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†Fossil Hexactinellida: An Overview

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Hexactinellida (Porifera) are known from hexactin spicules from the Late Proterozoic of Mongolia (Brasier *et al.*, 1997) and China (Steiner *et al.*, 1993), possibly representing the oldest lineage of animals alive on earth today. Hexactinellida flourished and radiated rapidly during the Middle Cambrian times, giving rise to many new taxa and new skeletal plans (Rigby, 1986c; Walcott, 1920). Our knowledge of Early Paleozoic Hexactinellida is largely derived from isolated spicules from sediments. Both Amphidiscophora and Hexasterophora are known since the Early Paleozoic but most Paleozoic families did not survive the Paleozoic-Mesozoic boundary. Lyssacinosida are the first Hexactinellida known since the Proterozoic. They are an ultra-conservative group and their body plan still exists in living species today. The first representatives of Hexactinosida are known since the Devonian, with maximum radiation and diversity occurring during the Mesozoic. The first lychniscosidan sponges were described from the Middle Jurassic of Europe and during the Cretaceous where they reached their maximum peak of diversity. After the Jurassic-Cretaceous there has been a gradual decline in diversity leading up to the present. The present overview discusses about 120 genera in 18 families and two orders.
Keywords: Porifera; Hexactinellida; Amphidiscophora; Hexasterophora; Reticulosida; Lyssacinosida; Hexactinosida; Paleozoic; Mesozoic; fossil taxa.

PALEOZOIC HEXACTINELLIDA

History

Hexactinellida were not very diverse during the Early Paleozoic, certainly compared to later sponge faunas. The various species often differ remarkably in their spicule organisation, leading to the creation of many families containing only one or two genera and often monotypic. However, the fact that much of the fossil record from this era consists only of isolated spicules, with few whole-body remains, the systematics and position of these Early Paleozoic taxa are fairly unstable, having changed often over the last few decades, and as they are likely to change again in the future.

Both extant higher taxa the Amphidiscophora and Hexasterophora were present since the Paleozoic. Hexasterophora occur from the Ordovician (Mostler, 1986; Kozur *et al.*, 1996). Amphidiscophora are known since the Silurian (Mehl, 1996). Two major groups are recognised from the Paleozoic: Reticulosida and 'Rossellimorpha'. The order Reticulosida includes the two paleozoic superfamilies Protospongioidea and Brachiospongioidea, erected by Finks (1960). The superfamily Protospongioidea Finks, 1960 comprises the following families: Protospongiidae, Teganiidae, Dictyospongiidae, Hyphanteniidae and Stereodictyidae. Finks (1960) also included the family Vauxiidae within this superfamily, but after thorough re-examination of the Middle Cambrian sponges of the Burgess shale (British Columbia, Canada) Rigby (1986c: 17) moved the Vauxiidae to the Demospongiae order Verongida (Subclass Ceractinomorpha), given that it lacks mineralized spicules. *Vauxia* spp. have a skeleton of pith-cored fibres, as in living *Verongia* (Rigby, 1986c: 17) (=*Aplysina*). The superfamily Brachiospongioidea Finks, 1960 contains the following families: Brachiospongiidae, Stiodermatidae, Docodermatidae, Stromatidiidae and Pileoutidae.

Reid (1958a) erected the order Reticulosa, characterized by different Paleozoic groups of Hexactinellida with a reticulate organisation of their hexactin, stauractin or even diactin spicules. Mostler (1986) moved to his new taxon Reticulosida the Protospongiidae, Teganiidae, Dictyospongiidae Hyphanteniidae, Stereodictyidae, Brachiospongiidae, Stiodermatidae, Docodermatidae, Stromatidiidae and Pileoutidae. However, Mehl (1996: 25) suggested that the superfamilies Protospongioidea and Brachiospongioidea are paraphyletic as their members contain amphidiscs as well as hexasters, and thus she refuted this classification in order to align fossil systematics with a Recent classification.

At the Permian-Triassic boundary most of the Paleozoic hexactinellid sponge groups died out. Only the Docodermatidae continued into the Mesozoic, where they finally died out in the Late Jurassic (Mostler, 1986), and where they are known only from isolated spicules.

ORDER RETICULOSIDA REID, 1958

Scope

Both the superfamilies Protospongioidea and Brachiospongioidea are united in the order Reticulosida. As their members contain both amphidisc as well as hexasters, this taxon is polypyhletic and should be used only in a descriptive sense (Mehl-Janussen, 1999).

SUPERFAMILY PROTOSPONGIOIDEA FINKS, 1960

Definition

Globular to vasiform, sometimes prismatic sponges with a thin body wall; skeleton composed of simple hexacts or reduced derivatives of hexacts, of one or more orders of size and in one or more layers; if the spicules are uniformly oriented, their parallel rays commonly overlap; in some forms stout, continuous bundles are formed from greatly elongated overlapping rays; monaxial prostalia frequently present; root tuft commonly present (Finks, 1960: 101).

FAMILY PROTOSPONGIIDAE HINDE, 1887

Type species

Protospongia fenestrata Salter, 1864 (Cambrian – Ordovician)

Age

Middle Cambrian – Early Devonian.

Scope

Protospongiidae contains the following genera: *Protospongia* Salter, 1864 (Cambrian – Ordovician) (Fig. 1); *Diagoniella* Rauff, 1894 (Cambrian – Ordovician) (Fig. 2).

Diagnosis

Small, conical to subcylindrical sponges with a thin wall consisting of a single layer of unfused paratangential stauractins forming regular quadrules.

Remarks

Representatives of the family Protospongiidae Hinde, 1887 occur for the first time in sediments of Middle Cambrian age (Walcott, 1920). The family comprises only two genera, with all species small (only a few centimetres in size) with very thin walls. Their shape is in general sac- or vase-like to subtubular. The sponge wall consists only of a single layer of unfused paratangential stauractins in a parallel (*Protospongia*) or diagonal (*Diagoniella*) orientation to the main axes forming regular quadrules. Choanosomal spicules are not yet developed (Rigby, 1986c; Mehl, 1996). Rigby (1986c) assumed that Protospongiids are the primitive stem group for the hexactinellids. The discovery of hexactins from lowermost Cambrian rocks of China and Australia (Wei-Ming & Qian, 1988), indicate they are an autapomorphy of Hexactinellida and that protospongiid stauractins are derived. The Protospongiidae, therefore, cannot be the stem group of Hexactinellida but are interpreted to be "a highly specialized clade of the Hexactinellida" (Mehl, 1991; 1996).

FAMILY DICTYOSPONGIIDAE HALL, 1884

Type species

Dictyospongia sceptrum Hall, 1898 (Devonian).

Age

Vendian ?, Ordovician – Early Carboniferous.

Scope

Dictyospongiidae contains the following genera (among others): *Clathrospongia* Hall & Clarke, 1898 (Middle Devonian – Early Carboniferous); *Dictyospongia* Hall & Clarke, 1898 (Late Devonian – Early Carboniferous); *Hydriodictya* Hall & Clarke, 1898 (Late Devonian – Early Carboniferous); *Tiddalickia* Rigby & Webby, 1988 (Ordovician); *Hydnoceras* Conrad, 1842 (Devonian) (Fig. 3); *Griphodictya* Hall & Clarke, 1898 (Carboniferous).

Diagnosis

Dictyospongiidae have very thin body walls which are composed of diactin and sometimes hexactin dermalia (Mehl, 1996) in a regular rectangular pattern of longitudinal and transverse spicules forming a quadrangular meshwork tracts which is similar to the dictyid type. The outer part of the wall is clearly distinguished from the inner one, which is more irregular and consists of small hexactins.

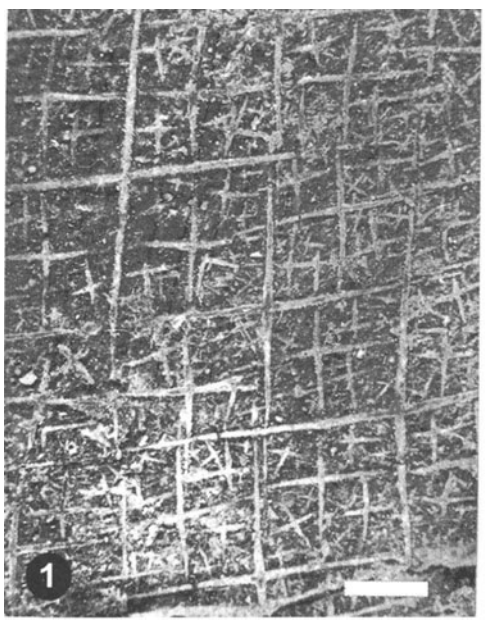

Fig. 1. Detail of *Protospongia hicksi* Hinde. Cambrian (Original of Rigby, 1966, modified after Mehl, 1996) (scale 7 mm).

Fig. 2. *Diagoniella robisoni* Rigby, 1978. Middle Cambrian, Wheeler Shale, Utah (modified after Mehl, 1996) (scale 5 mm).

Parietal gaps are not developed. The general shape of these sponges is vasiform, sometimes prismatic with eight sides, often with symmetrically arranged protuberances (Finks, 1960).

Remarks

If the Ediacara organisms of South Australia described by Gehling & Rigby (1996) are sponges, they are the first specimens with a dictyospongiid spicule architecture. The authors themselves are not absolutely sure and question their systematic placement. The first undoubted dictyospongiid sponges, however, are known from the Ordovician.

FAMILY STEREODICTYIDAE FINKS, 1960

Type species

Stereodictyum orthoplectum Finks, 1960 (Permian) (Fig. 4).

Age

Permian.

Scope

Monotypic.

Diagnosis

Skeleton composed of three sets of spicule bundles interlacing at right angles to one another. Each bundle consists of parallel monaxons or reduced derivatives of hexacts with greatly elongated rays (Finks, 1960: 107). Only sponge fragments are known. The shape is cone-like and it probably reaches sizes of 20 cm. The body wall may be 4–5 mm thick.

FAMILY HINTZESPONGIIDAE FINKS, 1983

Type species

Hintzespongia bilamina Rigby & Gutschick, 1976 (Ordovician)

Age

Ordovician.

Scope

Hintzespongiidae contains the following genera (among others): *Hintzespongia* Rigby & Gutschick, 1976 (Ordovician); *Cyathophycus* Walcott, 1879 (Ordovician); *Pleodioria* Öpik, 1961 (Ordovician); *Stephenospongia* Rigby, 1986c (Ordovician).

Diagnosis

Hintzespongiidae are characterized by two-layered wall. The dermal layer consist of hexactins, especially stauractins, arranged in a regular protospongiid manner. The inner, gastral layer consists of irregular arranged hexactins or hexactin-derived spicules. The general shape is cylindrical, sac- or vase-like and sometimes sphaeroidal. The sponges are small, not becoming larger than a few centimetres.

Remarks

Sponges of this group show characters both of the Protospongiidae (regular arrangment of stauractins) and of the Brachiospongiidae (irregular hexactins in the sponge wall), thus occupying an intermediate position between Protospongiidae and Brachiospongiidae.

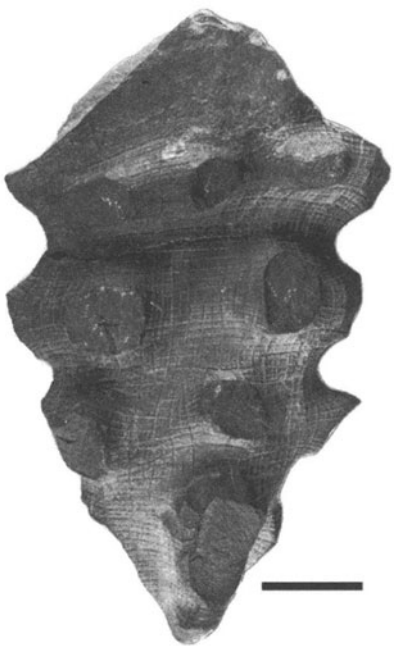

Fig. 3. *Hydnoceras* sp. Devonian (modified after Mehl, 1996) (scale 2 cm).

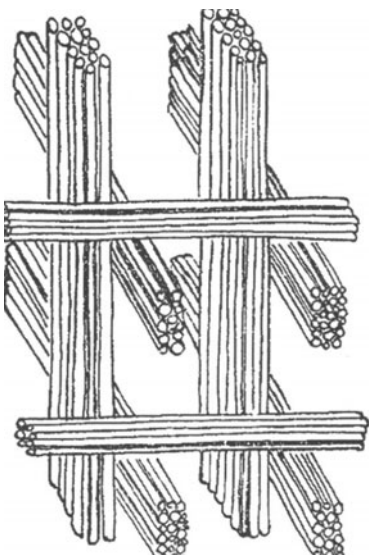

Fig. 4. *Stereodictyum orthoplectum* Finks, 1960. Permian. Part of the sponge wall showing alternate layers of horizontal and vertical spicule bundles. Atrium is towards the left (modified after Finks, 1960; Courtesy of the American Museum of Natural History).

SUPERFAMILY BRACHIOSPONGIOIDEA FINKS, 1960

Diagnosis

Vasiform sponges with large, circular, parietal gaps; specialized dermal layers of large spicules, usually pentacts, with characteristic processes on distal surface and in some species with extra tangential rays; a supradermal quadrate mesh of small pentacts or stauracts often present; interior spicules without uniform orientation (Finks, 1960: 115). Mehl (1996: 30) postulates a paraphyletic or even a polyphyletic character to the Brachiospongioidea *sensu* Finks (1960).

FAMILY BRACHIOSPONGIIDAE BEECHER, 1889

Type species

Brachiospongia digitata Owen, 1858 (Ordovician).

Age

Ordovician – Silurian.

Scope

Brachiospongiidae contains the following genera (among others): *Vaurelispongia* Rigby, 1974 (Late Ordovician – Silurian); *Twenhofella* Rigby, 1974 (Late Ordovician – Silurian); *Brachiospongia* Marsh, 1867 (Ordovician) (Fig. 5); *Strobilospongia* Beecher, 1889 (Ordovician); *Hyalostelia* Zittel, 1879 (Carboniferous).

Diagnosis

Brachiospongiidae have thick walls and a radial lobate, cup- or vase-like shape. The dermal layer consists of a fine net of stauractins in a regular quadrangular orientation. Hypodermalia are large Hexactins with long proximal rays protruding far into the sponge wall. Their distal and tangential rays are short and spherical. Parenchymal spicules are hexactins of different size and in an irregular orientation.

Fig. 5. *Brachiospongia digitata* (Owen, 1858). Ordovician (modified after Mehl, 1996) (scale 3 cm).

Remarks

Strobilospongia has a root tuft which is absent in *Brachiospongia*.

FAMILY STIODERMATIDAE FINKS, 1960

Type species

Stioderma coscinum Finks, 1960 (Permian).

Age

Permian.

Scope

Stiodermatidae contains the following genera (Mehl, 1996: 21, 31): *Stioderma* Finks, 1960 (Permian); *Hyalostelia* Zittel, 1879 (Permian); *Toomeyospongia* Rigby *et al.*, 1982 (Permian).

Diagnosis

Spicules of body wall almost entirely slender-rayed, regular hexacts, some spinose, in non-parallel alignment and never strongly fused with one another; dermalia similar but with distal, and often tangential, rays locally swollen; supradermal mesh, if present, non-quadrate and not covering the parietal gaps; gastral specialisation weak, but small oxeas in the plane of the surface may be present; well-developed root tuft present (Finks, 1960: 118). The dermalia of the type species are large hexactins with spherical distal rays and sometimes spherical tangential rays. The outer as well as the gastral surface are formed by a rigid layer of hexactins (Mehl, 1996: 21).

FAMILY DOCODERMATIDAE FINKS, 1960

Type species

Docoderma rigida Finks, 1960.

Age

Permian – ? Late Jurassic.

Scope

Docodermatidae contains the following genera: *Docoderma* Finks, 1960 (Permian); *Carphites* Finks, 1960 (Permian); *Acanthocoryna* Finks, 1960 (Permian).

Diagnosis

Dermalia very stout, often with distal excrescences and extra tangential rays; interior spicules triacts and diacts oriented parallel to the surface (Finks, 1960: 118). This family is mainly characterized by a rigid outer layer formed by dermalia fused together with the excrescences. The type pecies shows a root tuft which is 10 mm (Mehl, 1996: 21) or 50 mm (Finks, 1960: 121) thick formed by smooth monaxons longer than 200 mm (Finks, 1960: 121). General shape is thin (3 mm) to thick-walled (15 mm), cup-shaped sponges, sometimes 22 cm high.

Remarks

Hartman *et al.* (1980: 61) mention isolated spicules of docodermatids in Triassic sediments of Austria and Late Jurassic rocks of SW Germany.

FAMILY STROMATIDIIDAE FINKS, 1960

Type species

Stromatidium typicale Girty, 1909 (Permian).

Age

Permian.

Scope

Monotypic.

Diagnosis

Skeleton built of layers of pentacts with dichotomously branching rays; spicules within each layer fused into continous net; sponge not vasiform and parietal gaps not present (Finks, 1960: 136). Pentactins are horizontal arranged. Their flat and branched tangential rays are fused to one another and forming horizontal layers, so creating a rigid skeleton.

Remarks

This spicule architecture is unique within the Hexactinellida which makes a satisfying classification of the Stromatidiidae difficult.

REMARKS ON PALEOZOIC ROSSELLIMORPHA

Mehl (1997: 7) points out that 'Rossellimorpha' is not a natural monophyletic taxon but a diverse group of fossil and extant Hexactinellida characterized only by plesiomorph characters. The rossellimorph organisation is an ancient hexactinellid architecture. Thick-walled lyssacinosidan sponges mostly have spicules reduced to diactines in an irregular orientation. The diactines are often arranged tangentially to wall openings. This organisation is still today very abundant among lyssacinosidan Hexactinellids, such as among most Amphidiscophora and Rossellidae (Mehl, 1997: 7). Due to the rarity of autapomorphic characters this group defies further phylogenetic analysis.

Most of the oldest Hexactinellida belong to this group including sponges from Chengjiang (Yunnan, China) (Steiner *et al.*, 1993; Mehl & Erdtmann, 1994).

The following genera are included in this group (among others): *Hunanspongia* Qian & Ding, 1988 (Early Cambrian); *Hyalosinica* Mehl & Reitner, 1993 (Early Cambrian); *Sanshadictya* Mehl & Reitner, 1993 (Early Cambrian) (Fig. 6); *Triticispongia* Mehl & Reitner, 1993 (Early Cambrian) (Fig. 7); *Sanshapentella* Mehl & Erdtmann, 1994 (Early Cambrian); *Solactiniella* Mehl & Reitner, 1993 (Early Cambrian) (Fig. 8); *Stephenospongia* Rigby, 1986c (Middle Cambrian); *Ratcliffespongia* Rigby & Church, 1990 (Middle Cambrian); *Wongaspongia* Rigby & Webby, 1988 (Ordovician); *Malumispongium* Rigby, 1967a (Silurian); *Lumectospongia* Rigby & Chatterton, 1989 (Silurian);

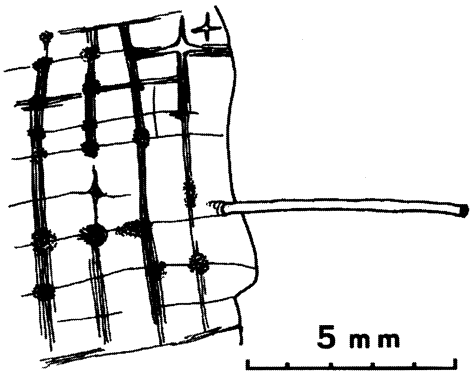

Fig. 6. *Sanshadictya microreticulata* Mehl & Reitner, 1993. Early Cambrian. China (modified after Mehl, 1996).

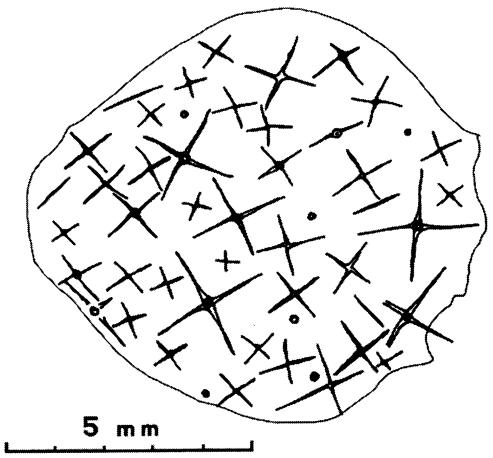

Fig. 7. *Triticispongia diagonata* Mehl & Reitner, 1993. Early Cambrian. China (modified after Mehl, 1996).

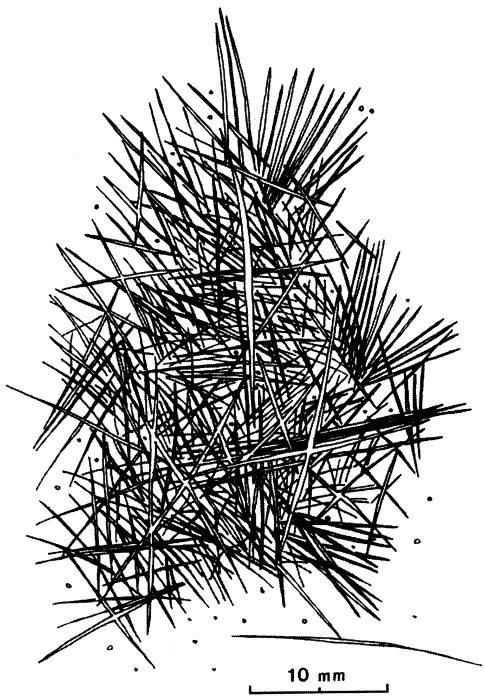

Fig. 8. *Solactiniella plumata* Mehl & Reitner, 1993. Early Cambrian. China (modified after Mehl, 1996).

Corticulospongia Rigby & Chatterton, 1989 (Silurian); *Teganiella* Rigby, 1979 (Late Devonian- Early Carboniferous) (Fig. 9); *Rufospongia* Rigby & Mehl, 1994 (Devonian); *Pileospongia* Rigby, Keyer & Horowitz, 1979b (Early Carboniferous); *Polylophidium* Finks, 1960 (Permian).

MESOZOIC HEXACTINELLIDA

ORDER LYSSACINOSIDA ZITTEL, 1877

Definition, diagnosis, scope and discussion

Refer to Tabachnick, this volume.

Age

Neoproterozoic to Recent.

Remarks

Bodily preserved Lyssacinosida are a rare exception. Usually the loose spicules desintegrate after death. Due to the low fossilisation potential of this group only a few mesozoic genera are known from the fossil record. The first mesozoic sponges mentioned (*Hexactinoderma*, *Silesiaspongia*) belonging to this group are described from the Middle Triassic of Poland (Pisera & Bodzioch, 1991). Only one taxon (*Tillichtia*) is described from the Early Jurassic of the Atlas Mountains in Morocco (Dresnay *et al.*, 1978). Three taxa (*Stauractinella, Polygonatium, Feifelia*) are known from the Late Jurassic of Europe and only *Regadrella* is described from the Cretaceous. Due to the rare fossil record no families are erected up to the present (Pisera, 1997).

Scope

The following fossil genera belong to this order: *Hexactinoderma* Pisera & Bodzioch, 1991 (Middle Triassic); *Silesiaspongia* Pisera & Bodzioch, 1991 (Middle Triassic); *Tillichtia* Dresnay, Termier & Termier, 1978 (Early Jurassic); *Stauractinella* Zittel, 1877 (Late Jurassic); *Polygonatium* Schrammen, 1937 (Late Jurassic); *Feifelia* Schrammen, 1937 (Late Jurassic); *Regadrella* Schmidt, 1880b (Cretaceous).

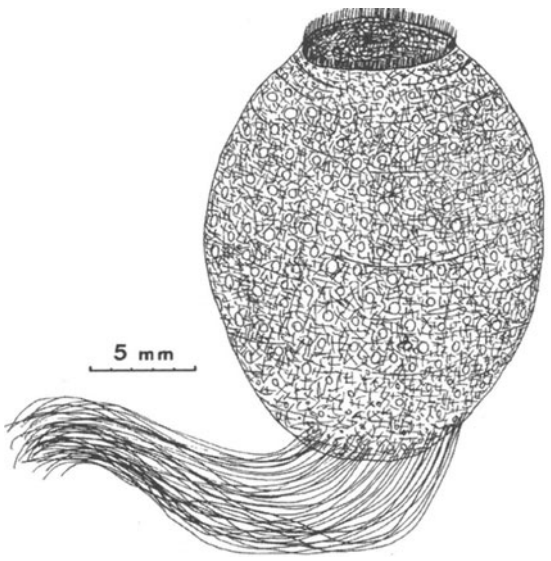

Fig. 9. *Teganiella* sp. Middle Devonian. Nevada (modified after Mehl, 1996).

ORDER HEXACTINOSIDA SCHRAMMEN, 1903

Remarks

Hexactinellida with a dictyid arrangement of the skeleton, known as Hexactinosida, appear in the Late Devonian (e.g., Pisera & Bodzioch, 1991; Rigby *et al.*, 1981; Rigby *et al.*, 2001). In Carboniferous and Permian times the fossil record of this order is extremely scarce, whereas in the Late Triassic these sponges begin to radiate worldwide. Localities are known from China (Wendt *et al.*, 1989) and the Southern Alps (Keupp *et al.*, 1989). In the Jurassic Hexactinosida radiate substantially reaching their maximum diversity during the Late Jurassic, forming (together with rare Lyssacinosida, Lychniscosida and the 'lithistid' Demospongiae) a discontinous deeper-water siliceous sponge reef belt spreading over more than 7000 km on the northern shelf of the Tethys (Krautter, 1995, 1997). After Jurassic times there is a remarkable decline in the diversity of Hexactinosida leading to the situation we have today.

Scope

Hexactinosida includes the following families known from the fossil record (see below for descriptions): Euretidae, Aphrocallistidae, Craticulariidae, Cribrospongiidae and Staurodermatidae.

FAMILY EURETIDAE ZITTEL, 1877

Type species

Eurete simplicissima Semper, 1868.

Definition, diagnosis, scope and discussion

Refer to Reiswig, this volume.

Age

Euretidae are known since the Late Jurassic with the genus *Verrucocoelia*.

Scope

Euretidae contains the following genera known from the fossil record: *Verrucocoelia* Etallon, 1859 (Late Jurassic – Early Cretaceous) (Fig. 10); *Periphragella* Marshall, 1875 (since Late Cretaceous); *Aulodomus* Schrammen, 1937 (Late Jurassic); *Pleurochorium* Schrammen, 1912 (since Late Cretaceous); *Eurete* Semper, 1868 (since Late Cretaceous); *Pararete* Ijima, 1927 (since Late Cretaceous).

Diagnosis (from Zittel, 1878)

Cup-shaped, cylindrical or branched sponges. Parenchymalia are fused hexactins. Sponge surface is not covered with a dermal layer or protected by a thickening of the outer skeletal parts.

Sometimes even covered with a very thin and fine-meshed net of fused spicules, which do not differ remarkably from those of of other skeletal parts. The reticulate dermal layer covers all 'ostia' (in the sense of canal openings). Skeletal architecture of the root portion is similar to the rest of the sponge body. 'Flesh spicules' (=isolated microscleres) are absent or present. Dictyonal framework euretoid with no primary canalization, though shallow epirhyses or aporhyses and/or ostia or postica may be formed as secondary features, or with similar but primary (intradictyonal) canalar features and sometimes also amararhyses. Sceptrules normally scopules in modern forms, but can be sarules, or be absent (Reid, 1963b).

Remarks

It is curious that Zittel (1878) included in this family *Archaeocyathus* and ?*Protospongia* among other hexactin sponges, such as *Cribrospongia* (=*Tremadictyon*), *Laocoetis* (= *Craticularia*) and *Sphenaulax*.

FAMILY APHROCALLISTIDAE GRAY, 1867

Type species

Aphrocallistes beatrix Gray, 1858b (Recent).

Definition, diagnosis, scope and discussion

Refer to Reiswig, this volume.

Age

Since the Late Cretaceous.

Scope

Aphrocallistidae contains the following genera known from the fossil record: *Aphrocallistes* Gray, 1858b (since Late Cretaceous); *Heterochone* Ijima, 1927 (since Late Cretaceous).

FAMILY CRATICULARIIDAE RAUFF, 1893

Type species

Laocoetis crassipes Pomel, 1872 (Tertiary) (Fig. 11).

Age

Since the Middle Jurassic.

Definition, scope and discussion

Refer to Reiswig, this volume.

Scope

Craticulariidae contains the following genera known from the fossil record: *Laocoetis* Pomel, 1872 (since Late Jurassic) (Figs 11–12); *Pachyascus* Schrammen, 1937 (Late Jurassic); *Pycnocalyptra* Schrammen, 1937 (Late Jurassic); *Sphenaulax* Zittel, 1877 (Late Jurassic – Early Cretaceous) (Fig. 13); *Psephosyllogus* Schrammen, 1937 (Late Jurassic); *Leptolacis* Schrammen, 1937 (Middle – Late Jurassic); *Leptophragma* Zittel, 1877 (?Jurassic, Cretaceous); *Andreaea* Schrammen, 1902 (Late Cretaceous); *Koleostoma* Regnard, 1926 (Late Cretaceous); *Stauronema* Sollas, 1877b (Late Cretaceous).

Diagnosis

Body tubular, funnel-like or cup-shaped; tubular epirhyses and aporhyses in quadrangular arrangement; strong diplorhysis, superficial dense meshwork, dictyonal euretoid arrangement of the skeleton.

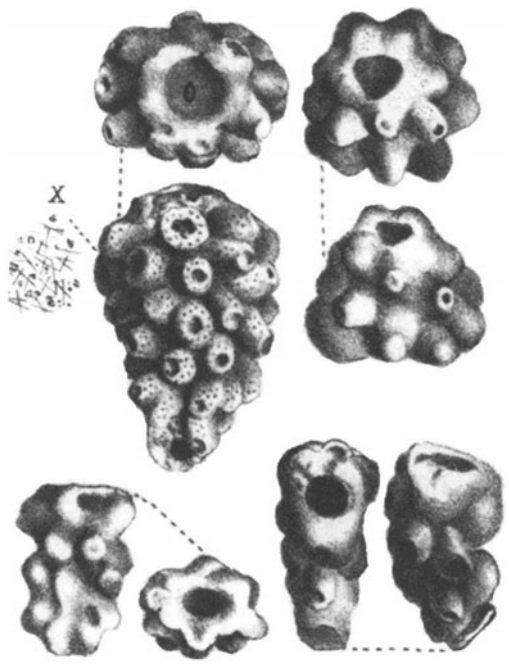

Fig. 10. *Verrucocoelia verrucosa* (Goldfuss, 1829). Late Jurassic. Germany (Original drawing from Quenstedt, 1878a) (×1.2).

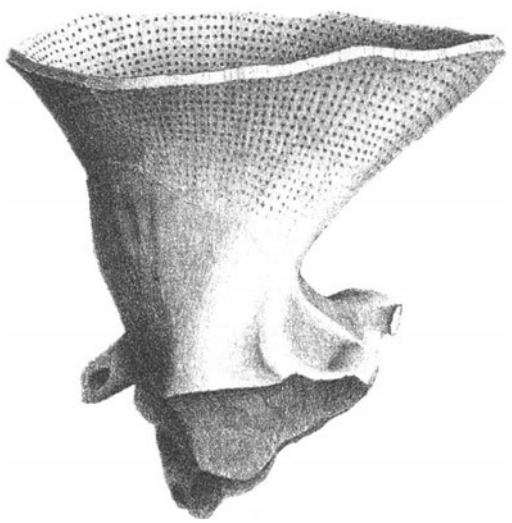

Fig. 11. *Laocoetis crassipes* Pomel, 1872. Tertiary. Algeria (Original drawing from Pomel, 1872) (height of the sponge 14 cm).

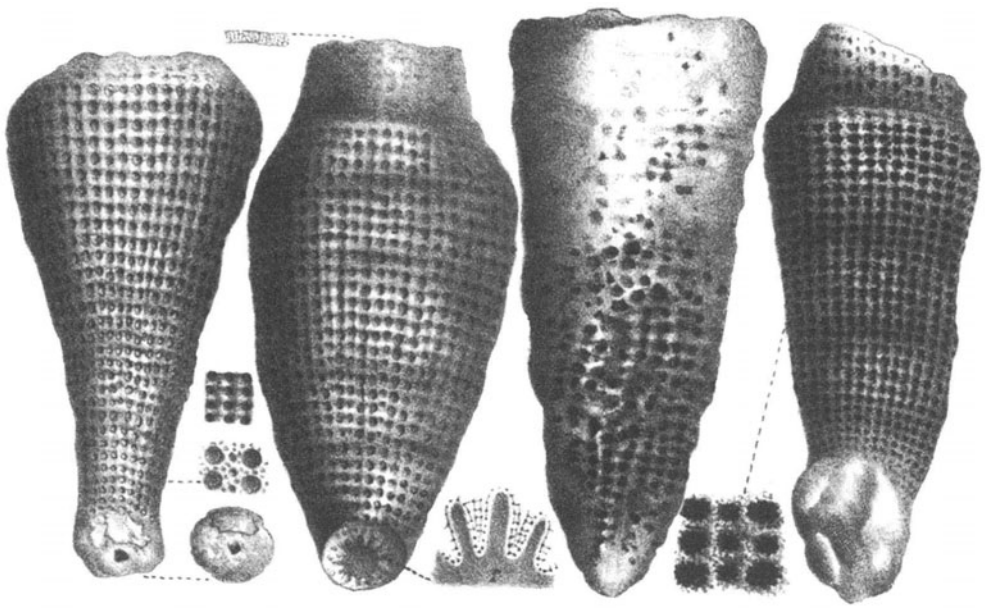

Fig. 12. *Laocoetis parallela* (Goldfuss, 1826). Late Jurassic. Germany (Original drawing from Quenstedt, 1878a) (×0.9).

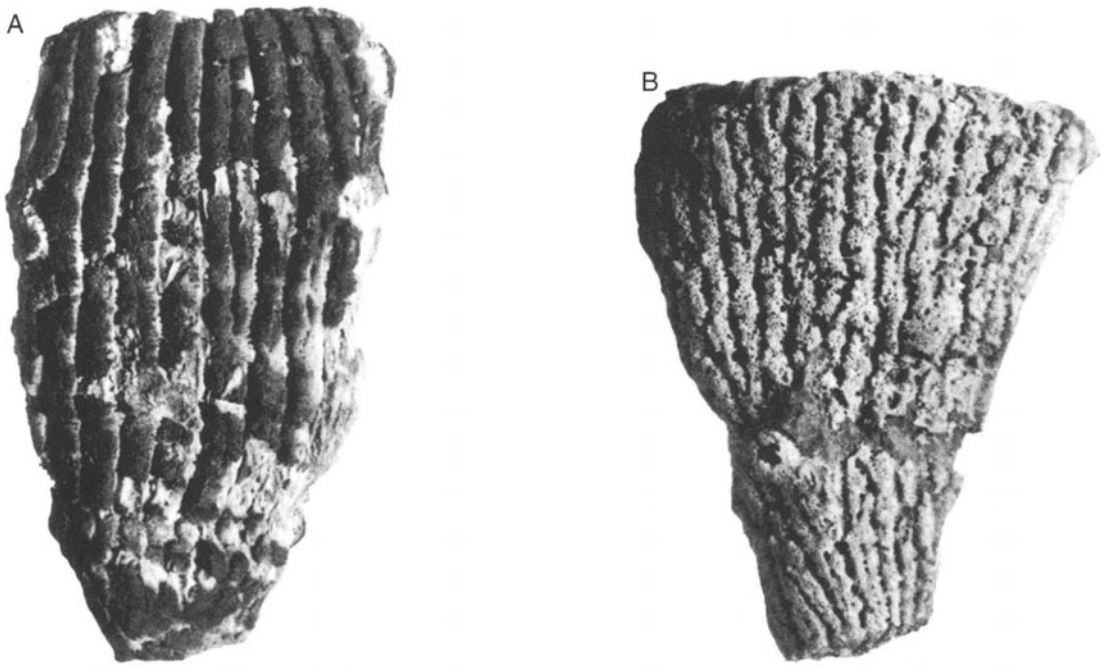

Fig. 13. *Sphenaulax* spp. Late Jurassic. Germany. A, *Sphenaulax progensis* (Schrammen, 1937) (from Schrammen, 1937) (natural size). B, *Sphenaulax costata* (Goldfuss, 1826) (from Schrammen, 1937) (natural size).

FAMILY CRIBROSPONGIIDAE ROEMER, 1864

Type species

Scyphia reticulata Goldfuss, 1826 (Late Jurassic) (Fig. 14B, C).

Definition, scope and discussion

Refer to Reiswig, this volume.

Age

Since the Late Jurassic.

Scope

Cribrospongiidae contains the following genera known from the fossil record: *Cribrospongia* d'Orbigny, 1849 (Late Jurassic – Cretaceous) (Fig. 14); *Tremaphorus* Schrammen, 1937 (Late

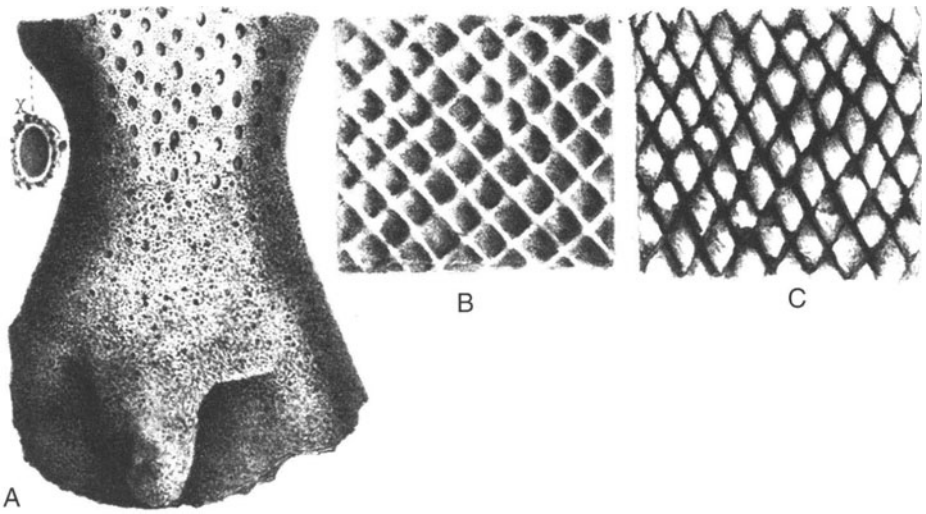

Fig. 14. *Cribrospongia* spp. Late Jurassic. Germany (Original drawing from Quenstedt, 1878a) (×0.9). A, *Cribrospongia radicata* (Quenstedt, 1878). B–C, *Cribrospongia reticulata* (Goldfuss, 1826). Late Jurassic. Germany. Detail of inner surface.

Jurassic); *Walcotella* de Laubenfels, 1955b (Late Jurassic); *Ordinatus* de Laubenfels, 1955b (Late Jurassic); *Erineum* Schrammen, 1937 (Late Jurassic); *Ramispongia* Quenstedt, 1878a (Late Jurassic).

Diagnosis

Body tubular, funnel-like or cup-shaped; epirhysis and aporhysis in regular series, so that openings of epyrhyses and aporhyses show alternate (or quincuncial) arrangement; often with superficial meshwork, which is sometimes wholly dictyonal, but may include dermal or gastral pentactines (Reid, 1963b). The pentactines are stauractines fused rigidly to the dictyonal framework. Root clods may be present.

FAMILY STAURODERMATIDAE ZITTEL, 1878

Type species

Spongites lochensis Quenstedt, 1858 (Late Jurassic).

Age

Late Jurassic.

Scope

Staurodermatidae contains only one fossil genus: *Stauroderma* Zittel, 1877 (Late Jurassic) (Fig. 15).

Diagnosis

Narrow conical to cup-shaped, dictyonal euretoid skeleton irregular with large meshes, canal openings on the outer surface (2 mm wide, 4–5 mm long) in alternating rows, on the inner (gastral) surface irregular in size and arrangement, canalization shows strong diplorhysis, epirhysis labyrinthical branching and anastomosing within the framework, aporhysis similar labyrinthic and

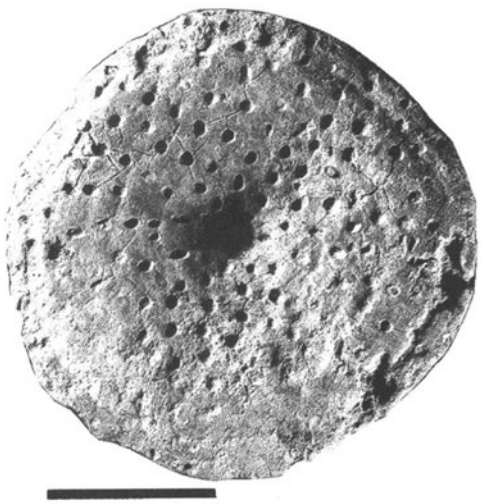

Fig. 15. *Stauroderma lochense* (Quenstedt, 1858). Late Jurassic. Spain (from Krautter, 1997) (scale 5 cm).

opening in groups into rounded cavaedial depressions in the gastral skeletal surface (Pisera, 1997; Reid, 1963b).

HEXACTINOSIDA *INCERTAE SEDIS*

Scope

The following fossil genera are listed as *incertae sedis* (among others): *Misonia* Krautter, 1996 (Early Jurassic); *Casearia* Quenstedt, 1858 (Late Jurassic) (Fig. 16); *Porospongia* d'Orbigny, 1849; emended Zittel, 1877 (Late Jurassic) (Fig. 17); *Multiloqua* de Laubenfels, 1955b (Late Jurassic); *Megalodictyon* Oppliger, 1926 (Late Jurassic); *Polypyge* Schrammen, 1937 (Late Jurassic); *Linonema* de Laubenfels, 1955b (Late Jurassic); *Nitidus* de Laubenfels, 1955b (Late Jurassic); *Rabdium* Schrammen, 1937 (Late Jurassic); *Guettardia* Michelin, 1847 (Cretaceous); *Strephinia* Hinde, 1883 (Cretaceous); *Pseudocavispongia* Hérenger, 1944 (Early Cretaceous); *Scleropegma* Schrammen,

1912 (Late Cretaceous); *Callibrochis* Schrammen, 1912 (Late Cretaceous); *Blondetia* Hérenger, 1944 (Late Cretaceous).

ORDER LYCHNISCOSIDA SCHRAMMEN, 1902

Definition, diagnosis, scope and discussion

Refer to Reiswig, this volume.

Age

Since the Middle Jurassic.

Remarks

This group includes Hexasterophora with a rigid dictyid skeletal arrangement and sometimes, or always, with perforated nodes of their hexactins so that the central part of the hexactins looks like a octohedron. This lantern-like perforation is restricted only to this group.

Scope

Lychniscosida includes the following families known from the fossil record (for descriptions see below): Cypelliidae, Sporadoscinidae, Ventriculitidae, Diapleuridae, Becksiidae and Coeloptychidae.

Fig. 16. *Casearia articulata* (Schmidel, 1780). Late Jurassic. Germany (Original drawing from Quenstedt, 1878a) (×0.9).

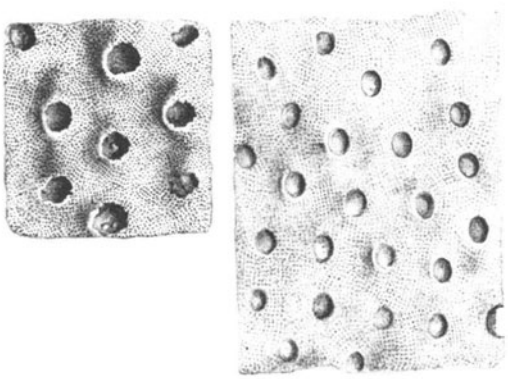

Fig. 17. *Porospongia marginata* (Münster in Goldfuss, 1829). Late Jurassic. Germany (Original drawing from Quenstedt, 1878a) (×0.75).

FAMILY CYPELLIIDAE SCHRAMMEN, 1937

Type species

Scyphia rugosa Goldfuss, 1833 (Late Jurassic).

Age

Late Jurassic.

Scope

Cypelliidae contains the following fossil genera: *Cypellia* Pomel, 1872 (Late Jurassic) (Fig. 18); *Placotelia* Oppliger, 1907 (Late Jurassic).

Diagnosis

Funnel-, conical- or plate-shaped lychniscosan sponges with well developed epi- and aporhyses variously organized. Dictyonal skeleton irregular near surface with numerous synapticulae. Dermal skeleton composed of irregularly organized pentactins fused with dictyonal skeleton and with their tangential rays (Pisera, 1997).

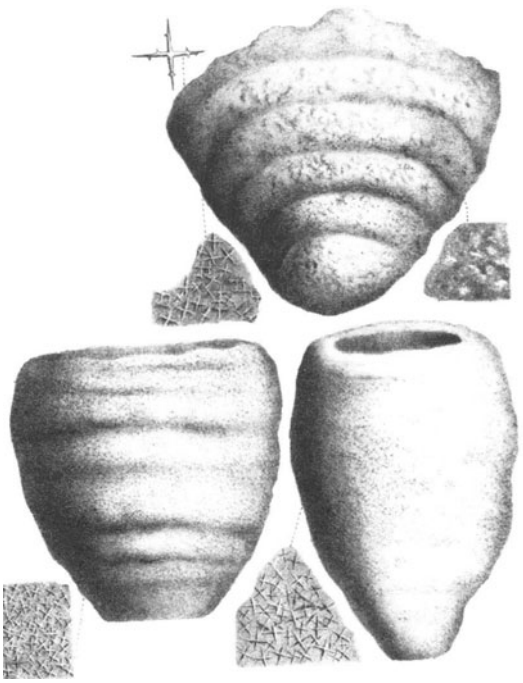

Fig. 18. *Cypellia rugosa* (Goldfuss, 1826). Late Jurassic. Germany (Original drawing from Quenstedt, 1878a) (2/3 of ×0.6).

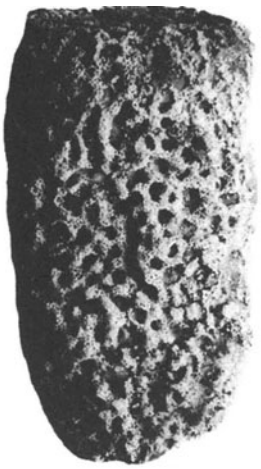

Fig. 19. *Sporadopyle pusilla* (Schrammen, 1937). Late Jurassic. Germany (from Schrammen, 1937) (4× natural size).

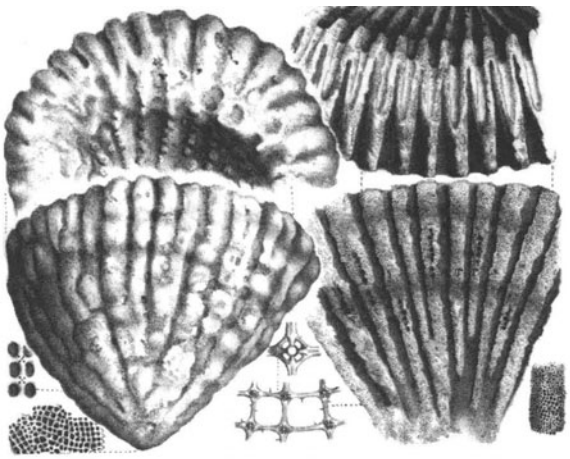

Fig. 20. *Pachyteichisma lamellosa* (Quenstedt, 1878a). Late Jurassic. Germany (Original drawing from Quenstedt, 1878a) (×0.5).

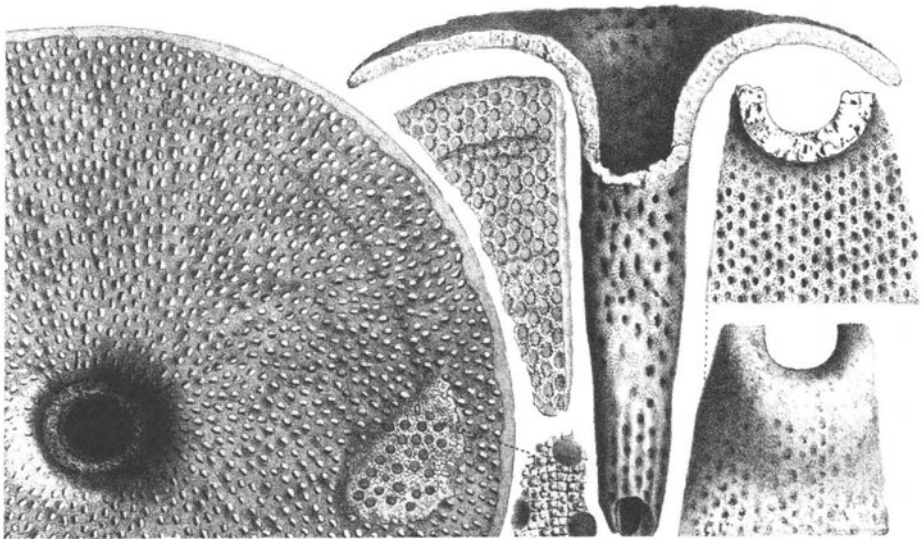

Fig. 21. *Ventriculites radiatus* (Mantell, 1822). Late Cretaceous. Germany (Original drawing from Quenstedt, 1878a) (×0.6).

FAMILY SPORADOSCINIDAE SCHRAMMEN, 1912

Type species

Scyphia retiformis Roemer, 1841 (Cretaceous).

Age

Late Jurassic – Tertiary.

Scope

Sporadoscinidae contains the following fossil genera: *Sporadoscinia* Pomel, 1872 (Cretaceous – Tertiary); *Sporadopyle* Zittel, 1877 (Late Jurassic – Cretaceous) (Fig. 19).

Diagnosis

Tube-, funnel- or cup-shaped lychniscosan sponges, canal openings on the exterior side are irregular in shape and arranged in an irregular manner whereas those of the interior side are sometimes oval and show alternate (or quincuncial) arrangement. The dictyonal skeleton is irregular, superficial gastral meshwork is developed.

FAMILY VENTRICULITIDAE SMITH, 1848

Type species

Alcynoidum chonoides Mantell, 1815.

Age

Late Jurassic – Cretaceous.

Scope

Ventriculitidae contains the following fossil genera: *Pachyteichisma* Zittel, 1877 (Late Jurassic – Cretaceous) (Fig. 20); *Desmoderma* Schrammen, 1937 (Late Jurassic); *Lepidospongia* Schlüter, 1870 (Cretaceous); *Ventriculites* Mantell, 1822 (Cretaceous) (Fig. 21); *Rhizopoterion* Zittel, 1877 (Cretaceous).

Diagnosis

Cup- or plate-shaped lychniscosan thick-walled sponges, on both sides covered with radial oriented skeletal ridges; large canal openings situated in furrows between the ridges, canals extend radially from both sides and end under the opposite side. The dictyonal skeleton is very regular showing a square meshwork (Pisera, 1997).

Remarks

The original concept of this family by Mantell (1815) was emended by Zittel (1877), and subsequently defined recently by Pisera (1997).

FAMILY DIAPLEURIDAE IJIMA, 1927

Type species

Diapleura maasi Ijima, 1927 (Recent).

Age

Since the Late Jurassic.

Scope

Diapleuridae contains the following fossil genera: *Trochobolus* Zittel, 1877 (Late Jurassic – Cretaceous); *Pachyrhachis* Schrammen, 1937 (Late Jurassic – Cretaceous).

Remarks

Pisera (1997) synonymized *Pachyrhachis* and *Trochobolus* under *Trochobolus* Zittel, 1877.

Diagnosis

Mostly conical- or cup-shaped lychniscosan sponges with original radially folded walls transformed into labyrinthically folded walls, schizorhysal canalisation, canals are crossing the wall in various angles, dictyonal skeleton is regular, no superficial meshwork developed.

FAMILY NEOAULOCYSTIDAE ZHURALEVLEVA, 1962

Type species

Neoaulocystis grayi (Bowerbank, 1867) (Recent).

Definition, diagnosis, scope and discussion

Refer to Reiswig, this volume.

Age

Since the Late Jurassic.

Scope

Neoaulocystidae contains the following fossil genera: *Phlyctaenium* Zittel, 1877 (Late Jurassic); *Cavispongia* Quenstedt, 1878a (Late Jurassic); *Centrosia* Schrammen, 1910 (Late Jurassic, Cretaceous); *Camerospongia* d'Orbigny, 1847 (Cretaceous); *Cystispongia* Roemer, 1864 (Cretaceous); *Cephalites* Smith, 1848 (Cretaceous); *Cameroptychium* (Cretaceous); *Tremabolites* Zittel, 1877 (Cretaceous).

Diagnosis

Spherical, mushroom- or plate-shaped, thin-walled lychniscosan sponge, sponge body consists of anastoming tubes, regular dictyonal skeleton, a superficial sometimes dense meshwork covering the tubes.

FAMILY BECKSIIDAE SCHRAMMEN, 1912

Type species

Becksia soekelandi Schlüter, 1868.

Age

Cretaceous.

Scope

Becksiidae contains only the following fossil genus: *Becksia* Schlüter, 1868 (Late Cretaceous) (Fig. 22).

Diagnosis

Cup-shaped, thin-walled lychniscosan sponges with cylindrical tubes surrounding a central atrial cavity. Very regular dictyonal skeleton showing a square meshwork. The rays of the dictyonal hexactins bear long, branching spines. Root-like extrusions are developed at the base. Dermal side with a dense cortex.

FAMILY COELOPTYCHIDAE ZITTEL, 1877

Type species

Coeloptychium agaricoides Goldfuss, 1826 (Late Cretaceous).

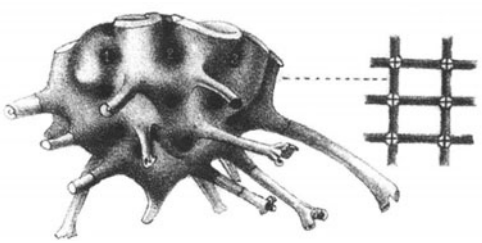

Fig. 22. *Becksia soekelandi* (Schlüter, 1868). Late Cretaceous. Germany (Original drawing from Quenstedt, 1878a) (×0.9).

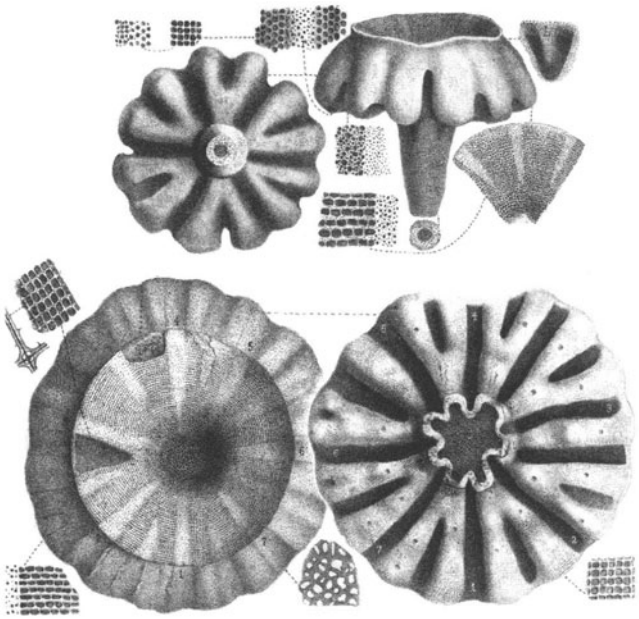

Fig. 23. *Coeloptychium* sp. Late Cretaceous. Germany (Original drawing from Quenstedt, 1878a) (×0.5).

Age

Cretaceous.

Scope

Coeloptychidae contains the following fossil genera: *Coeloptychium* Goldfuss, 1826 (Late Cretaceous) (Fig. 23); *Myrmecioptychium* Schrammen, 1912 (Late Cretaceous); *Troegerella* Ulbrich, 1874 (Late Cretaceous); *Loboptychium* Schrammen, 1924b (Late Cretaceous).

Diagnosis

Mushroom-, plate- or cup-shaped, thin-walled, stalked lychniscosan sponges. Sponge wall radially folded. Folded wall sometimes branching. Stalk diverging into a root-like base and may contain some septae which are relicts of former sieve plates. In addition, stalk may have round to oval pores with short epirhyses. Gastral surface covered with a dense dictyonal cortex. Canals are not developed. Dictyonal skeleton very regular. Dictyonal hexactins have spiny rays.

LYCHNISCOSIDA *INCERTAE SEDIS*

Scope

The following fossil genera are listed as Lychniscosida *incertae sedis*: *Xenoschrammenum* de Laubenfels, 1955b (=*Amphiblestrum* Schrammen, 1937) (Late Jurassic); *Porocypellia* Zittel, 1877 (Late Jurassic); *Rhogostomium* Schrammen, 1937 (Late Jurassic); *Coscinaulus* Schrammen, 1937 (Late Jurassic); *Lychniscaulus* Schrammen, 1937 (Late Jurassic); *Xylospongia* Hérenger, 1944 (Late Cretaceous); *Exanthesis* Regnard, 1926 (Late Cretaceous).

REMARKS ON FOSSIL HEXACTINELLIDA

The systematics of the fossil Hexactinellida remains largely unresolved, with many species and genera *incertae sedis*, as listed above, and the relationships between fossil and Recent taxa largely speculative, with continuing poor alignment between the fossil and contemporary classifications (see Reiswig and Tabachnick's contributions, this volume). This problem is related to both the quality of evidence (e.g., isolated spicules in sediments, without accompanying skeletal structures), the large gaps in knowledge of the existing fossil record, and the varying interpretations of this record by different authors, producing many different schemes.

Between the Carboniferous and Triassic the fossil record of Hexactinellida is very scarce. Only very few outcrops provide us with any useful fossil evidence. Phylogenetic hypotheses derived from this period are therefore still very vague and will certainly change in the future – including re-evaluation of existing material and incorporation of new evidence as it comes to hand. Most of the families described in this work are in urgent need of revision and interpretation in a contemporary framework. For example, most of the Cretaceous families are poorly described and even the most recent descriptions are older than 50 years. Many Recent publications dealing with sponge taxonomy are focused only on certain taxa, ignoring large portions of the existing literature. Revisions of entire families (including all constituent nominal genera – living and extinct) – is rare, with palaeontological efforts devoted mainly to certain eras/ strata, ignoring previous and subsequent faunas. However, this work is a beginning upon which future workers can build.