The biology and taxonomy of Mesozoic stromatoporoids

Thesis

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THE BIOLOGY AND TAXONOMY OF MESOZOIC STROMATOPOROIDS

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FRONTISPIECE

Dehornella crustans Hudson, 1960

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ABSTRACT

The presence of spicule pseudomorphs and an aquiferous filtration system in Mesozoic stromatoporoids confirms poriferan affinity for this previously problematic group. The form, and postulated original siliceous nature of most of the spicules, indicates that the possessors of these were calcified demosponges; others with originally calcareous spicules were calcareans. Different spicule types and arrangements indicate that the possession of a calcareous skeleton is a convergent feature. Previous defining characteristics are found to be invalid and Mesozoic stromatoporoids are redefined as calcified sponges, so that the term 'stromatoporoid' now only refers to a grade of organisation of the calcareous skeleton and not a taxonomic grouping. 'Chaetetids', 'sphinctozoans' and 'sclerosponges' are also polyphyletic groupings, representing grades, where some members of which are calcified demosponges. These groupings should no longer be considered in isolation, as this has previously obscured their true nature.

The original mineralogy of late Mesozoic stromatoporoids was probably low-Mg. calcite. Spicule and calcareous skeleton diagenetic lineages are given to enable workers to determine original microstructures.

Analogies with Recent calcified demosponges, suggests that the fossil stromatoporoid demosponges produced a primary framework of siliceous spicules bound together with an organic matrix, which probably provided the nucleation sites for subsequent precipitation of the calcareous skeleton.

A new taxonomic scheme is presented based on spicule type, arrangement and relationship of this framework to the microstructure of the calcareous skeleton. On the basis of spicule criteria, calcareous microstructure alone is found to be convergent and can no longer be used as a high-level taxonomic feature. Spiculate species are therefore redescribed and placed within the Recent poriferan classification framework. Synonyms are documented and intra-specific variation discussed. The present cnidarian-based nomenclature is replaced by one modified from Recent poriferan terminology.

The possession of a calcareous skeleton is probably a relict feature of a previously widespread calcified sponge fauna. It appears that the calcareous skeleton was acquired independently in a number of lineages in the early Palaeozoic, and has subsequently been lost in many.

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STATEMENT

None of this work has been previously submitted for a degree or any other qualification by the author. The finding of spicules in Mesozoic 'stromatoporoids' has been pulished in Palaeontology 29(3),469 - 475. A reprint of the paper is given in the Appendix. Work on the placing of Mesozoic stromatoporoids within the Porifera is in press, in the Proceedings of the Third International Conference on the Biology of Sponges, November 1985, Wood's Hole, Mass.,U.S.A.. All information has been derived by the author, except where otherwise indicated. New gen.and n. sp. A was found by Joachim Reitner, and material has been given to the present author for collaborative study; however, the present author is alone responsible for the observations on this material recorded herein.

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CHAPTER 1

INTRODUCTION

1.1. BACKGROUND

1.1.1. THEORETICAL INTENTION

The organisms of which the genus *Stromatopora* Goldfuss, 1826 is the type and which are known as 'stromatoporoids' constitute a major group of fossil invertebrates. They are calcareous, layered forms found in carbonate sequences from the Ordovician to the Cretaceous which reach their acme in the Silurian and Devonian. Palaeozoic stromatoporoids, especially those from the Ordovician to Devonian are known to have been important reef builders. Mesozoic forms range from the Bathonian to the Maastrichtian (excluding dubious Triassic and Permian forms) and are broadly Tethyan in palaeogeographic distribution.

Stromatoporoids are an abundant, geographically widespread and stratigraphically extensive group. They are found on every continent (with the possible exception of Antarctica) and form a significant, and often dominant part of certain fossil faunas. As geological tools, they are too long-ranging for stratigraphic use, but there is some indication that both Palaeozoic and Mesozoic forms could be useful ecological indicators. Stearn (1982) and Mitchell-Tapping (1980) suggest that Palaeozoic stromatoporoids are confined to reef crest and patch reef zones. Turnšek et. al. (1981) give evidence for an Upper Jurassic barrier reef complex in N.W.Yugoslavia which exhibits ecological zonation along suggested environmental gradients. Considering their abundance in many oil-bearing strata (they contribute to oil reservoirs in the Jurassic of the Middle East), investigation into stromatoporoid palaeobiology is of considerable practical use and importance.

The study of stromatoporoids has met with particular difficulties. With few general characters and no conclusive feature which would finally place them, diverse views have been proposed as to their affinity. As a consequence there is no agreed taxonomic framework and the descriptions are varied and often highly subjective. Without a workable taxonomy, meaningful ecological and phylogenetic reconstructions have been impossible and while other fossils are viewed from a biological standpoint, what appears as a scientific enquiry into stromatoporoids is really only a display of technical terms. There is therefore considerable scope for work on all aspects of this group.

This thesis provides a new and more valid framework for stromatoporoid study using Mesozoic forms. A positive placing in the natural classification is fundamental to further enquiry, and it is this which forms the foundation of my research. From this basis it has been possible to produce a biologically sound and workable taxonomy.

1.1.2. IDENTIFICATION OF PROBLEMS

Stromatoporoids have not received a scientific study commensurate with their importance. This stems from difficulties inherent in the material and the fact that few palaeontologists have been fired with enthusiasm by these comparatively unaesthetic and drab fossils. Perhaps they are only noteworthy as a contributary item in the downfall of the the biologist Kirkpatrick (1912, 1930)! As calcareous organisms found in carbonate strata, they are difficult to extract from their matrix. Moreover they possess few diagnostic surface features and the gross morphology is subject to environmental control. Their taxonomic study requires considerable thin section preparation and detailed knowledge of the microstructures. Microfabrics have been inadequately described and little consideration has been given to the effects of diagenesis, diagenetic fabrics often being confused with original skeletal ones. There is no consensus as to their biological placing (see Sections 1.2.1.and 2.1). No agreed descriptive terminology exists, each author preferring his own taxonomic schemes and character weightings. Homologies between the few characters present are difficult to determine. Definitions of the group as a whole and of families, genera and species, have been loose and subjective, producing an undisciplined heterogeneous grouping of forms and in desperation, even ecological definitions have been proposed (Stearn, 1982).

1.1.3.SCOPE AND ORGANISATION OF THESIS

This thesis is concerned with the biology and taxonomy of late Mesozoic stromatoporoids ranging from the Bathonian to the Maastrichtian. Co-existing and supposedly related groups will receive some attention. Discussion of related Palaeozoic, early Mesozoic and Recent organisms will be discussed when of relevance to these late Mesozoic forms.

Organisms can be considered at four levels: the closest inspection is at microstructural level, the second in terms of the functional units, the third is the arrangement of these units (the whole individual) and the fourth is the population level. These partially follow the rationalization of Goto (1972).

The first two levels contribute towards the biological conclusions presented in Chapter 2, and from these stem all other areas of research. A knowledge of the biology leads to the proposal of a new theoretical framework for Mesozoic stromatoporoids (Chapter 3) and provides the foundation of a taxonomic revision (Chapter 4). Together with stratigraphic information, this allows phylogenetic reconstruction (Chapter 5). Using functional units, comparison with nearest Recent relatives makes possible anatomical and functional analysis (Chapter 6).

The conclusions are presented in Chapter 7. Data which are not of direct relevance to the conclusions are given in the Appendix. A glossary of terms is given in the Appendix. Where possible, a diagram or Plate illustrating the feature is referenced therein.

1.1.4. APPROACH

The material used is from both existing museum and personal collections. Stromatoporoids have been collected from described faunas in the Upper Jurassic of Yugoslavia and Israel, the Lower Cretaceous of S.E. France and a previously undescribed fauna has been collected from N. W. Spain. The specimen numbers in the present author's collection are prefixed with 83/, 84/, or 85/.

Extensive use is made of the collections of the late R. G. S. Hudson held at the British Museum of Natural History, London (B.M.(N.H.)), and the Sedgwick Museum, Cambridge. B.M.(N.H.) numbers are prefixed with H, and Sedgwick Museum numbers with F. The collections of D.Turnšek (Upper Jurassic and Lower Cretaceous of Yugoslavia, and Lower Cretaceous of S.E.France) were examined. Additional selected holotype material was loaned to the author.

Where possible, gross morphology was noted but most information was obtained from polished slabs and thin sections. Many thin sections were stained with standard carbonate stains to enhance the visibility of the microstructure, using the technique outlined by Dickson (1965). Ultrastructures were studied using S. E. M. at the Open University and B.M.(N.H.).

S. E. M. stubs were coated for one to four minutes in an Emscope S C 500 sputter coater and examined with a Cambridge stereoscan 600 S. E. M. and photographed using Polaroid type positive/negative 35mm. film. Larger scale features upon uncoated material were examined using the environmental chamber of a Cambridge 160 A and recorded on Kodak Tri-X black and white negative film.

1.2. HISTORICAL PERSPECTIVE

1.2.1. HISTORY OF BIOLOGICAL INTERPRETATION

Stromatoporoids have long been in a disputed systematic position. The absence of any conclusive features, the lack of certainty as to the biological significance of astrorhizae and the characterless reticulum, have caused different workers to be impresssed by different analogies, and so these fossils have been shunted from one biological group to another. Table 1.1 lists the major proponents of the various biological proposals.

Goldfuss (1826), who founded the genus *Stromatopora*, placed it between the Millepores and the Madrepores. This idea was soon rivalled by Steininger (1834), who suggested that stromatoporoids might be sponges. D'Orbigny (1850) agreed, but the Sandbergers (1850) and Röemer (1851) proposed bryozoan affinity. Röemer later (1856) classed the stromatoporoids with the tabulate corals.

One of the most important studies was published by Baron von Rosen in 1869. Using for the first time microscopic study of thin sections, and beautifully illustrating his observations, he concluded from the minute structure of the skeleton and the presence of oscula and pores, that stromatoporoids were horny sponges which had become calcified.

Stromatoporoids have been referred to other sponge groups. Salter (1873) considered them calcareous sponges. Nicholson and Murie (1878) agreed but suggested that they were best regarded as a separate taxon, for which they proposed the name Stromatoporoidea. Sollas (1877) placed the genus *Stromatopora* among the Hexactinellida.

Table 1.1: List of major proponents of the various proposals of affinity for stromatoporoids.

ANTHOZOA (not including tabulate corals)	PORIFERA	BRYOZOA
Goldfuss 1826	Steininger 1834	Röemer 1851
de Blainville 1833	d'Orbigny 1850	Sandberger and Sandberger 1850
Lonsdale 1840	Eichwald 1860	
Römer 1843	von Rosen 1869	
von Keyserling 1843	Salter 1873	
Hall 1847	Nicholson 1873	
McCoy 1851	Sollas 1877	
Billings 1862	Nicholson and Murie 1878	
Winchell 1866	Solomko 1886	
Lindström 1880	Kirkpatrick 1912 (August)	
Mori 1976, 1984	Heinrich 1914	
	Twitchell 1929	
	Hartman and Goreau 1970, 1972	
	Stearn 1972, 1975	
	Wendt 1975, 1979, 1984	
	Hartman 1979	
	Stock 1984	
	Present author	

HYDROZOA	CYANOBACTERIA	TABULATE CORALS
Lindström 1873	Kazmierczak 1976-1983	Röemer 1856
Carter 1877,1880		Nestor 1981
Zittel 1877		
Steinmann 1878		
Champernowne 1879		
Bargatsky 1880		
Nicholson 1886		
Yabe and Sugiyama 1920 , 1935		
Dehorne 1920		
Steiner 1935-1		
Lecompte 1952, 1956		
Hudson 1955-1960		
Flügel 1958		
Galloway 1957		
Turnšek 1960-1974		
Kazmierczak 1971		
Turnšek and Masse 1974		

FORAMINIFERA	'VEGETABLE'	CEPHALOPODA
Dawson 1875, 1879	Billings 1857	Hyatt 1865
Lindström 1870		
Kirkpatrick 1912 (September)		
Hickson 1934		
Parks 1935		

Dawson (1875) in the "Dawn of Life" and later in "The Microscopic Structure of the Stromatoporidae"(1879) saw sufficient analogies between some members and the encrusting foraminifer *Gypsina* to propose classification with the Foraminifera. He compared the astrorhizal tubes to the canals of *Gypsina* . Hickson (1934) and Parks (1935) agreed, elaborating upon Dawson's theory .

Carter (1877) studied various species of *Hydractinia* and became impressed with the similarity of *H. echinata* to the Palaeozoic stromatoporoids *Labechia* and *Actinostroma*. In 1880 he suggested the term 'astrorhizae' to replace his previous 'stellate venation'. He proposed that the coenosarcal grooves, or 'hydrorhizae', on the surface of *H. echinata* were analogous to the astrorhizal canals of a stromatoporoid and that they housed the zooids. *Millepora* with its porous skeleton and tabulated zooidal tubes was considered to possess considerable similarities to stromatoporoids. So hydrozoan affinity was proposed. Nicholson (1886) also inferred the presence of zooidal tubes, although he had previously thought stromatoporoids were sponges (1873). Both Steinmann (1903) and Parks (1909) questioned the existence of zooidal tubes.

Although the main objection to hydrozoan affinity for stromatoporoids was the difficulty of proving the presence of suitable receptacles to lodge the zooids, hydrozoan affinity won general acceptance and was used as the biological basis for future classification. Little was done to find definite affinities for individual genera, and no critical examination was made to determine how the various organisations were related. Hydrocoralline affinity was commonly assumed for all genera.

The notable exceptions were Heinrich (1914) and Twitchell (1929). Twitchell convincingly used analogy between modern freshwater sponges and stromatoporoids to illustrate taxonomic similarities. He showed spinose structures within *Stromatopora* which he interpreted as spicules. He compared the aquiferous system of modern sponges to the canal and astrorhizal systems of stromatoporoids and proposed that they were based upon the same functional unit. This was one of the few detailed and scientifically argued proposals for the biological affinity for stromatoporoids.

Most workers accepted hydrozoan affinity for stromatoporoids until the late 1960's (Galloway 1957, Flügel 1958). Lecompte (1956) in the 'Treatise of Invertebrate Paleontology ' reviewed the main biological theories and he too decided to continue classification of the stromatoporoids within the Hydrozoa.

In the late 60's and early 70's some remarkable calcified sponges were described from the deep fore-reef of Jamaica, and two other genera, *Astrosclera* Lister, 1900 and *Merlia* Kirkpatrick, 1910 were redescribed (Hartman 1966, Hartman and Goreau, 1969,1970,1972). They were placed in a new class, the Sclerospongiae. These Recent sponges possess an aragonite or calcite skeleton which forms an encrusting or massive habit. A siliceous spiculate skeleton is also present. The soft tissue bears excurrent canal systems which leave traces in the skeleton surface. The authors noted their similarity to stromatoporoid astrorhizae, and proposed poriferan affinity for stromatoporoids. Kirkpatrick in August, 1912, whilst describing *Merlia*, had also noted the similarity between this Recent calcified sponge and the 'Monticuloporas' (which then included the stromatoporoids). He also stated that he possessed spicule proof of his assertion. Unfortunately by September, 1912, he decided that he was mistaken and that stromatoporoids were accretions of 'eozoon' foraminiferans, an idea which he later expanded to his Nummulosphere Theory, that all rock, irrespective of origin, was composed of Foraminifera (Kirkpatrick 1930).

The new evidence presented by Hartman and Goreau 1970 for poriferan affinity for stromatoporoids soon won wide, but not universal, acceptance.

Kazmierczak (1971) continued to support hydrozoan affinity for the group, but conceded that some Mesozoic forms were possibly related to the sclerosponges. He dismissed astrorhizae in Palaeozoic forms as being traces of boring symbiotic organisms and therefore not requiring further explanation.

Stearn (1972) strongly disputed this interpretation, the excurrent canal theory being generally more acceptable. Stearn (1972) reconstructed the stromatoporoid animal using the Recent sclerosponges *Astrosclera* and *Merlia* as models. Even though related to the sclerosponges, he considered them to be a separate sub-phylum of the Porifera. Stock (1984) also used the modern sclerosponge *Calcifibrospongia* to explain structures in the Ordovician genus *Cliefdenella*.

Having dismissed astrorhizae as of no biological significance to stromatoporoids, Kazmierczak (1976 and later), suggested that stromatoporoids were the permineralised colonies of coccoid cyanophytes. This was thought most unlikely and won little approval (Stearn 1984). Riding and Kershaw (1977) doubted that such complex structures as are found in stromatoporoids could be secreted by organisms as primitive as cyanobacteria.

Several workers still favoured stromatoporoids as Cnidaria. Mori (1976, 1984) preferred separation as a phylum related to the scleractinian corals. Nestor (1981) compared the coenosteum between the corallites of heliolitids to stromatoporoid organisation.

However, a new living sclerosponge, *Acanthochaetetes wellsi* was described by Hartman and Goreau (1975) which possessed a tabulate high-Mg calcite skeleton into which the spicules were not incorporated. *Acanthochaetetes wellsi* was assigned to a Mesozoic chaetetid genus and placed in a second sclerosponge order, the Tabulospongida. Poriferan affinity was thus proposed for Palaeozoic and Mesozoic chaetetids in the light of this 'living fossil'. The later finding of spicules in Mesozoic specimens of *Acanthochaetetes* confirmed this suggestion.

Alternative classifications among the Porifera have been proposed for stromatoporoids and chaetetids. Termier and Termier (1973, 1979) submitted that all calcified sponge forms should be united into one group, the Ischyrospongia. This has been heavily criticised by many workers, including Vacelet (pers. comm.) due to the highly polyphyletic nature of this collection of sponges.

The rediscovery of old, and discovery of new sclerosponges led to recognition of sclerosponges in the fossil record. During the 1970's sclerosponges were recognised in Mesozoic (Wendt 1975, Kazmierczak 1974) and Palaeozoic (Termier and Termier 1974) strata. Some authors (Dieci et. al. 1974b, Cuif 1973) assigned genera to the Sclerospongiae, seemingly on the basis of an aspicular spherulitic calcareous skeleton alone. Many forms were described from the Upper Triassic of the Dolomite Alps which often showed exceptional aragonitic preservation of the original microstructures. Some supposedly contained spicules (Dieci et. al. 1977). However the lack of indisputable spicules remained as evidence against poriferan affinities for stromatoporoids.

1.2.2. HISTORY OF TAXONOMIC INTERPRETATION

The arbitrary nature of accepted diagnostic features is the main reason why more and more stromatoporoid species have been erected. Numbers have markedly increased over the last twenty years. New taxa are described without critical examination of their morphological characters, which were determined as early as the late Nineteenth Century. Over 2,000 Palaeozoic species and 500 Mesozoic species have been described (Flügel 1975).

Nicholson (1886) established the first satisfactory working classification and he also gives a very comprehensive review of taxonomic work up to that date. Believing stromatoporoids to be Hydrozoa, he divided the Palaeozoic forms into two groups following the two Recent calcareous hydrozoan genera. His 'Milleporoid' group includes forms which possess the so-called 'zooidal tubes' and his 'Hydractinoid' group are without such structures. Nicholson's work was accepted by many later workers.

Nicholson's 1886 Classification

Stromatoporoidea Nicholson and Murie
- Hydractinoidea Nicholson: Forms without zooidal tubes, related to hydractinians;
  - Actinistromatidae, Idiostromatidae
- Milleporoidea Nicholson: Forms with zooidal tubes, related to the milleporoids;
  - Labechidae, Stromatoporidae.

Heinrich (1914) proposed that the families Labechidae and Idiostromatidae should be removed from the Order Stromatoporidea as they lacked a 'meshy' reticulum structure and there was an absence of astrorhizae. He believed that no zooidal tubes existed and that 'true stromatoporoids' always bore astrorhizae. He was the first to suggest subdivision of the stromatoporoids based on the microstructure of the structural elements. He divided the stromatoporoids into two families: the Actinostromatidae which bore homogenous microstructure and the Stromatoporidae with tubular or porous microstructure. Specific determinations were based upon the form of the astrorhizae.

Heinrich's 1914 Classification

Order Stromatoporoidea Nicholson and Murie:
- Actinostromatidae Nicholson. Homogenous microstructure and massive fibres.
  - subgroups: 1. Continuous pillars
  - 2. Pillars limited to one interlamellar space
- Stromatoporidae Nicholson. Porous or tubular microstructure and non-massive fibres.

subgroups: 1. Equally developed vertical and horizontal elements.
2. Dominant vertical elements.
3. Non-differentiated elements forming a reticulum.

The presence of stromatoporoids in the Mesozoic was not recognised until 1900, when Tornquist described a form, *Lithopora koeneni,* from the Upper Triassic near Vicentin, although Gregory (1898) had described what he believed to be a 'Milleporoid Hydrozoan' from the Turonian of Egypt which he named *Millestroma* and Steinmann had founded the Ellipsactinidae (with uncertain affinity) in 1878. In 1901, Tornquist mentioned the existence of two Lower Cretaceous stromatoporoids, *Actinostromaria stellata* and *Burgundia trinorchii,* from the collection of Munier-Chalmas. In 1903, Steinmann described *Milleporidium remesi* from the Tithonian of Stramberg which he considered to be ancestral to Recent *Millepora.* Yabe described *Stromatopora japonica* from the Torinosu Limestone of Japan, which was the first Mesozoic species to be assigned to a Palaeozoic genus. From then on a series of Mesozoic species were described and assigned to the Stromatoporoidea, by e.g. Bakalow (1906), Deninger (1906), Vinassa de Regny (1908-1915), Parona (1909), Osimo(1910) and Hayasaka (1917).

Dehorne produced a series of papers from 1915 and her final memoir was published posthumously in 1920, when she described many new species of stromatoporoids and pre-existing forms in the collections of Haug and Munier-Chalmas. She gives an extensive review of Mesozoic forms described until that date. This was the first study to assemble the current knowledge of Mesozoic forms. Dehorne (1920) suggested that the presence of both *Stromatopora* (Stromatoporinidae) and *Actinostromaria* (Actinostromatidae) illustrated the persistence of both Palaeozoic families into the Mesozoic and she continued to ascribe Mesozoic species to Palaeozoic genera.

Dehome (192O) adopted the essential features of Heinrich's classification for the Mesozoic forms. She added the Mesozoic family Burgundidae, considered intermediate between the Actinostromatidae and Stromatoporidae, due to the supposed presence of 'zooidal tubes'. Dehorne noted the similarity of *Burgundia* to the Palaeozoic genus *Clathrodictyon* , based upon its general appearance and the presence of closely spaced laminae. She believed the Actinostromatidae, Burgundidae and Stromatoporinidae formed a continuous lineage between the hydractinoides and the milleporelloids and that the stromatoporoids represented an order intermediate between the tubularids and the hydrocorallines.

Dehorne's 1920 Classification:

Family I: Actinostromides(Hydractinoides of Nicholson)
    Subfamily A Actinostromarines
    Subfamily B Clathrodictyonines
Family II: Burgundides
Family III:Stromatoporides (Milleporoides of Nicholson)
    Subfamily A Stromatoporellines
    Subfamily B Stromatoporines

Dehorne based her diagnoses upon the following characters:

GENERIC:

1. Form and dimensions of astrorhizae. Presence or absence of zooidal tubes.

2. Continuity of radial and horizontal elements.

3. Presence and form of tubercles.

SPECIFIC:

1. Number of tabulate zooidal tubes, their dimensions and form.

2. Size and form of skeletal elements.

3. Form of latilaminae.

She considered the general skeletal form to be subject to environmental control, but that some species and genera seemed always to possess the same gross morphological type.

Kühn's classification (1927, 1939) was based on his suggested evolutionary trends. He retained Heinrich's two families in which he included Mesozoic forms and added a Mesozoic family, the Stromatoporinidae, which were ancestors of the Recent Hydroida. Kühn placed some Mesozoic stromatoporoids in a new Order Sphaeractinoidea and removed the Order Labechioidea from the rest of the stromatoporoids.

Kühn's 1927/1939 Classification

Order Stromatoporoidea.(Cam.- Cret.)
    Family Actinostromatidae.(Cam- Cret.)
    Clathrodictydae.(Cam.- Perm.)
    Stromatoporidae. (Ord.- Perm.) evolving to the Disjectoporidae. (Perm.) evolving to the
        Stromatoporinidae (Trias-Cret)evolving to Order Hydroidea, (Recent).

Order Labechoidea. (Possibly derived from the Actinostromatidae). (Ord.- Perm.)
Order Sphaeractinoidea. (Possibly derived from the Disjectoporidae). (Jur.- Cret.)

Tripp (1929) believed that all stromatoporoids possessed characteristics approaching those of athecate hydroids. He did not propose a formal classification, but elaborated upon Nicholson's. In each of his two groups, based upon the nature of the lamellae and reticulum he had a further subdivision based upon microstructural features. He proposed three separate families for Mesozoic forms.

Tripp's 1929 Classification

Group 1: Closed tissue forms, with bipartite lamellae.
    Massive skeletal fibres.
    Porous skeletal fibres
Group 2: Open tissue forms. Simple lamellae.
    Massive skeletal fibres.
    Porous skeletal fibres.

Steiner (1932) used similar divisions, continuing analogies between Mesozoic forms and hydrocorallines. Her classification differed from Nicholson's and Dehorne's in that she placed the Ellipsactinidae within the hydractinoid group and the Milleporellidae in the milleporoid group. (Steinmann(1903) and Waagen and Wentzel (1887) concluded that the Ellipsactinidae, with their horizontal elements consisted of concentric laminae instead of lamellae, should be placed within the Tubularia).

Steiner agreed with Dehorne's placing of the Burgundidae, and also placed *Siphostroma* as intermediate between the hydractinoid and milleporoid groups, believing it to show many characteristics similar to forms belonging to the milleporoids, but with a microstructure that is similar to members of the Actinostromatidae. No diagnostic priorities had yet been established between the role of the microstructure and overall appearance of the skeleton in taxonomy.

Steiner(1932) stated that she was merely using the most practical classification to describe the fauna upon which she was working and that her classification might be illustrating convergent features. She based family definitions upon the form of the pillars and lamellae, and the presence or absence and form of zooidal tubes. Generic descriptions were based upon microstructure of the skeleton, the form of the astrorhizae, the relative developments of the pillar and lamellae and the form and dimensions of the zooidal tubes. Species she based upon the detail of the zooidal tubes, tabulae and the forms and dimensions of astrorhizal and skeletal elements.

Steiner's 1932 Classification

- Tubularia
- Hydrozoa
  - Stromatoporoidea:
    - Hydractinoidea:
      - Ellipsactinidae (Canavari)
      - Actinostromatidae (Nicholson)
    - Unnamed division:
      - Siphonostromatidae (Steiner)
      - Burgundidae (Dehorne)
    - Milleporoidea:
      - Stromatoporidae(Nicholson)
      - Milleporellidae (Yabe and Sugiyama)
  - Hydrocoralla
- Campanularids

In 1956, Steiner noted the considerable variability of the form of skeletal elements in *Burgundia trinorchii,* and suggested that a more consistent feature should be used to determine higher taxa. She noted that under the present classification system, the endpoints of her morphological continuum for this species would be placed within different sub-orders. She suggested that microstructure was a more consistent taxonomic criterion, but did not describe the microstructural type of *Burgundia.*

Although Steiner (1956) was the first to recognise variability in stromatoporoids, she did not extrapolate her findings to the logical extent of constructing a new taxonomic framework.

Yabe and Sugiyama (1935) also followed divisions similar to Tripp (1929). Their essential characters used in classification of the Japanese fauna were the development, form and microstructure of the vertical elements, the form of the interspaces and zooidal tubes, and surface features, the form of the coenosteum and mode of growth. They stated that '*Burgundia*, with massive or encrusting coenosteum composed of numerous concentric thin laminae supported by horizonal elements should, in our sense, be excluded from the stromatoporoids '. *Burgundia* was therefore not discussed.

Yabe and Sugiyama's Classification

Stromatoporidae: Trabecular skeletal elements, tabulate interspaces.
    Actinostromidae Nicholson
    Stromatoporidae Nicholson
Milleporelloidea: Vertical skeletal elements.
    Milleporellidae Yabe and Sugiyama : Tending to form closed tabulate tubes. Weak or no astrorhizae.
    Milleporiidae Yabe and Sugiyama: Large and small zooidal-type tubes. No astrorhizae.

Lecompte (1951) proposed five families within the Order Stromatoporoidea. These were based primarily upon the skeletal element arrangement and secondarily upon microstructure, although he emphasised the difficulty of using microstructure as a diagnostic feature. Lecompte followed his 1951 scheme in the 'Treatise of Invertebrate Paleontology' (1956), but he also included Mesozoic forms within the Palaeozoic framework. The basis for this 1956 classification is unclear and the descriptions brief.

Lecompte's 1956 Classification.

Class Hydrozoa.
    Order Stromatoporoidea (Cam.- Cret.)
        Actinostromatidae. (Cam.- Cret.)
        Clathrodictyidae. (Cam.- Jur.)
        Stromatoporellidae. (Sil.- Carb.?Trias.)
        Syringostromatidae. (Sil.- Jur.)
        Milleporellidae. (Jur.- Cret.)
        Milleporiidae (Jur.- Cret.)
        Labechiidae. (Ord.- Cret.)
        Aulaceridae. (Ord.- Sil.)
        Uncertain family. (Sil.- Jur.)

Yavorsky (1955) gives a brief discussion of the structure of Nicholson's classification and suggests modifications, including incorporation of six Mesozoic genera. Good block diagrams greatly aid his descriptions.

Galloway (1957) based his classification of Palaeozoic forms primarily on the microstructure, on the presence or absence of maculae ('dark' spheroidal bodies) within the skeletal elements. He assigned no taxonomic rank to these divisions. The maculate stromatoporoids corresponded to Nicholson's 'Milleporoid' group. Structural element arrangement was of secondary importance. He retained the four families founded by Nicholson and added the Clathrodictyidae (Kühn, 1939). The Idiostromatidae were recognised solely by their dendroid gross morphology. Galloway also gives a useful glossary of stromatoporoid morphological terminology, but with little attempt to eliminate repetitions and apparently useless terms.

In 1956, Hudson agreed with Kühn (1939) that the Milleporiidae were morphologically more closely comparable to the Hydroidea Dana, than to the Stromatoporoidea Nicholson and Murie, and allocated them to the former. Since the Mesozoic forms show little stratigraphic continuity with the Palaeozoic genera on one hand and the Recent Hydroidea on the other, their systematic allocation was controversial.

Hudson (1959, 1960) introduced a separate classification for Mesozoic forms. His two superfamilies were based upon the microstructure of skeletal elements and family subdivisions were made upon skeletal arrangement e.g.presence or absence of zooidal tubes. He introduced many new stromatoporoid terms to describe forms from the Upper Jurassic and Lower Cretaceous of the Middle East and was the first to denounce the practice of placing Mesozoic species in Palaeozoic genera. He made many revisions of forms which had been treated in this way. Turnšek (1966-1981) followed the taxonomic framework of Hudson. Believing the Burgundidae to possess irregular microstructure, she raised them to superfamiliy status in line with the two pre-existing superfamilies, erected by Hudson.

<u>Hudson's 1960 Classification</u>

Class Hydrozoa.
    Order Stromatoporoidea
        Superfamily Actinostromariicae.Orthogonal fibrous microstructure.
            Actinostromariidae
            ?Stromatorhizidae
            Siphostromidae
        Superfamily Milleporellicae. Cligonal fibrous microstructure.
            Milleporellidae
            Milleporiidae
            Parastromatoporidae

Incertae sedis. Family Burgundidae.

Yavorsky (1962) added little to previous classifications. He recognised Nicholson's four families to which he added Mesozoic genera. He also recognised two Mesozoic families, as had Lecompte (1956).

Flügel and Flügel-Kahler(1968) did not propose a formal classification, but suggested a division of forms into nine generic groupings. These were based upon microstructure and reticulum arrangement.

Bogoyavlenskaya (1965) suggested that astrorhizae were important in stromatoporoid classification. She divided astrorhizal types and partially based taxonomic divisions upon this. In 1969, she placed stromatoporoids as a subclass of the Hydrozoa, with five orders. Microstructures were not considered.

Bogoyavlenskaya (1974) proposed that more attention should be paid to stromatoporoid astogeny as well as astrorhizal form. Astrorhizae were used at generic level.

<u>Bogoyavlenskaya's 1969 Classification</u>
Order Labechiida
Order Clathrodictyda
Order Actinostromatida
Order Gerronostromatida
Order Syringostromatida

Kazmierczak (1971) divided stromatoporoids into informal morphological groupings and lineages. Astrorhizae were irrelevant to the classification as he believed them to be traces of organisms foreign to stromatoporoids.

Khalfina and Yavorsky (1973) produced a classification where divisions were based upon skeletal arrangement and microstructure, and phylogenetic considerations. Astrorhizae were not considered of higher taxonomic importance. Microstructures were viewed as derived features, believed to have arisen independently at different times in separate superfamilies.

Khalfina and Yavorsky's 1973 Classification

Superfamily Actinostromatacea.
Superfamily Clathrodictyacea
Superfamily Tienodictyacea
Superfamily Syringostromatacea
Superfamily Hermatostromatacea
Superfamily Stromatoporacea
Superfamily Labechiacea

Nestor (1974) presented a series of phylogenetic diagrams, which incorporated the following groupings.

Nestor's 1974 Classification

Superfamily Labechiacea
Superfamily Lophiostromatacea
Superfamily Clathrodictyacea
Superfamily Actinostromatacea
Superfamily Stromatoporacea

The latest classification to be proposed was that of Stearn (1980). He briefly reviewed previous classifications and presented a new framework for Palaeozoic forms based upon the form of structural elements. Microstructures were not used as diagnostic criteria because of their susceptibility to diagenetic alteration. Stromatoporoids were placed in the Porifera and divided into five orders. Some considerations of biomineralisation were included. However, Stearn (pers. comm.) has started to acknowledge the importance of, and extreme variability in stromatoporoid species and recognises the need for considerable modification of his taxonomic scheme.

Stearn's 1980 Classification

- Phylum Porifera
    - Class Stromatoporoidea
        - Order Labechiida
        - Order Actinostromatida
        - Order Clathrodictyda
        - Order Stromatoporellida
        - Order Stromatoporida

The many foregoing systems of classification reflect uncertainties in assessing the relative taxonomic value of features for making divisions above the generic level. Wide disagreement exists in the placement of major groups within the Stromatoporoidea and features are often considered without reference to proposed biological functions. The main controversy between classifications is the importance of microstructure of the skeletal elements compared with their arrangement. There are a large number of microstructures present in Palaeozoic forms, many of which may be diagenetic (Stearn, 1966). In Mesozoic forms microstructure is generally accepted to be of high-level taxonomic value.

1.2.3. PALAEOZOIC AND MESOZOIC STROMATOPOROIDS

The first bona-fide stromatoporoids have been recognised from the Middle Ordovician. They became abundant and widespread in the Silurian to Middle Devonian. However, numbers sharply declined at the end of the Frasnian (early late Devonian) although some members of the labechoids (thought to be the most primitive order) are found in the Famennian, but these became extinct at the end of the Devonian.

A second acme of stromatoporoids appeared in the Kimmeridgian (Upper Jurassic). Workers have related these to the Paleozoic stromatoporoids on one hand and the Recent Hydrozoa on the other. It should be noted however, that the type genus for 'stromatoporoids' is the Devonian genus *Stromatopora.* The Mesozoic forms possess a fibrous microstructure absent in most Palaeozoic forms. They appear to have become extinct by the end of the Cretaceous. Birenheide (1967, 1969) describes an Oligocene species, but attribution to the stromatoporoids is doubtful.

The transitional period in stromatoporoid history is from the lower Carboniferous to Upper Jurassic. This has been little studied and is poorly known. All published information suggests that the stromatoporoid fauna was considerably diminished. Yabe and Sugiyama (1935) compiled a part-list of late Palaeozoic occurrences of stromatoporoids mainly from Japan. Dehorne (1920), Steiner (1932) and Mori (1980) have doubted the validity of most of these forms, many of which are grouped within the Family Disjectoporidae. Most Triassic forms have been described by Vinassa de Regny (1901,1908, 1915) from Timor, and Wendt (1974) and Dieci et.al. (1974) from the Cassian Formation of Italy. Many sclerosponges have also been described from the Cassian Formation

(Wendt 1974, Dieci et al. 1974) but the basis for distinction between sclerosponges and stromatoporoids is not always clear in these works. In addition, Stanley (pers.comm.) has found new Upper Permian, Triassic and Lower Jurassic faunas from North and South America. These are as yet undescribed.

Figure 1.1 presents the diversity of stromatoporoids and sclerosponges through their geological history based upon the number of genera described as belonging to these groupings.

This scarce and uncertain record of stromatoporoid-like fossils in the Carboniferous, Permian and Triassic does not allow a systematic tracing of the geological history of the group, and has led to considerable debate. The similarities of gross morphology, structural arrangement and the presence of astrorhizae were sufficient for some workers to retain the word 'stromatoporoid' for both groups and to include Mesozoic and Palaeozoic genera together in the same families (Dehorne 1920, Kuhn 1939 and Lecompte 1956). Other workers felt that the discontinuous geological record and the microstructural difference between the Palaeozoic and Mesozoic forms warranted distinction of the two groups. Mesozoic forms were placed in a separate class within the Hydrozoa, termed the Sphaeractinoidea (Kuhn 1939, Galloway 1957, St.Jean 1967, Flugel and Flugel-Kahler 1968 and Flugel and Hotzl 1966).

Even though many workers recognised the two separate orders of stromatoporoid-like forms, they still continued to use the same generic names. Galloway 1957 implied that *Anostylostroma, Actinostroma, Hermatostroma* and *Stromatopora* are the ancestors of the Mesozoic stromatoporoids (Sphaeractinoidea). Comparable, but not identical microstructures to those of Mesozoic forms, are found in the Palaeozoic genera *Anostylostroma, Amphipora, Euryamphipora, Hammatostroma* and *Tienodictyon* (Stearn 1974).

Galloway (1957) thought the microstructure of *Tienodictyon* so similar to Mesozoic forms that he did not believe the specimen to have come from Palaeozoic rocks (Stearn 1969, 1974). The cellular (Stearn 1966) or maculate (Galloway 1957) tissue typical of many Palaeozoic forms has not been found in Mesozoic genera, even within skeletal arrangements thought similar (e.g. *Stromatopora* and *Steinerella*).

Stearn (1974) believes there is more microstructural similarity between the Palaeozoic and Mesozoic forms than has been suggested by previous authors, and that retention of two separate orders is not justified.

The geological 'gap' in the stromatoporoid history remains unresolved until further examination of possible stromatoporoid-bearing facies and reexamination of described intermediate forms. Galloway (1957) and St.Jean (1967) believe that the record can be best explained by a late Devonian extinction, then appearance of a group of hydrozoans showing convergent evolutionary features. Vacelet (1984) and Mistaen (1984) believe that the stromatoporids are calcified sponges, and suggest that the 'gap' represents a period of decalcification when the sponges persisted as (unfossilisable) soft-bodied forms. These theories are discussed in Chapter 5.

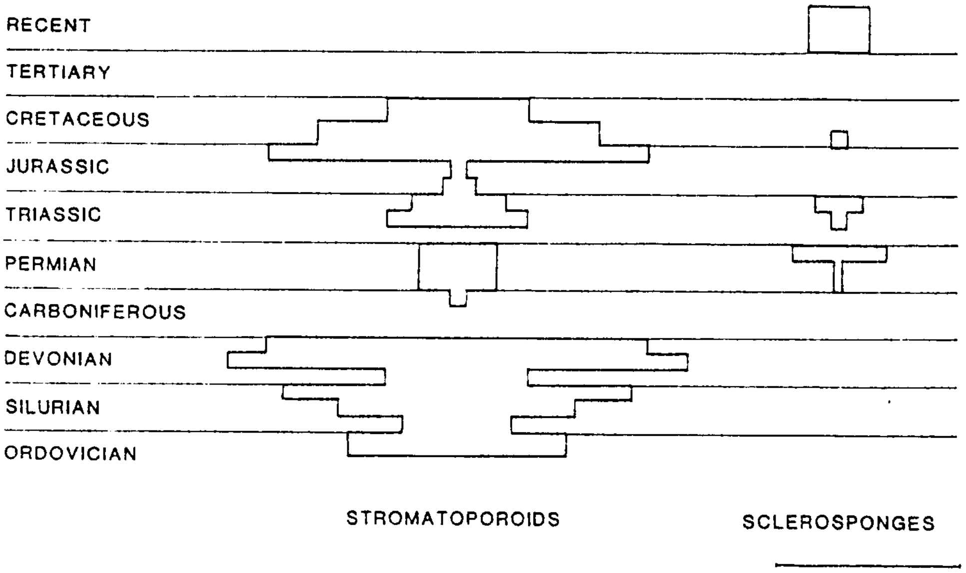


Figure 1.1 : Diversity of stromatoporoids and sclerosponges in terms of numbers of described genera attributed to these groups. (Partly after Wendt (1979) and Kazmierczak (1985)).
Scale bar = 10 genera.

1.3. GENERAL MORPHOLOGY OF LATE MESOZOIC STROMATOPOROIDS

Figure 1.2 shows the main morphological features of late Mesozoic stromatoporoids. The numbers below and in the figure refer to the various magnifications of inspection. The definition of terms can be referred to in the Glossary.

1. The gross morphology of the skeleton is highly variable and forms a continuum, where the end-points are encrusting, massive or branching forms. A single specimen can pass through several gross morphological types during development, often as an environmentally induced response.

Individuals range in size from a few millimetres to several metres in diameter.

2.There are few surface features. Sometimes the surface bears elevations, ranging from low relief mounds to pronounced chimneys. In well preserved specimens, there may be a stellate system of grooves, known as astrorhizae, or a system of single pores. The astrorhizae peter out into the fine meshwork of the skeleton.

3. The calcareous skeleton is constructed of radial or vertical elements (pillars or columns) and concentric or horizontal elements (laminae or pillar-lamellae). Either structure may be dominant, or where elements form reticulum, there may be no differentiation. A series of horizontal and vertical canals ramify the individual, which are in communication with the open framework of the skeleton and in turn open out onto the surface in the form of astrorhizae. Filling tissue might section-off older parts of the skeleton.

4. Four primary microstructures are known:

a) Irregular

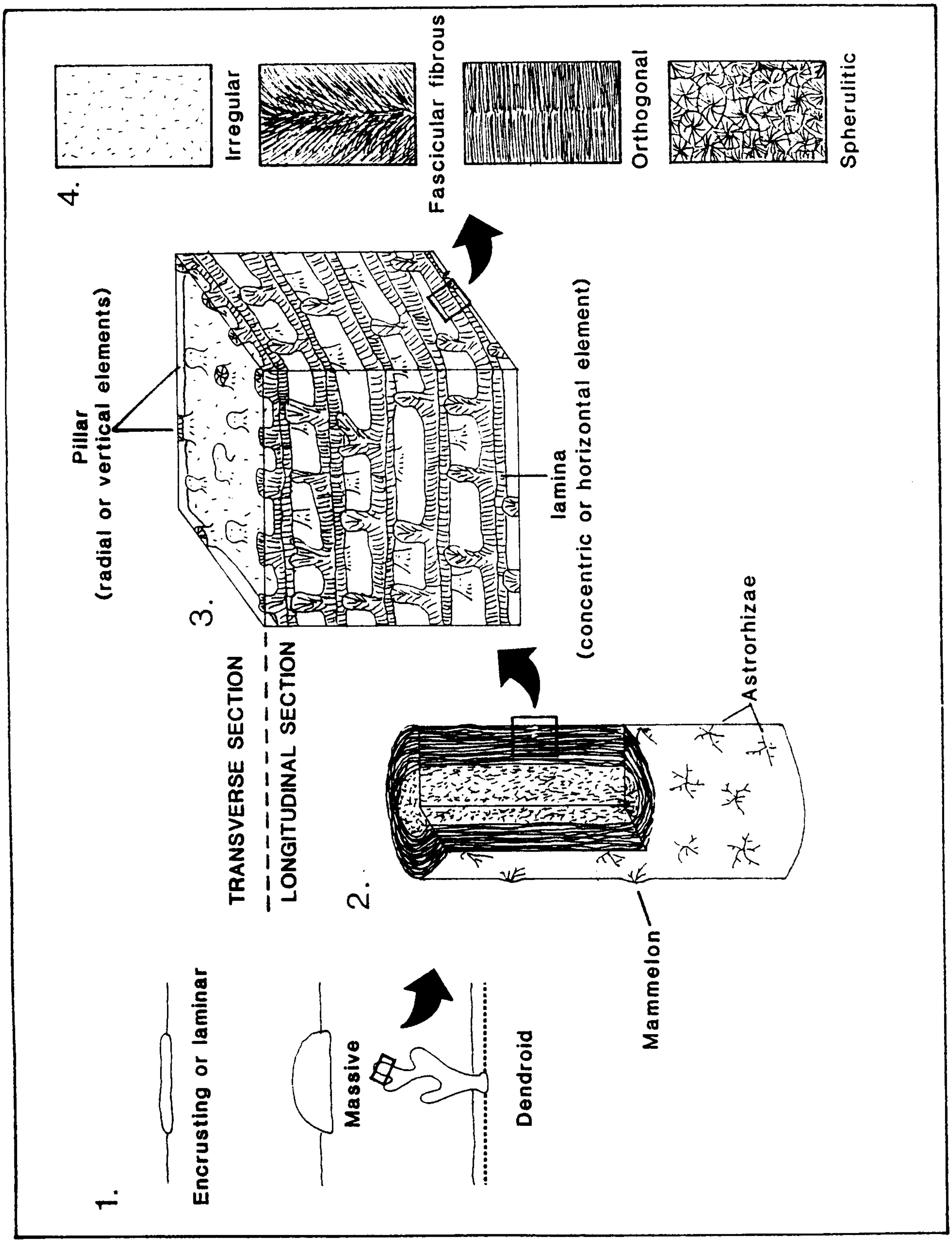
b) Fascicular fibrous

c) Orthogonal fibrous

d) Spherulitic

Some species possess combinations of these microstructures. Microstructure is decribed in detail in Section 2.2.1.2.

Figure 1.2: General morphology of Mesozoic stromatoporoids.
1. Gross morphology;
2. Surface features;
3. Internal structure;
4. Microstructure of skeletal elements.



CHAPTER 2

BIOLOGICAL AFFINITY OF MESOZOIC STROMATOPOROIDS

"Reasoning by analogy may not be the orthodox method of scientific analysis, but many conclusions in palaeontology have been reached in this way ...... and often cannot be reached in any other. There are a large number of fossils whose only guide to their biological affinity are faint analogies with living forms..... Here a palaeontologist without a good imagination is lost" *Twitchell 1929 p. 270.*

INTRODUCTION

Five main theories have been proposed for the biological affinity of stromatoporoids and of these the cnidarian and poriferan theories have gained most support. Discussion has largely concerned Palaeozoic forms, which are most abundant and widespread. However, they show secondary characteristics that differ from Mesozoic forms; therefore some of the arguments pertinent to Palaeozoic forms are only considered in detail here where relevant.

In this chapter, evidence to support the poriferan theory is presented for Mesozoic stromatoporoids and representatives are placed as precisely as possible within the Recent poriferan taxonomic framework. The consequences of these placings are discussed, but broader considerations as well as phylogenetic repercussions are developed in Chapter 5.

2.1. THE FIVE THEORIES OF BIOLOGICAL AFFINITY

Most theories for the affinity of stromatoporoids have been based not upon presentation of new morphological data, but upon negating the arguments of opposing theories and proposals of misguided 'homologies'. Once a palaeontologist assumes a paradigm for the biological affinity of a problematic fossil group, he will interpret all morphological characters from that particular stance. However, if one takes a different paradigm for that group, the same morphological characters will be interpreted in a different way. Therefore, objective appraisal between the two sets of interpretations is extremely difficult, as circular arguments are inevitable.

From evidence found in this study, I have assumed poriferan affinity for Mesozoic stromatoporoids. My criticisms of other paradigms can only be based upon this foundation.

The arguments for each theory are individually listed below, followed by critical appraisal (indented) and discussion where appropriate.

2.1.1. ANTHOZOAN AFFINITY

Many authors have postulated stromatoporoids to be anthozoans (See Section 1.2.1.). The most recent advocate is Mori (1982,1984), who advanced the following arguments:

1) The relationship between astrorhizal canals and the surrounding skeleton in stromatoporoids is comparable to that found between corallites and the coenosteal skeleton in scleractinian corals. He argues that the presence of marginal walls, tabulae in the astrorhizal canals, and skeletal thickening around these canals, are homologous with similar features found in the zooid/coenosteum relationship in the Cnidaria.

> The presence of tabulae in the astrorhizal canals can be explained in terms of a thinly-encrusting sponge, which separated away from abandoned parts of the skeleton as it grew. Several Recent calcified demosponges e.g.*Ceratoporella*, and *Acanthochaetetes* , secrete tabulae.
>
> The tubular or 'calicular' nature of many chaetetids (formed by marginal walls) has been given as evidence of a zooid or polyp influence upon the calcareous skeleton. However, living "chaetetids" (*Ceratoporella*, *Acanthochaetetes*) are known to be sponges.
>
> The skeletal thickening around astrorhizal canals in Palaeozoic stromatoporoids has not been noted in Mesozoic forms.

2) A great similarity is evident between the skeletal microstructure of stromatoporoids and scleractinian corals.

> Palaeozoic stromatoporoid microstructures are poorly preserved and described, since the calcareous skeleton was probably originally aragonitic; Mesozoic stromatoporoid skeletons are much better preserved and known. However, both groups share only one

microstructural type in common with scleractinian corals - the fascicular fibrous microstructure. Other microstructures found in Mesozoic stromatoporoids are known only from Recent and fossil sponges.

3) The essential skeletal features of stromatoporoids (laminae, pillars, cyst plates and amalgamated structures) are absent in sclerosponges.

Pillars are found in Recent sclerosponges e.g. *Calcifibrospongia actinostromariodes.* Laminae and pillars are found in representatives of many different phyla e.g. trepostome bryozoans. Not all Palaeozoic, and no Mesozoic stromatoporoids possess cyst plates and amalgamated structures. These are clearly not essential features of stromatoporoids.

4) Canals can be seen to cut across several laminae and sometimes across a marginal wall, indicating formation of the laminae after the astrorhizae. Recent sclerosponges lack traces of walls in their exhalent canals, unlike stromatoporoids which possess walled astrorhizae. In addition, astrorhizae are not generally confined to the skeletal surface as are sclerosponge exhalent canals.

No astrorhizae cross-cutting laminae have been noted in Mesozoic forms. Mori's example (1984 text-fig.1) may not be an astrorhizal canal. It could be a parasitic boring.

The astrorhizae of the Recent sclerosponges *Astrosclera* and *Calcifibrospongia* are not confined to the skeletal surface, but penetrate up to 2cm. into the calcareous skeleton, and both these sclerosponges possess 'walled' astrorhizae (Hartman and Goreau, 1970). Homologous structures in Mesozoic stromatoporoids are directly comparable and similarity of function can be confidently inferred.

5) The obvious "colonial" nature of stromatoporoids (the repeated stellate astrorhizal systems) is reminiscent of scleractinian corallites (Nicholson 1886, Hudson 1960, Turnsek and Barbulescu 1969).

The similarity between the hexameral symmetry of corals and the astrorhizae of stromatoporoids has led to confusion between the two groups, especially in forms where the corallites are not walled, e.g. the microsolenids. Brien (1967) discusses the apparent 'colonial' nature of thinly encrusting demosponges, which divide their aquiferous system into repeating units of oscula and stellate excurrent canals, giving the appearance of coloniality, but this is in no way homologous to the repetitive nature of scleractinian corallites. Microsolenid corals can always be distinguished from stromatoporoids by their characteristically beaded septa. The distinction between a colonial and a non-colonial organism appears to be ultimately a metaphysical one, which may transcend taxonomic boundaries and therefore cannot be used to argue affinity to a particular phylum.

2.1.2. HYDROZOAN AFFINITY

Before the discovery of sclerosponges, many authors (Flugel 1958, Turnsek 1969 -1981) preferred the allocation of the stromatoporoids to the Hydrozoa, following the innovative work of Carter (1878).

Their arguments are as follows:

1) The astrorhizae are analogous to the coenosarcal grooves, or hydrorhiza of Hydrozoa e.g. *Hydractinia*, or they may be traces of the tubes that contained specialised zooids, e.g.reproductive zooids. Astrorhizae are confined to one interlaminar space and may not always taper towards their tips, unlike sponge canal systems which vary in diameter according to position and ramify within the skeleton.

> Stromatoporoid and sclerosponge astrorhizae may either be expressed on the surface, or ramify within the skeleton. However, astrorhizal grooves on the skeletal surface and those preserved within the skeleton are always seen to converge on a central common opening. Away from that, they then peter out and branch into the open meshwork of the skeleton. The coenosarcal grooves of hydrozoa are expressed only on the skeletal surface; they are uniform in diameter and do not converge to a central point or opening, or peter out into the general meshwork of the skeleton.

2) Since the stromatoporoids are extinct and possess many unique features, the non-uniformity of the astrorhizal canal diameter as opposed to the hydrozoan hydrorhiza is a result of evolutionary divergence between the two structures (Mori 1984).

An argument evoking evolutionary divergence can be used to explain away any unwanted characteristic.

3) Some stromatoporoids possess zooidal tubes, as is found in Recent Hydrozoa housing zooids (Carter 1878, Galloway 1957).

Following the studies of Heinrich (1914) and Tripp (1929) of Recent gymnoblastic hydroids, the proposition that the stromatoporoids possess zooidal tubes (like the cyclosystems of the Recent *Millepora*) proved erroneous. No stromatoporoids possess zooidal tubes. Stromatoporoids could only then be compared with non-gymnoblastic hydroids e.g. *Hydractinia* , which secrete their skeleton only at the base of the colony.

What have been interpreted as zooidal tubes are probably tabulate oscula or tabulate interskeletal spaces between adjacent pillars. In a two-dimensional thin section these structures give the impression of three-dimensional tubes.

4) Stromatoporoid connective tissue is similar to that of *Millepora.*

The Mesozoic stromatoporoid skeleton is similar to *Millepora* only in terms of possessing laminae and pillars but its construction is quite different.

5) Interruptions of growth, latilaminar structures and a tendency to form thick reefal deposits are observed mainly in the Cnidaria (Mori 1984).

Growth interruptions (e.g. epithecal deposits) are known from Recent sclerosponges e.g. *Calcifibrospongia sp.* Although latilaminar structures are not known from Recent forms, many 'sclerosponges' do show a banded periodicity of growth (e.g.*Ceratoporella*,)even though found in tropical seas where little seasonality exists. Latilaminae in fossil 'stromatoporoids' may illustrate their sub-tropical niche, in a more seasonal climate.

The Cnidaria are not the main phylum which has produced reefal deposits in the geological record; many examples of calcareous sponge, bivalve and algal reefs are known from the Mesozoic.

6) The presence of tabulae in the astrorhizae indicates that they could not serve as a poriferan aquiferous filtration system. Tabulae in the astrorhizal canals are comparable with those developed

in the gastriopores (digestive zooids) and dactylopores (feeding zooids) of Recent *Millepora* (Carter 1878).

> Tabulae in astrorhizae can be explained by the animal sectioning off abandoned parts of the skeleton as it grew. Some Recent sclerosponges e.g. *Ceratoporella* produce a continuous secondary backfill to achieve this. Tabulae were not present in the astrorhizal canals when they were occupied by living tissue and functioning as a water-conducting system .

7) The apparent lack of sponge-type spicules in stromatoporoids suggests that they were not poriferan.

> Sponge-type spicules have been found in both Palaeozoic and Mesozoic stromatoporoids (e.g. Newell 1935, Wood and Reitner 1986).

8) Tabulae are characteristic of the Cnidaria.

> Tabulae are known from the Recent 'sclerosponges' *Ceratoporella* and *Calcifibrospongia* and are therefore not exclusive to cnidarians.

DISCUSSION

Many of the arguments for cnidarian affinity are contradictory. Mori (1984) argues for the anthozoan affinity that very few stromatoporoids possess astrorhizae which are confined to the skeletal surface, whereas proponents of the hydrozoan affinity suggest that the interlaminar, two-dimensional nature of astrorhizal systems supports their analogy with the coenosarcal grooves on the surface of hydrozoans.

Many of these arguments against poriferan affinity rest the case on the non-similarity of Palaeozoic stromatoporoids to the small number of Recent sclerosponge species. Stromatoporoids have not been considered in terms of features common to the Porifera as a whole.

2.1.3. FORAMINIFERAN AFFINITY

Classification of stromatoporoids among the Foraminifera has been based upon the resemblance of the Palaeozoic genus *Actinostroma* to the encrusting foraminifer *Gypsina plana*. The main advocate of this analogy was Hickson (1934), followed by Parks (1935).

They asserted:

1) Analogy by appearance of the reticulate structure seen in tangential sections of both genera.

> Calcareous organisms from many different phyla possess a reticulate skeletal arrangement e.g. Bryozoa, Anthozoa.

2) The coarse vertical astrorhizal canals of *Actinostroma* are interpreted as passages for protrusion of pseudopodia.

> There is no evidence to support this assertion.

3) Lamellae in *Stromatoporella* can be explained as a consequence of chamber alignment, with pillar supported interspaces serving only for separation of their rows.

> Only some stromatoporoids possess lamellae.

4) The basal layer of chambers different from others in the skeleton in *Actinostroma* , corresponds to the microspheric or megalospheric proculus of Foraminifera.

> Stromatoporoids do possess a basal layer of tissue different from the mature parts of the skeleton; all encrusting organisms possess juvenile tissue. This basal layer in no way corresponds to a foraminiferan proculus.

5) The occurrence of tubes called caunopores, in some stromatoporoids, is suggested to represent one of the alternating generations observed among foraminifers.

> Caunopore tubes are known to belong to tabulate corals symbiotic with stromatoporoids (Twitchell 1929).

6) Variability in size, form, and arrangement of chambers, is observed in both stromatoporoids and Foraminifera.

Chamber size variability is not specific to stromatoporoids and Foraminifera. Many encrusting organisms, from different phyla, show variability of chamber size.

DISCUSSION

The resemblance of two genera of Palaeozoic stromatoporoids to one species of Foraminifera cannot be extrapolated to a biological interpretation of the whole stromatoporoid group. These arguments relate only to secondary characters, and there is no evidence for these comparisons. The comparisons only refer to superficial similarities shared by all encrusting organisms.

2.1.4. CYANOBACTERIAL AFFINITY

This theory was proposed by Kazmierczak (1976, 1981, 1983) and he remains the only proponent.

1. He interprets the astrorhizae as traces of a plant or animal symbiotic or parasitic with the stromatoporoid (1969). This explanation is based upon specimens of *Hermatostroma* and *Stromatoporella* from the Devonian of Poland which show large tubes scattered throughout the coenosteum.

The large tubes described by Kazmierczak may be symbiont traces, but they are not typical of stromatoporoid astrorhizal canals. Astrorhizae are regularly spaced and constant in form within an individual and clearly form an integral and essential part of stromatoporoids. Criteria for this were given by Stearn (1975). The presence of astrorhizae has been a working diagnostic feature for 'stromatoporoids' and they are found in individuals throughout the history of this group. They cannot be explained away as traces of a foreign organism.

2. In 1983 Kazmiercak presented S.E.M. photographs of spherical bodies within a stromatoporoid skeleton. These forms are of the same dimensions as Recent coccoid bacteria/algae and Kazmierczak regards their presence as conclusive proof of cyanobacterial affinity for stromatoporoids.

The work of Vacelet (1985) has shown that all Recent sclerosponges (as well as corals) possess a large, symbiotic bacterial flora. The coccoid bodies desribed by Kazmierczak could be fossilised remains of this flora , neomorphic crystals or even artefacts.

3. He considers the overall laminate appearance to indicate algal bacterial affinity, comparing the stromatoporoid morphology with stromatolites.

Riding and Kershaw (1977) stated the improbability of organisms as simple as cyanobacteria being responsible for the formation of the complex structures, in addition to the lamellae, seen in stromatoporoids.

2. 1. 5. PORIFERAN AFFINITY

Since the discovery of the sclerosponges, most workers believe stromatoporoids to be sponges (Stearn 1972, 1975, Stock 1984). However, lack of indisputable sponge-type spicules has sustained uncertainty and prevented full acceptance.

The arguments for poriferan affinity have been as follows:

1. The astrorhizae of stromatoporoids are homologous to the excurrent canal system of sponges, and represent the traces of this system within or upon the calcareous skeleton.
2. The microstructure of the calcareous skeleton resembles that of the sclerosponges.
3. Sclerosponges bear tabulae, e.g.*Acanthochaetetes* spp. Therefore, this is not an exclusively cnidarian feature. Tabulae secreted across the astrorhizal canals and inter-skeletal spaces served to section off abandoned parts of the skeleton as the animal grew.
4. Spicules are not necessary to prove poriferan affinity. However, spicules have been noted within the skeletons of stromatoporoids, by Kirkpatrick (1912a), Twitchell (1929), Newell (1935) and Hartman and Goreau (1970). Those noted by Hartman and Goreau were considered to be calcite pseudomorphs of originally siliceous spicules. Spicules in Recent sclerosponges corrode during life, and so preservation in fossil material would be highly fortuitous. This would explain the apparent lack of documented spicules in stromatoporoids.
5. There are no suitable receptacles for the lodgement of zooids. Zooidal tubes do not exist in stromatoporoids.
6. The encrusting character of stromatoporoids is very like that of Recent and fossil sponges.
7. The skeletal framework resembles that of a sponge spicule network.

We must consider the evidence in detail.

2. 2. EVIDENCE FOR THE PORIFERAN THEORY.

Until the 1960's, stromatoporoids were generally considered to be calcified hydrozoans. The rediscovery of calcified sponges, the sclerosponges, in the deep fore-reef of Jamaica renewed interest and controversy in the stromatoporoid problem (Hartman and Goreau, 1966, 1970, 1972, 1975 and Hartman, 1969, 1979). It was proposed that the sclerosponges were "living fossils" and a relict fauna of Palaeozoic and Mesozoic reef-buiders, the stromatoporoids, chaetetids, and some tabulate "corals" (Hartman and Goreau 1970). They presented photographs of sponge-type spicule "ghosts" within the calcareous skeleton in Mesozoic stromatoporoids, but these were dismissed by many workers as being of diagenetic origin (Hartman, pers. comm.).

Evidence collected in this study suggests that the observations of Hartman and Goreau were valid, and their interpretation correct.

2. 2. 1. CONSTRUCTIONAL MORPHOLOGY.

2. 2. 1. 1. Spicular skeleton.

The presumed lack of spicules in stromatoporoids has been explained by the following possibilities:

1. Stromatoporoids were not sponges and therefore did not secrete spicules.
2. Stromatoporoids were sponges, but spicules were not secreted.
3. Spicules were secreted, but not incorporated into the calcareous skeleton and therefore not preserved e.g. acanthochaetetids.
4. The spicules present dissolved during the life of stromatoporoids (as in Recent sclerosponges), and were additionally susceptible to diagenetic loss.

There have been four reported finds of spicules within the calcareous skeleton of stromatoporoids. Kirkpatrick (August 1912) stated that he had found large numbers of sponge-type spicules in Palaeozoic stromatoporoids which confirmed his belief of their poriferan affinity. However, in the next month he refuted these findings (Kirkpatrick 1912b) and these 'spicules' have never been illustrated or verified by any other worker. In 1929 ,Twitchell reported spinose structures which he proposed to be spicules, from *Stromatopora centratum* (Silurian). These were examined by Finks (1986) and found to be composed of organic material, which he suggested is the remains of boring algae. Newell (1935) reported spicules from *Parallelopora mira* (Lower Carboniferous). However, they were dismissed by many workers as being of diagenetic origin, e.g.Stearn (1972). Stearn (op. cit.) agreed that *P.mira* does not possess the dissepiments and laminar structures crossing the galleries which he believes to be characteristic of a stromatoporoid and consequently sediment has infiltrated the open framework due to this lack of filling tissue. But, Mesozoic stromatoporoids do not characteristically show dissepiments and laminae. *P.mira* was interpreted by others as a true calcareous sponge (Flügel and Flügel-Kahler 1968). However, Finks (1983) reports that *P. mira* is found associated with calcareous sponges whose calcite spicules are unpreserved. Ron Clark (pers. comm.1986) has re-examined these specimens of *P.mira* and the species undoubtedly bears pseudomorphs of originally siliceous tylostyles and styles (Plate 20, fig.a). It appears that *P. mira* is a true spiculate stromatoporoid and may be one the ancestors of some Mesozoic stromatoporoids. This is discussed in section 5.2.1.

Hartman and Goreau (1970) suggested that several Mesozoic species showed clear, elongate areas within the pillars which were interpreted as calcite pseudomorphs of siliceous spicules. Since the nucleation points of radiating calcite fibres often appear "light" under transmitted light, these structures were considered diagenetic or non-existent by other workers (Hartman, pers. comm.)

Evidence presented in this section suggests that the observations of Hartman and Goreau were correct. Spicule pseudomorphs have now been found within the calcareous skeletons of 10 genera and 16 species of Upper Jurassic and Lower Cretaceous stromatoporoids (Wood and Reitner 1986, Wood in press). Table 2.1 presents details of the spicule findings together with information on the calcareous skeleton.

Spicules are clearly not absent or rare in Mesozoic stromatoporoids. Few workers have looked for spicules with any concentration and it is only since the discovery of sclerosponges that palaeontologists have been furnished with a search image for their recognition.

It should be noted that although sponges are not the only organisms to produce spicules (so do holothurians and octocorals) the spicules found in stromatoporoids are comparable in morphology and size only with those found in sponges.

In all examples studied, spicules are preserved as pseudomorphs (calcite, pyrite or silica) within the central zone of the skeletal elements. The pseudomorphs are of styles (or acanthostyles), tylostyles, strongyles and triaxines (or tetraxines) and are variously arranged within the calcareous skeleton of different genera. The ten spiculate genera can be sub-divided into four morphological types, each characterised by different spicule morphologies and arrangements and these coincide with four different microstructures of the calcareous skeleton. Individual spicule morphology and terminology is illustrated in Figure 2.1., which shows most spicule types referred to in this thesis. The four morphological types of spiculate stromatoporoids are described below and illustrated schematically in Figure 2.2.

These spiculate species are formally re-described in Chapter 4.

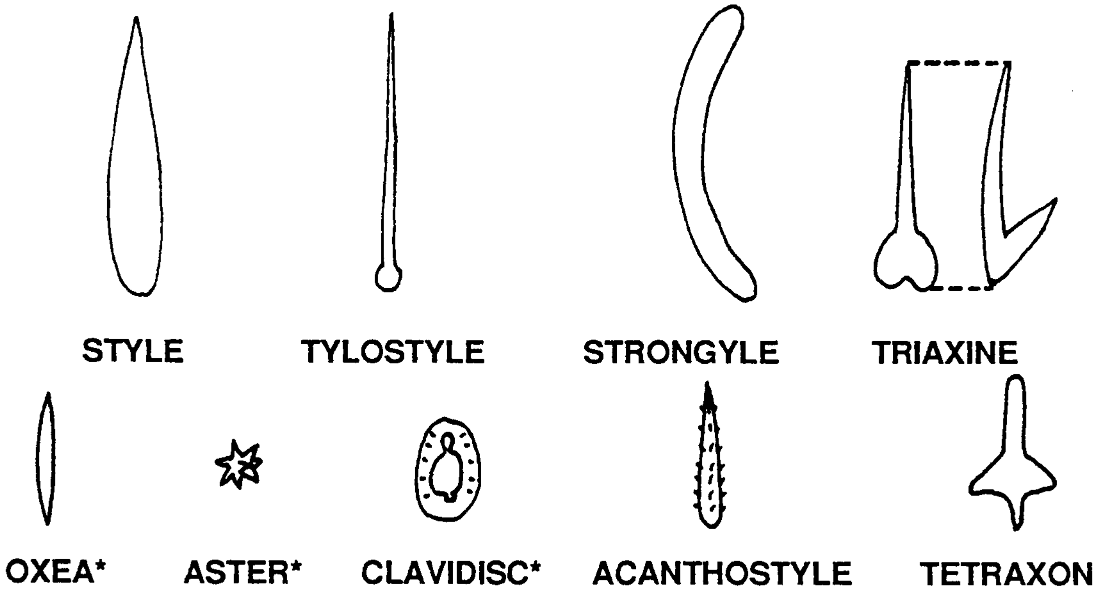
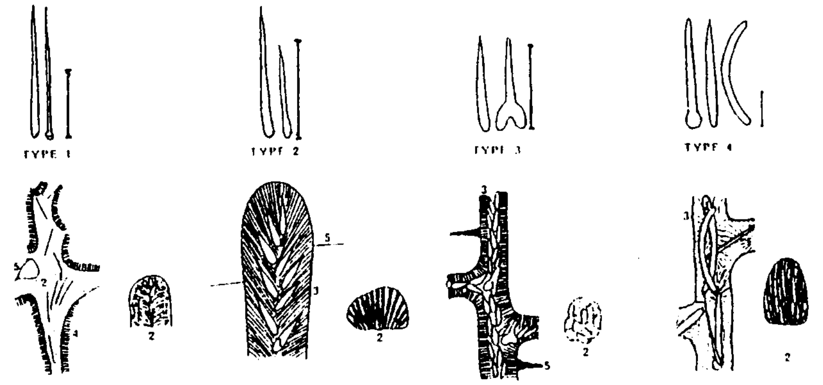


Figure 2.1 Terminology and morphology of spicule types found in Mesozoic stromatoporoids (top row) and other calcified demosponges (bottom row). Microscleres are asterisked.

Table 2.1: Mesozoic stromatoporoid spicule data (Modified after Wood and Reitner 1986 ,and Wood , in press).

SPECIES	AGE	LOCALITY	CALCAREOUS SKELETON			SPICULAR DATA				
			GROSS MORPHOLOGY	MICRO STRUCTURE	TRACES OF AQUIFEROUS SYSTEM	TYPE	DISTRIBUTION	PRESENT MORPHOLOGY	DIMENSIONS	
									LENGTH (um)	DIAMETER (um)
H DEHORNELLA CRUSTANS H5170c H5168a	L. KIMMERIDGIAN	MAKHTESH HAITHIRA, ISRAEL	NODULAR ENCRUSTING	FASC. FIB.	ASTRORHIZAE	STYLE	INTRAMURAL S.m.	CALCITE PYRITE	90 - 135	13.5 - 17
H New gen.n.sp.A JR 1001	U. APTIAN	ERENO, N. SPAIN	LAMINAR, ENCRUSTING	FASC. FIB.	ASTRORHIZAE	STYLE ACANTHOSTYLES	INTRAMURAL m.	CALCITE	75 - 250	5 - 20
STEINERIA SOMALIENSIS H4897b	LWR. KIMMERIDGIAN	MAKHTESH HAITHIRA ISRAEL	DENDROID	FASC. FIB.	TABULATE OSCULA ?astrorhizae	STYLE	INTRAMURAL S.m.	PYRITE	15 - 25	6.5 - 9
SHUQRAIA HETHIRA H5034a	L. KIMMERIDGIAN	WADI HATHIRA, ISRAEL	DENDROID	FASC. FIB.	ASTRORHIZAE	STYLE	INTRAMURAL S.m.	PYRITE	60 - 80	5 - 7
H ACTOSTROMA NASRI H 4893a	LOWER KIMMERIDGIAN JURASSIC	MAKHTESH HETHIRA ISRAEL.	MASSIVE or DENDROID	ORTHOGONAL FIBROUS	ASTRORHIZAE	STYLES	S.s. INTRAMURAL	CALCITE and PYRITE	80 max.	10 max.
ACTINOSTROMARIA SP. H 5480	OXFORDIAN - KIMMERIDGIAN JURASSIC	TRNOVSKI GOST, JUGOSLAVIA	MASSIVE	ORTHOGONAL FIBROUS	ASTRORHIZAE	STYLES and TRIAXINES	S.S. INTRAMURAL	CALCITE	100 max. 120 max.	10 max. 20 max.
PARASTROMATOPORA LIBANI H4789	M. KIMMERIDGIAN	TOUMATT, LEBANON	MASSIVE, NODULAR	FASC. FIB.	ASTRORHIZAE	STYLE	INTRAMURAL S.m.	PYRITE	60	18
H PROMILLEPORA KURNUBI H4898	L. KIMMERIDGAIN	MAKHTESH HAITHIRA, ISRAEL	DENDROID	FASC. FIB.	TABULATE OSCULA ?astrorhizae	STYLE	INTRAMURAL S.m.	PYRITE	50	12
P ACTINOSTROMARIANINA LECOMPTI H4608a H4608b	U. KIMMERIDGIAN	ALAM ABYADH, ARABIA	MODULAR ENCRUSTING FASCICULATE	GRANULAR AND ORTHOGONAL	ASTRORHIZAE	?TYLOSTYLE	INTRAMURAL S.s	CALCITE	180	8
ASTROPORINA ORIENTALIS H4850b	OXFORDIAN	AIN SAFRA YANTA LEBANON	NODULAR	FASC. FIB.	ASTRORHIZAE	STYLE	INTRAMURAL S.m.	CALCITE	100 - 140	32 - 18

H: HOLOTYPE, P: PARATYPE, FASC. FIB.: FASCICULAR FIBROUS, S.m.: SUB-PARALLEL TO MICRO STRUCTURAL FIBRES, S.s.: SUB-PARALLEL TO GROWTH AXIS OF SKELETON



	Actinostromarianina lecompti	Dehornella crustans	Actinostromaria sp.	New gen. n.sp. A
SPICULES 1 TYPE	Style Tylostyle	Style acanthostyle	Style and triaxine	Style, Tylostyle and Strongyle
2 ARRANGEMENT	Radial	Plumo-reticulate	Reticulate	Radial
CALCAREOUS SKELETON : 3 PRIMARY	Irregular	Fascicular fibrous	Orthogonal fibrous	Spherulitic
4 SECONDARY	Orthogonal fibrous	———	———	———
5 FILLING TISSUE	Tabulae	Tabulae	Fibrous Tabulae	———
REMARKS	Calcareous skeleton initiated by meniscus around spicule framework	Calcareous skeleton initiated in penicillules from spicule bases	Calcareous skeleton initiated perpendicular to dense spicule framework	Calcareous skeleton initiated around spicule lattice

Figure 2.2. Four skeletal types found in Mesozoic 'stromatoporoids', expressed in terms of spicule type, arrangement and relationship of this framework to the microstructure of the calcareous skeleton. Homologous structures are compared in the table below (modified from Wood, In press). Arrangement refers to the longitudinal section through an individual. Spicule scale bar = 100 µm.

Skeletal Type 1 Plate 1 ,Figs.a-f.

Representative: *Actinostromarianina lecompti* Hudson, 1955a

This genus was placed by Hudson into the Actinostromariidae Hudson, 1955a as he believed it to possess the orthogonal fibrous calcareous microstructure characteristic of that family . Contrary to Hudson's observations, *A. lecompti* possesses a primary calcareous skeleton of irregular microstructure (fine micritic) and a secondary skeleton of orthogonal fibrous microstructure. There is no microstructural differentiation of the skeletal elements, which form a network of pillars (radial elements) and pillar-lamellae (discontinuous and concentric elements, see Glossary) joined by tabulae of granular microstructure (Plate 1 ,fig.b).

Spicules are preserved as pyrite, and rarely calcite pseudomorphs. They are long, thin styles or tylostyles (Plate 1, fig.d, maximum 180 µm. length, 10 µm. width) which form a dense axial zone of parallel aligned spicules (Plate 1,fig.c) and which then radiate in tracts forming a fibro-reticulate arrangment towards the outer edges of the skeleton (Plate 1,fig.a). The preservation of the spicules is too coarse to detect with any certainty, the presence or absense of a basal boss enabling differentiation between styles and tylostyles.

The primary calcareous skeleton of irregular microstructure (fine micritic) has a meniscus-like form where it drapes over the projecting spicules (Plate 1,fig. e). The spicule pseudomorphs do not appear to pierce into the interskeletal spaces and appear to form the framework for the subsequent precipitation of the calcareous skeleton (Plate 1, fig.f.).

Skeletal Type 2: Plate 2, figs.a,b.

Representatives: *Dehornella spp., Shuqraia sp., Parastromatopora sp., Astroporina sp., Promillepora sp. , Steineria sp.*

All forms in this type are members of the superfamily Milleporellicae Hudson, 1959a. The calcareous skeleton is formed of radiating columns of fascicular fibrous microstructure, connected by irregular or fibrous tabulae (Plate 2, fig.a).

The spicules have been found preserved as pyrite, calcite or (secondary) silica pseudomorphs. They are club-shaped styles or possibly acanthostyles (50 - l35 μm length, 5 - 17 μm width) which radiate upwards with tapering tips in a plumose arrangement sub-parallel to the microstructural fibres of the columns, which initiate in tufts at the spicule bases (Plate 2 ,fig. a).

Spicules are found in the columns only, and sometimes project into the interskeletal spaces (Plate 2,fig. b). They have been found in profusion in some specimens of *Dehornella crustans.* In other species, spicules are found singly or in clusters but are obviously the remnants of a far denser spicular skeleton whose present distribution has been diagenetically determined.

Although spicule type remains constant in all representatives of this group, spicule dimensions and arrangements vary, providing generic and species recognition criteria which are further discussed in Chapters 3 and 4.

PLATE 1: TYPE 1 SPICULE ARRANGEMENT *Actinostromarianina lecompti* Hudson, 1955a

All light photomicrographs of B.M.(N.H.) H 4608a . Alam Abyadh, Arabia. Upper Kimmeridgian.

Figure a: Longitudinal section showing fibro-reticulate skeletal arrangement and latilaminae formed by intermittent precipitation of the orthogonal fibrous rim (arrowed).
Scale bar = 5 mm.

Figure b: Longitudinal section showing reticulate network of pillars (vertical) and pillar-lamellae (horizontal), with granular tabulae. Primary irregular calcareous skeleton only in lower part of photograph; secondary orthogonal fibrous rim development in upper part of photograph. Older area at base.
Scale bar = 200 µm.

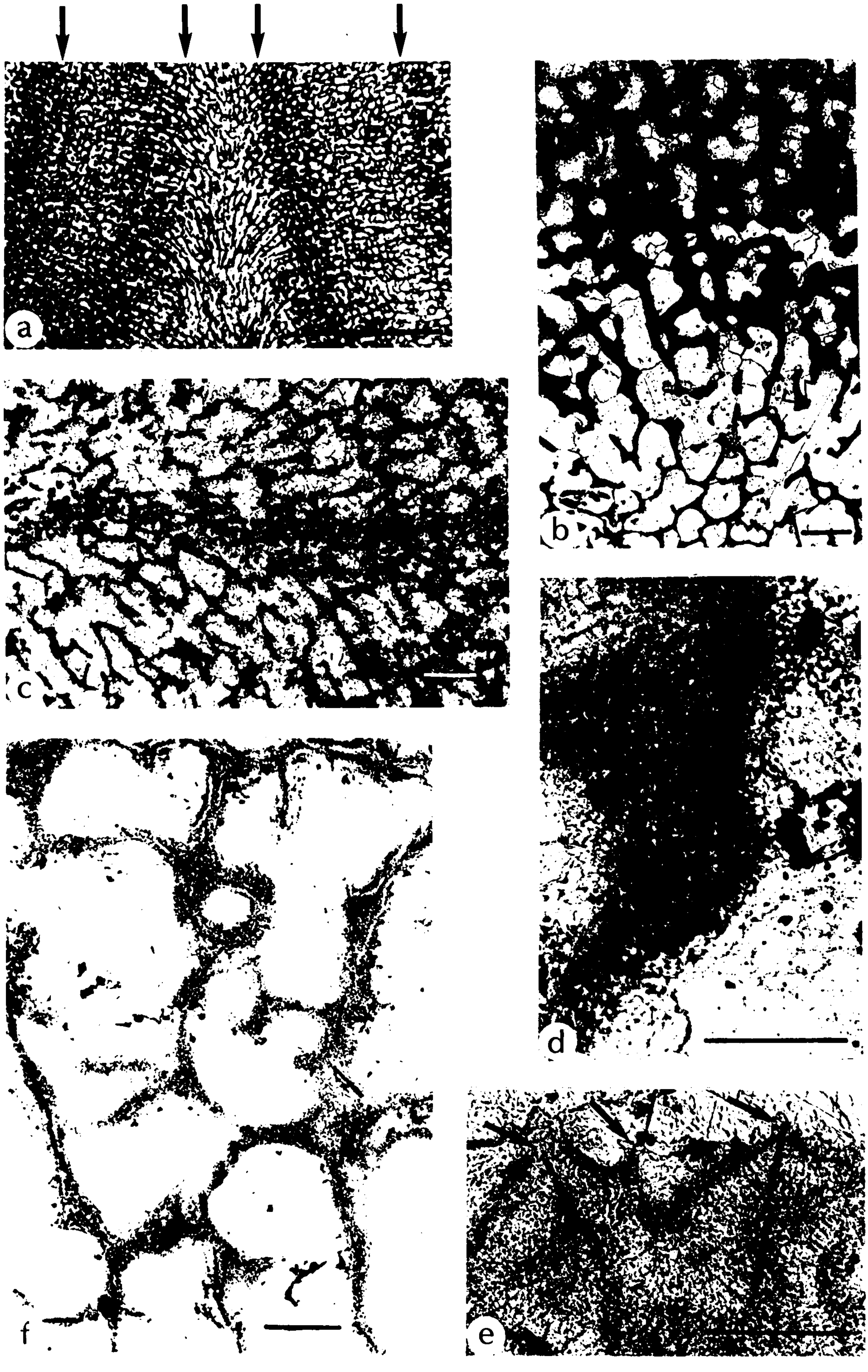
Figure c: Longitudinal section showing axial condensation and fibro-reticulate arrangement of skeleton.
Scale bar = 200µm.

Figure d: Pyrite pseudomorphs of long, thin styles (or tylostyles) within the primary irregular calcareous skeleton.
Scale bar = 100 µm.

Figure e: Projecting spicules (arrowed) with meniscus-like arrangement of primary irregular calcareous skeleton.
Scale bar = 100 µm.

Figure f:. Longitudinal section showing arrangement of spicule framework with primary irregular calcareous skeleton .
Scale bar = 200 µm.

PLATE 1 TYPE 1 SKELETAL ARRANGEMENT *Actinostromarianina lecompti* Hudson



Rachel A.Wood

PLATE
MISSING IN
ORIGINAL

PLATE 2 :TYPE 2 SPICULE ARRANGEMENT Milleporellidae Hudson,1959a

Dehornella crustans Hudson, 1960. H 5479. Makhtesh Hagadol, Israel. Lower Kimmeridgian. Light photomicrographs of stained thin-sections. The calcareous skeleton is stained pale pink (non-ferroan calcite) and calcite pseudomorphs are stained pale blue (ferroan calcite).

Figure a: Radiating columns of fascicular fibrous microstructure and fibrous tabulae with many calcite pseudomorphs of club-shaped styles radiating upwards and outwards with tapering tips sub-parallel to the microstructural fibres of the columns, which appear to initiate at the spicule bases. Scale bar = 200 µm.

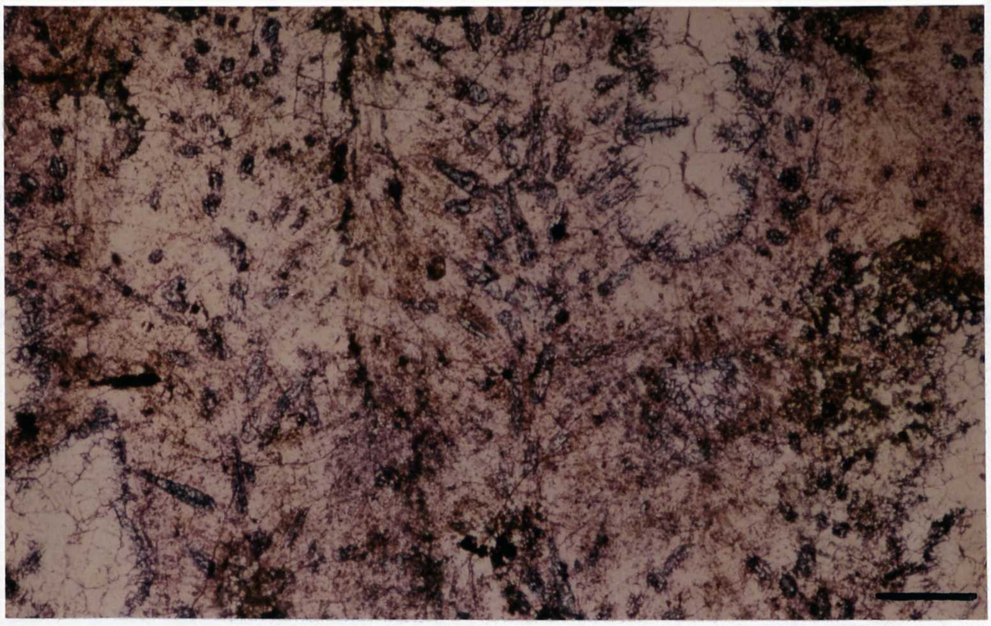


Figure b: Spicule pseudomorphs projecting into the interskeletal space (arrowed). Scale bar=100µm.

Skeletal Type 3: Plate 3, figs. a-d.

Representatives: *Actinostromaria* Haug, 1908, *Actostroma* Hudson, 1956.

These two genera are members of the Family Actinostromariidae Hudson, 1955a characterised by a reticulate skeleton of dominant pillars and pillar-lamellae of orthogonal fibrous microstructure , with irregular tabulae(Plate 3, figs.a,b).

Within the central zone of the skeletal elements there are closely packed styles (100 µm length, 10 µm width (maximum)) and triaxine or possibly tetraxine spicules (l20 µm long, 20 µm wide (maximum) Plate 3, figs. b-d) orientated sub-parallel to the longitudinal axis of the skeletal elements. The triaxine spicules have only been seen in thin section and their three dimensional form is uncertain (Plate 3, fig.c). They are rare, but appear to be placed at the pillar /pillar-lamellae junctions (Plate 3, fig. c). The orthogonal fibres form a rim around the spicule framework (Plate 3, fig.b.).

Skeletal Type 4 : Plate 4, Figs.a-d.

Representative: New gen . and sp. A

The calcareous skeleton is composed of columns and pillar-lamellae of spherulitic microstructure. No secondary tabulae are present (Plate 4, fig.a).

Spicules are found sub-parallel to the longitudinal axis of the skeletal elements. Spicules appear to form a lattice, composed of enmeshed tylostyles, strongyles and styles (75-250µm. length, 5-20µm. width, Plate 4, figs. b,c). Only calcite pseudomorphs have been found.

The centres of spherulite calcification might be initiated from the spicule bases(Plate 4, fig.d).

PLATE 3 : TYPE 3 SPICULE ARRANGEMENT *Actinostromaria sp.* Turnsek, 1966 and *Actostroma nasri* Hudson, 1960

Figures a-c: H 5480 (B.M. (N.H.)). Trnovski Gost, Slovenia, Yugoslavia. Oxfordian - Kimmeridgian. Light photomicrographs of stained transverse thin-sections.

Figure a: Reticulate skeleton of pillars and pillar-lamellae with an orthogonal fibrous microstructure. Specimen is encrusted by *Shuqraia sp.* (E).
Scale bar= 1mm.

Figure b: Closely packed spicule framework of calcite pseudomorphs within central area of skeletal elements(S), orientated sub-parallel to the growth axis of the skeleton. Primary orthogonal fibrous calcareous skeleton forms around the spicule framework (O). Granular tabulae (T) separate abandoned parts of the skeleton.
Scale bar=200µm.

Figure c: Pseudomorphs of styles and triaxines (or tetraxines). Triaxines appear to be placed at the pillar / pillar-lamellae junctions (arrowed). A triaxine in side-view is shown by the paired arrows (see Figure 2.1).
Scale bar= 100µm.

Figure d: Slightly micritised calcite pseudomorphs of styles in *Actostroma nasri.* (S). Primary orthogonal fibrous calcareous skeleton (O). H 4893b. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 100µm.

PLATE 3 TYPE 3 SKELETAL ARRANGEMENT *Actinostromaria sp.* Turnsek

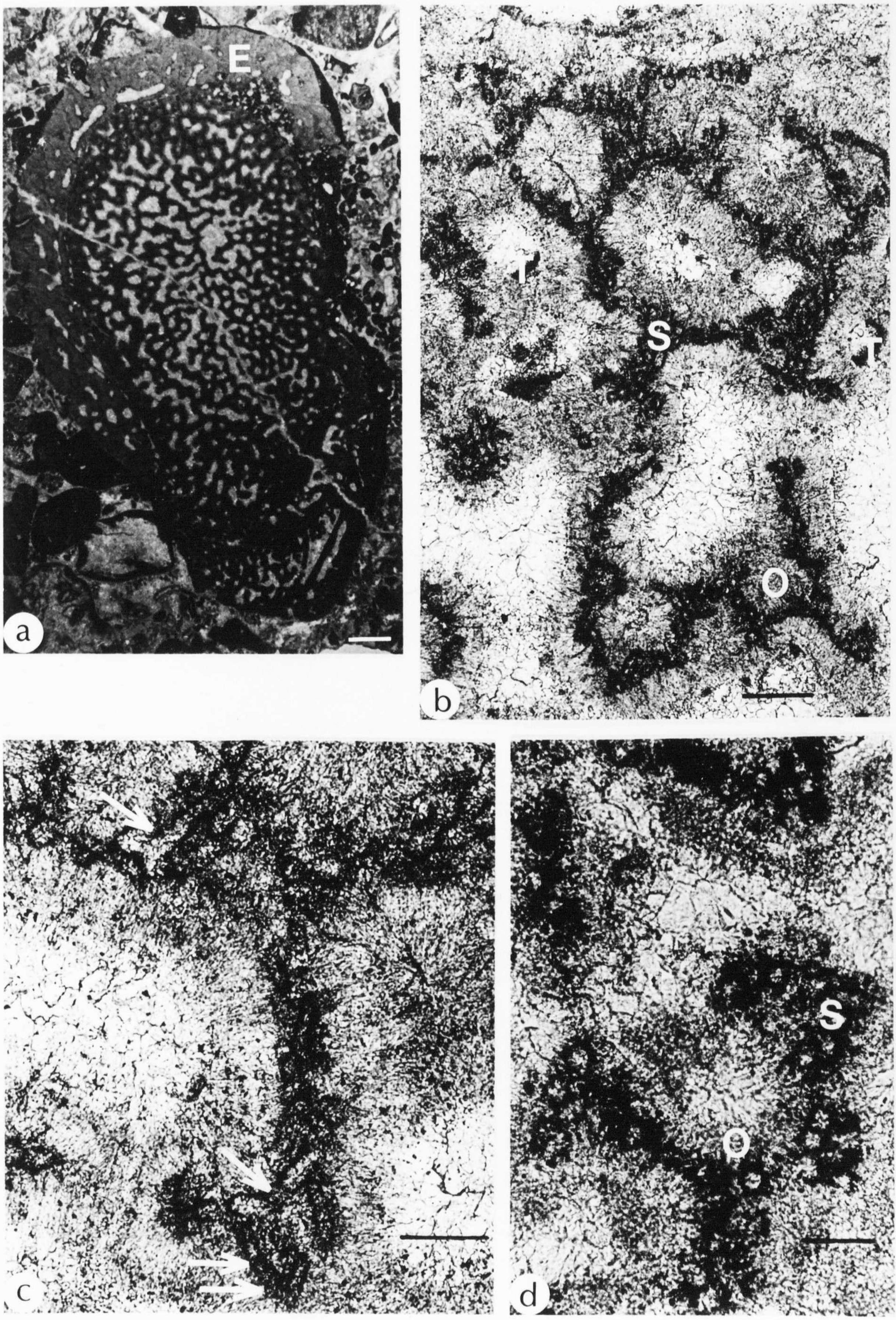


PLATE 4: TYPE 4 SPICULE ARRANGMENT New gen. and n.sp. A

Light photomicrographs of longitudinal thin-section H 5481 (B.M.(N.H.). Ereño, N.Spain. Upper Aptian.

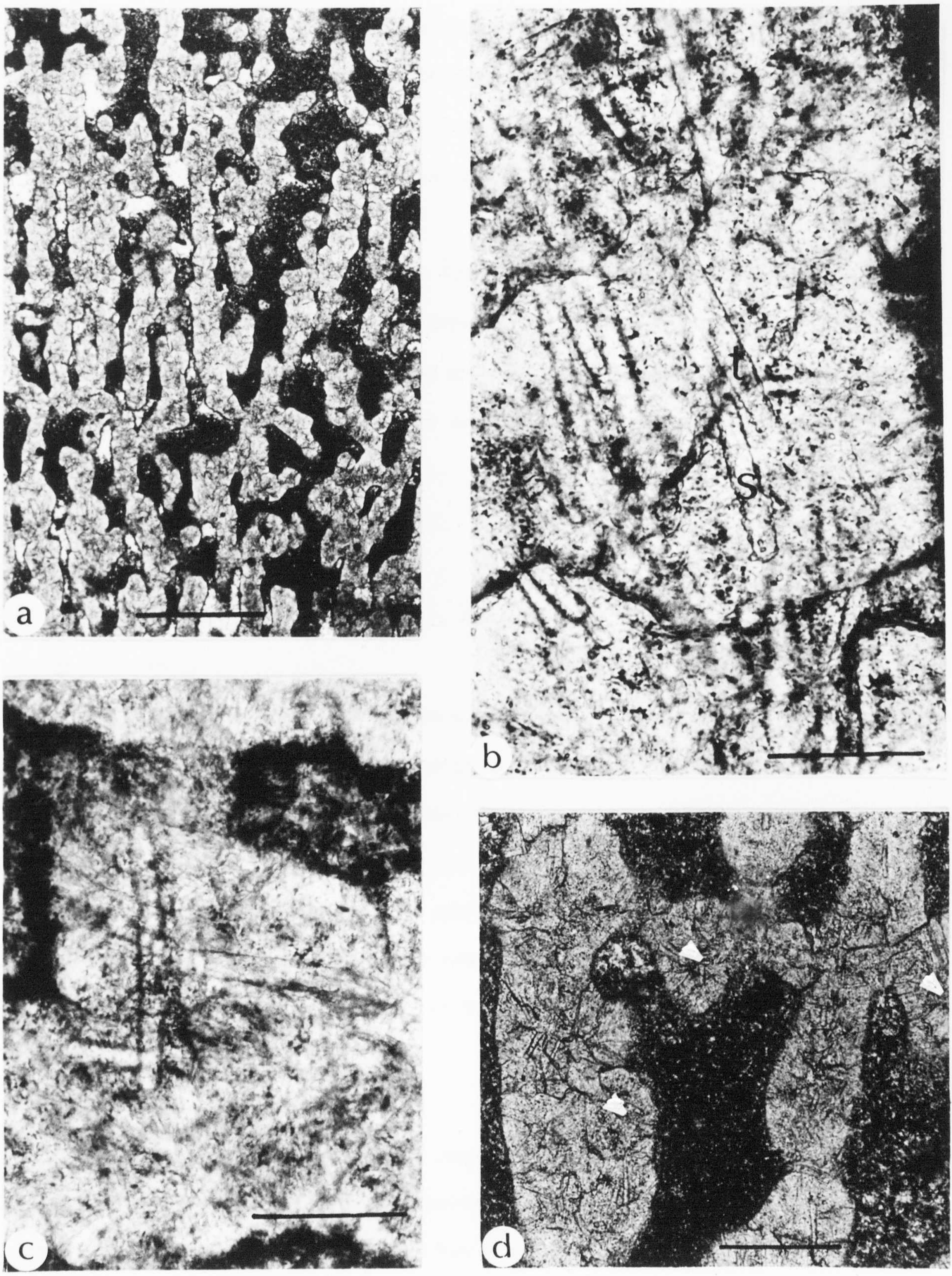
Figure a: Skeletal arrangement of columns (vertical) and pillar-lamellae (transverse) of spherulitic microstructure. No secondary tabulae are present.
Scale bar = 1mm.

Figure b:Tylostyles or styles (**t**) with a tapering tip, and strongyles (**S**) of uniform diameter, within column.
Scale bar=100µm.

Figure c: Spicule lattice placed vertically in columns and horizontally in pillar-lamellae.
Scale bar = 100µm.

Figure d: Calcite pseudomorphs of spicules forming a lattice within calcareous skeleton. Centres of spherulites are arrowed; calcification may be initiated from the spicule bases.
Scale bar = 200µm.

PLATE 4 TYPE 4 SKELETAL ARRANGEMENT *Euskadiella n.gen. n.sp.* Reitner



2. 2. 1. 2. MICROSTRUCTURE OF THE CALCAREOUS SKELETON

> *" The small size and indifferent preservation of these microstructures seem to have discouraged objectivity and encouraged idealisation, so that they have been described in terms of what they might have been rather then what they are now".* *Stearn, 1966.p.77.*

The need for distinction between skeletal (i.e. those formed by the soft tissue) and diagenetic fabrics was not always appreciated before Stearn (1966). He reviewed the microstructures of Palaeozoic stromatoporoids and described 14 skeletal fabrics. He considered that many of the 20 microstructures were of diagenetic origin and that they could be resolved to 4 primary microstructures:

1. Irregular
2. Melanospheric.
3. Compact
4. Fascicular fibrous

Unfortunately, Stearn perpetuated the erroneous description of "dark" areas under transmitted light. These "dark areas" are very often aggregates of finely crystalline carbonate; the darkening effect being due to the dense number of Becke lines.

Stearn concluded that due to the difficulty of determining primary microstructures from the array of diagenetic ones and the frequent bad preservation of specimens, microstructures should not be used as a taxonomic criterion and could not be used as an indicator of biological affinity for Palaeozoic stromatoporoids.

The dilemma of distinguishing primary from diagenetic fabrics was partially solved for Mesozoic forms by the finding of stromatoporoids, sclerosponges, sphinctozoans and inozoans from the Cassian Formation of the Upper Triassic of Italy and the Upper Permian of Tunisia which show preservation of original aragonite (Cuif 1973, Cuif and Fischer 1974, Wendt 1977, 1979).

The poriferan nature of Mesozoic stromatoporoids is supported after a comprehensive appraisal of Recent and fossil calcified sponge microstructure. Irrespective of present taxonomic placing, Wendt described the form and distribution of four primary microstructures, three fibrous and one irregular, found throughout these groups of calcified sponges. The occurrence of these four types is here confirmed in late Mesozoic stromatoporoids, and they are described below, modifying the scheme of Wendt (1984). Microstructural types are illustrated schematically in Figure 2.3 and in Plates 5-8.

1. **SPHERULITIC** Plate 5,figs. a-f

Globular arrangement of aragonite or low Mg-calcite crystals radiating from common centre forming spheres or ellipsoids.

Dimensions of aggregate: 20 - 160 µm diameter.

Dimension of single crystals: 10 - 80 µm length.

Occurrence: Carboniferous to Triassic sphinctozoans and inozoans (aragonite); Recent Inozoa (Mg-calcite); Permian (aragonite) and Lower Cretaceous (low Mg-calcite) stromatoporoids; Permian, Triassic and Recent sclerosponges (aragonite).

Modifications: Spherules may form a single series within a skeletal element (Plate 5, figs.e,f), or several series, named here as compound spherulitic microstructure(Plate 5, figs.b-d.). In ceratoporellids, the crystals parallel to the growth direction of the skeleton are elongated to form a microstructure intermediate between spherulitic and fascicular fibrous (Plate 5, fig.a.). This has previously been erroneously described as fascicular fibrous microstructure (Hartman and Goreau 1970).

Spherulitic microstructure can form primary, secondary or filling tissue(see Section 2.2.1.3.)

2. **ORTHOGONAL** (Synonyms; radial fibrous, transversly fibrous). Plate 6,figs. a-d.

Crystals of low Mg-calcite or aragonite arranged perpendicular to a central axis in the skeletal element.

Dimensions of single crystal :15 - 50 µm length, 0.7 - 1.4 µm width.

Occurrence: Mesozoic stromatoporoids (low Mg-calcite), chaetetids (aragonite); and Mesozoic inozoans (low Mg-calcite).

PLATE 5 SPHERULITIC MICROSTRUCTURE IN CALCIFIED SPONGES

Figures a-d, f: light photomicrographs of thin-sections.

Figures e: S.E.M.photomicrograph of broken surface.

Figure a: Tangential section of Recent *Ceratoporella nicholsoni* ("sclerosponge") with modified spherulitic microstructure, where crystals are elongated parallel to the growth axis of the skeleton. Transverse sections of spherules in bottom part of photograph ; tangential section in top left corner showing elongate crystals. J.Reitner Collection. Jamaica.
Scale bar = 100µm.

Figure b: Longitudinal section of Recent *Astrosclera willeyana* ("sclerosponge") . Compound spherulitic. J.Reitner Collection.
Scale bar = 100µm.

Figure c: Transverse section of an unnamed sclerosponge. Compound spherulitic. J.Reitner Collection. Tjebel Tebaga, Tunisia. Upper Permian.
Scale bar =100µm.

Figure d: Longitudinal section of an unnamed sclerosponge. Compound spherulitic primary skeleton with fascicular fibrous secondary skeleton and tabulae. J.Reitner Collection. Cassian Formation, N.Italy. Upper Triassic.
Scale bar = 100µm.

Figure e: S.E.Micrograph of Recent *Calcifibrospongia actinostromariodes* ("sclerosponge") showing detail of sclerodermites. Present author's collection.
Scale bar = 50 µm.

Figure f: Longitudinal section of New gen.and n. sp. A. ("stromatoporoid'), shown under cross-polars with centres of spherulites arrowed. Upper Aptian. Ereño, N.W.Spain.
Scale bar = 100µm.

PLATE 5 SPHERULITIC MICROSTRUCTURE IN CALCIFIED SPONGES

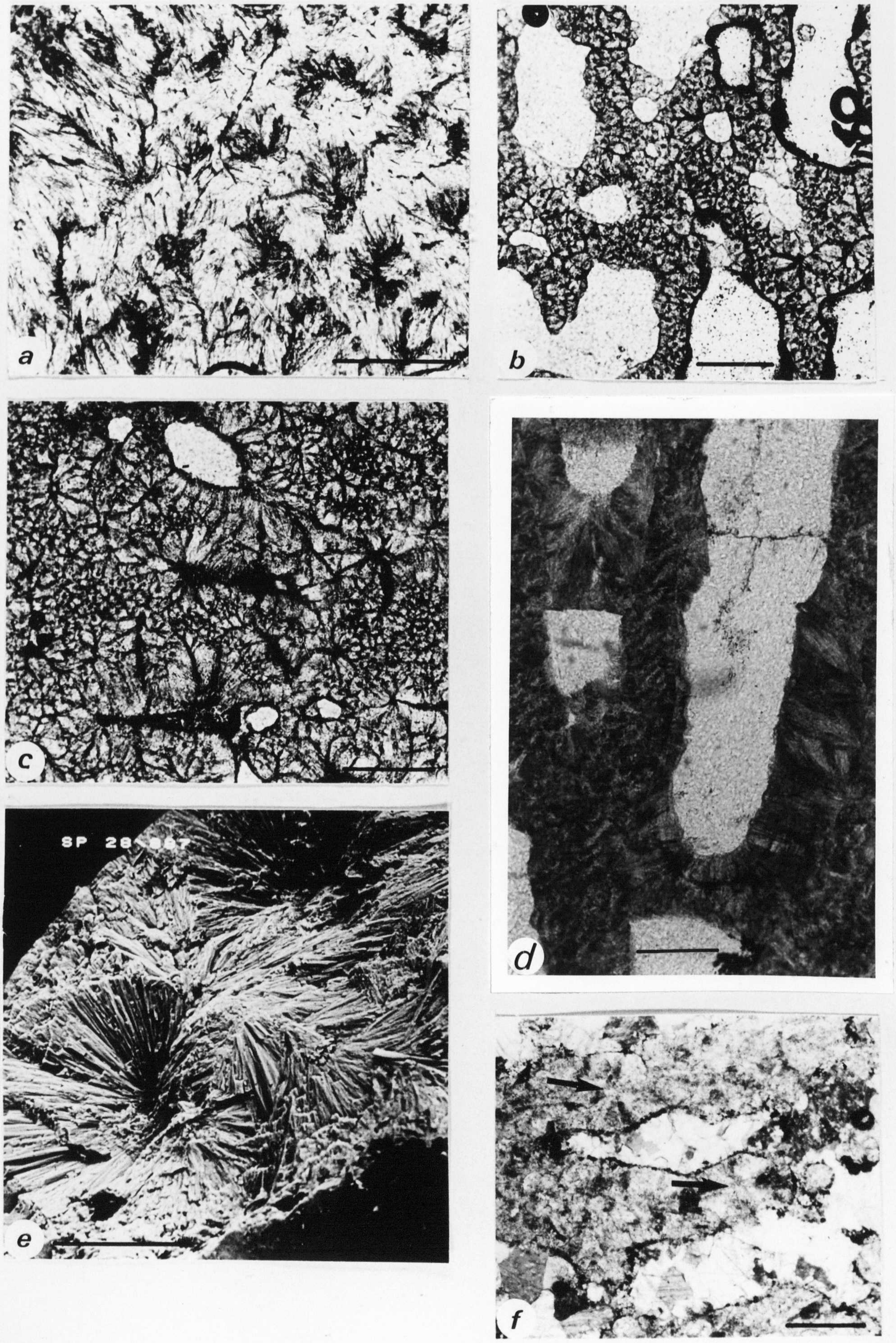


PLATE 6 ORTHOGONAL MICROSTRUCTURE IN CALCIFIED SPONGES

Light photomicrographs of thin-sections.

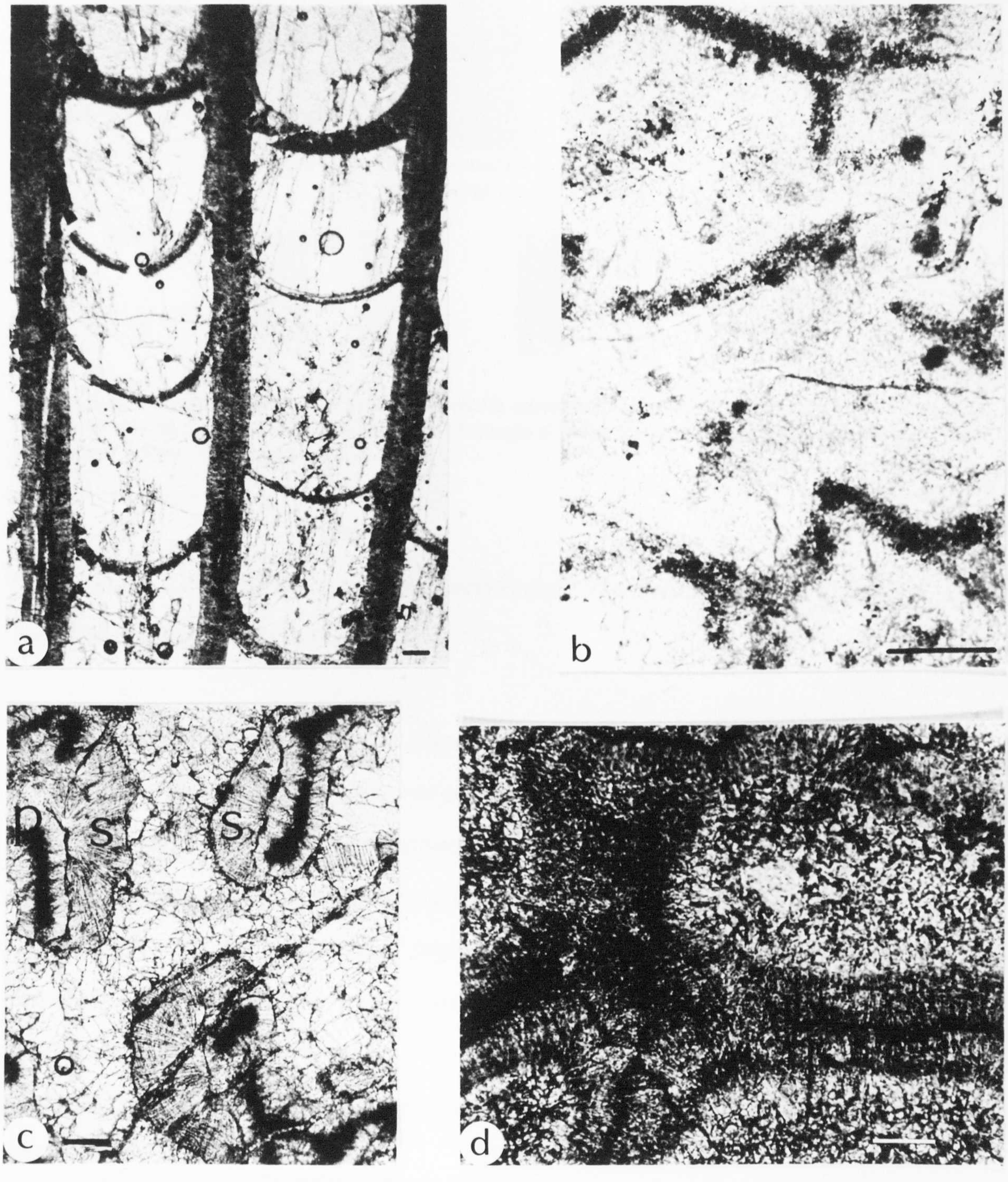
Figure a: Longitudinal section of an unnamed "chaetetid". J.Reitner Collection. Cassian Formation, N.Italy. Upper Triassic. Scale bar= 100µm.

Figure b: Tangential section of *Lymnoporella inclusa* (inozoan) with calcareous triaxine spicules (dark areas). H 3585 . Dudley, Gloucestershire. Upper inferior Oolite.
Scale bar= 100µm.

Figure c: Longitudinal section of unnamed 'sclerosponge' with primary orthogonal fibrous (**p**) and secondary fascicular fibrous calcareous skeleton (**S**). The central part of the skeletal elements is partially micritised. J.Reitner collection. Djebel Tebaga, Tunisia. Upper Permian.
Scale bar= 50µm.

Figure d: Longitudinal section of *Actinostromaria sp.* ('stromatoporoid") 83/62. Trnovski Gost, Slovenia, Jugoslavia. Oxfordian - Kimmeridgian.
Scale bar= 100µm.

PLATE 6 ORTHOGONAL MICROSTRUCTURE IN CALCIFIED SPONGES



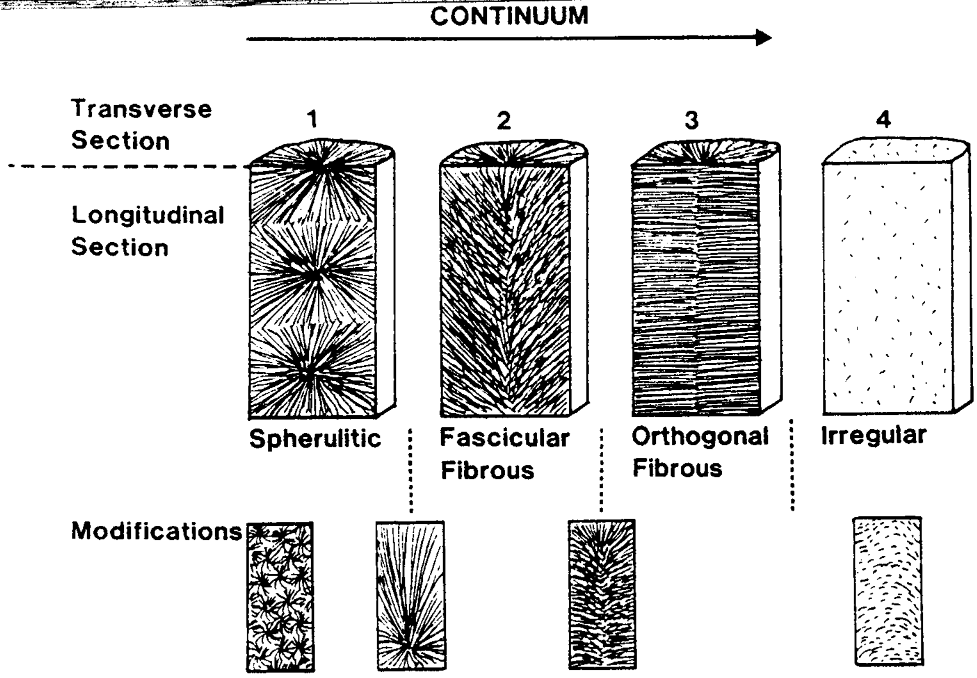


Figure 2.3. Four main microstructural types of the calcareous skeleton found in sponges, illustrated schematically as they appear in thin-sections through a radial element. Modifications of these types are shown below. Full explanation in text.

Modifications: Some forms produce a microstructure intermediate between orthogonal and fascicular fibrous. (See Plate 29, fig.h)

3. FASCICULAR FIBROUS (synonyms: cligonal, penicilliate, jet d'eau, trabecular). Plate 7, figs.a-d.

Radiating, fan-like arrangement of aragonite or low Mg-calcite crystals sub-parallel to the longitudinal axis of the skeletal elements showing fanning extinction under cross-polars.

Dimensions of single crystals: 80 µm length, 0.5 µm width.

Occurrence: Cretaceous sphinctozoans (Mg-calcite); Permian and Triassic (aragonite) and Recent (Mg-calcite) inozoans; Mesozoic stromatoporoids (Mg-calcite); Recent,Permian and Triassic sclerosponges (aragonite or Mg-calcite).

Modifications: Some forms produce a microstructure intermediate between orthogonal and fascicular fibrous (See Plate 29, fig.h).

4. IRREGULAR (Synonyms; granular) Plate 8,figs. a-c . Plate 1, fig.e,f.

Tangled, disorientated crystals.

Dimensions of crystals :4 - 8 µm length , 0.1 - 0.5 µm width.

PLATE 7 FASCICULAR FIBROUS MICROSTRUCTURE IN CALCIFIED SPONGES

a-c: light photomicrographs of longitudinal thin-sections.

d: S.E.Micrograph of broken surface.

Figure a: *Dehornella crustans* ("stromatoporoid") with calcite spicule 'ghosts'. H 4788. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 100µm.

Figure b: *Parastromatopora libani* ("stromatoporoid") with calcite spicule 'ghosts' and fibrous tabulae. H 4789. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 100µm.

Figure c: *Blastochaetetes irregularis* ("chaetetid"). 85/JP 2. Collades de Bastus, N.Spain. Santonian. Stained .
Scale bar = 100µm.

Figure d: S.E.M. of *Dehornella crustans*. 83/0519. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 10µm.

PLATE 7 FASCICULAR FIBROUS MICROSTRUCTURE IN CALCIFIED SPONGES

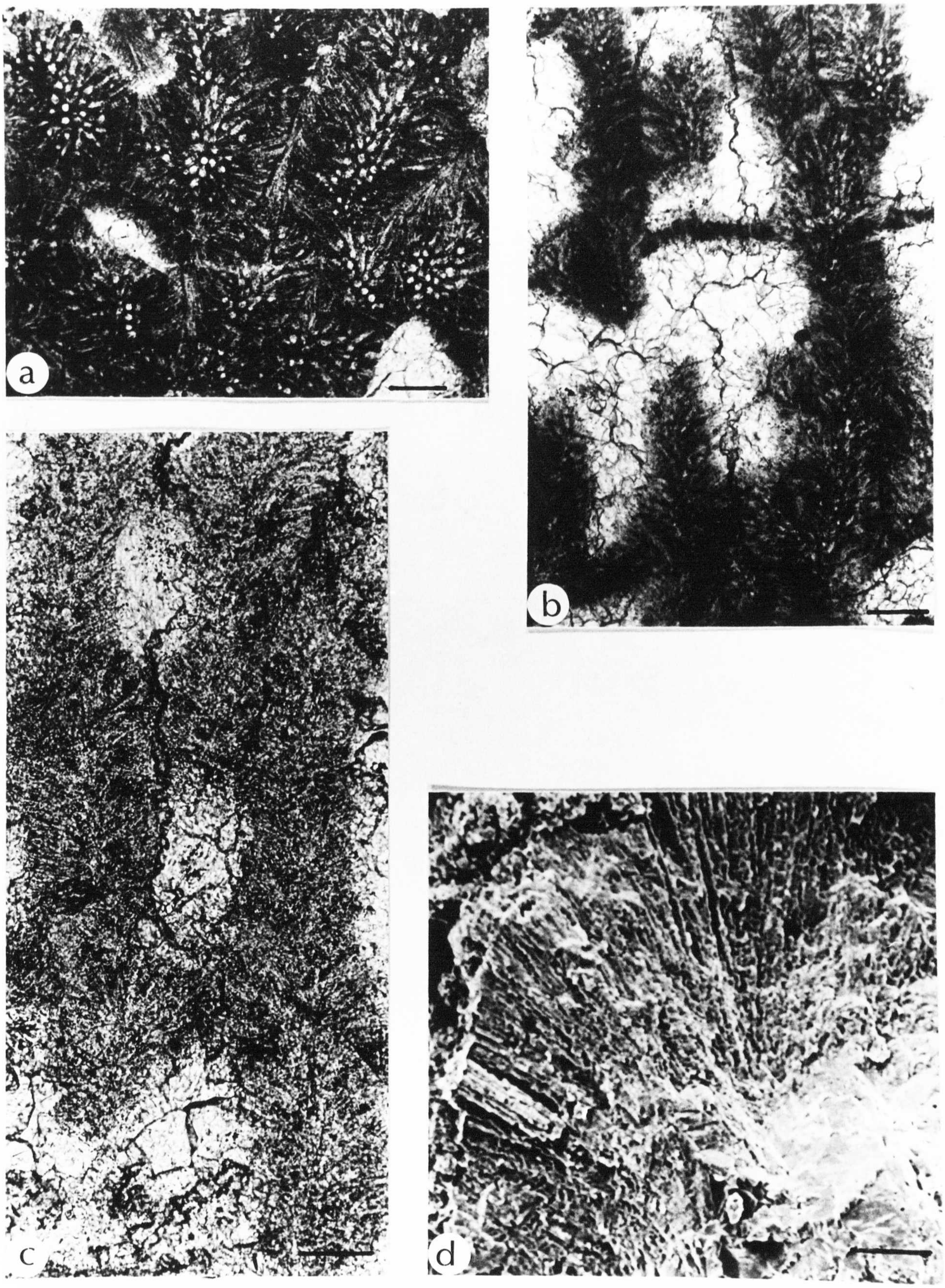


PLATE 8 IRREGULAR MICROSTRUCTURE IN CALCIFIED SPONGES

Light photomicrographs of longitudinal thin-sections.

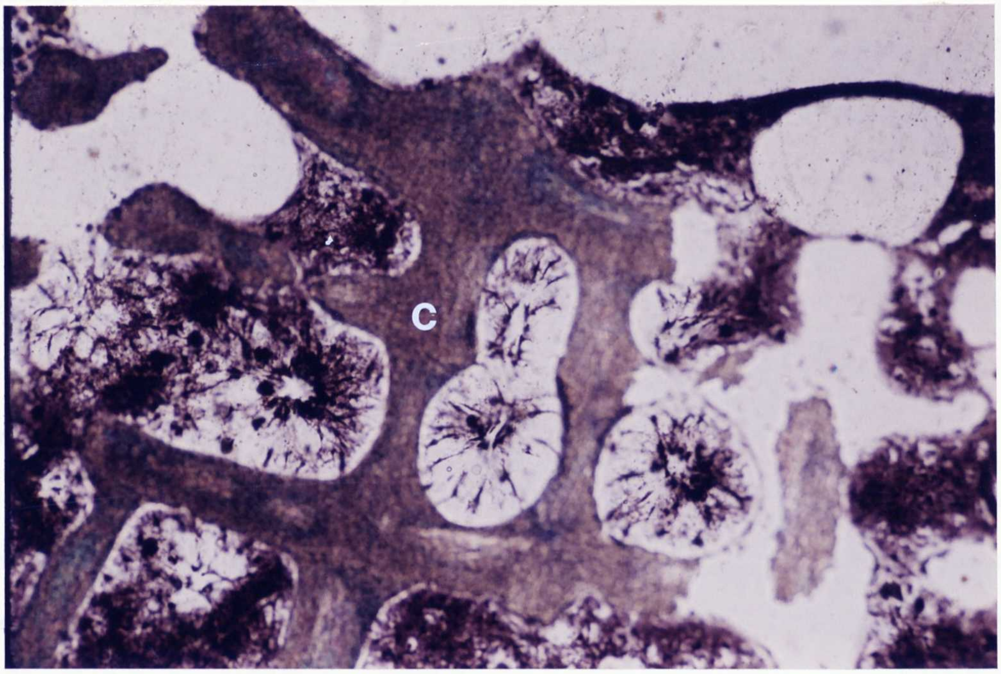
C: Irregular calcareous skeleton.

Figure a: Recent *Vaceletia crypta* (sclerosponge) with soft tissue . J.Vacelet Collection. Jamaica.
Scale bar= 1mm.

Figure b: Recent *Acanthochaetes wellsi* (sclerosponge) with stained soft tissue. Crystals orientated in one plane only, parallel to the living tissue, giving a ' lamellar' appearance. J.Vacelet Collection. Jamaica.
Scale bar= 1mm.

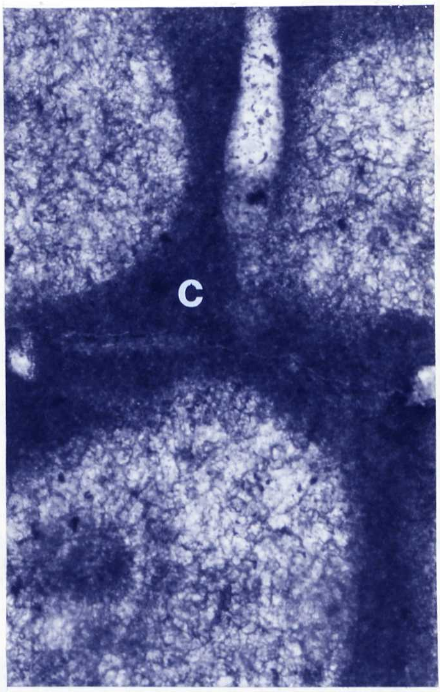
Figure c: Undescribed 'sphinctozoan', with triaxon spicule. 85/1 Caniego, N.Spain. Lower Cretaceous.
Scale bar= 200µm.

PLATE 8 IRREGULAR MICROSTRUCTURE IN CALCIFIED SPONGES



a

b



c

Occurrence: Triassic and Recent sphinctozoans (aragonite and Mg-calcite); Permian and Triasssic stromatoporoids (aragonite); Jurassic stromatoporoids (Mg-calcite); Mesozoic and Recent sclerosponges (aragonite and Mg-calcite).

Modifications: Irregular microstructure may sometimes show a preferential orientation in one plane, giving an appearance of lamellated structure in thin section e.g. the calcareous skeleton of the Recent sclerosponge *Acanthochaetetes* appears, in longitudinal thin-section, with arched growth lines orientated parallel to the inner surface of the living tissue (Plate 8, fig.b). This feature is highly characteristic, and unique to this genus.

Discussion:

Wendt (1979) did not observe any transitition from one microstructural type to another but he did note that some species possessed more than one type. However, it has been noted in this study that the three fibrous types form a continuum, with forms which show transitional microstructures. *Ceratoporella*, for example although described as possessing fascicular fibrous microstructure (Hartman and Goreau, 1970), possesses a modified form of spherulitic structure. There are also modifications upon the microstructural types, e.g. compound spherulitic, as found in *Astrosclera*. It should be noted that the three fibrous microstructural types can appear identical in transverse sections through the skeletal elements.

Wendt also stated that there was no consistency of microstructures within apparently well defined taxonomic units. For example, Upper Permian *Stellispongia sp.* has spherulitic microstructure whereas Upper Triassic forms of this genus have fascicular fibrous or irregular microstructures. He therefore questioned the taxonomic and phylogenetic use of microstructural criteria, but did not question the taxonomic validity of his examples.

The fossil aragonite and Recent sclerosponge microstructures are very similar. Mesozoic stromatoporoids possess all four types. Sclerosponges and sphinctozoans lack orthogonal fibrous microstructures and inozoans lack irregular microstructure.

Thus, Mesozoic stromatoporoids share the same microstructural types as found in all other Recent and fossil calcified sponges. The distribution of these microstructural types throughout their geological record is shown in Figure 2.4., after Wendt (1984).

Diagenesis frequently obscures the original microstructure, and this is described later in Section 3.2.

2.2.1.3. CONSTRUCTION OF THE SKELETON.

Wendt (1979) described the skeletal construction of calcified sponges in terms of four successive component growth stages:

a. spicular framework
b. primary calcareous skeleton
c. secondary calcareous skeleton.
d. filling tissue.

The construction of the Mesozoic stromatoporoid *Actinostromarianina lecompti* is used to decribe these stages, illustrated in Figure 2.5 and Plate 9.

a.Spicular framework

Spicules are orientated in characteristic ways in a sponge, and the shape of spicules may change progressively with position within the individual (Jones, 1970). Four types of spicule form and arrangement in Mesozoic stromatoporoids have been determined in this study, of which *Actinostromarianina lecompti* is characteristic of Type 1, with long, thin styles or tylostyles forming a plumo-reticulate arrangement, with a densely packed axial zone of parallel aligned spicules. The spicules appear to form the framework for the subsequent precipitation of the primary irregular calcareous skeleton(Plate 9, fig.a.).

b. **Primary calcareous skeleton**

This consists of irregularly arranged microcrystalline calcite, forming meniscus-like around the projecting spicules (Plate 9, fig.a.).

Figure 2.4. The distribution of microstructures and mineralogies in calcified sponges through geological history and present taxonomic groupings. Note shift in mineralogy from aragonite to calcite in the Middle Jurassic / Early Cretaceous (See Section 3.).
1: spherulitic; 2: irregular; 3: fascicular fibrous; 4: orthogonal; 5: recrystallised; 6: spicules; A: aragonite; C: Calcite. Modified from Wendt (1984).

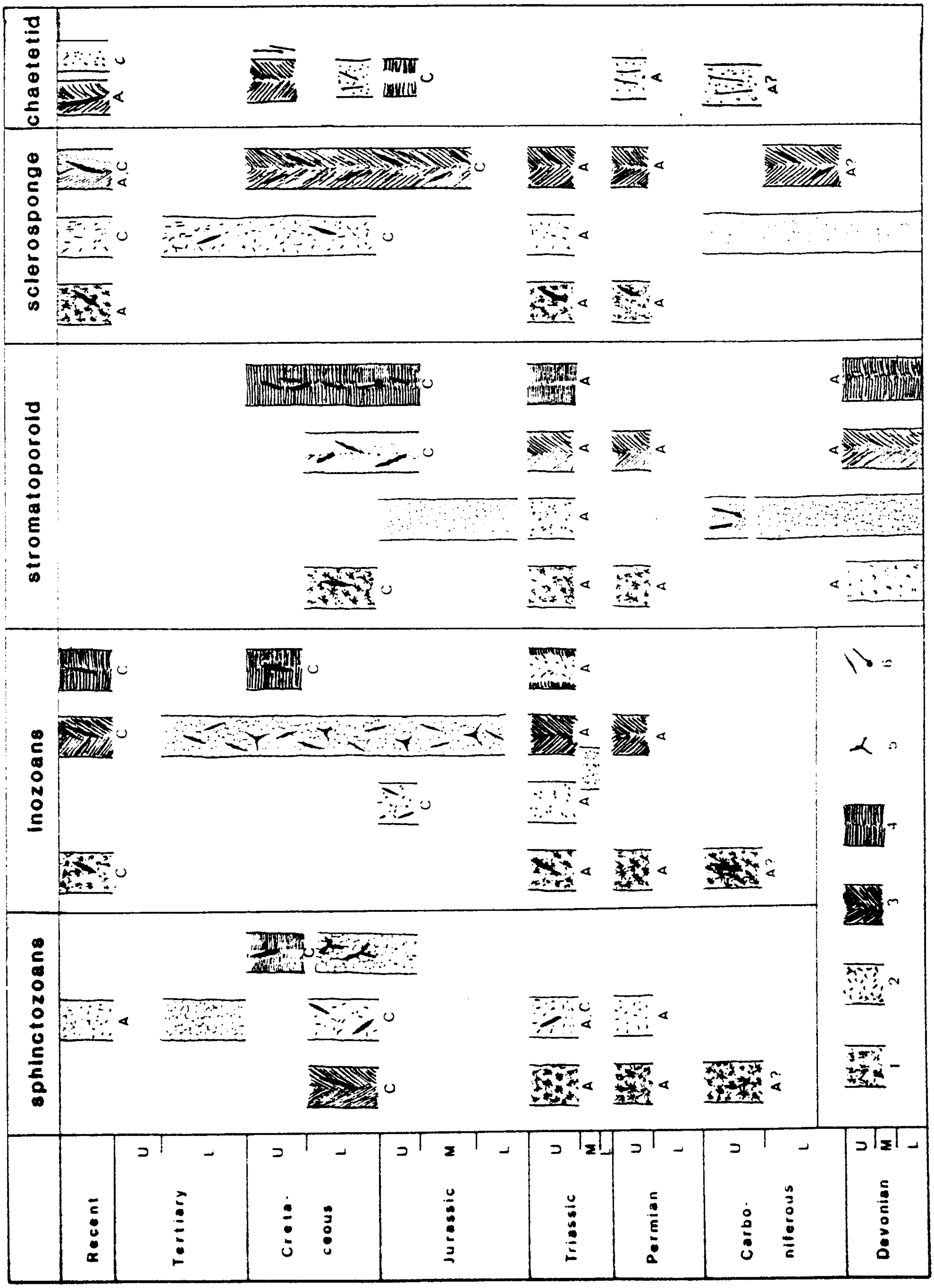


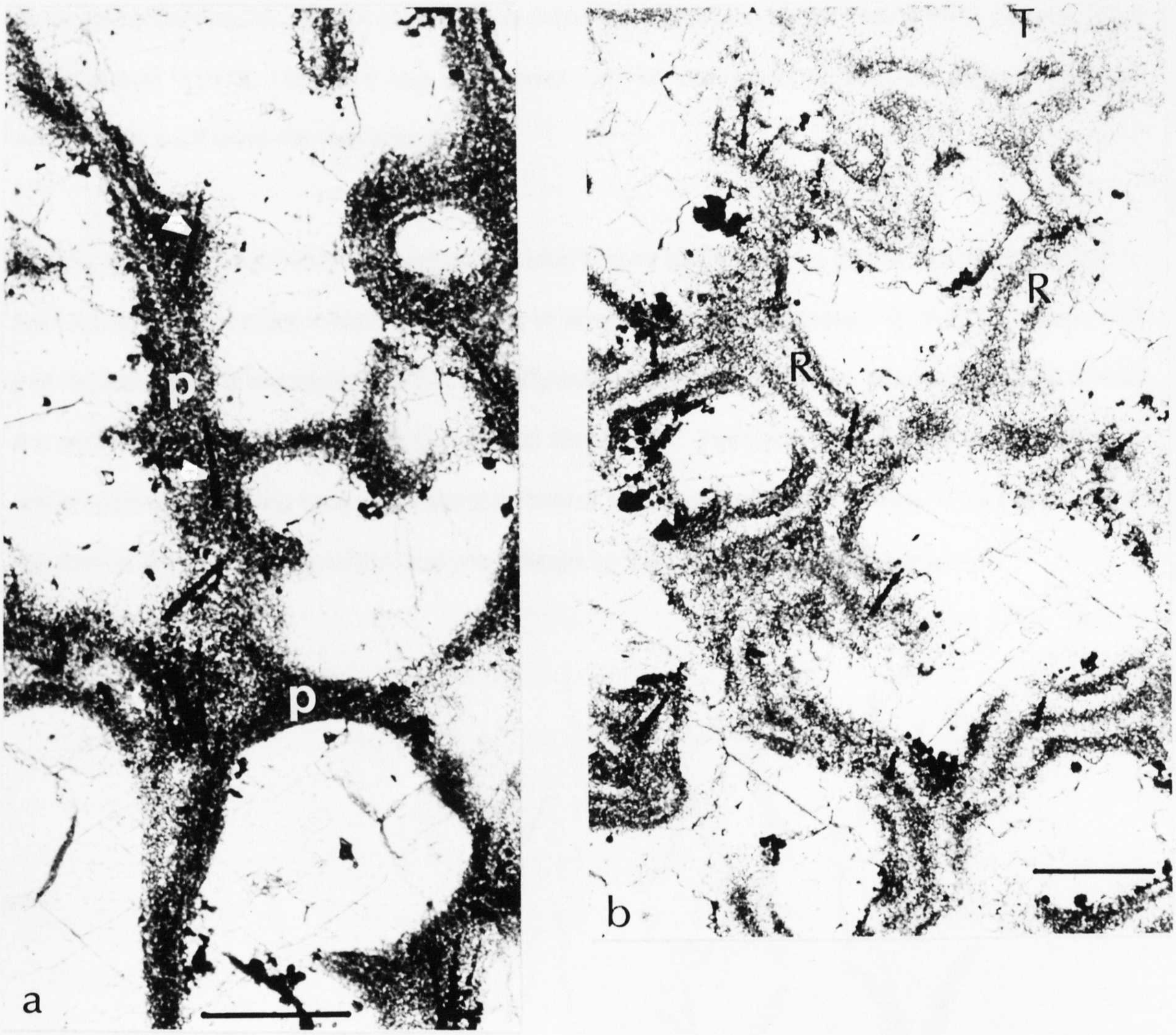
PLATE 9 CONSTRUCTION OF THE SKELETON OF *Actinostromarianina lecompti* Hudson ,1955a

All light photomicrographs of longitudinal thin-section H 4608a. (B.M.(N.H.)). Alam Abaydh, Arabia. Upper Kimmeridgian.

Figure a: Spicule framework (arrowed) and primary calcareous skeleton (**P**) of irregular microstructure .
Scale bar= 200 µm.

Figure b: Secondary orthogonal fibrous rim (**R**) and filling tissue in the form of irregular tabulae (**T**) . Banding of skeletal tissue is partially a result of recrystallisation forming pseudo-lamellar structure (See section 3.2.4.)
Scale bar = 200 µm.

PLATE 9 SKELETAL CONSTRUCTION OF *Actinostromarianina lecompti* Hudson



c. **Secondary calcareous skeleton**. Plate 9, fig.b.

The term 'secondary' has been introduced to describe the partial skeletal infilling of pore spaces in the skeleton framework when it is seen to be a continuation of the primary calcareous skeleton (Cuif 1973, Wendt (1979, 1984)). It can sometimes only be distinguished from the primary skeleton when it is of a different microstructure.

In *A.lecompti* the secondary calcareous skeleton occurs periodically as an orthogonal fibrous rim to form latilaminae, and is probably a response to environmental fluctuations. It could be argued that this deposit is not of organic origin, but an early marine cement. However, tabulae are found across the pore spaces, starting from the orthogonal fibrous rim. The orthogonal fibrous rim and tabulae are precipitated by living tissue, of necessity before its withdrawal from the area. This suggests that the fibrous rim is of organic origin and precipitated by the soft tissue of the organism.

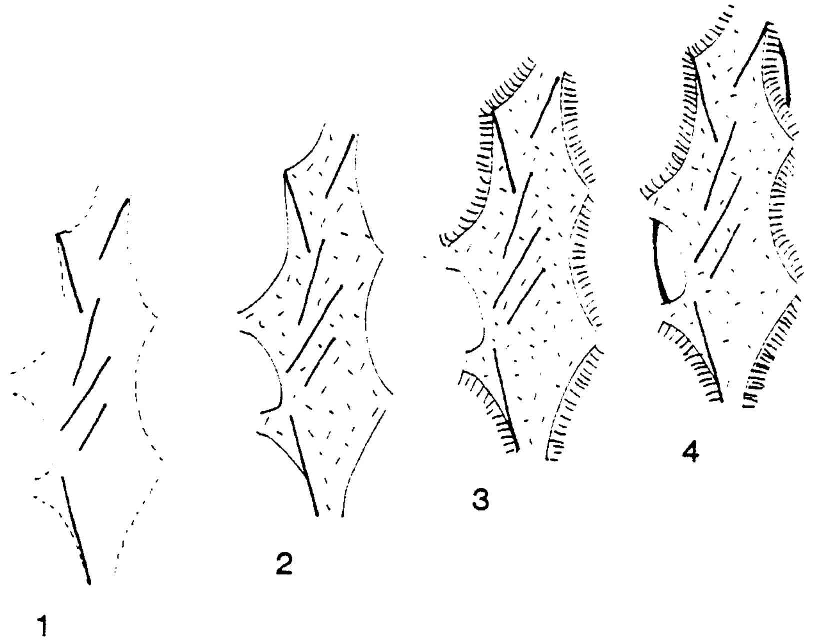


Figure 2.5. Skeletal construction in calcified demosponges, as shown by the Mesozoic stromatoporoid, *Actinostromarianina lecompti* Hudson ,1955a.

1. Primary spicule framework, probably bound with an organic matrix (dotted lines, see Section 6.3.2.);

2. Primary calcareous skeleton of irregular microstructure (perhaps due to mineralisation of the organic matrix, see Section 6.3.2.);

3. Secondary calcareous skeleton forming an orthogonal fibrous rim;

4. Filling tissue of irregular tabulae.

d. **Filling tissue.**

Only the peripheral part of most calcified sponge skeletons is an open water-supplied framework and this is covered or filled by living tissue.

Abandoned, older parts of the skeleton not occupied by living tissue are sectioned off or secondarily infilled by skeletal tissue. Secondarily precipitated partitions (tabulae, vesiculae, dissepiments and trabeculae) are common in sphinctozoans, stromatoporoids, and chaetetids. Some Recent sclerosponges possess tabulae (*Merlia spp., Acanthochaetetes spp.*, and *Ceratoporella sp.*) but most other forms, especially the Ceratoporellidae, form a backfill of solid skeleton which completely closes the original tubular pore-spaces which housed the living tissue. The backfilling tissue forms the same microstructure in optical continuity with the primary modified spherulitic skeleton and, generally, they cannot be distinguished. Often, secondary backfill can initiate from a tabula. Here, the distinction between types of filling tissue and secondary skeleton can be an arbitrary one. It is not clear whether this epitaxial overgrowth of crystals to fill primary pore space and produce a secondary skeleton is an organic or inorganic process (See Section 3. 2.).

In inozoans, the living tissue is thicker and so larger parts of the skeleton have an active filtration system. The filling tissue is restricted to the basal parts of the skeleton and disused exhalent canals (Wendt 1979).

The filling tissue of calcareous sponges, including Mesozoic stromatoporoids, is variable in form and microstructure. Table 2.2 and Plate 10, figs.a-g illustrate the various forms and microstructure of filling tissue in calcified sponges.

Thus, the primary and secondary calcareous skeleton and filling tissue in Mesozoic stromatoporoids show strong constructional similarities to Recent and fossil sponges which possess a calcareous skeleton.

2. 2. 2. FUNCTIONAL MORPHOLOGY.

Stromatoporoids possess an intricate canal system, generally expressed as ramified unwalled

PLATE10 FILLING TISSUE IN CALCIFIED SPONGES

All light photomicrographs of longitudinal thin-sections.

Figure a: Unnamed 'chaetetid' showing curved fibrous tabulae, between columns of the primary orthogonal skeleton. J.Reitner Collection. Cassian Formation, N.Italy. Upper Triassic.
Scale bar=200 µm.

Figure b: Unnamed 'sclerosponge'. Aligned straight tabulae **(T)** of spherulitic microstructure plus spherulitic secondary backfill in older parts of skeleton **(b)** in bottom third of photograph. J.Reitner Collection. Cassian formation, N.Italy, Upper Triassic.
Scale bar=200 µm.

Figure c: Recent *Astrosclera willeyana* ("sclerosponge"). Secondary spherulitic backfill in older parts of individual **(S)** in bottom third of photograph . J.Reitner collection. Jamaica.
Scale bar=200 µm.

Figure d: *Shuqraia arabica* ("stromatoporoid") . Secondary fibrous epitaxial calcareous skeleton completely infilling primary pore-space, except for former position of the astrorhizal canals. H5074a. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar=200 µm.

Figure e: *Shuqraia arabica* ("stromatoporoid"). Secondary epitaxial skeleton **(S)** forming an orthogonal fibrous rim, initiated from fibrous tabulae **(T)**. Tabulae are flat-based and have a curved upper surface, which grows epitaxially upon the primary fibrous skeleton **(FT)**. H 4639b. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar=200 µm.

Figure f: Unnamed 'sclerosponge'. Primary spherulitic calcareous skeleton (**P**). Secondary fascicular fibrous skeleton **(S)** forming fascicular-fibrous backfill **(B)**, initiated from tabulae **(T)** and primary columns. This illustrates the arbitrary distinction between filling tissue types and secondary skeleton. The fibrous tabula also grows epitaxially from the primary skeletal walls to produce what could be described as a secondary skeleton or backfill. J.Reitner Collection. Cassian Formation, N.Italy, Upper Triassic.
Scale bar=200 µm.

Figure g: *Burgundia wetzeli* ('stromatoporoid"). Laminae filling tissue (arrowed) forming continuous platforms. H 4424a. Bekhme Gorge, Iraq. Lower Cretaceous.
Scale bar=200 µm.

PLATE 10 FILLING TISSUE IN CALCIFIED SPONGES

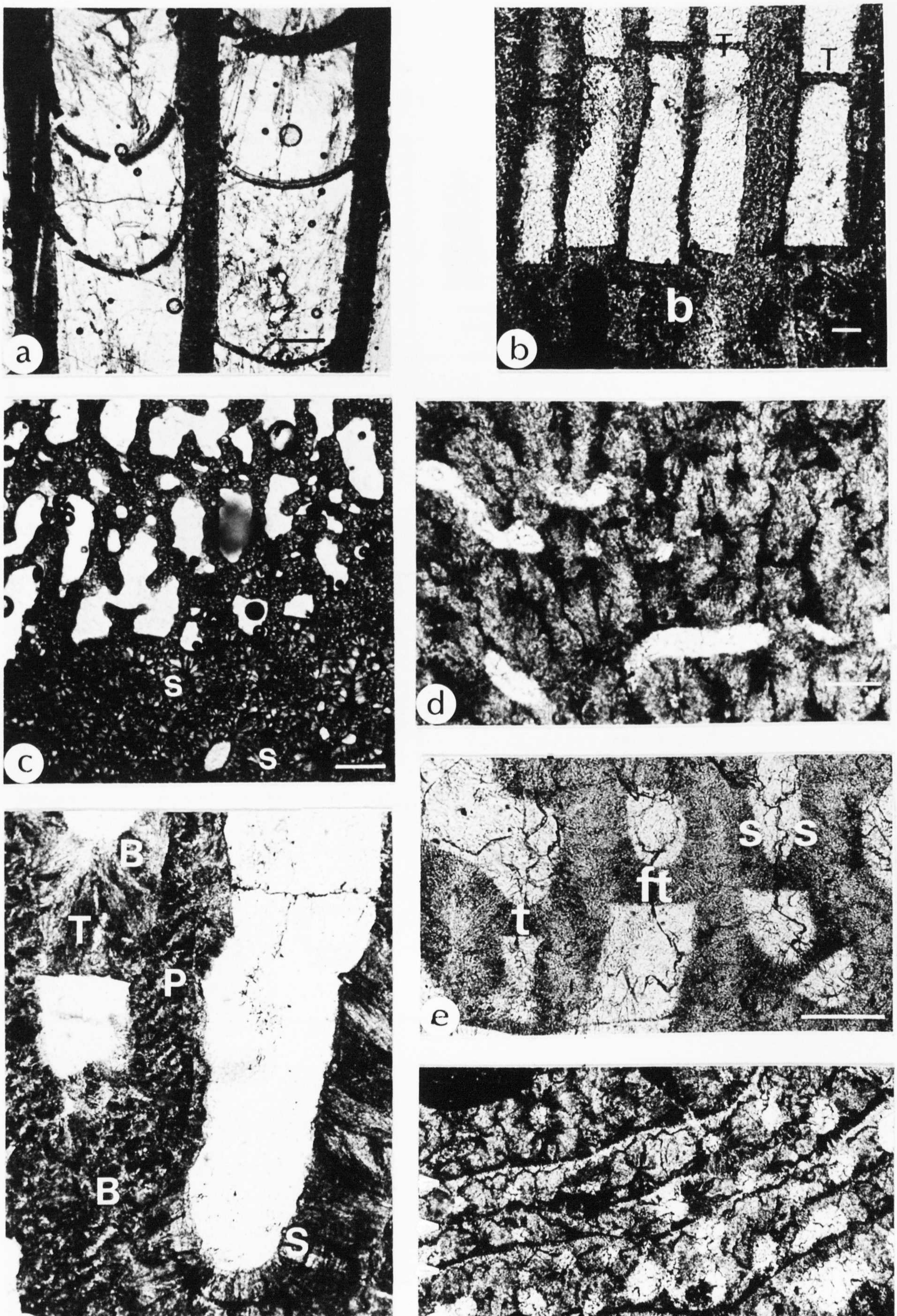
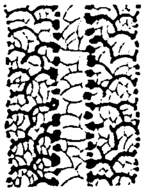
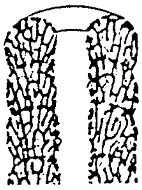
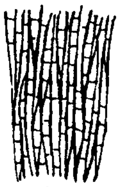
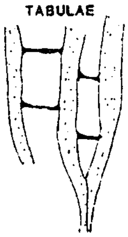
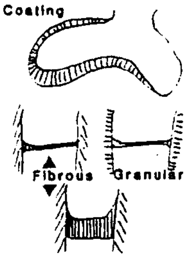
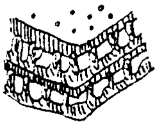
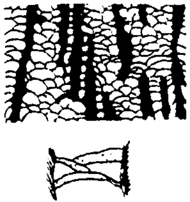
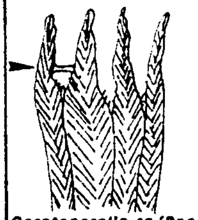
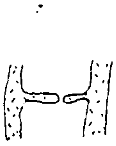
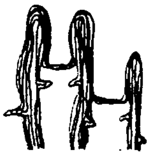
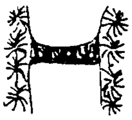


Table 2.2: Illustrates the similarity of filling tissue types found in the various present groupings of calcified sponges. Full explanation in text.
(Columns merely divide the various types of filling tissue within each grouping, and no relationship is implied within them)

GRADE	FILLING TISSUE			
SPHINCTOZOAN	 VESICULAR *Cystothalamia*	 TUBULAR *Polytholosia*	 TRABECULAR *Dictyocoelia*	 RETICULAR *Vesicocaulis*
CHAETETID	 *Blastochaetetes sp.* *(Up.Cret.)*	SECONDARY TABULAE 		
STROMATO- -POROID	 *Steinerella* *(Lwr.Cret)*	SECONDARY TABULAE 	LAMELLAE  *Burgundia sp.* *(Up.Cret.)*	 *Labechia* *(Silurian)* CYST PLATES
SCLEROSPONGE	EPITAXIAL BACKFILL & RELICT TABULAE  *Ceratoporella sp.(Rec.)*	PRIMARY TABULAE  *Merlia sp.* *(Rec.)*	 *Acanthochaetetes sp.* *(Rec.)*	SECONDARY TABULAE  *Preceratoporella* *(Permian)*

spaces within the skeleton, opening out to form repeated astrorhizae on the upper surface. These stellate structures appear as grooves on the skeletal surface which decrease in diameter and peter out into the fine meshwork of the skeleton. As the animal grows incrementally upwards, successive astrorhizae-bearing layers are superimposed. Since astrorhizae are considered to be one of the few characteristic features of stromatoporoids, their functional (and therefore biological) interpretation is fundamental in determining biological affinity.

Baron von Rosen (1869) and Twitchell (1929) noted the similarity between stromatoporoid astrorhizae and poriferan aquiferous filtration systems. This similarity between the sclerosponge excurrent canal system and the stromatoporoid astrorhizae was later highlighted by Hartman and Goreau (1970) . Examples are ilustrated in Plate 11,figs.a-f.

Although sclerosponges are the only Recent forms where traces of these excurrent canals are expressed in the calcareous skeleton, many other non-calcified sponges, especially thin encrusting demosponges, possess the same repeated system of aquiferous units within their soft tissue, e.g.*Spongilla uvirae* and *Potamolepsis leubnitzae.* (Fig.2.6) and some branching demosponges also show excurrent canal traces, e.g. *Axinella polypoides*, (Plate 11,fig. f). The visual similarity between stromatoporoid astrorhizae and the aquiferous units of many Recent sponges is a function of them both being based upon the same unit of organisation, the rhagon unit.

In the sponge aquiferous system, water enters through a series of small pores, known as ostia , and passes through a ramified system of canals which supply and drain the tissue. Water passes through inhalent canals supplying the flagellated chambers, then leaves through excurrent canals (astrorhizae) and leaves the sponge through a common exit; a localised canal terminating in a pore, known as the osculum. The rhagon unit is the first, juvenile aquiferous unit formed in demosponges. Consisting of a large cavity, the paragastric cavity, it opens out to the exterior by an osculum. Over the upper surface, about the osculum as a centre, are numerous ostia, leading to flagellated chambers. From these chambers the excurrent canals pass to the paragastric cavity. The rhagon unit is modified and then repeated to form the aquiferous system of mature individuals.

PLATE 11 EXCURRENT CANAL TRACES AND ASTRORHIZAE

Light photographs

Figure a: Transverse thin-section showing astrorhizae of *Actostroma damesini* (stromatoporoid). H 4892b. Thin-section. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 1mm.

Figure b: Transverse thin-section showing astrorhizae of *Shuqraia n. sp.* (stromatoporoid) H 4561. Alam Abaydah, Arabia.Lower Kimmeridgian.
Scale bar = 1mm.

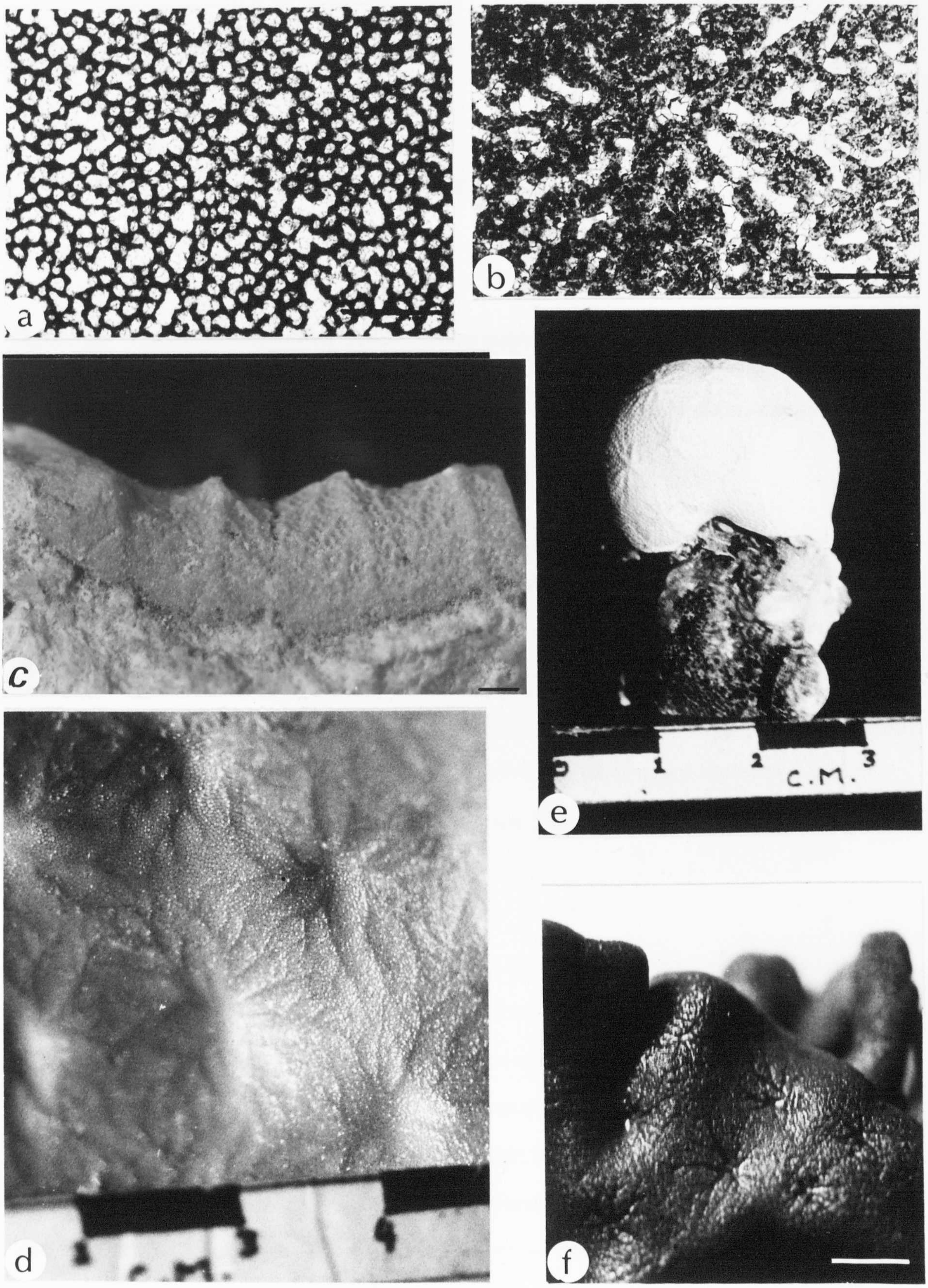
Figure c: Stromatoporoid raised astrorhizae. 86/36. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 1mm.

Figure d: Surface excurrent canal traces in preserved soft-tissue of Recent *Ceratoporella nicholsoni* (sclerosponge). J.Vacelet Collection. Jamaica.
Scale bars = 1cm.

Figure e: Excurrent canal traces in calcareous skeleton of Recent *Acanthochaetetes wellsi* (sclerosponge). J.Vacelet Collection. Jamaica.
Scale bars = 1cm.

Figure f: Surface excurrent canal traces in preserved soft-tissue of Recent *Axinella polypoides* (non-calcified axinellid demosponge). B.M. (N. H.) Sponge Collection (unnumbered).
Scale bar = 1cm.

PLATE 11 RECENT EXCURRENT CANAL TRACES AND FOSSIL ASTRORHIZAE



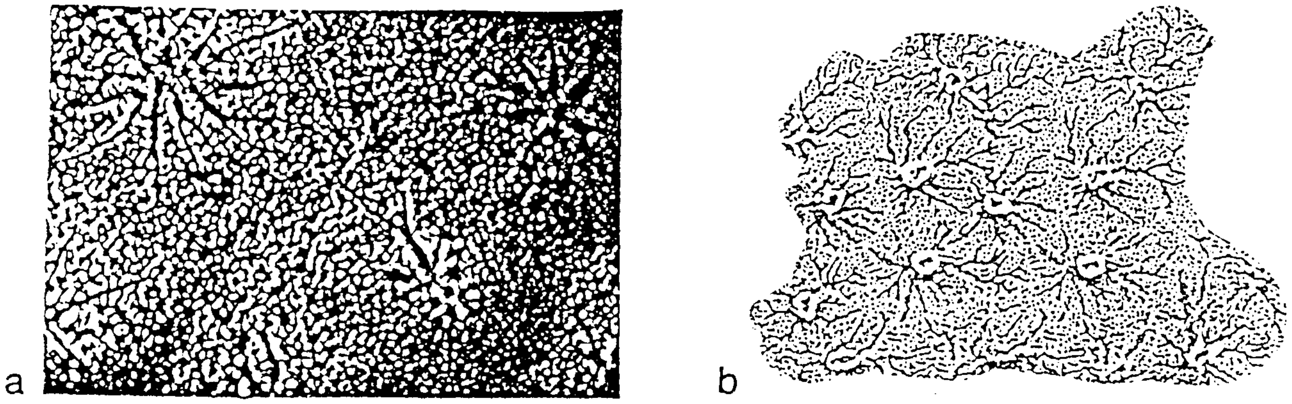


Figure 2.6. The external aquiferous systems of the freshwater sponges:
a) *Spongilla uvirae*, and
b) *Potamolepsis leubnitzae*
showing repeated and regular partition of oscula onto which converge stellate excurrent canals. From Brien (1967).
Scale bar = 1cm.

The stromatoporoid aquiferous units are based upon the derived leucon form of rhagon unit, where the paragastric cavity has been modifed to form excurrent canals. This idea was first proposed by Twitchell (1929) and is here confirmed. The rhagon unit and the modified leucon form are shown in Figure 2.7a and b. A stylised stromatoporoid aquiferous unit is shown in Figure 2.7c, based on *Burgundia wetzeli* and represented in terms of the form of enclosed space, rather than that of the skeleton. Stromatoporoids, like Recent sponges, show great variety in construction, organisation and spacing of these units.

Comparison of Recent and stromatoporoid aquiferous units can yield biological information. Figure 2.8 compares transverse and longitudinal thin sections of a modern sclerosponge *Calcifibrospongia actinostromarioides* with those of an Upper Jurassic stromatoporoid, '*Burgundia*' *astrotubulata.* The osculum, ostia and astrorhizal canals are directly comparable. Likewise, the canal system of *Burgundia wetzeli* (Lower Cretaceous) is formed of stacked rhagon units, where the osculum has been repeatedly truncated by secondarily precipitated tabulae, which have sectioned off abandoned parts of the skeleton as the animal grew (Figure 2.9).

This also explains the presence of tabulae across the ostia and within the astrorhizal canals. The

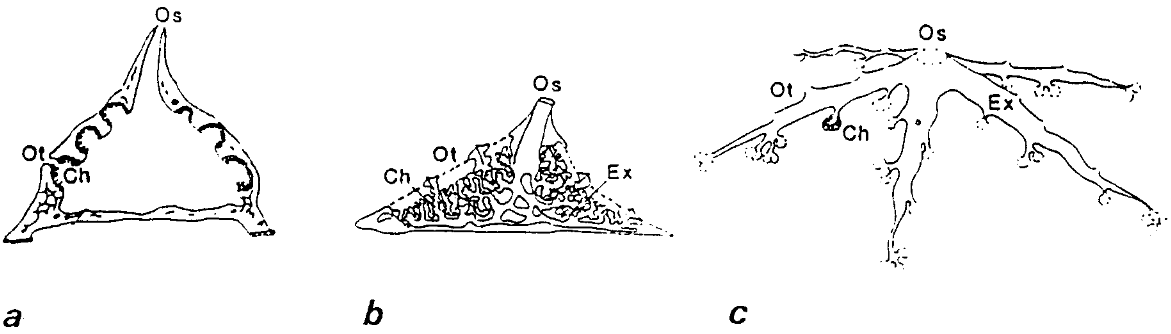


Figure 2.7. The Rhagon aquiferous unit. All diagrams are schematic.
Os: Osculum, **Ot**: Ostium, **Ex**: Excurrent canal. **Ch**: Choanocyte chamber
a) The basic rhagon (longitudinal section);
b) the tetractinomorph leucon, where the paragastric cavity has been modified to form excurrent canals (longitudinal section);
c) a 'stromatoporoid' aquiferous unit based on *Burgundia wetzeli* (represented three-dimensionally).

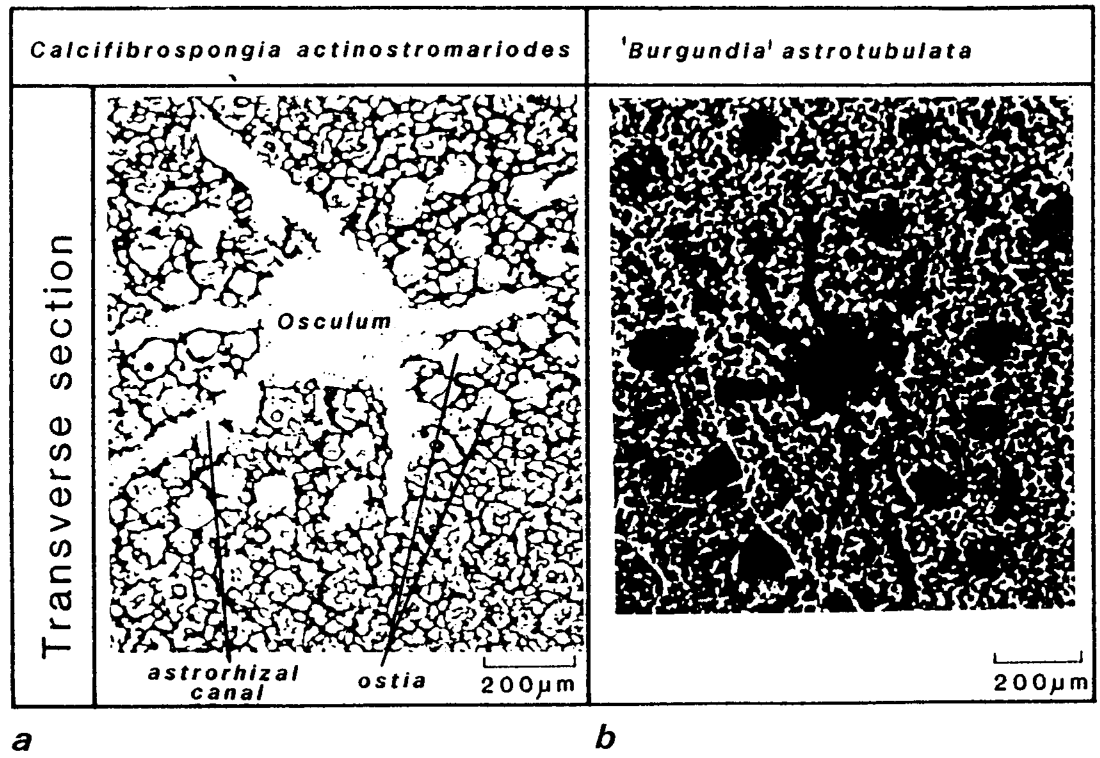


Figure 2.8. Comparison of transverse sections of the Recent sclerosponge *Calcifibrospongia actinostromarioides* (**a**) and the Upper Jurassic stromatoporoid *'Burgundia' astrotubulata* (**b**) . The osculum, astrorhizal canals and the ostia are directly comparable.
(Figure **a** from Hartman 1979, figure **b** from Turnšek 1967).

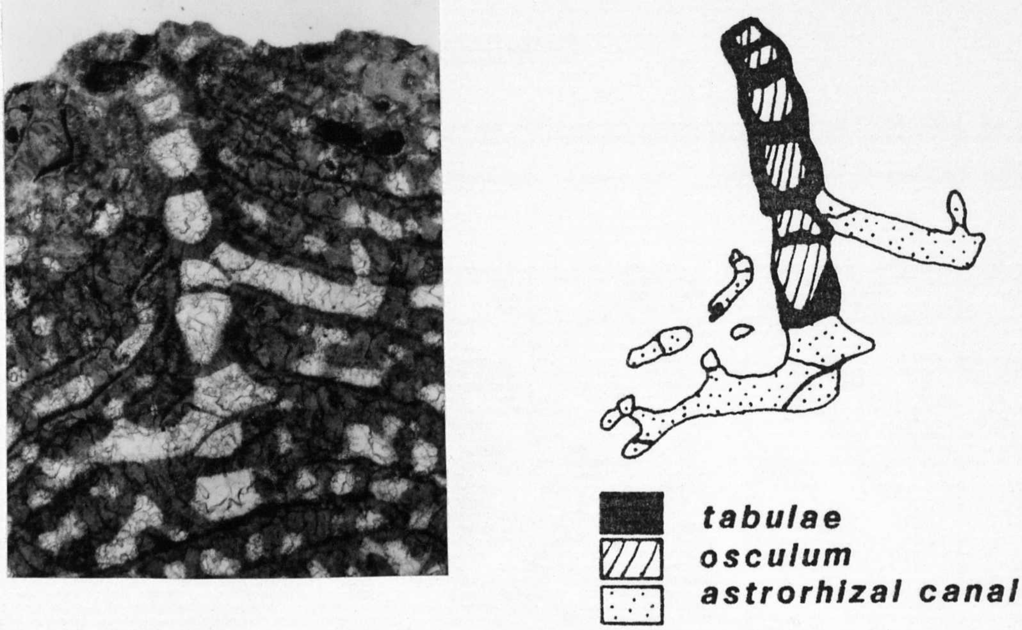


Figure 2.9. A longitudinal section through stacked aquiferous units of *Burgundia wetzeli,* showing the osculum, astrorhizal canals and secondarily precipitated tabulae separating-off abandoned parts of the skeleton as the animal grew.
Scale bar = 100 µm.

position of these secondary tabulae coincides with continuous lamellae, suggesting that this animal possessed a thin veneer of tissue, perhaps only limited to one interlamellar space, with superficial astrorhizal systems. The animal probably grew in an incremental way with only a thin layer of living tissue.

2.3 DISCUSSION

The finding of sponge-type spicule pseudomorphs within the calcareous skeleton of Mesozoic stromatoporoids confirms poriferan affinity for some representatives of this group and the canal system of Mesozoic stromatoporoids can best be interpreted in terms of a poriferan filtration system, based upon the rhagon unit, characteristic of thin encrusting demosponges. Studies of spicule type and arrangement allow a more precise placing within the Porifera .

The positioning of the spicules of Type 1(*A.lecompti*) clearly determines the form of the primary irregular calcareous skeleton, in a way reminiscent of spongin fibres enmeshing a spicule framework. The primary irregular calcite may have formed by the mineralisation

PLATE 12 RECENT NON-CALCIFIED DEMOSPONGES

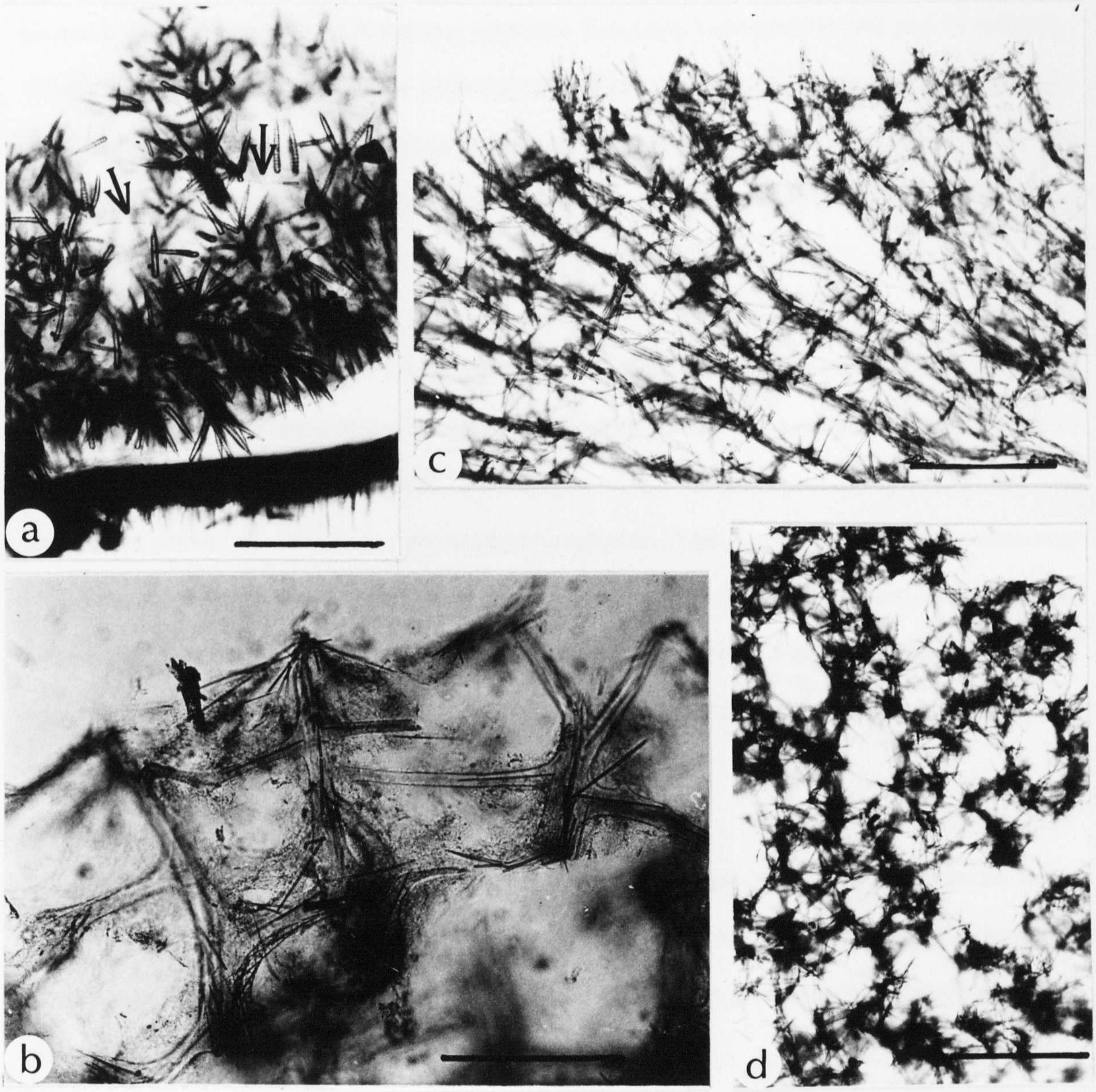
Light photographs of thin-sections. All specimens from the B.M.(N.H.) Sponge Collection.

Figure a: *Agelas mauritanis.* Longitudinal section showing plumose tracts of club-shaped acanthostyles held in place by strips of spongin (arrowed).
Scale bar= 1mm.

Figure b: *Esperiopsis anomala.* Longitudinal section showing spongin matrix enmeshing style spicules.
Scale bar = 1mm.

Figures c,d: *Renieria vasiformis.*
c: Longitudinal section showing fibro-reticulate arrangement of strongyle spicules in plumules bound by spongin forming tracts.
d: Transverse section through plumose tracts.
Scale bars = 1mm.

PLATE 12 RECENT NON-CALCIFIED DEMOSPONGES



of a network of spongin, and may be related to Recent forms, where spongin plays a similar role (See Section 6.) e.g.*Esperiopsis anomala* (Plate 12, fig. b) . The radial arrangement of the spicules is similar to that of the Recent Axinellida, within the Sub-class Tetractinomorpha and *Renieria sp.*, within the order Haplosclerida, class Demospongiae (Plate 12, fig.c,d.). However, the presence of an axial condensation of spicules is highly characteristic of the Axinellida. The orthogonal fibrous rim, present periodically, is a secondary skeletal feature ,and is possibly related to environmental fluctuations.

The plumose framework of Type 2 spicules (members of the Milleporellidae) appear to determine the presence and orientation of the fascicular fibres which construct the columns of the calcareous skeleton. The fibres are initiated in tufts at the spicule bases, sub-parallel to the spicule shafts. The tabulae are secondary filling tissue and contain no spicules. Type 2 arrangements show similarities in form, and their calcareous skeleton, in microstructure, to the Recent sclerosponge family Ceratoporellidae, especially to the fossil genus, *Murania sp.* and to members of the Agelasidae, e.g. *Agelas mauritanis* (Plate 12, fig. a.). There are also some similarities in spicule form and arrangement to the order Poecilosclerida.

The triaxine (or tetraxine) spicules of *Actinostromaria sp.* (Type 3) show some affinities to the sub-class Tetractinomorpha e.g. the genus *Syamon,* within the Axinellida. The three-dimensional morphology of these spicules is unclear and as only calcite pseudomorphs have been found, the possibility of this form being a calcarean cannot be dismissed.

The presence of strongyles in *New. gen. n. sp.* A (Type 4), indicates affinity to the Order Haplosclerida, within the Ceractinomorpha (e.g. *Renieria vasiformis* Plate 12, fig.c,d.).

Mesozoic stromatoporoids appear to have produced a calcareous skeleton upon a primary spicule framework. The four types possess different spicule complements, which coincide with different calcareous microstructures and differing relationships between these two parts of the skeleton. The strong correlation between spicule type, arrangement and calcareous skeleton has important biological consequences. Varied modes of biomineralisation are required to produce different microstructures and this could suggest profound original soft-tissue differences (See Section 3.5.

and Section 6.2.4).

Detailed spicule and histological examination of the Recent sclerosponges shows that these forms do not represent a monophyletic group. Different spicule complements, soft tissue organisations and larval types, indicate that members can be better placed within the pre-existing demosponge classification framework (Vacelet 1983). Members of the Ceratoporellidae and *Astrosclera sp.*, represent calcified members of the Order Axinellida (Plate 12, fig. a). *Calcifibrospongia* is a member of the Reneridae, within the Order Haplosclerida. The living "sclerosponges" are calcified demosponges , and their closest relatives are various non-calcified forms.

On the basis of this new spicule information, we are in a position to review the systematic position of Mesozoic stromatoporoids. Table 2.3 shows the proposed placing of spiculate stromatoporoids within the Recent demosponge taxonomic framework. The placing of the living sclerosponges is after Vacelet (1983).

The possession of a calcareous skeleton is a convergent feature in both stromatoporoids and sclerosponges. Chapter 4 discusses to what extent the retention of Mesozoic stromatoporoid higher taxonomic categories is necessary.

It is clear that the features thought characteristic of 'stromatoporoids', especially the astrorhizae, are shared by a wide range of different sponges. They are convergent and can no longer be used to define the group.

Mesozoic stromatoporoids must be redefined. Firstly, to redefine the group as calcified demosponges and secondarily, since the word stromatoporoid has been made indispensable by widespread use, to redefine the term to express a grade of organisation, rather than a taxonomically valid grouping:

PREVIOUS DEFINITION (Taxonomic)

Hydrozoans distinguished by a calcareous coenosteum basically of trabecular nature, generally with distinct transverse elements (lamellae) and vertical elements (pillars); exclusively colonial, massive, sheetlike or dendroid growth. Astrorhizae may or may not be present. Surface may or may not possess tubercles. (From Lecompte 1956).

(It should be noted however, that the type genus for 'stromatoporoids' is the Palaeozoic genus *Stromatopora* (Devonian)).

PROPOSED REDEFINITION (Organisational)

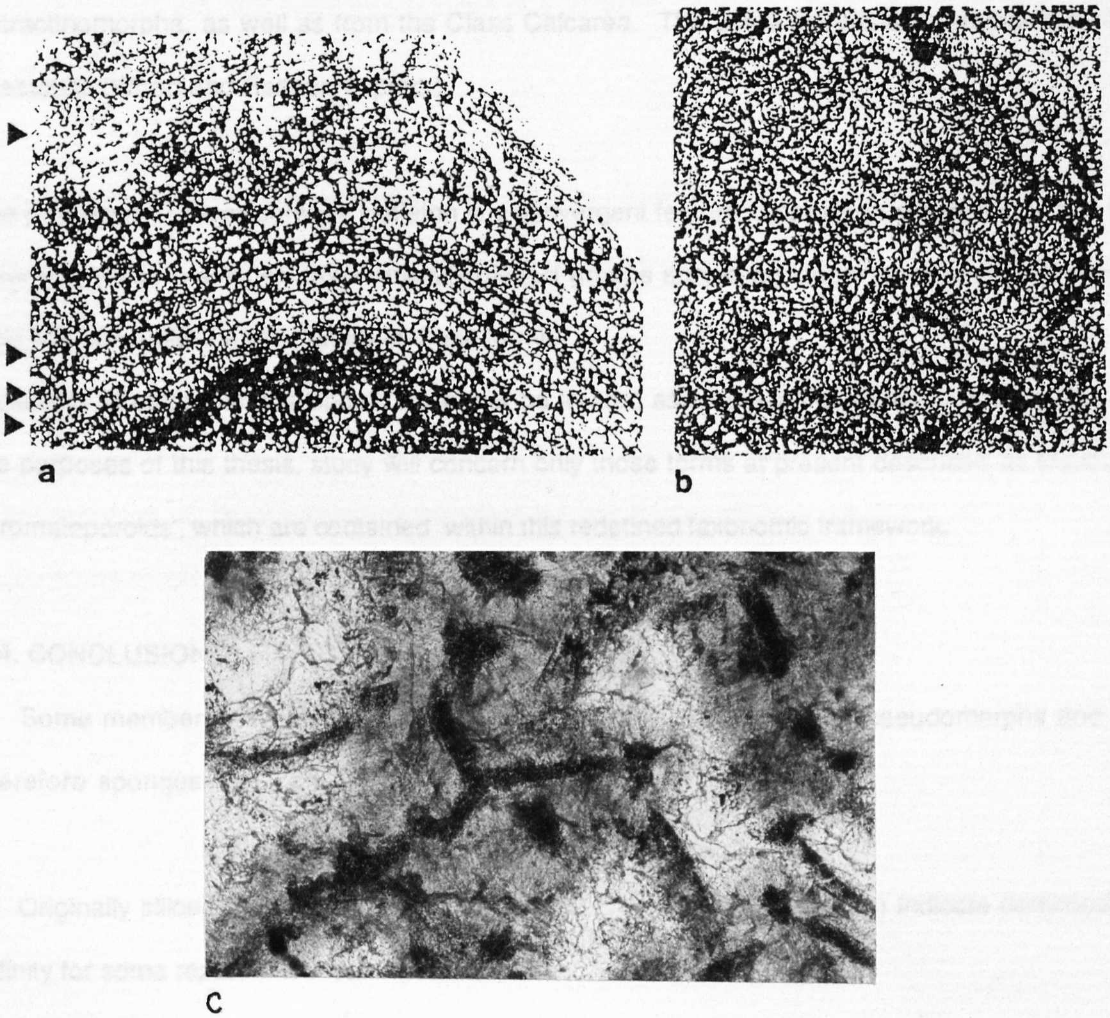
Calcified sponges which normally show a regular repetition of astrorhizal-bearing aquiferous units.

CLASS DEMOSPONGIA

SUB-CLASS TETRACTINOMORPHA		SUB-CLASS CERACTINOMORPHA	
POESCILOSCLERIDA	- *Merlia sp.**	**HAPLOSCLERIDA**-	*Vaceletia sp.**
AXINELLIDA		**RENIERIDAE**-	*Calcifibrospongia sp.**
AGELASIDAE	- *Astrosclera sp.**		- New.gen. n. sp. A**
	- Ceratoporellidae *		(Nov.fam.B)
	- Milleporellidae **(**TYPE 2**)		(**TYPE 4**)
	(*Actinostromarinina lecompti*) **		
	(Nov. fam. A) (**TYPE 1**)		
INCERTAE SEDIS	- Actinostromariidae **		
	(**TYPE 3**)		

Table 2.3 Distribution of 'stromatoporoids' (**) and 'sclerosponges' (*, after Vacelet 1985) within the Class Demospongiae, according to their spicule complement (Modified from Wood, In press.). The Types 1-4, refer to the skeletal types descibed in Section 2.2.1.1.

An example of this convergent "grade of organisation" is '*Burgundia' tutcheri* (Figure 2.10) a stromatoporoid described from the lower Cretaceous Faringdon Sponge Bed, Berks. This species fulfills the present characteristic features of a stromatoporoid, as satisfying the definition, but bears calcareous triaxine spicules; so one must ask, is it a calcarean, a stromatoporoid or both?



<u>Figure 2.10.</u> *'Burgundia' tutcheri* Kellaway and Smith, 1938.
a) Longitudinal thin-section showing a layered calcareous skeleton, pillars and lamellae (arrowed),
b) a transverse thin section showing astrorhizae.
c) orthogonal fibrous microstructure and calcareous spicules.
(Figures a and b from Kellaway and Smith 1938).

An important consequence of this redefinition is that as organisational terms the distinction between 'stromatoporoids' (in the Mesozoic sense) and 'sclerosponges' is purely an arbitrary one.

A similar conclusion was reached by Vacelet (1985) and Reitner (in press) for the sphinctozooid sponges, previously classified as a sub-class of the Class Calcarea. Reitner has shown from spicule complements that the thalamid skeleton characteristic of sphinctozoans has evolved six times in the history of the group, with representatives from the sub-classes Ceractinomorpha and Tetractinomorpha, as well as from the Class Calcarea. The same story is also emerging for the chaetetids (Wood and Reitner, in prep.).

The possession of a calcareous skeleton is a convergent feature in calcified demosponges and it is clear that these previously taxonomically distinct groups should no longer be studied in isolation. This has obscured the true nature of these forms.

Mesozoic 'stromatoporoids 'should no longer be treated as an independent taxonomic group. For the purposes of this thesis, study will concern only those forms at present described as Mesozoic 'stromatoporoids', which are contained within this redefined taxonomic framework.

2.4. CONCLUSIONS.

1) Some members of the Mesozoic "stromatoporoids" possess spicule pseudomorphs and are therefore sponges.

2) Originally siliceous styles (or acanthostyles) and triaxines (or tetraxines) indicate demosponge affinity for some representatives of the Mesozoic 'stromatoporoids'.

3) The calcareous skeleton is precipitated on a primary spicule framework.

4) Four different spicule types and arrangements indicate that possession of a calcareous skeleton is a convergent feature.

5) Four original microstructures of the calcareous skeleton can be determined: Irregular, fascicular fibrous, spherulitic and orthogonal fibrous. The microstructures shown by Mesozoic 'stromatoporoids' are identical to those found in Recent and fossil calcareous sponges.

6) The construction of the skeleton of Mesozoic 'stromatoporoids' (spicule framework, primary and secondary calcareous skeletons and filling tissue) is also identical to that of other calcified sponges.

7) The organisation of the skeletal elements, and the canal and astrorhizal system of stromatoporoids are best explained in terms of a poriferan aquiferous filtration system, based upon the rhagon unit.

8) Mesozoic 'stromatoporoids' should no longer be used as a taxon, but as an indication of the grade of organisation of the calcareous skeleton. As organisational terms, 'stromatoporoid' and 'sclerosponge' are synonyms.

9) The previously taxonomically distinct Sphinctozoa, Stromatoporoidea, Chaetetidae and Sclerospongiae all have representatives that are calcified demosponges and these forms should no longer be studied in isolation.

CHAPTER 3

A NEW SYSTEMATIC FRAMEWORK FOR MESOZOIC 'STROMATOPOROIDS'.

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3. 1. PRESENT TAXONOMIC FRAMEWORK.

No agreed taxonomic framework exists for the study of stromatoporoids. Each author has preferred his or her own system of taxonomic characters and weightings. In addition, much confusion and argument exists over the usefulness of certain features, e.g. microstructure. Diagenetic fabrics are frequently confused with original ones (i.e. those formed by the soft tissue) and there is a confusing plethora of descriptive terms, e.g. 'tabulate osculum' has five synonyms.

Significant contributions have been reviewed in Section 1. 2. 2. Because of the lack of a functional and constructional basis to systematic enquiries, the study of stromatoporoids has been haphazard. Such a basis is only possible when biological affinity has been determined. Having established Mesozoic stromatoporoids to be sponges, we are now in a position to apply this biological information to morphological and taxonomic investigations.

This chapter presents the rationale behind a new proposed systematic framework for Mesozoic stromatoporoids. Diagenetic lineages are presented which will enable workers to determine original skeletal microstructures where possible. The present nomenclature is reviewed and a revised and simplified system is given, based upon Recent poriferan terminology. Stromatoporoids are three-dimensionally complex and the study of structures using two dimensional thin sections can obviously lead to interpretational problems. Such erroneous interpretations are here eliminated and new or previously poorly recognised taxonomic features are described. The last three sections outline the new taxonomic framework. Constructional features are described and their taxonomic validity and position assessed.

3. 2. DIAGENESIS.

3.2.1.DIAGENESIS OF THE CALCAREOUS SKELETON.

Diagenetic alteration is significant in stromatoporoids because of its effects upon internal features which are of taxonomic importance. A good understanding of stromatoporoid diagenesis is necessary to evaluate the taxonomic validity of microstructure, and if found valid, to enable the construction of a taxonomic scheme which removes any diagenetic imprint.

Nicholson (1886) first recognised diagenetic alteration in stromatoporoids. Since then, there have been few attempts to distinguish between primary and secondary microstructure (St. Jean 1962, Stearn 1966, Wendt 1979, 1984). Wendt has been the only worker to present a reasonably comprehensive outline of the progression of skeletal alteration effects, but he dealt only with Mesozoic and Recent calcareous sponges (including stromatoporoids) .

Calcareous sponges are susceptible to all forms of diagenetic alteration including pyritisation, silicification and dolomitisation. Diagenetic alteration may enhance, modify or destroy primary skeletal characteristics. Wendt (1984) suggests that the l4 microstructures described in Palaeozoic stromatoporoids by Stearn, can be resolved to four types which he describes in Mesozoic calcified sponges including stromatoporoids:

1. Transversly fibrous (Synomous with striated): derived from orthogonal.
2. Melanospheric, cellular, microreticulate, ?vacuolate ?flocculent ?transversely-porous ?tubulate: derived from spherulitic.
3. Jet d'eau: synonomous with or derived from fascicular fibrous.
4. Compact: derived from irregular microstructure via micritisation or cementation.

Four pseudo-structures described by Stearn (peripherally fibrous, tripartite, laminae and meshed fibre) cannot be referred to the above four original microstructures. Through extensive study of mainly originally aragonitic material, Wendt broadly described diagenetic trends in the four microstructure types.

Diagenetic processes are extremely variable and cannot be discussed here, but diagenetic lineages are proposed which will enable workers to determine original skeletal microstructures and aid taxonomic determination in calcified demosponges.

Wendt (1984) distinguished three independent processes of diagenetic origin: alteration of mineralogy, alteration of microstructure and formation of diagenetic pseudostructures. Here, these categories are followed, with additional observations.

3. 2.1.1 Mineralogy

As established in Section 2.3 none of the calcified sponge groups, with the exception of Recent families (and possibly the inozoans) are valid taxonomic groupings. The distinction between 'sclerosponge' and 'stromatoporoid' is an arbitrary one, and any discussion of the distribution of original mineralogy in these forms can have no true taxonomic basis. So reference to these groups in the following sections is based upon their original assignment in the literature, and not upon the revised taxonomic criteria proposed in this thesis.

Extant sponges which bear a calcareous skeleton secrete aragonite (e.g. *Ceratoporella*, Plate 13 fig. a) or high magnesium-calcite (e.g. *Acanthochaetetes*, Plate 13, fig.c) in their basal skeletons. Different genera within the same family appear to share the same mineralogical composition. Vacelet (1980) has suggested that *Merlia normani* (generally found encrusting aragonitic gastropods) has a facultative aragonitic or calcitic skeleton. However, this sponge forms such a thin (few mm.) encrustation that contamination from the molluscan aragonite substratum was quite possible during analysis, and it is most likely that *Merlia normani* produces only a calcite skeleton.

Most fossil sponge material, including most Mesozoic stromatoporoids, is now low Mg. calcite. Primary aragonitic mineralogy with perfectly preserved microstructures has been documented from 'sphinctozoans' (Cuif, 1973), 'inozoans' (Wendt, 1974), ceratoporellids (Veizer and Wendt, 1976) other ' sclerosponges',(Dieci et al., 1974b), and 'stromatoporoids' (Wendt, 1975) from the Upper Triassic of the Alps, Hungary and Turkey, and from the Upper Permian reefs of Southern Tunisia (Plate 13, fig.b), but the 'stromatoporoid ' status of many of these forms is doubtful. Some genera

PLATE 13: MINERALOGY OF CALCIFIED DEMOSPONGES.

Light photomicrographs of thin-sections.

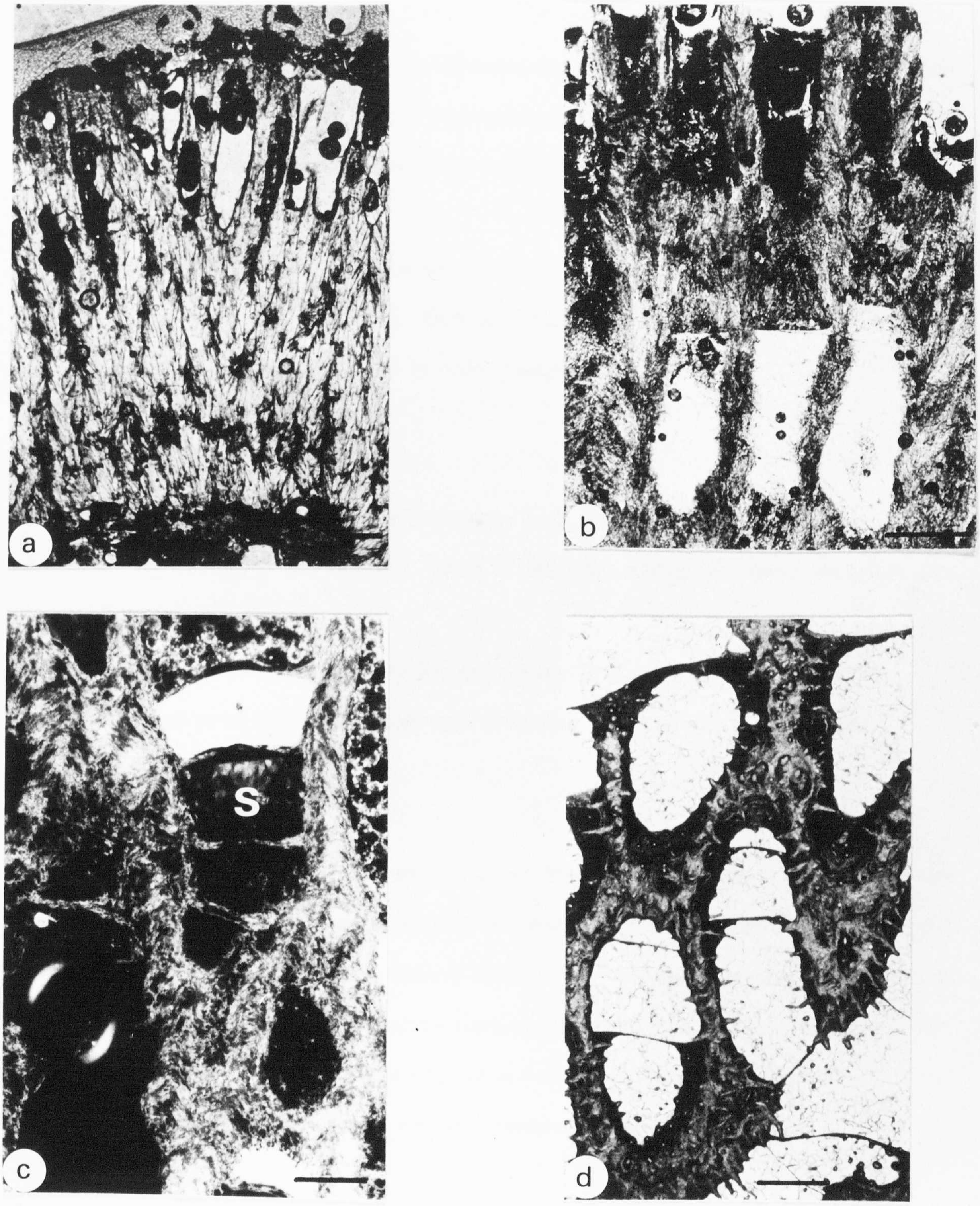
Figure a: Recent *Ceratoporella nicholsoni*. Original aragonitic calcareous skeleton with modified spherulitic microstructure. J.Reitner collection. Jamaica.
Scale bar = 1mm.

Figure b: Permian *Ceratoporella sp.* Original aragonitic calcareous skeleton with modified spherulitic microstructure. J.Reitner Collection. Djebel Tebaga, Tunisia.
Scale bar = 1mm.

Figure c: Recent *Acanthochaetetes wellsi.* Original high-Mg calcite calcareous skeleton with irregular microstructure orientated in one plane parallel to the growing surface. J.Vacelet Collection. Jamaica.
Scale bar = 200 µm.

Figure d: Eocene *Acathochaetetes sp.* Low-Mg calcite skeleton of originally high-Mg calcite with irregular microstructure orientated in one plane parallel to the growing surface. J.Reitner Collection. N.W. Spain.
Scale bar = 200µm.

PLATE 13 MINERALOGY OF RECENT AND FOSSIL CALCIFIED DEMOSPONGES



Rachel A.Wood

of Sphinctozoa within the well-preserved faunas of the Alps were originally calcitic.

Alteration of Mineralogy

Clearly, some originally aragonitic and high-Mg calcite calcareous sponges skeletons have inverted to low-Mg calcite (with varying degrees of microstructural loss) during diagenesis. Criteria for the recognition of these original mineralogies are discussed below.

The in-situ transformation from aragonite is said to occur via a thin solution film (Wardlaw et al. 1978) or a chalky solution zone (James 1974). Sandberg (1984) gave a list of criteria for recognition of original aragonite mineralogy, here given in order of decreasing reliability:

1. Still aragonite (e.g. Stehli, 1956)
2. Relatively coarse calcite mosaic cross-cutting original structure, with inclusions of original aragonite (e.g.Sandberg and Hudson, 1983). Mosaic crystals are often brownish and pseudopleochroic (Sandberg, 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. Moulds or subsequently filled moulds.

According to Sandberg (1984), calcite with preserved fine textures and regular optic orientations has often been attributed to a "pseudomorphic" or "paramorphic" transformation of aragonite, but there is no basis for accepting this 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 Besenecker (1983, fig. 4). Even that fine scale change produced textural and presumably also optical disruption.

Wendt (1979) postulates that the transformation of aragonite to calcite produces a secondary fabric which may retain some detail of the primary microstructure, but is frequently totally micritised, recrystallised or partially dolomitised (Wendt 1977).

Wendt (1984) suggests that Carboniferous Pharetronida were aragonitic, as their recrystallised skeletons sometimes reveal traces of spherulitic microstructure. According to Stearn (1972, 1986), Palaeozoic 'stromatoporoids', (generally recrystallised and rarely with traces of primary microstructure) were also probably aragonitic. This has been confirmed by Reitner (1986 pers.comm.) who has found relict aragonite inclusions in Palaeozoic 'stromatoporoid' material from S.Germany. However, Palaeozoic 'stromatoporoid' material, although recrystallised, does not show the same fabrics as associated fauna also postulated to have been aragonitic, e.g. molluscs.

The transformation of high- to low- Mg. calcite involves a paramorphic incongruent dissolution process (Plummer and Mackenzie, 1974). Fine detail may often be preserved. Lohmann and Meyers (1977) described calcite rich in microdolomite inclusions as evidence of original high -Mg calcite mineralogy. Richter and Fuchtbauer (1978) use the preservation of primary structures by ferroan calcite as a criterion for the recognition of original high Mg- calcite. Reitner and Engeser (1983) have postulated high-Mg mineralogy for *Acanthochaetetes* using this criterion in Cretaceous and Eocene specimens (Plate 13, fig d).

Low-Mg calcite is the most stable mineralogy under normal diagenetic conditions. Low-Mg forms tend to retain their original mineralogy and possess well-preserved microstructures.

Discussion

All microstructures found in Mesozoic 'stromatoporoids', as well as pharetronid and 'sclerosponge' material from the Upper Jurassic and later, is frequently well preserved. Associated fauna of undoubted aragonite composition is preserved either as moulds or with strongly re-crystallised shells. None of the typical characteristics of original aragonitic skeleton is found.

The well preserved calcite ultrastructures comprising late Mesozoic 'stromatoporoids' cannot reasonably be derived by calcitisation of aragonite precursors. If late Mesozoic 'stromatoporoids' had originally possessed aragonite skeletons, their preservation states would be dominated by the disruptive textures which are universally characteristic of the associated, altered scleractinian corals. Forms described as 'stromatoporoids', from the Middle Jurassic to Upper Cretaceous, were probably calcitic. Originally high-Mg calcite *Acanthochaetetes spp.* is known from the Cretaceous and Eocene of Spain (Reitner and Engeser 1983; 1986) and an aragonitic species of the genus *Ceratoporella* is known from the Upper Permian of Tjebel Tebaga, Tunisia.

Using these criteria to determine original mineralogy, Wendt (1984) proposed that most Carboniferous to Lower Jurassic calcareous sponges were aragonitic and most Middle Jurassic to Cretaceous forms were calcitic. However, Wendt (1979) suggested that the lamellar calcite skeleton found in some Jurassic and Cretaceous inozoans was possibly originally aragonitic, like the related aragonitic preserved sponges from the Permian and Triassic. Sandberg (1984) disputed this, stating that the textural regularity is incompatible with the calcitisation of original aragonite. This study confirms Sandberg's assertion and suggests that pseudo-lamellar structure in Mesozoic stromatoporoids is caused by recrystallisation of probably originally low-Mg calcitic material (See Section 3.2.1.3.).

Wendt (1979) postulates a shift in the mineralogical composition of sponges from aragonite to calcite during the Upper Jurassic, and compares this to a comparable shift in the Cnidaria e.g. from calcitic Palaeozoic Rugosa to Mesosoic and Recent aragonitic scleractinians.

Sandberg (1983), describing the original nature of ooids, suggests that there have been several cycles in original non-skeletal carbonate mineralogy, from low-Mg calcite, to high-Mg calcite with aragonite. He distinguishes two "aragonite-inhibiting" episodes (Late Ordovician to Mid-Carboniferous and Middle Jurassic to Late Cretaceous), alternating with three "aragonite-facilitating"ones.

Mistiaen (1984) and Kazmierczak et al. (1985) have suggested that there is a good correlation between the cycles described by Sandberg and the distribution of 'stromatoporoids', mainly described from strata deposited during the "aragonite-inhibiting" episodes. However, it is to be expected that the aragonitic forms would have a generally poorer record at these times due to diagenetic loss. Mistiaen and Kazmierczak et al. concluded that the bulk of Palaeozoic and Mesozoic forms were probably composed of low-Mg calcite.

An increasing number of Permian, Triassic and Lower Jurassic stromatoporoid-like calcareous sponges are being noted by G.Stanley (pers. comm. 1986). However preservation by silicification has made their systematics difficult to determine, but these forms might prove to be linking forms between the Palaeozoic and Mesozoic stromatoporoids. Their mineralogy is unknown.

It is clear that the calcareous skeleton mineralogy of the sponges has varied throughout their history, though we have few records of calcareous sponges from the Tertiary. We require more well-preserved material, a valid systematics and a finer diagenetic understanding if we are to fill in the many obvious "gaps" in the mineralogical record. Only then can we assess the taxonomic weighting and phylogenetic significance which should be given to mineralogical composition in calcareous sponges.

The distribution of mineralogies through time across the various calcareous sponge "grades" proposed here, is given in Figure 2.4.

3. 2. 1.2. Alteration of microstructure

Wendt (1984) has described microstructural alteration from aragonitic Permian and Triassic material in terms of micritisation, cementation and recrystallisation (transformation) . Diagenesis of aragonite is likely to differ from that of high Mg-calcite. Diagenetic lineages are described here from the four microstructure types and combinations found in low-Mg calcite late Mesozoic stromatoporoids. My purpose is to recognise original microstructure from diagenetic structures. I do not attempt to describe the processes involved. Figure 3.1. shows suggested diagenetic trends found in the calcareous skeletons of fossil calcified sponges. Completely micritised , recrystallised structures and solution precipitation may be derived from any of the four original microstructures.

Micritisation

Micritisation is attributed to the decomposition of organic matrices with associated biominerals. The final result is the complete breakdown of the original crystal arrangement and the formation of irregularily organised granular crystals between 1 - 8 µm length.

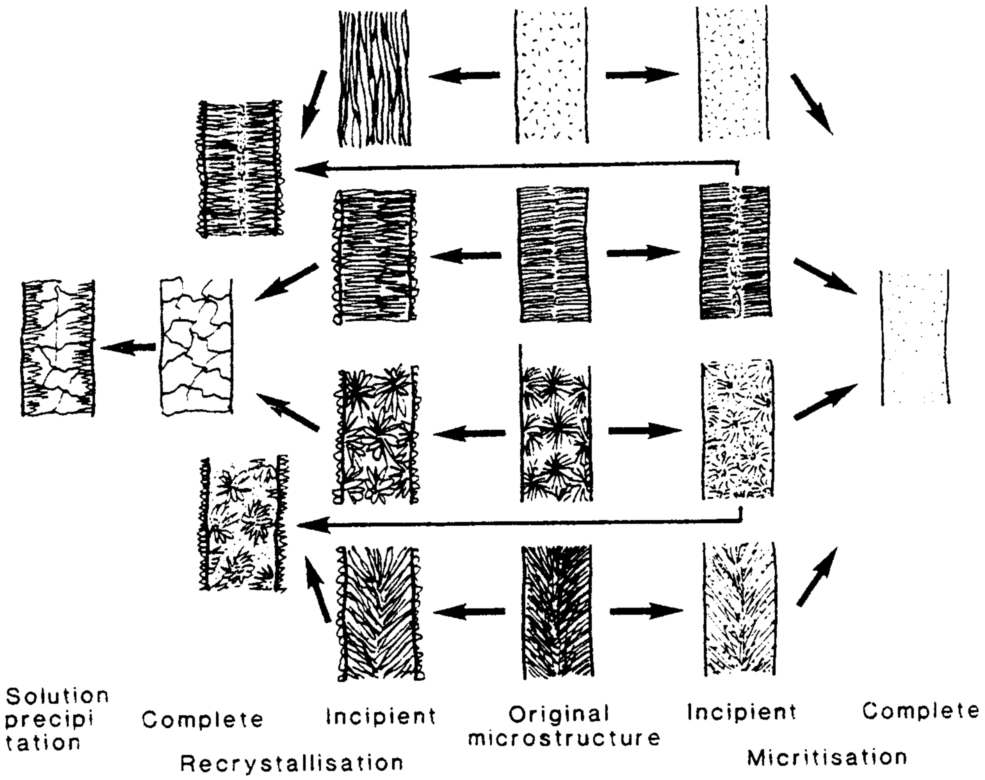


Figure 3.1: Trends of diagenetic alteration in the calcareous skeleton of sponges. Microstructure symbols as in Figure 2.4. Top-most diagram on left is pseudolamellar structure. Full explanation in text. (Modified from Wendt 1984)

Non-diagenetic irregular microstructure has only been noted from one Mesozoic'stromatoporoid' genus, *Actinostromarianina lecompti*, which bears a primary irregular microstructure, and a secondary orthogonal fibrous rim which is periodically precipitated to form latilaminae (see Section 2. 2. 1. 3.).

Micritisation appears preferentially to attack areas of weakness in the microstructure. In aragonitic spherulitic specimens it starts at the centre of the sphere and in the inter-spherulitic areas (Plate14, fig. a). Micritisation has not been noted from the one supposed calcitic spherulitic form. In orthogonal microstructure, micritisation starts at the centres of calcification. It appears as a "dark" central axis in thin-section increasing in width, and eventually totally obscuring the orthogonal fibres (Plate14,fig. b; Plate 16, fig.h). Micritisation also attacks calcite spicule pseudomorphs in this form, as noted in Section 3. 2. 2. 2. (Plate 16, figs. e-h).

PLATE 14: MICRITISATION AND RECRYSTALLISATION

figures a-c:Light photomicrographs of thin-sections.

Figure d: S.E.Micrograph.

Figure a: Recrystallisation of spherulitic microstructure to a fibrous microstructure in areas marked (**R**). Original microstructure remains in areas marked (**S**). 'Sclerosponge'. J.Reitner Collection. Tjebel Tebaga, Tunisia. Upper Permian.
Scale bar = 100 µm.

Figure b: Recrystallisation of orthogonal fibrous microstructure producing crystal size increase. Central area of skeletal element is micritised. *Disparastromaria sp.* 83/9b. La Mounine, Marseille, France. Upper Hauterivian.
Scale bar = 100 µm.

Figure c: Total dissolution and recrystallisation (Solution precipitation). Crystals are precipitated within the mould of former skeletal elements. *Disparastromaria sp.* 83/13. La Mounine, Marseille, France. Upper Hauterivian.
Scale bar = 100 µm.

figure d: S.E.Micrograph of *Actinostromaria sp.* with sparry calcite infill. H 5480. Trnovski Gost, Slovenia, Yugoslavia. Oxfordian - Kimmeridgian.
Scale bar = 100 µm.

PLATE 14 MICRITISATION AND RECRYSTALLISATION

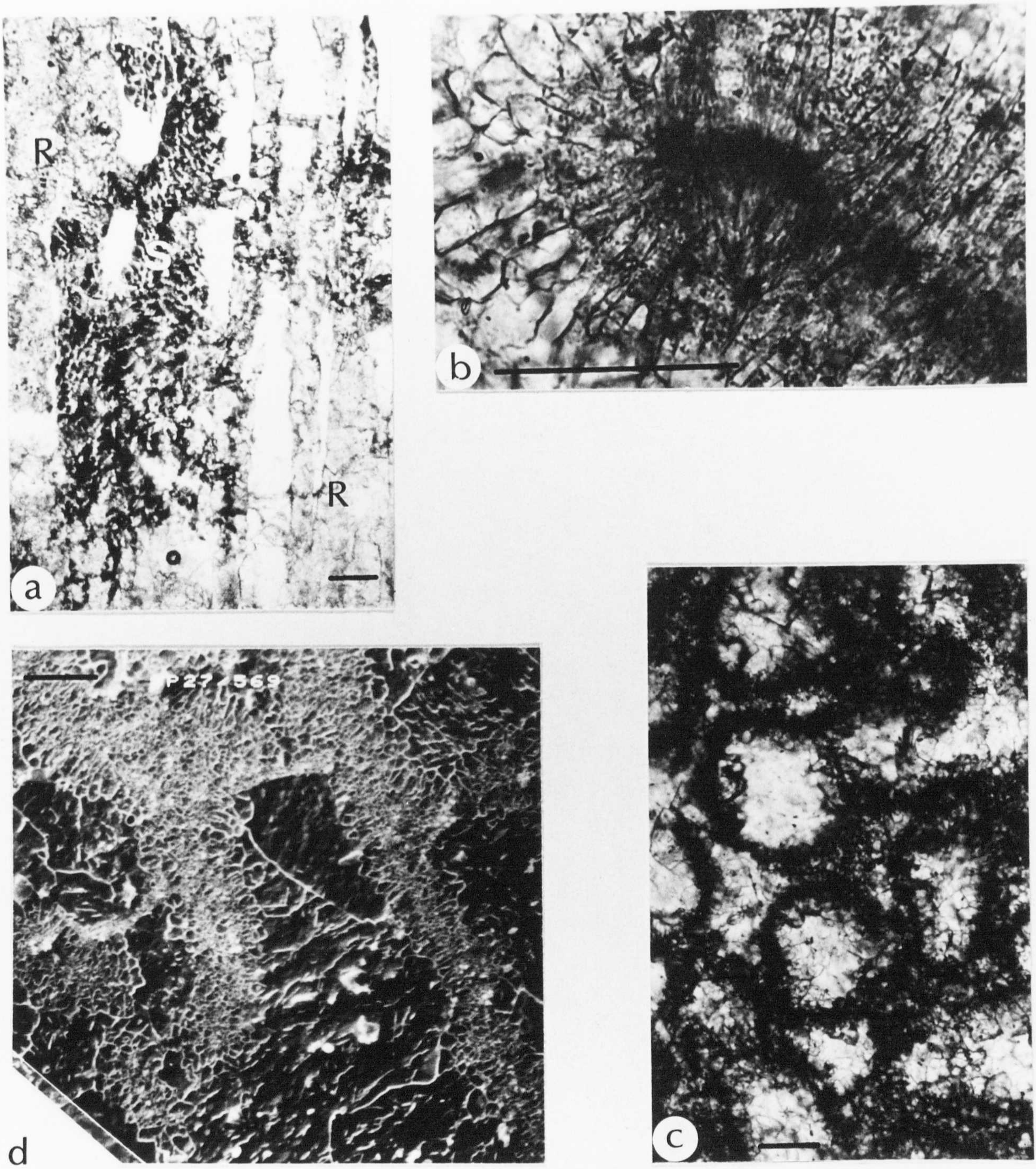


PLATE 15: CEMENTATION AND SKELETAL THICKENING

Figures a,b,d: Light photomicrographs of thin sections.

Figure c: S.E.Micrograph of broken surface.

Figure a: Rim calcite cement (**C**) and totally micritised skeletal element (**M**). Originally orthogonal fibrous strand. *Disparistromaria sp.* 83/5. La Mounine, Marseille, France. Upper Hauterivian.
Scale bar = 100 µm.

Figure b: Recrystallised fascicular fibrous columns. Note increase in crystal size and crystal growth from both sides of tabulae (**T**). *Parastromatopora libani.* H 4789 . Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 100 µm.

Figure c: Rim calcite (**R**) and sparry calcite infill (**S**) in interskeletal space. *Disparistromaria sp.* 84/52. Trnovski Gost, Slovenia, Yugoslavia. Oxfordian - Kimmeridgian.
Scale bar = 100 µm.

Figure d: Skeletal thickening in *Shuqraia sp.* H 4516. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 100 µm.

PLATE 15 CEMENTATION AND SKELETAL THICKENING

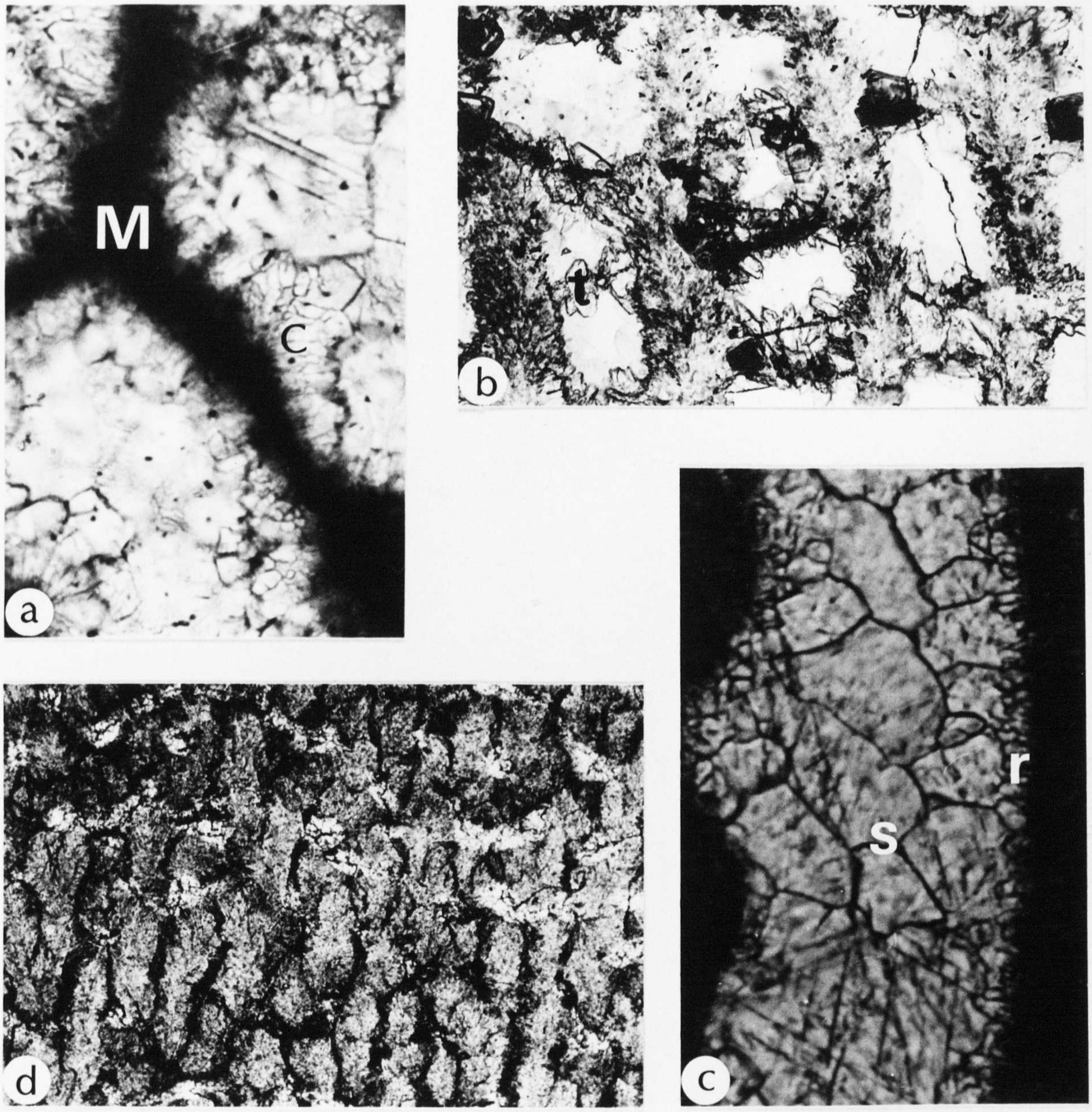


PLATE 16: SPICULE DIAGENESIS

Figures a - d : S.E.M. photomicrographs.

Figures e - h : light photomicrographs of longitudinal thin-sections.

Figure a: Pitting of siliceous spicule in Recent *Calcifibrospongia actinostromariodes* (arrowed). Jamaica.
Scale bar = 20 μm.

Figure b: Totally dissolved spicules leaving moulds in Recent *Calcifibrospongia actinostromariodes* (arrowed). Jamaica.
Scale bar = 20 μm.

Figure c: Epitaxial lumen infill in Recent *Ceratoporella.* J.Reitner Collection. Jamaica.
Scale bars = 30 μm.

Figure d: Epitaxial infill in Recent *Ceratoporella,* showing corrosion of spicule tip (arrowed). Backfill will eventually overgrow the mould left by the spicule. J. Reitner Collection. Jamaica.
Scale bars = 10 μm.

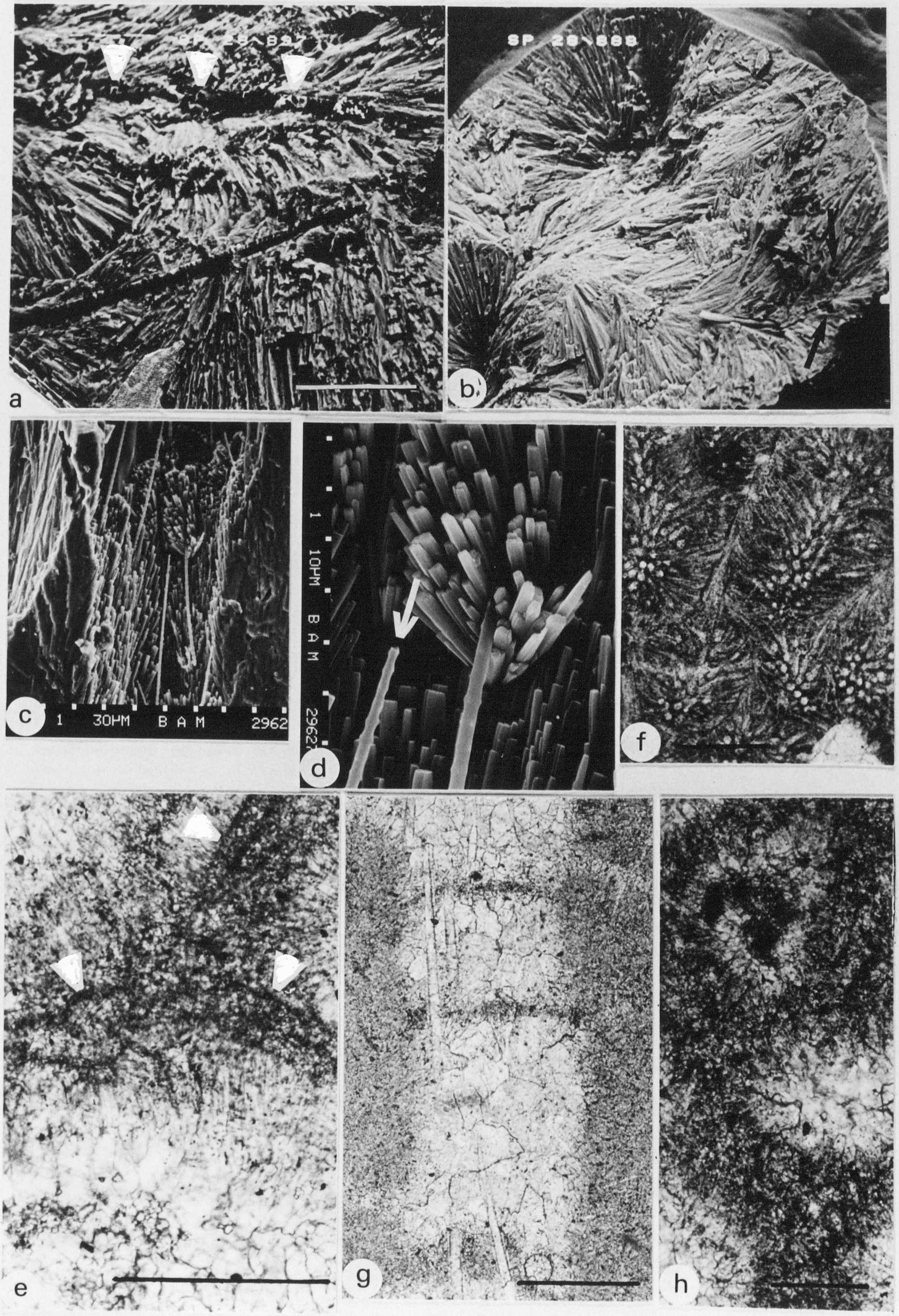
Figure e: Micritic envelope around siliceous spicule pseudomorphs in *Actinostromaria sp.* (arrowed). H 5480 Trnovski Gost, Slovenia, Yugoslavia. Oxfordian - Kimmeridgian.
Scale bar = 100 μm.

Figure f: Spicule 'ghosts' in *Parastromatopora libani.* H 4788. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 100 μm.

Figure g: Calcite pseudomorphs in *Blastochaetetes irregularis* in lumen of calicle, trapped by tabulae. 85/JP 2 .Collades de Bastus, N.Spain. Santonian.
Scale bar = 100 μm.

Figure h: Totally micritised spicule pseudomorphs (previously polycrystalline calcite) with only faint boundaries and incipient micritisation of orthogonal fibrous calcareous skeleton. *Actinostromaria sp.* H 5480.Trnovski Gost, Slovenia, Yugoslavia. Kimmeridgian - Oxfordian.
Scale bar = 100 μm.

PLATE 16 SPICULE DIAGENESIS



Rachel A.Wood

Fascicular fibrous microstructure appears to be least susceptible to micritisation; it is sometimes preserved in Lower Palaeozoic 'stromatoporoids' presumed to be originally aragonitic. In aragonitic forms the alignment of inclusions which appear as dark specks under transmitted light, accentuate this fibrous structure.

Cementation

All skeletal elements in calcitic Mesozoic 'stromatoporoid' microstructures show two phases of cementation.

1. Early rim cements, precipitated epitaxially to the microstructural fibres of the skeletal elements. Orthogonal fibrous cements are shown in Plate 15,fig.a,c and cements from fascicular fibrous microstructures in Plate 15 fig. b. Aragonitic calcareous sponges often show acicular aragonite crystals growing isopachously from the skeletal elements, including the tabulae.
2. Late drusy or equant cements . (Plate 15 , fig.c)

Cementation affects the interskeletal spaces or lumina of a sponge skeleton when the living tissue has abandoned the area or has decayed, but does not affect skeletal microstructure itself. Preservation of spicules not incorporated into the calcified skeleton within the interskeletal spaces, and spicules projecting into the lumina from the calcareous skeleton, indicates that cementation can occur before the diagenetic breakdown of the spicules (Plate 16,fig. g). Since Recent "sclerosponge" spicules are known to dissolve during the lifetime of the sponge (Hartman and Goreau 1970), cementation must be simultaneous, or pre-date, spicule dissolution.

Wendt (1984) states that irregular microstructure is the most porous, and therefore most susceptible to early cementation. At present, no evidence from Mesozoic 'stromatoporoids' is available to comment upon this.

The frequently observed longer crystals in fossil specimens compared with Recent and aragonitically preserved counterparts, is probably due to syntaxial crystal growth. This leads to skeletal thickening (Plate 15,fig. d) and is noted in all types of fibrous microstructures. Syntaxial crystal growth could be under organic or inorganic control. Inorganic crystal growth can only be distinguished from organic growth when it is seen to extend beyond the extent of the filling tissue e.g.tabulae, in the older part of the animal (Figure 3.2). Retreating tissue may precipitate syntaxial crystals onto the surrounding skeletal walls.

Recrystallisation

Aragonite skeletons frequently recrystallise to form a coarse calcite mosaic, with no or few traces of the primary microstructure or mineralisation. Recrystallisation can ultimately destroy the internal organisation of the skeleton as well as the microstructural fabric. In calcitic Mesozoic 'stromatoporoids' recrystallisation leads to a general increase in crystal size (Plate 14, figs.b,d). In early recrystallisation the individual crystals in the three fibrous microstructures will maintain their acicular nature. Continued recrystallisation will cause the growth of more equi-dimensional crystals (Plate Plate 15, figs. b). Previously micritised specimens can be recrystallised to form coarse mosaics with residual micritised areas. Recrystallisation trends are shown in Figure 3.1.

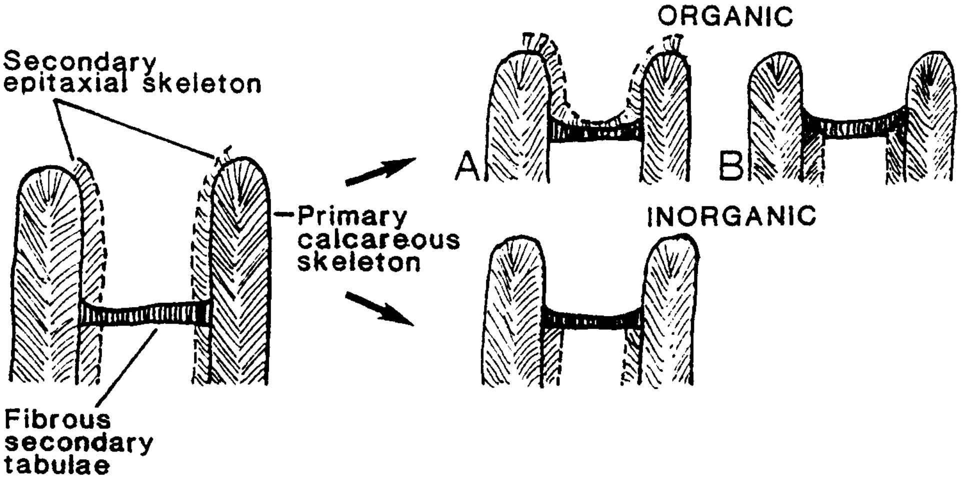


Figure 3.2: Criteria for differentiation between organically and inorganically precipitated secondary epitaxial skeleton. Inorganic crystal growth can only be distinguished from organic growth when it can be seen to postdate the secondary filling tissue e.g. tabulae, in the older part of the animal. Retreating tissue may precipitate syntaxial crystals onto the surrounding primary skeletal walls as a continuation of the tabulae (a), or tabulae are seen to postdate the epitaxial secondary skeleton (**b**).

3. 2. 1.3. Diagenetic Pseudostructures

Two diagenetic pseudostructures have been noted in Mesozoic 'stromatoporoids'; Pseudolamellar and scalenohedra. These are discussed below.

Pseudolamellar structure. (Plate 18, figs. a,c)

Although some species of calcified demosponge possess original lamellar microstructures e.g. *Acanthochaetetes spp.,* diagenesis can form pseudolamellar structures, e.g. *Actinstromarianina spp.*. *Actinostromarianina spp.* bears a primary irregular microstructure and a secondary orthogonal fibrous rim which is precipitated periodically to form latilaminae.

Flügel (1969) described a new species of this genus based upon skeletal form and organisation which possessed what he described as lamellar microstructure. This forms a banded appearance within the skeletal elements in thin-section, sub-parallel to the skeletal element boundaries. Wendt (1984) describes this structure under S.E.M. as consisting of interlocked, curved bladed crystals 5 - 10 µm thick and a few µm long. He suggests that lamellar structure is probably derived from a calcitic irregular microstructure showing some parallel orientation.

In *Actinostromarianina spp.* the lamellar nature is probably primarily due to recrystallisation of the irregular microstructure, enhanced by the recrystallisation of the orthogonal fibrous rim , producing crystals of a different size and therefore birefringence under transmitted light.

Pseudolamellar structure from Permian corals has also been described (Oekentorp, 1984). He suggests that it is a consequence of the recrystallisation of orthogonal fibrous cements deposited during early diagenesis in the pore space between the septa, which grow epitaxially on the septa to produce skeletal element thickening. *Shuqraia somaliensis* has an orthogonal to fascicular fibrous calcareous skeleton and shows pseudolamellar structure, that appears to delimit growth increments in the secondary orthogonal skeleton. It is unclear whether this structure is organic or inorganic. It may represent subsequent growth increase or increments of the fibrous tabulae as the animal grew upwards. Fenninger and Flajs (1974) suggest that this pseudostructure may result from orthogonally arranged crystals, affected by a migrating solution front parallel to the skeletal element surface. Due to the presence of this pseudostructure in *Steineria somaliensis* (which possesses orthogonal to fascicular fibrous microstructure) pseudo-lamellar structure is clearly not confined to orthogonal microstructure only.

PLATE 17: PYRITE SPICULE PSEUDOMORPHS

All light photomicrographs of thin-sections.

Figure a: Pyrite pseudomorph composed of a chain of aligned crystals. *Dehornella harrarensis.* H 5164a . Makhtesh Ramon, Israel. Lower Kimmeridgian.
Scale bar = 50 µm

Figure b: Agglomeration of pyrite forming pseudomorph. *Parastromatopora libani.* H 4789. Makhtesh Ramon, Israel. Lower Kimmeridgian.
Scale bar = 100 µm

Figure c: Incipient pyritisation of calcite pseudomorphs initiating as a thread of pyrite on axial filament of spicule (arrowed). *Dehornella crustans.* 29/4. Makhtesh Ramon, Israel. Lower Kimmeridgian.
Scale bar = 100 µm.

Figure d: Large numbers of pyrite pseudomorphs in outer zone of specimen. *Promillepora kurnubi.* H 4898a. Makhtesh Ramon, Israel. Lower Kimmeridgian.
Scale bar = 1mm.

Figure e: Silicification of entire individual obliterating the calcareous skeleton but leaving the more resistant pyrite pseudomorphs. H 4756a. '*Stromatopora*' *choffati.* Bakkin, ?S. Yemen.
Scale bar = 200 µm.

PLATE 17 PYRITE SPICULE PSEUDOMORPHS

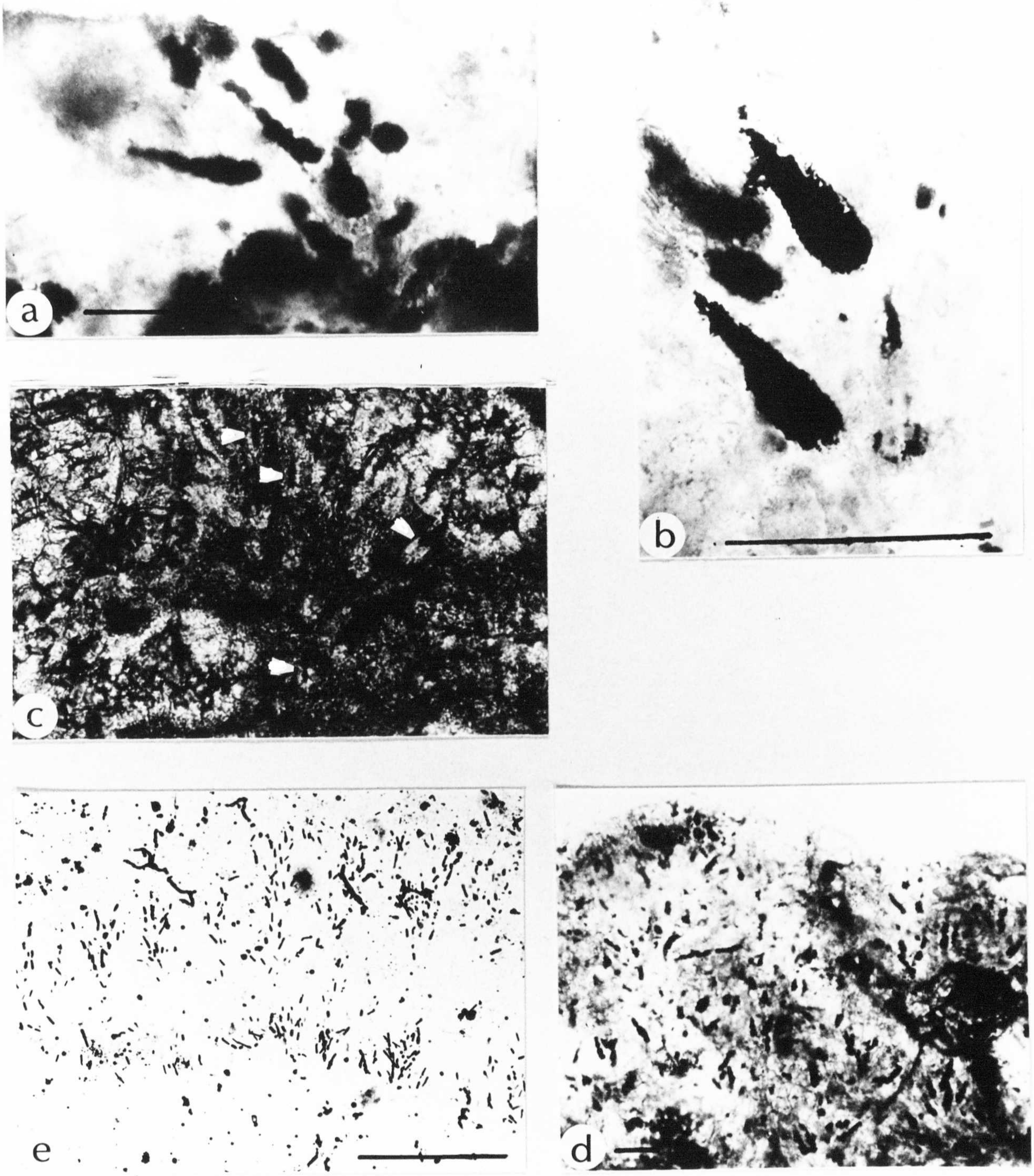


PLATE 18: DIAGENETIC PSEUDOSTRUCTURES

All light photomicrographs of thin-sections.

Figures a,c: Pseudolamellar structure:

Actinostromarianina lecompti. H 4608b. Alam Abaydah, Arabia. Upper Kimmeridgian.

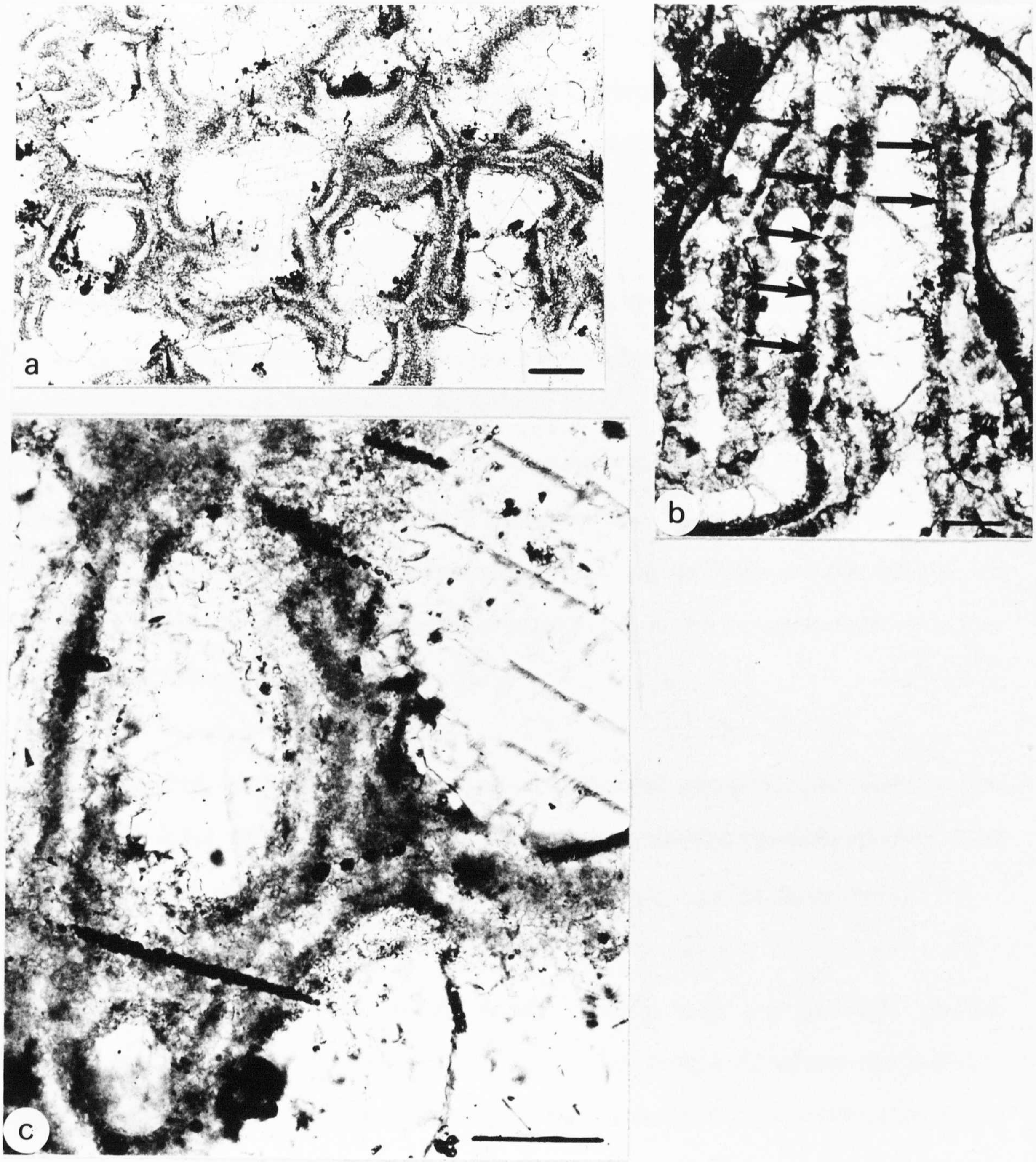
a: Scale bar = 200 µm.

c: Scale bar = 100 µm.

Figures b: Scalenohedra (arrowed) in *Burgundia ramosa.* H 4664. Alam Abyadh, Arabia. Upper Jurassic.

Scale bar = 100 µm.

PLATE 18 DIAGENETIC PSEUDOSTRUCTURES



Scalenohedra (Plate 18, fig. b)

Another possible diagenetic pseudostructure is "saw-toothed" formations or indentations projecting towards the centre of the skeletal elements. A similar structure has been characterised by Bathurst (1975) as being a recrystallisation fabric. In this study, it has been found in the Mesozoic "stromatoporoid" species *Shuqraia spp.* and *Burgundia ramosa*. This structure has also been reported from Upper Permian rugose corals from Timor (Oekentorp 1984).

3. 2. 2. DIAGENESIS OF SPICULES.

One of the reasons given for the presumed lack of spicules in 'stromatoporoids' was that spicules dissolved during life, as in Recent 'sclerosponges' and were susceptible to diagenetic loss.

Spicules are clearly not rare in Mesozoic stromatoporoids. They are incorporated into the calcareous skeleton and have been found in a large number of genera, and from localities with differing diagenetic histories. Use of standard carbonate stains greatly enhances their visibility. It is still unclear, however, whether the absence of microscleres is due to non-secretion or to their greater susceptibility to diagenetic loss.

In Recent calcified demosponges, spicules consist of hydrated amorphous silica (Hartman and Goreau, l970, Jones, 1979). Recent calcareans have single crystal High Mg-calcite spicules. Minor amounts of SO_4^{2-}, Sr^{2+} and Na^+ have also been found in calcitic spicules (Jones, 1979).

The original mineralogy of fossil "stromatoporoid", "sphinctozoan" and "chaetetid" calcified demosponge spicules was probably similar to that of their living descendants and relatives. However, early diagenetic processes have nearly always replaced the amorphous silica by a secondary polycrystalline mosaic of $CaCO_3$, SiO_2 or FeS_2. Single crystal pseudomorphs of SiO_2 have also been found, as well as calcareous spicules which remain as single crystals.

Spicule diagenesis begins during the life-time of Recent calcified demosponges. The processes are not fully known, but have been partially described by Hartman and Goreau 1970, and Hartman, 1979. Figure 3.3 illustrates suggested progressive stages of siliceous spicule diagenesis, as noted in Recent and fossil calcified demosponges.

3.2.2.1 Early diagenesis

During life the spicules are precipitated by the soft tissue and therefore occupy the original pore spaces of the skeleton. If the spicules are not in some way trapped in the calcareous skeleton, they will not be preserved. If preserved,

1) they may become accidentally trapped by:

a) secondary backfill growing epitaxially from the calicle walls or tabulae (e.g. *Ceratoporella spp.*), or,

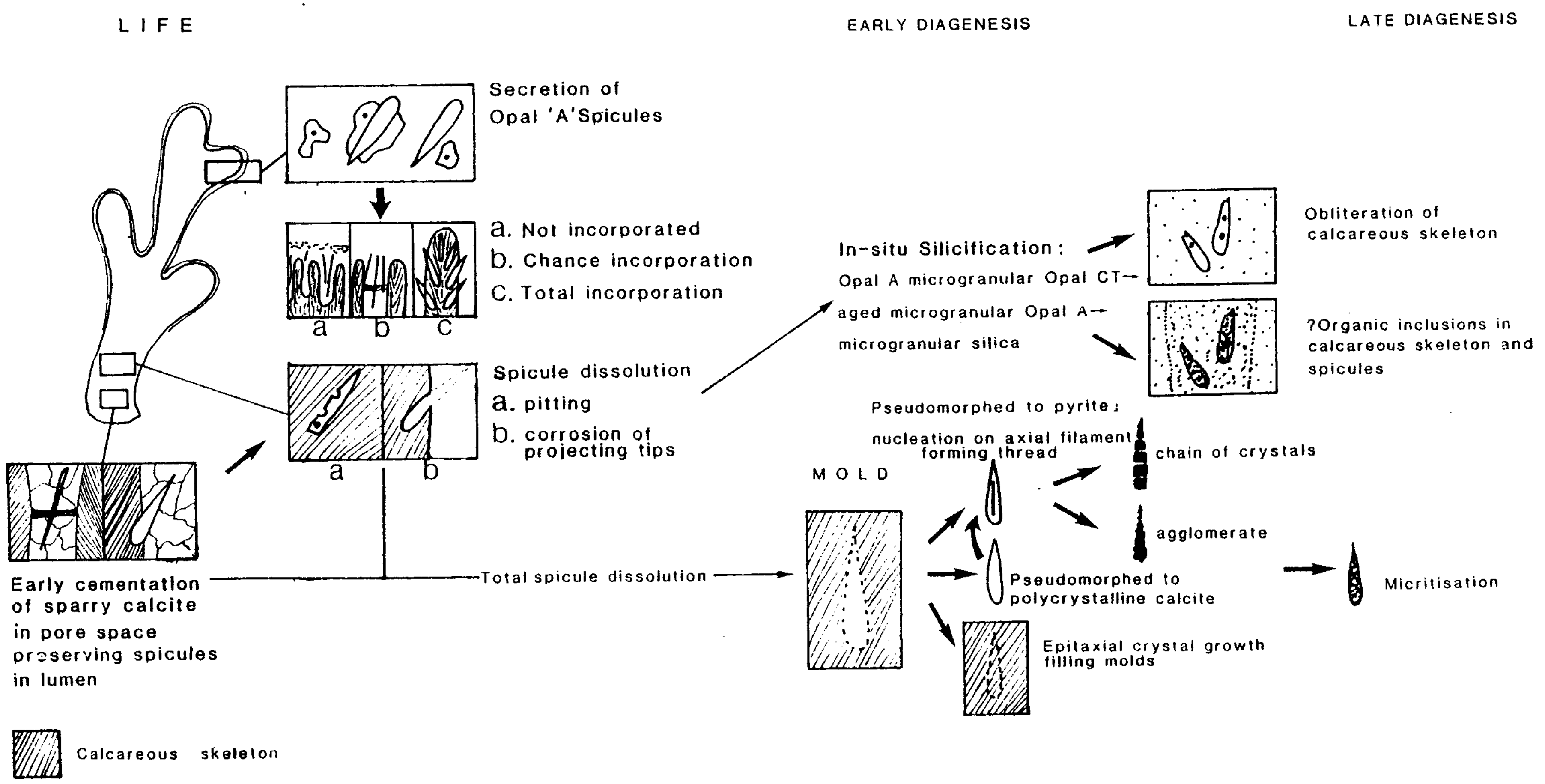
b) secondary tabulae (e.g. *Acanthochaetetes spp.*), or

2) they may to varying degrees have determined the positioning of the primary framework for the subsequent precipitation of the primary calcareous skeleton.

Due to the thermodynamic instability of in-phase silica and calcite, the silica spicules begin to corrode at high pH. In Recent *Ceratoporella nicholsoni* and *Calcifibrospongia actinostromariodes*, pitting of the spicule surface, corrosion of the acanthostyle spines and of the projecting tips have been noted (Plate 16,fig.a,b,d). These features have also been noted in fossil forms (Gray 1980). Corrosion of the spicules during the lifetime of the sponge starts in the older parts of the specimen. Hartman and Goreau (1970) noted that spicule dissolution sometimes starts from the axial filament, which enlarges and moves outwards. In other cases the head of the spicule is most susceptible. Eventually, spicule cavities or moulds are left. The subsequent diagenetic history of the spicules appears to be determined by the role they played in relation to the calcareous skeleton.

In forms which produce a secondary backfill, the moulds become filled with an epitaxial growth of calcite crystals, which can totally fill the original pore space e.g. *Ceratoporella* (Plate 16, figs.d) It is impossible to distinguish between the calcite crystals of the primary skeleton and the epitaxial infill i.e. to determine the original placing and presence of siliceous spicules.

Figure 3.3: Spicule diagenesis in calcified demosponges. Full explanation in text.



Blastochaetetes irregularis has been found with calcareous pseudomorphs preserved within the calicles, and only accidentally incorporated into the calcareous skeleton by secondary skeletal growth (epitaxial overgrowth or tabulae). *Blastochaetetes* does not produce a solid epitaxial backfill. Very early cementation of the original interskeletal spaces (in this case with non-ferroan blocky sparry calcite) prior to spicule dissolution, must account for this remarkable preservation; the resultant moulds left by the dissolved silica spicule in the calcite cement would then become calcite-filled. As spicule dissolution in Recent calcified demosponges begins during the lifetime of the organism (Hartman and Goreau ,1970), this interskeletal cemention must also have occurred during life. In areas of spicule contact with the calcareous skeleton, poorer preservation is noted than in areas encased by spar in the pore-space.The skeletal calcite appears to have a greater corrosive effect upon the spicules.

Spicules in late Mesozoic 'stromatoporoid' demosponges form the primary framework for the calcareous skeleton. Calcite pseudomorphs are often found in the older parts of the skeleton, suggesting that the original spicules were more diagenetically stable than those in Recent calcified demosponges, which produce a secondary backfill with apparent corrosive qualities.

3.2.2.2. Later diagenesis

If not totally obliterated by epitaxial skeletal growth, the mould may be filled with other minerals.

1. Polycrystalline calcite pseudomorphs.

Where calcite pseudomorphs are found ,the microstructure of the calcareous skeleton is always well preserved. Pseudomorph boundaries are only apparent when they are covered with a thin micrite envelope (Plate 16, fig. e) or when they are of a different calcite mineralogy to the calcareous skeleton (shown by staining, Plate 2) Otherwise, the pseudomorphs appear as spicule "ghosts" (Plate 16, fig.f) as in *Parastromatopora japonica* , described by Hartman and Goreau (1970). Here ,the spicules are recognised by their crystallographic difference from the fibres of the calcareous skeleton microstructure. The calcite pseudomorphs tend to be found in the central areas of the specimens, which have been partially protected from the later leaching of corrosive pore-waters by the outer parts of the skeleton.

In forms where the originally siliceous spicules formed a primary sketetal framework, the calcite pseudomorphs are rarely found projecting into the interskeletal spaces (Plate 2, fig.b). Most frequently they terminate abruptly due to corrosion of the projecting tips.

Calcite pseudomorphs are also susceptible to micritisation (Plate 16, fig. e,h). All stages, from well-preserved pseudomorphs with a thin micritised "coating" , through badly micritised but discernible spicules forming diffuse elongate and circular "lighter" areas, to a totally micritised central zone within the calcareous skeletal elements are noted .

2. Pyrite pseudomorphs

Pyrite pseudomorphs appear as agglomerates or as chains of pyrite crystals (Plate17, fig s. a,b.) They are often shorter than calcite pseudomorphs and are frequently found together in the same specimen (Wood and Reitner, 1986) indicating that pyritisation has occurred either after partial dissolution of the silicious spicule or as replacement of the calcite pseudomorph. Examples have been found where threads of pyrite are seen forming within calcite pseudomorphs (Plate 17,fig.c and Plate 19, fig.e.). Pyritisation appears to nucleate upon the organic axial filament, probably due to bacterial activity.

Pyrite pseudomorphs are often found in large numbers near the outer edges of specimens (Plate 17, fig . d). Kazmierczak (1979) , Gray (1980), and Wood and Reitner (1986), have suggested that pyritisation is a product of prolonged leaching by iron-rich pore waters, being due to the presence of reducing conditions, H_2S and a source of iron.

Pyrite pseudomorphs can remain after total obliteration of the calcareous skeleton by subsequent silicification (Plate 17, fig. e).

3. Siliceous spicule pseudomorphs

Siliceus spicule pseudomorphs are occasionally found in Mesozoic stromatoporoids. They are found in chertified areas of specimens, often where the calcified skeleton has been totally obliterated (Plate19, fig . d) or where 'dark 'inclusions have preserved the boundary of the calcified skeleton (Plate 19, figs. a,b).

Where the calcareous skeleton has been totally obliterated by silicification, the siliceous pseudomorphs are exceptionally well preserved. The typical corrosion and pitting features noted by Hartman and Goreau (l970) in Recent 'sclerosponge' spicules are seen on these pseudomorphs (Plate 19 fig.e). Axial canals are preserved but no acanthostyle spines are noted. Considering their excellent preservation it is unlikely that they were originally acanthostyles. Discontinuous siliceous pseudomorphs have not been found in late Mesozoic stromatoporoids, as noted by Gray (1980) in his description of siliceous pseudomorphs .

Siliceous spicule pseudomorphs sometimes appear dark brown and microgranular. The axial canals are not visible, and the brownish granular appearance and high relief of some pseudomorphs suggests that the original spicule mineralogy has been altered (Plate 19, fig.c).

Plate 20 shows S.E.M. photomicrographs of microgranular silica spicule pseudomorphs . Gray (1980) suggested that the original biogenic opal "A" of siliceous spicules converted to opal or opal CT (cristobalite-tridymite silica polymorph). With increasing diagenetic maturity opal CT occurs as bladed microspherules or lepispheres. No such structures have been noted in late Mesozoic stromatoporoid spicules. Robertson (1977) suggested that opal CT might further break down to form microgranules. The origin of the microgranular silica is unclear; it may be diagenetically aged opal A or relict microgranular opal CT.

Gray (1980) notes that the occurrence of this microgranular silica within spicule pseudomorphs and not within the chalcedonic silica walls, as well as the retention of delicate spicule corrosion features, are good evidence of an original mineralogy of opal "A" in fossil calcified demosponges, as in their extant relatives.

PLATE 19: SILICEOUS SPICULE PSEUDOMORPHS.

All light photomicrographs of thin-sections.

Figures a-c: Siliceous spicule pseudomorphs in *Dehornella crustans*. 85/0519. Makhtesh Hagadol, Israel. Lower Kimmeridgian. Note ?organic inclusions in the spicules and calcareous skeleton.

a: Scale bar = 1mm.

b: Scale bar = 100 µm.

c: Detail of ? organic inclusions.

Scale bar = 50 µm.

Figures d,e: Siliceous spicule pseudomorphs in?*Shuqraia arabica*. H 4888a. Makhtesh Hagadol, Israel. Lower Kimmeridgian.

d:Scale bar = 1mm.

e: Corrosion of spicule tip (small single arrows), pitting of spicules (large arrow) and pyrite thread following axial filament (double arrow).

Scale bar = 100 µm.

PLATE 19 SILICEOUS SPICULE PSEUDOMORPHS

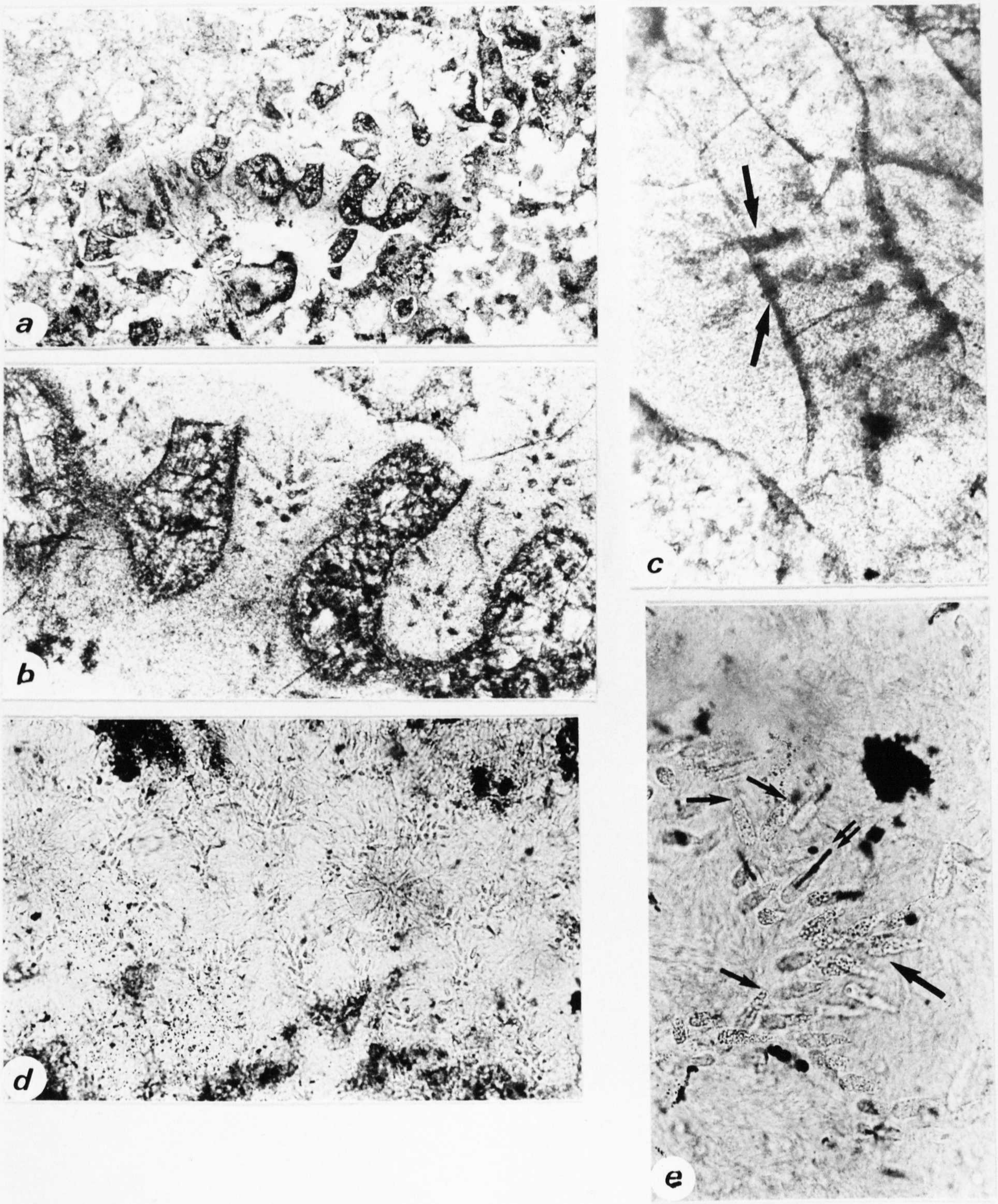


PLATE 20: S.E.M. MICROGRAPHS OF SILICEOUS SPICULE PSEUDOMORPHS.

Figure a: *Parallepora mira* . Pseudomorphs of styles and tylostyles in a perpendicular network. Newell Collection (American Natural History Museum). Kansas. Mid-Pennsylvanian.
Scale bar = 100µm.

Figures b,c: ?spicule pseudomorphs in *Burgundia wetzeli* (arrowed). 85/85. St. Mateo, Maestrazgo, Spain. Hauterivian.
Scale bar = 10 µm.

PLATE 20 SCANNING ELECTRON MICROGRAPHS OF SILICEOUS SPICULE PSEUDOMORPHS

3.3. NOMENCLATURE

3.3.1. REVIEW

The absence of a precise and universally accepted terminology make additionally difficult any accurate comparison and interpretation of systematic papers on stromatoporoids.

Table 3.1 presents a comparison of the salient terms applicable to Mesozoic stomatoporoids as used by major workers. Nicholson (1886) first proposed a set of terms which were widely accepted by later workers, e.g. zooidal tubes, pillars, lamellae, astrorhizae. Dehorne (1920) and Steiner (1932) followed Nicholson's usage in their description of Mesozoic stromatoporoids. Lecompte (1956) in the "Treatise" established terms gathered mainly from the Palaeozoic literature. Hudson(1953 - 1960) coined a large number of new terms specific to Mesozoic 'stromatoporoids'. These were wholly accepted and used by Turnšek (1966 - 1981).

Galloway (1957) was the only author to produce a glossary of morphological terms collected from the scattered literature. The list is extensive but uncritical, and the descriptions incomplete. Terms specific to Mesozoic 'stromatoporoids' were not included and no elimination of synonymous or unnecessary terms was attempted. There is no agreement on the use of some terms, the same term having different meanings for different workers or different words referring to the same structure e.g. lamellae and laminae. Hudson's proposed terms are awkward and their meaning frequently obscure. By giving a "structure" a name you cannot bring it into existence. He frequently confuses terms describing the skeletal tissue with those describing the spaces within the skeleton, but this is symptomatic of much stromatoporoid terminology.

Nomenclature of a group of organisms should reflect biological affinity. In early papers assumption of cnidarian affinity resulted in the introduction of terms bearing cnidarian prefixes, e.g."coeno", a term specific to "coelenterates" meaning hollow gut. Since stromatoporoids are re-interpreted as Porifera, this prefix is inappropriate and misleading. They should be replaced with general poriferan terms, or those specific to calcified demosponges, e.g. 'coenosteum' becomes skeleton, 'zooidal tube' becomes oscular tube.

Table 3.1: A comparison of the salient terms applicable to Mesozoic stomatoporoids as used by major workers
Terms used in this thesis are shown in bold.

STRUCTURE	HUDSON 1956-1960	TURNŠEK 1966-1981	DEHORNE 1920	STEINER 1932	LECOMPTE 1951, 1956	GALLOWAY 1957	NICHOLSON 1886	NON-ALLOCATED SYNONYMS
Fascicular-fibrous.	cligonal	cligonal	fasciculate	-	-	-	-	boutique jet d'eau
Irregular	granular	granular	irregular	-	-	-	-	-
Orthogonal	orthogonal	orthogonal	heterogonal	-	-	-	-	-
Tabulae	tabulae	tabulae	tabulae	tabulae	tabulae	tabulae	tabulae	-
Pillar-lamella	transverse lamella	horizontal lamella	-	lamella	lamella	-	concentric lamella	-
Lamina	lamina	lamina	-	lamella lamina	lamella	-	lamina	-
Aquiferous unit	astrosystem		-	astrorhizal system	-	-	-	-
Osculum	axial astrotube		-	-	-	-	-	-

Table 3.1 continued

STRUCTURE	HUDSON 1956-1960	TURNŠEK 1966-1981	DEHORNE 1920	STEINER 1932	LECOMPTE 1951, 1956	GALLOWAY 1957	NICHOLSON 1886	NON-ALLOCATED SYNONYMS
Excurrent canal	transverse astrotube		-	-	-	-	-	-
Superimposed aquiferous units	astro-corridor		convergent vertical corridors	superimposed astrorhizae	astrorhizal cylinder	-	astrorhizal cylinder	astrorhizal columns
Tabulate osculum	autotube	zooidal tube		super-posed galleries		zooidal tubule	zooidal tube	major tubule
Astrorhizae	<ASTRORHIZAE>							-
Inhalent canals	lateral tubes lateral canals		-	lateral canals	-	-	-	-
Pillars/ column	vertical elements / columns		-	pillars	<RADIAL PILLARS>			-
Inter-skeletal	coenospace	interspace	-	-	chamber / gallery	-	interlamellar space	cells space
reticulum	<RETICULUM>							-
Skeleton	<COENOSTEUM>							
	coenochyme		skeleton	colony	skeleton			coenosarcal tissue
Epitheca	<EPITHECA>							holotheca
Mamelons	<MAMELONS>							monticules
Latilamina	<LATILAMINA>							

There is a great need for simplification in stromatoporoid terminology. Repetitive, vague and unsound terms should be rejected, accepting only inaccuracies which common usage has made virtually obligatory. One such is 'astrorhizae ', which are the traces of excurrent canals of sponges, found in many Recent and fossil sponges.

Table 3.1 gives a list of terms accepted, amended or new to this study. Poriferan terms follow those recommended by Borojeric et al. 1968 and synonyms are given in brackets following the term deemed to be the senior. A glossary is given in the appendix.

3. 4. IMPLICATIONS OF FUNCTIONAL MORPHOLOGY FOR SYSTEMATICS

Sponges filter-feed by passing water through their bodies and retaining nutrient particles. A sponge skeleton serves only to support this aquiferous system and will reflect the internal organisation of this system when the living tissue has gone. The movement of water will influence the entirety of the individual (Fry 1979). A circulatory canal system is required to separate unfiltered and filtered water. A large opening, known as an osculum, is needed for exhalant water. Associated with each osculum are collecting ducts which supply and drain the surrounding tissues. Water initially enters the system through numerous inhalant pores known as ostia (Figure 2.7a). A single oscular system can only serve a fixed volume of sponge cells and this might be defined as a single functional unit.

Aquiferous units are often ephemeral in life. Sponges frequently reorganise their aquiferous systems, even daily (S.Stone 1985 *pers. comm*.). New oscula may arise in old sites or in different positions. However, when a Recent non-calcified sponge is preserved, or in calcified sponges, these previously ephemeral aquiferous units may become fixed and can be used as sources of taxonomic and functional information.

The defining characteristic of the Stromatoporoidea was thought be the possession of repeated stellate canals, or astrorhizae, seen on the surface or internally in thin-section. In Section 2.2.2., astrorhizae are shown to be the traces of the excurrent canal system of sponges, as found in many Recent species and the former position of the oscula and ostia can now be recognised. The presence of astrorhizae can no longer be used to define the 'stromatoporoids', for they are a convergent feature common to a variety of Recent sponges.

As outlined in Section 2.2.2., the functional or aquiferous units of 'stromatoporoids' are based upon the rhagon unit, as are demosponges. Figure 2.7c shows a stylised 'stromatoporoid 'aquiferous unit, expressed in terms of the architecture of the space within the skeleton, rather than the skeletal tissue. The 'stromatoporoid 'aquiferous unit can be defined by the astrorhizal canals and the extent of their influence.

The 'stromatoporoid' rhagon unit (Figure 3.4A) shows modifications in construction and homologous structures can be compared within different forms. The type of modification of the rhagon unit appears to be partially determined by the growth habit of the individual. Some 'stromatoporoids' possess tubular oscula which bear many radiating canals in successive layers . These penetrating drainage systems are generally associated with hemispherical or massive forms which probably bore several centimetres of living tissue (Figure 3.4D). The exhalant canal system of many encrusting 'stromatoporoids' and Recent demosponges (Figure 3.4B), consists of a set of superficial canals radiating from each osculum, through sub-dermal spaces tangential to the surface of the sponge. These superficial canals are confluent with adjacent aquiferous units and are usually regularly distributed over the lateral surfaces.

The lateral surface serves both inhalant and exhalant systems and the water flow is bidirectional; a characteristic of encrusting sponges with only a thin veneer of tissue. For a sponge to grow beyond a certain size, it must possess several of these functional units and become an aggregate.The form of the astrorhizae has been used to define higher taxonomic categories. Nicholson (1886) used the presence or absence of zooidal tubes to divide the Palaeozoic stromatoporoids, and Hudson (1956-60) used this criterion to discriminate between families within the superfamily Milleporellicae. The finding of similar spicule types and arrangements in families of the Milleporellicae shows that sub-division based upon the form of the aquiferous system is erroneous. The form of the aquiferous system clearly cannot be used as a high-level taxonomic characteristic.

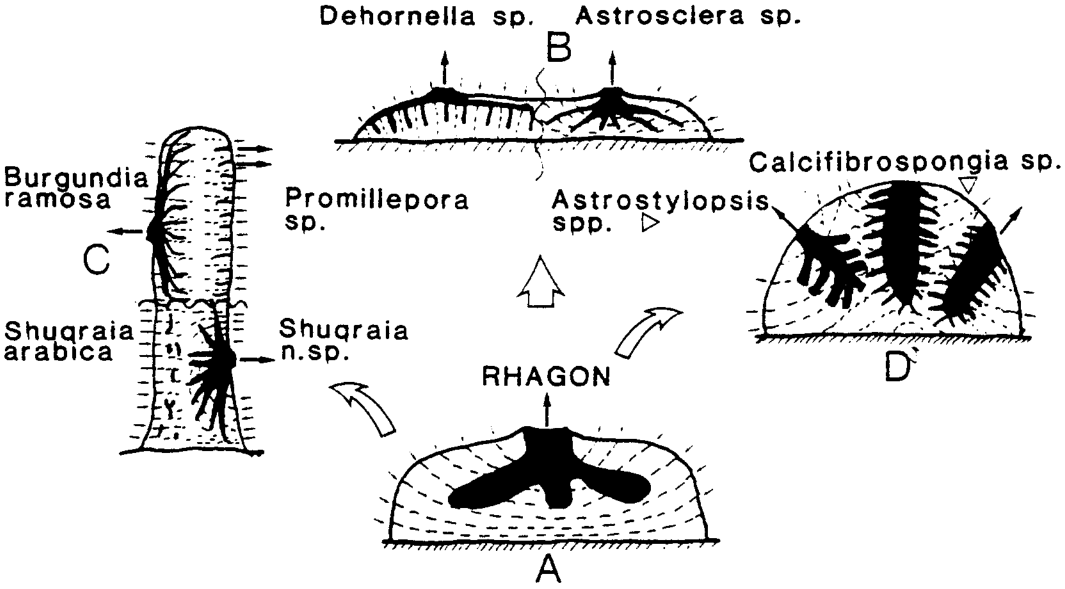


Figure 3.4: Diagrammatic representation of the derivation of aquiferous system organisational types in Mesozoic 'stromatoporoids'. Examples are given of each type.
A: Un-modified rhagon unit;
B: Encrusting forms;
C: Branching or cylindrical forms;
D: Massive forms.
–> Indicates flow of inhalent water.
—> Indicates flow of exhalent water. (Modified from Reiswig 1975)

Reiswig (1975) studied the aquiferous systems of three marine demosponges. He stated that the aquiferous systems of two unrelated species, *Halichondria panicea* (Order Halichondria) and *Haliclona permollis* (Order Haplosclerida) were so similar that it was impossibe to make species determinations of desilicified sections on the basis of canal organisation alone. This suggests that the organisation of the aquiferous system represents a very low level taxonomic criterion, and can only be used in conjunction with other more specific characteristics e.g. spiculation.

In Mesozoic "stromatoporoids", I propose that aquiferous system organisation be used as a species-specific criterion, but with caution.

Aquiferous units are diverse within a single genus and within a single ontogeny. Their study can yield taxonomically valid data, as well as information describing the response of an individual's aquiferous system (e.g.the formation of chimneys and mamelons) to the environment in which it grew. However, insufficient work has been conducted to distinguish between those aquiferous units characters which are genetically induced and those that are ecophenotypic.

Analysing the space within stromatoporoids as an aggregate of functional units, is a useful proceedure in a group devoid of other chararaters. The construction and organisation of aquiferous units can be used as low-level taxonomic characteristics.

3. 5. IMPLICATIONS OF CONSTRUCTIONAL MORPHOLOGY FOR SYSTEMATICS

Levi (1956) in his study of the Recent Demospongiae maintained that the Porifera are the last major group of organisms in which orders were not clearly defined.

There are several reasons for this lack of fundamental understanding. Early systematic work underlined the plasticity of sponges in response to the environment and all the attributes of sponge structure were considered to vary within such wide limits as to make the definition and description of species a specialist task. There is no objective test for sponges in order to decide if similar discontinuously distributed forms are different species or reproductively related variants of the same species. Many features of sponge morphology are subject to variation unrelated to genetic differences. This has made the choice of characteristics to be used in the delimitation of major systematic categories very difficult and subjective. The lack of a stable, agreed classification has made any work with sponges a hazardous undertaking, and the problem with fossil material is compounded. Only hard fossilisable parts, i.e., the spicular and calcified skeleton are available as taxonomic characteristics.

Evidence suggests that the possession of a calcified basal skeleton is a convergent feature in Recent sponges (Wood and Reitner 1986). This also appears to be the case in fossil calcified sponges, including Mesozoic "stromatoporoids". Information presented in Section 2.4. also suggests that there are but a few microstructure types secreted by fossil sponges irrespective of their taxonomic placing according to spicular criteria.

Considerable studies in Recent material have indicated the high intra-specific variation of spicule compliment. No Recent species are now defined on spiculation alone. Soft tissue characteristics, aquiferous system characteristics and larval type are more valid and important at lower and higher taxonomic levels. With fossil material we are in the unhappy situation of having illogically to define taxonomic categories at all levels on features which in Recent forms, have been shown to be invalid or misleading.

What follows is a critical review of the taxonomic characters available to a Mesozoic stromatoporoid systematist . Figure 3.5 represents the use of discussed criteria within the hierarchy of taxonomic categories. The character weightings reflect the bias of the author, based upon the evidence available.

TAXONOMIC CATEGORIES > **TAXONOMIC FEATURES** V	**CLASS**	**ORDER**	**FAMILY**	**GENUS**	**SPECIES**
SPICULES:					
TYPE	X————	X————	X————	X————	X
ARRANGEMENT	X————	X————	X————	X————	X
CALCAREOUS SKELETON:					
MICROSTRUCTURE			X		
GROSS MORPHOLOGY				X————	X
INTERNAL ORGANISATION					X
FILLING TISSUE				X————	X
MINERALOGY			?- - - - - - - - - -	X————	X
SURFACE FEATURES					X
RELATIONSHIP BETWEEN SPICULE AND CaCO3 SKELETONS			X- - - - - - - - - -	?	
AQUIFEROUS SYSTEM					X

Figure 3.5: Diagrammatic representation of use of discussed criteria within the hierarchy of taxonomic categories for calcified demosponges. Full explanation in text.

3.5.1. GROSS MORPHOLOGY

There have been many documented cases of the gross morphological plasticity of 'stromatoporoids' in response to environmental conditions, both inter- and intra-specifically (e.g. Kissling et al. 1967, Kershaw 1981). There are two opposing theories: one, that branching forms are found in shallow, high energy conditions and massive and encrusting forms in deeper, low-energy conditions. The other theory states the opposite.

In Mesozoic stromatoporoids however, some species and genera do appear to have a stable gross morphology e.g.*Burgundia wetzeli* has only been found in branching forms. This may be due to lack of widespread material. Gross morphology can be used as a taxonomic criterion, but only as a subsidiary generic or specific feature, and then only with caution.

3.5.2. SURFACE FEATURES

Stromatoporoids may possess mamelons, oscular chimneys, vermiculate meshworks or astrorhizal grooves, expressed upon their surface. Astrorhizae are discussed in sections 3.4 and 3.5.5. Some species of Recent sponges show a wide variation of general surface elevations, others always have characteristic surface features. Variation cannot always be attributed to apparent environmental differences e.g. adjacent *Ceratoporella nicholsoni* individuals show a wide range of mamelon development (Vacelet 1985 pers. comm.). A few stromatoporoid species however, always appear to possess specific surficial characteristics, and these can be used as a subsidiary characteristic.

3.5.3.SPICULAR SKELETON

On first study, spicule type would appear to be a valid and important taxonomic criterion at all levels. In Mesozoic "stromatoporoids" spicule type and arrangement are probably the best criteria available. However, there are several attendant problems.

It is highly likely in the evolution of demosponges, that the basic monaxon megasclere spicule has evolved several times. For this reason much stress has been laid upon the use of microscleres for demosponge systematics. The majority of Mesozoic stromatoporoid spicules are monaxon megascleres. No microscleres have been found. We have no choice but to use differences between monaxon spicule types as distinguishing criteria for taxonomic groups, but cannot rely on this feature alone. Defining phylogenetics on a probable convergent feature is also undesirable.

3.5.3.1.Spicule type

Spicule type characteristics are taken as taxonomically valid features at all levels.

3.5.3.2.Spicule arrangment

The arrangement of spicules within the tissue of Recent and fossil sponges is used as a taxonomic criterion. Mesozoic "stromatoporoids " which possess the same spicule type, show variations upon a common spicule arrangement. This can determine the placing of the calcareous skeleton. Spicule arrangement has taxonomic validity at family and lower taxonomic levels.

3.5.4. CALCIFIED SKELETON

We know of three species of *Merlia*, only one of which produces a calcified skeleton (Vacelet 1979; Hoshino 1985). Therefore, the presence of a calcified skeleton is not essential for uniting forms and can be of no taxonomic importance.

3.5.4.1. Microstructure

Sponges from widely differing taxonomic groups can produce the same microstructure of the calcareous skeleton. *Actinostromaria sp.* ("stromatoporoid" demosponge, siliceous styles and triaxons) and *Lymnoporella sp.* (Calcarea, calcareous triaxons); both produce an orthogonal fibrous calcified skeleton (Plate 21, figs.c,d). This is an example where a bona-fide calcareous sponge has been classified as a stromatoporoid due to its possession of characteristics thought diagnostic of the group e.g. the presence of astrorhizae and possession of an orthogonal microstructure. Other examples are *Dehornella spp.* ("stromatoporoid" demosponge, siliceous club-shaped styles arranged intramurally) and *Blastochaetetes irregularis* ("chaetetid" demosponge, siliceous long, thin styles only in the calicle spaces) which both possess a fascicular fibrous calcareous skeleton (Plate 21, figs.a,b.). In addition, the two Recent calcified demosponges, *Astrosclera willeyana* and *Ceratoporella nicholsoni* possess similar spicule types, soft-tissue organisations and larval types, which clearly place them in the same family, the Agelasidae within the Order Axinellida. However, *Astrosclera sp.* intracellularly secretes spherulites to form its reticulate calcareous skeleton, in which the spicules play no constructional role, and the calcareous skeleton of *Ceratoporella sp.* forms as

PLATE 21: CONVERGENCE OF MICROSTRUCTURAL TYPE OF THE CALCAREOUS SKELETON

All light photomicrographs of thin-sections.

Thin-sections shown in Figures c and d are stained.

Figures a,b: Fascicular fibrous microstructure:

a: *Dehornella crustans* ('stromatoporoid' calcified demosponge) with calcareous pseudomorphs of club-shaped originally siliceous spicules. H 5479. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 100 µm.

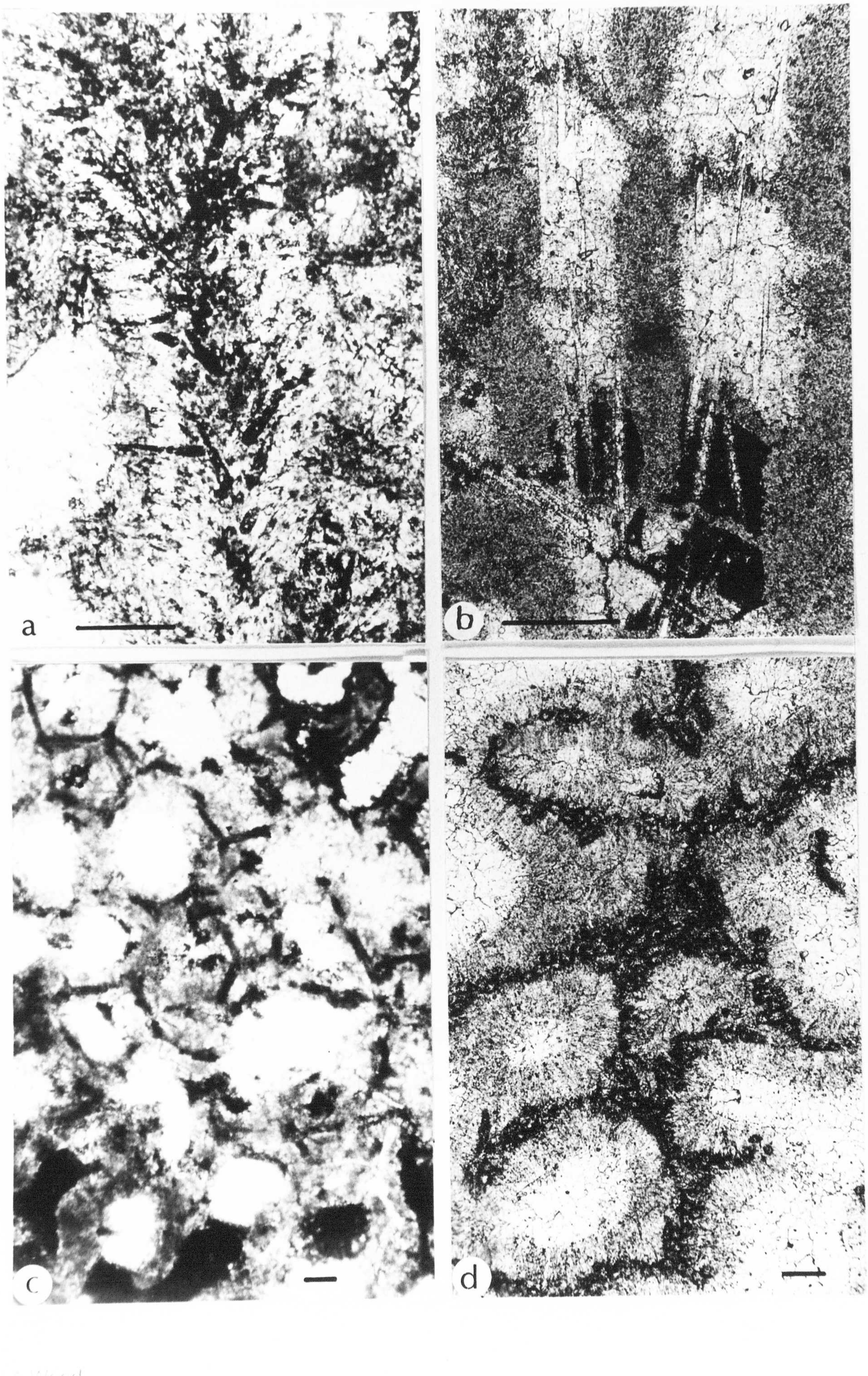
b: *Blastochaetetes irregularis* ('chaetetid' calcified demosponge) with calcareous pseudomorphs of long, thin originally siliceous styles trapped in lumen of calicle by tabulae. JP 2. Collades de Bastus, N.Spain. Santonian.
Scale bar = 100 µm.

Figures c,d: Orthogonal microstructure:

c: *Lymnoporella inclusa* (inozoan, synonym: *Bugundia tutcheri var. Huttonae*), with calcareous triactine spicules. H 4279a. Faringdon sponge gravel, Faringdon, Berks. Aptian.
Scale bar = 100 µm.

d: *Actinostromaria sp.* ('stromatoporoid' calcified demosponge) with calcite pseudomorphs of siliceous spicules. H 5480.Trnovski Gost, Slovenia, Jugoslavia. Oxfordian - Kimmeridgian.
Scale bar = 100 µm.

PLATE 21 EXAMPLES OF THE CONVERGENCE OF CALCAREOUS SKELETON MICROSTRUCTURE IN CALCIFIED DEMOSPONGES



R. Wood

penicillate tufts which initiate from the spicule bases to form a solid calcareous skeleton. If these two species were found as fossils, with no spicules preserved, they would undoubtedly be placed in different families, or superfamilies according to the present taxonomic scheme.

Therefore, microstructure alone cannot define superfamilies as used at present, and this feature can only be used in conjunction with spicule type and arrangement.

3.5.4.2. Relationship of the calcareous skeleton microstructure to the spicule framework

The relationship of microstructure type to spiculation appears to be consistent . However, relationships between the primary spicule framework and the secondary calcified skeleton differ. The following relationships have been determined:

I. A calcified skeleton without spicular skeleton e.g. *Vaceletia, Burgundia.*

2. Spicules present, but placing is independent of calcified skeleton i.e. spicules are incorporated into the skeleton by chance e.g. *Blastochaetetes irregularis, Ceratoporella sp..*

3. The calcified skeleton is precipitated around a primary spicule framework or lattice e.g. *Actinostromaria sp.,* Nov.gen. A.

4. The calcified skeleton crystals initiate from spicule bases e.g. *Dehornella spp..*

5. The calcified skeleton is precipitated meniscus-like around a spicule framework e.g. *Actinostromarianina lecompti.*

The differing relationships between the spicule and calcareous skeletons, i.e. the way in which forms construct their skeletons, is taken to be of family-level and lower taxonomic significance (when combined with spicule type data); variation should reflect soft tissue differences.

3.5.4.3. Internal organisation of the calcareous skeleton.

Most stromatoporoid workers have placed considerable emphasis upon this criterion. However, certain features have been found in this study to be extremely variable e.g. presence or absence of laminae and consistency of interlaminar space width. These can no longer be used as significant taxonomic features.

It is more meaningful to base taxonomic features upon ways in which different families, genera and species, construct their skeletons, rather than the subsequent minor "pattern" similarities or differences seen in thin section. For example, in transverse thin-section, the Palaeozoic genus *Clathrodictyon* and the Mesozoic *Burgundia* appear similar; they both have laminate skeletons. They are, however, constructionally distinct , a feature which will reflect true taxonomic differences, rather than convergent visual similarities (see Chapter 4). Having established that members of a group construct their skeletons in a similar way, dimensional differences can be used to define genera and species.

3.5.4.4. **Filling tissue**

Filling tissue may be in the form of straight or curved tabulae (irregular or fibrous) or a secondary backfill. The distinction between an "organically "and "inorganically" precipitated secondary calcified skeleton can be academic (See Section 3.2.1.2.) Tabulae may be precipitated at irregular intervals (independently) during the life time of the sponges or aligned as periodical growth increments.

Hartman and Goreau (1972) stated that the distinction between tabulae and backfill is "one of degree". In fact, relict tabulae can be found in Recent *Ceratoporella sp.,* even though the dominant form of filling tissue is backfill. Filling tissue form can be used as a subsidiary specific characteristic.

3.5.5. INTERNAL SPACE (AQUIFEROUS SYSTEM)

The role of the aquiferous unit in species level taxonomy was discussed in section 3. 4. Previous family definitions were based upon these criteria e.g. presence of 'zooidal tubes'. There is some consistency in the type of aquiferous unit found within "stromatoporoids" sharing the same spicule type, arrangement and microstructure. Aquiferous unit architecture can be used as a specific character.

3.5.6. MINERALOGY.

The role of mineralogy in taxonomy is not clear. The proposed shift from aragonite and high-Mg calcite, to low-Mg calcite during the Jurassic has been discussed (see Section 3.2.1.1.). Since all

Middle Jurassic to Upper Cretaceous "stromatoporoids " appear to have had original low-Mg calcite skeletons , this question is not discussed with regard to the internal systematics. But this question is raised in the phylogenetic analysis of the calcified demosponges (Chapter 5).

Table 3.2 presents the revised taxonomic framework for Mesozoic 'stromatoporoids' based upon the hierarchy of criteria discussed. The present taxonomic framework is given for comparison.

PRESENT CLASSIFICATION	**PROPOSED CLASSIFICATION**
Phylum Cnidaria	Phylum Porifera
Class Hydrozoa Dana	Class Demospongiae Sollas, 1875
	Subclass Tetractinomorpha Levi, 1953
Order Stromatoporoidea Nicholson and Murie, 1878	Order Axinellida Levi, 1956
Superfamily Actinostromariicae Hudson, 1959	
Family **Actinostromariidae Hudson, 1955**	Family **Actinostromariidae Hudson, 1955**
Family Stromatorhizidae Hudson, 1957	
Family Siphonostromaridae Steiner, 1932	Family A. nov.fam.
Superfamily Milleporellicae Hudson, 1959	
Family **Milleporellidae Yabe and Sugiyama, 1935**	Family **Milleporellidae Yabe and Sugiyama, 1935**
Family Milleporiidae Yabe and Sugiyama ,1935	Order Haplosclerida Topsent, 1898
Family Paratromatoporidae Hudson, 1959	Family B. nov.fam.
Family Stromatoporinidae Kuhn, 1928	
Superfamily Burgundiicae Turnsek, 1967	?Subclass Ceractinomorpha Levi, 1953
Family **Burgundidae Dehorne, 1920**	Family **Burgundidae Dehorne, 1920**
	Class Calcarea
	Family Pharetrones Zittel, 1878

Table 3.2: Present and proposed classification framework of late Mesozoic 'stromatoporoids'. Present classification after Hudson (1960). Pre-existing families considered valid in this study are shown in bold.

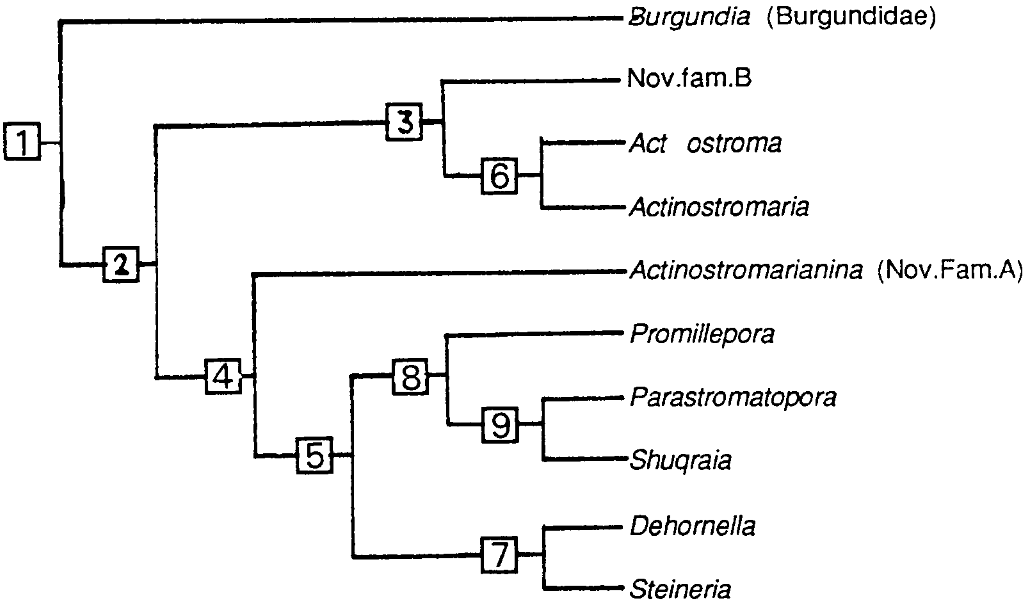
3.6. KEY

A key is here presented to enable the reader to distinguish between genera described in this study, which as far as the author is aware, includes all reported spiculate late Mesozoic 'stromatoporoid' calcified demosponges. Figure 3. 7 illustrates the structure of the key in the form of a dendrogram, where each bifurcation refers to the numbered pair of statements. This dendrogram in no way follows the suggested phylogenetic relationships of this group.

Table 3.3. KEY TO THE GENERA DESCRIBED IN THIS STUDY

1. Ability to produce laminae.No spicules.......................... *Burgundia*
   (Burgundidae)
   No laminae. Presence of spicules.......................... 2.
2. Presence of styles and triaxines, strongyles and/or tylostyles.......................... 3.
   Presence of styles only.......................... 4.
3. Club-shaped styles and triaxines.......................... 6. (Actinostromaridae)
   Styles, tylostyles and strongyles. Spherulitic microstructure
   of the calcareous skeleton.......................... Nov.fam.B
4. Club-shaped styles in a plumose arrangement and/or fascicular fibrous
   microstructure of the calcareous skeleton.......................... 5. (Milleporellidae)
   Long, thin styles in a fibro-reticulate arrangement. Irregular
   microstructure of the calcareous skeleton.......................... *Actinostromarianina*
   (nov. fam. A)
5. Radial elements generally between 200 - 300 µm in diameter.
   With or without a secondary skeleton.......................... 7.
   Radial elements generally between 80 - 180 µm in diameter.
   Abundant secondary skeleton.......................... 8.
6. Radial elements 50 - 70 µm in diameter. Orthogonal to fascicular
   fibrous microstructure.......................... *Actostroma*
   Radial elements 80 - 130 µm in diameter.
   Orthogonal fibrous microstructure.......................... *Actinostromaria*
7. Abundant styles (up to 130 µm) projecting into the interskeletal spaces.
   Continuous radial elements, abundant, possibly conjoined astrorhizae and
   aligned tabulae. No or little secondary skeleton.......................... *Dehornella*
   Discontinuous radial elements. Extensive development of secondary skeleton.
   Tabulate astrorhizal canals.......................... *Steineria*
8. Astrorhizae.......................... 9.
   Abundant tabulate oscula.......................... *Promillepora*
9. Fascicular-fibrous microstructure of calcareous skeleton.
   Tabulate astrorhizae.......................... *Parastromatopora*
   Orthogonal-fascicular fibrous microstructure of calcareous skeleton.
   Abundant fibrous tabulae forming latilaminae.......................... *Shuqraia*

Figure 3.6: Dendrogram showing structure of paired statements referred to in the key shown in Table 3.3.



3.7.CONCLUSIONS

1) The original mineralogy of late Mesozoic 'stromatoporoids' was probably low-Mg. calcite.

2) Original siliceous spicules have not been found in fossil calcified demosponges. Spicules are pseudomorphed to calcite, pyrite or secondary silica by replacement of mouldic porosity. Very early cementation, during the lifetime of the individual, can be evoked to explain some examples of spicule preservation.

3) Spicule preservation may be partially determined by the role played by the spicules in the overall skeletal construction.

4) Pyrite pseudomorphs appear to nucleate along the axial filament of the original spicule, perhaps due to bacterial activity, and can replace calcite pseudomorphs. Pyrite pseudomorphs are highly resistant to silicification of the skeleton.

5) The calcareous skeleton of Mesozoic 'stromatoporoids' is susceptible to alteration of microstructure (micritisation, cementation and recrystallization). Diagenetic lineages can be determined to enable workers to trace original microstructural types.

6) Two diagenetic pseudostructures are recognised; pseudolamellar and scalenohedra.

7) Present cnidarian-based terminology is replaced by one modified from Recent poriferan nomenclature. Synonyms are noted and meaningless terms eliminated.

8) Different spicule types and arrangements are found in forms with the same calcareous microstructural type, and members of the same Recent calcified demosponge family (same spicule type) possess different microstructures and biomineralisation mechanisms. Microstructure of the calcareous skeleton is a convergent feature and can no longer be used to determine superfamilies in Mesozoic 'stromatoporiods'.

9) The architecture and arrangement of the aquiferous units can be used as a species-specific characteristic, but with caution. They can no longer be used to determine families in Mesozoic 'stromatoporoids'.

10) Spicule type, arrangement, and relationship to the calcareous skeleton are the only vaild high-level taxonomic criteria in fossil calcified demosponges.

CHAPTER 4

SYSTEMATICS

4.1 INTRODUCTION

Material in the collection of the late R.G.S.Hudson, housed at the British Museum (Natural History) plus collected material and forms described by other workers to which the present author has had access, is here formally redescribed using the proposed taxonomy outlined in Section 3.6. In addition, possible allocation of forms not examined by the author, have been suggested.

The systematics of Mesozoic "stromatoporoids" has developed in a random manner, with no organised or widely accepted basis. Too many species are known from only single or a few specimens and there has been a tendency to establish new species rather than to review our knowledge of pre-existing ones. It is scarcely possible to identify many genera, for few adequate descriptions and figures have been published. Authors tend to depart wildly from the type of the genus, even when adequate figures and descriptions have been given. Different meanings of terms from those intended by the original author are frequent and the true relationships between forms are obscured by the diversity of the methods and viewpoints used for their description. Most importantly, there has been little allowance for intra-specific variability within anatomical features.

The logical remedy is to revise the species by having all the holotypes assembled in one place for comparison. This is unfortunately not practicable for this thesis. Some holotypes are lost and most are scattered and could never be brought together. Therefore, the best option is to prepare a survey of the characters of each species as they appear from written descriptions and illustrations and to check as many as possible by re-examination of the holotypes and authentically named species. The next step is to assess the limits of variability within forms by intensive studies of those species for which a long series of specimens can be obtained from one horizon and locality and which have well developed morphological characters.

Systematic descriptions here follow the rules of open nomenclature, as outlined by Matthews (1973), following Richter (1948). This method offers a clear expression of uncertain allocation of forms, and also some indication of the degree of uncertainty involved. The nomenclature remains open to possible future improvements and indicates where these improvements are needed and in which direction they may be sought. Improvements can be built into the nomenclature without upsetting established names.

After the recommendations of Matthews 1973, the following signs for synonymy lists have been adopted, which express the judgements of the author of the list:

1. Signs which should obviate needless searches.

1956 Year in italics: this work has a mention of the species, but without description or illustration. It may be ignored by anyone who wishes to check the morphological information, rather than the total data arising out of the occurrence.

1956 Year in roman: the work contributes to our knowledge of the species. If such a reference includes an illustration, an indication of the nature of the illustration is given:

I have introduced the following three rules to indicate the form of the specimen illustrated:

(W.S.): Indicates that the whole specimen has been figured.

(T.S.): Indicates that one or more thin-sections have been figured.

(cop.Dehorne 1920, type); the illustration is not a new one, merely a repetition of one already produced by Dehorne in 1920. The illustration is also part or all of the type material.

2.Signs before the year, which indicate the degree of confidence with which particular items in the list are referred to the species under discussion:

*1956 *in front of the year: with the publication of this work the species can be regarded as valid under the terms of Article 11 of the ICZN (earlier mentions of this name are to be regarded as *nomina nuda*).

.1956 .in front of the year: I accept responsibility for attaching this reference to the species under discussion.

1956 No sign in front of year: I have no right expressly to accept responsibilty for attaching this reference to the species under discussion; but I have no cause to doubt such an allocation.

?1956 ?in front of year: the allocation of this reference must be subject to some doubt because of the way in which it is presented.

v1956 v in front of year: *vidimus.* I have checked the deposited specimens that relate to the work cited, and on their evidence I have chosen the additional sign used:

v*1956 I have seen the type of the species.

v.1956 because of the evidence of the deposited specimens the author is able to take responsibility for this assignment.

v1956 I do not accept responsibility.

v?1956 the condition of the original specimens is such that no clear decision is possible.

(1956) year in parentheses: the year of publication is uncertain.

p.1956 p before the year: *partim*: the reference applies to only part of the species under discussion.

Numbers preceded by F are deposited in the Sedgwick Museum, Cambridge, those preceded by H are in the collections of the British Museum(Natural History) and those preceded by 83/,84/ or 85/ are in the present author's collection. Material from other collections is noted in the text where relevant.

4.1.1. TAXONOMIC DISCLAIMER

This publication is not deemed to be valid for taxonomic purposes (see Article 8b in the International Code of Zoological Nomenclature, 3rd Edition (1985), edited by W.D.L.Ride et al.)

(The purpose of this statement is so as not to pre-empt publication of these results elsewhere, which is intended for the near future).

4.1.2. THE CLASSIFICATION OF THE DEMOSPONGIAE

Among the classes of sponges, the Demospongiae have proved the most difficult to classify due to the great variety of modern forms and the generalised character of fossil forms. The earliest comprehensive classification of Recent forms was that of Topsent (1928). Laubenfels (1936) followed with a revised classification of Recent forms and followed through his philosophy to fossil genera (1955). Levi (1956) re-evaluated this classification, and incorporated reproductive characteristics for the first time, to define higher taxonomic categories. Later workers have modified this with biochemical approaches (Bergquist and Hartman 1969, Bergquist and Hogg, 1969).

The classification of fossil forms remains uncertain. Early workers (Hinde 1887-1912, Schrammen 1910, 1924) developed reasonable classifications of lithistid sponges, which bear solid skeletons of fused spicules, but the remaining, loosely spiculate sponges posed particular problems. Classifications were mainly based on growth form, major structures and megasclere spicule features. Reid (1963, 1968) developed a classification based upon the diagnostic priority of the component microscleres. His classification covered both fossil and Recent demosponges. However the difficulty of using microscleres in fossils (small size and rarity of preservation) make his classification extremely impractical to apply to non-lithistid sponges.

Many fossil workers prefer the utilization of early suggested sub-divisions based on megasclere morphology (Rigby 1983); the Tetraxonida (four-rayed spicules) and Monaxonida (single-rayed spicules) after Sollas (1880, 1883). These sub-divisions may be the most utilitarian, but as Reid (1968, 1970) noted, they probably represent 'grades' present in several lineages (as indicated by microscleres) and are thus polyphyletic.

Since orders and sub-orders are highly conjectural in non-lithistid demosponges and the present Recent classification is more precise, this study places fossil spiculate calcified demosponges within the Recent poriferan classification as far as possible. However, when discussing the origin of Recent Mesozoic 'stromatoporoid' ancestors, and therefore the Mesozoic 'stromatoporoids' themselves, reference will be made to the classification of Reid (1968), which incorporates fossil forms and appears to be the best one available for phylogenetic appraisal.

Here, the revised list within the proposed taxonomic framework is given, with an indication of those genera and species examined.

TABLE 4.1 List of redescribed genera and species of late Mesozoic stromatoporoids within proposed taxonomic framework.

- Phylum Porifera Sollas, 1875
  - Class Demospongiae Sollas, 1875
    - Subclass Ceractinomorpha Levi, 1953
      - ?Incertae sedis: Burgundidae Dehorne, 1920
        - *Burgundia* Dehorne, 1916
          - *B.trinorchii* Dehorne , 1916
          - *B.ramosa* Pfender, 1937
          - *B.wetzeli* Hudson ,1954
    - Subclass Tetractinomorpha Levi , 1953
      - Order Axinellida Levi,1956
        - Family Milleporellidae Yabe and Sugiyama, 1935
          - *Dehornella* Lecompte, 1952
            - *D.hydractinoides* (Dehorne, 1920)
            - *D.choffati* (Dehorne, 1920)
            - *D.harrarensis* (Wells, 1943)
            - *D.crustans* Hudson, 1960
            - *D.valanginiensis* (Schnorf-Steiner , 1960)
          - *Shuqraia* Hudson, 1954
            - *S.zuffardi* (Wells, 1943)
            - *S..n.sp*
          - *Promillepora* Dehorne, 1920
            - *P.pervinquieri* Dehorne, 1920
          - *Steineria* Hudson, 1956
            - *S.somaliensis* (Zuffardi-Comerci, 1932)
          - *Parastromatopora* Yabe and Sugiyama, 1935
            - *P.libani* Hudson, 1955
        - Family Actinostromariidae Hudson, 1955
          - *Actinostromaria* Haug, 1908
          - *Actostroma* Hudson, 1956
            - *A.damesini* Hudson, 1956
        - Incertae sedis nov. fam. A.
          - *Actinostromarianina* Lecompte,1952
            - *A.lecompti* Hudson, 1955
            - *?A.? beauvaisi* Flügel, 1969
            - *?A.praesalevensis* Zuffardi-Comerci, 1932
  - Order Haplosclerida Topsent, 1898
    - Nov. fam. B.
      - New gen. A
        - New gen and n. sp. A

PHYLUM PORIFERA Sollas, 1875

CLASS DEMOSPONGIAE Sollas, 1875

Diagnosis:

Sponges with siliceous spicules, siliceous spicules and spongin, spongin alone or no skeleton. Spicules are tetraxons or derivatives with more or fewer rays. Megascleres and microscleres differentiated except in primitive examples; many forms with megascleres only, due to loss of microscleres; some with microscleres only. May possess a secondary calcareous skeleton in addition to the siliceous spicular one.

SUB-CLASS CERACTINOMORPHA Levi, 1953

Diagnosis:

Demosponges characterised by the presence of incubated parenchymella larvae. When present, the siliceous megascleres are always monaxonid and microscleres exhibit a broad range of shapes, generally exclusive of the aster category. May or may not possess a secondary calcareous skeleton.

Discussion: The family Burgundidae is tentatively assigned to this subclass.

FAMILY BURGUNDIDAE Dehorne, 1920

Diagnosis:

?Aspiculate calcified demosponges with a fibrous microstructure, and an ability to produce concentric perforated laminae. Aquiferous system may or may not bear tabulate oscula and astrorhizae.

Assigned genera:

Burgundia Dehorne, 1916

Discussion:

The present systematic standing of the genus *Burgundia* and its species epitomises the lack of rationale in Mesozoic "stromatoporoid" taxonomy. Nowhere have so many authors so inadequately described and illustrated new forms, misunderstood diagnoses and used invalid taxonomic criteria.

The systematic position of the Burgundidae has never been clear within the Mesozoic "stromatoporoids". The genus *Burgundia* was first used in the literature by Tornquist (1901) to describe a fossil in the collection of Munier-Chalmas. No formal description was given. This specimen was subsequently described by Dehorne (1916, 1920), when she assiged the genus to the independent, monogeneric family, the Burgundidae. Dehorne separated it from the Actinostromaridae and Stromatoporoidae on the presence of dominant concentric elements, the laminae. Steiner (1932) placed the Burgundidae between the hydractinoids and milleporoids, on account of being characterised by distinct "zooidal tubes". Yabe and Sugiyama (1935) stated that *Burgundia,* "with a massive or encrusting coenosteum, composed of numerous concentric laminae supported by horizontal elements, should, on our sense be excluded from the stromatoporoids". Lecompte (1952) noted, as had Dehorne (1920) that *Burgundia* is very similar to the Palaeozoic genus *Clathrodictyon* Nicholson and Murie, 1878 and that the two genera should be classified together in the Clathrodictyidae. Turnšek (1967) raised the Burgundidae to superfamily status, following Hudson's (1960) classification based upon microstructural types. Hudson determined two superfamilies, the Actinostromariicae and the Milleporellicae which have orthogonal and fascicular fibrous microstructure respectively. Turnšek considered the Burgundidae to possess a "homogenous or zonate granular " microstructure, therefore constituting a third superfamily, the Burgundiicae.

Since 1920, sixteen species of the genus have been described from the Upper Jurassic and Lower Cretaceous of North-west Europe to Japan, including additions from revisions of other genera.

Examination of Hudson's collection of *Burgundia spp.*, shows that this genus possesses a fibrous microstructure, as Hudson noted when describing *B.wetzeli* in 1954, and Pfender (1937) when describing *B.ramosa*. There are therefore no grounds for retaining the Burgundiicae, based upon either Hudson's (and Turnšek's) criteria or those proposed in this study.

No definitive spicules have been found in any specimens of *Burgundia* . This may be a diagenetic loss or a true absence. For the present, I feel that the genus should retain familial independence based upon this apparent aspicularity. However, spherical bodies of silica which resemble microscleres have been found within the central area of the skeletal elements in *B.wetzeli* (Plate 20 figs. b,c; Plate 24, fig.g). Their identification as spicules remains problematic.

The presence of laminae is the diagnostic feature of the type species, *B.trinorchii*, as used by Dehorne 1916, and was used by subsequent authors to define further species of the genus. However, the presence of laminae is not consistent or characteristic within the type species, suggesting that laminae should not be the main diagnostic feature of the genus. Schnorf-Steiner (1953, 1955) had noted this but had not taken her observation to the logical taxonomic conclusion.

Constructionally, members of the genus *Burgundia* are nevertheless united in the way in which they form their laminae. This is decribed in Figure 4.1. The perforate lamina is precipitated upon the terminations of the radial elements, and partially encloses them. The next series of radial elements form upon this lamina. Although *Clathrodictyon* Nicholson and Murie, 1878 produces laminae, their construction is quite different; the construction of the lamina is continuous with the radial elements, but in *Burgundia* the lamina is secondarily precipitated and acts as filling tissue.

Specific differences in *Burgundia* have been based upon the spacing and the form of the vertical elements within the interlaminar spaces. These elements have been variously described as straight, curved, meandriform or bifurcating. Study of *Burgundia spp.* shows that there is no consistency in these previously proposed diagnostic features (Plates 22 - 24) and they should be used with caution.

Of the sixteen species allocated to *Burgundia*, four are eliminated from the genus, three are too badly illustrated to allow allocation and the remaining nine species are synonymised into three species. Much of this reallocation is based upon literature descriptions, and is therefore tentative.

The position of the Burgundidae in the Porifera:

The Burgundidae are apparently aspiculate. Without soft-tissue and larval type information, their

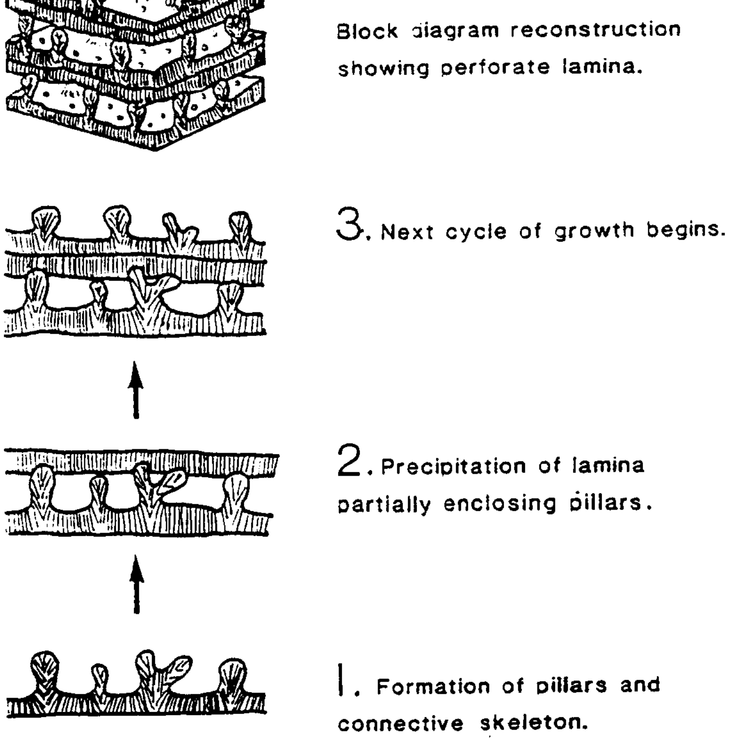


Figure 4.1: Construction of the laminae in *Burgundia*

position with in the Phylum Porifera is impossible to determine. The closest analogy to the skeleton of *Burgundia* is that of the Recent "sphinctozoan" genus *Vaceletia* which is aspiculate and has a thalamid (chambered) skeleton, somewhat reminiscent of the laminar periodicity exhibited in *Burgundia*. *Vaceletia* is considered to be a member of the Ceractinomorpha (Vacelet 1985). On the basis of these rather uncertain characters, the Burgundidae is very tentatively placed in the Ceractinomorpha.

Burgundia Dehorne, 1916

1917 *Circoporella* Hayasaka p.57
1930 *Plassenia* Yabe and Sugiyama p.113
1915 ?*Stromatoporidium* Vinassa de Regny p.108
1954 *Bekhmeia* Hudson p.48

Diagnosis:

?Aspiculate calcified demosponges with an ability to produce perforated concentric laminae, as well as tabulae. Fibrous microstructure of the calcareous skeleton, ranging from orthogonal to fascicular fibrous. Massive, nodular or dendroid gross morphology. Aquiferous units may possess tabulate oscula and/or astrorhizae.

Type species:

Burgundia trinorchii Dehorne, 1916 . Vers (Saone et Loire), France. Upper Jurassic, Portlandian.

Distribution:

Europe, U.S.S.R., Japan

Upper Jurassic to Lower Cretaceous (Upper Oxfordian - Hauterivian)

Discussion:

This genus is characteristically very variable in form, but Schnorf-Steiner (1953, 1955) is the only author to have drawn attention to the plasticity of *Burgundia.* In 1953, she described forms from a new locality, Rissoux in Switzerland. She noted that laminae were not always present in these specimens. The laminae broke-down through the ontogeny of the individual and the pillars became more continous to form an arrangement characteristic of the Family Milleporellidae. This caused her to question the validity of using the presence of laminae to define *B.trinorchii* and hence the genus and family, as well as generally questioning the use of skeletal organisation in Mesozoic stromatoporoid taxonomy. She suggested that more "stable" features, such as microstructure of the calcareous skeleton, were more acceptable.

In 1955, Schnorf-Steiner described a large number of specimens of *Burgundia trinorchii* from various European localities. She found that there was considerable variation in form both within "populations" of one locality and between different localities. She determined a morphological continuum of the internal organisation along the growth axis of an individual , based upon observations of a large number of thin-sectioned specimens.

She divided this continuum of internal arrangement into four types:

TYPE 1:"Lamellaire-ponctue": The dominant concentric elements are laminae, which are perforated and continuous. The radial elements are short, straight and isolated pillars, restricted to one inter-laminar space.

TYPE 2:"Lamellaire-meandriforme": The concentric, perforated laminae are dominant, but the radial pillars are not isolated, and form a meandriform arrangement in tangential section.

Type 2 corresponds to *Burgundia semiclathrata* (Hayasaka, 1917)

Types 1 and 2 tend to be in smaller, and more irregular, nodular individuals.

TYPE 3:"Vertical - meandriforme": Concentric elements are discontinuous aligned fibrous tabulae, not continuous laminae. Radial elements are meandriform in tangential section.

Type 3 corresponds to *Burgundia alpina* (Yabe and Sugiyama, 1930)

TYPE 4:"Tubulaire": Tabulae are unaligned and granular. Pillars are continuous and form a tubular, "chaetetid" arrrangement.

Types 3 and 4 tend to be in larger, and more regular, massive individuals.

Some individuals showed only one type; others possessed several types throughout ontogeny. Some specimens exhibited a cyclicity of repeated types. Apart from reversal, the order in which these types occurred in one individual always remained the same.

These differences were attributed to differing environmental conditions in which these forms grew. Where laminae were present (Types 1 and 2), she postulated that these specimens grew in adverse conditions, and non-laminate areas and forms (Types 3 and 4) in conditions which enabled the individual to flourish.

The present author confirms the findings of Steiner and agrees with her conclusions. Due to the sequential and cyclic nature of the variation of *B.trinorchii,* it is likely that this continuum of variable internal organisation can be attributed to seasonal fluctuations, in for example, temperature, light in the environment. The closely spaced laminae probably sectioned off abandoned parts of the skeleton and the area where laminae dominate is comparatively narrow. It is possible that the individual grew slowly and possessed only a thin veneer of tissue. In other areas, the pillars are more continuous and tabulae, of varying spacing and degree of alignment, are present instead of laminae. The individual at this stage may have grown faster and the tissue thickness would be greater. The tabulae tend to be more widely spaced than the laminae, when present.

Such regular periodicity has not been found in *B.ramosa.* The laminar spacing and the structure of the pillars in the inter-lamellar spaces is variable; pillars may be straight or branched. Cyclical transition from laminar to non-laminar areas has not been noted, but individuals in which one form predominates, can show laminar "break-down" or appearance respectively (Plate 23 ,fig. g).

The ability to produce laminae has not been noted in other genera as yet, and for this reason the presence of laminae is still acceptable as one of the diagnostic feature of the genus. In addition, there are dimensional differences within the three species here defined, which are given below.

Dimensions:

	B.trinorchii	*B.ramosa*	*B.wetzeli*
Vertical element width:	40-70 µm	50-100 µm	50-90 µm
Aquiferous system dimensions:			
Density of aquiferous units:	1/cm^2	1-4/cm^2	1/cm^2
Diameter of oscula :	100-300 µm	200-300 µm	100-200 µm
Length of oscular tube:	up to 1cm	up to 4mm	up t0 5mm
Diameter of astrorhizal canals:	100-300 µm	200-300 µm	100-200 µm
Lamina width		60-120 µm	60-100 µm

Several species are rejected from *Burgundia* under the proposed redefinition of this genus. They are as follows:

B.astrotubulata Turnsek, 1967;

B.tutcheri Kellaway and Smith, 1938 (Plate 36, fig.b, a calcarean);

B.tutcheri var. huttonae Kellaway and Smith, 1938 (Plate 36, fig.c, a probable synonym of *Lymnporella inclusa* (Hinde, 1883), a calcarean);

B.?sp. Fenninger et al. 1963, 1965;

B.tertia Zuffardi-Comerci ,1938 and *Stromatoporidium globosum* Vinassa de Regny, 1915 are too badly illustrated and described to allocate anywhere.

Burgundia trinorchii Dehorne, 1916

Plate 22. figs.a-h

1901 Burgundia Trinorchii Munier Chalmas (1883 in coll'n.), Tornquist p.1116 (*nomen nudum*).

1909 Burgundia trinorchii Munier-Chalmas (1883 in coll'n); Haug p.931 (*nomen nudum*).

* 1916 *Burgundia trinorchii* Munier-Chalmas (1883), Dehorne p.430 . Fig.1. (T.S.) .

1917*Circoporella semiclathrata* Hayasaka p.58.Plate 14, figs.1-8.(T.S.) .

1920*Burgundia trinorchii* Munier-Chalmas (1883 In coll'n.); Dehorne p.72 PlateIX,fig.8; Plate X, fig.6; Plate XI, fig.4; Plate XII, fig.3. (G.S.,T.S.) .

1920 *Burgundia semiclathrata* (Hayasaka, 1917), Dehorne p.73 text-fig.8 (T.S.).

1930*?Plassenia alpina* Yabe and Sugiyama p.11 Plate XI, figs.1-5. (G.S.,T.S.).

1932 *Burgundia Trinorchii* Munier Chalmas ,1883; Schnorf-Steiner p.183 Plate 12, fig.3 (T.S.).

1932 *Burgundia trinorchii*, Munier Chalmas ,1883; Pfender p.742 Plate XLI, figs.1-3; Plate XLII, figs.1-2. (T.S.).

1932 *Burgundia semiclathrata* (Hayasaka, 1917);Schnorf-Steiner p.184 (no illustration).

1937 *Burgundia (Circoporella) semiclathrata* (Hayasaka, 1917); Pfender p. 134 (no illustration).

1938 *Burgundia cf. semiclathrata* (Hayasaka , 1917); Kellaway and Smith Plate XXI, Fig.5 (T.S.).

1939 *Burgundia trinorchii* Munier Chalmas 1883; Kühn p.42 text-fig.57 (cop. Dehorne 1920, type T.S.).

1939*?Plassenia alpina* Yabe and Sugiyama, 1930; Kühn p.56 text-fig. 90 (cop. Yabe and Sugiyama 1930. T.S.).

1939 *Circoporella semiclathrata* Hayasaka , 1917; Kühn p.55 (no illustration).

1940 *Burgundia trinorchii* Munier Chalmas, 1883; Firton p.161(no illustration).

1941 *Circoporella semiclathrata* Hayasaka , 1917; Yabe and Sugiyama p.39 (no illustration).

1952 *Burgundia trinorchii* Munier Chalmas, 1883; Lecompte p.12 Plate 3, figs.4-5.(T.S.).

1953 *Burgundia trinorchii* Munier Chalmas, 1883;Schnorf-Steiner p.464 text-figs.1-3 (T.S.).

v . 1955 *Burgundia trinorchii* Munier Chalmas, 1883;Schnorf-Steiner p.545 text-figs 1-15, Plates1,2. (T.S.).

1956 *Burgundia trinorchii* Chalmas in Dehorne, 1915; Lecompte p.131 text-fig. 105, fig.1a-c. (T.S.).

1957*Burgundia barremensis* Yavorsky p.27 Plate 12, figs.2,3. (T.S.).

1965*?Burgundia alpina* (Yabe and Sugiyama, 1930), Fenninger and Hotzl p.39 Plate 5, fig.4; Plate 6, fig.5; Plate 8, fig.1. (T.S.).

Non 1973 *Burgundia semiclathrata* (Hayasaka , 1917) ;Turnšek and Masse 1973 p.21 Plate 21, fig.1-3. (T.S.).

Diagnosis :

Massive or nodular *Burgundia* in which the vertical elements are 40-70 µm in diameter.

Holotype: Dehome, 1916. Fig.1. From collection of Munier-Chalmas, Laboratoire de Geologie, La

Sorbonne, Paris. Vers (Saone et Loire), France. Upper Jurassic, Portlandian.

Material studied:

B.M. (N.H.) H 3425, 3395, 3396, 3594, 3595, 3597, 4032 and 4044 plus thin-sections. Villereousune, France. Lower Kimmeridgian (Upper Jurassic).

Description:

Massive or nodular gross morphology, up to 20 cms diameter. Filling tissue characteristically varies through the ontogeny of the individual, and may show cyclicity. May possess laminae, aligned tabulae or unaligned tabulae. Laminae are perforated concentric plates of orthogonally fibrous microstructure; tabulae may be of fibrous or irregular microstructure. In laminate forms, the vertical elements tend to be simple, unbranched and limited to one inter-laminar space. Laminae grade into aligned tabulae, and the pillars become more continuous. Pillars remain unbranched, but may be meandriform. Aligned tabulae grade into unaligned tabulae, and the pillars form a tubular, "chaetetid" arrangement. Aquiferous units bear tabulate oscula and astrorhizae. Continuous, long, tabulate oscula are more strongly developed in the non-laminate areas of the skeleton.

Distribution:

South-west Europe, Japan, U.S.S.R.

Upper Jurassic (Upper Oxfordian-Portlandian)

Remarks :

B. semiclathrata and *B. alpina* appear to be synonyms of *B. trinorchii* within the amended diagnosis for this species. *B. semiclathrata* was distinguished by Hayasaka (1917) from *B. trinorchii* by the meandriforme arrangement of the interlaminar pillars in tangential section. This form corresponds to Type 2 of Steiner's morphological continuum for *B.trinorchii.* Likewise, *B. alpina* (Yabe and Sugiyama, 1930) appears to correspond to Steiner's Type 3, where aligned tabulae are present instaed of continous concentric laminae are not present. *Stromatoporidium globosum* was suggested by Hayasaka (1917) to be a synonym of *B.trinorchii,* but the specimen is to poorly described and illustrated to be assigned with any certainty to this species.

Figure a: Massive gross morphology. Polished specimen showing laminae. H 4032. Villereousune, France. Upper Jurassic.

Figure b: Longitudinal thin-section showing periodicity of lamina formation forming latilaminae. Arrows indicate where lamina breakdown begins . A tabulate osculum is seen in the centre of the photograph. H 3395. Villereousune, France. Upper Jurassic.
Scale bar= 1mm.

Figure c: Longitudinal thin-section of laminate specimen showing variability of lamina spacing, interlaminar space width and form of interlaminar pillars. Central area shows slightly tangential section. H 3595. Villereousune, France. Upper Jurassic.
Scale bar = 1mm.

Figure d: Longitudinal thin-section of non-laminate specimen, with continuous pillars and aligned tabulae. A tabulate osculum is seen in centre left. H 3597. Villereousune, France. Upper Jurassic.
Scale bar= 1mm.

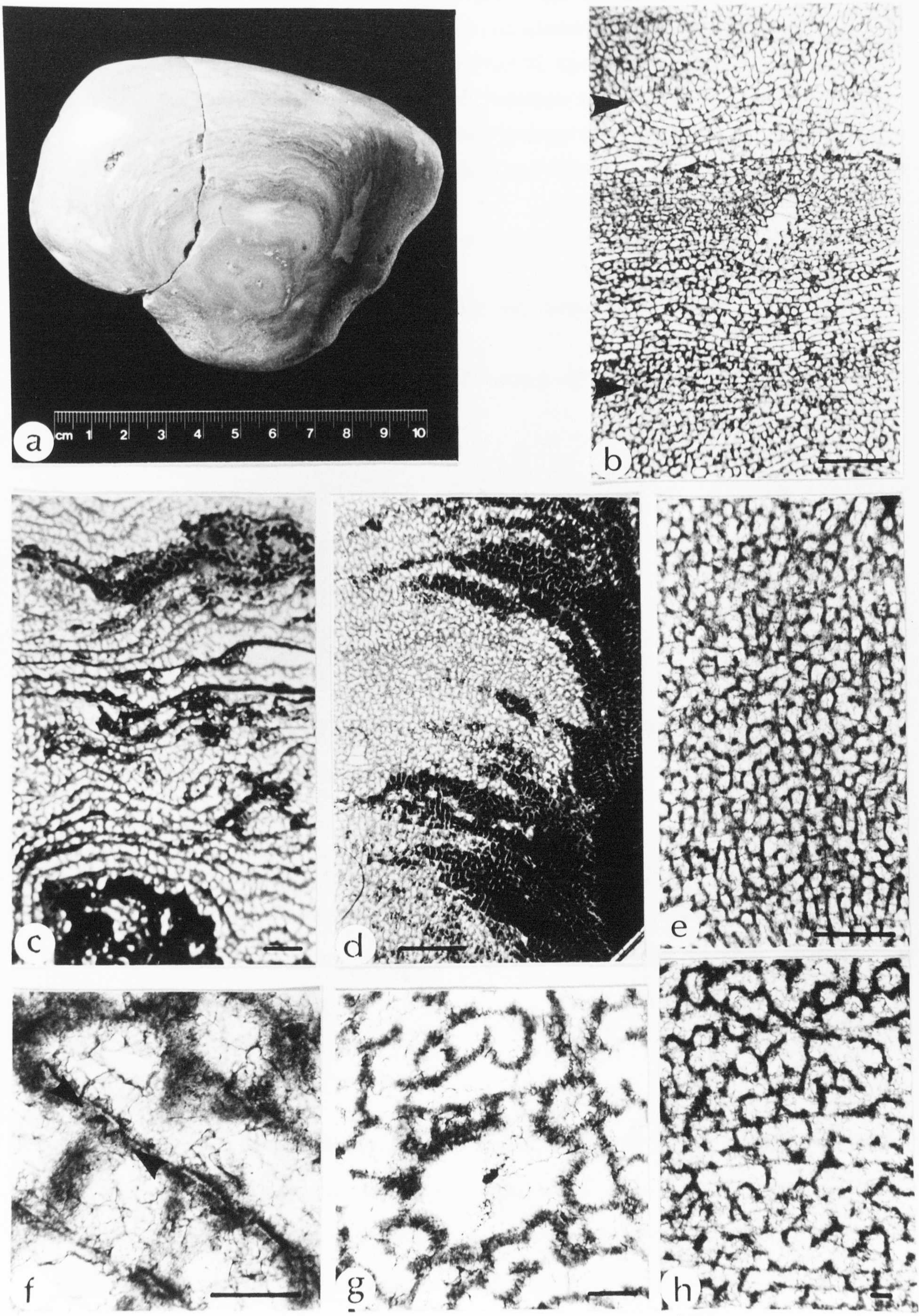
Figure e: Detail of Figure d showing continuous vertical elements, and absence of laminae and presence of aligned tabulae. H 3597. Villereousune, France. Upper Jurassic.
Scale bar = 200 µm.

Figure f: Pillar terminations by overlapping lamina (arrowed). Note fibrous nature of calcareous skeleton. H 3594. Villereousune, France. Upper Jurassic.
Scale bar = 100 µm.

Figure g: Transverse section of oscular tube in non-laminate form. H 4044. Villereousune, France. Upper Jurassic.
Scale bar = 100 µm.

Figure h: Detail of Figure b showing breakdown of laminae in upper part of photograph. H 3395. Villereousune, France. Upper Jurassic.
Scale bar = 100 µm.

PLATE 22 *Burgundia trinorchii* Dehorne 1916



Burgundia ramosa Pfender, 1937

Plate 23 figs.a-h

* 1937 *Burgundia ramosa* Pfender p.133 Plate III, figs.4-6; PlateIV, fig.5 (T.S.)

? 1937*Burgundia campanae* Pfender p. 135 (no additional information available)

v 1955 *Burgundia steinerae* Hudson p.228 Plate 22, figs.1-3 (T.S.)

1963 *Burgundia steinerae* Hudson , 1955; Fenninger et al. p. 235 (no illustration)

1965 *Burgundia steinerae* Hudson , 1955; Fenninger and Hotzl p.40

1965 *Burgundia mammelonata* Fenninger and Hotzl p. 40 Plate 6, fig.1; Plate 7, fig.4 (T.S.)

1973 *Burgundia semiclathrata* (Hayasaka, 1917); Turnšek and Masse p.21 Plate 21, figs.1-3 (T.S.)

v 1973 *Burgundia massiliensis* Turnšek and Masse p.21 Plates 22, 23, Plate 27, fig.4.(T.S.)

1983 *Burgundia steinerae* Hudson , 1955; Dong p.417 Plate II, fig.2a and b.(T.S.)

Diagnosis:

Burgundia , usually with a coarse reticulum of normally short branched vertical elements (pillars) of 50-90 µm diameter. No axial reticulum.

Holotype:

The original of Pfender , 1937. p.133 Plate III, figs.4-6; Plate IV, fig.5. Djebel Akra, N.W. Syria. Upper Oxfordian to Lower Kimmeridgian (Upper Jurassic).

Material studied:

H 4615a,b; 4644a. Wadi Leeben, Ras Sharwain range, Qishn, South Arabia. Upper Jurassic. 83/14-17, 83/19b, 83/58, 83/63, 83/64, 83/71, 83/77 . La Mounine, Marseille, France. Upper Hauterivian (Lower Cretaceous).

Description:

Nodular , encrusting or dendroid gross morphology, up to 5cms diameter. No discernable surface features, though mamelons may be present. Filling tissue varies through the ontogeny of the individual, forming laminae or unaligned tabulae. These may grade into one another. Laminae are sinuous, fibrous and perforated, the tabulae granular or fibrous. Vertical elements may be simple or

PLATE 23: *Burgundia ramosa* Pfender, 1937

Figures a-e: Upper Jurassic (Lusitanian) of Wadi Leeben, Ras Sharwain range, Qishn, South Arabia.
Figures f-h: Lower Cretaceous (Upper Hauterivian) of La Mounine, Marseille, France.

Figure a: Gross morphology showing branch of dendroid form.H 4644.
Scale bars = 1mm.

Figure b: Longitudinal thin-section showing variability of inter-laminar space width, both between a pair of successive laminae and laterally within a pair of laminae. H 4615ab.
Scale bar = 200 μm.

Figure c: Tangential section, showing transverse sections of oscula and astrorhizal canals .
H 4615a.
Scale bar = 200 μm.

Figure d: Vertical tubular structures which may be oscular walls. Note upturning of laminae (?mamelon) around uppermost tube. H 4615a.
Scale bar = 1mm.

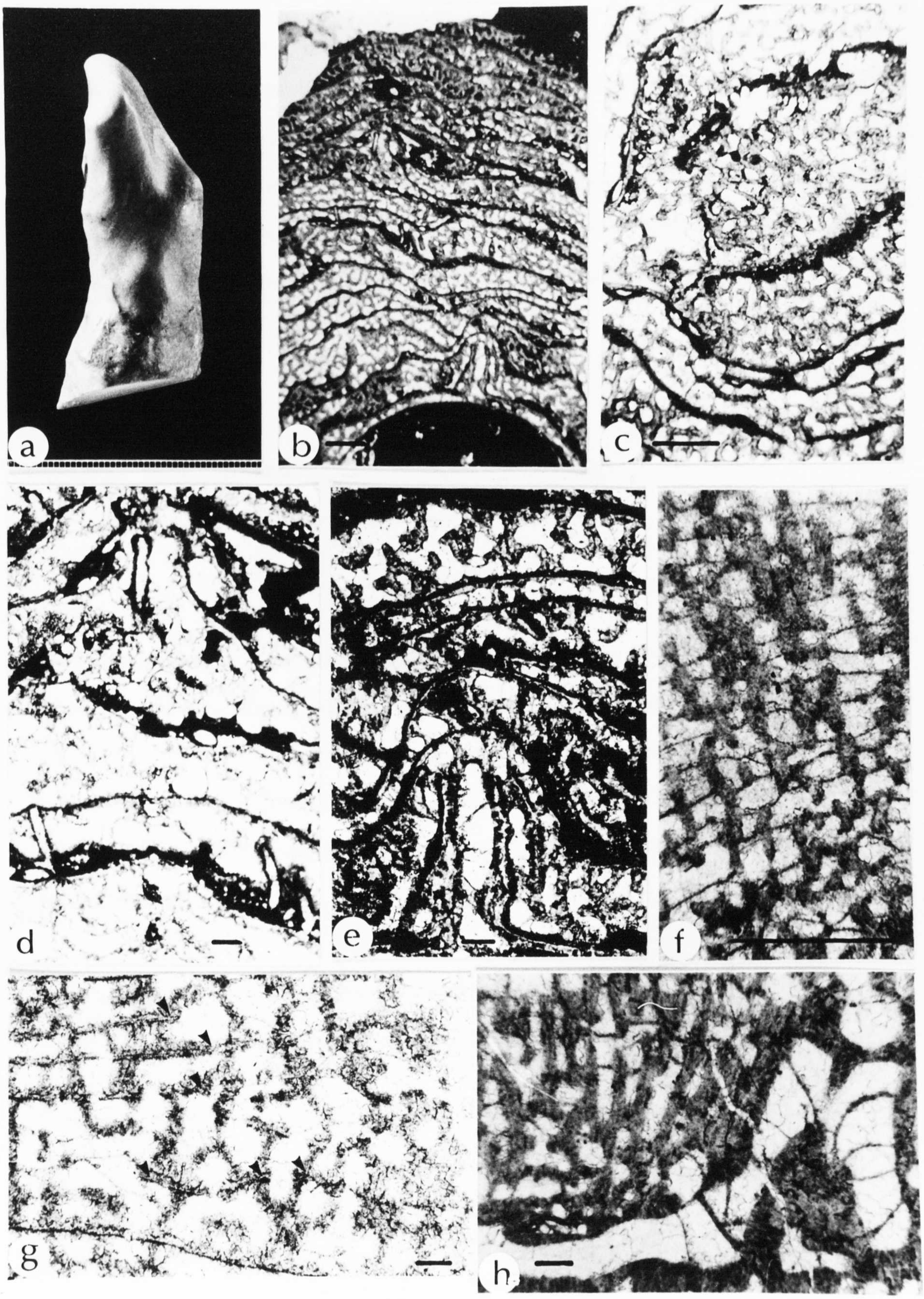
Figure e: Detail of oscular tube, where the walls are formed by an upturned and disrupted laminae. The oscular tube is tabulate and successive laminae have totally covered it and the mamelon. H 4644a.
Scale bar = 100 μm.

Figure f: Longitudinal section showing non-laminate area with continuous fibrous pillars and aligned tabulae. 83/58.
Scale bar = 100μm.

Figure g: Detail of figure f, showing lamina breakdown (arrowed). 83/64.
Scale bar = 100 mm.

Figure h: Detail of astrorhizal canals coalescing towards an osculum in non-laminate area. Note curved, fibrous tabulae in astrorhizae and osculum. 83/71.
Scale bar = 100 μm.

PLATE 23 *Burgundia ramosa* Pfender 1935



branched. When laminae are present they are generally 2-3mm apart and the pillars do not extend beyond one interlaminar space. Pillars become branching and anastomosing in the non-laminar areas. In tangential section the pillars appear meandriform. There is no tubular, "chaetetid" development of the skeleton. Aquiferous units with tabulate oscula , and astrorhizal canals form in the laminate areas, or non-tabulate oscula with sharply up-turned lamellae above them, which may have formed mamelons upon the skeletal surface. Oscula and astrorhizal canals bear abundant straight or curved tabulae, and may possess fibrous walls produced by skeletal element thickening and secondary calcareous skeleton precipitation. In the non-laminate areas of the skeleton, astrorhizal systems are common, and consist of short, tabulate oscula and tabulate astrorhizal canals.

Distribution:

S.W.Europe, Syria ,Iraq,China.

Upper Jurassic to Lower Cretaceous (Upper Oxfordian to Hauterivian)

Remarks:

Hudson suggested that *B.steinerae* differed from *B.ramosa* in that the interlaminar structures were mainly meandrifiorme tubules, whereas in *B.ramosa* they were regular pillar-lamellae. However, scrutiny of the figures of *B.ramosa*, suggests that these discriminatory criteria are not present. There is no cyclical alternation of laminar and non-laminar generations in *B. ramosa* as can be found in *B.trinorchii.* The separation of *Burgundia trinorchii* and *B.ramosa* has been based upon the criteria shown in Table 4.2.

Table 4.2: Criteria used for the separation of *Burgundia trinorchii* and *Burgundia ramosa.* (Terms used are relative to homologous features in the two species.)

Burgundia trinorchii	*Burgundia ramosa*
1. In non-laminate areas:	1. In non-laminate areas:
i) pillars tend to be straight and form a a tubular, "chaetetid" arrangement (Plate 22 ,fig. f)	i) pillars tend to be branched and anastomosing (Plate 23 ,figs. e,g)
ii)oscula are long, straight	ii)oscula are shorter, and the astrorhizal canals

and continous, and the astrorhizae poorly developed (Plate 22 ,fig. b).	"well" developed (Plate 23 ,fig. h).
2. Vertical element diameter is 40-70 µm.	2. Vertical element diameter is 50-90 µm.
3. Dendroid morphology not present (Plate 22 ,fig. a)	3. Dendroid morphology present (Plate 23 ,fig. a)

Burgundia wetzeli (Hudson,1954)

Plate 24, figs. a-g.

v * 1954 *Bekhmeia wetzeli* Hudson p.49 Plates 7,8 (T.S.)
1956 *Burgundia wetzeli* Hudson, 1954, Schnorf-Steiner p.570 (no illustration)
v . 1973 *Burgundia wetzeli* Hudson, 1954; Turnšek and Masse p.20 Plate 20, fig.1-3 (T.S.)

Diagnosis:

Nodular or dendroid *Burgundia* with an axial non-laminate reticulum formed of tubules and an outer laminate reticulum with generally simple, unbranched pillars limited to one interlaminar space. Stacked astrorhizal systems are present with tabulate oscula.

Holotype:

H 4428a,b; H 4429a-d; H 4430a,b. Eight thin-sections and the three remaining pieces of same branch.Bekhme Gorge, 4.5km N. of Bekhme, Iraq. Lower Cretaceous (Hauterivian)

Material studied:

H 4467-9, 4431 Bekhme Gorge, Iraq. Hauterivian (Lower Cretaceous).

83/1, 83/8, 83/21, La Mounine, Marseille, France . Hauterivian (Lower Cretaceous).

85/29, 85/30, 85/47, 85/54, 85/60, 85/74, 85/78, 85/80, 85/82, 85/85a, 85/85b, 85/87, 85/90a, 85/90b, 85/95. St. Mateo, Maestrazgo, E.Spain. Hauterivian (Lower Cretaceous).

Description:

In dendroid forms, the branches (2-20 mm diameter) appear to initiate from a basal nodule. Branching is by budding from the axial reticulum and not by dichotomy. In the axial reticulum (5-20 mm diameter), the reticulum is composed of parallel aligned sinuous tubules (100-120 µm diameter) of pillars and pillar-lamellae, intially parallel to the branch axis, but then normal to it. These tubules appear meandiform in tangential section. Tabulae are not present in this area. In the peripheral reticulum, the concentric laminae dominate and are usually 1mm apart. The interlaminar structures are generally simple and unbranched pillars usually terminate abruptly at the laminae base, but may be more complex. Laminae may be upturned directly over the stacked astrorhizal systems to produce feebly developed mamelons on the surface. Laminae beakdown occurs in directions of more vigourous growth, where a non-laminar axial-type reticulum dominates. Astrorhizal canals are generally confined to the interlaminar spaces, and the main branches often bifurcate. Astrorhizal canals appear to be in communication with both the osculum and the interskeletal spaces around and above them. Astrorhizae and osculum are commonly crossed by secondary fibrous tabulae, which are frequently curved and with a cyst-plate form, especially when they cross the junctions between interlaminar spaces. They may also be lined with secondary fibrous tissue. Nodular specimens may be markedly latilaminate due to a periodic variation of laminae spacing.

Distribution:

Europe (France, Spain) and Middle East (Iraq)

Lower Cretaceous (Hauterivian)

Remarks:

Hudson (1954) described *B.wetzeli* as having 'peripheral' and 'axial' reticulum. This is confirmed here. *B.wetzeli* often shows interlaminar pillar structures characteristic of *B.ramosa*. However, the dendroid gross morphology and the univeral presence of an axial reticulum, without laminar development, is felt sufficient to retain specific distinction for this form.

Spheroidal bodies of silica with a diameter of 5-10 µm have beeen found within the central area of the skeleal elements of *B.wetzeli*, which may be spicule microscleres. However, their indentification as spicules remains problematic.

PLATE 24 *Burgundia wetzeli* (Hudson, 1954)

All Hauterivian.

Figures a-f: Bekhme Gorge, Iraq.

Figure g: St.Mateo, Maestrazgo, Spain.

Figure a: Nodular or dendroid gross morphology. Nodular example shows latilaminar development due to periodic variability in laminar spacing. H 4468-9.
Scale bar = 1mm.

Figure b: Longitudinal thin-section showing non-laminate axial reticulum and outer reticulum with laminae. Note curve inwards and breakdown of laminae in centre of axial reticulum, due to the greater growth rate along the long axis of the branch. H 4429a.
Scale bar = 1mm.

Figure c: Stacked astrorhizal system with osculum. Note secondary fibrous tabulae precipitated across osculum and astrorhizal canals, and slight upturn of laminae to form a mamelon. H 4428b.
Scale bar = 1mm.

Figure d: Longitudinal section showing astrorhizal canals and variability of laminar spacing and vertical element form. H 4467a.
Scale bar = 1mm.

Figure e: Tangential section showing perforations (foramina) in fibrous laminae. H 4431.
Scale bar =100 μm.

Figure f: Tangential section showing astrorhizal canals.H 4431.
Scale bar = 1mm.

Figure g: Possible siliceous spicule pseudomorphs of ?microscleres within the central area of the fibrous skeletal elements. 85/85a.
Scale bar = 100 μm

PLATE 24 *Burgundia wetzeli* (Hudson)1954

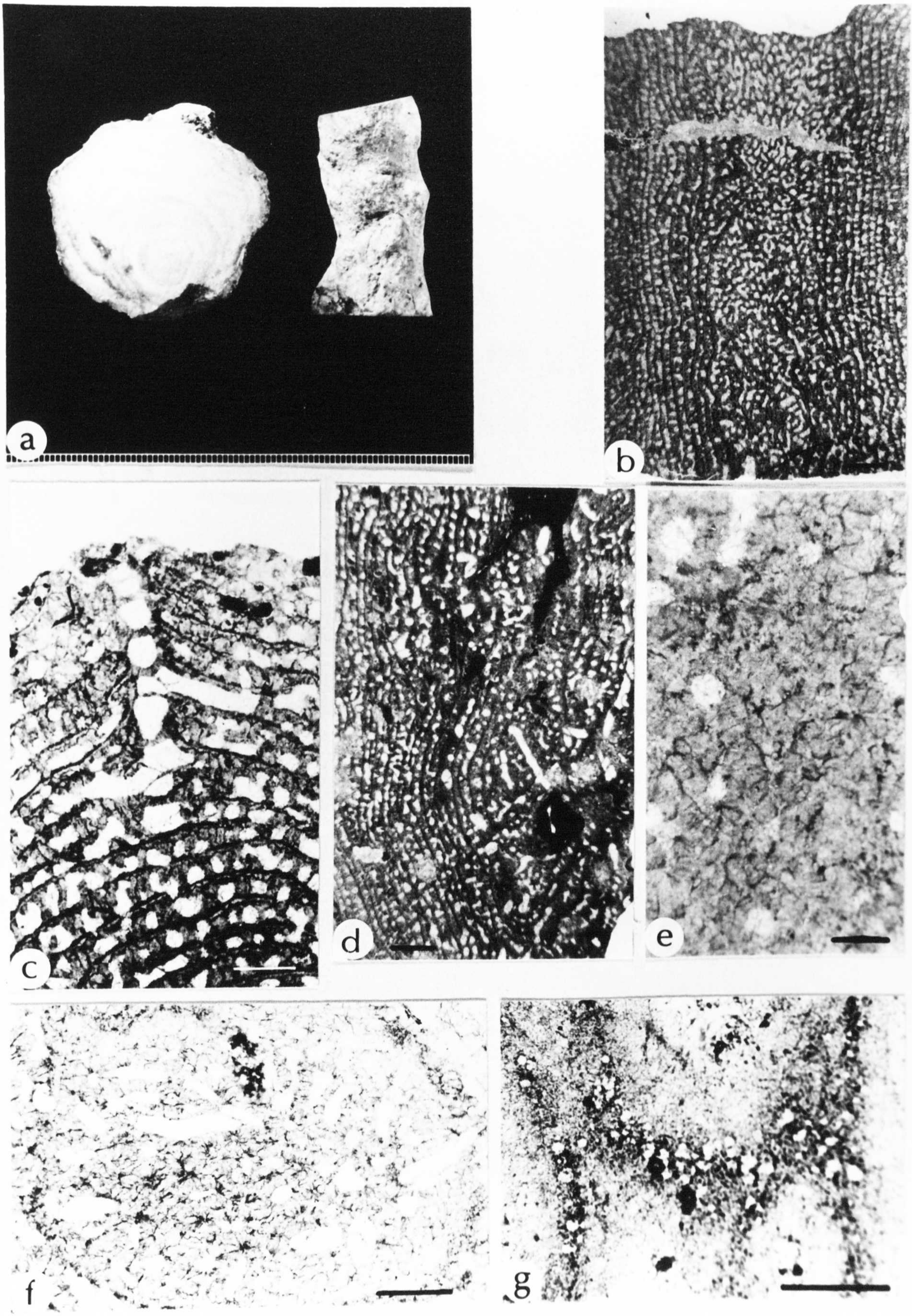


TABLE 4.3 Summary table showing the proposed amended status of species previously allocated to the genus *Burgundia* .

SPECIES	**ORIGINAL DESCRIPTION**	**REVISED PLACING**
B.trinorchii	*B. trinorchii* Dehorne, 1916	*B.trinorchii* Dehorne, 1916
B.wetzeli	*Bekhmeia wetzeli* Hudson, 1954	*B. wetzeli* (Hudson, 1954)
B.semiclathrata	*Circoporella semiclathrata* Hayasaka, 1917	*B. trinorchii* Dehorne, 1916
B.steinerae	*B. steinerae* Hudson, 1955	*B.ramosa* Pfender, 1937
B.tutcheri	*B. tutcheri* Kellaway and Smith, 1938	NOT BURGUNDIA (A calcarean)
B.tutcheri var. huttonae	*B. tutcheri* Kellaway and Smith,1938	NOT BURGUNDIA (A calcarean)
B.massiliensis	*B. massiliensis* Turnšek and Masse, 1973	*B.ramosa* Pfender, 1937
B.ramosa	*B. ramosa* Pfender, 1937	*B.ramosa* Pfender, 1937
B.campanae	*B. campanae* Pfender ,1937	?
B.mammelonata	*B. mammelonata* Fenninger et al. ,1965	*B.ramosa* Pfender, 1937
B.alpina	*Plassenia alpina* Yabe and Sugiyama, 1930	*?B. trinorchii* Dehorne, 1916
B.tertia	*B. tertia* Zuffardi-Comerci ,1938	?
B.astrotubulata	*B. astrotubulata* Turnšek ,1967	NOT BURGUNDIA
B.barremensis	*B. barremensis* Yavorsky, 1957	*B.trinorchii* Dehorne, 1916
B?. sp.	*B?. sp.* Fenninger et al.,1965	NOT BURGUNDIA
Stromatoporidium globosum	*Stromatoporidium globosum* Vanessa de Regny, 1915	?

SUB-CLASS TETRACTINOMORPHA Levi 1953

Diagonosis:

Demosponges which generally reproduce sexually by oviparity and which possess tetraxonid and monaxonid megascleres occurring together or separately and organised in a radial, plumose or axial pattern. Spongin is variable in amount. Microscleres include asters. May possess a calcareous skeleton.

ORDER AXINELLIDA Levi, 1956

Diagnosis:

Spongin and monaxonid spicule skeleton in the form of a stiff axis and a plumose or plumo-reticulate extra-axial system issuing from it. Extra axial elements project through the body surface. Microscleres are often absent. May possess a calcareous skeleton.

FAMILY MILLEPORELLIDAE Yabe and Sugiyama, 1935

Diagnosis:

Calcified axinellids with spicule framework of club-shaped styles in a plumose arrangement in vertical elements only. No microscleres are present. Primary calcareous skeleton dominated by radial elements of fascicular fibrous microstructure initiated at the bases of the spicules. Massive, encrusting or dendroid gross morphology. Secondary calcareous skeleton , where present , growing epitaxially on the primary one. Traces of aquiferous system as astrorhizae and /or oscula.

Genera described:*Dehornella* Lecompte,1952 ; *Shuqraia* Hudson,1954 ; *Promillepora* Dehorne, 1920; *Parastromatopora* Yabe and Sugiyama ,1930; *Steineria* Hudson, 1956.

Genera not discussed: *Tosastroma* Yabe and Sugiyama, 1930; *Steinerella* Lecompte,1952; *Ceratostroma* Kühn, 1926 ; *Stromatoporidium* Germovsek, 1954; *Myriopora* Volz, 1904; *Milleporella* Deninger, 1906 ; *Millestroma* Gregory, 1898; *Stromatoporellina* Kühn, 1928; *Milleporidium* Steinmann, 1903.

Distribution:

Europe, Middle East

Upper Jurassic to Lower Cretaceous (Upper Oxfordian - Valanginian)

Discussion:

This family replaces the superfamily Milleporellicae Hudson 1959.

Hudson gave the diagnostic feature of the Milleporellicae as the possession of cligonal fibrous (fascicular fibrous) skeletal tissue. The possession of fascicular fibrous microstructure is now known to be convergent (See section 3.5.4.1.). The division of the Milleporellicae into families by Hudson, was based upon differences in the arrangement of the aquiferous system arrangements e.g.the presence or absence of "zooidal tubes" (oscula, this work). In the opinion of the present author, aquiferous system differences are not significant at this taxonomic level. In addition, the presence of club-shaped styles in a pluomse arrangement in members of both the Milleporellidae and Milleporiidae suggests the distinction between the two families is an artificial one. The Milleporellidae Yabe and Sugiyama ,1935 takes priority as the senior family name.

Generic diagnoses are based upon differences in spicule size, arrangement and calcareous skeletal arrangement, dimensions and orientation. These variations are illustrated in Figure 4.2.

The position of the Milleporellidae within the Porifera:

The superfamily Milleporellicae has been reduced to family status, due the similarity of the spiculation in the Milleporellidae to that found in the order Axinellida, the convergent nature of the calcareous microstructural type and the reinterpretation of zooidal tubes. The family is placed within the order Axinellida, with closest affinities to the family Agelasidae. The Agelasidae bear club-shaped concentrically spinose acanthostyle megacleres, of similar dimensions to those in the Milleporellidae and generally in a plumose arrangement .

Dehornella Lecompte, 1952

1960 *Astroporina* Hudson p.196

Diagnosis: Milleporellidae with a densely packed plumose spicule skeleton, where spicules are

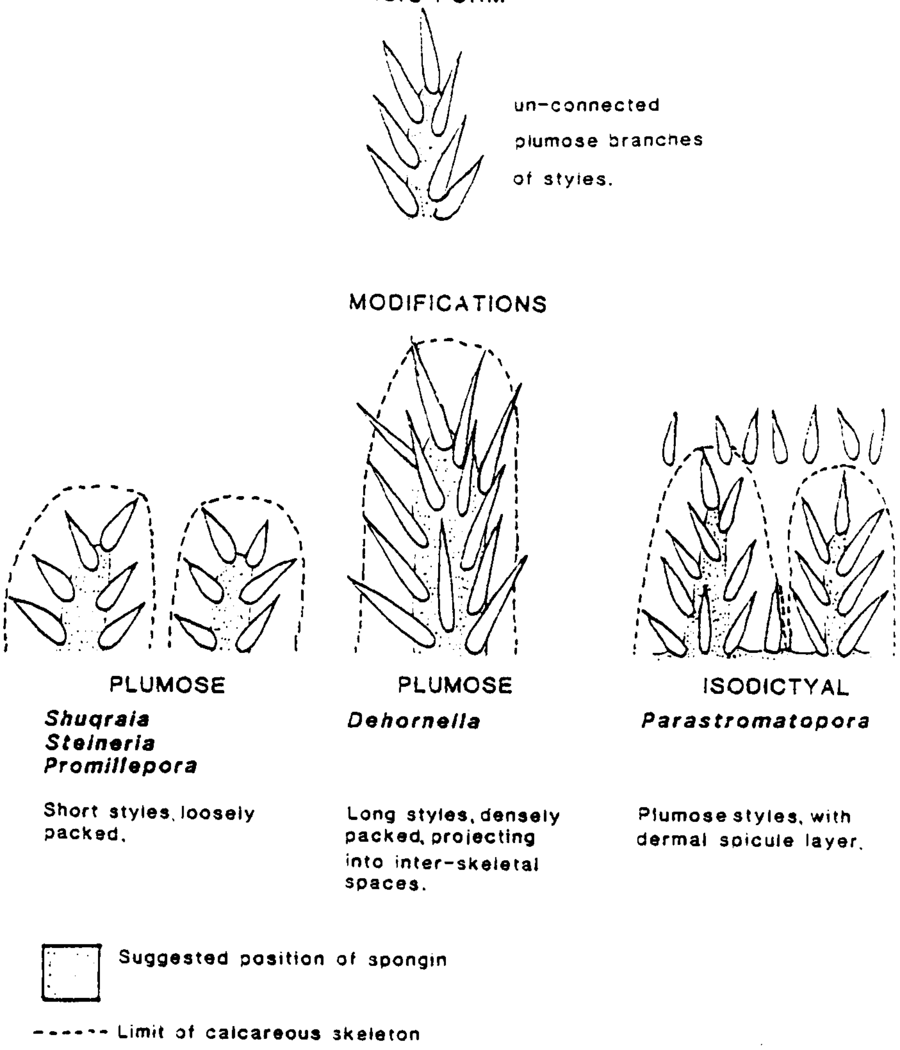


Figure 4.2: Modifications of spicule dimensions and arrangements of the spiculate genera within the Milleporellidae.

110-135 µm long and 13.5-17 µm wide, and may project into the interskeletal spaces. Vertical elements form continuous, often adjoined columns of fascicular fibrous microstructure, 100-300 µm wide. Pillar-lamellae are generally subordinate. Encrusting or massive gross morphology. Astrorhizae often common and obvious, sometimes conjoined. Tabulae are often common and sometimes aligned. May be markedly latilaminate.

Type species:

Stromatoporella hydractinoides Dehorne, 1920. Abbadia Marls, Silveiras, Arrabida Massif, Portugal. Lower Kimmeridgian (Upper Jurassic).

Included species: *Dehornella hydractinoides* (Dehorne, 1920) ; *D. choffati* (Dehorne, 1917) ; *D. harrarensis* (Wells,1943); *D. crustans* Hudson,1960; D. *valanginiensis* (Schnorf-Steiner, 1960).

Distribution:

Europe, Middle East

Upper Jurassic to Lower Cretaceous (Upper Oxfordian - Valanginian)

Remarks:

The genus *Dehornella* was founded by Lecompte on one specimen described by Dehorne (1920) as *Stromatopora hydractinoides.* Lecompte defined the genus as having:

1) Stellate astro-systems forming mamelons; 2) Continuous vertical pillars (columns); discontinuous transverse lamellae beneath the mamelons and continuous between the mamelons and 3) a skeletal tissue that was possibly originally chitinous.

In agreement with Hudson (1960), the possession of mamelons is considered in this study as being a subsidiary species-specific, not a generic characteristic.

The possession of a chitinous skeleton was suggested by Dehorne(1920) based on the similarity of the skeletal tissue growth stages of *Dehornella,* to that of Recent *Hydractinia echinata.* Lecompte agreed with this suggestion, on the dubious grounds that the pigmented cores of the pillars showed 'single extinction' (pseudopleiochroism). There is however no convincing evidence to suggest that *Dehornella,* or any other Mesozoic "stromatoporoids" were chitinous.

Hudson (1960) stated that the foundation of *Dehornella* on this particular specimen was unfortunate as the individual is thinly encrusting and bears a juvenile specialised reticulum. He redesignated the main features of the genus to be the dominant vertical pillars or lamellae, and the irregular, tabulate inter-skeletal spaces ("coeno-spaces") or superimposed astrorhizae ("astrocorridors").

With this definition, he could include *Stromatopora choffati* Dehorne and *S.harrarensis* Wells, so avoiding the erection of a slightly different new genus in which to place them.

Hudson stated that there were few differences in the *D. choffati* species group, which includes *D.hydractinoides, D.crustans, D.harrarensis and D.omanensis,* and that their distinction was probably intra-specific. In the opinion of the present author, *D.crustans* can be distinguished specifically from the other species. *D.hydractinoides* and *D.choffati* have not been examined. The remaining species are synonomous, together with *D.aff.harrarensis* Hudson, 1960 and *Astroporina sp.* Husdon, 1960 and possibly *D.kurtchensis* (Wells, 1943).

In 1960 Hudson founded the genus *Astroporina*, which he placed within the Parastromatoporidae.

The diagnostic feature of the genus was the "abundant conjoined astrosystems". In the opinion of the present author, the nature of the aquiferous system alone is an insufficient diagnostic characteristic on which to base a new genus.

In addition, spicules have been found in *Dehornella* and *Astroporina.* The spiculation of members of the genus *Astroporina* is identical to that of *Dehornella*, and in addition the character of the calcareous skeleton is very similar. *A.stellifera* , *A.stellens* and *A.orientalis* have been found to be conspecific with *D.crustans,* and *A.sp.* Hudson, 1960 conspecific with *D.harrarensis.* Species of the genus *Astroporina* should be included within the senior synonym *Dehornella.*

Dehornella hydractinoides (Dehorne, 1920)

Plate 25, figs.a,b

1920 *Stromatoporella hydractinoides* Dehorne p.77 Plate 6, fig.2; Plate 17, fig.3; Text-fig.9 (not Plate15, fig.3) (G.S.,T.S.)
1923 *Stromatoporella hydractinoides* Dehorne, 1920; Dehorne p.19 Plate 1, figs.2a and b.(T.S.)
1932 *Stromatoporella hydractinoides* Dehorne, 1920;Steiner p.80 (no illustration)
1928a Stromatoporella hydractinoides Dehorne, 1920; Kühn p.550
1928b Stromatoporella hydractinoides Dehorne, 1920;Kühn p.39
1952 *Dehornella hydractinoides* (Dehorne, 1920), Lecompte p.16 Plate 2, figs.1,1a.(T.S.)
1956 *Dehornella hydractinoides* (Dehorne, 1920); Lecompte p.133 Text-fig.109,5. (T.S.)
1960 *Dehornella hydractinoides* (Dehorne, 1920); Hudson p.190 (no illustration)

Diagnosis:

Dehornella, with possible spicule ghosts of club-shaped styles within the fascicular fibrous columns, with an irregular development of pillars and pillar-lamellae and abundant aligned fibrous tabulae. Encrusting gross morphology. Common astrorhizae, 2.5-3mm diameter. Conical mamelons are present, 5mm in diameter and usually 5-7mm apart.

Holotype:

Dehorne, 1920. p.77 Plate 6, fig.2; Plate 17, fig.3; text-fig.9. 1923. Plate 1, fig.2a. Specimen and thin-section a of *Stromatoporella hydractinoides.* Laboratoire de Geologie, La Sorbonne, Paris. Abbadia Marls, Silveiras, Arrabida Massif, Portugal. Lower Kimmeridgian.

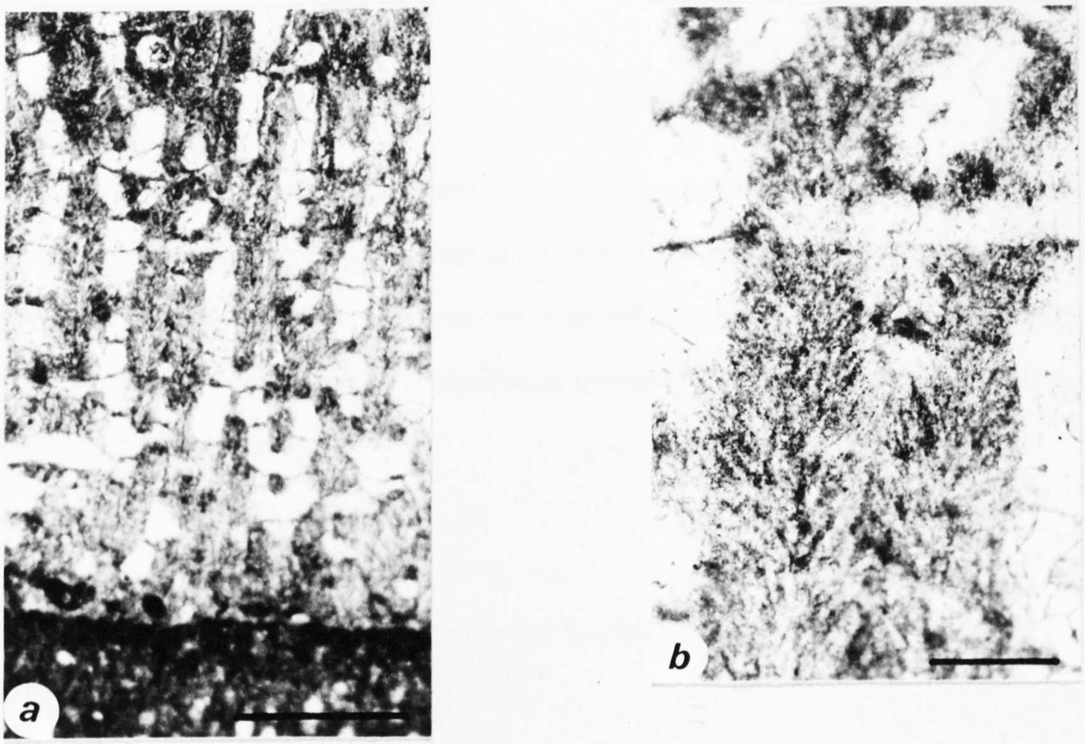
PLATE 25 *Dehornella hydractinoides* (Dehorne, 1920)

Longitudinal thin section. Abbadia marls, Silveiras, Arrabida Massif, Portugal . Lower Kimmeridgian. J. Reitner collection.

Figure a: Columns of fascicular fibrous microstructure with fibrous tabulae.
Scale bar = 1mm.

Figure b: Spicule 'ghosts' of club-shaped styles in columns.
Scale bar = 100 µm.

PLATE 25 *Dehornella hydractinoides* (Dehorne) 1920



Material studied:

One longitudinal thin section from the type locality (Abbadia marls (Lower Kimmeridgian)), Silveiras, Arrabida massif, Portugal. J.Reitner Collection.

Description:

Club-shaped styles in a plumose arrangement within the central areas of the columns. Fascicular fibrous microstructure appears to be initiated at the base of the spicules. Parallel arranged dominant columns 200-300 μm in diameter, which may be conjoined, by secondary calcareous skeleton, with subordinate pillar-lamellae development producing an open reticulum. Abundant aliged tabulae, 100-300 μm apart and 10-30 μm thick.

Remarks:

The present author does not feel sufficient material has been examined for a full examination of the species.

Dehornella choffati (Dehorne, 1917)

1917 *Stromatopora choffati* .Dehorne p.117 text-fig.1,2. (G.S.,T.S.)

p 1920 *Stromatopora choffati* Dehorne, 1917; Dehorne p. 83 text-figs.12,18,25,26. Plate 5, fig.6,Plate 7,fig.1;Plate 13, figs.1,2.(Not Plate 6, figs.3,4)(G.S.,T.S.)

1923 *Stromatopora choffati* Dehorne , 1917; Dehorne p.15 Plate1, fig.1a-c; Plate 2, fig.1(T.S.)

1928a Stromatoporina choffati (Dehorne, 1917) , Kühn p.550

1928b Stromatoporina choffati (Dehorne, 1917) ;Kühn p.90

1932 *Stromatopora choffati* Dehorne , 1917; Steiner p.82 (no illustration)

1952 Stromatoporina choffati (Dehorne, 1917) ;Lecompte p.20 (no illustration)

1955b *'Stromatopora" cf. Stromatopora choffati* (Dehorne, 1917); Hudson p.318 (no illustration)

1956 *Stromatoporina choffati* (Dehorne, 1917) ;Lecompte p.137 (no illustration)

Non 1956 *Syringostroma choffati* (Dehorne, 1917), Lecompte p.132 (no illustration)

1960 *Dehornella choffati* (Dehorne, 1917), Hudson p.190 (no illustration)

Type material:

Lectotype (Chosen by Lecompte 1952, p.20) *Stromatopora choffati* specimen 25 and sections 25a-e. Laboratoire de Geologie, La Sorbonne, Paris.Figured by Dehorne 1917. text-fig.1,2.

Nerinea elsgaudiae Limestones, Pedreiras, Cezimbra Massif, Portugal. Upper Oxfordian to Lower Kimmeridgian.

Material examined:

H 4752, 4756. (*'Stromatopora' cf. Stromatopora choffati* Hudson, 1955). Bakkin, ?South Yemen, Arabia. Upper Oxfordian to Lower Kimmeridgian (Upper Jurassic).

Remarks:

'Stromatopora' cf. Stromatopora choffati, described by Hudson in 1955b was based upon two highly recrystallised specimens. The thin-section H 4756a bears numerous pyrite spicule pseudomorphs comparable to *Dehornella*, but the calcareous skeleton is almost totally recrystallised. However, insufficient material of *D.choffati* has been examined and it is therefore not described.

Dehornella harrarensis (Wells,1943)

Plate 26, figs. a-e. Plate 38, fig.b.

* 1943 *Stromatopora harrarensis* Wells p.50. Plate 8, figs,1-5. (G.S.,T.S.)
1943*Stromatopora kurtchensis* Wells p. 50 Plate 9,fig. 2 (T.S.)
? 1954 *'Stromatopora' kurtchensis* Wells, 1943 ; Hudson p. 219 Plate VII, fig.5. (T.S.)
v . 1954*'Stromatopora' harrarensis* Wells,1943; Hudson p.219, Plate 7, fig.4. (T.S.)
1955b *Stromatopora cf.harrarensis* Wells, 1943; Hudson p.318 (no illustration)
v . 1960 *Astroporina sp.* Hudson p.197(no illustration)
v . 1960 *Dehornella omanensis* Hudson p.191. Plate 28, figs.1,2,5-8; text-fig.3b,4,5.
? *1960 Dehornella kurtchensis* (Wells, 1943), Hudson p.194
v . 1960 *Dehornella harrarensis* (Wells 1943), Hudson p.194 Plate 28, figs.3,4,9,10. text-fig.3a.(T,.S.)
v . 1960 *Dehornella aff. harrarensis* Hudson p.196 (no illustration)
1963 Dehornella aff. ?harrarensis Hudson, 1960; Fenninger et. al. p.326
1965 *Dehornella aff. ?harrarensis* Hudson, 1960; Fenninger et. al. p.35 Plate2, fig.6 (T.S.)
? 1974 *Dehornella aff.harrarensis* Hudson, 1960; Turnsek and Masse p.15 Plate 10 (T.S.)

Diagnosis:

Dehornella in which the vertical elements are generally 250-300μm (range 100 -300 μm) in diameter and form an open reticulum of short anastomosing columns, where average length is 5-9 mm. The club-shaped styles have not been noted to project into the interskeletal spaces. Few tabulae are present. Common, but not conjoined astrorhizae .

Holotype:

Amer. Mus. Nat Hist. Spec. no. 25285. Kurtcha, Harrar Province, Ethiopia. Upper Jurassic.

Other material:

H4833-49, 4851-63, 4865-69 Wadi Bih, Ruus al jibal, Oman. Lower Kimmeridgian. H4832 Jebel Moghara, Sinai, Egypt. Oxfordian. H5159-62, H5164, 5165, 5167, 5169. and 85/60/11, 85/60/12 Makhtesh Hethira, Israel. Lower Kimmeridgian.

Description:

Club-shaped styles arranged in a plumose arrangement within the central area of the vertical skeletal elements. Spicules do not appear to project into the inter-skeletal places. Encrusting, nodular or massive gross morphology, which may be an aggregate of nodules. Often with surface elevations; low, rounded bases, mamelons, or conical mamelons and astrorhizae. Astrorhizae consist of several braching, often tabulate canals, radially arrranged, which are the same diameter as the interskelatal spaces and show no decrease in diamater along their length. There may be latilamination due to a cyclical increase in the column width by secondary tissue development and variation in the spacing of these elements. In tangential section pillars become fused to form meandriform tubules. Tabulae are few (10-30 µm thick) and may or may not be aligned, when their vertical spacing is between 100-400 µm apart. Astrorhizae are commonly 5-6mm across and 7-9mm apart.

Distribution:

Middle East (Oman, Sinai, Israel)Europe (Austria, France)

Upper Jurassic to Lower Cretaceous (Upper Oxfordian to Lower Aptian)

Remarks:

Hudson noted that there was little difference between *D. harrarensis* and *D. omaniensis* and that their distinction was probably intraspecific. This is confirmed here. Hudson initially separated

PLATE 26 *Dehornella harrarensis* (Wells, 1943)

Figure a: Massive specimen with mamelons and astrorhizae on surface. H 4883. Wadi Bik, Ruus al Jebel ,Trucial Oman. Beni Zaid Limestone. Upper Jurassic (Oxfordian).
Scale bars = 1mm.

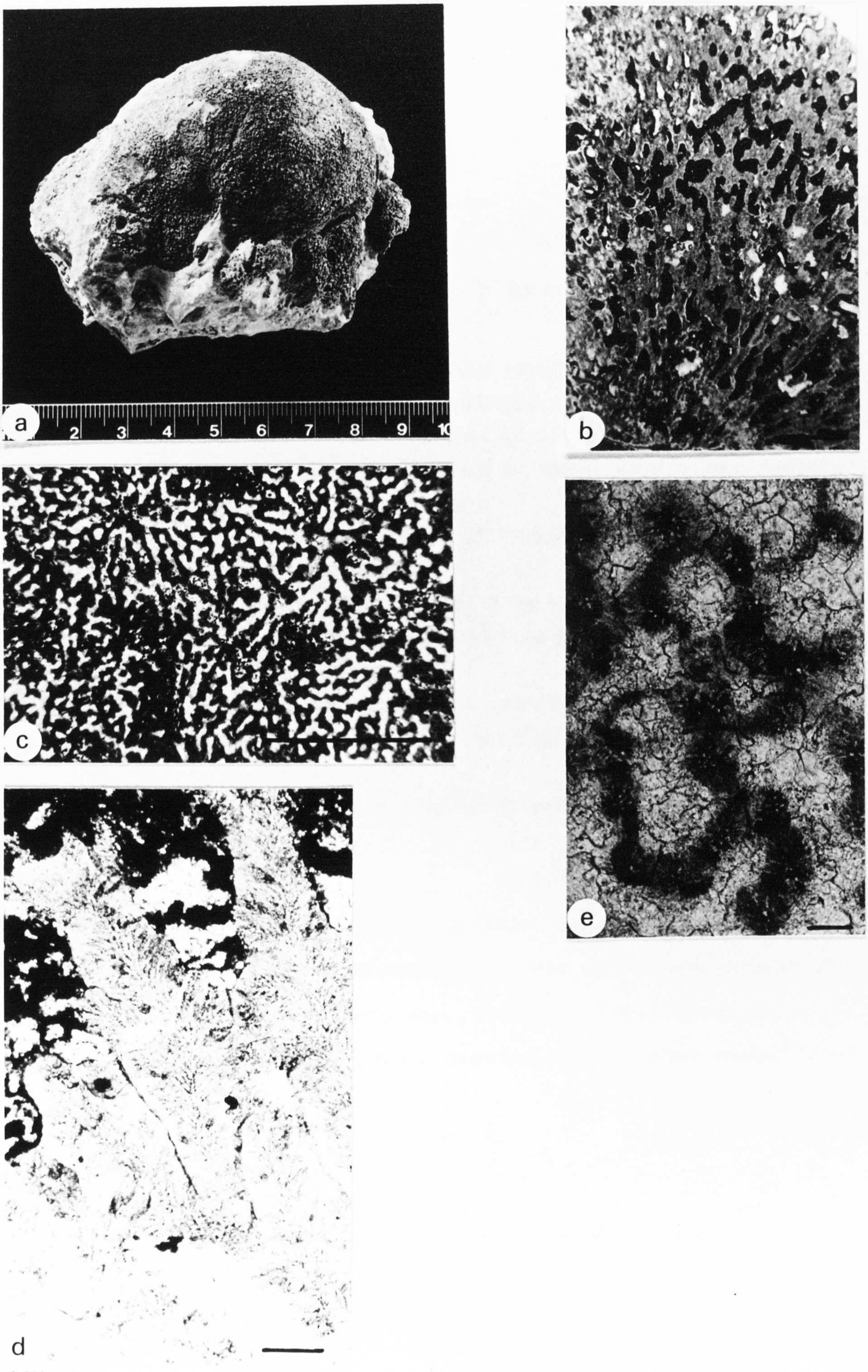
Figure b: Anastomosing columns of fascicular fibrous microstructure with few tabulae. No latilaminar development. H 4868a. Wadi Bik, Ruus al Jebel, Trucial Oman. Beni Zaid Limestone. Upper Jurassic (Oxfordian).
Scale bar = 1mm.

Figure c: Transverse section showing astrorhizal form and spacing. H 4844c. Wadi Bik, Ruus al Jebel, Trucial Oman. Beni Zaid Limestone. Upper Jurassic (Oxfordian).
Scale bar = 1cm.

Figure d: Fascicular fibrous columns with possible spicule 'ghosts' of club-shaped styles. H 4844c.
Wadi Bik, Ruus al Jebel ,Trucial Oman. Beni Zaid Limestone. Upper Jurassic (Oxfordian).
Scale bar = 100 µm.

Figure e: Transverse sections of calcite pseudomorphs of spicules in the central areas of the fascicular fibrous columns.85/60/11. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 100 µm.

PLATE 26 *Dehornella harrarensis* (Wells) 1943



D.omaniensis by its generally coarser reticulum, with smaller astrorhizae and fewer tabulae.

D. harrarensis and *D.crustans* can be distinguished as the astrorhizae of the former are more widely spaced (6-9mm) and generally less well developed than *D.crustans*, and there is considerable pillar-lamellae development. In addition, the reticulum is more open and anastromosing and there are relatively few tabulae.

Dehornella crustans Hudson,1960

Plate 2, figs.a,b. Plate 27, figs.a-j.

v . 1935 *Actostroma praesalevensis* Zuffardi-Comerci, 1932; Thomas p.38 (no illustration)
v * 1960 *Dehornella crustans* Hudson p.191 Plate 25, figs.5-7; Plate 26, fig.1. (T.S.)
v . 1960 *Astroporina stellifera* Hudson p.196 Plate24 ,figs.1-5; Plate 27, fig.1,2. (T.S.)
v . 1960 *Astroporina stellens* Hudson p.197 Plate 24, figs.6,7; Plate 25, fig.4; Plate 26, figs.5,6.(T.S.)
v . 1960 *Astroporina cf.orientalis* Hudson p.197 Plate 25, figs.1-3; Plate 26, figs.2,3. (T.S.)
v 1960 *Astroporina orientalis* Hudson p.196 Plate 26, figs.1,2; Plate 27, figs.6,7. (T.S.)
v 1960 *Astroporina cf. orientalis* Hudson p.197 Plate 25, figs.1-3; Plate 26, figs.2,3. (T.S.)
1983 *Astroporina stellifera* Hudson, 1960; Dong p.422 Plate IV, figs. 2a and b. (T.S.)
? 1983 *Parastromatopora menoria-naumanni* Yabe, 1927; Dong p.420 Plate III, figs.2a-c. (T.S.).
? 1983 *Epistromatopora eleganta* Dong p. 421 Plate III, figs.4a and b. (T.S.)

Diagnosis:

Dehornella with a densely packed isodictyal spicule skeleton which projects into the interskeletal spaces. Vertical elements form extensive anastomosing columns, often diverging and composite, and forming foramina. Subordinate pillar-lamellae. Secondary, epitaxial calcareous skeleton is present at intervals. Abundant, often conjoined astrorhizae. Abundant, aligned tabulae. Often latilaminate.

Type material:

Holotype: H 5170. Makhtesh Hagadol, Israel. Lower Kimmeridgian (Upper Jurassic).

PLATE 27 *Dehornella crustans* Hudson, 1960

Figure a: Variation in gross morphology; massive forms with variously developed surface elevations. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Lens cap = 6cms. diameter

Figure b: Broken tangential surface showing confluent astrorhizae. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale in centimetres.

Figure c: Longitudinal section showing micritised spicule pseudomorphs of club-shaped styles within columns of fascicular fibrous microstructure. DK23 6600'. Dakar, Egypt. (Un-registered bore-hole material at B.M.(N.H.)). Upper Jurassic.
Scale bar =- 100 µm.

Figures d,e,g: Variation in radial element arrangement:

Figure d: Longitudinal section showing latilaminae due to periodic secondary skeleton development, and arrangement of anastomosing columns and aligned tabulae. H 5170c. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 1mm.

Figure e: Longitudinal section showing columns and aligned tabulae with large tabulate inter-skeletal spaces, encrusting a recrystallised scleractinian coral. H 5168a. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 1mm.

Figure f: Surface showing selective weathering of latilaminae. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 1cm.

Figure g: Longitudinal section showing more widely spaced columns. F 1774a. Daghani section, Bihendula, Somalia. Upper Jurassic.
Scale bar = 1mm.

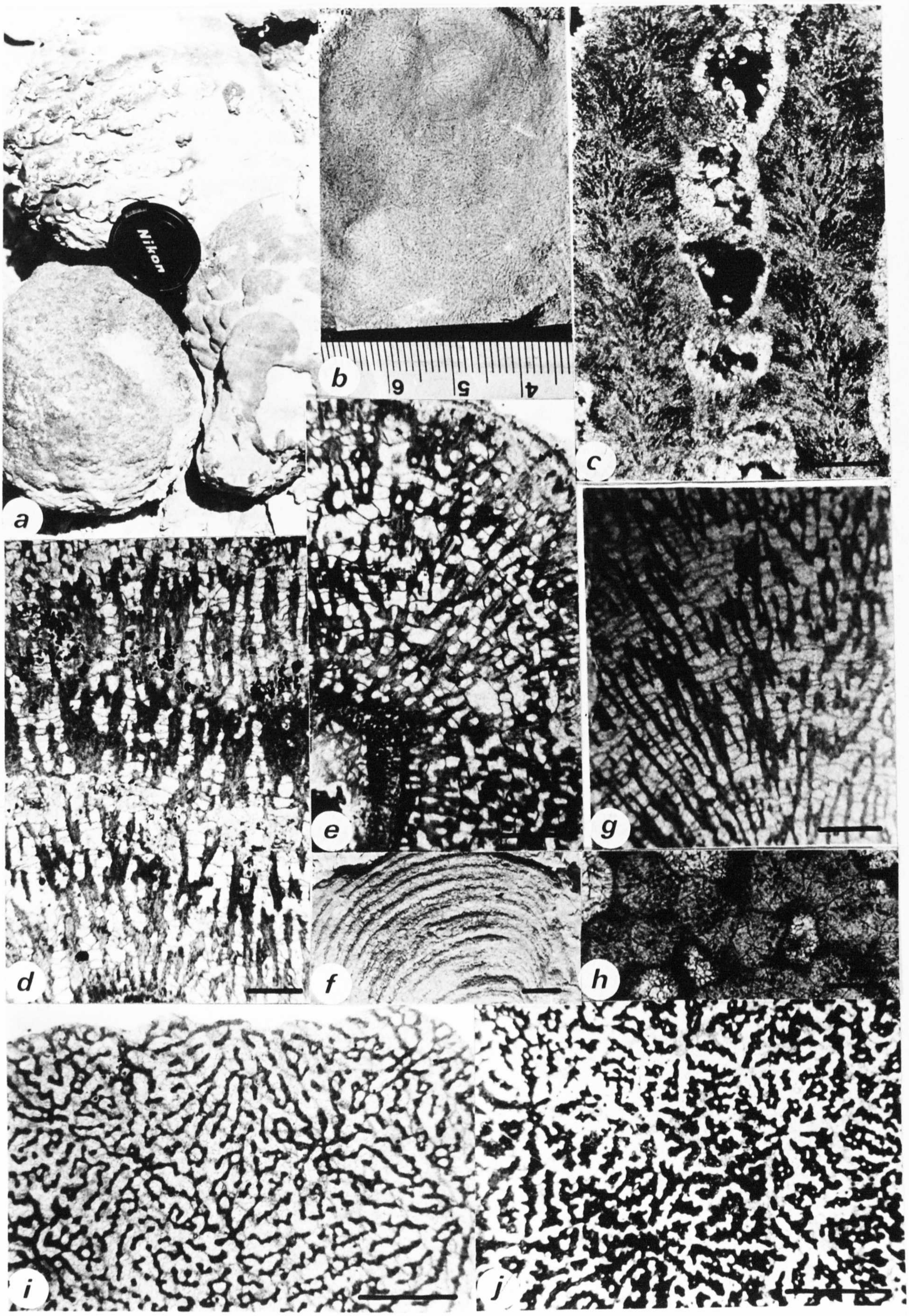
Figure h: Transverse section showing spicule pseudomorphs in central area of columns. 85/64/3. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 100 µm.

Figures i,j: Variability of astrorhizae:

Figure i: Transverse section showing confluent astrorhizae. H 4850 Ain Safra, Yenta, Lebanon. Upper Oxfordian to Lower Kimmeridgian.
Scale bar = 1cm.

Figure j: Transverse section showing conjoined astrorhizae. H 1775b. Daghani section, Bihendula, Somalia. Upper Jurassic.
Scale bar = 1cm.

PLATE 27 *Dehornella crustans* Hudson 1960



Material examined:

F 1773,1774. Bihen limestone, Daghani Section, Bihendula, Solamia. Upper Jurassic. F 1775. Ahankon Tug, Inda district, Somalia. Upper Jurassic. H 4850 Ain Safra, Yenta, Lebanon. Upper Oxfordian to Lower Kimmeridgian (Upper Jurassic). H 4850 Ein Safra, Yenta, Lebanon. Upper Oxfordian to Lower Kimmeridgian (Upper Jurassic).

H 4837, 5168, 5479, 85/ 62/2, 85/64/3, 85/66/7, 85/66/9, 85/68/12 Makhtesh Hagadol, Israel. Lower Kimmeridgian. DK 23 6600' Dakar. Upper Jurassic.

Description:

Spicule skeleton of club-shaped styles in a plumose arrangement within the central area of the vertical skeletal elements, with a dermal layer of parallel arranged spicules, producing an isodictyal arrangement. Encrusting to massive gross morphology up to 20cm diamater, often with well developed surface elevations; mamelons, conical mamelons or branch-like chimneys. Vertical columns (100-200 µm diameter) are continuous and adjacent columns are often united by secondary epitaxial skeleton (25-50 µm diameter), and sometimes extends outwards to form fibrous tabulae up to 100 µm thick. Up to four columns may be united in this way, for up to 2mm length. Vertical columns frequently diverge in longitudinal section to form a herring-bone pattern. In tangential section the columns unite to form a 'beaded' arrangement, sometimes enclosing tubes (200-300 µm diameter). Common and well developed astrorhizae, which are characteristically variable in form and show little decrease in diameter (250-400 µm) along their length. They are often conjoined, with their centres between 3.5-5mm apart. Astrorhizal canals are generally unbranched. Latilamine are formed by periodic secondary skeletal precipitation. Abundant aliged tabulae are present (10-30 µm width) and spaced 300-400 µm apart.

Distribution:

Middle East (S.Israel, Dakkar) and N.Africa (Somalia)

Upper Jurassic

Remarks:

Spicules have been found in the holotype.

No adequate transverse thin-section of *D.crustans* was made by Hudson. Otherwise, he would have noticed the similarity of the conjoined astrorhizal systems with those of the genus *Astroporina,* which he defined, in the same paper, by the presence of abundant and conjoined astrorhizal systems. Badly orientated thin-sections of the specimens F 1773-5, (originally collected by Thomas and erroneously allocated by him (1935) to *Actostroma praesalevensis* Wells, 1934) led Hudson to detect non-existent differences among these specimens, both between themselves and in comparison with the genus *Dehornella.* Hudson founded the genus *Astroporina* upon the specimens of Thomas and based the definition of the genus on the form of the aquiferous systems. He erected four species of *Astroporina.* The genus and species are here found to be invalid, and can be incorporated into pre-existing taxa of *Dehornella* under the revised diagnosis. *A.stellens, A.orientalis* and *A.stellifera* are all junior synonyms of *D.crustans,* which has page priority. *D.crustans* is a mammellate form, contrary to Hudson's observations.

Dehornella valanginiensis (Schnorf-Steiner, 1960)

Plate 28, figs. a-c.

1960 *Astroporina valanginiensis* Schnorf-Steiner p. 729-730.Plate 1,fig. 1-4; Plate 2, fig1; Plate 3, figs.1-2; text-fig.1,2.(T.S.)

1974 *Astroporina valanginiensis* Schnorf-Steiner, 1960; Turnšek and Masse p. 17. Plate 13, fig.1-3 (T.S.)

Diagnosis:

?*Dehornella* with an open reticulum of short pillars and pillar-lamellae with common aligned tabulae.

Type material:

Original of Schnorf-Steiner, 1960 p. 729-730.Plate 1,fig. 1-4; Plate 2, fig1; Plate 3, figs.1-2; text-fig.1,2. Steiner Collection, Lausanne Museum, Switzerland. Jura, Switzerland. Lower Valanginian (Lower Cretaceous).

Material studied:

83/33. Mont Rose, Marseille, France. Upper Lower Valanginian.

PLATE 28 *Dehornella valanginiensis* (Schnorf-Steiner, 1960)

83/33. Mont Rose, Marseille, France. Upper Lower Valanginian.

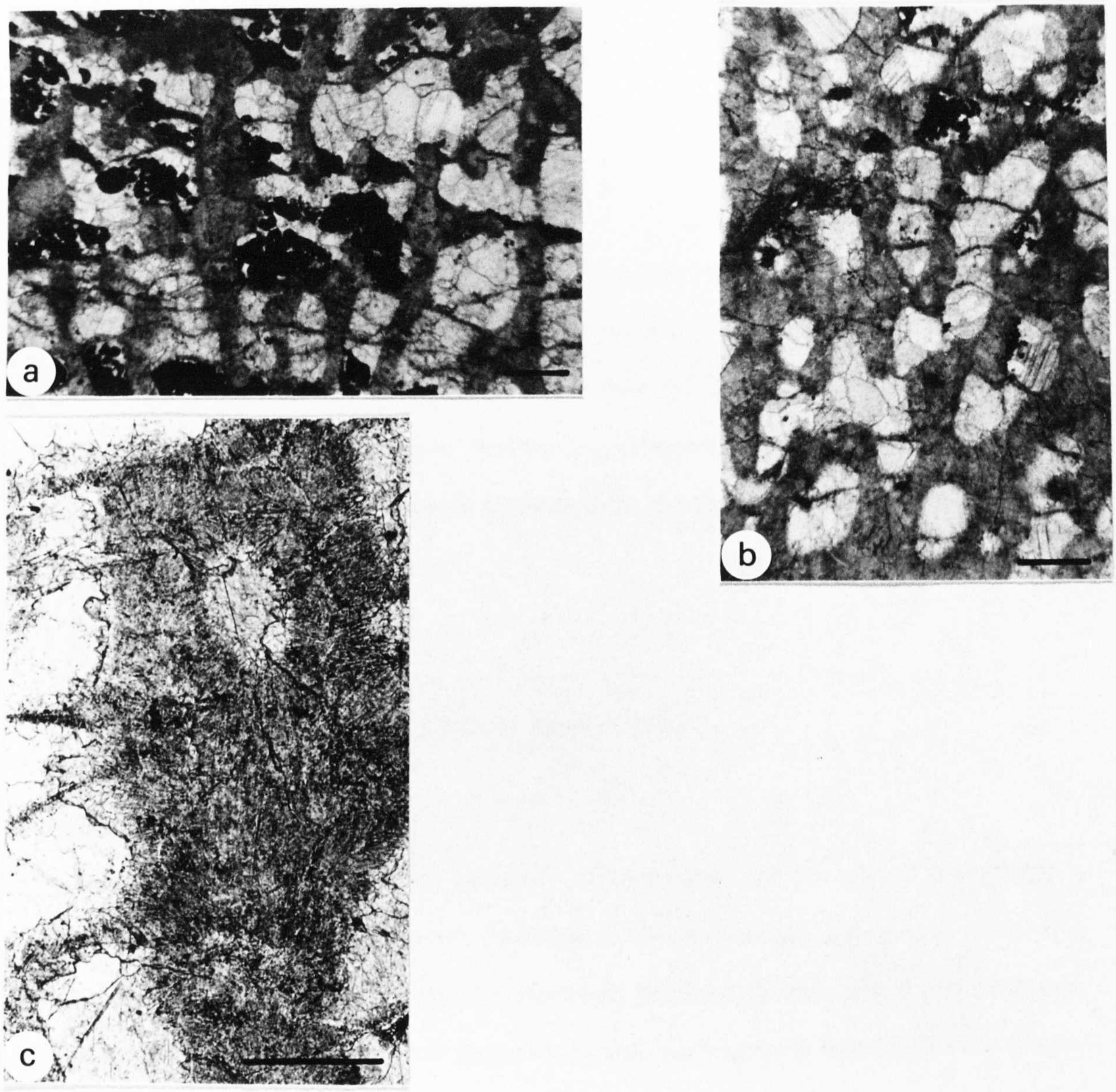
Figure a,b: Longitudinal sections showing widely spaced anastomosing fascicular fibrous columns with aligned fibrous tabulae.

Scale bar = 1mm.

Figure c: Detail of fascicular fibrous column and fibrous tabulae.

Scale bar= 100 µm

PLATE 28 *Dehornella valenginiensis* (Schnorf-Steiner) 1960



Description:

Massive or encrusting skeleton. Open reticulum of parallel arranged, short pillars (100-300 µm diameter) and pillar lamellae, which may enclose foramina. Pillar spacing is 30-500 µm apart. Few conjoined pillars and no secondary skeletal development. Tabulae are common, aligned and may be curved.

Remarks:

The material examined has been collected by the author from the locality of Turnsek (S.E.France, Valanginian). A full description of the species cannnot be given as no spicules have been noted as yet and the form of the astrorhizae is not known. However, the calcareous skeletal dimensions and form, and form of the tabulae, conform to those found in *Dehornella.*

D. valangiensis shows many similarities to *D.harranensis*, but possesses common aligned tabulae and has a more open reticulum.

Shuqraia Hudson, 1954

Diagnosis: (See Figure 4.2)

Milleporellidae with a primary spicule framework of styles (max. 80 µm long, 7 µm wide) in a loosely-packed, plumose arrangement. Dendroid gross morphology. Calcareous skeleton of regular columns forming tubules (140 µm in diameter) parallel to branch axis, then normal to it. These appear as a vermiculate mesh in tangential section. Orthogonal to fascicular fibrous primary calcareous skeleton in which the pillar diameter is 80- 130 µm. Thin, aligned tabulae (5-20 µm thick), form in the younger, central area of the skeleton. Secondary epitaxial calcareous skeleton (up to 50 µm thick) and fibrous aligned tabulae (up to 130 µm thick), often present in mature areas of the individual. This is often concentrically zoned. Pillars are shorter in the mature, outer areas. Tabulae often with periodicity to define latilaminae. No mamelons. May or may not possess astrorhizae.

Type species:

Milleporidium zuffardi Wells, 1943. Mt.Aiya Makkeran, Harrar Province, Ethiopia. Upper Jurassic (Upper Oxfordian to Lower Kimmeridgian).

Description:

Massive or encrusting skeleton. Open reticulum of parallel arranged, short pillars (100-300 µm diameter) and pillar lamellae, which may enclose foramina. Pillar spacing is 30-500 µm apart. Few conjoined pillars and no secondary skeletal development. Tabulae are common, aligned and may be curved.

Remarks:

The material examined has been collected by the author from the locality of Turnsek (S.E.France, Valanginian). A full description of the species cannnot be given as no spicules have been noted as yet and the form of the astrorhizae is not known. However, the calcareous skeletal dimensions and form, and form of the tabulae, conform to those found in *Dehornella.*

D. valangiensis shows many similarities to *D.harranensis*, but possesses common aligned tabulae and has a more open reticulum.

Shuqraia Hudson, 1954

Diagnosis: (See Figure 4.2)

Milleporellidae with a primary spicule framework of styles (max. 80 µm long, 7 µm wide) in a loosely-packed, plumose arrangement. Dendroid gross morphology. Calcareous skeleton of regular columns forming tubules (140 µm in diameter) parallel to branch axis, then normal to it. These appear as a vermiculate mesh in tangential section. Orthogonal to fascicular fibrous primary calcareous skeleton in which the pillar diameter is 80- 130 µm. Thin, aligned tabulae (5-20 µm thick), form in the younger, central area of the skeleton. Secondary epitaxial calcareous skeleton (up to 50 µm thick) and fibrous aligned tabulae (up to 130 µm thick), often present in mature areas of the individual. This is often concentrically zoned. Pillars are shorter in the mature, outer areas. Tabulae often with periodicity to define latilaminae. No mamelons. May or may not possess astrorhizae.

Type species:

Milleporidium zuffardi Wells, 1943. Mt.Aiya Makkeran, Harrar Province, Ethiopia. Upper Jurassic (Upper Oxfordian to Lower Kimmeridgian).

Distribution:

Middle East (S,Arabia, S.Israel) N.Africa (Ethiopia, Somalia) Japan?

Upper Jurassic (Upper Oxfordian to Lower Kimmeridgian)

Remarks:

Spicules have only been found in *S.hethira* (Hudson, invalid name; in collection, synonymised here with *S.zuffardi*) and in specimens collected by the present author. Due to the similarity of the construction of the calcareous skeletons, a similar spiculation is inferred for other specimens allocated to this genus.

Hudson described the fibrous tabulae (filling tissue), as transverse or coenosteal lamellae, or concentric laminae. These 'laminae' are merely aligned and periodically precipitated tabulae which form concentric bands and are not laminae as recognised and defined in this work. Since these aligned fibrous tabulae are generally found in the older, outer parts of the skeleton, Hudson described the skeleton as having an 'axial' and 'peripheral' reticulum.

In Hudson's (1954b)original description of Shuqraia, he allocated it to the family Stromatoporinidae. The type genus of this family, *Stromatoporina* was redescribed by Hudson (1955a), and he felt that *Shuqraia* could no longer be included in the family. In 1956, he placed *Shuqraia* in the Milleporidiidae, due to the presence of ancestral 'zooidal tubes'(Dehorne) or 'autotubes'(Hudson). The new-found spiculation indicates that it is a member of the Milleporellidae, within the order Axinellida.

Shuqraia zuffardi (Wells, 1943)

Plate 29, figs.a-i. Plate 39.

v . 1935 *Milleporidium somaliense* Zuffardi-Comerci, 1932; Thomas p.37-38 Plate 5, fig.5 (T.S.)
1943 *Milleporidium zuffardi* Wells p.51-52 Plate 9, figs.1,3,6,9. (T.S.)
v . 1954b *Shuqraia zuffardi* (Wells, 1943), Hudson p.218 Plate VII,fig.7;Plate VIII, fig.1a and b. (T.S.)
v . 1954b *Shuqraia heybroeki* Hudson p.214-215 Plate VI, fig.1-6 (T.S.)
v . 1954b *Shuqraia arabica* Hudson p.214-215 Plate VII, fig.3a-c; Text-fig.2 (T.S.)
v . 1954b *Shuqraia cf. Stromatopora douvillei* Hudson p.218 Plate VII, figs.2,6 (W.S.,T.S.)
v . 1955a *Shuqraia zuffardi* (Wells, 1943); Hudson p.237-238 Plate XXIII, fig.2 (T.S.)

1955b *Shuqraia arabica* Hudson, 1954; p.316 (no illustrations)

v . (1958) *Shuqraia hethira* Hudson (Invalid name; named in collection)

1969 *Shuqraia heybroeki* Hudson, 1954; Turnsek p.80-81. Plate 7-8. (T.S.)

Diagnosis:

Shuqraia with fibrous tabulae in the peripheral (i.e.older) areas of the skeleton. Rare tabulate oscula and no astrorhizae. Primary spicule framework of styles (max.80 µm long, 7 µm wide) in a loosely-packed, plumose arrangement. Orthogonal to fascicular fibrous primary calcareous skeleton. Secondary epitaxial calcareous skeleton often appears as concentric bands to form latilaminae, but may almost fully fill the primary skeletal pore-spaces leaving only aquiferous system canals. Pillar diameter is 80- 130 µm . Fibrous aligned tabulae, up to 130 µm thick, often arranged in groups to form latilaminar bands. Dendroid or possibly fasciculate gross morphology.

Holotype:

Amer. Mus. Nat. Hist. 252900-259001. Wells, 1943 . Plate 5, fig.5 . Mt. Aiya Makkeran, Harrar Province, Ethiopia. Upper Jurassic (Upper Oxfordian to Lower Kimmeridgian).

Material examined:

H4516 Ras Sharwain range, Qishn, South Yemen, Arabia. H4481-97 and F26/18-35, H 4516, H4517, H4769 ,H 4502, H 4505 Shuqra, South Yemen, Arabia. H4569, H4573, H4614, H4691 Alam Abyadah, North Yemen, Arabia. H 4508-15. Mahra, South Yemen, Arabia. Lower Kimmeridgian.

Specimen 29 (thin-sections 2-5 and ?6, and two branch segments) Geological Laboratory of the Sorbonne, Paris. Upper Jurassic, (Upper Oxfordian to Lower Kimmeridgian) of Guelb-el-Anze, S.Tunisia.

H 5034a 85/60/8, 85/60/9, 85/61/3, 85/61/4, 85/61/9, 85/68/11 Makhtesh Hagadol, Israel. Lower Kimmeridgian. H 3635-6 Bihendula, Somalia. Upper Jurassic.

Description:

Dendroid gross morphology (3-25 mm diameter), often with rounded terminations and showing a surface meshwork, which may show a vermiform or tubular arrangement. Branches often formed at 45^{o} by bifurcation. The axial reticulum is composed of dominant pillars forming sinuous tubules

PLATE 29 *Shuqraia zuffardi* (Wells, 1943)

Figure a: Dendroid and nodular gross morphology. H 3635-6. Bihenelula, Somalia. Upper Jurassic.
Scale bars = 1mm.

Figure b: Complete development of secondary skeleton except for astrorhizal canal traces. H 4508a. Mahra, South Yemen, Arabia. Lower Kimmeridgian.
Scale bar = 500 µm.

Figure c: Growing tip of branch showing aligned tabulae in peripheral area . H 4485. Shuqra, South Yemen, Arabia. Lower Kimmeridgian.
Scale bar = 1mm.

Figure d: Arrangement of radial elements and secondary skeletal development in outer area. H 4515. Mahra, South Yemen, Arabia. Lower Kimmeridgian.
Scale bar = 1mm.

Figure e: Transverse section showing band of secondary skeleton development and fibrous tabulae to form latilaminae. H 4481. Shuqra, South Yemen, Arabia. Lower Kimmeridgian.
Scale bar = 1mm.

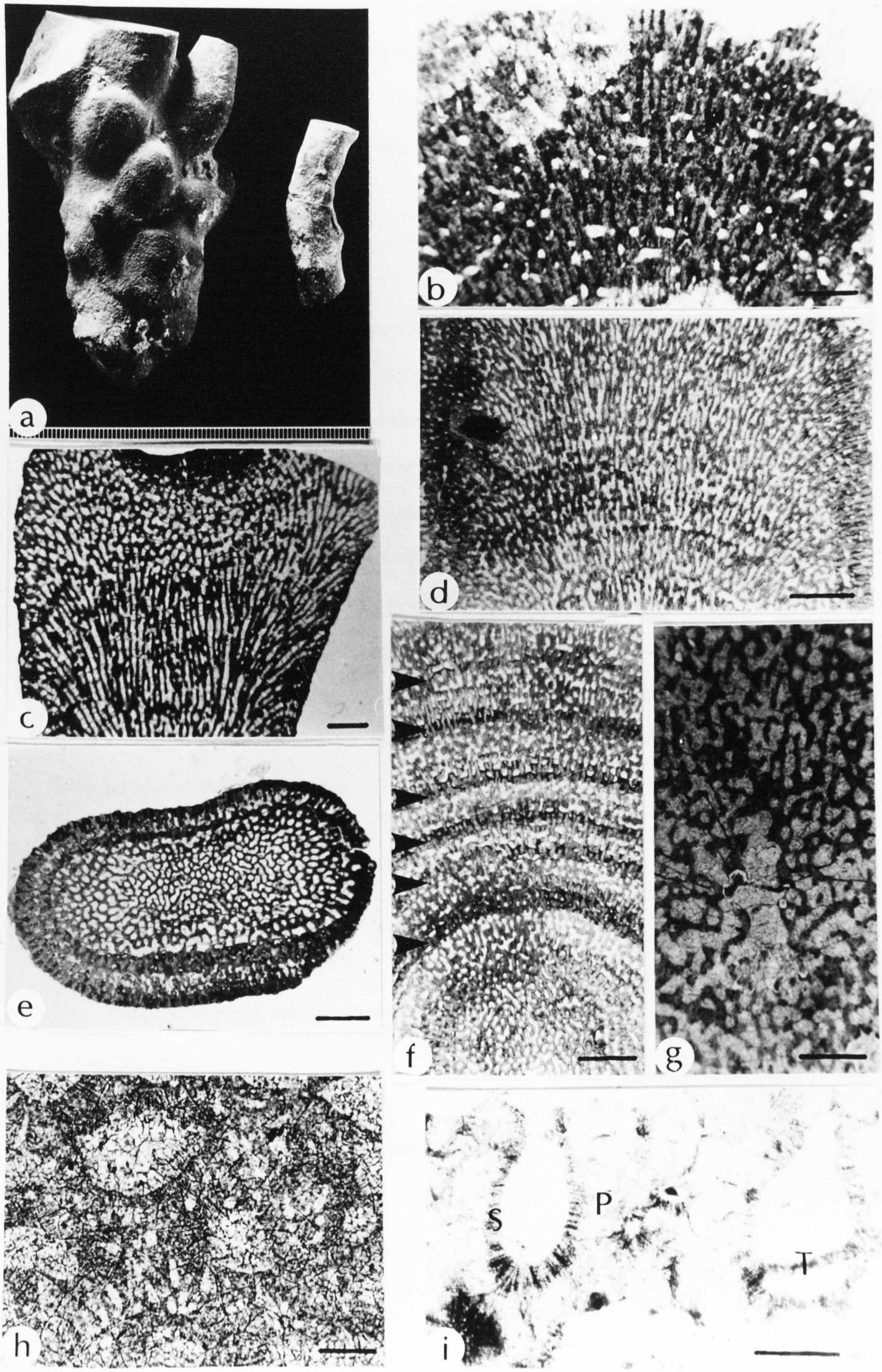
Figure f: longitudinal section showing secondary skeleton development and fibrous tabulae to form latilaminae. H 4515. Mahra, South Yemen, Arabia. Lower Kimmeridgian.
Scale bar = 1mm.

Figure g: Tabulate oscular tube. H 4505. Shuqra, South Yemen, Arabia. Lower Kimmeridgian.
Scale bar = 500 µm.

Figure h: Calcite pseudomorphs of club-shaped styles. 85/61/3. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar =100 µm.

Figure i: Orthogonal to fascicular fibrous microstructure (P) and secondary calcareous skeleton (ST) with fibrous tabulae (T). H 5034a. Makhtesh Hagadol, Israel. Lower Kimmeridgian.
Scale bar = 100 µm.

PLATE 29 *Shugraia zuffardi* (Wells) 1943



(90-190 µm diameter), initially parallel to the branch axis and then normal to it. In tangential section these appear rounded or polygonal. Few, aligned tabulae in the axial reticulum. Secondary calcareous skeleton often present in the outer reticulum, forming concentic zonation, producing latilaminae 1-3 mm apart. Secondary tissue present as fibrous epitaxial coating around pillars, continuous with thickened tabulae. Excurrent canals are common , but do not seem radially arranged to form recognisable astrorhizae. Tabulate oscula are up to 560 µm diameter. Excurrent canals do not appear to be tabulate.

Remarks:

The medial zone within the skeletal elements decribed by Hudson (1954b p.216) for *S.heybroeki,* represents the alignment of centres of calcification. Forms allocated to *S.heybroeki* differ from other specimens by the thinness of the skeletal branches. The reticulum pattern is not, as noted by Hudson (1954b p.216), significantly finer than *S.zuffardi.* This difference is not felt sufficient to retain the taxon; *S.heybroeki* may represent an immature population or ecophenotypic variation, as specimens allocated to this species show little secondary calcareous skeletal development, which has been shown to form in the outer i.e. older parts of the skeletal branches. *S.arabica* Hudson probably represents a more mature population of this species, as shown by the larger diameter of the skeletal branches and the degree of secondary calcareous skeleton formation.

Hudson only noted the formation of latilaminae (aligned fibrous tabulae) in *S.arabica.* It has now been noted in all the above forms.

Shuqraia n.sp.

Plate 30, figs.a-f.

v * 1955 *Shuqraia cf. arabica* Hudson p.238 Plate XXII, figs.4,5 (T.S.)

Diagnosis:

Shuqraia with stacked, common astrorhizae.

Type material:

Holotype: H 4639

PLATE 30 *Shuqraia n. sp.*

All from Alam Abaydah, North Yemen, Arabia. (Upper Oxfordian to Lower Kimmeridgian)

Figure a: Longitudinal section showing radial element arrangement and secondary skeleton development in outer areas. H 4639a.
Scale bar = 1mm.

Figure b: Longitudinal section showing stacked astrorhizal system. H 4639b.
Scale bar = 1mm.

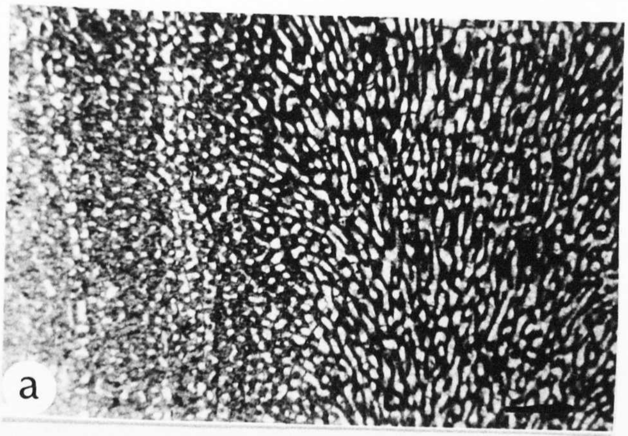
Figure c: Latilaminae formed by secondary skeleton and fibrous tabular development . H 4639b.
Scale bar = 1mm.

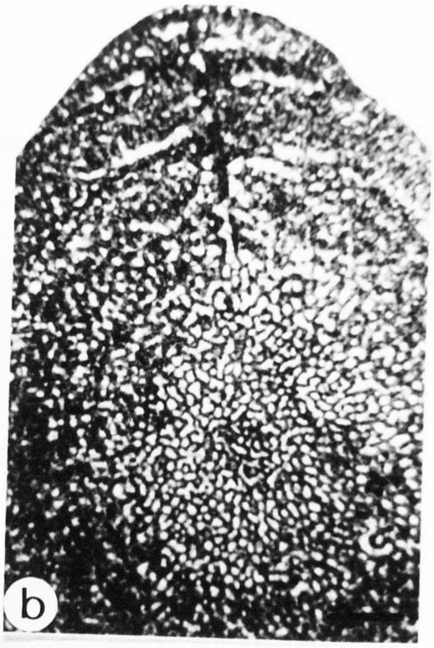
Figure d: Transverse section through confluent astrorhizae. H 4570.
Scale bar = 1mm.

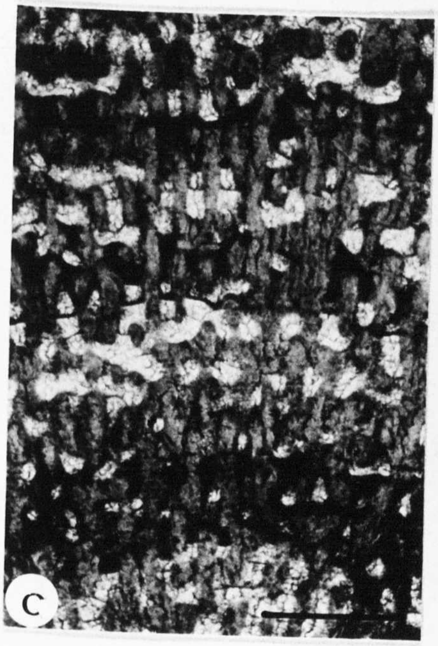
Figure e: Detail of fascicular fibrous primary skeleton **(P)** secondary epitaxial skeleton (S) and fibrous tabulae (T) . H 4581a.
Scale bar = 100 µm.

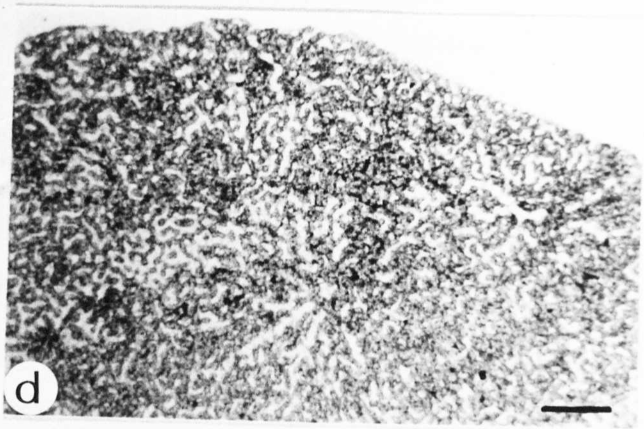
Figure f: Detail of fibrous tabulae (T) and secondary epitaxial skeleton (S). H 4581a.
Scale bar = 100 µm.

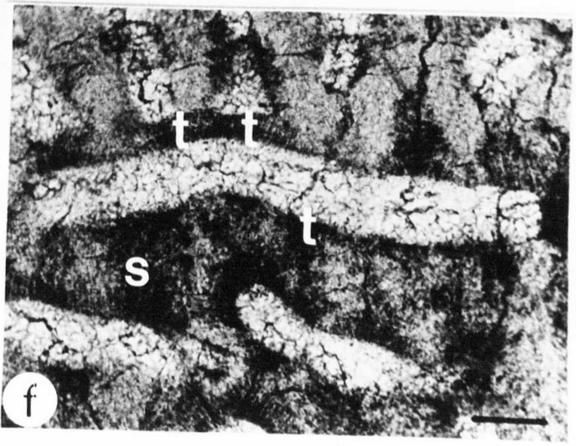
PLATE 30 *Shuqraia n.sp.* (Hudson)











Rachel A.Wood

Paratypes: H 4544, 4561-3, 4567, 4570, 4581, 4639-40.

Alam Abaydah, North Yemen, Arabia.

Upper Jurassic (Upper Oxfordian to Lower Kimmeridgian)

Description:

Dendroid gross morphology (10-30mm diameter, 15 mm average), often with rounded terminations and showing a surface meshwork, which may show a vermiform or tubular arrangement, with common astrorhizae up to 6mm radius, generally 4mm. No mamelons are present. Branches often formed at 45° by bifurcation. The axial reticulum is composed of dominant pillars (80-160 µm diameter) forming sinuous tubules (120-200 µm diameter), initially parallel to the branch axis and then normal to it. In tangential section these appear rounded or polygonal. Few, thin aligned tabulae in the axial reticulum. Secondary calcareous skeleton often present in the outer reticulum, developing peridically to form concentric zones of grouped tabulae, producing latilaminae 1-4mm apart. Secondary tissue present as fibrous epitaxial coating around pillars, which is continuous with thickened tabulae, up to 300 µm thick. Tabulate oscula are up to 300 µm diameter, with radially arranged astrorhizal canals. Excurrent canals do not appear to be tabulate.

Remarks:

No spicules have been noted as yet in these specimens.

The possession of a primary and secondary orthogonal to fascicular fibrous calcareous skeleton of regular columns where pillar diameter is 80- 160 µm, which form tubules proximally parallel to the branch axis and distally normal to it, indicates this form to be a member of the genus *Shuqraia.* The presence of astrorhizae, not found in other species of *Shuqraia* , suggests specific status for these specimens.

In the plate caption for Plate XXII, Fig.4, Hudson (1955) mistakenly ascribed this species to the fictitious genus *Dehornea.*

Promillepora Dehorne, 1920

Diagnosis:

Milleporellidae with a primary spicule framework of short styles (maximum length 50 µm, 12 µm width) in a loose, plumose arrangement. Fascicular fibrous primary calcareous skeleton with pillars and pillar-lamellae (diameter 30- 110µm), forming an irregular meshwork in tangential section. In mature parts a secondary epitaxial skeleton and fibrous aligned tabulae up 10-90 µm thick, which form latilaminae. Abundant, radially extensive tabulate oscula (140-280 µm) in outer mature areas, with no mamelons or astrorhizae. Gross morphology tends to be dendroid.

Type species (by monotypy) :

Promillepora pervinquieri Dehorne 1920 Upper Jurassic (Upper Oxfordian to Lower Kimmeridgian). Tatahouine, S.Tunisia.

Distribution:

Middle East (Israel,) Tunisia

Upper Jurassic (Upper Oxfordian to Lower Kimmeridgian)

Remarks:

This genus shows many constructional similarities to *Shuqraia*, as noted by Hudson. *Promillepora* however, as indicated in its name, was thought to be an ancestor of the Recent hydrozoan *Millepora*, whose tabulate zooidal tubes resemble the abundant tabulate oscula.of *Promillepora* . They both possess a differentiated reticulum; a juvenile part with a primary calcareous skeleton only and relatively thin, widely spaced tabulae, and an outer mature part with considerable secondary epitaxial skeletal growth and fibrous aligned tabulae. However this appears to be a feature of many dendroid calcified sponges including *Bugundia wetzeli* and *Steineria somaliensis.* This may be a function of living tissue surface:volume criteria, where individuals possessed only a thin veneer of tissue.

Hudson described the secondary tabulae as transverse lamellae and the oscular tubes as autotubes.

Promillepora pervinquieri Dehorne, 1920

Plate 31, figs. a-i

p 1918 *Stromatopora douvillei* Dehorne p. 219

1920 *Stromatopora douvillei* Dehorne, 1918; Dehorne p.20 Plate III, figs.5,6; Plate V, figs.1-5; Plate X, fig.9; Plate XIV, fig.1 (G.S. T.S.)

? 1920 *Promillepora pervinquieri* Dehorne p.97,98, 100 Plate 8, fig.12 (W.S.)

1928 *Milleporidium Douvillei* (Dehorne, 1918), Kühn p.87

? 1931 *Milleporidium arrabidense* Zuffardi-Comerci p.69 Plate 2, fig.5 (T.S.)

1932 *Stromatopora douvillei* Dehorne, 1918; Steiner p. 186

1932 *Promillepora pervinquieri* Dehorne, 1920; Kühn p. 34

? 1938 *Stromatopora douvillei* Dehorne, 1918; Zuffardi-Comerci p.6 Plate 1, figs.3,4 (T.S.)

? 1943 *Stromatopora douvillei* Dehorne, 1918; Wells p.50 Plate 9, fig.5 (T.S.)

? 1952 *Stromatoporina douvillei* (Dehorne, 1918), Lecompte p.23 (no illustrations)

v 1954a *Stromatoporina (Shuqraia?)douvillei* (Dehorne, 1918); Hudson p.228 Plate XXIV, fig.2 (T.S.)

v 1954b *Shuqraia cf. Stromatopora douvillei* (Dehorne, 1918), Hudson p.218 Plate VII, figs.2,6 (T.S.)

v 1955 *Shuqraia cf. arabica* Hudson p.238 Plate XXII, figs.4,5 (T.S.)

1955b *Stromatopora douvillei* Dehorne, 1918; Hudson

v 1956 *Promillepora douvillei* (Dehorne, 1918), Hudson p.722 (no illustration)

v 1956 *Promillepora pervinquieri* Dehorne, 1920; Hudson p.720 Plate 76, figs. 1-6 (T.S.)

v . 1956 *Promillepora kurnubi* Hudson p.721 Plate 77, 3-11; text-fig.6. (T.S.)

v . p 1956 *Steineria somaliensis* Hudson p.727-28 Plate 77, figs.1,2 (T.S.).

Diagnosis:

Promillepora often with common straight tabulate oscula 140-300 μm in diameter.

Type material:

Lectotype (chosen by Lecompte 1952 p.23). Specimen 29/1 in Stromatoporoid collection, Sorbonne. (Thin section figured as *Stromatopora douvillei* by Dehorne 1920 Plate 9, fig.9 and Hudson 1955b, text-fig.1). From *Stromatopora douvillei* beds, Upper Jurassic of Guelb-el-Anze, S.Tunisia.

Second, invalid holotype chosen by Hudson 1956 is now lost. Specimen figured by Dehorne 1920, Plate 8, fig.12, and sections cut from it. Formerly in the Pervinquiere collection, Geological Laboratory, Sorbonne, Paris.

Material studied:

H 4896-98,H 4900-4906, H4899 and 85/66/1, 85/64/7, 85/64/12, 85/72/12 from Makhtesh Hethira, Israel. Upper Jurassic (Lower Kimmeridgian)

PLATE 31 *Promillepora pervinquieri* Dehorne, 1920

Makhtesh Hagadol, Israel. Lower Kimmeridgian.

Figure a: Dendroid gross morphology and smooth surface. H 4896.
Scale bars = 1mm

Figure b: Longitudinal section showing tabulate oscular tubes and secondary skeletal development forming latilaminae (arrowed) . H 4898a.
Scale bar = 1mm.

Figure c: Transverse section showing oscula. H 4901c.
Scale bar = 1mm.

Figure d: Longitudinal section showing axial reticulum. H 4900a.
Scale bar = 1mm.

Figure e: Longitudinal section showing aligned tabulae in axial reticulum and secondary skeletal development. H 4901a.
Scale bar = 1mm.

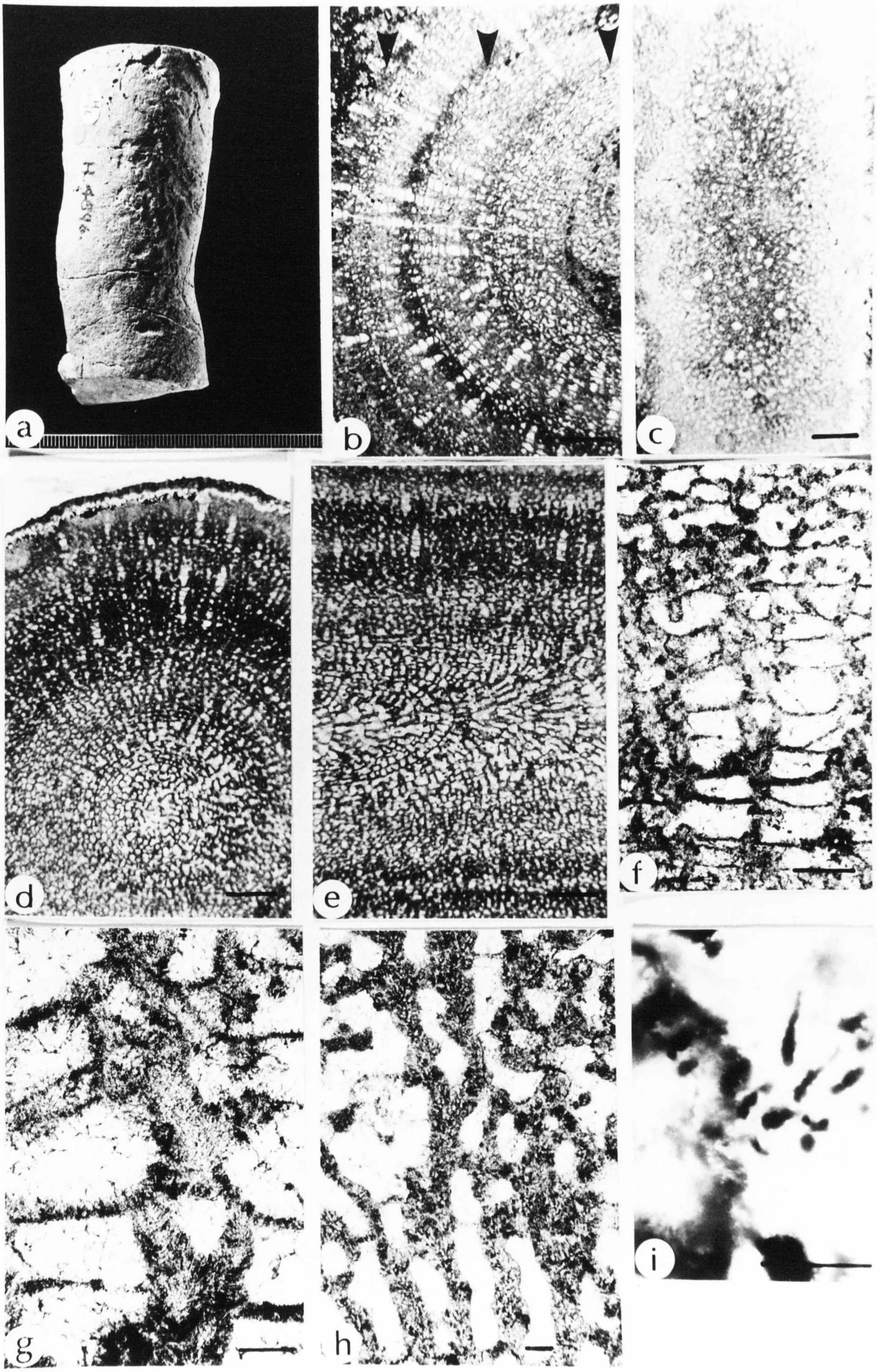
Figure f: Detail of Figure e showing tabulate oscular tubes. H 4901a.
Scale bar - 200 µm.

Figure g: Detail of fascicular fibrous microstructure and fibrous tabulae. H 4901a.
Scale bar = 100 µm.

Figure h: Fascicular fibrous columns with ?spicule ghosts. H 4898a.
Scale bar = 100µm.

Figure i: Pyrite spicule pseudomorphs of club-shaped styles. H 4898a.
Scale bar = 100 µm.

PLATE 31 *Promillepora pervinquieri* Dehorne 1920



Description:

Club-shaped styles (maximum length 50 µm, 12 µm width) in a loose plumose arrangement. Dendroid gross morphology. Surface shows a fine meshwork of elements, sometimes with oscular openings. Dendroid gross morphology (10-40mm diameter, 20 mm average), often with rounded terminations and showing a suface meshwork, which may show a vermiform or tubular arrangement with many oscular openings. No astrorhizae and mamelons are present. The axial reticulum (5-15mm diameter) is composed of pillars and pillar-lamellae (30 -90µm diameter) forming irregular tubules (100-120- µm diameter), initially parallel to the branch axis and then normal to it. In tangential section these appear rounded or polygonal. Few, thin aligned tabulae in the axial reticulum. Secondary calcareous skeleton often present in the outer reticulum, developing peridically to form concentric zones of grouped tabulae, producing latilaminae 1-4mm apart. Tabulae are generally 100 µm apart. Secondary tissue present as fibrous epitaxial coating around pillars, which is continuous with thickened tabulae, is up to 55 µm thick, making the secondary skeletal pillar diameter 55-110 µm. Straight tabulate oscula , of constant width are up tpo300 µm diameter, and spaced 1.2mm apart and up to 5mm long, and are found in the peripheral, mature reticulum.

Distribution:

Tunisia and Middle East (Israel)

Upper Jurassic (Upper Oxfordian to Lower Kimmeridgian)

Remarks:

No topotypes are available which can definitely be allocated to the species. Hudson used Dehorne's original description for his diagnosis and description of the species. He supplemented this with material from Israel, collected from "beds of the same age and belonging to the Tethyan province of sedimentation".

Hudson noted that *P.kurnubi, P.pervinquieri* and *P.douvillei.* were closely related, and that there were undescribed morphological linking forms between *P.pervinquieri* and *P.douvillei.* The present author has only had access to the material from the Middle East (Israel) and these specimens are found to be conspecific. The two size groups of the tabulate oscula, noted by Hudson in *P.pervinquieri*, have not been noted by the present author.

There is considerable variability in the amount of secondary epitaxial skeleton and in the distribution of the oscula, like that in *Shuqraia*. The two size categories of oscula noted by Hudson ("autotubes") have not been distinguished.

Steineria Hudson, 1956

1920 *Romanactis* Munier-Chalmas nom. nud., MS in coll. Dehorne p.88

Diagnosis:

Milleporellidae in which the short pillars are of fascicular fibrous microstructure and are up to 300 µm in diameter. Secondary epitaxial skeleton and aligned tabulae in mature areas forming latilaminae. Outer, mature areas of skeleton dominated by abundant tabulate astrorhizal canals up 560 µm diameter. Dendroid, often fasciculate gross morphology. Common, aligned tabulae.

Type species:

(chosen by Hudson 1956) *Stromatopora romanica* Dehorne, 1918 Dobrogea, Rumania. Upper Oxfordian to Lower Kimmeridgian (Upper Jurassic).

Distribution:

Europe (Rumania) and Middle East

Upper Jurassic

Remarks:

Hudson (1956) describes areas with and without secondary epitaxial thickening of the skeletal elements as coarse and fine-textured latilaminae respectively. The coarse latilaminae are sometimes termed concentric laminae.

No spicules have yet been found, but *Steineria* is constructionally extremely similar to *Promillepora* and *Shuqraia*. Hudson did not mention the diameter of the vertical elements , which are characteristically large in *Steineria.*

Steineria somaliensis (Zuffardi-Comerci, 1932)

Plate 32, figs.a-h

(1932)*Milleporidium somaliense* Zuffardi-Comerci p.70 text-figs.10,11 (T.S.)

1938 *Milleporidium somaliense* Zuffardi-Comerci, 1932; Zuffardi-Comerci p.7 Plate 1, figs. 5a and b (T.S.)

1943 *Milleporidium somaliense* Zuffardi-Comerci, 1932; Wells p.51 Plate 9, fig.8 (T.S.)

v . 1954b *Milleporidium somaliense* Zuffardi-Comerci, 1932; Hudson p.219 Plate 7, figs.1a -c; Plate 8, figs. 3a andb (T.S.)

v . 1955b *Milleporidium somaliense* Zuffardi-Comerci, 1932; Hudson p.5 (No illustrations)

v . 1956 *Steineria somaliensis* (Zuffardi-Comerci, 1932), Hudson p.727-728. (*Non* Plate 77, figs.1,2. (T.S.)).

Diagnosis:

Open textured reticulum, with primary calcareous skeleton of fascicular fibrous microstructure, sometimes orthogonal fibrous in axial, juvenile part, forming pillars up to 230 µm diameter, with a secondary epitaxial thickening up to 70 µm in the mature, outer parts, which may form latilaminae. Tabulate oscula up to 560 µm in diameter, sometimes extending the full radius of the skeletal branches. Dendroid gross morphology. Secondary calcareous skeleton may completely fill primary pore space except for the aquiferous system canals.

Type material:

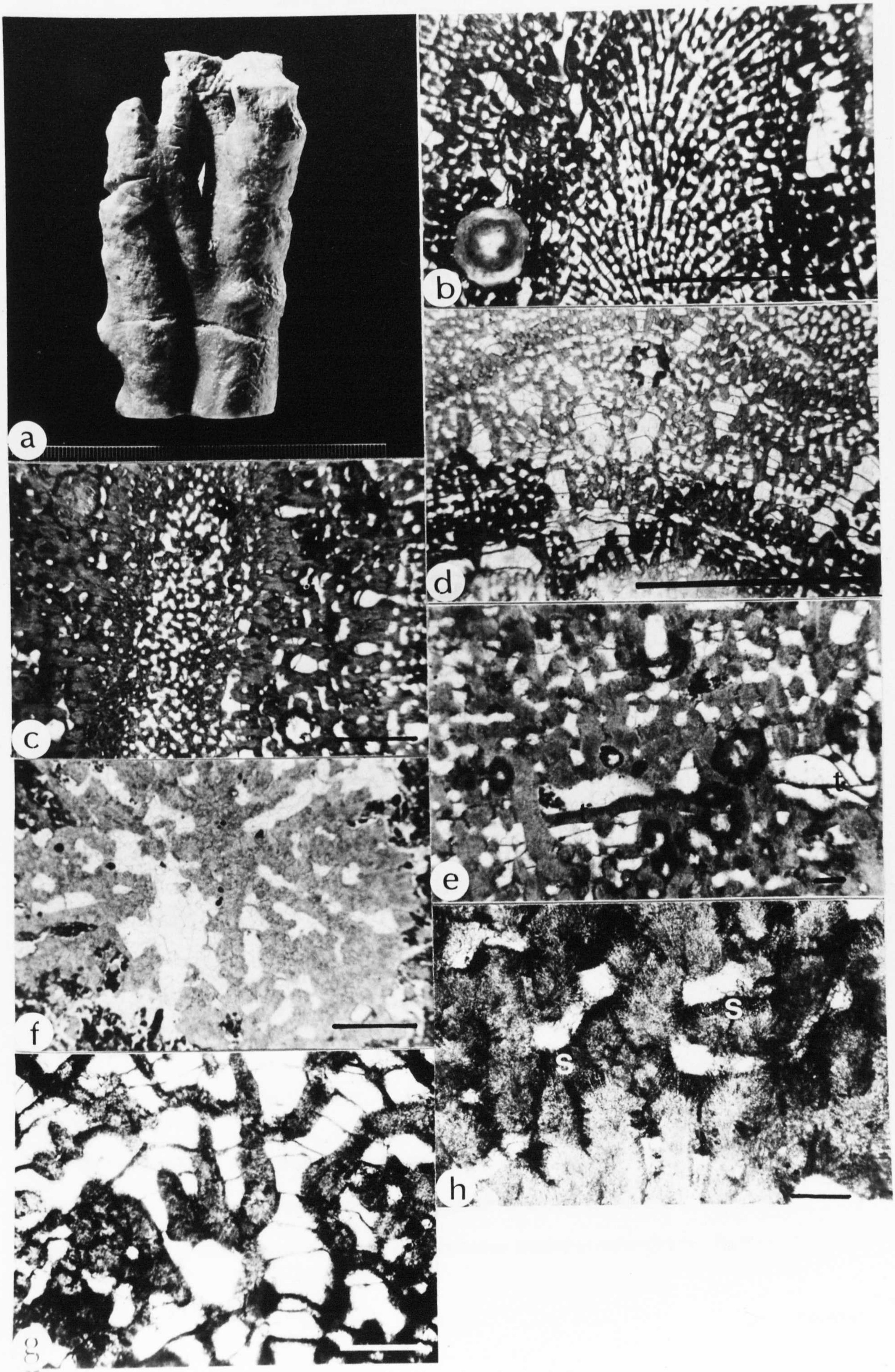
Original of Zuffardi-Comerci, 1932 p. 70 text-figs. 10,11. Collection unknown. Oolitico medio, bed b, of Bur Budulca, Uddur Plateau, southern Somalia. Upper Oxfordian to Lower Kimmeridgian (Upper Jurassic).

Other material:

H 4778,4973, 4995, 4996 Wadi Bakr, Haushi, Oman. Upper Jurassic.

not H 4896-4897, 4873, 4898, 5008-9, which are *Promillepora pervinquieri.* Makhtesh Hagadol, Israel. Lower Kimmeridgian.

PLATE 32 *Steineria somaliensis* (Hudson) 1956



Description:

Nodular or anastromosing, dendroid gross morphology, where the branch diameter may reach 5 cms. diameter. No surface markings are discernable. The axial reticulum (5-20 mm diameter) is composed of pillars and subordinate pillar-lamellae (55-140µm diameter) forming tubules (140-560-µm diameter), initially parallel to the branch axis and then normal to it. In tangential section these appear meandriform, rounded or polygonal. Common, thin aligned tabulae in the axial reticulum. Secondary calcareous skeleton often present in the outer reticulum, developing periodically to form concentric zones of grouped tabulae, producing latilaminae 1-4mm apart. Tabulae are generally 140 -280µm apart and up to 280 µm thick. Secondary tissue present as fibrous epitaxial coating around pillars, which is continuous with thickened tabulae, and is up to 70µm thick, makng the secondary skeletal pillar diameter 140-300µm. Abundant tabulate astrorhizal canals, dominant in the peripheral retuiculum, are 280-560 µm wide. In transverse section the aquiferous system is dominated by tabulate oscula, up to 1mm long.

Remarks:

Although no spicules have as yet been found in *Steineria somaliensis*, the arrangement of the skeletal elements, the presence of the secondary calcareous tissue forming latilaminae and the form of the tabulate aquiferous system , clearly shows affinity to the Milleporellidae.

Distribution:

Middle East (Arabia) Africa (Somalia)

Upper Jurassic (Upper Oxfordian to Lower Kimmeridgian)

Parastromatopora Yabe and Sugiyama, 1935

1935 *Epistromatopora* Yabe and Sugiyama p. 183.

Diagnosis:

Spicule framework of short styles (maximum 60 µm length, 18 µm width) forming a plumose arrangement. Primary fascicular fibrous calcareous skeleton of continuous columns forming irregular tubules (120-250 µm diameter). Pillar-lamellae absent or subordinate. Numerous aligned and closely spaced tabulae. Nodular, massive or encrusting gross morphology. Astrorhizae may or may not be present. No latilaminae or secondary skeletal development.

Parastromatopora libani Hudson, 1955

Plate 33, figs.a-e.

v . 1954c *Parastromatopora libani* Hudson p. 235 Plate 2, figs.1,3,4. (T.S.).

v . 1955 *Parastromatopora libani* Hudson, 1954; Hudson p.235 Plate XXIII, figs.3a -c; Plate XXIV, fig.3; Plate XXV, fig.2 (T.S.).

Diagnosis:

Parastromatopora with continuous radial, sometimes joined, columns of fascicular fibrous microstructure, forming tubules. No pillar-lamellae. Abundant , closely spaced and aligned tabulae. Tabulate astrorhizae with the same diameter canals as pillar spacing. Canals converge towards a central osculum, with no decrease in diameter.

Holotype:

B.M. (N.H.) H4789. Upper Jurassic (Middle Kimmeridgian), Couches jaunes inferieures, Toumatt Djezine, Tourmatt, Lebanon.

Other Material:

B.M. (N.H.) H4651a-d, Alam Abyadh, N. Yemen (Upper Oxfordian to Lower Kimmeridgian).
85/64/9 Makhtesh Hagadol, Israel. Lower Kimmeridgian

Description:

Club-shaped styles (60 µm length, 18 µm width) forming loose plumose arrangement. Massive, nodular gross morphology with open tubules and stellate astrorhizal systems. Tubular meshwork, and astrorhizae on the surface. The reticulum is composed of continuous columns (120-250 µm diameter) forming irregular tubules (160-250µm diameter). In tangential section these appear rounded or polygonal where the columns are often conjoined. Abundant, thin aligned tabulae

PLATE 33 *Parastromatopora libani* Hudson, 1955

Figure a: Longitudinal section showing tabulate interskeletal spaces. H 4651b. Alam Abyadh, North Yemen.Arabia. Upper Kimmeridgian.
Scale bar = 1mm.

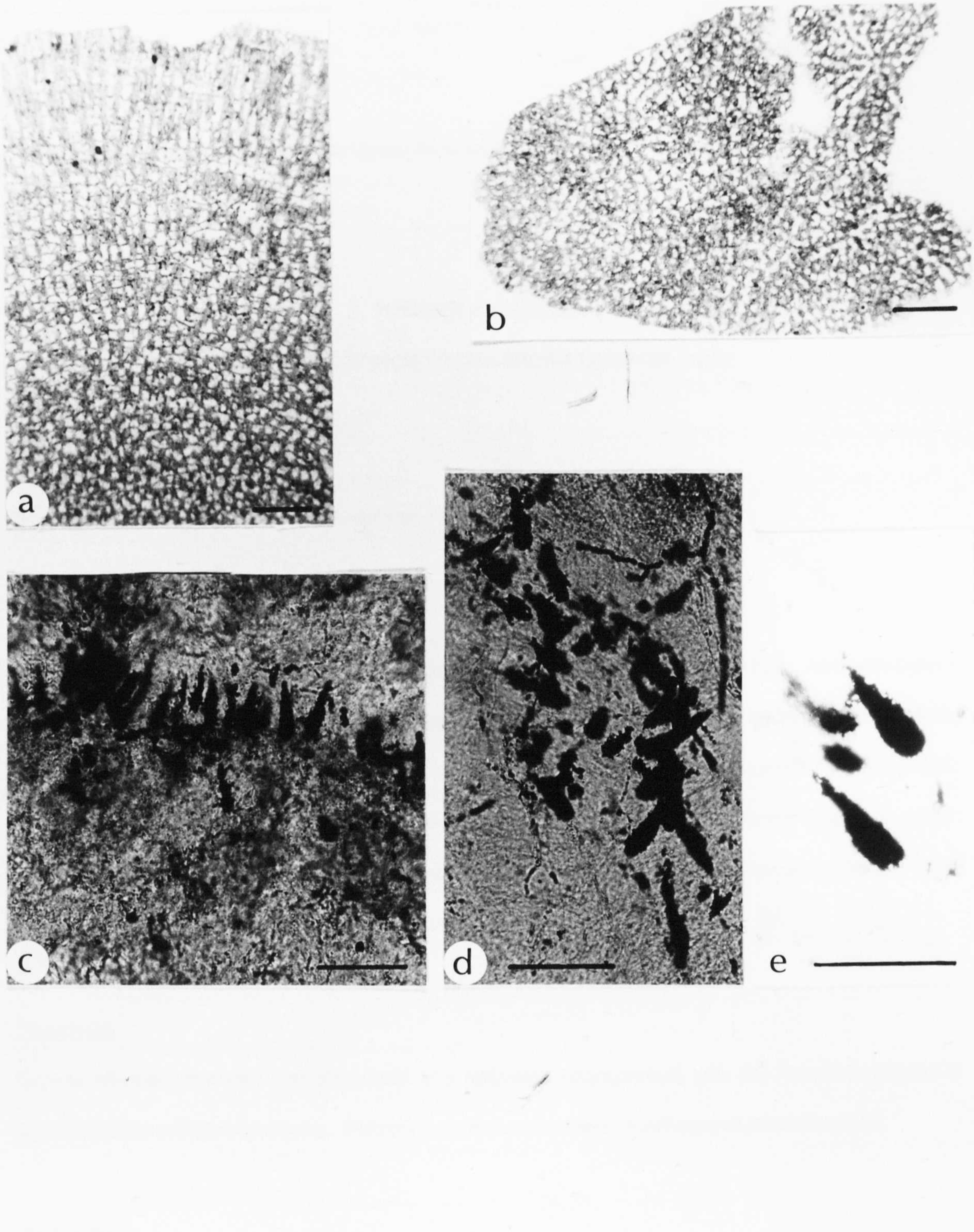
Figure b: Transverse section showing confluent astrorhizae. H 4651a. Alam Abyadh, North Yemen. Arabia. Upper Kimmeridgian.
Scale bar = 1mm.

Figure c: Pyrite pseudomorphs of club-shaped styles in isodactyal arrangement. H4789. Toumatt, Lebanon. Middle Kimmeridgian.
Scale bar = 100 µm.

Figure d: Plumose arrangement of spicule pseudomorphs. H4789. Toumatt, Lebanon. Middle Kimmeridgian.
Scale bar = 100 µm.

Figure e: Detail of spicule pseudomorphs. H4789. Toumatt, Lebanon. Middle Kimmeridgian.
Scale bar = 100 µm.

PLATE 33 *Parastromatopora libani* Hudson 1955



Rachel A.Wood

220-260 µm apart. No secondary calcareous skeleton. Common tabulate astrorhizae (6-10 mm apart), where the canal diameter is constant (160-250 µm), with tabulate oscula 160-200 µm.

Distribution:

Middle East (Lebanon, Israel)

Upper Jurassic (Lower Oxfordian to Upper Kimmeridgian)

?ORDER AXINELLIDA

FAMILY ACTINOSTROMARIIDAE HUDSON, 1955

Genera described:

Actinostromaria Haug, 1908 ; *Actostroma* Hudson, 1960.

Genera not described:

Actinostromina Germovsek, 1954; *Burgundostromaria* Turnsek, 1970; *Astrostylopsis* Germovsek,1954; *Desmopora* Yavorsky, 1947; *Disparistromaria* Schnorf-Steiner, 1960; *Stromatorhiza* Bakalow ,1966; *Sporadoporidium* Germovsek, 1954; *Coenostella* Turnsek ,1966; *Adriatella* Milan, 1969; *Tubuliella* Turnsek, 1966; *Siphostroma* Schnorf-Steiner, 1932; *Stromatostroma* Bakalow, 1910; *Paratubuliella* Dong, 1983; *Dongiastromaria* Dong ,1983; *Crimestroma* Yavorsky ,1947; *Tauripora* Yavorsky, 1947.

Diagnosis:

Spicule skeleton of styles and ?triaxines, in a reticulate arrangement, with the ?triaxines placed at the pillar/pillar-lamellae junctions. Primary calcareous skeleton of orthogonal microstructure.

Distribution:

Europe, Japan

Upper Jurassic-Lower Cretaceous

Remarks:

Hudson erected the superfamily Actinostromariicae in 1959. He defined this as "Stromatoporoids with radial or bilateral orthogonal or heterogonal fibrous trabeculae". No spicules had been found. Hudson divided the Actinostromariicae into two, possibly three families; the Actinostromariidae Hudson 1955, Siphostromaridae Steiner 1932 and ?Stromatorhizidae Steiner 1932. Germovsek (1954) named a fourth family, the Sporadoporiidae. Hudson (1956) thought this family invalid, members being incorporated into the Actinostromariidae. In 1966 Turnsek declared the Sporadoporiidae a valid family.

Spicules have only been found in two genera, *Actinostromaria* and *Actostroma*, within the family Actinostromariidae. The validity of the superfamily Actinostromariicae cannot be commented upon, but as existing familial diagnoses are based upon internal organisation, they are probably convergent features and insufficient criteria upon which to determine familial status. The placing of all other genera and species within this family is only conjecture, and is based upon their characteristics shared with these two spiculate forms. These are:

1) orthogonal microstructure of the calcareous skeleton;
2) Similar aquiferous system organisation;
3) Similar internal arrangement of the skeletal elements.

At present, these are the only characters available. As illustrated by *'A'.faringdonensis,* they are probably not synapomorphies.

Position of the Actinostromariidae in the Porifera:

We have spicular information for the genera *Actinostromaria* and *Actostroma.* The best preserved spicules have been found in *Actinostromaria sp.*.

The spiculation of *Actinostromaria* is difficult to associate readily with any Recent or fossil sponge. Spicules have only been found as calcite pseudomorphs and the triaxine spicules show a similar morphology to those of some calcareans, so the possibility of the genus being a member of the Calcarea cannot be dismissed. The only possible affinity determined is with the Recent genus, *Syamon,* a member of the Axinellida. *Syamon* possess megascleres only, which are often triaxines.

The family Actinostromariidae is tentatively placed in the Axinellida, within the Tetractinomorpha.

A.faringdonensis was described by Thomas (1971) from the Faringdon Sponge beds (Upper

Aptian, Lower Greensand), and assigned to the Actinostromariidae. Although it possesses features thought diagnostic of Mesozoic 'stromatoporoids' (a laminar skeleton, astrorhizae and orthogonal microstructure of the calcareous skeleton) *'A'.faringdonensis* possesses calcareous triaxine spicules and is a calcarean, and is probably a synonym of *Synopella pulvinaria* Hinde (Plate 36, fig.a).

This is a good example of the polyphyly of Mesozoic "stromatoporoids" , where members of different poriferan taxonomic groupings show the same grade of development of the calcareous skeleton.

Actinostromaria Haug, 1909

Diagnosis:

Primary spicule framework of styles (maximum:100 µm length, 10 µm width) and ?triaxines (maximum:120 µm length, 20 µm width) forming an open reticulate arrangement of pillars and pillar lamellae with a primary orthogonal fibrous calcareous skeleton. Fibrous or granular tabulae. Astrorhizae may or may not be present.

Type species:

Actinostromaria stellata Dehorne, 1915 L' Ile Madame, France. Lower Cretaceous (Cenomanian).

Distribution:

Europe

Upper Jurassic - Upper Cretaceous (Kimmeridgian- Santonian)

Actinostromaria sp.

Plate 4, figs.a-d. Plate 34, figs.a-d

v . 1966 *Actinostromaria* sp. Turnšek p.400. Plate 8, fig.5,6. (T.S.)

Diagnosis:

As for genus. Astrorhizae are present.

Original material:

P 42, 53a,b , 76, 134, 142, 194 (D.Turnšek Collection) . Turnsek p.400. Plate 8, fig.5,6. Trnovski Gost, Slovenia, Yugoslavia. Upper Oxfordian.

Material studied:

H 5480, 84/66, 84/95, 84/135 Trnovski Gost, Slovenia, Yugoslavia. Upper Oxfordian.

Description:

Encrusting or massive gross morphology. Spicular skeleton of abundant club-shaped styles and rare triaxines, which appear to be placed at the pillar/pillar-lamellae junctions. Calcareous skeleton is composed of dominant pillars and pillar-lamellae of orthogonal fibrous microstructure, forming a meandriform mesh in tangential section. Astrorhizae are not common, but are up to 8 mm diameter, with branching and ramfying canals, which bifurcate and peter out into the meshwork of the skeleton. There is little expression of the aquiferous system in longitudinal section. No latilamination and secondary tissue is present.

Actostroma Hudson, 1958

Diagnosis:

Calcified demosponges with style and ?triaxine spicules forming a reticulate arrangement in plan view. Open reticulum of primary calcareous skeleton of orthogonal to fascicular fibrous skeleton precipitated upon spicule framework forming pillars and short pillar- lamellae. Skeletal elements (dominant pillars and pillar-lamellae) are 50-70 µm wide and 50-70 µm apart forming tubules. Abundant traces of non-tabulate oscula and astrorhizae. No tabulae . Latilaminae and mamelons are often present. Nodular, encrusting or dendroid gross morphology.

Type species:

Actostroma damesini Makhtesh Hagadol, Israel. Lower Kimmeridgian (Upper Jurassic)

Distribution:

Middle East (Israel)?China

Upper Jurassic (Lower Kimmeridgian)

PLATE 34 *Actinostromaria sp.* Turnšek, 1966

Light photomicrographs of thin-sections.

Trnovski Gost, Slovenia, Yugoslavia. Upper Oxfordian.

Figure a: Transverse section through massive form, encrusting a scleractinian coral.84/95.

Scale bar = 1cm.

Figure b: Longitudinal section showing dominant pillars and pillar-lamellae. 84/135

Scale bar = 1mm.

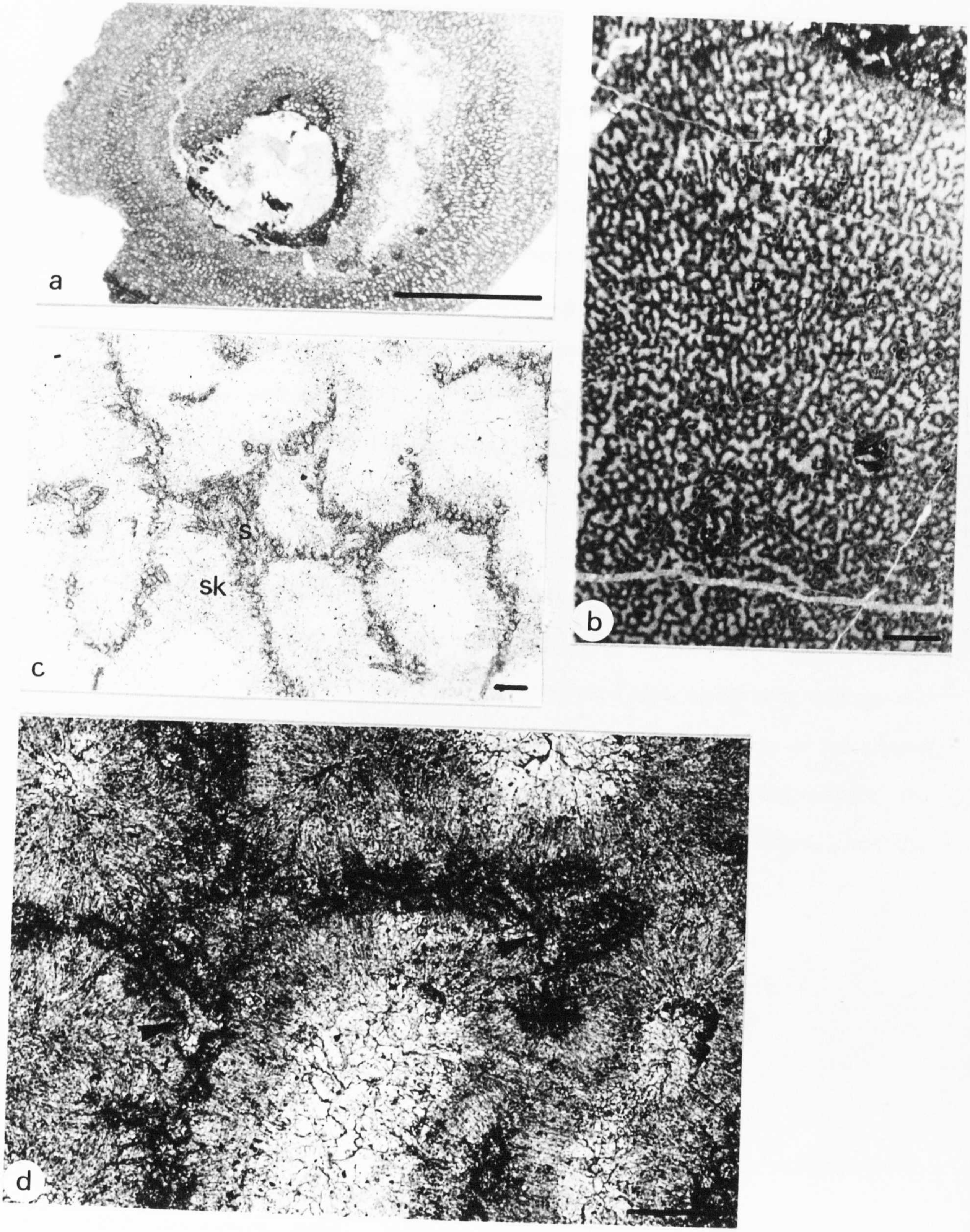
Figure c: Densely packed spicular skeleton **(s)** and orthogonal fibrous calcareous skeleton **(sk)** 84/66.

Scale bar = 100 µm.

Figure d: Detail of styles and ?triaxines (arrowed). 84/66.

Scale bar = 100 µm.

PLATE 34 *Actinostromaria sp.* Turnsek 1966



Remarks:

Spicules were not reported by Hudson (1958). They have been found by the present author in the type material, and in specimens from her own collection from Israel.

Hudson defined the genus *Actostroma* by the distribution of the oscula ("lateral astrotubes") and the lack of astrorhizae; he then described the form of the astrorhizae later in the paper. I suspect what Hudson meant was that the astrorhizae were not expressed as canals in radial section, as is the case in most other Mesozoic stromatoporoids. *Actostroma* clearly possesses astrorhizae, and this feature must be mentioned in the description. However, the spiculation and microstructural type of the skeleton justify the definition of a new genus, but not on the criteria used by Hudson.

Hudson described the astrorhizal system of *Actostroma* as having a six-fold symmetry (in two groups of three), in common with *Actinostromaria.* He postulated that this was a characteristic of the Actinostromariicae Hudson, and possibly of Mesozoic "stromatoporoids" in general. Examination of the astro-systems of this genus do not confirm the descriptions of Hudson. There is no regularity in the number or arrangement of the astrorhizal canals.

Hudson describes the calcareous skeleton microstructure as "orthogonal fibres which diverge slightly upwards; rarely clearly defined or constant". He named this microstructural type as heterogonal. His description of this microstructure is confirmed here, but the term heterogonal is not employed, to avoid unnecessary extra nomenclature. The microstructure of *Actostroma* illustrates the continuum between the fibrous microstructural types in calcified demosponges. The "broad composite axial strand or medial band" is probably the remains of micritised spicules or micritisation of the trabecular centres of the calcareous skeleton.

Actostroma damesini Hudson, 1958

Plate 35, figs.a-i. Plate 38, fig.a.

v * 1958 *Actostroma damesini* Hudson p.92-95. Plate15,figs.1,4; Plate 16,figs.3,5,8,10; Plate 17, figs.3-5,9; text-figs.1-3. (T.S.)

v . 1958 *Actostroma nasri* Hudson 1958 p.95 Plate 15.figs,2,3,5; Plate 16,figs.4,6,7,11-14; Plate 17, figs.1,10; text-figs.4,6.(T.S.)

v . 1958 *Actostroma kuhni* Hudson p.96 Plate 16, figs. 1.2.9; Plate 17, figs. 2, 6-8, 11.(W.S.,T.S.)

Diagnosis:

Primary spicule framework of styles and ?triaxines arranged intra-murally within the central area of the skeletal elements. Primary calcareous skeleton precipitated around the primary spicule framework, forming pillars and pillar-lamellae. Skeletal elements are 50-70 µm wide and 50-70 µm. apart. Encrusting, nodular, or massive gross morphology. Calcareous skeleton microstructure orthogonal to fascicular fibrous. Abundant astrorhizal canals and oscula are incorporated as the animal grows. Oscula may be tabulate.

Type material:

Holotype: H 4890, two pieces and thin sections a,b. Paratypes: H 4888, one piece and thin-sections a,b; H 4889, one piece and thin sections a,b,c. From the coral-stromatoporoid beds, Kumub Limestone, Makhtesh Hagadol, Israel. Lower Kimmeridgian.

Other material:

H 4893, two pieces and thin sections a,b. H 4891, two pieces and thin sections a,b. H 4892, two pieces and thin sections a,b. H 4887, two pieces and thin section, a. 85/29/4, 85/ 59/4, and 85/ 65/1 , 85/29.1 .Makhtesh Hagadol, Israel. Lower Kimmeridgian.

PLATE 35 *Actostroma damesini* Hudson, 1958

Makhtesh Hagadol, Israel. Lower Kimmeridgian.

Figure a: Nodular gross morphology and cut longitudinal sections showing latilaminae (arrowed). H 4890.
Scale bars = 1cm.

Figure b: Transverse section of astrorhizae. H 4891a.
Scale bar = 1mm.

Figure c: Longitudinal section showing pseudomorphs of club-shaped styles, partially micritised. H 4893a.
Scale bar = 100 µm.

Figure d: Transverse section, encrusting a calcareous algae. H 4891a.
Scale bar = 1cm.

Figure e: Longitudinal section. H 4893b.
Scale bar = 1cm.

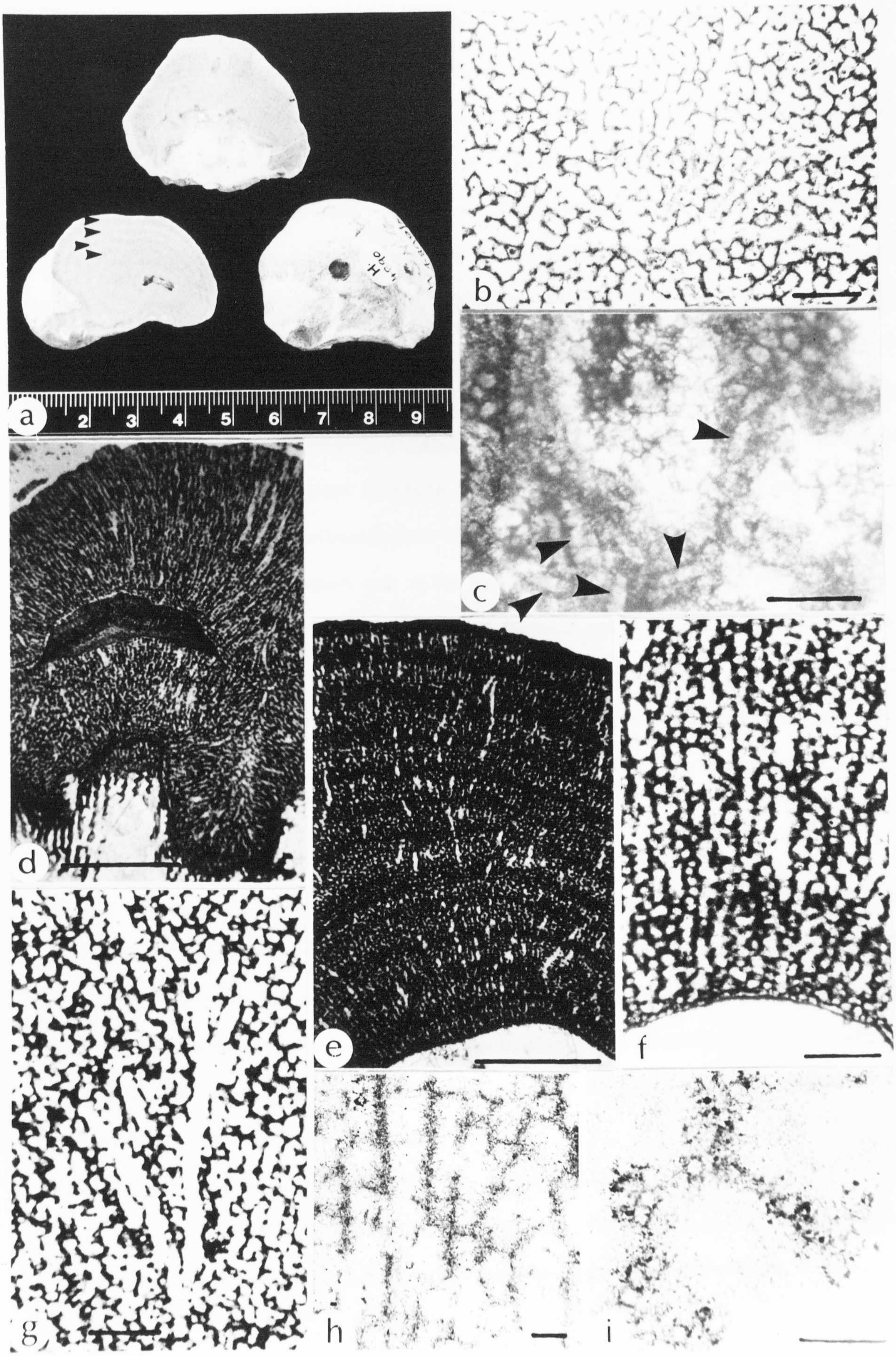
Figure f: Detail of oscular tubes .H 4893b.
Scale bar = 1mm.

Figure g: Non-tabulate oscular tube. H 4893b.
Scale bar = 1mm.

Figure h: Orthogonal fibrous microstructure. H 4893b.
Scale bar = 100 µm.

Figure i: Transverse section through partially micritised spicule pseudomorphs. H 4893b.
Scale bar = 100 µm.

PLATE 35 *Actostroma damesini* Hudson 1958



Description:

Spicule framework of styles (80 µm length, 10 µm width) and ?triaxines (at base: 100 µm length, 20 µm width) arranged intra-murally within the central area of the skeletal elements. Triaxines have been seen in side-view only and their three-dimensional configuration is uncertain. Nodular, encrusting or massive gross morphology. Skeletal arrangement of continuous dominant pillars (50-70 µm diameter), forming a "tubular" mesh in tangential section, and shorter transverse pillar-lamellae (50-70 µm diameter). Tubules are approximataely 70 µm apart. Astrorhizae are expressed as shallow, unwalled grooves on the skeletal surface and are abundant, small in total diameter relative to other Mesozoic stromatoporoids. Astrorhizal canals (100 µm diamater) commonly bifurcate. Astrorhizae (5-7mm diameter) are expressed as elongated and larger inter-skeletal spaces aligned along the astrorhizal traces, within the "tubular" ('chaetetid' like) arrangement of the skeletal elements in tangential section. These elongated areas continue in depth i.e. are continous through ontogeny to form elongate clear areas in radial section, representing generations of continuous astrorhizae. In radial section the oscula are common, and pronounced, following the growth axis of the skeleton perpendicular to the skeletal surface. Oscular tubes (100 µm diameter) are straight and unwalled and in communication with the open meshwork of the skeleton. Maximum length of oscula is 2.5mm, and they are spaced 0.3-1.00 mm apart. Tabulae may be present in astrorhizal canals. Mamelons and latilaminae may be present. Latilaminae are formed by an increase in the thicness of the skeletal elements.

Remarks:

Hudson did not report the presence of mamelons in this genus. They are here reported. No latilaminae were found in the specimens collected by the present author from the type locality. The presence of mamelons and latilaminae are therefore variable, and the latter are removed from the generic and specific diagnosis of Hudson. The placing of the astrorhizae correlates with the mamelons, but the traces do not always coincide with the summits of the mamelons; often, the astrorhizae are "displaced" onto the slopes or troughs.

Hudson described three species of *Actostroma; A.damesini* (type species), *A.nasri* and *A.kuhni.* He based their separation upon the form of the astrorhizae. From examination of the type material and specimens collected by the present author, there are not sufficient differences to warrant the existence of three species of this genus. Differences in astrorhizal development form a continuum and these three former 'species' are therefore resolved to one, *A.damesini.* The presence of latilaminae and the absense of mamelons are removed from the specific diagnosis. Latilaminae are formed by a thickening of the skeletal elements.

Spicules of a similar type and arrangement to *Actostroma* are found in the genus *Actinostromaria. Actinostromaria* also bears orthogonal microstructure and a similar form and density of the aquiferous units. This may indicate affinity.

INCERTAE ORDINIS

FAMILY A Nov. Fam.

Diagnosis:

Calcified demosponges which possess long, thin styles or tylostyles in a fibro-reticulate arrangement. Primary calcareous skeleton of irregular or orthogonal fibrous microstructure.

Assigned genera:

Actinostromarianina Lecompte, 1952

Remarks:

A new family is proposed based upon spicule type and arrangement which is unique among fossil calcified demosponges.

The placing of Nov.fam. A in the Porifera:

The simple spicule type of *Actinostromarianina lecompti,* (the only species within this family found with spicules) makes the placing of this genus in the Porifera difficult. However, the radial arrangement of the spicule framework is reminiscent of some members of the Axinellida, within the Tetractinomorpha, and so the family is tentatively placed in this order.

Actinostromarianina Lecompte, 1952

Diagnosis:

Calcified demosponges with long, thin styles, or tylostyles (180 µm length, 8 µm. width (maximum)) in a loose fibro-reticulate arrangement. A primary calcareous skeleton of irregular microstructure is arranged meniscus-like around the spicule framework forming pillars and pillar-lamellae. May or may not possess a secondary calcareous skeleton of orthogonal fibres, precipitated intermittently to form latilaminae. Filling tissue of aligned granular tabulae. Nodular or dendroid gross morphology.

Astrorhizae generally feebly developd or indistinguishable.

Type species:

Stromatopora milleporoides var romanica Dehorne, 1920. Dobrogea, Rumania. Upper Jurassic.

Distribution:

West and East Europe, Iraq.

Upper Jurassic (Upper Oxfordian)

Remarks:

Actinostromarianina was founded by Lecompte to describe two specimens from the collection of Dehorne. He named the new species *A.dehornae*, which he placed in the Palaeozoic family Actinostromidae Nicholson 1886. Lecompte defined *Actinostromarianina* by its dendroid gross morphology and by the presence of a central astrorhizal canal in the branch-axis. He does not mention microstructure of the calcareous skeleton or the presence of spicules. No specimens of this species have been examined. When Hudson (1955) described a new species of the genus, he modified the generic diagnosis. He stated that the presence of an axial astrorhizal canal is "not a common feature in Mesozoic stromatoporoids and does not occur in other stromatoporoids congeneric with *A.dehornae* . Hudson omitted this feature from his generic diagnosis, considering it to be of specific importance only. Hudson based his amended generic diagnosis upon the character of the internal arrangement of the calcareous skeleton; described as 'differentiated into a layered reticulum'.

Spicules have been found in holotype material of *Actinostromarianina lecompti* Hudson. The calcareous microstructure was undescribed by Lecompte, and incorrectly described by Hudson. The generic and species diagnosis are amended to include this new information.

Distribution:

Europe, N.W.Africa, ?U.S.A. (Texas)

Upper Jurassic

Actinostromarianina lecompti Hudson ,1955

Plate 1, figs. a-e

v * 1955 *Actinostromarianina lecompti* Hudson p.231PlatesXXII, fig.6; PLate XXIV, figs. 4-7; Plate XXV, figs.1,3; text-figs. 2-5.(W.S.,T.S.)

1969 *Actinostromarianina lecompti* Hudson, 1955; Milan p.179 Plate XVII, figs.4,5.(T.S.)

Diagnosis:

Long, thin styles or tylostyles (180 µm length, 8 µm width), arranged in a loose fibro-reticulate way, with a densely packed central axis. Primary calcareous skeleton of irregular microstructure precipitated in a meniscus-like way around the spicule framework, forming pillars and pillar-lamellae. Secondary calcareous skeleton in the form of an orthogonal fibrous rim, precipitated intermittantly to form latilaminae. Central area (juvenile) has no secondary skeleton. Granular, intermittantly aligned tabulae.

Holotype:

H 4580, 3 pieces and thin sections a,b,c. Alam Abyadh, N.Yemen. Upper Kimmeridgian (Upper Jurassic).

Other material:

H4564, H4565, H4568, H4571, H4572, H4574-79, H4582-90, H4592-H4613, H4616, H4619-21, H4623-31, H4633-38, H4642-43, H4645-49, H4653, H4655, H4561-72, H4674-90, H4692-4700. Alam Abyadh, Arabia. Upper Kimmeridgian. **Not** H4640 a-c.

Description:

Dendroid or sinuous gross morphology, where the diameter is up to 5 cm. Ajdacent branches may become joined for several centimetres. Central axial reticulum is up to 10 mm thick and bears elements with irregular microstructure only, 40 µm diameter, and with no tabulae. The axial condensation contains densley packed spicules with a thin irregular calcareous coating. In mature outer areas, the elements which bear a secondary fibrous sksleton are up to 100 µm wide and 140-200 µm apart. Astrorhizae are not well defined, as the diameter of the canals is the same as the inter-skeletal spaces. Latilaminae are 2.25 µm apart.

Distribution:

Upper Jurassic (Upper Oxfordian-Upper Kimmeridgian)

Iraq, ?Europe

Remarks:

Hudson failed to notice the spicules in his specimens and incorrectly described the microstructure of the calcareous skeleton. The species is here redefined.

The "differentiated reticulum" of Hudson corresponds to the latilaminar formation by the secondary orthogonal fibrous rim. The axial zone represents juvenile tissue with no orthogonal fibrous rim. Hudson described the axial zone as having been replaced by lime-mud i.e.micritised. This is here interpretated as the original irregular microstructure.

This species has also been described by Milan (1969), from Rumania. Specimens have not been examined , and allocation to this species cannot be confirmed.

Actinostromarianina? beauvaisi Flügel, 1969

1969 *Actinostromarianina? beauvaisi* Flügel p.127 Plate 1figs. 1-4 (T.S.)

Remarks:

Flügel describes a specimen from the Gosau beds of Austria with an "actinostromarid" internal arrangement, but with "circum-lamellar" microstructure. After the suggestion of Hudson, followed by Turnsek, that superfamilies should be defined by microstructure, Flügel suggests that this new form might constitiute a fourth Mesozoic "stromatoporoid" superfamily.

The "circum-lamellar" microstructure is likely to be a diagenetic pseudostructure of originally irregular or orthogonal fibrous microstructure. (See section 3.2.).

The photographs of Flügel show that this specimen bears "axial" astrorhizal canals. This species may be conspecific with *A.dehornae.*

Actinostromarianina praesalevensis (Zuffardi-Comerci, 1932)

Plate 36, figs. d,e.

v (1932)*Actinostroma praesalevensis* Zuffardi-Comerci p.38 Plate II, fig.6a and b. (T.S.)

1935 Actinostroma praesalevensis Zuffardi-Comerci, 1932; Yabe and Sugiyama

v 1943 *Actinostroma praesalevensis* Zuffardi-Comerci, 1932; Wells p.49 Plate 9,fig.4,7.(T.S., Holotype)

1955 *Actinostromarianina praesalevensis* (Zuffardi-Comerci, 1932); Hudson p.230 (no illustration)

Holotype:

Am.Nat.Hist.Mus. no. 25280. Zuffardi-Comerci, 1932. Plate 9, figs.4,7. Denaba, Harrar Province, Ethiopia. Upper Jurassic.

Description:

Nodular gross morphology. Primary calcareous skeleton of ?fascicular fibrous microstructure forming pillars and pillar-lamellae. Aligned tabulae. No recognisable astrorhizal systems.

Dimensions:

Diameter of pillars:	70-250 µm (average 170 µm)
Diameter (thickness) of pillar-lamellae:	50-70 µm
Spacing of pillars:	500-750 µm
Thickness of tabulae:	15-30 µm

PLATE 36 *'Actinostromaria' faringdonensis* Dighton-Thomas, 1971; *'Burgundia' tutcheri* and *'Burgundia' tutcheri var. huttonae* Kellaway and Smith, 1938; *Actinostromarianina praesalevensis* (Zuffardi-Comerici, 1932).

Figure a: Transverse section of astrorhizae of *'Actinostromaria' faringdonensis* (probable synonym of *Synopella pulvinaria* Hinde). H 4279c. Faringdon Sponge Beds. Lower Greensand. Scale bar = 1mm.

Figure b: *'Burgundia' tutcheri.* Transverse section showing calcareous triactine spicules (arrowed).
H 3397. Coombe Hill, Oxfordshire. Bathonian.
Scale bar = 200 µm.

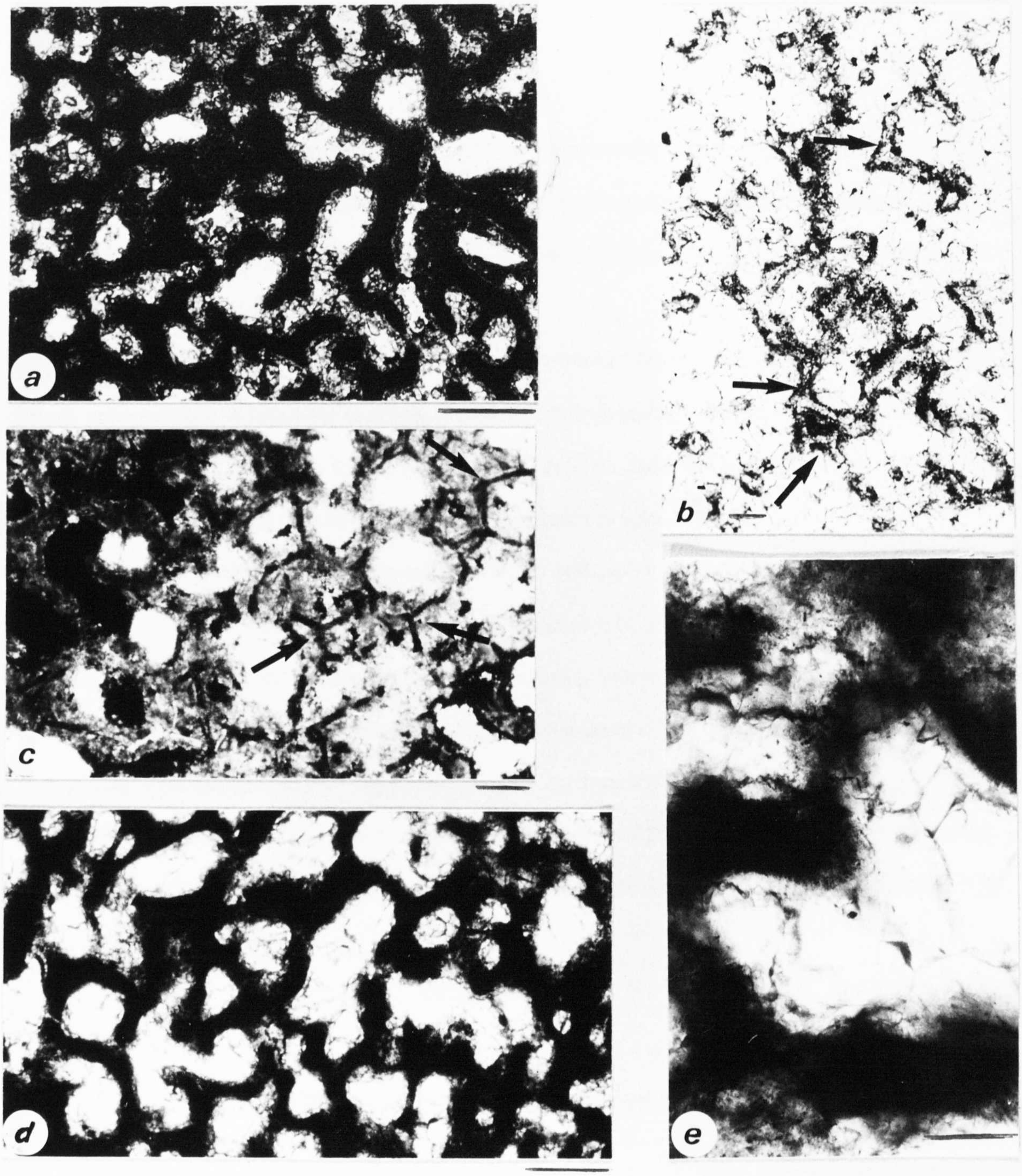
Figure c: *'Burgundia' tutcheri var. huttonae* (probable synonym of *Lymnoporella inclusa*) showing spicule pseudomorphs of triactine spicules (arrowed). H 3585. Dursley, Gloucestershire. Bathonian.
Scale bar = 200 µm.

Figures d, e: *Actinostromarianina praesalevensis* Amer. Mus.Nat. Hist. no. 25280. Denaba, Ethiopia. Upper Jurassic.

Figure d: Showing undifferentiated reticulum.
Scale bar = 200 µm.

Figure e: Detail of d showing ?irregular microstructure.
Scale bar = 100 µm.

PLATE 36 *'Actinostromaria' faringdonensis* Dighton-Thomas 1971 , *"Burgundia' tutcheri* and *'Burgundia' tutcheri var. Huttonae* Kellaway and Smith 1938, *Actinostromarianina praesalevensis* Zuffardi-Comerci 1931



Distribution:

Africa, (Somalia)

Upper Jurassic (Upper Oxfordian to Lower Kimmeridgian)

Remarks:

Hudson (1955) placed this species within *Actinostromarianina* due to its latilaminate reticulum, loosely marked and irregular pillar-lamellae and pillars, and "weakly" developed astrorhizae, despite the fact that this species is nodular rather than dendroid. It appears that he had not examined the holotype, but this is not clear.

Wells (1943) redescribed the holotype of Zuffardi-Comerci (1932). Yabe and Sugiyama (1935) merely recognised and listed the species. Thomas (1937) described new specimens of the species from a different site, but close to the type locality. Neither Zuffardi-Comerci , Wells or Hudson mentioned microstructural type of the calcareous skeleton or spiculation.

The holotype thin-sections have been cut too thickly sufficiently to study the microstructure of the calcareous skeleton. However, there is some indication of a fascicular fibrous structure. No spicules have been found. This specimen is doubtfully ascribed to *Actinostromarianina*. I do not feel able to give a formal diagnosis due to the bad preservation of this type material.

I have examined specimens ascribed to this species by Thomas (1935), from the Upper Jurassic of British Somaliland. These specimens conform to the descriptions of *Dehornella crustans* Hudson, 1960 (Family Milleporellidae), from the same area and are therefore not included in the species .

INCERTAE SEDIS

Stromatoporina tornquisti (Deninger,1906)

Plate 37, figs.a-c.

1901 *Stromatopora sp.* Tornquist p.19 (no illustrations)
v * 1906 *Stromatopora tornquisti* Deninger p.66 Plate 7, figs.7a and b. (T.S.)
Non 1910 *Stromatopora tornquisti* Deninger, 1906; Osimo p.289 Plate 1, figs.2,2a and b (T.S.)
1920 *Stromatopora tornquisti* Deninger, 1906; Dehorne p.82 (no illustrations)
1928a *Stromatopora tornquisti* Deninger, 1906; Kühn p.550 (no illustrations)
1928b *Stromatopora tornquisti* Deninger, 1906; Kühn p.90 (no illustrations)
1932 *Stromatopora tornquisti* Deninger, 1906; Steiner p.81 (no illustrations)

1935 *Stromatopora tornquisti* Deninger, 1906; Yabe and Sugiyama p.162 (no illustrations)

1955 *Stromatopora tornquisti* Deninger, 1906; Hudson p. 236

1958 *Stromatopora tornquisti* Deninger, 1906; Flügel p. 179

1960 *Stromatoporina tornquisti* (Deninger, 1906), Hudson p.185 Plate 27, figs.3-5; text-fig.1 (T.S.)

Holotype:

Sections a,b and c recorded by Deninger 1906. Collections of the University of Freiburg, Austria. ?Keuper (Tornquist 1901) or Bathonian (Deninger 1906) Monte Zirra, Nurra, N.W.Sardinia.

Desription:

No spicules have been noted. Reticulum is differentiated into laminae (40-60 µm diameter) and pillars(diameter 40-80 µm), which may or may not be limited to one inter-laminar space. Laminae are between 200-500 µm apart. Vertical elements are spaced 60-110 µm apart. Microstructure is poorly preserved, but appears to be irregular. Irregular, non-tabulate canals are present, which may be traces of an aquiferous filtration system. Canals are 100-170 µm in diameter. They do not form stellateor radially astrorhizae.

Remarks:

Kühn 1928a founded a new genus, *Stromatoporina* for Mesozoic stromatoporoids which had previously been allocated to the Palaeozoic genus *Stromatopora*. *Stromatopora tornquisti* was included in the new genus and made the type species. Other species included *S.choffati* Dehorne,1917, *S.costai* Osimo, 1911, *S.franchi* Osimo, 1911, *S.molluccana* Dehorne, 1918, *S.virgiloi* Osimo, 1911.

S.choffati, *S.costai* and *S.virgiloi* have since been allocated to *Dehornella* (Hudson 1960). (However, I have not examined the holotypes and cannot confirm this).

PLATE 37 *Stromatoporina tornquisti* (Deninger, 1906)

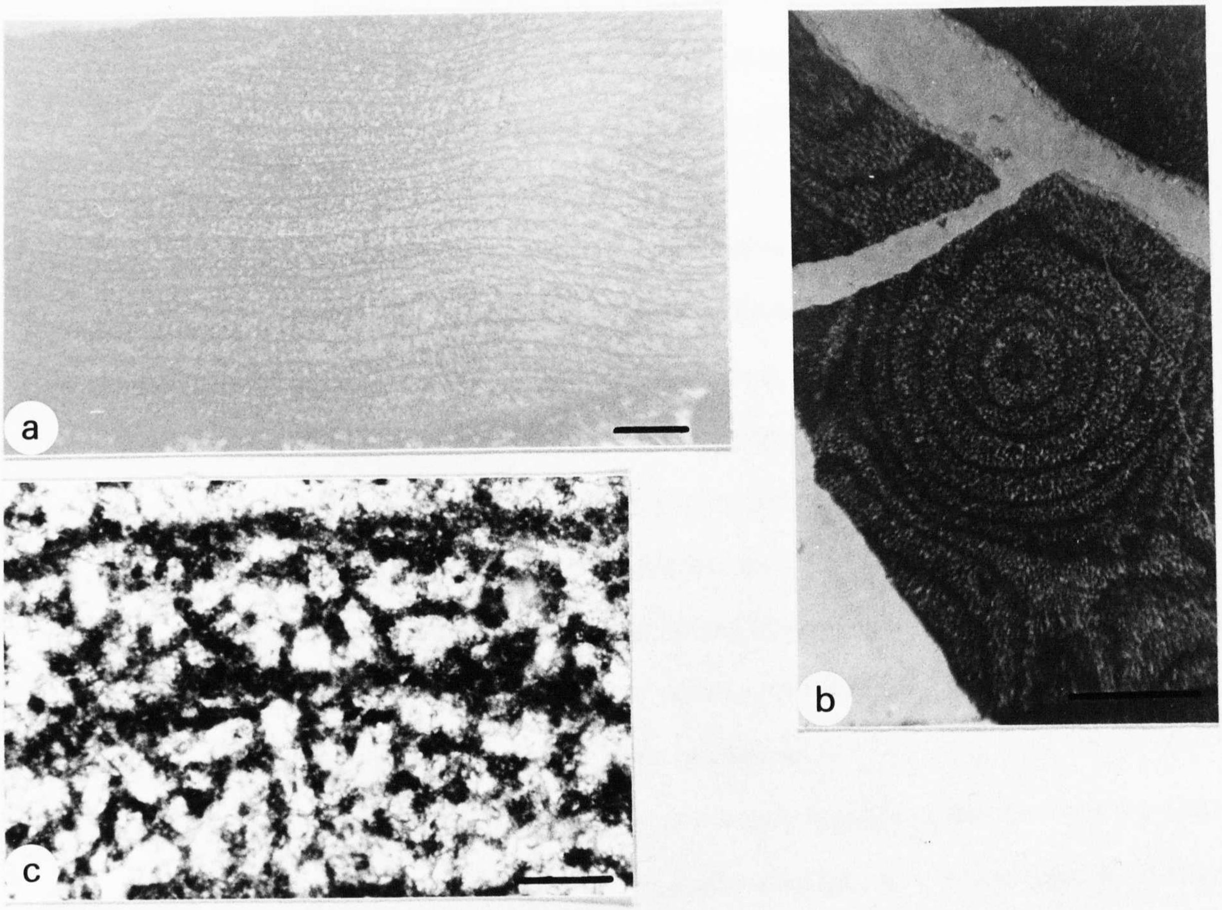
Monte Zirra, Nurra, N.W.Sardinia. ?Keuper or Bathonian. Collections of the University of Freiburg, Austria.

Figure a: Longitudinal section showing laminar development.
Scale bar = 1cm.

Figure b: Tangential section showing pillar-lamellae development.
Scale bar = 1cm.

Figure c: ?Irregular microstructure of calcareous skeleton, with poorly differentiated reticulum.
Scale bar = 1mm.

PLATE 37 *'Stromatoporina' tornquisti* (Deninger) 1906



Kühn considered that the straight and parallel vertical elements of the reticulum were the main characteristic feature of this genus. The description and illustrations by Deninger of *S.tornquisti* are poor. Hudson (1960) suggested that Kuhn's conception of the species was based upon the redescription of Osimo (1911) and not upon the holotype. From Deninger's description, it is clear that *S.tornquisti* does not possess the vertical elements thought characteristic of other species of the genus. Indeed, straight and parallel vertical elements are characteristic of *Dehornella*, which now includes species previously allocated to *Stromatopora*, and then to *Stromatoporina*. As reported by Hudson (1960), *Stromatoporina* was admitted by Kühn to be a genus of convenience, where the only feature which species held in common, was that they were not *Stromatopora*. Lecompte redefined the genus *Stromatoporina* Kühn, basing his definition on *S.choffati* (Now *Dehornella choffati*) and ignoring the type species *S.tornquisti*. In 1955, he attempted to redefine the genus based upon the type species. He did not find the holotype, and defined the genus on the topotype figured by Osimo (1911, Plate 7; figs.7a and b) and made this specimen a neotype. The holotype was relocated by Hudson, who redescribed the species, genus and family Stromatoporinidae Kühn 1928, into which he placed the genus.

The thin-sections are too thickly cut (as are many of the early types) and the specimen too badly preserved to discuss fully the microstructure of the calcareous skeleton. No spicules have been found. Insufficient information exists formally to redescribe this species, let alone the genus and family placing. The definition of the genus must be based upon this species in future. However, I cannot determine any similarity of this species to other forms which have been examined. Therefore, until spicules and microstructure of the calcareous skeleton are known, the species should retain its generic status. That this species constitutes a Mesozoic 'stromatoporoid' under the proposed redefinition, cannot be confirmed here.

Diagnosis:

Demosponges with a reticulate skeleton of triangular, rectagonal or polygonal meshes formed of monaxial megascleres joined at their ends by spongin; megascleres pointed at both ends; microscleres, if present are sigmas or bow-shaped. Parenchymella larvae, with incomplete ciliation, incubated. A calcareous skeleton may be present.

FAMILY B nov.fam.

Assigned genera:

Nov.gen. A

Diagnosis:

Haplosclerids with a spicule framework of styles, strongyles and tylostyles and a spherulitic calcareous skeleton.

The placing of Nov.fam. B in the Porifera:

This family shows a similar spiculation and calcareous skeleton microstructure to the Recent genus *Calcifibrospongia*, which is placed in the Reneiridae, within the Haplosclerida by Vacecet (1985). However, representatives of this family possess styles and tylosyles, which are lacking in *Calcifibrospongia* . The presence of strongyles clearly indicate affinty within the Haplosclerida for both *Calcifibrospongia* and this family.

Nov.gen. A

Type species:

Nov.gen. and n. sp. A. Ereño, N. W.Spain. Upper Aptian (Lower Cretaceous).

Diagnosis:

Primary spicule framework of styles strongyles and tylostyles forming a lattice of dominant vertical elements (length 75-250 µm, 5-20 width µm), and connecting horizontal elements. Primary calcareous skeleton of spherulitic microstructure, possibly initiated from the spicule bases.

Nov.gen. and n. sp. A

Plate 4, figs.a-d.

v * 1986 *Dehornella n. sp.* Wood and Reitner.p.469. Plate 35, fig. 2. (T.S.)

Type material.

Holotype. H 5478 Aptian of Ereño, N.W,Spain.

Diagnosis:

Primary spicule framework of styles, strongyles and tylostyles (length 75-250 µm, width 5-20 µm) forming a lattice within dominant vertical elements (columns), and connecting pillar-lamellae. Primary calcareous skeleton of spherulitic microstructure, possibly initiated from the spicule bases. Astrorhizae. No filling tissue.

Description.

Spicule framework of styles strongyles and tylostyles forming a lattice within both the dominant vertical elements and the pillar-lamellae. Nodular to massive gross morphology. No discernable surface features. The skeleton is dominated by closely spaced radial columns (100-250 µm diameter) with short connecting pillar lamellae (70-150 µm diameter) of spherulitic microstructure. The individuial spherules are between 70-135µm diameter and are spaced 35-70 µm apart. The astrorhizae bear bifurcating canals which peter out into the fine meshwork of the skeleton. The diameter of the canals is 200-350 µm. Latilaminae are formed by an increase in the diameter of the columns. No secondary tissue is present.

Distribution.

Ereño , N.W.Spain.

Lower Cretaceous (Aptian)

Remarks.

Apart from *Calcifibrospongia*, this is the only known calcified demosponge with strongyle spicules and a spherulitic microstructure.

PLATE 38: Spiculate late Mesozoic stromatoporoids.

All light photomicrographs of stained thin sections.

Makhtesh Hagadol, Israel. Lower Kimmeridgian.

Figure a: Longitudinal section of *Actostroma damesini* Hudson, 1958 showing club-shaped styles and orthogonal microstructure of calcareous skeleton. 85/29/1.

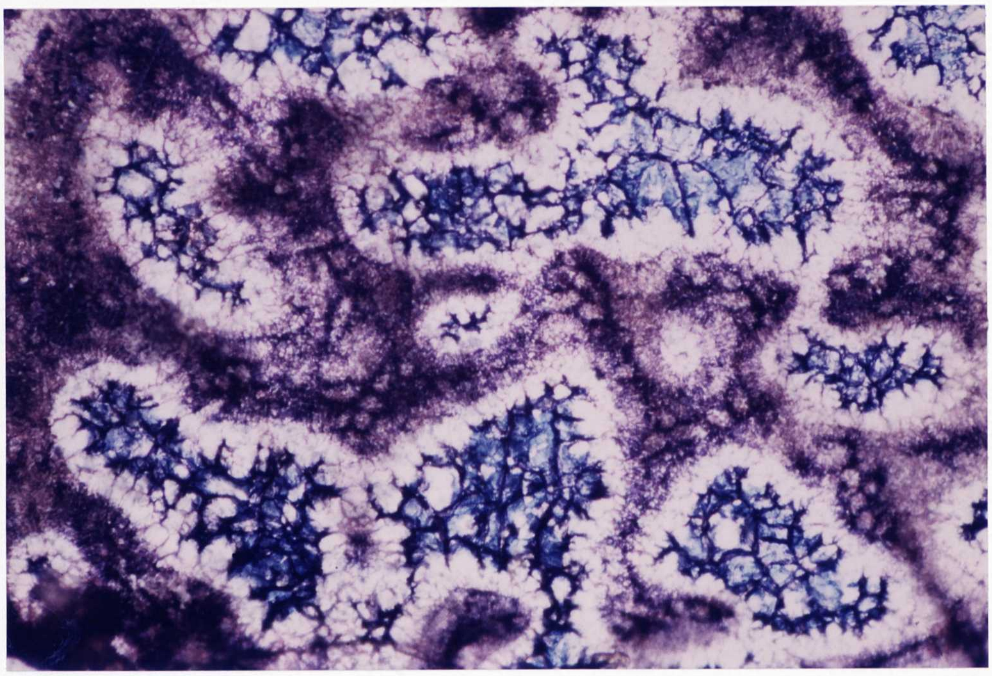


Figure b: Transverse section of *Dehornella harrarensis* (Wells, 1943) showing sections of club-shaped styles in central area of fascicular fibrous columns. 85/60/11

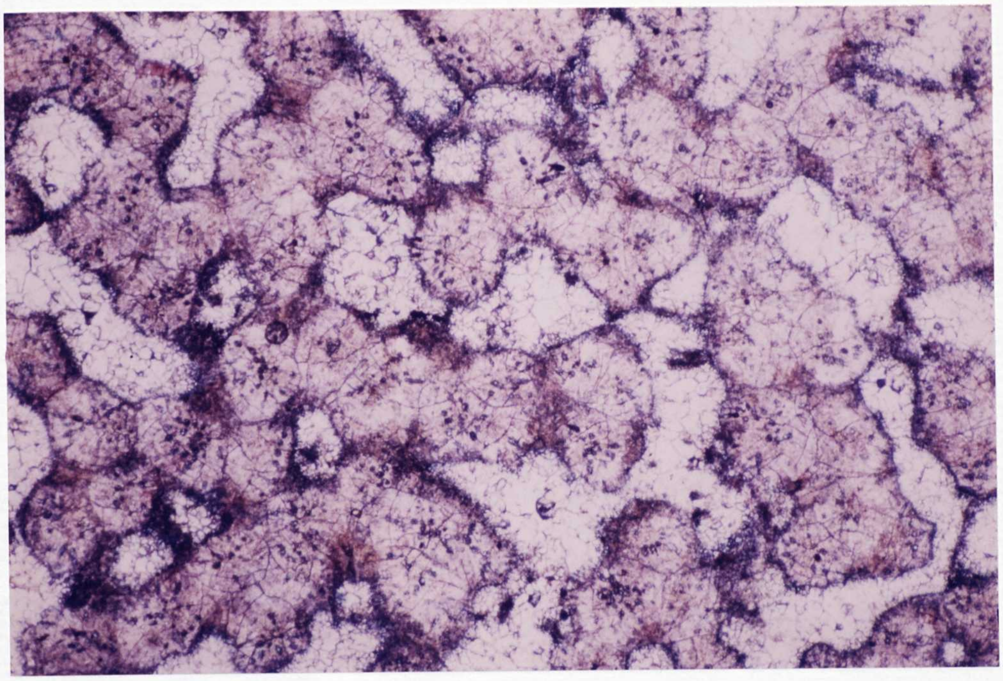
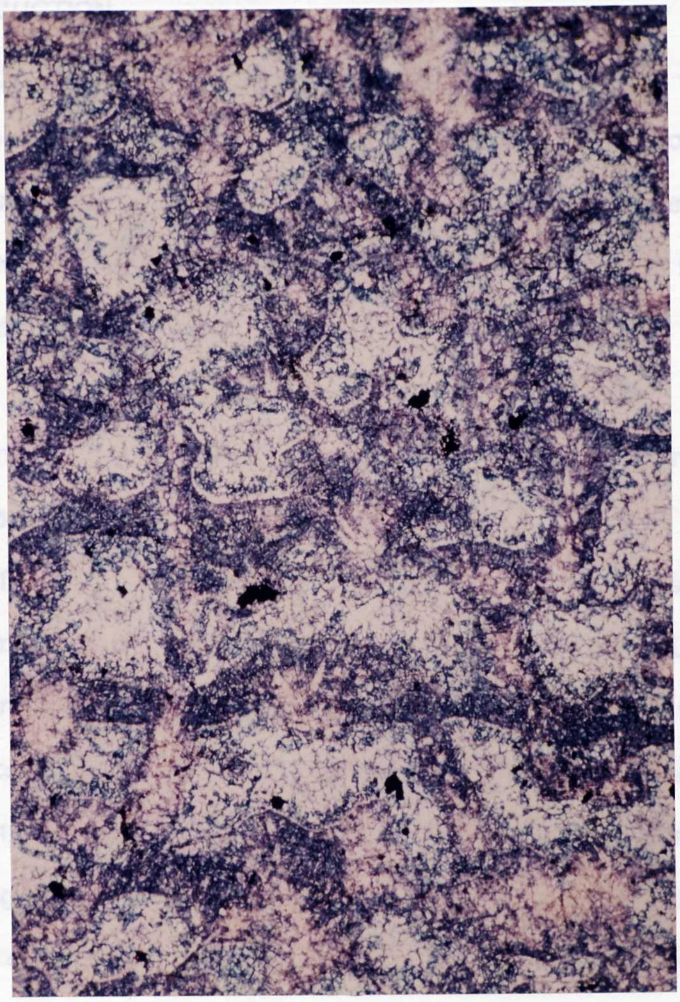


PLATE 39: *Shuqraia zuffardi* (Wells, 1943)

Longitudinal stained thin section showing loose plumose arrangement of club-shaped styles (pink) in the fascicular fibrous calcareous skeleton (blue).

85/69/11 Makhtesh Hagadol, Israel. Lower Kimmeridgian.



CHAPTER 5

PHYLOGENY OF THE CALCIFIED SPONGES

5.1 INTRODUCTION.

The finding of spicules in several previously problematic groups of fossil reefbuilders and the discovery of their survivors, has considerably enlarged the fossil record of the Porifera and radically modified our views on the evolutionary history of the phylum. We are now in a position to speculate upon the phylogeny of the calcified sponges, but the ramifications of this new information make the exercise extremely difficult.

Hartman and Goreau (1970) proposed that the living calcified sponges should be regarded as a fourth class of the Porifera, the Sclerospongiae, as all members possess a basal calcareous skeleton. This was disputed by Vacelet (1980, 1983) who suggested that these sponges differ greatly from one another and have strong similarities with various other Recent non-calcified sponges, and could therefore be incorporated into the pre-existing taxonomy. He distributed the Recent calcareous sponges within the Porifera on the basis of spicule type, soft-tissue organisation and larval type (criteria which he considered to be more taxonomically valid) and found the 'sclerosponges' to be calcified demosponges. The finding of pseudomorphs of siliceous spicules in certain stromatoporoids show that they too have representatives that are calcified demosponges.

Calcareous skeleton characteristics, and sometimes the spicule type and arrangement, are the only features available to the palaeontologist for taxonomic and therefore phylogenetic analysis. To appraise the phylogeny of the calcified sponges, we must first consider which features are taxonomically valid, and at what level. This has been discussed in Section 3.5 and the consequences have formed the basis for the revised taxonomic framework for Mesozoic stromatoporoids.

Macro-structures of the calcareous skeleton have been previously used to define several taxonomic groups of calcified sponges: the Chaetetida, Stromatoporoidea and the Sphinctozoa.

The microstructure of the calcareous skeleton has also been used by many workers to define high taxonomic ranks, even though only four microstructures are known in sponges, regardless of their taxonomic and stratigraphic placing. However, spicule data in fossil and Recent sponges shows the basal calcareous skeletons to have convergent characteristics. Different taxonomic groups based on spiculation, share the same microstructure, and members of the same group may possess different microstructures. Therefore microstructure type and macro-skeletal organisation alone, cannot determine the taxonomic placing in calcified sponges. These previous taxonomic groups are now known to represent grades of organisation (where the distinction between 'stromatoporoids' and 'sclerosponges' is an arbitary one) and it is clear that they should no longer be considered in isolation. At high taxonomic levels, only spicule characteristics can be used to unite forms.

Since features thought characteristic of 'stromatoporoids' have now been demonstrated to be convergent, phylogenetic determinations can be reached only for forms where spicule information is available This necessarily precludes the majority of forms described as 'stromatoporoids', 'chaetetids' and 'sphinctozoans', whose present taxonomic placings are based upon characteristics now considered misleading. However, the spicular forms can at least provide taxonomic guidelines for closely similar forms in which spicules have not as yet been found.

If one accepts the diagnostic priority of spicules, a discussion of the phylogeny of calcified sponges will concern several aspects:

1) The evolutionary development and inter-relationship of the sponge spicule types found in calcified sponges, which will be based upon what is known or suggested of the development of non-calcified sponge spicules,

2) The timing of the appearance, and subsequent development of, the calcareous skeleton within these different lineages as defined by spicule complements,

3) The taxonomic and phylogenetic significance of the relationship between the spicule framework and the calcareous skeleton, and the evolutionary modifications, if any, of this relationship through time,

4) The phylogenetic significance of mineralogy of the calcareous skeleton.

Only megasclere spicules have been found in stromatoporoid demosponges. Most of these are monaxons and it is highly probable that they have arisen independently in several demosponge lineages. This suggests that we may be in the unhappy situation of defining phylogenetic lineages upon convergent characters. But until other features are found, we have no alternative.

Our present scant spicule record has only allowed a broad phylogenetic analysis, but the presence of many types of calcareous sponges, which have not as yet yielded spicules, assures us that the fossil record of the calcified sponges was complex and diverse.

5.2 PHYLOGENY

Table 5.1 lists details of all known occurrences of spiculate calcifed sponges, excluding inozoans. This table contains all the data at present available for phylogenetic interpretation. Table 5.2. diagrammatically presents the information considered valid for phylogenetic study ; spicule type, arrangement and microstructure of the calcareous skeleton. These are arranged stratigraphically and in as precise (revised) taxonomic groupings as possible, within the proposed organisational grades. Stromatoporoid and sclerosponge data are combined. The ceratoporellids and acanthochaetetids are placed within the chaetetid grade.

For ease of management, characters will be described and summarised within these organisational grades. Common trends are discussed based on the features identified.

The Phylum Porifera is divided into three classes: the Hexactinellida, with siliceous spicules based upon a six-rayed form; the Demospongiae, with one- to four rayed siliceous spicules, and the Calcarea, which bear calcareous spicules. The Demospongiae is divided into three sub-classes: the Tetractinomorpha, Ceractinomorpha and the Homoscleromorpha.

Table 5.1: All known spicule data for Recent and fossil calcified sponges (excluding inozoans). 'Stromatoporoids' and 'sclerosponges' are listed together.
I: Spicules incorporated into the calcareous skeleton; C: Spicules incorporated by chance (See p.); E: Spicules not incorporated.

STROMATOPOROIDS

AGE	FORM	SPICULAR SKELETON		CALCAREOUS SKELETON		ORIGINAL REFERENCE
		TYPE	ARRANGEMENT	MINERALOGY	MICROSTRUCTURE	
	Astrosclera sp.	Acanthostyles	E.	Aragonite	Compound Spherulitic	Kirkpatrick 1910
	Calcifibrospongia sp.	Strongyles	I.lattice	Aragonite	Spherulitic	Hartman 1979
Lower Cretaceous	*Murania lefeldi*	Club-shaped styles	I.plumose	Calcite	Fascicular fibrous	Kazmierczak 1974
	Neuropora pustolosa	Style or ?Acanthostyle	I.	?Aragonite	?Orthogonal	Kazmierczak and Hillmer 1974
	Euskadiella erenoensis	Strongyles Styles, tylostyles.	I.lattice	Calcite	Spherulitic	Reitner. In press
Upper Jurassic	*Actinostromaria sp.*	Styles and ?triaxines	I,lattice	Calcite	Orthogonal	Wood. In press
	Milleporellidae	Club-shaped styles	I.plumose	Calcite	Fascicular fibrous	Wood and Reitner 1986
	Actinostromariania lecompti	styles	I.fibro-reticulate	Calcite	Irregular and orthogonal	"
	Actostroma damesini	styles and ?triaxines	I.lattice	?Calcite	Orthogonal	Wood . In press
Upper Cretaceous	*Actinostromaria sp.*	tylostyles microscleres	I.	Calcite	Orthogonal	Wood. In prep.
	'Burgundia' tutcheri	Calcareous trianes	I.	?Calcite	Orthogonal	Kellaway and Smith. [illegible]
	'Burgungia' tutcheri var. huttonae	"	I.	?Calcite	Orthogonal	"
	'Actinostromaria' faringdonensis	Calcareous trianes	I.	?Calcite	Orthogonal	Dighton Thomas 1977

Table 5.1 Continued

STROMATOPOROIDS Continued

AGE	FORM	SPICULAR SKELETON TYPE	SPICULAR SKELETON ARRANGEMENT	CALCAREOUS SKELETON MINERALOGY	CALCAREOUS SKELETON MICROSTRUCTURE	ORIGINAL REFERENCE
Upper Carboniferous	Parallelopora mira	Tylostyles	I.lattice	?	?irregular	Newell 1935
Middle Devonian	Stromatopora sp.	?styles ?microscleres	I.	?Aragonite	?Fascicular fibrous ?Spherulitic	Reitner pers.comm.

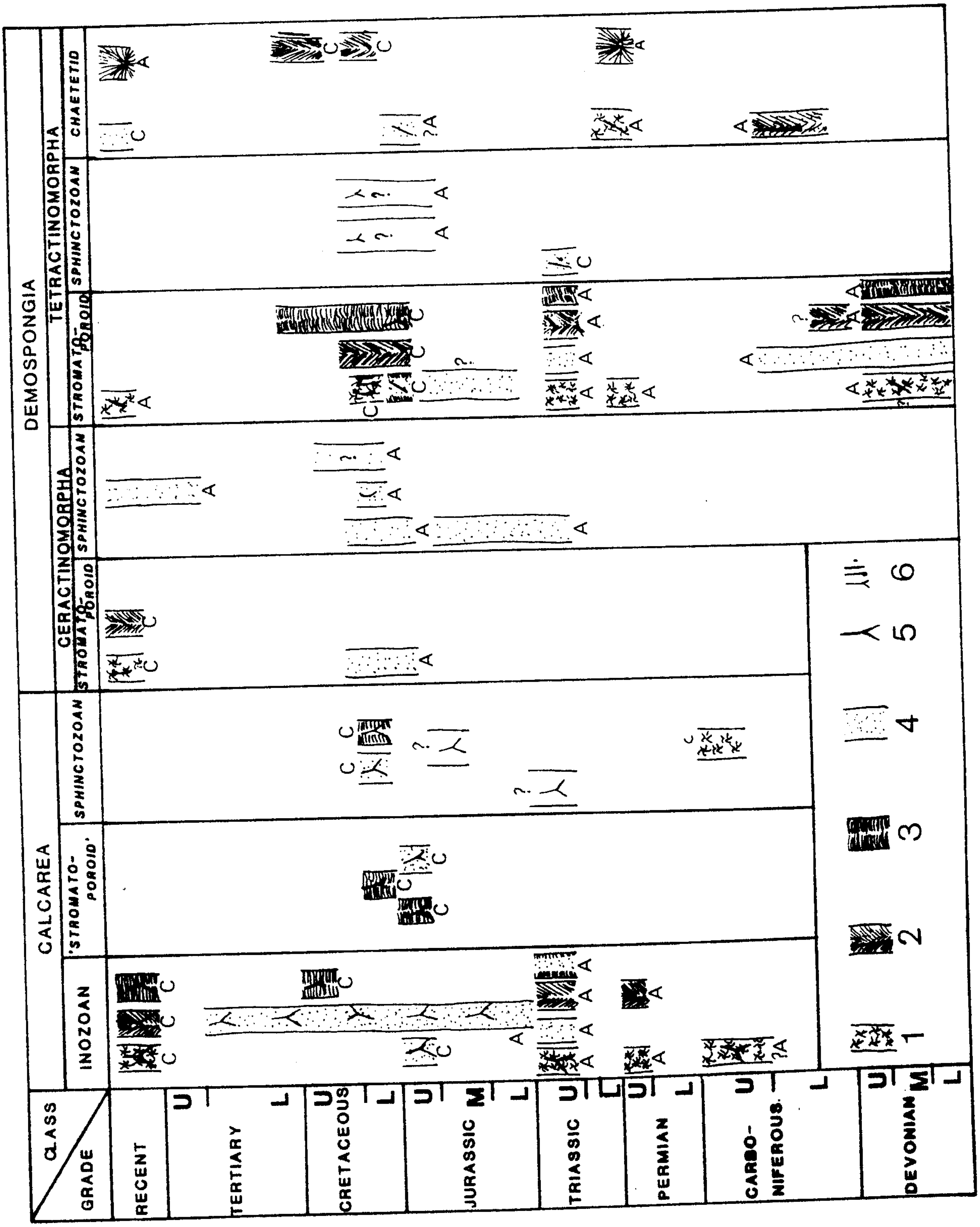
SPHINCTOZOANS

AGE	FORM	SPICULAR SKELETON TYPE	SPICULAR SKELETON ARRANGEMENT	CALCAREOUS SKELETON MINERALOGY	CALCAREOUS SKELETON MICROSTRUCTURE	ORIGINAL REFERENCE
Recent	Vaceletia sp.	-	-	Aragonite	irregular	Vacelet 1979
Lower Cretaceous	Barroisia sp.	Calcareous triactines fusiform .	I.lattice	Calcite	Irregular	Reitner . In press.
	Trematystia sp.	"	"	"	?Orthogonal	"
	Vascothalamia sp.	Fusiforme	I.	Aragonite	Irregular	"
	?Amblysiphonia sp.	Triaxons	I.	?	Orthogonal	"
Middle Jurassic to Lower Cretaceous	Murguithalamidia sp.	Trianes	I.	Aragonite	Irregular	"
	Boikothalamia sp.	"	"	"	"	"
Upper Jurassic	Undescribed sp.	Triaxons, fusiforme.	I.	Calcite	?	"
Upper Triassic	Sphaerocoelia sp.	Triactines	I.	?	?	"
	Cassianothalamia sp.	Styles and asters*	I.	High Mg. calcite	Irregular	"

Table 5.1 Continued

CHAETETIDS						
Recent	Acanthochaetetes sp.	Tylostyles, asters	E.	High Mg. Calcite	Irregular	Hartman et. al. 1975
	Ceratoporella sp.	Acanthostyle	I.C. plumose	Aragonite	Modified spherulitic	Hartman and Goreau 1970
	Stromatospongia spp.	"	"	"	"	"
	Goreauiella sp.	Acanthostrongyle	"	"	"	"
	Hispidopetra sp.	Style	"	"	"	"
	Acanthochaetetes sp.	Tylostyle	E.	High-Mg. Calcite	Irregular	Hartman 1975
	Merlia normani	Tylostyle Clavidisc Rhaphide	E.	Calcite	Fascicular fibrous	Kirkpatrick 1909
Upper Cretaceous	Blastochaetetes irregularis	styles	E.C. plumose	Calcite	Fascicular fibrous	Wood and Reitner. In prep.
Lower Cretaceous	Chaetopsis favrei	tylostyles ?asters	I.	Aragonite	"	Kazmierczak 1979
Upper Jurassic	Ptyochaetetes sp.	styles	I.	Aragonite	Irregular	Termier et al. 1976
Upper Triassic	Atrochaetetes medius	styles	I.	Aragonite	Spherulitic	Dieci et. al. 1977
Upper Permian	Preceratoporella sp.	styles	I.	Aragonite	"	Termier et al. 1976
	Ceratoporella sp.	?Acanthostyles	I.C.plumose	Aragonite	Modified spherulitic	Reitner and Wood. In prep.
Lower Carboniferous	Chaetetes (Boswellia) mortoni	Tylostyle ?raphide	I.	Aragonite	Fascicular fibrous	Gray 1980

Table 5.2: The distribution of spicule types , mineralogy and calcareous microstructures in calcified sponge grades through geological history . **A**: Aragonite; **C**: Calcite.
1: spherulitic; **2**: orthogonal; **3**: fascicular fibrous; **4**: irregular; **5**: calcareous spicules; **6**: originally siliceous spicules (ǀ styles; ǀ tylostyles; ⅄ triaxines; ⅄ tetraxons; • microscleres).



5.2.1. FOSSIL STROMATOPOROIDS / SCLEROSPONGES

Two theories have been presented for the evolutionary history of Mesozoic stromatoporoids. Lecompte (1956) suggested an evolutionary progression from forms with:

1) prominent laminae and short pillars (i.e. the Burgundidae) , to

2) vertical walls and some laminar structures (i.e.the Milleporellidae), to

3) vertical walls with no laminae, to

4) those with closed vertical tubes, resembling chaetetids , considered to be approaching a 'Milleporoid' hydrozoan state.

This contention was also held by Dehorne 1920, Steiner 1932 and Hudson 1960 . Evidence from this study suggests this idea to be erroneous : Firstly, because stromatoporoids are not hydrozoans; and secondly, Lecompte's types 2), 3) and 4) have been found to contain the same spicule type and are present in sediments of the same age. Moreover, a number of differing spicule types and arrangements have been found in forms described as stromatoporoids, suggesting a polyphyletic origin.

The second theory was proposed by Stock (1983). He speculated that if the Mesozoic stromatoporoids evolved from the Palaeozoic forms, it was probably the Order Clathrodictyida (due to its proposed similarities with the Mesozoic Family Burgundidae) or the Order Stromatoporellida which served as the ancestral (?sister) group. These two orders, in common with Mesozoic forms contain stromatoporoids with fibrous microstructures of the calcareous skeleton. However, from evidence in this study, it is clear that the same microstructural type does not taxonomically unite forms and evolutionary scenarios cannot be based upon the development of this feature alone.

The first stromatoporoids appeared in the Middle Ordovician, although some dubious forms have been described from the Cambrian. The first spiculate stromatoporoid has been determined from the Upper Carboniferous (Newell,1935). This form, *Parallelopora mira* bears styles and tylostyles in a perpendicular lattice arrangement (Plate 20 fig. a) and its affinities are with the tetractinomorph demosponges. The calcareous skeleton is heavily recrystallised, suggesting original aragonite mineralogy, but the original microstructure may have been fascicular fibrous. The calcareous skeleton is clearly precipitated around the spicule framework.

J.Reitner (pers.comm. 1986) has suggested that a species of *Stromatopora* from the Devonian of S.Germany is also spiculate, but I have examined the specimen and am not convinced of the presence of spicules. However, for completeness these spicules are indicated, with doubt, in Tables 5.1 and 5.2.

No further spicule information is available until the Upper Jurassic (Kimmeridgian), where three spicule types are found , all with probable affinities with the Order Axinellida, within the Tetractinomorpha. (Spiculate Upper Triassic forms have been decribed by Dieci et al. 1977 from the Cassian formation in Italy, but the author strongly suspects that these 'spicules' are algal borings)
1) Club-shaped styles in a plumose arrangement, with a fascicular fibrous calcareous skeleton. Specific affinities are with the Family Agelasidae (Upper Jurassic of the Middle East; Lower Cretaceous of East Europe (*Murania sp.*)).
2) Styles and ?triaxines in a reticulate arrangement with an orthogonal fibrous calcareous skeleton (Upper Jurassic of Yugoslavia).
3) Long-thin styles in a plumo-reticulate arrangement , with a primary irregular skeleton and an orthogonal fibrous rim (Upper Jurassic of the Middle East).

The apparently aspiculate Burgundidae, ranging from the Upper Jurassic to Lower Cretaceous , have been placed tentatively in the Ceractinomorpha (see p. 120).

In the Lower Cretaceous, a fourth type with strongyles, styles and tylostyles and a spherulitic microstructure is known from N.W.Spain. Affinities are with the Order Haplosclerida, within the Ceractinomorpha. There are no other records of this spiculation type. Also from the Lower Cretaceous, are three stromatoporoid calcareans which can be synonymised with pre-existing calcarean species.

The aragonitically preserved forms from the Upper Permian and Triassic appear to be aspiculate, although the author has not examined those forms descibed as stromatoporoids. There are no records from the Tertiary.

Summary

1) Fossil stromatoporoids appear to have representatives within the Ceractinomorpha, Tetractinomorpha and the Calcarea. All spiculate forms produce their calcareous skeleton upon a primary spicule framework, and no microscleres are present.

2) With no spicules, the more precise affinity of the possible ceractinomorph stromatoporoids (Burgundidae) cannot be determined.

3) The tetracatinomorph forms appear to be calcified axinellids, although no clear inter-relationships or lineages can be determined within this group. The stromatoporoid axinellids possess a diverse number of microstructural types of the calcareous skeleton.

4) The calcarean stromatoporoids may have a totally independent phylogentic history from the demosponge stromatoporoids.

5) The Palaeozoic tetractinomorph stromatoporoids may have been aragonitic, but the late Mesozoic tetractinomorph forms were probably low Mg-calcite.

5.2.2. SPHINCTOZOANS

The taxon Sphinctozooida was originally established by Steinmann in 1882, as a sub-order of the Order Pharetronida within the Class Calcarea. The type genus of the 'sphinctozoans' is *Sphaerocoelia* which possesses calcitic spicules and is certainly a member of the Calcarea, together with the Mesozoic genera *Barroisea* and *Tremacystia.*

The sphinctozoans are sponges with a thalamid or chambered skeleton. They do not possess astrorhizae, but often a central exhalent siphon or spongocoel. The development of the sphinctozooid skeletal type has been examined by Reitner (in press) and he proposes that the sphinctozoan organisational grade has occurred six times during the history of the Porifera. There are representatives from the Class Calcarea e.g. *Barroisia*, the Class Demospongiae e.g. extant *Vaceletia* and even one species from the Hexactinellida, *Caesaria,* which does not possess a calcareous skeleton.

The representatives of the sphinctozoid demosponges produce calcareous skeletons of aragonite or high-Mg calcite, with a trabecular internal structure.

The oldest known species belonging to the tetractinomorphs is *Cassianothalamia*, from the late Triassic Cassian beds in North Italy. This has a spiculate skeleton of fusiform megascleres and aster microscleres in a high-Mg calcite skeleton with an irregular microstructure. No regularity of the spicules has been observed. Further tetractinomorph sphinctozoans are placed in the Order Murguiathalamida and are known from the Callovian, Albian and Cenomanian. . They possess triane megascleres in an originally aragonitic skeleton.

In the late Triassic, the first representatives of the ceractinomorph sphinctozoans are found. Ceractinomorphs are only known in the Order Verticelletia, which have an aragonitic skeleton of irregular microstructure. Spiculate ceractinomorphs are known from the Jurassic, Cretaceous and Tertiary. e.g. *Vascothalamia* from the Late Albian has incorporated monaxon fusiform spicules. Reitner infers ceractinomorph affinity for other members of this order which possess no spicules, due to the similarity of their calcareous skeleton to Recent *Vaceletia e.g.Stylothalamia* from the Upper Triassic.

Conclusions

1) The sphinctozoan grade appears to have developed in the Calcarea, the Hexactinellida as well as the Tetractinomorpha and Ceractinomorpha within the Demospongiae.

2) The oldest spiculate form is a Triassic tetractinomorph which bears both megascleres and microscleres incorporated within a high-Mg calcareous skeleton, but with no discernible regular arrangement of spicules. The younger representatives of this sub-class are members of the Murguiathalamida, containing megascleres only, which form the framework for the calcareous skeleton. Therefore, within this lineage, the incorporation of both spicule types within the calcareous skeleton might be a plesiomorphic feature, and the subsequent loss of microscleres might be an apomorphic feature. Tetractinomorphs can produce either a high-Mg or aragonite calcareous skeleton.

3) Only one form of ceractinomorph sphinctozoan, is known to possess megascleres incorporated within the calcareous skeleton. The majority of fossil ceractinomorphs and extant *Vaceletia* possess no spicules at all. The apparent total loss of spicules in this lineage might be an apomorphic feature. All bear aragonite skeletons.

4) Reitner (op. cit.) suggests that the ceractinomorph sphinctozoans are more advanced than the tetractinomorph sphinctozoans due to the total spicule loss in many forms.

5.2.3. CHAETETIDS

The chaetetid grade of organisation is that characterised by a calcareous skeleton formed of conjoined tubules or calicles. Astrorhizae and filling tissue may or may not be present. Chaetetids are a diverse group with apparently separate Palaeozoic and Mesozoic histories. Palaeozoic chaetetids increase by pseudoseptal division (as do ceratoporellids) and basal fission and Mesozoic forms increase by intramural offset (as do acanthochaetetids).

The oldest reported spiculate chaetetid is from the Upper Carboniferous of Britain. Tylostyles and possibly rhaphides are incorporated into a probably originally aragonitic skeleton with fascicular fibrous microstructure (Gray 1980). Dieci et al. (1977) reported styles and acanthostyles from Upper Triassic chaetetids. These forms, including *Atrochaetetes* Cuif and Fischer (1974) possess a fascicular fibrous microstructure with a discontinuous backfill extending into the lumen. Termier and Termier (1976) described 'monaxons' in a 'scaly, porous' calcareous microstructure in an Upper Jurassic form. Kazmierczak (1974, 1979) has described styles or acanthostyles from two genera with microgranular microstructure. One of these, *Neuropora pustulosa*, was originally described as a bryozoan. Only the form decribed by Gray (1980) has been examined by the author.

In addition, Reitner and the present author have found spiculate specimens of *Blastochaetetes irregularis* from the Santonian of S.W.France and N.W.Spain. These bear long, thin styles within the calicles which are only incorporated into the fascicular fibrous calcareous skeleton by chance entrapment within tabulae and secondary epitaxial growth. This form was probably originally low-Mg calcite.

All these spicules show similarities with the Ceratoporellida, within the order Axinellida. *Atrochaetetes,* described by Cuif and Fischer (1974) is the only spiculate chaetetid which bears a discontinuous backfill. The other forms possess tabulae. However, this is probably not an important (high-level) distinguishing feature between these 'chaetetid' forms, as suggested by Gray (1980). Extant *Ceratoporella* possesses relict tabulae but Permian species of the same genus has abundant tabulae and a backfill. As Hartman noted, the distinction between secondary backfill and tabulae can be only 'one of degree'. None of the spicules in chaetetids appear to form the primary framework for the subsequent precipitation of the calcareous skeleton.

In addition to the described fossil spiculate 'chaetetids', the monogeneric family Acanthochaetetidae has a distinct and separate history extending to the Upper Triassic. This family possess microscleres as well as megascleres incorporated within a high-Mg calcite skeleton. Also, the present author and J.Reitner have found specimens of the genus *Ceratoporella* from Tjebel Tebaga , Tunisia (Upper Permian) with aragonitic preservation. These specimens do not contain spicules, but are clearly members of the same genus, thus considerably extending the Ceratoporellidae into the fossil record.

The calcareous skeleton of *Merlia* , when present, bears prismatic calicles partitioned horizontally by incomplete tabulae. Affinities are with the Family Biemidae, within the Order Poescilisclerida. There are no fossil representatives.

Summary

1)The fossil spiculate chaetetids appear to divide into two tetractinomorph groups, one with spicule and constructional similarities to the ceratoporellids (order Axinellida) with aragonite or low-Mg calcareous skeletons , and the other to the Acanthochaetetidae (order Hadromerida) with high Mg-calcareous skeletons. All members bear a calicular skeleton and probably possessed only a thin veneer of living tissue.

2) The chaetetids do not appear to use a primary framework of spicules to build their calcareous skeletons; spicules are merely incorporated by chance entrapment within filling tissue. When compared to the incorporation of spicules in stromatoporoid tetractinomorph demosponges, this

may be an apomorphic condition.

5.2.4. RECENT CALCIFIED DEMOSPONGES

The Recent calcified demosponges fall into both the chaetetid and stromatoporoid grades. There are no organisational differences between 'stromatoporoids' and 'sclerosponges' but Recent sclerosponge demosponges tend to have a secondary backfill which fills the primary pore space, whereas fossil stromatoporoid demosponges possess tabulae which perform the same function. The only distinction is that since the discovery of the 'sclerosponges', new fossil forms have been ascribed to this group, when previously they would have been placed within the stromatoporoids. *Calcifibrospongia* and *Astrosclera* show the stromatoporoid grade of organisation, and are placed in the Haplosclerida (Ceractinomorpha) and the Axinellida (Tetractinomorpha) respectively.
The Recent calcified demosponge fauna is diverse but small. The allocation of these forms within the Demospongiae is given in Figure 5.1., after Bergquist (1978).

5.3 EVOLUTION OF SPICULE TYPES

A discussion of the inter-relationship of these various calcified sponges rests on the present knowledge of the evolution of the Porifera as a whole, based on spicule development, and especially the origin and inter-relationship of the Calcarea with the demosponge sub-groups.

There are three significant theories on the general evolution of the demosponges and their relationship to the Calcarea. The Recent Calcarea are well characterised by a number of synapomorphies, but the origin of the group is difficult to establish as there are few plesiomorphic characters.

The theory of Reid (1970) is based upon the ideas of Dendy (1924). They believed the Hexactinellida to have a totally separate history and neither mentioned the origins of the Calcarea. The demosponge theory of Dendy and Reid proposed a system which followed microsclere development. Reid (1968) judged microscleres to be acceptable for differentiating high-level taxonomic divisions in non-lithistid sponges. He suggests that structural grades cut across lines of descent. In Reid's opinion, the two main sub-classes of demosponges evolved at the Pre-Cambrian /Cambrian boundary from a sponge group comparable to the Homoscleromorpha and

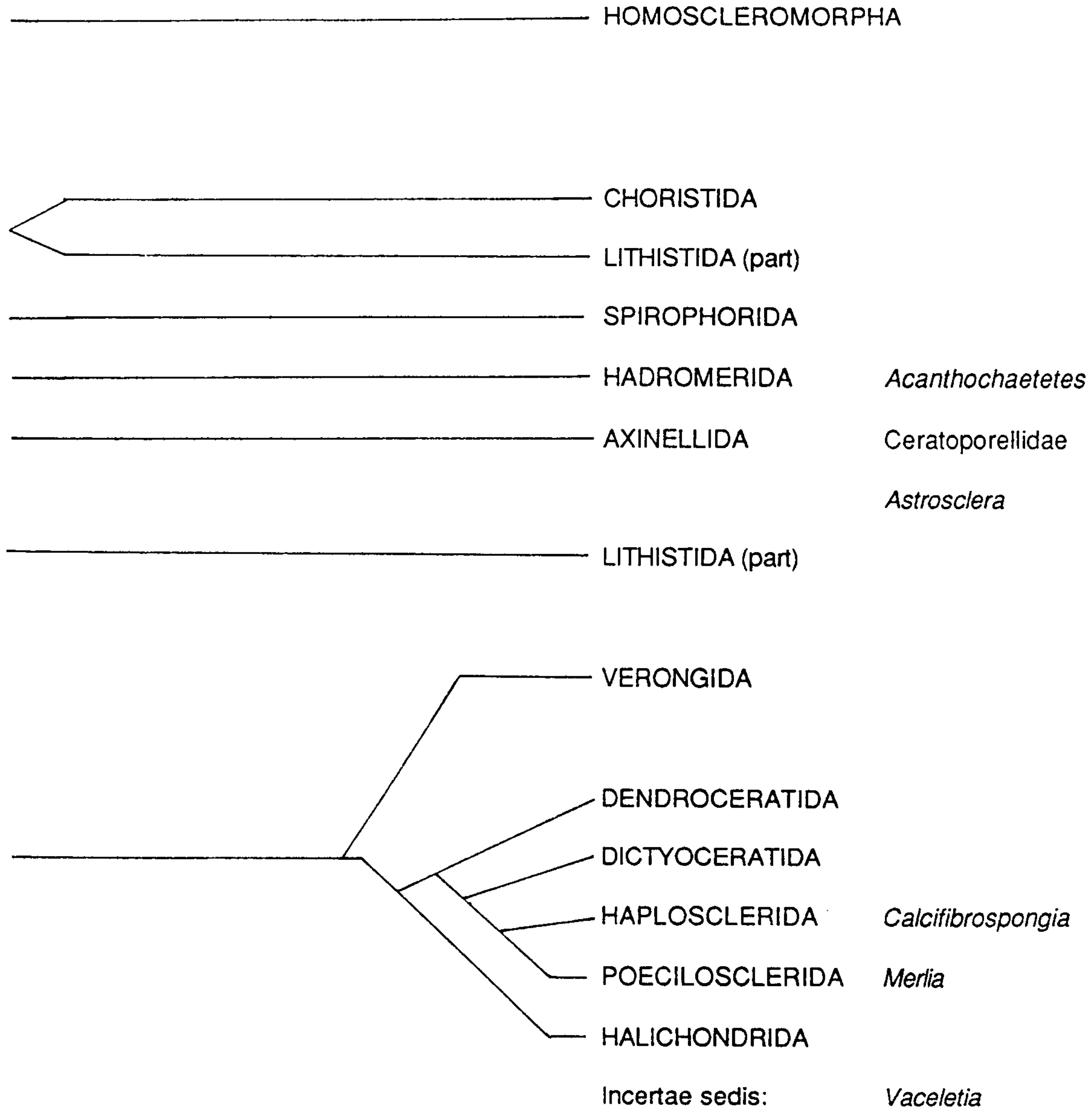


Figure 5.1: Distribution of Recent 'sclerosponge' genera over the currently recognised demosponge orders and the inter-relationship of modern orders. (modified from Bergquist 1978, fig.8.8).

that the Homoscleromorpha themselves have had the longest independant history. The extant members of this group are microspiculate sponges, characterised by very small tetractine spicules, known as calthrops. Reid suggests that some of the primitive demosponges possessed radiate (including tetraxon) spicules, and others only monaxons. Thus, many monaxonid demosponges, especially those with sigma (s-shaped) microscleres known as sigmatomonaxonids e.g. *Saccospongia,* may never have had tetraxon ancestry. *Saccospongia* bears tracts of plumose styles coated with microscleres. However Reid does not totally dismiss the possibility that monaxial megascleres have arisen several times during geological history, with major groups having separate origins.

According to the theory of Reid (op. cit.), the tetractinomorph calcified sponges would be related to the sigmatomonaxonids (as are their Recent ancestors , the axinellids and haplosclerids) within the Tetractinomorpha, which are characterised by sigma-microscleres. These microscleres have been lost in the stromatoporoids; an apomorphous feature. Reid suggests that the sigmatomonaxonids have no close relatives except the keratose sponges (those with a skeleton of spongin only) which are probably iterative derivatives of the spiculate sigmatomonaxonids at various stages of their history. Reid suggests the sigmatomonaxonids represent direct descent from the primitive Demospongiae without tetraxons.

Finks (1970) and Bergquist (1978) propose that all calcareous sponges may have a common Precambrian ancestry, separate from that of the Hexactinellida, and that the Calcarea and the Demospongiae evolved from a common ancestor. Finks also uses basic microscleres as a systematic frame for modern higher taxa of demosponges, but does not extrapolate back to the roots of post-Palaeozoic lineages throughout. Many of these origins are left open. Only a few phyletic lines are tied to Ordovician forms and only *Hazelia* among the Cambrian genera is considered a direct ancestor. *Hazelia* is a tubular, thin walled form found in the Middle Cambrian Burgess Shale and bears oxeas in an isodictyal plumose arrangement . In agreement with Reid, lithistids are considered polyphyletic. Finks believes that the Demospongiae derived from a monaxon ancestor and not from a tetraxon ancestor as suggested by Reid (1970). The monaxon is thought more primitive because of its wider distribution among sponges in general, and it may have given rise to early tetraxon-bearing forms by increasing its complexity. The Homoscleromorpha are suggested to be a relatively young sponge group, perhaps emerging in the Triassic. According to Finks (op.cit.), *Hazelia* and related genera are the ancestors of Recent Axinellida, Ceractinomorpha and some lithistids. However, in contrast Bergquist (op. cit.) argues that the evolution of these groups is more complex. She believes the Recent axinellids to be very disparate and so divisions of various axinellid groups from *Hazelia* stock must have occurred early. However, in the Middle Cambrian, tetraxon spicules can be found with monaxons (Van Kempen. In Press). Therefore, it is more probable that separation of the two main demosponge classes occurred in the Precambrian, or early Cambrian.

The third theory suggested by Van Soest (1984) is that the Homosclerophora and the Calcarea have close phylogenetic relationships. He bases this on the shared similarities of the calthrops-like spicules, the amphiblastula larva and the large choanocyte chambers found in both groups. However, Tuzet (1948) considered the larval similarity a parallel development as the embryology differs substantially in both cases. This question remains unresolved. Van Soest proposes the calthrops spicule to be a synapomorphy, impling that the Homosclerophorida and Calcarea are sister groups. *Verticillites* and *Vaceletia* , and the murrayonids (calcareans) are examples of relics of these lineages which have diverged from this evolutionary sequence.

Any common ancestor of the Calcarea and Homosclerophorida must have lived at least as far back as the Devonian. The Calcarea would have to be incorporated at sub-class level, in accordance with homosclerophorid taxonomic rank. Van Soest presented a tentative diagram of presumed phylogenetic relationships (Figure 5.2B).

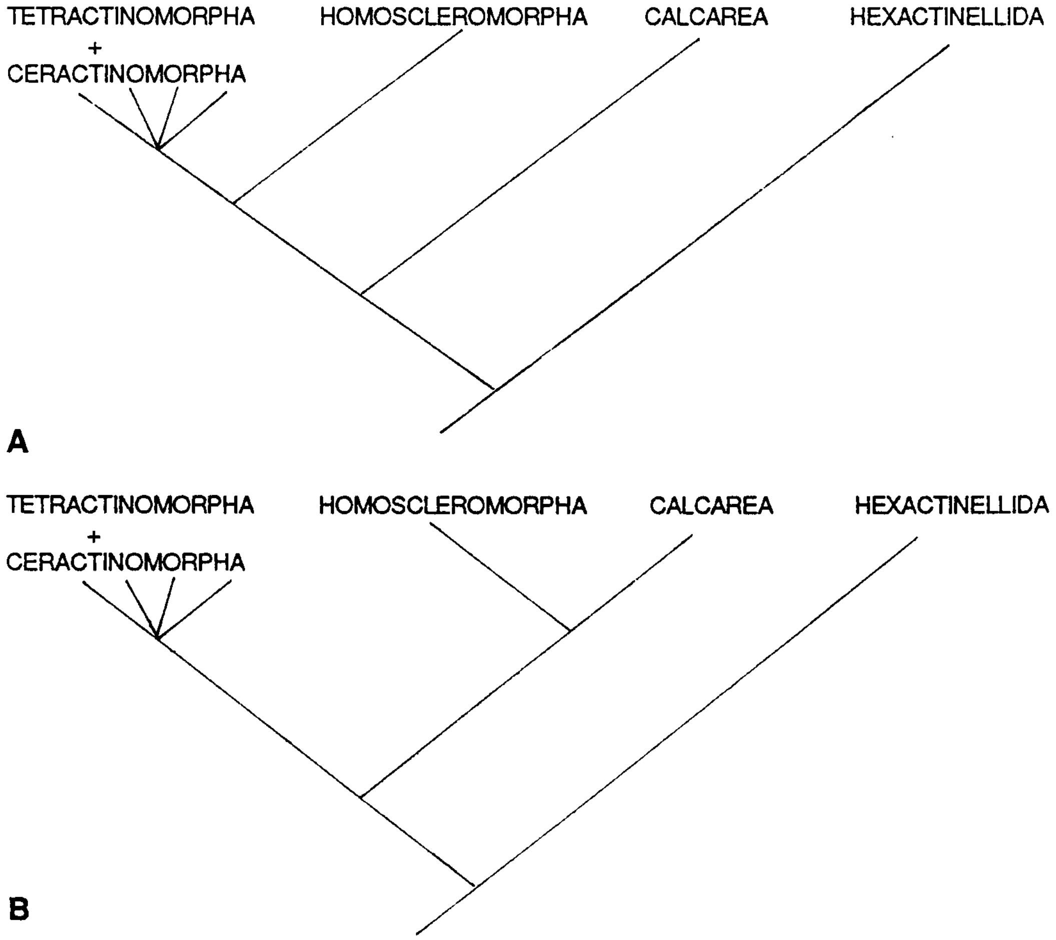


Figure 5.2: Diagrams representing the overall phylogenetic relationships of the major sponge taxa.
A: Generally accepted view (e.g. Finks (1970) and Reid (1970) with classes Hexactinellida, Calcarea and Demospongiae (Tetractinomorpha + Ceractinomorpha + Homoscleromorpha).
B: view suggested by Van Soest (1984) based on the idea that the hypercalcified skeleton has developed once only and that the similarities between the Calcarea and Homoscleromorpha are homologous.

Van Soest suggests that the origin of the Calcarea was from a calcified demosponge (stromatoporoid / sphinctozoan) stock. First, primitive sphinctozoan-like sponges evolved from stromatoporoids by losing their siliceous spicules (this tendency to lose spicules is seen in *Astrosclera* and most other Recent calcified demosponges have poorly developed spiculation compared with their non-calcified relatives). A progressive loss of the basal calcareous skeleton occurred, unrelated to the loss of spicules, in the same way as has occurred in Recent calcified demosponges. The resulting total loss of a supporting skeleton would be compensated by the development of a new support, the calcareous triactine or tetractine spicule, in a similar form to certain siliceous spicules (calthrops).

Discussion

It is clear that there is no consensus of opinion as to whether the monaxon or tetraxon spicule is the most primitive, when the Demospongiae diverged from the Calcarea (or vice versa) or the nature of the interelationship between these two groups. The present author does not have sufficient knowledge of Palaeozoic sponges to be able to favour any one theory. However, Reid's 1970 suggested phylogeny of the Demospongiae is reproduced in Figure 5.4 and the proposed position of the tetractinomorph stromatoporoids is shown. Following Reid's analysis, the calcified tetractinomorph demosponges appear to be the calcified relicts of an extremely conservative and primitive group, with origins in the Pre-Cambrian / Cambrian.

What lineages can be discerned within stromatoporoid demosponges are shown in Figure 5.3a. Little more can be said upon the origin of the lineages of the various calcified sponge groups, until more information and conclusive evidence has been gleaned from Recent and non-calcified fossil sponges.

5.4 ORIGIN OF THE CALCAREOUS SKELETON

Reitner (In Press) supports Van Soest's (1984) theory and uses this as the basis for study of the sphinctozoans. However, he disputes the idea of the monophyletic origin of the calcareous skeleton within the Demospongiae. He suggests that the different skeletal types within the sphinctozoan grade differ fundamentally in mineralogy, microstructure of the skeleton, and spicule type and arrangement. He believes the development of the calcareous skeleton to be apomorphic, the process of biomineralisation being a simple one for an organism to 'acquire', and lose.

Van Soest (1984) believes the calcareous skeleton to be an archaic feature. He believes the possession of a calcareous skeleton to be a symplesiomorphic feature, in that the divergence of calcarean and demosponge spicule types is postulated to have postdated this calcification.

The crux of this dispute rests on the timing of the origin of the Calcarea and demosponge sub-classes in relationship to the development of a calcareous skeleton.

Recent calcified demosponges are few but diverse. Several spicule types are unusual and have a limited distribution.

We must decide between two possible explanations: either a basal calcareous skeleton has developed separately in each lineage or, it is an ancestral characteristic of a large group of demosponge and calcarean orders, for which we only now have the occasional 'taxonomic' window.

Five facts are at our disposal:

1) We have a large fossil record of calcareous sponges, many of which were reef-builders,

2) A small but diverse number of Recent calcified sponges,

3) Recent calcified demosponges are generally found in cryptic habitats, e.g. caves,

4) There is an example of a calcified demosponge , *Merlia normani.*, which has a facultative calcareous skeleton. This species may be in the process of losing its calcareous skeleton.

5) Different microstructural types and modes of biomineralisation are present in members of the same family (as defined by spicule and soft-tissue criteria)

It appears that the most likely and parsimonious explanation is that the modern fauna are relict remnants of a previously widespread calcified sponge fauna. Many lineages of calcified forms are clearly now extinct e.g. the Mesozoic 'stromatoporoid ' Actinostromaridae, but some have persisted almost unchanged since the Upper Permian (ceratoporellids). However, it is more plausible to suggest that the calcareous skeleton in sponges developed after the divergence of the spicule types, as otherwise one would have to postulate parallel evolution of spicule types and calcareous skeleton types within each lineage. Many of the Cambrian and early Palaeozoic sponges are not calcified and also there are many different macro-organisations, microstructural types and mineralogies present in calcified sponges. A cladogram illustrating the convergent development of the stromatoporoid calcareous skeleton is given in Figure 5.3B.

The calcareous skeleton has appeared in most lineages of the Porifera, since the early Phanerozoic. Only the Hexactinellida and Homoscleromorpha do not produce a calcareous skeleton. The Hexactinellida are very different from other sponges because of their syncitial organisation (Mackie and Singla 1983). Vacelet (1985) suggests that the Hexactinellida may be archaecyathans which have lost their calcareous skeletons. However, without the presence of spicules we cannot resolve this.

The possession of a calcareous skeleton has allowed sponges to be the main carbonate reef-builders in the Palaeozoic and early Mesozoic. Vacelet postulates that in parallel with these calcified sponges there were non-calcified close relatives leaving no fossil remains.e.g. the Acanthochaeteidae (calcified) and the Spirastrellidae (non-calcified). In the Mesozoic, the scleractinian corals proved more successful reef-builders and so calcareous reef sponges declined. A few remained in the dark protected refuges of coral reefs.

5.5 EVOLUTION OF THE RELATIONSHIP BETWEEN SPICULAR AND CALCAREOUS SKELETON

Few microscleres have been found in calcified sponges; no microscleres have been found in Mesozoic 'stromatoporoids'. Within lineages, their loss could be interpreted as an apomorphic feature (as in Reitner (in press) for the 'sphinctozoans'). However, there are few records of microscleres in Palaeozoic sponges. The lack of microscleres could be a primitive feature shared by a now relict group which may have little relationship to the other groups of monaxonid demosponges that do possess microscleres. But perhaps with such a poor Palaeozoic record we should be wary of any firm conclusion.

It is true, however, that the Recent calcified sponge fauna has a reduced spiculation and that some forms e.g. *Vaceletia* and *Astrosclera* may not possess any spicules. This would suggest that the gain of a rigid calcified skeleton removes the need for support by spicules, and so they are progressively lost.

The relationship of the spicular to the calcareous skeleton in tetractinomorph chaetetids seems to be consistantly different to that found in stromatoporid tetractinomorphs. However, the relationship between spicule and calcareous skeleton is not consistant within Recent famillies of calcified sponges, and this suggests that it is of low taxonomic and therefore phylogenetic importance.
The proposed linages of the spiculate stromatoporoid demosponges and their affinities are shown in Figure 5.3A.

5.6 SIGNIFICANCE OF MINERALOGY

The mineralogical type of the calacreous skeleton within one family of calcified sponges appears to be constant e.g the acanthochaeteids (Triassic to Recent) are high-Mg calcite and the ceratoporellids (Upper Permian to Recent) are aragonite. However, different mineralogies are found within members of the same sub-classes and even orders e.g.within the Axinellida, *Ceratoporella* has an aragonitic sksleton and the Milleporellidae have a low Mg-calcite mineralogy. Mineralogy appears after all to be of low phylogenetic significance, having arisen independantly within different families.

Yet, it is clear that forms with different mineralogies must have co-existed e.g the acanthochaetetids (high Mg-calcite), the ceratoporellids (aragonite) and the milleporellids (low Mg-calcite) were all present in the Upper Jurassic to Lower Cretaceous, during a so called 'aragonite inhibiting' time according toSandberg (1983), and Wendt (1984). However, it is possible that these groups actually arose during their respective facilitating phases, but this remains conjecture until we possess a larger data base.

Figure 5.3: Lineages and affinities of the spiculate stromatoporoid demosponges, and the Acanthochaetetidae and Ceratopoellidae.

Figure 5.3a: Proposed affinity and phylogenetic relationships of the spiculate stromatoporoid demosponges.

5.4a

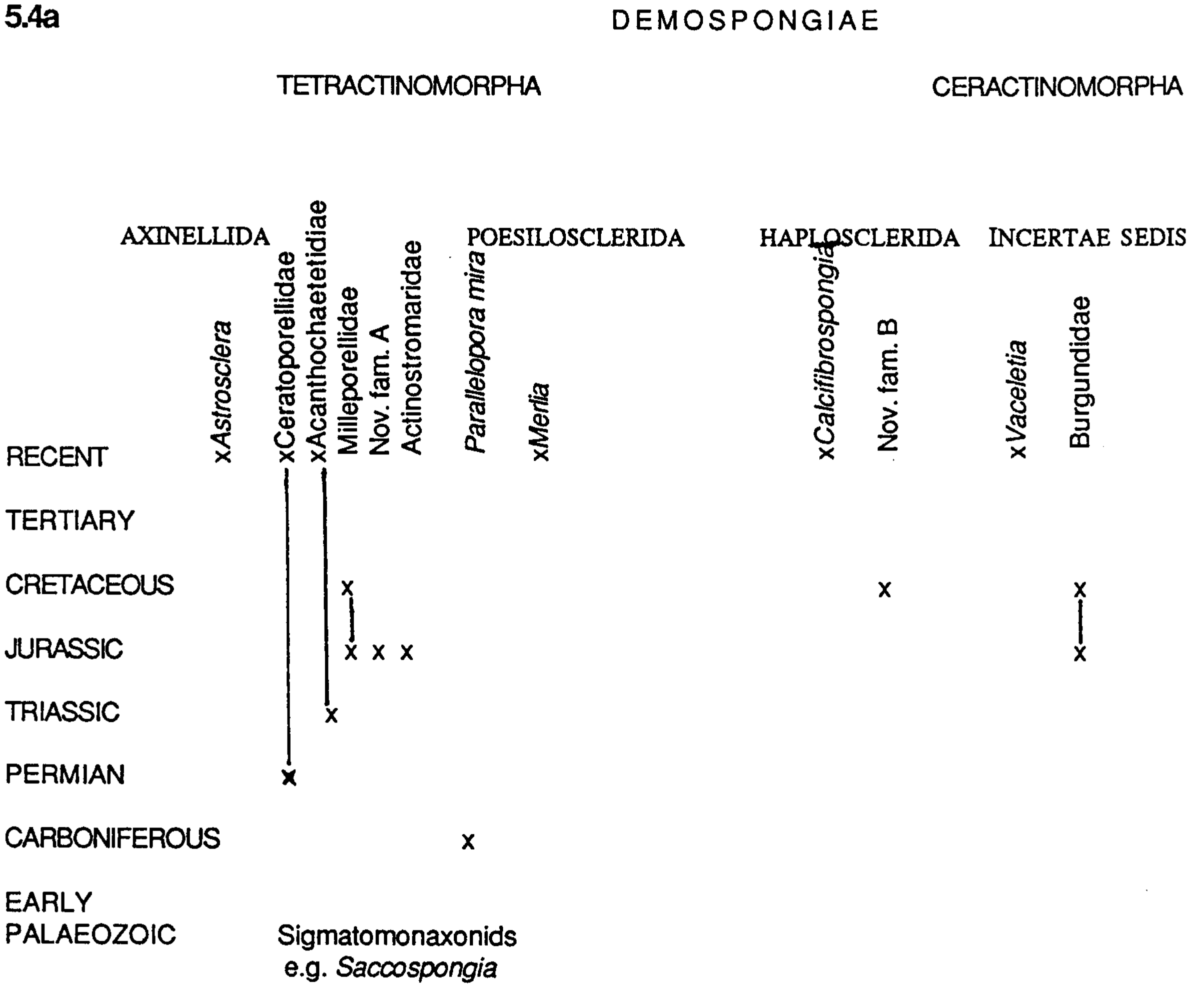


Figure 5.3b: Cladogram illustrating the convergent development of the stromatoporoid calcified skeleton, following Van Soest's generalised phylogeny. The Demospongiae and Calcarea are characterised by parenchymella and amphibastula larval types respectively. The Ceractinomorpha and Tetractinomorpha are also characterised by reproductive habits.

1) Layered calcareous skeleton with radial and concentric elements and repeated astrorhizal-bearing aquiferous units.
2) Spicules incorporated into the calcareous skeleton.
  2a) Megascleres and microscleres incorporated into calcareous skeleton.
  2b) Megascleres incorporated into calcareous skeleton.
3) No spicules present.
4) Loss of calcareous skeleton.

5.3b

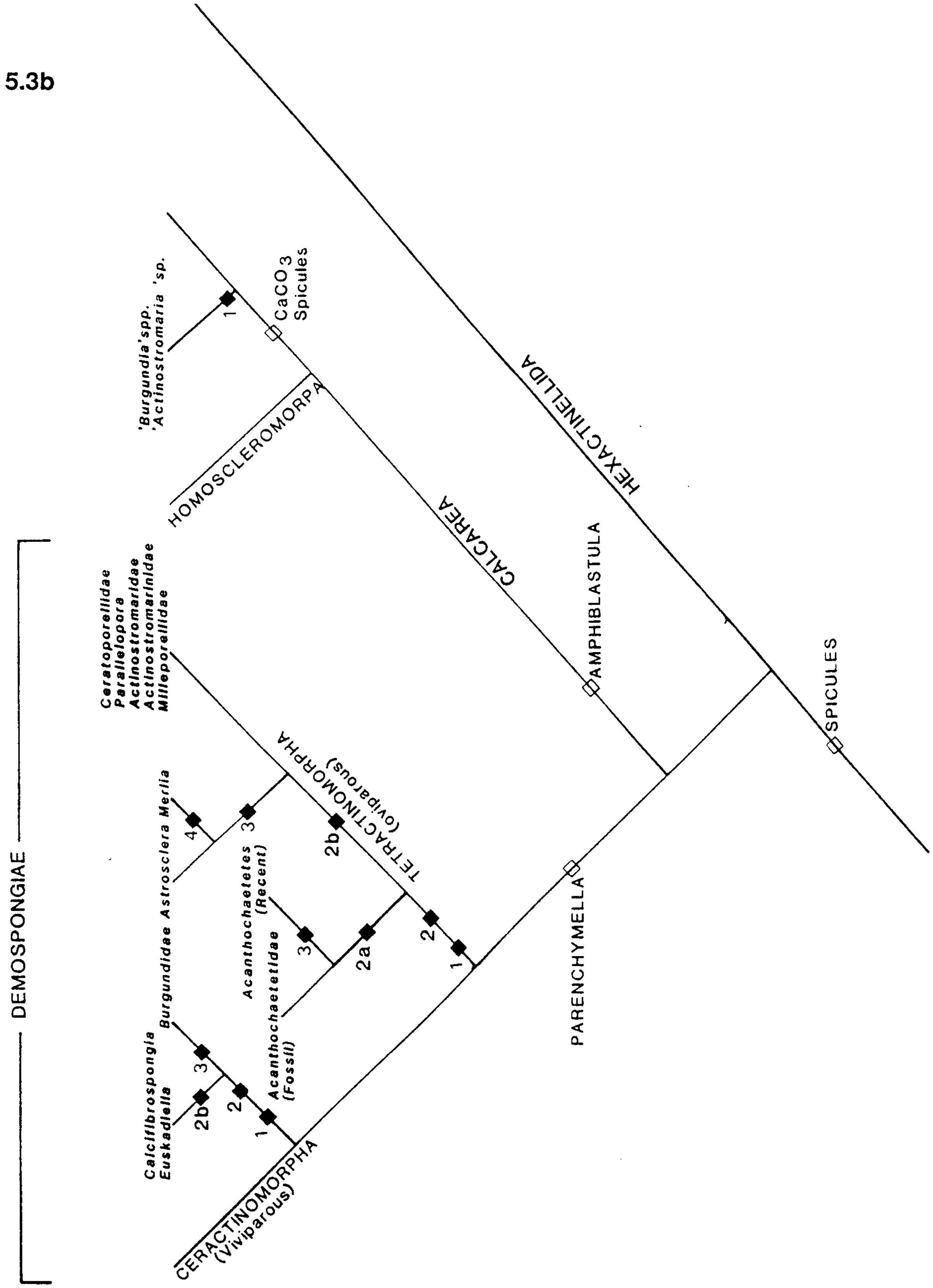
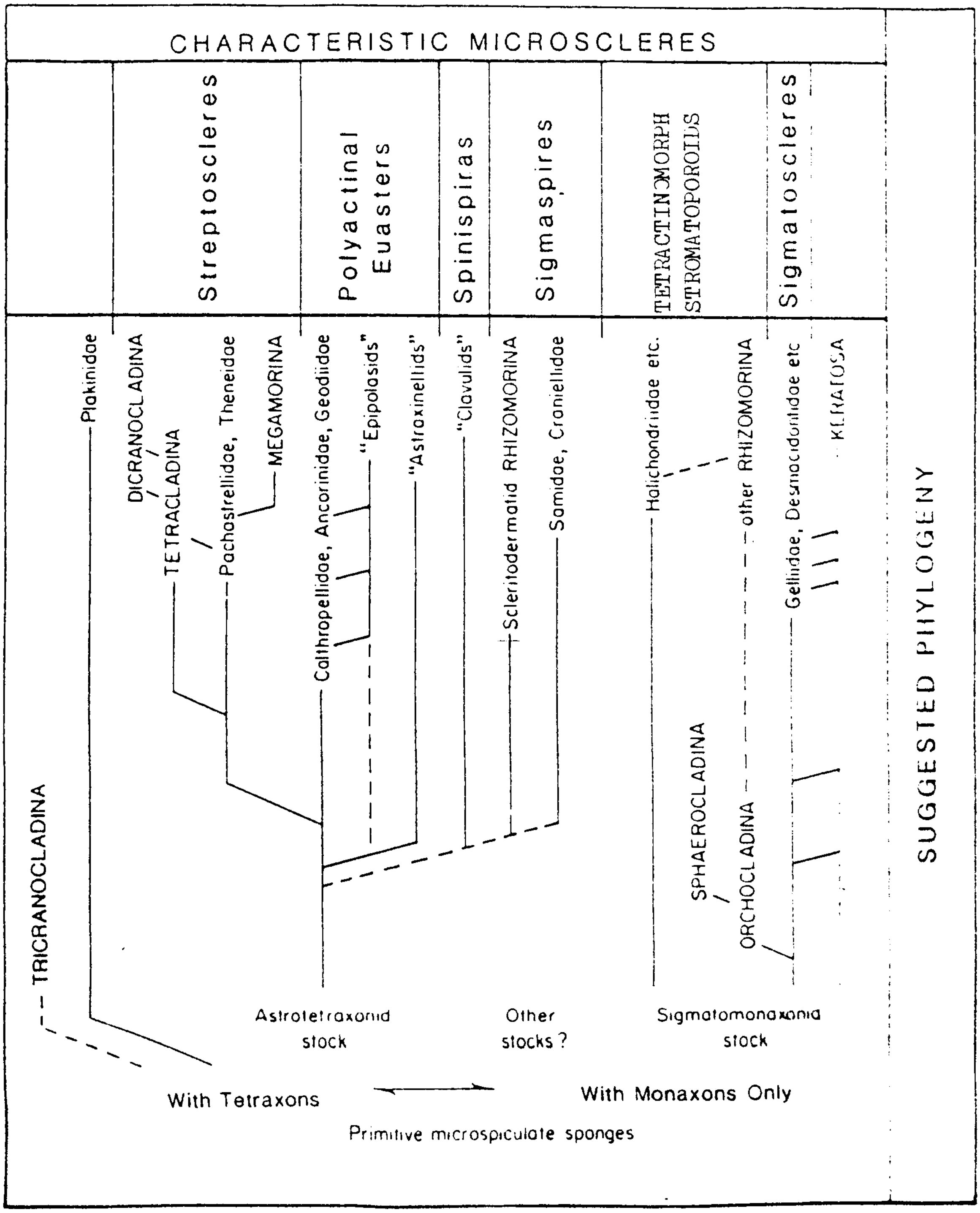


Figure 5.4: Phylogeny of the Class Demospongiae based upon spicule distribution. Suborders are shown in capital letters, family names in inverted commas and lower case. Those in quotation marks are invalid taxa, according to Reid (1970).
(modified after Reid1970).



5.6 CONCLUSIONS

1) The sphinctozoans and stromatoporoids have representatives in the Calcarea and both main sub-classes of the Demospongiae. These groups are polyphyletic.

2) The chaetetid grade appear to have developed only in tetractinonmorph demosponges.

3)The Recent calcified demosponges are the remnants of once diverse and successful lineages of calcified forms.

4)Two Recent families, the ceratoporellids and the acanthochaetetids have histories going back to the Upper Permian and Upper Triassic respectively. They show little, or no change in spicule and calcareous skeletal organisation and appear to be very conservative families.

5)The diverse compositions of the calcareous skeleton suggests that it has appeared and been lost in many different lineages.

6) The possesion of a calcareous skeleton has been aquired independantly within each lineage and within different genera at present thought to be part of the same lineage e.g.:

Ceractinomorpha:

Incertae sedis	?Burgundidae
	Verticelletia
Haploscleridae:	Calcifibrospongia (and possibly Nov. fam. B)

Tetractinomorpha:

Incertae sedis:	Cassianothalamia
	Murguithalamida
Axinellida:	Ceratoporellids
	Astrosclera sp.
	Milleporellidae
	Actinostromaridae
	Nov. fam. A
	some chaetetids

Hadromerida	Acanthochaetetids
	some chaetetids
Calcarea	Sphinctozoans
	Stromatoporoids

7) It is likely that calcified and non-calcified forms evolved in parallel.

8) Compared with their non-calcified relatives, the spiculation of Recent calcified demosponges is reduced. Reduced spiculation may be an apomorphic feature.

9) The incorporation of spicules within the calcareous skeleton may be a plesiomorphic feature within each lineage.

10)The loss of microscleres may be an apomorphic feature within each lineage.

11) The precipitation of a calcareous skeleton upon a primary framework of spicules, as seen in Mesozoic 'stromatoporoids', may be a plesiomorphous feature within each lineage.

12) Mineralogy type probably developed independantly within each calcified family.

CHAPTER 6

BIOMINERALISATION AND SOFT TISSUE RECONSTRUCTION

6.1.INTRODUCTION

Reconstructing fossil organisms is a tentative and difficult exercise, but understanding their functional and constructional morphology is essential to sound taxonomy and phylogenetic study.

Despite the rapid increase in the number of species described, few papers have discussed the biological interpretation of skeletal formation in 'stromatoporoids' , and the distribution of the living tissue during growth.

Flügel (1958), believing 'stromatoporoids' to be Hydrozoa, presented soft-tissue reconstructions based upon the arrangement of *Hydractinia*. He proposed that the calcareous skeleton was secreted by a folded basal coenosarc. After the discovery of 'sclerosponges', Stearn (1975) reconstructed representatives from the Palaeozoic 'stromatoporoids' using comparison with *Merlia* and *Astrosclera*, dismissing the ceratoporellids as having no analogies with Palaeozoic forms.

With conclusive evidence that Mesozoic 'stromatoporoids' are poriferan and probably largely members of the Demospongiae, and the discovery of two new calcified demosponges since Stearn's paper (*Calcifibrospongia* and *Vaceletia)* we are in a more confident position to reconstruct the Mesozoic 'stromatoporoid' animal.

With no evidence to the contrary, Stearn (1975) believed that spicules were not secreted by stromatoporoids and therefore their role in the soft tissue and biomineralisation of the skeleton was not discussed in his reconstructions. In addition, he did not appreciate the significance of organic fibres in the biomineralisation process. He had to evoke folding of secretory membranes to account for various skeletal structures, except in forms for which he proposed an originally spherulitic microstructure, where the mechanism found in *Astrosclera* could be proposed. Stearn only discussed the formation of calcareous microstructures found in Palaeozoic forms. He did not discuss possible biomineralogical mechanisms for microstructures found in Mesozoic forms.

Since 1975, there has been unfortunately little advance in our knowledge of Recent calcified demosponge biomineralisation and until more is known of the mechanisms, reconstructions will have to be tentative. They serve to illustrate the suggested inter-relationships between the soft tissue and secreted products: siliceous spicules, organic fibres and calcareous basal skeleton. Reconstructions can only be based upon what is known of the nearest postulated living relatives of Mesozoic 'stromatoporoids' and deductions from their skeletons. Therefore, soft tissue and biomineralogical processes of the Recent calcified demosponges are described. Being polyphyletic, the Mesozoic 'stromatoporoid' families will be dealt with separately. Calcarean stromatoporoids will not be discussed.

6.2. RECENT DEMOSPONGES

6.2.1. General Histology

The living demosponge (Figure 6.1) is covered with a single layer of cells, known as the pinacoderm, which delimits the organism from the external environment. Two kinds of openings occur in the pinacoderm.

1) ostia: pores for incurrent water,

2) oscula: larger exhalent water openings.

An aquiferous canal system connects several ostia to each osculum by way of two inter-digitating canal systems; an inhalent and exhalent system, each lined with pinacoderm. Between these two systems lies the mesohyl, a region containing the spicule and organic skeleton and other cell types of the sponge. Water passes through the ostia into a pinacoderm-lined vestibule, a cavity which lies beneath the outer pinacoderm (exopinacoderm) . From this cavity the water is distributed to the entire sponge from outpocketings of the pinacoderm which form inhalent canals. The only way the water can pass from the inhalent canal-mesohyl system to the exhalent canal is via hemispherical choanocyte chambers. These chambers (10-60 µm in diameter) are composed of choanocyte cells, each bearing a flagellum surrounded by a collar of microvilli. Two or three spaces, each about 5 µm in diameter, occur between the choanocytes of each chamber, and it is through these openings that water enters from the mesohyl. A larger opening (the apocyte) 25-30 µm in diameter , is on the opposite side of the chamber and allows passage of water into the exhalent canal. The distal exhalent canals converge to form larger and larger canals which eventually open out into a central exhalant cavity , leading to the osculum.

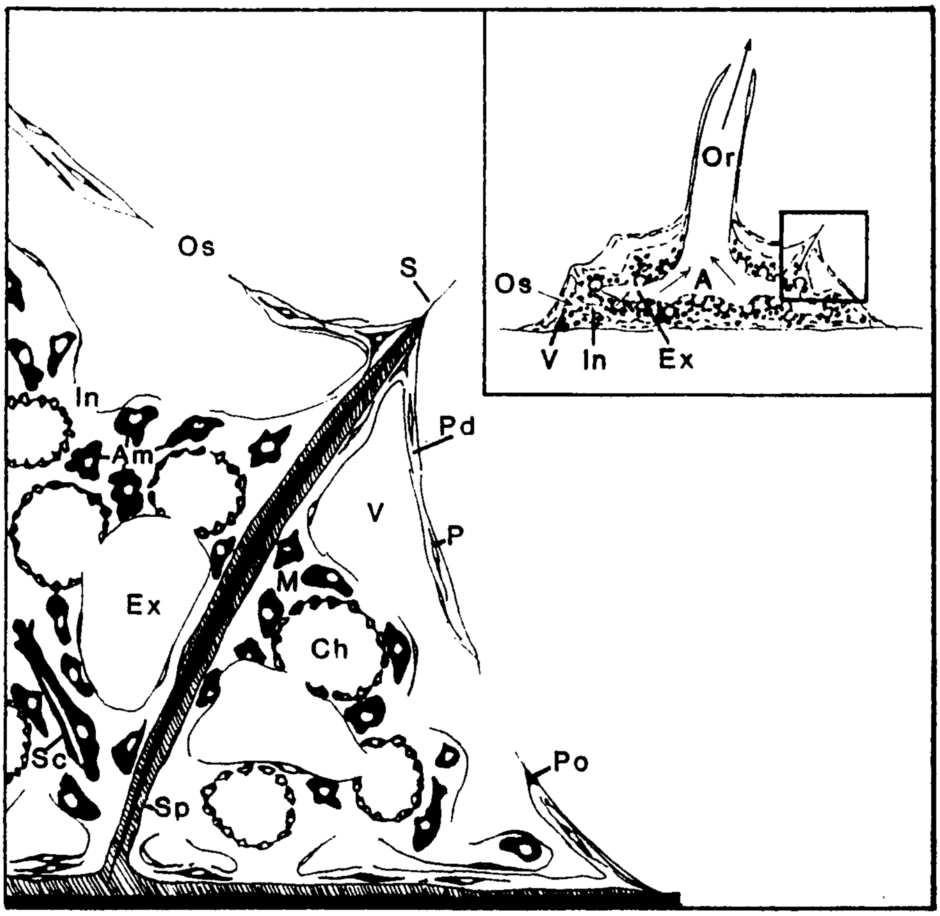


Figure 6.1: Soft tissue organisation of a demosponge.
Inset shows aquiferous organisation of a young fresh-water sponge, *Epydatia fluviatilis* .
Main diagram enlarges a portion showing how spicules are covered with spongin which isolates them from the internal milieu of the sponge.
A: Atrium; **Or**: Oscular tube; **O**: Osculum; **Am**: Amoebocyte; **Ex**: Exhalent canal; **Os**: Ostium; **In**: Inhalent canal; **Ch**: Choanocyte chamber; **M**: Mesohyl; **S**: Spicule; **P**: Pinacocytes; **Pd**: Pinacoderm; **Po**: Porocyte; **Sc**: Sclerocyte; **Sp**: Spongin; **V**: Vestibule.
(Modified from Weissenfels 1978)

The following salient cell types are found in demosponges (Hartman 1980):

1) Pinacocytes: Flattened cells which form the outer covering of a sponge and line the aquiferous system.

2) Choanocytes: Flagellated and collar-bearing cells which form the choanocyte chambers and maintain through- flow of water around the aquiferous system.

3) Collenocytes: Cells which bear filopodial extensions spanning the mesohyl, where they function as supports. Collenocytes are also important in the morphogenesis of sponges. They are thought to move fully formed spicules into place for incorporation into the skeletal framework, and may

secrete collagens and glycoproteins (Hartman 1980).

4) Sclerocytes: cells which secrete spicules intracellularily.

5) Spongocytes: Cells which secrete spongin around spicules. They often act in groups.

6) Choanoderm: Area of soft tissue where the choanocyte chambers occur.

6.2. 2. Non-calcified relatives

In Section 2.4 and Chapter 5 , it was suggested that the nearest relatives to the Mesozoic 'stromatoporoids' are non-calcified forms, which have perhaps evolved in parallel with calcified forms. In terms of spicule type and arrangement, the Milleporellidae, Actinostromariidae and nov.fam. A show similarities to the Recent Order Axinellida within the Tetractinomorpha . The Milleporellidae show a more specific relationship to the Family Agelasidae, within the Axinellida. The Burgundidae are of uncertain placing.

Fine collagen fibres occur in the ground substance of all demosponges. Spongin is found in varying quantities, the axinellids possessing abundant spongin. Often skeletal tracts (bunches of spicules) show an axial condensation from which they diverge in plumose (as in Milleporellidae) , or in plumulo-reticulate tracts (as in nov.fam. A) running to the surface of the sponge. The spicules are trapped and interconnected by the skeleton of spongin, from which the spicules echinate (protrude upwards and outwards from the fibres). Spongin fibres are a few mm. in diameter and are formed by numerous collagenous fibres 10 µm. or less in diameter. Collagen fibres of the intercellular matrix range from 20-30 µm. diameter.

Siliceous spicules are secreted by sclerocytes. Within the sclerocyte appears an axial filament 0.2 µm. diameter and reaching 0.3 µm long, lying in an elongate residence within the cell, thought to possess both protein and carbohydrate moieties (Shore 1972). It serves for the basis of silicification, a process first recognisable as a thickening around the axial filament. The spicule grows at a rate of 7.5 µm/hr during early development. According to Weissenfils and Landschoff (1977) there is a periodicity apparent in the elongations of the spicules, with a phase of growth of the axial filament of a few µm. followed by a period of silica deposition. A membrane, the silicalemina, surrounds the developing spicule and presumably functions in depositing the silica. After a spicule is completely formed, it punctures the sclerocyte which contracts to one end of the spicule. It is unclear whether the sclerocyte is phagocytised by amoebocytes or renews spicule formation (Hartman 1980). Collenocytes are probably active in moving the spicule to their final positions. In juvenile forms, spicules protrude from a basal plate of spongin in a radial orientatation. Basal exopinacocytes cover the spicule and then secrete a layer of spongin over it. As more spicules are moved into place and join the skeletal network, all parts of the spicule-spongin complex become covered with a similar layer of exopinacocytes. The skeleton of siliceous spicules and spongin fibres provides support for the soft parts of the sponge, for in sponge cultures raised in a silica-free medium, the aquiferous system fails. A flat cell mass forms, without a vestibular cavity; the sponge breaks up into numerous aggregates of cells (Weissenfels 1978).

6.2.3. Calcified demosponges

In Recent calcified demosponges little is known of the process of biomineralisation and inter-relationships between spicule, spongin and calcareous skeletons. What is known, and that deduced, is described for the various forms of Recent calcified demosponges below. Characteristics are summarised in Table 6.1.

6.2.3.1. **Ceratoporellids.** Figure 6.2 Plate 40

The four Caribbean genera comprising the Ceratoporellidae are now placed as a family within the Order Axinellida, with their closest affinities to the Family Agelasidae. These are the encrusting and massive forms *Ceratoporella* and *Hispidopetra*. The two species of *Stromatospongia* bear an irregular gross morphology and both are obligate commensals of serpulid worms. *Goreauiella* is saucer-shaped and attached to the substrate by a peduncle.

The basal skeleton of ceratoporellids is aragonite. The living tissue forms a thin veneer, no more than 1mm. thick over the calcareous mass, dipping 1-1.2 mm. into calicles (0.2-0.5 mm. diameter) or meandroid furrows in the surface of the aragonite (Plate 40,fig. a) The siliceous spicules (acanthostyles and acanthostrongyles) and spongin become trapped in the aragonite as the calcareous skeleton grows upwards. The calicles increase by longitudinal fission and are filled solidly with an epitaxial growth of aragonite as the living tissue moves upward (Plate 16, fig.c).

Table 6.1: Characteristics of Recent calcified demosponges (Modified after Vacelet 1985)

SPECIES	SPICULES	CALCAREOUS SKELETON: MICROSTRUCTURE	MINERALOGY	TRACES OF AQUIFEROUS SYSTEM	REPRODUCTIVE AFFINITIES	GEOGRAPHIC DISTRIBUTION	SYM BIOTIC FLORA
Astrosclera willeyana	Acantho-styles. (May be absent.) Partially enclosed.	Spherulitic, Intracellular.	Aragonite	Astrorhizae	Agelasidae, Tetractino-morpha.	Indopacific	Yes
Ceratoporellidae	Acantho-styles. Partially enclosed.	Modified Spherulitic	Aragonite	Astrorhizae	"	Caribbean & Pacific.	Yes
Calcifibrospongia actinostromarioides	stron-gyles. Enclosed.	Spherulitic, Collagen matrix.	Aragonite	Stacked astrorhizae	Renieridae, Haplosclerida, Ceractino-morpha.	Caribbean	?
Merlia spp.	Tylo-styles and micro-scleres.	(Facultative) Fascicular fibrous.	Mg-calcite.	- Tabulae	Poescilosclerida, Tetractino-morpha	Circum-tropical & Mediterr-anean.	No
Acanthochaetetes spp.	Tylostyles micro-scleres.	Irregular	High-Mg calcite.	astrorhizae	Spirastrellidae, Hadromerida, Tetractino-morpha.	Pacific.	No
Vaceletia crypta	-	Irregular, external spongin template.	Aragonite	siphon & pores.	Ceractino-morpha.	IndoPacific	Yes

PLATE 40: Living tissue of *Ceratoporella nicholsoni*

Thin veneer of stained soft-tissue (pink) and trapped acanthostyle spicules, at whose bases (arrowed) the penicilliate tufts of calcareous skeleton fibres are initiated.
Scale bar=1mm.

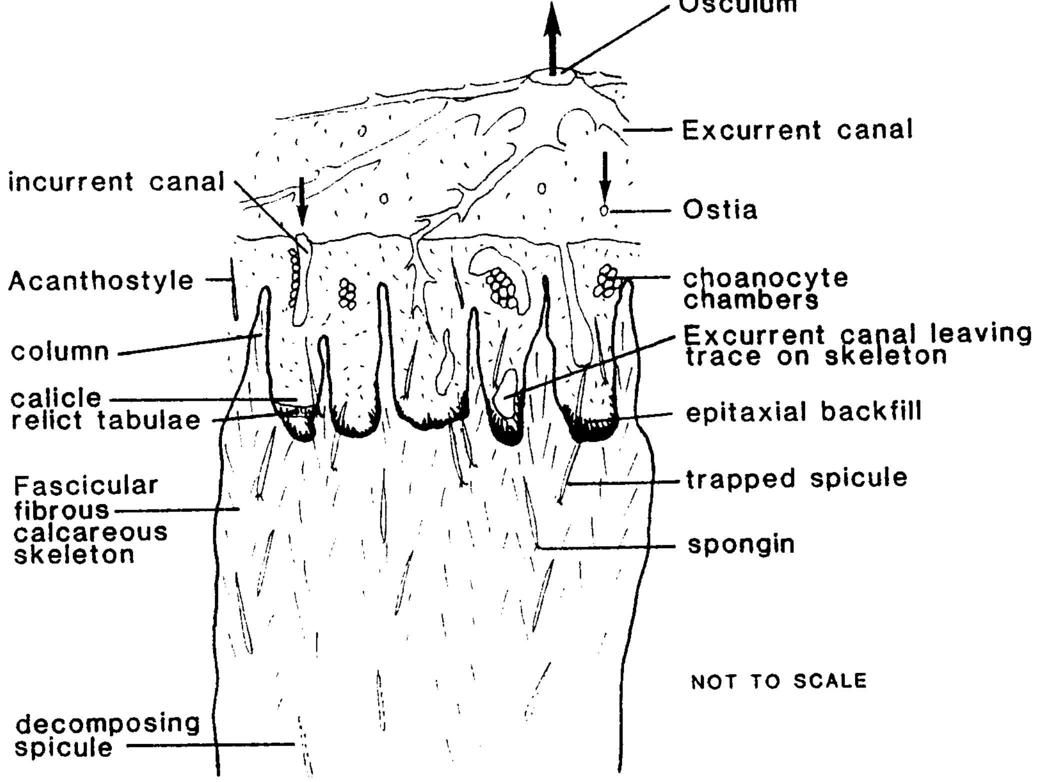


Figure 6.2: Longitudinal section showing general histology of *Ceratoporella* and relationship of the spicule, spongin and calcareous skeletons to the living tissue. Aquiferous system is shown in surface view. Fascicular fibrous skeleton is initiated in tufts at the spicule bases. Epitaxial backfill is continuous. Excurrent canal leave traces on the skeleton surface, but are not enclosed by it. (Not to scale).

The calcareous skeleton is formed of acicular or fibrous crystals arranged in what was described as a fascicular-fibrous microstructure. On examination of thin-sections, however , the microstructure is in fact a modified spherulitic form, where preferential crystal growth, parallel to the growth axis of the skeleton, has taken place (Plate 5,f ig.a) This confirms the observations of Cuif (1973). These bunches of crystals are termed sclerodermites, which Hartman and Goreau (1975) observed to form around blobs of organic matrix (?spongin) surrounding the heads of some spicules. In *Ceratoporella*, the spicules project upwards and outwards from the calicle walls. The secondary epitaxial growth is continuous, and the siliceous spicules are eventually totally enclosed in aragonite.

In *Hispidoptera*, the basal skeleton bears upright lamellae, knobs and branched processes at the surface. They characteristically enclose dense 'bushes' of stylote siliceous spicules.

Thus, to some extent, the positioning of the calcareous skeleton appears to be determined by the placing of the spicule and spongin frameworks.

One ostium, or sometimes two, open out into the tissue filling a single calicle. These lead to inhalent canals which give off branches that communicate with the choanocyte chambers. The chaonocyte chambers are small, 12-23 µm. in diameter. These in turn open out into the fine excurrent canals that become gradually larger and run to the surface where they join other such canals, increasing in size, and converging upon oscular openings. In living specimens the surface is covered with star-shaped patterns of excurrent canals. (Plate 11 fig. d). These canals often converge upon an osculum at the summit of a mamelon, which may extend 5 mm. above the general sponge surfaceof *Ceratoporella* .

Oscula generally occur at the convergence of excurrent canals, but sometimes occur along their length. In *Goreauiella* , the oscules open out at the edges of the calcareous skeleton.

6.2.3.2. ***Astrosclera*** Figure 6.3 Plates 41 and 42

Astrosclera , a nodular form ranging from a few mm. to 15 cm. in diameter, is known from the Pacific, Caribbean, Red Sea and Mediterranean (Plate 41, fig. a). Vacelet (1983) suggests that the closest affinities are to the family Agelasidae within the Axinellida.

The basal calcareous skeleton consists of a fine reticulum of aragonite with no differentiation into pillars and lamellae. The microstructure is spherulitic (Plate 41,fig. b) . The calcareous spherules are formed intracellularly by amoebocytes as small nuclei near the surface of the sponge and then transported to a position where they grow larger and add to the general calcareous skeletal network (Plate 42). The living tissue penetrates the mesh of the skeleton to a depth of approximatately 1 cm., and a secondary deposit of acicular calcite crystals partially fills the abandoned inner skeletal reticulum(Plate 10, fig.c). In the Indian Ocean, *Astrosclera* secretes siliceous acanthostyles but Pacific populations largely lack them, although when present , the spicules are incorporated into the calcareous skeleton. There appears to be no discernible direct relationship between the spicules and the positioning of the calcareous skeleton; they are incorporated by chance.

Below the pinacoderm are large exhalent canals 60-80 µm. in diameter which branch downwards and outwards into the skeletal tissue to form astrorhizal-like structures. No tabulae are found.

Figure 6.3: General histology of *Astrosclera willeyana*

Figure 6.3A: Longitudinal section showing relationship between skeletal elements and the soft tissue and aquiferous system.
The excurrent canals are enclosed by the calcareous skeleton. Spicules do not appear to play any role in the calcareous skeleton formation. The spherules are secreted by mesenchymal amoebocytes and are then moved to their position. No filling tissue is present.
(Modified from Stearn 1975)

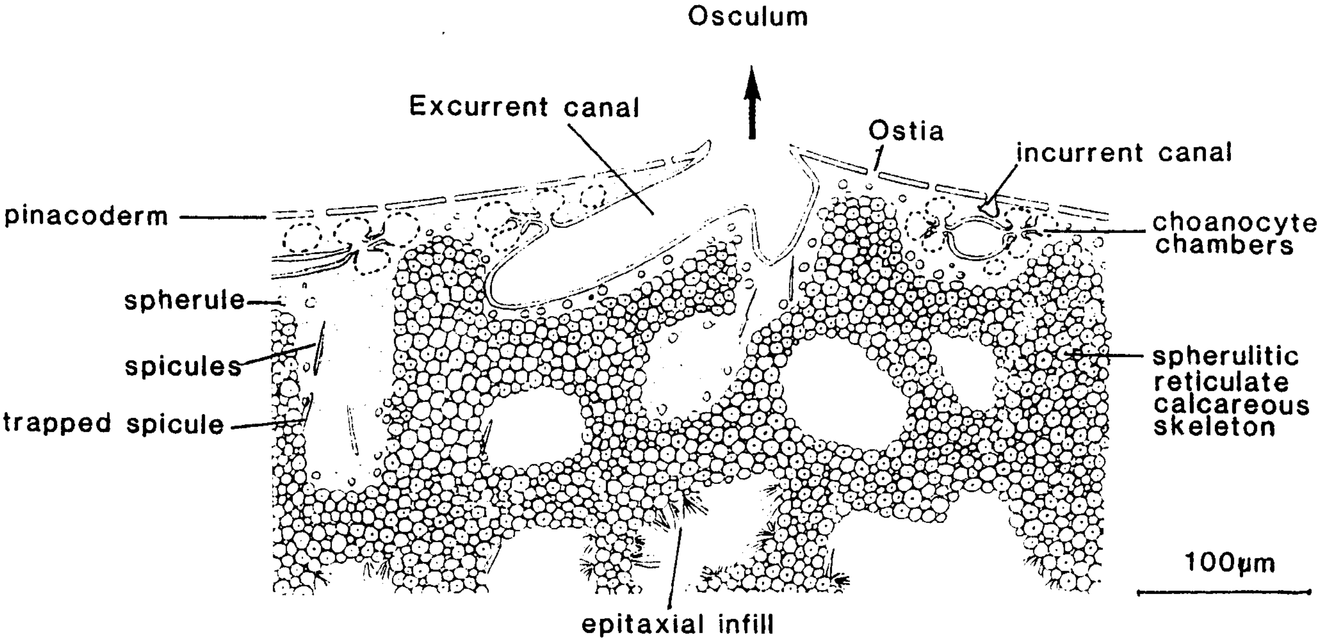


Figure 6.3B: Transverse section through the stellate exhalent canals showing the relationship between the choanoctye chambers and the calcareous skeleton. Section is taken near the top of the skeleton. Pinacoderm is depicted as a single layer only.
(Modified from Stearn 1975)

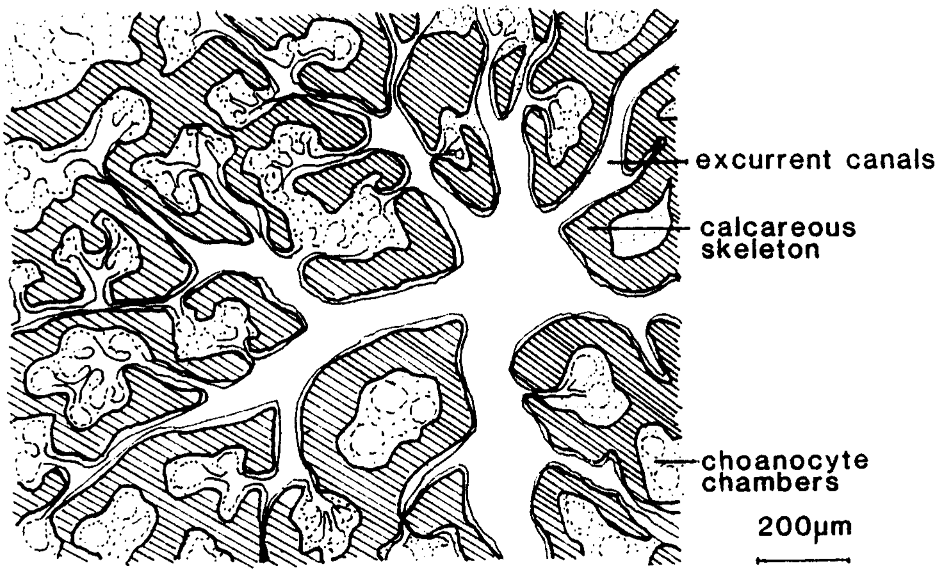


PLATE 41: Living tissue of *Astrosclera willeyana.*

Figure a: Living specimen showing nodular gross morphology, yellow-coloured soft-tissue and excurrent canals (not to be confused with the ophiuroid). Great Barrier Reef, Australia. (From 'The Great barrier Reef' Published by Reader's Digest)
Scale bar=1cm.

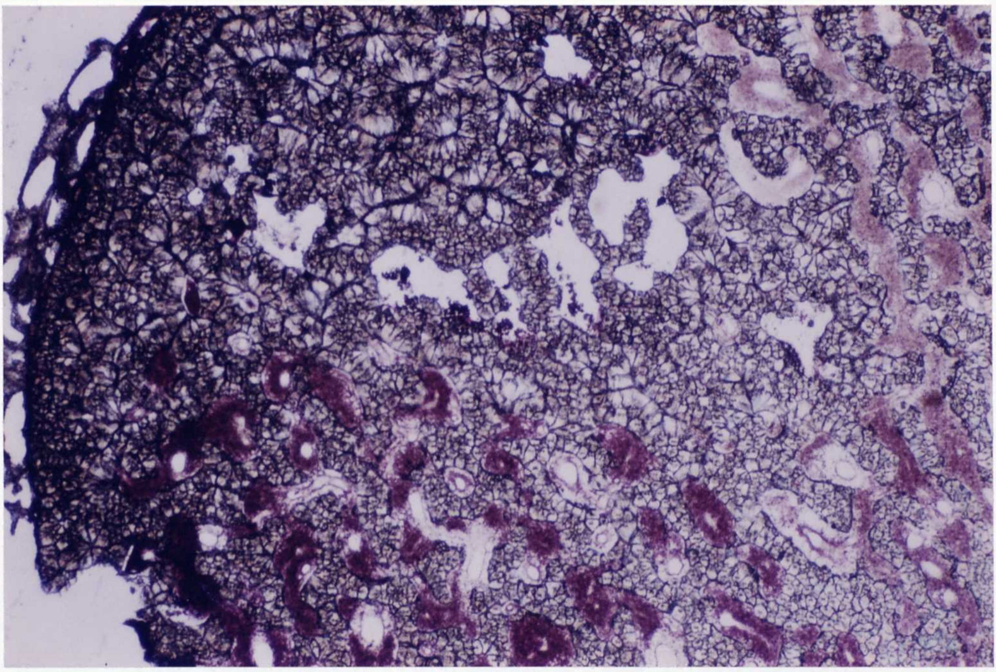


Figure b: Tangential thin-section showing stained living tissue (pink) and compound spherulitic calcareous skeleton. Jamaica.
Scale bar=1cm.

PLATE 42: *Astrosclera willeyana*

Tangential thin-section showing intracellular spherule formation within living tissue.

C: Calcareous skeleton; **S**: Soft-tissue; **I**: Spherule forming in soft-tissue. Sponge Collection. B.M. (N.H.). Jamaica.

Scale bar = 1mm.

6.2.3. 3. ***Calcifibrospongia*** Figure 6.4.

Calcifibrospongia is known only from the Caribbean. Vacelet (1985) proposes that it is a haplosclerid sponge with affinities to the family Renieridae, within the Ceractinomorpha.

Calcifibrospongia possesses a massive reticulate skeleton of aragonite. The exopinacoderm bears a reticulum of tracts of thin strongyles covering the entire sponge surface. The calcareous skeleton begins at the floor level of the vestibule and has the form of irregular sheets of aragonite , pierced by holes allowing a continuity of living tissue to occupy the interskeletal spaces up to a depth of 3 cm. beyond the vestibule floor, the mesohyl and choanoderm occurring in the interstices of the calcareous skeleton. The entire skeletal meshwork encloses a lattice of siliceous strongyles and some protrude beyond the surface of the skeleton (Hartman 1979).

When the aragonite is dissolved, a fibrous organic matrix remains with exactly the same reticulate structure as the aragonite skeleton. The aragonite appears to be laid down within a collagenous fibrous network. The calcareous skeleton is formed of elongated sclerodermites 60-110 µm long (Plate 5, fig. e). The centres of calcification may form simultaneously along or within a particular length of fibre; the acicular crystals of aragonite grow out in all directions from each centre until they reach the boundary of the organic fibre ,or are stopped by the crystals of a neighbouring sclerodermite. It is noted that the spicules frequently serve as the centres for calcification . Double rows of sclerodermites are also found (Hartman 1979).

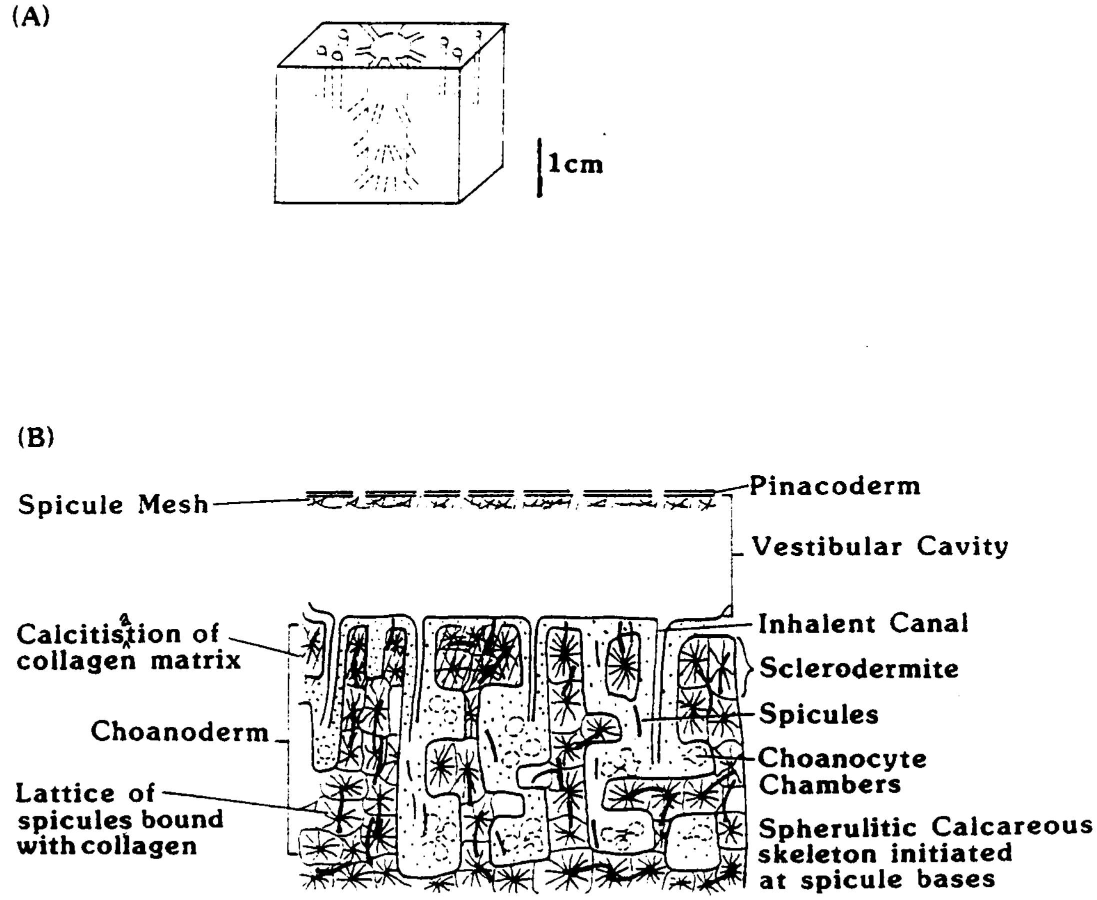
The sheets of aragonite form a meshwork that totally encloses the aquiferous system. Closely spaced vertical tubes, up to 0.4mm. in diameter, run from the vestibular cavity (an extensive water-filled cavity directly beneath the pinacoderm) to the interior of the sponge. Vertical tubes of greater diameter run to the outer surface, carrying exhalent canals that open out at intervals of 15-20 mm. via oscula, 1-5-2mm. diameter. As the oscula pass to the surface, each receives several vertically stacked, stellate whorls of 4-6 secondary exhalant canals, which drain the choanosomal region of the sponge (See Figure 6.9). The choanocytes chambers are exceptionally small, 17-18 µm. in diameter.

Calcifibrospongia can show deposits of epithecal material varying from 40-250 µm. thick. These

Figure 6.4: General histology of *Calcifibrospongia actinostromarioides*.

A: Stylised block diagram showing the form of one aquiferous unit within the calcareous skeleton. Scale bar = 1cm.

B: Longitudinal section showing soft tissue arrangement and biomineralisation. Spicules are bound in a lattice by collagenous fibres. Calcitisation appears to initiate at the spicule bases within this matrix. Relationship of the aquiferous system is not shown.
(Not to scale)



represent planes of the successive dieback and regrowth of the skeleton (Figure 6.9, longitudinal section). Some secondary thickening of the skeletal elements is noted, but never completely filling the original pore space as in the ceratoporellids.

6.2.3.4. ***Acanthochaetetes*** Figure 6.5. Plate 8. Fig.b.

Vacelet (1985) placed the Family Acanthochaetetidae in the Order Halichondria within the Tetractinomorpha, with close affinities to the Spirastrellidae.

The basal calcareous skeleton is high-Mg calcite, with an irregular microstructure of crystals (1-8 µm. long) orientated in one plane only, giving the appearance of a lamellar microstructure in longitudinal section. The living tissue forms a thin veneer. The surface of the skeleton is pitted with calicles reminiscent of *Ceratoporella*, but spines project from the walls of the calicles, either irregularily clumped or arranged in vertical rows. The calicles are 1.2-2 mm. deep and 0.3-0.6 µm in diameter. Instead of the abandoned parts of the skeleton being filled with a secondary epitaxial backfill, the portions below the living tissue are sectioned off by a series of tabulae or horizontal partitions .

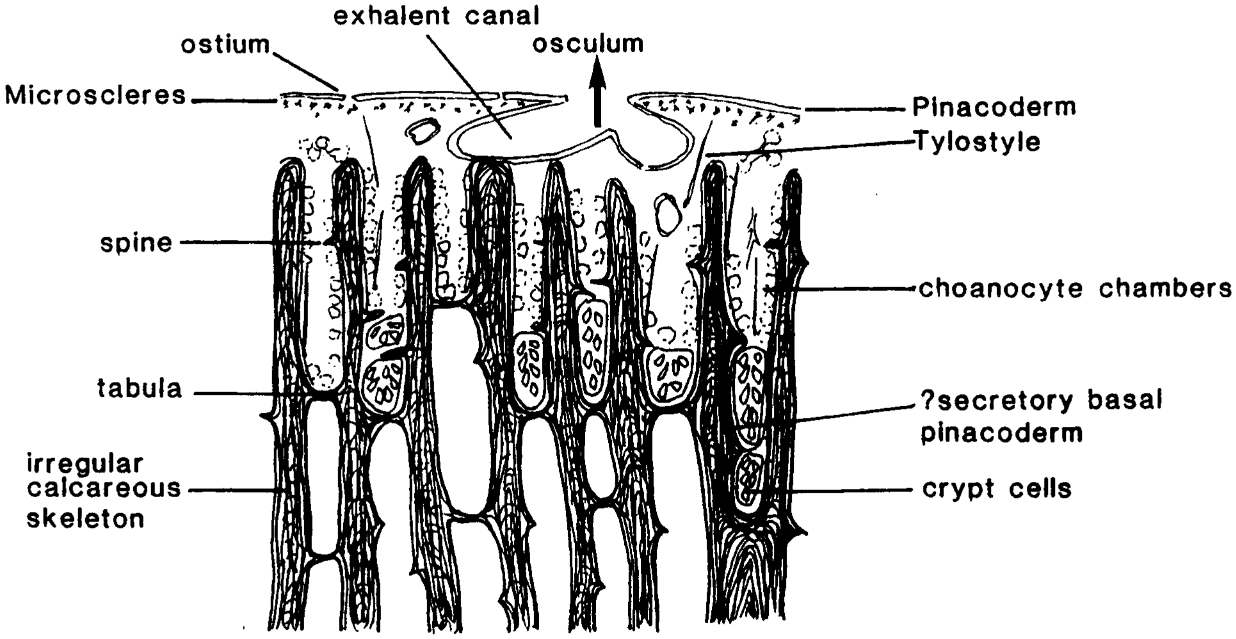


Figure 6.5: General histology of *Acanthochaetes wellsi.* Longitudinal section showing relationship between living tissue and skeletal elements. Excurrent canals leave an impression on the skeletal surface, but are not enclosed. The basal pinacoderm appears to secrete the irregular calcite skeleton. The tabulae and spines are precipitated as part of the primary calcareous skeleton; there is no secondary skeleton. The crypt cells may play a part in calcification.
(Not to scale)

Growth of the calicle walls is incremental and layered, tabulae and spines being outgrowths from the calicle walls, and not secondarily precipitated filling tissue. The siliceous spicules are megascleres (tylostyles) and microscleres (asters, spirasters) . The microscleres form a dense layer at the surface of the living tissue while the tylostyles are aligned parallel to the calicle walls. In living forms, the spicules are not incorporated into the calcareous skeleton, but in fossil representatives they are , although by chance. The megascleres tend to occur parallel to the calicle walls, and the microscleres within the tabulae.

The pillars, spines and tabulae grow incrementally and in an integerated way. Nannometre sized organic fibres act as the matrix for calcification. The calicle wall centres are richest in organic matrix. The excurrent canals sometimes leave impressions on the skeletal surface as in ceratoporellids

6.2.3.5. ***Merlia normani*** Figure 6.6. Plate 43.

Merlia is an extremly thin encrusting sponge, usually found on gastropod shells. It is known from the Mediterranean, Indian Ocean and West Indies. The characteristic spiculation of megascleres (tylostyles) and microscleres (clavidiscs, rhaphides and commatas) places it in the familiy Biemidae within the Poescilosclerida(Tetractinomorpha). Three species are known and only one bears a calcareous skeleton. Therefore the calcareous skeleton is a facultative production and its mere presence is of no taxonomic importance. The basal calcareous skeleton is low Mg-calcite, composed of contiguous rows of calicles with openings 0.12-0.15 μm in diameter. Tabulae, each perforated with a central hole are laid down as the skeleton is built up. No more than four tabulae occur, dividing the calicle into a maximum of five compartments. The pillars are stout fibre fascicles which form the calicle corners and from these form three vertical flanges at 120^{o}, which join with adjacent pillars to form hexagonal spaces (See Figure 6.6.). Kirkpatrick (1911) showed that the tabulae are precipitated by the basal pinacoderm horizontally across the calcicles.

The choanosome lies above and extends into the uppermost compartment of the calicles. Deeper compartments house crypt cells which accumulate reserves. They may function as gemmules or construct the calcareous skeleton.

The canal and choanocyte chambers occupy the depressions between the growing flanges at the tip of this structure. There are no traces of the aquiferous system on the skeleton, the tissue being relatively thick compared with the ceratoporellids.

PLATE 43: Soft tissue arrangement in *Merlia normani.*

Merlia normani encrusting a gastropod shell. Longitudinal section showing thin veneer of stained soft-tissue (pink), dipping into calicles of fibrous calcareous skeleton (**C**). Tabulae (T). J.Vacelet Collection. Jamaica.

Scale bar = 1mm

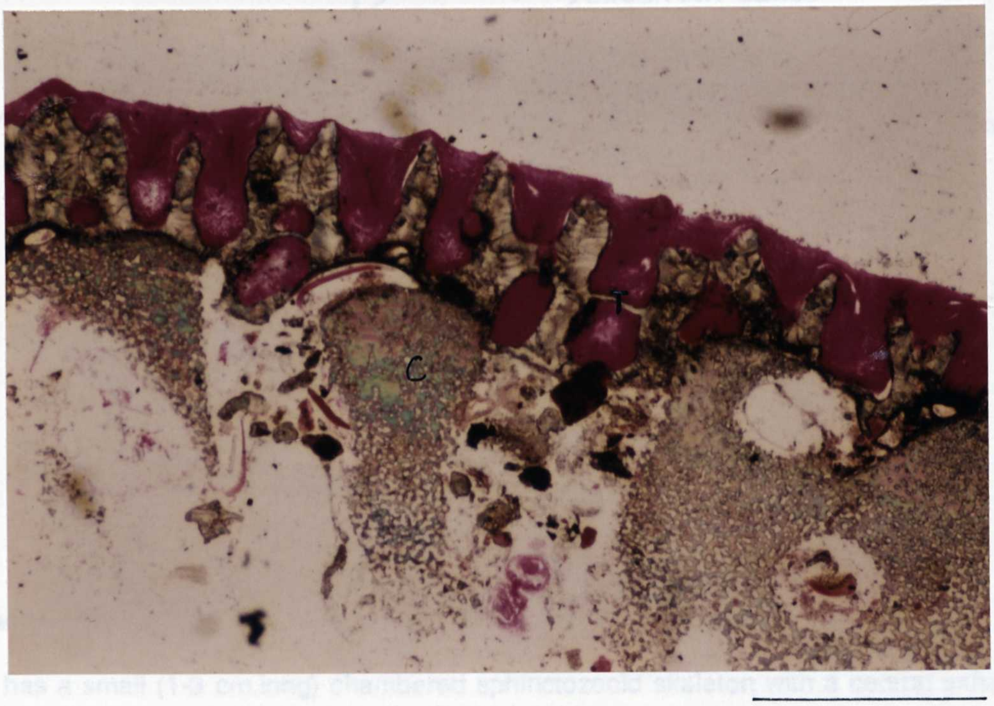
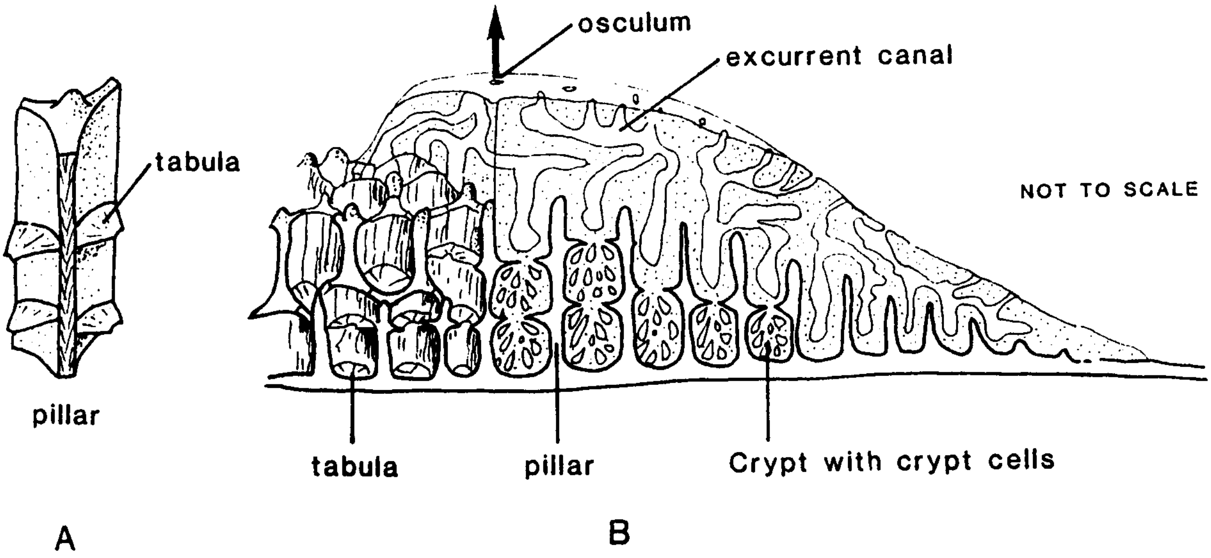


Figure 6.6: General histology of *Merlia normani.*
A: Cross section through pillar showing fascicular-fibrous microstructure and tabulae.
B: Longitudinal section showing relationship of soft tissue to calcareous skeleton. Crypt cells may function in the calcification process. No traces of the aquiferous system are left on the calcareous skeleton.
(Modified after Kirkpatrick 1910. Not to scale)



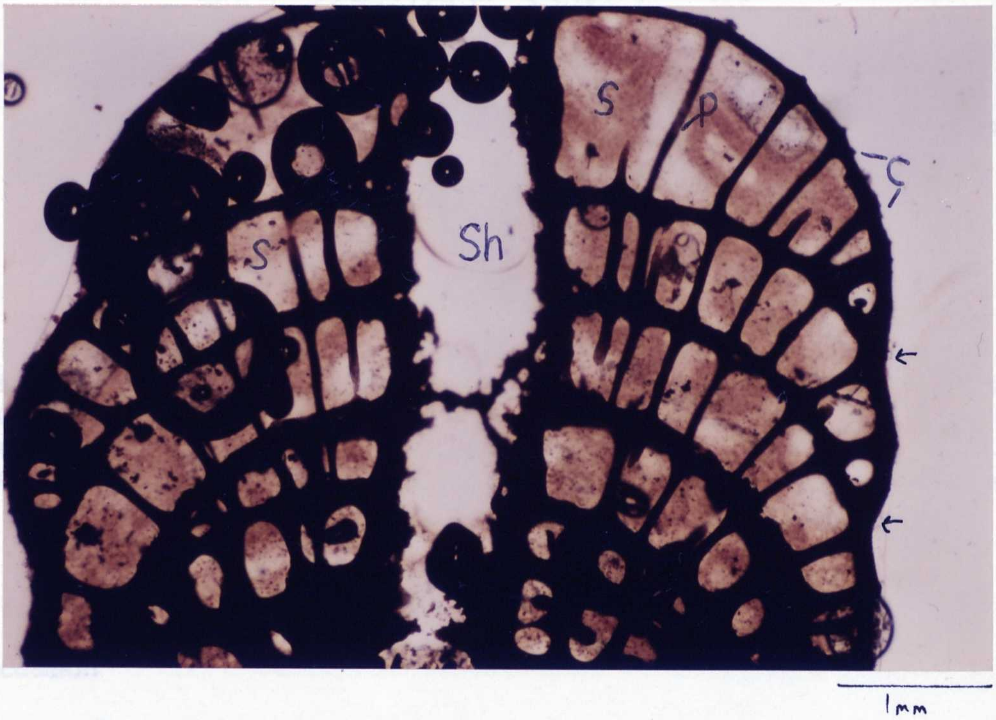
6.2.3.6. ***Vaceletia*** Figure 6.7 Plate 8, fig.a and Plate 44.

Vaceletia has a small (1-3 cm.long) chambered sphinctozooid skeleton with a central exhalent siphon (Plate 44) and is found only in the Mediterranean. It bears a leuconoid, dense choanosome with small choanocyte chambers. The ectosomal layer is thin. No spicules are secreted. These soft tissue chracteristics and possession of a parenchymella larvae place *Vaceletia* in the Ceractinomorpha (Vacelet 1985).

The living tissue is totally internal within the hemispherical chambers (Plate 44). The chamber walls are perforated and composed of a feltwork of aragonitic microfibrils (irregular microstructure, see Plate 8, fig. a). The skeleton of a new chamber appears first as an organic matrix, forming the template for the later calcification.The perforations of the outer chamber serve as inhalent pores passing to the choanocyte chambers and out through the central exhalent siphon. The trabeculae (or pillars) are secondarily precipitated to support the hemispherical chambers and are formed by mineralisation of organic strands (Plate 44).

PLATE 44: Soft tissue arrangement in *Vaceletia crypta.*

Longitudinal thin section of top four chambers. Living tissue (**S**) and calcareous skeleton (**C**). Successive chambers are arrowed. Pillars (**P**); Siphon (**Sh**).



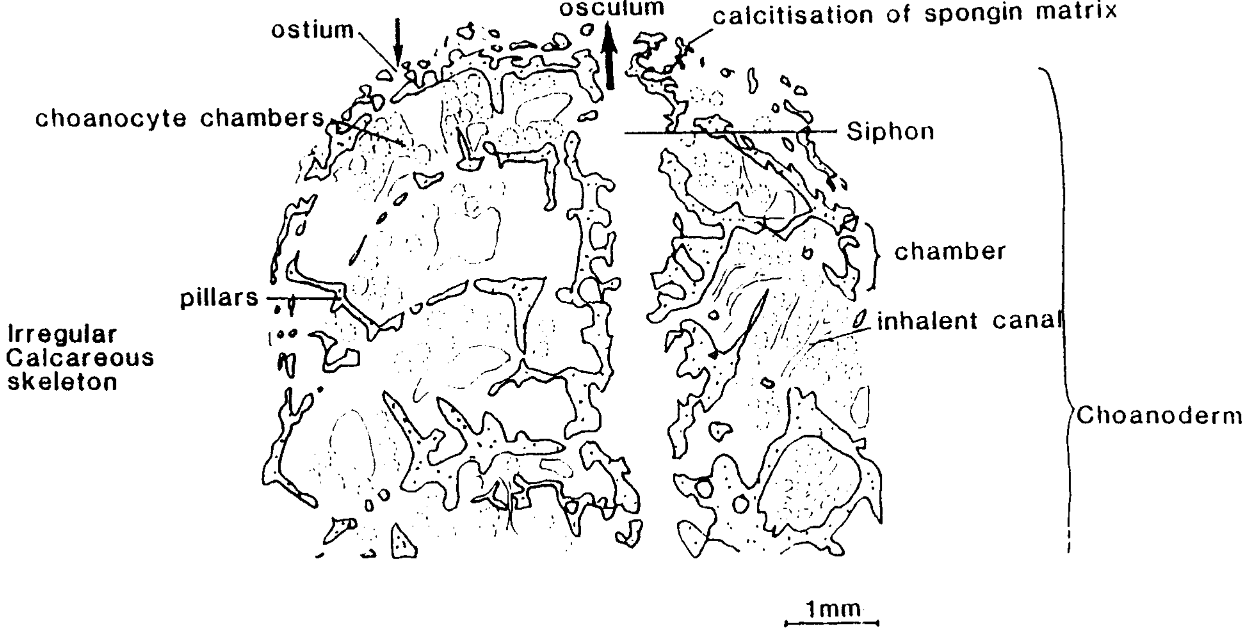


Figure 6.7: Longitudinal section of *Vaceletia crypta*, showing relationship of soft tissue to calcareous skeleton. Only four chambers are shown. Lower-most chambers are abandoned. Pillars are secondariliy secreted. All biomineralisation is by calcification of an organic matrix. Detail of the mechanism for the formation of new chambers is not known. (Drawn from photograph ,Vacelet 1979)

6.2.4. Discussion

Even though the Recent calcified demosponges are clearly a polyphyletic group, they share certain features, probably convergent, which are perhaps a consequence of possessing a calcareous skeleton.

1) All the Recent calcified demosponges have extremely small choanocyte chambers (12-23 µm). Hartman and Goreau (1970) suggested that this might be a function of possessing a very thin veneer of tissue. However, *Calcifibrospongia*, which bears the smallest diameter of chamber, has up to 3 cm. of tissue and is a massive sponge (up to 50cm. diameter).

Stearn (1975) suggested that in *Stictostroma* the choanocytes chambers might be 250 µm in diameter. From Recent calcified demosponge analogies, it is likely that the 'stromatoporoids' possessed very small choanocyte chambers and perhaps all calcified demosponges had small choanocyte chambers.

2) All have a cryptic niche habitat in sub-tropical and tropical reef environments.

3)When all three skeletal elements are present, the sequence of precipitation is always the same:

a) Spicule formation, transportation and orientation,

b) Spongin/collagen fibres to bind the spicules in place,

c)Calcareous skeleton precipitation.

The calcareous skeleton is always initiated from an organic matrix (with the possible exception of *Astrosclera*), and often at the spicule bases.

Only the calcareous skeletons of *Merlia* is possibly formed by the secretion of a folded basal pinacoderm.

4)Forms which have a thin veneer of tissue show traces of the excurrent canal system as astrorhizal grooves or ridges in the surface of the calcareous skeleton. In these forms the calcareous skeleton has a calicular 'chaetetid' grade of organisation .

5) Forms which have a greater thickness of living tissue have aquiferous systems which penetrate the skeleton and leave internal traces. e.g. *Astrosclera.*

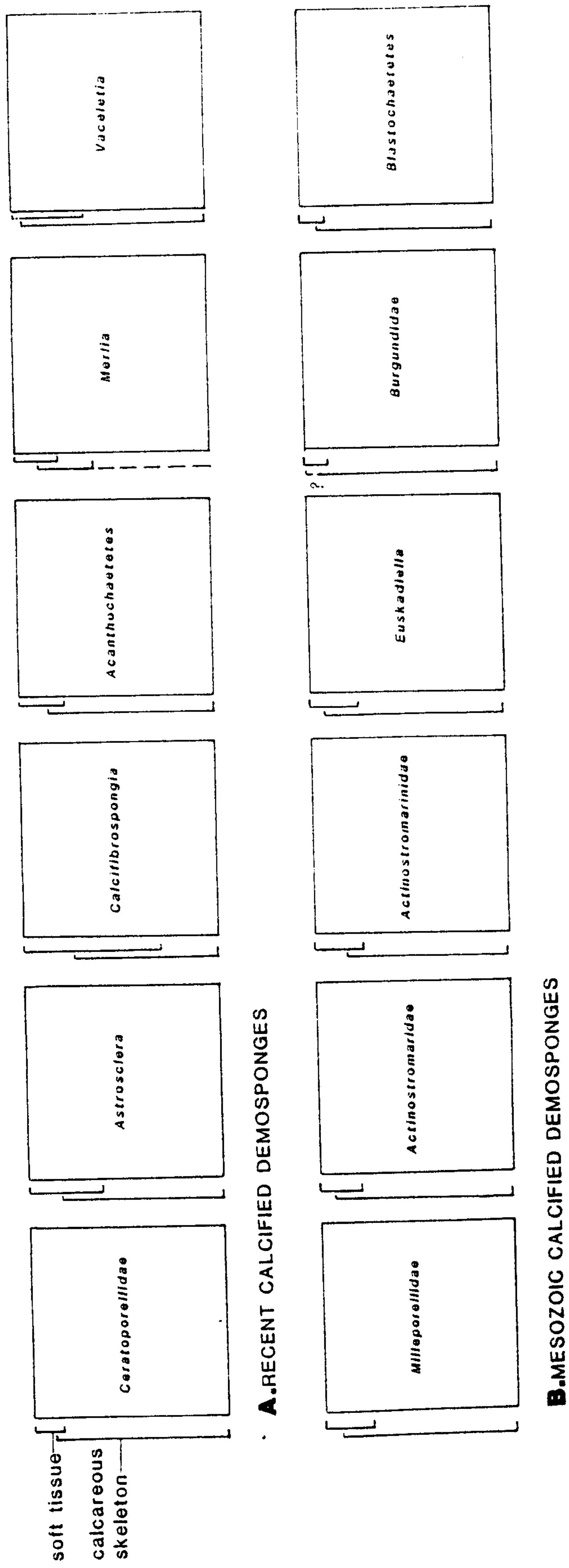
The form of the astrorhizae is related to the thickness of the tissue. A greater thickness of tissue requires a greater penetration of the aquiferous system to drain it, thus producing an 'open' calcareous skeleton.

A diagrammatic comparison of the thicknesses of living tissue in Recent calcified sponges and penetration into the calcareous skeleton is shown in Figure 6.8A.

6) Not all Recent calcified demosponges show traces of their excurrent canal system on the skeletal surface or interior, but all Recent calcified demosponges bear stellate exhalent canals. Only some canals must be in a position to affect the secretion of the calcareous skeleton and so are preserved. A commonly held theory is that the pressure of water flow, through the exhalent canals causes the presence of exhalent traces on the calcareous skeletal surface . But, it is more likely that the very

Figure 6.8 (overleaf): Diagrammatic representation of comparative thicknesses of living tissue and extent of penetration into the calcareous skeleton in calcified demosponges. Dotted lines indicate possible or occasional extent of tissue.
Figures are not to scale, but show relative arrangements.
A: Recent calcified demosponges;
Merlia never has a calcareous skeleton more than a few mm. thick. *Vaceletia* has a totally external calcareous skeleton, except during periods of new chamber growth. The occasional migration of living tissue beyond the calcareous skeleton is represented by a broken line.
B: Suggested relationships for Mesozoic 'stromatoporoid' demosponges. The possibility of *Burgundia* possessing a totally external skeleton is indicated by a broken line.

Figure 6.8



A.RECENT CALCIFIED DEMOSPONGES

B.MESOZOIC CALCIFIED DEMOSPONGES

position of the astrorhizal canals would prohibit any precipitation of calcareous material below them.

7) Siliceous spicules eventually dissolve when trapped in the calcareous skeleton of all Recent demosponges. Demosponge spicules are covered by a layer of spongin, which isolates them from the internal medium of the sponge and therefore serves as protection. Once the spongin coating breaks down the spicules decompose. When trapped by a calcareous skeleton the supporting function of the spicules is no longer required.

8) The same microstructure of the calcareous skeleton can be formed by totally different mechanisms. e.g. *Astrosclera* secretes spherules internally, then transports and attaches them to the calcareous skeleton. *Calcifibrospongia* forms spherulites in situ, initiated at spicule bases within a collagenous network. Here, quite different roles are played by the spicular and spongin elements.

9) The characteristics of *Calcifibrospongia* appear tc present the best general analogue for Mesozoic 'stromatoporoids':

This genus bears:

a) A reticulate skeleton of lamellae and pillars,

b) the presence of aquiferous system traces within the calcareous skeleton and

c) A primary spicule framework, about which the secondary calcareous skeleton is initiated.

10) As noted in 3, the placing of the calcareous skeleton fibres appears to be initiated from some organic skeletal component.

It is not necessary for the calcareous skeleton to have grown around the aquiferous system in situ, merely for the organic matrix to be emplaced. For, if tabulae are present within the astrorhizal tubes, which are themselves encased in calcareous tissue, the living tissue must have been present to lay down spongin, which perhaps formed the basis for the precipation of the tabulae.

In most Recent sponges the aquiferous system shows great mobility; oscular positions are often rearranged on a daily basis to adjust to fluctuating environmental conditions or adjust to soft tissue growth (S.Stone pers. comm.1985). Enclosing the aquiferous system in skeletal substances, e.g spongin or $CaCO_3$, would greatly restrict aquiferous system mobility and the aquiferous system would antedate all skeletogenic products . We could conclude either that the environments in which calcified demosponges lived were relatively stable , dispensing with the frequent need to alter aquiferous system arrangement or that the risks of tissue abrasion were more important for them than aquiferous system flexibility. Instead, they could produce a wave resistant skeleton that would raise the animal above the general substrate surface. The possession of a rigid calcareous skeleton enclosing the aquiferous sytem might also account for the incremental growth pattern of many stromatoporoids.

However, if the sponge had a thin veneer of tissue, where the aquiferous system was surficial and not in contact with the area of skeletogenesis, the sponge could maintain mobility of its aquiferous system.

6.3. MESOZOIC 'STROMATOPOROID ' DEMOSPONGES

To understand the nature of skeletal growth in Mesozoic'stromatoporoids', it is necessary to determine :

a) the proximity to and influence of the aquiferous system in relation to the skeletal elements,

b) the thickness of living tissue present.

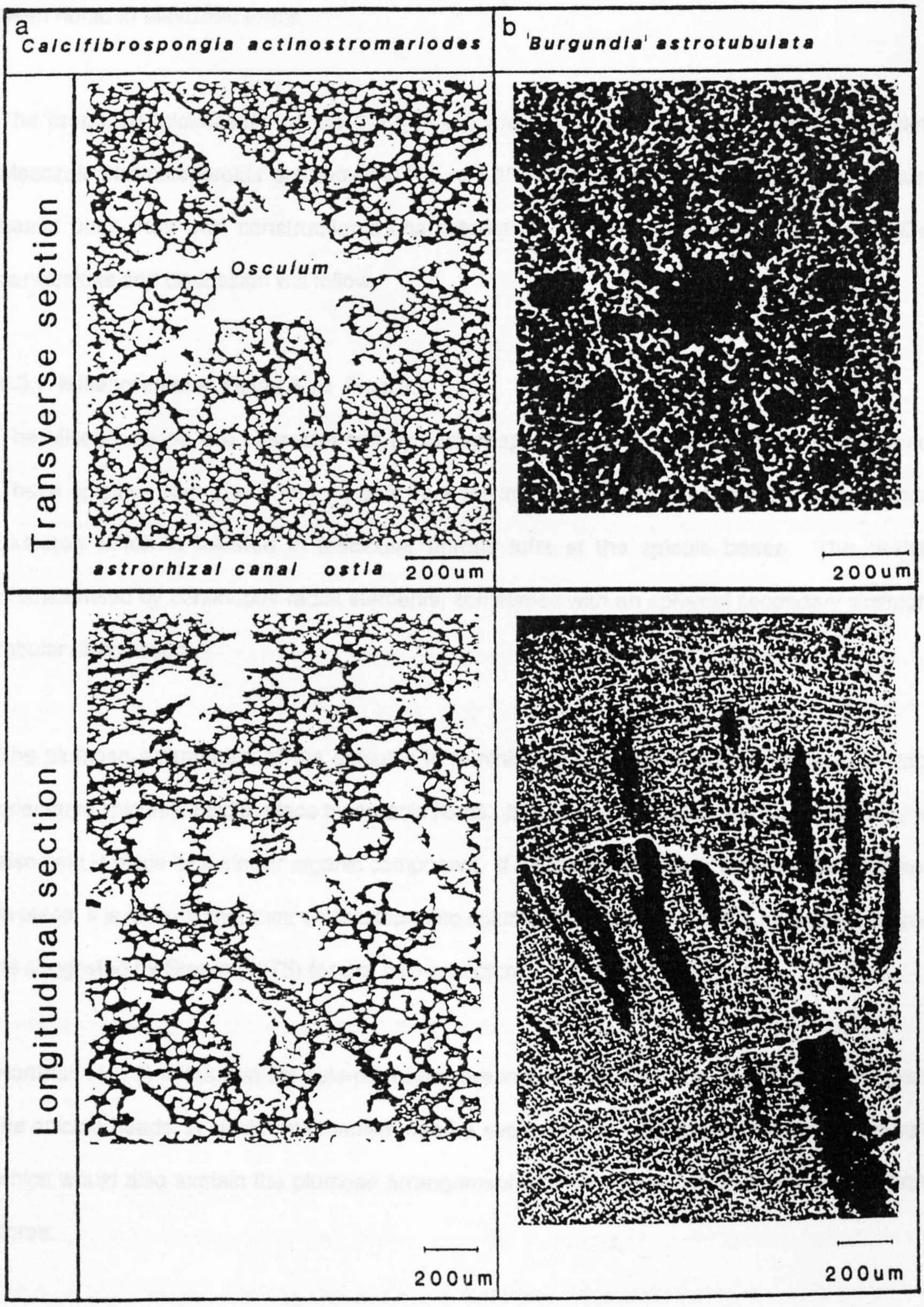
c) The zone occupied by the living tissue in succesive growth stages of the skeleton,

d) the direct relationship between the soft tissue and its skeletal elements,

e) the biomineralisation mechanisms of the primary and secondary precipitated calcareous skeleton.

The aquiferous unit type can give some indication of the amount of tissue present . E.g. Figure 6.9 shows the aquiferous system of a Mesozoic stromatoporoid compared with *Calcifibrospongia.* Similar aquiferous units imply similar depths of living tissue. Likewise Figure 2.10 shows the stacked astrorhizal units of *Burgundia wetzeli,* where secondarily precipitated tabulae have repeatedly sectioned off abandoned parts of the skeleton as the animal has grown. Tissue was probably limited to one interlamellar space. If the aquiferous system is enclosed within the skeleton, there must have been some thickness of tissue.

Figure 6.9: Comparison of the aquiferous system of **A:** Recent *Calcifibrospongia actinostromarioides* , with **B**: the Upper Jurassic stromatoporoid *'Burgundia' astrotubulata*. The ostia, osculum and astrorhizal canals are directly comparable. The length of the osculum, with no secondary tabulae sectioning off abandoned parts of the skeleton,i ndicates that *"B." astrotubulata*, like *C.actinostromarioides* , possessed a considerable thickness of tissue.
Also note the epithecal deposit seen in the longitudinal section of *Calcifibrospongia sp.*



Before detailed discussion of Mesozoic 'stromatoporoid' soft-tissue reconstruction, I would like to mention the finding of Twitchell (1929), who noted the presence of a possible spicular network above the calcareous skeleton surface in an undescribed species of the Palaeozoic genus *Clathrodictyon,* similar to that found in Recent *Calcifibrospongia sp.* However, this structure has not been noted in Mesozoic forms.

The proposed thicknesses of the living tissue and penetration into the calcareous skeleton in Mesozoic 'stromatoporoids' are shown in Figure 6.8B. Since Mesozoic stromatoporoid families are based upon their own constructional characteristics, they are dealt with individually. General conclusions and discussion will follow.

6.3.1. **Milleporellidae** Figure 6.10 Plate 2.

The Milleporellidae are characterised by club-shaped styles arranged in a plumose orientation. These spicules form the primary framework for the subsequent precipitation of the calcareous skeleton which is initiated in fascicular fibrous tufts at the spicule bases. The skeleton is characterised by continuous radial elements, sometimes with an epitaxial secondary skeleton, and tabular filling tissue.

The plumose arrangment of the spicules is reminiscent of axinellid echinating spicule tracts of orientated spicules, held in place by organic fibres. It is likely that the Milleporellidae spicules were also held in place by a similar organic component. If a network of organic fibres did hold the spicules in place, it is unlikely that their calcification into columns was due to a folded secretory pinacoderm, as suggested by Stearn (1975) for this microstructure.

Hartman (1970) notes that the sclerodermites are initiated from isolated blobs of organic matter at the spicule heads. A similar mechanism can be evoked for the calcification of the Milleporellidae, which would also explain the plumose arrangement of the spicules, parallel to the microstructural fibres.

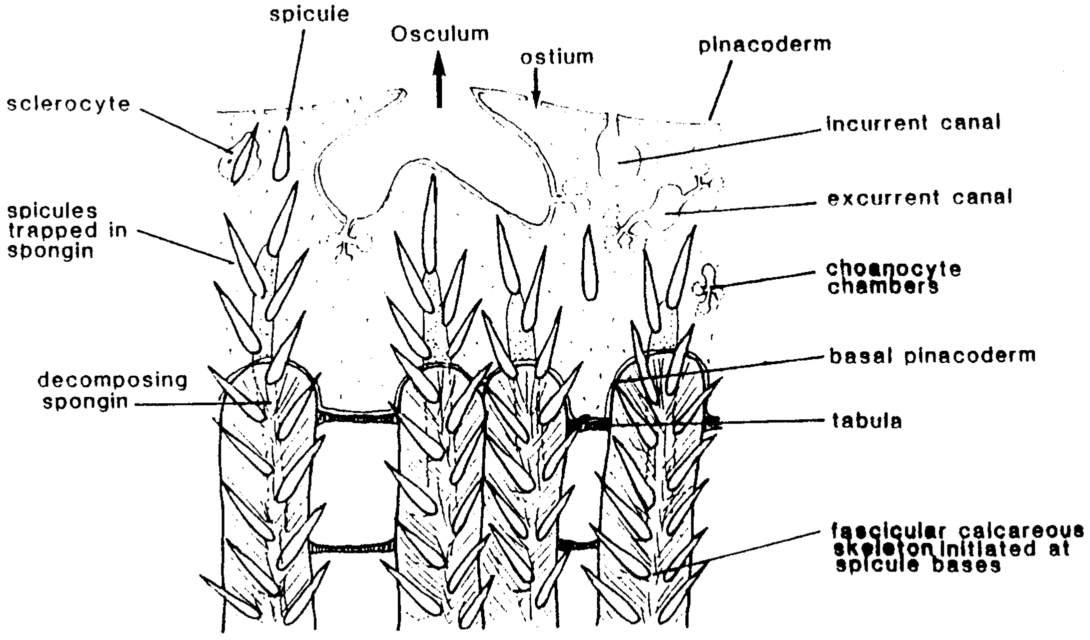


Figure 6.10. Soft-tissue reconstruction of a member of the Milleporellidae.
Spicules are secreted by sclerocytes and transported into position by collenocytes. When arranged in a plumose way, they are bound with spongin to produce an echinating tract. Calcification of the primary calcareous skeleton is initiated in peniciliate tufts at the spicule bases. The tabulae are fibrous; they may be formed by mineralised spongin or secreted by the basal pinacoderm. The excurrent canals inhibit skeletal formation (spicule positioning, spongin secretion and possibly calcitisation) below and possibly around them. (Not to scale).

The spicules would project beyond the spongin fibres and become partially or wholly trapped by the calcareous skeleton. The limits of the organic fibres may have determined the width of the calcareous elements, as in *Calcifibrospongia*. Calcification probably proceded continuously upwards as the animal grew, or from a closely spaced series of calcification sites.

Traces of the aquiferous system are found incorporated within the calcareous skeleton of the Milleporellidae. Therefore, the spicules and spongin skeleton must have formed around the aquiferous canals, but not necessariliy encasing them. The thickness of the living tissue must have been thin above the skeleton, but penetrated below the calcareous skeleton to some degree.

The vertical spacing of the tabulae might indicate the thickness of living tissue within the skeleton . The astrorhizal canals are relatively wide in diameter (2-300μm) The tabulae are formed as a single series of fibres at right angles to the skeletal surface and might have been secreted by the upwardly migrating basal pinacoderm, or by mineralisation of a spongin plate.

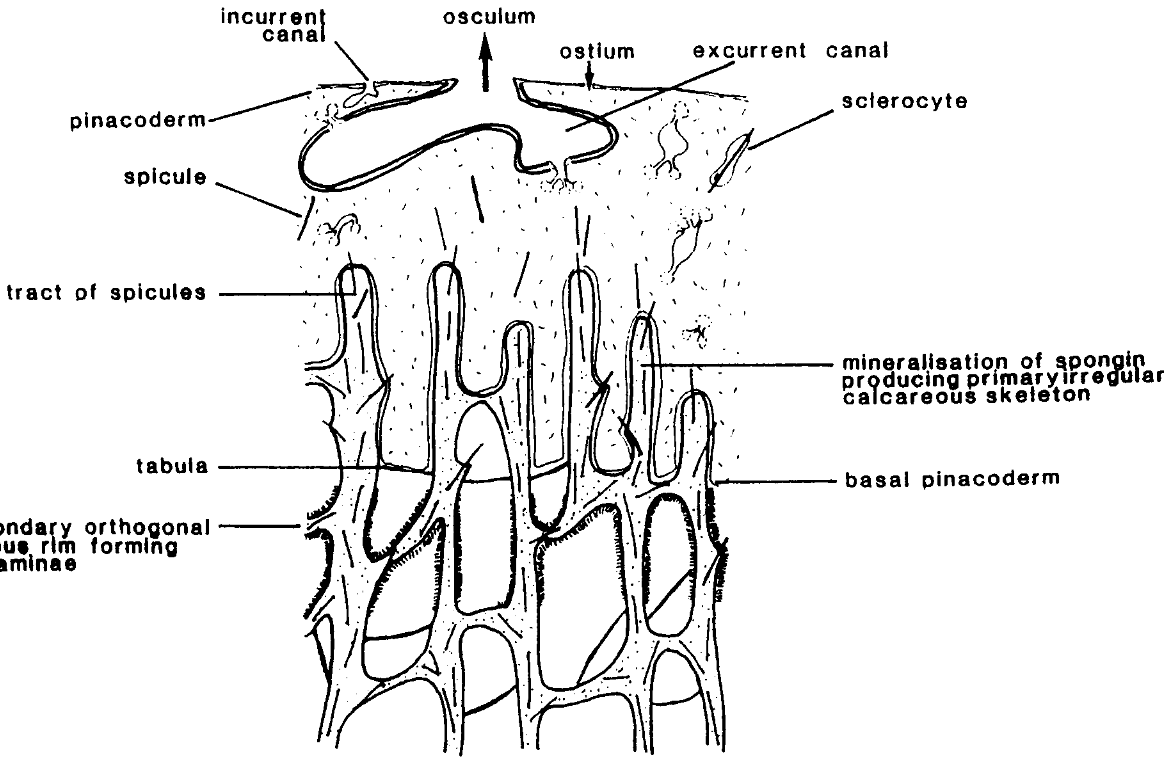
Some members of the Milleporellidae show a secondary backfill of epitaxial growth, which may almost completely fill the primary pore space (Plate 15, fig.d) Epitaxial backfill begins as the soft tissue vacates the area and may act as a support.

6.3.2. **Nov.fam.A** Figure 6.11 Plate 1.

Nov.fam.A is based upon *Actinostromarianina lecompti*. *Actinostromarianina* is characterised by long, thin styles or tylostyles with a dense axial zone from which spicules form a fibro-reticular arrangement towards the skeletal surface.

The primary irregular skeleton is precipitated around the spicule framework and appears to drape meniscus-like around the projecting spicules. The orthogonal fibrous rim is precipitated intermittently to form latilaminae and may be a seasonal deposit.

Figure 6.11: Soft-tissue reconstruction of *Actinostromarianina lecompti*.
Spicules are trapped by a meniscus-like coating of spongin. Spongin is mineralised to form a primary calcareous skeleton of irregular microstructure. A secondary orthogonal fibrous rim is precipitated intermittently to form latilaminae, possibly as a result of cyclical environmental changes. The granular tabulae may be formed by mineralisation of spongin plates or by secretory action of the basal pinacoderm. The traces of the aquiferous system are only rarely left on the surface of *A.lecompti*. A thicker depth of tissue can be postulated above the area of skeletogenesis than that in members of the Milleporellidae. (Not to scale)



The form and microstructure of the primary irregular skeleton, suggests direct mineralisation of organic fibres , as in *Vaceletia*. A large quantity of organic matrix was probably present in *Actinostromarianina*. The same might apply to the irregular tabulae which sectioned off the abandoned parts of the skeleton.

The orthogonal fibrous rim may be a' passive' deposit formed during times of higher temperatures. Alternatively, it may have been precipitated by a secretory pinacoderm. The rim predates the filling tissue.

Traces of the aquiferous system are not apparent in *Actinostromarianina*. The aquiferous canals were probably some distance from the area of skeletogenesis and did not penetrate the calcareous skeleton. Some thickness of tissue, above the calcareous skeleton, can be postulated.

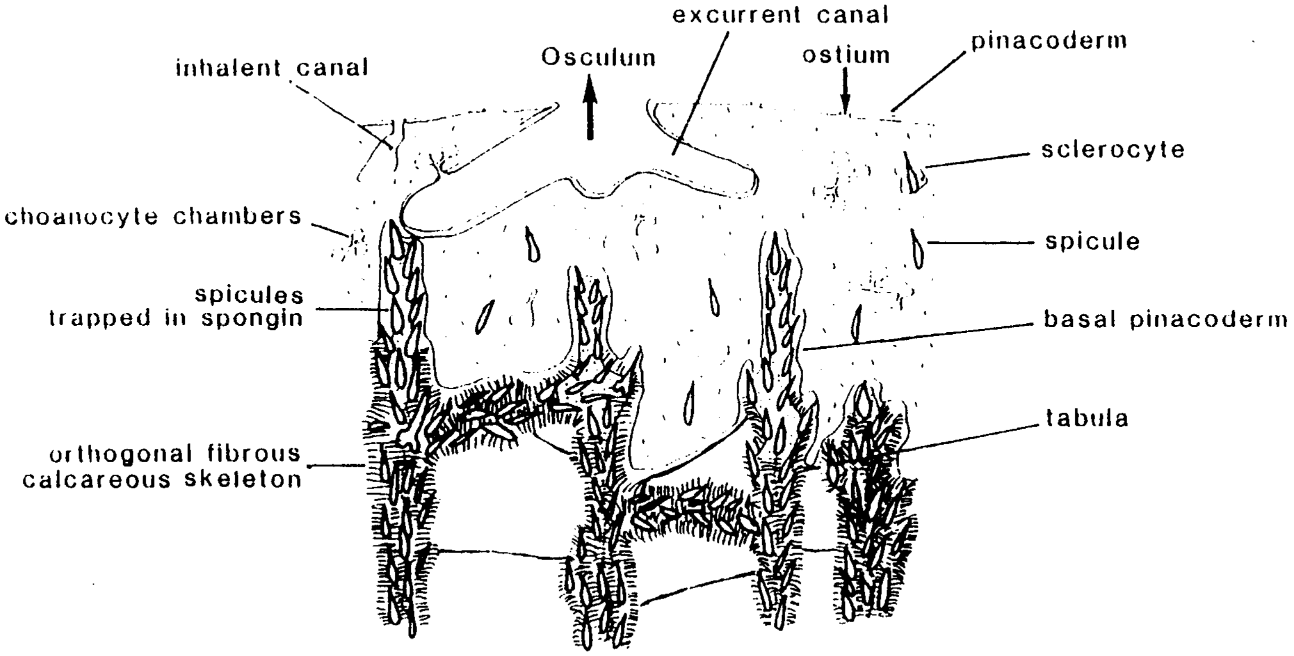
6.3.3. Actinostromariidae Figure 6.12. Plate 3 .

Actinostromaria sp. secretes a dense spicule skeleton of styles and triaxines in a reticulate arrangement. There is an orthogonal fibrous skeleton and irregular tabulae. The orthogonal fibrous rim may be formed in a way similar to that found in *Actinostromarianina lecompti.*

It is probable that the dense spicule skeleton was held together by organic fibres. The primary calcareous skeleton must have been secreted upon or within these fibres, either 'passively' or by a folded secretory pinacoderm. Granular tabulae postdate the orthogonal fibrous skeleton. No Recent analogue is available for orthogonal microstructure.

Astrorhizae are found in *Actinostromaria sp.* . The excurrent canals were clearly in contact with the area of skeletogenesis implying some penetration of the soft tissue into the skeleton, but little above it.

Figure 6.12: Soft-tissue reconstruction in *Actinostromaria sp.*
Spicules are trapped by spongin in echinating tracts. A primary orthogonal fibrous skeleton is precipitated around this framework. The granular tabulae may be formed by mineralisation of spongin or by the basal pinacoderm. The excurrent canals affect the secretion of the skeletal materials, which sectioned off the abandoned parts of the skeleton. (Not to scale).



6.3.4. Burgundidae Figure 6.13. Plates 24 and 45

No convincing spicules have been found in *Burgundia spp.* Models for soft tissue reconstruction are therefore based upon this apparent aspicularity.

Burgundia spp. are able to secrete continuous concentric laminae, enclosing various widths of interlamellar space supported by radial pillars The laminae are perforated with foramina (Plate 24, fig. e). The aquiferous systems are stacked and show numerous secondarily precipitated tabulae which have sectioned off the abandoned areas.

Plate 45, fig.a shows that *Burgundia* secreted pillars first, and then laid a perforated concentric plate over their tops.

The presence of closely spaced (1-4mm.) concentric laminae indicate a fine growth periodicity. *B.ramosa* and *B.wetzeli* have been found with isolated encrusting forams, algae layers and layers of sediment incursion upon the concentric lamellae, but never on the pillars (Plate 45, fig.b). This would suggest that the concentric laminae were either permanently or periodically devoid of soft tissue, and therefore colonised by epibiont larvae which required a hard substrate. After the resumption of the skeletal growth, the organisms would die and be enclosed by new stromatoporoid growth . Normal secretion of biominerals resumed after completion of the previous growth increment, regardless of the earlier deposition. The growth discontinuity surfaces then determine the boundary of the soft tissue in a given growth increment, so that *Burgundia* probably did not have soft tissue which extended down beyond two successive growth discontinuity surfaces i.e one interlaminar space. The construction of *Burgundia* indicates a necessary period of cessation of growth and reorganisation of skeletal tissue, and probable soft-tissue migration upwards to construct the next series of radial elements. The soft tissue must have had considerable lateral and upward mobility. In Mesozoic stromatoporoids this type of skeletal construction is only seen in *Burgundia.*

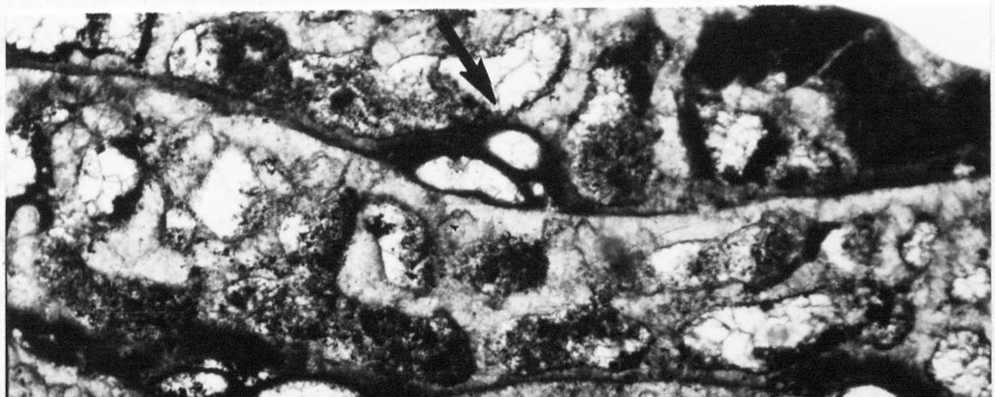
The junction between one growth cycle and the next appears to be a thin 'dark' line, running within the centre of the laminae. This line represents the junction between successive cycles and the new orientation of crystals above and below it (Plate 45, fig.a). The dark colouration can be explained by either the plane at which two crystal fronts of different orientations have met, a decrease of calcification causing fine grain material to be precipitated, or an increase of organic matter secretion. The formation of the skeletal tissue is not clear. The microstructure is similar to that of *Merlia,* which secretes calcite from a basal pinacoderm.

The laminae may have formed by the wholesale movement of tissue upwards producing a flat pinacoderm which could secrete a concentric plate. This would not , however explain the perforate nature of the laminae. It may have formed within the soft tissues and the pores , were spaces to allow the escape of soft tissue to the next upper surface. Alternatively, *Burgundia* could have possessed an external skeleton, like *Vaceletia,* with the pores being ostia.

PLATE 45 _*Burgundia ramosa*_

Figure a: Longitudinal section showing pillar - terminations and structure of lamina.

Figure b: Longitudinal section showing isolated encrusting forams (arrowed) upon concentric lamina.



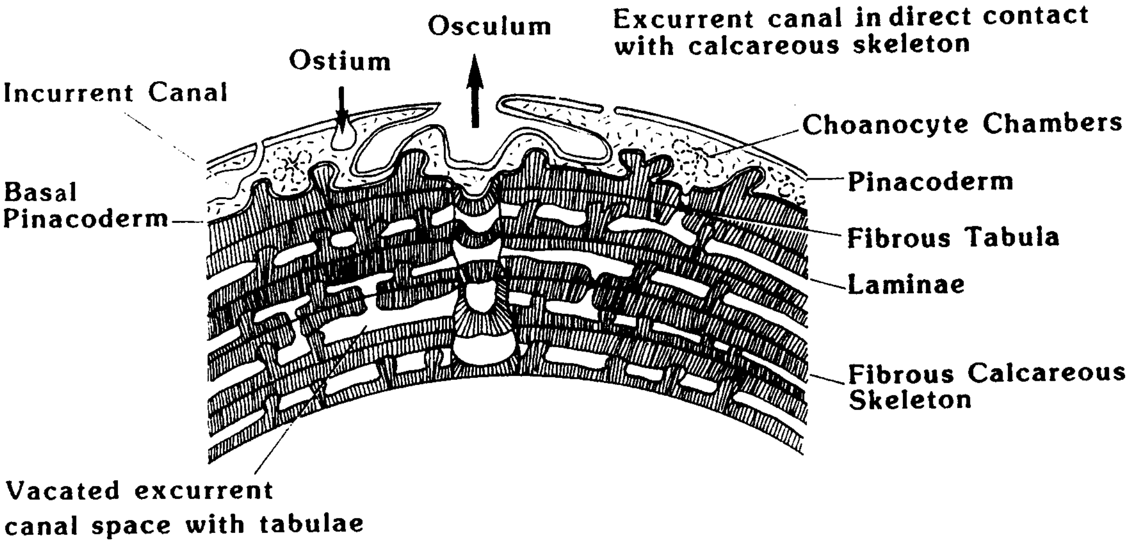


Figure 6.13: Soft-tissue reconstruction of *Burgundia wetzeli*.
No spicules are known. Living-tissue is limited to one inter laminar space. The calcification process is not known; perhaps mineralisation of spongin or the secretory action of a convoluted basal pinacoderm. Secondary fibrous tabulae separate-off abandoned parts of the skeleton. The excurrent canals were in direct contact with the area of skeletogenesis. Laminae may be upturned to form mamelons. (Not to scale).

6.3.5. New. Fam. B. Figure 6.14 Plate 4.

New Gen.A., the type of New Fam. B,possesses a spiculation and calcareous skeleton very similar to *Calcifibrospongia*. Therefore, a similar biomineralisation mechanism can be evoked.

The primary spicule framework of strongyles, styles and tylostyles was covered by an organic matrix. The calcification centres were isolated within this matrix and developed along the strand, perhaps initiated at particular spicule bases. The spherule growth would stop when it reached the edge of the organic matrix or met the crystals of the neighbouring sclerodermite. Both radial and transverse elements would be formed in this way.

Astrorhizae are found within the skeleton, and therefore were in intimate association with areas of skeletogenesis, with only a thin veneer of tissue above, and some penetration of the canals below. *New gen.A* does not have such penetrating oscula as *Calcifibrospongia* ; a similar depth of tissue within the skeleton cannot be suggested.

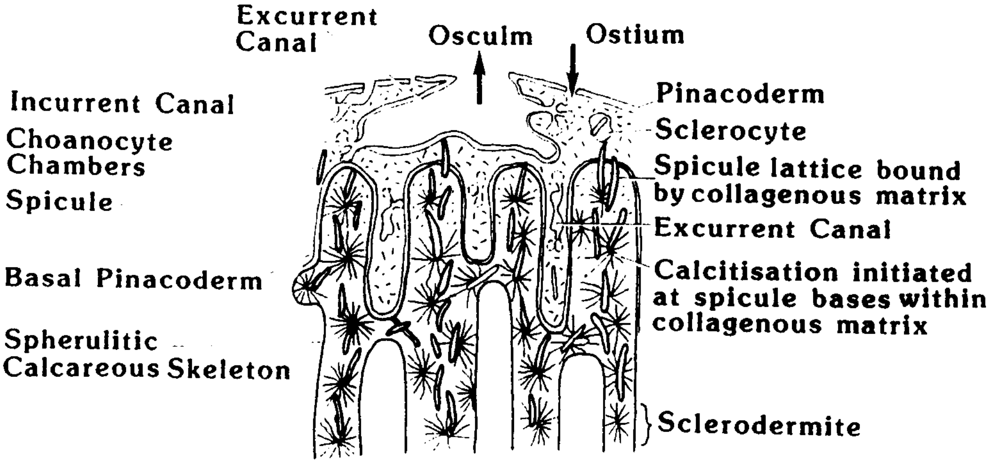


Figure 6.14: Soft-tissue reconstruction of *New gen. and n. sp. A*
Spicules form a lattice, trapped by large amounts of collagenous fibres. Calcitisation is initiated at spicule bases forming spherulites. The basal pinacoderm does not appear to play any role in the biomineralisation process. The aquiferous system lies just above the area of skeletogenesis. (Not to scale).

6.4 CONSTRAINTS ON SKELETOGENESIS THROUGH ONTOGENY

Few Mesozoic 'stromatoporoids' possessed skeletons which appear to have formed as a result of continuous growth. Continuous growth is usually manifested by the occurrence of long, uninterruped radial elements in the calcareous skeleton. Most Mesozoic 'stromatoporoids' display various types of periodicity.

Basal phases: are secreted by the juvenile stromatoporoid when overgrowing substratum.

Latilaminae: Cycles of growth possibly reflecting a periodicity of environmental changes. Latilaminae can be formed by a change in the rate of spacing of horizontal elements (Plate 24, fig.a), subtle changes in the microstructure (Plate 1,fig. a), or thickness of individual elements (Plate 27, fig. d).

Epithecae: Periods of dieback and regrowth (Figure 6.9)

Stromatoporoids can often show variation in rate of growth in one direction (Plate 24, fig.b) . There are two possible manifestations of growth rate differences:

1) throughout the individual (e.g.latilaminae) ,

2) in specific areas (e.g. mamelons), where they may be a lengthening of vertical elements relative to non-mamelate areas or an increased density of vertical elements.

Considering the criteria previously discussed, a greater thickness of tissue can also be postulated these areas.

6.5.CONCLUSIONS

1)All calcified demosponges may have possessed extremely small choanocyte chambers.

2) Without other indicators, the same biomineralisation mechanism cannot be presumed for the same microstructural types of the calcareous skeleton.

3) The presence and form of impressions of the aquiferous system on or in the skeleton is a good indicator of soft tissue thickness, both above and below the area of skeletogenesis.

4) Few Recent calcified demosponges secrete the calcareous skeleton from a folded basal pinacoderm. This mechanism cannot explain the biomineralisation features seen in several types of Mesozoic stromatoporoids; perhaps only members of the Burgundidae, Nov. fam. A. and the Actinostromariidae possessed a basal secretory pinacoderm

5) Spiculate Mesozoic 'stromatoporoids' precipitated a skeleton of calcium carbonate on a primary framework of spicules and organic matrix. The spicules were the first component to be emplaced.

6) Calcification was probably initiated from an organic matrix.

7) Some 'stromatoporoids' (e.g. *Clathrodictyon sp.*) may have possessed a reticulate net of spicules above the calcareous skeleton like that found in *Calcifibrospongia sp.*.

CHAPTER 7

CONCLUDING DISCUSSION

"We describe things not as they are, but as we are"

Kant

For many years, the fossil record of the Phylum Porifera was thought to be restricted to forms with a skeleton of fused spicules. However, about 12 Recent sponge species have been discovered in the last decade, with a solid calcareous basal skeleton, as well as a spicular one, and which bear a superficial resemblance to corals. These 'coralline sponges' were placed in a new class of the Porifera, the Sclerospongiae, in addition to the three pre-existing classes. They are generally found in cryptic habitats of tropical coral reefs. [illegible] ew evidence that the stromatoporoids, chaetetids and sphinctozoans are sponges, suggests that the living coralline sponges are survivors of these abundant and widespread fossil reef-builders. Most of these problematic groups were previously allocated to the Cnidaria, so these findings not only considerably enlarge the fossil record of the Porifera, but greatly modify our views on the evolutionary history of the phylum.

Many previous workers, thinking stromatoporoids to be hydrozoans, looked and only found features which they could name and describe within that biological framework. Not furnished with a search image for spicules, they were unaware of their existence, even within their own type material. Spicules are clearly not rare or difficult to detect in Mesozoic stromatoporoids; the finding of the Recent relict calcified sponge fauna has therefore had far-reaching palaeontological consequences and provided the much-needed biological handle for the study of these problematic fossil reef-builders.

It would appear that flexibility, a broad biological knowledge and a good imagination are some of the most valuable assets for a palaeontologist to possess. With only a fraction of the features available to a biologist, he or she must try to make scientific the study of fossil forms. The characters perceived, and those given importance, will be constrained ultimately by what the observer believes the object under study to be . All too often, only those features sought are found and those which do not tally with a conceptual paradigm are ignored.

The often quoted demise of one sponge biologist illustrates this phenomenon. Randolf Kirkpatrick descibed *Merlia normani* and *Astrosclera willeyana* in 1910, and was the first worker to recognise what is now accepted as the true affinity of these forms. While other workers continued to allocate other calcified sponges to the octocorals (e.g.*Ceratoporella*), Kirkpatrick perceived *Astrosclera* and *Merlia* to be sponges which possessed not only a siliceous spicule skeleton, but also a calcareous one. He even suggested them to be related to the fossil reef-builders, the Monticuloporas, in which he included the stromatoporoids. However, at some stage this respected and competent biologist gained the notion that stromatoporoids were composed of nummulitic foraminifera. It is not clear if his ideas stemmed from the study of stromatoporoids, but he gradually, over the years, developed his foraminiferal theory to cover all of geological matter - granite, meteorites and stromatoporoids were all interpreted as being composed of nummulites. Kirkpatrick can not be criticised for his lack of imagination - it bore him away - but having the fixed idea that stromatoporoids were Foraminifera meant that he was unable to see anything else in his thin sections and eventually it seems, within everything that he placed under his microscope for scrutiny.

The study of fossils is clearly not scientific without some understanding of biological affinity and placing within the natural classification, and if a scientific study is to be attempted, all aspects of palaeontological enquiry must be based upon this foundation.

The finding of spicule pseudomorphs and the presence of a water filtration system in this study has established poriferan affinity for some representatives of forms described as late Mesozoic stromatoporoids. Using inferences from Recent calcified sponges, this has allowed a revision of taxonomic methodology, phylogenetic analysis and soft tissue reconstruction to be extrapolated from these findings.

Detailed spicule and histological examination of the Recent calcified sponges has shown that these forms do not represent a monophyletic group. Different spicule complements, soft-tissue organisations and larval types indicate that members can be better placed within the pre-existing Recent poriferan taxonomic framework (Vacelet 1983). They are calcified demosponges, where their closest relatives are to non-calcified forms and have representatives in both sub-classes Tetractinomorpha and Ceractinomorpha. They are a polyphyletic grouping and the possession of a basal calcareous skeleton is therefore a convergent feature, representing a grade of organisation rather than a taxonomically valid characteristic.

On the basis of this new spicule information, we have reviewed the taxonomic position of the Mesozoic 'stromatoporoids' and 'sclerosponges'. The possession of a calcareous skeleton is a convergent feature in all these forms. According to spicule criteria they represent a wide variety of calcified demosponges and calcareans, which share the same grade of organisation of the calcareous skeleton. Within this definition, the distinction between 'sclerosponge' and 'stromatoporoid' becomes an arbitrary one (Wood, In press.)

A similar conclusion has been reached by Vacelet (1985) and Reitner (1985) for the sphinctozooid sponges, previously classified within the Class Calcarea. Reitner has shown from spicule data that the chambered, thalamid skeleton characteristic of the 'Sphinctozoa' has arisen six times in the history of the group, with representatives from both sub-classes of the Demospongiae as well as from the Calcarea and Hexactinellida.

The same story is also emerging for the chaetetids, characterised by a 'tubular' skeleton of conjoined calicles (Wood and Reitner, In prep.)

The possession of a calcified skeleton is a convergent feature in all calcified sponges and it is clear that these groups can no longer be studied in isolation; this has obscured the true nature of these forms.

The placing of the Mesozoic stromatoporoids in the Porifera has far reaching consequences for the

group. The present cnidarian-based terminology is replaced by one modified from Recent poriferan nomenclature and the many synonyms and meaningless terms have been eliminated.
If one accepts the diagnostic priority of spicules in sponge classification, as Vacelet has shown should be followed for the Recent calcified sponges, the use of calcareous skeleton characteristics becomes highly problematic. In fact, the presence of spicules, whilst giving stromatoporoid classification a more valid grounding, has eliminated many of the characteristics used by classical stromatoporoid systematists.

Viewed as a whole, these calcified sponges share many similar morphological features. The microstructure, skeletal construction and filling tissue types are comparable. Many of these sponges produce a secondary calcareous skeleton upon a primary spicular skeleton; the spicules determining the positioning and form of the calcareous skeleton. In other forms, which may possess identical calcareous microstructures, there is no such close relationship between the two skeletal components. The biological and taxonomic significance of this is not fully understood, but may be a further indication of the poor taxonomic standing of calcareous skeleton characteristics. Microstructures, used by many Palaeozoic and all Mesozoic workers to define higher taxonomic categories are, on the basis of spicules, convergent, and can no longer be used to define higher taxonomic ranks of stromatoporoid calcified sponges.

Due to the diversity of calcified skeletal types within members of the same families, the possession of a calcareous skeleton in calcified sponges probably appeared and disappeared independently in and within many different lineages. Recent calcified demosponges show reduced spiculation compared with non-calcified forms and few fossil calcified demosponges (including stromatoporoids) possess microscleres. Spicule reduction, leading to total loss could well be an apomorphic feature within each lineage and be a response to the possession of a calcareous skeleton.

Some members of the calcified demosponges are certainly conservative groups e.g. members of the Ceratoporellidae have persisted little changed for over 300 million years. But many other families appear to be extinct, and the inter-relationships within these groups is obscure.

Even though some lineages of the calcified sponges appear to be phylogenetically conservative, a radical ecological niche shift occurs somewhere between the Upper Cretaceous and Recent times. Recent calcified sponges tend to live in cryptic niches, whereas Mesozoic forms often formed bioherms and even reefs. This may have been a staggered change across the different lineages, e.g. the acanthochaetetids in the Upper Cretaceous reefs of North Spain had a cryptic niche habitat whereas Upper Cretaceous stromatoporoids in the same area still produce bioherms in the photic zone. Perhaps only a few lineages which were already cryptic niche dwellers survived to the Recent or those which could most successfully adapt to a reclusive niche in response to the new competition from scleractinian corals did so. It would make an interesting study to chronicle ecological niche changes throughout the history of the calcified sponges within the various lineages, noting differences and common trends.

A considerable problem in fossil sponge classification is the choice of valid taxonomic features and at which rank they can be used. The taxonomic scheme outlined here for the Mesozioc stromatoporoids is my personal preference based on information available from Recent forms and from the study of variability in fossil forms. The classification of fossil calcified sponges is extremely difficult given the few characters available and the variability of those present. Since Recent workers have rejected spicule data as being unreliable, we remain in the unhappy situation of having to define illogically taxa on characteristics judged to be unsound. Any classification will be subject to the personal bias of the author and what is given here is only my version of the truth. Classifications undergo constant change as our descriptive knowledge increases and higher level classification is usually based upon our understanding of phylogeny. Since we have a poor knowledge of the phylogeny of calcified sponges, this classification is an expression of our knowledge at this time. The palaeontologist's and biologist's approaches to classification differ, as a palaeontologist has an added time dimension, but lacks many of the discriminatory tools available to the biologist. Since I have attempted to place the Mesozoic stromatoporoids within the Recent poriferan classification as far as possible, there may be irresolvable discrepancies. A few characters have been singled out to as being of greater evolutionary and taxonomic significance than the rest and division has been based upon these characters. Character weighting should be based upon as objective a judgement as possible. At this early stage in the development of stromatoporoid taxonomy I feel it is important to state assumptions and reasons for them at the outset. The taxonomist rarely follows a clear routine and may not always be aware of the logical steps followed. Therefore in this study I have attempted to outline the system of character weightings I have chosen to follow and the reasons for choosing this system in preference to the pre-existing one and other possibilities. Hopefully, new information will be forthcoming , enabling modifications of this initial work. Unfortunately, there do not appear to be wholly reliabledefinitive characters for establishing higher groups of species. The cladistic approach, although attempted has been extremely difficult to adopt due to the lack of such characters and deciding which are primitive and which derived.

One possible solution to this taxonomic subjectivity and lack of morphological characters available may be to use palaeo-immunological techniques. This might provide a more objective taxonomic basis for calcified sponge taxonomy, working on Recent forms and then with fossil forms to work out recency of common ancestry.

Although the biological affinity of some late Mesozic stromatoporoid genera has been established in this study, there remains a large number of forms whose placing within or alliance with the stromatoporoids e.g. Ellipactinids and Disjectoporids, has been based either on the shared presence of secondary characteristics now known to be convergent e.g. radial and concentric elements, or on an inability to place these forms anywhere else. Certainly Palaeozoic and Mesozoic stromatoporoids have provided a repository for forms for which distinctive characters could not be determined to enable placement elsewhere.

Mechanisms of biomineralisation are another interesting avenue of inquiry, especially considering the different biomineralogical mechanisms used by organisms to produce the same microstructure: e.g. *Astrosclera* secretes spherules intra-cellularily and *Calcifibrospongia* forms spherules by mineralisation of a collagenous matrix initiated from spicule bases. The variability of mechanisms found within one taxonomic group is another problem. This variability suggests that biomineralisation mechanisms have a low taxonomic significance. Since members of the same genus may or may not produce a calcareous skeleton (*Merlia spp.*), and members of the same family, e.g. *Astrosclera* and *Ceratoporella*, both in the Agelasidae produce strikingly different skeletons by different mechanisms, it seems that sponges may be able to produce calcareous skeletons with relative ease. Therefore biomineralogical mechanisms are unlikely to be of taxonomic value, eliminating another of the few possible taxonomic characteristics available to palaeospongologists.

These new spicule findings not only give a sounder taxonomic basis for the reclassification of these previously problematic forms, but also allows investigation into this biomineralogical problem. A large data base from both Recent and fossil calcified sponges from different groupings and stratigraphic positions is needed to solve these questions.

Technological innovations seem to come late to palaeontology, and more use should be made of the now standard techniques of stained thin section analysis and S.E.M. studies to help to elucidate the precise nature of the relationship between the calcareous skeleton and the spicule framework for low level taxonomic work.

This study has not been able to solve the problem of the late Palaeozoic to early Mesozic 'gap' in the 'stromatoporoid' record. It has always been disputed that the two stratigraphically separated groups are related. Unfortunately, there is only one bona-fide Palaeozoic stromatoporoid which bears spicules, *Parallelopora mira*, from the Middle Pennsylvanian. Without spicule information the inter-relationship of these two groups cannot be assessed as the previously uniting features (presence of astrorhizae, a layered skeleton and a reticulate skeletal arrangement) are now known to be convergent.

G.Stanley (pers. comm. 1986) has found extensive calcified sponge faunas in the North and South

Americas, ranging from the Lower Permian to the Upper Triassic. These faunas neatly fill the presumed 'gap' in the stromatoporoid record. Therefore, I suggest that the since 'stromatoporoids' cannot be taxonomically differentiated from other calcified sponges on calcareous skeletal characteristics alone, their history has not been punctuated by a 'gap'; some lineages became extinct e.g. the labechiids, whereas others have persisted to Recent times e.g. the Ceratoporellids.

APPENDIX

GLOSSARY

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* A poriferan term applied to stromatoporoids.

\+ An amended definition.

** A new term

Synonyms, and where possible references to illustrations, are given in brackets.

ACANTHOSTYLES*: (Figure 2.1) One-axis spicules which bear small spines. One blunt end and one pointed end. Normally a megasclere.

APOPYLE*: Any aperture through which water leaves a choanocyte chamber.

AQUIFEROUS UNIT SPACE:** Three dimensional space enclosed by the aquiferous unit.

AQUIFEROUS UNIT*: (Figure 2.7): Functional unit of the poriferan aquiferous filtration system consisting of incurrent pores (ostia) , a connective canal system and excurrent canals (astrorhizae), and a common exhalent opening (osculum). An aquiferous unit serves a fixed volume of cells, and is defined by the extent and influence of the astrorhizae.

AQUIFEROUS SYSTEM*: The whole water-conducting system between the ostia and the oscula.

ASTER*: (Figure 2.1) Any polyactinal microsclere in which the processes appear to be emitted from a common centre or axial shaft.

ASTRORHIZAE+: (Plate 11) (stellate venations, excurrent canal traces, astrosystem). The collective name for the traces of the excurrent canal system. Appears as radiating and branched grooves or raised threads on the surface, or as canals within the skeleton which peter out into the fine meshwork of the skeleton. Usually unwalled.

ASTRORHIZAL CANAL+: (lateral tubes, transverse astrotube, lateral canals). One excurrent canal trace.

ATRIUM*: An exhalent aquiferous cavity receiving water from one or more exhalent canals or apopyles and conducting it to one or more oscula.

AXIAL : The central (older) part of a skeletal branch.

CALCAREOUS SKELETON: (Coenosteum, skeleton) The calcareous skeletal tissue.

CALTHROPS*: Four-rayed spicule with rays of similar length, arranged as though following the axes of a tetrahedron. So-called from resemblance to the four pointed weapon known as a calthrop. Can be a mega-or microsclere.

CHIMNEYS*:Vertically developed mamelons, which protrude beyond the general surface.

CHORISTID*: Demosponge with tetractinial megascleres or some other radiate type if tetractines are lacking. Member of the Order Choristida (Sollas)

CLAVIDISC* : (Figure 2.1) Specialised microsclere, comprising an ovate disc with an elongate central perforation.

COLLENOCYTE*: Anucleolate cells or with a small nucleolus, which by means of filopodial extensions span the mesohyl, where they function as supports.

COLUMN: (Plate 27, fig.e) (Vertical lamellae, vertical elements, radial pillar)
Radial structural element of the calcareous skeleton, which appears vertical in longitudinal section. Greater degree of continuity and size than pillars.

ECHINATING*(Figure 6.10): Spicules arranged in a plumose orientation from a central organic strand.

EPITHECA: A thin, wrinkled basal layer of finer structure than the superjacent, normal stromatoporoid tissue. Occurs at the base of many calcareous demosponge skeletons.

EXCURRENT CANAL SYSTEM*:(Figure 3.4.) The part of the aquiferous system between the apopyles and osculum.

FASCICULAR FIBROUS MICROSTRUCTURE+ (Figure 2.3.):(Cligonal) Fibrous microstructure of the skeletal elements. Crystal fibres are fanned and radiate upwards and outwards

FIBRE: Acicular calcite crystal of the calcareous skeleton.

FILLING TISSUE : (Table 2.2.) Secondary calcareous skeleton which partitions or fills abandoned parts of the skeleton as the animal grows.

FORAMINA : Circular pores in laminae connecting adjoining interlamellar spaces.

GROSS MORPHOLOGY: (Figure 1.2.) The overall shape of the calcareous skeleton.

Nodular (globular , irregular, sub-spherical, bulbous, massive): Almost spherical, often composed of a number of nodular growths.

Branching (dendritic or dendroid, foliose, fasciculate, ramose, digitate, phaceloid): Composed of ramifying branches.

Cylindrical; elongate forms with a circular or sub-circular cross-section.

Conical; Having the form of an inverted cone.

Encrusting (lamellar, tabular, mat-like): Forms seen to encrust a substrate or other organism, with a low height to width ratio.

Hemispherical (massive, domal); Having a flat base and a convex upper surface.

INDIVIDUAL (previously referred to as colony)*: A single 'stromatoporoid' skeleton representing one individual. In biological terms, this represents all the cellular components and all the interactions of their components within the pinacocyte envelope.

INTERLAMINAR SPACE: (Figure 6.13.) area or space enclosed between two successive laminae.

INTERSKELETAL SPACES: (galleries, chambers, coenospaces, coenotubes).
Spaces between any skeletal elements.

IRREGULAR MICROSTRUCTURE: (Figure 2.3) (granular, compact, finely micritic). Calcareous microstructural type of the skeletal elements where calcite crystals are small (1-5 ɥm) and without preferred orientation, or orientated in one plane only.

ISODICTYAL*: (Figure 4.2) Modification of plumose spicule arrangement , where spicules are also aligned parallel in connective spongin strands between the plumose tracts.

LAMINA (plural:laminae): (Synonyms: lamella (pars), coenosteal lamella, thecal lamella) (Figure 6.13.) Uninterrupted concentric calcareous plate, perpendicular to radial skeletal elements .

LAMINAR: A stromatoporoid dominated by laminae.

LATILAMINAE (Plate 27, fig.; Plate 29, fig.): A concentric banding, naked to the eye, showing a marked periodicity of the calcareous skeleton.

LITHISTID*: Demosponge with the main spiculate skeleton consisting of articulated megascleres, known as desmas.

MAMELONS: (Plate 27, fig. a) Rounded regular or irregular elevations of the surface of skeleton. May or may not show some correlation with astrorhizae.

MEGASCLERES:* (Figure 2.1) Major supporting spicule;the larger size group when two distinct size categories exist .Generally with a length greater than 0.2mm.

MESOHYL*: All the living tissue within the pinacoderm.

MICROSCLERES:* (Figure 2.1) Accessory spicules; the smaller size group when two size categories exist. Spicules generally smaller than 100μm.

MICROSTRUCTURE: (ultrastructure) (Figure 2.3) The arrangement of calcite crystals which form the skeletal elements as seen under high powers of a light microscope or under S.E.M.

MONAXON:* (Figure 2.1) A spicule with a single growth axes.

ONTOGENY * (Astogeny, when stromatoporoids were considered to be colonies): The development during the course of an individual's life history .

ORGANIC SKELETON*: (Plate 12, fig.a) Spongin or collagenous part of mechanical support found in Recent demosponges.

ORTHOGONAL MICROSTRUCTURE: (Figure 2.3.) Microstructure of the calcareous skeleton where fibres are orientated perpendicular and radially to a central axis.

OSCULUM (Plural: OSCULA)*: (axial astrotube) (Figure 6.1) Common exhalent opening of one aquiferous unit where water leaves a sponge.

OSTIUM (Plural : OSTIA) *: (pores) (Figure 6.1) Incurrent pore of aquiferous system where water enters a sponge.

PERIPHERAL : Outer (younger) part of a skeletal branch.

PILLAR : (Figure 1.2) (vertical lamella) Radial skeletal element. Relatively short and discontinuous cf. column.

PILLAR-LAMELLAE :(Synonym: transverse lamellae, lamellae(pars)) Horizontal elements which are part of the primary calcareous skeleton.

PINACODERM: (Figure 6.1) Outer covering of a sponge which is composed of flattened cells.

PLUMOSE* : (Figure 4.2) Herring-bone or feather-like arrangement of spicules radiating upwards and outwards with tapering tips.

POLYACTINAL*: A spicule with many growth axes.

PRIMARY CALCAREOUS SKELETON: (Figure 2.5) Initially precipitated calcareous skeletal tissue e.g. columns.

PRIMARY SPICULE FRAMEWORK*: (Figure 2.5) Framework of arranged spicules around which the calcareous skeleton is precipitated.

PSEUDO-LAMELLAR STRUCTURE**: (Plate 18, figs.a,b) Diagenetic alteration of the microstructure producing parallel plates of recrystallised crystals giving an internally layered appearance in transverse section.

RADIAL*: (Figure 1.2) Elements radiating outwards from a central point or area.

RADIATE (n.)*: Spicule with three or more radiating growth axis.

RADIATE (adj.)*: Referring to radiating arrangement of megascleres.

RETICULUM: Meshwork of skeletal elements, often where radial and horizontal elements cannot be distinguished.

RHAGON*: (Figure 3.4) Earliest development of a sponge with a functional aquiferous system of a thin-walled hollow cone, the walls of which contain choanocyte chambers, but no canal system.

SCALENOHEDRAL STRUCTURE:**(Plate 18, fig.c) Diagenetic alteration of microstructure due to recrystallisation. Forms a "saw-tooth" arrangement of fibres which appear "darker" under thin-section.

SCLEROCYTE *:(e.g. Figure 6.4)Nucleolate cells that secrete siliceous spicules.

SCLERODERMITE*: (Figure 6.4) Aggregate of crystals forming a microstructural unit of the sponge calcareous skeleton.

SECONDARY CALCAREOUS SKELETON: (Figure 2.5) Calcareous skeletal tissue precipitated after the primary calcareous tissue e.g. most tabulae.

SKELETAL TISSUE: Microstructure of the calcareous skeleton.

SKELETAL TRACTS* : (Figure 6.5) Strands of organically bound spicules.

SKELETON: (coenosteum) All structures where the primary function is the consolidation and mechanical protection of the sponge.

SPICULE*: (Figure 2.1) A discrete autochthonous element of the skeleton consisting of mainly silica or calcium carbonate

SPICULAR SKELETON:*(Figure 2.5) Framework of arranged spicules.

SPONGIN * : (Plate 12, fig.a)A skeletal organic matrix found in sponges which helps maintain cell integrity.

SPONGOCYTE *: Nucleolate cells which secrete spongin around spicules.

STYLE:*(Figure 2.1) One-axis spicule with a rounded base and which tapers to a point. No other ornamentation. Normally a megasclere.

STRONGYLE:*(Figure 2.1) Two-axis spicule, curved, rounded at both ends with no marked decrease of diameter.

SPHEROIDAL MICROSTRUCTURE: (Figure 2.3)Fibrous microstructure where fibres are arranged in aggregates radiating from a common centre

SUPERPOSED ASTRORHIZAE: (Astrorhizal Cylinder, Astrorhizal corridor, stacked astrorhizae). (Figure 2.9)Successive generations of Astrorhizae which have formed along the same radial axis.

TABULAE: (Plate 10) A form of filling tissue. Usually secondarily precipitated discrete plates, generally flat or slightly curved. Not continuous elements.

TABULATE OSCULUM:* (Figure 2.9) Osculum which has been repeatedly partitioned by secondarily precipitated tabulae. Interpreted as being characteristic of forms with a thin veneer of tissue which migrated upwards as the animal grew.

TRIAXINES:* (Figure 2.1) 3-rayed spicules

TUBULAR: Arrangement of skeletal elements with appearance of closely packed tubes.

TYLOSTYLE:*(Figure 2.1) One-rayed spicule with a basal, rounded boss and a tapered tip. Normally a megasclere.

REFERENCES

References marked with an asterisk have not been read, and the author has had to rely upon other sources for the information quoted from them.

BAKALOW, P. 1906. *Stromatorhiza*, eine Stromatoporide aus dem oberem Rauracien des Schweizer Jura. *Neues Jahrb. Mineral. Geol. Palaeontol.* **1**, 13-15.

BATHURST, R.G.C. 1975. Carbonate sediments and their diagenesis. *Dev.Sedimentol.* **12**. 658pp.

BERGQUIST, P.R. 1978. *Sponges.* Univ. Calif. Press. 268pp.

BERGQUIST, P.R. and HOGG, J.J. 1969. Free amino acid patterns in the Demospongiae: a biochemical approach to sponge classification. *Cahiers Biologique marin* **10**, 205-220.

BERGQUIST, P.R. and HARTMAN, W.D. 1969. Free amino acid patterns and the classification of the Demospongiae. *Marine Biology* **3**, 247-268.

BIDDER, G.P. 1923. The relation of a form of a sponge to its currents. *Q. J. microscop. Sci.* **67**, 293-323.

BIRENHEIDE, R. 1967. Mikrostruktur zweier stromatoporen aus dem Mitte-Oligozän. *Nat. Mus. Frankfurt* **97**, 313-328.

BIRENHEIDE, R. 1969. A new stromatopore from the Rupel clay of Germany. In: K.W.S. Campbell (ed.), *Stratigraphy and Palaeontology*, 43-49. A.N.U. Press, Canberra.

*BOGOYAVLENSKAYA, O.V. 1965. O taksonomicheskcom znachenii astroriz u stromatoporoidei. In: Sokolov, B.S. and Dubatolov, V.N. (eds.), Tabulyamorfnyne Korally v devona i carbona SSSR. *Akad. Nauk Sibir. Otd. Inst. Geol. Geofiz.* **1**(2), 105-112.

*BOGOYAVLENSKAYA, O.V. 1974. Printsipy sistematizatsii stromatoporoidei. In: Drevnie Cnidaria. *Akad. Nauk. Sibir. Otd. Inst. Geol. Geofiz.* **201**(1), 20-27.

BOROJEVIC, R., FRY, W.G., JONES, W.C., LEVI, C., RASMONT, R., SARA, M. and VACELET, S. 1968. A reassessment of the terminology for sponges. *Bull. Mus. natl Hist. nat. Paris,* 2^{e} ser., **39**, 1224-1235.

BRIEN, P. 1967. Les éponges: leur nature metazoares: leur gastrolation: leur état colonial. *Ann. Soc. zool. Belg.* **97**, 197-235.

*CANAVARI, M. 1892. Idrozi titoniani della regione mediterranea appartenenti alla famiglia delle

Ellipscatinidi. *Mem. R. Com. geol. d'Italia* **4**(11).

CARTER, H.J. 1877. On the close relationship of *Hydractinia, Parkeria* and *Stromatopora*; with descriptions of new species of the former, both Recent and fossil. *Ann. Mag. nat. Hist. London* **4**(19), 44-76.

CARTER, H.J. 1878. On the probable nature of the animal which produced the Stromatoporidae, traced through *Hydractinia, Millepora alcicornis* and *Caunopora* to *Stromatopora. Ann. Mag. nat. Hist. London* **5** (2), 304-314.

*CARTER, H.J. 1880. On the mode of growth of *Stromatopora* , including the commensalism of caunopora. *Ann. Mag. nat. Hist. London* ser. 5, **4**, 101.

CUIF, J.-P. 1973. Histologie de Quelques sphinctozoaines (Porifera) Triassiques. *Geobios* 6 (2),115-125.

CUIF, J.-P., FISCHER, J.C. and MARCOUX, J. 1972. Découverte d'une faune de Chaetetida (Cnidaria, hydrozoa) dans le Trias superieur de Turquie. *C. r. Seances Acad. Sci. Paris* 275.

CUIF, J.-P. and FISCHER, J.C. 1974. Étude systematique sur les Chaetetida du Trias de Turquie. *Ann. Palaeont. Invertebres* **60**, 3-23.

* DAWSON, J.W. 1875. *The Dawn of Life.*

*DAWSON, J.W. 1879. On the microscopic structure of Stromatoporidae and on Palaeozoic fossils mineralized with silicates in illustration of *Eozoon*. *Q. J. geol. Soc. London,* **35**, 48-67.

DEBRENNE, F. and VACELET, J. 1984. Archaeocyatha: Is the sponge model consistent with their structural organisation? Proc. Fourth International Symposium on Fossil Cnidaria. *Palaeontogr. Am.* **54**, 358-370.

DEHORNE, Y. 1915. Sur un Actinostromidé du Cénomanien. *C. r. Seances Acad. Sci. Paris* **161**, 733.

DEHORNE. Y. 1916a. Stromatopores du Givetien de Glageon (Nord). *Bull. Soc. geol. Fr.* 4^{e} ser.16, 180-185.

DEHORNE, Y. 1916b. Sur un stromatopore milleporoide du Portlandien. *C.r. Seances Acad. Sci. Paris* **162**, 430-433.

DEHORNE, Y. 1917. Sur la presence du genre *Stromatoporella* Nicholson dans le Senomanien des environs de Martigues (Bouches du Rhône). *C.r. Seances Acad. Sci.Paris,* **165**, 67.

DEHORNE, Y. 1917. A propos de la continution microscopique du squelette des stromatoporoides. *C.r. Seances Acad. Sci. Paris* **165**, 764.

DEHORNE, Y. 1917. Sur une éspèce nouvelle de stromatopore du Calcaire à *Hippurites: Actinostroma kiliani. C.r. Seances Acad. Sci. Paris* **164**, 225.

DEHORNE, Y. 1917. Sur un stromatopore nouveau du Lusitanien de Cezimbra, Portugal. *C.r.Seances Acad. Sci. Paris* **164**, 117.

DEHORNE, Y. 1917. Stromatoporoides Jurassiques du Portugal. *Com. Serv. geol. Portugal* **13**(1), 12-21.

DEHORNE, Y. 1918. Répartition des chaetitidés et des stromatoporoidés dans les terraines crétacés de la Basse-Provence. *C. r. Somm. Soc. geol. Fr.* 39-40.

DEHORNE, Y. 1918. Sur les analogies de la forme branchue chez les polypiers constructeurs des récifs actuelles avec celle des stromatopores des terrains secondaires. *C. r. Seances Acad. Sci. Paris* **166**, 219-222.

DEHORNE, Y. 1920. Les stromatoporoides des terraines secondaires. *Mém. Serv. Explic. Carte géol. Fr.* 1-161.

DEHORNE, Y. 1923. Stromatoporoidés Jurassiques du Portugal. *Com. Serv. geol. Portugal* **13**, 12-21.

DeLAUBENFELS, M.W. 1936. The sponge fauna of the dry Tortugas. *Carnegie Institute of Washington Publication,* **467**, 1-225.

DeLAUBENFELS, M.W. 1955. Part E, Archaeocyatha and Porifera. In Moore, R.C. *Treatise on Invertebrate Paleontogy, Geological Society of America and University of Kansas Press,* Lawrence, 122p.

DENDY, A. 1924. On an orthogenetic series of growth forms in certain tetraxonid sponge spicules. *Proc. R. Soc. London* ser.2, **18**, 164.

DENINGER, K. 1906. Einige neue Tabulaten und Hydrozoen aus Mesozoischen Ablagerungen. *Neues Jahrb. Mineral. Geol. Palaeontol.* **1** (V-VII), 61-70.

DICKSON, J.A.D. 1965. A modified staining technique for carbonates in thin section. *Nature. London* **205**, 587.

DIECI, G., RUSSO, A., RUSSO, F. and MARCHII, M.S. 1977. Occurrence of spicules in Triassic chaetitids and ceratoporellids. *Boll. Soc. palaeont. Ital.* **16** (2), 229-238.

DIECI, G., RUSSO, A. and RUSSO, F. 1974a. Nota preliminaire sulla microstructura di spunge aragonitche del Trias medio-superiore. *ibid.* **13** (1-2), 99-107.

DIECI, G., RUSSO, A. and RUSSO, F. 1974b. Revisione del genere *Leiospongia* d'Orbigny (Sclerospongia triassica). *ibid.* **13** (2), 135-146.

DONG DE YUAN, and WANG MING-ZHOU 1983. New materials of the Upper Jurassic stromatoporoids in the Ando county of Xizang . *Acta palaeontol. Sin.* **22** (4).

FENNINGER, A., FLÜGEL, E. and HÖTZL, H. 1963. Bricht über palaeontologischen-mikrofazielle Untersuchungen an ostalpinen Plassenkalken s.1. An2. *Osterr. Akad . Wiss., math-naturwiss* **15**, 234-327.

FENNINGER, A. and HÖTZL, H. 1965. Die Hydrozoa und Tabulozoa der Tressenstein und Plassenkalke (Oberjura). *Mitt. Mus. Bergball Geologica Technik Landes Mus. 'Joanneum' Graz* **27**, 3-61.

FENNINGER, A. and FLAJS, G. 1974. Zur mikrostrukturenzenter und fossiler Hydrozoa. *Biomineralisation* **7**, 69-99.

FINKS, R.M. 1970. The evolution and ecologic history of sponges during Palaeozoic times. *Symp. zool. Soc. London* **25**, 3-22.

FINKS, R.M. 1983. Pharetronida: Inozoa and Sphinctozoa. In: Broadhead, T.W. (ed.) Sponges and Spongiomorphs. *Univ. Tennessee Stud. Geol.* **7**, 55-70.

FINKS, R.M. 1986. "Spicules" in *Thamnopora* . *Fossil Cnidaria* **15** (1-2), 22.

FIRTION, F. 1940. Sur la présence de *Burgundia trinorchii* dans le Portlandien de la région de Morteau (Jura). *Bull. Soc. géol. France* Ser. F, **9**, 161-162.

FLÜGEL, E. 1958. Fossile Hydrozoaen - eine wenig bekannte gruppe riffbuildender meerestiere. *Veroff. naturhist. Mus. Wien* **1**, 27-32.

FLÜGEL, E. 1969. Hydrozoen mit circumlamellarer Mikrostruktur aus den Gosau-Schichten (Senon) des Gosau-Beckens (Oberösterreich/Salzburg). *Verh. Geol. Bundesanst.* **2**, 126-132.

FLÜGEL, E. 1975. Fossile Hydrozoen-kenntrisstand und probleme. *Palaeontol. Z. Berlin* **49** (4), 369-406.

FLÜGEL, E. and HÖTZL, H. 1966. Hydrozoen aus dem ober Jura der Hesperischen kelten (Ost-Spanien). *Neues Jahrb. Geol. Palaeontol. Abhandlungen* **124** (2), 103-117.

FLÜGEL, E. and FLÜGEL-KAHLER, E. 1968. Stromatoporoidea (Hydrozoa Palaeozoica). *Foss. Cat.1, Animalia,* **115-116**. Junk, The Hague, 681pp.

FLÜGEL, H.W. and FLÜGEL-KAHLER, E. 1975. Stromatoporen aus dem Unteren kohlenkalk (Tn 1b, strunium) von Aachen (Stromatoporen aus dem deutschen palaozoikum Z). *Neues Jahrb. Geol. Palaeont. Abhandlungen* **149**, 1-38.

FRY, W.G. 1979. Taxonomy, the individual and the sponge. In: Larwood G. and Rosen, B.R. (eds.) *Syst. Assoc. Special Vol.* **11**, 49-80.

GALLOWAY, J.J. 1957. Structure and classification of the Stromatoporoidea. *Bull. Am. Paleontol.* **37**, 345-470.

GALLOWAY, J.J. and St JEAN, J.Jr. 1956. A bibliography of the Order Stromatoporoidea. *J. Paleontol.* **30** (1), 170-185.

GERMOVSEK, C. 1954. Les Hydrozoa du Jura supérieur aux environs de Nova Mesto. *Razprave* **2**, 341-386.

*GOLDFUSS, G. 1826-1833. *Petrefacta Germiniae.* Dusseldorf, **1**, 42-82.

GOTO, H.F. 1982. Animal taxonomy. Institute of Biology. *Studies in Biology* No.143, 1-60.

GRAY, D.I. 1980. Spicule pseudomorphs in a new Paleozoic chaetetid and its sclerosponge affinities. *Palaeontology. London* **23**, 803-820.

GREGORY, J.W. 1898. *Millestroma,* a Cretaceous Milleporoid coral from Egypt. *Geol. Mag.* Dec.4, **5**, 337-342.

HARTMAN, W.D. 1969. New Genera and species of coralline sponges (Porifera) from Jamaica. *Postilla* **137**, 1-39.

HARTMAN, W.D. 1979. A new sclerosponge from the Bahamas and its relationship to Mesozoic stromatoporoids. *Colloques internationaux du C.N.R.S.* No.291, Biologie des Spongiaire, 467-475.

HARTMAN, W.D. 1980. Structure and function of a Recent sponge. In: Hartman, W.D., Wendt, J.W. and Wedenmayer, F. Living and Fossil Sponges. *Sedimenta* **7**, 1-52.

HARTMAN, W.D. 1985. Personal communication.

HARTMAN, W.D. and GOREAU, T.E. 1966. *Ceratoporella,* a living sponge with stromatoporoid affinities. *Am. Zool.* 6 (4), 563-564.

HARTMAN, W.D. and GOREAU, T.E. 1970. Jamaican coralline sponges: Their morphology, ecology, and fossil representatives. *Zool. Soc. London Sympos.* **25**, 205-243.

HARTMAN, W.D. and GOREAU, T.E. 1972. *Ceratoporella* (Porifera: Sclerospongiae) and the chaetetid 'corals'. *Trans. Connecticut Acad. Arts Sci.* **44**, 133-148.

HARTMAN, W.D. and GOREAU, T.E. 1975. A Pacific tabulate sponge, a living representative of a new order of Sclerosponges. *Postilla* **167**, 1-13.

HAYASAKA, T. 1917. On a new hydrozoan fossil from the Torinosu limestone of Japan. *Sci. Rep. Tohoku imp. Univ.,* ser.11, **4** (2).

HAUG, E. 1909. *Traite de geologie.* II. Les periodes géologiques, 1242.

*HEINRICH, M. 1914. Studien in den Riffkalken des Rheinischen oberen Mittledevons Pt. III. *Dissert. Bonn.* Freiberg pp.1-58.

HICKSON, S.J. 1934. On *Gypsina plana* and on the systematic position of the stromatoporoids. *Q. J. micro.Sci.* new ser., **303** (76), 433-480.

HINDE, G.J. 1887-1912. A monograph of the British fossil sponges. *Palaeontogr. Soc.* **40,** 92pp.

HOSHINO, T. 1985. A new *Merlia* (Poescilosclerida) from Japanese Waters. *Proceedings of the 3rd International Conference on the Biology of Sponges,* 31.

HUDSON, R.G.S. 1953. The stromatoporoid genus *Millestroma* Gregory. *J. Paleontol.* 27 (6).

HUDSON, R.G.S. 1954a. Jurassic Stromatoporoids from South Arabia. *Notes Mém.Moyen-Orient.Paris* **5**, 207-221.

HUDSON, R.G.S. 1954b. A new lower Cretaceous stromatoporoid *Bekhemia wetzeli* from Northern Iraq. *J. Paleontol.* **28** (1), 48-51.

HUDSON, R.G.S. 1954c. Jurassic stromatoporoids from the Lebanon. *J. Paleontol.* **28**, 657-661.

HUDSON, R.G.S. 1955a. Séquanian stromatoporoids from south-west Arabia. *Notes Mem. Moyen-Orient. Paris* **6**, 225-204.

HUDSON, R.G.S. 1955b. On the Jurassic stromatoporoids: I. The type of *Stromatopora douvillei* Dehorne II. *Milleporidium* and *'Stromatopora'* from Central Arabia, III. *Stromatopora arrabidensis* Dehorne, *Ann. Mag. nat. Hist.* **12** (8), 13-20, 313, 705.

HUDSON, R.G.S. 1956. Tethyan Jurassic hydroids of the family Milleporidiidae. *J. Paleont.* **30** (3), 714-730.

HUDSON, R.G.S. 1957. *Stromatorhiza* Bakalow, stromatoporoide du Jurassique superieur. *Bull. Soc. geol. Fr.* (6^e séries) **7**, 3-10.

HUDSON, R.G.S. 1958. *Actostroma* gen. nov. A Jurassic Stromatoporoid from Makhtesh Hathira, Israel. *Palaeontology* **1** (2), 87-98.

HUDSON, R.G.S. 1958. The Upper Jurassic faunas of S. Israel. *Geol. Mag.* **95** (5), 415-425.

HUDSON, R.G.S. 1959. The stromatoporoid genus *Milleporella* Deninger. *Geol. Mag.* **96** (4), 311-316.

HUDSON, R.G.S. 1959. A revision of the Jurassic stromatoporoids *Actinostromina, Astrostylopsis* and *Trupetostromaria*. *Palaeontology. London* **2** (1), 28-38.

HUDSON, R.G.S. 1960. The Tethyan Jurassic stromatoporoids *Stromatoporina, Dehornella* and *Astroporina*. *Palaeontology. London* **2** (2), 180-199.

JAMES, N.J. 1974. Diagenesis of scleractinian corals in the subaerial vadose environment. *J. Palaeontol.* **48**, 785-799.

JONES, W.C. 1970. The composition, development, form and orientation of calcareous sponge spicules. *Symp. zool. Soc. London* **25**, 91-123.

JONES, W.C. 1979. The microstructure and genesis of sponge biominerals. *Coll. Internat. C.N.R.S.,* **291**, 425-447.

KAZMIERCZAK, J. 1969. A new interpretation of astrorhizae in the Stromatoporoidea. *Acta palaeontol. Pol.* **14**, 499-535.

KAZMIERCZAK, J. 1971. Morphogenesis and systematics of the Devonian Stromatoporoidea from the Holy Cross Mountains, Poland. *Acta palaeontol. Pol.* **26**, 1-146.

KAZMIERCZAK, J. 1974. Lower Cretaceous sclerosponges from the Slovakian Tatra Mountains. *Palaeontology. London* **17**, 341-347.

KAZMIERCZAK, J. 1976. Cyanophycean nature of stromatoporoids. *Nature. London* **264** (5581), 49-51.

KAZMIERCZAK, J. 1979. Sclerosponge nature of chaetetids evidenced by spiculated *Chaetetopsis taurei* (Deninger 1906) from the Barremian of Crimea. *Neues Jahrb. Geol. Palaeontol.* **2**, 97-108.

KAZMIERCZAK, J. 1981. Evidences for Cyanophyte origin of stromatoporoids. In: Monty, C. (ed.), *Phanerozoic stromatolites* , 230-241. Springer-Verlag, Berlin.

KAZMIERCZAK, J. 1984. Favositid Tabulates: evidence for Poriferan affinity. *Science* **225**, 835-837.

KAZMIERCZAK, J. and KRUMBEIN, W. 1983. Identification of calcified coccoid cyanobacteria forming stromatoporoid stromatolites. *Lethaia,* **16** (3), 207-213.

KAZMIERCZAK, J., HEBBOT, V. and DEGENS, E.T. 1985. Biocalcification through time: Environmental challenge and cellular response. *Palaeontol. Z.* **59** (1/2), 15-33.

KAZMIERCZAK, J. and HILLMER, G. 1974. Sclerosponge nature of the lower Hauterivian 'Bryzoan' *Neuropora pustulosa* (Roemer 1839) from W. Germany. *Acta palaeontol. Pol.* **19** (4), 443-453.

KELLAWAY, G.A. and SMITH, S. 1938. Stromatoporoids from the Inferior Oolite of S.W. England. *Q. J. geol. Soc. London* **94**, 321-330.

KERSHAW, S. 1981. Stromatoporoid growth form and taxonomy in a Silurian biostrome, Gotland. *J. Paleontol.*, **55** (6), 1284-1295.

*KHALFINA, V.K. and YAVORSKY, V.I. 1973. Klassifikatsiya stromatoporoidey. *Palaeontol. Zhur.* **8**, 118-120.

KIRKPATRICK, R. 1910. Further notes on *Merlia normani.* *Ann. Mag. nat. Hist.* **5**, 288-291.

KIRKPATRICK, R. 1912. *Merlia normani* and its relation to certain Palaeozoic fossils. *Nature. London* •, 502-503.

KIRKPATRICK, R. 1912. On the stromatoporoid and Eozoon. *Ann. Mag. nat. Hist.*, ser.8, **10**, 341-347.

KIRKPATRICK, R. 1912. On the nature of stromatoporoids. *Nature* **87**, 607.

KIRKPATRICK, R. 1930. *The Nummulosphere.* Private publication.

KISSLING, D.L. and LINEBACK, J.A. 1967. Palaeoecological analysis of corals and stromatoporoids in a Devonian biostrome: Falls of Ohio, Kentucky, Indiana. *Bull. geol. Soc. Am.* **78**,157-174.

*KÜHN, O. 1927. Zur systematik und Nomenclatur der Stromatoporen. *Zbl. Geol. Palaönt. Abt. B,* 546-551.

*KÜHN, O. 1928. Hydrozoa: *Fossilum Catalogus* I. (Animalia) pt.36, 2, 76-94. Mesozoicium. Berlin.

KÜHN, O. 1928. Zur Systematik und Normenklature der Stromatoporen. *Centralbl. Mineral. Geol. Palaeontol.* B **12**, 546-551.

KÜHN, O. 1939. Hydrozoa. In: Schindenoy, O.H. (ed.) *Handbuch der Palaozoologie,* **2a** (5), 1-68. Berlin.

LECOMPTE, M. 1951. Les stromatoporoides du Dévonien moyen et supérieur du Bassin de Dinant, Première partic. *Institut R. Sciences Naturelles de Belgique* **11**, 215.

LECOMPTE, M. 1952. Revision des stromatoporoides Mesozoiques des collections Dehorne et Steiner. *Institut R.Sciences Naturelles de Belgique* **28** (53).

LECOMPTE, M. 1956. *Treatise on Invertebrate Palaentology.* Part F. Coelenterata, Stromatoporoidea. F108-144.

*LÉVI, C. 1956. Étude des *Halisarca* de Roscoff. Embryologie et systematique des demosponges. *Archs. Zool. exp. gen.* **93** (1), 1-181.

LÉVI, C. 1973. Systématique de la classe des Demospongia (Demosponges). In: Grassé P.P. (ed.), *Traité de Zoologie* **1** (3), 577-631. Masson, Paris.

*LINDSTROM, G. 1870. A description of the Anthozoa *perferacta* of Gotland. *Kongl. Svenska Vet. Akad. Handl.* **9** (6).

*LINDSTROM, G. 1873. Nagra anteckingar om Anthozoa tabulata. *O Efversigt. Kongl. Vetenskaps Akad. forhandl.,*B, 30.

LISTER, J.J. 1900. *Astrosclera willeyana* the type of a new family of sponges. Wiley, A. (ed.) *Zoological results* **4**, 459-482.

LOHMANN, K.C. and MEYERS, W.J. 1977. Microdolomite inclusions in cloudy prismatic calcites: A proposed criterion for former high-magnesium calcites. *J. sediment. Petrol.* **47**, 1078-1088.

*MACKIE, G.O. and SINGLA, C.L. 1983. Studies on hexactinellid sponges. I. Histology of *Rhabdocalyptus dawsoni* (Lambe, 1873). *Philos. Trans. R. Soc. London* B, **301**, 365-400.

MATTHEWS, S.C. 1973. Notes on open nomenclature and on synonymy lists. *Palaeontology.* **16** (4), 713-721.

*MAZZULLO, S.J. 1980. Calcite pseudospar replacive of marine acicular aragonite, and implications for aragonite cement diagenesis. *J. sediment. Petrol.* **50**, 409-422.

MILAN, A. 1969. Facijelni odnosi i hidrozo ska fauna malma prinorskog dijela sjevernog velebitaj velike kapele. *Geological Inst. Zagreb* **22** (11-16), 135-218.

*MISTIAEN, B. 1984. Disparition des stromatopores Palaeozoiques ou survie de groupe: hypothese et discussion. *Bull. Soc. geol. Fr.* **26** (7), 1245-1250.

MITCHELL-TAPPING, H. 1980. Use of stromatoporoids as an indicator of a coral reef environment. *Florida Sci.* **43**(1), 14-19.

MORI, K. 1970. Stromatoporoids from the Silurian of Gotland. Part 2. *Stockholm Contrib. Geol.* **19**, 1-100.

MORI, K. 1980. Revision of the Permian 'Stromatoporoids' reported from Japan. *Trans. Proc. Pal. Soc. Japan,* New Series, **117**, 237-241.

MORI, K. 1982. Coelenterate affinities for stromatoporoids. *Stockholm Contrib. Geol.* **37**, 167-175.

MORI, K. 1984. Coelenterate affinities of stromatoporoids. *Proc. Fourth International Symposium on Fossil Cnidaria. Palaeontogr. Am.* **54**, 354-358.

NESTOR, H. 1974. O filogenii paleozoiskikh stromatoporoidei. In: Sokolov, B.S.(ed.) Drevnie Cnidaria. *Akad. Nauk. SSSR Sibirskoe otdel.Tr. Inst. Geol. Geofiz.,* **201**, 27-38.

NESTOR, H. 1981. The relationship between stromatoporoids and heliolitids. *Lethaia* **14**, 21-25.

NEWELL, N.D. 1935. Some mid-Pennsylvanian invertebrates from Kansas and Oklahoma. II. Stromatoporidea, Anthozoa and Gastropoda. *J. Paleontol.* **9**, 341-355.

NICHOLSON, H.A. 1873. On a new species of *Stromatopora*. *Ann. Mag. nat. Hist.* Ser.4, **12**, 89.

NICHOLSON, H.A. 1886. British fossil stromatoporoids. *Palaeontogr. Soc. Monogr.* **39**, 77-79.

NICHOLSON, H.A. and MURIE, J. 1878. On the minute structure of *Stromatopora* and its allies.

J. Linnean Soc. Zool. **14**, 187-246.

d'ORBIGNY, A.P. 1850. *Prodrome de paleontologie stratigraphique universelle des animaux mollusques et rayonnés.* Vols.1 and 2. Paris.

OEKENTORP, K. 1984. Aragonite and diagenesis in Permian Corals. Proceedings of the Fourth International Symposium on Fossil Cnidaria. *Paleontogr. Am.* **54**, 282-293.

OSIMO, G. 1910. Alcune nuove stromatopore giuresi e cretacee delle Sardegna e dell 'Appennino. *R. Acad. Sci. Torino* **61**, 277-299.

PARKS, W.A. 1907-1910. Silurian stromatoporoids of America, excluding Niagara and Guelph. *Univ. Toronto Stud.* 4-7.

PARKS, W.A. 1935. Systematic position of the Stromatoporoidea. *J. Paleont.* 9, 18-29.

PARONA, C.F. , CREMA, C. and PREVER, P.L. 1909. La fauna coralligena del Cretaceo dei Monti d'Ocre nell'Abruzzo Aquilano. *Mem. Carta geol. Ital.* **5**, 148.

PARONA, C.F. 1933. Di alluci idrozoi dei Giurassico e Cretacico in Italia. *Mem. R. Accad. Sci. Torino,* 2ndSer.,**17**, 2-13.

PFENDER, J. 1932. Sur la presenie de stromatoporides du genre *Burgundia* dans les calcaires Portlandiens de Grand Corent, pres Villereversure (Ain). *Bull. Soc. geol. Fr.*, ser.5, **1**, 739-742.

PFENDER, J. 1937. Quelques hydrozoaires de la Syrie septentrionale. *Notes Haut. Comm. Syrie Liban* **2**, 125-136.

PLUMMER, L.N. and MACKENZIE, F.T. 1974. Predicting mineral solubility from rate data: application to the dissolution of magnesian calcites. *Am. J. Sci.* **274**, 61-83.

REID, R.E.H. 1963. Preliminary notice of a classification of the Demosponges. *Irish Nat. J*. **14**, 90-94.

REID, R.E.H. 1968. Microscleres in demosponge classification. *Paleontol. Contrib. Kansas Univ.* **35**, 1-37.

REID, R.E.H. 1970. Tetraxons and demosponge phylogeny. In: Fry, W. (ed) *Biology of the Porifera. Symp. Zool. Soc. Lond.* **25**, 63-89.

REISWIG, H.M. 1975. The aquiferous system of three marine Demospongiae. *J. Morphol.* **145**(4), 493-502.

REITNER, J. 1986. Personal communication.

REITNER, J. [in press]. The polyphyletic nature of the 'Sphinctozoa'. *Proceedings of the 3rd International Meeting on the Biology of Sponges.*

REITNER, J. and ENGESER, T. 1983. Contributions to the Systematics and Palaeoecology of the family Acanthochaetetidae Fischer 1970 (Order Tabulospongida, Class Sclerospongidae). *Geobios* **16**(6), 773-779.

REITNER, J. and ENGESER, T. 1985. Revision der demospongier mit einem Thalamiden, araginitischen Basalskelett und Trabekularer Internstukher ("Sphinctozoa" *pars*). *Berliner Geowiss Abh.* (A)**60**, 151-193.

*RICHTER, R. 1948. *Einfuhrung in die Zoologische Nomenklatur.* 2nd edition. Kramer, Frankfurt a.M., 252pp.

RICHTER, R. and FUCHTBAUER, H. 1978. Ferroan calcite replacement indicates former magnesian calcite skeletons. *Sedimentology* **25**, 843-860.

*RICHTER, D.K. and BESENECKER, H. 1983. Subrecent high-Sr aragonite ooids from hot springs near Tekke Ilica (Turkey). In: Peryt, T. (ed.) *Coated grains.* Springer-Verlag, 154-162.

RIDE, W.D.L.*et al.* International code of zoological nomenclature. 3rd edition. International Trust for Zoological Nomenclature.

RIDING, R. and KERSHAW, S. 1977. Nature of stromatoporoids. *Nature. London* **268**, 178.

RIGBY, R. 1983. Sponges of the Middle Cambrian Marjum Limestone from the House Range and Drum Mountains of western Millard County, Utah. *J. Paleont.* **57**, 240-270.

RIGBY, J.K. and STEARN, C.W. 1983. Sponges and Spongiomorphs. *Univ. Tennessee Studies in Geology* **7**, 220pp.

ROBERTSON, A.H.F. 1977. The origin of framboids. *Lithos* **3**, 269-293.

ROEMER, F. A. 1851-56. Lethaea Geognostica. 3rd edition, **1**, 166.

ROEMER, F. A. 1880. Lethaea Geognostica, 538.

ROSEN, B.R. 1979. Modules members and communes: A postscript introduction to social organisms. In: Larwood, G. and Rosen B.R. (eds.) *Biology and Systematics of Colonial Organisms.*

Syst. Assoc. Spec. Vol. **11**, xiii-xxxv.

ROSEN, F. von 1869. Uber die Natur des Stromatoporen und uber die Erhaltung der Hornfaser der Spongien im fossilen Zustande. *Verh. Russ-K. mineral. Ges. St. Peterburg* *4* (2),1-98.

SALTER, J. 1873. *Catalogue of Silurian fossils,* p.99.

St. JEAN, J. 1967. Maculate tissue in stromatoporoids. *Micropaleontology* **13**, 419-444.

SANDBERG, P.A. 1983. An oscillating trend in Phanerozoic non-skeletal carbonate mineralogy. *Nature. London* **305**, 19-22.

SANDBERG, P.A. 1984. Recognition criteria for calcitized skeletal and non-skeletal aragonites. Proceedings of the Fourth International Symposium on Fossil Cnidaria. *Paleontogr. Am.* **54**, 272-282.

SANDBERG, P.A. and HUDSON, J.D. 1983. Aragonite relic preservation in Jurassic calcite-replaced bivalves. *Sedimentology* **30**(6), 879-862.

SANDBEGER, G. and SANDBEGER F. 1850-1856. Die Versteinerungen des rheinischen Schlichten systems in Nassau, 380.

SCHNORF-STEINER, A. 1955. Polymorphisme chez *Burgundia trinorchii* Munier-Chalmas. *Eclog. geol. Helv.* **48**, 464-467.

SCHNORF-STEINER, A. 1956. Étude du squelette chez *Burgundia trinorchii. Schweiz. palaeontol. Ges.* **49**, 545-71.

SCHNORF-STEINER, A. 1960. Parastromatoporidae nouveau du Jurassique superieur et du Valanginien inferieur du Jura. *Eclog.geol. Helv.* **58**, 729-732.

*SHORE, R.E. 1972. Axial filament of siliceous sponge spicules, its organic components and synthesis. *Biol .Bull.* **143**, 689-698.

SCHRAMMEN, A. 1910. Die Kieselspongien der oberen Kreide von Nordwest-deutschland. I. Teil, Tetraxonia, Monaxonia und Silicea incert.sedis. Paleontogr. suppl. **5**, 385pp.

SCHRAMMEN, A. 1924. Die Kieselspongien der Oberen Jura von Süddeutschland. *Palaeontogr.* **84**, 149-194; **85**, 1-114.

SOLLAS, W.J. 1877. On *Stauronema*, a new genus of fossil Hexactinellid sponges, with a description of its two species. *Ann. Mag. nat. Hist.* Ser. 4, **19**, 1-25 .

SOLOMKO, E. 1886. *Stromatoporoides décriens de la Russie*. These. St. Petersbourg. 48pp.

STANLEY, G. 1986. Personal communication.

STEARN, C.W. 1966. The microstructure of stromatoporoids. *Palaeontology* **9** (1), 74-124.

STEARN, C.W. 1972. The relationship of the stromatoporoids to the sclerosponges. *Lethaia* **5**, 369-388.

STEARN, C.W. 1975. The stromatoporoid animal. *Lethaia* **8**, 89-100.

STEARN, C.W. 1980. Classification of the Palaeozoic stromatoporoids. *J. Paleont.* **54** (5), 881-902.

STEARN, C.W. 1982. The unity of stromatoporoidea. *Proc. 3rd North Amer. Palaeo. Convention.*

STEARN, C.W. 1986. Diagenesis and Mineralogy of the Palaeozoic stromatoporoids. *Proc. 4th North Amer. Palaeo. Convention,* p. A45.

STEHLI, F.G. 1956. Shell mineralogy in marine invertebrates. *Science* **123**, 1031-1032.

*STEINMANN, G. 1878. Über fossile Hydrozoen aus der Famille der Coryniden. *Palaeontographica* **25**, 101.

STEINMANN, G. 1903. Nachtrage zur fauna von Stramberg *Milleporidium*, aine Hydrocoralline aus dem Tithon von Stromberg. *Beitr. Palaontol. Geol. Ost.-Ung.* **15**,1.

STEINER, A. 1932. Contribution a l'étude des stromatopores secondaires. *Mem.Soc.Vaud Sci. Nat.* **4** (3), 105-221.

*STEINMANN, G. 1882. Pharetronen-Studien. *Neues Jahrb. Mineral. Geol. Palaeontol.* **2**, 139-191.

STOCK, C. 1983. Stromatoporoids: Geologic History. In: Broadhead, T.W. (ed.) Sponges and Spongiomorphs. *Univ. Tennessee Stud. Geol.* **7**,167-173.

STOCK, C. 1984. The function of tube-pillars in the Ordovician stromatoporoid *Cliefdenella* inferred by analogy with the Recent sclerosponge *Calcifibrospongia.* Proceedings of the Fourth International Symposium on Fossil Cnidaria. *Palaeontogr. Am.* **54**, 349-354.

STONE, S. 1985. Personal communication.

STUCKENBURG, A. 1895. Die Korallen und die Bryozoender Stein-Kohlenablageringen des Ural und des Timan. *Mem. Com. Geol., St. Petersbourg,* **10,** 230-470.

TERMIER, H. and TERMIER, G. 1973. Stromatoporoids, sclerosponges and Pharetores. *Ann. Mines Geol. Tunisie* **26**.

TERMIER, H. and TERMIER, G. 1976. Spongiares hypercalcifés et ectoproctes stenolemes fossiles. *C.r. Seances Acad. Sci. Paris* **282D**, 1269-1272.

TERMIER, H. and TERMIER, G. 1979. Temps-fortes de l'evolution des Spongiares. Theorie environmentale et symbiotique de leur origine. *Colloques Internationale de C.N.R.S.* **291**, 513-521.

THOMAS, H.D. 1935. Jurassic corals and Hydrozoa, together with a redescription of *Astraea caryophylloides* Goldfuss. *Geol. Palaeont. British J.* **2**, 23-39.

THOMAS, H.D. 1971. A new stromatoporoid (*Actinostromaria faringdonensis*) from the Lower Greensand of England. *Proc. Geol. Assoc. London* **82** (1), 13-15.

TOPSENT, E. 1928. Une Mycaline productrice de desmas *Desmatiderma asbuscula,* n. g., n.sp. *Bull. l'Institut Oceanographic, Monaco,* **519**, 1-8.

*TORNQUIST, A. 1900. Neue Beitrage zur Geologie und Paleontologie der Umgebung von Recoaro und Schio. IV. Die Stauia-Kalk. *Zeitschr. Deutsch. geol. Ges.* **52**, 128.

TORNQUIST, A. 1901. Uber mesozoische stromatoporide. *Sitzungsber Preuss. Akad. Wiss. Berlin* **1116**, note 2.

TRIPP, K. 1929. Untersuchungen uber den Skelettbau von Hydractinien zu einer vergleichenden Betrachtung der Stromatoporen. *Neues Jahrb. Mineral.* **62**, 467-508.

TURNŠEK, D. 1966. Upper Jurassic hydrozoan fauna from Southern Slovenia. *Razprave* **9**(8), 337-428.

TURNŠEK, D. 1967. Sistematski polozaj rodu *Burgundia* (Hydrozoa). *Razprave* **4**(10), 265-275.

TURNŠEK, D. and BARBULESCU, A. 1969. Upper Jurassic hydrozoa from Central Dobrogea (Romania). *Geologija* **12**, 73-84.

TURNŠEK, D. and MASSE, J.P. 1973. The lower Cretaceous hydrozoa and Chaetetidae from Provence (SE France). *Razprave* **16**(6), 219-244.

TURNŠEK, D. and BUSER, S. 1974. The Lower Cretaceous corals, hydrozoans, and chaetetids of

Banjska Planota and Trnovski Gozd. *Razprave* **17** (2), 85-124.

TURNŠEK, D. and MIHAJLOVK, M. 1981. Lower Cretaceous Cnidarians from Eastern Serbia. *Razprave* **23** (1), 1-53.

TURNŠEK, D. BUSER, S. and OGORELEC, B. 1981. An Upper Jurassic reef complex from Slovenia, Yugoslavia. In: Toomey, D.F. (ed.) *European Fossil Reef Models.* S.E.P.M. **30**, 361-371.

TUZET, O. 1948. Les premiers stades du development de *Leucosolenia botryoides* Ellis et Solander et de *Clathrina (Leucosolenia) coriacea Mont. Ann.Sci. nat. Paris,* **11**, 103-113.

TWITCHELL, G.B. 1929. The structure and relationships of the true stromatoporoids. *Am. Midl. Nat.* **11**, 270-306.

VACELET, J. 1979. Description et affinities d'une éponge sphinotozoaire actuel. *Collques internat. du C.N.R.S.* **291**, 483-493.

VACELET, J. 1980. Squelette calcaire faculatif et corps de regeneration dans le genre *Merlia* , éponges apparentées aux chaetetides fossiles. *C.r. Seances Acad. Sci. Paris* **290**, Series b, 227-230.

VACELET, J. 1983. Les éponges hypercalcifées, reliques des organismes constructeurs de recifs du Paleozoique et du Mesozoique. *Bull. Soc. zool. Fr.* **108** (4), 547-557.

VACELET, J. 1985. Coralline sponges and the evolution of the Porifera. In: Conway Morris,S. *et. al.* (eds.) *The orgins and relationships of Lower invertebrates. Syst. Assoc. Spec. Vol.* **28**, 1-13.

VACELET, J. 1985. Personal communication.

VAN SOEST R.W.M. 1984. Marine sponges from Curaçao and other Caribbean localities pt.3. Poescilosclerida. *Studies on the fauna of Curacao and other Caribbean Islands* **199**, 161-171.

VEIZER, L. and WENDT, J. 1976. Mineralogy and chemical composition of Recent and fossil skeletons of calcareous sponge. *Neues Jahrb. Geol. Palaeontol. Monatshefte,* 558-573.

*VINASSA DE REGNEY, P. 1901. Trias tabulalen, Bryozoen and Hydrozoen aus dem Bakony. *Res.d. Wissensch. Frj. d. Balatonsees Bd.* **1** (1).

VINASSA DE REGNEY, P. 1908. Neue Schwanme, Tabulaten und Hydrozoen aus dem Bakony. *Res.*

Wiss. Ertorschung d. Balatonsees, **1** (3).

VINASSA DE REGNEY, P. 1915. Triadische Algen, Spongien, Anthozoen und Bryozoen aus Timor. *Palaeontologie von Timor.* Stuttgart, **4** (8), 75-116.

WAAGEN, W. and WENTZEL, J. 1887. Salt range fossils. *Palaeontol. Indica*,Ser. 13, **7**, 1-947.

WARDLAW, N., OLDERSHAW, A. and STOUT, M. 1978. Transformation of aragonite to calcite in a marine gastropod. *Can. J. Earth Sci.* **15**, 1861-1866.

*WEISSENFELS, N. 1978. Bau und funktion des susswasserschwamms *Ephydatia fluviatilis* L. (Porofera) V. das Nadelskelet und seine Enstehung. *Zool. Jahrb. Abt. Anat.* 99, 211-223.

*WEISSENFELS, H. W. and LANDSCHOTT. 1977. Bau und Funktion des susswasserschwamms *Ephydatia fluviatilis* L. (Porofera). IV. Die Entwicklung der monaxialen SiO_2 - Nadeln in Sandwich-Kulturen. *Zool. Jahrb. Abt. Anat.* **98**, 355-371.

WELLS, J.W. 1934. A new species of stromatoporoid from the Buda Limestone of Central Texas. *J. Paleontol.* **8**, 169-170.

WELLS, J.W. 1943. Palaeontology of the Harrar Province, Ethiopia: Jurassic Anthozoa and Hydrozoa. *Bull. Am. Mus. nat. Hist.* **82** (2), 31-54.

WENDT, J. 1974. Der Skelettbau aragonitishen kalkschimmine aus dem alpinen obertrias. *Neues Jahrb. Geol. Palaeontol. Monatshefte* **8**, 498-511.

WENDT, J. 1975. Aragonitische Stromatoporen aus der alpinen Obertrias. *Neues Jahrb. Geol. Palaontol. Abhandlungen* **150** (1), 111-125.

WENDT, J. 1977. Aragonite in Permian reefs. *Nature* **267** (5609), 335-337.

WENDT, J. 1979. In: Hartman, W.D. *et al.* (eds.) Living and fossil sponges. *Sedimenta* **8**,169-223.

WENDT, J. 1984. Skeletal and spicular Mineralogy, Microstructure and Diagenesis of Coralline Calcareous Sponges. Proceedings of the Fourth International Symposium on Fossil Cnidaria. *Palaeontogr. Am.* **54**, 326-337.

WEST, R. Personal communication.

*WINCHELL, A. 1866. Stromatoporidae: their structure and zoological affinities. *Proc. Am. Assoc. Adv.Sci.* **15**, 91.

WOOD, R.A. [in press]. The placing of the Mesozoic stromatoporoids in the Porifera. *Proceedings of the3rd International Conference on the Biology of Sponges.*

WOOD, R.A. and REITNER J. 1986. Poriferan affinities for Meozoic Stromatoporoids. *Palaeontology.* **29**(3), 469-473 .

YABE, H. 1901 Uber *Myriopora verbeeki* Volz und *Stromatopora japonica* Yabe. *J. geol. Soc. London* **21**, 43.

YABE, H. 1903. On a Mesozoic stromatoporoid. *Jour. geol. Soc. Japan* **10**, 123.

YABE, H. and SUGIYAMA, T. 1930-31. Note on a new hydrozoan, *Plassenia alpina* gen. et sp. nov., from the Plassen Limestone of Plassen, Austria. *Jpn. J. Geol. Geog.* **8**, 113-116.

*YABE, H. and SUGIYAMA, T. 1931. Note on a New Form of *Lophiostroma* from the Permian of Japan. *Sci. Rep. Tohoku imp. Univ.* Ser.2, Geology **10** (1-2), 17-19.

YABE, H. and SUGIYAMA, T. 1935. Jurassic stromatoporoids from Japan. *Sci. Rep. Tohoku imp. Univ.* Ser.2, Geology **14**, 135-192.

YABE, H. and SUGIYAMA, T. 1941. Discovery of *Circoporella semiclathrata* Hayasaka from Hokkaido. *J. geol. Soc. Japan* **48,** 38-42.

YAVORSKY, V.I. 1955/56. Stromatoporoidea of the Soviet Union. *Trudy vsesoyuznogo Nettyanogo i geologicheskogo Institute*, novaya seriya, **8,** 1-261.

*YAVORSKY, V.I. 1957. Stromatoporidea Sovjetskugu sojuza. *Cast. Z. Trudi. USEG EJ N.S.* **18**, 1-78.

*YAVORSKY, V.I. 1962. Gruppa Stromatoporidea. In: Orlov, Y.A. *Osnovy Paleontologii* **2**, 157-167.

*ZITTEL, K.A. 1877. Supplementary note on the English Translation of Tornquist 1900. *Ann. Mag. Nat. Hist.* **4**, 19.

ZUFFARDI-COMERCI, R. 1931. Corallari e idrozoi del Guiralias della Somalia. *Palaeontogr. Ital.* **32**, 49-75.

ZUFFARDI-COMERCI, R. 1938. Corallari e idrozoi giurassici dell ogaden (A.O.I.) *Palaeontogr. Ital.* **32,** suppl. 1-9.

PORIFERAN AFFINITIES OF MESOZOIC STROMATOPOROIDS

by R. A. WOOD *and* J. REITNER

ABSTRACT. The finding of calcite and pyrite spicule pseudomorphs of monaxon spicules in six genera of Mesozoic stromatoporoids confirms poriferan affinities for at least some representatives of this group. Previously, the systematic position has been speculated upon solely from the internal organization of the skeleton.

STROMATOPOROIDS, tabulates, and chaetetids have achieved some notoriety owing to their proposed reclassification from the Cnidaria to the Porifera on the basis of their morphological similarity to some recently discovered sponges, the sclerosponges, which possess both a calcareous and a spicular siliceous skeleton (Hartman 1969, 1979; Hartman and Goreau 1970, 1972). Evidence in the form of spicule pseudomorphs has confirmed the poriferan affinity of chaetetids (Gray 1980; Kazmierczak 1979), and possibly some tabulates (Kazmierczak 1984), but the biological standing of stromatoporoids has remained problematic (for example, see Kazmierczak and Krumbein 1983; Mori 1984; Stearn 1972).

MATERIAL EXAMINED

Several specimens of Mesozoic stromatoporoids that contain spicule pseudomorphs have been found in the collections of the late R. G. S. Hudson, housed in the British Museum (Natural History). They are from the Upper Jurassic of the Middle East and include several holotypes and paratypes. The same feature has also been found by one of us (J. R.) in an undescribed species of stromatoporoid from the Lower Cretaceous of Spain.

Table 1 summarizes spicular data and information on the age and localities of the specimens. Stratigraphical, geographic, and systematic details are given in the cited references. All the spicules are preserved as pyrite or calcite pseudomorphs, either as styles/acanthostyles or possibly as tylostyles, and are arranged intramurally within the axial zone of the skeletal elements. The pyrite pseudomorphs are found as aggregates or chains of crystals arranged along the length of the spicules similar to previously described fossil chaetetid and sclerosponge spicules (Gray 1980; Kazmierczak 1979). These pseudomorphs are found in large numbers, towards the outer edge of the specimen where their original siliceous mineralogy has been replaced, probably as a result of the prolonged leaching by iron-rich pore-waters (Pl. 35, figs. 3 and 4).

The calcite pseudomorphs appear as rods of monocrystalline calcite of a higher transparency than the surrounding microstructural fibres, and are generally preserved in the central areas of the specimen. In *Dehornella crustans* Hudson, where both pyritic and calcitic pseudomorphs are found, the length of the pyrite type is considerably reduced, indicating that pyritization has occurred after partial dissolution of the spicules, producing imperfect replacement, especially of the distal tips. In species where both pseudomorph mineralogies are found, or where obvious corrosion has taken place, only the maximum figures are given. These figures, therefore, certainly represent reduced dimensions of the original spicules.

According to the most recent classification of Mesozoic stromatoporoids (Hudson 1960), all the spiculate species belong to the Milleporellicae, except *Actinostromarianina lecompti* Hudson, which belongs to the Actinostromariicae.

The skeleton of the Milleporellicae consists of fascicular-fibrous microstructure, connected by thin

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tabulae of granular microstructure. There is no lamellar development. The spicules found in these have tapering points, and diverge distally, subparallel to the fibres of the columns (Pl. 35, figs. 1-3). Pseudomorphs do not project into the lumina, and are found singly or in assemblages. Such isolated clusters appear to be remnants of a much denser spicule skeleton, the sporadic distribution of which is now diagenetically determined.

In the Actinostromariicae there is no microstructural differentiation of the pillars and lamellae. The reticulum forms a rectangular meshwork where the elements have a granular central zone and an orthogonal fibrous outer zone. Tabulae of granular microstructure are secreted across the interskeletal spaces. In *A. lecompti* the pseudomorphs are long and thin. They are probably tylostyles, with possible bosses at their proximal end (Pl. 35, fig. 5). The calcite and pyrite pseudomorphs occur side by side and are found both within the pillars and lamellae, where they are generally aligned subparallel to the growth axis of the skeleton. The spicules are evenly distributed, irrespective of their position relative to the skeletal elements. Pseudomorphs can be seen to project into the interskeletal spaces or to terminate abruptly at the skeletal surface due to the corrosion of the projecting length. The spicular positioning appears to form the framework for the subsequent secretion of the calcareous skeleton (Pl. 35, fig. 6).

CONCLUSIONS

The size and distribution of the spicules and the microstructure and arrangement of the calcareous skeleton of these species of Mesozoic stromatoporoid show similarities to representatives of the sclerosponge genera *Murania* (Kazmierczak 1974), *Astrosclera*, *Ceratoporella* (Hartman 1969; Hartman and Goreau 1970, 1972), and *Calcifibrospongia* (Hartman 1979). The systematic position of the sclerosponges is open to question. Some workers (Vacelet 1970, 1985; Levi 1973) believe that the sclerosponges form a polyphyletic and unnatural group and that the members can be better placed in the pre-existing taxa of the Demospongiae. It is likely that the sphinctozoans, tabulates, and the stromatoporoids are also unnatural groupings and that the finding of spicules will enable the construction of a more meaningful classification and phylogenetic reconstruction of these convergent groups. However, spicules cannot be used as a species-specific characteristic due to the rarity of their preservation.

The positive placing of at least some representatives of the stromatoporoids in the Porifera has several other consequences. The terminology, at present based on cnidarian nomenclature, will have to be revised and a classification that, where possible, incorporates spicule data needs to be developed. This will enable stromatoporoids to be studied from a biological standpoint, and allow a valid appraisal of their ecological role as locally significant faunal elements in Mesozoic carbonate buildups.

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EXPLANATION OF PLATE 35

Figs. 1-6. Spiculated Mesozoic stromatoporoids; transmitted light photomicrographs of thin sections. 1, ***Dehornella crustans*** (Hudson), H5170c. Calcite pseudomorphs of style/acanthostyle spicule arranged subparallel to the microstructural fibres of the calcitic skeleton. × 100. 2, ***Dehornella n. sp.***, H5478a. Calcite pseudomorphs of style/acanthostyle spicules arranged in ?lattice. × 175. 3, ***Parastromatopora libani*** (Hudson), H4789. Large numbers of pyrite pseudomorphs in outer leached zone. × 10. 4, detail of individual pseudomorphs of specimen shown in fig. 3. × 600. 5, ***Actinostromarianina lecompti*** (Hudson), H4608a. Pyrite pseudomorphs of ?tylostyle spicules. × 330. 6, Spicule framework of specimen shown in fig. 5. × 50.


1


2


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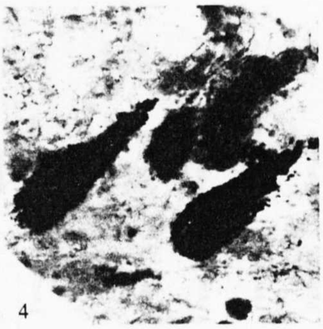
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3

WOOD and REITNER, spiculated Mesozoic stromatoporoids

TABLE 1. *Specimen and spicule data*

Species	Age	Locality	Calcareous skeleton			Spicular data					References
			Gross morphology	Micro-structure	Traces of aquiferous system	Type	Distribution	Present mineralogy	Dimensions		
									Length (μm)	Diameter (μm)	
H *Dehornella crustans* H5170c H5168a	L. Kimm.	Makhtesh Haithira, Israel	Nodular, encrusting	Fasc. Fib.	Astrorhizae	Style	Intramural s.m.	Calcite and pyrite	90–135	13·5–17·0	Hudson (1960)
H *Dehornella n. sp.* H5478a and b	U. Apt.	Ereño, Spain	Laminar, encrusting	Fasc. Fib.	Astrorhizae	Style acanthostyle	Intramural s.m.	Calcite	75–250	5–20	Reitner, pers. obs.
H *Steineria somaliensis* H4897b	L. Kimm.	Makhtesh Haithira, Israel	Dendroid	Fasc. Fib.	Tabulate oscula ?astrorhizae	Style	Intramural s.m.	Pyrite	15–25	6·5–9·0	Hudson (1955*a*)
Shuqraia hethira H5034a	L. Kimm.	Wadi Haithira, Israel	Dendroid	Fasc. Fib.	Astrorhizae	Style	Intramural s.m.	Pyrite	60–80	5–7	Hudson (1955*a*)
Parastromatopora libani H4789	M. Kimm.	Toumatt, Lebanon	Massive, nodular	Fasc. Fib.	Astrorhizae	Style	Intramural s.m.	Pyrite	60	18	Hudson (1954)
H *Promillepora kurnubi* H4898	L. Kimm.	Makhtesh Haithira, Israel	Dendroid	Fasc. Fib.	Tabulate oscula ?astrorhizae	Style	Intramural s.m.	Pyrite	50	12	Hudson (1955*a*)
P *Actinostromarianina lecompti* H4608a and b	U. Kimm.	Alam Abyadh, Arabia	Nodular, encrusting, fasciculate	Granular and orthogonal	Astrorhizae	?Tylostyle	Intramural s.s.	Calcite and pyrite	180	8	Hudson (1955*b*)

H = holotype; P = paratype; Fasc. Fib. = Fascicular Fibrous; s.m. = subparallel to microstructural fibres; s.s. = subparallel to growth axis of skeleton. Specimen numbers refer to the R. G. S. Hudson Collection housed in the British Museum (Natural History).

REFERENCES

GRAY, D. I. 1980. Spicule pseudomorphs in a new Palaeozoic chaetetid and its sclerosponge affinities. *Palaeontology*, **23**, 803-820.

HARTMAN, W. D. 1969. New genera and species of coralline sponges from Jamaica. *Postilla*, **137**, 1-39.

—— 1979. A new sclerosponge from the Bahamas and its relationship to Mesozoic stromatoporoids. *In* LEVI, C. and BOURY-ESNAULT, N. (eds.). Biologie des Spongiares. *Coll. Internat. du C.N.R.S.* **291**, 467-474.

—— and GOREAU, T. E. 1970. Jamaican coralline sponges: their morphology, ecology and fossil representatives. *Symp. Zool. Soc. Lond.* **25**, 205-243.

—— —— 1972. *Ceratoporella* (Porifera; Sclerospongiae) and the chaetetid 'corals'. *Trans. Conn. Acad. Arts. Sci.* **44**, 133-148.

HUDSON, R. G. S. 1954. Jurassic stromatoporoids from the Lebanon. *J. Paleont.* **28**, 657-661.

—— 1955*a*. Tethyan Hydroids of the Family Milleporiidae. Ibid. **30**, 714-730.

—— 1955*b*. Sequanian stromatoporoids from South-west Arabia. *Notes Mem. Moyen-Orient*, **6**, 225-240.

—— 1960. The Tethyan Jurassic stromatoporoids, *Stromatoporoina*, *Dehornella*, and *Astroporina*. *Palaeontology*, **2**, 80-99.

KAZMIERCZAK, J. 1974. Lower Cretaceous sclerosponges from the Slovakian Tatra Mountains. Ibid. **17**, 341-347.

—— 1979. Sclerosponge nature of chaetetids as evidenced by spiculated *Chaetopsis favei* (Denninger 1906) from the Barremian of Crimea. *Neues Jb. Geol. Palaeont., Mh.* **2**, 97-108.

—— 1984. Favositid tabulates: evidence for poriferan affinity. *Science*, **225**, 835-837.

—— and KRUMBEIN, W. E. 1983. Identification of calcified coccoid cyanobacteria forming stromatoporoid stromatolites. *Lethaia*, **16**, 207-213.

LEVI, C. 1973. Systematique de la classe des Demospongia (Demosponges). *In* GRASSE, P. P. (ed.). *Traite de Zoologie*, vol. 3, 577-632. Masson et Cie., Paris.

MORI, K. 1984. Comparison of skeletal Structures among Stromatoporoids, Sclerosponges and corals. *Palaeontographica Am.* **54**, 354-358.

STEARN, C. 1972. The relationship of the stromatoporoids to the sclerosponges. *Lethaia*, **5**, 369-388.

VACELET, J. 1970. Les éponges pharetronid actuelles. *Symp. Zool. Soc. Lond.* **25**, 189-204.

—— 1985. Coralline sponges and the evolution of the Porifera, 1-13. *In* CONWAY MORRIS, S., GEORGE, J. P., GIBSON, R. and PLATT, H. M. (eds.). The origins and relationships of lower invertebrates. *Syst. Assoc. Spec. Publ.* **28**, 390 pp. Oxford University Press.

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