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Monophyly of the Porifera

By
Joachim Reitner, Göttingen & Dorte Mehl, Berlin

With 9 Figures

Abstract: The monophyly of the Porifera is well established. According to our hypothesis the Hexactinellida are the adelphotaxon of the Pinacophora (new taxon = Calcarea + Homoscleromorpha + Demospongiae). The Porifera are the adelphotaxon of the Eumetazoa/Placozoa. Sponge spicules are considered not to be a constituent character of the Porifera. Mineralized spicules developed independently within the three poriferan main taxa the Hexactinellida, Calcarea, and Demospongiae. Demospongian microscleres are not derived from megascleres in contrast to those of Hexactinellida. Accordingly, spicules probably developed several times within the Demospongiae. Remains of Porifera are known since the late Proterozoic.

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A. Introduction

According to traditional classifications, the Porifera GRANT, 1836, comprise the taxa Demospongiae SOLLAS, 1885, Calcarea BOWERBANK, 1864, "Sclerospongia" HARTMAN & GOREAU, 1972, and Hexactinellida SCHMIDT, 1870. Few attempts have been made to discuss the phylogenetic relationships between these taxa (e.g., BERGQUIST 1978; SOEST 1984, 1991; REISWIG & MACHIE 1983; VACELET 1985; BÖGER 1988; REITNER 1992; MEHL 1992). Phylogenetic systematic methodology (introduced by HENNIG 1950, 1966; improved by AX 1984, 1987, 1988) pursues intersubjectively falsificable hypotheses, since taxonomy is based on established assumptions of phylogenetic relationships. Thus systematics should deal with natural groups (= monophyla) exclusively. The methods of analysis offered by phylogenetic systematics give rise to critical re-examination of traditional taxonomic classifications within every group of organisms. As far as the Porifera are concerned, phylogenetic systematic analyses have been accomplished by specialists for various groups, e.g. the Calcarea (see REITNER 1987a), the "Sclerospongia" (shown to be a polyphyletic grouping by SOEST 1984, VACELET 1985, 1991; REITNER 1987b, 1992; REITNER & ENGESER 1987; WOOD 1987), the Hexactinellida (see SALOMON 1988; MEHL 1992), and the Demospongiae (see SOEST 1991). Only Böger (1988) made the attempt to develop a phylogenetic systematization of the Porifera as a whole, and to establish the monophyly of this taxon.

As a basic metazoan group, the Porifera might provide the key to a better understanding of the Metazoa and to a directed search for the metazoan adelphotaxon among the "Protozoa". The purpose of this paper it to establish the monophyly of the Porifera, to develop a model for their basic pattern, and to present a comprehensive and well-established phylogenetic system of this group. Further, we want to contribute to the establishment of a phylogenetic system for the Porifera by presenting an approach, that differs in many respects from and thus competies with a previous hypothesis of BÖGER (1988). The reader is encouraged to compare both hypotheses and to consider probabilities. Also we want to contribute to the discussion of possible phylogenetic implications of the Porifera with regard to hypotheses of basic patterns in the Metazoa.

B. Systematics

I. Metazoa (Fig. 9)

Recent examinations show that the status of the Metazoa as a monophylum, can be considered to be well-established. The constituent characters of the Metazoa (partly after AX 1989) are as follows:

(1) Multicellularity with cell-differentiation
(2) Oogenesis with tiny polar bodies
(3) Spermatogenesis
(4) Omnipotent cells
(5) Collagen

By character (I) in the cladogram (Fig. 9), we refer to a feature widely distributed within all major groups of organisms: Ca^{2+} detoxification (SIMKISS 1977).

The fact that Ca^{2+} seems to occur as a metabolic product within different organism groups phylogenetically as far apart as e.g. Vertebrata, Mollusca, Porifera, Protozoa, Bacteria and Cyanobacteria might be in our opinion an indication that the Ca^{2+} detoxification is a basic character of the organismic cell.

DEGENS and co-workers have proposed the idea of the Precambrian "Soda"-ocean (Na_2CO_3 dominance versus the NaCl dominance in modern ocean waters). This means high alkalinity of the seawater, in combination with minor Ca^{2+} concentrations (about 10^{-7} mol/l). At the end of the Precambrian, the soda oceanic conditions were converted into the Phanerozoic halitic oceans. This infers a rapid increase of the Ca^{2+} (10^{-2} mol/l) and further metallic ion concentrations of seawater (DEGENS 1979; Kazmierzcak et al. 1985; Kempe et al. 1989).

Within the cytoplasma of the cell, Ca^{2+} concentrations higher than 10^{-4} mol/l are toxic (DEGENS 1989). This chemical shift of seawater was probably a catastrophic event for most organisms at the late Proterozoic till the Precambrian/Cambrian boundary. In order to survive, the cells were obliged to detoxify their Ca^{2+} surplus. One possibility of detoxification is an extracellular deposition of metallic salts (e.g. $CaCO_3$) (Reitner 1992). Our hypothesis considers this character to be a symplesiomorphy of the Metazoa. It might be a potential, cryptotypic (SALLER 1952; OSCHE 1965; Sudhaus 1980) feature of all organisms. This assumption is of importance to our phylogenetic model when discussing the significance of basal skeletons in coralline sponges (KAZMIERCZAK et al. 1985; REITNER 1992).

New data supporting this hypothesis were published in MACKIE (1990). In his paper on the elementary nervous system, Mackie (1990) stated that certain ion channels, the most important pathways of ion exchange between cytoplasm and the surrounding environment, are keys to the understanding of early metazoan evolutionary history. Ion channels are specific for major groups of organisms. Presence of ion channels open for Ca^{2+} and K^+ seems to be important in all organisms from the level of *Paramecium* species (Ciliata) onwards. Na^+ ion channels do not appear until the

Cnidaria level. Yeast cells have only K^+ open ion channels and thus might represent a primordial evolutionary stage.

This observation supports the theory of Soda (Na_2CO_3) oceanic conditions of the early Precambrian oceans, indicating that ciliates and other protozoans might have evolved under conditions poor in Ca^{2+}, whereas cnidarians evolved in a modern NaCl dominated, Ca^{2+} enriched oceanic water.

II. Placozoa / Eumetazoa

The constituent characters are as follows (Fig. 9):

(6) Differentiation into dorsal and ventral epithels with belt desmosomes.
(7) Gland cells
(8) Fibre cells within the mesenchyme of the Placozoa (?), (the Placozoa may belong to a higher taxon within the Eumetazoa, and their simplicity could be the result of a secondary development, BÖGER, pers.comm.)
(9) Tissues and organs of the Eumetazoa.

III. Porifera

Monophyly of the Porifera has been the subject of some controversy. BERGQUIST (1978, 1985) considered the Hexactinellida to have arisen independently from other sponges. However, such an assumption would be a mere transfer of problems within the phylogenetic system of organisms. At any case we are inevitably confronted with the question of the adelphotaxon of the Hexactinellida or the Pinacophora respectively.

The constiuent characters are as follows (Fig. 9):

(10) Poriferan choanomeres

Originally choanocytes, but in the Hexactinellida "collar units" of choanosyncytia, each with a central flagellum surrounded by a ring of about 40 microvilli (Figs. 1 A, B). The flagellum is provided with two fibrous, wing-0: Poriferan choanomeres (originally choanocytes) with a central flagellum surrounded by a shaped appendage arranged perpendicular to the flagellar long axis (Fig. 1 b) as documented for all poriferan main taxa, although up to now only within single species: Demospongiae, e. g., *Ephydatia fluviatilis* (LINNÉ, 1758) (see FEIGE 1969; BRILL 1973); Calcarea, e. g., *Sycon ciliatum* (FABRICIUS, 1780) (see SIMPSON 1984); Hexactinellida, e. g., *Aphrocallistes vastus* SCHULZE, 1886 (see MEHL & REISWIG 1991) (Fig. 1 B), and

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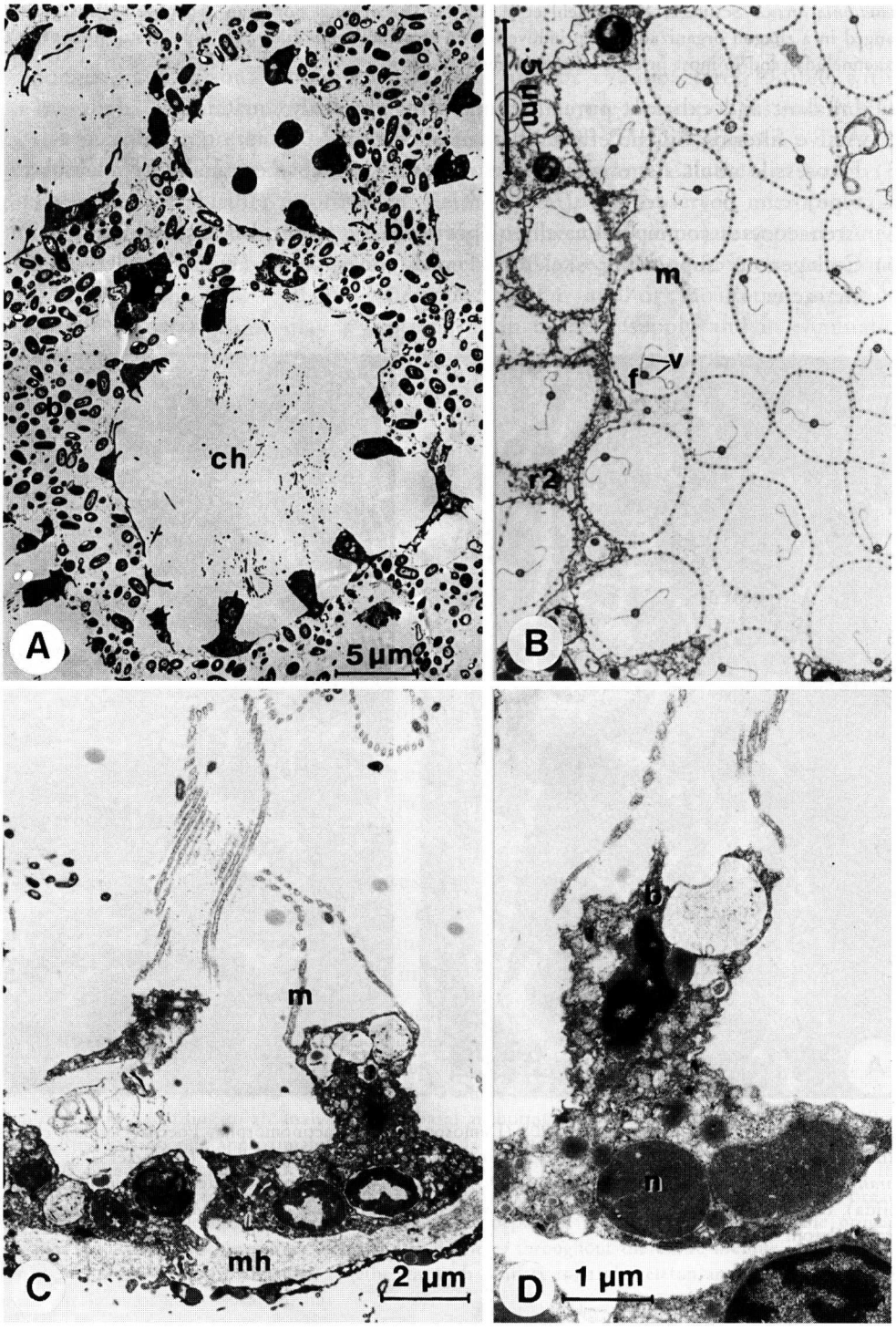
Fig. 1: Poriferan choanosomes: A) Demospongiae: *Vaceletia crypta;* choanocyte chamber (characters *10*, *20*), SEM. B) Hexactinellida (Hexasterophora): *Aphrocallistes vastus*; choanomeres (cut at the level of the secondary reticulum **r2**) with flagellar vanes (character *10*) in cross section; TEM. C, D Calcarea (Calcaronea): *Petrobiona massiliana* VACELET & LEVI, 1958, choanocyte chambers (characters *10*); TEM. – **b:** basal body, **ch:** choanocyte chamber, **m:** microvilli, **mh:** mesohyle, **n:** nucleus; **fl:** flagellum, **v:** vanes, **LM:** light microscope, **SEM:** Scanning electron microscope, **TEM:** transmission electron microscope.


A
b
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5 µm
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Schaudinnia arctica SCHULZE, 1900 (Mehl et al. 1994). The original poriferan choanosome was probably arranged in a rhagon organization, a primitive leucon structure *sensu lato*. This type is still present in the Hexactinellida, and in most juvenile demosponges.

(11) Inhalant and exhalant pores (delimited by glycocalyx material).
(12) Active filtering by the effect of flagella beating.
(13) Fixosessile adult stage with planktic larvae (probably originally of coeloblastula type).
(14) Archaeocytes (omnipotent cells of poriferan type; derived from character *5*).
(15) Collagenous supporting skeletons, partly of spongin (Fig. 3 A) (derived from character 4).

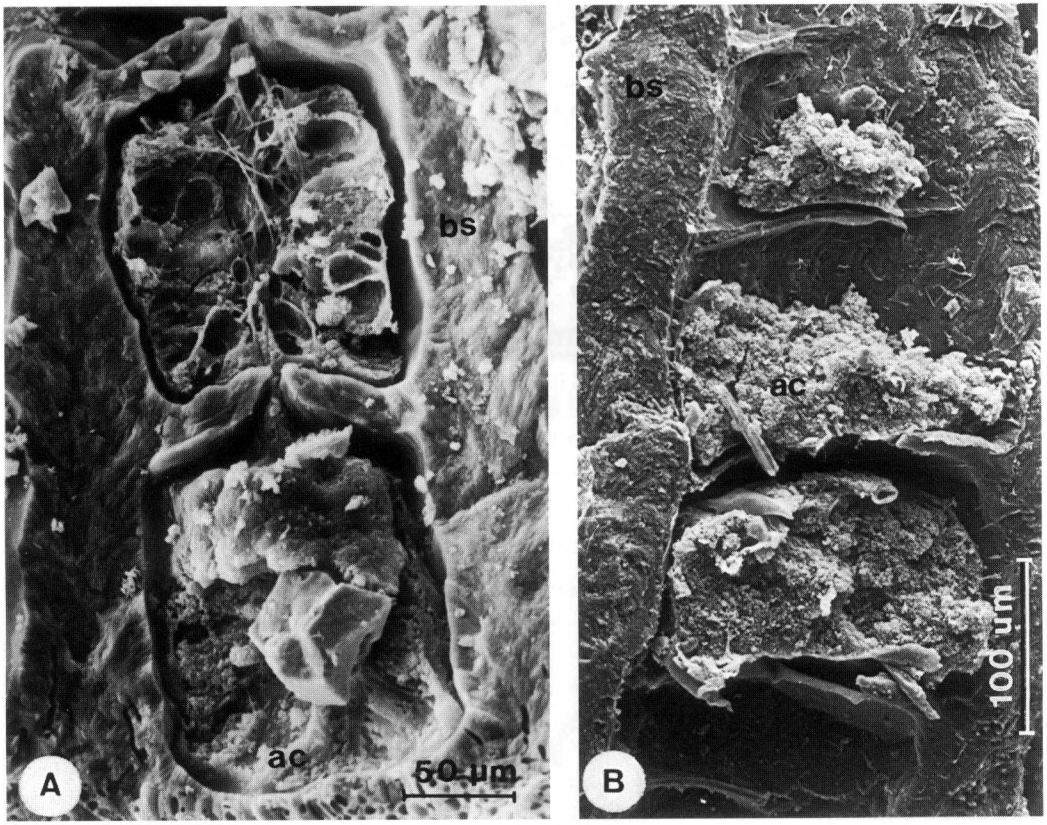

Fig. 2: A) *Merlia normani* KIRKPATRICK, 1908 (Demospongiae, Ceractinomorpha, Poecilosclerida), chamber with modified archaeocytes (character *14*) within the Mg-calcitic basal skeleton (character *21*); SEM. B) *Spirastrella (Acanthochaetetes) wellsi* (HARTMAN & GOREAU, 1975) (Demospongiae, Tetractinellida, Hadromerida), calicle subdivided by tabulae filled up with modified archaeocytes; SEM. – **ac**: archaeocytes, **bs**: basal skeleton.

1. Symbiontic microbes

All sponges have various amounts of bacteria and/or cyanobacteria located within their mesohyle. Microbes are very common in most marine demosponges and in some taxa the microbes represent 20-50% of the total biomass (Fig. 1 A, Fig. 4 A). They are less common, probably reduced, in fresh water sponges and Calcarea as well as in the Hexactinellida (further information: Reitner 1993). The observed microbial community is very strange and probably ancestral. The physiological parameters are known only from 15% of the observed taxa (Reitner 1993), i. e. that of 85% the taxonomic status is unknown. Most of microbes are aerobic and/or facultative anaerobic *Vibrio*-type bacteria which play a central role in nutrient supply and in elimination of metabolic waste products of the sponge. The phylogenetic importance of these symbionts is still unknown but it seems that microbes are an important character of the sponge animal. Despite of the importance of microbes for the vitality of the sponges, we have not enough informations on the plesiomorphic or apomorphic character of this feature upto now.

2. Spicules, a constitutive character of the Porifera?

a) Spicule formation in Hexactinellida

Within the Hexactinellida spicule secretion takes places intrasyncytially by means of an organic axial filament. Only few publications on the ontogenesis of hexactinellid sponges are basically dealing with the formation of spicules. According to Ijima (1901), Schulze (1904), and Okada (1928), hexactinellid spicules are formed within a "scleroblast mass", which contains numerous nuclei. This observation led Ijima (1901) to assume a syncytial organization in these sponges, long before this was documented ultrastructurally (Reiswig 1979).

Ijma wrote (1901: 194): "The numerous, closely packed nuclei do not differ, either in size or appearance after staining, from those of either the trabeculae or the archaeocytes. Not a trace of cell-outlines is discernible around them, which in fact makes me believe that the scleroblast mass represents a syncytium."

The primary axial filament is a semicrystalline protein fibre, which is rectangular in cross-section (Fig. 3 D). In many cases spicule features of the Hexactinellida are different from those of the Demospongiae. The largest poriferan spicule is formed by a hexactinellid sponge, the amphidiscophoran *Monoraphis chuni* Schulze, 1904, which is rooted in the substrate by a single basal spicule, about 1 cm in diameter and up to 3 m in length. According to an analysis of the basal anchoring spicule of *M. chuni* by Schulze (1904), the chemistry corresponds approximately to the formula $H_2SiV_4OV_7$. The central part of a hexactinellid spiculum is cylindriform and called "Protoshipho" by Schulze (1904) and covers the axial filament. It is surrounded by concentric opaline rings ("Siphonen") alternating with thin "Spiculin" lamellae rich in organic material. Such concentric opaline rings are continuously deposited at the outer surface of the principal parenchymal spicules, which are thus increasing in diameter throughout the entire lifetime of the sponge. Often these principal spicules are fused together by such a siliceous basal skeleton and thus form the rigid spicular skeletons of many hexactinellids.

Hexactinellid microscleres are always triaxial in origin, and they are apparently secreted in the same way as megascleres (new observation from *Schaudinnia arctica*

SCHULZE, 1900). Even amphidiscs have been shown to be reduced triaxones (Fig. 5 B). This observation is in contrast to the demospongian mode of spicule formation, and it supports the autapomorphic nature of the triaxial spicule within the Hexactinellida.

The mode of silica deposition on hexactinellid spicules (siliceous basal skeletons) seems to be analogous to a certain degree with the secretion of a cytoplasmatic Ca^{2+} surplus in calcareous basal skeletons of coralline sponges.

b) Spicule formation within the taxon Demospongiae – Homoscleromorpha
Within the Demospongiae, including the Homoscleromorpha, spicule formation partly differs from that of the hexactinellids. The spicules are of intracellar origin and are formed in general by single sclerocytes within the mesohyl. The megasclerocytes are relatively large with many mitochondria and ribosomes. They have prominent nucleoli, and well-developed Golgi bodies closely related to the silicalemma- and axial filament formation. The cells are mobile and often in contact with the pinacoderm. They are always surrounded by connective tissues (e. g. collagen or spongin) and thus, strictly speaking, represent extracellular spaces and originate directly from archaeocytes.

An organic, axial filament first develops, and the silica is deposited around it. In most cases the axial filament exhibits the semicrystalline hexagonal structure of a protein fibre. The young axial filament is surrounded by a special membrane called silicalemma. Silica deposition occurs between the axial filament and this membrane. In older spicules the membrane is no longer present, and the spicule comes in contact with other sponge tissues. The silicalemma has the function of a silica acid pump: For megasclerocytes of freshwater sponges SCHROEDER (1936) reported of small vacuoles in which gelated silicic acid is transported to the silicalemma. Within the space between the silicalemma and axial filament/spicule the silicic acid will mineralize to opaline according to the mode mineralization indicated by the organic matrix (SIMKISS & WILBUR 1989) (for further data on spicule formation see SIMPSON 1984; WEISSENFELS 1989; WEISSENFELS & LANDSCHOFF 1977; GARRONE et al. 1981).

The siliceous spicule formation is strongly affected by silica acid concentrations and the presence of Germanium. Spicules can only be formed by silicic acid concentrations in water of more than 0,005 mM (JEWELL 1935). JORGENSEN (1944) and PÉ (1973) have observed that very high concentrations of silicic acid (0,5–1 mM) inhibit the spicule formation. These observations were made on freshwater sponges (*Ephydatia fluviatilis, Spongilla lacustris*). The most favourable silica acid concentration for spicule formation found in experiments, was 0,02–0,16 mM (*S. lacustris*) and 0.25 mM (*E. fluviatilis*).

An important controlling factor of the secretion of siliceous spicules is certainly Ge concentration. SIMPSON (1990) used this feature to study diactine and monactine spicule formation under conditions of varying Ge-concentrations, to test the hypothesis of reduction of rays in a calthrop spicule during its evolution into diactines and further types. This idea is widely accepted, but there is no evidence, such as e. g. crosses of the axial filaments and central channels, as is the case in all types of hexactinellid spicules. SIMPSON found centers of silicic acid processes within diactines and tylostyles when incorporating germanic acid into the structures. This experiment exhibits that

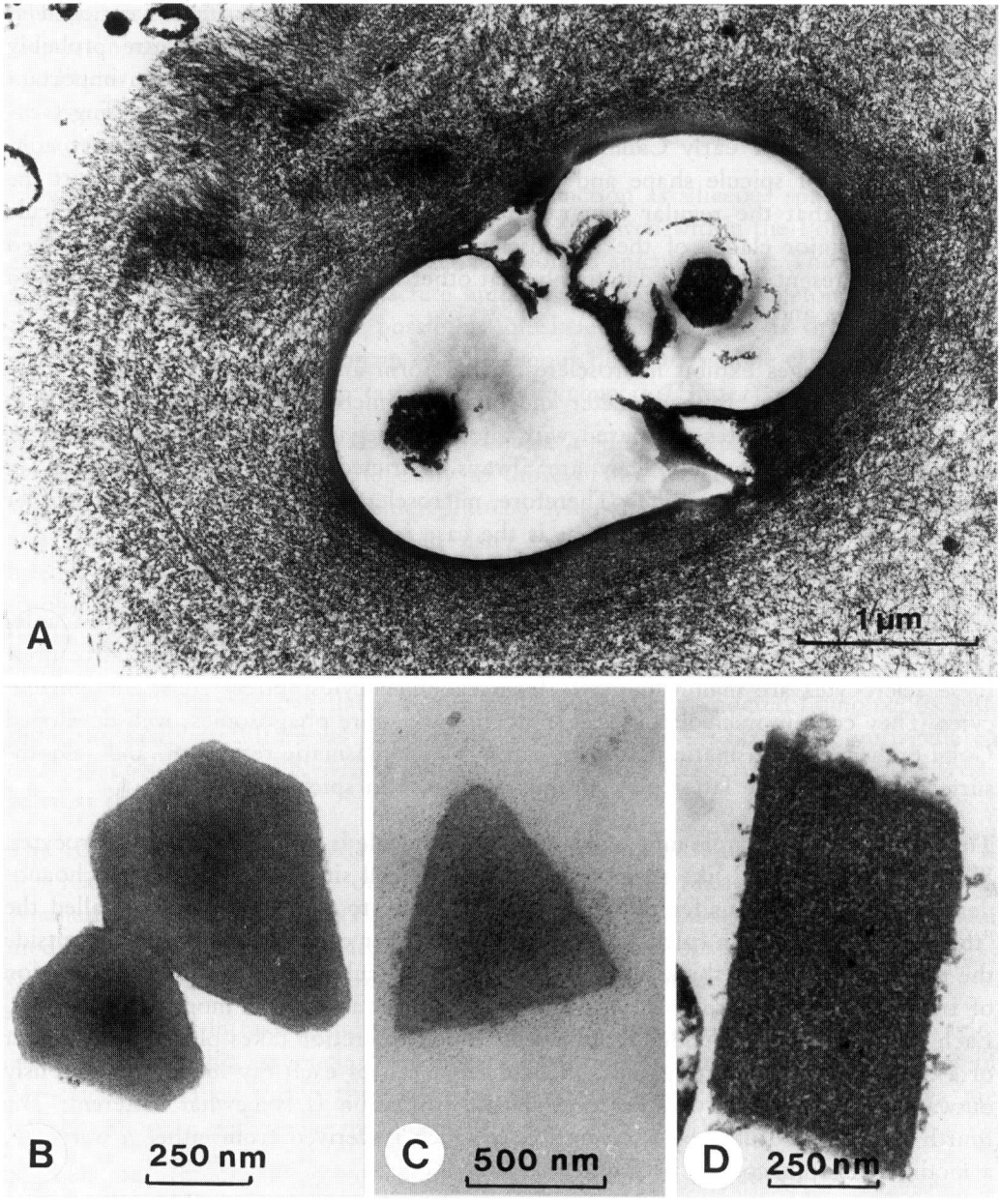

Fig. 3: Siliceous spicules with axial filaments; TEM: A) *Astrosclera willeyana* Lister, 1900 (Demospongiae, Agelasidae), two young spicules coated by spongin in cross section with hexagonal axial filaments (character *24*). B) Ceractinomorpha, poecilosclerid demosponge, two hexagonal axial filaments in cross section (character *24*). C) *Cladorhiza* sp. (Poecilosclerida), triangular axial filament in cross section (character *24*). D) *Schaudinnia arctica* (Hexactinellida, Hexasterophora), square axial filament in cross section (character *18*).

Ge is an important controlling factor of spicule formation, and silica is enriched at certain locations on monaxone spicules. These special spicule types are probably cryptotypic remains of a former tetractine spicule shape. This study is an important contribution to understand the evolution of demospongian megascleres. Varying Ge – concentrations in the early Cambrian oceans might have been an evolutionary controlling factor of spicule shape and reduction. The studies by SIMPSON support the classical idea that the regular four-rayed spicule (calthrops) is the primary spicule type. In all major clades of the Homoscleromorpha and Demospongiae four-rayed spicules are present. All these data imply that other demospongian megascleres evolved from calthrops and not vice versa.

Many demosponges exhibit microscleres. Their form and formation are autapomorphies of certain taxa. Both diameter and nuclei of microsclerocytes are smaller than those of megasclerocytes compared with those of megasclerocytes. Microsclerocytes originate from pinacocytes. They are always restricted to the mesohyl matrix, in contrast to the megascleroscytes. Therefore, microscleres in Demospongiae are neither reduced nor modified megascleres, as is the case in the Hexactinellida.

c) Spicule formation in Calcarea

Within the Calcarea, spicules of Mg-calcites are elaborated in extracellular vacuoles by special sclerocytes (LEDGER & JONES 1977). According to their internal structures, these sclerocytes are mainly derived from exopinacocytes, rarely from endopinacocytes. They contain nucleolate nuclei, mitochondria, rare phagosomes, well-developed Golgi bodies, cytoplasmatic filaments, a rough endoplasmatic reticulum, and smooth-surfaced vesicles. The latter play an important role in spicule formation.

The formation of a simple monaxone calcareous spicule is initiated by two sclerocytes. Within each cell a rod-like structure appears. The cell situated closer to the choanoderm is called the "founder cell" and the one closer to the pinacoderm is called the "thickener cell". During calcite deposition the founder cell pushes the spicule outside the tissue, whereas the thickener cell thickens the spicule during its growth. Secretion of triactine spicules takes place in the same fashion as that of monaxonic spicules. Each spicule ray is surrounded by two cells. Calcite secretion takes places in the center of a cluster of six coexisting cells, the thickener cell of each ray moves continuously outward to form the ray. Tetractine spicule formation is somewhat different: The fourth ray is constituted by a seventh cell, which is derived from either a porocyte, a modified exopinacocyte, or from an endopinococyte.

The spicules are secreted within thin organic layers separated from the mesohyl extracellurlarly within intercellular spaces. These spaces are bordered by sclerocytes, and each spicular ray is delimited by septate junctions. Each ray is secreted as a single Mg-calcite crystal. Calcium concentration of sea water is a limiting factor to spicule formation. LEDGER (1976) has described an increase of both growth rates and total amount of spicules if Ca^{2+} concentrations are increased from 1mM up to 20 mM. At 40 mM less spicules were secreted, that exhibit strange morphologies (Ca^{2+}-stress). Below 1 mM Ca^{2+} and HCO_3^- no spicules are formed.

This process might explain the absence of calcareous spicules in sediments older than Cambrian age and thus support the hypothesis of low Ca^{2+} concentration Soda oceanic conditions during the Precambrian (DEGENS 1979). During the Lower Cambrian a diverse fauna of the Calcarea (e.g.: *Gravestockia pharetroniensis* REITNER, 1992), already existed (REITNER 1992) (Fig. 7).

However, the calcitic spicules have the same function as siliceous spicules. Additionally, further modes of supporting skeletons have evolved within the Porifera: In some groups of the "Keratosa" (Demospongiae) spongin spicules occur. These spicules are not mineralized, but they are discrete units of the supporting skeleton analogous to the mineralized ones. Another possibility of skeletal supporting is the agglutination of detrital material within spongin or collagenous fibres by mobile cells. This strategy is realized in many keratosan taxa (e.g. *Phoriospongia*, *Dysidea*).

According to our hypothesis (Fig. 9), it follows *a posteriori* that hexactinellid spicules evolved convergently, and analogously to those of the Demospongiae. Alternatively, siliceous spicules might be considered to be synapomorphic between Hexactinellida and Demospongiae which were then sister taxa. This competing hypothesis would infer the reduction of the character pinacocytes within the Hexactinellida. According to observations made by BOURY-ESNAULT & VACELET (1994) on the embryogenesis of the hexactinellid sponge *Oopsacas minuta* TOPSENT, 1927, hexactinellid larvae seem to possess some kind of specialized dermal layer composed of cells. However, these "pinacocytes" are multiflagellated and cannot simply be considered homologous with the demospongian/calcareous pinacocytes. Some demosponge taxa have uniflagellated endopinacocytes, e.g. *Vaceletia crypta* (VACELET, 1977) (Fig. 6A), but never multiflagellated exopinacocytes.

The consequent regular triaxial symmetry of hexactinellid spicules (character 18) is not realized in any of the other poriferan taxa. The fundamental differences in symmetry of axial filaments (Fig. 3) in the spicules of Demospongiae (hexagonal and modified to triangular) and Hexactinellida (square), first observed by REISWIG (1971) (Figs. 3, A, B), might imply a different chemical composition.

The intracellular intrasyncytial secretion of SiO_2 demospongian + hexactinellid spicules can hardly be assumed to be homologous with the extracellular secretion of Mg-calcitic spicules within the Calcarea. In any case spicules of the Calcarea are non-homologous with those of siliceous sponges.

Spicules are not considered to belong to the poriferan basic pattern.

3. Hexactinellida

The constituent characters are as follows (Fig. 9):

16: Syncytial organization of soft tissues, including the choano-syncytia with "collar-units" separated from nucleated choanoblasts by plugged junctions (derived form choanocytes, character 10) (Fig. 4A) (MACKIE & SINGLA 1983; REISWIG & MEHL 1991).

17: A "secondary reticulum" supporting the "collar units" about midway above the microvilli basis (Fig. 4 B).
18: Intrasyncytial secretion of siliceous triaxial spicules (originally hexactins, according to the triaxial symmetry of the central canals, Fig. 5) with an axial filament square in cross section (Fig. 3 D) in all hexactinellid spicule types.
19: Parenchymella larvae (derived from 13) with stauractinic larval spicules (OKADA 1928).

All recent Hexactinellida possess hexactine spicules. In more simple hexactinellid spicules, like monactins and diactins, an axial cross can often be observed indicating their triaxial derivation (see, e. g. IJIMA 1927; MEHL 1991, 1992). Even amphidiscs are triaxial in origin (Fig. 5 B). Thus we can assume that the triaxon belongs to the hexactinellid basic pattern.

Earliest fossil record. – The Hexactinellida are the oldest Porifera documented. The earliest record of hexactin spicules is from the late Proterozoic (STEINER et al. 1993). From the lowermost Tomotian (early Cambrian) highly diverse hexactinellid sponge faunas are known (MEHL 1991, 1992; STEINER et al. 1993). A completely preserved fossil with hexactinellid affinities from the late Proterozoic Ediacaran of South Australia due to be described by RIGBY (1993, conference talk). The first definite poriferan spicules, diactins and stauractins (Hexactinellida) from the late Proterozoic of China were described recently (STEINER et al. 1993).

4. Pinacophora (nom. nov.)

This name is based on the pinacoderm cell type, which is a constituent character of the taxon. The Pinacophora comprise Demospongiae, Homoscleromorpha, and Calcarea.

We consider the term "Cellularia" (*sensu* REISWIG & MACKIE 1983) as misleading and not particularly informative, because multicellular structures are symplesiomorphic within the Metazoa.

The constituent characters are as follows (Fig. 9):

20: Pinacoderm with pinacocytes and porocytes (Fig. 6 A)
21: Ball-shaped choanocyte chambers (Leucon-organization *s. str.*) of the adult sponge (Fig. 1 A). Juveniles still show the rhagon organization.
22: Potential ability of formation of calcareous basal skeletons (from symplesiomorphy I) (Fig. 2).

a) Calcarea

Remarks on the "Sphinctozoa" STEINMANN, 1882:
The "Sphinctozoa" were erected by STEINMANN for sponges possessing thalamid calcareous basal skeletons. RAUFF (1913) presented the first definite proof of calcareous triaene spicules in the sphinctozoan skeleton of *Barroisia anastomas* (MANTELL, 1838).

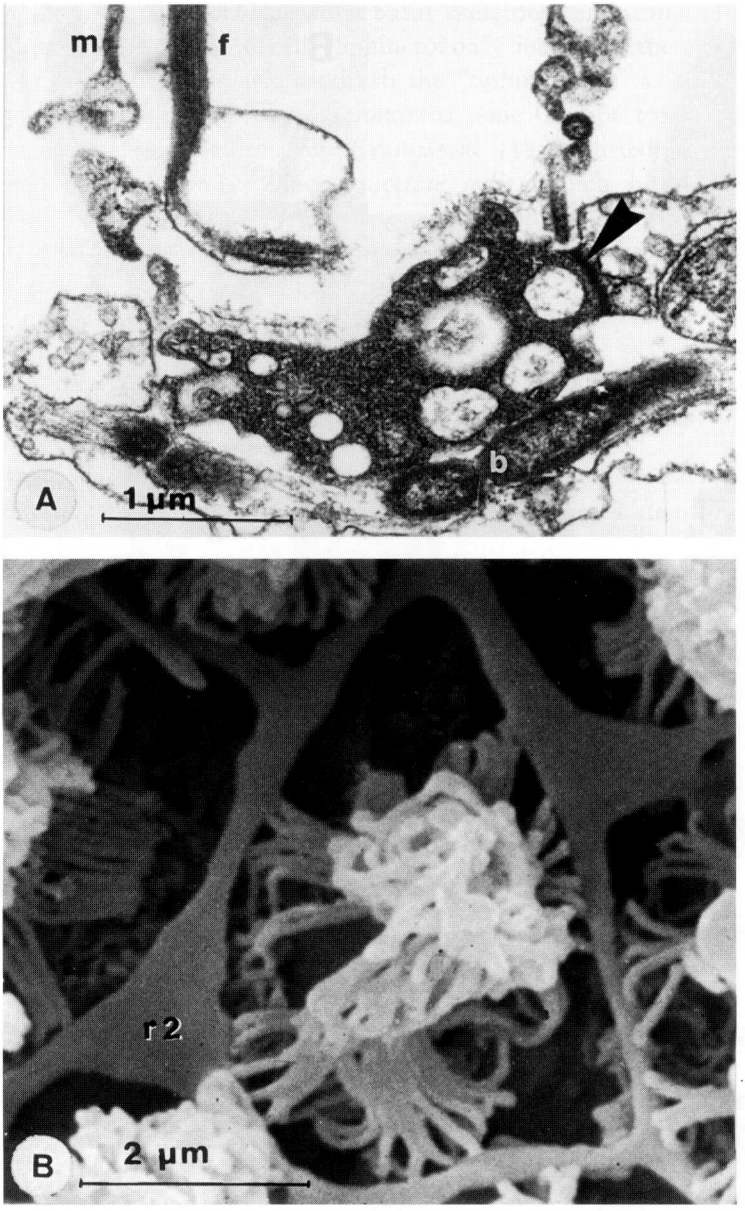

Fig. 4: Syncytial choanosomes of Hexactinellida (character *16*).: A) *Farrea occa* Bowerbank, 1862 (Hexactinellida, Hexasterophora), choanomere in cross section; collagen strands with bacteria, arrow shows semipermeable plug, which separates different syncytial areas, TEM. B) *Aulorossella vanhoeffeni* Schulze & Kirkpatrick, 1910 (Hexactinellida, Hexasterophora), collars of microvilli supported laterally by meshes of the secondary reticulum (character *17*); SEM. – **fl:** flagellum, **m:** microvilli, **ch:** nucleated choanoblast, **c:** collagen, **b:** bacteria, **r2:** secondary reticulum.

A
5 µm
B
5 µm
20 µm
C
250 µm
D
100 µm

By analyzing the internal structure of the basal skeletons, SEILACHER (1962) was able to verify the poriferan nature of all "Sphinctozoa", including the non-spiculiferous ones. However, SEILACHER did not establish the "Sphinctozoa" as Calcarea (in spite of the title of his work [1962] "Die Sphinctozoa, eine Gruppe fossiler Kalkschwämme"). In his original characterization STEINMANN (1882) listed an assemblage of Demospongiae, Calcarea and Porifera *incertae sedis*, which he attributed to five families of the so-called "Sphinctozoa"; a grouping which, according to STEINMANN himself, represents merely a morphological designation. Thus the term "Sphinctozoa" represents a polyphyletic grouping (REITNER 1990, 1992).

Constituent character are as follows (Fig. 9):
23: Extracellular secretion of Mg-calcitic spicules, originally probably triaenes (Fig. 6 B–D; Fig. 7 A–B), without any axial filament (JONES & LEDGER 1991).

a[1]) Heteractinida HINDE, 1888 (Fig. 7)
The Heteractinida, extinct since the end of the Permian, are a stem-group representative of the Calcarea. The Heteractinida first occurred in the lowermost Cambrian. In contrast to the other calcarean taxa, this group does not exhibit triaene spicules. RIETSCHEL (1968) concluded that the Heteractinida belong to the Calcarea because of the monocrystalline calcitic structure of the spicules.
The constituent characters are as follows (Fig. 9):
23 a: Regular octactine (Fig. 7 E) and irregular polyactine (Fig. 7 D) monocrystalline calcitic spicules.

a[2]) Calcinea – Calcaronea
Constituent characters are as follows (cladogram, Fig. 9):
23 b: Regular triaene and four-rayed Mg calcitic spicules

a[3]) Calcaronea BIDDER, 1898
Constituent characters as follows:
23 c: Amphiblastula larvae with true polarity, flagellated at one pole only = Calcaronea-type (derived from the coeloblastula larvae, character 13).
23 d: Choanocytes with an apical cell nucleus and the flagellum attached to the nucleus.

a[4]) "Calcinea" BIDDER, 1898
Remarks: It is difficult to establish the monophyly of the "Calcinea", because a large number of the characters are only "weak" apomorphies. Some of them are questionable, and may be symplesiomorphies. Hence, the features used to characterise this

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Fig. 5: Triaxial hexactinellid spicules from *Hyalonema* sp. (Amphidiscophora) (character *18*): A) Microamphidisc; B) Mesoamphidisc, the axial cross of the central canal exhibits the traxial derivation of these spicules, LM. C) Hexactinellid pentactin megasclere with relic of atrophied fifth ray from late Cambrian sediments of Sweden, SEM. D) Macroamphidiscs, SEM.

A
5 µm
pinc
pc
B
50 µm
C
10 µm
D
20 µm

taxon are mainly plesiomorphic (e.g. coeloblastula larva, basal cell nucleus, free flagellum).

BOROJEVIC et al. (1990) have revised the taxon "Calcinea". They presented a cladogram to establish a monophylum Clathrinida. They propose a stem group with an olynthus grade of tissue organisation which is similar to the Recent genera *Clathrina* and *Soleniscus.*

They further propose several parallel and continuous evolutionary lines in the Clathrinida. In their opinion the Murrayonida are a highly advanced taxon but they do not comment on the phylogenetic relationships of this taxon. VACELET (1991) has completed the cladogram and includes the Murrayonida taxon but without establishing the autapomorphic character.

They use constituent calcarean characters to define the subtaxon Calcinea: basinucleate choanocytes, coeloblastula larvae, regular, equiradiate and equiangular spicules, the early ontogenetic occurrence of triradiate spicules, and an olynthus grade of tissue organisation. In our opinion, all these characters, except the spicule types, are plesiomorphies.

The "constituent characters" used in this study are admittedly weak. At the present stage the "Calcinea" are, rather a paraphyletic grouping.

Possible constituent characters are as follows:

23e: Equiangular triaene spicules (Fig. 6 B) and extremely light $\delta^{13}C$ isotope values (-1 to -3,5) of basal skeletons (*Murrayona*) and spicules of Clathrinida in contrast to those of the Calcaronea ($\delta^{13}C$ -1,5 to +3) (REITNER 1989, 1992, 1993). This character indicates a strong isotopic vital fractionation during the formation of calcinean Mg-calcite spicules in contrast to the more kinetic fractionation observed in the calcaronean spicules.

Earliest fossil record - The earliest fossil record of calcarean spicules, mainly Heteractinida, is from the Lower Cambrian (Atdabanian) (RIGBY 1991). Important phylogenetic observation is the new record of regular calcitic triactine spicules with calcaronean affinities from Atdabanian archaeocyathid limestones of the Flinders Ranges of South Australia (REITNER 1991, 1992, REITNER & MEHL 1995) (Fig. 7 A–C).

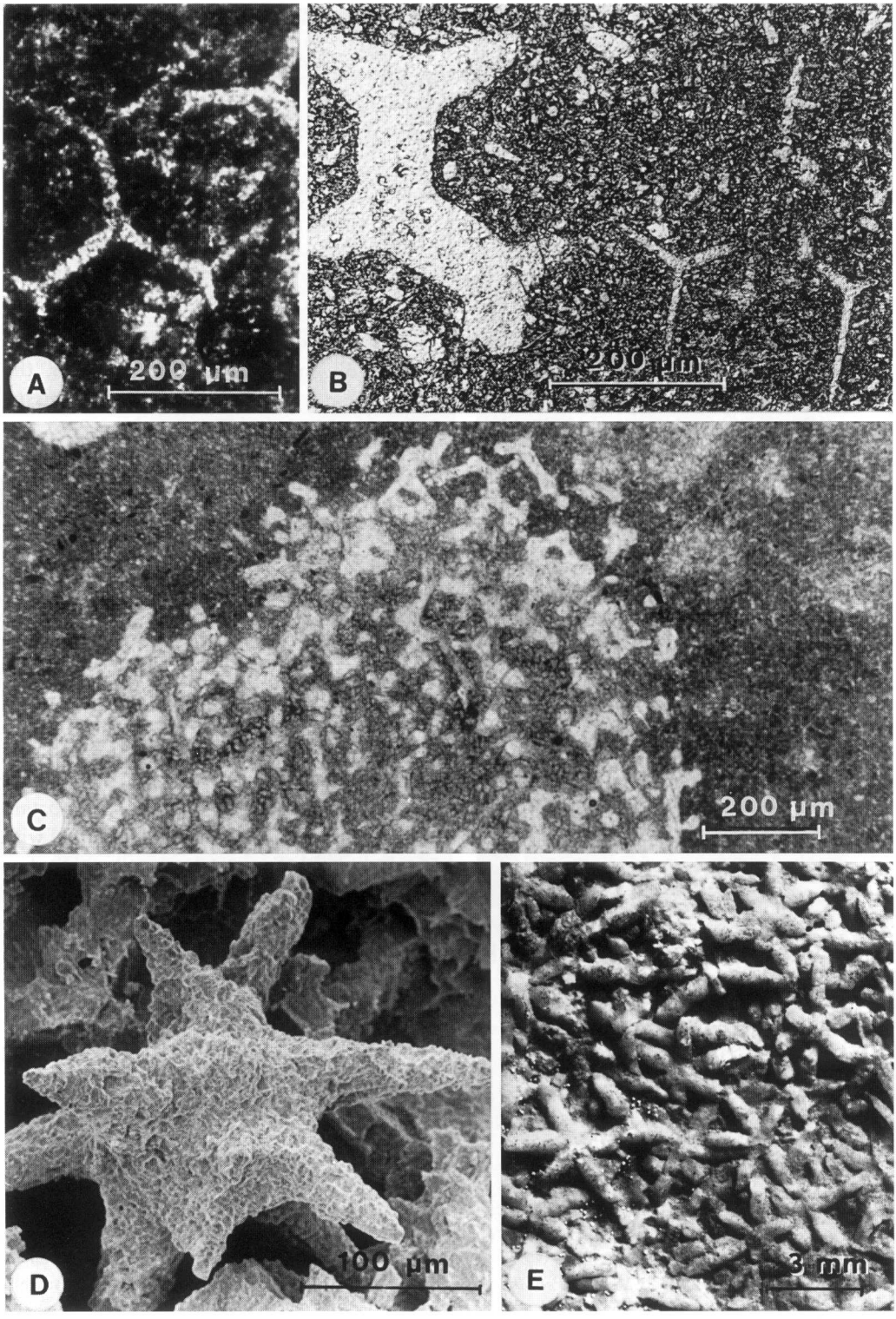
b) Demospongiae – Homoscleromorpha

The constituent characters are as follows (Fig. 9):

24: Intracellular secretion of siliceous spicules (originally regular calthrops/tetractinellid spicules and monaxons) (Fig. 6 B) by sclerocytes. The spicules possess axial filaments, which are triangular in cross section.

25: Desmatose spicules *sensu lato* (Fig. 8 A).

Fig. 6: Pinacophoran characters: A) Endopinacoderm of *Vaceletia crypta* with flagellated pinacocytes and porocytes (Demospongiae, Ceractinomorpha) (character *20*), SEM. B) *Plakina* sp. (Homoscleromorpha), calthrops spicules (character *24*), SEM. C) *Plectroninia hindei* KIRKPATRICK, 1900 (Calcarea, Calcaronea); tuning fork spicules (*23*), SEM. D) *Petrobiona massiliana* (Calcaronea, Calcarea), tuning fork spicules (character *23*), SEM. - **pinc:** pinacocytes, **pc:** porocytes.


A
200 µm
B
200 µm
C
200 µm
D
100 µm
E
3 mm

c) Homoscleromorpha

The only constituent character currently known as follows:

26: "Amphiblastula larvae" entire margin flagellated (= Homoscleromorpha-type [derived from character 13]).

d) Demospongiae

We only used species with microscleres in this study. Sponges without microscleres, e. g. the Axinellida, Halichondrida etc., have not been considered. Within the proposed cladogram these taxa are mentioned as paraphyletic. For possible taxonomic relationships of these taxa compare SOEST (1991).

The constituent characters are as follows (Fig. 9):

27: Parenchymella larvae of the Demospongiae-type (derived from character 13) with or without larval spicules, and occasionally developed choanosome. Demospongian parenchymella larvae often develop ontogenetically via a coeloblastula-stage.

28: Organic skeletons of spongin (derived from 15).

d^1) Tetractinellida

29: Aster microscleres (Fig. 8 B)

d^2) Ceractinomorpha

30: Viviparous mode of reproduction (it is questionable whether or not vivipary is a constituent character for all Demospongiae or only for certain demospongian groups).

31: Sigmatose microscleres (Fig. 8 C, D).

A main problem is the homologization of these microsclere types. DENDY (1921) presented an overview of all types of sigmatose microscleres. He regarded these scleres to be homologous. FROMONT & BERGQUIST (1990) – "When is a sigma not a sigma?" – discussed this problem in their paper entitled. In their opinion the spicules of similar form and shape are not, per se, homologous, and therefore the homology of the different sigmatose spicules is questionable. Problematic are the sinispirae with respect to their phylogenetic origin (WIEDENMAYER 1994). The main problem is the differential establishment of homology of the character in question: It must exhibit basically the same morphogenetic processes combined with genetic identity. In most cases it has been impossible, so far, to test these factors. Further arguments of FROMONT & BERGQUIST (1990) for a polyphyletic origin of the sigmatose spicules are basic

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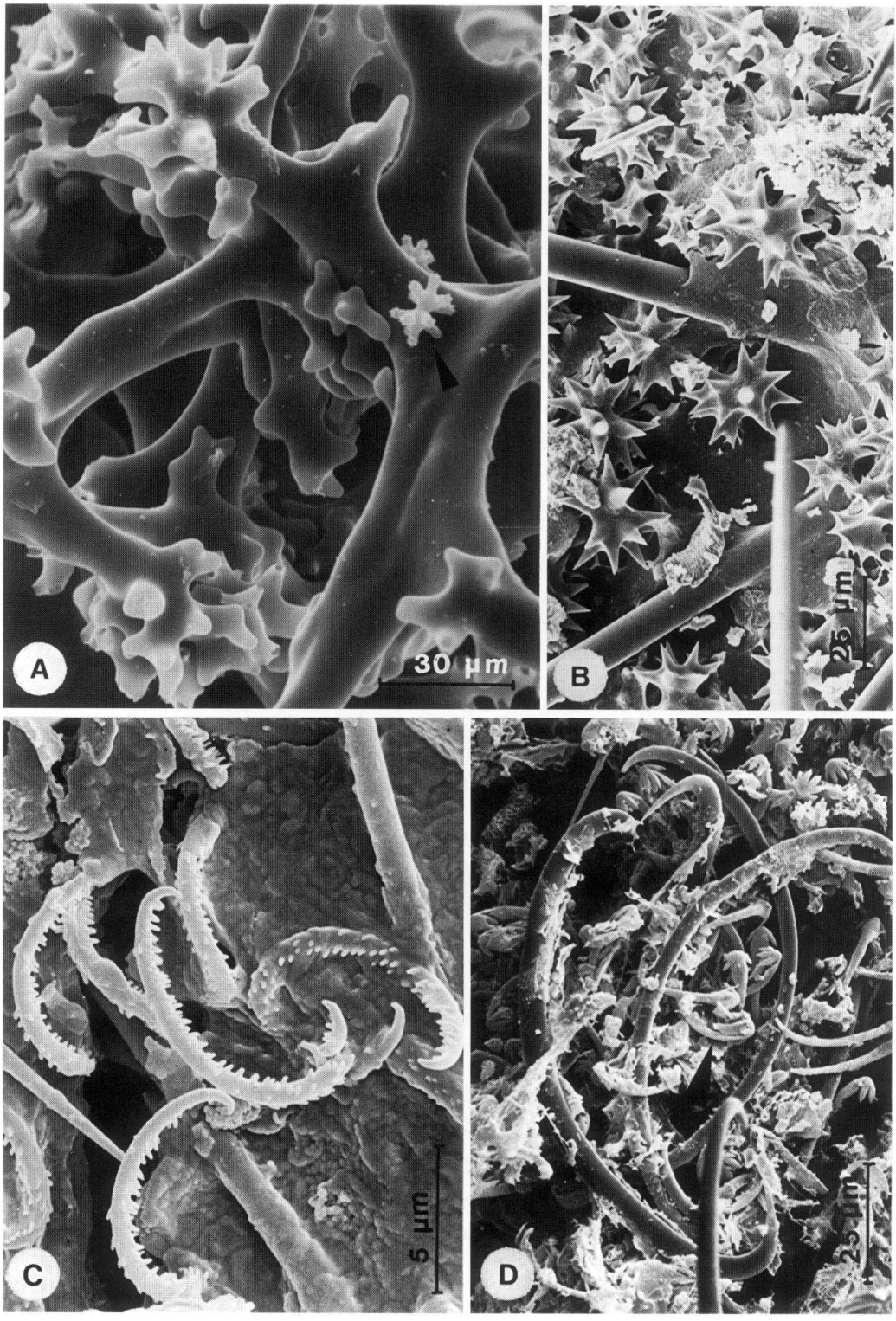
Fig. 7: Oldest known early Cambrian modern type calcarean spicules (A–C) from the Lower Cambrian (Atdabanian) of the Flinders Ranges (South Australia): A) Regular triaene with dichotomous split distal rays (character *23*), LM. B) Different calcaronean triaenes exhibiting the monocrystalline calcitic structure examined under SEM back scatter mode; SEM. C) Calcarea with calcaronean affinities, *Gravestockia phraretroniensis*, exhibiting fused choanosomal tetractine spicules (pharetronid); LM. Heteractinida (Calcarea). D) *Jawonya gurumal* KRUSE, 1987 (Wewokellidae); Middle Cambrian of North Australia. Polyactine dermal spicule (character *23a*); SEM. E) *Astraeospongia meniscus* ROEMER, 1848 with calcitic octactine derived spicules (character *23a*); Upper Silurian of the Isle of Gotland.


A
30 µm
B
25 µm
C
5 µm
D
25 µm

functional differences between sigmas. In our opinion this argument is weak, because microscleres may have changed their functionality and their location within the sponge tissue during the very long existence of the group Ceractinomorpha. We assume that all sigmatose microscleres are evolved from a "proto" sigmatose spicule. Maybe the sigmaspira of some "lithistids" (Scleritodermitae) and the Spirophorida (Tetillidae) are still close to the "proto" sigmatose spicule. Sigmatose and aster microscleres are *never* combined within one demosponge species, and therefore we are convinced of the homologous nature of both microsclere types.

Earliest fossil record of Demospongiae. – Regular four rayed spicules (calthrops) and advanced forms of spicules with tetractinellid affinities are known from rocks as old as the Lower Cambrian (Atdabanian) (REITNER 1992). KEMPEN (1985, 1990) has shown the great variety of tetraxon spicules within the early Middle Cambrian Ranken Limestone of the Georgina Basin (Australia). KRUSE (1990) reported the first doubted classical little spined sigmatose microscleres from the Middle Cambrian of the Daly – and Georgina Basin. This infers the presence of taxon Haplosclerida + Poecilosclerida of the Ceractinomorpha at least since that time. -Keratose- = dictyoceratid demosponges may be represented by the Lower-Middle Cambrian genus *Vauxia* very common within the Burgess Shale facies (RIGBY 1991). All these records indicate the very early phylogenetic branching points of the different Demospongiae + Homoscleromorpha taxa, probably before the early Cambrian radiation.

C. Discussion

The possibility of a homologization of the poriferan choanomeres with choanoflagellates, implying a close phylogenetic relationship of the Porifera and the "Craspedomonadina", has long been subject of discussion. KENT (1878) actually considered sponges to be nothing but colonies of choanoflagellates. SCHULZE (1885), however, argued that sponges are true metazoans because of their mode of reproduction.

The monophyly of the Metazoa is well established, and the Porifera are definitely metazoans (AX 1989). However, the adelphotaxon of the metazoan is still unknown. The assumption that it is some choanoflagellate group is questinoable because a planktic choanoflagellated stage has not been found within the ontogenesis of any metazoans. Also the presence of choanoflagellated cells in some Eumetazoa is very uncertain (for discussion see NORREWANG & WINGSTRAND 1970).

Fig. 8: Pinacophora; demospongian spicules: A) *Corallistes* sp. ("Lithistida", Tetractinellida), desmata (character *25*), aster microsclere (**arrow**) (character *29*), SEM. B) *Spirastrella* sp. (Tetractinellida, Hadromerida), dermal spiraster microscleres (character *29*), SEM. C) *Rhabderemia* sp.(Ceractinomorpha, Poecilosclerida); spined and curved sigmatose microscleres (character *31*), SEM. D) *Cladorhiza abyssicola* SARS, 1872 (Ceractinomorpha, Poecilosclerida); classical sigma microscleres and small cheloid microscleres (**arrow**) (character *31*), SEM.

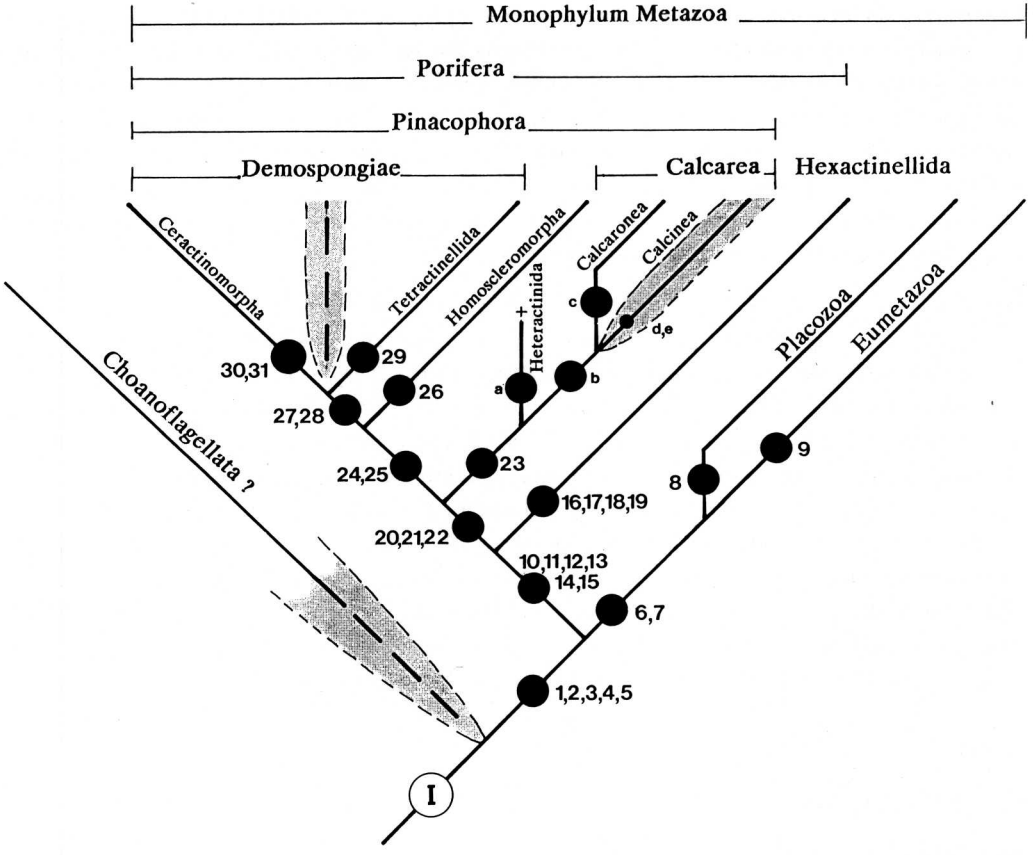


Fig. 9: Proposed phylogenetic relationships of the Porifera. For character numbers see text. Stippled areas indicate paraphyletic groupings; dark points are autapomorphies; open circles are plesiomorphic characters.

However, especially since AFZELIUS (1961 a, b) claimed the presence of "whip flimmer flagella" in poriferan choanocytes (of some Demospongiae and Calcarea), the hypothesis of some choanoflagellate taxa being the metazoan adelphotaxon was claimed in some publications (DOHLE 1986). Unfortunately, the TEM documentation of "flimmer flagella" (in cross section only) by AFZELIUS (1961 b) was not ultrastructurally informative, and a lot of doubt always remained about his interpretation. MEHL & REISWIG (1991) presented an indubitable SEM documentation of two appendages ("vanes") perpendicular to the proximal flagella axis of choanomeres from the hexactinellid sponge *Aphrocallistes vastus*. This was the first clear documentation of such structures in the choanomeres of Hexactinellida. Moreover, it completed the report of this structure from the main poriferan taxa: Demospongiae, Calcarea, and Hexactinellida. This allows us to assume that this flagellar appendage is part of the poriferan basic pattern. The vanes seem to be attached to the outer surface of the

flagellar membrane (Fig. 1C) and thus basically differ from mastigonemes of "flimmer-flagella", since the latter are connected with the microtubuli directly, penetrating the flagellar membrane (e.g. *Poterioochromonas*, see HERTH, 1982). Ultrastructural studies (FEIGE 1969 and BRILL 1973) were of the fresh water sponge *Ephydatia fluviatilis*. According to these authors, the flagellar vanes are attached to the microtubuli directly, their pictures, however do not allow any conclusive statements about the mode of attachment. New investigations with TEM and x-ray microanalysis are necessary in order to reconstruct the exact ultrastructure of poriferan flagellar vanes.

True flimmer-flagella have not been recognized within the Choanoflagellata (PATTERSSON; LEADBEATER, pers.comms.). Delicate bilateral flagellar appendages were reported from a few choanoflagellates only: *Salpingoeca* sp., *Monosiga* sp., and *Codosiga* sp. (HIBBERD 1975). The latter species often forms cell pairs connected by cytoplasmic bridges with median partitions (HIBBERD 1975: Figs. 8, 9), which seem similar to the "plugs" of hexactinellid syncytial tissues. However, in spite of similar dimensions, it is uncertain, whether or not the flagellar vanes of choanoflagellates are homologous with those of Porifera. The longitudinal sections of *Codosiga botrytis* flagellar appendages as figured by HIBBERD (1975, Figs. 12–14) from chromium-shadowcast preparations only, seem to be of extreme delicacy compared to the prominent and rigid-appearing vanes of, e.g. *Aphrocallistes vastus* (Fig. 1 C). According to HAUSMANN and PATTERSSON (pers. commun.), the homology of these structures is unlikely. However, only detailed ultrastructural studies on well fixated tissues of choanoflagellates and sponges will finally settle these questions.

MACKIE (1990) has pointed out affinities of the ciliate cell with metazoans. Ciliary movement within ciliates works in similar ways as observed in metazoans based on the common interactions between tubulin-dynein. Ciliates, however, possess binucleate stages within their ontogenetic cycle which makes their close relationship to the metazoans very unlikely.

The fossil record documents that all main poriferan groups have been present since the lowermost Cambrian. This implies that the important phylogenetic branching points of the Porifera occurred in the Precambrian before the so called "Cambrian Explosion". The sponges, thus, are in many respects plesiomorphic metazoans, which have survived and evolved since the Precambrian. Acording to MÜLLER et al. (1984), the hexactinellid sponge *Aphrocallistes vastus,* possesses a species unspecific aggregation factor (probably a primitive mode of cell to cell aggregation), whereas aggregation factors in other sponges are always species-specific. This suggests that the hexactinellid phyletic line separated from that of other sponges at a very early (early Proterozoic?) stage in poriferan evolution. This observation fits with new molecular biological data (PFEIFER et al.1993; HIRABAYASHI & KASAI 1993). PFEIFER et al. (1993) have analysed S-type lectins, which are important for cell recognition and aggregation, in *Geodia cydonium* (MÜLLER, 1776) which are highly conservative carbohydrates and were found only in nemathods and vertebrates (HIRABAYASHI & KASAI 1993). They considered that sponge S-type lectines are the ancestors of vertebrate S-tpye lectines. This means that

the responsible gene occured before 800 my, calculated by HIRABAYASHI & KASAI (1993). Further very important new data on sponge phylogeny were found by MOLDOWAN et al. (1994). They have analysed a strictly demosponge related C30 steranes and 24-isopropylecholestanes in an 1.8 Mrd year old black shale. In summarising all the known facts it is clear that sponges are metazoans which originated probably in early Proterozoic times and therefore survived true Precambrian metazoans.

D. Conclusions

1. The Porifera are definetely monophyletic.
2. The Porifera are the adelphotaxon of the Eumetazoa/Placozoa-Taxon.
3. Pinacophora (Demospongiae/Homoscleromorpha/Calcarea) and Hexactinellida are considered as sister groups.
4. Sponge spicules are not a constitutive character of the Porifera. Spicules developed independently within the three poriferan main taxa Hexactinellida, Calcarea, and Demospongiae. Within the Demospongiae, microscleres developed independetly from the megascleres.
5. Sponges are Precambrian animals which ocurred first in the Proterozoic. Sponges originated probably from a choanoflagellate stock which was related with microbial biofilms.

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Authors addresses:
Prof. Dr. J. REITNER, Institut und Museum für Geologie und Paläontologie, Goldschmidtstr. 3, D-37077 Göttingen, Germany.
Dr. D. MEHL, Institut für Paläontologie, Freie Universität Berlin, Malteserstr. 74-100, D-12249 Berlin, Germany.