Berliner geowiss. Abh.	E **18**	243 - 255	Berlin 1996

Observations on *Astraeospongium meniscum* (Roemer, 1848) from the Silurian of western Tennessee: Constructional morphology and palaeobiology of the Astraeospongiidae (Calcarea, Heteractinellidae)

Dorte Mehl & Joachim Reitner

Mehl, D. & Reitner, J. (1996): Observations on *Astraeospongium meniscum* (Roemer, 1848) from the Silurian of western Tennessee: Constructional morphology and palaeobiology of the Astraeospongiidae (Calcarea, Heteractinellidae).- Berliner geowiss. Abh., E 18: 243-255; Berlin.

Abstract: *Astraeospongium* is found to form secondary calcareous basal skeletons and thus may be attributed to the morphological grouping "coralline sponges". In *A. meniscum*, a bowl-shaped sponge with a massive skeleton of octactins, the ontogenetically youngest and still uncemented spicules are found at the upper, concave surface, particularly close to the edge. Towards the bottom, the spicules soon become altered through epitaxic cementation and recrystallization. From this skeletal architecture can be inferred that the soft tissues occupied only the uppermost portions of the basal skeleton. The skeletal structure is in many respects similar to that of the recent *Petrobiona massiliana*, although the ecological adaptations of the two species are fundamentally different.

Kurzfassung: *Astraeospongium* bildet ein sekundäres kalkiges Basalskelett und kann somit der morphologischen Gruppierung "koralline Spongien" zugerechnet werden. In *A. meniscum*, ein schüsselförmiger Schwamm mit einem massiven Skelett aus Octactinen, befinden sich die ontogenetisch jüngsten und noch unzementierten Spicula an der oberen, konkaven Seite, insbesondere nahe dem Rand. Zum Basis hin ändern sich bald die Spicula durch epitaktische Zementation und Rekristallisation. Aufgrund dieser Skelettarchitektur kann geschlossen werden, daß sich der Weichkörper nur in den obersten Bereichen des Skeletts befand. Die Skelettstruktur ist der der rezenten *Petrobiona massiliana* in vielerlei Hinsicht ähnlich, wenngleich sich die ökologischen Anpassungen der beiden Arten grundlegend unterscheidet.

Authors addresses: Dr. Dorte Mehl, Institut für Paläontologie, Freie Universität Berlin, Malteserstraße 74-100, D-12249 Berlin. Prof. Dr. Joachim Reitner, Institut und Museum für Geologie und Paläontologie, Universität Göttingen, Goldschmidtstr. 3, D-37077 Göttingen.

Introduction

The Heteractinellidae are an extinct group of Porifera belonging to the Calcarea, as stated by Reid (1967) and verified by Reitner (1992) on account of the mineralogy and diagenesis of their calcitic spicules. They were a long-living group of sponges, common in shallow reefal and platform environments throughout the Paleozoic. The earliest representative of the Heteractinellida in body preservation is *Jawonya* from the Middle Cambrian Daly Basin, Australia (Kruse 1987), and the latest is *Wewokella* from the Early Permian of Texas (Finks 1960).The taxon Heteractinellida currently comprises the *Eiffelia*-taxon (Rigby 1983) Octactinellidae Hinde, 1887 (= Astraeospongiidae Miller, 1889), and the Late Palaeozoic Wewokellidae King, 1943, as defined by Rigby (1983). It is uncertain at this point, whether or not *Jawonya* can be attributed to the Wewokellidae.

Some Heteractinellida, like *Eiffelia*, have skeletons composed of lose spicules only, whereas other representatives, such as *Jawonya* and *Astraeospongium,* are "coralline sponges" i.e. the spicules are integrated into a secondary basal skeleton. The Octactinellidae, to which the Astraeospongiidae belong, are characterized by octactins, which are bilaterally symmetrical spicules with a central, vertical ray and 6 tangential rays equally distributed around spaced in mutual distances of ca. 60°. The central rays may be partly atrophied, especially in spicules located at the outer surface of the sponge. *Astraeospongium meniscum* is the most common representative of the Octactinellida

Astraeospongium Roemer, 1854, the most common and best known genus within the Heteractinellidae, has been definitely documented from the Late Ordovician to Late Devonian, while isolated octactinellide spicules may indicate its presence in the Early-Middle Ordovician and Early Carboniferous as well. It is certainly characteristic of the family Astraeospongiidae. Several species have been described from the Silurium and Devonian of USA and Canada, from the Ordovician to Devonian of the Baltic region, including erratic blocks found in northern Europe, and also from the Silurian and Devonian of Middle Europe, Scotland and Russia (Rietschel 1968, Rigby 1983).

Material and methods

The fossiliferous strata, in which these sponges were collected, are of Late Silurian age from localities described by Rauff in his major work 1893-95. A large collection of Silurian sponges from western Tennessee have been kindly lent to D. Mehl by the Chicargo Field Museum. About 150 well preserved specimens of *Astraeospongium meniscum* in partly siliceous, partly calcitic preservation are included in the collection. According to Rigby (pers. comm.), *Astraeospongium* is most common in the Late Silurian Brownsport Formation in western Tennessee, and this is most probably the locality of the specimens here investigated. Due to the correspondence in the fossil content with that of Late Silurian sponge-bearing strata of New York, this series in Tennessee is often called "Niagara Group". It is a sequence of grey carbonates intercalated with thin marly fossiliferous beds. Siliceous concretions are common within these layers, and most organic remains are silicified as well (Roemer 1860). The Porifera contained are mainly desma-carrying Demospongiae ("Lithistida"), but also *Astraeospongium* and some stromatoporoid demosponges are common.

Most specimens are completely silicified and their large star-shaped spicules, well visible on the outer surface, have normally become internally obscured due to recrystallization. Measuring of spicule sizes was carried out on the most completely preserved silicified specimens. A few specimens in calcitic preservation were processed into thin sections and studied in light microscope. The distribution of spicules throughout the entire sponge was investigated, as well as the microstructure of single spicules in polarized light and also by UV-microscopy. The specimens will be returned to the Chicargo Field Museum.

Systematics and nomenclature of the Heteractinellidae and *Astraeospongium*

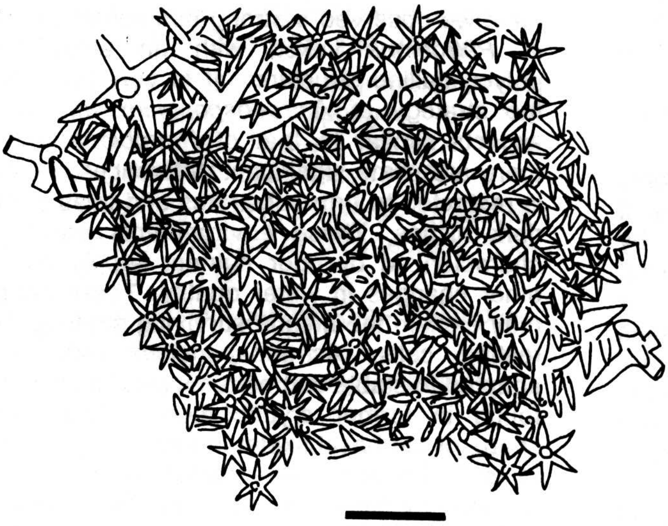
The taxonomic name "Heteractinida" was introduced by Laubenfels (1955) to include the families Chancelloriidae, Astraeospongiidae, and Asteractinellidae. This grouping is definitely non-monophylitic, since Chancelloriidae do not belong to the Calcarea, and may not be sponges at all (Bengtson & Missarzsky, 1981). We here prefer the use of the original taxonomic name Heteractinellida Hinde (1888), as recommended by Rietschel (1968).

The genus *Astraeospongium* Roemer,1854 was based on the type species *Astraeospongium meniscum*, first described as *Blumenbachium meniscum* Roemer, 1848. In his later publication, Roemer (1860) described the species as *Astraeospongia meniscus* and listed *Blumenbachium meniscus* and *Astraeospongium meniscus* as younger synonyms. But in Roemer (1860) there is no indication of any argument or intention to change original name. As correctly stated by Rietschel (1968), such a correction would be invalid according to the international rules of nomenclature, but in this case, a correction has not even been introduced, because no evidence of an emendation of intention of changing the name can be recognized in Roemer (1860). In the literature, both names have been used (e.g. Reitner 1992), but *Astraeospongia* is an invalid name! The correct name of this genus and type species is *Astraeospongium meniscum.*

Morphology and spicule organization of *Astraeospongium meniscum*

Astraeospongium meniscum is thick-walled, bowl to saucer shaped with a skeleton composed of large, star-like octactins. The size of the sponges varies between 3 and 9 cm, most of the specimens being 3.5-5 cm in diameter. Largest are the spicules found at the slightly concave surface, which in reconstructions is generally considered to be the upper side of the sponge. The sponge body is very variable from flat dish-like to conical, almost cup-shaped, but the central depression (paragaster) is normally very shallow (Pl. 1, Figs. 1-2; Pl. 2, Fig. 1). Generally at the concave surface, the large spicules with their six paratangential rays parallel to the surface and the distal rays atrophied look most clearly star-shaped. They appear to be without any special orientation, often rays of neighbouring spicules overlap or show various patterns of overlapping and interfingering (Pl. 2, Figs. 3, 5; Pl. 3, Fig. 1; Pl. 4). Comparing the concave (assumed) top with the convex (assumed) bottom, it can be seen that there are no signs of attachment to be found and that the spicules of the bottom are considerably smaller and less distinctive than the pronounced star-shaped ones of the top (Pl. 1, Figs 3-6). At the convex side of most specimens, the limits between the spicules are more or less obscured, and it is hard to distinguish or measure single spicules. Further, the largest spicules are always seen in the central area of the convex side, whereas smaller ones are found on eigther side of the sponge body, but mainly close to the edge. In some of the silicified specimens, especially the larger spicules exhibit central cavities running through the rays similar to weathered out central canals (Pl. 2, Fig. 2; Pl. 3, Fig. 2).

Most specimens in the collection are silicified through and through, and they are hollow or internally completely recrystallized with all originall structures destroyed.Thin sections were made through some of the few specimens in calcitic preservation, which still reveal relics of internal features (Pl. 2, Fig. 3-6) The thin sections show single spicules fairly well distinguishable in the top region of the sponge body, especially close to the edge.



Text-figure 1: Spicule arrangement in a well preserved heteractinellid sponge from the Eifelian Freilingen Formation (Middle Devonian, Rommersheim near Prüm/Eifel, Germany) with strong affinity to *Astraeospongium* with respect to the spicular skeleton, but the spicules appear less densely cemented. Also, the sponge body as well as the spicules are considerably smaller alltogether, and the sponge body is irregular to platy in stead of saucer shaped. These sponges might be attributed to *Magenia davidi* Finks 1995 from the Silurian (Niagara) Henryhouse Formation of Oklahoma, a genus so far unknown in Europe, Scale 1 mm.

About 1-2 mm towards the base, the spicules become obscured, successively recrystallized and fused together by cements (Pl. 2, fig. 3). In the middle of the sponge, the spicules are fused into a massiv calcareous basal skeleton without any open spaces or channels. When viewed under the light microscope, single spicules from the upper, marginal area show a central core, which behaves as a single crystal of calcite, giving unit extinction under crossed nicols.

On the five best preserved specimens, measurements of total ray sizes in spicules were carried out if possible at the inner and outer surfaces to get a significant number of measurements (according to the .preservation). Spicule ray lengths were measured from centers of spicules to ray ends. Thicknesses of rays were measured at the middle of the rays. Following mean values were found:

Mean Size (mm)	**Length**	**Thickness**	**Thickn./ Length**
Spec. no. 1			
Inner center	3.67	0.70	0.19
Inner edge	2.62	0.28	0.12
Outer edge	1.80	1.19	0.11
Spec. no. 2			
Inner center	3.00	0.52	0.18
Outer center	1.88	0.65	0.36
Spec. no. 3			
Inner center	3.16	0.69	0.22
Inner edge	1.41	0.14	0.09
Outer center	2.39	0.58	0.25
Outer edge	0.85	0.08	0.10
Spec. no. 5			
Inner center	2.44	0.46	0.19
Outer edge	1.88	0.16	0.09
Spec. no. 14			
Inner center	1.98	0.43	0.22
Outer edge	1.35	0.15	0.11

Obviously, the size of individual spicules, between different specimens as well as within the same sponge, is very variable. However, mainly the total size of spicules seems to vary throughout the sponges. The relationships between spicule thickness and length show relatively constant values, depending only on the position within the sponge body. Here three main regions can be distinguished:

Inner central region:	0.18-0.22
Outer central region:	0.25-0.35
Inner and outer side close to edge:	0.09-0.12

Thus follows that the spicules of the outer basal region are rather small and stout with ray thicknesses up to 1/3 of the length. In the inner central region, where mainly the largest spicules, > 5 mm in diameter, are found, the relationship between thickness and length is about 1/5. Interestingly, close to the edge on both inner and outer surface the smallest spicules occur, some of which measure only 0.85 mm in length and 0.07 mm in thickness of the rays. In this area, spicules are compareably thin, thickness of rays only about 1/10 of total ray length. These local differences in spiculation are obvious and can be seen by close observation of the sponge in a light microscope, or using a good hand lense (see Pl. 3).

Structure and function of the entire skeleton *of Petrobiona massiliana* and *Astraeospongium mensicum*

The spicules of *Astraeospongium* are characterized by an optically uniform core of surrounded by a thick shale that shows diffuse extinction patterns under crossed polars. This indicates that the spicules were formed in two phases by diffent processes: In the first place, the spicules were secreted as single crystals of calcite, secondly calcitic cements precipitated around the initial spicules and multiplied their thickness. Similar processes have been documented and described in detail by Reitner (1989a) on the formation of basal skeletons in the recent pharetronid sponge *Petrobiona massiliana*.

P. massiliana (Pl. 4, Figs. 1-4) is the only modern pharetronid sponge with a true basal skeleton. The basal skeleton is formed by aggregates of elongated units and flat crystal structures (cement chips). The elongated units are *in vivo* and early diagenetically altered spicules often enlarged by epitaxial crystal growth (Reitner 1989a, 1992). The flat crystal bodies (cement chips) grow in spaces made by the exopinacoderm when growing sideward and formed the rigid basal skeleton frame. In old portions of the basal skeleton, the monocystalline spicules are extremly altered into polycrystalline spherulites, prismatic, and granular structures. The stable isotope composition of the basal skeleton differs only little from that of normal marine water, and the formation is controlled mainly by kinetic effects. Vital effects, such as high amounts of respirative CO_2, may be responsible for the slightly lighter values than expected when formed only under equilibrium conditions (Reitner 1989a). The mean values are δ13C +2,1 and δ18O +1.

The living tissue of the sponges is restricted to the top area of the massive basal skeleton. The tissue is thin and charaterized by large choanocyte chambers (< 100 µm). The mesohyle is weakly developed and only few symbiontic bacteria are present. Within the choanocyte chambers, bacteria are often filtered and trapped by the microvilli. The tissue also exhibits cryptic areas which are located in canals within the basal skeleton (Vacelet 1990, Reitner 1992). Within these canals, resting cells are enriched which probably allow to recover dead portions of the basal skeleton. The unique basal skeleton has probably the function to protect the crypt cells. Comparable strategies are realized by the chaetetid demosponge *Spirastrella* (*Acanthochaetetes*) *wellsi* and the poecilosclerid demosponge *Merlia normani* (Vacelet 1990, Reitner 1989b, 1992). The basal skeleton of *P. massiliana* is a modified chaetetid-type basal skeleton and could be described as a large modified gemmula cyst comparable with so-called "aporate sphinctozoans" (*Celyphia* sp., see Reitner 1992).

The entire skeletal structure of *Petrobiona* is to some degree comparable to the extinct heteractinellid calcareous sponge *Astraeospongium*. This sponge is meniscus-shaped and formed by layers of large flat regular octactins. The central part of the skeleton is made of epitactically enlarged spicules, which close the major parts of the open space. Only the upper portions of the sponge exhibit open spaces, which indicate that in this area the living tissue was located.

Neither in other recent nor in fossil sponges, have we observed a strong neomorphism as seen in *Petrobiona* linked with an alteration into polycrystalline structures. It is very probable that the strategy of *Astraeospongium* was in some aspects similar to that of *Petrobiona*. However, there are some significant differences: *Petrobiona* is restricted to firm substrates and lives in cryptic, dark niches, These environments are normally characterized by poor nutrient supply and some other changes in water quality. These conditions may explain the unique surviving strategy through resting cells. *Astraeospongium* was probably adapted to stable soft bottoms and has never been found in former cryptic niches. The meniscus shape of the basal skeleton reflects the adaptation to soft bottoms. The formation of the basal skeleton by early diagenetically altered spicules is comparable with that of *Petrobiona*. However, no traces or remains of internal canals which might have contained resting cells were observed. It is of course possible that such narrow canals were secondarily closed through diagenetical cementation. The closely related *Astraeoconus calcarius* Rietschel, 1968 is described to have well defined pores between the spicules. Also new species from the Devonian Eifel (Germany), which is well attributable to the Astraeospongiidae, appears to be have a skeleton of lose, or hardly cemented spicules with cavities inbetween (Text-Fig. 1). So there may well be variations in the intensity of cementation, and the inclination to build basal skeletons within the Astraeospongiidae. However if there were originally no canals in the basal skeleton, we must assume that *Astraeospongium* did not store any resting cells. This hypothesis corresponds with the adaptation to open marine shallow water conditions, where, contrary to cryptic niches, food supply is normally not the main limiting factor. The survival strategy by storing resting cells is a special method of long term survival in the extreme environments of cryptic niches.

Acknowlegdements

D. Mehl thanks the Chicargo Field Museum for the generous loan of a large collection of sponges from the Silurian of Tennessee, which contains, among others, the specimens here studied. Mr. R. Leunißen (Kreuzau) is thanked for sending heteractinellid sponges from the Eifel, and Mr. U. von Hacht (Hamburg) for interesting discussions. The Deutsche Forschungsgemeinschaft (DFG) is acknowledged for financing research on the Porifera (Me 1151-2/2).

References

Bengtson, S. & Missarzhevsky, V.V. (1981): Coeloscleritophora - a major group of enigmatic Cambrian metazoans.- U.S. geol. Surv. Open-File Rep., **81-743**: 19-21

Finks, R.M. (1960): Late Paleozoic sponges from the Texas region. The siliceous sponges. Bull. Amer. Mus. Nat. Hist, **120**: 160 pp

Hinde, G. J. (1887-1888): A monograph of British fossil sponges, 1. Sponges of the Palaeozoic and Jurassic strata.- 1-92 London (1887), 93-188 London (1888)

Laubenfels, M. W. de (1955): Porifera.- *In*: Moore, R. C. (edit.): Treatise of Invertebrate Paleontology, **E**: 21-112

Rauff, H. (1893): Paleospongiologie.- Palaeontographica, **40**: 1-232.

Rauff, H. (1894): Paleospongiologie.- Palaeontographica, **41**: 233-346.

Rauff, H. (1895): Paleospongiologie.- Palaeontographica, **43**: 223-272.

Reid, R.E.H. (1967): *Hyalostelia* Zittel and the Heteractinellida.- Geol. Mag., **104**: 398-399

Reitner, J. (1989a): Struktur und Diagenese der Basalskslette bei rezenten Pharetroniden unter besonderer Berücksichtigung von *Petrobiona massiliana* Vacelet & Levi 1958 (Minchinellida, Porifera).- Berliner geowiss. Abh., (A), **106:** 343-383; Berlin

Reitner, J. (1989b): Lower and Mid-Cretaceous coralline sponge communities of the boreal and Tethyan realms in comparison with the modern ones.- In: Wiedmann, J. (ed.) Cretacous of the Western Tethys. Proc.3rd Internat. Cretaceous Symp. 851-878, Tübingen 1987; Schweizerbart (Stuttgart)

Reitner, J. (1992): „Coralline Spongien". Der Versuch einer phylogenetisch-taxonomischen Analyse.- Berliner geowiss. Abh.(E), **1**: 1-352 S

Rietschel, S. (1968): Die Octactinellida und ihnen verwandte paläozoische Kalkschwämme (Porifera, Calcarea).- Paläont. Z., **42** (1/2): 13-32

Rigby, J. K. (1983): Heteractinida.- *In*: Rigby, J. K. and Stearn, C. W. "Sponges and Spongiomorphs. Notes for a short course".- Univ. Tennessee Dep. Geol. Sci. Stud. Geol., **7**: 70-89.

Roemer, F. (1848): Über eine neue Art der Gattung *Blumenbachium* (König) und mehrere unzweifelhafte Spongien in obersilurischen Kalkschichten der Grafschaft Decatur im Staate Tennessee in Nord-Amerika.- N. Jb. Miner. Geogn. Geol. Petrefaktenkunde, **1848**: 680-686, Stuttgart.

Roemer, F. (1854): Palaeo-Lethaea, Kohlen-Periode.- *In*: Bronn, H.G. & Roemer, F. "Lethaea Geognostica", **1** (2): 1-788, Stuttgart.

Roemer, F. (1860) Die silurische Fauna des westlichen Tennessee. Eine palaeontologische Monographie.- 100 s.s., Eduard Trewendt-Verlag, Breslau.

Vacelet, J. (1990): The storage cells of calcified relict sponges.- In: Rützler K. (ed), New Perspectives in sponge Biology, Proc.3rd. internat. Conf. Sponge Biology 1985, 144-152.

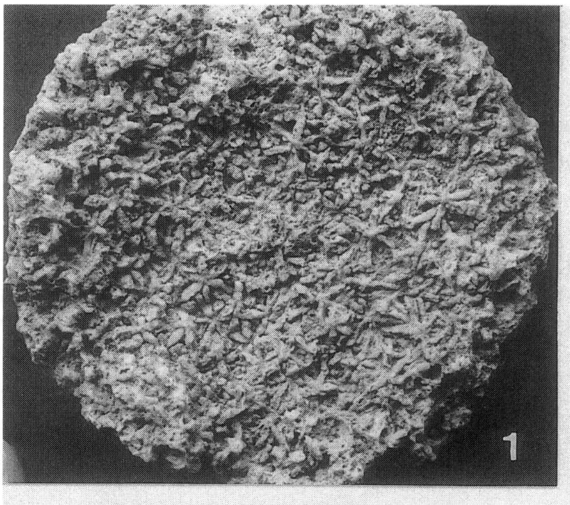
Plate 1

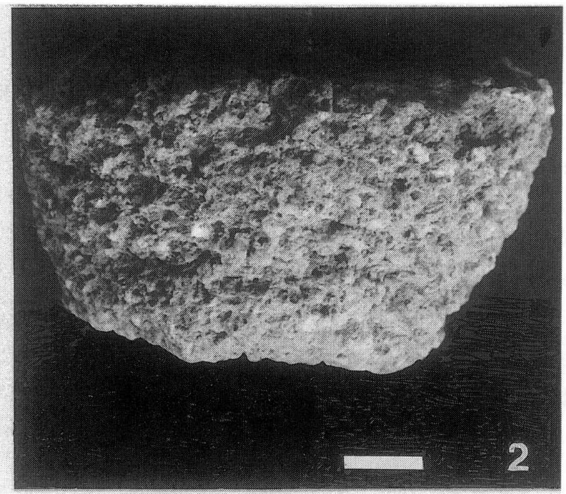
Astraeospongium meniscum

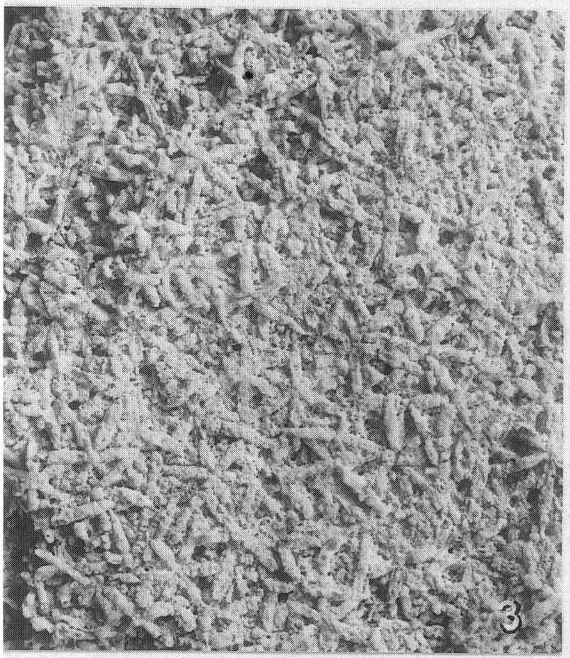
Figs. 1-2: Specimen 9, view of the upper concave surface and lateral view, scale 5 mm.

Figs. 3-4: Specimen 12, upper surface shows large star-shaped interfingering spicules and convex bottom surface where the spicules are smaller and strongly cemented, scale 5 mm.

Figs 5-6: Specimen 26, star-shaped spicules of the weathered upper surface exhibit pseudo central canals, and the heavily cemented bottom shows no more open spaces between spicules, scale 5 mm.


1


2


3


4


5

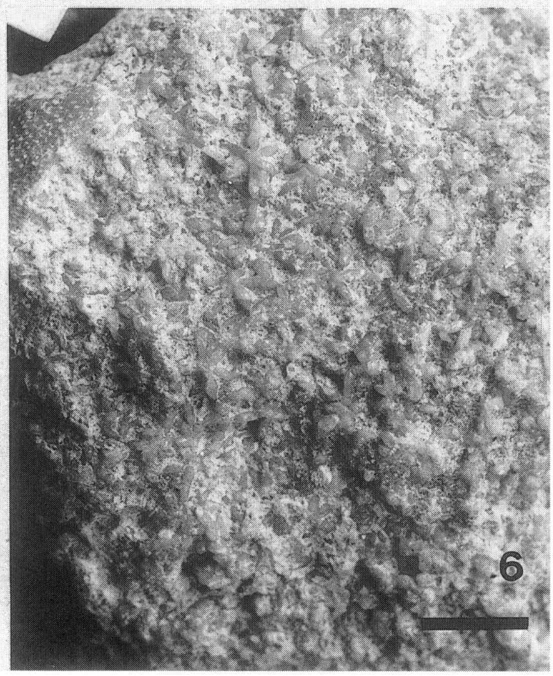

6

Plate 2

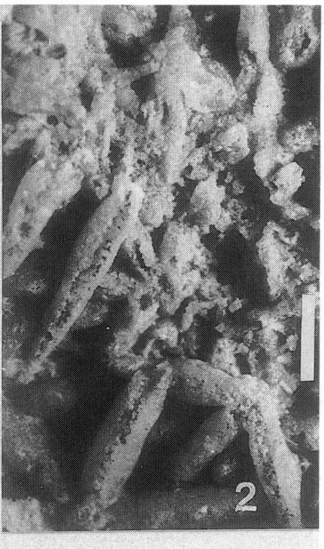
Fig. 1: *Astraeospongium meniscum* (spec. 26) seen from the concave surface with the interfingering pattern of star-shaped spicules and pseudo central chanals well visible, scale 5 mm.

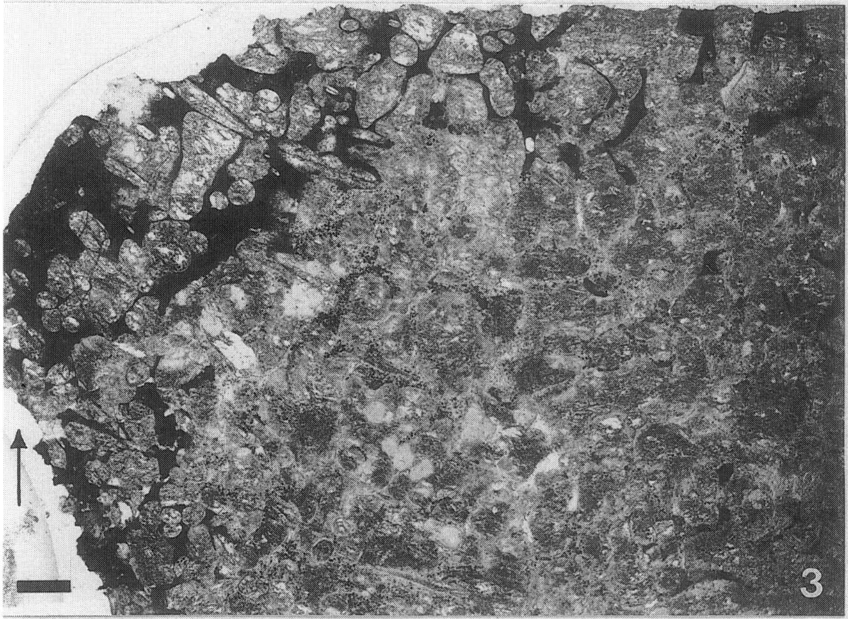
Fig. 2: Focus view of single spicules from the surface with pseudo central canals which result from weathering out of the primary cores within the calcitic spicules, scale 1 mm.

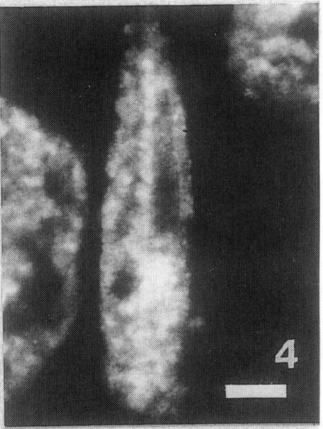
Fig. 3: Vertical thin section through *Astraeospongium meniscum* (spec. 32) in polarized light. The entire sponge is massive built up by calcitic spicules embedded in the secondary basal skeleton. In the uppermost part, interpreted as the ontogenetically youngest, the spicules are still only losely attached. Successively towards the base, they are cemented into a dense basal skeleton, scale 1 mm.

Figs. 4-6: Focus on single spicules in polarized light shows the central core as a single crystal giving unit extinction under crossed polars, all scales 100 µm.


1


2


3


4


5

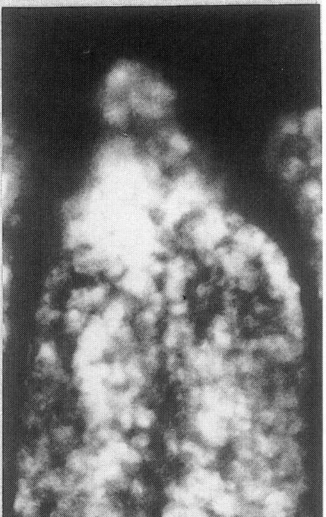

6

Plate 3

Astraeospongium meniscum, details of spicules at the upper concave surface.

Fig. 1: (spec. 14) outer margin of the concave surface with the spicules loosely attached, most spicules are relatively thin rayed, since the secondarily cemented basal skeleton has not become massive yet. This area is interpreted as the ontogenetically youngest part of the sponge, there are still large open spaces (now filled with sediment) between single spicules.

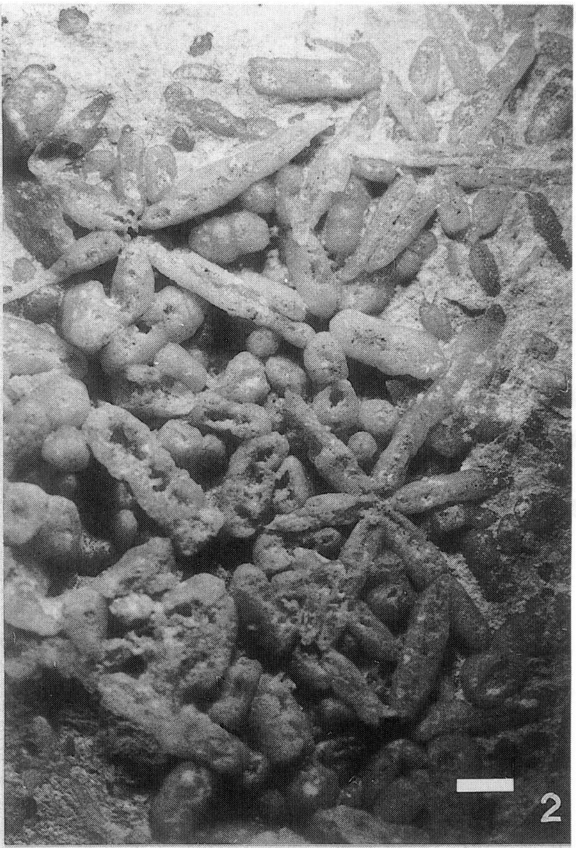
Fig. 2: Central area of concave surface (spec. 26) shows very large spicules with pseudo central canals from weathered out primary spicule cores. Secondary cementation of basal skeleton is already well developed, and there is practically no room left between single spicules.

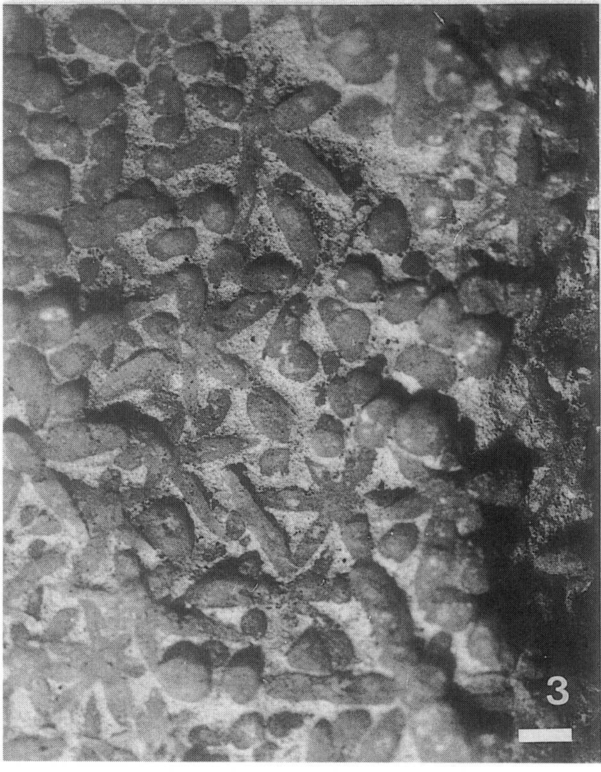
Fig. 3: Close to the margin (spec. 5) of concave surface, Most spicules are rather thick rayed, although generally smaller than those of the central area.

Fig. 4: Outer marginal area (spec. 23) of concave surface, where the recently secreted, youngest spicules are found. The spicules here are generally small and thin rayed, since the cementation of the secondary calcitic skeleton is not yet very advanced.

All scales 1 mm


1


2


3

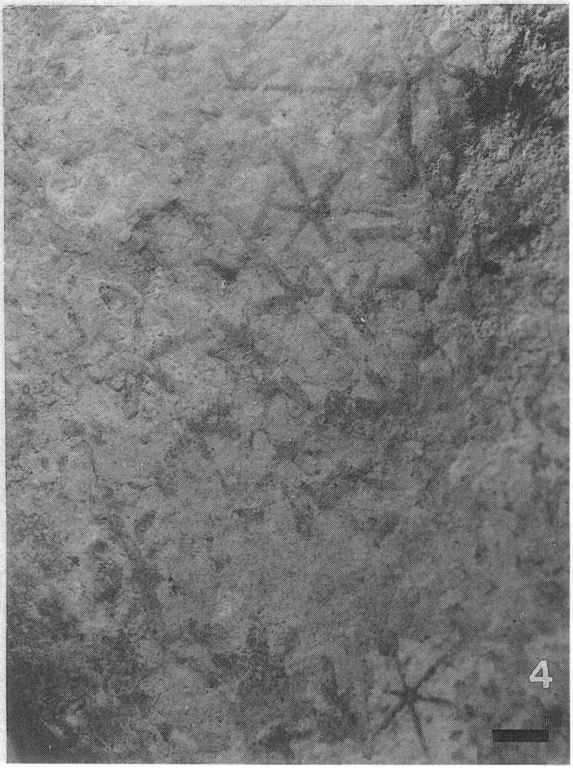

4

Plate 4

Figs. 1-4: *Petrobiona massiliana* Vacelet & Levi 1958 (Minchinellida, Calcaronea)

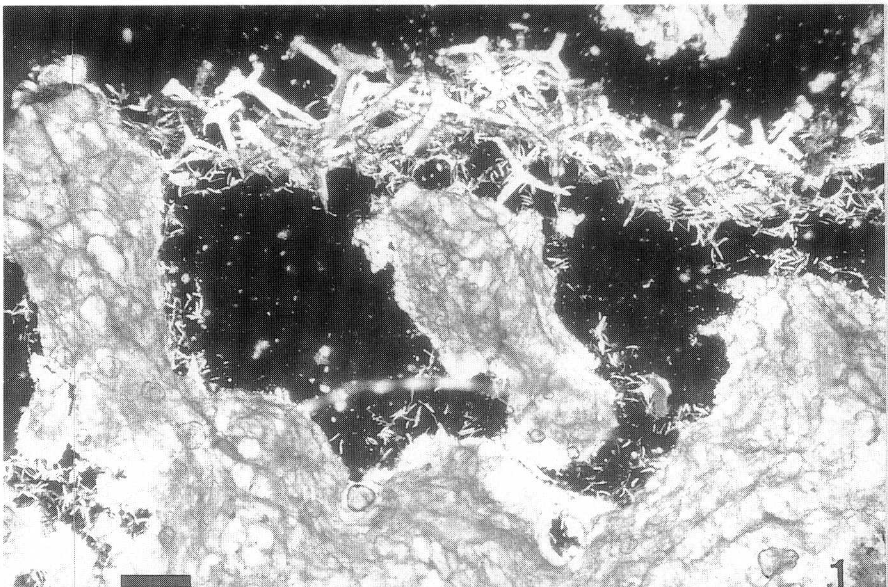
Fig. 1: Vertical section of the youngest portion of *P.massiliana*. The top area is characterized by a prominent cover of modified triaenes and calthrops calcitic spicules. The basal skeleton is formed by older spicules modified by an intense *in vivo* neomorphism and epitaxial crystal growth. The areas inbetween are filled with living tissue. The actively living tissue is restricted to the uppermost portion. Resting cells are located within canals inside the massive basal skeleton, scale 100 µm.

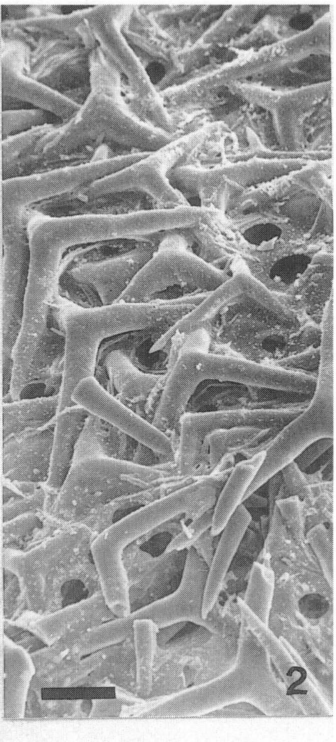
Fig. 2: Spicule arrangement of the dermal layer with ostia. Critical point dried specimen. SEM, scale 50 µm.

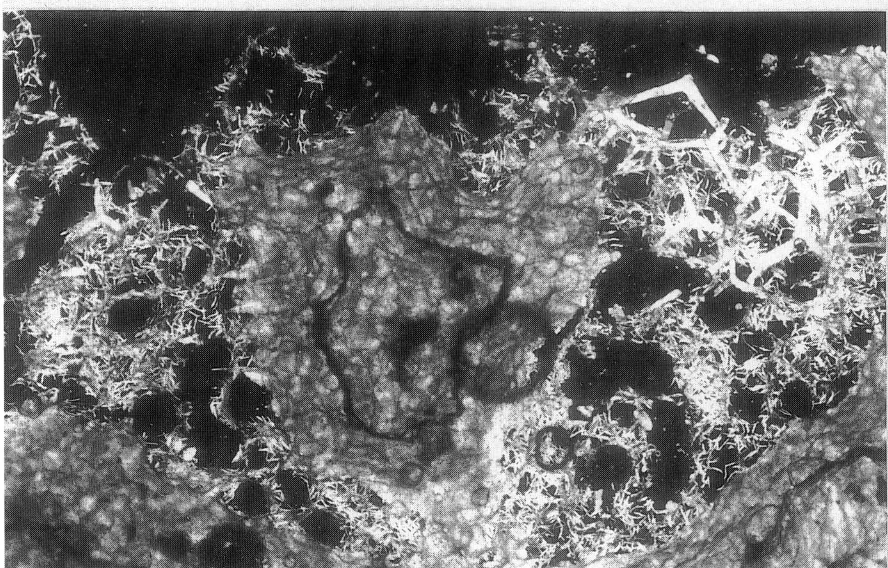
Fig. 3: Horizontal section through the dermal area, scale 100 µm.

Fig. 4: Boundary layer between the basal living tissue and the basal skeleton. Entrapped spicules and already altered spicules are present, SEM, scale 25µm.

Fig. 5: *Astreaspongium meniscum*, upper surface. The dermal area exhibits a comparable spicule pattern as that seen in *Petrobiona*. This type of heteractinid sponge exhibits a basal skeleton formed by modified epitaxially enlarged octactine spicules. Only the upper part of the sponge was occupied by living tissue as observed in *Petrobiona*. Traces of resting cells canals were not observed, scale 5 mm.


1


2


3


4


5