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A variety of meroms and affinity of receptaculitids

JERZY DZIK

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The dasycladacean nature of the receptaculitids, originally a result of misunderstanding of the fossil evidence, is widely accepted and entered textbooks but their alternative interpretation as sponges remains a possibility. Phosphatized, originally aragonitic, late Ordovician receptaculitid meroms, more complete than those previously known, may help in determining more precisely their taxonomic identity. Some of them may lack column or cap, but acutely-pointed arms parallel to the body surface are invariably present, which supports the poriferan ties. The spinose character of meroms and the presence of growth increments on meroms' caps and feet in advanced receptaculitids preclude their algal affinity. The walls of underived receptaculitids with conical body cemented to the substrate were perforated with pores that may be interpreted as inhalant canals in terms of the sponge model. Possibly, the receptaculitid lineage emerged more or less synchroneously with those of sponges having siliceous, aragonitic or calcitic skeletons in result of selective pressure from newly evolved macroscopic predators. The meroms of advanced globular receptaculitids were fused in the basal portion of the body and remain loose in the upper part, where their caps remain tightly arranged. In both body regions no space was left for any porosity. This suggest that the meroms were free to move in a certain extend allowing water to penetrate the body. Such ability would not be consistent with their algal nature but is within potential of the physiology of sponges owing to contractile action of the pinacoderm. Presumably, in the post-Cambrian evolution of the receptaculitid lineage the ability of aneural signal transduction by pinacocytes was mastered. □ *dasyclads, Ordovician, phosphatization, Poland.*

Jerzy Dzik ✉ [dzik@twarda.pan.pl], Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warszawa and Institute of Evolutionary Biology, Faculty of Biology, Biological and Chemical Research Centre, University of Warsaw, Warszawa, 02-089 Żwirki i Wigury 101, Poland; *manuscript received on 08/02/2024; manuscript accepted on 26/04/2024; manuscript published on 21/08/2024 in* Lethaia 57(2).

Receptaculitids are relatively common fossils in Palaeozoic strata of shallow marine origin, but their taxonomic identity remains obscure, although the most popular view is that they are relatives of the dasycladacean algae. Their skeleton was composed of radially arranged spinose aragonitic units called meroms, usually terminating with polygonal plates (caps) at the surface of the body (reviewed by Nitecki *et al.* 1999).

Receptaculitids were made algae by Kesling & Graham (1962) who claimed identification of gametocysts beneath the outer wall plates of the Ordovician *Ischadites*. It had already been pointed out by Byrnes (1968, p. 369) that the supposed gametocysts are actually cross sections of the diagonal rays of meroms. Although such interpretation was rejected, another aspect of the receptaculitid fossils was used to support their dasycladacean nature: the most common preservation of only the 'bottom' portion of their articulated skeletons. Instead of interpreting this as the original *in situ* preservation of meroms kept together, touching on the bedding plane by stabilizing sediment load, a hypothesis was forwarded that the 'bottom, was actually the top of the 'thallus' (e.g. Byrnes 1968; Campbell *et al.* 1974). This was the orientation of the skeleton opposite to that proposed by Rietschel (1969) who indicated also that the mineral skeleton of dasycladacean algae (including cyclocrinitids) is in reverse relationship to that of receptaculitids. What is calcified in these algae corresponds to empty space in the receptaculitids and *vice versa*. Despite these problems with the body plan, the idea of dasycladacean nature of receptaculitids was grasped by Nitecki (1970) who unified them with the early Palaeozoic cyclocrinitid algae, classifying the cyclocrinitids as a lower rank taxon among receptaculitids and even placing some receptaculitids within this taxon. The algal interpretation of receptaculitids entered textbooks and still dominates there.

In this work I describe phosphatized late Ordovician meroms more complete than those previously known. They may help in resolving the enigma of receptaculitid affinity.

Material and methods

The specimens that are the subject of this study were extracted with dilute acetic acid from about 10 kilograms weight sample Ma-192. It was taken from near

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the top of the Mójcza Limestone Formation at its type locality in village Mójcza within the administrative boundaries of the city Kielce. The Mójcza quarry is now densely overgrown with blackthorn bush that makes difficult measuring the section, but the sample most likely comes from the same layer as sample Ma-99 in Dzik & Pisera (1994). The rock matrix is an organodetrital limestone rich in phosphatic ooids and skeletal debris coated with calcium phosphate. Some fragmented calcareous skeletons are more or less completely replaced with phosphate and such is the preservation of most receptaculitid meroms. Owing to similarity between aragonite and apatite molecules aragonitic skeletons are preferentially replaced with phosphate (e.g. Mutvei 1983), whereas associated calcitic ones tend to be silicified (Dzik 1994). Apatite replicas of meroms show that they were originally built of acicular aragonite radially arranged in the merom head (Dzik 1994, fig. 19A-B, 1997; Dzik & Pisera 1994; Nitecki & Mutvei 1996; Nitecki *et al.* 1999, p. 46, fig. 1.5).

The material studied is housed at the Institute of Palaeobiology, Polish Academy of Sciences (ZPAL) in Warsaw, Poland. Sample Ma-192 of the Mójcza Limestone yielded 18 phosphatized meroms representing a *Tetragonis* species with flap-like plates; 44 specimens with irregularly hexagonal plates represent an unnamed sphaerospongiid genus. Several articulated specimens of *Tetragonis* were collected from glacial erratic boulder E-223 at the Baltic shore in Międzyzdroje, Pomerania. A large size articulated receptaculitid of unnamed genus has been found preserved in another erratic boulder of the micritic Ostseekalk lithology (its age and provenance was discussed by Brummer 1980) in Zgierz, central Poland.

Morphology of meroms

The anatomical terminology proposed by Brummer (1980) is here used (Fig. 1B).

Overlapping caps

More or less completely phosphatized meroms probably representing a species of *Tetragonis* are common in the Mójcza Limestone. As shown by articulated specimens from erratic boulders their heads did not touch each other laterally to form a continuous armor of polygonal units. Unlike typical receptaculitids, the *Tetragonis* imbricated caps overlapped in a way resembling the spruce cone (Fig 3A; Brummer 1980). The external surface of merom caps is glossy (Fig. 2C) like their arms (Dzik 1992, fig. 6.3B), which means that they were covered with secretive tissue. Arms are somewhat flattened in cross section (Figs 1B, 2A, E). The nuclead arms emerge from the column near the cap; the level of latitudinal arms is somewhat below (Figs 1B, 2 A, D, E), and the minute apicad arm is even more basal (Figs 1B, 2A). Probably because of the apicad arm small size it was not identified in acetate peels by Brummer (1980). Thus, in the disposition of arms *Tetragonis* does not differ from typical Ordovician receptaculitids.

As shown by the erratic boulders material, the merom column tips in *Tetragonis* are usually acute, like those of the Devonian *Ischadites* (Byrnes 1968), but Brummer (1980) identified small feet in some of them. At least in the nuclead end of the articulated *Tetragonis* specimens, the column tips are so close to each other that no space for any central cavity is left there. This suggest that such specimens do not reflect the *in vivo* arrangement of meroms but represent a kind of tetanus constriction. A suggestion that meroms were movable is offered also by the narrow concavity along the nuclead margin of the *Tetragonis* merom caps of various shape (Fig. 1B$_1$). Apparently, the meroms from the row closer to the nuclead end of the body partially overlapped those located apicad to them.

The closest relative of *Tetragonis* was probably *Ischadites*. Its type species, *I. koenigii* Murchison, 1839 from the early Ludlow beds at Ludlow, England shows similarly thin columns although the caps apparently did not overlap (Nitecki 1969).

Reduced column and diagonal arms

According to Hinde (1984; also Byrnes 1968, p. 368) *Sphaerospongia* meroms sometimes lack columns and, consequently, feet. Byrnes (1968, fig. 1B) reconstructed meroms arrangement in *Sphaerospongia* with perpendicular disposition of arms, similar to that in typical receptaculitids. Campbell *et al.* (1974) noticed that in the Silurian sphaerospongiid *Hexabactron* 'the cups at the apertural end of the smaller [...] specimens are unfused' but 'the largest specimens have the cups fused and pores well developed right up to the aperture. [...] It is clear, therefore, that a stage is reached when these plates increase in size and fuse together, thus rendering further growth impossible' (Campbell *et al.* 1974, p. 64). This means that the actual orientation of the body was opposite to that proposed by the authors, with the acute tips completing its growth first. They assumed that the apertural end was the basal one because many specimens were found with this part of the body oriented downward and the central cavity partially filled with laminated sediment,

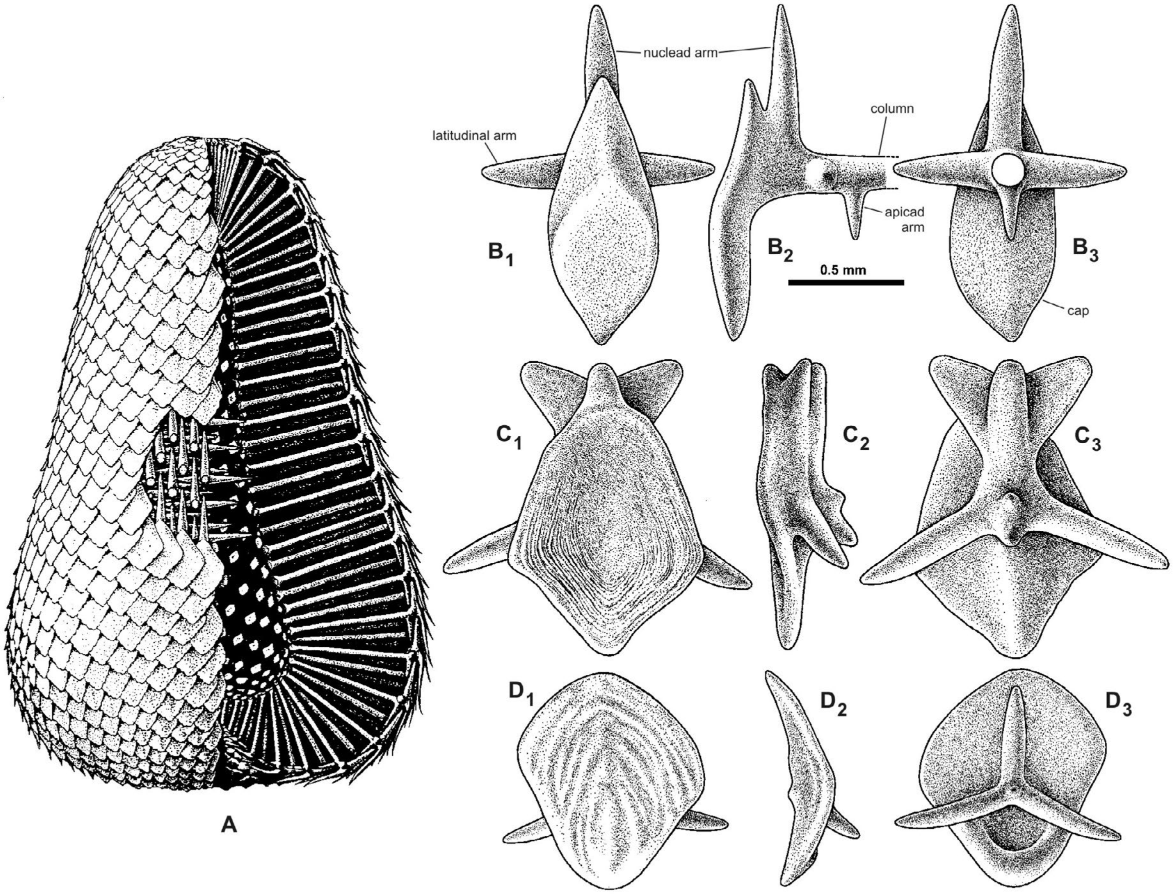

Fig. 1. Restored complete skeleton of *Tetragonis* sp. (A, modified after Dzik 1992, fig. 6.3A), its merom (B), and meroms of an unnamed sphaerospongiid (C, D) in external, lateral, and internal views.

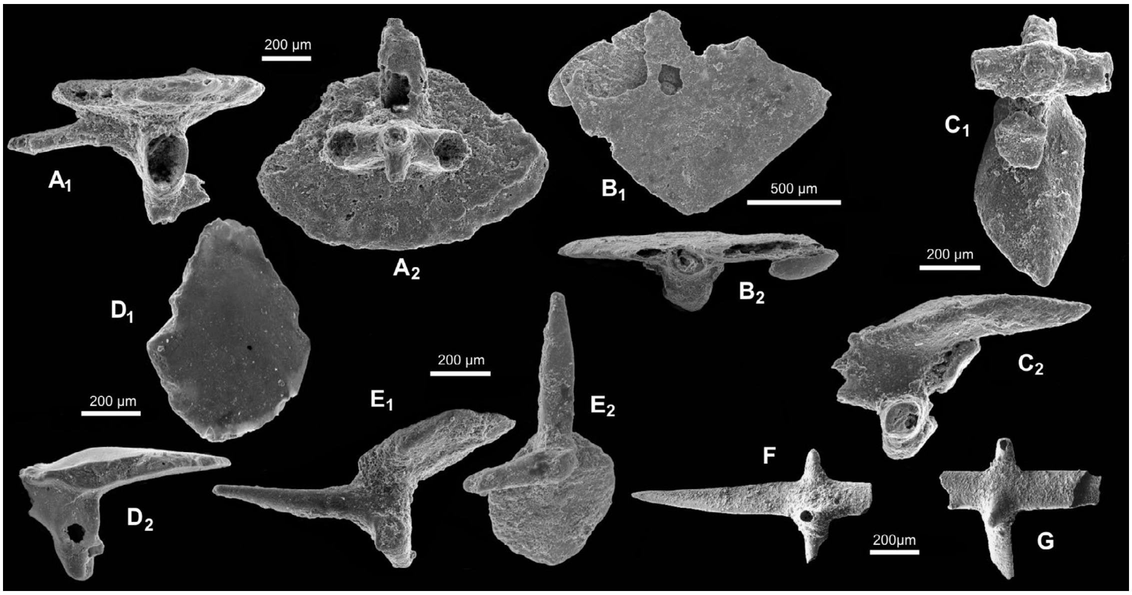

Fig. 2. Phosphatized meroms of receptaculitids. A–E, Katian *Tetragonis* sp. from the topmost Mójcza Limestone (sample Ma-192), Mójcza, Holy Cross Mts., Poland; specimens ZPAL V12/65 (A), 67 (B), 68 (C), 66 (D), and 60 (E). F, G, unnamed receptaculitid lacking caps from the Ludlow Kok Formation at the Cellonetta Lavinerinne, Carnic Alps, Austria (modified after Dzik 1994b, fig. 26).

apparently entering it through the pores. Alternative interpretation for such orientation of the fossil is that the mature specimens settled down with the apertural end of the body downward because it was heavier, loaded with large fused meroms. In more advanced receptaculitids, meroms near the opening remained unfused (e.g. Gould & Katz 1975; Finney *et al.* 1994) and usually, unless catastrophically covered with the sediment load, only the basal part of the body had a chance to be preserved with meroms still in contact to each other.

The most common kind of phosphatized merom heads from Mójcza shows the disposition of arms unusual for the receptaculitids. The latitudinal arms are oriented diagonally towards corners of the cap (Fig. 3E), instead of being perpendicular to the nuclead arm. The shape of the cap is irregularly hexagonal and both the column and apicad arm are reduced to minute tubercles (Figs 1C, 3A–E), which suggests a relationship to the Devonian *Sphaerospongia*, but this is not consistent with the orientation of arms that are perpendicular both in *Sphaerospongia* (Hinde 1884, pl. 37:1) and in *Hexabactron* (Campbell *et al.* 1974, fig. 6). Additional blunt rays developed on sides of the nuclead arm in the Mójcza receptaculitid. The apicad arm is missing in associated small merom heads that show also reduced column and diagonal transverse arms (Figs 1D, 3F, G). The apicad end of the cap is not pointed there but thickened into a kind of callus.

Another variety in disposition of arms is represented by '*Ischadites*' *tenuis* Nitecki & Dapples, 1975 from the Wenlock age Laurel Limestone in Indiana, as well as the conical receptaculitid from the Late Ordovician of Sardinia. Both their latitudinal and meridional arms of their meroms are at the same level immediately below the cap, or even incorporated into the cap (Nitecki & Dapples 1975; Hammann & Serpagli 2003).

Missing caps

Some of the Silurian receptaculitids represent strongly derived morphologies. An unnamed receptaculitid from the Ludlow age Kok Formation of the Carnic Alps had the cup and the apicad arm reduced to a tubercle (Fig. 2F, G; Dzik 1994). The protective scaly

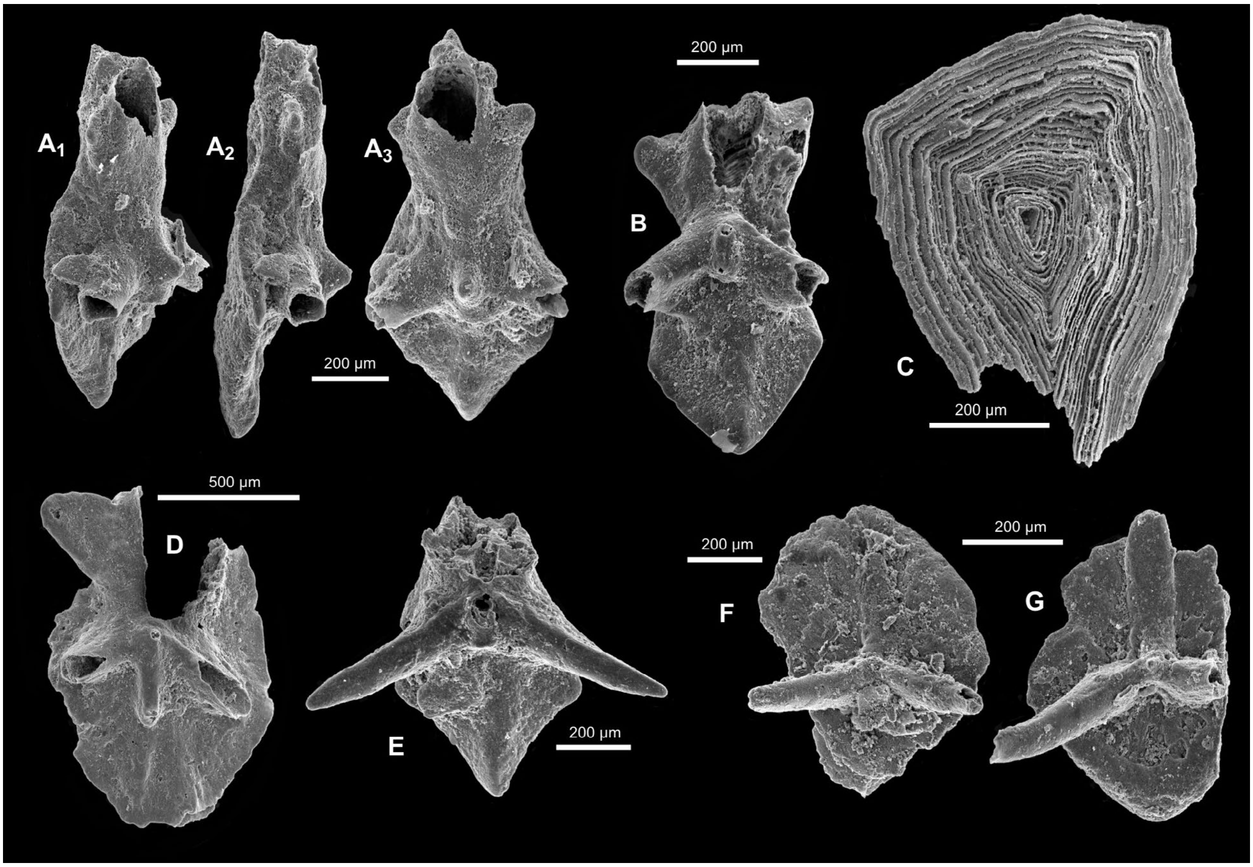

Fig. 3. Phosphatized meroms of an unnamed Katian sphaerospongiid from the Katian Mójcza Limestone (sample Ma-192), Mójcza, Holy Cross Mts, Poland; specimens ZPAL V12/76 (A), 73 (B), 74 (C), 75 (D), 72 (E), 71 (F), and 70 (G).

armour so typical for other receptaculitids was apparently missing and only prominent flat latitudinal arms and merom columns remained to perform the skeleton function.

Branching merom roots

The opposite end of the spectrum of merom morphology in respect to *Ischadites* represents an unnamed receptaculitid species from the late Ordovician (Katian) Ostseekalk (Fig. 4). Like other advanced globular receptaculitids, its juvenile meroms fusion prevented their further growth. In result, the merom size gradient at the apicad pole is preserved (Fisher *et al.* 1994). The columns of this Ostseekalk receptaculitid are relatively thick but their basal ends are divided into narrower and narrower rootlets (Fig. 4B). These branching feet are entangled in a way probably preventing movement of the apicad meroms. This resembles complex feet of meroms in the conical receptaculitid from the Darriwilian Antelope Valley Limestone of California (Foster 1973). The root-like meshwork forms a kind of spongiose inner wall. Possibly, the internal and external fibrous outgrowths typical for the Tremadocian *Calathium* (Fig. 5A) were of similar origin.

Conical cup with holdfast

Nitecki *et al.* (1999) referred to earlier works by other authors showing that the usually well preserved apicad (nuclear) part of globular receptaculitids

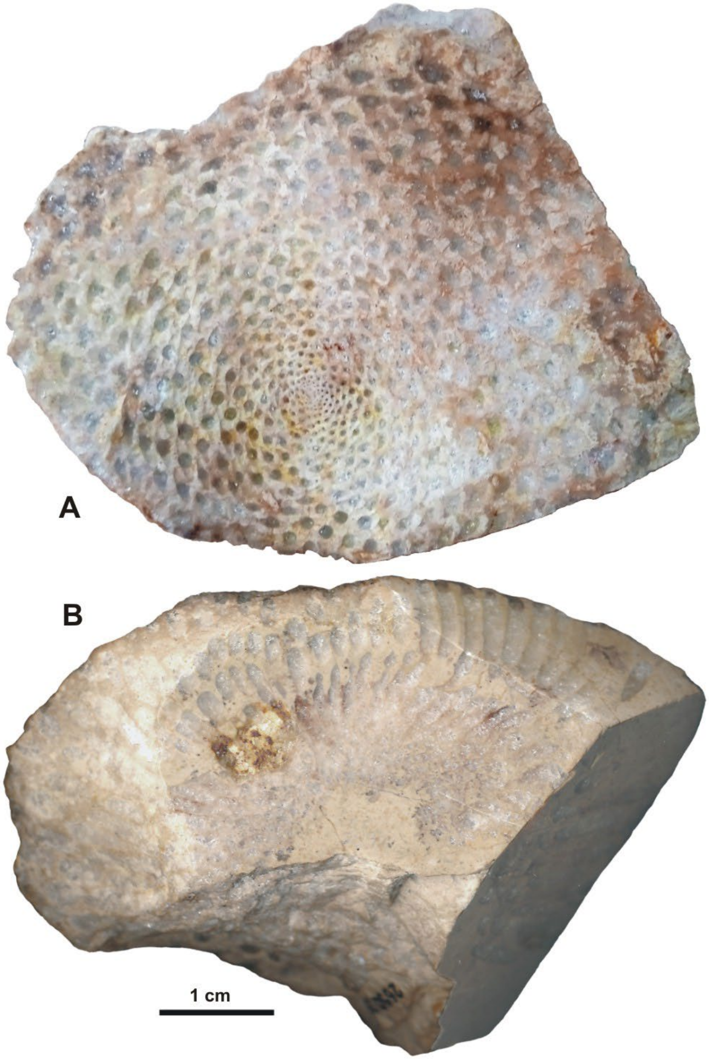

Fig. 4. Articulated apicad part of an unnamed receptaculitid ZPAL V12/77 with dendroid feet of meroms from the Katian erratic boulder of Ostseekalk lithology, Zgierz, Poland; photographed under water in basal (A) and upper (B) views. Note that the originally aragonitic meroms are diagenetically changed into translucent calcitic sparite.

was their base and that meroms were added on the opposite upper end. This interpretation is consistent with the course of ontogeny proposed for the Late Ordovician *Fisherites* by Finney *et al.* (1994). Some mature receptaculitids, as well as the earliest growth stage of globular ones (corniculum), were more or less conical in shape (Finney *et al.* 1994; Hammann & Serpagli 2003), grading into the cup-like *Calathium*. *Calathium* had an almost cylindrical, branching body and an extensive basal attachment area with a network of calcareous fibres around it and within the cup (Fig. 5A; dismissed by Nitecki *et al.* 1999 as epibionts). Accordingly, 'since *Calathium* are the oldest receptaculitids, branching of their body may be a primitive character' (Nitecki *et al.* 1999, p. 114). This is in contradiction to Nitecki (1986, p. 29) claim who allegedly 'collected in the Ordovician of Nevada an adult and a juvenile calathiid that may be complete; they are ovoid and entirely free of any overgrowths'. If true, perhaps Guo (1983) was right suggesting that *Soanites* differs from *Calathium* in having well developed outgrowths at the base of its cup. The medially sectioned specimen of *S. delicatus* Guo, 1983 (Fig. 5A) leaves little doubt that the outgrowth of meroms formed the basal attachment holdfast. Otherwise, the *Calathium* meroms had perpendicular rays closely similar to those of typical receptaculitids (Church 1991, fig. 6) except for that their caps and feet were less regular. They were fused into a rigid porous wall, transitional to the outgrowths of the cup (Church 1991, fig. 4.5; Li *et al.* 2015).

Receptaculitid relationships

An intriguing aspect of the acutely-pointed receptaculitid merom arms is their invariable presence, despite the diversity of merom caps and columns (or even the lack of them). This may be a result of either their functional significance or the developmental constrains.

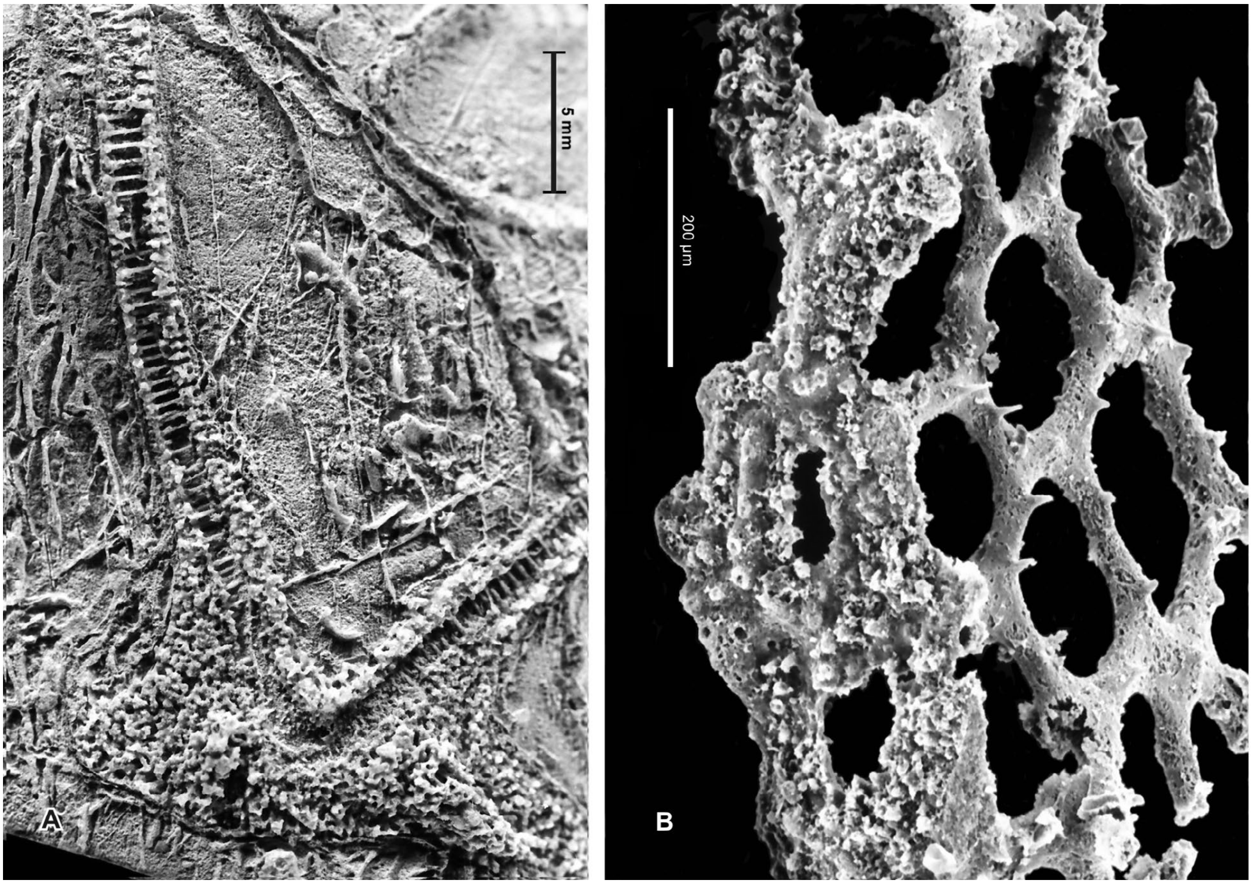

Fig. 5. A, longitudinal section etched with dilute acetic acid of the cup of *Soanites delicatus* Guo, 1983 from the early Ordovician Liangjioshan Formation of Hunjiang District in the southernmost part of Jilin in China (modified after Dzik 1991, fig. 6.4B; specimen donated by Zhu Mao-yan). B, phosphatized juvenile archaeocyathid cup ZPAL V29/26 from the Tommotian *Dokidocyathus regularis* Zone at Bydjangaia, Jakutia; note spinosity of the radial wall network (different view in Dzik 2003, fig. 6.3A).

Notably, the latitudinal and nuclead arms are always well developed, even in cases that the cup and apical arms are reduced (Fig. 2F, G). Rietschel (1969, figs 9, 10) explained how the latitudinal arms of neighboring meroms may overlap at the same level and how the apicad arm overlaps at different levels with the nuclead arm. Perhaps this served as a measure to keep the skeleton cohesive even when the meroms moved with the body volume change. This seems to be functional also in the case of diagonal disposition of latitudinal arms in the Mójcza sphaerospongiid. The presence of regularly spinose arms also in *Calathium*, in which the meroms were probably not movable, suggests that the development of arms was inherited after a sponge-like ancestor.

Completely preserved skeletons of the receptaculitids *Hexabactron* (Calloway *et al.* 1974) and *Tetragonis* (Nitecki *et al.* 1999) have an opening at the nuclead end. In *Calathium* and *Hexabactron* both the inner and outer walls of the cup have pores enabling flow of water. These are aspects consistent with the poriferan Bauplan. Perpendicular disposition of merom arms resembles that of spicules of the hexactinellid sponges. The similarity is superficial as the merom arms are located at different levels of the column. Moreover, they are diagonal in the Mójcza sphaerospongiid. The organization of its meroms is even not radial. A subdivision into radially arranged rays, column, and root-like foot characterizes calcitic spicules of the octactinellid sponges (e.g. Rietschel 1968; Dzik 1994; Mehl & Reitner 1996), but their rays are not arranged in the way similar to arms in merom. This makes the octactinellids related rather to the early Cambrian radiocyathids (Nitecki & Debrenne 1979; Zhuravlev 1986) but not to the post-Cambrian receptaculitids.

Two aspects of the typical receptaculitid skeleton Bauplan are of crucial importance in understanding their physiology and in determining their taxonomic position (Nitecki 1986, p. 29): 'in younger parts [...] the plates were not fused and may have been free to move in a certain extend' and 'with the exception of calathiids, the plates in the outer 'wall' show no evidence of pores'. Either a muscular action or hydraulic forces were involved in enabling contact of the soft tissues with external environment. Both possibilities are not consistent with their algal nature but is within potential of the sponge physiology. Many extant sponges can contract their bodies owing to contractile abilities of the pinacoderm (Nickel 2004).

The external surface of the merom cap and the inner surface of their feet in many receptaculitids bears distinct growth increments, which indicates that the body was not permanently covered with the secreting tissue from outside. Incremental lines may be well developed also on the meroms feet (e.g. Rietschel 1969, pl. 2:6). This precludes presence of any living tissue within the receptaculitid main cavity, especially the dasyclad-type main axis. The soft body was apparently restricted to the space between caps and feet.

A replica of growth increments by the phosphatic coat shows their distinctly regular pattern (Fig. 3C; Hammann & Serpagli 2003, fig. 6B_2). It is possible that they reflect a daily rhythm in secretion of the aragonitic tissue of about 7μm per day. Perhaps the body contractions, similar to those in extant demosponges, had the same cause.

A frequently revoked candidate for the receptaculitid ancestry, based on similarity to *Calathium*, are the early Cambrian archaeocyaths (e.g. Nitecki 1986). An additional argument in favour of their (and perhaps also receptaculitid) poriferan affinity is offered by phosphatized remains of juvenile growth stages from the Tommotian of Siberia (Fig. 5B; Dzik 1994, fig. 2C). They show a spinose appearance at the earliest stages of calcification that became obliterated later in the histogeny. This may or may not be used to support relationship between archaeocyaths and receptaculitids (Nitecki & Debrenne 1979). The skeleton and the aquiferous system of extant calcareous sponges are highly homoplastic (Manuel *et al.* 2003) and this obviously refers to their extinct forms. Any direct archaeocyathid-*Calathium* evolutionary connection is precluded by the difference in radial elements of their cups and mineralogy of the skeleton.

Unlike the receptaculitids, spicules of extant and fossil calcareous sponges are built of calcite (Manuel *et al.* 2003). Although the evolutionary change from aragonite to calcite was not a rare phenomenon (e.g. Stolarski *et al.* 2007; Conci *et al.* 2021) particular groups of sponges are conservative in this respect. Also, the siliceous skeletons of Hexactinellida, Demospongiae, and Homoscleromorpha sponges developed independently, as they use different, non-homologous protein machineries to control skeletogenesis (Shimizu *et al.* 2024). Therefore, it seems likely that the receptaculitid inherited their aragonitic skeleton after a Cambrian ancestor.

Probably the siliceous, aragonitic and calcitic poriferan skeletons developed synchroneously close to the Ediacaran-Cambrian boundary (Botting & Muir 2018) in result of selective pressure from newly evolved macroscopic predators (Dzik 2007). In the post-Cambrian evolution, the receptaculitid lineage developed skeletal elements (meroms) tightly packed in resting position. Perhaps the meroms moved in a daily rhythm to open ostia and allow water to enter canal system owing to the mastered ability of aneural signal transduction by pinacocytes.

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