

## EARLY PALEOZOIC DIVERSIFICATION OF SPONGES: NEW DATA AND EVIDENCES

Joachim Reitner & Dorte Mehl

With 1 figure and 2 plates

### Abstract:

Sponges are primitive metazoan organisms which occur since the late Proterozoic. The oldest sponge remains (hexactinellids) are from a shallow marine carbonate facies of the late Sinian Shibantan Member (China). From the Tommotian (Sansha, China) protospongiid and rossellimorph hexactinellids were discovered in shallow marine silicified rocks. The middle part of this section consists of silty shales with entirely preserved hexactinellid sponges: *Sanshadiictya*, *Hyalosinica*, *Solactinella*, *Triticispongia*, *Huanospongia*. The hexactinellids typically are soft bottom dwellers, which sometimes grow on and form *in situ* spiculites (spicule mats). The sponges from the Chengjiang deposits of Atdabanian age, which show a rossellimorph spicule organization typical of the conservative hexactinellid groups, which inhabited the deep sea during most of the Phanerozoic, were also typical soft bottom dwellers. All sponge taxa (*Leptomitella*, *Leptomitus*, *Paraleptomitella* etc.) described from this locality we consider to be hexactinellids and not demosponges, as originally classified.

The sponge communities of carbonate-dominated archaeocyathid mounds are completely different from the above described sponge mounds. The sponges from the archaeocyath mounds of the Flinders Ranges (S. Australia) are characterized by *Calcarea* and demosponges ( $\leq$  modern type of pharetronid *Calcarea Gravestockia pharetroniensis*, and many tetractinellid demosponges, *Geodiida*). Questionable is the origin of four-rayed demosponge spicules found in some archaeocyaths. The oldest ceractinomorph demosponges are documented from the middle Cambrian (*Vauxia* – an aspicular sponge with keratose affinities, and isolated sigmata microscleres).

Sponge communities of the Early Cambrian were highly developed, and already then they were taxonomically strongly dependent on substrates and trophic conditions.

### Zusammenfassung:

Schwämme sind primitive Metazoen, die seit dem späten Proterozoikum vorkommen. Die ältesten Schwammfragmente (Hexactinelliden) stammen aus einer flachmarinen Karbonatfazies im späten Sinium des Shibatan Members in China. Aus dem Tommotium (Sansha, China) wurden protospongiide und rossellimorphe Hexactinelliden innerhalb flachmariner, verkieselter Gesteinsformationen entdeckt. Der mittlere Abschnitt dieses Profils besteht aus siltigem Tongestein mit körperlich erhaltenen hexactinelliden Schwämmen: *Sanshadiictya*, *Hyalosinica*, *Solactinella*, *Triticispongia*, *Huanospongia*. Die Hexactinelliden sind typische Weichbodenbewohner, die manchmal *in-situ*-Spiculite (Spicula-Matten) bilden und auf diesen wachsen. Die Schwämme der Chengjiang Lagerstätte (Atdabatium), die eine rossellimorphe Sklerenanordnung, typisch für konservative Hexactinellidengruppen des tieferen Wassers während des Phanerozoikums, zeigen, waren ebenfalls charakteristische Weichbodenbewohner. Alle Spongien-Taxa, die von dieser Lokalität beschrieben sind (*Leptomitella*, *Leptomitus*, *Paraleptomitella*, ect.), werden von uns als Hexactinellida angesehen und nicht als Demospongiae, wie sie ursprünglich klassifiziert wurden.

Die Schwamm-Gemeinschaften der karbonatreichen Archaeocyathidenmounds unterscheiden sich von den oben beschriebenen Spongienmounds signifikant. Die Schwämme aus den Archaeocyathenmounds der Flinders Ranges (Südaustralien) sind charakteristischerweise *Calcarea* und Demospongiae (pharetronide *Calcarea* von „moderner“ Organisation wie *Gravestockia pharetroniensis* und viele tetractinellide Demospongiae der *Geodiida*). Umstritten bleibt der Ursprung der vierstrahligen demospongiiden Spicula, die in einigen Archaeocyathen gefunden wurden. Die bisher ältesten ceractinomorphen Demospongien sind aus dem mittleren Kambrium nachgewiesen (*Vauxia* – ein aspiculärer Schwamm mit Affinität zu den Keratosen, und isolierte Sigmata-Mikroskleren).

Spongien-Gemeinschaften des frühen Kambriums waren hochentwickelt und in ihrer taxonomischen Zusammensetzung schon damals sehr vom Substrat und Nahrungsangebot abhängig.

## Introduction

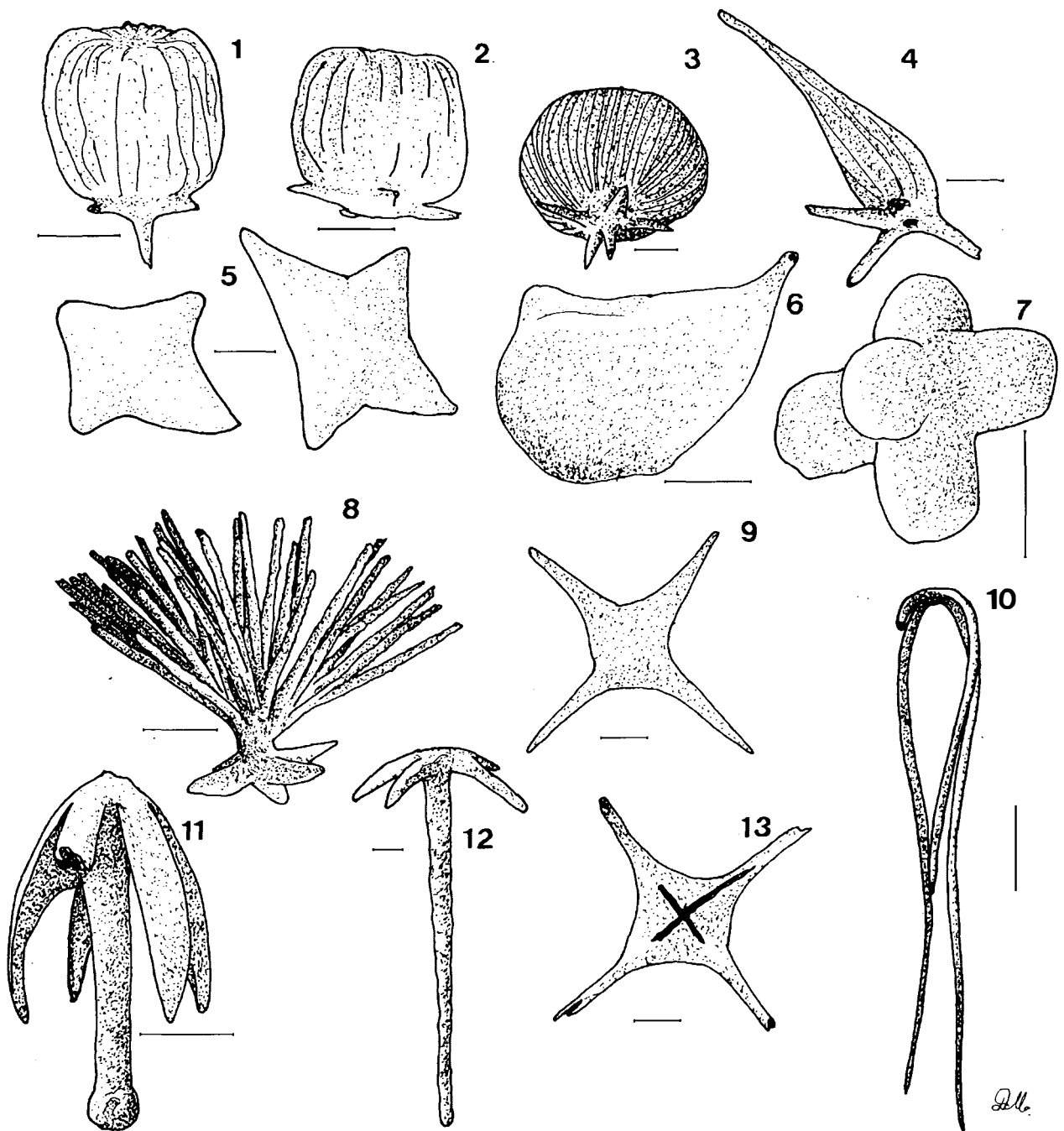
Sponges are a monophyletic metazoan group characterized by choanoflagellate cell types (choanocytes). Based on studies of MEHL & REISWIG (1991), REITNER (1992), REITNER & MEHL (in press) and MÜLLER et al. (1994) the first sponge-metazoans originated in the Proterozoic from a choanoflagellate ancestor. Probably the original sponge was an aggregate of choanoflagellates closely related to various microbial communities. It is evident that all known sponge taxa bear various amounts of often species-specific bacterial associations within their mesohyle. Very important data give the analyses of the metazoan  $\beta$ -galactose-binding lectins (S-type lectins) in sponges which was hitherto analysed only from vertebrates and the nematode *Caenorhabditis elegans* (PFEIFER et al. 1993, MÜLLER et al., 1994). The development of this sponge lectin may have occurred before 800 my (HIRABAYASHI & KASAI, 1993). This biochemical hypothesis that sponges are Proterozoic metazoans is tested by the new findings of indubitable sponge spicules from the Shibantan Member (Dengying Formation, late Sinian of the Hubei Province, China, STEINER et al., 1993). RIGBY (talk on the 4<sup>th</sup> internat. Porifera Congress, Amsterdam 1993) has presented a nearly complete specimen of a hexactinellid sponge from the Ediacara type locality of South Australia. Remarkable are also biomarker analyses made by MOLDOWAN et al. (1994) who detected C<sup>30</sup> sterane which are characteristic for demosponges in 1,8 mrd.y. old black shales!

The diversification of the demosponges and calcareous sponges is linked with the shallow calcareous facies often related to the archaeocyaths. Within archaeocyath mounds sponge spicules are very common, and beside hexactines, tetractines and modified monaxonic ones do occur. One of the authors (JR) has studied the spicules of the Atdabanian and Botomian Archaeocyath mounds of the South Australian Flinders Ranges intensively (REITNER, 1992; DEBRENNE & REITNER, in press).

## Hexactinellida

According to the data presently available, the Hexactinellida are the oldest metazoan group, which can be definitely attributed to an extant taxon. Spicule remains with clear relics of axial canals, mainly monaxons but also including typically hexactinellid triaxones, probably stauractins, were documented from thin sections of limestones from the Dengying Formation in South China (STEINER et al., 1993). These spicules are from the Shibatan Member of Late Proterozoic age (stratigraphic equivalent of the Australian Ediacara Member).

Well-preserved sponge fossils have been described earlier from the famous Burgess Shale (RIGBY, 1986) and from the House Range Mountains and Wheeler Shale, Utah (RIGBY, 1978, 1983; a.o.). A hexactinellid sponge fauna of comparably high diversity is known from Lower Cambrian (Tommotian) strata of the Sansha section, Yangtze Platform, South China. Six genera and species of sponges, most of which, or maybe all, are Hexactinellida, including the earliest representatives of several large Paleozoic groups, were found in the Sansha section as well-preserved natural spicule-assemblages. *Sanshadictya microreticulata* MEHL & REITNER (in: STEINER et al., 1993) is the earliest sponge with regular horizontal-vertical rows of diactins and stauractins. This reticulate spicule organization is the diagnostic feature of the Dictyospongiidae HALL, 1884, known from the Ordovician till the end of the Permian. However, the monophyly of Dictyospongiidae is not definitely established, and it is uncertain whether or not *Sanshadictya* really belongs to this group, since no Middle or Late Cambrian representatives are known so far. The species *Hyalosinica archaica* MEHL & REITNER was described on account of isolated root tufts of long monaxial spicules, twisted in a clockwise direction. The attachment of the main sponge body by a long, flexible stalk like a glass rope is a feature of the recent amphidiscophoran group, Hyaloneametidae GRAY, which comprise a large number of species (e.g. SCHULZE, 1877). *Hyalonema* GRAY, 1832, known from Late Cretaceous



**Fig. 1:** Drawings of hexactinellid spicules from Georgina Basin (Australia, Middle-Cambrian).

1: Follipinules of new hexactinellid (MEHL, 1995: holotype). 2–4: Various follipinules attributed to this species. 5–7: Heavily inflated stauractins, diactins, and hexactins which are associated with follipinules, and which may probably be attributed to the same taxon as those. 8: Kometiaster. 9, 13: special type of Cambrian stauractins flattened in the area of the axial cross (axial canal broken up in 13). 10: Stauractin with its paratangential rays all bent to point in one direction. 11: Tylodisc similar to those described as *Nabaviella elegans* MOSTLER & MOSLEH-YAZDI, 1976. 12: Clavule. All scales = 100 µm.

(MEHL, 1992) till today is characterized by a twisted root tuft of anchoring spicules, which may be more than 1 m long and is colonized by sym-

biotic soft corals encrusting and thus additionally stabilizing the “glass rope”. It was a strategy also of many fossil Hexactinellida, such as many Or-

dovician Protospongiidae (DAWSON & HINDE, 1888, 1889) of Little Métis, Canada, the Early Devonian *Retifungus rudens* RIETSCHEL, 1970, from the Hunsrückschiefer, Germany, or *Hyalostelia smithii* YOUNG & YOUNG, 1877, from the Carboniferous of Ayrshire, England. These are groups which may or may not belong to the Hyalonematidae. *Triticispongia diagonata* MEHL & REITNER (in: STEINER et al., 1993) most probably is a precursor of *Diagoniella* RAUFF, 1894, a Middle Cambrian representative of the Early Paleozoic Protospongiidae SALLER. *Sanshapentella dapingi* MEHL & ERDTMANN, 1994, exhibits a dermal skeleton very similar to the isolated hexactins with all their paratangential rays bent in one direction, which gave rise to *Hunanospongia delicata* QIAN & DING, 1988. Similarly triaxial spicules, stauractins, with all rays curved in one direction are found in sediments of the Georgina Basin (fig. 1:10). No post-Cambrian Paleozoic representatives of this type of hexactins with their paratangential rays all bent in one direction, but they are found in the Late Cretaceous (Coniacian) Amagerkalk from Bornholm, Denmark (MEHL, 1992). *Solactiniella plumata* MEHL & REITNER, characterized by diactin spicules radiating from a center in all directions represents a conservative bauplan of the Porifera. A radiating spicule organization is very common within the Demospongiae, e.g. the Middle Cambrian *Choia ridley* WALCOTT, 1920. Hexactinellids which exhibit a similarly conservative skeletal architecture were called "rossellimorph", which is not the name of a monophyletic group, but merely the designation of a very persistent morphological trend within the Hexactinellida (MEHL, 1995). *Quadrolaminiella* CHEN et al., 1990, from the Lower Cambrian Atdabatian of Chengjiang from Hunan, China, was originally attributed to the Demospongiae. However, *Quadrolaminiella* exhibits a spicular architecture with strong affinity to the Tommotian hexactinellid *Solactiniella*. According to our observations on unpublished material from Chengjiang, comprising also specimens which most probably belong to *Quadrolaminiella*, all Chengjiang sponges including the species described by CHEN et al. (1990), are He-

xactinellida. So far, no definite triaxons have been observed within these sponges. However, their spiculation is very similar to that of other Paleozoic "rossilimorphs", some of which do, others apparently do not possess triaxial spicules. Although the Hexactinellida are characterized by triaxons, basically hexactins, most of the hexactins of the so-called "lyssacinosaurs" are reduced to stauractins, e.g. the Protospongiidae (compare MEHL, 1991) or diactins. Thus, occasionally fossil or recent hexactinellids are found with exclusively diactin "megascleres". In recent representatives and in very well-preserved fossils, their hexactinellid nature can easily be recognized because of the typical soft tissue organization and the triaxial "microscleres" (hexasters and amphidiscs). However, in fossil sponges normally no "microscleres" are preserved, and thus the classification of sponges with exclusively monaxial "megascleres" is often problematic. Hexactinellid "microscleres" are mainly found as isolated spicules washed out of sediments (MEHL & MOSTLER, 1995). One criterion of distinction is the fact that hexactinellids often have much larger and coarser spicules than Demosponges. The largest poriferan spicules are found in the recent amphidiscophoran hexactinellid *Monorhaphis* SCHULZE, 1904, which is rooted in the sediment by a single anchoring spicule, up to 3 m long and 1 cm thick. The root-tuft spicules of *Hyalonema* may exceed 1 m in length and several mm in thickness. Of course some hexactinellids have small, only delicate "megascleres", but especially fossil sponges characterized by coarse spicules, several cm in length, in almost every case can be proven by the presence of triaxons to be hexactinellid. In the case of *Quadrolaminiella*, with coarse spiculation and strong affinity to *Solactiniella* the hexactinellid identity is very probable, even though the examination of further material would be necessary to definitely prove this hypothesis.

From the Late Atdabatian (Qiongzhusi Stage) of the Shaanxi province, southern China, a highly diverse association of isolated ? demospongian, calcarean (heteractinid), and mainly hexactinellid spicules has been described (ZHANG & PRATT, 1994). It contains oxypentasters and

-staurasters with 2 or 3 secondary rays which are often clading into Tertiary branches, before they end as simply pointed rays. These peculiar spicules, so far known from the Cambrian only, might be precursor forms of true oxyhexasters (compare MEHL & MOSTLER, 1995).

The Middle Cambrian phosphorites of the Georgina Basin in South Australia are being studied by one of the authors (DM). They contain microfossils in extraordinary, often soft-part preservation. Further, a diverse association of sponge spicules has been washed out of dissolved samples of these sediments. Their major part consists of hexactinellid spicules, but also the Demospongiae and Calcarea (Heteractinida) are represented. Hexactins are found in high variability of shapes. Generally, the hexactins are rather large and commonly measure up to several mm in total length. Average hexactins measure about 2–500  $\mu\text{m}$  and show six rays of approximately equal length, which may be a little curved or inflated to various degrees (fig. 1: 7). One or more rays can show various degrees of reduction and thus the spicules grade into pentactins, stauractins (fig. 1: 9, 13), or other triaxial derivatives. Some of the smaller triaxons, commonly stauractins, may be inflated like pillows, and the triaxial nature of such heavily inflated spicules is hardly recognizable. *Pinules* are tree-like spicules, hexactins or stauractins with their distal rays pinulate and often inflated, which, according to the functional morphology and position in recent hexactinellids, are marginal, normally dermal spicules. Classical pinules of the Georgina assemblage are rather large, average size 500 to 1000  $\mu\text{m}$ .

**Follipinules** (MEHL, 1995) are special pinules, average size only about 400  $\mu\text{m}$ , with their distally extremely inflated rays decorated with longitudinal ridges, ball-shaped, and almost “absorbing” the other reduced rays, so the axial cross sometimes is not visible (fig. 1: 1–4). A new taxon is erected on account of a hypothetical reconstruction of the Cambrian sponges carrying this special type of dermal spicules in MEHL (1995). Inflated pentactin pinules with some similarity to follipinules from the Cambrian of Texas were interpreted as dermal spicules

by RIGBY (1975). MOSTLER & MOSLEH-YAZDI (1976) documented smooth hexactins with one or more swollen rays from Late Cambrian sediments of Iran and based on these spicules the taxon *Rigbyella ruttneri*. Heavily inflated spicules like “pillow-stauractins” (fig. 1: 5–6) and follipinules are a widespread feature within Paleozoic, especially Cambrian, Hexactinellida. This type of probably dermal armouring layers indicates a special strategy of Early Paleozoic hexactinellida, which was realized beside the fragile skeletal architecture known from e.g. the Protospongiidae (compare MEHL, 1995). The armouring strategy probably reflects the adaptation to another type of environment as that of the fragile hexactinellids, either as stabilizer by higher water energies or as a defence against sponge-feeding predators.

**Kometiasters** (gr. *Kometes* = long-haired star) (Fig. 1: 8). These are triaxons 400–800  $\mu\text{m}$  in diameter with numerous short pointed secondary rays. One or two of these principalia are split up into a large number (ca. 30–50) of secondary rays, which are long (350–500  $\mu\text{m}$ ), gently curved, and slightly barbed at their distal ends. From the Late Ordovician of New South Wales a highly interesting hexactinellid spicule assemblage has been documented recently by WEBBY & TROTTER (1993). The hexasters of the new species *Kometia cruciformis* WEBBY & TROTTER, 1993, are similar to those from the Georgina Basin. If they can be regarded as true hexasterophorid spicules, these hexasters, which are called kometiasters (MEHL 1995), are the oldest ones found so far. Thus, the major hexactinellid group Hexasterophora might be traced back as far as to the Middle Cambrian.

**Tylodiscs**: Only one spiculum of this type was found within the collection (fig. 1: 11). It is 290  $\mu\text{m}$  long with one end like a clavule from which at least six spines are curved back about 2/3<sup>rd</sup> of the entire length of the spiculum. The other end is inflated and forms a small bud. This spicule, though much smaller, shows great similarity to *Nabaviella elegans* described by MOSTLER & MOSLEH-YAZDI (1976) from Late Cambrian sediments of Iran. Some clavules also occur (fig. 1: 12).

## The Early Paleozoic radiation of the Hexactinellida

The monophylum Hexactinellida comprises the sister groups Amphidiscophora and Hexasterophora, which can be traced back to the Early Paleozoic (MOSTLER, 1986; MEHL, 1991, 1995). Oxyhexasters from the Late Ordovician and amphidiscs from the Late Silurian were documented by MOSTLER (1986). From Late Cambrian sediments MOSTLER & MOSLEH-YAZDI (1976) documented large (about 0.6–3.2 mm) monaxon spicules with one clavulate and one swollen, turbulated end. These spicules, first classified as cancelloriides, were re-interpreted as hemidiscs by MOSTLER (1986). In case the spicules *Nabaviella elegans* are really hemidiscs, it would imply that they were amphidiscs with partly atrophied rays. Further, this would infer that both sister groups, Amphidiscophora and Hexasterophora, were documented since the Cambrian. However, no true amphidiscs are known older than Silurian, in spite of careful investigation of sediments from many different localities and facies types (MOSTLER, pers. comm.). For this reason, MEHL (1992) chose the name *tylodiscs* for the Early Paleozoic paraclavule-like spicules with one inflated end. The alternative hypothesis that the amphidisc are phylogenetically derived from hemidiscs (FINKS, 1970), is considered even more unestablished (MEHL, 1991). The oldest true Hemidiscs found so far were reported from the sponges, *Uralonema karpinskii* and *Microhemidiscia ortmanni* of the Late Carboniferous from Ural and Uruguay, respectively (LIBROVITCH, 1929; KLING & REIF, 1969). According to close observations of the type material to those species by one of the authors (DM), in St. Petersburg and Tübingen, respectively, these true hemidiscs are quite different from the Cambrian tylodiscs. Hemidiscs are thus most probably derived from amphidiscs by ray-reduction, and tylodiscs can be considered as convergently evolved, may be related with the paraclavules (the latter spicules are known from some Dictyospongiidae, e.g. *Griphodictya epiphanes* HALL & CLARKE, 1898). The occurrence of highly evolved hexactinellids, such as *Hyalos-*

*sinica archaica* already in the Early Cambrian (Tommotian) as well as the very rich and diverse assemblages of hexactinellid spicules found in Cambrian sediments (also by BENGTON, 1986; BENGTON et al., 1990) indicate an Early Cambrian radiation within the Hexactinellida.

## Archaeocyatha

The archaeocyaths are probably representatives of coralline sponges which secrete a secondary calcareous skeleton of high Mg-calcite (REITNER, 1990, 1992; VACELET & DEBRENNE, 1984; WOOD et al., 1992; ZHURAVLEV, 1989). Within some irregular archaeocyaths of the Flinders Ranges (South Australia) tetractine and monaxonic spicules were found (REITNER, 1992). The spicules are often intramurally enriched within endo- or exothecal buds (pl. 2, figs. 3–6). The calcifying tissue of the archaeocyaths has overgrown more or less entirely the primary spicular skeleton which is presumably related to the buds (pl. 2, figs. 3–4). The biomineralization of calcareous buds was a fast process which explains that the spicules are often more or less in their natural position. The special biomineralization of the buds may explain the scarcity of spicules within archaeocyath basal skeletons (pl. 2, figs. 5–6). The incorporation of spicules within the basal skeleton is probably a calcification artefact, a phenomenon which is also seen within the basal skeletons of Triassic coralline sponge *Cassianothalamia zardinii* REITNER (REITNER, 1987) and Lower Cretaceous *Acanthochaetetes* sp. (REITNER & ENGESER, 1987). The observed spicule types are modified tetractines (“dodecaactine”, triaenes) (pl. 2, figs. 4, 6) and monactine spicules (pl. 2, fig. 4) with demosponge affinities. The spicules exhibit the characteristic diagenesis which is known from fossil siliceous spicules: The early dissolution molds are cemented by a granular and/or equant calcite often associated with early prismatic marine cement. In contrast, fossil calcareous spicules still exhibit their mono- to paucicrystalline character.

The validity of the relationship of these spicules to the host archaeocyaths is under discussion. The spicules are doubtless tetractine spicules and therefore not related to hexactinellids.

However, the archaeocyath tissue was able to incorporate allochthonous material, as trilobate remains, isolated spicules, further organic remains, and overgrow sessile benthic organisms (e.g., *Gravestockia pharetroniensis* REITNER). To decide whether or not spicules were a constituent character of the archaeocyathid animal always depends on a paleobiological reconstruction of the studied specimen.

## Demosponges

Only few informations on the early history (Cambrian) of demosponges are available (BENGSTON et al., 1990; RIGBY, 1991; KRUSE, 1983, 1990; VAN KEMPEN, 1990) and are restricted to the Middle Cambrian. The sponges described by CHEN et al. (1990) from the Chengjiang deposits, as explained above, are most probably no demosponges but hexactinellids. Identifiable articulated demosponges from the Lower Cambrian are until yet not known.

The spicules of the demosponges in Archaeocyath mounds are exclusively restricted to the Tetractinellida. First Ceractinomorpha do occur during the Middle Cambrian (KRUSE, 1990; REITNER, 1992; REITNER & MEHL, in press). Beside tetractine spicules, typical modified dermal spicules (nail-types) (pl. 1, fig. 1–3), monaxonic spicules (large tylostyles) (pl. 1, fig. 3) and large aster microscleres (autoapomorphy of the Tetractinellida) (sterrasters, Geodiidae) (pl. 1, fig. 4) were found which proves the high level of tetractinellid evolution in the early Cambrian (GRUBER & REITNER 1991). The tetractinellid spicules of the Lower Cambrian differ in some aspects from modern ones. Most of the observed Cambrian spicules are generally larger (500  $\mu\text{m}$  to 3 cm) and thicker (ca. 50  $\mu\text{m}$ ) than the recent ones.

The second main tribe of the demosponges, the Ceractinomorpha, occurs first in the Middle

Cambrian. KRUSE (1990) has found sigmata microscleres (autapomorphy of this taxon) in the Middle Cambrian Daly and Georgina Basin. First record of a probable keratose sponge is *Vauxia* sp., e.g. known from the Lower Cambrian of Greenland (RIGBY 1987). Desma type megascleres (orchoclad lithistids with dendroclones) occurred latest in the Middle Cambrian (anthaspidellid sponge *Rankenella*, KRUSE, 1983). Based on phylogenetic reconstruction this spicule type should be an archaic one, but no desmas are known from the Lower Cambrian up to now.

## Calcarea

The Heteractinida are the most characteristic calcareous sponges in the Paleozoic (RIGBY, 1991; RIETSCHEL, 1968). They extinct at the end of the Permian. Within Lower Cambrian strata these sponges are rare and only few spicules are known (*Eiffelia* sp.) (pl. 2, fig. 2). The spicule types of the Heteractinida are extremely variable and completely different from the “modern” type Calcarea. It is astonishing that the “modern” type of calcitic spicules is common in Lower Cambrian strata. Up to now, regular calcitic triaene spicules were first known from Mesozoic strata. The modern type of spicules of Calcarea from the Lower Cambrian give absolutely new aspects of the phylogeny of this group. Remarkable is this evidence of calcareous sponges with “modern” affinities. The main problem is that typical Paleozoic Calcarea are the Heteractinida with their multi-rowed spicules or characteristic octactines. Entirely preserved sponges with regular triaene or tetractine calcitic spicules are not known from the Paleozoic. Beside isolated regular calcitic spicules one taxon is known from the archaeocyath mounds of the Flinders Ranges with cemented choanosomal spicules (“Pharetronida”), *Gravestockia pharetroniensis* REITNER, 1992 (pl. 1, fig. 5–6). This pharetronid sponge exhibits a rigid skeleton of simple

tetractine calcareous spicules and diactine-free dermal ones. These sponges grew preferably on archaeocyaths and are sometimes overgrown by the secondary skeletons of the archaeocyaths. This “intramural” spicule record is not to be confused with the isolated tetractinellid spicules with demosponge affinities, as described above.

Most of the observed calcarean spicules have affinities to the modern Calcaronea (pl. 1, fig. 1), only few with calcinean affinities are known (pl. 2, fig. 1).

## Conclusions

- The Hexactinellida are the oldest definite Porifera documented, their record goes back to the Late Proterozoic, and their radiation took place in the Early Cambrian.
- The Archaeocyatha were most probably demospouges with secondary calcareous basal skeletons. Evidence of “intramural” spicules within archaeocyaths may be interpreted as trapped dermal spicules that belong to the budding archaeocyath specimens.
- The main radiation of the Pinacophora (Demospongiae/Calcarea-taxon) took place in the Middle Cambrian.
- All main sponge taxa occur latest in the Middle Cambrian. New fundamental evolutionary trends were not realized during the following time.

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*Authors' addresses:*

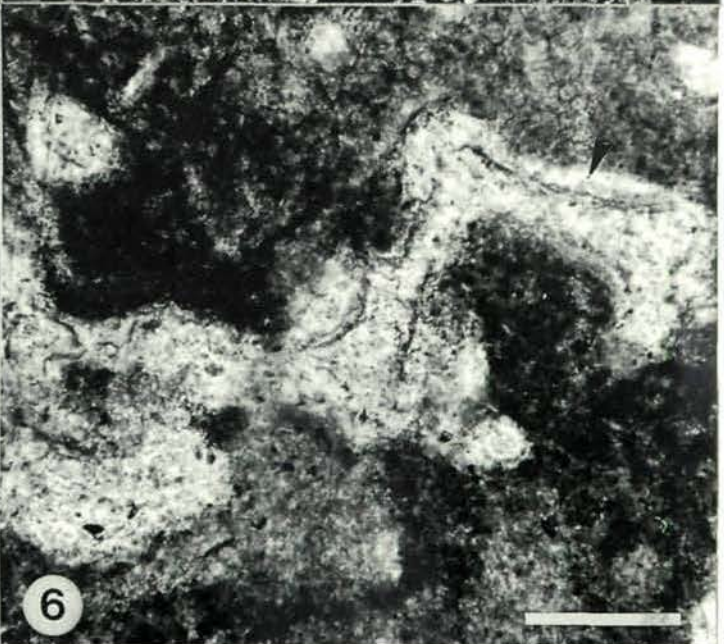
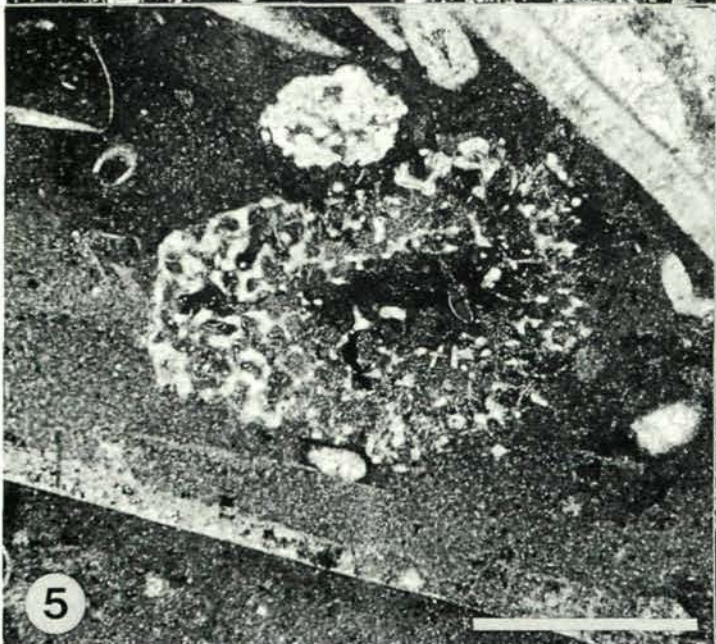
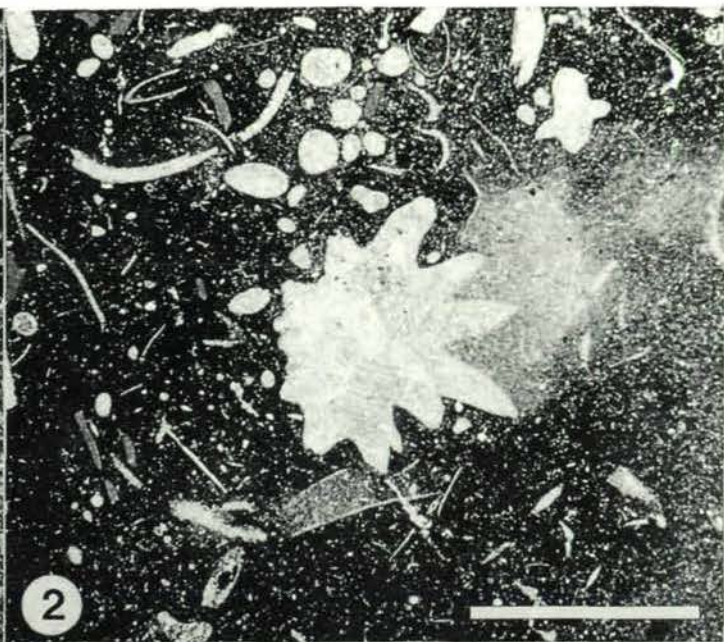
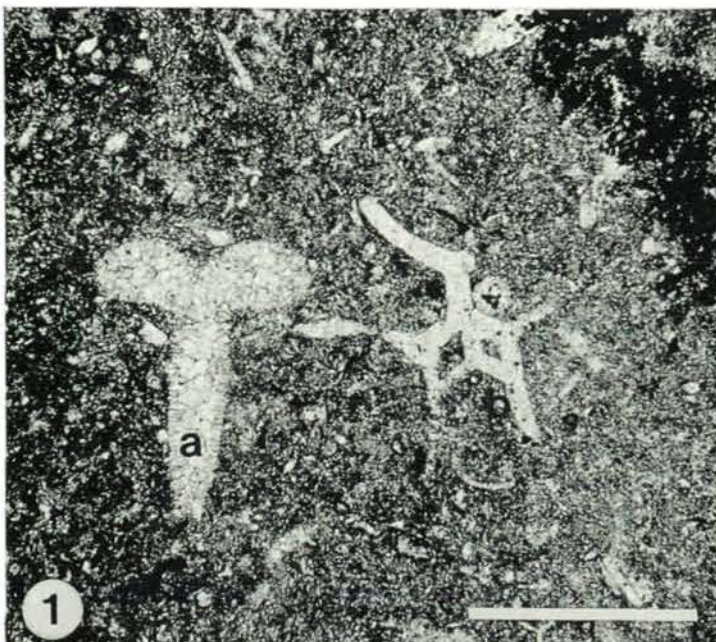
*Prof. Dr. Joachim Reitner, Institut und Museum für Geologie und Paläontologie, Universität Göttingen, Goldschmidtstr. 3, D-37077 Göttingen; Dr. Dorte Mehl, Institut für Paläontologie der Freien Universität Berlin, Malteserstr. 74-100, D-12249 Berlin.*

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**Plate 1:** Atdabanian archaeocyath mound of the Flinders Ranges, Wilkawillina Limestone

- Fig. 1: Vertical section of a triaene dermal spicule of a tetractinellid demosponge (a). The spicule exhibits the characteristic granular cements of former siliceous scleres. In contrast to the diagenetically altered siliceous spicule, the calcarean spicule (b) exhibits a monocrystalline structure. Scale 500 µm.
- Fig. 2: Horizontal section of a phylotriaene dermal spicule (Demospongiae). Scale 500 µm.
- Fig. 3: Tylostyle (a) and triaene (8b) demospongian megascleres. Scale 500 µm.
- Fig. 4: Modified kidney-shaped sterraster microscleres with demosponge affinities (Geodiidae). Scale 300 µm.
- Fig. 5: *Gravestockia pharetronensis* REITNER 1992; Calcaronea with pharetronid affinities. This sponge preferred to settle on archaeocyathids. Scale 500 µm.
- Fig. 6: Detailed magnification of the rigid spicular skeleton of *Gravestockia pharetroniensis* which shows the secondary calcite cement (arrow) of the pharetronids. Scale 150 µm.







**Plate 2:** Atdabanian archaeocyath mound of the Flinders Ranges, Wilkawillina Limestone

Fig. 1: Regular monocrystalline calcitic triactine spicule with Calcinean affinities. Scale 250  $\mu\text{m}$ .

Fig. 2: Sexiradiate spicule with heteractinid affinities (*Eiffelia* ?). Scale 300  $\mu\text{m}$ .

Fig. 3: Endothecal bud of an archaeocyathid with intramural spicules (arrows). Scale 500  $\mu\text{m}$ .

Fig. 4: Detailed magnification of the basal skeleton with intramural spicules of Fig. 3. Clearly visible are triaenes and cross sections of the long spicule axis (white dots). Scale 100  $\mu\text{m}$ .

Fig. 5: Entrapped spicules within the primary layer of the main skeleton of an archaeocyath (white dot and arrow). Scale 1 mm.

Fig. 6: Detailed magnification of a dodecaactinellid shape of spicule, a modified siliceous caltrop spicule (Fig. 5, arrow). Scale 200  $\mu\text{m}$

