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NUMBER 54

DECEMBER 28, 1984

**Recent Advances in the  
Paleobiology and Geology of the Cnidaria**

*Proceedings  
of the  
Fourth International Symposium on Fossil Cnidaria  
(and Archæocyathids and Stromatoporoids)  
held in Washington, DC, U.S.A., August, 1983*

edited by  
William A. Oliver, Jr., William J. Sando, Stephen D. Cairns,  
Anthony G. Coates, Ian G. Macintyre, Frederick M. Bayer,  
and James E. Sorauf

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## JEAN-PIERRE CHEVALIER (1926–1981)

Jean-Pierre Chevalier was born and completed all his studies in Paris. He spent his working life in the National Museum of Natural History, Paris, where he was a research scientist in the National Scientific Research Center. By virtue of his classic works on the Miocene corals of the Mediterranean and the Recent corals of the Pacific his preeminence as a biologist and paleontologist was established. We await with pleasure the posthumous publication of his review of the Cnidaria in the Grassé Treatise of Zoology. Among his many achievements he was awarded the Tchihatcheff Prize as Laureate of the French Academy of Sciences (1971) and the Silver Medal of the National Scientific Research Center (1978).

We remember Jean-Pierre Chevalier however, especially for his important contributions to the development of our Association. He was a founder member of our organization, undertaking the planning and development of the "Cnidarian Newsletter" following the First Symposium on Fossil Cnidaria (Novosibirsk, 1971). He was President of our International Association from 1975 to 1979 and organized the second symposium in Paris (1975).

We missed his gracious presence at our meeting and this volume is dedicated to his memory.

A. G. Coates

## JEAN-PIERRE CHEVALIER (1926–1981)

Jean-Pierre Chevalier, né à Paris, y a fait toutes ses études. Assistant au Muséum National d'Histoire Naturelle en 1950, il entre au Centre National de la Recherche Scientifique en 1952, organisme dans lequel se déroulera toute sa carrière. Sa renommée internationale en biologie et en paléontologie provient de ses publications devenues classiques sur les coraux et les récifs du Miocène de la région méditerranéenne et les coraux actuels du Pacifique.

J.-P. Chevalier est nommé par le Professor Grassé co-directeur des tomes du *Traité de Zoologie consacrés aux Cnidaire*s. Il en avait rédigé le long chapitre sur les scléactiniaires qui paraîtra à titre posthume dans l'un de ces volumes. Lauréat de l'Académie des Sciences en 1971 (Prix Tchihatcheff), il avait reçu la médaille d'argent du C.N.R.S. en 1978.

Lors du premier symposium sur les Cnidaire fossiles (Novosibirsk 1971) J.-P. Chevalier est chargé de créer et de rédiger notre bulletin de liaison, "Cnidaire Fossiles," ainsi que d'organiser le second symposium à Paris en 1975. Il a été Président de 1975 à 1979 de l'International Committee for the Study of Fossil Cnidaria.

Sa présence nous manque. Cet ouvrage est dédié à sa mémoire.

A. G. Coates

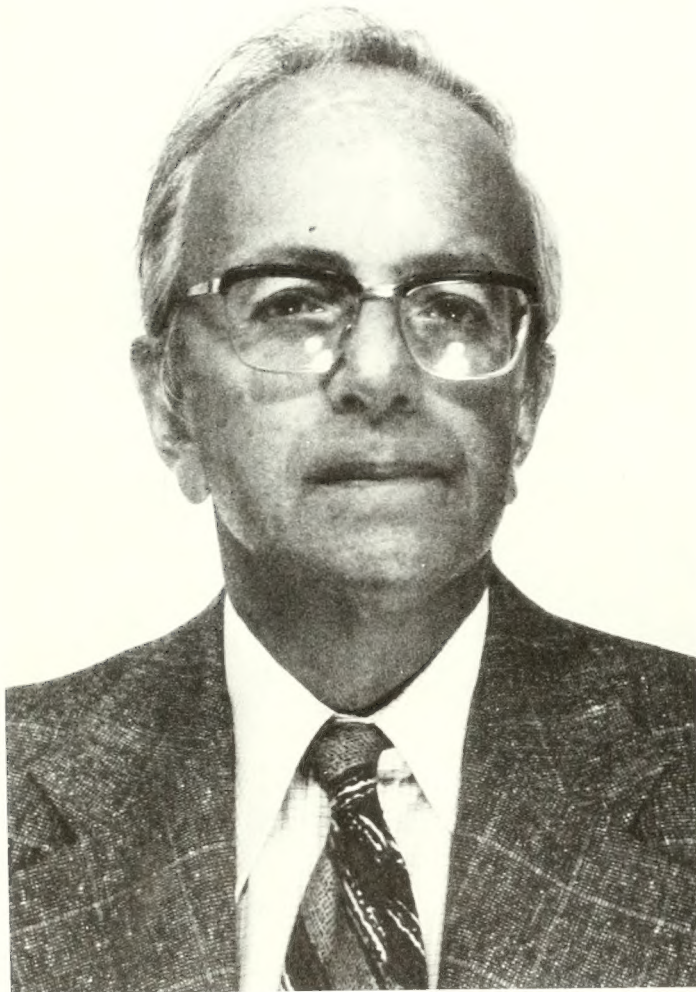
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## INTRODUCTION

William A. Oliver, Jr.

U.S. Geological Survey, Washington, DC, U.S.A.

The International Association for the Study of Fossil Cnidaria had its start in 1971, in Novosibirsk, USSR. Two All-Union Symposia on Fossil Corals of the USSR had been held in 1963 (Novosibirsk) and 1967 (Tallin). For their third meeting (1971), the USSR Commission on the Study of Fossil Corals, under the leadership of Academician B. S. Sokolov, issued invitations to specialists from other countries, thus making this meeting the First "International Paleontological Symposium on Corals (and some other Coelenterata)." In addition to specialists on the Cnidaria proper, workers on archeocyathids and stromatoporoids were well represented at the Novosibirsk meeting and have been significant contributors to the organization ever since.

At a final plenary session of the First Symposium it was agreed that an International Committee should be formed, that a newsletter would be appropriate, and that additional symposia should be held. Officers were "elected" and these, acting as an organizing committee, appointed a Council to represent countries and institutions that were most active in fossil Cnidaria research. The International Committee on Fossil Cnidaria was subsequently accepted as a working group of the International Palaeontological Association.

A biannual newsletter, *Fossil Cnidaria*, was begun in 1972 in Paris, under the editorship of Dr. J.-P. Chevalier and continued there for four years through the Second International Symposium (Paris, 1975). *Fossil Cnidaria* was then edited and produced for four-year periods in Washington/Binghamton (1976–79), Brisbane (1980–83), and is now moving to Münster (1984–). *Fossil Cnidaria* communicates news and ephemera of all kinds relating to the special field(s) involved; as one of its important functions it has published, and periodically updates, a master list of specialists on fossil cnidarians, archeocyathids, and stromatoporoids.

At the Paris meeting it was decided that the organization should become more formal. Under the leadership of Dr. Chevalier a constitution was written and adopted during 1976 (*Fossil Cnidaria*, 1976, vol. 5(2), pp. 2–4). With this, the Committee structure became the International Association for the Study of Fossil Cnidaria. At the Paris meeting and again at the Third Symposium (Warsaw, 1979), the Council was expanded to more accurately reflect the world distribution of cnidarian specialists. These and subsequent changes in the organization are fully recorded in *Fossil Cnidaria*.

The First International Symposium in Novosibirsk was very successful. It demonstrated the value of periodic meetings at which specialists could discuss their current work, find out what was being done elsewhere, and establish professional contacts that could be further developed by correspondence and other meetings. The Novosibirsk meeting was particularly notable for the establishment of contacts. The Symposium provided the first opportunity for meetings between most non-Soviet workers and their Soviet counterparts who, at that time, comprised nearly half of the known, active specialists. The program itself was varied, arranged by topic, and set the general pattern for succeeding symposia. The Proceedings were published in 1974 and 1975, and this too set a precedent.

Subsequent symposia in Paris (1975), Warsaw (1979) and Washington (1983) have experimented with different subject arrangements, invited 'keynote' speakers, and arranged invitational symposia, but all have held to the basic plan of inviting all specialists to report, formally or informally, on their current work. In addition, each symposium has published an abstract volume at the time of the meeting and has followed with full publication of the proceedings (see bibliography below).

The Washington Symposium had a long gestation period. A first invitation was made in 1975 at the Paris meeting, but it was rejected in favor of the Polish proposal which was more detailed and included specific plans for Proceedings publication. A second invitation was issued well in advance of the Warsaw meeting (*Fossil Cnidaria*, 1979, vol. 8(1), pp. 3–4). There was no shortage of countries willing to host the fourth meeting, but Washington was selected without a formal vote.

The organization of coral specialists in North America began in 1965 with the arrangement of the first of a series of topical sessions for the Paleontological Society (Geological Society of America Program, 1965, p. 33A). These topical sessions led shortly to the formation of the "Friends" groups, meeting annually at the Paleontological Society/Geological Society of America national meetings. The North American "Friends of the Corals and Stromatoporoids" first met in 1970 and is still continuing. An informal newsletter, begun in 1970, was issued irregularly, then merged with *Fossil Cnidaria* when that began publication in 1972. Special "Friends" meetings have been held in 1972 (Montreal, International Geological Congress) and 1974 (Symposium on Pennsylvanian and Permian Corals, South-Central Section, G.S.A., March, 1974).

The "Friends of the Corals and Stromatoporoids" provided much of the substructure for the 1983 Washington Symposium. The Organizing Committee included Washington-based specialists and others who were interested in and willing to do particular jobs. Plans were regularly discussed at "Friends" meetings and in *Fossil Cnidaria* and the Committee profited greatly from the resulting advice. A five day format with mornings being devoted to organized symposia was adopted, and a general invitation was issued to specialists, asking them to propose topical areas of current interest. The first five subject groupings of these Proceedings were selected by the Committee and, for each symposium, one or two specialists, in most cases the initial proposers, were invited to serve as organizers. Once launched, the organizers took more and more responsibility for their sessions. They selected speakers and subjects, established time limits and discussion arrangements, and eventually edited and prepared the papers from their symposium for this volume.

As had been customary at previous meetings, all specialists were invited to attend and give papers. However, the five "morning" topics were announced early and additional contributions in these subject areas were invited. As a result, one-third of the volunteered papers were added to the 'morning' symposia, extending them into or through the afternoons. In this volume, those volunteered papers that were submitted and accepted for publication are integrated with the appropriate invited papers.

Other volunteered papers fell easily into five subject areas and were so arranged in the program. A similar arrangement is used in the Proceedings for those papers that were submitted and accepted for publication. Sections six through ten represent significant areas of current research, but the included papers were not intended to cover the field and no attempt has been made to fill gaps. The introductions to these sections outline the coverage and give some background for each area as a whole. The volume editors took responsibility for soliciting reviews and editing these individual papers as well as generally overseeing the scientific editing of the volume.

Throughout the preparation of this volume, the editors, subeditors, and authors have been advised by Peter R. Hoover, Publications Editor and Director of the Paleontological Research Institution. We all appreciate the interest and care that he has taken to help produce these Proceedings.

The Washington Symposium and these Proceedings were made possible by the generous help of the sponsors listed below. This assistance has been in kind as well as financial, and has involved the skills, knowledge and experience of individuals too numerous to list. On behalf of the Organizing Committee, I take this opportunity to thank our organizations and our many friends and colleagues for their help.

Four benefactors made contributions to our publication fund that enabled us to assure publication of the Proceedings. These too are listed and acknowledged with thanks.

A grant from the National Science Foundation (EAR-8116559) made possible the invitation of several foreign specialists and launched our Publication Fund drive. A second grant, from the International Palaeontological Association, was also very helpful. Both grants are gratefully acknowledged.

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**Sokolov, B. S.** (ed.)

1974–75. Ancient Cnidaria, vol. 1, 364 pp. (1974), vol. 2, 280 pp. (1975). Acad. Sci. USSR, Siberian Branch, Trans. Inst. Geol. Geophys., Issues 201 and 202 (Proceedings of the First Symposium, 1971, Novosibirsk; Russian, English and French).

**Chevalier, J.-P. et al.** (eds.)

1977. Second Symposium International sur les Coraux et Récifs Coralliens Fossiles, Paris, 1975. Mém. du B.R.G.M. 89, 542 pp. (French and English).

**Osmólska, Halszka, Roniewicz, Ewa et al.** (eds.)

1980 (1981). Third International Symposium on Fossil Cnidarians, Warszawa, 1979. Acta Palaeont. Polonica, vol. 25(3–4), pp. 291–679 (English and French).



E R R A T U M

On page 11 of *Palaeontographica Americana* Number 54, the first paper following the Introduction to Section 6 should be:

Community Patterns on the Jamaican Fore Reef (15-56 m)..... 385  
*W. David Liddell, Sharon L. Ohlhorst, and Stephen K. Boss*

instead of:

Community Structure of Reef-Building Corals on a Recently Raised Holocene Reef on Guam, Mariana Islands..... 394  
*R. H. Randall, H. G. Siegrist, Jr., and A. W. Siegrist*

Please accept our apologies for any inconvenience this may cause.

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SECTION 1  
INVITATIONAL SYMPOSIUM

**Taxonomic Methods in Living Corals and their  
Paleontologic Implications**

Organized, Convened and Edited  
By

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INTRODUCTION

ANTHONY G. COATES

The species concept, particularly for lower metazoans, has always been a thorny issue in taxonomy and nowhere more so than in the scleractinian corals. There is clearly a major contrast between neontological and paleontological data regarding the availability of soft part and ecological characters for use in taxonomy.

Of prime importance therefore in any reconciliation of taxonomic procedures between neontologists and paleontologists is the role of non-skeletal characters in the systematics of living corals. This topic has been thoroughly reviewed by Lang in the opening article of the symposium. Ohlhorst augments this review with an elegant application of the use of polyacrylamide gel electrophoresis to coral taxonomy. It is certainly important that paleontologists become familiar with all aspects of living corals that are used in taxonomy.

However, it is clear from Lang's review that the vast majority of living coral species are defined on skeletal features even though a wide variety of morphological, physiological and behavioral aspects of the polyp have or could be incorporated into coral taxonomy. She indicates that although these polyp features may be important or even occasionally the primary features for defining coral species, for practical purposes, living coral species need to be recognizable in terms of their skeletal features.

It seems therefore that there need be no fundamental difference in approach to taxonomy between coral neontologists and paleontologists. However both groups are far from understanding the full range of microstructural and micro- and macroarchitectural characters which must be accurately described and measured before a common systematic approach is possible.

Three aspects of paleontological data have traditionally separated the taxonomy of fossil corals from that of living corals. Firstly, diagenetic changes modify critical surface microarchitecture in fossil corals (Section 4, Diagenesis, this volume) and lead to errors in the recognition of living taxa in the fossil record. Secondly, the fact that fossil specimens are frequently lithified and incorporated in rock matrix means that many fossil species are described only from thin sections and these are not easily compared to descriptions of three-dimensional surface features which form the basis for taxonomy in living corals (also see Hubbard, this volume). Finally, because paleontologists often have few specimens from temporally and geographically scattered localities, population variability is often underestimated and there is a strong tendency to create too many species based on too few specimens. The dangers of this are referred to by both Borel-Best and Zibrowius.

In recent years the work of Wijsman-Best (1972, 1974) is perhaps the most important in bringing to paleontologists' attention the nature and extent of phenotypic variation in certain corals and its implication for taxonomy. In her paper in this symposium she extends and develops her thesis, pointing out that we do not yet understand the functional significance of variation as a species attribute. Indeed the ecological implications of high versus low variability are not yet documented for any species or correlated with such factors as taxonomic longevity and geographic distribution.

Variability will remain an acute problem if paleontologists continue to ignore its extensive develop-

ment in many coral taxa [see Foster 1979a, b, 1980, and this volume, Veron and Pichon (1976), Pfister (1977) for examples]. It seems ironic that the nature of much paleontologic data tends to make fossil coral taxonomists "splitters" when the evidence from living corals suggests that we should be "lumpers."

The subtlety and complexity of morphological variation in modern hermatypic coral species have led to the use of detailed statistical analyses within and between populations (Brakel, 1977; Foster, 1979a, 1980, and this volume; Wallace, 1974; Wallace and Dale, 1977) to delimit within colony, within and between habitat, and eventually total species variability. It seems highly likely that the only real hope of fully understanding the nature, distribution and degree of variability within and between species lies in using a numerical population approach, with detailed accurate measurements on carefully selected morphological features. The pioneering work in this area is that of Foster. By defining phenotypic plasticity using canonical variate analysis on control and transplanted specimens she can precisely delimit intraspecific variation. It is also possible to allocate particular variation to specific habitats. Armed with this information she is able to define similar ranges of variation in the fossil record of the same groups and hence make accurate taxonomic assignments, as well as interpret the nature of the ecophenotypic variation she measures. This is exemplary work and should point the way for future paleontologists.

Cairns' application of cladistics to the Fungiidae is in its way also pioneering, providing a concise description of the methodology for this type of coral phylogenetic reconstruction. The scene is now set for applications to the fossil record. A cautionary note is provided by Fedorowski who outlines the dangers of an improperly designed numerical taxonomic method. Questionable relationships are suggested between genera if the morphologic characters: 1) are ranked for a given taxonomic level; 2) are not precisely and narrowly defined; and 3) substantial numbers of morphological attributes are missing in many descriptions of the taxa being analyzed. According to Fedorowski this seems to be the case for much rugosan taxonomy.

The contribution of Zibrowius gives us insight into the taxonomic problems involved in the ahermatypic corals. Some of these taxa are zooxanthellate and colonial and it is perhaps not surprising that they turn out to be highly variable. However, conventional wisdom, no doubt influenced by the work of Weber (1974), holds that non-zooxanthellate ahermatypes are likely to have significantly less intraspecific variation than their reef-building counterparts. With the exception of the free-living solitary forms this is apparently not the case. In addition Zibrowius indicates a variety of taxonomically valuable characters in the ahermatypes that

are not usually employed in hermatypes. The conclusions of Zibrowius are supported by Mori who records a large range of morphological variation within 1090 specimens from a single locality, in the Pleistocene solitary ahermatype *Caryophyllia compressa* (Yabe and Eguchi) from Japan.

The symposium seems to highlight three areas where progress and consensus in taxonomic procedures are needed. Firstly, if specimens are not numerous and well preserved taxonomy should not be attempted at the species or even generic levels. Secondly, some standard techniques might now be agreed to by both neontologists and paleontologists so that their respective descriptions are directly comparable. Finally, some standardization must be developed for both the description and figuration of coral taxa throughout the world.

What this seems inexorably to point to is the organization, perhaps under the auspices of the International Committee on Fossil Cnidaria, of an international body to unify coral taxonomic procedure. It is surely obvious that no meaningful paleobiogeographic or evolutionary patterns that require comparable taxonomic units for their analysis can satisfactorily use existing species or genus level data. The problem has an historical and a procedural aspect. Clearly, much paleontological evidence comes from older monographs which describe taxa that have never been revised, are inadequately or inaccurately figured, that are poorly known stratigraphically and for which, in many cases, no type specimens remain. This is probably also true of a significant number of extant coral species. The first project that an international group might undertake is to arrange for a specialist for each geologic period (including the Recent) to inventory the species published in his or her country and establish whether or not the type specimens exist. Those for which the specimens exist could then be systematically revised following some standard format to be agreed on by the international body. A decision could then be taken as to the fate of those taxa for which revision was not possible. This would include rendering them officially null and void. The next step would be to establish an agreement, by international consensus, as to what measurements and descriptions of morphological features (including illustrations) would constitute the minimum requirement for a valid coral taxon to be accepted. This involves the thorny problem of agreeing on a lexicon of precisely defined terms which would be used by all coral taxonomists.

Finally each taxon should be photographed and a file of valid taxa built up, duplicates of which would be available at the major national museums as a universal standard reference set.

These suggestions are made primarily to provoke

action. Already we have seen some small personal efforts (Gill and Roniewicz, 1982) to develop a catalogue of coral taxa, but satisfactory progress will come only from a broad based international agreement. The International Commission on Zoological Nomenclature provides a broad framework for taxonomic procedures but current problems are particular to phyla and need to be addressed at that level. Similar developments have occurred in stratigraphic procedures, for example, the International Commission on Stratigraphy, which has a working Subcommittee for each System, and it seems apparent that the time is ripe for parallel developments in taxonomy and systematics.

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## WHATEVER WORKS: THE VARIABLE IMPORTANCE OF SKELETAL AND OF NON-SKELETAL CHARACTERS IN SCLERACTINIAN TAXONOMY

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### ABSTRACT

Species of scleractinian corals are primarily defined by skeletal traits as these are most readily available for laboratory study. At present, the success with which they are differentiated varies greatly from one genus to another. That coral skeletons show a considerable range of variation in many characters is well known, and overlap between species can occur. Other problems arise from generic differences in the shapes and in the relative development of the various skeletal structures.

An array of non-skeletal characters may help to distinguish living corals, and would be particularly useful for cryptic species in problematic genera. The range of variability of these features is generally less well known, and needs documentation comparable to that which is available for some skeletal traits. Their value would obviously be enhanced by correlation with distinctive skeletal characters, which may require detailed microstructural, geochemical or other forms of analysis.

Modern scleractinian corals could thus be differentiated by whatever combination of skeletal and non-skeletal characters works most reliably and efficiently for any particular species.

### INTRODUCTION

Scleractinian corals are classified primarily by skeletal traits (Vaughan and Wells, 1943; Alloiteau, 1952). Species and subspecies are usually defined by such characters as "dimensions of corallites, number, arrangement and structural details of septa and costae, habit of colonial coralla and shape of solitary corals, and features of the coenosteum" (Wells, 1956, p. 368). Specimens are usually considered to belong to a single species when they form part of a series whose skeletal morphology intergrades (*e.g.*, Vaughan, 1901; Bourne, 1903); hence different species are expected to be separated from each other by distinct morphological gaps (Vaughan, 1907).

The advantages of characterizing scleractinian species by skeletal traits are obvious: the ease of storage and of observation; the direct correlations which exist between many aspects of the hard and soft tissues; the potential for accurate morphometric measurements of dimensionally stable (non-contractile) structures; the necessity for establishing phylogenies and for compatibility with the classification systems of fossil scleractinians. Nonetheless, there are difficulties with this morphological approach. For example:

1. Highly simplified, or reduced, skeletal elements provide little information of systematic value (Crossland, 1952; Wallace, 1978). Not surprisingly, species designations have been especially controversial in small-polyped genera such as *Acropora*, *Montipora*, *Porites*, and *Agaricia*.

2. Extremely complicated features, such as the coenosteal structures of some stony corals, are difficult to describe (Bernard, 1897).

3. Scleractinians are notorious for the high levels of

skeletal variability which characterize many genera (Quelch, 1886; Veron, 1982; Borel Best, this volume; and many others). Overlap between the skeletal traits of congeneric species has often been reported (*e.g.*, Vaughan, 1918; Brakel, 1977; Wijsman-Best, 1977; Wallace, 1978). Foster (1982) has quantified such overlap in the otherwise well-delineated western Atlantic congeners *Montastraea annularis* (Ellis and Solander) and *M. cavernosa* (Linnaeus).

4. That scleractinian skeletal morphology may be affected by local environmental conditions is now well established experimentally (*e.g.*, Foster, 1979; Graus and Macintyre, 1982). Ecological information can be used to distinguish between phenotypic and genotypic sources of variability (*e.g.*, Bell, 1895; Gardiner, 1904; Vaughan, 1907); particularly when two closely related species maintain their morphological differences in the same habitat (Yonge, 1935). At least in some plants, however, the patterns and extent of phenotypic plasticity are affected by genetic relatedness in addition to ecological requirements (Schlichting and Levins, 1984). Thus morphological overlap could actually be enhanced when congeneric species with similar phenotypic responses grow in the same habitat (C. Schlichting, pers. comm.). Indeed such overlap has occasionally been noted in stony corals (*e.g.*, *Pocillopora*—Veron and Pichon, 1976, 1982; *Acropora*—Wallace, 1978).

5. Variability within the skeletal structures of a single corallum is thought to reflect a suite of developmental and/or physiological responses to microhabitat variations (*e.g.*, Bell, 1895; Chevalier, 1971), which may differ with "age," *i.e.*, growth stages and, for colonial corals, location on the colony (*e.g.*, Brook, 1893). Other potential sources of within-colony variation may



include "aggregated" colonies formed by the fusion of conspecifics (see review of Rinkevich and Loya, 1983), especially juveniles; non-lethal somatic mutations (*e.g.*, Buss, 1983); or possibly other forms of "stress" (Wallace, 1978; Lamberts, 1982). Specimens with unusually high levels of within-colony variation can resemble several species (*e.g.*, Duncan, 1877; Bell, 1895)—or even genera (Whitfield, 1901; Matthai, 1948)—in different parts of the corallum.

6. We are unlikely to recognize any cryptic species as may exist in stony corals (*e.g.*, Wijsman-Best, 1972, 1977; Veron and Pichon, 1980). Cryptic species (often called sibling species—see Ross, 1974) are very similar morphologically. They rarely or never interbreed in nature, and usually differ in other biologically important characteristics (Mayr, 1970). Since they act as independent evolutionary lineages, cryptic species deserve species names, despite the problems of identifying them by morphological criteria (*e.g.*, Ross, 1974; Wiley, 1981). Distinguishing between "ecomorphs" (*sensu* Veron and Pichon, 1976) of a single species, and pairs or complexes of cryptic species, would be particularly difficult in scleractinian genera characterized by high levels of skeletal variability.

7. The genetic control of skeletal characters may be especially complicated in the zooxanthellate scleractinians with their populations of the dinoflagellate endosymbiont, *Symbiodinium microadriaticum* Freudenthal. Trench (1981, in press) has reviewed the evidence for genetic heterogeneity among cultured strains of this algal complex. When present, zooxanthellae usually accelerate the calcification rates (*e.g.*, T. F. Goreau, 1959; Vandermeulen and Muscatine, 1974), and perhaps alter the skeletal morphology (see review of Dustan, 1979) of their stony coral hosts.

Hence, for these and other reasons, systematists may experience great difficulty in delineating species limits in some scleractinian genera (*e.g.*, Wells, 1966, 1969; Chevalier, 1971; Wijsman-Best, 1977; Wallace, 1978). Moreover, other coral reef scientists often use these specific names with considerable imprecision in the field.

Problems such as these are certainly not unique to the Scleractinia. In response to similar difficulties, some systematists have expanded the traditional morphological species concept to include other kinds of information. For example, Mayr (1969, p. 143) has defined a systematic character as "any attribute by which a member of a population may differ from other populations of organisms." For purposes of identification, a species may be considered to be a group of populations which share similar morphological, genetic, biochemical, physiological, behavioral and ecological

characteristics. Note that the emphasis on shared similarities within a species (Mayr, 1970), rather than on gaps between species (as in Vaughan, 1907), somewhat diminishes the impact of overlapping characters—skeletal or otherwise (see 3 and 4 above). Examples of such "multi-character" approaches to the recognition and description of species are given in Mayr (1969), Doyen and Slobodchikoff (1974), Bush and Kitto (1978), Davis (1978), Davis and Fuller (1981), Trüper and Krämer (1981), Wiley (1981) and many others.

To the advocates of this approach, systematic progress is frequently accelerated when "new" or previously neglected characters (including "underutilized" anatomical features) are explored. In general, however, the inclusion of a larger array of traits has increased the number of species recognized by systematists (*e.g.*, Schopf, 1979)—a trend opposite in direction to that of many modern scleractinian systematic works (*e.g.*, Veron and Pichon, 1976; Zlatarski, 1982; but see Wells, 1969, p. 319; Veron and Pichon, 1982, p. 133).

#### SOME NON-SKELETAL ATTRIBUTES OF SCLERACTINIAN SPECIES

Non-skeletal features have figured prominently in the characterization of only a few species of scleractinians (Table 1).<sup>1,2</sup> J. W. Wells (encouraged, one suspects, by R. Catala and T. F. Goreau) has been a major contributor to this trend. To date, the most spectacular instance of "live coral" taxonomy is Veron and Pichon's (1980) distinction of two new species of *Euphyllia* (*Fimbriaphyllia*) exclusively on polypal characters.

Biological information about scleractinians is currently scattered among a wide, and ever increasing array, of scientific journals. For this reason I have attempted to summarize published data on non-skeletal attributes which are—or might be—of value in the recognition of species (Table 2<sup>2</sup> and below). Some of these features have already been used in a few species descriptions (Table 1), or in Powers and Rohlf's (1972) numerical taxonomic study of scleractinian classification. Unfortunately many areas of active research

<sup>1</sup> Not included in Table 1 are the numerous examples in which (a) ecological information is used only in the interpretation of skeletal structures, or (b) non-skeletal traits are treated only as useful field identifiers, even when these allow species to be described more easily than do the corresponding skeletal characters.

<sup>2</sup> To conserve space, many references are to recent review articles or, when these are unavailable, to a few, selected papers. I am very conscious of my inability to read all the appropriate scleractinian literature during the preparation of this paper, and welcome further information from my readers.

Table 1.—Examples of non-skeletal traits which have been used to characterize genera, subgenera, species and formae of scleractinians.

Non-skeletal trait		Use in systematics
General	Specific	
Sexual reproduction	planulation	Van Moorsel (1983) separated the <i>humilis</i> form of the agariciid <i>Agaricia agaricites</i> (Linnaeus) as a new species, <i>A. humilis</i> Verrill, partly on the basis of differences in seasonality of planulation, planula output, and maximum diameter of the smallest planulating colonies.
Asexual reproduction	budding patterns	Matthai (1928) keyed "astraoid" (=faviid and mussid) genera partially by their patterns of asexual reproduction. <sup>1</sup>
External morphology	unusual polypal sizes and shapes	Vaughan and Wells (1943) characterized the siderastroid genus <i>Siderastrea</i> in part by its bifurcated entocoelic tentacles. Wells (1966) erected <i>Heliofungia</i> as a new subgenus of <i>Fungia</i> , largely on polypal characters, especially its exceedingly long tentacles; Veron and Pichon (1980) used similar arguments to raise <i>Heliofungia</i> to the rank of a new genus. Wells (1971a) described a new eusmiliid genus, <i>Catalaphyllia</i> , primarily on polypal characters, particularly those of the oral disc and peristome, and by the shape and location of the tentacles. Eguchi (1973) described <i>Euphyllia sabiuraensis</i> , a new eusmiliid species, primarily by the morphology of its tentacles. <sup>2</sup> Veron and Pichon (1980) distinguished <i>Fimbriaphyllia</i> , a new subgenus of <i>Euphyllia</i> , and differentiated two new species, <i>E. (F.) divisa</i> and <i>E. (F.) ancora</i> , by pronounced differences in tentacular morphology. Veron and Pichon (1982) characterized <i>Alveopora marionensis</i> , a new poritid species, partially on the shapes of its tentacles.
	counts of repeated structures	Wells (1961) described the new oculinid species <i>Bantamia merleti</i> , and noted the uncertain taxonomic value of its rings of tentacles which are not associated with the septa. <sup>3</sup> Wells (1971a) also separated <i>Catalaphyllia</i> from <i>Euphyllia</i> by differences in the number of tentacle rows.
	relative tissue fleshiness	Lang (1971) considered differences in relative tissue fleshiness when reinstating the mussid <i>Scolymia cubensis</i> (Edwards and Haime). <sup>4</sup>
	tissue colors	Lang (1971) also treated tissue color as an attribute when reinstating <i>Scolymia cubensis</i> . <sup>4</sup> Wijsman-Best (1972) weighted tissue color quite heavily in the characterization of <i>Favites rufa</i> , a new faviid species. <sup>5</sup>
Internal morphology	mesenteries	Matthai (e.g., 1928) separated "astraoid" genera partly on the basis of mesenterial characters. <sup>6</sup>
	cnidom	Matthai (1914, 1928) also used the location, size and density of the different types of nematocysts in the tissues to characterize genera of "astraoid" corals. Best (1968) similarly characterized the nematocysts and spirocysts of <i>Polycyathus banyulensis</i> and <i>P. mediterraneus</i> , two new caryophylliid species. <sup>7</sup>
Behavior	expansion	Wells (1966) separated the new subgenus <i>Heliofungia</i> partly because its polyps are continually expanded except during planulation; Veron and Pichon (1980) raised <i>Heliofungia</i> to the rank of a new genus in part for similar reasons. Best (1968) also noted differences in the expansion patterns of <i>Polycyathus banyulensis</i> and <i>P. mediterraneus</i> . <sup>7</sup>
	feeding	Crossland (1952) "unhesitatingly" placed <i>Tridacophyllia</i> in the Fungiidae in part on its "surely Fungiid" mode of feeding—yet retained <i>Merulina</i> in the Merulinidae, without comment on its identical feeding response (Yonge, 1930). <sup>8</sup>
	coral-coral interactions	Lang (1971) and Wells (1971b) considered the occurrence of unilateral, extracoelenteric destructive reactions between two morphs of <i>Scolymia lacera</i> (Pallas), and differences in the relative positions of these morphs in a scleractinian destructive dominance hierarchy in Jamaica and Curaçao, as primary characters when reinstating <i>S. cubensis</i> . <sup>4</sup> Wells (1973) used similar destructive reactions among some of the morphs of the mussid <i>Mycetophyllia lamarckiana</i> Edwards and Haime in Jamaica when reinstating <i>M. danaana</i> Edwards and Haime, and in describing the three new species <i>M. ferox</i> , <i>M. aliciae</i> and <i>M. reesi</i> . <sup>9</sup>

Table 1.—Continued.

Non-skeletal trait		Use in systematics
General	Specific	
Ecology	habitat distribution patterns	Lang (1971) treated differences in the overall depth ranges of populations of <i>Scolymia lacera</i> and <i>S. cubensis</i> as a systematically relevant feature. <sup>4</sup> Maragos (1977) described the species of Hawaiian corals partly by depth distributional data. Head (1983) characterized the new species <i>Merulina scheeri</i> in part by contrasting the range of environments which it inhabits with those of <i>M. ampliata</i> (Ellis and Solander).
	non-scleractinian associates	Scott (1980) noted that the restriction of the boring mytilid <i>Lithophaga simplex</i> Iredale to <i>Favia</i> spp. and to <i>Barabattoia mirabilis</i> Yabe and Sugiyama, and its absence from species of the three other faviid genera present in Hong Kong, supports Wijsman-Best's (1972) inclusion of <i>Barabattoia</i> in <i>Favia amicorum</i> (Edwards and Haime) (=the <i>Favia amicorum</i> complex of Veron <i>et al.</i> , 1977). <sup>10</sup>
Physiology	environmental tolerance levels	Yonge (1935) correlated sediment shedding behavior with habitat, overall colony shape, and with corallite size and structure, in two forms of the siderastreid <i>Siderastrea radians</i> (Pallas).

<sup>1</sup> As the asexual budding patterns of the polyps are usually reflected in the skeleton, this tissue trait rarely provides additional systematic information.

<sup>2</sup> Eguchi and Miyawaki (1975) transferred this species to *Cattalaphyllia* (= *Catalaphyllia*).

<sup>3</sup> Wells (1968) transferred this species to the new mussid genus *Blastomussa*.

<sup>4</sup> Zlatarski (1982) resynonymized all the Western Atlantic species of *Scolymia*.

<sup>5</sup> Veron *et al.* (1977) synonymized *Favites rufa* with *F. russelli* Wells.

<sup>6</sup> Septa alternate with mesenteries (Vaughan and Wells, 1943; N. I. Goreau, 1983a); since then this approach has not been pursued further.

<sup>7</sup> Zibrowius (1978) synonymized *Polycyathus banyulensis* and *P. mediterraneus* with *P. muelleriae* (Abel).

<sup>8</sup> Vaughan and Wells synonymized *Tridacophyllia* with *Pectinia*; Alloiteau (1952) synonymized this genus with *Echinopora*.

<sup>9</sup> Zlatarski (1982) synonymized *Mycetophyllia ferox*, *M. aliciae* and *M. danaana* with *M. lamarckiana*.

<sup>10</sup> Veron and Pichon (1982) reinstated the genus *Barabattoia* to include most of the forms contained in the "*Favia amicorum* complex."

have had to be omitted due to a lack of comparable information for congeneric species.

Reproductive attributes are integrated in the first section. Wiley's (1981, p. 319) definitions are used for the necessarily somewhat arbitrary classes of characters into which other traits are grouped. Given the importance which systematists place on variability, I have emphasized the kinds of intraspecific variation which have been described for these characteristics. I have also noted attempts to relate non-skeletal features to skeletal morphology. Occasional references are made to other cnidarians (mostly actiniarians) when appropriate information is unavailable for stony corals.

### Reproductive Characters

Replication is a fundamental property of living organisms, and may occur as either sexual or asexual reproduction (Barrington, 1979). As in many other organisms (*e.g.*, G. C. Williams, 1975; Harper, 1977), the relative investment into each of these modes of reproduction may vary among stony corals (*e.g.*, Dana, 1846; Fadlallah, 1982), including different species in such taxonomically difficult genera as *Acropora* (Bothwell, 1982), *Porites* (Kojis and Quinn, 1982; Hunter and Kehoe, 1983) and *Agaricia* (Chornesky, pers. comm.).

### Sexual Reproduction

Sexual reproduction is biologically important because it increases genetic variability in the offspring (Mayr, 1970). For sexually reproducing organisms, extensive interbreeding among natural populations whose ranges overlap, and reproductive isolation from other groups, constitute the "ultimate" test of conspecificity (*e.g.*, Mayr, 1970; Chevalier, 1971). Many cryptic species were first recognized by sexual reproductive criteria (*e.g.*, Mayr, 1970; Ross, 1974).

Although the systematic importance of "experimental breeding" studies was early appreciated (Wood Jones, 1907), little is known of the circumstances under which scleractinian eggs are fertilized (Fadlallah, 1983a). Nevertheless, some aspects of scleractinian reproduction are perhaps correlated with skeletal morphology (Fadlallah, 1983a). Moreover, information on various developmental and behavioral aspects of sexual reproduction is rapidly accumulating for some congeneric species (*e.g.*, see reviews of Fadlallah, 1983a; Harriott, 1983a). Van Moorsel (1983) has even characterized a new species of *Agaricia* in part by its sexual reproductive patterns (Table 1); while Richmond and Jokiel (in press) are using similar information in a reexamination of "the 'species' problem" in *Pocillopora damicornis* (Linnaeus).

Regarding intraspecific variability, decreased fecundity has been noted in populations of *Stylophora pistillata* (Esper) stressed by chronic oil pollution (Rinkevich and Loya, 1977) and of *Acropora palifera* (Lamarck) exposed to high sedimentation rates (Kojis and Quinn, 1983). Geographic variation has been noted in the seasonal and lunar periodicity of planulation for *Stylophora pistillata* in various localities (see review of Rinkevich and Loya, 1979). The predominant developmental stage of the expelled larvae may also vary geographically in *S. pistillata* (Rinkevich and Loya, 1979).

#### Asexual Reproduction

The means by which new polyps (or stomodaea, when intratentacular division is incomplete) develop in colonial scleractinians are considered systematically important characters at the levels of subgenera to families (e.g., Matthai, 1928; Vaughan and Wells, 1943), and can usually be deciphered in the skeleton.<sup>3</sup> In other kinds of asexual reproduction, organic continuity between the parent and "daughter polyps" is lost (Vaughan and Wells, 1943). Thus various kinds of transverse fission occur in diverse scleractinians (e.g., Bourne, 1903; Wells, 1966), and a form of fragmentation affects species of *Diaseris* (e.g., Veron and Pichon, 1980). Apparently more restricted means of asexual reproduction and dispersal may include the "polyp balls" of *Goniopora stokesi* Edwards and Haime (Rosen and Taylor, 1969),<sup>4</sup> the planula-containing polyps which detach from *Seriatopora hystrix* Dana (Sammarco, 1982) and the "asexual planulae" of *Pocillopora damicornis* (Stoddart, 1983; see also Harriott (1983b) for data on gonad structure and development).

#### Morphological Characters

Structural attributes of organisms at the cellular level or above are termed morphological characters (Wiley, 1981).

<sup>3</sup> The predominant mode of asexual reproduction is, however, a species-specific diagnostic trait in some genera (e.g., Chevalier, 1971; Veron *et al.*, 1977; Head, 1978, 1982). Asexual budding patterns also vary between populations in *Astrangia lajollaensis* Durham (Fadlallah, 1982) and within a single colony in a number of species (e.g., Wood Jones, 1907; Matthai, 1928; N. I. Goreau, 1983b).

<sup>4</sup> During these asexual reproductive periods relatively less skeletal material is deposited in the calices of the parents, whose coralla then resemble those of *Alveopora*. Presumably its tissues can still be identified as a *Goniopora* by having 24 tentacles/polyp, whereas *Alveopora* has 12 tentacles in each polyp (Veron and Pichon, 1982).

#### External Morphology

External features of organisms are a primary source of systematic information in most groups of multicellular organisms (Wiley, 1981), including the various groups of anthozoans which lack skeletal structures (e.g., Stephenson, 1928; West, 1979; den Hartog, 1980; Manuel, 1981).

*Unusual sizes and shapes.*—Because the scleractinian skeleton "reflects the character of the polyp between the oral disc and base of the column wall" (Vaughan and Wells, 1943, p. 31), much can be inferred about the organization of the soft tissues by examining the corresponding skeletal structures (Duerden, 1902). Moreover, according to Porter (1976), tentacle lengths usually correlate with polypal (and hence corallite) diameter. The location of the tentacles on the oral disc is related to calicular shape in many corals (Vaughan and Wells, 1943). Nevertheless, unusual soft tissue characters, most notably in the sizes and shapes of the tentacles, do sometimes occur, especially in a few eusmiliinid, fungiid, poritid and siderastroid genera (Table 1). Veron and Pichon (1980) have also described intraspecific variations in the number of subbranches per tentacle in *Euphyllia (Fimbriaphyllia) divisa* Veron and Pichon, and between-colony variations in the shape of the tentacle caps in *E. (F.) ancora* Veron and Pichon.

*Sweeper tentacles.*—Elongate sweeper tentacles can develop in some scleractinian species when specimens come into contact with certain other sessile organisms (see review of Chornesky, 1983). At any given time, sweepers are only present on some polyps or specimens of those species which are known to possess them (Chornesky, 1983), and would thus appear to be of little diagnostic value. In fact, closely related species may differ in their ability to form these unusual tentacles. For example, sweeper tentacles are commonly found in *Montastraea cavernosa*, but have never been seen in its congener *M. annularis* (Richardson *et al.*, 1979; Chornesky and Williams, 1983).

*Counts of repeated structures.*—Most scleractinians have one tentacle per septum (Vaughan and Wells, 1943), and interesting exceptions may have some specific diagnostic value (see Table 1). Moreover, in *Cynarina lacrymalis* (Edwards and Haime), several tentacles are associated with each primary septum (Veron and Pichon, 1980). Tentacles are apparently "uncertain in number" in *Cyphastrea chalcidicum* (Förskal) and *Caulastrea tumida* Matthai (Eguchi and Miyawaki, 1975); and appear to be absent altogether in a few genera (*Pachyseris*—Yonge, 1930), or species (*Mycetophyllia reesi*—Wells, 1973). Tentacle number is an important specific diagnostic character in soft-bodied

hexacorals such as actiniarians, corallimorpharians and zooanthids (*e.g.*, Stephenson, 1935; West, 1979; den Hartog, 1980; Manuel, 1981).

*Relative tissue fleshiness.*—Tissue fleshiness, *i.e.*, the relative thickness of the mesogleal layer (Duerden, 1902), appears to vary between two closely related species of *Scolymia* (see Table 1). Veron and Pichon (1980) have also noted the presence of unusually fleshy tissues in *Scolymia australis* (Edwards and Haime) and in *Acanthastrea* sp. (now = *A. lordhowensis* Veron and Pichon, 1982).

*Tissue colors and color patterns.*—Tissue colors are undoubtedly the most common "live coral" trait mentioned by systematists, but very little use appears to have been made of this information when diagnosing species (Table 1). In some scleractinian genera, at a given locality and habitat, coloration can be an important specific character (*e.g.*, Maragos, 1977; Wallace, 1978). Color is, however, routinely used as a systematic trait in actiniarians, corallimorpharians, zooanthids and some octocorals (*e.g.*, Stephenson 1928, see especially pp. 67–72; Bayer, 1956, 1961; West, 1979; den Hartog, 1980).

Color morphs are associated with distinctive skeletal morphologies in some species (*e.g.*, Barnes, 1973; Lehman and Porter, 1973; Lasker, 1981), whereas such correlations are lacking in others (*e.g.*, Veron and Pichon, 1980, p. 238; Veron and Pichon, 1982, p. 118). Intraspecific color variation may also be related to habitat (*e.g.*, Duerden, 1902; Kawaguti, 1937) or to regional or geographic location (*e.g.*, Crossland, 1952; Veron and Pichon, 1980; Wijnsman-Best, 1980). Even seasonal variability in the colors of *Favites abdita* (Ellis and Solander) in eastern Australia has been noted by Veron *et al.* (1977).

Within colonies, coloration may vary with polyp age and/or position (*e.g.*, Wood Jones, 1907; Veron and Pichon, 1980, p. 395). In addition, the colors of the zooxanthellate scleractinians are affected by the number (*e.g.*, Duerden, 1902; Yonge and Nicholls, 1931) and photoadaptive capabilities (Chang *et al.*, 1983) of their algal endosymbionts. Some of the pigments in these stony corals are, however, of animal origin (see review of Jokiel and York, 1982).

#### Internal Morphology

Internal morphology includes any structural attributes not found on the surfaces of organisms. In protists, many algal and some small multicellular animal groups, most systematic characters are provided by these internal features (Wiley, 1981). The number and arrangement of mesenteries, and the position, pattern and relative development of muscles, are also impor-

tant systematic features of actiniarians and zooanthids (*e.g.*, Stephenson, 1928; West, 1979). In scleractinians, however, the arrangement of the mesenteries can be deduced from the septal patterns of the skeleton (Vaughan and Wells, 1943; N. I. Goreau, 1983a; see also Table 1). Scleractinian muscles are relatively small (Matthai, 1914). Nevertheless, numerous histological and histochemical (Table 2) differences do occur among stony coral genera (see reviews of Bourne, 1887; Duerden, 1902; Matthai, 1914, 1928), and some congeneric species too (E. C. Peters, pers. comm.; A. Szmant-Froelich, pers. comm.).

*Cnidom (nematocysts and spirocysts).*—Scleractinian tissues contain several kinds of nematocysts (Schmidt, 1974), each of which is anatomically variable (Table 2). Their dimensions, relative proportions and distributions within the polyps may also vary (*e.g.*, Matthai, 1928). Although few (*e.g.*, Abe, 1938) have attempted to determine the systematic value of scleractinian nematocysts, Matthai (1914, 1928) and Best (1968) have included data about the cnidom in formal species descriptions (Table 1). Wijnsman-Best (1972), however, subsequently referred to the high within-polyp diversity of nematocyst types. Presently documented between-tentacle variation includes the unusual nematocysts in the sweeper tentacles of *Montastraea cavernosa* (den Hartog, 1977), and the increased nematocyst to spirocyst ratios in sweepers of *Pocillopora* spp. (Wellington, 1980). In actiniarians, corallimorpharians and zooanthids, nematocysts are important specific characters (*e.g.*, Stephenson, 1928; West, 1979; den Hartog, 1980).

#### Karyological Characters

Studies of chromosome number, size and shape have provided invaluable systematic information in many plant and animal groups. Chromosome data can be used to help recognize cryptic species (*e.g.*, Mayr, 1969; Wiley, 1981). Niiyama (1944) reported minor, but consistent, differences in chromosome number and/or shape in three species of hydroids (*Hydra*—2 spp., *Pelmatohydra*—1 sp.). A. Heyward (oral commun., 1984) had adapted histological techniques for visualizing scleractinian chromosomes with a light microscope.

#### Behavioral Characters

Behavioral characters are nonstructural traits resulting from actions taken by organisms (Wiley, 1981). Species-specific behavioral patterns are well known in many groups of animals (*e.g.*, Hinde, 1970), and there is abundant evidence that behavior is genetically controlled (*e.g.*, Erhman and Parsons, 1976). Behavior can, however, be modified by learning, and by ecolog-

ical or age factors (e.g., Ross, 1974). Intraspecific behavioral variations may also occur (e.g., McKillup, 1983). Behavioral characters have contributed to the classification of many animal groups, and have been particularly important in the recognition of cryptic species (e.g., Mayr, 1969; Ross, 1974). Moreover, the behavior of organisms is clearly related to, and partially constrained by, their morphology (e.g., Colbert, 1958). Thus the potential does exist, at least to some extent, to correlate behavioral and skeletal traits in scleractinians.

#### *Expansion Behavior*

Like many other anthozoans (e.g., Preston and Preston, 1975; Sebens and DeReimer, 1977), distinctive patterns of expansion and contraction have been noted for some stony corals. To date only one scleractinian (Table 1) has been formally diagnosed in part by its expansion behavior. Diurnally expanded polyps are, however, treated as field traits in a few genera (*Goniopora*, *Alveopora*—Ditlev, 1980; Veron and Pichon, 1982) and species (*Leptastrea pruinosa* Crossland—Veron *et al.*, 1977; Wijsman-Best, 1980). Several other species are known which are seldom expanded, even at night (e.g., *Moseleya latistellata* Quelch—Veron *et al.*, 1977; *Pectinia lactuca* (Pallas)—Veron and Pichon, 1980). Interspecific differences in expansion behavior apparently occur in other scleractinian genera (e.g., Matthai, 1928; Best, 1968; Porter, 1974; Bak and Elgershuizen, 1976). Cycles of expansion activity, and height of the expanded polyps, which vary between morphs of *M. cavernosa*, are also affected by habitat depth and by their zooxanthellae (e.g., Lasker, 1979; 1981). Geographic location does not appear to affect expansion behavior (compare Porter, 1974; Lewis and Price, 1975; Bak and Elgershuizen, 1976).

#### *Feeding Behavior*

Reef scleractinians primarily capture particulate food with their tentacles and/or by various forms of ciliary-mucoid suspension feeding activities (e.g., Yonge, 1930; T. F. Goreau *et al.*, 1971; Muscatine, 1973; Johannes, 1974). Capture rates seem to correlate with tentacle length; the behavioral responses of the polyps to food and to ambient water velocity; colony morphology; the presence of any zooxanthellae; and with the density, morphology, and behavior of their prey (Hubbard, 1974; Chamberlain and Graus, 1975; Lasker, 1976; Clayton and Lasker, 1982; Brunet, in review). Nevertheless, details of the specific feeding responses of different corals are rather controversial (compare Lewis and Price, 1975; Porter, 1976; Sorokin 1982). Hence Crossland's (1952) inclusion of the morphologically

problematic genus *Tridacophyllia* in the Fungiidae, partly on the basis of its feeding patterns, now seems somewhat naive (see Table 1). Nonetheless, according to Lewis (1976), interspecific differences in suspension feeding behavior may occur in some genera.

Regarding intraspecific variability, the larger polyped, nocturnally expanded morph of *M. cavernosa* ingests *Artemia* nauplii significantly faster than the smaller polyped, continuously expanded morph (Lasker, 1976). Zooxanthellate and nonzooxanthellate colonies of *Astrangia astreiformis* Edwards and Haime, however, consume similar quantities of live zooplankton prey (Brunet, in review). *Porites* has been characterized as feeding primarily with its tentacles in Australia (Yonge, 1930) and in Barbados (Lewis and Price, 1975); whereas *Porites lobata* in Hawaii (Johannes and Tepley, 1974) and the Jamaican species of *Porites* (N. I. Goreau, pers. comm.) are considered to be essentially non-tentacular, suspension feeders.

#### *Coral-Coral Interactions*

Partitioning of space between neighboring scleractinians may occur by various mechanisms (e.g., Shepard, 1982) resulting from direct tissue contact, or indirectly without such contact (see Table 2). Interactions between any two stony corals are probably affected by their genetic relatedness and by morphological constraints (Bak and Criens, 1982a), by demographic processes (Neigel and Avise, 1983), and by such ecological variables as the frequency with which each encounters conspecific, congeneric or other scleractinians. As noted by Bak *et al.* (1982) and by Chornesky (1983), within colonies, positional effects and other factors may also influence the outcome of such interactions.

Lang (1971) and Wells (1971b) used extracoelenteric destructive reactions (Table 1) to separate two species of *Scolymia*.<sup>5</sup> Similar behavioral patterns were considered by Wells (1973) in his treatment of the Jamaican *Mycetophyllia*. Considerable geographic differences do, however, occur in the extent to which extracoelenteric mesenterial reactions, and other traits, intergrade in the *Mycetophyllias* (Lang, 1973; Zlatarski, 1982). I currently suspect that this genus consists of a cluster of closely related species, or semispecies (incipient species), that may be introgressing at least in parts of their areas of sympatry.

Various kinds of overgrowth and filling (also collec-

<sup>5</sup> Other differences between these species of *Scolymia* (Table 1) include tissue coloration and fleshiness, relative abundance, depth distribution and their relative positions in a scleractinian destructive dominance hierarchy (Lang, 1971; 1973). Usually their skeletons can also be separated by some minor, but distinctive traits (Wells, 1971; N. I. Goreau, pers. comm.).

tively called cementum) reactions may occur between congeneric species of *Acropora* (e.g., Hildemann et al., 1975; Bak and Criens, 1982a), *Montipora* (Bernard, 1897), *Porites* (Brüggemann, 1887), etc. The sweeper tentacles of *Montastraea cavernosa* batter polyps of *M. annularis* when colonies are separated by distances of several cm, and may thereby deter the latter from deploying its mesenterial filaments (Richardson et al., 1979).

Antagonistic intraspecific interactions include extra-coelenteric mesenterial attacks between specimens of *Montastraea annularis* (Dustan, 1975), and of sweeper tentacles in *M. cavernosa* (K. B. Sebens, pers. comm.), and various overgrowth and filling reactions within species of *Acropora* (e.g., Hildemann et al., 1975; Potts, 1976), *Pocillopora* (Hildemann et al., 1975) and *Montipora* (Hildemann et al., 1980). According to Rinkevich and Loya (1983), diverse responses characterize interactions among colonies of *Stylophora pistillata*, with color and size being most important. Contact avoidance has also been described within species of *Acropora* (e.g., Hildemann et al., 1975).

Since contact between different parts of the same colony invariably leads to compatible fusion of tissues and skeletal elements (e.g., Dana, 1846; Brook, 1893), grafting experiments have been used to approximate intraspecific clonal diversity and population structure in a few species of *Acropora* (Bothwell, 1982; Neigel and Avise, 1983), *Montipora* (Jokiel et al., 1983) and *Porites* (Hunter and Kehoe, 1983).<sup>6</sup>

Interclonal fighting restricted to members of the same sex has been described in an actiniarian (Kaplan, 1983). In hydroids, abnormal interclonal overgrowth reactions may occur between the stolons of related (half-sibs, parent-offspring) strains (Ivker, 1972). Furthermore, heteroclonal grafts of medusae may fuse compatibly, despite interclonal incompatibility of the stolons of the corresponding polypal stages (Buehrer and Tardent, 1980).

#### *Mucus Sheet Formation*

Mucus released by scleractinians of different genera may vary considerably in appearance (Coles and Strathmann, 1973), and in rate of production (Richman et al., 1975). Lewis (1973) noted the mucus sheets which occasionally overlie tissues of the western Atlantic species of *Porites*. Recently Coffroth (1983) has reported that the formation of these sheets is independent of environmental factors, but occurs at different

times of the lunar cycle in *Porites astreoides* Lesueur and *P. furcata* Lamarck (? = *P. porites* (Pallas)). Organic products of endosymbiotic algal photosynthesis are incorporated in the mucus released by the zooxanthellate corals (e.g., Crossland et al., 1980).

#### Ecological Characters

Ecological traits encompass a wide array of non-structural characters resulting from the interactions of organisms with the abiotic and biotic components of their environment (after Wiley, 1981). They have been especially important in the recognition of cryptic species (Mayr, 1969; Ross, 1974).

#### *Habitat Distribution Patterns*

In other groups of animals, a number of cryptic species have been discovered by habitat differences (e.g., Mayr, 1969, 1970). Depth ranges, or more detailed distributional data, have been listed in systematic treatments of stony corals for many years (see Vaughan, 1918). As far as I am aware, only Head (1983) has clearly utilized this kind of information in the description of a scleractinian species (Table 1).

Chang et al. (1983) have suggested that the photoadaptive capabilities of three strains of *S. microadriaticum*, including one isolated from *Montipora verrucosa* (Lamarck), are positively correlated with the ecological distribution patterns of their respective hosts. Hence the habitats occupied by zooxanthellate corals may be partially determined by their algal endosymbionts.

#### *Demography*

Demographic information for scleractinians is still fairly rare (e.g., Connell, 1973; Fadlallah, 1983b; Rylaarsdam, 1983). Sympatric populations of *Agaricia agaricites* and of *A. lamarcki* Edwards and Haime show distinctive differences in larval recruitment rates; mean colony sizes; and patterns of mortality, tissue repair and longevity, both in Curaçao (Bak and Engel, 1979; Bak and Luckhurst, 1980) and Jamaica (Hughes and Jackson, 1980, in review).<sup>7</sup> Algal endosymbionts may contribute to the expression of some of these features (e.g., corallum sizes, tissue repair rates) in the zooxanthellate corals.

#### *Non-Scleractinian Associates*

Although living scleractinians are overgrown or bored by a wide variety of sessile protists, algae, fungi and animals (e.g., see reviews of Sheppard, 1982; Macintyre, this volume), I have found few examples of

<sup>6</sup> Note, however, the possibility for interclonal fusion among conspecific scleractinians, as discussed by Neigel and Avise (1983) and by Rinkevich and Loya (1983).

<sup>7</sup> Zlatarski (1982) has, however, synonymized all the western Atlantic *Agaricias* into a single, polytypic species.

species-specific associations (Table 1).<sup>8</sup> At least several species of the boring bivalve *Lithophaga* appear to distinguish between congeneric species of *Acropora* (Kleeman, 1977), *Montipora* (Highsmith, 1980) and, perhaps, *Heteropsammia* (Arnaud and Thomassin, 1976; but see Veron and Pichon, 1980), yet geographic variation in host specificity is fairly high (see also Scott, 1980). Furthermore, overlap of host species does not occur between the two species of West Indian barnacles which inhabit the skeletons of live scleractinians (P. J. B. Scott, pers. comm.).

Stony corals shelter numerous motile animals, some of which are permanent obligate associates. Many of these *e.g.*, cyclopoid copepods, xanthid shrimps and decapods (*e.g.*, Bruce, 1976; Patton, 1976, 1983) are associated with a particular family or genus of corals. Exceptions include the three species of pontoninid shrimps and the alpheid which Bruce (1976, 1977) reports are obligatory associates of *Galaxea fascicularis* (Linnaeus). In Australia the dark color morph of *Paragobiodon echinocephalus* Rüppell (= *Paragobiodon* sp.) is restricted to *Stylophora pistillata*, whereas the light color morph (= *P. xanthosoma* Bleeker) is only found among colonies of *Seriatopora hystrix* Dana (Tyler, 1971; Lassig, 1976).

Host discrimination by most of the described predators and parasites of scleractinians is similarly limited (*e.g.*, Robertson, 1970; Jokiel and Townsley, 1974; Wellington, 1982). Some stony coral species do, however, experience either disproportionately high levels of predation—or relative immunity from predators—at least in some environments (*e.g.*, fishes—Neudecker, 1979; perhaps nudibranchs—Rudman, 1981). Endoparasitic coralloveniid copepods appear to discriminate among several congeneric species of scleractinians in Curaçao (Stock, 1975); but Herriott and Immermann (1979) found some cases of geographic variation in these associations in St. Croix. A few corallivores may digest zooxanthellae (see review of Robertson, 1970; Rudman, 1981). Alternatively, self-autolysis of these algae may occur (Trench, pers. comm.).

Those scleractinians which do escape predators or parasites may be protected by unusually toxic nematocysts and/or chemicals (*e.g.*, Barnes *et al.*, 1970; Brauer *et al.*, 1970; Moore and Huxley, 1976). The obligate crustaceans associated with some stony corals can also prevent attacks by *Acanthaster planci* (Linnaeus) (*e.g.*, Glynn, 1976, 1983), as can some fishes (Weber and Woodhead, 1970).

<sup>8</sup> In this section I have omitted numerous reports in which (a) the host scleractinian is the only species of its genus apparently living in the habitat in which the particular association occurs, or (b) data are not given for other congeners known to occur in the area.

## Diseases

Susceptibility of corals to various presumed infections (such as the white and black band diseases; perhaps neoplasia) is apparently restricted to certain genera or congeneric species, at least in the western Atlantic (*e.g.*, Ramos-Flores, 1983; Rützler *et al.*, 1983; Peters, in press). Apparently identical signs of disease in different species of corals may, however, be caused by different pathogens (Dustan, 1977), and/or by different environmental conditions (Peters, in press). Nonetheless, in the early 1980's, *Acropora cervicornis* (Lamarck) was disproportionately susceptible to a white band disease in Curaçao, Bonaire (Bak and Criens, 1982b; van Duyl, 1982) and in Jamaica (Knowlton *et al.*, 1981). Moreover, the proportion of colonies of *Acropora palmata* (Lamarck) which are affected by a white band disease varies horizontally along the reef crest in St. Croix, and geographically in the western Atlantic (Gladfelter, 1982).

## Biochemical Characters

The structural, or other physical, attributes of molecules (including DNA and its products), constitute biochemical characters (Wiley, 1981). Specificity in molecular structure occurs at every taxonomic level, and biochemical techniques are now being applied to systematic problems of all types, and in many different organisms (*e.g.*, Mayr, 1969; Ferguson, 1980; Wiley, 1981), including such anthozoans as alcyonaceans (Kashman *et al.*, 1980) and gorgonians (Gerhart, 1983).

## Allozymes

Many proteins exist in natural populations in two or more molecular forms called allozymes, some of which can be detected electrophoretically (Bush and Kitto, 1978). Despite the well-known limitations of this method (Avisé, 1974), it has made important contributions to the systematics of species of morphologically simple organisms (Ferguson, 1980). Often suspected cryptic species are easily distinguished by electrophoretic techniques (Rollinson, 1980). Interspecific differences in allozyme patterns have been reported for three species of zoanths in Venezuela (Lin, 1979). In actinarians, electrophoretic data have been used to infer genetic relationships among clonemates (*e.g.*, Shick *et al.*, 1979; Ayre, 1983), and between brooding polyps and brooded juveniles (Ottaway and Kirby, 1975; Black and Johnson, 1979; Orr *et al.*, 1982), to separate color morphs (Quicke *et al.*, 1983), and to characterize species (Carter and Thorpe, 1981; Bucklin and Hedgecock, 1982). Evidence of geographic variation in allozyme patterns has also been provided by Bucklin and Hedgecock (1982).



For scleractinians, the electrophoretic approach, first suggested by Lamberts (1979), is presently under active investigation in several laboratories. For example, the "asexual planulae" of *Pocillopora damicornis* were identified electrophoretically (Stoddart, 1983). On the basis of polymorphism in five enzyme systems, Ohlhorst (this volume) could distinguish, with varying degrees of certainty, all 12 described species in 5 genera of West Indian corals. In this study allozyme patterns were related to collection site along the Jamaican north coast in some species, but no correlations were found with colony shape or tissue coloration.

#### Lipids

Scleractinians have unusually high concentrations of lipids (e.g., Patton *et al.*, 1983). Some western Atlantic species appear to have distinctive fatty acid signatures, whilst others show substantial temporal and geographic variability (Meyers, 1977). Temporal variations in lipid content can be related to diet and nutritional state; the presence or absence of zooxanthellae; and probably also to stage of the sexual reproductive cycle (e.g., Meyers *et al.*, 1978; Szmant-Froelich and Pilson, 1980; Patton *et al.*, 1983).

#### Chemical Activation of Feeding

Lenhoff *et al.* (1976) have suggested that actinarians and zooanthids generally exhibit a greater degree of feeding specificity than do scleractinians (but see Goreau *et al.*, 1971; Lehman and Porter, 1973). Slight differences in the chemicals which stimulate feeding have been noted for *Pocillopora damicornis* and *P. meandrina* Dana (Mariscal, 1971). The two morphs of *Montastraea cavernosa*, however, differ greatly in the range of stimuli which initiate feeding responses (Lehman and Porter, 1973). Geographic variability has not been studied in stony corals, but the chemicals which stimulate feeding in the actinarian *Diadumene* (= *Haliplanella*) *luciae* (Verrill) do vary between California and England (see review of R. B. Williams, 1973).

#### Release of Dissolved Organics

There is considerable indirect evidence that actinarians, gorgonians and alcyonaceans naturally release organic chemicals to the surrounding sea water (e.g., Martin, 1968; Wahle, 1980; Coll *et al.*, 1982; Sammarco *et al.*, 1983). Scleractinians may also secrete substances such as cytotoxins (*Fungia*—Hildemann *et al.*, 1977) and riboflavins (*Acropora* sp.—Fontaine *et al.*, 1982). Rinkevich and Loya (1983) have suggested that pheromones or other biochemicals are released by *Stylophora pistillata*, perhaps in mucus, since many of its natural interactions with nearby conspecifics appear

to occur without physical contact between the reacting colonies.

#### Physiological Characters

Physiological characters result from the metabolic activities of organisms (Wiley, 1981). In the relatively few instances in which closely related species have been carefully studied, physiological differences have been found between them (e.g., Mayr, 1969). Indeed Vaughan (1907) stressed that physiological investigations were needed to resolve the problems of morphological variation in stony corals, and to understand the environmental factors influencing their distribution. Nonetheless, physiological characters are rarely utilized as systematic characters, despite their potential utility, especially in the discrimination of cryptic species (Prosser, 1973).

The physiological behavior of zooxanthella-containing stony corals is also related to the activities of their algal endosymbionts (e.g., T. F. Goreau, 1959; Muscatine, 1980; Jacques *et al.*, 1983). Genetic differences among zooxanthellae have been suggested as potentially influencing the thermal tolerances (Jokiel and Coles, 1977) and photoadaptation responses (Dustan, 1979; Jokiel and York, 1982) of their scleractinian hosts. In support of this concept is Chang *et al.*'s (1983) demonstration of different photoadaptive capabilities in three strains of *S. microadriaticum*.

#### Environmental Tolerance Levels

Congeneric scleractinian species (inhabiting either the same or nearby habitats) sometimes vary in their relative abilities to tolerate extreme temperatures (Mayer, 1914; Jokiel and Coles, 1974), salinities (Mayer, 1918; Mayor, 1924; Wells, 1932; Goreau, 1964), or to shed sediments (Mayor, 1924; Hubbard and Pockock, 1972; Bak and Elgershuizen, 1976; Schuhmacher, 1977).

Yonge (1935) related intraspecific differences in sediment shedding (Table 1) to skeletal characters and habitat in two morphs of *Siderastrea radians* (Pallas). Similar differences have been described for *Montastraea cavernosa* by Lasker (1980), and for *Heterocyathus aequicostatus* Edwards and Haime by Fisk (1982). Coles *et al.* (1976) have quantified geographic variation in the upper lethal temperatures tolerated by specimens of *Fungia scutaria* Lamarck in Hawaii and Enewetak.

#### Respirometry

The respiratory rates of *Montastraea annularis* from any habitat are consistently higher than those of *M. cavernosa* from similar environments (Spencer Davies,

1980; Porter *et al.*, in prep.). In several scleractinian species with wide depth ranges, specimens from "deep" habitats have been shown to have lower compensation light intensities than their "shallow" counterparts on the same reefs (Wethey and Porter, 1976; Porter, 1980; Fallowski and Dubinsky, 1981). Lasker (1981) related rates of oxygen flux in the two morphs of *M. cavernosa* to polypal number and size, expansion behavior and to density of zooxanthellae. Morphs of *Stylophora pistillata*, some of which were formerly considered to be different species (Veron and Pichon, 1976) also have different oxygen flux rates (Porter *et al.*, in press). Coles and Jokiel (1977) found that rates of photosynthesis and respiration were closely adapted to ambient temperature conditions for geographically separated populations of four scleractinian species in Enewetak and Hawaii respectively.

#### *Electrophysiology*

Stony corals which have been stimulated with a localized electrical shock respond by retracting some or all of their polyps (Horridge, 1957). According to Anderson (1976), the maximum area of the polyp retraction response is twice as great for colonies of *Goniopora columna* Dana as it is for colonies of *G. lobata* Edwards and Haime.<sup>9</sup> The number of electrical shocks needed to generate pulses in the ectodermal slow-conduction system differs between the two morphs of *Meandrina meandrites* (Linnaeus), but is not affected by the gradual loss of zooxanthellae in the laboratory (McFarlane, 1978).

#### OVERVIEW

The recent technological improvements in microscopy, biochemistry, physiology, and in diving procedures (which allow extended time underwater for behavioral, ecological, and many other kinds of research) provide an unparalleled opportunity to use a "multi-character" approach in identifying scleractinians. Thus far I have emphasized published accounts of those non-skeletal attributes which appear to differentiate congeneric species of stony corals. Other novel characteristics could, however, also be explored by systematists.

In particular, the ultrasculptural and ultrastructural features of scleractinian gametes, planulae and polyps (*e.g.*, Lyons, 1973; Mariscal 1974a; Hayes and N. I. Goreau, 1977a, b; Schmidt and Schäfer, 1980; Schmidt and Höltken, 1980; Fadlallah and Pearse, 1982) could be examined under the scanning electron-microscope

(SEM) and the transmission electron microscope (TEM) respectively (J. E. Rawlins, pers. comm.). The cnidae of stony corals could be investigated with SEM (Mariscal, 1974b), TEM (Schmidt, 1974), perhaps with X-ray microanalysis (Mariscal, 1980), and with various biochemical (*e.g.*, Mariscal, 1974b; Hessinger, 1983) and quantification (*e.g.*, Bode *et al.*, 1983) procedures. Even scleractinian chromosomes could be counted by use of appropriate spreading techniques (see Kligerman and Bloom, 1977). Spread preparations of the synaptonemal complexes of meiotic cells (Counce and Meyer, 1973) would give additional information about chromosome length and the location of the centromeres (J. R. Ellison, pers. comm.).

Moreover, the chemicals which are presumably involved in such species-specific recognition phenomena as sperm chemotaxis (*e.g.*, Miller, 1980, 1982), control of nematocyst discharge (*e.g.*, Lubbock, 1979; Ertman and Davenport, 1981), and activation or inhibition of feeding responses (*e.g.*, Lenhoff *et al.*, 1983) might receive greater attention. Electrophysiological techniques can be applied to the study of chemoreception, and to many allied components of behavior such as expansion, feeding, and "self" versus "non-self" recognition (see review of Shelton, 1982). Perhaps the metabolic costs associated with these specific behavioral patterns could be compared using the new generation of *in situ* respirometers (Porter, 1980; Pearson *et al.*, 1984) and methods of data analysis (Muscatine *et al.*, 1981). Dissolved organics released by scleractinians could be concentrated under reasonably natural field conditions (Coll *et al.*, 1982) prior to analysis in the laboratory.

My tentative assessments of the kinds of non-skeletal attributes which might help to characterize species of scleractinians are given in Table 2. As this review illustrates, such characteristics have been studied in a limited number of stony corals, few of which are congeners. Hence the data which are currently available have little to offer the systematist. Such pertinent information as does exist is, however, rarely considered when scleractinian species are delineated (but see Table 1).

A few cautionary observations may be appropriate at this stage. That the systematic utility of any particular skeletal character varies among groups (*e.g.*, Vaughan and Wells, 1943; Alloiteau, 1952; Wallace, 1978; Dinesen, 1980) or geographic regions (Crossland, 1931) is well known. Similar constraints apply to the non-skeletal features described above. For example, evidence to date suggests that some fungiids and eusmiliinids can be recognized by unusual polypal characteristics and by their expansion behavior. Nevertheless, species of siderastreids (Szmant-Fro-

<sup>9</sup> According to Veron and Pichon (1982), *Goniopora columna* and *G. lobata* are very similar morphologically, and can seldom be distinguished *in situ*.

lich, pers. comm.) and agariciids will probably be separated more readily by sexual reproductive and, perhaps, distributional or demographic patterns. The ability to deploy sweeper tentacles may yet prove to be of diagnostic value for some favioid, pocilloporid or caryophylliid species. And so on.

Like many skeletal traits, these attributes can be difficult to describe and/or highly variable. Furthermore, many nonskeletal components of the zooxanthellate corals are probably affected by their algal symbionts. As noted in the above review, however, non-morphological characteristics are valuable in the diagnosis of cryptic species. In morphologically variable organisms such as scleractinians, where species limits in some genera are confused or seemingly impossible to define with skeletal traits, this ability could potentially be exceedingly important.

Once recognized, cryptic species in many other groups have been separated by a number of minor, but consistent, morphological differences (*e.g.*, Mayr, 1970; Ross, 1974). For "practical purposes" (Heywood, 1973), whenever possible, cryptic scleractinian species should also be identifiable by some distinctive skeletal structures. Sometimes new approaches to the characterization of stony coral skeletons may be needed to accomplish this secondary goal.

As Wallace and Dallwitz (1981) have illustrated, the ranges of variability of diagnostic skeletal structures can be portrayed by coupling SEM photography with a precise descriptive terminology. Patterns of variation in skeletal microstructure can be quantified (*e.g.*, Chevalier, 1971; Foster, this volume). Other skeletal characteristics which appear to differentiate congeneric scleractinian species include linear extension rates (*e.g.*, Hughes and Jackson, in review), density banding patterns (Jokiel, pers. comm.), stable isotope geochemistry (*e.g.*, Haggerty *et al.*, 1980), architectural design (Constanz, this volume) and ontogenetic changes (*e.g.*, N. I. Goreau and Hayes, 1980; N. I. Goreau, 1983a).

In addition, complex skeletal shapes can be visualized with SEM stereophotography (*e.g.*, Benson, 1972; Cairns, 1983). The three-dimensional data contained in paired stereo photographs and micrographs can be quantified with computer graphic analysis (Schooley *et al.*, 1982).

Finally, systematic decisions should never be based on a single trait (*e.g.*, Alloiteau, 1952; Veron *et al.*, 1977), regardless of what that character is. No trait is invariably constant,<sup>10</sup> and each attains its value to systematists through the reliability of its correlations with

other characters (*e.g.*, Darwin, 1859; Cronquist, 1980; Wiley, 1981). Particularly when morphological analyses are ambiguous, all available information, drawn from as wide a range of organizational levels as possible, should be considered (*e.g.*, Mayr, 1969; Avise, 1974; Rollinson, 1980; and Richmond and Jokiel, in press), with special regard for evidence of sexual reproductive isolation. Then particular emphasis should be given to whichever combination of characters appears most effective for any given scleractinian species. At this stage, statistical methods of character analysis may be necessary (*e.g.*, see reviews of Wiley, 1981; Foster, this volume).

A number of the approaches suggested here require specialized equipment and/or prolonged periods of observation. To test some of these suggestions, most systematists would need to collaborate with specialists in other fields, although they would retain ultimate responsibility for any systematic interpretations (Johnson, 1974). Fortunately, many other scientists are currently studying such potentially relevant attributes as scleractinian reproductive patterns, ecological relationships, metabolic activities, physiological, biochemical and geochemical aspects of skeletogenesis, etc. Concern for the lack of a stable species nomenclature is sometimes evident in their writings. I suspect that some of these scientists would willingly collaborate on the problematic genera of stony corals. In other words, systematists should not fear that they would personally have to generate all the unconventional forms of data suggested here. Surely everyone would benefit from the knowledge gained, because a soundly based identification system for scleractinians would certainly enhance the development of all branches of stony coral biology and geology.

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<sup>10</sup> As Cronquist (1979) noted of chemical characters, "they work when they work, and they don't work when they don't work."

Table 2.—Provisional assessments of the kinds of non-skeletal attributes which might help to characterize species of scleractinians.

Non-skeletal attribute	Likely to be modified by		Provisional assessment
	Local environment	Endo-symbiotic zooxanthellae	
<b>SEXUAL REPRODUCTION</b>			
Sexual patterns:	yes	?	In a number of problematic genera, <i>e.g.</i> , <i>Agaricia</i> , <i>Acropora</i> , <i>?Favia</i> , <i>Porites</i> , <i>?Siderastrea</i> , at least some species can probably be characterized by distinctive sexual reproduction patterns; obtaining adequate data can be very time consuming and tedious, but is potentially of great systematic value; some aspects of gonad development and of embryonic and larval ontogenesis can probably be related to skeletal morphology.
Gonochorists (=dioecious) versus adolescent gonochorists (=protandrous or protogynous hermaphrodites) versus simultaneous hermaphrodites;			
Gonads develop as thickenings within septa versus stalks in the coelenteron;			
Number of eggs and/or spermaries per gonad;			
Mean oocyte size;			
Mean spermary size;			
Length of breeding season;			
Lunar, seasonal and annual variations in gonad development and of breeding;			
Extent of synchrony of gonad development and of breeding;			
Number of eggs or planula larvae released;			
If brooders (=release planulae)			
Planulae develop within gonads versus within coelenteron;			
Developmental stage at which planulae are released;			
Planktonic versus benthic planulae;			
If planktonic			
Lecithotrophic versus planktotrophic planulae;			
Age or size of adults at first sexual reproduction;			
If gonochorists			
Sex ratios of adults			
<b>ASEXUAL REPRODUCTION</b>			
"Polyp balls" ( <i>G. stokesi</i> )	?yes	?	Although each of these unusual forms of asexual dispersal has been described for only one scleractinian species, their potential systematic importance cannot be assessed at present, due to a lack of data for other scleractinians.
"Planula-containing polyps": ( <i>S. hystrix</i> )			
"Asexual planulae": ( <i>P. damicornis</i> )			
<b>EXTERNAL MORPHOLOGY</b>			
Unusual polypal sizes and shapes	?	?	For some scleractinians, tentacle morphology appears to be a useful systematic trait at the level of (perhaps) species to genera; easily observed, and probably most of the obvious cases have already been described; SEM has not yet been used to look for any specific differences as may exist in ultrasculptural features of scleractinian gametes, planulae and polyps.
Sweeper tentacles	yes	?	In some genera, <i>e.g.</i> , <i>Agaricia</i> , <i>?Dichocoenia</i> , <i>?Euphyllia</i> , <i>Montastraea</i> , <i>?Pocillopora</i> , variability in the ability to develop and, perhaps, maintain sweeper tentacles, could potentially be used as a species-level character somewhat difficult to observe in species with tiny (<3 mm diam.) polyps.
Counts of repeated structures	?	?	Tentacle number and/or location is perhaps a useful specific trait in some genera, <i>e.g.</i> , <i>?Blastomussa</i> , <i>?Caulastrea</i> , <i>?Cyphastrea</i> , <i>?Cynarina</i> , <i>?Mycetophyllia</i> .

Table 2.—Continued.

Non-skeletal attribute	Likely to be modified by		Provisional assessment
	Local environment	Endo-symbiotic zooxanthellae	
<b>EXTERNAL MORPHOLOGY (Continued)</b>			
Relative tissue thickness	?no	?	At least in a few mussid genera, the relative development of the mesogleal layer could probably be used as a systematic character at the species level; easily observed.
Tissue colors and color patterns	yes	yes	Within any given geographic area, tissue colors could be used to distinguish scleractinian species in many genera; easily observed, but requires careful descriptions or good color photographs; in some species color patterns correlate with skeletal morphology.
<b>INTERNAL MORPHOLOGY</b>			
Muscular development; Mesenterial filament morphology and cell composition; Supporting and mucosecretory cells of the epidermal layer; Gastrodermal cells; Pigment cells and pigment accumulation; Cell size and vesicles of the calicoblastic epithelium; Desmoidal processes; Relative number of mesogleal cells; Quantity and arrangement of fibers in the mesoglea	?	?	Probably many histological, histochemical and, perhaps, ultrastructural characters could be used as species-level systematic characters, at least in some scleractinian genera.
Cnidom: For each type of nematocyst Size and shape of the capsule; coiling of the threads; relative abundance; location in the tissues; If sweeper tentacles Any associated differences in nematocyst type, size, relative abundance or location	yes	?	The systematic potential of scleractinian nematocysts should be evaluated with adequate microscopical, biochemical and quantification techniques.
<b>KARYOLOGY</b>			
Chromosome number; Chromosome lengths; Position of centromeres	?no	?no	Scleractinian chromosomes could be counted by use of spread preparations; synaptonemal complexes of meiotic cells would also indicate chromosome lengths and the position of the centromeres.

Table 2.—Continued.

Non-skeletal attribute	Likely to be modified by		Provisional assessment
	Local environment	Endo-symbiotic zooxanthellae	
<b>BEHAVIOR</b>			
Expansion: Diel activity patterns	yes	yes	Unusual patterns of expansion and contraction are apparently a useful character for recognizing species in at least a few problematic scleractinian genera; easily observed in many species.
Feeding: Relative use of Tentacles, Ciliary-mucoid suspension feeding, Extracoelenteric feeding, Mucus sheets, Microvilli on epidermal cells, Zooxanthellae; Kinds of food used Zooplankton, Phytoplankton, Bacterioplankton, Dissolved organic matter; For any kind of food Feeding rates, Feeding selectivity, Amounts eaten, Diel cycles in feeding activity	yes	yes	Until scleractinian feeding responses can be accurately predicted from skeletal morphology (combined, perhaps, with information on expansion behavior and nematocysts), quantitative feeding data might be a useful systematic trait; its potential as a species-level character cannot be assessed at present, due to a lack of comparable information for congeneric species.
Coral-coral interactions: In interactions with any given species Direct (tissue contact) versus indirect (no tissue contact); If direct, relative use of Mesenterial filaments, Sweeper tentacles, Sweeper polyps, Overgrowth reactions (=cementum), Filling reactions (=cementum), Border lines, Nematocyst discharge, ?Release of cytotoxins, Any other forms of immuno-incompatibility reactions as may occur, Complete fusion of soft and skeletal tissues, Complete cessation of growth and no apparent interaction (? =some stand-off interactions); If indirect, relative use of Retreat growth (? =contact avoidance reactions), Growth from above (=shading), ?Release of pheromones or other organic chemicals, perhaps in mucus	yes	?	When they occur, extracoelenteric mesenterial (esp. in the Faviina), sweeper tentacular ( <i>Montastraea</i> ), and overgrowth or filling ( <i>Acropora</i> , <i>Porites</i> , <i>Montipora</i> , etc.) reactions sometimes distinguish congeneric species, but intraspecific interactions may also occur; the systematic potential of the other kinds of coral-coral interaction cannot be assessed due to a lack of information on congeners; presumably the types of interactions and their frequency are affected by morphology, and by demographic or other ecological factors, in addition to the genetic relatedness of the interacting scleractinians.
Mucus sheet formation: Lunar periodicity of formation and release; ?Appearance	?	?yes	Not enough information at present to speculate on the systematic potential of lunar variations in the formation of mucus sheets in <i>Porites</i> .

Table 2.—Continued.

Non-skeletal attribute	Likely to be modified by		Provisional assessment
	Local environment	Endo-symbiotic zooxanthellae	
<b>ECOLOGY</b>			
Habitat distribution patterns	yes	?yes	At least in some scleractinian genera, e.g., <i>?Acropora</i> , <i>?Agaricia</i> , habitat or microhabitat data might help in the recognition of cryptic species.
Demography: Larval recruitment rates; Mean adult colony size; Patterns of mortality; Mechanisms and rates of tissue regeneration; Mean longevity patterns	yes	?yes	Demographic information is potentially useful in clarifying specific relationships, particularly for such problematic genera as <i>?Acropora</i> , <i>Agaricia</i> , <i>?Pocillopora</i> , <i>?Porites</i> , in which at least some species grow rapidly.
Non-scleractinian associates: Epibenthic overgrowers; Endobenthic borers; Motile animals; Predators; Parasites	yes	?yes	Although relatively few non-scleractinian associates are known to be associated with a single host species, some highly restricted relationships—or the avoidance of certain scleractinians by these organisms—could potentially be used to help distinguish species in such problematic genera as <i>Acropora</i> , <i>Montipora</i> , <i>Pocillopora</i> , <i>Porites</i> , etc.
Diseases: Identity of pathogens; External signs of the disease; Rate of progress of the disease Within colonies, Within populations, Between populations	yes	?	Until more is known about the identity and distribution patterns of the pathogens which cause diseases in scleractinians, speculations about the extent of their host-specificity are premature; nonetheless, congeneric species of <i>Acropora</i> differ in the extent to which they are killed by the “white band” disease(s).
<b>BIOCHEMISTRY</b>			
Allozymes: One-dimensional electrophoresis; ?Two-dimensional electrophoresis	yes	?	Different allozyme systems could potentially provide a suite of useful systematic characters at the levels of clones to genera; relatively rapid and inexpensive; procedures are now fairly well established for cnidarians.
Lipids: Wax ester to triglyceride ratios; Fatty acid compositions; Percent saturation values of fatty acids; Lipid to protein ratios	yes	yes	Differences in lipid composition may perhaps help to characterize species in such genera as <i>Acropora</i> , <i>Madracis</i> , <i>Porites</i> , ?other.
Chemical activation of feeding: Specific activators; For each activator Concentration range over which activation occurs	?	?	The chemicals which initiate feeding responses apparently differ in two species of <i>Pocillopora</i> and in two morphs of <i>Monastrea cavernosa</i> ; overall there is too little information on congeneric species to assess its systematic potential at present.
Release of dissolved organics: Riboflavins; ?Cytotoxins; ?Pheromones	?yes	?	Until the dissolved organic compounds which may be released from scleractinians have been collected under natural field conditions and identified chemically, speculations as to their potential level of systematic importance are obviously premature.

Table 2.—Continued.

Non-skeletal attribute	Likely to be modified by		Provisional assessment
	Local environment	Endo-symbiotic zooxanthellae	
<b>PHYSIOLOGY</b>			
Environmental tolerance levels:	yes	?yes	Differences in the relative abilities of some congeneric species to tolerate various environmental extremes have been observed both experimentally and in nature, and might contribute useful systematic information in such problematic genera as <i>Acropora</i> , <i>Montastraea</i> , <i>Porites</i> , ? <i>Siderastrea</i> .
Temperature;			
Salinity;			
Desiccation;			
Sediments;			
?Ambient illumination			
Respirometry:	yes	yes	Oxygen flux rates appear to differ between species ( <i>Montastraea</i> ) and morphs ( <i>Montastraea cavernosa</i> , <i>Stylophora pistillata</i> ), and may correlate with some aspects of skeletal morphology; analytical techniques have improved greatly in the last few years, and their systematic potential can be assessed as information becomes available.
Oxygen flux			
Electrophysiology:	?	?	Various kinds of electrophysiological responses may differ between species (polyp retraction— <i>Goniopora</i> ) or morphs (pulse generation— <i>Meandrina meandrites</i> ) but more data are needed for congeneric species before their systematic potential can be assessed; many specific chemorecognition responses (coral–coral interactions, activation of feeding, etc.) could be analyzed electrophysiologically.
Type of system			
Nerve net,			
Ectodermal slow conduction;			
Type of response			
Polyp retraction,			
Polyp expansion;			
If colonial			
Extent of integration between polyps			

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## THE USE OF POLYACRYLAMIDE GEL ELECTROPHORESIS IN CORAL TAXONOMY

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### ABSTRACT

Twelve species of Jamaican corals [*Montastrea annularis*, *M. cavernosa*, *Diploria labyrinthiformis*, *D. strigosa* (F. Faviidae); *Acropora cervicornis*, *A. palmata*, *A. prolifera* (F. Acroporidae); *Mycetophyllia aliciae*, *M. ferox*, *M. lamarckiana*, *M. reesi* (F. Mussidae); and *Meandrina meandrites* (F. Meandrinidae)] were analyzed using the technique of polyacrylamide gel electrophoresis. Five enzyme systems were successful in producing useful protein bands. Most species can be distinguished from each other by a distinctive "fingerprint" of banding patterns, reflecting differing protein mobility within an electric field. Patterns of band polymorphism do not correlate with variability in coral colony shape or color but are often correlated with different collection sites along the north coast of Jamaica.

### INTRODUCTION

Coral taxonomists have, with few exceptions, relied upon differences in skeletal characteristics for coral species determinations. A number of workers have demonstrated the difficulties associated with the sole use of this approach (Foster, 1977, 1979; Wijsman-Best, 1974), due especially to variability of colony form in relation to environmental parameters. Lang (these proceedings) has encouraged the use of characters from the living animal and used one such character, digestive dominance, in addressing one coral species problem (1971).

Protein electrophoresis is another approach to the study of the taxonomy and species variability of living corals and one which to date has been rarely applied to corals (Lamberts, 1979). Electrophoresis is a technique whereby proteins are separated on the basis of differences in net electrical charge of the macromolecules. When electrophoresis is conducted in gels of polyacrylamide or starch the mobility of the proteins is also influenced by their size and configuration. Through use of this technique Markert and Møller (1959) discovered the existence of isozymes, electrophoretically distinct forms of the same enzyme. The isozymes, with their different mobilities through the gel, are revealed by specific histochemical stains which produce visible bands reflecting regions of enzyme activity.

The degree and pattern of isozyme polymorphism have been examined for a wide range of vertebrate, invertebrate and some plant groups (see review in Powell, 1976). Electrophoresis has been utilized in this manner primarily by population and evolutionary geneticists (see review by Ayala, 1976), but also by taxonomists (Avise, 1974).

This paper reports on the successful use of polyacrylamide gel electrophoresis with corals. The technique

allows the separation of most of the species investigated and reveals differences existing between certain populations. Variation in coral colony morphology and tissue color does not correlate with any banding pattern polymorphism.

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### METHODS

Coral samples were collected primarily from reefs off the central north coast of Jamaica, W.I., although specimens of certain species were also collected from Colombia, Curaçao and Barbados. At Jamaica, 350 specimens were collected from depths of 3–39 m on the reefs at Discovery Bay and Pear Tree Bottom (5 km east of Discovery Bay). When possible, a single species was collected from a variety of depths and colonies with different tissue colors and morphologies sampled. The coral species studied were *Montastrea annularis*, *M. cavernosa*, *Diploria labyrinthiformis*, *D. strigosa* (F. Faviidae); *Acropora cervicornis*, *A. palmata*, *A. prolifera* (F. Acroporidae); *Mycetophyllia aliciae*, *M. ferox*, *M. lamarckiana*, *M. reesi* (F. Mussidae); *Meandrina meandrites* (F. Meandrinidae).

Table 1.—Jamaican coral esterase band frequencies. Protein bands are numbered in order of increasing mobility towards the anode. N = # specimens with EST bands/# total.

Coral species	N	Protein bands											
		1	2	3	4	5	6	7	8	9	10	11	12
<i>Montastrea annularis</i>	121/132	.23	.38	.05	.05	.10	.02	.08	.08	.43	.33	.07	.08
<i>Montastrea cavernosa</i>	48/51			.02		.02	.08	.44	.42	.12	.02		
<i>Diploria labyrinthiformis</i>	5/5						.20			.20	.80		
<i>Diploria strigosa</i>	5/6					.20	.20			1.0			
<i>Acropora cervicornis</i>	27/29	.06				.61	.39		.04	.04	.59	.07	
<i>Acropora palmata</i>	26/27	.04	.04	.08	.08	.42	.50		.04	.15	.65		
<i>Acropora prolifera</i>	29/30		.03		.07	.31	.66			.03	.52	.03	
<i>Mycetophyllia aliciae</i>	22/22				.05			.05	.82	.14			
<i>Mycetophyllia ferox</i>	5/5	.20			.20			.20	.20		.40	.20	.40
<i>Mycetophyllia lamarckiana</i>	18/18		.06	.06	.11				.67	.28	.06		
<i>Mycetophyllia reesi</i>	14/14				.07	.07	.07	.07		.36	.36	.21	
<i>Meandrina meandrites</i>	9/9			.22	.11	.22		.44	.33	.22			

Pieces of coral colonies (2 × 2 cm) were removed with a chisel and hammer in the field (coral tissue regrew to cover the "wound," indicating this method is non-destructive) and tissue was removed from the skeleton in the laboratory by scraping with a scalpel. Use of a "water-pik" for tissue removal resulted in a dilute, foamy "coral shake" and is not recommended unless a way of later concentrating the solution is available. The resulting tissue, mucus and skeletal fragments were mixed with one-half to equal volume of phenoxyethanol buffer (85.6 gm sucrose, 2.3 gm KH<sub>2</sub>PO<sub>4</sub>, 14 gm K<sub>2</sub>HPO<sub>4</sub>, 15 ml phenoxyethanol made to one liter with distilled water) and centrifuged in a table top centrifuge at 2500 rpm for five minutes, or sufficient time to spin down skeletal fragments and zooxanthellae without heating the sample. The supernatant was pipetted off and placed into 0.4 ml plastic mini-centrifuge tubes, frozen and stored for later electrophoresis. Samples were collected between 1975–1977 and were run within 4 months of collection. The phenoxyethanol buffer helps considerably in maintaining enzyme activity and samples in the buffer can sit several days at room temperature and give the same banding pattern as when freshly thawed. Replicate samples of specimens run over the course of several years maintained the same patterns. Samples preserved in phenoxyethanol cannot, however, be compared to those frozen without the buffer.

The coral tissue solutions were run on acrylamide gel slabs in refrigerated gel apparatuses (see Brewer, 1970, for a general discussion of techniques). Electrophoresis was conducted in gels of 7% acrylamide at 5 mA per gel for 3–4 hours, resulting in a maximum protein migration of 3–4 cm. Starch gels were also tried but gave less satisfactory results for all assays. A control coral sample to which a bromphenol marker dye had been added was included on each gel as a reference

point. Enzyme assays and buffer solutions outlined by Ayala *et al.* (1972) and Shaw and Prasad (1970) and modified for acrylamide gels were utilized.

## RESULTS

Esterases (EST), acid phosphatase (ACPH), alkaline phosphatase (APH) and leucine amino peptidase (LAP) assays all yielded a number of coral protein bands (8–12 each) and are useful in distinguishing species and/or genera. Malate dehydrogenase (MDH) was useful in species determination of the *Acropora* spp. group. Only specimens which had bands for at least one of EST, ACPH or APH assays are included in the total sample size.

Although it is quite probable that several bands may represent heterozygous expressions of single loci, the exact relationships of these bands to the genetic loci of these enzymes is unclear.

### Taxonomic Determinations

The genera *Montastrea* and *Diploria* (F. Faviidae) are distinguishable on the basis of assays for EST, ACPH, APH (Tables 1–3) and LAP. Each genus possesses either bands of unique mobility or different frequencies of similar bands.

Within the genus *Montastrea* the species are also distinguishable on the basis of certain of these assays. *M. annularis* possesses EST bands not encountered in *M. cavernosa* and bands of differing mobility predominate in each (Table 1). Assays for ACPH do not separate the species well (Table 2), although it does serve to separate these species from any others quite readily. The APH assay distinguishes the two species due to the total absence of bands for *M. annularis* specimens in contrast to *M. cavernosa* (Table 3). LAP appears to separate the species although success of this assay for *M. annularis* was low (20%).

Table 2.—Jamaican coral acid phosphatase band frequencies. Protein bands are numbered in order of increasing mobility towards the anode. N = # specimens with ACPH bands/# total.

Coral species	N	Protein bands							
		1	2	3	4	5	6	7	8
<i>Montastrea annularis</i>	131/132	.02	.06	.06	.17	.17		.75	.08
<i>Montastrea cavernosa</i>	46/51					.06		.89	.04
<i>Diploria labyrinthiformis</i>	4/5					.25	.50	.25	
<i>Diploria strigosa</i>	2/6					.50	.50		
<i>Acropora cervicornis</i>	21/29	.14	.76	.14	.05				
<i>Acropora palmata</i>	0/27								
<i>Acropora prolifera</i>	0/30								
<i>Mycetophyllia aliciae</i>	14/22					.07	.57	.36	
<i>Mycetophyllia ferox</i>	2/5							.50	.50
<i>Mycetophyllia lamarckiana</i>	13/18					.16	.77	.08	
<i>Mycetophyllia reesi</i>	7/14					.57	.14	.28	
<i>Meandrina meandrites</i>	9/9			.33	.56	.56			

Although the sample size was small, the *Diploria* spp. seem to be easily separable. They possess unique EST bands and differing frequencies of those bands shared (Table 1) and possess unique LAP bands. Neither assays for ACPH nor APH were useful in this study for distinguishing these species from each other (Tables 2, 3).

The *Mycetophyllia* spp. also separate well (Tables 1–3), possessing either unique bands and/or strikingly different band frequencies from each other.

The *Acropora* spp. are the least readily separable. The three species have slightly different EST frequencies, *A. palmata* sometimes possesses a unique APH band, and most strikingly, neither *A. palmata* nor *A. prolifera* produced any ACPH bands (Tables 1–3). Malate dehydrogenase yielded useful results for these species. Over 50% of the specimens produced bands for this assay and the different species possessed unique bands and/or differences in band frequencies.

*Meandrina meandrites* possesses unique protein band frequencies which readily separate it from the other species analyzed.

#### Species Polymorphisms

*Montastrea annularis* is quite polymorphic with respect to both colony morphology and tissue color. Records were kept of these parameters and neither correlated with the observed enzyme band polymorphisms.

Band polymorphism did correlate, however, with the location of collection of the coral species as illustrated in Table 4 for *Montastrea annularis*, *M. cavernosa* and *Acropora cervicornis*. These collection sites differed by at least 10 m in depth and/or were located 0.5–5 km apart. To investigate the possibility that these polymorphisms were environmentally induced, six pieces from each of three *M. annularis* colonies from six reef localities were moved to each of the other sites. The colonies were retrieved and processed as above after one year. In all cases the transplanted specimen

Table 3.—Jamaican coral alkaline phosphatase band frequencies. Protein bands are numbered in order of increasing mobility towards the anode. N = # specimens with APH bands/# total.

Coral species	N	Protein bands								
		1	2	3	4	5	6	7	8	9
<i>Montastrea annularis</i>	0/132									
<i>Montastrea cavernosa</i>	32/51					.03	.13	.50	.63	.06
<i>Diploria labyrinthiformis</i>	2/5								1.0	
<i>Diploria strigosa</i>	3/6								1.0	
<i>Acropora cervicornis</i>	29/29		.41	.59						
<i>Acropora palmata</i>	27/27	.18	.45	.37	.04					
<i>Acropora prolifera</i>	27/30		.48	.52	.04					
<i>Mycetophyllia aliciae</i>	13/22		.15			.08			.85	
<i>Mycetophyllia ferox</i>	2/5								.50	.50
<i>Mycetophyllia lamarckiana</i>	15/18							.73	.27	
<i>Mycetophyllia reesi</i>	0/14									
<i>Meandrina meandrites</i>	9/9			.22			.33	.67	.33	

Table 4.—Esterase band frequencies for specimens of three coral species from different reef sites.

Coral species	Site	N	Protein bands												
			1	2	3	4	5	6	7	8	9	10	11	12	
<i>Montastrea annularis</i>	A	27	.33	.41	.11	.04				.04	.07	.41	.22	.15	.04
<i>Montastrea annularis</i>	B	7		.29		.29				.14	.14	.14	.43	.29	
<i>Montastrea annularis</i>	C	15	.07	.40				.27	.13			.13	.73	.13	
<i>Montastrea annularis</i>	D	10		.90	.10					.10		.40	.30		
<i>Montastrea annularis</i>	E	16	.06	.19	.06	.13	.38			.31	.25	.06	.56		.38
<i>Montastrea annularis</i>	F	16	.56	.13							.13	.63	.19		
<i>Montastrea annularis</i>	G	8	.13	.38		.13	.25			.25		.75	.25		.25
<i>Montastrea annularis</i>	H	22	.32	.45	.05						.05	.77	.14		
<i>Montastrea cavernosa</i>	A	10							.20	.30	.70				
<i>Montastrea cavernosa</i>	B	10						.10	.40	.30	.20				
<i>Montastrea cavernosa</i>	D	11								.55	.27	.18			
<i>Montastrea cavernosa</i>	E	8								.63	.38				
<i>Montastrea cavernosa</i>	H	9			.11			.11	.11	.33	.44	.22	.11		
<i>Acropora cervicornis</i>	I	11						.64	.36				.73		
<i>Acropora cervicornis</i>	J	8						.88	.13		.13	.13	.38	.25	
<i>Acropora cervicornis</i>	K	8						.30	.70				.60		

bands remained identical to those of the "parent" colony.

#### Other Caribbean Localities

A limited number of specimens of *Montastrea* spp. and *Mycetophyllia* spp. were collected from the reefs of Curaçao, Colombia and Barbados. Banding pattern frequencies for all species analyzed were consistent with those found for the Jamaican species.

#### CONCLUSIONS

This study has demonstrated that polyacrylamide gel electrophoresis is a useful technique for those interested in coral taxonomy or coral population variations. The corals analyzed are separable on the basis of distinctive protein banding patterns. Certain of the enzyme assays indicate that distinct populations, located in some cases as close as 100 m along a depth gradient, exist within species. That these polymorphisms are not a reaction to environmental parameters is demonstrated by a transplantation experiment where banding patterns did not change following a year in a new location.

Although there is enzyme polymorphism within a species at a reef site, it can not be correlated with either coral colony morphology or tissue color. It would be of great interest to use electrophoretic analysis on coral specimens for which detailed morphometric measurements were also made.

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AN APPLICATION OF PHYLOGENETIC ANALYSIS TO THE  
SCLERACTINIA: FAMILY FUNGIIDAE

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## ABSTRACT

The terminology and principles of phylogenetic analysis (cladism) are briefly discussed. Three myths commonly ascribed to cladism are discussed and dispelled. They are: 1) that cladism is completely objective, 2) that complete reliance is placed on evolutionary parsimony, and 3) that fossil evidence is not relevant. A step-by-step procedure is outlined for the phylogenetic analysis of the genera and subgenera of the Fungiidae. The procedure includes: 1) construction of a character table, 2) selection of an out-group, 3) polarizing and ordering the character states by out-group comparison, 4) coding the character states, and 5) interpretation of the computer-generated cladogram. The advantages of the cladogram over the previous phylogeny of the Fungiidae (Wells, 1966) are: 1) a more reasonable interpretation of the evolution of the subgenera of *Fungia*, 2) a significantly more parsimonious tree including less homoplasy, 3) an understandable methodology subject to verification and modification, and 4) a better basis for the interpretation of characters. This is the first application of phylogenetic analysis to the Scleractinia and its fourth usage in the Coelenterata.

## INTRODUCTION

Phylogenetic Systematics, frequently called cladism, is not often used to establish the phylogeny of a group of lower invertebrates. This report represents only its fourth usage within the Coelenterata (Schmidt, 1972 and 1974; Gerhart, 1983; Cairns, in press) and its first application to the Scleractinia. The infrequent use of cladism probably stems from the paucity of characters found in lower invertebrates and the difficulty of character analysis. It is the purpose of this paper to apply the cladistic method to an analysis of the fungiid genera in order to serve as a guide and example for other such studies. All procedural steps are explained and the resultant cladogram is interpreted and compared to the traditional phylogeny of the Fungiidae proposed by Wells (1966). The Fungiidae was chosen for this analysis because there is a good data set available for the characteristics of the genera and a proposed evolutionary scheme for the family to serve as a comparison, both provided by Wells (1966). Only those characters described by Wells (1966) are used in the cladistic analysis in order to allow for a valid comparison. Other characters, such as corallum microstructure, histology of soft parts, and characters observed in the field, can and should be used in any subsequent, more thorough analysis of the group. The methodology of cladism is particularly amenable to deletions, additions, and changes within the data set.

Before I proceed with the analysis, I would like to dispel three myths commonly ascribed to cladism. Firstly, the idea that cladism is an entirely objective method. There are elements of subjectivity at several points of the analysis, e.g., choice of out-group, ordering of multistate characters, and choice of alter-

native, equally parsimonious cladogram branches. Secondly, the claim that evolution proceeds in the most parsimonious manner. This also is not true. Cladism will arrange taxa such that their character states change with the least amount of convergence and reversal, i.e., most parsimoniously; however, the decision to invoke parsimony is simply a philosophical choice employed to minimize our acceptance of assumptions, not necessarily the method of determining truth (Cracraft, 1983). The third myth is that fossils should not be used in a cladistic analysis. Fossils *can* be used both as taxa in a cladistic analysis and as an out-group for cladistic analysis. Their stratigraphic ranges can serve to falsify or substantiate a cladistic model, and fossil taxa can also be integrated into a classification with minimal disruption (Wiley, 1981, pp. 214–225).

A cladistic analysis is best performed by an expert on the group being analyzed and preferably on a group recently revised. I acknowledge that I am not an expert on the Fungiidae, but I have relied on the excellent work of Wells (1966), updated by Veron and Pichon (1980) and Pillai and Scheer (1976), and I have examined 31 of the approximately 62 species of fungiids, including specimens of the type-species of every genus and subgenus and a representative of *Acrosmilia*.

TERMINOLOGY AND PRINCIPLES OF  
CLADISM

The three basic methods of determining relationships among organisms are phenetics, evolutionary taxonomy, and phylogenetic analysis or cladism. Phenetics is a numerical approach that groups by overall similarity and does not weight characters. This method does not necessarily reflect the evolutionary history of

the group being analyzed. Traditional evolutionary taxonomists attempt to reflect evolutionary history, by giving more weight to some characters, using the fossil record to identify missing links, and intuitively constructing evolutionary trees based on experience. Cladism also attempts to portray the evolutionary history of a group by determining shared derived characters among the taxa. In the simplest example, among three taxa the two considered most closely related are those that share a unique character. This shared derived character is called a *synapomorphy* and its expression in the two taxa is considered homologous. In Text-figure 1, the acquisition of character 1 is a synapomorphy for taxa A–D and unites them in a *monophyletic* assemblage (a *clade*). Character 2 is a synapomorphy for the monophyletic group A–C. Character 4 is unique to taxon A and therefore is derived but not shared. It is therefore not a synapomorphy but instead is termed an *autapomorphy*.

Cladism is highly dependent on accurate character analysis, *i.e.*, the determination of which character states are ancestral (*plesiomorphic*) and which are derived (*apomorphic*). Character states are *polarized* by a method called *out-group comparison*. For example: assume that in Text-figure 1, A–C is considered to represent all fungiid genera and D represents the most closely related genus to the fungiids, *Acrosmilia*, the out-group. If the theca of *Acrosmilia* and fungiid genus C are imperforate and that of taxa A–B perforate, then the imperforate character state is considered plesiomorphic and the perforate state is considered derived, the change occurring where number 3 → p is drawn on the diagram. This also implies there was a common ancestor, X, to both *Acrosmilia* and the fungiids that had an imperforate theca, a character state that remained in *Acrosmilia* and fungiid genus C. The character state of perforate is also considered a synapomorphy for taxa A–B. If C is considered to represent *Cycloseris*, *Diseris*, and *Heliofungia*, and A–B represents the remaining fungiid genera, then the previously described example reflects the representation of character 5 (thecal porosity) on the cladogram of Text-figure 3. Out-group comparison provides the most reliable basis for polarizing character states. Therefore, choosing the correct sister group (that out-group most closely related to the group being studied) is of great importance.

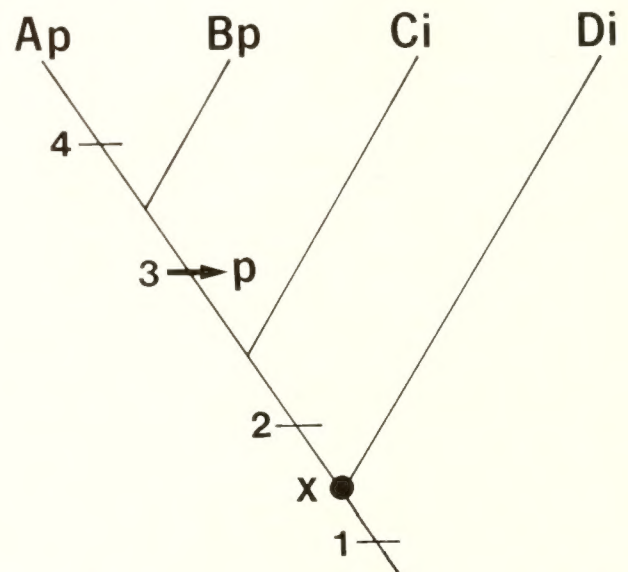
General references on cladism that explain methodology and terminology are: Eldredge and Cracraft (1980), Wiley (1981), and Funk and Humphries (in press). There are several computer algorithms available for cladistic analyses; I used the Wagner 78 program, developed by J. S. Farris (State University of New York, Stony Brook, New York).

#### PROCEDURE FOR OBTAINING THE CLADOGRAM

The first step of the analysis was to produce a character table or tabular key for the fungiid genera and subgenera (Appendix 1). The information for this table was taken from Wells (1966) and Veron and Pichon (1980) and verified by personal observation. Only generic level characters used by Wells (1966) were included in the analysis; however, additional information, such as number of species and stratigraphic range, can be included at this point for informational purposes (but not to be considered as characters).

Next, the Cretaceous synastreid *Acrosmilia* was chosen as the out-group. This was based on hypotheses of the higher classification of the Scleractinia proposed by Vaughan and Wells (1943, pp. 91, 95), Wells (1956, pp. 363, 366), and Wells (1966, pp. 226–227, 230). It was also chosen to be consistent with Wells' premise in his fungiid revision. If subsequent study reveals a group of corals that is more closely related to the fungiids than *Acrosmilia* then this closer relative should be used as the out-group and as the basis for character polarization.

The third step was to polarize and order the character states used in Appendix 1 based on out-group comparison. Seven of eleven of the characters were easily polarized from the out-group because they are two-state characters for which the out-group state is known



Text-figure 1.—Cladogram illustrating the hypothetical interrelationships among four taxa, A–D. Numbers 1–3 represent character state changes or synapomorphies for the taxa they define. Synapomorphy 3 represents the change from an imperforate theca (i) to a perforate theca (p). Character 4 is an autapomorphy. X is a hypothetical ancestor.



(Text-fig. 2a). Thus, because *Acrosmilina* is solitary, this state is considered ancestral, and colonial is considered derived (character 1). Likewise, because *Acrosmilina* has fine costae, this state is considered ancestral and coarse costae is considered derived (character 6), and so forth. The remaining four characters, however, are multistate characters, each having three to five character states. Thus, for character 3 (shape of upper corallum), discoidal was chosen as the ancestral state because of its occurrence in *Acrosmilina*, but out-group comparison does not provide a basis to order the other two states. Therefore, parsimoniously these two states were both provisionally assumed to originate from the discoidal state (Text-fig. 2b). For character 9 (septal dentition), the small state was chosen as ancestral because of its occurrence in *Acrosmilina*, and a trend was hypothesized leading from small septal teeth to large to very large (Text-fig. 2c). Character 10 (budding pattern) is more complicated, with five character states. The lack of budding was considered ancestral and it was intuitively hypothesized that the circumoral/marginal state

proceeded through an exclusively circumoral state, and that the intramural/circumoral state proceeded through an exclusively intramural state. This progression is supported by the ontogenetic development of the corals. These two lines were kept separate, resulting in Text-figure 2d. (Because ordering of these multistate characters includes varying degrees of subjectivity and intuition they are subject to reevaluation once the cladogram has been constructed.) Character 11 (costal ornamentation) could not be polarized from the out-group and no intuitive scheme could be suggested for its transformation, therefore it was not included in the analysis.

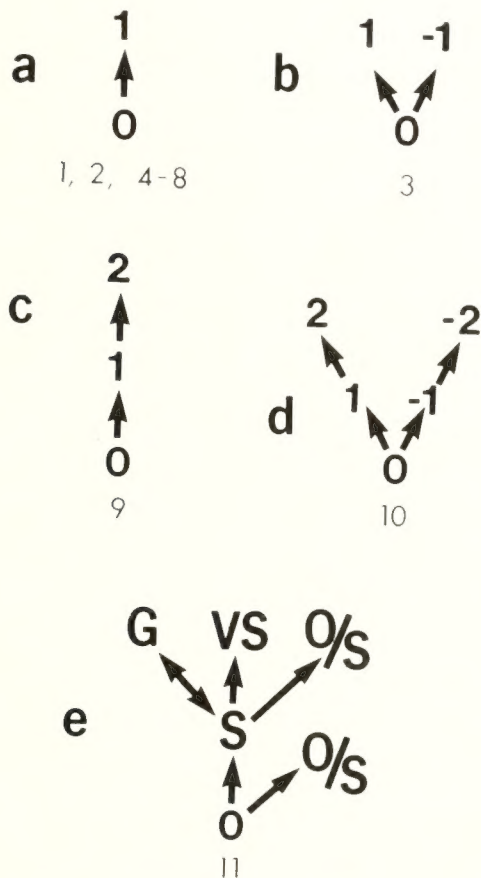
The fourth step of the analysis was to code the data for the computer. Usually a binary code is used, customarily with zero representing the plesiomorphic state and the number one representing the derived state. For multistate characters higher numbers may be used; for series of branching character states, negative numbers and even multiple columns may be used to code one character. The coding of the ten characters used in the analysis is given in the explanation to Appendix 1 and the coded data matrix is provided in Appendix 2. Two taxa, *Cycloseris* and *Danafungia*, were subdivided because they possess two character states for the same character. For example, some species of *Cycloseris* have equal costae, whereas others have unequal costae; thus, *Cycloseris* A was coded for those species having equal costae and *Cycloseris* B coded for those with unequal costae.

In the final step the computer algorithm linked the taxa together, one at a time, ultimately producing a tree "rooted" at the out-group (Wiley, 1981, pp. 178–192). Theoretically, the tree produced is the shortest one possible, *i.e.*, the one with the least number of steps or character state changes (*i.e.*, the most parsimonious). For small data sets, as in this example, it is not always necessary to run a computer program; a tree can be produced manually by trial and error. The resultant cladogram from the Wagner 78 program is illustrated in Text-figure 3. Autapomorphies and characters such as costal ornamentation, which were not used in the analysis, can be added at this stage for informational value; they will not change the branching sequence.

### DISCUSSION

#### Comparison to the Phylogeny of Wells (1966)

To facilitate a comparison of the cladogram and Wells' (1966) tree, the latter was redrawn with the following modifications: 1) straight lines were used, 2) *Diaseris* was added as a derivative of *Cycloseris*, 3) *Cycloseris* and *Danafungia* were subdivided as they



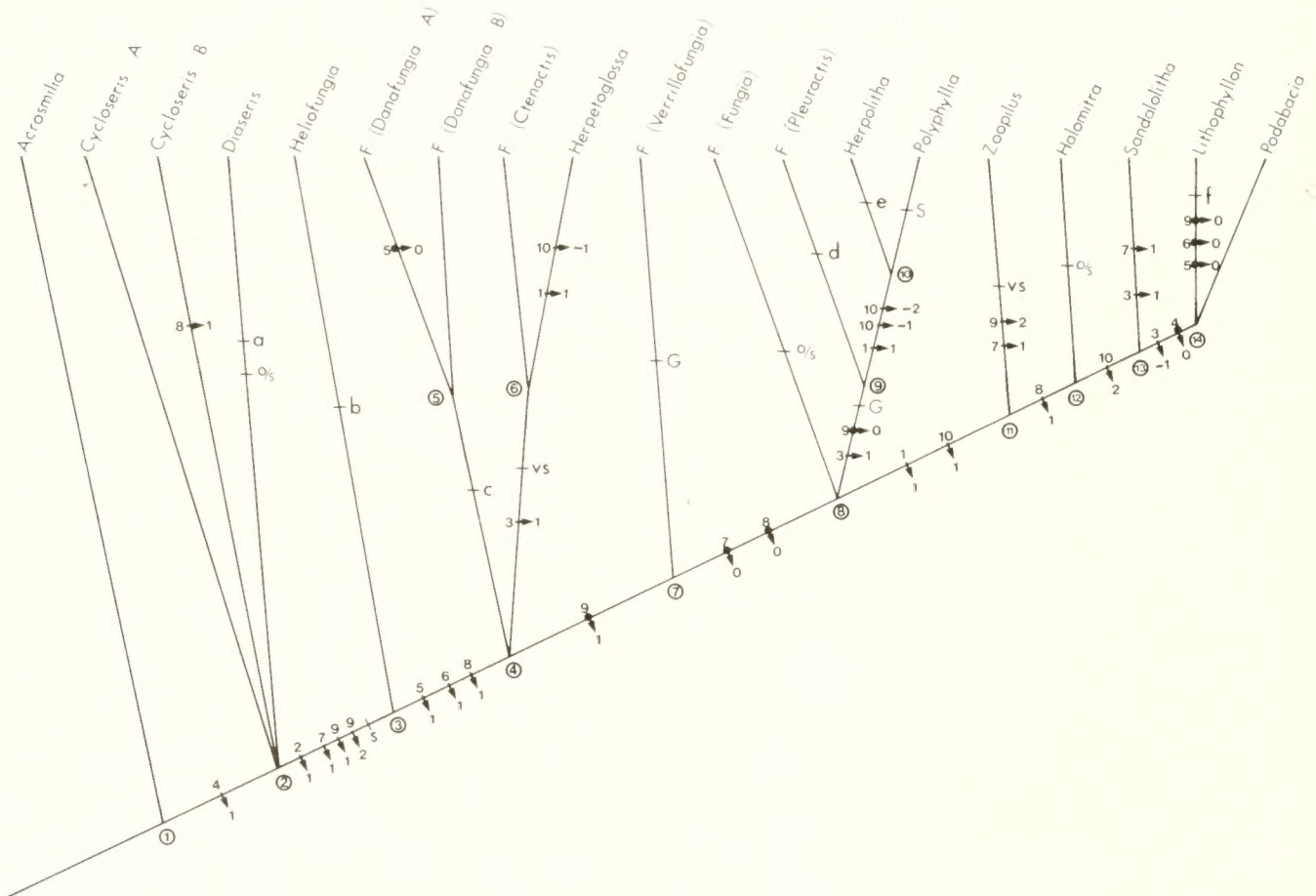
Text-figure 2.—Proposed character state transformation series for the characters used in the analysis. The numbers and letters correspond to the coding found in Appendix 1. The numbers in light-face indicate the characters in Appendix 1 that follow that pattern.

were for the coding in the cladogram, 4) *Parahalomitra* was changed to *Sandalolitha* (see Pillai and Scheer, 1976), and 5) *Heliofungia* was considered as a separate genus (see Veron and Pichon, 1980). None of these changes was thought to affect the intent of Wells' phylogeny. Finally, the character state changes used in the phylogenetic analysis, which were also those used by Wells, were placed on his diagram in such a way as to produce the least number of steps. Autapomorphies and characteristics of costal ornamentation were also added. This resulted in Text-figure 4.

The two trees are similar in that they both place *Cycloseris*, *Diaseris*, and *Heliofungia* near the ancestor, and they both maintain the clade composed of *Pleuraeractis*, *Herpolitha*, and *Polyphyllia*; however, they differ in most other points. Wells' diagram arranges the remaining taxa in four groups, labelled I-IV on Text-figure 4, each originating in the Miocene as a separate subgenus of *Fungia*. Each subgenus persists to the Re-

cent and each produces a small adaptive radiation of colonial genera starting in the late Miocene and extending to the Recent. Each group of genera is distinguished by a distinctive combination of septo-costal characteristics described by Wells (1966, p. 235, fig. 4) and represented in my character table as characters 6-9 and 11.

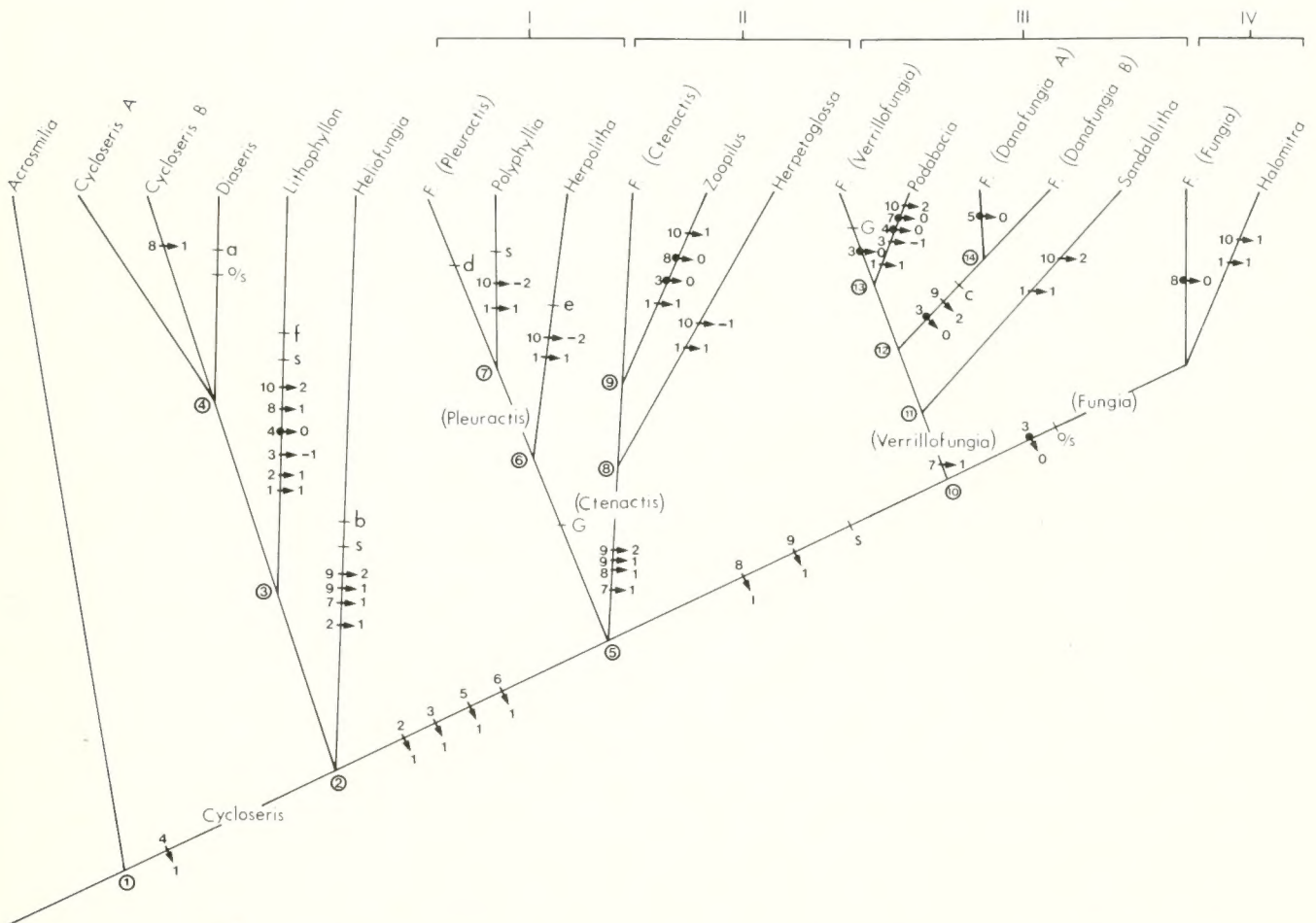
Whereas the Wells phylogeny is strongly influenced by the weighting of septo-costal structures, the cladogram is strongly influenced by the synapomorphy of coloniality (characters 1 and 10). Directly after *Heliofungia*, the cladogram branches off the remaining solitary taxa, the subgenera of *Fungia*, almost in sequential order. Then coloniality is evolved twice: at internodes 9-10 and 8-11. The rudimentary coloniality of *Herpetoglossa* is different from that of the other colonial genera and apparently evolved quite recently (Veron and Pichon, 1980). The last three genera on the cladogram are further differentiated by a synapomorphy of increasing complexity of coloniality.



Text-figure 3.—Cladogram of the fungiids. Encircled numbers are arbitrarily numbered nodes. Numbers at the origin of arrows denote characters; numbers at the arrow tips denote character states of those characters (Appendix 1: columns 1-10). Lowercase letters indicate autapomorphies (Appendix 1: column 12); uppercase letters indicate characteristics of costal spine ornamentation (Appendix 1: column 11). Character state reversals are indicated by a square on the arrow.

My main objection to the phylogeny of Wells is that, although it evolves most of the subgenera of *Fungia* in a relatively tight clade in the Miocene, the subgenera are subsequently scattered throughout the Recent genera. For instance, according to the Wells diagram *F. (Fungia)* is more closely related to *Halomitra* and *Sandalolitha* than it is to any of its other sister subgenera. Cladistically this is unacceptable because the subgenera of *Fungia* do not form a monophyletic group (clade) in the Recent. The cladogram does not group the subgenera of *Fungia* as a monophyletic genus either; however, the subgenera are at least sequentially derived, thus all occur in the same area of the cladogram. A strict interpretation of the cladogram would require each subgenus of *Fungia* to be a separate genus unless a synapomorphy could subsequently be found to unite them. Currently, *Fungia* is defined on plesiomorphic characters and characters that are also shared with other genera; it has no uniquely derived characters of its own.

In addition to a more meaningful arrangement of the fungiid subgenera, the cladogram offers several other advantages over the traditional phylogeny: 1) The Wells phylogeny required 48 character state changes, including 35 cases of convergence or parallelism and nine reversals, to fit the character states to each taxon, whereas the cladogram required only 34 steps, including 16 cases of convergence or parallelism and nine reversals. The cladogram is therefore considerably more parsimonious. This is also reflected in the character consistency indices (CI) listed in Appendix 1. The CI is defined as the range of a character state transition series divided by the number of times this character changed on the cladogram (Farris, 1969). For example, character 1 has a range of one and it changed from state 0 to state 1 three times on the cladogram, producing a CI of  $\frac{1}{3}$  or 0.33. A CI of 1.0 implies a perfectly congruent character for a cladogram. The average CI for the cladogram is 0.48; that for the Wells phylogeny, 0.38. 2) The cladogram is more repeatable in meth-



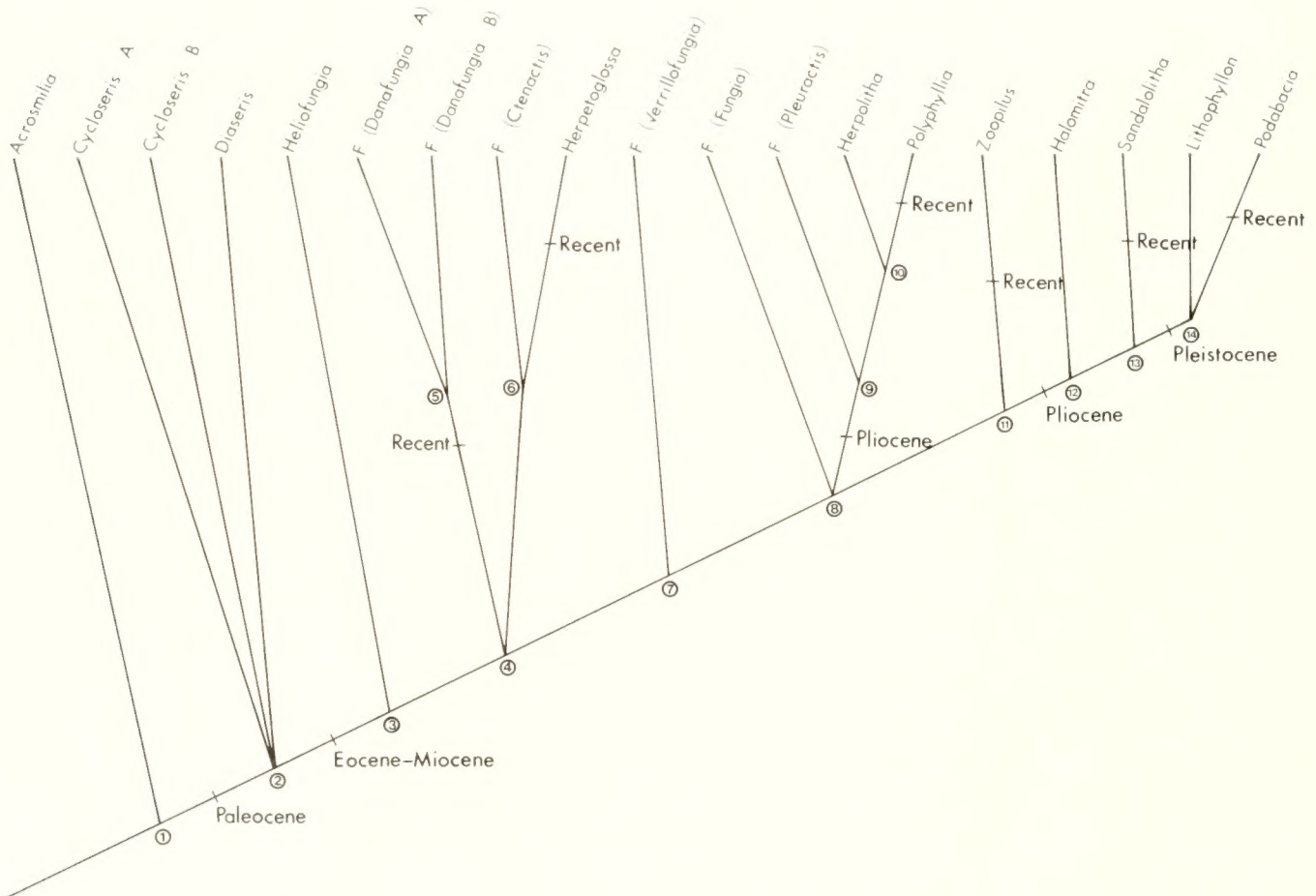
Text-figure 4.—Modified phylogeny of Wells (1966, fig. 3). Labelling conventions are the same as for Text-figure 3. Roman numerals I-IV indicate the four groups of genera implied by Wells.

odology and easily allows for additions or changes of data in the matrix. Each stem is justified by at least one character state change. The reasoning supporting the Wells phylogeny is not explained and five of the stems are not supported by character state changes (internodes 2–3, 6–7, 8–9, 11–12, and 12–13 of Text-fig. 4). 3) The cladogram allows a better interpretation of the characters. Character 11 (costal ornamentation) was not used in the analysis because its states could not be ordered; however, the cladogram suggests a reasonable hypothesis, which is illustrated in Text-figure 2e.

### Proposed Scenario

If the earliest fossil record of each taxon is placed on the cladogram as a character, using the transformation series of Paleocene to Recent (Text-fig. 5), then the following scenario may be suggested. *Cycloseris* evolved from *Acrosmilina*, or a common ancestor of the two (node 1), in the Paleocene, differing from it primarily by its free corallum. But it was not until the Miocene that the adaptive radiation of the fungiids

began. The hypothetical ancestor of the remaining fungiids (node 3) became larger and acquired arborescent costal spines. *Heliofungia* evolved from this ancestor. Then two significant changes occurred: the hypothetical ancestor represented at node 4 developed a perforate theca and coarse costal spines, which paved the way for the evolution of the closely related subgenera of *Fungia*, each differing from the others by various combinations of septo-costal characteristics. The earliest record of *F. (Danafungia)* is the Recent, but one would infer from the cladogram an older fossil record. *Herpetoglossa* evolved from *F. (Ctenactis)* in the Recent by acquiring a rudimentary coloniality. *F. (Pleuractis)* evolved from the common ancestor to *F. (Fungia)*, node 8, in the Pliocene. The ancestor of *F. (Pleuractis)*, node 9, gave rise to two colonial genera, *Herpolitha* and *Polyphyllia*, the latter in the Recent. Still in the Miocene, the hypothetical ancestor to the remaining genera, node 8, evolved circumoral budding, which produced *Halomitra* in the Pliocene and the stem that produced *Zoopilus* in the Recent. The ancestor represented at node 12 acquired marginal



Text-figure 5.—Cladogram with earliest known fossil records of taxa superimposed on the branching pattern.

budding in addition to circumoral budding and gave rise to the stem that produced *Sandalolitha* in the Recent and the Pleistocene stem that resulted in *Lithophyllon* and *Podabacia*. The implication of the analyses of both Wells (1966) and Veron and Pichon (1980, p. 195) is that *Lithophyllon* belongs at the opposite end of the cladogram as a polystomadeal derivative of *Cycloseris*. On the cladogram, the stem supporting *Lithophyllon* includes three reversals, which suggests that this is a questionable placement; in fact, the most poorly supported stem of the cladogram. However, the stem supporting *Lithophyllon* in the Wells phylogeny includes seven character state changes, including one reversal, which is the longest stem on the tree and also an indication of a questionable placement. The position of *Lithophyllon* in either phylogeny is unsatisfactory; analysis of additional characters might resolve the problem.

Because they are highly speculative, scenarios extrapolated from cladograms and stratigraphic ranges should be accepted only as working hypotheses.

CONCLUSIONS

Phylogenetic analysis is a logical method of producing a phylogeny which, in many ways, does not differ from that used for many years by evolutionary taxonomists. Cladism simply forces one to justify and explain every step of the analysis and thus to scrutinize organisms and characters more closely. It allows for verification by others and easy modification of the data set as new information is discovered. For some, the cladogram is the final product, but for others it is just the beginning, laying the foundation for additional character analyses, zoogeographical considerations, coevolutionary studies, and paleontological predictions.

APPENDIX 1

Character table for the genera and subgenera of the Fungiidae.

	Ten characters used in cladistic analysis												Presumed septo-costal homologues	Number of species	Stratigraphic range
	1	2	3	4	5	6	7	8	9	10	11	12			
<i>Acrosmitia</i>	S	S	D	A	I	F	S	E	S	O	?		<i>Cycloseris</i>	?	Jur.-Cret.
<i>Cycloseris</i>	S	S	D	F	I	F	S	E/U	S	O	O			14+	Paleo.-Rec.
<i>Diaseris</i>	S	S	D	F	I	F	S	E	S	O	O/S	a	<i>Cycloseris</i>	4+	? ?
<i>Heliofungia</i>	S	L	D	F	I	F	A	E	VL	O	S	b		1	Mio.-Rec.
<i>F. (Danafungia)</i>	S	L	D	F	I/P	C	A	U	VL	O	S	c		11-12	Recent
<i>F. (Ctenactis)</i>	S	L	E	F	P	C	A	U	VL	O	VS			1	Mio.-Rec.
<i>Herpetoglossa</i>	C	L	E	F	P	C	A	U	VL	I	VS		( <i>Ctenactis</i> )	1	Recent
<i>F. (Verrillofungia)</i>	S	L	D	F	P	C	A	U	L	O	G			5-6	Mio.-Rec.
<i>F. (Fungia)</i>	S	L	D	F	P	C	S	E	L	O	O/S			1	Mio.-Rec.
<i>F. (Pleuractis)</i>	S	L	E	F	P	C	S	E	S	O	G	d		3	Plio.-Rec.
<i>Herpolitha</i>	C	L	E	F	P	C	S	E	S	I/C	G	e	( <i>Pleuractis</i> )	2	Plio.-Rec.
<i>Polyphyllia</i>	C	L	E	F	P	C	S	E	S	I/C	S		( <i>Pleuractis</i> )	1	Recent
<i>Zoopihus</i>	C	L	D	F	P	C	A	E	VL	C	VS		( <i>Ctenactis</i> )	1	Recent
<i>Halomitra</i>	C	L	D	F	P	C	S	U	L	C	O/S		( <i>Fungia</i> )	1	Mio.-Rec.
<i>Sandalolitha</i>	C	L	E	F	P	C	A	U	L	C/M	S		( <i>Verrillofungia</i> )	2	Mio.-Rec.
<i>Lithophyllon</i>	C	L	F	A	I	F	S	U	S	C/M	S	f		1-2	Mio.-Rec.
<i>Podabacia</i>	C	L	F	A	P	C	S	U	L	C/M	S		( <i>Verrillofungia</i> )	1	Mio.-Rec.

Key to character states listed above, their computer coding and character consistency indices for both Wells' tree and cladogram

Characters	Computer code	Consistency indices	
		Wells	Cladogram
1. Coloniality:		0.12	0.33
S = Solitary (monostomous)	0		
C = Colonial (polystomous)	1		
2. Corallum size:		0.33	1.0
S = Small (usually less than 5 cm diameter)	0		
L = Large (adult usually more than 5 cm)	1		
3. Shape of upper corallum:		0.28	0.50
D = Discoidal (round to slightly elliptical)	0		
E = Strongly elliptical to elongate rectangular	1		
F = Foliaceous (irregular in shape)	-1		
4. Corallum attachment as an adult:		0.33	0.50
A = Attached	0		
F = Free	1		
5. Porosity of theca:		0.50	0.33
I = Imperforate	0		
P = Perforate	1		
6. Density of costal spines:		1.0	0.50
F = Fine (3-7 per mm)	0		
C = Coarse (0.5-2.0 per mm)	1		
7. Shape of costal spines:		0.25	0.25
S = Simple	0		
A = Simple and arborescent	1		
8. Width of adjacent costae:		0.17	0.25
E = Equal	0		
U = Unequal	1		
9. Size of septal dentition:		0.33	0.33
S = Small (3-6 teeth per mm)	0		
L = Large (1-2 teeth per mm)	1		
VL = Very large (less than 1 tooth per mm)	2		
10. Budding pattern:		0.50	0.80
O = No budding (solitary)	0		
C = Circumoral budding	1		
C/M = Circumoral plus marginal budding	2		
I = Intramural budding	-1		
I/C = Intramural plus circumoral budding	-2		
11. Ornamentation of costal spines:		Not coded or used in analysis	
O = No ornamentation (smooth)			
O/S = Smooth sides and spinose tips			
S = Spinose			
VS = Very spinose			
G = Granular			
12. Autapomorphies:		Not coded or used in analysis	
a = Corallum reproduces by fracturing			
b = Tentacles and polyps very large			
c = Higher cycle costae not spinose			
d = Supernumerary calices sometimes present			
e = Circumoral calices are small and few in number			
f = Encrusting growth form			

## APPENDIX 2

## Coded data matrix used in the phylogenetic analysis.

	1	2	3	4	5	6	7	8	9	10
<i>Acrosmilina</i>	0	0	0	0	0	0	0	0	0	0
<i>Cycloseris A</i>	0	0	0	1	0	0	0	0	0	0
<i>Cycloseris B</i>	0	0	0	1	0	0	0	1	0	0
<i>Diaseris</i>	0	0	0	1	0	0	0	0	0	0
<i>Heliofungia</i>	0	1	0	1	0	0	1	0	2	0
<i>F. (Danafungia A)</i>	0	1	0	1	0	1	1	1	2	0
<i>F. (Danafungia B)</i>	0	1	0	1	1	1	1	1	2	0
<i>F. (Ctenactis)</i>	0	1	1	1	1	1	1	1	2	0
<i>Herpetoglossa</i>	1	1	1	1	1	1	1	1	2	-1
<i>F. (Verrillofungia)</i>	0	1	0	1	1	1	1	1	1	0
<i>F. (Fungia)</i>	0	1	0	1	1	1	0	0	1	0
<i>F. (Pleuractis)</i>	0	1	1	1	1	1	0	0	0	0
<i>Herpolitha</i>	1	1	1	1	1	1	0	0	0	-2
<i>Polyphyllia</i>	1	1	1	1	1	1	0	0	0	-2
<i>Zoopilus</i>	1	1	0	1	1	1	1	0	2	1
<i>Halomitra</i>	1	1	0	1	1	1	0	1	1	1
<i>Sandalolitha</i>	1	1	1	1	1	1	1	1	1	2
<i>Lithophyllon</i>	1	1	-1	0	0	0	0	1	0	2
<i>Podabacia</i>	1	1	-1	0	1	1	0	1	1	2

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## THE SPECIES CONCEPT IN FOSSIL HERMATYPIC CORALS: A STATISTICAL APPROACH

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### ABSTRACT

The complex, widespread variability now recognized within modern scleractinian species requires redefinition of species using a numerical population approach. This study demonstrates a technique for re-evaluating fossil species, using one genus (*Montastraea*) from several Caribbean localities of lower Miocene age as an example. First, phenotypic plasticity in modern populations is estimated by means of transplantation experiments. The observed responses are documented by measuring numerous morphologic characters on thin-sections at fixed positions on each colony. These data are then compared with those on fossil populations. Clusters of individuals approximating species are isolated using multivariate statistical procedures, such as canonical variate analysis. Each cluster is further refined by studying variation within colonies and between modern populations. In the example, this method reduced the number of common lower Miocene Caribbean species from the six previously described to three. Some fossil colonies were shown to belong to the two modern species, thus representing the earliest known occurrences of the modern species.

Comparison between populations within fossil and modern clusters allows interpretation of environmental conditions at each fossil locality and the evolutionary history of species. In the example, colonies from Anguilla appear to have grown in more turbid habitats than those from Panama or Chiapas. The modern species appear to have originated in early Miocene time in nearshore areas and spread at varying rates across the Caribbean.

### INTRODUCTION

Recent work in biogeography has shown that studies of phylogeny are essential to explaining coral distribution patterns (Heck and McCoy, 1978; Frost, 1981). However, the evolutionary history of most hermatypic scleractinian lineages is still poorly understood. This is partially due to the difficulty of clearly distinguishing species, the basic unit through which evolution occurs. Especially in fossils, one species may have originally been given several names at one locality, because of slight differences in morphology. It may have received several names in different geographic areas and at different stratigraphic levels (see Vaughan, 1919; Pfister, 1977; Frost, 1981). Using such inaccurate fossil data in phylogeny reconstruction would only lead to faulty interpretations of the interrelationships between species and their stratigraphic and geographic distribution.

Many fossil workers have advocated resolving this problem by extensively synonymizing species, based on knowledge of the widespread variability recognized within so many living species (see Veron and Pichon, 1976). Some have suggested that highly variant characters be disregarded altogether, leaving only a few "stable" characters to diagnose species. It has been further maintained that, if individuals are found intermediate between morphologic groups, the groups should be interpreted as one species.

However, in contradiction to such a broad approach, work on modern species has shown that, in addition to being widespread, variability within species (as well as between species) is subtle and complex, involving

numerous characters which must be studied in populations from a range of habitats (Wijsman-Best, 1972; Foster, 1980). Both the pattern and magnitude of variation differs from one species to another, and different species may sometimes overlap morphologically (Foster, 1982). As a result, species boundaries may not always be truly discontinuous, and species may even form continuous morphologic series [*e.g.*, in *Agaricia* and *Mycetophyllia* (Wells, 1973; Lang, 1973) and in *Porites* (Brakel, 1977)]. Therefore, fossil taxonomic interpretations must be carefully re-evaluated by detailed analysis of within- and between-species variation and by directly comparing fossil patterns with well-documented modern examples.

The purpose of the present paper is to demonstrate a method for objectively delimiting fossil species by analyzing variation within and between populations. An example consisting of five early Miocene groups of populations of Caribbean *Montastraea* is discussed in detail. Since scleractinian species are generally distinguished using linear dimensions of several morphologic features and septal counts, this study uses continuous quantitative measurements and counts as characters. To insure consistency, these characters are enumerated in thin-sections. Because work on living species has shown the necessity for describing many characters simultaneously in many populations, the data are analyzed statistically using multivariate procedures. Throughout the paper, the term "population" means all colonies collected from one stratigraphic horizon at one locality (usually <50–100 m in length).



No assumption is intended of a common gene pool within each population or of mutually exclusive gene pools between populations. The term "species" is used to mean a lineage of populations, descended from one another, which has a unique evolutionary history (as defined by Wiley, 1978). No assumption is intended of complete reproductive isolation (as defined by Mayr, 1970) or of complete morphologic distinctiveness (as defined by Eldredge and Cracraft, 1980).

#### STATISTICAL METHOD FOR DISTINGUISHING CORAL SPECIES

Multivariate statistical techniques have been used most frequently to differentiate species in mammals (*e.g.*, Jenkins, 1976; Bogan, 1978). Some work has been done in marine invertebrates such as bryozoans (*e.g.*, Cook, 1977), foraminifers (*e.g.*, Malmgren, 1974), and ostracods (*e.g.*, Reyment, 1980). However, few coral workers have attempted to distinguish species by analyzing populations using multivariate techniques. One exception is the work of Brakel (1977) which analyzes 20 corallite characters in modern *Porites* populations from seven nearby Jamaican reef habitats using cluster analysis. In this study, Brakel found as many as six "phenons" in what were originally believed to be three species. In another example, Wallace (1974) used cluster analysis and principal coordinate analysis to determine the relative weighting of characters in distinguishing four modern species of *Acropora*. Other multivariate statistical studies of coral species include: (1) work by Wallace and Dale (1977) which analyzes distribution patterns of *Acropora* species using procedures similar to Wallace (1974), and (2) work by Foster (1979, 1980) which analyzes patterns of variation within two Caribbean species using canonical variate analysis.

In the present study, data on fossil corals of one genus from one time interval are analyzed together with data on two modern coral species to determine how the fossils can best be grouped into distinct species clusters. The data were initially explored using principal component analysis (SAS PRINCOMP procedure, Helwig and Council, 1979), a technique that explains the maximum variation among corallites using a minimum number of dimensions (each dimension being a linear combination of characters). To determine what (if any) groups could be defined from these principal component results, the principal component scores for each corallite, regardless of colony affiliation, were first analyzed using cluster analysis (SAS FASTCLUS procedure, Helwig and Council, 1979). To incorporate additional information on within-species variation in the analysis, cluster assignments were then

modified so that: (1) all corallites from the two known modern species were assigned correctly to their corresponding species cluster, and (2) all corallites from one colony were assigned to the same species cluster.

The species clusters were then re-evaluated by performing canonical variate analysis (SPSS DISCRIMINANT procedure, Nie *et al.*, 1975) on the original data set. Canonical variate analysis is a technique that finds the minimum number of dimensions that maximize the variation between *a priori* groups (in this case, the species clusters). Afterwards, Mahalanobis distances from group centroids are calculated to determine if individuals are correctly assigned to groups. Groups having the highest percentage of correctly classified corallites are the most discrete. Cluster assignments for colonies lying at cluster margins were further modified by trial and error to obtain the highest percentage of correctly classified corallites. Details of the statistical procedures are given in numerous books on morphometrics (*e.g.*, Neff and Marcus, 1980; Reyment, 1980).

#### CHOICE OF A MODERN ANALOG

Taxonomy in living hermatypic corals is based primarily on skeletal morphology (see Veron and Pichon, 1976; Zlatarski and Estalella, 1982). Species limits are commonly defined by qualitative study of patterns of variation in skeletal characters within and between populations. However, since such studies are inferential, it is often unclear if the observed variation is caused by genetic differences between colonies or by phenotypic plasticity. One way of overcoming this uncertainty is to perform experiments whereby living corals are subjected to controlled changes in their environment (artificial treatments) and their phenotypic responses directly monitored. Because the resulting variation is caused only by phenotypic plasticity, a minimum limit can be objectively defined for the species. Moreover, by correlating phenotypic plasticity with specific environmental factors, morphology can serve as an environmental indicator and its adaptive significance explained.

The initial experiments in morphology involved transplanting coral colonies from one natural reef habitat to another and documenting the resultant changes in colony extension rate (Vaughan, 1915; Mayor, 1924; Edmondson, 1928). From these studies, it is difficult to interpret exactly which environmental factors were causing the observed morphologic response. More recently, experiments have been designed to isolate one specific environmental factor in the laboratory or field and study morphologic responses to that factor (Table 1). However, research has focussed on changes in col-

Table 1.—Some selected examples of experiments testing the effect of isolated environmental factors on coral growth.

Reference	Skeletal attributes studied	Experiment duration	Environmental treatments	Species
Franzisket (1970)	mass	4 months	laboratory: light intensity, zooplankton	<i>Fungia scutaria</i> <i>Pocillopora elegans</i> <i>Montipora verrucosa</i> <i>Porites compressa</i> <i>Dendrophyllia</i> sp.
Wellington (1982)	linear extension rate	1 year	field: light intensity, zooplankton	<i>Pocillopora damicornis</i> <i>Pavona clavus</i> <i>Pavona gigantea</i>
Jokiel (1978)	linear extension rate	70 days	laboratory: water movement	<i>Pocillopora damicornis</i> <i>Pocillopora meandrina</i> <i>Montipora verrucosa</i>
Bak <i>et al.</i> (1977)	regeneration rate	80 days	field: physical disturbance (lesions)	<i>Montastraea annularis</i> <i>Agaricia agaricites</i>
Neudecker (1977)	linear extension rate, mass	70 days	field: fish predation, light intensity, temperature	<i>Pocillopora damicornis</i>

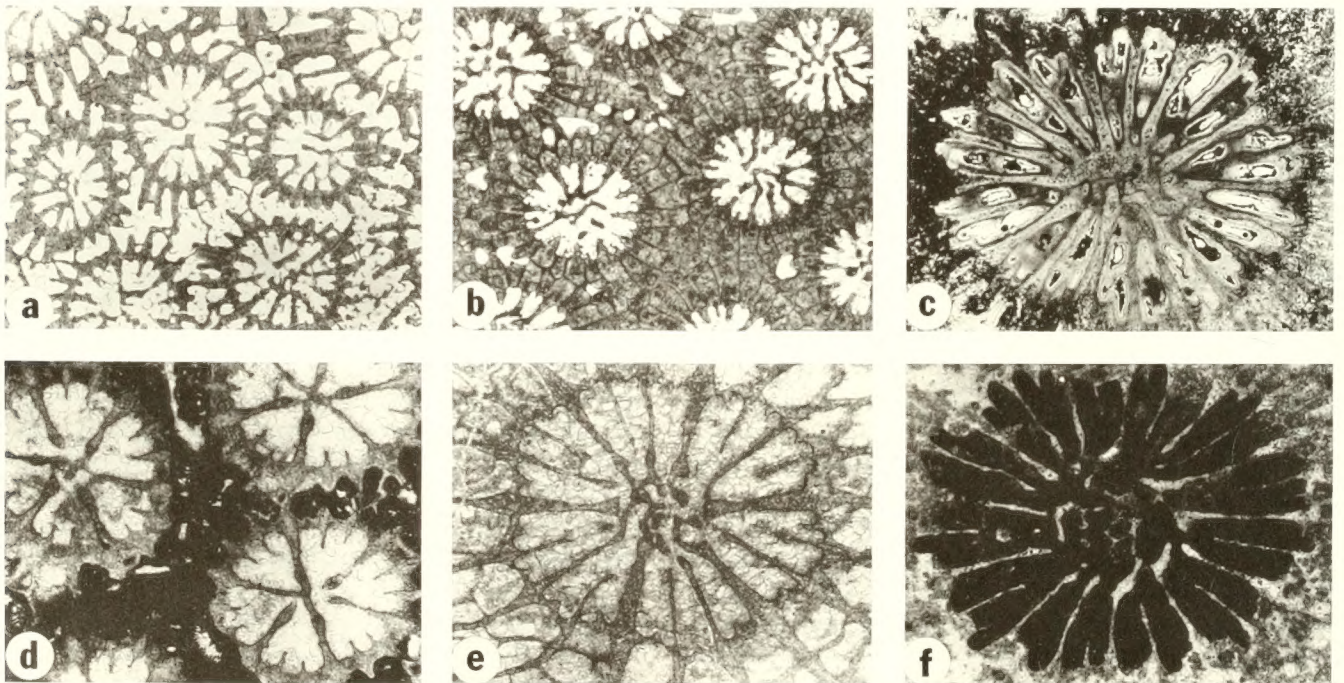


Figure 1.—Transverse thin-sections showing representative corallites from the species clusters recognized in the statistical analyses. [A.] Corallites in a modern colony transplanted from the lagoon (LAG) to the sand channel (SC) habitats near Discovery Bay, Jamaica. Skeletal material deposited before transplantation is shown. (SUI45537D) 6×. [B.] Corallites from the same colony as A showing skeletal material deposited after transplantation. (SUI45537C) 6×. As seen by comparing A and B, the corallites of the lagoon colony have changed to become smaller in diameter with thicker thecae and a denser coenosteum, as a result of transplantation, and now have an appearance characteristic of corallites from the sand channel. [C.] Fossil corallite from Georgia belonging to the *M. cavernosa* cluster. The corallite size is intermediate to large, and the first three septal cycles extend to a well-developed columella. (USNM M324880(NF188D)) 6×. [D.] Fossil corallite from Panama belonging to fossil cluster A (fcA). The corallites are small with six prominent primary septa which extend to a thin columella. The secondary septa are reduced and form in pairs between the primary septa. (USNM 63471(NF397A)) 6×. [E.] Fossil corallite from Chiapas belonging to fossil cluster B (fcB). The corallite size is intermediate and six prominent primary septa extend to a porous columella. The secondary septa are reduced in length and thickness and occur irregularly (singly or in pairs) between the primary septa. (UI x3673B) 6×. [F.] Fossil corallite from Anguilla belonging to fossil cluster C (fcC). The corallite size is very large, and the primary and secondary septa extend to a porous columella. The tertiary septa are reduced in thickness and in length. (USNM M324845(NF124D)) 6×.

Table 2.—Distinguishing morphologic characteristics of some common *Montastraea* species reported from the lower Miocene localities studied.

Species	Corallite diameter	No. septal cycles	Paliform lobes	Costae	Major septa
<i>M. limbata</i> (Duncan) <sup>2</sup>	3–4 mm	3	no	subequal	subequal in thickness
<i>M. imperatoris</i> (Vaughan) <sup>1</sup>	3.5–5 mm	3	no	equal	thick, long primaries
<i>M. canalis</i> (Vaughan) <sup>1</sup>	5–9 mm	4	?no	subequal	thick, long primaries
<i>M. tampaensis</i> (Vaughan) <sup>1,2,3</sup>	6–10 mm	4	no	equal	subequal in thickness
<i>M. costata</i> (Duncan) <sup>1</sup>	7.5–8.5 mm	4	yes	equal	subequal in thickness and low
<i>M. bainbridgensis</i> (Vaughan) <sup>1</sup>	6–7 mm	4	yes	equal	subequal in thickness and low

References: <sup>1</sup> Vaughan, 1919; <sup>2</sup> Frost and Langenheim, 1974; <sup>3</sup> Weisbord, 1973.

ony extension rate (Table 1) or calcification rate (e.g., Muscatine and Cernichiaro, 1969) and not on corallite architecture *per se*. Exceptions include transplanting stained coral colonies between habitats (Dustan, 1979; Foster, 1979; Graus and Macintyre, 1982) and laboratory experiments subjecting coral colonies to varying mud concentrations (Dodge, 1982).

In the present analysis, living populations of *Montastraea annularis* were selected that had been used in transplantation experiments between four environmentally-distinct stations near Discovery Bay, Jamaica (Foster, 1979) (Appendix I). The stations include: (1) a nearshore patch reef, 3 m depth (PR); (2) a nearshore turbid lagoon, 16 m depth (LAG); (3) a forereef coral thicket, 20 m depth (RF); and (4) a forereef sand channel, 20 m depth (SC) (see Foster, 1980). The transplant experiments showed that skeletal morphology changed after transplantation from one which was typical of the original habitat to one characteristic of the transplantation habitat (Fig. 1a, b). Therefore, between these *M. annularis* populations, corallite variation is exclusively environmental, and it can be used to estimate the limits of ecophenotypic variation in the species. In addition, populations of *Montastraea ca-*

*vernosa*, a closely-related species, from identical collecting stations but not yet studied using transplantation experiments, are included in the analysis (Appendix I).

#### FOSSIL MATERIAL AND MEASUREMENTS

Populations of early Miocene *Montastraea*, representing a wide range of locations within the Caribbean, have been selected for study (Fig. 2, Appendix I). The genus and time period were selected, because it has been suggested that *Montastraea* had an adaptive radiation in the Caribbean during the early Miocene, following the extinction of many common massive reef-building corals in the Caribbean at the end of the Oligocene (Frost, 1977). The early Miocene age of the fossils studied has been established by Puri and Vernon (1964), Bold (1970), Woodring (1957), and Frost and Langenheim (1974). In the present study, the specimens were initially identified by the author to genus level without making any *a priori* judgement concerning species identifications. Earlier studies of the material, however, indicated that as many as six species may be represented (Table 2). These six species were distinguished on the basis of five imprecise, often poorly preserved characters (Table 2), making accurate species diagnosis difficult, if not impossible.

Previous work has shown that: (1) 8–12 colonies are required to obtain a normal distribution in modern populations (Foster, 1980) and (2) 2–3 species of any one genus occur on the average within modern Caribbean reef habitats (Goreau, 1959). Therefore, 16–36 colonies were examined from each collecting locality (Appendix I). Study of growth bands suggests that all the examined colonies were mature and roughly similar in age (i.e., 15–40 years old). *Montastraea* colonies are typically non-polymorphic and not known to vary significantly with astogeny (see Foster, 1980); therefore no corrections were made for these sources of variation. However, because of extensive ecophenotypic variation known to exist within colonies of the genus (Foster, 1980), 8–12 mature corallites were measured from fixed positions within each colony. Similarly, ten



Figure 2.—Map showing the locations of areas where the fossil material was collected (P, Emperador Lm. in Panama; A, Anguilla Fm. in Anguilla; C, Modelo Gp. in Chiapas, Mexico; F, Tampa Fm. in Florida, U.S.A.; G, Chattahoochee Fm. in Georgia, U.S.A.).

Table 3.—List and description of characters analyzed. Measurements in characters 1–6 were made at maximum to the nearest 0.10 mm, those in characters 7–12 to the nearest 0.05 mm, and those in characters 13–16 to the nearest 0.025 mm.

Character	Abbreviation	Description
1. corallite diameter	CD	Linear measure between theca/corallite cavity margins; average of longest and shortest lengths (CD lines)
2. total number of septa	NS	Count
3. corallite spacing	NND	Linear measure between theca/corallite cavity margins of nearest neighboring corallites
4. coenosteum diameter	CND	Linear measure between theca/coenosteum margins of nearest neighboring corallites
5. coenosteum density	CNNV	Linear measure, parallel to the CND line, of non-void material across the coenosteum
6. coenosteum density	CNP	Linear measure, perpendicular to the CND line, of non-void material crossing a 1 cm line
7. columella width	CLW	Linear measure between outer columella/corallite cavity margins; average of longest and shortest lengths
8. columella density	CLNV	Linear measure, parallel to 2 CD lines, of non-void material across the columella; average
9. theca thickness	TT	Linear measure between theca/corallite cavity and theca/coenosteum margins; average at 2 CD lines
10. septum length (1st cycle)	SLP	Linear measure between columella and theca margins; average at 2 CD lines
11. septum length (2nd cycle)	SLS	Linear measure similar to SLP on major septa adjacent to SLP; average
12. septum length (highest cycle)	SLT	Linear measure between septum tip and theca margin of septum between SLS and SLP; average
13. septum thickness (1st cycle)	STP	Linear measure of thickness of septa at SLP at septum midpoint; average
14. septum thickness (2nd cycle)	STS	Linear measure of thickness of septa at SLS at septum midpoint; average
15. septum thickness (highest cycle)	STT	Linear measure of thickness of septa at SLT at septum midpoint; average
16. costa thickness (1st cycle)	CST	Linear measure of costa thickness at SLP; ~.15 mm from corallite cavity; average

corallites in colonies of both modern species were measured at fixed positions within each colony. These fossil and living data were then analyzed simultaneously.

Surface preservation is irregular and often poor in the fossil populations studied; therefore, all characters were examined in thin-section. Measurements were made of sixteen characters (Fig. 3, Table 3) on each corallite. The distributions of most characters within

colonies were found to be approximately normal by comparing skewness and kurtosis values.

## RESULTS ON SPECIES DIFFERENCES

The results of the multivariate statistical analyses show that the *a priori* groups (in this case, the species clusters) are most distinct in canonical variate analysis (93.9 percent correctly classified) when (1) three fossil species clusters are distinguished in the samples and (2) some fossil colonies are placed within the two modern species clusters (Table 4, Fig. 4). This indicates that as many as five *Montastraea* species may have existed during the early Miocene in the Caribbean region. The three fossil species clusters form a morphologic continuum with slight overlap at the margins of groups (Figs. 1d–f; 4). Fossil representatives of the two modern species are less common in the samples and do not form part of the continuum.

Comparison with the original species names given to the specimens (Table 2) shows that this statistical designation of species leads to a substantial reorganization of early Miocene Caribbean species within *Montastraea*. The number of fossil species is reduced from six to three, and the stratigraphic range of the two modern Caribbean *Montastraea* species is extended back to early Miocene time. Some fossil species are combined, while others are further separated (Table 4).

The canonical variate that best distinguishes species clusters (CV1) in the present statistical analysis weights columella width (CLW) most heavily; and corallite diameter (CD), columella porosity (CLNV), and costa thickness (CST) next in importance (Table 5). Secondary septum length (SLS) and thickness (STS) are most

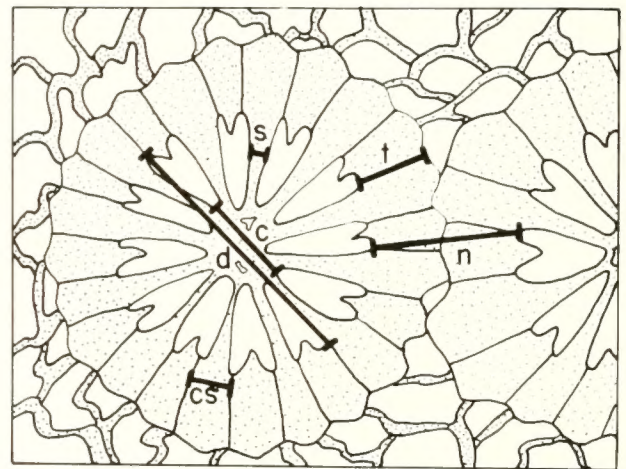


Figure 3.—Line drawing showing some of the characters measured: d (corallite diameter CD), n (corallite spacing NND), c (columella width CLW), t (theca thickness TT), s (septum thickness STP), cs (costa thickness CST).

Table 4.—The three fossil species clusters found using the canonical variate (CV) analysis including comparisons of intraspecific variation using Box's test. n = number of corallites. N = number of colonies. 'MA' and 'MC' represent the modern species *M. annularis* and *M. cavernosa* respectively.

	Fossil cluster A (fcA) n = 266 N = 27	Fossil cluster B (fcB) n = 352 N = 39	Fossil cluster C (fcC) n = 189 N = 22
Former species names	<i>M. imperatoris</i> <i>M. limbata</i>	<i>M. canalis</i> <i>M. bainbridgensis</i> <i>M. tampaensis</i>	<i>M. costata</i> <i>M. tampaensis</i>
Within-colony variation (CV1)	>MA, <MC <fcB, <fcC	>MA, =MC >fcA, <fcC	<MA, =MC >fcB, >fcA
Within-population variation (CV1)	>MA, =MC =fcB, =fcC	>MA, =MC >fcA, =fcC	>MA, =MC =fcB, =fcA

important in the second canonical variate (CV2), whereas coenosteum porosity (CNP) and theca thickness (TT) are most important in the third canonical variate (CV3). Therefore, the first canonical variate (CV1) is most heavily influenced by corallite size, the second canonical variate (CV2) by the development of the secondary septa, and the third canonical variate (CV3) by the thickness of the theca and coenosteal structures. Study of the canonical discriminant function coefficients in Table 5 further indicates that subtle contrasts between characters can be interpreted within each canonical variate. For example, the four characters which appear related to size (CD, CLW, CLNV, CST) are positively weighted on the first canonical

variate (CV1), whereas features describing coenosteal thickness (CND, CNP), minor septum length (SLT), and septum thickness (STP, STS, STT) are negatively weighted on it. Similarly, coenosteum porosity (CNP) increases as theca thickness (TT) decreases in the third canonical variate (CV3).

Comparison of these results with the conventional characters used to designate species in *Montastraea* (Table 2) shows basic similarities in the first two canonical variates. Columella width and corallite diameter, two corallite size characters, are most important using both approaches. The character of the columella, the development of costae, and the relative development of the primary and secondary septa are also considered highly significant in both. However, in

Table 5.—Results of the canonical variate (CV) analysis between clusters in which the highest percent (93.9%) of corallites were correctly classified. Standardized canonical discriminant function coefficients are listed for the 16 measured characters. The first canonical variate (CV1) explained 73.8% of the variation, the second (CV2) 20.2%, and the third (CV3) 4.8%. Data on 1577 corallites from 164 colonies were used in the analysis.

	CV1	CV2	CV3
CD	.260*	-.296	-.009
NS	.225	-.233	-.015
NND	.111	.003	-.254
CND	-.126	.068	.387
CNNV	.078	-.155	.157
CNP	-.139	.280	.790**
CLW	.304**	.362	.373
CLNV	.278*	.123	-.441
TT	.067	.252	-.606*
SLP	.200	-.399	.025
SLS	.140	.634**	.092
SLT	-.039	-.106	.238
STP	-.060	-.161	.248
STS	-.029	.474*	.106
STT	-.186	.124	.215
CST	.298*	-.378	.058

\*\* Most heavily weighted in the canonical variate.

\* Heavily weighted in the canonical variate.

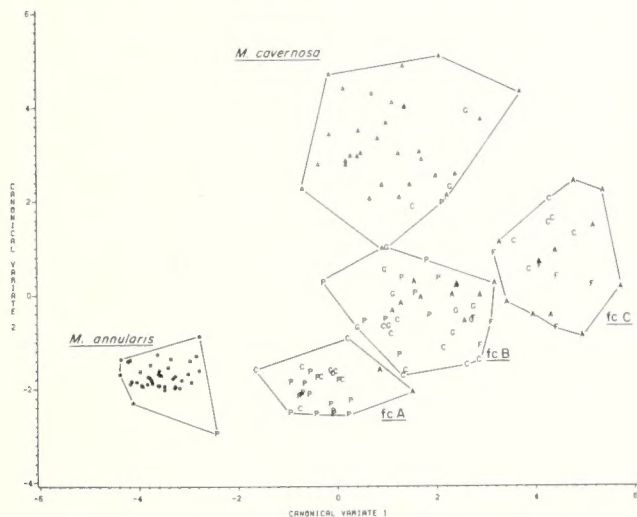


Figure 4.—Plot of scores on the first two canonical variates showing polygons outlining the range of variation between colonies in the five clusters defined by the statistical analyses. The points represent means for each colony. (A, colonies from Anguilla; C, colonies from Chiapas; F, colonies from Florida; G, colonies from Georgia; P, colonies from Panama; star, modern *M. annularis* colonies from Discovery Bay, Jamaica; triangle, modern *M. cavernosa* colonies from Discovery Bay, Jamaica. fcA, fossil cluster A; fcB, fossil cluster B; fcC, fossil cluster C).

Table 6.—Results comparing populations of corallites within each species cluster. Means ( $\pm$  standard deviation) of the first canonical variate scores (CV1) are listed for each population. Relative groupings based on t-tests using Duncan's multiple range test are given in the last column. N = number of colonies sampled. n = number of corallites sampled. 'LAG', 'PR', 'RF', and 'SC' refer respectively to modern populations from the lagoon, patch reef, reef, and sand channel habitats.

Species cluster	Population	N	(n)	CV1	
				Mean	Grouping
<i>M. annularis</i>	Panama	1	(10)	-2.43 (.30)	A
	LAG	10	(100)	-3.19 (.44)	B
	PR	10	(100)	-3.34 (.50)	C
	SC	10	(100)	-3.75 (.32)	D
	RF	10	(100)	-4.10 (.33)	E
<i>M. cavernosa</i>	Georgia	2	(20)	2.44 (.59)	A
	Panama	1	(10)	2.12 (1.04)	A/B
	LAG	10	(100)	1.65 (1.16)	B
	Chiapas	1	(10)	1.52 (.86)	B/C
	SC	10	(100)	1.10 (1.42)	C
Fossil cluster A (fcA)	Anguilla	2	(20)	1.18 (1.05)	A
	Chiapas	9	(88)	-.39 (.82)	B
Fossil cluster B (fcB)	Panama	16	(158)	-.41 (.62)	B
	Florida	3	(26)	2.93 (1.14)	A
	Anguilla	10	(93)	2.14 (1.06)	B
	Georgia	9	(74)	1.74 (1.17)	C
	Chiapas	8	(80)	1.68 (.98)	C
Fossil cluster C (fcC)	Panama	9	(79)	1.18 (1.04)	D
	Anguilla	11	(96)	4.51 (1.52)	A
	Florida	5	(35)	4.30 (1.13)	A
	Chiapas	6	(58)	4.16 (1.12)	A

the traditional approach, number of septa is relatively more important, and in the statistical analyses, wall (theca) thickness and coenosteum porosity are more heavily weighted. One significant difference between the two approaches is that the statistical approach corrects for redundancies between correlated characters. The statistical analysis more explicitly shows the interrelationship between characters used in describing species and the contrasts between characters.

#### INTRASPECIFIC VARIATION

Intraspecific variation was analyzed using the canonical variate axes which best separated the species clusters in the statistical analysis. To focus on the species problem, only those axes or vectors that distinguish species were considered. Tests for homogeneity of variance (SAS TTEST procedure, Helwig and Council, 1979) suggest that overall variance is slightly higher in *M. cavernosa* and fossil cluster C and lower in *M. annularis* and fossil cluster A (cf. Fig. 4). Box's test (Miller, 1968) was used to compare magnitudes of within-colony and within-population variation within each species cluster (Table 4). The results suggest that *M. annularis* has the least intraspecific variation and *M. cavernosa* the most. Magnitudes for fossil species clusters A, B, and C lie between the two extremes and increase from A to B to C. Hence, as desired when

grouping fossils into species, the fossil species clusters have magnitudes of intraspecific variation roughly comparable to each other and to the modern species.

Differences between populations within species clusters were further studied to determine if any environmental interpretations could be made using fossil populations. Analysis of variance using Duncan's multiple range test (SAS GLM procedures, Helwig and Council, 1979) shows that populations are discrete in both modern species and, to a lesser degree, in fossil clusters A and B (Table 6, Fig. 5). The fossil specimens in both modern species clusters lie closest to the modern lagoon (LAG) population. The fossils in *M. cavernosa* are from various widely-separated areas along the western and northwestern margins of Caribbean reef-coral distribution during early Miocene time. The fossils in *M. annularis* are only from Panama. Consequently, assuming that the fossil samples are drawn from roughly equivalent facies and they adequately represent their distribution in the early Miocene throughout the Caribbean, the *M. annularis* fossils appear to have had a more restricted geographic distribution. The results suggest that the two modern species may have originated in early Miocene time in near-shore areas having low water energies and high turbidities (as in the modern lagoon) and spread at varying rates across the Caribbean.

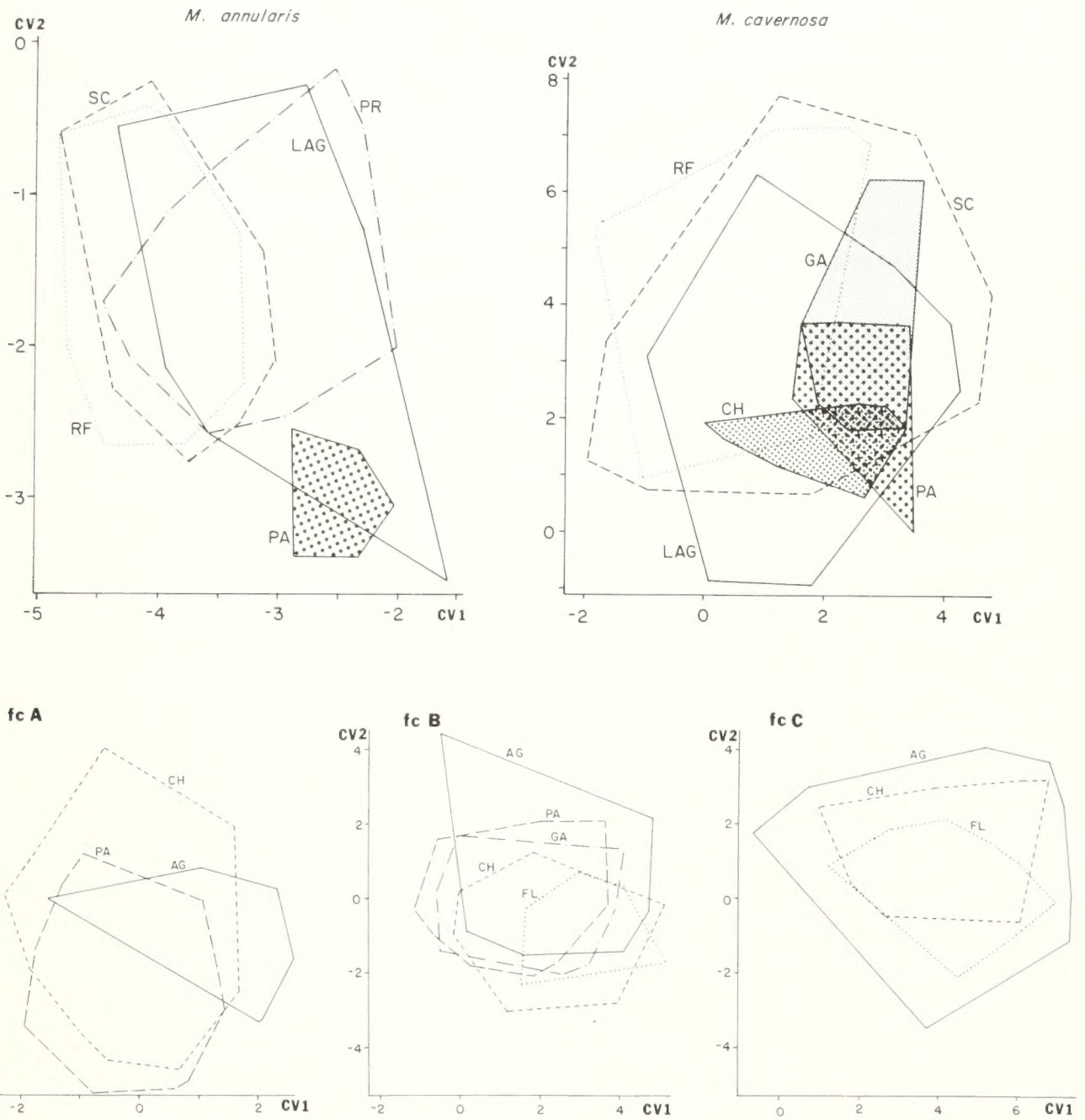


Figure 5.—Plots of the first two canonical variates (CV1, CV2) showing variation between populations within each species cluster. Each polygon outlines the range of variation between corallites within a population. Fossil corallite populations within modern species clusters are shaded. (PA, fossil corallites from Panama; AG, fossil corallites from Anguilla; CH, fossil corallites from Chiapas; FL, fossil corallites from Florida; GA, fossil corallites from Georgia; LAG, modern corallites from lagoon (Discovery Bay, Jamaica); PR, modern corallites from the patch reef (Discovery Bay, Jamaica); RF, modern corallites from the reef (Discovery Bay, Jamaica); SC, modern corallites from the sand channel (Discovery Bay, Jamaica); fcA, fossil cluster A; fcB, fossil cluster B; fcC, fossil cluster C).

Trends of variation between populations can be further interpreted by comparison with *M. annularis*, the species shown by transplantation experiments to have between-population variation caused exclusively by the environment. In *M. annularis*, the two nearshore populations (PR, LAG) have significantly higher values for the first canonical variate (CV1). No difference could be seen between populations in the second canonical variate (CV2). Parallel trends are seen between populations within fossil species clusters (Table 6, Fig. 5) as follows:

(1) Populations from Anguilla have higher CV1 values than populations from Panama in both fossil clusters A and B. Similarly, Anguilla specimens belong to three species clusters which have a higher overall CV1 value than those from Panama.

(2) Populations from Chiapas and Georgia generally have CV1 values between those from Panama and Anguilla within fossil clusters A and B, whereas populations from Florida are more similar to those from Anguilla.

Correlations between trends in *M. annularis* and those in fossil clusters suggest that colonies from Anguilla (and perhaps Florida) may have grown in significantly more turbid habitats with lower water energies (as in the modern lagoon) than those from Panama. The interpretations between populations presented here assume, of course, that all species vary similarly in response to the environment. Since this may not be true (see Foster, 1980), trends need to be analyzed in more living species to establish a pattern that can more confidently be projected to the fossil data.

### CONCLUSIONS

One ultimate goal of systematics is the reconstruction of phylogenies at the species level. However, work on corals is still at a primitive stage, because our knowledge of variation in fossils is limited and inadequately documented. Such variation in modern species is known to be subtle and complex both within and between species. This study has presented a preliminary

demonstration of how both statistics and experiments can be used in the systematics of fossil species to offer more rigorous descriptions and interpretations of coral variation. It has shown that a statistical analysis of variation within and between populations can lead to substantial reorganization of fossil species within genera. Such reorganization could strongly affect reconstructions of species distribution patterns (ecologic, biogeographic or stratigraphic) and, consequently, phylogenies.

Furthermore, this study has shown that transplantation experiments that document responses in taxonomic characters are fundamental to defining species limits in fossils and in interpreting patterns of variation between populations. Such experimental results can be directly incorporated into statistical analyses of fossil data. They can be used to estimate magnitudes of variation within fossil species and morphologic distances between species. Experimental results also permit environmental interpretations of fossil populations, that allow better understanding of the importance of geography and ecology in coral evolution.

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## APPENDIX 1

## List of specimens in the statistical analyses.

Formation	Locality	Specimens
Culebra Fm. (Panama)	USGS 6015	USNM-M324890(NF238)
	USGS 6016	USNM-M324872(NF244), M324875(NF246, 247), M324867(NF258, 260, 261, 263), 63471(NF386–388, 390, 391, 394–399, 405, 407, 410, 415)
Anguilla Fm. (Anguilla)	USGS 6017	USNM-M324889(NF240)
	USGS 6444	USNM-M324907(NF248)
	USGS 6893	USNM-M324910(NF113), M324930(NF118), M324848(NF123), M324845(NF124, 125), ?M324853(NF131), M324869(NF139, 140)
	USGS 6894	USNM-M324844(NF119), M324848(NF121), M324848(NF126), M324854(NF130), M324871(NF137, 141–145)
	USGS 6965	USNM-M324870(NF138)
	USGS 6966	USNM-M324839(NF127), M324857(NF132)
	USGS 6967	USNM-M324849(NF135), M324850(NF136)
Modelo Group— Santa Ana Fm. and Rio Lajas Lm. (Chiapas, Mexico)	Finca Santa Ana: Unit 9 (FSA 5)	UI-x3671
	Unit 15 (FSA 6)	UI-x3704, 6253, 3673, 3674, 3676
	Unit 31 (FSA 8)	UI-x6257
	Unit 35 (FSA 10)	UI-x3682
	Unit 37 (FSA 12)	UI-x3712, 3714, 3686, 3687, 6342
	Unit 69 (FSA 27)	UI-x3720, 3721, 3691, 3692, 3694–3696
	Colonia Modelo: Unit 39 (CM 1)	UI-x3699–3701
Tampa Fm. (Florida, USA)	USGS 2115	USNM-M324899(NF169)
	USGS 3694	USNM-M324877(NF235)
	USGS 4999	USNM-M324891(NF172), M324890(NF176–178)
	USGS 7754	USNM-63447(NF174, 175)
Chattahoochee Fm. (Georgia, USA)	USGS 3383	USNM-M324881(NF192)*, M324882(NF209)
	USGS 3790	USNM-M324892(NF191)
	USGS 6084	USNM-M324880(NF184, 185, 187, 188)
	USGS 7074	USNM-63443(NF205–208)
Modern <i>M. annularis</i> (Discovery Bay, Jamaica)	patch reef (PR)	SUI 45425–45434
	lagoon (LAG)	SUI 45435–45444
	reef (RF)	SUI 45445–45454
	sand channel (SC)	SUI 45455–45464
Modern <i>M. cavernosa</i> (Discovery Bay, Jamaica)	patch reef (PR)	SUI 48768–48769
	lagoon (LAG)	SUI 48758–48767
	reef (RF)	SUI 48770–48779
	sand channel (SC)	SUI 48748–48757

\* Primary type only 2 corallites measured.

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## SPECIES CONCEPT AND ECOMORPH VARIATION IN LIVING AND FOSSIL SCLERACTINIA

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### ABSTRACT

Coral taxonomists are confronted with the problem of considerable variation within coral species. Many systematically important characteristics, such as calice diameter and septal structure, vary widely within species. The cause of this variation is not clear, but a matter of intensive research. Basic patterns of skeletal morphology in corals are not yet functionally understood. The limit of variation within a coral species is therefore difficult to define. This has all resulted in the description of an excessive number of fossil as well as Recent coral species. The species concept in modern corals has been drastically changed as a result of variability studies carried out in the field using underwater observation. However, species are still largely based on morphological and not genetic characters. Intraspecific variability may be intracolony, intrapopulation and interpopulation. These aspects are overprinted by geographical variation. Evolutionary morphogenesis involves variability that ranges geographically and through time and both combine to determine the character of any species.

### INTRODUCTION

A great amount of intraspecific variability occurs within coral species (Wijsman Best, 1974). What factors caused the variability? Is the effect the same in all coral species? What is the limit of variation? Intraspecific variation has been summarized recently by Veron and Pichon (1976). Different micro-ecological factors give rise to heterogeneous colonies, while the various macro-ecological factors result in a heterogeneous series of coral colonies of the same species from different populations.

At the beginning of this century most coral specialists were paleontologists. In Europe the traditions established by Milne Edwards and Haime and Alloiteau were followed by Chevalier (1961) who contributed much to coral classification. In the United States, building from the collections and studies of Dana and Vaughan, Wells (1956) presented the classification of fossil and recent coral genera, which is now commonly followed. Coral species were described according to the 19th century typological species concept, which remains entrenched in much paleontological systematics. However, recent biological coral research has resulted in a reorientation of the approach of many paleontologists. In Europe, Pfister (1977) incorporated modern concepts of variation in her study of fossil corals from northern Italy, as did Frost (1977) for Caribbean Cenozoic reefs. However, in his Oligocene reef coral biofacies study, although Frost (1981) often compared these reefs and their ecology with recent ones, he did not discuss the environmental factors causing intraspecific variation in reef corals in detail. At the same time the problem of environmentally related in-

traspecific variation in corals and the degree in which this potentially can be employed as a sensitive paleo-ecologic indicator in suitable fossil situations was discussed by Haggerty *et al.* (1980). This topic was amplified by Foster (1979), who compared intraspecific variability in fossil and recent corals of related genera.

### INTRASPECIFIC VARIATION

The larvae of a coral species, having a genetically determined "specific diagram," will express a certain degree of ecophenotypical modification, depending on the site it settles (Wijsman Best, 1972).

In both fossil and Recent coral species, within a geographically limited area, intraspecific variation may be intracolony, intrapopulation and interpopulation. Examples of these three types of variation will be described from species belonging to the family Faviidae.

#### Intracolony Variation

Intracolony variation is exemplified in *Hydnophora exesa* (Pallas) (Pl. 1, figs. 1-2) where the top branches, which are in a higher energy environment, show increased calcium carbonate secretion, manifested in higher monticules, a denser corallum and more septa (Fig. 1). Towards the base of the colony the hydnae become flatter, the septa are sparser and the coenosteum is more vesicular (Fig. 2). This intracolony variation has important paleontological implications (see: *Turbinaria* p. 73), because fossils are often found as fragments of a colony and in this case two species might be erected from two different fragments of the same colony.

### Intrapopulation Variation

Intrapopulation variation is demonstrated by *Favia amicornum* (Edwards & Haime) (Pl. 1, figs. 3–4). The colonies are small and plocoid to phaceloid or subdendroid. The variability therefore does not apply within one colony. However, within one population, the adaptation to sedimentation is so strong that colonies from a sandy substratum develop into subdendroid colonies, which have been identified as specifically, and even generically, different from the plocoid *Favia* colonies encountered in reefs. Intermediate growth forms were also observed. This aspect of variability is of importance for paleontology when comparing different facies within a well preserved reef complex (see also *Tarbellastrea* p. 73).

### Interpopulation Variation

*Cyphastrea serailia* (Forskal) (Pl. 1, figs. 5–6) demonstrates an example of interpopulational variability, which is common in the Indo-Pacific and occurs in all reef biotopes. Although intracolony very homogeneous the interpopulational variability is high, four ecomorphs having been recognized by Veron *et al.* (1977, p. 172).

Although much has now been written about variability in coral species and the agencies which cause variation (energy, light intensity, nutrient supply), there remains the problem that there is no general rule for all species. Every coral species has its own range of variability with its own variety of causes. The causes however are mostly obscure.

Intracolony variability is the result of adaptation to microecological factors; the different sectors of the colony are objective ecomorphs of the same species. Intrapopulational variability may be partially genetic however (Hildemann *et al.*, 1977). Since these subjective ecomorphs may be the result of genotypic variability studies we must use the polytypic species concept. According to Mayr (1963) most species consist of a group of potentially interbreeding populations which fill the same niche geographically or ecologically. Among these, the neighbouring ones intergrade or interbreed whenever they are in contact. Foster has done some experiments to test the morphologic plasticity in different coral species. In her studies she found varying degrees of phenotypic plasticity (Foster, 1979a), which suggests that all variability is not exclusively the result of environmental influences, but also of genetic polymorphism. Direct protein analysis may in the future produce sound systematic information, but research by enzyme electrophoresis has as yet not fully succeeded with corals but see Lamberts (1979) and Ohlhorst (this volume).

The three types of variability, which of course do intergrade, are overlain by geographic variation. In variation studies we are usually dealing with one or more of the above discussed variations because most studies are carried out in restricted areas. When dealing with coral collections from the whole Indo-Pacific one is struck by the different distribution and variation patterns. There are species with: 1) small geographic domain and little variation (*Oulastrea crispata* (Lamarck)); 2) very large geographic distribution and little intraspecific variation (*Diploastrea heliopora* (Lamarck)); 3) small geographic distribution but high variability (*Echinopora forskaliana* (Edwards & Haime)); and 4) very large geographic range and high variability (*Leptastrea bottae* (Edwards & Haime)). In a study on the Montastreinae, Wijsman Best (1980) discussed genera with respect to their geographic distribution and variability. It was assumed that species occupying a large geographic area while showing little variation could be regarded as an old and stable species, in contrast to the highly variable species in the same area which could be regarded as young and diversified.

An example of this pattern is seen in the genus *Leptastrea* (Pl. 2, figs. 1–4). Of the five species belonging to *Leptastrea*, three have an Indo-Pacific distribution. In these three (*L. purpurea* (Dana), Fig. 1; *L. transversa* Klunzinger, Fig. 2; *L. bottae* (Edwards & Haime), Figs. 3–4), the geographic variation extends beyond the interpopulational variation, and therefore they may be regarded as dynamically evolving species. *L. bottae* ranges from the Red Sea to the Hawaiian Islands, and although its interpopulational variation is great, the overall geographic variation extends even beyond this range. Populations from adjacent areas overlap in intraspecific variation, so that only populations from widely separated areas vary significantly from one another. One may consider the ecomorphs of this species as “races” or subspecies. However it is possible that the degree of variation within the species is not closely related to the age of the genus from an evolutionary viewpoint. The degree to which a genus is stabilized or in full speciation probably has to do with the extent of genotypic polymorphism within the species; morphological plasticity may be more genetically based than we as yet have previously assumed. Finally, evolutionary morphogenesis involves variability which ranges geographically and through time and both combine to determine the character of the species. Paleontology proves the limited plasticity of such a seemingly plastic feature as calice diameters in colonial corals. In the Middle Triassic, the suborders Astrocoeniina, Fungiina and Faviina appeared simultaneously. The first suborder has retained its small

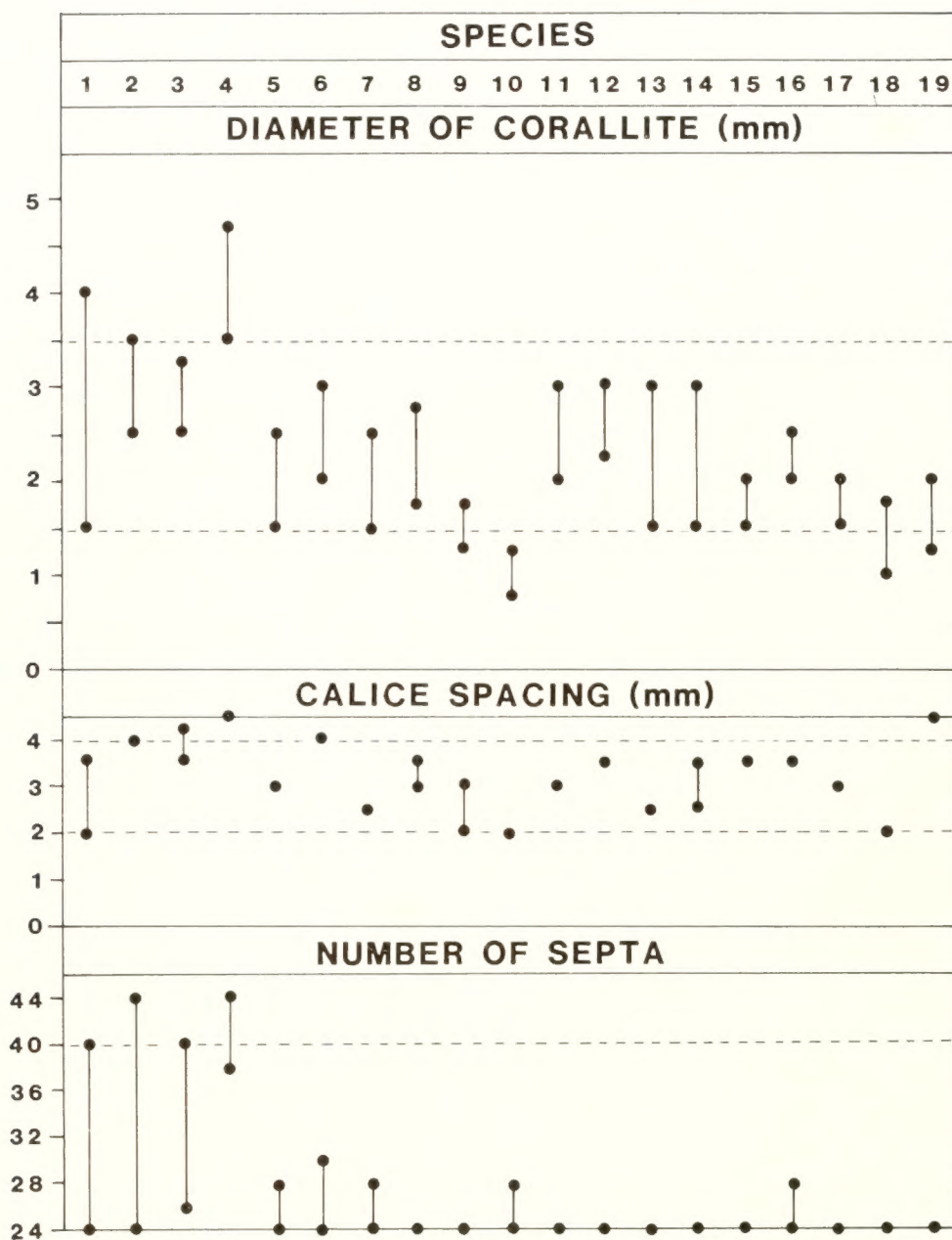


Table 1.—Distinguishing characteristics of *Tarbellastraea* (after Chevalier, 1961, p. 1984). Calice spacing measured from the centers of adjacent corallites. Variability in our specimens is indicated within dashed lines.

1. <i>ellisiana</i>	7. <i>mimbastensis</i>	13. <i>eggenburgensis</i> var. <i>andalousianensis</i>
2. <i>ellisiana</i> var. <i>manthelanensis</i>	8. <i>raulini</i>	14. <i>reussiana</i>
3. <i>carryensis</i>	9. <i>aquitaniensis</i>	15. <i>reussiana</i> var. <i>echinulata</i>
4. <i>carryensis</i> var. <i>major</i>	10. <i>aquitaniensis</i> var. <i>termofuriae</i>	16. <i>prevostiana</i>
5. <i>carryensis</i> var. <i>minor</i>	11. <i>eggenburgensis</i>	17. <i>siciliae</i>
6. <i>conoidea</i>	12. <i>eggenburgensis</i> var. <i>formosa</i>	18. <i>abditaxis</i>
		19. <i>distans</i>

corallites during the ensuing 200 million years. A sound genetic and/or functional cause probably exists for this conservatism. In general, it may be stated that in Oligocene and Miocene reefs, species with larger corallite diameters often occurred in many genera. However, rapid growth developed in species with smaller corallites. In the genus *Montastrea*, species with both larger and smaller corallites have evolved:

- Montastrea curta* (Dana), large, Indo-Pacific
- Montastrea annuligera* M. Edwards & Haime, small, Indo-Pacific
- Montastrea cavernosa* (Linnaeus), large, Caribbean
- Montastrea annularis* (Ellis & Solander), small, Caribbean

(See Pl. 3, figs. 1–4.) This suggests that corallite diameter has functional significance.

#### FOSSIL EXAMPLES

To compare variability in fossil corals with that in modern corals, the classical, and exceedingly well preserved Burdigalian fauna from Le Peloua near Saucats (South East of Bordeaux, France) was studied. The most recent revision of this fauna is that of Chevalier (1961). In most cases poor preservation makes variability studies in fossil corals difficult. Dubious stratigraphic control hampers paleobiogeographic reconstructions. However, this does not apply to Le Peloua, which is only a few kilometers from the stratotype of the Burdigalian, where the corals are still aragonitic. Even so, it was difficult to obtain a series of specimens large enough to study intraspecific variability. Only the specimens of *Tarbellastraea* (90) and the specimens of *Turbinaria* (150) warranted special consideration.

*Tarbellastraea* Alloiteau, is an extinct genus in which some Neogene species were grouped that Reuss (1871) had placed in *Heliastrea* Milne Edwards & Haime, to which *Tarbellastraea* is closely related. We identified all *Tarbellastraea* material from Le Peloua as *Astraea ellisiana* DeFrance. Chevalier (1961) distinguished not less than nineteen species and varieties of *Tarbellastraea* from the Mediterranean Neogene; he recorded five of these from Le Peloua. Table 1 presents characteristics of *Tarbellastraea* forms as described and distinguished by Chevalier, combined with the observations on our material. Large overlaps exist in characteristics that usually identify separate systematic entities. The variability is extremely large in number of costae, diameter of corallites, distance between corallites and columellar shape. Moreover, all of these variations intergrade. We do not hesitate therefore, to ascribe all Le Peloua specimens of *Tarbellastraea* to one species, *T. ellisiana* (Pl. 4, figs. 1–6).

The causes underlying the variability in this case are

not clear. Material from the Burdigalian of St. Paulles Dax is less variable. It is conceivable that the large blocks from St. Paul are derived from one reef with a more or less stable environment, whereas the Le Peloua material is a deposit derived from a gully system in which the coral fragments washed together from various places and conditions.

*Turbinaria* Oken is an Oligocene to recent cupuliform coral genus. Recent specimens of *Turbinaria mesenterina* (Lamarck), from the Leiden Museum were studied for comparison with Le Peloua material because entire fossil colonies of this genus are exceedingly rare. Our numerous finds from Le Peloua consist of fragments only. Two stems of colonies were encountered, and it is probable that some of the fragments were derived from one colony. The stem of the skeleton as well as the disk consist largely of coenosteum. At the colony surface, only the upper side of the disk contains many calices. The corallites originate from a branching level situated in the disk midway between the upper and lower surface. The coenosteum above this branching level is finer in structure and trabeculae are less densely packed than at the level below. All corallites are directed upward. Because the bottom of the cupuliform colony is more or less horizontal in the center of the cup (above the stem), the corallites there are perpendicular to the branching level and the colony surface. At the edges of the colony they are situated oblique to these surfaces. This causes the sides of the calices at the downslope half of the upper surface of the colony edge to be heightened by a protruding rim.

The fossil *Turbinaria cyathiformis* (Blainville) (Pl. 5, figs. 1–4) has calices with diameters from 1.2 to 2.8 mm. The smallest calices have 12 septa, the largest 40. The distance between neighboring calices varies from 1.0 to 50 mm or more. Most lie 2–4 mm apart, just as in *Turbinaria mesenterina*. Fragments in which the corallites are situated oblique to the surface (and to the branching plane) show heightened calices arranged in short rows, as do recent colonies. Chevalier (1961) created the variety *lamelliformis* for fragments with a dense coenosteum and corallites perpendicular to the surface. Another species name, *Turbinaria grandis*, was coined for fragments with calice diameters ranging from 1.2 to 2.0 mm and perpendicular corallites. It is clear that skewness or perpendicularity in *Turbinaria* colonies is covered by intracolony variation and that reported differences in calice diameter and density of coenosteum are very probably also due to intracolony variability. There remains no doubt that *Turbinaria grandis* and *Turbinaria cyathiformis* var. *lamelliformis* are both synonyms of *Turbinaria cyathiformis* s.s. We found some indications of ecologically controlled intercolony variability in the *Turbinaria* species. We

collected 40 fragments from the Graviere de Cante locality, in Burdigalian strata a few kilometers west of Le Peloua. This material is more worn than that from Le Peloua. The thickness of the trabeculae varies from 0.20 to 0.22 mm as compared with 0.18–0.20 mm in Le Peloua and their calices are slightly larger, their mean diameter is 2.0 mm as compared with 1.8 mm at Le Peloua. The mean number of septa is therefore, also somewhat higher: 22 at Graviere de Cante, 19 at Le Peloua.

### CONCLUSIONS

The examples discussed of *Tarbellastraea* and *Turbinaria* make abundantly clear that fossil coral species must be based on comparisons with the skeletal morphology of recent scleractinians. On the other hand, modern species can only be understood by study of their fossil ancestors.

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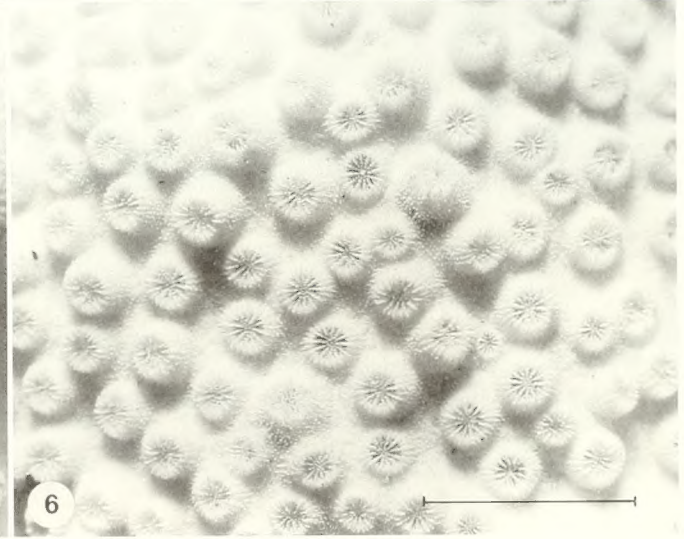
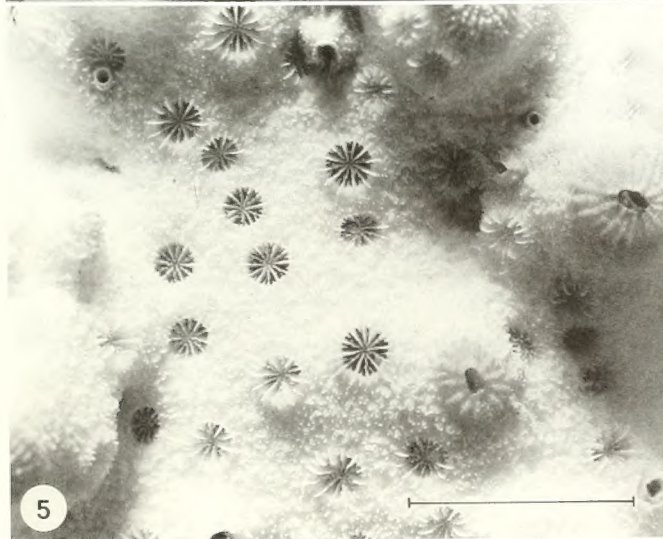
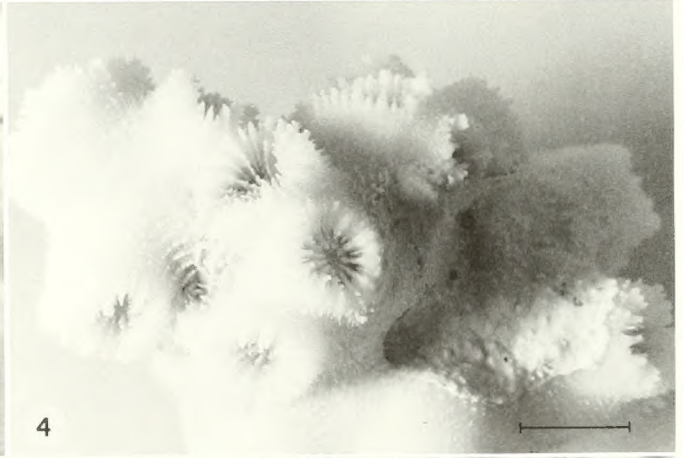
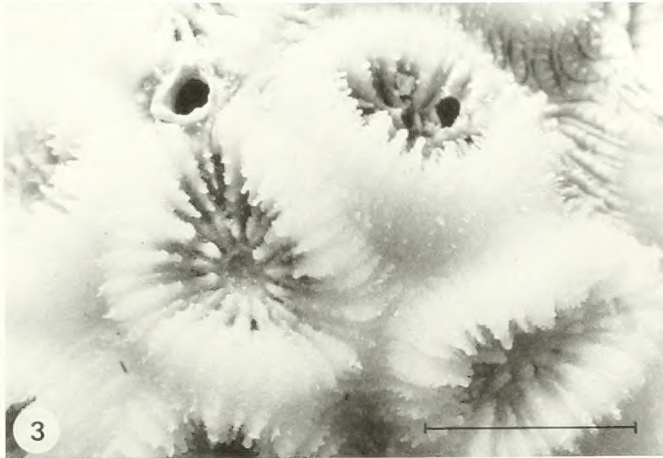
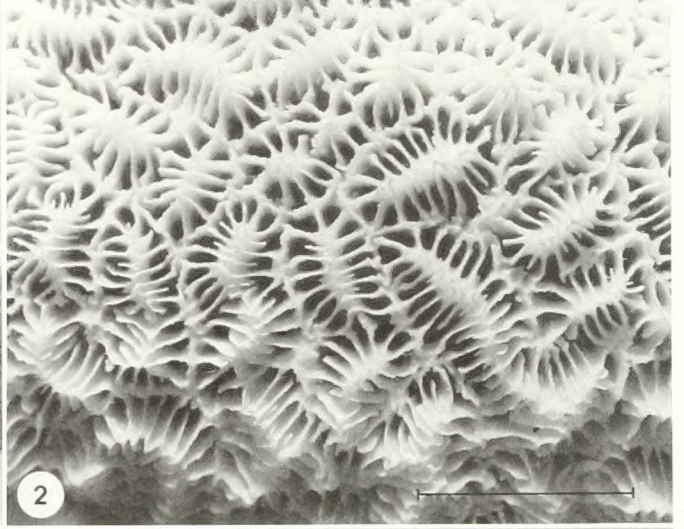
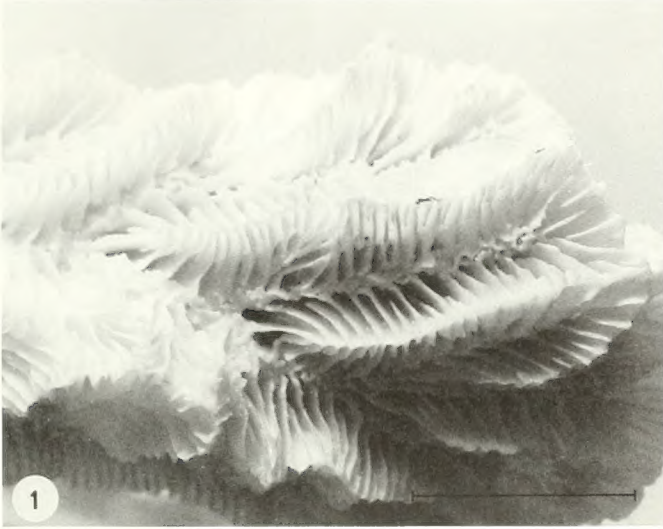
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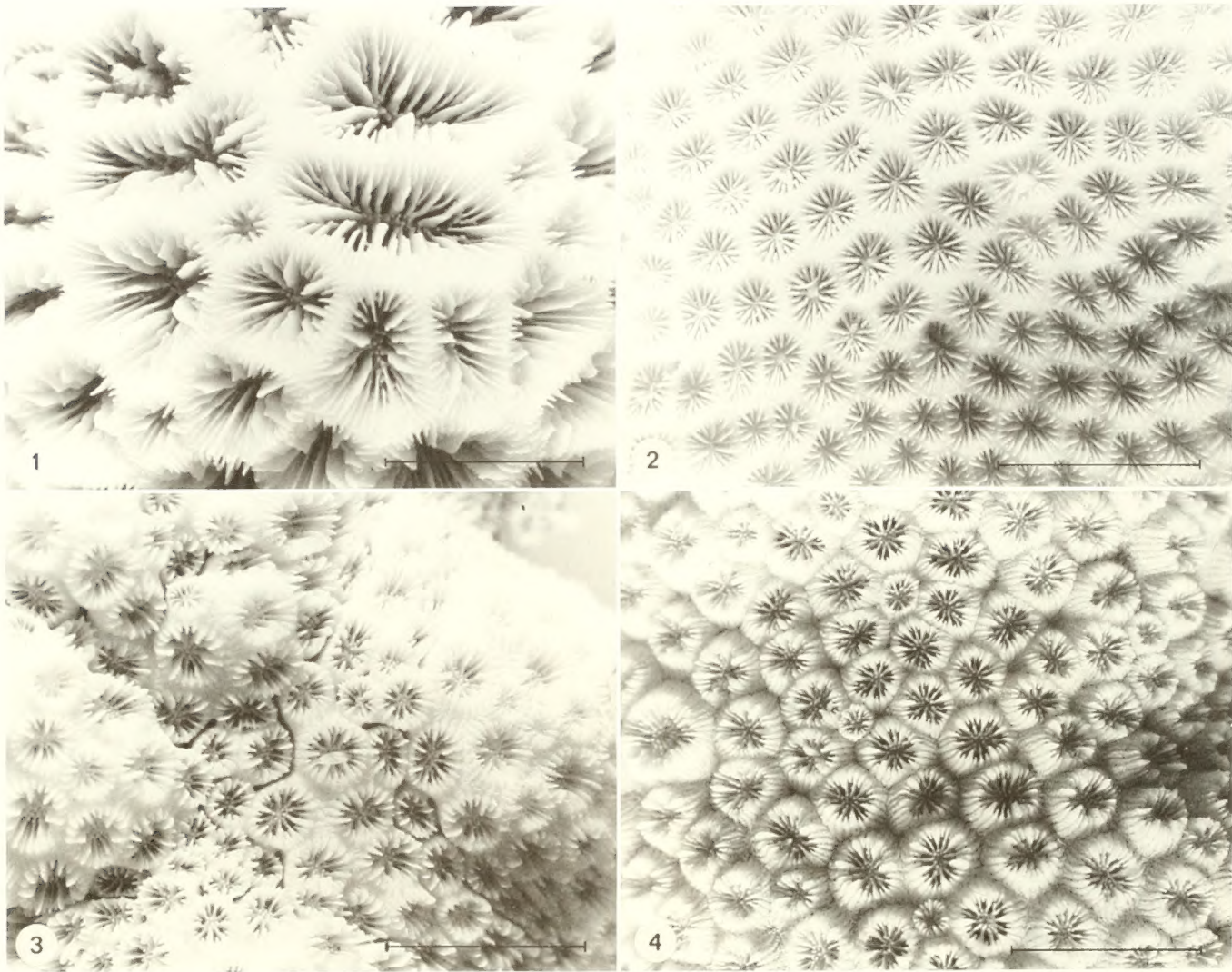
(Scale-bar = 1 cm; RMNH = Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands)

#### Figure

- 1–2. Intracolony variation in *Hydnophora exesa* (Pallas)  
 RMNH Coel 9626 from the Red Sea.  
 1. Corallites from top branch.  
 2. Corallites from base of colony.
- 3–4. Intrapopulation variability in *Favia amicorum* (Edwards & Haime)  
 3. RMNH Coel 14357, a plocoid colony from Enewetak atoll, Marshall Islands.  
 4. RMNH Coel 14349, a phaceloid colony from Enewetak atoll, Marshall Islands.
- 5–6. Interpopulation variability in *Cyphastrea serailia* (Forsk.)  
 5. RMNH Coel 12654 ecomorph *C. suvadivae* from Prony Bay, New Caledonia.  
 6. RMNH Coel 12658 ecomorph *C. hemprichiana* from Ricaudy reef, New Caledonia.







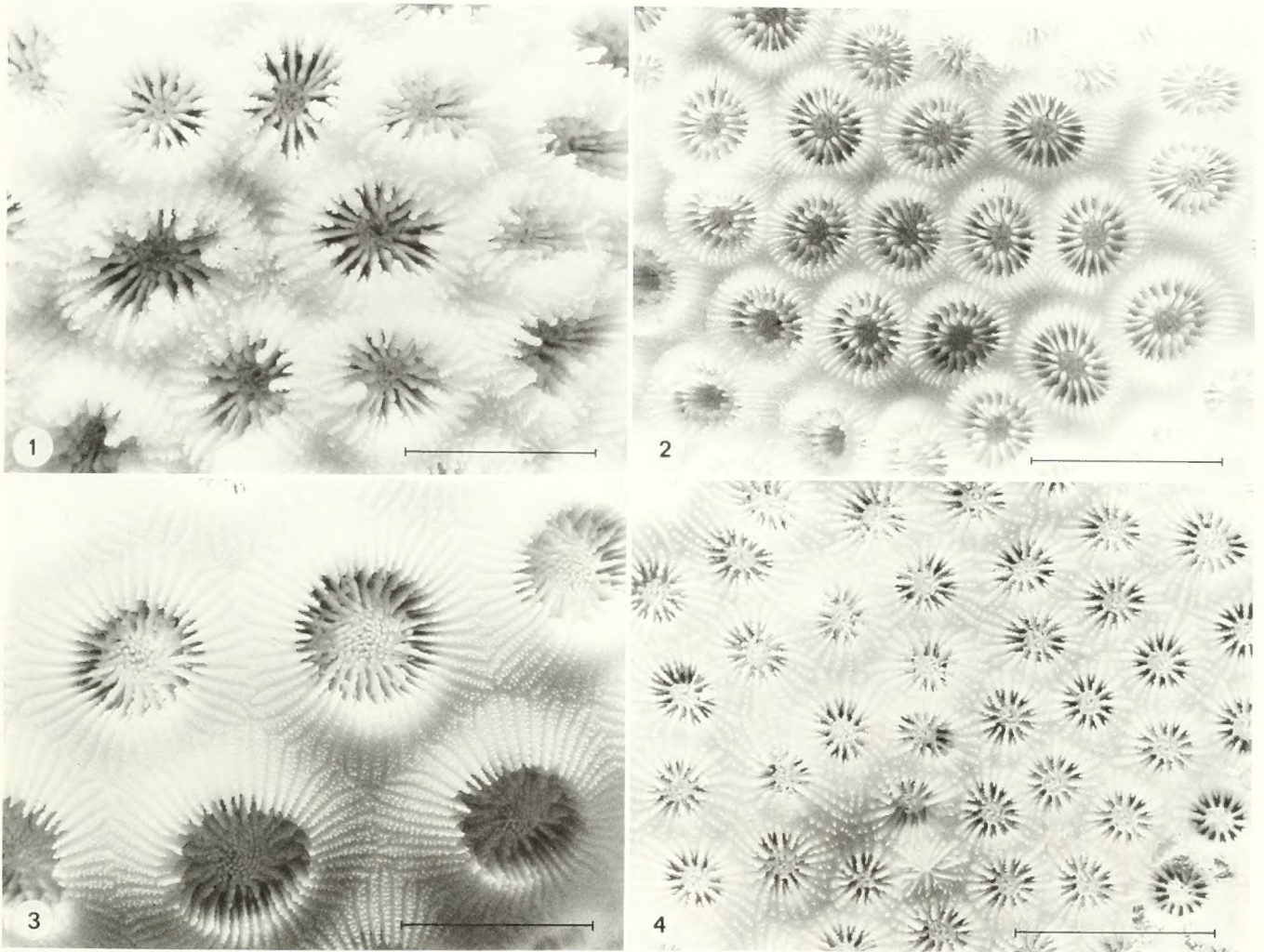
## EXPLANATION OF PLATE 2

(Scale bar = 1 cm; RMNH = Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands)

## Figure

1-4. Geographical variability in the genus *Leptastrea*

1. *L. purpurea* (Dana), RMNH Coel 10755 from Spermonde shelf, Sulawesi, Indonesia.
2. *L. transversa* Klunzinger, RMNH Coel 12721 from Enewetak atoll, Marshall Islands.
3. *L. bottae* (Edwards & Haime), RMNH Coel 12869 from Honolulu, Hawaiian Islands.
4. *L. bottae* (M. Edwards & Haime), RMNH Coel 12673 from Gulf of Elat, Red Sea.



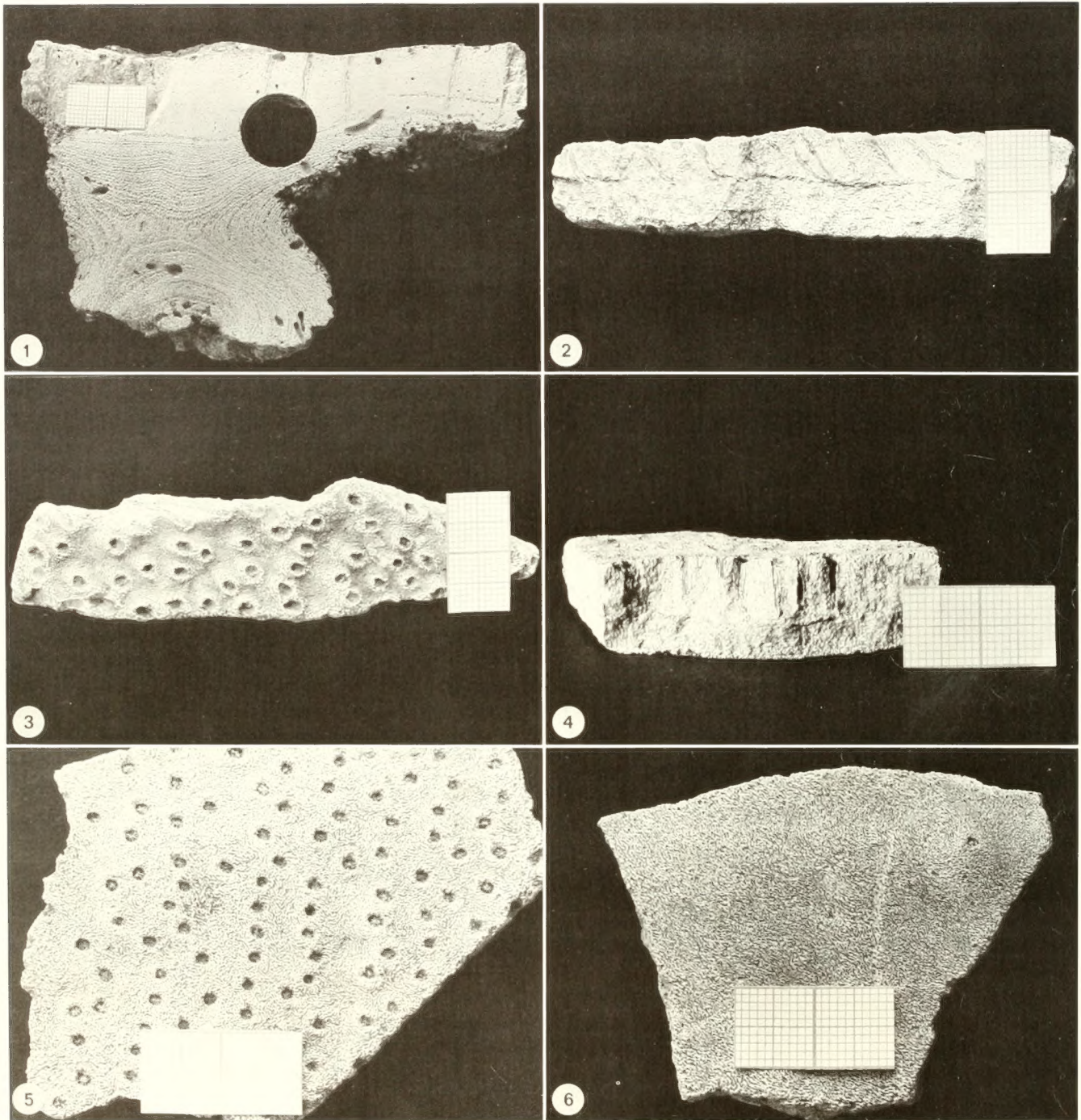
## EXPLANATION OF PLATE 3

(Scale bar = 1 cm; RMNH = Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands)

## Figure

1-4. Parallel evolutionary processes in species differentiation in the genus *Montastrea*

1. *M. curta* (Dana), RMNH Coel 9528 from Noumea, New Caledonia.
2. *M. annuligera* Edwards & Haime, RMNH Coel 10718 from Heron Island, Great Barrier Reef.
3. *M. cavernosa* (Linnaeus), RMNH Coel 8630 from Saba bank, Caribbean Sea.
4. *M. annularis* (Ellis & Solander), RMNH Coel 8642 from St. Eustatius, Caribbean.



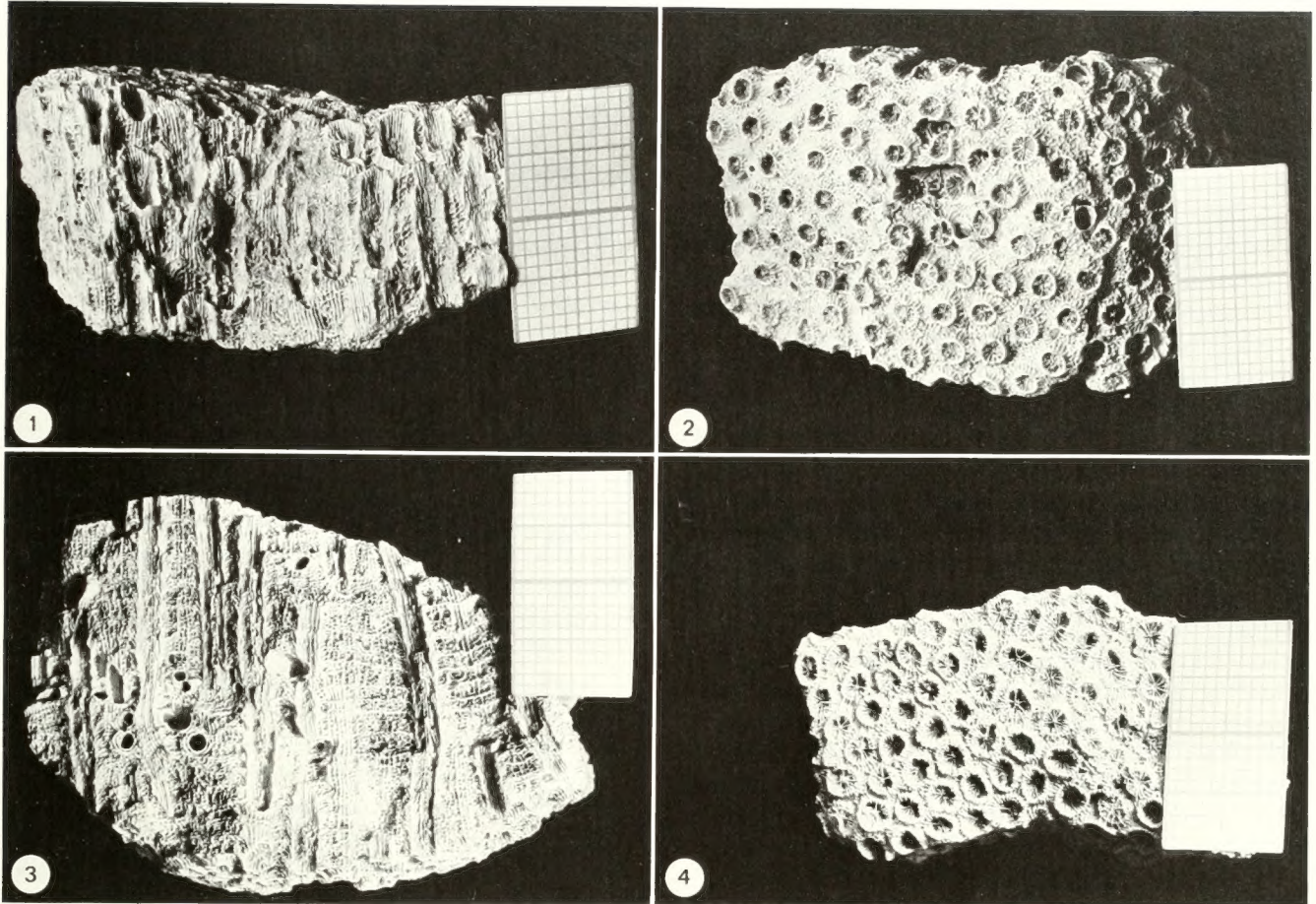
## EXPLANATION OF PLATE 4

(Scale bar = 1 cm; RGM = Rijksmuseum van Geologie en Mineralogie, Leiden, Netherlands)

## Figure

1-5. Intracolony variation in *Turbinaria cyathiformis* (Blainville) from the Burdigalian, Le Peloua, Saucats, France

1. Cross section of central stem of colony. Coenosteum below corallite branching plane less dense than above; corallites perpendicular to colony surface. RGM 299.801.
2. Lateral aspect of fragment from steep part of colony hood. Corallites oblique to colony surface. RGM 299.802.
3. Surface of fragment (same as 2); calices surrounded by rims. RGM 299.802.
4. Lateral aspect of fragment from horizontal part of colony hood. Corallites perpendicular to surface. RGM 299.803.
5. Surface of fragment (same as 4); calices not surrounded by rims. RGM 299.803.
6. Reverse side of same fragment as in 5. RGM 299.803



## EXPLANATION OF PLATE 5

(Scale bar = 1 cm; RGM = Rijksmuseum van Geologie en Mineralogie, Leiden, Netherlands)

## Figure

1-4. Intercolonial variation in *Tarbellastraea ellisiana* (Defrance) from the Burdigalian, Le Peloua, Saucats, France

1. Lateral aspect of colony fragment. Densely packed corallites, no laminae. RGM 299.804.
2. Surface of same fragment as in 1; calices closely spaced together, costae numerous and well-developed. RGM 299.804.
3. Lateral aspect of colony fragment. Corallites widely spaced, laminae well-developed. RGM 299.805.
4. Surface of same fragment as in 3; calices widely spaced, costae not covering the corallite wall. RGM 299.805.

## TAXONOMY IN AHERMATYPIC SCLERACTINIAN CORALS

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## ABSTRACT

The basic task of coral taxonomy is to recognize species in relation to their ecologic and biogeographic range. A considerable range of variation, despite references to the contrary, can be found in the skeletal characters not only of the reef-building corals, but also of those from other environments. Growth form variation may be particularly large in colonial species and seems limited only in solitary species living free on soft bottoms. Results are most satisfactory when based upon a large series of specimens. In recent studies of non-reef-building coral faunas (including both zooxanthellate and non-zooxanthellate forms) various previously neglected characters are shown to be taxonomically important. These include: attached or free early stages, monocyclic or polycyclic structure of the base, reinforcement of the base, type of adventive attachment to the substrate, respective width of the septa, the spatial relationship of calicular elements and the type of asexual reproduction. Examples of large intraspecific variation and of the usefulness of particular taxonomic characters in ahermatypic scleractinians are provided.

## INTRODUCTION

Mayr (1969) defined a taxonomic character as "any attribute of a member of a taxon by which it differs or may differ from a member of a different taxon." For Scleractinia, finding these characters appears particularly difficult.

The order Scleractinia combines high morphological and ecological diversity (Wells 1956) and this is manifest in the concept of ecomorphs (Veron and Pichon, 1976), which are defined as "intraspecific skeletal variations phenotypically and/or genotypically determined in response to specific ecological conditions."

A review of the literature shows that there is now wide agreement that a considerable range of intraspecific variation exists in coral skeletons, which are the basis for taxonomic studies.

As far as hermatypic (reef-building) corals are concerned, Veron and Pichon (1976) summarize the history of the problem and the evolution of concepts. Referring to reef-building scleractinians from Eastern Australia, Veron (1982) mentions seven forms of variation: 1) among nearby corallites on the same corallum branch, 2) within whole colonies, 3) among different colonies within the same biotope, 4) on a single reef face or in a single lagoon, 5) within a single major geographic region such as the Great Barrier Reef, 6) between geographic regions, 7) within geologic time.

Multilevel variations are not restricted to colonial reef-building corals, but are now also well documented for various ahermatypic (not reef-building) species, some of them from shallow water being zooxanthellate, those from deeper water non-zooxanthellate. Weber (1974) underestimated the high degree of plasticity in non-zooxanthellate corals when he hypothesized that zooxanthellae, in their role of metabolite removal, account for the high degree of plasticity within species.

Among the older authors, Gravier (1920) was aware of the considerable range of variation in ahermatypic (in this case deep-water) corals and especially noted the influence of size and stability of the substrate on the resulting attachment structures and shapes of solitary corals, such as *Caryophyllia*.

Intraspecific variation has also been a major concern in more recent studies of ahermatypic coral faunas, especially from the Mediterranean and the northeastern Atlantic (Zibrowius, 1980), and from the western Atlantic, Antarctica and Subantarctic regions (Cairns, 1979, 1982).

Variation in ahermatypic corals can be recognized when many specimens are available, preferably from throughout the ecological and geographical range of the species. Early coral workers were not in this privileged position and quite frequently described as distinct species that which we can now integrate into one variable species.

## EXAMPLES OF VARIATION IN AHERMATYPIC SCLERACTINIANS

Colonial zooxanthellate ahermatypes and constructors of deep-water coral banks provide examples of a wide range of variation in skeletal structures.

*Cladocora caespitosa* (Linnaeus, 1767), as a colonial zooxanthellate species, is limited to the euphotic zone of the Mediterranean, compatible with the life of its symbionts. But inside this zone it has a wide ecological range on hard and on soft bottoms from near the surface to about 50 m (?) depth, and from calm water to sites exposed to strong currents and wave action. The general aspect of the colonies varies considerably with the sedimentation and mechanical requirements. Extreme forms range from phaceloid colonies with short

corallites on exposed rocks in shallow water to loosely branched colonies with long slender corallites on deeper soft bottoms. There is also a tendency in the slender calm water form to have fewer septa, more loosely packed in individual calices. Dentation of the septa also varies considerably. It is no surprise that early authors having little material considered extreme forms as belonging to distinct species.

Abel (1959) was aware of the polymorphism of *C. caespitosa* and tried to correlate the growth forms with the main environmental factors (light and water movement). The underlying idea was good, but unfortunately he included in the diagram a second species of *Cladocora* and a species of *Polycyathus*, both non-zooxanthellate.

Extreme forms of the potentially zooxanthellate *Madracis asperula* Milne Edwards & Haime, 1849, as found in the eastern Atlantic, would surely have been taken for distinct species, had they been known to early authors. Growth form varies between slender branches and thick crusts, with all intermediates. Although the calices are simple (few septa, no pali) variation at this level is considerable, mainly as the result of more or less crowding of individual calices. Various sectors of the same colony may differ considerably from each other, and occasionally isolated parts are difficult to recognize as *Madracis*.

So far, zooxanthellate colonial ahermatypes have been presented as examples of wide intraspecific variation. Being zooxanthellate and colonial, these forms may be considered as being physiologically similar to typical reef-building zooxanthellate corals whose wide intraspecific variation is widely known. However, as the following examples will show, intraspecific variation appears no less extensive in various non-zooxanthellate ahermatypes.

*Astroides calycularis* (Pallas, 1766) is a shallow-water dendrophylliid from the Mediterranean in which considerable calical variation is found both between and within colonies. Wells (1956) characterized the genus *Astroides* as constituting submassive colonies in which the corallites are united by noncostate coenosteum. This, in fact, characterizes only colonies exposed to strong water movement in the type species *A. calycularis*. Other colonies are phaceloid with branching, elongate, and laterally free corallites.

Variation in the deep-water bank-forming species *Madrepora oculata* Linnaeus, 1758, *Lophelia pertusa* (Linnaeus, 1758), and *Solenosmilia variabilis* Duncan, 1873, is most evident at the level of individual calices, although coenosteal development and packing of calices are also subject to variation, thereby influencing the general aspect of the colonies. In *L. pertusa* and *S. variabilis*, the septa vary considerably in exsertness

and the calices in width. In *S. variabilis* calicular variation is accentuated by the mechanism of intratentacular budding. Calices may be crowded together in dense clusters or, at the other end of variation, be spaced out by long slender tubular structures. A particularly slender form of *L. pertusa* had been named *L. tubulosa*. In *M. oculata* the development of the columella and the last cycle septa are highly variable. The first cycle septa may be strongly exsert and extend into sharp costae. Distinct pali may occur, a detail which does not conform to the conventional definition of the genus *Madrepora*. The sympodial type of budding with calices occurring in opposite and alternating rows is fairly typical of end branches, but obscured in older and basal parts, with calices more randomly oriented. Frequently there is a contrast between calices of the end branches and those of older and basal parts, the latter appearing shallower and filled in more closely by a thickened columella and septa.

Extensive intraspecific variation is not restricted to colonial corals. Examples abound among solitary forms. Only in species not attached throughout their benthic life or becoming free at a very early stage and characterized by a low flattened corallum is variation minor, manifesting itself mostly in thicker or thinner radial structures (*Fungiacyathus*, *Stephanophyllia*, and some species of *Deltocyathus*).

The Mediterranean and eastern Atlantic *Caryophyllia smithii* Stokes & Broderip 1828 has a wide ecological range and may live on hard as well as on soft bottoms. On soft bottoms, the younger stages are always attached to some object, such as a mollusc shell or *Ditrupa* tube, but often become free at a later stage. On stable, rocky substrates, the base covers a larger surface, grows considerably thicker, and the specimen normally remains attached throughout its life. A wide range of variation is observed in corallum size, shape (from free and turbinate to attached and cylindrical), and proportions as well as general solidity, number of septa, and development of columella and pali. It is not surprising that the synonymy of this species, known for a long time, is abundant and complicated, the confusion with other species having been frequent.

*Caryophyllia inornata* (Duncan, 1878), occurs in the Mediterranean but is less widely distributed in the northeastern Atlantic than the preceding species, and has a narrower ecological range, being limited to hard bottoms especially under overhangs and in caves. It had been little known before diving became a common technique in marine biological investigations. It also exhibits considerable variation, including different pigmentations of the polyp. Distinct pali are often absent in this species and unusual individuals have been found that may not even possess a columella.

The solitary dendrophylliid *Leptopsammia pruvoti* Lacaze-Duthiers 1897, typical of hard bottoms in the Mediterranean and the northeastern Atlantic, is another example of a variable species which became better understood thanks to extensive collecting by diving. The columella, originally used for the distinction of two species, varies enormously, from almost nonexistent to filling the greater part of the calice. The septal pattern of branching called the Pourtalès plan, common to many dendrophylliids, can mostly be seen only in very young stages, but rather exceptionally persists in some adult specimens.

In solitary corals, a high degree of variation can also be found in deep-water forms. The northeastern Atlantic *Desmophyllum cristagalli* Milne Edwards & Haime 1848 exhibits considerable variation in spite of its rather simple structure (no pali and a reduced columella in only very young stages). The shape of the corallum is largely conditioned by the substrate available for the settling larva. Specimens attached to loose fragments of sponge skeleton or isolated large spicules lying on soft bottom are elongate, slender and curved (once described as *D. serpuliforme*), whereas those in an elevated exposed position on banks of colonial deep-water corals (*Madrepora*, *Lophelia*, etc.) or on rock are greatly flared and have strongly exsert septa. The outer surface varies from rather smooth to strongly costate. *D. cristagalli* is considered worldwide in distribution and local forms can not be precisely distinguished on the basis of skeletal characters (Zibrowius, 1974a; Cairns, 1982). In populations of the southern hemisphere persistence of the columella in more advanced stages, as well as a higher number of septa (exceeding 96 of four cycles), appear more common than in the northeastern Atlantic, which is the type locality.

In populations of *Leptopsammia formosa* (Gravier, 1915) from the Azores, adult specimens with and without the Pourtalès septal arrangement coexist. Thecal thickness and a tendency for the septa to become free are correlated. Gravier (1920) even assigned distinctive specimens of this species to two different genera: *Balanophyllia formosa* and *Thecopsammia imperfecta*.

The preceding examples illustrate that variation occurs extensively in ahermatypic corals and no one morphological structure can be used for separating taxa. A tendency to "split" taxa among early coral workers was largely because they were less informed on environmental variation and had less material. For much the same reasons, the tendency to "split" taxa may still be stronger with paleontologists than with people studying living corals.

Sequenza's work (1864, 1880) on the Pleistocene of Sicily and Calabria well illustrates excessive splitting and over-estimation of the number of species. This Pleistocene deep-water coral fauna is very similar to that of the present northeastern Atlantic and it is most unlikely that some genera comprised many more species in the Mediterranean Pleistocene when they now have only one or a few species in the present Atlantic fauna, each with significant intraspecific variation.

#### EXAMPLES OF PARTICULAR TAXONOMIC CHARACTERS IN AHERMATYPIC CORALS

The above review of variation shows that the use of simple morphological criteria (e.g., exsert septa, Pourtalès plan, regular crown of pali, and large columella) may lead to error when uncritically accepted. Coral workers should therefore test other taxonomic characters in order to see whether these can improve the definition of the species or a higher taxon. Evidently, there can be no precise procedure to this kind of approach. Recent studies of ahermatypic corals reveal many taxonomic characters useful at different levels: some new and others already known to earlier authors but subsequently neglected.

#### Attachment Structures

The nature and structure of the base of a scleractinian, whether free or attached, simple or consolidated, may be useful taxonomically at the level of species, species group, genera, or higher taxa.

Durham's (1949) considerations of the type of ontogenetic development recorded in the base of the corallum has received the attention it deserved only recently (Cairns, 1978, 1979; Zibrowius, 1980). Durham distinguished between two types which he considered significant taxonomic characters: monocyclic development by simple conical enlargement of the prototheca to form the adult corallum, and polycyclic development by growth through successive stages of concentric overlapping thecal rings which takes place before the adult corallum is formed by conical enlargement of the most peripheral post-embryonic thecal wall.

Up to now, one or the other type of development has typically been demonstrated in different species. The complex situation in *Caryophyllia* suggests, however, that it can not always be taken as a generic character. In fact, the type species, *Caryophyllia cyathus* (Ellis & Solander 1786), has a monocyclic base reinforced by exterior stereome, the well-known *C. smithii* Stokes & Broderip, 1828, has a polycyclic base more or less reinforced by exterior stereome, and many deep-



water species like *C. ambrosia* Alcock, 1898, and *C. sequenzae* Duncan, 1873, have a monocyclic base without any reinforcement.

Generally many bathyal species typical of soft bottoms are monocyclic, without consolidation of the base. They settle on small unstable objects (such as pteropod shells) from which they detach at an early stage, continuing their growth as completely free individuals. This is the case in various species of the genera *Caryophyllia*, *Stephanocyathus*, and *Flabellum*.

Cairns (1978) demonstrated that in some species the corallite base increases in diameter by adding exothecal dissepiments over raised costae, thereby producing concentric rings of partitioned chambers. The resulting concentric rings resemble the thecal rings of polycyclic development, but are structurally and ontogenetically different, since they are formed much later in development and not developed from overlapping thecal walls.

In the family Flabellidae, attention to the structure of the base (mostly monocyclic) turned out to be useful for the distinction of genera (Zibrowius, 1974b, 1980; Cairns, 1979). In *Flabellum* the corallum arises from the simple initial skeleton (prototheca) without exterior reinforcement of any kind. In *Monomyces* (= *Rhizotrochus*) the attachment is consolidated by additional stalk-like rootlets not fused to the pedicel. In *Polyomyces* Cairns, 1979, the attachment is consolidated by rootlets fused along the pedicel. In *Javania* the base is consolidated by concentric layers of stereome. In *Platocrochides* the base is similar to that in *Javania*, but the genus is distinguished by transverse fission.

Within the large genus *Flabellum* young stages belonging to the group of *F. pavoninum* Lesson, 1831, are characterized by a pedicel with only 6 septa arising from the lowermost level (prototheca), whereas in forms more closely related to *F. curvatum* Moseley, 1881, and *F. inconstans* Marenzeller, 1904 (the latter characterized by transverse fission) 12 septa are present at the lowest level.

Attached stages are entirely unknown in various groups where the base does not show the slightest trace of former attachment, even at the youngest age (*Fungiacyathus*, *Stephanophyllia*, some *Deltocyathus* spp., and most Turbinoliinae). This suggests that the planula larva metamorphoses in the benthic stage with a skeleton without needing any substrate to settle on. For the distinction of two otherwise similar and previously confused species of *Flabellum*, such a detail has been decisive: The southern hemisphere *Flabellum apertum* Moseley, 1876, is originally attached to a substrate by a short and cylindrical pedicel and generally becomes

free early in ontogeny. On the contrary, no trace of attachment could ever be found even in the youngest and smallest stages of the North Atlantic *Flabellum angulare* Moseley, 1876.

#### Spatial Relationships of Calicular Elements

Spatial relationship of calicular elements, such as the relative exsertness and length of different cycle septa (extension from the wall towards the columella) and the width of the pali has proved particularly useful for the distinction of species in *Caryophyllia*, especially when combined with various other characters.

For example, in various species the septa of different cycles are progressively less exsert and smaller, whereas in others (in the case of 4 cycles of septa) the quarteraries equal in size the paliferous tertiaries and are even more exsert, being more closely associated with the primaries and secondaries. The precise number of septa is often of minor interest, being subject to rather great variation in some species. However, it is fairly constant in others.

In the genus *Deltocyathus* various living species have now been distinguished (Cairns, 1979; Zibrowius, 1980) from the Miocene *D. italicus* (Michelotti, 1838). The latter, which is the type species of the genus, had been considered by previous authors to persist in the present fauna and to be highly polymorphic, cosmopolitan, eurybathic and eurythermic (reported from tropical reef lagoons as well as from abyssal depths!). A cup-shaped or conical free corallum is not a sufficient character for referring a species to the genus *Deltocyathus*. Valuable new characters which can be used are the successive development of different cycle septa and their junctions, relative size and arrangement of costae, and absence or presence of a basal scar. The latter detail leads to the hypothesis that in some species of *Deltocyathus* the free cup-shaped corallum corresponds to the "anthocyathus" stage of the free-living *Fungia*, detached by transverse fission from an attached still unknown "anthocaulus" stage, following Wells' (1966) terminology.

#### Septal Ornamentation

Septal ornamentation may provide a taxonomic character useful for the definition of species. Generally the lateral faces of the septa are covered by distinct, roughly conical granules formed by the horizontal growth of strongly diverging trabecular elements (Wells, 1956). As noted by Zibrowius (1980), some extant species belonging to the genera *Caryophyllia*, *Paracyathus* and *Sclerhelia* possess horizontal ledge-like to basket-like outgrowths (upper side concave) on the septa which resemble the pennular structures described

from Mesozoic and Cenozoic corals (Gill, 1967; Gill and Russo, 1980). For example, *Caryophyllia alberti* Zibrowius, 1980, from the Azores, is rather similar to the northeastern Atlantic and Mediterranean *Caryophyllia calveri* Duncan, 1873, in the spatial relationships of calicular elements but is distinguished by its well formed pennula-like septal ornamentation.

#### Asexual Reproduction

The type of asexual reproduction can be a good diagnostic feature in ahermatypic scleractinians, as illustrated by the following examples from Zibrowius (1980).

*Flabellum macandrewi* Gray, 1849, is morphologically similar to *Flabellum alabastrum* Moseley, 1873, but is characterized by splitting easily into longitudinal pieces, each of which regenerates a new individual.

Besides morphological features, transverse fission can be retained as a character distinguishing *Peponocyathus folliculus* (Pourtales, 1868) from the other Atlantic species, *Peponocyathus stimpsonii* (Pourtales, 1871).

The northeastern Atlantic and Mediterranean *Sphenotrochus andrewianus* Milne Edwards & Haime, 1848, reproduces asexually by opposite budding from the base, followed by separation. This does not appear to be a common feature in the genus *Sphenotrochus* and should be taken into account at the species level.

A particular type of budding is characteristic of the extant Atlantic and Indo-Pacific species referred to the genus *Asterosmilia* Duncan, 1868: small individuals are formed in the edge zone and fall off the parent, generally at an early stage. The resulting easily recognizable scars are highly diagnostic, even on dead fragments found in the sediments.

#### CONCLUSIONS

In contrast to statements made in previous works, high levels of intraspecific variation occur in ahermatypic corals and must be taken into account in species definition.

As is the case for reef-building zooxanthellate corals, good taxonomy in ahermatypic taxa requires abundant specimens to measure variation through a wide ecological and geographic range.

Good taxonomy in ahermatypes also requires, in many cases, the description of new or previously neglected characters such as attached or free early stages, monocyclic or polycyclic basal structure, type of reinforcement of the base, adventive attachment structures, and asexual reproductive mode as well as the width of successive septal cycles and the spatial relationships of various calicular elements.

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SUBJECTIVITY IN THE EVALUATION OF DIAGNOSTIC CHARACTERS  
AND ITS INFLUENCE ON THE TAXONOMY OF THE RUGOSE CORALS

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ABSTRACT

A numerical objective technique for comparing pairs of genera in the Suborder Metriophyllina Spassky, is illustrated. Pairs are ranked as closely related when they score highly in points assigned either for having selected morphological characters in common (Evaluation 1) or for sharing different variations of such characters which are given fractions of points according to whether they are universal, dominant, common or rare variants (Evaluation 2). Although this technique may help to eliminate subjectivity in taxonomy the arbitrary selection of characters to define a given taxonomic rank is shown to produce artificial groups. Only characters which are precisely known and correlated with corallite growth stage possess real value for taxonomy.

A more natural classification will only be attained when ontogeny, microstructure of septa, morphology of calices and morphogenesis and composition of basal and radial elements are described.

INTRODUCTION

The present paper is a by-product of the detailed analysis of taxa included by Hill (1981) in the suborder Metriophyllina Spassky, 1965. The full analysis is too extensive to be included here and is published separately (Fedorowski, in press). However, I present here some conclusions based on that analysis which seem to be rather general in character, and applicable to most studies of Rugosa. The object of this paper is to show that assigning morphological characters a taxonomic rank value and applying it mechanically to define rugosan taxa does not work and leads to highly subjective groupings. In particular, some morphological characters, e.g., "minor septa," "split septa" and "septal carinae" are often derived in different ways and on different septa among rugosans so that applying them to define taxonomic categories often brings together genera which are otherwise not closely related. Also morphological features must be compared between taxa when they are at the same ontogenetic stage. This paper outlines an 'objective' numerical technique for evaluating the similarity of genera in the suborder Metriophyllina using data of the kind widely utilized in published works on rugosan taxonomy. In particular, the subfamily Sutherlandinina, Weyer 1972, is examined, using the same technique, and shown to be a subjective 'artificial' grouping. It is proposed that a wider variety of factors must be evaluated for each taxon before good taxonomy can be achieved. These factors are discussed below.

METHODS

The number of genera included in the suborder Metriophyllina Spassky of Hill (1981) is so large that for the purposes of this numerical analysis, I arbitrarily removed the families Hadrophyllidae Nicholson, 1889;

Kielcephyllidae Rozkowska, 1969; and Combophyllidae Weyer, 1975. I also excluded the taxa considered by Hill (1981, pp. F204–F205) as "Uncertain" and

Table 1.—Characters of genera of Sutherlandininae, Weyer, 1972.

Character	Genera
<b>1. MAJOR SEPTA</b>	
a. Aulos	5, 27 (major).
b. Permanently meet axially	9.
c. Temporarily withdrawn from axis and free	22 (some), 27 (rare).
d. Permanently withdrawn from axis and free	20, 22 (some).
<b>2. CARDINAL SEPTUM</b>	
a. Equals major septa	5, 9, 20, 22 (some), 27 (rare).
b. Slightly elongated	22 (some), 27 (major).
c. Slightly shortened	22 (temporary in some).
<b>3. COUNTER SEPTUM</b>	
a. Equals major septa	5, 20, 22 (some), 27 (rare).
b. Slightly elongated	22 (rare), 27 (major).
c. Shortened	5, 22 (rare).
<b>4. MINOR SEPTA</b>	
a. Contratingent	5, 9, 22 (some), 27.
b. Contraclined	20, 22 (some).
<b>5. CARINAE</b>	
a. Present	5, 9.
b. Absent	20, 22, 27.
<b>6. EXTERNAL WALL</b>	
a. Thick	5, 9, 27 (some).
b. Thin	20, 22, 27 (some).

Key to Tables 1 and 2.—1, *Amplexocarinia*; 2, *Alleynia*; 3, *Barrandeophyllum*; 4, *Bitraia*; 5, *Boolelasma*; 6, *Duncanella*; 7, *Gorizdronia*; 8, *Gymnaxon*; 9, *Haptophyllum*; 10, *Kabakovitschiella*; 11, *Laccophyllum*; 12, *Lindstroemia*; 13, *Metriophyllum*; 14, *Metrionaxon*; 15, *Metrioplexus*; 16, *Nalivkinella*; 17, *Neaxon*; 18, *Neaxonella*; 19, *Paralleynia*; 20, *Pedderelasma*; 21, *Petraia*; 22, *Petraiella*; 23, *Petronella*; 24, *Protozaphrentis*; 25, *Saucrophyllum*; 26, *Schindewolfia*; 27, *Sutherlandinia*; 28, *Syringaxon*; 29, *Trochophyllum*.

Table 2.—Characters of selected genera of *Metriophyllina* Spassky, 1965.

Character	Genera
<b>1. MAJOR SEPTA</b>	
a. Aulos	1 (some), 2–5, 6 (?), 8, 11, 14, 17, 18, 19, 24–29.
b. Permanently met axially	9, 12, 13 (major), 21 (major), 23 (some).
c. Temporary withdrawn from axis and free	1 (some), 13 (rare), 21 (rare), 22 (some), 23 (some).
d. Permanently withdrawn from axis and free	7, 10, 15, 16, 20, 22 (some).
<b>2. CARDINAL/SEPTAL/FOSSULA</b>	
a. Present	15, 18, 19.
b. Absent	Other taxa.
<b>3. CARDINAL SEPTUM</b>	
a. Equal other major septa	1–6, 7 (major), 8–14, 16 (major), 17, 20, 21, 22 (some), 23, 24, 25, 26 (major), 27 (major), 28.
b. Slightly elongated	8, 22 (some), 26 (rare), 27 (rare).
c. Differently shortened	7 (rare), 15, 16 (rare), 18, 19, 29.
<b>4. COUNTER SEPTUM</b>	
a. Equal major septa	1, 2, 3 (some), 4–8, 10–21, 22 (some), 23, 25, 27 (some), 28, 29.
b. Slightly elongated	3 (some), 22 (rare), 24, 26, 27 (some).
c. Differently shortened	9, 22 (rare).
<b>5. MINOR SEPTA</b>	
a. Contratingent (+ amalgamate)	2–6, 8, 9, 11, 12, 21, 22 (some), 23–28.
b. Contraclined	10, 20, 22 (some).
c. Triad only	15.
d. Short, radial	1, 7, 13, 14, 16, 17, 18, 19, 29.
<b>6. SPLIT OF MAJOR SEPTA</b>	
a. Present	5, 9, 20, 21 (some?), 22 (some), 27 (major).
b. Absent	1–4, 6, 7, 8, 10–19, 21 (some?), 22 (some), 23–26, 27 (rare), 28, 29.
<b>7. CARINAE AND SIMILAR STRUCTURES</b>	
a. Present	4, 5, 6, 9, 13, 14, 15.
b. Absent	Other taxa.
<b>8. EXTERNAL WALL</b>	
a. Thick	5, 6, 9, 14.
b. Thin	Other taxa.
<b>9. BIFORM TABULARIUM</b>	
a. Present	2–5, 9, 10, 11, 20, 22, 25–28.
b. Absent	Other taxa.

“Doubtfully assigned to *Metriophyllina*” and the columnate and dissepimentate genera. Such a selection is certainly subjective and one can easily demonstrate the relationship of some excluded taxa to the analyzed ones

Table 3.—Frequency response of pairs of genera of *Sutherlandininae* Weyer, 1972.

Evaluation		Evaluation		Pairs of genera
Table 1		Table 2		
1	2	1	2	
6	4¼	9	6½	<i>Pedderelasma/Petraiella</i>
5	2¼	10	6¾	<i>Petraiella/Sutherlandinia</i>
4	4	7	7	<i>Boolelasma/Haptophyllum</i>
4	2¼	7	6	<i>Boolelasma/Sutherlandinia</i>
4	2	7	5¾	<i>Pedderelasma/Sutherlandinia</i>
3	1¾	5	3	<i>Boolelasma/Petraiella</i>
3	1¼	5	3	<i>Haptophyllum/Petraiella</i>
2	2	4	4	<i>Boolelasma/Pedderelasma</i>
2	1¼	4	3½	<i>Haptophyllum/Sutherlandinia</i>
1	1	3	3	<i>Haptophyllum/Pedderelasma</i>

but this procedure does not affect the purpose of the article and does not change the conclusions.

Using a list of morphological characters considered important in the Suborder *Metriophyllina* (Table 2), two kinds of evaluation were made: Evaluation 1 scored 1 point for each occurrence of a character in a given taxon; this was independent of the variability of the character. Evaluation 2 awarded points in accordance with the variability of a character as follows: 1 point for a constant character; ¾ point for the dominant variant; ½ point for the more or less equally represented variants; ¼ point for a minor variant. In both evaluations, taxonomic rank of characters was not graded. Single occurrence of a character in a taxon was not counted in spite of its possible taxonomic value.

An analysis was made to select the most similar and the most dissimilar pairs of genera. The analysis first involved establishing a set of morphological features to be used in the comparison of taxa. All genera occurring in a given character class (Table 2) were compared to each other and either one point (Evaluation 1) or the smaller point value of the two genera (Evaluation 2) was assigned to the given pair of genera (Table 4). After applying the criteria as indicated, only Evaluation 2 scores of more than 7 points (Tables 2 or 4) or 4 points (Tables 1 and 3) were considered to show close similarity of pairs.

Lack of data for some or many generic type species made it necessary to delete from the tables the following important characters: presence or absence of a cardinal, tabular fossula; the insertion and increase of major and minor septa in early ontogeny; the stage of growth of a specimen at the moment of the first appearance of minor septa inside its lumen; the morphology of calices; and the microstructure of septa.

Although this greatly reduces the taxonomic precision of this analysis it does reflect the level of information upon which much current rugosan taxonomy is based.

Table 4.—Frequency response of pairs of genera of Metriophyllina, Spassky, 1965 (note that Evaluation 1 and 2 of Sutherlandinae are given in Table 3).

Evaluation		Pairs of genera	
1	2		
10	8¾	<i>Barrandeophyllum/Sutherlandinia</i>	
10	7½	<i>Schindewolfia/Sutherlandinia</i>	
10	6¾	<i>Petraiaella/Sutherlandinia</i>	
9	9	<i>Alleynia/Laccophyllum</i> <i>Alleynia/Saucrophyllum</i> <i>Alleynia/Syringaxon</i> <i>Barrandeophyllum/Syringaxon</i>	<i>Laccophyllum/Syringaxon</i> <i>Laccophyllum/Saucrophyllum</i> <i>Saucrophyllum/Syringaxon</i>
9	8½	<i>Amplexocarinia/Neaxon</i>	<i>Barrandeophyllum/Laccophyllum</i> <i>Barrandeophyllum/Saucrophyllum</i>
9	8¾	<i>Alleynia/Barrandeophyllum</i>	
9	8	<i>Gorizdronia/Nalivkinella</i> <i>Gymnaxon/Neaxon</i>	<i>Gymnaxon/Petronella</i> <i>Gymnaxon/Protozaphrentis</i>
9	7½	<i>Alleynia/Sutherlandinia</i> <i>Laccophyllum/Sutherlandinia</i> <i>Saucrophyllum/Sutherlandinia</i>	<i>Gymnaxon/Sutherlandinia</i> <i>Syringaxon/Sutherlandinia</i>
9	6½	<i>Kabakovitschiella/Petraiaella</i>	<i>Pedderelasma/Petraiaella</i>
8	8	<i>Alleynia/Bitraia</i> <i>Alleynia/Gymnaxon</i> <i>Bitraia/Saucrophyllum</i> <i>Bitraia/Syringaxon</i> <i>Duncanella/Metrionaxon</i>	<i>Gymnaxon/Laccophyllum</i> <i>Gymnaxon/Saucrophyllum</i> <i>Gymnaxon/Syringaxon</i> <i>Kabakovitschiella/Pedderelasma</i> <i>Neaxonella/Trochophyllum</i>
8	7¾	<i>Amplexocarinia/Gorizdronia</i> <i>Amplexocarinia/Nalivkinella</i> <i>Gorizdronia/Neaxon</i> <i>Nalivkinella/Neaxon</i>	<i>Barrandeophyllum/Schindewolfia</i> <i>Laccophyllum/Schindewolfia</i> <i>Saucrophyllum/Schindewolfia</i> <i>Syringaxon/Schindewolfia</i>
8	7	<i>Alleynia/Schindewolfia</i> <i>Gymnaxon/Schindewolfia</i>	<i>Metriophyllum/Metrionaxon</i> <i>Metriophyllum/Neaxon</i>
8	6½	<i>Bitraia/Sutherlandinia</i>	<i>Protozaphrentis/Sutherlandinia</i>
8	6	<i>Alleynia/Petraiaella</i> <i>Barrandeophyllum/Petraiaella</i> <i>Laccophyllum/Petraiaella</i>	<i>Saucrophyllum/Petraiaella</i> <i>Syringaxon/Petraiaella</i>
8	5¾	<i>Petraiaella/Schindewolfia</i>	
8	5½	<i>Gymnaxon/Petraiaella</i>	<i>Petronella/Petraiaella</i>
8	5¼	<i>Petraia/Petraiaella</i>	

## ANALYSIS OF RESULTS

The results show that 44 pairs of genera show high levels of similarity (more than 7 points in Table 4). How reliable are these measures for good taxonomy?

Morphological characters must be described in detail and their differentiation during ontogeny clearly understood if their taxonomic evaluation is to be accurate. For instance, the introduction of the character class "Carinae and similar structures" to Table 2 brings such genera as *Boolelasma*, *Haptophyllum*, *Bitraia*, *Metriophyllum*, *Metrionaxon* closer to each other by one full point. But in *Haptophyllum* and possibly also in *Boolelasma* these structures are septa-like plates, in *Metriophyllum* and *Metrionaxon* they are metriophylloid

carinae, and in *Bitraia* they are the yard-arm or zig-zag types. Each of these structures is morphogenetically different and has different taxonomic value. They were introduced here, as a single character class on purpose, because the term "carinated septa" remains a commonly used expression in the literature. There is quite commonly no further description of this character, although it may have a large value for taxonomy in some instances, or may be hardly used on the species level in others.

The character class "Minor septa," although subdivided in Tables 1 and 2, also does not appear to be appropriate when examined more closely. The subclass "Triad only" (Table 2), commonly used in descriptions

of taxa, exemplifies the value of the proper evaluation of a character. We may interpret it either as a structure newly evolved from a taxon with short septa (*Metriophyllum* in this case) or as a rudiment left in ontogeny (of *Metrionaxon* for instance) after the contratingency of other minor septa was already eliminated. Only with the recognition of such relationships as these can valid families be identified.

Comparison of characters in relationship to the ontogenetic stage of growth should be discussed in a similar context. *Protozaphrentis* Yu, 1957, exemplifies two aspects of this problem. First, the cardinal septum of this genus may be described as either longer than, or equal to other major septa, or slightly shortened. The choice depends on the arbitrary decision of which part of the corallite we consider most typical. Second, if the original statement that tabulae are lacking in this genus is correct, we are dealing only with a calice, which immediately brings in two other problems: a) if different lengths of the cardinal septum depend on the growth stage of the coral, then in *Protozaphrentis* it might have been elongated in the middle part of the calice if the coral had continued its development long enough; b) if differences in the length of the cardinal septum were genetically determined in accordance with the stage of growth, then only the stage with the shortened cardinal septum may be considered fully mature and, as such, used for comparison. In addition, such

a corallite can be compared only with calices, not with sections beneath calices of corallites of other genera. My recent study of etched calices of Permo-Carboniferous corals from S.W. Texas, U.S.A., shows that the most important morphological changes may take place on, or just above a calice floor. There are corals, for instance, that have only very short minor septa on a calice wall, while on the bottom of the calice and beneath the calice these septa are long and contratingent.

As is common in the rugose corals, there are also examples of the opposite situation, *i.e.*, where calices are of no use for generic and family determination. Two genera from the Texas Permian (Fig. 1) have a similar morphology in mature portions of growth, but this resulted from totally different early ontogenies.

Examples similar to the cited ones are surely present in several, if not in all higher taxa of rugosans. They are mentioned here to illustrate the thesis that only the characters that are clearly placed in the ontogeny of a given taxon are useful for comparisons. It is a truism that location of a character in a given growth stage of an individual specimen, or the lack of some characters in the specimen means nothing until we determine what stage of growth is represented by the investigated specimen itself.

#### ANALYSIS OF THE SUTHERLANDININAE

Given the general reservations about the significance of similarity between genera based upon morphological characters in the above analyses and the absence of several important taxonomic characters, I wished to find out whether an analysis based on this technique using only the available data would be adequate to recognize the artificiality of a taxon of subfamilial rank. I selected for this purpose the subfamily Sutherlandininae Weyer, 1972, synonymized by Hill (1981) with the Laccophyllinae Grabau, 1928. The morphologic features used for analysis of this taxon are listed in Table 1.

When analyzed by Evaluation 2 from criteria in Table 1 only two pairs of genera, *Boolelasma/Haptophyllum* and *Pedderelasma/Petraiaella*, score 4 or above.

This seems to indicate firstly that *Boolelasma/Haptophyllum* are not closely comparable to any other members of the subfamily on any analysis, which may be due to their relative isolation in the Australian province during Early Devonian time. *Pedderelasma* and *Petraiaella* belong to the Western European Province but the incompletely known, stratigraphically much older *Pedderelasma* shows details of morphology that are not known later. It seems easier to accept iterative evolution in this case rather than close evolutionary linkage to explain the high similarity scores, and in

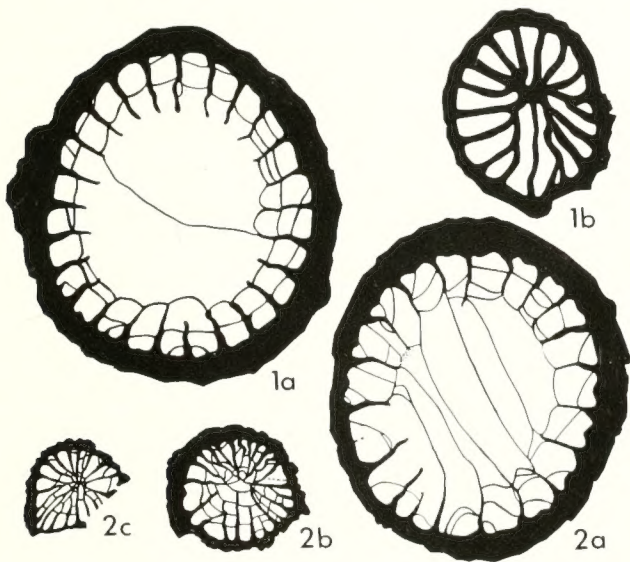


Figure 1.—Transverse sections showing common morphology in mature portions of two genera with different ontogenies. 1. New genus 1; a, mature portion,  $\times 5$ ; b, neanic portion,  $\times 7$ . 2. *Paraduophyllum* Wu and Zhou, 1982; a, mature portion,  $\times 5$ ; b, c, successive sections of the neanic portion,  $\times 7$ . Both species are from the Permian of Texas. See text discussion.

any case scores based on characters in Table 2 show that they fall below 7 points in similarity for Evaluation 2. Lastly, the case of *Petraia* and *Sutherlandinia*, which shows fairly high similarity with Evaluations 1 and 2 when compared on data from Table 2, appears to be a consequence of high variability causing a taxon to score with several variants of a character and thus enter into several relationships.

It seems therefore that this analysis demonstrates the artificiality of the present grouping of the above five genera into the Sutherlandiniinae. This leads us to question the criterion used to define the Sutherlandiniinae.

The genera all possess a biform tabularium, but as is shown in Table 2 there are at least 13 genera of the 29 analyzed that possess this character and several are not included in the Sutherlandiniinae. All of them possess split peripheral parts of some major septa. However, in *Haptophyllum* and *Pedderelasma* (genera indicated above as being distant), only the counter septum is split; in *Sutherlandinia* the cardinal, counter and the counter-lateral minor septa are split (or none if *Petraia? squarrosa* Sutherland, 1965, is included in this genus; see below); in *Boolelasma* the same septa plus the counter-lateral septa are split. Such variable occurrence of a subfamily character, with no stratigraphic sequence in the appearance of individual variants, appears to be either random or artificially grouped and, in fact, this is the case. In contrast to Weyer (1972), Hill (1981) evaluated the split of some major septa as having only generic value. She located members of the Sutherlandiniinae in either the Petraiidae de Koninck, 1872 or Laccophyllinae Grabau, 1928. This placing, however, was not less subjective than that of Weyer, because it was only supported by a higher ranking of different characters. It thus seems that such a simple analysis as has been described can demonstrate subjectivity in taxonomy. It may also offer some indications of the more or less close similarity of genera. It will not identify synonyms, however. This may properly be done when individual characters are objectively graded in their taxonomic value.

#### DISCUSSION

Besides the dangers of confusing several different features under one character heading and of comparing characters from different ontogenetic stages, which I discussed above, other factors must also be brought into the analysis if a natural classification is to be achieved. It would seem important to distinguish between those variations which are on the decline and those which are new and evolutionarily significant. This is a difficult, but the only procedure leading toward a natural systematics.

Also, when large collections are available for study it may be that a small proportion of the specimens (5% or less) differ from the rest only in a single morphologic feature which, however is the one used to define the taxa being studied. For example, *Sutherlandinia arbucklensis* in this analysis showed 10 specimens out of more than 200 which have no split of the peripheral portions of the major septa, a feature which allowed Sutherland (1965) to place these 10 specimens in *Petraia? squarrosa*, and to include them in a distinct family.

In the case of *Sutherlandinia arbucklensis* and *Petraia? squarrosa* the peripheral split of septa appears to represent the retention of the older feature. This determines *Petraia? squarrosa* as very closely related to *Sutherlandinia arbucklensis*, although a variety of possibilities exists to explain this; the population of 10 specimens represents: 1) a small, isolated species, 2) a subspecies, 3) an ecophenotypic variant. If the given character is qualitatively new, it may represent the initiation of a new evolutionary line and its bearer should be distinguished on a high level of the classification. Thus it is difficult to conceive of any satisfactory taxonomic analysis which systematically and mechanically places equal weight on the presence or absence of any morphological characters or indeed on different variations within one character given the nature of the morphologic plasticity of living organisms.

#### CONCLUSIONS

A study of Tables 1 through 4 suggests that a comparison of taxa using only the presence or absence of certain morphological characters has a rather restricted value in good systematics.

In order to achieve data which are satisfactory for developing a 'natural' classification a wide variety of morphological features should be used, which incorporate comparisons based on similar stages of development in ontogeny and astogeny, microstructure of the septa, and where possible, an understanding of the morphogenesis of horizontal and radial skeletal elements.

In addition, possible convergence or divergence of morphological features due to factors such as homeomorphy, iterative evolution, varying evolutionary rates as well as vicariance and dispersal factors should be evaluated as an intrinsic part of the taxonomic method.

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INTRASPECIFIC VARIATION OF SEPTAL ARRANGEMENT AND  
NUMBERS IN A FOSSIL SOLITARY SCLERACTINIAN  
CORAL AND ITS GENETIC IMPLICATION

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ABSTRACT

Intraspecific morphological variations in a Pleistocene solitary coral, *Caryophyllia (Premocyathus) compressa* (Yabe and Eguchi), were investigated based on 1090 specimens collected at a single locality. The fossil population shows large variations in skeletal features. 1) Nine different septal arrangements, hexameral to decatetrameral, are recognized, with specimens having a decameral plan predominating. Hexameral and dodecameral plans can be distinguished from each other by septal sizes and the position of pali. 2) Septal numbers are genetically determined. Even if the last cycle of septa in a given specimen is "incomplete," it is considered to be a mature form. 3) Pali are in one crown, but their numbers are different from specimen to specimen, being intimately related to insertion of last cycle septa. Some mature specimens, however, lack pali. 4) Many specimens do not show bilateral symmetry owing to their septal arrangement or the position of the last cycle of septal insertion. The results indicate that many septal and related skeletal features are genetically controlled and several criteria hitherto used for specific or generic distinction should be carefully reconsidered.



SECTION 2  
INVITATIONAL SYMPOSIUM

**Late Precambrian and Early Paleozoic  
History of Cnidarians**

Organized, Convened and Edited  
By

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INTRODUCTION

COLIN T. SCRUTTON

There is a compelling fascination in the search for origins and relationships in the organic world. The evidence we have to work on is usually fragmentary, often tantalizingly incomplete in the fossil record even for organisms with skeletons, and even more drastically reduced for the period preceding the acquisition of hard skeletal parts. Other lines of evidence, from the biology of living relatives, are indirect and, in the case of most invertebrates, some 600 to 700 Ma distant. However, the data base is constantly improving with new discoveries and new techniques, in part stimulated by earlier phylogenetic speculation and in turn fostering new scenarios. For the Cnidaria there is the added interest that the body fossil record goes back further in time than for almost all other animal phyla.

This collection of papers represents all facets of this area of research, from reviews of current ideas on phylogeny to the presentation in detail of new and important information. The invited contributions were intended to be broad summaries of various aspects of early cnidarian evolution. Thus the latest work on the famous Ediacaran fauna and its stratigraphic setting is reviewed (Jenkins) and illustrates that the Cnidaria underwent a major radiation prior to the Cambrian. Of the contentious frondose fossils, some are considered octocorals whilst others probably represent an unrelated and extinct phylum of organisms. This Precambrian event preceded by some 100 Ma the appearance and diversification of the two main skeletonized cnidarian groups of the Paleozoic, the Tabulata (Scrutton) and Rugosa (Neuman). However, there is

an increasing number of coralline fossils known from the Cambrian, which are largely of uncertain affinities (Jell). Some may be anthozoan but none so far is accepted as a direct ancestor of either the rugose or the tabulate corals. Also no direct relationship between these two groups is envisaged, at least among Ordovician forms secreting a skeleton. The Tetradiida seem not to be closely related to the rest of the Tabulata, which are considered to be monophyletic. For the rugose corals, a new division is proposed of equal rank to the streptelasmatids and columnariids, and these also are considered monophyletic although the relationships of the Calostylidae are uncertain.

In terms of the origins of the cnidarian classes, the fossil evidence does little more than show that all three were already present in the late Precambrian. One approach to these fundamental relationships is through a biomechanical analysis of cnidarian soft-body construction (Grasshoff). Given the likely construction of a primitive metazoan ancestor, the adoption of a sessile mode of life is seen as a key step for the evolution of the Cnidaria. Evolution of a hydrostatic body system led to the anthozoan polyp as the ancestral cnidarian. The Scyphozoa evolved from the Anthozoa and ultimately, the Hydrozoa from the Scyphozoa, through changes in body plan largely consequent upon the refinement of different methods for the production of medusae.

Among the other contributions, an account of recent discoveries in the Precambrian of China extends our knowledge of the Ediacaran fauna (Wang *et al.*). Some

Phanerozoic non-coralline cnidarians are also discussed. The Ordovician medusaemorph *Conchopeltis* may be a chondrophore or a scyphozoan, or even a member of a separate cnidarian class rather than a conulariid (Oliver). There is also the probability that putative monoplacophorans placed in *Scenella* and *Macroscenella* should in fact be assigned to the Chondrophora (Yochelson), although positive evidence one way or the other is difficult to establish. Four additional papers are concerned with corals. Some of the problems associated with the pre-Ordovician ancestry of the Tabulata and Rugosa are reviewed (Iwanowski), which suggests the need for a more critical examination of the Cambrian gastroconids. Valuable new observations on the type species of what may be the earliest tabulate coral genus (*Lichenaria*) are described (Laub). Lower Ordovician species assigned to this genus clearly need revision. Finally, two papers outline important revisions and redescriptions of Ordovician tabulate coral faunas. It now appears that the Heliolitida evolved and diversified first in eastern Australia, where critical steps in the development of different coenenchymal structures can be demonstrated (Webby and Kruse). British Ordovician tabulate coral faunas are also revised and show provinciality in the Ashgill with Scot-

tish faunas of American aspect and English and Welsh faunas of European aspect (Yang). Caradocian tabulate coral faunas, however, appear to show no distinct provincialism.

There is clearly still much to be done in establishing and clarifying Ordovician coral phylogenies and in refining our ideas on the broader problems of cnidarian class relationships. Hopefully these contributions provide new data and new ideas which will stimulate further researches throughout this wide and interesting field.

#### ACKNOWLEDGMENTS

It is a pleasure to acknowledge secretarial and drafting assistance during editing from Miss E. Walton and Miss C. Jeans (University of Newcastle upon Tyne). I am also grateful to Professor R. B. Clark (University of Newcastle upon Tyne), Dr. O. A. Dixon (University of Ottawa), Dr. R. J. Elias (University of Manitoba), Dr. R. J. F. Jenkins (University of Adelaide), Dr. R. S. Laub (Buffalo Museum of Science) and Dr. K. M. Towe (Smithsonian Institution, Washington) for providing technical reviews of the papers published in this section.

## INTERPRETING THE OLDEST FOSSIL CNIDARIANS

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## ABSTRACT

Fossil remains of soft-bodied metazoans characteristic of the Ediacaran Period (~590 Ma to 2545–540 Ma) are known from more than twenty world localities. About 70% of these fossils may represent cnidarians; the remainder consist principally of annelids, several kinds of arthropods, and various problematica.

Problematic discoidal markings showing little internal detail occur in the Early Ediacaran and are common in the type Ediacara assemblage; they may reach 70–80 cm in diameter. Discoidal imprints showing ordered concentric and radial structures appear late in the Early Ediacaran; study of selected forms in conjunction with modern material suggests that some were porpitiid chondrophores with fragile floats. Rare examples of bilateral chondrophores occur in the Late Ediacaran. Other medusoids with ordered internal structures probably represent scyphozoans, while the bell-shaped *Kimberella quadrata* (Glaessner and Wade) appears to be an early cubozoan.

Chance preservation of complete organisms and certain trace fossils show that various stalked discs are actually holdfasts of frond-like fossils, such as *Charniodiscus* Ford. Frond-like fossils exhibit several degrees of structural complexity. Some may be compared to modern pennatulaceans; others comprise a primary stolon or initial polyp and multiple fronds. Forms consisting of chambered vanes (e.g., *Pteridinium* Gürich) and related sack-shaped organisms (e.g., *Ernieitta* Pflug) do not resemble known cnidarians and probably represent a separate phylum.

## INTRODUCTION

## Geological Occurrence and Faunistic Association

Fossil remains of soft-bodied metazoans of sub-Cambrian age are known at more than 20 localities in the world (cf. Glaessner, 1979, fig. 2). The best documented occurrence is in the Flinders Ranges, South Australia, where about 40 kinds of animal remains and a dozen different trace fossils characterize a thin interval towards the base of the Rawnsley Quartzite, the upper formation of the Pound Subgroup (Jenkins *et al.*, 1983). I have formally proposed that the rocks including these fossils represent an Ediacaran System and Period, with a stratotype at Bunyeroo Gorge, central Flinders Ranges (Jenkins, 1981; Gostin and Jenkins, 1983). Broadly parallel, but different opinions as to possible time-rock divisions in the Flinders Ranges have also been put forward (Cloud and Glaessner, 1982; Harland *et al.*, 1982). Metazoan assemblages predating or including *Charnia* Ford, 1958, may be considered as belonging to an Early Ediacaran Epoch; the type Ediacara assemblage and closely similar assemblages characterize the Late Ediacaran (Jenkins, 1981, 1983). The place name "Ediacara" is Aboriginal in origin and from the dialect of the 'Kujani Tribe; it is a word combination, possibly *iltya-kara* or *itya-jakara*, meaning 'vein-spring,' or more loosely translated, 'vein-like spring of water.'

On the basis of a review of radiometric data, Jenkins (1983) concluded that the fossiliferous Ediacaran rocks of Newfoundland and Western Europe are dated between approximately 590 Ma and about 565–560 Ma. Early Cambrian shelly assemblages in these regions

postdate a significant tectonic event, with orogenic uplift and formation of thick molassic sequences. The tectonic event is associated with metamorphism and intrusion at ~565 to ~550 Ma. Presuming that the molassic sequences are largely post-tectonic, the start of the Cambrian is probably not earlier than about 545–540 Ma.

Though statistics are available only for the assemblage from the Rawnsley Quartzite (e.g., Cloud and Glaessner, 1982) it appears that about 70% of the body-fossil imprints from Ediacaran rocks represent cnidarians; the remainder consist of distinctive kinds of worms, several sorts of arthropods, and various problematica. The cnidarians are discussed in numerous works, chief among which are studies by Glaessner and Wade (1966), Wade (1968, 1969, 1971, 1972), Glaessner (1979), Scrutton (1979) and Fedonkin (1981). The remains are often of large size, with medusoids, creatures resembling sea pens and worms approaching 1 m in maximum dimension. The assemblages are of marine aspect and considering the diversity of taxa and the size which some forms attain, the waters in which they lived were probably relatively well oxygenated.

## Preservation of Remains

The key to interpreting the possible structure of Ediacaran fossil remains lies in understanding processes of alteration which occurred before and during preservation, and in appreciating the way in which the remnant markings in the sediment were formed. Most of the remains in the type Ediacara assemblage occur as markings on the bottom surface of sandstone or

quartzite flags, and the majority may represent organisms stranded during ebb tide on muddy tidal flats and buried by the shifting sands of later tides (Jenkins *et al.*, 1983). Wade (1968) described the several processes of casting or moulding involved in preservation. Analysis of preservation in the manner she suggested in conjunction with comparative studies of modern animals may provide a basis for deductions about both the external and internal anatomy of the original organism.

Wade (1968, pp. 264–265; 1971) also recorded a process which formed ‘external moulds with counterpart casts’ in unbedded sands deposited by some form of grain flow mechanism. Fossils from the Nama Group, Namibia, showing a ‘three-dimensional’ structure (*e.g.*, Pflug, 1970) are preserved in this way. Ediacaran fossils from Newfoundland and the Charnian Supergroup, Charnwood Forest, Leicestershire, England, are chiefly preserved as external moulds formed by impression of organisms into upper surfaces of beds.

All numbered specimens discussed are curated by the South Australian Museum, Adelaide.

#### ACKNOWLEDGMENTS

I am indebted to Dr. Hans Pflug, Justus Liebig University, Giessen, West Germany, for allowing study of his large collection of Ediacaran fossils from Namibia, and for his hospitality and discussion. Dr. Trevor Ford, University of Leicester, helped with study of the Charnian material and assisted with photographs and latex impressions of Newfoundland specimens; he and Dr. Helen Boynton, Leicester, are especially thanked for demonstrating the Charnian succession.

#### THE OLDEST CNIDARIANS

An extensive literature reports supposed indications of metazoans predating the Ediacaran (*e.g.*, Glaessner, 1983). I continue to remain sceptical as to the significance of these claims (*e.g.*, Jenkins *et al.*, 1981). Hofmann and Aitken (1979) described possible cnidarian burrows of suggested Riphean age from northwestern Canada. The structures are on a single rock flag and the same authors admit that the markings should be “temporarily assigned to the dubiofossils”; questions also remain concerning the age.

Problematic markings which may be of organic origin are known from the older part of the Ediacaran in several areas. Possible megascopic remains are reported from the Briscall Formation of the Conception Group on the Avalon Peninsula, Newfoundland, and from the underlying Drook Formation (Hofmann *et al.*, 1979). Unfortunately this material remains undescribed. Unusual sub-circular markings also occur

in the lower part of the Charnian Supergroup (Dr. Helen Boynton, pers. comm.).

Ten or so discoidal markings ~3.5–~7 cm in diameter have recently been located on an upper bedding plane surface in a sandstone near the top of the Wonoka Formation at Bunyerroo Gorge (Gostin and Jenkins, 1983). The discs show a well marked annulation about  $\frac{1}{2}$  the diameter of a faintly impressed, smooth outer flange (Pl. 1, fig. 2). Their seemingly simple form and imperfect preservation preclude any systematic placement. A possible frond-like fossil also occurs on the same surface as the discs. This specimen shows a stalk passing into a fusiform body which seems to be overlapped by very imperfectly preserved casts of fronds (Pl. 1, fig. 1). The beds containing these specimens show ripple marks and mud-cracks indicating a littoral environment. Peculiar wrinkled surfaces apparently mould organic films which were likely of algal origin. Trace fossils made by worm-like creatures are also present.

#### LATE EARLY AND LATE EDIACARAN MEDUSOIDS

Various world occurrences of late Early and Late Ediacaran rocks include numerous imprints of discoidal fossils. These remains commonly show several concentric grooves or annulations and perhaps an indication of radial structure. However, in many instances the detail is insufficient to provide a basis for classification.

The remarkable specimens from Ediacara illustrated in Plate 1, figure 3 show two discs associated with casts of a mass of radiating ‘tentacles’ extending as much as  $\frac{3}{4}$  the diameter of the discs. The discs were peaked, with a central ring 3.5 mm in diameter, and faint annulations spaced at ~1.5 mm. The specimens are comparable with *Eoporpita medusa* Wade, 1972, and there can be little doubt that they represent porpitud chondrophores. Some of the imprints of similar discs in various Ediacaran rocks are probably also porpitud floats which became separated from the soft tissues as decomposition proceeded (*cf.* Glaessner in Føyn and Glaessner, 1979).

Several new specimens of casts of the zooids of *E. medusa* have been collected at Ediacara and one (P.18614) split accidentally through the centre shows overlapping internal moulds of 8 or 9 rings of zooids comprising a zone ~4.5 cm wide in radius, and the mould of part of the large central gastrozooid ~3 cm in diameter. The specimen augments Wade’s (1972) evidence for placement of this form as a chondrophore.

Other discoidal remains in the type Ediacara assemblage show well defined radial and concentric mark-

ings. These forms comprise a more or less intergrading plexus including the name taxa *Cyclomedusa* Sprigg, 1947, *Tateana* Sprigg, 1949, and *Spriggia* Southcott, 1958 (e.g., Glaessner and Wade, 1966; Wade, 1972). The holotype of *Cyclomedusa davidi* Sprigg, 1947, the type species of the genus, is rather poorly preserved, posing an initial systematic problem. Several newly collected specimens of reasonably large "medusoids" (11–17 cm in diameter) show central structures resembling *C. davidi*.

*Tateana inflata* Sprigg (1949), = *Cyclomedusa radiata* Sprigg (1949), consists of well defined discoidal imprints 30 to 80 mm in diameter and marked by strong, regularly spaced radial grooves, and occasional concentric grooves (Pl. 1, fig. 4). An overfolded or wrinkled marginal flange indicates a fleshy 'skirt' and there is evidence of tissue covering inner parts of the disc. The specimen illustrated in Plate 1, figure 5 may show faint indications of zooids. The float of the one modern porpitiid held by the South Australian Museum shows strong radial ribs on its upper surface and deep, fragile, narrow, radial pleats on its lower surface. The concentric float chambers are filled with preserving fluid and on partial drying of the specimen air enters the chambers which may then crinkle to form annulate wrinkles. These tend to be more closely crowded near the thin, peaked center. The characteristics of *T. inflata* closely parallel this configuration, suggesting that it also represents a chondrophore. *Spriggia annulata* (Sprigg, 1949) clearly shows the annulation of the float chambers, and on a different surface within the rock, moulds of the fine radial pleats which probably formed the lower surface of the float (Pl. 1, fig. 6). Large numbers of such specimens on some rock surfaces suggest that these chondrophores underwent periodic blooms or formed swarms in the manner of their modern counterparts. Porpitiid chondrophores evidently evolved during the Early Ediacaran: an annulate imprint in hornstones within the Beacon Hill Formation of the Charnian Supergroup at Beacon Hill, Charnwood Forest, may represent one of the oldest known examples.

The rare bilateral chondrophores *Ovatoscutum concentricum* Glaessner and Wade, 1966, and *Chondroplon bilobatum* Wade, 1971, occur in the Late Ediacaran of the Flinders Ranges. While the early porpitiids seem to have had relatively fragile floats, those of the bilateral forms were evidently rather tough or resilient and left sharply imprinted moulds in the sediments (Pl. 1, fig. 7). The later fossil history of the chondrophores is summarized by Stanley (1982). Glaessner (1971) and Scrutton (1979) have reviewed the relationships of the conchopeltid *Conomedusites* Glaessner and Wade, 1966.

Large circular imprints occurring at Ediacara reach 70 to 80 cm in diameter. The medusoids represented seem to have been mostly preserved exumbrellar side down and commonly the casts of their bodies show little surface detail. The edges are usually wrinkled and sometimes fold and curve upwards into the overlying sand layer, possibly reflecting desiccation and contraction prior to burial. In an energetic wave environment, medusoids tend to be stranded exumbrellar side up as this offers the least resistance to turbulence. Observation of the stranding of scyphozoans with short tentacles in a quiet, shallow marine embayment suggests they may settle exumbrellar side down if torpid or dead before settling. This condition may be induced by heating of the shallows during hot weather; perhaps the organisms represented by the fossil assemblage inhabited warm waters.

New material of identifiable scyphozoans available since Wade's (1972) study is limited. One new form of lobate medusoid and another new taxon with pronounced radial structure have been discovered. Several new specimens of *Rugoconites enigmaticus* Glaessner and Wade, 1966, show deep imprints of subrounded, discoidal bodies near the center. There is an indication of similar structures in specimen F.17458 shown in plate 43, figure 4 of Wade (1972). It is tempting to interpret the discoidal elements as moulds of the gonads; the greatly distorted centers of many specimens of *R. enigmaticus* (e.g., Wade, 1972, p. 221) may reflect collapse of the stomach and comparatively deep gastric pouches which contained the gonads (Text-fig. 1). No indication of oral arms is known.

Five new specimens shed further light on the structure and likely relationships of the enigmatic bell-shaped form *Kimberella quadrata* (Glaessner and Wade, 1966). These specimens indicate new limits to the known size range (bell length 32 mm to 71 mm) and one seems to show the attached tentacles (Pl. 1, fig. 8). I disagree with Wade's (1972) suggestion that the gonads are rotated along their length in one specimen (P.13775) and consider that they probably attached to 'perradial' membranes and comprised paired structures exactly as has been described in the living Carybdeidae. The 'smooth zones' apparently represent the walls of the subumbrellar funnels lying beneath the gonads (Pl. 1, fig. 10), and the 'puckered zones' must surely reflect the circular muscle system of the subumbrella (cf. text-figure 9 of Southcott, 1956). Modern box-jellies are powerful and fast swimmers.

Another characteristic requires explanation; this is the longitudinal fold or deep groove which roughly bisects the 'puckered' zone in the majority of specimens (Pl. 1, fig. 9). While the shape and positioning

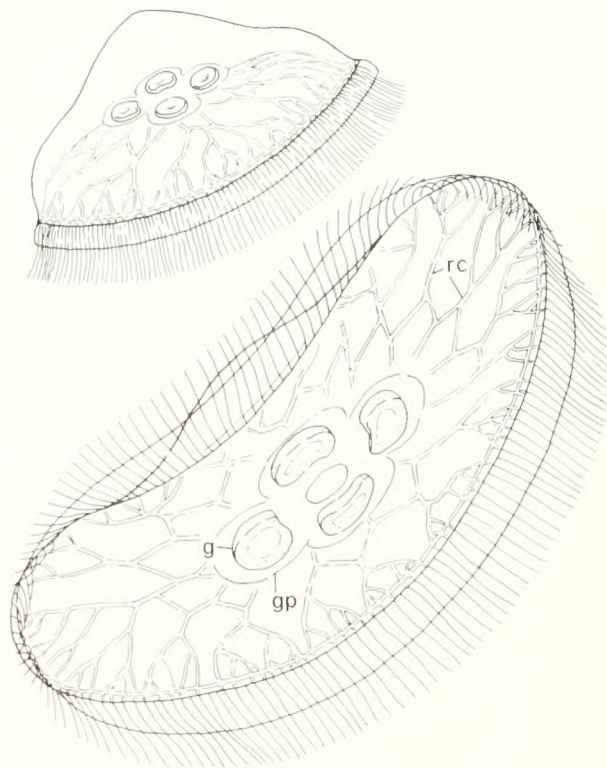
of this fold seem to have an accidental component, the fold generally becomes deeper and more accentuated at about the position where the rhopalia are located in living Carybdeidae. The rhopalia of the modern box-jellies occur in pockets situated in thickened expansions of the mesogloea within a wider zone bounded by aradial grooves (Southcott, 1956, 1967); internal to the bell, the perradial septa project into the central subumbrellar space and extend from the corners of the manubrium to below the rhopalia (Southcott, 1967, fig. 2). The groove and fold in the fossil remains evidently represent composite moulds of these structures (Text-fig. 2).

The gonads and bell margin of P.23526 (Pl. 1, fig. 8) are greatly deformed as though dragged about and folded by the grounding of the twisted and anastomosing fan of spreading tentacles. The tentacles appear to have been supported by large pedalia such as in the living *Chiropsalmus* L. Agassiz, 1862.

*Kimberella* appears to be a direct ancestor of the chirodropid sea wasps, and the extraordinary antiquity of these creatures certainly lends weight to Werner's (1975) separation of the Cubozoa and Scyphozoa. Werner considered the cubozoans to be the most highly evolved cnidarians and suggested that their ancestry lies between the hydrozoans and scyphozoans. Their incredibly potent venom comprising active agents of high molecular weight (Burnett and Carlton, 1977) has doubtlessly been refined and perfected by continued test and selection over the vast eons spanned by their existence.

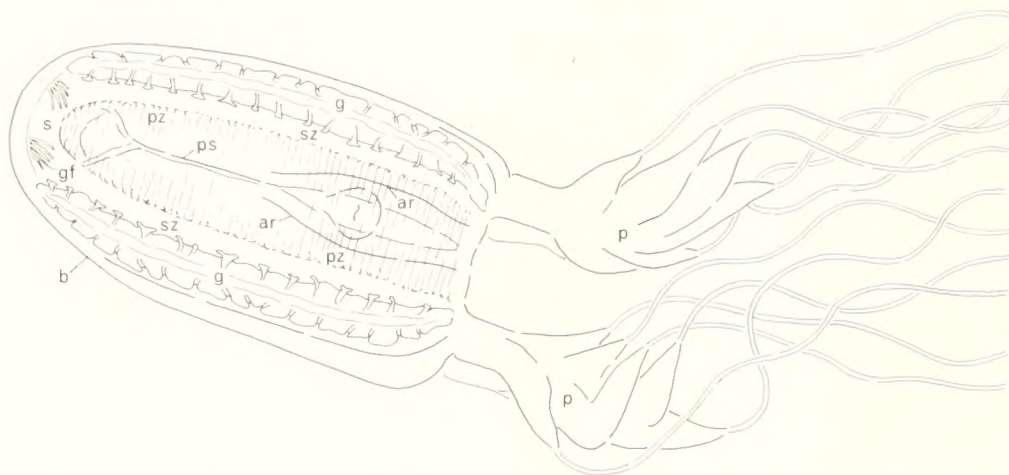
#### FROND-LIKE FOSSILS

Several kinds of discoidal objects occurring in the type Ediacara assemblage are attached to broad, ta-



Text-figure 1.—Reconstruction of possible early scyphozoan *Rugoconites enigmaticus* Glaessner and Wade, 1966. Oblique ventral view of lower specimen showing branched radial canal system, rc, and inferred relationship between gastric pouches, gp, and gonads, g. About life size.

pering stalks. In rare instances the stalk passes into the axial zone of frond-like fossils (Jenkins and Gehling, 1978; Text-fig. 3). These remains are referable to *Charniodiscus* Ford, 1958. *Charniodiscus*-like stalks sometimes extend from a round plug of sediment with a diameter about that which may be expected for the



Text-figure 2.—Reconstruction of early cubozoan *Kimberella quadrata* (Glaessner and Wade, 1966): b, bell, s, stomach, g, gonads, sz, smooth zones inferred to represent walls of subumbrellar funnels, pz, puckered zones inferred to reflect parts of circular muscle system of subumbrella, ar, aradial grooves, ps, perradial septum, and p, pedalia. Compare with Pl. 1, figs. 8–10. About life size.



attached disc. The plug is a cast of a collapse crater in the original substrate, and is inferred to mark the position of the buried disc, which is interpreted as an anchoring device. Rare specimens of the whole organism are preserved bent over from their point of anchorage. Radial grooves on the flange of the disc of *Charniodiscus oppositus* Jenkins and Gehling, 1978, probably reflect a radial musculature analogous to that in the bulb of living pennatulaceans. In contrast, the disc of *Charniodiscus arboreus* (Glaessner, 1959) shows a wide, almost smooth central area and peripheral, annular grooves.

Most specimens of *Charniodiscus* are broken at the stalk suggesting that they were torn free of their anchor. Glaessner and Wade (1966) reconstructed the frond as an entire, fusiform, foliate element with the laterally joined branches supporting free standing 'polyp-leaves' and this interpretation is maintained here. The 'polyp-leaves' were subdivided by resistant transverse structures indicated by serial grooves imprinted into the flag bearing the fossil. Similar short grooves characterize the stalk and axial zone of the frond, and are rarely seen as discrete needle-shaped imprints. Most students have interpreted these markings as indications of spicules. Following Glaessner and Wade (1966), Jenkins and Gehling (1978) interpreted the fleshy lobes between the spicules on the 'polyp-leaves' as the actual polyp anthosteles.

In a large specimen of *C. oppositus* (P.19687) in which the frond was in excess of 28 cm wide and probably more than 1 m long, the spaces between the spicular impressions on the 'polyp-leaves' are up to 8 mm in width. In places the fleshy lobes between these spicules show rather complex patterns of wrinkling and it

is possible that the true polyps were small (1–1.5 mm diameter) and numerous, possibly arranged in a manner more or less similar to that in the modern sea pen *Pteroeides* Herklots, 1858. *Charniodiscus* thus shows a degree of complexity analogous to that of modern sea pens, but differs in that the clearly defined branches were linked together by a foliate base or connective tissue. Several taxa exhibit a membranous marginal zone or 'skirt' extending from the edges of the frond.

The genus *Glaessnerina* Germs, 1973, had large polyp anthosteles. In the compressed state reflected by the fossil imprint the moulds of these overlap the median zone of the frond to give the effect of a zig-zag median line. The gross geometry of *Glaessnerina* seems comparable to that of the living Pennatulidae.

In *Charnia*, which is so far known only from northern hemisphere localities, the stalk also terminated in an expanded basal structure. The secondary divisions of the frond show finer third order divisions (see Fedonkin, 1981, pl. 29, fig. 1) which may represent anthosteles. This characteristic is a complexity not paralleled in living sea pens.

*Rangea* Gürich, 1929, from lower parts of the Nama Group, Namibia, is correctly interpreted by Pflug (1970) and Germs (1973) as a complex foliate structure, but I am not in agreement with Pflug that its fronds formed an enclosed body. *Rangea* consisted of some four or five fronds arranged 'back to back' and surrounding a central conical structure. This central element was evidently hollow and frequently became infilled by sediment which formed an internal mould. Individual fronds were entire or foliate, with a marginal 'skirt.' 'Polyp-leaves' present on the 'branches' of the fronds were double, but still able to fold to and fro as in



Text-figure 3.—Specimen, a, of 'ventral' aspect of *Charniodiscus oppositus* Jenkins and Gehling, 1978, showing stalk passing into axial zone of frond; fine striae on axial zone are interpreted as imprints of spicules; and, b, probable holdfast of *Charniodiscus*, with faint indication of stalk extending to left. Rock slab in upper part of Ediacara Member of Rawnsley Quartzite, near Bunyerroo Gorge, central Flinders Ranges.  $\times 33$ .

*Charniodiscus*. The secondary divisions of the 'polyp-leaves' show fine third order markings (.3-.4 mm) which branch in a sympodial pattern.

Spindle-shaped remains from the Conception Group on the Avalon Peninsula, Newfoundland (Anderson, 1978; Anderson and Conway Morris, 1982) appear to comprise serial groups or clusters of diverging branches extending in an alternate manner on either side of a slightly zig-zag median axis or median stolon. The form and complexity of the fine structure of the branches is closely comparable to that in *Rangea*. Other extraordinary forms occurring in association with the spindle-shaped remains consist of a number of frond-like elements (9-15) branching alternately from either end of a narrow trace which tends to be somewhat zig-zag (Anderson, 1978, p. 148). An organism consisting of a large number of complexly overlapping small fronds is present in association with *Charnia* in the Maplewell Group, Charnwood Forest (Ford, 1980, p. 82). The fine structure of the small fronds is also comparable with that of fronds of *Rangea*.

The systematic placement of these complex frondose organisms is problematic. Forms such as *Charnia* and *Rangea* show evident resemblances to *Glaessnerina* or *Charniodiscus*, suggesting a common relationship between them; their configuration superficially resembles that of several families of pennatulaceans and the likely presence of spicules in some supports the view that they represent highly evolved octocorals. The ordering within individual fronds of *Rangea* is seemingly greater than within living pennatulaceans. The other kinds of organisms with multiple fronds show similarities to either *Rangea* or *Charnia*. In some the fronds appear to be connected by a branching stolon, while in *Rangea* the fronds were outgrowths of a large, primary oözooid; such an oözooid presumably constituted the basal bulb and stalk in *Charnia*. Anderson and Conway Morris (1982) consider that different forms of preservation of the spindle-shaped fossils indicate that the original organisms were contractile, an observation which would seem to preclude their other suggestion that the 'polyps' had a stiffened cuticle resembling that of some modern hydrozoans. It is notable that *Rangea* seems to have had tissues interconnecting the branches of the fronds and *Charnia* was apparently rather fleshy; these characteristics probably indicate the presence of mesogloea. I consider that the complete group constituted a divergent Ediacaran radiation of the octocorals (Text-fig. 4).

Other distinctive Ediacaran remains have been confused with the plexus just described. These are the forms *Pteridinium* Gürich, 1933, *Ernietta* Pflug, 1966, and near relatives. *Pteridinium* consisted of three elongate vanes joined to a common axis and tapering to-

wards either end of the 'colony.' Each vane comprised at least two rows of elongate narrow tubes which constitute the ribbing seen on the surface. Sometimes the walls of the tubes show fine, enigmatic transverse striae or possible growth lines. *Ernietta* was a bizarre, sack shaped organism which grew upwards after attaching to the substrate (Jenkins *et al.*, 1981). It also consisted of several layers of elongate tubes; these were arranged in a mathematical way such that there were ~64 tubes in each circle. These remains show no particular resemblance to any known cnidarian and I agree with Pflug's (1972) suggestion that they represent a separate phylum.

### CONCLUSIONS

The soft-bodied assemblages of Ediacaran age indicate that the cnidarians underwent major radiation prior to the Cambrian. Knowledge of the life of the early part of the Ediacaran is limited to microfossils and algal laminates. Enigmatic discoidal markings may constitute some of the earliest indications of metazoans. By the "mid" Early Ediacaran, colonial hydrozoans such as the porpitiid chondrophores seem to have evolved. The appearance of the Anthozoa in the late Early Ediacaran is heralded by diverse assemblages of plumate or frondose octocorals inhabiting the benthonic realm. Medusoids were frequent and reached large size.

During Late Ediacaran time porpitiid chondrophores with fragile floats swarmed on the world's warmer seas and rare bilateral chondrophores with stiffened floats drifted amongst them. Various true scyphozoans appeared, but the deadliest predators were likely to have been fast swimming, voracious cubozoans. The evolution of the octocorals continued towards singly-frondose forms approaching pennatulaceans. These had adapted to become more robust in order to better withstand the currents and turbulence of near-shore waters. The specialized worms and early arthropods which also appeared foreshadow the major radiation of invertebrates characterizing the Cambrian.

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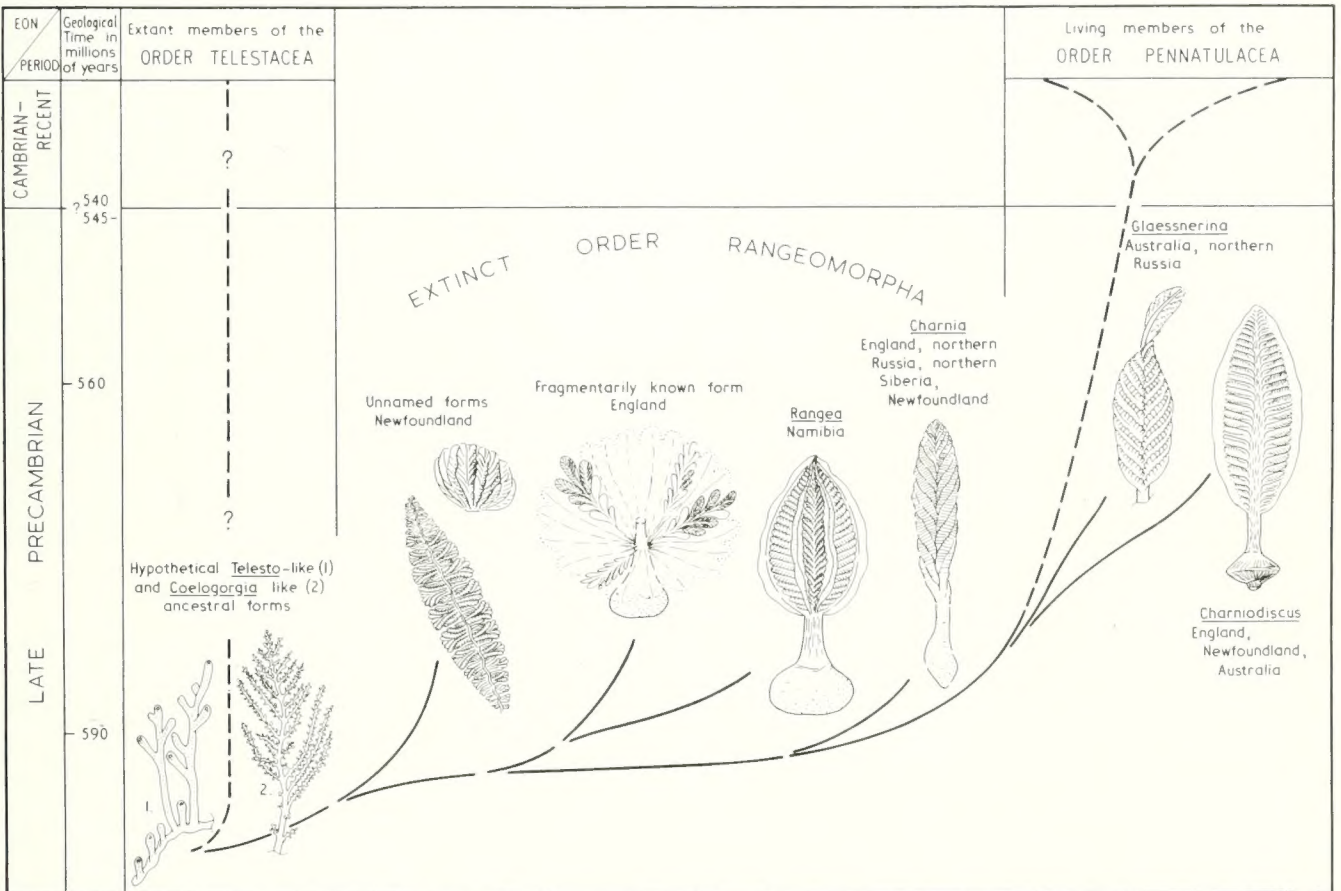
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Text-figure 4.—Hypothetical phylogeny of Precambrian frond-like octocorals, showing inferred position of members of Pflug's (1972) division Rangeomorpha between presumed ancestral representatives of the living Telestacea, and "mid" Ediacaran genera near the Pennatulacea. Known distribution of fossil genera indicated.

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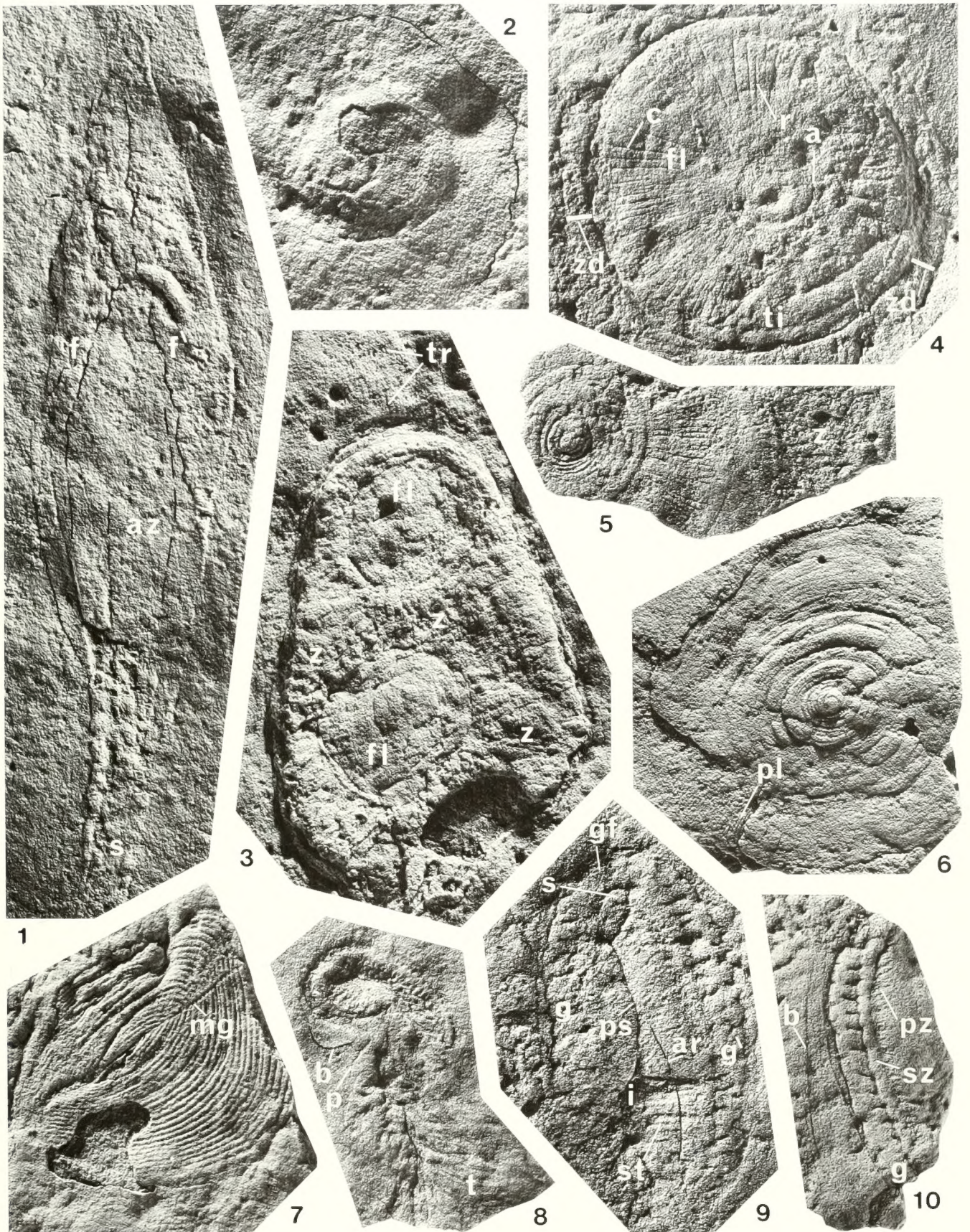
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## EXPLANATION OF PLATE I

## Figure

1. Unnamed frond-like fossil  
Photograph of plaster cast of specimen on an upper bedding plane surface in sandstone interval near top of Wonoka Formation, Bunyerroo Gorge, Flinders Ranges, South Australia;  $\times 1$ . Stalk, s. (cropped for reasons of space), appears to pass into faintly marked axial zone, az. with boundaries indicated by short dashed lines; edges of presumed overlapping parts of fronds, f, f', indicated by long dashed lines.
2. Unnamed medusoid fossil  
Photograph of plaster cast of one of several similar specimens on same bedding plane as fossil shown in figure 1;  $\times 1$ . Margin of preserved part of outer flange indicated by dashed line.
3. Unnamed remains of presumed chondrophores  
P.24299 a, b; preserved as casts on lower surface of quartzite flag, Ediacara Member of Rawnsley Quartzite, Ediacara Range, Flinders Ranges;  $\times 1$ . Floats, fl, and indications of zooids, z, of two individuals evident. Zooids probably contracted due to desiccation; faint traces, tr, on substrate indicate their length at time of grounding of remains.
- 4–5. *Tateana inflata* Sprigg  
Preserved as casts on lower surface of quartzite flags, Ediacara Member, Ediacara Range; both  $\times 1$ .  
4. Holotype, T.11;2017, showing float, fl, with radial grooves, r; closely spaced faint concentric markings, c, may indicate float chambers; collapsed float chambers form annulae, a; tissues, ti, overlap part of float and parts of zooid disc, zd, are evident.  
5. T22;2027 (paratype of *Cyclomedusa radiata* Sprigg), with possible indications of zooids, z, extending beyond margin of disc.
6. *Spriggia annulata* (Sprigg)  
Holotype, T.30;2031, preserved as a cast and partial mould on lower surface of quartzite flag, Ediacara Member, Ediacara Range;  $\times 9$ . Annulate structure of float clearly evident; fine radial pleats, pl, apparently present on lower surface of float.
7. *Ovatoscutum concentricum* Glaessner and Wade  
P.24300, preserved as a cast and partial mould on lower surface of quartzite flag, Ediacara Member, Bunyerroo Gorge;  $\times 1$ . Annulate float chambers clearly visible, with median groove, mg, bisecting distorted float.
- 8–10. *Kimberella quadrata* (Glaessner and Wade)  
Preserved as composite internal moulds and ? casts (gonads), with one specimen showing moulds of tentacles; all on lower surface of quartzite flags, Ediacara Member, Ediacara Range; all  $\times 1$ .  
8. P.23526; bell deformed and bell-margin, b, displaced; pedulum, p, joins spreading fan of overlapping tentacles, t.  
9. P.24301; faint grooves which may represent gastric filaments, gf, occur lateral to collapsed corner of stomach cavity, s, or part of manubrium joining groove representing perradial septum, ps, which passes into impressed area, i, in proximity to likely position of rhopalium; aradial furrow, ar, overlapped by striae, st, representing circular muscle system of subumbrella; gonads g, g'.  
10. P.23532; well preserved fragmentary specimen showing bell margin, b, pleated double-gonad, g, and smooth zone, sz, forming a ridge lateral to gonad; pz, puckered zone reflecting part of circular muscle system.



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## CAMBRIAN CNIDARIANS WITH MINERALIZED SKELETONS

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## ABSTRACT

The Cambrian record of cnidarian or supposed cnidarian fossils with mineralized skeletons is reviewed. It is sparse and the known occurrences are widely scattered both geographically and stratigraphically. The relationships of the various forms are doubtful and as presently known none can be confidently regarded as ancestral to the Rugosa or Tabulata.

## INTRODUCTION

Cnidarian coelenterates are well represented in the 'Ediacaran Fauna' of the late Precambrian. They consist entirely of remains and imprints of soft bodied forms, some showing evidence of chitinous or minor spicular strengthening elements but none had mineralized shells or solid skeleton. Although rare, this fauna is now known to have a worldwide distribution and to include representatives of the three cnidarian classes, Hydrozoa, Scyphozoa and Anthozoa. Both polypoid and medusoid forms were common, colonial polypoid organisms had developed, and sessile and planktonic habits were established.

The 'Cambrian Radiation Event' which began in latest Precambrian was one of the most dramatic in the evolution of the metazoans. It is characterized by the development of animals with hard parts. Many new phyla developed, exploiting the usefulness of shells or solid skeletons primarily for better musculature, better support with the possibility of raising the organism above the benthic boundary layer, and for better protection. The development of hard parts also meant that traces of the organism had a better chance of fossilization and thus the record of their evolution would be more complete than it had been in the Precambrian. However, cnidarians although well established in the Precambrian appear not to have successfully exploited this new development until the Ordovician.

Scrutton (1979) provided a comprehensive review of early fossil cnidarians and discussed possible cnidarian affinities of all Cambrian forms that had been referred to the Coelenterata by various authors. He considered many to have no cnidarian affinities and these are not discussed herein. In the succeeding five years little additional information has been published; although several new finds have been recorded their detailed description will be required before they can be properly evaluated.

## RECORDS OF CAMBRIAN CNIDARIANS WITH MINERALIZED SKELETONS

There do not appear to be any Cambrian forms with mineralized skeletons that can confidently be referred to the Hydrozoa or Scyphozoa. The conulariids with their chitinophosphatic skeletons and possible scyphozoan affinities have several records from the Cambrian. Scrutton (1979) discussed their relationships and concluded that they are of uncertain affinities but may form a separate class of cnidarians. However, evidence for this relationship is very tenuous and, as pointed out in this volume by Oliver (1984), they are yet to be shown to be cnidarians. The Cambrian byroniids are also sometimes regarded as scyphozoans but they have only chitinous skeletons. *Petaloptyon danei* Raymond, 1931 from the Middle Cambrian of western Canada was described as a probable anthozoan (gorgonian coral) with possible spicules associated with fan-shaped network of presumed chitinous material.

A number of small Cambrian forms with mineralized skeletons that may be of cnidarian affinities may not be referable to the more commonly recognized classes. They may represent the first "attempts" by polyps to develop skeletons for protection but may not have been adaptable enough to evolve further.

## Small Colonies of Slender Calcium Carbonate Tubes

Several forms consisting of slender, irregular, polygonal tubes, less than 1 mm in diameter, and forming small massive colonies have been described from a number of Cambrian localities.

The oldest is possibly *Bija sibirica* Vologdin (1932) from the Lower Cambrian of the Altay and western Sayan of central Asia. It consists of very slender, prismatic tubes closely adpressed and radiating outwards, with thin walls and without trace of septa, tabulae or mural pores. Vologdin originally referred it to the Alcyonaria, whereas Sokolov (1962) suggested that it showed affinities with the Tabulata (Family Lichenariidae). This was questioned by Hill (1981), and Scrut-

ton (1979) on account of its meandrine appearance in cross section and very small corallite size which suggested that it may represent a primitive chaetetid.

*Labyrinthus soraufi* Kobluk, 1979, first described from the Early Cambrian Forteau Formation of southern Labrador, Canada and later (Kobluk, 1982) from the late Early Cambrian Shady Dolomite in south western Virginia, U.S.A., is formed of splaying and branching irregular polygonal tubes which are often incomplete giving the appearance of a labyrinthine open network in tangential section. The tubes are aseptate and atabulate although some irregular infolding of the wall gives a suggestion of incomplete tabulae. The wall is thickened, consisting of an outer thin layer and a thicker layer of elongate calcite crystals that appear to be arranged in tufts based on the outer wall. Some colonies are up to 20 cm in diameter. These fossils show similarities to *Lichenaria* and also to *Tetradium*.

*Cambrotrypa sudetia* Gunia, 1967 from the ?Lower Cambrian of the Sudetes Mountains, Poland also consists of diverging irregularly polygonal corallites without septa but in this case with what appear to be irregularly spaced tabulae. They form massive cerioid colonies up to 10 cm by 18 cm. Preservation is poor and the microstructure is obliterated but the species does resemble the type species of the genus *C. montanensis* Fritz and Howell, 1959 from the Middle Cambrian Silver Hill Formation of Montana, U.S.A. The latter species has corallites up to 1 mm in diameter either in contact or separated by narrow spaces. When separated the tubes are joined periodically by small outgrowths of the wall. The tubes are hollow and only small colonies less than 2 cm diameter have been found. Bolton and Copeland (1963) referred specimens from the Middle Cambrian Albertella zone as recognized in Alberta and British Columbia, to this species.

A similar form is *Cambrophyllum problematicum* Fritz and Howell, 1955 described initially from the early Late Cambrian Maurice Formation of Montana, U.S.A. This species is characterized by slightly twisted polygonal to rounded tubes sometimes interconnecting and giving in cross section a meandrine appearance due to stout blunt processes projecting into the tubes but not completely crossing them. These processes were interpreted as initiating fission. No tabulae are observable and the microstructure is obliterated. Forms referred to this species have been found in the Lower Cambrian of the Salair, U.S.S.R. (Sokolov, 1962).

*Archaeotrypa prima* Fritz, 1946 and *A. secunda* Fritz 1947, both from the late Cambrian of the Ram Range of the Foothills of the Rocky Mountains, Alberta Canada are similar to *Cambrophyllum* but the diameter of the tubes is much smaller, less than 0.5 mm, and the

tubular walls are irregular. These latter characters suggest bryozoan affinities.

The relationship of these different forms is not known but as Sokolov (1962) suggested, their morphology is like that which might be expected of an ancestor to the Lichenariidae, and indeed other Tabulata.

#### Small Branching Colonies of Cylindrical or Trumpet-like Corallites Composed of Calcium Carbonate

The second group comprises Cambrian ramose or loosely fasciculate colonies of cylindrical or trumpet-shaped corallites originally constructed of calcium carbonate.

The early Middle Cambrian *Lipopora lissa* Jell and Jell, 1976 and *L. daseia* Jell and Jell, 1976 from the Coonigan Formation, western New South Wales, Australia, are both small irregular fasciculate colonies consisting of long cylindrical to scolecooid corallites up to 3 mm diameter with their external wall showing distinct transverse growth banding and with short septa (16 in *L. lissa* and 8 in *L. daseia*). Unfortunately, these forms are rare and unsilicified material has not yet been found so that their microstructure remains unknown. As Jell and Jell (1976) suggested these forms are similar to *Coelenteratella antiqua* Korde, 1959 from the Middle Cambrian of the southeastern part of the Siberian Platform, U.S.S.R., and they referred both genera to a new family Lipoporidae. *Coelenteratella* lacks septa and the rejuvenescences are more regular and more pronounced than in *Lipopora*. Their tabular corallites, lateral gemmation, and solid walls sheathed in transversely wrinkled epitheca resemble the Auloporida of the Tabulata.

*Protoaulopora* Sokolov, 1952, the type species of which is *Syringopora ramosa* Vologdin, 1931, from the Chingiz Range, Kazakhstan, U.S.S.R., is described as consisting of minute (on the order of 0.1 mm) slightly conical, prostrate corallites in cluster forming small colonies and having their calices slightly raised. The walls are thin and there are no septa and no tabulae. The holotype has not been traced (Hill, 1981) and the microstructure is unknown. Sokolov (1962) included it in the Auloporidae and as he and other Russian coral workers have regarded the auloporiids as ancestral to some if not all the tabulates, this Cambrian form has assumed great significance. However, its identity as an ancestral auloporiid is questionable especially as its corallites are so slender.

Whether these forms are closely related or not is arguable but the forms with larger corallite diameters appear to have cnidarian if not tabulate affinities.



### Solitary Cups Sometimes Forming Loose Colonies and Originally of Calcium Carbonate

This third group contains small cup-shaped or conical solitary forms originally composed of calcium carbonate and sometimes showing several generations of offsets to form loose fasciculate colonies.

Korde (1963) described four new genera and species *Hydroconus mirabilis*, *Tuvaconus rarus*, *Dasyconus porosus*, and *Gastroconus venustus* from the Lower Cambrian of the Bolshoy Shangan River, Tuvanian ASSR, central Asia, referring them to an independent class of cnidarians, the Hydroconozoa. They are small (up to 1.5 cm in height), conical or cylindrical, solitary, attached forms probably of calcite although this was not definitely stated by Korde in her descriptions. The lumen is filled by quite dense skeletal material showing a lamellar structure and, in some, radially arranged vertical plates that are like septa in appearance. There is some suggestion of tabulae. There is frequently a series of longitudinal and radial canals in the axial region. In the available figures these are difficult to differentiate and to interpret.

Handfield (1969) described *Tabulaconus kordeae* from the lower Cambrian Sekwi Formation, Northwest Territories and the Atan Group, Cassiar Mountains, British Columbia, Canada. This form consists of small thin-walled cylindrical corallites and can be either solitary or colonial. It contains closely spaced tabulae and in thin sections of the material examined there is a suggestion that short septa are developed in the early growth stages. The microstructure of the wall appears to be of elongate calcite fibers perpendicular to the inner wall of the corallite and crossed transversely by prominent growth lines. The microstructure is not unlike that of some tabulate corals. Debrenne and Lafuste (1981) reported results of ultra-thin section examination of this species and their description is in press. Specimens from similar horizons in Alaska have been referred to this species (Handfield, 1969).

Another small conical form that sometimes develops into bushy colonies up to 10 cm in height is *Cothonion sympomatum* Jell and Jell, 1976 from the early Middle Cambrian Cooigan Formation of western New South Wales, Australia. It is peculiar in that it is operculate. Recently a considerable amount of additional material has become available and is currently being described in detail. Also unsilicified material has allowed a better study of the microstructure. The thickening of the wall and the infilling of the lumen consist of elongate tufts of long calcite crystals, the tufts based on a thin outer epithecate wall. Vertical rows of tufts may be more elongate than adjacent tufts and form the low septal ridges. The elongate tufts appear trabecula-like but no

axis of divergence of fibres can be distinguished, all fibres seem to originate from the base of the tuft. This microstructure is interpretable as primitive coralline with the elongate tufts being incipient trabeculae. Many of the other features as outlined by Jell and Jell (1976) suggest rugosan affinities but the plan of septal insertion has not been demonstrated as rugosan.

Jell and Jell (1976) considered *Cloudina? borrelloii* described by Yochelson and Herrera (1974) from the Early Cambrian of Argentina more like *Cothonion* and of cnidarian affinities than like *Cloudina*, the type species of which is now considered to be a serpulid. This material was not available to the author so that no further comment is possible.

These small cup-like forms all show resemblances to small primitive corals. It is likely they are unrelated but may be of cnidarian affinities.

### Minute Colonies of Microtubules

Very small colonies 1 to 1.5 mm in size of tubules only 0.06 mm in diameter bearing clear septal spines; tabulae and mural pores have been recorded from the Early Cambrian Dengying Formation, Yangtze Platform of Sichuan, China (He, Yang, and Wang, 1983).

### Small Conical Tube-like Forms Composed of Fluorspar

Tynan (1981) reported the discovery of small cups of tube-like forms composed of fluorspar from the Early Cambrian Campito and Poleta Formations, White-Inyo Mountains, California. These were described too late for meaningful discussion here (Tynan, 1983).

### SUMMARY

The number of occurrences of Cambrian forms that might have Cnidarian affinities and have mineralized skeletons is very small. Considering the amount of paleontological collecting from Cambrian sequences, this paucity does not appear to be due to collection failure. Table 1 shows these occurrences to be widespread both geographically and stratigraphically.

It is questionable that any of these forms are related and indeed if all are cnidarians. There is very little evidence that supports any of these forms as direct ancestors to the Ordovician and younger coral groups. They probably represent unsuccessful attempts to establish lineages with mineralized skeletons and thus could all be considered as belonging to different classes, but at present this would only confuse the basic classification of the cnidarians. On the other hand, if they are just left as isolated genera and *incertis sedis*, they may be neglected. Perhaps the most useful course is to group them in an informal category, the Coralomorpha.

Table 1.—Summary of Cambrian cnidarians with mineralized skeletons.

Early Cambrian	Middle Cambrian	Late Cambrian
Group 1		
<i>Bija sibirica</i> (Altay-Sayan, U.S.S.R.)	<i>Cambrotrypa montanensis</i> (Montana, U.S.A.; British Columbia, Alberta, Canada)	<i>Cambrophyllum problematicum</i> (Montana, U.S.A.)
<i>Cambrophyllum problematicum</i> (Salair, U.S.S.R.)		? <i>Archaeotrypa prima</i> <i>A. secunda</i> (Rocky Mts., Canada)
<i>Cambrotrypa sudetia</i> (Sudetes Mts., Poland)		
<i>Labyrinthus soraufi</i> (S. Labrador, Canada; Virginia, U.S.A.)		
Group 2		
	<i>Lipopora lissa</i> , <i>L. daseia</i> (Western NSW, Australia)	<i>Protoaulopora ramosa</i> (Kazakhstan, U.S.S.R.)
	<i>Coelenteratella antiqua</i> (S.E. Siberia, U.S.S.R.)	
Group 3		
<i>Hydroconus mirabilis</i>	<i>Cothonion sympomatum</i> (Western NSW, Australia)	
<i>Tuvaconus rarus</i>		
<i>Dasyconus porosus</i>		
<i>Gastroconus venustus</i> (Tuva, U.S.S.R.)		
<i>Tabulaconus kordeae</i> (Western Canada; Alaska)		
? <i>Cloudina? borrelloi</i> (Argentina)		
Group 4		
Microcoralla of minute tubes (Sichuan, China)		
Group 5		
Small solitary fluorspar forms (California, U.S.A.)		

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## ORIGIN AND EARLY EVOLUTION OF TABULATE CORALS

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## ABSTRACT

The subclass Tabulata is considered to have appeared in the early Ordovician when *Lichenaria* evolved from a soft-bodied anthozoan ancestor by the acquisition of a skeleton. Some pre-Ordovician skeletal tabulatormorphs may be closely related but none is a lineal ancestor to *Lichenaria*. Tabulate corals (Tabulata of Hill, 1981 excluding chaetetids and tetradiids) are concluded to be monophyletic. All orders arose in the Ordovician and some are likely to be polyphyletic groupings of broadly homeomorphic stocks. The chaetetids are thought not to be corals, and the tetradiids, which may have a different mineralogy from that of the tabulate corals as a whole, are of uncertain affinity.

## INTRODUCTION

The origin and early evolution of tabulate corals have been widely discussed (Bassler, 1950; Sokolov, 1955, 1962a, b; Flower 1961; Flower and Duncan, 1975; Bondarenko, 1966; Scrutton, 1979; Hill, 1981, for example). The amount and quality of the contributing data are steadily increasing although there is still a pressing need for the careful revision of early and middle Ordovician material.

The criteria on which phylogenetic reconstructions are based should include an assessment of all aspects of skeletal morphology as well as stratigraphical and paleogeographical data. The weighting given to structural features will vary. Some, apparently stable within one group of corals (and therefore presumably more or less tightly controlled genetically), may show considerable variation in others. Furthermore, we can be more certain of some lines of evidence than of others. Our knowledge of microstructure in early corals, for example, is very variable and the distinction between primary and diagenetic effects far from clear. Finally, neat gradational series cannot be expected between the early representatives of various groups of tabulate corals, although the magnitude of the gaps seems to vary. Work with corals in general has convinced me that the origin of new stocks is frequently sudden and sharply distinctive, thereby minimizing the clues to phylogenetic descent. The only approach is to weigh all the evidence and to invoke a rule of parsimony, proposing relationships that require the minimum of important structural innovation. Structures such as well-developed mural pores and coenenchyme can be regarded as advanced and characterize major groups of corals. Although their secondary loss is possible, I regard primitive morphologies as generally more likely to have evolved from other primitive forms.

I broadly follow the definition of the tabulate corals that I previously adopted (Scrutton, 1979), essentially the Tabulata of Hill (1981) excluding her Chaetetidae,

Desmidoporidae and Tiverinidae, although I am now less certain about the affinities of the Tetradiida. I also now follow Hill (1981) and Sokolov (1962a) in classifying the major groups at the ordinal rather than at the subordinal level. The aim here is to attempt to identify the ancestry of the earliest members of each order. It is likely that not all orders are monophyletic, but I have only commented on this if polyphyly is suggested by the Ordovician records.

Stratigraphical correlations used here are based on various sources and are related to Ross *et al.* (1982). The terms Lower, Middle and Upper Ordovician as used in this paper refer to the Ibexian Series (approximately Canadian of authors), the Whiterockian plus Mohawkian Series (Champlainian of earlier usage) and the Cincinnati Series respectively.

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## ORIGIN OF THE TABULATE CORALS

A number of pre-Ordovician coralline fossils show some similarity to the main established body of tabulate corals (Scrutton, 1979). These are geographically and stratigraphically scattered records, mainly from North America but including Russian and Australian material. I have accepted *Tabulaconus*, *Cambrotrypa*,

*Lipopora* and *Coelenteratella* as possible anthozoans of tabulate appearance. *Protoaulopora* from the Upper Cambrian of Kazakhstan, classified as Auloporidae by Sokolov (1962a), is of doubtful affinity and requires redescription (Scrutton, 1979). Subsequently, *Labyrinthus soraufi* (late Lower Cambrian–early Middle Cambrian, eastern North America; Kobluk, 1979, 1982) showing some possible anthozoan features and *Rosellatana jamesi* (late Lower Cambrian, western Canada; Kobluk, 1984), with similarities to *Paleoalveolites*, have been described.

The earliest usually accepted tabulate corals are *Lichenaria claudi* and *L. simplex*, of early and mid Lower Ordovician age respectively, in Texas, Missouri and the eastern U.S.A. (Bassler, 1950; Flower, 1961; McLeod, 1979) and *Cryptolichenaria miranda* and *C. baikitica* from the Chunya of the Siberian Platform close to the Lower-Middle Ordovician boundary (Kaljo and Klaamann, 1973). These early Ordovician forms, although requiring redescription, appear to be much more comparable with the more diversified and widespread “Chazyan” tabulate corals and tetradiids than with anything in the Cambrian, and despite the early Middle Ordovician gap in the coral record I am inclined to accept direct descent over this interval and to suspect that new finds will bridge the gap. The scattered Cambrian records so far known, however, I am more inclined to regard as the result of the independent acquisition of a skeleton, possibly on several different occasions, by soft bodied stocks some of which may indeed have been anthozoan. None of these, however, led directly to the earliest *Lichenaria* although they may have had a common ancestor in the earlier Cambrian with the stock that gave rise to *Lichenaria*. I therefore restrict the subclass Tabulata to *Lichenaria* and its descendants.

No rugose corals are known before the Middle Ordovician. Although the origin of rugose corals from tabulate coral ancestors, in whole or in part, has been widely suggested (see Scrutton, 1979), I do not think that any groups of tabulate corals have been claimed as descending from rugosan ancestors. Certain genera present problems in their assignment to one or other of the subclasses but this is usually because clear diagnostic structural characteristics appear to be lacking (for example, *Fletcheria* in Hill, 1981, p. 104). In other cases, genera apparently combining rugosan and tabulate features (for example *Agetolites*, *Karagemia* and *Rhaphidophyllum*) require further investigation to clarify their affinities, but seem unlikely to require any fundamental revision of our concepts of rugose and tabulate corals. The vast majority of corals can be readily placed in one or other of the subclasses and I conclude that any common ancestry is likely to be

among soft bodied Cambrian precursors (Scrutton, 1979).

#### EARLY EVOLUTIONARY DIVERSIFICATION OF THE TABULATE CORALS

Species of *Lichenaria* are in need of redescription. Early forms, *L. claudi* and *L. simplex* from the Ibexian, are silicified but appear to be simple cerioid colonies of prismatic corallites, lacking septa, both ranging from 0.7 to 1.0 mm in diameter (R. S. Laub, pers. comm.). Possible tabulae are reported in one case (McLeod, 1979) but no mural pores have been detected and wall structure is unknown. However, *L. simplex?*, again atabulate, is recorded from the mid Whiterockian of Utah with fibrous non-trabecular walls (Rigby and Hintze, 1977).

Beds of a similar age yield the earliest *Eofletcheria* (Text-fig. 1), together with more diversified and tabulated *Lichenaria* (Duncan, 1956; Ross, 1964). *Eofletcheria* B (of Oliver and Duncan in Ross, 1964) appears to have fibrous walls, whilst semiphaceloid *Lichenaria* A possesses sporadic and irregular septal spines. *E. utahia*, with well spaced but well developed tabulae, is described as possessing an initially cerioid structure, becoming phaceloid in later stages of colonial growth (Rigby and Hintze, 1977). The conclusion that *Eofletcheria* descended from *Lichenaria* seems logical and is widely held (Flower, 1961; Flower and Duncan, 1975; Rigby and Hintze, 1977, for example) although the earlier species may simply be growth-form variants of the same genetic stock. Later *Eofletcheria* have a wall composed of thick monacanthine trabeculae (for example, Sokolov, 1955, fig. 73, pl. 54, figs. 4, 5) which may be extended as septal spines; these may have arisen via a septal condition like that in semiphaceloid *Lichenaria* A. A thorough description of the Whiterockian material is required to clarify the possibilities. I earlier classified *Eofletcheria* as a syringophyllid in view of its apparently trabecular wall structure (Scrutton, 1979). As earlier forms have a simple fibrous wall, however, it may be better to retain it in the Lichenariida, as Sokolov (1962a) has done and I have done here, or even to distinguish two separate genera split between the two orders.

Later Mohawkian *Lichenaria* of the *L. typa* group appear to have very sparse mural pores (Flower, 1961; Laub, 1984) and these may therefore have evolved in this genus if further work confirms the aporous nature of earlier species. This would appear to buttress the proposed descent of *Saffordophyllum*, in which mural pores are rather sparse but well developed, from a *Lichenaria* ancestor, except that the earliest species, *S. deckeri*, from the late Whiterockian McLish Formation, predates any known porous *Lichenaria*. This still

seems to be the most likely evolutionary sequence, however, and either pores will be found in earlier lichenariids, or they have evolved independently in these two genera. *Saffordophyllum* possesses fibrous walls without a clear axial plane and in this respect agrees closely with better preserved *Lichenaria* according to Flower (1961).

*Foerstephyllum* and *Lessnikovaea* are aporous Lichenariida in which the axial plane is more clearly developed and septa are variably prominent. Where septa are lacking, the wall structure appears to be very similar to that in *Lichenaria* rather than that in contemporary sarcinulids and I regard these two genera as evolving septal structures independently of that group. I also disagree with Flower (1961) in interposing *Saffordophyllum* between *Lichenaria* and *Foerstephyllum*, which would appear to require the loss of mural pores. I have already argued that late Ordovician porous "*Foerstephyllum*" with favositid wall structure should be referred to *Paleofavosites* (Scrutton, 1979) and I do not regard true *Foerstephyllum* as ancestral to any other major group of tabulate corals.

*Lamottia*, considered a synonym of *Lichenaria* by some (e.g., Bassler, 1950), was thought by Flower (1961) to have longitudinal light lines in the microstructure of the walls comparable to similar features in *Nyctopora* and *Trabeculites*. Laub (1984) regards the type material of *Lamottia heroensis* as distinct from *Lichenaria* and probably related to *Nyctopora*.

The Lichenariida are a difficult group to define. If, as all writers on tabulate coral phylogeny agree, *Lichenaria* is the root of much diversification and ultimately ancestral to many or all other orders, it is not surprising to find the evolution of features taken as diagnostic of these orders within various genera immediately descended from *Lichenaria*. I have chosen to retain these "transitional" genera in the Lichenariida together with the few genera apparently descended directly from *Lichenaria* but not leading to any other major groups of tabulate corals.

The earliest favositid appears to be *Paleofavosites* from the upper Middle Ordovician of the Urals (Sokolov, 1951). The genus spreads through Eurasia to Australia and to North America by early Upper Ordovician times but does not become common in the latter area until as late as Richmondian times. Flower (1961) favoured descent from *Foerstephyllum* but I have argued for a *Saffordophyllum* ancestor as species of this latter genus already possess mural pores of paleofavositid type and position (Scrutton, 1979; Text-fig. 1). Both genera are recorded in Europe in mid Mohawkian times (Sokolov, 1951; Klaamann, 1966; Yang, 1984). A supposedly distinguishing characteristic of the paleofavositids is the well defined "axial

plate" (Flower, 1961) in the intercorallite wall, which presumably could develop equally readily in either of the two proposed ancestral stocks. Furthermore, the distinctive crenulate walls of *Saffordophyllum* in cross section are a feature also occurring in some later *Paleofavosites* (see, for example, Sokolov 1951b, pl. 1). A similar axial plate certainly seems to develop in the Upper Ordovician *Foerstephyllum vacuum* group but apparently not in earlier species (Flower, 1961), and may therefore be a later and independent event to the origin of *Paleofavosites*. I am unhappy about the microstructural evidence in general, however, and I suspect the presence of an "axial plate" in at least some earlier lichenariids.

The favositids do not diversify to any great degree until the Silurian, although *Favosites* and the first probable pachyporic *Kolymopora* both appear in the Upper Ordovician, the latter very early (Volkova *et al.*, 1978). The Upper Ordovician *Agetolites* is regarded as a favositid with well developed septa; rugosan septal insertion (claimed by Kim, 1974) has not been convincingly demonstrated in this genus.

Sarcinulids are among the earliest tabulate corals to diversify (Text-fig. 1), with *Billingsaria* appearing in the upper Whiterockian of both North America and the Siberian Platform (Bassler, 1950; Pitcher, 1964; Sokolov, 1955). First records of *Lyopora* seem to be contemporary in the Siberian Platform, although this genus did not reach Europe, Australasia and North America until the mid Mohawkian. *Nyctopora* is recorded slightly later in the upper Whiterockian of North America, but *Lamottia* occurs a little earlier than *Billingsaria* and may be a precursor of *Nyctopora* (see above). Both *Billingsaria* and *Nyctopora* are effectively cosmopolitan by the early to mid Mohawkian.

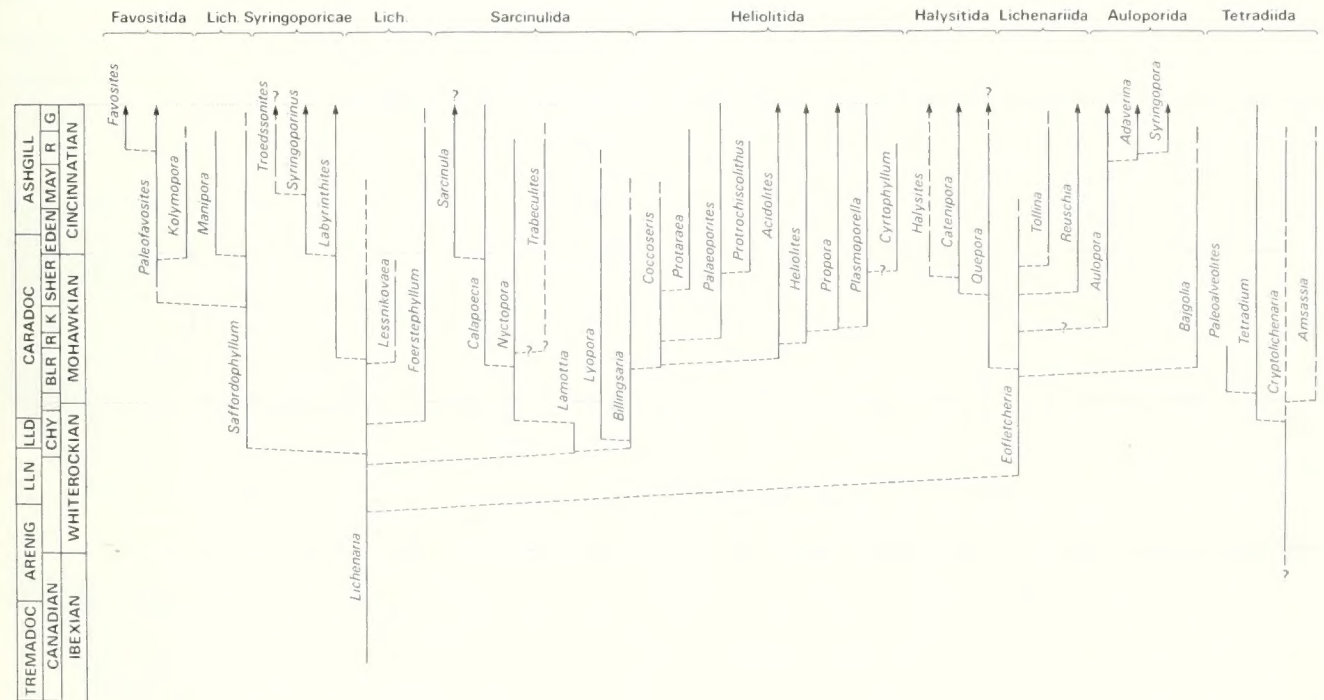
The evidence seems to suggest the origin of *Nyctopora* and *Billingsaria* via *Lamottia* (if it be distinct from *Nyctopora*) from *Lichenaria*, probably in the North American area, by the development of trabeculae in the corallite walls (Flower, 1961). Alternatively, they may be a branch of the stock leading to trabeculate *Eofletcheria*, which would require the evolution of thick wall-trabeculae on one occasion only, possibly in a phacelo-ceroid ancestor. *Nyctopora* and *Billingsaria* are very close and undoubtedly had a common origin, separated as they are by little more than the columella of the latter, constructed of poikiloplasm according to Flower (1961) but considered trabecular by Hill (1981). *Billingsaria* has no mural pores and although Hill (1953, 1961, 1981) and Jull (1976) claim rare, very small pores or intertrabecular spaces in *Nyctopora*, these are denied by Duncan (1956) and Flower (1961). In any case, there appear to be no pores present of similar form to those in *Saffordophyllum*, which to my mind

makes derivation of *Nyctopora* via that genus, as advocated by Flower and Duncan (1975), unlikely. Furthermore, the inclusion of *Trabeculites* in this lineage is not supported by its stratigraphic distribution (Text-fig. 1), even if *S. tabulatum* from the late Black Riveran proves to belong to this genus (Flower, 1961; Flower and Duncan, 1975). The aporous *Trabeculites* seems unlikely to have evolved from an ancestor with mural pores and may therefore be descended either from *Lichenaria* with the independent development of trabeculae or from *Nyctopora* by the partial degeneration of the trabecular wall.

The present stratigraphic and paleogeographic evidence point to the evolution of *Lyopora* from *Billingsaria* or trabeculate *Eofletcheria* in the region of the Siberian Platform through the development of zones of wall pores by the localized thinning of the trabeculae and, in the case of the former, by the loss of the columella. In either case, *Lyopora* migrated outwards from Siberia and its first occurrence in the U.S.A. (Kirkfieldian) post-dates the earliest *Calapoecia* which appears there in the early to mid Mohawkian (late Black Riveran). This suggests that the derivation of *Calapoecia* from *Lyopora* (Hill, 1953; Scrutton, 1979) is unacceptable unless new evidence comes to light. The most likely alternative is descent from *Nyctopora* through the development of coenenchyme, increased

potential septal number and the much more orderly and extensive thinning of the trabeculae to form wall pores. This is an evolutionary sequence previously favoured by Flower (1961) and Flower and Duncan (1975). Some species of *Nyctopora* show the beginning of coenenchyme in the form of what appear to be persistently juvenile offsets with closer-spaced tabulae, which eventually develop into fully mature corallites. *N. goldfussi* shows this well (Fig. 2A, B), but is itself too young to be ancestral to *Calapoecia* (wall structure and lack of obvious mural pores in material of *N. goldfussi* I have seen suggests that this species is a *Nyctopora* and not a *Saffordophyllum* as proposed by Flower (1961)). I certainly do not regard coenenchymal structures to be the sites of specialized polyps, but the evolutionary origin of tabulate 'coenosarc' may be via the proliferation of extrapolypal tissue, as in the early stages of extratentacular budding, with the suppression of polypal differentiation. It is relatively easy to see also how coenenchymal increase may have arisen by this route. It seems likely that coenenchyme in halysitids and heliolitids evolved in a similar manner, although apparently in two further separate events.

*Tollina* apparently has lyoporid microstructure in corallite walls in at least some species, which led Hill (1981) to classify the genus with the sarcinulids. If this is a persistent feature then it may have evolved from



Text-figure 1.—Stratigraphic ranges and suggested phylogenetic descent for selected Ordovician tabulate coral genera. Some alternative linkages are outlined in the text. Abbreviations: LLN — Lanvirn; LLD — Llandeilo; CHY — Chazyan; BLR — Black Riveran; R — Rocklandian; K — Kirkfieldian; SHER — Shermanian; EDEN — Edenian; MAY — Maysvillian; R — Richmondian; G — Gamachian; Lich. — Lichenariida.

either *Lyopora* or *Eofletcheria* late in the Mohawkian. The apparent lack of mural pores suggests the latter alternative but *Tollina* needs to be better known before its relationships can be resolved.

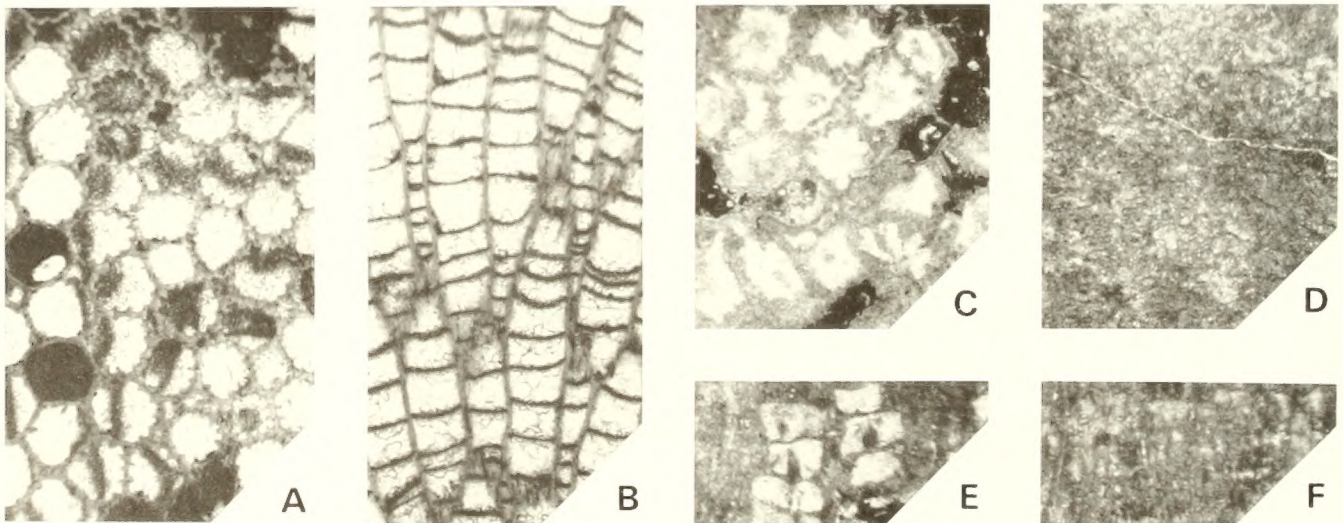
The origin and early diversification of the heliolitids departs from the more usual paleogeographical pattern. *Coccoseris* first appears low in Fauna I (Webby, 1969, 1975) of early mid Mohawkian age in N.S.W., Australia and is joined higher in that division by several other genera including, in sequence, *Acidolites* and *Heliolites*, together with *Palaeoporites*. *Propora* and *Plasmoporella* are added to this diversifying heliolitid assemblage by upper Mohawkian Fauna II times (Webby and Kruse, 1984). *Coccoseris* did not reach Europe and North America (as *Protaraea*), however, until upper Mohawkian times (*Coccoseris* may be synonymous with *Protaraea* as suggested by Sokolov (1955)). Diverse faunas of heliolitids are of similar age in China (Lin and Zou, 1980) but first appear in the U.S.S.R. in late Caradoc times (Sokolov and Tesakov, 1975; Volkova *et al.*, 1978) and in Europe and North America by late Caradoc or early Ashgill times (Bolton, 1977; Flower, 1961; Yang, 1984).

Flower (1961) derived *Coccoseris* from *Nyctopora* via *Protrochischolithus* but this is clearly not supported by the stratigraphic evidence. I now regard *Coccoseris* as evolving from *Billingsaria*. A specimen of *B. parva* from the upper Whiterockian Lenoir Limestone of Tennessee, whilst possessing 16 septa of alternating length in at least some corallites of normal billingsarid character, has zones in the corallum in which the septal trabeculae are thickened to contiguity and become wedge-shaped (Text-fig. 2C-F). In these cases, septal

number appears to be variable but is frequently 10 or 12 (it is very difficult to distinguish individual trabeculae). The appearance in both cross section and longitudinal section is very like *Coccoseris* and differs only in the single element columella and the variable septal number. *Billingsaria* is present in the N.S.W. Fauna I but I do not know if it exhibits the features described here in *B. parva*.

The evolution of *Palaeoporites* and later *Protrochischolithus* (either linearly or separately) from *Coccoseris* seems a reasonable proposition, but the origins of *Heliolites*, *Propora* and *Plasmoporella* have been much less certain. Flower and Duncan (1975) considered this group to be of unknown but independent origin to the coccoserids, whilst Sokolov (1955, 1962b) regarded *Heliolites* as descending from *Protaraea* via *Esthonia* and *Acidolites*. Webby and Kruse (1984) have now produced the evidence, formerly lacking, that seems fully to justify the principle of Sokolov's scheme. Not only do *Coccoseris*, *Acidolites* and *Heliolites* appear in sequence in the N.S.W. faunas, but some forms in early Fauna II times show alternating levels of *Heliolites*-like and *Propora*-like coenenchyme in the colony. This latter evidence suggests the further step that the Proporicae evolved in turn from a heliolitid ancestor. Thus all the main subdivisions of the Heliolitida were in existence by the mid-late Mohawkian and the order appears to be a monophyletic group arising from the sarcinulids.

From this discussion it is clear that I do not accept Nestor's (1980) contention that heliolitids are related to the stromatoporoids. His comparisons of internal structure are very superficial but a detailed discussion



Text-figure 2.—A, B. *Nyctopora goldfussi*. Waynesville Limestone, Richmondian, Upper Ordovician; near Oxford, Ohio, U.S.A. A, cross section,  $\times 8$ ; B, longitudinal section,  $\times 8$ . USNM 40100. C-F. *Billingsaria parva*. Lenoir Limestone, Whiterockian, Middle Ordovician; 4 km SE of Whitesburg, Tenn., U.S.A. C, D, cross sections,  $\times 8$ ; E, F, longitudinal sections,  $\times 8$ . USNM 133681.



is unfortunately outside the scope of this paper.

*Quepora*, the earliest halysitid from the early Mohawkian of Canada, was considered by Sinclair (1955) to be a cateniform lichenariid. With its thickened, fibrous walls, it suggests the possibility of microstructural similarity with *Eofletcheria*, some species of which show cateniform growth in part (Hill, 1953), and an origin among the non-trabeculate members of this genus. *Tollina* was suggested as an intermediate between *Lichenaria* and *Quepora* by Bondarenko (1966) and although this represents an apparently logical morphological series, the earliest *Tollina* appears to be late Mohawkian or even early Cincinnatian in age (Sokolov, 1962a; Sokolov and Tesakov, 1975; Volkova *et al.*, 1978). With its aporous, trabeculate wall, *Tollina* may represent a later independent descendant of *Eofletcheria*. I earlier regarded *Manipora* as synonymous with *Tollina*, but I now agree with Hill (1981) that the two genera are separate. The sparsely porous *Manipora* is closely related to *Saffordophyllum* (Sinclair, 1955; Flower, 1961; Scrutton, 1979).

*Catenipora* first appears in the late Mohawkian in England, China and Australia (Yang, 1984; Lin and Zou, 1980; Webby and Semeniuk, 1969) and seems to represent the acquisition of septal spines by a *Quepora*, of which there are contemporary species in Australia. In general, the difficulty of detecting septal spines in less than perfectly preserved material means that the relative ranges of these two genera are uncertain. In view of the variable growth form and septal development in at least some *Eofletcheria*, the possibility cannot be dismissed that *Catenipora* evolved directly from that genus, and indeed may be polyphyletic. The first *Halysites* also appears in Australia in the latest Mohawkian, and although Webby and Semeniuk (1969) regard it as unlikely to have evolved from locally known species of *Quepora*, this in general seems to be the logical line of descent. Pre-Silurian *Halysites* is very rare and the genus again may represent a polyphyletic collection of species stocks derived on more than one occasion from *Quepora* initially or later *Catenipora*.

Preobrazhenskii (1977, 1979) has suggested that the halysitids might be polyphyletic at a more fundamental level, with the *Quepora*, *Catenipora*, *Eocatenipora*, *Tollina* group related to the lichenariids and the *Halysites*, *Cystihalysites*, *Spumaeolites*, *Hexismia* group close to the heliolitids and proporicids. Although cateniform growth has clearly developed in several unrelated lineages, there seems to be little to recommend this drastic dismemberment, except that *Spumaeolites* may well be a proporicid. Otherwise the halysitids have a similarity of basic wall structure and a manner of origin of coenenchyme within the colony—even in some cases its partial development—which suggests a

broadly homogeneous evolutionary lineage, even if some form genera may themselves be polyphyletic.

The earliest records of auloporids are of uncertain status. The late Cambrian *Protoaulopora* is considered to be of problematical affinities and I have been unable to substantiate any records of *Aulopora* prior to those of Webby (1977), of mid Mohawkian age, which include the aspinous, atabulate *A. walliensis*. The slightly earlier *Bajgolia*, appearing in the early Mohawkian of N.S.W., Australia, however, may also be an auloporid. I had earlier favoured a pre-Ordovician separation of the auloporids and lichenariids as soft bodied stocks later independently acquiring skeletons (Scrutton, 1979). If the stratigraphic evidence is taken at its present face value, however, the widely suggested possibility that the auloporids descended through an *Eofletcheria* with a non-trabeculate, fibrous wall seems a reasonable proposition (Hill, 1953; Flower, 1961; Flower and Duncan, 1975; Webby, 1977). *Bajgolia* and *Aulopora* could be independently derived from *Eofletcheria*, but a study of increase in early *Aulopora* may show that its derivation from *Bajgolia*, with its unequal adaxial increase (Webby, 1977), is a reasonable hypothesis. *Aulopora* forms small encrusting colonies easily overlooked and new records may well throw more light on these relationships.

The earliest syringoporid appears to be the early to mid Mohawkian *Labyrinthites* (Bolton, 1965), which at the moment seems to predate *Aulopora*. Sokolov (1962a) considered this genus (as *Tetraporella*) to evolve from a lichenariid ancestor, which I have accepted as a likely possibility (Scrutton, 1979). In addition, however, Yang (pers. comm.) has recently discovered a new genus in the mid Mohawkian of Scotland which he describes as a "*Reuschia* with connecting tubules." *Reuschia* itself first appears in China at about the same time (Lin and Zou, 1980) but apparently later elsewhere. It seems likely to be a descendant of *Eofletcheria* as advocated by Hill (1953). When the distribution of the new genus and *Reuschia* are better known, the evolution of the former from the latter may be supported. Finally, the possibility remains that some or all syringoporids with infundibuliform tabulae evolved independently from auloporids through the aulocystids. The first of the aulocystids appears to be *Adaverina acritos* from the mid to late Cincinnatian (Richmondian) of N.S.W. (Webby, 1977) and the earliest syringoporids with comparable internal structure are approximately coeval records from the Urals and N.E. U.S.S.R. (Sokolov, 1962a; Preobrazhenskii, 1976). Thus the Syringoporicae of Hill (1981) could be a polyphyletic grouping of as many as three independent stocks.

The Tetradiida have had an uncertain history with their separation from other tabulate corals being advocated by Okulitch (1936), Flower (1961) and Flower and Duncan (1975), whilst Bassler (1950), Sokolov (1962a), Scrutton (1979) and Hill (1981) have regarded them as true tabulates, if a somewhat specialized side branch. The distinctive tetrameral increase of *Tetradium* seems to be unique but additionally they appear to be characterized as a group by a standard of preservation much poorer than that of contemporary tabulate corals. The implication is that they may have had a different wall structure and composition, perhaps aragonitic, whilst the tabulate corals as a whole were calcitic. Of all the groups discussed here, I am least happy to maintain the tetradiids as closely related to the rest of the tabulate corals.

*Tetradium* (interpreted here *sensu lato*, as by Webby and Semeniuk, 1971) first appears in the latest White-rockian and is widespread and highly diversified by the early Mohawkian. It is predated by *Cryptolichenaria*, first recorded near the Lower-Middle Ordovician boundary, which has been taken as an intermediate between early *Lichenaria* and *Tetradium*. In fact the Ibexian lichenarids have been tentatively referred to *Cryptolichenaria* by Sokolov (1955, 1962a) and Kaljo and Klamann (1973) although there is little detailed similarity between the Russian and the North American material. *C. miranda* Sokolov (1955, p. 234, pl. 58, figs. 1-6) shows wall processes developed in zones, usually back to back, two per corallite but on adjacent rather than opposite walls, which are reported to meet and result in an unequal form of longitudinal fission. Corallite shape and size is peculiarly irregular. It is not an unreasonable precursor to *Tetradium* but I am doubtful of any relationship with *Lichenaria*. This will be clarified by better information on *L. simplex* and *L. claudi*. I therefore follow Sokolov and Mironova (1959) and place *Cryptolichenaria* (with *Amsassia* and *Porkunites*) as a separate group within the Tetradiida, but keep an open mind on the affinities of the group as a whole.

Another early genus with unequal adaxial increase is *Bajgolia* which appears later than North American *Tetradium* in the early Mohawkian of N.S.W., Australia (Webby, 1977). It is therefore not likely to be an intermediate between lichenariids and tetradiids. In *Bajgolia*, I am not sure that the pattern of increase is of particular significance and other features suggest affinity with the auloporids.

#### CONCLUSIONS

The origin of the Tabulata is ultimately obscure and its definition to some extent a taxonomic convenience.

However, the most significant break at the moment precedes the Ibexian lichenarids. This I take as the limit of the subclass and suggest as the point at which the ancestor of all tabulate corals acquired a skeleton. Earlier "tabulatomorphs" may well represent skeleton acquisition by closely related stocks, or even by branches of the pre-tabulate stock, but none appears to show lineal descent to the first lichenariids. No direct evolutionary relationships are envisaged between the Tabulata and Rugosa in post-Cambrian times.

Despite much debate in the past concerning the unity of the tabulate corals (see discussion in Hill, 1981), it is concluded here that a monophyletic origin for the bulk of the subclass as traditionally conceived in recent major reviews is a reasonable hypothesis. Only the chaetetids are removed (Scrutton, 1979), whilst the affinities of the Tetradiida are considered problematical. An examination of the morphology, biostratigraphy and paleobiogeography of early tabulate corals suggests that several orders as currently defined are probably polyphyletic.

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## ORIGIN AND EARLY EVOLUTION OF RUGOSE CORALS

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## ABSTRACT

The oldest rugose corals reliably reported to date are lower Caradocian forms with monacanthine septa belonging to the genera *Hillophyllum* (from Australia), *Primitophyllum* (Estonia and USSR) and *Lambeophyllum* (N. America). During the middle Caradoc several new monacanthine corals appeared, and a few Silurian and Devonian genera (such as *Palaeocyclus* and *Stauromatidium*) are clearly developed from Ordovician ancestors. All corals with monacanthine septa are here included in the new suborder Monacanthina. The streptelasmatic corals with fibro-normal septa appeared somewhat later in the Middle Ordovician and they dispersed and developed rapidly. Streptelasmatic and monacanthinid corals probably developed from a common ancestor. The Tryplasmatic (with rhabdacanthine/holacanthine septa) appeared in the Upper Ordovician and could have developed from monacanthinid forms. The Calostylidae, with their porous and synapticular septa, do not seem to be related to monacanthinid corals.

By analyzing the first appearances of morphological structures in faunas from different faunal realms, new information on the development, dispersion and ecology of the early rugose corals can be obtained. During the Middle and Upper Ordovician the phylogeny of septal and fossular structures and the presence of tabellae seem to be important in discussing the still very hypothetical connections between different faunal realms.

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## ORIGIN OF RUGOSE CORALS

The origin of rugose corals has been enthusiastically discussed for more than 100 years. The early discussions were comparatively sterile because the oldest rugose coral faunas had been examined very little. During the last 30 years our knowledge of Ordovician corals has increased considerably, but much work remains to be done before reliable phylogenetic lines can be distinguished.

The different theories about the origin of rugose corals have been summarized by many authors, for example Hill (1956, 1960 and 1981), Ivanovski (1972), Webby (1971), Sytova (1977), Scrutton (1979) and Oliver (1980). I will give a short review of the most important. The earliest rugose coral genera discovered to date are *Lambeophyllum* recorded by Welby (1961) from the Chazyan in North America (but more reliably known from the Blackriveran), *Hillophyllum* Webby, 1971 from the Gisbornian (middle lower Caradoc) in Australia and *Primitophyllum* Kaljo, 1956b from the

Idavere, Jöhvi and Keila Beds (upper lower Caradoc) from Estonia and the Leningrad area. All these genera have monacanthine septa and slightly predate the streptelasmatic and columnariid (=stauriid) corals with fibro-normal septa.

Possible ancestors of the rugose corals are: 1) one of the Vendian or Cambrian cnidarians (e.g., *Cothonion*), 2) a tabulate coral, or 3) a sea anemone which developed the ability to secrete a skeleton.

Analyzing the first possibility, *Cothonion sympomatum* Jell & Jell, 1976 could be "an early skeleton-evolving side branch to the main line of rugosan descent" (Scrutton, 1979). All other Vendian and Cambrian Cnidaria do not seem to be closely related to rugose corals.

Tabulate corals as possible ancestors for the Rugosa have been widely discussed. Several Russian authors have suggested auloporoid corals as possible ancestors (Soshkina in Soshkina *et al.*, 1962; Ivanovski, 1972). A diphyletic origin is suggested by a number of authors. Sokolov (1955) proposed that *Lichenaria* could be ancestral to colonial columnariid corals and *Aulopora* to the solitary rugose corals. This opinion was also shared by Kaljo (1956a) and Spassky (1967). The latter author claimed that all solitary rugose corals developed separately from the colonial ones. He erected the groups Rugosa Solitaria and Rugosa Associata for solitary and colonial corals respectively (see Sytova, 1977).

Based on observations of the corals from the Montoya group (Cincinnatian), Flower (1961) suggested *Foerstephyllum* as an ancestral form to both *Paleofavosites* (Tabulata) and *Favistina* (Rugosa), and that *Favistina* gave rise to the three genera *Cyathophyl-*

*loides*, *Palaeophyllum* and *Crenulites*. Later *Streptelasma* was developed from *Palaeophyllum*. I agree with Sytova (1977) that these genera have such different septal microstructures that it is difficult to accept such a proposal.

Hill (1960) and Webby (1971) considered *Foerstephyllum* (of the *F. halli* group) as the ancestor of the cystiphyllid rugose corals. Later, however, Jull (1976) and Fedorowski and Jull (1976) showed that the septal insertion during increase in *Foerstephyllum* and *Palaeophyllum* was "fundamentally dissimilar."

I agree with Scrutton (1979) that it is unlikely that a colonial form could be the ancestor for all rugose corals, colonial as well as solitary. Either a solitary form was ancestral or we have to consider a diphyletic or polyphyletic origin for the rugose corals which is also unlikely. Hill (1960) concluded that "there is no unequivocal evidence of intermediates between the Alcyonaria and the Tabulata, between the Tabulata and the Rugosa or between the Rugosa and the Scleractinia," and in my opinion this is still true today.

In agreement with Scrutton (1979) and Weyer (1973) I believe that a possible ancestor to rugose corals should resemble *Primitophyllum primum* Kaljo, 1956. This species was recently revised by Weyer (1980a) who convincingly showed that it is an ordinary lambelasmatic coral with at least two cycles of monacanthine septa (a third cycle of septa, called hyposepta, indicated as faint septal grooves on the epitheca/septotheca, was also observed). This species has very short, monacanthine septa and no tabulae or dissepiments. Morphologically it is probably near the non-skeletal ancestral form. Generally, it is easier to believe in development from a simple form into a more advanced one, and from a solitary coral into a colony.

I also agree with Oliver (1980) that the development of corals from one or more stocks of skeletonless zoantharian polyps (sea anemones) by the addition of a skeleton is most probable. A polyphyletic origin for a particular group of corals (*e.g.*, rugose corals), however,

is unlikely. It is hard to accept that the same mode of septal insertion would develop repeatedly.

## EARLY EVOLUTION OF RUGOSE CORALS

### Development of Morphological Structures

An analysis of the first appearances of different morphological structures within early rugose corals aids further discussion on the development and dispersion of faunas during the Early Palaeozoic. The following morphological structures are discussed below: septa, tabulae, tabellae, dissepiments, fossular structures and axial structures.

### Septa

Both major and minor septa are present in the oldest rugose corals (*e.g.*, *Hillophyllum*, *Primitophyllum*, *Lambeophyllum*, *Lambelasma* among the monacanthinid forms, *Streptelasma* among the streptelasmatic forms and *Favistina* and *Palaeophyllum* among the columnariid forms). Tertiary septa are observed in late Ordovician corals (at least in one probably undescribed species from Russia) and hyposepta are observed by Weyer (1980a) in both the oldest monacanthinid forms as well as in Upper Ordovician and Silurian streptelasmatic forms. Septal insertion typical for rugose corals is also clearly seen in the earliest genera (*e.g.*, *Hillophyllum* and *Primitophyllum*). As mentioned earlier, the first forms with monacanthine septa appear at approximately the same time in Australia and North America and slightly later in Baltoscandia. Forms with fibro-normal septa, including streptelasmatic and columnariid genera, are reported from somewhat younger strata in Australia (*Palaeophyllum* from lower Estonian, upper lower Caradocian, and *Streptelasma* and *Favistina* from upper Estonian, middle Caradocian), in the East Baltic area (*Leolasma* from the Jöhvi Beds) and in North America (*Streptelasma* and *Palaeophyllum* from the Blackriveran).

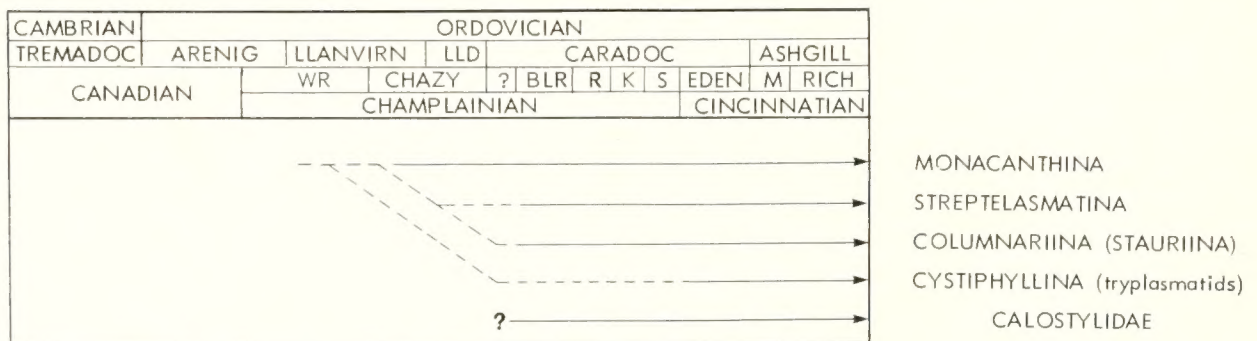


Figure 1.—Stratigraphic ranges and suggested phylogenetic links for the main groups of Ordovician rugose corals. Abbreviations: LLD—Llandeilo; WR—Whiterock; BLR—Black River; R—Rockland; K—Kirkfield; S—Sherman; M—Maysville; RICH—Richmond.

Tryplasmatisms have been reported from Middle Ordovician strata, but subsequent examination has shown most of these species to be monacanthine forms. True tryplasmatisms are characterized by having rhabdacanthine or holacanthine septa and a lamellar sclerenchyme. Weyer (1980b, pp. 26–27) claimed that the earliest true tryplasmatisms are of Upper Ordovician age (e.g., *Tryplasma tubulus* (Dybowski) and *T. spinulatum* Neuman). Our present very limited state of knowledge of tryplasmatisms corals indicates that they develop later than monacanthinid and streptelasmatisms corals. Even if the structure of rhabdacanthine and monacanthine trabeculae is very different (see Hill, 1936), it is possible to imagine the first developing from the latter by minor modification of the secretory centers in the epithelium, and a step by step rather than continuous septal construction.

Weyer (1973) stressed a close resemblance between the porous septa of Middle Ordovician genera with monacanthine septa and the Calostylidae (e.g., *Calostylis* and *Helminthidium*). It is difficult to agree with this interpretation from what can be seen of the septal structures in the genera involved. The thick monacanthine trabeculae, sometimes equipped with secondary trabeculae where septa are especially strongly dilated (interpreted by Weyer 1973 as rhabdacanthines), are either joined directly in an almost massive septum without pores or are separated from each other. Certainly, they can also interfinger with trabeculae from an adjacent septum which results in a pseudo-porous structure.

Studies of septal structures in well preserved specimens of *Calostylis concavotabulata* from the upper Visby and lower Höglint Beds on Gotland, on the other hand, revealed that separate trabeculae are difficult to distinguish in the septa which, both in longitudinal and transverse section, show a nodular structure of sectioned sclerodermites which are never arranged in the pattern we find in monacanthine septa. In addition, the irregular synapticulae are never observed in genera with monacanthine septa. The classification of the Calostylidae and their relationship to other rugose corals is still very uncertain. Further studies of the microstructures based on well preserved material are necessary.

Observations of the length of septa during the ontogeny of the oldest rugose corals have not revealed any special trend. *Primitophyllum* and *Hillophyllum* have comparatively short septa throughout ontogeny. On the contrary, *Lambeophyllum* has comparatively long septa during early ontogeny. All three genera have a deep calice and short septa within the calice. A deep calice is also common in almost all lambelasmatisms genera of Middle and Upper Ordovician age from Baltoscandia. Among the earliest streptelasmatisms and col-

umnariid corals there are no consistent trends in the length of major septa.

#### The New Suborder Monacanthina

On the basis of extensive studies of forms with monacanthine septa, I propose a new suborder, Monacanthina (see below), for the following reasons:

- 1) The first rugose corals have monacanthine septa.
- 2) Monacanthinid genera are known from: the Chazy (=upper Llanvirn), Caradoc and Ashgill (genera belonging to the family Lambelasmatisms), Llandovery (Palaeocyclusidae), Wenlock (Wenlockiinae) and from the Ludlow and Lower Devonian (Stauromatidiidae Pedder & Oliver, 1982). In addition several new undescribed genera and species have already been identified.
- 3) The morphological structures show a development almost parallel to those of streptelasmatisms corals (although globose dissepiments are not yet known in monacanthinid forms).
- 4) Monacanthinid forms have a wide distribution within possible faunal realms.
- 5) Monacanthine trabeculae seem to be comparatively resistant to diagenetic changes and are easy to identify.

#### Tabulae, Tabellae and Dissepiments

Complete tabulae are developed among the earliest rugose corals (e.g., *Hillophyllum*). Also a few complementary plates (incomplete tabulae in the periphery of the corallite which buttress the complete tabulae) can be seen in this genus. Other monacanthinid genera with tabulae are *Estonielasma*, *Rectigrewingkia* and a new genus recorded from Sweden. Otherwise, the majority of the monacanthinid corals do not have tabulae (e.g., *Lambelasma*, *Lambeophyllum*, *Primitophyllum*, *Coelolasma*, *Coelostylis*). *Neotryplasma* Kaljo, 1957 as revised by Weyer (1982) has centrally placed tabularium with complementary plates and a peripheral dissepimentarium of large lonsdaleoid dissepiments. Also the earliest streptelasmatisms (e.g., *Streptelasma*) and columnariid corals (e.g., *Palaeophyllum* and *Favistina*) have numerous complete tabulae often with complementary plates. In North America, Siberia, China and Australia tabellae are well represented in Upper Ordovician streptelasmatisms corals, but Baltoscandian Ordovician Rugosa do not have structures which can be interpreted as tabellae. Dissepiments of lonsdaleoid type seem to be the oldest kind, represented in *Neotryplasma* and *Paliphyllum* from Baltoscandia (of upper Middle Ordovician and Upper Ordovician age, respectively). Several genera with lonsdaleoid dissepiments developed during the Llandovery (e.g., *Arachnophyllum* and *Microplasma*). The first genus with small, globose dissepiments seems to be *Protocyathactis* from the Upper Ordovician and during the Llandovery a number of genera with globose dissepiments developed.

## Fossulae and Pseudofossulae

The definition of a fossula is so variable among coral specialists, that it is difficult to compare usage from one author to another.

Hill (1956, p. 248) defined a fossula as an "interseptal space distinguished by its unusual shape and size," and in the same work (p. 242) declared that these "interseptal loculi of unusual shape and size occur at the point of insertion" (of new major septa).

Schouppé and Stacul (1959) examined fossular structures in detail. They pointed out that the original definition of Edwards and Haime (1851, p. 325) specifically included the depression of tabulae in the zones of septal insertion. The word fossula is derived from *fossa* which means a depression or pit. Schouppé and Stacul (1959, p. 44) convincingly showed that a fossula *sensu stricto* with depressions in either tabulae, tabellae or dissepiments (see Fig. 2B) is an important structure, a useful taxonomic feature at the generic level and a correlative feature for higher taxonomic groups (*e.g.*, subfamilies). In series of transverse sections a real fossula can be recognized during the whole ontogeny where a tabularium or dissepimentarium is present. Unfortunately, fossular structures are not present in modern corals so it is difficult to reconstruct their function. A fossula *sensu stricto* is, with few exceptions, present only in combination with the cardinal septum. The rugose coral animal (polyp) must have developed a basal pouch on the cardinal side responsible for the fossular pit in the skeleton. The cardinal septum, and to some extent the counter septum, must be essential structures in rugose corals and are among the first formed. An enlarged gastro-vascular cavity on the cardinal side and an elongate food apparatus could be of importance for a more efficient food supply, although authors (*e.g.*, Birenheide, 1965, fig. 5) have suggested that the fossular pouch was the site for the gonads. Whatever its function, a *fossula* with tabular or dissepimental depression ought to be counted as an important morphological structure which must be taken into consideration in taxonomic work at least at the generic level.

A *pseudofossula* is normally more or less developed in all rugose corals as an enlarged interseptal space at points where septal insertion takes place and is not especially important in taxonomic work. A considerable shortening of the cardinal septum compared to the laterally situated major septa causes a depression in the calice on the cardinal side. This may also provide space for a minor gastrovascular pouch and should be taken into consideration as a morphological structure almost as important as a fossula, and of use at least at the specific level. For such structures I here introduce

the term *septofossula*. A septofossula is never combined with tabular depression, although a *septofossular stage* can often be distinguished in rugose corals with a fossula at a late subcalicular epehebic stage. Nelson (1981) interpreted this as a pseudofossula.

## The Development of Fossular Structures in Baltoscandian Rugosa

The Middle and Upper Ordovician monacanthinid corals are nonfossulate or sometimes equipped with a pseudofossula. Ordovician and Lower Silurian streptelasmatic corals (which dominate the fauna in that interval) show a clear trend in the development of fossular structures. In the middle Ashgill (Pirgu Stage in Estonia, Etage 5a in the Oslo Region, lower part of the Boda Limestone in the Siljan District) the streptelasmatic corals are equipped with a pseudofossula only (Fig. 2D). The only species with a somewhat fossula-like pseudofossula, but without marked tabular depressions, is *Grewingkia buceros* (Fig. 2E). In the upper Ashgill (Porkuni Stage in Estonia, Etage 5b in the Oslo Region and the *Dalmanitina* Beds and Upper Boda Limestone in Sweden) several species have a septofossula, for example *Streptalasma unicum* (Fig. 2F) and *Ullernelasma svartoeyensis*, and other as yet undescribed new species. Several other species are equipped with a pseudofossula.

In the early Llandovery (Etage 6 in the Oslo Region) several genera of rugose corals suddenly developed a cardinal fossula *sensu stricto* with pronounced depression of the tabularium (Fig. 2A). Later in the Llandovery and Wenlock, a fossula combined with depression in the dissepimentarium became more frequent (*e.g.*, *Ketophyllum* (Fig. 2C)). Fossulae in counter- and alar-quadrants also began to appear in the Wenlock. Parallel to the development of true fossulae, Silurian species with a pseudofossula or septofossula (*e.g.*, *Rhegmaphyllum conulus* and *Dalmanophyllum dalmani*) are also present in Scandinavia. It is important to notice that a fossula *sensu stricto* is never clearly developed in Ordovician rugose corals in Scandinavia. In Estonia a few corals seem to have a fossula (*e.g.*, *Bighornia orvikui* Kaljo, 1960 with a clear septofossular stage), but mainly the development is similar to Scandinavia. In Siberia and China several Upper Ordovician genera have fossulae developed. A true fossula appears first in the North American Midcontinent (as defined by Jaanusson and Bergström, 1980), where the majority of rugose coral genera have such a structure from the Middle Ordovician/Upper Ordovician boundary. Several of the American species from the uppermost Ordovician have a septofossular stage developed during late ontogeny (Elias, pers. comm., and my own observations).



It is interesting that a septofossula and the septofossular stage of fossulate forms appear in many parts of the world in the uppermost Ordovician. Could this be connected with the general regression of the seas in uppermost Ordovician time with adaptation to new niches by representatives of several genera?

#### Axial Structures

An axial structure consisting of the fused ends of major septa is seen in the early ontogeny of several monacanthinid corals (e.g., *Lambeophyllum*, *Lambe-lasma*, *Coelolasma* and *Dybowskinia*; see Weyer, 1973). *Coelostylis* has the same type of axial structure, forming an irregular boss in the deep calice. Even *Grewingkia*-like axial structures, consisting of numerous

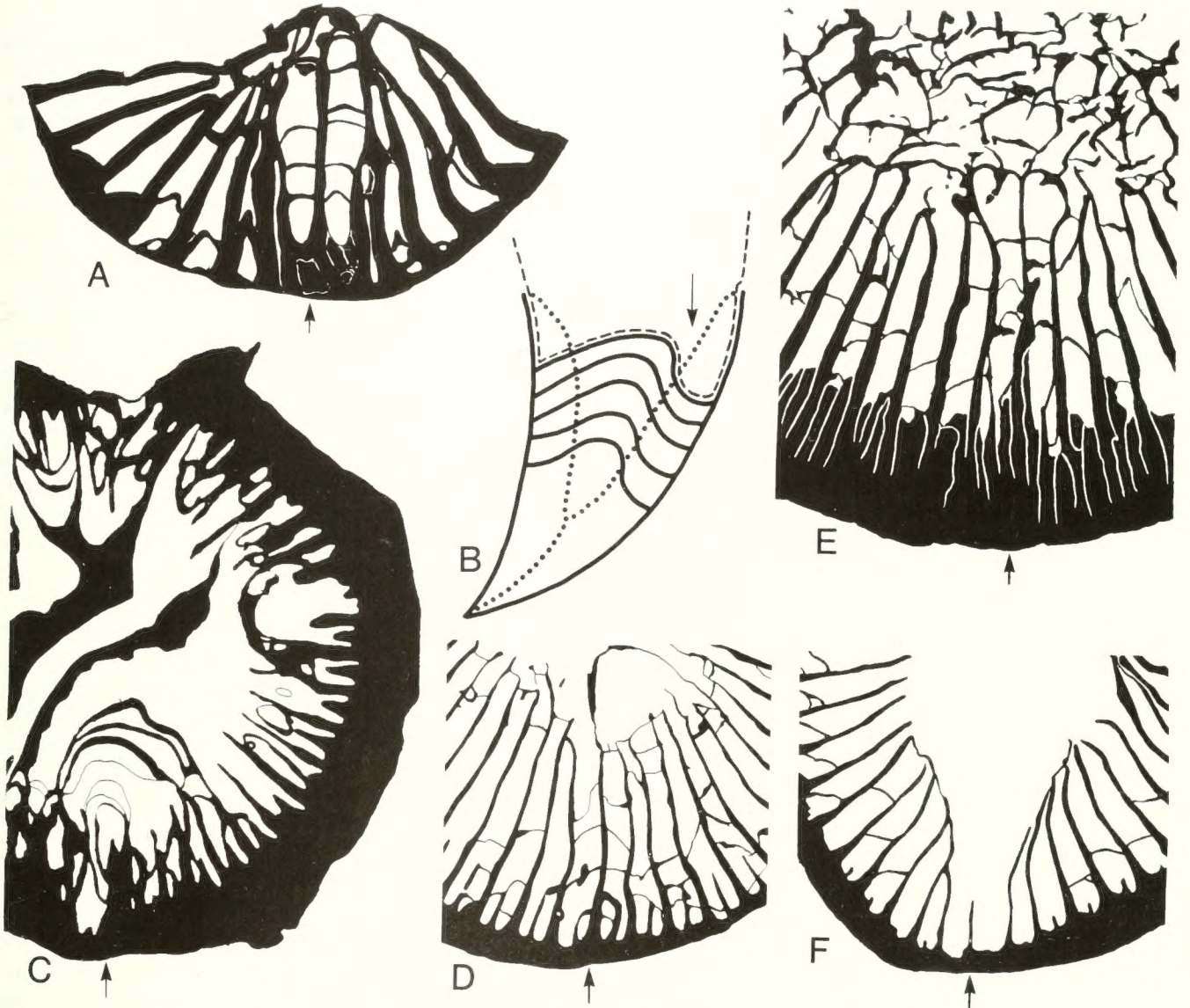


Figure 2.—Different types of fossular structures. *A*, cardinal fossula in *?Streptelasma* sp. a Neuman, 1982 (BN UB 2, Presteveien, Asker; Llandover, Etage 6b). *B*, schematic longitudinal section of a fossula. Dotted lines indicate the inner border of major septa, dashed lines the soft body of the polyp. *C*, cardinal fossula in *Ketophyllum kutscheri* (Wedekind, 1927), (BN UB 38, Båta, Fårö Island, Sweden; Wenlock, Slite Beds) (picture from O. Pettersson, unpublished thesis). *D*, cardinal pseudofossula in *Streptelasma primum* (Wedekind, 1927), (UM Nor 6, Stannestangen, Ringerike, Oslo Region, Norway; Upper Ordovician Etage 5a). *E*, an almost fossula-like pseudofossula in *Grewingkia buceros* (Eichwald, 1856), (PMO 39961, Skramnes Farm near Mjøndalen railway st. Nedre Eiker, Oslo Region; Upper Ordovician, Etage 5a). *F*, typical septofossula in *Streptelasma unicum* Neuman, 1975 (RM Cn 59327, Borensult, Östergötland, Sweden; Upper Ordovician *Dalmanitina* Beds). Explanation of the abbreviations: BN = B. Neuman collection; UB = University of Bergen, geological collections; UM = Museum of the Palaeontological Institute, University of Uppsala; RM = Palaeozoological Department, State Museum of Natural History in Stockholm; and PMO = Palaeontological Museum in Oslo.

irregularly bent septal lobes and lamellae occupying a large central area of the lumen, are present in monacanthinid corals (e.g., *Rectigrewingkia anthelion*). A median boss was observed by Elias (1983) in ?*Lambeophyllum* sp. A from the Middle Ordovician Tyrone and Curdsville Limestones of central Kentucky. Those axial structures, so typical of early streptelasmatic corals, are thus also represented in monacanthinid corals.

*Grewingkia*-like axial structures are most frequently represented in upper Middle Ordovician and Upper Ordovician *Grewingkia* and *Densigrewingkia* as well as typical American genera like *Lobocorallium* and *Bighornia*. Several of the Middle Ordovician corals earlier placed in *Grewingkia* seem, however, to be monacanthinid forms. In the Silurian, a great variety of axial structures developed. Sometimes tabulae and tabellae also assisted in forming an axial structure (e.g., *Dinophyllum*, in which a pronounced axial vortex is also present forming a prominent calicular boss). The aulos of the syringaxonid corals is another important type of axial structure.

A calicular boss must be considered as an important structure at both generic and specific level as it must have been formed in close connection with the soft body of the polyp.

#### The Development of Ordovician and Lower Silurian Rugose Corals in Different Faunal Realms

Hill (1981, pp. 49–54) gave an excellent review of the current knowledge of Ordovician and Silurian rugose faunas in different regions. Further information on the Upper Ordovician and Lower Silurian rugose corals of North America is given by Elias (1982) and on the Oslo Region by Neuman (1982). In agreement with Hill (1981) I must admit that comparatively little is known about faunal realms based on Ordovician and early Silurian rugose corals, often because of taxonomic uncertainties. My simple analysis of morphological structures, based on my own examinations and extensive studies of publications, reveals that only a few morphological structures appear to have a different evolution in various faunal realms. These structures are: monacanthine septa, fibro-normal septa, fossular structures and tabellae.

1) Monacanthinid corals appeared first (Chazyan) in the North American Midcontinent (as specified by Jaanusson and Bergström, 1980) and in Australia (Gisbornian). Somewhat later they are also found in Baltoscandia (Idavere or Jöhvi horizons). The monacanthinid corals show a comparatively high diversity in Baltoscandia during the upper Middle Ordovician and are also represented in the lower Upper Ordovician (Vormsi horizon). In all areas outside Baltoscandia only Middle Ordovician forms are reported.

2) Forms with fibro-normal septa, the streptelasmatic and columnariid (stauriid) corals, also appear first in North America (Blackriveran) somewhat later in Australia (Estonian) and still later in China, Siberia and Baltoscandia.

3) A fossula *sensu stricto* is first seen in North America (lowermost Upper Ordovician), later in Australia, China and Siberia (Upper Ordovician) and latest in Baltoscandia (Lower Silurian) with one or two Estonian exceptions.

4) A septofossula is a common structure in the uppermost Upper Ordovician rugose corals from most areas. A septofossular stage in corals with a fossula *sensu stricto* is also common at the end of the Ordovician.

5) The first development of tabellae shows the same distribution pattern as for the fossula.

In addition, the following information is of interest in this connection:

6) No certainly conspecific and very few congeneric rugose corals are recorded before the Llandovery from the North American Midcontinent and Baltoscandia. In part, the Appalachian area shows a closer relationship at the generic level to Baltoscandia than to elsewhere in North America (Elias, 1982, text-fig. 24).

7) Tetradiid tabulate corals (*Tetradium* and allied genera) have approximately the same distributional patterns as for the fossula (see above). These corals, however, appear earlier in North America and China (Blackriveran).

#### CONCLUSIONS

We still do not know enough about the systematics, ecology and distribution patterns of early rugose corals to reach any safe conclusions about rugosan faunal realms and their connections. Jaanusson and Bergström (1980) convincingly showed the complexity of distribution patterns for well known Middle Ordovician shelly, graptolite and conodont faunas in Baltoscandia and in the Appalachians. Upper Ordovician and Lower Silurian distribution patterns are not expected to be less complex, so further discussion is very hypothetical.

Pickett (1975) discussed continental reconstructions on the basis of the distribution of coral faunas during the Silurian. By correlating the genera represented in Europe, North America, Asia, Australia, Japan and South America, Pickett found that there were only minor tendencies towards provincialism (and endemism) from upper Llandovery to middle Ludlow times. Richard's and Belbin's reconstruction (see Pickett, 1975) of the position of the continents was, according to Pickett, the most suitable for a reasonable distribution pattern of the coral genera, assuming that most rugose

corals lived under tropical or subtropical conditions. The distribution of reef structures, calcium carbonate deposits, evaporites and red beds also supports this model which collects the continents mentioned above near the equator (Pickett, 1975, p. 150, fig. 4). Rugose corals with a fossula *sensu stricto* and tabellae are very common in these continents in Silurian strata. Monacanthinid corals with coarse trabeculae are, on the contrary, very rare.

If we assume that monacanthinid corals with coarse trabeculae and nonfossulate Streptelasmatis are favoured by temperate climate and that corals with fossula and tabellae are favored by tropical climate, the development of the Ordovician and Silurian rugose corals could be more readily interpreted.

In most modern palaeogeographical reconstructions, based on palaeomagnetic studies and plate tectonics, the North American and the European plates were moving northwards towards the equator during the Ordovician. Such a trend could explain why the Ordovician epicontinental sea of the North American Midcontinent was first invaded by monacanthinid corals, somewhat later by nonfossulate streptelasmatis and columnariid corals, and last by fossulate streptelasmatis corals with tabellae. The same trend can be observed in Baltoscandia but somewhat later, which could indicate more temperate conditions than in North America (and also than in Greenland, Siberia, China and Australia) during the Middle and Upper Ordovician.

A full discussion of the evidence bearing on this theory is beyond the scope of this paper. For example, only a few of the ecological factors normally controlling faunal distributions are included in the discussion above. The model is proposed as a basis for further discussion and as an inspiration for further detailed examinations of the morphological structures, ecology and faunal distribution of rugose corals.

#### SYSTEMATIC PALEONTOLOGY

Suborder **MONACANTHINA** suborder nov.

*Diagnosis.*—All rugose corals with monacanthine septa.

*Discussion.*—The following families are included:

Family *Stauromatidiidae* Pedder & Oliver, 1982. *Original diagnosis:* Members are characterized by having a septothecal marginarium that normally lacks dissepiments and coarse monacanthine locally bifurcating trabeculae. Parricidal increase normal. *Genera included:* *Stauromatidium* Oliver & Pedder, 1979; *Farabophyllum* Lavrusevich, 1971.

Family *Lambelasmatisidae* Weyer, 1973. *Original diagnosis:* Corals with porous septa without synap-

ticulae and never everted calice (translation). *Remarks:* Weyer (1973) placed this family in the superfamily Calostylaceae Zittel, 1879 because of the supposed porous septa. The superfamily was in turn placed in the suborder Streptelasmatina. Because of the septal structure (see above). I see no close relationship between lambelasmatisid and calostylid corals. Therefore, only the former group is here included in the Monacanthina.

Subfamily *Lambelasmatinae* Weyer, 1973. *Original diagnosis:* Lambelasmatisidae with zaphrentoid pinnately arranged septa and predominantly a concave cardinal side. *Genera included:* *Lambelasma* Weyer, 1973; *Dybowskiina* Weyer, 1973; ?*Lambeophyllum* Okulitch, 1938.

Subfamily *Coelostylinae* Weyer, 1973. *Original diagnosis:* Lambelasmatisidae with radially arranged septa and predominantly a convex cardinal side (translation). *Genera included:* *Coelolasma* Weyer, 1973; *Coelostylis* Lindström, 1873; *Estonielasma* Weyer, 1973; *Rectigrewingia* Kaljo, 1961; *Hillophyllum* Webby, 1971.

Subfamily *Primitophyllinae* Ivanovski, 1968. *Diagnosis herein:* Lambelasmatisidae with extremely short septa throughout ontogeny. No tabulae. *Genus included:* *Primitophyllum* Kaljo, 1956.

Subfamily *Wenlockiinae* Spassky & Kratsov, 1974. *Diagnosis* (Hill, 1981): Monacanthine septa and short cardinal septum in notable fossula. *Genus included:* *Wenlockia* Kato, 1966.

Family *Palaeocyclidae* Dybowski, 1873. *Diagnosis herein:* Discoid or patellate rugose corals with septa of small monacanthine trabeculae. *Genus included:* *Palaeocyclus* Edwards & Haime, 1849; Hill (1981) included *Bojocyclus* Prantl, 1939 and *Rhabdocyclus* in this family, but they are here excluded because of their rhabdacanthine septa.

The ontogeny is not yet known in detail for several of the monacanthinid genera listed above so their inclusion in different subfamilies is uncertain. *Lambeophyllum* is one of the most problematic genera and needs careful revision. Forms with tufted monacanthine trabeculae are at present not included in the suborder Monacanthina.

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## CNIDARIAN PHYLOGENY — A BIOMECHANICAL APPROACH

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## ABSTRACT

An analysis of cnidarian evolution must begin with the biomechanical properties of the soft body, since its construction determines the form and arrangement of hard skeletal parts. Cnidarians can be derived from free living early metazoans, the body of which was supported by a jelly-like substance containing connective tissue, fibers and muscles. Adaptive changes in consequence of sessility led to polyps of anthozoan type, with the gelatinous body support replaced by a fluid filled hydrostatic skeleton and a grid of connective tissue and muscles arranged on the mesenteries and the body wall. Scyphozoa arose through the improvement of regular oral-disc delamination, thus developing medusae. Decrease of polyp size and reduction of the mesenteries are interpreted as adaptations facilitating this process. Evolution of both Hydrozoa and Cubozoa started from the scyphozoan form. The key event was the development of polyp colonies, enabling the transformation of strobilation into medusa budding.

## INTRODUCTION

Evolution is a process that gradually changes animal body construction. Because of this, the following arguments on cnidarian evolution will be based mainly on considerations of the soft-body system and on the possibilities for evolutionary change determined by soft-body construction. In this methodological approach the organism is understood as an energy transforming apparatus (Gutmann and Bonik, 1981), and evolutionary development is seen as a process of internal and external economies of input and output. This method tries to answer the question, how and why certain steps in evolution took place, in that it outlines the conditions under which the transformation of a certain body construction was possible. (This is always implied, even when the text flows in a more narrative style, making complicated transformations easier to describe and to understand.) The method cannot resolve the phylogenetic relationships of all the groups, but neither can any phylogenetic approach.

There is no difference in kind in the interpretation of extant animals and fossils, though the interpretation of fossils, because of their often rather fragmentary nature, may be difficult or even impossible. Moreover, fossil evidence shows us that the main cnidarian groups were already present at the beginning of the metazoan fossil record. Thus the general outline of phylogeny based on changes in soft-body constructions cannot hope to get direct support from fossil evidence.

## THE HYDROSTATIC SOFT-BODY SYSTEM

The most important principle of animal body construction is the hydrostatic soft-body system. In a technical sense it is always established once a soft membrane is placed under tension by a filling of gas, fluid, or fine-grained material, for example the soap bubble, the balloon, the sugar sac, or the fire brigade hose. Such

biological systems are numberless: cells, organs such as lungs and digestive tracts, growing zones such as cartilage and, in soft-bodied animals, the whole body. Since hard skeletal parts are always preformed and produced in soft bodies, it is not an exaggeration to say that the hydrostatic soft-body system is the principle on which organic forms are built up.

If composed of uniform membranes, these systems would be spherical like soap bubbles. However, the spherical form is normally suppressed and altered by fibers of a certain tensile strength. The fibers may be arranged in the membraneous soft wall of the system itself (as in the sugar sac), or may run through the open inner space as in the dissepiments of the earth worm, or the mesenteries of the coral polyp.

Since the form and arrangement of all sclerites are determined by soft-body conditions, skeletal material can be explained only insofar as it is possible to study or reconstruct the soft-body system by which it was formed. If this is not possible, as in fragmentary fossils or parts of animals such as conodonts, or in vague soft-body impressions in the sediment, such forms must remain unexplained as "problematica."

## THE ORIGIN OF CNIDARIA

There is little doubt that the cnidarians originated from primitive metazoans, and further discussion is decisively conditioned by what kind of body construction we must assign to those early animals. The development of metazoans is no longer seen as an aggregation of cells forming hollow balls, but, on the contrary, as a development of systems which had mechanical support from the beginning on (Bonik, Grasshoff and Gutmann, 1976, 1978). This was made possible by the deposition of a jelly-like substance in the endoplasmic reticulum of a multinuclear protozoan, increasing the body size and producing an arrangement

of cell membranes around the nuclei. Connective tissue fibers were formed by the gelatinous substance, and muscle cells were differentiated. Canals in various forms, lined with ciliated epithelium, may have penetrated the body. At this level of construction many different forms were already possible.

In such hypothetical gelatinous animals we see the technically necessary and basic construction for all further animal evolution by adaptive changes under the conditions of different ways of life. The only animal group in which this basic form has not essentially changed is the ctenophores. They have only modified some features, such as the ciliar arrangement in plates and rows, and show part of the range of forms possible at this constructional level.

The key event for cnidarian evolution was the adoption of a sessile way of life. Sessility often arises in the animal kingdom at different levels of organisation and the most important condition for it is always that the food catching system functions independently of the locomotory system. Adaptations to sessile life are always similar: reduction of the locomotory system, increase of the food catching (often filtering) system (the latter often in the form of tentacle crowns more or less radially arranged), sometimes the development of a holdfast, the development of muscles for rapid withdrawal, and often allowing Siamese twins, thus beginning to build up colonies.

These are paradigms towards which the body construction of gelatinous animals must have been improved when assuming sessility. Radial arrangement of tentacles and a more cylindrical body form were probably not the greatest changes. Far-reaching transformations, however, started with the retraction of the exposed upper parts of the body with mouth and tentacles (Text-fig. 1).

The jelly substance is rather stiff, and changes in form require some effort. Under these circumstances, retractor muscles arranged themselves around the mouth region extending down to the base. However, the stiffness of the jelly must have inhibited withdrawal, chiefly in the center of the body, and any replacement of jelly by fluid would have been an advantage. This was a technical dilemma, since the longitudinal muscles in the center of the body could not be abandoned. The well known solution was that the gastric cavity, narrow in the beginning, enlarged by the formation of pouches passing between the muscles. These remained on sheets of body tissue, which developed into the thin "mesenteries." The process of hollowing out could proceed because the body support was not lost: the gelatinous wall became thinner, but it was placed under tension by the fluid filling of the cavity. A totally hydrostatic system was the result when the

inner wall reached the outer wall. When the fine structure of the "combined walls" was adapted towards a highly contractile body, the epithelial muscle cells developed by packing the voluminous cell body containing the nucleus aside into the epithelium and attaching the long, thin contractile part onto the sheet of jelly and connective tissue fibers. Once developed, epitheliomuscular cells are used throughout the cnidarian stem because of their high contractility.

The mesenteries, arranged symmetrically in couples, hold the pedal and oral discs flat, and the pharynx in its introverted position. The pharynx works as a valve, protecting the animal from collapse by loss of pressure, and bearing the siphonoglyph which acts as a water pump.

The resulting multimesenterial hydrostatic body is the basic cnidarian body plan and is technically identical with the anthozoan polyp (Text-fig. 1).

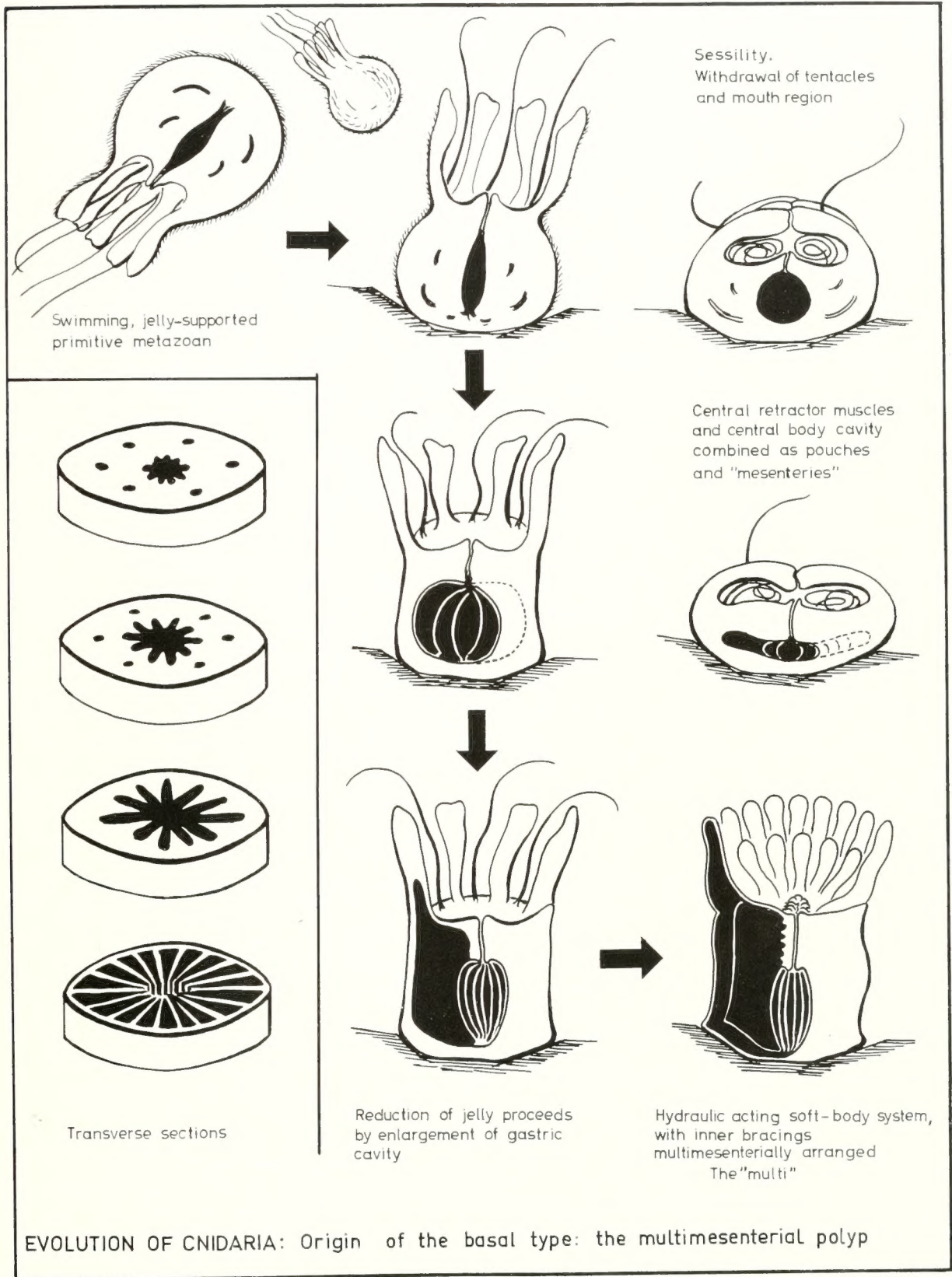
## RADIATION OF THE ANTHOZOA

The Octocorallia, with a minimal number of mesenteries and a gelatinous coenenchyme penetrated by canals lined with a ciliated epithelium, which is used for budding and building up colonies, seems to be one line of anthozoan evolution. The other line, the "Hexacorallia," developed bigger polyps equipped with more mesenteries.

The extant hexacoral groups, with mesenteries in couples but not in pairs, have a small adult body size (*Antipatharia*) or they grow to a larger size along a median strip of the body cylinder (*Ceriantharia*, which burrow into the substrate, have a reduction of mesenteries in the hind part of the long body; *Zoantharia*, polyp colonies with lacunate coenenchyme). None develop large oral or pedal discs.

The groups with paired mesenteries grow all around the body cylinder and thus develop very large, flat pedal discs and oral discs with many regularly arranged tentacles (*Actiniaria*, *Corallimorpharia*, *Scleractinia*). This body form permits essentially endless growth. In stony corals, this is combined with a calcareous platform which enables this construction to give up the cylindrical body form, since the basal disc is no longer mobile, but fixed to the (self made) substrate.

In the *Rugosa* the well known mode of septal insertion makes it extremely probable that the mesenteries were not paired. However, their arrangement allowed growth in four large quadrants, which encompass practically the whole body cylinder. Thus the *Rugosa* were able to deposit a calcareous platform, as this is technically possible only for those Anthozoa growing all around the body cylinder. The unpaired mesenteries



Text-figure 1.—Evolutionary transformation of the primitive metazoan body plan into the multimesenterial polyp of anthozoan type.

and their mode of addition, however, prevented the rugosan body plan from becoming transversely elongate or meandroid. This possibility is confined to those anthozoans with paired mesenteries (Hand, 1966).

Septal arrangement in the Heterocorallia and their relatively thin, tubelike growth makes it probable that they also had unpaired mesenteries. The Tabulata require further consideration as their relationships remain open to question.

#### THE TETRARADIAL POLYP

Further cnidarian development was probably induced by a certain mode of asexual reproduction, oral disc delamination (Text-fig. 2). Actinians show us that the multimesenterial construction is capable of transverse fission. If a multimesenterial polyp used this procedure for regular propagation, increased efficiency could have been obtained by size reduction, since it is advantageous to divide smaller quantities of body tissue. This size reduction, however, could not go too far, since gonads need space for ripening. When the gonads were no longer confined to the polyp stump alone, but began to ripen in the swimming stage as well, the condition was reached whereby the swimming stages no longer needed to settle down, but ripened the gonads earlier whilst still swimming. From this point on, nothing prevented increase in size of the swimming stage (which we may now call medusae), and total adaptation of the polyp for disc delamination. With diminishing polyp size, the mesenteries were reduced and body support was more or less assumed by the now relatively thick wall, whilst the hydrostatic functions were lost. The development of the basal cuplike periderm, to which the polyp is fixed by desmonemes, was necessary since fixation to the substrate by means of a flattened pedal disc was no longer possible after the loss of the mesenteries.

The medusae develop by constriction of the polyp body. To prevent the premature release of the medusae, it was necessary that tissue bridges of some tensile-strength were retained axially. Mesenterial structures were available for this purpose. Big longitudinal muscles were superfluous in this polyp, but the small muscle fibers in the funnels pulled down from the oral disc were evidently sufficient for this task. Since the coupling of mesenteries established an even number, an even number of such cord muscles, functioning as guyropes, remained. Two evidently were not enough for stability, so four remained as the smallest effective number.

The result is the sterile, tetradial, medusa-producing polyp, fixed to a chitinous basal periderm or enclosed in such a tube. This construction is the starting point for tetradiality, inherited by all descendants

and used in one way or the other in polyps and medusae.

#### THE SCYPHOZOAN LEVEL

Scyphozoan polyps are essentially such "tetra"-polyps, but specialised in having no circular muscles in the body wall. The loss of this muscle layer, which is present in anthozoans and hydrozoans, could perhaps be explained as a consequence of periderm tube dwelling. Development of the periderm tube provided external support to the polyp so that the polyp wall became thinner. The Coronata show this construction (Werner, 1966; Chapman and Werner, 1972), which seems to me highly derived, not primitive.

Radiation on the scyphozoan level (Text-fig. 2) can be explained by the different modes of managing the medusae. In the Rhizostomeae and the Semaestomeae (which differ in the construction of the medusae) the nude "strobila"-type of polyp produces numerous medusae; in the Stauromedusae, a solitary medusa ripens and remains on the polyp stump (Thiel, 1966).

In the Conulariida the fossil evidence is against strobilisation. The four apertural lappets were evidently closed by four longitudinal muscles, which would have had to be cut during medusae development, a very improbable presumption. Fossils show, moreover, that fully developed polyps were severed from their bases by the growth of a diaphragm near their tip (=base). Because of these observations Kiderlen (1937) supposed that the bigger Conulariida were swimming organisms. We may add today that they probably were solitary medusae attached to their polyp stumps and subsequently dehisced.

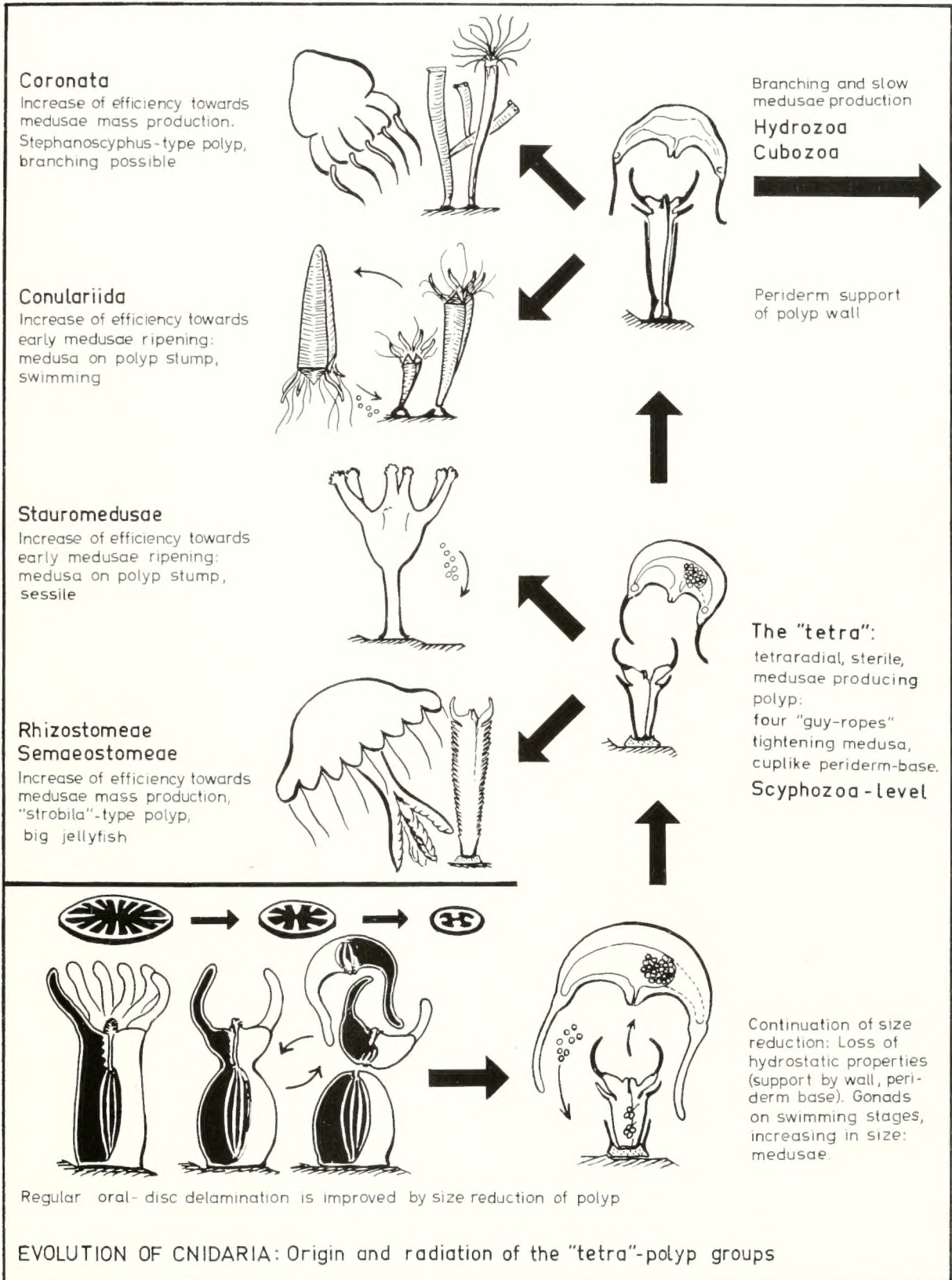
The periderm tube is mechanically a very important feature, because it enables the polyp to branch. Branching occurs already in some species of Coronata, but they are so highly specialized towards mass-production of medusae that they could not escape the constructional level of what we call the Scyphozoa.

#### THE SIMPLE, HIGHLY EVOLVED POLYPS: CUBOZOA AND HYDROZOA

Probably two evolutionary lines (Text-fig. 3) started from such periderm-supported, branched tetradial polyps, which were not so efficient in the production of medusae. This constructional level sets conditions leading to the differentiation of polyps for feeding and for production of medusae. Since the latter are nourished from within the colony, it was no longer necessary to retain the old method of oral-disc delamination.

In one line, efficiency increased towards few branches and a high frequency of medusae release (Text-fig. 3, right). The medusae-producing polyps were reduced to buds, which are detached so early that they must

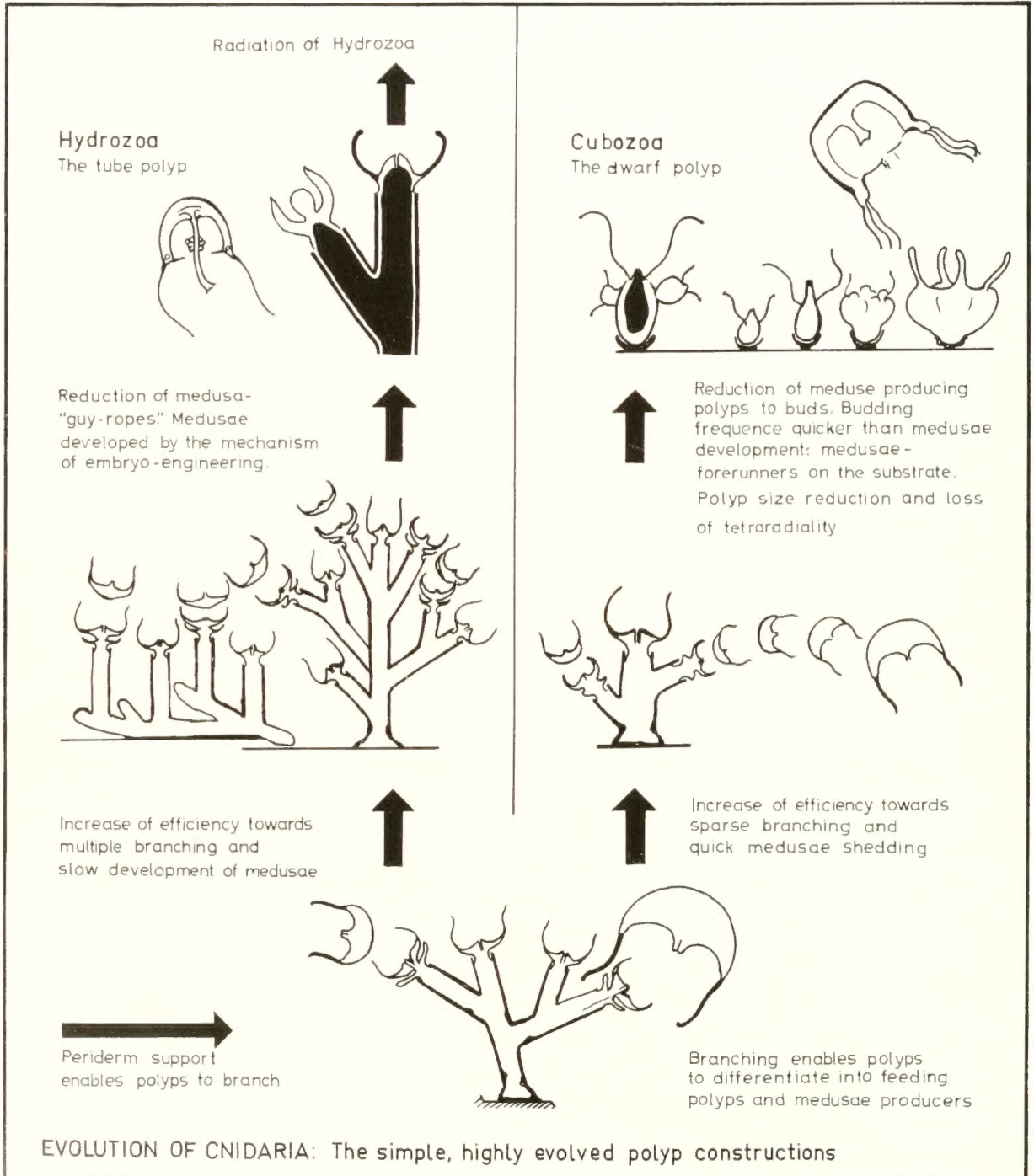




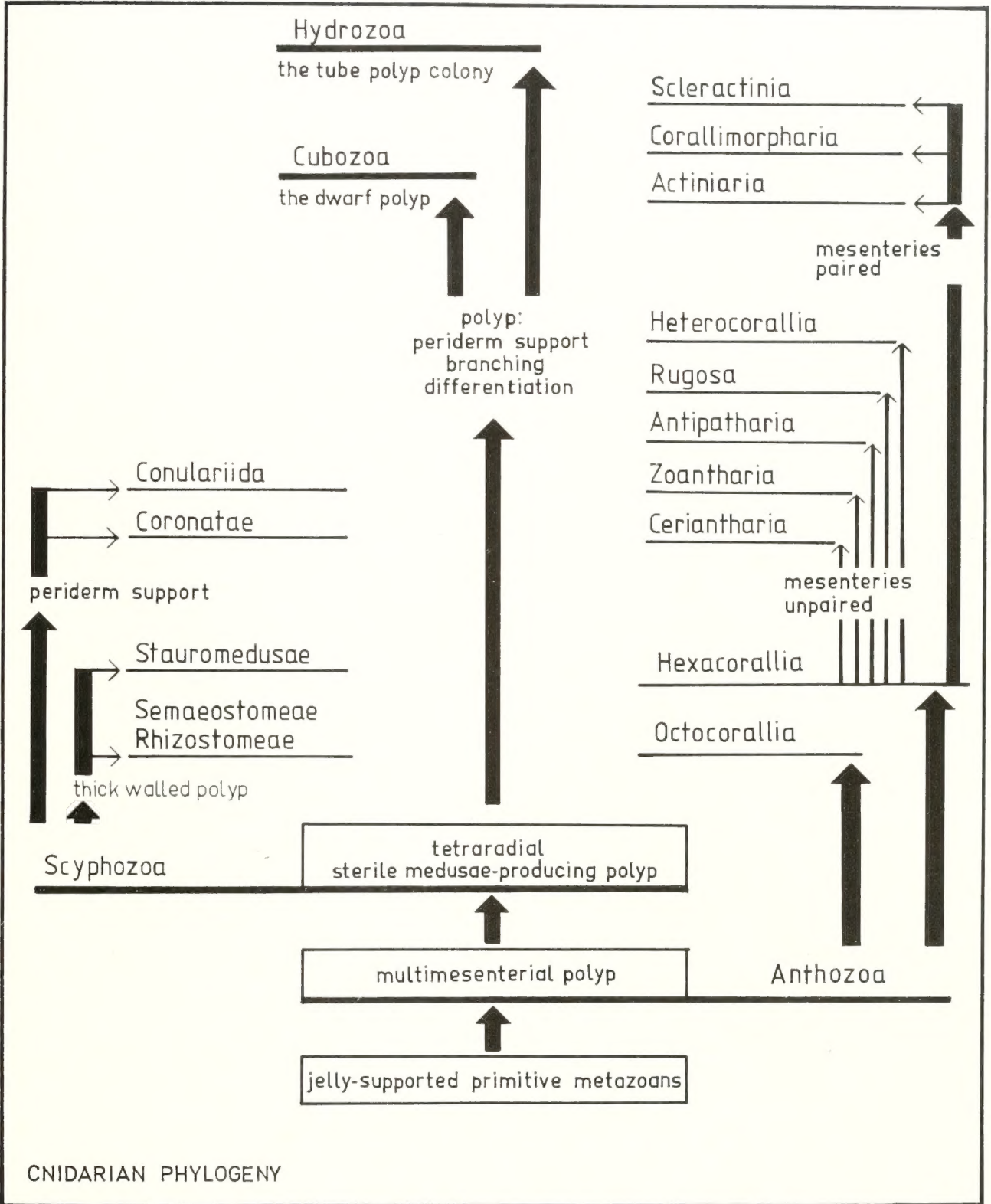
Text-figure 2.—Transformation of the multimesenterial polyp into the tetradial polyp of scyphozoan type. Radiation at the scyphozoan level.

make the final development into medusae resting on the substrate (in a periderm cup). All tetra-radial structures were lost, since they were not needed in this process, but tetra-radiality remained in the medusa. The reduction of polyp size must be seen in connection with this budding process. The result is the dwarf polyp of the Cubozoa, recently described by Werner (1975).

In the other evolutionary line (Text-fig. 3, left) efficiency was increased towards multiple branching and slow medusae development and transformations are also far reaching. Here the old oral disc delamination was gradually changed into medusa bud formation profiting from all the advantages of embryo engineering. The tetra-radial inner structures associated with me-



Text-figure 3.—Development of the periderm supported hydrozoan polyp colony (left) and the dwarf polyp of the Cubozoa (right).



CNIDARIAN PHYLOGENY

Text-figure 4.—Evolutionary levels of cnidarian construction. The Tabulata are not included because of their uncertain position.

dusae delamination were reduced and the result was the tubular polyp of the Hydrozoa. The medusa buds can be shifted to any place in the polyp wall, and the very simple tubular polyp construction is architecturally almost unlimited in colony design. This explains the enormous radiation of the Hydrozoa.

#### CNIDARIA, AN EVOLUTIONARY DEAD END

Several other body systems have not been dealt with here, for example, cnidae, position of the gonads, arrangement of muscles, and the architecture of medusae. They at least do not contradict the view of cnidarian evolution presented (Text-fig. 4), and in some points they strongly support it.

There is good reason for the radial arrangement of the mesenteries in the basic cnidarian polyp, which cannot be transformed in a technically reasonable way into a basic coelomate construction, a cylindrical body transversely compartmented by dissepiments (Bonik, Grasshoff and Gutmann, 1976). Neither could the coelomate body plan be derived from any other cnidarian construction.

The Cnidaria are, in consequence, an evolutionary dead end, not a transitional stage between "lower" and "higher" animal constructions. The special structure of their body wall and their "hollow" body were often interpreted, without any respect to the biomechanical implications, as indicating a primitive level of organization. These features, however, can be explained as adaptations of the primitive metazoan body to sessility. The Cnidaria reached a high level of variation and organization, no less than in any other animal group.

#### OTHER HYPOTHESES ON CNIDARIAN PHYLOGENY

An overview of the literature shows that almost every possible polarity of morphological sequence of the main cnidarian groups had been suggested. In one way or another all these hypotheses are based on the germ layer theory of Haeckel, which he developed in connection with his gastraea theory of metazoan evolution. Both theories do not take into account important morphological constraints and hence are biomechanically untenable (Bonik, Grasshoff and Gutmann, 1978). Haeckel's theories have been modified, but essential biomechanical difficulties have never been eliminated. The animal body was envisaged as a configuration of characters, not as the construction of a living apparatus. Thus a rather simple body plan must be taken as evolutionarily primitive, and a more complicated body plan as more advanced.

(1) The traditionally most widely held hypothesis takes the Hydrozoa as the primitive cnidarian group. In connection with his gastraea theory, Haeckel re-

garded the hydrozoan polyp as the initial form. However, transformation of the tube-like polyp into polyps with taenioles and oral-disc delamination, or with mesenteries cannot be accepted.

(2) An early objection to Haeckel's assumption was that it did not explain the development of medusa budding. Brooks (1868) assumed that not the polyp, but the medusa was the first cnidarian. This hypothesis, discussed and favoured by Hyman (1940) and Hand (1959) has been practically abandoned by all recent workers. The assumption that the larva of the medusa (actinula larva) settled down and formed a branched colony of hydrozoan type is not explained in a gradualistic sense, nor are other important features, such as tetradiality in the medusae, oral disc delamination in scyphozoans, or the mesenterial arrangement of anthozoan polyps.

(3) Recently, the tetradial polyp was proposed as the starting point of cnidarian evolution by Chapman (1966) and Werner (1973). The implications of this hypothesis as far as the evolution of the Hydrozoa and the Cubozoa are concerned, can be explained, as I try to show here. However, the theory does not explain the origin of the tetradial polyp, but holds tetradiality as a principle ("Grundbauplan") of the cnidarian and acnidarian form. Here again the problem of the transformation of the tetrapolyp into the anthozoan polyp arises. The tetrapolyp of scyphozoan type is regarded as the most primitive cnidarian because of its simple construction, such as the lack of circular muscles in the body wall. However, just this feature points to a high degree of specialisation, since it is not the presence of muscle layers (and in any case not a single muscle layer) that is the primitive, general condition, but a more or less gelatinous connective tissue and muscle fiber grid, containing all the mechanical properties necessary for further specialisations.

(4) The Anthozoa were considered to be the primitive cnidarian group by Hadzi (1963). This concept was primarily based on configurational similarities of larvae and adult forms. It could not gain ground, since it was developed as an appendix to a hypothesis on metazoan evolution which was refuted because of erroneous morphological evidence. The resemblance of Hadzi's hypothesis with the phylogenetic model presented here is merely superficial.

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## CNIDARIAN FOSSILS FROM THE SINIAN SYSTEM OF CHINA AND THEIR STRATIGRAPHIC SIGNIFICANCE

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### ABSTRACT

Cnidarian faunas of Sinian age have been discovered in three localities in China: Jixi, northeast China, with *Arumberia* and *Glaessnerina* in addition to the local genera *Mashania* and *Jixiella*; Yichang, south China, containing *Charnia*; and Fu Xian, northeast China, including *Cyclomedusa* and *Medusinites*. The first two localities are of Late Sinian age and comparable with the Ediacara fauna of Australia. The third is also Late Sinian, but may occupy a slightly lower position.

### INTRODUCTION

The most outstanding cnidarian fossils of Late Precambrian age come from the famous Ediacara fauna of Australia, which was described and discussed at length by Glaessner (1971, 1979). In the past decade important progress in the study of the Sinian System (ca. 800–600 my BP) and its faunas has been made in China (Xing, 1978; Wang *et al.*, 1978; Xing and Liu, 1979; Liu, 1981; Ding and Chen, 1981). The aim of the present paper is to give a brief review of the Sinian cnidarian fossils so far known in China and of their stratigraphic significance. We are grateful to Professor M. F. Glaessner and Dr. B. Daily (both University of Adelaide) who have kindly examined some of the specimens and made constructive suggestions during their visit to China in 1979.

### GEOGRAPHIC AND STRATIGRAPHIC DISTRIBUTION

Up to the present, Sinian cnidarian fossils are known to occur at three localities (Text-fig. 1):

1. Near Jixi in the eastern part of Heilongjiang (Text-fig. 1-1) the metamorphic Proterozoic belonging to the Xingkaian Fold Zone includes the Mashan Group (Middle to Upper Proterozoic), which is probably unconformably overlain by the Longshancun Group. Rich fossils known as the Mashan fauna (Liu, 1981) have been found in intercalated limestones in the Zhong-sanyang Formation within the upper group. The main forms are: *Glaessnerina* sp., *Arumberia banksi* Glaessner and Walter, *Mashania sinensis* Liu, *M. minuta* Liu, *M. longshanensis* Liu, *M. angusta* Liu, *M. deformata* Liu, *M. annulata* Liu and *Jixiella capistratus* Liu.

2. In Liaoning Province cnidarian fossils were found in carbonate rocks in the Sinian sequence of Fu Xian, which was situated in the eastern subsiding belt of the North China Platform in the Sinian Period. Here the

Sinian begins with the Qiaotou quartzitic sandstone, followed by the Changlingzi Formation mainly composed of variegated shales and thin-bedded micritic limestones amounting to 1500 m in thickness. Medusoid fossils associated with sabelliditids were reported by Xing and Liu (1979) in the uppermost part of the Changlingzi Formation, including the following forms: *Cyclomedusa annulata* (Sprigg), *C. davidi* Sprigg, *C. aff. davidi* Sprigg, *C. gracilis* Xing and Liu, *C. minus* Xing and Liu, *C. simplicis* Xing and Liu, *Medusinites simplex* Xing and Liu, *M. cf. asteroides* (Sprigg) Glaessner, *Planomedusites* sp., *Lianoningia fuxianensis* Xing and Liu (Text-fig. 1, 2).



Text-figure 1.—Sketch-map showing geographic distribution of fossil Cnidaria in the Sinian System of China. 1. Jixi, Heilongjiang Province. 2. Fu Xian, Liaoning Province. 3. Yichang, Hubei Province.

Table 1.—Comparison of some genera of the Mashan fauna of the Jixi region.

Genera	Size of cup	Deformation of cup	Ribs	Median suture of ribs
<i>Arumberia</i>	large, over 100 mm long	slight	strong and multiply bifurcated	unknown
<i>Mashania</i>	small, less than 100 mm long	strong, folded or enrolled	slender, bifurcated	clear
<i>Jixiella</i>	small, less than 100 mm long	not evident	slender, weakly bifurcated	unknown

3. In the type section of the Sinian System in Yichang, Hubei Province (Text-fig. 1-3), the Upper Dengying Formation has a thickness of about 906 m and is divisible into four members. The lower Hamajing Member is a dolomite containing *Trematosphaeridium holtedahli* and *Oncholites*; the succeeding Shiban Member consists chiefly of thin-bedded, sometimes bituminous limestones bearing abundant *Vendotaenia*. Two specimens were obtained from the middle part of this member, which were described by Ding and Chen (1981) as *Charnia dengyingensis*. The Baimamiao Member above is a thick-bedded, light grey, usually micritic dolomite containing the peculiar *Sinotubulites* in its lower part. Finally the topmost Tianzhushan Member consists of only 2–3 m of phosphatic beds, which contain a very rich small shell fauna evidently referable to the basal Cambrian. The Early Cambrian Shuijingtuo Formation carrying a *Tsunyidiscus* fauna rests on the Tianzhushan Member with a clear sedimentary break and yields an Rb-Sr isochron age of 572 my (Yichang Institute of Geology and Mineral Resources, 1981) from the black shale in the basal part.

In addition to the three localities cited above, problematic medusoid fossils have also been reported from the Upper Sinian Liuchapo Formation in Xupu, Hunan Province.

#### FAUNAL CHARACTERISTICS AND CORRELATION PROBLEMS

As far as is known, nearly all the older established genera and species cited above from the Sinian of China are known in the Ediacara fauna of Australia. Some genera, such as *Glaessnerina* and *Cyclomedusa*, are of wide distribution in the world. But the Mashan fauna is characterized by the local genera *Mashania* and *Jixiella*, of interest in their structure as well as in their mode of preservation. Furthermore, in the Mashan fauna, *Arumberia* and *Glaessnerina* are of special significance. *Arumberia banksi* was originally found in the upper part of the lower member of the Arumbera sandstone. The middle and upper members of the Arumbera sandstone rest on the lower member with a disconformity and contain trace fossils and trilobite remains of Early Cambrian age. The Arumbera sand-

stone is underlain by the upper tillites of the Pertataka Formation about 670 my in age. *Glaessnerina* is an important member of the Ediacara fauna and is widely known outside Australia, being found in the Kuibis quartzite of the Nama Group of southwestern Africa, and probably also represented in the Maplewell Series of Charwood Forest, England and in the Vendian, northwest of the Olenek Uplift of northern Siberia.

The local genus *Jixiella* is conical or cylindrical in shape and has a smooth outer "mantle" (*J. capistratus*, Pl. 1, fig. 1), but ribs and grooves and sometimes a sinus are clearly shown on the lower side of the "mantle." *Mashania* is another conspicuous cup-shaped genus but of variable form, sometimes enrolled or folded up in preservation. The characteristics of the three genera are summarized in Table 1.

With regard to the mode of preservation, soft-bodied cnidarians occur mostly as imprints on the lower surfaces of clastic beds, as in the Pound quartzite in Australia and the Kuibis quartzite in southwest Africa. In China, however, they are usually found in dark colored organic or siliceous carbonate rocks not as impressions, but with the soft parts probably gradually filled and replaced by fine sediments or precipitates in a low energy environment. This situation is especially displayed by the Mashan fossils in which rib and groove structures may be observed on different levels in the specimen, and sometimes the variable preserved thickness of the soft body may be estimated (Pl. 1, fig. 1c). The structures of the different parts of the "mantle" surface enable an anterior and posterior side of the specimen to be distinguished, probably related to the current direction that carried the food supply at the time (Pl. 1, figs. 3–4).

In view of the primitive nature of the Sinian faunas, provincialism was certainly not so obvious as in the Early Cambrian. In the Mashan fauna, apart from the local forms *Mashania* and *Jixiella*, the genus *Arumberia* is probably most akin to *Baikalina*, found in the Ayankan Formation of late Eudomian age near Lake Baikal, to which *Mashania* is also closely related. *Glaessnerina*, although widespread in the world, is known in the Khatyspit Formation of Olenek, in the Valdai Formation near Moscow, and in the Vendian

of the western Ukraine Massif, all within the scope of the ancient Eurasian continent. The common presence of the platyhelminthian *Palaeoplatoda* in the Mashan fauna and in the Valdai on the Russian Platform is a further indication of the kinship between the faunas.

Specimens representing *Charnia dengyingensis* from the Yangtze Platform are not very well preserved. The nearest related forms are probably *Charnia masoni* from Charwood Forest, England and a similar form found in the Conception Group of Newfoundland, Canada. It is interesting to note that these three localities may have been distributed to the south of the northern continental massifs and probably occupied a position intermediate between them and Gondwanaland, in the realm of the Palaeo- or Protero-Tethys.

The Ediacara fauna has an age ranging from 680 to 700 my (Glaessner, 1971). There is no direct isometric age data for the Mashan fauna, but it may be correlated with the Ediacaran with some confidence. The *Charnia*-bed in Yichang occurs in a position about 400 m above the base of the Doushantuo Formation (700 my BP) and about 490 m below the Sinian-Cambrian boundary (605 my BP). Thus 650 my may be a reasonable age for that particular horizon.

There seems to be some discrepancy in the stratigraphic position of the *Cyclomedusa*-bed of Liaoning.

The fossiliferous horizon is situated in the middle of the Sinian sequence of 4400 m of carbonate and clastic sediments, but several stromatolite assemblages not comparable with other Sinian sequences occur above the fossil bed, and the top of the Sinian is disconformably overlain by the mid Early Cambrian Jianchang Formation. Indeed, some doubt has been expressed as to the real nature of the medusoid remains, but the recent discovery of sabelliditids indicates that they are at least Late Sinian in age. It is highly possible that they occupy a stratigraphic position lower than the Mashan fauna and the *Charnia*-bed of Yichang (Table 2).

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#### EXPLANATION OF PLATE 1

All specimens are from the Zhongsanyang Formation, Jixi, Heilongjiang Province, China and are housed in the Shenyang Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences, Shenyang, China.

##### Figure

1. *Jixiella capistratus* Liu, No. M.E. 770007, ×1
  - a. Showing the flat, elliptically conical external form and smooth surface.
  - b. Separated end part of the same specimen showing the ribs, grooves and sinus covered by the smooth "mantle."
  - c. Interior of the end part of the flat, elliptically conical body showing impression of ribs and grooves and variation of thickness of the "mantle."
2. *Arumberia banksi* Glaessner and Walter, No. M.E. 807006, ×1
 

Large compressed specimen showing the cup-like shape with weak radial grooves; the grooves are shallow and the ribs are flat to gently convex; the straight apex of the specimen is broken; maximum width about 11.8 cm.
3. *Mashania sinensis* Liu, No. M.E. 827001
  - a. Side view of cup-like or turbinate external form, ×1.
  - b. Anterior view showing the intersecting suture of the bilateral ribs and grooves, ×1.
  - c. Posterior view opposite to Fig. 3b, ×1.
  - d. Basal view, ×1.
  - e. Side view opposite to Fig. 3a, ×1.
  - f. Top view, ×1.
4. *Mashania longshanensis* Liu, No. M.E. 770006, ×1
 

Anterior view showing the intersecting suture of the bilateral ribs and grooves.
5. *Mashania* sp., No. M.E. 807013, ×1
 

Showing various orientations of ribs and grooves because of folded preservation.
6. Specimen showing *Glaessnerina* sp. (upper left) associated with *Arumberia banksi* (lower right) on the same piece of rock. No. M.E. 770012, ×1
  - a. *Glaessnerina* sp., ×3.
 

Showing leaflike bodies, bent near the terminal part of the frond. Primary grooves generally straight, joining the median line at angles of 30–50°; secondary grooves at a high angle to the primary ones, defining about 6–7 secondary branches between each pair of primaries.
  - b. Fragment of *Arumberia banksi* Glaessner and Walter, ×1.





Table 2.—Correlation of the Sinian cnidarian fossil horizons in China (\*my BP, figures adopted from Yichang Institute of Geology and Mineral Resources).

	Yichang, Hubei		Fu Xian, Liaoning	Jixi, Heilongjiang
Cm <sub>1</sub>	Dengying Formation	Tianzhushan small shell fauna	Jianchang Formation	
		605*	-----	-----
Z <sub>2</sub>		Baimamiao Member	Jinxian Group	Longshancun Group
	Dengying Formation	Shibantan Member	Wuhangshan Group	Zhongsanyang Formation
		<u>Charnia</u> -bed		Ganjingzi Formation
		Hamajing Member	Nanguanling Formation	Mashan-fauna
		Doushantuo Formation	Changlingzi Formation	
		700*	<u>Cyclomedusa-Sabelidites</u> bed	
Z <sub>1</sub>		Nantuo Formation	Qiaotou Formation	
		Liantuo Formation 740*		
		800*	-----	-----
		Pt <sub>1</sub> Sandouping Gr.	Pt <sub>3</sub> Nanfen Formation	Pt <sub>2-3</sub> Mashan Gr.

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## CONCHOPELTIS: ITS AFFINITIES AND SIGNIFICANCE

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## ABSTRACT

*Conchopeltis alternata* Walcott, a Middle Ordovician medusoid, is known from only a few specimens. Because of its "square" outline and low-pyramidal form, the genus has been considered a conulariid (Subclass Conulata). One *C. alternata* specimen, remarkable for showing tentacles, has fueled arguments relating *Conchopeltis* (and the conulariids) to the Scyphozoa. However, this and other specimens are bilaterally symmetrical, having one of the four sides distinctly shorter and steeper than the others. I suggest that this side was anterior and that this symmetry makes assignment to the Conulata and to the Scyphozoa doubtful. *Conchopeltis* can be interpreted as a hydrozoan or scyphozoan offshoot, or as a separate class of the Cnidaria. The relationships of the conulariids are unknown, but they are not close to the conchopeltids, and they have not been shown to be cnidarians.

## INTRODUCTION

The genus *Conchopeltis* and its type species, *C. alternata* Walcott, were first described in 1876 from seven specimens stated to be from the upper third of the Trenton Limestone at Trenton Falls, New York. There is some question about the precise stratigraphic position and locality of these and other known specimens, but all seem to be from the general area and formation named. They are either late Middle or early Late Ordovician in age.

Specimens of *Conchopeltis alternata* are uncommon. Only two specimens in addition to the seven in the type lot have been reported in the literature, and six more are reported here for the first time (see Table 1). This study is based on laboratory examination of eight specimens (the others could not be located) plus the published illustrations of three more. Table 1 lists all known specimens, their principal illustrations, and their repositories, if known.

## CONCHOPELTIS

*Conchopeltis* has a low pyramidal form (Pl. 1) and a very thin test of unknown composition. In most specimens four lobes give a "square" outline and may suggest at first glance a fourfold radial symmetry. The lobes are separated by grooves that radiate from the apex, and each lobe is divided into two equal parts by shallower grooves. In addition, the surface bears fine radiating striae and concentric growth lines. Specimens are 5 to 6 cm in diameter and 1 to 1.6 cm high; they are very low pyramids.

The most interesting specimen known is now in the collection of the New York State Museum (NYSM; see Table 1, specimen 8; Pl. 1, figs. 1, 2). This specimen is remarkable for the clear preservation of a number of tentacles which extend beyond the margin of the test in such a way as to suggest that the animal was washed along the substrate, dragging its tentacles be-

hind. The tentacles and their preservation pattern provide convincing evidence that the specimen was a cnidarian and probably a medusoid. Glaessner's (1971, p. 7) suggestion that *Conchopeltis* was a polyp, cannot be ruled out but seems unlikely in view of the evidence of drifting, and the bilateral symmetry discussed below.

The "rectangular" margin of the NYSM specimen is 53 by 62 mm in short and long diameters and is 15

Table 1.—Known specimens of *Conchopeltis alternata*. (\* Present location not known.)

Type lot, Museum of Comparative Zoology, Harvard Univ. (MCZ):

- 1) 27930, holotype, illus. Knight (1937), Moore and Harrington (1956), and herein; positive and negative composite molds.
- \*2) 27928, paratype, illus. Ulrich and Scofield (1897), p. 823, and herein.
- \*3) 27927a, paratype, illus. Knight (1937), fig. 4.
- \*4) 27927b, paratype, illus. Knight (1937), fig. 5.
- \*5), \*6), \*7) not described or illustrated.

Mentioned by Moore and Harrington (1956), p. F32, as exhibiting tentacles (formerly in Cornell Univ. collection):

- 8) Illus. Moore and Harrington (1956), fig. 22, and herein, not previously described; preserved in New York State Museum (NYSM 12914A, B); positive and negative composite molds.
- \*9) "Somewhat smaller specimen," not illus. or described; present repository unknown.

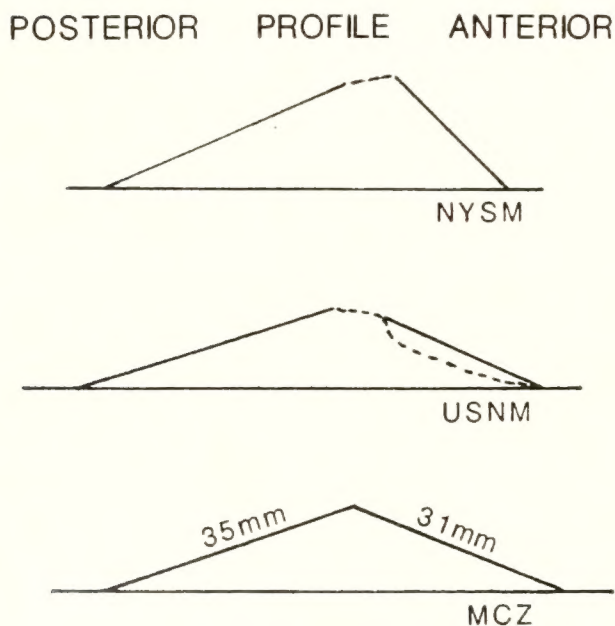
U.S. National Museum of Natural History (USNM):

- 10) 375444, positive mold; profiled herein.
- 11) 375445, positive and negative molds, illustrated herein.
- 12) 375446, positive mold.
- 13) 375447, positive mold.
- 14) 94235, positive mold.

New York State Museum (NYSM) (see no. 8 above):

- 15) 14077, positive mold; originally in Rust collection as specimen no. 8 (and ?9); but this is apparently not specimen 9 as 9 seems to have been in the Cornell collection in 1956 whereas specimen 15 was "Purchased of Wm. P. Rust, July, 1890" by the NYSM according to NYSM records; illustrated herein.

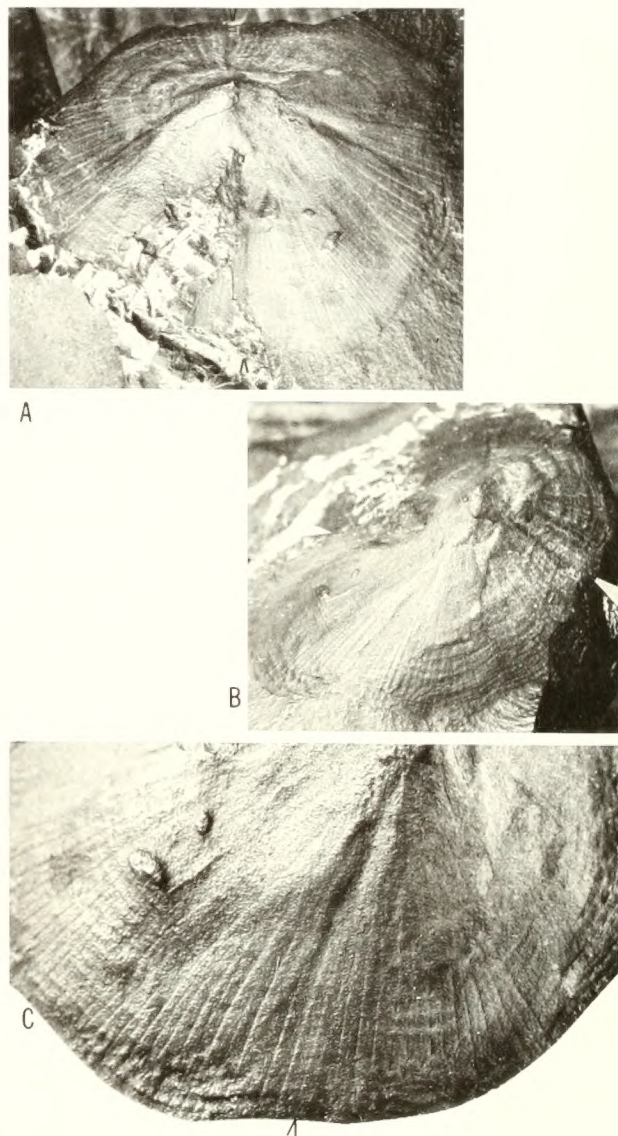
mm high (as preserved). The apex is not exposed; its exact nature is unknown, but it can be assumed to be like that of the holotype (Pl. 1, figs. 5–6). On this assumption, the apex is 24 mm from the “anterior” margin (measured along the surface of the test) and 40 mm from the posterior margin (Text-fig. 1a). Four distinct lobes are apparent, and their arrangement gives a distinct bilateral symmetry to the test. The shortest lobe is arbitrarily termed “anterior” (toward the top of plate in each specimen); the two lateral lobes are narrower (measured along the test margin) than the anterior and posterior lobes but have approximately the same radial length (apex to margin) as the posterior lobe. Each lobe seems to be bisected by a weak radial depression. Fine radiating striae are uniformly spaced on the surface of the test; at the test margin, these are commonly  $\pm 1$  mm apart (0.7–1.2 mm). Only a few striae extend to the apex; most extend only part way and are intercalated between longer striae in such a way that the space between striae is more or less constant. The striae are crossed by two or more series of concentric growth lines; the coarser lines are 3–4 mm apart on the posterior and lateral lobes, somewhat more closely spaced on the anterior lobe. The anterior slope of the test is slightly wrinkled, presumably because of compression during preservation, but the wrinkling is not enough to suggest that the animal may have originally had four lobes of equal length. Indeed, the bilateral symmetry



Text-figure 1.—Simplified anterior-posterior profiles of three symmetrical specimens. The dashed line on *a* marks broken apex; the dashed line in *b* marks the broken apex and the true anterior profile. Specimens are: *a*, NYSM 12914; *b*, USNM 375444; *c*, MCZ 27930, holotype.

with short steep anterior slope seems to have been fundamental.

Tentacles are preserved extending away from the test on its posterior half (Pl. 1, fig. 1). These are seen on both the positive and negative composite molds as clearly delimited black marks on the gray limestone matrix. The longest tentacle extends 19 mm from the



Text-figure 2.—*Conchopeltis alternata* Walcott; positive composite mold, NYSM 14077, “Trenton Limestone (middle). From the diggings owned by Wm. P. Rust and C. D. Walcott, in Herkimer Co., near Trenton Falls. Purchased of Wm. P. Rust, July, 1890”. (From NYSM Catalog). A. Dorsal view, “anterior” to top of figure,  $\times 1$ . B. Oblique view of dorsal right anterior,  $\times 1$ . C. Surface detail, radiating grooves and faint concentric lines on “right” side of same specimen,  $\times 2$ . Arrows mark anterior and posterior grooves in Figs. A, B; right groove in C.

The specimen is torn (anterior margin) and slightly distorted but shows its bilateral symmetry and short, steep “anterior” lobe very clearly.

Table 2.—Length of anterior and posterior lobes in studied specimens. Specimen numbers correspond to those in Table 1 of this paper.

Specimen	Anterior lobe	Posterior lobe	Remarks
1	31 mm	35 mm	Profiled in Text-fig. 1c; Pl. 1, figs. 5, 6.
2	21	35	Based on publ. illustr.; Pl. 1, figs. 3, 4.
8	24	40	As restored in Text-fig. 1a; Pl. 1, figs. 1, 2.
10	27	38	Profiled in Text-fig. 1b.
11	25	35	See Pl. 1, fig. 7.
12	±21	37	
13	27	36	
14	25	35	
15	19+ est. 5	37	See Text-fig. 2.

test margin but 8–12 mm is the common length. The tentacle impressions are parallel-sided but gently tapering at their distal ends (Pl. 1, fig. 1). Only one kind of tentacle is preserved and there is no suggestion that they had bulbous ends. Exact counts are not possible but where best seen (Pl. 1, Fig. 1, left) there is approximately one tentacle for each sector defined by the radiating striae that reach the margin. I originally termed these tentacles “apparent” to avoid being overly positive, but I can see no other explanation for these morphologic features.

Other known specimens of *C. alternata* are similar to the NYSM specimen, although several are distorted (Pl. 1, fig. 7) or torn in various ways (*e.g.*, Knight, 1937, pl. 29, figs. 4 and 5). Individual variation in height, apical angle, and in the eccentricity of the apex are shown in Text-figure 1 and on Table 2. The MCZ holotype is low and has an “anterior” lobe that is only slightly shorter (31 vs. 35 mm) than the posterior one (Text-fig. 1c). Knight (1937, p. 187) considered this as “the only specimen that is not obviously distorted or distorted and torn.” However, one of the type lot (Table 1, specimen 2) was illustrated in a pen and ink sketch by Ulrich and Scofield (1897, p. 823; herein Pl. 1, figs. 3–4), as having the short steep “anterior” lobe. Knight (p. 187) dismissed this specimen as “considerably distorted” but this interpretation is unlikely in view of the symmetry and the similarity of the illustrations to several other specimens now known (Text-figs. 1 and 2, and Table 2). Indeed, I consider the Ulrich and Scofield illustrations to represent excellently the common appearance of the test.

The composition of the periderm or test is unknown. Walcott (1876, p. 93) referred to it as “of a membranous character” and described folded and torn periderms in the type lot. Knight (1937, p. 186) emphasized the fragility also, “exceedingly thin and fragile, flexible.” Moore and Harrington (1956, p. F57) described the periderm as “very thin and presumably consisting mainly of a chitinous substance.” This composition was apparently deduced from the preservation characters noted but is reasonable. The periderm was apparently organic, possibly chitinous, and the mate-

rial itself has probably not been preserved in any of the specimens. It was extremely thin, it wrinkled easily, and was torn in some specimens before fossilization. There is no evidence that the test was mineralized.

### CONULATA

Conulariids have four-sided pyramidal tests with a squarish cross section. They have a very acute apical angle (they are high pyramids, rather than low ones), and their relatively rigid tests are composed of a chitinophosphatic material. Fossils are locally common and range from the Upper Cambrian to the Permian or Triassic. Tests are mineralized and often well preserved. Detailed discussions of the group are included in Moore and Harrington (1956, p. F54–F66), and Kozłowski (1968).

### RELATIONSHIPS

All 19th-century descriptions of *Conchopeltis* referred to it as a patelliform mollusk (gastropod). Knight (1937) showed that this interpretation was erroneous and suggested that because *Conchopeltis* specimens were four-sided pyramids, they must be related to the Conulata. This assignment was based on his interpretation (discussed above) of the almost equidimensional holotype as typical and all other specimens (then known) as distorted.

In the same year that Knight proposed the *Conchopeltis*-Conulata relationship, Kiderlen (1937), suggested that the Conulata were scyphozoans, basing his argument on the fourfold symmetry and the presence in some conulariids of internal structures that he termed “septa.” Kiderlen’s reconstructions of medusoid and polypoid conulariids (1937, text-figs. 45–47) were based on his interpretation of the so-called septa and other internal markings. Kiderlen’s interpretations were, and still are, extremely interesting even though speculative, but, at best, he suggested possible interpretations of conulariid features that are still little known and questionably understood.

A discussion of the Conulata is beyond the scope of this paper. “Septa” such as those described and illus-

trated by Wiman (1894) and by Knod (1908) need to be studied and described in detail and, because conulariids are common in many places, this is certainly feasible. I do not know how to interpret these so-called septa or the internal ridges of other conulariids, but I see no particular reason to relate them to the internal divisions, "septa," of living scyphozoans. However, they do support the interpretation of a fourfold radial symmetry in the conulariids.

A circle was completed when *Conchopeltis* was shown to have tentacles. Moore and Harrington (1956) used this new morphologic detail to further support their assignment of the conulariids to the Cnidaria. They formally proposed the Subclass Conulata (in the Class Scyphozoa) to include *Conchopeltis* (Suborder Conchopeltina Moore and Harrington).

The most extensive additional published contribution to this question of relationships is found in a series of papers by Bernhard Werner (*e.g.*, Werner, 1973), in which Werner argues that the living *Stephanoscyphus* is a descendant of the conulariids. *Stephanoscyphus* is the polyp stage of a scyphozoan. It has a peridermal tube, circular in cross section, but with external markings that are not unlike those on some conulariids. The polyp strobilates within the tube, releasing medusae in the usual scyphozoan way. The key feature is the peridermal tube, which is apparently composed of chitin or a chitin-like material. This tube may well indicate that *Stephanoscyphus* is a primitive scyphozoan, but it is not evidence of a linkage to the conulariids.

Kozłowski (1968), in a detailed study of conulariid ontogeny and morphology, argued against any relationship of the conulariids to *Conchopeltis* or the Cnidaria. Kozłowski used many of the same arguments that I am using but from the conulariid point of view. Scrutton (1979, p. 172–174) provided an excellent review of this and other work; he also questioned any direct phylogenetic link between *Conchopeltis* and the conulariids, but tentatively, at least, kept the Conulata in the Cnidaria.

*Conomedusites* Glaessner and Wade, from the Ediacaran beds in South Australia is similar to *Conchopeltis* in having four radial lobes that are subdivided in larger specimens, and concentric growth lines that suggest the presence of a periderm. Two specimens of

*Conomedusites* are said to preserve tentacles (Glaessner, 1971, p. 8, pl. 1, fig. 1). Glaessner (1971) assigned *Conomedusites* to the Conchopeltina giving the group a stratigraphic range from late Precambrian to Ordovician. *Conomedusites* appears to have a fourfold radial symmetry (Glaessner, 1971, p. 8–9), but this does not exclude relationship with the bilaterally symmetrical *Conchopeltis* which, in any case, would be assumed to have developed from a radially symmetrical ancestor.

*Conomedusites* is preserved with the apex of the cone pointed downward (Glaessner, 1971, p. 8) and Glaessner interprets this as the living position (*loc. cit.*). Because of this he interprets both *Conomedusites* and *Conchopeltis* as polypoid, rather than medusoid, cnidarians. The life orientation of *Conchopeltis* is not known but most workers have assumed the apex to have been up rather than down. Support for this orientation is found in the evidence that the NYSM specimen (with tentacles) was drifting along the bottom (see above), and in the bilateral symmetry. In addition it is noted that where well preserved (*e.g.* Pl. 1, figs. 6–7) the apex of *Conchopeltis* shows no evidence of an attachment scar. For these reasons, I find it easiest to interpret *Conchopeltis* as a pelagic or weakly nektonic medusoid. I am not convinced of the similarities to *Conomedusites*, but I have not had the opportunity to study that form.

Glaessner (1971, p. 12–14), Stanley (1982, p. 503–4) and others (see cited discussions) have suggested the possibility that *Conchopeltis* was a condrophoran (Hydrozoa). The Chondrophora are pelagic hydroid colonies (conventionally) or individuals (Fields and Mackie, 1971) that have a medusoid form and life style as adults. A chitinoid float (pneumatophore) is shaped like an inverted saucer and consists of concentric air-filled chambers. The pneumatophore is enveloped by soft tissues; on the ventral side, a central mouth is at the end of a proboscis and this is surrounded by descendant reproductive appendages and one or more outer rings of tentacles. *Porpita* and *Veleva* are familiar living condrophorans and several convincing Paleozoic examples have been described (reviewed by Scrutton, 1979, p. 165–6; Stanley, 1982; and Yochelson, Stürmer and Stanley, 1983).

#### EXPLANATION OF PLATE I

##### Figure

##### 1–7. *Conchopeltis alternata* Walcott

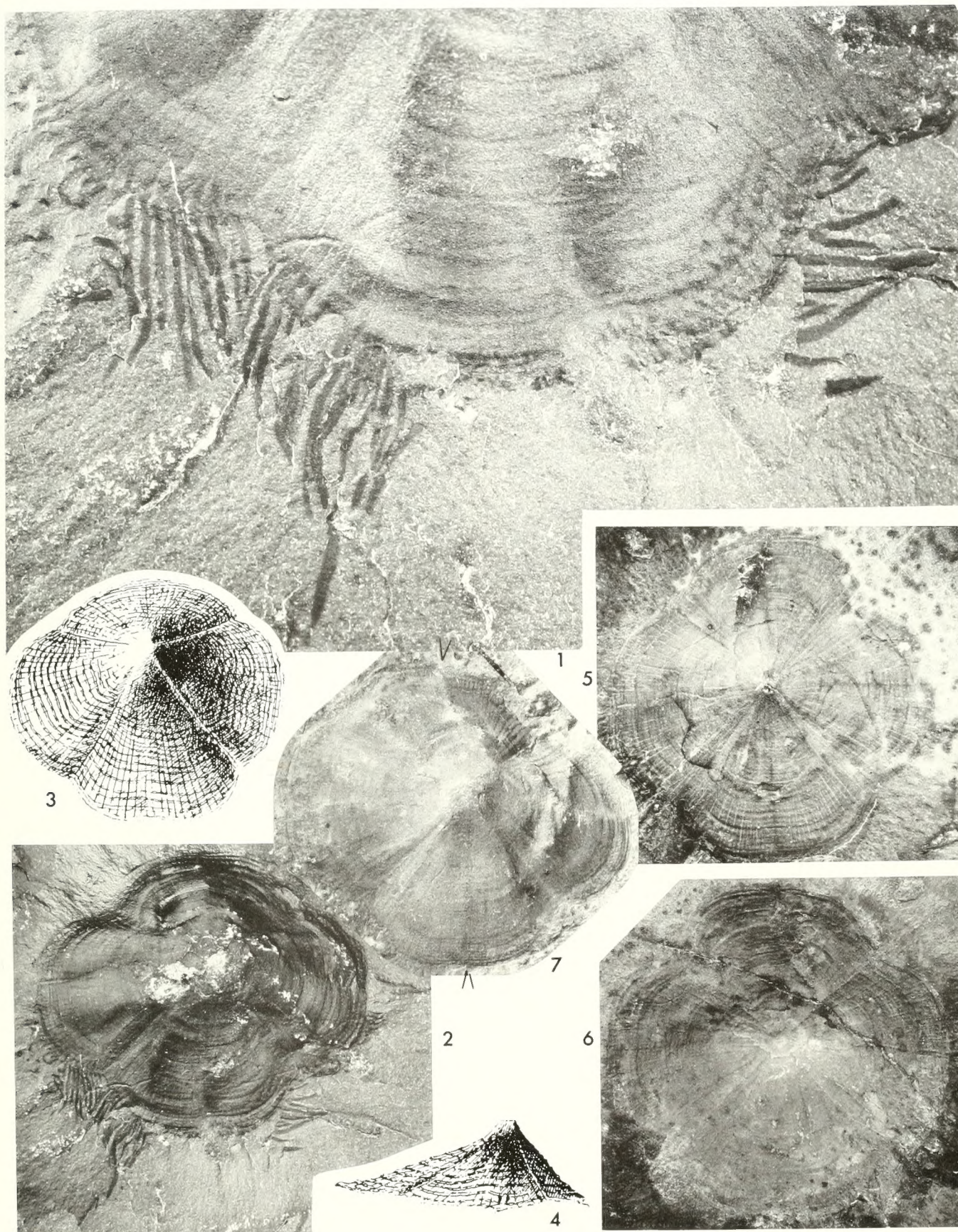
(Trenton Limestone, vicinity of Trenton Falls, New York.)

1–2. NYSM 12914A, positive composite mold of specimen preserving tentacles;  $\times 3$  and  $\times 1$ . See also Text-fig. 1a.

3–4. Paratype from Walcott's original collection, present repository unknown. Top and side views of specimen; sketch prepared under supervision of H. N. Winchell and published by Ulrich and Scofield, 1897, p. 823. See text discussions of this rendition.

5–6. MCZ 27930, holotype, internal and external composite molds,  $\times 1$ . Short lobe is toward top. See also Text-fig. 1c.

7. USNM 375445, positive mold,  $\times 1$ . Specimen is distorted in upper right area; arrows mark central grooves of anterior and posterior lobes.



*Conchopeltis* differs from chondrophores in lacking the pneumatophore with its concentric air-filled chambers. In contrast, the periderm of *Conchopeltis* is extremely thin and one-layered. It is tempting to consider this as an intermediate stage between sessile tubularian hydroids (Fields and Mackie, 1971, p. 1596) and typical chondrophorans as suggested by Glaessner (1971, p. 13). Such a relationship is equally possible whether one interprets *Conchopeltis* as a polyp (apex down, sessile) or medusoid (apex up, pelagic). If this relationship is accepted, *Conchopeltis* is biologically a polyp (conceivably a polyp colony) while functionally a medusoid, as is true of the Chondrophora.

The most pervasive and attractive element in discussions of these relationships, over nearly 50 years, is the apparent fourfold radial symmetry that has been described both in *Conchopeltis* and the conulariids and that has been used to relate them to the living Class Scyphozoa in which this symmetry is also well developed. Almost the only additional cnidarian characters of significance are the presence of tentacles and a chitinoid test in *Conchopeltis*.

In analyzing the *Conchopeltis* relationships, I am very impressed by the nature of the tentacles and by the bilateral symmetry. It seems to me that the tentacles are strong evidence that *Conchopeltis* is cnidarian. The presence and nature of the chitinoid test may relate *Conchopeltis* to the Hydrozoa as an early offshoot of the Chondrophora or to the polypoid group from which the chondrophorans were derived. The presumed fourfold radial symmetry of *Conomedusites* and *Conchopeltis* have seemed to be more at home in the Scyphozoa whose medusae characteristically show this symmetry. However, this is countered by the bilateral symmetry of *Conchopeltis* and by the presence of possibly homologous chitinoid structures in hydrozoans and *Conchopeltis*. In my original abstract (Oliver, 1983) I concluded that *Conchopeltis* was closest to the Scyphozoa but should possibly be recognized as a separate class within the Cnidaria. I now lean toward a hydrozoan connection and see analogs in the Chondrophora although the lack of a chambered float in *Conchopeltis* presents difficulties. The bilateral symmetry of *Conchopeltis* may indicate that the animal was weakly nektonic and suggests that it may not have been ancestral to later medusoids, whatever its relationships.

Arguments relating *Conchopeltis* to the conulariids are reduced to both being four-sided pyramids. Against such a relationship is the great difference in the shape of the pyramids—low versus high, the difference in test composition—chitinoid versus chitinophosphatic, and the bilateral nature of *Conchopeltis*. It is very difficult to prove that the two groups are not related, but none

of the arguments that have been used to support a relationship are significant. I think that the groups are unrelated, but at the very least I would argue that no relationship has been demonstrated.

The conulariid-scyphozoan relationship has been based on the symmetry, on the presence of internal septa and marginal tentacles, and the nature of the living *Stephanoscyphus*. Against these arguments, I note that the so-called septa are not generally present and are of unknown significance when they are present, and that there is absolutely no evidence for tentacles. *Stephanoscyphus* is interesting, but it could as easily be used to relate the scyphozoans to any number of tubular Paleozoic fossil groups. The Ordovician *Byronia* is more like a polypoid scyphozoan than any conulariid (Scrutton, 1979, p. 173). I conclude that there is no satisfactory evidence that conulariids are cnidarians of any kind.

## CONCLUSIONS

The Moore "Treatise on Invertebrate Paleontology," the Soviet "Osnovi," and many of our textbooks, classify *Conchopeltis* as a conulariid and the Conulata as scyphozoans. Arguments set forth in this paper show that these proposed relationships are very questionable and probably false. *Conchopeltis* is a bilaterally symmetrical medusoid and has tentacles. It is probably a cnidarian and may be either a hydrozoan or scyphozoan.

New and fundamental studies of the conulariids are needed to determine the nature and significance of the so-called septa and other internal structures that have been observed in a very few specimens. Are these structures common and representative of the group? Intensive study of the conulariids should provide better answers to the questions of their relationships. At present, the relationships of the conulariids are speculative. However, they are not related to *Conchopeltis* and have not been shown to be cnidarians.

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Photographs are by R. H. McKinney and H. E. Mochizuki.

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NORTH AMERICAN MIDDLE ORDOVICIAN *SCENELLA* AND *MACROSCENELLA*  
AS POSSIBLE CHONDROPHORINE COELENTERATES

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ABSTRACT

Middle Ordovician species currently placed in the presumed monoplacophoran *Scenella* probably are coelenterates rather than mollusks. Features are considered which may distinguish fossil chondrophores that floated from low-conical mollusks that clung to the substrate. *Macroscenella* cannot be proved to be a coelenterate, but likewise cannot be proved to be a mollusk; it may represent a new form of chondrophorine.

INTRODUCTION

*Porpita* and *Veleva*, the only living chondrophorines, each develops a chitinous-like float. Yochelson and Stanley (1982) redescribed the Early Ordovician *Palaeolophacmaea* as a chondrophorine, suggesting it resembled a float of *Veleva* but lacked a "sail"; this work extends that concept. *Scenella* was first described from the Early Cambrian; whether it is a mollusk remains an open question. However, at least some post-Cambrian species assigned to *Scenella* are not Mollusca.

PALEOZOIC LIMPETS

Malacologists use the term "limpet" to refer to a clinging mollusk that has a broad low shell; it has no systematic significance, for limpets occur in many gastropod superfamilies. The foot expands rapidly, and the shell is essentially not coiled, except in the earliest stages. Some of these "cap-shaped" forms have the apex distinctly anterior or posterior, but others develop a nearly symmetrical cone.

Three types of Paleozoic limpets are known. Most common are platyceratacean gastropods that clung to the anal opening of echinoderms; many show some remnant of trochiform coiling. Low cones of patellacean gastropods are the second type; a horseshoe-shaped muscle scar within the shell reflects torsion of the soft parts, but they are bilaterally symmetrical on the exterior. Monoplacophorans are the third type; these form a molluscan class recognized only within the last three decades and have paired muscle scars which indicate bilateral symmetry of soft parts, and external bilateral symmetry.

Historically, cap-like Paleozoic forms were assigned to the Patellacea, whether or not there was evidence of a horseshoe-shaped muscle scar, for there were no geometric alternatives to consider. When monoplacophorans were recognized, pre-Mississippian limpets were assigned to that class, but again no critical study was made to determine the presence of paired muscle

scars. Few fossil monoplacophorans show muscle scars and assignments were made on external form. Authentic fossil monoplacophorans occur from Cambrian to Devonian, but transfer of some species will modify views on class diversity and abundance.

DISTINGUISHING MONOPLACOPHORANS  
FROM CHONDROPHORINES

No one criterion distinguishes all mollusks from all chondrophorines. No monographic study of American Paleozoic monoplacophorans has been made. Likewise, reinterpretation of *Palaeolophacmaea* by Yochelson and Stanley (1982) constitutes only the second report of chondrophorines in the American Ordovician (first was Caster, 1942). We know little of variation in either group; caution is urged in assignment of these early Paleozoic fossils. Confirmation by Oliver (1984) of bilateral symmetry in *Conchopeltis* strengthens the concept that conical Paleozoic "shells" need not be mollusks. Features which may differentiate limpets and chondrophorines are summarized below.

*Thickness.*—In mollusks, shell thickness varies widely. As a rule, cephalopod shells are thin and pelecypod shells thick. Gastropods and monoplacophorans are intermediate; both trochiform gastropods and limpets have about the same average shell thickness. Chondrophorine pneumatophores are paper thin after death, far thinner than the shell of even tiny cephalopods.

*Composition.*—Characteristically mollusks are composed of aragonite. Sedentary forms also secrete calcite and some living patellaceans are calcitic; nothing suggests that any Ordovician monoplacophorans were composed of calcite. The chondrophorine pneumatophore is organic. In some kinds of matrix it appears chalky white, in others it is black; in certain diagenetic environments it may be replaced by calcite or even show a phosphatic sheen.

*Apical position.*—Characteristic monoplacophorans are the Silurian *Tryblidium* and *Pilina*; these are best

described as "spoon-shaped," having an apex distinctly anterior on a low cone. Specimens having the apex overhanging or at the margin probably are not chondrophorines. Chondrophorine affinities may be indicated by a central or slightly off-center apex. Some living patellaceans have a central or subcentral apex, and differentiation of chondrophorines from this shape of patellaceans is more difficult.

*Outline.*—The apertural outline of all monoplacophorans seems to be distinctly oval. No authentic monoplacophorans have a circular aperture, and so far as known, none are elliptical. Some chondrophorines may have a slightly oval margin. Individuals that are circular or elliptical to irregular in outline may be chondrophorines.

*Profile.*—All monoplacophorans in which muscle scars are known and almost all patellaceans maintain the same shape throughout growth; specimens that have a short concave slope on one side of the apex and a long convex slope on the other may be mollusks. In contrast, study of *Veleva* and *Plectodiscus* (see Yochelson *et al.*, 1983) suggests that some chondrophorine pneumatophores have stronger curvature in early growth stages than at later growth stages.

*Growth lines.*—In mollusks, growth lines tend to be uniform in strength, although some forms periodically develop a "frill"; except in late stages, growth lines are virtually constant in spacing. In large chondrophorines, pneumatocysts seem to be slightly variable in width, or at least taphonomic processes impose some variability. In chondrophorines the edge of each pneumatocyst is prominent, whereas in many mollusks growth lines are faint.

*Course of growth lines.*—Mollusk shells are subject to breakage and repair, causing irregularity in growth lines. Predation, the principal cause of shell breakage, is rare in the Paleozoic (Vermeij *et al.*, 1981) and no undoubted monoplacophorans show irregular growth lines. In some chondrophorines, the pneumatocysts have local irregularity in width around the circumference. Specimens appear to have been tattered and torn; in keeping with their relative thinness and delicacy, subsequent repair causes irregularity for several rings. This possible tearing is analogous to breakage of a molluscan shell, but its appearance is different. Not all fossil specimens can be expected to show this effect, but several "tattered" individuals are known.

*Surface irregularities.*—Mollusk shells commonly are smooth. Compacted pneumatophores show some surface irregularities, and impressions of fleshy parts even more. Tissue may show concentric features like a pneumatophore. "Jellyfish" and mollusks are unlikely to be confused, but three years ago no one was concerned with the similar appearance of pneumatophores and

limpet shells (see Yochelson *et al.*, 1983, for preservation of chondrophorine tissue, separate from the pneumatophore).

*Ridge and sinus.*—Authentic monoplacophorans and patellaceans have a simple margin, uncomplicated by any indentation. Some specimens of *Palaeolophacmaea* and *Plectodiscus* have a ridge that forms a slight marginal sinus; this may be a good indicator of chondrophorine affinities, but it appears subject to individual variation. The limpet *Siphonaria* has a sinus and, apart from its thick calcareous shell, superficially resembles *Palaeolophacmaea*.

*Radial ornament.*—No authentic monoplacophoran having paired muscle scars shows radial ornament; other forms assigned to the class—even though information is lacking on muscle scars—do show such ornament. Most patellacean gastropods do not have radial ornament, but a few show this ornament prominently, forming a cross-hatched pattern with growth lines. A strengthening of the pneumatophore by faint radial elements, which give the appearance of radiating ribs, occurs in *Veleva*; conspicuous radial flutes and folds characterize the float of *Porpita*. Radial ornament on a lower Paleozoic conical specimen suggest chondrophorine affinities, but do not prove them.

#### DIAGENETIC EFFECTS

In addition to compression of the pneumatophore, other diagenetic effects may assist in distinguishing chondrophorines from monoplacophorans.

*Surface texture.*—Mollusk shells either break cleanly from a limestone or exfoliate, leaving a smooth steinkern (internal filling). Splitting along shell layers almost never occurs. Some chondrophorines do not break clean of the matrix. A papillose texture seen on some partially exfoliated chondrophorines (Yochelson and Stanley, 1982) has no equivalent within the mollusks. We do not know whether the texture is original and part of internal strengthening of the float, or whether it is a diagenetic effect; its equivalent has not been described in living material. This texture may be the single feature which is most convincing of chondrophorine affinities, but it is also unlikely to be preserved.

*Three-dimensional form.*—Mollusk shells preserved in limestone are not crushed, and in most shales, breakage by compaction is extremely rare. One remarkable feature of chondrophorine pneumatophores in limestone is preservation of a conical form without compaction, although the cone is rarely preserved uniformly. Surface irregularities or indentations may occur; such irregularity is not seen on the exterior of mollusk shells.

*"Growth" markings.*—On steinkerns, lateral slopes of most monoplacophorans appear smooth below the

area of muscle scars. In contrast, some impressions of pneumatophores show concentric undulations. These may result from differential compaction associated with the stronger walls of individual pneumatocysts relative to their weaker centers.

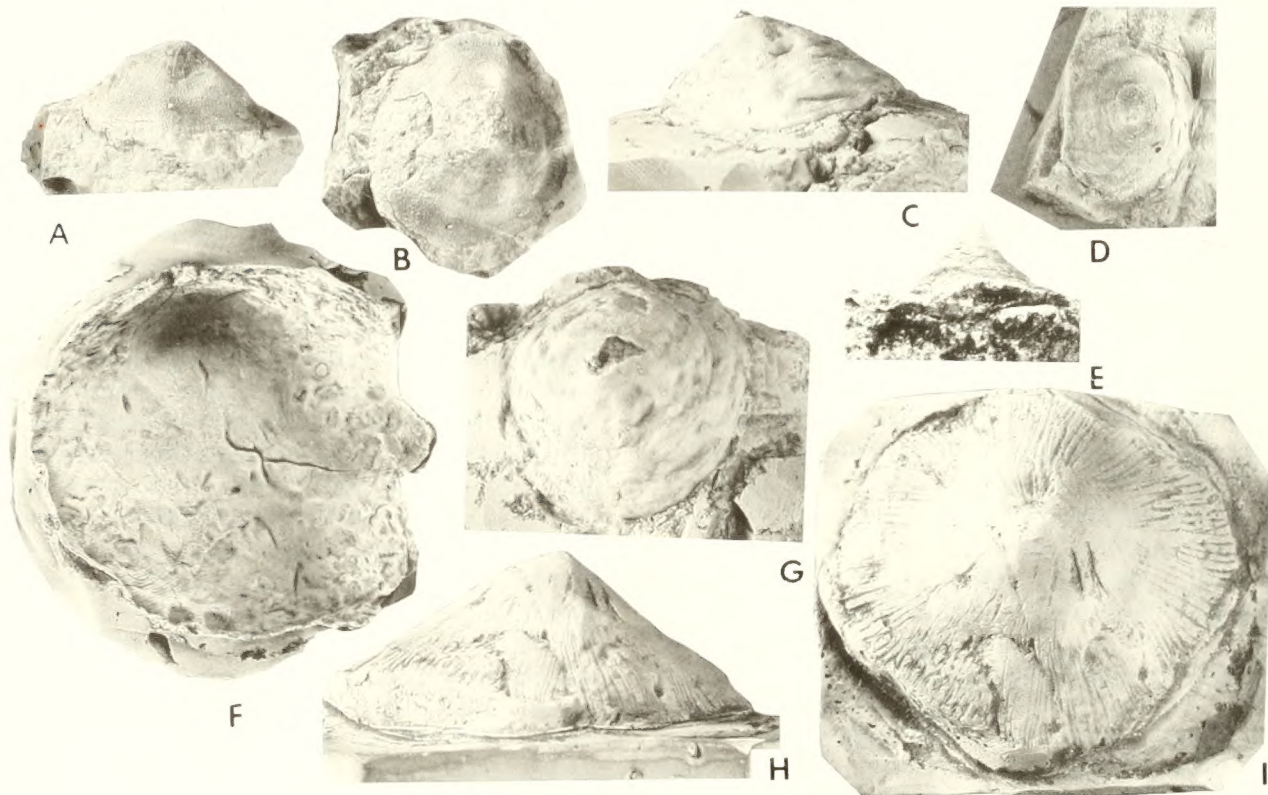
#### DIFFICULTIES IN COMPARISON OF FOSSILS

Unfortunately most of the fossils in question are not well preserved. Many specimens of presumed mollusks in the lower Paleozoic are based on steinkerns and, of course, these lack all external features. Most steinkerns are correctly assigned to the mollusks, but among the low conical forms the problem of distinguishing between mollusks and coelenterates is more difficult. Indentations formed by imperfect preservation of original shape will be reflected on the steinkern, but some mollusks do thicken the shell internally, particularly in the apical area, and irregularities on a steinkern must be treated with caution.

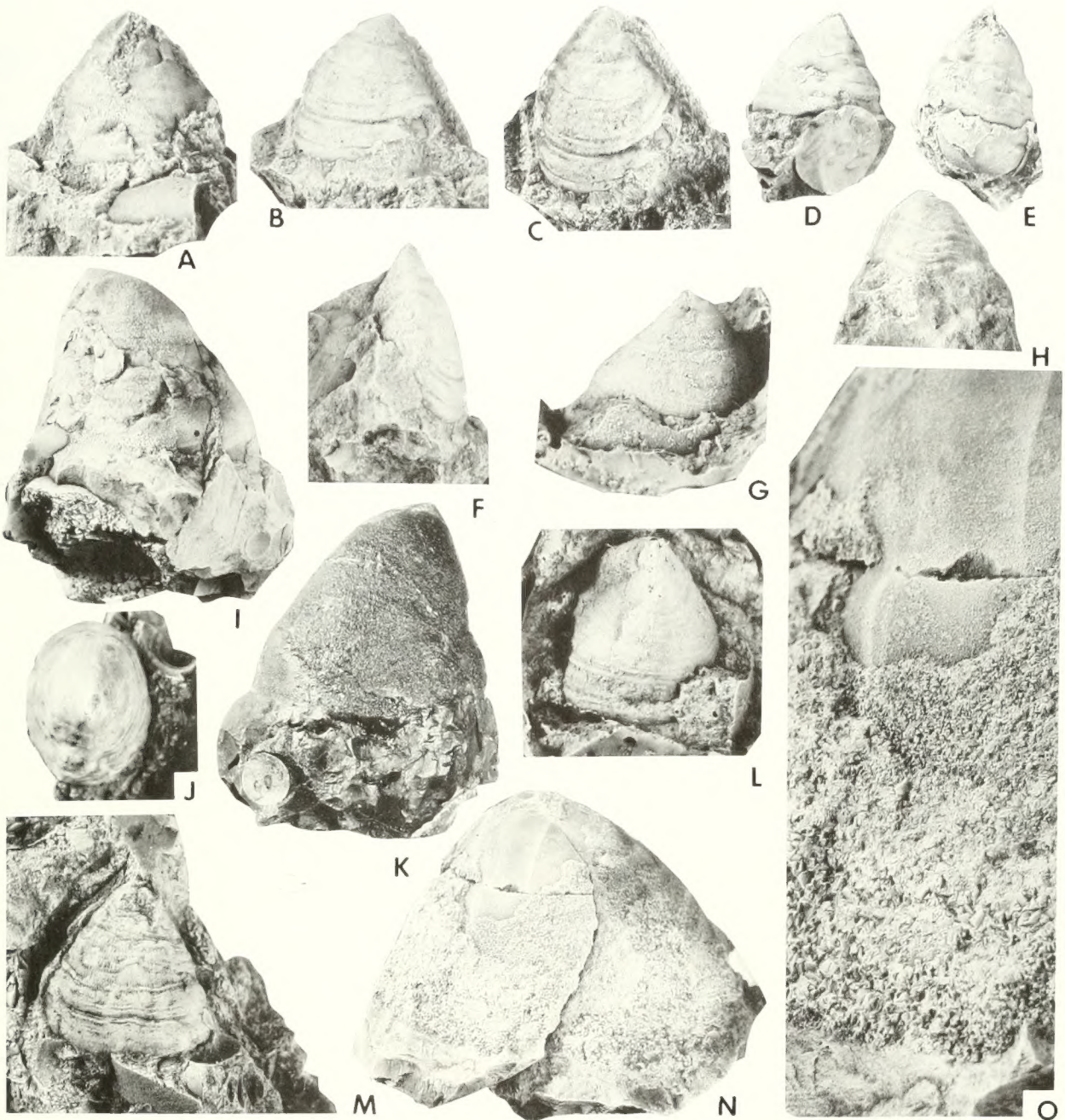
On the other hand, chondrophorines are not the only

unlikely coelenterates to be preserved as fossils. The pneumatophores provide the homeomorphy for growth lines, but most planktonic coelenterates lack a float. Likewise, many living mollusk shells are extremely smooth and hardly show the growth lines; on many fossil mollusks, growth lines cannot be discerned. Confusion with other fossil groups is possible. The impression of an inarticulate brachiopod may be a conical shape showing concentric annulations. Worn prasinopoid bryozoan colonies are another source of potential confusion, for concentric impressions of the base may simulate pneumatocysts.

In the final analysis, assignment of a subcircular conical form to Mollusca or to Coelenterata is subjective. My illustrations show that most species mentioned below are not based on adequate material. Features suggestive of coelenterate affinities are difficult to photograph and are almost never seen on drawings. Because of time limitations, only specimens in the U.S. National Museum of Natural History, Washington, DC, were studied.



Text-figure 1.—Middle Ordovician *Scenella*; all specimens coated with ammonium chloride. A, B. *Scenella beloitensis* Ulrich and Scofield, Platteville Limestone, Wisconsin, lateral and oblique-apical views of holotype,  $\times 1$ ; USNM No. 136718. C, G. *Scenella cassienensis* Bassler, Chazy Limestone, Vermont, lateral and oblique-apical views,  $\times 1$ ; USNM No. 33435. D, E. *Scenella analoga* Walcott, Pogonip Group, Nevada, lateral and oblique-apical views of holotype,  $\times 2$ ; USNM No. 17358. F. *Scenella obtusa* (Sardeson), Decorah Shale, Minnesota, interior view of wax impression of holotype,  $\times 1$ ; USNM No. 24221. H, I. *Scenella radialis* Ulrich and Scofield, Prosser Limestone, Minnesota, lateral and apical views of plaster cast of holotype, with radial ornament near the margin "improved,"  $\times 1$ ; USNM No. 45990.



Text-figure 2.—Middle Ordovician *Macroscenella*; all specimens coated with ammonium chloride, except K. A–H, J, L, M. *M. montrealensis* (Billings), Chazy Group, Isle La Motte, Vermont. A. Lateral view of crushed specimen lacking tip of the apex, showing steinkern to the right; the opposite side of the specimen shows concentric lines and faint radial elements continuous with same region to left where little detail is evident,  $\times 2$ ; USNM No. 369703. B, C, F. Two slightly different oblique lateral views and an end view of narrow specimen; note that a prominent concentric line is both irregular and not parallel to those above and below,  $\times 2$ ; USNM No. 369704. D, E. Lateral and end views of wide specimen; note margin infolding on E,  $\times 2$ ; USNM No. 369705. G, L. Two views of latex impression of exterior, showing radial elements,  $\times 3$ ; USNM No. 369706. H. End view of specimen lacking apex, showing a prominent marginal "lobe",  $\times 2$ ; USNM No. 369707. J. Apical view of steinkern having smooth slopes laterally and near apex, but an irregular wrinkled area below  $\times 2$ ; USNM No. 369708. K. Lateral view of specimen showing irregularity of concentric lines, an irregular surface, and faint radial elements,  $\times 2$ ; USNM No. 369709. I, K. Two lateral views of *M. magnifica* (Ulrich and Scofield) showing general shape and irregular texture of paper thin integument between steinkern and matrix, Lowville Formation, Black River Group, 2 miles below Poland, N.Y.,  $\times 1$ ; USNM No. 99024. N. Very slightly oblique lateral view of small specimen of *M. superba* (Billings), upper part of Black River Group, Montreal, Canada,  $\times 1$ ; USNM No. 92437. O. Enlargement of part of same specimen, showing smooth steinkern above, irregular texture of thin integument, and matrix below,  $\times 3$ .

## SYSTEMATIC SUMMARY

References to Ordovician species are given by Bassler (1915), who listed 17 species assigned to *Scenella*. The type species of *Scenella* is Early Cambrian, and although no muscle scars are known from the type specimen (Knight, 1941), or any Early Cambrian specimen, it has been considered the oldest known monoplacophoran (Knight, 1952). Four of the 17 species are Early Ordovician and were not investigated. *Scenella conica* Whiteaves is Silurian; after examining specimens from Buffalo, New York, I am certain that this species is non-molluscan and could be a chondrophorine of some sort. The remaining dozen species are all Middle Ordovician. The latest American work that includes Middle Ordovician patelliform mollusks (Wilson, 1951) was completed before the concept of Monoplacophora (see Knight, 1952) gained general acceptance. I am not aware that any North America post-Cambrian species assigned to *Scenella* were described between the time of Bassler's compilation and the descriptive work by Wilson.

*Scenella beloitensis* Ulrich and Scofield is known from a steinkern (Text-fig. 1A, B). *Scenella radialis* Ulrich and Scofield is represented in the collection by a plaster cast, again apparently that of a steinkern (Text-fig. 1H, I). A wax impression of the only known specimen of *S. obtusa* (Sardeson) is also illustrated (Text-fig. 1F). Wilson (1951) assigned all three species of *Macroscenella*, but because of their irregularities all of these low conical forms might be impressions of chondrophorines. A single small specimen is known of *S. analoga* (Walcott) (Text-fig. 1D, E); the change in shape with growth and some slight irregularities indicate non-molluscan affinities. From drawings, *S. robusta* Raymond is known to be a low cone, irregular in height, outline, and surface. The name may be a senior synonym of *S. cassiensis* Bassler. A specimen of that species which shows considerable surface irregularity is illustrated in Text-figure 1C, G.

*Macroscenella* Wilson is a high cone, the depth being greater than the longest apertural dimension. Some specimens are remarkably large, up to 6 cm in height. Muscle scars are unknown in the holotype of *M. superba* (Billings), the type species, and its exterior is obscured almost entirely by silics deposited in small concentric rings (beekite); radial ornament may be seen in one place (Wilson, 1951). No specimens are well preserved (Text-fig. 2N, O), and this negative information may suggest that no calcium carbonate shell was present. *Macroscenella magnifica* (Ulrich and Scofield) is relatively higher but similar. Only a few specimens are known and none shows external features or muscle scars on the steinkern; a small, but well pre-

served individual is illustrated (Text-fig. 2I, K) which again shows no indication of a distinct shell.

*Scenella affinis* Ulrich and Scofield, *S. affinis obsoleta* Ulrich and Scofield and *S. compressa* Ulrich and Scofield are each based on single specimen; types are either poor external molds or a steinkern and none warrants illustration here. All are high cones and despite much smaller size could fit in *Macroscenella*. *Scenella pretosa* Raymond from the Chazy Limestone may be a junior synonym of *S. compressa*.

*Scenella montrealensis* (Billings) is probably a species of *Macroscenella*, in spite of its smaller size. Identity of *S. pretosa* to this species is evident. In contrast to the other species discussed, specimens of *M. montrealensis* are abundant. In a collection from the Chazy Limestone on Isle LaMotte, Vermont, a thin calcified "shell" appears present, but no uniform growth lines are to be seen (Text-fig. 2A-H, J, L, M); gastropods from this same unit are well known for delicate preservation of uniform growth lines. The species shows a great deal of individual variation in shape and some specimens are irregularly rugose. Rare specimens have radial ornament, as noted by Raymond (1908). If *M. montrealensis* is a mollusk, it is a strange one. If it is a coelenterate, it was a deep, bilaterally symmetrical bell with a relatively thick and tough integument, perhaps without any chondrophorine-like float. I do not know where to assign the species, but I prefer that it and all other *Macroscenella* species be considered bizarre coelenterates rather than bizarre mollusks. If this concept is accepted, perhaps the poorly known *Micropileus* Wilson (1951) may also find a home outside of the Monoplacophora.

Although information has improved slightly in a century, Whiteaves (1884, p. 32) was most perceptive. "The genus *Scenella* of Billings has never been properly defined and consequently ought either to be reconstituted or abandoned."

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## THE EARLIEST STAGES IN THE EVOLUTION OF CORALS

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## ABSTRACT

The Vendian was marked by the rapid appearance of Metazoa, many of them attributed to the Coelenterata. They are medusoids like "*Cyclomedusa*," problematical Hydrozoa and Pteridiniida (*Pteridinium*, *Rangea*, *Charniodiscus*, etc.). The latter have been considered problematical Octocorallia, but this point of view does not seem well founded. The oldest octocoral spicules have been found in the Silurian, but they have nothing in common with the Pteridiniida which are here considered to have been representatives of an independent but very short-lived metazoan phylum.

Many Cambrian forms were directly or indirectly related to Anthozoa. Among them, *Gastroconus* and *Tabulaconus* are the most similar to corals, but they had not yet developed true septal elements. The Gastroconida could be the ancestors of corals. True Anthozoa are known from the Ordovician.

## CORAL EVOLUTION

Cnidarians may be the oldest metazoans. Certainly medusoids, except for doubtful forms such as *Gakarusia*, are known from the early late Precambrian. A very important review of the oldest Cnidaria has been published by Scrutton (1979) and he is certainly right in stating that the first well documented and acceptable cnidarians come from the Vendian (=Ediacarian).

Among late Precambrian and Cambrian medusoids were perhaps representatives of Hydrozoa, Scyphozoa and some actinians. This paper is concerned principally, however, with those forms which may be ancestral to corals. Here I wish to consider those organisms with which I am well acquainted.

Paleontology proves that the main phylogenetic branches of organisms appeared geochronologically "instantly" and associated with rapid divergence. We know that at the end of the late Precambrian different Metazoa, including problematical Coelenterata, appeared suddenly and immediately inherited the Earth. At the beginning of the Middle Ordovician all main groups of Paleozoic corals appeared, and the beginning of the Middle Triassic was marked by a rapid appearance of various Scleractinia.

The origin of different phyla, classes or orders of the Metazoa hardly occurred in the procaryotic stage of evolution. Dacque (1935) supposed that the divergence of the genetic branches of corals occurred at the beginning of their history, and groups with skeletal representatives might have existed as nonskeletal ancestors at earlier periods; that the Tabulata, Heliolitoidea and Rugosa existed in the Precambrian and Cambrian. Why should corals have lived without a skeleton when all the conditions for skeleton formation were present?

All late Precambrian fossils have been described on the basis of imprints and their position in the organic world has almost always been supported by compar-

ison of their outlines with living animals that appeared later by some 650–600 my. Is it possible to consider this similarity as proof of relationship? What was the tempo of evolution in these cases? The diversity of successful morphotypes among living forms is not infinite and convergence has always to be considered. Any such suppositions of taxonomic relationship are incorrect and Precambrian fossils can only be compared with those of the Cambrian.

I'll try to examine this problem, but proceeding from the living relatives of Precambrian fossils and not from superficial similarities between imprints and living organisms.

Following the work of Prof. M. F. Glaessner and Dr. M. Wade (Wade, 1972; Glaessner, 1977; see Cloud and Glaessner, 1982), numerous workers have shown that no less than two thirds of the Ediacaran fauna were cnidarians, assigned to the Hydrozoa, Scyphozoa and Anthozoa (Octocorallia, Pennatulida). Leaf-shaped organisms like *Pteridinium* belong to the latter group. Precambrian Metazoa similar to Cnidaria are characterised by the following living forms:

1. Medusaemorphs. Conventionally included here are all organisms with a rounded imprint, sometimes more than 20 cm in diameter. They are reminiscent of recent medusae. Medusae are known from the Cambrian, from throughout the Palaeozoic, beautiful specimens of *Rhizostomites* have been described from the Jurassic lithographic limestones and they are still successful. On the surface all seems straightforward; it is quite natural to suppose that all such medusoids are Coelenterata. Many generic names for these forms have been proposed but the most popular among them is *Cyclomedusa*. This "genus" is rather all embracing.

The end of the late Precambrian was the beginning of Metazoan evolution. Organisms began to occupy an infinite number of ecological niches, planktonic and



benthonic, suitable for both animals and algae. In the first stages of metazoan evolution different attempts by living organisms to adjust to the environment might be expected to take similar analogous forms. In this case, "*Cyclomedusa*" was indisputably both the simplest and the most convenient morphotype. Among the oldest organisms, medusaemorphs could be the representatives not only of coelenterates, no doubt one of the oldest and most primitive groups of organisms, but also of completely different groups which did not pass the sieve of natural selection.

2. Bowl-like organisms (*Tirasiana* and possibly the similar *Ediacaria*). Judging by Vendian material from the Dnestr River, *Tirasiana* had a very low conical shape with a distal edge like the rugosan calicular platform. They attached to the substrate by the apex of the cone, and are reminiscent of some Archaeocyatha, or Sponges such as Hexactinellida (*Ventriculites*). *Tirasiana* reproduced by gemmation, by division or by throwing out a special filament, on whose end a daughter organism began to grow. But this process cannot be recognized as an analogue of stolonial increase, which is well-known among some Stolonifera and Telestacea (Octocorallia). Naturally, these organisms had no relationship to the corals.

3. Petalomorphs. Numerous workers such as Glaessner (1977), have claimed these to be octocorals. These very spectacular feather-like benthic organisms were the first Precambrian Metazoa discovered and they are an element of all Vendo-Ediacarian biotas. There are many generic names erected for petalomorphs, the most widespread of which are *Pteridium*, *Rangea* and *Charniodiscus* (Pl. 1, figs. 1-3).

Judging by their complexity and morphological diversity, this group, as with the "medusoids," could include representatives of some taxa ranking even higher than family. As a living form, this could also be seen as one of the most convenient of early morphotypes; the organism was attached to the bottom, and would appear to have been well suited to filtering microplankton.

The petalomorphs consisted of two or three petaloids, sometimes leaf-like. Imprints have a common marginal contour, so that an analogy with feathers is inadmissible.

Sea pens (Octocorallia Pennatulida) are non-branching, and not firmly attached. They consist of an oozyoid, that elongates to produce a barren, proximal stalk which anchors the colony in mud, and a polypiferous distal rhachis, from which secondary polyps spring, either directly or from ridge-like or broadly expanded polyp leaves. Spicules are present. They look like a lamp-brush (Pl. 1, fig. 4), but not like petals or leaves.

They appeared in the Mesozoic (their "Paleozoic representatives," for example *Spirophyton* Hall and *Alectonurus* Schimper, are doubtful).

The Vendo-Ediacaran organisms had neither oozyoid, nor a rhachis with pennatuloid polyps and we can only follow Pflug (1970a, b) and unite all these forms in the phylum Petalonamae, which existed at the end of the late Precambrian only.

There are few late Precambrian Metazoa which can be compared with Early Paleozoic Coelenterata. The point of view that Cnidaria, including true Anthozoa, constituted three quarters of the Ediacaran biota cannot now be accepted. The late Precambrian Metazoa, arising almost instantaneously in an "empty" ecosystem cannot be compared with later biotas in Earth history. Although the late Precambrian biota differs distinctly from that in the Cambrian, it is much more similar to that than to the Cryptozoic biota.

Many paleontologists following Sokolov (1955, for example) considered the ancestors of Paleozoic skeletal corals to be so called "auloporids." Auloporids are one of the most ancient groups to form a skeleton. Among all known corals they are characterized by the simplest morphology, confirmed not only by a simple skeletal structure (compare Ordovician *Aulopora*, Devonian *Ceratopora* and Permian *Sinopora*), but by simple coloniality and by a simple ecological plasticity (Iwanowski, 1981).

From the Cambrian to early Ordovician interval some skeletal forms are known which have been considered as the hypothetical ancestors of corals. Naturally, all insufficiently studied forms and those occurring in strata of uncertain stratigraphic position should be excluded, for example *Protoaulopora ramosa* (Vologdin), *Bija sibirica* Vologdin, *Mendoconularia lasherensis* Rusconi, *Cambrophyllum prolematicum* Fritz and Howell, and *Cambrotrypa montanensis* Fritz and Howell. Also the ancestors of corals cannot be sought among organisms with a porous skeleton like typical Hydroconozoa (*Coelenteratella* Korde, *Lenaella* Korde, *Tuvaconus* Korde, *Dasyconus* Korde). *Cothonion* and *Lipopora*, described by Jell and Jell (1976) from the Middle Cambrian of Australia, are not true corals. I agree with Hill (1981) that all the above-named forms are neither Rugosa nor Tabulata.

Handfield (1969) described *Tabulaconus kordeae* from the Lower Cambrian of Canada and assigned it (conditionally) to the family Gastroconidae and subclass Zoantharia. These are forms with a lamellar wall, numerous tabulae, lacking pores and without distinct septa. The general structure of this organism much resembles corals such as "*Fletcheriella*," *Pycnostylus* or "*Aphyllum*" (I do not mean that they are genetically

related, but I want to draw attention to the fact that such a primitive morphological type has appeared more than once among Paleozoic corals). *Cloudina? borreloi* (Yochelson and Herrera, 1974) is also known in the Lower Cambrian, but from Argentina. This is a small organism which looks like a solitary rugose coral, with a lamellar skeleton but without an operculum. The study of topotypes of *Cloudina hartmannae* Germs (without touching upon their systematic position) has shown that the material from the Cambrian of Argentina differs considerably from *Cloudina* as well as from *Cothonion* according to Jell and Jell (1976) who considered *C? borreloi* to resemble the Gastroconidae. Solitary attached *Gastroconus venustus* Korde (Pl. 1, fig. 5), with a lamellar skeleton lacking pores and septal elements, is known from the Lower Cambrian of Tuva.

Thus, in the Cambrian, there were organisms with a lamellar nonporous skeleton which had some similarity with Anthozoa. But, insofar as these simple organisms existed more than 50–70 my before the first accepted Tabulata and Rugosa, their genetic relationships are not clear. Handfield (1969) was possibly right in uniting *Tabulaconus* and *Gastroconus* in one family assigned to the Zoantharia and not to the Hydroconozoa. However, the absence of distinct septal elements distinguishes gastroconids from all Anthozoa, including the Zoantharia.

Around the boundary of the early and middle Ordovician, during some 10 my, all the main genetic branches of Paleozoic corals, Tabulata, Heliolitoidea and Rugosa, appeared. The first representatives of these groups were similar not only morphologically but genetically and the problem of their origins is a common one. As in the late Precambrian this is another example of the sudden appearance of new branches followed by rapid divergence.

Following the work of Hartman and Goreau (1970, 1972) there is the possibility that the Chaetetida are sclerosponges (they had earlier been assigned variously to the Algae or the Hydroidea, or the Tabulata). It has also been suggested that the favositids might be sclero-

sponges (Flügel, 1976), but this point of view has not been supported (see for example Oliver, 1979).

In conclusion there are three main problems associated with the earliest stages of coral evolution: (1) were there any true corals among Precambrian organisms? (2) are there any relationships between the latter and Cambrian gastroconids? (3) were the gastroconids the ancestors of auloporids and other corals?

I thank Dr. J. Jell (Brisbane) for topotypes of *Cothonion* and *Lipopora*, Dr. R. Birenheide (Frankfurt-am-Main) for topotypes of *Pteridinium* and *Rangea* and Dr. K. Korde (Moscow) for types of all Hydroconozoids and topotypes of *Cloudina*.

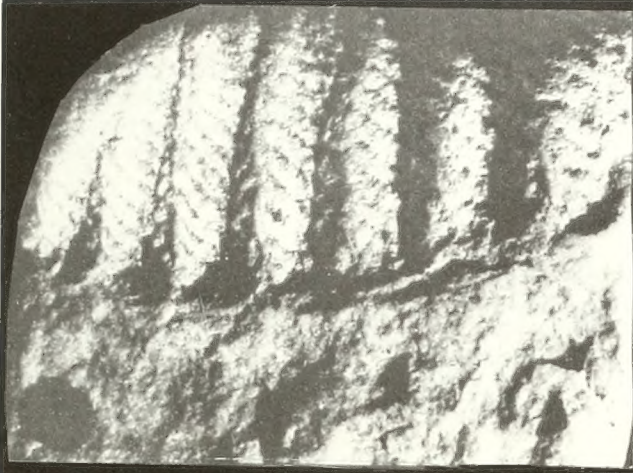
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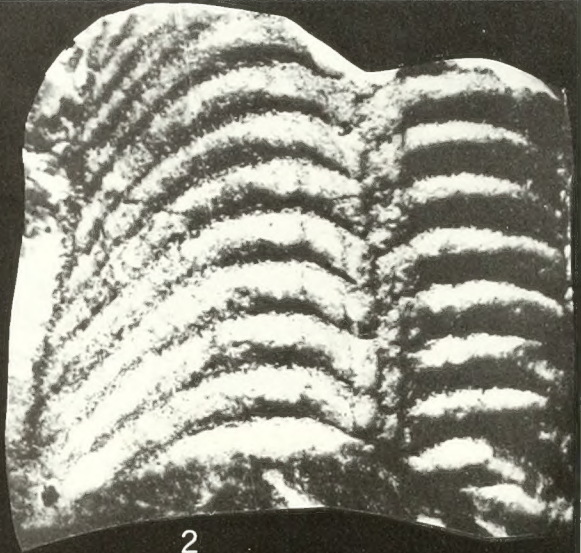
#### EXPLANATION OF PLATE I

##### Figure

1. *Rangea schneiderhöhni* Gürich  
Topotype. Nama system, Kuibus quartzite; SW Africa (Pflüg, 1970), ×2.
2. *Pteridinium simplex* Gürich  
Topotype. Nama system, Kuibus quartzite; SW Africa (Pflüg, 1970), ×2.
3. *Charniodiscus concentricus* Ford (= *Arborea arborea* Glaessner, 1982)  
Charnwood series, Great Britain (Cloud and Glaessner, 1982), ×0.25.
4. *Pennatula phosphorea* Linnaeus  
Type species of the type genus of pennatulids. Colony from the side. Recent, ×1.
5. *Gastroconus venustus* Korde  
Lower Cambrian; Tuva (Korde, 1963), ×10. Longitudinal section of holotype.



1



2



4



3



5

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LICHENARIA WINCHELL & SCHUCHERT, 1895, LAMOTTIA RAYMOND, 1924 AND  
THE EARLY HISTORY OF THE TABULATE CORALS

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ABSTRACT

*Lichenaria* Winchell & Schuchert is commonly viewed as a possible ancestral tabulate coral due to the simple structure attributed to it (no septa or mural pores) and its alleged occurrence in the basal Ordovician, below other accepted tabulates. The lectotype of the type species, *L. typa* W. & S., has very sparse mural pore-like features, faint longitudinal wall fluting, no trabecular septa, and affects increase by lateral offset. *Lamottia* Raymond, commonly treated as a junior synonym of *Lichenaria*, is actually a distinct tabulate genus, probably allied with *Nyctopora*. Available evidence does not substantiate reports of *Lichenaria* below the Chazyan. Consequently, there are other tabulate corals of equal or greater age.

INTRODUCTION

The name *Lichenaria* was introduced by Winchell and Schuchert (1895) for a genus of tabulate corals of favositoid form, but lacking mural pores and septal structures. To date, about 20 nominal species have been reported or described from the United States, Canada, the U.S.S.R., China, and doubtfully Tasmania (Text-fig. 1), ranging from the basal Ordovician through the basal Edenian (upper Caradocian). Because of its supposed simple structure and greater reported antiquity than any other tabulates, it is commonly considered representative of the most primitive stock of this group. To date, however, no detailed studies have been made of its morphology, so that *Lichenaria* remains poorly understood.

STRUCTURE OF *LICHENARIA*

The type species of this genus is *L. typa* Winchell & Schuchert, 1895. Bassler (1950, p. 310) designated as lectotype a specimen figured by Winchell and Schuchert (1895, pl. G, fig. 13, which is U.S. National Museum of Natural History specimen no. 42949, from the Rocklandian Guttenberg beds of the St. Paul, Minnesota area). Some time in the past, part of this specimen had apparently been removed for thin-sectioning. The remainder was prepared for study by the author using soft sodium bicarbonate grit in an air abrasive unit to remove the matrix from the corallite lumens with minimal erosive damage. This afforded a clear view of the internal structure of the corallum. In addition, thin-sections registered with this specimen were studied.

The portion of the lectotype remaining after thin-sectioning is an irregular fragment, approximately  $1.4 \times 1.4 \times 1.1$  cm across (Plate 1, figs. 1, 2). It contains roughly 100 polygonal corallites in various growth stages, the largest having a diameter of 1.9 mm.

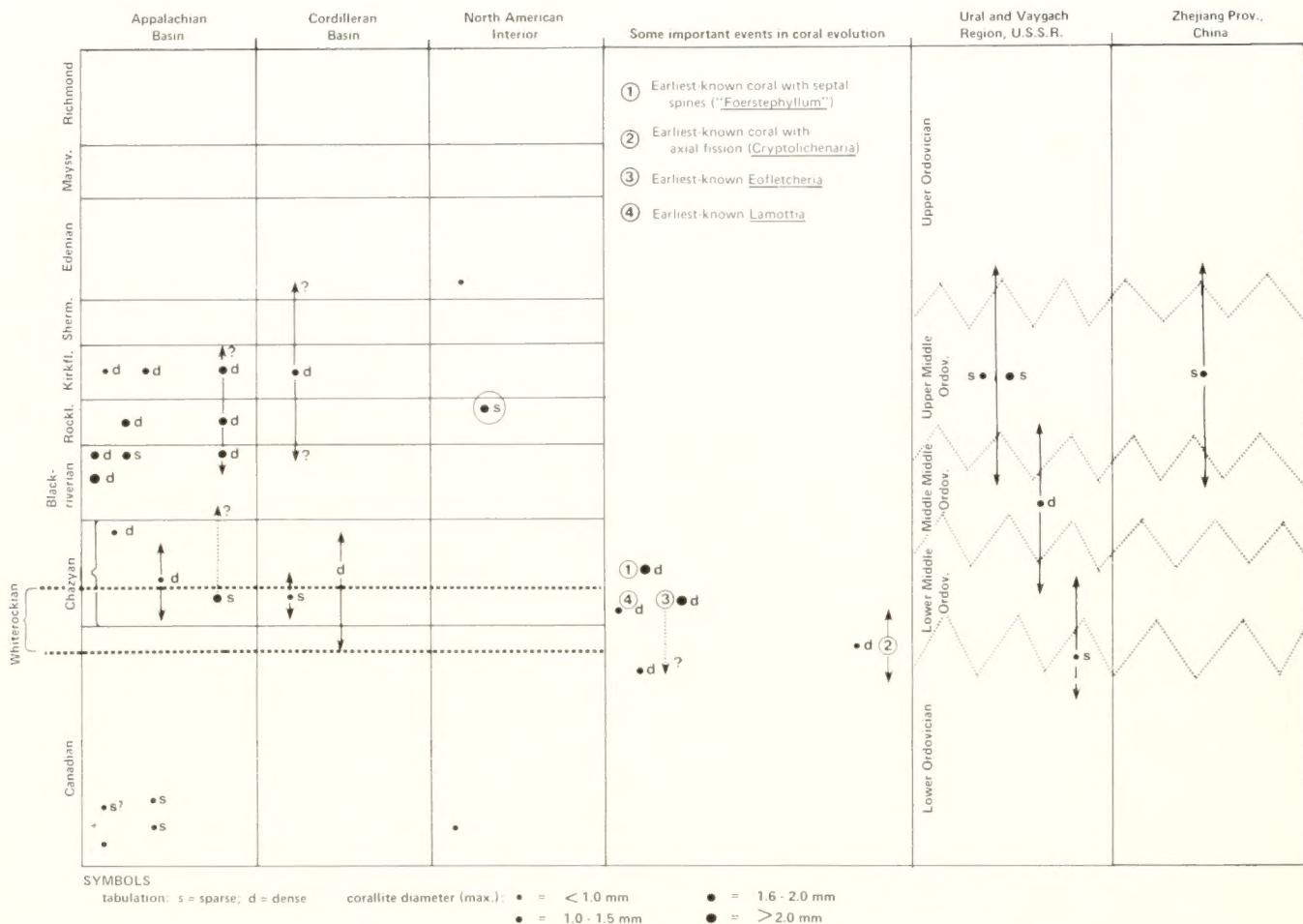
Tabulae are complete and sparse, spaced at intervals greatly exceeding the lumen diameter (Plate 1, figs. 1, 3). As the specimen is a fragment (albeit probably a large portion of the original corallum, judging by the typically small size of topotypes), it may be that the lectotype represents a sparsely-tabulated part of a corallum with zonally-spaced tabulae. Topotypes do, however, seem to confirm sparse tabulation.

True septal structures are absent. There is, however, a faint longitudinal fluting of many corallite walls (Plate 1, fig. 3), apparently due to varying longitudinal wall thickness, and possibly to some actual corrugation of the walls (Plate 1, fig. 7).

Corallites clearly arise by lateral offsetting (Plate 1, fig. 4), with parent and daughter joined through a pore characteristically shaped like a rounded triangle, apex pointing upward.

Four pores were found, comparable to mural pores in the favositids (Plate 1, figs. 5, 6). These are vertically-elongate, about 0.1 mm in maximum diameter. Three lie near wall corners, while the position of the fourth is unclear due to indistinctness of the corner. If growth lines were originally present, they have not been preserved. The sparseness of these pores is striking, and contrasts with the abundance and relative order of mural pores in *Favosites* and its allies. An origin through an agency other than the living coral, such as boring or breakage, seems unlikely. The bi-concavity of the holes, and their uniformly vertical elongation are inconsistent with the former, and their small size and relative smoothness do not support the latter alternative. (A broader hole with a thinner, less regular rim, shown in the lower right-hand corners of Plate 1, figs. 5 and 6, is more likely due to breakage.)

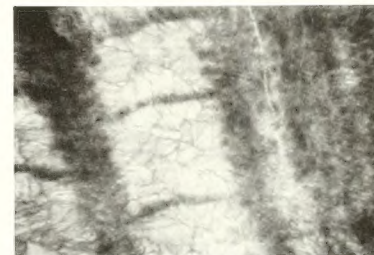
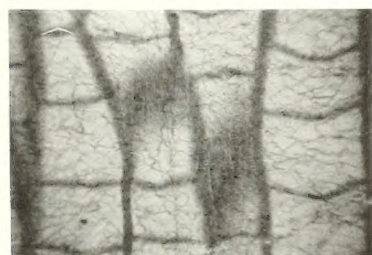
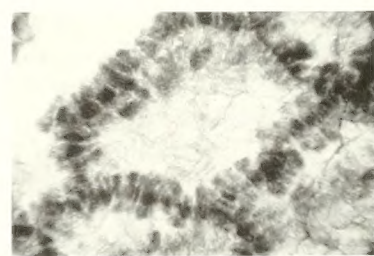
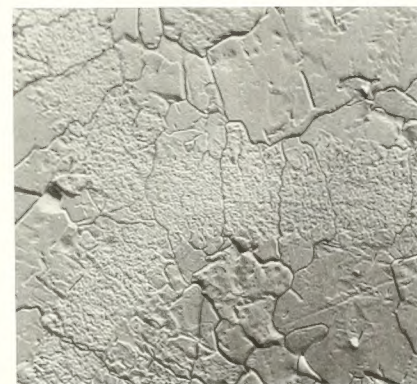
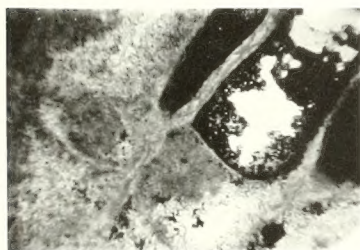
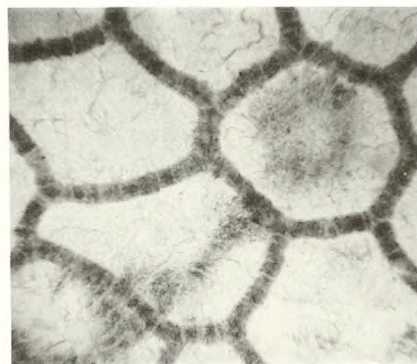
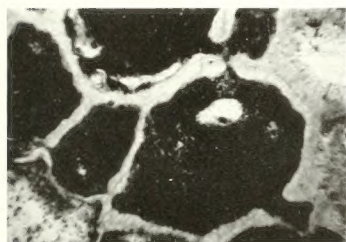
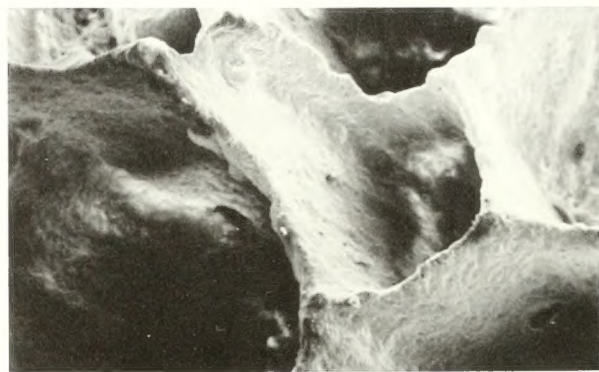
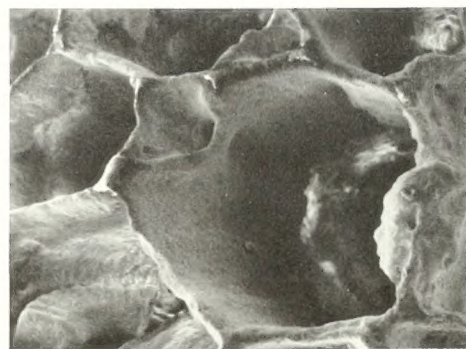
No logical pattern, such as an association with offsets, has been found for these mural pore-like features, and they have not yet been identified in superficial examination of topotype material.



Text-figure 1.—Stratigraphic distribution of material assigned to *Lichenaria* in the literature, correlated with some significant evolutionary developments in tabulate corals. Vertical scale is proportional to time duration of each stage. Arrows indicate uncertainty of precise stratigraphic position of material, and zig-zagged lines on right reflect imprecision of correlations between North America, and the Soviet Union and China. A doubtful occurrence in Tasmania is not included. The position of the holotype of *Lichenaria typa* is circled.

#### EXPLANATION OF PLATE I

- Figure
- 1-8. *Lichenaria typa* Winchell & Schuchert, 1895  
 USNMNH 42949 (lectotype); Guttenberg Mbr., Decorah Shale, St. Paul, Minnesota.  
 1-2. Lateral and distal surfaces. Bar = 5.0 mm.  
 3. SEM showing wall fluting. Bar = 1.0 mm.  
 4. SEM showing lateral offset. Bar = 1.0 mm.  
 5-6. SEM showing two views of a mural pore-like feature (below down-pointing arrows). Note possible mechanically-produced hole in lower right (near left-pointing arrow in Fig. 5; at edge of shadow just above and to left of the number 6 in Fig. 6). Bar = 1.0 mm.  
 7-8. Transverse and vertical thin-sections (respectively), supposedly cut from lectotype. Bar = 1.0 mm.
- 9-12. *Lamottia heroensis* Raymond, 1924  
 MCZ 9410 (holotype); Lower Chazy, W. C. Hall's Pasture, South Hero, Vermont.  
 9-10. Vertical and transverse sections (respectively). Note longitudinal striations in Fig. 9 where wall is in plane of section. Bar = 1.0 mm.  
 11. SEM of transverse polished surface, showing crystal boundaries crossing walls in preferentially radial manner. Bar = 0.2 mm.  
 12. Transverse section showing cracks (crystal boundaries) parallel to transverse wall stripes. Bar = 0.5 mm.
- 13-14. *Nyctopora vantuyli* Bassler, 1950  
 USNMNH 102159 (holotype); Upper Chazyan, near Middlebury, Vermont. Transverse and vertical sections (respectively). Bar = 1.0 mm.



Two thin-sections are associated with the lectotype, bearing the same catalogue number and data, and labelled as type material. The size of the corallum, corallite proportions and matrix are consistent with the lectotype. These sections present an enigma, as in contrast with the specimen they show numerous gaps in the walls (Plate 1, fig. 7). Bassler (1950), in his analysis of the lectotype, illustrated its microstructure with line drawings, and showed no mural pores. Either these thin-sections are not from the lectotype, or the portion of the specimen from which they came was more richly endowed with pores than the unsectioned portion. Museum records shed no light on the matter. The safest course would be to characterize the lectotype by the unsectioned portion, as its structure is readily visible, and to conclude that the mural pore-like features are sparse over-all, though possibly not of uniform abundance throughout the corallum.

#### STRUCTURE OF *LAMOTTIA*

*Lamottia* Raymond, based on *Lamottia heroensis* Raymond, 1924 (Lower Chazyan of the New York-Vermont border area) is a very early genus of favositoid form, commonly placed in synonymy with *Lichenaria* on the basis of its lack of mural pores and septal structures. It is peculiar, however, in having a pattern of alternating light and dark stripes, considered diagenetic features by some authors, crossing the walls in a radial manner as seen in transverse section (Plate 1, figs. 10, 12). Unlike typical *Lichenaria*, it is furnished with abundant tabulae. Serial peels of topotype material have so far revealed no mural pores. They do show clearly that increase was by lateral offset, and therefore coral-like.

The holotype of *L. heroensis* (specimen no. 9410 in the Museum of Comparative Zoology paleontology collection, Harvard University) was studied in thin-section and under the scanning electron microscope. In transmitted light a crack could be seen along the axis of some stripes (Plate 1, fig. 12). Under the SEM (Plate 1, fig. 11) it became clear that the rock was recrystallizing, and that the cracks are crystal boundaries preferentially crossing the corallite walls in a radial manner, parallel to the striping. It was initially assumed that the stripes are an alteration pattern controlled by the cracks, but the presence of distinct longitudinal striations in the walls (Plate 1, fig. 9) suggests instead that the cracks follow a primary structural grain in the walls.

It may be noted that the earliest cases of trabecular septa in corals occur in this New York-Vermont border area: *Foerstephyllum? wissleri* Welby in the Crown Point Fm., just overlying the *Lamottia*-bearing Day Point Fm., and slightly higher in the Chazyan, *Nyc-*

*topora? vantuyli* Bassler (Plate 1, figs. 13, 14), and *Billingsaria parva* (Billings). Perhaps *Lamottia* represents an early stage in the evolution of these structures.

It may be concluded that *Lamottia* 1) was a tabulate coral; 2) had a primary grain in its walls, visible in longitudinal and transverse section; and 3) is distinct from *Lichenaria*, and probably related to *Nyctopora*, as suggested by Flower (1961, p. 39).

#### THE EARLIEST TABULATE CORALS

*Lichenaria's* phylogenetic significance lies in its reputed simple form, and existence prior to other corals, the latter point being founded on basal to mid-Lower Ordovician coral-like fossils reportedly lacking mural pores and septa. These include *L. simplex* (Bassler, 1919); *L. claudi* Bassler, 1950; *L. claudi* Bassler, of Sando, 1957; *L. sp. cf. L. claudi* Bassler, of McLeod, 1979; and unpublished material from the basal Ordovician of Virginia. Only the third (Sando's) is reasonably well-preserved, and numerous features show that it is not a *Lichenaria*, and probably not a coral (for example, broad openings in the walls; increase through axial fission by one to four partitions; and "tabula" formation by distally-concave sheets smoothly tangential to the tube walls, and commonly not meeting in the tube axis). The fifth specimen is insufficiently known for comment. The remainder are all too poorly-preserved to allow confident analysis.

Text-figure 1 shows that all of these early specimens had narrow corallites (under 1.0 mm), and are separated by an appreciable time gap from later *Lichenaria*, most of which have broader corallites. Further, by Chazyan time, corals were undergoing important changes: marked corallite diameter increase, and development of trabecular septa, axial fission, and fasciculate growth habit. If the Chazyan was a time of high evolutionary activity among corals, then the stratigraphic gap separating Lower Ordovician supposed *Lichenaria* from more typical *Lichenaria*, the universally narrow corallites of the former, and the unsatisfactory preservation of the older material leave serious questions about the antiquity of this genus, and the identity of these older specimens. The earliest formally-described material that may be confidently assigned to *Lichenaria* is the Chazyan *L. prima* Okulitch from Tennessee, which post-dates or at best is coeval with *Lamottia*, *Eofletcheria*, and *Cryptolichenaria*. Reports of *Lichenaria*-like corals in the upper Pogonip beds of the western United States are promising, but not yet confirmed by published descriptions. In light of the potential for error (for example, the proximal phase of an *Eofletcheria* corallum can be quite similar to that of a *Lichenaria*; see Rigby and Hintze, 1977, p. 110), these reports must be treated with caution.



Hence, the true role of *Lichenaria* in the evolution of the Tabulata has yet to be established.

### CONCLUSIONS

1. *Lichenaria* is a true tabulate coral, distinct from *Lamottia*. It lacks septal structures. Mural pore-like features occur adjacent to corners, but seem either extremely sparse, or at least unevenly distributed, and lack obvious order (compared to *Favosites* and its allies).

2. Available material is inadequate for confidently extending *Lichenaria* below the Chazyan. Other tabulate corals equal or exceed the age of material that seems confidently referable to *Lichenaria*, though studies of Pogonip specimens may change this.

3. In view of the sparseness of mural pore-like features in *Lichenaria* and some other early tabulates, serial peel techniques are clearly preferable to traditional thin-sectioning for their study.

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THE EARLIEST HELIOLITINES: A DIVERSE FAUNA FROM THE ORDOVICIAN OF NEW SOUTH WALES

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ABSTRACT

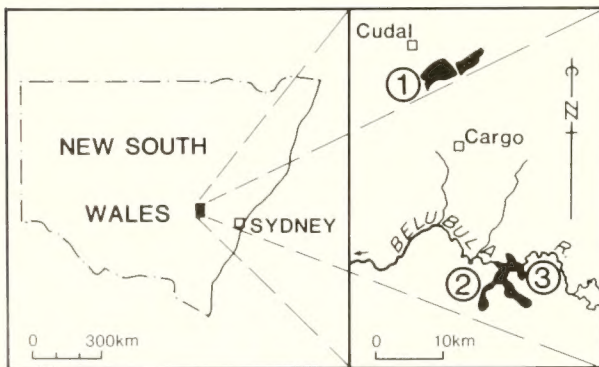
Heliolitines are among the most common corals in Middle-Late Ordovician successions of New South Wales. In fauna I of the biostratigraphically distinct coral-stromatoporoid faunas I-IV only encrusting *Coccoseris* is well represented, but in fauna II a wealth of small hemispherical, encrusting and digitate forms appears, including species of *Heliolites*, *Plasmoporella*, *Propora* and *Palaeoporites*. Fauna I is probably of late Early or early Middle Caradoc age (Blackriveran or Rocklandian-early Kirkfieldian) based on conodont determinations, and fauna II from its position beneath a disconformably overlying graptolitic sequence is older than the zone of *Dicranograptus hians kirki*. This represents an age older than or equivalent to the British zone of *Dicranograptus clingani* (either early or late Middle Caradoc). The pattern of earliest appearances of coccoseridids followed by a diverse fauna is matched elsewhere in the world but the timing is different. In Kazakhstan and China the diverse fauna appears in the latest Caradoc; in eastern North America, Scotland and Baltoscandia, in the Ashgill. The main diversification of the heliolitines is therefore inferred to have taken place in the comparatively isolated N.S.W. island-arc setting off the Australian sector of Gondwana during the Middle Caradoc. The fauna first spread to Kazakhstan, then achieved a circum-equatorial distribution during the Ashgill.

INTRODUCTION

Hill (1957) originally described nine species of heliolitines from the Ordovician of New South Wales, but it has only been more recently that these faunal elements could be placed in their correct stratigraphic context (Webby, 1969; Webby and Packham, 1982). The heliolitines are widely distributed in the Ordovician limestone successions, forming conspicuous components of all the biostratigraphically distinct coral-stromatoporoid faunas I-IV, especially faunas II-III. This paper, however, only focusses on the earliest heliolitines, that is, those represented in faunas I and II of the Bowan Park, Licking Hole Creek and Cliefden Caves areas (Text-figs. 1 and 2).

The lower limits of age of the *Tetradium*-dominated fauna I have not been settled. Packham (*in* Webby, 1969) suggested that conodonts of the Fossil Hill Lime-

stone (Text-fig. 2) were of late Porterfield? or early Wilderness (*i.e.*, Blackriveran) aspect. C. R. Barnes (*pers. comm.*, July 1983) who is currently studying these faunas has noted the presence of *Panderodus* spp., *Belodina* spp., *Bryantodina* n. sp., *Phragmodus* cf. *P. flexuosus*, *Histiodela?* sp., *Pseudooneotodus beckmanni*, *Drepanoistodus suberectus*, and many new taxa. Much more taxonomic work is required to allow precise correlations, but general indications are in favor of a Blackriveran age. Another approach to cor-



Text-figure 1.—Map showing location of Ordovician limestones in Bowan Park area (1), Licking Hole Creek area (2) and Cliefden Caves area (3).

C/S FAUNA	BOWAN PARK AREA ①	LICKING HOLE CREEK AREA ②	CLIEFDEN CAVES AREA ③	
III	Ballingoole Limestone	Malongulli Formation Ea3		
II	Quondong Limestone (34m)	Mt. Lewin Limestone Member	Vandon Limestone (58m)	
		Trilobite Hill Limestone Member		
	Davyesford Limestone (250m)	Belubula Limestone	Belubula Limestone (290m)	
	Davy's Plains Limestone Member			'Aulopora' unit
	Glenrae Lst Member			'E' horizon
Gerybong Lst Mbr				
I	Manooka Lst Mbr	Fossil Hill Limestone ('Big Shell' unit)	Fossil Hill Limestone (110m)	
	Bourimbla Lst Mbr			
	Ranch Member			
	Transmission Lst Mbr			
	Dunhill Bluff Lst Mbr			
			Taplow Lst Mbr	
			Wyoming Lst Mbr	
			Kalimna Lst Mbr	
			Gleesons Lst Mbr	

Text-figure 2.—Subdivision and correlation of Ordovician limestones on Molong High. Note the biostratigraphically distinct coral/stromatoporoid faunas I-III. Ea3 represents the Eastonian zone of *Dicranograptus hians kirki*.

relation is with Tasmanian assemblage OT14 of Banks and Burrett (1980), which is similarly dominated by species of *Tetradium*. It has associated conodonts of North American Midcontinental type, regarded by Banks and Burrett (1980) as suggesting a Rocklandian or early Kirkfieldian age. Succeeding fauna II is similarly comparable with Tasmanian faunal assemblage OT16. It has the first *Palaeophyllum*, and conodonts suggesting to Banks and Burrett (1980) a Kirkfieldian or early Shermanian age.

Upper limits of age of fauna II can be established in the Cliefden Caves area where the Vandon Limestone is overlain disconformably by the graptolitic Malongulli Formation (Text-fig. 2). The basal Malongulli graptolite fauna includes *Leptograptus eastonensis*, *Climacograptus tubuliferus*, *Dicellograptus elegans* and *Dicranograptus* cf. *D. hians kirki*, and may be assigned to the Eastonian (Ea3) zone of *Dicranograptus hians*

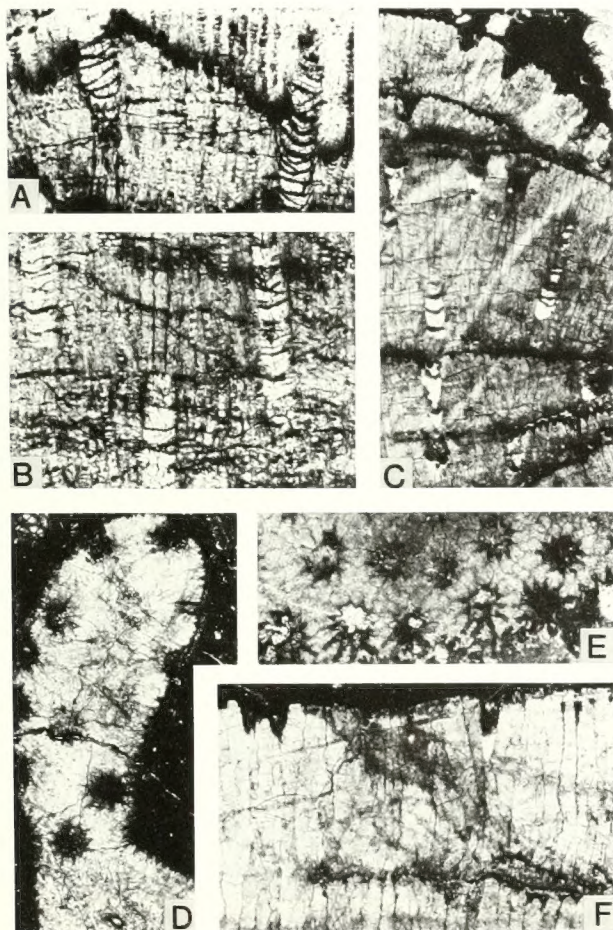
*kirki* (VandenBerg, 1983). The disconformity is unlikely to represent a large gap in time and so markedly effect the validity of the correlation of the directly underlying Vandon Limestone and its fauna II with a level in the early Eastonian. However a problem remains as to how precisely this part of the Australian graptolite zonal scheme correlates with the British standard succession. The zone of *D. hians kirki* (Ea3) has been suggested by Williams (1982) to correlate with an interval spanning the boundary between the British zones of *Dicranograptus clingani* and *Pleurograptus linearis* whereas VandenBerg (1983) equated it entirely within the zone of *P. linearis*. If VandenBerg proves to be correct, then fauna II correlates with the *clingani* Zone. Fauna I is presumably about one graptolite zone older, possibly equating with a level about the British zone of *Climacograptus wilsoni*. The alternative, if Williams's (1982) correlations are adopted, is that the N.S.W. faunas I and II may each have appeared almost one graptolite zone earlier.

## HELIOLITINE SUCCESSION

### Fauna I

The earliest heliolitines in the New South Wales Ordovician sequences are members of Coccoserididae. The sheet-like encrusting *Coccoseris* (Text-fig. 3E-F) and the less common ramose *Pragnellia* (Text-fig. 3D) first appear in the Kalimna Limestone Member (Fossil Hill Limestone) of the Cliefden Caves area (Text-fig. 2). In the stratigraphically higher Dunhill Bluff Limestone Member, *Coccoseris* is accompanied by two other distinctive forms—representatives of sheet-like *Acidolites* (Text-fig. 3C) and *Esthonia*. A similar species of *Acidolites* (Text-fig. 3B) occurs in the 'Big shell' unit of the Licking Hole Creek area. Then in the Ranch Member of the Bowan Park succession the first indubitable members of the Helioliticae appear—these are dome-like to hemispherical colonies of *Wormsipora* and *Heliolites* (Text-fig. 3A). The same species of *Heliolites* is represented in the lower part of the Belubula Limestone (below the 'E' horizon) of the Licking Hole Creek area, along with *Coccoseris* and the first *Palaeoporites*. The equivalent beds in the Bowan Park area include a possible *Wormsipora* in the Bourimbla Limestone Member and a *Coccoseris* which encrusts branches of *Tetradium tenue* to give a digitate *Pragnellia*-like appearance in the Gerybong Limestone Member.

The species of *Coccoseris*, *Acidolites* and *Heliolites* exhibit an almost continuous gradation in morphology from typical *Coccoseris* in the lowest beds of the Fossil Hill Limestone through *Acidolites* in the upper part of the Fossil Hill Limestone to *Heliolites* in the lowest



Text-figure 3.—A, *Heliolites* sp., longitudinal section of SUP 92191,  $\times 8$ ; B, *Acidolites* sp., longitudinal section of SUP 81159,  $\times 8$ ; C, *Acidolites* sp., longitudinal section of SUP 93181,  $\times 5$ ; D, *Pragnellia* sp., SUP 93177,  $\times 7$ ; E-F, *Coccoseris* sp., transverse and longitudinal sections of SUP 80207,  $\times 8$ .

beds of the Belubula Limestone. There is an accompanying change in growth form from encrusting laminar to hemispherical. Rare digitate forms also appear.

#### Fauna II

Silicified heliolitines are found in a number of horizons through the upper part of the Belubula Limestone in the Licking Hole Creek area (Text-fig. 2). In the 'E' horizon, *Wormsipora* and the first indubitable *Propora* occur and, in the immediately overlying beds, a slender digitate *Heliolites*. A hemispherical *Heliolites* (Text-fig. 4F–G), more *Propora* and *Plasmoporella* are represented in the next interval below the 'Aulopora' unit, and in the equivalent Davys Plains Limestone Member at Bowan Park this same species of *Heliolites* is associated with a much larger species of *Heliolites*, *Propora* and *Plasmoporella*. Colonies with a morphology alternating between *Heliolites* and *Propora* also occur (Text-fig. 4C–E).

The greatest diversity and abundance of heliolitines is seen at the level of the Quondong Limestone (Text-fig. 5) and the Trilobite Hill Limestone Member of the Vandon Limestone (Text-fig. 4A–B). Especially abundant in both silicified and unsilicified preservation are the hemispherical colonies of *Plasmoporella*, *Propora bowanensis*, *P. mammifera* (incorrectly attributed to a lower stratigraphic horizon by Hill, 1957), *Heliolites* sp., ramose *H. digitalis* and less common encrusting-laminar *Palaeoporites serratus*, *Acidolites* and *Coccoseris*.

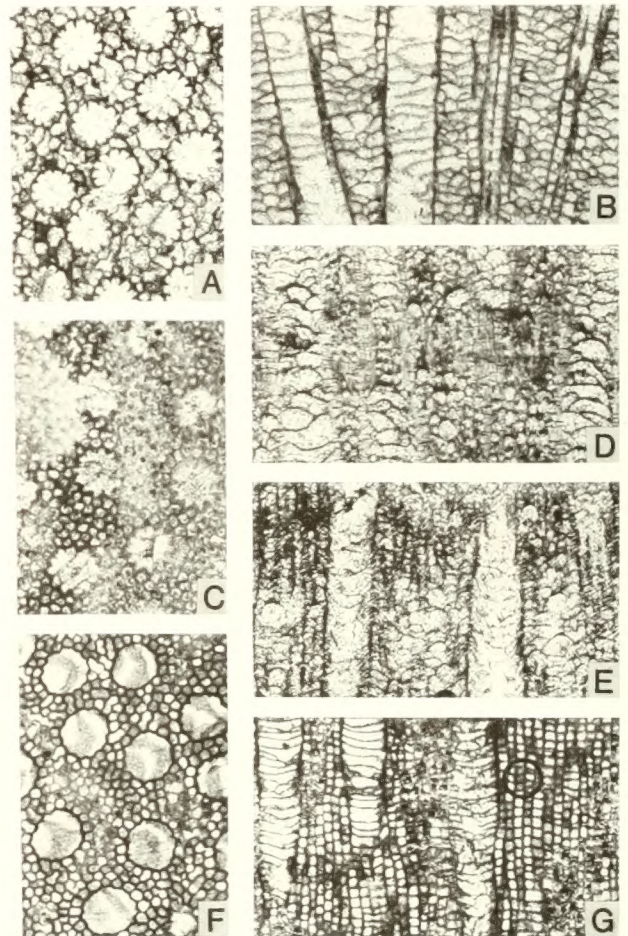
#### DISCUSSION

The extent of the diversification of heliolitines in the ?late Gisbornian–early Eastonian (approximately Middle Caradoc) of New South Wales is without parallel in successions of similar age in other parts of the world. In terms of Hill's (1981) classification the fauna includes representatives of all three superfamilies Coccoseridicae, Helioliticae and Proporicae, and about half the known families. Indeed, all three major 'designs' of heliolitines—with their distinctively different bacular, tubulose and cystose coenosclerenchyme (Text-fig. 6)—had appeared in the N.S.W. region by the end of the Middle Caradoc.

These earliest N.S.W. heliolitines occupied shallow carbonate seas flanking and mantling an offshore volcanic 'high' in an island-arc setting off the Australian sector of Gondwana (Webby and Packham, 1982). The rapid diversification may then have been promoted by their initial geographic isolation. However pathways for the dispersal of the stocks must also have existed to allow colonization of the Tasmanian shelf (a part of the Gondwana continental shelf) with its less diverse

'Caradoc' fauna of *Coccoseris*, *Acidolites*, *Protaraea?* and *Wormsipora* and, perhaps a little later, to permit dispersal along island chains to China (Lin and Zou, 1980) and Kazakhstan. *Protoheliolites* is recorded from the Otarsky horizon of probable *Dicranograptus cligani* age in the Chu-Iliysk mountains of Kazakhstan, and succeeded by a more diverse fauna of *Heliolites*, *Plasmoporella* (12 species), *Acdalopora*, *Protoheliolites* and *Taeniolites* in the Dulankara horizon of *Pleurograptus linearis* age (Bondarenko, 1967).

In many other areas, for example, in eastern North America, Scotland, Norway and Estonia, the Middle-early Late Caradoc record is limited to encrusting-laminar members of the Coccoseridicae (*Protaraea* and/or *Coccoseris*). A few representatives of the Proporicae are recorded in the latest Caradoc (*Pleurograptus linearis* Zone) of Norway (*Kiaeriolites*) and the Siberian Platform (*Sibriolites*), but the major spread of the group



Text-figure 4.—A–G,  $\times 8$ . A–B, *Propora bowanensis* Hill, transverse and longitudinal sections of SUP 80176; C–D, transverse and longitudinal sections of SUP 81153 and E, longitudinal sections of SUP 81200 showing alternating *Heliolites*- and *Propora*-type growth; F–G, *Heliolites* sp., transverse and longitudinal sections of SUP 81201.

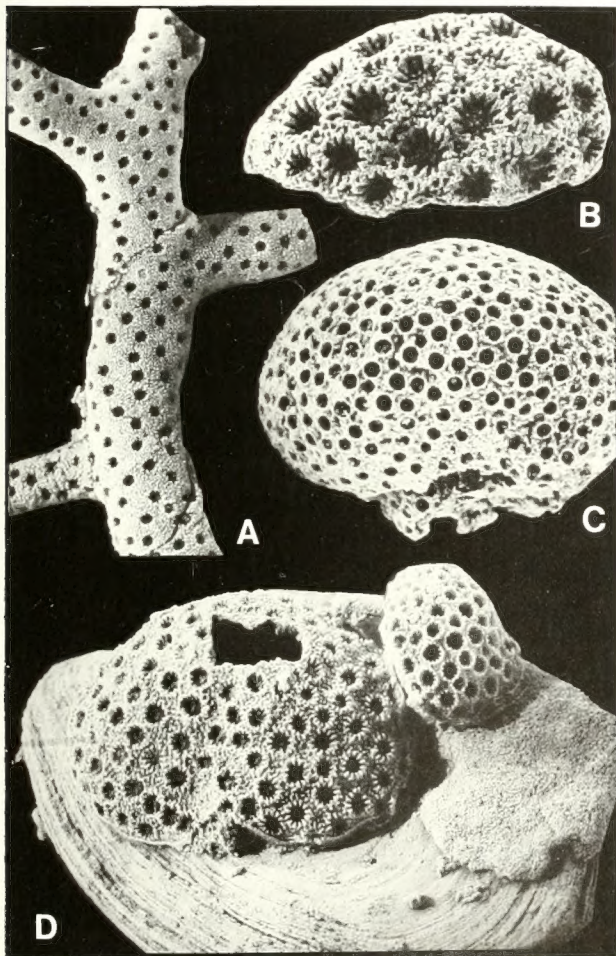
throughout the circum-equatorial belt, to North America, Greenland, the British Isles, Baltoscandia, other parts of the Soviet Union (notably Central Asia, the Urals and north-eastern U.S.S.R.), and Mongolia, occurred in the Ashgill.

The close morphological interrelationships between the main groups of heliolitines in the New South Wales 'Caradoc' faunas gives strong support to the view of the essential unity of the suborder, as already emphasized by Sokolov (1962) and Hill (1981). There seems little justification for arbitrarily separating off the *Coccoseridicae* and implying that the suborder is polyphyletic (Flower and Duncan, 1975; Bondarenko, 1980). The most ancient N.S.W. heliolitines do not show any forms with markedly narrow areas of coenosclerenchyme, nor evolutionary trends towards wider areas of coenosclerenchyme in successively younger

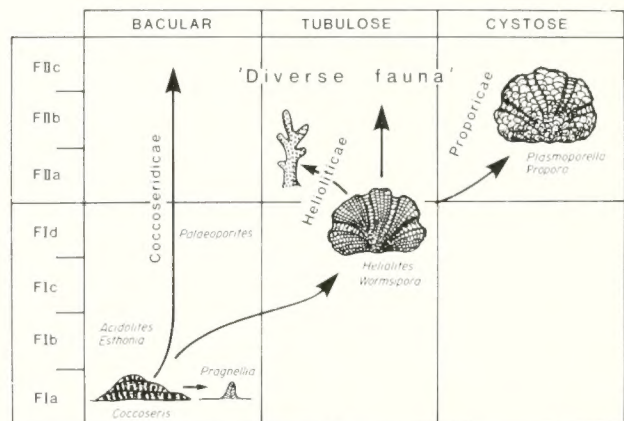
faunas, as claimed by Bondarenko (1975). Furthermore the presence of digitate colonies in both fauna I and II (Text-figs. 3D, 5A and 6) does not support Bondarenko's (1975) contention that they were phylogenetically the most advanced heliolitines.

From the pattern of heliolitine appearances in the New South Wales succession, it is possible to suggest, in agreement with Sokolov (1962), that the Helioliticae were derived directly from a coccoseridid-ancestor. Accompanying the morphological trend from *Coccoseris* → *Acidolites* → *Heliolites* of fauna I is a change in growth form from laminar encrusting to hemispherical (Text-figs. 3 and 6). This appears to reflect substrate adaptation from a role as a low-level encrusting, to a higher level, more independent, habit. Possibly the much thickened bacular tissue of *Coccoseris* reflects the slower growth rate of such an encrusting form. In contrast, at the other end of the 'series' is the hemispherical (and digitate) *Heliolites* with a tubulose coenosclerenchyme which possibly formed during more rapid upward and outward growth.

A second morphological trend in the early part of fauna II may help to explain the nature of the relationship between the Helioliticae and the Proporicae. A few individual colonies show tubulose, relatively more thickened coenosclerenchyme of *Heliolites*-type alternating with cystose coenosclerenchyme of *Propora*-type (Text-figs. 4C–E and 6). The alternation may be interpreted in terms of changes in growth rate—from vertical and horizontal elements (tubules and diaphragms) of slower growth, to only cystose horizontal elements (dissepiments) developed during relatively faster periods of growth. From the ordering of early N.S.W. appearances it may be presumed that repre-



Text-figure 5.—A, *Heliolites digitalis* Hill, lateral view of SUP 94210,  $\times 3$ ; B, oblique-lateral view of *Plasmoporella* sp. B, SUP 94211,  $\times 3$ ; C, lateral view of *Propora bowanensis* Hill, SUP 94212,  $\times 2.5$ ; D, oblique view of *Plasmoporella* sp. A and *Propora bowanensis* Hill (top right) growing on large *Eodinobolus* brachiopod, SUP 94213,  $\times 2$ .



Text-figure 6.—Diagram illustrating the inferred pattern of diversification of major groups of heliolitines in the New South Wales region during ?late Gisbornian–early Eastonian (about Middle Caradoc) time; that is, through the biostratigraphically distinct subdivisions of faunas I and II (F<sub>1a</sub>–F<sub>1c</sub> inclusive).

representatives of the Proporicae were derived from a heliolitid-ancestor (not the other way round), with the loss of vertical components of the coenosclerenchyme.

Specimens illustrated in Text-figures 3–5 are housed in the paleontology collections of Sydney University (SUP).

#### ACKNOWLEDGMENT

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## ORDOVICIAN TABULATE CORAL ASSEMBLAGES OF BRITAIN AND THEIR ZOOGEOGRAPHICAL RELATIONSHIPS

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### ABSTRACT

Details of previously undescribed British Ordovician tabulate coral faunas are given. In the Caradoc Series of south-west Scotland, the Craighead Limestone contains three assemblages comparable with the Blackriveran and Trentonian faunas of North America and with Australian faunas.

Scottish Ashgillian assemblages are also closely related to those of North America. In contrast English and Welsh occurrences match those of Norway and Estonia.

From a review of current available data it is concluded that no distinct Caradocian tabulate coral provinces can be distinguished. However, there is evidence of two provinces in Ashgill times. A North American–North Asian Province consists of an American Subprovince to which the Scottish assemblages belong and an Arctic American–North Asian Subprovince. The second, a West European–Central Asian–Chinese Province includes a West European Subprovince to which the English and Welsh assemblages belong, and a Central Asian–Chinese Subprovince.

### INTRODUCTION

Ordovician tabulate corals in Britain were first recorded by Lonsdale (1839) who briefly described and illustrated two species from south-west Wales. Subsequently McCoy (1850, 1851), Milne-Edwards and Haime (1851, 1855) and Nicholson and Etheridge (1878) described other occurrences in Scotland, northern England, North Wales and south-west Wales, for the most part assigning them incorrectly to existing taxa. Tabulate corals from the Portrane Limestone (Ashgill Series) of Portrane, Eire were described by Klaamann (*in* Kaljo and Klaamann, 1965) but no systematic work on British representatives of this fossil group has been published in the last 100 years.

A comprehensive study of British Ordovician tabulate corals has reached an advanced stage and a detailed systematic account is being prepared for publication. The object of the present paper is to provide details of tabulate coral assemblages in the British Ordovician and to compare them with those of similar age recently reported from other countries and to discuss their zoogeographical relationships.

### ACKNOWLEDGMENTS

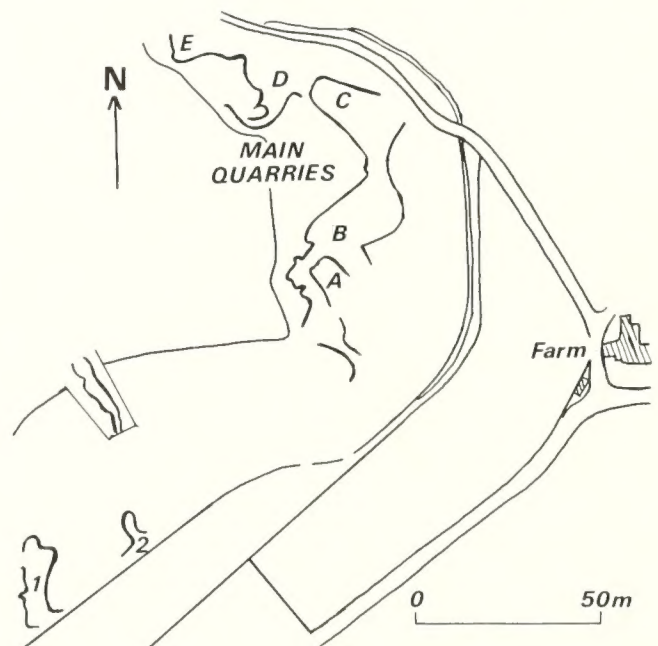
This research was carried out at the Institute of Geological Sciences, Exhibition Road, London. I am very grateful to Dr. D. E. White of the Institute for his encouragement and constant advice during the course of this work, and for his help in the preparation of this paper. The world map was drawn by Mr. J. A. J. Proctor of the IGS Drawing Office.

### SUMMARY OF BRITISH OCCURRENCES

The geographical and stratigraphical distribution of British Ordovician tabulate coral assemblages are summarized in Table 1. Apart from rare isolated examples

in the Welsh Borderland, Caradocian occurrences are limited to the diverse coral fauna of the Craighead Limestone in south-west Scotland. However, Ashgillian faunas are well represented in northern England, North Wales and South Wales as well as in south-west Scotland.

In terms of modern plate tectonic theory, the Scottish faunas are believed to have originated on the margin of an American plate, separated by the basin of the Iapetus Ocean from a European plate, along the margin of which the English and Welsh faunas were located.



### Craighead Quarries

Text-figure 1.—Craighead Quarries, near Girvan, Ayrshire, Scotland.

Table 1.—Stratigraphical relationships of British tabulate coral assemblages (indicated by black bars).

STAGES		NORTH WALES		NORTHERN ENGLAND		SCOTLAND
A S H G I L L	HIRNANTIAN			KEISLEY LIMESTONE	CONISTON LIMESTONE GROUP	
	RAWTHEYAN	CONWAY CASTLE GRIT	GLYN LST. DOLHIR FORMATION			DRUMMUCK GROUP
	CAUTLEYAN	SOUTH WALES ROBESTON WATHEN LST.	DOLHIR LIMESTONE			CRAG HILL LIMESTONE
	PUSGILLIAN					WHITEHOUSE GROUP (UPPER)
C A R A D O C	8 stages				NORTH AMERICA TRENTONIAN BLACKRIVERAN	CRAIGHEAD LIMESTONE (CORRELATION UNCERTAIN)
	recognized					

Caradocian Faunas

The only important British occurrence of Caradocian tabulate corals is in south-west Scotland at the Craighead quarries, near Girvan (Text-fig. 1), where the following three distinct assemblages can be recognized:

3. Main quarries C-E: *Bajgolia scotica* (Nicholson & Etheridge), *Lichenaria* sp., *Paratetradium* sp. nov., *Lyopora favosa* (McCoy), *L. americana* Bassler, *L. sp. nov. 1*, *L. sp. nov. 2*, *Eofletcheria* cf. *irregularis* Hill, *Nyctopora* sp. nov., gen. nov. A, *Catenipora* sp. nov., *Coccoseris tumulosus* Hill.

2. Main quarries A-B and Quarry 2: *Bajgolia furcata* Webby, *Rhabdotetradium tenue* (Webby & Semeniuk), *Eofletcheria laxa* Bassler, *Catenipora* cf. *wrighti* Klaamann.

1. Quarry 1: *Billingsaria occidentalis* (Nicholson & Etheridge), *B.* (subgen. nov. C) sp. nov., *Rhabdotetradium tenue* (Webby & Semeniuk).

There is no local evidence for establishing their stratigraphical relationships. However, assemblages 1

and 2 are closely comparable with Australian coral/stromatoporoid Faunas I and II of Webby (1969, 1975) and with the Blackriveran coral fauna of North America as described by Bassler (1950). Assemblage 3 is believed to equate with Webby's Fauna III and the Trentonian coral fauna of North America as listed by Bassler. It is concluded that the Craighead Limestone spans a greater stratigraphical range than has previously been suspected.

Assemblage 3 also compares very closely, to specific level in some cases, with a tabulate coral assemblage described by Hill (1953) from the Mjøsa and Encrinete limestones of the Oslo region, Norway. It is evident that the Iapetus Ocean was not a barrier to migration and mixing of coral faunas at that time.

Caradocian tabulate corals are rare in England and Wales; only *Foerstephyllum simplissimum* (Okulitch) from the early Caradoc Series of North Wales has so far been recognized.



## Ashgillian Faunas

The stratigraphical distribution of British tabulate coral assemblages in the Ashgill Series is given in Table 1. Faunal details are as follows:

*Girvan District, South-west Scotland*

Upper Drummuck Group: *Calapoecia* sp., *Paleofavosites* sp., *Catenipora* sp., *Propora* sp.

Lower Drummuck Group: *Calapoecia ungava* Cox, *Foerstephyllum halli* (Nicholson), *Paleofavosites* sp., *Catenipora* sp., *Propora* sp.

Upper Whitehouse Group: *Nyctopora mutabilis* Flower, *N. cf. nondescripta* Flower, *N. zeehanensis* Hill, *Catenipora tapaensis* (Sokolov), *Falsicatenipora* sp. nov., *Propora speciosa* (Billings), *Schmidtilites schmidti* (Bondarenko), *Khangailites cf. sinkiangensis* (Yü).

*Northern England*

Keisley Limestone (Cross Fell): *Coccoseris* sp., *Catenipora* sp.

Crag Hill Limestone (north-west Yorkshire): *Protoheliolites goldfussi* (Billings), *Catenipora* sp.

Coniston Limestone Group (Lake District): *Sarcinula* sp. nov. 2, *Paleofavosites* sp., *Catenipora* sp., *Propora* sp., *Wormsipora hirsuta shiyangensis* Lin & Chow, *Protoheliolites norvegicus* Bondarenko, *P. sp. nov. 1*.

*North Wales*

Conway Castle Grit: *Paleofavosites* sp., *Propora* sp.

Glyn Limestone: *Sarcinula cf. organum* (Linnaeus), *S. sp. nov. 2*, *Paleofavosites* sp., *Catenipora* sp., *Acidolites* sp., *Wormsipora hirsuta* (Lindström), *Propora* sp., *Protoheliolites norvegicus* Bondarenko.

Dolhir Formation: *Calapoecia* sp. nov., *Paleofavosites* sp., *Catenipora* sp., *Acidolites* sp., *Propora* sp.

Dolhir Limestone: *Sarcinula* sp. nov. 1, *Catenipora* sp., *Wormsipora hirsuta* (Lindström) *Acidolites* sp., *Propora* sp.

*South Wales*

Robeston Wathen Limestone: *Sarcinula* sp. nov. 1, *Catenipora tapaensis* (Sokolov), *C. tractabilis* (Sokolov), *C. wrighti* Klaamann, *Rhabdotetradium* sp., *Coccoseris* sp., *Esthonia asterisca* (Roemer), *E.? inordinata* (Lonsdale), *E.? sp. nov. 1*, *E.? sp. nov. 2*, *Wormsipora hirsuta* (Lindström), *Wormsipora hirsuta shiyangensis* Lin & Chow, and *Propora* sp.

The Scottish assemblages, characterized by *Calapoecia*, *Foerstephyllum* and *Nyctopora*, are closely related to those of North America. The assemblage from the upper Whitehouse Group, containing abundant *Nyctopora*, may equate with that of the Second Value Formation, New Mexico, described by Flower (1961)

as of Red River age, which is generally considered to be equivalent to the earliest Ashgill of Britain. The coral faunas from the Drummuck Group are comparable with those of Richmondian age listed from eastern North America by Bassler (1950).

In contrast the English and Welsh tabulate coral faunas are dominated by heliolitoids (*Coccoseris*, *Esthonia*, *Acidolites*, *Wormsipora*, *Protoheliolites*) and *Sarcinula*, and are closely related to faunas from the Norwegian 5a and Estonian Vormsi and Pirgu (F1 b-c) stages described by Kaljo, Klaamann and Nestor (1963).

## ORDOVICIAN TABULATE CORAL PROVINCES

Ordovician coral zoogeography was reviewed by Leshus (1970) and by Kaljo and Klaamann (1973) but since then much new information has been published. This, together with results obtained during the recent study of British tabulate coral assemblages, have been synthesized in order to establish whether or not tabulate coral provinces can be recognized.

Caradoc faunas: Kaljo and Klaaman (1973, p. 39) recognized Americo-Siberian and Euroasiatic provinces, the latter being characterized by the presence of specific forms of Rugosa. Certainly, no distinct tabulate coral provinces can be distinguished although *Calapoecia* is confined to North America, *Cyrtophyllum* is confined to Siberia and the Urals of the U.S.S.R., whilst *Plasmoporella* and *Heliolites* are only recorded from eastern China and eastern Australia. All these genera have a much wider distribution in Ashgill times.

Ashgill faunas: The world distribution of selected Ashgill tabulate coral genera is listed in Table 2. Two tabulate coral provinces can be distinguished, each of which may be subdivided into two subprovinces. Their distribution is shown in Text-figure 2.

A North American-North Asian Province, characterized by an association of *Calapoecia*, *Foerstephyllum* and *Sibiriolites* consists of an American Subprovince in which *Calapoecia* and *Foerstephyllum* are predominant and an Arctic American-North Asian Subprovince in which these genera are much less common, but *Sibiriolites*, *Cyrtophyllum*, *Labyrinthites* and *Troedssonites* are abundant; in contrast, these four genera are absent from the American Subprovince.

A West European-Central Asian-Chinese Province can also be recognized, characterized by an association of *Sarcinula*, *Plasmoporella* and *Agetolites*. It consists of a West European Subprovince in which heliolitoids (*Coccoseris*, *Esthonia*, *Acidolites*, *Trochiscolithus* and *Wormsipora*) are predominant, and a Central Asian-Chinese Subprovince in which those heliolitoids are rare but, in contrast, *Plasmoporella* and *Agetolites* are abundant.

Table 2.—Distribution of selected Ashgillian tabulate coral genera. The cosmopolitan genera *Catenipora*, *Paleofavosites* and *Propora* are omitted, together with those of restricted distribution. Abbreviations as for Text-figure 2.

<i>Agetolitella</i>	Z, EC	heliolitoids:	
<i>Agetolites</i>	Z, WC, EC, K, Y, AL	<i>Acdalopora</i>	Z, EC
<i>Amsassia</i>	SI, NB, Z, AT, SC	<i>Acidolites</i>	N, ES, IE, EA
<i>Baikitolites</i>	SI, AT, WC	<i>Coccoseris</i>	N, ES, IE
<i>Calapoecia</i>	N. America, S, IE, U, SI, T, K, AT, NC, EC, AU	<i>Cyrtophyllum</i>	U, NB, SI, T, Y, AT
<i>Eofletcheria</i>	U, AT, EC	<i>Esthonia</i>	ES, N, IE
<i>Fletcheriella</i>	SI, K, AT, EC	<i>Heliolites</i>	ES, Z, M, WC, SC, EC, K, AU
<i>Foerstephyllum</i>	EA, WA, G, S, SI, AT	<i>Karagemia</i>	AT, M
<i>Kolymopora</i>	K, EC	<i>Khangailites</i>	M, X, AT, S
<i>Labyrinthites</i>	B, AL, G, AT	<i>Plasmoporella</i>	N, ES, Z, AT, X, WC, SC, EC, TC, U, K, EA, AU
<i>Nyctopora</i>	WA, EA, H, G, S, N, SI, NB, T, Y, AT, M	<i>Protoheliolites</i>	N, ES, Z, EA, G
<i>Priscosolenia</i>	ES, Z	<i>Protochiscolithus</i>	WA, MA, H, EL, G
<i>Reuschia</i>	AL, WA, EA, N, NB, Z, AT, WC, EC	<i>Rhaphidophyllum</i>	AL, K, SI, T, M
<i>Saffordophyllum</i>	N. America, SI, T, AT, Z, WC	<i>Schmidtites</i>	ES, Z, WC, EC, G, AU
<i>Sarcinula</i>	IE, N, ES, WC, EC, AL	<i>Sibiriolites</i>	SI, Y, AT, M, NC, EC, EL
tetradiids	AL, MA, EA, G, U, NB, T, SI, AT, EC	<i>Stelliporella</i>	N, ES, Z, AT, EC, K
<i>Tollina</i>	SI, T, K, AL, H	<i>Taeniolites</i>	Z, EC
<i>Trabeculites</i>	AL, WA, H	<i>Trochiscolithus</i>	N, ES
<i>Troedssonites</i>	G, EL, K	<i>Wormsipora</i>	ES, IE, X, WC, EC
<i>Vacuopora</i>	SI, T, AT, K		

Although differing in detail, these four subprovinces correspond broadly to the four late Ordovician tabulate coral provinces recognized by Sokolov (1962, pp. 56–58) and mentioned by Leleshus (1970, pp. 85–87). Similarly there is broad agreement with conclusions reached by Kaljo and Klamann (1973, pp. 39–40).

The Scottish assemblages belong to the American Subprovince of the North American–North Asian Province, whereas those of England and Wales belong within the West European Subprovince of the West European–Central Asian–Chinese Province (Text-fig. 2).

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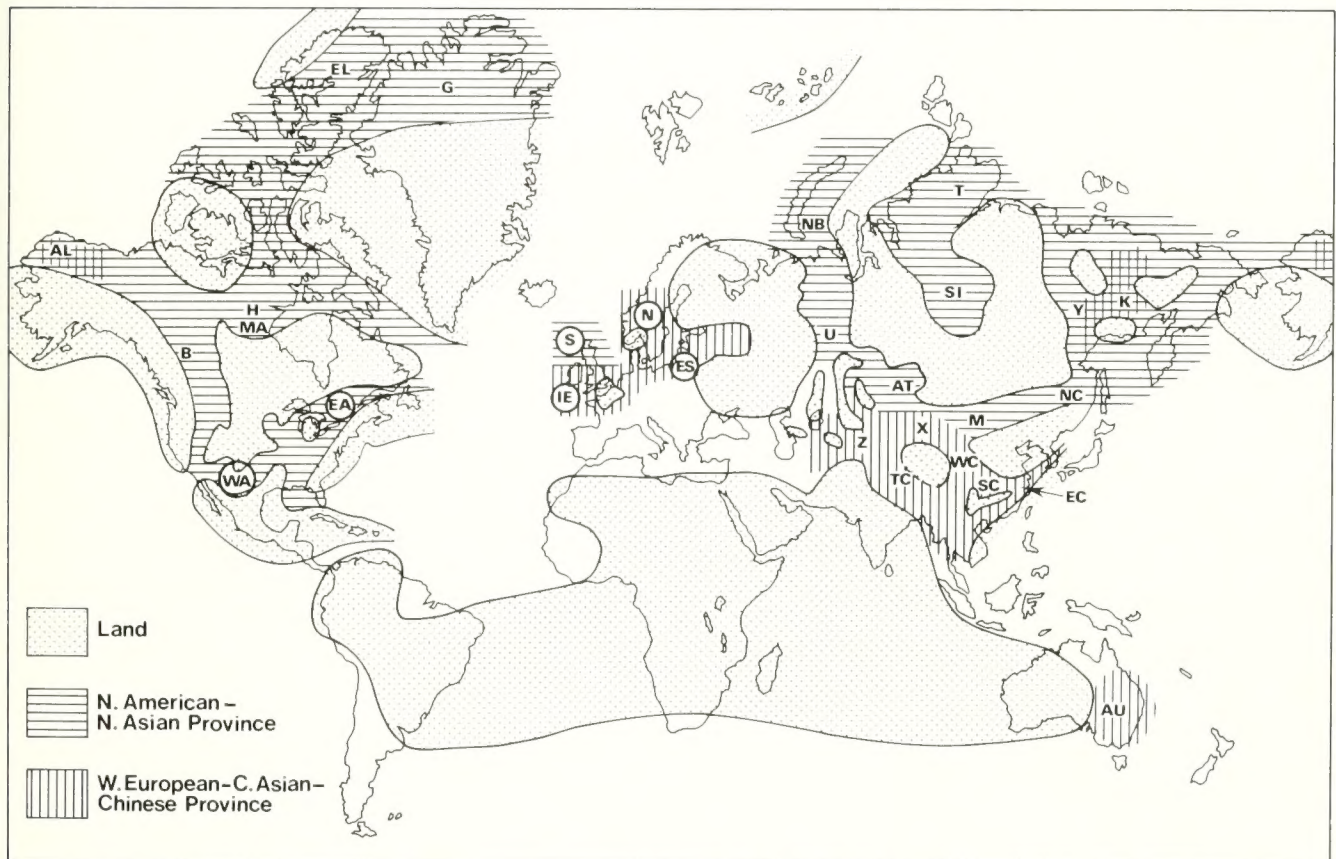
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Text-figure 2.—Ashgillian Tabulate Coral Provinces: AL = Alaska; AT = Altai; AU = Australia; B = British Columbia; EA = Eastern North America; EC = East China; EL = Ellesmere Island; ES = Estonia; G = Greenland; H = Hudson Bay; IE = Ireland, England and Wales; K = Kolyma; M = Mongolia; MA = Manitoba; N = Norway; NB = Novaya Zemlya and Baigach; NC = Northeast China; S = Scotland; SC = Southwest China; SI = Siberia; T = Taymyr; TC = Tibet; U = Urals; WA = Western USA; WC = West China; X = Xinjiang; Y = Yakut; Z = South Kazakh, Kirgiz and Tadzhik.

Circled symbols indicate either the American subprovince or the West European Subprovince, as appropriate.

Symbols without circles indicate either the Arctic American–North Asian Subprovince or the Central Asian–Chinese Subprovince, as appropriate.



SECTION 3  
INVITATIONAL SYMPOSIUM

**The Post-Paleozoic Reorganization, Evolution, and  
Ecologic Development of Reef-Building Cnidaria**

Organized and Convened  
By

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Edited by

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INTRODUCTION

GEORGE D. STANLEY, JR.

The theme of this session was developed as a result of the International Triassic Reef Symposium (1981) organized by Prof. Erik Flügel and held in Erlangen, West Germany, under the support of the German Research Society (Deutsche Forschungsgemeinschaft). This meeting allowed interactions and lively discussions and it underscored the advanced state of our knowledge of Triassic as well as Permian reefs and reef-building organisms. Since the 1981 meeting, there has been a flurry of publications dealing with the subject of Triassic reefs. This is readily apparent by glancing at the extensive bibliographies that accompany each of the following papers. We now have reached a point in the production and refinement of information on the subject of Triassic reefs and reef organisms where we are able to approach the subject of the post-Paleozoic reorganization with appreciable resolution power.

The Permo-Triassic extinctions had a profound effect on the evolution of reefs and reef-building cnidarians. The first post-Paleozoic period, the Triassic, was especially critical in the ecologic development of reefs and the evolutionary histories of the reef-building organisms. Events taking place during the Triassic reshaped the biologic structure of reefs producing the

modern characteristics that readily set them apart from their Paleozoic counterparts.

The reorganization of reef communities in the post-Paleozoic did not occur as a single event but rather as a series of events that lasted some 60 million years, beginning with the earliest Triassic and not completed until Jurassic time. Central to this theme and of paramount interest to cnidarian workers, is the vexing problem of just what happened to the corals after the Paleozoic. In any case, reef organisms of the Triassic cannot properly be discussed without clear knowledge of the last Permian reefs and reef organisms. While no new definitive and unequivocal data can be brought to bear on the origin and ancestry of scleractinian corals, we do have considerable insight into their evolutionary history and ecologic roles in reef environments from the Middle Triassic through the rest of the Mesozoic. While corals are the central interest, we cannot fully appreciate their evolution and ecologic development without also considering their close reef associates (both cnidarian and non-cnidarian).

The six papers and two abstracts in this symposium address different aspects of the post-Paleozoic reorganization and the roles of cnidarians and other or-

ganisms in reef environments of Permian through Jurassic times. The international scope of these papers is apparent with contributions coming from China, the Soviet Union, Yugoslavia, West Germany, Italy, France, and the U.S.

The first paper by Flügel and Stanley, in addition to providing an introduction and overview of the symposium theme, also discusses and summarizes new findings on little-known Permian reefs in South China and Yugoslavia. New discoveries of the first Lower Triassic "potentially" reef-building organisms provide a link in the 20 million year gap between Permian and Middle Triassic reefs. This paper also outlines various periods of reorganization of reef communities and offers some biological innovations to explain changes in these communities, changes ultimately leading to the dominance of scleractinians in the reef environment.

Qi Wentong, in the next paper, describes some of the earliest and most remarkably well preserved scleractinians yet known. They are Anisian (Middle Triassic) from South China and their apparent taxonomic diversity and complexity of growth forms challenge previous ideas about the early evolution of Scleractinia. The following paper by Fois and Gaetani on late Anisian to Ladinian (Middle Triassic) reefs of the Italian Dolomites reveals the ecologic structure and succession of highly diverse communities whose recovery followed the post-Paleozoic crisis.

Ladinian to Carnian age reefs of Yugoslavia are the subject of the next paper by Turnšek and others whose subject bridges the Middle to Upper Triassic interval. This paper provides insight into the increasingly important roles that scleractinian corals began to play.

The latest Triassic reef sequences are presented by

Schäfer who draws extensively from her experience in the Northern Limestone Alps of Austria. The Rhaetian reefs she describes contrast markedly with those of previous papers and leave no doubt that by the end of the Triassic, corals had risen to positions of dominance and true ecologic coral reefs existed. The continuing importance of corals is reaffirmed by Beauvais whose paper completes the reorganizational theme of the symposium. Giving a succinct, stage-by-stage account, she discusses evolution and dramatic radiations of scleractinians from Late Triassic through the Jurassic. Her analysis relates evolutionary patterns in Jurassic corals to environmental changes.

The two abstracts include one by Schäfer and Hillebrandt on Lower to Middle Jurassic coral faunas of South America and another by Krasnov on evolutionary trends in post-Paleozoic corals. The theme of the symposium is well brought out by Krasnov who also offers additional data on the coral-zooxanthellae relationship.

Each contribution in this symposium gives insight into cognate issues during various stages of the post-Paleozoic reorganization. The chronologic unity originally planned for the symposium is maintained and time-overlap between many of the papers such as Qi, Fois and Gaetani, and Turnšek and others, provides cohesion and permits more complete development of the overall theme. The variety of approaches emphasized in the papers, underscores the increasingly interdisciplinary nature of reef research and the combined stratigraphic and paleontologic approach provided by the authors, affords the kind of insight and synthesis not previously possible.

## REORGANIZATION, DEVELOPMENT AND EVOLUTION OF POST-PERMIAN REEFS AND REEF ORGANISMS

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### ABSTRACT

Permian and Triassic reef biotas differ in the taxonomic composition of frame-building or potential framework building organisms (*e.g.*, corals, calcisponges, bryozoans) but are similar with respect to sessile and encrusting organisms (some calcisponges, various algae) which were important sediment binders in Middle and Upper Permian reefs (Bled reef, Slovenia) as well as in Middle Triassic and Carnian buildups (Betic Cordillera, southern Spain). Seven major types of Permian reefs can be recognized according to the dominant binding, baffling or frame-building organisms. Only the calcisponge/algal reefs and the *Tubiphytes*/algal crust reefs are known both from the Permian and from the Triassic. These reef types were also developed in the uppermost Permian (*Palaeofusulina* zone: Hubei, China; Skyros, Greece). No reefs existed during the Lower Triassic, but the first potential reef-builders (calcisponges) discovered just recently indicate an uninterrupted range of some binding organisms. A significant break in the biotic composition took place during the Carnian. Anisian, Ladinian and early Carnian reefs were characterized by calcisponges and algae together with only a few corals, whereas Norian and Rhaetian reefs exhibited more highly diverse reef biotas, consisting of abundant corals, calcisponges, spongiomorphids and foraminifers. Anisian and Ladinian reefs are also distinguished by abundant isopachous carbonate cement crusts growing upon and between sediment-binding organisms (cyanobacterial crusts). Comparable "algal/cement reefs" have been described from the Upper Permian. The stages of reorganization of Triassic reefs are triggered by the following factors: the survival of Permian reef organisms especially adopted to stabilization and binding of initial buildups including organisms that promoted precipitation of early cements; the diversification of reef organisms connected with the expansion of shallow-water habitats; the reappearance of fasciculate coelenterate growth forms lost during the Permian; the rapid evolutions of secondary frame builders; and the fostering of symbiotic associations between scleractinian corals and dinoflagellate algae.

### INTRODUCTION

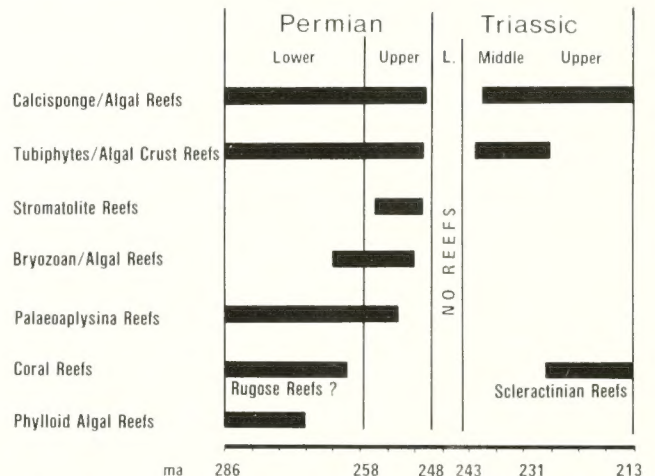
The Triassic was an important period in the evolution of reefs and reef-building organisms. It records the first appearance of scleractinian corals and the transition from Permian-type reef organisms to coral-dominated reefs more reminiscent of those of today. Any discussion of Triassic reefs necessitates examination of those Late Permian examples. Difficulties in comparing Permian and Triassic reefs stem from different approaches and states of knowledge. Very few Permian reefs have been thoroughly studied with respect to systematic descriptions of the reef biota and ecology, whereas about 45 Triassic reefs have become well known. Seventy-five percent of these come from the Alpine-Mediterranean area and western North America. Current concepts and problems in the evolution of Triassic reefs already have been discussed by E. Flügel (1982).

New discoveries of Lower Triassic potential reef-building organisms have shed new light on the subject and reinforce previous ideas that many of the first Triassic reef organisms were holdovers or survivors from the Permian. Several periods of reorganization of reef-building organisms can be recognized. The term "reef" in this paper is used in the loose sense to refer to a variety of organic carbonate accumulations or buildups (Heckel, 1974).

### PERMIAN BUILDUPS

Based on composition, seven types of organic buildups (including reefs and reef mounds; James, 1979) can be differentiated in the Permian according to the most important frame building, binding or baffling organisms involved in the formation of the reefs (Text-fig. 1):

1. Calcisponge/algal reefs: Characterized by the abundance of sphinctozoan and inozoan calcareous



Text-figure 1.—Major types of Permian and Triassic reefs. Time scale after Harland *et al.* (1982).

sponges, which occur together with various algae (*Tubiphytes*, "algal crusts," e.g., *Archaeolithoporella*; selenoporaceans), and bryozoans. These reefs have been formed in shelf-edge or downslope positions. Examples are parts of the Permian Reef Complex in Texas and New Mexico (Newell *et al.*, 1953; Finks, 1960; Newell, 1957), the Late Permian Djebel Tebaga reef in southern Tunisia (Newell *et al.*, 1976; Termier *et al.*, 1977; Wendt, 1980), uppermost Permian reefs in Hubei, Southern China (Fan *et al.*, 1982), and the Late Permian reef facies, represented by allochthonous blocks, near Sosio, Sicily (Montanaro-Gallitelli, 1954). Allochthonous reef limestones of uppermost Permian age (Palaeofusulina zone), found on the Greek island of Skyros, are characterized by abundant calcisponges and bryozoans (E. Flügel, in preparation).

2. *Tubiphytes*/algal crust reefs: Calcisponges are of minor importance in these reefs as compared with encrusting species of *Tubiphytes* Maslow and micritic algal crusts which might have been responsible for the intensive formation of syndimentary carbonate cements. This type seems to have flourished during the Lower Permian (Troglkofel reefs, Southern Alps, E. Flügel, 1981a; Ural region, U.S.S.R., Chuvashov, 1983), but is also important in the Middle and Upper Permian (Bled reef, Julian Alps, Slovenia, E. Flügel and Ramovš, in preparation; Permian reef complex, U.S.A., Babcock, 1977, Toomey and Cys, 1979; Southern China, Fan *et al.*, 1982, He *et al.*, 1981; Caucasus region, U.S.S.R., Pisera and Zawidzka, 1981). Types 1 and 2 can not always be strictly preserved, but type 2 often corresponds to the stabilization phase of buildups.

3. Stromatolite reefs: Buildups composed predominantly of stromatolites and cryptalgal laminites with only minor amounts of bryozoans have been described from the Late Permian of the Central European Zechstein basin (Kerkmann, 1967, 1969; Paul, 1980; Smith, 1981a). These reefs are believed to have been formed under normal marine, subtidal as well as under hypersaline conditions, sometimes in close spatial and temporal connection with bryozoan/algal reefs.

4. Bryozoan/algal reefs: fenestrate bryozoans in conjunction with sediment-binding algae can be regarded as principal frame builders in Late Permian reefs of the Zechstein basin (Cuffey, 1977; Füchtbauer, 1980; Smith, 1981b).

5. *Palaeoaplysina* reefs: *Palaeoaplysina* Krotow, variously attributed to stromatopora or sponges, is the predominant binding and framing organism in some Pennsylvanian and many, mostly Lower Permian buildups known from the western margins of the Urals (Chuvashov, 1973), on Ellesmere Island (Davies and Nassichuk, 1973), in the Yukon territory (Davies,

1974), in Central Spitsbergen (Skaug *et al.*, 1982), in Idaho (Breuninger, 1976), and in Southern China (Fan *et al.*, 1982).

6. Rugose coral reefs: Rugose corals are of minor or most likely of no importance in the formation of Permian reefs. Descriptions of Permian coral framestones or bafflestones are scanty (Hashimoto, 1979). During the latest Permian, cerioid and fasciculate colonial growth forms disappeared leaving only solitary, probably deeper water corals at the end of the Permian. (H. W. Flügel, 1970; Taraz *et al.*, 1981).

7. Phylloid algal reefs: Buildups, characterized by abundant leaflike calcareous algae, are common in Pennsylvanian and Lower Permian shelf limestones of the central and western United States (Wray, 1968; Toomey, 1976), in the U.S.S.R. (Kulik, 1978; Chuvashov, 1983), and in the Southern Alps (E. Flügel, 1980).

Only the *Tubiphytes*/algal crust reefs and the calcisponge/algal reefs are known both from the Permian and the Triassic. Rugose coral reefs are said to have occurred in the Lower Permian but evidence for this is equivocal. Scleractinian corals first appeared in the Middle Triassic and they began to take up important reef-building roles in the Upper Triassic. This leaves a gap of about 40 million years during which coral reefs did not exist.

There are no striking differences with regard to the major frame-building and binding organisms, in the



Text-figure 2.—Distribution of Permian Calcisponge/Algal Reefs and *Tubiphytes*/Algal Crust reefs.



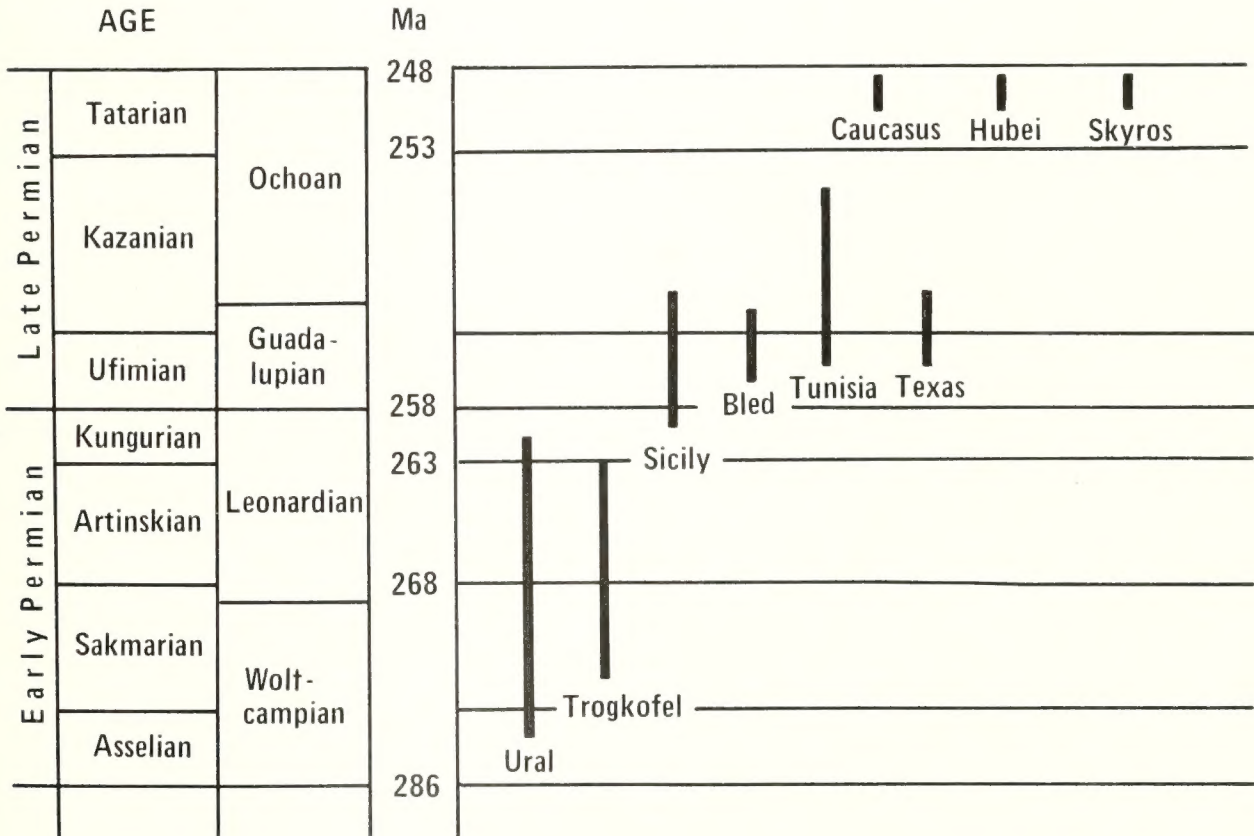
gross composition of *Tubiphytes*/algal reefs and calcisponge/algal reefs from the Early and Late Permian and from the latest Permian (Text-figs. 2 and 3). Reefs, described by Fan *et al.* (1982) from the Changxing Formation (late Tatarian or late Ochoan) of the Lichuan District in West Hubei, Southern China, yield a rich sphinctozoan fauna (together with *Tubiphytes* and algal crusts), partly congeneric with the rich calcisponge fauna of the Capitan reef of West Texas. The depositional fabrics of these Chinese reef limestones seem to be very similar to those of the Capitan reef-complex. The reef facies of the Hubei reefs are overlain by lagoonal limestones, indicating a shallowing-upwards sequence, which seems to continue into the Lower Triassic; a stratigraphical gap may exist near the Permian/Triassic boundary (Kahler, 1974).

In contrast to the Chinese reef limestones, allochthonous blocks of reef carbonates, shown by fusulinid dating to be coeval with the Hubei reefs (Palaeofusulina zone), of the island Skyros (Northern Sporades, Greece), are characterized by a micritic matrix, the predominance of inozoan sponges instead of sphinctozoans, and the abundance of bryozoans. Epizoans and algal crusts are very rare. Microfacies and biotic composition of the Greek reef limestones cannot be

compared with Triassic reefs, whereas the facies types as well as the major reef-building biotic elements (with the exception of the bryozoans) of the Chinese Hubei reefs are similar to Anisian or Ladinian calcisponge/algal reefs (Wetterstein limestone reefs of the Northern Alps and the Carpathians). The same holds true in a comparison of the Middle Permian Bled reef in Slovenia with Middle Triassic *Tubiphytes*/algal crust reefs, developed in the Betic Cordillera, southern Spain (E. Flügel, Martin and Martin-Algarra, in preparation). Details are summarized in Text-figure 4.

POTENTIAL REEF-BUILDING ORGANISMS IN THE LOWER TRIASSIC

No reefs are known from the Early Triassic (Text-fig. 1). The time gap between the latest Permian reefs and the oldest Anisian reef described by Scholz (1972), from northern Hungary, is about 8 million years (Harland *et al.*, 1982). The causes of this worldwide phenomenon have been discussed in terms of regression/transgression patterns, salinity crises, changes in the water circulation patterns and their effect on the productivity of oceanic plankton, and the extinction of potential reef-building organisms (Hüssner, 1983; Kummel and Teichert, 1973; Kozur, 1980; Oliver,

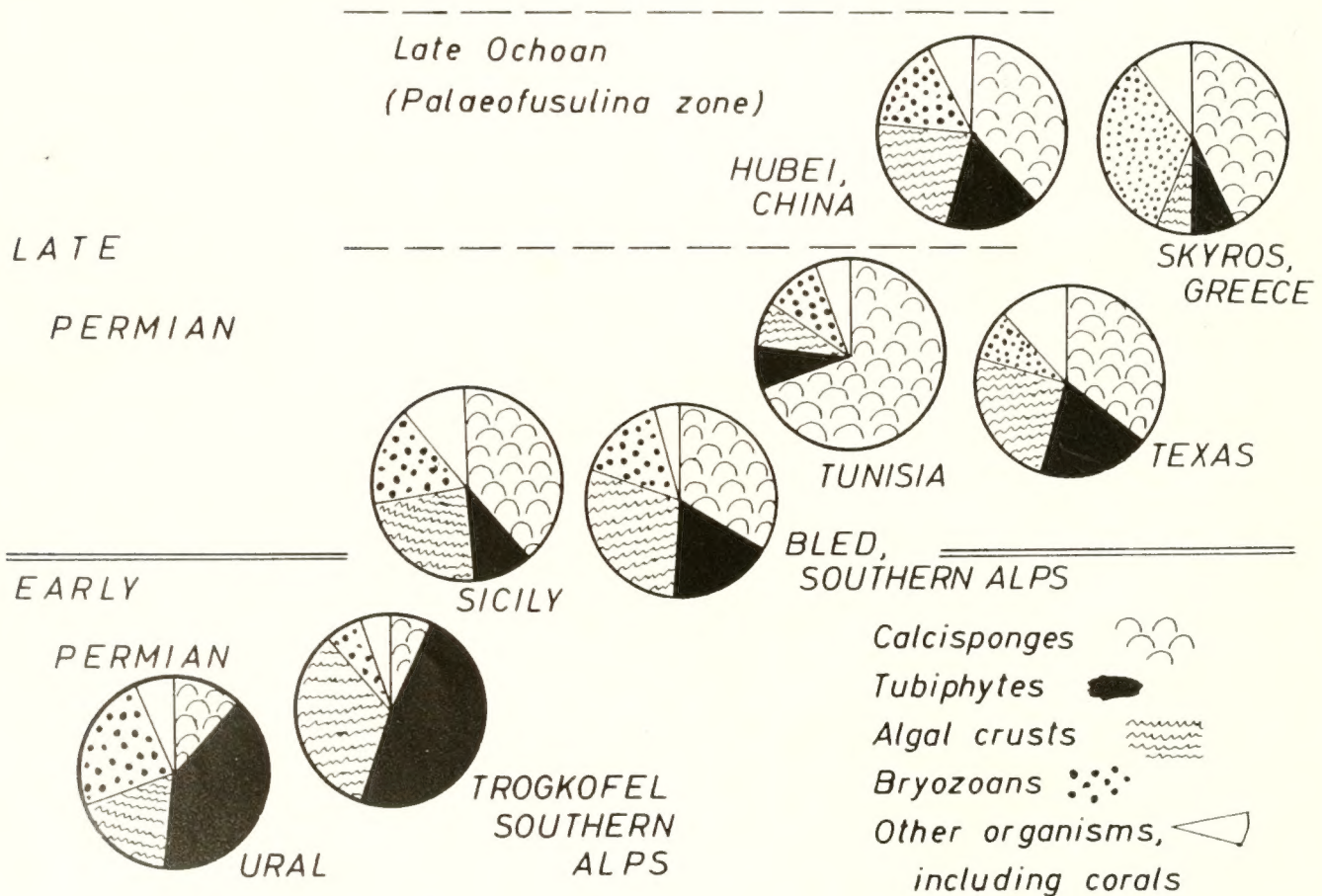


Text-figure 3.—Approximate age of some Permian Calcisponge/Algal Reefs and *Tubiphytes*/Algal Reefs.

1980). The extinction of the principal reef-building groups might have been responsible for the disappearance of bryozoan reefs (and of course, rugose corals) but this seems questionable for calcisponge reefs, because sphinctozoan calcisponges have just recently been discovered in Lower Triassic (Upper Scythian) platform carbonates near Vienna, Austria (E. Flügel and Mostler, in preparation). These low-growing, very small calcisponges, found together with some ostracods, gastropods and foraminifera, belong to the Permian genus *Girtyocoelia* King, and seems to be identical with the Permian species, which is, thus evidence that some potential reef builders spanned the systemic boundary without interruption. The lack of epizoans and of calcareous algae, (this group is missing all over the world in the Lower Triassic!) as well as the paleoenvironmental parameters, point to a rather restricted biotope for these sponges.

#### "PERMIAN" REEF BUILDERS IN TRIASSIC REEFS

The systematic paleontological study of some Middle Triassic and early Upper Triassic reefs (Ladinian reefs in Spain; E. Flügel *et al.*, in preparation; Carnian reefs of Hydra Island, Greece; Schäfer and Senowbari-Daryan, 1983) indicates that encrusting algae and many microproblematica as well as some stromatoporoids occur both in Permian and Triassic reefs. Examples are *Archaeolithoporella hidensis*, *Colonella* sp., *Tubiphytes obscurus* and *T. carinthiacus*, *Koivella permien-sis*, and various species of porostromate algae as well as some disjectoproids. Even some relicts of late Paleozoic phylloid algae may still be present in the Triassic (P. Reid, pers. comm.). All long-ranged species were active in the formation of bindstones, characteristic of the early phases of Middle Triassic reefs (Fois and Gaetani, this volume).



Text-figure 4.—Frame-building and binding organisms within some Permian Calcisponge/Algal Reefs and *Tubiphytes*/Algal Crust Reefs. Estimations are based on the following sources: Ural, Chuvashov, 1973, 1983; Trogkofel, Flügel and Flügel-Kahler, 1980; Sicily, samples from the Sosio region; Bled, Flügel and Ramovš, in prep.; Tunisia, Termier *et al.*, 1977, Wendt, 1980; Texas and New Mexico, Babcock, 1977; Hubei, Fan *et al.*, 1982, and own samples; Skyros island, own samples.

## TURNING POINTS IN TRIASSIC REEF BUILDING

After the long biologic hiatus in the Early Triassic distinguished by a worldwide absence of reefs and thick carbonates in general, the first reefs of the Middle Triassic began to take shape. As discussed above, the biotas of these first Triassic reefs were very similar to those of the Permian. Two major turning points marked by reorganization of the reef biota can be recognized within the Triassic. These are the Middle to early Late Triassic (Anisian–Early Carnian) and the latest Triassic (Norian–Rhaetian). It is possible within these intervals to discuss the general composition of the reef biota on a group, genus, and species level, the principle reef organisms producing the major reef framework as well as their taxonomic diversity and provinciality (E. Flügel, 1982).

### Anisian to Early Carnian

Reefs and large-scale carbonate sedimentation resumed in Anisian time. This stage is also characterized by the first scleractinians that appear in the lower Muschelkalk of the Germanic facies of the Silesian region of Poland (Weissermel, 1925). These are fairly diverse, consisting of 12 species of solitary and colonial scleractinians. Eight species were reported in slightly younger Upper Anisian rocks of Hungary (Kolosváry, 1958). Anisian reef limestones also come from the Southern Alps, Karawanken, and the Northern Calcareous Alps (E. Flügel, 1982). New discoveries of unusually diverse and well-preserved Anisian corals have been made in South China (Qi, this volume). Even though they were potentially reef building, Anisian corals did not construct reefs but instead occurred as small, localized patches. They do not appear to have been particularly cosmopolitan. Those of China represent many new species and are quite different in composition from corals of the Muschelkalk or Alpine facies. The succeeding Ladinian reef-complexes of both the Northern and Southern Alps (Brandner and Resch, 1981; Henrich, 1981; Gaetani *et al.*, 1981, and Fois *et al.*, this volume) show also that while corals were producing localized biostromal accumulations, they were still not reef building.

The roles of reef building during this time seem to have been relegated to organisms of the Permian such as calcisponges, encrusting algae, and *Tubiphytes* (Text-fig. 1). Although early Carnian carbonate sequences reveal increased abundance of scleractinians, they still played rather subordinate roles as reef builders. Regions where detailed paleoecologic studies have been undertaken show that while diversity of scleractinians is high, the primary framework builders were stromatoporoids and/or calcisponges (Fürsich and Wendt,

1977). The same holds true for Ladinian and Carnian (Cordevolian) reefs of Yugoslavia (Buser *et al.*, 1982; Turnšek *et al.*, this volume), although quiet and probably deeper-water coral bioherms show a great abundance of corals and an apparent preponderance of coral framework.

Ladinian biostromal limestone of North America occurs in Nevada (Stanley, 1979; Gaździcki and Stanley, 1983). Here, corals are found only in localized lenses and calcareous algae and benthic foraminifera are more abundant. The absence of calcareous sponges in Nevada is in contrast to other sequences where they are especially conspicuous, and in the absence of any larger organisms, perform the role of reef builders.

While most genera of calcisponges have broad time ranges, species are restricted to the Anisian–Carnian time interval. The same holds true for the corals, dasycladacean algae flourishing in back-reef settings, and some microproblematica. There are no conspicuous differences in the specific composition of calcisponge faunas from the Ladinian and Early Carnian reefs from different parts of Europe, western Anatolia, or China. Diversity (based on the number of species) seems to be different, however, perhaps due to the different stages of investigations and by different potentials for preservation. In general, diversity is rather low in most reefs. This is especially true for the biota within the base of larger, high-energy reef-complexes. Middle Triassic and Early Carnian reefs exhibit about eight communities; at a high taxonomic level, only three however, can be regarded as long-lived units.

### Norian and Rhaetian

Norian and Rhaetian reef communities of the Late Triassic differed greatly from those of the Carnian. The geographic distribution of Norian and Rhaetian reefs shows a distinctly wider distribution pattern, from the western Tethys across this vast, near tropical seaway to Asia and possibly also to North and South America (Text-fig. 5).

A major change in Norian and Rhaetian reefs that distinguishes them from older examples is the increase in importance of scleractinians, especially in shallow-water, higher energy regions of the reef. These corals played dominant roles in the construction of extensive patches in the central reef area such as in the Dachstein reef/complex of the Northern Calcareous Alps (Zankl, 1971). In these Norian reef settings they began to diversify and increase in importance. Details of the paleoecology of Norian–Rhaetian reefs was given by E. Flügel (1981b) who pointed out that areas of the reef-crest and reef-flat became occupied by large, rapidly growing scleractinian colonies. In comparison with the Norian, those of the Rhaetian such as the Röteland

and Adnet reefs (Schäfer and Senobari-Daryan, 1981) show dramatic increases in cover and percent surface area occupied by actively growing corals. Other examples such as the Steinplatte reef (Piller, 1981) reveal domination of a narrow reef crest by gigantic coral colonies, leaving little doubt of the presence of true, wave-resistant coral framework in these Upper Triassic reefs.

In addition to corals, secondary framework builders included abundant calcisponges, spongiomorphs, disjunctoporida and "tabulozoans" (including some sclerosponges). Aside from spongiomorph colonies, few of these organisms ever attained sizes matching some species of the colonial corals such as "*Thecosmilia*" (= *Retiophyllia* Cuif). Other organisms such as sessile foraminifers, various microproblematica, spongiostromate algae and other types of calcareous algae played important roles in building and cementing the framework.

Norian and Rhaetian reefs cannot be differentiated by the composition of their reef-building organisms. Differences occur in contemporaneous species of reef biota from different geographical positions (reefs in the Northern Alps, in northwestern Sicily, and in the Pamir Range). In contrast, western North American buildups yield coral faunas, very similar to those of the Tethyan region (Montanaro Gallitelli *et al.*, 1979; Stanley, 1979) with up to 60 percent of the taxa conspecific. The provinciality of Norian and Rhaetian frame builders seems to be more pronounced in non-coral associations (calcisponges, tabulozoans, spongiomorphids). The diversity of Norian and Rhaetian reef-builders is rather high, especially in reefs developed at platform margins (Gosaukamm reef, Austria; Wurm, 1982), and in back-platform basins (some Upper Rhaetian reefs in Austria; Schäfer and Senobari-Daryan, 1981). Reef communities are rather monotonous and widely distributed; six major communities may be defined by the quantitative predominance of a few reef-building genera or species, and by regular associations with epibionts (E. Flügel, 1982).

The significant turnover of reef biotas between Anisian to Early Carnian and the Norian to Rhaetian intervals can only be explained by adaptive radiations of the reef-building organisms (sphinctozoan calcisponges, scleractinian corals).

A number of extrinsic and intrinsic biological and geological factors may have worked together or singly to control or influence the evolution of organisms of Triassic. Some of these factors are discussed below.

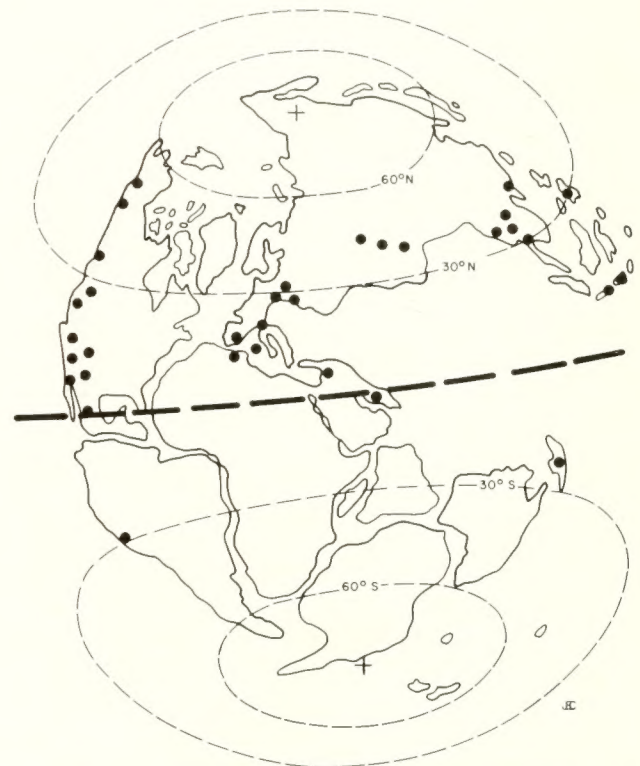
## FACTORS INFLUENCING THE EVOLUTION OF TRIASSIC REEFS

### Survival of Permian Organisms

The survival into the Triassic of Permian organisms such as algae, calcisponges, foraminifers, and *Tubiphytes* resulted in Middle Triassic reefs that were so reminiscent of those of the Late Paleozoic. Some of these were framework builders and other organisms stabilized and colonized organic buildups on the lower part of gently dipping paleoslopes. Encrusting organisms were very important. In the Anisian to Early Carnian interval, cyanobacteria and algae aided in binding and also stimulating syndimentary cements, which along with the frame builders, were so important in producing reefs (E. Flügel *et al.*, 1981; Biddle, 1980).

### Sedimentation and Tectonics

The Middle Triassic was characterized by extensive carbonate sedimentation and widespread shelf areas. This resulted in extended carbonate platforms and platform margins; settings ideal for reef growth. In the Southern Alps this was also closely associated with active volcanism and volcanoclastic deposition. Tensional tectonics were active during this time with block-



Text-figure 5.—Distribution of Triassic reefs. Stippled area in western North America is the site of possible allochthonous "displaced terranes" and may not have been part of North America during Triassic time.

faulting movements accompanied by synsedimentary tectonics (Brandner 1978; 1983). This coincided with early rifting (Bechstädt *et al.*, 1978) which facilitated platform-basin development and seems to have promoted reef building. Such tectonic styles were apparently not present in contemporaneous carbonate rocks of western North America and this may explain radical differences in carbonate facies and the apparent lack of reef development there (Stanley, 1980; 1982).

Extensive shelf areas coincided with a major transgression of epicontinental seas. These seas attained their maximum extent in Ladinian to Early Carnian times, flooding an estimated 16 to 19 percent of the continental margins (Hallam, 1981). This flooding and the increased habitat area it afforded, may explain in part, the increased diversity and rapid evolution of reef organisms. By Late Triassic (Norian) time we find a different reef community and extensive high-growing corals inhabiting the back reef, central reef areas and the reef crest.

#### Reappearance of Colonial Framework

Colonial growth forms lost before the end of the Permian, occurred again in the first Triassic reefs of the Anisian due to the appearance of scleractinian corals. The first scleractinians of the Anisian were both solitary and colonial, and seem to be relatively diverse, representing at least five distinct families. In addition to taxa known from the Anisian Muschelkalk (Weisermel, 1925) an exceptionally well-preserved and diverse Anisian fauna has been recently discovered in South China. Here 20 different taxa occur (Qi, this volume). Potentially framework building (fasciculate) growth forms are present. These corals are all small and some thamnasteriid species show rather complex corallum morphologies which according to Coates and Oliver (1973), can be considered highly integrated.

Included in the Anisian fauna are low-growing branching fasciculate coral colonies of "*Thecosmilia*" (= *Retiophyllia* Cuif). Although potentially reef-building, these corals did not produce extensive framework in reef settings but occurred instead as small, rather localized patches or thickets. The same can be said for most Ladinian to Carnian examples, where corals preferred protected, lower/energy settings. The corals were subordinate to other organisms in both abundance and volume of framework and do not appear to have formed the type of framework found on the reef crest or the upper forereef slopes today (Jackson, 1979). During the Ladinian, branching spongiomorphs appeared but the principal framework during the Ladinian to Carnian interval was produced by *Tubiphytes* and calcisponges. Sphinctozoan calcisponges became very diverse during this time.

In the Norian and Rhaetian interval, scleractinians began contributing extensively to organic framework, especially by high-growing, fasciculate species, some of which achieved gigantic sizes. Many developed in high-energy, reef crest settings. The paleoecology of the Latest Triassic coral reefs shows great similarity with living reefs (Schäfer, this volume).

A vexing question emerging from this discussion is why potentially reef-building scleractinians of the Triassic inhabited reef environments for nearly 20 million years yet remained subordinate to calcisponges and other noncolonial organisms. An idea put forward by Stanley (1981) is that scleractinians did not acquire symbiosis with zooxanthellate algae until the Late Triassic. This subtle association and the inherent advantages it bestowed in improved metabolism and accelerated growth rates in corals, may have been decisive in establishing a competitive edge over other reef organisms. The firm establishment of this association sometime later in the Mesozoic could explain the dramatic adaptive radiation that occurred in post-Triassic reef corals (Wells, 1956).

#### CONCLUSIONS

The Triassic history of reef building and the evolution of reef-building organisms cannot be properly appreciated without a firm understanding of Permian counterparts. New studies of uppermost Permian reefs and newly discovered, potentially reef-building organisms of the Lower Triassic, reinforce the idea that many organisms survived uninterrupted through the Permian-Triassic crisis to reemerge as reef builders of the Middle Triassic. Foraminifers, calcisponges, *Tubiphytes*, and algae established a relatively long-lived reef association somewhat reminiscent of the Permian and lasted from Anisian to Carnian time.

The nature of this association can be attributed to the survival of Permian organisms and intricate relationships between reef dwellers and encrusting organisms, such as cyanobacteria and algae crusts, capable of binding, trapping and promoting rapid cementation of the reef. The tectonic-depositional setting may also have resulted in the expansion of carbonate shelves, all along the Tethys region, which consequently facilitated the diversification of the reef organisms.

The reorganization of the reef ecosystem took place in the latest Triassic and resulted in Norian and Rhaetian communities characterized by abundant scleractinians and diverse calcisponges, spongiomorphs, and foraminifers. It was a time of rapid development of extensive organic framework produced principally by scleractinian corals. Reefs of this interval were of more modern aspects and by Rhaetian time, true coral reefs were present. Part of the success of scleractinian corals

and their continued importance until today may have been linked to their early symbiosis with dinoflagellate algae.

#### ACKNOWLEDGMENTS

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## AN ANISIAN CORAL FAUNA IN GUIZHOU, SOUTH CHINA

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## ABSTRACT

A rich and varied Anisian coral fauna was found in Guizhou, South China, including a new genus and 13 new species of *Thamnasteria*, *Cyathocoenia*, cf. *Stylophyllopsis*, "*Montlivaltia*" and "*Thecosmilia*." More than 200 specimens were studied, including the microstructure through thin sections. This Anisian coral fauna was located in front of an algal reef, together with very abundant benthic fossils. The colonial corals in this fauna are commonly broken or rounded, while the solitary corals are usually well preserved; they may have lived in a relatively high-energy environment. These early Scleractinia were neither large nor important in volume and seemed not to be reefbuilders. The origin and early history of the Scleractinia is an interesting subject. Due to this discovery of rich and well preserved Anisian coral fauna, the early history of corals can be restudied.

## INTRODUCTION

The origin and early history of Scleractinia remains a problem that attracts the interest of scholars and scientists, and many papers have been published dealing with its relationship with Rugosa, Tabulata and other groups (Wells, 1956; Oliver, 1980; Cuif, 1977, 1980). The absence of Scleractinia, Rugosa and Tabulata in the lower Triassic leaves a large gap and provides few answers to the question of the origin of Scleractinia. The earliest known Anisian Scleractinia corals may give clues for further investigation.

Weissermel (1925) described a coral fauna from Lower Muschelkalk and Kolosváry (1958, 1966) reported Anisian corals from Hungary. Flügel (1961) described a species from Vicentin.

So far no Anisian corals have been described in China. Ssu Dehyou and Chen Kang (1943) reported 91 species of Anisian bivalves, gastropods, ammonids, brachiopods and crinoids and mentioned a few corals from Guizhou Province. Yang Zunyi and Hsu Guirong (1966) studied Middle and Upper Triassic brachiopods in this district and listed several Anisian coral species. Yin Hong-Fu and Yochelson (1983a, b, c) studied the gastropods from Qingyan. A systematic study of the corals collected from Qingyan has shown them to be astonishingly rich and well preserved (Qi, 1980).

## STRATIGRAPHY

Qingyan is a small town, located 25 km south of Guiyang, the capital of Guizhou Province (Text-fig. 1). Paleogeographic and stratigraphic studies have shown a Middle Triassic barrier reef crossing Guizhou (Fan Jiasong, Li Juying and Zhao Shengcai, 1979; Ho Zhiai, Yang Hong and Zhou Jingcai, 1980). It extended about 1000 km, roughly in a NE-SW direction in the form of an elongated "S," forming the border between the Southern China Province of the open sea basin at southeast and the carbonate platform of the Yangtze

Province at northwest. Qingyan is located in front of the barrier reef facing the open sea (Fan, 1979).

In this zone of barrier reef, the Middle Triassic is divided into two formations, the Anisian Qingyan Formation and the Ladinian Falang Formation. The stratigraphic section of the Qingyan Formation is given in Text-figure 2.

The ammonids in Qingyan Formation are fairly rich and Wang Yigang and He Guoxung (1980) listed the ammonite zone in Qingyan Formation and correlated it with the Anisian in the Yomolonga District and in Europe.

The corals in Qingyan Formation are concentrated in the upper part of horizon 4, together with *Paraceratites trinodosus*, *Paraceratites binodosus* and *Discoplychites* sp., etc., indicating an Upper Anisian age.

## THE CORAL FAUNA

In recent years, we have used different classifications for Mesozoic corals, for example, that of Wells (1956), Alloiteau (1957), Cuif (1972, 1980), etc. In this paper, I follow the older system raised by Wells with some modifications.

*Thamnasteria silesiaca*, occurring as both massive and foliaceous forms, is the only species in common with Lower Muschelkalk of central Europe (Weissermel, 1925). I have established several species of this genus, based upon the important differences in the distance between the corallite centers, the number of the septa, the arrangement of the trabeculae in the septa and the presence of the columnella (Qi, 1980).

I found genera such as *Cyathocoenia*, *Stylophyllopsis*, "*Montlivaltia*" and "*Thecosmilia*," etc., to be present and they seem to represent many new species, though with further study some of these genera may prove congeneric with those in Europe. I present below a preliminary listing of the taxa (Table 1). Research now in progress with G. D. Stanley, Jr. will treat details

of the systematic standing of these corals more thoroughly.

The diversity of the Anisian coral fauna mentioned above is surprising. Altogether they represent five families, four superfamilies and three suborders.

Wells (1956) proposed an evolutionary pattern of the scleractinian suborders and families which is extensively recognized. He pointed out that the Scleractinia at the earliest recorded appearance already include widely divergent groups at the subordinal level. This is verified by the Anisian corals in China. He deemed *Isastrea*, for example, to range from Middle Jurassic to Cretaceous. *Calamophyllidae* also appeared in Middle Jurassic. Detailed study of the Guizhou corals now underway may lead to the modification of the evolutionary pattern raised by Wells.

At the genera level the coral found in the Anisian strata in China, such as *Thamnasteria*, *Cyathocoenia*, *Stylophyllopsis*, "*Montlivaltia*" and *Thecosmilia* are also found in Anisian and Ladinian strata in Europe, indicating that the Tethys Sea made a wide seaway for corals to distribute themselves. By the time of Anisian, they had been able to spread in the Tethys area, almost from the western to the eastern end.

#### PALEOECOLOGY

The Qingyan Anisian corals are in grey, thin-bedded biogenic limestone, which is intercalate with yellow, calcareous shale in the upper part of horizon 4 (Text-fig. 2). The strata containing corals are only a few meters in thickness and probably are not an organic mound or build-up.

The coral fauna is located in front of the Anisian algal reef, together with very rich brachiopods, bivalves, crinoids, gastropods and ammonids, among which, brachiopods constitute approximately 50–60 percent volume, with bivalves 20–25 percent, corals 10–15 percent, crinoids 10 percent, and ammonids and gastropods less than 10 percent.

Table 1.—List of coral taxa from Qingyan, Guizhou, South China.

Order SCLERACTINIA Bourne, 1900
Suborder ASTROCOENIINA Vaughan et Wells, 1943
Family THAMNASTERIIDAE Vaughan et Wells, 1943
Genus <i>Thamnasteria</i> Lesauvage, 1823
<i>Thamnasteria silesiaca</i> Beyrich, 1879
<i>Thamnasteria</i> sp. A
<i>Thamnasteria</i> sp. B
<i>Thamnasteria</i> sp. C
Suborder FUNGIINA Verrill, 1865
Superfamily AGARICIICAE Gray, 1847
Family PROCYCLLOTITIDAE Vaughan et Wells, 1943
Genus A (new genus)
new genus, new sp. A
Family ASTROCOENIIDAE Vaughan et Wells, 1943
Genus <i>Cyathocoenia</i> Duncan, 1867
<i>Cyathocoenia</i> sp. A
<i>Cyathocoenia</i> sp. B
Suborder FAVIINA Vaughan et Wells, 1943
Superfamily STYLOPHYLLICAE Volz, 1896
Family STYLOPHYLLIDAE Volz, 1896
Genus cf. <i>Stylophyllopsis</i> Frech, 1890
cf. <i>Stylophyllopsis</i> sp. A
Superfamily FAVIICAE Gregory, 1900
Family MONTLIVALTIIDAE Dietrich, 1926
Subfamily MONTLIVALTIIDAE Dietrich, 1926
Genus <i>Montlivaltia</i> Lamouroux, 1821
<i>Montlivaltia</i> sp. A
Genus <i>Thecosmilia</i> Edwards et Haime, 1848
<i>Thecosmilia</i> sp. A
<i>Thecosmilia</i> sp. B
<i>Thecosmilia</i> sp. C
<i>Thecosmilia</i> sp. D
<i>Thecosmilia</i> sp. E

Among the corals, branching "*Thecosmilia*" and massive *Thamnasteria* dominate. The massive colonies are usually oval in outline, 7–11 cm in length diameter. Many massive specimens are rounded and branching specimens are often broken. Together with broken shells and disarticulated crinoid stems, they indicate a relatively high energy environment on the foreslope or deep shelf margin.

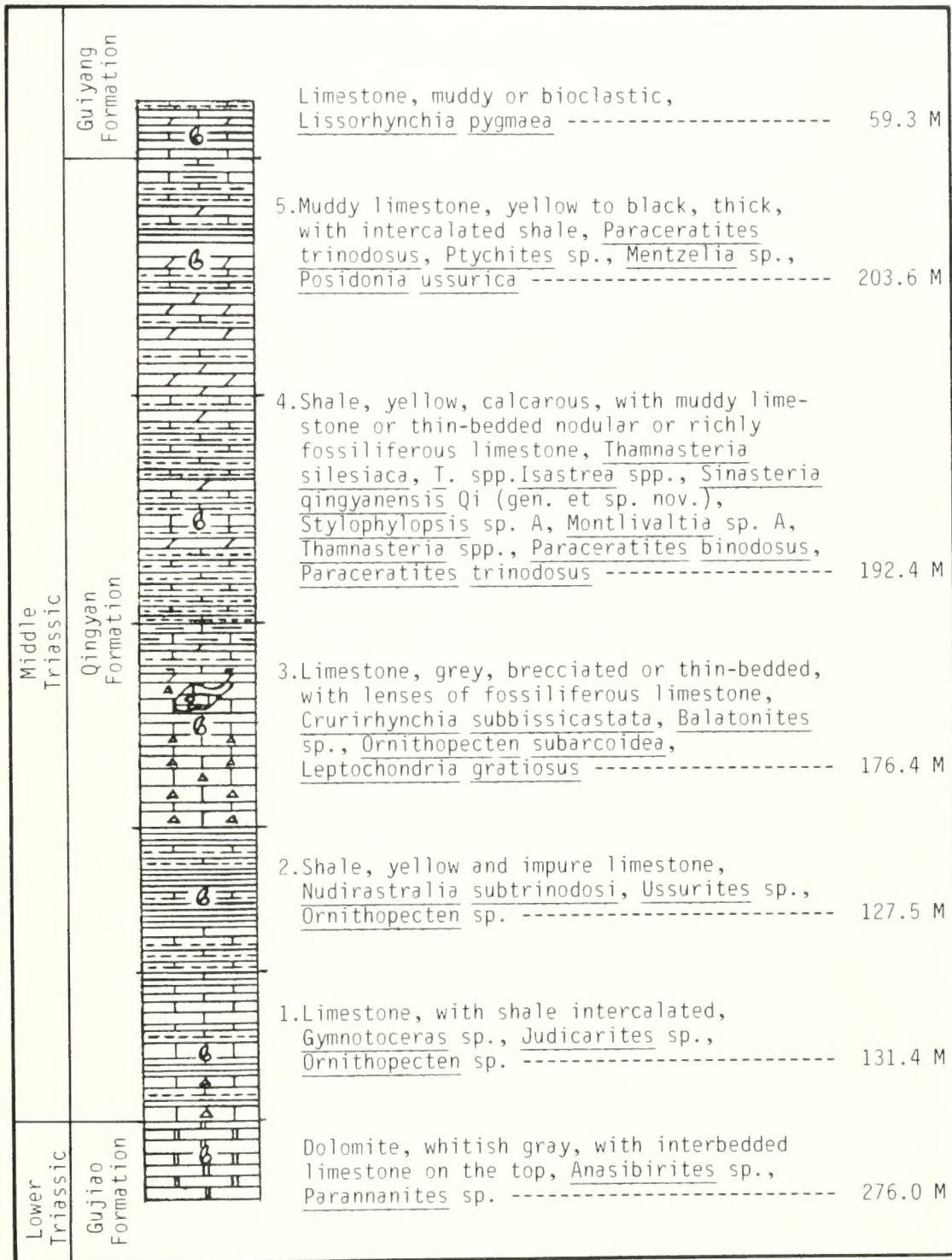


Text-figure 1.—The locality of the Qingyan section.

The solitary corals are usually small, with the diameter less than one cm. In a few specimens, a circular ring of growth can be seen on the flattened apical end, representing a form of life lightly attached on the soft,

muddy sea bottom. However, I did not find the trace of attachment in these corals.

Stanley (1979, 1981) raised a hypothesis that the earliest Scleractinia of the Middle Triassic were aher-



Text-figure 2.—Stratigraphic section of the Anisian Qungyan Formation.

matypic, instead of hermatypic as suggested by Wells (1956), and it was only by the end of Triassic that a few corals, such as *Thecosmilia* were producing extensive ecologic reefs.

The Qingyan corals were small and were neither the major group in the benthic invertebrates or major reef-builders during the Anisian in South China.

#### ACKNOWLEDGMENTS

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## THE RECOVERY OF REEF-BUILDING COMMUNITIES AND THE ROLE OF CNIDARIANS IN CARBONATE SEQUENCES OF THE MIDDLE TRIASSIC (ANISIAN) IN THE ITALIAN DOLOMITES

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### ABSTRACT

Late Anisian carbonate sequences in the Dolomites (Italy) give the best case history of the earlier Triassic "reefy" communities in the Southern Alps. Small (few cubic meters) mud mounds developed in a deep infralittoral environment not far from islands. A pioneer community is made of *Olangocoelia otti* Bechstädt and Brandner growing on peloidal packstones, and of blue-green algae laminae and/or *Tubiphytes obscurus* Maslov developing on muddy substrata. Over the latter a second stage characterized by abundant encrusting Sphinctozoan *Celyphia zoldana* Ott might develop. A third stage marked by more diversified communities (*i.e.*, trepostomatid bryozoans, sphinctozoans/inozoans, porostromate blue-green algae, solenoporaceans) characterizes the full development of the mounds. Scanty scleractinians appear at this stage, characterized by fairly high evolutionary complexity and diversity in contrast with the low density.

### INTRODUCTION

The recovery of the "reef" building communities after the Permo-Triassic crisis in the Southern Alps occurred during the Anisian. In order to illustrate those communities and the pattern of the recovery, a number of Anisian units and sequences in the Southern Alps have been studied. *In situ* mud mounds and boulders embedded in the topmost Dont Formation, as well as the very base of the Cernerer Dolomite in the Mt. Cernerer and Valdaora areas (Eastern Dolomites) are the richest and most diversified sites. The age is Late Anisian (Illyrian, Trinodosus Zone).

The main characters of the microfacies of the Valdaora area have been described by Bechstädt and Brandner (1970). Other localized occurrences are in carbonate lenses in the Agordo Formation (Ott *et al.*, 1980), and in the Upper Serla Formation (Pisa *et al.*, 1979; Farabegoli and Guasti, 1980; Gaetani *et al.*, 1981) in the Dolomites. Similar facies are also present in the Upper Serla Formation of Carnia (Jadoul, pers. comm.). Consequently the present paper deals with the outcrops we consider more suitable for this case history.

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### GEOLOGICAL SETTING

The paleogeographic setting of the Dolomites during the Anisian has been described by Assereto *et al.* (1977). Land was located westward and possibly north in the form of islands, and deltas were intermittently spreading clastics on an open platform. Towards the beginning of the Trinodosus Zone the terrigenous input temporarily decreased and small micritic mounds developed (Text-fig. 1). The tectonic framework was unstable and limited displacement of the mounds may be noted. The decrease and end of the clastic supply allowed the mud mounds to coalesce and form a continuous subtidal carbonate bank (Cernerer Dolomite; the informal name is introduced for the first Illyrian carbonate bank which grows onto the Dont Formation and is interrupted by the Richthofen Conglomerate (see Text-fig. 1). Renewed uplifting caused an increased terrigenous input from the neighboring islands (Richthofen Conglomerate). In the Valdaora area the uplifting also disrupted the Cernerer Dolomite, and boulders from it and the topmost Dont Formation are embedded in breccias and conglomerates.

Consequently three different settings are present (Text-fig. 2):

A) *In situ* mud mounds (Text-fig. 2A). They form lenticular bodies varying in size from about 1 to 10 cubic meters. Exceptionally several small lenses have been observed to coalesce forming a wall about 15 m high and 8–10 m wide. They have been interpreted as *in situ* mounds because: 1) most of the organisms are in growth position; 2) geopetal infillings, including cavities within the organisms, are concordant with the present orientation of the outcrop; 3) basal and lateral

contacts with the marly limestone of the Dont Formation are gradual, the mound growth being preceded by irregularly nodular facies (up to 1–2 m thick) made of blue-green algae bindstones with calcareous sponges and solenoporaceans increasing upwards; the same nodular facies characterizes the flanks of the mounds.

The mounds normally develop on planar marly limestone of the Dont Formation, which some 2 m before the true mound show a distinct increase in  $\text{CaCO}_3$  due to the activity of calcareous blue-green algae and subordinate calcareous sponges; the increasing binding produces first planar nodular limestone (outlined by diagenetic processes) passing upwards to very irregularly nodular facies (Text-fig. 2A).

The mounds consist of several smaller micritic lenses welded together and enveloped by veneers of marly limestone, which frequently correspond to tiny patches of different organisms. In the case of the biggest mound recorded, among the smaller lenses are veneers of crinoidal calcarenites, likely formed by *in situ* remains of crinoids which could attach onto the other organisms. A comparison to the present day Halimeda sands filling the hollows in patch reefs might be suggested. The mound when fully developed must have reached a relief of at least 1 m over the sea bottom. They are capped by crinoidal calcarenites (few meters) rapidly passing into a thick sequence of marly limestone and marls of the topmost Dont Formation. The best preserved mounds crop out in the Mt. Cenera area (Col Toront). In the Valdaora area the base of the Cenera Dolomite is made of mud lenses welded together, separated by marly veneers, displaying a binding community in growth position.

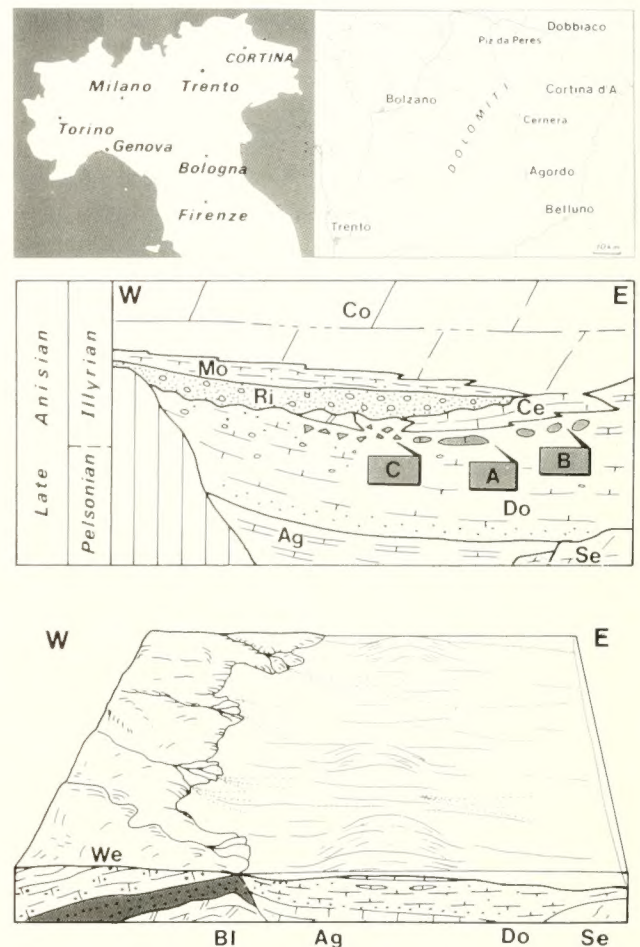
B) Displaced mud mounds (Text-fig. 2A–B). They consist of lenticular carbonate bodies comparable in size and composition to the *in situ* mud mounds. They have been interpreted as displaced mounds because of: 1) tilting of geopetal infillings in relation to the present orientation of the mound; 2) presence of slump structures in the basal and surrounding beds; 3) occasional tilting of the internal bedding of the mound.

The degree of displacement is variable; in some cases it consists of a gentle sliding of the mound on its flat base, thus not affecting the original orientation, but truncating the lateral connections (Text-fig. 2A top). More intense displacement may cause tilting, breaking up of the mounds and formation of swarms of monogenic carbonate lenses (Text-fig. 2B). We do not consider them as boulders which slid from an active margin of the Cenera Dolomite because the latter is younger than the mounds and forms a tabular body. They crop out throughout the area examined.

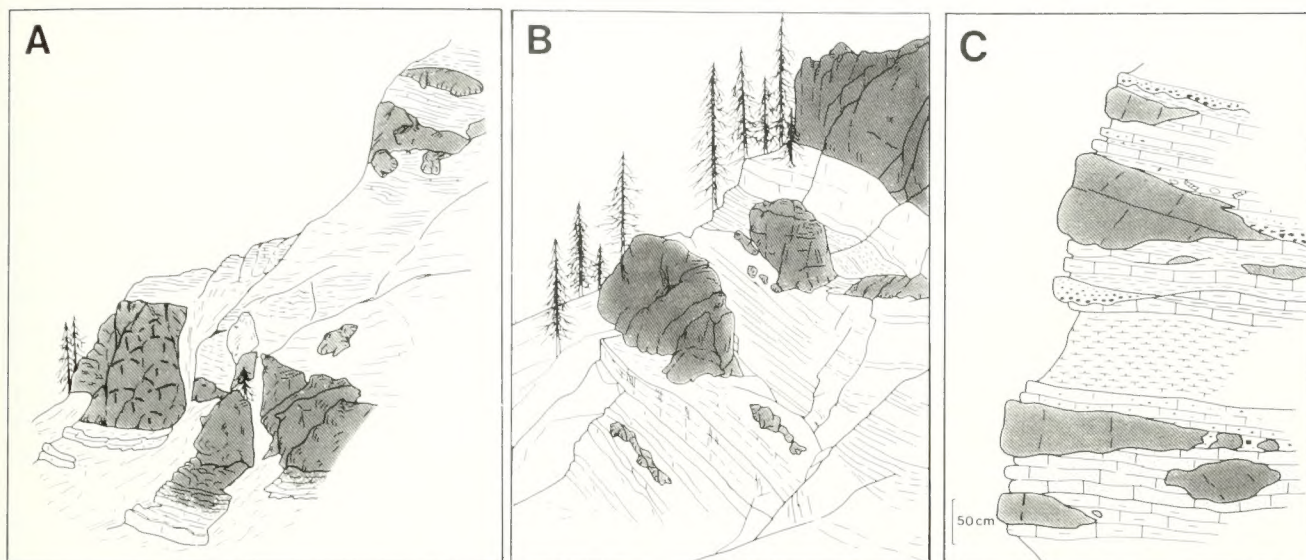
C) Boulders (Text-fig. 2C). They are carbonate blocks up to some tens of cubic meters in size derived from

the erosion of the Cenera Dolomite and Contrin Formation. They are interbedded in the topmost part of the Dont Formation associated with conglomeratic-arenitic layers announcing the Richthofen Conglomerate event. They crop out in the area of Piz Tre Dita (Valdaora area) where no Illyrian carbonate bodies are recorded in the sequence. As the Cenera Dolomite crops out in the neighboring regions, the area is interpreted as a paleofurrow into which the clastics were funneled with erosion of the adjacent carbonate banks.

The three different settings yield similar microfacies and may be considered as part of the same stage of evolution of the recovery of the “reefy” communities in the Late Anisian.



Text-figure 1.—Top: location map. Center: stratigraphic scheme; Ag = Agordo Fm.; Se = Upper Serla Fm.; Do = Dont Fm.; Ce = Cenera Dolomite; Ri = Richthofen Conglomerate; Co = Contrin Fm. Capital letters A, B, C refer to the three settings of Anisian mounds and boulders illustrated in Text-fig. 2. Bottom: block-diagram showing the paleogeographic setting during the late Anisian. The mounds and the Cenera Dolomite developed on a continental shelf polluted by clastics from the islands of the Western Dolomites. BI = Bellerophon Fm.; We = Werfen Fm.; Ag = Agordo Fm.; Do = Dont Fm.; Se = Upper Serla Fm.



Text-figure 2.—Mounds and boulders setting. *A.* Col Toront (W side of Mt. Cenera). The lower belt of mounds is in growth position, reaching a thickness greater than 10 m. Note the irregularly nodular basal part corresponding to stages I and II of the growth model. Communities are well developed and diversified. In the topmost part the mounds appear to be slightly displaced, sliding for a short distance on its flat base; communities do not reach the highest diversification. *B.* Col Vallaccia (Valdaora area) NW side. Large mounds are displaced and even tilted, originating from a neighboring area within the topmost part of the Dont Fm. They are interpreted as not derived from the Cenera Dolomite, which forms the bank at the upper side of the sketch and is younger in age. Communities are dominated by *Olangocoelia otti*. *C.* NE side of Piz Tre Dita (=section D of Bechstädt and Brandner, 1970). Carbonate boulders are embedded in a marly-silty sequence which laterally substitutes for the Cenera Dolomite. Blocks dominated by the *Olangocoelia* community may be derived both from the topmost Dont Fm., and from an active/passive margin of the Cenera Dolomite. Conglomeratic layers (Richthofen Conglomerate) increase upwards.

#### NATURE OF THE REEF COMMUNITIES

The organisms involved, notwithstanding local variations, form a single broad facies. An assemblage of building organisms in which blue-green algae, sphinctozoans and bryozoans play the main role has been detected. Solenoporacean algae, inozoans, vermetid gastropods, annelids, sessile foraminifers and scleractinians are subordinate forms. Several, often exclusive communities dominated by one or two groups of organisms, have been recognized, which develop at different stages of the sediment colonization.

##### 1. *Olangocoelia* Community (Text-fig. 3)

*O. otti* Bechstädt & Brandner appears to form an exclusive community rarely associated with other organisms (*Celyphia zoldana* Ott, spongiostromate laminae, *Tubiphytes obscurus* Maslov, agglutinating worms) which if present are totally subordinate; sometimes those forms are well developed too, but colonize adjacent but separate areas.

*Growth morphology.*—*O. otti* acted as sediment stabilizer and baffle. Its pearl necklace shaped skeleton

Text-figure 3.—*Olangocoelia* community. *O. otti* colonizes fine peloidal packstone creating irregular cavities with geopetal infilling. Spongiostromate laminae are subordinate. Burrow at the topmost left. Scale bar 5 mm. Thin section EF 173. Piz Tre Dita, Valdaora area.

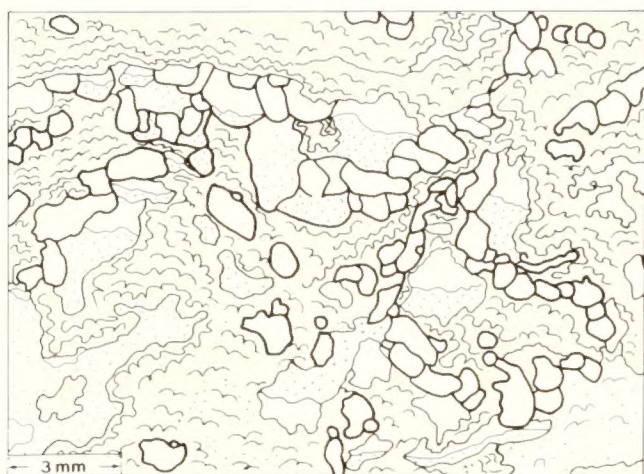


with the wandering growth direction created many irregular cavities later infilled by peloidal packstone. The problematic sphinctozoan must have formed a fairly rigid framework as most of the cavities show geopetal infilling. Nevertheless rare burrowings in the sediment surrounding the sponge skeleton rule out early lithification of the whole rock. That community normally grows on fine peloidal packstones, where it seems to represent the first and last stage of colonization of the sediment (Text-fig. 11, below).

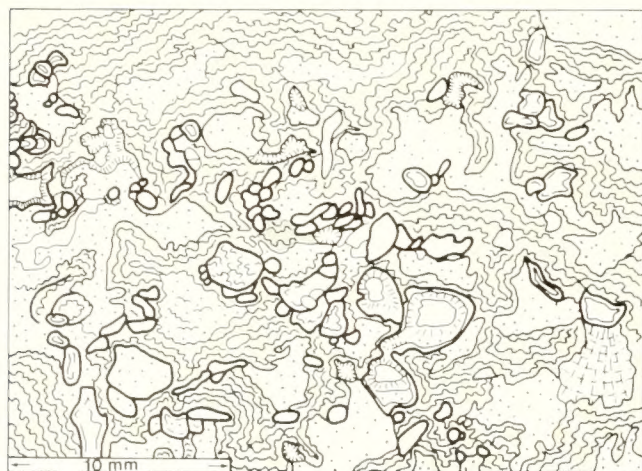
*Location.*—The community is fairly widespread in the area east of Piz da Peres (case C) where it is the main constituent of the smallest boulders. It is subordinate west of Piz da Peres and in the Cerneria area in the upper displaced mounds (case B).

## 2. Blue-Green Algae, *Celyphia zoldana*, *Tubiphytes* Community (Text-figs. 4–5)

Blue-green algae (spongiostromate laminae and very rare porostromate algae, *i.e.*, *Cladogirvanella*-like tufts) and *C. zoldana* form irregular encrusting layers; *Tubiphytes obscurus* forms tiny erect tufts when not very abundant while it grows as irregular nodules when it is a main constituent of the community. Locally one of the organisms becomes predominant. Associated forms are vermiform gastropods (*Spirorbis* sp.), agglutinating worms and occasionally trepostomatid bryozoans, solenoporaceans, other sphinctozoans (*Deningeria*-type forms) and inozoans. Sessil foraminifers (*i.e.*, *Alpinophragmium* sp.) are secondary encrusters.



Text-figure 4.—Spongiostromate/*Celyphia* community. Spongiostromate laminae (A) create a network of irregular cavities with frequent geopetal infilling; *C. zoldana* (B) grows onto the firm surfaces formed by the algal laminae. In the drawing, spongiostromate laminae are in grey. Scale bar 3 mm. Thin section EF 170 c. Piz Tre Dita, Valdaora area.



Text-figure 5.—Spongiostromate community. Blue-green algae laminae create a framework of cavities with geopetal infilling. *Celyphia zoldana* (A) and agglutinating worms (B) are secondary forms. In the drawing, spongiostromate laminae are in grey. Scale bar 10 mm. Thin section EF 155. Piz da Peres, Valdaora area.



*Growth morphology.*—The spongiostromata and/or *Tubiphytes* colonize mud substrata forming hard or at least firm surfaces; they created a network of irregular cavities on and inside which *C. zoldana* developed, intergrowing with following spongiostromate laminae. However occasionally, *C. zoldana* appears to be able to grow directly on mud as well. The community created a framework with several tiny cavities (the largest connected to spongiostromate laminae) in which the sediment was trapped as secondary geopetal infilling. The community is the pioneer colonizer of muddy substrata and if following stages are present, it represents the base the other organisms could grow on (Text-fig. 11). In the succeeding communities dominated by

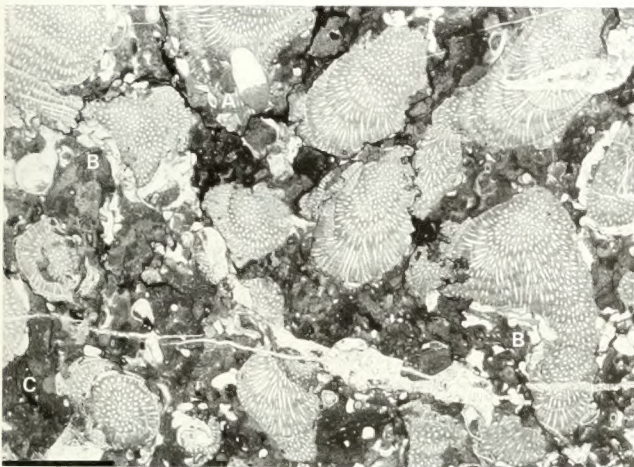
other organisms (stage III) it helps strengthen the framework.

*Location.*—The community is common throughout the area wherever a muddy substratum develops. It contributes to form the base of mud mounds in the Cernera area (case A); in the Valdaora area it normally occurs in boulders (case C) except for a mud lens cropping out in a gully under Piz da Peres (case B) and the base of the Cernera Dolomite (case A).

### 3. Bryozoan-Rich Community (Text-fig. 6)

The bryozoans can either create an almost exclusive community or are abundant components of a more heterogeneous assemblage. All the specimens belong to a new genus and new species of Trepostomata. Associate forms are spongiostromate laminae, sphinctozoans (*C. zoldana* and new genus 1), inozoans and solenoporaceans. Secondary encrusters are *Tubiphytes obscurus*, vermiform gastropods, agglutinating worms and *Ladinella porata* Ott.

*Growth morphology.*—The substratum the bryozoans grow on consists either of encrusting forms (*i.e.*, spongiostromates, sphinctozoans) or of scattered bioclasts in muddy peloidal sediment (*i.e.*, crinoid fragments, pelecypod shells, calcareous sponges). They normally become abundant in an advanced stage of development of the building community. It appears that when they found a favorable environment, the bryozoans rapidly outpaced the other organisms, forming almost exclusive communities. The digitiform to platy colonies grew laterally and downward in sheltered spaces (created by shells and the algal-sponge community) presently very difficult to detect because they are totally filled by sediment. On the basis of recent



Text-figure 6.—Trepostomatid bryozoan community. Bryozoans grow laterally and downward in a framework partially built and strengthened by spongiostromate laminae. They are the preferential substratum for boring bivalves (A) and secondary encrusters such as *Celyphia zoldana* (B) and *Ladinella porata* (C). Scale bar 5 mm. Thin section EF 190. Piz da Peres, Valdaora area.



Text-figure 7.—Sphinctozoan/inozoan community. Sphinctozoans (Fam. *Cryptocoeliidae* n. gen. 1 (A), *Celyphia zoldana* (B)) and inozoans (n. gen. 2) (C) grow in a framework of spongiostromate laminae (in grey in the drawing). Scale bar 6 mm. Thin section EF 199. Col Toront mud mound, Cernera area.



data on bryozoan ecology (Hammelin, 1976) the presence of slightly erect colonies could be interpreted as a response to constant currents. The bryozoans represent a preferential substratum for boring pelecypods and in turn they can be encrusted by *C. zoldana*, *Tubiphytes* tufts and *Ladinella porata*.

*Location.*—They are abundant in the Cernera area (case A) where they have been observed to be the dominant community in a series of coalescent mounds forming a wall some 10 m high. They are diffuse also in the Piz da Peres area (case B).

#### 4. Sphinctozoan/Inozoan Community (Text-figs. 7–8)

Different sphinctozoans (Fam. *Cryptocoeliidae*, n. gen. 1, *Thaumastocoelia* sp., *Deningeria*-type forms, *C. zoldana* and very rare *Follicatena irregularis* Senowbari-Daryan & Schaefer) and inozoans (n. gen. 1, n. gen. 2) dominate this assemblage in which scattered trepostomatid bryozoans and solenoporaceans can be found.

*Growth morphology.*—They normally grow on blue-green algae and/or *Celyphia* crusts, thus not forming a pioneer assemblage, but can be secondary forms in the initial stage of mound development. They acted as sediment stabilizers (mainly sphinctozoans) and bafflers, forming a microfacies with poorly developed cavities and rare geopetal infillings, due to the erect growth form.

*Location.*—The community is present in the mounds of Mt. Cernera area (case A) and less frequently in Valdaora area (case B, i.e., base of Cernera Dolomite, and case C).

#### 5. Porostromate and/or Solenoporacean-Rich Community (Text-fig. 9)

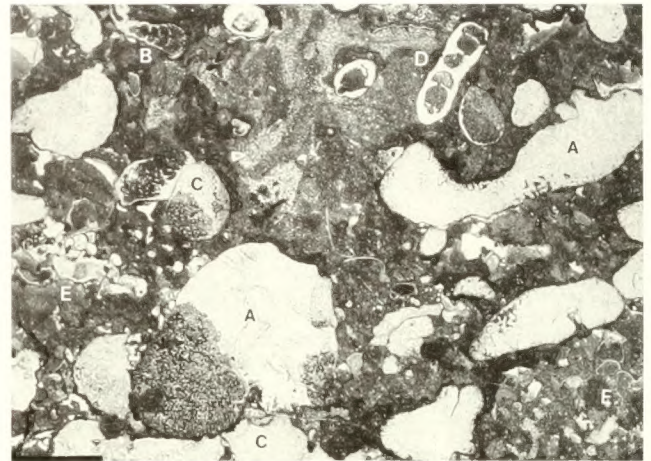
Porostromate blue-green algae (*Garwoodia*-type forms) and solenoporaceans (*Solenopora* cf. *cassiana*, *Solenopora* sp.) can locally dominate the faunal and floral assemblage although they normally play a secondary building role. They are associated with *C. zoldana*, *Thaumastocoelia* sp., spongiostromate algae and inozoans (n. gen. 1, n. gen. 2).

*Growth morphology.*—They normally grow on community 2 as nodular to branching thalli not close enough to create cavities; the peloidal mud between the tufts is colonized by spongiostromate algae which, together with *C. zoldana* and vermiform gastropods encrust the thalli as well.

*Location.*—The community is present in the mounds of Mt. Cernera area (case A) and in boulders at Prati di Cotz (Valdaora area, case C).

When the building community reaches a higher degree of diversity other organisms appear, which however never become abundant. This is the case of (1) the scleractinians and (2) a microproblematic form similar to *Radiomura cautica* Senowbari-Daryan.

1. Scleractinian corals occur in some communities. Unfortunately only 10 poorly preserved specimens of



Text-figure 8.—Sphinctozoan/inozoan community. Inozoan n. gen. 2 (A) and sphinctozoans (*Thaumastocoelia* sp. (B), *Deningeria* type (C), Fam. *Cryptocoeliidae* n. gen. 1 (D) and *Celyphia zoldana* (E)) grow on spongiostromate laminae mainly acting as bafflers. Scale bar 5 mm. Thin section EF 200. Col Toront mud mound, Cernera area.



Text-figure 9.—Porostromate, blue-green algae community. *Garwoodia* sp. and sphinctozoans (Fam. *Cryptocoeliidae* n. gen. 1 (A)) act as sediment bafflers. Scale bar 3 mm. Thin section EF 205. Col Toront mud mound, Cernera area.

scleractinian colonies have been found. One specimen is possibly related to the group of *Isastrea profunda* Reuss (Text-fig. 10 left) while other small massive colonies show striking similarities to the genus *Cassianastrea* Voltz (Text-fig. 10 center). Two other specimens are referable to the “*Thecosmilia*” group, belonging to two species and possibly different genera too, based on the difference of wall organization.

They appear when the building community is well differentiated and form tiny (hand size) colonies which grow in sheltered spaces among the previously described communities. Thus they do not play a primary role in the building of the mud mound, being more as guests, settling only when the environment is particularly suitable and protected niches have been created by other organisms.

Corals have been found only in the Cernera area and they are generally different from the forms quoted in Bechstädt and Brandner (1970) as *Calamophyllia* sp., cf. *Thecosmilia* sp. except for the form referred to as tabulate *incertae sedis*. Specimens must be rare as we searched at length in the localities sampled in Valdaora area, but no other corals were obtained.

Huge coral colonies (meter size) have been found in the Contrin Formation (Latest Anisian) in the Marmolada area; they show strong similarities with *Thecosmilia cyclica* Senowbari-Daryan & Schaefer in the morphology of septa and dissepiments with ring-like arrangement, the thick wall and the general size of corallites which average 7 mm diameter (Text-fig. 10 right).

The density of scleractinians is very low; however the diversity is fairly high, with 5 genera and at least 4 families.

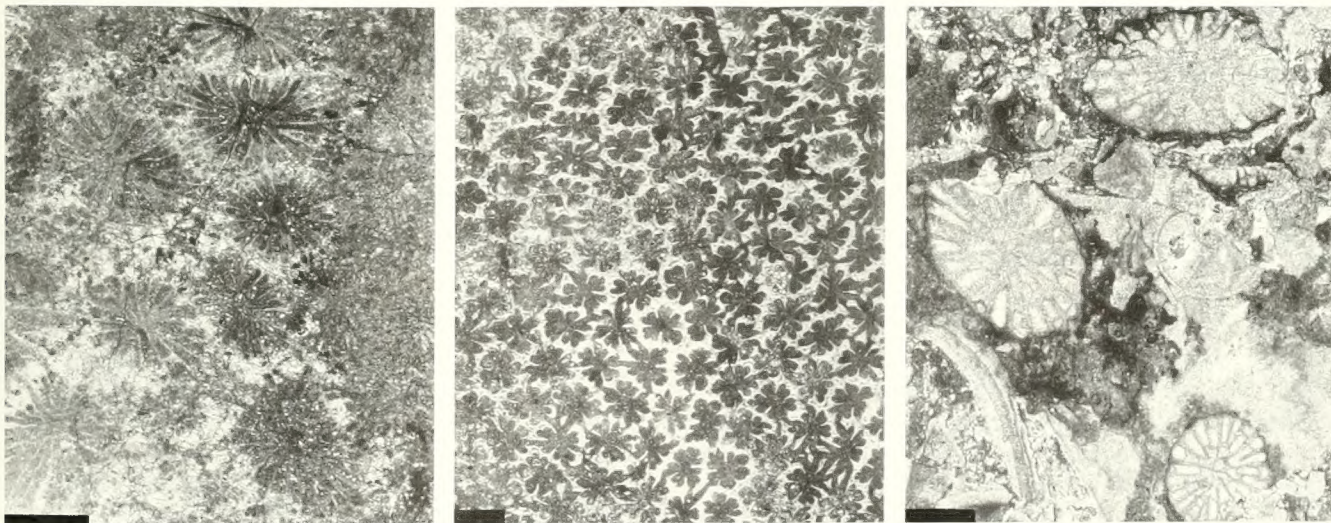
2. The problematic microorganism similar to *Radiomura cautica* can create very rare communities appearing in a later stage of the mound development. It is associated with rare *C. zoldana* and grows on mud forming a network of tiny cavities in which the sediment settled creating geopetal infillings. It has been found only in the Cernera area (case A).

#### REEF COMMUNITY GROWTH MODEL AND MOUND DEVELOPMENT

Field observations and microfacies analysis suggest the following interpretation for the Anisian “reefy” community.

1. The substratum the building community grows on consists of muddy peloidal sediment (wackestone versus packstone). The sand size sediment (bioclastic/grapestone packstone versus grainstone) is never colonized by organic communities possibly because it was too mobile to offer a suitable substratum and poor in nutrients. In contrast modern examples of non-skeletal blue-green algae growing on muddy bottom in Florida Bay and the Bahamas suggest colonization of muddy substrata by blue-green algae is not unusual; moreover the Anisian *Spongiostromata* were calcifying forms, thus rapidly forming a firm substratum for hard bottom organisms.

These patterns contrast with the development of better known mud mounds (Ordovician-Silurian) which often grow on biocalcarenes (Pitcher, 1964; Albersstadt *et al.*, 1974; Crowley, 1973) nevertheless growth on muddy sediment has occasionally been recorded (Scoffin, 1971). However, it is worth remembering that the Anisian pioneer community is mainly made of blue-green algae while the Middle Paleozoic ones con-



Text-figure 10.—Scleractinian corals. Left: colony referable to the *Isastrea profunda* group; thin section EF 203, Col Toront mud mound, Cernera area. Center: colony showing striking similarities to the genus *Cassianastrea*; thin section EF 202, Col Toront mud mound, Cernera area. Right: colony showing similarities with *Thecosmilia cyclica* for the ring-like arrangement of septa; thin section G 1414, Contrin Fm., Marmolada area. Scale bars 2 mm.

sist of tabulate, stromatoporoids, and bryozoans which seemed to prefer coarser and above all firmer substrata. This interpretation is supported also for the Anisian bryozoans and corals that grew either on algal/sponge crusts or on single bioclasts, *i.e.*, a firm bottom.

2. No evidence of growth on identifiable topographic highs has been detected but growth on flat bottoms, not protected from moderate mud input, did not prevent the algal growth as previously discussed.

3. Growth sequence. A model of growth for the "reefy" community has been hypothesized on the basis of observations of mud mounds (Cernera and Piz da Peres areas case A and B) and boulders (Piz Tre Dita-Col Vallaccia area, case B and C) yielding similar faunal and floral assemblages.

*Stage I.*—A first stage of sediment colonization has been detected in which two different communities can develop. A. *Olangocoelia otti* stabilizes fine peloidal packstones and creates an irregular framework with several cavities. Secondary encrusting forms such as blue-green algae, rare *Celyphia zoldana* and *Tubiphytes* contribute in strengthening the framework. This community has never been observed to form the substratum for the succeeding more diversified assemblages. However scattered *O. otti* may be present in other communities. (Text-fig. 11A). B. Blue-green algae and/or *Tubiphytes* nodular masses start binding the muddy sediment and form hard, at least rubbery irregular crusts which create a framework with several cavities. This community is generally strictly connected to the development of stage II (Text-fig. 11B).

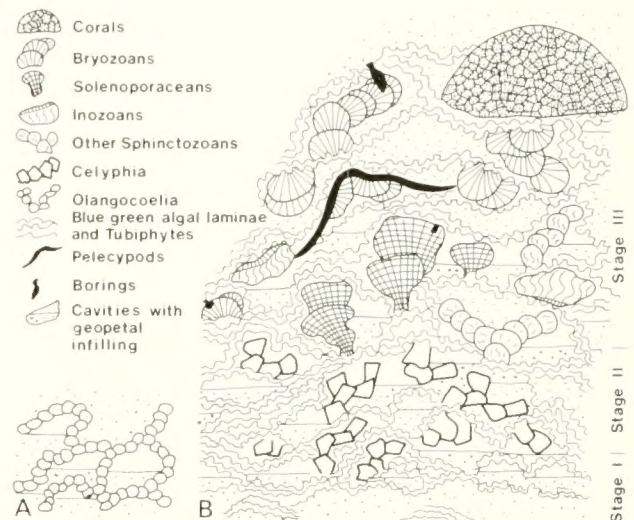
*Stage II.*—It is marked by the appearance, closely related to stage IB, of encrusting sphinctozoans (*i.e.*, *C. zoldana*) which are interlayered with spongiostromates. The second stage is characterized by the development of a true framework in which the mud is trapped mainly as secondary infilling often with geopetal structures. Secondary encrusters contribute to build the framework. Scattered different organisms such as bryozoans, inozoans and other sphinctozoans can be present but always subordinate. Stages IB and II form irregularly nodular facies which create the base and the flanks of the lenticular mounds.

*Stage III.*—Diverse and often mutually exclusive groups of organisms (*i.e.*, sphinctozoan/inozoan community, porostromate blue-green algae and solenoporacean community, bryozoan community, corals) develop on a substratum formed during the previous stages. Depending on the particular growth morphology of the organism involved (erect tufts for solenoporaceans, sphinctozoans and sometimes bryozoans too, platy thickets for inozoans and bryozoans) either a framework or a sequence of crusts can form. In both cases blue-green algae laminae and sometimes *Cely-*

*phia* too are still growing between and on the other organisms. Secondary encrusting forms such as *Ladinella porata*, tiny *Tubiphytes* tufts and Vermetids, commonly grow onto the other organisms. No burrowers have been detected, while several borings, mainly affecting the bryozoan colonies, testify that the organic framework was not rapidly covered by sediment (Text-fig. 11). No early cementation has been detected although the presence of micritic cement cannot be excluded.

4. The mound attained some relief (0.50–1 m, exceptionally more) over the bottom which prevented it from being covered by the constant input of sediments. However, the relief was not enough to protect the community from larger inputs of onlapping sandy calcarenites, and of marly limestone and marl of the topmost Dont Formation.

5. Death of the mound. Data are obviously obtained from the analysis of case A. Apparently the growth of the mound is interrupted by inputs of sand size sediment, either crinoidal packstones/grainstones or silty packstones, thus confirming that calcarenites do not represent a suitable substratum for the reef community. On the contrary a moderate input of mud does not definitely interrupt the mound development. The



Text-figure 11.—Mud mound growth model. A pioneer stage (stage I) is recognizable in which either *Olangocoelia otti* (A) or spongiostromate laminae and *Tubiphytes obscurus* (B) stabilize the sediment. *O. otti* seems to prefer fine peloidal packstones and has never been observed to create the substratum for succeeding communities. It creates a network of cavities with geopetal infilling. In the case B, a second and third stage might be present growing on stage I. Stage II is characterized by the appearance of the encrusting sphinctozoan *Celyphia zoldana* which, together with the spongiostromate laminae, create a true framework. Stage III is marked by a higher diversity, with communities of bryozoans, porostromate blue-green algae, solenoporaceans, sphinctozoans/inozoans and scattered scleractinian corals.

interpretation is strengthened by the absence of colonization in sequences made of biocalcarenes throughout (southern side of Mt. Cenera).

6. On the basis of the following elements a deep infralittoral environment is inferred for the Anisian mounds. 1) No evidence that the mounds were growing in a protected area, thus the mud is related to fairly deep water. 2) Absence of dasycladacean algae which are present in under- and overlying units of similar lithology (marly limestone of the Agordo Formation = Algenwellenkalk of Bechstädt and Brandner, 1970; silty limestone of Calcari di Pontebba, Fois and Jadoul, 1983). 3) Community morphology and organisms growth form. Some similarities with the Squamariacean facies of the "Biocenose du Détritique côtier" of the present Mediterranean at the limit between infra- and circalittoral zones (Perès and Picard, 1964) have been noticed. Obviously the various roles in the community are played by different organisms but in both cases an initial mud encrusting stage is present. Blue-green algae and recent squamariaceans crusts and blades form special microenvironments for the succeeding cryptic and epibiontic communities (red algae, bryozoans). Among the Anisian organisms the bryozoan growth morphology (erect to platy colonies) might be indicative of an environment dominated by currents but with mud input still present (Hammelin, 1976). 4) Parallel laminations in the biocalcarenes indicate current influence.

On the other side, the fairly high calcium carbonate productivity and the general trend leading upwards to a continuous carbonate bank (Cenera Dolomite), suggest a depth not higher than 30 m, possibly 50 m.

#### DISCUSSION OF THE SIGNIFICANCE OF THE SCLERACTINIANS

In the Late Anisian mud mounds of the Southern Alps, scleractinians play a subordinate building role. In fact only a few specimens confined to a few areas and appearing in the most diversified communities have been found. Despite the low number, the coral assemblage shows surprisingly high diversity and evolutionary advancement. At present five families, seven genera and ten species have been detected also on the basis of similar assemblages reported from the Sturia limestone of the Recoaro area, which is time-equivalent to the sequence of the Dolomites (Flügel, 1961; De Zanche and Mietto, 1981).

Although they are the oldest scleractinians found in the Southern Alps up to now, the high diversity suggests the existence of an environmentally optimal area possibly located far eastward along the Tethys. From that area the coral planulae occasionally reached the Dolomites, situated at the "cul-de-sac" of the Tethyan

seaways. The distance from the source area was a tool for selection, explaining the striking ratio of density to diversity.

The coral occurrence which is confined to few areas, and the low density suggest that most of the Dolomites were too polluted by clastics and had very muddy substrata. Moreover other groups such as blue-green algae, calcareous sponges and bryozoans still were able to out compete the scleractinians.

The same scenery persists during the Ladinian and only in the Carnian the role of scleractinians in the reef-building communities becomes more important (Fürsich and Wendt, 1977).

#### CONCLUSIONS

A fairly homogeneous "reefy" community has been identified in the Anisian of the Dolomites (Southern Alps, Italy). At the moment similar microfacies have not been detected in coeval units outcropping westwards (Lombardian Alps) possibly because the latter area was more protected and muddy. In the Dolomites, constant characters of the building community have been detected in different Upper Anisian units (Ott *et al.*, 1980; Farabegoli and Guasti, 1980; Bechstädt and Brandner, 1970). The community consists of blue-green algal laminae and encrusting sphinctozoans playing the pioneer role, followed by sphinctozoans, inozoans, trepostomatid bryozoans, porostromate blue-green algae, solenoporaceans and rare scleractinians, together with subordinate encrusters (vermetids, microproblematics, sessile foraminifers). Corals are thought to have reached the area occasionally, drifted as planulae from a climax area situated far away.

Distinctive elements which differentiate the Upper Anisian building assemblage from the topmost Anisian/Lower Ladinian one (Gaetani *et al.*, 1981) are: the encrusting sphinctozoan *Celyphia zoldana*, the problematic sphinctozoan *Olangocoelia otti* and the trepostomatid bryozoans. On the whole the Anisian community is not less differentiated than the Ladinian one; it is just smaller in the number of specimens, less widespread, and appears to be able to create small mud mounds in a deep infralittoral environment.

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## THE ROLE OF CORALS IN LADINIAN-CARNIAN REEF COMMUNITIES OF SLOVENIA, YUGOSLAVIA

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### ABSTRACT

The first Triassic scleractinian corals in Slovenia are known from the Ladinian-Carnian coral-sponge reef complexes. The Ladinian faunal community is not distinguishable from the Carnian fauna. It leads to the supposition that these complexes may be lateral equivalents. Their beginning should be put into the Cordevolian.

Corals represent 35 to 50 percent of the organic framework. In the entire mass of limestone their proportion varies from 15 to 30 percent of its volume. The starting species of scleractinians are quite heterogenous. They belong to 13 genera and 5 suborders. It supports the supposition that most scleractinians evolved from soft ancestors in several lines at the same time. Among the identified corals, only in the genus *Protoheterastraea* may direct descendants of *Rugosa* be sought.

The examined buildups are small patch reefs within limestones of the Julian and Dinaric carbonate platforms, and small mud mounds within clastic beds of the deeper Slovenian trough, where corals and sponges played the role of baffling or trapping carbonate mud.

### INTRODUCTION

We have started the study of the Triassic reef communities in Slovenia only recently. They appear in two periods, in the Ladinian-Carnian and the Norian-Rhaetian, in several places, and in various reef types (Buser *et al.*, 1982). Only the localities of reef fauna at Jesenica (Čar *et al.*, 1981) and Hudajužna (Senowbari-Daryan, 1981) have been studied in detail. The fossil reef assemblage of Begunjščica was presented by Flügel and Ramovš (1961), and identifications of individual corals from various sites have been made by Kolosváry (1967).

In this paper we present the entire picture of the older, Ladinian-Carnian, reef complex; its distribution, paleogeographic evolution, depositional environment, mode of formation of reef complex, fossil association, and contribution of corals in the reef framework.

### ACKNOWLEDGMENTS

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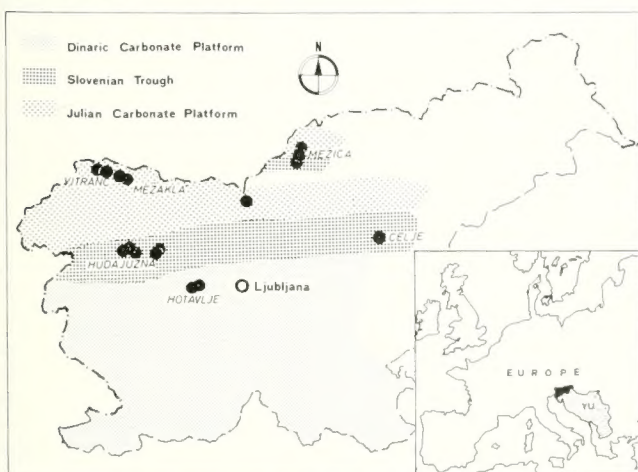
### DEVELOPMENT OF TRIASSIC REEFS IN SLOVENIA

After the Groden clastic beds were deposited during the Upper Permian in the major part of present-day Slovenia, an extended carbonate platform developed. Only the area of northern Karavanke and the extreme part of the southern Slovenia remained land. In rare places on the platform grew smaller coral reefs with the coral *Waagenophyllum indicum*.

The Lower Triassic witnessed the expansion of the carbonate platform to an even greater extent. The carbonate deposition was frequently interrupted by influxes of terrigenous material which made this period completely unfavorable for reef growth.

The Anisian is characterized by the extension of the carbonate platform into the area of the northern Karavanke. Extended algal mats appeared in places during this time which formed several hundred meters of limestone beds. On the major part of the platform, layered dolomite of littoral development was deposited. Coral reef structures are not known from these intervals. Between the Middle and Upper Anisian, long and narrow intraplatform troughs formed and platy limestone with chert was deposited.

Ladinian was, for the major part of the present-day Slovenian territory, one of the most agitated stages of the Triassic. The carbonate platform which was up to

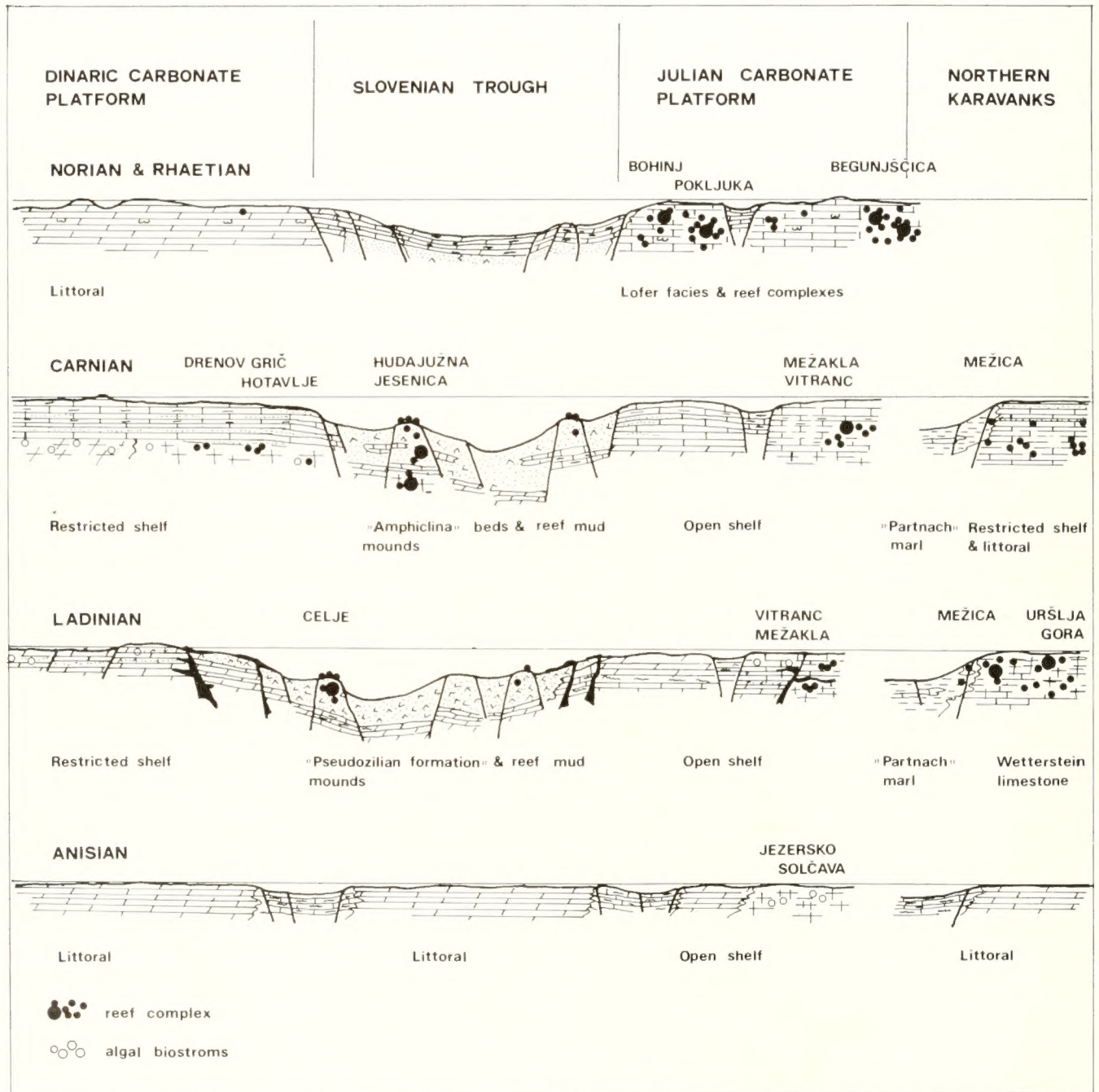


Text-figure 1.—Location map of Slovenia with localities of Ladinian-Carnian coral-sponge reef complexes.

then stable, became dissected by long faults forming numerous tectonic blocks. Deep subsidence in central Slovenia started formation of the Slovenian trough. This trough divided the formerly uniform carbonate platform into the Dinaric platform in the south and the Julian platform in the north.

In shallow areas were deposited carbonate sediments, and in deeper troughs various clastic materials.

Along fault-lines rose lava and pyroclastic materials of spilitic-keratophytic association. These mixed with clastic and carbonate rocks. Smaller reefs appeared on some relatively uplifted blocks in the trough. Formation of deeper marine areas promoted the growth of organic framework, since water currents became stronger, and aeration of water and supply of nutrients increased. Among the reef structures, one buildup near



Text-figure 2.—Simplified paleogeographical development in Slovenia from Anisian to the end of the Triassic with positions of coral-sponge reefs.

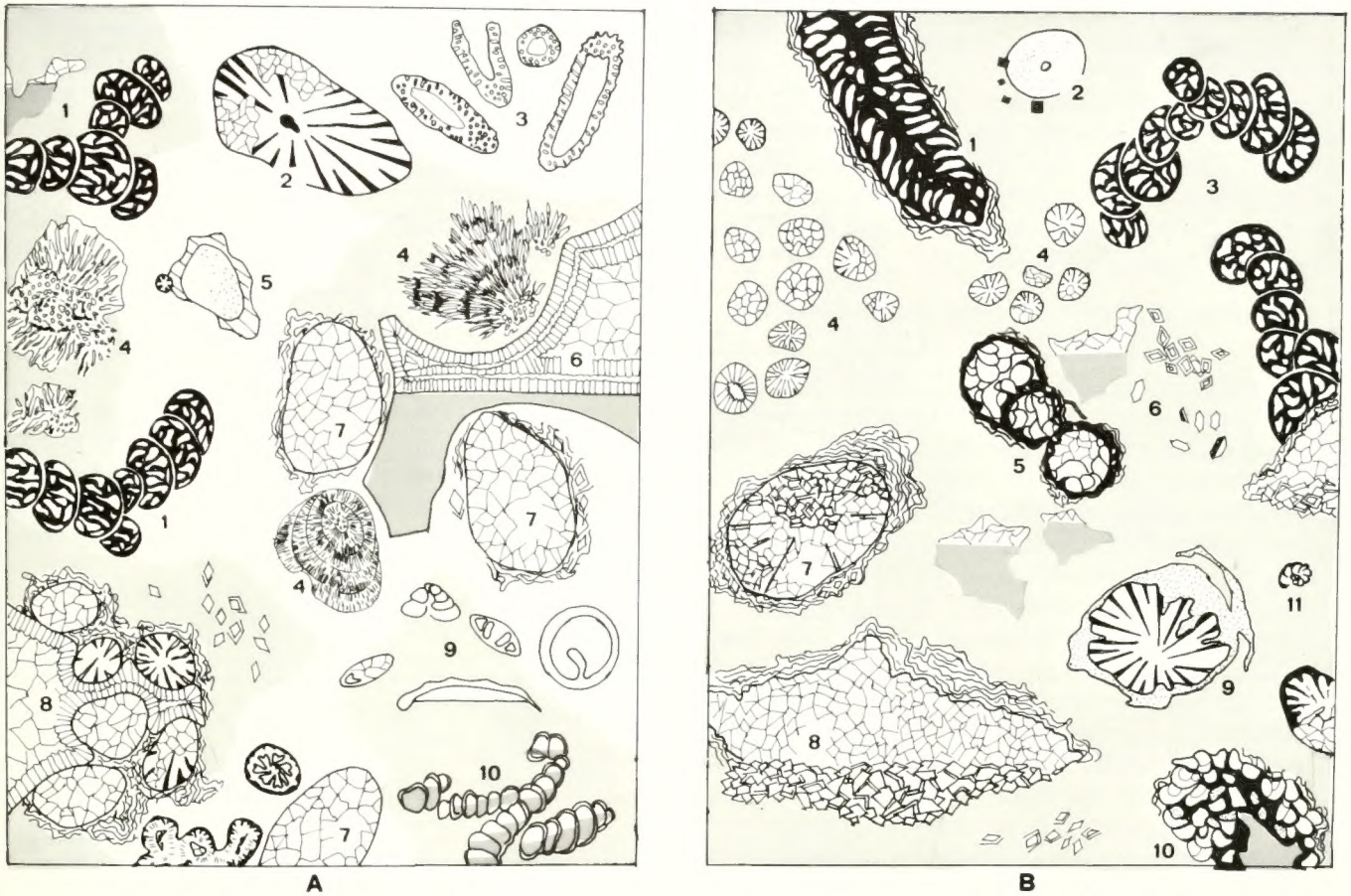


Celje is almost one hundred meters thick and some hundred meters long and consists of corals and sponges. It is situated among argillites and graywackes cut by keratophyre intrusions (Pseudozilian Formation). According to its position the buildup is assigned to the Ladinian stage, since in its upper part the lamellibrach *Daonella lomelli* was found.

Also in the northern Karavanke, in the wider area of Mezica, a broader trough formed during the Ladinian. Here argillites and marls, as well as platy limestones of the Partnach type were deposited. At the

periphery of the carbonate platform on the northern Karavanke and northern Julian Alps, deposition of nonbedded Wetterstein limestones began.

During Carnian (Cordevolian, Julian) the deposition of carbonate sediments continued with coral-sponge buildups in Mezica area and Julian Alps. In the Slovenian trough argillites, sandstones and platy limestones (Amphiclina beds) were deposited. In its southern part on uplifted blocks 10 to 130 m thick and up to 5 km long grew coral-sponge reef structures which outcrop in western Slovenia between the Blegoš Mountain, Hu-



Text-figure 3.—Schematic presentation of diagenetic forms and microfacial characteristics in the Triassic reef limestone: A, reefs of the carbonate platforms; B, reefs of the Slovenian trough. Grey fields represent the micritic groundmass, white is sparitic cement. A. Reefs of the Carbonate Platforms: 1) Various species of calcisponges (Carnian stage). 2) Solitary coral, partly recrystallized. 3) Section of algae *Diplopora* sp. (Ladinian stage). 4) Various species of skeletal algae of Dasycladacea and Solenoporacea. 5) Plate and spicule of echinoderm, coated with syntaxial sparitic cement. 6) Part of a larger solution cavity is filled with micrite and clay, and the upper part with sparitic calcite of several generations. 7) Section of completely recrystallized solitary corals, incrustated with nonskeletal algal envelopes. In places rare dolomitic rhombohedrons occur. 8) Colony of ramosely corals incrustated with nonskeletal algae; individual corallites are partly or completely recrystallized; in a part of the colony appears a cavity filled with two generations of cement. 9) Group of mollusks and foraminifers. 10) Sponge *Cheilosporites tyrolensis* (Norian-Rhaetian stage). B. Reefs of the Slovenian trough: 1) Calcisponge *Cystothalamia bavarica*, encrusted with envelopes of nonskeletal algae. 2) Crinoid plate with grains of authigenic pyrite. 3) Calcisponge *Cryptocoelia zitteli*, one of the most abundant reef building organisms. 4) Section of a ramosely coral; the septal structure in individual corallites is recrystallized. 5) Calcisponge *Colospongia* sp., encrusted with envelopes of nonskeletal algae; in surroundings, pores with geopetal texture. 6) Isolated crystals of authigenic quartz, albite (twins) and dolomitic rhombohedrons with zonal growth. 7) Entirely recrystallized solitary coral coated with envelopes of nonskeletal algae, partly recrystallized. 8) Stomatactis texture; lower parts of pores filled with late diagenetic dolomite, upper parts of pores filled with coarse sparitic calcite. 9) Solitary coral with a moderately well preserved septal structure; along borders silicified (authigenic microcrystalline quartz). 10) Calcisponge *Uvanella* sp. with rare crystals of authigenic quartz. 11) Foraminifera *Endothyra* sp.

dajužna and Tolmin. Due to strong supplies of clastic materials, growth of the reefs was periodically interrupted. These reefs are assignable to the Upper Cordevolian–Julian stages. In clastic sediments overlying the reefs, conodonts of the Tuvallian age were found (Buser and Krivic, 1979; Turnšek *et al.*, 1982).

On the Dinaric carbonate platform during the Carnian, limestone with *Diplopora annulata* was deposited. Small coral-sponge patch reefs grew only in the surrounding area of Hotavlje. Growth of all Carnian reef structures partially ceased in the Julian and Tuvallian substages (Text-fig. 1).

The largest Triassic reefs appeared during Norian and Rhaetian at the periphery of the Julian platform. According to their extensions and morphology they may be attributed to barrier type of reefs, being several hundred meters thick and several kilometers long. It is interesting to note that during this time no reefs occur either on the Dinaric platform, or in the area of the Slovenian trough (Text-fig. 2).

#### SEDIMENTOLOGICAL CHARACTERISTICS OF THE REEF COMPLEXES

According to the environment of deposition in Slovenia two types of Triassic reefs can be distinguished, reef complexes within the Slovenian trough, and reef complexes on the carbonate platforms. Organic, ecological, and diagenetic characteristics of the two reef types are shown schematically (Text-fig. 3).

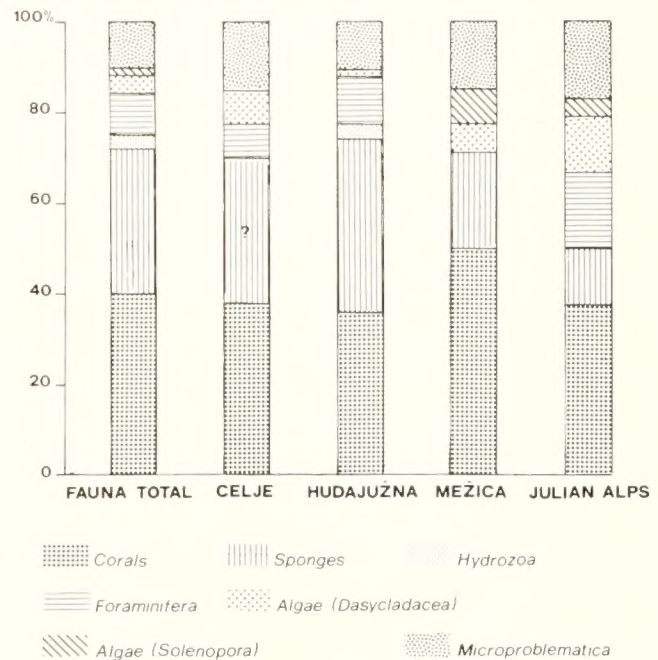
The reef complexes within the Slovenian trough occur in the form of mud mounds having steep slopes up to 50° (Čar *et al.*, 1981; Buser *et al.*, 1982). They always grew in rather exposed parts of the basin. Thick beds of turbiditic breccias served usually as solid ground for attachment of reef organisms. Dimensions of bioherms depend largely on the stage in which their life was interrupted by the supply of terrigenous material. The reef cores consist of organisms which chiefly played the role of trappers and stabilizers of carbonate mud (bafflestone-boundstone). Micrite must have been mostly a product of micritization and disintegration of *in situ* skeletons of sponges, since the carbonate content in clastics of the immediate surroundings of the bioherms does not exceed 3 percent.

In the reef, limestone frequently occurs with the texture of the "stromatactis." Cavities up to 15 cm in diameter often display geopetal internal texture in which their lower parts are filled by sparitic ferruginous dolomite, and the upper parts by calcite. Due to admixture of iron the dolomite is brownish on the surface. The ceilings of the "stromatactis" cavities are often coated with envelopes of nonskeletal algae which enabled their preservation, and respectively the collapse

of the micritic groundmass. The majority of sponges, corals, and other organisms are encrusted with thinner or thicker coatings of nonskeletal algae. Dolomite, frequent also in the form of isolated dolomitic rhombohedra in the micritic groundmass, is of late diagenetic origin. It crystallized, according to our opinion, in the domain of the mixed marine-freshwater environment at times when the reefs reached closer to the sea surface. Along with dolomitization in the considered reefs, quite often silicification, pyritization, and to a smaller extent albitization occur. Quartz appears in authigenic crystals. The primary source of silica is thought to have been from the surrounding clastic beds. Pyrite occurs as a uniformly dispersed pigment which gives the rock a dark color, an indication of frequent reducing environments within the sediment.

Characteristic of the reef complexes on the platforms is growth largely in very shallow environments of the open carbonate shelf having high energy. Their dimensions are usually much greater than those previously described and they are, in contrast, surrounded by different types of limestones. Their boundaries are therefore not easily determined, and morphologically they are not protruding from the terrain.

Fossils are usually very recrystallized and therefore not easily determined. Mostly they can be recognized only by their shapes which are still preserved because of micritic envelopes and algal incrustations. The micritic groundmass is mostly washed out. Organic skel-



Text-figure 4.—Quantitative analysis of the fossil assemblage in the Ladinian–Carnian reef complexes. Diagram shows percent of fauna in the total and in the four separately studied areas.

SUBORDO	SPECIES	Carnian		Cellje	Hudajuzna				Mežica		Julian Alps					
		Ladinian	Cordevolian	Julian	Cellje	Hudajuzna	Jesenica	Zakriž	Leskoviča	Hlevnik	Pristava	Vitranc	Prisojnik	Mojstrana	Mežakla	Kamniško sedlo
Archaeocoeniina	Cassianastraea reussi (LAUBE)		—									○				
	Koilocoenia decipiens (LAUBE)		—											○		
Faviina	Margarophyllia capitata (MÜNSTER)	—	—		●	●	●									
	Margarophyllia crenata (MÜNSTER)	—	—		●	●	●	●								
	?Margarophyllia michaelis (VOLZ)		—			●										
	"Montlivaltia" cipitensis VOLZ		—		●	●	●			●						
	"Montlivaltia" obliqua MÜNSTER		—				○	○						○		
	? "Coryphyllia" sp.		—		?									○		
	Craspedophyllia cristata VOLZ	—			○											
	Margarosmia zieteni (KLIPSTEIN)		—		●	●	●		●	●						
	Margarosmia septanectens LORETZ		—			●			●	●						
	Margarosmia confluens (KLIPSTEIN)		—			●	●		●							
	Volzeia badiotica (VOLZ)		—			●	●				●					
	Volzeia sublaevis (MÜNSTER)		—		?	●				●	●	●				
	Tropidendron rhopalifer CUIF		—													●
	Tropidendron sp.		—			●		●		?	?		●		●	
Meandriina	Andrazella labyrinthica (KLIPSTEIN)		—			●	●					●		●		
Amphiastreaeina	Protoheterastraea leonhardi (VOLZ)		—			○	●	○								
	Protoheterastraea fritzchi (VOLZ)		—				?									
	Protoheterastraea hudajuznensis TURNŠEK		—			●										
Fungiina	Myriophyllum badioticum (VOLZ)		—			●	●									
	Myriophyllum dichotomum (KLIPSTEIN)		—				●	●								
	Myriophyllum gracilis (LAUBE)		—		○								○			
	Myriophyllum mojsvari (VOLZ)		—					○								
	Omphalophyllia boletiformis (MÜNSTER)		—			●										
	Omphalophyllia radiciformis (KLIPSTEIN)		—			●		●		●						
	Omphalophyllia bittneri VOLZ		—							○						
Other fossils	Sponges		—		●	●	●	●	?	●	●		●		●	
	Foraminifera		—		●	●	●				●		●	●		
	Algae (Dasycladacea)		—		○	○				○			●			
	(Solenopora)		—							●	●		●			
	Microproblematica		—		●	●	●	●		●	●	●	●	●	●	

Text-figure 5.—List of coral species in reef localities of Slovenia. Other noncoral fossils are included at bottom.

etons and their debris, mixed with thin intraclasts, are chiefly cemented by fine-grained sparitic calcite.

The reef limestone of the platform type is light in color. It usually does not contain terrigenous admixtures and authigenic quartz. With the exception of the Wetterstein reef complex of Mežica, it shows less intensive dolomitization. The latter is of late diagenetic origin characterized by dolomitic rhombohedrons which are concentrated mostly in micritic nests and in laminae of nonskeletal algae. The textural forms of "stromatactis" are very rare in the platform type of reefs. They contain, however, many solution cavities up to several dm in diameter. These cavities indicate periodical emersions of shelf areas followed by paleokarst development. Solution cavities are filled by several generations of coarse-grained calcite which give them the appearance of cocode texture. In places, mostly those in reefs of the Dachstein Formation, the cavities are filled in part by red carbonate clay of karst origin.

## THE ROLE OF CORALS IN REEF COMMUNITIES

### The Fossil Assemblages

According to present findings, the oldest finds of Triassic corals in Slovenia can be attributed to the Ladinian–Carnian stages. At that time smaller reef complexes appeared in which corals and sponges are most frequently found. Attached organisms include hydrozoans, *Solenopora* algae, and crinoids. Frequent constituents of reef framework are the microproblematica, and much rarer foraminifers. The algae (*Dasycladacea*) are found only as individual fragments. Lamellibranchs and gastropods are found along reefs in several places (Text-fig. 4).

The fauna and flora of the Ladinian–Carnian beds can not be extensively subdivided into stratigraphically distinct horizons, therefore, they will be considered as one stratigraphic unit.

### Lateral Coral Diversity

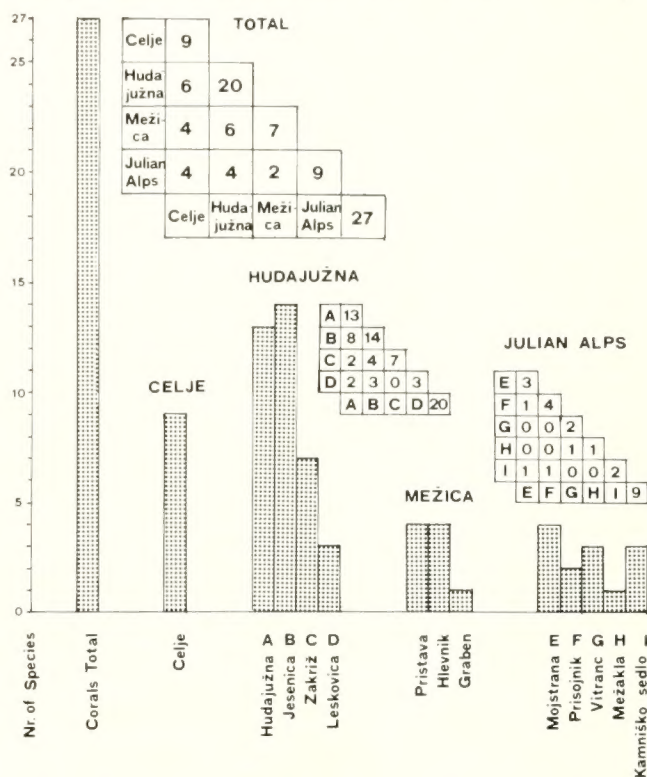
Corals have been found at numerous smaller localities. According to the paleogeographic position and tectonic units these localities have been divided into four areas: (1) Celje, (2) Hudajužna and surroundings, (3) Mežica and surroundings, and (4) Northern Julian Alps. Celje and Hudajužna occur in the Slovenian trough. Also included here are some of the localities at Mežica. Karavanke and the Northern Julian Alps are located on the Julian platform. Corals from the Dinaric platform are so recrystallized that they can not be determined (Text-fig. 5).

Analyses of coral species in various localities have shown great lateral variability. Species from one locality never appear together at the next locality. In the studied areas approximately half of the coral species are common to several areas. Also, within the same area the coral fauna varies greatly between localities. About 60 percent of the species are common to several localities (Text-fig. 6).

### Stratigraphic Comparison of Corals

The coral species found in the Ladinian–Carnian beds in Slovenia have been described from the Dolomites in Italy (Volz, 1896; Montanaro-Gallitelli *et al.*, 1973), Hungary and Czechoslovakia (Kolosváry, 1966a, b), and the Pamir Mountains (Melnikova, 1980; Dronov *et al.*, 1982). A similar facies has also been mentioned in several places in the Alps (see review of all investigations in Flügel, 1981, 1982) and in North America (Stanley, 1982).

In all these areas and localities the corals and coral-sponge buildups were generally thought to have developed during the Ladinian–Cordevolian–Julian stages. Where one finds the same facies, the same fossil assemblage occurs (Cassian Formation, Wetterstein beds; Wendt 1982; Turnšek *et al.*, 1982).



Text-figure 6.—Similarity matrix for coral species in the Ladinian–Carnian reef complexes of Slovenia. Diversity and similarity between four studied areas and between localities within individual areas are shown.

In Slovenia the various coral localities have been described in various ways, according to their geographic position: Celje to Ladinian, Hudajužna to the Upper Cordevolian-Julian, Mežica to the Upper Ladinian and Cordevolian, and the Northern Julian Alps to the Upper Ladinian–Cordevolian, or possibly Julian (Text-fig. 7). If we compare the collections of identified fossils, they are all generally similar in composition. Of the nine coral species at the Celje locality (Ladinian in age), six species are the same as those found at Hudajužna which is Julian. This is the highest similarity of coral fauna between two localities in all of Slovenia. Somewhat similar to Hudajužna are the localities at Mežica and the Julian Alps (Text-fig. 6). According to other workers, abundant Ladinian–Cordevolian sponges occur at Hudajužna (Ott, 1967; Dieci *et al.*, 1968; Senowbari-Daryan, 1981).

The corals and other reef fauna from the Ladinian and Carnian stages are actually identical. Because of this fact it can be inferred that all mentioned reef localities are time equivalent. Their appearance coincides with the beginning of the Cordevolian. Only with such explanation does the former transfer of the Cordevolian from the Ladinian into the Carnian become meaningful, due to the supposition that the Cordevolian fauna is closer to that of the Upper Triassic than to the Middle Triassic. In this case, the position or even the meaning of Ladinian becomes problematical and dubious.

The Share of Corals in Reef Building

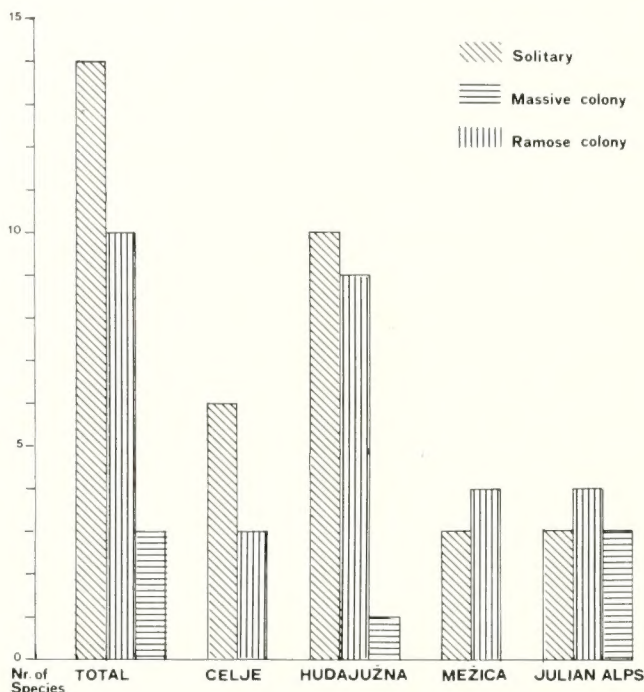
In estimating the contributions of corals in the building of reef structures, qualitative and quantitative anal-

		CELJE	HUDAJUŽNA	MEŽICA	JULIAN ALP
Rhaetian					Grid pattern
Norian					Grid pattern
Carnian	Tuvalian		?		?
	Julian		Grid pattern	Grid pattern	Grid pattern
	Cordevolian		Grid pattern	Grid pattern	Grid pattern
Ladinian		Grid pattern	Grid pattern	Grid pattern	Grid pattern
Anizian					

Text-figure 7.—Stratigraphical positions of the four studied areas. In all areas, the fauna are identical and it infers localities to be time equivalent. It is proposed that the first appearance of the coral-sponge reefs should be put into the beginning of the Upper Triassic.

ysis must be taken into consideration. The latter has shown clear predominance in all localities of sponges and corals which make up 50 to 80 percent of all organisms. In places sponge species prevail, but in the entire mass of organisms the percentage of coral volume is higher, since some colonial corals attain considerable size. However, corals are to a high degree recrystallized and thus not determinable, which gives a false impression in the qualitative analysis. According to the number of species, corals represent 35 to 50 percent of the investigated organisms. By volume corals represent approximately 30 to 60 percent of the organisms. Based on field data on the entire volume of the reef limestone, their proportion varies from 15 to 30 percent.

The coral forms are mostly solitary (14 species) and ramose dendroid-phaceloid colonies (10 species). In the massive colonies, two species are cerioid forms, and one species is meandroid (Text-fig. 8). These corals do not build large reefs. Instead, they build in several depths, small patch reefs and mud mounds within the carbonate and clastic beds. Those in the Slovenian trough could have lived without zooxanthellae as presumed by Stanley (1981). Also Fricke and Hottinger (1983) have found coral bioherms in the Red Sea between depths of 120 and 200 m. They established that the “absence of symbiotic algae below the euphotic zone does not hamper the building of bioherms by stony corals.” The growth depends on temperature,



Text-figure 8.—Growth forms of the corals and their quantitative importance in the building of the reef limestone.

currents providing nutrients, and submarine topography. All of these conditions may have been met in the deeper platform basins of the Carnian Tethys Sea.

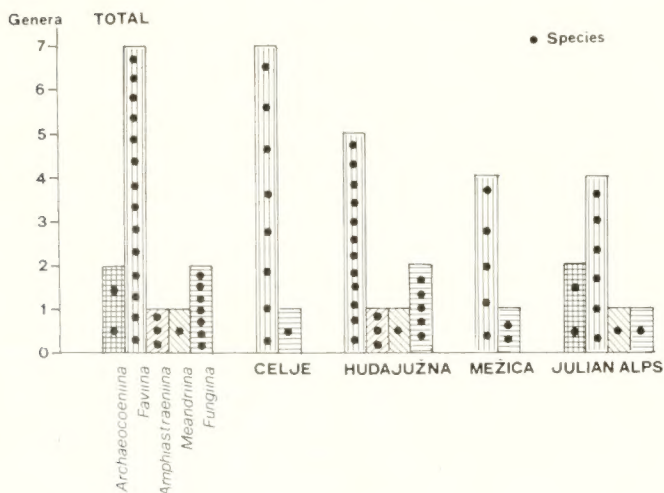
### Evolution of Scleractinia

Identified "Ladinian-Carnian" corals from Slovenia belong to 5 suborders of Scleractinia based on Melnikova (1968) and Roniewicz (1974), rather than Beauvais (1980). The most abundant are representatives of Faviina (14 species) and Fungiina (7 species); two species belong to Archaeocoeniina, 3 species to Amphistraeina and one species to Meandriina. No species assignable to suborders Stylinina and Caryophyllina were found (Text-fig. 9). The fact that the earliest fauna of Scleractinia in the Middle Triassic is quite heterogeneous and diverse adds more credence to Oliver's (1980) opinion that these corals evolved from soft-bodied ancestors along several lines at a time. Such soft-bodied ancestors started secreting calcareous skeletons when favorable conditions arose. In most of these corals the radial symmetry and cyclical septal insertion are characteristic of Scleractinia. The only exception in our collections is the genus *Protoheterastraea* which shows peculiar bilateral symmetry and irregular growth of septa. Similar to this coral is the genus *Zardino-phyllum* (Montanaro Gallitelli, 1975) and the Pachy-thecalidae (Cuif, 1977). Bilateral symmetry occurs in amphistraeins throughout the Mesozoic. Perhaps only in this suborder should direct descent from rugose corals be postulated.

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Text-figure 9.—Number of Ladinian-Carnian coral genera and species in the different scleractinian suborders.

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## DEVELOPMENT OF ECOLOGIC CORAL REEFS DURING THE LATEST TRIASSIC (RHAETIAN) OF THE NORTHERN LIMESTONE ALPS

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### ABSTRACT

Ecologic coral reefs in the Latest Triassic (Rhaetian) of the Northern Limestone Alps south of Salzburg, Austria developed in different paleogeographic positions in the northern transitional area of a Dachstein platform and the adjacent Kössen basin. This caused both the distinct facies developments and paleoecologic zonations of the two reef areas.

### INTRODUCTION

Facies and paleoecologic investigations of Upper Triassic reef structures in the Salzburg area, Austria (Schäfer, 1979; Schäfer and Senowbari-Daryan, 1981) are part of the project "Reefs of the Tethys" that has been carried out at the Paleontological Institute, University of Erlangen under generous financial support provided by the Deutsche Forschungsgemeinschaft.

The investigated reef structures of Adnet and the Rötelwand are located about 15 km south of Salzburg, Austria. They tectonically belong to the Osterhorn group as part of the Tyrolian nappe.

The quarries of Adnet near Hallein have been used for several hundred years in an area of 1 to 0.5 square km and provide a fantastic insight into the different levels of the Adnet reef structure. The Rötelwand reef lies north of Adnet in the Mörtebach valley, Gaissau. Good outcrops occur in dried up rivulets cutting the reef structure vertically and along a forest road. The lower portion of the reef structure is cut by a steep cliff about 80 m high.

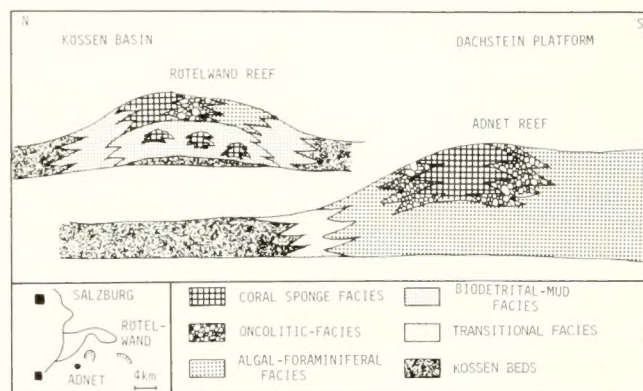
### FACIES DEVELOPMENT

The reef structures of Adnet and the Rötelwand developed during the latest Triassic (Rhaetian) in the northern transitional area of an extended, open marine Dachstein platform with shallow water carbonate sedimentation and the adjacent, somewhat deeper marine Kössen basin with more restricted carbonate deposition. The difference in relief between the Dachstein platform and the sea floor of the Kössen basin might have been some tens of meters during the time of deposition due to the difference in thickness of the Triassic and overlying Jurassic rocks. The different paleogeographic position of the reef structures caused the distinct facies development and paleoecologic zonation of the two reef areas.

The Adnet reef grew directly on the northern ramp of the Dachstein platform and is underlain by shallow water sediments (algal-foraminiferal facies) (Text-fig. 1). These are shallow subtidal dasycladacean and in-

volutinid calcarenites being well known from other localities with bedded Dachstein Limestones (Piller, 1976). The reef core (coral-sponge facies) interfingers with oncolitic, reef-detrital sediments (oncolitic facies) and shallow marine, lagoonal carbonates (algal-foraminiferal facies) on all sides. Northwards these Dachstein platform carbonates interfinger with Kössen basin sediments (alternation of limestones, marls and shales).

Ecologic conditions for reef growth were reduced on this backward side of the Dachstein platform, where the influence of the open Tethyan ocean was less distinct. Therefore the diversity of reef organisms is low and only a few framebuilders dominate. More locally changing water currents on the platform and the high amount of movable carbonate sands prevented the construction of one extended, massive reef framework. Instead the reef core is composed of several smaller reef patches isolated from each other and surrounded by a zone of reef-detrital, oncolitic grainstones. Each reef patch displays a distinct ecologic zonation of frame-builders and reef dwelling organisms that can be studied in vertical and horizontal sections in the Adnet quarries (Text-fig. 1).



Text-figure 1.—Facies development of the Adnet and Rötelwand reef structures grown in different paleogeographic position in the northern transitional area of a Dachstein platform and the adjacent Kössen basin.



The Röteland reef structure developed out of the northern adjacent Kössen basin and is totally surrounded by Kössen basin sediments. Reef development within the basin took place on preexisting relief differences of the sea floor formed by mechanical accumulation of sand shoals (oolitic or pelecypodal banks) and/or by the formation of coral biostromes (Kuss, 1983).

Two developmental stages can be distinguished in the Röteland reef structure. In a deeper water stage the formation of a carbonate mud-mound is caused by sporadic reef growth on these shoals and by mechanical-biological baffling of lime mud between the frame-builders and the pelecypodal and crinoidal banks. Growing actively into the wave base the mud-mound was capped by thick pelecypodal banks that prevented the carbonate mound from being destroyed by erosion. Thus the structure had developed into a shallow water zone providing environmental conditions comparable to those of the Dachstein platform. A small platform was formed in shallow water with reef growth on its northern slope (coral-sponge facies) and with the deposition of carbonate sands (oncolitic, algal-foraminiferal facies) under high energy water conditions in the south that correspond with subtidal, lagoonal facies types of the Dachstein platform (Text-fig. 1). Slope sediments (biodetritral mud facies) interfinger with

Kössen basin sediments on all sides of the structure. The whole carbonate complex is overlain by pelecypodal banks and buried under shallow subtidal grainstones (oncolitic and algal-foraminiferal facies).

The central reef area in the shallow water stage of the Röteland structure consists of a few interfingering reef belts composed of different reef communities of framebuilders and reef dwellers. Because of the predominance of highly diverse sponge communities it is assumed that the Röteland reef was formed in somewhat deeper water than the Adnet reef patches on the Dachstein platform (Text-figs. 2-3).

#### CORAL COMMUNITIES

Among all framebuilding organisms the scleractinians are the most widespread and display the most significant distributional patterns within the two reef environments. In contrast to the sponges, which are restricted to the central reef area in both reefs, the corals also occur in oncolitic and algal-foraminiferal limestones as well as in the Kössen basin sediments. However, the fauna in the Kössen facies is limited to only a few species.

Twenty-five coral species have been identified that belong to the following genera: 1. phaceloid and dendroid growth forms: "*Thecosmilia*" Milne-Edwards & Haime, *Pinacophyllum* Frech and *Stylophyllum* Reuss;

DIFFERENCES IN FACIES	RÖTELWAND	ADNET
VERTICAL DEVELOPMENT	DISTINCT 2. REEF STAGE 1. MUD MOUND STAGE LOWER KÖSSEN BEDS	INDISTINCT REEF DEVELOPMENT ON A BASEMENT OF PLATFORM CARBONATES (DACHSTEIN FACIES)
HORIZONTAL FACIES DISTRIBUTION OF UPPER REEF STAGE	DISTINCT 5 FACIES UNITS	INDISTINCT 5 FACIES UNITS
1. ZONATION	STRONG ZONATION	WEAK ZONATION
2. ONCOLITIC FACIES	ONE-SIDED	EXTENDED, ON ALL SIDES
3. BIODETRITAL MUD FACIES	ON ALL SIDES	REDUCED, ONE-SIDED
DISCONFORMITIES OF REEF GROWTH	LACKING	PRESENT
OVERLAYING LIASSIC SEDIMENTS	GREY FACIES PREVAILING (CONTINUOUS DEVELOPMENT)	RED FACIES PREVAILING (DISCONTINUOUS DEVELOPMENT)

Text-figure 2.—Differences in facies development between the Adnet and the Röteland reef structures.

2. solitary growth form: *Montlivaltia* Lamouroux, *Procycololites* Frech, *Stylophyllopsis* Frech and *Stylophyllum* Reuss; 3. massive growth form with cerioid, thamnasterioid or plocoid corallites: *Elysastraea* Laube, *Astrocoenia* Frech, *Phyllocoenia* Milne-Edwards & Haime, *Palaeastraea* Kühn, *Stephanocoenia* Winkler, *Astraeomorpha* Reuss and *Thamnasteria* Lesauvage; 4. foliaceous growth form: *Seriastraea* Schäfer & Senowbari-Daryan. Since skeletal microstructures of all corals are mostly destroyed by diagenesis, systematic names are still based on the classic work of Frech (1890) and others.

The Adnet reef shows the predominance of "*Thecosmilia*" *clathrata* form A. The large, thick branched colonies cause the mainly vertical growth of the reef framework that provides the formation of the various reef biotopes (Text-fig. 3). Less important are the fine branched "*Thecosmilia*" *clathrata* form B forming dense, monospecific thickets, and the nodular thamnasterioid species *Astraeomorpha confusa* (Winkler).

In the Röteland reef "*Thecosmilia*" *clathrata* form A is replaced by "*Thecosmilia*" *cyclica* Schäfer & Senowbari-Daryan living together with *Stylophyllum polyacanthum* Reuss, both species that are lacking in the Adnet reef. They are associated with *Pinacophyllum* sp., whereas the species "*Thecosmilia*" *clathrata* form A is relatively rare. In some parts of the reef area the fine branching, smaller "*Thecosmilia*" *clathrata* form B dominates over the large phaceloid species typical for the reef crest. In contrast to the Adnet reef,

species with massive nodular or platy colonies (*Thamnasteria* Lesauvage, *Elysastraea* Laube, *Palaeastraea* Kühn and other genera) are more common in the Röteland reef and dominate on the lower reef slope.

Besides scleractinians, sphinctozoans are also present with a comparable high species diversity, followed by less numerous spongiomorphids, tabulozoans and red calcareous algae. All of these organisms acted as primary reef framebuilders. Reef dwellers representing various groups of organisms colonized the resulting reef biotopes and display significant distributional patterns (Schäfer, 1979; Schäfer and Senowbari-Daryan, 1978; Senowbari-Daryan and Schäfer, 1979; Schäfer and Senowbari-Daryan, 1981).

Overall nine reef communities are characterized by their biogenic and sedimentary fabric (Schäfer and Senowbari-Daryan, 1981) (Text-fig. 5):

1. "*Thecosmilia*" *cyclica*-*Stylophyllum polyacanthum*-*Pinacophyllum* community;
2. "*Thecosmilia*" *clathrata* form A-massive coral species community;
3. "*Thecosmilia*" *clathrata* form A-*Pinacophyllum* community;
4. "*Thecosmilia*" *clathrata* form B-*Astraeomorpha confusa* community;
5. *Astraeomorpha confusa*-*Spongiomorpha ramosa* community;
6. *Disjectopora*-Sphinctozoa-Tabulozoa community;
7. *Montlivaltia norica*-*Disjectopora*-Sphinctozoa-Tabulozoa community;
8. *Montlivaltia norica*-*Seriastraea multiphylla*-Sphinctozoa community;
9. "*Thecosmilia*" *clathrata* form B-Sphinctozoa community.

These communities can be related to two hydro-

DIFFERENCES IN ECOLOGY	RÖTELWAND	ADNET
REEF BUILDING ORGANISMS IN ORDER OF THEIR ABUNDANCE	CORALS/CALCISPONGES SPONGIOMORPHIDS CALCAREOUS ALGAE	CORALS CALCISPONGES/SPONGIOMORPHIDS CALCAREOUS SPONGES
DEGREE OF DIVERSITY	HIGH DIVERSITY	MODERATE DIVERSITY
TYPE OF ECOLOGIC ZONATION	COARSE ZONATION OF ONE EXTENDED REEF PATCH	FINE ZONATION OF NUMEROUS, CLEARLY SEPARATED REEF PATCHES
TYPE OF INTERNAL STRUCTURE OF REEF PATCHES	WIDELY SPACED DISTRIBUTION OF REEF ORGANISMS	DENSE FRAMEWORK, MAINLY BUILT BY CORALS
TYPE OF REEF COMMUNITIES	HETEROTYPIC COMMUNITIES PREVAILING	HOMOTYPIC AND HETEROTYPIC COMMUNITIES IN MONO- AND POLYMICT REEF PATCHES

Text-figure 3.—Differences in paleoecologic zonation between the Adnet and the Röteland reef areas.

dynamically distinguished reef zones (Text-fig. 6). Higher energy, outer (Adnet) and topographically higher zones of patches (Röteland and Adnet) were occupied by phaceloid, dendroid and massive cerioid scleractinians with thick corallites withstanding water turbulence. Almost no sphinctozoan sponges, spongiomorphids and tabulozoans occurred in this environment. Diversity of the communities is rather low. Incrustations on the framework can be very intensive as evidenced by *Lithocodium aggregatum* Elliott, *Bacinella irregularis* Radoičić and *Alpinophragmium perforatum* Flügel, but is always restricted to a few species. The reef framework is sparse (bafflestone) and the interstitial sediment was a relatively coarse calcarenite indicating higher energy conditions in this environment. Only a few reef cavities gave space for a reef dwelling fauna and flora (Text.-fig. 4).

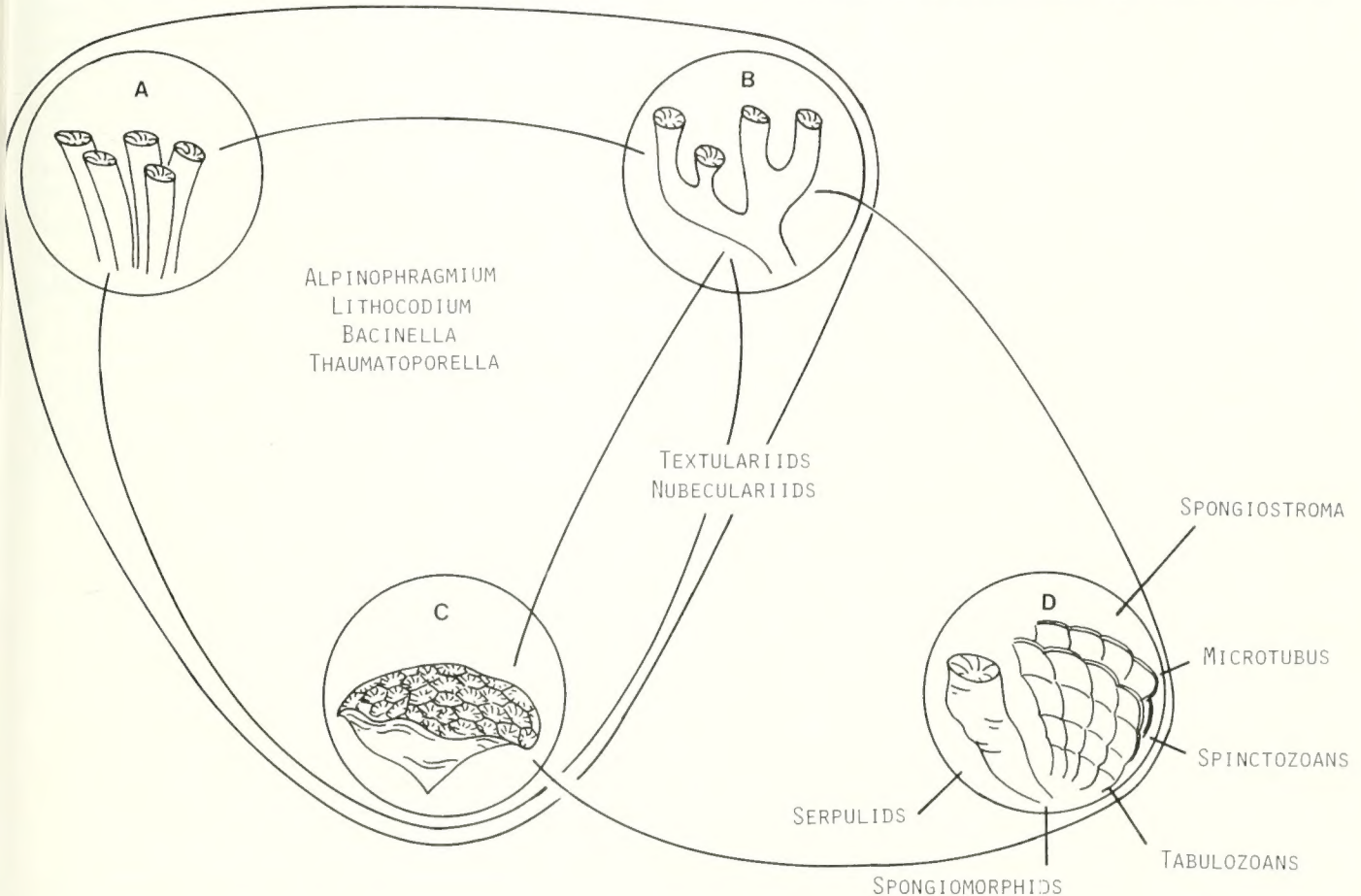
The lower energy interior (Adnet) and topographically deeper zones of patches (Röteland and Adnet) were biotopes for highly diverse reef communities including sphinctozoans, tabulozoans, spongiomorphids and solitary, foliaceous and massive thamnasterioid

corals. Intensive organic overgrowth produced a massive framework (framestone) with numerous reef cavities providing biotopes for a great number of reef dwelling organisms (foraminifers, ostracods, echinoids, crustaceans and other organisms).

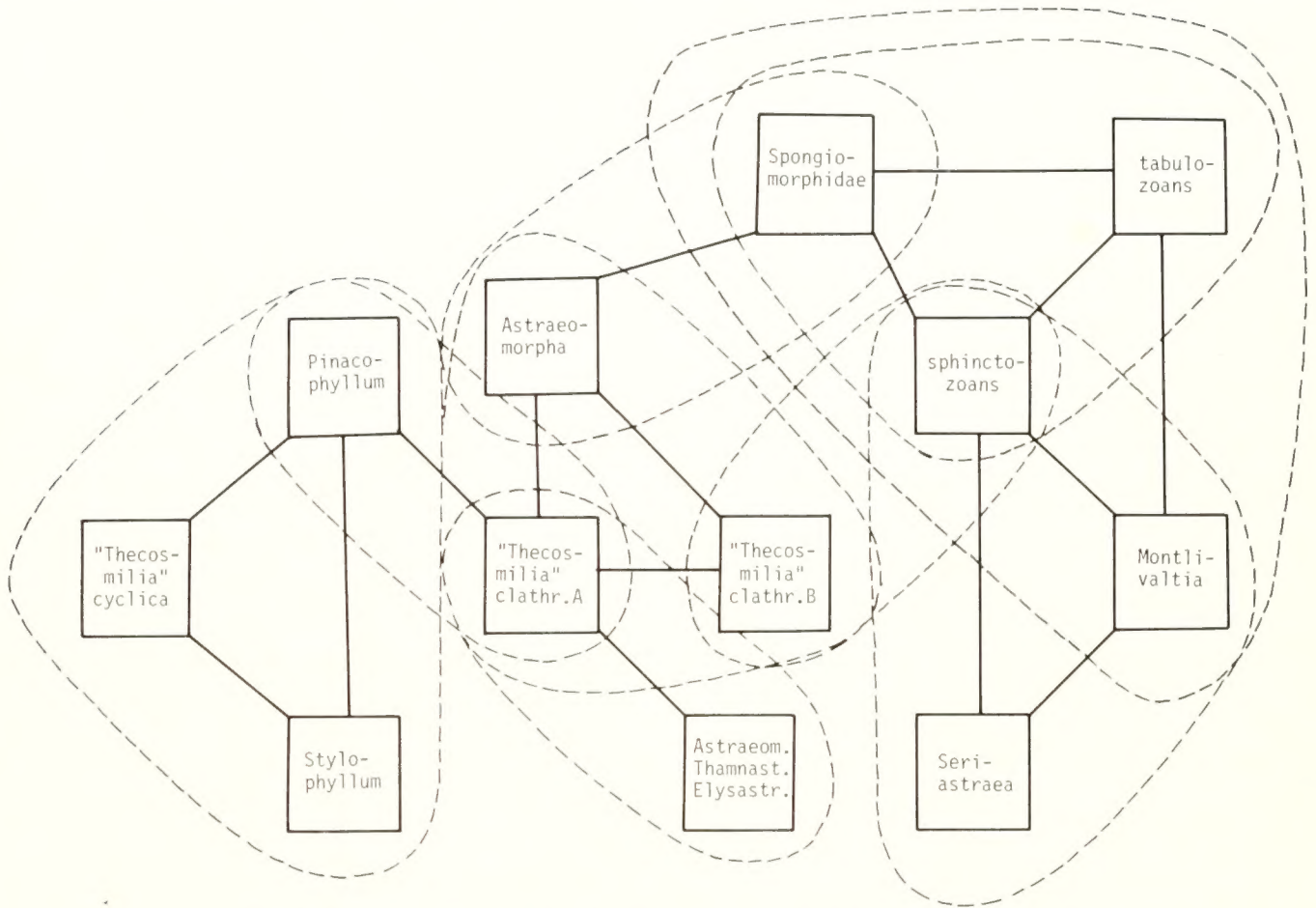
ECOLOGIC ZONATION

Recent as well as fossil reefs are thought to be ecologic structures of different complexity. Organic components of all reefs are individuals or colonies of one or more monospecific populations or heterospecific associations (Text-fig. 7).

The Adnet and the Röteland reef structures meet all requirements that are necessary to call them true ecologic reefs (Heckel, 1974; Schuhmacher, 1976; Longman, 1981). In the upper reef stages the rigid framework has been formed mainly by the carbonate secreting activity of organisms, thus causing positive topographic, wave resistant relief and stimulating the formation of different biotopes with various, highly diverse and interacting reef communities. Additionally the reefs controlled sedimentation processes in the sur-



Text-figure 4.—Association model for scleractinians in the Adnet and Röteland reef structures. Associations are characterized by the distinct growth forms of the coral species, by their assemblage of epibionts and by the interstitial sediment.



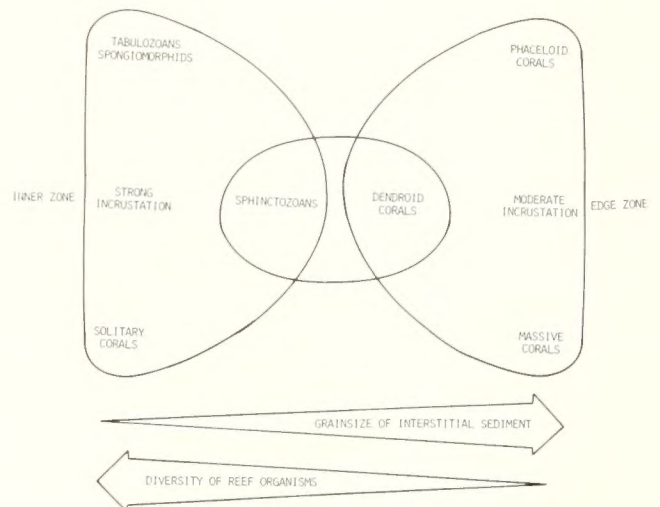
Text-figure 5.—Associations of framebuilding organisms in the Adnet and Röteland reef areas.

rounding depositional environment. Only the lower mud-mound stage of the Röteland structure is still lacking a rigid organic framework; it displays however all criteria of a carbonate buildup.

The numerous small and isolated reef patches of the Adnet reef area display the various ecologic categories taking part in reef constructions. Almost all possible combinations (Text-fig. 7) are found from single colonies to polymict reef patches composed of a sequence of heterospecific reef associations. Their distribution within the reef area was evidently controlled by water depth and water agitation. The size of the patches and the complexity of the communities forming the framework increase from the periphery towards the center of the reef area.

Monomict patches, consisting of just one colony, are restricted to the periphery of the reef area (oncolitic and algal-foraminiferal facies) and are interpreted to be initial reef patches. Only the large sized, phaceloid-dendroid colonies of "*Thecosmilia*" *clathrata* form A (this form is replaced by "*Thecosmilia*" *cyclica* Schäfer & Senowbari-Daryan in the Röteland reef) were able to colonize the sandy, shifting substrate of this high energy, unprotected biotope.

Very often several colonies occur together, thus forming pure "*Thecosmilia*" *clathrata* form A thickets of considerable size. "*Thecosmilia*" *clathrata* seems to be the pioneer of the Adnet reef, where form A with



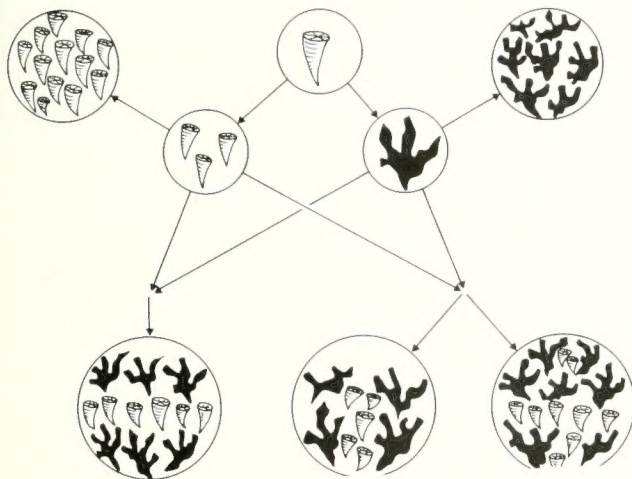
Text-figure 6.—Reconstruction model for reef patches in the Adnet and Röteland reef structures illustrating the type of reef communities and their position within the reef patches.

thick and few branching coralites could colonize the loose sandy bottom, whereas the small sized, frequently branched form B needed a firm substrate to settle. All other framebuilders (corals, sphinctozoans, tabulozoans, spongiomorphids) only occurred after their biotopes had been prepared by these pioneer forms.

Solitary framebuilders do not occur as monospecific populations in the Adnet and Rötelswand reefs. *Montlivaltia norica* Frech, a very common species, exclusively occurs in very sheltered areas of the reef patches. It obviously preferred low light reef cavities, where the species lived together with sphinctozoans, tabulozoans and the spongiomorphid *Disjectopora* sp. The same heterospecific association is typical for the lower reef slope of the Rötelswand reef structure.

All other patches of the Adnet reef are polymict sedimentary structures that are composed of a succession of several monospecific or more often of heterospecific communities (Text-fig. 7).

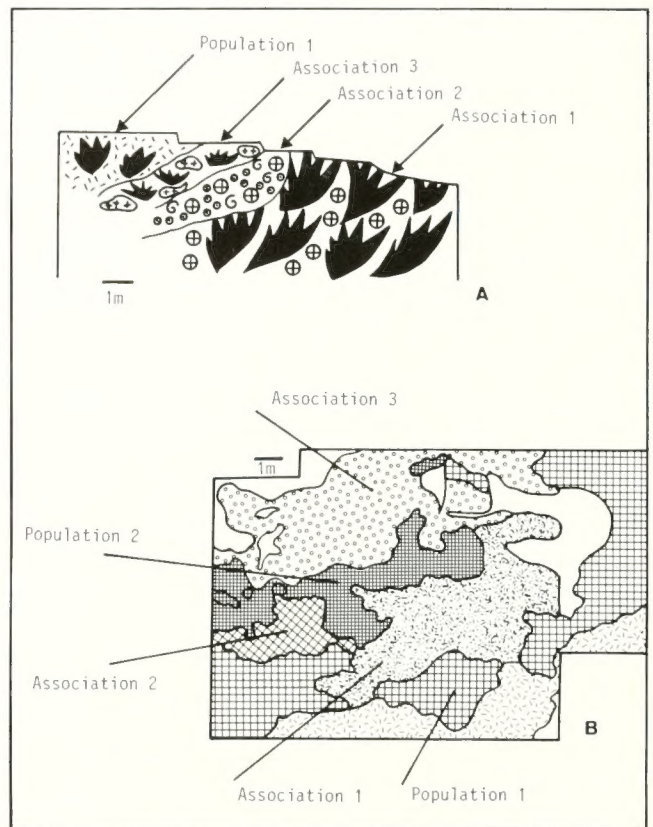
Polymict patches, composed of monospecific populations, are more common in the periphery of the Adnet reef area. Very often the interstitial sediment is stained by ferruginous minerals in these patches and extended solution surfaces indicate discontinuity of reef growth. The dominant coral in these patches is the fine branched "*Thecosmilia*" *clathrata* form B forming dense thickets. Other common species are *Astraeomorpha confusa* (Winkler), *Pinacophyllum* sp. and "*Thecosmilia*" *clathrata* form A. These monospecific communities form vertical successions. The underlying substrate of the patches is arenitic to ruditic, reef detrital and crinoidal sands and pelecypod banks.



Text-figure 7.—Ecologic categories included in the construction of reefs illustrated by a hypothetical coral reef. Complexity of communities from the top (one individual forming a monomict reef patch) to the base (polymict reef patch built by a vertical succession of monospecific populations and heterospecific associations of corals).

However the framebuilders mostly do not form true monospecific populations but live in heterospecific associations with one dominant and several additional species. Thus "*Thecosmilia*" *clathrata* form A and form B very often occur together. The fine branched form B associates with *Astraeomorpha confusa* (Winkler), the larger form A with *Pinacophyllum* sp. but also with *Thamnasteria rectilamellosa* Winkler. Characteristically the corals predominate against all other framebuilders within these patches in the periphery of the reef area.

Polymict reef patches in the Adnet reef, which consist of several mono- and heterospecific communities, show a very distinct vertical and horizontal zonation (Text-fig. 8). They dominate the inner part of the reef area. The margins of the patches are mostly occupied



Text-figure 8.—Vertical and horizontal section through reef patches in the Adnet quarries displaying the zonation of reef communities. A. Vertical section through a distal reef patch; association 1: "*Thecosmilia*" *clathrata* form A—*Montlivaltia norica*; association 2: *Montlivaltia norica*—*Paradeningeria*; association 3: "*Thecosmilia*" *clathrata* form B—*Astraeomorpha confusa*—*Thamnasteria rectilamellosa*; population 1: "*Thecosmilia*" *clathrata* form A. B. Horizontal section through a proximal reef patch; population 1: "*Thecosmilia*" *clathrata* form A; association 1: *Paradeningeria*—*Astraeomorpha confusa*—*Montlivaltia norica*—*Spongiomorpha*; population 2: "*Thecosmilia*" *clathrata* form A and form B; association 2: "*Thecosmilia*" *clathrata* form B; association 3: *Paradeningeria*—*Disjectopora*—*Tabulozoa*.

by large bushes of "*Thecosmilia*" *clathrata* form A, growing into the surf zone and providing a protected biotope for other framebuilders and reef dwellers in the center of the patches (Text-figs. 6, 8). With decreasing water energy the framework is constructed by monospecific thickets of "*Thecosmilia*" *clathrata* form B, followed by a heterospecific association of sphinctozoans, spongiomorphids, tabulozoans and the solitary coral *Montlivaltia norica* Frech in the very center of the structures. These most complex patches in the center of the Adnet reef area display several associations of framebuilders at one time causing a horizontal zonation. This and the abundance of sponges, spongiomorphids and tabulozoans and the reduced diversity of corals are the main differences, in contrast to the patches formed at the periphery of the reef area, where corals predominate and a horizontal zonation is mostly lacking.

Patches at the periphery of the reef area, which are built mainly by a succession of monospecific populations, have a lenticular shape, while patches in the reef center formed by heterospecific associations are domal.

Comparing the ecologic zonation of the Adnet and the Röteland reef structures one can find the same general features. While in the Adnet reef each patch shows its own zonation, the reef core of the upper reef stage of the Röteland structure consists of some broad interfingering ecologic belts that can be related to their position on the reef slope. The reef crest is colonized by large bushes of "*Thecosmilia*" *cyclica* Schäfer & Senowbari-Daryan, *Stylophyllum polyacanthum* Reuss and *Pinacophyllum* sp. This community also colonized the high energetic oncolitic facies. Down the reef slope below the zone of turbulence a "*Thecosmilia*" *clathrata* form B-sphinctozoan community occurs, followed by a highly diverse sphinctozoan-spongiomorphid-tabulozoan-solitary coral community and a "*Thecosmilia*" *clathrata* form B-sphinctozoan community. Instead of both a vertical and horizontal zo-

nation of the reef communities in the Adnet reef patches, the central reef area of the Röteland structure displays a horizontal zonation of the reef communities.

In both reef complexes each community type is characterized by a distinct composition of framebuilders and associated reef dwellers. They occur repeatedly with predictable groupings. Their composition and distribution within the patches were controlled by the changing ecologic conditions. Topographic relief and water energy seem to be very significant factors controlling the vertical and/or horizontal zonation of reef communities in both the Adnet and Röteland reef structures.

### CONCLUSIONS

Rhaetian patch reefs in the Upper Triassic of the Northern Limestone Alps south of Salzburg, Austria developed in different paleogeographic positions in the northern transitional area of a Dachstein platform and the adjacent Kössen basin. This caused the distinct facies development and paleoecologic zonation of the reef areas.

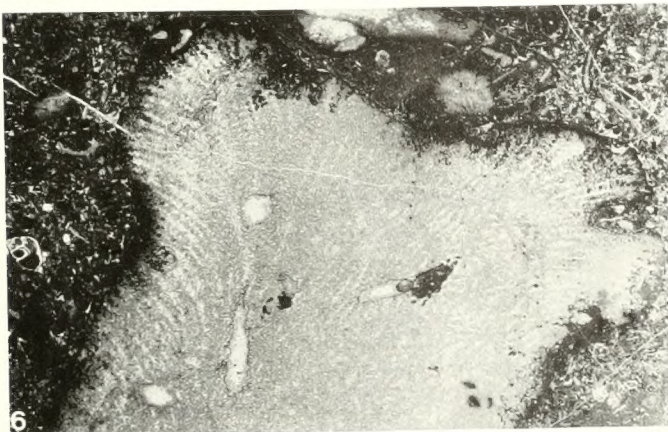
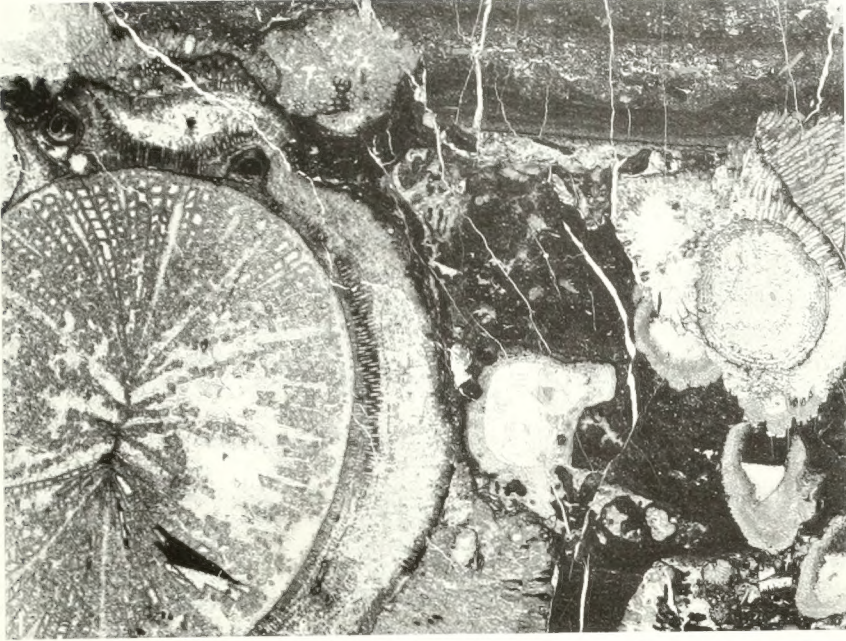
The Adnet reef grew directly on the platform in a shallow water carbonate setting. The reef area is composed of numerous smaller patches, each of them displaying an internal ecologic zonation. Restricted conditions for reef growth on this leeward side of the platform are indicated by a reduced diversity and the predominance of only a few reef builders. The mostly polymict patches are composed of several communities. Dendroid and massive coral species prevail.

The Röteland reef structure grew isolated out of the Kössen basin and shows two growth stages. A deeper water mud-mound stage is followed by an upper reef stage that represents a true ecologic reef including a shallow marine, high energy and a low energy environment. The reef core consists of a few interfingering reef belts composed of heterospecific communities. The

### EXPLANATION OF PLATE I

#### Figure

1. Reef community in the inner part of a reef patch; massive framestone; *Montlivaltia norica* Frech, overgrown by tabulozoans, serpulids and *Microtubus-Spongiostroma* crusts; reef cavity, filled with graded sediment consisting of a specific foraminifer assemblage, of echinoid fragments, ostracods and crustacean coprolites; upside down. Adnet, A/14,  $\times 1.5$
2. Colony of "*Thecosmilia*" *cyclica* Schäfer & Senowbari-Daryan; strong incrustation by the foraminifer *Alpinophragmium*; reef crest; Röteland; o/54;  $\times 1.3$
3. Colony of "*Thecosmilia*" *clathrata* (Emmrich) form A, dominant reef framebuilder in the Adnet reef patches; Adnet, A/41,  $\times 2$
4. Colony of *Thamnasteria rectilamellosa* Winkler; frequent species in lenticular polymict patches in the periphery of the Adnet reef area. Adnet, A/126,  $\times 3$
5. Reef community of the reef crest; bafflestone; cross section through corallites of "*Thecosmilia*" *cyclica* Schäfer & Senowbari-Daryan and *Pinacophyllum* sp. Röteland, z/21,  $\times 2$
6. Colony of *Astraeomorpha crassisepta* Reuss; common species in oncolitic, reef detrital sediments surrounding the reef patches. Adnet, s/87,  $\times 2.5$
7. Colony of *Stylophyllum polyacanthum* Reuss, frequent species on the reef crest of the Röteland reef structure. Röteland, o/56,  $\times 1.5$



diversity is high and sponges predominate over scleractinians.

Among the framebuilders the corals are most widespread and display the most significant distributional pattern. Overall nine reef communities are characterized by their biogenic and sedimentary fabric that can be related to two hydrodynamically distinguished reef zones. Higher energy zones are occupied by phaceloid, dendroid and cerioid scleractinians. Diversity and in-crustation are low. The reef framework is sparse with only a few primary reef cavities. Lower energy zones are biotopes for a highly diverse community dominated by solitary and thamnasterioid corals, sponges, tabulozoans and spongiomorphids. Intensive organic overgrowth formed a massive framework with numerous reef cavities.

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## EVOLUTION AND DIVERSIFICATION OF JURASSIC SCLERACTINIA

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## ABSTRACT

An attempt at a new taxonomy of the Mesozoic Madreporaria based on microstructural evolution was made by Beauvais (1980b). It allows examination of the phylogenetic relations existing between scleractinian suborders, families and genera.

In the present paper, appearance and processes of diversification of these different taxa are studied stage by stage from the Triassic to the Upper Jurassic. Then a study of the evolutionary trends of some genera (*Actinastraea*, *Isastraea*, *Andemantastraea* and *Microsolena*), based on an examination of their species variations through the Jurassic, is given. This study shows that it is difficult to determine species among these genera and that both qualitative and quantitative characters are intergrading and thus do not allow the separation of real, distinct species. However, an evolutionary trend based on an increase in the number of septal trabeculae is seen in the genus *Isastraea*.

The variations of the genera in the Families Actinastraeidae and Andemantastraeidae show examples of an evolutionary trend from intercalicinal to intracallicinal budding. An increase in the number of genera from Liassic to Upper Malm is also found.

Finally, the biogeographic evolution of the Jurassic scleractinian formations is outlined. It shows correlations between the distribution of reefs, plate tectonics and paleoenvironments. It is also possible to see a parallel between the distribution in time of reef formations and the evolution of the scleractinian taxa.

## INTRODUCTION

It is difficult to study evolution and diversification of Jurassic Scleractinia without having previously examined how this group appeared in the Middle Triassic. In fact, scleractinian evolution consists of a succession of steps that began as early as the Middle Triassic and continued unbroken until now. The Jurassic period is actually only a stage in this continuous phenomenon.

In 1981, I approved Cuif's hypothesis that the Scleractinia descended from Paleozoic Madreporaria. The pattern of septal insertion can not be said to mark the difference between the two groups because the first process of setting of the septal apparatus is nearly the same in both Tetracorallia and Hexacorallia. Also, I tried to explain that the difference in mineral composition of skeletons (calcite vs. aragonite) is probably true and not a diagenetic phenomenon. It is probably a result of important paleoenvironmental modifications occurring during the Permo-Triassic period.

In this paper, the scleractinian suborders and families will be studied from the Triassic to the present and I will show how these taxa were diversifying through the Jurassic Period.

## I. ESTABLISHMENT OF SUBORDERS, FAMILIES AND GENERA

An attempt at a new taxonomy, based on the microstructures of septa, allowed me (1981b) to study the evolutionary development of the different taxa. In this work, I distinguished two fundamental scleractinian groups. The first includes Scleractinia whose radial elements do not possess trabecular structure and which

today have completely disappeared. These are almost exclusively confined to the Triassic and Liassic and are divided into three suborders. The second group includes Scleractinia whose radial elements exhibit a trabecular structure. These forms were present, although scarce, in the Triassic. They increased markedly in the Lower and Middle Jurassic. This group is divided into eight suborders. During Early Jurassic time, the three suborders with nontrabecular microstructure that appeared in the Triassic were still present. These are discussed here.

A. Suborder Stylophyllina: This suborder is the most primitive. Septa are sclerenchyme laminae, arranged in uninterrupted connection with the other skeletal elements (dissepiments and wall) from which they are not differentiated. It includes two families: The Family Stylophyllidae, with discontinuous septa, is well represented in the Liassic with the genera *Stylophyllopsis*, *Phacelostylophyllum*, *Heterastraea* and *Discocoeniopsis*. It continues through the Dogger with the genus *Bathmosmilia* and through the Malm with *Palaeosmilia*. The Family Zardinophylliae, with entirely compact septa, began also with Triassic forms and continued during the Liassic with the genera *Archaeosmilia*, *Archaeosmiliopsis*, *Alloiteausmilia*, *Parapleurosilia*, *Plesiophyllum* and *Epismilia*, reaching the Lower Cretaceous. *Carolastraea* and *Intersmilia* were placed in this family with doubt because their microstructure is unknown.

B. Suborder Pachythealina: In this suborder, septa became independent of the theca and fibers and became arranged along a medio-septal plane. The suborder includes two Triassic families. However, only

the Family Volzeiidae, with one genus, *Volzeia*, persisted to the end of the Lower Jurassic.

C. Suborder Disticophyllina: This third suborder confirms an important evolutionary step in the Hexacorallia history (Cuif, 1974, 1976). It includes five families among which three appeared in the Triassic and persisted to the Lower Jurassic; they are: The Family Coryphyllidae exhibits an undulated medio-septal plane but no lateral axis; it disappeared at the end of the early Liassic. The Family Distichophylliidae is a little more evolved; lateral axis appear in the septa; this family became extinct at the end of the Middle Liassic. In the Family Margarophylliidae lateral axis appear progressively earlier, so that the phase with medio-septal plane becomes barely visible; this family disappeared at the end of the Late Liassic. The Family Amphistraeidae is more complex and evolved during late Liassic with the genus *Amphistraea* and became extinct in the Middle Cretaceous. In the Family Heterocoeniidae the lateral axis changed into rudimentary septa; it appeared in the Dogger and continued until the end of the Upper Cretaceous.

Eight suborders possess a trabecular microstructure. Three of them appeared as early as the Triassic. They are:

D. Suborder Archaeocoeniina which appears in the Triassic with two families: The Family Pinacophyllidae, exhibiting entirely dissociated trabeculae, is found only in the Triassic. The Family Tropiphyllidae, in which trabeculae became coalescent, appeared in the Triassic with the genera *Chorisastraea*, *Beneckastraea* and *Margarastraea*, continued in the Liassic with *Duncanosmia* and *Macgeopsis* and finished in the Middle Cretaceous with the genus *Ellipsosmia*.

E. Suborder Archaeofungiina. This suborder seems related to the Archaeocoeniina but possesses synapticulae. It appears in the Triassic with only one genus: *Myriophyllum* (Family *Cyclastraeidae*) but it is well represented during the Jurassic with the following families: The Family Cyathophyllopsiidae includes the genera *Oppelismilia* (Liassic), *Cyclophyllopsis* (Liassic to Middle Cretaceous), *Placocoenia* and *Blastosmia* (Upper Jurassic). The Family *Cyclastraeidae* includes the genera *Ellipsoidastraea* and *Omphalophylliopsis* (Liassic) and *Isastrocoenia* (Liassic to Dogger).

F. Suborder Fungiina. It is characterized by the appearance of compound trabeculae and synapticulae. It is the suborder including the more numerous families, genera and species in the Mesozoic. It is already present in the Triassic with two families represented, each by only one genus: *Araiophyllum* (Family *Microsoleniidae*) and *Thamnasteriamorpha* (Family *Thamnasteriidae*). Six families of this important suborder appeared in the Middle Liassic and continued to the end of Up-

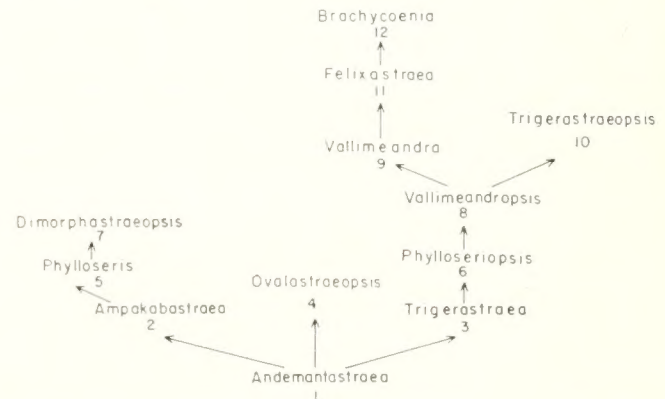
per Cretaceous; these families are: *Latomeandriidae*, *Synastraeidae*, *Siderastraeidae*, *Dermosmiliidae*, *Funginellidae*, *Andemantastraeidae*. Three new living families (*Agariciidae*, *Fungiidae* and *Agathiphyllidae*) replaced the six Mesozoic ones in the beginning of the Tertiary.

Finally, the last five suborders appeared during the Jurassic.

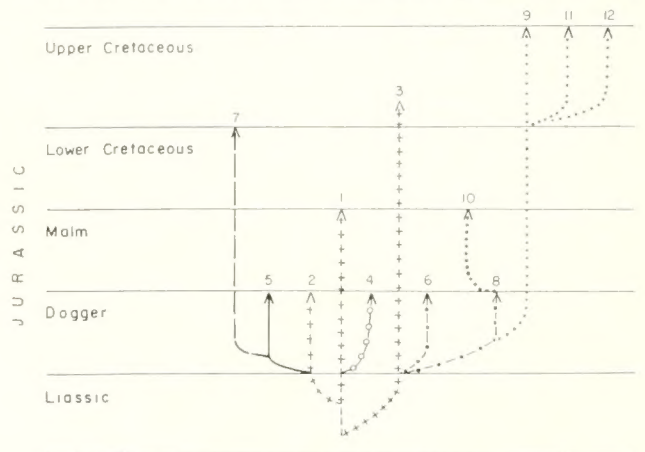
G. The Suborder Stylinina is a small and relatively archaic suborder, comprising a few genera grouped in two families: *Cyathophoridae* and *Stylinidae*.

H. The Suborder Faviina begins in the Liassic with the Family *Montlivaltiidae* in which Beauvais (1981) included all genera possessing septa with large-sized, simple and compound trabeculae arranged in a divergent system; devoid of synapticulae; with upper edge of the septa adorned with sharp, equal and equidistant teeth, inner edge undenticulate and lateral faces covered with thick granulations often joined into vertical carina.

The two following suborders possess a multitrabecular and thus already complex microstructure: The Suborder *Meandrinina* which appeared in the Middle Ju-



Text-figure 1.—Evolution of the family Andemantastraeidae. Top (a), evolutionary relationships based on manner of budding. Bottom (b), geologic distribution of the various genera given in (a), above.



assic with the Meandriidae, a living family and the Suborder Caryophylliina, which ranges from Liassic to Recent. The Suborder Dendrophylliina, the most evolved scleractinian suborder, is also the richest in living species and genera. It possesses the most complex microstructure with septa that are irregularly perforated and made of trabeculae that are discontinuous and incompletely joined.

II. EVOLUTION OF THE SPECIES WITHIN GENERA

Recent papers (Beauvais, 1982, 1983) examined how the species of the genera *Actinastraea* and *Isastraea* evolved. *Actinastraea* and *Isastraea* seem to include only one species each and, if no evolutionary tendency is evident in the genus *Actinastraea*, we can observe in the genus *Isastraea* a tendency of increase in the number of the septal trabeculae from Lower to Upper Jurassic. This evolutionary change is continuous and does not allow us to distinguish species. The variations of the quantitative characters (diameter of corallites, number of septa, etc.) seem to be either individual variations or variations related to the changing environments. Evolution of species in *Andemantastraea* and *Microsolena* was somewhat different.

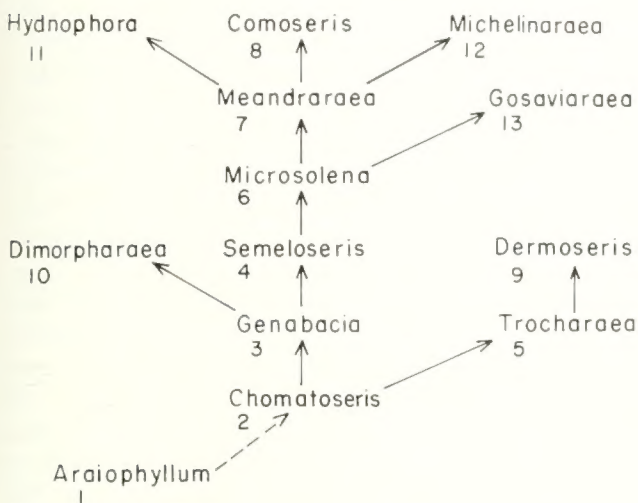
*Andemantastraea*, Liassic to Upper Jurassic. When we examine stage by stage, the quantitative characters used to distinguish the species of the genus *Andemantastraea*, we can not note any evolution based on these characters. Variations between the species are independent of the stratigraphic position. We see that it is difficult to determine valid species with these characters. In fact, several zoologists (Labrel, 1967; Pichon, 1972; Wijsmann-Best, 1974; Chevalier, 1975; Zlatarski and Martinez-Estalella, 1982) studying variations of these characters on living corals have already shown that they are dependent on environmental changes.

*Microsolena*, Bajocian to Middle Cretaceous. In the same manner, we can see that it is impossible to distinguish valid species within this genus and it is thought that the observed variability is the result of the changing environment.

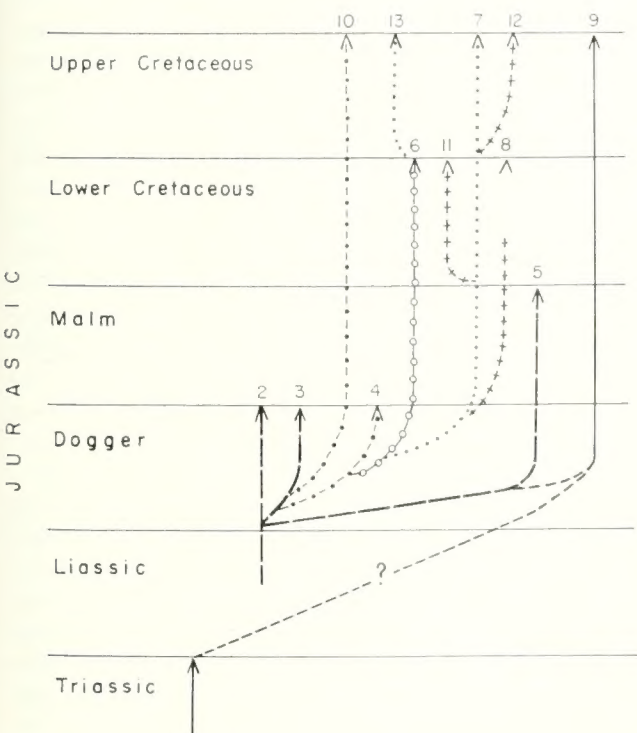
Similarly, we saw that the species of the genus *Ovalastraea* found in the Bathonian of Madagascar are already known in the Upper Jurassic (Beauvais, 1977b).

It seems that many Jurassic genera include only one species, each with ecotypes depending on the surrounding conditions. This great longevity of species (biological stasis of about 110 to 120 million years) may be explained by the strong relationship between the corals and their environment.

Beauvais (1983) studied evolution of the genera of the Family *Actinastraeidae*. Two evolutionary tendencies were noted: 1) Evolution in the manner of budding—in the oldest genera I observed a simple budding (fissiparity); this budding passes to a mixed one (intra- and intercalicinal gemmation) and, in the younger genera, only intercalicinal budding is present. 2) Disappearance of the trabecular dissociation—trabecular dissociation in adult septa disappears in the Dogger and it is continued only in the immature septa of the Cretaceous genus *Platycoenia*.



Text-figure 2.—Anagenetic evolution of the family Microsolenidae according to the manner of budding. Top (a), solitary corals and dendroid forms become thamnasteroid and finally meandroid (based on Alloiteau, 1957). Bottom (b), geologic distribution of the genera shown in (a) above.



A similar study was conducted within the Jurassic families *Andemantastreaeidae* (Text-fig. 1) and *Microsolenidae* (Text-fig. 2). In both cases, the evolutionary tendency observed in the *Actinastreaeidae*, based on the mode of budding, may be seen. This evolution was previously demonstrated by Alloiteau (1957). According to him, in the Paleozoic 80 per cent of the genera are solitary and among the few colonial forms known, only extracalicular budding is observed. No meandroid genera lived in the Paleozoic.

I note the fact that this evolutionary tendency in the budding may also be the result of an evolution of the paleoenvironments. It has been shown on living corals that dendroid, cerioid and meandroid forms are related to environmental conditions.

Conclusions: Very frequently fossil scleractinian species, based on the typologic method of determination (almost exclusively based on quantitative characters) are ecotypes, characteristic of one particular environment. The species taxon can be considered an ecotype-form, the genus-taxon is transferred to the species level and the family to the genus level. I think that parallel studies between the morphology of Scleractinia and the sedimentology of the formations where they occur must be made to ensure accurate understanding.

### III. INCREASE IN THE NUMBER OF GENERA THROUGH THE JURASSIC

The number of scleractinian genera increased through the Jurassic. In the Triassic, about fifty genera are known. In Liassic, approximately sixty; in Dogger they attain nearly one hundred, and in the Upper Jurassic more than one hundred and thirty are known.

Liassic—Eleven genera survive from the Triassic into the Liassic at the end of which they die out. Only twenty-one genera are known in the Liassic. Five genera that begin in the Liassic continue to the Middle Jurassic, five to the Malm and sixteen up to the Cretaceous. It seems that among all the genera which appeared in the Lower Jurassic none survived later than the Cretaceous.

Dogger—No remainder of the Triassic scleractinian fauna has been found in Middle Jurassic. Five genera appearing in the Liassic are still living by Middle Jurassic time. Five genera which appeared in the Liassic go through to the Dogger and into the Malm. Sixteen reached the Cretaceous. Twenty-nine genera appeared in the Dogger and are limited to this stage. Eleven appearing in the Dogger continued to the Malm and twenty-six to the Cretaceous. No Middle Jurassic genera reached the Tertiary.

Malm—Twenty-one genera which appear in the Liassic are still found in the Upper Jurassic. Five be-

came extinct there, while sixteen continued to the Cretaceous. Thirty-seven genera which appeared in the Middle Jurassic were still living in the Upper Jurassic. Eleven stopped at the end of this stage and twenty-six went on into the Cretaceous. Seventy new genera appeared in the Malm. Fifty-six were limited to this stage and fourteen extended to the Cretaceous. As mentioned before, it is apparent that no Upper Jurassic genera continued in the Tertiary.

### IV. PALEOBIOGEOGRAPHIC EVOLUTION OF REEF FORMATIONS AND PARALLEL EVOLUTION OF THE CORAL FAUNA

After the complete disappearance of the *Madreporearia* during the Early Triassic, they reappear in the Middle Triassic (Anisian) in northern Europe. Then, from Ladinian time, they extend throughout the Tethys basin. To the east, they reach Indonesia and Japan. In the other direction, they appear in England and North America. Paralleling this geographical dispersal, during Upper Triassic there began an important evolution of the fauna. During the Middle Triassic, the genera were still very similar to the Paleozoic ones, but from the end of the Triassic period onwards, there began an evolutionary trend which continued into the Lower Jurassic. This trend established almost all of the families which were going to characterize the rest of the Mesozoic as well as some Cenozoic and Recent reefs.

#### Lower Jurassic

True reefs are very uncommon during the Liassic. In almost all the areas where Liassic Scleractinia occur, they are solitary species or small colonies scattered in the sediments. An exception may be noted in Morocco where Middle Liassic bioherms were described by du Dresnay (1971, 1975). Fifty-nine genera are known from the Liassic. The hermatypic genera were derived from the Upper Triassic of Austria, Poland, Turkey, Pamir and Afghanistan (Beauvais, 1977a). Thirty-five per cent of the Moroccan species are endemic. These facts demonstrate that the greatest part of the scleractinian fauna from the Liassic of Morocco is derived from Triassic reefs of the Tethys and then evolved locally and endemically in this end of the basin, perhaps analogous to the present Red Sea coral fauna.

In a general way, the endemism observed in the reefs seems to be the result of a local evolution according to the environmental conditions prevailing in each basin. In previous works, I showed that the small-scale development of the Lower Jurassic reefs was probably due to a general deepening of the seas in early Liassic times. During the Lower and Middle Liassic we may observe the continuance of the Triassic genera *Stylo-*

*phyllopsis*, *Phacelostylophyllum*, *Heterastrae*, *Volzeia*, *Parathecosmilia*, *Procycolites*, *Retiophyllia*, *Margarosmilia* and *Thamnasteriomorpha*.

In the Upper Liassic all these genera suddenly disappear, and with the beginning of a new period of reef extension new families including about forty new genera appear. About half of them continue through the Mesozoic. They are *Epismilia*, *Amphiastraea*, *Cyclophyllopsis*, *Allocoeniopsis*, *Coenastraea*, *Actinastraea*, *Microphyllia*, *Brachyseris*, *Dimorphastraea*, *Epistrephtophyllum*, *Funginella*, *Andemantastraea*, *Mesomorpha*, *Stylosmilia*, *Goniocora*, *Stylinia*, *Montlivaltia*, *Rhabdophyllia*, *Goldfussastraea* and *Thecocyathus*. The following families appeared in the Liassic: Amphiastraeidae, Cyclophyllopsidae, Actinastraeidae, Latomeandriidae, Synastraeidae, Dermosmiliidae, Funginellidae, Andemantastraeidae, Stylinidae, Montlivaltiidae, Thecocyathiidae and Flabellidae. The Families Volzeiidae, Coryphyllidae and Margarophyllidae died out during or at the end of the stage.

#### Middle Jurassic

**Bajocian**—The distribution of Madreporaria during the Bajocian is almost the same as during the Upper Liassic. However, hermatypic genera became more numerous. These genera were cosmopolitan but the species distribution allows us to distinguish five distinct basins: an Anglo-Parisian basin, an Alsace-Swabia-Jura basin, a North African basin, a North American basin and a South American one. Seventy genera appeared in the Bajocian; twenty-nine of them are only known in the Middle Jurassic. The others (about forty) lived through the Mesozoic.

**Bathonian**—Reefs of Bathonian age disappeared from North America and at about this time the limits of boreal belemnites dropped down to 50° in north latitude. Elsewhere, reefs continued to grow and the number of genera eventually reached about one hundred. Many species became cosmopolitan, although some remained endemic, probably reflecting differences in sedimentary deposits. Two basins may be distinguished, European and Indo-Madagascan.

**Callovian**—The southern boreal belemnite limit reached the center of the United States. In Europe, it went down to Portugal, entailing the disappearance of reefs from the Anglo-Parisian basin. However, the contemporaneous uplifting of the Ardennes formed a ridge that stopped the cold currents coming from the north and allowed the scleractinians to continue their growth south of the Paris Basin. With this reef regression, the number of genera decreased since only thirty-nine genera are known in the Callovian. All the new species which appeared were endemic. The genera *Allocoeni-*

*opsis*, *Macgeopsis*, *Chomatoseris*, *Ampakabastraea* and *Paraphyllogyra*, which appeared in the Liassic, died out at the end of the Dogger. The families Heterocoeniidae, Acroporidae, Cyathophoridae and Meandriidae appeared in the Middle Jurassic. No family is known to have died out at the end of the Dogger.

#### Upper Jurassic

**Lower Oxfordian**—The cooling trend that started as early as the Bathonian in North America and extended into Europe during the Callovian persisted during the Lower Oxfordian. The boreal belemnites remained in Portugal and reefs are only found in the Crimea, Sinai and Somalia. They reappeared in North America, in northern Mexico and Wyoming.

**Middle and Upper Oxfordian and Kimmeridgian**—Favorable conditions for reef development reappeared in the Middle Oxfordian and reefs began their extension all over the earth. The resulting reef formations have a wide distribution from Middle Oxfordian time through the Kimmeridgian. Reefs grew and extended north as far as Scotland, Greenland and Sakaline Island and south as far as Argentina and Chile. This broad geographical distribution added a wealth of genera and species. Almost one hundred and fifty genera are known from the Upper Jurassic. Among them, about twenty continued from the Liassic and forty from the Dogger. About seventy genera appear in the Malm. All of the genera are cosmopolitan and the extent of this reef realm recalls, on a larger scale, the present reef formations found in the Indo-Pacific Ocean. It seems that a uniform and warm climate was prevailing during the Malm, allowing the Scleractinia to migrate through very variable latitudes. Floras and some bivalves confirm this hypothesis.

Only one family (Guyniidae) appeared in the Malm. During this time all of the Mesozoic families were already present. No families died out at the end of the Malm. It is only at the end of Cretaceous (period of the great Maestrichtian and Danian reef regression) that almost all the families which appeared during the Jurassic died out. Thus the Heterocoeniidae, Amphiastraeidae, Dermosmiliidae, Funginellidae, Andemantastraeidae, Cyathophoridae, Stylinidae, Montlivaltiidae and Thecocyathidae all disappeared. The Acroporidae, Faviidae, Meandriidae, Guyniidae and Flabellidae continued through this time and are still living.

**Tithonian**—Toward the end of the Upper Jurassic another reef regression commenced. True reefs are only known in Germany, Czechoslovakia and in southern France. Some small and scattered reefs are still found in the Jura Mountains.

## GENERAL CONCLUSIONS

We can see that the changes of the reefs and evolution of the fauna are closely connected. Thus it may be observed that for each variation in the reef conditions (climate, depth, salinity, etc.), there is a parallel evolution of the coral fauna in increasing or decreasing in the number of genera and in the disappearance or appearance of families. However we do not note evolution at the species level and we have to revise the species concept of the Jurassic Scleractinia and to research new micro- and macrostructural details. Dr. G. Gill (pers. comm.) has said that new data must be obtained to distinguish species. We must also study in parallel fashion how the variations of these details changed with the environmental conditions. A big area of new research is presently open.

## ACKNOWLEDGMENTS

This paper is dedicated to the memory of J. P. Chevalier. I am grateful to Professor J. Labrel from Marseilles for his perspicacious suggestions about species evolution. To Mr. P. E. Negus who so kindly corrected my English text, I send my best thanks and to Mrs. Y. Benkheiri and Mrs. M. Mannu who helped me in preparation and drawing tables and figures I express sincerely my acknowledgments.

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## A JURASSIC CORAL FAUNA FROM SOUTH AMERICA (CHILE)

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## ABSTRACT

Jurassic scleractinian corals in sediments of the Northern Andes of Chile (25–32°S) are of Hettangian to Callovian age. Solitary and dendroid forms are restricted to the Hettangian and Pliensbachian. Cerioid, phaceloid and thamnasterioid corals occur both in Liassic and Dogger sediments. Meandroid colonial forms have been found in strata of Middle Jurassic age only.

This trend of increasing coloniality corresponds with the general renovation of the scleractinians in post-Triassic time. A first attempt is made to compare the corals from Chile with faunas known from other Jurassic paleobiogeographic provinces.

## EVOLUTIONARY TRENDS OF SCLERACTINIANS AND CORAL COMMUNITIES IN POST-PALEOZOIC TIME

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## ABSTRACT

Scleractinian corals from the Tethys as well as Pacific realms range from Middle Triassic to Recent and are represented by three heterogeneous groups: 1) mostly solitary forms with fibrous skeletal parts, porous septa absent or rare (*Montlivaltiidae*); 2) colonial forms with primary lamellar microstructure, porous septa developed only in Cenozoic (*Pinacophyllidae*); 3) solitary and colonial corals with increased septal porosity ranging from early Mesozoic *Triadophyllum*, and *Conophyllia* to living *Fungia* (*Fungiidae*).

The three groups of corals should be compared by similar but not identical modes of their reproduction. The main tendency in this connection would be characterized from one side by increased colonial forms developed from solitary polyps (*Anabacia-Microsolena*, *Fungia-Polyphyllia*, etc.) and from the other side by stable coexisting solitary and colonial polyps (*Caryophyllia*, *Porites*, etc.). In this context, trends can be discussed. These include symbiotic relationships from parasitism and commensalism to mutualism between corals, algae, bivalves, and some other groups which inhabited reef biotopes. It is possible to recognize a correspondence between symbiotic algae development in coral soft tissues, their biogeochemical interaction and the increase or decrease in the coral's growth potentials.

Coral-zooxanthellae symbiosis began in the Late Triassic (Carnian stage) in the Far East of the U.S.S.R. as evidenced by recently discovered Carnian reefal limestone with framework branching "*Thecosmilia*" s.l., reaching as much as 2–3 m in height. By Ca/Mg and oxygen isotope methods, long standing paleotemperature of *Thecosmilia* growth was determined and found to range between 12–15°C.

Ecologic differentiation of hermatypic vs. ahermatypic corals in terms of Wells' definition began in the Early Jurassic but their most important development occurred in Late Cretaceous time due to tectonic movements and consequently to the changing relationships of shallow- and deep-water biotopes. The Late Jurassic was distinguished by an increase of species and genera of reefbuilding and reef-like corals.

The Cretaceous to Paleogene taxonomic composition and structure of the coral reef ecosystem was radically changed, probably by the influence of cosmic radiation. Nevertheless three main evolutionary lines of coral and ecological divergence were prolonged throughout Neogene and Quaternary time. Diversity, biomass, and number of some symbiotic groups corresponded in taxonomic position to their reefbuilding and reef-like hosts.

According to new dates, it is now possible to propose coral-zooxanthellate coevolution as a direct means of coral reef development in the post-Paleozoic.





SECTION 4  
INVITATIONAL SYMPOSIUM

**Diagenesis of Carbonate Material:  
Implications for the Study of Fossil Cnidaria**

Organized, Convened and Edited  
By

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INTRODUCTION

J. E. SORAUF AND I. G. MACINTYRE

Paleontologists immersed in systematic, paleobiological, and biostratigraphic investigations may be unaware of the research being done on carbonate diagenesis—a field of study that can have important implications in paleontological research, particularly in the study of corals, stromatoporoids, and archeocyathids. This symposium was organized, in part, to remedy this situation by bringing together carbonate petrologists and paleontologists to discuss various aspects of carbonate diagenesis and to present papers that provide insight into petrographic problems arising in the study of fossil cnidarians.

In keeping with this idea, this symposium begins with Ian Macintyre's examination of the skeletal alterations that take place in modern scleractinian corals during growth and following their death during early stages of burial. Using thin-sections to identify these skeletal alterations, Macintyre describes examples of the earliest phases of skeletal diagenesis (which are related to both biological and physical processes) as well as examples of contemporaneous and postdepositional submarine cements. If, as he suggests, early diagenesis is by and large associated with characteristic environmental settings, similar alterations in fossil corals may shed light on the conditions under which these corals grew or were transported and deposited.

This discussion is followed by Bob Halley's presentation of the latest information concerning the diagenesis of the metastable carbonates aragonite and magnesium calcite (especially in skeletal carbonates) as it relates to different diagenetic environments. Halley

discusses differences in pore water chemistry of various environments (fresh, saline, mixed fresh and marine, marine below compensation depth, and deep basinal connate water). Halley notes that the mineralogy of the altered materials can be superficially similar, but that in fact considerable differences do exist because of the dissolution of metastable carbonate and replacement of it by calcite or dolomite, each of which inherits markedly different petrographic and chemical details from the characteristic pore waters. Halley suggests that cnidarian paleontologists should be aware of techniques (petrographic, trace element, stable isotope, and fluid inclusion studies) that can aid in differentiating the diagenetic environments that metastable carbonates have experienced. Such data can help these paleontologists recognize the original mineralogy of various taxonomic groups.

Next, Johannes Schroeder describes how diagenetic alterations recorded in scleractinian corals from the Miocene of Sudan and the Paleocene of Egypt have been used to develop a technique that can assist in unravelling complex diagenetic sequences. This technique, known as the petrographic genetic dendrogram (petrogenetogram), can be useful in illustrating the multiple pathways present as alternative diagenetic possibilities during the numerous stages of the diagenetic process. Diversifying factors include skeletal morphology as well as skeletal mineralogy, both of which may cause temporal changes related to dissolution and/or neomorphism of the original carbonate. Other diversifying factors include the amount and sa-

linity of water in the diagenetic environment. As a result, diagenetic effects may be complex and vary greatly in degree. The petrogenetogram, according to Schroeder, is a useful means of ordering data for study of the evolution and distribution of pore spaces and diagenetic fabrics.

Christian Dullo follows with a paper on progressive diagenesis of aragonitic material in a sequence of raised Pleistocene reefs and reefal deposits on the eastern coast of the Red Sea. From a comparison of the biotic composition of modern and ancient deposits and their diagenetic alteration, Dullo concludes that algae and various marine invertebrates have different fossil records owing to differences in their susceptibility to solution and diagenetic change. He also notes that bioclasts are more susceptible to such change than are whole skeletons, that nonbiogenic aragonite is more easily modified than biogenic, and that coral-generated aragonite crystallites are more susceptible than mollusc-generated aragonite biocrystals (formed within complete envelopes of organic tissue). Dullo also shows that the timing of diagenetic modification provides further possibilities for selectivity. Thus, early dissolved aragonitic corals may be preserved as calcite-filled casts whereas later dissolved corals or molluscs may be absent or present only as molds.

Philip Sandberg focuses directly on the occurrence (and absence) of aragonite in ancient limestones and fossils. He notes the implications of analogy that have been made between modern and fossil corals, and between modern and ancient ooids, and emphasizes the dangers of overextending these analogies. Sandberg presents criteria for recognizing formerly aragonitic constituents of fossil skeletons and shows how neomorphic mosaics of calcitized aragonites can be recognized by pleochroism, orientation of crystal boundaries, size of crystals, inclusions (organic matter, fluid inclusions, relic aragonite) and elevated strontium content. His presentation concludes with arguments in support of the hypothesis that the rugose corals originally had a calcitic skeleton and that their microstructures were more variable than is the case in living scleractinian corals. The calcitization of scleractinian skeletons produces irregular mosaics quite unlike skeletal structures in any rugosan.

Turning to Permian corals, Klemens Oekentorp presents the interpretation that most septal microstructures in specimens he has studied are the result of either recrystallization or of blanketing of thin septa by uniform layers of fibrous calcite cement. He raises again

the interpretation that the rugosan skeleton may have originally been aragonite. In reviewing a number of unusual septal microstructures, Oekentorp suggests that these resulted from recrystallization, which in turn led to the deformation of internal features. He also suggests that the manifold number of septal structures indicates that for the most part they are secondary structures developed during diagenesis. Septal thickening (generally thought to be caused by biogenic stereome) is here attributed to the deposition of inorganic cement; and, according to Oekentorp, only the central zone of the septa is biogenic. Oekentorp also discusses the occurrence of inferred recrystallization fronts within the septa of these Permian corals and what they may suggest about the original mineralogy. In conclusion he calls for further study of patterns of recrystallization in calcitized aragonitic scleractinian corals as a means of understanding recrystallization phenomena in the Paleozoic rugosans.

The symposium on diagenesis closes with Jim Sorauf's description of Permian corals from Timor, which appear to be virtually unmodified by diagenesis. These corals, Sorauf suggests, can provide not only analogies for other corals, but also more general models for rugosan skeletal structures. He notes that broken sections of these corals lend themselves to study by scanning electron microscopy, which in this study has revealed that observed microstructures are formed by actual crystals and crystal boundaries, whose regular morphologies and arrangement argue against the occurrence of widespread recrystallization of biogenic carbonate. Other evidence of this is the orientation of early, syntaxial rim cements, and the occurrence of a pseudo-uniaxial cross in the genus *Euryphyllum*. The latter also indicates that the c-axis of rugosan biogenic calcite crystallites is the axis of elongation of fibers, just as the c-axis is the elongation axis of aragonite crystallites in the modern Scleractinia. In addition, Sorauf shows that the septal microstructure of some Permian rugosans does differ from that in modern corals, thus reinforcing Sandberg's argument that the analogy between living and Paleozoic septate corals does not hold for either mineralogy or microstructure.

The work presented in this symposium provides some of the most up-to-date information on the diagenesis of carbonate materials. We hope that the contributions here will be of special interest not only to cnidarian paleontologists, but also to carbonate sedimentologists and petrographers.

## PREBURIAL AND SHALLOW-SUBSURFACE ALTERATION OF MODERN SCLERACTINIAN CORALS

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### ABSTRACT

The nature and extent of alteration of modern scleractinian coral skeletons can help to explain the state of preservation of fossil corals and can provide some insight into their environment of deposition. The preburial and shallow subsurface alteration of modern coral skeletons is directly related to the types of environment in which corals grow, or into which they may be transported after death. The environmental conditions are related, overall, to the amount of ambient light and water movement present, and, locally to water temperature and turbidity. These physical parameters determine reef zonation, which includes both areal distribution of encrusting organisms and corals as well as the organisms that destroy coral tissues or skeletons. These parameters control the environment of deposition, and thus also the degree of mechanical damage experienced by coral tissues and coral skeletons, as well as the type and rate of substrate accumulation and submarine lithification that in some cases may completely replace coral skeletons. Paleontologists may find it helpful to review current information on skeletal alteration in modern corals with a view to understanding the numerous factors that can leave their imprint on fossilized coral skeletons.

### INTRODUCTION

Before coral skeletons become part of the rock record, they generally undergo various degrees of alteration related to certain biological, geological (physical and chemical) factors. These factors, in turn, are influenced by conditions of light and water agitation, both of which decrease in intensity with water depth. Biological alterations refer to encrustation, bioerosion, and the destruction of coral tissue by organisms having specific distributional patterns. Geological alterations refer to (a) physical changes in corals that are the result of tissue abrasion or the breakage and abrasion of coral skeletons, and (b) chemical alterations, such as the deposition of submarine cements in coral-reef substrates. The degree of both biological and geological alteration depends on the length of time that a coral colony is exposed to the agents of alteration, which depends on the rate of framework and sediment accumulation.

Paleontologists may find it useful to consider how such alterations might appear in fossil corals and what environments of deposition are associated with each type of alteration. This paper therefore presents a review of the principal types of skeletal alteration that have been documented in modern scleractinian corals, particularly by the more recent studies.

### BIOLOGICAL ALTERATION OF CORAL SKELETONS

#### Encrustation

As corals grow, encrusting organisms compete for the space that is unoccupied by living coral tissue. Many of these are cryptic organisms that tend to concentrate on the underside of coral colonies or in cavities

formed through bioerosion (discussed below). Under the right environmental conditions, some encrusters can completely dominate a reef community, as crustose coralline algae commonly do in forming pavements or ridges. Of the wide variety of encrusters (for a detailed review, see Jackson and Winston, 1982; Choi and Ginsburg, 1983), crustose coralline algae, bryozoan, foraminifera, molluscs, and polychaete worms are most notable for their heavy encrustations of coral skeletons, which can assist in preserving the skeletons.

#### Bioerosion

Bioerosion is a term introduced by Neumann (1966) to denote the organic erosion of calcareous substrates. Bioeroders are generally divided into two size categories: endolithic microorganisms and macroscopic borers.

#### *Endolithic Microorganisms*

This group comprises algae, fungi, and some bacteria (May *et al.*, 1982) that form a microscopic network of borings (1–100  $\mu\text{m}$  in diameter) in calcareous substrates. Boring is believed to take place through chemical, or a combination of chemical and mechanical, processes (May *et al.*, 1982). Golubic (1972) has demonstrated that the patterns of microboring networks can be used to identify these organisms in both recent and fossil carbonates. (For detailed information on endolithic organisms, see Golubic *et al.*, 1975 and the bibliography compiled by Kobluk and Kahle, 1977.)

Algal microborings, which are ubiquitous in modern corals (Fig. 1), occur most commonly as green bands directly under the live surface of coral colonies. These bands are formed principally by species of the siphonaceous green alga *Ostreobium*. In the massive corals,

the green bands document the growth pattern of the colony. Kanwisher and Wainwright (1967) demonstrated that only the outermost bands consist of live *Ostreobium* filaments and that the coloration in the deeper bands is the result of green algal pigmentation "adsorbed by the aragonite of the skeleton" (p. 384). In the Gulf of Panama, these bands have been found to coincide with dense annual growth bands that appear to form in coral skeletons during warm intervals between periods of cold upwelling in this area (Macintyre and Smith, 1974). Glynn (1974a) has calculated growth rates for *Pavona gigantea* off Saboga Islands on the basis of the spacing between the green bands.

In many coral skeletons, the microborings are filled by aragonite and magnesium calcite (see Alexandersson, 1972). Such infilling, if not recognized, may distort chemical and mineralogical analyses of coral skeletons. For example, a head of *Porites lobata* collected off Waikiki, Hawaii, thought to contain about 46 percent skeletal calcite was said to indicate an "alternate form of calcification" in corals and to have important implications for coral genetics and the history of coral skeletal mineralogy (Houck *et al.*, 1975). Later, however, the calcite was found to be associated with a network of algal microborings rather than being the primary biogenic skeletal deposit of the coral (Macintyre and Towe, 1976).

Although endoliths are widely distributed across the Belizean Barrier Reef, microboring activity appears to be most prevalent in the shallow back-reef zone. The green algae *Ostreobium brabantium* and *Phaeophila engleri* are restricted to the shallow-water fore reef, reef crest, and back reef zones (May *et al.*, 1982). Among the blue-green algae only one—*Hyella tenuior*—is restricted to shallow water. The other two common blue-green species (*Plectonema terebrans* and *Mastigocoleus testarum*) are found across this reef transect to depths of 30 m. The red alga *Porphyra* sp. appears to be most abundant in the deeper fore reef off Belize, while fungal endoliths are present in all reef zones.

Little information is available on the rate and extent of microboring activity. From an algal-filament count in the darkest green band in *Dichocoenia stokesii*, Kanwisher and Wainwright (1967) estimated that *Ostreobium* can destroy 12 percent (by volume) of a coral skeleton. To study the rate of infestation of this endolithic alga, Kobluk and Risk (1977) placed calcite crystals in the nearshore subtidal zone off Discovery Bay, Jamaica, where they found that 0.5 percent of the crystal surface was infested after eight days. The infestation progressed slowly up to about 15 days of submarine exposure, and thereafter increased markedly, at a rate of 0.9 percent surface area per day. The entire surface was infested to a depth of 30  $\mu\text{m}$  at the end of 213 days.

### Macroscopic Borers

The important role of macroscopic boring organisms in reef destruction was recognized in some early studies of Maldivian and Laccadive reefs (Gardiner, 1903a, b), Red Sea reefs (Bertram, 1936), and the Australian Barrier Reef (Otter, 1937). Recent reviews (Stoddart, 1969; Bromley, 1970; Warne, 1975, 1977) indicate, however, that interest in this subject lapsed until the 1960s, when researchers resumed work on the nature and distribution of macroscopic borers in reef habitats and began to investigate the rate of skeletal destruction by these organisms, which include boring sponges, echinoids, molluscs, polychaete worms, sipunculan worms, fish, and crustaceans.

*Boring sponges.*—Otter (1937) was among the first to recognize the damaging effect of boring sponges on coral skeletons, which was later confirmed in several studies (see Odum and Odum, 1955; Goreau and Hartman, 1963; Rützler, 1975; MacGeachy and Stearn, 1976; Stearn and Scoffin, 1977; Bromley, 1978). In their study of macroborings in coral heads off the west coast of Barbados, MacGeachy and Stearn (1976) found that sponges accounted for more than 90 percent of the skeletal destruction. Another study of the bioerosion of coral heads off Florida reported an average of 12 percent by volume destruction of coral skeletons (Hein and Risk, 1975). Extensive bioerosion caused by sponges has also been reported in geological studies, which have noted that boring sponges produce a large volume of sediment (see Futterer, 1974; Rützler, 1975; Moore and Shedd, 1977). The distribution of these organisms ranges from the shallow subtidal to depths greater than 20 m (Goreau and Hartman, 1963; Pang, 1973; Bromley, 1978).

The two dominant sponge-boring genera present in coral reefs are *Cliona* and *Siphonodictyon*. Clionids characteristically form a complicated network of connecting galleries or chambers 1–15 mm in diameter that generally penetrate no more than 2 cm below the coral surface. *Siphonodictyon*, on the other hand, tend to form one large cavity (10–100 mm in diameter) and are able to penetrate 10–12 cm into a coral colony (Rützler, pers. comm., 1983).

The surface of clionid sponge borings is characteristically pitted or scalloped (Rützler, 1975, fig. 1) as the result of the cellular etching of silt-size chips from the substratum, which are subsequently ejected by the sponge through its exhalant system (see Goreau and Hartman, 1963; Rützler and Reiger, 1973).

The rate of clionid bioerosion has been studied in a few areas. In Bermuda limestones, for example, it was estimated to be 23  $\text{kg m}^{-2} \text{y}^{-1}$  (Neumann, 1966), but later work in this area revealed that this value applied only to the initial stages of sponge infestation of the

carbonate substrate and that long-term rates are closer to  $7 \text{ kg m}^{-2} \text{ y}^{-1}$  (Rützler, 1975). Comparable rates ( $5.8 \text{ kg m}^{-2} \text{ y}^{-1}$ ) were calculated for sponge-chip production in the fore-reef off Jamaica (Moore and Shedd, 1977). In an innovative study of paired x-radiographs of core slabs in which skeletal erosion could be established, the loss of growth bands in cores of dead corals collected at various time intervals suggested that 1 m of *Montastrea annularis* could be eroded away in 150 years (Hudson, 1977). It should be remembered, however, that in all these cases clionids have limited substrate penetration and therefore the long-term rate of sponge bioerosion will ultimately be controlled by the rate of removal of the surficial network of sponge borings by other destructive forces.

*Echinoids*.—Even the most casual observer cannot fail to notice the effects of echinoid bioerosion. It is therefore not surprising that the boring activities of echinoids were documented in some of the earliest marine studies (Cailliaud, 1856, 1857; John, 1889). Several genera are known to erode carbonate substrate, particularly *Echinometra*, *Diadema*, *Echinostrephus*, and *Lytechinus* (see Russo, 1980) but only *Diadema* dominantly erode coral heads. The others are noted for their erosion of algal ridges, limestone, and beach-rock.

*Diadema* generally erode the dead surfaces of coral colonies in protected back-reef environments in depths less than 3 m. They rasp the coral surface with their teeth, and in doing so remove not only the coral but also the coralline, filamentous, and endolithic algae encrusting the coral. Although *Diadema* feeds primarily on algae, it has been reported to graze on live coral surfaces in the reefs off Curacao (Bak and van Eys, 1975) and Jamaica (Knowlton *et al.*, 1981). Similarly, in the Galapagos Islands the dominantly algal grazer *Eucidaris thouarsii* was found grazing heavily on "all hermatypic pocilloporid corals" (Glynn *et al.*, 1979, p. 47).

Although the characteristic radial scraping marks of *Diadema* are readily recognized on fresh crustose coralline algal surfaces (Hunter, 1977), they are not preserved on eroded coral surfaces. In thin section the coral surfaces eroded in this way usually appear uneven and the corallite growth pattern is truncated in a series of scalloped depressions or ridges (Fig. 2). In many cases, the density growth bands in the coral skeleton (see Macintyre and Smith, 1974) have been differentially eroded so that the erosional surface appears to have a banded pattern (Miller and Macintyre, 1977, fig. 14).

The rate of coral bioerosion by *Diadema* has been estimated by measuring the amount of carbonate that passes through the gut of the organism. Values of  $9 \text{ kg/}$

$\text{m}^2/\text{y}$  (Stearn and Scoffin, 1977) and  $9.7 \text{ kg/m}^2/\text{y}$  (Hunter, 1977, who introduced a correction factor for an estimated 43 percent reworked sand passing through the gut) have been reported in studies off Barbados. The rate for *Diadema* off St. Croix, where 50 percent reworked sediment was taken into account, is estimated to be  $4.6 \text{ kg/m}^2/\text{y}$  (Ogden, 1977).

*Molluscs*.—A number of molluscs are responsible for bioerosion in coral skeletons, notably the boring bivalves *Lithophaga* and *Gastrochaena*. In Bermuda reefs, these genera occur in a wide depth range, but are most abundant in depths less than 10 m; below this depth, *Lithophaga* appear to outnumber *Gastrochaena* (Bromley, 1978). Both of these bivalves have bifurcated apertures, through which their inhalent and exhalent siphons protrude. These apertures are a distinctive feature of their borings.

These bivalves reportedly account for 2.8 percent of the destruction in coral heads collected from patch reefs off Florida (Hein and Risk, 1975) and for 1.9 percent of the bioerosion found in *M. annularis* from Barbados (MacGeachy and Stearn, 1976), where a few other species were also observed boring into coral heads.

*Lithophaga* and *Gastrochaena* both have club-shaped borings that vary greatly in size, depending on the species and maturity of the individual. The average length and width of *Lithophaga nigra* borings are reported to be 14 and 2 cm, respectively, and 18 and 0.8 cm for *Gastrochaena hians* (James, 1970). Borings of both genera are characterized by aragonite linings (Fig. 3). The outer edge of *Gastrochaena* borings is lined with aragonite that extends beyond the substrate surface to form tubes which accommodate the siphons. In contrast, the lining of *Lithophaga* borings occurs in the lower part of the bore hole and varies considerably in degree of development, depending in large part on the strength of the substrate being bored (MacGeachy and Stearn, 1976). Species of both genera appear to use a combination of mechanical and chemical techniques to penetrate coral skeletons (see Carter, 1978; MacGeachy and Stearn, 1976), but little information is available on the boring rate of these or other boring bivalves, except for the large boring clam *Tridacna crocea*, which bores into coral rubble on the reef flats of the Great Barrier Reef at a rate of about  $140 \text{ gm/m}^2/\text{y}$  on the average (Hammer and Jones, 1976).

Some gastropods are noted for their radular rasping of the algal-covered substrate in the intertidal zone (see Ginsburg, 1953; North, 1954; Craig *et al.*, 1969), but on the whole they account for only a small proportion of coral-head bioerosion. Two species are reported to bore living coral: *Magilopsis*, off the Mariana Islands (Cloud, 1959), and *Leptoconchus*, in the Red Sea (Soliman, 1969).

Chitons, like gastropods, rasp the substrate with their radulae as they forage for filamentous algae (Otter, 1937) and coralline algae (Steneck and Watling, 1982). The borings of these gregarious animals tend to be densely packed and interconnecting (Fig. 4), and are wider at the surface. They truncate the coral skeleton with a smooth surface, and the debris from the rasping action is commonly cemented in the base (Fig. 5). Because chitons are shallow subtidal dwellers, they damage shallow-water coral species, notably *Acropora palmata* (pers. observ.) in the Belizean Barrier Reef. They commonly enlarge preexisting borings (Otter, 1937).

*Polychaete worms.*—Despite being considered “perhaps really the most important boring animals in coral rock” in Indian Ocean reefs (Gardiner, 1903a, p. 336), polychaete worms have been given relatively little attention in recent bioerosion studies. They form various types of borings that penetrate deep into coral skeletons—but never into the live surface. Eunicid polychaetes, the dominant coral borers (Gardiner, 1903a), form sinuous and anastomosing borings that range from 0.5 to 2 mm in diameter off Barbados (MacGeachy and Stearn, 1976) and reach 4 mm in diameter off Bermuda (Bromley, 1978). Most borings are circular in cross section, but some are oval (Bromley, 1978). These borings cut roughly through coral skeletons and commonly have a lining of fine debris in a brown matrix (Fig. 6).

Boring polychaete worms appear to have a wide distribution in coral reefs (James, 1970). Off Barbados,

they are most common at depths of less than 20 m (MacGeachy and Stearn, 1976), but off Bermuda they are most abundant in depths less than 10 m (Bromley, 1978). Off Florida, they appear to be responsible for about 13.2 percent of the bioerosion in massive shallow-water corals (Hein and Risk, 1975).

Eunicid polychaetes are thought to bore into corals mechanically with the aid of strong jaws (Hartman, 1954). This hypothesis is supported by Ebbs (1966), who noted that the gut contents of *Eunice schemacephala* grade from fine sand near the mouth to mud that is excreted to fill the organism's borings. In correlating the distribution of boring polychaetes with algal bands in coral skeletons, MacGeachy and Stearn (1976) suggested that the worms might rely on endolithic algae as a source of nutrients. At present no information is available on the rate at which eunicid polychaetes destroy coral skeletons.

*Sipunculan worms.*—Sipunculans, too, have long been recognized for their destruction of reef corals (Gardiner, 1903a; Otter, 1937), but their distribution appears to vary considerably. A recent study of coral heads from a patch reef off Florida, for example, found no evidence of sipunculan boring (Hein and Risk, 1975), and a study off Barbados found that sipunculans accounted for only one percent of the borings in living coral heads (MacGeachy and Stearn, 1976). In other studies, only two boring sipunculans were found in the reefs off Bermuda (Bromley, 1978), whereas six species

Figure 1.—Photomicrograph of a green band in the skeleton of *Pavona gigantea*, Saboga Islands, Pacific coast of Panama. Note the network of microscopic borings of the green alga *Ostreobium*.

Figure 2.—Section through a colony of *Montastrea annularis* that exhibits bioerosion by the echinoid *Diadema*. The uneven bioeroded surface truncates the corallite growth pattern which extends to the living flank of the colony. Shallow Back Reef, Carrie Bow Cay, Belize.

Figure 3.—Details of the aragonitic lining of a *Lithophaga nigra* boring in a *Pavona gigantea* colony, Saboga Islands, Pacific coast of Panama.

Figure 4.—Surface of a crustose coralline algal-coated *Acropora palmata* colony showing the closely spaced and interconnecting pattern of chiton borings. Rubble Reef Crest, Carrie Bow Cay, Belize.

Figure 5.—Photomicrograph of a section of a chiton boring from Figure 4 showing the smooth surface of the walls and cemented debris at the base of the boring.

Figure 6.—Section through a eunicid polychaete boring in *Acropora palmata*. Note the ragged wall surface and the brown debris-laden lining. Rubble Reef Crest, Carrie Bow Cay, Belize.

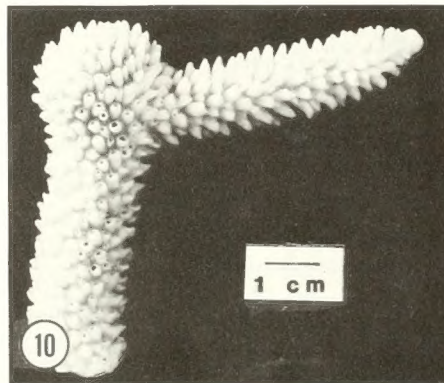
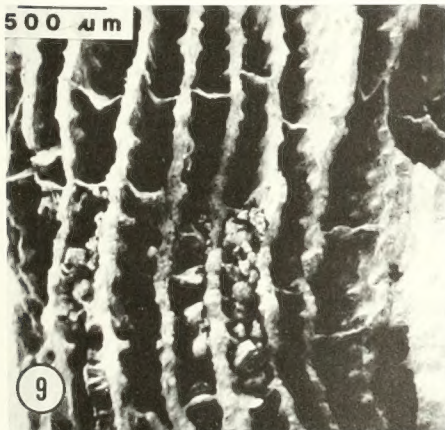
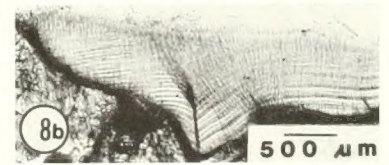
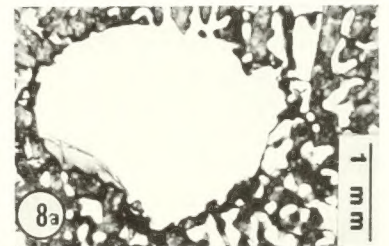
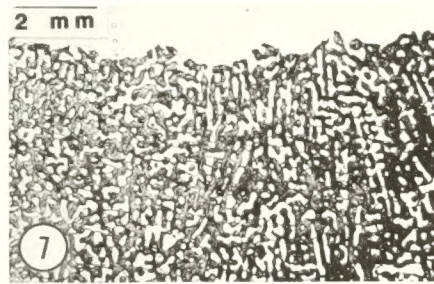
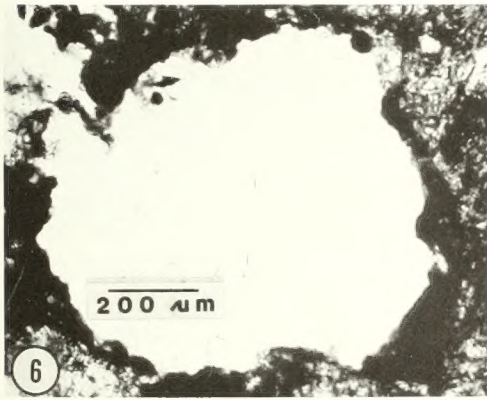
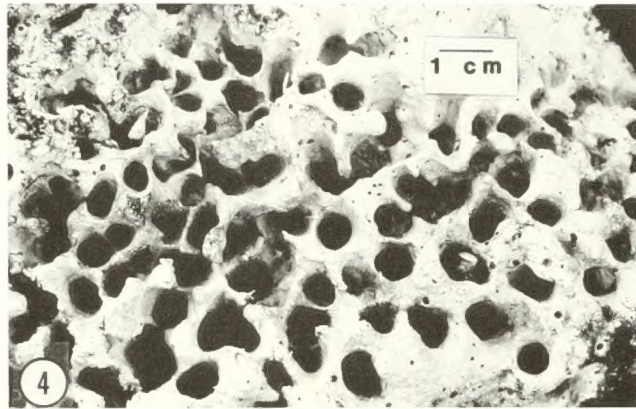
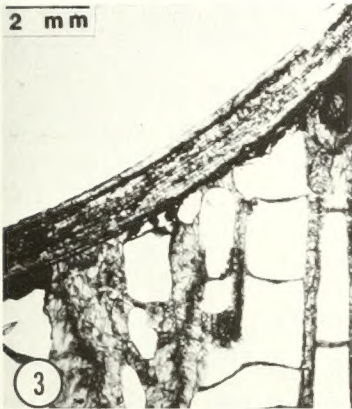
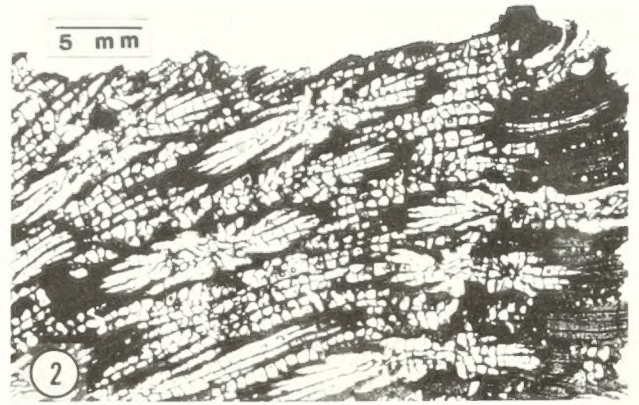
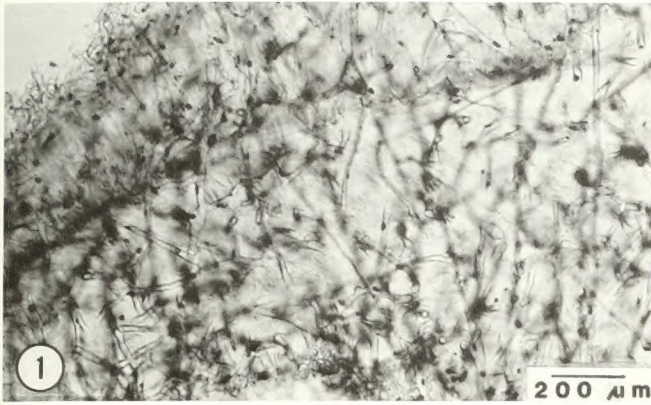
Figure 7.—Parallel grooves cutting into the surface of a colony of *Porites astreoides* indicate the biting action of a parrotfish. Shallow Back Reef, Carrie Bow Cay, Belize.

Figure 8.—Section through a *Lithotrya* barnacle boring in *Acropora palmata*, Rubble Reef Crest, Carrie Bow Cay, Belize. a) Note the oval shape of the boring and the calcite attachment plate on the wall. b) Detail of the calcite plate showing a pattern of growth bands.

Figure 9.—Scanning electron micrograph showing detrital material trapped under the dissepiments of a corallite of *Solenastrea hyades* from the continental shelf off North Carolina. This indicates that the coral colony was alive when this sediment entered the skeletal cavities.

Figure 10.—Regenerated branch of *Acropora cervicornis* after storm damage, Shallow Back Reef, Carrie Bow Cay, Belize. Fractured tip has been overgrown but apical polyp, rather than reestablishing at the end of the branch, forms a new branch on the flank.

Figure 11.—Section through the bulbous tip of a *Acropora cervicornis* branch tip that has recovered from storm damage, Shallow Back Reef, Carrie Bow Cay, Belize. The new growth covers the “die-back” original surface that is encrusted by coralline algae. Note the abrupt termination in the growth pattern of the apical corallite.



were collected from the Belizean Barrier Reef (Rice and Macintyre, 1982).

On a transect across the outer reef platform off Belize, sipunculans showed the highest concentration in the reef-crest zone, and somewhat less concentration in the inner and outer fore reef to depths of 20 m. They decreased markedly—with respect to surface area and weight of coral fragment in both the shallow back-reef zone and on the deep fore-reef slope (35 m). Bromley (1978) and MacGeachy and Stearn (1976) have reported that boring sipunculans have a wide depth range in reef areas.

Sipunculan borings vary in length and sinuosity, but all are cylindrical and they cleanly truncate the coral skeleton. Patches of sediment are commonly found packed into skeletal cavities adjacent to the borings (Rice and Macintyre, 1972, fig. 4).

Most of the sipunculan borings in the Belizean Barrier Reef are attributed to four species (Rice and Macintyre, 1982): *Lithacrosiphon alticonus* occurs in a great variety of corals, most commonly in deeper water, and usually forms a straight boring with a rounded termination; *Aspidosiphon brocki* is a shallow-water species found predominantly in coral rubble of *Porites porites*, *P. astreoides*, and *Acropora palmata*, and is noted for a near-surface, short and narrow boring that penetrates the surface with no particular angle of preference; *Phascolosoma perlucens* is also a shallow-water species but it favors *Acropora palmata* and *Agaricia* sp., in which it forms long sinuous borings that can penetrate deep into the coral skeleton; *Paraspidosiphon steenstrupi* is most common in the shallow reef crest, but occurs in a variety of corals from all depth ranges and its borings are similar to those of *P. perlucens*, but less sinuous.

The boring technique of sipunculans has not been established. Gardiner (1903a) and Hyman (1959) have favored physical processes, but Rice (1969) has pointed out that since the hard parts are all oriented toward the bore-hole opening, they are probably not used in the boring process. Rice suggested instead that sipunculans use some form of chemical dissolution to bore into coral heads, which they accomplish through secretions from epidermal glands. A more recent study found evidence of both chemical alteration and mechanical abrasion in the walls of sipunculan borings (Rice and Macintyre, 1972).

*Fish.*—Probably the first report of coral being eroded by fish was Darwin's (1842) observation of fish browsing on coral in the reefs off Cocos-Keeling. The damage fish cause to both living and dead corals has been of wide interest, particularly in studies of sediment production (Wood-Jones, 1910; Grabau, 1913; Nesteroff, 1955; Odum and Odum, 1955; Newell, 1956; Cloud,

1959; Bardach, 1961; Bakus, 1966; Glynn *et al.*, 1972; Gygi, 1975; Frydl, 1977).

Parrotfish (Scaridae) and surgeonfish (Acanthuridae) are the principal bioeroders, rasping both algal-covered dead corals and live corals in shallow back-reef environments (Bakus, 1964; Stoddart, 1969; Gygi, 1975; Ogden, 1977), although parrotfish have also been reported grazing widely at a depth of 15–20 m off Barbados (Frydl, 1977). In the Belizean Barrier Reef, the highest concentration of rasp-marks on corals has been noted in the inner margin of the reef-crest zone and in the rubble and pavement zone directly shoreward of the reef crest.

Recent studies have concentrated on the effects of parrotfish, of which at least ten species browse on coral in the Caribbean (Ogden, 1977). These fish have "heavy beaklike jaws and a pharyngeal mill which acts as a grinder, breaking down pieces of coral skeleton and calcareous red and green algae into fine sand and silt before it enters the gut" (Ogden, 1977, p. 281). The sediments from the gut of these fish have been examined in terms of content (Cloud, 1959; Ogden, 1977) and size (Gygi, 1975; Frydl, 1977), but little is yet known about characteristics that might be used to identify the source of this material after it has been deposited on the sea floor.

On the coral heads themselves, parrotfish leave a highly distinctive bite pattern: parallel grooves, 1–2 mm apart (Gygi, 1975; Bromley, 1977; Frydl, 1977). In thin section the grooved surface is easily recognized (Fig. 7). Furthermore, the repeated grazing from the same orientation can produce a series of scalloped depressions on dead coral surfaces (see Rützler and Macintyre, 1982, fig. 12) that could be used to identify fish bioerosion in the rock record.

The amount of sediment produced by these fish is thought to give some indication of the rate of bioerosion by fish. Cloud (1959), for example, estimated that fish "browsing on coral-algal rock or eating coral" (p. 399) can produce 1100–1600 metric tons of sediment per square mile per year. Frydl (1977) cautioned, however, that such calculations should take into account the fact that many parrotfish feed on sediment, and should, where possible, be based on the sediment produced by species such as *Sparisoma viride* which rarely feed on sand. Accordingly, Scoffin *et al.* (1980) estimated that bioerosion by this parrotfish off the west coast of Barbados occurs at a rate of  $34 \pm 5$  g/m<sup>2</sup>/y. In working with the same species off Bermuda, Gygi (1975) noted two other possible sources of error—the carbonate lost through the gills during feeding, and the sediment trapped in the algal growth on which the fish feeds. After correcting for the recycled sediment in the algal cover, Gygi estimated fish bioerosion to occur at a rate of 174 kg/ha/month. Ogden (1977), meanwhile,



assumed that half of the material excreted by *Scarus croicensis* off the Caribbean coast of Panama is recycled sediment, and on that basis calculated a sedimentation rate of 0.49 kg/m<sup>2</sup>/y.

It should also be pointed out that parrotfish appear to favor certain live corals, particularly the massive *Porites* off Palao (Motoda, 1940), Eniwetok Atoll and Fanning Island (Bakus, 1967), in the Eastern Pacific near Panama (Glynn *et al.*, 1972), Bermuda (Gygi, 1975), and Belize (pers. observ.).

*Crustaceans.*—The predominant bioeroder of this group is the barnacle—particularly *Lithotrya*, which occurs in the intertidal of the Great Barrier Reef (Otter, 1937) and Puerto Rico (Ahr and Stanton, 1973) and the shallow subtidal in water depths less than 1.5 m off Bermuda (Bromley, 1978). *Lithotrya* are abundant in Belize in the algal-covered rubble fields that are common on the reef crest of the barrier reef (pers. observ.). They appear to thrive under slightly turbulent conditions (Bromley, 1978).

Interestingly, *Lithotrya* tend to bore upward into calcareous substrates (Ahr and Stanton, 1973; Bromley, 1978). The borings are oval (Fig. 8a), measuring 5 × 8 mm and 7 cm long (Ahr and Stanton, 1973) to 7 × 5 mm and 3 cm long (MacGeachy and Stearn, 1976). Borings in the base of live coral heads tend to be inclined “so that the animal hangs downward” (MacGeachy and Stearn, 1976, p. 728). In rubble, however, *Lithotrya* appears to penetrate vertically into the coral skeleton. Some borings are found to have other orientations (Andre and Lamy, 1933).

Another characteristic of *Lithotrya* borings is a series of overlapping attachment plates (Fig. 8a, b) that are deposited in the boring whenever the individual molts (Andre and Lamy, 1933). Some of the basal plates, which are formed of calcite and deposited early in the boring, tend to be removed by the boring action of the barnacle (Bromley, 1978). This action appears to take place by mechanical abrasion “with the calcified plates that dot the surface of the peduncle [hollow base] and cover the capitulum [the head]” (Ahr and Stanton, 1973, p. 21).

Some other bioeroders of the crustacean group are crabs and shrimp (Warme, 1977). Hermit crabs—*Trizopagurus magnificus* and *Aniculus elegans*—feeding on the soft parts of *Pocillopora* on the Pacific coast of Panama were found to destroy branch tips at the rate of 10.3 mg dry wt/day and 1.24 mg dry wt/day, respectively.

#### Soft-Tissue Destruction

The degree of damage inflicted on the soft tissue of coral colonies by predators varies from minor, temporary injury, with almost no recognizable skeletal alteration (as is caused by some fish predators), to ex-

tensive and permanent damage, followed by encrustation or bioerosion by other organisms (such as the starfish *Acanthaster*). The devastating effect of *Acanthaster planci* on entire coral communities was first reported in the Red Sea (Goreau, 1964) and in the western Pacific Ocean (Barnes and Endean, 1964; Barnes, 1966; Chesher, 1969; Endean, 1969). This starfish can destroy large areas at one feeding because of its size—mean diameters range from 13.8 cm (Chesher, 1969) to 17–19 cm (Glynn, 1973)—and its ability to extrude its stomach through its mouth, which allows the starfish to cover and digest an area of soft tissue extending almost to its arm tips (D. Pawson, pers. comm., 1983). *Acanthaster* feeds on a wide variety of corals as well as hydrocorals (Glynn, 1974b), and only the corals in areas of heavy wave action appear to escape predation in a heavily infested area (Endean, 1974).

Estimates of the feeding rates of individuals vary from 12 m<sup>2</sup>/y off Guam (Chesher, 1969) to 5.3 m<sup>2</sup> and 5.4 m<sup>2</sup>/y in the eastern Pacific (Dana and Wolfson, 1970; Glynn, 1973). Population explosions of *Acanthaster* in recent times—700 were reported on one coral pinnacle of the Great Barrier Reef (Endean and Stablum, 1973a)—can lead to the destruction of entire coral coverings in some localities (Endean and Stablum, 1973b). Off Guam, for example, 90 percent of the corals in depths from low spring tide to the limit of coral growth were killed in a period of 2.5 years (Chesher, 1969). Off Okinawa, only 1–10 percent of the corals at the reef margin were eaten, compared with 20–50 percent on the reef flat, but some stations were almost “entirely devastated” (Nishihira and Yamazato, 1974, p. 595).

Another common predator is the polychaete *Hermodice carunculata*, which in the Caribbean favors *Porites porites* (Marsden, 1962), *Acropora palmata* (Glynn, 1962), dominantly *P. porites* and *P. astreoides* (Ott and Lewis, 1973) and *Acropora cervicornis* (Kaplan, 1982). Although this fireworm is known to feed on flat surfaces, it has the unusual feeding habit of folding its proboscis over the tips of branching corals and digesting the soft tissue, leaving behind clear white coral tips. In some areas it is capable of destroying one tip in about 24 hours (Kaplan, 1982). Ott and Lewis (1973) noted that large *Hermodice* “could consume up to 3 cm<sup>2</sup> of living coral tissue in a 3 h period” (p. 1651). In the Marshall Islands another polychaete *Eurythoe complanata* has been observed feeding on coral tissue (Hartman, 1954).

Cyanobacterial infections are also known to cause extensive damage to coral tissue (Antonius, 1973, 1981a, b; Garrett and Ducklow, 1975). The blue-green alga (cyanobacterium) responsible for this infection—known as black band disease (Antonius, 1981b)—was

only recently identified as *Phormidium corallyticum* (Rützler and Santavy, 1983) when corals were experimentally infected with this cyanobacterium. Corals that have succumbed to the disease are readily identified by the white zone devoid of tissue directly behind the advancing front or band of black *P. corallyticum* filaments (Rützler *et al.*, 1983). A variety of Caribbean corals have been found infected by black band disease. Dustan (1977) reported that the most susceptible species off Florida appear to be *Mycetophyllia ferox*, *Mycetophyllia lamarckiana*, *Montastrea annularis* and *Colpophyllia nathans*. Later Antonius (1981a) found a high incidence of this disease in *Diploria strigosa* and *Montastrea annularis*, off Florida, as well as several other localities.

Black band disease can spread at rates as high as 1 cm per day (Antonius, 1981a). Off Belize, it has been observed spreading at 3.1 mm per day and destroying about 14.1 cm<sup>2</sup> of tissue per day (Rützler *et al.*, 1983). *Phormidium corallyticum*, aided by bacteria and protozoans, appears to be active predominantly in water depths of 0.5–4 m, but has been observed at a maximum depth of 6 m off Belize (Rützler, pers. comm. 1983) and to 18 m off Florida (Dustan, 1977). Although *P. corallyticum* is a common phenomenon in shallow-water areas of the western Atlantic, there is still no information on how the disease is transmitted in nature. As yet, the disease has not been observed in Indo-Pacific corals (Rützler *et al.*, 1983).

Some corals contract white band disease, which is recognizable by the stark white band that appears behind the front of diseased tissue, which contains no "distinct accumulations of destructive agents" (Antonius, 1981b, p. 4). This disease occurs mainly in three species of western Atlantic corals: *Acropora palmata*, *Diploria strigosa*, and *Montastrea annularis* (Antonius, 1981b). Off St. Croix, the disease appears to affect mainly *A. palmata*, which is being rapidly killed off at the rate of 5.5 mm per day (over a three-month period) (Gladfelter, 1982). White band disease has been noted in pre- and post-storm-damaged *Acropora cervicornis* off Jamaica (Knowlton *et al.*, 1981) and storm damaged *A. cervicornis* and *A. palmata* off Antigua (Multer, pers. comm. 1983).

Fish constitute still another group of well-known coral predators (for a comprehensive review, see Reese, 1977). Those that feed on the live tissue of corals are mainly the butterflyfish (Chaetodontidae) and damselfish (Pomacentridae). The former family includes omnivorous species and plankton feeders along with coral feeders. Some species appear to depend almost solely on coral mucus for food (Hobson, 1974). Some butterflyfish have fine "bristle like" teeth (Reese, 1977, p. 270) particularly suited to nipping coral polyps, while

others suck out the polyps, and still others irritate the coral and then feed on the mucus released in response.

Damselfish appear to be more destructive than butterflyfish; permanent coral damage has been observed in the Caribbean (Kaufman, 1977), Australia (Potts, 1977), and the eastern Pacific (Wellington, 1982). These territorial species tend to bite the live coral surface repeatedly, and thus leave behind areas that are soon taken over by algal mats or "algal lawns" (Kaufman, 1977, p. 560). In the Caribbean, damselfish seem to prefer *Montastrea annularis* and *Acropora cervicornis*, whereas in the eastern Pacific, they favor *Pavona* sp. (Wellington, 1982). Apparently little or no damage is suffered by the coral skeleton during the feeding activity of damselfish, which in one month can convert 0.1 m<sup>2</sup> of live surface of *M. annularis* into an algal mat.

Many gastropods feed on the live tissue of corals (see, for example, Robertson, 1970). Two that have recently been studied in detail are *Coralliophila abbreviata* from the Caribbean and *Jenneria pustulata* from the Pacific coast of Panama. *C. abbreviata* appears to feed on coral tissue by means of chemical breakdown and proboscis pumping (Ward, 1965). It has been observed feeding on *M. annularis* (Ward, 1965), *A. palmata* (Brawley and Adey, 1982), and a number of other corals (Ott and Lewis, 1973; Miller, 1983). The damage reported ranges from minimal *in situ* (Ott and Lewis, 1973) to 16 cm<sup>2</sup>/animal/day in an aquarium (Brawley and Adey, 1982). The difference between these observations may be related to the concentration of fish predators on *Coralliophila* (Brawley and Adey, 1982). The cowrie *J. pustulata* feeds on the branching *Pocillopora* off the Pacific coast of Panama, where it has been observed destroying 5.26 metric tons/ha/year of coral (Glynn *et al.*, 1972).

Hermit crabs, as mentioned earlier, are well-known predators particularly *Trizopagurus* and *Aniculus*, which off Panama, scrape the tissue from and destroy *Pocillopora* branches at rates of 1.3 metric tons/ha./year and 0.09 metric tons/ha./year, respectively (Glynn *et al.*, 1972). In the Caribbean, the green reef crab *Mithrax sculptus* feeds on *Porites furcata* and *P. porites* by cutting polyps with its claws (Glynn, 1962, 1973).

Corals that prey on other corals by extruding mesenterial filaments form still another group of tissue destroyers (Lang, 1973). An interesting observation is that Caribbean corals can become established according to their place in the feeding-order hierarchy, so that slow growers like *Mussa angulosa* and *Scolymia lacera* are positioned at the top, and faster growers such as *Montastrea annularis*, acroporids, and *Agaricia* are near the base. Recent studies show more complex interspecific aggression strategies involving for example, the development of sweeper tentacles (Wellington, 1980;

Bak *et al.*, 1982), and variations in growth rates (Bak *et al.*, 1982).

It is almost impossible to recognize the agents of coral-tissue damage in fossil corals. Where only a small amount of tissue has been affected and has regenerated, it may not be possible to determine whether such damage occurred at all. In some cases, however, the presence of fine detrital sediment trapped in original skeletal cavities (Fig. 9) may indicate minor tissue destruction and recovery. Barnard *et al.* (1974) noted that "dissepiments [may be] commonly arched to accommodate trapped sediment" (p. 219), and thereby suggested that cavities were filled when the coral colonies were still alive. Apparently the detrital sediment can become trapped in temporarily damaged surfaces of live colonies and then becomes sealed into the skeleton after the polyps regenerate.

Needless to say, extensive coral-tissue damage will be readily recognized by the subsequent bioerosion of the coral skeleton. On the other hand, it will be impossible to determine what caused the tissue to be destroyed, or whether it was a biological or physical agent.

## GEOLOGICAL ALTERATION OF CORAL SKELETONS

### Mechanical Destruction

The mechanical destruction of coral communities during tropical storms is the single most important cause of catastrophic coral mortality (Stoddart, 1969). During periods of intensive water turbulence, coral colonies—both living and dead—are subject to breakage and extensive abrasion. The extreme damage inflicted on reef communities exposed to violent tropical storms has been documented in many reef areas, notably the Great Barrier Reef (Moorhouse, 1936; Stephenson *et al.*, 1958), Belize (Stoddart, 1963, 1969; Rützler and Macintyre, 1982), Puerto Rico (Glynn *et al.*, 1964), Fiji (Cooper, 1966), Florida (Ball *et al.*, 1967; Perkins and Enos, 1968), Jamaica (Woodley *et al.*, 1981), and the U.S. Virgin Islands (Rogers *et al.*, 1982, 1983). An excellent review of storm damage to reef areas has been compiled by Stoddart (1971).

The effects of a hurricane can be particularly awesome: during Hurricane Hattie in October, 1961, a section of the Belizean barrier reef 8 km in length was "stripped of living corals" (Stoddart, 1969, p. 451), and the shallow fore-reef spur and groove formations were entirely destroyed, along a 40-km section of this reef. The hurricane passed over Rendezvous Cay reef which suffered 75–80 percent damage in the shallow reef zones; in addition, 100 percent of *A. cervicornis* was lost and 80 and 50 percent of *A. palmata* and *M. annularis*, respectively, destroyed.

The reefs of Discovery Bay, Jamaica, experienced similar damage after Hurricane Allen—the most powerful storm to be recorded in the Caribbean—passed immediately north of this reef in 1980 (Woodley *et al.*, 1981). Here the shallow *A. palmata* framework was completely destroyed, with coral rubble mantling the breaker zone and reef flat. Interestingly, in one area *A. cervicornis* at a depth of 6 m was almost entirely destroyed, whereas heads of *M. annularis* suffered only a 9 percent loss. Physical damage extended to depths of 50 m, however, where platy *Agaricia* spp. were broken and many other species were damaged by the impact of reef debris and scouring sand.

Characteristically, fast-growing corals such as *A. cervicornis* sustain greater damage in shallow reef areas than do slower growing head corals such as *M. annularis* (see Moorhouse, 1936; Ball *et al.*, 1967; Perkins and Enos, 1968; Rogers *et al.*, 1982). Another characteristic of storm-damaged reefs is the subaerial accumulation of extensively water-worn and fractured coral debris, known as "shingle ridges" (Stoddart, 1963, p. 107). Although they are common in the Caribbean, the most spectacular storm ridge deposits are found in the Pacific. Baines *et al.* (1974), for example, reported that a "storm beach 19 km in length and up to 4 m in height" (p. 485) formed after a cyclone hit Funafuti Atoll in 1972.

A high percentage of coral colonies are able to recover by growing over the fractured or abraded surfaces left behind by severe storms. The extent of recovery depends largely on the species of coral and the depth of water in which it grows. Bak and Steward-van Es (1980), for example, demonstrated that the regenerative capacity of corals varies greatly with respect to species and water depth—*M. annularis* being at the high end (8–12 m), and *Agaricia agaricites* (8–12 m), *Porites astreoides* (18–23 m), and *A. agaricites* (25 m) being at the lowest end. Off St. Croix, fractured branches of *A. palmata* "healed at a rate of 0.01 to 0.05 cm/day" (Rogers *et al.*, 1982, p. 538). Within a period of less than seven months, small branches up to 2 cm were sprouting from the healed fractured surfaces.

Similarly, *A. cervicornis* off Belize was able to recover by growing over fractured tips that had died back and developed a cover of filamentous and encrusting coralline algae (pers. observ.). As was noted in the reefs off St. Croix, the new coral grew over the algal cover, sealing it within the skeletal structure (Rogers *et al.*, 1982). Apparently once the damaged area becomes covered, the apical polyp does not regenerate at the top of the tip, but develops on the flank of the bulbous overgrowth to form a new offshoot tip (Fig. 10).

Although storm damage is greatest among the branching corals such as *A. cervicornis* and *A. palmata*, these species are usually able to survive the breakage

and transportation and to reestablish themselves as new colonies. This ability is a well-known dispersal characteristic of *A. cervicornis* (Shinn, 1976; Gilmore and Hall, 1976; Tunnicliffe, 1981; Rützler and Macintyre, 1982). In sections through coral colonies the fractured surface will appear as a sharp break in the corallite growth pattern, which, if overgrown, will show up as a buried hiatus. In branching corals such as *A. cervicornis*, the break may show up as a sudden termination in the growth of the apical corallite (Fig. 11). Evidence of bioerosion or encrustation buried within a coral skeleton may also indicate a period of partial destruction and the subsequent recovery of the damaged area.

Heavily abraded coral colonies that are unable to recover or that are extensively water-worn after death are typically well rounded and lack all delicate surficial features (Fig. 12a, b). In addition, water-worn colonies commonly exhibit micritization at the outer edge—that is, a dense microcrystalline rim forms as the result of the infilling of endolithic borings by secondary carbonate (Fig. 13). This feature—originally described in water-worn mollusc grains as “micrite envelopes” (Bathurst, 1966)—has been well documented in carbonate sedimentological and petrographic studies (see Alexandersson, 1972). Another prominent characteristic of water-worn coral colonies, particularly the more porous skeletons of genera such as *Porites*, is that fine detrital sediment tends to be packed in the outermost skeletal cavities (Fig. 14).

Abrasion of the live surface of corals accompanied by minor skeletal damage will be difficult to identify after a colony recovers unless detrital sediment becomes sealed within skeletal cavities (Fig. 9).

Two other causes of the death of coral colonies are exposure during unusually low tides and smothering by heavy sedimentation; in both cases, the tops of coral colonies are affected. In areas near the northern or southern limits of reef development, incursions of cold water can also kill off entire reef communities and thus

pave the way for extensive bioerosion and cementation of the coral colonies (Lighty *et al.*, 1980).

### Cementation

Submarine cements have been well documented from numerous tropical reef areas (see Macintyre, 1984), but the processes responsible for the precipitation of these cements are still poorly understood. Submarine cements consist mainly of dense to chalky, submicrocrystalline to microcrystalline magnesium calcite (14–19 mole percent  $MgCO_3$ ) that “coats, infills and forms a matrix around various reef components” (Macintyre, 1977, p. 514). Except for one instance in the Red Sea (Friedman *et al.*, 1974), aragonite is generally a minor component of coral reef cements and is usually found as a rim cement in the skeletal cavities of corals (see Macintyre, 1977).

Magnesium calcite tends to be best-developed in coral-reef facies that have accumulated slowly under conditions of high agitation (see James *et al.*, 1976; Macintyre, 1977). These submarine magnesium calcites can occur as multicyclic cemented agglomerate or pavement limestones and as cement crusts and infilled rims (Macintyre, 1977, 1983). On the other hand, sediment floors of quiet water lagoonal environments generally show little evidence of submarine lithification.

Pavement limestone is generally a well-indurated agglomeration consisting of a high-energy coral-reef assemblage that has been extensively bored and filled and surrounded by micritic (less than 30  $\mu m$ ) calcite. In many cases, most of the skeletal framework has been lost as a result of multicyclic boring and lithification. In both these shallow-water pavement limestones and in slowly accreting limestones of the deeper fore-reef slopes, the skeletons of coral colonies can be converted to micritic limestone with “floating” remnants of the original coral (Fig. 15). Under conditions of slow accumulation, much of the evidence of a reef’s original framework may be destroyed.

The magnesium calcite cement crust and infilled rims are of particular interest because they generally exhibit

Figure 12.—Photomicrographs of *Montastrea cavernosa*. a) Living colony with well preserved surface details of the corallites, Inner Fore Reef, Carrie Bow Cay, Belize. b) Smooth abraded surface of a colony from a storm-ridge deposit, Discovery Bay, Jamaica.

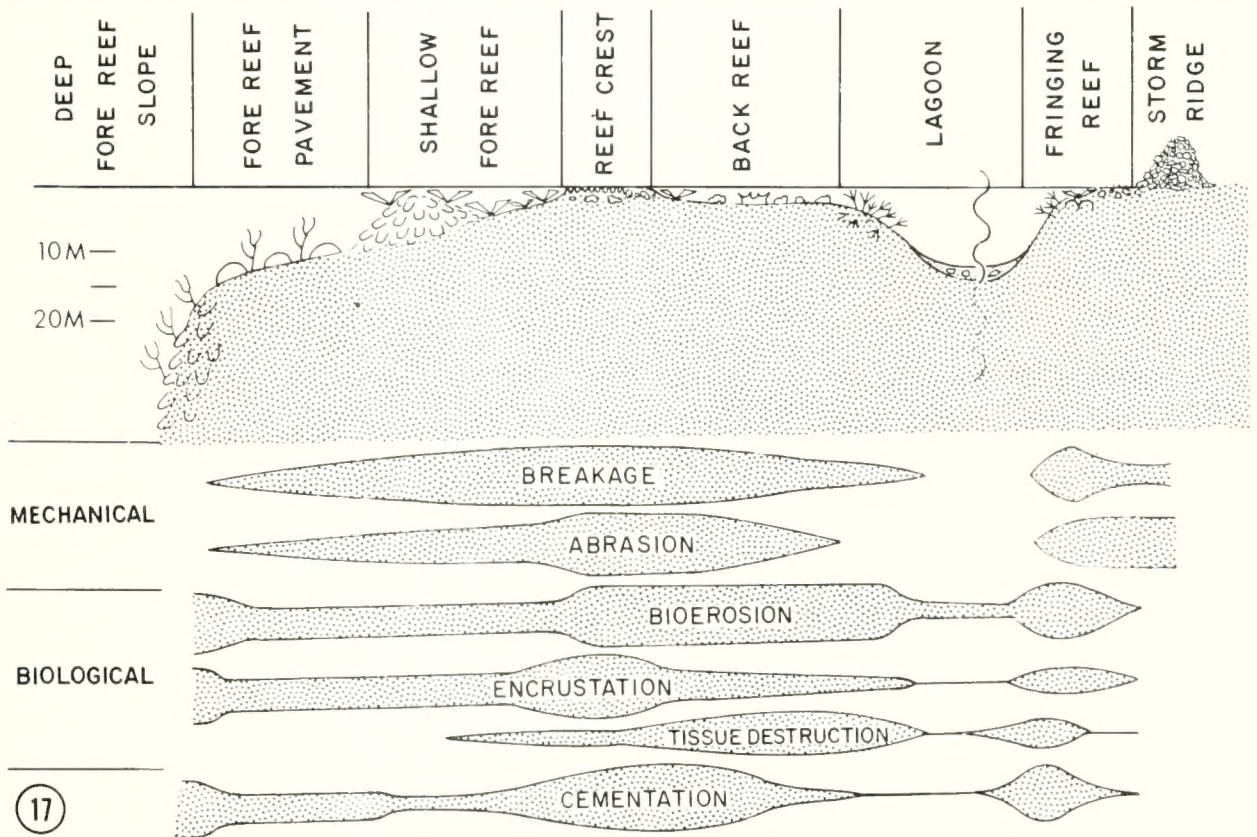
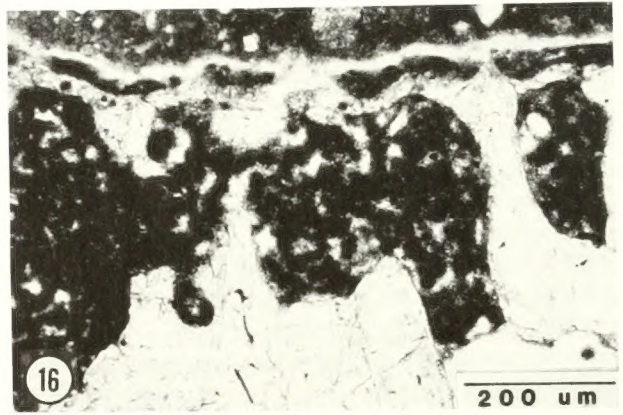
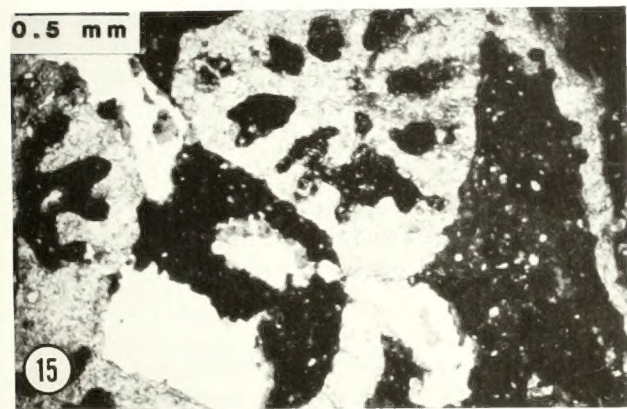
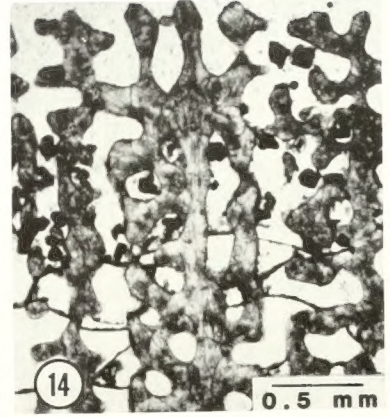
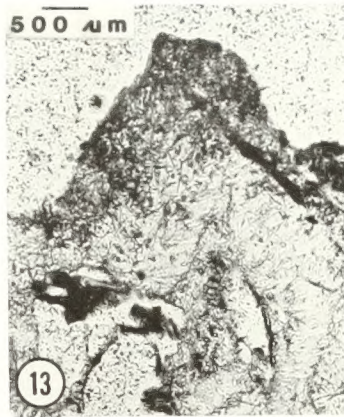
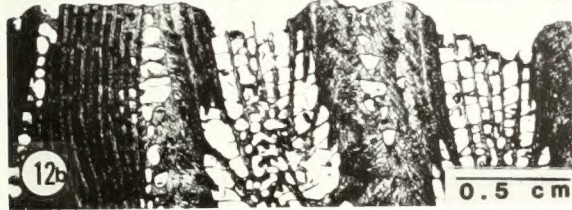
Figure 13.—Micrite rim formed around the outer edge of a water-worn colony of *Montastrea annularis*, beach, Carrie Bow Cay, Belize. Opaque rim formed by secondary carbonate infilling of endolithic borings.

Figure 14.—Water-worn *Porites astreoides* exhibiting an outer zone of sediment packing of skeletal cavities, storm-ridge deposit, Discovery Bay, Jamaica.

Figure 15.—Photomicrograph of extensively bored and submarine lithified colony of *Siderastrea siderea*, Fore-reef coral head facies, Galeta Reef, Panama. Remnants of the original coral skeleton “float” in a matrix of dense sediment-rich submicrocrystalline magnesium calcite.

Figure 16.—Photomicrograph of magnesium calcite cement crust and infilled rim on *Acropora palmata*, Reef *A. palmata* facies, Galeta Reef, Panama. Note cement zonation from sediment-rich crust to peloidal infill of skeletal cavities at the outer edge of coral.

Figure 17.—Schematic profile extending from the outer edge of a barrier reef to a fringing reef bordering a lagoon, showing the relative distribution of processes responsible for preburial and shallow-subsurface alteration of corals.



"a distinct zonal pattern in the outer edge of the coral that, if recognized in the fossil record, could provide evidence of submarine lithification" (Macintyre, 1983, p. 582). The cement crust is commonly 1–3 cm thick, and it coats and infills the encrusting biota on the coral surface. It also penetrates the outer edge of the coral skeleton to less than 2 cm, unless the coral is bored. The sediment-rich outer crust, which consists of a dense interlocking crystal mosaic of micritic magnesium calcite grades into a sediment-free magnesium calcite infilling of the coral skeletal cavities. This outer infilling has a distinct peloidal or pelleted texture (diameter of 20–60  $\mu\text{m}$ ; Fig. 16), which tends to be well developed "in restricted or isolated microcavities" (Macintyre, in press) and is a diagnostic characteristic of submarine cements. The inner edge of the magnesium calcite infilling consists of a porous or sugary micrite that also "commonly exhibits a peloidal or clotted texture" (Macintyre, 1983, p. 582). Within the porous magnesium calcite zone, and well within the coral skeleton, acicular aragonite rim cement up to 100  $\mu\text{m}$  thick coats the lining of original skeletal cavities (Macintyre, 1977). This aragonite cement occurs as a "syntaxial overgrowth of the sclerodermites in the coral skeleton" (p. 508). Because spherulitic clusters of aragonite needles form the sclerodermites, the aragonite cement radiates at widely varying angles into the coral cavities (Macintyre, 1977, fig. 4d).

The zonal pattern of submarine cements, particularly the gradation from a sediment-rich crust into a peloidal or pelleted skeletal infilling, could be useful in identifying submarine cements in the fossil record. Even in pavement limestones, restricted cavities such as the skeletal openings or borings commonly contain the diagnostic peloidal texture.

The dense cement rims may play an important role in the later diagenesis of the coral skeleton. This dense magnesium cement coating can, under subaerial conditions, become altered to calcite, with no significant change in the dense crystalline texture. Because this barrier is impervious to the interstitial waters, it can inhibit the alteration of the aragonitic skeleton (Adey *et al.*, 1977).

### CONCLUSIONS

Skeletal alteration is a widespread and rapidly occurring phenomenon in modern scleractinian corals. Much of it takes place while the colony is still alive. The extent of skeletal alteration depends on the reef habitat in which the coral grows or the environment to which it is transported after death. In turn the habitat determines both the distribution of processes responsible for coral-skeleton alteration and the amount of time that the coral skeletons are exposed to these elements of destruction.

The general distribution of the processes responsible for coral alteration can be presented in an idealized profile extending from the outer edge of a barrier reef to a fringing reef bordering a lagoon (Fig. 17). As might be expected, the area of most extensive coral alteration occurs in the shallow turbulent waters of the reef-crest zone. Here mechanical destruction and biological alteration are highly concentrated. In addition, the substrate is constantly swept free of sediments and tends to become well indurated by submarine cements. The processes of alteration are also highly active at the outer edge of the inshore fringing reef. The deep fore-reef slope, another area of slow framework accretion, is a site of relatively high biological alteration and cementation but is too deep to receive any significant mechanical damage.

The lagoon (Fig. 17), an area of relatively rapid accumulation of sediments—tends to contain some of the best-preserved corals, as well as highly altered corals that have been transported here. Well-preserved corals may also be found transported well below the depths associated with coral alteration processes to the deep fore-reef talus deposits not considered in this review.

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POST-DEPOSITIONAL DIAGENESIS OF METASTABLE  
CARBONATES: AN OVERVIEW

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## ABSTRACT

Aragonite and magnesian calcite are the dominant minerals of modern, shallow-marine carbonate sediments. In most sedimentary sequences these minerals alter quickly to more stable carbonate phases. The diagenetic environments in which these alterations take place can be classified by the type of pore waters in the sediments. These pore waters include: 1) fresh (meteoric) water; 2) saline brines; 3) mixed fresh water and sea water; 4) sea water below the carbonate compensation depth; and 5) water buried and modified during basin subsidence. Alterations which take place in these diagenetic environments may lead to mineralogically similar end products (usually resulting in the dissolution of the original mineral and/or its replacement by calcite or dolomite) which vary widely in morphological, petrographic and geochemical detail. Numerous techniques are employed to study these details in order to differentiate various diagenetic environments and establish original mineralogy. The techniques include petrographic observations, analyses of trace and minor elements, determination of stable isotope ratios of carbon, oxygen and strontium, and study of solid and fluid inclusions. Diagenetic alterations may enhance, modify or destroy primary skeletal characteristics and confuse their interpretation in fossil cnidarians as well as in other types of marine skeletons which were originally composed of metastable carbonate minerals.

## INTRODUCTION

Shallow-water marine carbonate sediments are composed of metastable minerals that precipitate organically and inorganically from sea water. Their alteration to stable minerals is an extremely complicated process which is not yet fully understood. This article is a review of the major factors controlling alteration and the resulting products of carbonate diagenesis. The review is necessarily brief and merely serves as an introduction to several of the more detailed diagenetic topics discussed in other papers (for example Sandberg, this volume and Schroeder, this volume).

The bulk of shallow marine carbonate sediments are composed of aragonite and magnesian calcite (calcite with more than 4 or 5 mole percent  $MgCO_3$ ). Although both minerals are generally considered to be metastable, sedimentary aragonite is known to occur in lower Paleozoic rocks (Grandjean *et al.*, 1964) and obviously may persist for hundreds of millions of years. Considerable thicknesses of aragonitic sediments of Tertiary age occur at depths up to 700 m beneath Enewetak atoll (Schlanger, 1963) attesting to the occasional persistence of the mineral. Key factors in aragonite preservation appear to be the isolation of aragonite from water dissimilar to that in which it was formed, for example by encasement in bitumen. In most cases, however, aragonite is exposed to other than normal shallow marine water early in its history and alteration processes begin. These processes lead to mineralogical stabilization and the production of calcite and dolomite, the common carbonate phases of the geologic record.

In the following sections we will review the factors that affect carbonate diagenesis, the settings in which diagenesis occurs as characterized by types of diagenetic waters, some of the products of diagenesis which may be similar despite having formed by different mechanisms, and the methods currently in use to determine early stages of diagenesis and original mineralogy.

FACTORS INFLUENCING THE ALTERATION  
OF METASTABLE CARBONATES

It is premature to presume all the factors that control aragonite and magnesian calcite alteration in sedimentary settings are known. To date, the best summary of carbonate diagenesis available is in *Carbonate Sediments and Their Diagenesis* by R. G. C. Bathurst (1975). Despite the decade of research and progress made since the publication of this text, there is still a great deal left unknown about carbonate diagenesis. But certainly many of the major factors are understood. These include: 1) mineralogy and crystal chemistry; 2) chemistry of surrounding water; 3) water movements; 4) dissolution and precipitation rates; 5) grain size; and 6) various interactions with organic substances.

## Mineralogy and Crystal Chemistry

Both aragonite and magnesian calcite are more soluble than calcite. The trace and minor element content of magnesian calcite varies more than aragonite and its solubility varies accordingly. Recent experimental evidence (Walter, 1983) suggests magnesian calcite with about 12.5 mole percent  $MgCO_3$  has the same solu-

bility as aragonite. Magnesian calcites containing more magnesium have considerably higher solubilities (Fig. 1) than either calcite or aragonite. The lattice structures of aragonite and calcite are arranged so that calcium accommodates small cations and aragonite accommodates large cations. For example, calcium, with an ionic radius of 0.99 angstroms fits well into either the orthorhombic aragonite crystal lattice or the rhombohedral calcite lattice. Metallic elements with larger ionic radii (such as strontium or barium) substitute for calcium in aragonite. Those with smaller ionic radii (such as magnesium, manganese, and iron) substitute for calcium in calcite. These minor element substitutions have considerable effect on the solubility of aragonite and calcite. Tracing the minor element changes during diagenesis has proven useful in determining subtle alterations.

#### Water Chemistry

Although aragonite and magnesian calcite are stable in warm, shallow seawater, they may alter quickly once placed in porewater of some other composition. In a geologic context, it is common to find the original pore fluids surrounding metastable carbonates replaced by fresh water, brines, mixed waters, deep oceanic water, or waters that have altered during sediment burial. In these waters both major and minor constituents may have profound effects on the precipitation and dissolution characteristics of carbonate minerals. Major factors are dissolved  $\text{CO}_2$ , temperature and pressure. Important minor constituents are magnesium/calcium ratios (Folk, 1974), dissolved ammonia (Towe and Malone, 1970), and dissolved sulfate (Baker and Kastner, 1981). Some of these factors are discussed in more detail in following sections.

#### Water Movement

Water movement is critical to the removal and re-supply of dissolved constituents during carbonate diagenesis. Although, in theory, aragonite can dissolve in and calcite precipitate from stagnant fresh water, in actuality this process occurs much faster in areas of active water flow. Particularly important in this process is the variability of dissolved  $\text{CO}_2$  in water which greatly affects its ability to carry dissolved  $\text{CaCO}_3$ . Although some  $\text{CO}_2$  may be from the atmosphere, a particularly rich source of  $\text{CO}_2$  in ground water is soil gas. Water movement is also important because so little  $\text{CaCO}_3$  is dissolved in water that it takes large volumes of water (*i.e.*, water flow) to move significant amounts of limestone. Several authors (Dunham, 1969; Bathurst, 1975) have pointed out that it takes tens of thousands to hundreds of thousands of pore volumes of water to fill a pore with calcite. It is therefore readily

apparent that the rate of water movement may control the rate of dissolution and precipitation of carbonate minerals.

#### Dissolution and Precipitation Rate

The dissolution and precipitation rates of carbonate minerals vary widely and may exert some control on resulting fabrics. In some instances precipitation may follow dissolution almost immediately resulting in considerable retention of original fabrics and structures in the new mineral. Rapid precipitation may be accompanied by rapid nucleation of new crystals. Because large crystals are more characteristic of relatively slow growth and few nucleation sites, the resulting fabric may be characterized by many small crystals rather than few large crystals. Rapid recrystallization, with its resultant fine-grained texture, tends to favor the preservation of original textures because the resulting fabric tends to be fine-grained. One of the best documented cases of this effect is the tendency for magnesian calcite skeletal fragments to be better preserved than those that are aragonite during fresh-water diagenesis. It has been known for almost twenty years that magnesian calcite alters to calcite more quickly than aragonite in the presence of fresh water (Friedman, 1964; Land, 1967). Magnesian calcite recrystallization releases magnesium to surrounding water while retaining most calcium. The resulting increase in the Mg/Ca ratio of water during the alteration of magnesian calcite is an example of incongruent dissolution. Along with that rapid stabilization, skeletal magnesian calcites preserve more skeletal detail than aragonite during alteration (Sandberg, this volume).

#### Grain Size

Grain size has a dramatic effect on the solubility of carbonate grains that are less than one micron in diameter. Chave and Schmaltz (1966) illustrated the ef-

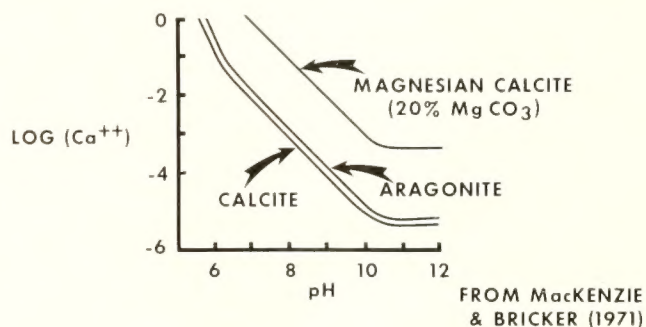


Figure 1.—Illustration of the relative solubilities of calcite, aragonite and magnesian calcite. The solubility of magnesian calcite is a function of magnesium content and Walter (1983) considered magnesian calcite with about 12.5%  $\text{MgCO}_3$  to have a solubility similar to that of aragonite.

fect of grain size on the activity of calcite (Fig. 2), the activity being related to the solubility. The solubility of calcite increases exponentially with decreasing grain size below about one micron in diameter (for examples see Bathurst, 1975, chapter 1). This finding is particularly significant when combined with the observation that most modern carbonate grains and skeletal structures are composed of subcrystals that approach an effective diameter of about one micron. Ooid grains, for example are composed of needle-shaped, aragonite subgrains, or nannograins of Loreau and Purser (1973), a few microns long and often less than a micron wide. Similar sized magnesian calcite needles form veneers on the surfaces of some foraminifera (Towe and Cifelli, 1967). *Acropora palmata* and many other corals construct their skeletons from aragonite subgrains with at least two dimensions much less than one micron (James, 1974). Even echinoderm grains, that are petrographically recognized because they behave optically like large single crystals, may be composed of subcrystals (Towe, 1967). So too are most, if not all, marine carbonate sediments composed of ultrastructural elements which are of a size small enough to affect their solubility.

#### Organic Matter

The role of organic substances in carbonate diagenesis is not very well understood, either as they may affect precipitation or dissolution. The works of Mitterer (1971), Suess (1970), Suess and Fütterer (1972) continue to be the basis for and understanding of pos-

sible non-biological relationships between organic constituents of sea water and carbonate precipitation. Some amino acids, particularly aspartic acid and glycine are commonly associated with organically and inorganically precipitated carbonates and may act as a catalyst or template to aid nucleation.

Shearman *et al.* (1970) suggested that the organic matrix of aragonitic ooids may serve as a template for later replacement by calcite. In this way an organic matrix may passively serve to control later diagenetic fabrics. But Sandberg (1975) cites evidence for little selectivity in calcite replacing Pleistocene aragonitic ooids. Earlier studies by Hudson (1962) suggest that inclusions of original organic matter in pelecypod shells may help preserve skeletal detail. However, a review of this material by Sandberg (*pers. comm.*, 1983) suggests the inclusions are preserved in calcite that has lost most of the ultrastructural detail of the original skeletal aragonite.

As organic matter changes with time and temperature it releases products that may interact with skeletal carbonates. In particular,  $\text{CO}_2$ ,  $\text{H}_2\text{S}$ , and organic acids may make formation waters more acidic, promoting dissolution of carbonate minerals. Aliphatic acids and acetic acids have been found in significant concentrations in some subsurface waters near hydrocarbon reservoirs (Surdam *et al.*, 1982). Organic matter may also act indirectly to produce large amounts of  $\text{H}_2\text{S}$  and  $\text{CO}_2$  by reaction with minerals. Orr (1974) has suggested that methane may react with dissolved sulfate to produce  $\text{H}_2\text{S}$  and  $\text{CO}_2$  in the subsurface at elevated temperatures. This mechanism could be responsible for the remobilization of large amounts of calcium carbonate at depth.

Although organic substances are generally considered important, much more documentation of specific organic/inorganic interactions is necessary to establish their significance to carbonate diagenesis.

#### FACTOR INTERDEPENDENCE

The factors affecting carbonate diagenesis described above are by no means independent of each other. In any given setting where alteration is taking place, all of these factors contribute in various proportions to the diagenetic milieu. Rather than describe the endless combinations and proportions that these factors might contribute to diagenesis, researchers have tended to describe a particular style of diagenesis by the characteristics of water involved during alteration. This has given rise to phrases such as "fresh-water alteration," "phreatic diagenesis," and "mixing zone dolomitization."

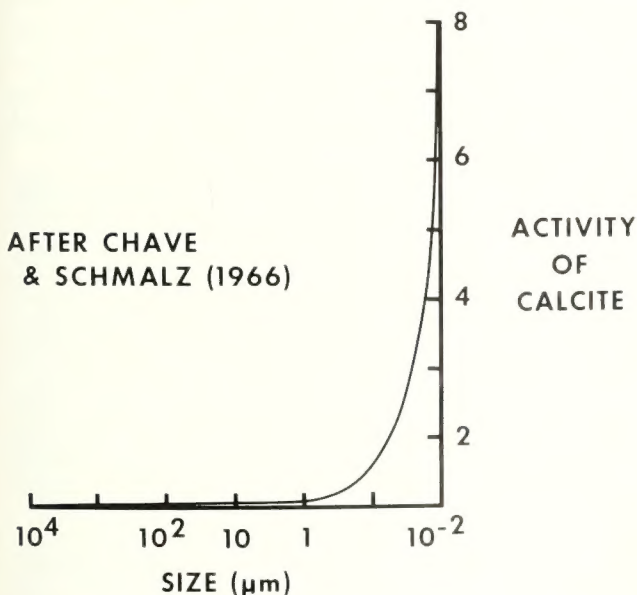


Figure 2.—The solubility of calcite as a function of grain size. Subgrains, or nannograins, common to the ultrastructure of most modern carbonate sediments fall near the size range characterized by increased solubility due to small grain size and high surface area.

## DIAGENETIC WATERS

Water of any composition may be involved in carbonate diagenesis, but there are six general categories of water that are commonly cited in studies of the alteration of carbonate sediments. These are: 1) shallow sea water; 2) fresh water; 3) brines; 4) mixed waters; 5) deep sea water; and 6) burial water. Diagenesis in shallow marine water has been covered previously (Macintyre, this volume) so that this outline deals briefly with the last five types of water and the diagenetic settings in which they occur.

### Fresh Water

Fresh-water diagenesis is the longest studied and best understood of the types of diagenesis to be described here. An excellent review of early, fresh-water diagenesis is presented by Longman (1980). He noted that the fresh-water diagenetic environment may be divided into two zones following common hydrologic usage, a zone above the water table called the vadose zone and that below the water table termed the phreatic zone. The differentiation of these diagenetic zones is usually based on subtleties of cement morphology (Halley and Harris, 1979). Both zones have several characteristics in common. These include the replacement of aragonite by calcite, recrystallization of magnesian calcite to calcite, development of molds (usually after aragonite) and the precipitation of calcite cement. Aragonite is replaced by dissolution and precipitation of calcite on a variety of scales. If replacement involves the development of visible (with the light microscope) pore space the process is dissolution and cementation. If the scale of replacement does not develop visible porosity the process is termed neomorphism (Folk, 1965). Neomorphic replacement of aragonite by calcite often preserves more detail than dissolution/cementation, usually in the form of fine inclusions in the calcite outlining former grain characteristics (Fig. 3). However, even neomorphism involves general coarsening of the fabric and considerable loss of petrographic detail (Sandberg, this volume). Much more detail is preserved during the alteration of magnesian calcite to calcite in fresh water. The development of molds or visible porosity rarely occurs. Early studies of magnesian calcite alteration identified fresh-water alteration by geochemical methods because petrographic changes were not evident (Gross, 1964). Dissolution and reprecipitation occur on such a fine scale that alteration is often recognized only on the ultrastructural scale (Buchbinder, 1979).

### Brine

The alteration of carbonate sediments in brines has received considerable attention, and is particularly well

known in the Holocene from studies of carbonates in coastal brines developed along the arid shores of the Persian (Arabian) Gulf (see several papers in the volume edited by Purser, 1973, and the most recent treatment by Patterson and Kinsman, 1982). In these areas aragonite is dissolved and dolomite is precipitated. Illustrations by Illing *et al.* (1965) suggest that aragonite skeletons are left as molds during this process and skeletal detail is destroyed. However, most studies of carbonate alteration in this diagenetic environment have dealt with details of geochemistry and little attention has been given to petrographic changes in the sediments. The Persian Gulf data indicate that dolomitization in these sediments occurs because of unusually high ratios of magnesium to calcium in the surrounding water. These elevated ratios result from the widespread precipitation of calcium sulfate as gypsum or anhydrite which removes calcium from pore fluids thus elevating the magnesium/calcium ratio.

### Mixed Waters

Mixing zones have become recognized as active zones of carbonate dissolution and precipitation. Runnells (1969) pointed out that mixed fresh water and sea water may be undersaturated or supersaturated with respect to a variety of carbonate minerals depending on the original compositions of the unmixed waters. A number of authors have documented evidence for the replacement of calcite and aragonite by dolomite in mixing zones (Hanshaw *et al.*, 1971; Badiozamani, 1973; Land, 1973a,b). Massive dissolution of calcite is occurring today in mixing zones along the eastern coast of the Yucatan Peninsula (Hanshaw and Back, 1980). Along portions of the coast, areas of Pleistocene limestone several meters thick and hundreds of meters wide have been removed by mixing-zone dissolution. Below

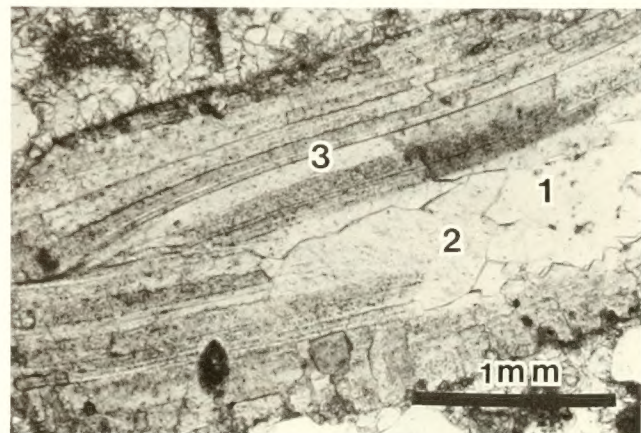


Figure 3.—Calcite-replaced mollusk fragment from the Pleistocene Miami Limestone. Originally aragonite, area 1 has dissolved leaving pore space, area 2 has filled with calcite cement, and area 3 has been neomorphosed and preserves some skeletal details.

the land surface, vuggy porosity and caverns form in the mixing zone. In addition, Ward and Halley (1982) have shown that dolomite has formed in the Yucatan mixed-water areas. The geochemistry of these mixed waters, studied by Back *et al.* (1976) suggest that mixtures of sea water with Yucatan aquifer fresh water produce a zone where the water is undersaturated with respect to calcite and oversaturated with respect to dolomite. It is in this zone that calcite dissolution and dolomitization takes place (Fig. 4).

#### Deep-Sea Water

Although metastable carbonates are quite stable in shallow sea water, the deep sea is generally undersaturated with respect to aragonite and, deeper still, is undersaturated with respect to calcite. Shallow-water carbonate sediments may be transported by a number of transport mechanisms or submerged into deeper waters where they may be dissolved or altered. Here they may take on the petrographic and chemical characteristics surprisingly similar to those that develop during fresh-water diagenesis (Schlager and James, 1978). These characteristics include alteration to calcite, dissolution of aragonite, loss of magnesium from magnesian calcite and calcite neomorphism. There is some evidence that dolomite may form as a cement or as a replacement mineral in the deep sea below the level of calcite saturation. Deep waters are supersaturated with respect to dolomite and may explain the dolomitization of Miocene corals on Enewetak Atoll (Schlanger, 1963; Saller, 1984).

#### Subsurface Waters

Perhaps the least known environment of alteration occurs when metastable carbonates are buried deeply before alteration. Burial diagenesis has been so little

studied because access to the environments of burial diagenesis is limited by all the difficulties associated with subsurface studies (Scholle and Halley, in press). At depth, diagenesis is bolstered by increased pressure and temperature but is limited by the sluggishness of water circulation. Nevertheless, pressure dissolution and cementation, compaction, dolomitization and fluid alteration by organic acids, CO<sub>2</sub>, hydrocarbons, H<sub>2</sub>S, and other temperature and pressure related processes and products clearly alter carbonate minerals at depth. The study of burial diagenesis in carbonate rocks received a great boost from the Deep Sea Drilling Project which made available cores through great thicknesses of carbonate sediments that had never been exposed to fresh water. Studies of these cores showed that burial diagenesis requires tens of millions of years and hundreds of meters of burial to convert deep-sea calcite sediments to chalks (Schlanger and Douglas, 1974; Matter *et al.*, 1975). Schmoker and Halley (1982) show a persistent decrease in porosity of shallow-water carbonates of the south Florida platform suggesting that burial processes are also mainly responsible for porosity loss in shelf carbonates. However, the specific processes responsible for diagenetic changes associated with porosity loss and the petrographic alterations associated with deep, subsurface, diagenetic changes are still subjects of considerable research and debate (Scholle and Halley, in press).

#### DISCRIMINATING DIAGENETIC PRODUCTS

The alteration of metastable carbonates in differing diagenetic environments leads to a variety of products that may resemble each other in considerable detail. It is the pursuit of the carbonate petrologist to determine the original mineralogy and diagenetic conditions from which these final products evolved. A number of geochemical approaches are in wide use or are rapidly gaining acceptance as methods for determining earlier diagenetic conditions. These generally fall into three categories: trace and minor element analyses; stable isotope studies; and inclusion analyses. Although these techniques have been primarily used in the study of carbonate cements, their application to studies of skeletal carbonates should be equally productive.

#### Trace and Minor Elements

Trace and minor element distributions in carbonates often reveal patterns not readily visible during light microscopy. They also may be used to estimate compositions of the fluids involved in diagenesis. Petrographic characteristics of carbonate rocks are often enhanced by staining techniques or through cathodoluminescent petrography, both of which reflect elemental distributions in carbonate minerals. The staining techniques

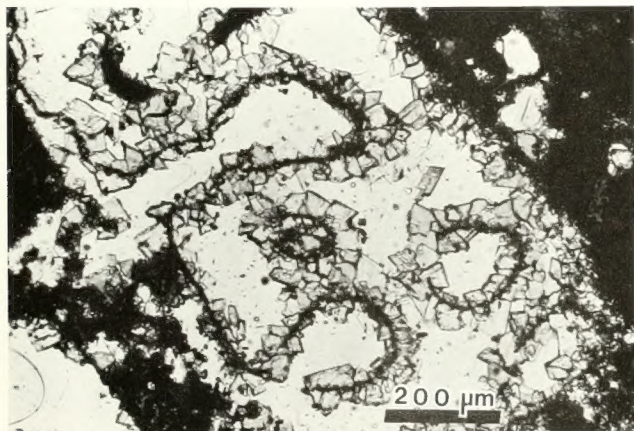


Figure 4.—Coral fragment from Pleistocene, mixing-zone dolomite of the east coast of the Yucatan Peninsula. The coral septa have been replaced by transparent dolomite rhombs.

for iron described by Friedman (1959) have proved among the most useful. Although not the main point of their paper, James and Klappa (1983, fig. 16) illustrate the use of cathodoluminescent petrography to differentiate skeletal elements from cement in archeocyathids and echinoderm fragments.

A more quantitative approach to trace and minor element geochemistry of carbonate cements suggests that the concentration of an element in a carbonate mineral may be directly related to the concentration of that element in the precipitating water at a specified temperature. The concentrations of magnesium, strontium, sodium, iron and manganese in calcite have been used to estimate original concentrations in diagenetic waters. This approach received considerable attention during the past fifteen years and appears to be applicable to near surface processes, especially for early diagenetic changes in fresh water (Benson, 1974) and sea water (Kinsman and Holland, 1969). However, the effects of time and temperature on incorporation of cations in calcite are still subject to question and may not always be predictable (Baker *et al.*, 1982). It remains to be determined to what level of detail trace and minor element studies may be extended.

#### Stable Isotope Studies

Two approaches to diagenesis have evolved from stable isotope studies of carbonate rocks. One approach is to establish constraints on diagenetic conditions based on stable oxygen and carbon isotope ratios. The other is to estimate the timing of diagenetic events based on known temporal variation of stable strontium isotope ratios in sea water.

Oxygen and carbon isotope analyses have proven extremely useful in discriminating types of diagenetic waters and the imprints they leave on carbonate sediments. Hudson (1975 and 1977) summarizes the variability of analyses in carbonate rocks and outlines the major trends of diagenetic alteration. These include diagenesis in waters described above as well as some special situations such as carbonates derived from the oxidation of methane and fermentation of organic matter. Major trends produced during deep-sea alteration, burial diagenesis, or fresh-water diagenesis are apparent; brine and mixing zone alteration are not. Overlap between trends remains a problem in many cases, but these isotope ratios remain one of the most powerful tools used to discriminate different types of carbonate diagenesis.

Several authors have published estimates of the variation of stable strontium isotope ratios in sea water during the Phanerozoic. The most recent of these, that of Burke *et al.* (1982), is based largely on carbonate analyses, and provides a standard against which anal-

yses from diagenetically altered materials may be compared. For example, Stueber and Pushkar (1983) have shown that carbonate cements in the Jurassic Smackover Formation yield a ratio of  $^{87}\text{Sr}/^{86}\text{Sr}$  that is much larger than that expected from Jurassic sea water. They suggest that the cements precipitated from fluid originating outside the Smackover. Saller (in press) has used stable strontium isotopes to date the timing of dolomitization in portions of the subsurface of Enewetak Atoll. Similar analyses of well-dated skeletal material may reveal if and when it underwent diagenetic alteration.

#### Inclusion Analyses

Analyses of solid and liquid inclusions in skeletal and nonskeletal carbonates yield direct and indirect evidence of original mineralogy and subsequent diagenetic change. Sandberg *et al.* (1973) found inclusions of aragonite in calcite-replaced skeletal grains. Such aragonite relics are known to occur in replaced skeletal and nonskeletal aragonite grains at least as old as mid-Paleozoic (Grandjean *et al.*, 1964). Such aragonite inclusions are direct evidence of the original mineralogy of carbonate grains (Fig. 5). Lohmann and Meyers (1977) describe microdolomite inclusions in calcite echinoderm grains and cement that they interpret to be the product of diagenetic alteration of magnesian calcite. A similar interpretation for Ordovician microdolomites in echinoderm grains is made by Blake *et al.* (1982) who attempt to explain the mechanism of alteration. It is now generally agreed that whatever the mechanism, microdolomite in calcite is a strong indication of a magnesian calcite predecessor, either organic or inorganic.

Liquid-filled inclusions also commonly occur in calcite cements and replaced skeletal fragments. These

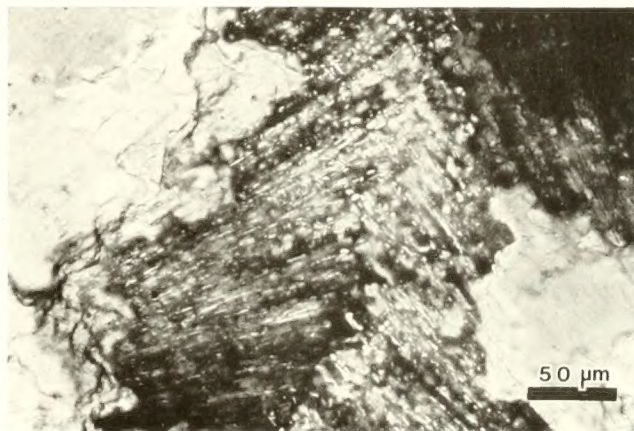


Figure 5.—Inclusions of aragonite (light rays) in calcite (dark) from the Pennsylvanian Holder Formation of New Mexico. The presence of aragonitic inclusions like these in calcite cements or skeletal grains is strong evidence of an aragonite precursor.



may often be analyzed to determine the temperature and salinity of water during formation of the inclusion. If the inclusion is primary, then these determinations apply also to the conditions of precipitation of the surrounding mineral. Studies of fluid inclusions in sedimentary rocks are rare and were summarized by Roedder (1979). The equipment required and analytical techniques are described in Hollister and Crawford (1981). Although little used in the determination of replaced skeletal carbonates to date, it is clear that fluid inclusion analyses will play an increasingly important role in carbonate diagenesis in general and perhaps in particular, the determination of altered skeletal carbonates.

### SUMMARY

It is not always possible to determine the original mineralogy or structure of skeletal carbonates from diagenetically altered remains. Although progress is being made at determining original mineralogy, arguments persist concerning several major and many minor groups of organisms. New problems continue to arise. For example, Buchbinder and Halley (in press) illustrate a very well preserved squamariacean alga from the Eocene of Tonga. Modern representatives of this family are entirely aragonite. The Eocene example has been exposed to fresh water and is now calcite. Exquisite ultrastructural detail is preserved in these samples suggesting that at least occasionally skeletal aragonite is not replaced by blocky calcite. As yet there is no satisfactory explanation for such detailed replacement of aragonite. Perhaps the organism was not aragonite initially. In any event, the example points out that there may still be significant exceptions to the general rules for carbonate diagenesis. In this manuscript many of the factors involved during skeleton alteration have been listed to illustrate the complexity of the processes resulting in the stabilization of carbonate minerals. It is clear that although we have made significant progress and understand many of the generalities of transformation, the details of many processes await clarification.

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PROGRESSIVE DIAGENETIC SEQUENCE OF ARAGONITE STRUCTURES:  
PLEISTOCENE CORAL REEFS AND THEIR MODERN COUNTERPARTS  
ON THE EASTERN RED SEA COAST, SAUDI ARABIA

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ABSTRACT

Uplifted coral reefs on the eastern Red Sea coast and the Gulf of Aqaba compared to their modern analogues reveal faunal differences due to diagenesis. Whereas all biota show more or less the same amount of diagenetic reduction in numbers, aragonitic mollusks are more reduced in number. Although the skeletons of many organisms and also marine cements, consist of aragonite, their reaction to diagenesis in the vadose environment differs. The diagenetic alteration of aragonite cements into calcite occurs earlier than that of aragonitic coral skeletons. The diagenesis of aragonitic mollusks begins only after the complete replacement by calcite of aragonite in corals and cements. In this stage the diagenetic environment can be already so well advanced that leaching predominates with little concomitant calcite precipitation. This leads to a major loss of aragonite mollusks. This diagenetic sequence can be related to the differing influence of organic matrices formed during aragonite precipitation; to the density of the crystal fabric; and also to the degree of undersaturation of the meteoric water with respect to  $\text{CaCO}_3$ .

INTRODUCTION

The present morphology of living reefs along the coast of the Gulf of Aqaba and the Red Sea is predominantly related to the erosion of the last glacial lowstand of sea level (Gvirtzman *et al.*, 1977). Lagoons are missing or are very small in those areas where fringing reefs develop along steep cliffs. The same situation is found on the flanks of drowned canyons. In those areas where the sea bottom is more nearly flat or is horizontal fringing reefs with lagoons are developed. Relic structures within the present day reef crest, such as pools or radially arranged furrows, indicate old erosional patterns, which become more and more masked by active reef growth. In addition to these fringing reefs, in some areas there are reefs which have the characteristics of barrier reefs. These are more common south of the Tiran strait.

Fringing reefs with larger lagoons show the most complete sequence of differing shallow water sedimentary environments. The beach deposits are characterized by gravel and sand of different composition, depending on the rocks of the hinterland, and containing various bioclasts. These gravels sometimes form beachrocks. According to Mergner and Schuhmacher (1974) the following zones can be distinguished. Behind the beach channel, predominantly characterized by the same material as that of the shoreline itself, follows the seagrass zone which consists of carbonate sand with many tests of the larger foraminifera *Marginozoum*. Next the coral-rock zone yields dead corals in a cemented carbonate sand matrix. Only octocorals may occur. The seaward zone of microatolls contains massive corals together with branching colonies of *Stylophora* and *Acropora*. The density of living sclerac-

tinians increases towards the backreef. The reef flat is barren. Dense coral growth is developed only on channel margins which cut through the reef flat, and also on the reef slope. For detailed information about the Recent environments see Friedman (1968), Friedman *et al.* (1974), Mergner and Schuhmacher (1974, 1981), and Braithwaite (1982).

This distribution pattern of zones is also recorded in uplifted Pleistocene reefs. This provides an extraordinarily good opportunity for comparative studies of the quantitative biotic composition of Recent and

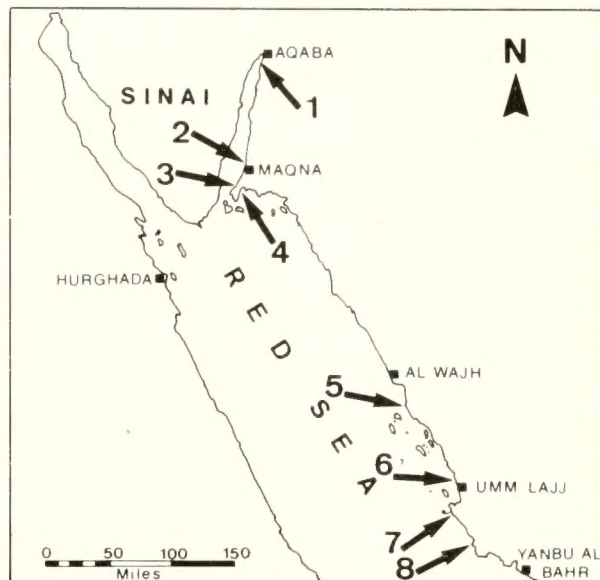


Figure 1.—Location map of the modern fringing reefs studied and their uplifted counterparts on the eastern coast of the Red Sea. 1, Aqaba; 2, 10 km north of Maqna; 3, Sharm Mujawwan; 4, Ra's al Qasbah; 5, Ra's Karkuma; 6, Umm Lajj; 7, Ra's Abu Madd; 8, Ra's al Lakh.

Pleistocene reefs in this area (Fig. 3A, B). Depending on where they are studied, different marine reef terraces are developed. The northern part of the Gulf of Aqaba is characterized by four terraces, whereas in the south only three terraces are developed (Behairy, 1983; Dullo, 1983).

Different localities were sampled, as shown in Figure 1. Recent samples were collected from unlithified skeletal sands of different sedimentary environments as well as from a few recently cemented parts of the reef crest. Comparative samples from Pleistocene terraces were sampled from the equivalent environments. The quantitative biotic composition of each was established by point counter method using fifty large scaled thin sections ( $10 \times 15$  cm). The diagenetic alteration of differing aragonitic materials was studied with the SEM.

#### COMPARISON OF QUANTITATIVE BIOTIC COMPOSITION OF MODERN AND PLEISTOCENE REEFS

Differences regarding the biotic composition between living and fossil reefs are obvious in the field (Fig. 3C). Fossil reefs exhibit approximately two thirds of the primary biota. Owing to different mineralogies, calcareous skeletons of algae and marine invertebrates thus show differing fossil records. Especially aragonite skeletons are reduced or missing, although those consisting of Mg-calcite are normally more unstable under conditions of freshwater diagenesis. Bathurst (1971) and others have pointed out that Mg-calcite can be altered to calcite by incongruent dissolution without changing the structure. In addition, Mg-calcite can be more stable than aragonite if orthophosphates are present (Walter and Hanor, 1979). The framebuilding or-

ganisms, which are predominantly scleractinians all consist of aragonitic material (Sorauf, 1980; Flügel, 1982). Their frequency of occurrence is reduced in the Pleistocene reefs (Fig. 2). However, it is still possible to identify the facies zones of fossil reefs, for which some typical representatives remain, like *Platygyra* or *Millepora*. There are no essential differences in the occurrence of massive or branching framebuilders. Small aragonitic bioclasts, derived from corals or hydrozoans, are much more affected by diagenesis and are completely lost in the oldest terraces.

Among the calcareous algae, the green alga *Hali-medea* is frequently lost during diagenesis. Even molds or recrystallized fabrics are lacking to indicate the prior existence of this alga. In contrast, coralline algae are better preserved due to their original composition of Mg-calcite. In a few cases their primary microstructure is still visible in SEM, although x-ray diffraction analyses indicate that they are low Mg-calcite.

Just as the coralline algae, the echinoderms consist of Mg-calcite, but they are more reduced in number than coralline algae. This seems to be a result of the primary microstructure of these organisms. The highly porous stereome of echinoderms is apparently more easily affected by diagenesis than is the dense crystal fabric of the coralline algae.

Foraminifers as a whole are numerically reduced at a normal rate for other organisms in the terraces (Fig. 2). Certain taxonomic groups show different fossil records however. Rotaliids, except those consisting of aragonite, are well preserved in all terraces, whereas small miliolids or textulariids are rare or absent by solution.

Calcitic mollusks are not reduced in number. They occur in the same frequency in the Pleistocene as in the Recent sediments (Fig. 2). Even their microstructure is still preserved in the older terraces. Only a few crystal overgrowths are seen (Dullo, 1983). In contrast, aragonitic mollusks are much reduced in number, more so than other aragonitic organisms. Only thick-shelled representatives such as *Tridacna* or *Strombus* are preserved and sometimes even show preservation of primary colors, although rarely. Although very frequent in the Recent, the small tests of juvenile forms are not recorded in the fossil reefs (compare Fig. 3D with 3E). The bulk of aragonitic mollusks in the diagram for the Pleistocene terraces (Fig. 2) includes not only those shells which show primary structures, but also all mollusk molds and recrystallized shells. This clearly shows faunal modifications in preserved reef biotas due to different reaction of aragonitic organisms during diagenesis.

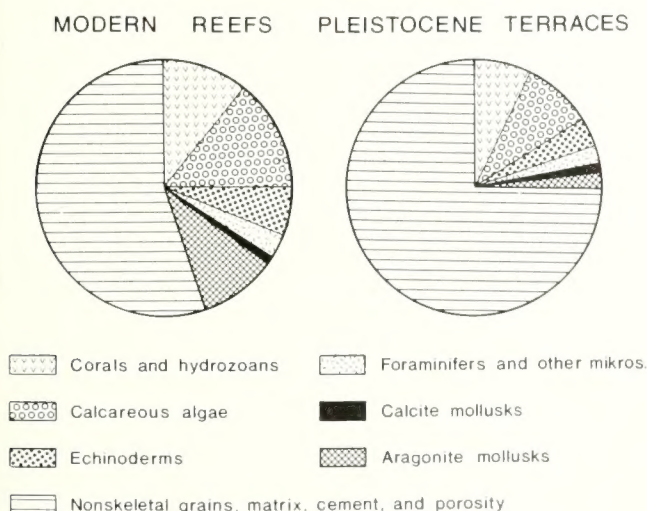


Figure 2.—Quantitative difference of the biotic composition of modern reefs and Pleistocene terraces.

## GRADUAL ALTERATION OF ARAGONITIC STRUCTURES

At the northern end of the Gulf of Aqaba four marine terraces are developed (locality 1; Fig. 1). The fossil record of aragonitic skeletons here is extremely poor. Only the lowermost terrace contains a few thick-shelled mollusks bearing relics of original colors. All other terraces are characterized by leached or recrystallized aragonitic mollusks. Corals and aragonite cements are also replaced by calcite. Similar diagenetic alterations are exhibited in the terraces north of Maqna, of Ra's Karkuma, and Umm Lajj (localities 2, 5, 6; Fig. 1).

A completely different situation is found farther south at Sharm Mujawwan, at Ra's al Qasbah, Ra's Abu Madd, and Ra's al Lakh (localities 3, 4, 7, 8). Well preserved mollusks of different sizes, some with relics of original colors, can be found in the uppermost terraces. The reduced degree of diagenetic alterations in the latter localities depends on climatic factors and the geological setting (Dullo and Hötzl, 1983).

All aragonite structures remain unaltered in marine environments studied, although submarine lithification has begun, leading eventually to cementation of isolated skeletons and their fragments. The common cement minerals in the marine environment are aragonite and Mg-calcite (Bathurst, 1971). Although Mg-calcite cement has been reported in the Red Sea reefs (Friedman *et al.*, 1974), it is not included in this study—only aragonite cements are considered. Besides lithification cement filling of intraskeletal cavities also occurs. Figure 3F shows fibrous aragonite cement within an interseptal cavity of *Stylophora pistillata*. The marine environment is also characterized by microborers (Fig. 3G). These microborers form the widely known micritic envelopes of Bathurst (1966). Primary structures of the aragonite sclerodermites that construct the coral skeleton (Hubbard, 1975; Sorauf, 1980) are not altered in the vicinity of these microboreholes (Fig. 3H).

The lower terrace already shows the gradual alteration of aragonite cements. Portions of these cements are replaced by calcite through the influence of meteoric waters (Fig. 4A, B). The coral skeletons remain unaltered and there is no hint of calcite replacement. Only a few leaching cavities may occur within the microstructure.

The middle terrace, which lies between 8 m and 12 m above present sea level, is characterized by the complete calcitic replacement of aragonite cements. The corals here exhibit the beginning alteration of microstructure. Newly formed calcite crystals always occur in the centers of the trabeculae and gradually replace the trabecular structure (Fig. 4C). This type of alteration of the coral skeleton is commonly reported (Gvirtzman and Friedman, 1977; Sorauf, 1980; Hubbard and Swart, 1982). Aragonitic mollusks are still unaltered in this terrace and exhibit their primary microstructure (Fig. 4E) as well as relics of original colors.

Macroscopically well preserved corals occur in the uppermost terrace (Fig. 3C), which corresponds in diagenetic degree to the lowermost terraces at the northern end of the Gulf of Aqaba, north of Maqna, Umm Lajj, and Ra's Karkuma. However, the complete alteration of the coral skeleton is obvious in the SEM, even at low magnification (Fig. 4D). Although the corals are characterized by complete replacement of their aragonitic skeleton by blocky calcite, aragonitic mollusks are only beginning to be altered.

## CONCLUSIONS

Although aragonitic cements, corals, and aragonitic mollusks all consist of the same carbonate mineral, a significant variation in their degree of diagenetic alteration was observed. The different and gradual alteration of these aragonitic materials is summarized in Figure 5. Several factors must be taken into consideration, which are apparently responsible for these progressive diagenetic sequences.

The precipitation of marine aragonite cements without the direct influence of organic action of algae or bacteria can presently be excluded. Formation of cements is dependent on the activity of these organisms in producing chemical microenvironments (Longman, 1980). The trace elements of these cements are in equilibrium to the seawater (Folk, 1974), regardless of the influence of organic activity. The biomineralization of corals is more complicated (Sorauf, 1980). The organic matrix of the coral controls the formation of the aragonite skeleton. However, growth of these aragonite crystals still follows crystallographic laws. Also the trace elements in the crystals are more or less in equilibrium with the sea water (Swart and Hubbard, 1982). The biomineralization in aragonitic mollusks is one of the

Figure 3.—A, Recent fringing reef with *Goniastrea* sp., *Porites lutea*, and *Acropora variabilis* near Maqna. B, Pleistocene fringing reef with *Lobophyllia corymbosa* near Maqna. C, upper terrace of Ra's al Qasbah. The coral is already replaced by calcite, whereas the aragonite mollusks occur only as molds. D, Recent carbonate sand from the coralrock zone. Note the frequent occurrence of aragonite mollusks. Gulf of Aqaba. Thin section rez. 2,  $\times 10$ , crossed nicols. E, coralrock zone of uplifted reefs. The few mollusks occur only as molds, whereas fine bioclasts are lost. Second terrace south of Aqaba. Thin section VI/2,  $\times 10$ , crossed nicols. F, marine aragonite cement in an interseptal cavity of *Stylophora pistillata*. Sample SA82/315b, SEM foto 48400,  $\times 1760$ . G, microborings on the outer wall of *Acropora variabilis*. Sample SA82/316, SEM foto 44825,  $\times 800$ . H, microborings in the trabecular structure of *Goniastrea* sp. Sample SA82/321, SEM foto 44885,  $\times 160$ .

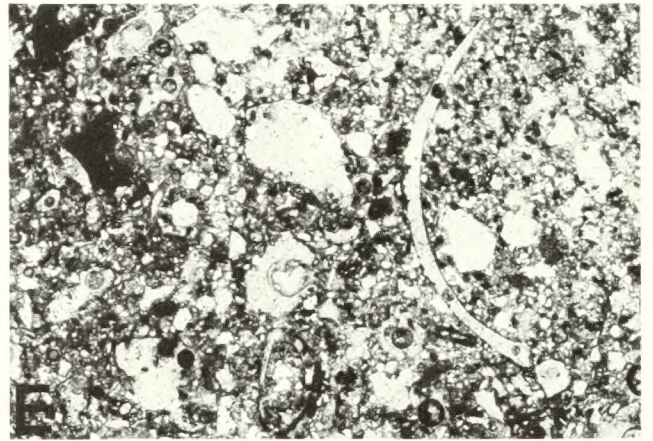
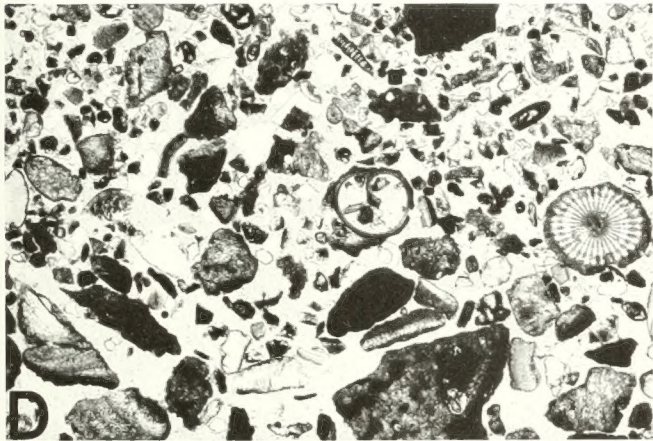
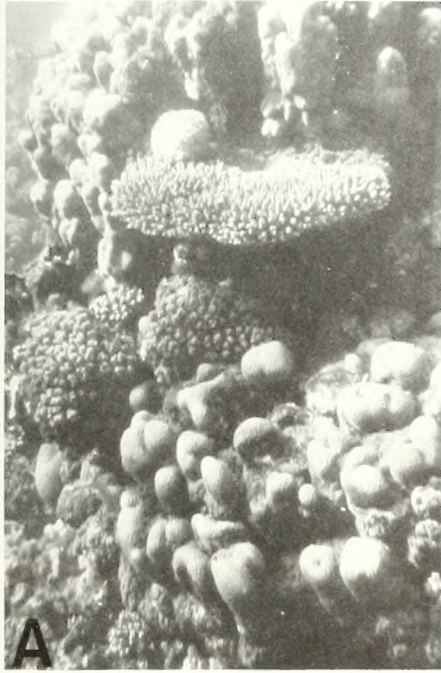


Figure 4.—Gradual replacement of aragonite cements by blocky calcite. Sample SA82/340, SEM foto 44904,  $\times 760$ . B, the corals in the lower terrace of Sharm Mujawwan exhibit blocky calcite cements in their interseptal cavities as well as few remaining aragonite cements. Sample SA82/321, SEM foto 44850,  $\times 80$ . C, the middle terrace of Ra's al Qasbah is characterized by the beginning of the alteration of the coral microstructure. All aragonite needles, forming the sphaerulitic structure of the trabecules are already leached, whereas in the center of the sphaerulites newly formed calcites occur. Sample SA82/341, SEM foto 44892,  $\times 720$ . D, completely altered coral septum of *Stylophora pistillata*. Upper terrace of Sharm Mujawwan, sample SA82/359, SEM foto 48413,  $\times 56$ . E, unaltered nacre structure of *Trochus erythraeus*. Middle terrace of Sharm Mujawwan, sample SA82/345, SEM foto 44937,  $\times 1440$ . F, beginning alteration of aragonite mollusks in the lower terrace of Aqaba. The crossed lamellar structure of *Conus* sp. is partly replaced by blocky calcites. Sample Aq VI/3/2, SEM foto 38392,  $\times 800$ .

most complex known among the invertebrates. The shell consists of a well defined connection of organic matrix and aragonite crystals, characterized as real biocrystals (Bandel and Hemleben, 1975), exhibiting a constant size of  $0.2 \mu\text{m } \phi$ . These biocrystals can be arranged in different structures; among them nacrous and crossed lamellar structures are well known. Formation of these structures is completely controlled by the extrapallial liquid. Even the trace elements in the crystals are controlled by this organic liquid and are not in equilibrium with sea water, but rather are genetically fixed (Pilkey and Goodell, 1963).

The increasing influence of organic matrices during the mineralization of aragonitic material leads to the increasing complexity of structures. The microorganisms, like algae or bacteria contributing in the formation of cements by organic action (Longman, 1980) are not preserved for a longer time (Krumbein, 1979). When these cements are exposed to the vadose environment, undersaturated meteoric water affects them, and leaching of aragonite and precipitation of calcite results (Longman, 1980). The more complete interconnection of organic matrix material with aragonite crystals in corals and mollusks provides protection against leaching meteoric waters. The increasing complexity of microstructure reflects also the increasing complexity of the organic matrix. The coral skeleton is formed more simply than that of mollusks and the organic matrix in corals is less complex than that of mollusks. Besides inorganic diagenesis there also exists biological diagenesis, caused by bacteria, algae, and fungi, which feed on organic material remaining within the skeleton. The organic materials within coral skeletons are decomposed more easily by endolithic organisms than are those of mollusks, complexly interconnected with biocrystals (Bandel, 1981). Therefore coral skeletal aragonite can be leached and transformed into calcite earlier than that of mollusks. Another important factor affecting this progressive diagenetic alteration of aragonitic structures is the density of the crystal fabric of various carbonate components. For example, meteoric waters can circulate more easily through the open structures of aragonite cements and therefore affect them more readily than the dense skeletal fragments of mollusks.

Corals and aragonite cements are altered earliest. Their alteration occurs even in a vadose environment

with less reactive waters. Such an environment is present in the lower terraces of Sharm Mujawwan, Ra's al Qasbah, Ra's Abu Madd, and Ra's al Lakh. If the vadose water becomes more reactive, mollusks are also affected by diagenesis and are reduced in number, because of disappearance by leaching. Corals and cements, already replaced by calcite remain unaffected. Such a situation is seen in the terraces at the northern end of the Gulf of Aqaba, north of Maqna, at Ra's Karkuma, and Umm Lajj, characterized by the complete lack of preserved aragonitic mollusks.

This diagenetic modification of biotic compositions occurs also in ancient carbonates, which have been exposed to vadose environments. Examples of this are the Miocene Leitha limestone in the Vienna basin (Dullo, 1983) and the Upper Triassic reefs of the Alps (Flügel, 1981).

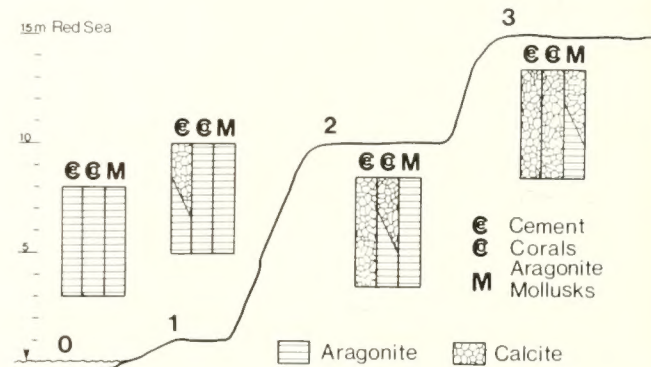
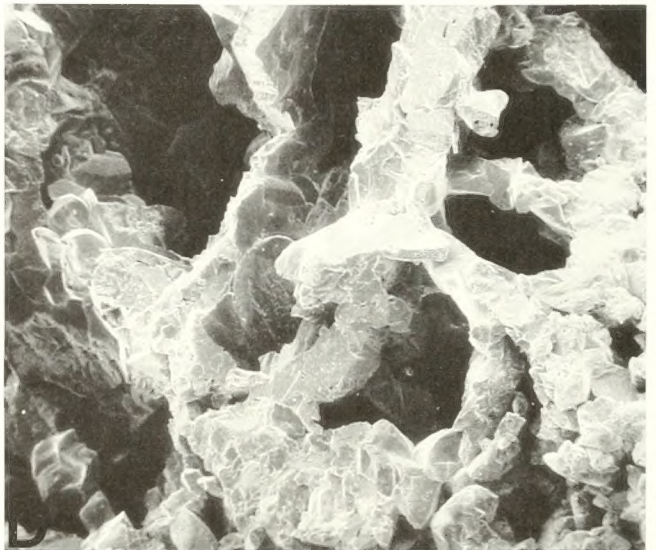
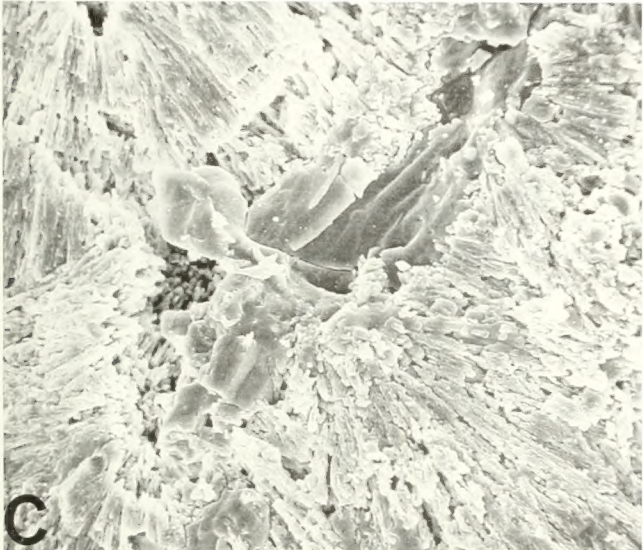
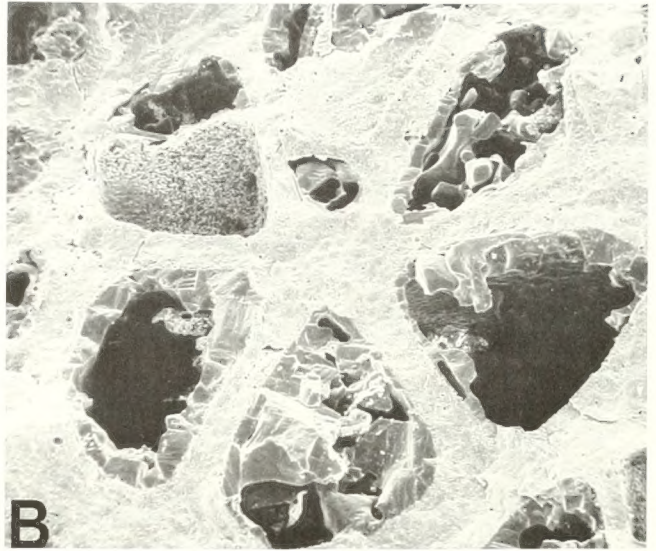
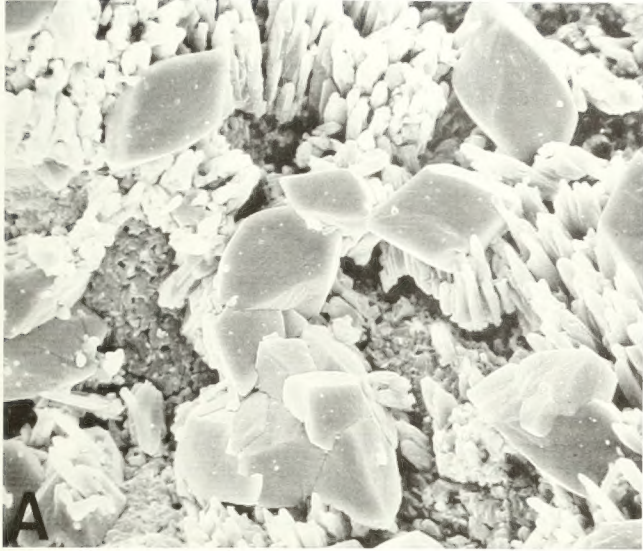


Figure 5.—Summarizing sketch of the progressive diagenetic alteration of aragonite structures.

#### ACKNOWLEDGMENTS

These investigations were carried out with the financial support of the Deutsche Forschungsgemeinschaft (Du 129-1) and the University of Petroleum and Minerals in Dhahran (Saudi Arabia). I am deeply indebted to both organizations. I wish to thank Prof. Dr. Altherr, Dr. Bayer, Prof. Dr. Blümel, Dr. Briem, Prof. Dr. Hötzel, Dr. Quiel, Prof. Dr. Jado, Mr. Koch, Prof. Dr. Puchelt, and Mr. Stefan for their help in the field as well as Prof. Dr. Flügel and Dr. Bandel for their critical reviews. Mrs. Neufert and Mrs. Sporn kindly prepared the photo micrographs of thin sections and prints of scanning electron micrographs.





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## THE PETROGENETOGRAM OF CORALS: SPATIAL VARIATIONS IN DIAGENETIC SEQUENCES

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### ABSTRACT

The diagenesis of Paleocene corals from the Bir Abu El Husein area of S. Egypt and Miocene corals from Khort Eit, N.E. Sudan, was studied by means of petrographic, cathodoluminescence and scanning electron microscopes as well as by X-ray diffractometer and electron microprobe.

In both cases complex diagenetic sequences were recognized, comprising in broad terms 1. Skeletal growth, bioerosion, sediment filling and early cementation; 2. Neomorphic alteration (leaving relics or ghost features) or complete dissolution, with either process affecting early cement, sediment filling or borers; 3. One or more stages of cementation in remnant or newly formed pore spaces with intermittent or subsequent sedimentation or dissolution phases.

Neither the resultant complete diagenetic sequence with all stages nor even the basic pattern in very broad terms is characteristic for a given limestone or even for a given coral colony. The variety of parallel and subsequent developments in each case is illustrated in petrogenetograms. These dendrograms, based on petrographic observation, indicate that coral diagenesis is a matter of multiple choices in space and time. The rationale behind the pathway taken at a given junction remains largely a matter of speculation at present, apart from readily apparent changes in diagenetic environment.

### INTRODUCTION

In his review of carbonate diagenetic textures Longman (1980) stressed the importance and variability of the diagenetic sequence. The purpose of this paper is to draw attention to the spatial variation of diagenetic sequences in a given thin section, hand specimen, outcrop, or lithofacies.

As documented earlier (Schroeder, 1972a, figs. 10-12; Schroeder and Zankl, 1974, figs. 6 and 9), both diagenetic sequences and the spatial variations thereof occur in Holocene reefs within the submarine environment, and can be traced to the Pleistocene. James (1974) illustrated the co-existence of different stages of preservation in Pleistocene corals, and Scherer (1975) showed a variety of diagenetic pathways in Pleistocene corals. Armstrong (1980) observed alternative stages in the evolution of porosity in Upper Miocene reefs, and Bebout *et al.* (1979) distinguished different diagenetic pathways in intra-skeletal, interskeletal and secondary pores of Lower Cretaceous rudist reefs.

The present paper is based on the studies of two occurrences of Tertiary corals (Schroeder, in prep.), which offer a considerably larger number of diagenetic pathways than hitherto recognized.

### THE PETROGENETOGRAM

The petrogenetogram (Fig. 1) is a diagrammatic illustration of spatial variations and temporal sequences of genetic/diagenetic products. As such it reflects spatial variations and sequences of genetic/diagenetic processes as well as spatio-temporal variations of the respective environments or micro-environments. The frame of reference is a matter of choice: A petrogenetogram

may be drawn for a single pore, a thin section, a hand specimen, an outcrop (as in the cases presented) or a lithofacies.

Basically, the petrogenetogram reflects the petrogenesis and its variations; therefore, in the case of corals, it starts out with the skeletal material. Immediately after the formation of the skeleton, still in the submarine environment, the next series of products follows: submarine cements, internal sediments, bioerosive pores or no addition. This is when and where the petrogenetic differentiation begins, where diagenetic pathways bifurcate for the first time. As a rule subsequent diagenetic processes simply by affecting or not affecting portions of the coral complicate the picture and gradually a complex diagenetic patchwork develops. The increasing variety with time is indicated by downward branching dendrograms composing the petrogenetograms.

### CASES STUDIED

Paleocene corals from the Bir Abu El Husein area in southern Egypt and Miocene corals from Khor Eit in northeastern Sudan exemplify spatial variations in diagenetic history. These corals were studied by means of petrographic, cathodoluminescence and electron microscopes and analyzed by X-ray diffraction and electron microprobe. Full documentation and illustration of the results obtained by these analytical means cannot be presented here due to the limited space available for contributions in this volume; detailed reports are in progress. In this paper, to introduce the approach of spatio-temporal diagenetic studies, the examples are illustrated in two ways: For each case one thin section

has been selected to show variation and proximity of some diagenetic products encountered (Figs. 3 and 5). Corresponding observations on spatial and sequential relations of various diagenetic products were made in other thin sections, in polished and in fractured samples; the many observations, complemented by appropriate mineralogical and chemical analyses formed the basis for the synthesis presented in the respective petrogenetogram (Figs. 4 and 6).

To provide the geological context for these observations, some information on location, stratigraphy and sedimentology as well as brief descriptions of the diagenetic products are given. As indicated by the question marks in Figures 4 and 6, some questions are not thus far answered: Some of these require more detailed analysis. The answers of the remaining ones, for example regarding questions concerning the precursor of some altered sediment or the original composition and fabric of a neomorphosed cement, remain a matter of speculation. In both cases studied, only the diagenetic history of the coral skeletons themselves were considered, not that of surrounding, underlying or overlying sediments.

### Paleocene Corals from the Bir Abu El Husein Area, S. Egypt

#### *Location, Stratigraphy, Sedimentology*

The outcrop is located 45 km East of Bir Abu El Husein and is part of the Upper Cretaceous/Lower Tertiary escarpment marked in Figure 2B. A measured section of 130 meters includes the Lower and Middle Paleocene Kurkur Formation, the Upper Paleocene Garra Formation, and the Eocene Thebes Formation (Issawi, 1971). In the uppermost portion of the Kurkur Formation, 65 m above the base of the section, an 80 cm layer of marly limestone marks the general change from shales to the overlying limestone and marl sequence (the exact stratigraphy of this section is being studied in detail by Luger, Technische Universitaet, Berlin). Above this layer follows a soft, carbonate-bearing shale unit; as a result the marly limestone layer forms a ledge in the escarpment and, where small valleys cut the slope, it forms terraces. Horizontal partings of the limestone form a series of terraces in the outcrop investigated.

The 80 cm layer concerned is a biocalcarenite con-

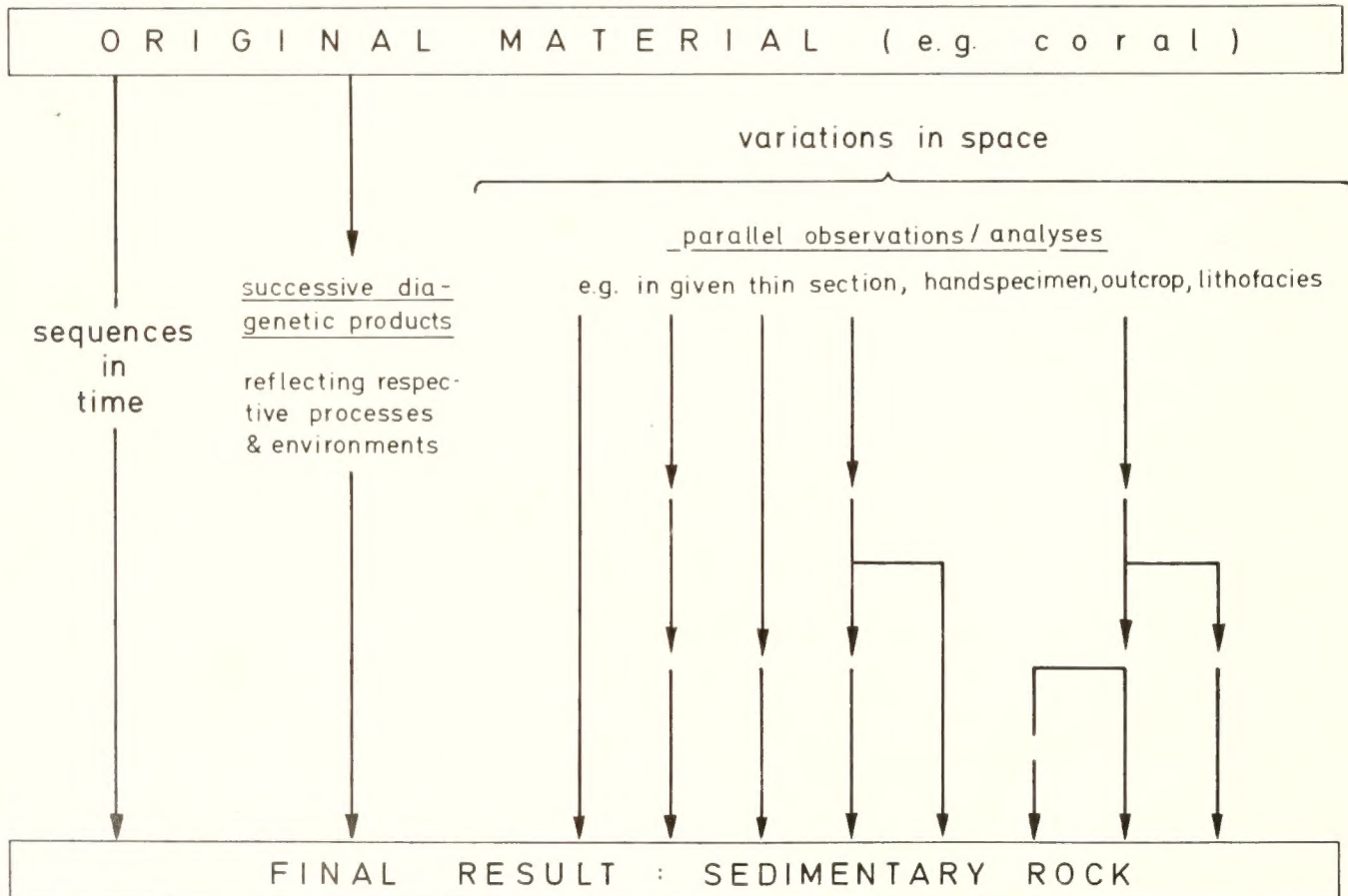


Figure 1.—Basic idea of the petrogenetogram: Temporal sequences proceed from top to bottom; spatial variations are indicated in horizontal direction.

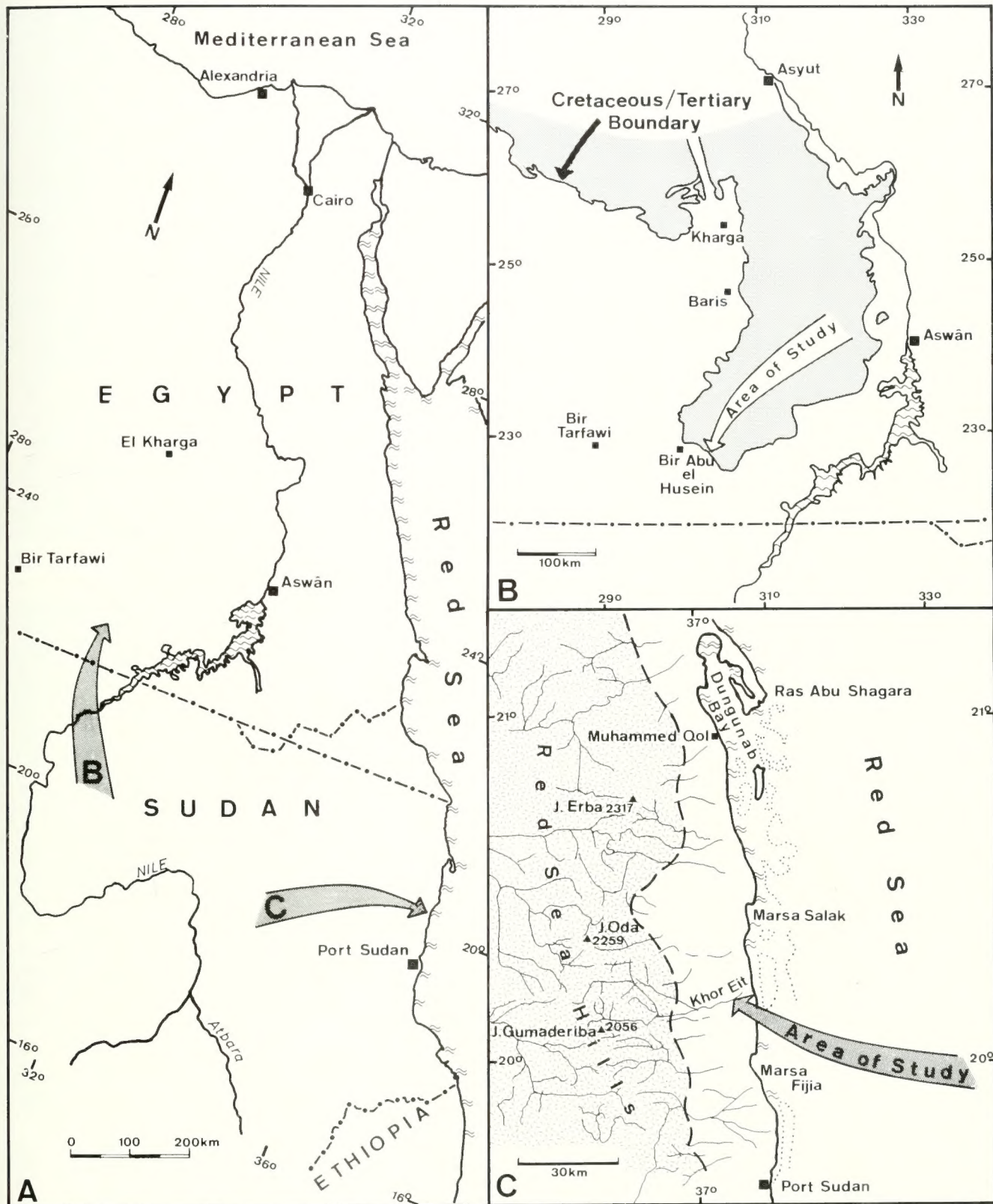


Figure 2.—Location of the areas of study.

taining a shallow water fauna; at a level 50 cm from the base coral knobs are found. These knobs, composed of one or more colonies of one or more coral species, are subcircular and disc-shaped. Their diameter ranges from 25 to 125 centimeters; the maximal height observed is 18 cm. Twenty-eight of these knobs were found to be irregularly scattered in the horizontal outcrop which is a square of  $100 \times 20$  m. The layer and its coral knobs were traced for about 5 km along the escarpment. The corals involved include six species of four genera. The most abundant are three species of *Actinastraea*; in addition, colonies of *Astraraea* sp., *Koilonomorpha* sp., and *Procladocora* sp. were found. While the first five species form domal to disc-shaped colonies, the last one is branching.

At the underside of some coral colonies bryozoan crusts and serpulid tubes were found. Many knobs are affected by bioerosion. Most abundant and most effective are bivalves with their millimeter- to centimeter-sized date-shaped holes, frequently containing the shell of the borer; very common are sponges attacking the coral from the underside and producing series of millimeter-sized holes. Elongate tube-shaped holes with diameters of about 1–3 millimeters are attributed to worms. The boreholes frequently are filled with sediment; in some cases calcified filaments (Schroeder, 1972b) were observed in bivalve boreholes.

### Diagenesis

Ghost structures indicate that submarine cements existed (Fig. 3c), but were largely obliterated by neomorphism and dissolution. These two processes largely determine the diagenetic picture in that skeletons and early cements, were either altered by neomorphism (Fig. 3b) and remaining primary pores filled by one or two generations of calcite cement or they were dissolved and secondary pores formed (Figs. 3a, d). These pores are generally larger and better interconnected than remaining primary pores, due to the movement of the solvent to which they owe their origin. As a result the secondary pores are the sites of more intensive and more varied diagenetic action.

A complex sequence of cements or portions of this sequence are found (Figs. 3 and 4): Calcite cement (II) is followed by an ankerite cement  $[(Ca_{0.60}Mg_{0.24}Fe_{0.15}Mn_{0.01})CO_3]$ . This ankerite may be converted neomorphically into another ankerite, which is relatively enriched in magnesium and impregnated by goethite and hematite. The next diagenetic product in the sequence is a calcian dolomite cement  $[(Ca_{0.59}Mg_{0.41})CO_3]$ . It may be followed by one or two calcite cements; these two generations of calcite cement can be distinguished only by their respective crystal orientation where the one grows on top of the other. Remaining secondary porespace is frequently filled by a gypsum/anhydrite cement (Figs. 3d, e). Last in the sequence are microspherulites of 10–20  $\mu$ m size, which are irregularly distributed in these pores. They contain Ca, Si, and Fe as ascertained by EDAX analysis; due to their size and scarcity further analysis was impossible.

The spatial variation of this sequence is immediately evident at several scales. A given ankerite crystal may be neomorphically altered at one side, but not on the other (Fig. 3e); the sequence at one side of a given pore may differ from that on the other side (Fig. 3d); between different pores the differences may be still greater. Figure 3 provides some idea of the variations encountered in one thin section, while Figure 4 shows the variations observed within 20 coral colonies from this one outcrop. Considering the level between thin section and outcrop, that is the individual coral colony, very few or almost all diagenetic sequences shown in the petrogenetogram may occur.

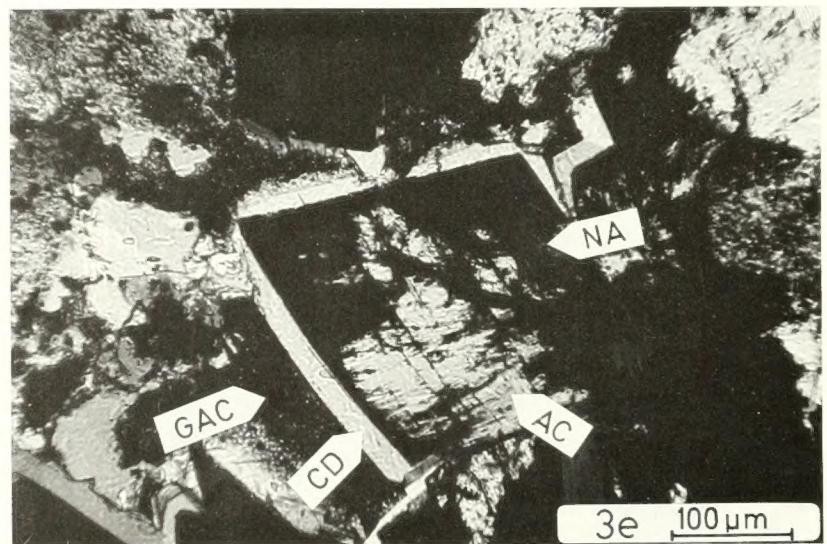
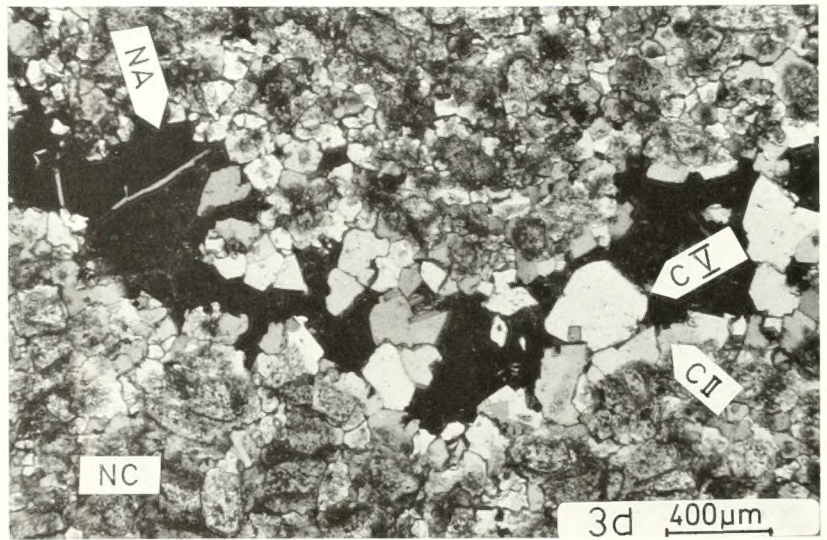
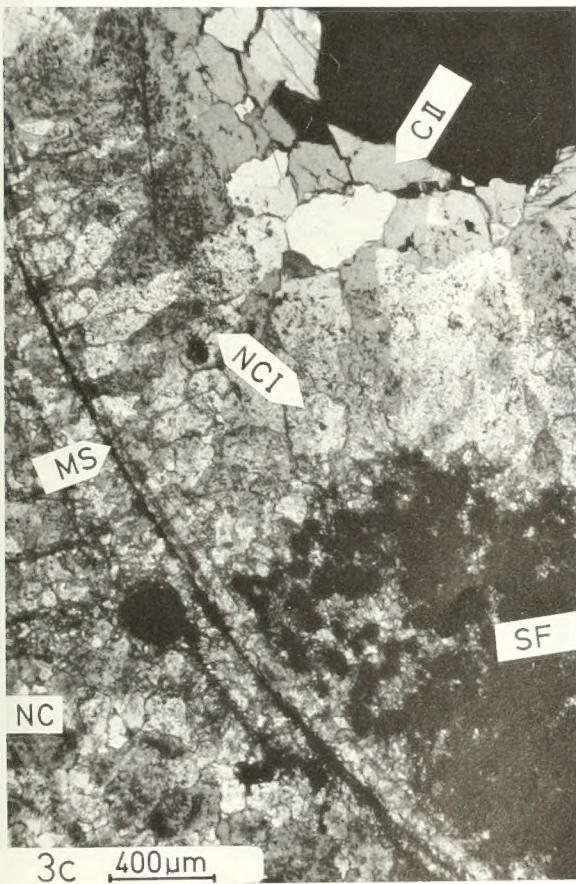
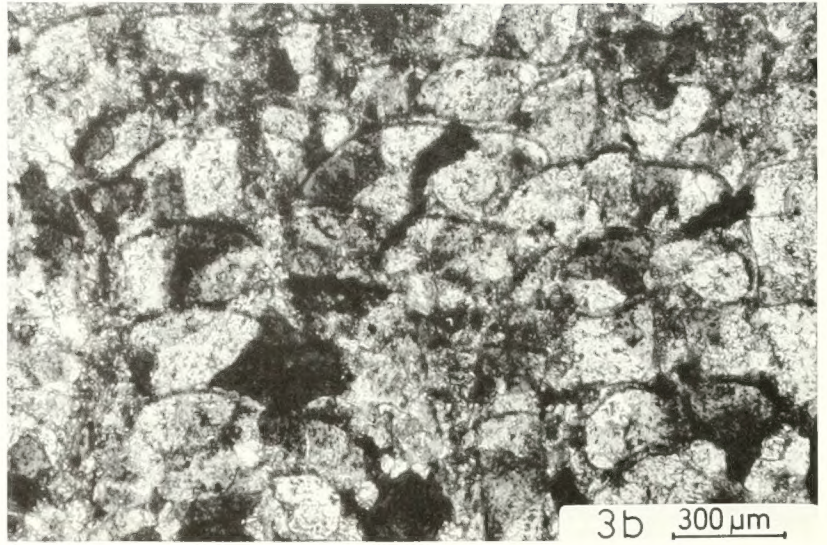
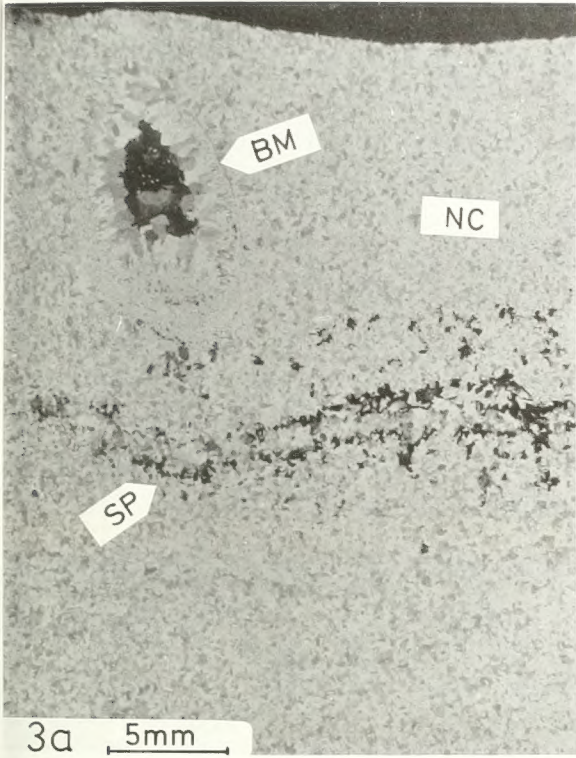
### Miocene Corals from Khor Eit, N.E. Sudan

#### *Location, Stratigraphy, Sedimentology*

Khor Eit is the valley of an ephemeral stream extending from the Red Sea Hills across the coastal plain to the Red Sea (Fig. 2C). On its flanks one of the few exposed profiles of the Tertiary sequence of the coastal plain is found which has been described in detail by Sestini (1965). The corals studied are from Sestini's unit 3 of the Middle Miocene Abu Imama Formation from the outcrop located about 1 kilometer East of Eit Well as shown in his fig. 9. Sestini called this unit "reef

Figure 3.—Diagenetic variations in a Paleocene coral from Bir Abu El Husein, S. Egypt, as seen in petrographic microscope analysis of one thin section (vertical = sub-parallel to corallites).

- General view of part of the thin section showing neomorphosed coral (NC), bioerosive hole of boring pelecypod (BM), and secondary pore (SP) due to dissolution.
- Neomorphosed coral with neomorphic calcite crystals cutting across ghost structures of original skeleton.
- Borehole of pelecypod surrounded by neomorphic coral (NC) with neomorphosed shell (MS), sediment fill (SF) and neomorphosed early cement (NCI) with ghost structures and overlain by calcite cement (CII) with further porespace left open.
- Secondary sheet shaped pore in section; neomorphic ankerite (NA) with calcian dolomite (white line) on one side, and calcite cement generations II and V (CII, CV) on the other side. Remaining porespace filled by gypsum/anhydrite cement.
- Diagenetic sequence in the same pore as shown in Fig. 5d: Ankerite cement (AC) is partly and unevenly neomorphosed (NA); the entire crystal is covered by a thin layer of calcian dolomite (CD), which in turn is followed by gypsum/anhydrite cement (GAC).



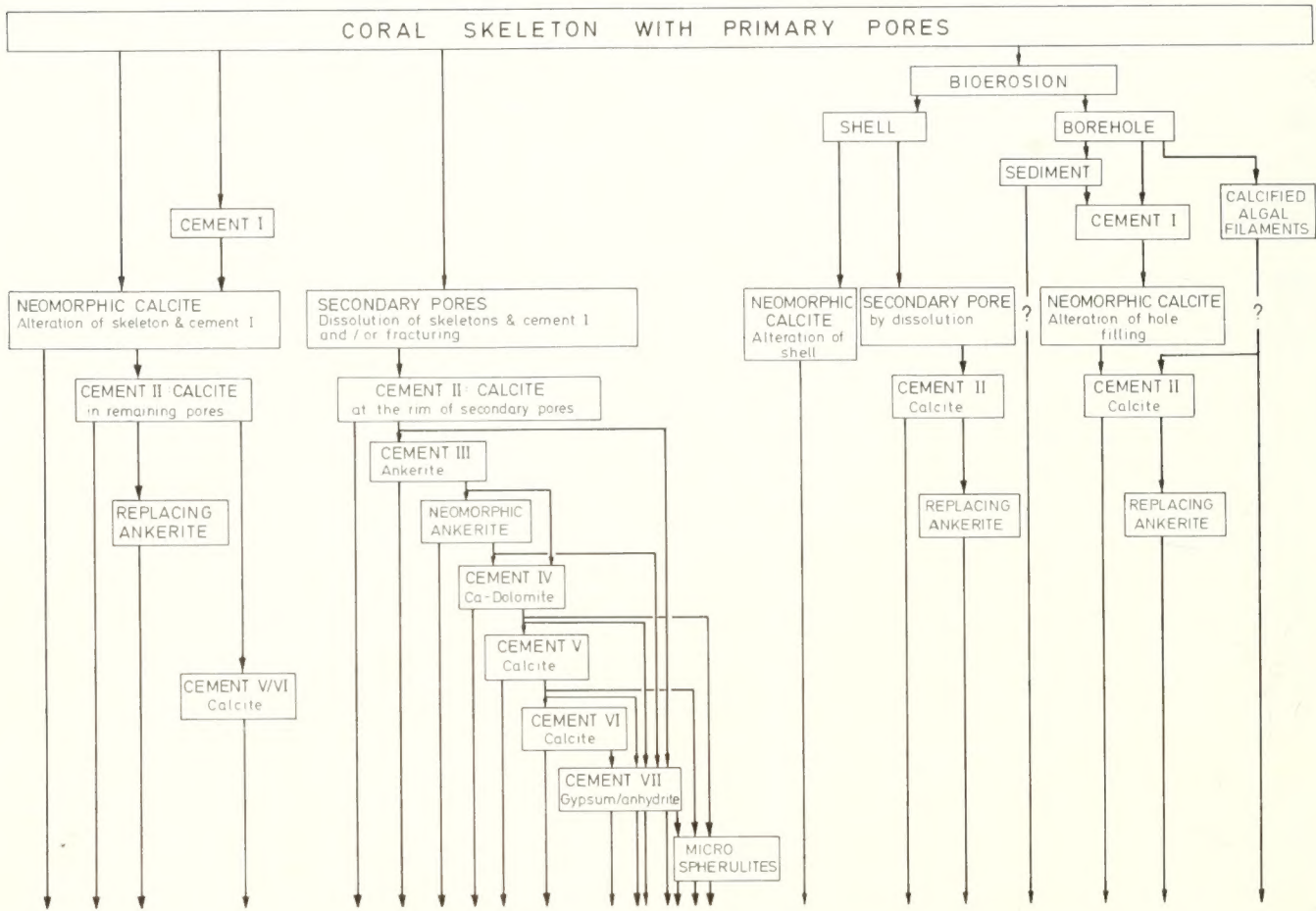


Figure 4.—The petrogenetogram of Paleocene corals from the Bir Abu El Husein area, S. Egypt.

limestone"; however, in this particular outcrop there are many corals, but no contiguous framework. Numerous colonies of poritid and faviid corals up to 30 cm in size are found in growth position within a matrix of biocalcarenite. According to Sestini the thickness of the unit varies between 0 and 11.5 m, and in this outcrop it is about six meters. The environment of deposition possibly corresponds to the "coral zone" of the present fringing reef, which near Port Sudan is found in 1.50 to 3.80 m water depth in a protected nearshore position (Schroeder and Nasr, 1983).

Most corals were subject to bioerosion, mainly by bivalves, but also by sponges. Internal sediment is not only found in the boreholes, but also in intra-skeletal pores of the corals.

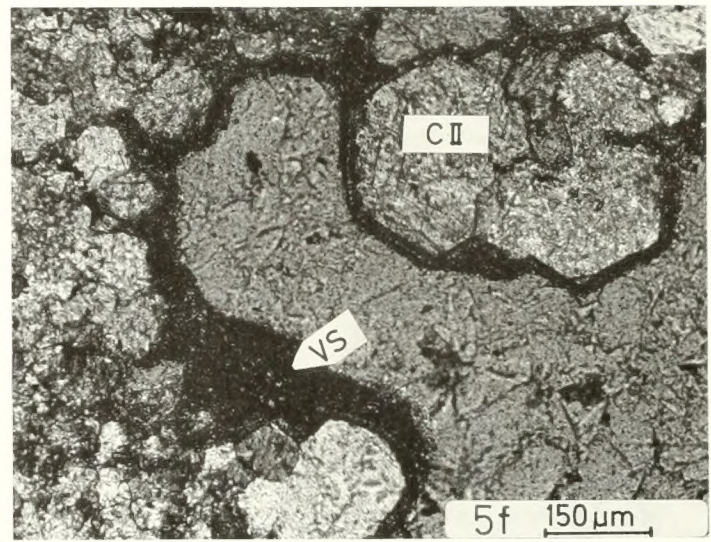
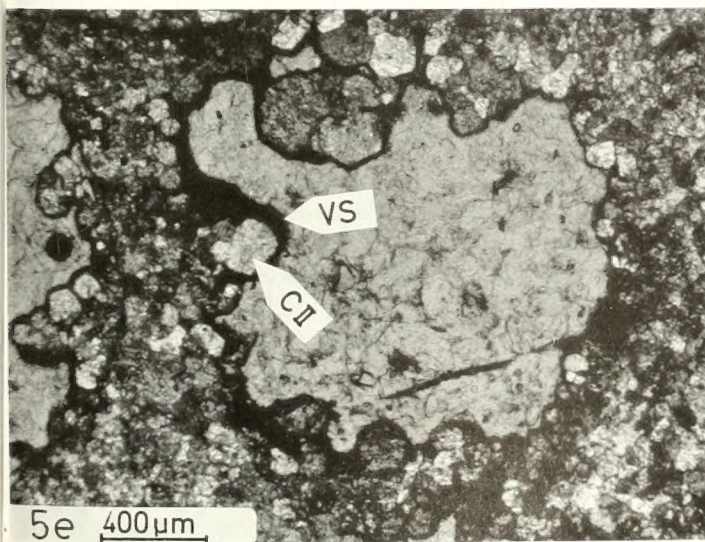
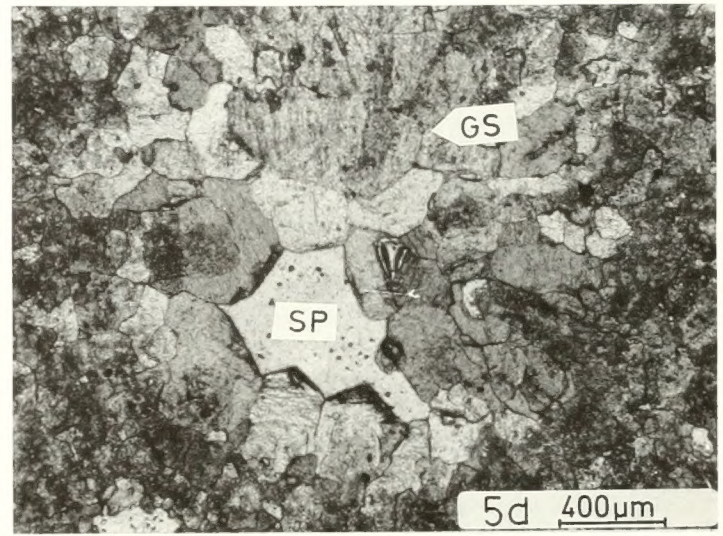
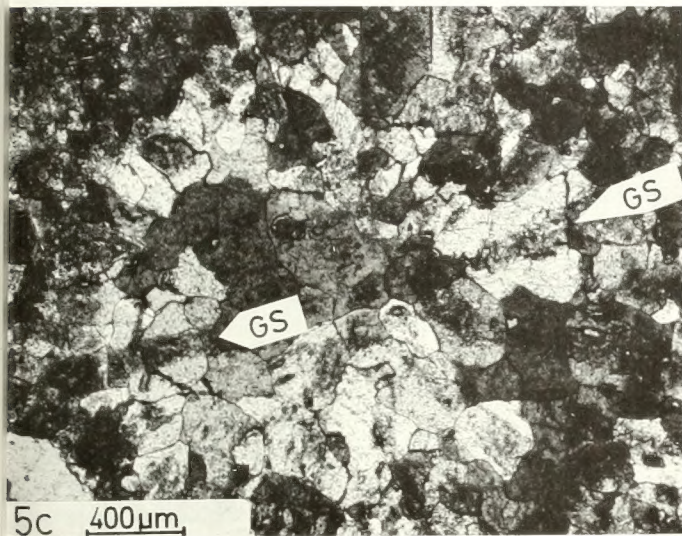
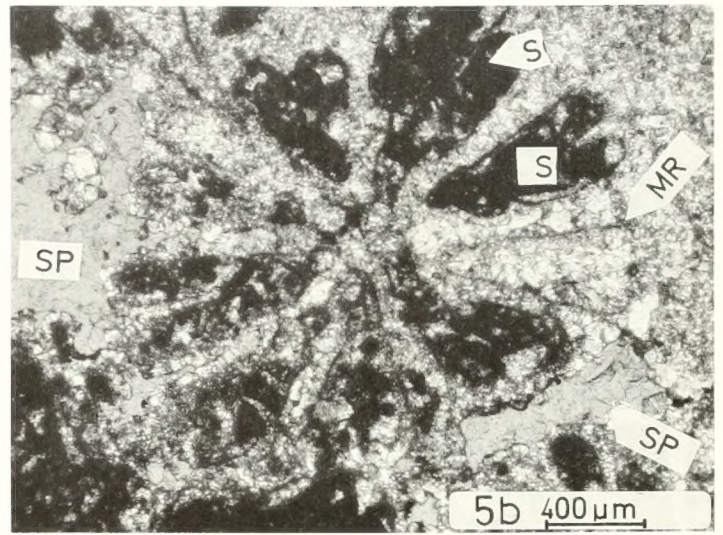
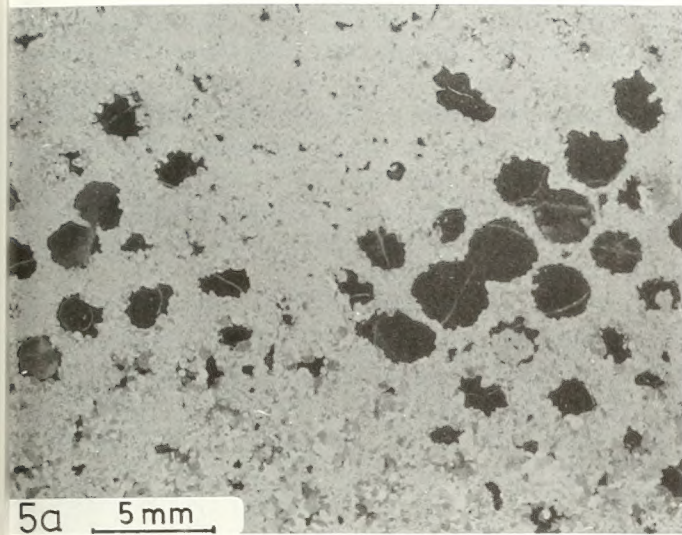
*Diagenesis*

Ghost structures suggest the former presence of an early submarine aragonite needle cement, and relics of the original skeletal aragonite are also observed. However, both skeletal material and early cement have been partly neomorphically altered to calcite. A relatively

Figure 5.—Diagenetic variations in a Miocene coral from Khor Eit, N.E. Sudan, as seen in petrographic microscope analysis of one thin section.

- a. General view of thinsection cut horizontally across coral colony with some corallites dissolved (top right), others closed by coarse crystalline mosaic (center bottom), others with large crystals growing into secondary pore (top left).
- b. Corallite partly filled by sediment; inter-corallite skeletal material dissolved to form secondary pores (SP), sediment fill preserved (S); micritic rim (MR) serving as substrate for crystals growing into moldic as well as intra-skeletal porespace.
- c. Corallite totally neomorphosed with coarse crystalline mosaic and ghost structures of septae (GS).
- d. Corallite partially neomorphosed with ghost structures (GS) and partially dissolved leaving secondary pore (SP), into which the calcite cement crystals grow with idiomorphic terminations.
- e. Corallite fully dissolved with calcite cement (CII) growing into the secondary pore and covered by carbonate vadose silt/micrite (VS).
- f. Detail of Fig. 5e showing blocky crystals of calcite cement (CII) and vadose silt/micrite (VS).





coarse blocky crystal mosaic with ghost structures results (Fig. 5c). Other portions of the skeletal material (and probably early cements) have been dissolved and secondary pores formed (Figs. 5a, e). Dissolution may affect only part of the corallite, while the remainder may be neomorphosed (Fig. 5d). The secondary pores formed are usually lined or filled by calcite cement; in cases of partial neomorphism, neomorphic crystals may continue to grow as cement crystals and assume idiomorphic terminations (Fig. 5d around SP).

Some corallites may be filled with sediment which apparently resisted dissolution in its entirety, although some individual particles probably are altered. The remaining coral may be dissolved and the secondary pores may be filled by calcite cement (Fig. 5b). Neither the sediment filling nor its preservation necessarily involves the entire corallite. Parts may be filled while

others are entirely altered (Fig. 5b). Another feature observed is a micritic rim lining the original corallite; this may have been a micritic envelope produced by boring algae (Bathurst, 1966) or a thin layer of isopachous micritic cement. In the process of dissolution it resisted while the surrounding material was removed and thus forms a substrate for the calcite cement subsequently precipitated. In this way the internal outline of the corallite is preserved.

The calcite cement which follows neomorphism and dissolution (Fig. 5e and f, CII) is zoned as seen in cathodoluminescence. Up to 20 alternate dark red and bright orange zones have been observed and indicate alternating Mn and/or Fe contents, hence fluctuations in the conditions of the diagenetic environment.

The calcite cement may be followed by a vadose carbonate silt/micrite (Fig. 5e and f), an authigenic

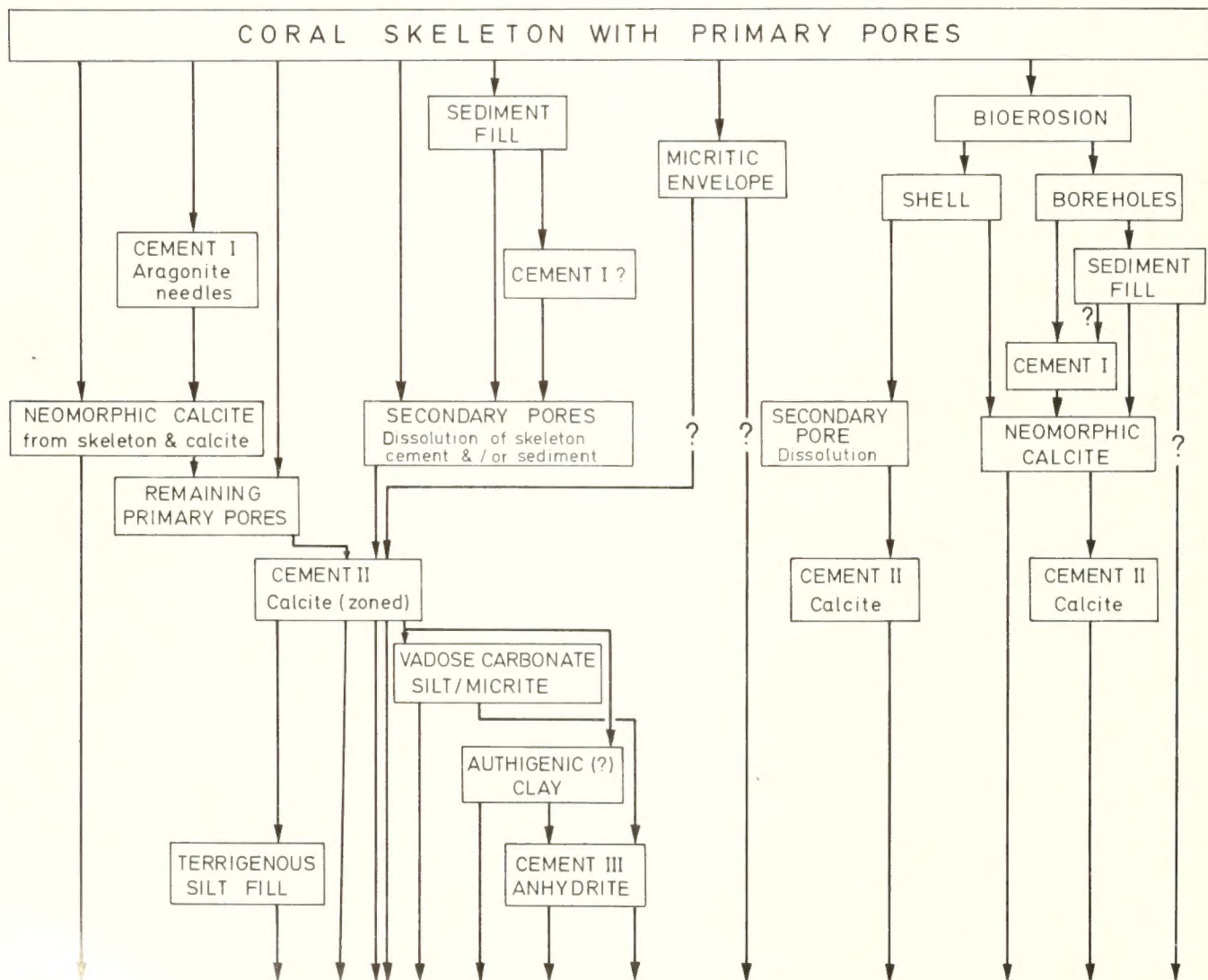


Figure 6.—The petrogenetogram of Miocene corals from Khor Eit, N.E. Sudan.

clay mineral and/or by an anhydrite cement. Finally, terrigenous sediment may fill some pores partly or completely.

The diagenesis of these corals is illustrated in Figure 5, presenting different modes of preservation in one given thin section ( $5 \times 5$  cm), and in the petrogenetogram (Fig. 6) referring to 12 coral colonies from various levels of this vertical outcrop of  $50 \times 6$  m.

## DISCUSSION

The two examples of coral diagenesis briefly presented include many individual features requiring further explanation, interpretation and discussion; the interested reader is referred to forthcoming reports. At present the discussion is restricted to spatial variations in diagenetic processes and sequences. First, diversifying factors and processes will be considered, second the petrogenetogram.

### Diversifying Factors and Processes

Skeletal morphology alone appears to be one factor giving rise to diagenetic differentiation; thus solid skeletal elements react diagenetically in a different way from delicate parts, and connected pores and occluded pores react differently. In domal or disc-shaped colonies the polarity between its top with the living organism present, and cementation occurring immediately underneath on one hand, and the underside with encrusting and boring organisms present already during the colony's lifetime should cause variation. Bioerosion with resultant cross-cutting pores provides another element of spatial variation.

Another diversifying factor can be the unstable mineralogy of the coral skeleton, which makes it diagenetically sensitive. Due to this sensitivity a coral may be affected by a slight change in local diagenetic environment, while other biogenic materials more resistant to diagenesis would require more drastic, hence more general and widespread changes in environmental conditions.

An important element of variation is introduced when the skeleton is changed by neomorphism and/or dissolution. These two processes seem to occur in close proximity and simultaneously or nearly so. Possibly these processes are only different responses to the same cause, proceeding at different rates, as an example, to different rates of fresh water movement through the material. Experimentation and extensive observations on these processes are needed to verify this suggestion or find alternative explanations. The effect of the two processes is markedly different, in that while neomorphism closes the diagenetic history or leads to a relatively uneventful continuation, dissolution opens

new pores and thus avenues to varied and intensive diagenetic action.

Many of the subsequent variations, for example, in neomorphism around a crystal or in sequence within a pore seem to reflect differences in micro-environmental flow patterns. On this broad and somewhat unsatisfactory explanation subsequent observations on spatial variations will necessarily add much.

It should be kept in mind, however, that in the above examples the limitation of study to coral colonies only means considerable simplification. Including the sediment around, between, above and below the corals, leads to the realization that the diagenetic patchwork is much more complex, and spatial variations are much greater than illustrated.

### The Petrogenetogram

#### *Conceptual Considerations*

This paper certainly is not intended to question the value and importance of sequential diagenetic analyses of corals, reef carbonates, or carbonates in general. Sequence studies such as those by Meyers (1974), Scherer (1977), and Machel (1983), to mention a few, have contributed significantly to the understanding of the evolution of porosity.

The examples presented, however, suggest considering such sequences and variations in sequences within their spatial framework. The spatial aspect is important with respect to the distribution of pores and pore types within a coral or, for that matter, in any carbonate rock. The petrogenetogram may be a useful means to visualize various bifurcating or parallel diagenetic pathways, and its use can be further enhanced when the relative importance of respective pathways is considered. A semi-quantitative or even a quantitative aspect can thus be introduced, depending on the purpose for study.

Application of the petrogenetogram is by no means limited to corals. It can be applied to other rocks exhibiting similar degrees of diagenetic variation. As an example, the same basic approach (although less explicit) was used in the study of Quaternary beachrock from Kenya (Schroeder, 1979) where a sequence of cements and various successive or coexisting alterations of cements and skeletal particles were recognized.

#### *Practical Aspects*

For the practical purpose of understanding evolution and distribution of the pore space of a limestone under study, the actual occurrences of diagenetic products, sequential or coexisting, are relevant; therefore only those actually observed are entered into the petroge-

netogram. There are many more theoretical possibilities of coexisting or successive diagenetic products; some of these may be of interest: The absence of a combination or a sequence may indicate mutually exclusive processes or conditions of origin.

The temporal correlation of diagenetic sequences observed in thin section, specimen, or outcrop may present a problem: for example, if three generations of calcite cement are found in one sequence, but only one in another. The respective position within the sequence may enable correlation, but more likely further analyses and thus more detailed characterization of the cements will be required, for example by staining, cathodoluminescence, or microprobe.

Correlation of different diagenetic processes and products may be still more difficult. For example, whether or not neomorphism and dissolution are actually simultaneous and occur in the same diagenetic environment, remains an open question. Thus, the petrogenetogram may help to realize the spatial variation in diagenesis and at the same time draw the attention to the resultant problems in genetic interpretation.

### CONCLUSIONS

Two case studies of the diagenesis of Tertiary corals from N.E. Africa strongly suggest that the sequence of diagenetic products or events should be considered when investigating lithification and porosity evolution. The spatial variations of these sequences must also be considered in order to improve understanding of the distribution of pores and to appreciate the coexistence and interaction of diagenetic processes and environments.

The petrogenetogram is introduced to illustrate observations on the genetic/diagenetic history and its variations with respect to fossil corals as well as other carbonates.

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## RECOGNITION CRITERIA FOR CALCITIZED SKELETAL AND NON-SKELETAL ARAGONITES

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### ABSTRACT

Assertions of pseudomorphic or near pseudomorphic transformation of aragonite to calcite have occasionally been made in the literature, usually for extinct organisms. Observations on alteration behavior of known aragonite skeletons do not support such assertions. Observed states vary from total solution removal of the aragonite to calcitization across a solution film very much thinner than aragonite crystal dimensions. Even the latter process produces significant textural disruption; the resulting mosaic of considerably larger neomorphic calcite crystals irregularly cross-cuts original structure. Fluid inclusions are common, and elevated Sr values and even relics of original aragonite frequently remain in the replacement calcite. Such aragonite relics are preserved in calcites replacing skeletons at least as old as Carboniferous, *i.e.*, they do not represent transitory, "partially altered" states inexorably destined to calcitize. Alteration of non-skeletal aragonite constituents (ooids and cements) does not differ from the general modes just described for skeletal aragonites.

### INTRODUCTION

Examples in the paleontological literature of efforts to understand original skeletal microstructure in fossils have commonly resorted to "analogy" with skeletal microstructure in a modern group as closely related as possible, ideally the same species. Similar analogies with modern examples are made for non-skeletal carbonates. Such arguments based on comparison with modern correlatives are to be made cautiously and with awareness that potentially erroneous conclusions could be derived. The difficulties which can arise are well exemplified in the study of rugose corals and ooids. Both of these have been treated in some detail earlier (Sandberg, 1975a, b).

#### The "Coral Analogy"

It has been suggested that trabecular and fibro-lamellar microstructures of aragonite, the only ones that occur in modern, scleractinian corals, are to be accepted, on the basis of analogy, as the only primary ones for ancient corals, including rugosans (Oekentorp, 1972). This "coral analogy" is a common implicit or explicit basis for many interpretations of microstructure in corals, and, by extension, other fossil groups as well. It is important to note that the assumption, in the "coral analogy," of equivalence of original states in rugosan and scleractinian corals leads logically to several subsidiary conclusions: *first*, that non-trabecular microstructures must be the product of recrystallization; *second*, that, because trabecular structures occur in both modern aragonitic and ancient calcitic corals, calcitization of aragonite can occur pseudomorphically (or "paramorphically"). As discussed in the following sections, both conclusions are spurious.

Like the analogy from which they follow, they are tenable only by ignoring actual textural consequences of calcitization of scleractinian corals or, for that matter, of aragonites in general, skeletal or non-skeletal.

Comparison of skeletons of fossils with those of their nearest living counterparts is a natural first step in the study of original microstructure and composition in those skeletons. As the taxonomic distance increases, however, the danger in that approach lies in taking too strict a view of equivalence. Understanding of skeletal genesis and diagenesis in any and all groups is better served by seeking to identify properties which are consistently found (or consistently not found) in calcitized examples of known aragonites, regardless of taxonomic origin (or even non-skeletal origin).

The general uniformity in properties of calcitization mosaics replacing aragonite skeletons of diverse taxa is striking, as noted so eloquently by Sorby (1879). In the face of that uniformity, which transcends phylum and even kingdom boundaries, it is unreasonable to invoke unusual, taxonomically-restricted diagenetic behavior to account for presently fine, regular calcite ultrastructures in skeletons of extinct groups inferred to have had originally aragonite skeletons. Wendt (1980) argued that the lamellar calcite skeletons of Jurassic-Cretaceous inozoan sponges were originally aragonitic, like related inozoan sponges in the Permian and Triassic. The illustration of a Jurassic example (Wendt, 1980, fig. 12e) suggests a textural regularity incompatible with origin by calcitization of aragonite. Dauphin (1983) reviewed the suggestions of various authors that the rostra of the belemnite cephalopods were, like those of the aulacocerids (Dauphin and Cuif, 1980), originally aragonite. That interpretation is re-

futed by the regular radial calcite crystals with closely-spaced concentric growth increments that compose belemnite rostra. Such textural and optic regularity does not characterize calcite after aragonite. Furthermore, there is a drastically different diagenetic behavior of the calcitic rostra and the aragonitic layers known to compose the other parts of the skeleton. In well-preserved belemnite specimens in which the aragonitic skeletal parts are preserved (Mutvei, 1964) the rostra are, nevertheless, still calcite. Dauphin (1983, p. 419, 431) implied that the work of Spaeth (1971) indicates an aragonitic mineralogy for the belemnite rostrum. Reexamination of Spaeth's paper shows that he suggested only secondary infilling and recrystallization to produce the dense calcite rostrum, not a calcitization. The descriptions by Dauphin and Cuif (1980, p. 43) of the textural differences of belemnite rostra ("conserve toujours un disposition générale radiaire") and presently calcitic aulacocerid rostra ("grands cristaux calcitiques totalement indépendants des structures histologiques . . ."), effectively describe the differences between skeletons that were, respectively, originally calcitic and originally aragonitic.

#### The "Ooid Analogy"

This striking non-paleontological parallel of the "coral analogy" has caused much confusion and misunderstanding in the study of non-skeletal and even skeletal carbonates (see Sandberg, 1975b). Although recent work has demonstrated a diversity of microstructures and mineralogies in modern and Pleistocene ooids, ooids of Bahamian type were long regarded as the characteristic original state for marine ooids. The Bahamian ooids are composed of concentric layers of aragonite needles arranged in statistically tangential orientations. Ancient marine ooids generally also show concentric layering, but, in well-preserved examples, are commonly composed of radially oriented calcite crystallites. Adherence to the "ooid analogy" explicit or implicit in older ooid studies would require that, because known modern marine ooids (*i.e.*, Bahamian type) are tangential aragonite, ancient ooids must have also been so originally. Therefore, fine radial calcite microstructure in ancient ooids must have been acquired by a process of very fine-scale replacement, preserving the regular, concentric structure and regular optic orientation.

Such a concept of calcitization of aragonite with retention of fine regular texture is not based on the observed diagenetic behavior of aragonites. Rather, it follows (as in the "coral analogy") as a logical consequence of the initial assumption of equivalence. Despite that lack of support, the concept continues to be

applied, even in quite recent literature. The mischief worked by the "ooid analogy" extends well beyond the interpretation of textural states in ancient ooids. In even quite recent works, the assumption of original aragonite mineralogy for fine-textured calcite ooids (*e.g.*, in the Jurassic) has led to questionable interpretations related to such things as diagenetic changes in Sr content, differences in diagenetic environment, timing of cementation, and paleohydrology (Chowdhury, 1982; Scudeler Baccelle, 1983). Interpretation of the original mineralogy of ancient ooids (or cements) based on the "ooid analogy" assumes "same initial conditions," *i.e.*, like today. Recent work indicates that long intervals of the geologic past had significantly different, "aragonite-inhibiting" conditions (see Sandberg, 1983, and references therein).

It is important to note that some ancient ooids do indeed have properties indicative of original aragonite mineralogy. Most notable among such properties are: disruptive calcite textures like those found in calcitized examples of Pleistocene aragonite ooids and aragonite skeletons from throughout the Phanerozoic (Dodd, 1966; Bathurst, 1964; Sandberg, 1975a, 1983). Less commonly, there is retention of aragonite relics (Sandberg, 1975b; Sandberg and Popp, in preparation). Such ooids may co-exist with ooids possessing regular textural-optic properties indicative of original calcite (Sandberg, 1983, figs. 4, 5).

## DISCUSSION

### Criteria for Recognition of Aragonite Constituents

Sandberg (1983) suggested that the criteria which have been used in the literature as indicative of original aragonite mineralogy can be arranged into a hierarchy of decreasing reliability (Table 1). Calcitization mo-

Table 1.—Criteria for recognition of ancient aragonites. A hierarchy of decreasing reliability (from Sandberg, 1983).

1. Still aragonite (*e.g.*, Stehli, 1956).
2. Relatively coarse calcite mosaic cross-cutting original structure, with inclusions of original aragonite (*e.g.*, Sandberg, 1975a, b; Sandberg and Hudson, 1983).
3. Calcite mosaic as for 2, no aragonite relics, but elevated Sr content (*e.g.*, Mazzullo, 1980).
4. Calcite mosaic as for 2, no relics, no elevated Sr content, or Sr content not yet analyzed.
5. Molds or subsequently filled molds.

*Note:* Calcite with preserved fine textures and regular optic orientations has often been attributed to "pseudomorphic" or "paramorphic" transformation of aragonite. There is no basis, in the alteration behavior of known aragonites, for accepting that commonly cited state as a likely fate of aragonite in natural diagenetic environments. The only textural approximation of such a change is the unusual hot spring alteration of some aragonite ooids reported by Richter and Beseneker (1983, fig. 4). Even that fine scale change produced textural and presumably also optical disruption.

saics are most readily recognized petrographically by the transecting relationship between the replacement crystals and the original structure reflected by relics (Bathurst, 1964; Sandberg, 1975a). Those organic relics commonly render the calcite pseudopleochroic (Hudson, 1962) and delineate original structures, especially growth lineations. The Sr content remaining after calcitization is dependent on the openness of the diagenetic system (both intergranular flow and intragranular diffusion, Pingitore, 1976) and on the original Sr content of the aragonite. Hence some calcitized aragonites may have significantly lower Sr content than co-existing ones (*e.g.*, of other taxa). Molds are equivocal indicators of allochem mineralogy. Although they are common for aragonitic components, they are also known for calcitic components, even in undolomitized rocks.

If the pseudomorphic calcitization so commonly alluded to in the literature were a reasonable diagenetic fate of aragonite it is curious that it only seems to affect skeletons of extinct taxa, plus ooids and cement, all *inferred* to have been originally aragonitic. In effect, it is an example of the "taxonomically selective" unusual alteration rejected in the previous section of this paper. Even instances of solid state alteration of aragonite produce irregular calcite mosaics like those seen in natural aqueous diagenesis (Land, 1967; Kamiya, 1974).

#### Neomorphic Calcite Mosaics

Calcitized known aragonites, whether skeletal or non-skeletal, have a variety of textural, optical and compositional properties in common: 1. Crystals are commonly brownish, often pseudopleochroic (Hudson, 1962; Talbot, 1972; Bathurst, 1975; Zorn, 1977; Sandberg and Hudson, 1983); 2. Boundaries of calcite crystals commonly transect irregularly the original aragonite microstructure revealed by inclusions; 3. Calcite crystals are 5 to 1000+ times larger than original aragonite crystals; 4. Inclusions of organic matter (Bathurst, 1975), fluid inclusions, and often even oriented relics of the original aragonite occur throughout the replacement calcite (Sandberg *et al.*, 1973; Sandberg, 1975a, b); 5. Commonly the calcites have elevated Sr content, which is at best only partly attributable to incorporated aragonite relics (Sandberg and Hudson, 1983, table 1). Bathurst (1964) presented additional properties for differentiation of calcitized aragonite from calcite cements, based mainly on morphology and arrangement of crystal mosaics and crystal boundaries.

The brownish color and pseudopleochroism appear to be controlled by the included organic matter (Hud-

son, 1962; Sandberg and Hudson, 1983). Although the positions of calcite crystal boundaries are sometimes determined by organic sheets at microstructural boundaries (most notably in calcitized molluscan shells), their positions commonly show little influence by organic structures preserved as relics. Continuation of growth of a neomorphic calcite crystal must depend largely on crystallographic orientation relative to adjacent crystals and to the direction of advance of the alteration front, as well as the behavior, at the front, of impurities (incorporation as inclusions, locking of grain boundaries, serving as nucleation sites, etc.). The combination of textural disruption and elevated Sr content is indicative of a calcitized aragonite. The inclusions (item 4 above) are distinctive and important enough to warrant a separate discussion.

#### Inclusions in Calcitization Mosaics

The organic matter responsible for pseudopleochroism or for brown structural relics in light microscopy is apparently composed of individual elements so small and so finely disseminated that they are not, in my experience, generally recognizable on polished, etched surfaces in the SEM.

The incorporation of fluid inclusions during calcitization of aragonite appears to be facilitated by the transformation of a complex array of minute aragonite crystals, with organic matrix and abundant intercrystalline spaces of diverse sizes, into much larger, inclusive calcite crystals. The larger fluid inclusions which permeate calcitized skeletons (*e.g.*, in the Key Largo Limestone) are readily seen in the light microscope, down to the resolution limits of that instrument. If one examines highly polished (0.05  $\mu\text{m}$  alumina), very slightly etched (0.1% formic acid, 15–20 sec.) surfaces of such calcitized skeletons in the SEM, two very small-scale properties become visible. Most surprising of these is the presence of oriented inclusions of the original aragonite throughout the neomorphic calcite of many calcitized skeletons. These relics, in their original orientations, give evidence of the very fine scale of the replacement process (Sandberg *et al.*, 1973). Their location, enclosed within large crystals of the stable polymorph, would seem likely to protect them from further alteration. The presence of abundant similar relics in diverse Paleozoic and Mesozoic calcitized aragonites (Sandberg and Hudson, 1983; Sandberg and Popp, 1981 and in preparation; Sandberg, unpublished data), both skeletal and non-skeletal, supports this interpretation. Once one is aware of the presence and appearance (Sandberg, in press, fig. 5) of the aragonite relics as seen with the SEM and confirmed by X-ray and/or staining, many even quite small relics can be recognized with



the light microscope. They are detectable primarily through difference in extinction angle, relative to the larger, enclosing calcite crystal. It is evident, however, that many calcitized aragonites contain very small, sometimes relatively uncommon aragonite relics which would not be detectable by light microscopy.

The presence of aragonite relics as oriented solid inclusions is unequivocal evidence of the original aragonite mineralogy of that carbonate constituent. In some calcitized aragonites, the relics are extremely abundant, comprising perhaps 10–15 percent of the carbonate (Pl. 1, fig. 1; and Sandberg and Hudson, 1983). Fluid inclusions are not so common in such specimens. In some specimens, perhaps aided by a relative rarity of aragonite relics, one can see numerous pits (Pl. 1, figs. 2–4). A first interpretation of these might be that they are molds of former aragonite relics dissolved away before complete engulfment at the diagenetic front, or during specimen preparation. The abundance of those pits on some very slightly etched (Pl. 1, fig. 4), or even unetched, polished sections indicates that most of them are fluid inclusions. Sizes down to 0.2  $\mu\text{m}$  are not uncommon.

The near absence of such fluid inclusions from the coarse calcite cements adjacent to such calcitized skeletons (Pl. 1, figs. 3, 5, 6) is noteworthy. Combined with the absence of aragonite relics and the clear, colorless appearance of those cements, it indicates that the cements are not calcitized aragonite. Note that fluid inclusions alone are *not* diagnostic for calcitized aragonites. They occur commonly in finer, often drusy calcite cement sequences which may be recrystallized high Mg calcite cements. Aragonite cements certainly do occur adjacent to calcitized skeletons in the Pleistocene. An apparently common fate of such aragonite cements in the Key Largo Limestone, in contrast to Pingitore's findings (1976, p. 988) in Barbados, is encasement in meteoric calcite cement. Surprisingly, similar first-generation aragonite cements have survived, encased in calcite cement, in rock as old as Carboniferous (Sandberg and Popp, in preparation). The skeletons on which such cements grew are calcitized, like their Pleistocene counterparts. That condition is further support of the general observation (*e.g.*, Land, 1967) that skeletal aragonites are more susceptible to alteration than non-skeletal.

It appears that, even within a skeleton, void-fill calcite and neomorphic calcite may be differentiable using distribution of relics and fluid inclusions. James (1974, text-fig. 7d) noted the occurrence, in trabecular centers in *Acropora palmata*, of clear calcite contrasting to surrounding calcite with "ghost texture." Chalkification of coral skeletons prior to calcitization (James,

1974; Pingitore, 1976) increases the microvoids in the skeleton. Because these microvoids contain no skeleton to calcitize, it is cement which precipitates into them. More complete removal of aragonite, as in the trabecular centers, can produce substantial voids visible in the light microscope (*e.g.*, James, 1974; Pingitore, 1976). When the diagenetic regime later changes from dominantly dissolution to calcite deposition, cement deposited in such voids may be differentiable if the voids are sufficiently large. Some apparent examples of such intermixing of cement and neomorphic calcite on a very fine scale occur (Pl. 1, figs. 5, 6) in corals from the Key Largo Limestone. The calcite cement in the trabecular center shows the same crystallographically dependent etching pattern as the surrounding neomorphic calcite, but no fluid inclusions or aragonite relics. One must be cautious about interpreting absence of relics as indicative of cement. In some calcitized shells with abundant organic relics of original structure there may be few or no aragonite relics. In some, the aragonite relics have a patchy distribution. Presence of cement regions is best supported by clear (versus brownish) calcite in thin section, and is most likely in some morphologic locations, such as the trabecular centers in scleractinian corals (Pl. 1, figs. 5–7; James, 1974, figs. 7c, d; Pingitore, 1976, fig. 8).

That cement and neomorphic calcite should occur intermixed is hardly surprising. Effectively, all neomorphic calcites replacing polycrystalline aragonite have a cement component, commonly not differentiable, occupying what was intercrystalline space in the original aragonite. In some quite porous skeletons (*e.g.*, many codiacean algae), the cement component can be considerable. Such easily overlooked "hidden" void spaces in many aragonites could be more than enough to absorb the 8 percent "excess" carbonate generated by calcitization.

Only when the dimensions of the intraskeletal microporosity become relatively large, as in the illustrated coral, can the cement be differentiated from adjacent neomorphic calcite. Both calcites are part of the same crystal (Pl. 1, figs. 5, 6), an intraskeletal example of Pingitore's (1976) cross-cutting mosaic. All these last observations serve to underscore the earlier observation (Sandberg *et al.*, 1973, p. 133) that processes of dissolution of aragonitic shells and precipitation of void-fill calcite differ mainly in scale and relative timing from calcitization of aragonite across a thin diagenetic front. On a larger scale, the presence of aragonitic and fluid inclusions allows ready differentiation of replaced skeleton and adjacent inclusion-free calcite cement in larger intra- or interskeletal pores (Pl. 1, fig. 3). The presence of apparent void-fill calcite in the

trabecular centers suggests a significant dissolution phase prior to the inception of calcite deposition as void-fill and neomorphic spar. However, other partially calcitized aragonite skeletons from Key Largo material indicate that leaching and a chalkified state are not necessary precursors of calcitization. Indeed, chalky alteration is notably less common than thin-film alteration, when calcitization fronts are preserved.

#### The Calcitization Front

Partially calcitized aragonite skeletons of diverse taxa can be frequently observed in the Pleistocene, less commonly in older rocks (Sandberg and Hudson, 1983). The characteristic appearance of that alteration is a contact between replacement calcite and original aragonite along which there may be considerable chalky porosity, or more commonly only a thin interface perhaps no more than a few hundred Ångströms across (Wardlaw *et al.*, 1978). The position and orientation of the diagenetic front may be spatially controlled at least locally by skeletal structures and organic matrix distribution in and between microstructural units of the skeleton (*e.g.*, Kamiya, 1974). Typically, however, the front transects original structure of the aragonite quite irregularly. Both the alteration front and the processes acting at it have been described in diverse ways in the literature (*e.g.*, Folk, 1965; Matthews, 1968; Kinsman, 1969; Spiro and Hansen, 1970; Pingitore, 1970, 1976; Brand and Veizer, 1980). A few of the terms applied, most notably "inversion," have unfortunate implications of dry, solid-state alteration not found in natural diagenetic environments (Bathurst, 1975, p. 475). Both the general textural properties and the observed changes in isotopic and cation compo-

sition in natural calcitized aragonites show that a solution phase is involved at the alteration front. Despite demonstrable alteration across "very thin" fronts, calcitization of aragonite skeletons of diverse taxa does not retain the fine texture. Not only are the neomorphic calcite crystals 5 to 1000+ times larger, their shapes and boundaries are usually very irregular, relative to the replaced aragonite.

As noted by Matthews (1968), the rate-limiting step in calcitization of aragonite is the nucleation of calcite crystals. In the monomineralic mass of an aragonite skeleton, scattered nucleation and subsequent porphyroid growth of calcite have not been observed. Calcitization often begins at the periphery, perhaps commonly nucleating on calcite in the matrix, and proceeds inward. Frequency of calcite nucleation at the messenger film must be influenced by degree of supersaturation and the effect of organic matrix "impurities" in locking grain boundaries. The typical overall textural result of calcitization is a considerable, even extreme, increase in crystal size. In polyminerally but aragonite-dominated lime muds, generally much smaller crystals are produced by the calcitization because of the abundant, pre-existing calcite nuclei. Those "micrite" crystals are normally about 2–20  $\mu\text{m}$  in diameter, and their other neomorphic properties are, on a small scale, quite like those found in calcitized ooids, cements, and skeletons (Lasemi and Sandberg, 1983 and in preparation).

#### Calcitization of Non-Skeletal Aragonites

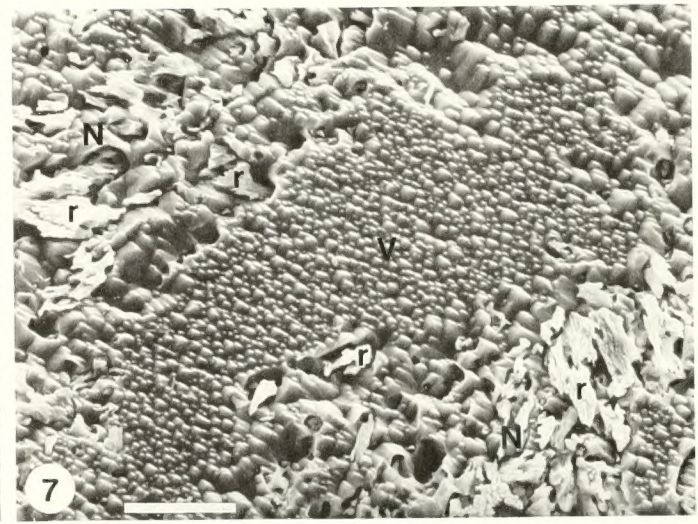
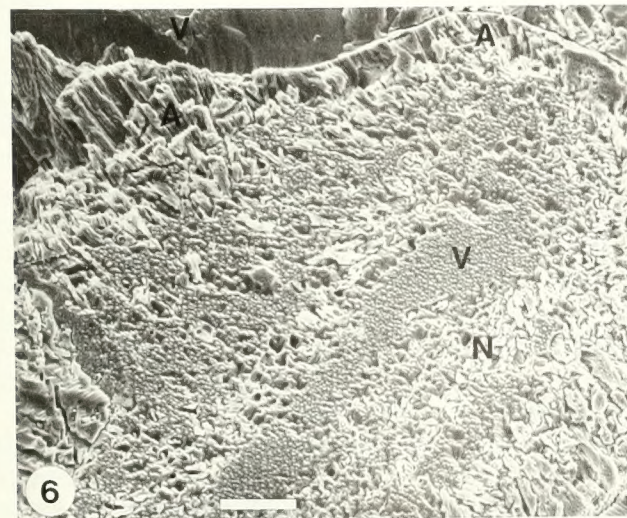
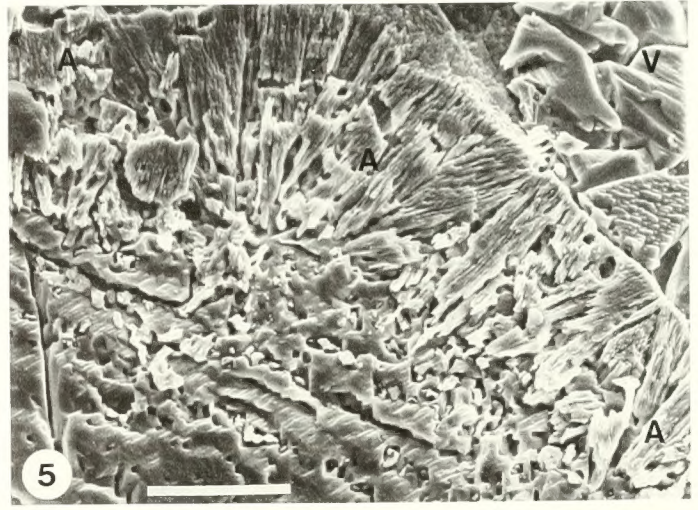
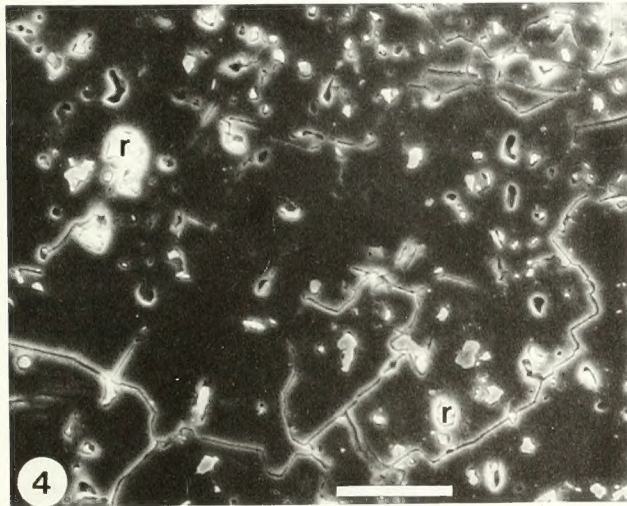
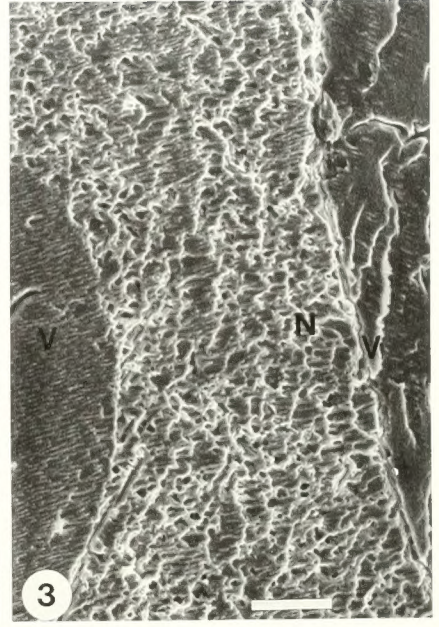
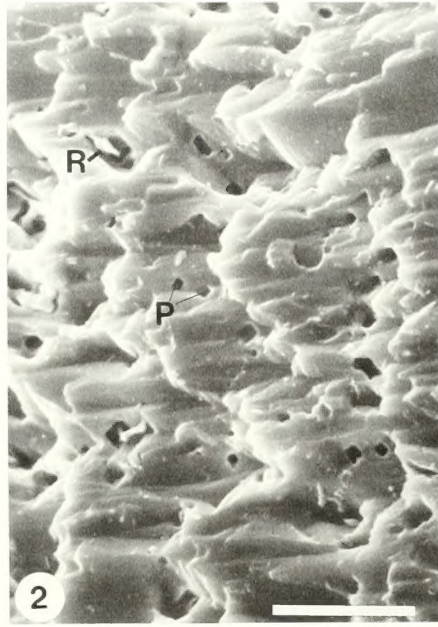
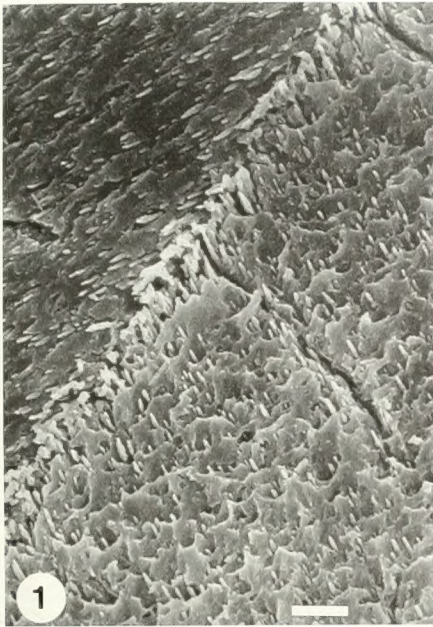
Non-skeletal constituents known to be aragonite do not alter differently from skeletal aragonites discussed above. Calcitized ooids in the Miami Oolite exhibit the same coarse calcite mosaic irregularly transecting

#### EXPLANATION OF PLATE I

All figures are scanning electron micrographs of polished, etched sections of skeletons of calcitized or partially calcitized gastropods (fig. 1) or scleractinian corals (figs. 2–7), Key Largo Limestone, Pleistocene, S. Florida.

#### Figure

1. *Strombus* species  
Boundary between two adjacent crossed-lamellar units. Note the two orientations of the included aragonite relics. The entire field of view lies within one replacement calcite crystal. Bar scale = 2  $\mu\text{m}$ .
2. *Porites divaricata*  
Rather strongly etched section. Note partly dissolved relics (R) and numerous pits (P, mainly etched defect structures and/or fluid inclusion voids). Bar scale = 5  $\mu\text{m}$ .
3. Same specimen shown in figure 2  
Pitted neomorphic calcite (N) and unpitted relic-free void-fill cement (V) forms a cross-cutting mosaic to the left (shown by continuity of crystallographic etching pattern), but a fabric-selective boundary to the right. Bar scale = 20  $\mu\text{m}$ .
4. *Montastrea annularis*.  
Polished, very slightly etched (0.1% formic acid, 15–20 sec.) section. Note scattered bright aragonite relics (r) and somewhat more numerous dark pits (fluid inclusions). Bar scale = 10  $\mu\text{m}$ .
- 5–7. *Porites divaricata*  
Note the irregular, ragged alteration front between unaltered trabecular skeletal aragonite (A) and neomorphic calcite (N) with relics (r) of the original aragonite. Void fill calcite cement (V) occurs both externally (as a fabric-selective cement) and within open space in the skeleton, such as the trabecular centers (figs. 6, 7). Bar scales = 20  $\mu\text{m}$  (figs. 5, 6) and 10  $\mu\text{m}$  (fig. 7).



the original layering, and preserve aragonite inclusions in their original orientation (Sandberg, 1975b, figs. 17–19). Similar calcitized ooids, with few aragonite relics, occur in the Upper Carboniferous of the North American mid-continent (Sandberg and Popp, 1981 and in preparation). Botryoidal cements, morphologically similar to the modern botryoidal aragonite from the Belize barrier reef (Ginsburg and James, 1976), occur in various locations in early Mesozoic and late Paleozoic rocks (Sandberg, 1983 and in press). Those ancient botryoids: 1. have the same coarse, irregular textures as the calcitization mosaics described earlier, 2. are sometimes pseudo-pleochroic, and 3. often have elevated Sr content (Mazzullo, 1980). In the Upper Carboniferous of southeastern Kansas, small botryoids have similar calcitization mosaics and also contain oriented relics of the relatively large aragonite rays which originally composed the botryoids (Sandberg, in press).

The essential identity of replacement properties in the botryoids and in the ooids and diverse skeletons discussed above underscores another point: the supposed role of variation in organic content as a means of preservation of fine texture during calcitization is not supported. Calcitization of molluscs, with their high organic contents, co-existing scleractinian corals with relatively low organic contents, and botryoidal aragonite cements with quite low organic contents produces comparable coarse, irregular mosaics of neomorphic calcite.

#### Calcitization and Rugosan Skeletons

One may reasonably ask what independent external data support the contention that calcitization of aragonite could have produced the fine, regular textures seen in rugose coral skeletons. The ooid examples appear to have been important here. In fact, the “coral and ooid analogies” have been mutually supportive. However, both lack support in observed calcitized aragonites. Rugosan skeletons, even when co-existing in impermeable lithologies with very well preserved aragonite skeletons of other taxa (Stehli, 1956), are invariably calcite. Calcitization, in the Pleistocene, of skeletons of still-living species of aragonitic scleractinian corals (and mollusks, algae, etc.) does not produce even a remote approximation of the regular skeletal microstructures found in rugose corals.

Arguments are sometimes voiced that diagenetic states in Pleistocene carbonates are transitory, destined to be obliterated by more “complete” alteration. That view is testable, particularly by combining light microscope and SEM study with mineralogic-elemental analyses (X-ray, atomic absorption spectroscopy, microprobe, etc.). Such integrated studies show that cal-

citization products which are essentially indistinguishable from those in the Pleistocene occur well back, even into the Paleozoic (Sandberg and Hudson, 1983; Sandberg, 1983; Sandberg and Popp, 1981 and in preparation). Furthermore, there is nearly identical alteration of molluscan shells from near-surface conditions (Pleistocene, South Florida; Sandberg *et al.*, 1973) and deep burial conditions (Jurassic, Scotland; Sandberg and Hudson, 1983). These latter observations refute possible claims that texturally retentive calcitization is the product of alteration in relatively less understood or studied burial environments.

Zorn (1977, p. 344) suggested that, if one accepts the view of Oekentorp (1972) that rugose corals were originally aragonite, like scleractinians, then occurrences of the two in similar facies should produce diagenetic products similar to one another and to other co-existing taxa with originally aragonite skeletons. Zorn's data on Triassic scleractinians and Devonian rugosans (and associated fauna) do not show that predicted similarity. Rather, as noted by Sorby (1879) and Sorauf (1971, p. 29), rugosans behaved diagenetically like coexisting calcitic forms. If rugosans were originally aragonitic, then at least statistically they should show diagenetic behavior similar to that of coexisting taxa with aragonite skeletons, *e.g.*, gastropods, bivalves, and nautiloid cephalopods, and dasyclad algae. In the Ordovician of the mid-continent U.S.A., the latter taxa are essentially universally preserved as molds or as void-fill calcite casts. Coexisting rugosans, in contrast, show well-preserved calcite skeletal structures. Data do not support “explanation” of that distinction on the basis of differential diagenetic susceptibility among different aragonite skeletal ultrastructures. Highly porous algal aragonite and dense molluscan aragonite are similarly affected. Furthermore, in the Pleistocene, there are reversals of the sequence of susceptibility among ultrastructures. For example, the relatively coarsely prismatic myostracal layers in bivalves may be generally more resistant (Sandberg and Hudson, 1983, fig. 4E, F) or less resistant (Sandberg, unpublished data) than adjacent, fine crossed-lamellar or complex crossed-lamellar aragonite. The difference does not lead to fine regular calcite in any case; it is basically a question of when the textural disruption (or dissolution) will occur. The approach suggested by Zorn is applicable to the investigation of original mineralogy in stromatoporooids, tabulates, or, as suggested by Sorby (1879, p. 68–69), any “doubtful” fossil group.

Cuif (1974) suggested that similarities existed between the calcitized trabecular centers of a Triassic scleractinian coral and skeletal calcite of Paleozoic chaetid tabulate corals. The implication was that skel-

etal calcite of Paleozoic corals could be derived by calcitization of aragonite as in the Triassic specimen. Although light microscope data were not supplied, the details of the SEM photos provided do not, in my view, support that suggestion. The calcitized portion of the scleractinian is large relative to the skeletal crystallites of either the chaetitids or the scleractinian but appears, from the general alignment of crystal margins, to be a single crystal. The magnified region of the non-porous chaetitid skeleton shows sutured crystals that are probably spherulite calcite (compare Sandberg, 1971, figs. 4–6).

A recrystallization front proceeding from the outside inward was suggested by Sorauf (1971) as potentially responsible for generating lamellar structure in rugose corals. Recrystallization fronts beginning at the exterior are common in scleractinian corals, as noted by Matthews (1968) from the Pleistocene of Barbados. I have seen such fronts commonly in the Key Largo Limestone, particularly in columnar colonies of *Montastrea annularis* (well portrayed in the walls of the Coral Gables City Building and the Key West Post Office). It is true that the general orientation of such fronts is parallel to the outer colony surface. However, in detail, the fronts are not at all parallel to the individual skeletal elements of the corallites composing the colony. They cut quite irregularly across septa and walls, leaving behind an irregular mosaic of calcite crystals. These crystals are drastically different in size, shape and orientation from the crystals comprising lamellar ultrastructure, or any other ultrastructure, in rugosans.

### CONCLUSIONS

1. Diagenetic behavior of aragonite shows a surprising uniformity among skeletons of diverse taxa. Where calcitization has occurred, the texture is disruptive, transecting original structure, *i.e.*, “pseudomorphic” or “paramorphic” alteration does not occur. Relics (both organic and aragonitic), fluid inclusions, and elevated Sr content are common in the replacement calcite.

2. There does not appear to be any justification for inferences that differences among aragonitic ultrastructures can account for retention or obliteration of fine texture in ancient, presently calcitic constituents, or that differences in diagenetic environments can explain such preservation differences (assuming starting material was aragonite in all cases).

3. The calcite ultrastructures composing rugose corals cannot reasonably be derived by calcitization of aragonite precursors. If rugosans had originally possessed aragonite skeletons, then at least statistically

their preservation states should be dominated by the disruptive textures (and moldic or void-fill preservation) that universally characterize altered scleractinian corals.

4. The preceding conclusions are equally applicable to other carbonates inferred to be calcitized aragonite, *e.g.*, inozoan sponges, belemnite rostra, radial fibrous calcite cements, ooids, etc.

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## ARAGONITE AND DIAGENESIS IN PERMIAN CORALS

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## ABSTRACT

Permian corals of Afghanistan and Timor are characterized by greatly thickened structural elements; septa touch one another. These skeletal elements display a fibrous structure which has been regarded as representing "an extremely well-preserved microstructure" and of primary origin. Thus, it was formerly postulated that the skeleton was calcitic. However, these microstructures, in spite of their seemingly excellent preservation, are not primary. Micritised septa are often enveloped by thick fibrous carbonate coating. In other cases, distinct recrystallization fronts with irregular margins have been observed, and simultaneously occurring fibrous, pseudolamellar and zigzag structures are found. The two latter structures have previously been recognized as being secondary. Dark, saw-toothed growths within the septa are calcite scalenohedra resulting from recrystallization without destroying the skeletal architecture or the previously developed secondary skeletal texture. In contrast to the Scleractinia, Permian Rugosa possess a variety of different microstructures: fibrous, micritic, fan-shaped and fountain-like, pseudolamellar or zigzag structures, recrystallization fronts, septal foldings, development of cement and scalenohedra, which indicate their secondary nature. Alteration and septal folding took place before the formation of cement, and recrystallization was prior to burial, as shown by algal borings. These complex alterations can perhaps be explained if the skeleton was not composed of calcite. Recrystallization fronts suggest that the skeletons were initially composed of a different material, aragonite, as is the case in Scleractinia. However, calcite-to-calcite transformation should not be excluded, as a possible cause of the structures noted.

## INTRODUCTION

The first detailed investigations of the microstructure of the skeleton in Permian corals were carried out by Schindewolf (1942). Schindewolf proposed a standardization of skeletal microstructures and outlined the morphogenesis of the skeleton, especially of the septa. These considerations were accepted by later authors, e.g., Schouppé and Stacul (1955, 1959, 1966). Most authors believed that the excellent microstructural preservation was primary (*i.e.*, controlled by the polyp).

Kato (1963) first doubted the primary nature of certain of these structures, as did Oekentorp (1972, 1974, 1977, 1980), Schouppé and Oekentorp (1974), and Sorauf (1971, 1977, 1978, 1979). The existence of diagenetic artifacts in skeletal structure was confirmed. At the same time, discussion of the original nature of the skeletal material was revived: aragonite versus calcite. The possibility of aragonite being the original skeletal material, as in the Scleractinia, was discussed by Oekentorp (1980). This question remains unsolved, although arguments in favor of calcite predominate. Increased knowledge of mineralogical reaction of calcite during diagenesis will help to solve the questions raised in the following sections.

## SKELETAL STRUCTURES IN PERMIAN CORALS

In Scleractinia two microstructures exist: trabecular and fibrolamellar. In Paleozoic corals a multitude of

septal structures have been described. Some of them, in particular those of Permian corals, are briefly mentioned and illustrated here (see also Oekentorp, 1980):

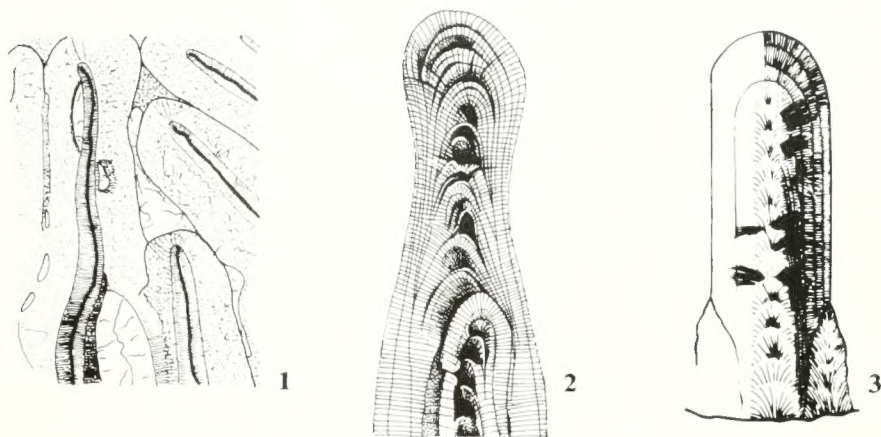
1. fibro-lamellar structure, with distinct median line
2. fibro-lamellar structure, with frontal zones
3. fountain-like structure
4. zigzag structure
5. pseudolamellar structure
6. trabecular structure

In comparing the Scleractinia with the Rugosa, the unavoidable question which arises is, how is this multitude of structures established and genetically controlled in simple animals such as rugose corals? These problems are emphasized by numerous cases in which several clearly discernable microstructures, some of which have been described as primary, occur in the same corallum and are recognized in one thin section. The following discussion of these septal microstructures may help to elucidate the problem.

## Septa with Fibro-Lamellar Microstructure and Median Line

This type of microstructure is frequently observed in Permian and other Paleozoic corals. The septum contains a complete, dark median line with calcitic fibers orientated normal to it on both sides and to the front (Text-fig. 1; Pl. 1, figs. 1, 2). Schindewolf (1942) proposed that the septal pocket grew to a predetermined length prior to formation of the septum. The





Text-figures 1–3.—(1) *Timorphyllum wanneri wanneri* Gerth, 1921, Lower Upper Permian of Afghanistan. Septa with dark median line and fibers oriented normal to it are enveloped by diffusely fibrous to cloudy carbonate (compare Pl. 1, figs. 1, 2). (2) *Calophyllum (C.) rossica* (Schindewolf, 1942), Lower Upper Permian of Samara, U.S.S.R. Septum thickened by fibro-lamellar carbonate and median line interrupted by semicircular recrystallization fronts. (3) *Wannerophyllum cristatum* (Gerth, 1921), Lower Upper Permian of Timor, Indonesia. Septum formed by semicircular “Stirnzonen” (frontal zones) coated by fibro-lamellar carbonate with saw-toothed formations, *i.e.*, scalenohedra. (Drawing from Schouppé and Stacul, 1966, fig. 27).

growth lamellae may be suppressed and the fibers appear uninterrupted. In some specimens, the fibers are not discernable; they appear diffuse, or the skeletal material is cloudy (Pl. 1, fig. 2). The fibrous/cloudy carbonate is separated from the central area of such septa by a dark line (Text-fig. 1; Pl. 1, fig. 2).

#### Septa with Interrupted Median Line and Fibro-Lamellar Structure

The median line of these septa is interrupted by the intercalation of semicircular, lighter lamellae composed of fibers oriented perpendicular to the semicircle. These semicircular lamellae only occupy a small

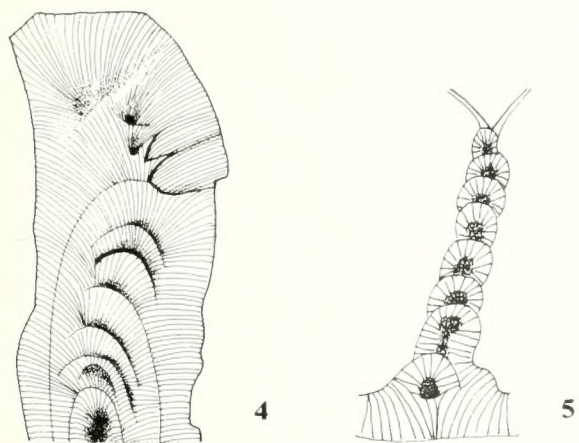
area and are limited at the core of the septum. Schindewolf's interpretation was that this type of septum was built up in single steps, in the axial direction until reaching its full length, similar to the type that follows. Only then was the carbonate coating formed which enveloped the septal core (Text-fig. 2; Pl. 1, fig. 2). In this context, frequently occurring changes of direction of the median line are striking and, according to Schindewolf (1942), are connected with the lateral shift of the front of the septal pocket.

#### Fibro-Lamellar Structure Without Median Line

This type of microstructure is marked by a fountain-like orientation of the fibers in the core region of the septum. A median line is absent (Pl. 1, fig. 4). At the flanks, the septum, after reaching its full length is coated by a fibro-lamellar carbonate coating (Text-fig. 3). Here, it should be stressed that the dark triangular, saw-toothed structures observed in the carbonate coating, and which protrude into the septal area, are due to crystallization (Text-fig. 3; Pl. 1, fig. 5). This mode of septal formation grades into the following type.

#### Septa with Frontal Zones

Here no median line exists, or if so, it is only partially developed. In many cases, the uniform coating by fibro-lamellar calcite is absent. The septa are built up by widespread rims, the so-called “Stirnzonen” (frontal zones) in the sense of Schindewolf (1942) and Schouppé and Stacul (1966), which are composed of fan-like oriented fibers (Text-figs. 4, 5; Pl. 2, fig. 7).



Text-figure 4.—*Calophyllum (C.) rossica* (Schindewolf, 1942), Lower Upper Permian of Samara, U.S.S.R. Septum consists of broad semicircular, brightened “Stirnzonen” (frontal zones).

Text-figure 5.—*Amplexocarinia jonkeri* (Koker, 1924), Lower Upper Permian of Timor, Indonesia. Septum consists of semicircular “Stirnzonen” only; the darker parts perhaps are relics of the dark median line. (Drawing from Schouppé and Stacul, 1959, fig. 4.)

According to Schindewolf and other authors, successive secretional layers are assumed to have been deposited without additional accumulation of a carbonate coating. It should be stressed that these frontal zones are remarkably lighter in color than the other skeletal material.

#### Septa with Zigzag Pattern

Widely different from the above structural features is the so called zigzag pattern. Here, no fibers oriented normal to the skeletal surface are seen, but only fiber-like units, which with adjacent lamellae produce a zigzag pattern (Pl. 1, fig. 6). This pattern seems relatively regular but not in detail. The secondary nature of these structures has been established by Oekentorp (1972) and was discussed by Sorauf (1978).

#### Pseudolamellar Structure

This term was introduced by Oekentorp (1972) and used for a microstructure in which (as in the zigzag pattern) no fibers are recognizable. This structure is characterized by fine lamellar-like structural units oriented mostly obliquely to the skeletal surface (Pl. 1, fig. 7). This microstructure is attributed by me to shearing processes. The "lamellar structure" discussed by Yü and Oekentorp (1983) however, seems to be quite different from the pseudo-lamellar structure.

#### Discussion

The examples listed above are only a small selection of the total known, but indicate how manifold the problems concerning microstructures are, especially when one takes into account that these structures may occur together in the same corallum. This multitude of structures makes it less likely that these are all primary in nature. Furthermore, it should be noted that the appearances of the structures themselves may be quite variable. Thus, fibers may be arranged in distinct lamellae, or lamellae may be absent. The fibers themselves show all transitions from distinct to diffuse fibrous structures to a "fiberless" cloudy structure. Localized brightening is also characteristic, as well as the development of darker triangular features with apparently spindle-like cluster of fibers (Pl. 1, figs. 5, 10; Pl. 2, fig. 1). Zigzag lamellae interchange with those of normally oriented fibers and occur together with pseudolamellae (Text-fig. 6). In addition, the development of septal margins is important; the margin can either be blurred or the septal rims may be irregularly toothed (Pl. 1, fig. 4). Distinct septal margins occur as primary structures. The microstructural appearances in Permian corals seem more likely to have developed in the course of diagenesis.

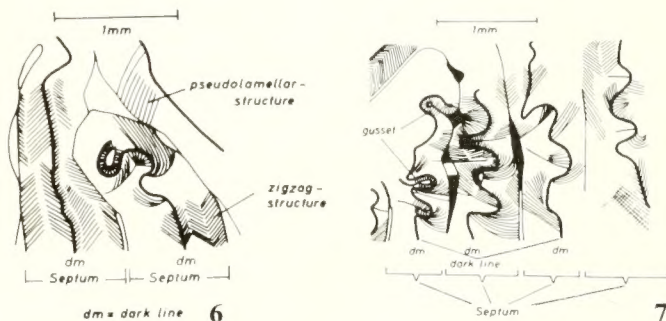
As already mentioned, these structures were assumed to be primary and regarded as revealing the morphogenesis of the coral skeleton. Possible recrystallization and diagenetic changes were not considered. Thus, it was postulated that the skeletal carbonate must have been initially calcitic, either as high-Mg calcite (Richter and Füchtbauer, 1978) or low-Mg calcite (Sorauf, 1978). It is, of course, not possible to prove whether the Rugosa were initially aragonitic or calcitic. It is my concern here to show that the so-called primary nature of the microstructures described must be looked at with the greatest caution. These microstructures are, in my opinion, largely of secondary origin and developed in the course of diagenesis.

#### DIAGENETIC STRUCTURES

Modifications of skeletal structures in Paleozoic corals can be observed, but cannot always be proved. The primary structure of the skeleton can be transformed into a secondary, more or less well-ordered structure due to recrystallization during diagenesis. Furthermore, thickening of the skeleton by cements can develop and can even simulate primary skeletal thickening.

#### Septal Thickening by Cement Formation

My observations concerning the secondary nature of skeletal structures originated with Permian corals from Afghanistan. In different individuals extreme septal folding was found that could hardly have developed during the lifetime of the polyp (Pl. 1, figs. 7, 8). In most cases this folding only affects the dark median line which varies from slightly waved, in part rectangularly bent, to extremely folded with a sinuous course (Pl. 1, figs. 7, 8; Text-figs. 6, 7). The pattern of development within one corallum can differ greatly: this deformation can be absent in some parts, while in others extreme folding is present. The foldings largely



Text-figure 6, 7.—Gen. et sp. indet., Upper Permian of Afghanistan. The drawings are to make clear the situation figured in Plate 1, figs. 7–8, but note that the "septum" mentioned in the drawing does not correspond to a true biogenic septum.

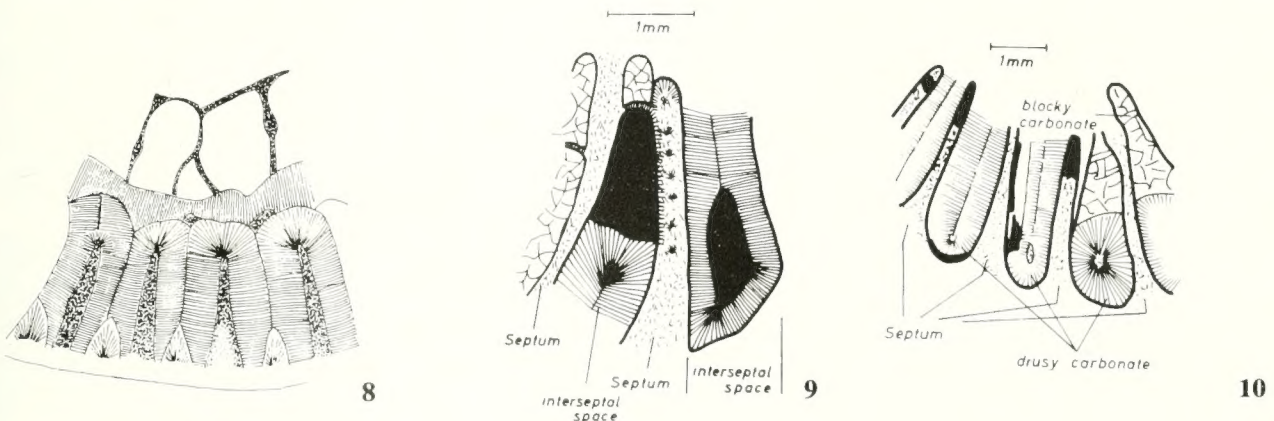
affect primary septa which have been coated by cement, and then recrystallized, and can only be identified in certain kinds of preservation. In addition, the formation of a pseudolamellar or zigzag pattern hinders the identification of this feature. During the folding of the septa (including the median line) neighboring parts of one and the same septum come to lie next to each other. Smaller wedges or recesses were formed which now are not filled by biogenic carbonate. These recesses, produced by the folds, lie within a thick carbonate coating, thus giving "septa" which seem to be of primary origin. These "septa" touch each other, and because of the development of zigzag and pseudolamellar structures, septal boundaries are not recognizable.

*Discussion.*—Initially it appears that the formation of wedges and recesses indicates the presence of a primary septum. The original thickness of the septum may be derived from the distance between the median line and the rim of the recess (Text-fig. 7), and consequently, the carbonate coating must have been deposited after the folding. Another indication of this is the group-coating of several septa.

How did this peculiar skeletal structure form? The folding is not of primary origin, because the recesses are devoid of skeletal material. The folding, therefore, has to be attributed to lateral compression, the cause of which is not easily understood. Compaction, as well as tectonic strain can be excluded, as these factors normally occur in the later phase of diagenesis. The folding is probably of early diagenetic origin, because the carbonate coating of the recesses produced by the folds is not a biogenic feature, but was deposited after deformation of the septa. This coating is cement, and de-

position took place at a very early stage of diagenesis. There is no obvious reason why changes in structure and architecture should have been produced by a simple calcite transformation. It is more logical to attribute these changes in structure to a change in the primary material, *i.e.*, a possible change of aragonite to calcite, especially as calcite needs about 8 percent more space than aragonite. This is only one possible interpretation, but it will be taken as the hypothesis for this investigation.

Folding of the septa led me to the assumption that the material coating and thickening the skeletal elements must be regarded as secondary cement that filled the empty spaces between the septa. It was deposited with perpendicular orientation of the fibers and in part shows marked lamellae. At times the cements are only present as a rim of cloudy carbonate (Pl. 1, fig. 2). These observations and assumptions must be corroborated, especially as similar thickenings are of special significance in the taxonomic and morphogenetic understanding of many groups of Paleozoic corals. This has led to extensive investigations of large collections of corals; the most important information in connection with this problem was gained by study of corals from the Permian of Afghanistan and Indonesia. From here, numerous corals show marked thickening of the septa, almost leading to touching of adjacent septa (Pl. 1, figs. 5, 9, 10; Text-fig. 8). In many cases it is difficult to determine how much secondary carbonate has coated a primary septum. Without the deformation described above one would not have regarded these thickenings as cements. The thickenings may affect the entire corallum (Pl. 1, fig. 9) and fill all interseptal spaces; they can fill all but the axial area or fill only the axial



Text-figures 8–10.—*Verbeekiella* sp., Upper Permian of Afghanistan.

8. Micritized septa are coated by fibrous carbonate not arranged in lamellae.
9. Septa micritized with occasional fan-shaped orientation of fibers. Interseptal spaces filled by fibrous cement, coarse grained cement, and ankerite. (Compare with Plate 1, fig. 12: right side.)
10. Septa micritized; interseptal spaces filled with perpendicularly oriented fibrous cement, and coarse grained cement.

spaces (Pl. 1, figs. 9, 11, 12). The thickening may be limited to quadrants (Pl. 1, fig. 12) or absent in all upper parts; it may occur only on parts of the septa, e.g., only one flank, or may be deposited only on peripheral parts (Pl. 1, figs. 11, 12). The "septa" themselves have either light or dark central areas (Pl. 1, figs. 5, 9, 13), in which a median line is hardly or not at all recognizable. The microstructure in the core region differs from that in the flanks; it is fibrous or fountain-like, sometimes interrupted by dark triangular protrusions which originate from the carbonate flanks (Pl. 1,

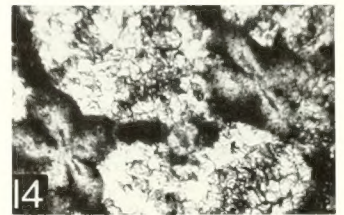
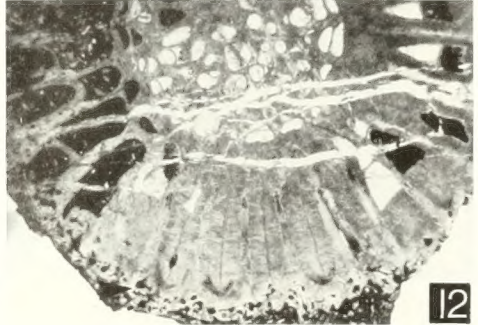
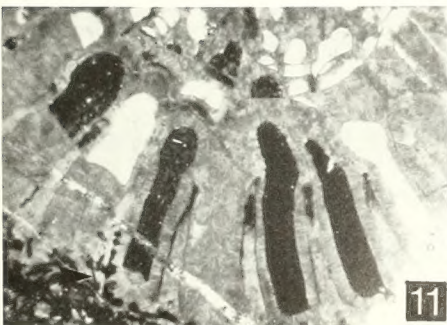
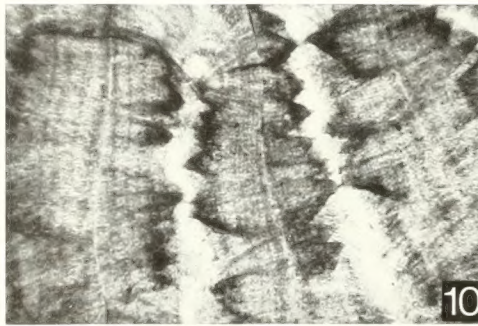
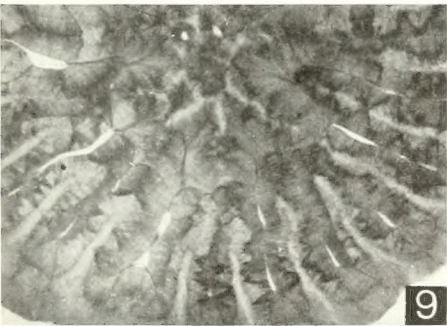
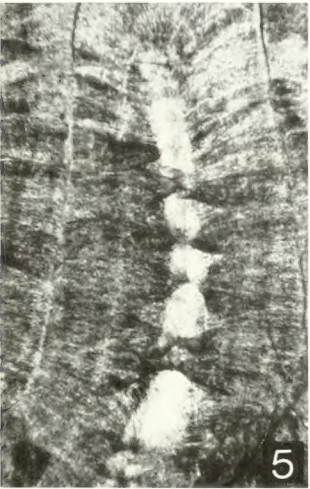
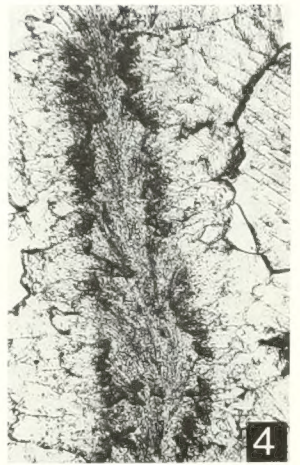
figs. 5, 10; Pl. 2, fig. 1). At times the microstructure is diffusely fibrous to micritic (Pl. 1, fig. 13; Text-fig. 8-10). The width of this central zone corresponds to the septal thickness of unthickened septa, as for instance in the calyx.

The central zone, in my opinion, corresponds to the true primary, biogenic septum, and is surrounded by a partly lamellar carbonate coating of varying thickness composed of normally oriented fibers (Pl. 1, figs. 5, 9-13). Outside the core, the fibers may be more pronounced or diffuse or cloudy structures may occur. It

#### EXPLANATION OF PLATE 1

##### Figure

1. *Timorphyllum wanneri wanneri* Gerth, 1921  
Lower Upper Permian of Indonesia,  $\times 8.5$ .  
Septa with dark median line and fibrous and cloudy coating material.
2. *Timorphyllum wanneri wanneri* Gerth, 1921  
Lower Upper Permian of Timor, Indonesia,  $\times 25$ .  
Septum thickened by fibrous to cloudy carbonate; the core is limited by dark algal rims and consists of median line and perpendicularly oriented fibres.
3. *Calophyllum (C.) rossica* (Schindewolf, 1942)  
Lower Upper Permian of Samara, U.S.S.R.,  $\times 33$ .  
Septa with median line interrupted by semicircular recrystallization fronts. The carbonate coating shows a fibro-lamellar structure.
4. *Plerophyllum (P.) radiciforme* Gerth, 1921  
Upper Permian of Timor, Indonesia,  $\times 42$ .  
Septum with fountain-shaped arrangement of crystals. Note the irregular saw-like margins.
5. *Duplophyllum (D.) zaphrentoides* Koker, 1924  
Lower Upper Permian of Timor, Indonesia,  $\times 25$ .  
The core of the thickened septum is brightened and shows a fan-like orientation of crystals. The carbonate coating shows a fibro-lamellar texture and saw-toothed indentations.
6. *Pentaphyllum (Prionophyllum) crassiseptatum* Schindewolf, 1942  
Lower Upper Permian of Timor, Indonesia,  $\times 40$ .  
Septum with zigzag pattern.
7. Gen. et sp. indet.  
Upper Permian of Afghanistan,  $\times 25$ .  
Dark lines and the septa are strongly folded. Note the recesses (arrow) and the zigzag and pseudolamellar texture in the coating.
8. Same as in Fig. 7  
Note the recess (arrow) built by septal folding and enveloped by zigzag structured carbonate.
9. *Wannerophyllum cristatum* Gerth, 1921  
Lower Upper Permian of Timor, Indonesia,  $\times 8.5$ .  
The brightened septa are mutually thickened by fibrous cement in which saw-toothed features (scalenohedra) occur.
10. *Wannerophyllum cristatum* Gerth, 1921  
Lower Upper Permian of Timor, Indonesia,  $\times 25$ .  
The brightened small areas with micritic to diffusely fibrous carbonate are the true septa. They are coated by fibro-lamellar carbonate in which saw-toothed scalenohedra occur.
11. *Verbeekiella* sp.  
Upper Permian of Afghanistan,  $\times 8.5$ .  
The true septa are visible as small brightened and micritic areas and only partly thickened by fibrous cements. The interseptal spaces are filled either with fibrous cement A, or coarse cement B, or ankerite (black). Algal borings (black tubes) can be seen at the periphery (arrow).
12. Same as in Fig. 11,  $\times 12$   
The micritized and brightened septa are limited by dark rims of algal cement, coated by cement A. Black infillings are ankerite. Note the algal borings (arrow).
13. Same as in Fig. 11,  $\times 4.5$   
Thickened and unthickened septa together in one cross section. Algal borings visible as black tubes at the periphery of the corallite (arrow).
14. *Favosites* sp.  
Lower Devonian of Turkey,  $\times 25$ .  
Cross section showing four- to five-rayed star-shaped swellings in the walls of corallite corners, previously assumed to be tubes of commensal worms.





Text-figure 11.—*Calophyllum (C.) clausa rara* (Niermann, 1974), Lower Upper Permian of Timor, Indonesia. "Septa" with dark median line all mutually thickened. Conspicuous is the brightening with exception of some septal "relics." (Drawing compares with Plate 2, Figs. 3 and 4.)

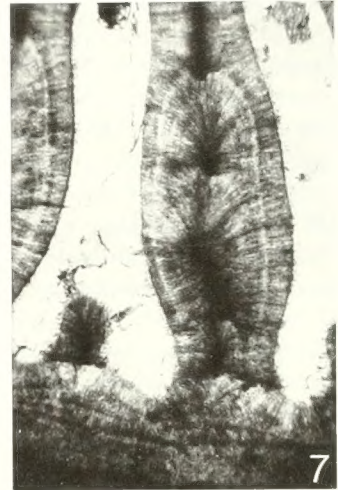
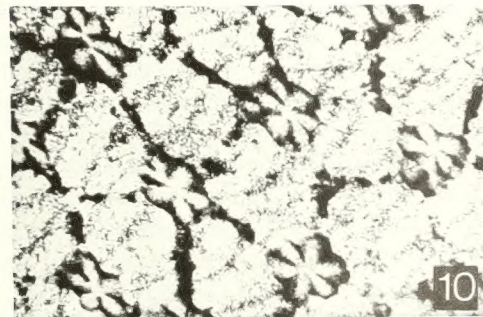
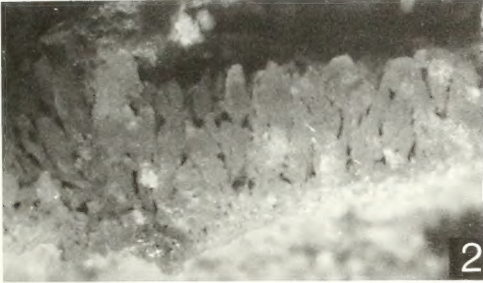


Text-figure 12.—*Favosites* sp., Lower Devonian of Turkey. Cross section showing the star-shaped swellings in the walls at corallite corners, assumed up to the present to be tubes of commensal worm. (Compare with Plate 2, fig. 10.)

#### EXPLANATION OF PLATE 2

##### Figure

1. *Wannerophyllum cristatum* Gerth, 1921  
Lower Upper Permian of Timor, Indonesia,  $\times 25$ .  
The small, brightened septa are micritized or show a fan-like structure. They are enveloped by fibrous carbonate with distinct scalenohedra.
2. *Timorphyllum wanneri wanneri* Gerth, 1921  
Lower Upper Permian of Timor, Indonesia,  $\times 25$ .  
Weathered septum with distinct scalenohedra.
3. Same as in Fig. 2,  $\times 175$   
Scanning electron micrograph of the columella showing scalenohedra.
4. *Calophyllum (C.) clausa rara* (Niermann, 1974)  
Lower Upper Permian of Timor, Indonesia,  $\times 23$ .  
"Septa" with dark median line, all mutually thickened. Conspicuous is the brightening of the carbonate with exception of some septal "relics" (arrow).
5. Same as in Fig. 4  
The brightened and thickened septa touch each other. Note the wedge-like septal base within the wall, caused by recrystallization of the wall.
6. *Duplophyllum (D.) zaphrentoides* Koker, 1924  
Lower Upper Permian of Timor, Indonesia,  $\times 10$ .  
Septa in the peripheral part of the section are club-shaped, swollen, with "Stirnzonen" (frontal zones) annularly growing to the corallite axis.
7. Same as in Fig. 6,  $\times 25$   
Club-shaped septum with "Stirnzonen" which consist of fan-like arrangement of needle-like crystals. Wall with zigzag pattern and fibrous lamellae.
8. Same as in Fig. 6,  $\times 25$   
Changing of growth direction of the "Stirnzonen."
9. *Favosites squamuliferus* Philip, 1960  
Lower Devonian of Australia,  $\times 11.5$ .  
The corallite walls are brightened by recrystallization, sometimes showing star-shaped pattern.
10. *Favosites* sp.  
Lower Devonian of Turkey,  $\times 14$ .  
Cross section showing the star-shaped swellings in the walls at corallite corners, previously assumed to be tubes of commensal worms.
11. Same as in Fig. 10,  $\times 35$   
Six-armed star-shaped swelling without any internal structure.



should also be noted that the central core and the carbonate coating are sometimes separated by a dark micritic band which apparently can be regarded as algal micrite (Pl. 1, fig. 13; Text-figs. 9, 10). Smaller cavities between the core (that is the septum), and the cement coating support these conclusions (Text-fig. 1). The conditions mentioned, especially in the central zone of light, diffusely fibrous to micritic carbonate and in the distinct fibro-lamellar coating, very much resemble the features described by Land (1967) in the recent scleractinian coral *Diploria strigosa* from Florida. This showed interseptal spaces filled by acicular aragonitic cement that was precipitated after the inversion of the skeletal aragonite. The skeletal architecture remained but the skeletal microstructure had been destroyed. My investigations on Permian corals have shown similar features, but with the carbonate coating preserved as calcite. Algal borings (within both cement and skeletal material) also are of significance concerning the timing of changes in structure. As these borings could only have been effected before burial of the coral skeleton, the changes, *i.e.*, micritization of the central region of the "septum," as well as the formation of cements, must have taken place at a very early phase of diagenesis (Pl. 1, figs. 11–13).

Other corals are slightly different. The central parts of the septa show a distinct median line with bilateral, more or less perpendicularly oriented fibers of carbonate, which again are enveloped by thick carbonate coating the structure of which is diffusely fibrous or cloudy in appearance (Pl. 1, figs. 1, 2). This is reminiscent of known cements and supports the hypothesis of skeletal thickening due to postmortem diagenetic formation of cement coatings, even if its appearance at first resembles biogenic septal thickening. One further argument will be made: saw-toothed septal cores (Pl. 1, figs. 5, 10; Pl. 2, figs. 1–3), already characterized as being recrystallizations by Bathurst (1959) are nothing more than scalenohedra that developed by recrystallization as suggested by Oekentorp (1980). The saw-toothed formations are generally limited to the cement coating (Pl. 1, fig. 10; Pl. 2, fig. 1). This may be caused by the cement being a separate structural unit which behaves differently during recrystallization than does the septal core because the crystals in the cements are less densely packed (Dullo, 1982; Jux, 1982). This again suggests that only the core corresponds to the primary septum, and that the carbonate coating was deposited later as cement.

To summarize, diagenesis apparently leads to significant changes in the microstructure of the coral skeleton. Micritization of septal carbonate is most common, and septal thickening is seemingly not of biogenic

origin but results from fibrous cements deposited during early diagenesis. Recrystallization, and the formation of zigzag and pseudolamellar structures may later affect the thickened septa. These tend to obliterate the original differences in the carbonate material. The result may be a septum-like architecture with a seemingly primary microstructure. The initial processes of change, as shown by algal boring, are early diagenetic, but other changes occur later.

#### Septal Thickening by Recrystallization

The processes changing the skeletal structure and architecture discussed above, were due to deformation, micritization, and cement deposition. A fundamentally different diagenetic process can also be recognized as causing septal thickening. This occurs within the septum itself during recrystallization. Such thickening often occurs but has, until now, always been regarded as biogenic.

As noted previously, septa may be extremely thickened so as to almost touch one another. Their microstructure consists of a dark median line with a thick carbonate layer of relatively long, normally orientated fibers (Pl. 2, figs. 4, 5; compare Text-fig. 11). There is a brightening of carbonate, a characteristic feature that is an indication of recrystallization in many cases (Pl. 2, figs. 4, 5). In one special case, *Calophyllum (C.) clausa rara* (Niermann, 1974), the light carbonate is additionally accentuated by remnants of darker material which occur as relics between the brightened and very thick septa (Pl. 2, fig. 4; compare Text-fig. 11). In this case it seems that the smaller and darker parts occur or pass below the strongly lightened septa. This appearance is, in fact, brought about by recrystallization; a new "septum" was developed at the expense of the primary biogenic septum by an *in situ* dissolution and precipitation that led to the successive destruction of the earlier structure. The newly grown coarser-grained crystals cause the brightening of the carbonate. Further, the new, mineralogically controlled "septum," again has an almost regular microstructure that has been misinterpreted as being primary. To recognize the possible development of regular secondary structures is of very great significance in the interpretation of microstructures in Paleozoic corals.

This alternative development of skeletal thickening makes it possible to interpret further structural peculiarities in Permian corals. Different solitary rugosans from the Permian of Indonesia show decrease in septal thickening in the direction of the axis, revealing an annular zonation in transverse thin sections (Pl. 2, figs. 6–8). In the axial parts, the septa are relatively thin and dark and show a pronounced median line with



fibers oriented perpendicular to it, but the median line in the enlarged central part is interrupted by fan-like structures. In the peripheral parts the septa are club-shaped and swollen and only relics of the median line can be detected. Here the structure consists mainly of a fan-like arrangement of fibers in successive arcs. These arcs correspond to the term introduced by Schindewolf (1942) (cf. Schouppé and Stacul, 1966) as "Stirnzonen" (frontal zones). I should like to further use this term but in a different way. Schindewolf thought these were biogenic structures, but in my opinion these are caused by recrystallization. Present usage of the term "Stirnzonen" only applies to secondary, diagenetically dependent microstructures. Features supporting this interpretation are the brightening, frequent changes of direction ("oscillation") of the frontal zones (Pl. 2, fig. 8), and relics of the median line. In some cases a V-shaped indentation at the frontal part of the "Stirnzonen" is seen, into which the median line protrudes like a wedge (Pl. 2, fig. 7). This indicates that the secondary fibers have grown past the more resistant median line. This appearance can not be explained morphogenetically.

Features comparable to the frontal zones are very commonly observed. Often they are narrow, partly semicircular and reminiscent of a string of pearls (Text-fig. 5) so that the lateral margin of the septum is always indented (Schindewolf, 1942; Weyer, 1979). The ring-like arrangement shown in transverse sections is here interpreted as a succession of recrystallization fronts, starting from the outer wall of the coral and following the structural pattern of the skeleton toward the axis. The problem lies in the striking regularity of the newly built, non-biogenic structures: the arrangement of the fiber-like crystals and the orientation of the fronts directed towards the axis. Such fronts can also be observed directed toward the periphery of the corallum. Schindewolf (1942, p. 30, pl. 18, fig. 1) pointed out this peculiarity but attributed it to dome-like septal growth.

A further phenomenon is here described so that it can be clarified on the basis of the above considerations. It is the star-shaped tubes described as commensal worms and named *Asterosalpinx* Sokolov, 1948, *Actinosalpinx* Sokolov, 1962, and *Antherosalpinx* Sokolov, 1962 (see Oekentorp, 1969; Hill, 1981). These appear as star-like swellings of portions of the wall, especially at the corners of corallites in cerioid favositoid colonies (Text-fig. 12; Pl. 1, fig. 14; Pl. 2, figs. 10, 11), with a lightening of the coral skeleton material. The number of rays varies from three to eight and is not regular. Of some significance is the number of neighboring polyps with respect to the walls built by

these polyps. Normally the corner is formed by three walls, so that the star-arms are three, or a multiple of three. New material from the Devonian of Turkey and Southern China reveal that recrystallization alone, comparable to that in frontal zones, was the factor which led to these peculiar features. A similar phenomenon was described by Philip (1960) in *Favosites squamuliferus* (see Schouppé and Oekentorp, 1974, p. 130) (Pl. 2, fig. 9). The "worm" genera mentioned above therefore do not exist biologically (Oekentorp, Yü and Deng, in preparation).

*Discussion.*—It is suggested here that recrystallization may lead to certain, barely understood changes in skeletal structures. A well-ordered texture, simulating primary structure can be produced not only by cement deposition but also by recrystallization of the skeletal elements themselves. In a calcite-to-calcite transformation, from unstable, high-Mg calcite to stable low-Mg calcite (if calcite is presumed to be the primary skeletal material) the crystal lattice of the calcite would not suffer any changes or deformation apart from ion exchange and is unlikely to produce alterations leading to skeletal thickening. In this case, recrystallization in the form of grain growth would occur, as present in the scalenohedra; but these were formed after alteration of the skeletal carbonate had taken place. The septa were micritized at an earlier stage. Moreover, the scalenohedra are, without doubt, late diagenetic in origin, whereas the principal alteration must have occurred early in the diagenetic history, as indicated by algal borings.

Recrystallization processes, especially the septal thickening described here can perhaps be readily explained if a material other than calcite is considered. Aragonite is an obvious choice since it is used as skeletal material in the related Scleractinia. Aragonite is metastable; when transformation into calcite occurs, an enlarged space and greater volume is needed; the increase in volume amounts to about 8 percent. An appropriate replacement of aragonite by calcite can be achieved by different means; 1) By solution of the skeletal carbonate and subsequent void-filling precipitation. This would result in a mosaic of relatively coarse grains as observed by Bøggild (1930), and which has been repeatedly quoted since as evidence that aragonite was replaced by calcite. 2) By solution and precipitation *in situ*, where the needle-like crystal fabric of the aragonite can be retained if micritization does not occur. Then, if the volume increases by 8 percent, it will be seen that both narrowings and foldings as well as thickening of skeletal elements will be the consequence. This would be accompanied simultaneously by a brightening if the carbonate material is not dissipated

and precipitated as cement. This is, indeed, also known to occur.

Oekentorp (1980) thus proposed that aragonite was the original skeletal material at least in those Permian corals investigated by him. There are, of course, numerous opposing arguments. One is that the Rugosa commonly have a calcitic skeleton, normally without obvious or remarkable changes of the microstructures. In this connection, it seems likely that during an assumed recrystallization of aragonite into calcite the excess carbonate has been carried away in solution or deposited as cement. Thus, the supposition of a primary calcitic skeleton would be logical. But the question remains, how could such conspicuous recrystallization features occur, especially in the Permian corals dealt with here. Further investigations are imperative.

### CONCLUSIONS

The microstructures which occur in the Rugosa, at least as far as the material under investigation is concerned, are not primary. They instead represent completely new structures that occurred in different ways and followed one another during diagenesis. It has been suggested that septal thickening developed either by formation of cement or transformation of skeletal carbonate. The changes that followed were due to recrystallization forming scalenohedra as well as zigzag and pseudolamellar structures. Transformation of the skeletal material without doubt mostly occurred early in diagenesis. Furthermore, it seems that in the course of diagenesis, a needle-like and well-ordered fabric can again be formed, based on and derived from the structure of the skeletal elements.

Unfortunately, no Paleozoic coral having an aragonitic skeleton has yet been found to provide direct evidence. On the other hand, it seems quite advantageous to explore this question from a different point of view: *i.e.*, not to necessarily look for evidence within the Rugosa. Could we not ask: what kind of structural changes do occur in the Scleractinia and what do they look like, aside from those in which the structure is destroyed, as shown by Bøggild (1930)? On the other hand, it has been shown, and this presents the main concern of these investigations, that knowledge of carbonate diagenesis has largely been neglected in coral research. Only with the aid of this knowledge can coral microstructure be explained and used in systematic considerations.

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## UPPER PERMIAN CORALS FROM TIMOR AND DIAGENESIS

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## ABSTRACT

Diagenesis of the Upper Permian coral fauna of Timor has occurred within the phreatic zone in great part, resulting in characteristic cements and in partial silicification. Early epitaxial cements show control by substrate and thus accurately reflect biogenic structure. Silicification preferentially occurs in septal trabeculae of *Lophophyllidium* and recrystallization under pressure has resulted in the zigzag wall structures seen within *Calophyllum* and *Euryphyllum*. *Wannerophyllum* and *Calophyllum* show unaltered, non-trabeculate septal structures. In *Euryphyllum*, the presence of a pseudo-uniaxial cross under crossed polarization is due to preferred c-axis orientations of septal biocrystallites, and underlines the lack of diagenetic change.

## INTRODUCTION

The use of living counterparts to provide insight into fossil groups is only partially successful in the case of the Paleozoic corals. The Paleozoic Rugosa had basic differences in skeletal mineralogy and structure, as compared to the modern Scleractinia. Thus, it is especially important in the study of this extinct group to identify exceptionally well-preserved faunas and study them intensively. Such a rugosan fauna is known from Upper Permian rocks near Basleo, Timor, Indonesia. These superbly preserved specimens provided much data for the classic report by Schindewolf (1942) and also for a series of papers by Schouppé and Stacul beginning in 1955, culminating in their extended study

of the skeletal structure of the Rugosa (1966). The present paper is an extension of earlier reports on the structure and composition of *Calophyllum*, *Lophophyllidium* and *Timorphyllum* (Sorauf, 1978), and on the structure and diagenetic history of *Timorphyllum* (Sorauf, 1983); and also includes data on genera not previously treated, *Euryphyllum* and *Wannerophyllum*.

The diagenetic history of these Permian rugosans from Timor must be inferred from evidence derived from the corals themselves, as little is known regarding the details of the strata yielding the fauna. Brad Macurda reports that the Basleo corals come from blocks of Permian limestone which have accumulated as allochthonous boulders (wildflysch) in Tertiary deep

## EXPLANATION OF PLATE I

## Cements

Figure

1-2. *Timorphyllum wanneri* Gerth

1. Two septa with early rim cement and later, blocky cement filling interseptal space, characterized by numerous enfacial angles. Septa composed of somewhat dark biogenic calcite forming crystallites perpendicular to septal flank surface.  $\times 75$ , crossed polarizers.
2. Scanning electron micrograph of septum, with tip at base of micrograph, characterized by fine biocrystallite size in septum, somewhat larger rim cement crystals (arrow) and later, larger crystals of dog-tooth spar filling partially interseptal spaces.  $\times 50$ .

3-6. *Wannerophyllum cristatum* (Gerth)

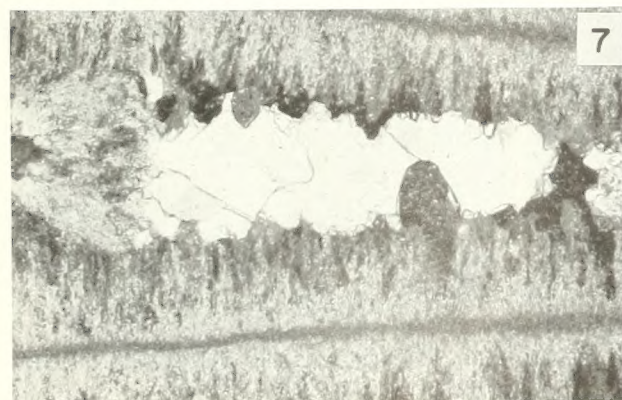
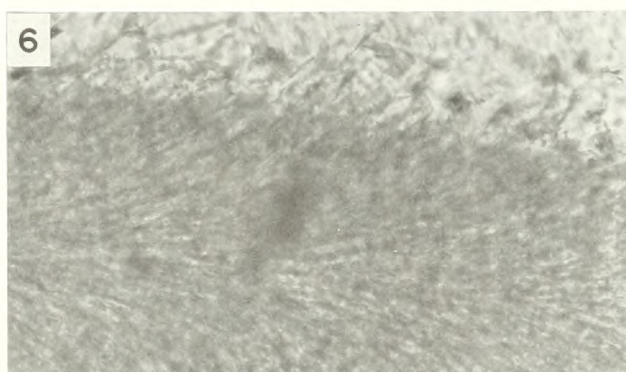
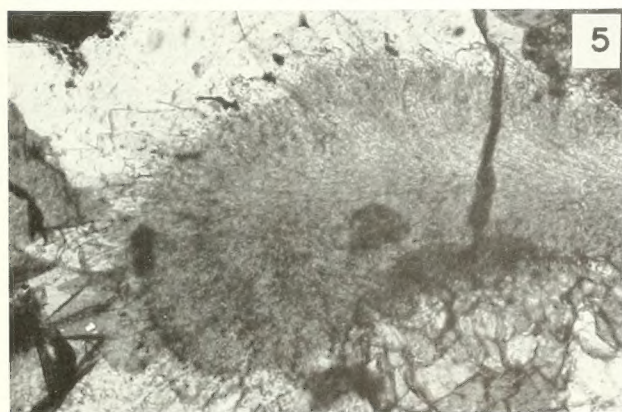
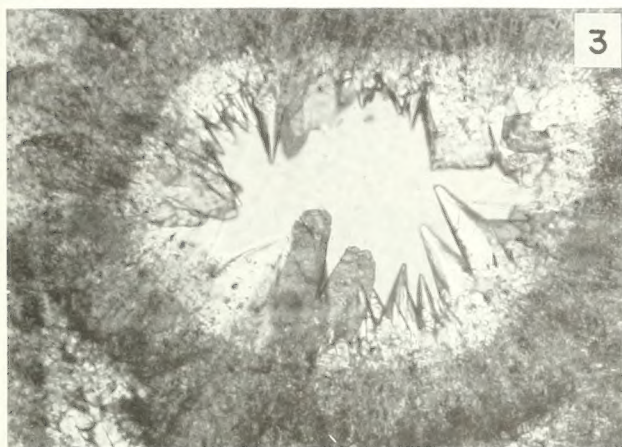
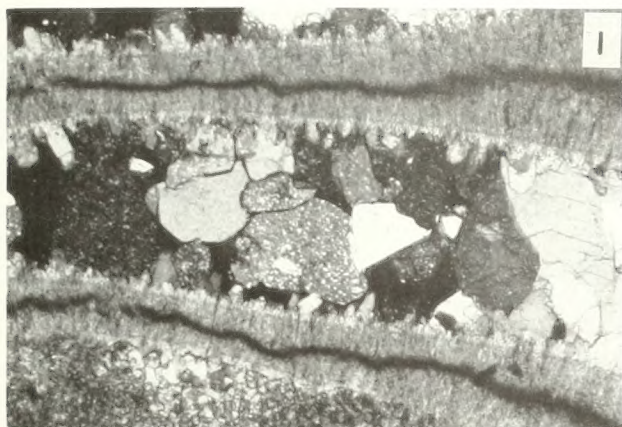
3. Void formed by dissepiments and septa, with early epitaxial cements overgrown by dog-tooth spar partially filling void space.  $\times 75$ , partially crossed polarizers.
4. Scanning electron micrograph illustrating fine-grained nature of biogenic septal calcite and dog-tooth spar overgrowths on septa, projecting into, but not filling interseptal spaces.  $\times 50$ .
5. Septum showing epitaxial rim cement with orientation of cement crystals epitaxial on biocrystallite structure, fanning around septal tip. Note that cement long axes are continuation of biogenic crystallites, and not perpendicular to septal flank.  $\times 75$ , crossed polarizers.
6. Septum below and cements above, to illustrate epitaxial nature of early rim cement growing on and continuing orientation of septal biocrystallites. Early cement is not here perpendicular to septal flank, but accurately reflects fanning structure of septum.  $\times 200$ , plane polarized.

7. *Euryphyllum cainodon* (Koker)

7. Septa, early epitaxial cement and later blocky cement filling interseptal space. Seen under cross polarization early cement and septal flanks apparently show some slight recrystallization.  $\times 63$ , partially crossed polarizers.

8. *Lophophyllidium spinosum* (Martin)

8. Septa and dissepiments with extremely acicular early cement, late cement filling many void spaces, but with chalcedony filling one interseptal space, and with silicification of septa concentrated in septal trabeculae, as shown here by bright spots in transverse section (arrow).  $\times 25$ , partly crossed polarizers.



water shales (pers. comm., 1982). We thus infer that the corals accumulated in shelf deposits and that their later diagenetic history probably occurred within a low permeability sequence of siliciclastic muds. Other conditions must at present be inferred through study of cements and other diagenetic features.

## CEMENTS

### First-Generation Cement

The early cement in these rugosans is almost invariably of the same type, isopachous rim cement growing into intraskeletal void spaces (Pl. 1, figs. 1–3). The cement is identical to that illustrated by numerous authors, notably Cullis (1904, p. 394) and Bathurst (1975, p. 432), and referred to as “micro-dog-tooth spar” by many. A sufficient body of data exists to make certain the knowledge that this rim cement did not result from the recrystallization or inversion of aragonitic needle cement. None of the common features of such calcitized, formerly aragonitic cements are noted in cements within these corals (radial-axial fibrous cements, and other fabrics, as summarized by Mazzullo, 1980).

This early rim cement is typically present within void spaces in the rugosan skeleton, and it appears to be peculiar to rugose and tabulate corals exclusively among fossil corals. There are several aspects of this rim cement that are of interest to the student of fossil corals; its substrate specificity, common epitaxial nature, and recrystallization.

Substrate specificity of cements was noted by Cullis (1904, p. 394) who suggested that normally, aragonite rim cements form only on aragonite substrates, while calcitic rim cements are found on either calcitic or

aragonitic substrates. This has since been observed by a number of petrologists (notably Glover and Pray, 1971; Schroeder, 1972). Also, early aragonitic needle cements only form on bare aragonitic skeletal material, and the slightest organic film or impurity coating the skeleton causes calcite to form instead (Schroeder, 1972). Sandberg (1975), studying Pleistocene bryozoa found that calcitic rim cements are consistently formed on calcitic bryozoan skeletal material, while penetrative fabrics indicate altered (calcitized) aragonitic cements and skeleton.

The early rim cement in the rugosans from Timor is generally also epitaxial in nature. The common situation is that rim cement crystals grow perpendicular to the flanks of septa or whatever skeletal part they coat (Pl. 1, figs. 1–4). The rim crystals are thus an extension of septal crystallites (biogenic) which are also perpendicular to the flank. In this case the argument can also be made that it is the surface which controls the orientation of the cement crystals, rather than biogenic structure influencing and/or dictating the organization of cement crystals, such as illustrated by Schroeder, in aragonite needle cement within a gastropod shell chamber (1973, p. 184). In at least one of the Timor rugosans, this skeletal influence over epitaxial cement is clearly shown. In *Wannerophyllum*, rim cement is noted in which calcite crystals are clearly continuous with biogenic crystallites of calcite, but neither is perpendicular to the septal flank (Pl. 1, figs. 5, 6). This is a great aid in determining the biogenic microstructure of the septum, in this case a clearly fanning structure of septal calcite crystallites, with crystallites forming an angle to both the septal flanks at the lateral position; but parallel to the length of the septum in the

## EXPLANATION OF PLATE 2

### Septal and Wall Structure

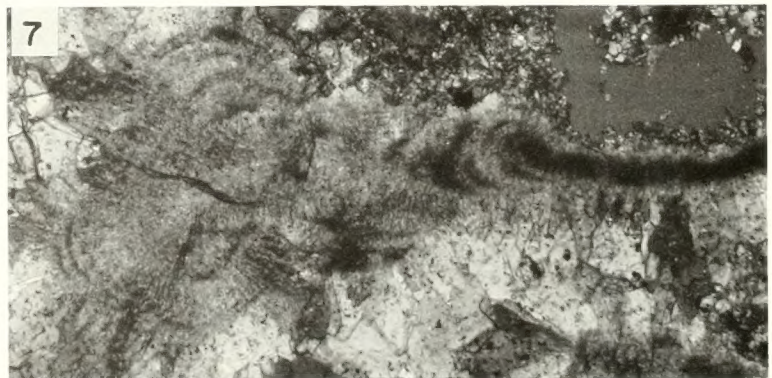
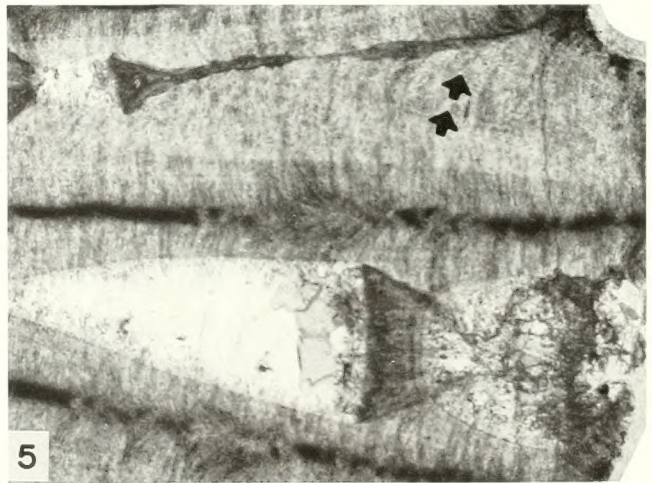
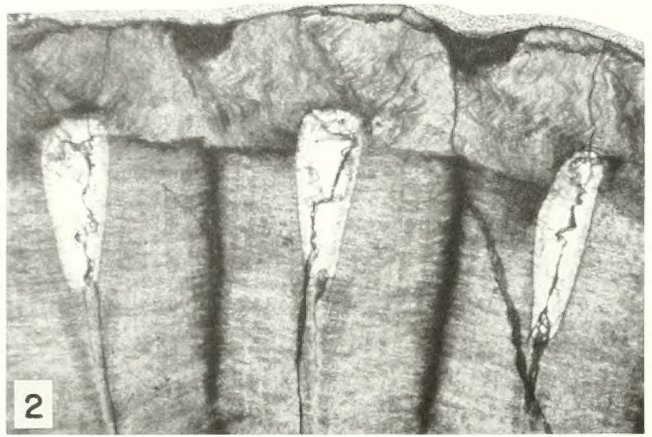
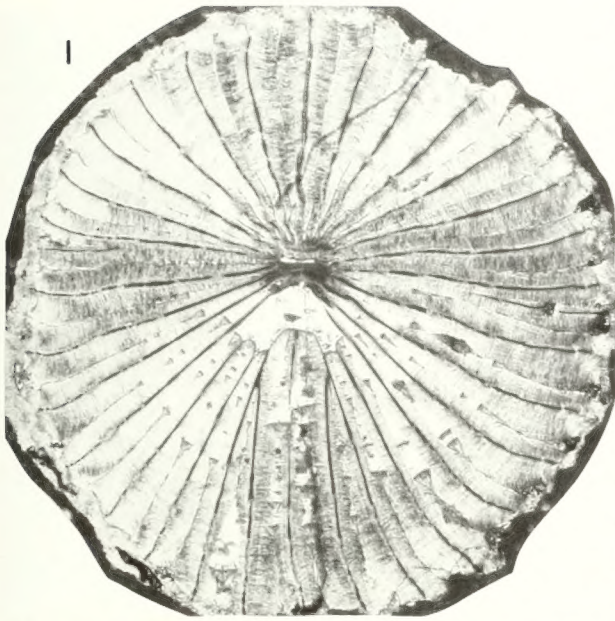
Figure

1–5. *Euryphyllum cainodon* (Koker)

1. Transverse section of corallum showing pseudo-uniaxial cross under crossed polarization, caused by c-axes of septal biocrystallites (=axis of elongation of crystallites) all lying in the plane of the thin-section, mostly perpendicular to the central planes of the septa, thus roughly parallel to the periphery of the coral.  $\times 5$ , crossed polarizers.
2. Wall and peripheral portion of 4 septa, illustrating the fibro-normal structure of septal flanks, zigzag structure of the coral wall, and recrystallization front separating the two.  $\times 25$ , plane polarized.
3. Wall and septa in specimen illustrated in Fig. 2, under crossed polarizers showing wall with zigzag structure and recrystallization front between wall and septa. Recrystallization also affected cement filling interseptal spaces as shown at left center (arrow).  $\times 25$ , crossed polarizers.
4. Illustrating axial portion of cardinal septum to illustrate growth lamellae in septa and relationship to dissepiments.  $\times 25$ , partly crossed polarizers.
5. Peripheral portion of septa illustrating septal structure, growth lamellae in septa and dissepiment, as well as continued infilling of interseptal space shown above (arrows).  $\times 25$ , partly crossed polarizers.

6–7. *Calophyllum angustum* (Rothpletz)

6. Transverse section illustrating rhopaloid nature of septa, bilateral symmetry and prominent nature of 4 protosepta.  $\times 10$ , non-polarized.
7. Enlargement of alar septum illustrating lamellar nature of expanded, rhopaloid tip, with radiating biocrystallites, as well as thin nature of remainder of septum to the right.  $\times 75$ , partly crossed polarizers.



center of the septum as seen in cross-section (Pl. 1, figs. 5, 6). The occurrence also indicates that neither the septal structure nor the early rim cement crystals have undergone any reorientation during diagenesis.

However, septal flanks and early cements in some corals do suggest that some recrystallization has taken place, even if minor. *Euryphyllum* (Pl. 1, fig. 7), illustrates this phenomenon, in that rim cement is in optical continuity with septal crystals, and together they show a wedge-like pattern of extinction extending as much as two-thirds of the way to the central zone of the septum. Provided that this is truly a recrystallization phenomenon, and not merely a reflection of radiating crystalline structure in the septal flanks, minor recrystallization may then have occurred prior to deposition of late cement. Septal flanks and early cements might show this modification if each were originally high-magnesium calcite, modified to low-magnesium calcite prior to the later phreatic zone cementation by low-magnesium calcite. Schroeder (1973, p. 185) has noted that modern early rim cements on calcareous substrates are commonly high-magnesium calcite. Some genera of the Timor rugosans may have had more magnesium in their skeletal carbonate than others, and recrystallization seems to occur to differing degrees in different taxa.

Also, the only type of recrystallization seen to affect the Timor rugosans occurs solely at the septal flanks. More central trabecular zones are not affected and remain unaltered by this or other carbonate recrystallization phenomena. This is the exact opposite of the situation in aragonitic scleractinian corals, where septal trabeculae are the first to be dissolved or calcitized, due to the small sizes of biogenic crystallites, as noted by James (1974).

### Late Cements

The second generation (late) cement seen in skeletal voids of the Timor rugosans is low-magnesian, blocky calcite. Preliminary study of the isotopic compositions of these cements confirms that the precipitating agent was a relatively fresh ground water in the phreatic zone (P. Choquette, pers. comm., 1977). The Timor rugosans quite commonly still retain voids in intraskeletal spaces due to incomplete cementation. This may reflect relatively effective isolation of voids from migrating solutions, or a relative lack of the solutions themselves or lack of saturation within solutions. The voids cannot easily be compared to normal pore spaces between sediments because of differing geometries and lack of connections between pores. Generalizations concerning pore spaces in permeable sedimentary rocks are not always applicable to closed spaces such as the interseptal spaces in corals with disseminations and tabulae.

The late cements not only vary in the percentage of each void that is filled by them, but also there is a considerable variation in crystal size. As shown in figure 8 on Plate 1, *Lophophyllidium spinosum* has the largest cement crystals noted in the Timor fauna. It is perhaps noteworthy that this genus is also characterized by partial silicification of septal structures. The slow growth of very large cement crystals (and the resultant smaller number of them) is perhaps the result of the characteristics of the pore fluids, and thus related to diagenetic factors favoring silicification.

### SILICIFICATION

In corals examined during this study, only specimens of *Lophophyllidium spinosum* show any silicification. Schindewolf (1942, p. 29) also reported that specimens

### EXPLANATION OF PLATE 3

#### Septal and Wall Structure

Figure

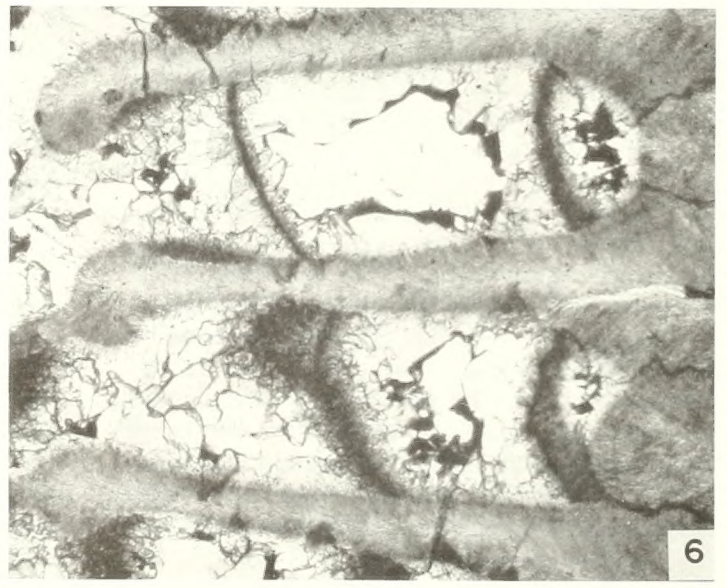
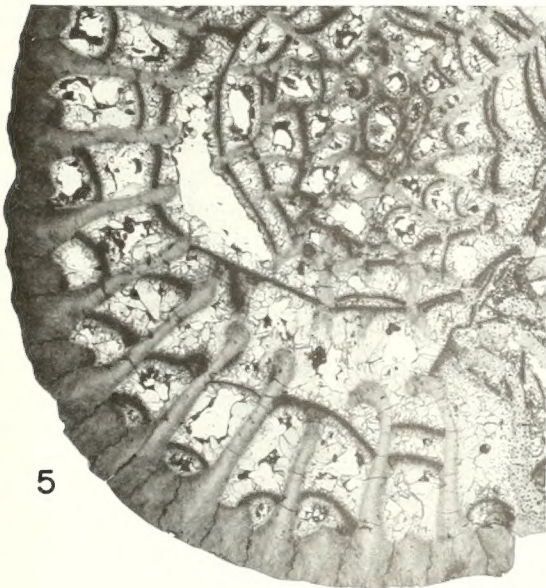
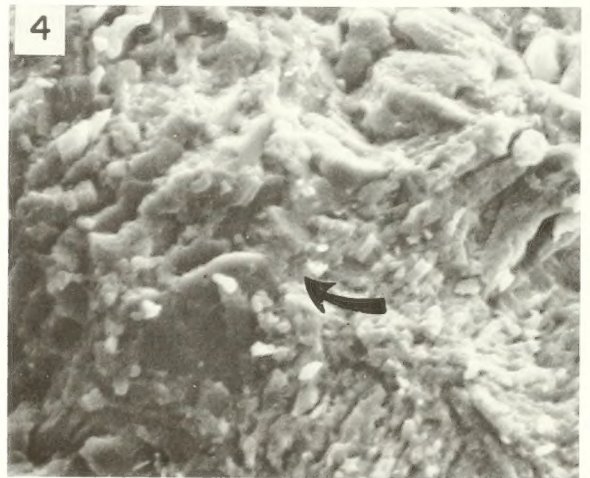
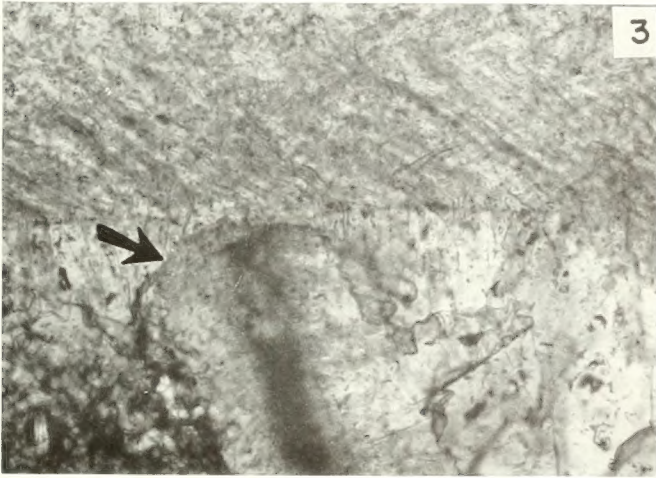
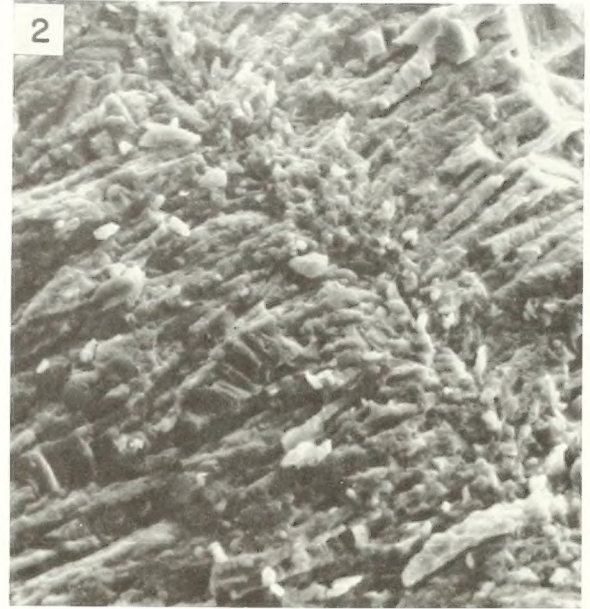
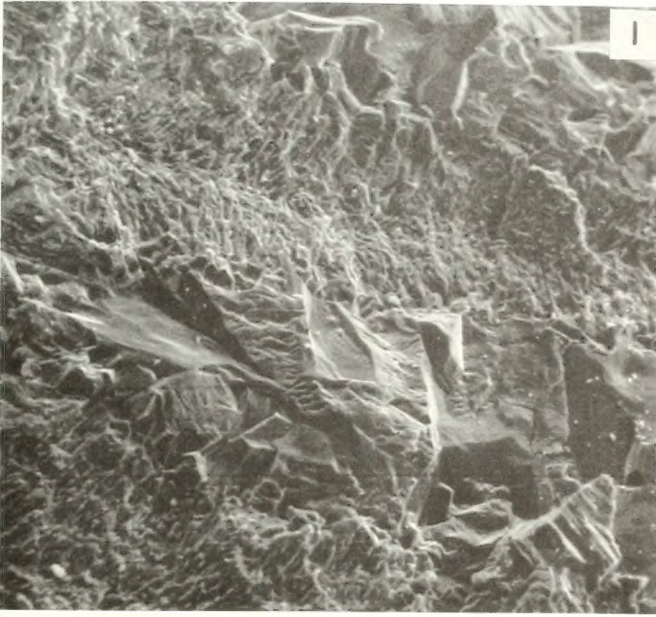
#### 1-4. *Calophyllum angustum* (Rothpletz)

1. Septa at bottom and upper portion of this micrograph show fibro-normal septal structure. Wall is shown at upper left corner. Interseptal spaces are completely filled by blocky calcite.  $\times 200$ , Scanning Electron Micrograph.
2. Enlargement of septum to show absence of septal trabeculae and fibro-normal structure in the thin, peripheral portion of septum.  $\times 1000$ , Scanning Electron Micrograph.
3. Contact between septum below and wall above, with zigzag structure in wall and discontinuity between it and septum below.  $\times 200$ , crossed polarizers.
4. Junction (at arrow) of wall above and to the left and septum to the lower right, with septum showing structure similar to that illustrated in Fig. 2 above. Wall is seen to be composed of larger, lath-like crystals resulting from recrystallization and forming zigzag structure.  $\times 1000$ , Scanning Electron Micrograph.

#### 5-6. *Wannerophyllum cristatum* (Gerth)

5. Overview of individual with typical basket-like columella, septa with "bright" centers and incomplete blocky cement.  $\times 7.5$ , non-polarized.
6. Three septa in another individual. Septum at top is that illustrated in Fig. 5 of Plate 1. Septa show absence of trabeculae and uniform fanning structure of crystallites as well as early epitaxial and later blocky cements.  $\times 25$ , plane polarized.





of *Pleramplexus* are characterized by the silicification of the central plane of their septa, while the septal flanks remain calcite. As seen in *Lophophyllidium*, silicification begins first in septal trabeculae within septa (Pl. 1, fig. 8), also seen in Sorauf (1978, pl. 33, figs. 3–5). As observed in polished and etched section in the scanning electron microscope, the early silica imitates the radiating structure of the trabeculae (Sorauf, 1978, pl. 33, fig. 4). Silica is also rarely present as cement, filling voids left after late cementation (Pl. 1, fig. 8). This seems remarkable in that silica-bearing solutions have not re-dissolved early cements, although they must have been undersaturated with respect to calcite in order to have dissolved away the fine calcite of the trabecular centers. Knauth (1979) suggests that solutions such as these and also simultaneously supersaturated with respect to silica can be found in the phreatic fresh-marine mixing zone.

#### IRON OXIDE FILMS

Many of the Timor corals show cavity surfaces coated by hematite films that appear opaque in thin-section. These films are seen coating septa in some corals, especially *Timorphyllum* (Sorauf, 1983, figs. 3, 5), preceding deposition of early cement. They also coat early cements and even occur later to coat some of the late cement crystals (Pl. 3, fig. 8), occurring between several late, phreatic zone cementation events. It is assumed that iron-oxide films were cemented in phreatic zone waters at various times, perhaps as a result of development of terra rosa soils. The films thus outline features of skeleton or cement and can aid in interpretation of both.

#### PRESSURE RECRYSTALLIZATION

##### (Zigzag Structure)

In the cross-sectional view of *Euryphyllum*, a pseudo-uniaxial cross is seen under crossed polarizers (Pl. 2, fig. 1). This extinction phenomenon does not extend into the wall of the corallum, nor even to the outermost part of the septa. The wall of *Euryphyllum* shows the zigzag structure, recognized by Schindewolf (1942, p. 38), regarded by him as biogenic (p. 42), but regarded as diagenetic by Sorauf (1978) and by Oekentorp (1972, 1974, 1980). As shown in *Euryphyllum* (Pl. 2, figs. 2, 3), the structure is somewhat irregular at the inner margin of the walls, and there is a very pronounced discontinuity between the area affected, here the wall or the outermost portion of the septa, and the rest of the septa where septal structure is unaltered and typically fibro-normal and trabecular. This discontinuity thus separates the outer recrystallized zone (walls, etc.) and an inner unrecrystallized region. It occurred rel-

atively late in the diagenetic history of the corals, because it also affected late cements (Pl. 2, fig. 3).

The same structure is seen in *Calophyllum* (Pl. 3, fig. 3) with a recrystallization discontinuity between septa and wall which is very similar to that noted in *Euryphyllum*. Scanning electron microscopy shows (with higher magnification) that this junction occurs where crystals in the wall are notably enlarged in the long direction of the coral (Pl. 3, fig. 4), and form the zigzag only in the transverse section (Sorauf, 1978, pl. 32, fig. 4).

This recrystallization is regarded as having taken place under external pressure, probably compactional in nature, with preferred crystal growth forming laths elongate in the direction perpendicular to maximum pressure.

#### BIOGENIC STRUCTURES

As has been noted previously, the biogenic structures of the Rugosa from Timor are extremely well-preserved, as evidenced by the small crystallite sizes of biogenic calcite, as seen in broken section by scanning electron microscopy, and by similarities in trabeculae, dissepiments, growth lamellae and general skeletal microstructure between the calcitic rugosans and modern or fossilized aragonitic scleractinian corals, as long as they have not been calcitized. In all specimens of rugosans studied from the Timor fauna, at least parts of each are well enough preserved that original biogenic structure can be recognized. Structures are described in genera, grouped by septal type.

##### Trabecular Septa

By far the greatest majority of all septate corals, whether belonging to the Rugosa or Scleractinia, have trabeculate septal structures. Most of the Permian rugosans from Timor do also. A few are described here.

##### *Euryphyllum*

*Euryphyllum* is characterized by trabecular septa, and septa are laterally inflated by biogenic stereome until in lateral contact with each other. The cardinal septum characteristically forms a fossula (Pl. 2, figs. 1, 4), and open interseptal spaces characteristically occur only in the cardinal quadrant. Under crossed polarizers a pseudo-uniaxial cross appears, with four radiating arms at extinction (Pl. 2, fig. 1). This is a common feature of both modern and fossil oolites and is familiar to carbonate petrologists. The pseudo-uniaxial cross indicates that the c-axes of calcite crystals in the skeleton are virtually all in the plane of the thin-section, and in this thin section the fibrous calcite is generally oriented parallel to the outer periphery of the

corallite. Thus, a good analogy can be made to the occurrence of the pseudo-uniaxial cross in modern ooliths. This also indicates that the c-axis is the axis of elongation in the calcitic septal biocrystallites, just as the c-axis is the elongation axis in skeletal aragonite crystallites of modern corals. The cross also provides a very positive indication that recrystallization is virtually non-existent in these septa.

The septal microstructure in *Euryphyllum* reflects the quality of preservation of these specimens. Adjacent to the cardinal septum, septa have interseptal void spaces rather than being in lateral contact as in the counter quadrants. The structure here is clearly fibro-normal at the flanks, with well-defined growth lamellae distinctly visible (Pl. 2, fig. 4). These growth lamellae show that septal flank growth continued on the peripheral side of dissepiments, as shown clearly in figure 5 of Plate 2. The trabecular nature of the septa is likewise well-displayed here, but this trabecular structure is not a "well-contained" structure; rather, the trabeculae are broad and show clear fanning within the trabeculae. Septal construction is shown by growth lamellae to be more continuous peripherally, and actually seems to reflect continued growth upward and outward from the corallite axis, rather than towards the axis as in most rugosans.

#### *Lophophyllidium*

*Lophophyllidium* is best characterized in the Timor fauna by its diagenetic features, both cements and silicification (Pl. 1, fig. 8). The septa of *Lophophyllidium* do clearly have a trabecular structure where unaltered and in addition show trabecular structure where partly silicified because of the preferential silicification of trabecular centers, resulting in bright spots recognizable as the trabeculae, previously discussed.

#### Non-Trabeculate Septa

It is unusual to find rugose corals that are well-preserved, as the Timor corals are, but without discernable septal trabeculae. This is one of the peculiarities of Permian rugosans, and possibly, a character by which Carboniferous and Permian coral faunas can be differentiated from earlier Paleozoic corals.

#### *Calophyllum*

*Calophyllum* from the Permian of Timor is modified by diagenesis to varying degrees. The genus, called *Polycoelia* by numerous past authors, is typically characterized by its small size, bilateral symmetry, rhopaloid septa that are greatly inflated at the tips, but thin elsewhere, and thick walls that are generally more or less modified to form the zigzag structure (Pl. 3, fig.

3). The tip of the septum (Pl. 2, fig. 7), shows fanning of septal biocrystallites, seen in this figure in the radiating fine structure perpendicular to the very prominent growth lines (alternating dark and light) which show the pattern of expansion of the tip. The thin part of the septa is characterized by fibro-normal structure, with septal biocrystallites perpendicular to the outer flanks of the septum and almost perpendicular to the center line of the septum. Seen at higher magnification, the septa are clearly lacking septal trabeculae (Pl. 3, figs. 1, 2). This is somewhat unusual in the Rugosa, but the feature is consistent within the genus, and is not regarded as diagenetic.

The walls of *Calophyllum*, with their zigzag structure, have been discussed above.

#### *Wannerophyllum*

*Wannerophyllum* as a genus was proposed by Schouppé and Stacul (1955), in part characterized by what they called a "bright central zone" in the septa. The genus has been regarded as a synonym of *Verbeekiella* by Hill (1981), but I favor retaining *Wannerophyllum* until more is known about the septal structure of *Verbeekiella*.

*Wannerophyllum* possesses a rather singular septal structure composed of fanning biocrystallites without any sign of septal trabeculae, with the light appearance of the septa in thin-section due to the orientation of calcite crystals (Pl. 3, figs. 5, 6). That this fanning orientation is original is evidenced by its constancy within septa and within the fauna, and shows fanning extinction when rotated under crossed polarizers. Early epitaxial cement on the septa likewise shows fanning around septal tips (Pl. 1, figs. 5, 6). Since biocrystallites are not perpendicular to septal flanks, neither are epitaxial cements. This is one of the few instances in which it can clearly be shown that the biogenic structure is truly controlling the orientation of cement crystals.

The walls of *Wannerophyllum* show a similar fanning orientation of crystallites and generally are well-preserved (Pl. 3, fig. 5).

#### SUMMARY AND CONCLUSIONS

These are as follows:

1) There is an early, first generation cement, which is commonly epitaxial, and thus reflects septal structure. This is usually but not always perpendicular to septal flanks, because biogenic calcite crystals are usually perpendicular to the septal flanks.

2) Generally a late cement of blocky calcite is noted, which is phreatic in origin. This cement commonly does not completely fill void spaces in the Timor corals.

3) Biogenic septal structures occur in well-preserved septa, and are usually trabecular, as in most Rugosa. However, both in *Calophyllum* and *Wannerophyllum*, the septal structure is non-trabecular; *Calophyllum* having a generally fibro-normal structure, except for fanning at the rhopaloid tips. Fanning septal structure is also present in *Wannerophyllum*.

4) Recrystallization is noted as zigzag patterns in the walls of *Euryphyllum* and *Calophyllum*. In both cases, a discontinuity is noted between unaffected portions of septa and the recrystallized wall and/or outer part of the septa.

5) Silicification in septa of *Lophophyllidium* preferentially replaced the fine crystallites of trabecular centers.

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SECTION 5  
INVITATIONAL SYMPOSIUM

**The Paleobiology of Sclerosponges, Stromatoporoids, Chaetetids,  
Archæocyathids and Non-Spicular Calcareous Sponges**

Organized, Convened and Edited

By

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INTRODUCTION

J. A. FAGERSTROM

Discoveries of "living fossils" in biologically remote areas (*e.g.*, the deep sea and in shallower cryptic habitats) are of particular interest to both biologists and paleobiologists. In the early 1900's some rare and unusual sponges (combined solid and spicular skeletons) were described from reefs (Lister, 1900; Kirkpatrick, 1911; Hickson, 1911) and then largely forgotten. More than 50 years later these sponges were rediscovered by divers in cryptic habitats in Jamaican reefs and subsequently placed in a new poriferan class (Sclerospongiae).

It is noteworthy that some of the biologists who studied these sclerosponges also compared them to such abundant, extinct and enigmatic fossils as the stromatoporoids, tabulate corals and chaetetids (*e.g.*, Hartman and Goreau, 1966, 1970, 1972). These comparisons induced paleobiologists who formerly were skeptical of the sponge affinities of these fossils (largely because they lacked spicules) to re-evaluate their materials with new insights into the functional aspects of several skeletal features (*e.g.*, Stearn, 1972; Kaźmierczak, 1969, 1981; Flügel, 1976; Cuif *et al.*, 1973; Gray, 1980).

In the present volume, Hartman summarizes the gross morphology and function of sclerosponge astrorrhizae, mamelons and symbionts, features that have been stressed by paleobiologists in recent interpretations of taxonomic affinity. Next, Stearn compares the nature of other gross skeletal features among several taxa and uses these features to draw some new general conclusions regarding their taxonomic importance.

Similarities in skeletal mineralogy and crystal structure among living calcareous sponges and their fossil counterparts have considerable potential value in phylogeny reconstruction if diagenetic alterations can be correctly interpreted; the mineralogic and crystal structure data are summarized and interpreted by Wendt.

The chaetetids are major constituents of many Paleozoic and Mesozoic reef and biostromal communities. Until the rediscovery of the Recent sclerosponges, most paleobiologists regarded the extinct chaetetids as unusual tabulate corals (*e.g.*, Hill, 1981) but after reviewing their paleoecology and morphological similarities with stromatoporoids, tabulates, Bryozoa and sclerosponges, West and Clark conclude that chaetetids are sclerosponges.

Next, Stock compares the detailed morphologies of an unusual Ordovician stromatoporoid and a Recent sclerosponge stressing probable similarities in the manner by which seawater circulated through their skeletons. Then, Mori reviews similarities among some gross morphological features (including astrorrhizae) in sclerosponges, selected coelenterates and stromatoporoids and concludes that those between the coelenterates and stromatoporoids are of greatest taxonomic importance.

Because nearly all fossil sphinctozoans lack spicules their placement among the calcareous sponges was somewhat uncertain until the discovery of a living species in Indo-Pacific reefs (Vacelet, 1979). This sponge, also lacking spicules, has thus expanded the morphological "domain" of both living and fossil Po-

rifera in ways that make it very appropriate for Debenne and Vacelet to re-open the long-standing debate on the taxonomic affinities and functional morphology of the extinct Archaeocyatha.

Except for the Archaeocyatha, none of the major fossil taxa noted above have proven to be of great value as chronostratigraphic indices. However, their abundance and varied functional rôles (guild placement) in ancient reef communities, many of which are enormously productive of oil and gas, have attracted the interest of both paleoecologists and exploration geologists. In the final paper in this section, Fagerstrom reviews the ecology and paleoecology of the sclerospores and sphinctozoans with particular emphasis on their guild placement in the structure of reef communities.

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## ASTRORRHIZAE, MAMELONS AND SYMBIONTS OF RECENT SCLEROSPONGES

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## ABSTRACT

Astrorhizae are stellate configurations of depressions or elongate conical, branching channels occurring in the basal calcareous skeletons of certain marine organisms. In Recent sclerosponges, to which this discussion is confined, astrorhizae may lie at the surface of the basal calcareous skeleton (*Ceratoporella*), may lie in part on the surface and also course into the interior of the skeleton (*Astrosclera*) or may occur entirely within the skeleton (*Calcifibrosporgia*).

The living structures, the presence and configuration of which result in the skeletal vacuities known as astrorhizae, are the terminal, cell-limited water-conducting canals of the excurrent aquiferous system as they converge upon the oscule, the opening through which water leaves the sponge. These living elements of the exhalant aquiferous system are never preserved in fossil sponges; in dead, cell-free Recent and in fossil sclerosponges, astrorhizae give evidence of the sites of the converging exhalant canals that were present in the living sponge.

Mamelons are elevations rising above the general surface of the basal calcareous skeleton in sclerosponges. Characteristically, in life, an osculum opens at the apex of each mamelon and a system of exhalant canals radiates down its sides. Within a particular species of sclerosponge, mamelons may be present or absent and strongly or weakly developed.

Symbionts of Recent sclerosponges include zoanthideans and scleractinians, both of which leave evidence of their presence in the basal calcareous skeleton. Serpulid polychaete tubes overgrow and are overgrown by sclerosponge skeletons. Other animal symbionts associated with the living surface of Recent sclerosponges are the excavating sponge genus *Siphonodictyon*, barnacles, brachiopods, vermetid snails and sphinctozoans.

Intercellular symbiotic bacteria occur in some sclerosponge species, but cyanophytes and zooxanthellae have not been found in the tissues. Endolithic green algae, cyanophytes and fungi occur in the surface processes of the basal skeleton of sclerosponges.

## INTRODUCTION

The purpose of this paper is to present a descriptive account of astrorhizal configurations and mamelons as they occur on the basal skeletons of Recent sclerosponges. The occurrence of symbiotic organisms with sclerosponges will also be discussed.

## ASTRORRHIZAE

The term "astrorhiza" was coined by Carter (1880) for stellate systems of shallow grooves found on the surface and at deeper levels of the skeleton of stromatoporoids. He regarded them as homologs of the branching coenosarcal grooves on the surface of the skeleton of species of *Hydractinia*. Nicholson (1886-1892) accepted Carter's "apt name" for these structures which he noted consist of stellate groups of "comparatively large-sized shallow gutters, which spring from a central point and branch as they radiate outwards, diminishing at the same time in diameter, and giving off more or less numerous lateral branches." He pointed out that the furrows lack walls of their own, that neighboring astrorhizal configurations are confluent and that deep-lying astrorhizae are converted into canals as newly deposited laminae build up. Nicholson (*op. cit.*) observed that astrorhizae occur on successive laminae and are either superposed and joined together by a vertical central tube or are placed irregularly without vertical alignment. He noted also that not all stro-

matoporoid species have astrorhizae. The term "astrorhiza" is now generally accepted to refer to stellate patterns of surface depressions or stellate arrangements of canal traces associated with fossil stromatoporoid skeletons (see, *e.g.*, Lecompte, 1956).

Hartman and Goreau (1970, 1975) adopted the term "astrorhiza" for stellate patterns of depressions on the surface of Recent sclerosponges or for stellate configurations of canal traces within them (see also Hartman, 1979). Surficial astrorhizae are the simplest types found in sclerosponges. They occur as depressions on the surface of the basal calcareous skeletons of *Ceratoporella nicholsoni* (Hickson), *Stromatospongia norae* Hartman and *Acanthochaetetes wellsii* Hartman and Goreau. These astrorhizal configurations in Recent sclerosponges are traces of the exhalant water canal systems that carry water that has already passed through the sponge to the oscules (sites of water expulsion), situated at the center of each such circlet of canals. The canal systems are tubes delimited by living cells arranged in thin epithelial layers. Upon death of the sponge they decay and disappear, at which time only traces of the canal systems remain impressed into the calcareous skeleton. Astrorhizae in living sclerosponges result when the living tissues of the sponge form a very thin veneer over the basal calcareous skeleton so that the exhalant canal systems, rendered turgid by the pressure of water running through them, inhibit

the upward growth of the calcareous skeleton beneath them. In forms like *Hispidopetra miniana* Hartman and *Stromatospongia vermicola* Hartman where the living tissues are somewhat thicker and less dense and the calcareous skeleton has spicule-rich processes at its surface, astrorhizae are not present, although stellate patterns of living exhalant canals are evident (see Hartman, 1969, p. 36, fig. 29 and p. 38, fig. 31). Elegant stellate patterns of exhalant canals are also present at the surface of many species of thin, encrusting sponges of the Class Demospongiae (see, e.g., Hartman and Reiswig, 1973, p. 571, fig. 2), but no astrorhizae are formed in the absence of a basal calcareous skeleton.

There is considerable intraspecific variation in the occurrence of surficial astrorhizae among sclerosponges. In *Ceratoporella nicholsoni*, especially, the depressions range from being deep (about one mm) and readily visible on the surface of the calcareous skeleton in some specimens (Fig. 1) to complete absence in others. When present, the astrorhizae of *Ceratoporella* cover circular to ellipsoidal surface areas with individual diameters ranging from  $21 \times 20$  mm to  $8 \times 8$  mm (based on measurements of six specimens with eight measurements per specimen). Dimensions of astrorhizae for individual specimens range from  $14 \times 14$  mm to  $8 \times 8$  mm in a specimen with relatively small astrorhizal traces and from  $21 \times 20$  mm to  $16 \times 14$  mm in a specimen with large traces. The individual radial furrows of an astrorhiza may show several primary branches and a few peripheral secondary branches in this species.

In the Indo-Pacific sclerosponge, *Acanthochaetetes wellsi*, the astrorhizae are shallow, difficult to see and not infrequently completely absent. The individual radial furrows are usually unbranched but occasionally show primary branches (Fig. 10; see also Hartman and Goreau, 1975, figs. 1, 3, 4). Most astrorhizae cover circular areas ranging from  $13 \times 13$  mm to  $5 \times 5$  mm (based on measurements of five specimens with eight measurements per specimen). Dimensions of astrorhizae for individual specimens of *A. wellsi* range from  $13 \times 13$  mm to  $10 \times 10$  mm for Belauan (Palau Is.) specimens and from  $7 \times 7$  mm to  $5 \times 5$  mm for the smallest astrorhizae measured on specimens from the Mariana Islands.

In *Astrosclera willeyana* Lister, widely distributed in the Indo-Pacific biogeographic realm, astrorhizae are manifest at the surface as three to six curving furrows (Fig. 2), clearly incised into the reticulate skeleton to depths of 250 to 300  $\mu$ m. The individual furrows usually do not branch at the surface; only the longest occasionally show a few primary branches. The furrows characteristically course beneath the surface of the

skeleton peripherally and there may show primary and secondary branching. At the surface the furrows range from 8 to 1 mm in length in six specimens measured; in individual specimens the furrows range in length from 8 to 2 mm in a specimen with larger astrorhizae and from 3 to 1 mm in a specimen with small astrorhizae.

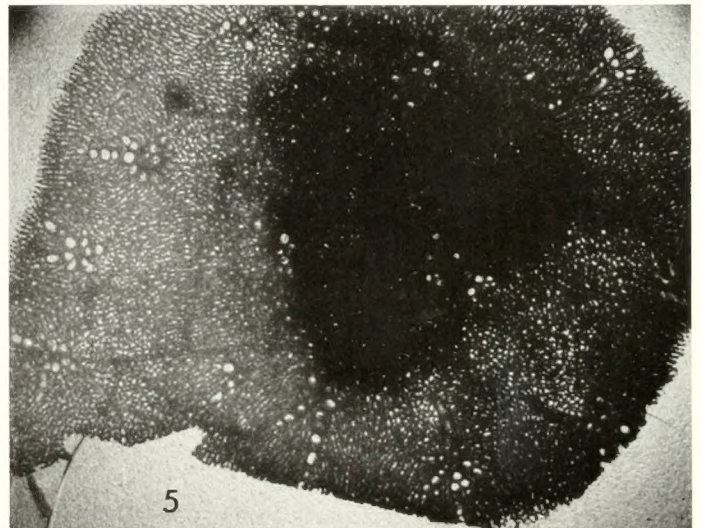
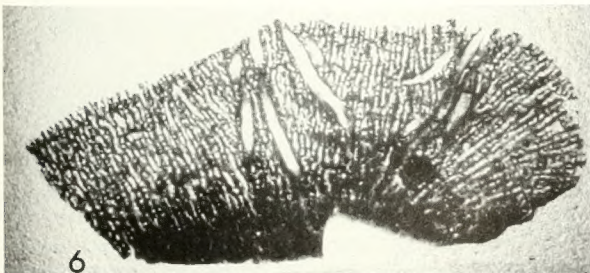
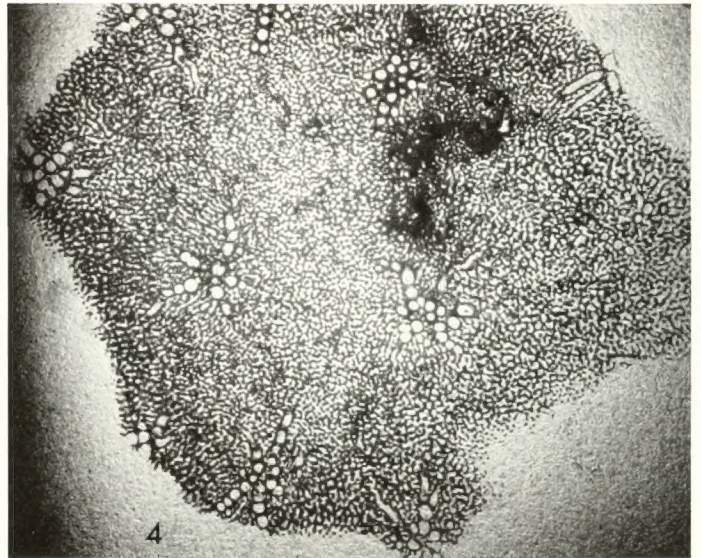
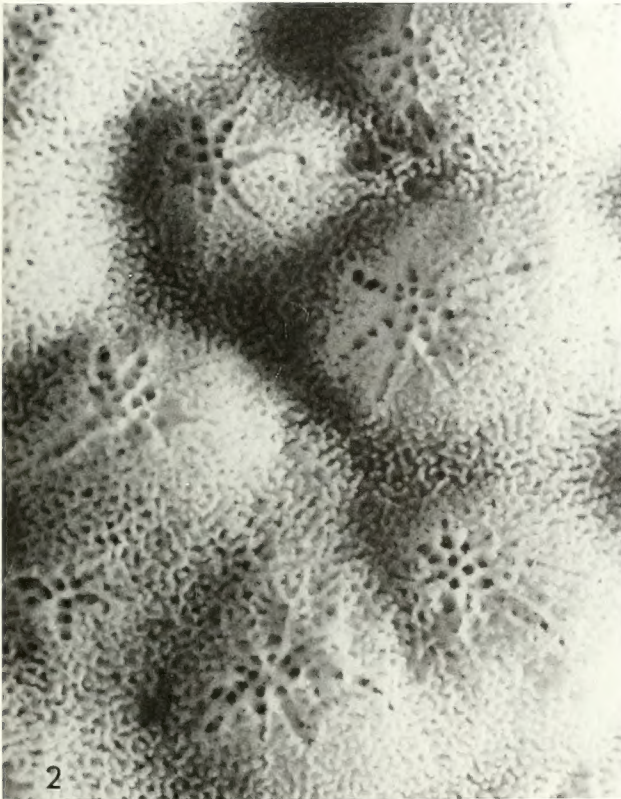
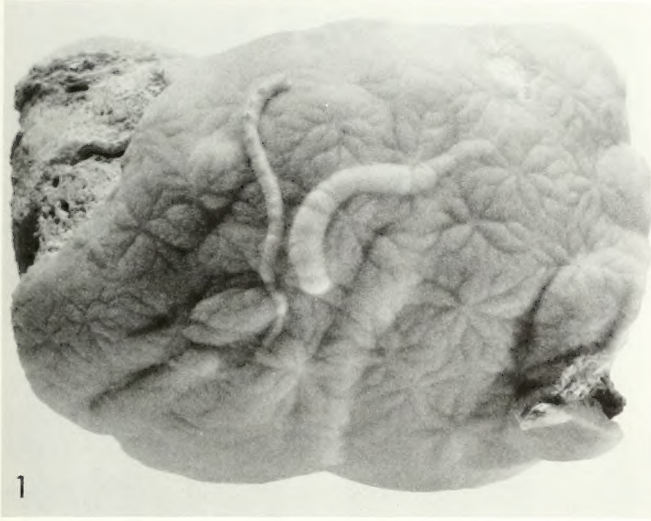
The astrorhizae of *Astrosclera* are three-dimensional, with only part of the configuration at the surface. Two to five, or occasionally six, astrorhizal canals course vertically into the interior of the skeleton (Fig. 6) from a central position which lies beneath the oscule in life. The lateral astrorhizal canals lie to a greater or lesser extent at the surface (Fig. 3), rising from a sub-surface position at varying distances from the central oscular region. Each of these lateral canals gives off a succession of branches from its floor and these course into the interior of the skeleton (Figs. 4, 5), quite vertically near the center of the system and more diagonally toward the periphery. The direction of the exhalant water current in the exhalant canal system of the living sponge runs from the deeper and more peripheral parts of the system to the center, but it is easier, in talking about the postmortem astrorhizal canals, to speak of them running from the oscular center to the deeper and more peripheral parts of the skeleton.

In *Astrosclera*, as the sponge grows upward, laying down more skeletal material at the surface, it also recedes a comparable amount from its innermost habitation of the skeleton. The interstices of the skeletal reticulum, now deprived of living tissue, as well as the deeper parts of the astrorhizal canals, are filled in with

Figures 1-6.

1. *Ceratoporella nicholsoni* (Hickson). Skeleton with surficial astrorhizae. Note also symbiotic serpulid tubes. Runaway Bay, Jamaica. 26 m. YPM (Yale Peabody Museum) No. 9293.  $\times 0.85$ .
2. *Astrosclera willeyana* Lister. Astrorhizae on portion of the skeleton. Saipan, Mariana Is. 6 m. YPM No. 9301.  $\times 8$ .
3. *Astrosclera willeyana* Lister. Tangential section of skeleton just beneath surface. Note astrorhizal configurations with central channels in cross section and lateral channels in longitudinal section. Fijis. 25 m. YPM No. 9294.  $\times 5.1$ .
4. *Astrosclera willeyana* Lister. Tangential section of skeleton about 0.5 mm deeper than Figure 3. Note that central channels and those issuing from the bottom of the lateral channels are seen in cross section. Fijis. 25 m. YPM No. 9294.  $\times 4.1$ .
5. *Astrosclera willeyana* Lister. Tangential section of skeleton about 1 mm deeper than Figure 4. Note that cross sections of central channels and more peripheral vertical or diagonal channels are still seen in cross section or diagonal section. Fijis. 25 m. YPM No. 9294.  $\times 2.7$ .
6. *Astrosclera willeyana* Lister. Vertical section through skeleton showing central vertical channels and diagonal channels of astrorhizae. Spaces between skeletal reticulum were filled with living tissue down to darkened region where secondary infilling has occurred. Fijis. 25 m. YPM No. 9294.  $\times 4$ .



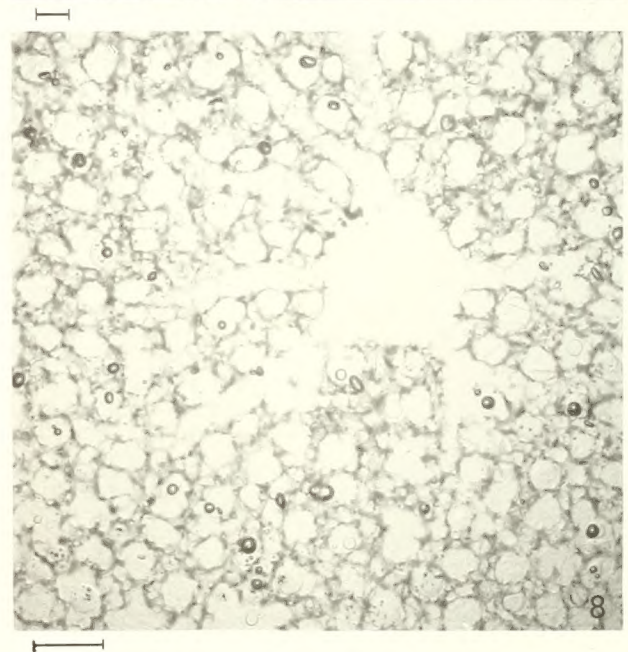
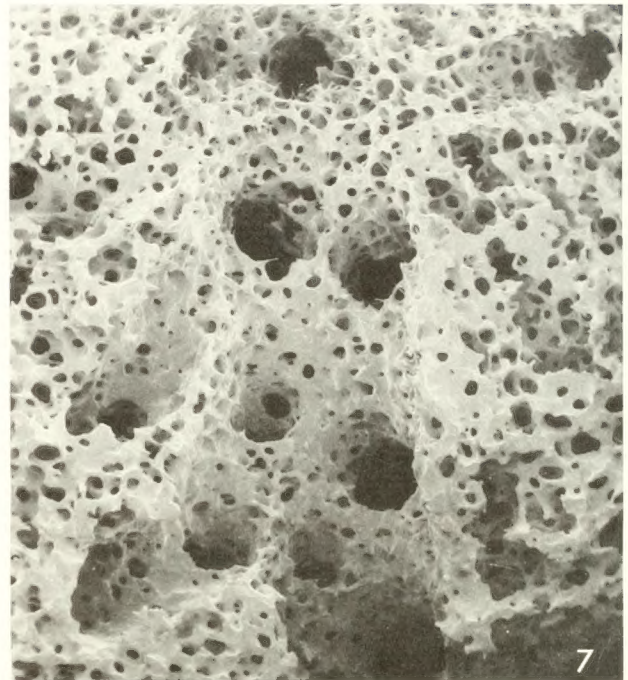


developmentally younger deposits of aragonite so that eventually the courses of the canals will no longer be evident a distance below the innermost level of the living tissue. Adjustments must be made as well in the positioning of the surface astrorhizal canals as the sponge grows upward and the living exhalant canals are refashioned at a higher level. Probably skeletal reticulum is laid down beneath the epithelial floor of the exhalant canals as they are repositioned; in this way the former position of the astrorhizal canals in the skeleton is filled in and becomes unrecognizable in these tropical animals that probably grow continuously.

In *Calcifibrospongia actinostromarioides* Hartman astrorhizae are internal. In this species a dermal membrane provided with a reticulate skeleton of siliceous spicules held together with spongin, but lacking a calcified skeleton, lies at the surface of the sponge, above a vestibular cavity about 0.5 mm deep in preserved specimens. The vestibule receives sea water by way of pores in the dermal membrane and distributes the water to the inhalant canals that lie in the subvestibular tissue, the choanosome (internal, choanocyte chamber-bearing tissues) where a reticulate skeleton of aragonite is present. In the skeleton a series of closely spaced tubes, 360 to 600  $\mu\text{m}$  in diameter, that house the inhalant canals of the water-conducting system in the living sponge, extend vertically from the vestibular cavity into the interior of the sponge. Larger tubes, 1.5 to 2.0 mm in diameter, that house the major exhalant canals of the aquiferous system, rise vertically to the surface at intervals of 15 to 20 mm. Whorls of horizontal exhalant canals, draining the surrounding choanosome, open into the vertical canals at intervals (Fig. 7). The traces in the skeleton of these canal systems have the appearance of internal astrorhizae in thin sections (Fig. 8).

Yet another variant among astrorhizal structures of Recent sclerosponges occurs in the ceratoporellidan genus *Goreauiella* Hartman. The oscules of the exhalant canal systems in the living sponge open along the edge of the sponge, and their positions are marked by indentations along the periphery of the calcareous skeleton. The astrorhizae, composed of traces raised above the general level of the skeleton, occur beneath the living exhalant canals. (See Hartman, 1969, p. 18, fig. 10.) The mechanism of formation of these raised astrorhizal patterns, unique among Recent sclerosponges, is not yet understood.

The astrorhizal patterns described from the skeletons of Recent sclerosponges provide three kinds of models for comparison with astrorhizal configurations on skeletons of extinct animals. These are (1) surficial,



Figures 7, 8.—7. *Calcifibrospongia actinostromarioides* Hartman. Portion of calcareous skeleton sectioned vertically and showing an exhalant canal trace (shaded) running on a slight diagonal from top center to bottom right of photograph. Large holes are lateral exhalant canal traces entering the vertical one. Scanning electron micrograph. Scale = 300  $\mu\text{m}$ . (From Hartman, 1979.) 8. *Calcifibrospongia actinostromarioides* Hartman. Cross section of calcareous skeleton showing internal astrorhiza (main vertical exhalant canal trace with lateral canal traces entering it) and numerous inhalant canal traces (small, circular holes). Scale = 1.5 mm. (From Hartman, 1979.)

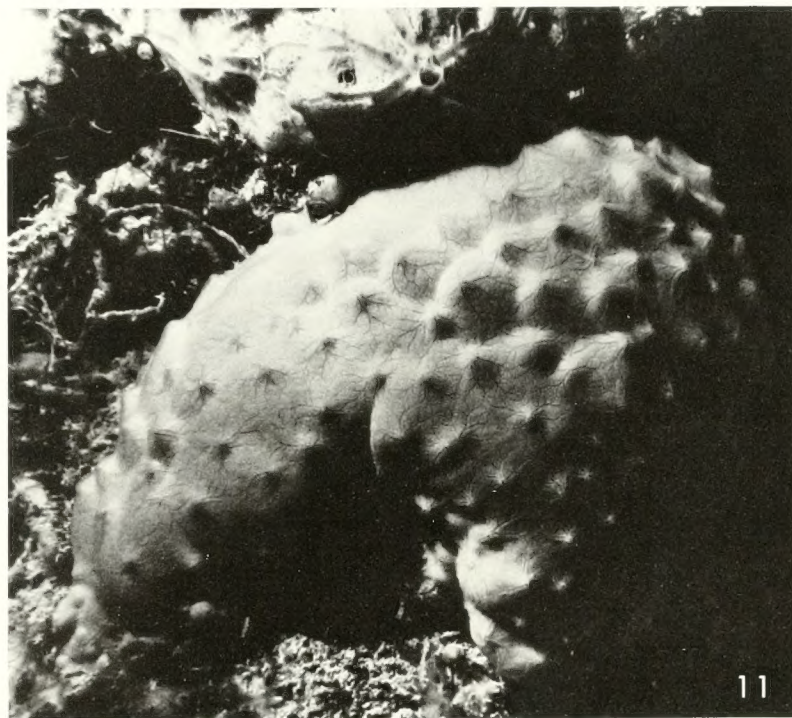
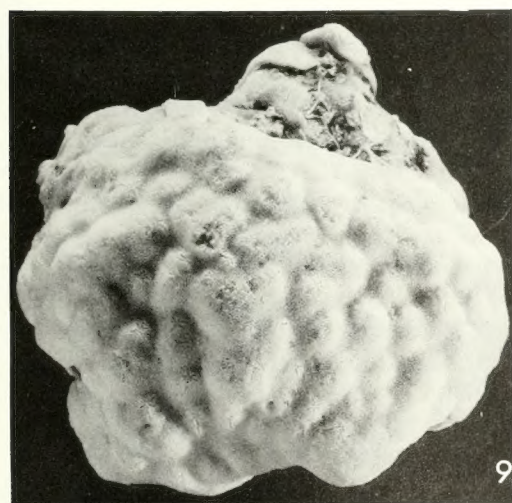
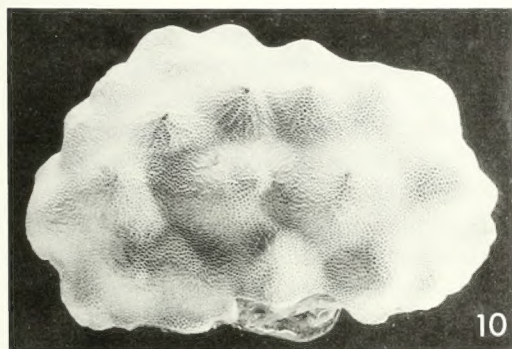
(2) those with some astrorhizal canals lying at the surface and others extending into the interior of the skeleton and (3) those occurring solely within the skeleton. It is important in making comparisons with fossil specimens to keep in mind that whether it is a question of stellate systems of depressions on the surface of a skeleton or the radiating patterns in the interior of the skeleton, the canal traces in sclerospenges are widest at the center of the system and decrease in diameter peripherally. It should also be noted that neighboring systems may be confluent, especially in the case of surficial traces.

### MAMELONS

The term "mamelon" has been widely used by students of stromatoporoids to refer to rounded or pointed elevations on the surface of the skeleton, often provided apically with the opening of an axial astrorhizal canal (see, e.g., Lecompte, 1956, p. F110). Hartman and Goreau (1970) described such features in sclerospenges where, in life, an oscule typically opens at the

apex of each mamelon and a system of exhalant canals radiates down its sides. Astrorhizae may occur beneath the stellate arrangements of exhalant canals. Mamelons occur on the skeletons of *Ceratoporella nicholsoni*, *Stromatospongia norae*, *Astrosclera willeyana* and *Acanthochaetetes wellsi*.

In *Ceratoporella nicholsoni* mamelons (Fig. 11) vary up to 7 mm in height and occur 10.5 to 22 mm apart (center to center). Astrorhizal traces are frequently present on the mamelons (see Hartman and Goreau, 1970, p. 211, fig. 6). As the skeleton increases in surface area mamelons, together with their systems of exhalant canals, divide and separate until two mamelons exist spaced in the usual manner. Centers of mamelons in the process of dividing on two specimens examined lie 6 to 7 mm apart. In one specimen, two buds are present, one on each side of the parent mamelon. These observations suggest that a maximal volume of tissue exists that can be drained by an exhalant canal system. When the volume exceeds this amount a new system forms by "fission" of an existing system. In two spec-



Figures 9–11.—9. *Astrosclera willeyana* Lister. Specimen with mamelons. Saipan, Mariana Islands. 6 m. YPM No. 9301.  $\times 1.6$ . 10. *Acanthochaetetes wellsi* Hartman and Goreau. Specimen with prominent mamelons and astrorhizae. Ngargol, Belau. YPM No. 9122.  $\times 1$ . 11. *Ceratoporella nicholsoni* (Hickson). Living specimen *in situ* showing exhalant canal systems in relation to mamelons. Note encrusting demosponge above with stellate system of exhalant canals. Tunnel near Runaway Bay, Jamaica. 28 m.  $\times 1$ . Photo by T. F. Goreau.

imens of *Ceratoporella* with well-developed mamelons the maximal volume of tissue drained by a single exhalant canal system of one approximates  $400 \text{ mm}^3$  (in the formula for the volume of a cylinder,  $r = 8.5$  and  $h = 1.5$ ); in another, the maximal volume is  $570 \text{ mm}^3$ . It is estimated that about 30–40% of specimens of *Ceratoporella nicholsoni* in the Jamaican North Coast populations are provided with mamelons of varying height. The rest lack these features.

*Stromatospongia norae* is the only other ceratoporellidan sclerosponge that bears mamelons, and these range up to 16 mm in height and are 10 to 14 mm apart. A majority of specimens of this species are provided with mamelons. (See, e.g., Hartman, 1969, p. 9, fig. 4; note exhalant canal systems on sides of mamelons.)

Mamelons are rare in *Astrosclera*. In the single specimen available to me (Fig. 9) the mamelons are about 2 mm in height and range from 3.5 to 6 mm apart (center to center). Each is provided with a surface astrorhizal configuration, and a few, with two astrorhizae close together, appear to be dividing in response to growth of the skeleton.

In *Acanthochaetetes wellsi*, conspicuous mamelons occur on specimens from Belau (Palau Is.). Mamelons on specimens from these populations (Fig. 10) range from 3 to 5.5 mm in height and are 5 to 18 mm apart (center to center). Less conspicuous mamelons characterize specimens from the Mariana Islands where these structures rarely exceed 1.5 mm in height and range from 5 to 10 mm apart (center to center). As in previously mentioned species, oscules of exhalant canal systems open at the apex of mamelons and the canals extend down the sides of the mounds. Growth of the sponge and its skeleton is accompanied by binary fission of the mamelons and associated systems of exhalant canals and their astrorhizae. Centers of mamelons in the process of dividing are 4 to 5 mm apart. In Belauan specimens the maximum volume of tissue drained by a single exhalant canal system approximates  $500 \text{ mm}^3$ ; in Mariana Islands specimens the maximum volume is about  $160 \text{ mm}^3$  (each figure based on two specimens). In Belauan populations mamelons are of general occurrence (see also Mori, 1976, pl. 1, figs. 3, 4) while in populations from the Mariana Islands mamelons are present in about half of the twelve specimens examined and are absent in the rest.

There is a possible advantage for a sponge living in quiet water to elevate its oscules on tubules that lie above the major inhalant surfaces of the sponge (see, e.g., McNair, 1923). This separation of exhalant and inhalant openings together with optimal oscular diameter provides an excurrent flow of water with a di-

ameter of supply (Bidder, 1923) great enough to allow previously filtered water, poor in nutrients, rich in  $\text{CO}_2$  and nitrogenous waste materials, to be dissipated before reentering the sponge. Vogel and Bretz (1972) and Vogel (1974) have pointed out a further advantage to a sponge in having its exhalant openings elevated above its inhalant pores. The external medium travels fastest over an encrusting sponge as it passes the highest points since a velocity gradient exists at the boundary layer between medium and object. As the external medium passes over an elevated oscule a reduction in pressure passively drives a secondary flow from the lower-lying, small, inhalant openings of the sponge in the direction of the higher, large exhalant openings. This passive flow can augment the rate at which water passes through a sponge (Vogel, 1977) with resulting favorable metabolic consequences.

Do these considerations help provide an explanation of the mamelons of sclerosponges? The variable occurrence of mamelons among sclerosponge species that manifest them suggests that an environmental explanation of their presence is possible, but our imperfect knowledge of the ecology of sclerosponges prevents a definitive answer to the question at this time. It is of interest to note, however, that the only three specimens of *Acanthochaetetes wellsi* known to me (two from Yale Peabody Museum collections (see Fig. 10) and one figured by Mori, 1976) from shallow caves on Belau have prominent mamelons. Unfortunately I do not know if these caves are protected from strong wave action. Twelve specimens of the same species with inconspicuous or no mamelons come from caves in the Mariana Islands where moderate surge action is of regular occurrence.

In the case of *Ceratoporella nicholsoni* five of six specimens in Yale Peabody Museum collections or known from underwater photographs (see Fig. 11) from a tunnel near Runaway Bay, Jamaica, at 90 ft., have low to prominent mamelons. One specimen lacks these features. I do not know, however, if the mamelon-bearing specimens were collected in protected recesses of the tunnel. Among specimens in our collection from deeper waters at Runaway Bay and from Discovery Bay, Jamaica, mamelons are of rare occurrence. Of particular interest in this regard is the distribution of specimens with or without mamelons on the deep fore reef off Discovery Bay. A set of photographs of this zone (55–120 m) made during a survey of its fauna by submersible (Lang, 1974; Hartman, 1973) indicates that at least 40% of specimens of *Ceratoporella nicholsoni* have mamelons (see, e.g., Hartman, 1973, figure on p. 16) while the remainder lack them. In several photographs a specimen with mamelons occurs

directly adjacent to one without mamelons, indicating that an environmental explanation does not apply in these populations.

### ANIMAL SYMBIONTS

In discussing the symbionts of sclerosponges the term "symbiosis" will be used to mean "living together" in line with the original definition by de Bary (1879; see discussion in Henry, 1966, p. ix-xi, xiii-xiv). As such the term embraces mutualism, commensalism and parasitism.

Among West Indian sclerosponges the most frequent animal symbionts are serpulid polychaetes. All known specimens of *Stromatospongia vermicola* are associated with many serpulids. The three species of serpulids involved—*Pseudovermilia occidentalis* (McIntosh), *P. multispinosa* (Monro) and *P. fuscostriata* Hove—are not restricted to a relationship with sclerosponges, however, but may attach to other hard substrata such as sponges without a basal calcareous skeleton or scleractinian corals (Hove, 1975). Young specimens of *S. vermicola* lack serpulid associates (Hartman and Goreau, 1972, figs. 10, 11), but older ones become a tangle of worm tubes and the calcareous skeletal mass of the sclerosponge (Hartman, 1969, p. 4, fig. 1; Hartman and Goreau, 1970, p. 214, fig. 9).

*Stromatospongia norae* invariably encrusts at least one serpulid tube and tends to assume bizarre shapes when it does (see Hartman, 1969, p. 9, fig. 5). The only serpulid species so far recorded in association with *S. norae* is *Pseudovermilia multispinosa* (see Hove, 1975). A high percentage of the skeletons of *Ceratoporella nicholsoni* enclose at least one serpulid tube and many enclose several (Figs. 1, 13). In a few instances the skeleton is covered with the tubes of *Pseudovermilia multispinosa* (Fig. 12), the only species reported from this sclerosponge (Hove, 1975).

*Hispidopetra miniana* almost always grows in association with one or two species of serpulids (see Hartman, 1969, p. 14, figs. 8, 9); namely, *Pseudovermilia multispinosa* or *P. fuscostriata* (Hove, 1975). Specimens of the first-mentioned serpulid have a unique type of operculum when associated with *H. miniana* and may represent a distinct species which in itself, however, is not restricted to sclerosponges. Serpulid tubes also grow occasionally on the living surface of the Indo-Pacific species *Astrosclera willeyana*.

Zoanthideans are not infrequent symbionts of sponges and are especially common in the West Indies (see, e.g., West, 1979). An unidentified species of *Parazoanthus* with yellow to tan polyps lives with *Ceratoporella nicholsoni* (Fig. 13). The polyps are spaced 5 to 10 mm apart and each forms a depression, 1 to 2

mm deep and 1.5 to 3 mm in diameter, in the sponge skeleton where the aragonite has grown up around the base of the polyp. It is not known if the coenenchymal bridges that connect adjacent polyps are enclosed within the calcareous skeleton or if they are confined to the soft tissues of the sponge. West (1979) reports the zoanthidean *Parazoanthus puertoricense* West living with *Stromatospongia vermicola* in Jamaica. An orange-tan zoanthidean growing with *Goreauella auriculata* induces the formation of skeletal processes ranging up to 1 cm in height and 6 mm in width. The polyps, distributed at intervals of 6 to 8 mm, sit in depressions on the processes (Hartman, 1969, p. 18, fig. 11). Among Indo-Pacific sclerosponges, yellow and tan species of *Parazoanthus* occur with *Astrosclera willeyana* in Guam and another species is known from a single specimen in association with *Acanthochaetetes wellsii* from Saipan. Aposematic coloration is apparent in the following associations: dark maroon *P. puertoricense* growing on salmon pink *S. vermicola*; an orange-tan zoanthidean growing with light yellow *Goreauella auriculata*; a yellow to tan *Parazoanthus* sp. living on *Ceratoporella nicholsoni*, orange to maroon in color; yellow or tan species of *Parazoanthus* sp. growing on salmon-, peach- or orange-colored *Astrosclera willeyana*. The significance of these more or less contrasting color patterns in deterring fish predation (West, 1976; Lewis, 1982) is uncertain, however, in view of the shaded habitats of sclerosponges.

The only scleractinian coral known to overgrow sclerosponges is *Madracis pharensis* (Heller) which encrusts *Ceratoporella nicholsoni* in the West Indies, apparently killing the sponge tissue beneath it and causing a change in form of the sponge skeleton in a zone up to 2.25 mm in width around the coral (Hartman and Goreau, 1972, figs. 15, 16, 17). At the far end of the affected zone the calices of the sponge lose their regularity, becoming elongate in shape and provided with tall, pointed processes. Closer to the coral, the skeleton loses all semblance of calicular structure and is composed of lamellate processes comparable to those that characterize *Stromatospongia norae*.

Excavating sponges of the family Clionidae are common inhabitants of the basal skeleton of sclerosponges, but only *Siphonodictyon* sp., an excavating sponge of the family Adociidae, sends its oscular and ostial processes through the living surface of the sclerosponge *Ceratoporella* (Fig. 14), leaving holes, 1.5 to 2.5 mm in diameter and spaced from 5 to 16 mm apart, in the skeleton. (See, e.g., Rützler, 1971.)

Other less common animal symbionts include pyrgomatid barnacles (Fig. 15) which settle on the skeleton of *Astrosclera willeyana* and become partially over-

grown by the sponge skeleton in a manner similar to that which obtains in scleractinian corals (see, e.g., Ross and Newman, 1973). Another symbiont is the brachiopod *Thecidellina* which commonly settles on the dead undersides of sclerosponges (Jackson *et al.*, 1971) and only occasionally occurs on the living surfaces of *Stromatospongia micronesica* Hartman and Goreau (1976) in caves in Saipan. Bryozoans may also grow over *Astrosclera* (Fig. 16). A single example of a small vermetid snail has been found on the living surface of an *Astrosclera* (Fig. 17) from Saipan. Another unusual occurrence is a pair of sphinctozoan sponges, *Vaceletia crypta* (Vacelet), growing on the living surface of an *Astrosclera* from the Fijis (Fig. 18).

Sclerosponges provide unusual opportunities for other organisms to grow in close association with them in view of their habit of dying back locally only to overgrow the same region at a later time. Ample opportunity exists for larvae to settle on a dead portion of the skeleton; later the settled organism may be overgrown by renewed growth of the sclerosponge, and survival of the symbiont will depend upon whether its growth rate is equal to or greater than that of the host. I believe most of the examples of animal symbionts cited here will have begun the relationship by way of this mechanism.

A greater diversity of organisms settle and grow on the epithelial surface or underside of sclerosponges, but these do not interact with the living tissues of the sponge.

#### MONERAN, ALGAL AND FUNGAL SYMBIONTS

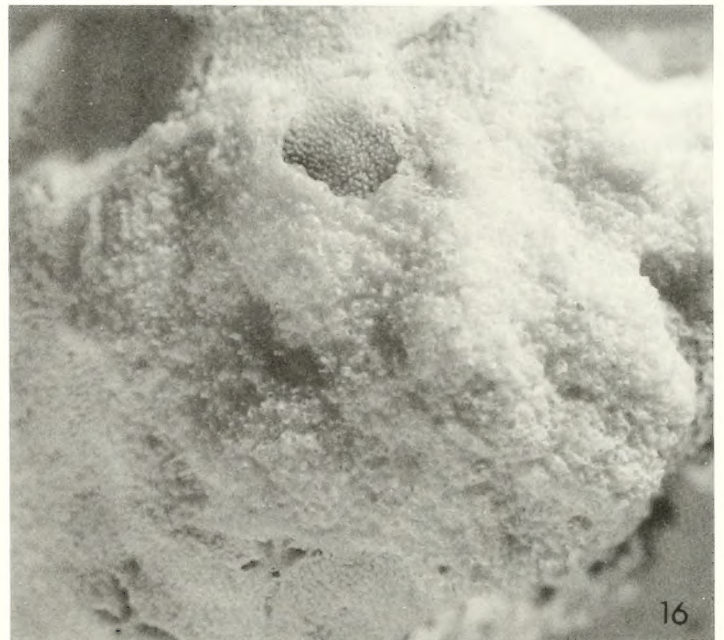
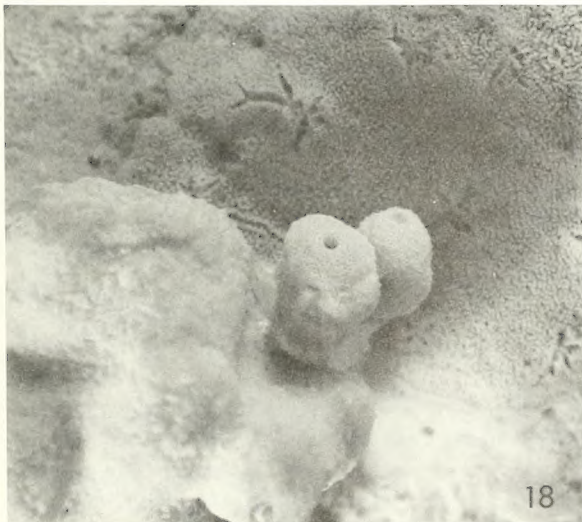
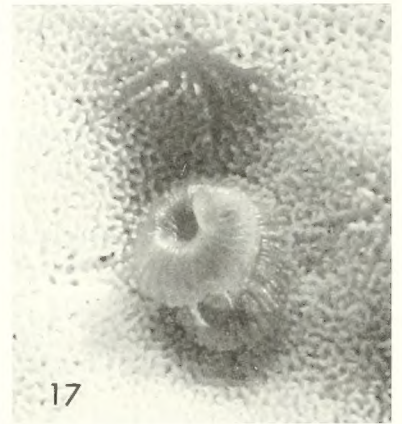
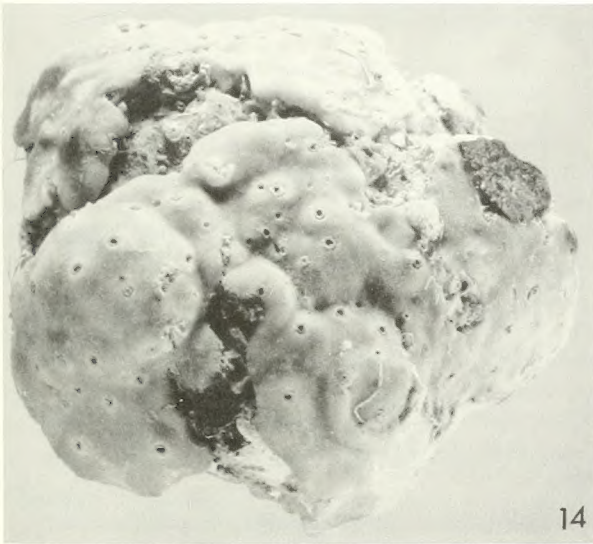
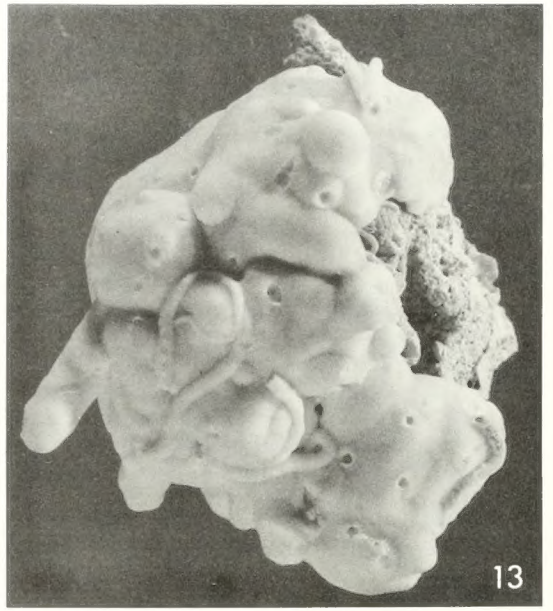
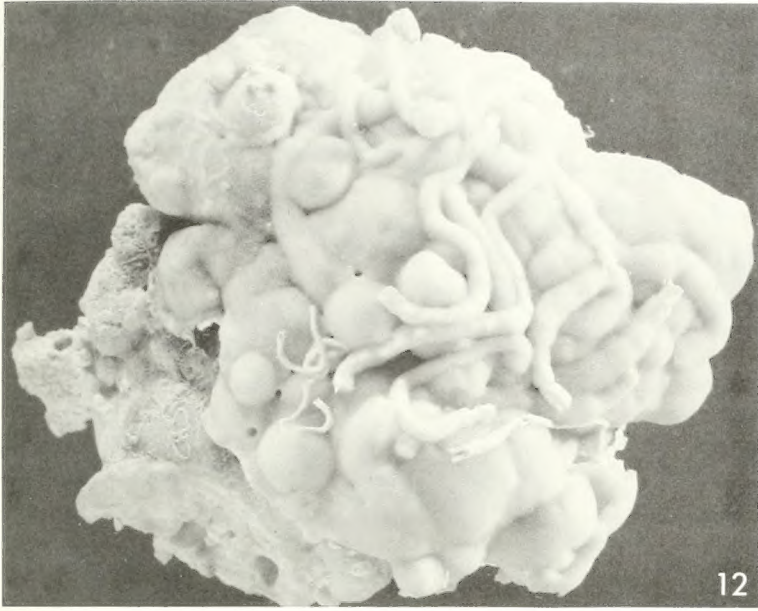
Endolithic algae and possibly endolithic bluegreen algae (Cyanobacteria) as well are of general occurrence in the skeletons of sclerosponges. Chlorophyta, possibly of the genus *Ostreobium*, are most apparent in the tips of the skeletal processes of *Hispidopetra miniana* when this sponge is alive (Hartman, 1969), but comparable organisms occur in the skeletons of other West Indian and Indo-Pacific sclerosponges. They appear to be absent only from the skeleton of *Acanthochaetetes wellsi*. Other endolithic organisms present in sclerosponge skeletons (Hartman, 1969) are believed to be bluegreen algae and fungi comparable to those figured by Duncan (1877, pl. 7, figs. 39–44), but all these symbionts need further study in sclerosponges. Unidentified unicellular eucaryotic algae have been observed in electron micrographs of the tissues of *Astrosclera* and *Stromatospongia micronesica* (pers. observ.). Zooxanthellae are unknown, however, in any sclerosponges at this time.

Intercellular bacteria are of common occurrence in the tissues of *Astrosclera* and *Stromatospongia micronesica* (pers. observ.). They have also been reported

by Vacelet (1981) from Caribbean sclerosponges. Their possible role in the uptake of dissolved organic substances, as demonstrated by Wilkinson and Garrone (1980) for demosponges, has yet to be shown for sclerosponges. Bacteria are apparently absent from electron micrographs of the tissues of *Acanthochaetetes wellsi* (pers. observ.). Bluegreen algae have not been reported from the tissues of sclerosponges.

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- Figures 12–18.
12. *Ceratoporella nicholsoni* (Hickson). Skeleton overgrown by numerous serpulid tubes which the sponge in turn is overgrowing. Note single row of zoanthidean depressions. Andros Island, Bahamas. 65 m. YPM No. 9298.  $\times 1.2$ .
  13. *Ceratoporella nicholsoni* (Hickson). Skeleton showing depressions where zoanthidean polyps occurred in life. Serpulid tubes are also present. Runaway Bay, Jamaica. 37 m. YPM No. 6450.  $\times 1$ .
  14. *Ceratoporella nicholsoni* (Hickson). Holes in surface of skeleton represent sites through which ostial and oscular tubes of the excavating sponge, *Siphonodictyon* sp., protruded in life. Discovery Bay, Jamaica. 86 m. YPM No. 9302.  $\times 0.85$ .
  15. *Astrosclera willeyana* Lister. Skeleton with barnacle embedded. Saipan, Mariana Islands. 6 m. YPM No. 9303.  $\times 1.3$ .
  16. *Astrosclera willeyana* Lister. Portion of skeleton overgrown by unidentified bryozoan. Fijis. 27 m. YPM No. 9304.  $\times 4$ .
  17. *Astrosclera willeyana* Lister. Unidentified vermetid snail attached to surface of sponge. Saipan, Mariana Islands. 6 m. YPM No. 9305.  $\times 6$ .
  18. *Astrosclera willeyana* Lister. Two individuals of the sphinctozoan sponge, *Vaceletia crypta* (Vacelet), attached to surface of *Astrosclera*. Encrusting bryozoan lies to the left of the sphinctozoans. Fijis. 27 m. YPM No. 9306.  $\times 2.25$ .



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GROWTH FORMS AND MACROSTRUCTURAL ELEMENTS  
OF THE CORALLINE SPONGES

COLIN W. STEARN

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## ABSTRACT

The chaetetids, sclerosponges, and stromatoporoids are organisms that combine many features of the phyla Porifera and Cnidaria. Like several groups of encrusting invertebrates and cyanobacteria, these organisms secreted a continuous calcareous skeleton, abandoned the inner parts and lived on, and near, the upper surface only. Causal relationships between their growth forms and environmental parameters have been postulated but are not firmly established. Although some members of the group show rhythmic growth that has been attributed to seasonal variations, no proof of the annual nature of these bands has been presented nor has their presence been connected to environmental variations. A morphologic gradient can be demonstrated from corallites of cnidarians, through the hexagonal individuals of the favositids and the tubes of chaetetids to the calicules of sponges and the inter-coenosteole space of stromatoporoids. A spectrum of forms exists from scleractinians with corallites surrounded by coenosteum through heliolitids and millepores to stromatoporoids with no evidence of individuals. The definition of morphologic boundaries is difficult between tabulates with well defined corallites, chaetetids, sclerosponges with tabulate design (*Merlia*), sclerosponges with calicules (*Ceratoporella*), sclerosponges without calicules (*Astrosclera*) and stromatoporoids. Likewise, no definite morphologic boundaries exist between sponges that are entirely spicular, those with spicules embedded in a nonspicular skeleton, those with spicules embedded in soft tissue and an aspicular skeleton, and those with only an aspicular skeleton such as the stromatoporoids. The morphologic field of the stromatoporoids is much closer to that of the poriferans than to that of the cnidarians.

## INTRODUCTION

The sponges have traditionally been divided into three major groups: the hexactinellids, the demosponges, and the calcareous sponges. The hexactinellids have soft-tissue structures that justify their separation from other sponges as a separate subphylum (Reiswig and Mackie, 1983). They secrete six-rayed siliceous spicules that join into frameworks of rectilinear design and are commonly referred to as the "glass sponges." By far the largest number of fossil sponges belong to the other two groups: the demosponges and the calcareous sponges.

The demosponges secrete a siliceous skeleton of spicules that may be loose in the soft tissue or fused to form a rigid framework. To paleontologists, the most familiar of the latter are the lithistid sponges of the Paleozoic and Mesozoic which have large rigid skeletons composed of complex spicules of basically tetraxon design. Although all living demosponges are characterized by siliceous spicules, most fossils from Paleozoic rocks placed in this group are composed of calcite and their siliceous spicules are assumed to have been replaced. This replacement in fossil materials of opaline spicules by calcite makes the assignment of some fossil groups to the demosponges or calcisponges uncertain.

Workers do not agree on a classification of calcareous sponges but for purposes of this discussion I have distinguished 3 classes (Table 1). These three classes are here referred to informally as the calcareous sponges.

The classes Sclerospongiae and Stromatoporoidea may be considered to form an informal group called the coralline sponges.

The Calcarea secrete a skeleton composed of an assembly of calcite spicules or a continuous skeleton of fibrous, or spherulitic, calcium carbonate referred to as an aspicular skeleton. The Calcinea and Calcaronea whose spicules are isolated in the soft tissue have a poor fossil record.

To paleontologists the most familiar calcareous sponges belong to the order Inozoa. These are composed of spicules which are cemented together by lamellar or spheroidal calcite to form fibers that build rigid skeletons. They are particularly abundant in Mesozoic reefal facies but have been recorded in rocks as old as Permian and persist in modern seas. The Heteractinida (or octactinellids) are a group of early and mid-Paleozoic sponges composed of star-like spicules that are now calcite but could originally have been silica (if so the group should be placed in the demosponges). *Astraeospongium* from the Middle Silurian is the heteractinid genus most familiar to North American paleontologists. The Sphinctozoa are an aberrant group of sponges that have chambered skeletons and are particularly characteristic of the late Paleozoic but have recently been discovered in modern oceans (Vacelet, 1979). The sphinctozoan skeleton, like that of many of the coral-like sponges is aspicular and the presence of spicules in this group is a matter of discussion (Vacelet, 1970).

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cation of this pattern directly by the environment may have taken place, but was usually of minor significance. The latter influence can only be separated from the former if different forms of the same species are compared. Such a study has recently been completed by Kershaw (1981).

Many stromatoporoids grew in areas of sediment accumulation and in order to keep their upper surfaces free for feeding and other life-processes, maintained relief between themselves and the sediment that was accumulating around them. Such stromatoporoids secreted skeletons that interfinger at the lateral edges with the accumulating sediment. The degree of this inter-fingering was referred to by Kershaw and Riding (1978) as the raggedness of the growth form. Variations in the ratio of the rate of growth of the stromatoporoid and the rate of sedimentation cause changes of shape of a single stromatoporoid (Tsien, 1974). Stromatoporoids that were broadly laminar in form, and were using most of their growth potential in spreading along the substrate under conditions of slow sedimentation, in order to avoid being overwhelmed by an influx of sediments, may be forced to grow more rapidly upwards, concentrating their growth potential in a smaller area. Such stromatoporoids may change from laminar to domal or digitate forms as the sediment accumulated around them. The growth of stromatoporoids to a bulbous form appears to have been controlled by a rapid rate of sedimentation (Fig. 1F). The lateral edges of laminate, bulbous, or skirted stromatoporoids may end abruptly against the accumulating sediment or may appear to seal against each other. Unfortunately in many stromatoporoid skeletons the relations of the edge zones to the surrounding sediment is obscure because this area is preferentially altered, presumably by contact with the pore waters expressed from the compacting sediment. Most stromatoporoids are successful in excluding sediment from the skeleton but in some the space between the skeletal elements contains sedimentary grains near the edges and in others lenses and layers of sediment are incorporated as the organism was locally overwhelmed and grew over the deposit.

#### Growth Rates

The stromatoporoids were the largest and the most successful of the coralline sponges if success is measured by some combination of abundance, diversity, and racial longevity. When the stromatoporoid is embedded in limestones the boundaries of individual skeletons may be obscure. For this reason the maximum size of stromatoporoids is difficult to determine. Mounds that appear to be single individuals 4 or 5 m across are known from Middle Ordovician rocks of

northern Vermont. A laminar stromatoporoid in the Middle Devonian rocks of Iowa appears to cover an area several tens of square meters. The sclerosponges grow to 1 m in diameter.

The latilaminae of many stromatoporoids have been interpreted by paleontologists as formed by annual environmental cycles. Meyer (1981) has related the latilaminar thicknesses of two species of *Parallelostroma* and one of *Stictostroma* to rhythmic changes in a favositid which they overgrew. He assumed that these rhythmic changes are annual and determined that the stromatoporoids grew vertically at rates of 1.3 to 3 mm per year and laterally at rates of 10 to 23 mm per year. Until some independent evidence is offered that the layering of either the stromatoporoids or the corals is annual, these rates must be considered conjectural. Hartman and Goreau (1972) state that the rate of growth of sclerosponges such as *Ceratoporella* is unknown and the aspicular skeleton is not conspicuously marked by concentric growth lines. The epitheca of sclerosponges is marked by growth lines but these have not been related to its rate of growth.

## MACROSTRUCTURAL ELEMENTS

### Individual and Colony

The fossil coralline sponges secreted hard tissue that is so similar to that of colonial corals that many paleontologists place them in the phylum Cnidaria. Yet sponge hard tissue is secreted by an individual and the comparable hard tissue of colonial corals by the concerted action of many polyps. Hartman and Reisinger (1973) have reviewed the question of the coloniality of sponges, and have clearly shown that a sponge operates its systems as an individual. The trophic units which are repeated throughout the sponge body are choanocyte chambers, ostia through which water is taken in and directed to the chambers, and the larger excurrent canal systems which lead to oscula. None of these units can be homologized with the polyps that form the colonial skeleton of the cnidarian nor can the whole trophic system of the encrusting sponges be closely compared with that of cnidarians. The similarity of the hard tissue of such coralline sponges as *Tabulispongia* (= *Acanthochaetetes* of Hartman and Goreau, 1975) to that of primitive corals and ectoprocts should be a warning to paleontologists that skeletal form may be a poor guide to trophic function of extinct organisms.

The living sclerosponges are proven to be sponges by their soft tissue; certain fossils identified as sclerosponges on the basis of skeletal similarity, may be sponges; the chaetetids, once widely regarded as cnidarians, since they have been shown to be very similar

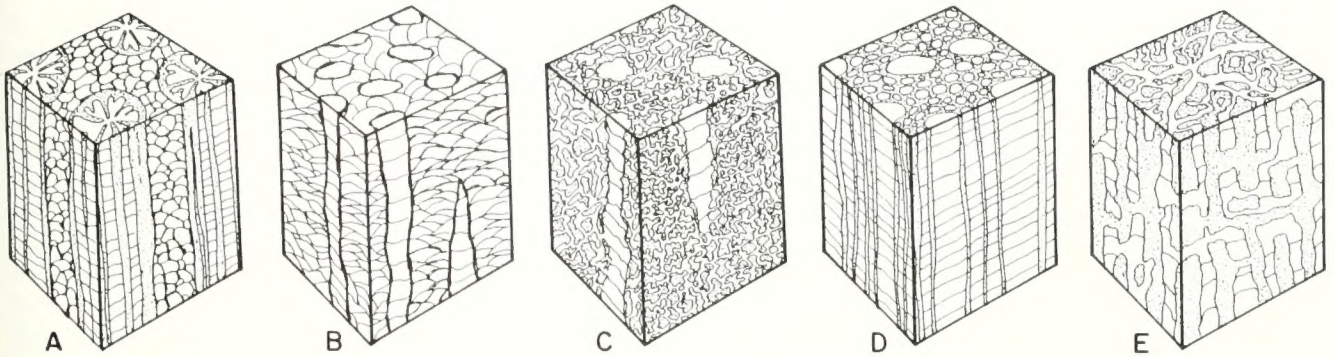


Figure 2.—Block diagrams,  $\times 7.5$  (approx). A, a scleractinian, B, a heliolitid, C, the hydrozoan *Millepora*, D, *Milleporidium*, E, stromatoporoid of amalgamate structure.

to some living sclerospoenges and to have spicules, are widely accepted as sponges; but the stromatoporoids are considered by some paleontologists to be sponges and by others to be cnidarians. If they were sponges, each mass of hard tissue housed an individual; if they were cnidarians, each housed many polyps. Although it may be misleading the skeleton of the stromatoporoid is all that remains to bear evidence of its coloniality or individuality.

#### Corallites and Calices

In the Scleractinia and Rugosa the corallites may make up the whole of the hard tissue of the colony or soft tissue between the polyps may secrete cystose or tubular skeletal tissue called coenosteum. I use the term coenosteum in the sense of Hill (1956) and Wells (1956). Hill in her revision of 1981 uses the term coenenchyme for the intercorallite tissue in the tabulates. This intercorallite tissue is similar to the skeletons of stromatoporoids (Mori, 1982) and a spectrum exists of forms that lie between the stromatoporoids composed of cysts,

laminae, and pillars without trace of corallite tubes and the corals composed solely of adjacent corallites (Fig. 2).

The extinct heliolitids have structures similar to those of the scleractinians, that is, corallites separated by coenosteum. However, septa are absent or poorly developed in the corallites unlike those of the scleractinians. The coenosteum of the heliolitids may be tubular or cystose and in the latter state is so similar to the hard tissue of labechiid stromatoporoids that the similarity has been used by Nestor (1981) in arguing that the stromatoporoids are cnidarians.

The hydrozoan *Millepora* can also be placed in this spectrum of forms. Between the tabulated tubes that house the zooids is coenosteal hard tissue composed of irregular strands of carbonate that forms a "spongy" irregular structure (Fig. 3). The strands are formed of both spherulitic and lamellar calcite (Fenninger and Flajs, 1974) and the skeletal surface shows the spherules in the process of secretion. The similarity of the milleporid coenosteum to the macrostructures of the amalgamate stromatoporoids was a factor in convincing Nicholson (1886) that the stromatoporoids were hydrozoans and he used the name Milleporoidea to describe the amalgamate subdivision of the stromatoporoids. He also referred to the vertical openings crossed by dissepiments that are found in the order Stromatoporida (as the Milleporoidea are now known) as zooidal tubes because he thought they were analogous to the tabulated tubes that house the polyps of *Millepora*. These openings are now generally referred to as "pseudozooidal tubes."

The fossil *Milleporidium* can also be assigned a position on this spectrum of hard tissue forms between skeletons composed solely of corallites and those composed solely of coenosteum (Fig. 2). This Mesozoic form has what appear to be zooidal tubes much like those of *Millepora* separated by a finely tabulate coenosteum. Both smaller and larger tubes are crossed by tabulae. *Milleporidium* is commonly regarded as a

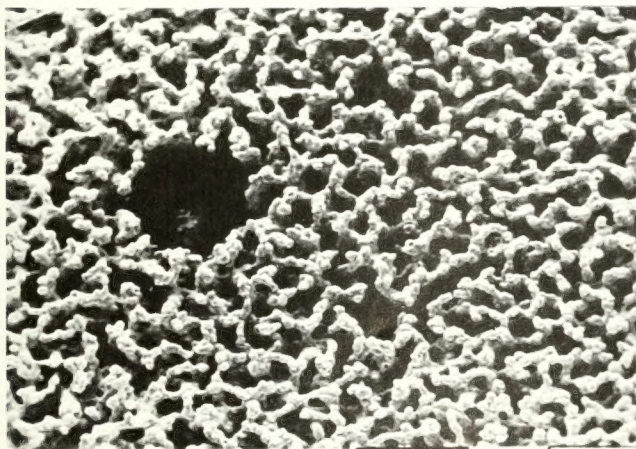


Figure 3.—Scanning electron micrograph of growth surface of *Millepora* sp., Recent, Barbados. The scale bar is 200 micrometers. Redpath Museum, McGill University, No. 14.776.

stromatoporoid because it appears to represent the end product of trends toward the increasingly tubular nature of the skeleton, the dimorphism of the tubes, and the suppression of the astrorhizae that are followed through several genera of Mesozoic stromatoporoids. If these morphologic transitions are ignored, *Milleporidium* would be placed in the hydrozoans. It occupies a step along the "ladder" from scleractinian septate corallites without coenosteum, corallites with coenosteum, aseptate tubes within cystose or tubular coenosteum, tubes within an amalgamate coenosteum, and the stromatoporoid hard tissue consisting solely of amalgamate "coenosteum." This gradient has led many paleontologists to regard the stromatoporoids as cnidarians that have lost skeletal traces of their corallites.

The hard tissue of some of the sclerosponges appears to be composed of individual units; that of others, does not. Genera such as *Ceratoporella*, *Tabulispongia*, and *Merlia* have regularly arranged cavities called calicules in their growing surface that resemble corallites but are a fraction of corallite-size. In some sclerosponges one or two incurrent canals or ostia open into each calicule, in others there is no obvious relationship between the ostia and the underlying calicule (Hartman and Goreau, 1975). In *Merlia* the bases of the calicules are partitioned off and contain what Kirkpatrick (1911)

referred to as "crypt cells." The similarity in form of the tubes in chaetetids to the corallites of corals persuaded most paleontologists before 1970 that they were cnidarians with small polyps; but the similarity of these tubes to calicules in both form and size (and the discovery of chaetetid spicules) has now convinced many that the chaetetids are sponges.

A second type of "individual" structure in the sclerosponges is associated with the excurrent canal systems or oscula. Sinuous radial canals just beneath the surface gather water from the choanocyte chambers and bring it to an excurrent pore on the surface. In some genera such as *Astrosclera* and *Calcifibrospongia* the traces of the canal system penetrate the hard tissue, in others they are lightly impressed on the surface of the hard tissue (*Ceratoporella*, *Tabulispongia*) and in still others (*Merlia*) they are confined to the soft tissue and make no impression on the hard tissue. These canals have been homologized with similar structures in the hard tissue of stromatoporoids by Hartman and Goreau (1970) and the name astrorhizae has been used for each (Fig. 4). Some paleontologists (for instance, Tripp, 1929; Mori, 1982) have suggested that the astrorhizae were the sites of modified polyps of a cnidarian and Tripp, following Carter (1877), compared them in detail with the hydrorhizal system that connects and transfers nutrients between the zooids of the common Atlantic

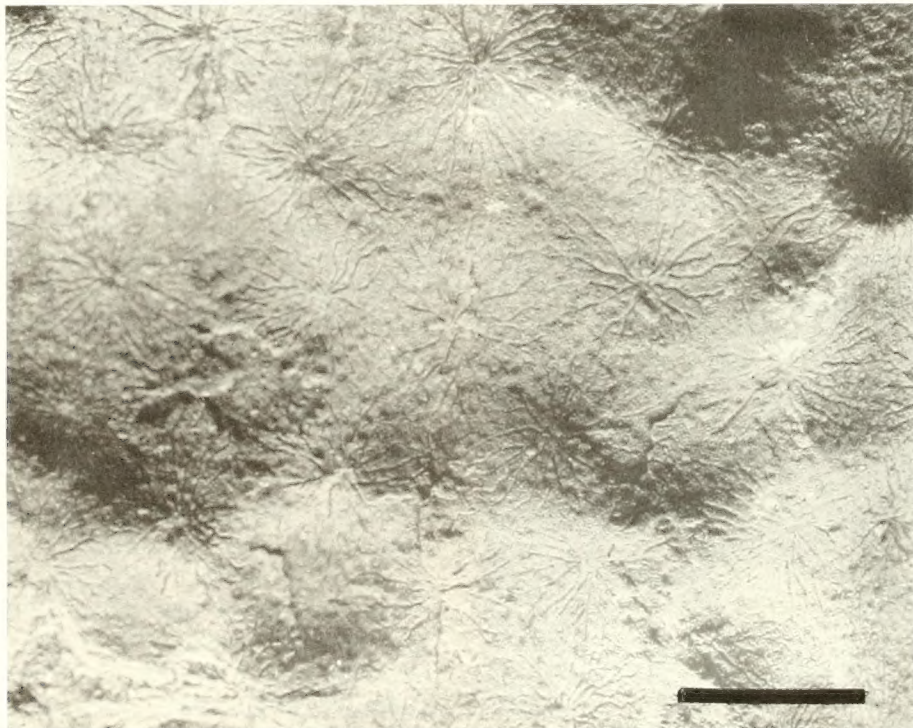


Figure 4.—Surface of a stromatoporoid showing astrorhizal grooves. Devonian, Michigan. Scale bar is 1 cm. Redpath Museum, McGill University, No. 14.777.

hydrozoan *Hydractinia*. The main evidence for rejecting this hypothesis is the river-and-tributary form of the astrorhizal canal system which is unlike the network of constant diameter tubes connecting polyps in hydrozoans yet is remarkably like the excurrent canal systems not only of sclerosponges but also of encrusting demosponges.

Just as the calicules of the sclerosponge can be homologized with the tubes of the chaetetids to show that the latter are non-colonial poriferans; in the same way, the excurrent canal systems of the sclerosponges can be homologized with the astrorhizae of the stromatoporoids to show that the latter are also non-colonial and of poriferan affinity.

#### Tabulates, Chaetetids and Stromatoporoids

A morphologic gradient exists between the favositids that have corallite-sized tubes with septa (or pseudo-septa) and the stromatoporoids without tubes of any sort (Fig. 5). The favositids have been compared with the sclerosponges (Hartman and Goreau, 1975; Flügel, 1976) but differ in the presence of septa (generally spiny but lamellar in some), the possession of mural pores, the larger size of the individual tubes, and their morphological affinity with other tabulates (for example, the halysitids) that are difficult to interpret as sponges. However, the morphological step to the chaetetids from the favositids is a small one and many specimens with "corallites" about 1 mm in diameter (for example many alveolitids) may be difficult to classify as one or the other. The chaetetids form a bridge to the sclerosponges for, despite having tabulated tubes and spine "septa" (*Acanthochaetetes*), they also have spicules and astrorhizal systems. The sclerosponge closest to the chaetetids is *Tabulispongia* (referred to as *Acanthochaetetes* by Hartman, 1983). It has polygonal tabulated calicules of about the same size as those of the chaetetids. *Merlia* also has tabulated polygonal calicules but its spicules are dissociated from the aspicular

skeleton as they apparently were in most, but not all, chaetetids. In *Ceratoporella*, the next step in the morphological gradient, the tubular nature of the hard tissue is evident only near the surface and in the lower part of the skeleton the calicules are filled with fibrous aragonite. Still the basic honey-comb packing of polygonal units is evident at the hard tissue surface. In the next step to *Astrosclera* this tubular nature is entirely lost and the hard tissue has become an irregular network of interlocking fibers of aragonite that would, in the stromatoporoids, be called an amalgamate structure. The astrorhizae that in the chaetetids and *Ceratoporella* are rarely seen or superficially impressed on the hard tissue, are prominent and penetrate the skeleton in *Astrosclera*. The step to the stromatoporoids with amalgamate structure, such as *Stromatopora*, is such a short one that *Astrosclera* has been called a living stromatoporoid (Hartman and Goreau, 1972). Dissepiments dividing the space between the skeletal fibers must be added and laminate skeletal elements parallel to the growth surface but little else to bridge this morphologic gap. A final step in this gradient is that from amalgamate stromatoporoids characterized by an irregular mass of labyrinthine fibers to those whose hard tissue is composed of distinct laminae and pillars. Although they are placed arbitrarily here on the extreme end of the gradient, these laminate stromatoporoids have many features in common with sclerosponges such as *Tabulispongia* and *Merlia*.

#### Spicular to Aspicular Hard Tissue

The spicules that are present in the sponges that secrete a calcareous skeleton may be calcareous and isolated in the soft tissue, or joined by aspicular skeleton to produce a rigid framework (Pharetronida); or they may be siliceous and confined to the soft tissue or incorporated in an aspicular skeleton as it grows. The calcareous sponges can be arranged in a morpho-

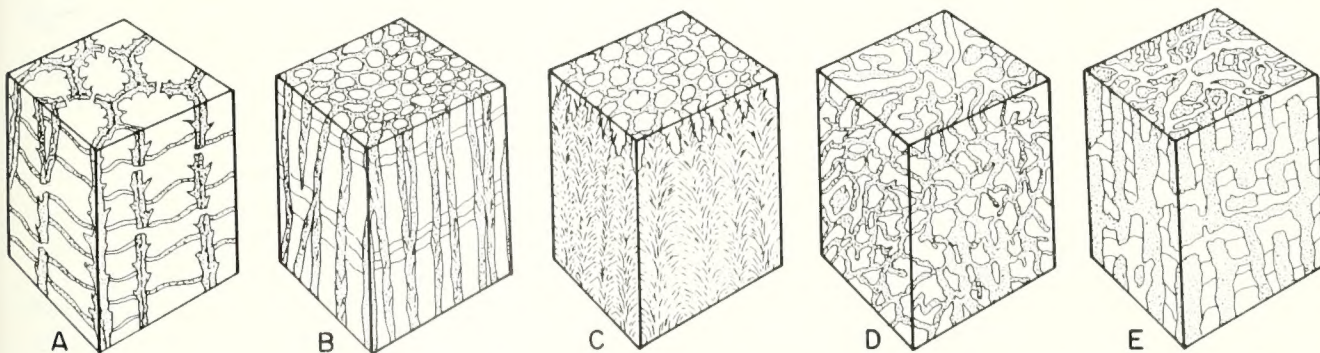


Figure 5.—Block diagrams,  $\times 7.5$ . A. favositid, B. chaetid (*Chaetetopsis*), C. the sclerosponge *Ceratoporella*, D. the sclerosponge *Astrosclera*, E. a stromatoporoid of amalgamate structure.

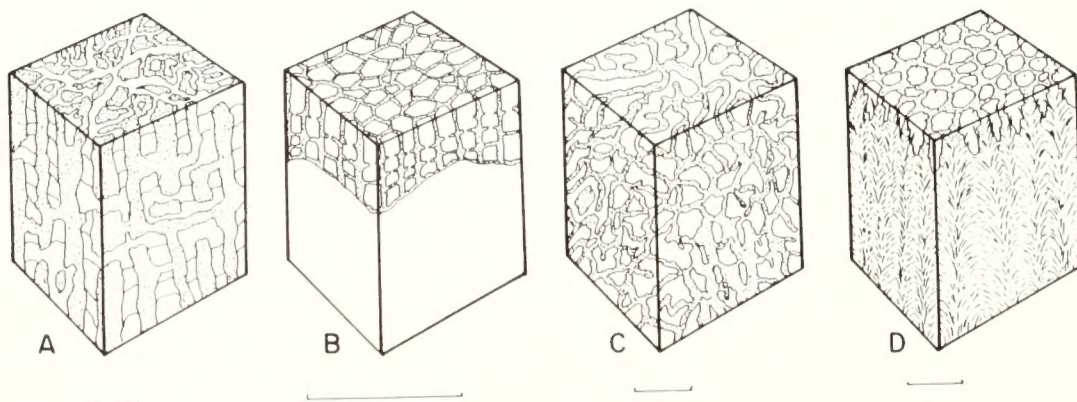


Figure 6.—Block diagrams. Scale bars represent 1 mm. A, a stromatoporoid of amalgamate structure, B, the sclerosponge *Merlia*, C, the sclerosponge *Astrosclera*, D, the sclerosponge *Ceratoporella*.

logic gradient with respect to the relationship of the spicular and aspicular skeleton (Fig. 6).

At one end of the gradient are the stromatoporoids which have a completely aspicular skeleton in which no spicules have been confirmed although several writers have suggested they may be present (Kirkpatrick, 1912; Hartman and Goreau, 1970). In the sclerosponge *Merlia* the aspicular hard tissue does not incorporate spicules but siliceous spicules are contained in the soft tissue. Presumably *Merlia* would leave behind a fossil not unlike a stromatoporoid. A similar condition is found in some populations of *Astrosclera* which do not contain spicules in the hard tissue (Stearn, 1972) but other populations do incorporate siliceous spicules in the hard tissue. Siliceous spicules in aspicular hard tissue are the normal pattern in most other sclerosponges and are identified in some specimens of chaetetics. The recognition in the fossil record of siliceous spicules in aspicular hard tissue is made difficult by the tendency of opaline silica to dissolve completely in a carbonate environment or to be replaced by calcite, pyrite, or other materials. Thus the absence of spicules in the hard tissue of fossil calcareous sponges may be owing to their complete absence in the organism during life, their presence during life only in the soft tissue, or their dissolution or replacement by minerals indistinguishable from the aspicular skeleton during preservation of the rest of the hard tissue. Their absence from stromatoporoids is not detrimental to the hypothesis of the sponge affinity of this group but their discovery in a stromatoporoid would be convincing corroboration of the hypothesis first put forward by Rosen (1867) nearly 120 years ago.

#### Tabulae, Dissepiments and Laminae

As a cnidarian polyp grows forward in its corallite it lifts itself and secretes a central basal plate (tabula) or a series of peripheral curved plates (dissepiments).

These plates serve to support the growing surface of the colony and its individual members and also to seal the living tissue from the abandoned older parts of the colony. In most non-encrusting sponges the soft tissue with its water circulating systems permeates the whole organism and partitions which isolate the surface layers are not needed. However, tabula-like partitions that isolate part of the sponge skeleton are found in some sphinctozoans and rarely in some pharetonids (Ziegler and Rietschel, 1970). In the coralline sponges that live only on the surface of the hard tissue, structural elements which serve the same purpose as tabulae and dissepiments are secreted. In *Merlia* structures much like tabulae progressively seal off the dying crypt cells as the organism grows higher. In *Tabulispongia* the plates secreted by the basal parts of the sponge are essentially identical to the tabulae of corals and the dissepiments of the stromatoporoid stromatoporoids. The stromatoporoids went a step further and secreted more-or-less continuous structures parallel to the growth surface called laminae. These sheet-like structures evolved from the union of tiers of cysts in Ordovician time. In the Clathrodictyida and the Stromatoporellida, they became the dominant structures. With respect to these transverse structures no significant morphologic discontinuities can be drawn between the cnidarians, the sclerosponges, the favositids, the chaetetics and the stromatoporoids.

#### CONCLUSIONS

The morphologic gradients described in this paper are not presented to show phylogenetic relationships. In them living and extinct, recent and ancient organisms are arranged without regard to their stratigraphic positions. The gradients are presented to illustrate the difficulty of defining these groups of lower invertebrates on the basis of morphologic criteria.



Taxa of all ranks can be thought of as solids defined by variates which express morphologic features enclosing sets of lower taxa in multidimensional space. As multidimensional space is impossible to illustrate in a single plane (this sheet of paper) the relationships between the taxa discussed above as steps in morphological gradients or spectra are illustrated in only three dimensions in Figures 7, 8 and 9. On the three axes of the solid are plotted: 1. the relationship of the spicular skeleton to the aspicular (vertical axis), 2. the gradient from radially septate corallites of the scleractinians to the laminate structures of the hard tissue of stromatoporoids (one horizontal axis), and 3. the gradient from (corallite) tubes only, through tubes in coenosteum, to coenosteum-like structures without tubes. The shapes of the solids depend on the arbitrary divisions of the gradients. Four of the groups have hard tissue that is exclusively aspicular (Fig. 7). The scleractinians, favositids, and heliolitids plot in the lower left corner, with the heliolitids on the side toward the stromatoporoids in the lower right corner. The similarity of the stromatoporoids and the pharetronids is shown by the position of the former immediately above the latter; their separation is an expression of the spicular nature of one and the entirely aspicular nature of the other. Figure 8 shows that the chaetetids occupy a large volume which overlaps the volume of the favositids but extends upward into spicular space. The sclerosponges however occupy the largest volume, an expression of their wide morphologic range overlapping all the other fields except that of the scleractinians and pharetronids (Fig. 9). The representation of the sclerosponge morphology as two separate volumes is caused by the choice of divisions of the right horizontal axis and reflects the fact that some of the sclerosponges have tubes, some amalgamate hard tissue but none combine tubes with coenosteal tissue. The sclerosponges are seen to span the morphologic fields between the Cnidaria and the Porifera, a fact that was early recognized when Hartman and Goreau (1970) called them the coralline sponges.

These figures summarize the morphologic gradients considered in this paper and illustrate the position of the stromatoporoids in morphometric space far on the sponge side of cnidarian-poriferan morphologic gradient.

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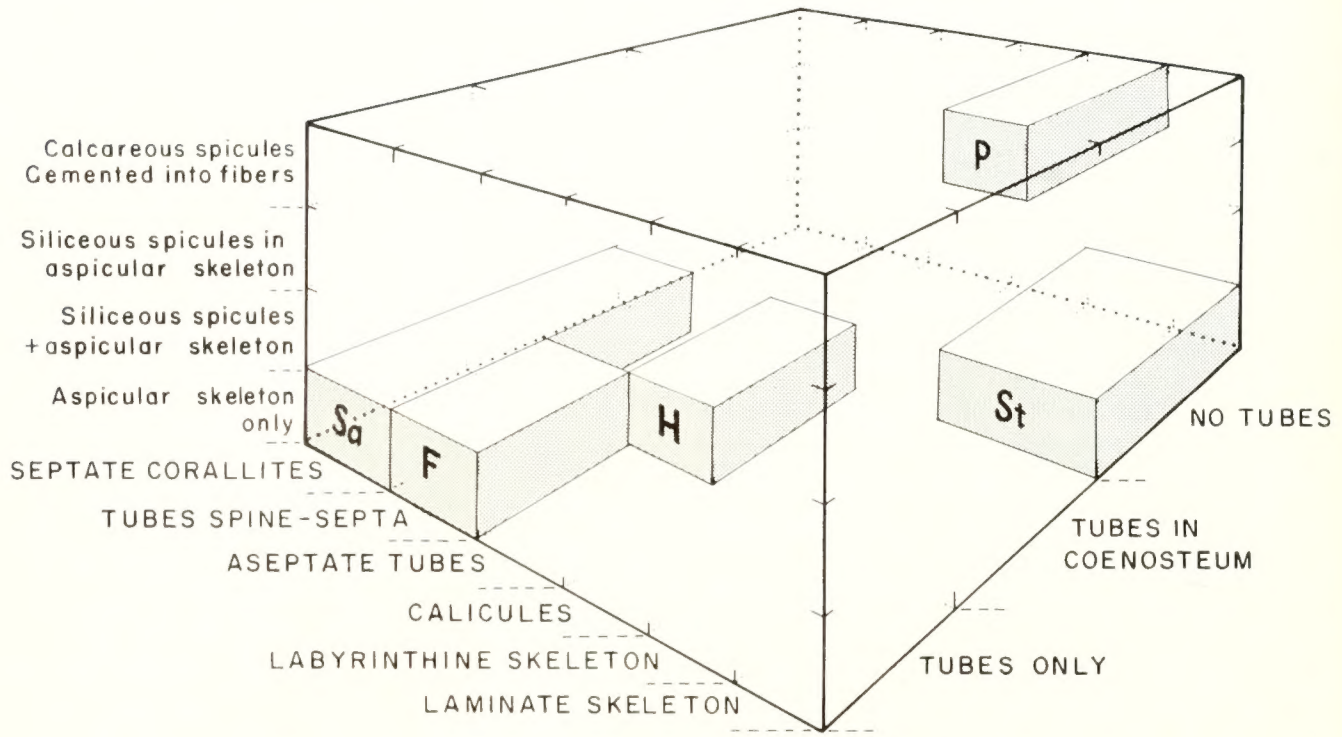


Figure 7.—Solids representing the range of morphologies occupied by corals and calcareous sponges in space defined by three morphologic gradients. Sa—scleractinians, F—favositids, H—heliolitids, St—stromatoporoids, P—pharetronids.

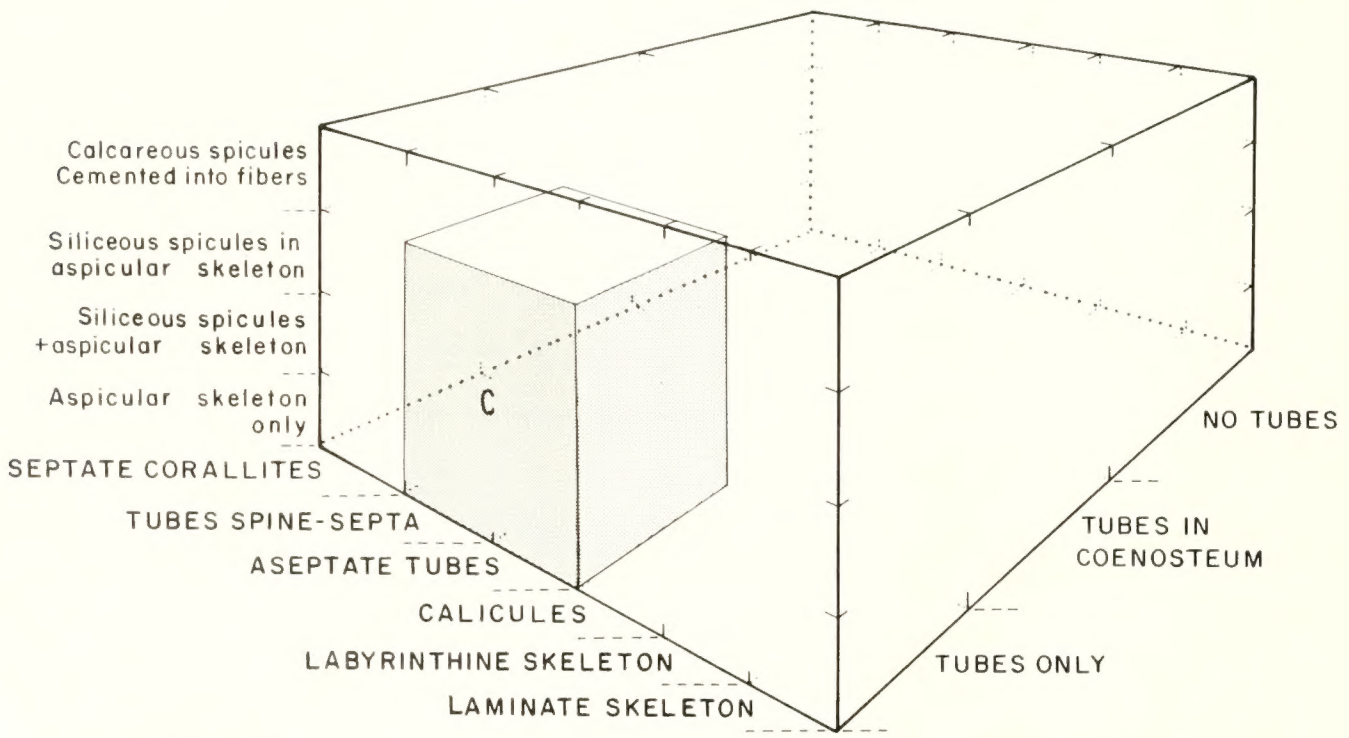


Figure 8.—Solid representing the range of morphologies in chaetetids in space defined by three morphologic gradients.

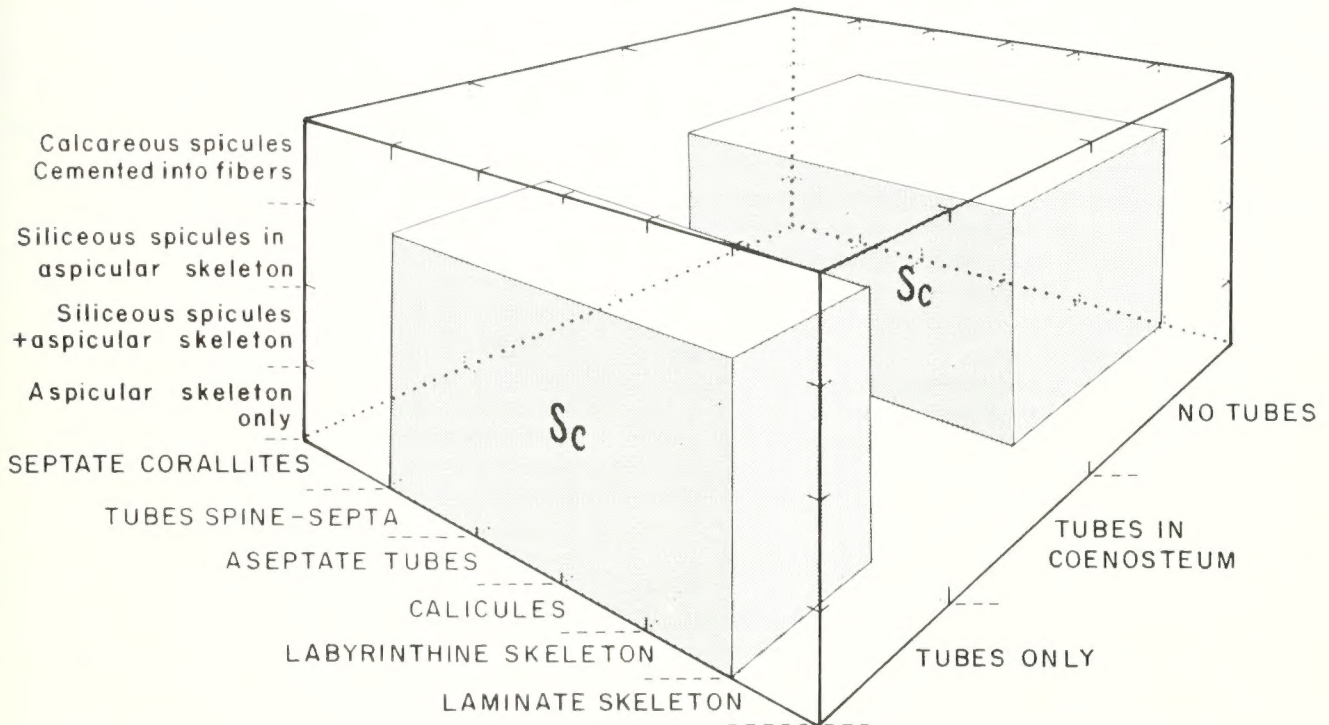


Figure 9.—Solids representing the range of morphologies in sclerosponges in space defined by three morphologic gradients.

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SKELETAL AND SPICULAR MINERALOGY, MICROSTRUCTURE AND  
DIAGENESIS OF CORALLINE CALCAREOUS SPONGES

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## ABSTRACT

Devonian to Recent non-spicular calcareous sponges (Pharetronida, Stromatoporoidea, Sclerospongiae, Heteractinida) construct a massive aragonitic or Mg-calcitic skeleton. Spicules, calcitic in Heteractinida and Pharetronida and siliceous in Sclerospongiae, are generally rare, randomly oriented and may be completely lacking in the non-spicular skeleton. This skeleton is constructed of acicular crystals, 0.1–1.4  $\mu\text{m}$  in width and 15–60  $\mu\text{m}$  in length, which are arranged in four well-defined microstructures: irregular, spherulitic, clinogonal and orthogonal. Diagenetic alterations of the massive skeleton include incipient to complete micritization and recrystallization, and cementation of intercrystalline voids. These processes lead to the formation of diagenetic pseudostructures and to a total obliteration of primary microstructure and mineralogy.

## INTRODUCTION

During the last fifteen years the scientific interest in fossil and living calcareous sponges has increased considerably. Spectacular discoveries of living representatives of different groups which were believed to have become extinct during the late Cretaceous or the early Tertiary have enlarged and modified our views on the once rather homogeneous Class Calcarea. Archaeocyathids, stromatoporoids and chaetetids are now more or less unanimously regarded as calcareous sponges, but the systematic relationship among them and their position within the classification of modern sponges are still controversial. A satisfactory answer to these problems can only be expected from an examination and comparison of histological and cytological features of living calcareous sponges. In addition, a sound knowledge of the microstructure and mineralogic composition of calcareous sponges is necessary in order to classify extinct groups and to compare them to living counterparts. Diagenetic alterations must be recognized and correctly interpreted in order to avoid creation of new taxa based on pretended original microstructures. Diagenetic factors have often been neglected in the past, especially in stromatoporoids. It is the aim of the present paper to summarize our knowledge on microstructure and mineralogy in Late Paleozoic to Recent calcareous sponges as two important diagnostic characters in this heterogeneous and polyphyletic group.

## MATERIAL AND METHODS

The present paper is based on the examination of 205 species of calcareous sponges (86 Inozoa, 32 Sphinctozoa, 42 Sclerospongiae, 41 Stromatoporoidea, 4 Heteractinida). Data on skeletal microstructure and its diagenetic alteration were obtained from thin sec-

tions and SEM observation. SEM photographs were all made from broken, unetched surfaces. Qualitative distribution of aragonite and calcite in massive skeletons is most easily revealed by staining thin sections with Feigl-solution which is capable of indicating the presence of aragonite as low as 1%. Percentages of aragonite were calculated from X-ray diffraction (diffractometer) and those of  $\text{Mg}^{++}$  by atomic absorption. If possible, modern material was examined, both in a dried state (to avoid dispersal of spicules not embedded in the skeleton) and after leaching of the tissue with  $\text{NaOCl}$ .

## ACKNOWLEDGMENTS

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## CLASSIFICATION

In this paper, the term "coralline calcareous sponges" is given preference to "non-spicular calcareous sponges" because many living and fossil genera included in this group actually possess spicules. Spicules are generally so small and scattered, however, that strengthening is only achieved by the rigid massive calcareous skeleton.

The discovery of a living sphinctozoan sponge without spicules and its histological and cytological examination (Vacelet, 1979) has shed new light on the systematic position of the Sclerospongiae (Hartman and Goreau, 1970) and some Sphinctozoa which might partly be attributed to the Class Demospongiae. Until such an attribution is supported by further evidence, the present author prefers a classification which is comprised of the following groups:

Class Sclerospongiae

Order Stromatoporoidea (Ordovician–Eocene, Recent?)

Order Chaetetida (Ordovician–Eocene)

Order Ceratoporellida (Upper Triassic, Recent)

Order Tabulospongida (Upper Jurassic–Recent)

Order Merliida (Recent)

Class Calcarea

Subclass Calcinea (Recent)

Subclass Calcaronea (Lower Carboniferous? Jurassic–Recent)

Subclass Heteractinida (Cambrian–Lower Permian)

Subclass Pharetronida

Order Inozoa (Carboniferous–Recent)

Order Sphinctozoa (Middle Cambrian–Recent)

Class Archaeocyatha (Lower–Middle Cambrian)

Non-spicular calcareous sponges comprise the Class Sclerospongiae, the Subclasses Heteractinida and Pharetronida and the Class Archaeocyatha. Representatives of all groups, except Archaeocyatha, are examined in this paper.

## MINERALOGY

### Non-Spicular Skeleton

The massive skeleton of recent sclerosponges and pharetronids consists of aragonite or Mg-calcite (Mg-contents range from 14 to 20 mol % of  $MgCO_3$ , see Wendt, 1979). It seems that different species within the same genus have all the same mineralogical composition, but more information on this subject is wanted. According to Vacelet (1979) only *Merlia* (which may even lack a non-spicular skeleton) has a facultative aragonitic or calcitic composition. Primary aragonitic mineralogy has been documented in many Upper Triassic Sphinctozoa (Cuif, 1973), Inozoa (Wendt, 1974; Dieci *et al.*, 1975), Sclerospongiae (Cuif, 1974; Wendt, 1974; Dieci *et al.*, 1975) and Stromatoporoidea (Wendt, 1975) from the Alps, Hungary and Turkey. Only a few genera of Sphinctozoa within the same well-preserved faunas are originally calcitic. High proportions of aragonite have been documented in the same groups from Upper Permian reefs of southern Tunisia

(Wendt, 1977). Carboniferous Heteractinida and Pharetronida are always recrystallized, but occasionally still reveal traces of a spherulitic microstructure suggesting a primary aragonitic mineralogy. According to Stearn (1972), Paleozoic stromatoporoids, generally strongly recrystallized and with only minor traces of primary microstructure, were probably all aragonitic.

In contrast to the rather uniform aragonitic mineralogy of coralline calcareous sponges during the Paleozoic and early Mesozoic, a predominance of calcitic mineralogies is obvious since the Upper Jurassic (Text-fig. 1). This is demonstrated by the presence of pharetronids, sclerosponges and stromatoporoids that suffered little diagenetic alteration in Upper Jurassic and Cretaceous sediments, while in the same rocks other organic remains of undoubted aragonitic composition (gastropods, ammonoids etc.) are preserved either as moulds or with strongly recrystallized shells. The most striking examples of this mineralogical change are found among the chaetetids; the Triassic representatives are aragonitic, and those from the Cretaceous are calcitic. Apart from modern species, aragonite has not been found in post-Triassic calcareous sponges; however, neomorphic calcite, most probably derived from primary aragonite, is present in some Jurassic and Cretaceous Pharetronida and Stromatoporoidea indicating that the change from an aragonitic to calcitic mineralogy was neither total nor simultaneous. More well-preserved material is necessary to fill the gaps in the structural and mineralogical evolution of calcareous sponges sketched in Text-figure 1. The most obvious gap in this scheme in the Tertiary, however, has a phylogenetic reason: apart from a few survivors in the Lower Tertiary, the bulk of coralline calcareous sponges became extinct by the end of the Cretaceous. Tertiary and Pleistocene ancestors of Recent sclerosponges remain to be discovered.

### Spicules

In Recent sclerosponges, spicules consist of hydrated amorphous silica (Hartman and Goreau, 1970; Jones, 1979). Recent pharetronids have Mg-calcitic spicules (single crystals). Apart from  $CaCO_3$  and  $MgCO_3$ , minor amounts of  $SO_4^{--}$ ,  $Sr^{++}$  and  $Na^+$  have been found in calcitic spicules (Jones, 1979). The original mineralogy of fossil sclerosponge spicules was probably similar to that of their living descendants, but early diagenetic processes have always replaced amorphous silica by a secondary, polycrystalline mosaic of  $CaCO_3$ ,  $SiO_2$  or  $FeS_2$ . Calcitic spicules have lost their  $Mg^{++}$  but generally remain preserved as single crystals. In stromatoporoids, most sphinctozoans and many inozoans, spicules are totally absent. This may be attributed to

the fact that they were restricted to the soft tissue (as in the modern *Acanthochaetetes wellsi* and *Merlia normani*) and were scattered after its decay, or even totally missing (as in *Vaceletia crypta*).

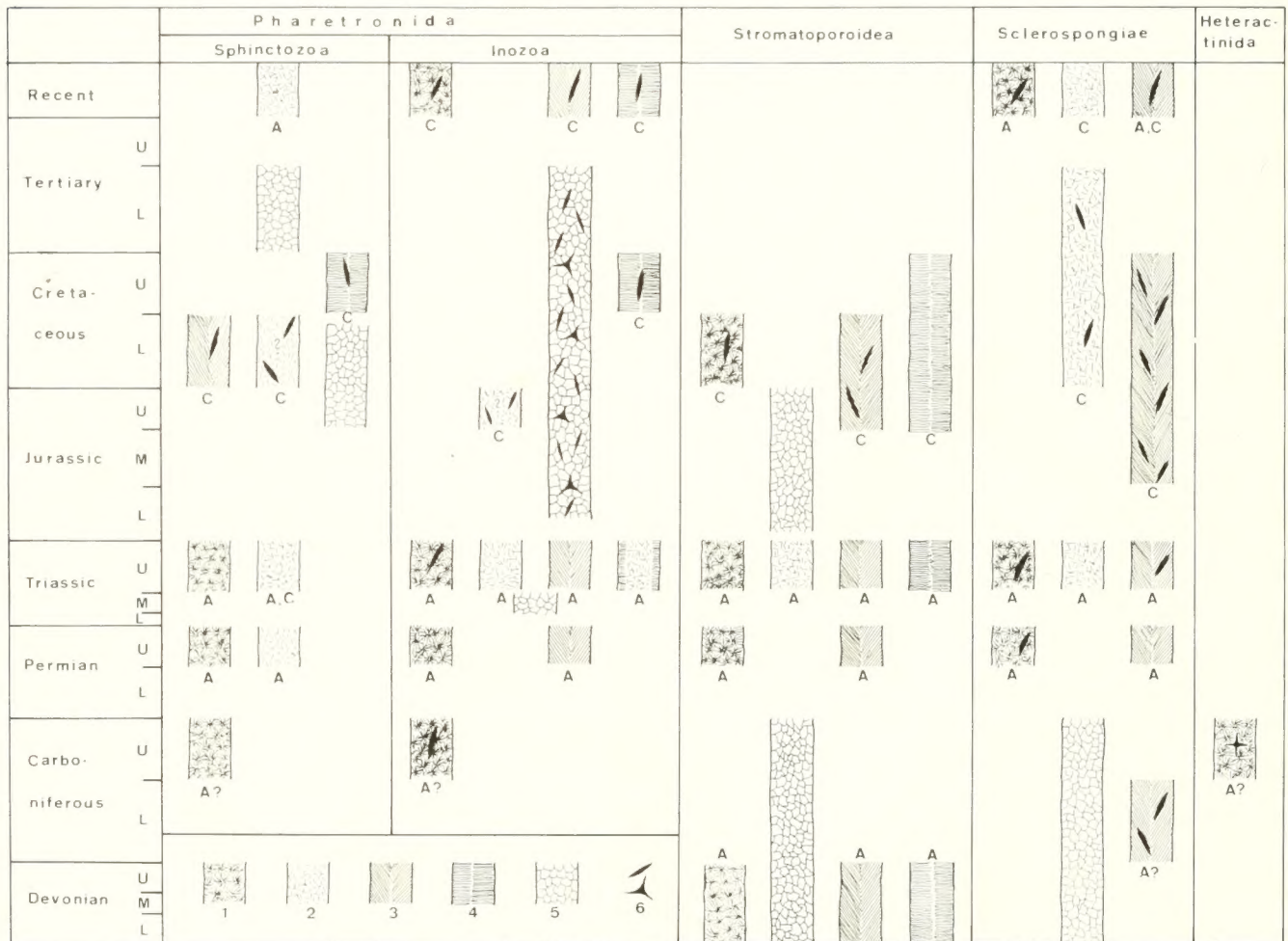
MICROSTRUCTURE OF THE NON-SPICULAR SKELETON

Microstructure should be defined as the three-dimensional arrangement of the smallest crystalline units visible at SEM magnifications of several hundred to more than a thousand times. Light-optical examination of thin sections under crossed nicols at lower magnifications may reveal original microstructure as well, but generally does not allow one to recognize incipient diagenetic alteration which may be confused with primary microstructure (e.g., the lamellar structure). The massive non-spicular skeleton of calcareous sponges is

constructed of acicular crystals of aragonite or Mg-calcite. Crystal dimensions vary between 0.1–1.4 μm in width and 15–60 μm in length. They are arranged in four different modes:

Irregular

Irregular microstructure (Plate 1, figs. 3, 4) is the arrangement of loosely packed crystals, 0.1–0.5 μm wide and 4–8 μm long, generally with random orientation. In some cases the crystals are parallel aligned simulating a lamellar structure in transmitted light (compare figures in Hartman and Goreau, 1975 and Mori, 1976). SEM magnifications reveal that these “lamellae” are not sheets but, in fact, closely-packed acicular crystals. In Cretaceous and recent *Acanthochaetetes* these pseudolamellae are distinctly arched (convex up) reflecting growth lines with the single crys-



Text-figure 1. — Distribution of microstructures and mineralogies in non-spicular calcareous sponges. Note shift in mineralogic composition from aragonite to calcite in the late Jurassic/early Cretaceous. 1 = spherulitic, 2 = irregular, 3 = clinogonal, 4 = orthogonal, 5 = recrystallized, 6 = spicules, A = aragonite, C = (Mg)calcite. Recrystallized (calcitic) structures (probably originally aragonitic) have been included only where better preserved material was not available. Gaps in the microstructural/mineralogical record are due to lack of material, gap in the Tertiary is due to extinction of most groups by the end of the Cretaceous.

tals oriented parallel to the inner surface of the pinacoderm. Typical examples of irregular microstructure are known from Triassic Sphinctozoa (aragonite or calcite), Inozoa (aragonite), Stromatoporoidea (aragonite), Cretaceous and Recent Sclerospongiae (Mg-calcite) and living *Vaceletia crypta* (aragonite). High magnifications of the last reveal that the acicular crystals have a polygonal cross section with concave facets and may therefore be composed of still smaller sub-crystals (Plate 1, fig. 3).

Spherulitic

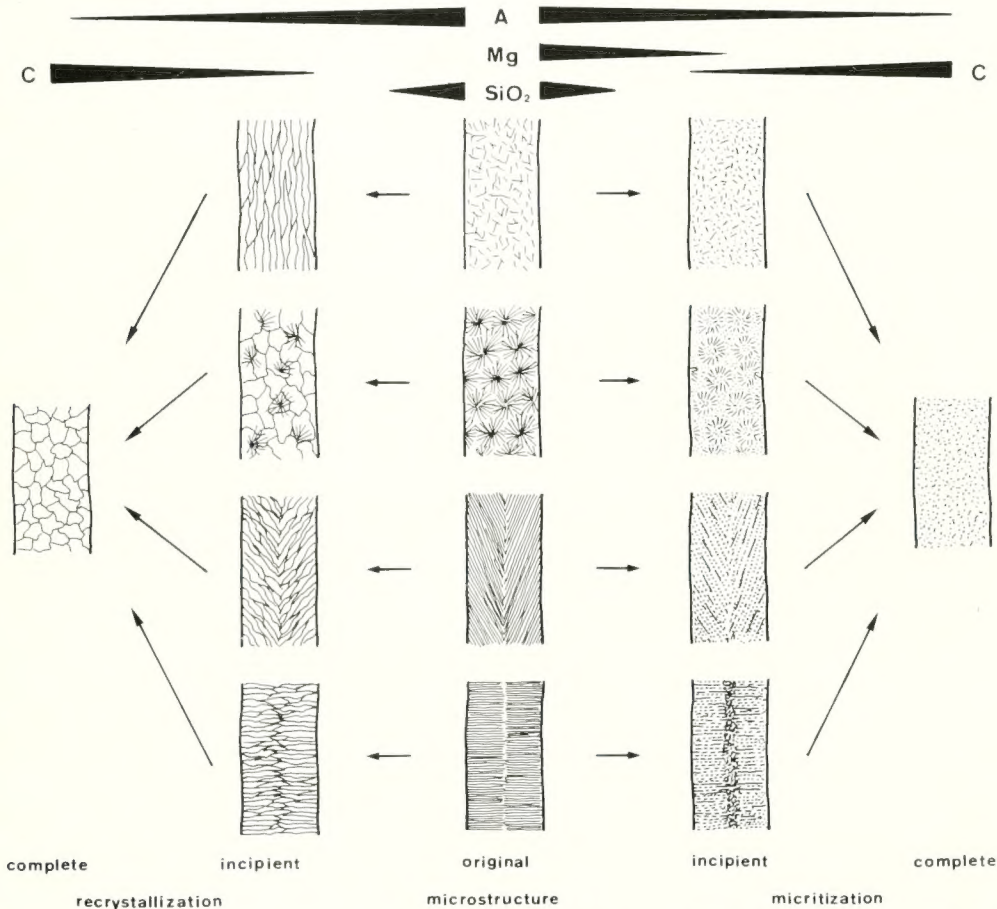
Spherulitic microstructure (Plate 1, figs. 1, 2) is the globular arrangement of crystals radiating from a common center to form regular or irregular (eccentric) spheres ranging in diameter from approximately 20 to 100  $\mu\text{m}$ . Eccentric spherulitic structure (partially spherulitic in Fenninger and Flajs, 1974) is common in peripheral parts of skeletal units which have been added to the primary skeleton at later growth stages (secondary skeleton, Wendt, 1979). Spherulitic micro-

structure is the most common type in Carboniferous and Permian Heteractinida, Pharetronida and Sclerospongiae which were probably all aragonitic. The best examples are known from aragonitic Upper Triassic Sphinctozoa (Cuif, 1973), Inozoa and Sclerospongiae (Wendt, 1974; Dieci *et al.*, 1975). In the Cretaceous, this microstructure is known only from one species of a stromatoporoid which was most probably calcitic (J. Reitner, Tübingen, pers. comm.). The modern *Petrobiona massiliana* has an ill-defined spherulitic structure composed of Mg-calcite crystals which seldom show a regular orientation. Typical spherulitic structure is also found in the modern aragonitic sclerosponge *Astrosclera*.

Clinogonal

(synonyms: water jet, trabecular, penicillate)

Clinogonal microstructure (Plate 1, figs. 5, 6) consists of long (up to 60  $\mu\text{m}$ ), closely-packed crystals which diverge at a very low angle. This microstructure is perfectly preserved in aragonitic Upper Triassic chaetetids



Text-figure 2.—Stages of diagenetic alteration in non-spicular calcareous sponges. Symbols as in Text-figure 1 (upper left is lamellar pseudo-structure). A = aragonite, C = low-Mg-calcite, Mg = Mg-calcite, SiO<sub>2</sub> = amorphous silica.

and stromatoporoids, and, less distinctly, in calcitic representatives of the same orders in the Jurassic and Cretaceous (Hudson, 1959). Clinogonal microstructure, strongly obscured by diagenesis and therefore probably of aragonitic origin, is also known from Paleozoic stromatoporoids. In contrast to Stearn (1966), the present author considers this structure as one of the four basic microstructure types present in Paleozoic stromatoporoids. Among living sclerosponges, *Merlia* shows a calcitic, *Ceratoporella* and *Hispidopetra* an aragonitic clinogonal microstructure. The only living pharetronid with calcitic clinogonal structure is *Murrayona phanolepis*.

#### Orthogonal (synonym: fibro-normal)

Orthogonal microstructure (Plate 1, figs. 7, 8) consists of relatively short (15–25  $\mu\text{m}$ ) closely-packed and parallel crystals which are arranged perpendicular to the surface of skeletal elements. This microstructure is rare in coralline calcareous sponges and seems to be limited to some Stromatoporoidea and to a few pharetronids (e.g., *Minchinella*). It is known from Paleozoic (Stearn, 1966), Jurassic (Hudson, 1959) and Cretaceous stromatoporoids (Turnšek and Masse, 1973). Its good preservation in Jurassic and Cretaceous species (with accompanying scleractinians that are heavily recrystallized) suggests a primary calcitic mineralogy. Aragonitic orthogonal microstructure was found in the Upper Triassic stromatoporoid *Cassianostroma kupperi* (Wendt, 1975).

Sponge skeletons may be constructed of only one type of microstructure. This is most common in the irregular microstructure which is the only one found in Cretaceous and Recent *Acanthochaetetes* and in some Triassic and Recent Sphinctozoa. In calcareous sponges with various growth stages (primary skeleton, second-

ary skeleton, filling tissue), different microstructures are commonly present. This is well exemplified by *Sestrostomella robusta* from the Upper Triassic in which the primary skeleton is irregular and spherulitic, the secondary skeleton eccentric spherulitic to clinogonal and the filling tissue (tabulae) spherulitic (Wendt, 1979).

On the other hand, different species of the same genus have been found to be constructed of different microstructures. This is the case in the inozoan *Stellispongia* whose Permian species are spherulitic while Upper Triassic species are irregular or clinogonal. In some well-preserved Triassic pharetronids it can be observed that one microstructure passes into another, thus emphasizing the "omnipotent" nature of the pinacoderm cells.

#### DIAGENESIS

The distinction of original microstructure from diagenetic pseudostructure (Text-fig. 2) and the determination of the primary mineralogy of sponge skeletons are necessary to avoid specific and generic misinterpretations. A great deal of the tremendous taxonomic splitting in Paleozoic Stromatoporoidea could have been avoided if the presumed great variety of original microstructures in this group (Stearn, 1966) had been recognized as diagenetic products (Stearn, 1972; Scherer and Wendt, 1977). Three interdependent processes of diagenetic alteration must be distinguished:

#### Alteration of Mineralogy

$\text{SiO}_2$ : Hartman and Goreau (1970) and Land (1976) have observed that siliceous spicules in living sclerosponges begin to dissolve when they are exposed to normal seawater. Corroded and partially dissolved spicules have been found in living *Ceratoporella* and *Goreauella* in the basal parts of the skeleton some cm below the surface covered with living tissue (Plate 2,

#### EXPLANATION OF PLATE 1

##### Original Microstructures (A = aragonite, C = calcite)

##### Figure

1. Spherulitic structure in *Astrosclera willeyana* Lister. Recent, Europa Island, Strait of Mozambique. Note eccentric spherulites almost closing residual void in massive skeleton,  $\times 530$
2. Spherulitic structure in *Sestrostomella robusta* Zittel, U. Triassic, Dolomites (Italy),  $\times 800$
3. Irregular structure in *Vaceletia crypta* (Vacelet). Recent, Great Barrier Reef. Note polygonal cross section of crystals with concave facets (twins?). Inner surface of pore on left margin,  $\times 8000$
4. Irregular structure in *Acanthochaetetes seunesi* Fischer. Albian, N-Spain. Note patchy parallel orientation of acicular crystals,  $\times 10,000$
5. Clinogonal structure in *Stromatospongia norae* Hartman. Recent, Jamaica,  $\times 180$
6. Clinogonal structure in *Atrochaetetes medius* Cuif and Fischer, U. Triassic, Dolomites (Italy),  $\times 500$
7. Orthogonal structure in *Murrayona phanolepis* Kirkpatrick. Recent, Christmas Island. Note broken spicule in the center of skeletal element,  $\times 900$
8. Orthogonal structure in *Cassianostroma kupperi* Flügel, U. Triassic, Dolomites (Italy),  $\times 1150$



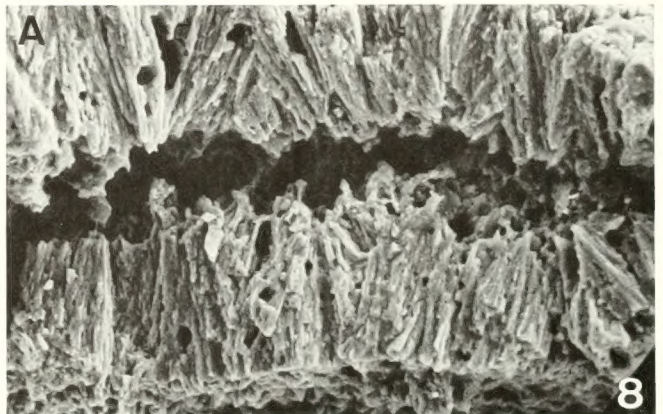
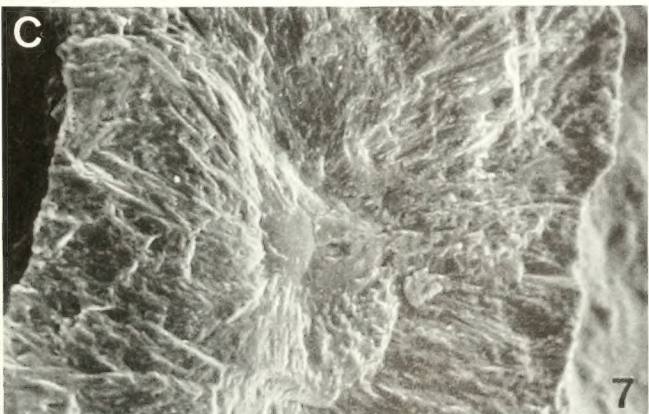
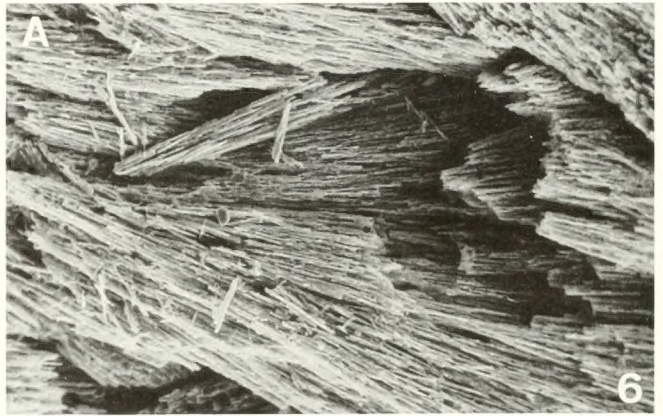
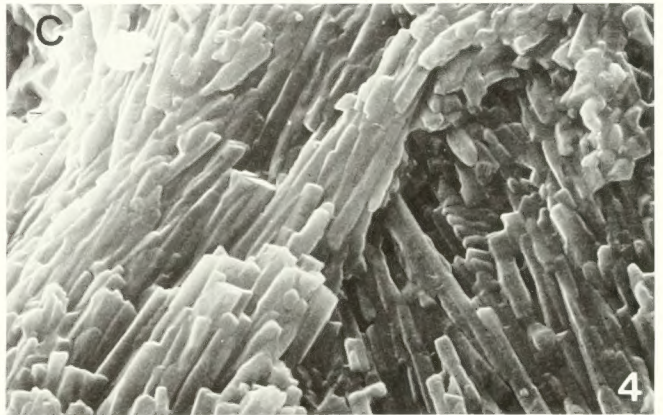
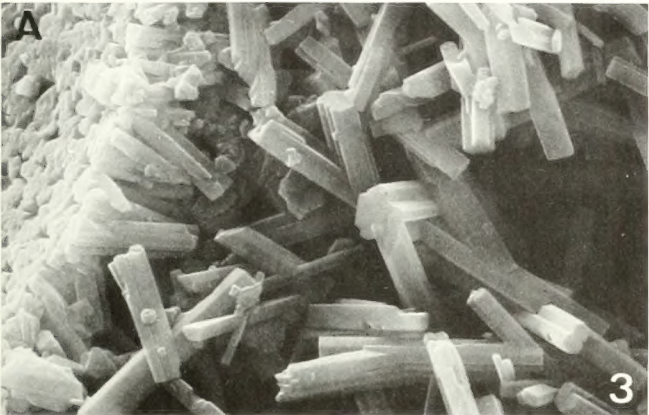


fig. 1). In fossil sclerosponges (e.g., chaetetids), spicules, if present, are always preserved as calcitic, siliceous or pyritic pseudomorphs (Gray, 1980; Reitner and Engeser, 1983) (Plate 2, fig. 2).

$Mg^{++}$ : High magnesian calcite is generally more easily transformed into calcite than is aragonite and is therefore not preserved as such in fossil organic remains. Primary Mg-calcitic mineralogy in fossil non-spicular skeletons can therefore only be inferred from comparison with modern analogues. During the process of recrystallization,  $Mg^{++}$  must have been lost at a very early stage of transformation. In the well-preserved sponge faunas from the Permian of Tunisia (Scherer and Wendt, 1977) and from the Upper Triassic of the Dolomites (Italy) where partial or total aragonitic preservation occurs, no trace of  $Mg^{++}$  was found in calcitic skeletons. Amounts of up to 13,500 ppm  $Mg^{++}$  reported by Veizer and Wendt (1976) must be attributed to the formation of secondary Mg-calcite cements (Scherer, 1976). Only in calcitic *Acanthochaetetes* from the Spanish Albian, have minor amounts of  $Mg^{++}$  been found (J. Reitner, Tübingen, pers. comm.).

Aragonite: Occasionally aragonite is preserved in early diagenetic stages. A few totally micritized and/or cemented calcareous sponges from the Alpine Upper Triassic have retained their original aragonitic mineralogy (Plate 2, fig. 6). Also partially dolomitized specimens from the Upper Permian of Tunisia have been found to contain up to 5% of aragonite in bulk samples (sponge skeleton + cement; Wendt, 1977). Even in totally recrystallized calcareous sponges from the Alpine and Hungarian Upper Triassic minor amounts of aragonite have been found. The fact that aragonite was never found in Jurassic and Cretaceous calcareous sponges supports the interpretation noted above of a general shift from an aragonitic to calcitic mineralogy in calcareous sponges during the Jurassic.

### Alteration of Microstructure

The following observations are based mainly on well-preserved, aragonitic specimens from the Permian of Tunisia and the southern Alpine Upper Triassic.

#### Micritization

This process, called intragranular cementation or cryptocrystallization by Milliman (1974), is very common in fossil calcareous sponges. It is attributed to carbonate precipitation inside individual grains or micro-environments. Its final result is a complete breakdown of the original crystal arrangement and the formation of granular crystals with sizes of 1–5  $\mu\text{m}$ , generally without any preferred orientation (granular pseudostructure, p. 334). Apparently the irregular microstructure is most susceptible to this diagenetic alteration. Aragonitic and presumed calcitic irregular microstructure often shows transitions from well-preserved crystal sizes and arrangements to micritized patches in the same specimen (Plate 2, figs. 3, 4). In the spherulitic microstructure, micritization starts in the center of the spherulites and in the inter-spherulitic areas, whereas in orthogonal structures it affects the central axis of the skeletal elements. The "dark line" which is often observed in stromatoporoids and chaetetids in transmitted light, is obviously a result of micritization in the center of the skeletal elements. Clinogonal microstructure seems to be least susceptible to micritization and is often preserved even in Lower Paleozoic stromatoporoids. It is assumed that completely micritized structures may be derived from any of the four original microstructures.

#### Cementation

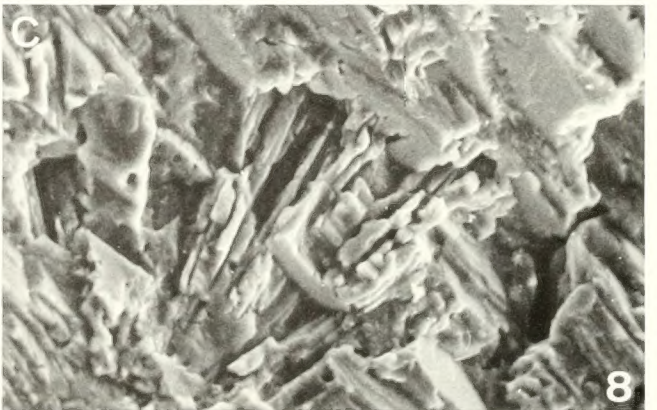
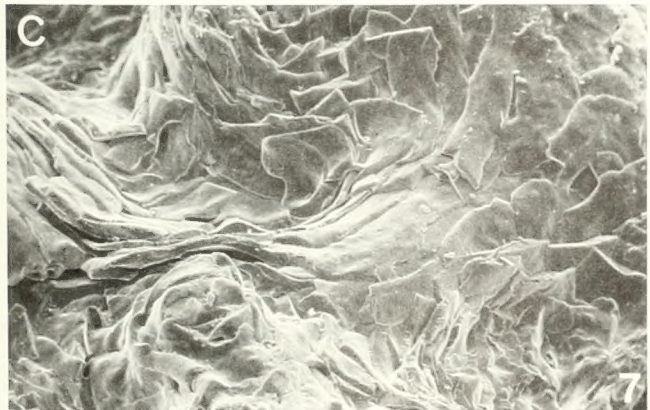
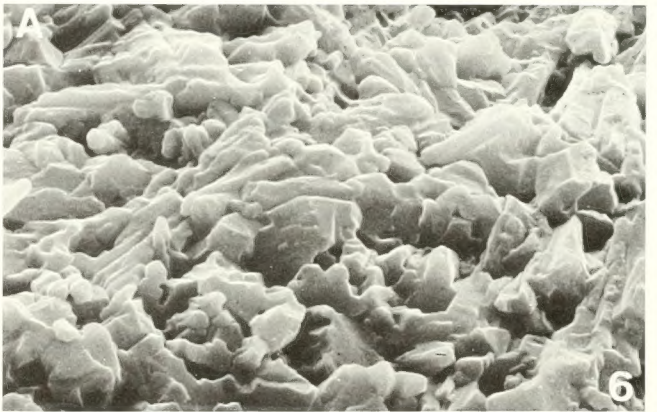
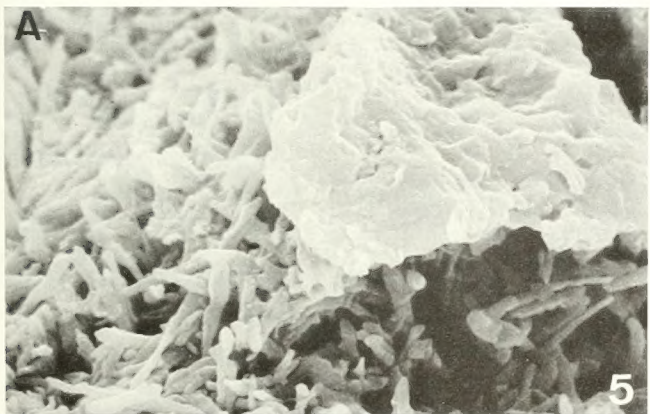
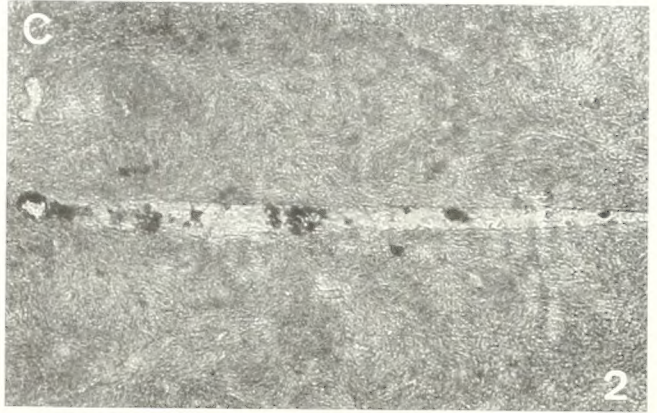
Cementation processes affect the intercrystalline spaces and the larger voids in the sponge skeleton after the retreat or decay of the living tissue. Irregular microstructure appears to be the most porous one, and therefore probably the first to be affected by early ce-

### EXPLANATION OF PLATE 2

#### Diagenetic Alterations (A = aragonite, C = calcite)

##### Figure

1. Corroded and partly dissolved siliceous spicule in *Ceratoporella nicholsoni* (Hickson), 2–3 cm below living tissue. Recent, Caribbean,  $\times 2300$
2. Tylostyle (calcitic pseudomorph) in *Acanthochaetetes ramulosus* (Michelin), Albian, N-Spain. Thin section,  $\times 270$
3. Nearly perfectly preserved irregular structure (slightly micritized) in *Actinofungia astroites* (Münster), U. Triassic, Dolomites (Italy),  $\times 2300$
4. Same specimen as Fig. 3 with incipient micritization (upper right) and ?syntaxial cementation (lower left),  $\times 8000$
5. Same specimen as Fig. 3. Growth of neomorphic crystals (upper right) in irregular microstructure,  $\times 8000$
6. Syntaxial grain growth in irregular structure of *Eudea polymorpha* (Klipstein). U. Triassic, Dolomites (Italy),  $\times 10,000$
7. Lamellar pseudostructure in *Enaulofungia cf. glomerata* (Quenstedt). U. Jurassic, Normandy,  $\times 190$
8. Incipient recrystallization with spherulitic relic structure in *Cystothalamia* sp., U. Permian, Tunisia,  $\times 1900$



mentation. The commonly observed larger crystals in fossil specimens compared to modern counterparts is probably the effect of syntaxial grain growth (Plate 1, fig. 4). Later, the spaces between the crystals become completely infilled by cement (Plate 2, fig. 6). It is difficult to document if this cement is also syntaxial because the resulting crystals do not show clear crystallographic orientations. The final stage is a homogeneous, granular mosaic of interlocked anhedral crystals. In the remaining, more compact microstructures, the effects of cementation are more difficult to interpret, but they probably play only a minor role. It cannot be decided if abnormally long, spherulitic or clinogonal crystals in the peripheral parts of skeletal elements represent a late growth stage before the final retreat of the living tissue from the skeleton, or if they are the result of early syntaxial cementation. Cementation of the skeletal pores and canals does not affect skeletal microstructure (apart from an obliteration of the outlines) and therefore can be ignored here.

#### *Recrystallization (Transformation)*

Aragonitic skeletons, when recrystallized, are generally completely transformed into a coarse calcitic mosaic without any traces of primary microstructure. Consequently, from such a mode of preservation a primary aragonitic mineralogy can be inferred. This conclusion is supported by the presence of unaltered calcitic fossils in the accompanying faunas (brachiopods, bryozoans, some groups of pelecypods etc.). Partial recrystallization may occur in both aragonitic and calcitic skeletons and may lead to an increase of the crystal size (Plate 2, fig. 5). The original microstructure is still visible at this stage and can generally be distinguished better under crossed nicols than with the SEM because the original orientation of the crystals has remained unchanged. This kind of incipient recrystallization corresponds more or less to Stearn's (1977) stage B. Even in a coarse mosaic of neomorphic spar, traces of spherulites may sometimes be observed in Carboniferous Heteractinida and Pharetronida and in Permian Sclerospongiae and Pharetronida (Plate 2, fig. 8).

#### Formation of Diagenetic Pseudostructures

Irregular, spherulitic, clinogonal and orthogonal microstructures have been found in many well-preserved (mostly aragonitic) Permian, Triassic, Cretaceous and Recent species of coralline calcareous sponges. These four crystal arrangements are probably the only original microstructures which were developed by the Porifera (including Lower Paleozoic Stromatoporoidea). The present author considers all other structures as diagenetic pseudostructures.

#### *Lamellar Structure*

Lamellar structure (Plate 2, fig. 7) consists of more or less parallel, interlocked, curved calcitic blades with crystals 5–10  $\mu\text{m}$  thick and up to a few mm long, which are commonly found in seemingly well-preserved Jurassic and Cretaceous Inozoa and Sphinctozoa (Veizer and Wendt, 1976, fig. 2). However, the crystal size of the lamellae is about ten times larger than that of organically secreted crystals and therefore appears to be a result of diagenetic grain growth. Lamellar structure is probably derived from a calcitic irregular microstructure which often shows a parallel orientation of individual crystals (Plate 1, fig. 4). Such a crystal arrangement pretends a lamellar structure when examined with a light microscope at low magnifications (compare Cretaceous and Recent *Acanthochaetetes* in Hartman and Goreau, 1975, figs. 10, 12), but it is not a primary microstructure as proposed by Jones (1979). It might also be possible that the same diagenetic pseudostructure results from orthogonally arranged crystals affected by a migrating solution front parallel to the surface of the skeletal elements as suggested by Fenninger and Flajs (1974) for Mesozoic Hydrozoa and Stromatoporoidea.

#### *Granular Structure*

Light-optical examination of thin sections sometimes shows a completely homogeneous structure; SEM observation of the same specimens reveals a fine-grained aggregate of interlocked crystals 1–5  $\mu\text{m}$  in diameter without any preferred orientation. Such fine-grained mosaics are reminiscent of micritized structures, especially those derived from irregularly arranged primary crystals (p. 332). The present author considers granular structure as a result of a complete micritization of aragonitic or calcitic microstructures, syntaxial grain growth and cementation of the intercrystalline spaces.

#### *Diagenetic Pseudostructures in Paleozoic Stromatoporoidea*

Only a very limited number of Paleozoic stromatoporoidea has been examined so far by the present author. All specimens are heavily recrystallized, suggesting a primary aragonitic mineralogy, as proposed by Stearn (1972). Stearn's (1966, 1972, 1977) light optical and SEM examinations of well-preserved specimens show that original microstructures are often preserved as relics. The fourteen presumed types of microstructure in Paleozoic stromatoporoidea described by various authors can tentatively be referred to the above four original ones as follows (Scherer and Wendt, 1977):

1. Compact: derived from the irregular structure (micritized and/or cemented).

2. Cellular, microreticulate, melanospheric, vacuolate, ?flocculent, ?transversely porous, ?tubulate: derived from the spherulitic structure.

3. Water jet, ?striated: synonymous with or derived from the clinogonal structure.

4. transversely fibrous: synonymous with orthogonal structure.

Three other pseudostructures (peripherally vesicular, tripartite laminae, meshed fiber) cannot be referred to one of the above four original microstructures but are certainly of diagenetic origin. If only original microstructures are taken into account, a considerable simplification in the systematics of Paleozoic Stromatoporoidea should be achieved.

### CONCLUSIONS

1. Coralline calcareous sponges are a heterogeneous and polyphyletic group comprising Pharetronida, Stromatoporoidea, Sclerospongiae (including the Chaetetida), Heteractinida and Archaeocyatha (the last not examined in this paper).

2. These organisms secreted a massive skeleton originally constructed of acicular crystals which are organized into four microstructures: irregular, spherulitic, clinogonal, orthogonal.

3. Paleozoic and Triassic non-spicular calcareous sponges were almost exclusively aragonitic; since the Upper Jurassic/Lower Cretaceous calcitic (probably Mg-) mineralogies prevail.

4. Spicules, unknown from Stromatoporoidea, are siliceous in Sclerospongiae and Mg-calcitic in the Pharetronida, and play only a subordinate role for the strengthening of the skeleton.

5. Diagenetic alterations include early loss of amorphous silica, subsequent loss of Mg<sup>++</sup> (but preservation of monocystal structure of spicules), transformation of aragonite to calcite and various interacting stages of micritization, neomorphism and cementation of the non-spicular skeleton.

6. Diagenetic alterations may preserve traces of original microstructures and mineralogies, but may also result in the formation of pseudostructures (lamellar, granular).

7. Recognition of original microstructure and their diagenetic histories are important clues for the classification of coralline calcareous sponges. This principle should especially be applied to Paleozoic Stromatoporoidea whose presumed fourteen original microstructures are here interpreted as diagenetic variations of the four types listed in 2 above.

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PALAEOBIOLOGY AND BIOLOGICAL AFFINITIES  
OF PALAEOZOIC CHAETETIDS

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ABSTRACT

In parts of the Upper Palaeozoic, chaetetids are a conspicuous component of the fossil benthos. Three dominant growth forms are recognized: laminar; ragged, low domical; and domical (columnar). These are frequently *in situ* or overturned in the immediate vicinity of growth. All require a stable, firm substrate for initial attachment. Smaller colonies occur in abundance in mudstones while some of the columnar forms merge to form conspicuous reefs in the carbonate beds. In all cases, chaetetids appear to have lived within the photic zone, and in many cases exhibit evidence of wave action. Phylloid algae, rugose corals, echinoids, articulate brachiopods, bivalves, and *Aulopora* are associated with these reefs. At some localities the chaetetid colony surfaces are bored (*Trypanites*) and encrusted (bryozoans).

Middle Pennsylvanian chaetetids were examined and compared with published data on other Palaeozoic and post-Palaeozoic chaetetids, stromatoporoids, tabulate corals, bryozoans, and extant sclerosponges. While diagenesis often obscures the microstructure, there is evidence (Lustig, 1971; Mathewson, 1977) that Palaeozoic chaetetids had a trabecular wall structure, as do some sclerosponges (Hartman and Goreau, 1972) and many stromatoporoids (Stearn, 1972). Post-Palaeozoic chaetetids had a wall composed of spherulites (Cuif, 1974) which also occur in some sclerosponges (Hartman, 1979). Spicules are present in living and fossil sclerosponges and in some chaetetids (Gray, 1980) but are lacking in the other groups (listed above). With documentation of astrorhizae in Middle Pennsylvanian chaetetids (Mathewson, 1977), astrorhizae occur in all groups except the Tabulata. We consider Palaeozoic chaetetids to be sclerosponges.

INTRODUCTION

Chaetetids, like other Problematica, have been considered members of a number of phyla, including sponges (Kirkpatrick, 1909, 1910, 1911, 1912; Hartman and Goreau, 1972); coelenterates (Milne-Edwards and Haime, 1850–1854); bryozoans (Lindstrom, 1873); and even algae (see Hill, 1981). They have, likewise, been included in a number of the major divisions of the Coelenterata: hydrozoans (Sokolov, 1939, 1955, 1962; Tesakov, 1960; Fischer, 1970); tabulates (Milne-Edwards and Haime, 1850–1854); tetracorals (Bassler, 1950); alcyonarians (Duncan, 1872); hexacorals (Neumyer, 1889; Struve, 1898); and several other categories no longer recognized (Schizocoralla and Chaetokorallen). Interestingly, Lecompte (1936, 1952) rejected Thallophyta, Bryozoa, and Coelenterata as appropriate phyla for chaetetids. According to the coelenterate supplement to the Treatise on Invertebrate Paleontology (Hill, 1981), Palaeozoic chaetetids are classified as tabulate corals, but it is suggested, indirectly, that post-Palaeozoic chaetetids might be sclerosponges and these taxa are not included in the stratigraphic distribution charts of the Tabulata.

Stratigraphically, chaetetids range from Ordovician to Miocene (Hill, 1981) but they are most conspicuous in rocks of Carboniferous and Permian age, especially the Lower and Middle Pennsylvanian (Upper Carboniferous). As seems to be the case with Mesozoic occurrences of chaetetids, these Carboniferous occurrences are associated with other framebuilding

organisms or are the dominant frame builder of small "buildups" (bioherms).

To our knowledge there has been no attempt to plot, on a world wide scale, the occurrence of chaetetid genera, Palaeozoic or post-Palaeozoic. Thus one is limited to the more inclusive papers on coelenterate biogeography such as Hill (1973) and the more current summary in Hill (1981). Relying on these two sources it appears that three palaeobiogeographic provinces are recognized for the Lower Carboniferous: North American, Eurasian, and Australian. These three apparently continue through the Upper Carboniferous and Permian. Each of these three are further subdivided into subprovinces, the number depending on whether one follows Hill (1973) or the Russian workers (see Hill, 1981). Lack of precise data prevents any meaningful comments on the distribution of chaetetids with respect to palaeolatitudinal positions. It would appear that localities where chaetetids are a conspicuous component of the fauna (Middle Carboniferous) were tropical to low temperate when these localities are plotted on Map 61 of Smith, Harley, and Briden (1981).

Chaetetids actually examined by us, in the field and laboratory (via thin section, polished surfaces, scanning electron microscopy and stereo light microscopy), were collected from the Upper Carboniferous (Morrowan, Atokan, and Desmoinesian Stages) rocks of Iowa, Missouri, Kansas, Oklahoma, Texas, and Nevada. The most concentrated study was done on specimens collected from two quarries in southeastern

Kansas (Text-fig. 1) which expose the Amoret Limestone Member (Text-fig. 2). These are two of the localities studied by Mathewson (1977). Currently we are studying in detail the ecology of chaetetid reefs exposed in quarries of Desmoinesian rocks of south-eastern Kansas.

GENERAL MORPHOLOGY AND ECOLOGY

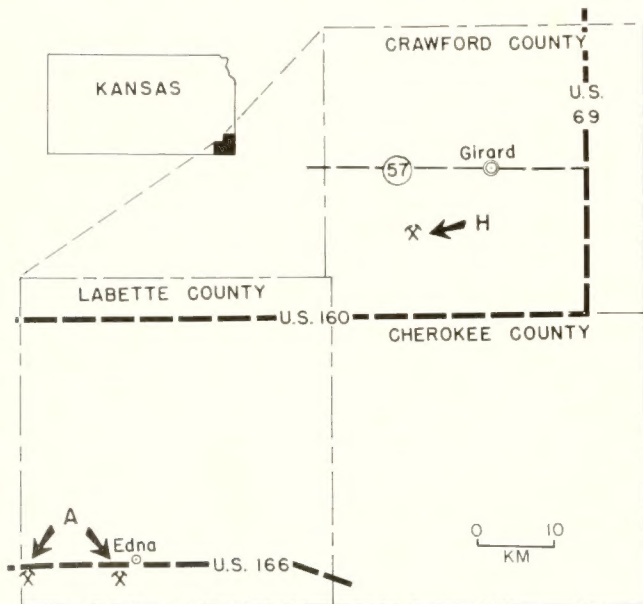
Introduction

Chaetetids are massive colonies composed of numerous polygonal (in cross section) cerioid to meandroid tubes (Pl. 1, fig. A). These individual tubes are horizontally partitioned by irregularly spaced tabulae (Pl. 1, fig. B). Structures termed pseudosepta (neophragms of Lustig, 1971) also project toward the center of the tubes. Our observations suggest that these structures have limited vertical extent and some (seen in transverse section) may be spines. These "spines" are not a conspicuous feature and if they are spines the chaetetids could be said to resemble *Acanthochaetetes wellsii* in this respect. Colony increase is by longitudinal fission (pseudosepta extending completely across a calicle to divide it into two), by peripheral expansion (new, full sized calicles initiated at basal margin), or by intercalicle budding (new calicles arising by separation of existing calicle walls). Colony surfaces (Pl. 1, figs. C, D, and E; Pl. 2, fig. A) presumed to be living surfaces, exhibit tubercles, mamelons (monticles), and

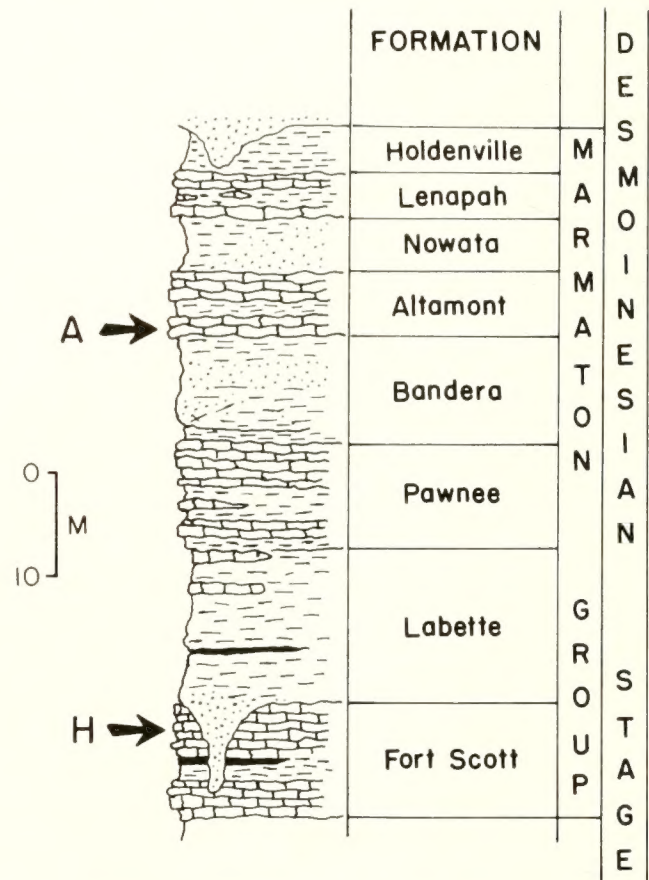
astrorrhizae. Tubercles are most often observed with the others being very rare features. Astrorrhizae are most often found on protected vertical surfaces while mamelons are so rare that it is impossible at this time to make any generalizations. There seems to be no relationship between mamelons and astrorrhizae as there is in some stromatoporoids, bryozoans, and sclerosponges. Spicules have not been recognized in our specimens but Gray (1980) has documented nicely spicule pseudomorphs in the Lower Carboniferous form *Chaetetes (Boswellia) mortoni*. Microstructure in the Palaeozoic forms we have studied is frequently obscured by diagenetic alteration. However, illustrations by others (Lustig, 1971 and Mathewson, 1977) and our observations support an interpretation of a fibroradial (trabecular) wall structure (Pl. 1, figs. A and B).

Growth Form, Substrate, and Habitat

The growth form of these colonial organisms can be characterized using a modified version of the param-



Text-figure 1.—Map of extreme southeastern Kansas showing the geographic localities of three quarries containing chaetetid-bearing limestones. The large A refers to the Amoret Limestone Member of the Altamont Formation and the large H refers to the Higginsville Limestone Member of the Fort Scott Formation.



Text-figure 2.—Stratigraphic section of the rocks of the Marmaton Group, Desmoinesian Stage, Middle Pennsylvanian Series of southeastern Kansas. The large A denotes the position of the Amoret Limestone Member and the large H denotes the position of the Higginsville Limestone Member (modified from Zeller, 1968).



eterization scheme proposed by Kershaw and Riding (1978) for stromatoporoids. Using this scheme three dominant growth forms are recognizable: 1) laminar; 2) ragged, low domical; and 3) columnar (Text-fig. 3). These correspond to what Mathewson (1977) called shingles, mounds, and columns. Spaw (1977) recognized two chaetetid growth forms in the Morrow-Atokan of Texas and New Mexico: 1) shingle forms and 2) club forms; this latter corresponds to the "bulbous" form of Kershaw and Riding (1978).

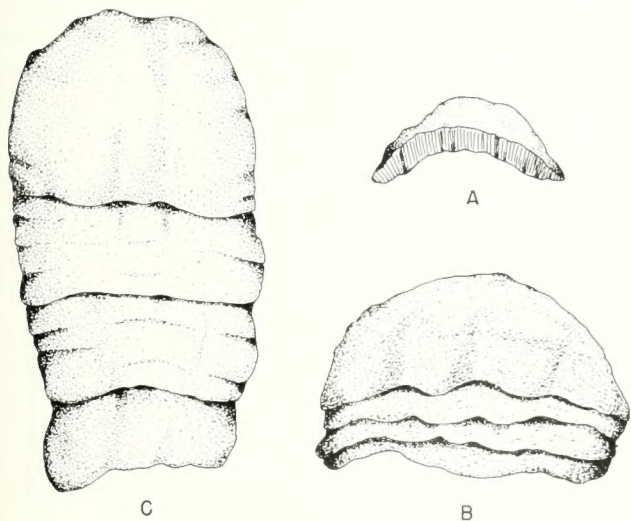
Different growth forms have been related to general environmental conditions by various authors. Spaw (1977) suggested that laminar forms were adapted to areas of frequent fluctuations of the physical and biological environment while club (bulbous) forms were adapted to stable, deep-water environments. Bottjer (1976) recognized four growth forms in the Devonian stromatoporoid *Syringostroma barretti*. Laminar and hemispherical (low domical) forms grew in areas where circulation was sufficient to provide adequate incur-rent-excurrent mixing with the former developing on a loose substrate and the latter on a firmer substrate. Mamelonated and digitate forms grew in areas of less circulation where greater surface area was beneficial and possessed laminar or hemispherical bases depending on the substrate characteristics. Our interpretation of the growth forms we observed are, in part, as suggested by Bottjer. Laminar and ragged to smooth low domical colonies occur in mudstones and could reflect the degree of substrate firmness and sedimentation rate. Domical to high domical (columnar) forms occur in "cleaner" carbonate units suggesting both a firmer substrate and less sedimentation. A firmer carbonate substrate is supported by the presence of phylloid algae

and *Osagia* in the carbonate immediately below the columnar chaetetid colonies (Mathewson, 1977). It is also possible, as suggested by Mathewson (1977), that crowding may have been important in controlling the growth form. Colonies would have less space for lateral growth in areas of high colony density and indeed domical forms are high (columnar) and dominant where colony density is high. Spaw (1977, pp. 44-45) suggested that competition with algae for space may have been important to chaetetid occurrence. Certainly a number of factors are important in understanding the significance of growth form and factors dominant in one situation may be subdominant or unimportant in another.

Studies of stromatoporoids (Kershaw, 1981) and stromatoporoids and scleractinian corals (Stearn, 1982) indicated that different species exhibit different growth forms in the same environment. Thus genetic, as well as environmental, factors are important in controlling growth form. Detailed studies of chaetetids are needed to determine which of these two, or other, factors may be the most important in shaping chaetetid colony growth.

While the general aspect of substrate firmness could have been variable it was essential that a firm surface be available for initial chaetetid colonization. In most cases, examined by us, a shell, shell fragment, or an algal encrusted grain (oncolite) served as the "nucleus" of the chaetetid colony. Often the shell or shell fragment had been algal encrusted before chaetetid attachment. While the majority of the chaetetids encrusted algal coated grains, this did not seem to be a necessary prerequisite because a few cases were noted in which chaetetids grew on lithic fragments. Such fragments of sediment had to have been at least partially lithified, so these occurrences do not invalidate the need for a stable, firm substrate. Shells and shell fragments consist of articulated valves of *Composita*, and hydrodynamically stable valves of linoproductids and neospiriferids.

Chaetetid-free oncolites, found in association with chaetetids, are 2 to 4 cm in minimum diameter. Small laminar chaetetid colonies 3 cm across and up to 1.5 to 2 cm in height are present. Thus, the oncolite-producing environment must have had sufficient energy to "roll around" objects up to 4 cm in size, and of the density of calcite/clay minerals. There are small chaetetid colonies which have been tumbled around with several directions of growth apparent because of overlap. Once a critical maximum size was reached there was little movement of the object and chaetetid colonies grew up to heights of 1.5 m and diameters of 0.8 m (high domical, columnar forms). Laminar and low



Text-figure 3.—Three dominant growth forms of chaetetids; A = laminar; B = ragged, low domical; and C = columnar.

domical forms reached a diameter of 0.25 m and 0.5 m respectively. These do not represent maxima as Winston (1963) has illustrated colonies over 10 feet (3 m) tall in the Llano area of Texas. We have observed overturned colonies on which upward growth continued but these are interpreted as a result of higher than "normal" turbulence such as storms. Such turbulence is also supported by the presence of angular fragments of chaetetid colonies of different sizes incorporated into the intercolony lithologies. Some of these form "chaetetid breccias."

Both Lustig (1971) and Spaw (1977) noted that chaetetid colonies occurred on slight topographic highs of a hummocky sea floor. Commonly chaetetid colonies encrust a layer of sediment which overlies a *Multithecopora* colony (Lustig, 1971, p. 102). Lustig suggested that the sediment had been stabilized by a sediment-binding organism, possibly algal mats, while Spaw indicated that sub-mound areas were either a shell fragment (cephalopod shells or rugose corals) or outlined by encrusting foraminiferids. Spaw, more or less, rejected algal mats as a binding agent because (1977, p. 39) "... hardened algal mats are restricted to intertidal zones." However, Dravis (1983) has reported the occurrence of hardened subtidal stromatolites in the Bahamas. Additionally, Spaw notes the exclusion of chaetetids from grainstones because grainstones indicate a rather rapidly shifting sea floor. Again, such generalizations can be misleading because Connolly and Stanton (1983) record chaetetids colonizing non-mobile oolite bars between intervals of ooid formation in the Morrowan rock of the Hueco Mountains, Texas. Our observations that chaetetids colonized oncolites and shell fragments, etc., support the general observations of others that slight topographic highs were preferred and further illustrates that there are undoubtedly a number of physical, chemical, and biological mechanisms that can produce such areas.

The inference that chaetetids lived within the photic zone is based upon the presence of algae in the rocks below and between (intermound) the colonies. Winston (1963) and Mathewson (1977) reported chaetetids and algae in the same rock units. Lustig (1971) sug-

gested algal mats as binding agents in the chaetetid substrates (see above) and reported (p. 101) *Girvanella* type algae within chaetetid colonies. Ota (1968) illustrated (pl. 7, fig. 1) sheet-like chaetetid laminae closely associated with stromatolites in his "true reef facies." The occurrence of oncolites as colony nuclei also supports a photic zone environment and Spaw (1977) suggested, as mentioned above, that chaetetids competed with phylloid algae and *Cuneiphyucus* for space on the sea floor. Connolly and Stanton (1983) suggested very shallow water and Kotila (1973), as interpreted by Wray (1977), placed chaetetid occurrences in the Upper Carboniferous (Morrowan) of Arkansas and Oklahoma on the seaward side of algal banks with the surface of the algal banks exposed at low tide. Certainly the extent of the photic zone is dependent on turbidity of the water and there is evidence that there was some turbidity (clay fraction in carbonate rocks and chaetetid occurrence in mudstones) but such turbidity did not eliminate algal growth in these environments.

#### Associated Organisms

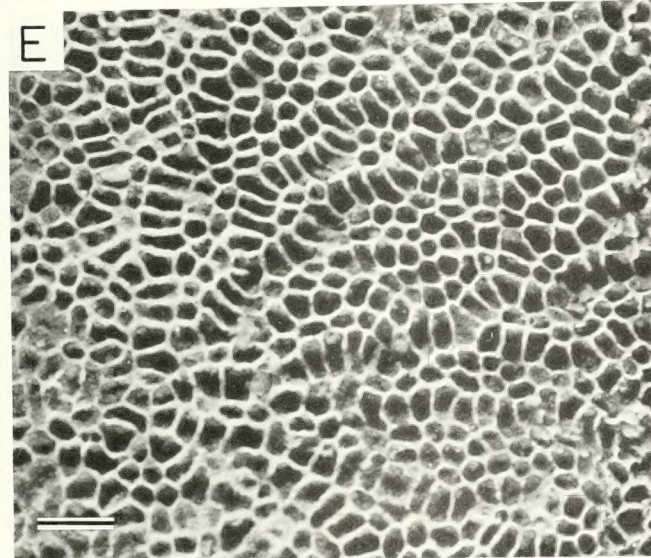
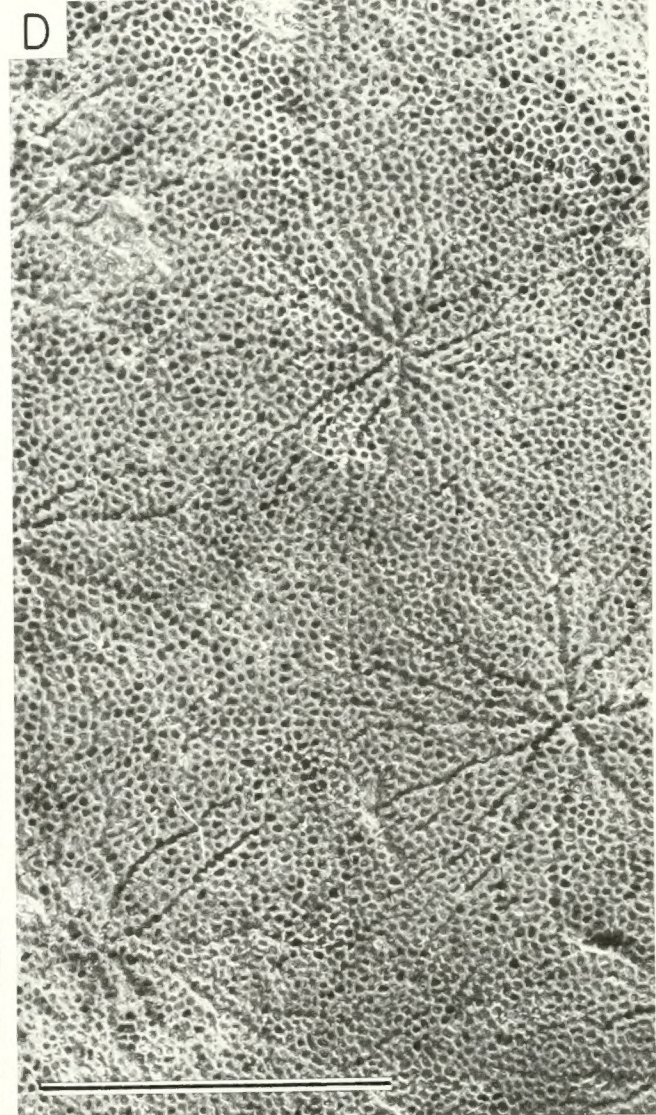
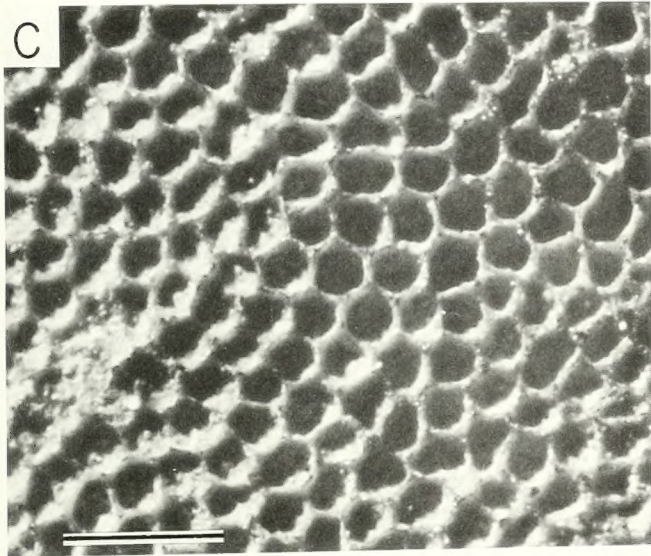
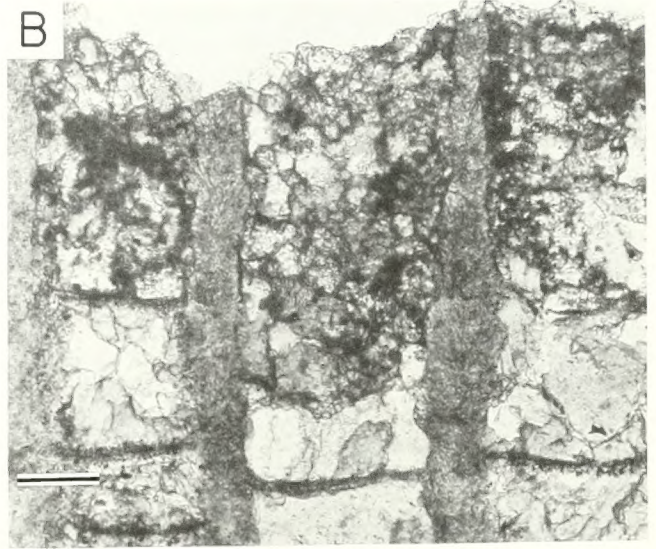
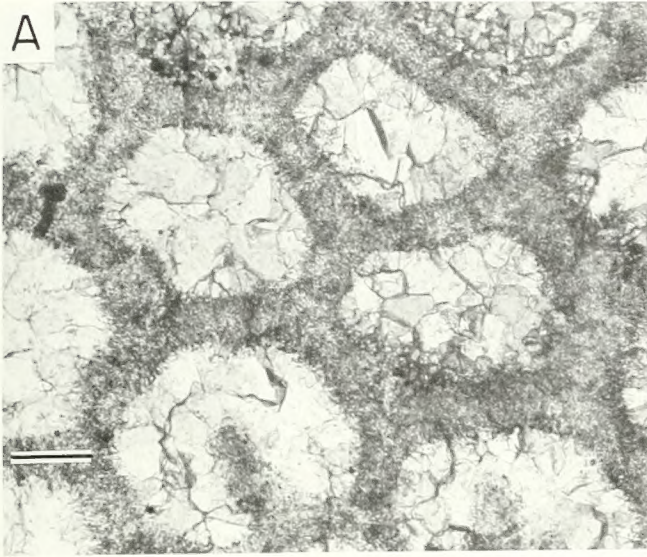
Numerous benthic marine invertebrates are found in the lithologies containing chaetetids and those underlying and overlying the chaetetid bearing beds. It is not our purpose to enumerate all of these invertebrates or their environmental-ecological significance. Rather, we will confine our remarks to those invertebrates which lived on or in the colonies or within cavities or overhangs created by the colonies. It has already been noted that shells and fragments of shells of marine invertebrates are important to the colonization of chaetetids, but these are cases of dead invertebrates; we will here further confine our remarks to those invertebrates which can be inferred to have 1) been alive at the same time as the chaetetids, though they may have caused the death of part of the colony at times; and 2) lived shortly after other causes resulted in death of part of the chaetetid colony.

The tabulate coral *Aulopora* encrusts parts of the chaetetid colonies (Pl. 2, fig. D). Lustig (1971) reported a similar situation in which *Multithecopora*, a tabulate coral, and *Caninostrotion*, a large phaceloid coral, grew

#### EXPLANATION OF PLATE I

##### Figure

- A. Transverse section of *Chaetetes* from the Amoret Limestone. Note fibroradial microstructure in calicle walls and pseudoseptum in calicle at bottom left. Scale bar is 0.1 mm
- B. Longitudinal section of *Chaetetes* from the Amoret Limestone. Surface of colony is at top. Note calicle walls, tabulae, and microstructure. Scale bar is 0.1 mm
- C. Surface of *Chaetetes* from the Amoret Limestone. Note numerous tubercles at junctions of calicle walls. Scale bar is 1.0 mm
- D. Surface of *Chaetetes* from the Amoret Limestone. Note numerous astrorhizae. Scale bar is 1.0 cm
- E. Surface of *Chaetetes* from the Amoret Limestone. Enlargement of part of Figure D. Note elongation, slight depression, and more orderly arrangement of calicles to form astrorhizae. Scale bar is 1.0 mm



over and were overgrown by *Chaetetes*. A similar relationship between just *Multithecopora* and *Chaetetes* was also reported by Wilson (1963). Spaw (1977) reported "large encrusting foraminiferids" encrusting chaetetids, but her illustration (text-fig. 14) looks more like a tabulate coral both in arrangement and size of "chambers" and wall thickness.

In the southeast Kansas localities we have found small caninid-like solitary rugose corals attached to chaetetid surfaces in the Higginsville Limestone (Upper Carboniferous). Jameson (1980) found solitary rugose corals attached to some chaetetid colonies in the Lower Carboniferous Petershill Formation of Scotland. We have found in chaetetid-bearing beds of the Marble Falls Limestone (Upper Carboniferous) in the Llano area of Texas specimens of a colonial rugose coral which Sutherland (pers. comm.) has identified as *Petalaxis*.

Ota (1968), in addition to documenting the close association of chaetetids and stromatolites in the "true reef facies" of the Akiyoshi Limestone Group (Lower Carboniferous to Upper Permian), also noted (figs. 12 and 13) the intimate association between chaetetids and cerioid corals, dendroid corals (*Lonsdaleoides*), bryozoans (*Fistulopora*, *Fenestella*, *Polypora*, and *Hexagonella*) and crinoids. Ota's illustrations indicate that these different taxa grew over and were overgrown by chaetetids.

Microcrinoid holdfasts and small colonies of fistuliporoid bryozoans have been noted attached to chaetetid colonies by Jameson (1980). On the undersides of some ragged, laminar colonies from the Pawnee Limestone of south central Iowa there are holdfasts of fenestellid type bryozoans as well as very small colonies of fistuliporoid type bryozoans. The upper surfaces of these colonies are bored by what appears to be *Trypanites*; this has also been noted by Mathewson (1977) in domical colonies from the Amoret Limestone of southeast Kansas. DeVries (1955) recognized borings

in chaetetid colonies from the Amoret Limestone of southern Iowa and from his illustrations some of these could be *Trypanites*, *Rogerella*, *Zapfella*, and/or *Caulostrepsis*. *Trypanites* is thought to be the result of boring by a polychaete and *Caulostrepsis*, formerly called *Polydorites* (Hantzschel, 1975), is probably the result of boring by a *Polydora*-type worm. Both *Rogerella* and *Zapfella* are interpreted as the borings of barnacles.

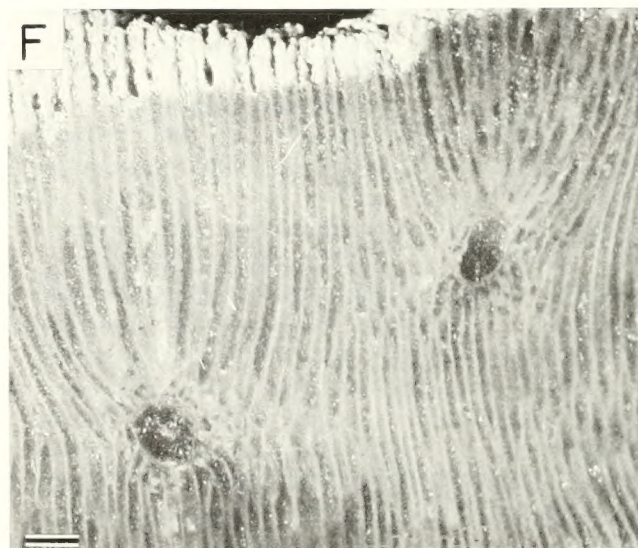
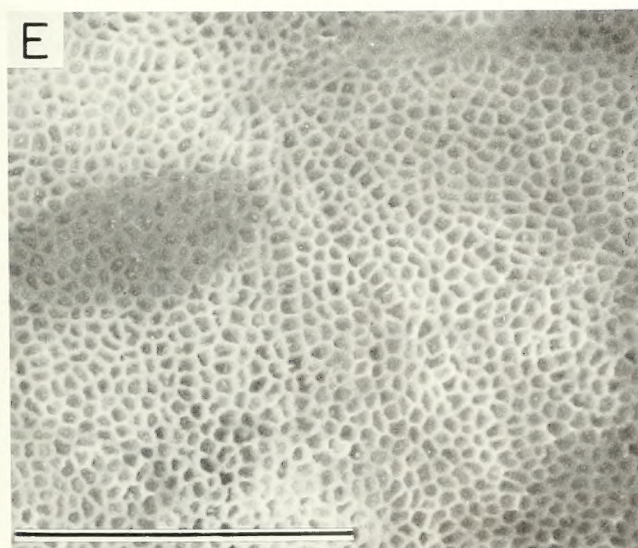
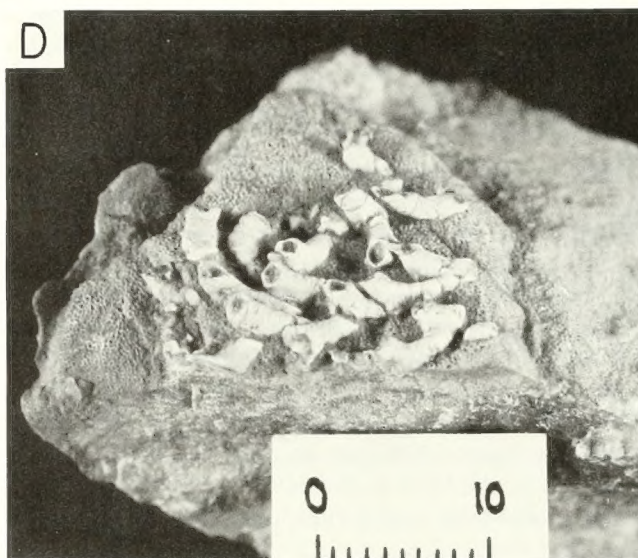
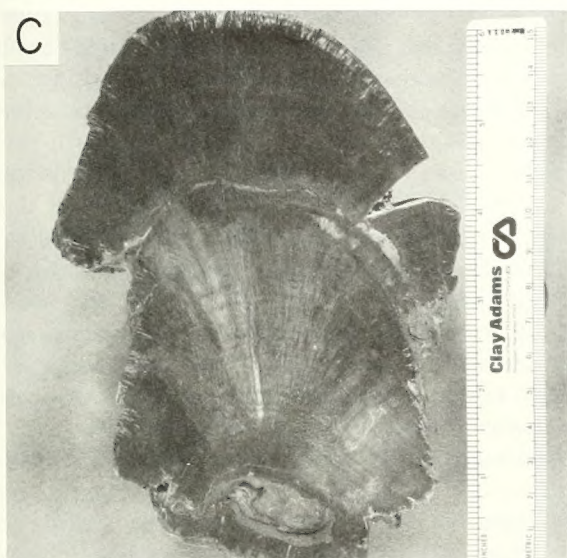
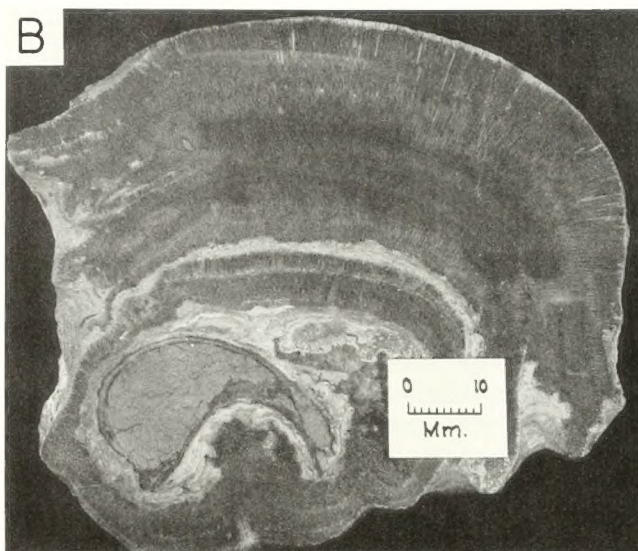
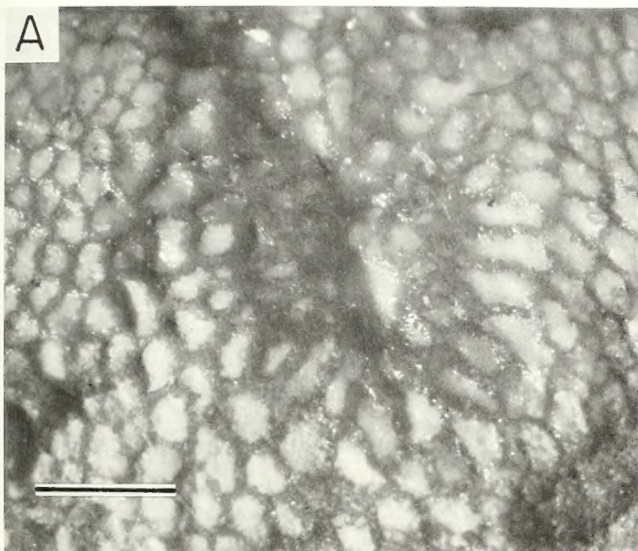
*Composita* and other spiriferid brachiopods are closely associated with chaetetid surfaces, suggesting that they may have attached to them. As yet we have found no evidence of brachiopod pedicle pits (Bromley and Surlyk, 1973) but these, if present, could be obscured by the irregular surface topography of the colonies. We have observed some articulated specimens of *Composita* (immature and adult) closely adpressed to the lateral surfaces of the colonies in the area of the pedicle opening. Jameson (1980) illustrated the underside of a chaetetid colony from the Petershill Formation (Lower Carboniferous) containing attached aulostegid productoids, spirorbid worms, and possibly a costate spiriferid brachiopod (fig. 14-3, p. 356). He also stated (p. 357) that *Composita* and *Dielasma* were attached to the undersides of some chaetetid colonies. None of the brachiopods observed by Jameson were found attached to the upper surfaces of chaetetid colonies, suggesting a possible relationship during life.

Jameson (1980, p. 365) described an interesting association between a "... large unadorned form ..." of *Spirorbis* and *Chaetetes*. This form is found on the upper surface of some colonies and "... after landing on the growing surface, uncoiled and grown (sic) upwards to keep pace with its hosts." Other occurrences suggested to Jameson that *Spirorbis* detached itself from its host before being engulfed, leaving a circular print on the chaetetid colony surface. He suggested that the relationship between these two was commensal. The description of this association suggests that these "spi-

#### EXPLANATION OF PLATE 2

##### Figure

- A. Surface of *Chaetetes* from the Amoret Limestone. Note abnormal calicle growth in vicinity of vermiform symbiont. Scale bar is 1.0 mm
- B. Polished vertical section of *Chaetetes* colony from the Amoret Limestone. Note original settlement on algal-coated productid brachiopod shell and evidence of overturning during early growth. Note also the prominent interruption partings and the subsequent irregular "ragged" growth at the margins
- C. Polished vertical section of *Chaetetes* colony from the Amoret Limestone. Note original settlement on oncolite and evidence of overturning during early growth. Also note the numerous growth lines and the interruption partings marking a change in growth form
- D. Surface of *Chaetetes* colony from the Higginsville Limestone. Note partial overgrowth by an *Aulopora*. Scale bar is in mm
- E. Polished vertical section of *Chaetetes* from the Amoret Limestone. Note parts of astrorhiza revealed by regular arrangement of calicles and apparent lower position of tabulae in astrorhizal calicles. Scale bar is 1.0 cm
- F. Polished longitudinal section of *Chaetetes* from the Amoret Limestone. Note abnormal growth of calicles below and above vermiform symbionts. Scale bar is 1.0 mm



rorbids" may be vermiform gastropods as reported by Burchette and Riding (1977).

We have observed two different bivalves associated with chaetetid colonies. Part of one valve of a large form which might be a pseudomonotid is oriented such that it could have been cemented to the upper surface of a colony. The other bivalve is a very small, articulated, smooth form which is contained within a "sediment" filled pocket in a low domical colony. The general morphology and living position raises the possibility that the bivalve had developed a boring habit, but in the absence of additional examples it seems better to consider it a nestling form which found a protected place in an unoccupied cavity within the chaetetid colony.

Within another small cavity in the side of a high domical colony is the disarticulated partial skeleton of a regular echinoid. The plates and spines suggest that it is a species of the common Palaeozoic genus *Archaeocidaris*. Here again we see little evidence that the organism created the hole.

#### Associated Depositional Environments

Winston (1963) suggested that chaetetid development was best during the deposition of regressive phases but that they occurred, in lesser abundance, during transgressive phases as well. This seems to be the case in Kansas, at least in terms of our rather preliminary investigations. Using Heckel's (1977) model to explain the Kansas Upper Carboniferous sequences, the Amoret Limestone Member would be a transgressive limestone, and while chaetetids are abundant in some localities they are not nearly as conspicuous or well developed as they are in the Higginsville Limestone Member, which is interpreted as a regressive limestone.

### SKELETAL STRUCTURE

#### Surface Features

Chaetetids possess certain features in common with tabulate corals, stromatoporoids, bryozoans, sclerosponges, and post-Palaeozoic chaetetids. Tubercles (Pl. 7, fig. C), small (0.14 mm high) conical structures, occur at the confluence of calicle walls on the surfaces of some chaetetid colonies. Unfortunately they are not common, probably because these small features are easily removed by erosion or covered by matrix and/or encrusting algae. Kirkpatrick (1911) described structures he called tubercles on *Merlia* and noted that they extend above the calicle edges. Similar features are reported by Hartman and Goreau (1972) on other extant sclerosponges though they did not call them tubercles. In some extant sclerosponges these structures

may be present or absent. To our knowledge tabulate corals and stromatoporoids lack these features, but the acanthopores of some bryozoans may be analogous.

Mamelons (monticles in bryozoans) are very rare features on Palaeozoic chaetetids. We have only one specimen from the Amoret on which some few weakly developed mamelons can be seen, but Gray (pers. comm.) has found mamelons on "many Carboniferous chaetetids . . ." Mamelons, a rather common feature on stromatoporoids, some bryozoans, sclerosponges, and post-Palaeozoic chaetetids, have not been found on tabulate corals. In some stromatoporoids, post-Palaeozoic chaetetids, sclerosponges, and bryozoans mamelons or monticles are the sites of the radial canal system termed astrorhizae. In Palaeozoic chaetetids this relationship has not yet been observed.

Astrorhizae (Pl. 1, figs. D and E) in Palaeozoic chaetetids have been described by Mathewson (1977). These stellate patterns of linearly arranged calicles range from 0.8 to 1.8 cm in diameter and up to 40 are present on a single chaetetid colony. Unlike the astrorhizae of some stromatoporoids, sclerosponges, and post-Palaeozoic chaetetids, these astrorhizae are primarily surface features and it is very difficult to trace them downward into the coenosteum. We are aware of only one case where astrorhizae have been reported in the interior of a Palaeozoic chaetetid colony (Mathewson, 1977) (Pl. 2, fig. E). Our own attempts to trace these stellate patterns downward by closely spaced horizontal and vertical thin sections has proved unsuccessful. Chaetetid astrorhizae are not common features and are easily removed by erosion and obscured by encrustations and/or matrix. Our experience suggests that astrorhizae are most likely to be found on vertical surfaces of the colonies or on protected overhung surfaces. Cuffey (pers. comm.) suggested (believes) that bryozoan astrorhizae appear to be similar to those we have observed in Palaeozoic chaetetids.

The function of these structures is not clearly understood but it seems reasonable to suggest that they are in some way related to the exhalent system of the organism. The general absence of mamelons in Palaeozoic chaetetids even in the presence of astrorhizae may mean that while localization of excurrent water was necessary (thus astrorhizae) the turbulence of the water in the habitat was such that raised areas (mamelons/monticles) were not necessary to prevent the fouling of incurrent water.

It is not the purpose here to dwell at length on the secondary surface features found in Palaeozoic chaetetids. These are well discussed by Mathewson (1977) and others. It is important, ecologically, to comment briefly on those secondary features which are biological

in origin. Borings in Palaeozoic chaetetid colonies were discussed above. Any available firm surface will be colonized by benthic organisms and chaetetids were no exception.

Structures tentatively identified as "worm tubes" are present on some colony surfaces (Pl. 2, fig. A) and also on some polished sections (Pl. 2, fig. F). Previous workers have noted the deformation of calicles around these cylindrical features. Kirkpatrick (1911, p. 673) referred to such deformation of calicles in *Merlia* (an extant sclerosponge) as occurring around "the mouth of a worm tube." Okulitch (1936) in his study of *Heliolites*, *Tetradium*, and *Chaetetes* suggested such deformation was due to serpulid worms. Similar features in *Ceratoporella* (another extant sclerosponge) were ascribed to serpulid worms by Hartman and Goreau (1972) and Mathewson (1977) felt this to be the cause of calicle deformation in the Pennsylvanian chaetetids he studied. While we have no additional data, we feel that such features need to be re-examined carefully before excluding the possibility that they may be the result of vermiform gastropods (see Burchette and Riding, 1977).

#### Internal (Within Colony) Features

Structures within the individual colonies which are of secondary importance are interruption partings (Pl. 2, figs. B and C), which occur in all growth forms of chaetetids we have observed. Interruption partings may represent periods of death of the chaetetid colonies as suggested by Hartman and Goreau (1975) for some sclerosponges, or they may be caused by sudden influxes of sediment or overgrowth by other encrusting organisms. Such partings are commonly found in most, if not all, colonial organisms and have been reported, with different possible explanations, in Palaeozoic chaetetids by Lustig (1971), Mathewson (1977), and Spaw (1977).

Another feature conspicuous in polished vertical sections is growth bands. Basically these are alternating light and dark bands with abrupt to gradational contacts and contained growth laminae. Widths of these bands range from 0.09 to 0.86 cm in the Pennsylvanian chaetetids of southeastern Kansas (Mathewson, 1977). Studies of Atokan chaetetids from Nevada by Lustig (1971) revealed that from 10 to 13 growth laminae comprised each growth band; using these data Lustig suggested a growth rate of 2 mm per year for these chaetetids, which agrees well with the growth rates for sclerosponges as reported by Lang *et al.* (1975) and Goreau and Land (1974) and for the estimated growth rates for tabulate corals of the family Halysitidae (Hamada, 1959; and Buehler, 1955).

Calicles within chaetetid colonies are cerioid in arrangement with a few being meandroid. In transverse section (Pl. 1, figs. A and E) these calicles are circular, polygonal, elliptical, and irregularly shaped, ranging in "diameter" from 0.08 to 0.57 mm, approximately within the range of corallite diameters in tabulates (0.1 to 10 mm) and sclerosponges (0.18 to 0.5 mm). There does not appear to be any dimorphism within the colonies but there does seem to be some change in calicle shape, from regular to irregular, following a disturbance of colony growth. Similar growth variation has been noted in sclerosponges by Kirkpatrick (1911) and Hartman and Goreau (1972). Calicle size, shape and characteristics before and after overgrowth are thus of little help in the "correct" taxonomic placement of Palaeozoic chaetetids.

Tabulae (Pl. 1, fig. B), are nearly always present in chaetetids, tabulate corals, sclerosponges, and other groups to which chaetetids have been referred. In Palaeozoic chaetetids the tabulae may be complete, incomplete, concave, convex or flat. Additionally they may occur at the same level in adjacent calicles or be irregularly spaced. Tabulae in Palaeozoic chaetetids average 0.021 mm in thickness and range from 0.007 to 0.051 mm and are spaced from 0.08 to 0.5 mm apart with average spacing of 0.23 mm (Mathewson, 1977). Lustig (1971) suggested that diagenetic factors were responsible for the diverse distribution pattern of tabulae in the Upper Carboniferous (Atokan) chaetetids of Nevada. Additionally, Lustig (1971) concluded that tabulae in chaetetids were not continuous with the calicle wall structure, but Mathewson (1977), studying thin sections and SEM photographs, disagreed with her conclusions. He felt the two were continuous as they are in the extant sclerosponge *Merlia* (Kirkpatrick, 1911). This is perhaps one reason that Lustig considered chaetetids tabulate corals while Mathewson considered them sclerosponges.

Calicle increase, in chaetetids is interpreted to occur via longitudinal fission, peripheral expansion, and intercalicle budding. Longitudinal fission is accomplished by the development of one or more pseudo-septa which divide a calicle into equal or subequal parts. As these pseudo-septa grow toward each other the "parent" calicle increases in size. Generally, this division of a calicle is along the calicle's shortest dimension. Coenenchymal enlargement as described by Kirkpatrick (1911) for the extant sclerosponge *Merlia* has been documented by Mathewson (1977) in Palaeozoic chaetetids. Mathewson suggested that the features supporting this enlargement in Palaeozoic chaetetids is rare and could easily be obscured by abrasion and/or coatings of sediment or encrustations by chae-

tetids or other organisms. Intercalicle budding begins with the separation of calicle walls at an intersection and the increase of this space into a full sized calicle with upward growth.

#### Microstructure

Basically the microstructure of the calicle walls and tabulae in chaetetids differ little from that in skeletal coelenterates and living sclerosponges. A rather good summary of the microstructure of skeletal coelenterates and chaetetids is given by Lustig (1971), who considered chaetetids to be tabulate corals. Our studies, to date, support the conclusions of Mathewson; the microstructure of the walls is fibroradial and the walls and tabulae are continuous. As Mathewson (1977) has pointed out, fibroradial is synonymous with trabecular, fascicular, and "jet d'eau" of other authors and is a common microstructure in extant sclerosponges (Hartman and Goreau, 1972).

The only documented example of spicules in Palaeozoic chaetetids known to us is the study by Gray (1980). Spicules in *Chaetetes (Boswellia) mortoni* occur as intramural pseudomorphs of calcite, pyrite, and silica. While some of the chaetetids we are studying, particularly those in southeastern Kansas, are partially silicified and the presence of iron staining suggest the presence of pyrite, we have to date, observed no spicules or pseudomorphs of spicules. The absence of spicules in chaetetids should not, in our opinion, be considered as detracting from their poriferan affinities. Not only are spicules not always incorporated into the skeletons of extant sclerosponges (Kirkpatrick, 1911; Hartman and Goreau, 1975), but due to the instability of silica in the presence of calcium carbonate, such spicules are commonly corroded completely away in older parts of the skeletons of still-living sclerosponges (Hartman and Goreau, 1970, 1972). Thus the usual absence of spicules in chaetetids is exactly what should be expected.

#### BIOLOGICAL AFFINITIES AND CONCLUSIONS

As pointed out in the introduction, chaetetids have been assigned to a variety of biological phyla. While there are certain gross morphological similarities between chaetetids and certain calcareous algae, we think that most investigators would agree that such similarities are superficial. However, if the studies by Kaźmierczak (1969, 1976, 1981) are substantiated we may need to revise our thinking once again.

The major animal phyla considered to be "home" for Palaeozoic chaetetids are bryozoans, coelenterates (tabulates), and sponges. Comparison of the Upper Carboniferous (Middle Pennsylvanian) chaetetids we

have studied, with published data on other Palaeozoic and post-Palaeozoic chaetetids, stromatoporoids, tabulate corals, bryozoans, and extant sclerosponges provide the following results.

1) Size of "individuals" within the colonies of all these groups are quite similar, as is the occurrence of what are, or can be, considered tabulae. However, tabulae are not universally present in the Tabulata or in the extant members of the Sclerospongiae. Structures referred to as septa or pseudosepta occur in tabulates and chaetetids but are absent in the other groups. Mural pores, or similar structures, are present in some tabulates and in some bryozoans but absent in the remaining groups.

2) Surface features, such as mamelons or monticles are not particularly unique to any one group, as they have been observed in bryozoans, tabulates, stromatoporoids, post-Palaeozoic chaetetids, and sponges, including sclerosponges. They are, however, rather rare features on Palaeozoic chaetetids. The same is true of astrorhizae except that we are unaware that they have been reported on tabulates.

3) Intimate skeletal associations with tubular organisms is common in extant sclerosponges, chaetetids, and some tabulate corals.

4) There is considerable variety in the microstructure of chaetetids, both Palaeozoic and post-Palaeozoic, as well as stromatoporoids and sclerosponges (Gray, 1980). As pointed out by Cuif (1974), post-Palaeozoic chaetetids generally have a wall composed of spherulites, as do some sclerosponges (Hartman, 1979) and some stromatoporoids (Stearn, 1977). The Palaeozoic chaetetids we have studied possess a fibroradial microstructure as do some sclerosponges (Hartman and Goreau, 1972) and many stromatoporoids (Stearn, 1972). Tabulate wall structure is summarized by Hill (1981) and is also fibroradial, and Lustig (1971) discusses the similarities between the wall structure of Upper Carboniferous (Atokan) chaetetids and skeletal coelenterates.

5) Spicules have been observed and reported in sclerosponges, post-Palaeozoic chaetetids, and some Palaeozoic stromatoporoids (Gray, 1980). They have not been reported in bryozoans or tabulates.

In conclusion, the bulk of the evidence supports the assignment of the Palaeozoic chaetetids to the Sclerospongiae with the primary evidence being the presence of astrorhizae, spicules, and the continuity between the structure of the calicle walls and the tabulae. Thus, we support the placement of the Palaeozoic chaetetids in the Order Chaetetida of the Class Sclerospongiae (Hartman and Goreau, 1972).



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THE FUNCTION OF TUBE-PILLARS IN THE ORDOVICIAN  
STROMATOPOROID *CLIEFDENELLA* INFERRED BY ANALOGY WITH  
THE RECENT SCLEROSPONGE *CALCIFIBROSPONGIA*

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ABSTRACT

The internal macrostructure of the Ordovician *Cliefdenella* Webby is unique among the stromatoporoids in that all the pillars are hollow tubes (tube-pillars) crossed by cyst-plates. The function of the tube-pillars has remained an enigma. They did not house exhalant canals, as astrorhizae are also present in *Cliefdenella*. The Recent sclerosponge *Calcifibrospongia* Hartman from the Bahamas contains an unusual characteristic, vertical tubes which house inhalant canals. Astrorhizal exhalant canals are also present. Close examination of *Cliefdenella* specimens from Alaska shows a characteristic not seen before, pores in the walls of the tube-pillars. These pores allowed communication between the hollow centers of tube-pillars and the galleries. Apparently, water entered *Cliefdenella* through the tube-pillars, circulated to the galleries, and was exhaled *via* the astrorhizae.

INTRODUCTION

The biological affinities of stromatoporoids have long been a subject of study and speculation. Stearn (1972, 1975) has summarized the history of thought on stromatoporoid affinities. Although some modern workers espouse a coelenterate affinity (*e.g.*, Nestor, 1981), or a grouping with cyanobacteria (*e.g.*, Kaźmierczak, 1981), most paleontologists today agree that stromatoporoids are allied to sponges, following the lead of Hartman and Goreau (1970) and Stearn (1972, 1975). Recently it has been proposed that the stromatoporoids should be considered a class of Phylum Porifera (Stock, 1979; Stearn, 1980), most closely related to Classes Demospongea and Sclerospongea. These poriferan relationships will be employed in the determination of the probable function of tube-pillars in the stromatoporoid *Cliefdenella* Webby, 1969.

The Middle to Upper Ordovician stromatoporoid *Cliefdenella* is known from Australia (Webby, 1969; Webby and Morris, 1976), the Altai region of Siberia (Khalfina and Yavorsky, 1974), Alaska (Stock, 1981), and possibly China (Ozaki, 1938) and California (J. K. Rigby, pers. comm., 1980). This present-day circum-Pacific distribution is seen to be more or less equatorial when plotted on paleogeographic maps showing Middle to Late Ordovician continental positions (*e.g.*, Scotese *et al.*, 1979).

Specimens described in this paper are housed in the United States National Museum of Natural History (USNM) and the Yale Peabody Museum (YPM).

INTERNAL MACROSTRUCTURE

The internal macrostructure of *Cliefdenella* is dominated by two features: sheetlike laminae, and pillars which are hollow tubes crossed by horizontal to inclined cyst-plates. The aforementioned tube pillars are

unique to *Cliefdenella* in relation to other Ordovician stromatoporoids. Other macrostructures include the many cyst-plates in the galleries, and multi-canaled astrorhizae.

In tangential section the tube-pillars are seen as isolated circles. The astrorhizae appear as bundles of circles from which extend branching astrorhizal canals. By analogy with other sponges, the astrorhizae in *Cliefdenella* are believed to be exhalant canal systems, but what was the function, if any, of the tube-pillars?

TUBELIKE STRUCTURES IN  
STROMATOPOROIDS

It is doubtful that the tube-pillars served an exhalant function, since astrorhizae also are present, and the two are not associated. Astrorhizal canals by-pass tube-pillars (Pl. 1, fig. 2). They are not the tubes formed by the symbiotic tabulate coral *Syringopora*, the presence of which served as the diagnostic characteristic of the now invalid stromatoporoid genus *Caunopora* Phillips, 1841. The skeletal material of *Syringopora* is clearly different from that of the surrounding stromatoporoid, the corallites contain infundibular tabulae, and the corallites are connected by horizontal tubes. In *Cliefdenella*, the tube-pillars have the same microstructure as the laminae and there is no suture separating the two macrostructures.

Ring-pillars, characteristic of the Devonian stromatoporoid *Stromatoporella* Nicholson, 1886, resemble tube-pillars in cross section, but the ring-pillars typically cross only one gallery. Ring-pillars are formed by upward inflections of laminae, and laminae in *Cliefdenella* are deflected downward where they intersect tube-pillars. Tubelike pillars in the Devonian stromatoporoid *Tubuliporella* Khalfina, 1968, arise from upward inflections of laminae, as in ring-pillars, but

the inflections are superposed to form a tube. However, in both *Tubuliporella* and *Stromatoporella* the tubes and rings represent the minority of vertical macrostructures in the coenosteum, as most are spool-shaped, nonsuperposed pillars. There are no stromatoporoids known from the Silurian through earliest Devonian containing tubelike pillars. Hence, the tube-pillars in *Tubuliporella* and *Cliefdenella* are regarded as the result of diachronous convergent evolution.

Goold (1980, p. 111) has warned that one must resist assigning an adaptive function to any particular structure. However, tube-pillars in *Cliefdenella* are well-developed structures, unique among genera of their time, which persisted through at least parts of the Caradocian and Ashgillian. They must have served some special function, beyond the obvious role as supporters of the laminae, since almost all other stromatoporoids were able to survive without tube-pillars.

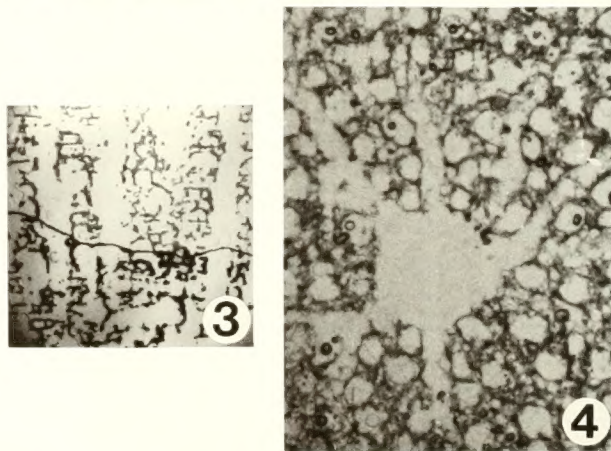
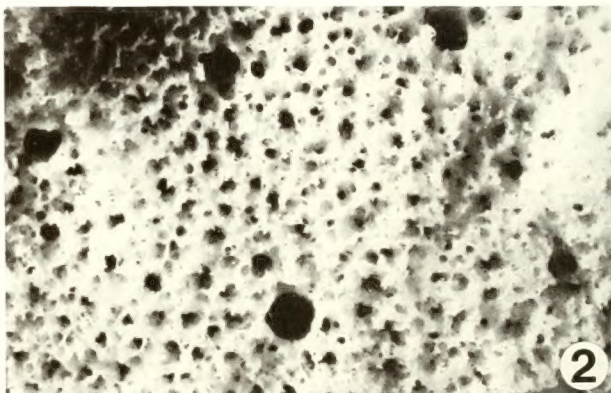
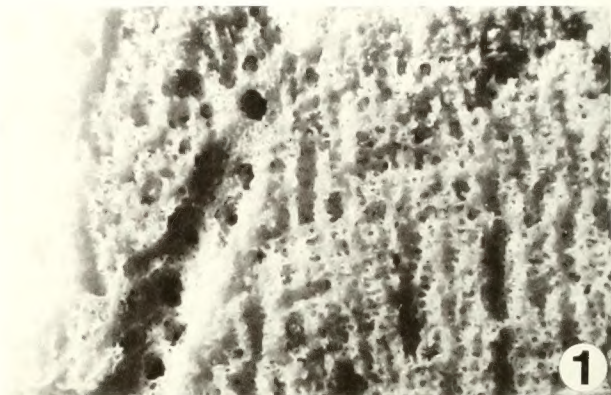
#### CALCIFIBROSPONGIA

An insight on the nature of tube-pillars is gained through study of a recently named sclerosponge, *Calcifibrospongia* Hartman, 1979, from the Recent of the Bahamas. Hartman's (1979) publication presents a thorough description of the anatomy of *Calcifibrospongia*. Briefly, the skeleton is composed of three structures, one organic, another calcareous, and a third siliceous. Within the soft tissue is found a reticulum of sponginlike organic fibers. The aragonitic skeleton is secreted within the fibrous network, mimicking the original reticulation. The open skeletal network of *Calcifibrospongia* is quite different from the solid calcareous exoskeleton constructed by some other sclerosponges (e.g., *Ceratoporella* Hickson (1911)). Siliceous monaxon spicules (strongyles) are also secreted in the soft tissue, and also form a reticulum. These spicules can become enclosed within the aragonitic skeleton, and eventually erode away completely during the life of the sponge. Aragonite fills the spicule molds, totally obliterating evidence of the spicules' presence.

The macrostructure of *Calcifibrospongia* is quite irregular (Text-fig. 1), not very much like *Cliefdenella*. The upper surface of the skeleton of *Calcifibrospongia* exhibits two types of circular to oval openings. Some of the openings are large (1.4–2.2 mm in diameter), and many more are small (0.4–0.6 mm in diameter). Canals extend down into the skeleton from the openings.

Study of the soft tissue by Hartman (1979) revealed that the large openings are the sites of vertical exhalant canals, fed by horizontal tributaries, and that vertical inhalant canals are located at the small openings. Water enters the small, inhalant canals, passes laterally through

small canals and flagellated chambers, is collected by the horizontal canals, and exits *via* the large exhalant canals.

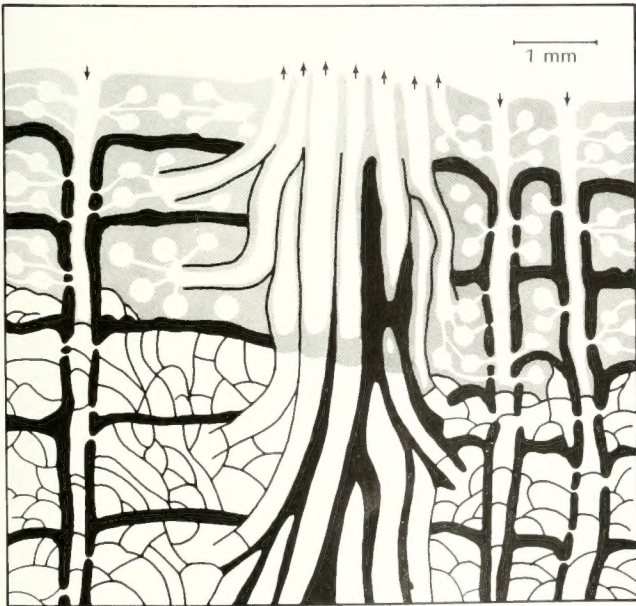


Text-figure 1.—*Calcifibrospongia actinostromarioides* Hartman, 1979. 1. Vertical view of cut surface,  $\times 3$ , holotype YPM 9114, showing large, diagonal, axial astrorhizal canal with horizontal tributaries, and smaller, vertical inhalant canals; 2. View of upper surface,  $\times 3$ , paratype YPM 9135, showing a few, large, exhalant canals, and many, small, inhalant canals; 3. Vertical section,  $\times 5$ , holotype, YPM 9114, showing irregular skeleton, a few inhalant canals, and a thin transverse layer sealing off the previous year's growth; 4. Tangential section,  $\times 5$ , specimen number unknown (from Hartman, 1979, fig. 6), showing an astrorhiza and many inhalant canals.

## COMPARISONS

Recent close inspection of a vertical surface of a paratype specimen of *Cliefdenella alaskaensis* Stock, 1981 (p. 1000) has revealed the presence of small, sub-circular pores (0.04 mm in diameter) in the walls of tube-pillars (Pl. 1, fig. 6). These pores can also be seen in thin sections of another paratype specimen of *Cliefdenella alaskaensis* from Alaska (Pl. 1, figs. 3, 4), and of a topotype specimen of *Cliefdenella etheridgei* from New South Wales, Australia (Pl. 1, figs. 7, 8). The presence of pores in the walls of two species of *Cliefdenella* from two distant localities supports the occurrence of the pores as a generic characteristic, and decreases the possibility that they are a product of diagenesis. The pores apparently allowed some sort of communication between the galleries and the tube-pillar interiors.

Just as comparisons with sclerosponges revealed the exhalant nature of astrorhizae in stromatoporoids, the inhalant nature of the tube-pillars in *Cliefdenella* is inferred by analogy with *Calcifibrospongia*. This interpretation is enhanced by the presence of a few tube-pillars which bifurcate upward (Pl. 1, fig. 5). Astrorhizal canals often merge in stromatoporoids (e.g., Stock, 1982, pl. 4, figs. 6, 7) as do exhalant canal systems in sclerosponges (e.g., Hartman, 1969, fig. 30; Hartman and Goreau, 1970, fig. 5). The merger is always in the direction of water flow, as in a river's tributary system. If the same is true for tube-pillars, the flow was downward, into the stromatoporoid.



Text-figure 2. — Reconstruction of the stromatoporoid *Cliefdenella* as seen in vertical section. The stippled pattern represents soft tissue; skeletal material is solid black. Arrows represent sites of inhalation and exhalation of sea water.

Water entered the coenosteum of *Cliefdenella* via the inhalant canals and perhaps through fine pores on the upper surface of the soft tissue (Text-fig. 2). At some distance below the upper surface, the calcareous exoskeleton was being deposited. The inhalant canals were encased by the tube-pillars as skeletal calcium carbonate deposition continued. The water flowing down the inhalant canals laterally entered fine canals. When the tube-pillars were deposited, the fine canals remained functional for a time, and are represented by the pores in tube-pillar walls. Apparently, the fine canals then carried the water to flagellated chambers where feeding and excretion by the choanocytes took place. This conclusion is based on the idea that stromatoporoids are most closely related to sclerosponges and demosponges, both of which display a leucon-style architecture. Stearn (1975) inferred similar soft-part architecture in stromatoporoids. Waste water passed out of the flagellated chambers via fine exhalant canals, which coalesced into astrorhizal canals. The astrorhizal canals carried the water out of the animal. The lower reaches of the skeleton were not occupied, but were closed off by cyst-plates in the galleries, tube-pillars, and lateral astrorhizal canals.

## CONCLUSIONS

Tube-pillars in *Cliefdenella* are unusual structures for a stromatoporoid to contain. Detailed examination of internal macrostructures, especially the tube-pillars, has revealed pores which allowed communication between the hollow axis of the tube-pillars and adjacent galleries. Study of *Calcifibrospongia* indicates this sclerosponge contains vertical inhalant canals. In addition, *Calcifibrospongia* contains exhalant astrorhizal canals, as does *Cliefdenella*. It is concluded that tube-pillars in *Cliefdenella* housed inhalant canals which carried water from the surface to the galleries. Water circulated back to the surface via exhalant astrorhizal canals.

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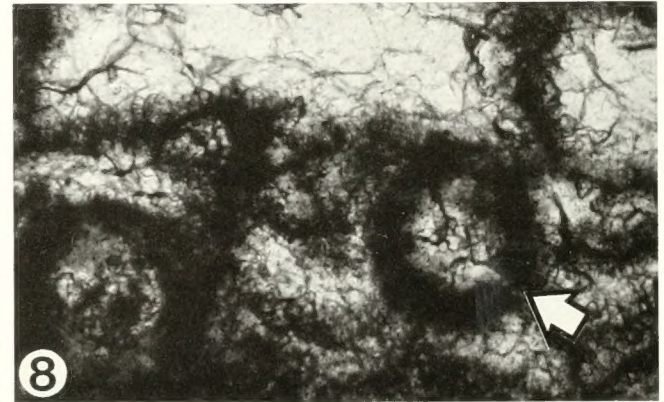
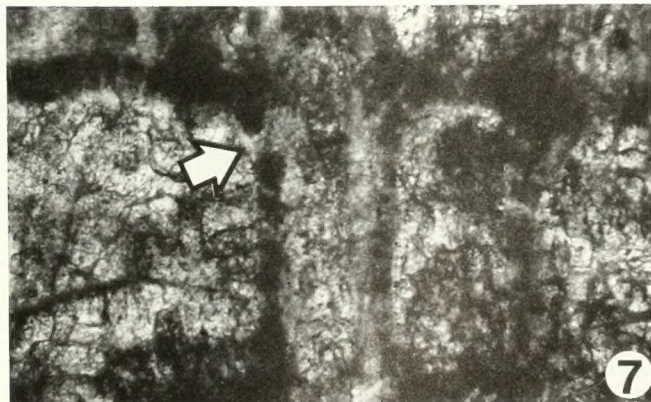
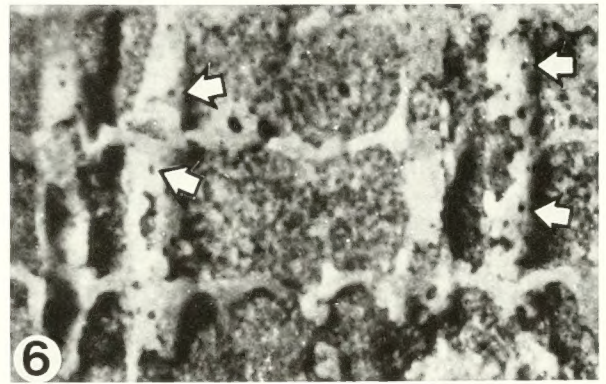
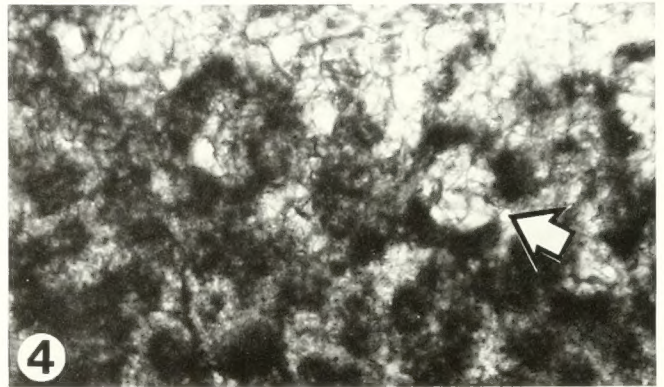
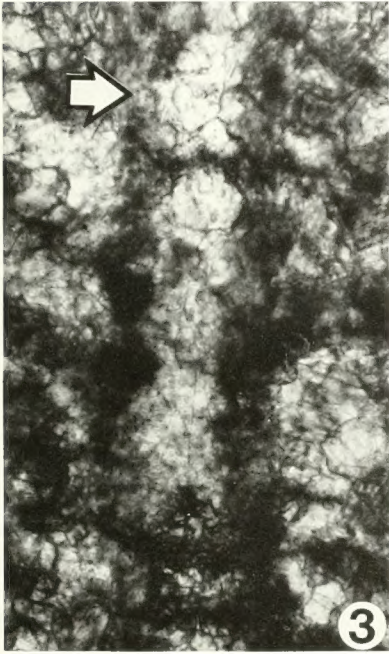
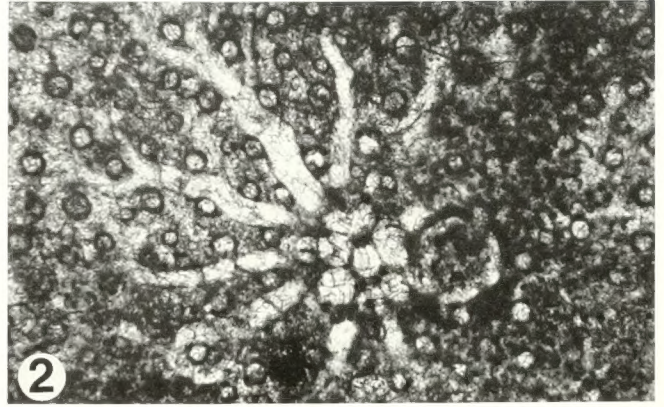
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## EXPLANATION OF PLATE 1

## Figure

- 1–6. *Cliefdenella alaskaensis* Stock, 1981  
1. Vertical section,  $\times 10$ , paratype USNM 292680, showing laminae, tube-pillars and an astrorhiza.  
2. Tangential section,  $\times 10$ , paratype USNM 292684, showing tube-pillars and an astrorhiza.  
3. Vertical section,  $\times 50$ , holotype USNM 292685, showing tube-pillar with pore (arrow) in wall; 4. Tangential section of same specimen,  $\times 50$ , showing pore (arrow) in tube-pillar wall; 5. Vertical section of same specimen,  $\times 10$ , showing upward-bifurcating tube-pillar.  
6. Vertical view of weathered specimen,  $\times 14$ , paratype USNM 292680, showing pores (arrows) in tube-pillar walls.
- 7–8. *Cliefdenella etheridgei* Webby, 1969  
7. Vertical section,  $\times 50$ , topotype USNM 327459, showing tube-pillar with pore (arrow) in wall; 8. Tangential section of same specimen,  $\times 50$ , showing pore (arrow) in tube-pillar wall.



## COMPARISON OF SKELETAL STRUCTURES AMONG STROMATOPOROIDS, SCLEROSPONGES AND CORALS

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### ABSTRACT

Stromatoporoid skeletons show a coelenterate relationship in many aspects. The following skeletal features observed in several stromatoporoid species can be better explained by coelenterate affinity than by poriferan affinity: 1) similarity of gross skeletal structures between stromatoporoids and the coenosteum of plocoid or dendroid scleractinian corals, 2) similarity of supposed original microstructures of the stromatoporoid skeleton to scleractinian corals, 3) thickening of the stromatoporoid skeleton around astrorhizal canals similar to the thickened coenosteum in the vicinity of some scleractinian corallites, 4) presence of astrorhizal canals with walls which clearly cut laminae, indicating formation of such laminae after the astrorhizal canals, 5) presence of tabulae in the astrorhizal canals and 6) presence of spaces lacking any traces of astrorhizal canals between the canal margin of one astrorhiza and those of neighboring astrorhizae. Sclerosponges lack any direct evidence of structures or conditions comparable with the stromatoporoid features mentioned above, especially in 3-5.

### INTRODUCTION

Stromatoporoids are an extinct and enigmatic fossil group; their taxonomic affinities are controversial largely because their soft tissues are unknown. However, stromatoporoid skeletons have characteristics of both the Porifera and Coelenterata whose soft tissues and modes of life are distinctly different. Porifera filter nutrients through canal systems, whereas many coelenterates are partially carnivorous with tentacular polyps that function individually. Stearn (1972) pointed out that "without knowledge of whether the stromatoporoids were filter-feeders or actively sought their food like a coelenterate, their role in ancient reefs will not be understood." The relationship of the stromatoporoids to the Porifera or Coelenterata is also important if a solution to their taxonomic problems is to be found, assuming that their origin is monophyletic. Other opinions on the affinities of the stromatoporoids as foraminifers, archaeocyathids or as aggregates of cyanobacterial cells are not considered here, because the evidence presented so far seems weak.

Many recent investigations support the view proposed by Hartman and Goreau (1970) that there is a close relationship between sclerosponges and stromatoporoids. Stearn (1972, 1975, 1982) discussed the relationship between these two groups in detail and suggested that the stromatoporoids should be a subphylum (Stromatoporata) in the Phylum Porifera. Alternatively, coelenterate affinities of the stromatoporoids have been propounded by Mori (1976, 1977, 1982), Bogoyavlenskaya and Boyko (1979) and Nestor (1981). The purpose of the present paper is to review the gross skeletal structures (including astrorhizae) of the stromatoporoids so as to judge their relationship to the Porifera and Coelenterata. Because even those workers

supporting the poriferan affinity of the stromatoporoids have accepted the microstructural similarities between the stromatoporoid and scleractinian skeletons (see Stearn, 1972, 1975; Mori, 1982), these are not discussed herein.

### GROSS SKELETAL STRUCTURES

The skeletons of Recent sclerosponges are composed of honeycomb structures which are strikingly similar to those of Paleozoic and Mesozoic chaetetids but are clearly different from stromatoporoids. Stearn (1972, 1975) also separated the stromatoporoids from the sclerosponges on differences in gross structure, tabulae and spicules although he reconstructed stromatoporoid soft parts by comparison with the sclerosponges *Merlia* and *Astrosclera*. As far as gross skeletal structures are concerned, these two genera are similar to other sclerosponges in showing no close resemblance to any stromatoporoids (see Stearn, 1972, fig. 8; Kirkpatrick, 1911, figs. 16, 17). Also, Hartman (1979) noted that skeletons of the Recent sclerosponge *Calcifibrospongia* and the Mesozoic stromatoporoid *Actinostromaria* are similar, but their three-dimensional reconstructions are entirely different: *C. actinostromarioides* consists of closely spaced vertical tubes whereas species of *Actinostromaria* contain vertical pillars and radial rods. Essential skeletal features of stromatoporoids are laminae, pillars, cysts and amalgamated structures which are absent in sclerosponges.

On the other hand, Mori (1982) has noted the similarity between stromatoporoid skeletal structure and the coenosteum of colonial scleractinian corals. Despite the difference in geologic age of these two groups, it is important to note that the corals precipitate similar gross structures to those in stromatoporoids. Stromatop-



toporoid skeletons are also similar to those of Recent *Hydractinia* and *Millepora*. Although dissimilarities in skeletal structure between stromatoporoids and sclerosponges alone is not conclusive in deciding stromatoporoid taxonomic position, strong evidence exists to suggest that the coelenterates are closely related to stromatoporoids.

#### MORPHOLOGY OF ASTRORRHIZAE

Stromatoporoid astrorhizae show many morphological varieties. They can be divided into the following categories, although there are intermediate forms between them:

A. Astrorhizae consist of a vertical canal associated with delicately ramified radial canals. Canal diameters decrease towards their tips.

B. Astrorhizae consist of a vertical canal associated with simple radial canals. In some cases the radial canals do not taper towards their tips.

C. Astrorhizae consist of a simple vertical tube; radial canals are absent.

#### Radial Canals

In *Clathrodictyon djupvikense* Mori from the Silurian of Gotland (Text-fig. 1; see also Mori, 1970, p. 89, pl. 3, figs. 6, 7) the astrorhizae belong to Type B (above) and possess a marginal wall. The fact that the canals cut across several laminae indicates that they existed prior to formation of the laminae. In contrast, Recent sclerosponges lack traces of walls in their exhalant canals. In addition, there are very few examples of stromatoporoid astrorhizae that are confined to the skeletal surface as is the case in some sclerosponge exhalant canals. These differences are evidence of differences in function between stromatoporoid astrorhizae and poriferan canal systems.

#### Tabulae

The astrorhizal canals in some stromatoporoids contain tabulae. However, in sclerosponges tabulae are present throughout the skeleton but are absent in the exhalant canals again suggesting a difference in function between stromatoporoid astrorhizae and sclerosponge canals.

Tabulae in the astrorhizal canals more closely correspond to those developed in the gastropores and dactylopores of Recent *Millepora* and thus can be used in support of the coelenterate affinities of the stromatoporoids.

#### Skeletal Thickening

Thickening of skeletal structures in the vicinity of the astrorhizal canals has been described in stroma-

toporoids (Kaźmierczak, 1969; Stearn, 1975; Mori, 1982). Tangential and vertical sections of *Stromatoporella saginata* Lecompte (Text-figs. 2, 3) clearly show that the skeleton is more dense in the vicinity of the astrorhizal canals than elsewhere. Similar skeletal thickening is present in Recent corals, e.g., *Acropora* sp. and *Dendrophyllia micranthus* (Ehrenberg) (Text-figs. 6, 7). In *Acropora* sp. dense skeleton surrounds the axial corallites and in *D. micranthus* there are gradients in skeletal densities which are related to distance from corallites. Sclerosponges lack thickened structures comparable to the skeletal modifications in stromatoporoids and corals mentioned above.

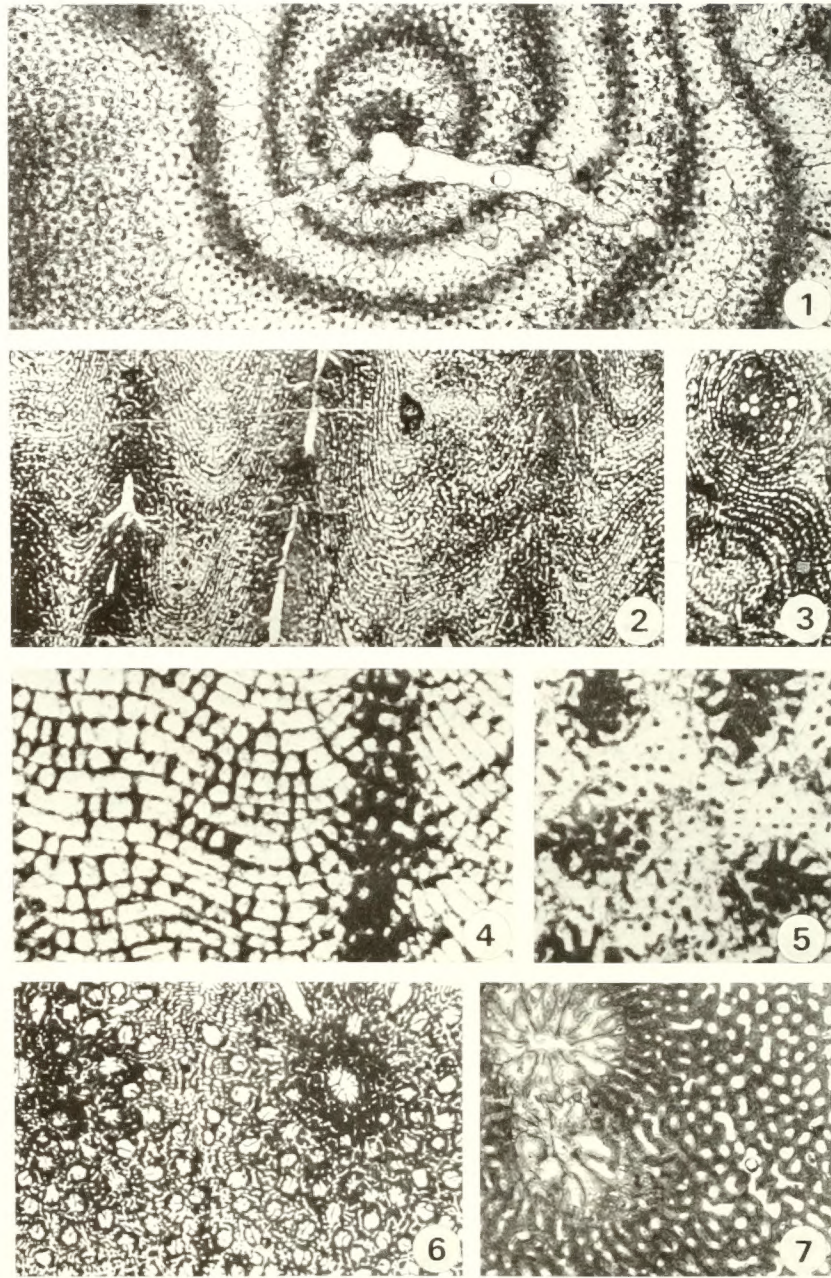
It is highly probable that these skeletal thickening features did not occur during diagenesis, but rather by biogenic processes related to the function of the astrorhizae. Goreau and Goreau (1959) noted that calcification rates and Ca uptake of colonial scleractinians fluctuate widely even within a single colony. Skeletal thickening around scleractinian corallites is considered to be a consequence of accelerated Ca uptake and calcification of the surrounding coenosteum by the polyps. Variation in skeletal density around the astrorhizal canals supports the idea that the astrorhizae are traces of zooids and are thus comparable to scleractinian corallites.

#### INTERPRETATION OF STROMATOPOROIDS LACKING ASTRORRHIZAE

Many genera and species of stromatoporoids lack traces of astrorhizae. It is uncertain whether this can be better explained by a poriferan or a coelenterate affinity for the group. Stearn (1972, 1975) believes that exhalant canals were present in these stromatoporoids but that they did not interfere with secretion of the skeleton. However, Recent hydrozoans have a variety of zooids whose differences may or may not be reflected in their skeletons. Thus, in *Millepora* the zooids leave pits or depressions in the skeleton but in *Hydractinia* there are no such traces (Lecompte, 1956). Therefore, stromatoporoids lacking astrorhizae are equally comparable to poriferans and coelenterates.

In the stromatoporoid *Anostylostroma subcolumnare* Galloway and St. Jean astrorhizae are absent but mamelon columns are prominent (Text-figs. 4, 5). In Fagerstrom's (1982) description, these columns are filled with dark, dense skeletal material composed of greatly thickened pillars which was regarded by Fagerstrom as original. This thickening is comparable to that noted above in *Stromatoporella saginata* and in both these species it is probable that zooids were located on the surface of each mamelon but did not interfere with skeletal secretion and left only dark and

Text-figures 1-7.—1. Tangential section of the Silurian stromatoporoid, *Clathrodictyon djupvikense* Mori, showing an astrorhizal canal associated with a marginal wall (Inst. of Geol. Stockh. Univ. Strom. Coll. no. 104),  $\times 10$ . 2,3. Devonian stromatoporoid, *Stromatoporella saginata* Lecompte, showing thickened skeletons surrounding the astrorhizal canals; 2, Vertical section; 3, Tangential section;  $\times 3$  (After Lecompte, 1951, pl. 23, figs. 1-3). 4,5. Devonian stromatoporoid, *Anostylostroma subcolumnare* Galloway and St. Jean, showing thickened pillars in mamelon columns; 4, Vertical section; 5, Tangential section.  $\times 10$  (After Fagerstrom, 1982, pl. 5, figs. 8, 9). 6. A Recent scleractinian coral, *Acropora* sp., showing thickened skeleton surrounding axial corallites,  $\times 3$  (Inst. of Geol. Paleont. Sendai, coll. cat. no. 44829). 7. A Recent scleractinian coral, *Dendrophyllia micranthus* (Ehrenberg), showing gradients of coenosteal skeletal densities,  $\times 3$  (Inst. of Geol. Paleont. Sendai, coll. cat. no. 57428).



dense tissues. No comparable skeletal features are present in any Porifera.

### CONCLUSIONS

1. Poriferan affinity of the stromatoporoids is primarily based on similarity between exhalant canals of the sclerosponges and astrorhizal morphology of some stromatoporoids. It is true that the superficial morphology of exhalant canals observed in the living tissue of *Ceratoporella nicholsoni* shown by Hartman and Goreau (1970) is similar to that of the astrorhizae (Type A above) in some stromatoporoids. However, whether

these similarities prove conclusively the poriferan affinity of the stromatoporoids is still controversial.

Mori (1982) suggested that the relationship between astrorhizal canals and the surrounding skeletons in stromatoporoids is comparable to that between corallites and coenosteal skeletons in scleractinians and between zooidal tubes and surrounding skeletons in hydrozoans. The presence of marginal walls and tabulae in astrorhizal canals and skeletal thickening around astrorhizal canals in stromatoporoids may be regarded as homologous with similar features in the zooid/coenosteum relationship in Coelenterata.

2. Stromatoporoid skeletons show coelenterate affinities in the similarity of their gross structures to those of Recent hydrozoans (e.g., *Hydractinia* and *Millepora*) and to the coenosteum of plocoid and dendroid scleractinian corals. There is also great similarity in the skeletal microstructure between stromatoporoids and scleractinian corals.

3. The difficulty which the coelenterate affinity hypothesis encounters is the lack of direct evidence to explain the ramified astrorhizal canals which decrease in diameter toward their tips. The analogy of the astrorhizal canals of stromatoporoids and the hydrorhizae of hydrozoans was accepted by several authors (e.g., Carter, 1877; Nicholson, 1886), but Kaźmierczak (1969) and Stearn (1972) pointed out that hydrorhizae differ from astrorhizae in having canals of uniform diameter throughout their length. Since the stromatoporoids are extinct and possess many unique skeletal features, highly modified canal structures comparable to the hydrorhizae in function might have existed in the stromatoporoids. A simple explanation of the considerable variation in astrorhizal morphology ranging from Type A to Type C above is difficult but canals composed of vertical tubes (Type C) containing tabulae are more coelenterate than poriferan in character as has been suggested by Nestor (1981) in reference to heliolitids. The similarities between poriferan exhalant canals and some stromatoporoid astrorhizae are here regarded as the result of evolutionary convergence.

4. On balance, stromatoporoid skeletons show more important coelenterate features than poriferan features. If stromatoporoids are monophyletic then they are best included among the Coelenterata in which case the ramified astrorhizae probably mark the location of zooids. Thus, the stromatoporoids have their closest phylogenetic relationship with the hydrozoans, especially the milleporines. The chief difference is that the hydrozoans are polymorphic and there is no evidence of such in stromatoporoids.

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## ARCHAEOCYATHA: IS THE SPONGE MODEL CONSISTENT WITH THEIR STRUCTURAL ORGANIZATION?

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### ABSTRACT

The arguments advanced previously to include the Archaeocyatha within the Phylum Porifera employed superficial morphological similarities which do not correspond to the present state of knowledge. Two major errors are frequently found in previous studies. The first is the emphasis on the presence or absence of spicules as a definitive argument. The second is the direct comparison of fossilized skeletal structures with living, soft tissue. We base our arguments on the study of unusual recent sponges, the calcareous skeleton of which can be fossilized. The skeletal microstructure of the Archaeocyatha is constant and does not correspond to any known type of microstructure in calcified sponges. Nevertheless, there is such a great variety in microstructural types within calcified sponges that it is conceivable to consider archaeocyathan microstructure as one of their primitive forms. The Archaeocyatha belong to a single group, despite their considerable diversity of morphotypes. Analysis of functional morphology indicates that Archaeocyatha were filter-feeding organisms that functioned in the same way as sponges, *i.e.*, they were active filter-feeders and not passive ones, with the same direction of water flow as sponges. None of the structural features of Archaeocyatha is inconsistent with a sponge model, even those which have no equivalent in calcified sponges, such as complex porous channels or imperforated basal regions. Recent discoveries of Antarctic Archaeocyatha and Australian sphinctozoan sponges in Upper Cambrian rocks show that there is no stratigraphical gap between the two groups. We consider that there are no valid arguments against the inclusion of the Archaeocyatha within the Phylum Porifera.

### INTRODUCTION

Archaeocyatha have been interpreted to have affinities with many different groups of organisms (Table 1), but most frequently with sponges. In these interpretations there is a recurring tendency to: a) Attribute to preserved calcified features directly, the functions of soft non-fossilizable tissues; and b) Base the interpretations primarily on sponges with spicules without adequately taking into account living sponges with potentially fossilizable calcareous skeletons which, although minor today, were widespread in the past.

These calcified sponges are also characterized by a water filtering system of choanocyte cells—a system which could also be applied to Archaeocyatha. In particular, the comparison should focus on: a) functional morphology, b) structure of the skeleton, c) mode of life, and d) stratigraphic position.

### MORPHOLOGY OF A CALCIFIED SPONGE

Sponges are filter organisms, fitted with an aquiferous system the driving element of which is the choanocyte, a special, well-individualized cell in the Classes Calcarea and Demospongea, but partly syncytial in the Class Hexactinellida (Reiswig, 1979; Pavans de Ceccatty and Mackie, 1982). The small inhalant pores (generally about fifty micrometers in diameter) are placed on the outer part in the cup-shaped forms, contrary to the larger exhalant pores. In recent forms, the skeleton is essentially made of spicules, calcitic among the Calcarea, siliceous among the Hexactinellida and

Demospongea. Among the latter, it must be remembered that spicules are frequently absent and that usually in the above three classes the skeletal structures are only fossilizable when the spicules are fused with one another, *e.g.*, lithistid group among the Demospongea, dictyonines among the Hexactinellida and some pharetronids among the Calcarea. Most of the Recent forms are not fossilizable; when the skeleton, or part of the skeleton, is fossilized, the corresponding living structures do not leave any remains.

Some Recent forms regarded by some as a fourth class of Porifera (Sclerospongea, Hartman and Goreau, 1970; Ischyrospongea, Termier and Termier, 1973) possess a fossilizable solid calcareous skeleton, not built by spicules and when spicules are present, they do not have any major structural role. These "coralline sponges" are not frequent in the Recent; they contain features of relict forms and are commonly thought to be survivors of different Paleozoic to Mesozoic groups of reef builders (stromatopores, sphinctozoans, chaetetids). These coralline sponges were not very well known at first. Their existence was debated even when the main evaluations of the relationships between Archaeocyatha and sponges were first established (see Okulitch and de Laubenfels, 1953). Therefore, discussions have to be resumed taking the new data into account. It is now known in particular that calcareous skeletons which are not built by spicules are present within the Porifera; in some cases (sphinctozoans), the living tissues are located in the chambers delimited by the skeleton.

The main features of the known forms are summarized in Table 2. The great variety of these few sponges must be emphasized, in considering the living tissues as well as the composition and the type of formation of the calcareous skeleton (Vacelet, 1979–1983).

From this variety and the obvious similarities with numerous non-calcified Recent sponges, we conclude that the forms listed in Table 2 have to be classified in different groups of the classes Calcarea and Demospongia (Table 3).

### MORPHOLOGY OF AN ARCHAEOCYATHAN

Archaeocyatha were marine organisms with calcium carbonate skeletons. Remains of their cups are found in carbonate shelf and reef environments of the Early Cambrian seas. A few representatives of the Family Archaeocyathidae persist through the Middle Cambrian into the Upper Cambrian (Debrenne *et al.*, in press).

The basic skeleton of Archaeocyatha is relatively simple: an individual "cup" comprising two coaxial inverted generally porous cones (the walls) connected by more or less radial and sometimes horizontal elements (Zhuravleva, 1960; Debrenne, 1964; Hill, 1972).

The worldwide distribution of Archaeocyatha within the Lower Cambrian has suggested that they had planktonic larvae which cannot be seen in the fossil record. Changes during the development of the skeleton provide useful indications on the hierarchy of characters that may be used for systematics. At the beginning of the development, there is a one-walled cup with no pores, attached to the substratum by a solid sole. Two ways are thus possible: 1) in Regulares, the cup is rapidly perforated, radial rods appear and then the inner wall; septa, tabulae also are developed. Complexity appears sooner in the outer wall than in the inner wall; 2) in Irregulares, the imperforate cup persists during a period variable in time and the inner cavity is filled by dissepiments and disoriented rods or plates. Complexity of walls appears late in development and never reaches the variety displayed in Regulares. The rods, circular in section, are later associated in three directions forming a dictyonal network (Pl. 1, fig. d); the plates build wavy pseudosepta. Dictyonal types of Irregulares are very similar to some sponges (Pl. 1, fig. c).

In both the Regulares and the Irregulares, the pores of the outer wall are smaller than the pores of the inner wall (Pl. 2, fig. c).

## STRUCTURE OF THE SKELETON

### Dimensions

The dimensions are similar in Archaeocyatha (mean diameter 20 mm, height 50 mm) and sphinctozoans; the sphinctozoans are sponges which bear the most striking similarities with Archaeocyatha (mean diameter 10–20 mm, height 50 mm). Exceptionally, the maximum size of an archaeocyathan cup reaches 600 mm in diameter or 500 mm in height although they are only of 400 mm maximum in sponges.

### Form

Slightly more variety exists among Archaeocyatha than sponges in the shape of the conical skeleton which ranges from a cylinder to a saucer or sheet. Sponges, especially Sphinctozoa, are frequently cylindrical; no fusiform individuals are known in Archaeocyatha. Sheetlike forms are not known among sphinctozoans but are common among non-segmented sponge taxa (*e.g.*, *Goreauiella* and numerous fossil groups such as stromatoporoids). Spherical forms are rare in Archaeocyatha and are present only in small taxa (Globosocyathina); they are well known (not in the Sphinctozoa) among other calcified sponges such as *Astrosclera*. Segmentation in superposed chambers is the rule in the polyphyletic sphinctozoans and also in both Regular (Putapacyathida, Coscinocyathida) and Irregular (Archaeosyconida) Archaeocyatha (Pl. 1, figs. a, b). It is perhaps in these forms that the most abundant and fruitful comparisons can be made between sponges and archaeocyathans.

### FUNCTIONAL MORPHOLOGY

Both Archaeocyatha and Sphinctozoa have a similar basic design, a double perforated wall with a central cavity. However, several differences occur: a) There is a more clearly defined opening of the central cavity in the majority of the Archaeocyatha although it may not be discerned in *Agastrocyathus* and is filled in *Prismocyathus*. b) The interwall structures are predominantly vertical in Archaeocyatha and horizontal in Sphinctozoa. c) In the Archaeocyatha, the pores are generally different in both size and shape between the two walls whereas they are generally similar in the Sphinctozoa, with a few exceptions such as *Vaceletia progenitor* (Pickett, 1982).

### MODE OF LIFE

#### Calcified Sponges

Water flows through the external pores (generally about 50  $\mu\text{m}$  in diameter within the cells), circulates by active pumping to the interior and leaves through

Table 1.—Place of Archaeocyatha in the organic world.

Author and date	Systematic assignment	Taxonomic rank	Reasons for placing in this group
Billings (1861)	Zoantharia-Perforata (corals)	Genus	External form; presence of septa
Dawson (1865, 1875)	?Protozoans	Genus	Presence of chambers
Meek (1868)	Foraminifera or giant Protista	Genus	Presence of chambers
Zittel (1880)	Sponges	Genus	Presence of central cavity
Roemer (1880)	Receptaculites as sponge	Family	Same construction of the intervallum; porous skeleton
Bornemann (1884, 1886)	New class of Coelenterata	Class	Septa comparable to those of <i>Cyathophyllum</i>
Hinde (1889)	Zoantharia Sclerodermata	Family	Perforation similar with those of perforated corals
von Toll (1899)	Close to Siphonales Acetabularia	Family	"Cells" and central cavity
Taylor (1907, 1910)	Separate group intermediate between Porifera and Coelenterata	Class	Principal features are sometimes similar to sponges and sometimes to corals
Broili <i>in</i> Zittel (1915)	Sponges	Family	Central cavity and pore system
Douvill� (1915)	Sphinctozoans	Genus	External form of the skeleton and arrangement of chambers
Gordon (1920)	Independent group near to sponges	Class	Cf. Taylor
Grabau (1922)	Corals	Class	Morphological similarities
Hekker (1928)	Calathium	Genus	General features of external form
Vologdin (1931)	Porifera	Class	External form of cup; central cavity and porous skeleton
Raymond (1932)	Porifera or intermediate forms between corals and sponges	Class or phylum	Cf. Taylor
Okulitch (1935)	Porifera (Cyathospongia)	Class	External form of cup; central cavity and porous skeleton
Okulitch (1937)	Porifera (Pleospongia)	Class	External form of cup; central cavity and porous skeleton
Vologdin (1937)	Extinct group close to sponges	Sub-phylum (type)	Porous skeleton with different evolution than sponges
Ting (1937)	Siliceous sponges	"Tribe"	Presence of siliceous spicules (misinterpretation)
Simon (1939)	Siliceous sponges	Superfamily	Same error than Ting
Bedford (1936–1939); Okulitch (1940–1943)	Pleospongia	Class	External form of cup; central cavity, porous skeleton
Vologdin and Zhuravleva (1945); Vologdin (1952); Okulitch and de Laubenfels (1953)	New taxonomic group	Phylum	Absence of spicules in the construction of chambers
Vologdin (1948); Yakovlev (1954)	Spongiomorph ancestor of the corals	Phylum	"Central organ" in the central cavity of the calice
Zhuravleva and Rezvoi (1956)	The most primitive type among multicellular organisms: "blastea"	Phylum	Multiforms; similarities with the most simple animals in the construction of the skeleton
Zhuravleva and Rezvoi (1956)	Hypothetic ancestor of metazoans: Haeckel's blastea	Phylum	Multiforms; similarities with the most simple animals in the construction of the skeleton

Table 1.—Continued.

Author and date	Systematic assignment	Taxonomic rank	Reasons for placing in this group
Zhuravleva (1960)	Hypothetic ancestor of metazoans: Haeckel's blastea	Class within a primitive independent phylum	The most simple among multicellular organisms with porous calcareous skeleton. 3 "classes": Euarchaeocyathi (Cambrian), Aphrosalpingoidea (Upper Paleozoic), Sphinctozoa (post-Paleozoic)
Debrenne (1964)	Type of primitive organism	Phylum	Convergence to many groups without a single dominant affinity
Hill (1965)	Type of primitive organism	Phylum	Convergence to many groups without a single dominant affinity
Beklemishev (1964)	Organisms not included within the major subdivisions of animal kingdom	Superdivision of metazoans within a new subkingdom	3rd subkingdom different from the Enantiozoa (Porifera) and Enterozoa (Coelomates)
Khalfina and Yavorskii (1967)	Stromatoporoids	Subdivision	Morphological similarities of some forms
Termier H. and G. (1968)	Development arrested at the blastula stage	Phylum	Monoblastic individuals
Zhuravleva (1970)	Development arrested at the blastula stage	Archaeozoa with superphylum Archaeocyatha	Group of primitive organisms with two walls
Zhuravleva and Miagkova (1970, 1972)	Development arrested at the blastula stage	Part of Archaeata (Archeozoa pre-occupied)	Comprises the Euarchaeocyatha (Cambrian), Radiocyatha (Cambrian), Receptaculitida (Ordovician to Permian) and Aphrosalpingata (Silurian). Different development stages to those of the sponges
Balsam and Vogel (1973)	Porifera	Class	Passive filtering system similar to sponges
Oepik (1976)	Chlorophycean algae	Class	Impossible to reconstruct a water circulation model compatible with an animal
Termier H. and G. (1979)	Ischyrosponges	Class Irregulares (in part)	Choanocyte stage reached in several forms
Wendt (1980)	Sponges	Class	Porous calcareous skeleton
Nitecki (1982)	Calcareous algae	Class	Organizational plan
Bondaref (1982)	Calcareous algae	Class	Mode of growth related to light

the osculum (*i.e.*, the central siphon in sphinctozoans). Passive circulation, if it occurs, involves only a very slight percentage of the water filtered (Vogel, 1977).

#### Archaeocyatha

Considered filter feeders by most authors; however, opinions differ as to the direction of water flow. Vogel has tested an aluminum model, constructed by Balsam, which is a scale representation of the archaeocyathan skeleton (Balsam and Vogel, 1973; Vogel, 1977). In this model, each of the two walls has holes drilled through it but the vertical and horizontal partitions do not have pores, a situation which does not exist in Archaeocyatha (Pl. 2, fig. e).

The true relative surface area of pore-space to skeleton has not been strictly followed in these models. The minimum size of external pores (20–30  $\mu\text{m}$ ) is not compatible with the passive flow model of Balsam and

Vogel but would be functional with an active pumping mechanism such as that possessed by sponges.

Zhuravleva has proposed a different model based upon a particularly well-preserved thin section (Zhuravleva and Elkina, 1974, pl. 2, fig. 1) which contains calcified membranes that fill each vertical loculus and bend outwards towards the exterior. This latter feature led the authors to deduce that the current must have been pushed from the central cavity outwards and then have passed out through the pores in the outer wall.

However, the "membranes" are only hard parts, similar to the vesicular horizontal plates (tabulae) and they do not necessarily reflect the exact position of the soft parts when under pressure from the water current.

In fact, among syconid sponges the concavity of the radial tubes (non-skeletonized) is in the opposite sense to that of the water current (Pl. 2, fig. d, a sycon). If the current direction directly influenced the orientation of the curvature of the tissues then all pores in sponges

Table 2.—Characters and affinities of living sponges with a solid calcareous skeleton. (Note that only two of them belong to the Class Calcarea; the others are calcified demosponges.) (After Vacelet, in press.)

	<i>Murrayona</i> (1 species)	<i>Petrobiona</i> (1 species)	Ceratoporellidae (6 species)	<i>Astrosclera</i> (1 species)
Spicules	Calcareous, free. Class Calcarea, Calcinea	Calcareous, free. Class Calcarea, Calcaronea	Siliceous, in part enclosed in skeleton. Demospongea, affinities Agelasidae	As Ceratoporellidae. May be absent in the Pacific forms
Calcareous skeleton and mode of formation	Calcite, reticulate. Spherulitic and trabecular. Formation ?	Calcite, massive. Spherulitic and trabecular. Formation ?	Aragonite. Penicillate spherolithes. Formation ?	Aragonite. Spherulitic, regular. Formation: intracellular
Trace of aquiferous system on skeleton	Yes	No	Yes, astrorhizae	Yes, astrorhizae
Affinities according to the soft parts	Calcarea, subclass Calcinea	Calcarea, subclass Calcaronea	Demospongea, affinities Agelasidae	Demospongea, affinities Agelasidae
Reproduction	Calcarea, subclass Calcinea	Calcarea, subclass Calcaronea	?Perhaps Demospongea subclass Ceractinomorpha for 1 sp.	Demospongea, Ceractinomorpha
Rich symbiotic microflora	No	No	Yes	Yes
Resting bodies	No	Yes	No	No
Geographic distribution	Indopacific	Mediterranean	5 Caribbean spp., 1 Pacific sp.	Indopacific
Corresponding fossil groups	? Probably some pharetronids (inozoan)	? Probably some pharetronids (inozoan)	Triassic Ceratoporellidae and some inozoan pharetronids	Some stromatoporoids and inozoans

would be housed on concavities, which is not the case. Thus, Zhuravleva's argument does not hold up in view of the arrangement of soft parts in living sponges which actively filter water.

If one accepts the Archaeocyatha as filtering organisms, then the above system is not functional; the extremely small pores of the outer wall will be rapidly choked by particles coming through the larger pores of the inner wall. In addition, the central cavity will also be rapidly choked up by an accumulation of particles too large to be evacuated by the pores of the inner wall. No such system of filtering is known in living animals.

Rozanov derisively presented a non-functional model in which the inhalant current was presumed to pass through both outer and inner walls and the exhalant to leave by the upper part of the intervallum (Rozanov, 1973, p. 77, fig. 100). It has not always been realized that this flow pattern is dynamically impossible.

Apart from sponges there are few organisms which possess a large number of external pores. Examples are unicellular Foraminifera and to a lesser degree calcareous algae. An obvious question to ask is do the pores of archaeocyathans function as conduits of water? If not, what function could they have?

One line of investigation is to compare archaeocyathans with known organisms having porous skeletons, e.g., a) Openings for pseudopodia in unicellular, syncytial forms; b) Genital openings in calcareous algae, such as corallinaceans and dasycladaceans.

The difference in size and form between outer and inner wall pores and the presence of porous structures in the intervallum (septa, tabulae, taeniae and rods) make no sense in any of these hypotheses. Furthermore, it is difficult to imagine the role of pseudopodia (in a, above) in the interior of the central cavity or in the intervallum. As for the second hypothesis (b, above), the large number of openings, their size, and their regular arrangement in archaeocyathans do not seem appropriate for a reproductive function, particularly if one compares them to the distribution of pores of living calcareous algae.

We fall back then to the most plausible hypothesis, that of an active filtering organism. This mode of functioning (directed current with pumping) is compatible with that of sponges, that is, flow in through the pores of the outer wall to irrigate the soft tissues of the intervallum and then evacuation through the central cavity.



Table 2.—Continued.

<i>Vaceletia</i> (1 species)	<i>Calcifibrospongia</i> (1 species)	<i>Merlia</i> (1 species)	<i>Acanthochaetetes</i> (1–3 species)
Absent	Siliceous, in part enclosed in skeleton. Demospongea, Ceractinomorpha	Siliceous, free. Demospongea with uncertain affinities	Siliceous, free. Demospongea, Tetractinomorpha (Spirastrellidae)
Aragonite, external. Stacking of microcrystals. Mineralization of a non collagenous matrix	Fibro-radiated aragonite. Mineralization of a collagenous matrix	Calcite and aragonite. Vertical trabeculae. May be absent. Formation ?	Calcite. Stacking of microlamellae. Formation ?
Yes, pores and siphon	Yes, astrorhizae	No, tabulae	Yes, astrorhizae. Tabulae
Demospongea, Ceractinomorpha	Demospongea, ?	Demospongea, Tetractinomorpha	Demospongea, Tetractinomorpha
Demospongea, Ceractinomorpha	?	?	?
Yes	?	No	No
No	No	Yes	Yes
Indopacific	Caribbean	Circumtropical and Mediterranean	Pacific Ocean
Some sphinctozoans	Mesozoic stromatoporoids	Stromatoporoids	Chaetetidae and some Tabulomorpha

### MICROSTRUCTURE OF THE SKELETON

In calcified sponges as in archaeocyathans, the skeleton is calcareous and not spicular. In the calcified sponges, the skeleton can be either calcitic or aragonitic with various microstructural types: a) either centered or asymmetric spherulites, b) a felt of entangled microcrystals, or c) stacking of microlamellae. These microstructures are formed by either intracellular secretion (centered spherulites) or extracellular secretion (various types of microstructure) (Debrenne and Lafuste, 1970; Lafuste and Debrenne, 1977; Dieci *et al.*, 1977; Cuif *et al.*, 1979; Wendt, 1979).

There is good correlation between skeletal microstructure and the systematic grouping of living types, also taking into account other characters (type of spicule, living tissue; cf. Table 2). By contrast there has been no correlation between microstructural characters and habitat. The skeleton is even more varied in fossils. In the Triassic, the aragonitic skeleton is preserved intact. When there was diagenesis, it never destroyed or fundamentally modified the basic microstructure except in a few cases where the skeleton has been replaced completely by silica.

Spicules, which in living forms may be siliceous or calcareous, are either completely absent or free in the

soft parts (and thus not fossilized) or successively trapped in the skeleton by its growth. Even in this last case fossilization is highly uncertain because dissolution is rapid and may take place even during the life of the sponge. In some fossils, traces of the spicules remain (Dieci *et al.*, 1977).

In archaeocyathans the original skeleton was apparently calcite, with a microstructure formed of polyhedral microgranules which are equidimensional, have embossed surfaces, and are interlocked. There are no spicules. Several different granule types are recognized either by their size or density of interlocking depending on whether there is primary skeleton with coarse granules or vesicular tissue and secondary thickening developed in successive laminae covering the primary skeleton and filling up the chambers, rendering them non-functional. This secondary layer is finer grained and smoother. This type of skeletal microstructure is not known in living or fossil calcified sponges, but this alone does not justify completely separating the two groups.

It is not possible to know by simple inspection of the skeleton the manner in which it was secreted by the living animal. One can assume that, as in *Vaceletia* (pro *Neocoelia* which is preoccupied), secretion proceeds by rapid mineralization of a primary organic

Table 3.—A classification of modern sponges listing only those with solid calcareous skeleton, including some indications of their affinities to fossil groups. Stromatoporoids and sphinctozoans can be seen to have affinities with ceractinomorph demosponges, while the “tabulates” have affinities with tetractinomorph demosponges. These speculations concern particularly systematic and phylogenetic studies, but are also relevant to other disciplines such as paleobiogeography. Larval dispersal is weak in sponges, but particularly in tetractinomorphs which are oviparous. Incubated larvae of ceractinomorphs have a free swimming life of about 2–3 days (after Vacelet, in press).

CLASS HEXACTINELLIDA	{ No known calcified form		
Siliceous spicules with 3 axes			
CLASS CALCAREA	{ —Subclass Calcinea —Subclass Calcaronea	: Murrayonidae (1 sp.)	: ? Pharetronid sponges (in part).
Calcareous spicules		: Petrobionidae (1 sp.)	: ? Pharetronid sponges (in part).
CLASS DEMOSPONGEA	{ —Subclass Homoscleromorpha —Subclass Tetractinomorpha —Subclass Ceractinomorpha	: No known calcified form	
		Acanthochaetetidae (3 spp.)	: Chaetetidae and some Tabulomorpha.
		Merliidae (1 sp.)	: Uncertain affinities with tabulates and stromatoporoids.
		Ceratoporellidae (6 spp.)	: Pharetronid sponges (in part).
Siliceous spicules with 1 or 4 axes		Astroscleridae (1 sp.)	: Stromatoporoids (in part).
		Cryptocoelidae (1 sp.)	: Sphinctozoans (in part).
		Calcifibrospongiidae (1 sp.)	: Stromatoporoids (in part).

template. This assumption is hypothetical in our present knowledge; it is based on the similarities of *Vaceletia* and *Archaeosyconida*, and extended to the other members of the group.

#### Secondary Structures

In both calcified sponges and archaeocyathans, there occur infillings of chambers formed by the skeleton; some of the infillings are secreted during life and reinforce the basal skeleton which has been abandoned by the animal.

Among living calcified sponges these infillings are the rule but less so among fossil forms. In archaeocyathans secondary thickening of the skeleton (described above) extensively chokes the loculi rendering them either completely dysfunctional or that part of the calice partially so if some connections remain open. It is this situation which was described by Zhuravleva in demonstrating “proof” of the reversed flow of water in archaeocyathans (see above). The microstructure of the infilling tissue may be either similar to or different from the primary skeleton in calcified sponges, but in archaeocyathans the microgranules are smaller than those of the primary skeleton.

#### Exostructures

These structures are absent in living calcified sponges unless the external extra covering known from the base of *Vaceletia*, or epithecae present in various forms are considered a particular type of exostructure. In fossil sponges in the Triassic there are, exceptionally, exostructures known from sphinctozoans (Pl. 2, fig. a). This type of exostructure is very close to that in archaeocyathans (Pl. 2, fig. b). In archaeocyathans, exostructures are common and in great variety; they are interpreted as anchoring processes or growth surfaces and they can build significant amounts of skeletal tissue between calices, functioning like coenosteum (Debrenne and James, 1981, p. 362, pl. 51, fig. 1).

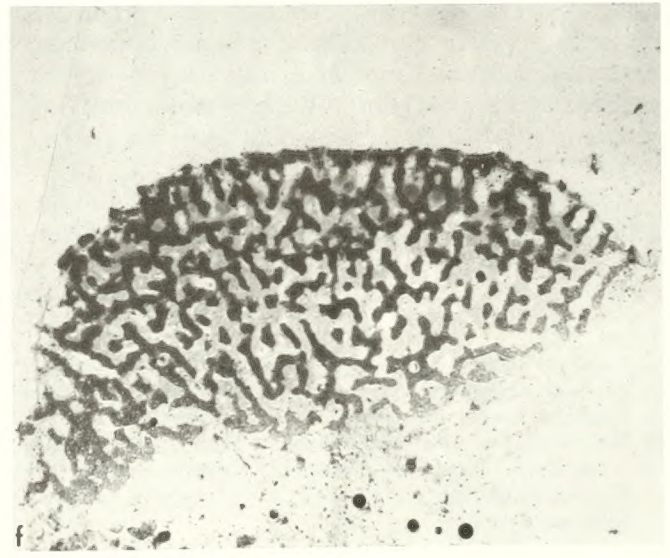
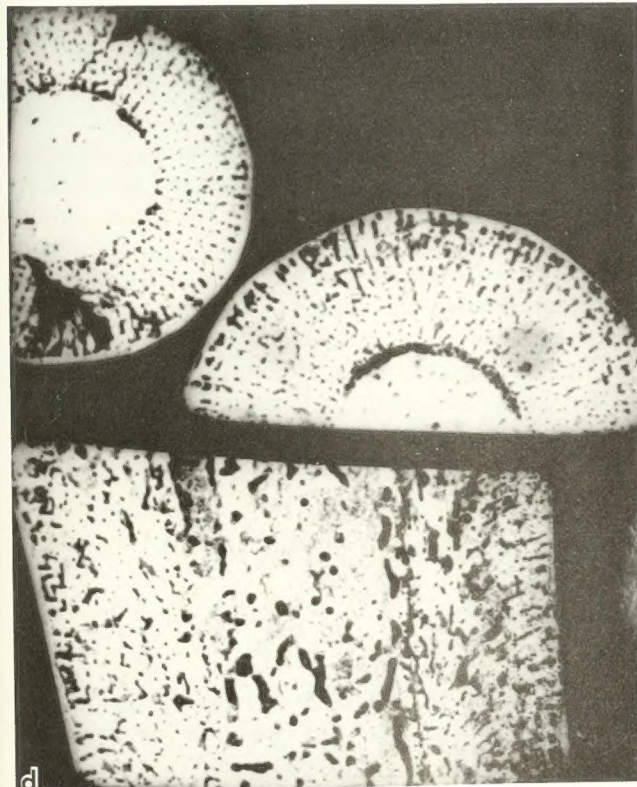
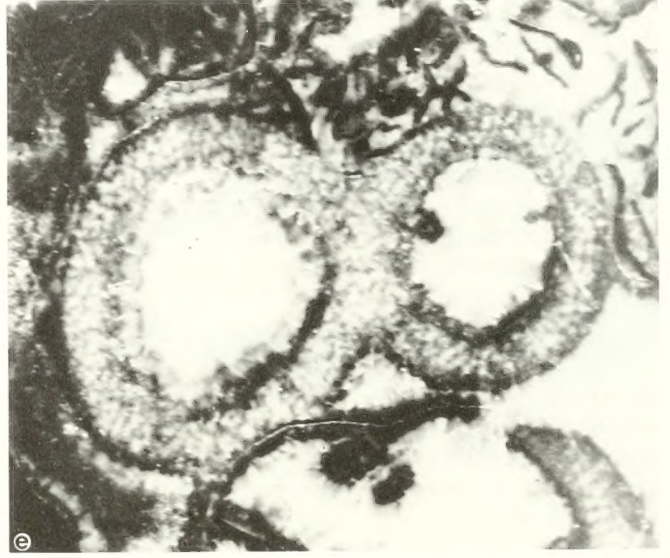
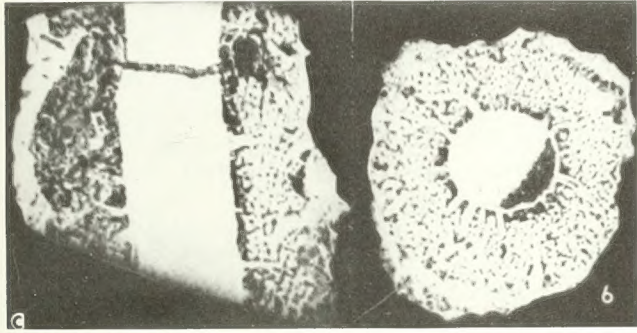
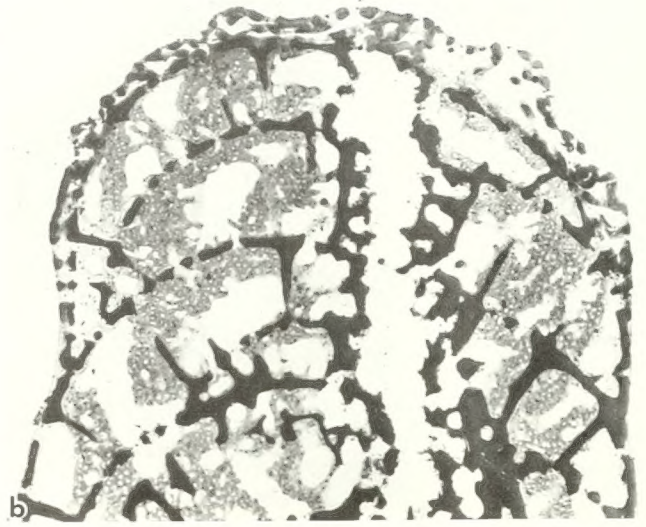
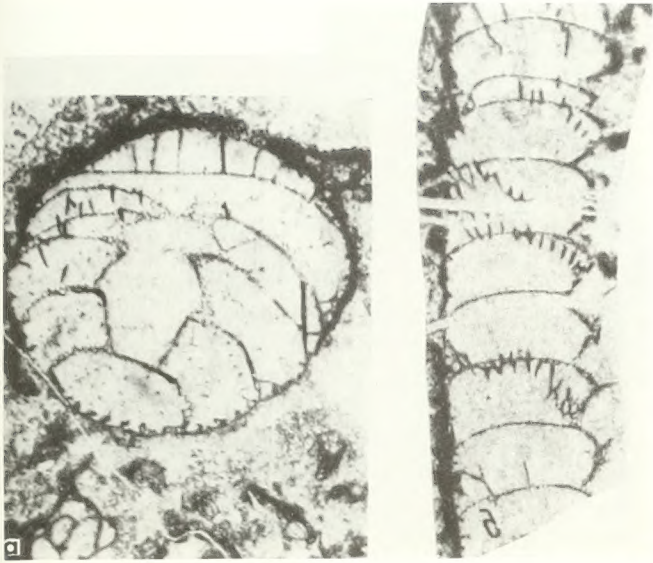
#### BUDDING-REGENERATION

The possibility of budding and regeneration of partially broken (“wounded”) skeletons occurs in both sponges and archaeocyathans. In archaeocyathans, budding is the way colonial forms develop either in series (Regulares) or as arborescent forms (Irregulares). In lesions, regeneration occurs after isolation of the area by membranous vesicular tissue and reconstruction often of structures different from that of the orig-

#### EXPLANATION OF PLATE I

Figure

- Vertical successive chambers in an archaeocyathan. *Tabulacyathellus bidzhaensis* Missarzhevsky, Lower Cambrian, U.S.S.R. × 5.6. After Missarzhevsky, 1964
- Vertical successive chambers in a sphinctozoan. (Note the living tissue inside the chambers and the formation of a new apical chamber.) *Vaceletia crypta* (Vacelet), Recent, Indian Ocean. × 30. After Vacelet, 1979
- Dictyonal framework in a demosponge. *Coelocladia spinosa* Girty, Pennsylvanian, U.S.A. × 5. After Girty, 1908
- Dictyonal framework in an archaeocyathan. *Dictyocyathus translucidus* Zhuravleva, Lower Cambrian, Siberia. × 6. After Zhuravleva, 1960
- Reticulate skeleton in an archaeocyathan. *Antarcticocyathus* Debrenne and Rozanov, Upper Cambrian, Antarctica. × 5. After Debrenne, Rozanov and Webers, in press
- Reticulate skeleton in a living calcified demosponge. *Astrosclera willeyana* Lister, Recent, Pacific Ocean. × 15. Original



inal calice and generally more simple. Rebuilding of the initial calice generally occurs after a certain period of growth.

In calcified sponges, regeneration occurs by means of specialized cell masses similar to gemmules, the existence of which is known in some living forms *e.g.*, *Merlia* (Vacelet, 1980), *Acanthochaetetes* (Vacelet, 1983) and is assumed to have occurred in certain fossil taxa.

#### ONTOGENETIC DEVELOPMENT OF THE SKELETON

Developmental stages in the ontogeny of Archaeocyathans can be known only from the beginning of skeleton formation. The base of the archaeocyathan skeleton had no pores; in sphinctozoans they are clearly developed even though sometimes overgrown by secondary deposits once the basal chambers had become non-functional (see above).

Another developmental difference concerns the order of appearance of the walls. In *Vaceletia*, and thus in at least some sphinctozoans, new chambers appear everywhere together. The chamber and siphon walls (corresponding to the outer and inner walls respectively) as well as the pillars (intervallum structures in archaeocyathans) all appear simultaneously.

In Archaeocyatha the outer wall is formed first, then the intervallum structures and then the inner wall. This bears on the problem of the functioning of the archaeocyathan during the early stages of fixation, if one assumes the active filtration mode of life. There would have been no mural pores in the outer wall during quite a long period of early growth, sometimes up to 5–7 mm high. Perhaps at this stage, during secretion of the basal skeleton, there was functioning non-skeletalized tissue above it.

Secretion of the basal skeleton would have used considerable larval reserves. When they were exhausted the archaeocyathan must then have begun to build the functional skeleton. In sphinctozoans the very earliest growth stages are not known. We know from the living *Vaceletia* that the larvae are small and with few reserves.

It should be noted that in calcified sponges and the sphinctozoans, the development of the carbonate skeleton

does not fundamentally alter the functional morphology of the sponge. For example *Merlia*, which does not always possess a skeleton, functions in the same manner with or without skeleton (Vacelet, 1980). This at least suggests that the proposed model for the early functioning of the archaeocyathan is plausible.

#### STRATIGRAPHIC POSITION

##### Archaeocyatha

They first appeared at the very beginning of the Cambrian and then rapidly diversified during the Middle Lower Cambrian. Regulares, after an explosion of forms with complex walls, become extinct at the end of the Lower Cambrian. Irregular forms, with a less elaborate skeleton that is more convergent with sponges, continued to survive, by virtue of some 'relict' taxa belonging to the Family Archaeocyathidae, throughout the Middle and into the Upper Cambrian.

##### Calcified Sponges

The first appearance of sponges with calcified skeletons goes back as far as the Cambrian with forms doubtfully attributed to stromatoporoids (*Korovinella*) and sphinctozoans (?*Amblysiphonella*, *Blastulospongia*; Pickett and Jell, 1983).

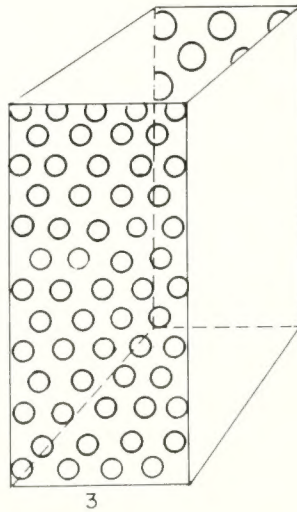
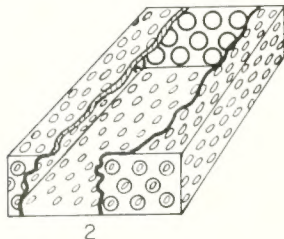
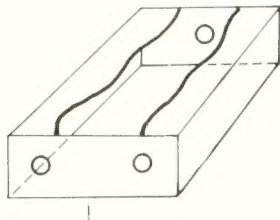
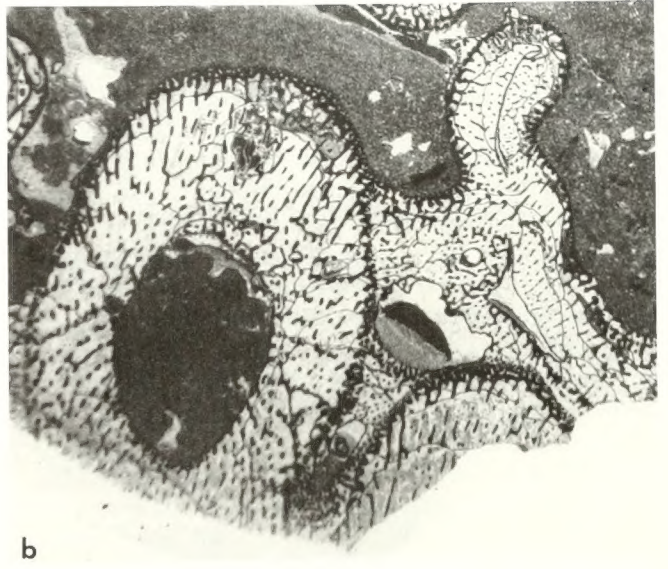
The polyphyletic group of sphinctozoans is well-developed from the Carboniferous to the end of the Cretaceous; some relicts are present in recent seas. The stromatoporoids have two times of expansion: Paleozoic (Ordovician to Middle Carboniferous) and Mesozoic (Jurassic to end of the Cretaceous). No fossil remains have yet been found in between; some forms are still living. Chaetetids are present from the Ordovician, expanding through the Paleozoic and part of the Mesozoic, and disappearing at the end of the Cretaceous; one genus persists today. The Ceratoporellidae have their acme in the Mesozoic; only six forms are still present. Among the Calcarea, pharetronids have the same stratigraphic range (Mesozoic); two genera have survived to the Recent.

The Recent forms are not able to give a proper idea of the variety and of the extension in space and time of such a large Paleozoic and above all Mesozoic flourishing group as were the calcified sponges.

#### EXPLANATION OF PLATE 2

Figure

- a. Exothecal tissue in a sphinctozoan. Triassic, Turkey.  $\times 2$ . Coll. Cuif (Université d'Orsay). Original
- b. Exothecal tissue in an archaeocyathan. Lower Cambrian, Australia.  $\times 3$ . Coll. Kruse. Original
- c. Regular archaeocyathan with microporous outer wall. Lower Cambrian, Australia.  $\times 8$ . Coll. Kruse. Original
- d. Non-fossilizable radial organization in a recent sponge. *Sycon sycandra*, Mediterranean.  $\times 25$ . Original
- e. 1. Element for a functional model of Archaeocyatha with imperforate septa and tabulae. After Balsam and Vogel (1973). 2. Element for a functional model of Archaeocyatha with perforate septa and tabulae (*Coscinyathus*). 3. Loculus of Ajacicyathid with imperforate septa and no tabulae



e

## CONCLUSIONS

The arguments put forward until recently to demonstrate either the closeness or the separateness of the sponges and Archaeocyatha have each made reference to a particular feature or structure and not to an assessment of the characters combined overall. In these arguments the structures were chosen for their apparent contrasts or similarities. Furthermore, these arguments are rather outdated as they were based on knowledge now more than fifteen years old and during this time both groups have been subject to intense study. The earlier works placed great weight on the presence or absence of spicules when deciding to attach, especially the Archaeocyatha, to the sponges. This concept has been reappraised in detail in this article.

Another common source of error in the earlier works was to compare, directly, the skeletal structure of archaeocyathans with the functioning non-calcified soft parts (choanocytes, chambers, *e.g.*) of sponges, a risky and doubtful method of argument (Pl. 2, figs. b,e).

The problem is here taken up again but based upon a study of living forms in which the calcareous skeleton is well-known so that interpreting it as a paleontologist (who usually has only the skeleton to study), one can also subject the functional interpretation to current biological tests. Thus, systematic study of the microstructure of the skeleton can become a diagnostic tool equal in importance to the more classical biological data.

Analysis of the different archaeocyathan skeletal morphologies (herein) has sought to establish whether or not a viable sponge model is possible. The resemblances have been known for a long time and are often striking, *e.g.*, with sphinctozoans, Archaeosyconina, *Gerbicanaecyathus* (Regulares) and with other calcified sponges, *Dictyosyconina* (Pl. 1, figs. a-d). However, even though archaeocyathans form a morphologically varied group, no argument can be made to split off one of the taxonomic units to make a polyphyletic group *e.g.*, with descendants like Radiocyatha and dasycladacean receptaculitids, an enigmatic group (Soanitida) and the sponges. The unity of the archaeocyathans is based primarily upon their microstructure, their general organization, the existence of transitional forms between major groups and the stages of regeneration.

The diverse and complex array of archaeocyathan skeletal structures can be broken down into a few basic types with the Archaeocyathidae found in the Upper Cambrian as a 'relict' survivor. Fossil calcified sponges never attained the level of elaboration of some of the more complex regular Archaeocyatha at the end of the Lower Cambrian, just before their demise, but they parallel the trend towards simplification demonstrated

by the archaeocyathans in the Upper Cambrian. In living sponges the calcified skeleton has been largely replaced by a spicular or collagenous one except in a few relict forms. A functional morphological analysis of the two groups strongly suggests that the archaeocyathans were filtering organisms using active pumping to force currents through the organism in the same manner as sponges. No specific anatomical feature of the archaeocyathans, even those with no known equivalents in calcified sponges such as complex wall canals and the non-porous initial stages, contradicts this hypothesis.

The "stratigraphical gap" which was formerly evoked to separate the Archeocyatha and the calcified sponges has been removed by new discoveries in the Upper Cambrian of archaeocyathans in Antarctica and sphinctozoans in Australia (Debrenne *et al.*, in press; Pickett and Jell, 1983).

Can the proposition of similar modes of life for archaeocyathans and sponges suffice to place them both in the same phylum? In favor is the fact that the majority of modern authors place within the Porifera all syncitial forms with a filter mode of life, such as Hexactinellida (Reiswig, 1979), which are as far from sponges *sensu stricto* as are archaeocyathans.

It would, therefore, not be unreasonable to propose that the Archaeocyatha should be included in the Phylum Porifera.

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THE ECOLOGY AND PALEOECOLOGY OF THE SCLEROSPONGIAE  
AND SPHINCTOZOA (*SENSU STRICTO*): A REVIEW

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ABSTRACT

Living sclerosponges and the sphinctozoan *Vaceletia crypta* are confined to tropical reef communities, except for *Merlia normani* which also occurs in the Mediterranean. Most fossil sclerosponges and sphinctozoans were also members of reef communities, but a few inhabited level-bottoms. Cryptic habitats in water 20–100 m deep are most common for living sclerosponges and *V. crypta*; very few of their fossil ancestors were cryptic and their common association with abundant and varied algae in Late Paleozoic and Triassic reefs indicates shallow water. The predominance of aragonite in living sclerosponge and sphinctozoan skeletons, coupled with their tropical shallow water occurrence, indicates that warm water (>25°C) is another important influence over their distribution. Generally high turbulence and low turbidity in cryptic habitats also minimize water circulation problems from sediment deposition on the sponge surfaces.

Near Jamaica, sclerosponges are subordinate to Scleractinia in depths less than 70 m where they sporadically encrust rocky surfaces, but at 70–105 m sclerosponges are the chief reef constructors where they may cover up to 50 percent of the surface. Middle Permian Sphinctozoa functioned in three ways in reef communities: 1) dense entanglements of thin-walled digitate forms acted as baffles and sediment traps, 2) thick-walled, cup- to vase-shaped forms were most important in frame construction, and 3) sheet-like forms were encrusters and sediment binders. In Middle and Late Triassic reefs, some Sphinctozoa continued to function as baffles and traps, others with small, blister-like chambers and chamber-filling pillars, struts and vesiculae, were important frame constructors and still others encrusted hardgrounds and bound skeletons and sediment into the framework. Triassic Sclerospongiae functioned primarily as binders, but locally were important constructors. The reduced importance of both sclerosponges and sphinctozoans in post-Middle Triassic reef construction appears to be related to the rise of the Scleractinia and the thermodynamic efficiency of their symbiotic association with zooxanthellae.

INTRODUCTION

The rediscovery of sponges with massive aragonitic skeletons and siliceous spicules living in Jamaica, their comparison with extinct stromatoporoids (Hartman and Goreau, 1966) and their subsequent assignment to a new class (Hartman and Goreau, 1970, 1972) has aroused considerable interest among both biologists and paleobiologists. Since 1966 there have been a great many papers dealing with the morphology of several previously described species as well as new ones belonging to the Class Sclerospongiae, comparisons of their biological affinities not only with the Stromatoporoidea, but with other paleontologically important, extinct major taxa and discussions of their paleoecologic significance.

Most of the taxonomic and morphologic comparisons have centered on the old problem of the affinities of the stromatoporoids, especially whether they were indeed sponges (first suggested long before 1966) or whether they were coelenterates. Solution of this problem also has important paleoecological consequences because of the sharply different trophic levels of the microphagous herbivorous sponges and the partially macrophagous carnivorous coelenterates. Stromatoporooids, chaetetids and other even more enigmatic fossils are present in many ancient communities and before their paleoecologic significance and the trophic structure and other feeding relationships of the com-

munities to which they belong can be interpreted, their biologic affinities must be determined. However, such problems no longer exist for the fossil sclerosponges and sphinctozoans; the discovery of living species of these taxa permits much more direct comparison of their ecology and paleoecology.

The purposes of this paper are to review the autecology and synecology of the living sclerosponges and sphinctozoans and compare them with the paleoecology of their ancestors as interpreted from the fossil record; emphasis is placed on presumed shifts in their ecological functions (guild placement) during geologic history and possible causes for these shifts.

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AUTECOLOGY

Biogeography

The distribution of the major taxa (Text-fig. 1) indicates the general association of sclerosponges and sphinctozoans with the world tropical reef belt; the presence of *Merlia* spp. in the Mediterranean is the



Table 1.—Frequency of reported habitats of living Sclerospongiae and Sphinctozoa (species listed in Fig. 2).

Habitats	Frequency of Reported Occurrences		
	Atlantic	Indo-Pacific	Miscellaneous
Caves, grottos, caverns	4	*6	1
Tunnels	1	3	—
Canyons, crevices, fissures, rock walls	2	4	2
Under coral or rock ledges	3	—	—

\* Includes the sphinctozoa *Vaceletia crypta*.

only exception. They are notable for their absence in the major areas of upwelling (eastern margins of ocean basins), the northern Indian Ocean and Florida, where the water may be too cold (Dustan *et al.*, 1976). The Tabulospongida are confined to the Pacific, the Merliida (*Merlia* spp.) are the most cosmopolitan and the Ceratoporellida are the most diverse and reported from the most localities.

#### Habitats

Although previous authors have used a variety of terms to describe the habitats of sclerosponges and sphinctozoa (Table 1), they are in general agreement that they grow best in darkness or subdued light (cryptic). Hartman (1980) has suggested that because sclerosponges lack zooxanthellae they are commonly out-competed (overgrown) by hermatypic scleractinians and thus confined to cryptic habitats from which the hermatypes are excluded. At depths of about 100 m sponges grow at least as rapidly as scleractinians. Thus, differ-

ences in sclerosponge and scleractinian growth rates appear to be major biologic controls over the bathymetric distribution of sclerosponges as well as their functions in reef communities.

#### Depth

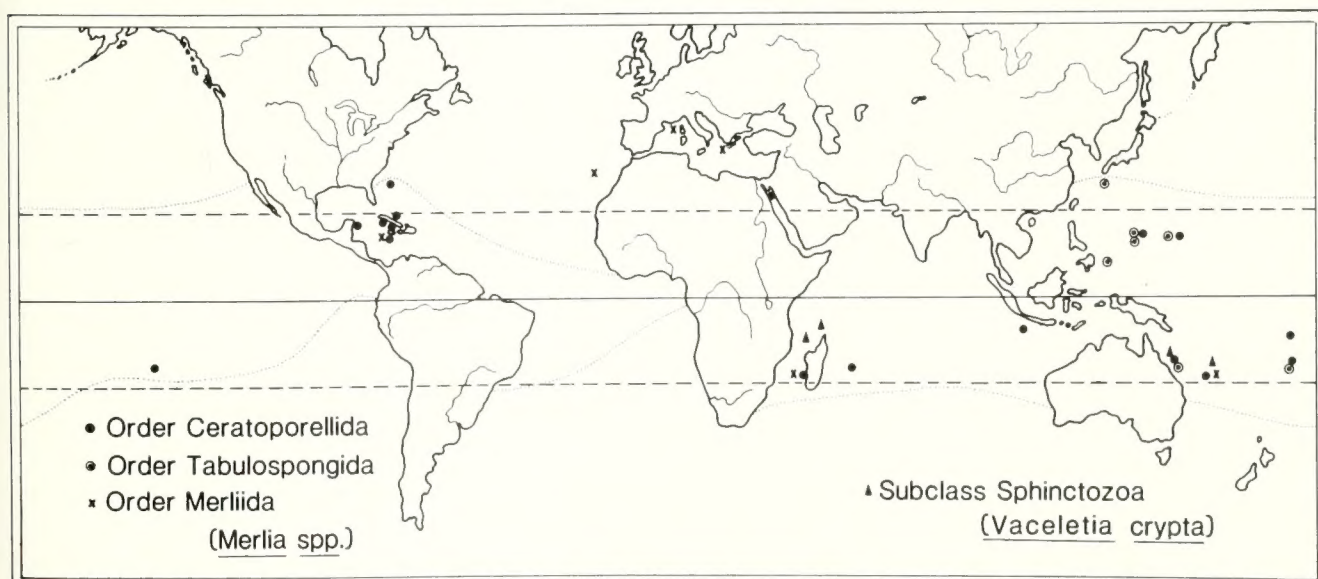
The data of Text-figure 2 clearly indicate that the Indo-Pacific sclerosponges and sphinctozoa live in much shallower water than those of the Atlantic and that the Tabulospongida are generally shallower than the Ceratoporellida. The vertical range of *Astrosclera willeyana* exceeds all other species, except perhaps *Ceratoporella nicholsoni*. Of the fourteen extant species, only about half extend below about 100 m. Thus, all species are cryptic and have successfully entered these habitats even where they exist in shallow water.

The lack of staggered bathymetric ranges and optima among the diverse co-existing sclerosponge species near Jamaica suggests that interspecific competition is not an important control over their occurrences. Sarà (1970) also noted the general lack of inter-specific competition among other co-existing sponges.

#### Temperature

The absence of sclerosponges and sphinctozoa in areas of upwelling cold water and the predominance of aragonite rather than calcite in the rigid parts of their skeletons suggests that water temperature exerts an important influence on their distribution both geographically and bathymetrically.

Lang (1974) and Hartman (1980) have described the general vertical temperature profile near Jamaica. The following three zones can be recognized:



Text-figure 1.—Biogeography of the living sclerosponges (dots, dots within circles, crosses) and sphinctozoa (triangles). The area between the dotted lines contains the modern reefs where surface water temperatures are at least 21°C.

a. Temperatures are remarkably stable ( $\cong 27\text{--}28^\circ\text{C}$ ) in the upper 105 m. Sclerosponge diversity is maximal (6 species) and all species attain their maximal density and size (Text-fig. 2).

b. Between 105 and 125 m there is a weak thermocline with temperatures of about  $26\text{--}27.5^\circ\text{C}$ . Although there are five sclerosponge species here, only *Ceratoporella nicholsoni* is abundant.

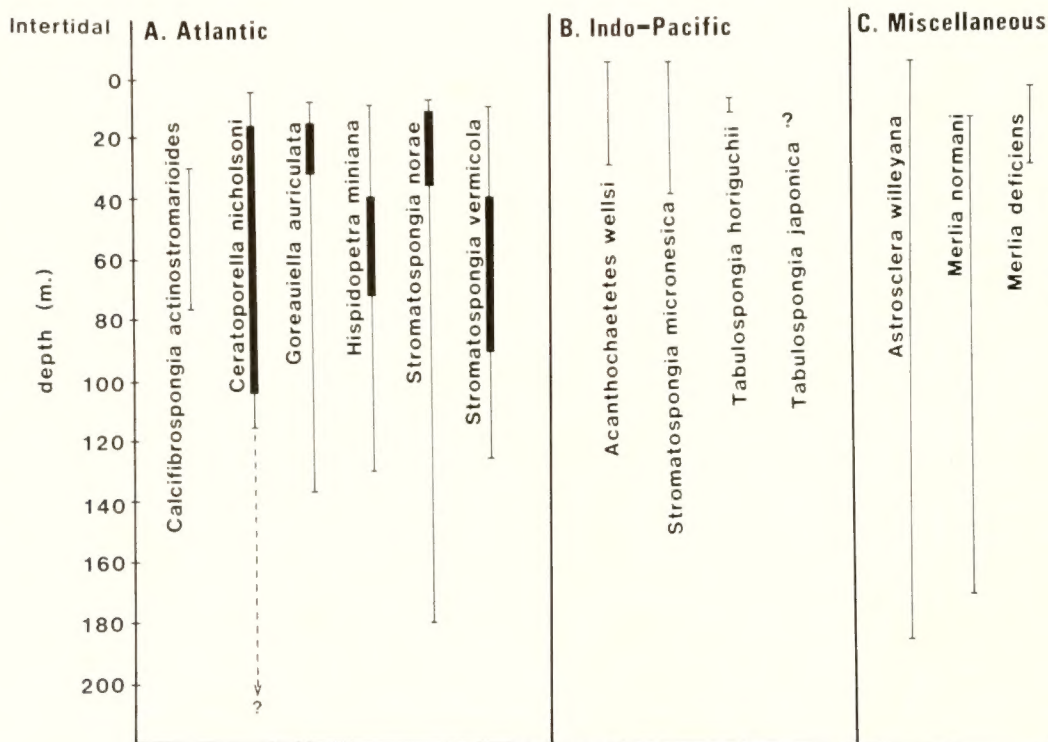
c. From 125 to 200 m there is a relatively uniform decrease in temperature with depth from about  $26^\circ\text{C}$  to about  $23^\circ\text{C}$ . Four sclerosponge species live here; none is abundant and only one (possibly two) species occurs below about 130 m in water colder than about  $25^\circ\text{C}$ .

Hartman (1980) suggested that the top of the thermocline is an important control over the lower bathymetric limit of sclerosponges; however, the presence of four of the six shallow water species below the thermocline casts some doubt on the ecologic importance of the thermocline. The restriction of sclerosponges and sphinctozoans to tropical waters where thermoclines are generally weak also suggests that their lower bathymetric limits are not as strongly influenced by a steep temperature gradient as by the overall need for warm water ( $>25^\circ\text{C}$ ).

### Sedimentation: Turbidity

Sclerosponges and sphinctozoans are typical of most living sponges in having a low tolerance to highly turbid water from which sediment is deposited on their surface and may also enter the canal system. Dustan and Sacco (1983) believed that sclerosponge species vary in their tolerance to turbulence and turbidity and have noted that highly turbid water may result when divers enter caves containing sclerosponges. In the Jamaican fore-reef, promontories jutting out from the cliff are covered by loose sediment rained down from above, but are encrusted by *Ceratoporella* sp. on their undersurfaces (Hartman, 1973). In cases where sedimentation has killed sclerosponges, the skeleton is commonly encrusted by coralline algae and hermatypic scleractinians in shallow water and by demosponges in deeper water.

Because of the usual low turbulence/low turbidity relationship that exists in sheltered and recessed habitats and in deep water, one of the major physical environmental controls over sclerosponge and sphinctozoan distribution may be turbidity; turbulence and depth may have only indirect influence.



Text-figure 2. — Bathymetry of the thirteen species of extant sclerosponges and one species (*V. crypta*) of extant sphinctozoan. The sclerosponge orders and the included genera are: Order Merliida (*Merlia*), Order Tabulospongida (*Acanthochaetetes*; *Tabulospongia*) and Order Ceratoporellida (the remaining genera). Optimum depths, where known, indicated by thickened bars.

SYNECOLOGY

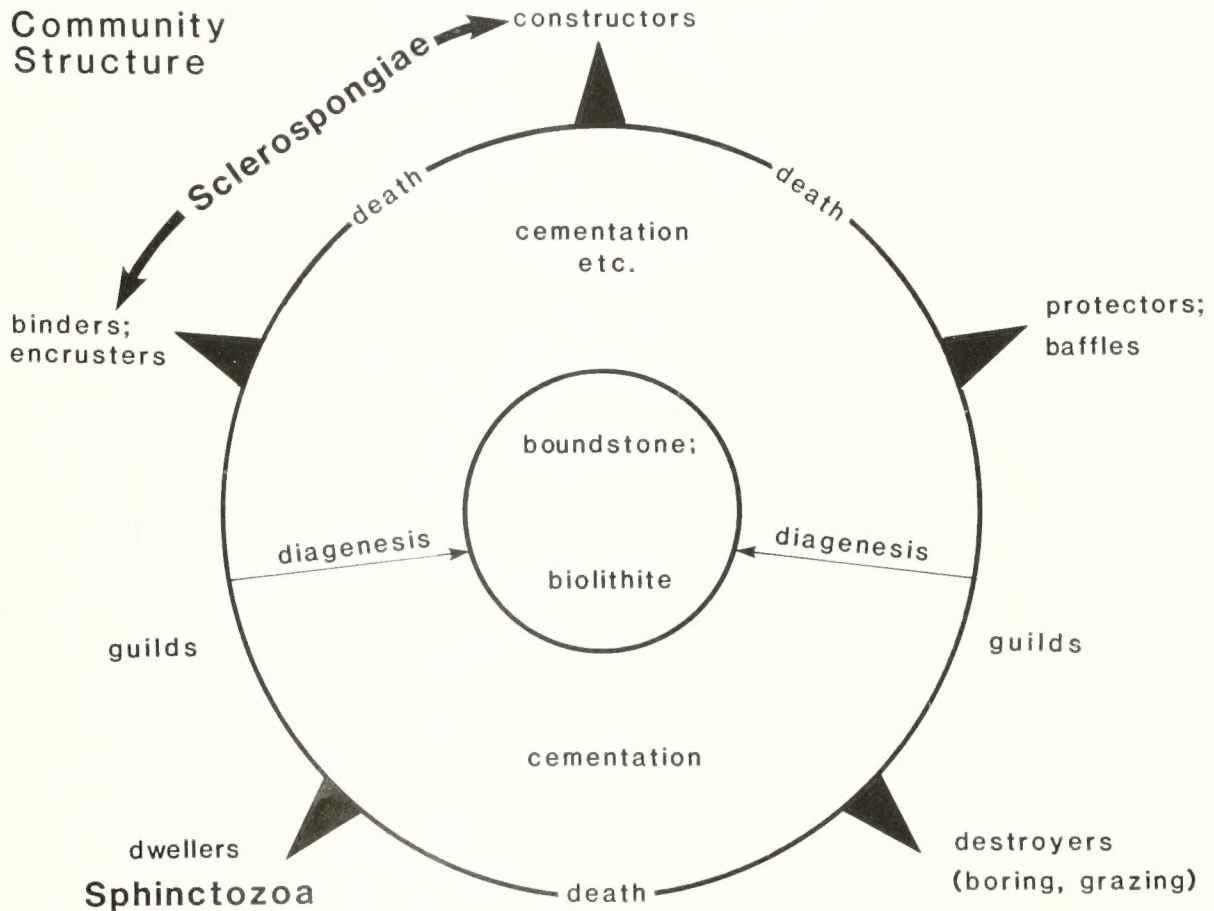
Guild Structure

The exceedingly complex functional relationships among species in taxonomically diverse Holocene reef communities may be simplified by subdividing the community into major functional units or guilds (Root, 1967). Each guild contains several species and each such species contributes to the same overall function in the community. By contrast, niches are confined to single species.

Previous authors have disagreed on the numbers and names of the guilds in Holocene as well as in ancient reef communities. In the scheme discussed below, the present author recognizes five guilds (Text-figs. 3-5): constructors, binders/encrusters, dwellers, destroyers and protectors/baffles. The constructors are commonly the largest organisms in the community and thus provide volume to the reef framework, the dwellers are the most diverse and the binders/encrusters are im-

portant in maintaining the constructors in their growth positions in the turbulent reef environment. The function of the protectors/baffles is to reduce turbulence and destruction of the reef and enhance the accumulation of sediment within the framework.

The functional roles (guild placement) of the sclerospoges in Jamaican reef communities vary with depth. In the shallow waters of the main fore-reef escarpment and fore-reef slope (0-55 m), construction of the framework is dominated by hermatypic scleractinians, *Montastera* spp. above 50 m and *Agaricia* spp. below. Although both sclerospoges and sphinctozoans are present in shallow waters such as these, neither group is abundant except in local cryptic habitats. Most of the cave-, tunnel-, fissure-dwelling, etc. (Table 1) sclerospoges encrust the surfaces of corals and rocks and bind skeletons and sediments to the coral-built reef framework (Text-fig. 3); only rarely do they contribute to frame construction (Dustan and Sacco, 1983). Skeletons of *Vaceletia crypta* are too uncommon to be



Text-figure 3.—Community structure of Holocene reef communities (outside outer circle) showing the major functional units (guilds) to which the Sclerospongiae and Sphinctozoa belong. Shallow water sclerospoges encrust hardgrounds and bind skeletons and sediments to the framework constructed by hermatypic scleractinians. Near Jamaica in water 70-105 m deep sclerospoges construct the reef. Sphinctozoa are so rare that they play no important rôle in reef construction or in baffling/binding of sediment; they are dwellers.

significant contributors to frame construction, binding or baffling; thus, *V. crypta* is a reef dweller. At Discovery Bay, Jamaica, there is a nearly vertical cliff with numerous caves, tunnels and promontories at 55–145 m depth. The assemblage of organisms encrusting these surfaces is dominated by demosponges, crustose coralline algae and sclerosponges, in order of decreasing importance. Hermatypic corals remain the chief constructors on sloping surfaces to depths of about 70 m.

From 70–105 m the reef is constructed by sclerosponges (chiefly *Ceratoporella nicholsoni*); hermatypic corals and algae are present but rare (Text-fig. 3). Sclerosponges are most abundant in the cliff recesses where they may cover up to 50% of the surface; they are present also in lesser abundance in more exposed locations such as under promontories and ledges. The approximate base of the photic zone for zooxanthellae and the top of the thermocline at about 105 m marks the lower bathymetric limit of the true reef community.

#### Community Composition

Goreau (1959) has listed and described the distribution of the hermatypic scleractinians in the shallow waters (0–15 m) off the north coast of Jamaica. Although these corals completely dominate this part of the reef, the upper bathymetric limits of five sclerosponge species occur here as well as a surprisingly high density and diversity of brachiopods (one terebratulacean, two thecideaceans and one craniacean; Jackson *et al.*, 1971). The brachiopods are important to depths of at least 55 m and extend in fewer numbers to the deeper sclerosponge-built portion of the reef (70–105 m).

The non-framebuilding associates in the sclerosponge-built reef also include antipatharians, gorgonaceans, hermatypic and ahermatypic corals, *Halimeda*, hydroids, comatulids, decapods, urchins, ophiuroids, Bryozoa, encrusting Foraminifera, cemented bivalves, serpulids, and lithistid sponges (Lang, 1974; Lang *et al.*, 1975).

Below about 105 m the seafloor is covered by reef-derived debris encrusted by demosponges, coralline algae and sclerosponges (especially *Ceratoporella nicholsoni*; the other species are rare).

In New Caledonia and the Glorious Isles (Malagasy Republic), *Vaceletia crypta* (Text-fig. 1) lives in association with both sclerosponges (*Acanthochaetetes wellsii*; *Astrosclera willeyana*) and more typical spicular/fibrous sponges (Vacelet, 1979). Hartman (1977) has also described the great importance of reef-dwelling sponges in Holocene Caribbean reefs. Although in Jamaica the sclerosponges play very important roles in both the reef construction and binding guilds, it was

the Sphinctozoa that dominated construction and binding in Permo-Triassic reef communities.

#### PALEOECOLOGY: GENERAL

The presence of Holocene sclerosponges and sphinctozoa in tropical reef communities noted above is also a characteristic of their fossil distribution. [Although siliceous sponges may occur in reef communities, they are relatively uncommon (Rigby, 1971), and only rarely do they contribute significantly to reef construction; cf. Gwinner, 1976.] The Sphinctozoa were major contributors to the construction of Permian reefs in North America and Triassic reefs in Europe. These occurrences were within the tropical Tethyan belt.

Among Holocene sponges there is also a general bathymetric division between deep, cold water (100–1000+ m) assemblages containing only siliceous taxa and shallower, warmer water assemblages (0–100 m) including both siliceous (especially Heliospongiidae; Demospongia) and calcareous taxa (Finks, 1960; Reid, 1968). This same division appears to also exist in the fossil record, *i.e.*, the calcareous sponges were confined to the shallower and presumably warmer water and reached their optima in the upper 50 m (Reid, 1968). Furthermore, the common close association of the Sphinctozoa with a variety of fossil calcareous and non-skeletal algae lends additional support to their apparent restriction to shallow water.

Thus, the conclusion is inescapable that warm water was an essential requirement for fossil sclerosponges and sphinctozoa just as it is for their living descendants.

#### PALEOECOLOGY: SCLEROSPONGIAE

The recognition of fossil sclerosponges is made difficult by the mineralogic instability of their siliceous spicules before and during diagenesis of the adjacent aragonite (Hartman, 1977, p. 131) or hi-Mg calcite (Friedman *et al.*, 1976; Land, 1976; Rützler and Macintyre, 1978). The only fossil sclerosponges described thus far that contain spicules (and these are calcite pseudomorphs presumably after the original silica) are from the Lower Cretaceous of southern Poland (Kaźmierczak, 1974). Cuif (1973) described aragonitic skeletons from the Triassic of northern Italy with regularly arranged pits in the calicle walls that he regarded as cavities that contained the original sclerosponge spicules. Wendt (1975) described aragonite specimens (either stromatoporoids or sclerosponges?), also from the Triassic of the Italian Alps, that lack spicules but have irregularly arranged pits (questionably ascribed by Wendt to boring algae) that may have been spicule cavities. Kaźmierczak (1979) reviewed some other uncertain fossil sclerosponges.

Table 2.—Composition of a Late Carboniferous level-bottom (evenly bedded wackestone) community, Midcontinent region, U.S.A. (after Toomey, 1979).

Algae		
* <i>Archaeolithophyllum missouriense</i>		<i>Cuneiphycus</i>
<i>Tubiphytes</i>		"oncolites"
Foraminifera		
* <i>Tetrataxis</i> spp.	<i>Reophax</i>	* <i>Hyperammina</i> spp.
<i>Ammovertella</i>	<i>Calcivertella</i>	
<i>Apterrinella</i>	<i>Tolypamma</i>	
Sphinctozoa		
* <i>Cystauletes mamilosus</i>		<i>Girtyocoelia</i>
Rugosa		
<i>Dibunophylloides</i>		
Ectoprocta		
fistuliporids	acanthocladids	diploporarids
polyporids	fenestellids	
pennireteporids	septaporids	
Brachiopoda		
* <i>Ambocoelia</i>	<i>Juresania</i>	<i>Neochonetes</i>
<i>Cliothyridina</i>	<i>Leptalosia</i>	<i>Heteralosia</i> (?)
<i>Crurithyris</i>	* <i>Composita</i>	<i>Lingula</i>
<i>Antiquatonia</i>	<i>Beecheria</i>	
Gastropoda		
<i>Euphemites</i>		
Other Taxa (mostly fragmented)		
Bivalvia	"sponge spicules"	Holothuroidea
Ostracoda	<i>Spirorbis</i>	conodonts
Crinoidea	Trilobita	
"fish"		

\* Abundant taxa.

The oldest fossil sclerosponges reported, thus far, are from small Upper Permian reefs in Tunisia (Termier *et al.*, 1977) where they are found in dense association with other calcareous sponges and both non-skeletal and calcareous algal crusts. The earliest record of sclerosponges playing an important role in frame construction is in the Middle Triassic (Ladinian) patch reefs of the southern Alps (Fürsich and Wendt, 1977). The Cretaceous sclerosponge reported by Kaźmierczak (1974, p. 341) was collected from reef-derived skeletal (algae, hydrozoans?, echinoderms, etc.) debris. These occurrences clearly indicate that the sclerosponges have been intimately associated with, or perhaps confined to, reef communities since at least the Late Permian. Their apparent absence from Lower Triassic and Lower Cenozoic rocks may simply reflect the general worldwide paucity of reefs of these ages (Newell, 1972). The reason for the absence of sclerosponges from Middle and Late Tertiary and Pleistocene reef communities is uncertain; perhaps increasing biologic efficiency of the zooxanthellae-scleractinian symbiosis allowed the scleractinians to over-grow and to out-compete the sclerosponges (Dustan and Sacco, 1983) except in deep water; deep water reefs are rare in the fossil record.

## PALEOECOLOGY: SPHINCTOZOA

### Cambrian to Devonian

Although the Sphinctozoa first appear in the fossil record in the Cambrian (Pickett and Jell, 1983), they are very rare in Early and Middle Paleozoic rocks (see Rigby and Potter, 1980; Pickett and Rigby, 1983; Rigby and Blodgett, 1983). These occurrences all suggest that early sphinctozoans were confined to level-bottom communities.

### Carboniferous

Sphinctozoans were relatively unimportant elements (dwellers) in Carboniferous reefs and banks built by various combinations of rugose corals, chaetetids, stromatolites (Ota, 1968), and phylloid algae (Toomey, 1980). However, in the Midcontinent region of the United States, Late Carboniferous (Desmoinesian to Virgilian) level-bottom (mudstone-wackestone) fossil assemblages locally contain abundant digitate sphinctozoans and the taxonomic diversity of these level-bottom communities (*e.g.*, Table 2) commonly exceeds the diversity of the adjacent banks (algal and chaetetid boundstone).

Many late Carboniferous sphinctozoans are coated by the phylloid (red?) alga *Archaeolithophyllum lamellosum* (Toomey, 1969, pl. 124, fig. 3; 1974, fig. 1c; 1975, figs. 3a, 4). In most cases, the failure of the first algal lamina to completely encircle the sponge suggests that the alga encrusted loose, dead fragments. Alternatively, the algae may have overgrown and killed the filter-feeding sponges by "suffocation," a process difficult to prove in the fossil record. Nonetheless, this common alga-sphinctozoan association in level-bottom carbonate substrates is excellent presumptive evidence for deposition in warm, shallow water. Wray (1964) and Toomey (1974, 1979) estimated the bathymetric range of *Archaeolithophyllum* spp. from low tide to about 15–30 m; perhaps by mere coincidence this lower limit is remarkably similar to the depth of the living sphinctozoan *Vaceletia crypta* ( $\cong$  15–38 m; Text-fig. 2).

### Permian

The Sphinctozoa reached their North American acme (both abundance and diversity) in the Middle Permian (Guadalupian) and their European acme in the Middle and Late Triassic (Ott, 1967, pp. 53–54). Finks (1960, p. 10) has noted the very low taxonomic turnover at the genus level in his system-to-system comparison of the Permian and Triassic sphinctozoan faunas and Wendt's (1980, p. 174) stage-by-stage compilation indicates their total absence from Lower Triassic rocks.

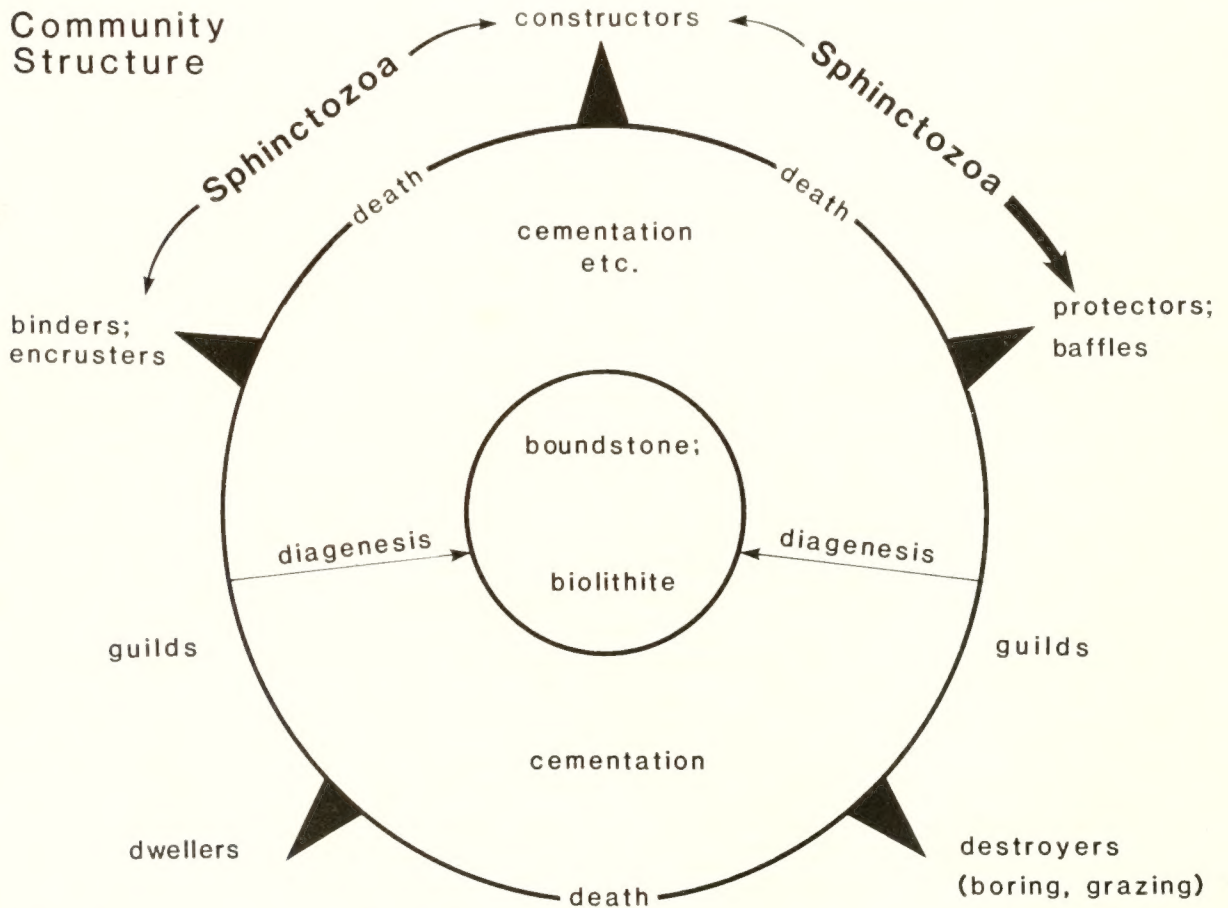
At the beginning of the Permian there was a sudden increase in the abundance and species-level diversity

of the Sphinctozoa (Finks, 1960, pp. 23–24) that coincides with the initiation of an extended reef-building episode marginal to the Delaware Basin in west Texas and New Mexico. The earliest Permian (Wolfcampian) reefs were relatively small but somewhat later (Leonardian) reef size began to increase and culminated in the extensive barrier reef system (Newell *et al.*, 1953) of the Late Middle Permian (Guadalupian  $\cong$  Kungurian). The Leonardian-Guadalupian also marks the dramatic rise in importance of two major features in sphinctozoan morphology and evolution: 1) abundant thick-walled, sheet-like and cup- to vase-shaped forms of the Family Guadalupiidae and 2) development of varied pillars, dissepiments and struts within the chambers. Pre-Leonardian sphinctozoans were thin-walled, digitate forms with open chambers lacking a cloaca or with a simple thin-walled cloaca.

The ecological role of the Sphinctozoa in the Middle Permian (Guadalupian) reefs in west Texas and New

Mexico has been disputed for years. However, there is no doubt that they were important members of the community now preserved in the thickest and most massive parts of the reef system. The Sphinctozoa in these rocks are here assigned to particular guilds (Text-fig. 4) on the basis of their overall growth form and their presumed structural ability to withstand breakage in the shallow, turbulent water of the reef crest. Thus, the cup- and vase-shaped guadalupiids strengthened by thick walls and internal pillars were the dominant sponge constructors (Finks, 1960; Rigby, 1971; Yurewicz, 1977). Other important constructors included the enigmatic algae? *Archaeolithoporella*, *Eugonophyllum* and *Tubiphytes* (Babcock, 1977; Toomey and Babcock, 1983, pp. 262–281; Yurewicz, 1977), inozoans, richthofenids and leptodids (Grant, 1971, pp. 1450, 1455).

In contrast, the more abundant, fragile digitate forms (*e.g.*, *Girtyocoelia*, *Amblysiphonella*) growing in dense



Text-figure 4.—Community structure of Middle Permian (Guadalupian) reef communities marginal to the Delaware Basin in west Texas and New Mexico showing the major functional units (guilds) to which the Sphinctozoa belonged. The thin-walled, digitate forms living in dense entanglements with the similarly shaped fenestellid Bryozoa and the dasycladacean alga *Mizzia* acted as baffles and traps to hold loose sediment. The cup- and vase-shaped forms with thick, tubular walls were important in the construction guild and sheet-like forms were binders and encrusters.

entanglements acted as sediment baffles and traps in much the same manner as the associated fenestellid Bryozoa, pelmatozoan columns and digitate algae (e.g., *Mizzia*). Finally, the sheet-like forms of *Guadalupia* probably functioned as encrusters and binders in concert with various calcareous algae of similar growth form.

Associated dwellers and destroyers included an enormous diversity of brachiopods, fusulinids, ammonites (Cooper and Grant, 1977, pp. 3163–3322), Bryozoa, Tabulata, Gastropoda (Yochelson, 1956, 1960; Batten, 1958) and siliceous sponges (Finks, 1960).

The work of Babcock (1977, 1983) and Yurewicz (1977) indicates that there are important temporal and lateral variations in the relative importance of the numerous forms of Guadalupian calcareous algae but no comparable work has been published on variation in the Sphinctozoa. Although sphinctozoans of both the constructor and binding guilds are abundant and closely associated in the massive rocks of the main reef, they were probably subordinate to the calcareous algae (*sensu lato*) in construction of the reef framework, at least during the Late Guadalupian. Coeval digitate algae and Sphinctozoa increase in abundance from the main reef toward the reef-to-shelf transition; the larger size and *in situ* position of many sphinctozoan clusters indicates that they are the dominant baffles. The much greater abundance of encrusting algae indicates that they were more important in the binding/encrusting guild than the sheet-like Sphinctozoa.

Contemporaneous deeper water benthic communities within the Delaware Basin were dominated by siliceous sponges (Finks, 1960); calcareous sponges are absent from these rocks. Newell *et al.* (1953, p. 190) estimated basinal water depths from about 5–10 m during the Early Guadalupian to nearly 600 m during the Late Guadalupian. This led Finks (1960, p. 25) to suggest that cold temperatures in deep water confined the calcareous sponges and other reef-builders to the warmer, shallow water of the basin margin. This same general bathymetric separation of siliceous (deep, cold water) and calcareous sponges (especially Sphinctozoa and Inozoa) also probably existed during the Jurassic (Arkell, 1935; Wendt, 1980). In contrast, there is a general similarity between the calcareous sponge faunas of the Guadalupian reefs and the adjacent shallow water shelf lagoon to the north (Finks, 1960, pp. 22–23).

The biologic association of sphinctozoans with sclerosponges appears to have begun in the Late Permian (Termier *et al.*, 1977) and has continued with varying degrees of closeness to the present.

During the Late Permian and Middle to Late Triassic there was increased development of sphinctozoans with small, densely packed blister-like chambers containing an even greater variety of internal structures (pillars, vesiculae and thickened cloacae) than previously. These features are present in Late Permian faunas of China (pers. comm., J. K. Rigby) and are of even greater importance in Middle and Late Triassic reef Sphinctozoa from the Alps (Ott, 1967, p. 65; Dieci *et al.*, 1968, pp. 105, 107, pl. 27–33).

### Triassic

The Early Triassic was a time of general world-wide restriction in reef development that coincides with the virtual absence of sponges having well-calcified non-spicular skeletons (Wendt, 1980, pp. 169–177).

During the Middle Triassic there was an important increase in the genus-level diversity of the Sphinctozoa (Ott, 1967, pp. 53–54). This also coincides approximately with the reappearance of numerous Inozoa, Stromatoporoidea and Sclerospongiae in the fossil record, the origin of the Scleractinia and numerous “spongiomorphs, tabulozoans, etc.” of uncertain biologic affinities and the advent of an important reef-building episode in Europe that continued to the end of the Triassic. The coincidence of the waxing of these numerous calcareous “sponges” (*sensu lato*) and the building of reefs is clear but the nature of the cause and effect relationship is uncertain. Nonetheless, the association between reef communities and well-calcified calcareous sponges was indeed intimate, perhaps even obligatory and self-reinforcing.

The newly evolved, diverse and structurally rigid Sphinctozoa (e.g., *Cryptocoelia*, *Vesicocaulis*, *Deningeria*) and those with more massive skeletons (e.g., *Uvanella*) were the chief constructors of Middle Triassic reefs (Text-fig. 5). Sphinctozoans with thin, encrusting skeletons (e.g., *Ascossymplegma*) functioned to bind the sediment and framework together whereas those with more fragile, digitate skeletons (e.g., *Amblysiphonella*, *Girtyocoelia*) acted as sediment baffles in the same manner as their Permian congeners. All of these forms are also present in Upper Triassic reefs but the Sphinctozoa have now been supplanted by the Scleractinia as the chief constructors (Fischer, 1969; Flügel, 1981, pp. 344–345).

The Alpine Triassic reefs vary enormously in size (1–1000 m thick; Bosselini and Rossi, 1979). The taxa involved in construction as well as their relative proportions also vary considerably among reefs as well as from place to place in the same reef as exemplified below:

a. In the Middle Triassic Seelandalpe patch reef in northern Italy, Fürsich and Wendt (1977) and Wendt (1980) have clearly distinguished between species diversity changes in dominance of major taxa in an ecological sere. The corals (30 species) and sclerosponges (32 species) are the most diverse. The pioneer constructing guild was dominated by stromatoporoids; sclerosponges and sphinctozoans were not important. The intermediate stage was dominated by inozoans, sclerosponges and sphinctozoans and the climax assemblage was predominantly encrusting Foraminifera, Sphinctozoa and Sclerospongiae. The most diverse taxa of reef dwellers were the gastropods (58 species), bivalves, especially epibyssate forms (29 species), brachiopods (19 species) and echinoderms (17 species). Fürsich and Wendt (1977, p. 259) have estimated total reef and inter-reef macro-invertebrate diversity at about 1000 species. Brachiopods were the predominant reef dwellers at Seelandalpe followed by gastropods and bivalves; echinoderms were rare.

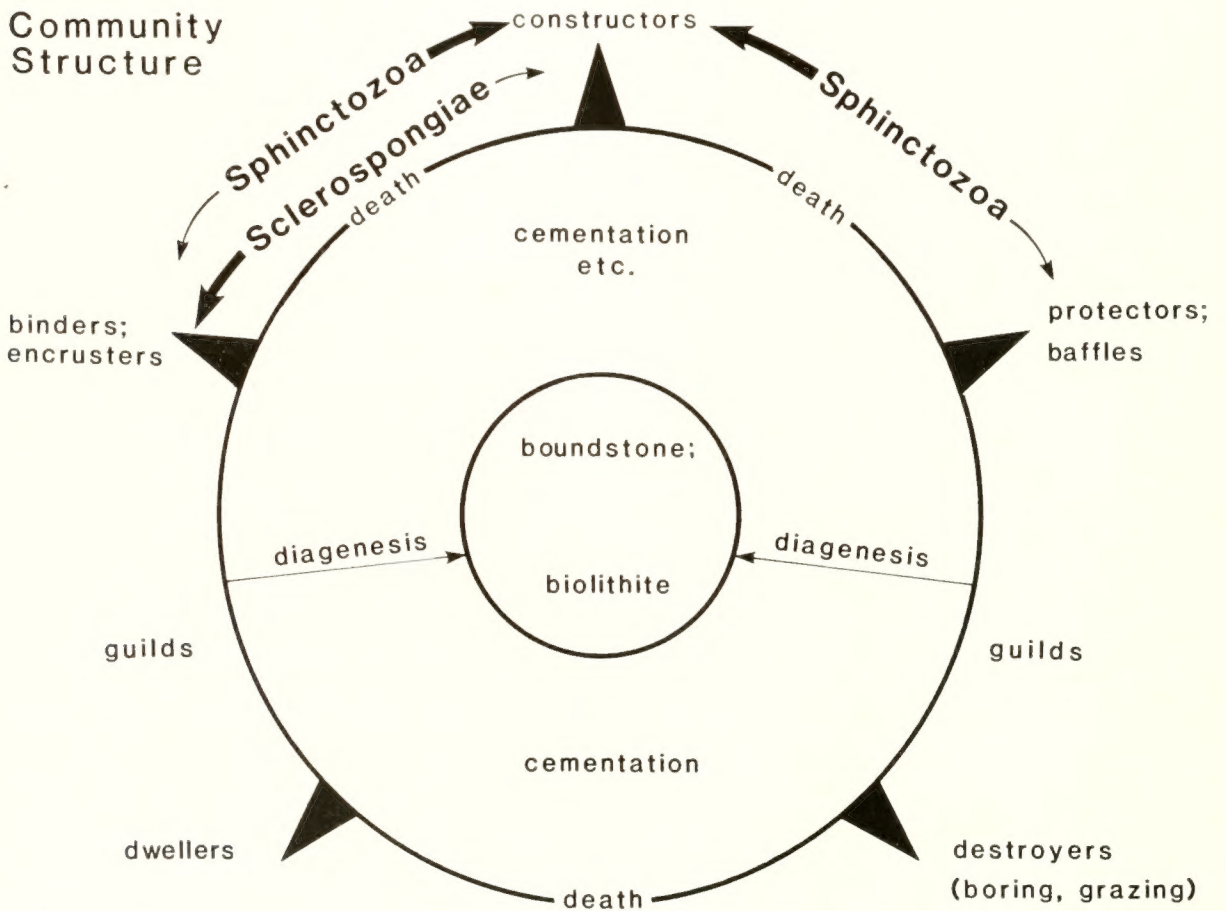
b. In reefs spanning the Middle–Upper Triassic boundary near Innsbruck, Austria, Bradner and Resch (1981) consider corals to be the dominant constructors, especially near the reef margins. The Sphinctozoa chiefly encrust the coral framework and the interiors of reef cavities.

c. In the Upper Triassic Steinplatte reef near Salzburg, Austria, the sphinctozoans are of only minor importance as constructors but are abundant as encrusters in both the near-reef slope and lagoon (Piller, 1981).

Post-Triassic

All aporate Sphinctozoa and nearly all of the forms with internal chamber-filling structures became extinct at the end of the Triassic; Jurassic and Cretaceous species (a few were spicular) are morphologically similar to those of the Late Carboniferous (Ott, 1967). This abrupt extinction of most sphinctozoans coincided with another general collapse in the organization

Community Structure



Text-figure 5.—Community structure of Triassic reef communities in the Alps showing the major functional units (guilds) to which the Sphinctozoa and Sclerospongiae belonged. Thin-walled, digitate sphinctozoans acted as baffles (Text-fig. 4); digitate species with calcareous chamber fillings helped construct the reef framework; encrusting species of both the Sphinctozoa and Sclerospongiae bound skeletons and sediment into the framework.



and distribution of reef communities; Early Jurassic reefs are small, rare and coral-built. Reef-building progressively increased in importance again in the Middle and Late Jurassic and continued to the end of the Cretaceous but the Sphinctozoa were inconspicuous members of these communities. The thin-walled, digitate post-Triassic forms apparently were unable to construct the reef framework as effectively as the thermodynamically more efficient calcareous algae and scleractinians.

Only two species of Cenozoic Sphinctozoa (both rare) are known: *Vaceletia progenitor* (Pickett, 1982) from the Eocene of Australia and *V. crypta* (Vacelet, 1979) from the Holocene (Text-fig. 1).

### CONCLUSIONS

On the basis of the data presented above, the following conclusions may be drawn:

1. The association of Sclerospongiae and Sphinctozoa in reef communities began at least as long ago as the Permian and continued with varying degrees of closeness to the end of the Triassic. Jurassic and Cretaceous sclerosponges and sphinctozoa are rare and none of the former are known from the Tertiary. Holocene Sclerospongiae are also confined to reefs, but are most common in communities lacking Sphinctozoa (e.g., Jamaica). The reef occurrence and the preponderance of aragonitic skeletons indicates a general restriction of both groups to warm water; living sclerosponges and sphinctozoa are most abundant and diverse in water warmer than about 25°C.

2. Holocene sclerosponges and sphinctozoa are most abundant on hardgrounds in cryptic habitats (caves, tunnels, crevices, etc.). Although a few fossil species may have occupied such habitats, most species appear to have lived on open (non-cryptic) hardgrounds. This shift to cryptic habitats may have been due to the more rapid growth rates of the hermatypic scleractinian corals; competition may have "forced" the shallow water sclerosponges and sphinctozoa to occupy cryptic habitats in which the advantages of the hermatypic corals are less pronounced.

3. Living sclerosponges and sphinctozoa are most abundant and diverse in the photic zone for zooxanthellae (0–100 m). The very common association of fossil sphinctozoa with abundant and diverse algae strongly suggests that they also inhabited shallow water. Although the fossil record of sclerosponges is much poorer, they occur also with algae. Living and fossil sclerosponges and sphinctozoa are closely associated with brachiopods, mollusks, Foraminifera, and Bryozoa.

4. The functional role (guild placement) of the Sphinctozoa in reef communities has shifted during geologic time. In the pre-Permian they were relatively uncommon dwellers. By the Middle Permian they had become important elements in the constructor, binder and baffle guilds in reefs marginal to the Delaware Basin in Texas and New Mexico. Early Triassic sphinctozoa are unknown but in the Middle Triassic they were the chief reef constructors. By the Late Triassic the Sphinctozoa had been supplanted by the Scleractinia as the major elements of the reef constructing guild. Cenozoic species all belong to the dweller guild.

5. Permian sclerosponges were probably dwellers but by the Middle Triassic they had become important members of both the binding and construction guilds. Jamaican Holocene sclerosponges in shallow water (<70 m) encrust and bind skeletons and sediment whereas those in deep water (70–105 m) are the main members of the construction guild.

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## SECTION 6

**Fossil and Recent Reef Communities**

## INTRODUCTION

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The study of Cnidarians often leads to the study of the reef-like structures and communities they generate. At the most basic level of study, reefs can be physically described, *i.e.*, the component taxa are identified, or at least distinguished, and usually the taxa are mapped both stratigraphically and topographically. At the next level of study, these data can be analyzed by various methods, such as measures of species diversity, percentage substrate cover, and evidence of species zonation, all of which contribute to a better understanding of the reef community. At this level well defined sampling methods are usually employed to give statistical validity to the results. A third level of study involves paleoecological interpretation, wherein the investigator uses the organisms and/or characteristics of the fossil community to hypothesize what the environment might have been at the time. This is invariably done with reference to Recent organismal or community analogs, making the study of Recent reefs of critical importance. In the case of a study of an exclusively Recent reef, this form of conjecture could take the form of suggesting why species are distributed as they are. To reiterate, three levels of study of reef communities are descriptive, analytical, and hypothetical, each building on the former.

In addition to the six papers presented in Section 3 on post-Paleozoic reef-building and Cnidaria, another 11 papers were volunteered that dealt with various aspects of fossil and Recent reefs, most of them addressed to community structure within a reef. These 11 papers are presented in this section, six in entirety and five as abstracts only. These papers are quite diverse in time period (Cambrian to Recent), geographic area (Caribbean, Guam, Italy, China, and Canada), and kinds of organisms studied (corals, stromatoporoids, and rudists), and employ all three levels of study discussed above. They are presented in reverse chronological order.

The first paper, by Liddell, Ohlhorst, and Boss, describes community structure on a Recent reef in Discovery Bay, Jamaica, and is an example of all three levels of study. The authors first identified the corals, algae, and sponges on a line transect and then calculated coral species diversity for various areas of the reef. Coral diversity was highest on the fore-reef escarpment. Percentage substrate cover of fleshy algae and sponges increased with depth, whereas cover of coralline algae and boring sponges decreased with depth. They hypothesized that the increase in fleshy algae with depth was a result of the attenuation of the urchin herbivore below the fore-reef escarpment.

The next three papers, all coauthored by A. W. Siegrist, H. G. Siegrist, and Randall concern an emergent Holocene reef at Ylig Point, Guam. Based on analogous Recent zonal indicator species, they suggest that the Holocene reef was a high energy reef margin zone. This is also supported by their petrographic analysis. Using line transects and point count sampling methods, they statistically described functional morphological groups (*e.g.*, cespitose corals, massive corals) in an attempt to quantitatively define community structure and variability.

In contrast to the high energy Guam reef, Pfister (abstract only) describes a low energy fringing reef from the Oligocene of Northern Italy. The community consists of about 20 species and shows only a weak zonation.

The early Cretaceous reefs of the Gulf of Mexico are discussed by Scott in the next two contributions. According to Scott, the early Cretaceous demise of coral reefs was not caused by competition with rudists but rather by environmental changes, such as an increase in water temperature, decrease in oxygen content of the water, and perhaps by a shift in the planktonic trophic structure. Rudists occupied a slightly different niche, above the wave base, and were less affected by

the environmental changes, allowing them to dominate at this time. In his second paper (abstract only), Scott describes community succession of the coral-algal-rudist reefs of the Gulf of Mexico.

Likewise, Pope (abstract only) describes a possible community succession of stromatoporoid reefs in the Upper Silurian West Point Formation in Quebec. In a related paper, Copper and Fay (abstract only) report 302 bioherms from the early Llandoveryian of the northern fringe of the Michigan Basin, Ontario, Canada. These bioherms are of three types: bryozoan, stromatoporoid-tabulate, and rugosan. This constitutes the largest early Silurian reef belt known. Qi Wen-ton and Copper (abstract only) briefly review some of the reef

formations in China from the Cambrian to the Cretaceous, suggesting parallels with other parts of the world.

The last paper, by Tsien, is a generalized account of how corals can be used in paleoecological analysis. He presents several examples drawn mainly from Paleozoic corals and stromatoporoids and stresses that fossil assemblages are more significant than individual organisms as environmental indicators. But he cautions that a fossil assemblage is not necessarily a fossil community; for instance it may be a paleoethanacoenosis, and therefore urges caution in paleoecological interpretation.

## COMMUNITY PATTERNS ON THE JAMAICAN FORE REEF (15–56 M)

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## ABSTRACT

Patterns of community composition, percent cover and species diversity were determined for sites on the fringing reef in the vicinity of Discovery Bay, Jamaica. Sites sampled range from the fore reef terrace (15 m) to the boundary (56 m) between the fore reef slope and the vertical to overhanging deep fore reef.

Coral diversity ( $H'$ ; Shannon and Weaver, 1948) increases from the fore reef terrace (15 m,  $H' = 1.87$ ) to the fore reef escarpment (22 m,  $H' = 2.12$ ) and then decreases on the upper fore reef slope (30 m,  $H' = 1.54$ ) with the lowest value occurring at the boundary between the lower fore reef slope and the deep fore reef (56 m,  $H' = 1.49$ ). Coral cover decreases from 35.9% at 15 m to 27.9% at 22 m (due to the unstable nature of the steeply sloping fore reef escarpment) and then increases to a high of 58.9% at 30 m before declining to 38.5% at 56 m. Coral diversity is not correlated with coral percent cover. Cover by fleshy and filamentous algae (8.0–32.0% range) and fleshy and encrusting sponges (1.7–14.5%) increases with depth while cover by coralline algae (25.6–3.6%) and boring sponges (20.0–0.0%) decreases with depth. The increase in fleshy algae correlates with the nearly complete absence of the urchin herbivore *Diadema antillarum* below the fore reef escarpment. Total living cover is highest on the fore reef slope (90.6–94.7% versus 81.8–83.8% on the terrace and escarpment). Total reef diversity (all cnidarians, algae and sponges) is fairly constant over the range of 15 m–56 m.

## INTRODUCTION

The well developed fringing reefs occurring along the north central coast of Jamaica display a striking, depth-related biotic zonation which has been described in several papers (Goreau, 1959; Goreau and Goreau, 1973; Kinzie, 1973; Lang, 1974; and others). In addition, these reefs have been the location of numerous studies dealing with the physiology, functional morphology, biotic interactions and other aspects of reef organisms. As such, the dearth of quantitative data on the community composition of the Jamaican reefs is surprising. To date, only a few studies (Bonem and Stanley, 1977; Liddell and Ohlhorst, 1981; Jackson and Winston, 1982; Huston, in preparation) have presented data which enable the quantitative documentation of depth-related trends in species composition and diversity over the range of 0–30 m. Such studies at Jamaica and elsewhere in the Caribbean have been restricted to the shallower reefs ( $\leq 30$  m), with few exceptions (Ott, 1975; Bak, 1977; Bak and Luckhurst, 1980). The present paper extends our knowledge of patterns of species diversity and community composition on a Jamaican reef to 56 m, which is near the lower depth limit of reefs dominated by scleractinians and algae. Such information may aid in the recognition of different reef environments in the geologic record.

## ACKNOWLEDGMENTS

We wish to extend our appreciation to Michael Huston (University of Michigan) for providing us with a copy of his manuscript on Jamaican coral reef diversity from 0–30 m, and to Steve Kohut (University of New

Orleans) for his assistance with the reef transects described in this paper. This represents contribution number 308 from the Discovery Bay Marine Laboratory.

## STUDY LOCALITY

Discovery Bay lies on the north central coast of Jamaica at Lat.  $18^{\circ}30'N$  and Long.  $77^{\circ}20'W$ . The fringing reef studied is known as "Zingorro" and lies on the West Fore Reef, approximately 0.5 km west of the Discovery Bay ship channel (Text-fig. 1, line A–A').

Study sites on Zingorro were located at 22 m on the fore reef escarpment and at 30 m, 45 m and 56 m on the fore reef slope (Text-fig. 2). The last site lies near the edge of the fore reef slope, only 1 to 2 m from the vertical escarpment of the deep fore reef (terminology after Goreau and Land, 1974). One additional site at 15 m on the fore reef terrace of nearby Watertower Reef (separated from Zingorro by a 10 m wide sand channel) was also studied (Liddell and Ohlhorst, 1981).

## METHODS

Data from 15 m on the fore reef terrace of Watertower were collected during May of 1980. Data from the fore reef escarpment and fore reef slope of Zingorro were collected during August and September, 1982. Although shallower reef sites were still recovering from the August, 1980 Hurricane Allen, and not in species equilibrium, deeper sites, such as those on the fore reef slope ( $\geq 30$  m), were less affected by the hurricane (Woodley *et al.*, 1981; Ohlhorst and Liddell, 1981) and may represent moderately undisturbed communities.

Table 1.—Mean percent community composition from 15–56 m on the Jamaican fore reef as determined by line transects. 95.0% confidence intervals in parentheses.

Site:	Terrace <sup>1</sup> 15 m N (transect points/lines): (606/12)	Escarpment 22 m (453/9)	Slope		
			30 m (244/5)	45 m (286/7)	56 m (222/5)
Category					
Corals	35.9 (±3.2)	27.9 (±5.1)	58.9 (±9.7)	45.0 (±12.4)	38.5 (±14.1)
Cnidarians (non-coral)	3.8 (±1.4)	0.9 (±0.8)	1.2 (±2.2)	0.7 (±1.2)	1.6 (±4.4)
<i>Gypsina</i> (foraminiferan)	1.1 (±1.0)	4.4 (±2.1)	2.9 (±5.0)	2.6 (±3.3)	0.8 (±1.3)
Coralline algae	13.3 (±3.4)	25.6 (±5.9)	3.2 (±3.8)	5.5 (±3.3)	3.6 (±5.9)
Filamentous algae	5.2 (±2.8)	12.0 (±3.7)	4.1 (±3.5)	5.3 (±4.8)	7.6 (±11.0)
Fleshy algae	2.8 (±3.2)	2.7 (±1.3)	8.2 (±7.9)	26.5 (±5.4)	24.4 (±21.0)
Fleshy sponges	1.5 (±1.3)	2.2 (±1.6)	4.5 (±3.4)	7.5 (±5.7)	7.8 (±9.7)
Encrusting sponges	0.2 (±0.4)	0.0	1.7 (±3.4)	0.3 (±0.8)	6.7 (±3.9)
Boring sponges	20.0 (±5.6)	6.9 (±3.2)	10.3 (±9.2)	1.4 (±1.7)	0.0
Bare hard substrate	12.4 (±3.4)	1.3 (±1.1)	4.5 (±4.5)	1.1 (±2.8)	0.4 (±1.1)
Sand/mud	3.8 (±2.4)	16.8 (±4.2)	0.8 (±1.4)	4.4 (±3.7)	9.1 (±6.6)
Living cover	83.8 (±3.4)	81.8 (±3.8)	94.7 (±5.8)	94.4 (±4.6)	90.6 (±7.5)
No. <i>Diadema antillarum</i> /m <sup>2</sup> (m <sup>2</sup> surveyed)	3.2 (±1.1) (90)	2.2 (±0.8) (90)	0.1 (±0.1) (70)	0.0 (50)	0.0 (50)

<sup>1</sup> Data from Liddell and Ohlhorst (1981).

Although the fore reef escarpment site almost certainly suffered some hurricane damage, diversity and percent living cover data from the site on Zingorro are very similar to such data from the fore reef escarpment of nearby Watertower Reef collected in March, 1977 by Huston (manuscript in preparation).

Data were collected by a line transect method in which 10 m lines with points marked every 20 cm were draped over the reef at 1 m intervals and the identity of every item beneath a transect point recorded (line intercept method; Lucas and Seber, 1977; Eberhardt, 1978). From 5 to 12 lines (approximately 250–600 points) were surveyed at each site (Table 1). Due to bottom time limitations (e.g., 5 minutes “no decompression” limit at 45 m), this method was consid-

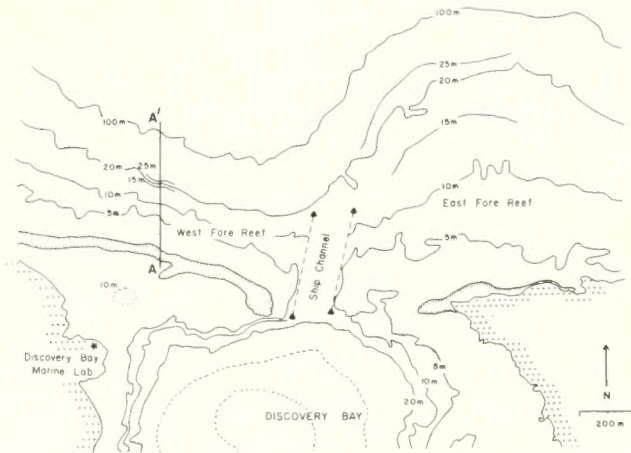
ered to be preferable to others, such as the quadrat method (Kissling, 1965; Weinberg, 1981), in that it allowed for a greater area of reef to be censused and is, therefore, less subject to biasing by heterogeneous distributions of reef benthos. Although the quadrat method may provide a better estimate of the composition of the reef area covered by the quadrat, only a small area of reef per unit time is covered—a serious disadvantage for time-limited deep reef surveys.

Transect data were used in the determination of general community composition, coral species abundance and percent living cover and in the calculation of values for diversity ( $H'$ , natural log; Shannon and Weaver, 1948) and evenness ( $J'$ ; Pielou, 1968).

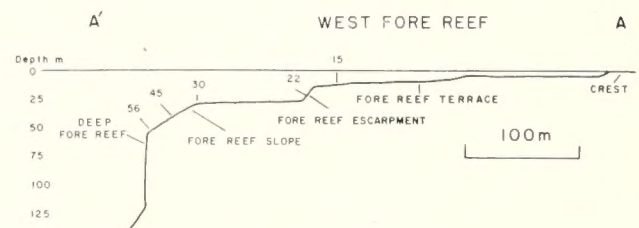
Data were also gathered on the density of the urchin *Diadema antillarum*, one of the principal herbivores on the Caribbean reefs (Sammarco *et al.*, 1974; Carpenter, 1981), which was counted in 1 m wide strips adjacent to the transect lines.

## RESULTS

Cumulative plots of coral species censused versus



Text-figure 1.—Bathymetric map of the Discovery Bay area showing study site (profile line A-A'). Modified from Liddell and Ohlhorst (1981).



Text-figure 2.—Profile of Zingorro Reef showing transect sites. Location of profile indicated on Text-figure 1. Modified from Liddell and Ohlhorst (1981).

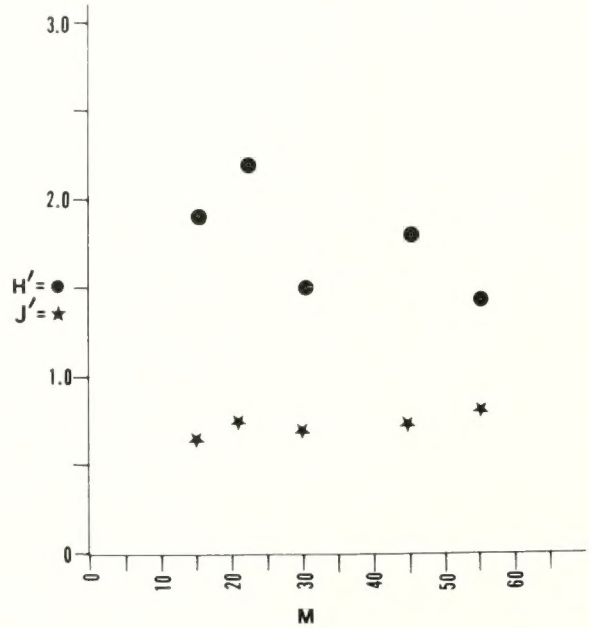


number of transect lines surveyed were utilized as a test of sample adequacy (Loya, 1972). For all sites the cumulative species curves were either level (no new species being added with increasing sample size) or at least rising at a low rate, suggesting that the samples are nominally adequate for describing the reef community.

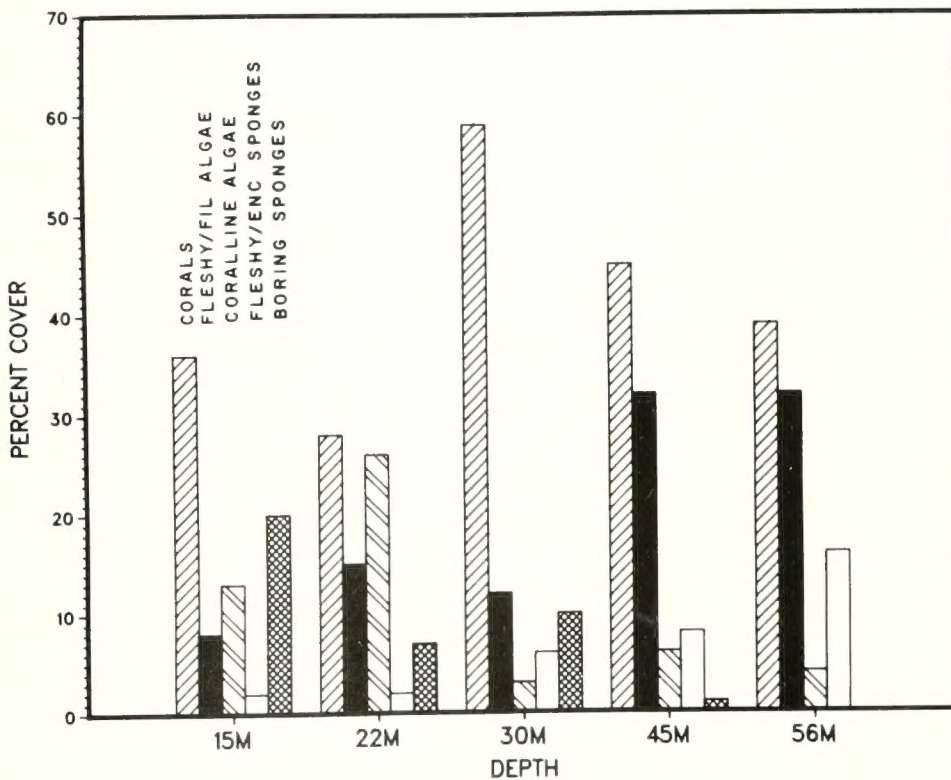
Total living cover varies from 81.8–94.7% of the reef surface and is typically highest on the fore reef slope (Table 1). At all sites the reef is dominated (76.6–91.2%) by corals, algae and sponges. Although coral abundance does fluctuate over the five sites (27.9–58.9%), the most striking depth-related trends are displayed by the algae and sponges (Text-fig. 3, Table 1). “Fleshy” (largely brown and green) and filamentous (largely red) algae and fleshy sponges increase dramatically in abundance (% cover) with increasing depth (Spearman Rank Correlation 0.90 and 0.98, respectively; both are significant at the 0.05 level) while coralline red algae and boring sponges (principally *Cliona* spp.) decrease in abundance with increasing depth (SRC -0.60 and -0.90, respectively; the latter is significant at the 0.05 level). In most cases the greatest change in a group’s abundance occurs at the boundary between the fore reef escarpment and the fore reef slope.

Depth-related trends at the species level are pre-

sented only for the corals (Text-fig. 4, Table 2). The number of coral species present remains relatively constant over the range of 15–22 m (15–17), but then declines to 12 at 30 m, 11 at 45 m and 7 at 56 m.



Text-figure 4.—Coral diversity ( $H'$ ) and evenness ( $J'$ ) versus depth.



Text-figure 3.—Abundance of major groups at different depths.

Table 2.—Mean percent composition and diversity values for coral communities from 15–56 m as determined by line transects. 95% confidence interval presented in parentheses.

Site: N (transect points over coral): Category	15 m <sup>1</sup> 214	22 m 127	30 m 143	45 m 123	56 m 82
<i>Acropora cervicornis</i>	45.3 (±12.2)	0.6 (±1.4)	1.5 (±4.3)		
<i>Agaricia agaricites</i>	20.3 (±6.8)	28.7 (±14.5)	16.2 (±9.9)	20.5 (±19.9)	
<i>Agaricia fragilis</i>					21.1 (±10.3)
<i>Agaricia lamarcki</i>		0.6 (±1.4)	6.7 (±7.4)	34.1 (±23.5)	17.5 (±7.0)
<i>Agaricia undata</i>					43.5 (±13.1)
<i>Colpophyllia natans</i>	1.1 (±2.4)	1.7 (±2.6)	3.9 (±7.3)		
<i>Dichocoenia stokesi</i>		0.6 (±1.4)			
<i>Diploria labyrinthiformis</i>	0.4 (±0.9)				
<i>Diploria strigosa</i>		4.3 (±7.2)	0.8 (±2.1)		
<i>Eusmilia fastigiata</i>	0.4 (±0.8)	1.4 (±2.2)			
<i>Helioseris cucullata</i>	1.0 (±1.5)	2.7 (±3.3)	8.3 (±9.1)	6.2 (±3.0)	3.3 (±9.3)
<i>Madracis decactis</i>	1.5 (±2.3)				
<i>Madracis mirabilis</i>	7.6 (±5.6)	27.2 (±11.7)	0.6 (±1.7)		
<i>Meandrina meandrites</i>	0.7 (±1.6)	0.8 (±1.8)		1.1 (±2.7)	
<i>Montastrea annularis</i>	6.1 (±3.2)	2.3 (±2.7)	54.2 (±29.3)	19.1 (±16.0)	
<i>Montastrea cavernosa</i>			0.8 (±2.1)	12.3 (±12.9)	11.1 (±13.9)
<i>Mussa angulosa</i>				0.6 (±1.6)	
<i>Mycetophyllia aliciae</i>					1.0 (±2.7)
<i>Mycetophyllia lamarckiana</i>		1.4 (±2.1)		1.1 (±2.7)	
<i>Porites astreoides</i>	9.8 (±4.7)	5.7 (±4.0)	5.6 (±9.3)	1.6 (±2.6)	
<i>Porites furcata</i>	2.6 (±2.6)	1.5 (±2.4)			
<i>Porites porites</i>	4.1 (±3.4)	4.6 (±4.9)			
<i>Siderastrea siderea</i>	1.3 (±2.2)	6.8 (±5.5)	0.6 (±1.7)	1.3 (±2.1)	
<i>Stephanocoenia michelinii</i>	1.7 (±2.9)	9.2 (±7.5)	0.8 (±2.1)	2.1 (±3.3)	2.5 (±4.3)
No. coral species	15	17	12	11	7
H' (Shannon and Weaver, 1948)	1.87	2.12	1.54	1.76	1.49
J' (Pielou, 1968)	0.69	0.75	0.62	0.73	0.76

<sup>1</sup> Data from Liddell and Ohlhorst (1981).

Diversity (H', Shannon and Weaver, 1948) reaches its highest value at 22 m on the fore reef escarpment (2.12) and its lowest value at 56 m on the fore reef slope (1.49). Coral diversity is not correlated with coral abundance (% cover).

The corals clearly show species replacement along a depth gradient with *Acropora cervicornis* dominating at 15 m (45.3% of corals), *Madracis mirabilis* (27.2%) and *Agaricia agaricites* (28.7%) dominating at 22 m, *Montastrea annularis* (54.2%) dominating at 30 m and various species of *Agaricia* dominating at 45–56 m (54.6–82.1%).

## DISCUSSION

The observed changes in community composition along a depth gradient cannot be ascribed to a single causal factor. The spectral characteristics of light change and its intensity decreases with increasing depth. Water turbulence also decreases with increasing depth. These and other abiotic factors may be responsible for depth-related shifts in species abundance, resulting in the domination of deeper reef areas by "depth-adapted" corals such as the *Agaricia* species.

Biotic interactions may also play a role in species distributions. The great increase in fleshy algae on the fore reef slope is almost certainly related to the near-total absence of the important herbivore *Diadema antillarum* below the fore reef escarpment (Table 1). The reasons for the urchin's depth limitation are unknown.

Controls on coral species diversity (H') are also far from clear. The fore reef slope sites represent areas of both lowered physical (wave and storm action) and biological (grazing by *Diadema*) disturbance as well as lowered resource (light) levels. In contrast, the shallower sites (terrace and escarpment) experience higher levels of disturbance and increased light levels. In addition, the escarpment site is on a steep (approx. 45°), potentially unstable slope, which may introduce an additional element of disturbance. The effects of these varying factors are difficult to ascertain as increasing disturbance, to a point, may be expected to increase diversity by preventing the attainment of community equilibrium and competitive displacement while decreasing resource (light) levels, to a point, may also be expected to increase diversity by lowering growth rates and reducing competitive displacement (Huston, 1979).

The similarity of coral species diversity at 15 and 45 m ( $H'$  1.87 and 1.76, respectively) may reflect a balance between these effects. The high diversity at 22 m ( $H'$  2.12) may reflect exceptionally high rates of disturbance while the low diversity at 56 m ( $H'$  1.49) may reflect the point at which the light resource level is approaching a limiting value.

It should be stressed that the data presented herein are from a single reef at Jamaica. Further study is certainly in order before attempting to extrapolate the data from this deep reef to other areas. Comparison with quantitative studies of deep reefs at Curacao (Bak, 1977; Bak and Luckhurst, 1980) and Barbados (Ott, 1975) indicate a number of differences in community percent cover, coral species depth distributions and diversity at the three localities.

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## FUNCTIONAL MORPHOLOGICAL GROUP VARIATION WITHIN AN EMERGENT HOLOCENE REEF, YLIG POINT, GUAM

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### ABSTRACT

Line transect and orthogonal grid (point count) sampling methods yield multivariate descriptions and geologic interpretations of the spatial distributions of functional morphological groups (f.m. groups) on a raised windward reef on Guam ( $3655 \pm 150$  b.p.). Sampled reef corals and detrital sediments are categorized into the f.m. groups encrusting (8%), massive (9%), submassive (6%), cespitose (29%) and corymbose (24%). Detritus (24%) is treated as a separate group.

Time series analysis of a 150-meter seaward to shore transect describes the distribution in one direction of dominant groups. Cespitose is best fitted by an autoregressive model and corymbose by a moving average model. Detritus is statistically random. Trend surface analysis within seaward and landward grids describes their distributions in two geographical dimensions. The trend in cespitose abundance is represented by a planar surface increasing toward the seaward edge of the raised reef. Trends for corymbose are represented as quadratic and cubic surfaces increasing landward and exhibiting NW-SE oriented peaks. Surfaces representing trends in diversity values are planar and cubic in form, and increase toward the landward edge.

### INTRODUCTION

Multivariate techniques applied to the study of *in situ* forms from modern or ancient coral reefs generate quantitative descriptions of the community structure and variability of a reef system. Such descriptions are powerful in the amount of readily interpretable information they contain and in the variety of research purposes for which they are useful. Sufficient detail on the occurrence and spatial distribution of species is obtainable by multivariate methods so that subtle patterns or zonation within a single reef may be identified. Moreover, the accuracy with which the results represent the entire reef system allow for comparisons between several reefs. Multivariate techniques prove to be efficient (economical); thus, it is feasible to study very large or complex reef systems.

The objective of this research is to demonstrate the usefulness of systematic sampling and statistical analyses to describe the spatial distribution of reef corals and detrital sediment on a recently raised reef. The study concentrates on the Holocene Merizo Limestone cropping out at Ylig Point on the east-central coast of Guam (Fig. 1) and is part of an ongoing research program focusing on Neogene and Quaternary limestone in the southern Mariana Islands.

The Merizo Limestone is named in Tayama (1952), described and dated in Tracey *et al.* (1964) and mapped and redated by Easton *et al.* (1978). At Ylig Point, the formation disconformably overlies the Pliocene-Pleistocene Mariana Limestone. Recently completed drilling at this location indicates that the Merizo averages approximately 3.5 meters in thickness. From the outcrop of the formation at Ylig Point, mineral compo-

sitions and textures of reefal and detrital facies are described by Siegrist *et al.* (1983, and in this volume). Also from Ylig Point, the community structure of the reef corals and the occurrence of crustose calcareous algae and detrital sediments are discussed by Randall *et al.* (1983). Methods of systematically sampling reefs are reviewed and compared recently by several authors (Stoddart, 1972; Loya, 1978; Dodge *et al.*, 1982). Most stress the inherent advantages and disadvantages of each method in terms of the type and amount of information recorded per time spent sampling. Statistical analyses of the spatial distribution of reef corals appear to be scarce in the literature. However, time series analysis is used extensively to identify patterns of occurrence in economic events (Nelson, 1973) and trend surface analysis is a common mapping tool in geologic research (Davis, 1973).

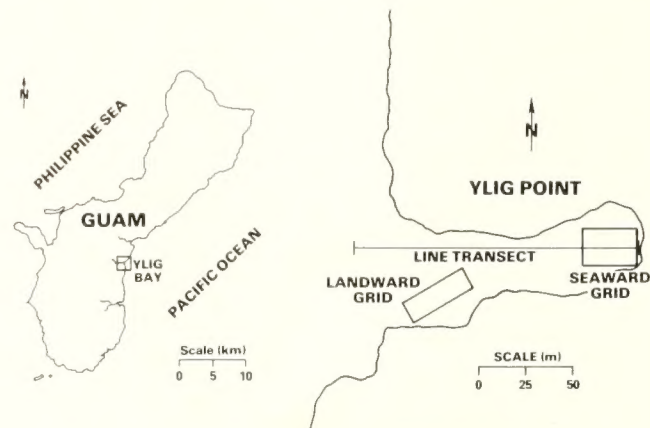


Figure 1.—Locations of transect, seaward and landward grids.

## METHODS AND PROCEDURES

Two complementary sampling techniques are chosen to study community structure and its variability within the Ylig site. Initially, the line transect method described by Loya (1978) is used to continuously sample a 150-meter transect oriented east to west over the raised reef (Fig. 1). This seaward-landward transect is first run to establish a reasonable sample spacing or grid interval. The raw transect data are systematically sampled at 0.50-, 0.75-, 1.00-, 1.50- and 2.25-meter spacings and, using a Markov approach (Davis, 1973), an optimum interval of 0.75 meters is established. This is the smallest distance between samples wherein no dependency between adjacent points is evident.

Two separated (seaward vs. landward) orthogonal grids are then point-counted on the 0.75-meter interval. This sampling technique, similar to the point method described in Dodge *et al.* (1982), is extensively modified to collect independent samples along two directions. The seaward grid shown in Figure 1 is oriented with its long axis N-S and covers an area 29.25 by 20.25 meters. Also shown is the landward grid oriented with its long axis N37°E and samples an area 31.5 by 11.25 meters.

Sampling is preceded by operationally defining reproducible categories of functional morphological groups (f.m. groups): cespitose; corymbose; encrusting; massive; submassive. Individuals located along the transect or on grid intersections are recorded within one of these f.m. groups. Two additional counting categories established are detritus and miscellaneous. Detritus includes concentrations of wackestone, packstone and grainstone textures dominated macroscopically by algal, coral, molluscan and/or foraminifer clasts (Siegrist *et al.*, 1983). Miscellaneous encompasses segments that are subtidal and encrusted with recent algae, deep depressions filled with recent wave detritus or thick vegetation.

Measures used to compare line transect and point-counted data are total coral coverage, relative f.m. group coverage and diversity. For the transect data, total coverage is calculated as the total length of all f.m. groups intersected by the transect divided by the length of the transect. Relative coverage is computed by dividing the total length of a particular f.m. group by the total length of all f.m. groups. Point-counted data are counts only so that total and relative coverages must be estimated indirectly. Total coverage is estimated as the total number of counts or points of all f.m. groups divided by the number of points within the grid. Similarly, relative coverage is found by dividing the total number of points of a particular f.m. group by the total number of points of all f.m. groups. A Shannon-Weav-

er information index of f.m. group diversity is calculated

$$H' = - \sum_{i=1}^S p_i \ln p_i,$$

where  $p_i$  is the proportion of coverage of the  $i$ th f.m. group ( $i = 1, 2, \dots, S$ ).

Time series analysis (Box and Jenkins, 1970) offers a refined description of a sequence of measurements made at regular intervals along a linear dimension, usually time, but in our case distance along the transect. The objective of the analysis is to formulate the simplest statistical model which best describes the observed occurrence of a f.m. group. The resulting models are linear regressions which express the length of a f.m. group within a given interval along the transect as a function of lengths of that group within previous intervals and random errors. The significance of the fit of any model to the observed behavior of the f.m. group of interest may be tested statistically.

Only cespitose, corymbose and detritus are modeled as time series since they dominate the line transect data. The lengths of each of these are summed over regularly spaced intervals of 2.25 meters. The data are analyzed by BMDP (Dixon, 1981) computer program P2T, Box-Jenkins Time Series Analysis.

Like time series, trend surface analysis is a type of regression technique which describes the spatial distribution of a sequence of measurements. Instead of predicting lengths along a single dimensional transect however, trend analysis predicts occurrences located by several dimensions. Applied to our data, trend analysis searches for a statistical model which estimates the proportions and distributions of f.m. groups conditional on their geographic location within the seaward and landward grids. The significance of the derived trend equations is tested by analyses of variance.

Again, only cespitose, corymbose and detritus are modeled since these groups dominate. Grids are divided into square cells, 2.25 meters on a side; thus, each cell includes nine grid intersections. Derived data from each cell include the proportions of each f.m. group, detritus and miscellaneous, and the f.m. group diversity of the cell. These data are analyzed by the computer program TREND (Davis, 1973).

## RESULTS

Table 1 presents the total coral coverage, relative f.m. group coverage and f.m. group diversity from the line transect and point-counted data. Large variations in these measurements are obvious between the transect and the grids as well as between the grids themselves. Oriented normal to the probable reef edge, the transect samples along the strongest gradients in the

Table 1.—Measurements from transect, seaward and landward grids. Includes total coral coverage (%), relative f.m. group coverage (%) and f.m. group diversity.

	Transect	Seaward grid	Landward grid
Relative coverage (%)			
Cespitose	38.30	55.32	19.91
Corymbose	30.70	24.24	34.42
Encrusting	11.25	9.67	16.45
Massive	12.18	4.40	19.91
Submassive	7.36	6.73	9.31
Total coral coverage (%)	74.13	77.59	73.33
Diversity	1.425	1.208	1.528

reef population (Stoddart, 1972) and possibly crosses several zones oriented parallel to the reef edge. Orthogonal grids, purposely located to sample the seaward and shore reef edges, provide detailed measurements of the reef at these specific locations.

Several tables are necessary to present the results of time series and trend surface analyses. Due to space constraints, only a discussion of these results are presented here. All data are available on request to the authors.

From time series analysis, the cespitose series is best fitted, in terms of accuracy and parsimony, by a first-order autoregressive model. As a given length of cespitose departs from the average length of all cespitose, the succeeding length measured also will depart from the average about the same amount and in the same direction, either higher or lower. The model implies a patchy or clumped distribution and that cespitose forms occur both with abundance and scarcity from seaward to land. A more modulated behavior, expressed by a first-order moving average model, is exhibited by corymbose forms. The model estimates that, if a given length of corymbose departs from the average of all corymbose, the next length encountered will tend to return to the average. Thus, corymbose forms occur across the width of the reef with an average frequency plus gradual fluctuations. The detritus series proves to be statistically random. No dependency is evident between successive lengths. Its distribution is constant along the direction of the transect.

First-order trend surfaces best fit the observed distribution of cespitose forms in both the seaward and landward grids. Figure 2a, a contour map of the computer trends in cespitose proportions, shows a planar surface increasing, or rising, toward the seaward reef edge. The trends in corymbose abundance are modeled by a second-order equation in the seaward grid and a third-order equation in the landward grid. Figure 2b illustrates the quadratic surface (seaward) increasing toward a NW-SE ridge and the cubic surface (land-

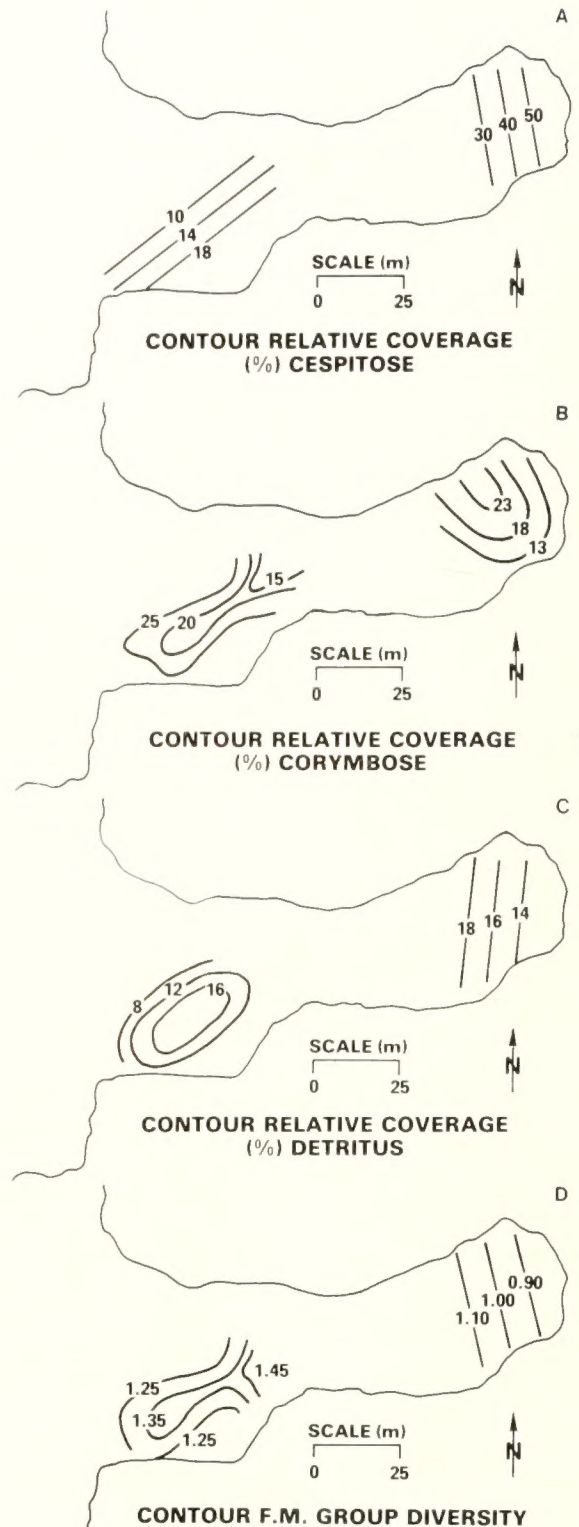


Figure 2.—Maps of significant trend surfaces for f.m. groups and diversity. Contours of relative coverage (%) cespitose (2a); corymbose (2b); detritus (2c); and diversity values (2d).

ward) decreasing toward a NE-SW valley. Although statistically random along the transect, the distribution of detritus within the grids shows very localized trends. Seaward, the first-order equation fit to detritus abundance is mapped in Figure 2c as a planar surface increasing away from the seaward edge. Landward, the trend in detritus is a quadratic surface which increases to a NE-SW ridge. F.m. group diversity follows a first-order trend surface in the seaward grid and a third-order surface in the landward grid. Displayed in Figure 2d, both the planar and cubic surfaces increase away from the seaward edge.

### CONCLUSIONS

Transect sampling offers a sectional view of the raised reef. If oriented parallel to major variability gradients, the transect provides unbiased estimates of average total coral coverage, relative coverage and diversity for the entire raised reef.

Point-counting is a rapid and informative sampling method for assessing two dimensional variation. Grids purposefully located within specific portions or zones of the reef provide detailed coverage and diversity measures for those zones. Moreover, because data are collected within orthogonal grids, point-counting in the sampled population may resolve both strong and subtle patterns oriented in any direction within the plane of the grids.

Complementary conclusions are drawn from the results of time series and trend surface analyses and are supported by coverage measurements from both sampling techniques. Cespitose forms increase markedly in abundance toward the seaward edge of the raised reef. Their patchy distribution allows them to contribute to the landward reef population (relative coverage 20%) and, yet, to dominate the seaward population (relative coverage 55%). The proportion of corymbose forms only gradually increases landward. The modulated distribution of the group is reflected in the slight fluctuations in its relative coverage from seaward to land. Detritus does not follow a pattern across the reef yet exhibits subtle patterns along the seaward edge and the landward edge. It contributes a constant amount to the reef population regardless of its location on the reef. Finally, diversity values increase landward.

By categorizing species into f.m. groups, systematically sampling the reef and analyzing the data with

widely accepted and available statistical methods, a reproducible procedure for studying modern or ancient coral reefs has been demonstrated. Results obtained by this multivariate procedure accurately reflect local patterns in the Ylig Point raised reef and will be readily comparable to results obtained in future studies of Neogene limestones throughout the southern Mariana Islands.

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COMMUNITY STRUCTURE OF REEF-BUILDING CORALS ON A  
RECENTLY RAISED HOLOCENE REEF ON  
GUAM, MARIANA ISLANDS<sup>1</sup>

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ABSTRACT

Line intercept and grid-point sampling methods were used to determine the community structure of reef corals and the occurrence of crustose calcareous algae and detrital sediments on an emergent Holocene (Merizo Limestone) reef at Ylig Point, Guam.

Data from the line intercept transect and grid-point sampling areas revealed the presence of a flourishing shallow-water reef complex that could be separated into two distinct coral communities consisting of a high-energy seaward reef facies and a low-energy landward (backreef) facies. The seaward reef facies contained 16 reef-building coral species (species diversity index 1.461) which occupied 72.2 percent of the substrate and the landward reef facies contained 21 reef-building coral species (species diversity index 1.724) which occupied 68.2 percent of the reef substrate. On the seaward reef facies cespitose colony forms, composed predominantly of the high-energy indicator species *Pocillopora setchelli*, make up 42.9 percent of the coral community, while on the landward reef facies corymbose and massive colony forms make up a more heterogeneous coral community that includes several low-energy indicator species. Detrital matrix and crustose calcareous red algae respectively occupy about 16 and 5 percent of the reef substrate in both the seaward and landward reef facies.

Geomorphic and community structure interpretations of Guam's shallow reef platforms require not only the consideration of a general post-Wisconsin transgression, but features inherited as the result of relatively rapid emergence of vigorously growing Holocene reefs (Merizo Limestone) as well.

INTRODUCTION

One of the most conspicuous features of Guam's shallow reef-flat platforms is the presence of supratidal Merizo Limestone that forms low (up to 2.5 meters above mean sea level) discontinuous terraces along the shoreline and isolated patches, projecting peninsulas, and long narrow ridges on its surface. The upper surface of the limestone is weathered into a jagged pitted and pinnacled topography (karrenfeld) which at all but the most exposed locations supports a prostrate growth of *Pemphis acidula* scrub. A superficial layer of endolithic and encrusting algae imparts a grey color to the supratidal surfaces. At most outcrops on the reef platform the weathered limestone surface reveals a profuse abundance of close-packed reef-building corals in their original position of growth.

The formation was named from extensive outcrops along the southwest coast by Tayama (1952), re-described and dated at  $3400 \pm 250$  years primarily from the same outcrops by Tracey *et al.* (1964), and redated at 2975–5115 years and further traced around most of the shoreline of Guam by Easton *et al.* (1978).

A study of the community structure of reef-building corals in the Merizo Limestone is part of a larger program to investigate all the raised limestones of Guam. We expect information from such a study to be useful in interpreting reef geomorphology patterns and strati-

graphic correlations in other Guam limestones, and ultimately in limestones of other southern Mariana Islands.

The objective of the present study is to determine the species composition, diversity, and substrate coverage, and colony size distribution for the reef-building coral community within an extensive outcrop of Merizo Limestone on the windward exposed coast at Ylig Point (Fig. 1). At this location a low, flat-surfaced peninsula with an area of about 3000 m<sup>2</sup> projects eastward from the shoreline onto a wider intertidal reef platform. Relief of the Merizo Limestone peninsula is gen-

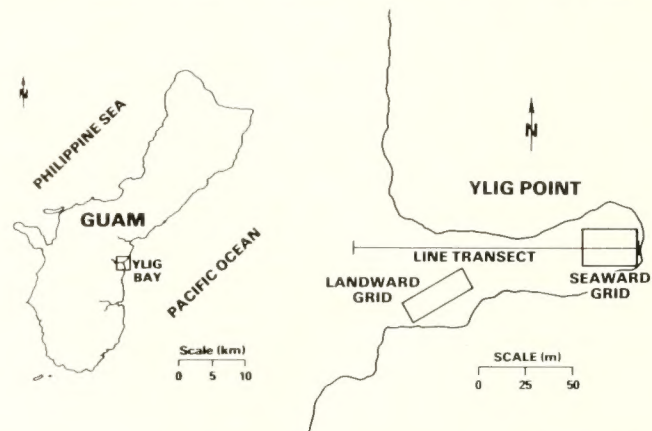


Figure 1.—Map of Guam showing the location of Ylig Bay and a map of Ylig Point showing the locations of the line transect and seaward and landward grid-point sampling areas.

<sup>1</sup> Contribution No. 175, University of Guam Marine Laboratory.



erally less than 0.5 meters above the adjacent intertidal reef platform and in the sampling areas is believed to disconformably veneer the Pliocene and Pleistocene Mariana Limestone with which it is in lap contact along the shoreline approximately 75 meters north of the peninsula (Fig. 1).

The Merizo Limestone outcrop at Ylig Point was selected for a study of the community structure of reef-building corals because: 1) it is the widest supratidal exposure of Merizo Limestone on Guam, and 2) such a wide exposure is more likely to show community structural differences from the outer (seaward) high-energy region to the inner (shoreward) lower-energy region, especially since the long axis of the peninsula is oriented normal to the fringing reef platform axis.

## METHODS

Community structure of the raised coral reef at Ylig Point was determined by using line intercept and orthogonal grid-point sampling methods. Initially the reef community was sampled by using the line intercept method of Loya (1978) along a 150-meter transect that followed the long axis of the peninsula (Fig. 1) to determine colony size distribution data and the proper space interval to use for the orthogonal grid-point sampling method. By sampling raw data from the line intercept transect at 0.50, 0.75, 1.00, 1.50, and 2.25 meter spacings, and using a Markov approach (Davis, 1973), an optimum interval to use for the orthogonal grid-point sampling method was 0.75 meters (A. Siegrist *et al.*, 1983, and in this volume). Two grid-point sampling areas were established, one at seaward and one at the landward ends of the peninsula, by placing parallel transects on the reef surface spaced 0.75 meters apart and point sampled at 0.75 meter intervals along their length (Fig. 1). The reef surface beneath each grid-point interval was identified and recorded as matrix, calcareous red algae, reef coral, or "other." Matrix is any consolidated or unconsolidated detrital material, calcareous red algae refers to crustose types that could be identified as *in situ* encrusting and nonarticulated ramose forms, reef corals include any *in situ* scleractinian, stoloniferan, coenothecalian, or hydrozoan species, and "other" refers to reef cavities or *in situ* organism other than reef corals or calcareous red algae. Reef corals were first identified and then categorized into one of five functional morphologic groups that include encrusting, massive, submassive, corymbose, or cespitose forms. Although it was possible to identify most corals to the species level, some could only be referred to a genus and given a species number. If it was suspected that the genus identification included

more than one species the group was referred to as a genus complex.

Measures used to determine the community structure of reef corals at Ylig Point are total coral coverage, coral coverage by individual species, coral coverage by functional morphologic groups, and the diversity index of functional morphologic groups of corals. For the line transect data total coral coverage (or calcareous red algae or matrix) is calculated as the total length of all coral species intercepted by the transect line divided by the length of the transect line; coral coverage by individual species is calculated as the total length of the transect line intercepted by all the corals of a given species divided by the length of the transect line; and coral coverage by a functional morphologic group of corals is calculated as total length of all the species of a functional morphologic group intercepted by the transect line divided by the length of the transect line. Grid-point data are counts only, so coral coverages must be estimated indirectly. For the grid-point data total coral coverage (or calcareous red algae or matrix) is estimated as the total number of grid-points occupied by corals divided by the total number of grid-points; coral coverage by individual species is estimated as the total number of grid-points occupied by all the corals of a given species divided by the total number of grid-points; and coral coverage by a functional morphologic group of corals is calculated as the total number of grid-points occupied by all the species of a functional morphologic group divided by the total number of grid-points. A Shannon and Weaver information index of the five functional morphologic groups of corals, plus matrix, is calculated

$$H' = - \sum_{i=1}^s p_i \ln p_i,$$

where  $p_i$  is the proportion of coverage of the  $i$ th functional morphologic group ( $i = 1, 2, \dots, s$ ).

## RESULTS

Observations and data from the transects at Ylig Point revealed the presence of a flourishing, shallow-water, Holocene reef complex composed of 31 reef-building coral species (Table 1). Twenty-six of the 31 species were recorded directly from the transects and an additional five species (*Psammocora* sp. 1, *Stylophora mordax* (Dana, 1846), *Porites cylindrica* (Dana, 1846), *Acanthastrea echinata* (Dana, 1846), and *Heliopora coerulea* (Pallas, 1766)) were recorded from outside the transect areas in the vicinity of the landward grid-point area. Species abundance is actually somewhat higher than that indicated, because the species list includes five species complex groups which

Table 1.—Percent of substrate coverage by reef corals, calcareous red algae, and matrix calculated from a line intercept transect and two (landward and seaward) grid-point sampling areas at Ylig Point. Colony size distribution is given for the line intercept transect.

Species and f.m. (functional morphological) group	Line intersect transect size distribution (cm)				Landward grid-point area		Seaward grid-point area	
	Occurrence (counts)	$\bar{x}$	St. Dev.	Percent coverage	Occurrence (counts)	Percent coverage	Occurrence (counts)	Percent coverage
Cespitose (f.m.)								
<i>Pocillopora setchelli</i>								
Hoffmeister, 1929	151	22.5	15.9	21.9	2	0.3	391	37.1
<i>Pocillopora</i> (spp. complex)	43	19.3	14.2	6.2	90	14.3	61	5.8
Total Cespitose (f.m.)	194	—	—	28.1	92	14.6	452	42.9
Encrusting (f.m.)								
<i>Millepora platyphylla</i>								
Hemprich & Ehrenberg, 1834	5	16.0	13.0	0.7	10	1.6	4	0.4
<i>Leptastrea</i> (sp.1)	—	—	—	—	4	0.6	—	—
<i>Montipora</i> (spp. complex)	27	20.4	14.1	3.9	30	4.8	18	1.7
<i>Pavona</i> (sp.1)	4	20.8	6.4	0.6	—	—	—	—
Total Encrusting (f.m.)	36	—	—	5.2	44	7.0	22	2.1
Submassive (f.m.)								
<i>Aeropora monticulosa</i>								
Brueggemann, 1879	15	40.7	54.1	2.2	3	0.5	38	3.6
<i>Pavona duerdeni</i> Vaughan, 1907	—	—	—	—	2	0.3	—	—
<i>Acropora</i> (spp. complex)	13	16.1	8.1	1.9	38	6.0	17	1.6
Total Submassive (f.m.)	28	—	—	4.1	43	6.8	55	5.2
Corymbose (f.m.)								
<i>Acropora humilis</i> Dana, 1846	11	28.6	12.7	1.6	7	1.1	1	0.1
<i>Acropora nasuta</i> Dana, 1846	6	25.3	7.8	0.9	—	—	—	—
<i>Acropora irregularis</i> Brook, 1892	9	84.3	100.2	1.3	74	11.9	36	3.4
<i>Acropora</i> (spp. complex)	121	18.7	10.7	17.5	78	12.2	161	15.4
Total Corymbose (f.m.)	147	—	—	21.3	159	25.2	198	18.9

contain more than one species in each. As fossils, these complex groups are difficult to discriminate into distinct species because of the loss of characteristic calicular and coenosteal features. Conservative estimates of the number of species in each complex group are three for encrusting *Montipora*, four for corymbose *Acropora*, two for branching *Pocillopora*, two for submassive *Acropora*, and three for massive *Porites*, which would add another nine species to the present 31 for a total of 40 species for the entire Holocene reef complex at Ylig Point. With a detailed search of the study area the species list would most likely reach 50 or more species.

Transect data show the presence of two distinct coral communities consisting of a high-energy seaward reef facies with 16 reef-building species occupying 72.2 percent of the substrate and a low-energy landward (back-reef) reef facies with 26 reef-building species (21 from the grid-point sampling area plus 5 from outside the area) occupying 68.2 percent of the substrate (Table 1).

The seaward reef facies is dominated by cespitose *Pocillopora* species which occupy nearly 43 percent of

the substrate. The high-energy indicator species, *Pocillopora setchelli*, accounts for 86 percent of the corals within the cespitose groups and at places forms nearly monospecific patches up to four meters across. Another high-energy indicator species in the seaward reef facies are large colonies ( $\bar{X}$  dia. 40.7 cm) of *Acropora monticulosa* which occupy 3.6 percent of the reef substrate. Although acroporid corymbose corals are common in the seaward reef facies (18.9 percent substrate occupancy) they become the predominant group in the landward reef facies where they occupy 25.2 percent of the substrate. Other morphologic groups (encrusting, massive, and submassive) in the seaward reef facies are widely scattered among the dominant cespitose forms with a combined substrate coverage of only 10.4 percent. The Shannon Weaver diversity index for the five morphologic coral groups, plus matrix, in the seaward reef facies is 1.461.

In the landward reef facies cespitose forms occupy 14.6 percent of the substrate with the high-energy indicator species, *Pocillopora setchelli*, only accounting for 2.1 percent of the corals within the group. In contrast to the low substrate coverage (10.4 percent) in the

seaward reef facies, encrusting massive, and submassive forms in the landward reef facies collectively occupy 28.4 percent of the substrate. Other indications that the landward reef facies developed in a lower-energy environment include: 1) the presence of large ( $\bar{X}$  dia. = 42.2 cm) massive *Porites* species (7.5 percent coverage), which are absent in seaward reef facies, 2) the presence of ramose colonies of *Porites cylindrica*, which is rarely seen in high-energy environment, and 3) the low occurrence and substrate coverage (0.5 percent) by the high-energy indicator species, *Acropora monticulosa*. The Shannon Weaver diversity index for the five morphologic coral groups, plus matrix, in the landward reef facies is 1.724.

Although the community structure of the Ylig Point Holocene reef indicates the presence of a leeward low-energy reef facies, the occurrence of some high-energy indicator species in reduced abundance and coverage suggests the environment was not as protected as that of quiet lagoons or backreef moat zones of fringing reefs. Such protected reef communities can generally be recognized by the pervasive presence of both *in situ* and fragmented skeletal material of arborescent *Acropora*, ramose *Porites*, finely branched *Psammocora* and *Pocillopora*, and foliaceous *Pavona* species.

Crustose, ramose and encrusting species of calcareous red algae occupy 5.1 to 5.4 percent of the substrate in both the line transect and seaward and landward grid-point sampling areas (Table 1). Encrusting algae species were more prevalent as secondary encrustations around the basal regions of coral colonies and intercolonial substrate surfaces. At places, these algal encrustations were two or more centimeters in thickness. Small finely-divided ramose algal species were less common, but when encountered formed conspicuous masses up to 15 cm in thickness. No zone was encountered that could be interpreted as an algal ridge which is a common feature on the outer edge of Guam's present windward reef platforms.

Matrix, mostly consisting of coral-algal-mollusc fragments, foraminifers, articulated calcareous algal segments, mollusc shells, and angular to subrounded detritus ranging in size from pebbles to coarse silt (H. Siegrist *et al.*, 1983), forms a conspicuous element that occupies about 16 percent of the substrate in both the seaward and landward reef facies (Table 1). A detrital-rich zone with reduced coral coverage was encountered between the seaward and landward grid-sampling areas which accounts for the higher matrix coverage of 26.1 percent for the line intercept transect (Table 1). This detrital zone may represent a depositional region where storm-transported detrital material accumulated behind the seaward reef facies.

The "other" group recorded along the transects includes holes too deep to sample that have been infilled by recent sediments or filled with water, soft coral spicularite rock, vermetid molluscs, and *in situ Tridacna* shells (Table 1). The high substrate occupancy by this group in the landward reef facies (10.5 percent) was a result of a greater frequency (5.9 percent) of sediment-filled holes occupied by a scrub growth of *Pemphis acidula*, which were mostly absent in the seaward reef facies. Low substrate occupancy by the "other" group along the line intersect transect was a result of it being laid along a vehicle path through the axis of the peninsula where *Pemphis acidula* scrub was absent.

#### DISCUSSION AND CONCLUSIONS

The uniform elevation of the Ylig Point exposure, and of the Merizo Limestone in general, plus a flattened even exposure of *in situ* corals on its upper surface and the occurrence of large massive corals with flattened upper growth surfaces, indicate that the Holocene reefs reached sea-level equilibrium at approximately the same time as emergence. Dating of corals from the upper reef surface at Ylig Point by Easton *et al.* (1978) indicates that this emergence occurred about 3000 years B.P.

The community structure of the emergent Holocene reef at Ylig Point reveals the development of a wide reef platform over a seaward-dipping Pleistocene terrace by rapid upward growth of a flourishing reef facies composed of closely packed corals with spaces between and within colonies mostly occupied by calcareous algae and detrital matrix. Based primarily upon the present distribution patterns of zonal coral indicator species, the emergent Ylig Point reef represents a shallow reef platform that can be divided into two distinct coral communities. The outermost seaward reef facies represents a high-energy zone dominated by *in situ* cespitose *Pocillopora* species that are interspersed with scattered corymbose and submassive *Acropora* species and a few widely scattered encrusting and massive species. In a shoreward direction the seaward reef facies grades into a lower-energy zone dominated by a more heterogeneous coral community that consists of increased numbers of corymbose, massive, encrusting, and submassive forms and few cespitose forms.

During the development of the Ylig Point reef platform, both the seaward and landward reef facies presented an extant upper level of closely-spaced, *in situ* reef-building corals that were secondarily encrusted by red calcareous algae at the substrate level and finally infilled by detrital material in inter- and intra-colonial voids at the lowest level. The final stage of reef platform development to sea-level equilibrium level was inter-

rupted by subsequent subaerial and intertidal weathering and erosion about 3000 years b.p. The present platform consists of a relatively flat solution-pitted and pinnacled surface with principal macro- and micro-relief features controlled to a large extent by differential weathering rates between the detrital matrix and *in situ* coral heads.

The community of corals and geomorphic interpretation of Guam's modern reef platforms require not only the consideration of a general post-Wisconsin transgression, but features inherited directly or indirectly as the result of a small amount of relatively rapid emergence of vigorously growing Holocene reef platforms as well. Most conspicuous of these features is the presence of fringing reef platforms that are out of equilibrium in respect to the present sea level, and during low spring tides are completely or partially exposed. Exceptions to such low-tide exposure are found at wide reef platforms, such as the one at Tumon Bay on the west coast of Guam, where an outer elevated part is exposed and an inner depressed part retains a shallow moat of water. Possibly these wide reef platforms consisted of an outer part that supported a flourishing growth of corals and reached sea-level equilibrium before emergence (present exposed zone) and a deeper backreef detrital depositional part that supported a less vigorous growth of corals and did not reach sea-level equilibrium before emergence (present moat zone).

When the Ylig Point raised reef community is compared with that of present-day reef platforms around Guam, conspicuous differences arise. Transect studies conducted by Randall (1978) on present-day leeward (13 transects) and windward (7 transects) fringing reef platforms revealed that coral species richness, density, and substrate coverage were quite variable, depending upon the nature of the substrate (stable consolidated or unstable unconsolidated) and whether or not the platforms were exposed or submerged during low tides. On the inner (backreef) parts of fringing reef platforms along leeward coasts, species richness ranged from 0 to 12, density from 0.0 to 13.2 colonies per m<sup>2</sup>, and substrate coverage from 0.0 to 12.8 percent; and on the outer (seaward) parts species richness ranged from 0 to 13, density from 0.0 to 10.6 colonies per m<sup>2</sup>, and substrate coverage from 0.0 to 5.3 percent. On the inner (backreef) parts of fringing reef platforms on the windward coasts along the north and south sides of Ylig Bay (200 meters north of the present study site), species richness ranged from 0 to 4, density from 0.0

to 0.7 colonies per m<sup>2</sup>, and substrate coverage from 0.0 to 1.7 percent; and on the outer (seaward) parts species richness ranged from 0 to 3, density from 0.0 to 0.01 colonies per m<sup>2</sup>, and substrate coverage from 0.0 to 0.001 percent. Many of the narrow reef platforms as well as most of the outer parts of wide platforms with moats are completely exposed during low spring tides. Such exposed platforms lack corals and other reef builders that can not tolerate long periods of exposure, or if present, are restricted to a few holes and depressions that retain water during such times. Most moat zones also have large areas without corals, or the community is significantly reduced in species richness and substrate coverage because of reduced water circulation and temperature elevation during low spring tides.

#### ACKNOWLEDGMENTS

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PETROGRAPHY OF THE MERIZO LIMESTONE, AN EMERGENT  
HOLOCENE REEF, YLIG POINT, GUAM

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ABSTRACT

The Merizo Limestone on Guam represents a flourishing Holocene reef complex that has emerged one to two meters above present sea level. Petrographic analysis and interpretations of outcrop samples collected along a 150-meter line transect across a major windward Merizo exposure at Ylig Point are presented.

Two texturally distinct intercalated facies characterize the samples: 1) coral-algal boundstone and 2) silty to sandy micritic packstone and wackestone. Early submarine high-magnesium calcite cements are widespread in the boundstones and in the body cavities of detritus. Finely comminuted silt- to sand-sized reefal detritus appears to be a later infilling, possibly representing an energy drop associated with emergence. Freshwater vadose diagenetic processes have not been effective.

INTRODUCTION

The Holocene Merizo Limestone crops out around the low supratidal (0.5 to 2.5 meters above sea level) perimeter of Guam as pinnaced and pitted stumps and discontinuous karrenfeld terraces. The formation was named by Tayama (1952) from extensive southwest coastal outcrops; subsequently redefined and dated at  $3400 \pm 250$  years by Tracey *et al.* (1964); and mapped (Fig. 1) and redated at 2975–5115 years by Easton *et al.* (1978). It is but one of the controversial "2-meter" limestones occurring around many western Pacific high islands. At least four other islands in the Marianas chain: Pagan, Rota, Tinian, and Saipan have comparable limestones. Their presence has led to the unresolved question of whether they represent a brief post-Wisconsin eustatic or regional +2-meter sea level stand or if their present supratidal position results sole-

ly from tectonic adjustments (Tracey, 1964; Curray *et al.*, 1970; Easton *et al.*, 1978).

This study is part of a broader program focusing on Neogene and Quaternary limestones in the Marianas undertaken to develop an understanding of the chronologic trends in reef structure, depositional facies geometries, and styles of diagenetic overprinting. Ultimately, we expect to apply these studies to stratigraphic and event correlations throughout the southern Marianas.

The objective of the current work is to describe trends in depositional and diagenetic textures and features within one major outcrop of the Merizo Limestone. This report presents petrographic data on a windward exposure at Ylig Bay along the central east coast of Guam (Fig. 1). Here, the Merizo veneers disconformably the Pliocene-Pleistocene Mariana Limestone

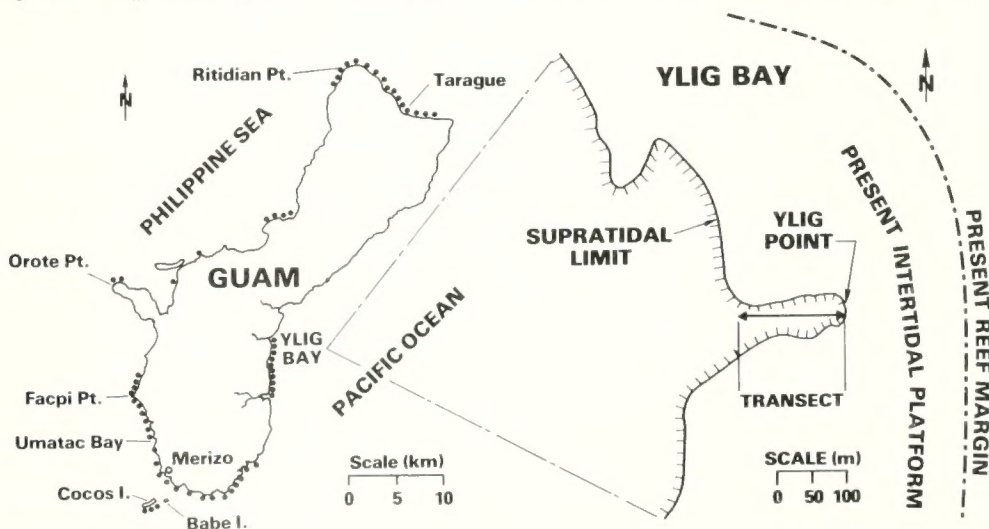


Figure 1.—Locality maps. Dots on Guam map (after Easton *et al.*, 1978) refer to outcrop areas of Merizo Limestone. Sampled localities designated by name.

forming a prominent, low-lying, and flat-surfaced peninsula jutting eastward onto the present intertidal reef platform. The peninsula covers about 3000 m<sup>2</sup> of Ylig Point. Merizo outcrops of Ylig never exceed 1.5 meters above mean low tide; preliminary thickness estimates based upon a just-completed drilling program indicate an average vertical section of Merizo at Ylig to be about 3.5 meters. The Mariana-Merizo contact is not traceable in outcrops at Ylig, but can be approximated at about 160 meters west of the seaward limit of Merizo outcrop.

## METHODS

Sampling for petrographic variation was carried out at approximate 10-meter interval stations along a 150-meter east-to-west line transect. Within a diameter of 2 meters at each station, 2 to 4 samples were removed for thin sectioning. Additional Merizo Limestone localities around Guam were spot sampled for comparison (Fig. 1).

Mineral composition and textural features were studied on stained and unstained slabs under low-magnification with a binocular microscope and on stained and unstained resin-impregnated thin sections with a petrographic microscope. Modal analyses were performed at 150 $\times$  magnification on 37 detrital-rich samples; between eleven and fourteen thin-section traverses of approximately 80 points per traverse provide the estimated compositions. Fine-grained mineral phases were identified by X-ray diffraction of whole rock and insoluble residues.

Texture nomenclature used in this report follows the terminology and definitions of Dunham (1962). Trace element distribution,  $\delta^{13}\text{C}$ , and scanning electron microscopic (SEM) analyses of cement compositions and morphologies are currently in progress on these as well as on drill-core samples.

## RESULTS

As viewed by binocular microscope, the Merizo Limestone generally is composed of greater than 60 percent *in situ* corals and/or encrusting algae with locally varying admixtures of coral fragments, foraminifers, vermetid gastropods, branching algae, and large reef mollusks occurring as poorly sorted, angular to sub-rounded detritus ranging in size from pebbles (1.5 cm) down to at least coarse silt (.06 mm). At Ylig, the formation varies landward from a coral-algal seaward boundstone facies dominated by cespitose coral growth forms (especially *Pocillopora*), and to a lesser extent by corymbose forms, through two conspicuous localized detrital-rich facies, then into a landward boundstone facies. The latter is rich in diversity but domi-

nated by corymbose coral growth forms (especially *Acropora*) (Fig. 2a).

The average thin-section modal analysis of detrital-rich specimens at each station along the line transect is given in Table 1 and summarized graphically in Figures 2b and 2c. Constituents are grouped into petrologically important end-members (Fig. 2b): grains (silt-sized and coarser bioclastic material); inter- and intragranular micrite; inter- and intragranular pores; and sparry calcite or aragonite pore-filling cements. Figure 2c shows the variation along the transect of the various components which make up the category "grains."

Several interdependent trends are suggested by the thin-section analyses. Silt and sand gradually decrease

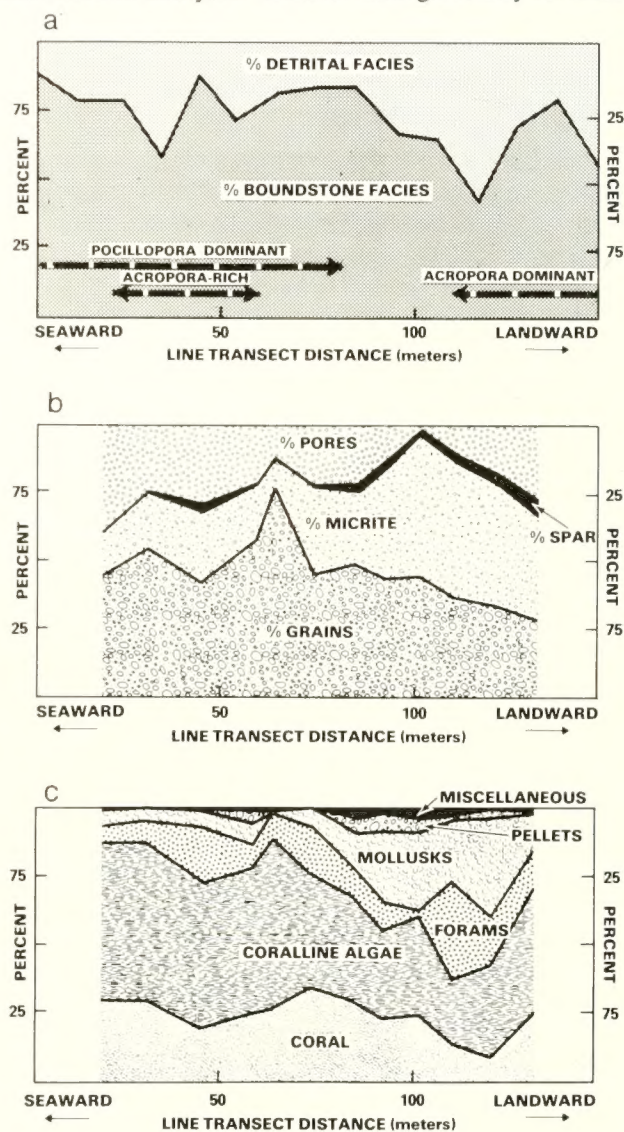


Figure 2.—Distribution of facies (a); textural end-members within detrital facies (b); and grain composition within detrital facies (c), across Ylig Point transect of Merizo Limestone.

Table 1.—Petrographic data from Merizo Limestone, Ylig Point.<sup>1</sup>

Line transect station	Meters landward of seaward outcrop limit											
	18	30	43	59	63	70	84	90	101	110	121	130
<i>In situ</i> coral-algal coverage (%)	80	79	67	74	75	80	81	86	70	68	46	74
Grains												
Corals	13.5	16.0	8.5	14.5	20.5	17.0	14.0	9.5	11.0	5.0	3.0	7.5
Algae	26.0	31.5	24.0	31.5	48.0	19.5	13.0	13.0	16.0	9.0	11.5	12.5
Forams	3.0	5.0	8.5	6.0	5.0	9.0	7.5	5.0	1.0	6.5	5.5	4.0
Mollusks	3.5	1.5	2.0	4.0	2.0	3.0	4.5	10.5	12.5	14.0	9.3	4.5
Pellets	—	—	—	0.5	0.5	—	2.5	4.0	3.5	1.0	3.0	1.5
Total grains	46.0	54.0	43.0	56.5	76.0	48.5	41.5	42.0	44.0	35.5	32.5	30.0
Micrite												
Intergranular	12.0	16.5	17.5	16.5	10.5	24.0	28.0	40.0	45.0	46.0	38.5	29.5
Intragranular	3.0	4.0	7.0	3.0	1.0	7.5	4.5	3.0	8.5	7.0	8.5	7.0
Total micrite	15.0	20.5	24.5	19.5	11.5	31.5	32.5	43.0	53.5	53.0	47.0	36.5
Pores												
Intergranular	30.0	20.0	18.5	17.0	8.5	17.5	20.0	10.0	2.0	6.5	11.0	20.5
Intragranular	8.5	5.0	12.5	6.0	4.5	4.0	3.5	3.0	0.5	2.0	6.0	7.5
Total pores	38.5	25.0	31.0	23.0	13.0	21.5	23.5	13.0	2.5	8.5	17.0	28.0
Sparry cement	—	—	1.0	—	—	—	1.0	1.0	0.5	2.0	3.5	4.0
Miscellaneous	1.0	—	1.0	2.0	0.5	—	1.0	—	—	—	—	2.0

<sup>1</sup> Averages rounded to nearest 0.5%.

landward in importance as the percentage of micrite increases. Highest percentages of micrite occur between 80 and 130 meters landward but micrite is conspicuous throughout the transect.

Thin-section pore count estimates increase both landward and seaward from the 101-meter station. Scanning electron microscopy (with energy-dispersive X-ray capability) reveals that the pores observed in thin-sections as well as those that are too small for

optical microscopic resolution are invariably lined with secondary carbonate cements. Scalenohedral-habit, high-magnesium calcite crystals (Figs. 3 and 4) and acicular aragonite have grown along both internal body-cavity walls and intergranular pore linings. These secondary cements constitute one mode of occurrence of the "micrite" as point counted.

A volumetrically more important mode of occurrence of micrite is as a light tan and optically dense

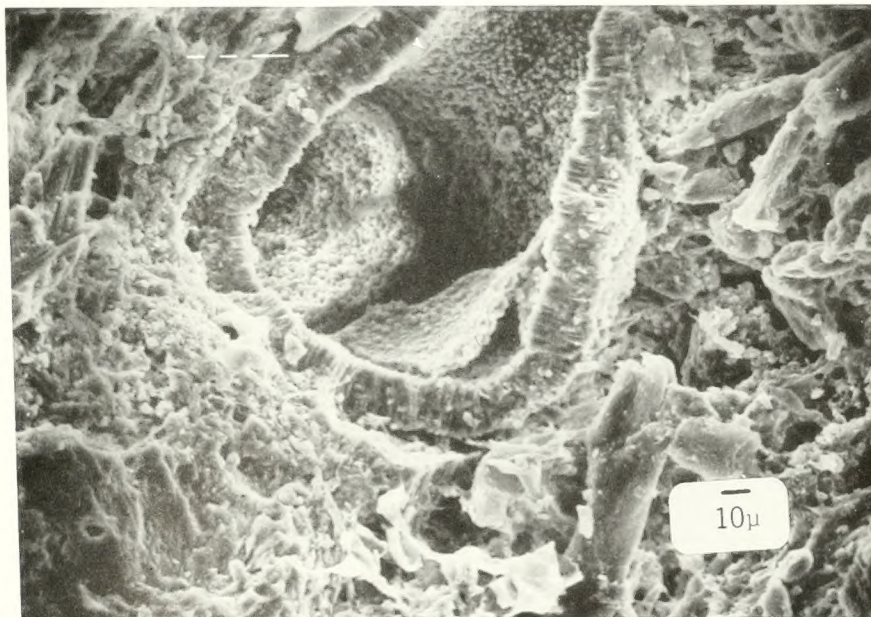


Figure 3.—SEM micrograph (430 $\times$ ) showing body cavity pore enclosing microcrystalline drusy pore-lining cement in Merizo Limestone, Ylig Point.

microcrystalline (4–30  $\mu\text{m}$ ) to submicrocrystalline material (<4 $\mu\text{m}$ ). Under the SEM, it is seen as an intimate mixture of predominantly high-magnesium calcite cement with far lesser amounts of indeterminate aragonite bioclastic debris. This material supports fine-sand and silt grains and commonly occludes the body cavity pores where it appears to be distinctly younger than the high-magnesium calcite and aragonite linings.

Sparry low-magnesium calcite cements are never a high-percentage constituent yet persist and increase landward from the 84-meter station. Feigel's solution staining and X-ray diffraction analysis of fifteen genera of *in situ* corals from the Merizo at Ylig reveal almost no aragonite-to-calcite conversion. However, because minor low-magnesium calcite is present, some conversion from either aragonite or high-magnesium calcite is indicated. (Conversion is complete in the underlying Mariana Limestone.)

Coralline algal fragments comprise the major grain type throughout most of the Ylig Merizo samples but are more dominant seaward than landward. Fragmented and abraded corals, and foraminifer grains are uniformly persistent throughout most samples. Mollusk pieces and fecal pellets only become important detrital ingredients landward from the 84-meter station. Echinoid spines, silt-size phosphatic grains and otoliths are among the very minor constituents throughout.

Conspicuous for their scarcity within the coarser than fine-silt size grains of Merizo at Ylig are either fresh or weathered volcanoclastic materials. Only occasional

goethite-hematite clumps and questionable chlorite flakes comprise the microscopically visible terrigenous assemblage in these rocks.

Photomicrographs of two typical fabric relationships exhibited by transect samples are presented in Figure 5 and 6. Figure 5 shows a geopetal infilling of an apparently unaltered coral by fine-grained angular bioclastic sand, supported by submicrocrystalline high-magnesium calcite (<4 $\mu\text{m}$ ). Figure 6 is a fairly typical packstone with angular bioclastic sand supported by the same type of submicrocrystalline micrite as Figure 5 (black in photo).

## DISCUSSION

An interesting aspect of the petrography of the Merizo Limestone on Ylig Point is the joint occurrence of exceedingly high coral coverages throughout the outcrop with high concentrations of high-magnesium calcite cements. We observe on the one hand a fossil reef community that flourished directly in the teeth of translational wave energy from the northeast trade-winds yet, on the other hand, a pervasive silty micritic matrix, occluding intergranular and body-cavity pores alike. The expectation of a well-winnowed grainstone facies never proved correct.

Fine-grained sediments are certainly not alien to reef front lithologies. Macintyre (1977) described a modern fringing reef at Galeta Point, Panama, with similar composition and style of cements to those at Ylig Point. His conclusion that highly agitated reef front waters intensified submarine cementing processes is certainly

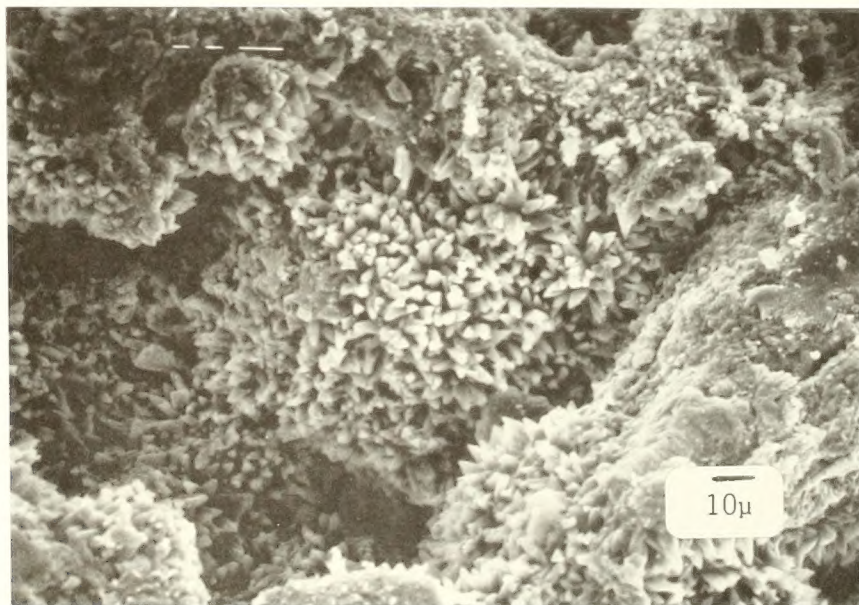


Figure 4.—SEM micrograph close-up (530 $\times$ ) of same body cavity pore as in Figure 3. Clusters of dogtooth high-magnesium calcite form pervasive pore-lining cement throughout the Merizo Limestone outcrop at Ylig Point.



applicable to the situation in our study; the Holocene reef at Ylig Point must have flourished in as severe a surf as existed anywhere on Guam.

Dryer and Logan (1978, fig. 8), report between 25 and 40 percent mud along the reef fronts in Castle Harbour, Bermuda. However, there the reefs are almost totally circumscribed by landmasses and the harbor is a low-energy sink for fine-grained sediments. Uplifted Pleistocene reef front facies described in Barbados are likewise very high in silt and clay-size de-

tritus (Mesolella *et al.*, 1970). Similar textures are reported for a lower Cretaceous reef front development in Texas (Jacka and Brand, 1977). Bathurst (1970, p. 263) concludes that, "despite the vigorous hydraulic environment of the exposed surface of the reef, the internal cavity system forms a quiet environment with sufficiently reduced flow and turbulence to allow accumulation of silt- and clay-grade internal sediments on the floors of cavities."

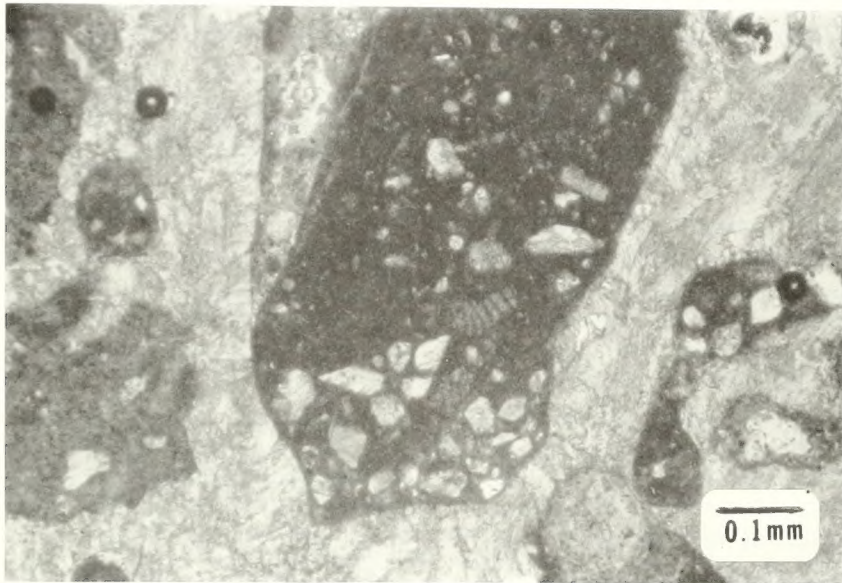


Figure 5.—Thin-section micrograph (60 $\times$ ) of body cavity geopetal infilling. Light-colored background is aragonite of *in situ* coral. Cavity is filled with submicrocrystalline magnesium calcite (black), supporting angular coral and algal silt.

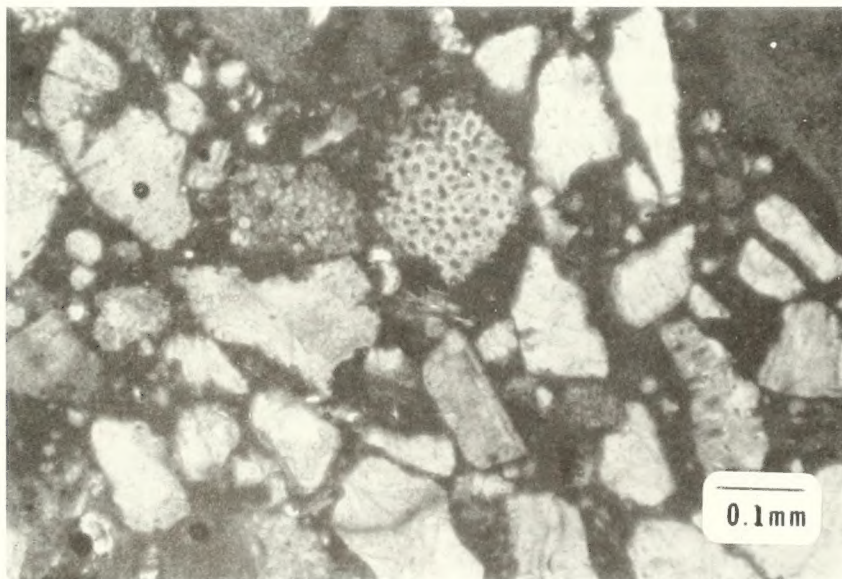


Figure 6.—Thin-section micrograph (60 $\times$ ) of packstone texture that typifies detrital portions of Merizo Limestone at Ylig. Microcrystalline to submicrocrystalline magnesium calcite (black) supports mixture of sand-size bioclastic reef detritus.

There is no dispute that the high-magnesium calcite and aragonite pore-linings are submarine in origin as advocated by Macintyre (1977) and earlier workers (e.g., Ginsburg and Schroeder, 1973). Similarly, the pervasive silt- and sand-supporting high-magnesium calcite cements are no doubt a marine accumulation, if based only upon the geometry of Ylig Point. It does appear that significant portions of this matrix are a later geopetal infilling of body-cavity pores because it blankets the pore-lining crystals. But the exact timing of the infilling is difficult to establish. A well-defined vertical gradient, from cores taken throughout the transect, indicating a rapid decrease in bioclastic matrix with depth would support any suggestion that the infilling is syn- or post-emergence. Absence of such a trend would point to early and continual mud accumulation in protected sites in an otherwise high-energy environment.

The general scarcity of terrigenous materials is further testimony to the winnowing efficiency that existed within the Holocene reef environment at Ylig Point. Today, during rainy seasons, significant quantities of weathered volcanoclastics move down the Ylig River into the estuary adjacent to the reef communities. Samples examined from the head of the bay and from previous bay sedimentation studies (Randall and Birkeland, 1978) confirm the availability of clay-through-sand-sized detritus. Even with the increased tendency of landward sediment trapping afforded by a +2-meter stand, it is doubtful that such a "clean" limestone could develop without direct and strong wave action throughout the reef community. This situation contrasts sharply with the low supratidal depositional environment today where periodically terrigenous sediment from the Ylig River estuary is driven up and onto the Merizo outcrop, becoming incorporated within the highly porous fabric of the rock.

Finally, there is very little thin-section evidence for freshwater vadose diagenesis. Solution porosity; neomorphism; rapid sparry cementation; and equant, isopachous, and interlocking crystals are scarce. The so-called unstabilized texture and mineralogy of the Merizo Limestone at Ylig clearly indicate short residence times in the subtidal marine environment of coral reef growth and the subsequent fresh- or mixed-water environment associated with the freshwater lens landward.

### CONCLUSIONS

Based upon our interpretation of the petrography of outcrop samples, we have concluded that a highly successful Holocene reef complex developed at Ylig Point, Guam, within a very high energy regime. Early sub-

marine cements crystallized first as high-magnesium calcite and aragonitic pore linings of the dominant boundstone frameworks and of body cavities of reefal debris, then subsequently as magnesium calcite pore occluding grain-supporting geopetal cements. Major accumulation of microcrystalline and submicrocrystalline reef or terrigenous detritus was constrained because of severe surf conditions.

Later, emergence terminated reef growth producing lower energy intertidal and subtidal regimes and depositional sites which favored infilling of the highly-porous Merizo Limestone outcrops.

Quantitatively little post-emergence freshwater vadose diagenesis has overprinted the mineralogy or texture of the Merizo Limestone at Ylig. No petrographic evidence exists from outcrop samples that the reef has ever been within a freshwater lens system.

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PALEOECOLOGICAL INVESTIGATIONS IN THE SMALL OLIGOCENE FRINGING REEF  
OF CAIRO MONTENOTTE, NORTHERN ITALY

THERÈSE PFISTER

Naturhistorisches Museum, Bern, Switzerland

ABSTRACT

In the Ligurian and Piemontese area of Northern Italy only a few small coral reefs and other coral formations could form during the Oligocene and early Miocene marine transgression. The reef of Cairo is characteristic for these reefs: It is a small fringing reef that established itself in shallow and calm water conditions. The coral limestone dovetails with detritic sediments. The reef shows a weak zonation, caused mainly by differences in water movement, abrasion and sedimentation rate. Correspondingly, several coral associations can be found. At good ambient conditions a dense growth of about 20 species of massive and, rarely, phaceloid coral colonies could become established. In places with greater accumulation of skeletal sand from water flows, massive *Porites* or *Actinacis* became predominant, growing in greater or lesser density. Where sedimentation of terrigenous mud was higher, few large massive corals, mainly *Astreopora* and *Porites*, and encrusted rubble of small branching species were found.

The coral limestone facies, unsorted micritic pack- and wackestones, mostly with many coral colonies in life position, are surrounded by sorted pack- and grainstones, partly with some coral colonies or coral rubble. The vertical succession and lateral changes in reef facies can be observed in the field. The total thickness of the reef is at least 30 m, much more than in any other known coral formation of Liguria and Piemont.

EVOLUTION OF EARLY CRETACEOUS REEFS IN THE GULF OF MEXICO

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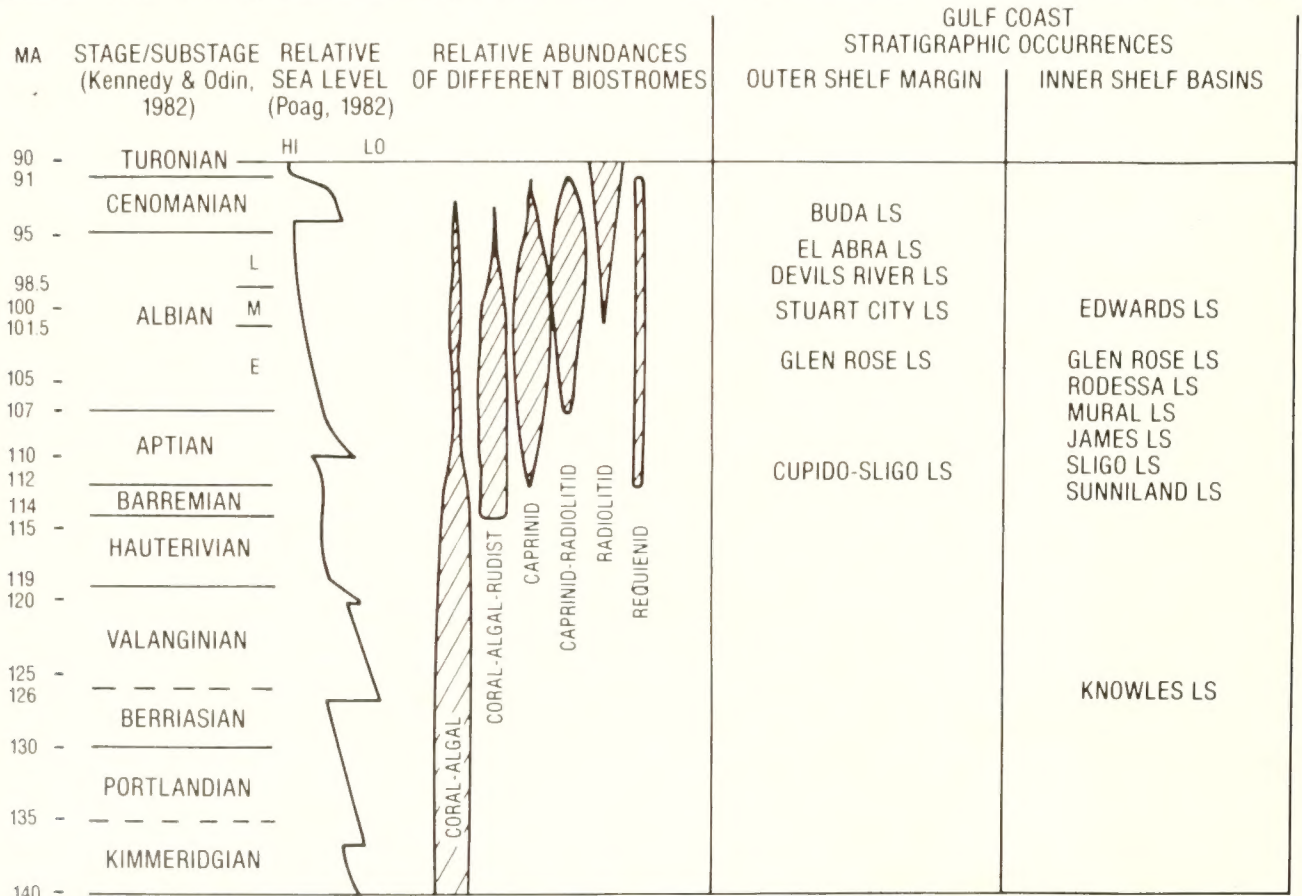
ABSTRACT

During the Aptian to Middle Albian, coral-algal-rudist reefs co-existed with rudist-dominated reefs in the Gulf Coast region. Six major biotic assemblages constructed buildups: coral-algal, coral-algal-rudist, caprinid, caprinid-radiolitid, radiolitid, and requienid. Early Cretaceous coral reefs did not fail because of widespread extinction of corals; in fact colonial corals diversified through the Cretaceous. Coral communities lived just below the zone of normal wave base and rudist communities occupied substrates generally within the zone of normal wave action. Further, the two communities probably did not compete for the same food resources. Therefore, causes of the demise of coral reefs were mainly environmental, and biotic interactions were of minor importance.

INTRODUCTION

Early Cretaceous coral-algal-rudist reefs in the Gulf of Mexico region were replaced by rudist-dominated reefs over a period of about 13–14 m.y., from Aptian to Middle Albian. Excellent examples of these types of reefs have been documented by facies analyses and a few by paleoecologic studies: Knowles Limestone by Finneran *et al.* (1984); Sligo and Cupido limestones

by Cunningham (1981), Wilson and Piali (1977), and Conklin and Moore (1977); James Limestone by Achauer and Johnson (1969); Mural Limestone by Scott and Brenckle (1977), Scott (1979, 1981), and Warzeski (1978); Glen Rose by Wells (1932), Perkins (1974), and Lozo and Stricklin (1956); Edwards Limestone by Young (1959), Roberson (1972), and Jacka and Brand (1977); Stuart City Limestone by Bebout and Loucks



Text-figure 1.—Stratigraphic distribution of Cretaceous reefs in the Gulf Coast.

(1974); and the El Abra Limestone by Griffith *et al.* (1969), Aguayo (1978), Enos (1974), and Coogan *et al.* (1972). This list is not complete and many units remain to be studied in detail.

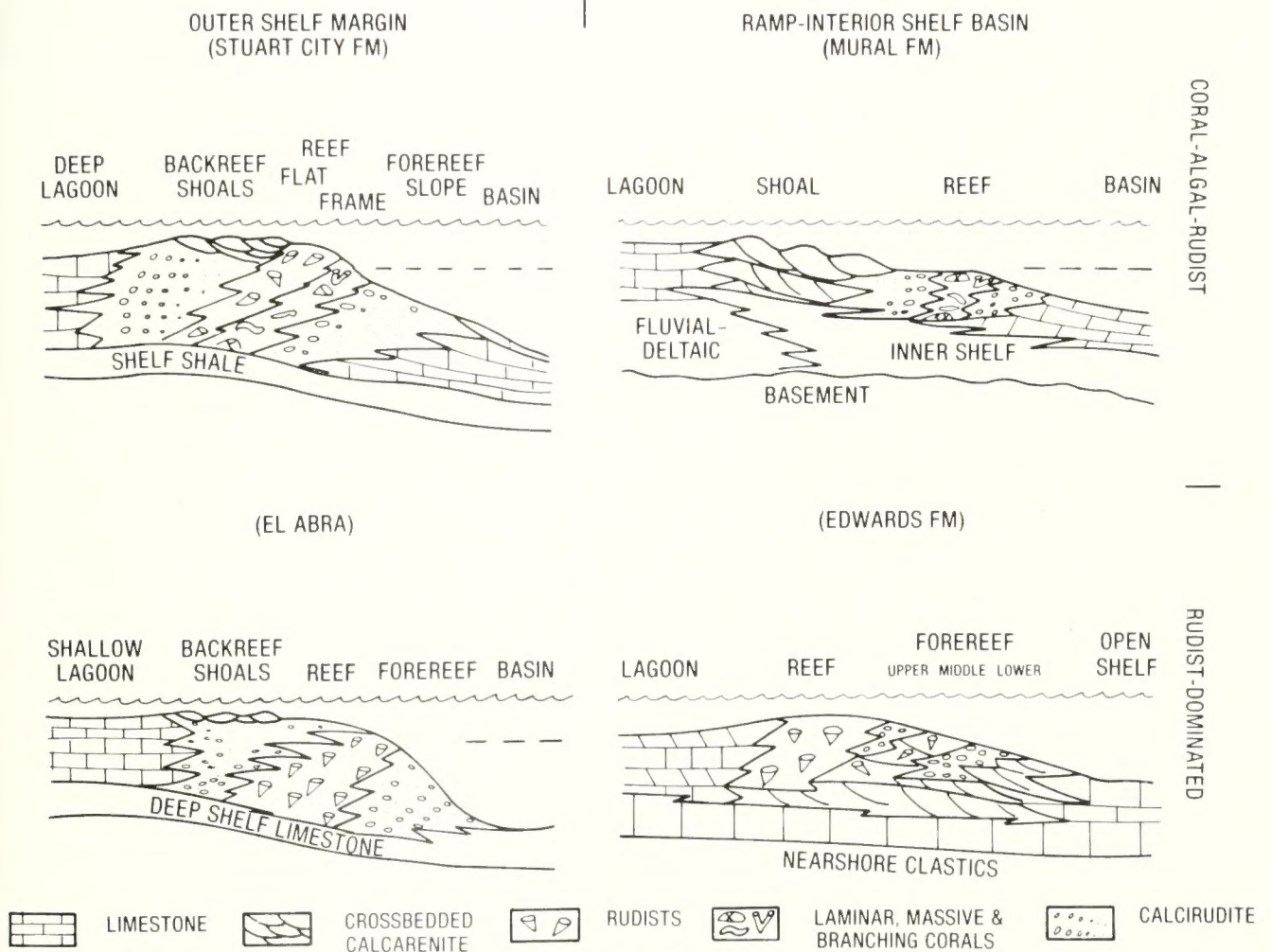
In the Mediterranean Basin the rudist reefs replaced coral-algal-rudist reefs during the Cenomanian and Turonian in a 4 to 7 m.y. period (Philip, 1980). After the Turonian, corals played only a subsidiary role in Late Cretaceous reefs (Beauvais and Beauvais, 1974; Coates, 1977), except perhaps locally where abundant massive corals formed local shelf margin reefs in Yugoslavia and the Mediterranean (Turnšek and Buser, 1976; Turnšek and Polšak, 1978). Radiolitid and hippuritid rudists dominated most Late Cretaceous reefs and formed tabular biostromes intercalated with high-energy carbonate sands (Kauffman and Sohl, 1974; Bein, 1976).

Hypotheses to explain the replacement of corals by rudists either call upon environmental processes or

biological processes. Increased turbidity in Late Cretaceous seas (Beauvais and Beauvais, 1974) and Santonian regressions (Philip, 1980) were suggested as factors stressing reefal environments so that the supposedly more eurytopic rudists expanded and the more stenotopic corals diminished in abundance. The alternative set of hypotheses calls upon a competitive advantage of rudists over corals either because of more rapid growth rates (Coates, 1977) or because of a complex of evolutionary developments (Kauffman, 1977).

TYPES OF REEFS

Early to Middle Cretaceous reefs in the Gulf Coast are characterized by six main faunal assemblages defined not only by the distinctive species composition but also the dominance of key taxa (Text-fig. 1). Each assemblage has a known stratigraphic range and an acme of abundance. These assemblages do not have



Text-figure 2.—Cretaceous reef models based on examples from the Gulf Coast.

stratigraphic value because their local occurrence depends on local environments.

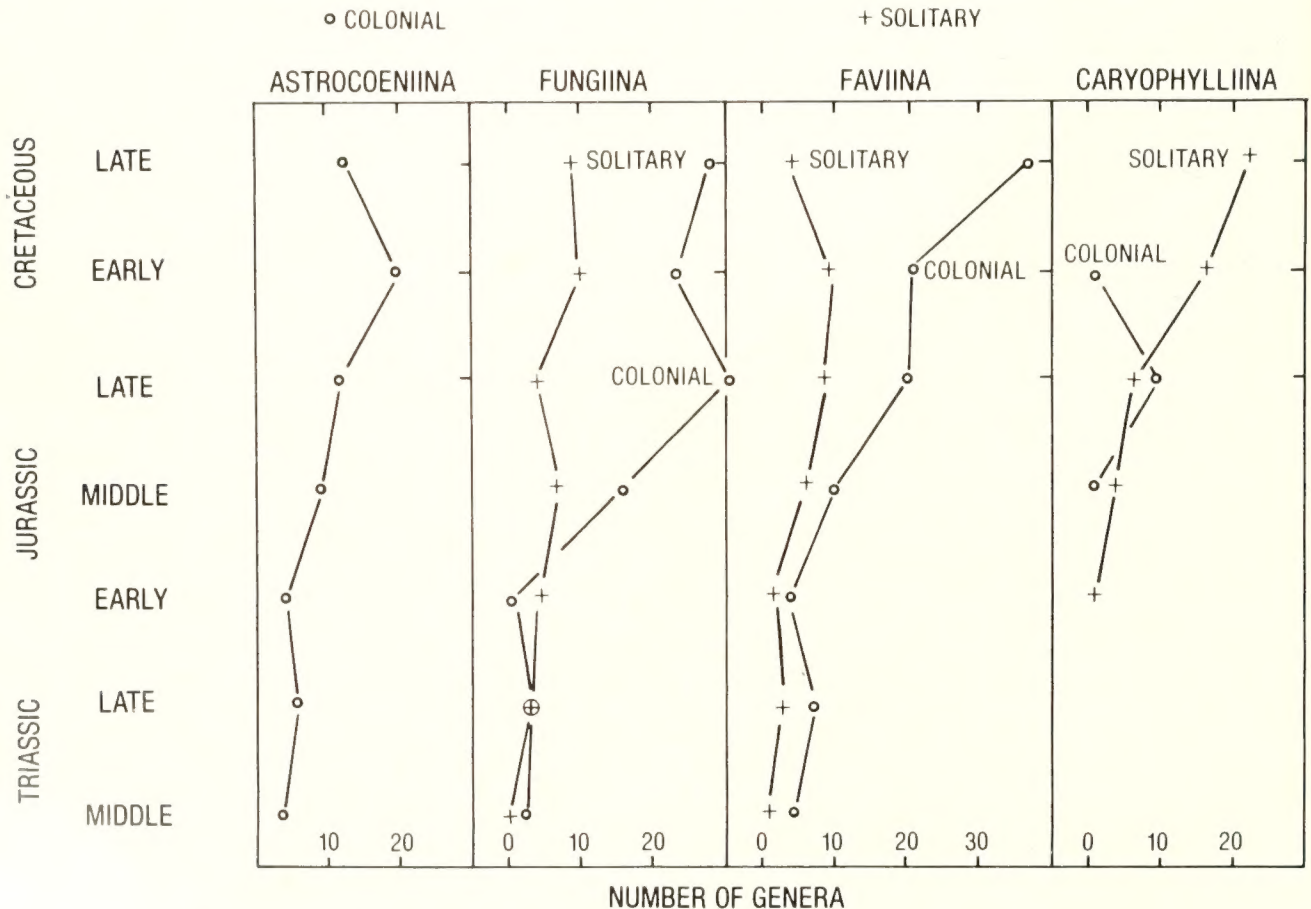
1. A coral-algal assemblage is characterized by a variety of hemispherical to massive corals encrusted by red and green algae. Stromatoporoids may be present but not abundant. This assemblage occurs in the basal Cretaceous Knowles Limestone where it is interpreted to have formed below normal wave base on a carbonate ramp facing the East Texas Basin (Fineran *et al.*, 1984). It may also occur in parts of the Cupido and Sligo limestones in Mexico and the U.S.

2. The coral-algal-rudist assemblage contains caprinids, monopleurids and requienids in addition to corals, algae, and stromatoporoids. The caprinids generally are thought to represent high energy reef conditions, and the corals low energy conditions below normal wave base. Reefs of this type developed on carbonate ramps around interior basins, as in the Aptian-Albian James, Mural (Text-fig. 2), Rodessa, and Glen Rose limestones (Scott, 1979; Achauer and Johnson, 1969). In the Gulf Coast the assemblage was first developed along an outer shelf margin during the Aptian in the Sligo and Cupido limestones (Wilson and

Pialli, 1977; Conklin and Moore, 1977); it is found in the Lower Albian Glen Rose Limestone, and it survived through the Middle Albian in the Stuart City Limestone (Text-fig. 2) (Bebout and Loucks, 1974). It persisted from the Aptian (Masse, 1980) into the Cenomanian in the Mediterranean (Philip, 1980).

3. Caprinid-dominated assemblages consist of one to a few species of these rudists encrusted with some epizoans and almost no other framework taxa. The associated grainstone sediments, with locally sorted bioclastic debris, reflect high-energy conditions. Numerous types of emersion surfaces also point to shallow water (Perkins, 1970). The caprinid assemblage apparently formed reefs on ramps marginal to interior shelf basins (Text-fig. 2) (Fisher and Rodda, 1969; Roberson, 1972; Perkins, 1974; Jacka and Brand, 1977), and it is also found in shelf margin reefs of the Sligo and Stuart City limestones (Bebout and Loucks, 1974).

4. Caprinid-radiolitid assemblages have a variety of framework rudists along with various associated species and epizoans. Normally the rock matrix is grainstone or packstone which suggests deposition within the zone



Text-figure 3.—Number of colonial and solitary coral genera in each suborder; data from Wells (1956).

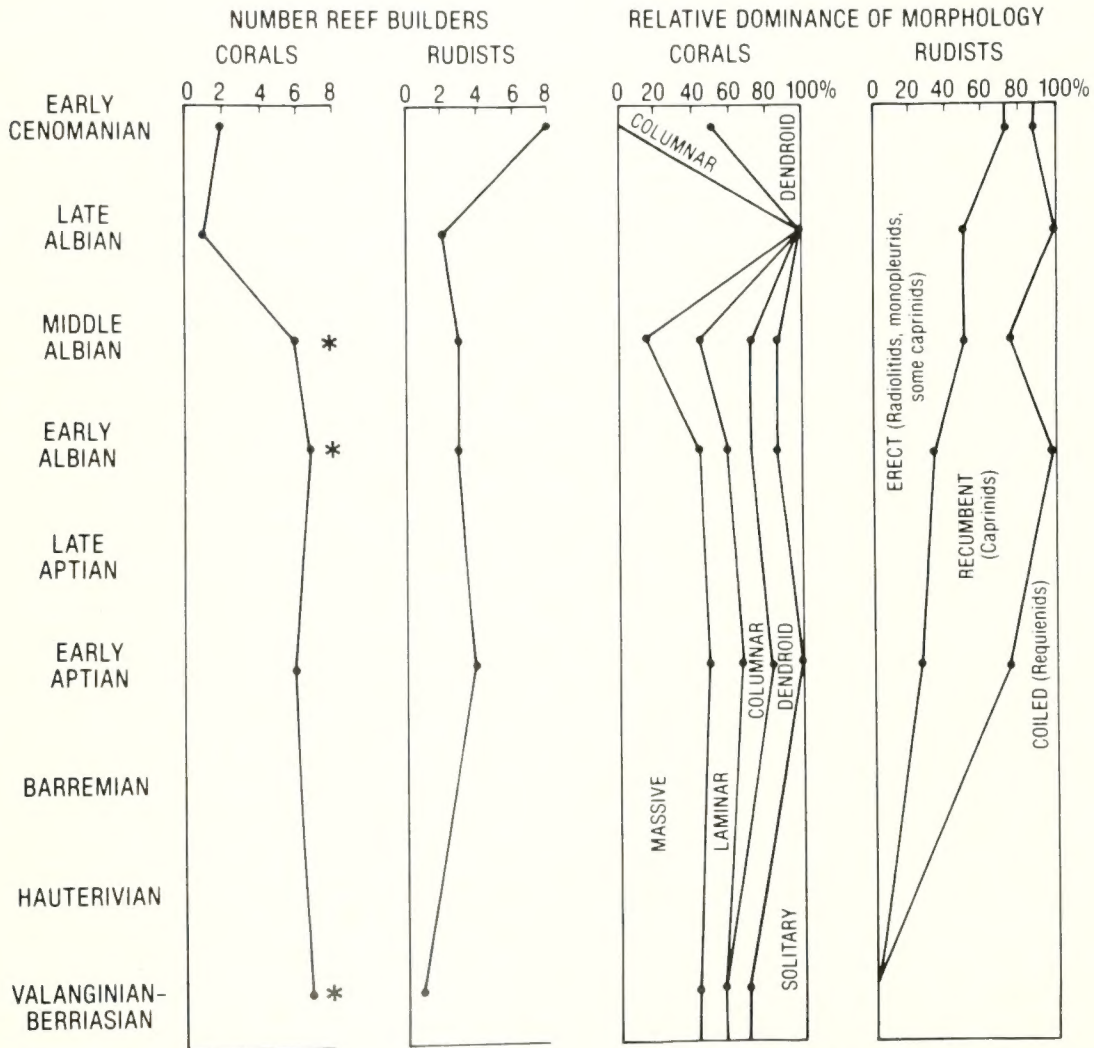
of wave action. The presence of intercalated well-sorted bioclastic gravel supports this interpretation. In the Stuart City Limestone this assemblage may represent a reef flat environment (Text-fig. 2) lying behind structures formed by the corals, algae, and rudists of assemblage 2. It also dominates the shelf-margin reefs of the Devils River and El Abra limestones (Aguayo, 1978) and is present locally in the Edwards Limestone in Central Texas along the ramp margin of the East Texas Basin (Fisher and Rodda, 1969).

5. The radiolitid assemblage is dominated by one or two erect rudists and sparse epizoans. It forms tabular biostromes, locally stacked into banks in the El Abra Limestone (Aguayo, 1978), where it is thought to have lain behind the reef crest at the shelf margin and in shoal areas on the carbonate platform. The radiolitid assemblage ranges into post-Cenomanian strata on the Yucatan Platform.

6. The requienid assemblage with a muddy matrix occurs in biostromes that are assumed to have formed low-energy areas of the shelf and in protected areas of ramp and shelf margin reefs (Scott, 1981). Locally requienids populated the reef flat as in the Cupido-Sligo and Stuart City limestones in association with the caprinid-radiolitid assemblage.

ANALYSIS OF BIOTIC COMPOSITION OF REEFS

The demise of coral reefs during the Mid-Cretaceous was not a result of widespread extinction of corals. In fact, the two largest suborders of colonial corals, Fungiina and Faviina, diversified from Early Jurassic into the Late Cretaceous (Text-fig. 3) (Wells, 1956). Only part of the coral expansion resulted from diversification of deeper water, ahermatypic, solitary corals; shal-



Text-figure 4.—Structure of selected Early-Middle Cretaceous reef communities in the Gulf of Mexico. Data marked \* based on detailed quadrat-thin section analyses; data from other units derived from field observations.

low water, hermatypic, colonial corals also expanded in protected niches among rudist biostromes (Coates, 1977; Coates and Jackson, 1984).

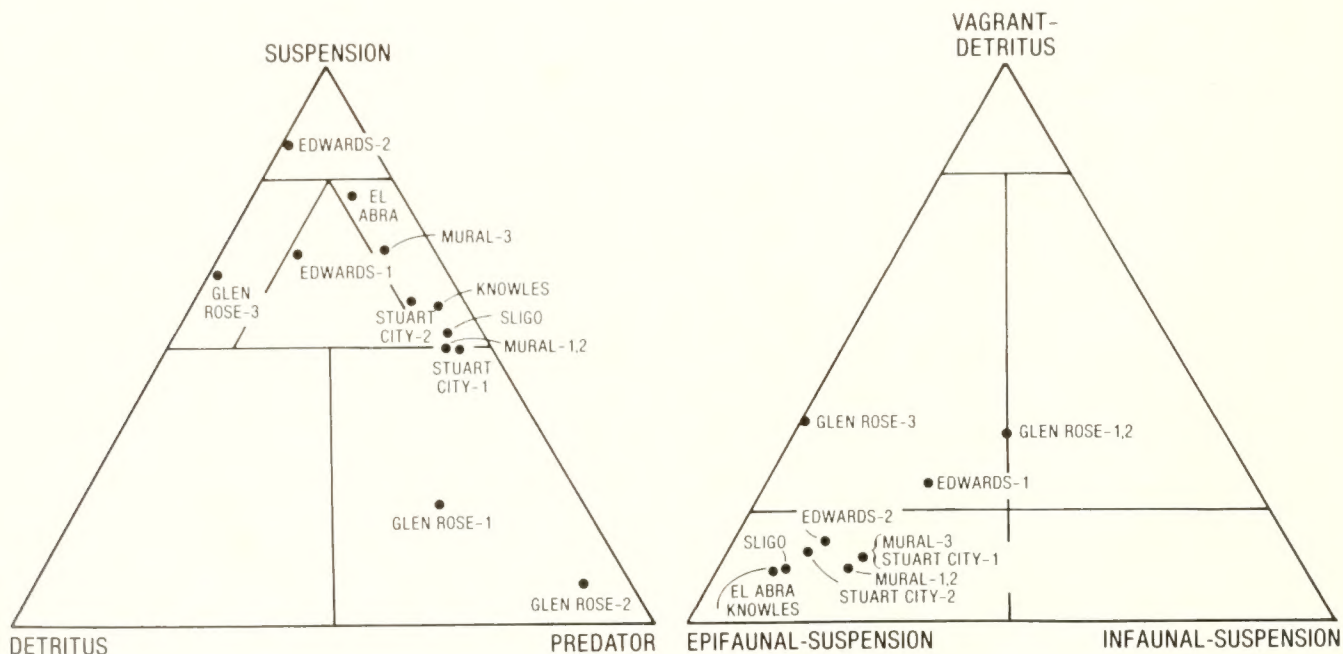
Rudists and corals coexisted in Cretaceous reefs from Early Aptian to Middle Albian (Text-fig. 4). But from Late Albian onward coral abundance decreased and rudists increased in reef communities. Rudist diversification started before corals began to decrease, perhaps because rudists adapted to high energy reef zones. The functional morphology of both groups may give a clue to this change. From Berriasian to Middle Albian times coral morphology in reefs was relatively constant, consisting mainly of massive and laminar corals. From the Middle Albian massive/laminar forms decreased (Text-fig. 4) and by Early Cenomanian times (El Abra Limestone) branching corals were dominant. Data are sparse for the Upper Albian. Rudist morphology also changed significantly as rudists diversified (Text-fig. 4). By the Early Cenomanian, erect conical types had replaced most of the recumbent and coiled encrusting forms. This probably resulted in more stable frameworks (Philip, 1972).

An analysis of preserved trophic structure, which is defined by feeding habits and substrate niches (Scott, 1976), suggests that corals and rudists did not occupy the same habitats nor compete for the same nutrients (Text-fig. 5). Coral assemblages in the Knowles, Sligo,

Mural 1-2, Glen Rose 1-2, and Stuart City 1 were dominated by passive predators. Rudist assemblages in the Mural 3, Glen Rose 3, Edwards 1-2, Stuart City 2, and El Abra were dominated by suspension feeders. Each assemblage contained a small number of preserved detritus feeders, mainly echinoids. Both are mainly epifaunal assemblages, though the Glen Rose assemblages appear anomalous because of low diversity of suspension-feeding taxa. With the demise of coral reef communities, feeding shifted from zooplankton to phytoplankton.

#### PALEOENVIRONMENTAL FACTORS

The demise of Early Cretaceous reefs was not a result of the extinction of corals, but of the reduction in coral reef communities just below normal wave base. The reefal rudist communities above wave base flourished and rudists diversified. Therefore, environmental changes seem to be more important than biologic processes such as competition in causing rudists to dominate. A combination of environmental effects seems more reasonable than the effect of any one factor. Surface water temperatures deduced from oxygen isotopes increased from 20 to 25°C during the Hauterivian to 25-30°C in the Albian-Cenomanian (Arthur, 1979). Anoxic conditions were widespread during the Aptian-Albian, the end of the Cenomanian, and at the end of



Text-figure 5.—Feeding habit-substrate niche diagrams of preserved megafossils. Mural 1 is the *Actinastrea* community; Mural 2 is the *Microsolena* community; Mural 3 is the *Coelcomana* community. Glen Rose 1 is from the Narrows of Blanco River (Wells, 1932); Glen Rose 2 is from Blanco River at Pleasant Valley (Wells, 1932); Glen Rose 3 is caprinid community in Perkins (1974). Edwards 1 is caprinid biostrome at Round Mountain Quarry, Comanche County, Edwards 2 is radiolitic biostrome at Watson Quarry, Comanche County. Stuart City 1 is a coral community and Stuart City 2 is a caprinid community in core of Shell No. 1, Chapman, Waller County, Texas.



the Coniacian (Arthur, 1979). These events probably were the result of local oceanographic-bathymetric conditions, rather than global factors (Waples, 1983). As sea level rose, however, the basinal oxygen-minimum layer could expand and flood onto the shelf (Waples, 1983). Stratigraphic evidence suggests that such flooding happened repeatedly during the Aptian-Albian in the Gulf of Mexico (Bebout and Loucks, 1974). Coral-algal-rudist reefs recovered following the Aptian and Early Albian transgressions, but after the Late Albian flooding, only rudist-dominated reefs repopulated the shelves (Devils River and El Abra limestones).

Composition of the pelagic ecosystem changed during the Aptian through Cenomanian as planktic algae and foraminifers diversified in a major evolutionary event (Tappan, 1971). New phytoplankton species of dinoflagellates and coccolithophores were added to the food chain, possibly others became extinct. New omnivorous grazers, the planktic foraminifers were added. This shift in the trophic structure coupled with perhaps stressful temperatures and periodic flooding of the shelves locally with oxygen-deficient waters may have altered the stability of the deeper communities in the reefal ecosystem.

Whatever the cause, the result was the extermination of coral-algal communities below normal wave base. Yet, rudists diversified in the new shallow-water habitats within the zone of normal wave action, and reduced coral populations took refuge in these widespread biostromes.

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## EARLY CRETACEOUS CORAL-ALGAL-RUDIST REEFS, GULF COAST

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### ABSTRACT

Early Cretaceous reefs in the Gulf Coast region comprised of complex communities of corals, algae and rudists are important biotic features of lower Cretaceous strata. Communities of various corals commonly encrusted by algae form bound frameworks that influenced the surrounding sedimentation. As the reef communities grew into the zone of wave action, shoal-water carbonate sands accumulated in the zones of highest energy. Various rudists occupied these mobile sandy substrates. In many places, these buildups were capped by well-sorted ooid grain shoals. Trends in species diversity and morphology clearly delineate these environmental patterns. The pioneer community is commonly massive *Actinastrea*, followed by hemispherical to laminar *Microsolena* commonly encrusted by stromatolites. In the Albian reefs, caprinid and monoplorid rudists such as *Coalcomana* and *Petalodontia* became abundant. Local biostromes of *Chondrodonta*, *Monopleura*, and *Toucasia* developed in the back reef on quiet-water, muddy substrates. These communities built both small-scale patch reefs upon carbonate ramps, such as in the Mural Limestone in Arizona, and larger reef complexes rimming the Early Cretaceous shelf margin, such as in the Stuart City Limestone in Texas. The corals and algae comprising these communities, like the rudists, were derived from the European Tethyan biogeographic province. The major distinction, however, is the markedly lower diversity of corals compared to the large number of species reported from the Tethyan province in Europe.

THE STROMATOPOROID FAUNA OF THE WEST POINT FORMATION  
(UPPER SILURIAN) ON THE GASPÉ PENNINSULA,  
QUEBEC, CANADA

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ABSTRACT

Stromatoporoids are a major constituent of many of the facies of the West Point reef complex around Port Daniel, Quebec. Several species of *Parallelostroma* and *Stromatopora*, some with commensal *Syringopora*, exhibiting morphologies ranging from laminar and tabular to hemispherical and domal, occur in the moderately diverse basal siliciclastic siltstones of the formation. The overlying three facies (sponge-supported? mud mounds, algal banks and crinoid debris shoals) contain fewer stromatoporoids and where they occur they are less diverse both taxonomically and morphologically. These facies are overlain by a stromatoporoid reef facies and an associated lagoon or mud-flat facies. The reef facies is dominated by laminar *Stromatopora* with minor laminar to tabular clathrodictyids while the lagoon facies is distinctive in containing a wide variety of stromatoporoid morphologies representing the genera *Stromatopora*, *Clathrodictyon*, *Amphipora* and *Parallelostroma*. Several small stromatoporoid patch reefs or bioherms are present in various facies throughout the section as well.

The West Point Formation has been interpreted as a community succession from pioneer stages to climax and dominance stages interrupted by a number of regressions. Evidence from the stromatoporoids and from the stromatoporoid-sediment relationships suggests a model of basin subsidence interrupted by periodic standstills during which there was increased siliciclastic sediment influx associated with contemporaneous volcanic activity in the area.

EARLY LLANDOVERIAN (SILURIAN) BIOHERMS OF ONTARIO, CANADA

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ABSTRACT

Some 302 bioherms of Early Llandoveryan (Rhuddanian) age have been plotted within an outcrop belt 40 km wide on the eastern side of Manitoulin Island, the northern fringe of the Michigan Basin. This is the world's largest and most extensive early Silurian reef belt known. These metazoan build-ups are graded into several types, dependent on size and faunal component: (1) *bryozoan* mud mounds, low relief <1 m, small diameter <5 m, (2) *stromatoporoid-tabulate* coral bioherms (relief 1-3 m, diameters about 20 m) and (3) *rugose* coral bioherms (relief 2-5 m, diameters averaging 10-100 m) containing phaceloid and cerioid rugosans and tabulates. The largest bioherms have a relief of >4 m and length up to 3 km, being flat-topped and elongate, barrier-type structures, and showing sequential series of coral-stromatoporoid elements. The Manitoulin Formation in which these occur is less than 13 m thick and was deposited directly on the Ordovician-Silurian unconformity: the largest reefs broke through the low tide mark, but most of the patch reefs were formed at or slightly below wave base on a relatively shallow, sheltered, marine intracratonic platform.

## PHANEROZOIC REEF DEVELOPMENT IN CHINA

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## ABSTRACT

A preliminary review of Phanerozoic reef evolution in China indicates some parallels with other parts of the world. Early Cambrian archaeocyathid-algal bioherms occur in Guizhou and calcareous algal mounds in Shanxi province. The early Ordovician featured algal mounds in Hebei, while Middle Ordovician calcisponge build-ups formed in Hubei. Llandoveryian coral-bryozoan biostromes occur in Guizhou, Hubei and Gansu, but Middle to Late Silurian and Early Devonian reefs are absent in China. Widespread Mid-Devonian stromatoporoid-coral reefs are found in Guizhou, Yunnan, Guangxi, Gansu, Shanxi and Inner Mongolia, with algal-sponge barrier reefs also in Guizhou. Only algal mounds occur during the Carboniferous, *e.g.*, Yunnan and the Tarim basin. Permian algal-sponge-bryozoan reefs are found in Hubei, Guizhou and Yunnan. Atoll and barrier-type reefs of Triassic age were formed by calcareous algae in Guizhou and Yunnan, calcisponge patch reefs in Sichuan. Cretaceous rudist-scleractinian mounds are present in Tibet.

## ORGANISMS: THEIR ECOLOGY AND FUNCTION IN CARBONATE CONSTRUCTION

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### ABSTRACT

Detailed paleoecological analysis of organisms shows that most can be regarded as indicators of particular environments (stenobiotic); others (eurybiotic) occur in several rock facies and show varied adaptive growth forms. There are a number of critical life requirements for most organisms and different organisms can construct carbonates in different ways. To demonstrate this the following problems and examples will be discussed: Indicators of 1) Reef and non-reef facies. 2) Water depth and energy. 3) Hard-ground and soft-ground. 4) Clear and muddy water. 5) Currents. 6) Cryptic environments. 7) Seasonality. 8) Salinity or water circulation. 9) Condition changes.

### INTRODUCTION

Organisms are commonly ecologically restricted. It has been found that the distribution of organisms is controlled by sedimentary facies and that some organisms lived in one environment only, whereas others lived in several different environments but were adapted differently to the different conditions (Tsien, 1968, 1969, 1971, 1974, 1980; Mouravieff and Tsien, 1983). The interpretation of skeletal features as environmental indicators is not easy. In many cases, the real role (or significance) and adaptation of the organism in an environment is masked by sedimentation and diagenesis. That is why the problem of organisms as paleoenvironmental indicators has been the subject of many discussions (Stearn, 1982).

The understanding of paleoecologic aspects of an organism is based on the observation and careful analysis of both the organism and the rock. Organisms show ecologic characteristics and generic or specific characteristics. Through careful paleoecological analysis, the ecologic characteristics (or aspects) of the organisms can be used as environmental indicators.

To demonstrate this, several examples are discussed.

#### REEF AND NON-REEF FACIES INDICATORS

Ancient reefs were built by organisms. But ecologic aspects of the reefs are less well studied than sedimentologic aspects. The presence of frame-building organisms has long been established as one of the best indicators of "reef" environments. But what does "frame-building" mean? In what conditions can an organism be considered as a frame-builder? To use organisms as reef facies indicators, it is important to understand the role of organisms in the construction of a reef.

Figure 1 shows five distinct ways in which reef-building organisms can construct reef carbonates (Tsien, 1982).

1. *In situ* sedentary massive organisms can form the supporting framework of a reef or part of a reef (Fig. 1, framestone). Framestones should not be confused with rudstones (Fig. 2A) that are composed of similar organisms not in living position. Further, some *in situ* globular, rounded or columnar organisms commonly embedded partly in muddy substratum and not in mutual contact (Fig. 2B) do not form rigid frames and are not reefs.

2. Bindstones of Embry and Klovan (1971) are formed by tabular, lamellar and encrusting organisms. But the role of tabular or lamellar organisms and encrusting organisms in the construction of reef carbonates are entirely different. *In situ* sedentary tabular or lamellar organisms cover broken debris to protect and stabilize them to form one type of reef carbonate (Fig. 1, coverstone).

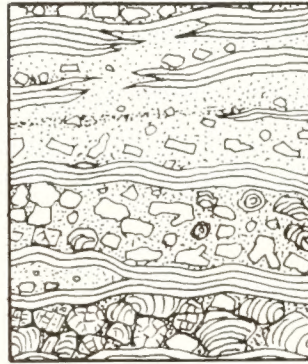
3. Encrusting organisms encrust or bind debris together to form a secondary reef framework (Fig. 1, bindstone).

4. *In situ* sedentary branching organisms slow down water movement and allow sediment to settle (Fig. 1, bafflestone). However, the role of branching organisms in the construction of a reef is multifold: a, Robust branching organisms may form a loose reef framework; or b, some fine delicate branching forms may act as a sediment stabilizer and supporter to form biogenic micrite.

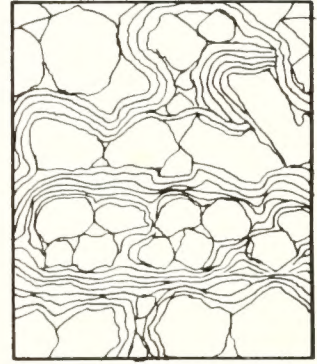
5. In mud mounds (some of them are reefs, Tsien, 1980; Mouravieff and Tsien, 1983), microorganisms (algae and bacteria) are important. They produce micrite, and trap, stabilize and support lime mud to form one type of reef carbonate that I called biocementsones (Tsien, 1982) (Fig. 1). The biogenic micrite and the lime mud can be cemented very rapidly to form a secondary reef framework. Some other microorganisms are specialized for living in cryptic habitats such as reef cracks, fissures, holes and cavities. Many of



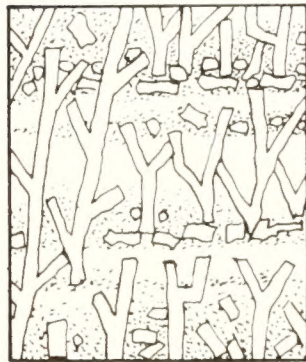
FRAMESTONE



COVERSTONE



BINDSTONE



BAFFLESTONE



BIOCEMENTSTONE

## REEF LIMESTONE

Reef building  
organisms built  
reefs in five  
distinct ways

Figure 1.—Five different reef-building organisms construct five different types of reef carbonates. See discussion in text (T sien, 1982).

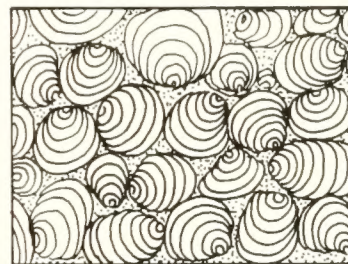
these microorganisms produced micrite, filling and cementing the reef debris into a solid rigid reef mass.

In these five ways different organisms form reef frameworks. But, if they have no function in the construction of the reef, the same organisms are not reef facies indicators.

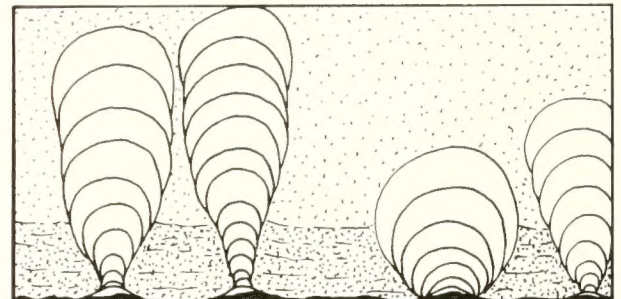
### WATER DEPTH AND ENERGY INDICATORS

The morphology of organisms has long been used as an important environmental indicator. But interpretations have often been oversimplified and overgeneralized. The morphology of some organisms is a good environmental indicator, but this is not the case for other organisms. Therefore, caution must be used.

*Stromatoporoids*.—The patch reef, at Fondry des Chiens, is built mainly by large irregularly shaped massive and encrusting stromatoporoids generally of the same species, with crinoidal grainstone matrix containing stromatoporoid debris in places (Fig. 3). No micrite has been found in the matrix of the massive forms. However, slight vertical variations occur in the reef facies with some layers of corals and lamellar stromatoporoids including some micrite matrix. Crinoidal



A



B

Figure 2.—The presence of frame-building organisms when not functioning as frame-builders is not an indicator of a reef environment. See text discussion. 2A, Stromatoporoid rudstone. 2B, Stromatoporoid floatstone.

grainstones with small stromatoporoid fragments, suggest that the most favorable condition for the irregular shaped massive stromatoporoids is in an environment of shallow agitated clear water, while the presence of micrite indicates that the lamellar stromatoporoids occurred in deeper, moderately agitated muddier water. However, massive stromatoporoids do not appear to be related only to wave resistance as would generally be assumed. They can be found in almost any environment. Their ecologic conditions range from shallow agitated clear water of the reef (irregular shape), to calm conditions (attached columnar form) to shallow restricted subtidal environments (tennis ball-like forms) (Tsien, 1974).

The massive rugose coral *Hexagonaria* and tabulate coral *Alveolites* are important in the upper part of the Lower Frasnian in Belgium. They are abundant in different rock facies suggesting that *Hexagonaria* and *Alveolites* were adapted to different kinds of bottom conditions. Both *Hexagonaria* and *Alveolites* have a thin disk-like form in open marine, calm, non-reef conditions. They have a globular shape with a deeper calice in the reef facies (Tsien, 1968, 1971).

In an open marine, moderately agitated water en-

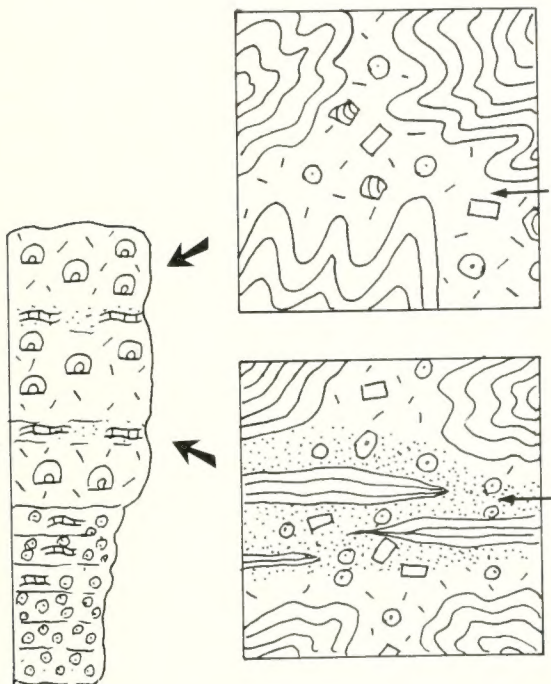


Figure 3.—Fondry des Chiens, Nismes, Belgium. Patch reef constructed by irregular massive stromatoporoids. Crinoidal grainstone with small stromatoporoid debris (arrow, upper right figure) suggests high energy, clear water environment. Lamellar stromatoporoids with lime mud (arrow, lower right figure) indicates moderately agitated muddier water conditions.

vironment, large amounts of *in situ* sedentary lamellar or tabular organisms can cover broken skeleton and other debris to protect and stabilize it, thus the debris can be cemented very rapidly to form reef carbonates. In many biostromes and bioherms, the reef facies are often distinctly graded with large organic fragments at the base and the fine-grained packstones or wackestones with lamellar or tabular organisms at the top of each sequence (Fig. 4). Fragments of organisms indicate the periods of destruction of the reef whereas the growth of lamellar or tabular organisms indicates the periods of construction of the reef.

#### HARD-GROUND AND SOFT-GROUND INDICATORS

On a hard substratum the corals attach with roots or talons (Figs. 5G, H), while in a soft muddy sea bottom the same coral species have a cylindrical form or a cylindrical protocorallite for stability (Figs. 5L, M). On a smooth hard level-bottom, rough hard surface or smooth soft level-bottom, the fossil assemblages are different. They are to be identified only after careful examination and deduction as shown in Figure 5.



Figure 4.—*In situ* lamellar or tabular stromatoporoids (S) cover skeletal and other debris such as *Hexagonaria* (H), *Thamnopora* (T) to form reef limestones. In this case, the rock sequence indicates that the reef facies has developed under varying conditions: broken organic fragments suggest strongly agitated conditions possibly caused by storms; the graded bedding of organic debris suggests a turbid suspension caused by a storm of short duration; the deposits of wackestones indicate relatively calm conditions; the growth of lamellar organisms indicates moderately agitated clear water conditions.

### CLEAR AND MUDDY WATER INDICATORS

The example of Fondry des Chiens (Fig. 3) suggests that irregular massive stromatoporoids indicate agitated clear water conditions. Some stromatoporoids and tabulate corals such as *Alveolites*, are extremely sensitive to terrigenous material; slight turbidity may influence the rate of growth. An alternation of a clear water season and a turbid water season may cause some organisms like *Stromatopora concentrica* and *Alveolites suborbicularis* to form layers (the so called latilaminae). This can be shown by the periodic presence of terrigenous material in their skeletons. Most bafflestones suggest muddy water conditions.

### CURRENT INDICATORS

Many organisms in a particular facies may show an asymmetric development. This can be interpreted as a structural adjustment to some external force. In most cases, these forms are influenced by unidirectional currents (Tsien, 1970, 1974).

### CRYPTIC ENVIRONMENT INDICATORS

A wide variety of large and small cavities occur in ancient reefs (Tsien, 1980; Mouravieff and Tsien, 1983). The roof of some cavities is coated with a thin irregular layer of milky, pale reddish brown or gray micrite containing the algae *Renalcis* and *Epiphyton*. The micrite cement is in turn coated by iron oxide with *Frutexitis* and *Epiphyton*. In this case, the algae can be observed growing from both sides of a fissure or downward from the roof of a cavity. The fact that they lived in the dark and that their growth form and direction are in contradiction to the usual orientation of an upward-branching organism, suggest that they are probably fossil microbial colonies that thrived in cavities and large fissures (Mouravieff and Tsien, 1983).

### SEASONALITY INDICATORS

*Temperature.*—The rate of growth of organisms generally varies according to seasons in the subtropics. Hence, the skeleton displays alternating thin, dense layers, the product of winter growth, and thick, porous layers, the product of summer growth, which together, make up a "year layer" (Tsien, 1968, 1969).

*Turbidity.*—Growth layers may be caused by the alternation of a clear water and a turbid water season. Stromatoporoids grew very slowly or ceased growing during the turbid water season and grew quickly during the clear, agitated water season. Hence the skeleton exhibits alternately thin, dense layers (sometimes with argillaceous materials), the product of the turbid water season, and thick, porous layers, the product of the

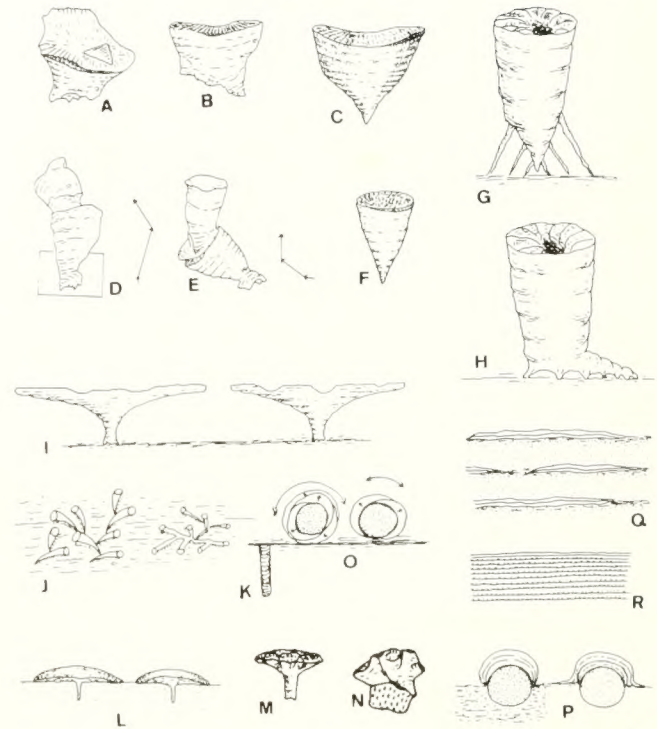


Figure 5.—Hard or firm ground indicators: A, B, D, E, G, H, I, J, K, N, O. Soft ground indicators: C, F, L, M, P, R. Soft or firm ground indicator: Q.

A, B, C: *Dohmophyllum* is very abundant both in shale and limestone beds of Co3 and Gi1 levels in Belgium. It shows conical form (C) in the shale beds (suggesting soft muddy sea bottom). When they are developed on a hard limestone surface (suggested by encrusting organisms on a limestone surface and by burrowers) or attached to a large skeletal fragment, they show roots and talons (A and B).

D–H: *Tabulophyllum*, abundant both on the platform limestone facies and in the shale peri-reef facies of Fr1 $\gamma$ ; shows conical form (F) in shale facies. The same species developed on a limestone hard ground, has roots and talons (D, E, G and H).

I: *Phillipsastrea goldfussi* and *Ph. pentagona* observed in the Upper Frasnian at Engis Quarry, Engis, Belgium, are generally attached to the upper surfaces of other *Phillipsastrea* colonies by talons; the same species at the same stratigraphic level in the shale facies in the Neuville area is disk-like without talons or roots.

J: *Aulopora*: generally developed on the skeletal surfaces of brachiopods, corals and stromatoporoids; on limestone surfaces it suggests a hard ground.

K: Evidence of burrowers.

L, M, N: *Hexagonaria davidsoni*, *H. mae*, *H. buxutiensis* and *H. gamboni* (Tsien, 1977) are very abundant in the shale, peri-reef facies near Lion Member (Frasnian) in Frasnian region, generally with a protocorallite. The protocorallites have different growth habits, either free of attachment (L, M), or attached to another coral or to a brachiopod. In this latter case, they have talons (N).

O: Alternating in growth direction and successive encrustations (Tsien, 1979).

P: Half encrusted debris (Tsien, 1979).

Q: Lamellar organisms on mudstones or wackestones.

R: Algal mats.



clear water season. If turbidity was too great, stromatoporoids ceased growing and the lateral margins of the latilaminae became invaginated flanks (Tsien, 1974). Many *Alveolites*, *Phillipsastrea* and stromatoporoids were buried by muddy sediments and only the highest part of the animal could remove the sediments (showing an autoclearing effect) and continue to survive (Mouravieff and Tsien, 1983).

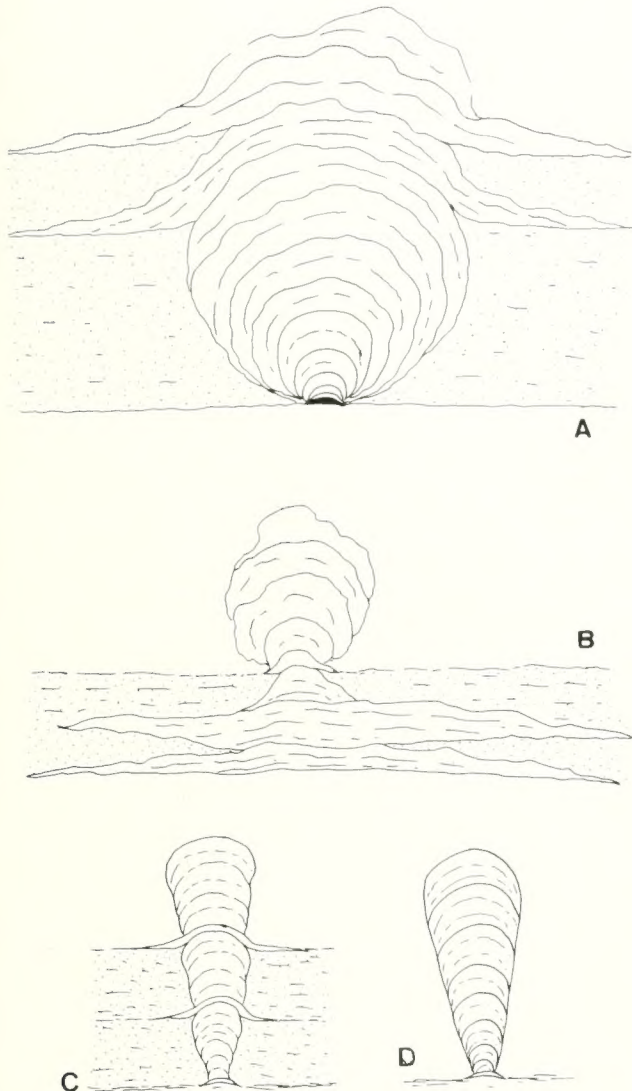


Figure 6.—Environmental control on the external form of stromatoporoids. A, Massive to lamellar form; *Hermatostroma polymorphum*, Lower Frasnian, Lion Quarry, Frasnes, Belgium. B, Lamellar to massive form; *Actinostroma verrucosum*, Givetian, Fondry des Chiens, Nismes, Belgium. C, Columnar alternating with lamellar form; Givetian, Chitzechiao Formation, Ma-an-Shan, Hunan, China. D, Columnar form; Givetian, Chitzechiao Formation, Ma-an-Shan, Hunan, China.

## SALINITY OR WATER CIRCULATION INDICATORS

*Coenites gradatus* of the Couvinian in Belgium shows different growth development in different facies. It is thin-laminar in high salinity conditions but thick-laminar in open marine, well circulated water conditions. This was discussed by Tsien (1974).

## CONDITION CHANGE INDICATORS

Organisms can reflect particular environments (Lecompte, 1958, 1968; Klovan, 1964; Fischbuch, 1968; Noble, 1970; Tsien, 1968, 1971, 1974, 1980). Many species in various environments exhibit ranges of shapes. In some, certain growth forms are restricted to specific stable environments (generally with low diversity), while in a fluctuating open marine environment (generally with high habitat diversity), the same species show varied growth forms reflecting varied living conditions. Some stromatoporoids such as *Actinostroma verrucosum*, were encrusting in calm, low sedimentation rate conditions, but were irregular massive in clear agitated conditions. The external morphology of some *Cystiphyloides* can reflect condition change. In calm conditions, the corallum was cylindrical, while in high energy conditions with strong, unidirectional water movements and a soft sea bottom, the corallum grew horizontally producing "marginatum" or "lamellosum" forms (Tsien, 1970). Figure 6 shows changes in the external form of some stromatoporoids as a result of changes in the environmental conditions.

## CONCLUSIONS

As environmental indicators, fossil assemblages are probably more significant than individual organisms or individual growth forms. But fossil assemblages are not communities of organisms. A bed containing organic remains in a certain rock facies represents only the location and the medium of their burial. These fossil assemblages may be paleobiocoenoses, paleo-thanatocoenoses or both together. Therefore, it is only through careful paleoecological analysis that we may obtain some real information from fossil assemblages. In this paper I have attempted to demonstrate this by describing and illustrating several examples.

## ACKNOWLEDGMENT

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## SECTION 7

**Paleozoic Biogeography**

## INTRODUCTION

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Biogeography is the study of distribution patterns of organisms during stated periods of time. In common with other fields of biology, it has two principal components, description and analysis. Historically, paleobiogeography has proceeded from largely descriptive works dealing with whole geologic periods to more analytic studies on the stage or even zone level. Studies of coral paleobiogeography have followed this general pattern and an extensive literature exists.

Descriptions and analyses of Paleozoic coral distributions began in the 1890's or earlier and many early workers recognized patterns of geographic relationships that we are only beginning to understand and explain today. The history of thought and interpretations of Devonian coral distributions was reviewed by Oliver (1977, pp. 89-91). So far as I know, no similar "history" has been published for other parts of the Paleozoic, but the early stages and general patterns of investigation are certainly very similar.

In most of the Paleozoic systems, coral distributions are well enough known to permit analysis of interregional faunal relationships and their use to test compatibility with the various proposed reconstructions of ancient land masses. Principal review papers for each system are cited below. These, with their bibliographies, provide an entrée to the literature on the subject.

The only summary of the entire Paleozoic, is that of Hill (1981, pp. F49-63, 481-489). This is a remarkably succinct review of broad scale distribution patterns and provides a feeling for the evolution of such patterns through the whole history of the rugose and tabulate corals.

Ordovician and Silurian coral biogeography has been reviewed most recently by Kaljo and Klamann (1973). This is a stage-level analysis of the distribution of genera along with broad discussion of provinces and faunal movements. Webby (1980) made a similar analysis of Ordovician stromatoporoids and used the distribution patterns as a test of proposed reconstructions of Ordovician geography. Similarly, Pickett (1975) used Si-

lurian coral distributions for testing Silurian reconstructions.

Devonian coral biogeography was reviewed by Oliver (1977) with emphasis on recognition of three realms (two with rich coral faunas), subdivision of the Eastern Americas Realm into provinces and their history, and testing of previously proposed Devonian geographies. Old World Realm provinces and history were dealt with in greater detail by Oliver and Pedder (1982/84), Dubatolov and Vassiljuk (1981), and in several earlier papers by V. N. Dubatolov and N. Ya. Spassky (cited by Oliver, 1977).

Dubatolov and Vassiljuk (1981) also discussed Carboniferous coral provinces and proposed biogeographic regions and provinces in some detail. Fedorowski (1981) provided more distribution data and more extensive discussions of the patterns in successive stages. Both of these reviews of the Carboniferous discuss the implications of their patterns for physical geography, but Fedorowski tested proposed geographic reconstructions and plotted his provinces on stage maps that he modified for the purpose.

The Permian has not been comprehensively reviewed in any one paper but, as noted by Hill (1981, pp. F62-63), a coherent picture of coral biogeography can be assembled from several regional studies. Rowett (1977) and Stevens (1982) are good introductions to the literature; both authors are notable for their use of Permian corals to test geographic reconstructions.

The Fourth Symposium attracted fewer biogeographic papers than its predecessors. Perhaps this indicates that we are in a period of consolidation after a decade of analysis and testing of proposed geographies resulting from the general acceptance of continental drift. Certainly more data are needed from all areas in each system to refine provincial boundaries and faunal assemblage relationships. However, significant change in our understanding of provinces through time, is more likely to come from the addition of data from previously unknown or poorly known faunal regions,

or from the proposal of significantly different geographies to test.

The most conspicuous geographic weakness in most of the review papers cited above is China. Fortunately, the past few years have seen a major increase in the volume of systematic studies of Chinese Paleozoic corals and these data are ripe for integration into the world biogeographic picture. Several papers on Chinese coral geography have been published but most are in Chinese and difficult for the average western coral specialist to use. For this reason the first two of the papers in this section are particularly welcome as they summarize, in English, current work on coral biogeography in China: Wang, Li, and Wang discuss the Silurian and Early Devonian, and Luo, the early Carboniferous.

The second two papers fill smaller, but significant gaps. Rodriguez deals with Carboniferous corals from the Cantabrian Mountains of Spain. The geographic position of Spain during the Carboniferous is in dispute and the faunal relationships discussed by Rodriguez may help resolve this question. Wilson (abstract only) discusses the provincial affinities of some Permian corals from northern California. The Permian location of this area is also in question.

The four papers of this section are presented in stratigraphic order, from oldest to youngest.

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## SILURIAN AND EARLY DEVONIAN RUGOSE CORAL BIOGEOGRAPHY OF CHINA

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## ABSTRACT

Silurian and Early Devonian rugose corals of China are analyzed on the basis of genera and epochs by using the percentage of endemic genera and the Otsuka similarity coefficient. Seven biogeographic provinces belonging to four biogeographic realms, the Boreal, the Tethyan, the Australo-Pacific and the Gondwanan(?) may be recognized in various epochs. The Yangtze epicontinental sea province has high endemism, especially in the Early Silurian and Early Devonian. The Yangtze fauna shows a close affinity to that of East Australia in the Early Silurian and was more akin to that of the Urals and Central Asia in the Middle and Late Silurian. The intimate relationship between the coral faunas of South China, East Australia and western North America in the Early Devonian may indicate the strong influence of the Australo-Pacific Realm at that time.

## INTRODUCTION

Rugose coral zones and assemblages in the Silurian and Devonian of China have been recently summarized by Yu *et al.* (1979) and by Wang and Ho (1980). Silurian and Devonian rugose coral biogeography in general has been discussed by Hill (1959, 1967), Ivanovsky (1965), Kaljo and Klaamann (1973), Oliver (1976) and Oliver and Pedder (1979), and was comprehensively summarized by Hill in 1981. Wang made a preliminary study of Chinese Devonian coral provincialism during 1975, and Wang and Ho (1981) discussed the Silurian coral biogeography of China. The present paper attempts to give a brief account of the distribution of Silurian and Early Devonian coral faunas in China and of their biogeographic significance (Fig. 1).

Various authors have regarded the Silurian corals as mainly cosmopolitan and noted a distinction in the late Llandoveryan between Australia and North America. Ivanovsky (1965) has recognized a north European Province and a North American Province, with an intermediate Siberian and a more or less isolated South China Province. Oliver (1976) and Oliver and Pedder (1979) emphasized the contrast between the Eastern North American and the much more extensive "Old World" Realms. Wang and Ho (1981) indicated that the different provinces in China could be assigned to four realms, the Boreal, the Tethyan, the Australo-Pacific and the Gondwanan(?) respectively. The following discussion is based on an evaluation of the genera recognized and on the well-defined regions of stratigraphic and tectono-palaeogeographic characteristics. By use of the percentage of endemic genera in each region and by Otsuka similarity coefficient comparison of regions within China and between China and other parts of the world, we have recognized two stages, the earlier of Early to Middle Silurian age and the later of Late Silurian and Early Devonian age. For

convenience, an approximate correlation table of Chinese and European Stage names with representative Chinese rugose coral zones or assemblage zones is given in Table 1.

Table 1.—Correlation of European and Chinese stages and coral zones.

D2	Eifelian	Yingtangian	<i>Brevisseptophyllum-Utaratuia</i>
	Dalejan	Sipaian	<i>Psydracophyllum</i> <i>Trapezophyllum</i>
D1			<i>Lyriellasma</i> <i>Heterophrentis-Amplexiphyl-</i> <i>lum</i> <i>Xystriphylloides</i>
	Pragian	Putongou'an	<i>Chalcidophyllum</i> <i>Eoglossophyllum</i>
	Lochkovian		<i>Mucophyllum-Pseudomicrocro-</i> <i>plasma</i>
	Pridolian	Miaokao'an	<i>Weissermelia-Altaja</i>
S3			<i>Micula-Ketophyllum</i>
	Ludlovian	Guandian	
S2	Wenlockian	Ningqiangian	<i>Kyphophyllum-Idiophyllum</i>
	Upper Llandoveryan	Shiniulianian	<i>Kodonophyllum-Maikotia</i> <i>Dinophyllum-Rhabdocyclus</i>
S1	L. & M. Llandoveryan	Longmachian	

Table 2.—Comparison of Silurian and Early Devonian rugose corals of China with other parts of the world. (Upper: number of genera; middle: number of genera in common; lower: Otsuka coefficient.)

		Siberia	Central Asia	Urals-Tianshan	NW Europe	N.A. West	N.A. East	Austral. East
D1	57	12	51	57	34	39	29	57
SW China		4	11	15	9	16	6	18
		.16	.21	.26	.21	.37	.15	.30
S3 Jilin-Nei Mongol	30	X	35	42	20	X	21	10
			12	13	8		4	5
			.37	.37	.31		.20	.29
S2 Yangtze Platform	40	X	24	28	29	X	X	17
			13	14	10			10
			.40	.61	.32			.36
S1 Yangtze Platform	55	30	26	X	21	X	X	25
		20	18		16			21
		.51	.49		.47			.58

### EARLY TO MIDDLE SILURIAN

In the late Early Silurian (Late Llandoveryan), rugose corals began to proliferate in the Yangtze epicontinental sea where endemic genera account for 35 percent of the total (19 out of 55 genera). Representative forms include *Paramplexoides*, *Lindstroemophyllum* and the stauriids *Paraceriaster* and *Cystostauria*. The fauna is on the whole rather uniform within the platform area and shows a high level of similarity with that of East Australia (Table 2). Less abundant, contemporary coral associations were found in the Zhaohuajing Formation to the north of the Qilian Mountains and probably also in the Jifuke Formation in Central Tianshan. The presence of the Siberian forms *Tungussophyllum* and *Protopilophyllum* indicates a possible northern connection. A small, interesting *Amplexoides*-fauna recently found near Dongkacuo, north of Lhasa, Tibet shows an affinity to the Yangtze fauna (belonging to the Tethyan Realm) and is different from the Qomolangma region which probably occupied the northern margin of the ancient Gondwanaland (Fig. 2).

Conditions changed somewhat in the Middle Silurian when the most abundant coral faunas occurred near Ningquiang in northern Sichuan. *Idiophyllum* and *Nanshanophyllum*, with well developed tertiary septa, are among the peculiar forms which are also found in the Qinling and Qilian Mountains. The Guandi fauna of late Wenlockian to earliest Ludlovian age was probably developed in a more-or-less restricted sea in eastern Yunnan and is not comparable with the faunas of other regions. Owing to more extensive transgressions, the Yangtze fauna has a decreased endemism (25 percent, see Table 3), and bears an intimate relationship with faunas of the Urals and Central Asia in the USSR (Table 2). The similarity of coral faunas between these regions may indicate that they were all located on the complicated margins of the Proto-Eurasian continent,

and that there were shallow sea connections between the Yangtze and the northern massifs across the Xiugou-Tongcheng crustal consumption zone (Fig. 2). The decreased similarity of the Yangtze fauna to that of East Australia (as compared with the Early Silurian) and its increased affinity with Central Asia might have some relation to the possible northern motion of the South China massif during the Middle Paleozoic. The biogeographical provinces in Early and Middle Silurian time are shown in Figure 2.

### LATE SILURIAN TO EARLY DEVONIAN

The Late Silurian and Early Devonian mark an episode of prominent marine regression in China and the coral faunas were restricted to marine regions between the uplifted land areas. The richest coral fauna occurs in West Qinling where Silurian and Devonian deposition was continuous (Fig. 3). In the Diebu area of West Qinling 38 rugose genera have been identified, among which six are endemic. Many Central Asian and northwestern European forms such as *Columnolasma*, *Micula* and *Strombodes* occur here, although the Otsuka similarity coefficient is not high owing to the abundance of peculiar forms. *Protopilophyllum* and *Evenkiella*, known from Siberia, were also found, but apart from these, few genera are common to both regions. The West Qinling fauna shows a remarkably low similarity to East Australia, in strong contrast to the Early and Middle Silurian situation. We have combined the coral faunas from Central Jilin and southern Nei Mongol, which lie close to each other, and have compared the combined fauna with other regions of the world (Table 2). Close connections are obvious with Central Asia and the Urals, and the relationship with East Australia persisted. It is noticeable that some common forms occur in Junggar and South Tianshan across the Aibi-Xilamulun crustal consumption zone, which is inferred to represent an open seaway during

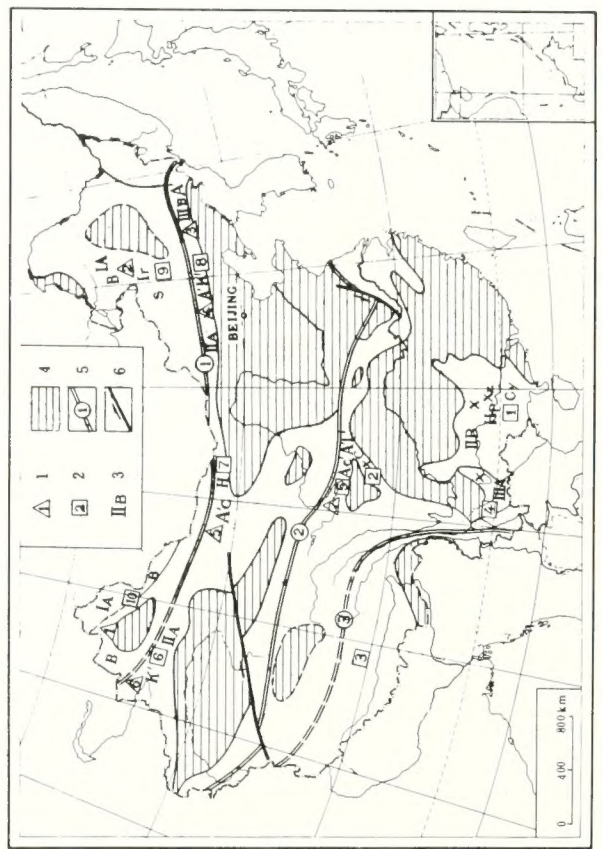
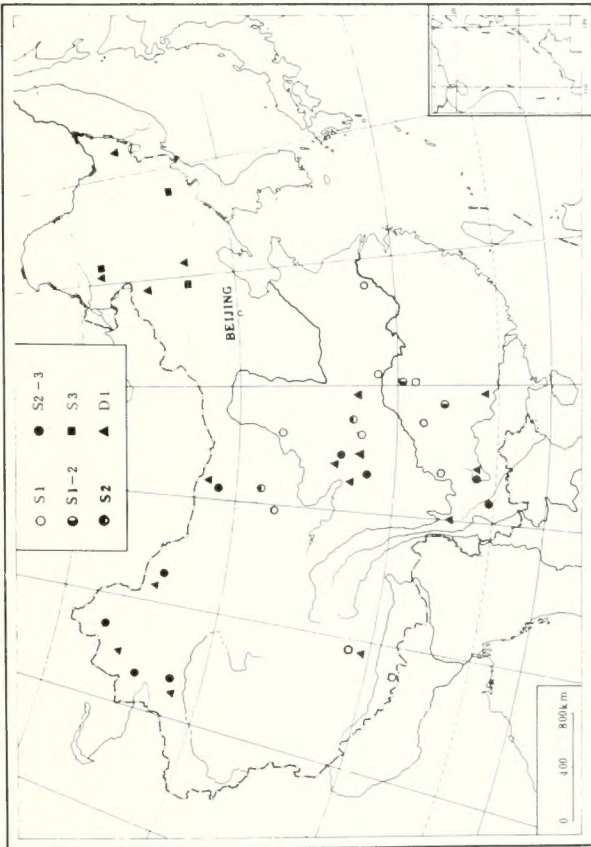
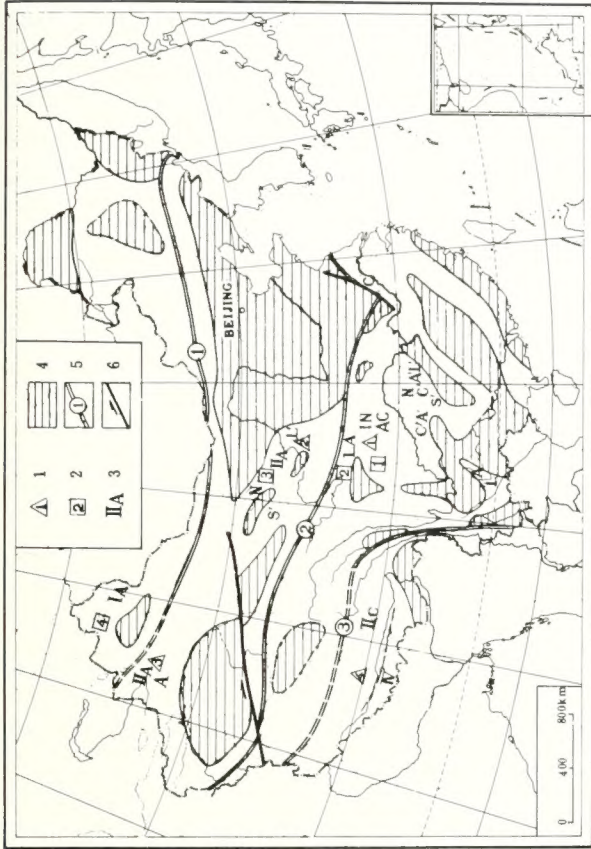


Figure 1.—Geographic distribution of Silurian and Early Devonian rugose coral localities in China.

Figure 2.—Early and Middle Silurian rugose coral biogeographical provinces and distribution of selected genera. Legends: 1, S1 coral localities; 2, S2 coral localities; 3, biogeographic provinces; 4, land; 5, later crustal consumption zones; 6, later transect faults. See Tables 2 and 3.

- I. Boreal (Siberian-Mongolian) Realm
  - IA. Junggar Province
- II. Tethyan (Eastern) Realm
  - IIA. Tianshan-Qilian Province
  - IIIB. Yangtze-Qinling Province
  - IIC. North Tibet Province
- IV. Peri-Gondwanan Realm
  - S1: A' *Amplexovoides*, C' *Cerastier*, L' *Lindstroemophyllum*, S' *Stauria*. S2: A' *Amplexovoides*, C' *Cerastier*, L' *Lindstroemophyllum*, I' *Idiophyllum*, N' *Nanshanophyllum*. Crustal consumption zones: (1) Albi-Xilamulun, (2) Xugou-Tongcheng, (3) Bangong-Nujiang.

Figure 3.—Late Silurian and Early Devonian rugose coral biogeographical provinces and distribution of selected genera. Legends: 1, S3 coral localities; 2, D1 coral localities; 3–6, as in Figure 2.

- I. Boreal (Siberian-Mongolian) Realm
    - IA. Junggar-Hingan Province
  - II. Tethyan (East) Realm
    - IIA. Tianshan-Net Mongol Province
    - IIIB. Southwest China Province
  - III. Australo-Pacific Realm
    - IIIA. W. Yunnan-Malaya Province
    - IIIB. Jilin-Japan Province
- S3: A' *Amplexovoides*, Ac' *Acerularoides*, K' *Kyphophyllum*, L' *Lindstroemophyllum*, D1: B' *Barrandophyllum*, C' *Crossoprentis*, Cy' *Cystobryelasma*, H' *Heterotrapezophyllum*, Hp' *Heterophaulactis*, S' *Sinochlamydophyllum*, X' *Xystriphyllodes*, Xz' *Xiangzhophyllum*.

the Paleozoic (Wang, 1981). To the north of this line rugose corals are small and solitary as in the Early and Middle Silurian.

The Early Devonian is the second epoch during which epicontinental sea faunas in South China (Guangxi and Guizhou Provinces) had a high degree of coral endemism (13 endemic out of 50 genera, Table 3). In this region rugose corals began to appear in the late Pragian and flourished in the Zlichovian (Yujiangian). Marine Silurian and Devonian deposits are continuous in West Qinling and western Yunnan, but the rugose coral zones have not been adequately established. Yu *et al.* (1979) have erected rugose coral zones or assemblage zones in the Guangxi-Guizhou region which contain many Australian genera (*Australophyllum*, *Chalcidophyllum*, *Trapezophyllum*, *Psydracophyllum*) and Australian-related genera (*Xystriphyllodes* with *Xystriphyllum*; *Xiangzhouphyllum* and *Tipheophyllum* with *Tropidophyllum* etc.). Thus there is a relationship between rugose coral faunas in South China and East Australia although the Oztuka similarity coefficient is not very high (Table 2). The Early Devonian corals recently reported from Hainza, Tibet are close to those of Lijiang, western Yunnan and are also of Australian affinity.

In the Tianshan-Nei Mongol Geosyncline along the northern border of the ancient Tarim-North China continent, rugose corals of similar aspect are distributed from Central Tianshan in the west to Central Jilin in the east, and are characterized by the presence of European forms such as *Schlotheimophyllum*, *Leptinophyllum* and *Glossophyllum* (Table 2). *Siphonophrentis*, *Aemulophyllum* and *Homalophyllum* of North American affinity were also found, especially in Badain Jaran, where the eastern North American forms are prominent. Two outstanding features in the distribution of Early Devonian rugose corals deserve notice: One is the high similarity of the South Chinese fauna with the western North American and the East Australian fauna (Table 2); this could be interpreted as reflecting the strong influence of the Australo-Pacific Realm. The western North American region seems to represent the eastern extension of the eastern province of the Australo-Pacific Realm (via Japan?; Fig. 3 IIIB), which may also account for the presence of North American forms in northeast China. The western branch of the Australo-Pacific, the W. Yunnan-Malayan Province (Fig. 3, IIIA), shows some connection

Table 3.—Comparison of total number of genera and endemic forms of Silurian and Devonian rugose corals of SW China (mainly Yangtze Platform).

	Late Early Silurian	Middle Silurian	Late Silurian	mid- late Early Devonian	Early Middle Devonian
Total genera	55	37*	38**	50	66
Endemic genera	19	9	5	13	15
Percent endemic	35%	25%	14%	26%	23%

\* Excluding genera in eastern Yunnan.

\*\* Including genera in Longmenshan.

with the West Qinling and the Hainza region of Tibet. No coral faunas are known in the Himalayan region, which represents one of the northern massifs of ancient Gondwanaland.

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## EARLY CARBONIFEROUS RUGOSE CORAL ASSEMBLAGES AND PALEOBIOGEOGRAPHY OF CHINA

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### ABSTRACT

The Early Carboniferous Rugosa of China may be grouped into six zones: 1) *Meniscophyllum xinjiangense* or *Ceriphyllum elegatum*, 2) *Kassinella* or *Caninia dorlodoti*, 3) *Enygmophyllum dubium* or *Cystophrentis*, 4) *Siphonophyllia oppressa* or *Pseudouralinia*, 5) *Dorlodotia mui* or *Thysanophyllum asiaticum*, 6) *Yuanophyllum*. The boundary between the Tournaisian and the Viséan is at the top of the *Siphonophyllia oppressa* Zone, and the *Yuanophyllum* Zone ranges from the Late Viséan to Early Namurian. Three biogeographic provinces, the Tianshan-Qilian, the Bayankela-Sanjiang and the Yangtze, are distinguished, which are represented by *Siphonophyllia oppressa*-*Gangamophyllum*, *Siphonophyllia*-*Pseudouralinia* and *Pseudouralinia*-*Kueichouphyllum* respectively. The main controlling elements of the biogeographic provinces, isolation of the ocean or the continent, ecological conditions, and convergence in parallel evolution are discussed.

### INTRODUCTION

Marine strata of Early Carboniferous age are widely distributed in China and contain abundant fossil corals. Professor C. C. Yu established four rugose coral zones in the 1930s.

Significant progress has been made in the study of Early Carboniferous corals since the 1950s, but many problems still exist. For example, the Rugosa in Northwest China show many differences from those of South China and belong to different paleobiogeographic provinces. Thus, the application of the rugosan zones of South China to Northwest China has caused confusion in stratigraphic correlation. Another problem is the evaluation of coral zones established in the thirties.

The aim of this paper is to analyze the data accumulated during the past three decades, to discuss the correlation of rugose coral assemblages, and to distinguish paleobiogeographic provinces.

### BIOGEOGRAPHICAL PROVINCES AND ASSEMBLAGES OF CHINESE EARLY CARBONIFEROUS RUGOSE CORALS

The Early Carboniferous Rugosa of China are distributed in three biogeographical provinces, the Tianshan-Qilian, the Yangtze, and the Bayankela-Sanjiang (Fig. 1). The characteristics of the faunas follow below.

#### Tianshan-Qilian Province

This province covers most of Xinjiang, Qinghai, Gansu, Ningxia and the western part of Nei Mongol. Sedimentary environments in the province are complicated because shelf seas existed only around the median massifs, such as Qaidam and Tarim, and the remaining areas are mostly geosynclines. There are many west European elements of Yanguanian Age, such as *Caninia*, *Siphonophyllia*, *Carruthersella*, *Sychnoelas-*

*ma*, *Lophophyllum*, *Cyathoclisia*, and *Campophyllum*, and also East European and Central Asian elements, such as *Keyserlingophyllum*, *Enygmophyllum*, *Humboldtia*, *Kassinella* and some North American genera, e.g., *Vesiculophyllum*, *Siphonophyllia*, *Humboldtia*, *Enygmophyllum* and *Kassinella* are representative genera of this fauna, which is distributed along the Qaidam Massif (Luo and Zhao, 1962; Wang, 1980, 1981). It is also reported in Tokesun, Jimunai and other localities in Xinjiang (Yu and others, 1978). The Datangian Stage is represented by *Gangamophyllum*, *Qinghaiphyllum*, *Dorlodotia*, and numerous colonial forms. Small reefs are found in the middle and upper Datangian Stage. The Rugosa of this province can be designated as the *Siphonophyllia*-*Gangamophyllum* fauna.

From more than ten stratigraphic sections where rugose corals were found (Luo and Zhao, 1962; Wang, 1981), the author has established a biostratigraphic sequence of five rugose coral zones (Table 1).

Wu and Zeng (1982) established, in Barkol of Xinjiang, the *Meniscophyllum xinjiangense* assemblage, characterized by small ceratoid corals without dissepiments, which may be older than the *Kassinella* Zone of Quinghai. Furthermore, this assemblage is associated with the ammonoid *Gattendorfia* at the base of the Carboniferous and may be the lowest coral zone of the Carboniferous in the Tianshan-Qilian Province.

#### Yangtze Province

This province includes all marine areas south of the Upper Yangtze and Qinling-Huaiyang Massifs, east of the Kangdian Axis, and west of the Cathysian Oldland. Corals of the Yanguanian Stage are characterized by *Cystophrentis* and *Pseudouralinia*. The Datangian Stage is indicated by *Kueichouphyllum*, *Heterocaninia*,



Table 1.—Early Carboniferous rugosan zones along North Margin of Qaidam Basin.

Units		Coral zones and subzones	Associated forms	
Datangian Stage	Huaitoutala Fm.	Yuanophyllum Zone	<i>Aulina (Aulina) rotiformis</i> Subzone	<i>Lithostrotion asiatica</i> , <i>L. portlocki</i> , <i>L. mccoynum</i> , <i>Lonsdaleia crassiconus</i> , <i>Aulina</i> sp., <i>Lonsdaleia crassiconus</i> , <i>Corwenia</i> cf. <i>rugosa</i> , <i>Yuanophyllum kansuense</i>
			<i>Gangamophyllum spiroides</i> Subzone	<i>Gangamophyllum rotiformis</i> , <i>Aulina (Pseudoaulina) cystoides</i> , <i>Carcinophyllum mendipense</i> , <i>Diphyphyllum echinatum</i> , <i>Corwenia longiseptata</i>
			<i>Qinghaiphyllum sinense</i> Subzone	<i>Qinghaiphyllum dimorphoides</i> , <i>Palaeosmia merophylloides</i> , <i>Yuanophyllum</i> sp.
	Sh.	<i>Dorlodotia mui</i> Zone	<i>Orionastraea huitoutalaensis</i> , <i>O. gigantea</i> , <i>Arachnolasma cylindrica</i> , <i>Carcinophyllum</i> sp.	
Yanguanian Stage	Chuanshangou Fm.	Ls. & Sh.	<i>Siphonophyllia oppressa</i> Zone	<i>Siphonophyllia delinghaensis</i> , <i>Caninia cornucopiae</i> , <i>Rotiphyllum yohi</i> , <i>Caruthersella lophophylloides</i> , <i>Campophyllum ovale</i> , <i>Lithostrotion</i> sp.
			<i>Enygmophyllum dubium</i> Zone	<i>Humboldtia qinghaiensis</i> , <i>Vesiculophyllum qinghaiense</i> , <i>Donophyllum primiticum</i>
			<i>Kassinella</i> Zone	<i>Lophophyllum densum</i> , <i>Amunikephyllum caninophylloides</i> , <i>Parakassinella sinensis</i>
	Cgl. & Ss.			

*Arachnolasma*, and *Neoclisiophyllum*. The Rugosa of this province can be designated as the *Pseudouralinia-Kueichouphyllum* fauna, which is characterized by endemic genera of the so-called "South-China Type." Based on the Shaodong section in Central Hunan (Wu, 1964; Wu and others, 1981) and the Dushan section in South Kueichou (Yu, 1931), the Early Carboniferous Rugosa of South China are distributed in six zones (Table 2).

#### Bayankela-Sanjiang Province

This province covers the vast regions west of the Kandian and Upper Yangtze Massifs, south of the Kunlun and Animaqing Mountains and north of the Amdo-Bangong Lake line, including mainly the Sanjiang geosyncline and its neighboring areas of complicated sedimentary facies. Rugose corals are often found in West Yunnan and in the Longmenshan Mountain of North Sichuan. Typical genera of the Yangtze Province, such as *Cystophrentis*, *Pseudouralinia*, *Kueichouphyllum*, are often associated with typical genera of the Tianshan-Qilian Province, such as *Siphonophyllia*, *Humboldtia*, *Gangamophyllum*, or they may appear

alternately. They may be called the *Siphonophyllia-Pseudouralinia* mixed fauna, which can be divided preliminarily into three zones in the Longmenshan region (Fan, 1980, and others) (Table 3).

Apart from the three provinces mentioned above, *Kueichouphyllum*, *Arachnolasma*, *Gangamophyllum*, *Sugiyamaella*, etc. have also been found in Northeast China, where some Japanese and Siberian forms were also discovered (Guo, 1980). This assemblage may represent a fourth province (Fig. 1).

#### Correlation of Early Carboniferous Rugose Coral Zones in China

The key point of correlation of the Early Carboniferous rugosan zones in China lies in the determination of the age of the *Siphonophyllia oppressa* Zone and of the duration of the *Yuanophyllum* Zone. The latter was established by Yu (1931) and was correlated with the *Dibunophyllum* Zone; it actually includes beds of Early Namurian age because the ammonoids *Platygoniatites* and *Dombarites* occur at the top of this zone in Guangxi. The *Siphonophyllia oppressa* Zone, of which *Siphonophyllia* accounted for about 60%, was estab-

lished by Luo and Zhao (1962) and was correlated with the C<sub>1</sub>-Lower C<sub>2</sub> Subzone of Avon, England. The *Meniscophyllum xinjiangense* or *Ceriphyllum elegantum* Zone may be the lowest coral zone of the Carboniferous in China. Correlation of the Early Carboniferous rugosan zones of China is summarized in Table 4.

FACTORS CONTROLLING EARLY  
CARBONIFEROUS  
RUGOSAN BIOGEOGRAPHICAL  
PROVINCES OF CHINA

Factors discussed below controlled the extension and

Table 2.—Early Carboniferous rugosan zones of South China.

Units		Coral zones and subzones	Associated forms
Datangian Stage	Zimengqiao Fm.	<i>Aulina (Aulina) carinata</i> Subzone	<i>Aulina (Aulina) rotiformis</i> , <i>A. (Pseudoaulina) senex</i> , <i>Palaeosmia regia</i> , <i>Dibunophyllum bipartitum</i> , <i>Lithostrotion asiatica</i> , <i>Neoclisiphyllum</i> sp.
		<i>Heterocania tholusitabulata</i> Subzone	<i>Hunanoclesia sinensis</i> , <i>Arachnolasma sinense</i> , <i>Clisiphyllum rigidum</i> , <i>Kueichouphyllum heishikuanense</i> , <i>K. sinense</i>
	(3)	<i>Thysanophyllum asiaticum</i> Zone	<i>Thysanophyllum grabaui</i> , <i>Kwangsiiphyllum pemicum</i> , <i>Caninia subbicum</i>
Yanguanian Stage	(2)	<i>Pseudouralinia gigantea</i> Zone	<i>Pseudouralinia tangpakouensis</i> , <i>Zaphrentoides parallelus</i> , <i>Siphonophyllia caninoides</i>
	(1)	<i>Cystophrentis kolaohoensis</i> Zone	<i>Cystophrentis tieni</i> , <i>Sychnoelasma konincki</i> , <i>Caninia cornucopiae</i>
	Shaodong Fm.	<i>Caninia dorlodoti</i> Zone	<i>Caninia patula</i> , <i>Zaphrentites steroseptatus</i> , <i>Dematophyllum minor</i>
		<i>Ceriphyllum elegantum</i> Zone	<i>Sychnoelasma konincki</i> , <i>Zaphrentites delanouei</i> , <i>Complanophyllum compressum</i>

(1) Menggongao Fm., (2) Liujiatang Fm., (3) Shidengzi Fm.

Table 3.—Early Carboniferous rugosan zones of Longmenshan.

Units		Coral zones	Associated forms
Datangian Stage	Qiangou Fm.	<i>Yuanophyllum</i>	<i>Arachnolasma sinense</i> , <i>Kueichouphyllum</i> sp., <i>Dibunophyllum</i> sp., <i>Gan-gamophyllum</i> sp., <i>Lithostrotion mccoynum</i> , <i>Kusbassophyllum</i> sp.
		?	<i>Thysanophyllum?</i> sp.
Yanguanian Stage	Maziauba Fm.	<i>Pseudouralinia</i>	<i>Pseudouralinia irregularis</i> , <i>Stelechophyllum</i> sp., <i>Siphonophyllia minor</i> , <i>Humboldtia</i> sp.
	Chang-tanzi Fm.	<i>Cystophrentis</i>	<i>Cystophrentis kolaohoensis</i> , <i>Caninia cornucopiae</i> , <i>Beichuanophyllum</i> sp., <i>Siphonophyllia irregulare</i>

division of the Early Carboniferous rugosan biogeographic provinces in China.

Distribution of Oceans and Continents

In the Late Tournaisian of West China many corals are often identified as *Siphonophyllia cylindrica*. The author believes that *Siphonophyllia* can be divided into two groups, the *Siphonophyllia oppressa* group and the *S. caninoides* group. The latter is characterized by larger lonsdaleoid dissepiments, and fewer and shorter septa, whereas the former is characterized by small lonsdaleoid dissepiments and many long septa dilated in the tabularium. *Siphonophyllia oppressa* is only found to the north of the Kunlun-Animaqing Mountains and extended northward through Xingjiang to Central Asia, but to the south of the Kunlun-Animaqing Mountains, in Longmenshan Mountain and West Yunan, only the *Siphonophyllia caninoides* group is found. Probably the *Siphonophyllia caninoides* group represented the fauna in the epicontinental sea on the south, while the

*S. oppressa* group occupied the north margin of the Tethyan Ocean, which acted as a barrier against passage of the coral planulae. Later crustal movement, the Hercynian and Indosinian orogenies, caused closure of the Tethyan Ocean, and folded zones were formed.

The Yangtze shallow sea was obviously an isolated inland sea.

Ecological Conditions

The distribution of the Yanguanian Rugosa implies that the coral community which dominated the Yangtze sea is usually characterized by thin epitheca and loose internal structure, probably related to the stable environment of the shallow, calm sea there. On the other hand, elements of the coral community in the broad seas of the Tianshan-Qilian and Bayankela-Sanjiang Provinces, such as *Siphonophyllia*, have thick epitheca, compact internal structure, and an oval, more or less stream-lined shape that could better resist the stronger waves.

Table 4.—Correlation of Early Carboniferous rugosan zones in China.

Western Europe		China					
		Tianshan-Qilian		Bayankela-Sanjiang	Yangtze		
Z	H	Yuanophyllum	<i>Aulina (Aulina) rotiformis</i>	Yuanophyllum	Yuanophyllum	<i>Aulina (Aulina) carinata</i>	Datangian
	E						
Viséan	D		<i>Gangamophyllum spiroides</i>				
		<i>Qinghaiphyllum sinense</i>					
	S	<i>Dorlodotia mui</i>	?	<i>Thysanophyllum asiaticum</i>			
Tournaisian	C	<i>Siphonophyllia oppressa</i>	<i>Pseudouralinia</i>	<i>Pseudouralinia gigantea</i>	Yanguanian		
	Z	<i>Enygmophyllum dubium</i>	<i>Cystophrentis</i>	<i>Cystophrentis kolaohoensis</i>			
	K	<i>Kassinella</i>		<i>Caninia dorlodoti</i>			
		<i>Meniscophyllum xinjiangense</i>		<i>Ceriphyllum elegantum</i>			

Table 5.—An illustration of rugosan convergent character during Late Tournaisian.

Bristol of England		Oulongbuluke of China	
Siphonophyllia bed	<i>Siphonophyllia cylindrica</i> mut. r <i>Caninia cornucopiae</i> "Zaphrentis" <i>omaliusi</i> <i>Cyathoclisia tabernaculum</i> <i>Carruthersella</i> sp. <i>Lophophyllum tortuosum</i>	<i>Siphonophyllia oppressa</i> <i>Caninia cornucopiae</i> <i>Rotiphyllum yohi</i> <i>Clisiophyllum qinghaiense</i> <i>Carruthersella</i> sp. <i>Lophophyllum</i> sp.	Siphonophyllia Zone

Finally, the apparent similarity of Early Carboniferous corals in the Bristol region of England and the Oulongbuluke area of China in the Late Tournaisian may represent parallel evolution, because they obviously belong respectively to the West European and Central Asian Provinces. The corals in both provinces show a close similarity (Table 5).

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## CARBONIFEROUS CORALS FROM EASTERN CANTABRIAN MOUNTAINS: PALEO GEOGRAPHIC IMPLICATIONS

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### ABSTRACT

During the Carboniferous Period, the Cantabrian Basin was covered by a warm sea. Corals are common in some stages there. During the Viséan, the sea was probably deep, and corals were associated with cephalopods. Cosmopolitan influence is remarkable. Tectonic movements were important from the Serpukhovian to the Kasimovian, and the corals flourished in three different structural regions. American faunal influences were important during the Viséan and Serpukhovian but disappeared during the Bashkirian, when faunal influences from eastern basins were still notable. That situation remained until the Moskovian. A rich coral fauna with a high level of endemism flourished during the Kasimovian, and same ancestors of Permian Mediterranean corals appeared then in the Eastern Cantabrian Mountains.

### INTRODUCTION

Corals from Eastern Cantabrian Mountains have been studied by the author during the last five years (Rodríguez, 1984). The stratigraphic and geographic distribution of genera identified in that region reveal some interesting data on Carboniferous palaeogeography which are summarized herein.

Palaeogeographical data and names of zoogeographic provinces are taken from Fedorowski (1981). Endemism index and similarity index are used in the sense of Sando and others (1977).

The Eastern Cantabrian Mountains include three structural regions (Martínez-García, 1981): the Picos de Europa Region, the North Palentian Region (or Liébana Region), and the Beleño Region (Fig. 1). Stratigraphic successions are different in each region (Fig. 2). During the Early Carboniferous, the sedimentation was very similar in all these regions, but during the Late Carboniferous there were notable differences. Upper Carboniferous sedimentary facies of the Beleño Region include silty mudstones and limestones, and alternation of mudstones and limestones is the most remarkable characteristic of this region. Corals are common in the limestones.

In the North Palentian Region (or Liébana Region) the sedimentation was predominantly turbiditic, but several limestone intercalations appear in the turbiditic series. These deposits represent temporary advances of a carbonate platform located to the south, and marl intervals containing corals are common in them.

Carbonate rocks predominate in the Upper Carboniferous of the Picos de Europa Region. Surprisingly, corals are not so abundant in this region as in the Liébana or Beleño regions. The richest fauna from Picos de Europa appears in the Kasimovian, where limestones are less abundant. Colonial corals were not recorded from this region.

### RUGOSE CORALS FROM THE CANTABRIAN MOUNTAINS

No rugose corals are known from the lower Tournaisian of the Cantabrian Mountains. The first record of corals is from the Genicera Formation, a condensed series of Late Tournaisian to Early Serpukhovian age. Genera recorded from that formation are:

<i>Rotiphyllum</i>	" <i>Syringaxon</i> "
<i>Cyathaxonia</i>	<i>Meniscophyllum</i>

This impoverished coral fauna includes genera that belong to the *Cyathaxonia* fauna; they are associated with cephalopods. Kullmann (1966, 1968) described the following genera from the Genicera Formation in the southern Cantabrian Mountains:

<i>Claviphyllum</i>	<i>Trochophyllum</i>
<i>Cyathaxonia</i>	<i>Ufimia</i>
<i>Fasciculophyllum</i>	<i>Zaphrentoides</i>
<i>Metriophyllum</i>	

Both Eastern Cantabrian and Southern Cantabrian associations are of Early Viséan age. No geographical barriers existed between the Cantabrian basin and other basins during the Early Viséan. The fauna is cosmopolitan (E.I. = 0). The influence of Western European, American and Asiatic faunas is remarkable. The impoverished coral fauna is due only to the environmental conditions; the Genicera Formation has been interpreted as warm, deep-water marine deposits, although the depth of the Genicera Formation is controversial.

During the Serpukhovian, the coral fauna became restricted geographically in the Cantabrian Mountains, but it also became richer than the Viséan fauna. Serpukhovian corals occur only in the Liébana Valley

(Cosgaya Formation), where they form algal-coral reefs. Rodríguez (1984) recorded:

<i>Caninostroton</i>	<i>Kizilia</i>
<i>Dibunophyllum</i>	<i>Nemistium</i>
<i>Fomichevella</i>	<i>Semenophyllum</i>
<i>Kionophyllum</i>	

The age of this association is latest Serpukhovian. *Nemistium*, *Kizilia* and *Dibunophyllum* show a European influence in the Cantabrian Mountains. These three genera are common in Western European basins (except *Kizilia*) and also in Eastern basins such as the Donetz or Voronezh. *Caninostroton* reflects an American influence (Easton, 1943). Relationships between faunas from the Cantabrian Mountains and other basins still were important during Late Serpukhovian and Early Bashkirian times (E.I. = 14). An interesting event is the appearance of new coral forms (*Fomichevella*, *Kionophyllum*) that were ancestors of Bashkirian genera. This was a general event during the Late Serpukhovian (Fedorowski, 1981).

A very poor coral fauna has been recorded from the Lower and Middle Bashkirian. Only two genera have been described from the middle part of the Vejo Formation in Liébana Valley:

<i>Allotropiophyllum</i>	<i>Kionophyllum</i>
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Much more important is the coral fauna from Dobres Limestone, at the top of Vejo Formation of latest Bashkirian age:

<i>Amygdalophylloides</i>	<i>Koninckocarinia</i>
<i>Asturiphyllum</i>	<i>Pseudoamygdalophyllum</i>
<i>Axolithophyllum</i>	<i>Pseudozaphrentoides</i>
<i>Kionophyllum</i>	<i>Spirophyllum</i>
<i>Caninia</i>	

The same association is present in the Beleño Region, but the following colonial corals also occur in it:

<i>Donophyllum</i>	<i>Petalaxis</i>
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This fauna is very similar to the fauna described by De Groot (1963) from the Santa María Limestone and Perapertú Formation in the Southern Cantabrian Mountains:

" <i>Carcinophyllum</i> " = <i>Kionophyllum</i>	<i>Koninckocarinia</i>
" <i>Clisiophyllum</i> " = <i>Asturiphyllum</i>	<i>Petalaxis</i>
" <i>Dibunophyllum</i> "	<i>Pseudozaphrentoides</i>
" <i>Hillia</i> " = <i>Petalaxis</i>	<i>Spirophyllum</i>

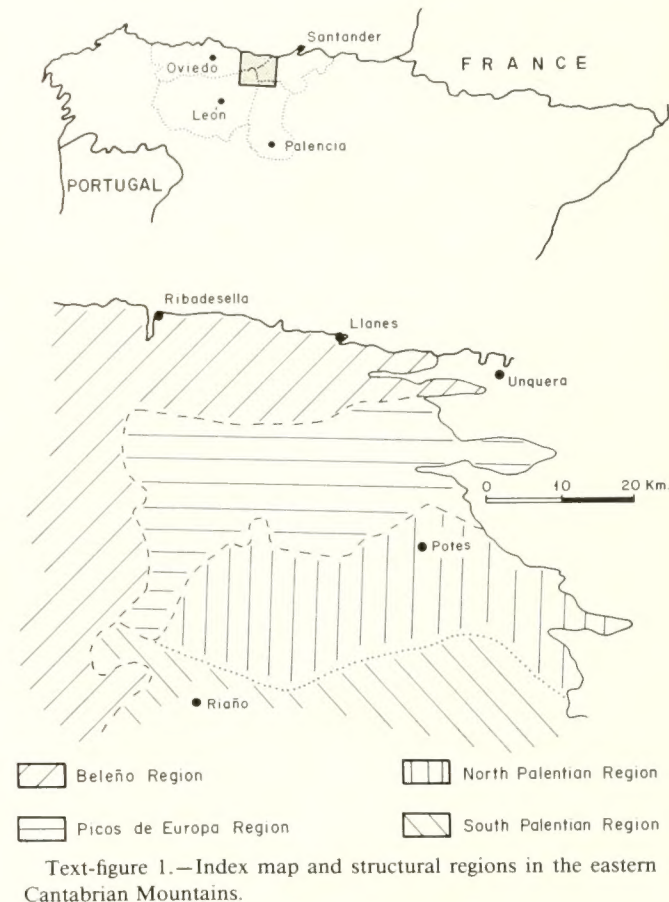
The age of the Santa María Limestone and Perapertú Formation is the same as that of the Dobres Limestone, i.e., Late Bashkirian to earliest Vereyan. The similarity index between both faunas is very high (79). Further, the presence of geyerophyllids, *Petalaxis*, *Donophyllum* and *Spirophyllum* indicates an important communication between the Cantabrian Late Bashkirian

sea and eastern basins such as Czechoslovakia, Donetz, Voronezh and China (Dianshan Formation; Yu, 1976). The similarity index with Czechoslovakia (Heritsch, 1935) is 55, with the Donetz basin (Fomichev, 1953) 53, and with the Dianshan Formation 36; on the other hand, relationships with the North American Province (see Fedorowski, 1981) are weak or absent.

The lowermost Moscovian coral fauna is nearly the same as the Upper Bashkirian coral fauna in Eastern Cantabria. The presence of some *Cyathaxonia* fauna corals is the only remarkable difference; *Cyathaxonia*, *Amplexocarinia* and *Bradyphyllum* appear in the Lower Vereyan and not in the Upper Bashkirian.

The coral record is very poor in the Upper Vereyan and the Lower Kashirian, but the richest coral fauna in the eastern Cantabrian Mountains lived during late Kashirian and Podolskian times. The following fauna has been recorded from the Kashirian–Podolskian boundary at the base of the Escalada Formation:

<i>Allotropiophyllum</i>	<i>Caninia</i>
<i>Amygdalophylloides</i>	<i>Corwenia</i>
<i>Arachnastraea</i>	<i>Cyathaxonia</i>
<i>Axolithophyllum</i>	<i>Ivanovia</i>
<i>Bothrophyllum</i>	<i>Kionophyllum</i>
? <i>Campophyllum</i>	





Similarities with the Eastern Mediterranean and Uralian-Arctic Provinces are so evident that communication is indubitable, but the genera appear later in the Cantabrian Mountains, suggesting east to west migration to Cantabria. Communication with the American Province was probably lacking or very indirect.

During the Podolskian and Myachkovian, the Cantabrian basin was gradually isolated; the Late Podolskian coral fauna was beginning to become endemic, and the Kasimovian coral fauna is quite endemic. The following genera have been described from the Upper Podolskian of the Beleño Region (Upper Escalada Formation):

- |                           |                        |
|---------------------------|------------------------|
| <i>Amygdalophylloides</i> | <i>Cystolonsdaleia</i> |
| <i>Arachnastraea</i>      | <i>Koninckocarinia</i> |
| <i>Bothrophyllum</i>      | <i>Lophophyllidium</i> |
| <i>Caninia</i>            |                        |

The Cantabrian fauna also includes some endemic forms not yet identified. This fauna still suggests a very important communication with European basins, but also shows a very small level of endemism. Colonial corals and dissepimented solitary corals are not so

abundant as in the Lower Podolskian, but the *Cyathaxonia* fauna is richer (Picos de Europa Region). The Picos de Europa Formation has yielded:

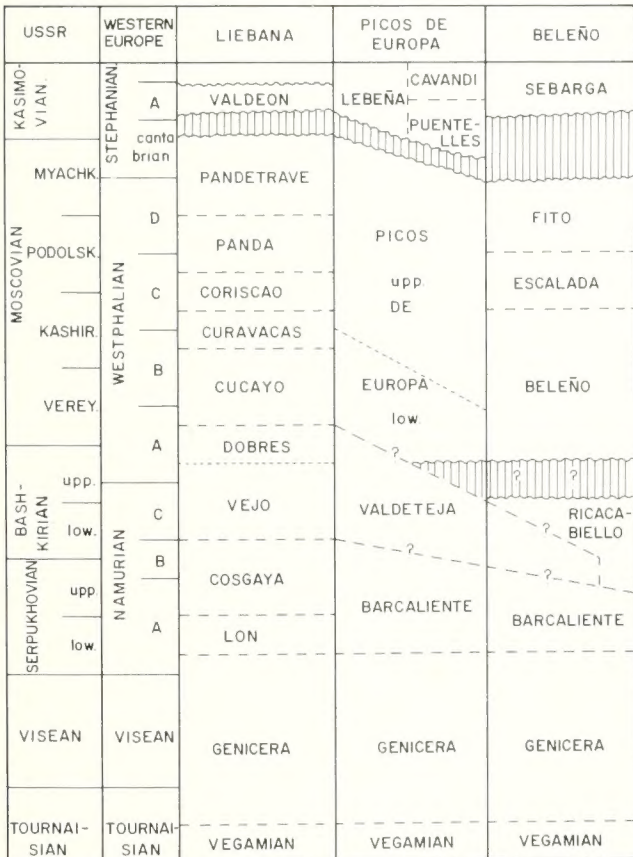
- |                       |                        |
|-----------------------|------------------------|
| <i>Amplexocarinia</i> | <i>?Hapsiphyllum</i>   |
| <i>Amplexus</i>       | <i>Lophophyllidium</i> |
| <i>Cyathaxonia</i>    | <i>Rotiphyllum</i>     |
| <i>Duplophyllum</i>   | <i>?Stereolasma</i>    |

These are all small solitary corals without dissepiments. The age of this association is also Late Podolskian.

The endemism trend attains its highest level during the Kasimovian and possibly involves an important change of environmental conditions. The Kasimovian coral fauna is restricted to a small basin (Cabrales Valley in the Picos de Europa Region), but it is very rich and has two different aspects: it is composed of many species of the *Cyathaxonia* fauna and only three species of solitary dissepimented corals, but specimens of these species are very abundant.

- |                          |                        |
|--------------------------|------------------------|
| <i>Allotropiophyllum</i> | <i>Duplophyllum</i>    |
| <i>Amplexocarinia</i>    | <i>Lophocarino-</i>    |
| <i>?Amplexus</i>         | <i>?Stereolasma</i>    |
| <i>Asserculinia</i>      | <i>Ufimia</i>          |
| <i>Bradyphyllum</i>      | <i>Verbeekiella</i>    |
| <i>Cyathaxonia</i>       | <i>Lophophyllidium</i> |
| <i>Cyathocarinia</i>     |                        |

- |                      |
|----------------------|
| <i>Sestrophyllum</i> |
| <i>Bothrophyllum</i> |
| <i>Geyeronaotia</i>  |



Text-figure 2.—Structural domains and formations of the eastern Cantabrian Mountains.

Dissepimented corals and some species of the *Cyathaxonia* fauna indicate a clear relationship with the Carnic Alps and Donetz Basin, but some genera that appear in the Cantabrian Mountains in the Kasimovian (*Cyathocarinia*, *Duplophyllum*, *Lophocarino-* *phyllum*, *Verbeekiella*, *Asserculinia*) are common in the Permian of the Mediterranean Province (Schouppé and Stacul, 1955, 1959; Soshkina, 1925, 1928), where they are restricted to the Permian. A possible error in age of this fauna is dismissed because the corals are associated with Foraminifera of the *Triticites* Zone.

CONCLUSIONS

During the Carboniferous Period, the Cantabrian Basin was occupied by a warm sea where a rich coral fauna flourished. That sea probably was deep at the beginning of the Carboniferous, but became increasingly shallower during the Serpukhovian.

During the Viséan, the coral fauna from the Cantabrian Mountains was poor because it lived in deep water, but it shows remarkable influences from different geographic directions.

Upper Serpukhovian and Lower Bashkirian coral faunas are restricted geographically, and they are characterized by development of new forms. Communi-

cation between the Mediterranean and North American Provinces probably was open across the Cantabrian basin.

Tectonic movements were important from Bashkirian to Kasimovian time, and several structural and sedimentary regions can be distinguished. During the Bashkirian and the Moscovian, corals were abundant in the Liébana and Beleño Regions, where there were periods of shallow water carbonate deposition. On the contrary, in the Picos de Europa Region, the carbonate environment was more constant, but the rugose corals are rare; only corals of the *Cyathaxonia* fauna have been recorded from very restricted levels.

The similarity of coral faunas in the Cantabrian and other Mediterranean basins is very great; communication between these basins is evident, and the corals probably migrated from east to west.

During the Kasimovian, the present day Cantabrian Mountains region was an almost closed basin, but environmental conditions continued to be favorable, so that a very characteristic coral fauna was developed in this region. Environmental conditions changed possibly during the Late Gzhelian or Early Permian, causing the migration of an endemic coral fauna from Cantabria towards the eastern basins.

#### ACKNOWLEDGMENTS

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STRATIGRAPHIC RANGE EXTENSIONS AND CORAL PROVINCE  
AFFILIATIONS OF STONY CORALS IN THE LOWER PERMIAN  
McCLOUD LIMESTONE OF CALIFORNIA

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ABSTRACT

The Permian McCloud Limestone of northern California ranges in age from Early Wolfcampian to Late Leonardian. Newly collected (1982) rugose corals from the uppermost Wolfcampian part of the formation at Tombstone Mountain represent three cerioid and one solitary coral species. One of the cerioid coral species also occurs lower in the formation in another section, a second also occurs in the Upper Wolfcampian Coyote Butte Formation of central Oregon, and the third cerioid coral is a new species. They extend ranges upward in the formation for three genera and two subgenera. The solitary coral represents a new genus and species. Tabulate corals have not been found in the uppermost Wolfcampian rocks. Identifiable corals have not been found in the highest (Leonardian) beds of the formation.

The overall generic composition of the coral fauna of the McCloud Limestone places it in the Durhaminidae coral province, with close affinity to the Permian coral faunas of the Cordilleran miogeosynclinal formations to the east. It has a more general affinity with the northern Durhaminidae coral province of the Arctic islands and western Russia. The fasciculate coral *Herit-schioides* may partly distinguish a western North American subprovince. Corals that characterize the Tethys coral province are not present in the McCloud Limestone, probably because the Permian Pacific Ocean constituted a distributional barrier. Consideration should be given to the idea of the Permian eastern Pacific Ocean as a source area for western American corals.



## SECTION 8

**Biostratigraphy**

## INTRODUCTION

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There is a pervasive view among many geologists that corals and other cnidarians are of little value in biostratigraphy because they are sedentary benthonic animals that did not attain widespread distribution in the short time spans needed for modern biostratigraphic discrimination. There is also some inclination to regard corals as too environmentally restricted for meaningful biostratigraphic constructions. Such prejudices are now largely outmoded by recent progress in coral biostratigraphy, particularly in Devonian and Carboniferous rocks.

Although living corals do not have great mobility, studies of scleractinian larvae (Connell, 1973) indicate that some larvae remain swimming for as long as two months before settling down and attaching themselves to the substrate. Clearly, this provides potential for rapid distribution over large areas. Moreover, from an empirical standpoint, the geochronometric resolutions of some coral zones in the ancient record compare favorably with those of traditionally respected biostratigraphic indices such as foraminifers, conodonts, and cephalopods (Sando, 1977).

At one time, Paleozoic corals were thought to be essentially restricted to shallow-water carbonate environments (Wells, 1957). Teichert (1958) called attention to modern deep-water occurrences, and this is now reinforced by many new localities discovered during several decades of ocean-bottom research. Teichert's admonition that occurrences of corals in deep water may be more common in the ancient record than generally recognized has been confirmed by later work (Kullmann, 1966, 1968; Sando, 1977, 1980). There is no evidence that Paleozoic corals were subject to the same bathymetric restrictions as many modern scleractinians because of dependence on phototropic symbiotic zooxanthellae.

Historically, corals have played a significant role in zonation and correlation of Paleozoic rocks since the advent of Twentieth Century biostratigraphic tech-

niques. Vaughan's (1905) zonation of the British Carboniferous is a notable example of a biostratigraphic scheme proposed shortly after the turn of the century that is still being used today, with modifications. More recently, geochronometric resolutions of one to three million years have been accomplished by coral zonation of the Mississippian of the Western Interior Province of North America, a huge area that includes most of western Canada and the western states of the U.S.A. (Sando and others, 1969; Sando and Bamber, 1979, in press). Oliver and Pedder (1979) have successfully demonstrated stage-level correlations by means of corals within biogeographic realms in the Devonian. Thus, recent biostratigraphic work with the Paleozoic corals indicates that significant zonal capabilities may be obtained within biogeographic provinces of continental or subcontinental areal extent. On the other hand, attempts at world-wide coral zonation (Hill, 1957; Ross, 1970, 1979) have provided only series-level discrimination.

Contributions to the Fourth Symposium include a potpourri of papers on biostratigraphy and closely related subjects. All but one of the nine papers in this section deal with Paleozoic cnidarians (predominantly corals), hence the emphasis on the Paleozoic in this discussion.

Five of the papers in this section present data specifically focussed on improving biostratigraphic capabilities. Qin and Yang describe stage-level discrimination in the Lower Cambrian of China using archaeocyathids. Lin proposes five coral assemblage zones in the Middle and Upper Ordovician of China. Niikawa recognizes four zones, based partly or entirely on rugose corals, in the Lower Carboniferous (Viséan) Onimaru Formation of Honshu, Japan and uses the zones to correlate the formation with strata in England, Belgium, the USSR, and China. Sando describes series-level discrimination by means of syringoporoids in the upper Paleozoic of the western interior region of the

U.S.A. Soto relates occurrences of rugose corals to conodont zones used to define boundaries between Lower and Middle Devonian rocks and Middle and Upper Devonian rocks in the Cantabrian Mountains of Spain.

The paper by Poty analyzes evolutionary patterns in five genera of lithostrotionid corals in the Lower Carboniferous of western Europe. Although Poty does not call attention to biostratigraphic applications, the patterns he describes for such widespread and abundant corals can be used for biostratigraphic discrimination of stages or finer divisions.

Two other papers represent initial data-gathering steps to using corals for biostratigraphic synthesis. McLean revises taxonomic and locality data for a rich rugose coral fauna from the Upper Devonian (Middle and Upper Frasnian) of the Northwest Territories in Canada. Turnšek, LeMone, and Scott (abstract only) catalog occurrences of scleractinian species in lithostratigraphic units of the Cretaceous (Albian and Cenomanian) in southern New Mexico and northern Mexico.

Finally, Tsien contributes to the modern controversy over tempo and mode of evolution by analyzing diversity and speciation patterns of two rugose coral genera in the Upper Devonian (Frasnian) of Belgium. This too has broad stratigraphic implications.

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## LOWER CAMBRIAN ARCHAEOCYATHA FROM SOUTHERN SHAANXI PROVINCE, CHINA

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### ABSTRACT

The Lower Cambrian archaeocyathan faunas dealt with in this paper were collected from the Guojiaba Formation (mainly calcareous sandy shales) and Xiannudong Formation (mainly algal limestones) in the Xixiang area of southern Shaanxi Province. The lower Guojiaba fauna is considered equivalent to the upper part of the Qiongzhusi Stage of southwest China. The younger Xiannudong fauna is considered equivalent to the basal part of the Canglangpu Stage of southwest China.

### XIXIANG AREA, SHAANXI

All Lower Cambrian Archaeocyatha dealt with in this paper were collected from the Xixiang area of southern Shaanxi Province by the writers in 1978–1983 (Text-fig. 1). This area, which lies between the Qinling Mountains and Micangshan Mountain, is a small basin crossed by the Han River, a northern branch of the Yangtze River. Micangshan Mountain is a watershed dividing the Han River Basin from the Sichuan Red Basin. This region is included within the ancient Yangtze Platform which was consolidated in the Late Precambrian.

The north side of Micangshan Mountain, where the specimens were obtained, is really a special stratigraphical subregion which differs from the neighboring Dabashan area to the east and Lungmenshan area to the west. A well-developed Lower Cambrian sequence crops out on the hillside along the Han River.

Four formations of Early Cambrian Age are distinguished in the Xixiang area, from upper to lower, as follows:

- Konmingdong Formation
- Yanwangbian Formation
- Xiannudong Formation
- Guojiaba Formation

The archaeocyathid assemblages are found in the lower two formations and are named after the formations.

The Xiannudong Formation is characterized mainly by algal limestones, about 58 meters in thickness, along with several layers of lenticular limestones which are mostly composed of archaeocyathid bioherms.

The faunal assemblage consists of the following species: Archaeocyatha (Irregulares): *Dictyocyathus* sp., *Dictyocyathus lepidus* Yuan and Zhang, *Dictyocyathus intextus* Yuan and Zhang, *Dictyocyathus* spp., *Reticyathus* sp.; (Regulares): *Aldanocyathus* sp., *Ajacycyathus sichuanensis* Yuan and Zhang, *Ajacycyathus* spp., *Rotundocyathus* sp., *Coscincyathus* sp. cf. *C. liangshuijingensis* Yuan, *Coscincyathus* spp., *Archaeofun-*

*gia* sp. cf. *A. dissepimentalis* Vologdin; Algae: *Epiphyton* sp., *Girvanella* sp.; Heteractinids: *Allonnia* sp., *Archiasterella* sp.; Hyolithids: *Hyolithellus* sp.; Tommotiids: *Fomithella* sp. In addition, many fragments of brachiopods and ostracods were found.

### SOUTHEAST AND CENTRAL CHINA

Recently, four archaeocyathid assemblages were established in northern Sichuan, western Hubei and other parts of southeast and central China (Yuan and Zhang, 1980). They are named in descending order as follows:

- Tienheban Assemblage
- Yinzuiyan Assemblage
- Liangshuijing or Xiannudong Assemblage
- Qiongzhusi or Guojiaba Assemblage

The Tienheban and Yinzuiyan assemblages are not represented in the Xixiang area. The fauna found in the Xiannudong Formation in this area is very similar to the Liangshuijing fauna in northern Sichuan. The same trilobites, such as *Yiliangella* and *Yunnanaspis*, found in the same horizon, are of Canglangpu Age (middle Early Cambrian).

The Xiannudong and the Liangshuijing Formations were deposited along the northern and western margins of the Yangtze Platform in a semicircular belt, and far from the Kangdian massive craton (Text-fig. 1).

Fossils belonging to the Liangshuijing assemblage and the Yinzuiyan assemblage were also found at Kurukttag Mountain in the South Tianshan Mountains of Xinjiang. The widely distributed faunal assemblages, which dominated the period of archaeocyathids in China, are the Xiannudong and the Liangshuijing, probably equivalent to the lower part of the Siberian Platform sequence.

It is interesting to note that the leading species, *Dictyocyathus* sp., with its numerous individuals in the Xiannudong Formation, has never been found with *Chengkoucyathus*, which is predominant in the Liang-

shuijing Formation. This may suggest that the two areas were then under quite different paleogeographical conditions. This opinion is in agreement with that of many Chinese geologists who subdivide the region into two different stratigraphical subareas.

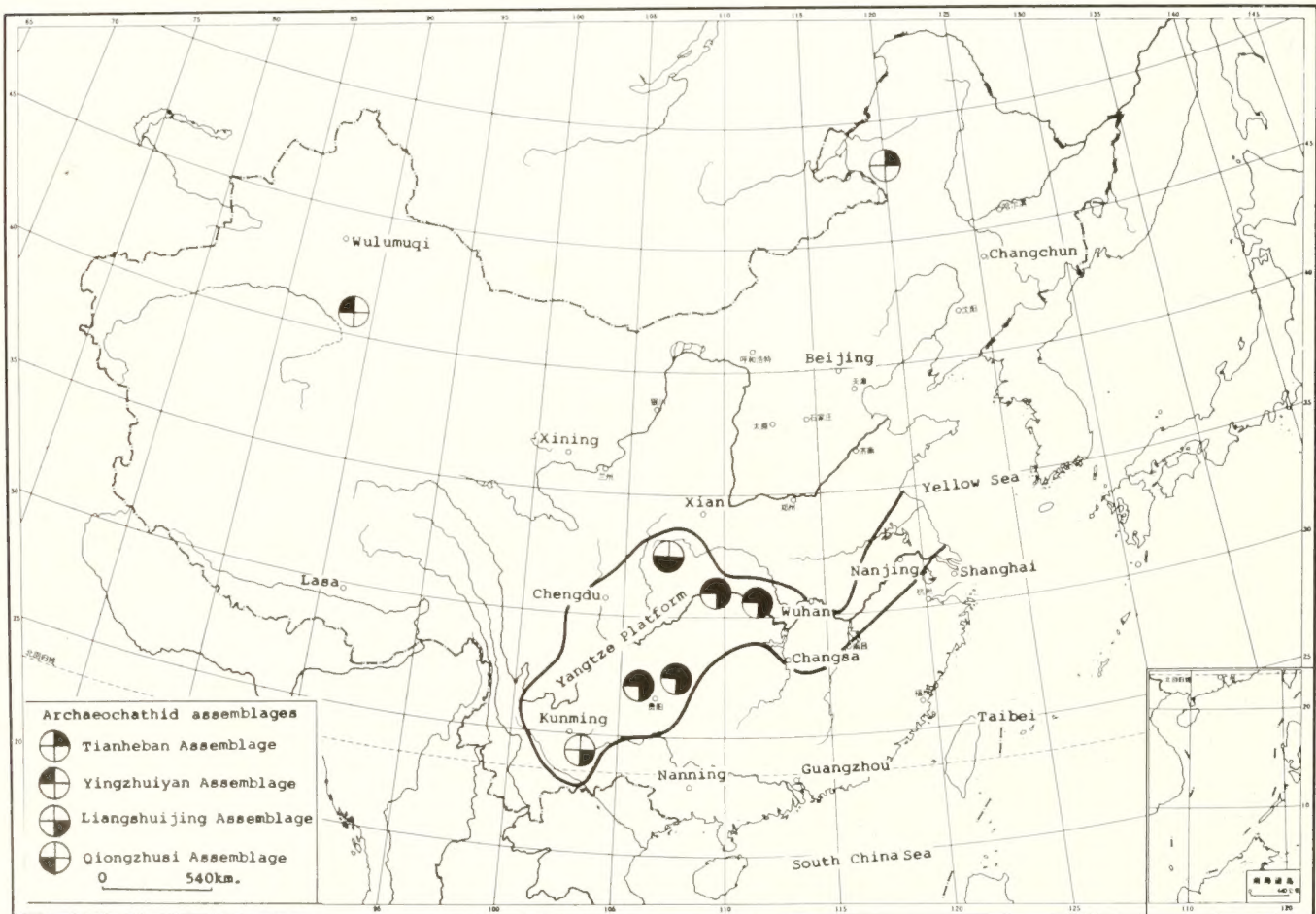
In the Xixiang area the Guojiaba Formation, underlying the Xiannudong Formation, is characterized mainly by yellowish sandy shales and argillaceous sandstones, about 188 m thick. The Guojiaba Formation is very similar to the Qiongzhusi Formation of eastern Yunnan, as the same trilobite fossils, such as *Eoredlichia* and *Wutingaspis*, have been found in both. They are evidently of the same age. At the topmost part of the Guojiaba Formation in the Xixiang area, carbonate lenses with rich archaeocyathid fossils have been found and are now reported for the first time. The fauna is mostly composed of the septoids of the Class Regulares and represents the lowest archaeocyathid horizon in China. It contains the following forms: Archaeocyathids: *Ajacyathus spinosus* Yuan and Zhang, *Rotundocyathus* spp., *Taylorcyathus* sp.,

*Coscinocyathus* sp., *Dictyocyathus* sp., *Archaeocyathus* sp.; Heteractinids: *Eiffella* sp., *Onychis* sp., *Chanceloria* sp.; Brachiopods: *Diandongia pista* Rurng; Hyolithids: *Hyolithellus* sp.; Tommotiids: *Tommotia* sp. The Guojiaba archaeocyathid assemblage is restricted to this area, and the Guojiaba Formation may be considered as equivalent to the upper part of the Tommotian of the Siberian Platform.

#### SUMMARY AND CONCLUSIONS

The archaeocyathid horizons in China can be well correlated with the trilobite zones established in China by Zhang (1981). The main points are the following:

1. The Guojiaba archaeocyathid fauna marks the lowest archaeocyathid horizon so far recognized in China.
2. The distribution of *Dictyocyathus* and *Chengkoucyathus* which occupied different regions in the same epoch may be used as a criterion for the recognition of biogeographical provinces.



Text-figure 1.—Map of China showing distribution of archeocyathid assemblages. The symbol closest to Xian marks the Xixiang Area. See text discussion.



3. The Xiannudong faunal assemblage is widespread and may be considered equivalent to the lower part of the Atdabanian Stage of the Siberian Platform.

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Series	Stage	Formation	Literal meaning	Section	Thickness	Main lithology	Biological group	Trilobites zonation and Archaeocyathid assemblages of the Lower Cambrian in Southwest China	
Cambrian	Longwangmiao	Kongmingdong	Bright cave		203m.	Grey sandy dolomites	Redlichia cf. chinensis	Hofferte-Redlichia murakamii	Tianheban Assemblage
						Grey fine sandstones	Palaeolenus Metaredlichioides	Megapalaeolenus	
	Canglangpu	Xiannudong	Fair cave		58m.	Red sandy shales	Dictyocyathus gemmutus D. lepidus D. intexus D. spp.	Palaeolenus Drepanuroides	Yingzhuiyan Assemblage
						Grey oolitic limestones Grey algal limestones	Coscinocyathus cf. liangshujingensis C. spp. Rotundocyathus micangshanensis R. xixiangensis Ajacicyathus sishuanensis A. Spp. Aldanocyathus sp. Retecyathus dubius Heteractinids Hyalithellus sp. Brachiopods and Ostracods	Yiliangella-Yunnanaspis	
Lower	Guojiaba	Guo's field		188m.	Yellow calcareous siltstones intercalated with limestone lenses	Ajacicyathus spinosus Rotundocyathus rotundo Taylorcyathus spp. Coscinocyathus dabashanensis Dictyocyathus intermedius Archaeocyathus sp. Hyalithellus sp. Tommotia sp. Tsunyidiscus sp. Hupeidiscus sp.	Eoredlichia-Wutingaspis	Qiongzhusi Assemblage	
					Yellow sandy shales and black shales		Parabadiella-Mianxiandiscus		

Text-figure 2.—Columnar section of the Lower Cambrian in the Xixiang area, Shaanxi Province.

## NEW DEVELOPMENTS IN CORAL BIOSTRATIGRAPHY OF THE ORDOVICIAN OF CHINA

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### ABSTRACT

Abundant Ordovician coral faunas occur in China and, based on their stratigraphic distribution, five Assemblage Zones can be recognized. In ascending stratigraphic order, the zones are: 1) *Rhabdotetradium-Lichenaria* Assemblage Zone; 2) *Yohophyllum-Ningnanophyllum* Assemblage Zone; 3) *Agetolites-Grewingkia* Assemblage Zone; 4) *Calapoecia-Favistella* Assemblage Zone; and 5) *Borelasma-Sinkiangolasma* Assemblage Zone. Zone 1 is of Llanvirnian age; Zone 2 is Middle Caradocian age; Zones 3 and 4 are of early Ashgillian age; and Zone 5 is of late Ashgillian age.

### INTRODUCTION

The Ordovician corals spread widely in China except in the northeastern part of China (including the northern part of Hebei, Shandong, Shaanxi, Liaoning, Jilin and Heilongjiang provinces); in addition they have not been found in Fujian, Taiwan, and Guangdong provinces. All the other provinces and regions contain Ordovician corals. Some of the Ordovician corals are similar to those in Siberia, North America, and the Baltic Region, but others occur only in China. Therefore China is one of the important areas of the world for Ordovician coral study.

### BIOSTRATIGRAPHY

Based on stratigraphic distribution, the Chinese Ordovician corals may be subdivided into five Assemblage Zones (A.Z.). They are (from oldest to youngest): 1) *Rhabdotetradium-Lichenaria* A.Z., 2) *Yohophyllum-Ningnanophyllum* A.Z., 3) *Agetolites-Grewingkia* A.Z., 4) *Calapoecia-Favistella* A.Z. and 5) *Borelasma-Sinkiangolasma* A.Z. The main faunal elements and geographic occurrence of each of these zones are described, in ascending stratigraphic order.

#### *Rhabdotetradium-Lichenaria* Assemblage Zone

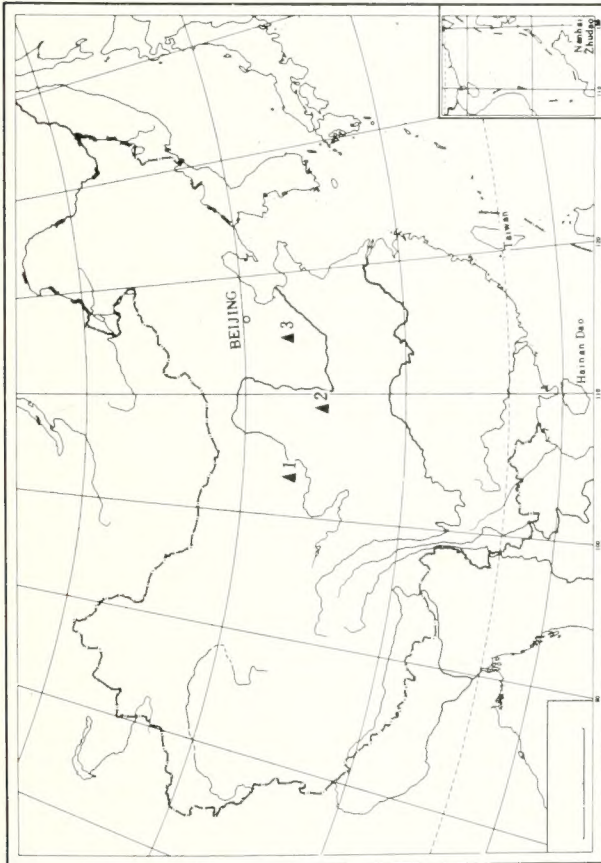
This Zone is recognized in the Sandaogou Formation (Lower Ordovician) of Northern Shaanxi Province (Li and Lin, 1982) and the Upper Majiagou Formation (Lower Ordovician) of South Hebei Province (Lin, 1980, 1983). The coral faunas of the Gulang Limestone (Yu, 1961) may belong to this Assemblage Zone. The principal corals are: *Rhabdotetradium tongchuanense* Lin, *R. fengfengense* Lin, *Lichenaria concava* Lin, *Yaoxianopora taoqupoensis* Lin, and *Y. gigantea* Lin (Text-fig. 1).

#### *Yohophyllum-Ningnanophyllum* Assemblage Zone

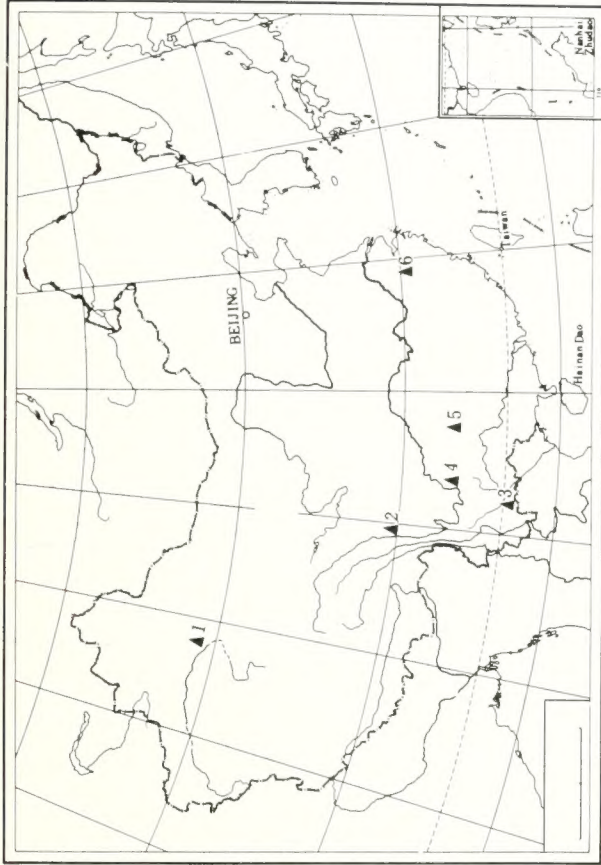
This Zone has been found in the Lower part of the Huanghuachong Formation (Middle Ordovician) in Guiyang, Guizhou Province (Yoh, 1959; Lin, 1965; Yi Nung, 1974), the Yanwashan Formation (Middle Ordovician) in Western Zhejiang Province (Lin and Zhou, 1980), the upper part of Qiaojia Formation (Middle Ordovician) in Ningnan, Sichuan Province (Lin, 1965) and in Jinping, Yunnan Province, Batang, Sichuan Province and Yuli (Lopnur), Xinjiang Uysur Autonomous Region. The principal corals are: *Yohophyllum kueiyangense* (Yoh), *Y. zhejiangense* Lin and Chow, *Y. kuruktageense* Lin, *Palaeophyllum irregulare* Lin and Chow, *Ningnanophyllum ningnanense* Lin, *N. minor* Lin, *N. shengi* Lin, *Calostylis ningnanense* Lin, *C. loai* Lin, *C. crassisepta* Lin, *C. sichuanensis* Lin, *C. huidungensis* Lin, *Streptelasma rariseptata* (Lin), *Protararea ningnanensis* Lin, *P. guiyangensis* Lin, *Eofletcheria zhejiangensis* Lin and Chow, *Reuschia intermedia* Lin and Chow, *Jiangshanolites multitabulatus* Lin and Chow, *Proheliolites* sp., *Plasmoporella* spp., *Catenipora* sp., and *Amssasia* sp. (Text-fig. 2).

#### *Agetolites-Grewingkia* Assemblage Zone

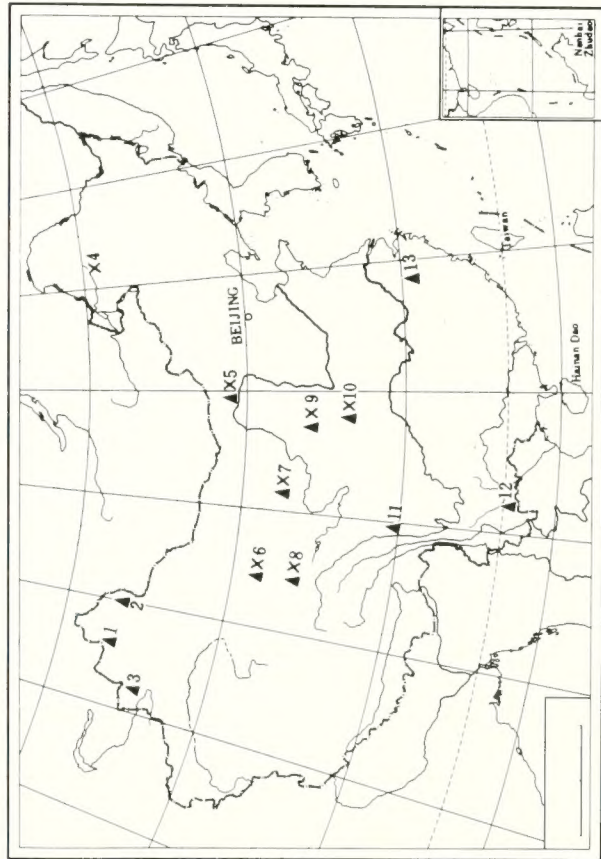
This Assemblage Zone is spread widely in South China and Northwest China. It is known from the Sanjushan Formation and Changwu Formation (upper part of Upper Ordovician) in Zhejiang and Jiangxi Provinces (Lin, 1960; Lin and Chow, 1977; Yoh, 1933; Yu, 1960), the Baguoshan Formation (Upper Ordovician) in Shaanxi Province (Li and Lin, 1982), the Baiyanhuashan Formation (Upper Ordovician) in Urad Qianqi, Nei Mongol (Lin *et al.*, 1983), the Koumenzi Formation (Upper Ordovician) in North Qinghai (Yu, 1960; Deng *et al.*, 1979), the Shihuichang Formation (late Upper Ordovician) in South Qinghai (Li and Lin,



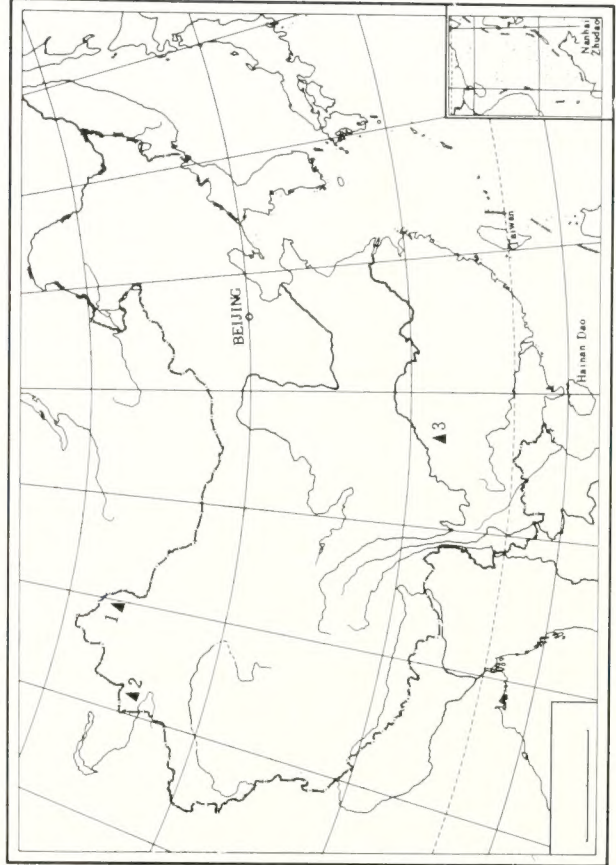
Text-figure 1.—Sketch-map showing geographic distribution of *Rhabdotetratidium-Lichenaria* Assemblage Zone of Llanvirnian age in China. 1. Gulang County, Gansu Province; 2. North Shaanxi; 3. South Hebei.



Text-figure 2.—Sketch-map showing geographic distribution of *Yohophyllum-Ningnanophyllum* Assemblage Zone of Middle Caradocian age in China. 1. Yuli County, Xinjiang; 2. Batang County, Sichuan Province; 3. Jinping County, Yunnan Province; 4. Ningnan County, Sichuan Province; 5. Guiyang, Guizhou Province; 6. Jiangshan County, Zhejiang Province.



Text-figure 3.—Sketch-map showing geographic distribution of *Agerolites-Grewinkia* Assemblage Zone and *Calapoecia-Favistella* Assemblage Zone of early Ashgillian age in China. 1. West Junggar, Xinjiang; 2. East Junggar, Xinjiang; 3. West Tianshan; 4. Great Hingan, Nei Mongol; 6. Da Qaidam, Qinghai Province; 7. Qilian County, Qinghai Province; 8. Golmud County, Qinghai Province; 9. Long Xian, Shaanxi Province and Guyuan County, Ningxia; 10. Shanyang County, Shaanxi Province; 11. Batang County, Sichuan Province; 12. Jinping County, Yunnan Province; 13. Yushan County, and Jiangxi Province, Jiangshan and Changshan Counties, Zhejiang Province.



Text-figure 4.—Sketch-map showing geographic distribution of *Borelasma-Sinkiangolasma* Assemblage Zone of late Ashgillian age in China. 1. Fuyun County, Xinjiang; 2. Hocheng County, Xinjiang; 3. Tongzi County, Guizhou Province.

1982), the Bulunguoer Formation (late Upper Ordovician) in West Junggar (Lin and Wang, 1981), the Jiaposaer Formation (late Upper Ordovician) in East Junggar (Lin and Wang, 1981) and the Hudukedaban Formation (Upper Ordovician) in West Tianshan of Xinjiang Uygur Autonomous Region (Lin and Wang, 1982). The principal coral genera are: *Agetolites*, *Agetolitella*, *Sarcinula*, *Reuschia*, *Eofletcheria*, *Eofletcheriella*, *Fletcheriella*, *Rhabdotetradium*, *Tetradium*, *Catenipora*, *Kolymopora*, *Taeniolites*, *Stelliporella*, *Parastelliporella*, *Wormsipora*, *Neowormsipora*, *Acdalopora*, *Proheliolites*, *Heliolites*, *Propora*, *Plasmoporella*, *Sibiriolites*, *Neosibiriolites*, *Streptelasma*, *Helicelasma*, *Grewingkia*, *Sinkiangolasma*, *Tryplasma*, *Cantrillia*, *Neocantrillia*, and *Palaeophyllum* (Text-fig. 3).

*Calapoecia-Favistella*  
Assemblage Zone

This Zone is known from the Zhinishan Formation (Upper Ordovician) of Great Hingan (Tchi, 1982), the Baguoshan Formation (Upper Ordovician) in Shaanxi Province (Lin, 1963; Li and Lin, 1982), the Baiyanhuashan Formation (Upper Ordovician) in Nei Mongol (Lin *et al.*, 1983), the Koumenzi Formation (Upper Ordovician) in North Qinghai (Yu, 1960, 1962; Yü *et al.*, 1963; Deng *et al.*, 1979), the Shihuichang Formation (late Upper Ordovician) in South Qinghai (Li and Lin, 1982). Characteristic corals include: *Calapoecia hinganensis* Tchi, *Catenipora dahinganensis* Tchi, *C. ramosus* Tchi, *Sibiriolites tumefactus* Tchi, *Proheliolites zhadunheensis* Tchi, *Saffordorphyllum*, *Rhabdotetradium*, *Favistella*, *F. (Parafavistella)*, *Cyathophylloides*, and *Sinkiangolasma* (Text-fig. 3).

*Borelasma-Sinkiangolasma*  
Assemblage Zone

This Zone was first recognized in the Guanyinqiao Formation, Guizhou Province (Ho, 1978). It is now also known from the upper part of the Upper Ordovician in North Xianjiang. The main faunal elements of the Assemblage Zone are: *Streptelasma* cf. *distinctum* Wilson, *S. kweichouense* Ho, *S. insolitum* Ho, *Grewingkia buceros fosulata* Ho, *G. sinensis* Ho, *Brachyelasma primum* (Wedekind), *B. brevisseptatum* Ho, *B. lindstroemophylloides* Ho, *B. simplotabulatum* Ho, *Crassilasma multitabulatum* Ho, *C. concava* Ho, *C. tuberculosum* Ho, *Borelasma sinensis* Ho, *B. corniculatum* Ho, *Kenophyllum* cf. *subcylindricum* Dybowski, *K. compactum* Ho, *Siphonolasma obliquitabulatum* Ho, *Paramplexoides cylindricus* Ho, *P. concavus* Ho, *Pycnactis* cf. *mitratus* (Schlotheim), *P. kweichowensis* Ho, *Sinkiangolasma* cf. *simplex* Yu, *Proheliolites* sp., and *Sibiriolites* sp. (Text-fig. 4).

## BIOGEOGRAPHIC SUMMARY

The *Rhabdotetradium-Lichenaria* fauna is very similar to that in the North American-Siberian Region. In contrast the *Yohophyllum-Ningnanophyllum* fauna is endemic. The *Agetolites-Grewingkia* fauna occurs mainly in South China and Northwest China, and occupied an independent zoogeographical region. The *Calapoecia-Favistella* fauna is most closely related to the faunas of the North American-Siberian Region. The youngest assembly, the *Borelasma-Sinkiangolasma* fauna is similar to that in the Baltic Region.

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## CORAL FAUNA OF THE UPPERMOST DINANTIAN ONIMARU FORMATION, HONSHU, JAPAN

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### ABSTRACT

The Onimaru Formation consists mainly of black, well-bedded limestone containing a very rich coral fauna. The formation is divided into four fossil zones, in ascending order: *Kueichouphyllum gracile*-*Actinocyathus japonicus* Zone, *Saccamminopsis* Zone, *Arachnolasma*-*Palaeosmilia regia* Zone and Barren Zone. The formation is correlated with Vaughan's (1905, 1906) D<sub>2</sub> and D<sub>3</sub> subzones (Brigantian Stage) of the British Dinantian and with the uppermost V<sub>3b</sub> and V<sub>3c</sub> of the Upper Viséan in Belgium. Among the coral fauna, *Kueichouphyllum* and *Yuanophyllum* occupy a unique position; the former is a typical element of the *Kueichouphyllum* sea province, while the latter has a very narrow distribution limited to eastern Central Asia and East Asia.

### INTRODUCTION

The southern Kitakami Mountains, northeastern Honshu, Japan is one of the typical areas for Paleozoic strata in Japan. Among the Paleozoic deposits in this area, black, well-bedded and fossiliferous limestone, formerly called the Coral limestone, is now referred to the Lower Carboniferous Onimaru Series. The name Onimaru Series was introduced for all the Carboniferous deposits by Onuki (1937, 1938). Minato (1943) redefined the Onimaru Series to include only the Coral limestone, Group VI of Minato (1941). He further correlated the Onimaru Series with the Upper Viséan *Dibunophyllum* zone in Britain and with the *Yuano-phyllum* zone of the Fengningian in China based on corals and brachiopods. Minato and others (1953) suggested that this series be divided into two biozones. This idea was further advanced by Minato and Takeda (1956) and Minato and others (1959), who proposed division of the series into a lower, Hotokezaka Stage and an upper, Hiishi Stage.

Studies of the lower Carboniferous coral faunas in Japan were summarized by Minato (1975) and Kato (1979), who considered that the coral fauna of the Onimaru Series and its correlatives consisted of elements of the extremity of the so-called *Kueichouphyllum* sea (Hill, 1948; Minato, 1953). Meanwhile, Minato (in Minato, Hunahashi, Watanabe and Kato, eds., 1979) is now of the opinion that the Onimaru "Series" is better treated as a formation, and the author now follows this opinion.

### BIOSTRATIGRAPHY OF THE ONIMARU FORMATION

The Onimaru Formation is widely distributed in the southern Kitakami Mountains, where it consists generally of black, well-bedded limestone and is about 94 m thick. Occasional chert nodules and bands occur. The formation is known also to have abundant well

preserved coralline and other fossils. The author divides the formation into four fossil zones based on lithofacies, corals and Foraminifera (Text-fig. 1).

***Kueichouphyllum gracile*-*Actinocyathus japonicus* Zone.**—This zone is characterized by a rich coral fauna consisting of 30 species in 9 genera, including *Kueichouphyllum gracile* Yü, *Actinocyathus japonicus* (Yabe and Hayasaka), *Diphyphyllum fasciculatum* (Fleming) and *D. furcatum* (Thomson); these species are chosen as index-fossils. *Kueichouphyllum gracile* and *Actinocyathus japonicus* are the most common corals in this zone.

***Saccamminopsis* Zone.**—This zone is characterized by the occurrence of the Foraminifera, *Saccamminopsis* sp. Among the corals, *Pseudodorlodotia kakimii* Minato and "*Tabulophyllum*" sp. occur rarely in this zone.

***Arachnolasma*-*Palaeosmilia regia* Zone.**—A coral fauna of this zone contains abundant species of the genus *Arachnolasma*, *Palaeosmilia regia* (Phillips), *Neoclisiophyllum xiangxiangense* Wu, *Lithostrotion columellata* Dobrolyubova, *Diphyphyllum hochangpingense* Yü, *Lonsdaleia duplicata* (Martin) and *Hexaphyllia mirabilis* (Duncan). Among the taxa listed above, *Arachnolasma* and *Palaeosmilia regia* are common at some localities.

**Barren Zone.**—These deposits consist of alternations of black, impure limestone and siliceous slate. This zone is partially developed in the southern Kitakami Mountains, where the maximum thickness is 10 m. Corals have not been found in this zone, but diagnostic conodonts are reported by Nakamura (in Minato, Hunahashi, Watanabe and Kato, eds., 1979), who concluded that the zone is equivalent to the *Gnathodus commutatus* zone of Western Europe.

Remarks

A twofold division of the Onimaru "Series," on paleontological grounds, was established by Minato and Takeda (1956) and Minato and others (1959). Their lower division, the Hotokezaka Stage, corresponds to the author's lower fossil zone, and their upper, Hiishi Stage, is equivalent to the author's upper three fossil zones (Text-fig. 1).

INTERNATIONAL CORRELATION

By direct comparison of common species of corals between the Onimaru Formation and the standard regions of the Carboniferous (Britain, Belgium, USSR, and China), the following international correlations become feasible.

Great Britain

Common species between the Onimaru Formation and the British Dinantian are *Diphyphyllum fasciculatum* (Fleming), *D. furcatum* (Thomson), *D. lateseptatum* McCoy, *Dibunophyllum bipartitum* (McCoy), *D. bristolense* Garwood and Goodyear, *Lonsdaleia duplicata* (Martin), *Palaeosmilia regia* (Phillips) and *Hexaphyllia mirabilis* (Duncan). These species are elements of the *Dibunophyllum* zone, especially the D<sub>2</sub> subzone, in Britain. *Palaeosmilia regia*, whose range is from D<sub>2</sub> to D<sub>3</sub>, would suggest that at least the upper part of the Onimaru Formation may be partly correlative with D<sub>3</sub>. George and others (1976) introduced a fresh approach to subdivision of the Lower Carboniferous in Britain by establishing six new stages in the Dinantian. The Onimaru Formation correlates with the Brigantian Stage of this new classification.

Belgium

Common species between the Onimaru Formation and the Belgian Dinantian are *Diphyphyllum fasciculatum* (Fleming), *D. furcatum* (Thomson), *Dibunophyllum bipartitum* (McCoy), *Lonsdaleia duplicata* (Martin) and *Hexaphyllia mirabilis* (Duncan). All of these species except *Dibunophyllum* range through uppermost V<sub>3b</sub> and V<sub>3c</sub> of the Upper Viséan.

U.S.S.R.

The Russian Platform (Dobrolyubova, 1958) and the Northern Urals (Sayutina, 1974) contain abundant corals in common with the Onimaru Formation. The common species are *Diphyphyllum fasciculatum* (Fleming), *D. lateseptatum* McCoy, *Siphonodendron rossicum* (Stuckenbergl), *Lithostrotion columellata* Dobrolyubova, *Arachnolasma cylindricum* Yü and *Dibunophyllum bipartitum* (McCoy). These species have relatively long ranges as a whole, but the ranges of taxa found in the Onimaru Formation overlap each other in the Oksky Superhorizon of the U.S.S.R.

China

Common species between the Onimaru Formation and the Hunan and Guizhou Provinces, which contain widely distributed Lower Carboniferous deposits, are *Arachnolasma sinense* (Yabe and Hayasaka), *A. minor* Wu, *A. simplex* Yü, *A. lophophylloidea* Wu, *A. multiseptatum* Yü, *A. equiseptatum* Yü, *Dibunophyllum bipartitum* (McCoy), *Kueichouphyllum sinense* Yü, *K. ephippium* Yü, *K. gracile* Yü, *Palaeosmilia regia* (Phillips), *Yuanophyllum kansuense* Yü, *Diphyphyllum hochangpingense* Yü, *Lithostrotion columellata* Dobro-

Niikawa (1983)		Minato and others (1959)		Onuki (1937, 1938)	
Nagaiwa Formation		Nagaiwa Series			Nagaiwa Stage
Onimaru Formation	Barren zone	Onimaru Series	Hiishi Stage	Onimaru Series	Upper Kanenokura Stage
	<i>Arachnolasma</i> - <i>Palaeosmilia regia</i> zone				
	<i>Saccaminopsis</i> zone				
	<i>Kueichouphyllum gracile</i> - <i>Actinocyathus japonicus</i> zone		Hotokezaka Stage		

Text-figure 1.—Summary of zonal usage in the Onimaru Formation of the southern Kitakami Mountains.

lyubova and *Neoclisiophyllum xiangxiangense* Wu. Most of these species are known from the Shangssu Member in Guizhou Province and from the Tzemenchiao Member in Hunan Province; *i.e.*, from the *Yuanophyllum* zone of the Fengninian in China.

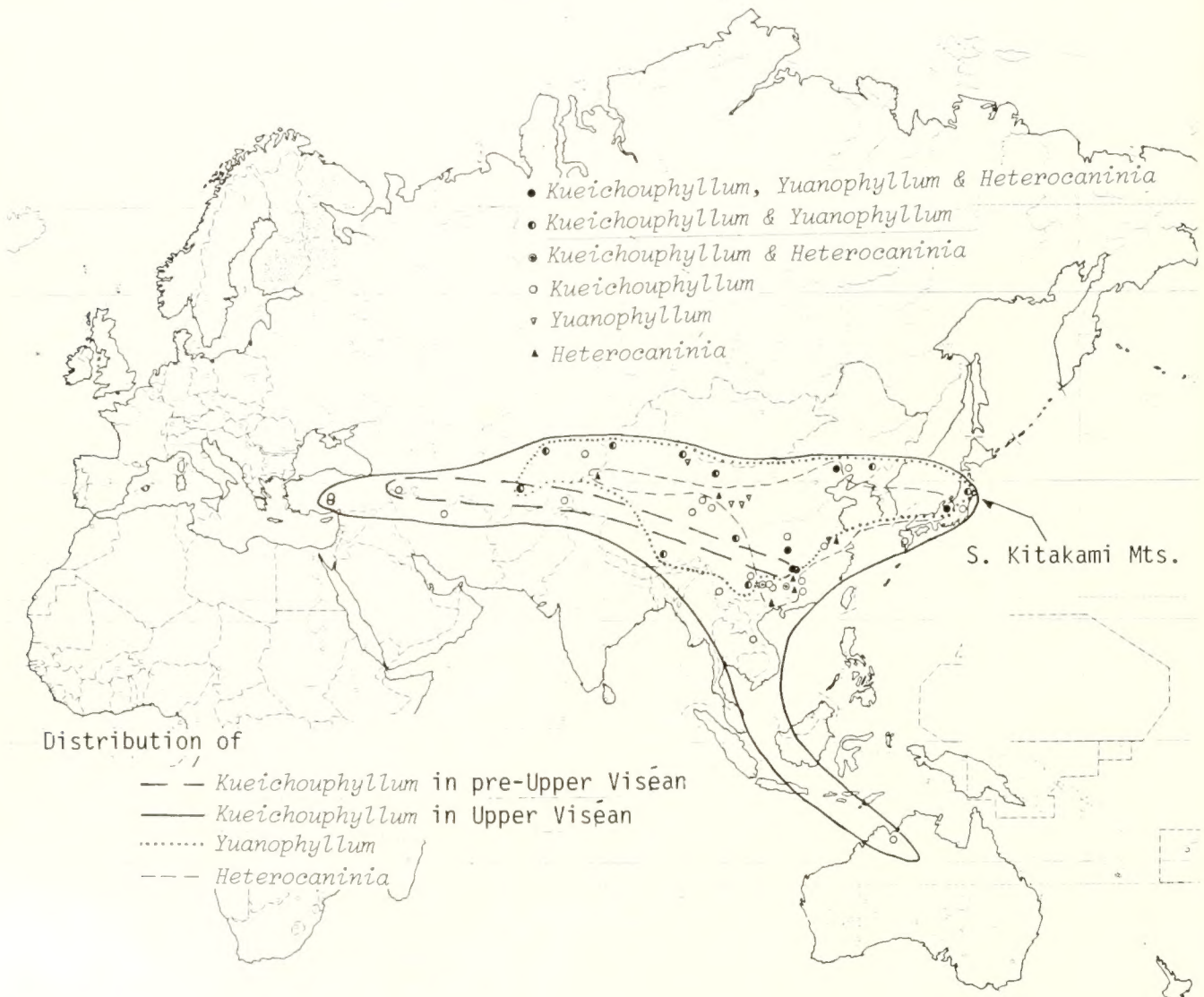
#### Remarks

The Onimaru Formation is thus correlated with the uppermost Dinantian, but the presence of the  $D_1$  subzone in the formation has not yet been ascertained. The absence of  $D_1$  may suggest that there is a hiatus between the Onimaru Formation and the underlying Hikoroichi Formation.

#### PALEOBIOGEOGRAPHY

Formations that contain Onimaru-type corals are widely distributed in Japan from Kyushu to Honshu.

Major contributions on these corals have been published by Minato (1944), Kanmera (1952), Sato (1954), Kato (1959) and others. The coral faunas described in these papers are so similar to those of the Onimaru Formation that they may be referred to collectively as the Onimaru fauna. Coral genera in this fauna include *Siphonodendron*, *Lithostrotion*, *Diphyphyllum*, *Aulina*, *Lonsdaleia*, *Actinocyathus*, *Pseudodorlodotia*, "*Tabulophyllum*," *Dibunophyllum*, *Arachnolasma*, *Koninckophyllum*, *Yuanophyllum*, *Palaeosmia*, *Kueichouphyllum*, *Heterocaninia*, *Neoclisiophyllum*, *Hexaphyllia* and *Heterophyllia*. Although cosmopolitan genera such as *Lithostrotion*, *Siphonodendron*, *Diphyphyllum* and *Koninckophyllum* are included, the fauna, as a whole, may be considered to have been situated in the eastern extremity of the Tethys faunal realm. Yü (1937) recognized "Sinican" elements in the



Text-figure 2.—Distribution of *Kueichouphyllum*, *Yuanophyllum* and *Heterocaninia*.



Carboniferous corals of China. Yü and Lin (1978) further mentioned Chinese type corals in the Fengninian. According to them, "Sinican" elements of the *Yuanophyllum* zone in the Fengninian are represented by *Kueichouphyllum*, *Yuanophyllum* and *Arachnolasma*. However, *Kueichouphyllum* was first known from the Upper Tournaisian in the Armenian SSR (Papojan, 1969). In the Lower Viséan, it was reported from the Uzbekian SSR (Anikina, 1962), the northern Pamir (Pyzhjanov, 1965), and from Hunan Province (Wu, 1963). From east to west, the localities from which *Kueichouphyllum* has been reported from the pre-Upper Viséan extend from China to Armenia and form a very narrow paleobiogeographical province within the Tethyan realm (Text-fig. 2). *Kueichouphyllum* later migrated more widely in all directions and marked the extension of the so-called *Kueichouphyllum* sea province in the Upper Viséan. *Arachnolasma* is widely known from Japan, China, Central Asia, northern Urals, Poland, and northwest Sahara. This distribution suggests that *Arachnolasma* is not a provincial Chinese-type coral but was cosmopolitan. *Yuanophyllum* definitely occurs in eastern Central Asia, China, and Japan, and may be considered to belong to a biogeographical subprovince of the *Kueichouphyllum* sea province. The distribution of *Heterocaninia*, which was not regarded as a "Sinican" element, is more narrowly limited than *Yuanophyllum* and occurs only in China and Japan.

### CONCLUSIONS

1) The Onimaru Formation consists mainly of black, well-bedded limestone about 94 m thick and is divided into four fossil zones in ascending order: *Kueichouphyllum gracile*-*Actinocyathus japonicus* Zone, *Saccamminopsis* Zone, *Arachnolasma*-*Palaeosmilina regia* Zone and Barren Zone.

2) The Onimaru Formation is correlated with the D<sub>2</sub> and D<sub>3</sub> subzones of the *Dibunophyllum* zone or the Brigantian Stage in the British Dinantian, uppermost V<sub>3b</sub> and V<sub>3c</sub> in Belgium, the Oksky Superhorizon in U.S.S.R., and the Shangssu and Tzemenchiao Members of the Fengninian in China.

3) The Onimaru fauna may be considered to have been situated at the extremity of the *Kueichouphyllum* sea province. *Yuanophyllum* and *Heterocaninia* may be regarded as the endemic corals of the East Asia.

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## BIOSTRATIGRAPHIC UTILITY OF UPPER PALEOZOIC SYRINGOPOROID CORALS, WESTERN INTERIOR REGION, CONTERMINOUS U.S.A.

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### ABSTRACT

The uppermost Devonian to Lower Permian sequence in the western interior region of the U.S.A. is characterized by a continuously evolving complex of syringoporoid corals that can be divided into eight genera and 24 morphogroups useful for biostratigraphic analysis. Major discontinuities in the phylogenetic succession occur at about the lower Meramecian–middle Meramecian boundary, the Meramecian–Chesterian boundary, the Mississippian–Pennsylvanian boundary, the Atokan–Desmoinesian boundary, and the Missourian–Virgilian boundary. The syringoporoids are particularly useful for distinguishing provincial series in the Upper Mississippian and Pennsylvanian. Although the potential for zonal resolution by these corals is not as great as present resolution attainable by fusulinids and conodonts, they afford a useful tool for biostratigraphic analysis because of their abundance, widespread distribution, and visibility.

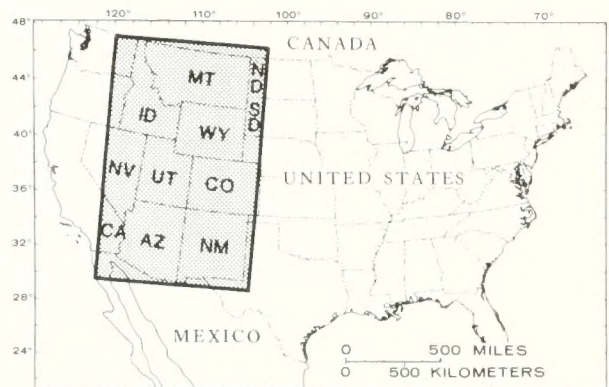
### INTRODUCTION

Tabulate corals having the general morphology of *Syringopora* Goldfuss are among the most common and widespread fossils in carbonate rocks of late Paleozoic age. Until recently, these syringoporoid corals received little attention as biostratigraphic indices, and even today the generic name *Syringopora* is applied indiscriminately to morphologically diverse corals throughout the Paleozoic. Pioneer work by Sokolov (1955) led the way to recognition of meaningful morphologic variations that have resulted in many new syringoporoid taxa. More recently, Chudinova (1975, 1980a, b) inferred a comprehensive phylogeny for the Paleozoic syringoporoids based on morphologic trends derived from careful study of many specimens.

In North America, intensive work by Nelson (1962a, 1977) on Mississippian syringoporoids in western Canada provided new taxonomic and biostratigraphic perspectives in the upper Paleozoic. Driscoll and Newton (1969), Harker and Thorsteinson (1960), Hoare (1964, 1966), Langenheim and McCutcheon (1959), McCutcheon (1961), Nelson (1962b), Rowett (1969), Sando (1960, 1965, 1969, 1975), Tischler (1963), Wilson (1963, 1982), and Wilson and Langenheim (1962) presented useful descriptions of genera and species from North American upper Paleozoic rocks. Syringoporoid genera were used as biostratigraphic indices in coral zonation of the Mississippian of western North America by Sando and others (1969) and Sando and Bamber (1979). Paleogeographic and paleoecologic syntheses including Mississippian syringoporoid corals were also presented by Sando and others (1975, 1977) and Sando (1980). Until now, most of the emphasis in North America has been on the Mississippian. The present report explores biostratigraphic patterns in the entire upper Paleozoic sequence of the western interior States.

### DATA BASE

Biostratigraphic conclusions presented herein are based on 581 occurrences of syringoporoid corals from rocks ranging in age from latest Devonian to Early Permian in the States of Arizona, California, Colorado, Idaho, Montana, Nevada, New Mexico, North Dakota, South Dakota, and Utah (Text-fig. 1). Most of the specimens studied are from collections made during the past 80 years by various geologists of the U.S. Geological Survey. All specimens were independently dated by other fossils as follows: Devonian, conodonts identified by C. A. Sandberg; Mississippian, foraminifers and algae identified by B. L. Mamet and conodonts identified by C. A. Sandberg; Pennsylvanian, fusulinids identified by R. C. Douglass and L. G. Henbest and brachiopods identified by M. Gordon, Jr. and T. W. Henry; Permian, fusulinids identified by R. C. Douglass and L. G. Henbest. The occurrences are overwhelmingly in shallow-water shelf carbonate facies, mostly free of terrigenous detritus, except for some



Text-figure 1.—Map of United States of America showing location of western interior region where syringoporoid corals occur in upper Paleozoic rocks.

MORPHOGROUP	NOMINAL NORTH AMERICAN SPECIES AND FORMAE		CORALLUM		CORALLITE		CONNECTIONS BETWEEN CORALLITES		CORALLITE WALL		VIS-CERAL CAVITY	TABULAE		SEPTAL SPINES				
			FORM	SHAPE	FORM	SHAPE	MEAN DIAMETER (mm)	MEAN FREQUENCY (per cm <sup>2</sup> )	TUBULI	MURAL PORES		PLATE OR STRIAE	WIDTH-MEAN THICKNESS (mm)	ARRANGEMENT	TRACES	ABUNDANCE	LENGTH	
<i>Syringopora</i>	A	<i>Syringopora aculeata</i> Girty, <i>S. harveyi</i> White, <i>S. tubifera</i> Easton	fasciulate	bush-like	phaceloid and dendroid	cylindrical	1.1-1.8	8-18	sparse, short to long	absent	lamellar	-0.25	suboval to oval	intubular	concentric to subconcentric	absent to abundant	short to long	
	B	<i>Syringopora compacta</i> Nelson, <i>S. pennsylvanica</i> Shimer, <i>S. surculifera</i> Girty	-do-	-do-	-do-	-do-	1.9-2.6	3-14	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-	
	C	<i>Syringopora rudyi</i> Nelson	-do-	-do-	-do-	-do-	2.7-3.3	3-10	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-
	D	None	-do-	-do-	-do-	-do-	3.8+	2-4	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-
<i>Pleurostrophomena</i>	E	? <i>Syringopora agglomerata</i> Nelson	massive	hemispherical	phaceloid and subconoid	cylindrical to subcylindrical	2.0-2.5	16-17	sparse, very short	rare	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-
	F	<i>Syringopora bassor</i> Nelson	fasciulate	bush-like	phaceloid and dendroid	cylindrical	3.0-4.1	2-4	sparse, short	absent	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-
	G	<i>Syringopora dingmanae</i> Nelson	-do-	-do-	-do-	-do-	2.0-2.5	9-13	abundant, short to long	rare	lamellar?	-0.25	suboval to lateral	intubular to vascular	concentric to subconcentric	-do-	-do-	-do-
	A	None	-do-	-do-	-do-	-do-	1.5-2.0	7-9	sparse, very short	-do-	fibrous	-0.25	lateral	-do-	-do-	-do-	-do-	-do-
<i>Multithecopora</i>	B	<i>Syringopora virginica</i> Butts	-do-	-do-	-do-	-do-	1.5-2.0	8-23	sparse, very short	common	-do-	-do-	-do-	-do-	-do-	sparse to abundant	absent to common	
	C	<i>Syringopora drummondii</i> Nelson	-do-	-do-	-do-	-do-	2.3-2.5	5-9	sparse, short	-do-	-do-	-do-	-do-	-do-	-do-	sparse to abundant	absent to common	
	A	<i>Multithecopora?</i> <i>amsdensensis</i> Sando	-do-	-do-	-do-	-do-	1.9-2.6	7-13	abundant, very short	-do-	fibrous or fibrillar	-0.3	oval to lateral	horizontal	concentric	sparse	rate	
	B	None	-do-	-do-	-do-	-do-	1.1-1.2	26-33	abundant, very short	-do-	fibrous	-do-	oval, very narrow	grouped	concentric	rate	absent	
<i>Duncanopora</i>	C	<i>Multithecopora hypotaenae</i> Wilson, <i>M. paucitubulata</i> Moore & Jeffords, <i>Syringopora minor</i> Rowett	repent	thin sheet (3 cm max.)	phaceloid and dendroid	cylindrical to subcylindrical	1.6-2.5	6-20	rare, short	rare	fibrous or encephaloid	-do-	oval to lateral	grouped	-do-	rare to common	absent to common	
	A	<i>Duncanopora duncanae</i> Sando	massive	hemispherical to discoidal	phaceloid and subconoid	cylindrical to prismatic	1.3-2.5	18-43	abundant, regular	common	platforms	-do-	-do-	-do-	concentric to subconcentric	common	rate	
	A	None	repent to fasciulate	thick sheet (5 cm max.)	phaceloid and dendroid	cylindrical	1.9-2.5	10-15	abundant, short	-do-	-do-	-do-	-do-	horizontal and intubular	concentric	abundant	absent to abundant	
	B	None	repent	thick sheet (4 cm max.)	-do-	-do-	1.6	23	absent or rare	absent or rare	-do-	-do-	-do-	-do-	-do-	-do-	absent?	
<i>Neosyringopora</i>	C	<i>Syringopora mcutcheonae</i> Wilson	fasciulate to submassive	tabular to hemispherical	-do-	cylindrical to subcylindrical	1.9-2.3	14-19	abundant, short	common	abundant, tabular and platform	-do-	-do-	-do-	-do-	absent to common	short	
	A	None	fasciulate	bush-like	-do-	cylindrical	1.8-2.3	9-19	rare, abundant, short	rare to abundant, tabular	fibrous, encephaloid	-0.25	-do-	vascular	subconcentric to nonconcentric	-do-	absent to abundant	
	B	<i>Syringopora centrocylindrica</i> Driscoll & Newton	-do-	-do-	-do-	-do-	2.4-2.6	10-15	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-
	C	None	-do-	-do-	-do-	-do-	3.0	10	abundant, short	abundant	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-
<i>Cornwallia</i>	D	None	-do-	-do-	-do-	-do-	1.9-2.3	11-13	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-	-do-
	A	<i>Cornwallia tabulana</i> Hoare	massive	tabular to hemispherical	subconoid to carinal	subcylindrical to prismatic	2.5	23	very rare, short	-do-	-do-	-0.3	suboval	horizontal, intubular	-do-	-do-	-do-	-do-
<i>Bayhaum</i>	B	None	-do-	-do-	-do-	-do-	2.5-3.0	15-23	-do-	-do-	-do-	-0.2	-do-	-do-	-do-	-do-	-do-	-do-
	A	<i>Bayhaum vallium</i> Hoare	submassive to massive	tabular to hemispherical	-do-	-do-	1.8-2.0	20-35	rare, short	common	rare, tabular	-0.3	-do-	intubular and horizontal	concentric to subconcentric	-do-	common	short

Text-figure 2.—Critical morphologic characters of syringopoid morphogroups. The nominal species *Syringopora multattenuata* McChesney was inadvertently left out for the morphogroup *Neosyringopora* A.



quartzose arenaceous rocks in the Pennsylvanian and some deep water carbonate rocks in the Mississippian.

### TAXONOMY

The upper Paleozoic syringoporoid fauna of the western interior region includes eight nominal genera divided into 24 morphogroups, which are tentative taxonomic groupings based on somewhat arbitrary and convenient morphologic criteria (Text-fig. 2). Statistical studies are needed to determine whether these morphogroups can be treated as species or species groups. For the time being, the morphogroups at least are determinants for biostratigraphic discrimination not previously recognized. The genera are generally based on criteria summarized by Hill (1981), the most important of which is the nature of the tabulae. Essential criteria for differentiation of morphogroups are summarized in Text-figure 2.

### BIOSTRATIGRAPHY

#### Devonian

The syringoporoid succession studied for this report begins in the Pinyon Peak and Fitchville Formations of Late Devonian (late Famennian) age in Utah. Here we find four morphogroups (A–D) that belong to the genus *Syringopora*, which is characterized by a fasciculate, bush-like corallum, cylindrical corallites, axial to subaxial visceral cavity, infundibular tabulae, connecting tubuli, and a lamellar wall microstructure (Text-fig. 3). The corallites of the Famennian forms range from about 1 mm to more than 3.5 mm in mean diameter, but they can be divided into four arbitrary clusters based on mean corallite diameter.

#### Mississippian

Lower and lower Upper Mississippian (Kinderhookian to lower Meramecian) strata, principally the widespread Madison Limestone and equivalent formations, are characterized by the same four *Syringopora* morphogroups found in the Famennian. The Famennian forms may, as a group, have a smaller corallite frequency than the Mississippian forms, but this suggestion has not been tested statistically and the Mississippian assemblages include many specimens that appear to be identical to the Famennian forms. Although highest Famennian and lowest Mississippian strata have yielded few syringoporoids, the Devonian–Mississippian boundary appears to be unmarked by any significant morphologic changes. Preliminary statistical studies of *Syringopora* A–D by the author and K. R. Moore have failed to reveal any biostratigraphically significant morphologic variations in the Lower Mississippian. *Syringopora* E, a distinctive form having close-packed subcerioid corallites and restricted to

Mamet Zone 7, is the only *Syringopora* morphogroup that appears to have stratigraphic significance in this part of the sequence. Osagean and lower Meramecian strata contain rare specimens of the earliest representatives of *Pleurosiphonella* (P. A), which is characterized by a lateral visceral cavity, short connecting tubes and mural pores, and a fibrous wall microstructure. *Pleurosiphonella* is undoubtedly an offshoot from the *Syringopora* stock. The Lower Mississippian–Upper Mississippian boundary is not distinguishable on present syringoporoid criteria.

Syringoporoids are common in thick, shallow-water carbonate complexes of Utah and Idaho and their extensions in Wyoming and Montana. A significant change in the syringoporoid fauna takes place in the Upper Mississippian at about the base of Mamet Zone 13. *Pleurosiphonella* is the dominant syringoporoid and is represented by P. B in the middle and upper Meramecian and P. C in the Chesterian. *Multithecopora*, characterized by horizontal tabulae, short connecting tubuli, and corallite walls of highly variable thickness and fibrous or fibrous-amorphous microstructure, appears for the first time, represented by fasciculate coralla of M. A in the upper Meramecian and Chesterian and M. B in the upper Meramecian. *Multithecopora* C, a reptant morphogroup in which the coralla are in the form of sheets, is represented by a single specimen of probable Chesterian age. The closely related *Duncanopora*, having a phaceloid-cerioid corallum and abundant, regularly spaced connecting tubuli and platforms, is an important index to upper Chesterian (Mamet Zones 17 and 18) strata. *Syringopora* is represented only by two rare morphogroups (S. F and G) in the upper Meramecian (Mamet Zones 14 and 15); these forms are quite distinct from and have no apparent connection to older representatives of the genus. These later *Syringoporas* are the youngest representatives of the genus. Chesterian strata are distinguished from Meramecian strata by the presence of *Pleurosiphonella* C and *Duncanopora* A. Highest Mississippian strata (Mamet Zone 19) have not yielded syringoporoids.

#### Pennsylvanian

Syringoporoids are common in thick, shallow-water Pennsylvanian carbonate sequences in Idaho, Utah and Nevada and are rare in mixed carbonate-terrigenous sequences elsewhere in the western interior. Pennsylvanian syringoporoid faunas are strikingly different from those of the Mississippian; *Multithecopora* is the only Mississippian genus that ranges into the Pennsylvanian.

Lower Pennsylvanian (Morrowan) strata contain only *Multithecopora* C, which is distinguished by its reptant,

sheet-forming corallum. *M. C* dominates the Middle Pennsylvanian faunas and continues up into the Lower Permian. Desmoinesian strata are marked by the first appearance of *Neosyringopora* and *Neomultithecopora*, advanced forms having complex tabulae, short connecting tubes and mural pores, and a fibrous or fibrous-amorphous wall microstructure. *Neosyringopora*, distinguished by its vesicular tabulae, is represented by three morphogroups in Desmoinesian through Virgilian strata. *N. A*, the commonest form, continues up into the Lower Permian. *Neomultithecopora*, distinguished by its horizontal and infundibular tabulae, is represented by four morphogroups, two (*N. A* and *B*) that range from Desmoinesian into Lower Permian and two (*N. C* and *D*) that are restricted to the Upper Pennsylvanian. Virgilian strata are marked by the first appearance of *Cornwallatia* and *Bayhaium*. *Cornwallatia* is a massive, subcerioid to cerioid form having the internal structure of *Neosyringopora*, whereas *Bayhaium* is a submassive to massive form having the internal structure of *Neomultithecopora*.

Permian

Syringoporoids are generally rare in shallow-water Lower Permian carbonate rocks in Nevada, California, Arizona, Utah, and Idaho. Differentiation of faunas at the Pennsylvanian–Permian boundary is minimal. *Multithecopora*, *Neomultithecopora*, *Neosyringopora*, *Cornwallatia*, and *Bayhaium*, which characterize the Upper Pennsylvanian, are all present in the Lower Permian. However the number of morphogroups is reduced from nine in the Virgilian to six in the Lower Permian. No syringoporoids have been recorded from rocks younger than Wolfcampian in the study area.

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## RUGOSE CORALS OF THE LOWER-MIDDLE AND MIDDLE-UPPER DEVONIAN BOUNDARY BEDS OF THE CANTABRIAN MOUNTAINS (NW SPAIN)

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### ABSTRACT

Most rugose corals from the Devonian of the Cantabrian Mountains (NW Spain) can be dated in terms of conodont zones.

At present the base of the *Polygnathus costatus partitus* Zone is accepted as being the Lower-Middle Devonian boundary. In the Asturo-Leonese region of the Cantabrian Mountains the equivalent to that boundary could be the base of the *Icriodus retrodepressus* Zone. The rugose corals of the Moniello and Santa Lucia Formations will be analyzed in relation to this stratigraphic position.

Recently, the Middle-Upper Devonian boundary has been interpreted as being the base of the Lower *Polygnathus asymmetricus* Zone, equivalent to the transition *Ancyrodella binodosa-Ancyrodella rotundiloba*. The association of rugose corals from the Candas and Portilla Formations are listed with respect to this transition which is well established in the Cantabrian Mountains.

### INTRODUCTION

The Devonian of northwest Spain is entirely marine and from a structural point of view it forms what has long been called the Asturian arc. Most of the outcrops belong to the Cantabrian Zone (Lotze, 1945), although some of them occur in the West Asturian-Leonese Zone. West and south of the Narcea anticlinorium (Fig. 1), Devonian outcrops almost disappear due to erosion, or by plunging below the Tertiary of the Duero basin.

The Devonian sequence in the Cantabrian Mountains is characterized by terrigenous formations alternating with calcareous ones, frequently reefal, and interpreted as originating in the shallow neritic environment. This sedimentation is similar in type of that of Erben's (1962) "mixed magnafacies," or more exactly, to that of Copper's (1966) "Eifel Magnafacies." To the southeast there exists an area with pelagic deposits bearing planktonic and nektonic fossils, which is very similar to Erben's (1962) "Hercynian Magnafacies." Brouwer (1964) distinguished two types of facies, Asturo-Leonese and Palentine facies respectively, in order to differentiate the two Devonian realms in the Cantabrian Mountains (Fig. 1).

The stratigraphic framework of the Devonian in the Asturo-Leonese facies was established by Barrois (1882) on the northern slope and by Comte (1936, 1938, 1959) on the southern slope of the Cantabrian Mountains. The stratigraphical units on both slopes, especially those formations which are dealt with in this paper (Moniello-Santa Lucia, Candas-Portilla, Piñeres-Nocedo), could be the same. However, the first name in each pair is used to refer to the formation situated on the northern slope and the second one, to that on the southern slope. The correspondence between units is not however, necessarily synchronous and there is a continuous change in facies, not only along each structural

unit but also from one unit to another (Reijers, 1972; Colmenero, 1976; Mendez-Bedia, 1976).

The stratigraphic framework of the Devonian in the Palentine facies was established by several Dutch geologists (Van Veen, 1965; Binnekamp, 1965; etc.), who distinguished a series of formations (Fig. 2) and tried to compare them, without a great deal of success, with those of the Asturo-Leonese realm.

The Lower-Middle Devonian boundary in the Asturo-Leonese region of the Cantabrian Mountains is situated within the Moniello-Santa Lucia carbonates and the Middle-Upper Devonian boundary is located within the Candas-Portilla calcareous formations or within the detrital sequence of the Nocedo Formation. Because of the reefal character, in at least some of the members of these formations, the rugose coral fauna is generally abundant, not only in number of specimens, but also in number of taxa.

In the present paper the general rugose coral associations present in the Cantabrian Mountains are shown in relation to conodont biozones presently being adopted for the establishment of the Lower-Middle and Middle-Upper Devonian boundaries. In those cases where conodonts are lacking due to unfavorable facies, the biostratigraphical units used are brachiopod zones. Conodont and brachiopod data have been provided by Drs. Garcia-Lopez and Garcia-Alcalde respectively, to whom I am greatly indebted. In addition, I am grateful to Dr. Mendez-Bedia for aid in preparing this paper in English.

### LOWER-MIDDLE DEVONIAN BOUNDARY

Agreement has been reached by the International Subcommittee on Devonian Stratigraphy regarding the position of the Lower-Middle Devonian boundary at the base of the *Polygnathus costatus partitus* Zone

(the Eifelian boundary). The exact position of this boundary in the Asturo-Leonese realm of the Cantabrian Mountains is unknown due to the absence of *P. costatus partitus*; however, the finding of other typical conodonts of the same biozone (*Icriodus retrodepressus*), as well as brachiopods with wide geographical distribution, allow us to locate it approximately at the top of the Moniello-Santa Lucia Formations (Fig. 2).

Conodont distribution in different sections of the Moniello Formation (Asturias), allows good comparison with the "Couvinian" boundary. The presence of *Icriodus corniger ancestralis* towards the base of the Moniello Formation and the first appearance of *Icriodus corniger corniger* a few meters above this, limits the interval in which the Emsian-Couvinian boundary can be placed (Arbizu *et al.*, 1979; Garcia-Alcalde *et al.*, 1979). The associated rugose coral fauna has earlier been listed for the type locality of the Moniello Formation (Soto *in* Arbizu *et al.*, 1979), but the present paper provides more information about the rugose cor-

al content at other outcrops of the Moniello: *Edaphophyllum sulcatum* (Billings), *Mesophyllum* (*Cystiphyllodes*) *originale originale* Birenheide, *Cayugaea hispanica* Birenheide and Soto, *C. sp.*, *Ufimia prior* (Kullmann), *Combophyllum* n. sp. A, *Petronella truncata* (Barrois), *Synaptophyllum* n. sp., *Papiliophyllum* sp., *Metriophyllum album* Soto, *Ceratophyllum* sp., *Stereolasma asturica* Altevogt, *Hapsiphyllum subguilieri* (Kullmann), *Pseudamplexus* n. sp. 1, *P. n. sp. 2*, *Prismatophyllum* sp. aff. *P. ovoideum* (Davis), *Heliohyllum* sp., *Acinophyllum* n. sp. and *Xystriphyllum* sp.

The Eifelian boundary, as defined above, cannot be directly identified in the Moniello Formation but only indirectly and approximately traced. The occurrence of *Icriodus retrodepressus* in the Santa Lucia Formation in Leon, a few meters above the first appearance of *Anathyris alejensis* and the last occurrence of *Euryspirifer paradoxus* permit indirectly the establishment of this boundary in the upper part of the Moniello

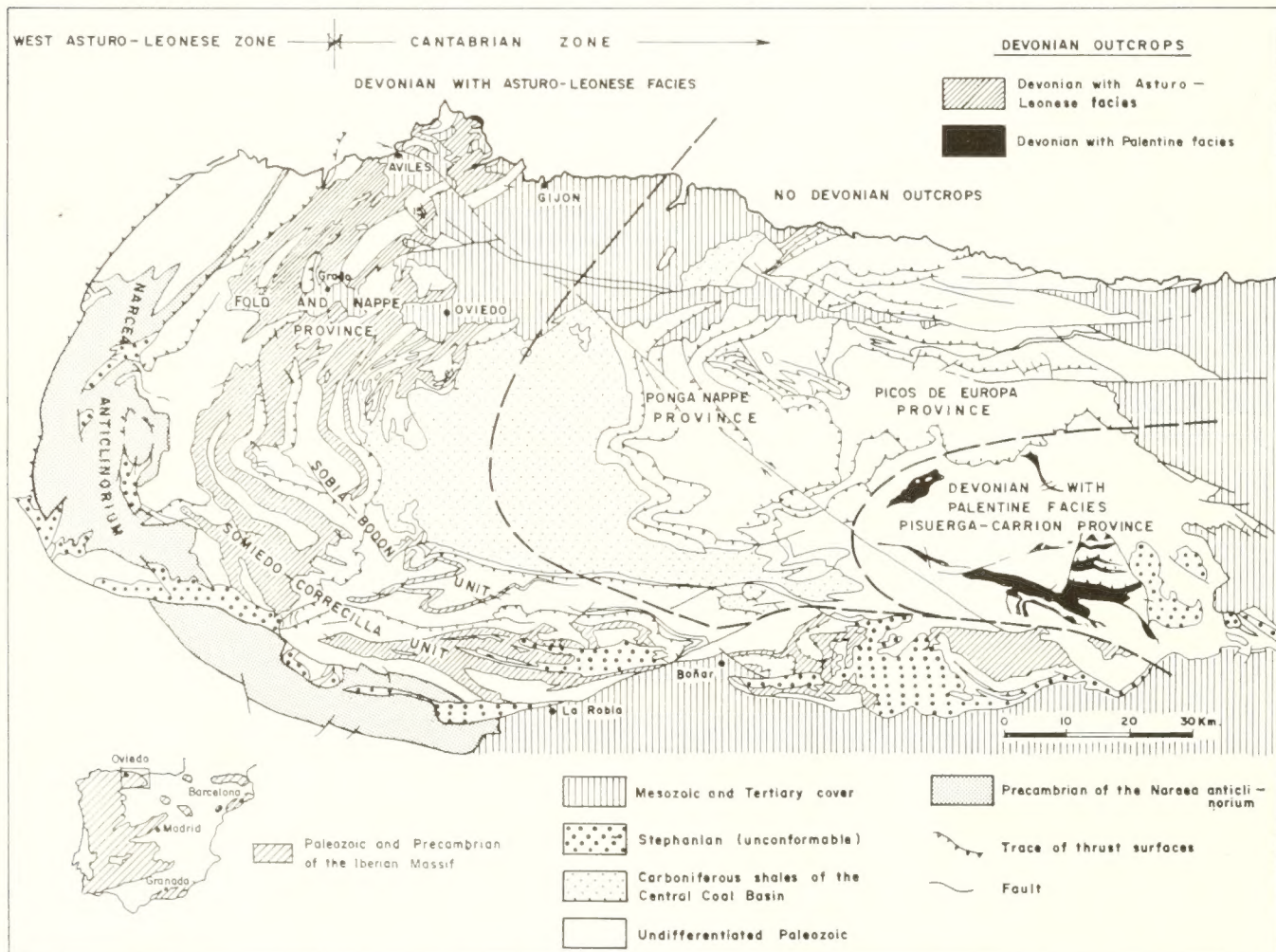


Figure 1.—Devonian outcrops of the Cantabrian Mountains (Garcia-Alcalde *et al.*, 1979).


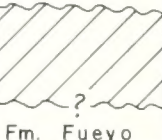
REGION		A S T U R I A S			L E O N		PALENCIA
AUTHORS	BARROIS	RADIG	TRUYOLS & GARCIA-ALCALDE	COMTE	TRUYOLS & GARCIA-ALCALDE	BROUWER	
STAGE	1.882	1.962	1.981	1.959	1.981	1.967	
FAMENNIAN	Grès de Cué	Marmol ? grioto	Fm. Candamo	Grès de L' Ermitage	Fm. Baleas	Vidrieros Fm.	
		Areniscas de Piñeres					
FRASNIAN	Calcaire de Candás	Calizas sup. de Candás	Fm. Piñeres	Grès de Nocedo	Fm. Fueyo	Murcia Fm.	
		Calizas inf. de Candás	Fm. Candás		Fm. Nocedo	Cardaño Fm.	
GIVETIAN	F <sub>1</sub>	Grès à Gosseletia	Fm. Naranco	Calcaires de la Portilla	Fm. Huergas	Gustalapedra Fm.	
	Gi						
EIFELIAN	COUVINIAN	Co 2	Areniscas de Gosseletia	Grès et Schistes de Huergas	Fm. Sta. Lucia	Gustalapedra Fm.	
		Co 1	Calcaire d'Arnao				Fm. Moniello
EMSIAN	Calcaire de Ferroñes	Capas sup. Moniello	Fm. Moniello	Calcaires de Sta. Lucia	Fm. Sta. Lucia	Abadia Fm.	
		Capas inf. Moniello					
SIEGENIAN	Schistes et Calcaires de Nieva	Capas de Aguión	Capas de Aguión	Calcoschistes et Calcaires de La Vid	Grupo La Vid	Abadia Fm.	
		Calizas de Ferroñes	Capas de Ferroñes				
GEDINNIAN	Grès de Furada	Margas de Ferroñes	Grupo Rañeces	Calcoschistes et Calcaires de La Vid	Grupo La Vid	Lebanza Fm.	
		Dolomias de Ferroñes					Dolomias de Bañuques
SILURIAN	Zona de Furada	Capas de Nieva	Fm. Furada	Grès de S. Pedro	Fm. S. Pedro	Carazo Fm.	
		Capas inf. de Nieva					

Figure 2.—Age of the Devonian lithostratigraphic units of the Cantabrian Mountains after several authors (Truyols and Garcia-Alcalde, 1981).

Formation (40–45 m below the top). However, 40 m below this level is the first occurrence of specimens comparable to *Arduspirifer(?) intermedius*. Thus a position between the two levels could be a more proper place for the Eifelian boundary (Fig. 2). The rugose fauna is composed of: *Mesophyllum (Cystiphylloides) tabulatum* (Wedekind), *M. (C.)* sp. cf. *M. (C.) secundum conistructum* (Quenstedt), *M. (C.) monielloense* Birenheide and Soto, *Cayugaea hispanica* Birenheide and Soto, *Calceola sandalina* (Linnaeus), *Combophyllum* cf. *lamellosum* Le Maitre, *Papiliophyllum multiseptatum* (Tsien), *P.* aff. *tabulatum* (Tsien), *Aulacophyllum* sp. cf. *A. sulcatum* (D'Orbigny), *Metriophyllum album* Soto, *Stereolasma asturica* Altevogt and *Acanthophyllum* sp. cf. *A. vermiculare* (Goldfuss).

In the Santa Lucia Formation in Leon (Fig. 2), the transition between *Icriodus corniger ancestralis* and *I. corniger corniger* occurs near the base of the Moniello Formation. Massive (*Favosites*), branching (*Thamnopora*) and lamellar tabulates are relatively abundant in these Emsian-Couvinian transition beds. However, rugose corals are rather scarce but include: *Mesophyllum (Cystiphylloides)* sp., *Stereolasma* sp., *Synaptophyllum* sp. cf. *S. multiseptatum* Soto, *Hapsiphyllum* sp. cf. *H. subguillieri* (Kullmann), *Calceola sandalina* (Linnaeus), *Papiliophyllum* sp. and *Pseudamplexus* sp. The finding of *Icriodus retrodepressus* towards the upper part of the formation (45–50 m below the top) allows good correlation with the Eifelian boundary. The coral fauna is very often affected by silicification. Rugose corals are numerous and represent the following taxa: *Mesophyllum (Cystiphylloides) originale ballonifer* Birenheide and Soto, *M. (C.) secundum secundum* (Goldfuss), *M. (C.) macrocystis* n. subsp., *Cayugaea* sp., *Stringophyllum* sp. cf. *S. acanthicum* (Frech), *Acanthophyllum heterophyllum* (Milne-Edwards and Haime), *Breviphrentis* n. sp., *Ceratophyllum* sp. aff. *C. salmense* (Wedekind), *Aulacophyllum* sp., *Papiliophyllum* sp., *Metriophyllum* sp. aff. *M. bouchardi* Milne-Edwards and Haime, and *Calceola sandalina* (Linnaeus).

In the Palentine realm (Brouwer's Palentine facies) of the Cantabrian Mountains (Fig. 1) the position of the Lower–Middle Devonian boundary on the basis of conodonts is still poorly known. To date, most papers published on this problem, locate the boundary in the upper part of the Abadia Formation (Fig. 2). De Sitter and Boschma (1966) consider this formation as being of Emsian age and only its uppermost part assignable to the Couvinian. Kullmann (1960, 1965) assigns an Eifelian age to the top of the Abadia Formation on the basis of the goniatites, *Anarcestes (Latanarcestes) noeggerati* and *Subanarcestes macrocephalus*. The associated rugose corals are scarce and exclusively soli-

tary, belonging to the "Cyathaxonia-fauna": *Syringaxon postsiluriensis* Kullmann, *S. pinguis* Kullmann, *Neaxon regularis* Kullmann, *Hapsiphyllum simplex* (Kullmann), *H. subguillieri* (Kullmann), *H. multiseptatus* (Kullmann), *Ufimia prior* (Kullmann) and *Pentaphyllum (Pentaphyllum) irregulare* Kullmann.

#### MIDDLE–UPPER DEVONIAN BOUNDARY

Discussion of the Middle–Upper Devonian boundary is centered here on the choice of a suitable level to define the base of the Frasnian in the Ardennes. This results from the long tradition of using the term Frasnian to represent the first stage of the Upper Devonian. Possible levels and biostratigraphic markers differ according to different authors. Maillieux (1942) considered the abundant appearance of cyrtospiriferid brachiopods to take place at the base of the F<sub>1</sub>; in other regions this seems to coincide with the boundary between the *Maenioceras terebratum* and *Pharciceras lunulicosta* ammonoid biozones (House and Ziegler, 1977). Finally, a level based on conodonts has recently been proposed, the base of the Lower *asymmetricus* Zone. This latter boundary can be indirectly drawn in Asturias (Candas Fm.), but in Leon (Portilla Fm.) it would be situated at an undetermined level in the lower half of the overlying detrital Nocedo Formation (Fig. 2), just below beds with *Ancyrodella rotundiloba rotundiloba*.

Conodont distribution in different sections of the Candas Formation (Asturias) allows good correlation with the Ardennes. The first appearance of *Polygnathus rhenanus* and *Icriodus latericarinatus*, almost at the base of the formation leads to the correlation of this part of the formation with the uppermost Givetian in the Ardennes. This boundary would be situated within the upper part of the Middle *varcus* Zone, but it is not possible to determine the boundary with the Upper *varcus* Zone because the characteristic elements are absent. Rugose corals at these levels are abundant and belong to diverse taxa: *Stringophyllum acanthicum* (Frech), *S.* sp. cf. *S. isactis* (Frech), *S.* sp. cf. *S. normale* Wedekind, *Sociophyllum elongatum* (Schlüter), *Mesophyllum (Mesophyllum) maximum maximum* (Schlüter), *Mesophyllum (Cystiphylloides) secundum secundum* (Goldfuss), *M. (C.) macrocystis macrocystis* (Schlüter), *Endophyllum* sp. cf. *E. abditum* Milne-Edwards and Haime, *Phillipsastrea* sp. cf. *P. hennai* (Lonsdale), *P.* sp. cf. *P. goldfussi* (Verneuil and Haime), *Disphyllum* sp. aff. *D. goldfussi* (Geinitz), *D.* sp., *Heterophrentis* sp. cf. *H. simplex* (Hall), *H. venezuelensis* (Weisbord), *H.* sp. cf. *H. prolifica* (Billings), *Thamnophyllum caespitosum* (Goldfuss), *Pterorrhiza* sp., *Heliophyllum halli* Milne-Edwards and Haime, *H.* sp., *Acanthophyllum concavum* (Walther), *A.* sp., *Grypo-*

*phyllum* sp., *Siphonophrentis gigantea* (Lesueur), *Temnophyllum* sp., *Pexiphyllum* sp. and *Charactophyllum* sp.

The disappearance of *Polygnathus latifossatus* and the appearance of *P. brevilaminus* in the middle part of the Candás Formation mark a suitable interval in which to draw the Givetian–Frasnian local boundary, conforming to the boundary that has been adopted by the Devonian Subcommittee (base of the Lower *asymmetricus* Zone). Conodont faunas occurring from this level up to the base of the overlying Pineres Formation are typically Frasnian: *Polygnathus webbi*, *Icriodus subterminus* and *Ancyrodella binodosa*. The associated rugose coral fauna is less varied than below, although biostromes of *Disphyllum* are abundant: *Disphyllum rugosum* (Wedekind), *D.* sp. cf. *D. lazutkini* (Ivanija), *D. goldfussi* (Geinitz), *D.* sp. aff. *D. geinitzi* Lang and Smith, *Thamnophyllum caespitosum* (Goldfuss), *Cyathophyllum* (*Cyathophyllum*) sp., *Tabulophyllum gorskii* Soshkina, *T. normale* (Walther), *Charactophyllum lotzei* Altevogt, *Breviphyllum occidentale* Altevogt and *Hexagonaria hexagona* (Goldfuss).

The conodont distribution in various sections of the Portilla Formation (Leon) does not permit the accurate drawing of the Givetian–Frasnian boundary, as it has been adopted at present (base of the Lower *asymmetricus* Zone). In the detrital levels of the overlying Nocedo Formation conodonts are lacking (Fig. 2). The Portilla Formation in the Bernesga section (Leon) belongs totally to the Upper Givetian (García-Alcalde *et al.*, 1979), whereas in other sections of the Leonese region a great part of the formation is Upper Givetian while the uppermost part of it either cannot be dated because of the lack of characteristic conodonts or could even be Frasnian (Frankenfeld, 1981). The Middle *varcus* Zone is always well characterized in the Portilla Formation, from the base of the sequence where *Polygnathus ansatus* occurs to 5 m below the top where *Spathognathodus semialternans* appears: The latter ranges in other regions from the Middle *varcus* Zone up to the Upper *hermanni-cristatus* Zone. Within the last 3.5 m of the succession, in some sections, is the first occurrence of *Schmidthognathus peracutus* which never occurs below the Upper *hermanni-cristatus* Zone. Thus, the Upper *varcus* and Lower *hermanni-cristatus* Zones are condensed to an interval of 1.5 m. The rugose coral species associated with these levels are numerous: *Stringophyllum isactis* (Frech), *S. acanthicum* (Frech), *S. buechelense* n. subsp., *S.* n. sp., *Sociophyllum elongatum* (Schlüter), *Heliophyllum halli* Milne-Edwards and Haime, *H.* n. sp. A, *H.* n. sp. B, *Thamnophyllum caespitosum*, *Disphyllum* sp. aff. *D. goldfussi* (Geinitz), *Temnophyllum* sp. cf. *T. rectum* (Walther), *T. majus* (Walther), *T.* sp. cf. *T. latum* (Walther),

*Pexiphyllum ultimum* Walther, *P. multizonatum* (Reed), *Pterorrhiza marginata* (Goldfuss), *P. bathycalix* (Frech), *P.* sp., *Metriophyllum bouchardi* Milne-Edwards and Haime, *M.* sp. cf. *M. skalense* Fedorowski, *Mesophyllum* (*Mesophyllum*) *maximum maximum* (Schlüter), *Mesophyllum* (*Cystiphyllodes*) *secundum schlueteri* (Wedekind), *M.* (*C.*) *pseudoseptatum* (Schulz), *M.* (*C.*) *secundum constrictum* (Quenstedt), *M.* (*C.*) *macrocystis leonense* Birenheide and Soto, *Acanthophyllum concavum* (Walther), *A.* n. sp., *Ceratophyllum* sp. 1, *C.* sp. 2, *Cyathophyllum* (*Cyathophyllum*) n. sp., *Pachyphyllum pradoanum* Haime, *Phillipsastrea hennai* n. subsp., *P.* sp. cf. *P. ananas* (Goldfuss), *Haplothecia* sp. cf. *H. pengellyi* Milne-Edwards and Haime, *Frechastrea* sp. cf. *F. micrommata* (Roemer), *F.* sp. aff. *F. frechi* Weyer, *Crassicycclus denseptatus* Soto, *Amplexocarinia* n. sp., *Siphonophrentis cantabrica* Birenheide, *S.* sp. A, *S.* sp. B, *Breviphrentis kullmanni* Birenheide, *B.* sp. A, *Tabulophyllum* sp. aff. *T. gracile* (Walther), *T.* sp. cf. *T. normale* (Walther), *Metrixonax schlueteri* Gliniski, *Neaxon* n. sp., *Famennelasma* n. sp., *Solipetra* n. sp., *Hapsiphyllum* sp. A, *Briantelasma*(?) n. sp., *Columnaria* sp. aff. *C. sulcata* Goldfuss, and *Calceola sandalina* (Linnaeus).

Rugose corals do not exist in the Upper *hermanni-cristatus* Zone and Lower *asymmetricus* Zone since they would fall within detrital beds of the Nocedo Formation as previously mentioned (Fig. 2). The only corals occurring in sandy limestones in the Nocedo Formation are very few and badly preserved samples of *Hexagonaria hexagona* (Goldfuss).

In the Palentine region of the Cantabrian Mountains, the Middle–Upper Devonian boundary is placed within the Cardaño Formation (Fig. 2). Adrichem-Boogaert (1965) assigns, on the basis of conodonts, a Frasnian age to the middle part of the formation and an Upper Frasnian to the top. Five meters below the top of the formation, *Ancyrodella curvata* and *Ancyrognathus triangularis* occur, and two meters below the top *Palmatolepis delicatula*, *P. minuta*, *P. gigas* and *Polygnathus normalis* are found (Lobato, 1977). In this unit rugose corals have not yet been found, as the facies is apparently unfavorable for them.

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AN EVOLUTIONARY PATTERN FOR THE WESTERN  
EUROPEAN LITHOSTROTIONIDAE

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## ABSTRACT

The oldest lithostrotionid in Western Europe is a new genus and species found in the Upper Tournaisian (Cf2 Foraminifera zone). It probably arose from the Chinese *Dematophyllum* and gave rise to the aulate *Solenodendron*. The first *Siphonodendron* appeared at the base of the Middle Viséan (base of the Cf46 subzone) and gave rise to *Lithostrotion araneum* (the first *Lithostrotion* species), to *S. martini*, and perhaps to *S. sociale*. Both the *Solenodendron* and the *Lithostrotion* lineages are characterized by a decrease in corallite size and septal number. *Siphonodendron* evolution is more complex and is mainly characterized by two opposite trends (both increase and decrease in the quantitative morphological characters). But the main morphological evolutionary trend in *Siphonodendron* is the replacement of lateral increase by parricidal increase resulting in the genus *Nemistium*, followed by the disappearance of the columella resulting in the genus *Diphyphyllum*.

## INTRODUCTION

Although numerous papers have contributed a good knowledge of the morphology, systematics, and stratigraphic distribution of the European lithostrotionids, only a few attempts have been made to explain their phylogenesis. Thus, Sando (1976) shed some light on the relationships between the aulate lithostrotionids, while Nudds (1979 and unpublished data) suggested a polyphyletic origin for *Lithostrotion* and *Diphyphyllum*.

This paper gives details about phylogenetic relationships among *Diphyphyllum*, *Lithostrotion*, *Nemistium*, *Siphonodendron*, *Solenodendron* and a new, undescribed Upper Tournaisian genus, and their Western European species. These relationships are inferred from: 1) morphological resemblances between the species, some of their morphotypes, developmental stages, or peculiar corallites such as "lost structures" (Fedorowski, 1978; Poty, 1981b); 2) corals showing a morphology and a stratigraphic position intermediate between two described species; and 3) comparison of stratigraphic distributions.

## SYSTEMATIC PALEONTOLOGY

Family LITHOSTROTIONIDAE  
d'Orbigny, 1851Genus *Lithostrotion* Fleming, 1828

*Diagnosis*.—Cerioid lithostrotionids having columellate corallites that usually show single dissepiments and a lateral ("intermural") non-parricidal increase.

*Discussion*.—The species of *Lithostrotion* (as well as species of the other lithostrotionid genera) can be determined mainly by statistical comparison of the number of septa and of the diameter of the tabularium (Nudds, 1981; Poty, 1981b).

*Western European species*.—*L. araneum* (McCoy,

1844), *L. vorticale* (Parkinson, 1808), *L. decipiens* (McCoy, 1849), *L. maccoyanum* Milne-Edwards et Haime, 1851.

Genus *Siphonodendron* McCoy, 1849

*Diagnosis*.—Fasciculate lithostrotionids having columellate corallites that show a lateral, non-parricidal increase.

*Discussion*.—The columella can be weak or absent, probably because of the influence of the environment (Poty, 1981a, b).

*Western European species*.—*S. ondulosum* Poty, 1981, *S. martini* (Milne-Edwards et Haime, 1851), *S. intermedium* Poty, 1981, *S. irregulare* (Phillips, 1836), *S. pauciradiale* (McCoy, 1844), *S. junceum* (Fleming, 1828), *S. sociale* (Phillips, 1836), *S. sp. A*, *S. sp. B*.

Genus *Nemistium* Smith, 1928

*Diagnosis*.—Fasciculate lithostrotionids having columellate corallites that show a parricidal increase.

*Discussion*.—For Smith (1928), the genus *Nemistium* was characterized by a weak but complex columella. Because this character is not constant and is known only in the type species *N. edmondsi*, I believe that it is not a generic but a specific character. Both lateral non-parricidal and parricidal increase have been recorded in *N. affine* (Fleming, 1828) but I have not verified this observation.

*European species*.—In Western Europe, *Nemistium* includes only two uncommon species: *N. edmondsi* and *N. affine*. It seems to be more common in Eastern Europe (i.e., *Lithostrotion* (*Siphonodendron*) *dobro-ljubovae* Nguyen Duc Khoa, 1977; *L. scoticum* Hill (Dobroljubova, 1958); *Diphyphyllum gracile* McCoy (Dobroljubova, 1958), *D. fasciculatum* (Fleming) (Dobroljubova, 1958), from where it probably migrated to Western Europe.

### Genus *Diphyphyllum* Lonsdale, 1845

*Diagnosis.*—Fasciculate lithostrotionids having non-columellate corallites that show a parricidal increase.

*Discussion.*—The axial tabellae of the  $\beta$  type of Smith (1928) can produce an aulos-like axial structure that differs from a true aulos by the non-participation of the ends of the septa in its construction. Parricidal increase was described in one of Lonsdale's syntypes of *D. concinnum* (type species of genus *Diphyphyllum*) by Rosen and Wise (1980).

*Western European species.*—*D. lateseptatum* McCoy, 1849, *D. furcatum* Hill, 1940, *D. fasciculatum* (Fleming, 1828), *D. gracile* McCoy, 1851, *D. maximum* Poty, 1981.

### Genus *Solenodendron* Sando, 1976

*Diagnosis.*—Fasciculate lithostrotionids having corallites that show an aulos formed by union of deflected axial ends of major septa. Increase parricidal.

*Discussion.*—Septal carinae are considered a diagnostic character of *Solenodendron* (Sando, 1976), but they are sometimes weak or absent in certain *Solenodendron* species, and they also occur in non-aulate species, i.e., *Lithostrotion araneum* (see Poty, 1981b, pl. IV, fig. 4) and *Diphyphyllum lateseptatum* (see Poty, 1981b, pl. XV, fig. 2).

*Western European species.*—*S. horsfieldi* (Smith and Yü, 1943), *S. hibernicum* (Clarke, 1966), *S. furcatum* (Smith, 1925).

### New Genus and Species

*Diagnosis.*—Fasciculate lithostrotionids having both aulate and columellate corallites. Increase probably parricidal.

Only one species is known.

### STRATIGRAPHY

The stratigraphic distribution of each species (Fig. 1) is reported in relation to the Belgian Dinantian zonation defined by Conil, Groessens and Pirlet (1976) and completed in Paproth, Conil, and others (1983). The Belgian distribution of Mamet's Foraminifera zones and an attempted correlation with North America are included on the figure for comparison.

### PHYLOGENY

*Oldest lithostrotionid in Western Europe.*—The oldest lithostrotionid known in Western Europe is a new genus and species found in the *Granuliferella* subzone (Cf2 Foraminifera zone, Upper Tournaisian) in the Avesne area, France. As mentioned above, some of its corallites have an aulos, while others are columellate. The aulate corallites show affinities with the Viséan *Solenodendron*, while the columellate ones show affin-

ities with the Chinese *Dematophyllum minor* Wu and Jiang, 1981. The genus *Dematophyllum* Wu and Jiang, 1981 (in Wu, Zhao and Jiang, 1981) includes *D. minor*, *D. hunanense* Wu and Jiang, 1981 and probably *Diphyphyllum antiquatum* Wu and Zhao, 1981. *Dematophyllum* is recorded by the authors from the Shaodong Formation in South China, which the Chinese consider to be of Etroeung age, but is probably younger (Middle Tournaisian?). Because its morphology and its stratigraphic position are intermediate between those of *Dematophyllum* and *Solenodendron*, the new Upper Tournaisian genus from France could be a European descendant of the former and the ancestor of the latter.

*Solenodendron lineage.*—The earliest *Solenodendron* is *S. horsfieldi* from the Lower Viséan (Cf4 $\alpha$  and  $\beta$  Foraminifera subzones) of England and Normandy, France. It is the first link of a continuous lineage mainly characterized by a decrease in corallite diameter, in aulos diameter, and in septal number (Sando, 1976). This lineage includes, from Early to latest Viséan, *S. horsfieldi*, *S. hibernicum* and *S. furcatum*. This evolution is probably neotenic.

*Siphonodendron phylogensis.*—The oldest *Siphonodendron* seems to be recorded from the upper part of the Banff Formation in Western Canada (Macqueen and others, 1972, p. 52), and from the Upper Tournaisian Rangari Limestone in Australia (Hill, 1973). Sando (1976) suggested that *Siphonodendron* could have arisen from the cerioid *Stelechophyllum* Tolmachev, 1933, but I believe that it arose from a *Dematophyllum*-like lithostrotionid, especially because it is not usual for a fasciculate form to evolve from a cerioid coral (Hill, 1956; Coates and Oliver, 1973).

In Western Europe, the oldest *Siphonodendron*, *S. ondulosum*, occurs at the boundary between the Cf4 $\gamma$  and the Cf4 $\delta$  Foraminifera subzones in Belgium and England (Poty, 1981b, 1983). It evolved from a non-European, indeterminate, older species of *Siphonodendron*.

The morphology of *S. ondulosum* varies according to three morphological trends which probably foreshadow the evolution of the species and even of the genus. The first trend is characterized by a widening of the dissepimentarium, a crowding of the divided tabulae and a more dense packing of the corallites, which sometimes form subcerioid colonies. Such morphotypes of *S. ondulosum* show numerous resemblances to *Lithostrotion araneum*, suggesting that the former could have given rise to the latter.

The second trend is characterized by a decrease in both septal number and corallite diameter, reaching the same values as observed in *S. martini*; this suggests close relationships between the two species.





The third trend is characterized by an increase in both corallite diameter and spacing of the tabulae, which are undivided. The resulting morphotype resembles *S. sociale*, but because such a morphologic trend also occurs in the earliest *S. martini*, *S. sociale* could have arisen either from *S. ondulosum* or from *S. martini*.

Thus, *S. ondulosum* probably gave rise, by adaptive radiation, to the genus *Lithostrotion*, to *S. martini* and perhaps to *S. sociale*.

Colonies of the early *S. martini* sometimes show corallites having young characters along their entire length (Poty, 1981b). These "lost structures" (Fedorowski, 1978) do not differ from the mature corallites either of *S. aff. S. intermedium* or of *S. irregulare*. This suggests (agreeing with their stratigraphic distributions) relationships between these species and *S. martini*.

*Siphonodendron* aff. *S. intermedium*, *S. irregulare* and the younger *S. pauciradiale* and *S. junceum* are the links in a lineage characterized by a decrease in both corallite diameter and septal number (and by the disappearance of the dissepiments in the youngest *S. junceum*). This neotenic evolution ranges from the early Cf5 Foraminifera zone to the Cf6 $\gamma$  subzone.

In contrast, another lineage characterized by an increase in corallite diameter and in septal number developed during the Cf5-Cf6 $\gamma$  time. It starts with larger morphotypes, either of *S. ondulosum* or of *S. martini*, and includes *S. sociale* (see above the discussion about the origin of *S. sociale*) and *S. sp. B*.

Other species such as *S. intermedium* and *S. sp. A* appear during the Upper Viséan. They can be related to previous species, as suggested on the figure, because of some morphological affinities.

*Lithostrotion* lineage.—The stratigraphic order in the appearance of the *Lithostrotion* species shows that each new species has a smaller tabularium diameter and septal number than the previous one. This suggests a neotenic pattern of evolution such as that described previously in *Solenodendron* and *Siphonodendron*. The *Lithostrotion* lineage includes, from the early Cf5 Foraminifera zone to the Cf6 $\gamma$  subzone, *L. araneum*, *L. vorticale*, *L. decipiens* and *L. maccoyanum*. Note that *L. decipiens* not only gave rise to *L. maccoyanum* but also to the genus *Orionastrea* Smith, 1916 (as suggested by Nudds, 1979), and that *L. maccoyanum* could have given rise to the subgenus *Aulina* Smith, 1916, emend. Sando, 1976 (as suggested by Sando, 1976).

*Relationships among Siphonodendron, Nemistium and Diphyphyllum*.—The main characters of *Diphyphyllum* are the lack of a columella and parricidal increase. In contrast, *Siphonodendron* has a columella

and lateral, non-parricidal increase. However, any fasciculate columellate lithostrotionids that we attribute to *Nemistium* show parricidal increase. This suggests that *Diphyphyllum* could arise from a *Siphonodendron* (of the *S. martini* group?) through an unknown *Nemistium* species. Considering their stratigraphic distribution, that evolution probably took place not long after the Cf6 $\beta$  subzone and, because *Nemistium* is not known before the Cf6 $\delta$  subzone, outside of Western Europe. The evolutionary pattern of *Nemistium* is not known.

*Diphyphyllum phylogenesis*.—*D. furcatum* appears in the Cf6 $\beta$  subzone and seems to be the earliest *Diphyphyllum* in Western Europe. It is probably at the origin of two divergent lineages. The first one, including *D. fasciculatum* and *D. gracile*, is characterized by a decrease in both corallite diameter and septal number. The second one, including *D. lateseptatum* and *D. maximum*, is characterized by an increase in both corallite diameter and septal number.

#### CONCLUSIONS

Evolutionary changes affecting qualitative morphological characters such as the axial structure (columella, aulos or nothing), the pattern of increase (lateral, intermural or parricidal) or the growth pattern (cerioid or fasciculate), can be regarded as changes at the generic level. In contrast, evolutionary changes affecting quantitative morphological characters, such as septal number or corallite diameter (tabularium diameter in cerioid colonies) can be regarded as changes at the specific level.

The evolution of the quantitative characters can follow two opposite trends: either an increase or a decrease in septal number and corallite (tabularium) diameter. This latter evolutionary trend seems to be the more common one and suggests a neotenic evolutionary pattern. Indeed, the corallites of each new species of a taxon usually have the same morphological characters as those of the young corallites of the previous species.

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## UPPER DEVONIAN (FRASNIAN) RUGOSE CORALS OF THE HAY RIVER REGION, NORTHWEST TERRITORIES, CANADA

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### ABSTRACT

Middle and Late Frasnian strata of the Hay River region of southern District of Mackenzie contain a diverse, well-preserved rugose coral fauna. Of the 76 species recognized at present, some 38 await formal description. Previous work on the Hay River coral faunas is reviewed, while current taxonomic assignments and likely type horizons are provided for forms described from the area. Type material of *Temnophyllum parvulum* (Whiteaves), *Tabulophyllum mcconnelli* (Whiteaves), *Phillipsastrea exigua* Lambe and *Macgeea proteus* Smith is illustrated in thin section for the first time.

### INTRODUCTION

The presence of well-preserved corals in the Upper Devonian strata of the Hay River region, west of Great Slave Lake in southern District of Mackenzie, has been known since the pioneering explorations of McConnell (1891). However, while approximately half of the species currently recognized in the area have been described (see below), they are in need of major revision in terms of taxonomy, description and illustration. The Frasnian rugose corals of the Hay River area, together with those from other regions in western Canada (over 120 species), are currently being studied by the writer, partly in conjunction with Alan Pedder of the Geological Survey of Canada. Initial results have been published (McLean, 1982) or submitted for publication (McLean and Pedder, in press).

The coral-bearing strata under consideration, occur in an outcrop belt that stretches from tributaries of the Liard River in the west (Blackstone, Birch, and Poplar Rivers), across tributaries of the upper Mackenzie River (Jean-Marie, Trout, Redknife, and Bouvier Rivers) to the Kakisa River, the escarpment north and east of Kakisa Lake and finally to Hay River itself in the east (Text-fig. 1). The stratigraphic subdivision of the Frasnian sequence in this area is basically that proposed by Belyea and McLaren (1962) with subdivisions of the Hay River Formation (Members A-F) adopted by Jamieson (1967). Stratigraphic terminology is illustrated in Text-figure 2. Corals are only sparsely present in the upper part of Member A of the Hay River Formation, a unit dominated by green silts and shales bearing abundant acritarchs and brachiopods. However the upper two thirds (approximately) of the Frasnian sequence has a diverse rugose coral fauna, generally showing excellent preservation, associated with abundant brachiopods, stromatoporoids, algae, conodonts, foraminifera and palynomorphs. Lithologies are dominated by limestones that are often silty, together with calcareous shales. Major and minor bio-

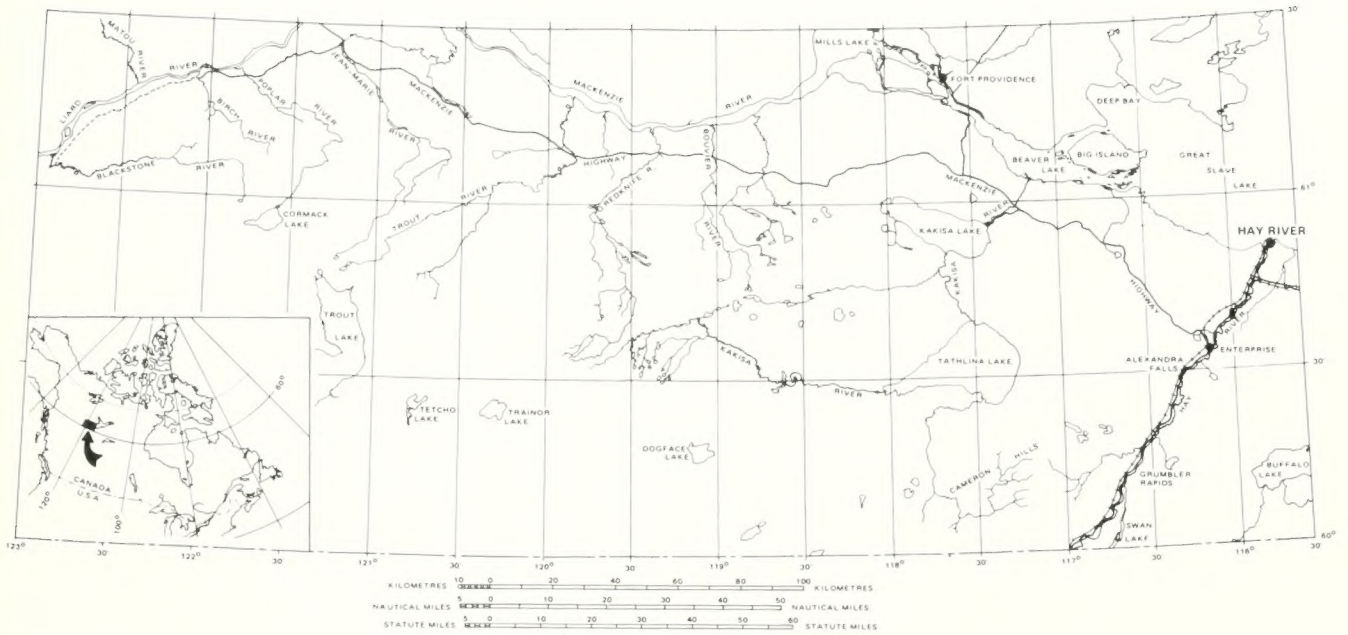
herms and biostromes are developed at a number of levels and a major stromatoporoid-algal reef complex (with minor rugose corals) is developed in the Hay River-Kakisa River area as the Alexandra Member of the Twin Falls Formation (Jamieson, 1971).

### PREVIOUS CORAL STUDIES

Of all the fossil groups represented in this study area, the corals have probably been most thoroughly studied. A major problem in dealing with much of the early literature is that locality data are unreliable in many cases. Whiteaves (1891) described and illustrated a number of forms collected by McConnell from "40 miles" above the mouth of Hay River. It is most probable that these faunas came from the upper part of the Hay River Formation (probably Members B and C on the basis of the fauna present) but their exact positions cannot be known. Only one new species was described by Whiteaves ("*Heliophyllum*" *parvulum*), but later (Whiteaves, 1898) he added a new name for a species from his collection ("*Cyathophyllum*" *mcconnelli*). Lambe (1901) redescribed a number of Whiteaves' forms and also proposed a new name ("*Phillipsastrea verrilli* var. *exiguum*") for one of them.

Lang and Smith (1939) erected a new genus, *Micrrophyllum*, based on material collected by Whittaker from beds on Redknife River now referred to the Kakisa Formation. The bulk of Whittaker's collection was described by Smith (1945) in the only major study of the corals of the region. However, much of this material was poorly located, both geographically and stratigraphically. Smith published extracts from Whittaker's field notes, but as McLaren (1959) has noted, there are discrepancies between Whittaker's original notes and the published versions. The type localities of some of Smith's type specimens must, for the present, remain a mystery.

Warren and Stelck (1956) illustrated externally a number of forms referred to their "*Macgeea* fauna"



Text-figure 1.—Locality map, southern District of Mackenzie.

from the “Hay River Shale” and their “*Spirifer stri-gosus* fauna” of the “Hay River Limestone” on the Hay River. Accurate geographic and stratigraphic locations for these forms were not given.

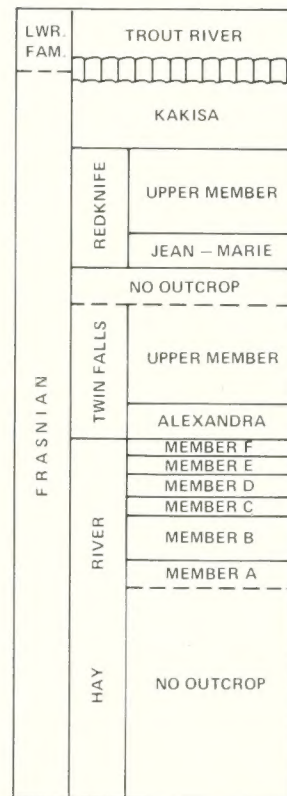
McLaren (1959) restudied some of Smith’s material and erected two new species (*Phacellophyllum fenense* and *P. tructense*). The need for detailed revision of the Hay River coral fauna was emphasized by McLaren’s work. McLaren *et al.* (1962) illustrated some new material from the region, although no new taxa were introduced.

Birenheide (1962) erected a new genus, *Smithiphyllum*, with type species *Spongophyllum imperfectum* Smith, 1945. Pedder (1965) redescribed this species, accurately locating it from the Jean-Marie Member of the Redknife Formation on Jean-Marie River, and proposed a new species (*S. whittakeri*) from the same horizon and locality. Rozkowska (1980) erected *Smithicyathus*, having *Phillipsastrea cincta* Smith, 1945 as type species. The type locality of this species is doubtful as Smith (1945, p. 70) recorded it from Redknife River, “5 miles above the falls.” As the highest Devonian coral-bearing beds on Redknife River occur *at* the falls, this locality information is obviously incorrect. The species has been re-collected by the writer at the falls, in the topmost beds of the Kakisa Formation, and this probably represents the type locality and horizon.

Lakhov (1982) included material from the Jean-Marie Member on Poplar River, referred by Pedder (1965) to *Smithiphyllum imperfectum* (Smith), in the new species *Pantophyllum pedderi*. Pedder’s material is clearly representative of *Smithiphyllum*, and is unre-

lated to the disphyllid *Pantophyllum* (a possible junior synonym of *Breviseptophyllum* Ermakova).

Most recently, McLean and Pedder (in press) introduced a number of new taxa from Frasnian strata of



Text-figure 2.—Composite stratigraphic column, Frasnian strata, southern District of Mackenzie.

western Canada. Included in these are representatives of the new genera *Mikkwaphyllum* from Member C of the Hay River Formation and *Parasmithiphyllum*, *Tarphyphyllum*, *Bouvierphyllum*, *Wapitiphyllum* and *Kakisaphyllum* from the Kakisa Formation.

#### TAXONOMIC ASSIGNMENT OF PREVIOUSLY DESCRIBED SPECIES

Listed below are species described from the Hay River region by earlier workers, with current taxonomic assignment given after each taxon. Type horizons for these species in terms of stratigraphic nomenclature adopted here are also given.

##### Whiteaves, 1891:

*Campophyllum ellipticum* (Hall and Whitfield), p. 202—*Tabulophyllum mcconnelli* (Whiteaves, 1898). ?Member B, Hay River Formation. (See Pl. 1, figs. 3, 4.)

*Heliophyllum parvulum*, p. 203—*Temnophyllum parvulum* (Whiteaves). ?Member B, Hay River Formation. (See Pl. 1, figs. 5, 6.)

*Phillipsastrea verrilli* Meek, p. 205—*Phillipsastrea exigua* Lambe, 1901. ?Member C, Hay River Formation (See Pl. 1, figs. 1, 2.)

##### Lang and Smith, 1939:

*Mictophyllum nobile*, p. 155—*Mictophyllum nobile* Lang and Smith, Kakisa Formation.

##### Smith, 1945:

*Charactophyllum* sp., p. 18—*Hunanophrentis* sp., Kakisa Formation.

*Disphyllum catenatum*, p. 21—*Disphyllum catenatum* Smith, Upper Member, Redknife Formation.

*Disphyllum* (*Synaptophyllum*) cf. *arundinaceum* (Billings) (= *Phacellophyllum fenense* McLaren, 1959), p. 22—pl. 12, fig. 1 = *Peneckiella* sp. cf. *P. densa* (Smith), Upper Member, Twin Falls Formation; pl. 12, fig. 2 = *Phacellophyllum colemanense* (Warren, 1928), same horizon.

*Disphyllum* (*Synaptophyllum*) *densum*, p. 22—*Peneckiella densa* (Smith), Upper Member, Twin Falls Formation.

*Disphyllum* (*Synaptophyllum*) *stramineum* (Billings), p. 23—pl. 13, figs. 1, 2, 4, 5, 7, 8, 10 = *Smithicyathus tructensis* (McLaren, 1959), Kakisa Formation; pl. 13, figs. 6, 11, 12 = *Peneckiella* sp., same horizon.

*Macgeea proteus*, p. 27—*Macgeea proteus* Smith, ?Member B, Hay River Formation. (See Pl. 1, figs. 7, 8.)

*Metriophyllum* sp. A, p. 29—*Hunanophrentis* sp., Kakisa Formation.

*Mictophyllum semidilatatum*, p. 31—*Mictophyllum semidilatatum* Smith, Kakisa Formation.

*Mictophyllum modicum*, p. 32—pl. 5, figs. 1, 2, 4–6; pl. 7, fig. 8 = *Temnophyllum modicum* (Smith) Kakisa Formation; pl. 5, fig. 3 = *Temnophyllum* sp., same horizon.

*Mictophyllum* near *modicum*, p. 33—*Temnophyllum* sp., Kakisa Formation.

*Mictophyllum multiseptatum*, p. 33—*Temnophyllum multiseptatum* (Smith), Kakisa Formation.

*Phillipsastrea whittakeri*, p. 39—*Frechastraea whittakeri* (Smith), Kakisa Formation.

*Phillipsastrea whittakeri*, large variety, p. 40—*Frechastraea whittakeri?* (Smith), Kakisa Formation.

*Phillipsastrea macouni*, p. 41—pl. 20, figs. 4–6, 8; pl. 23, fig. 6 = *Phillipsastrea nevadensis* Stumm, 1940, ?Member C, Hay River Formation; pl. 20, fig. 7; pl. 21, fig. 1; pl. 23, fig. 5 = *Phillipsastrea woodmani* (White, 1870), ?same horizon.

*Phillipsastrea exigua* Lambe, p. 41—*Phillipsastrea* sp. (*non* Lambe, 1901), Kakisa Formation.

*Phillipsastrea vesiculosa*, p. 42—*Phillipsastrea vesiculosa* Smith, Kakisa Formation.

*Phillipsastrea cincta*, p. 43—*Smithicyathus cinctus* (Smith), Kakisa Formation.

*Prismatophyllum* cf. *magnum* Fenton and Fenton (sic), p. 47—*Hexagonaria magna* (Webster and Fenton in Fenton and Fenton, 1924), Jean-Marie Member, Redknife Formation.

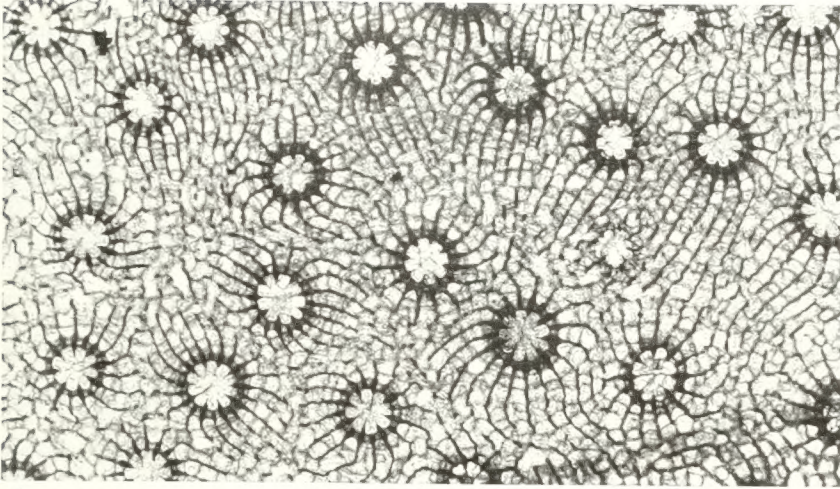
*Prismatophyllum reticulatum*, p. 48—*Hexagonaria bassleri* (Webster and Fenton in Fenton and Fenton, 1924), Upper Member, Twin Falls Formation.

#### EXPLANATION OF PLATE I

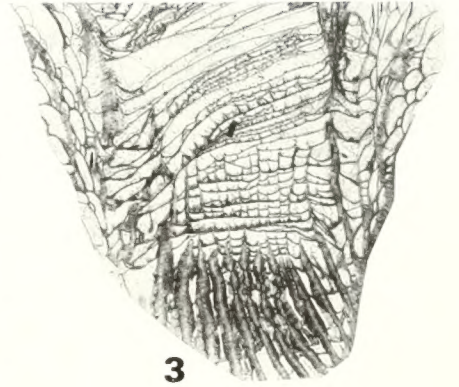
(All material housed at Geological Survey of Canada, Ottawa.)

##### Figure

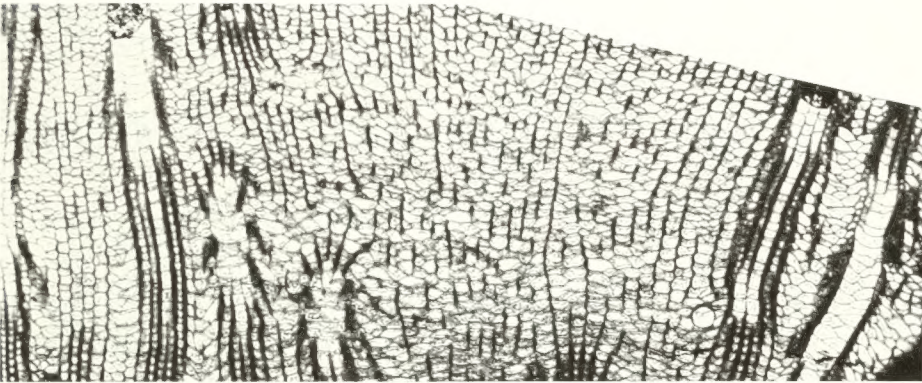
- 1, 2. *Phillipsastrea exigua* Lambe, 1901  
GSC 4306 (holotype); ?Member C, Hay River Fm., Hay River, N.W.T.; transverse and longitudinal sections,  $\times 4$ .
- 3, 4. *Tabulophyllum mcconnelli* (Whiteaves, 1898)  
GSC 4206 (lectotype); ?Member B, Hay River Fm., Hay River, N.W.T.; longitudinal and transverse sections,  $\times 2$ .
- 5, 6. *Temnophyllum parvulum* (Whiteaves, 1891)  
GSC 4209c (syntype); ?Member B, Hay River Fm., Hay River, N.W.T.; transverse and longitudinal sections,  $\times 4$ .
- 7, 8. *Macgeea proteus* Smith, 1945  
GSC 9300 (holotype); ?Member B, Hay River Fm., Hay River, N.W.T.; transverse and longitudinal sections,  $\times 3$ .



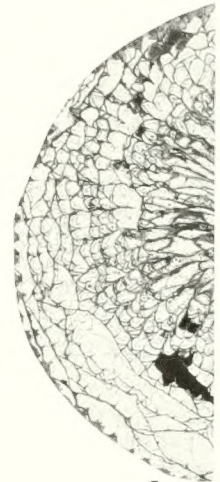
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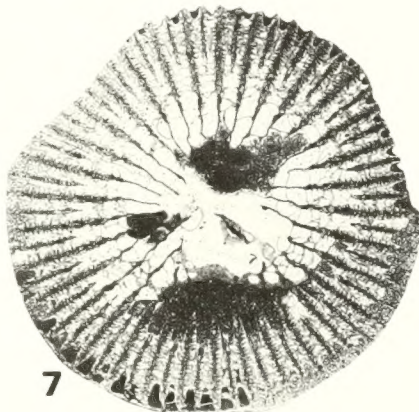
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8

- Prismatophyllum schucherti*, p. 48—*Hexagonaria schucherti* (Smith), Kakisa Formation.
- Prismatophyllum firthi*, p. 49—*Hexagonaria firthi* (Smith), Upper member, Twin Falls Formation.
- Prismatophyllum bompasi*, p. 49—*Hexagonaria bompasi* (Smith), Upper member, Twin Falls Formation.
- Prismatophyllum parvulum*, p. 50—*Hexagonaria caurus* Smith, 1953, Kakisa Formation.
- Ptychophyllum ? kindlei*, p. 52—*Mictophyllum ? kindlei* (Smith), Kakisa Formation.
- Ptychophyllum ? whittakeri*, p. 53—*Mictophyllum ? whittakeri* (Smith), Kakisa Formation.
- Spongophyllum* near *S. semiseptatum* Schlüter, p. 55—*Parasmithiphyllum kakisianum* McLean and Pedder, in press, Kakisa Formation.
- Spongophyllum imperfectum*, p. 55—*Smithiphyllum imperfectum* (Smith), Jean-Marie Member, Redknife Formation.
- Spongophyllum* near *imperfectum*, p. 56—*Smithiphyllum whittakeri?* Pedder, 1965, Jean-Marie Member, Redknife Formation.
- Spongophyllum lituus*, p. 56—*Smithiphyllum lituus* (Smith), Jean-Marie Member, Redknife Formation.
- Zaphrentis* aff. *phrygia* Rafinesque and Clifford, p. 66—*Hunanophrentis* sp., Kakisa Formation.
- Zaphrentis* sp. A, p. 66—*Hunanophrentis* sp., Kakisa Formation.
- Zaphrentis* sp. B, p. 66—*Hunanophrentis* sp., Kakisa Formation.
- Pedder, 1965:**
- Smithiphyllum imperfectum* (Smith), p. 622—text-figs. 4A–C, E, G, H, =*Smithiphyllum imperfectum* (Smith); text-figs. 4D, F, I; pl. 88, fig. 7; pl. 89, figs. 1–3, 10–12 =*Smithiphyllum pedderi* (Lakhov, 1982), Jean-Marie Member, Redknife Formation.
- Smithiphyllum whittakeri*, p. 626—*Smithiphyllum whittakeri* Pedder, Jean-Marie Member, Redknife Formation.

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CORALS FROM CERRO DE CRISTO REY, DONA ANA COUNTY,  
NEW MEXICO AND CHIHUAHUA, MEXICO

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ABSTRACT

Six of the nine lithostratigraphic units at Cerro de Cristo Rey contain corals. Twenty-one species, three new, from fourteen genera have been identified. One of the species was recovered from the Cenomanian Buda Formation (*Caryophyllia dentonensis* Wells, 1947). The remaining species are Albian in age and include in descending stratigraphic order: Mesilla Valley, *Parasmiliopsis cenomana* (Fromentel, 1862), *Diegosmilia complanata* (Collignon, 1931), *Sphaenotrochus* n. sp., *Conicosmilitrochus* n. sp., *Rennensismilia stainbrooki* (Wells, 1933), *Caryophyllia* sp. cf. *C. comanchei* Wells, 1933, *Budaia* n. sp.; Muleros, *Platytrichopsis lashensis* (Siharulidze, 1975); Smelertown, *Paratrochocyathus* n. sp., *Calostylopsis sakalavensis* (Alloiteau, 1958), *Columastraea wintoni* (Wells, 1933), *Axosmilia whitneyi* (Wells, 1933), *Rennensismilia stainbrooki* (Wells, 1933), *Dimorpharaea manchacaensis* Wells, 1933, *Stenocyathus* sp., *Actinaraea* sp. cf. *A. tenuis* Morycowa, 1971, *Microsolena distefanoi* (Prever, 1909); Del Norte, *Paratrochocyathus conulus* (Phillips, 1829), *Paratrochocyathus* sp. cf. *P. crassus* Alloiteau, 1958, *Paratrochocyathus collignoni* Alloiteau, 1958, *Paratrochocyathus androianensis* (Alloiteau, 1936), *Coelosmilia texana* (Conrad, 1857), *Platytrichopsis lashensis* (Siharulidze, 1975); and Finlay, *Paratrochocyathus crassus* Alloiteau, 1958, *Paratrochocyathus collignoni* Alloiteau, 1958.

ANALYSIS OF EVOLUTIONARY CHANGES IN  
*HEXAGONARIA* AND *PHILLIPSASTREA*

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ABSTRACT

In the Frasnian of Belgium, detailed population sampling through time is possible in different coral facies. *Hexagonaria* and *Phillipsastrea* show complex diversity and speciation patterns in different facies. In the Lower Frasnian, only slow rates of change (anagenesis) occurred. In this case, long periods of morphological stasis seem related to long periods of stability in the sedimentary basin and relatively small populations. Near the end of the Lower Frasnian and in the Upper Frasnian, there occurred complex diversity and speciation patterns in different environments (mainly cladogenesis). High habitat diversity and low habitat diversity have been observed in the same stratigraphic unit. Sedimentary facies and ecologic analyses suggest that high habitat diversity and complex speciation seem to be related to fluctuating environments. Very rapid faunal changes and mass extinction have been observed at the end of Lower Frasnian time concordant with maximum expansion of *Hexagonaria*. Very rapid faunal change seems to coincide with the beginning of a transgression or regression. The phyletic gradualism hypothesis seems to be satisfactory to explain the observed data in general. However, what appear to be examples of punctuated equilibria do occur at some stratigraphic levels. But detailed study shows that what seem to be punctuations do not suggest abrupt change, but coincide only with important evolutionary gaps caused by unknown factors (mass extinction in this case).

INTRODUCTION

Darwin and most of those who followed him, believed that the work of evolution was slow, gradual and continuous and that a complete phylogenetic lineage could be recognized for all fossil and living beings. However, the history of life on the earth, as revealed in the fossil record, is characterized by intervals in which fossils show evidence of mass extinction and sudden faunal change. These facts proved more of a problem for Darwin than a benefit. Many evolutionary theories have since been proposed. Among them, phyletic gradualism and punctuated equilibria are two current hypotheses about the tempo and mode of evolution at the species level. For all the echo and the excitement it has generated, punctuated equilibrium is still not accepted by many scientists. On the contrary it becomes the target of the attack.

In a recent paper, Gould and Eldredge (1977) reconsidered the problem and they are prepared to acknowledge the possibility of phyletic gradualism but argue that it is rare and of minor importance for evolution. They accept the existence of evolutionary trends but argue that they can be produced as a result of species selection. They are apparently ignoring the fact that closely related species of common genera are frequently met and are not easily distinguished from each other. As Boucot (1982, p. 19) pointed out "the proposers of punctuated equilibria neglected to consider the community ecologic and behavioral consequences implicit in their idea . . . . These situations led them

to the ecologically, behaviorally invalid concept of punctuated equilibria."

Based on intensive analysis and an extensive survey of the Devonian rugose corals from different facies in Western Europe, this paper provides some satisfactory examples of phyletic evolution, speciation, and extinction; that is, further insight into the tempo and mode of evolution at the species level.

GEOLOGICAL AND PALEOGEOGRAPHIC  
SETTING

Western European Devonian rugose corals first appear conspicuously in the Early Devonian rocks of the Armorican Massif of Western France (Barrois, 1889; Sorauf, 1969; Fontaine, 1977; Plusquellec, 1981). They are abundant in the Middle Devonian and Frasnian sedimentary rocks. Rugose corals show important endemism in the Eifelian. Decreasing endemism in the Givetian reflects the breaching of barriers (ecological and others) (Tsién, 1977). During Early Frasnian time, very complex reefs with high habitat diversity, developed in the subsiding basin contemporaneously with carbonate deposition, with low habitat diversity, on the relatively stable platform. During Late Frasnian time, different reef complexes, also with high habitat diversity developed near wave base, while formations with low habitat diversity developed below wave base or in the near shore restricted shallow marine environment. These situations are very interesting for studies of phyletic evolution and speciation. Figure 1 shows the main rugose coral bearing facies in the Devonian

of Belgium and Western Europe. The fossil record of rugose corals in the Lower and lower Middle Devonian shows that only slow rates of change occurred at these times. Coral assemblages are different in the different areas, suggesting the control of evolution by geographic isolation. In Frasnian time, complex diversity and speciation patterns occurred. Very rapid faunal changes and mass extinctions in corals have been observed near the boundary between the Middle and Upper Devonian and at the end of Early Frasnian.

In the Frasnian of Belgium, facies variation and rugose coral distribution patterns are quite different during the stable phases (tectonically calm periods) as compared to those during and in the transgressive phases (Tsien, 1978, fig. 1, 1980). Using lithic and faunal associations, it is possible to recognize several types of coral facies containing different coral assemblages in the Frasnian of the Dinant-Namur basins.

LOWER FRASNIAN EXAMPLE

General Geology

During Early Frasnian time, the rate of subsidence in the southern part of the Dinant Basin was different from that of its northern flank. Whereas, the southern area was a subsiding basin, the northern area was a relatively stable platform (Fig. 2).

Coral Assemblage and Environment

Two coral zones are found in the Lower Frasnian (Tsien, 1977a). Each zone can be laterally subdivided into several facies. Eight facies with different coral assemblages can be recognized in the *Hexagonaria* and *Tabulophyllum* acme-zone (Table 1). Within this acme zone, *Hexagonaria* is abundant in different rock facies suggesting that it was adapted to different kinds of bottom conditions. Very different isolated coral populations occur on the stable platform, while only one

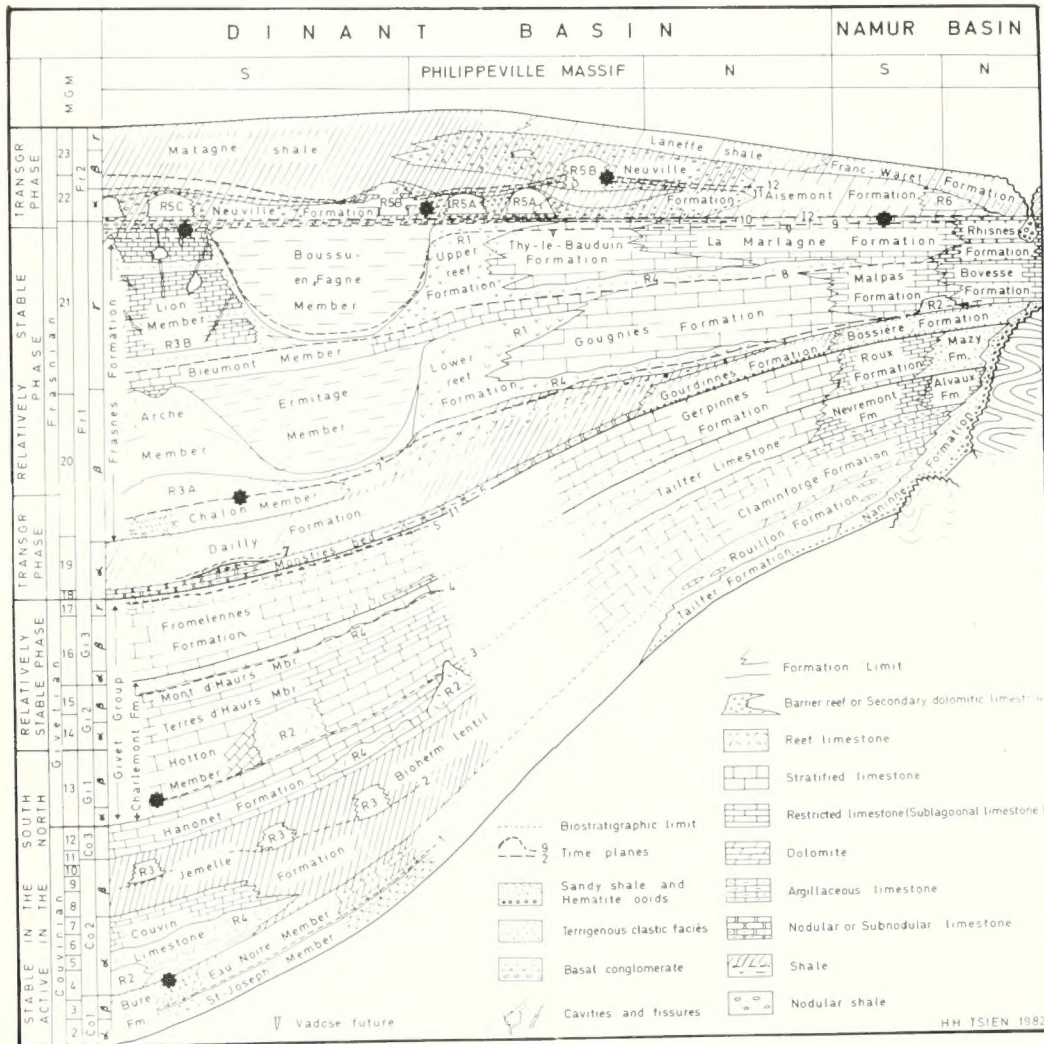


Figure 1.—Relationships of the different sedimentary facies in the Devonian sequence of Belgium. The stratigraphic correlation of different facies is shown by the time planes. (Modified from Tsien 1983b). \* = coral bearing facies.

widely distributed coral assemblage has been found in the open marine basin (Table 1). Different coral populations have gradually and continuously evolved in distinctive ways (Tsien, 1978, 1980). It seems that the differences between coral assemblages on the platform were caused by geographic isolation.

#### Very Rapid Evolution

Vadose features (gravitational cements) and karst solution cavities occur in the upper part of the reefs and in the platform carbonate sequences. This indicates that the reefs and platform were subaerially exposed and consequently, indicates a time plane (time plane no. 9, Fig. 3). The facts that: 1) no clay "sediment" has been found on the platform behind the barrier reef (R1 of Fig. 2), 2) all organisms occurring in the bioherm complex and on the platform indicate clear water conditions, together with 3) the pattern of the time planes 9 and 10 on Figure 3 suggests that the clays in the barren shales surrounding the reefs came from the south and were deposited after the development of the reefs. In the nodular shales (10 m thick) on the top of the reef, the compound cerioid coral species *Hexagonaria davidsoni*, *H. mae*, *H. buxutensis*, and *H. gamboni* are very abundant and show very rapid and continuous faunal change and complex speciation. Compared with the total thickness of biozone 21 (M.G.M.: Micropaleontological guide marks, defined by conodonts; Bouckaert and Streel, 1974) which is 275 m in the Frasnian area, this interval represents only 3.6 percent of one biozone.

The approximate amount of time represented by this 10 meters in the Frasnian area is 3.6 percent of one conodont zone or between 21,600 and 10,800 years (or less). This is using data from Ziegler (1978) who has indicated that a conodont zone lasted 0.6 to 0.3 million (or less) years. Regional geology and paleoecology show that, in the Frasnian area, this facies (nodular shales with different biofacies) was formed in a fluctuating basinal environment of high habitat diversity. On the stable platform (in the northern area), different coral assemblages show different isolated coral populations with low habitat diversity (Tsien, 1980). Rapid faunal change and complex speciation occurred only in the uppermost 2 m (Fig. 3), compared with the total thickness of biozone 21 at the northern part of the basin which is 47 m. This interval represents only 4.0 percent of one conodont zone, or between 24,000 and 12,000 (or less) years.

#### Diversity and Environment

The above example and Figures 4 and 5 demonstrate that in the fluctuating basinal environment, organisms are numerous in species as well as individuals (high habitat diversity of Neuville Formation), while in the stable environment of the stable platform, organisms are numerous as individuals but belong to few species (low habitat diversity of La Marlagne Formation). Punctuated equilibria as a valid model of the evolutionary process depends on whether speciation is dis-

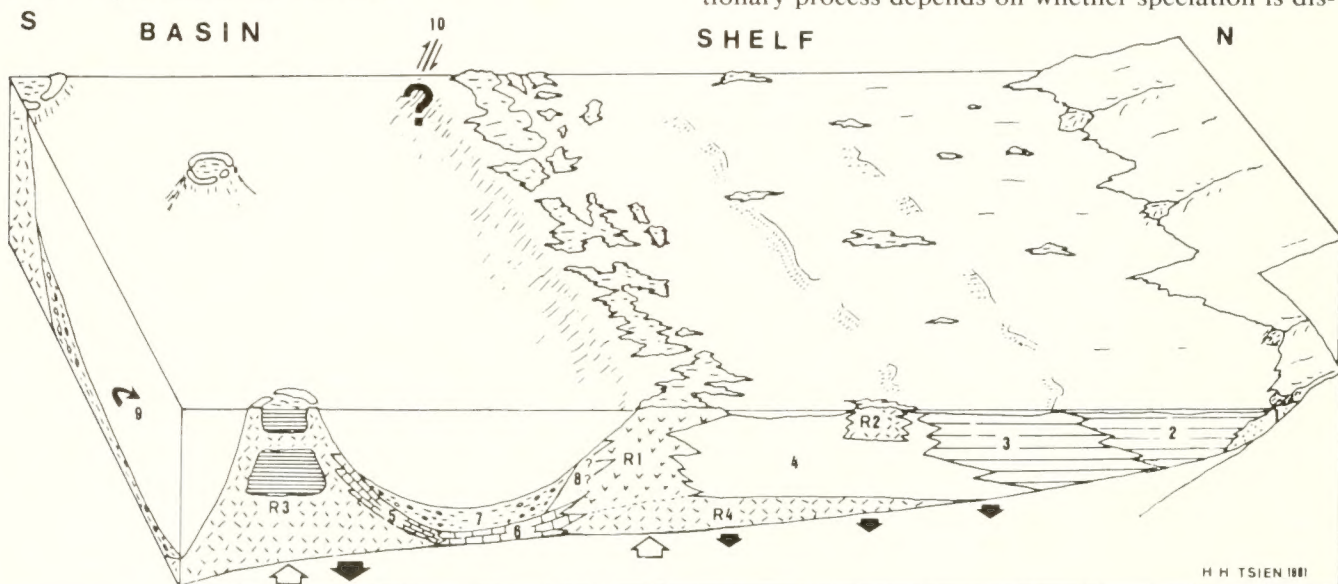


Figure 2.—Facies distribution during relatively stable phase. 1: littoral facies, 2, 3, 4: back-reef facies, 5: slope deposit, 6: open marine limestone facies, 7: off-reef facies, 8: fore-reef facies, 9: barren claystone facies which was deposited after the development of the reef, 10: the relationship between shelf and basin, it could be a syndimentary fault or a hinge, R1: barrier reef, R2: patch reef, R3: bioherm complex, R4: biostrome, solid arrow: rate of subsidence, open arrow: rate of reef growth, curved arrow indicating the source area of the claystones. (From Tsien, 1983a, fig. 19.)

Table 1.—Stratigraphic and facies distribution of the different coral assemblages. M.G.M. = Micropaleontological Guide Marks.

		MOBILE PLATFORM CONDITION (Basinal Condition)		Shelf Margin Reef Facies	STABLE PLATFORM CONDITION				
		Bionermal Complex Facies		Barrier Reef	Open Sea Platform Carbonate Facies			Restricted Platform Carbonate Facies	
MGM		Reef Facies	Peri-reef Facies		Assemblage 1	Assemblage 2	Assemblage 3	Assemblage 1	Assemblage 2
Fr2	22								
Frlγ	21	<i>H. hexagona</i> <i>H. davidsoni</i> <i>H. mae</i> <i>H. buxutiensis</i> <i>H. gamboni</i> <i>H. marmini</i> + numerous other organisms	<i>H. davidsoni</i> <i>H. mae</i> <i>H. buxutiensis</i> <i>H. gamboni</i> + numerous other organisms	<i>H. davidsoni</i> <i>H. mae</i> <i>H. hexagona</i>	<i>H. davidsoni</i> <i>H. fewata</i> new gen.	<i>H. hexagona</i> <i>H. marmini</i> <i>H. lecomptei</i>	<i>H. hexagona</i> <i>H. bracobanda</i>	<i>H. lecomptei</i> <i>H. fewata</i>	<i>H. marmini</i> <i>H. hexagona</i>
		<i>H. hexagona</i> <i>H. davidsoni</i> <i>H. marmini</i>		<i>H. davidsoni</i> <i>H. marmini</i>	<i>H. davidsoni</i> <i>H. marmini</i>				
Frlβ	20	<i>H. hexagona</i> <i>H. marmini</i> <i>H. davidsoni</i>			<i>H. hexagona</i> <i>H. davidsoni</i> <i>H. marmini</i>				<i>H. hexagona</i>
Frlα	19								
	18								

continuous or continuous. Studies of Frasnian *Hexagonaria* show that speciation is continuous (Tsien, 1978, 1980).

MASS EXTINCTION

Very rapid faunal change and mass extinction of coral faunas occur at the Lower/Upper Frasnian boundary (Tsien, 1978, 1980). Two nodular shale beds in normal succession show the same lithologic characteristics, but one is very rich in *Hexagonaria* while the second bed and the beds thereafter contain abundant *Phillipastrea*. These facts would appear to strongly support the punctuated equilibrium model. How-

ever, detailed studies of *Hexagonaria* show that these coral genera have evolved gradually and continuously and that closely related species of *Hexagonaria* and *Phillipastrea* are not easily distinguished from each other (Tsien, 1975, 1977, 1978, 1980).

Very Rapid Faunal and Environmental Change

The *Hexagonaria* that occur in the uppermost part of the Lower Frasnian show an interesting series of developmental stages beginning with a single proto-coralite. In longitudinal section, one observes: 1) fine septal trabeculae in fans, 2) horseshoe dissepiments,

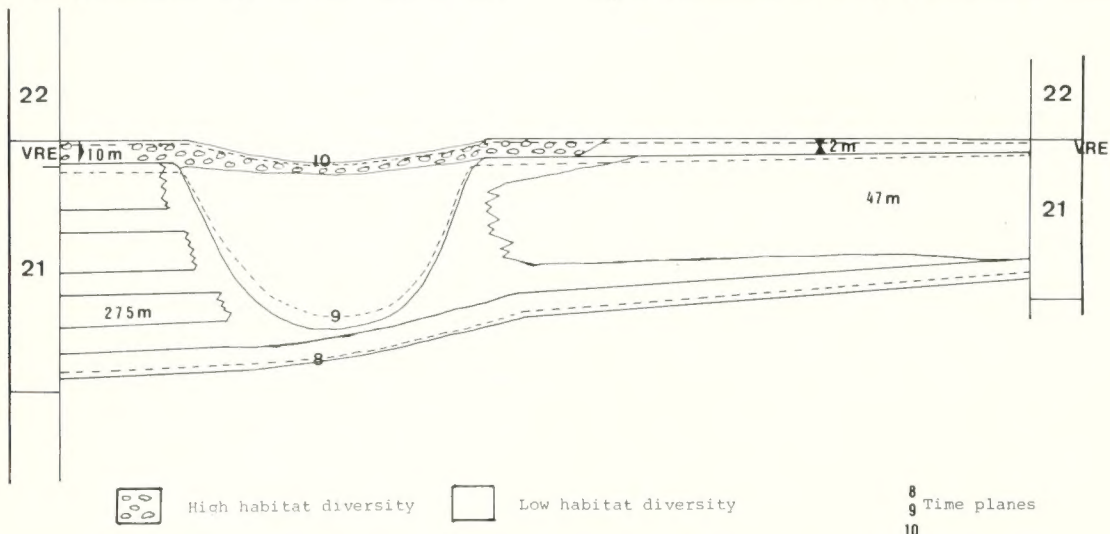


Figure 3.—*Hexagonaria*-bearing facies which record very rapid evolution (VRE).

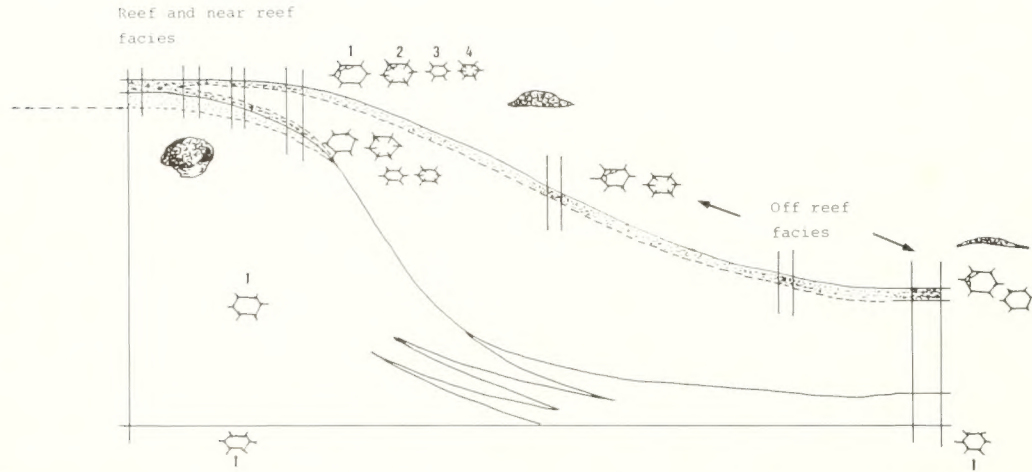


Figure 4.—Figure illustrating the distribution of certain *Hexagonaria* species in the reef and near reef facies in the southern part of the Dinant Basin. In open marine, relatively deeper water off reef facies, *Hexagonaria* has a thin disk-like form, with a large flat calicular platform. It has a globular colony shape, with a relatively deep calicular pit with a pronounced rim and a large calicular platform, in the reef facies. 1: *H. davidsoni*, 2: *H. mae*, 3: *H. buxutiensis*, 4: *H. gamboni*. *H. buxutiensis* and *H. gamboni* occur only in reef and near reef facies, associated with *H. davidsoni*, *H. mae*, *Alveolites*, *Thamnopora* and brachiopods, thus a high habitat diversity. While, in off reef facies (a deeper calm stable environment), only a few *Hexagonaria* species and brachiopods have been found indicating low habitat diversity.

and 3) specialized dissepiments (Tsien, 1977a, fig. 11). In transverse section, some colonies show, in part, a single layered wall. Fine septal structures are typical of *Phillipsastrea* not of *Hexagonaria*. The presence of horseshoe and specialized dissepiments, trabecular fans and a single layered wall indicate a phylogenetic relationship between *Hexagonaria* and *Phillipsastrea*.

Deposition of the beds of the uppermost part of the Lower Frasnian coincided with a general transgression

in Western Europe. This suggests that the rapid faunal change began at the end of Lower Frasnian time (Fig. 6) and was probably related to the beginning of the transgression. This also suggests that the appearance of *Phillipsastrea* is not "sudden" appearance. On the stable platform, the section at the abandoned quarry at Engis shows exactly the same phenomenon, two limestone beds, one containing *Hexagonaria*, the second one and the beds thereafter containing *Phillipsas-*

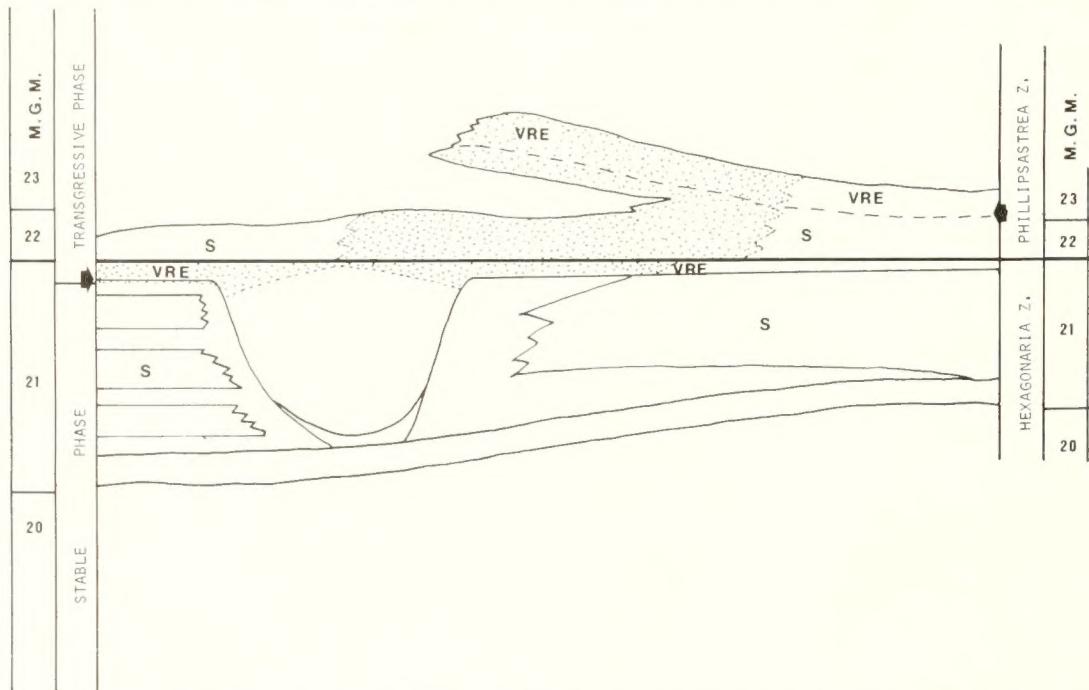


Figure 5.—Figure showing the main *Hexagonaria* and *Phillipsastrea* bearing facies in the Frasnian of Belgium. Stippled area: high habitat diversity, VRE: very rapid evolution, S: slow rates of change, solid arrow: revival of a transgression or a regression.

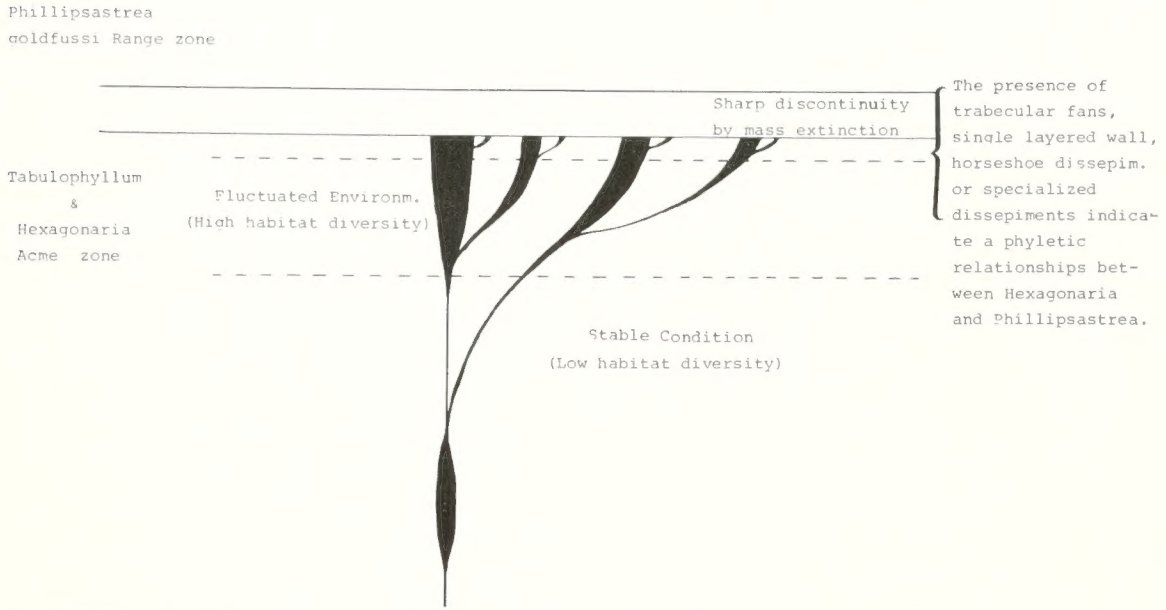


Figure 6.—Detailed study of *Hexagonaria* shows that there exists a phylogenetic relationship between *Hexagonaria* and *Phillipsastrea*, and also that the appearance of *Phillipsastrea* is not a “sudden” appearance, but coincides only with an important evolutionary gap caused by mass extinction.

*tree*. However, both the *Hexagonaria* assemblage and the *Phillipsastrea* assemblage show low habitat diversity. It is equally true that the periods of high extinction rates in rugose corals correspond to those in other groups.

Rapid faunal change in Late Frasnian time coincided with the beginning of a major transgression.

UPPER FRASNIAN EXAMPLE

General Geology

Coral facies occur in nodular shale facies and red mud mounds of the Neville Formation and in shallow argillaceous limestones and shales of the Aisemont Formation. In general, the coral facies occur in a gentle slope environment (Fig. 7). High habitat diversity occurs in and around the red mud mounds of R5A, R5B and R5D types. Low habitat diversity occurs in R5C type red mud mounds and in the Aisemont Formation (Tsien, 1983b and Fig. 1).

Diversity and Environment

Biofacies and sedimentary textures indicate that parts of type R5A, R5B and R5D mounds developed above or at wave base, whereas other parts of them and R5C type mounds formed below wave base (Tsien, 1980, 1983b).

Type 5RC mounds and the Aisemont Formation, both with low habitat diversity, developed in ecologically stable environments. In the facies with high habitat diversity, both in the mounds and around them, the organisms are numerous in species as well as individuals. Internal layerings, argillaceous interbeds, interfingering relationships to basin shales and vertical biozonation of the mounds suggest that the mounds and the surrounding shales developed in a fluctuating environment (Tsien, 1980, 1983b). High habitat diversity seems always related to fluctuating environments, while low habitat diversity is more likely to be

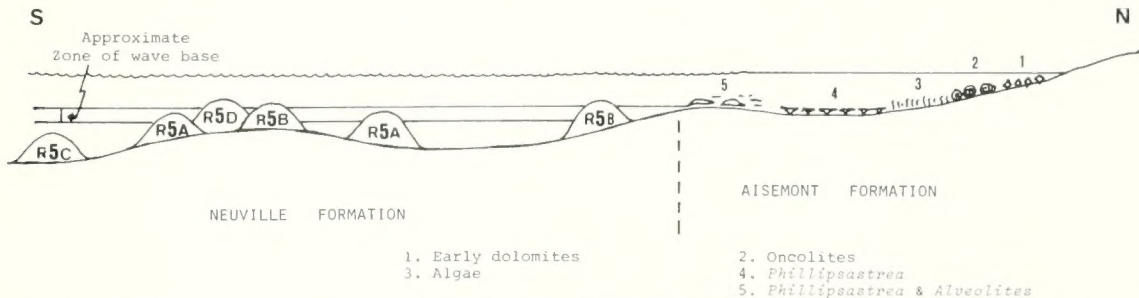


Figure 7.—Coral facies occur in a gentle slope environment, in nodular shale and red mud mounds of the Neville Formation, and in shallow argillaceous limestone and shale of the Aisemont Formation.

related to stable environments (Tsien, 1977, 1978, 1980, 1983b).

### CONCLUSIONS

In the discussed examples, faunal change coincides with a general transgression (Fig. 1). Maximum habitat diversity and much speciation is associated with fluctuating and/or changing benthic conditions. With such variable conditions the slightest environmental change can influence competition between species and thus encourage diversification and speciation. Low habitat diversity occurs during periods of stability (same condition persists for a long geological time). Some speciations are clearly caused by geographic isolation in the inner stable platform. The examples show clearly that most species level evolution takes place *in situ* through time and geographic isolation. Studies of lineages demonstrate progressive species transition. The study of population and ecological variation and phylogenetic lineages shows that slow rates of change and low diversity occurred in stable facies. High diversity coincides with fluctuating conditions and high rates of change correspond with general environmental change caused by a transgression or a revival of transgression (Fig. 5). The distribution of evolutionary rates documented in the fossil coral record conforms to phyletic gradualism rather than to punctuated equilibrium. Apparent punctuations do occur at some particular levels (Tsien, 1977, 1978), but detailed study shows that what seem to be punctuations do not suggest abrupt change, but coincide only with important evolutionary gaps caused by unknown factors (mass extinction, Tsien, 1978, 1980, in these cases).

### ACKNOWLEDGMENTS

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## SECTION 9

**Microstructure/Morphology**

## INTRODUCTION

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The relationship of most of the papers in this section to the symposium on diagenesis (Section 4) is evident. The symposium deals with modifications in skeletal carbonates. From the petrographic viewpoint, recognition of neomorphism within skeletal carbonates requires firm understanding of original materials and microstructures. There has been considerable study of this aspect of coral paleontology during the past decade, based largely on earlier reports by Schindewolf (1942), Schouppé and Stacul (1966) and Kato (1963), on rugose corals, and Wainwright (1964) and Kato (1968) on living scleractinians. These earlier reports were the result of excellent and incisive study of corals using light microscopy and thin section techniques.

Although the scanning electron microscope (SEM) has been of great importance in the study of cnidarian skeletal structure during recent years, the transmission electron microscope (TEM) has not. Probably this is because the very large minimum magnifications of the TEM has made the visual transition from lower magnification light microscopy too difficult. Nevertheless, the TEM has been of importance in developing an understanding of the biocrystallization process and the role of organic matrix in skeleton formation (Johnston, 1979). Scanning electron microscopy has led to the publication of a number of papers on the microstructure of both scleractinian and rugose corals (for references see Sorauf, 1980 and papers by Sorauf and Oekentorp in Section 4 of this volume). Many of these papers have dealt with diagenetic changes as well as microstructural analysis. Most SEM research on fossils has been carried out using the technique of etching polished surfaces for sample preparation, but some exceptionally well preserved fossils (Scleractinia by Cuif, 1975, 1977 and Rugosa by Sorauf, 1978, 1983) have been studied in broken section, just as modern material is.

Papers in Section 4 indicate that study by petrologists has continued to emphasize both standard petrographic microscope techniques and also electron beam methods, with SEM and microprobe X-ray systems providing morphological and chemical data. A somewhat newer development, luminescence microscopy, has provided data on cement generations and neomorphism.

A quite different outgrowth of earlier microstructural work is a refinement of a standard carbonate petrographic method. Ultra-thin sections were described and used in coral studies by Lafuste (1970); by grinding sections to a thickness of as little as 2 microns, the deleterious effect of high carbonate birefringence and small crystal size in many Paleozoic corals is lessened. Lafuste successfully used the technique in several studies and it has been adopted by other workers (see Lafuste and Semenoff references in Semenoff, 1984, this section).

The first three papers in this section are based on ultra-thin section studies. Lafuste describes the fine structure of sclerenchyme in a Silurian tabulate, and Semenoff-Tian-Chansky, the microstructure of septa, walls, and other parts of some Carboniferous rugosans. Both studies will aid in the interpretation of major groups of corals; in addition, Semenoff suggests an evolutionary change in structure through the Viséan. In the third paper, Mistiaen shows that the symbiotic caunopore tubes in a variety of stromatoporoids have a different wall microstructure from that of *Syringopora* with which these tubes are commonly identified; the author's interpretation of the differences suggests that the coral-stromatoporoid association was more intimate than heretofore recognized.

The next three papers use microstructure in somewhat different contexts. Webb describes and interprets variations in the columella of a Mississippian rugose

coral; the structure is a complex of septal lamellae and stereoplasmic laminae and Webb suggests that its significance has been misinterpreted in the past. Roniewicz uses microstructure to suggest ancestor-descendent relationships of two families of scleractinians. Owens correlates changes in septal microstructure with a change from shallow to deep water habitat in a Cretaceous to Recent scleractinian family. All three of these studies have broad implications for the classification of the corals involved.

The last paper in this section deals with overall coral morphology, of which microstructure is a key part. Hubbard and Pocock address an old but still important problem in coral studies—that which results from significantly different techniques being used in the study of living and fossil corals. The authors provide keys for the translation of morphologic data, but it is clear that students of living corals should add paleontological techniques to their work, in order to more profoundly influence the study of fossil corals.

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MICROSTRUCTURE OF *PLANALVEOLITES* LANG AND SMITH, 1939  
(TABULATA, SILURIAN)

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ABSTRACT

On an average, the microlamellae in the sclerenchyme of *Planalveolites* are about 25  $\mu\text{m}$  in diameter and 3  $\mu\text{m}$  in thickness; their surfaces are often planar and featured by cupules down to 1  $\mu\text{m}$  in diameter. It is suggested to denote them as scutellate microlamellae. *Planalveolites*, which differs from all those Alveolitidae that consist of fibers or cupular microlamellae, is considered as an *incertae sedis* unit in the Tabulata subclass.

INTRODUCTION

The genus *Planalveolites* was introduced by Lang and Smith (1939, p. 154) from the Gotland Silurian species *Alveolites fougti* Milne-Edwards and Haime (1851, pp. 257–258), whose only established features were limited to very inclined corallites and wide wall openings. Lang and Smith's diagnosis states that the new genus includes reptant corals composed of very reclined, thin-walled polyps, whose calices are provided with a protruding lower lip, with large diameter pores and complete lower walls. Acanthine septa are well developed, though hardly spiny.

In 1955, Sokolov repeated Lang and Smith's diagnosis, insisting on the fact that the septal system is characterized by numerous but short spines (p. 188).

Stumm (1964, p. 72 and 1967, p. 69) gave interesting additional information; in the revision of *P. fougti* and the description of *P. louisvillensis* (Davis) 1887, he noted that the very short septal spines are arranged in longitudinal rows.

Considering these established features of the genus *Planalveolites*, it becomes understandable that it could logically be related to the family Alveolitidae. However, because of its septal system, *Planalveolites* differs very much from *Alveolites* Lamarck, 1801. Such a disparity has led to this microstructural study.

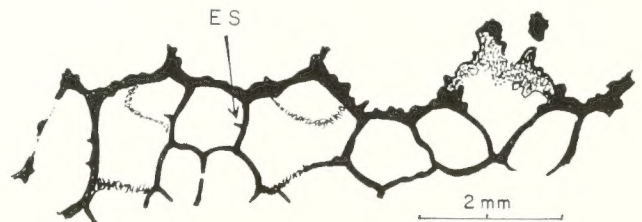
DESCRIPTION

*Material.*—Two specimens of *P. fougti* from the Gotland Silurian, R 1736 and R 25138, British Museum, London; a colony of *P. fougti* from Gotland Silurian, MNHN 40003, National Museum of Natural History, Paris. An ultrathin section was cut from the latter 3.5 mm thick sample, whose initial dimensions were 32 mm  $\times$  26 mm (Lafuste, 1970): Lafuste collection, MNHN, LFP S-280.

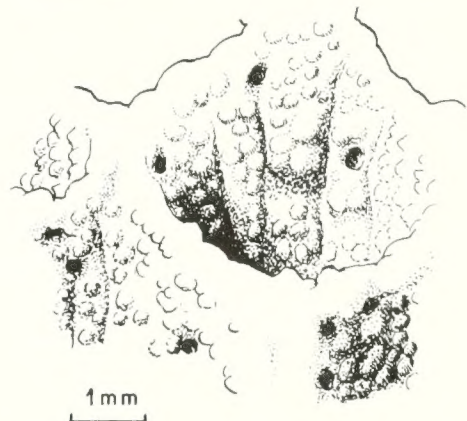
*Morphology.*—It is in conformance with the descriptions found in the literature. Examining the cross section of sample MNHN 40003 (as recorded when cut-

ting the ultrathin section) allows me to specify that the walls become conspicuously thicker as growth proceeds (Text-fig. 1). In the basal, very thin-walled part of the colony, large aciculate spines, far apart from each other, can be observed. At a higher level, more particularly observed in the calices (Text-fig. 2; Pl. 1, fig. 1), adjacent warts arranged in longitudinal rows or ridges cover the walls. The large diameter pores occur both along these ridges and between them.

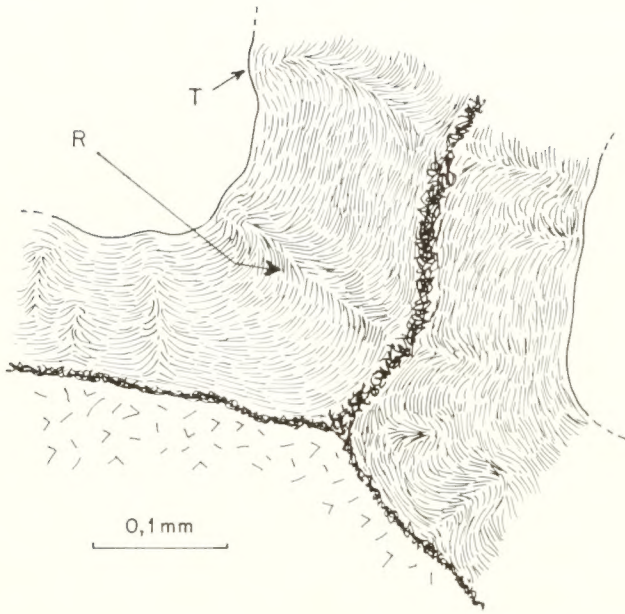
*Microstructure.*—Under low magnification (Text-fig. 3), the laminated structure of the sclerenchyme, resting on a dark primordial line of granular nature, can be observed. The lamination exhibits bulges (R) in places



Text-figure 1.—*Planalveolites fougti*. MNHN 40003. Transverse section. ES: septal spine.



Text-figure 2.—*Planalveolites fougti*. Brit. Mus., R 25138. Arrangement in longitudinal rows of the tubercles of the wall.

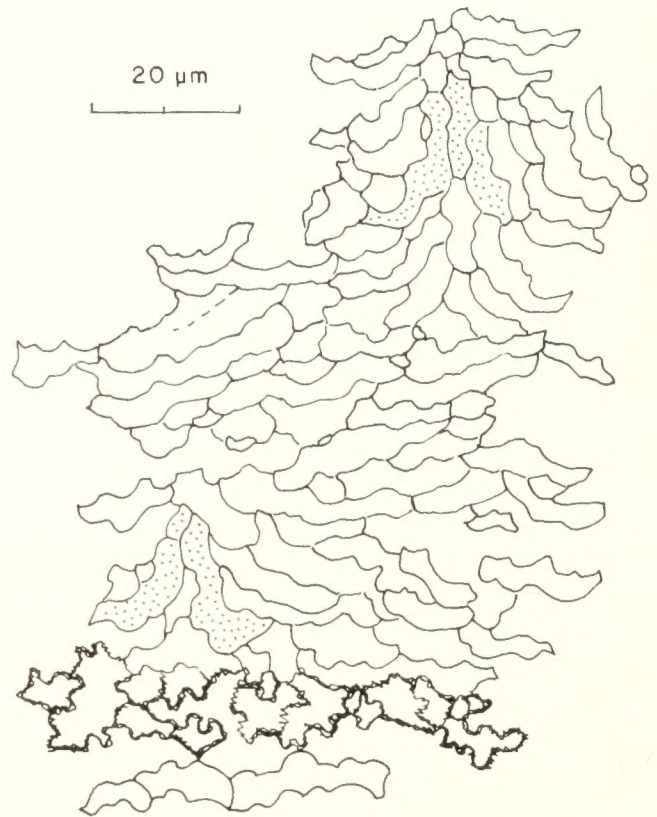


Text-figure 3.—*Planalveolites fougti*. Lafuste coll., LFP: S-280. Microlamellar sclerenchyme; the up-raising (R) correspond to the axes of the tubercles.

corresponding to the centers of warts (T) protruding at the surface of the wall.

The shapes and dimensions of the *Planalveolites* sclerenchyme components can be determined through the examination of the thinner parts of LFP S-280 (Text-fig. 4; Pl. 1, figs. 2, 3 and 4). The calcitic, flat or slightly curved areas can reach as much as 25  $\mu\text{m}$  in length; their thickness, usually ranging from 2 to 3  $\mu\text{m}$ , does not exceed 4  $\mu\text{m}$ . Their limits are outlined by incurvations the concavity of which always faces the internal cavity of the corallites. The gap between the ridges that separate these incurvations can vary to a large extent, since it ranges from 5  $\mu\text{m}$  to sometimes slightly less than 1  $\mu\text{m}$ . As a whole, the microstructural elements are parallel with both the middle lamella of the wall, and the periluminal border of the corallite. In contrast, in the bulging areas mentioned they are raised until at right angles with the general wall plane. Joined elements whose border concavities are diametrically opposed can even be observed (dotted area in Text-fig. 4) just in the direction of wall warts.

In addition, we must state that the aciculate spines consist of uneven fibers which are common in tabulates, and that the "dark middle lamella," when observed through the ultrathin section, is found to be



Text-figure 4.—*Planalveolites fougti*. Lafuste coll., LFP: S-280. Morphology and dimensions of the scutellate microlamellae. Dotted microlamellae are upturned at 90° with regard to the common orientation of the wall.

made up of isodiametric granules with highly intermingled limits (Text-fig. 4).

#### DISCUSSION

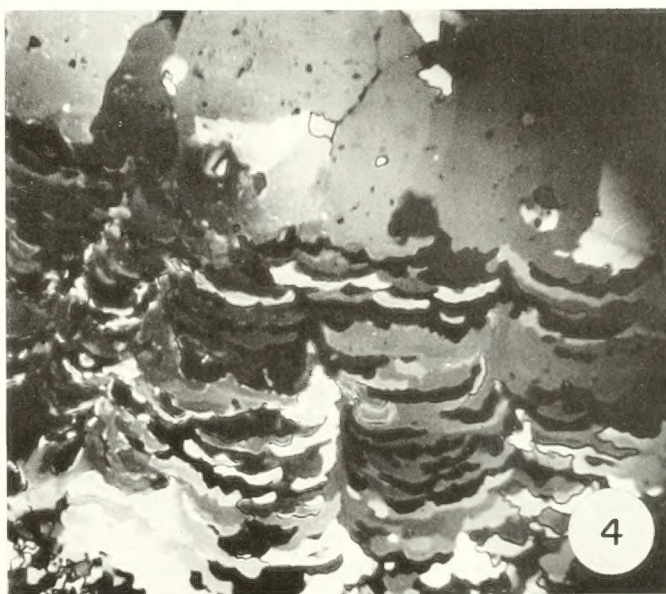
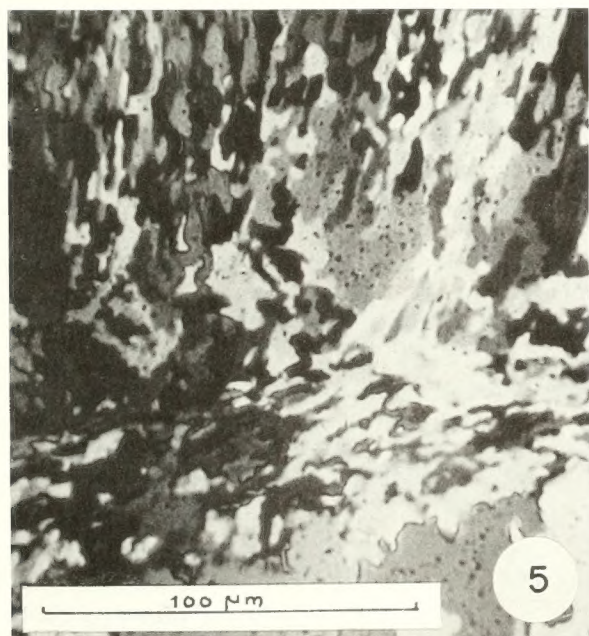
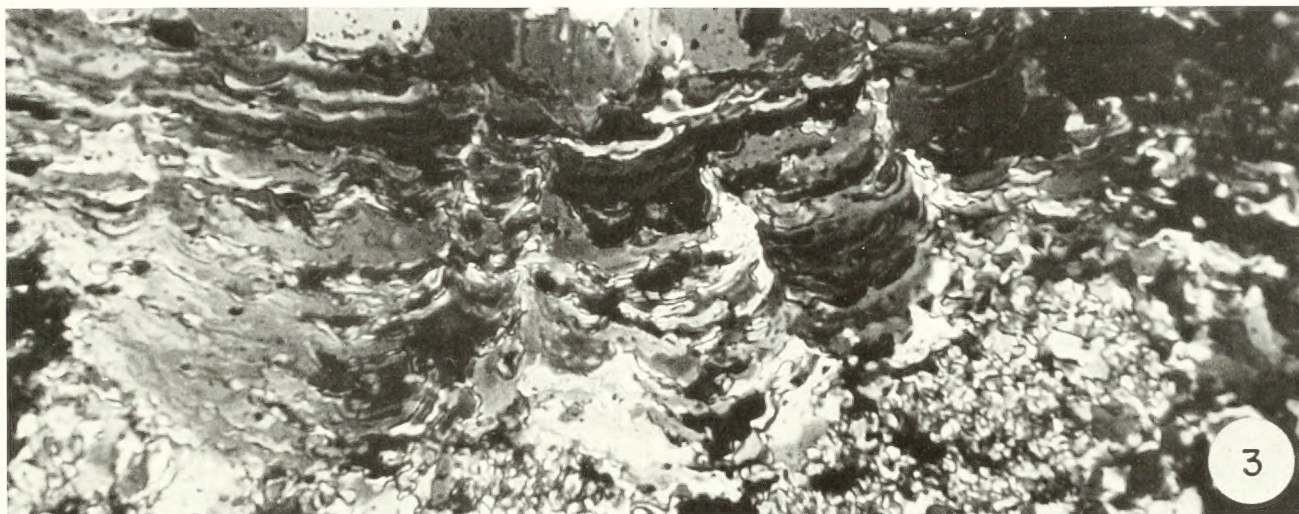
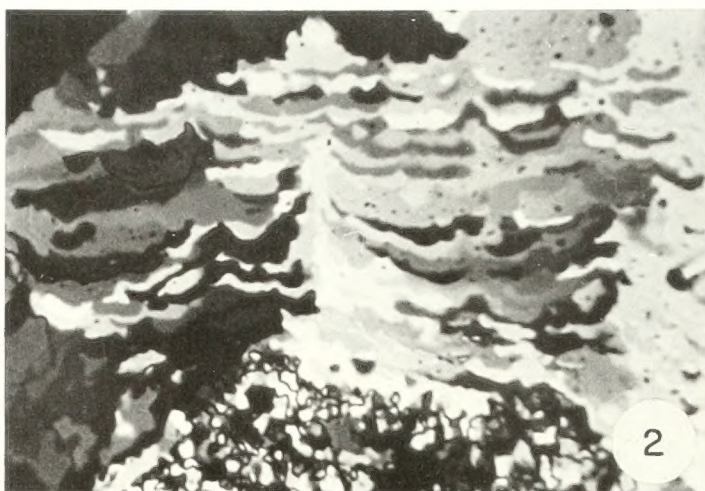
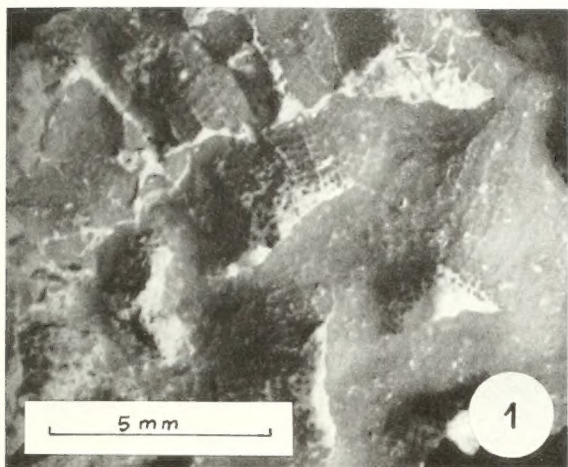
When being considered in space, the calcitic areas of the *Planalveolites* sclerenchyme correspond to sections of microlamellae. Microstructural elements were already termed this way in tabulates. They can be regarded as typical in *Parastriatopora* Sokolov, 1949, where they were specially investigated (Plusquellec and Tchudinova, 1976): featured by the following average dimensions: 15  $\mu\text{m}$  long (max. 20  $\mu\text{m}$ ) and 4 to 6  $\mu\text{m}$  (max. 7  $\mu\text{m}$ ) thick; they occur as an association of a small number of adjacent cupules. They were therefore termed "cupular" lamellae.

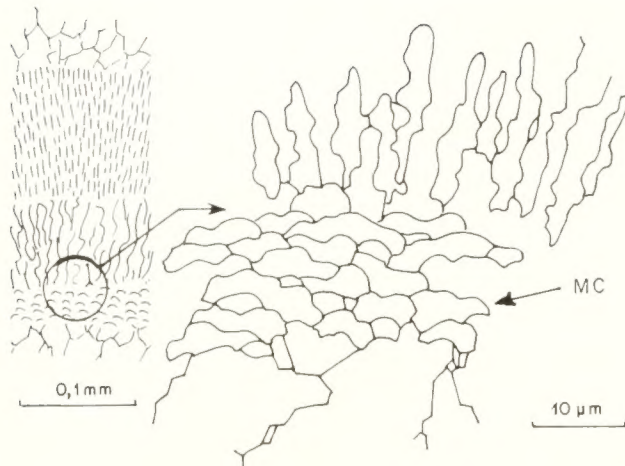
The corallum of the genus *Alveolites* Lamarck, is considered to be fully fibrous (Iven, 1980). Now the study of numerous ultrathin sections cut from samples

#### EXPLANATION OF PLATE I

##### Figure

1. *Planalveolites fougti*. Specimen MNHN 40003. Tubercles of the wall, in the calicular openings
- 2-4. *Planalveolites fougti*. Lafuste coll., slide LFP: S-230. Scutellate microlamellae. Same scale as Fig. 5
5. *Alveolites suborbicularis*. Lafuste coll., slide LFP: D-672. Cupular microlamellae topped with "fibroids"





Text-figure 5.—*Alveolites suborbicularis*. Lafuste coll., LFP: D-671. Morphology and dimensions of the cupular microlamellae (MC), topped with the "fibroid" elements of the median line of the wall.

of Upper Devonian *Alveolites suborbicularis* (Lamarck) from France, England, Balearic Islands and Morocco made it possible to find that the lower portion of the wall consists of a layer of microlamellae with features similar to those of *Parastriatopora* (Text-fig. 5; Pl. 1, fig. 5).

Projections to the same magnification of microlamellae sections of *Planalveolites*, *Parastriatopora*, and *Alveolites* have been compared in Text-figure 6. The difference between *Planalveolites* and the other two genera is obvious: in *Parastriatopora* and *Alveolites*, the microlamellae are shorter and much thicker, and the cupules at their surfaces, with a 5  $\mu\text{m}$  average diameter, reaching up to 7  $\mu\text{m}$ , are much wider.

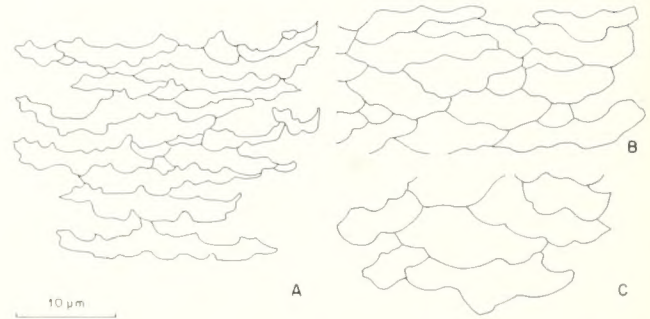
Considering the common flatness of the *Planalveolites* microlamellae and the possible flattening of the bottoms of elementary constitutive cupules, it is suggested to term them "scutellate" microlamellae, from the Latin word *scutella*, which means saucer.

### CONCLUSIONS

1) The study of *Planalveolites* leads to the identification of a new type of microstructural element in the Tabulata.

2) So far, the scutellate microlamellae have only been found in the Silurian genus *Planalveolites*.

3) The microstructural difference between *Planalveolites* and all the other genera from the Suborder Alveolitina, considered as fibrous (Hill, 1981, p. 589), leads me to remove it from that taxonomic unit.



Text-figure 6.—Comparison of the scutellate microlamellae of *Planalveolites* (A) with the cupular microlamellae of *Alveolites* (B) and *Parastriatopora* (C).

4) It is suggested that *Planalveolites* be retained as an *incertae sedis* genus, in the Subclass Tabulata for strictly morphological reasons.

No attempt at a preferential analogy with any taxonomic unit defined in the Tabulata may be contemplated. This point of view is the same as that adopted, for microstructural reasons as well, for the genus *Dendropora* Michelin, 1846.

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MICROSTRUCTURE OF *SIPHONODENDRON* (LITHOSTROTIONIDAE)

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## ABSTRACT

The microstructure of two species of *Siphonodendron* is described by the method of ultra-thin sections: *S. martini* (M.-Edw. & H.) and *S. sp. cf. S. dutroi* Armstrong, from the Lower Carboniferous of Northern Africa. They represent two types of microstructure observed among species of *Siphonodendron*. The first, prevailing in the early Viséan, is partly lamellar; the second, widespread in the late Viséan and Serpukhovian, is completely fibrous. In both cases, an internal periodic structure in the wall, which has a correlation with the external growth-ridges, is described.

## INTRODUCTION

The microstructure of the Lithostrotionidae, especially of the fasciculate forms like *Siphonodendron* has been little studied, except for reports by Struve (1898), Wang (1950), and Kato (1963).

Struve (1898), whose observations and accurate drawings are outstanding for his time, dealt with two species: *Siphonodendron junceum* (Fleming) and *S. irregularare* (Phillips). In the latter, he observed correctly the stereoplasm on the septa and the dissepiments (Struve, pl. V, fig. 12). On his drawings, the median fascicles of the columella can be recognized (Struve, pl. V, fig. 9) as well as the accurate orientation of the wall components (Struve, pl. V, fig. 10).

Wang (1950, p. 212, pl. 20, fig. 5) properly observed the fibrous microstructure and the wedge-like insertion of the septa into the wall of *S. pauciradiale* M'Coy.

Kato (1963, p. 623) correctly described the trabecular structure of the septa in the early forms of *Siphonodendron*, but he assumed that in later forms the septa evolved towards a "diffusotrabecular" structure. We shall see that slightly modified trabeculae are probably involved.

Most likely, all these authors had some trouble with too thick slides and with optical diffusion on a rough surface due to oversized grains of grinding powder. Ultra-thin polished slides (Lafuste, 1970) do not allow magnifications as high as those on the scanning electron microscope but do not have the disadvantages of acid etched surfaces. The thinness of the slides (2 or more microns) and their fine polish, as well as the varying orientation of the optical areas visible in polarized light, are suited for accurate recognition of compound or simple microelement outlines. This technique has been used here to investigate two main types of *Siphonodendron*, one of them fibrous and lamellar (*S. martini* M.-Edw. & H., 1851) and the other one exclusively fibrous (*S. sp. cf. S. dutroi* Armstrong, 1972). The possibility of an evolution from the first to the second type may be considered.

THE MICROSTRUCTURE OF  
*SIPHONODENDRON MARTINI*

The present study is based on specimens from three localities in the Tafilalt area, Morocco (Djebel Begaa, lower Viséan, specimens CP/13, 14) and in the Saoura valley, Sahara, Algeria (lower upper Viséan, Djorf el Morhabar and Akacha. Specimens CP 3179, 3181; PS 7094/11, 14b and 16). Slides: 27 standard and 29 ultra-thin. All the material here described is preserved in the Institut de Paléontologie, Muséum national d'Histoire naturelle, 8, rue de Buffon, 75005, Paris, France. In the Tafilalt and the Sahara, *S. martini* is recorded only in the lower Viséan and the lowermost upper Viséan stage. These specimens are identified as *S. martini* by their macroscopic and numerical characters. Both transverse and longitudinal sections are typical (Pl. 1, figs. 1, 2).

Up to now no detailed investigation on the microstructure of *S. martini* has been undertaken. Kato (1963, p. 599, fig. 114; *S. scoticum* (Hill) = *S. martini* M.-Edw. & H.) illustrated the middle layer and the lateral parts of a septal fragment. Such a development of the septal stereoplasm occurs only in some morphotypes of this species. The trabecular structure of the septa was briefly noted in the lectotype by Semenov-Tian-Chansky and Nudds (1979, p. 263): specimen E 1466, Phillips Collection, University Museum, Oxford, probable Asbian age, Yorkshire.

The ultra-thin slides made from the North African material show the trabecular structure of the septa. By this technique the fine microstructure of the septa as well as the wall and of the stereoplasm on the dissepiments and the columella can be investigated.

## Septa

The trabeculae, arranged in a single series, are gently inclined (10–30°) within the external two-thirds of the septa before turning up in the inner region. The trabeculae appear to be weakly individualized in longitudinal sections, while in transverse sections they show

blunt, serrate swellings (Text-fig. 1A). Sections cut at about 60° to the horizontal and perpendicular to the trabeculae (Text-fig. 1C) show them being roughly quadrangular in cross section with a diameter of 40 to 60  $\mu\text{m}$ . They are made of "embossed fibers," the margins of which are strongly and irregularly serrate (Text-fig. 1F; Pl. 1, fig. 8). The diameter of the smallest elements varies from 2 to 6  $\mu\text{m}$  depending on whether they are measured at trough or hump level. These elements, which seem to be monocrystalline, overlap each other and form larger composite groups approximately of the same shape (diameters up to 10 to 15  $\mu\text{m}$ ; Pl. 1, fig. 8). The embossed fibers have been defined by Lafuste (Lafuste and Fischer, 1971) in Carboniferous and Jurassic Chaetetida. They have been identified in numerous tabulate and rugose corals as well as in the Heliolitida and the Stromatopora (Lafuste and Fischer, 1971; Lafuste, 1970, 1972; Plusquellec and Semenoff-Tian-Chansky, 1972; Semenoff-Tian-Chansky, 1974a, b).

The trabeculae are monocanths, having fibers almost parallel to each other and to the axis of the trabecula. Such an arrangement, which accounts for their weak longitudinal individualization, is similar to the one described by Jell (1969) in some Phillipsastraeidae, but in this case the divergence is still weaker.

#### Wall

The septa meet the wall in a wedge-shaped junction without reaching the outer margin (Text-fig. 1A). The wall, which possesses wide interseptal segments, is thus a tangential, non-septal, structure. Its origin independent of the septal apparatus is emphasized by a lamellar microstructure, whereas the septa are fibrous.

The wall is made of small lamellae several tens of microns in diameter (mean value about 30  $\mu\text{m}$ ) and 4 to 10  $\mu\text{m}$  in thickness. These elements, having an overall concavity facing the interior of the coral and being sometimes geniculated, bear socket-like depressions, the hollows of the inner faces fitting the humps of the external faces of the adjacent lamellae (Text-fig. 1G; Pl. 1, fig. 7). The multicupulated form, as opposed to the large lamellae with a sinuous cross section, is typ-

ical of the elements defined by Lafuste as "microlamellae" in the genus *Striatopora* Hall (Lafuste, 1959, p. 86).

The epitheca is a narrow strip made of less regular elements, presumably however of lamellar nature (Text-fig. 1A, ep). The concept of epitheca is discussed below.

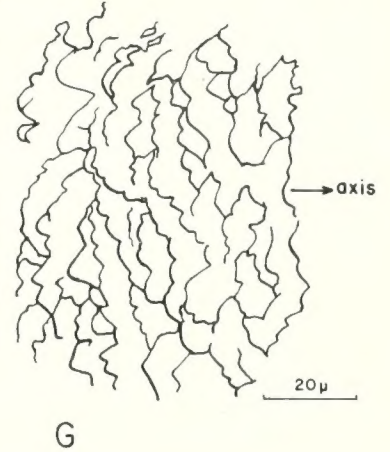
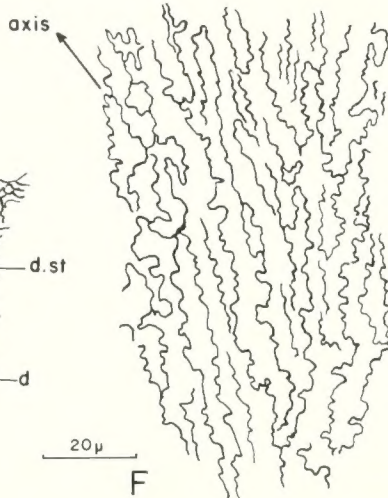
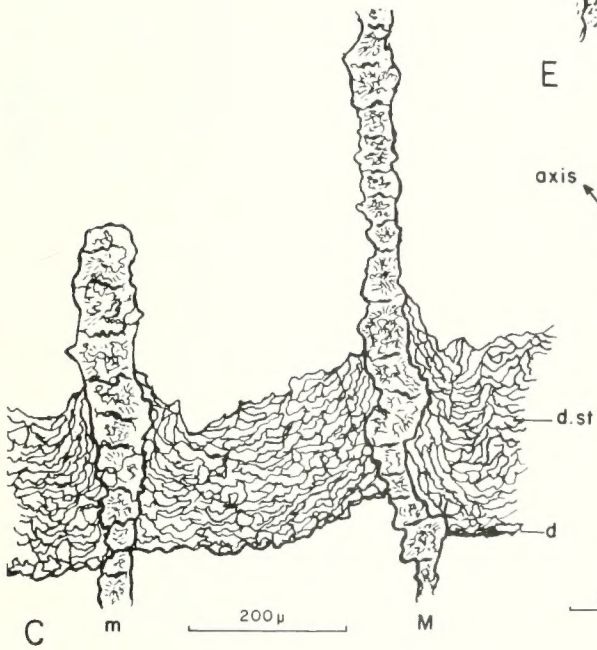
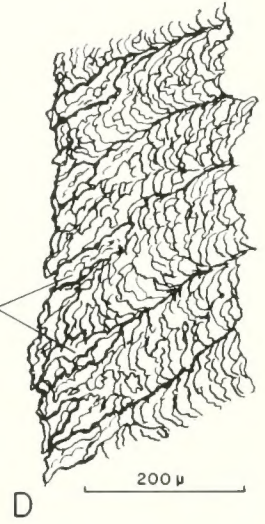
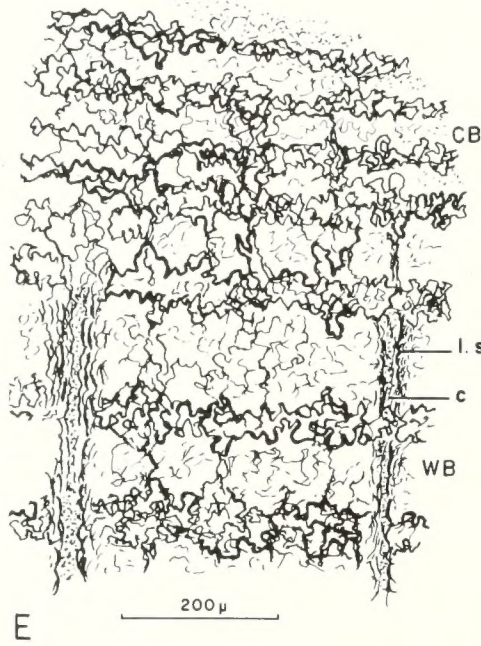
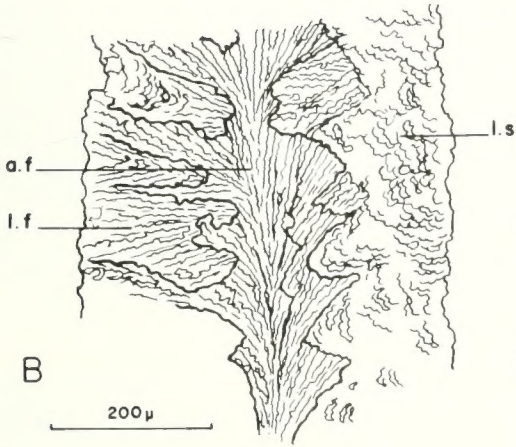
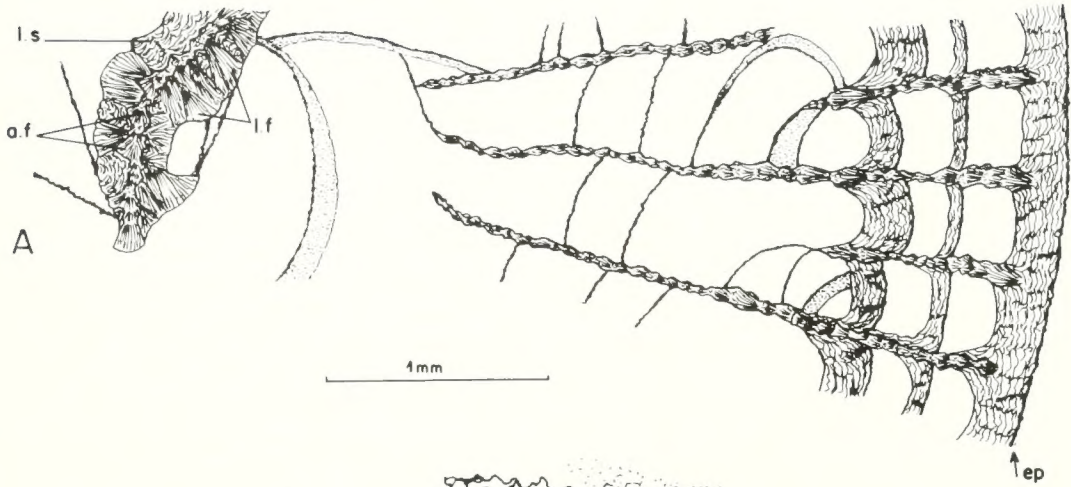
The outstanding peculiarity of the wall is the distribution of the microlamellae in regularly up-piled clusters. Longitudinal radial sections clearly show these piles directed upwards and inwards at 30 to 35° to the horizontal, following the same direction as the trabeculae (Text-fig. 1D; Pl. 1, fig. 10). The piles are separated from each other by turned-back lamellae, and in the external part of the wall, by sets of obliquely arranged microlamellae (Text-fig. 1D, ob).

There are 7 to 10 piles per mm of height (specimens CP 667/13 and 14; CP 3181). In the same specimens the fine growth-ridges seen on the outer side of the coral are respectively 12 to 15 (specimen CP 667/13) and 14 to 18 (CP 3181) per mm (in a total of 20 measurements). One slide of specimen 3181 shows two growth-ridges for each pile, with double piles at the periphery. The specimen is unfortunately rather poorly preserved in that area. According to these first measurements and observations, both periodicities, even if varying during the growth stages of each corallite, are linked by a 1 (pile) to 2 (ridges) ratio.

Longitudinal tangential slides, parallel to the lamellae, show a complex mosaic resulting from the intersection of the section plane with the cupules bearing interfaces between the adjacent microlamellae (Text-fig. 1E; Pl. 1, fig. 11). The first feature to be recognized within this mosaic is wide horizontal stripes (dark between crossed nicols) separated by narrow stripes (bright between crossed nicols). The former represent the main mass of the lamellae bundles seen in radial section. Because the c-axis of the calcite is perpendicular to the plane of the microlamellae (Lafuste in Fischer and Lafuste, 1972, p. 322), these are more or less near extinction in the central part of the stripes where the section is nearly parallel to the plane of the lamellae. The bright polarized zones correspond to the turned back lamellae.

Text-figure 1.—Microstructure of *Siphonodendron martini* (M.-Edw. and H.). A. Transverse section of corallite; general sketch-view of the trabecular fibrous septa and the microlamellar wall and stereoplasm of the dissepiments; columella made of fiber fascicles and microlamellae; ep, epitheca; af, axial fascicles; lf, lateral fascicles; ls, lamellar sclerenchyme. The term "fascicle" is used here in the same sense as "bundle" is used in the text. B. Columella, longitudinal section, perpendicular to sagittal plane; same symbols as for A. C. Oblique section through the dissepitheca (about 60° to horizontal line), perpendicular to the trabeculae; d, dissepiment; d st, dissepimental stereoplasm; M, major septum; m, minor septum. D. Wall, vertical radial section; periodic piled structure of microlamellae oriented upwards and towards the axis (coral axis at right hand of figure); ob, oblique groups of microlamellae; E. Wall, vertical tangential section; horizontal zonation produced by the sections (parallel to lamellae) of piles of lamellae seen in fig. D; CB, close spaced banding in the outer part of the wall; WB, wide spaced banding in the inner part of the wall, with two septa cut at right angles; l st, lamellar stereoplasm of septum; c, core of the septum (fibrous mesoplasm). F. Embossed fibers in a longitudinal section of a septal trabecula; arrow points to axis of corallite; note the slight divergence of fibers towards upper left. G. Microlamellae; section perpendicular to their plane, in a radial section of the wall; concavity of cupules facing the coral axis (way of secretion). All these ultra-thin sections are cut from specimen CP 667/13, lower Viséan. Djebel Begaa, Tafilalet, Morocco.





These stripes are sometimes wide-spaced (Text-fig. 1E, WB), and sometimes closer together (Text-fig. 1E, CB). The reason for this is that the tangential section cuts through the wall at different depths. The wide-spaced stripes belong to a deep (internal) zone of the wall (see Text-fig. 1E, where two septa are cut). The more closely spaced stripes are nearer to the surface. Moreover, their spacing (15 per mm) corresponds to that of the fine external ridges of the wall. Finally, their interval matches half the interval of the widely equidistant stripes as well as the width of the lamellae piles. The double equidistance of these stripes sustains the 1 to 2 ratio observed or measured in radial slides between lamellae clusters and growth ridges.

The outermost periphery is often worn or recrystallized. Thus, further observations are needed for a better understanding of the microstructural relationship between the external ridges and the inner structure of the wall (splitting into two lamellae piles; and significance of the oblique lamellae), as well as of the secretion process of the ridges, obviously linked to that of the "epithec." Furthermore, the tangential mosaic displays a zonation too, consisting of vertical stripes, not quite as obvious, yet perceptible and independent of the septa. These zones are equidistant at about 100  $\mu\text{m}$  and coincide with the partial upturning of the lamellae in the interseptal segments as seen in cross section.

#### Dissepiments

The dissepiments proper, are made of a unique, thin layer of microelements of granular type, as a rule recrystallized on account of its very thinness. Most dissepiments are coated by a microlamellar tissue identical with that of the wall. This is the "stereoplasm" of the dissepiments which is locally bent against the middle fibrous part ("mesoplasm") of the septa (commonly poorly coated by stereoplasm). The terms ste-

reoplasm and mesoplasm are provisionally used because they are suitable for descriptive purposes. They were defined in Semenoff-Tian-Chansky (1974, p. 38), but should be abandoned on account of their etymological inadequacy (D. Hill, pers. comm.).

#### Columella

The columella includes a central part, consisting of fiber bundles, bound on each side by lateral sclerenchyme made of fibers and microlamellae (Text-fig. 1A). The axial bundles are one above another. They may be slightly flared and somewhat inclined on either side of the axial plane of the columella. They may also form a continuous structure for some vertical distance where the succession of the narrow proximal parts of the bundles and their lateral expansions, look like a pennatifid leaf (Text-fig. 1B).

The bundles are made of embossed fibers identical with those of the septa, diverging from the base of the bundle or from the area nearest to the columellar axial plane where they are vertical. These structures may locally look like pieces of trabeculae, yet they are true fiber bundles (or fascicles) and not trabeculae because they do not display the typical rod pattern with a symmetry axis from which the fibers are regularly radiating. Moreover, in cross section, they are poorly, or not at all, individualized from each other, and they make sharp angles which correspond to their lateral expansions (Pl. 1, fig. 5).

The lateral sclerenchyme is formed by fibers grouped into bundles and by microlamellae. These lateral bundles, which are always made of the same embossed fibers, are inserted into the indentations of the axial bundles and widen outwards. They are either horizontal or inclined upwards and outwards.

The microlamellar tissue coats the different elements of the fibrous tissue, so that the microlamellae hold

#### EXPLANATION OF PLATE 1

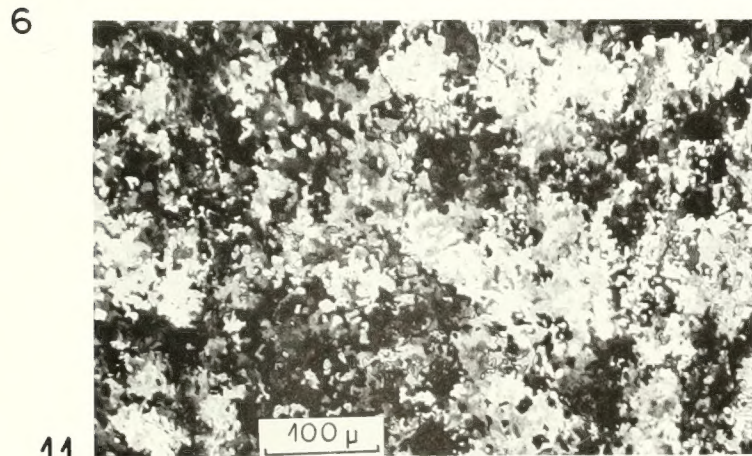
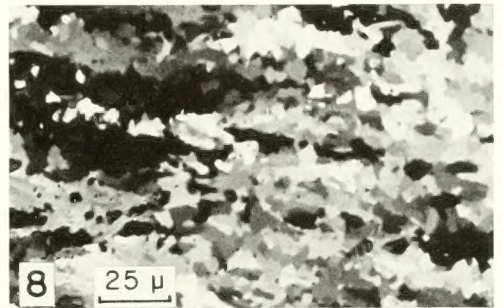
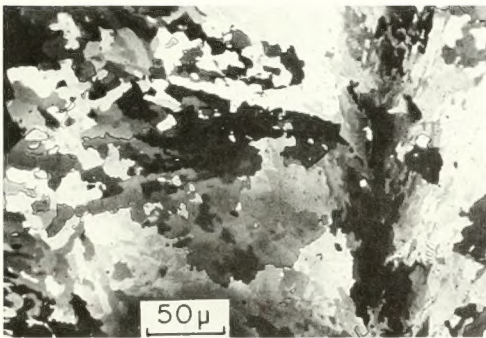
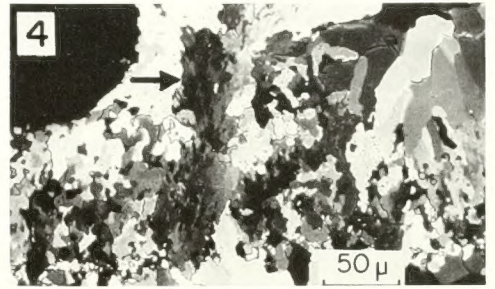
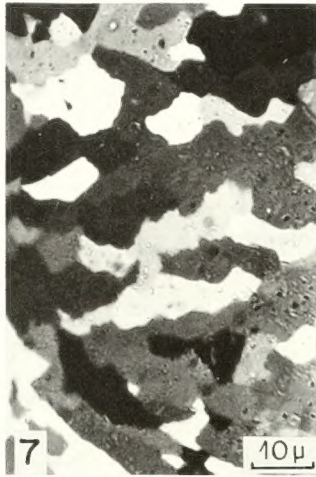
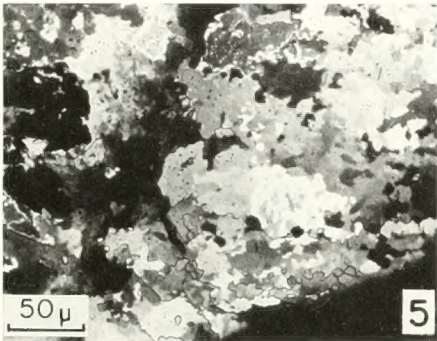
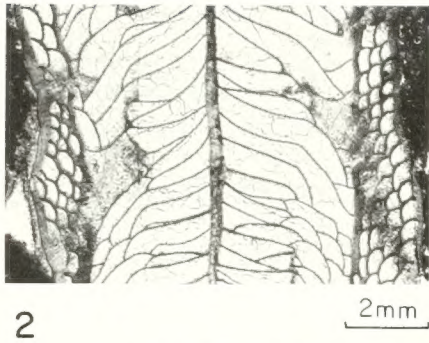
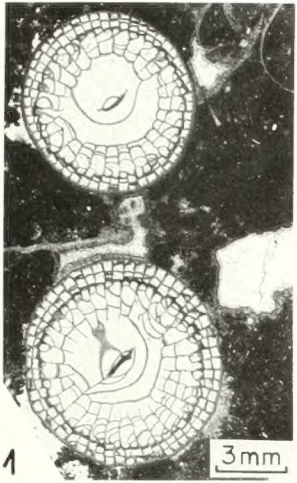
##### Figures

1-3, 5-11. *Siphonodendron martini* (M.-Edw. and H.)

1, 2. Transverse and longitudinal sections, standard slides;  $\times 3$ ,  $\times 5.3$ . 3, 5-11. Ultra-thin sections, crossed nicols. 3. Wall, cross section; microlamellar structure with concavity of cupules facing the coral axis (upwards in the figure); the core of a septum inserted as a wedge into the wall is indicated by the arrow;  $\times 200$ . 5. Columella, transverse section; on left, angular shaped sections of axial fiber fascicles; on right, lateral microlamellar sclerenchyme;  $\times 200$ . 6. Columella, longitudinal section, perpendicular to sagittal plane; on right, axial fiber bundles with their lateral expansions; on left, microlamellar sclerenchyme;  $\times 200$  (see Text-fig. 1B). 7. Microlamellae; section perpendicular to their plane, in a radial section of the wall; coral axis upwards;  $\times 800$  (see Text-fig. 1G). 8. Embossed fibers in a longitudinal section of a septum; they form composite groups with smaller diameter than those of trabeculae,  $\times 400$  (see Text-fig. 1F). 9. Trabeculae, longitudinal section; low angle divergence of fibers;  $\times 360$ . 10. Wall, vertical radial section; periodic piled structure of microlamellae; coral axis to right (see Text-fig. 1D);  $\times 120$ . 11. Wall, vertical tangential section; wide spaced stripes of microlamellae cut in a direction parallel to their plane, giving a complex mosaic;  $\times 150$  (see Text-fig. 1E). All these sections are cut from specimen CP 667/13, lower Viséan, Djebel Begaa, Tafilalet, Morocco.

4. *Siphonodendron irregulare* (Phillips)

Specimen PS 7052/14, upper Viséan, west of Bibane-el-Arjem, Saoura District (Sahara, Algeria). Wall, cross section; contrary to *S. martini*, the microlamellae are turned back towards the axis almost as fibers in a fibrous wall; the arrow indicates the core of a septum; coral axis upwards; crossed nicols;  $\times 200$ .



varying positions. Some of them are vertical with concavities facing outwards. Most of them are oblique with concavities facing upwards and outwards. Still others are fixed in, and bent back between neighboring bundles. This variation in position of the microlamellae accounts for the confusing appearance of this tissue as seen in longitudinal sections (Text-fig. 1B; Pl. 1, fig. 6).

The orientation of the fibers and microlamellae, especially of their cupule concavities suggests the growth direction. As a whole, the axial bundles were secreted upwards, whereas the lateral ones along with the microlamellae were secreted towards the periphery or, alternatively, in an intermediate direction, upwards and outwards.

Finally, it seems reasonable to suggest that the axial or lateral bundles belong to the septal apparatus, forming its axial structure. The microlamellar tissue is the axial homologue of that of the wall or the dissepiments.

#### THE MICROSTRUCTURE OF *SIPHONODENDRON* SP. CF. *S. DUTROI*

This species is a fasciculate lithostrotionid, quite abundant in the Serpukhovian stage ( $E_2$  zone) of the Béchar Basin (Algeria). Its tabulae are strongly raised towards the axis, interfering with the columella; this suggests that it is very close to *S. dutroi* described by Armstrong (1972) from the upper Meramecian of northeast Alaska. It differs from that species mainly by a greater number of septa and a larger diameter (mean value of  $n/d = 15/3$  instead of  $11/1.5$ ). Three sections, transverse and longitudinal (Pl. 2, figs. 1–3) provide a general picture of the macrostructure. It is completely fibrous and is a good example of the fibrous type of *Siphonodendron*.

The studied material was sampled at four localities on either margin of the Béchar Basin. All specimens are from the Djenien Formation  $E_2$  Zone, upper Serpukhovian; a) LY 562, Chebket Mennouna; b) PS 7072/1, Oued Djihani; c) PS 701/1, 2, Hassi Arlal; d) PS 703/2, Djebel Arlal. Slides: 14 standard and 30 ultra-thin.

Text-figure 2.—Microstructure of *Siphonodendron* sp. cf. *S. dutroi* (Armstrong). A. Transverse section of the wall and the outer part of two septa; ep, epitheca; c, core of the septum (fibrous mesoplasm); st, stereoplasm. B. Oblique section (about  $45^\circ$ ) perpendicular to the trabeculae; M, major septum; m, minor septum; d st, dissepimental stereoplasm; st, septal stereoplasm. C. Embossed fibers in a longitudinal section of the septum; arrow indicates coral axis. D. Columella, transverse section; af, axial fascicles; lf, lateral fascicles; s lam, septal lamellae. E. Columella, longitudinal section perpendicular to the sagittal plane; af, axial fascicles; ex, lateral expansion of axial fascicle; lf, lateral fascicles; i tr, incipient trabecula. F. Wall, vertical radial section; periodic superposition of the fiber bundles; ep, epitheca; the arrows indicate the growth direction of the epitheca and of the fiber bundles. G. Wall, vertical radial section showing concordance between external ridges and fiber bundles; figure as seen in natural light for the ridges and between crossed nicols for the bundles; cr, crests of the fine growth-ridges; fb, fiber fascicles between the growth-ridges. H. Wall, vertical tangential section; horizontal zonation produced by sections approximately perpendicular to fiber bundles seen in F and G; WB, wide spaced banding in the inner part of the wall, with two septa cut at right angle; CB, close spaced banding in the outer part of the wall; c, core of a septum (fibrous mesoplasm); st, septal stereoplasm. The ultra-thin sections figured on A, B, C, D, F and H are cut in specimen PS 7072/1, Serpukhovian (zone  $E_2$ ), Oued Djihani, Béchar Basin (Algeria). The ultra-thin section figured in E and G is from specimen PS 703/2, same level, Djebel Arlal, Béchar Basin (Algeria).

#### Septa

The septa are made of trabeculae arranged in single series, oblique upwards and towards the axis. Although strongly inclined in the dissepimentarium ( $45$  to  $60^\circ$  to the horizontal), the trabeculae are bent down in the tabularium where their slope is only about  $30^\circ$  (Pl. 2, fig. 6). Their diameter, which is smaller than in *S. martini*, varies from 20 to 40  $\mu\text{m}$ , rarely reaching 60  $\mu\text{m}$ .

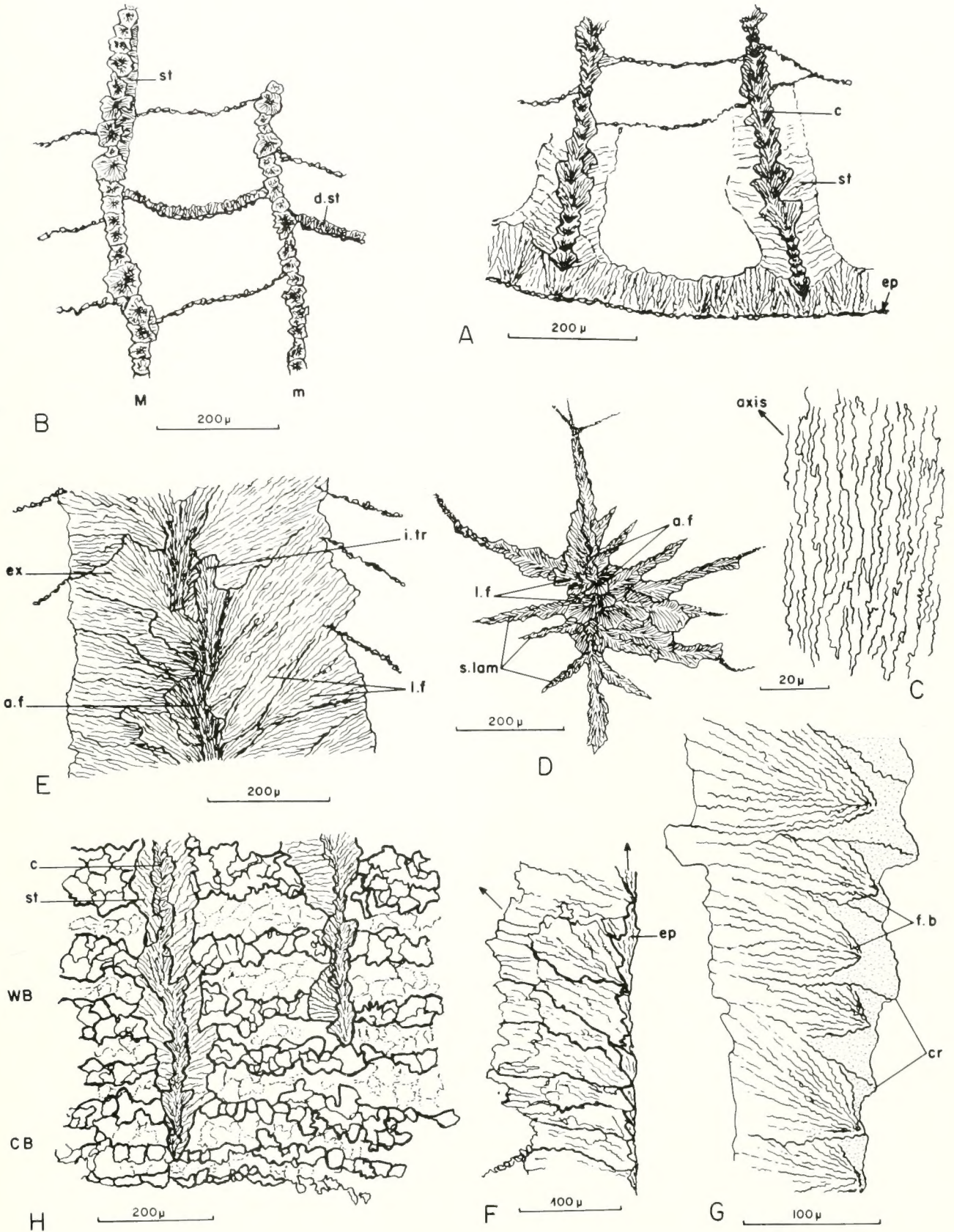
Oblique slides, cut at about  $45^\circ$  to the horizontal, show sections of various, more or less polygonal, often angular shape. Considered in space, these angles are dihedrons which are responsible for the sharply serrate outline of the mesoplasm, as seen in transverse sections (Fig. 2A). In some other fibrous species, a similar strongly serrate structure was termed "diffuso-trabecular" by Kato (1963, p. 623). Oblique sections show, at least in our species, a true trabecular structure (Fig. 2B).

The trabeculae are made of embossed fibers the size and morphology of which are rather different from the fibers of *S. martini*: the diameter is smaller (1 to 4  $\mu\text{m}$ , rarely more) and the indentations are weaker (Text-fig. 2C; Pl. 2, fig. 5).

At the periphery, the mesoplasmic trabecular part of the septa is often coated by a fibrous stereoplasm. The fibers of the latter, approximately perpendicular to the septal plane, stand also at an angle to the fibers of the wall at the sites where the wedge-shaped junction of the septa with the wall occurs (Text-fig. 2A). In our specimens, the stereoplasm is generally less well preserved than the remainder of the skeleton. Its fibers progressively disappear within the large calcite crystals of the sparry infilling. While unquestionably belonging to the skeleton of the coral as far as embossed fibers can be recognized within it, the stereoplasm may be merely a drusy coating at some sites in the same colonies.

#### Wall

As in *S. martini*, the wall is a tangential, nonseptal structure, but in this species it is made of fibers. The



embossed fibers are identical with those of the septa. In cross section they show an average radial direction and are arranged in more or less distinct bundles (Text-fig. 2A; Pl. 2, fig. 4).

In longitudinal radial sections, the bundles are better outlined (Text-figs. 2F, G; Pl. 2, fig. 10). They are regularly superposed upon each other, giving rise to a periodic structure similar to that of the wall of *S. martini*, except that here the clusters of lamellae are replaced by the fiber bundles. The latter are also similarly directed upwards and towards the axis.

In many sections, the periphery displays some triangular, vertically arranged elements (Text-fig. 2F, ep). These are bundles or, better, half-bundles of fibers which in cross sections form a thin peripheral layer of small irregularly shaped elements (Text-fig. 2A; Pl. 2, fig. 4, ep). In all probability this is the "epitheca" of the authors who have distinguished this external layer of the properly so-called wall (Hill, 1981, p. F12).

During the growth of the coral, these external elements were probably secreted initially by the peripheral margin of the polyp in a vertical direction. Later on, the parts located immediately inwards secreted the bundles of the wall body, this time in an oblique direction. Thus, this "epitheca" is merely the first layer of the wall. This observation was made jointly with J. Lafuste. A new name should be coined for this initial layer, seemingly not homologous with the epitheca of the Scleractinia, which is a tangential, perimural or peri-costal structure as defined by Milne-Edwards and Haime (1848) and specified by Milne-Edwards (1857).

*Periodicity.*—The bundles are not as easy to count as the clusters of lamellae of *S. martini*. Their boundaries are not parallel because the fibers are diverging; moreover, some smaller bundles are imbedded between the major bundles. The results of 40 measurements (from 14 slides cut through 5 colonies from 3 localities) are: 11 to 29 bundles per mm height; most

frequent interval: 17 to 23; most frequent density: 19.6. Such different values may be explained by varying growth rates of the coral, often within the same corallite, but also by the greater or lesser frequency of observed secondary peripheral bundles, depending on the state of preservation of the outer part of the wall.

As in *S. martini*, I have tried to verify whether there is any relationship between the periodicity of the fiber bundles and that of the fine growth ridges visible on the outer surface of the coral. Because the colonies of *S. sp. cf. S. dutroi* are embedded in the rock, the counting of the ridges was carried out in the following way:

1) On petrographic standard slides, in the rare instances where the ridges are preserved, the ridges are visible because of the superposition of the finely recrystallized elements at the outmost periphery; observed values: 16 to 25.5 ridges per mm; the average value is 19.6 (for 10 measurements).

2) On the same slides through the wall; at first, of standard petrographic thickness (for ridge counting, with guide marks on microphotograph mosaics); then, after further grinding down to ultra-thin slides (for bundle counting).

The compared densities are as follows (specimen 703/2):

Sections	Measured height (in mm)	Number of ridges per 1 mm	Number of bundles per 1 mm
a-b	2.7	18.5	17.6
c-d	0.4	19.6	19.6
d-e	1.41	20.5	19.6
f-g	1.41	25.5	20.6
n-o	0.51	21.5	17.6
r-s	1.14	25	22.8

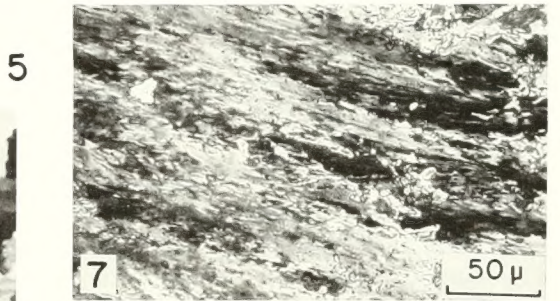
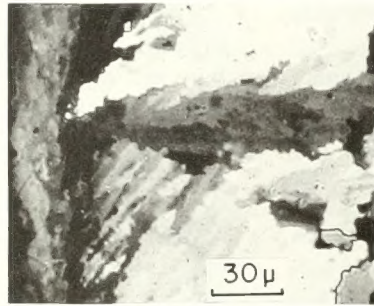
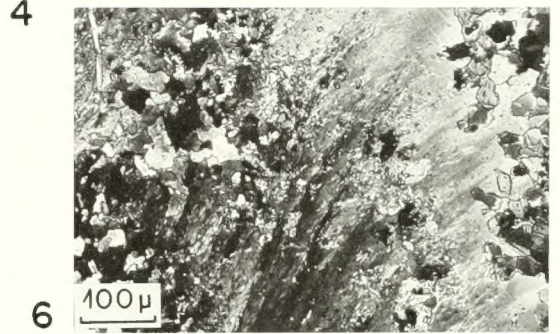
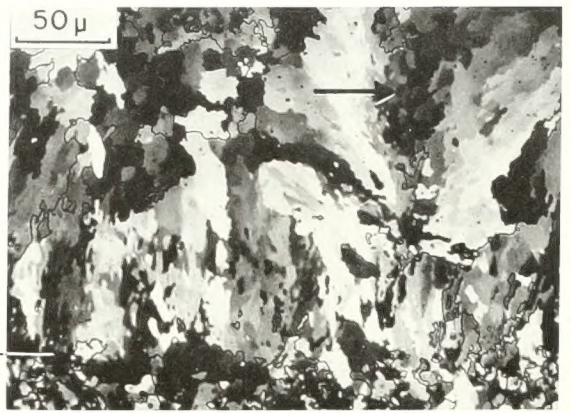
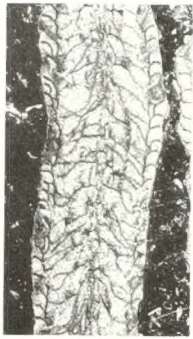
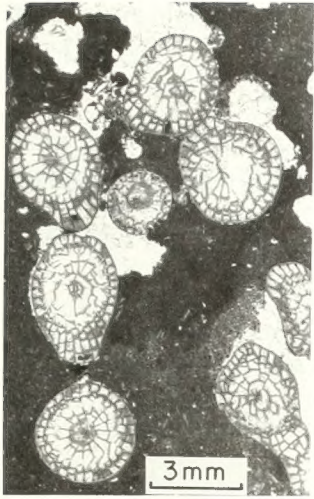
Both densities are close to each other, and even identical in some sections, although the number of bundles is often a little smaller than that of the ridges. This

#### EXPLANATION OF PLATE 2

##### Figures

1-11. *Siphonodendron* sp. cf. *S. dutroi* Armstrong

1-3. Transverse ( $\times 4$ ) and longitudinal ( $\times 5$ ) sections; standard slides; Figs. 2 and 3 show two extreme variations of the axial structure in this species from a more complex to a simple columella. 4-11. Ultra-thin sections, crossed nicols. 4. Wall, transverse section of the outer part of a septum; coral axis upwards ( $\times 250$ ); fiber bundles arranged in a radial direction; their homogeneous polarizing color, different from those of the matrix, is not clearly distinct on a black and white photograph; the core of the septum is indicated by the arrow; ep, epitheca, a narrow peripheral strip of small elements, mostly extinguished with crossed nicols (see Text-fig. 2A). 5. Embossed fibers in a longitudinal section of a septum,  $\times 800$ ; notice the weaker indentations than those of *S. martini* (see Text-figs. 1F and 2C). 6. Septum, longitudinal section; strongly inclined trabeculae, bent down towards the axis to the right,  $\times 100$ . 7. Trabeculae, longitudinal section; low angle divergence of fibers as in *S. martini*,  $\times 250$ . 8, 9. Columella, longitudinal section, perpendicular to sagittal plane. 8. Vertical series of fiber bundles bent alternatively on either side,  $\times 225$ ; middle-thin area of the slide. 9. On left, vertical axial fascicles with lateral expansions to the lower and upper right; on middle right, horizontal lateral fascicles,  $\times 320$  (see Text-fig. 2E). 10. Wall, vertical radial section; periodic superposition of the fiber bundles, with epitheca on the right as in Text-fig. 2F; coral axis to the left ( $\times 225$ ). 11. Wall, vertical tangential section; on middle and left, wide spaced horizontal banding with a vertical septum; on right, close spaced banding, the section cutting through the wall near periphery;  $\times 120$ . These sections are cut from 4 specimens collected at 3 localities in the Béchar Basin (Algeria): PS 701/1, 2, Hassi Arlal; PS 703/2, Djebel Arlal; PS 7072/1, Oued Djihani; Djenien Formation, E 2 zone, upper Serpukhovian.



deviation may be accounted for by the small secondary folds of the wall which may have been counted as ridges, along with the small recrystallized bundles at the outmost periphery that are more or less visible, as stated above. With these restrictions in mind, it seems quite likely that the two periodicities are equal.

One further observation corroborates this. In the parts of medium thickness of one of the sections, the morphologic correlation between ridges and bundles is visible (Text-fig. 2G). Each fiber-bundle is offset upwards and inwards from the corresponding ridge. A zigzag line resulting from the encounter of differently oriented fibers ends at the apex of each ridge and marks the border between the "clusters of fibrous structure." There remains a peripheral recrystallized zone (dotted area in Text-fig. 2G) where intercalated bundles are likely to occur along with the elements of the initial layer or "epitheca."

I noticed an almost perfect concordance between the periodicities of external ridges and fiber bundles of the wall in two other lithostrotionids as well: *Diphyphyllum furcatum* Thomson (upper Viséan of Ben Zireg, Algeria), and *Diphyphyllum maximum* Poty, 1981 (upper Viséan, zone 3b $\gamma$ , Royseux, Belgium).

All these data lead to the conclusion that during the growth of these corals with a fibrous wall, addition of any new external ridge keeps pace with the secretion of a whole sclerenchyme ring. This appears in radial section as a cluster of fibrous elements, the main part of which is a fiber bundle.

Vertical tangential slides cut through the thickness of the wall display a mosaic pattern similar to that of the tangential sections through the microlamellar wall of *S. martini*. In addition, however, they show a well marked horizontal banding with less jagged outlines (Text-fig. 2H; Pl. 2, fig. 11). These horizontal stripes of more or less polygonal patches reflect the cross sections of the fiber bundle systems. The spacing of the stripes varies in the ratio of one to two depending on whether the section crosses the inner zone of the wall, between the septa (Text-fig. 2H, WB) or the peripheral part (Text-fig. 2H, CB). The latter spacing, which is 12 to 20 per mm in the two examined slides, fits fairly well with the spacing of the ridges or the fiber bundles as measured in radial slides. The wider spacing (7 to 10 per mm) corresponds to the internal fiber system resulting from the inward coalescence of the external bundles (Text-figs. 2F and G, left).

#### Dissepiments

These are thin chains of small elements, the morphology of which has been changed by recrystallization. If the dissepiments are coated by stereoplasm, the latter consists of fibers arranged in small bundles

similar to that of the wall, more or less perpendicular to the dissepiments (Text-fig. 2B).

#### Columella

This is entirely made of fiber bundles forming a desmidoid (term by Lafuste, 1979), rather than trabecular, structure. Axial and periaxial parts are visible, but not always sharply separated (Text-fig. 2E). In the axial part, the bundles are in a vertical arrangement. They may overlap each other or bend alternatively on each side giving rise to a widely angular broken line (Pl. 2, fig. 8). Within these median bundles, the fibers nearest to the axis of the columella are vertical, while the lateral fibers diverge, forming fan-shaped expansions (Text-fig. 2E, ex; Pl. 2, fig. 9).

The axial parts with vertical fibers are like trabecular elements in some places. This aspect is enhanced between crossed nicols because the axial fibers are extinct when the columella is parallel to the polarizing plane. The likeness may be enhanced also by a narrow median bundle, by an angular discontinuity of the fibers, or by an incomplete separation of the axial part (Text-fig. 2E, i tr). In summary, this median structure seems to bear some crude kinds of incompletely shaped trabecular elements. In cross section, the median bundles show variable, often triangular or trapezoidal outlines (Text-fig. 2D). When rounded, one is dealing with the just noted primitive trabeculae.

The periaxial bundles are attached to the sides and in the indentations of the median bundles from which they are separated by a thin line emphasizing their change in direction. They are oriented horizontally or obliquely upwards and towards the periphery: they are open outwards. These are typical desmids. They form the "radial lamellae" of the columella as seen in cross section, but they may also be intercalated between these elements. In this case, they are the homolog of the infilling lamellar tissue of the columella of *S. martini*.

#### OTHER SPECIES

Ultra-thin sections have been cut through specimens belonging to twelve other lithostrotionid species of the following genera: *Siphonodendron*, *Diphyphyllum*, *Lithostrotion*, and *Solenodendron* (from Sahara, Belgium and the British Isles). They will be dealt with in future publications, particularly *Lithostrotion*, whose wall displays trabecular elements of a very peculiar type.

With regard to *Siphonodendron*, species such as *S. pauciradiale* (McCoy), *S. irregulare* (Phillips) and other forms from the lower Viséan and lowermost upper Viséan display a microstructure quite similar to that of *S. martini*. They possess a trabecular fibrous septarium, whereas the wall, the stereoplasm of the dis-



sepiments, and the lateral parts of the columella are microlamellar. The differences relate to the morphology and arrangement of the trabeculae or the fascicles, as well as to the ratio of microlamellar to fibrous tissue.

Higher up in the Viséan, one finds some completely fibrous species exhibiting a structure very close to that of *S. sp. cf. S. dutroi*. Such is the case of *S. intermedium* Poty, 1981 (Saoura: Boulmane and Igli Formations; Belgium: V 3b $\gamma$ ) and of two new species in the Serpukhovian stage. The microstructure of these fibrous forms differs from that of *S. sp. cf. S. dutroi* only in the dimensions and the outlines of the fibers and the compound elements (fascicles, trabeculae) they build up.

In some of the first, partly lamellar forms, a trend towards a more fibrous sclerenchyme may be observed. In *S. irregulare* for instance, the microlamellae of the wall are so strongly turned back towards the axis that they display an arrangement of a fibrous wall (Pl. 1, fig. 4). In *Siphonodendron sp. B* (lower upper Viséan, Saoura, Algeria), the lateral sclerenchyme of the columella is more fibrous than in *S. martini*, in the columella of which the "fibrous trend" is discernable.

From these examples, it seems likely that between the lower Viséan and upper Serpukhovian an evolution may have occurred leading from the partly lamellar forms of *Siphonodendron* to entirely fibrous ones. A detailed study of the intermediate species is needed to confirm the existence of phylogenetic relationships between both types of *Siphonodendron*.

### CONCLUSIONS

1) In the genus *Siphonodendron*, there are (at least) two kinds of microstructure. The first type displays a fibrous septal apparatus, whereas the tangential or lateral structures are microlamellar. In the second type, the microstructure is entirely fibrous. In both cases, the septa are trabecular, while the columella is made of fiber fascicles, at least in its median part.

2) In both types of microstructure, the internal structure of the wall shows a vertical periodicity correlating with the growth rhythms as recorded by the fine external ridges. In the microlamellar type, it can be almost taken for granted that each internal zone corresponds to two external ridges. In the fibrous type, each zone of fascicles corresponds to one ridge.

The fine growth ridges are thought to reflect a diurnal growth rhythm among numerous *Rugosa* (Wells, 1963, 1970; Scrutton, 1965). The study of the internal banding of the wall, quite easy to be seen in polarized light, may complete or replace the observation of the ridges which are often worn off. This zonation is present in many *Rugosa*. Its examination may notably contribute to the study of biological rhythms in these corals.

3) From the base of the Viséan up to the latest Serpukhovian stage, a probable evolutionary trend in the genus *Siphonodendron* leads from partly microlamellar to entirely fibrous forms.

### ACKNOWLEDGMENTS

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## COMMENTS ON THE CAUNOPORE TUBES: STRATIGRAPHIC DISTRIBUTION AND MICROSTRUCTURE

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### ABSTRACT

Caunopores are usually considered tubes of commensal tabulates in stromatoporoids, and have been noted in 27 stromatoporoid genera. The stromatoporoid genera most often allied with caunopores are *Stromatopora*, *Stromatoporella* and *Clathrodictyon*. Caunopores are very frequent in Middle Devonian stromatoporoids, and possibly disappear at the top of the Givetian; indeed, the presence of caunopores in Frasnian stromatoporoids is doubtful. Caunopores are usually referred to *Syringopora* but the microstructure of the caunopores is very different from the lamellar microstructure of *Syringopora*.

### INTRODUCTION

The generic name *Caunopora* was erected by Phillips, 1841 for two species: *C. ramosa* which is the type species of the genus *Amphipora* Phillips, and *C. placenta* (*Coscinopora placenta* Lonsdale). Phillips gave the following description of *C. placenta*: "Amorphous; composed of concentric or nearly plane masses, perforated by larger straight subparallel or radiating, open?, non-lamelliferous? tubes persistent through the whole mass."

Numerous authors have discussed the validity of *Caunopora* and the place of the caunopore tubes, or caunopores in the stromatoporoid coenosteum. The first, Roemer (1844) thought that *Caunopora* results from a *Syringopora* growing parasitically with a stromatoporoid. In 1878, Nicholson and Murie also discussed the caunopores. In the end, they rejected Roemer's opinion, however they admitted that there is a singular resemblance between *Caunopora* and *Syringopora* and they noted that all characteristic internal structures of *Syringopora* are present in *Caunopora*. Carter (1879) adopted Roemer's opinion. Carter (1880) considered that *Caunopora* is more closely related to *Syringopora* than to *Aulopora*. Bargatzky (1881) erected the genus *Diapora* on the basis of caunopores in the coenosteum of the stromatoporoid genus *Stromatoporella*. In Monograph of the British Stromatoporoids, Nicholson (1886–1892) gave a lengthy introduction and discussion of caunopores. He considered three theories regarding *Caunopora*. 1) *Caunopora* and *Diapora* are stromatoporoid genera; 2) *Caunopora* and *Diapora* are stromatoporoids with commensal *Syringopora* (or *Aulopora*); 3) *Caunopora* and *Diapora* are a particular state of other known stromatoporoid species. The "tubes" thus would belong to the stromatoporoids, representing reproductive zooids or structures of other function.

Since Nicholson, most authors have assigned caunopores to the syringoporids (Twitchell, 1928; Hill,

1981), but differing opinions have been proposed. Thus, Parks (1935) suggested that stromatoporoids are Foraminifera and that caunopores "may be regarded as representing one of the alternate generation."

### THE TAXONOMIC DISTRIBUTION OF CAUNOPORES

Several authors have noted that caunopores are present only in some stromatoporoid genera (Le Maître, 1933; Galloway, 1957; Mori, 1970). I have studied 191 citations or illustrations of *Caunopora* in Silurian and Devonian stromatoporoids. As Galloway (1957) first stated, caunopores have not been reported in Ordovician stromatoporoids. Forty seven out of the 191 citations referred to Silurian stromatoporoids. Thus caunopores are present in Silurian stromatoporoids but not as commonly as in Devonian stromatoporoids. Some caunopores referred to in Silurian stromatoporoids are not characteristic of *Syringopora* but are referred to *Syringoporinus*. Also in the Devonian some caunopores are referred to *Syringoporella*. However the numbers listed above do not take into account all papers on Silurian and Devonian stromatoporoids published to date, and do not reassign species but accept the generic assignments that were made by the original authors.

Twenty seven stromatoporoid genera are concerned with caunopores, but 5 of them only are concerned with more than 5 species with caunopores. *Stromatopora* is the most common stromatoporoid genus with caunopores: 62 citations, that is about 1/3 of the listed citations, or 28 species of *Stromatopora* are involved (12 in the Silurian, 16 in the Devonian). The species frequently associated with caunopores are *S. buecheiensis* (Bargatzky, 1881; Nicholson, 1886; Le Maître, 1934, 1937; Ripper, 1936; Lecompte, 1951; Flügel, 1956; Stearn *et al.*, 1970; Mistiaen, 1980) and *S. huepshii* (Bargatzky, 1881; Nicholson, 1886; Ripper, 1937; Yavorsky, 1955, 1961; Galloway, 1960; Sleumer, 1969;

Yang *et al.*, 1979; Dong *et al.*, 1982). Third most frequent is *S. concentrica* (Nicholson, 1886; Patrini, 1930; Yavorsky, 1931; Ripper, 1937; Spinar, 1946; Firtion, 1957; Sleumer, 1969). *S. buecheliensis*, *S. huepschii* and *S. concentrica* are Devonian species. The 12 Silurian species of *Stromatopora* with caunopores have only been cited once apiece. So, relating to *Stromatopora*, caunopores are more frequent in the Devonian than in the Silurian.

*Stromatoporella* is also often associated with caunopores. It has been cited 32 times. Only 4 Silurian species are concerned; but 14 Devonian species are mentioned. The most frequent species is *S. laminata* (Bargatzky, 1881; Nicholson, 1886; Lecompte, 1951; Turnšek, 1970; Cornet, 1975; Mistiaen, 1980).

Caunopores also occur frequently in *Clathrodictyon*, cited 16 times. Three Silurian and seven Devonian species are involved. The most often cited species with caunopores is *C. amygdaloides* (Lecompte, 1951; Yang *et al.*, 1979; Mistiaen, 1980; Dong *et al.*, 1982). *Stictostroma* is represented by five Devonian species with caunopores. *S. socialis* is the most frequently cited (Nicholson, 1886; Le Maître, 1943; Lecompte, 1951; Yavorsky, 1955; Kazmierczak, 1971). Five species of *Actinostroma* are cited with caunopores but some appear questionable. They are *A. aequale* (Yang *et al.*, 1979); *A. clathratum* (Le Maître, 1934; Schouppé, 1954); *A. hebbornense* (Firtion, 1957, doubtful). *A. stellulatum* (Turnšek, 1970, doubtful); *A. verrucosum* (Zukalova, 1958, doubtful?). *A. astroites* of Nicholson, 1886 with caunopores (Galloway, 1957, p. 388) is better referred to *Densastroma* Flügel, 1959. Mori (1970) noted that stromatoporoids with superposed pillars such as *Actinostroma* seem to have been unfavorable places for the settlement of *Syringopora* larvae. Admittedly, caunopores may be present in *Actinostroma* but are uncommon or poorly developed. Four Devonian species of *Anostylostroma* are associated with caunopores, *A. arvense* (Galloway *et al.*, 1960), *A. laxum* (Fagerstrom, 1982), *A. ponderosum* (Nicholson, 1875; Galloway *et al.*, 1957) and *A. substriatellum* (Nicholson, 1875). Three Devonian species of *Trupetostroma* are cited with caunopores, *T. saintjeani* (Stearn, 1966), *T. coalescens* and *T. laceratum* (Klovan, 1966). In the last species, I believe that the tubes are not true caunopores, rather they are *Aulostegites*. Also, three Devonian species of *Pseudoactinodictyon* are cited with true caunopores: *P. dartingtonense* (Kazmierczak, 1971), *P. robustum* (Fritz *et al.*, 1956) and *P. zonatum* (Yang *et al.*, 1979). Two Devonian species of *Hermatostroma* are cited with caunopores, *H. dolica* (Yavorsky, 1931) and *H. polymorphum* (Zukalova, 1971, who noted that they are doubtful). *Symplexodictyon* (= *Clathrodictyon*?) is only associated with caunopores

in two Silurian species, *S. podolicum* (Bolshakova, 1973) and *S. convictum* (Yavorsky, 1929; Ripper, 1937; Riabinin, 1951, 1953; Nestor, 1966; Mori, 1970; Tchudinova, 1971; Bogoyavlenskaya, 1973). The same is true for *Parallelostroma*. Two essentially Silurian species are cited as having caunopores, *P. tenellum* (Mori, 1970) and *P. typica* (Nicholson, 1886; Le Maître, 1934; Mori, 1970; Tchudinova, 1971).

The last 16 genera are represented by only one species with caunopores. These species are *Atelodictyon stelliferum* (Klovan, 1966), *Clathrocoilona abeona* (Fischbuch, 1969), *Densastroma astroites* (Nicholson, 1886), *Diplostroma yavorskyi* (Mori, 1970; Birkhead, 1976), *Ecclimadictyon robustum* (Mori, 1970), *Gerronostroma boutovi* (Yavorsky, 1955), *Hammatostroma delicatula* (Klovan, 1966), *Idiostroma oculatum* (Nicholson, 1886; Ripper, 1936), *Intexodictyon perplexum* (Birkhead, 1978), *Labechia socialis* (Yavorsky, 1961), *Parallelopora crassa* (Flügel, 1956), *Plectostroma scallense* (Tchudinova, 1971), *Plumatalinia balticivaga* (Birkhead, 1976), *Pseudoactinostroma porosa* (Tchernychev, 1951), *Schistodictyon conjugatum* (Lesavaya *et al.*, 1970), *Taleastroma irregulare* (Yang *et al.*, 1979).

Thus caunopores exist in stromatoporoid genera belonging to almost all stromatoporoid orders, but are more numerous in some than others.

#### THE POSSIBLE DISAPPEARANCE OF THE CAUNOPORES AT THE END OF THE GIVETIAN

As early as 1932, Le Maître emphasized the absence of caunopores in Strunian stromatoporoids. She also drew attention to their abundance in the Lower and Middle Devonian stromatoporoids. In 1934, she accepted the third of Nicholson's theories, that caunopores may be stromatoporoid reproductive zooids. She proposed that the disappearance of caunopores in Upper Devonian stromatoporoids results in not permitting reproduction by means other than by budding, causing the decrease in numbers of the stromatoporoids at the end of the Devonian.

Out of the 191 citations mentioning caunopores, 71 deal with Givetian stromatoporoids but only 19 with Frasnian and only 2 with Strunian stromatoporoids. Moreover, many of the caunopores reported from Frasnian or Strunian stromatoporoids appear questionable in nature.

Only one Strunian stromatoporoid with true caunopores is described, *Stromatoporella damnoniensis struniana* Conil (1961). It comes from a "very narrow outcrop in a puddingstone-like limestone" (1961, p. 349). Perhaps it is a reworked sample. The other possible caunopore from the Strunian consists of some circular sections in an illustration of Flügel *et al.*, 1975

(pl. 6, figs. 4, 5); it is doubtful and may be sections through an auloporid.

Zukalova (1958, 1971) described four stromatoporooids with caunopores in the "Lower Frasnian" from Hranice in Moravia: *Actinostroma verrucosum* (doubtful *Caunopora*), *Clathrodictyon paramygdaloides*, *Stromatoporella frasnensis* and *Hermatostroma polymorphum* (doubtful *Syringopora*). The "Lower Frasnian" from Hranice seems equivalent to the Fromelennes Formation (F1) in the Dinant Basin (Mistiaen, 1982). The Fromelennes beds correspond to the Upper *varcus*, *hermanni-cristatus* and lowermost *asymmetricus* zones, that is the Upper Givetian.

In Poland (Holy Cross Mountains), Kazmierczak (1971, 1976) has described five stromatoporooids containing *Syringopora* sp. One of them, within *Stictostroma sociale*, is not a true caunopore, but instead may be an *Aulostegites*. Another within *Stictostroma kolymense*, differs by its large dimensions (1–1.3 mm) and thick walls (0.3–0.5 mm) from all other described caunopores. Two others, within *Stictostroma lensiforme* and *Pseudoactinodictyon dartingtonense*, come from Givetian to Frasnian transitional beds. The last noted within *Parallelopora* aff. *planulata*, comes from strata the age of which was "estimated" by Kazmierczak (1971) as Lower Frasnian. It is also possibly from the *hermanni-cristatus* zone.

In the U.S.S.R., two Frasnian occurrences have been noted. One is an auloporoid growing within *Stromatoporella strelnensis* (Yavorsky, 1955). The second, within *Clathrodictyon tumulosum* (Yavorsky, 1957) has been found in the Upper Frasnian of the Kuznetsk Basin (Glubokinskie Beds), and it appears to be a true caunopore.

Eight Frasnian caunopores are from Canada (Northwest Territories and Alberta). Stearn (1966) described two true caunopores from the Kakiza Formation of the Upper Frasnian, within *Stictostroma maclareni* and *Trupetostroma saintjeani*. Stearn (1975) described another true caunopore within *Stromatopora cygnea*, from the Frasnian of Alberta (Ancient Wall Reef Complex). Klován (1966) described five stromatoporooids with *Syringopora* or *Syringoporella* from Redwater Reef Complex. One, within *Trupetostroma* aff. *laceratum*, is surely an *Aulostegites*. The four others are true caunopores. Klován described a rich stromatoporooid fauna with 27 species, among which are six new species. For the 18 species previously described, stratigraphic ranges are given below, following Flügel *et al.*, 1968. One (*Actinostroma matutinum*) is Silurian only. Seven species (*Anostylostroma laxum*, *Stromatoporella* cf. *subvesiculosum*, *S.* cf. *mirabilis*, *Trupetostroma warreni*, *T.* cf. *coalescens*, *Ferestromatopora dubia*, and *Syringostroma* cf. *perfuscum*) are Middle Devonian only;

three species (*Stromatoporella damnoniensis*, *Actinostroma clathratum*, and *Trupetostroma* aff. *laceratum*) are typically Givetian but seldom Frasnian; three species (*Actinostroma crassepilatum*, *Synthetostroma vesiculosum*, and *Stachyodes costulata*) are both Givetian and Frasnian. Thus the whole stromatoporooid fauna described by Klován shows much more affinity with Givetian faunas than with those of the Frasnian. It therefore seems that, in western Canada, relic Givetian stromatoporooids may have persisted into Frasnian.

Thus, caunopores seem scarce in the Frasnian while they are very common in the Givetian. Where stratigraphically does the extinction occur in exact terms? In the Dinant Basin, the Sourd d'Ave section contains the Givetian–Frasnian boundary, that is the lowermost to lower *asymmetricus* zone boundary (Bultynck, 1974). I have examined 181 coenostea from the *hermanni-cristatus* and lowermost *asymmetricus* zones (F1b–c); none of them has caunopores. Perhaps caunopores have their great decrease in number during the F1b? Perhaps, but the three genera often allied with caunopores (*Stromatopora*, *Stromatoporella* and *Clathrodictyon*) are also scarce among this stromatoporooid fauna, causing doubt regarding this interpretation.

#### THE MICROSTRUCTURE OF CAUNOPORES

Out of the 191 listed citations, 88 give a generic assignment for the caunopores: 72 are assigned to *Syringopora* (27 Silurian, 45 Devonian), ten to *Syringoporella* (all Devonian) and four to *Syringoporinus* (all Silurian). Caunopore and *Syringopora* microstructure have also been studied, using the ultrathin section method of Lafuste (1970).

The first observations have been made on caunopores in *Stromatopora* cf. *buecheliensis* from the Blacourt Formation, Givetian, of Ferques, Boulonnais (Brice *et al.*, 1979). In the specimen GFCL 1402, LUM 62, caunopore walls in transverse sections, are made up by small calcite crystals coarsely ordered (Figs. 3, 4) nearly forming a ring. In the inner part there are larger crystals filling in the tube. In the outer part, there are crystals of the stromatoporooid tissue that are difficult to explain. The crystal lengths within the caunopore wall are about 50–80  $\mu\text{m}$ , that is the thickness of the tubes. The crystal width is irregular but it often is rather large, 10–20  $\mu\text{m}$ . A second specimen (GFCL 1387, LUM 65) shows the same aspect. A third (GFCL 1046, LUM 61) has a thicker wall, as much as 100  $\mu\text{m}$  thick. It can locally have two layers of similar crystals (Figs. 5, 6). Longitudinal sections show other features of the caunopores' microstructure. In one section (GFCL 1406, LUM 60) locally very large crystals were observed, up to 400  $\mu\text{m}$  long and 15–40  $\mu\text{m}$  wide (Fig. 7), oriented parallel to the axis of the tubes and with

irregular contours. In another place the aspect is even more irregular where the section perhaps cuts irregular boundaries between two or more crystals. Another section (GFCL 1387, LUM 66) shows the same situation. Thus, the caunopore wall in specimens of *Stromatopora* cf. *buecheliensis* is apparently made up of long crystals with very irregular boundaries, which are disposed parallel to the axis of the tube and locally overlap one another. As a result, in transverse sections two crystal layers can be seen locally.

Caunopores have also been studied in other stromatoporoid species. In a specimen of *Clathrodictyon* cf. *amygdaloides subvesiculosum* from the same beds (GFCL 1132, LUM 58), caunopore transverse sections appear very similar to those described above. Some tubes however, have thicker walls (130–150  $\mu\text{m}$ ) and crystals seem more fibrous. A specimen of *Stromatoporella laminata* (GFCL 1304, LUM 59) from Boulonnais also has an identical appearance in transverse sections. Longitudinal (oblique) sections do not show the elongated crystals as in the other genera. These sections also show transverse connection tubes, the walls of which seem to be made up by small calcite crystals similar to those observed in transverse sections.

By comparison, syringoporoid microstructure is very different (Fig. 11). Ultrathin sections were made in a well preserved specimen of the Blacourt Formation (LUM 54, 55, 56), which show walls with a characteristic lamellar microstructure (Fig. 8), very similar to that described by Fischer *et al.* (1972), in the Mesozoic chaetetida *Acanthochaetetes*. The spines of *Syringopora* also appear completely lamellar. Lamellar microstructure in *Syringopora* has been interpreted both as a primary or secondary (diagenetic) structure (Hill, 1981). By observation in ultrathin section, it is possible to identify the microstructure of *Syringopora*. The wall appears in transverse section, to be made up by three layers. The middle layer, making up the greatest thickness, is about 200  $\mu\text{m}$  thick and is made of lamellar contorted crystals, oriented parallel to the wall

of the *Syringopora* tube. Dimensions of crystals are about 2–10  $\mu\text{m}$  wide and up to 60–80  $\mu\text{m}$  long. Locally there are knot-like structures corresponding to the spines of *Syringopora*. The outer layer (Fig. 9) varies in thickness, with an average of 150  $\mu\text{m}$ . It is made up of crystals that are narrower than in the middle layer. Locally the outer layer seems to continue the middle layer, corresponding to a change in crystal orientation (Fig. 9). The outer layer is not always present, it is at times eroded (?) away. The inner layer is about 30  $\mu\text{m}$  thick and it seems very similar to the walls of the caunopores but is more regular. The inner layer does not seem to be calcite cement; it is clearly limited by a regular boundary (Fig. 10), and is not present everywhere. Other sections have been cut in a poorly preserved specimen from the Frasnian of Hajigak (Central Afghanistan); here the outer and inner layer are very difficult or impossible to distinguish.

From these observations it is possible to draw some conclusions. 1) The caunopore microstructure is very different from the *Syringopora* microstructure. 2) It is difficult to think that *Syringopora*'s lamellar microstructure results from a diagenetic process. If this were true, why would not the inner layer have suffered the same diagenetic change? I thus agree with Lafuste that here the lamellar microstructure is primary. 3) If the inner layer of the wall in *Syringopora* corresponds to the caunopore wall, one could imagine that the caunopore animal did not need any protective layers (middle and outer layers) due to its life habit, living in the coenosteum of stromatoporoids. 4) Additional studies are needed to compare the microstructure of caunopores to the microstructure of the Tabulata (*Aulopora*, *Thecostegites* and others).

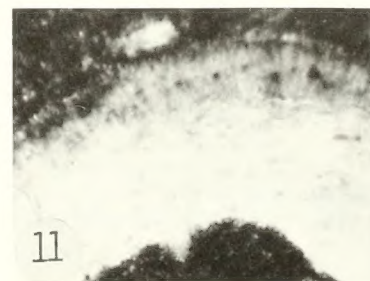
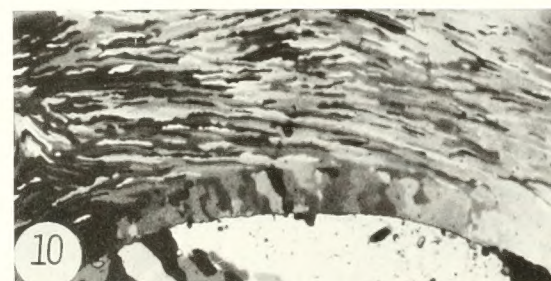
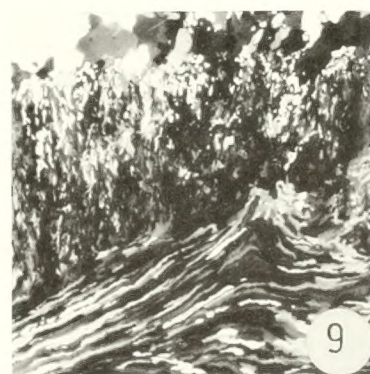
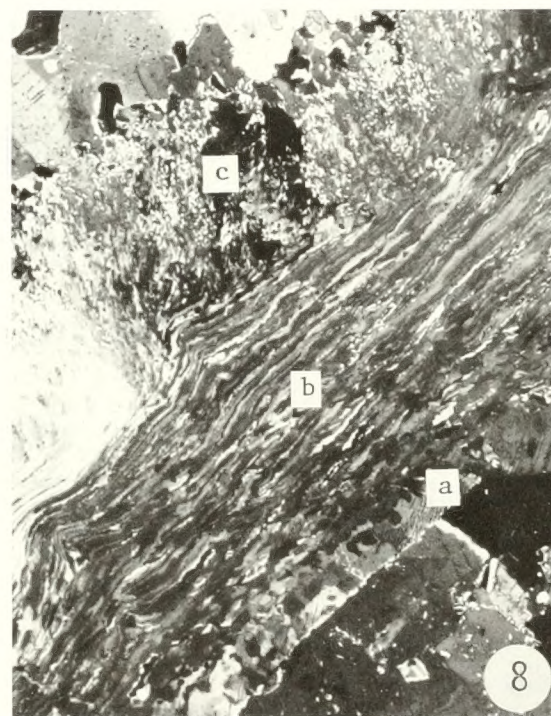
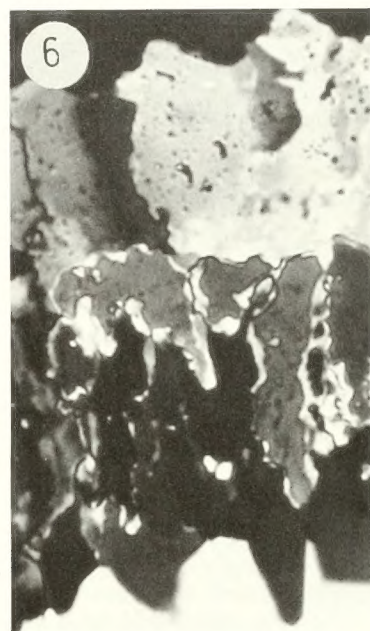
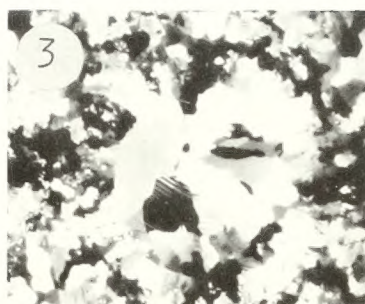
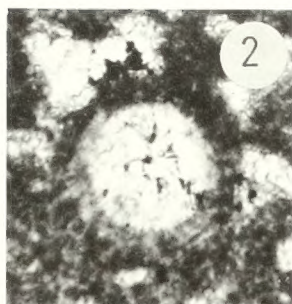
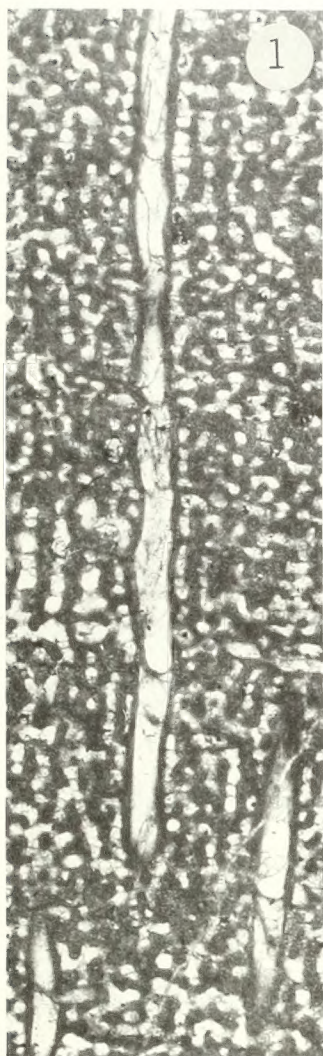
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#### EXPLANATION OF PLATE I

##### Figure

- 1–7. Caunopore tubes in different specimens of *Stromatopora* cf. *buecheliensis* (Bargatzky, 1881a), from the Formation de Blacourt, Givetian of Ferques area, Boulonnais, France
  1. GFCL 1387: Longitudinal sections in caunopore tubes. Typical thin section.  $\times 12$ .
  2. GFCL 1402: Transverse section in a caunopore tube. Typical thin section.  $\times 40$ .
  3. GFCL 1402-LUM 62: Caunopore tube in ultrathin transverse section.  $\times 65$ .
  4. Detail of the Fig. 3. Caunopore wall with a single crystal layer (slightly underlined).  $\times 170$ .
  5. GFCL 1406-LUM 61: A "two layers" wall of a caunopore tube.  $\times 170$ .
  6. Detail of the Fig. 5.  $\times 650$ .
  7. GFCL 1406-LUM 60: Longitudinal section in the wall of a caunopore tube, with elongated crystals.  $\times 170$ .
- 8–11. Microstructure of syringoporoids. Specimens from the same locality as the caunopores. All sections transverse
  8. LUM 54: Syringoporoid with its three crystal layers (a = inner; b = middle; c = outer).  $\times 170$ .
  9. LUM 54, Different place in the same thin section: relation between the middle lamellar and the outer fringed layer.  $\times 170$ .
  10. LUM 56: Another thin section of the inner layer.  $\times 170$ .
  11. Normal appearance of a syringoporoid wall. Typical thin section.  $\times 40$ .



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*Note added in press*

While this paper was in press, the author had the opportunity to examine the type-material of *Stromatoporella damnoniensis struniana* Conil, 1961, through the courtesy of Prof. R. Conil of Louvain-la-Neuve University. Prof. Conil does not agree with the opinion that it could be a reworked sample, because the micritic limestone inside the stromatopore coenosteum contains typical Strunian microfauna.

COLUMELLA DEVELOPMENT IN *LOPHOPHYLLIDIUM* N. SP., AND ITS  
TAXONOMIC IMPLICATIONS, IMO FORMATION, LATEST  
MISSISSIPPIAN, NORTHERN ARKANSAS

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ABSTRACT

A new species of the genus *Lophophyllidium*, from latest Mississippian strata from Arkansas, exhibits an extremely high degree of variability in the size and complexity of its columella. This variability is attributed to randomness in the relationships of the septal lamellae and stereoplasmic laminae, which are major constituents of the columella. The occurrence of structurally complex columellae in this Mississippian example of *Lophophyllidium* suggests that a complex columella should not be considered an "advanced" trait in the genus.

INTRODUCTION

Corals of the family Lophophyllidae have long been noted for their high degree of variability and confused taxonomic status (Jeffords, 1947; Fedorowski, 1974). The genus *Lophophyllidium* contains some of the most variable members of the family, and its most prominent morphological feature, the columella, has not been excluded from this variability. In North America, this genus has not previously been described from strata below the base of the Pennsylvanian, but a striking new species of the genus has been examined from the Imo Formation, latest Mississippian, of Arkansas. It is not the intent of this paper to describe this new species, but rather to outline the variability and construction of its columella, with an emphasis on its taxonomic importance.

The Imo Formation crops out in a small area on the southern flank of the Ozark Mountains in north-central Arkansas. The unit, composed primarily of dark gray shales, lies with apparent conformity on the Mississippian Pitkin Formation, and is unconformably overlain by Pennsylvanian strata. It contains the well known *Eumorphoceras richardsoni*-*Fayettevillea friscoense* ammonite zone, which suggests equivalency to the E<sub>2</sub>b-c zones of the European, Arnsbergian Stage (Saunders and others, 1977).

This new example of *Lophophyllidium* consists of solitary, conical to conico-cylindrical corals that reach a maximum observed length of 7.3 cm, and an average maximum diameter of 1.8 cm. They have a thick theca with prominent septal grooves and ridges (Pl. 1, fig. 1a). Internally, they exhibit extreme variability. The following is a typical ontogenetic sequence for the species, with the emphasis on the columella.

ONTOGENY

The earliest ontogeny, represented by the first five millimeters of growth, has not as yet been studied, but

is assumed to follow the typical pattern for the family, as illustrated by Jeffords (1947) for *Stereostylus*, where in the columella arises as an expansion of the axial end of the counter septum. After this, three main ontogenetic stages have been observed in the Imo species, each with a distinctive columellar structure. The first stage is characterized by the joining of the septa to the columella by stereoplasmic lamination, creating in many cases a solid mass (Pl. 1, fig. 2). Septal lamellae may or may not be present in the columella. The nature of the tabulae is obscured by the abundance of stereoplasm between the septa. This stage encompasses the apical region of the coral, and major septa are rapidly being introduced.

The second stage shows a decrease in the overall amount of stereoplasm, though its abundance is a highly variable character. Major septa are still being inserted, and, with the exception of the cardinal septum, still generally extend to the columella, where they may or may not be attached to it by stereoplasm. The tabulae are mostly complete and rise fairly steeply from the theca to the columella (Pl. 1, figs. 1b, c). The columella generally increases in diameter and projects far above the calice floor during this stage. Septal lamellae are commonly prevalent, although they may be lacking.

The last stage, or adult stage, is initiated when the maximum number of septa (usually 30 to 32) have been inserted, and the coral begins to take on a cylindrical shape. The major septa, with the exception of the counter septum, generally withdraw somewhat from the columella and are only rarely attached to it by stereoplasm. In rare instances, the columella may also become completely free of the counter septum (Pl. 1, fig. 3), although it is generally at least connected by the rising tabulae (Pl. 1, figs. 4a-d). The tabulae become much more numerous, more incomplete, and begin to flatten out (Pl. 1, figs. 1b, d). The columella becomes

smaller in diameter, and does not project as far above the calice floor. Septal lamellae are typically less prevalent in this stage, although new ones may still arise (Pl. 1, fig. 5a).

#### COLUMELLA DEVELOPMENT

The columella is made up of three major elements. The first, which is invariably present, is the medial lamella. It arises as a continuation of the midline of the counter septum, and may remain continuous with it throughout ontogeny, or become separated at an early age. The medial lamella is surrounded by stereoplasmic laminae which are continuous with those on the top surface of the tabulae (Pl. 1, fig. 5b). A columella, so composed (*i.e.*, of only laminae on a medial lamella), is termed "simple" by Fedorowski (1974). The third component consists of septal lamellae. They are composed of vertical plates which are laid down on top of the stereoplasmic laminae of the columella. Columellae which contain septal lamellae are termed "composite," by Fedorowski (1974).

Septal lamellae may be introduced at the axial end of a septum and extend up the surface of the columella to its peak, so that in serial section they appear to migrate inward toward the medial lamella (Pl. 1, figs. 6b-f). A septal lamella may penetrate to the medial lamella only if it is introduced at the peak of the growing columella. Once introduced, the lamella may grow continuously, or may be partially or completely eliminated by the overgrowth of stereoplasmic laminae. They may also migrate over the surface of the columella. Many septal lamellae appear to be introduced only high upon the columella, well above the calice floor, so that they appear not to be related to any specific septa. Although associated with septa, septal lamellae represent a fundamentally different type of deposition. The dark line of a septum may be cut by stereoplasmic laminae at its axial end, but the dark line of a septal lamella is not disturbed (Pl. 2, fig. 1). This indicates that the septal lamellae are deposited in a short period of time, as compared to the continually growing septa. Lamellae deposited on the surface of a tabula, at the base of the calice, must in fact be completely deposited in between the time of deposition of the two boundary tabulae.

Some evidence indicates a periodicity to the deposition of septal lamellae and stereoplasmic laminae. Although some septal lamellae, and certainly the medial lamella, appear to be maintained constantly throughout the columella, others periodically stop growing, are covered by laminae, and then may or may not be subsequently re-established (Pl. 2, figs. 2, 3). Septal lamellae may also be emplaced at the peak of the columella in such a way as to protect areas from lamination, thus creating hollow areas in the center of the columella (Pl. 2, fig. 4). This might suggest that the two types of deposition alternate, but it seems more likely that the deposition of stereoplasmic laminae is a slow, fairly constant process, which is only occasionally overtaken by events of rapid septal lamellae growth. Fedorowski (1974) terms columellae which contain both septal lamellae and stereoplasmic laminae, "lamello-tabellar," and attributes them to a "change in rhythm of the secretion of the structural elements," whereby the fundamental type of secretion changes from lamellar to laminar. Some individuals of this species do appear to undergo a rapid change from lamellar to laminar deposition, in moving from the second to third ontogenetic stage (Pl. 2, fig. 5), but they still retain the capacity to begin introducing new septal lamellae. Others retain a simple columella throughout ontogeny and never introduce septal lamellae. Therefore, though the relative percentages of the two types of deposition may vary, there is no fundamental change from one type to the other.

#### VARIABILITY AND TAXONOMIC IMPLICATIONS

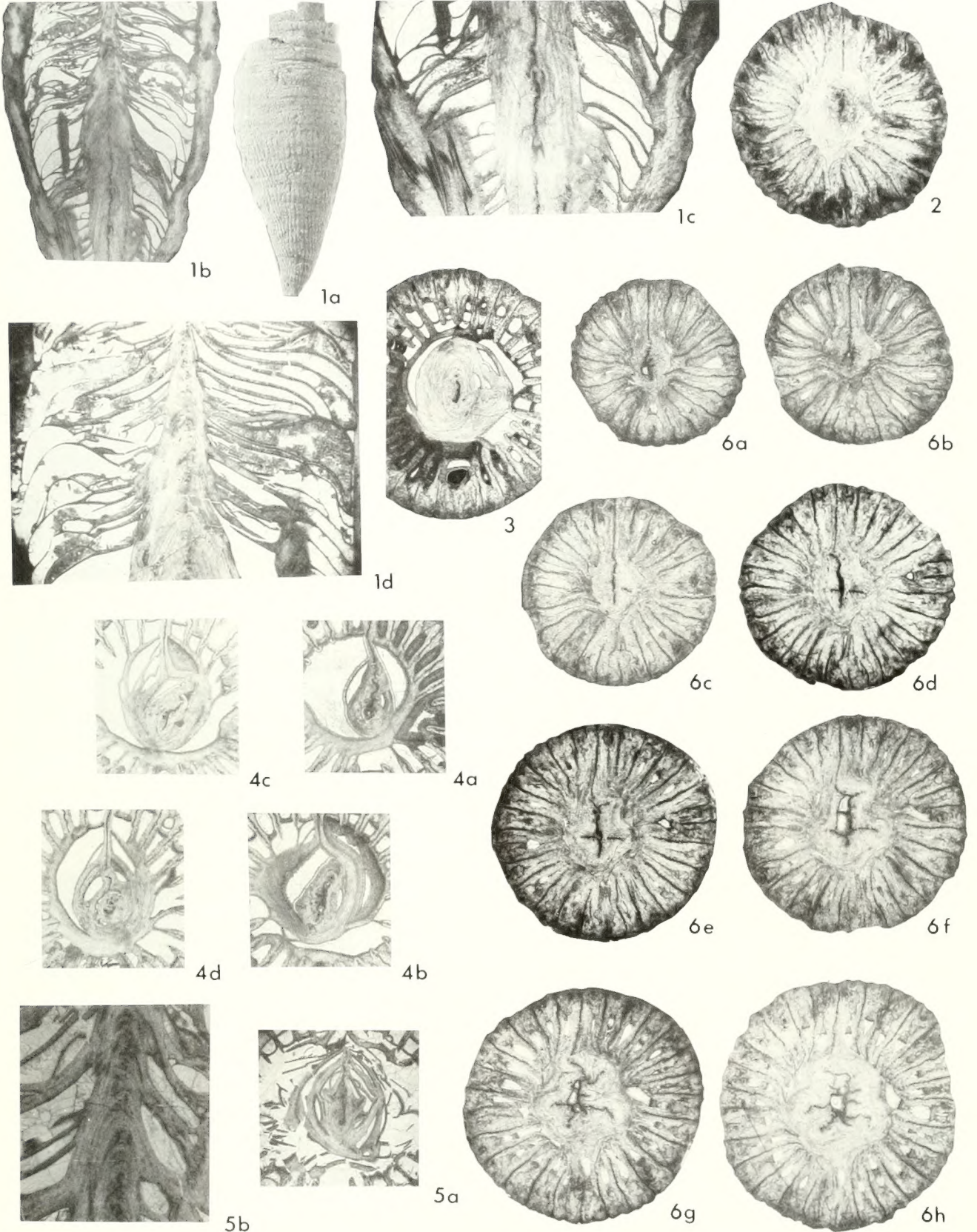
Historically, the character of the columella has been considered one of the primary diagnostic features of the lophophyllidid corals (Jeffords, 1947). More recently, however, Fedorowski (1974) has pointed out that the structure of the columella cannot be considered a diagnostic character on the generic level. The high degree of variability observed in this new species may even limit the usefulness of the columella on a specific level. Most of the columellar variability can be attributed to three factors. The component of variability due to the ontogenetic stage has already been discussed. The remaining variability is due to differences in both

#### EXPLANATION OF PLATE I

Figure

1-6. *Lophophyllidium* n. sp.

Specimens, unless otherwise noted, are from the Imo type section at Sulphur Springs Hollow in SE, SE, sec. 3, and NW, NW, sec. 11, T. 13 N., R. 17 W., Searcy County, Arkansas (USGS Loc. 15932-PC). 1) a. External view,  $\times 1$ . b. Longitudinal view,  $\times 2$ . c. Longitudinal view,  $\times 4$ . d. Longitudinal view,  $\times 4$ . USNM 314165, USGS Loc. 15793-PC. 2) Transverse section through juvenile stage,  $\times 4$ , USNM 314171. 3) Transverse section through adult stage,  $\times 3$ , OU 10214. 4) a-d. Serial sections,  $\times 4$ , OU 10217. 5) a. Transverse section through adult stage,  $\times 3$ . b. Longitudinal section through adult stage,  $\times 7$ . OU 10212. 6) a-h. Serial sections,  $\times 4$ , USNM 314173.



the abundance and distribution of septal lamellae and in the amount of stereoplasmic lamination. The size of the columella may range widely due to the varying thicknesses of stereoplasm (Pl. 2, figs. 6–9). The abundance and distribution of the septal lamellae may also have environmental controls, but they seem more likely to be a function of individual genetic makeup. The insertion of the septal lamellae does not appear to follow any set pattern. Their numbers may range from few to many (Pl. 2, figs. 4, 10–13), and they need not exhibit any particular symmetry (Pl. 2, fig. 14). They likewise need not radiate from the medial lamella, but may be oriented in any direction, including parallel to the medial lamella (Pl. 2, figs. 15a–j). They may also radiate from other septal lamellae. Thus, an individual of this species may exhibit any of several different columella “types,” so long as these “types” are distinguished by the relationships of the septal lamellae and stereoplasmic laminae (see Fedorowski, 1974, for several columella types).

The variability and potential complexity of the columella in this species has several taxonomic implications. The fact that many of the different “types” of columella, which are present in this species, seem to be random variants of each other, in itself, precludes any one “type” from being inherently more advanced than another. This could also explain the difficulty, which Fedorowski (1974) points out, in tracing the development of a single columella “type” through time. It is also interesting that structurally complex columellae were already present in the genus *Lophophyllidium* by latest Chesterian time. This does not seem to support the much disputed Biogenetic Rule (*i.e.*, the Law of Recapitulation, whereby ontogeny recapitulates phylogeny). Rugose corals make ideal subjects for the evaluation of this rule, in that the ontogenetic stages of each individual may be preserved. Jeffords (1947) lists the supposed primitive characteristics, obtained from ontogenetic studies of Pennsylvanian and Permian lophophyllidids, as: 1) prominent bilateral symmetry; 2) large alar pseudofossulae; 3) columella attached to counter septum; 4) long major septa; 5) irregular, anastomosing tabulae; 6) insertion of major septa throughout most of development and hence conical shape; 7) thick stereoplasmic deposits; and 8) a

laterally compressed, simple columella. Most of these “primitive” traits do occur in this Mississippian species of *Lophophyllidium*, but just as in the Pennsylvanian species, they occur, for the most part, only in the juvenile stages. The adult stage of this species exhibits many of the “advanced” traits, such as: shortened major septa, cylindrical shape, and a large, complex columella. It therefore undergoes the same basic ontogenetic trends as do the later species, with the only major exception being that the tabulae of the Imo species become more irregular and anastomosing through ontogeny. This does not rule out the possibility that this species could be ancestral to many later species of *Lophophyllidium*. It clearly could have given rise to forms with widely varying columellae. It does, however, rule out the assumption that a structurally complex columella is an “advanced” trait in this genus.

### CONCLUSIONS

- 1) The genus *Lophophyllidium* is represented in the North American Mississippian.
- 2) Structurally complicated columellae occur in the family Lophophyllidae in the Mississippian.
- 3) The columella of this species is highly variable and this variability is due to randomness in the relationships between septal lamellae and stereoplasmic laminae.
- 4) The emplacement of septal lamellae may not occur at all, or may occur in several separate cycles throughout ontogeny. The deposition of stereoplasmic laminae, on the other hand, appears to occur more slowly and steadily throughout ontogeny, but at variable rates.
- 5) The columella, by itself, cannot be considered a taxonomically diagnostic feature for this species.
- 6) Although a complex columella has previously been considered an “advanced” trait, its occurrence in this species as a random variant of a simple columella, indicates that this is not the case.

### ACKNOWLEDGMENTS

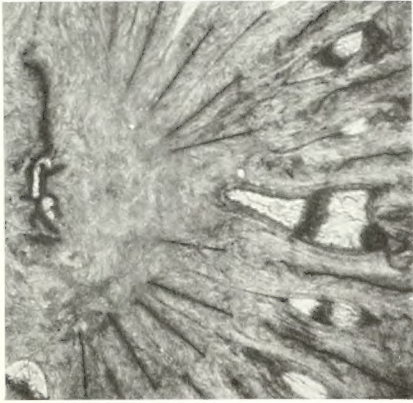
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### EXPLANATION OF PLATE 2

#### Figure

#### 1–15. *Lophophyllidium* n. sp.

Specimens are all from the Imo type section at Sulphur Springs Hollow in SE, SE, sec. 3, and NW, NW, sec. 11, T. 13 N., R. 17 W., Searcy County, Arkansas (USGS Loc. 15932-PC). All figures, unless otherwise noted, are transverse sections. 1)  $\times 10$ , OU 10216. 2)  $\times 4$ , USNM 314167. 3) Longitudinal section through calyx,  $\times 5$ , OU 10219. 4)  $\times 3$ , USNM 314173. 5)  $\times 3$ , USNM 314176. 6)  $\times 2$ , OU 10213. 7)  $\times 2$ , USNM 314170. 8)  $\times 2$ , USNM 314172. 9)  $\times 2$ , USNM 314175. 10)  $\times 3$ , USNM 314168. 11)  $\times 3$ , USNM 314169. 12)  $\times 3$ , OU 10215. 13)  $\times 3$ , USNM 314166. 14)  $\times 4$ , OU 10218. 15) a–j. Serial sections,  $\times 3$ , USNM 314174.



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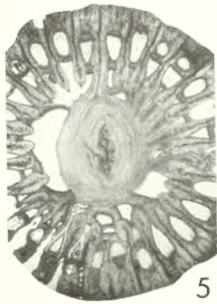
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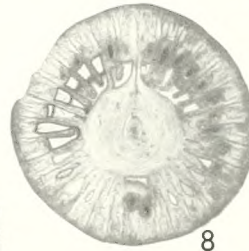
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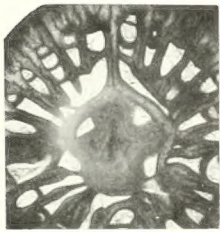
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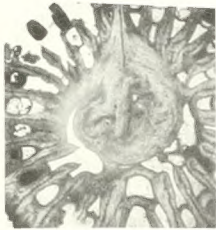
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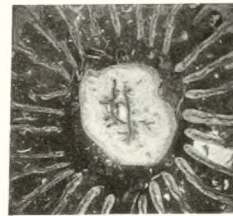
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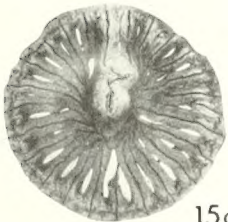
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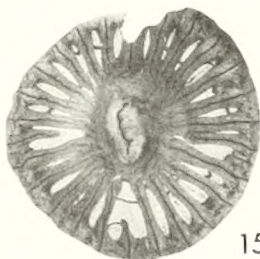
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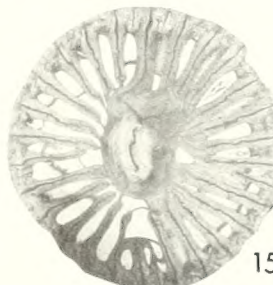
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15i



15j



14

Thanks also go to Will Hawkins for his aid in the field, and to the United States National Museum and University of Oklahoma for the use of their collections.

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MICROSTRUCTURAL EVIDENCE OF THE DISTICHOPHYLLIID AFFINITY  
OF THE CARYOPHYLLIINA (SCLERACTINIA)

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## ABSTRACT

The Triassic shallow-water corals of the family Distichophylliidae Cuif, 1977 display, in their septa, small (beginning with 10  $\mu$ ) trabeculae arranged in a fountain-like manner with fascicles of fibers or trabecular axes diverging from them laterally. The mid-septal line may be straight, undulating or zigzag. This type of microstructure of the septa and its characteristic diagenesis has so far been unknown in later shallow-water corals. It occurs, nevertheless, in the ahermatypic corals of the suborder Caryophylliina starting, at least, with the Albian. The caryophylliids are therefore considered as a descendant group of the Triassic distichophylliids.

## INTRODUCTION

The Triassic corals discussed in this paper come from the collections of the Geologisches Bundesanstalt, Wien (abbreviated GBA) and Naturhistorisches Museum, Wien (NHM). The Cretaceous and Miocene corals are housed in the Institute of Paleobiology, Polish Academy of Sciences (ZPAL).

MICROSTRUCTURE OF THE  
DISTICHOPHYLLIIDS

The corals of the family Distichophylliidae Cuif, 1977 occur commonly in the Late Triassic shallow-water deposits of the Tethys. They are solitary and colonial, primarily phaceloid corals, as well as massive ones of variable growth form. They are found together with a rich assemblage of fossil invertebrates and plants, embedded in fine-grained sediments of wackestone to packstone type, which fill up the intercorallite and intercolonial space.

Although all coral-bearing Triassic deposits are generally interpreted as reefs, the frequent domination of phaceloid corals in association with fine-grained sediments indicates that at least part of them was formed in a rather low energy and not very shallow-water environment. Under different conditions the phaceloid corals would be crushed, at least during storms, and form breccias. In reality, as debris they contribute insignificantly to the volume of the sediment, but are conspicuous as intact colonies occurring *in situ*.

Distichophylliids resemble faviids in the structure of their endotheca and radial elements; however, they display a very specific microstructure. The mid-septal zone is built by a row of small trabeculae (diameters between 10–30  $\mu$  in some species, reaching 40–60  $\mu$  in others), crowded closely to each other (Pl. 1, figs. 2–5), and composed of very thin fibers. Fascicles of thick fibers diverge from them laterally. These fibers may be organized into short, thick, lateral trabeculae provided with their own axes (Cuif, 1974, fig. 4). Grow-

ing from the mid-septal zone outward, the fascicles of thick fibers or lateral trabeculae cover practically the whole thickness of the septal blade. The small-trabecular midzone is very thin as compared with thick-fibrous layers of the stereom situated on either side. The midzone, usually of a high optical density, appears in transverse section as straight, undulating or a zigzag line (Pl. 1, fig. 1).

As a result of dissolution, the histology of the main trabeculae and the axes of lateral trabeculae is, on the whole, subject to destruction. Their fibers being dissolved, the calcium carbonate is carried away or recrystallized on the spot. A fissure is formed where the trabecular midzone occurred (Pl. 1, figs. 1–4). The septa easily split along the mid-septal line displaying surfaces marked by a characteristic sculpture (Cuif, 1974, fig. 8).

The distichophylliid microstructure was described and interpreted for the first time by Cuif (1974). His interpretation is correct only in part, since it does not take into account the occurrence of trabeculae in the mid-septal zone.

In the Triassic, next to corals with perhaps the most frequent, small-trabecular distichophylliid microstructure, there also occurred those with a non-trabecular microstructure, for example, pachythecaliids, astraeomorphids, stylophyllids and corals of large-trabecular microstructure developed in many variations (Cuif, 1977).

All shallow-water distichophylliids became extinct at the Triassic/Jurassic boundary (perhaps with one exception—a line leading to rhipidogyrids). This is most striking because various other Triassic corals, possessing distinctly archaic features, continued at least to the Lower and Middle Jurassic (stylophyllids) or even passed into the Tithonian (Hexanthiniaria, Montanaro-Gallitelli, 1975). The lithology and composition of the animal groups accompanying corals in the Jurassic and Triassic are comparable to each other.

One may presume that shallow-water corals occupied a similar habitat through both the Jurassic and Triassic times.

With the extinction of the distichophylliids late in the Triassic, there disappeared from the shallow-water environment corals of small-trabecular microstructure, and new types evolved with fibrous and large-trabecular microstructures. The Jurassic shallow-water corals reached a new level of histological organization of the skeleton but, generally, they did not mark any great progress in corallite or colony organization. A different situation would be observed in a group that colonized a new environment, *i.e.*, deep-water corals.

Corals of distichophylliid microstructure have not been noted in the interval between the uppermost Triassic and Albian. Recently, I recorded them in the Albian and Senonian, in deposits of non-reefal facies. These are ahermatypic corals of the suborder Caryophylliina. Russo (1976) recorded them in the Eocene.

#### MICROSTRUCTURE OF SOME CARYOPHYLLIIDS

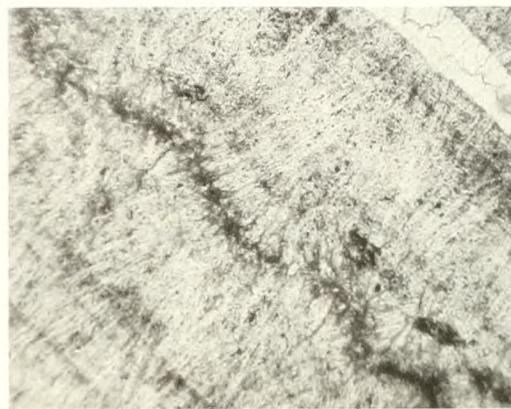
The microstructure of the caryophylliids is discussed on the basis of several examples of Recent corals described by Sorauf and Podoff (1977) and Sorauf and Jell (1977), as well as some fossil corals.

##### Family Caryophylliidae

(a) The subfamily Caryophylliinae: The first SEM micrographs of the microstructure of septa in the *Caryophyllia* were published by Sorauf and Podoff (1977, pl. 1, figs. 8, 9, pl. 3, fig. 3). A row of single or branched trabeculae, about 20  $\mu$  (or less) in diameter, and composed of very fine aragonite fibers, occurs along the septal midline of the Recent *Caryophyllia communis* Moseley. The growth of crystallites, connected with their abrupt thickening outward from the midline, takes place on these trabeculae. The fibers of the tissue forming the sides of the septa are subperpendicular to the midline, with a slightly marked organization of fasci-

cles. The authors remark that the primary septa display branched trabeculae and secondary septa discrete and simple trabeculae (pl. 3, fig. 3).

A similar structure is present in the Maestrichtian *Caryophyllia* sp. having partially preserved aragonite in its skeleton. The sides of the septa are composed of fibers subperpendicular to the midline. The latter shows locally traces of crowded trabeculae about 20–30  $\mu$  in diameter (Text-fig. 1).



Text-figure 1.—*Caryophyllia* sp. Maestrichtian, Kraśnik, Poland. ZPAL, H.II/2. Vestiges of trabeculae at the median septal zone,  $\times 100$ .

Similar in structure are septa of the Upper Albian caryophylliid coral from the Tatra Mts. Its zigzag mid-septal line is composed of closely spaced vestiges of trabeculae, about 30  $\mu$  in diameter (Text-fig. 2).

One can assume that the septal microstructure of corals of the subfamily Caryophylliinae is comparable in diameters, structure and arrangement of trabeculae to that observed in the Upper Triassic retiophylliids (Pl. 1, figs. 1–5).

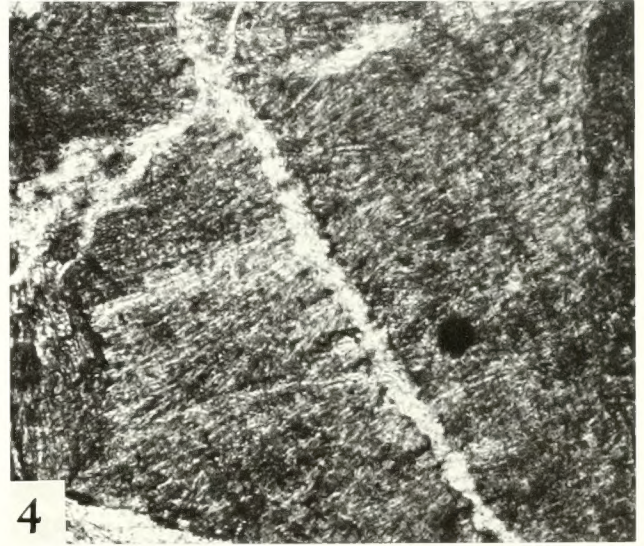
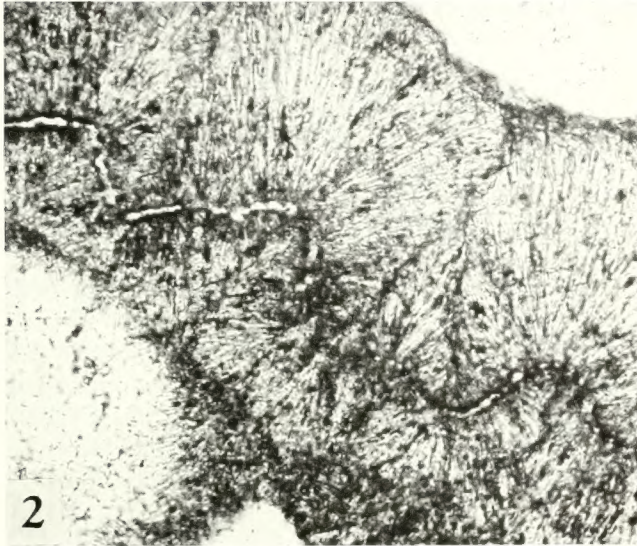
(b) The subfamily Desmophyllinae: The skeletal structure in the Recent *Desmophyllum cristagalli* Milne-Edwards et Haime, 1848 is presented by Sorauf and Jell (1977) in SEM micrographs. A longitudinal broken section shows the surface of the mid-septal plane (pl. 2, figs. 1–4) with fiber fascicles diverging

#### EXPLANATION OF PLATE I

Figure

1–6. Septal microstructure of the distichophylliid type

- 1, 2. *Retiophyllia fenestrata* (Reuss, 1854). (Rhaetian, Northern Alps), GBA 1982/12/26; transverse sections,  $\times 30$  and  $\times 110$ ; 1. Zigzag mid-septal line; 2. Feebly differentiated small trabeculae visible at the mid-septal line.
3. *Retiophyllia paraclathrata* Roniewicz, 1974. (Rhaetian, Northern Alps), NHM 1982/56/7; transverse section with completely recrystallized trabeculae,  $\times 120$ .
- 4, 5. *Retiophyllia* sp. (Rhaetian, Northern Alps), NHM 1982/56/14; transverse sections,  $\times 185$ ; 4. Trabeculae recrystallized; 5. Trabeculae well preserved of relatively large dimensions; thick fibers palisaded, subperpendicular to the mid-septal line.
6. *Flabellum zejszneri* Rózkowska, 1932. (Miocene, Poland), ZPAL H.I/345; scanning electron micrograph; longitudinal broken section at the median plane of septum showing a series of trabeculae,  $\times 600$ .



subperpendicularly from it (pl. 2, figs. 5, 6; pl. 5, figs. 1, 4; pl. 6, fig. 2; pl. 7, figs. 1, 2). The middle of the septum and one of the sides are visible in the longitudinal etched section approaching a mid-septal plane (pl. 5, fig. 1). The section is oblique: a longitudinal outline of trabeculae is visible on the left upper corner and a tangential section through the side of septum, with rows of distinctly convergent fascicles of large fibers at the bottom right corner of the micrograph.

The microstructure of some Tertiary caryophylliids (e.g., the Eocene "*Placosmilia*" and "*Parasmilia*" that was described by Russo (1976)) exposes, in SEM micrographs, all features typical of the family (pl. 2, figs. 5, 6; pl. 3, figs. 1–8; pl. 4, figs. 1–6). In "*Parasmilia*," well expressed lateral fascicles of fibers can be observed (pl. 4, figs. 2, 3).

The septal structure in the Triassic *Distichophyllia* and *Margarosmilia* (Cuif, 1974, text-figs. 5a, b, 8 and 11) is similar to the above presented. In the Triassic corals, the skeletal structure is, however, more complex, since the fibers of lateral fascicles are concentrated around the axis, thus forming short, thick, lateral trabeculae.

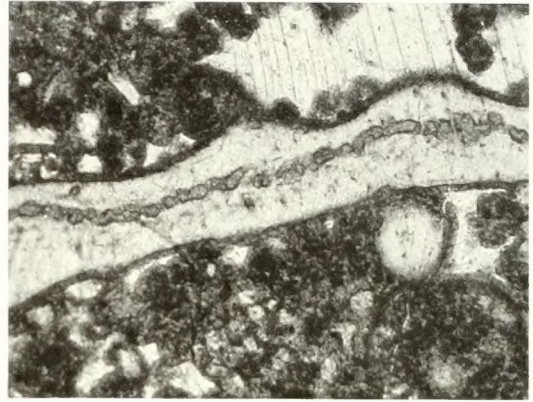
While etching the surface of the Recent corals for SEM observation, the trabecular axes are subject to a strong corrosion, much stronger than in any other skeletal part. Besides, on the etched surface an incipient fissure between the axes of trabeculae, running along the mid-septal line can be visible (compare Sorauf and Podoff, 1977, pl. 1, fig. 8 and Sorauf and Jell, 1977, pl. 4, fig. 2). These changes simulate the external effects of an early diagenesis. Similar stages of diagenesis are seen in the Triassic distichophylliids, where the well preserved thick-fibrous parts flank the generally destroyed trabecular midline (Pl. 1, figs. 1–4).

#### Family Flabellidae

I have traced the septal structure of *Flabellum zejszneri* Rózkowska, 1932 from the Miocene. The midline is straight or zigzag. Very thin trabeculae (20–25  $\mu$ ) arranged in a series (Pl. 1, fig. 6) are visible in the plane of natural splitting in two of the septa. The mid-septal plane is marked on the corallite surface as a furrow. Both sides of the septum deflect from each other peripherally and pass to a wall. Thus, the radial elements are here devoid of costal part, and strong external "costae" represent, in reality, peripheral parts of septa protruding outward. Trabeculae are distributed in series, not in a fountain-like pattern characteristic of distichophylliids.

#### CONCLUSIONS

Corals of the family Caryophylliidae, as well as Flabellidae have septa with small trabeculae displaying distichophylliid microstructural pattern. Thus, caryophylliids, the only post-Triassic corals with this type



Text-figure 2.—Caryophylliid indet. Upper Albian, Kominy Doudove, Tatra Mts. ZPAL, H.II/1. Vestiges of trabeculae at the median septal zone,  $\times 25$ .

of microstructure, can be considered to be a derivative group of distichophylliids. From strongly differentiated Rhaetian distichophylliids, the crisis at the Triassic/Jurassic boundary was survived probably by the few species which could live under conditions departing from optimum and capable of adopting a deep-water mode of life. Their considerable ability to radiate, which is observed on the generic and specific level (see Cuif, 1974, 1977), as well as their rather large bathymetric range within the shallow-water zone, would support such a hypothesis.

New conditions under which the pre-caryophylliids had to live stimulated the formation of new patterns of corallite structure with an unchanged, inherited pattern of microstructure. Reduction of dissepiments in some groups, development of pali, and, in the flabellids, a new structure of septa, distinguish the Caryophylliina from their distichophylliid ancestors.

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## MICROSTRUCTURAL CHANGES IN THE MICRABACIIDAE AND THEIR ECOLOGIC AND TAXONOMIC IMPLICATIONS

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## ABSTRACT

Microstructural changes in the septa of Cretaceous to Recent micrabaciid corals coincide with their migration from shallow to deep water. Corallum characters and septal construction of fifty-six specimens selected from the different genera of Micrabaciidae were examined, measured, and compared using a compound microscope and scanning electron microscopy (SEM). The microstructural changes thus observed indicate a tendency toward a lightening of the skeleton with increase in water depth through septal perforations and a reduction of trabecular elements. The resulting structural changes are significant enough to offer a valid basis for a revision of the family.

## INTRODUCTION

The Micrabaciidae is a family of small, solitary, ahermatypic corals. The major evolutionary trend of the family from the Cretaceous to the Recent is an adaptation to life at increasing depths of water. As the micrabaciids migrated from the shallow waters of the continental shelves and marginal seas of Europe and North America to the deep waters of the Atlantic, Pacific and Indian Oceans, the decreasing availability of calcium carbonate with depth caused a number of significant changes in their coralla.

This paper is concerned with the microstructural changes in the septum of the micrabaciids that resulted in a progressive modification of the corallum from the very small, compact, button-like skeleton of the Cretaceous coral to the open, delicate, nearly flat skeleton of the deep water coral in today's seas. Many of the corallum modifications are expressed externally by spines, septal perforations, or openness of the skeleton, and have been deemed sufficient for generalizations about generic characters and adaptive trends of the family. In some cases, however, such external expressions suggest generic identities that are not borne out by more detailed study. This present study, therefore, investigated the underlying microstructural changes in the septum that are manifested in these architectural modifications on the assumption that in the microstructure of the septum lay the key to a more definitive generic classification and to a greater insight into means by which the observed adaptive changes occurred.

Both Steinmann (1908) and Squires (1967) noted progressive changes in the genera of the Micrabaciidae. Steinmann observed that the porosity of the septum in *Stephanophyllia*—at that time, a very broadly defined micrabaciid genus—increased with succeeding geologic ages. Squires noted a trend toward lightening the skeleton that included a decrease in weight of the corallum and a reduction in number of septal trabec-

ulae. Neither, however, looked at the septum in thin section to see how these changes had been effected.

For this study, I obtained 56 specimens of the five genera of the Micrabaciidae—*Micrabacia*, *Stephanophyllia*, new genus A, *Letepsammia*, and *Leptopenus*—and examined them in whole specimen and thin section using a compound microscope and the SEM. My observations of these specimens revealed that the major changes in the coralla of succeeding genera, adapted to life at increasing depths of water, occurred in the number and spacing of trabeculae, frequency and distribution of synapticulae, and presence or absence of septal perforations and deltas. Such changes proved to be valid for identifying discrete clusters of specimens, and provided a basis for revision of the family.

## ACKNOWLEDGMENTS

The materials on which this investigation was based were made available to me by A. G. Coates of George Washington University and Stephen Cairns of the Smithsonian Institution. I owe them a special debt of gratitude for their unceasing willingness to locate and supply needed specimens as the scope of this study inevitably broadened. In addition I am particularly indebted to Dr. Coates for originally suggesting that I undertake this project, and for being a constant source of advice and assistance.

For assistance in the more technical aspects of this study, I wish to thank Donald A. Dean of the Smithsonian Institution and William C. Pinckney, Jr. of the U.S. Geological Survey for their help in thin-sectioning my specimens; and Diana Lipscomb and Thomas Waters for their help with the SEM.

Special thanks are also due to my husband, Frank A. Owens, not only for his constant encouragement throughout this project, but also for his assistance in critically reviewing and proofreading my manuscript.

### MICROSTRUCTURE OF THE SEPTUM

Microstructurally, the septum in micrabaciid corals is composed of trabeculae—stacks of sclerodermites which form the centers of calcification—arranged in a fan-like series radiating from a point near the base of the columella. Secondary trabecular elements consisting of the ends of individual sclerodermites project from the trabeculae. When these secondary elements merge with those of neighboring trabeculae, they form various patterns in the interarea between adjacent trabeculae; if they do not merge, the interarea is undifferentiated. When the secondary elements project at right angles to the plane of the septum, they either form tiny, teeth-like structures called vepreculae (Jell, 1974) along the flanks of the septum, or merge with similar elements from an adjacent septum to form synapticulae.

In some genera the projecting trabecular elements form porous triangular sheets which join the upper, proximal margins of secondary and tertiary septa. Such consequent structures are called deltas.

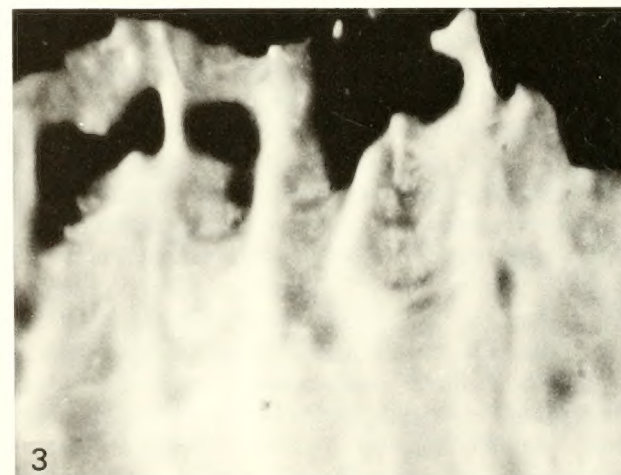
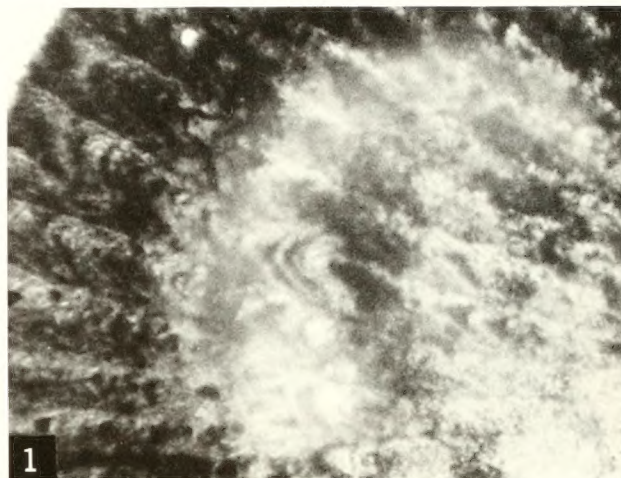
The interarea between trabeculae in a septum may be solidly filled with secondary elements, thereby producing an imperforate septum, or may be marked with regularly or irregularly spaced pores, thus forming a perforate septum. The septa in micrabaciid corals range from imperforate with numerous synapticulae and vepreculae to perforate with restricted synapticulae and no vepreculae.

### MICROSTRUCTURAL CHANGES IN THE MICRABACIIDAE

*Micrabacia*, the Cretaceous micrabaciid, is the oldest and shallowest-dwelling genus of the family, found only in association with fauna and sediments typical of water depths of less than 100 m. Its members are the smallest of the family, averaging less than 10 mm in diameter. Its corallum is small, compact, and cupoloid, with septa that rise steeply from a flattened basal wall, giving it the highest height : diameter ratio, exclusive of spines, of all the micrabaciids.

Microstructurally, the septum in *Micrabacia* is composed of 20–30 closely spaced trabeculae in a highly organized fan (Fig. 1). The secondary trabecular elements merge between trabeculae to form tight little chevron folds which completely fill the interareas. The septum therefore is imperforate.

Other secondary elements which diverge from the growth direction of the trabeculae project from the plane of the septum as numerous evenly-spaced synapticulae and vepreculae that are arranged radially along the full expanse of the septum. Both deltas and septal perforations are absent.

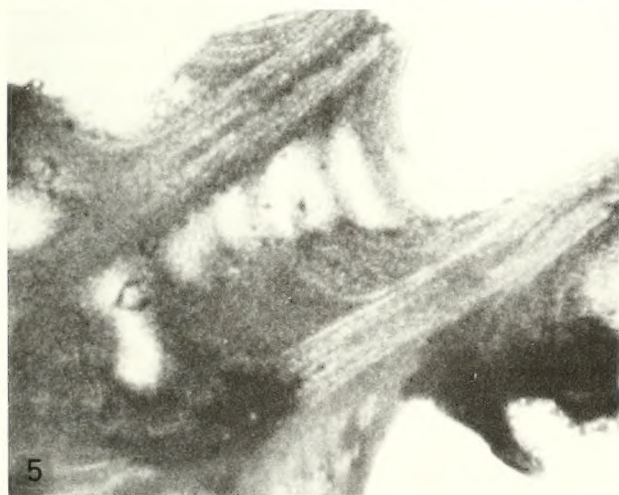
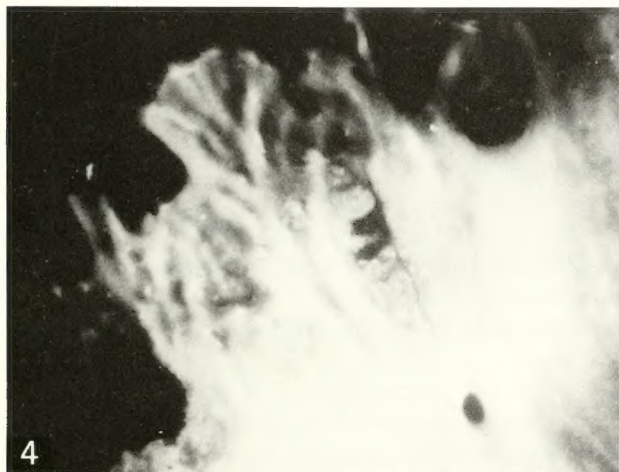


Figures 1–3.—1. *Micrabacia* sp. Thin section of septum showing close fan of trabeculae with chevrons in the interarea ( $\times 22$ ); 2. *Stephanophyllia* sp. Thin section of septum showing widely spaced trabeculae with undifferentiated interareas ( $\times 15$ ); 3. New genus A sp. Thin section of septum under reflected light showing thin, wavy trabeculae with arcuate pattern in the interarea ( $\times 8$ ).

After the Cretaceous, no species of the Micrabaciidae has been recorded until the Upper Tertiary when *Stephanophyllia*, a Miocene to Recent micrabaciid, occurs. By then the microstructure of the septum has made significant changes: the fan system of trabeculae has become less tightly organized, and perforations have begun to develop in the interarea between adjacent trabeculae.

The corallum in *Stephanophyllia* is a little larger than that in *Micrabacia*, ranging from 8–20 mm, but it is still rather compact. The bathymetric range of this genus, however, extends from shallow waters of about 70 m to deep waters in excess of 700 m.

In thin section, the septum of *Stephanophyllia* is seen to be composed of 15–25 trabeculae in a more loosely arranged fan (Fig. 2). They are set farther apart, like stiffly splayed fingers, with undifferentiated interareas in which the ends of the secondary elements do



Figures 4, 5.—4. *Letepsammia* sp. Thin section of septum under reflected light showing ramifying trabeculae ( $\times 3$ ); 5. *Leptopenus* sp. Thin section of reduced septum showing widely spaced trabeculae projecting as spines (broken) ( $\times 35$ ).

not merge. Near the base of higher cycle septa, five or six well-formed pores are developed in the interarea between trabeculae, making these septa slightly perforate. Synapticulae and vepreculae are still present, but the synapticulae are now restricted to the base and distal margin of the septum. Deltas, composed of porous trabecular sheets, appear for the first time with this genus.

New genus A, slightly succeeds *Stephanophyllia* both in geologic age and bathymetric range. It is Pliocene to Recent, and has been collected at depths of 500–950 m. Because of its relative age and bathymetric range, I had anticipated it would show an increase in number of perforations in the septum. Instead, they are essentially imperforate. There are one or two pores in some septa, but they are random in distribution when they do occur, and are not consistently present in any cycle of septa.

The corallum is larger (25–35 mm) than in either of the previous two genera, and it is more open—that is, the septa, though still of the same thickness, are set farther apart, making the skeleton less compact. The calice, however, is still strongly convex.

In thin section, the trabecular structure is also more open (Fig. 3). There are about 20 trabeculae per septum, and they are thin, wavy, and more widely spaced. In one species, the secondary elements between trabeculae merge in an arcuate pattern; in the other, the interarea is undifferentiated. In both species vepreculae are abundant and alternate in position on either side of the septum. The deltas are well developed, and the synapticulae are restricted to the basal and distal portions of the septa.

*Letepsammia*, a Plio-Pleistocene to Recent coral, is the largest of the micrabaciids, with a corallum diameter of 30–40 mm. The corallum is discoidal and very open, with septal interspaces several times wider than the septa themselves. The septa are highly porous. Its bathymetric range is slightly less than 100 to nearly 1000 m.

Microstructurally, the septum in *Letepsammia* is composed of 10–20 very thin, wiry, and widely spaced trabeculae which ramify at the septal margins (Fig. 4). The perforations, though numerous, are irregular in size, shape, and distribution. Some pores appear to cut across trabeculae; others sometimes appear as tiny pinholes in locally thinned areas of the septum, suggesting that pores develop through localized reabsorption of the calcareous material. The deltas are highly porous and well developed, and the synapticulae are again located basally and distally.

*Leptopenus*, an exclusively Recent genus of the family, is the deepest dwelling of the micrabaciids and second deepest of all solitary corals, having a bathy-

metric range of 2000 to somewhat less than 4500 m. Its corallum is small (less than 30 mm), spinose, and discoidal. The septa are greatly reduced, consisting mainly of spines.

In thin section, the trabeculae are seen to be reduced in number to 4–9 per septum, each projecting beyond the basal remnants of septa as long, recurved spines (Fig. 5). A reduction is also evident in secondary elements: synapticalae and vepreculae are absent, and the ends of only the lowermost sclerodermites extend in a loose arcuate pattern between adjacent trabeculae to form an imperforate septum. The deltas are similarly reduced to very small, imperforate sheets of only a few trabecular elements.

#### ECOLOGIC AND TAXONOMIC IMPLICATIONS

From my observations I conclude that microstructurally the Micrabaciidae have evolved an increasingly lighter, more open corallum through progressive ages and at increasing depths by: (1) a loosening of the fan system through thinner, less rigid, and more widely spaced trabeculae; (2) a reduction in number of trabeculae per septum; (3) a less densely packed interarea

between trabeculae; (4) a restriction in abundance and growth directions of secondary elements; and (5) an increase in porosity or decrease in skeletal material of the septum.

My study also reveals a relationship between delta formation and distribution of synapticalae. When deltas are absent, synapticalae occur in concentric rows along the full expanse of the septum; when deltas are present, synapticalae occur only basally and distally. I conclude that deltas and synapticalae serve the same purpose: a strengthening of the septa. By replacing synapticalae with deltas, there is a reduction in number of septal elements and thus in weight of the corallum without a loss of strength of the septa.

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SCLERACTINIAN FUNCTIONAL MORPHOLOGY: A KEY TO  
PALEOECOLOGICAL RECONSTRUCTION

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## ABSTRACT

Thirty live species of common genera from the Atlantic-Caribbean Province were subjected to behavioral experiments and also prepared by conventional paleontological methods and then related to their natural field occurrences. These species represent more than 90% of the live scleractinian populations of Bermuda and Florida. Comparisons with fossil counterparts are drawn from the Pleistocene of Florida, East Africa and Bahrain, the Triassic of Central Europe and the Jurassic of England. These data are synthesized in readily recognizable tabular form to aid field recognition. The resultant models have been verified in field reconnaissance mapping.

## INTRODUCTION

In recent years fossil corals have been studied fairly intensely, particularly as regards their taxonomy and paleobiogeography. At the same time much work has been done on the taxonomy and ecology of living Scleractinia, yet this has not translated into a commensurate amount of sound work on coral paleoecology. Partly this is due to a lack of researchers who are familiar with both living and fossil coral species. It is our contention that much useful paleoecological information is lost by not relating known behavioral and soft part anatomical patterns to skeletal types. These relationships can be used in functional morphological interpretations of fossil corals with corresponding morphologies.

Sound taxonomy is a fundamental prerequisite to any study of biogeography or ecology, whether living or fossil organisms are involved. Two major sources of confusion may cause living coral species not to be recognized in the fossil record. Firstly, taxonomic descriptions of fossil corals are frequently based on measurements and patterns taken from transverse and longitudinal sections. When living species are described three dimensional features of the corallum and surface architecture, particularly of the calice, are measured. It is extremely important that, where possible both sets of measurements are included in the species description, as is shown in Text-figure 1 for 10 common living Caribbean species.

A second reason for taxonomic confusion between fossil and Recent corals is the fact that surface microarchitecture, particularly of the skeleton of scleractinians, is prone to rapid and early diagenesis. Because of this, fossils that are preserved as three dimensional coralla extracted from sediment matrix, are often separated from their living counterparts taxonomically (Hubbard, 1972a; Crame, 1977) and hence biogeographically and ecologically.

In this paper we examine some living corals in such a manner as to demonstrate how function in fossil corals may be inferred from soft part/skeleton relations in living relatives, to allow easy comparison to fossil species and to reveal preservational biases in paleontological data due to artifacts of preservation and study technique.

## FUNCTIONAL MORPHOLOGY

The calice is the fundamental unit upon which functional morphological interpretations are based. The relationship of soft to hard parts in the calice is hard to determine directly because it is almost impossible to make thin sections of calices with soft parts in place but we have sectioned the skeleton at the level of the calice in species of corals whose behavior has already been monitored. We then infer the relationship of the polyp's anatomy to that of the underlying skeleton (Text-fig. 2). For example in *Diaseris* we can see that, in its contracted condition (Text-fig. 2A) septa are clearly evident, and that in a slightly expanded condition (Text-fig. 2B), each tentacle rests on the oral surface of a septum. We can thus infer for this coral that for each septum a tentacle is present in the polyp.

It can also be shown (Hubbard and Pocock, 1972) that the distentional potential of a polyp is about 400% and that this is related to the surface area of the calice. A rough estimate of the maximum tentacular length is thus possible from a study of calicular relief so that *e.g.*, *Agaricia* and *Pavona* bear only rudimentary tentacles and have short septa; *Cladocora*, *Montastrea*, *Galaxea*, *Diploria*, and *Coeloria* have relatively long tentacles when extended and fairly long exsert septa; and *Manicina* and *Mussa* have by far the longest tentacles and the most crudely dentate septal structure. However, the complex and structured responses of tentacles to various stimuli in some species, *e.g.*, *Porites*

(Hubbard, 1974a) are not apparently correlated with any particular skeletal structural patterns.

Laboratory experiments conducted over a one year period in an open circulating seawater aquarium show that drastic starvation can be detected through large scale skeletal malformation (Text-fig. 3A and 3B) and that lesser deprivation can be inferred from subtle red algal overgrowth (Text-fig. 3E). Also the amount of endolithic, fungal, algal and bacterial activity increases

in direct proportion to the hostility of the microcosm, a process which causes increasingly fuzzy outlines to the coral skeleton (Text-fig. 3). Thus further analysis of the endoliths and epibionts associated with the skeleton, which occur in that portion of the skeleton no longer covered by soft tissue, could add significantly to the interpretation of the paleoecology of corals (Hubbard and Swart, 1982).

Other attempts to infer anatomy and physiology from

	DIASERIS DISTORTA	EUSMILIA FASTIGIATA	MONTASTREA ANNULARIS	ACROPORA CERVICORIVIS	SIDERASTREA SIDERA	AGARICIA AGARICITES	PORITES PORITES	MANICENA AREOLATA	MUSSA ANGULOSA	DIPLORIA CLIVOSA
SURFACE VIEW OF CALICE										
CORALLITE IN TRANSVERSE SECTION										
CORALLITE IN LONGITUDINAL SECTION										
LATERAL LINKAGE OF CORALLITES	SOLITARY DISCOID	DENDROID or PHACELOID	PLOCOID	PLOCOID	CERIOID	CERIOID to MEANDROID	CERIOID	MEANDROID	MEANDROID	MEANDROID
SEPTA :										
- number	90-92	15-18 per cm.	24-26	12	50-60	36	12	15-20 per cm.	8 per cm.	30-40 cms
- arrangement	8 cycles	2 cycles	3 cycles	2 cycles	5 cycles	2 cycles	1 cycles	2 cycles	2 cycles	2 cycles
- ornament	finely dentate	smooth, exsert	dentate	dentate	finely dentate	finely dentate	dentate	dentate	dentate, exsert	dentate, exsert
- structure	imperforate (lower cycles) fenestrate (higher cycles)	imperforate	imperforate	imperforate	imperforate	imperforate	perforate	perforate	imperforate	imperforate
AXIAL STRUCTURE	none	weak parietal columella	parietal columella	none	small columella	small columella	tubercle 6 pali	large parietal columella	trabecular columella	parietal columella (continuous)
ANALOGUES :										
Recent -	<i>Fungia scutaria</i>	<i>Cladocora arbuscula</i> <i>Oculina diffusa</i>	<i>Favia solenastrea</i> <i>hyades</i> <i>Montastrea cavernosa</i>	<i>Acropora palmata</i>		<i>Agaricia fragilis</i> <i>Dichocoenia stokesii</i>	<i>Porites furcata</i> <i>P. divaricator</i> <i>P. astraeoides</i>		<i>Isophyllia sinuosa</i> <i>Isophyllastrea rigida</i>	<i>Diploria strigosa</i> <i>D. labyrinthis</i> <i>Colpophyllia natans</i>
Fossil - Jurassic (J)		<i>Thecosmilia</i> (J)			<i>Isastrea</i> (J)	<i>Thamnasteria</i> (J)	<i>Mesophyllia</i> (J)	<i>Montlivardia</i> (J)	<i>Thecosmilia</i> (J)	<i>Meandrina meandrites</i>
Oligocene (O)	<i>Leptomussa</i> (O) <i>Cricocyathus</i> (O)				<i>Thamnasteria</i> (O)					<i>Mycetophyllia lamarkiana</i>

Text-figure 1.—Illustrated key to the recognition of some common recent coral taxa and their fossil analogues as used in Bahrain (see Hubbard, in Doornkamp *et al.* (eds.), 1980) for mapping and facies reconstruction and equally applicable to the Triassic (Flügel, 1981), the Jurassic and the Oligocene (Frost, 1981) of Europe.

skeletons, such as the organization of muscle sheets (Hubbard and Pocock, 1972; Hubbard, 1973) and the presence of zooxanthellae (Swart, 1983) and skeletal accretion (Swart and Hubbard, 1982) have been by indirect means only.

#### PALEOECOLOGICAL RECONSTRUCTION

Fossil assemblages of reef corals rarely record accurately the full diversity of taxa which occurred with the assemblage in life. Taphonomic loss in reef corals can be traced to several causes. Just as species of coral survived for different lengths of time when subjected to various stresses imposed in the aquarium (Hubbard and Pocock, 1972; Hubbard, 1974b) so are the more sensitive taxa absent from the more stressful environments (Text-figs. 4, 5) on a living reef. This primary distributional pattern is then modified further by a variety of diagenetic or taphonomic factors, some of which can be detected in the surviving skeletons and others inferred by tracing the sedimentary history of dead coral on modern reefs.

Infestation by endolithic algae and epibionts can be shown to increase during transport of a coral from growth site to burial site (Hubbard and Swart, 1982; Hubbard, 1983). Many species do not survive transportation as long as others (Hubbard, 1976) so that fossil reef assemblages reflect not only primary patterns of spacial distribution but physical resistance. *Acropora*, which is highly sensitive to variation in water chemistry (Caribbean *Acropora* spp. died within hours of placement in an aquarium experiment) is neverthe-

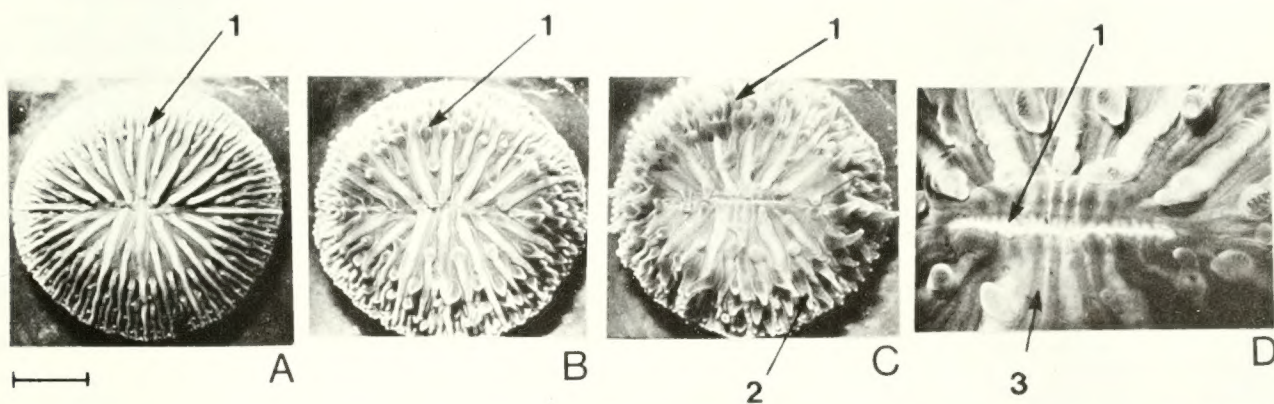
less highly resistant to abrasion and is readily fossilizable. *Porites*, on the other hand, is much more tolerant to changes in water chemistry, regenerates rapidly but is extremely fragile. Thus the abundance of these two species in a fossil assemblage can easily be the reverse of that in their living association. Faviids appear to be intermediate in both physiological tolerance and physical durability.

Field observations in the Pleistocene of the Caribbean, Florida and East Africa show the universal abundance and better preservation of the Acroporidae, the general abundance and poorer preservation of the Faviidae and the poor representation and highly altered condition of the Poritidae (for a detailed taxonomic analysis see Crame, 1981). Furthermore, grain size analysis of reef sediment shows that acroporids (and astrocoeniinids in general) dominate the rubble, faviids the coral sand and poritids the fine fractions. Vadose dissolution/cementation processes preferentially remove evidence therefore of faviids and poritids relative to astrocoeniinids (Hubbard, 1983).

#### CONCLUSIONS

Much useful data is currently being lost because of a lack of communication between paleontologists and biologists. This loss stems from four reasons:

1. Differences in technique result in corals being largely identified from transverse and longitudinal thin sections if they are fossilized but from three dimensional surface architecture if they are Recent.



Text-figure 2.—Serial photographs of *Diaseris* sp. to show the relationship of the tentacular units to the underlying eight cycles of septa in an oral view:

- A. The polyp is almost completely retracted to emphasize the position of the septa (1). Scale bar 10 mm long.
- B. Partially expanded polyp showing bulbous tentacular units (1) at the oral end of each septum and the mouth firmly closed in the center.
- C. Semi-distended polyp (approximately 75%), with extended tentacles (1) and nematocysts (2) on their surfaces and partially open mouth showing interlocking striped longitudinal muscle sheet tissue in the gullet.
- D. Close-up of the mouth in a semi-relaxed, expanded condition showing stomodeal musculature of both longitudinal (1) and circum-oral sheet muscle tissues; largely retracted oral tentacles (2) and traces of mesenteries appearing through the translucent body wall (3). These relationships can be compared to biological data on feeding (Fisk, 1981), tentacular reach (Bradbury and Young, 1981; Sheppard, 1981), and acrobatic mobility in *Diaseris* (Hubbard, 1972b)

2. Rapid and early diagenesis alters the surface three-dimensional architecture in fossil corals, further confusing the comparison of living with fossil species.

3. Soft part morphology, particularly features of the tentacles, as well as conditions relating to nutrition and microboring activity can in turn be related to different skeletal structures in living corals and hence inferred in fossil corals with the same skeletal types and geochemical signatures.

4. Differential disintegration rates of different higher taxa on modern coral reefs can be measured and used to interpret fossil reef assemblages. The more eurytopic taxa (poritids) are shown to disintegrate much more rapidly than do the more stenotopic acroporids with faviids occupying an intermediate position: the cause of this is of inherent architectural origin, but its rate can be enhanced by endolithic fungal and algal activity in adverse circumstances.

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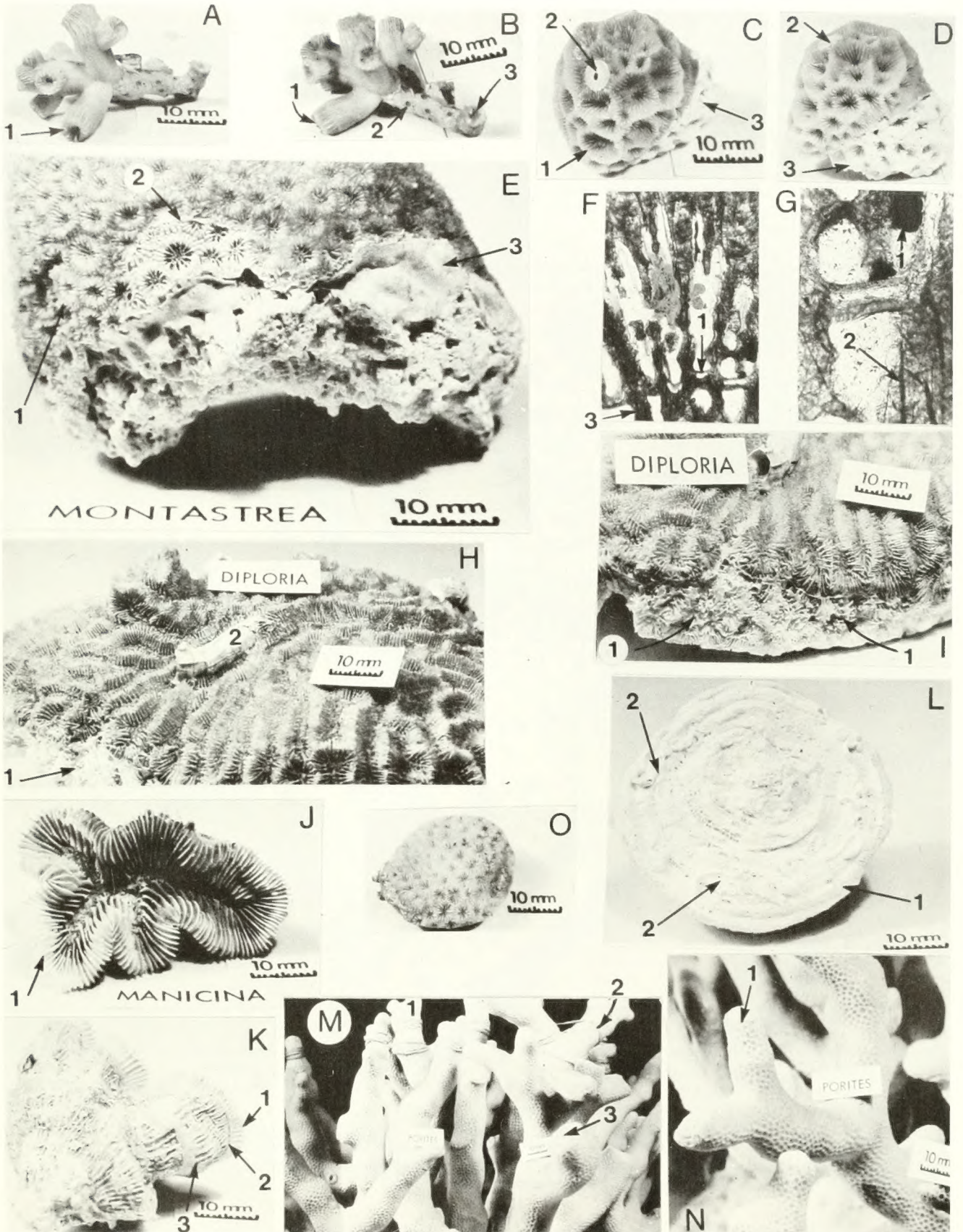
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Text-figure 3.—Examples of the relationship between paleoecologically detectable skeletal aberrations and physiological functions.

- A, B. Different views of the same specimen of *Cladocora* to illustrate, at A, inhibition of skeletal deposition by calical contraction (1) and at B, thecal malformity with associated exsert septa in a starved specimen which has a dead, bored (2) and red algal encrusted (3) base.
- C, D. Different views of the same specimen of *Agaricia agaricites*, which has at C, fine septa (1) and only rudimentary tentacles, with associated cirripede (C2, D2) and at D, well developed red algal overgrowth (C3, D3).
- E. *Montastrea annularis* (1) showing red algal encrustation in increasing thickness creeping up (2) from the base (3) formed during adverse conditions, notably oxygen starvation and oxygen depletion in the aquarium (see Hudson, 1981 for further details).
- F, G. Transverse section through calices of *Montastrea annularis* to show the close proximity of living polypal tissues (F1, G1) in their contracted state, to the endolithic borers (G2) infecting the septa (F3).
- H, I. Two views of *Diploria* to show the alteration of calical details (H1, I1) even in living materials shortly after vacation. It also features a polychaete worm (2) which has withstood adversity in the aquarium rather better than the coral whose initial skeletal overgrowth was subsequently inhibited (2).
- J, K. Oral and aboral views of *Manicina areolata*. The large septa with coarse ornament (J1, K1) pass from the calice seen in J to the aboral surface seen in K where their accretionary limit is marked by an edge zone (K2) below which there is no theca (K3).
- L. Aboral view of *Dichocoenia*, from a coarse carbonate sand substrate, showing unusually well developed growth rings (1) with encrusting polychaetes (2) and bryozoa.
- M, N. Views of *Porites furcata* which continued to grow healthily in the aquarium even when the tips (N1) were above the water level as marked by the rubber bands (M2). Specimens were also able to regenerate broken branches (M3).
- O. *Siderastrea* demonstrating the common feature of ball-like growth form which can be exhibited by most dislodged taxa including the most delicate agariciids.



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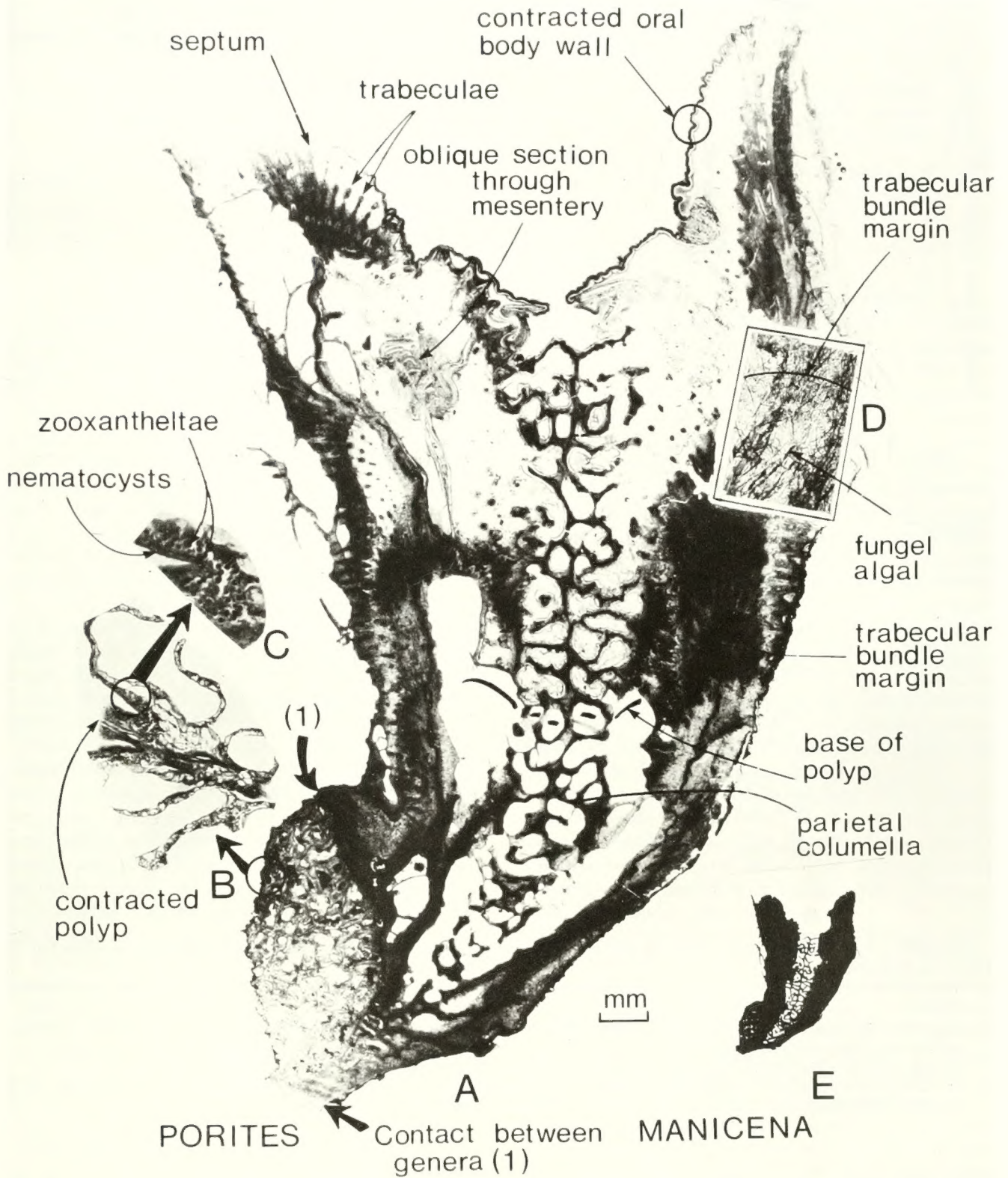
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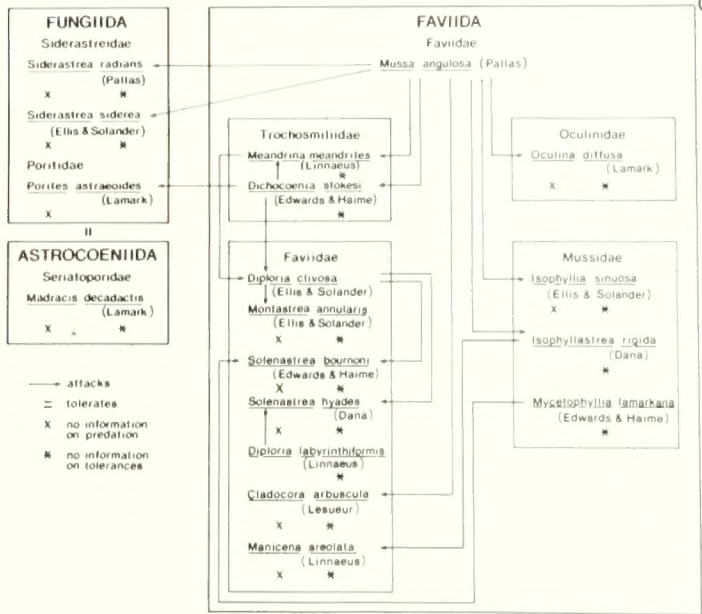
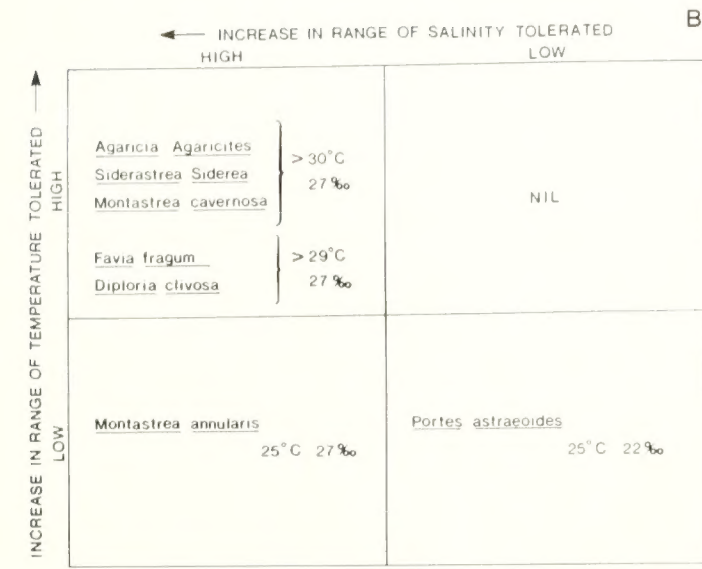
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Text-figure 4.—The relationship between the soft body, or hydrostatic skeleton and the hard calcareous skeleton, in longitudinal section through both solitary *Manicina areolata* and compound *Porites* sp. (lower left) to which the former is adhering.

- A. General view of the main anatomical features of *Manicina*, in which the polyp in life was contracted, to illustrate the state of the calical structures, and particularly the septal trabeculae. Bar scale is 50 mm long.  
 B. Close up of a semi-expanded, decalcified polyp of *Porites* to emphasize the features of the body wall.  
 C. Detail of B to show the nature and occurrence of nematocysts and symbiotic algae in the tissues.  
 D. Inset of a magnified trabecula showing increased alteration by fungal and algal boring during life in the aquarium.  
 E. Reduced inset of A in inked-in format used by some paleontologists.





**A**

<p>REEF FRAME BUILDERS FF MONTASTREA ANNULARIS</p>	<p>PROTECTED REEF ACCESSORIES PFF MONTASTREA CAVERNOSA OCULINA MANICENA EUSMILIA</p>	<p>SPECIALISTS FS ACROPORA CERVICORNIS SOLENASTREA</p>	<p>FPS GLADOCORA</p>
<p>SF NIL</p>	<p>SHELTERED AREAS SFF PORITES DIVARICATA PORITES FURCATA</p>	<p>SS DICHOCOENIA</p>	<p>SPS NIL</p>
<p>REEF FRAME ACCESSORIES PFF MYCETOPHYLLIA ISOPHYLLIA PORITES ASTRAEOIDES DIPLORIA LABYRINTHIFORMIS</p>	<p>HIGH ENERGY MARGINS PFPF DIPLORIA CLIVOSA</p>	<p>PFS NIL</p>	<p>PFP SIDERASTREA</p>

F = Fast P = Pause S = Slow

**D**

RANK CORRELATION COEFFICIENT DATA

	RANKING ACCORDING TO SEDIMENTATION	RANKING ACCORDING TO CURRENTS	RANKING ACCORDING TO CANIBALISM	RANKING ACCORDING TO SALINITY	RANKING ACCORDING TO TEMPERATURE
SUBORDER ASTROCOENIIDA					
FAMILY ACROPORIDAE					
Acropora cervicornis (LAMARCK)	7	9			
Acropora palmata (LAMARCK)	6				
FAMILY SERIATOPORIDAE					
Madracis decadactylus (LYMAN)			1.5		
SUBORDER FUNGIIDA					
FAMILY AGARICIDAE					
Agarcia agaricites (LINNAEUS)	5	10		2.8	5.6
Agarcia fragilis (DANA)	14.5				
FAMILY SIDERASTREIDAE					
Siderastrea siderea (ELLIS & SOLLANDER)	14.5	14.5	3.9	2.8	5.6
Siderastrea radians (PALLAS)			3.9		
FAMILY PORITIDAE					
Porites astreoides LAMARCK	16.8	6.6	1.5	1	1.5
Porites divaricata LESUEUR	16.8	18			
Porites furcata LAMARCK	16.8	16			
Porites porites (PALLAS)	16.8				
SUBORDER FAVIIDA					
FAMILY FAVIIDAE					
Diploria labyrinthiformis (LINNAEUS)	22	4	3.9		
Diploria clivosa (ELLIS & SOLLANDER)	16.8	1		2.8	3.5
Diploria strigosa (DANA)	10.75		14.6		
Colpophyllia natans (HOULTUYN)	23.75				
Manicena areolata (LINNAEUS)	21	5	3.9		
Cladocora arbuscula LESUEUR	4	11	3.9		
Solenastrea hyades (DANA)	2	6.6	3.9		
Solenastrea bournoni (EDWARDS & HAIME)			3.9		
Montastrea annularis (ELLIS & SOLLANDER)	10.75	2.5	3.9		1.5
Montastrea cavernosa (LINNAEUS)	10.75	2.5		2.8	5.6
Favia fragum (ESPER)				2.8	3.5
FAMILY OCULINIDAE					
Oculina diffusa LAMARCK	8	12	3.9		
FAMILY TROCHOSMITIDAE					
Meandrina meandrites (LINNAEUS)	1		3.9		
Dichocoenia stokesii EDWARDS & HAIME	9	14.5	17		
FAMILY MUSSIDAE					
Mussa angulosa (PALLAS)	10.75		18		
Isophyllastrea rigida (DANA)	23.75		14.6		
Mycetophyllia lamarckiana (DANA)	23.75	6.6	14.6		
Isophyllia sinuosa (ELLIS & SOLLANDER)	23.75	17	3.9		
SUBORDER CARYOPHYLLIDAE					
FAMILY CARYOPHYLLIDAE					
Eusmilia fastigiata (PALLAS)	3	13			

Text-figure 5.—Diagrams synthesizing various aspects of behavior in scleractinian polyps in laboratory experiments conducted at the University of Miami.

- A. Responses to variations in current velocities record rates of retraction on impact followed by relaxation on cessation (after Hubbard, 1974b).
- B. Toleration to variations in temperature and salinity (only the extreme end-members of all species tested are illustrated; for a detailed analysis see Marcus and Thorhaug, 1981).
- C. Pecking order records of digestive dominance by rival taxa following tentacular entanglement (see Lang, 1973).
- D. The ranking of experimental results using Spearman's Rank Correlation Coefficient does not yield significant correlation between any of the experiments performed on representatives of the total scleractinian population of Florida.



## SECTION 10

## Adaptation to Environment

## INTRODUCTION

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It has long been known that corals are capable of extreme intraspecific variation and that much of this variation can be attributed to adaptive responses to different environmental factors, such as illumination, hydrodynamics, sedimentation, and action of commensals or symbionts. Darwin was one of the first to notice this phenomenon but it was Quelch (1886) who first discussed these interrelationships in his monograph of the shallow-water corals collected by the *H. M. S. Challenger*. After spending over a year in the Cocos-Keeling Islands, Wood-Jones (1907) further elaborated on the effect of environment on growth form, concluding, rather discouragingly, that nothing was constant among the animals, not the colony form, the coenenchyme, or the calices. Needless to say, environmental adaptations have caused serious problems in the definition of coral species (Veron and Pichon, 1976; Zibrowius, this volume).

There are two classes of environmental adaptations: genetic (those that arise by mutation and are subsequently passed on to future generations by natural selection) and phenotypic or ecophenotypic (those that occur within one generation and are not part of the genome and thus not inherited). Laborel (1970) called this latter category an ecomorph and Wijsman-Best (1974) called it an ecotype. Genetic adaptation may lead to speciation, either by allopatric lineage splitting or by gradual transformation (phyletic speciation); phenotypic variation does not lead to speciation.

Each of the five papers in this section concerns an example of adaptation to environment; both genetic and phenotypic adaptations are included. The papers deal with rugosans, tabulates, and scleractinians from the Ordovician to the Recent, mostly from North America. They are presented in chronological order.

In the first paper Elias explains that most small conical solitary rugose corals could not survive after being overturned. In the Red River-Stony Mountain Province corals adapted to this situation by dilating their

septa and developing non-circular cross sections, both of which increased stability. On the other hand, *Strep-*telasma** of the Edgewood Province could survive a major attitudinal change by radical redirection of its growth axis (curvature). In both cases, because the adaptations were restricted to a few lineages in one province, Elias has interpreted them as genetic adaptations.

Conversely, Pandolfi assumes a purely phenotypic explanation for the differences between presumably the same species of massive tabulate corals of two different formations. In the Windom Shale the corals are mounded, presumably to shed sediment more efficiently in this environment of high turbidity and low light, whereas the corals of the Centerfield Limestone are sheet-like, which allows for a more efficient acquisition of nutrients in an environment of low sedimentation. Because these conclusions are just the opposite of what one would expect of a massive hermatypic coral, at least with regard to illumination, Pandolfi suggests that these corals did not have symbiotic algae.

The third paper, by Sutherland, describes unusually large coralla of *Chaetetes*, from the Marble Falls Limestone of central Texas. The size and shape of these colonies is probably the result of an increased influx of carbonate mud and therefore probably represents a purely phenotypic adaptive change.

Constantz compares the mechanical strength of two Recent species of *Acropora*, concluding that the shallower-water species, *A. palmata*, resists shear and torsion stress better than the deeper-water *A. cervicornis*. On the other hand, because the latter species fragments more easily, it is probably more efficient at asexual reproduction. Constantz makes an interesting analogy between the axial corallites of *A. palmata* and the structure of some aircraft tubular laminates, both of which have considerably higher shear and torsional strengths than the summed strength of their component tubes (*i.e.*, tubes or corallites) in isolation. This is clearly a genetic adaptation to hydraulic stress.

Page, Perrin, and Rosen (abstract only) indicate that symbiotic solitary scleractinia (hermatypes) are usually larger than non-symbiotic solitary (ahermatypes) and suggest that this relationship might be used as an indicator of fossil zooxanthellates and thus of shallow, warm-water environments.

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PALEOBIOLOGY OF SOLITARY RUGOSE CORALS,  
LATE ORDOVICIAN OF NORTH AMERICA

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ABSTRACT

Most North American Late Ordovician solitary rugose corals behaved as unattached objects on soft substrates soon after the larvae became fixed by their cardinal sides to grains of sediment. Straight corals lived in upright positions, whereas curved forms were oriented with their concave sides up. Curvature likely resulted from inclination into or away from currents. Corals in the Red River–Stony Mountain and Richmond Provinces were unable to grow upward after being overturned, and such events probably killed them. This inability was compensated for by improved stability resulting from septal dilation and, in the Red River–Stony Mountain Province, the development of coralla with noncircular cross sections. Dominant species in the Edgewood Province were able to grow upward after being overturned, and had unusually high growth rates. Rejuvenescence in response to random and periodic events was especially common in *Streptelasma* and *Paliphyllum*. Asexual development of offsets is known only in these genera.

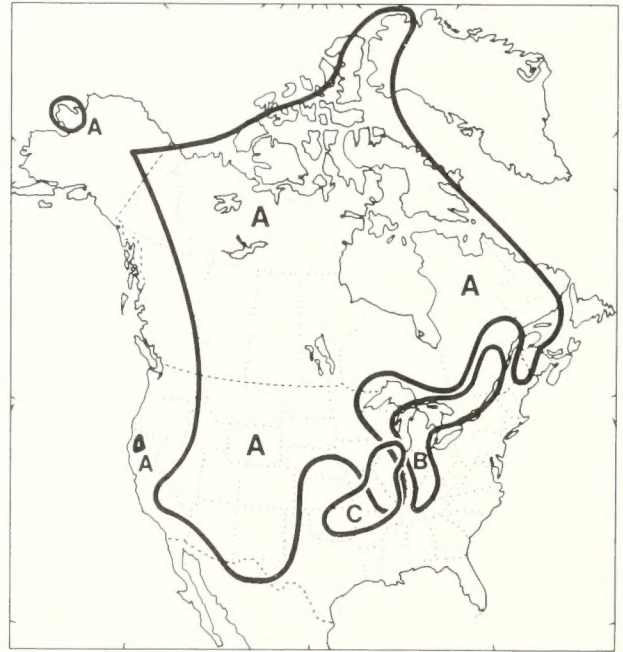
INTRODUCTION

This paper presents a synthesis of what is known about four aspects of the paleobiology of North American Late Ordovician solitary rugose corals. It is based on previous studies, plus new data and interpretations. The topics to be discussed are (1) orientation and growth, (2) the problem of instability, (3) records of events and growth rates, and (4) reproduction. Unless otherwise indicated, systematic treatments of rugosan taxa referred to herein are provided by Elias (1981, 1982a, 1983), Elias and Potter (in press), and Nelson (1963, 1981). Because the significance of several important observations is apparent only when considered in a paleobiogeographic framework, an introduction is provided in Text-figure 1.

ORIENTATION AND GROWTH

Few species of North American Late Ordovician solitary Rugosa were epizoic and attached throughout ontogeny. The only well known example of such a coral is *Streptelasma divaricans*, which was not substrate specific (Elias, 1982a, p. 23). The orientation of *S. divaricans* suggests a preference for elevated positions in areas suitable for feeding. The gregarious habit of this species, often resulting in pseudocolonies, was probably due to selection of favorable attachment sites by more than one larva (Elias, 1982a, p. 25). *Neotryplasma* sp. (undescribed) from the Second Value Dolomite at El Paso, Texas, was host specific. The larvae attached to dead portions on the upper surface of living colonies of the coral *Nyctopora mutabilis*.

Attachment structures are unknown or rare and small in most species. These corals must have behaved as unattached objects soon after skeletal secretion began.



Text-figure 1.—Paleobiogeography of Late Ordovician solitary Rugosa in North America. A, Red River–Stony Mountain Province of Edenian to Gamachian age included vast interior region characterized by carbonate sedimentation in somewhat restricted seas, plus continental margin with open, normal marine environments (Elias, 1981, pp. 2, 8, 10; 1982a, pp. 48, 49; 1983, pp. 927–931; Elias and Potter, in press). Isolated areas to west are Cordilleran terranes with possible Red River–Stony Mountain assemblages. B, Richmond Province of Richmondian age corresponded to carbonate platform bordering epicontinental sea that received clastic sediments from deltaic complex to east (Elias, 1982a, pp. 49–51). C, Edgewood Province coincided with Gamachian transgression that introduced open, high energy environments to continental interior (Elias, 1982a, pp. 51, 52).

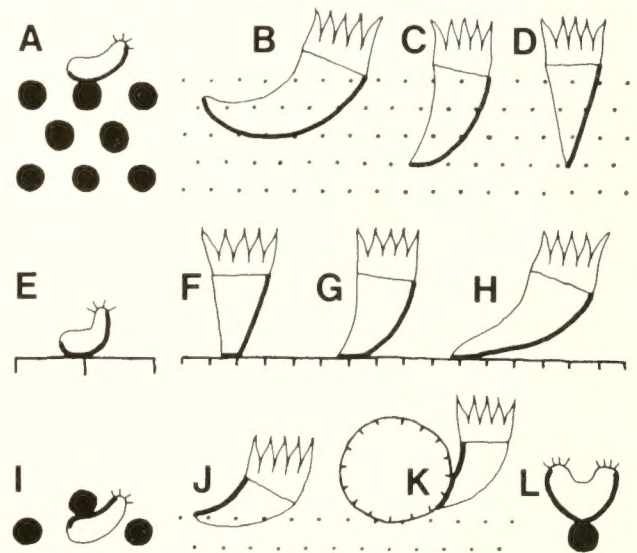
Their orientation during life is reconstructed using the distribution and abundance of borings, epizoans, and bioclastic material incorporated into outer walls (Elias, 1980, pp. 275, 276, fig. 5; 1981, pp. 5, 6; 1982b, pp. 1587, 1588, fig. 5a–d). Straight corals were oriented upright (Text-fig. 2D). Polyps producing them probably inhabited low energy environments in which their oral surfaces remained horizontal and the coralla slowly sank vertically into the sediment as weight increased during ontogeny (Elias, 1982a, p. 14). Curved corals lay with their concave sides facing upward and at least partly exposed above the substrate (Text-fig. 2B, C). Planes of bilateral symmetry were vertical. Curvature apparently resulted from redirection of growth axes in order to bring oral surfaces into horizontal orientations from inclined positions. Inclination is thought to have been related primarily to currents. A positive correlation between an increase in the degree of curvature and current energy is suggested by the observation that strongly curved coralla are generally more highly abraded than slightly curved to straight specimens in the same unit (Elias, 1981, pp. 5, 6). Curvature could have resulted if polyps were inclined into or away from currents. The observation that convex sides are often more abraded than concave sides (Elias, 1981, p. 5) may be used to support the conclusion that they faced into currents. However, although abrasion by shifting sediment probably began while the animals were alive, most seems to have occurred during post-mortem transportation (Elias, 1982b, p. 1590).

Attachment structures are virtually always located on the cardinal sides of coralla (Elias, 1981, p. 5; 1982a, pp. 53, 74, 78, 79; 1982b, p. 1588). It is concluded that larvae became attached to the substrate with their cardinal sides, and that oral surfaces were directed upward during subsequent growth. If larvae settled on the upper sides of objects, straight to curved coralla with convex cardinal sides would result (Text-fig. 2A–H). The only taxon having a concave cardinal side is *Bighornia*. Spoon-shaped depressions on the cardinal sides of some specimens have been interpreted as attachment sites, and their shape suggests that the substrate was a smooth, curved surface such as a cephalopod shell (Elias, 1981, p. 5, pl. 10, figs. 1, 2; 1982a, p. 80, pl. 14, figs. 19, 23, pl. 15, fig. 7; 1982b, p. 1588; 1983, p. 950, fig. 16a, b, h). If larvae fixed themselves to the undersides of objects, perhaps for protection, upward growth would result in concave cardinal sides (Text-fig. 2I–K). This ability was confined to a single genus, suggesting genetic control.

#### THE PROBLEM OF INSTABILITY

Coralla representing the vast majority of unattached species in the Red River–Stony Mountain and Rich-

mond Provinces are characterized by planar cardinal-counter surfaces of bilateral symmetry and straight to smoothly curved growth axes, indicating that they remained in stable positions throughout life (Elias, 1981, p. 6; 1982b, p. 1588). Slight bends in the cardinal-counter surfaces and (or) axes of a small number of specimens presumably developed when the polyps re-oriented their oral surfaces and directions of growth after being tilted (Elias, 1982b, p. 1588, fig. 4c). The absence of high-angle bends, despite the fact that most of the corals were oriented sideways at the time of burial (Elias, 1981, p. 5; 1982a, pp. 13, 28, 30, 31; 1982b, p. 1592), suggests that the polyps could not redirect their growth axes after being overturned. Such an event may have killed these organisms (Elias, 1981, p. 6; 1982b, pp. 1588, 1589). Irregularities in cardinal-counter surfaces and axes are more common and more pronounced in species of *Streptelasma* from these two provinces (Elias, 1982a, pl. 3, figs. 17, 18, pl. 5, fig. 4) and in *Paliphyllum* from the Red River–Stony Moun-



Text-figure 2.—Growth orientation of solitary Rugosa, cardinal side designated by heavy line. A–D on soft substrate: A, attachment of larva to upper side of grain and inclination of oral surface (shown with tentacles) into or away from strong current; B, resulting coral; C, D, corals in weak current and still water, respectively. E–H on hard substrate: E, attachment of larva and horizontal orientation of oral surface in still water; F, resulting coral; G, H, corals in weak current and strong current, respectively. I–K, development of concave cardinal side: I, attachment of larva to lower side of grain and inclination of oral surface into or away from current; J, resulting coral on soft substrate; K, coral attached to lower side of cephalopod shell. L, Siamese twins or twins resulting from aberrant development of oral surfaces at both poles of larva.

tain Province (Nelson, 1963, pl. 13, fig. 12; Elias, 1982a, pl. 15, fig. 12), but again high-angle bends have not been observed. *Streptelasma* is the dominant genus in the Edgewood Province. Irregularities are not uncommon in the most widespread species, *S. subregulare*, and in *Streptelasma* sp. (undescribed) from the Keel Formation of Oklahoma. Several specimens of each have right-angle bends. These are the only North American Late Ordovician taxa presently known that could grow upward after being fully overturned. The ability to survive major attitudinal changes during life by redirection of the growth axis must have been advantageous. It was restricted to a few genera and was well developed in only one province, suggesting genetic control.

Most species in the Red River–Stony Mountain and Richmond Provinces have dilated septa. Exceptions include representatives of *Streptelasma* and *Paliphyllum*. Dilation is especially pronounced in early ontogenetic stages, and in some taxa is commonly greatest on the convex side (Elias, 1981, p. 6; 1982a, p. 70). Thickened septa would have increased the weight of these corals, particularly in apical regions and on the sides that faced down during life, resulting in greater stability and decreasing the likelihood of being overturned. This would have compensated for the inability of the polyps to redirect their growth axes after such an event. Evolutionary trends in *Grewingkia*, *Lobocorallium*, and *Helicelasma* involved increases in the degree of dilation throughout ontogeny, suggesting that it was advantageous (Elias, 1981, p. 8; 1983, p. 932).

Solitary rugose corals are generally circular in cross section. Several taxa characteristic of the Red River–Stony Mountain Province are conspicuous exceptions (for terminology see Elias, 1981, p. 3). *Grewingkia* includes species that are triangulate and trilobate. *Deiracorallium* is compressed, and triangulate to slightly trilobate. Trilobation is pronounced in *Lobocorallium*. *Bighornia* is generally subcalceoloid, being depressed with an angulate concave side and flattened convex side. Most of these corals were curved and unattached. Their external forms would have provided greater stability as they lay in the sediment, and made overturning less likely than among corals with circular cross sections (Elias, 1981, p. 6, fig. 4; 1982b, p. 1588, fig. 5a–d). This would have compensated for the inability of these polyps to redirect their growth axes after such an event. That it was advantageous is suggested by the evolutionary lineage linking *Grewingkia* and *Lobocorallium*, which involved an increase in the degree of trilobation (Nelson, 1963, p. 34; 1981, pp. 19, 20, 39; Elias, 1981, p. 6; 1983, p. 932). The ability of polyps to form coralla with noncircular cross sections is thought

to have been genetically controlled because it was restricted to a few lineages in one province.

#### RECORDS OF EVENTS AND GROWTH RATES

Progressive constriction of calice rims has been observed at the tops of some coralla (Elias, 1982b, p. 1589). It suggests that adverse conditions such as disease or unfavorable environment eventually resulted in death of the polyps. Constrictions at irregular intervals followed by rejuvenations probably reflect less severe periods of stress with subsequent recovery. In one example, such a constriction coincided with tilting of the coral, followed by redirected upward growth and a return to normal size (Elias, 1982b, fig. 4c).

Prominent constrictions at apparently regularly spaced intervals have been recognized in portions of a small percentage of specimens representing three species, as follows: *Streptelasma* sp. (undescribed) from the Keel Formation of Oklahoma, 1 specimen, 6 consecutive intervals between regularly spaced constrictions, 6 to 7 mm between constrictions (average 6.8 mm); *S. affine*, 4 specimens, total of 21 intervals in consecutive series of 3 to 8 per corallum, 8 to 13 mm between constrictions (average 10.3 mm) (Elias, 1982a, pp. 46, 59, pl. 5, fig. 9); *Paliphyllum ellisense*, 5 specimens, total of 14 intervals in consecutive series of 2 to 4 per corallum, 7 to 11 mm between constrictions (average 8.1 mm) (Elias, 1982a, pp. 46, 47, 82). In another specimen of *P. ellisense* the regularly spaced constrictions are closer together, as follows: 7 consecutive intervals, 3 to 5 mm between constrictions (average 4.1 mm) (Elias, 1982a, pl. 15, fig. 20). During parts of their ontogenies, the polyps secreting these coralla responded to periodic biological or environmental events by constrictions and subsequent rejuvenations. In general, however, prominent constrictions in these species, in *S. subregulare* (Elias, 1982a, pl. 4, figs. 14, 15), and in *P. stummi* (Nelson, 1963, pl. 13, figs. 7, 12) are irregularly spaced, indicating that events occurred at random intervals or that growth rates between periodic events were not uniform. Polyps of *Streptelasma* and *Paliphyllum* may have been more sensitive to biological or environmental events than other taxa, or inhabited areas where events occurred that caused rejuvenescence. These polyps also had the ability to make significant adjustments in the direction of growth, as described in the previous section.

Periodicity was recorded internally by five zones of more closely spaced and dilated tabulae and dissepiments in a specimen of *Paliphyllum ellisense* (Elias, 1982a, pl. 15, fig. 18). The interval between zones varies from 4.3 to 5.0 mm (average 4.7 mm). This periodicity is not apparent externally, but the spacing is

similar to that of constrictions on one coral reported above. In a specimen of *Lobocorallium trilobatum vaurealense*, three zones of dilated tabulae spaced 10 to 12 mm apart are situated immediately above layers of sediment trapped in the corallum (Elias, 1982a, pl. 13, fig. 2). The base of the calice is 10 mm above such a layer, suggesting that the polyp died during a periodic influx of sediment. Periodicity with an average spacing of 10.7 mm recorded within this corallum is not reflected externally (Elias, 1982a, pl. 13, fig. 1s).

Fine growth ridges are seldom preserved on coralla from the Red River–Stony Mountain and Richmond Provinces. They were removed by abrasion primarily during post-mortem transportation (for examples see Elias, 1981, p. 5; 1982b, pp. 1589, 1590). The degree of abrasion was related to the duration of exposure before final burial, and therefore to sedimentation rate (Elias, 1982b, pp. 1590–1592). Wells (1970, p. 9) reported about 412 days per year based on a single specimen from Ohio. In the Edgewood Province, species of *Streptelasma* often have well preserved growth ridges, indicating rapid burial (Elias, 1982a, p. 39, pl. 4, figs. 11, 19). On three specimens of *Streptelasma* sp. (undescribed) from the Keel Formation of Oklahoma, a total of 378 ridges counted in 8 measured intervals have an overall average frequency of 7.68 per mm (averages for individual intervals range from 6.11 to 12.91 ridges per mm). This value is low compared with the average of 20 per mm that is commonly cited for corals in general, and the range of 12 to 60 per mm for specimens examined by Wells (1970, p. 5). It is concluded that this species had an unusually high growth rate. If the ridges represent daily periodicity and if one was secreted every day, an overall average growth of about 53 mm per year is calculated, using a figure of 405 days per year in the latest Ordovician (Wells, 1970, fig. 5). Unfortunately, monthly or annual bands cannot be recognized on these coralla. An average spacing of 6.8 mm between periodic constrictions in the specimen of *Streptelasma* sp. reported previously (which unfortunately has poorly preserved growth ridges) does not correspond with monthly or annual intervals that would be expected using the daily growth rate determined from these individuals.

Coralla of *Streptelasma* sp. (undescribed) from the Keel Formation of Oklahoma are very long and have slender ceratoid to cylindrical forms. Their walls, septa, and tabulae are extremely thin. Major septa are short and tabulae are far apart. These specimens are similar to some ceratoid individuals of *S. subregulare*, which is the most widely distributed species in the Edgewood Province (see Elias, 1982a, pl. 4, figs. 14–18). Such morphologic features are thought to correlate

positively with the high growth rate demonstrated above. Rapid growth, as well as the previously discussed ability to redirect the axis following tilting or overturning, would have been advantageous to corals inhabiting environments where sedimentation rates and energy levels were high. These conditions are indicated by the oölitic and bioclastic grainstones, some of them cross-bedded, that comprise most stratigraphic sequences in the Edgewood Province (see Elias, 1982a, pp. 39, 40).

## REPRODUCTION

Reproduction among these solitary Rugosa must have been primarily sexual. Asexual development of offsets was rare. From a single corallum of *Streptelasma divaricans*, one offset developed by peripheral increase and one by lateral increase (Elias, 1982a, pp. 55, 56, fig. 26, pl. 2, fig. 11). Single offsets may have formed in two other specimens of this taxon (Elias, 1982a, p. 56, pl. 2, figs. 12, 13). Single intracalicular offsets produced by peripheral increase are present in two coralla representing a new species of *Streptelasma* from the eastern Klamath Mountains of California (Elias and Potter, in press, fig. 2e). Small offsets apparently formed by lateral increase have been observed on the sides of several specimens of *Streptelasma* sp. (undescribed) cf. *S. leemonense* from the Keel Formation of Oklahoma. In one corallum of *Paliphyllum ellisense*, seven offsets developed simultaneously by peripheral increase (Elias, 1982a, p. 83, pl. 15, figs. 21, 22s). It is noteworthy that evidence of asexual reproduction has been found only in the two genera having polyps that responded significantly to random and periodic events as described in previous sections.

A unique specimen of *Lobocorallium trilobatum trilobatum* consists of twin corallites that rise from a single apex, are joined along their counter sides throughout ontogeny, and have cardinal sides facing in opposite directions (Elias, 1983, fig. 11w, x). The corallites are thus mirror images of one another and share a common plane of bilateral symmetry as defined by the cardinal and counter septa. Walls do not separate them where they are joined, and their calices are interconnected. Below the calice, one or two long septa that were shared by the two polyps form a partition. These corallites would represent Siamese twins if division into two parts that remained attached occurred very soon after conception. They could also have resulted from aberrant development of an oral surface at both poles of a larva that attached to the upper side of a grain of sediment with its cardinal side. The two oral surfaces would have been directed upward with subsequent growth, resulting in twin polyps joined along

their counter sides and having cardinal sides facing in opposite directions as observed (Text-fig. 2L).

An interconnected calice involving two corallites has also been noted in a specimen of *Streptelasma divaricans* (Elias, 1982a, p. 54, pl. 2, figs. 14, 15s). In earlier stages, however, normal walls in lateral contact separated these polyps, which are thought to be part of a pseudocolony.

#### ACKNOWLEDGMENTS

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ENVIRONMENTAL INFLUENCE ON GROWTH FORM IN SOME MASSIVE  
TABULATE CORALS FROM THE HAMILTON GROUP  
(MIDDLE DEVONIAN) OF NEW YORK STATE

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ABSTRACT

Colony growth forms of *Favosites*, *Alveolites*, and *Pleurodictyum* contrast markedly in two coral beds of the Hamilton Group of New York State. Within the Fall Brook coral bed (Windom Shale, Moscow Formation) they are predominantly of the 'mound' morphotype, whereas those of the *Eridophyllum* biofacies of the Centerfield Limestone (Ludlowville Formation) are most commonly of the 'sheet' morphotype. The mounds in the Windom Shale display large maximum corallite growth angles in response to a high sedimentation rate, a strategy which enabled efficient removal of sediment from the colony surface. The sheets in the Centerfield Limestone display a tabular growth form with small maximum corallite growth angles. Low sedimentation and clear, well-lit water enabled these tabulates to expand horizontally, thus allowing efficient acquisition of abundant nutrients. Colonial rejuvenescence occurred often in the Windom and occasionally in the Centerfield in response to episodes of rapid sedimentation. Tabulate mounds inhabited both the Centerfield and Windom environments, but were overshadowed in the Centerfield by sheets. Lower corallite growth angles occur in Centerfield tabulates than in Windom tabulates where light intensity was not as great. This negative correlation between light intensity and corallite growth angle gives indirect evidence against the presence of symbiotic algae in these corals.

INTRODUCTION

A major issue with which all coral specialists are concerned is the ecologic plasticity of ancient and modern coral morphology. Recent work by Foster (1979a, 1980a) and Graus and Macintyre (1976, 1982) has shown a high degree of ecophenotypic plasticity in modern reef corals. Detailed studies on fossil corals (e.g., Foster, 1979b, 1980b) are needed before corals can be usefully incorporated into paleoecological interpretations. Study of environmental variation of Paleozoic tabulate corals has been largely confined to reef habitats (see James, 1979).

In the present study, a detailed comparison of morphotypes of non-reef tabulate faunas is based on statistical examination of two coral beds in the Middle Devonian Hamilton Group in New York. The Fall Brook coral bed (Baird and Brett, 1983) is located in the Windom Shale (Moscow Formation), and the *Eridophyllum* biofacies is located in the Centerfield Limestone (Ludlowville Formation) (Text-fig. 1). The Fall Brook coral bed was sampled at Little Beard's Creek in Leicester, New York, and the Centerfield Limestone was sampled in Genesee County, New York, 4 km west of East Bethany (Text-fig. 2).

Tabulate corals collected in this study include *Favosites*, *Alveolites* and *Pleurodictyum*. Only massive tabulates from each locality were examined in order to document environmental response in this type of tabulate coral. Taxonomic work was not undertaken.

Ross (1953) noted that at least half of the favositid species which occur in the Moscow Formation also occur in the Centerfield Limestone. While there may be some minor variation in the trends outlined in this paper due to species-specific control over coral morphology, it is doubtful that this variation undermines these observed trends. In addition, it is probable that

SUBSYSTEM	SERIES	STAGE	GROUP	FORMATION AND MEMBER	EUROPE
MIDDLE DEVONIAN	ERIAN	TAGHANIC		Tully	GIVETIAN
		TIOUGHNOGH	HAMILTON	Windom	
				Moscow	
				Ludlowville	
	Centerfield				
SKANEATELES					
CAZENOVIA	Marcellus				
	SOUTHWOOD	Onondaga Limestone	EIFELIAN		

Text-figure 1.—Stratigraphic column of the Middle Devonian of New York State. Tabulate corals were collected from the Centerfield Limestone of the Ludlowville Formation and from the Windom Shale Member of the Moscow Formation.

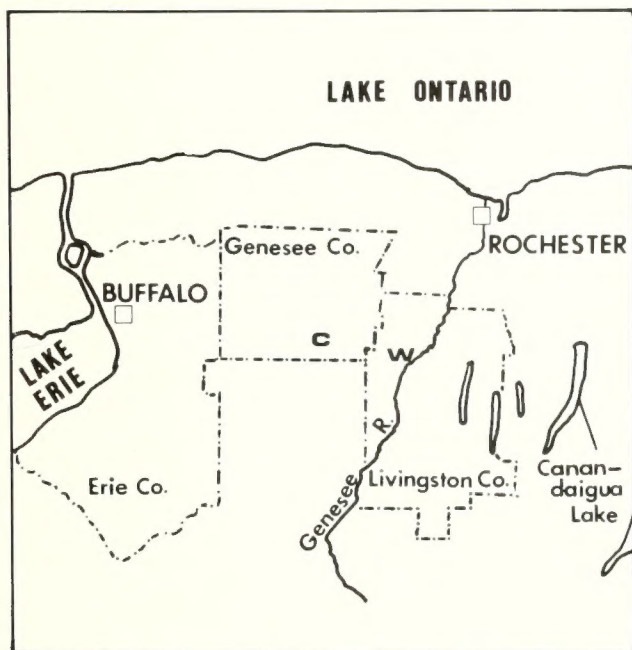
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the environment affected all species in a similar way and that adaptive strategies of various tabulate species were similar within both of the environments of this study. Morphologic response to individual environments seems to be consistent among different phyla of modern sessile marine invertebrates (Jackson, 1979). It is therefore assumed in the present paper that morphological response of tabulate corals in Centerfield and Windom environments was similar among species within each environment.

### SEDIMENTARY ENVIRONMENTS

The Centerfield Limestone near East Bethany is composed of gray fossiliferous shales interbedded with argillaceous limestones. Tabulate corals were collected from a soft, fossiliferous gray shale which occurs immediately below the "core" limestone of Gray (1983). Numerous favositid, auloporid and rugose corals, and infrequent alveolitids occur in this shale with the brachiopods *Longispina*, *Mediospirifer* and *Pseudoatrypa*. Brett and others (1983) interpret this shaly interval of Centerfield deposition as one with extremely low rates of sedimentation based on such taphonomic evidence as corrosion of large fossils, overgrowths of epibionts and a high incidence of fossil fragmentation. Many of the fossils were probably on the sea floor for some time after their death. Colonial rejuvenescence occurs in 30 percent of the observed tabulates, suggesting that while sedimentation rates were indeed slow, they were probably episodic.



Text-figure 2.—Location map of study area in western New York State. C = Centerfield Limestone locality near East Bethany and W = Windom Shale locality in Leicester.

The Fall Brook coral bed at Little Beard's Creek is composed primarily of shale. Baird and Brett (1983) have interpreted this coral bed as representing a composite of coral-rich lenses and patches which overlie one another or which may be intermixed due to bioturbation. They hypothesize that several events of coral colonization may have occurred. Baird and Brett recognized episodes of "exceptionally rapid fossil burial" (p. 433) from such evidence as delicate holdfasts of calceocrinid crinoids with adherent portions of jointed columnals occurring on one coral. Colonial rejuvenescence occurs in 64 percent of the tabulates collected. These corals were probably growing upward at a rate just rapid enough to keep up with sedimentation. There are also only a few occurrences of epibionts on the Windom tabulates. In one case, *Aulopora* encrusted *Alveolites* on the highest portion of the colony, suggesting that the alveolitid colony had died due to suffocation by sediment, leaving the *Aulopora* to encrust on whatever remnant of the coral skeleton that was not yet buried. The *Aulopora* in this case is composed of less than ten corallites, suggesting that either they too were quickly buried or that they quickly used up all available coral substratum to encrust.

The environments of the living massive tabulates differed between the two localities. Centerfield tabulates inhabited an environment in which sedimentation rates were usually very low, but were punctuated by episodes of increased sedimentation. In contrast, Windom tabulates lived in an environment of almost continuous sedimentation with recurrent "smothering" episodes. Light intensity was probably higher in the clear waters of the Centerfield than in the sediment-laden waters of the Windom. Centerfield tabulates may have remained on the sea floor for a while after their death, whereas Windom tabulates were buried *in situ*, resulting in their death. It is difficult to assess the relative input of nutrients into one locality versus the other; it is probable, however, that nutrients received by Centerfield tabulates were less diluted with detritus than those received by Windom tabulates.

### RESULTS

Table 1 shows the morphometric and statistical results of the present study. Height above substratum (H) refers to the maximum vertical distance above the sea floor that the coral grew. Diameter of encrusted substratum (D) was calculated as the average of the longest and perpendicular to the longest horizontal dimension. In cases of colonial rejuvenescence, H, D, and H/D were recorded for each episode of growth. H/D yielded a quantitative assessment of shape and gives a measure of the relative sheet- versus mound-

ness of the coral colony; therefore H/D may be related to Jackson's (1979) growth form classification for sessile marine invertebrates. Mean H/D values were significantly different between the two populations (Table 1). The mean maximum corallite growth angle, which has been used in the description of Recent reef scleractinians (Graus and Macintyre, 1982), is also significantly different between the two populations (Table 1).

Colonial rejuvenescence may be defined as a type of colony growth in which the diameter of the corallum is periodically suddenly reduced before increasing again. It does not generally result in reversion of internal structure to that of an earlier stage of development, as in some solitary corals. Colonial rejuvenescence was observed only in the massive corals at each locality. It is prolific in Windom tabulates and present in Centerfield tabulates (Table 1).

#### DISCUSSION

The corallum morphologies of the Centerfield and Windom tabulates differ principally in their H/D values, maximum angle of corallite growth, and incidence of colonial rejuvenescence. Tabulate morphotypes of this study, based on H/D values, fall into two of Jackson's (1979) six major morphotypes in modern sessile marine invertebrates. Centerfield tabulates have a lower H/D value than Windom tabulates and are predominantly sheets, whereas Windom forms are almost exclusively mounds (Table 1). Mounds may be arbitrarily defined as having H/D values greater than 0.5, whereas sheets are defined with H/D values less than 0.5. The mean H/D value of 0.513 for the Centerfield tabulate population does not indicate a mound strategy for these corals, but reflects an averaging of a majority of sheet morphotypes with a substantially smaller number of mound morphotypes (Table 1). The mounds have the effect of positively distorting the H/D mean, since their variance is more positively skewed than the variance associated with the sheets. The mean H/D value of 0.716 for Windom tabulates reflects a mound strategy for these corals.

Jackson (1979) related six major morphotypes of marine sessile invertebrates to various environmental parameters. He suggested that mounds should be more successful than sheets in environments with high sedimentation and limited food and light. Whereas sheets may not be able to withstand areas of high sedimentation and limited food and light, mounds are capable of living in areas of both abundant and scarce food and light (Jackson, 1979). Relative incidence of mounds and sheets in the two coral faunas (Table 1) indicates that mounds were capable of inhabiting both the Cen-

Table 1.—Morphometric results from tabulate corals from the *Eridophyllum* biofacies of the Centerfield Limestone and from the Fall Brook coral bed of the Windom Shale, New York. The sample ratio values (H/D) were tested for normality using the Rankits method (Sokal and Rohlf, 1969) and found to approximate a normal distribution.

	Center- field	Windom	t-test
Mean H/D*	0.513	0.716	p < .001 (t = 3.88, 76 df)
Mean maximum corallite growth angle	107°	137°	p < .05 (t = 2.63, 28 df)
% Rejuvenescent Coralla	30	64	—
% Sheets	63	12	—
% Mounds	37	88	—

\* H = height above substratum. D = diameter of encrusted substratum.

terfield and Windom environments, but the paucity of sheets in the Windom suggests that these forms were not well adapted to environments with rapid sedimentation rates. Mounds are well adapted to areas of continuous sedimentation because the steeply-sloping edges of the colony enable efficient sediment removal from the colony surface (Text-fig. 3-5 to 3-8).

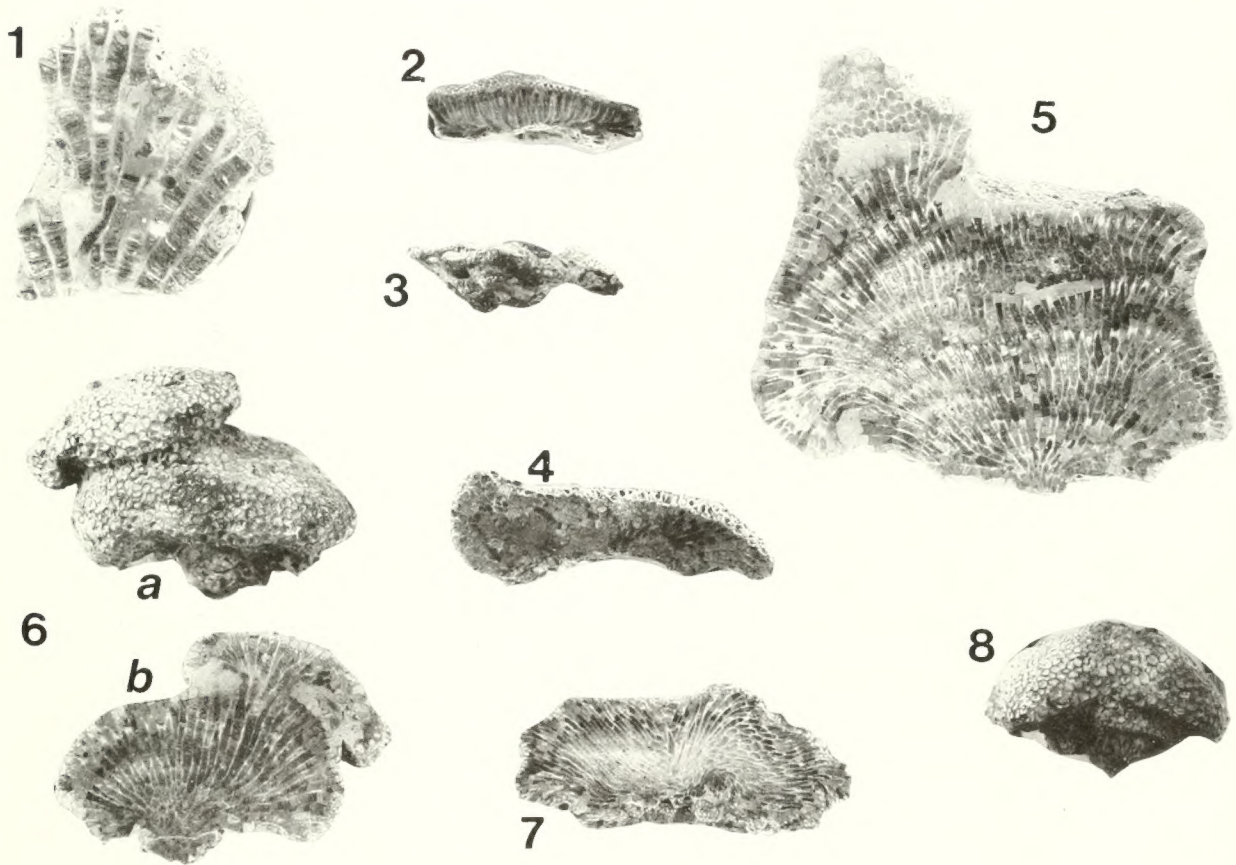
The sheets of the Centerfield probably represent an adaptation to a rich, continuous nutrient supply in which dilution of food particles was minimal due to low sedimentation. Sheets should be favorable in this type of environment since more food could be captured with increasing area of encrusted substratum. It was therefore advantageous for Centerfield tabulates to grow horizontally over the sea floor rather than vertically (Text-fig. 3-2 to 3-4).

Graus and Macintyre (1982) studied maximum corallite growth angles in the reef coral *Montastrea annularis* in a wide range of water depths at Carrie Bow Cay, Belize. These authors found a linear and continuous relationship of this morphologic character with depth, and classified five major morphotypes of *M. annularis* based on mean maximum corallite growth angle. They concluded that light intensity and distribution provide the major ecological control over skeletal morphogenesis in this species. Windom tabulates may be classified as hemispheres since their mean maximum angle of corallite growth of 137° (Text-fig. 3-5 to 3-7) falls within the hemisphere range (120–180°) defined by Graus and Macintyre. Centerfield tabulates have a mean maximum angle of corallite growth of 107° (Text-fig. 3-1, 3-2) which falls in the 'tapered hemisphere' range (105–120°) defined by Graus and Macintyre. The Centerfield mean, however, reflects an averaging of 'plate' forms with hemisphere forms and should not be taken as indicative of a population with a predominantly tapered hemisphere morphotype.

Decreasing maximum corallite growth angles should correlate with decreasing light intensity if calcification rate is dependent on light (Graus and Macintyre, 1982) as it is in modern hermatypic corals due to the presence of symbiotic algae. In Hamilton tabulates of this study, smaller maximum corallite growth angles occur in areas of greater light (*i.e.*, Centerfield Limestone) than those which occur in areas of less light (*i.e.*, Windom Shale). The lack of a positive correlation between maximum corallite growth angle and light intensity in the tabulates of the present study represents indirect evidence against the presence of symbiotic zooxanthellae in these corals. It is therefore suggested that light intensity was of secondary importance in governing the morphological ecophenotypes exhibited by Centerfield and Win-

dom tabulates. The fact that the sheet forms of the Centerfield were probably influenced more by nutrient supply than light intensity is illustrated by their horizontal expansion in clear, well-lit water. Conversely, mounds of the Windom, with their large maximum corallite growth angles, were not ecologically generated by poor light conditions, but rather by the need for efficient sediment removal under a continuous rain of sediment.

Incidence of colonial rejuvenescence differs substantially between the two localities (Table 1). Colonial rejuvenescence in the massive corals was brought on by increased sedimentation, since all corallites of the earlier growth stages in rejuvenated colonies are infilled with sediment except for the few corallites which rap-



Text-figure 3.—1–4. Centerfield Limestone; 5–8. Windom Shale. All figures  $\times 1$ . 1, 2. *Pleurodictyum* and *Favosites*; internal view of tabular colonies showing small maximum corallite growth angles which are typical of Centerfield tabulates. Note that *Pleurodictyum* would be classified as a mound by Jackson (1979) and as a plate by Graus and Macintyre (1982). 3. *Favosites* showing typical sheet morphotype characteristic of Centerfield tabulates with a low H/D value. 4. Sheet morphotype of *Favosites* in which H/D = 0.435; this sheet has an unusually high maximum corallite growth angle of  $131^\circ$ . 5. Mound morphotype of *Favosites* displaying a large H/D value; note shaly layers within the coral where sediment built up on the colony surface; the uppermost sedimentation event killed most of the coral, but the coral was able to continue growth on its left margin; note also large corallite growth angles conducive to efficient sediment removal at the colony margin. 6a, b. Internal and external view of mound morphotype of *Favosites* showing hemisphere form, large maximum corallite growth angle, and a sediment smothering event during which the coral underwent colonial rejuvenescence to form another mound. 7. *Alveolites* showing mound morphotype and large maximum corallite growth angle. 8. *Favosites* showing steeply sloping colony edges characteristic of the mound morphotype and used for sediment removal in areas of high sedimentation.

idly grow and reproduce to form the "rejuvenated" portion of the coralla (Text-fig. 3-6). Rejuvenescence is therefore directly correlated with the physical environment. The Centerfield sheet tabulates were able in many cases to survive during rare episodes of increased sedimentation through colonial rejuvenescence. These sheets, however, though apparently able to grow quickly through rejuvenescence, were unable to infiltrate the Windom environment with its continuous sedimentation. This suggests that colonial rejuvenescence alone is not an adequate adaptive strategy during times of high sedimentation and seems to be invoked only in cases of severe stress and as a last resort.

### CONCLUSIONS

1) A major difference in tabulate coral morphotype exists between the sheets of the *Eridophyllum* biofacies of the Centerfield Limestone and the mounds of the Fall Brook coral bed of the Windom Shale.

2) Tabulate colony mounds are better adapted for areas of high sedimentation than are sheets, but may also live in areas of low sedimentation.

3) Tabulate colony sheets of the Centerfield Limestone extended horizontally along the substratum to enable greater food access and not directly in response to availability of light.

4) Sedimentation rate was the predominant environmental parameter governing corallum morphotype in the Windom Shale, whereas the lack of stressful conditions and the pure nutrient supply of the Centerfield accommodated both sheets and mounds but gave preference to sheets which were capable of more efficient acquisition of nutrients than mounds.

5) Maximum corallite growth angle may not necessarily give clues to depth of life or light intensity in tabulate corals in non-reef habitats since the presence of symbiotic algae has not been demonstrated in these corals. Maximum corallite growth angle may instead reflect conditions of nutrient supply and/or sedimentation rate.

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CHAETETES REEFS OF EXCEPTIONAL SIZE IN MARBLE FALLS  
LIMESTONE (PENNSYLVANIAN), CENTRAL TEXAS

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ABSTRACT

Patch reefs composed predominantly of colonies of *Chaetetes* occur in the upper part of the Marble Falls Limestone, of early late Atokan age, in the Llano area of central Texas. These reefs are up to 3.3 m (11 ft) in height and typically about 4.6 m (15 ft) in diameter, but they may coalesce to form rather extensive barrier reefs. The *Chaetetes* colonies are globular in the initial growth stages but become free standing cylindrical pinnacles in later stages, possibly as a result of an increased influx of carbonate mud. The reefs are estimated to have had at least 1 to 2 m (3 to 6 ft) of relief above the sea floor during growth.

INTRODUCTION

*Chaetetes* colonies are the primary contributors to rather large patch reefs (Text-fig. 1) that occur in the upper part of the Marble Falls Limestone in the southwestern part of the Llano Uplift in central Texas. These reefs occur in association with medium bedded limestones that range from foraminiferal wackestones to packstones (Pl. 1, fig. 5). Most layers contain abundant fusulinids. Fusulinid samples collected from near the base of the lower patch reef interval have been examined by R. C. Douglass and M. K. Nestell who state that the species represented is close to *Fusulinella llanoensis* (Thomas), a primitive form of the genus. The age is early late Atokan.

The *Chaetetes* reefs described here occur in bluffs on Big Cedar Creek, located about 10 km (6 mi) southwest of Streeter, in Mason County, Texas. The Carboniferous stratigraphy of the Marble Falls Limestone in the southwestern Llano area has been described by Winston (1963) and the *Chaetetes* reefs described here are included in his measured sections (M.S.) 15 and 16.

CHAETETES REEF DEVELOPMENT

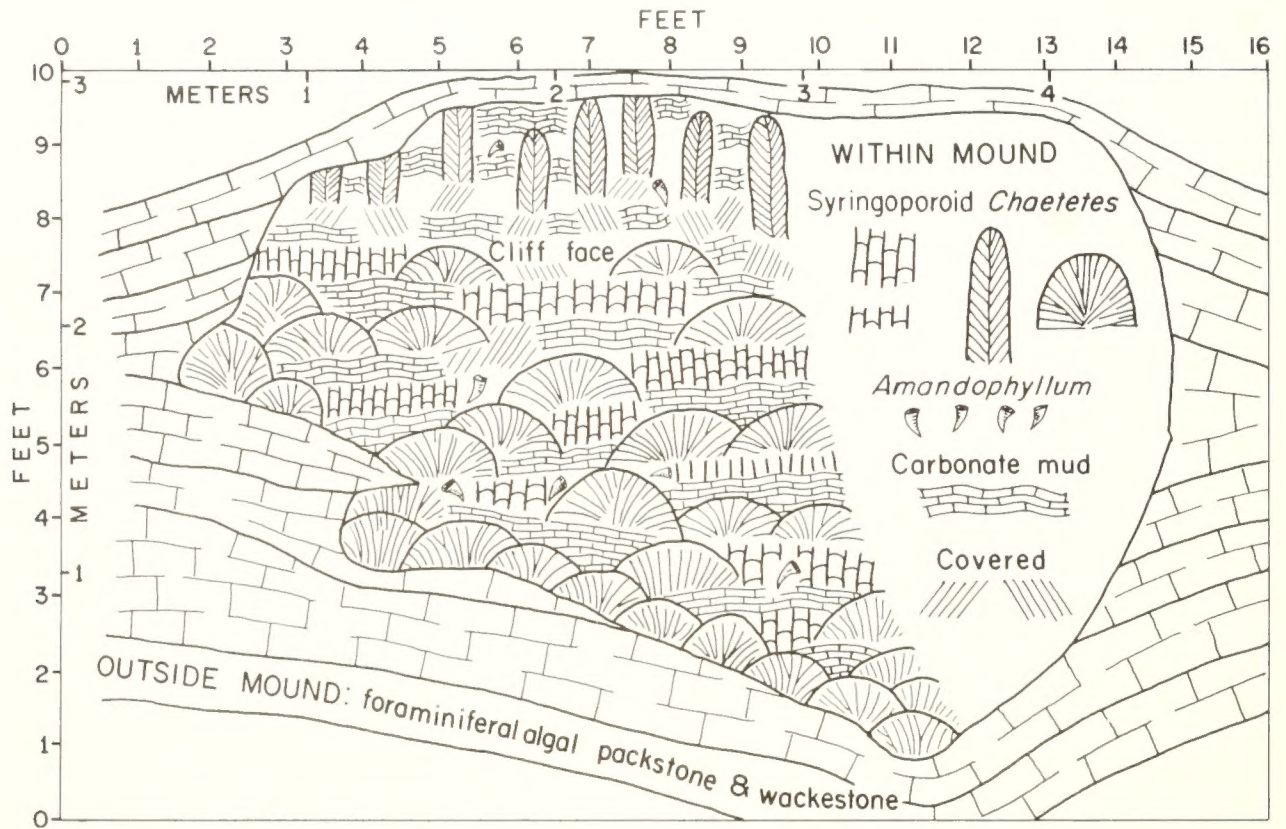
Two types of *Chaetetes* reefs occur at different horizons in the same limestone sequence, separated by about 7.5 m (25 ft) of strata. Both reef types occur in Winston's (1963) M.S. 15, located in bluffs on the east side of Big Cedar Creek about 2 km (1.25 mi) above its junction with the Llano River. The second type also occurs in Winston's (1963) M.S. 16, located in the bluff on the southwest (opposite side of the creek, 0.3 km (0.2 mi)) south of M.S. 15. It was at this second locality that the Type II reefs were examined in detail (Text-figs. 2, 3).

A problem in the examination of *Chaetetes* reefs is the differentiation of individual colonies within the

reef. In both reef types, here described, colonies can be examined mostly only in vertical cliff faces, and it is difficult to tell whether or not *Chaetetes* "heads," as observed, represent new colonies or buds from other colonies. These heads are globular in shape in the lower parts of both reef types. They show a range in size up to 0.5 m (1.5 ft) in diameter. In the upper part of the reefs, particularly in Type II, there is a significant increase in percentage of carbonate mud and the development of a cylindrical growth form for the *Chaetetes* colonies (Text-figs. 1, 3; Pl. 1, fig. 4). Each colony becomes isolated from lateral colonies and has vertical sides. The diameters of these cylindrical spires have been observed in Type II reefs to range from 0.15 to 0.3 m (0.5 to 1 ft) or more. Heights are more difficult to observe, but the maximum in these reefs is certainly in excess of 0.6 m (2 ft). It is assumed that the increase in rate of deposition of carbonate mud may have been a factor in this change in growth form to cylindrical spires.

Winston (1963), at an almost inaccessible locality in the southwestern Llano area, not yet visited, records the occurrence of a single cylindrical *Chaetetes* colony over 3 m (10 ft) in height that he interpreted as having grown as a free column before it was broken at the base and fell parallel to the bedding.

A feature found in all *Chaetetes* reefs observed is the pinch out of limestone layers below the lower half of the reef (Text-figs. 1-3; Pl. 1, fig. 3). These pinch outs are presumed to have developed depositionally during lateral and upward growth of the reef. There is also an inexplicable sagging of the limestone layers immediately below Type I reefs but not below Type II reefs (compare Text-figs. 1 and 3). The layers lateral to the reefs are mostly foraminiferal wackestones, and some of the available carbonate mud was periodically washed onto the reef. In the upper half of Type I reefs the



flanking beds pinch out against the reef and slope away from it (Text-fig. 1). These pinch outs are believed to substantiate the presence of relief on the reef during the time of deposition. It appears likely that the patch reef rose at least 0.5 to 1 m (1.5 to 3 ft) above the sea floor during early growth stages of the reef and possibly 2 m (6 ft), or more, during the later development of the reef.

Virtually all faunal elements within the reefs are in a growth position and there is no evidence of disorientation of the *Chaetetes* colonies. This seems to suggest that the reefs developed below normal wave base.

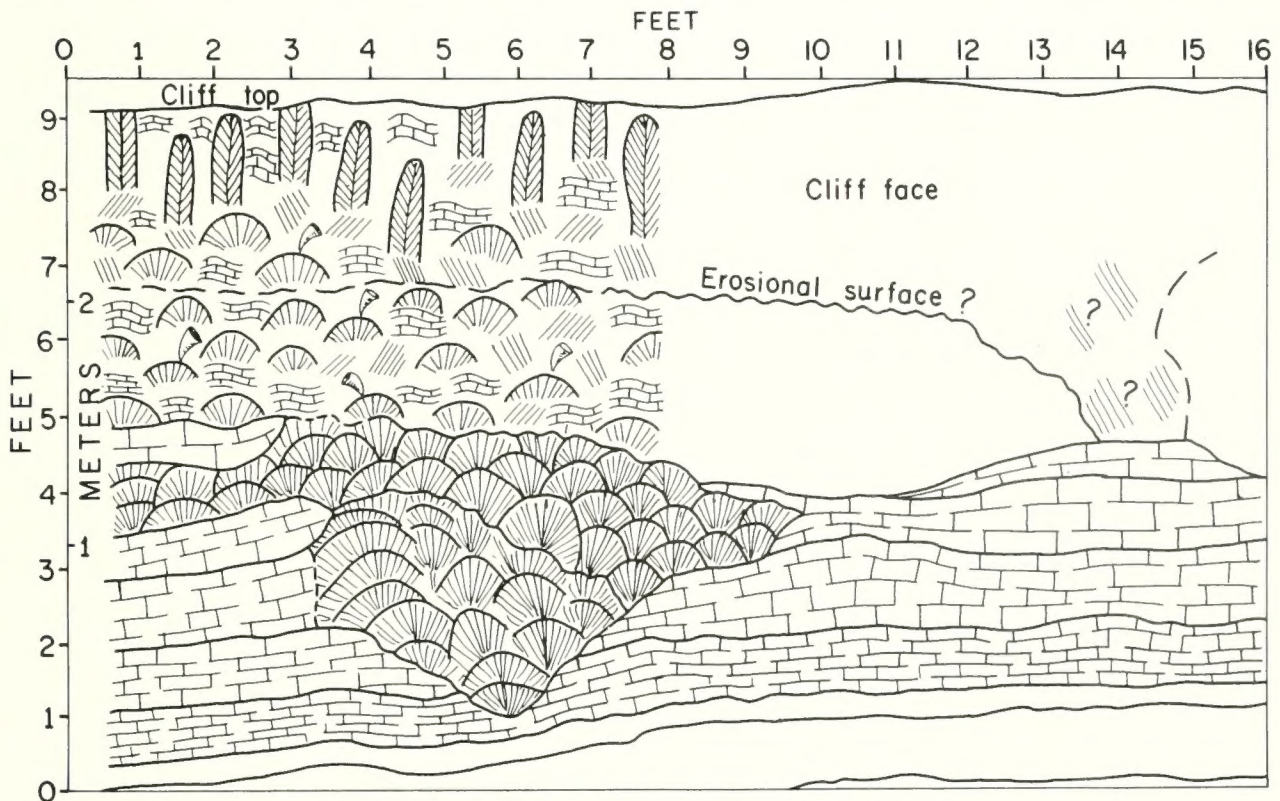
#### *Chaetetes* Reef: Type I

*Chaetetes* Reef Type I (Text-fig. 1; Pl. 1, figs. 1–6) has an observed maximum height of 3.2 m (10.5 ft) and the diameter of a single reef is typically 3.6 to 4.6 m (12 to 15 ft). Observed spacing between isolated reef patches along a cliff face ranged from about 3.6 to 9.2 m (12 to 30 ft), but three closely spaced reef patches grew together forming a single continuous reef barrier 14.5 m (47.5 ft) in length. Each reef varies in shape and symmetry but no preferred orientation could be detected.

Patch reefs of this type are composed predominantly of colonies of *Chaetetes* and each reef originated with a single *Chaetetes* colony apparently resting directly

on a wackestone surface that was not yet fully indurated. Important secondary constituents within the reef mass are irregular patches of carbonate mud with which are associated numerous irregular small colonies of syringoporoids seen mostly as thin tabular colonies. The only other faunal elements seen are encrusting algae and rare specimens of the small solitary rugose coral *Amandophyllum* (Text-fig. 1). Even the solitary corals are commonly in growth positions. Slabs cut from *Chaetetes* colonies show that encrusting algae either killed local patches of *Chaetetes* or grew on surfaces where the *Chaetetes* had been killed. Subsequently, however, *Chaetetes* grew back over the laminated algal surfaces (Pl. 1, fig. 6).

In this reef type, the patches of carbonate mud are scattered throughout the reef. It appears possible that the carbonate mud locally prevented further growth on the irregularly growing *Chaetetes* surface. This interpretation is supported over the alternative possibility, that the mud was subsequently washed in, because the numerous, small, thin, tabular colonies of syringoporoids are growing, in 90 percent of the cases noted, in a series of layers alternating with carbonate mud. In the remaining few cases the syringoporoid colonies are growing directly on the surface of *Chaetetes* colonies and may have caused them to stop growing. Conversely, the appearance of *Chaetetes* above a carbonate mud



Text-figure 3.—*Chaetetes* reef, Type II. Compare with Text-fig. 2.

interval is almost invariably directly overlying a syringoporoid colony.

#### *Chaetetes* Reef: Type II

*Chaetetes* reefs, Type II (Text-figs. 2, 3) form a well developed interval about 7.6 m (25 ft) stratigraphically above those described in Type I. Type II reefs have two distinct growth stages not seen in the earlier type. The first stage, found in the lower 1.2 to 1.5 m (4 to 5 ft) of vertical growth, is marked by closely spaced globular *Chaetetes* colonies or buds that include virtually no carbonate mud or other fossils. The upper surface of this stage is marked by what appears to be an erosional surface that arches upward axially over the core of the reef (Text-figs. 2, 3). Possibly this represents a storm surface in which the reef was ravaged, as is suggested by the coincidence of this surface with the encroachment of tongues of limestone onto the reef surface. Above this surface is the second phase of growth (Text-figs. 2, 3) which shows some characteristics similar to those found in Type I reefs. Carbonate mud is found in abundance as well as scattered specimens of *Amandophyllum*. Syringoporoids were not observed. Also, in the upper part of the reef the *Chaetetes* colonies become cylindrical and mostly isolated from each other and of greater size and scope than those found in Type I reefs. It was not possible, however, in the cliff exposures studied, to determine the relationship of globular *Chaetetes* below to cylindrical colonies above. In the middle of the upper phase of growth there is at least one additional possible erosional surface that appears to confirm the occurrence of differential relief on the reef surface during its development.

Type II *Chaetetes* reefs are equal in size to those of Type I. The maximum height observed is about 3.1

to 3.3 m (10 to 11 ft). Type II reefs begin growing 3.6 to 6.1 (12 to 20 ft) apart but in the stream bluff studied the Type II upper phase in each case grew together laterally forming a continuous barrier.

#### CONCLUSIONS

*Chaetetes* reefs in the Marble Falls Limestone have the following characteristics:

1. They are up to 3.3 m (11 ft) in height and may occur as isolated patch reefs about 4.6 m (15 ft) in diameter or they may coalesce into barrier reefs.
2. *Chaetetes* colonies form the primary ingredient of the reefs and the colonies are typically globular in the initial growth stages but become characteristically cylindrical in the upper parts of the reef, particularly in Type II reefs, possibly as a result of an increased influx of carbonate mud.
3. Faunal diversity in the reefs is low. Rare solitary corals (*Amandophyllum*) occur and syringoporoids may or may not be present.
4. Limestone layers (foraminiferal wackestones) pinch out depositionally below the lower half of each reef and slope into the reef. Lateral layers to the upper part of Type I reefs slope away from each reef.
5. The reefs are believed to have had moderate relief above the sea floor during growth, possibly in the range of 1 to 2 m (3 to 6 ft).

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#### EXPLANATION OF PLATE I

#### *Chaetetes* reefs, Type I, on Big Cedar Creek (except for Fig. 5).

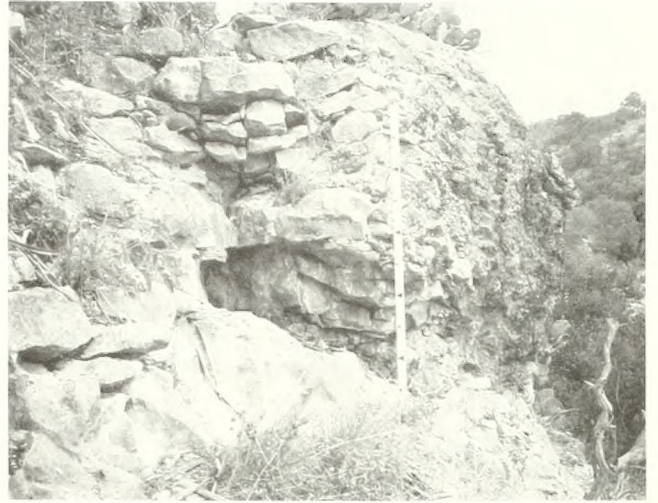
##### Figure

1. Bluff on east side of creek showing typical reef
2. Lateral limestone beds slope and pinch out towards lower part of reef; beds adjacent to upper part of reef slope away from it
3. Detail of lower part of reef seen in Fig. 2 showing pinch out of beds against lower flank of reef
4. Top of reef in creek bed showing circular cross-sections of cylindrical *Chaetetes* colonies separated by carbonate mudstone. Note overlying limestone layer is draped over reef crest
5. Sample of foraminiferal wackestone from layer near base of *Chaetetes* reef, Type II, shown in Text-figs. 2 and 3. Enlarged  $\times 8.5$
6. Slab of *Chaetetes* colonies taken from upper part of reef shown in Fig. 1, showing encrusting algae growing on lower *Chaetetes* surface and overgrown by higher *Chaetetes* colony. Enlarged  $\times 1.5$





1



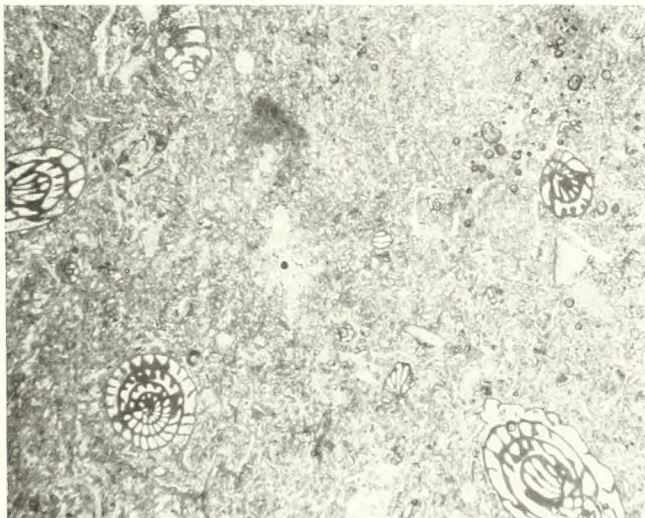
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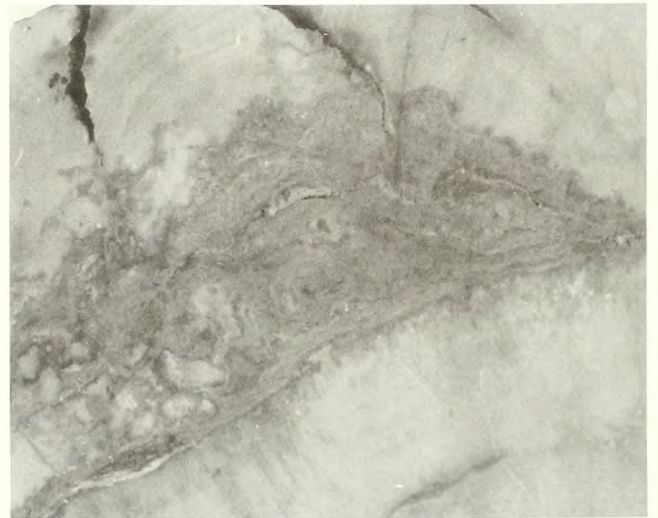
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6

## FUNCTIONAL COMPARISON OF THE MICROARCHITECTURE OF *ACROPORA PALMATA* AND *ACROPORA CERVICORNIS*

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### ABSTRACT

Differences in the mechanical strength of *Acropora palmata* and *A. cervicornis* skeletons result from their microarchitectural designs which are a consequence of their differing styles of axial extension. Branches consist of a core of axial corallites that extend up each branch as continuous tubes surrounded by a sheath of radial corallites. Extension of radial corallites increases branch diameter.

The core of *A. palmata* consists of a bundle of several axial corallites whereas the core of *A. cervicornis* consists of a single axial corallite. The skeletal design of *A. palmata* resists shear better because of the continuous multiple bundle of connected axial corallites in its branch core. By contrast, the skeletal design of *A. cervicornis* is particularly susceptible to fracture because of the greater proportion of radially oriented corallites in the shear plane of fracture. These interspecific microarchitectural differences have implications for the distribution and reproduction of both species.

### INTRODUCTION

This report considers whether the skeletal microarchitectures of *A. palmata* and *A. cervicornis* are adaptive with specific regard to hydrodynamic stresses. We expect mechanical damage to be a limiting factor for corals due to the magnitude of the hydraulic forces on reefs (Chamberlain and Graus, 1975). Specific mechanical adaptation of corals for withstanding hydro-mechanical stresses has been studied by analysis of colony growth form and skeletal physical properties (Graus and others, 1977; Chamberlain, 1978; Schumacher and Plewka, 1982). Graus and others (1977) demonstrated that overall colony growth form may minimize hydraulic drag. Chamberlain (1978) measured the compressive strength and elastic modulus of small cores of the skeletons of three common Caribbean coral species including *A. palmata* and concluded that mechanical properties of coral skeletons are an important factor in their design.

Given that *A. palmata* inhabits shallow waters (2–10 m) exposed to waves and swell, while *A. cervicornis* inhabits a deeper zone (4–20 m) of only moderate reef currents (Geister, 1977), *A. palmata* would be expected to be better adapted to withstanding hydraulic stresses. Schumacher and Plewka (1982), using small cores and sawn blocks of skeleton measured physical properties in *A. palmata* and *A. cervicornis* and found *A. cervicornis* skeleton to be stronger than *A. palmata* skeleton—an “unexpected” result in light of Chamberlain’s (1978) result. They concluded that skeletal mechanical properties are of minor adaptive significance to corals, but colony growth forms are of major significance. By contrast, *in situ* whole branch fracture experiments (Constantz, in prep.) indicate whole *A. palmata* branches are, in fact, stronger per unit cross sectional

area than are whole *A. cervicornis* branches. This result suggests that *A. palmata*’s larger, massive, branch morphology is not a factor determining its relatively lower susceptibility to fracture from hydraulic drag, because drag increases with larger branch area.

Skeletal microarchitecture and material ultrastructure must determine whole skeletal mechanical strength. The skeletal “microarchitecture” is the internal structural organization of the skeleton and the skeletal “ultrastructure” refers to the materials making up the skeleton with which the microarchitecture is fabricated. This report documents the skeletal microarchitectures of *A. palmata* and *A. cervicornis*, analyzes their respective designs for resistance to shear and torsional skeletal deformation and fracture, and comments on the adaptive significance of skeletal microarchitecture in both species.

### METHODS

Specimens are from a variety of Caribbean reef habitats in Barbados, Dry Tortugas, The Grenadines, Jamaica, and U.S. Virgin Islands. Specimens were studied by X-radiography, petrography, and scanning electron microscopy. For X-ray preparation, one cm thick, axial and serial radial sections were made of the uppermost meter of freshly dried branches. Specimens were X-rayed at 30 kVP for 2.5 to 5.0 minutes. Thin section material was impregnated with blue resin under vacuum prior to sectioning to enhance contrast. Specimens for SEM examination for surface microarchitecture and for internal ultrastructure in broken section were air dried. After washing with acetone, specimens were mounted on stubs with silver paint and sputter-coated with gold-palladium (approximate thickness 25 Å) in a high vacuum.

## RESULTS

The principal and most readily discernible morphological difference between *A. palmata* and *A. cervicornis* is a consequence of differing styles of axial extension. Tracking of corallite growth geometry in serial radial X-radiographic and petrographic sections showed that axial extension in *A. palmata* involves several axial corallites, whereas, for *A. cervicornis*, extension involves only one axial corallite. Therefore, *A. palmata* branches consist of a core of several axial corallites surrounded by a proportionately narrower sheath of radial corallites than *A. cervicornis* branches that consist of a core of only one axial corallite surrounded by a proportionately wider sheath of radial corallites. A useful way of expressing these differences is by the ratio of core radius to branch radius. This ratio near branch tips varies from 1/4 to 1/8 for *A. palmata* and for *A. cervicornis* is 1/8. In both species, basal parts of the branch have gradually increasing thickening due to radial corallite extension. For example, at one meter below the growth tip this ratio is almost 1/5 for *A. palmata* and 1/12 for *A. cervicornis*.

Scanning electron microscopy showed two interesting features of skeletal microarchitecture in *A. palmata* and *A. cervicornis*. First, the corallites of both species, both axial and radial, are constructed as porous tubes. The corallites of *A. palmata* and *A. cervicornis* are composed of axially extending rod-like septa connected together by rod-like synapticulae (Pl. 1, figs. D, I, K, J, M, N). This design gives corallites the structure of porous tubes. Axial corallites are about 2 mm across and the radial corallites are about 1.5 mm across. Aside from the manner in which these tubes are arranged, the most important difference between the microarchitecture of *A. palmata* and *A. cervicornis* is the robust coenosteal linkages between the axial corallites of *A. palmata*. These robust rod-like linkages are morphologically similar to the synapticulae of the corallites and form a sponge-like network of linkages connecting together *A. palmata*'s bundle of axial corallites (Pl. 1, figs. C, F, G). By contrast, the axial corallite of *A. cervicornis* is surrounded only by radial corallites.

The second feature seen under SEM is that the crystalline ultrastructure of both species is very similar. Aragonite fibers comprising sclerodermites of fully developed trabeculae in both species are about 10  $\mu\text{m}$  across and up to 120  $\mu\text{m}$  long, depending on the competitive interference of fibers from other sclerodermites (Pl. 1, figs. A, B, C, H, L). Every fiber is in fact a polycrystalline bundle of very fine acicular crystallites elongate with the fiber (Pl. 1, figs. H, L). The acicular crystallites are about 0.5  $\mu\text{m}$  across, and considerably longer. This general morphology occurs in all septa and

synapticulae of both species. On fractured surfaces (Pl. 1, figs. A, B) fractures appear to develop from cracks along cleavage planes that spread from one grain to another by nucleating new cracks in adjoining grains. Adjacent cracks then merge by a tearing action that produces steps in the fracture surface near the grain boundary (Pl. 1, figs. A, B). In some areas organic material may form grain boundary segregates that cause fractures to propagate along grain boundaries.

## DISCUSSION

The "materials science" of coral skeletal ultrastructure is outside the scope of this report and is discussed in Constantz (in prep.). However, two aspects of the ultrastructure are relevant here. First, the lack of any notable differences in skeletal fiber size or crystallite organization in the two species suggests that their mechanical properties are the same. Therefore, the skeletal materials probably do not play a role in determining the different skeletal strengths. Second, Johnston (1980) has shown that at least two separate organic components exist in coral skeleton. There are organic crystal sheaths associated with the calicoblastic epithelium that separate grain boundaries at the growing margin and a skeletal organic matrix consisting of sheets that delineate each individual fiber in older parts of the skeleton. In polycrystalline materials, brittle fracture is always preceded by some plastic deformation (Hayden and others, 1965). Therefore, although coral skeleton fractures in a brittle manner by sudden crack propagation, the organic skeletal matrix may increase the amount of plastic deformation allowable prior to brittle fracture.

The differing tubular arrangements of *A. palmata* and *A. cervicornis* corallites, produced by each species' style of axial extension, are of substantial adaptive significance. Hydraulic action across a reef produces shear and torsional forces on coral branches. An important advance in the aircraft industry has been the development of strong lightweight tubular laminates composed of tubes whose walls are fixed together to prevent slippage between the tubes (Plantema, 1966). Bundles of tubes connected in this manner have considerably higher shear and torsional strengths than the summed strength components of their tubes in isolation. Furthermore, the degree to which this summed strength is surpassed is a function of the strengths of the connections linking the tubes (Plantema, 1966). The robust coenosteal linkages connecting the axial corallites of *A. palmata* (Pl. 1, figs. F, G) fasten tube walls in the bundle together preventing slippage under the differential tension and compression caused by shear and torsional deformation. The tubular laminated construction in the axial corallite bundle of *A. palmata*

would be resistant to damage by wave and current forces. The "unexpected" low compressive and bending strengths for *A. palmata* reported by Schumacher and Plewka (1982) are probably an artifact of dissecting samples from their natural structural framework, thereby loosing the structural linkages of a tubular laminate so that they behave under compression and bending as isolated tubes. The lower breaking strength of *A. cervicornis* whole branches is caused not only by the lack of a bundle of axial corallites, but also by a preferential plane of fracture created by its proportionately wider sheath of radial corallites oriented away from the axial corallite (Constantz, in prep.). Ryshkewitch (1953) showed a considerable drop in a material's strength with a small increase in porosity, and Wainwright and others (1976) noted this relationship in coral skeletons. The greater proportion of small radial corallites in *A. cervicornis* lowers its porosity and increases its compressive and bending strength measured in small samples.

One final point to consider about the skeletal microarchitectures of *A. palmata* and *A. cervicornis* is secondary calcification, both by the coral and inorganically, that fills voids, reduces porosity, and masks primary microarchitecture. X-radiographs and thin sections showed evidence of significant amounts of secondary precipitation of skeletal aragonite and aragonitic marine cement in radial corallites and reduced amounts in the axial corallites. Gladfelter (1982) reported 18% per year infilling by organically mediated secondary calcification in the axial corallite of *A. cervicornis* for the first 2.5 years after growth, decreasing to 3.4% per year thereafter. Secondary calcification by the coral thickens the tubes of the tubular microarchitecture, and probably enhances their structural

strength. The void-filling, marine cements lining corallite walls on dead parts of the branch, because of their different material properties, may not be particularly effective in reducing stress concentrations (Wainwright and others, 1976).

The skeletal microarchitectures of *A. palmata* and *A. cervicornis* give these species different abilities to resist wave and current forces that may thereby limit their respective distributions, while creating different probabilities of skeletal fracture that may affect the degree to which each species reproduces asexually via fragmentation.

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#### EXPLANATION OF PLATE I Scanning electron micrographs

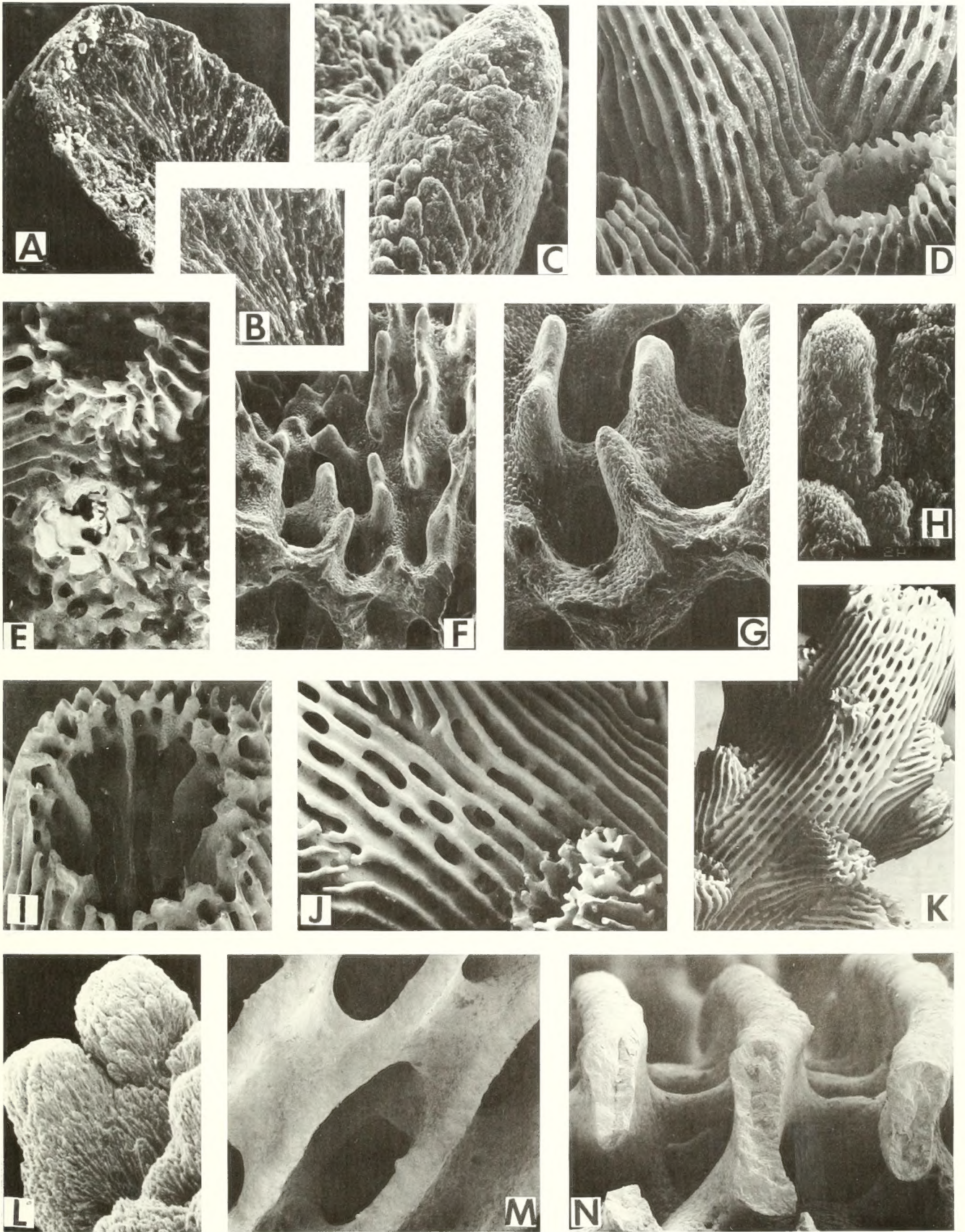
Figure

##### A-I. *Acropora palmata*

- A. Fractured synapticulae (field width 180  $\mu\text{m}$ , 15 kV).
- B. Detail of broken sclerodermite (field width 72  $\mu\text{m}$ , 15 kV).
- C. Polycrystalline fibers in sclerodermites building coenosteal linkage (field width 222  $\mu\text{m}$ , 15 kV).
- D. Radial corallites (field width 4800  $\mu\text{m}$ , 15 kV).
- E. Axial corallite (top) with new corallite emerging (below; scan illumination from behind) (field width 4800  $\mu\text{m}$ , 15 kV).
- F. Coenosteal linkages developing between axial corallites (field width 1750  $\mu\text{m}$ , 15 kV).
- G. Detail of "robust" coenosteal linkages between axial corallites (field width 960  $\mu\text{m}$ , 15 kV).
- H. Polycrystalline fibers (field width 18  $\mu\text{m}$ , 15 kV).
- I. Radial corallites (field width 3600  $\mu\text{m}$ , 5 kV).

##### J-N. *Acropora cervicornis*

- J. Axial corallite one cm from growth tip. Radial corallites branching off (field width 8500  $\mu\text{m}$ , 5 kV).
- K. Axial corallite and branching radial corallites; ring of septa interconnected by synapticulae define corallite (field width 14,400  $\mu\text{m}$ , 5 kV).
- L. Axial corallite septal extension; polycrystalline fibers (field width 24  $\mu\text{m}$ , 5 kV).
- M, N. Septal and synapticulae (field width 2800  $\mu\text{m}$ , 5 kV).



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## THE SIZE OF SOLITARY CORALS AS A POSSIBLE INDICATOR OF ZOOXANTHELLATE SYMBIOSIS

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### ABSTRACT

It has been well known for some time that symbiotic, solitary corals tend to be larger than non-symbiotic solitaries. The maximum size attained by non-zooxanthellates can be used on an empirical basis for inferring the symbiosis in fossil corals.

Preliminary results suggest that the symbiosis goes back to the Silurian, and that these large fossil corals might also, therefore, be used to infer warm, shallow paleoenvironments comparable to those occupied by living zooxanthellates.

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