

Non-Lithistid Fossil Demospongiae – Origins of their Palaeobiodiversity and Highlights in History of Preservation

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Available evidence suggests that the first demosponges occur in the Late Proterozoic, with forms characterized by bundles of long monaxonic spicules. In the Middle Devonian the first modern forms of Dendroceratida, ‘axinellids’ (mostly halichondrids), and first haplosclerids appeared. An important boundary for the demosponges is the Late Devonian extinction event, which caused a complete overhaul of demosponge communities. The Late Permian and the Triassic, especially the Late Triassic, are the main eras for coralline demosponge radiation and dominance, in which some modern taxa occur for the first time (*Ceratoporella*, *Astroscлера*, *Vaceletia*). In the Late Jurassic the freshwater environments were occupied by certain (marine) demosponges, mostly Haplosclerida. The importance of coralline demosponges as primary reef-builders decreases up to the Late Cretaceous.

Keywords: Porifera; Demospongiae; fossil taxa; coralline demosponges.

INTRODUCTION

Demospongiae are an important group of sessile benthic organisms showing a special potential for fossil preservation. Up to 60% of their biomass consists of microorganisms, predominantly bacteria, in some cases Archaea, and partly of anaerobic taxa (sulfate-reducing bacteria (SRB) and Archaea) (Reitner & Schumann-Kindel, 1997). The SRB play a central role in the formation of Porifera-rich mud mounds and certain microbialites. To a great extent the micrite in these structures was formed by various types of sponge related microorganisms, (and/or) degraded and reorganized organic material originated from sponges (Reitner *et al.*, 1995), but some portions of these build-ups are also influenced by seeps and seepage. In the Upper Devonian a fundamental push in the development of sponges took place, from the long-existing, stem-group Palaeozoic taxa to modern groups of which the monophyla are still present. The driving forces for this change are so far unknown, but most likely include medium-term fundamental oceanic changes (water chemistry, nutrient situation) producing new niches for new taxa, especially in deeper water and other protected areas. Porifera-rich build-ups and black shale environments provide a window to answer this question, which concerns reef-like structures, rich in micrites, without a metazoan framework. This increase in nutrient input could have impacted significantly on oceanic environments, possibly through a significant increase of alkalinity as well as by increased input of hydrothermal calcium and other metal cations. Porifera react very rapidly to such changes, whereas sponge-associated bacteria are even more sensitive to changes within the general nutrient environment (eutrophism of organic and inorganic nutrients), as we know from field experiments on modern Porifera. In this way, the rapid development during the Devonian of the polyphyletic coralline sponges (the so-called ‘sclerosponges’) may have been a reaction to the global oceanic change during this critical interval, and linked with increasing alkalinity and/or massive increase of the overall Ca²⁺ dissolved in ocean water (Arp *et al.*, 2001).

Little is known about the fossil record of non-lithistid demosponges, in contrast to the ‘lithistid’ demosponges, and taxa with a secondary calcareous basal skeleton, due to the poor preservation potential of the soft tissue, the collagenous spongin skeleton and,

most significantly, the discrete siliceous spicules that are often crucial to taxonomic identification. The silica of spicules is replaced by other minerals, mostly calcite or secondary silica or pyrite. Isolated spicules are common in certain deposits and some of them are of taxonomic and phylogenetic importance, but only few studies have yet been made, especially of the phylogenetically important Early Palaeozoic strata. In special fossil lagerstätten, like the Burgess shale deposits, entirely preserved sponges are present. Similarly, one of us (JR) has recently discovered entirely preserved non-lithistid demosponges in Cambrian and Middle Devonian microbialites. Due to the large numbers of sponge-related bacteria in many demosponges the sponge tissue may mineralize rapidly, controlled by sulfate reduction and/or ammonification. In this particular case certain sponge biomarkers (chemofossils) are preserved and thus allow chemotaxonomic examination.

This chapter does not provide a complete overview on fossil demosponges – which could occupy a volume in itself, and will be more comprehensively addressed in the forthcoming revision of the *Treatise of Invertebrate Paleontology* (J.K. Rigby *et al.*, editors). The purpose of this chapter is to demonstrate some highlights in the history of palaeontological preservation, which provides a general overview on the early development of the main monophyletic groups of non-lithistid demosponges. Some coralline sponge taxa are also included in this treatment, but these taxa are restricted to those with modern representatives and those that represent important phylogenetic lines.

PHYLOGENETIC ASPECTS

New data suggest that ‘sponges’ are probably not monophyletic (Borchiellini *et al.*, 2001), with Calcarea indicated to have greater similarities with Cnidaria (perhaps the Ctenophores) than to sponges with siliceous skeletons. These data include nucleic acid analysis (18s rDNA), the spectra of fatty acids and the occurrence of sponge-related bacteria. In these latter characters the Calcarea do not exhibit the very characteristic long-chained demospongiac acids, which are very good biomarkers for all demosponges and hexactinellids (Thiel *et al.*, 2001), and in most

Calcarea mesohyle bacteria are missing. This evidence certainly suggests a more distant phylogenetic position for the Calcarea, although it does not necessarily imply sponge paraphyly.

Demosponges demonstrate the following clades based on morphological characters:

- (1) Homosclerophorida.
- (2) Tetractinomophora, including the Astrophorida, Spirophorida and Hadromerida.
- (3) Ceractinomorpha, including the aspicular Dendroceratida, Dityoceratida and Verongida (so-called ‘Keratosa’) and spiculate taxa like the Poecilosclerida, Haplosclerida, Halichondrida (‘Axinellida’) and Agelasida.

THE CONCEPT OF SPONGE-BIOFILMS

The origin of the sponge bauplan is probably related to the development of special stromatolite-forming biofilms during the Early Proterozoic – at the same time as endosymbioses of eukaryotic cells evolved. This hypothesis is supported by direct evidence from 1.8 billion year old stromatolites containing sponge-specific C30 steranes and 24-isopropylcholestanes (Moldowan *et al.*, 1994a,b), which are extremely abundant in demosponges and therefore good biomarkers for these animals (Thiel, 1997). A further indirect argument for a phylogenetic relationship between the modern morphology of sponges and ancestral biofilms is the presence of mid-chain branched carboxylic acids (MBCA) in modern demosponges, which are probably related to anaerobic sulfate-reducing bacteria within the sponge mesohyl (Thiel *et al.*, 1999). This type of bacterial biomarker was previously unknown in any other marine environment but was recently discovered in heterotrophic biofilms of the modern highly alkaline Walker Lake in Nevada. We hypothesise that Early Proterozoic oceanic environments had a higher alkalinity than Recent seas (Kempe & Kazmierczak, 1994), and thus the occurrence of certain species of bacteria adapted to alkaline environments found in modern demosponges – especially in bacteria-rich demosponges like the possible ancestral astrophorid taxon *Geodia* – supports this assumption. Our working hypothesis – that sponges are highly developed biofilms with a close relationship to choanoflagellate eukaryotic cells – is based on the analysis of the sponge-related microorganisms and biofilm analyses from extreme environments. Demosponges exhibit a mesohyle community of Eubacteria, mainly gamma and alpha proteobacteria, few gram-positive bacteria and only in a few cases the Archaea (Schumann-Kindel *et al.*, 1997). In contrast to the demosponges all taxa of the Hexactinellida demonstrate a community of microorganisms dominated by Archaea (Thiel *et al.*, 2001).

PALAEONTOLOGICAL HISTORY OF DEMOSPONGES

Late Proterozoic Sponge Remains

The spicule record of sponges starts in the Late Proterozoic. In most cases these are simple monaxonic types with uncertain affinities. Some of them show hexactinellid affinities with simple hexactines and stauractines. The oldest spicules with demosponge affinities were found by the senior author in ca. 750my old Noon Day Dolomite in Nevada, and in the Neoproterozoic (ca. 555my) *Cloudina*-Reefs of southern Namibia. These latter reefs

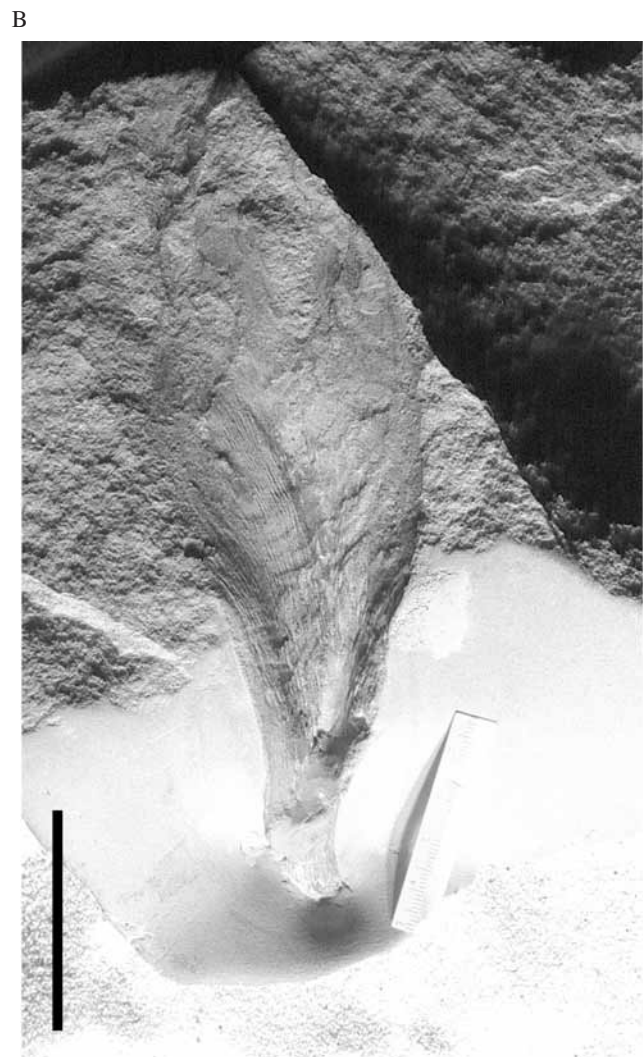
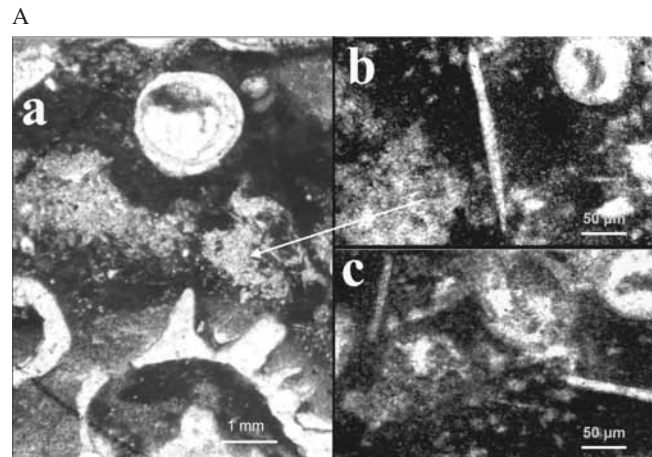


Fig. 1. A, Late Proterozoic (ca. 555my) sponge with demosponge affinities from the *Cloudina*-reefs of the Kuibis Formation (Zebra River, Southern Namibia). The small sponges with tylostyle-type spicules are located between *Cloudina*-tubes. *Cloudina* has probably pogonophoran affinities and represents the first organism in earth history with a calcified skeleton – onset of biomineralisation. B, Late Proterozoic (Ediacaran) sponge with demosponge affinities from the White Sea coast, Northern Russia. This organism is constructed of long monaxonic spicules (scale 7 cm).

demonstrate bundles of styles to tylostyles, typical demosponge spicules. *Cloudina* may be related to pogonophoran worms and the *Cloudina*-mound environment may be related to hydrothermal seepage. Small sponges are common between *Cloudina*-rich thrombolitic pillars (Fig. 1A). Sponge remains with demosponge affinities from the Ediacara-type environment of the White Sea coast (Russia) are currently under investigation (Fig. 1B). These consist of sponges with radiating monaxonic spicule bundles characteristic of early demosponges. This type is also known from the Early Cambrian (Atdabanian) Sansha formation of China (*Saetaspongia densa*) (Steiner *et al.*, 1993). The small 'sponges' and so-called 'sponge larvae' of the Wengan phosphorites are highly questionable as to their affinities to Porifera (Li *et al.*, 1998). Some of these phosphatized larvae exhibit some morphological similarities to simple demosponge parenchymella larvae (*Tethya*-type), but this interpretation of the fossil evidence is still equivocal.

Early Cambrian Non-Lithistid Demosponges

Archaeocyatha – demosponges with uncertain affinities.

The first sponges in the fossil record with a calcareous basal skeleton occur in the Early Tommotian – the Archaeocyatha (see Debrenne *et al.* chapter in this volume). Archaeocyatha are classified in two main taxa: the Regulares and the Irregulares (Debrenne & Zhuravlev, 1992, 1994; Debrenne & Reitner, 2000). The phylogenetic position of the entire Archaeocyatha is still unclear. Spicular skeletons are not known from most of these sponges, except in a few cases where tetractinellid spicules have been occasionally incorporated into rapidly calcified buds of some archaeocyaths

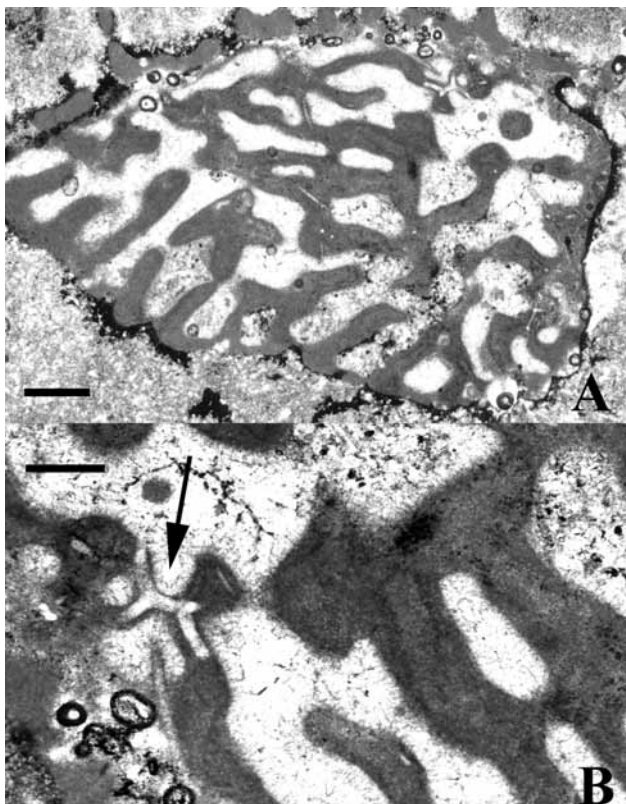


Fig. 2. A, Coscinocyath archaeocyath from the Flinders Ranges (South Australia) (scale 5 mm). B, Intramural, mostly tetractinellid spicules are common within the endothelial buds (Reitner, 1992; Reitner & Mehl, 1995) (scale 1 mm).

(Reitner, 1992, Reitner & Mehl, 1995), which suggest a close relationship to the Tetractinellida (Fig. 2). It is questionable, however, whether these spicules are part of the sponge skeleton or of allochthonous origin. The Archaeocyatha possess a Mg-calcite basal skeleton with distinctive microstructural characteristics which are also known from the modern demosponge aspicular 'sphinctozoan' taxon *Vaceletia*, which occur first in the Middle Triassic (Reitner, 1992; Reitner *et al.*, 1997). This taxon has some affinities to the ceractinomorph demosponges (see Vacelet, and Senowbari-Daryan & Garcia-Bellido chapters in this volume). In the older parts of the archaeocyath skeleton a calcification phenomenon of a lens-shaped microstructure is present, which is known from the deep skeletal structure of *Vaceletia* – called CWD (Ca-Waste-Deposits) (Reitner, 1992). This phenomenon is often observed in similarly formed fossil sphinctozoans, like the middle Triassic *Stylothalamia* Ott, 1967 and Late Triassic *Cassianothalamia* Reitner, 1987b and *Uvanella* (Reitner, 1987b). This type of a basic biomineralization process is based on Ca-detoxification and could be a model for all irregular, micritic-granular basal skeletons of 'stromatoporoid' and 'thalamid' grades of organisation. Of special interest is that all types of Archaeocyatha, the oldest known coralline sponges, exhibit this very specific type of calcification mode. The modern *Vaceletia* Pickett, 1982, thus, may be a modern 'archaeocyath' sponge (Reitner *et al.*, 1997, 2001b).

Early Cambrian Tetractinellida. The first record of tetractinellid spicules are four-rayed calthrope from the base of the Cambrian of the Flinders Ranges (South Australia) (Bengston *et al.*, 1990).

The Geodiidae are probably one of the most ancestral of demosponge groups as suggested by their fossil record. They exhibit the ancestral character of radially arranged larger spicules, a plesiomorphy of the stem group of demosponges (Reitner & Mehl, 1996). The oldest remains of geodiid spicules are known from the Early Cambrian deep water archaeocyath reefs of the Mount Scott Range near the Flinders Ranges (South Australia) (Reitner & Mehl, 1995) (Fig. 3). The observed spicules are various types of large triaene dermal spicules, phyllotriaenes, and peculiar kidney-shaped sterrasters with the characteristic impression of the spicule forming cell (Gruber & Reitner, 1991). These spicules are exclusively preserved in a polycrystalline calcite, in contrast to the associated spicules of calcareous sponges which exhibit a characteristic monocrystalline structure. However, these fossil astrophorid

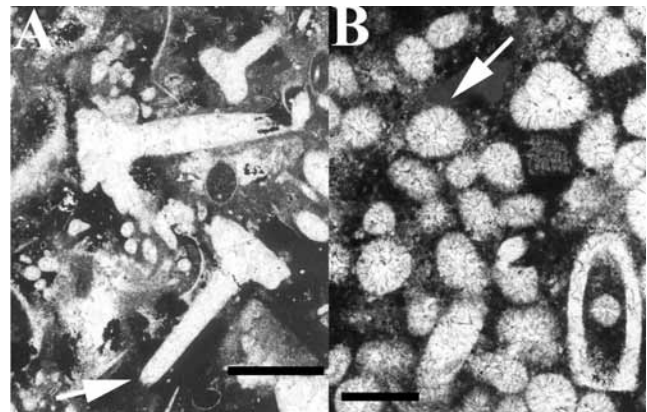


Fig. 3. Geodiid spicules remains from the archaeocyath reefs of the Mount Scott Range (Flinders Ranges, South Australia) (Reitner & Mehl, 1995). A, Megascleres resemble large triaenes (scale 200 μ m). B, The kidney-shaped structures are interpreted as remains of sterrasters (scale 100 μ m).

spicules differ in many aspects from Recent ones. Most of the observed spicules are larger ($600\ \mu\text{m} - 3\ \text{cm}$) and thicker (more than $50\ \mu\text{m}$) than those of modern species.

Early Cambrian Hadromerid-Type Spicules. In addition to the astrophorid spicule remains in the Early Cambrian deep water archaeocyath reefs of the Mount Scott Range there are also large tylostyle megascleres, which may have hadromerid affinities. Unfortunately, no hadromerid spicule arrangements were observed within these strata, and therefore their classification in the Hadromerida is equivocal (Reitner & Mehl, 1995, 1996).

Cambrian Demosponge Taxa with Uncertain Phylogenetic Affinity. From the Chinese locality Sansha a very diverse hexactinellid fauna is known with only one spherical sponge, *Saetospongia densa* Steiner *et al.*, 1993, which has alleged demosponge affinities (Steiner *et al.*, 1993). *Saetospongia densa* has bundles of small diactine spicules, an arrangement not seen previously in hexactinellids. Similar types of sponges from the lower Cambrian Sirius Passet of northern Greenland were investigated by the authors; they exhibit the same spicule arrangement. In this particular case the spicules are plumose in arrangement (Fig. 4).

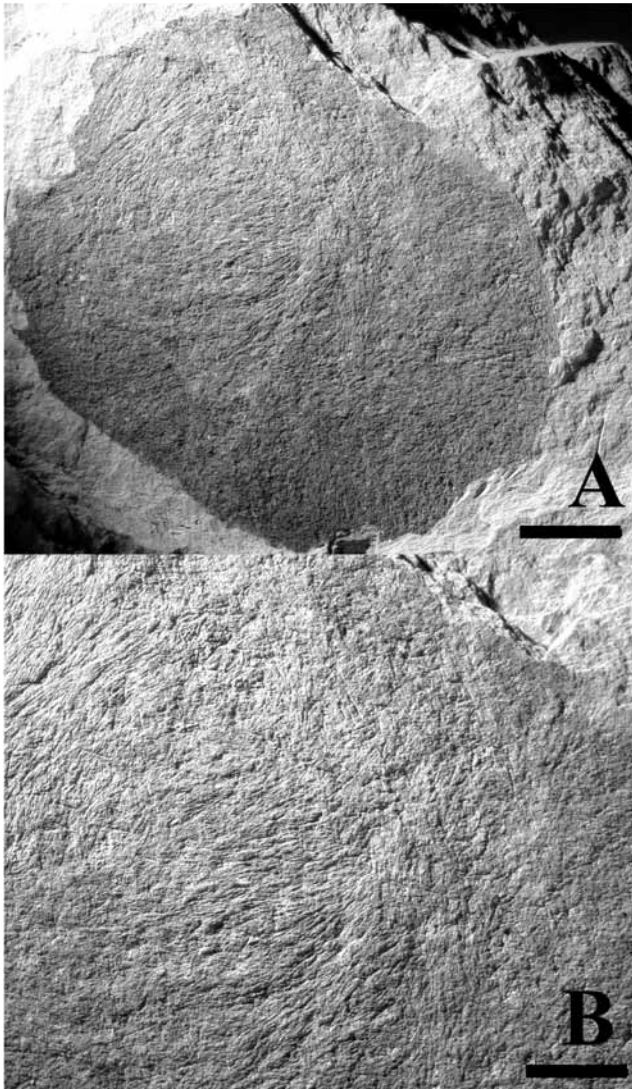


Fig. 4. *Saetospongia densa*, a demosponge from the Sansha fossil lagerstätten, China (Steiner *et al.*, 1993) (scales: A, 1 cm; B, 5 mm).

Early Cambrian Demosponges with 'Axinellid'-Type Spicule Arrangement. In the Lower Cambrian deep water archaeocyath reefs of the Mount Scott Range (Australia) entirely preserved small sponges were observed, constructed of radially arranged monaxonic spicules. These demosponges (about 1 cm in diameter and smaller) are extremely abundant within the deep water archaeocyath facies and they are part of a spiculitic matrix. This occurrence is the first record in Earth's history of an autochthonous spiculite which are otherwise common in modern temperate and polar seas (Henrich *et al.*, 1992). The preservation of these small demosponges is not so good as to allow their accurate classification. The monaxonic spicule arrangement is definitely not of the Tetractinellida model, but is reminiscent of the 'Axinellida' bauplan.

Choiidae de Laubenfels, 1955. From the Lower and Middle Cambrian strata relatively large demosponges are known which are called *Choia* Walcott, 1920 and *Choiella* Rigby & Hou, 1995. Both taxa are very similar and probably synonyms (Mehl, 1999). The Choiidae exhibit radially arranged, several cm long large styles, diactines and small styles (1 cm and less). They are typical ancestral demosponges with radially arranged simple spicules, with postulated affinities to the Halichondriidae. These sponges exhibit some similarities to modern hymeniacionids (family Halichondriidae). In any case, the Choiidae are members of the stem group of the Demospongiae (Fig. 5).

Halichondritidae Rigby, 1986c. These sponges exhibit a strong 'axinellid' spicule arrangement and probably developed from the Choiidae. They have lost the entirely radially arranged spicule architecture and the sponges are more cup-shaped. Oxeas and styles are arranged axially, and in this regard differ from the Choiidae. Both types occur in the same environments and are known from the lower Cambrian Sirius Passet from Greenland and from the middle Cambrian Burgess Pass (Canada). Two taxa are known, *Halichondrites* Dawson, 1889 and *Pirania* Walcott, 1920. The latter is characterized by very long styles (*Pirania*-style) which protrude from radially arranged small oxea. The Halichondritidae are very close to the Ordovician taxon

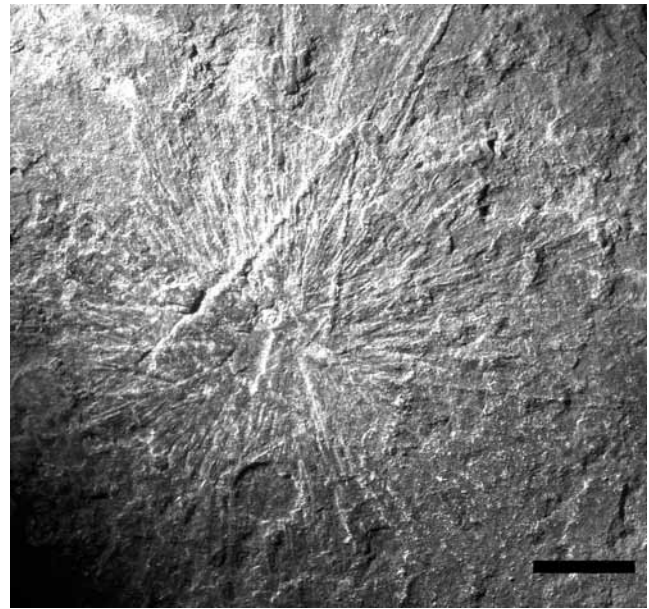


Fig. 5. *Choia* sp. from the Lower Cambrian Sirius Passet from Northern Greenland (coll. J. Peel). These spherical demosponges are good representatives of the demosponge stem line (scale 1 cm).

Saccospongia Bassler, 1889 which also contains a certain type of desma (heloclones) (Mehl, 1999). The occurrence of this latter body plan can be seen in the enigmatic *Esperiopsis desmophora* Hooper & Lévi, 1989 (Recent deep-water Poecilosclerida from the continental slope off the Great Barrier Reef). Thus, the 'axinellid' type of architecture is highly convergent within Demospongiae, with some of the Recent taxa assigned to Halichondrida (Van Soest, 1991; Reitner, 1992) (Fig. 6), Poecilosclerida (e.g., Raspailiidae) and Hadromerida (e.g., Hemiasterellidae) (see relevant chapters in this volume).

Choiidae and Halichondritidae are a well-defined monophyletic group and may be the stem group of the Saccospongiidae. In any case, these demosponges exhibit many typical 'axinellid' characters and they may be ancestors of the modern 'Axinellida'/Halichondrida, which were first documented from the Middle Devonian of the Boulonnais (France).

Early 'Keratose' Demosponges. Ceractinomorph sponges without spicules were summarized in the taxon 'Keratosa' Grant, 1861. 'Keratosa' s.s. excludes the Halisarcidae Vosmaer 1887, where the latter does not have spongin fibres common to all others. In the modern scheme the term 'Keratosa' has virtually disappeared as a clade, although they may represent a grade of construction, with Recent species assigned to the Dendroceratida, Dictyoceratida or Verongida. The fossil record of these sponges is poor due to the fact that they have no spicules. There are some exceptions, however, when the entire tissue has been preserved due to rapid calcification via sulfate reduction (see section on Devonian 'keratose' sponges). Some of these taxa agglutinate detritic material to support their spongin fibre skeleton. The amount of agglutinated material may reach more than 50% of the entire sponge volume. There are some Late Proterozoic small sand-structures which resemble possible fossil remains of 'sand-sponges' (Fig. 7).

The best known taxa are the middle Cambrian Vauxiidae Walcott, 1920 from the Burgess Shale. These sponges exhibit a basket-shape fibrous, aspiculate skeleton, probably made by strong spongin fibres. Based on this feature Rigby (1986c) discussed a strong affinity to modern 'Keratosa'. It is difficult to decide, based on this material, whether or not this assumption is correct. In any case, the Vauxiidae are representatives of the stem-group of the 'keratose' demosponges (which excludes the Halisarcidae) (Fig. 8).

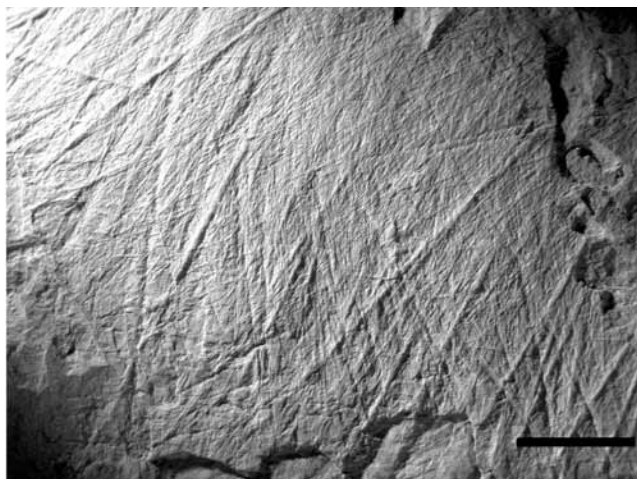


Fig. 6. *Halichondrites* sp. from the Cheniang fossil lagerstätten (China). This demosponge is probably evolved form *Choia* and exhibits some similarities to axinellid demosponges (scale 1 cm).

Highlights of the Cambrian Demosponges. In the Cambrian the diversification of the main demosponge clades was realised. It is possible to distinguish between tetractinellid taxa (Geodiidae), 'axinellid'/halichondrid taxa (Choiidae, *Pirania*), and ceractinomorph 'keratose' types (Vauxiidae). In the Middle Cambrian a new character evolved within both the main clades of the demosponges: desma spicules, which form rigid choanosomal skeletons and increased their preservation potential. Desma-bearing



Fig. 7. 'Sand-sponges' from the late Proterozoic Ediacaran of the Ukraine. These structures may be remains of so-called 'Psammosponges'. Many 'keratose' demosponges agglutinate sandgrains to support their collagenous skeletons (scale 1 cm).

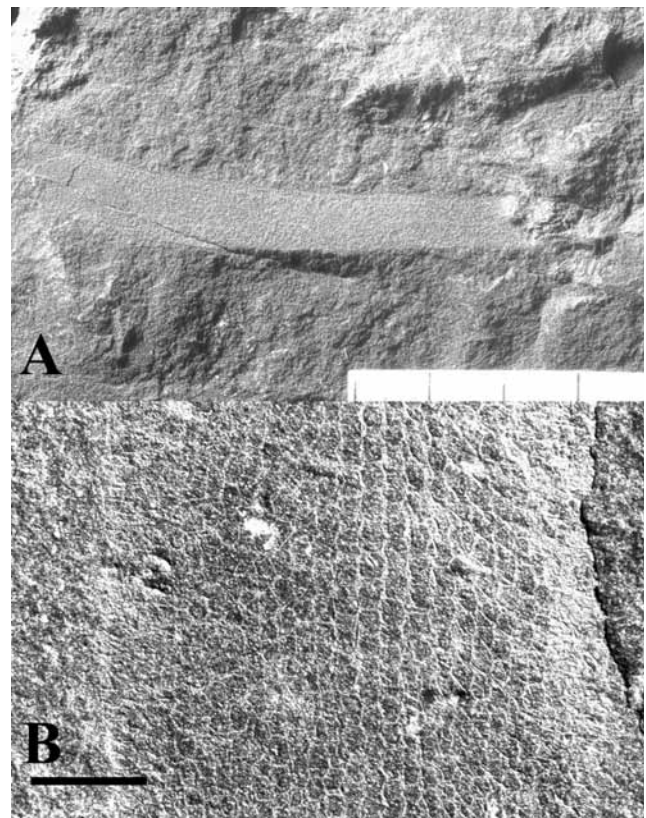


Fig. 8. *Vauxia gracilenta* from the middle Cambrian Burgess Shale. These sponges are 'keratose' demosponges with affinities to the Verongida (scales: A, 4 cm; B, 1 mm).

demosponges (see chapters on 'Lithistida') have dominated the fossil record of demosponges since this time. Important is the fact that sigma-type microscleres were recorded (Mehl, 1999) in a close relationship with the first middle Cambrian 'lithistid' demosponges (*Rankenella mors* Gatehouse, 1968) from the Ranken Limestone (Northern Territory, Australia) and the Georgina Basin, which illustrate the Cambrian diversification of the demosponges into the main clades Tetractinomorpha and Ceractinomorpha. Within the Middle Cambrian Australian Georgina Basin and Daly Basin characteristic tetractinomorph spicules are commonly documented as various types of triaenes (orthotriane, trichotriane) and aster-microscleres, such as oxyasters (Van Kempen, 1978, 1990a; Kruse, 1990; Mehl, 1999). However, most of these spicules are related to the 'lithistid' demosponges (e.g., Anthaspidellidae-Orchocladina). It is difficult to decide whether these free tetractinellid and ceractinomorph spicules are related to 'lithistids' or to desma-free demosponges. In any case, the main steps of demosponge phylogeny had been achieved in the Cambrian.

Middle Devonian Non-Lithistid Demosponges from the Boulonnais (Northern France): the Beginning of Modern-Type Demosponge Communities

The Middle Devonian microbialites from Boulonnais, Northern France (Mistiaen & Poncet, 1983) show a characteristic ecological sequence of rugose corals, cyanobacteria/algae (*Rothpletzella*), microbialite crusts, and Porifera (Demospongiae) documenting a facies poor in light (Reitner *et al.*, 2001a). Within cryptic space halichondrid/'axinellid' demosponges are common (Fig. 9), as well as relicts of dendroceratid demosponges (Fig. 10), which show an excellent preservation of the spicule skeletal frame due to automicrite formation. This result is supported by chemofossils, like sesquiterpenes, which are characteristic of (and potentially good biomarkers for) Recent halichondriids/'axinellids'. Biomarker investigations were performed on the decalcified residue of samples from the Porifera-*Rothpletzella* sequence from the small microbialite reefs. Compared to other Palaeozoic mud mounds, the material from

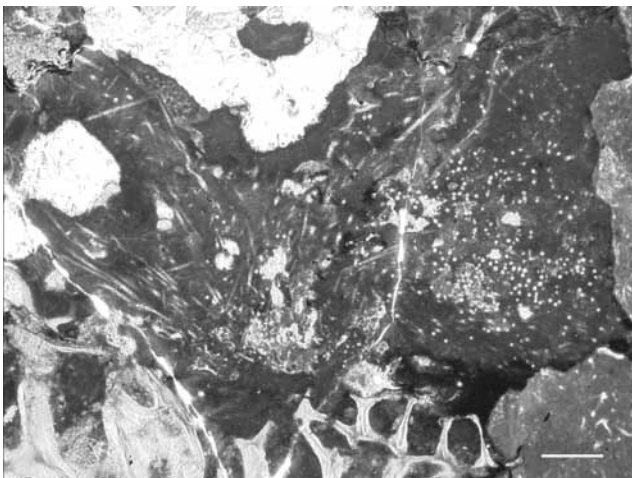


Fig. 9. Within the small microbialite reefs in the surroundings of Ferque (Boulonnais, Northern France) *Axinella*-type cryptic sponges are extremely abundant. Biomarker analysis of these rock have shown sesquiterpene biomarkers, characteristic for the Halichondrida/'Axinellida' (Reitner *et al.*, 2001a) (scale 200 μ m).

the Boulonnais displays a much better preservation of autochthonous compounds among the organic sediment fraction. This may be due to the tight sealing of the small carbonate deposits by fine-grained hemipelagic sediments and a low degree of alteration during carbonate diagenesis. A remarkable feature of the Boulonnais samples is the occurrence of a pronounced series of bicyclic sesquiterpenoid hydrocarbons, some of which displayed mass spectrometrical characteristics consistent with a drimane-type carbon skeleton (Reitner *et al.*, 2001a). The occurrence of fossil sesquiterpenoids has been demonstrated in several studies, but the significance of these compounds has not yet been fully unravelled (Peters & Moldowan, 1993). Some structures have been related to inputs from terrestrial sources, whereas others, including the drimanes, have been suggested as microbial biomarkers. Notably, sesquiterpenoid natural products occur as main compounds in numerous recent demosponges, and are particularly prominent among the Halichondrida, and notably in the Axinellidae (e.g., Bergquist, 1979). An interpretation of the sesquiterpenoids found as diagenetic derivatives of sponge natural products would be in full accordance with the palaeontological evidence found in these deposits.

This result is spectacular, since it gives evidence of the direct connection with the 'axinellid' plumose spicule bundles! In terms of Earth's history this shows the earliest appearance of this modern sponge taxon.

The palaeobiodiversity of non-lithistid demosponges within these cryptic environments looks very modern, and was never observed in comparable Early Palaeozoic environments. It is the first time in Earth's history that cryptic demosponges play a significant role in reef mound environments. The community is dominated by halichondrid demosponges, followed by 'keratose'/dendroceratid sponges, and few haplosclerid demosponges. Hexactinellids have never been observed within this facies. The history of modern demosponges started within these cryptic facies.

Late Devonian to Early Carboniferous

The interval between the middle-Late Devonian to the Early Carboniferous is one of the most critical times for the development

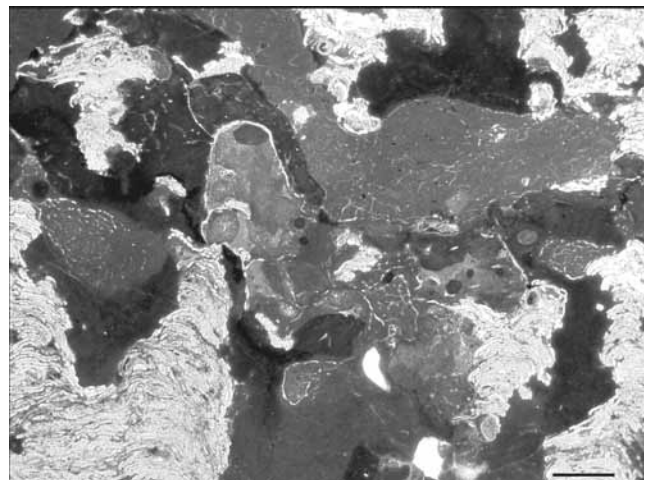


Fig. 10. Within the small microbialite reefs in the surroundings of Ferque (Boulonnais, Northern France) dendroceratid ceractinomorph sponges are common. Diagenetically calcified spongin fibres are preserved (Reitner *et al.*, 2001a) (scale 200 μ m).

of modern sponge taxa, especially the demosponge communities, due to fundamental changes in the oceanic systems and reorganisation and recovery of shallow shelf systems and reef environments. This critical interval is called the 'Late Devonian' crisis and involved one of the biggest worldwide extinction events during Phanerozoic Earth history (summarized in Walliser, 1996). In particular, a fundamental change in the 'lithistid' communities occurred in the Late Devonian (Famennian). The first tetractinellid 'lithistid' demosponges were found in small bacterial reef mounds located directly on submarine hydrothermal spring/vent systems. These sponges are part of a true vent-fauna with auloporid corals, certain small rugose corals, tube worms and stalked crinoids (Reitner *et al.*, 2001a). The reef-type Famennian strata are extremely rich in demosponges, although most of them are currently of unknown taxonomic position. Within the Lower Carboniferous most of the modern clades of demosponges existed, and in the Permian all modern major taxa were present. Remarkable is that the first record of the Homosclerophora, a simply-organized group of demosponges, occurred late in the Early Carboniferous with plakinid spicules and probably evolved from astrophorid tetractinellid ancestors. The first remains of poecilosclerid spicules are known from Permian strata. However, poe-

ilosclerid spicules from middle Triassic sediments are especially common (Mostler, 1976, 1986, 1990; Reitner, 1992; Wiedenmayer, 1994). The reorganisation of the modern taxon Demospongiae had been completed by the Early Triassic.

Only one fundamental new development happened, probably in the Early Jurassic – the invasion of some marine taxa, predominantly Haplosclerida, in freshwater environments. The oldest known remains of freshwater sponges are from the continental Late Jurassic of Portland (southern England). These are spiculites of spiny spongillid oxeas, *Spongilla purbeckensis* (Hinde, 1883). The fossil record of Mesozoic freshwater sponges is extremely poor and only one further locality from the Lower Cretaceous is known, the Chubut-Formation in Argentina, however, with excellent well-preserved modern-type freshwater sponges (Volkmer Ribeiro & Reitner, 1991b) (Fig. 11).

CORALLINE DEMOSPONGES WITH PRESERVED SPICULE SKELETONS

Characterization of Coralline Demosponges

Coralline sponges or 'sclerosponges' are a polyphyletic group with affinities to both Demospongiae and Calcarea (e.g., Hartman & Goreau, 1969, 1972; Vacelet, 1985; Wood, 1987; Reitner, 1987c, 1989, 1992; Reitner & Mehl, 1996), which construct a secondary basal skeleton of Mg calcite or aragonite (Reitner, 1992). Five basic types of basal skeletons can be distinguished: (1) simple thin crusts; (2) differentiation of tubes/calicles ('*Ceratoporella*-type'); (3) tubes/calicles separated by tabulae ('chaetetid-type'); (4) more-or-less irregular network of the primary organic skeleton with horizontal (laminae) and vertical elements (pillars) ('stromatoporoid basal skeleton'); and (5) chambered basal skeleton ('sphinctozoid' or 'thalamid basal skeletons'). The first three types of basal skeletons are related to sponges with thin organic tissue, the latter two are characterized by a thicker living tissue (Reitner, 1992).

The first Recent specimens of coralline demosponges were collected at the turn of the last century (Döderlein, 1897; Kirkpatrick, 1908d, 1910a,c, 1911, 1912a,b; Lister, 1900; Hickson, 1911), but from that time until relatively recently the knowledge of these organisms had been nearly forgotten – no doubt due to the diminished interest in the phylum during the mid-1900s (see general Introductory chapter and chapter on Phylum Porifera). During that time palaeontological investigations were also made on fossil sponges with basal coralline skeletons, as stromatoporoids and 'Pharetronida', and Calcarea with a rigid dense network of calcitic spicules (Rauff, 1913; Steinmann, 1882; Welter, 1910). However, from those 'halcyon days of sponge discovery' until relatively recently most of the fossil coralline sponges, especially the stromatoporoids, were misinterpreted as being hydrozoans, corals, foraminifera, cyanobacteria etc. (e.g., Lecompte, 1951; Flügel & Flügel-Kahler, 1968; Kazmierczak, 1981).

During the second half of the 1900s up to the present two groups of biologists have independently recovered Recent coralline sponges, including many new species, living especially in cryptic marine reef environments (Vacelet & Levi, 1958; Vacelet, 1964; Hartman & Goreau, 1969, 1972, 1975; Hartman 1979), and other new species with different types of basal coralline skeletons were found in the late 1900s (Reitner & Wörheide, 1996; Willenz & Pomponi, 1996). All these discoveries were important for the interpretation of many fossil sponge remains, which are now classified as 'coralline demosponges' or 'pharetronids'. Hartman & Goreau

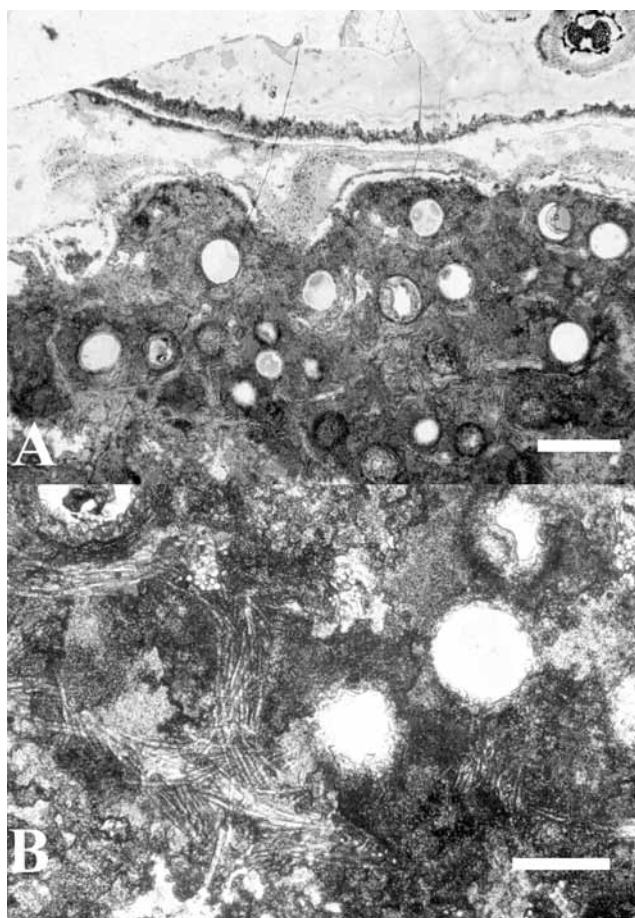


Fig. 11. *Palaeospongilla chubutensis* from the Lower Cretaceous continental Chubut-Formation in Argentina. This specimen is the best known preserved fossil spongillid (Volkmer-Ribeiro & Reitner, 1991b). The specimen shows lots of gemmules embedded within the silicified tissue. The gemmules are surrounded by reticulate tracts of haplosclerid oxea (scales: A, 1 mm; B, 300 μ m).

(1972) created a new class to accommodate sponges with a secondary basal skeleton, the Sclerospongiae Hartman & Goreau, 1970, but this taxon has clearly been shown to be invalid based on its polyphyletic origin (e.g., Van Soest, 1984a; Vacelet, 1985; Reitner, 1991, 1992; Wood, 1987). Sponges with coralline basal skeleton are now assigned to widely distributed clades within demosponges, and this feature is no longer recognised as a phylogenetic autapomorphy; significantly, hexactinellids with a calcareous basal skeleton have never been observed. The various basal skeletons are highly convergent, and represent a grade of construction (sharing functional similarities) rather than any common ancestry. Observations of spicule remains in fossil representatives of coralline sponges have shown that a lot of coral-like fossils are sponges, and that they were important reef dwellers and reef-forming organisms in the past up until the end of the Cretaceous (Dieci *et al.*, 1974, 1977; Kazmierczak, 1979; Gray, 1980; Reitner & Engeser, 1983, 1985, 1987; Wood & Reitner, 1986, 1988; Reitner, 1987a,b,c, 1989, 1991, 1992; Wood, 1987; Wood *et al.*, 1989).

Calcified sponges were the dominant reef-building organisms since the beginning of the Phanerozoic. They were replaced by scleractinian corals in modern reefs as primary structural organisms, but they have living relatives ('coralline sponges') in cryptic niches of almost all Recent coral reefs. They were the first metazoans to produce a carbonate skeleton and their microstructural features have remained completely unchanged over this very long period of time. Their biomineralization processes are extremely conservative and these still exist in extant calcified sponges (Reitner *et al.*, 1997, 2001b).

Coralline demosponges first occur along with the Archaeocyatha in the Lower Cambrian (Tommotian). At this time archaeocyaths were very diverse in their morphotypes, dominated the Cambrian reefs, and have strong poriferan affinities (Debrenne & Zhuravlev, 1993; Debrenne *et al.*, 1990), now ascribed as potential demosponges (refer to chapter on Archaeocyatha by Debrenne *et al.*, this volume). Although demosponge spicules have been discovered within the basal skeleton of few Archaeocyatha 'Irregulares' (Reitner, 1992; Reitner & Mehl, 1995), their allochthonous origin is possible. Coralline demosponges with a stromatoporoid basal skeleton occur in the Middle Ordovician, except a few enigmatic ones from archaeocyath-mounds. They play a major role as reef-building organisms in the Silurian and especially in the Devonian. After the Frasnian/Famennian boundary coralline demosponges with 'chaetetid' basal skeletal (Chaetetidae, Tabulata) construction play a major reef-building role, as well as chambered coralline sponges ('sphinctozoans'), which occur first in the Ordovician (Rigby & Potter, 1986). The first (problematic) taxa of 'sphinctozoan' sponges were known from the Lower Cambrian. During the Permian and Middle Triassic 'sphinctozoans' were one of the most important groups of reef builders, whereas modern forms of coralline sponges originated in the Late Permian and had a first maximum in the Late Triassic (Carnian-Norian). Special forms of stromatoporoids (e.g., *Dehornella*) were important reef dwellers during the Jurassic and Lower Cretaceous. Most of them are cryptic benthic dwellers and had adapted to living in nutrient-poor deeper shelf areas. In the Late Albian modern cryptic coralline sponge communities of the Pacific realm developed (Reitner, 1989, 1990, 1991, 1992, 1993). Since this time there have been no fundamental changes observed in the evolution of coralline sponges, with Recent taxa morphologically very similar to the Cretaceous faunas. Up until the Lower Cretaceous coralline sponges were important reef-building and reef-dwelling organisms, but since the development of

coralline algae in the Jurassic, the hermatypic corals became more dominant as reef-frame builders. Today coralline sponges are now virtually restricted to cryptic niches and deeper fore-reef areas, with less or no light and strict oligotrophic conditions.

After the Cretaceous-Tertiary (KT-) boundary the fossil record of coralline sponges is extremely poor.

Palaeozoic Record of Spicule-Bearing Coralline Demosponges

Hadromerida. Only few taxa of coralline sponges from the Palaeozoic bear spicules and allow an informed evaluation of their taxonomic affinities. The largest group of these in the Palaeozoic are the classical Stromatoporoidea Nicholson & Murie, 1878, which do not bear spicules. However, due to their characteristic exhalant canal systems (astrorhizae), most of the main taxa (*Stromatopora* Goldfuss, 1826, *Actinostromaria*, etc.) are now classified as demosponges. A more detailed classification and determination of the phylogenetic position has, up until now, been impossible.

Only one group of Palaeozoic stromatoporoids, the Early Devonian taxon *Syringostroma* cf. *borealis* (Nicholson, 1875), has a distinctive wall structure of densely packed spherical structures (Fig. 12). These spherical bodies are interpreted as aster microscleres, comparable to those known from the modern hadromerid taxon *Chondrilla*, and found in the Cretaceous chondrillid coralline sponges *Calcichondrilla crustans* Reitner, 1991 and *Calcistella tabulata* Reitner, 1991 (Fig. 13) (Reitner, 1992).

If this taxonomic assumption is correct, the diversification of the Hadromerida happened very early in the Phanerozoic. This assumption is supported by the spicule record in the 'chaetetid' early- to middle Devonian taxon *Pachythea* cf. *stellimicans* (Schlüter, 1885). Within the basal skeleton of this taxon hadromerid-like tylostyle spicules are preserved (Reitner, 1992). Both major clades of the hadromerid construction were realised in the Middle Devonian: on the one hand the *Suberites/Polymastia*-like taxon with reduction of aster microscleres (*Pachythea*), and on the other hand the *Chondrilla*-like taxon with a reduction of megascleres (*Syringostroma* Nicholson, 1875).

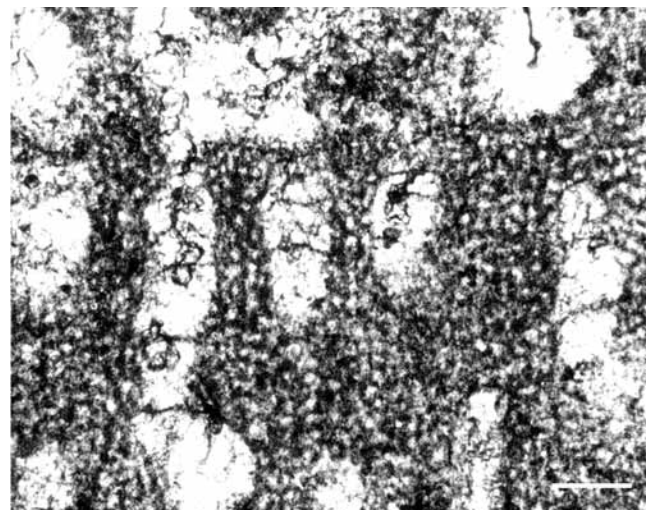


Fig. 12. *Syringostroma* cf. *borealis* from the middle Devonian of northern Spain with abundant spherical structures within the stromatoporoid basal skeleton. These structures are interpreted as densely packed aster microscleres with hadromerid affinities (scale 200 μm).

The 'chaetetid' basal skeleton bauplan is very important in the Lower Carboniferous, and some 'chaetetids' bear bundles of hadromerid tylostyles but no microscleres. An important representative of the Lower Carboniferous hadromerid 'chaetetids' is *Boswellia mortoni* Gray, 1980. However, most of the Carboniferous 'chaetetids' lack characteristic spicules and this may be due to diagenetic factors. The spicules in *Boswellia* are exclusively preserved

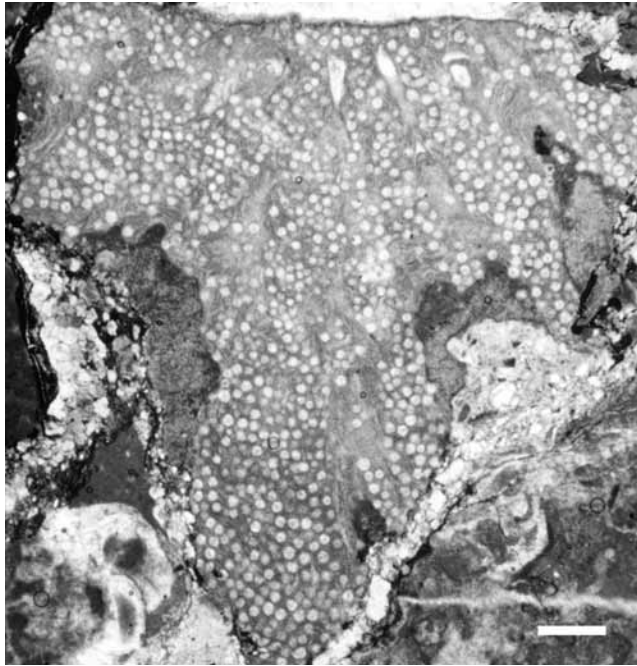


Fig. 13. *Calcichondrilla crustans*, a Lower Cretaceous hadromerid with affinities to the extant *Chondrilla*. The distribution of microscleres are similar to those seen in the Devonian *Sysringostroma* (scale 200 μ m).

in silicified specimens (Fig. 14). The opaline silica of sponge spicules is dissolved very fast and spicule remains, mostly calcitic pseudomorphs, are extremely rare. Therefore, it appears that the Hadromerida were well developed in the Palaeozoic.

Halichondrid/'Axinellid' Palaeozoic Coralline Demosponges.

There is only one record of coralline demosponge with 'axinellid' affinities from the Late Carboniferous (Pennsylvanian) from Kansas. This sponge was firstly described by Newell (1935), as *Parallelopora mira*. This taxon was revisited by Wood *et al.* (1989) and this was the first time that the spicular skeleton was described in detail. In that paper the authors favoured a classification within the Haplosclerida, due to the reticulate arrangement of the spicular skeleton. However, the arrangement of the subtylostyle spicules in the main pillars exhibit an axial condensation, which is more characteristic of an 'axinellid' bauplan (Reitner, 1992) (Fig. 15). Comparable skeletal features were seen in the Lower Cretaceous taxon *Euzkadiella erenoensis* Reitner, 1987b.

A very intriguing halichondrid coralline demosponge is the 'thalamid' *Subascosymplegma oussifensis* (Termier, Termier & Vachard, 1977) from the Late Permian of Djebel Tebaga in Tunisia. This locality is famous for of its masses of coralline sponges and aragonite preservation of most of the basal skeletons. The basal skeleton of *Subascosymplegma oussifensis* is formed by aragonitic spherulites and the inhalant pores of the 'thalamid' skeleton are surrounded by bundles of long styles (Reitner, 1992). The spicular types and arrangements are comparable with the modern taxa *Hymeniacion*, *Scopalina* and the coralline demosponge *Hispidopetra miniana* Hartman, 1969.

Agelasid Coralline Demosponges.

(1) Ceratoporellidae Hartman & Goreau, 1972 – agelasid coralline demosponges with a heavy aragonitic basal skeleton crust. The type genus of the Ceratoporellidae is *Ceratoporella* (Hickson, 1911), which is restricted to the Caribbean region. Only one species of Ceratoporellidae, *Stromatospongia micronesica*, is known from Pacific reefs. *Ceratoporella* is one of the extant

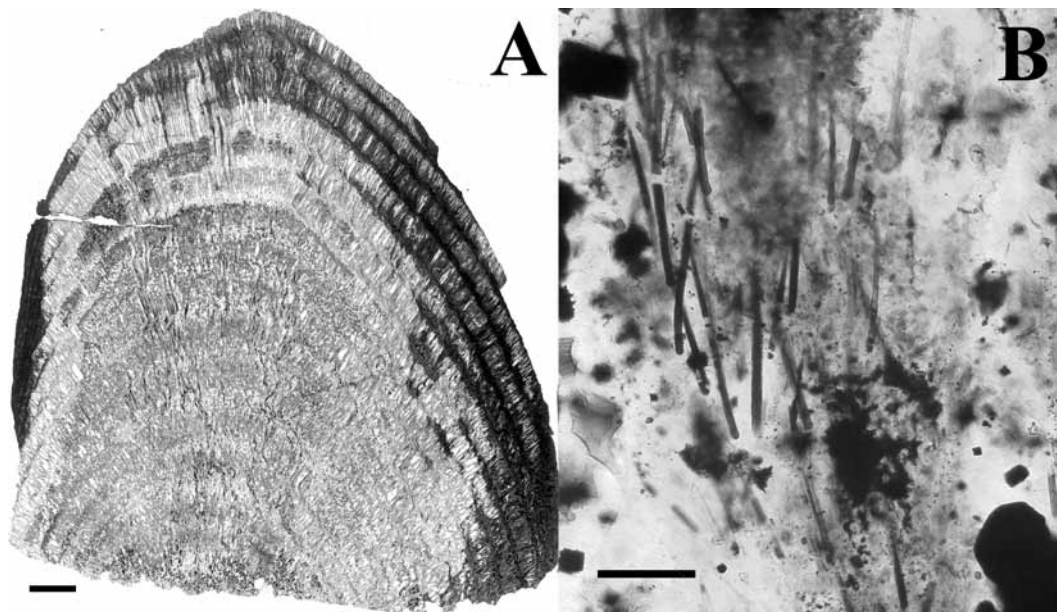


Fig. 14. *Boswellia mortoni* from the Lower Carboniferous from Wales. These chaetetid sponges are classified as hadromerids with strong affinities to *Suberites*. This specimen exhibits a clear regular chaetetid growth pattern. The specimen is partly silicified and within the silicified portions of the chaetetid the hadromerid-type tylostyles arranged in bundles are well preserved. All vertical elements of these chaetetids are primarily constructed of tylostyles spicules (scales: A, 1 cm; B, 150 μ m).

coralline demosponges ('living fossils') which first occurred in the Late Permian of the Djebel Tebaga (Reitner, 1992; Wood, 1987) (Fig. 16). The Ceratoporellidae are very common in the Late Triassic, especially from the Carnian Cassian Beds (Northern Italy). From one species, *Ceratoporella breviacanthostyla* Reitner, 1992, acanthostyle spicules are known (Fig. 17). The spicular skeleton of this taxon is made of verticillitid acanthostyles of the *Agelas* type. They form a heavy aragonitic basal skeleton on the top with small calicles in which most parts of the soft tissue of the sponge is located. The soft tissue is also characterized by high amounts of symbiotic bacteria (ca. 60% of the entire biomass) (Willenz & Hartman, 1989). In contrast to the 'sphinctozoan' *Vaceletia*, the aragonite is orientated in clinogonal arranged fibres ('water jet' structure). Shortly after the removal of the soft tissue the calicles are closed by rapid epitactical growth of the aragonitic fibres. The calcification fronts are easy to stain with calcein and therefore ideal for *in situ* growth measurements (Willenz & Hartman, 1985). These sponges are extremely slow growing, exhibiting only 200–500 μm yearly growth rates (Böhm *et al.*, 2000). We have investigated specimens with an age of more than 600 years. The entire basal skeleton is a thick aragonitic crust with high amounts of Sr (10,000 ppm) and additional extraordinary high amounts of U (7–8 ppm) which allows excellent age determination using the U/Th method. The carbon used for skeletal formation is heavy and in equilibrium with the ambient seawater ($\delta^{13}\text{C} + 5 - +3,8$).

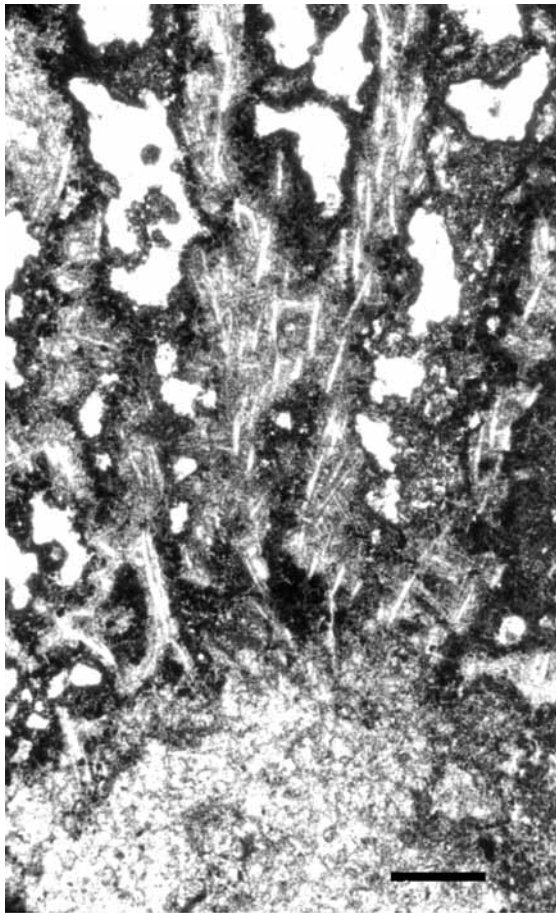


Fig. 15. *Newellia mira*, an 'axinellid' coralline demosponge from the Late Carboniferous of Kansas (USA) (Wood *et al.*, 1987) (scale 250 μm).

The main problem of this taxon is that it occurs first in the Late Permian, has a good fossil record in Triassic reefs, and then disappears at the end of the Triassic (Reitner, 1992) but reappears next in the Pleistocene. Palaeontologists refer to these taxa as 'Lazarus-taxa'. There is a time gap of about 210my. Modern representatives of Ceratoporellidae differ little from Triassic faunas, either in the basal skeleton geochemistry or in the spicular skeleton. The reason for this peculiar fossil record is unknown and could be related with varying ocean chemistry, early diagenetic aragonitic dissolution, or may be a facultative basal skeleton formation by one taxon dependent on the Ca^{2+} content of the ambient seawater. Permian and Triassic oceans were probably low in Ca^{2+} , similar to Recent oceans, whereas Jurassic, Cretaceous and Tertiary oceans were enriched in Ca^{2+} (Arp *et al.*, 2001). However, the detailed physiological influences on varying Ca-concentrations are still unknown and currently under investigation.

(2) *Astrosclera willeyana* Lister, 1900 – a stromatoporoid coralline sponge with a spherulitic basal skeleton. The main features of soft tissue and the processes of formation of the basal skeleton in *Astrosclera* have recently been described in detail, and therefore only a summary is provided here (refer to Wörheide, 1998).

The living tissue of *Astrosclera* penetrates the basal skeleton to a maximum depth of 50%, depending on specimen size. The soft

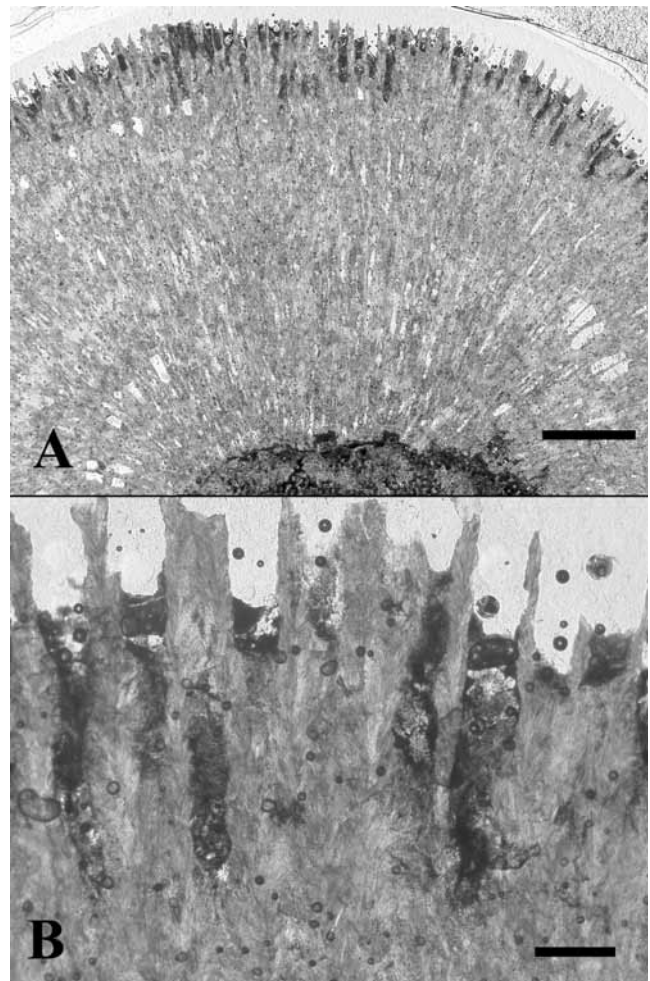


Fig. 16. A, this specimen is the oldest known Ceratoporellidae from the Late Permian Djebel Tebaga (Tunisia) (scale 1 cm). B, the aragonitic basal skeleton is comparable with Recent species, however, unfortunately no spicules are preserved (scale 1 mm).

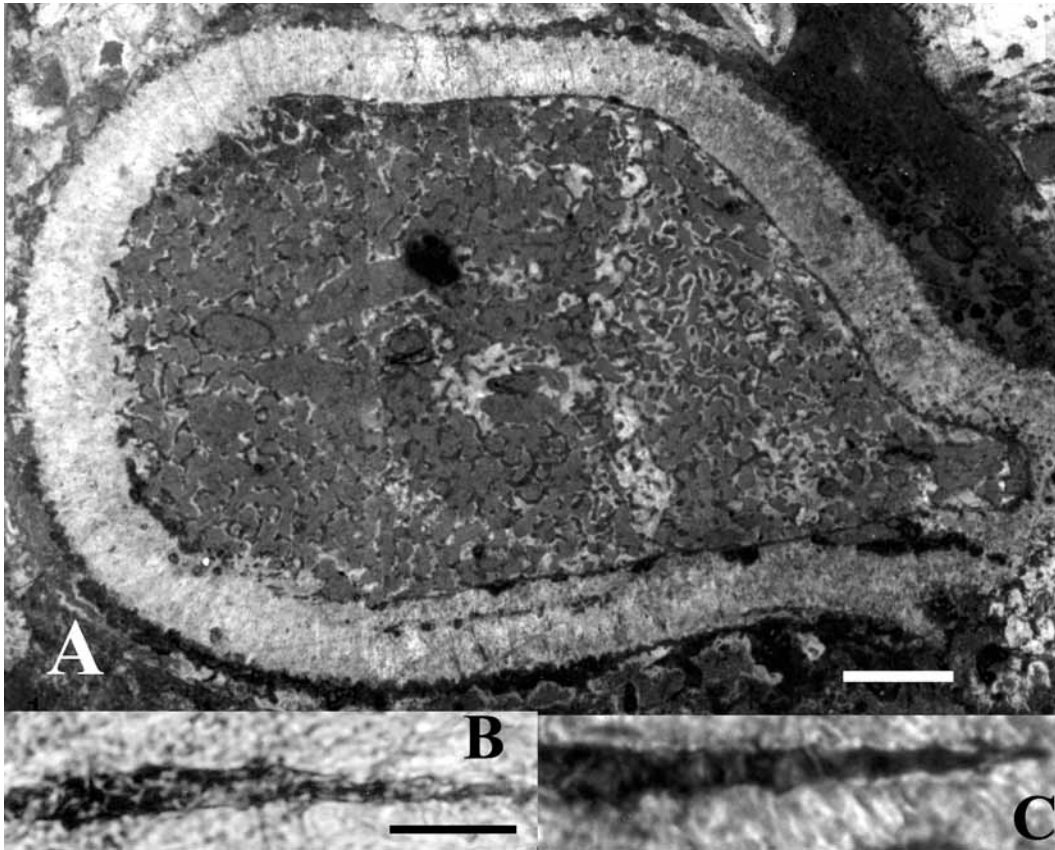


Fig. 17. A, this ceratoporellid specimen (*Ceratoporella breviacanthostyla*) from the Carnian of the southern Alps (Cassian Beds, Northern Italy) is the only known material with acanthostyle megascleres (B, C) (Reitner, 1992) (scales: A, 2.5 mm; B–C, 20 μm).

tissue shows a stromatoporoid grade of organization (e.g., Wood, 1987) and can be divided into three major zones:

(A) The ectosome is the area directly beneath the exopinacoderm, reaching a thickness of about 100–300 μm . This zone is characterized by the absence of choanocyte chambers, an enrichment of storage and supporting cells (SSC's), and archaeocyte-like large vesicle cells (LVC's), which are responsible for the initial formation of aragonitic spherulites. (B) The choanosome, contiguous with the ectosome but with a more-or-less sharp transition, comprises the major part of the living tissue in *Astrosclera*, characterized by small choanocyte chambers ($\pm 15 \mu\text{m}$ diameter) and a high density of bacterial symbionts. Other cellular components of the choanosomal mesohyle are archaeocytes, typical pluripotent, phagocytic demosponge cells, SSC's, and rare fiber cells. (C) The zone of epitaxial backfill (ZEB) is considered as a subzone of the choanosome due to its important role for the *syn vivo* cementation of the lowest parts of the basal skeleton. It is characterized by a reduced number of (or absence of) choanocytes and bacteria and sometimes an enrichment of SSC's.

The aragonitic calcareous skeleton of *Astrosclera* is formed by the combination of three processes. In the first, spherulites are formed in LVC's in the ectosome. The LVC's possess a large vesicle which is filled with a three dimensional network of sheets and fibers and acidic mucus. Sheets and fibers act as the insoluble organic matrix (IOM) and mucus as soluble organic matrix (SOM) for seed crystal nucleation. In the first stage, seed crystals are randomly oriented, later they are oriented in the direction of the

aragonite c-axis. When they attain a size of $\pm 15 \mu\text{m}$ spherulites are released from the cell and enveloped by basopinacocytes. In the second process, basopinacocytes transport the spherulites to the tips of skeletal pillars where they fuse by epitaxial growth. This epitaxial growth is controlled by acidic mucous substances in the extracellular space (ECS) between the growing aragonitic fibers and the basopinacoderm. The mucus is produced by basopinacocytes and acts as a buffer for Ca^{2+} ions. The ECS-mucus is thought to have a different composition from the mucus inside vesicles of the LVC's. The third process involves withdrawal of soft tissue during upward growth, when it is pulled upwards from the lowermost parts of skeletal cavities. The space remaining is subsequently filled by epitaxial growth of aragonite fibers. The zone of epitaxial backfill is characterized by an absence of choanocyte chambers and a reduced number of bacteria, but sometimes by an increased number of SSC's. The ECS in the ZEB is also filled with acidic mucus, which controls the speed and direction of epitaxial growth. The number of SSC's is sometimes increased, indicating their importance in nutrient supply during skeletal elaboration.

Astrosclera is a very slow growing species as measured by *in vivo* staining with fluorochromes, the mean growth rate being 230 μm per year, with an average growth rate of 0.63 μm per day, as determined by *in vivo* staining with Calcein- Na_2 , AMS, ^{14}C and U/Th data (Wörheide, 1998). The oldest known modern specimen has an individual age of more than 500 years (Wörheide, 1998).

Taxonomic Value of the Spherulitic Basal Skeleton. The spherulitic basal skeleton-type was much more widespread at the

end of the Palaeozoic (upper Permian, Djebel Tebaga, Tunisia), and in the Late Triassic (Carnian, St. Cassian, Dolomites, Italy; Norian, Antalya, Lycien Taurus, Turkey), than in Recent seas. Generally, this body plan can be elaborated by two distinct processes. The first is extracellular, where an organic skeleton (e.g., organic spongin) is calcified extracellularly, producing a 'pseudo-spherulitic' skeleton. This mode is seen in extant *Calcifibrospongia actinostromarioides* (Haplosclerida) from the Bahamas, and in the Aptian axinellid *Euzkadiella erenoensis* from northern Spain (see Reitner, 1987a, 1992). The second, an intracellular mode of spherulite formation is where no primary skeleton is calcified. This mode was described in detail by Wörheide (1998), and is summarized above, outlining early stages of skeletal formation in extant *Astrosclera willeyana*. Whether formed extra- or intracellularly, the spherulitic type of skeleton appears to be predominant amongst sponges from the Triassic deposits of St. Cassian and Antalya (Cuif & Gautret, 1991a), whereas the intracellular mode of formation is only now found in one extant taxon, *A. willeyana*.

The first occurrence of sponges with a spherulitic grade of construction was reported from the upper Permian of Tunisia (e.g., Termier *et al.*, 1977). One of the reported taxa, *Subascosymplegma oussifensis*, was described by Reitner (1992: 210), as possessing a basal skeleton made of intracellularly-formed aragonitic spherulites. Free spherulites, as found in the extant *Astrosclera* but with a larger diameter of 400–600 μm , were also found in the biogene pore space of that species. *Subascosymplegma oussifensis* had a spicular skeleton of irregularly arranged long thin styles, a plumose ectosomal skeleton also composed of long thin styles, and Reitner (1992) suggested affinities to the taxon 'Axinellida'/Halichondrida. Although the deposits of Djebel Tebaga contain a large variety of spherulitic-type basal skeletons, only some of them appear to be formed intracellularly. Intracellular formation of spherulites is only recognizable in spherulites with a dark centre, as found in extant *Astrosclera*.

Calcified coralline sponges with a spherulitic skeleton are present in the exceptionally well preserved Late Triassic deposits of Antalya and St. Cassian, previously described by Cuif (1974) and Cuif (1983), Engeser & Taylor (1989), Reitner (1992), and others. These sponges have well-preserved original aragonitic mineralogy and microstructure, and were used to compare the taxonomic value of spherulitic skeletons based on comparisons with Recent *Astrosclera* (Gautret, 1986; Cuif & Gautret, 1991b; Wood, 1991b; Reitner, 1992) (Table 1). These authors showed that the spherulitic grade of construction appeared independently in a large variety of skeletal grades of architecture in Triassic sponges (i.e., sphinctozoan, chaetetid, stromatoporoid; Wörheide, 1998: Plate 29), and in different taxa (e.g., *Sestostromella robusta*, Haplosclerida; *Chaetosclera klipsteini*, Halichondrida; Reitner

1992). Reitner (1992) also stated that different skeletal morphotypes appeared independently in various phylogenetic lineages, and suggested that intracellular formation of the aragonitic spherulites in general is not an apomorphy of *Astrosclera*. This grade of construction may be interpreted as a polyphyletic development of several distinct sponge taxa, with no synchronous development (i.e., a convergent character), or a plesiomorphic character, evolved in a common ancestor during the Precambrian/ Cambrian. Therefore, an 'intracellularly formed spherulitic skeleton' represents a character with no taxonomic value in the fossil record.

Wörheide (1998) screened and studied thin sections of samples from St. Cassian and from Antalya (the latter by courtesy of J.-P. Cuif), to determine the affinities of calcified sponges with 'astrosclerid-like' spherulitic microstructures, and to find relatives of the extant *Astrosclera* (if possible, spicule-bearing ones). A large variety of spherulitic microstructures was observed in thin sections of this collection, belonging to a large variety of skeletal architectures and taxa (e.g., Wörheide 1998: pls. 29/3, 29/4: the chaetetid *Cassianochaetetes* cf. *gnemidius* (Klipstein); Pls. 29/5–7: an unidentified sphinctozoan). Most of the different spherulitic skeletal morphologies of sponges from St. Cassian and Antalya were formed by an intracellular process in the early stage, and later by epitaxial growth as in the Recent *Astrosclera*, and therefore this mode was named 'astrosclerid-like' (e.g., Cuif & Gautret 1991b). It has been demonstrated in detail by Wörheide (1998) that the skeleton of *Astrosclera* is formed by three distinct processes. Only in the very early, initial stages are spherulites elaborated by an intracellular process, but the greater part of skeletal accretion happens by two different extracellular epitaxial growth processes. In some of the Triassic thin sections screened, there were signs of (A) initial intracellular growth of the spherulite (non-mineralized dark centre of spherulite), (B) epitaxial fusion of spherulites (elongated spherulites), and (C) epitaxial backfill. These specimens certainly belong to a different taxon from *Astrosclera* (Wörheide, 1998: Pls 29/3–7). Even if all these processes were found in one specimen, a definite decision could not be made about the taxonomic affinities given that a combination of the three processes appears to have no taxonomic value. As noted, this grade of construction has probably appeared independently in different phylogenetic lineages of coralline sponges, representing a convergent character, whereas taxonomic affinities can only be deduced if spicules are present. Hypercalcified spherulitic basal skeletons are clearly a grade of construction, as suggested by Wood (1991b), and no apomorphic character of particular taxa, as suggested by Hartman & Goreau (1970) in general, and by Cuif & Gautret (1991b) for *Astrosclera*.

Clearly, morphological characters are inadequate clues to the affinities of extant *Astrosclera* with Triassic species. Because the

Table 1. Examples of selected coralline sponges with a basal skeleton made of intracellularly formed spherulites. This type of skeleton occurs in distinct sponge taxa through time and represents a character with no taxonomic value (from Wörheide, 1998).

Taxon	Age	Diameter of intracellular spherulites	Spicular skeleton	Affinities to
<i>Subascosymplegma oussifensis</i>	Upper Permian	400–600 μm	Long, thin, styles, plumose	Axinellida/Halichondrida
<i>Sestostromella robusta</i>	Lower Carnian	20–50 μm	Long, thin, curved diactines	Haplosclerida
<i>Chaetosclera klipsteini</i>	Lower Carnian	10–20 μm	Long styles	Halichondrida
<i>Astrosclera willeyana</i>	Recent	15–60 μm	Thick, short, verticillate acanthostyles (basic form)	Agelasida

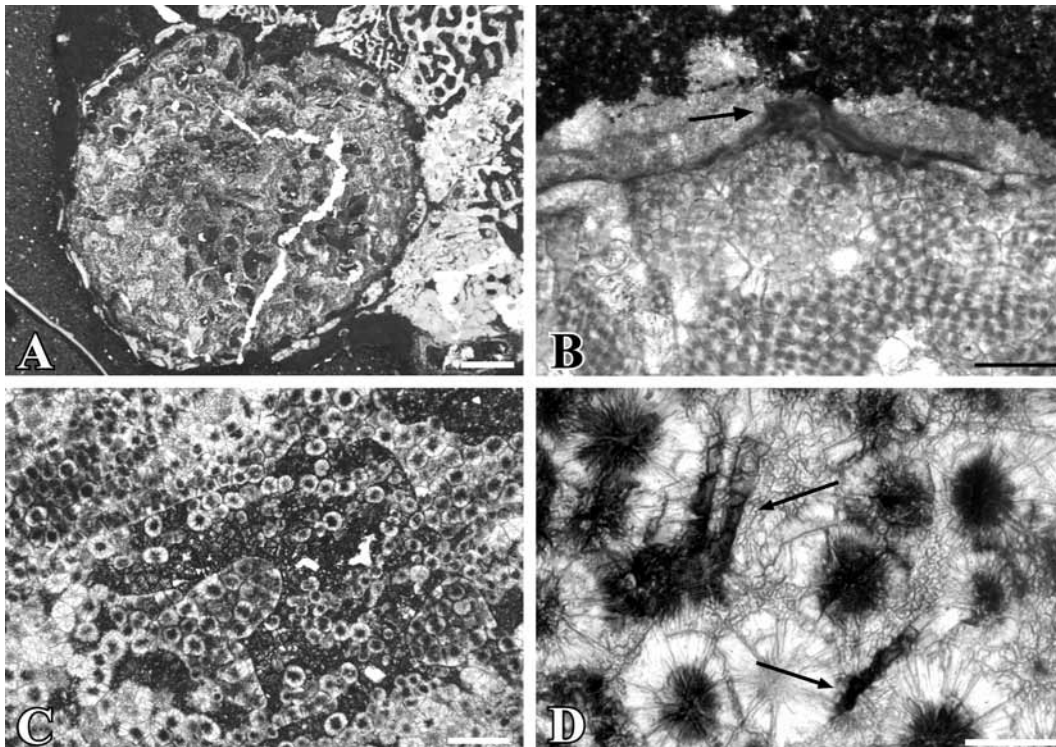


Fig. 18. A, holotype of *Astroclera cuifi* Wörheide 1998 from the Norian of Antalya (Turkey); horizontal section of specimen in thin section (scale 1 mm). B, one mamelon of *A. cuifi* (arrow) (scale 200 μm). C, detailed view of *A. cuifi* showing spherulitic basal skeleton. Note dark centers of spherulites and free spherulites in biogene pore space, similar to extent *Astroclera* (scale 150 μm). D, sub-acanthostyle megascleres (arrows) in the basal skeleton of *A. cuifi* (scale 50 μm). All figures from Wörheide (1998, Plates 29, 30).

Triassic material lacks spicules (Reitner 1992: 230), sponges, probably *Astroclera*, have to be identified initially from a combination of morphological criteria based on biocalcification. A definitive classification of Triassic ‘relatives’ is only possible based on spicule morphologies, but in most cases spicules are not present in the fossil record, leaving only the morphological criteria of the basal skeleton (i.e., central Pacific populations of extant *Astroclera* also lack spicules).

Thus, all of the microstructural features present in *Astroclera* must be present in fossil taxa to infer affinities, not only the character ‘intracellularly formed spherulitic’ basal skeleton, since the intracellular formation of spherulites appeared in the Triassic in different taxa. But even so, confirmation of phylogenetic affinity with *Astroclera* is at most only probable, and still uncertain if no spicules are present.

However, applying stringent criteria, Wörheide (1998) was able to discover and describe the first true relative of the taxon *Astroclera*. Only one sponge from Antalya (Turkey) complied with all the criteria, of all the sponges screened from both St Cassian and Antalya. Therefore, affinities to the taxon *Astroclera* were clear, and moreover, spicules were also found in this specimen (Fig. 18). *Astroclera cuifi* Wörheide (1998) showed signs of all three of the distinct biocalcification processes of *A. willeyana*, although the size of spherulites was larger than in extant *Astroclera*. These biocalcification characters indicate initial and subsequent biocalcification took place similar in a manner similar to the processes in extant *A. willeyana* (see above and Wörheide, 1998 for details). The spicular skeleton, although not ‘typical’ acanthostyles, generally showed

similarities to one of the ‘groups with similar spicule morphology’ (GSSMs) of extant *Astroclera*. Wörheide (1998) distinguished six different populations in *Astroclera*. One of these populations, from the western Indian Ocean, showed a medium intra-population variation in spicule morphology and normally contains acanthostyle megascleres, but also a few thick spicules without spines, or with reduced spines, which are comparable to the ones observed from the Antalya species. Affinities of the Triassic sponge *A. cuifi* to *Astroclera* were therefore obvious. The Triassic species was clearly new due to the slightly larger spherulite size, the rarer spicules, and the different spicule morphology (Fig. 18D).

However, although the first occurrence of *Astroclera* has been confirmed in the Late Triassic of southern Turkey (*Astroclera cuifi* Wörheide 1998), an important problem still remains: the lack of a record during younger times until the Holocene (thus, a ‘Lazarus’-taxon, see above).

***Vaceletia* Pickett, 1982: A ‘Thalamid’ Coralline Demosponge with Archaeocyathan Affinities.** The fossil record of this taxon is, in contrast to other aragonitic coralline sponges, very good and continuous from its first reported occurrence in the Middle Triassic to Recent seas. They are ‘thalamid’ or ‘sphinctozoid’ sponges that exhibit a soft tissue organisation and structure already known from sponges with a stromatoporoid skeleton. Normally they possess a central cavity (spongocoel) and a chambered basal skeleton.

The primary organic skeleton of *Vaceletia* is non-spicular (Vacelet, 1979). The choanocyte chambers are relatively large (50 μm) and the mesohyl is enriched with bacteria (ca. 50% of the entire biomass). Large rounded cells with large inclusions are very

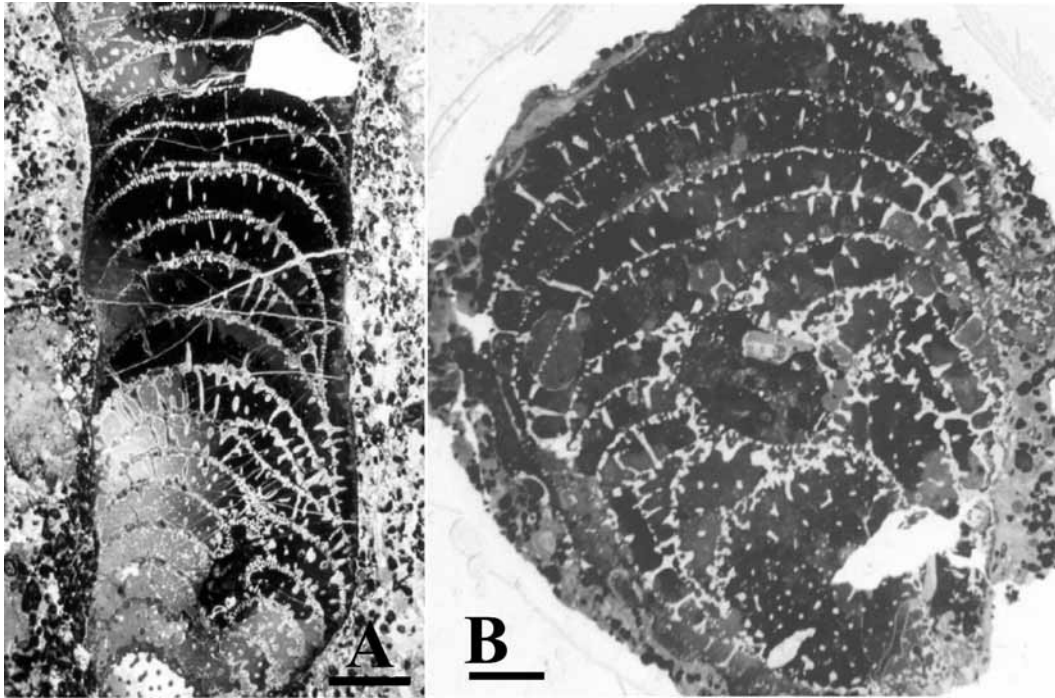


Fig. 19. Cenomanian *Vaceletia* from Liencre, northern Spain. These coralline sphinctozoan sponges are very common in the middle Cretaceous (Reitner, 1989, Reitner *et al.*, 1995) (scales: A, 5 mm; B, 2 mm).

characteristic of this sponge, comparable with the LCG cells of *Acanthochaetetes* Fischer, 1970 (Reitner & Gautret, 1996). It has a trabecular organisation and is overlaid by a hemi-spherical top-layer ('dermal-layer'). The trabeculae consist of irregular, organic filaments with a very thick central filament. This central filament has a supporting function and could be seen as an 'organic spicule'. A network of very thin fibers surrounds this central filament. The calcification of the secondary aragonitic skeleton starts between these organic fibers. This secondary skeleton consists of irregular aragonitic micrite. The central filament would not be calcified. The formation of the secondary skeleton is not a continuous process, it happens step by step in the following order (cf. Reitner, 1992; Reitner *et al.*, 1997, 2001b).

(1) Formation of skeletal-pillars. Formation of a new, non-calcified chamber with a hemispherical dermal top-layer and a trabecular organisation and organic skeletal-pillars containing a thick central filament. These skeletal-pillars are filled with thin fibres. The entire space inside the pillar is filled with acidic glycoproteic/proteoglycanic mucous. This space is filled successively during ontogenesis by aragonite crystals. The mineralization starts from the inside of the organic pillars. Further on the whole fibrous insoluble matrix of a newly formed pillar is substituted successively by aragonite crystals. The acidic mucous substances are reduced correspondingly. The thick central filament cannot be mineralized. This central filament has only a primary initial supporting function, because the irregular fibres inside the pillars are not able to support the choanosome on their own. Newly formed chambers never show the complete structure and size of the later calcified ones. Such a chamber *in statu nascendi* is increasing slowly in size. The crystallization seems to start from the borders of the uncalcified skeletal elements. An initial, prismatic layer of aragonite crystals is observed. Larger crystals overlay this layer forming a loose network. The density of calcification is higher in

the central part and the border of the pillars, in between the calcification is slower.

(2) Calcification of the inactive parts of the skeleton. In the ontogenetic development of the older parts of the skeleton a second calcification phenomenon is observed. The upwardly moving soft-tissue is able to form organic phragmas via the basopinacoderm. These phragmas separate chambers which are filled with acidic glycoproteic mucus ('soluble matrix', SOM). This SOM shows high concentrations of Asp (14.13 mol%) and Glu (11.42 mol%) in combination with high values of sugars ARA (14 mol%), XYL (16.5 mol%), and GLC (22 mol%) (Reitner, 1992). Within these chambers the toxic physiological surplus of Ca^{2+} is bonded to acidic macromolecules and deposited as an aragonitic waste product. The SOM is interspersed by polymerised mucus fibres which act as the insoluble organic matrix (IOM). The steps of mineralization are the same as seen in the pillars (Reitner, 1992; Reitner *et al.*, 2001b). This calcification phenomenon is often observed in many fossil sphinctozoans of the *Vaceletia*-type, and could be a model for all irregular, micritic-granular basal skeletons of stromatoporoid and 'thalamid' organisation. Most important is the mode of biomineralization because the Archeocyatha of the Lower Cambrian exhibit the same type. It is suggested that *Vaceletia* may be extremely ultraconservative and therefore comparable with certain taxa of the Archeocyatha (Reitner, 1992).

Highlights of the Mesozoic Coralline Demosponges. The earliest fossil taxon is *Stylothalamia dehmi* Ott, 1977, recorded from the Ladinian (Middle Triassic) (Ott, 1967) (Fig. 19). This type of 'sphinctozoan' is restricted to small caves and dark reef environments. The Stylothalamidae were extant in the Late Triassic and apparently survived until the lower Jurassic (Domerian). The Stylothalamidae are characterized by vesicular skeletal structures, and sometimes oxeas are found incorporated into the micritic, aragonitic basal skeleton. However, most vaceletids do not bear any spicules. The spicule types

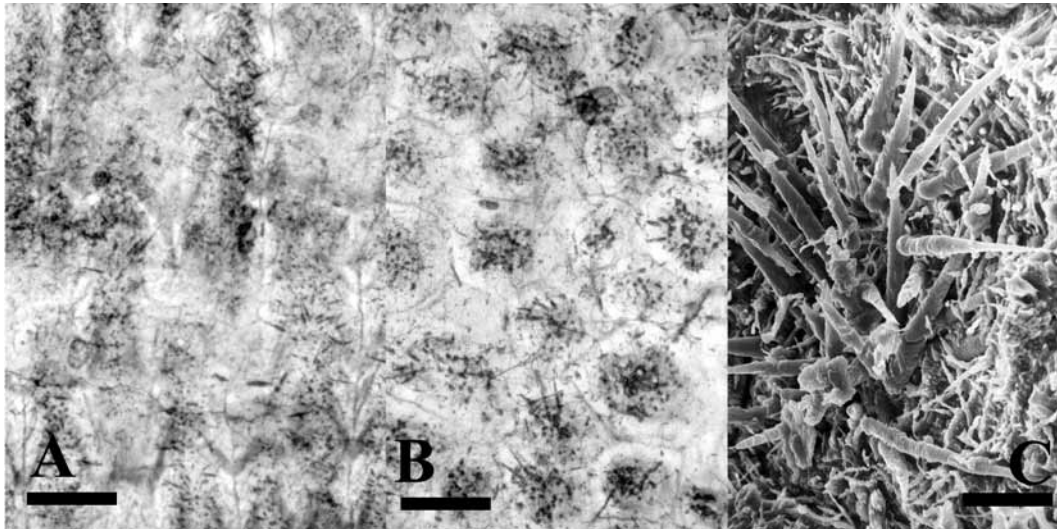


Fig. 20. Most of the Mesozoic coralline sponges are related to the Halichondrida/ 'Axinellida', with axial spicule condensation. One taxon of the Milleporellidae, the genus *Murania*, has a basal skeleton of aragonite in the Triassic and calcitic ones in the Lower Cretaceous. *Murania kazmierczaki* from the Carnian Cassian beds has an aragonitic basal skeleton with excellent preserved subtylostyle spicules (Reitner, 1992) (scales: A, vertical section, 1mm; B, horizontal section, 1mm; C, SEM micrograph – aragonite dissolved with EDTA (method described in Reitner & Engeser 1987), 100 μm).

and arrangement resembles the Haplosclerida, with some affinities to the Callyspongiidae. In the Cretaceous *Verticillites* DeFrance, 1829 is very common and forms large specimens of up to 10 cm in size. *Vaceletia* is known from various Tertiary localities (e.g., *Vaceletia progenitor* Pickett, 1982), and the deeper water form from the Danian of Faxø (Denmark), *Vaceletia faxensis*.

Recent *Vaceletia* are mostly non-branched solitary taxa and are restricted to dark reef caves. However, common frame building colonial forms were recently discovered in shallow water reef caves at Osprey Reef (Coral Sea) and at the Astrolabe Reef, Fiji (Wörheide & Reitner, 1996). According to a recent genetic analysis (Wörheide *et al.*, unpublished) both forms are clearly different species. There is also one deep-water (200–400 m) species from New Caledonia realm (Vacelet, 1988, Vacelet *et al.*, 1992). The genetic relationships of all these forms are currently under investigation.

Based on the ceractinomorph parenchymella larva and simple monaxonic spicules in some fossil taxa, with a callyspongid arrangement the fossil and Recent vaceletids may be classified close to the Haplosclerida.

Mesozoic Coralline Demosponges with 'Axinellid' Spicule Arrangement

In the Mesozoic, coralline demosponges with an 'axinellid' skeletal structure are major components of the benthos (Wood, 1987; Reitner, 1992). Most of the Jurassic stromatoporoids (Milleporellidae), like *Dehornella* Lecompte, 1952, exhibit the typical axial concentration of monaxonic spicules (oxeas, styles). They are important reef and shallow water dwellers, and exhibit in the Jurassic and Cretaceous a low Mg calcite basal skeleton. In the Triassic all of the coralline sponge with 'axinellid' affinities bear an aragonitic basal skeleton. Surprisingly, one taxon is able to do both, aragonite basal skeletons in the Triassic and calcitic ones in the Cretaceous. This taxon is a crust-forming coralline sponge called *Murania* Kazmierczak, 1974. The spicule-trees (axially condensed spicules) become calcified probably during the upward movement of the soft tissue. The taxon *Murania* occurs first in the Late Triassic (Carnian) of the Cassian Beds (northern Italy), with

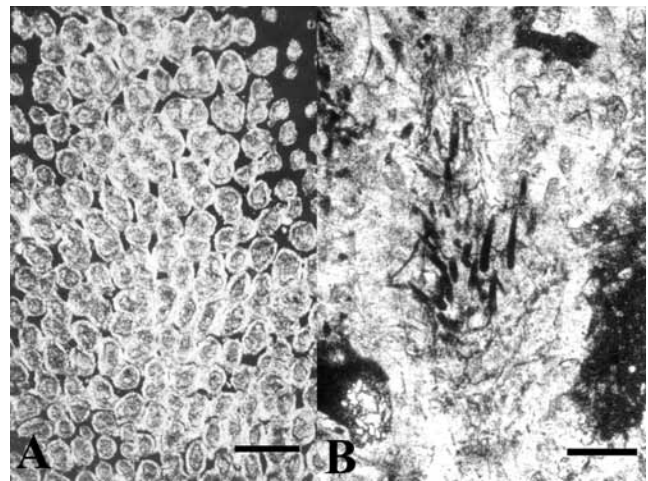


Fig. 21. A, *Murania merbeleri* from the Barremian Schrätenkalk (Bavaria, Germany) exhibits a calcitic basal skeleton (scale 1mm). B, This sponge shows the same spicule types and arrangements as *M. kazmierczaki* (scale 100 μm).

the species *Murania kazmierczaki* Reitner, 1992. The basal skeleton is constructed of a fibrous aragonite and the spicules are subtylostyles (Fig. 20). A good example of a Cretaceous representative is *Murania merbeleri* Scholz, 1984 from the Barremian Schrätenkalk reef facies (Fig. 21). The Milleporellida became extinct at the Cretaceous-Tertiary boundary.

Acanthochaetetes Fischer, 1970, a Lower Cretaceous Spirastrellid Coralline Demosponge. The modern representative of this taxon is the chaetetid *Acanthochaetetes wellsi* Hartman & Goreau, 1975, which has been associated with the Recent genus *Spirastrella* by Reitner (1991) but requires further molecular corroboration. The basal skeleton is made of high-Mg Calcite (15–19 mole% MgCO_3) with a generally tangential lamellar growth patterns (Reitner & Gautret, 1996). Only the 0.5–1 mm thick youngest generation of the calicles of the 'chaetetid'-type basal skeleton is occupied by the living soft tissue. *Acanthochaetetes wellsi* has an extremely slow growth rate of the basal skeleton of 50 $\mu\text{m}/\text{yr}$. The

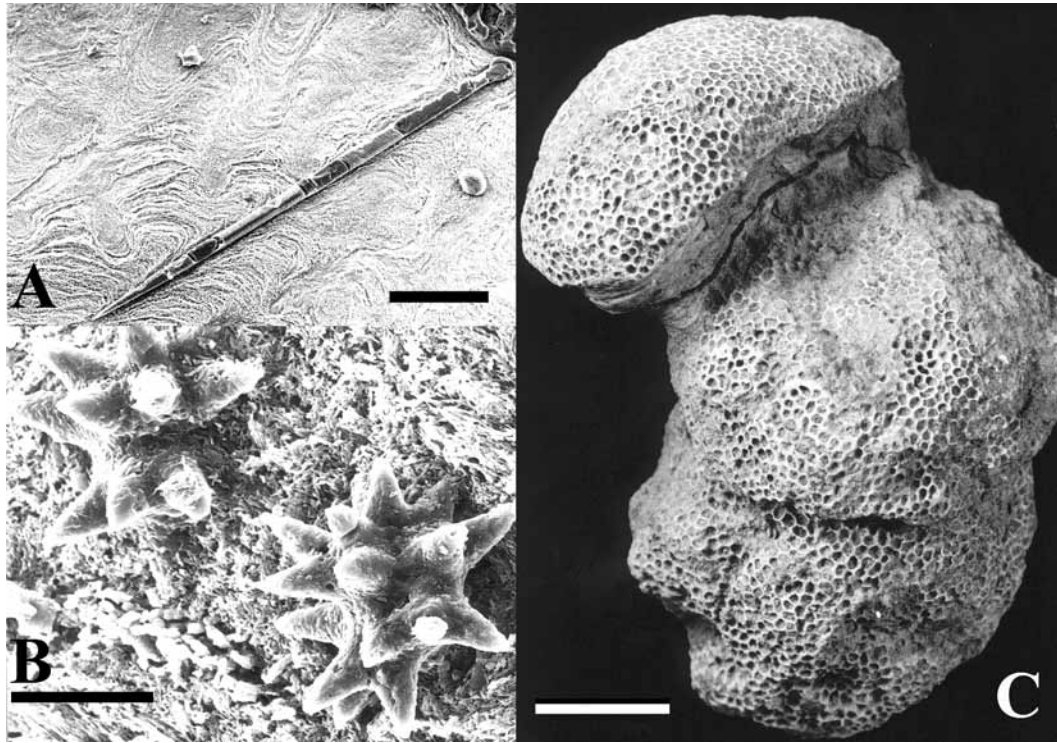


Fig. 22. *Acanthochaetetes* is an ultra-conservative taxon, which occurs first in the Lower Cretaceous of northern Spain. A, taxa from the Albian (Lower Cretaceous) incorporate parts of their spicular skeleton in the high Mg-calcite basal skeleton (scale 100 μm). B, the spicular skeleton is composed of hadromerid tylostyles and spiraster microscleres (scale 20 μm). C, Cretaceous specimen of *Acanthochaetetes* (scale 1 cm) (from Reitner & Engeser, 1997; Reitner, 1992).

soft tissue and basal skeleton exhibit a vertical anatomy divided in six major zones. The formation of the basal skeleton can be summarized as below (Reitner & Gautret, 1996).

(1) At the uppermost position there is a thick crust-like layer of spiraster microscleres (dermal area, zone I), and tylostyle megascleres which are arranged in clearly plumose bundles, demonstrating its alleged close relationship to the bauplan of Recent *Spirastrella*.

(2) Below the outer dermal area, the internal dermal area (zone II) is formed by mesohyle tissue, devoid of choanocyte chambers, and enriched in mobile cells. Large inhalant chambers (lacunae) and distributing canals cross this zone, serving the choanosome with water filtered through the ostiae. The choanosome is characterized by very large choanocyte chambers (80–100 μm). The mesohyle is characterized by large cells (ca. 10 μm) containing numerous inclusions (LCG: large cells with granules), and lying directly on the calcareous skeleton (Reitner, 1992; Reitner & Gautret, 1996). Mesohyl bacteria are rare (ca. 5% of the mesohyl biomass) and they are very small (500 nm). These highly mobile cells are undoubtedly responsible for the secretion of collagen fibres and they probably derive from a special type of lophocyte. Collagen fibres form strong bundles which traverse the basal pinacocyte layer, and anchor into the rigid skeleton (Vacelet & Garrone, 1985). Thin collagenous fibres produced by non-modified lophocytes are widely dispersed within the intercellular mesohyl. They condense and become organized into a frame-building matrix at the top of the walls and they stay entrapped inside skeletal structures after calcification. Calcite formation occurs as soon as these two types of fibres are present, supporting the interpretation that they have an ability to attract bivalent cations. However, the acicular shape of crystals and the

highly organized microstructure, both characteristic of the *Acanthochaetetes* skeleton, were never observed in these places. Skeletal formation starts inside the uppermost fibre template in the form of a soft structure in which elements have the shape and size of the future characteristic *Acanthochaetetes* crystals, but these are not rigid, and they look like ‘cooked spaghetti’ (Reitner & Gautret, 1996). This random structure becomes calcified and organized when a mucus is secreted in the narrow space between the basopinacoderm and the calcified skeleton, by the pinacocytes which are forming the most basal continuous cell layer. This mucus is highly soluble, making direct observations difficult to perform with electron microscopy. It is not preserved in TEM preparations and at best, it can be recognized with the SEM through the collapsed clumps which are closely related spatially to growing crystals in very well fixed specimens.

(3–5) The central part of the tubes (zone III) is characterized by the choanosome which exhibits large choanocyte chambers (80–100 μm) leading to large oscular channels. Few tylostyles are normally present. Typical for a ‘chaetetid’ skeletal type is the occurrence of tabulae stopping the tubes (zone IV). These are formed by the basopinacoderm, first as a thin organic phragma or sheet. Below the choanosomal zone, LCG cells become enriched and produce the mineralization of the organic sheet. Continuous upwardly moving basopinacoderm form a space filled with Ca^{2+} -binding and mineralizing organic mucus. This mineralization process happens only when LCG cells are present (Reitner, 1992). Within the closed spaces between tabulae, they contain accumulations of modified archaeocytes with numerous storage granules (thesocyte-like cells) and few spiraster microscleres (zone V). These cells may play a role in regeneration processes (Vacelet,

1985, 1990; Reitner, 1992), making the sponge able to start growing again when it has been drastically damaged.

The 'chaetetid' basal skeleton has a very specific function as a protective and resting body for special omnipotent cell types (thesocytes, archaeocytes), which are enclosed between two tabulae in a calicle (internal 'gemmulae'). This strategy allows the sponge to survive environmental crises. Due to this survival strategy the sponges may have many buds, representing a starting point for new growth on the top of one calicle.

The oldest known Recent specimen from a deep submarine cave of Cebu (Philippines) has individual age of more than 600 years.

The taxon *Acanthochaetetes* is very conservative and the first fossil record is known from the Lower Cretaceous (Fischer, 1970; Reitner, 1982, 1990; Reitner & Engeser, 1983). In contrast to the most aragonitic species of coralline sponges, this taxon has a continuous record since the Lower Cretaceous. During the Cretaceous three ecological niches were occupied, a shallow marine open water environment (*Acanthochaetetes ramulosus*), deep fore reef environment (cf. *A. seunesi*), and cryptic niches (*A. seunesi*). In contrast to modern *Acanthochaetetes* the Cretaceous species incorporate parts of their spicular skeleton within the basal skeleton (Reitner & Engeser, 1986) (Fig. 22).

CONCLUSIONS: MAJOR TRENDS IN THE EVOLUTION OF NON-LITHISTID DEMOSPONGES

The main problem in interpreting trends in evolution of non-lithistid demosponges is that their fossil record is generally poor and discontinuous for most taxa, and most palaeontologists are not able to recognize sponge spicules within sediments. Therefore, our knowledge of non-lithistid demosponges, and also of the coralline sponges, is poor, because only few bear spicules that allow a more-or-less unequivocal classification within the modern taxonomic framework. However, some trends are recognisable. Available evidence suggests that the first demosponges occur in the Late Proterozoic, with forms characterized by bundles of long monaxonic spicules. In the Early Cambrian spherical forms with long styles occur (*Choia*) and represent probably the stem line of the Phanerozoic demosponges. It is possible, or even likely, that some Archaeocyatha are demosponges, based on the occurrence of occasional tetractinellid spicules incorporated in the basal skeleton, but this interpretation requires further corroboration. In the Early Cambrian the tetractinellids diversified with the taxon *Astrophorida* (Geodiidae). At this time the first 'keratose', hadromerid and

'axinellid' sponges also radiated. In the Middle Devonian the first modern forms of Dendroceratida, 'axinellids' (mostly halichondrids), and the first haplosclerids occurred. Most of the Lower Palaeozoic stromatoporoids are probably demosponges although this also requires further corroboratory evidence given that in all except one form spicules are missing. An important boundary for the demosponges is the Late Devonian extinction event which caused a complete renovation of demosponge communities. In the Early Carboniferous most of the main modern demosponge taxa were present. The first Poecilosclerida are known from Permian sediments. Notably, most of the stromatoporoids became extinct during the Late Devonian extinction event and were replaced by the 'chaetetid' body plan. Most Carboniferous 'chaetetids' are representatives of the Hadromerida. In the Permian, coralline demosponges became very important and this development continued into the Triassic. Most of the spicule-bearing coralline sponges are 'axinellids', and most of these can be associated with halichondrid taxa, with only one appearing to be more closely related to the modern Poecilosclerida and some more closely related to modern Haplosclerida. The Late Permian and the Triassic, especially the Late Triassic, are the main eras for coralline demosponge radiation and dominance, in which some modern taxa occur first (*Ceratoporella*, *Astrosclera*, *Vaceletia*). At the Triassic-Jurassic boundary another fundamental change occurred to demosponge communities. Remarkable is the disappearance of the ceratoporellids and astrosclerids, which did not reappear again until the Pleistocene, 200 my later. In the Late Jurassic the freshwater environments were occupied by particular marine demosponges, mostly Haplosclerida. This was the last innovation in demosponge phylogeny until Recent seas. The importance of coralline demosponges as primary reef-builders decreased up to the Late Cretaceous. Today, nearly all coralline sponges are restricted to cryptic or deep marine environments and are considered to be relicts or 'living fossil' taxa. Their further study certainly holds clues to fossil sea environmental conditions and evolutionary trends within Porifera.

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