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The Upper Cretaceous "chaetetid" demosponge *Stromatoaxinella irregularis* n.g. (MICHELIN) and its systematic implications

By

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With 9 figures and 1 table in the text

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Abstract: The "chaetetid" *Blastochaetetes irregularis* (MICHELIN) is redescribed. The presence of calcite pseudomorphs of long, thin style spicules indicates poriferan affinities. Their type and arrangement is characteristic of the Order Axinellida (Class Demospongia), but the unique combination of spicule type and arrangement requires a new genus, *Stromatoaxinella*, and family, Stromatoaxinellidae. The distinction previously drawn between "stromatoporoids" and "chaetetids" is artificial.

Zusammenfassung: Die Beschreibung des "Chaetetiden" *Blastochaetetes irregularis* (MICHELIN) aus der mediterranen Oberkreide wird emendiert. Eine neue Gattung *Stromatoaxinella* wird erstellt. Neben einem kalzitischen Basalskelett, das Ähnlichkeiten mit dem oberjurassischen/unterkretazischen stromatoporoiden Demospongier *Dehornella* aufweist, findet sich ein Sklerenskelett aus langen Stylen, die sich in den Tuben des chaetetiden Basalskeletts befinden und in die Tabulae integriert sind. Anordnung der Stylen und Sklerentyp sind charakteristisch für die Ordnung Axinellida. Die Erhaltung der Skleren im Tubenraum und die Integration in die Tabulae indizieren unterschiedliche Mineralisationsphasen des Basalskeletts, die abhängig sind vom Weichkörper des Schwammes. Diskutiert wird die polyphyletische Natur des chaetetiden Basalskeletts. Eine neue Familie Stromatoaxinellidae wird aufgestellt.

1. Introduction

Our knowledge of the distribution and evolutionary history of sponges which bear a calcareous skeleton in addition to a siliceous spicular one, has been greatly modified in recent years. In the 1960's and 70's the rediscovery of living calcified sponges, the "sclerosponges", re-opened the debate as to the possible poriferan affinity of several problematic groups of fossil reef-builders e.g. HARTMAN & GOREAU 1970. Sponge spicule pseudomorphs have since been

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described from Mesozoic stromatoporoids (Wood & Reitner 1986; Wood, 1987a and b; Reitner, 1987(b), sphinctozoans (Reitner & Engeser 1985) chaetetids (e.g. Kaźmierckak, 1974; Dieci et al. 1977; Gray, 1980) as well as from fossil representatives of the living genus *Acanthochaetetes* (Reitner & Engeser 1983; 1987).

These fossil spicule findings have confirmed poriferan affinity for these forms and have allowed a more precise placement within the Recent poriferan classification framework. Due to the uncertainty of taxonomic features used in the fossil classification, placement within this system has been considered to emphasize convergent taxonomic characters and obscure true affinities (Reitner, 1987(b); Wood, 1987(b)). Many of these spiculate forms, including the "sclerosponges" can be placed within the Class Demospongiae (Vacelet, 1985). The possession of different spicule types and arrangements within members of these previously discrete taxonomic groups, has confirmed that the overall morphological form of sponge calcareous skeletons is convergent and that the "stromatoporoids" and "sphinctozoans" are polyphyletic groups, which represent different grades of calcareous skeleton organisation (Valcelet, 1985; Wood, 1987(a); Reitner, 1987(a)). The "sclerosponges" contain representatives of all these grades.

New spicule findings from an Upper Cretaceous (Coniacian-Santonian) "chaetetid" confirms the previously suggested polyphyletic nature of this group and also raises further taxonomic questions. The studied material is lodged in the British Museum (Natural History).

2. Systematic palaeontology

Phylum Porifera Grant, 1872
Class Demospongiae Sollas, 1875
Order Axinellida Levi, 1956

Discussion: The presence of calcareous pseudomorphs of style spicules with axial canal preservation indicates demosponge affinity for *Stromatoaxinella irregularis* nov. gen. (Fig. 2). The ubiquitous presence of smooth styles throughout the Demospongiae makes impossible a more precise placement on the basis of spicules type alone, however the organisation of the spicule in a loose, plumose arrangement and the apparent absence of microscleres probably indicates affinity to the Order Axinellida and the Family Stromatoaxinellidae n. fam. is tentatively assigned to this Order.

Family Stromatoaxinellidae n. fam.

Diagnosis: Calcified ?axinellids with extensive tracts of long thin styles in a loose low-angle plumose arrangement, which are only incorporated within the secondary calcareous tissue (filling tissue). The basal calcareous skeleton is composed of fascicular fibrous tissue which forms columns.

Discussion: The spicules found in *Stromatoaxinella irregularis* appear to

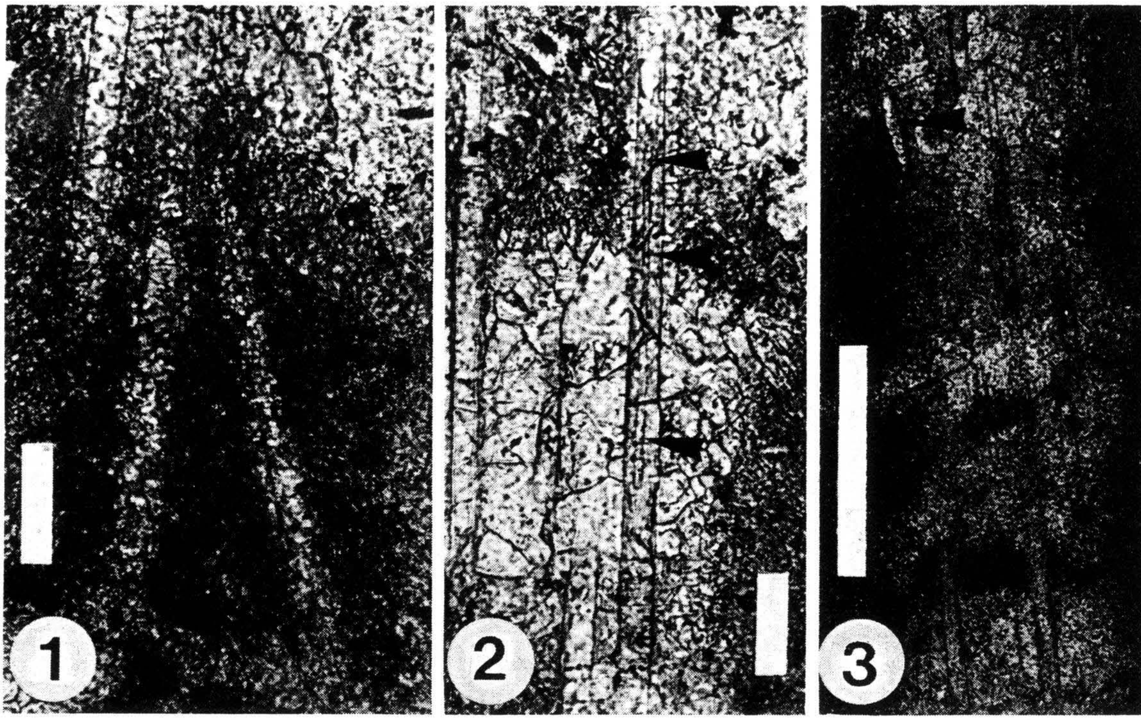

Fig. 1-3. Light photomicrographs of *Stromatoaxinella irregularis* n.g. H 5481, Collada de Bastus, Tremp, N.E. Spain, Santonian.

1: Corrosion (micritisation) of spicules enclosed within tabulae. Scale bar = 25 μm.

2: Axial canal preservation (arrowed). Scale bar = 25 μm.

3: Trapment of spicule within the secondary epitaxial skeleton (arrowed). Scale bar = 300 μm.

be incorporated into the calcareous skeleton only by chance entrapment within the secondary calcareous tissue, which was precipitated upon the primary calcareous tissue during soft-tissue retreat from abandoned skeletal areas. The spicules do not therefore form a primary framework for the subsequent precipitation of the calcareous skeleton, as is the case in most other known fossil spiculate calcareous sponges. A new family is proposed on the basis of this unique combination of spicule type, calcareous microstructural type, and relationship between the spicular and calcareous skeletons.

Type genus: *Stromatoaxinella* n. g.

Enclosed genera: Type genus.

Genus: *Stromatoaxinella* n.g.

Diagnosis: as for family.

Enclosed species: Type species.

Type species: *Blastochaetetes irregularis* (MICHELIN).

Etymology: *Stromato*: calcified demosponge possessing a stromatoporoid grade of calcareous skeleton development, *axinella*: with axinellid spicule affinities.

Remarks: A new genus is required to separate this spiculate species from the other, at present aspiculate, members of the genus. In addition, the variation of calcareous skeletal features in present members of *Blastochaetetes*, suggest this genus to be a poorly defined one.

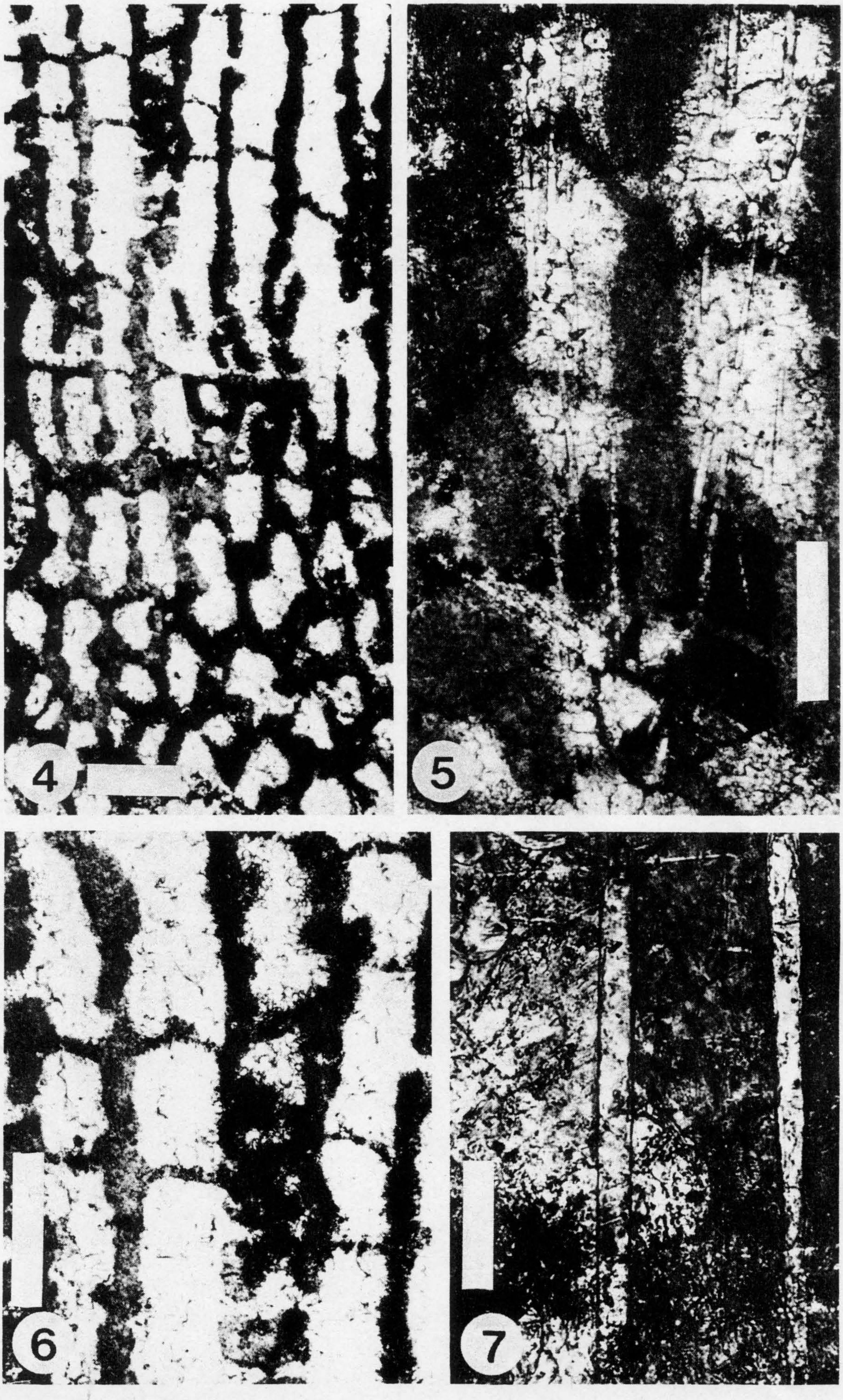

Fig. 4-7 (Legend see p. 217)

Stromatoaxinellia irregularis (MICHELIN)
(Fig. 1-7)

1848 *Chaetetes irregularis* MICHELIN, p. 306. Plate 73, figs. 2a and b.
1970 *Blastochaetetes irregularis* (MICHELIN) FISCHER, p. 36-38. Figs. 24-27; Plate C, figs. 6-9.
Emended diagnosis: Stromatoaxinellid where 2-5 adjacent columns are joined by pillar-lamellae, whose repetition vertically forms foramina when viewed in longitudinal thin-section. Abundant aligned fibrous tabulae and no astrorhizae.
Type material: Holotype: *Chaetetes irregularis* MICHELIN, 1848. p. 36, Plate 73, fig. 2a and b. Institut de Paléontologie du Museum, Paris. MICHELIN collection. L'Etang de Caronte, Martigues (Bouches-du-Rhône), France. Lower Senonian ('Terrain á *Hippurites*').
Material studied: B.M. (N.H.) 5481 and 5482 Collada de Bastus, Tremp, N-E. Spain. B.M. (N.H.) 5483 Haulin de la Roche, La Cadière (Var) France. Santonian (Upper Cretaceous).

Description: Spicule and calcareous skeleton data is given in Table 1. Laminar encrusting, nodular or dendroid gross morphology up to 30 cm in length. The encrusting forms frequently grow in a series of lobes over the substrate surface. The upper surface may be convoluted into elevations and layered into latilaminae (2-5mm) but there is no expression of these in thin-section. No mamelons or astrorhiza have been noted but often a fine meandriforme or cellular network is expressed on the weathered upper surface. The spicules are pseudomorphs of long, thin styles, preserved in multicrystalline calcite (Fig. 7) and are orientated into tracts with spicule tips pointing uppermost (Fig. 5). There is no differentiation into dermal or axial spicular skeletons. The spicules show a considerable, but continuous size range (300 x 5 μm - 900 x 20 μm, average 440 x 9 μm), and the remains of axial canals are sometimes visible (Fig. 2). The skeleton is composed of fascicular fibrous microstructure, where the calicle walls are formed of fused colums of either uninterrupted growth or an aggregate of units (Fig. 6). The columns are longitudinally joined to form calicles. In longitudinal section the columns are arranged into partially enclosed tubules perpendicular to the upper surface but are parallel to the lower surface (Fig. 4). Some specimens show a secondary calcareous skeleton of epitaxial growth of fascicular fibres which partially fill the interskeletal pore space (Fig. 3). Two types of tabulae (filling tissue) are present: prismatic fibrous tabulae which cross perpendicular to the tubule walls and a

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Fig. 4-7. Same as Fig. 1-3.

4: Longitudinal section showing transverse sections of calicles parallel to the substrate in the older areas (lower third of photograph), and then longitudinal sections of younger calicles which have subsequently bent upwards, and grown perpendicular to the substrate (upper two thirds of photograph). Note longitudinally joined columns forming foramina and aligned tabulae. Scale bar = 300 μm.

5: Longitudinal section showing low-angle plumose spicule arrangement in the calicles, trapped within secondary calcareous tabulae. Scale bar = 300 μm.

6: Detail of fascicular fibrous microstructure and fibrous tabulae. Scale bar = 400 μm.

7: Detail of style spicule morphology. Scale bar = 25 μm.

Table 1. Spicule and calcareous skeleton data of *Stromatoaxinellia irregularis* n.g.

Table 1. Spicule and calcareous skeleton data of *Stromatoaxinella irregularis*.
Enc.: Encrusting; Fasc. Fib.: Fascicular fibrous; P.I.: Partially enclosed; S.S.: Sub-parallel to growth axis of the skeleton.

Age	Locality	Calcareous Skeleton							Spicular Skeleton				
		Gross Morphology.	Microstructure.	Aquiferous System.	Present Mineralogy.	Dimensions			Type	Distribution	Present Mineralogy.	Dimensions	
						Calicles (μm)		Tabulae Thickness. (μm)				Length (μm)	Width (μm)
						Ø	Wall						
Santonian	Collada de Bastus, Spain.	Enc.	Fasc. Fib.	–	Low Mg. Calcite	220-800.	110-300.	40-80.	Styles	S.s. P.I.	Calcite	300-880.	5-20
	Haulin de la Roche, France	"	"	–	"	220-850.	110-310.	35-85.	"	"	"	330-900.	5-20

second, dark micritic or irregular form, of variable thickness and orientation (Fig. 7). The origin of this second tabular type is not known, but it may be the product of a parasitic organism.

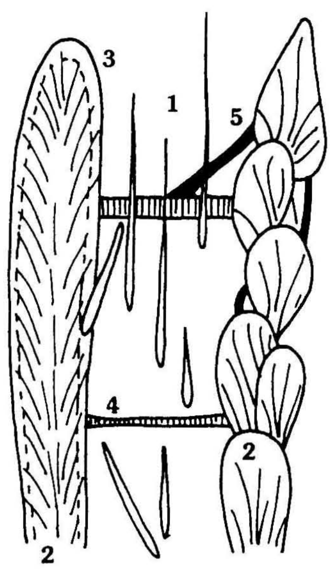
Distribution: West Europe. Cretaceous (Coniacian-Santonian). France: Foissac, La Roque-su-Ceze (Gard); la Grande-Pellet near Mornas (Vaucluse); la Cadier, le Castellet, le Beausset, Chaine de la Sainte-Baume near Plan-d'Aups, Mazaugues (Var); Martigues (Bouches-du-Rhône) and Haulin de la Roche, La Cadière, (Var), (Coniacian-Santonian).

Spain: Collada de Bastus, Tremp, (N.E.Pyrenees). (Santonian).

Remarks: The calcareous skeleton of the specimens here described conform to the description of FISCHER 1970, who emended the original description of MICHELIN 1848.

3. Mode of Growth

The spicules are found within the calicles, and are rarely incorporated into the calicle walls. When they do incorporate, it is only within the outer and not the central part of the columns (Fig. 3). The outer calicle wall is probably formed by secondary epitaxial growth of fibres which incorporated the prepositioned spicules. Spicules are also trapped by the filling tissue (Fig. 5). The inter-relationships of skeletal hard parts and the proposed developmental sequence are shown in Fig. 8.



SEQUENCE OF DEVELOPMENTAL EVENTS

1 Spicule framework held in soft tissue

2 Primary calcareous skeleton of columns or aggregate fascicular fibrous units, forming calicle walls

3 Secondary calcareous skeleton of epitaxial fibres, partially incorporating spicules

4 Filling tissue: fibrous tabulae, entrapment of spicules

5 Filling tissue: irregular tabulae

Fig. 8. Diagrammatic illustration of the developmental sequence of skeletal elements.

The calicles grow initially parallel to the substrate surface, and then curve upwards, perpendicular to it. This is presumably an adaptive feature to secure substrate area as rapidly as possible.

4. Diagenesis

The preservation of the calcareous microstructure is good, but the associated aragonitic and scleractinian coral fauna is recrystallised. The specimens lack the disruptive fabrics of aragonitic forms as outlined by SANDBERG, 1985 and others, and also lack the characteristic diagenetic features of high-Mg forms e.g. *Acanthochaetetes*. The original mineralogy of *Stromatoaxinella* irregularis was therefore probably low-Mg calcite.

Siliceous spicules are known to dissolve rapidly in Recent calcified demosponges, often during life (HARTMAN, 1979; REITNER, 1987(b)). Those spicules which are partially trapped within the calcareous tissue and/or which project into pore space are especially susceptible. Early cementation of the primary calicle spaces must have occurred prior to the dissolution of the siliceous spicules to allow the formation of moulds which produced the calcite and pyrite pseudomorphs in *Stromatoaxinella irregularis*. This interskeletal cementation of sparry calcite may therefore have occurred during life (compare REITNER, 1987(b)). To date, only epitaxial acicular crystal growth has been noted during the lifetime of Recent calcified sponges. In addition, substantial corrosion of spicules (micritisation) is noted in areas of contact with the organic calcareous skeleton as compared with the clean lines of sparry calcite enclosure (Fig. 1).

5. Palaeobiology

Apart from raising some interesting taxonomic questions, the arrangement of the spicules and the calcareous skeleton in *S.irregularis* also offers deductions as to the form of soft-tissue organisation from which the skeletal parts were produced.

The affinity indicated by the spicule type has already been discussed. The confinment of spicules to the primary pore space, indicates that the soft tissue was itself organised into almost discrete calicles. The absence of excurrent canal traces (astrorhizae) on the upper skeletal surface indicates the tissue thickness was not very thin and that the excurrent canals were not in direct contact with the area of skeletogenesis (WOOD, 1987(b)).

A similar soft tissue and spicule organisation is known from ceratoporellids and acanthochaetetids, both of which produce calicular calcareous skeletons, but excurrent canal traces are common as both these forms possess only a surfical soft-tissue veneer. Athough *Ceratoporella* possesses acanthostyles, the general arrangement and chance incorporation of the spicules into the calcareous skeleton is similar to that of *S. irregularis. Ceratoporella* produces a solid secondary epitaxial backfill which fills the original calicle pore spaces and traps the spicules, normally incorporating them into the primary calicle walls. No such trapment of spicules in *S. irregularis* has been noted. However, the calcareous skeleton does not have a well developed calicular nature and has many similarities to some genera of Mesozoic stromatoporoids. In addition, the microstructure and general dimensions of the calcareous skeleton of *S.irregularis* are closely comparable to those found in the Upper Jurassic/Lower Cretaceous stromatoporoid genus *Dehornella* (WOOD & REITNER 1986). However, these forms possess club-shaped styles in a plumose arrangement incorporated within the central area of the primary calcareous tissue, which is clearly precipitated upon this primary spicule framework; microstructural types are therefore convergent and can no longer be used as high-level diagnostic taxonomic criteria in the absense of spicule data (WOOD 1987(b); REITNER, 1987(b)). The general organisation of the calcareous skeleton is also similar to that of *Dehornella*. There is therefore a conflict between the information deduced from the spicular and that deduced from the calcareous skeletons. Although the spiculation of *S. irregularis* obviously reflects a similar soft-tissue arrangement to that found in Recent "chaetetid" demosponges, with a thin veneer of tissue lodged in pits, the surface soft-tissue is not a thin veneer as noted in Recent forms and the arrangement of the calcareous skeleton tends towards the labyrinthine, a supposed stromatoporoid characteristic, with only a weakly developed calicular skeleton. The supposed 'calicular' organisation is not well developed in *S. irregularis* and it seems the inability to place this form on present defining criteria highlights the artifical taxonomic distinction that has previously been drawn between chaetetids and stromatoporoids. Fig. 9 graphically illustrates this idea and examines the importance of characters previously thought diagnostic of the chaetetids and stromatoporoids.

Dehornella spicules determine the positioning of the calcareous skeleton and collagenous material must be present to hold the spicule tracts in place, but the microstructure of *S. irregularis* is identical to that of *Dehornella*. Clearly, the same biomineralization process can be postulated for both, with the spicules or organic skeleton in *Dehornella* providing the sites for calcification but exerting no influence over the calcification process. If taxonomic priority is given to spicule type, then calcareous skeleton microstructural type must also be taken to be convergent and to have been acquired independently in these two lineages of calcified demosponges.

6. The systematic position of "chaetetids"

Most Recent and fossil calcified sponges which bear a chaetetid grade of calcareous skeleton development appear to be members of the sub-class Tetractinomorpha within the Class Demospongiae, apart from the favositids, some of which are certainly cnidarian and some calcareous algae which have been erroneously assigned to the chaetetids. Of these spiculate forms, most appear to have affinities with the Order Axinellida, but as only very simple undifferentiated spicules (style megascleres) have been reported to date, their placing cannot be stated

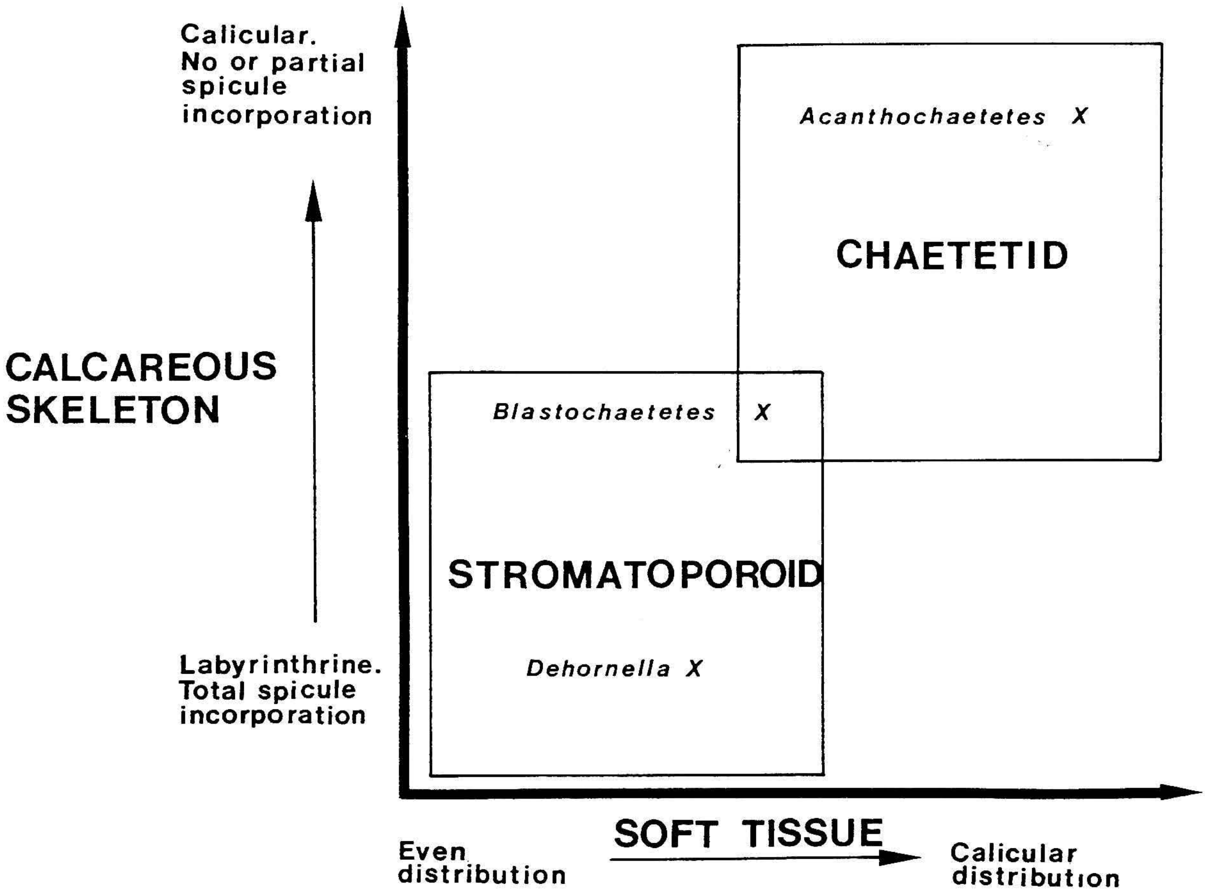


Fig. 9. Diagram illustrating the morphological continuum present in stromatoporoids and chaetetids.

with any certainty. The Recent genus *Merlia* shows affinities to the Poecilosclerida, within the Ceractinomorpha (Soest, 1984; Vacelet, 1985) and the acanthochaetetids to the Hadromerida (Vacelet, 1985; Reitner & Engeser 1985).

Acanthochaetetes is known from the Lower Cretaceous and *Ceratoporella* is known from the Upper Permian (present authors). Therefore, those lineages which can be determined are long-ranging and conservative. The morphological changes noted in these lineages are minor. In Recent *Acanthochaetetes* no spicules are incorporated into the calcareous skeleton and the microscleres show greater morphological diversity than the Cretaceous forms (Reitner & Engeser 1987). The Permian *Ceratoporella* has common tabulae producing considerable primary pore space, from which the secondary backfill initiates, in contrast to the Recent form which possesses only rare relict tabulae; primary pore space being almost entirely absent. In addition, both the acanthochaetetids and the ceratoporellids can be shown to be closely related to non-calcified forms i.e. the Spirastrellidae and the Agelasidae respectively.

The so-called Tertiary sclerosponge *Diplochaetetes mexicanus* Wilson, 1986 described from North America is suggested by the present authors to be the remains of a worm tube system; an idea that is now in complete agreement with the original author.

In conclusion, the chaetetids appear to be a diverse assemblage of calcified demosponges, which have independently developed a calicular calcareous skeleton, perhaps as a consequence of basal pinacoderm folding causing compartmentalisation of the soft-tissue into partially discrete units. The "chaetetid" grade of organisation is therefore a convergent one. Those lineages which can be determined are long-ranging and conservative, and appear to have had independent evolutionary histories since the late Palaeozoic/ early Mesozoic but with close affinities to extant non-calcified forms.

7. Conclusions

1. Partially incorporated calcite pseudomorphs of style spicules have been found in the calicles of an Upper Cretaceous chaetetid, *Stromatoaxinella irregularis* n.g., thus confirming poriferan affinity for this form.

2. *S.irregularis* shows affinities to the Order Axinellida within the Class Demospongiae, which includes the ceratoporellids.

3. The spicules do not form the primary framework for the subsequent precipitation of the calcareous skeleton, as previously noted in many fossil demosponges. A new family and genus are proposed on the basis of this, at present, unique characteristic.

4. A review of our present knowledge of spiculate chaetetids suggests that chaetetids are a polyphyletic group, where the development of a calcareous skeleton is a convergent feature representing a "grade of organisation" of the soft-tissue, reflected in the calicular form of the calcareous skeleton.

5. The microstructure and arrangement of the calcareous skeleton is very similar to that of the Mesozoic "stromatoporoid" genus *Dehornella*, which has a primary siliceous spicular skeleton of club-shaped styles, which form the framework for the fascicular fibrous calcareous skeleton. This emphazises the convergent nature of the form and microstructure of the calcareous skeleton in demosponges and reinforces the notion that present taxonomic distinctions are artificial and polyphyletic.

6. Siliceous spicules are known to dissolve during the lifetime of Recent calcified sponges. Therefore, the preservation of spicule pseudomorphs within the calicles of *Stromatoaxinella irregularis*, as opposed to trapment within the calcareous skeleton, suggests the occurrence of very early cementation of the primary pore space, perhaps during life.

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