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Palaeozoic record of *Thaumatoporella* PIA, 1927 (*incertae sedis*)?

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ABSTRACT

From Palaeozoic (mainly Devonian) shallow-water carbonates, spherical to irregular shaped microfossils with thin, apparently homogeneous or perforate micritic walls are widely reported. They are classically referred either to unilocular parathuramminid foraminifera, algae *incertae sedis* or calcispheres (e.g., *Bisphaera*, *Cribrosphaeroides*, *Uslonia*, *Vermiporella myna*, *Irregularina*). Due to their morphology and microstructural features, they are interpreted here as possibly belonging to *Thaumatoporella* PIA, a widespread Mesozoic-Early Cenozoic taxon of *incertae sedis* showing a remarkably high morphological variability. In analogy to Mesozoic thaumatoporellaceans, *Bisphaera malevkensis* BIRINA is interpreted as the cyst (i.e.= resting) stage of forms ascribed to different genera, i.e., *Cribrosphaeroides*, *Uslonia* and *Vermiporella* (here: *Vermiporella myna* WRAY). Note that in the Mesozoic many taxa were also synonymized with *Thaumatoporella*: *Polygonella* ELLIOTT, *Lithoporella elliotti* (EMBERGER), *Messopotamella* DRAGASTAN et al., *Vermiporella crisiae* DRAGASTAN et al., *Micritosphaera* SCOTT.

This new interpretation, based on material from the Devonian of W-Germany and the Czech Republic, leads to taxonomic reassessment as *Thaumatoporella*? *malevkensis* (BIRINA) nov. comb. As a consequence of our interpretation, the rather long Mesozoic to Early Cenozoic (Anisian? to Lutetian) record of thaumatoporellaceans is supposed to be significantly larger than formerly assumed. The possible gap of no records of thaumatoporellaceans between the Middle Carboniferous and the Lower Triassic cannot substantially be argued at the moment (Lazarus effect of one taxon?; two homeomorphic but taxonomically different taxa).

Keywords: Parathuramminida, calcareous algae, *incertae sedis, Thaumatoporella, Bisphaera, Cribrosphaeroides, Irregularina, Uslonia, Vermiporella*, Devonian

1. INTRODUCTION

Representatives of the microproblematicum *Thaumatoporella* PIA were successful inhabitants of different shallow-marine carbonate environments recorded so far over a very long period, from the Middle Triassic (Ladinian) until the Palaeocene (RADOIČIĆ, 1960; FLÜGEL, 1983; DE CASTRO, 1990; SCHMID, 1996). The possible oldest Mesozoic record is most likely that from the Anisian by EMMERICH et al. (2005: Fig. 14.3, “algal remains similar to *Thaumatoporella* cf. *parvovesiculifera*”). Later, thaumatoporellaceans were illustrated by NICORA et al. (1995: *Thaumatoporella*) also from the Lower Eocene (Illerdian) shallow water limestones drilled at the Limalok Guyot, southern Marshall Islands of the Central Pacific. At this site, they were also observed in younger sediments, up to the Middle Eocene (Lutetian) in age. Together with Lutetian findings in southern Italy (VECCHIO & BARATTOLO, 2006; VECCHIO & HOTTINGER, 2007), these represent the youngest records of thaumatoporellacean algae. From the published literature data, a final peak occurrence of thaumatoporellaceans in the Lower-Middle Eocene can be assumed. More important proliferation periods (increased abundance, acme) are concentrated in the Early/Middle Jurassic and Late Cretaceous time windows. While the Jurassic-Cretaceous occurrences derive almost exclusively from inter- to subtidal inner platform fa-

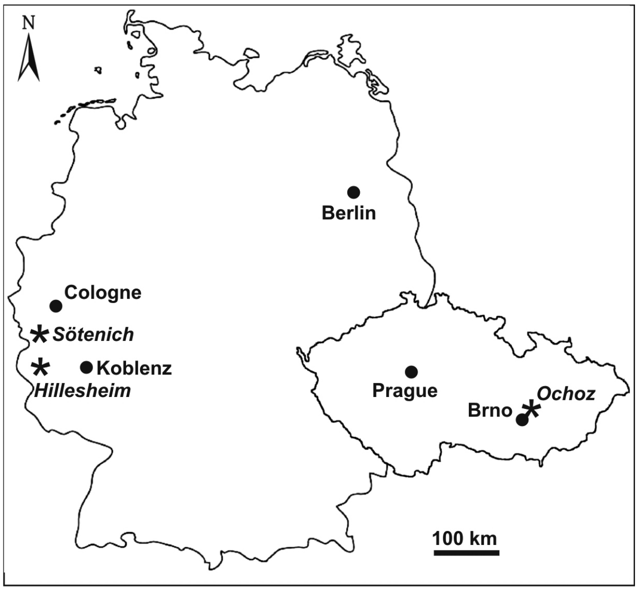


Figure 1: Map of Germany and the Czech Republic with the sample localites: Sötenich, Hillesheim and Ochoz (*stars*).

cies, in Triassic times, *Thaumatoporella* is also found in reefal carbonates (SENOWBARI-DARYAN, 1984). However, there are also records of *Thaumatoporella* from Late Jurassic reefal facies (e.g., LEINFELDER et al., 1993; SENOWBARI-DARYAN et al., 1994; BUCUR et al., 2005). In the exhaustive work of DE CASTRO (1990), thaumatoporellaceans were compared with living Volvocales and Cladophorales and tentatively assigned to the green algae. A possible faunal origin was put up for discussion by FLÜGEL (1983).

The interpretation of some Palaeozoic irregular-shaped to subsphaerical unilocular foraminifera (parathuramminids), and/or algae *incertae sedis* as thaumatoporellacean algae (in the sense of DE CASTRO, 1990) was proposed by VACHARD (1994) and VACHARD & CLEMENT (1994). These assumptions/interpretations are accepted here and are further corroborated with thin-section material of Middle to Late Devonian shallow-water limestones of the Czech Republic and Germany (Fig. 1) in comparison to Mesozoic material. Thereby further evidence for the possible presence of thaumatoporellaceans in Palaeozoic times is presented.

2. GEOLOGICAL SETTING AND MATERIAL

2.1. Czech Republic

The levels and patches with *Thaumatoporella*-like occurrences were traced in many places across a 15 000 km^2 large and, on average, 0.45 km thick segment of Middle–Upper Devonian platform and reef limestones, in the middle and eastern parts of Moravia, the SE part of the Czech Republic. About 98 % of these limestones occur in subsurface structures but were densely drilled and documented during the oil survey works of the second half of the 20th century (e.g., ZUKALOVÁ, 1981; HLADIL, 1994; GERŠL & HLADIL, 2004; HLADIL, 2007a; BÁBEK et al., 2007). The platform is dominated by shallow-water facies (reefs with flats and extensive lagoons dominated by *Amphipora*), whilst the rim of slope facies is fragmentarily preserved (HLADIL, 2002; BOSÁK et al., 2002). The basement compartments with deeply dissected Neoproterozoic and Early Cambrian rocks belong to a collage of southernmost Brunovistulian terrane fragments (KALVODA et al., 2008). The occurrences of *Thaumatoporella*-like fossil objects and related facies are notable features for the Late Givetian and Middle Frasnian (see Material below). In this paper, we concentrate on the latter. In the Devonian of Moravia, the "*Bisphaera*"-, "*Cribrosphaeroides*"-, "*Irregularina*"- and "*Vermiporella*"-shaped forms occur together, often in gently inclined aprons around sediment-starved, variously deteriorated intertidal reef flats. They are typically embedded in poorly washed packstones-grainstones with microsparitic clusters, interbedded micrite and occasionally co-occurring large *Parathurammina*.

2.2. Germany

Samples from the Middle Devonian of Germany with *Thaumatoporella*-like microfossils were acquired from shallow water platform carbonate sections of various localities within the Eifel hills. The limestone synclines of the Eifel hills are part of the western Rhenish Slate Mountains, within the Rhenohercynian fold-thrust belt of the European Variscides. Synclines are situated in a N-S trending, approx. 50 km wide, major depression of the Eifel nappe, the so-called Eifel North-South Zone (ONCKEN & WEBER, 1995; ONCKEN et al., 2000; FRANKE, 2000). The Eifel North-South Zone covers mainly the lower and middle parts of the Devonian sedimentary record of the Ardennes-Eifel shelf, developed at the southern margin of the Old Red Continent. In this succession, the Lower Emsian siliciclastics are possibly the oldest known (BELKA & NARKIEWICZ, 2008, p. 393). These molasse-like sediments are up to several kilometres thick and the transition to carbonate beds is in the Upper Emsian Heisdorf Formation. Carbonates containing a diverse reef-building fauna first occurred during the early Eifelian, followed by the widespread and intensive transgressive development of shallow water reef-bearing carbonates of Early to Middle Givetian ages. The Late Givetian to Early Frasnian platform is partly dolomitized. The Middle Frasnian has diverse facies, but argillaceous and black shales prevail in the youngest known parts of the succession (Late Frasnian and Early Famennian).

General large scale palaeogeographical models for the Devonian of the Rhenohercynian Belt in central Europe assume that shelf zonation parallels the SW-NE trending southern margin of the Old Red Continent (KREBS, 1974; BURCHETTE, 1981). The Emsian–Givetian shelf and platform configuration in the context of the Eifel hills is still debated, but a ramp configuration with a southward deepening trend is most likely, based on detailed facies studies (e.g., UTESCHER, 1992; SALERNO, 2008), though different models exist with postulated structural highs controlling platform development and resulting in a E-W shelf zonation pattern (STRUVE, 1963; FABER et al., 1977).

In terms of environmental distribution, "*Cribrosphaeroides*-", "*Vermiporella*-", "*Bisphaera*"-shaped forms occur in shallow marine, peritidal and shallow subtidal facies types including massive stromatoporoid, branching stromatoporoid (*Amphipora*) and rugose/tabulate coral biostromes and meadows. The Devonian examples studied herein point to an ecological preference of thaumatoporellid-like microfossils for fully marine environmental conditions, though they also occur in marginal marine euryhaline settings (e.g., FLÜGEL & HÖTZL, 1971; SALERNO, 1997; KALDUN, 1998; WILLMER, 1998).

2.3. Material

Czech Republic. – Based upon various studies during the last four decades from the Moravian segment, we can infer that the *Thaumatoporella*-like facies are not very common here, being found in less than 1 % of the cases. This ratio clearly indicates that the relevant occurrences correspond to specific rather than common environments. For this study, the main focus is on the material from the Ochoz Skalka Quarry situated in the southern part of the Moravian Karst area (coordinates 49 15 56 N, 16 44 30 E). Here, thin sections between 4 and 6 m of the measured section (nos. OCH 301 – 304, 250 – 254 and 223 – 227) represent rocks of the earliest Middle Frasnian and others, between 15 and 21 m (nos. OCH 221, 223, 230, 231, 234, 290, 292 and 293) represent the Middle Frasnian, around and above the ~*Pa. punctata* / *Pa. hassi* conodont zone boundary equivalent (HLADIL et al., 2009). The comparative material referred to in the study is from several other sites, e.g., the youngest occurrences of Middle/Upper Frasnian age can be exemplified by those in the Mokrá Central Quarry (49 13 46 N, 16 45 29 E; Neptunian dykes; thin section nos. JH 1659 and 1660), or the oldest occurrence in the latest Middle Givetian has been recorded in the Ostravice NP-824 well (49 33 25 N, 18 22 44 E; depth 1890 m; no. JH 2236 / 31814–G) (ZUKALOVÁ, 2004). The latter paper indicates several levels with *Thaumatoporella*-like fossils in the Jablůnka-1 well (49 22 21 N, 17 57 03 E) showing that there is repeated onset and cessation of the related facies in the Middle Frasnian.

Germany. – Samples studied herein stem from (a) the uppermost Eifelian of the Hillesheim syncline, (in an abandoned railway cut at Nohn mill between the villages of Üxheim and Niederehe, the middle part of the section, in the so-called Katzenley railway cut, Lower Ahbach-Formation, sample numbers K 39, K 41b, K 42, K44b, K 56, cf. KALDUN, 1998), (b) the Lower Givetian of the Hillesheim syncline ("Cisterziensis marble quarry", located between the villages of Kerpen and Niederehe, Rodert-Formation, sample no. SH 2/2, cf. WILLMER, 1998); "Meerbüsch quarry" between the villages Kerpen and Üxheim, Dreimühlen-Formation, sample number MP 2/3; cf. FISCHER, 1999), (c) the Lower Givetian of the Sötenich syncline ("Scheidberg quarry" south of Sötenich village, Urft River valley, Rodert-Formation, sample nos. SB 9, SB 15, SB 16; "Winter & Weiss quarry" south of the village Sötenich, Loogh-/Cürten-Formation, sample nos. B 14, 524, cf. SALERNO, 1997) and (d) the Lower Givetian of the Dollendorf syncline (a quarry at the abandoned railway station of Dollendorf, "Klotzige Bankkalke", ?Dreimühlen-Formation, sample numbers KBK 68, KBK 68-1, KBK 69; cf. SCHRÖDER & SALERNO, 2001).

3. MICROPALEONTOLOGY

3.1. Historical review and systematics of Mesozoic to Early Cenozoic thaumatoporellaceans

In 1922, RAINERI described the new species *Gyroporella parvovesiculifera* from the Upper Cretaceous of southern Italy and attributed it to dasycladalean algae. In 1927, PIA recognized the differences between RAINERI´s taxon with *Gyroporella* and introduced the new genus *Thaumatoporella* with the new combination *Thaumatoporella parvovesiculifera* maintaining its assignment to the dasycladalean algae. For the genus diagnosis given by PIA see Table 1. In 1938, PIA studied Upper Cretaceous material from Naxos Island, Greece, and remarked that *Thaumatoporella parvovesiculifera* represents a "curious" (merkwürdiges) fossil and "that the morphology........is such a bizarre one that I became completely crazy about its interpretation as a Dasycladale" (op. cit., p. 492-493, translated from German). As a peculiarity of the genus *Thaumatoporella*, PIA didn´t refer to the internal structure but to the general "thallus" morphology that is mostly not regular (e.g., cylindrical) but irregularly bent with branching and highly changing thickness. Therefore, PIA assumed that the thalli were not growing in an upright position as do dasycladalean algae but was creeping ("kriechend") on the sea floor. It is also worth mentioning that PIA stressed the high variability concerning both morphology and dimensions (e.g., width of "thallus", pore diameter, wall thickness). Identical microfossils were described several decades later from Upper Jurassic to Upper Cretaceous shallow-water limestones as *Polygonella incrustata* (ELLIOTT, 1957: Upper Jurassic of the Middle East; JOHNSON, 1965: Upper Cretaceous of Greece), *Lithoporella elliotti* (EMBERGER, 1957: Upper Jurassic of Algeria), *Polygonella shikokuensis* (IMAIZUMI, 1965: Upper Jurassic of Japan), *Thaumatoporella (Polygonella) occidentalis* (JOHNSON & KASKA, 1965: Upper Cretaceous of Guatemala), *Messopotamella angulata* (DRAGASTAN et al., 1985: Upper Triassic of Greece) and *Vermiporella crisiae* (DRAGASTAN et al., 1989: Upper Aptian of Romania). These forms were mainly interpreted as red algae (Corallinaceae, Solenoporaceae) or algae *incertae sedis* differing from *T. parvovesiculifera* by differences in "cell" (= pore) dimensions, e.g., "shorter and wider cells" in *T. occidentalis*, morphology etc. There seems to be a general consensus in the literature, however, that these parameters are highly variable (following PIA, 1938) and that therefore these forms should be included in the variability of *Thaumatoporella parvovesiculifera* (RAINERI), thus representing junior synonyms (SARTONI & CRESCENTI, 1959; RADOIČIĆ, 1960; FENNINGER & HÖTZL, 1967; FLÜGEL, 1983; DE CASTRO, 1990, 1991; DÜZBASTILAR, 1991; SCHLAGINTWEIT, 1992). This represents the widely accepted concept of polymorphic thaumatoporellaceans (Fig. 2). One of the oldest detailed studies was conducted by SARTONI & CRESCENTI (1959) based on

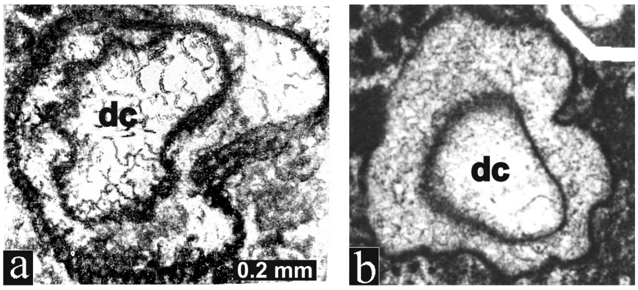


Figure 2: a: *Cribrosphaeroides permirus* (ANTROPOV), modified from CHUVASHOV (1965: Pl. 3, Fig. 7 Upper Frasnian of Russia). **b**: *Micritosphaera ovalis* SCOTT, modified from SCOTT (1978: Fig. 1g, Albian of Guatemala; no scale was indicated). Both forms are interpreted here as thaumatoporellaceans. dc = structures called daughter-colonies by DE CASTRO (1990).

Liassic specimens. Contrasting their material with that from the Upper Cretaceous type material, SARTONI & CRESCENTI (1959: p. 130) stated that it is impossible to distinguish between both, specifically due to intermediate gradations in dimensions, therefore indicating a rather long stratigraphic range for *Thaumatoporella parvovesiculifera*. Nevertheless, the authors mentioned a pure statistical difference, namely the occurrence of larger values (wall thickness, pore diameter) for the Upper Cretaceous forms. A detailed morphological description and analysis of thaumatoporellaceans was presented by DE CASTRO (1988, 1990, 1991). Besides new interpretations on internal structures, the order Thaumatoporellales and the family Thaumatoporellaceae were introduced by DE CASTRO (1988) (Tab. 1). However, an emendation of the genus diagnosis of PIA (1927) was not presented. Concerning the systematics of thaumatoporellaceans, DE CASTRO (1990, p. 204, translated from Italian) concluded that it is "probable that within the Middle Triassic to Palaeocene period more species and more genera of thaumatoporellaceans existed. However, the considerable intergradations of the morphological features, the great variability of the wall thickness in homeomorphic specimens.....make the distinction of different species very difficult at the present state of knowledge". The high morphological (e.g., shape, dimensions) variability of *Thaumatoporella* is here exemplified from Late Sinemurian specimens of Albania (Pl. 1).

3.2. Morphology of Mesozoic thaumatoporellaceans

The general morphology of thaumatoporellaceans does not correspond to a fixed bauplan but is highly variable including completely different morphotypes: irregular lobate, globose, ovoid, and more or less cylindrical shapes. Deeply constricted "thalli" (DE CASTRO, 1990: "deep invaginations") may display a chambered appearance due to the outer wall protruding into the interior. According to DE CASTRO (1990, p. 186), it cannot be excluded that these structures are connected to "reproduction phenomena". Thaumatoporellaceans can be free-living, attached to hard substrates, dwell as cryptoendoliths inside hollow bioclasts (see SCHLAGINTWEIT & VELIĆ, 2012) or dwell within microbial crusts (SCHLAGINTWEIT, 2013) (Pl. 1). Some of these modes of life are controversial and not fully understood with respect to possible life cycles or adaptations to different environmental conditions. For irregular-shaped morphotypes with elongated protuberances, reported from Liassic peritidal carbonates, a psammobiontic way of life was recently discussed (SCHLAGINTWEIT et al., 2013) in an analogy to the Palaeozoic *Irregularina* (VACHARD, 1994) (Fig. 3). In this connection, it is noteworthy that VACHARD (1994, p. 31) argues that *Irregularina*, due to its assumed psammobiontic way of life, may be the deformed stage of a microfossil whose free (= non-psammobiontic) stage is represented by *Bisphaera*.

Thaumatoporellaceans consist of an outer perforated micritic wall enclosing an internal cavity preserved as sparry calcite. In fixed specimens, the base is mostly thinner (FLÜGEL, 1983; DE CASTRO, 1990: "strato rudimentale"; SCHLAGINTWEIT, 2012). Internal structures typically with thinner walls than the enclosing one were interpreted as daughter-colonies (DE CASTRO, 1988, 1990), thus implying an algal origin, or ontogenetic stages of an animal (FLÜGEL, 1983). In some specimens, there are several stacked structures like a nested Russian doll (matryoshka) (see Pl. 1a). Leaving these interpretations open, they are neutrally referred to here as "internal bodies". Spheroidal morphotypes or morphotypes with a very thin wall seem to be non-perforate (or have pores that are not discernible?). As previously remarked by

Table 1: Diagnosis of *Thaumatoporella* and suprageneric classification referring to an algal origin (PIA, 1927; DE CASTRO, 1988).

DE CASTRO (1988, p. 249)	Order *Thaumatoporellales*	Benthic colonies, internally void, formed by a sheath layer at the periphery of the colonial cavity. Each sheath contains a single cell or a succession of cells. The vegetative reproduction leads to the formation of autocolonies.
DE CASTRO (1988, p. 249)	Family *Thaumatoporellaceae*	Colonies, presenting a more or less regular form, constituted of cells or filaments of variable length inside of sheats laterally joined to form a well defined "sheat-layer". The sheats, all perpendicular to the layer which they generate, are tightly joined among themselves and consequently form a polygonally shaped network in the belt sections of the layer. The sheats are simply or dichotomously branched. The sheat layer shows a various arrangement; in any case it delimits a colonial cavity completely occluded. It shows a variable number of openings, more or less pronounced and funnel shaped, with the wider part towards the internal cavity of the colony. A single colony may contain in its cavity one, two or three generations of daughter-colonies (autocolonies) of variable size, and of the same or different shape; the shape can be the same or different from the parent. Within the colony we can find daughter-colonies lacking a cavity, with sheats distributed according to open surfaces of variable form.
PIA (1927, p. 69, translated from German)	Genus *Thaumatoporella*	In general, morphology and disposition of pores ("Äste") compares to Triassic macroporellas. The shape of the thallus and the main axis though is very irregular, ramifying and bending. This recalls dasyporellas. However, a direct connection to these is unlikely. The genus may in fact go back to *Macroporella*.

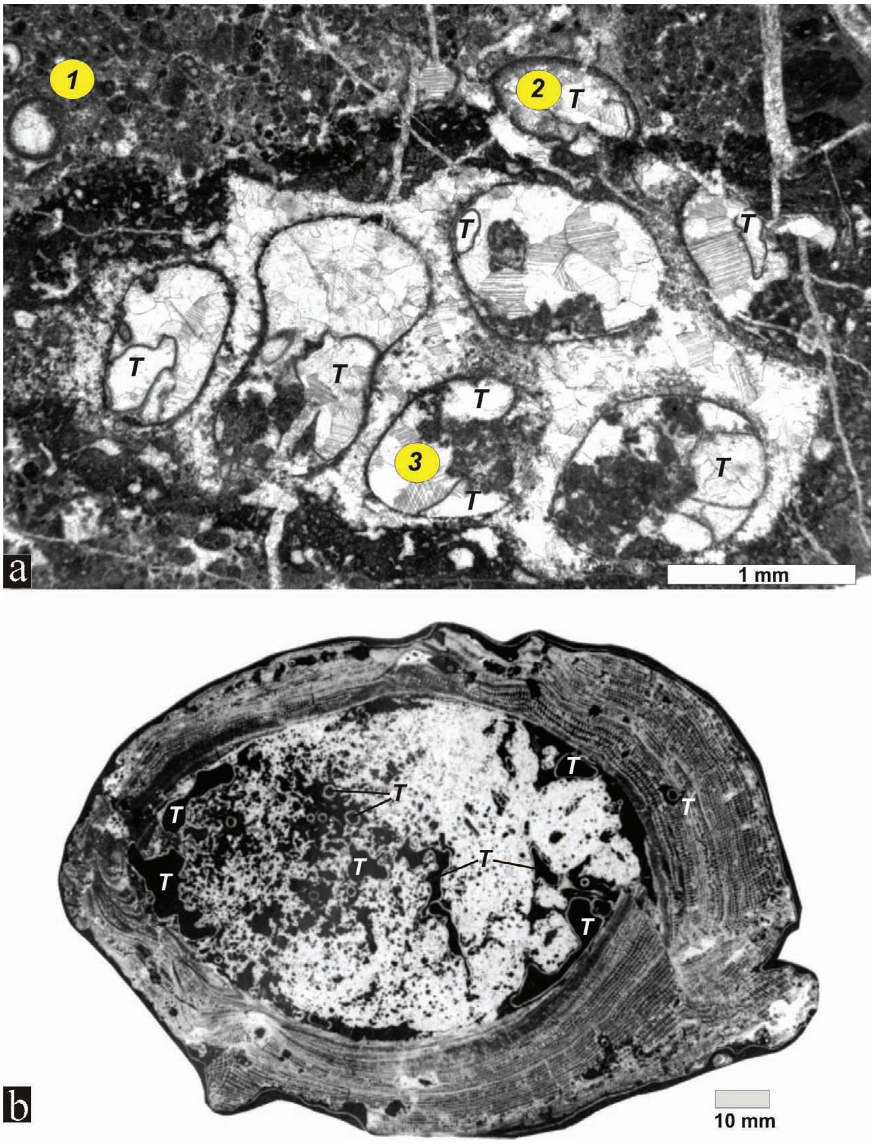


PLATE I

Examples for the way of life of Mesozoic thaumatoporellaceans (T).

a Specimens showing different life strategies: free in the micritic matrix (*1*), epilithic, attaching to microbial crusts that envelope a gastropod shell (*2*) and thus likely documenting a post-mortem colonization, and cryptoendolithically inside the inner whorls of the shell (*3*). Pliensbachian of Mount Biokovo, Croatia, thin-section VE 514-13 (see GUSIČ, 1977).

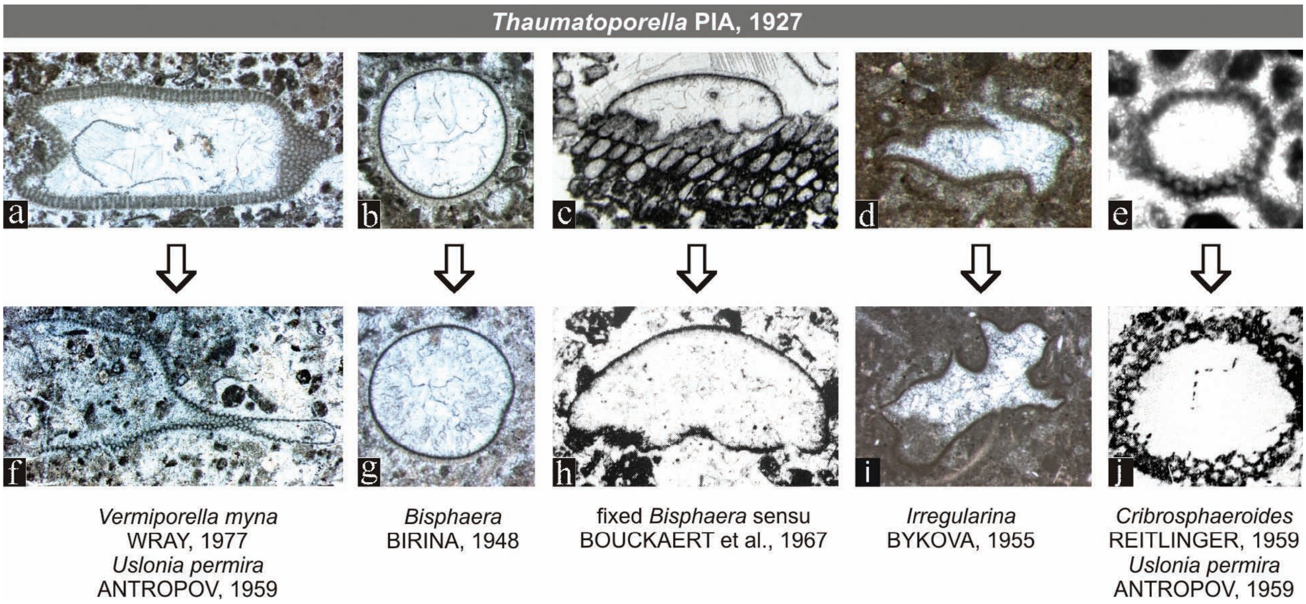
b Specimens inside rudist shell of *Praeradiolites acutilamellosus*. Some are attached to the inner side of the rudist shell others are dispersed in the micritic filling. Cenomanian of northern Italy (modified from CAFFAU et al. 1996: pl. 7, fig. 1). Note the sponge borings (ichnogenus *Entobia*) parallel to the shell surface (upper side).

PIA (1938), both the wall thickness and the dimensions of the pores (or alveoli) are highly variable (for details see section 3.4).

In general, the polymorphism of *Thaumatoporella* PIA and the resulting taxonomic splitting in the past is widely accepted among (Mesozoic) micropaleontologists (Tab. 2). This concept is now applied here to a variety of problematic Palaeozoic “foraminifera” and “algae” (Figs. 2–3, Tab. 2).

3.3. Generic interpretation of the Palaeozoic forms

The priority concept of the Linnean taxonomic system is it´s independence from the biological origin (plant or animal) of a taxon in question, and that it is mandatory for names below the rank of family (ICBN Art. 11). It refers to the oldest available name as the valid name of a taxon (ICZM Art. 23). In the present case study different taxa (in order of publication date) are considered:



Vermiporella myna WRAY, 1977 *Uslonia permira* ANTROPOV, 1959

Bisphaera BIRINA, 1948

fixed *Bisphaera* sensu BOUCKAERT et al., 1967

Irregularina BYKOVA, 1955

Cribrosphaeroides REITLINGER, 1959 *Uslonia permira* ANTROPOV, 1959

Figure 3: Variability of Mesozoic *Thaumatoporella* PIA (**a-e**) and application/transfer of this concept to a variety of Palaeozoic (Devonian) parathuramminid foraminifera-algae *incertae sedis* (**f-j**). Without scales. Mesozoic examples: Liassic of Albania (a, d-e) and Italy (c); Cenomanian of Serbia (b). Palaeozoic examples: Devonian of Germany (f-g, i), Luxembourg (h, from BOUCKAERT et al., 1977: Pl. 3, fig. 57), and Russia (from CHUVASHOV, 1965: Pl. 3, fig. 4).

- *Vermiporella* STOLLEY, 1893 (introduced as an alga)
- *Thaumatoporella* PIA, 1927 (introduced as an alga)
- *Bisphaera* BIRINA, 1948a (introduced as a foraminifer)
- *Irregularina* BYKOVA, 1955 (introduced as a foraminifer)
- *Uslonia* ANTROPOV, 1959 (introduced as a foraminifer)
- *Cribrosphaeroides* REITLINGER, 1959 (introduced as a foraminifer)

Vermiporella was described as a dasycladalean alga by STOLLEY (1893) from Ordovician-Silurian erratic boulders of the Baltic coast, as having bent and branching tubes with simple pores, either perpendicular or slightly inclined to the axis. Based on silicified and three-dimensionally preserved thalli from Ordovician boulders of the Baltic coast, a revised diagnosis was given by KOZLOWSKI & KAŹMIERCZAK (1968), showing that the structure of *Vermiporella* is “fundamentally different from that previously described by various authors” to this genus. The alga is characterized by dichotomously branching (in various planes), and anastomosing tubes, giving rise to a three-dimensional bush-like thallus structure, “forming a sort of a tangled network or lattice” (KOZLOWSKI & KAŹMIERCZAK, 1968: p 331). Inside the tubes, a central stem that occupies about 1/3 of the diameter occurs, displaying regular contractions. Attached to the stem, three orders of lateral branches are present forming regular whorls. In addition, sporadic septae and spores of the type of oospores occur in the central stem. Concerning the taxonomic position, KOZLOWSKI & KAŹMIERCZAK (1968) stress the mixed character, partly including features of dasycladalean (e.g., regular arranged branches) and ulotrichalean algae. Concerning “*Vermiporella myna*” (here considered a possible representative of the genus *Thaumatoporella*), the light-sparitic thick-walled appearance of representatives of *Vermiporella*, e.g., *V. canadensis* JOHNSON, 1970 is striking. This difference in the wall microstructure (aragonitic in *Vermiporella*) between both was previously stressed by VACHARD (1994, p. 37).

In the decades following the introduction of some of the listed taxa, they were controversially discussed including the proposal of synonymies and new combinations, and some were renamed:

- *Cribrosphaera* was renamed as *Cribrosphaeroides* by REITLINGER (in RAUZER-CHERNOUSOVA & FURSENKO, 1959).
- CHUVASHOV (1965) proposed the new combination *Cribrosphaeroides permirus* (ANTROPOV) by assuming the synonymy of *Uslonia* with *Cribrosphaeroides*.

Table 2: Taxonomic concept of Mesozoic to Early Cenozoic *Thaumatoporella* (e.g., SARTONI & CRESCENTI, 1959; RADOIČIĆ, 1960; FLÜGEL; 1983; DE CASTRO, 1990) confronted with possible Palaeozoic representatives.

Mesozoic	Paleozoic
Polygonella ELLIOTT, 1957	*Bisphaera* BIRINA, 1948
Lithoporella elliotti EMBERGER, 1957	? *Irregularina* BYKOVA, 1959
Messopotamella DRAGASTAN et al., 1985	*Cribrosphaeroides* REITLINGER, 1959
Vermiporella crisiae DRAGASTAN et al., 1989	*Uslonia* ANTROPOV, 1959
Micritosphaera SCOTT, 1978	*Vermiporella myna* WRAY, 1967

- *Bisphaera*, *Irregularina*, and *Cribrosphaeroides* were included in the family Irregularinidae by ZADOROZHNYY & YUFEREV (1984) (see also VACHARD, 1994) showing their inferred systematic relationships.
- VACHARD (1994: p. 38) transfered *Vermiporella myna* WRAY to the genus *Cribrosphaeroides*, a view followed by MAMET et al. (1999). Other authors, however, did not adopt this proposal (FENG et al., 2010).
- *Uslonia permira* was interpreted by VACHARD (1994: p. 29) as non-biogenic, corresponding to "large and irregular sparitic debris" namely cortoids.
- VACHARD (1994: Fig. 15) illustrated continuous morphological transitions between *Bisphaera* BIRINA, 1948 and *Irregularina* VISSARIONOVA, 1950, however without treating the latter as a synonym of the former.
- MAMET & PRÉAT (2009) treated *Vermiporella myna* as a synonym of *Uslonia permira* ANTROPOV, thus rejecting the cortoid interpretation of VACHARD (1994).
- AFANASIEVA & AMON (2011) considered *Bisphaera* as representing a radiolarian assigned to the genus *Trochodiscus* HAECKEL, 1887, thereby introducing the new combination *Trochodiscus malevkensis* (BIRINA, 1948). The aspect of a possible radiolarian nature of some parathuramminids (e.g., *Bisphaera*) was also envisaged by VISHNEVSKAYA & SEDAEVA (2002). It is worth mentioning that BYKOVA (1955: p. 15) also treated *Bisphaera* as a pelagic form, due to its spheroidal shape and the primitiveness of its structure. Further discussion of these issues is not necessary as they are not accepted here.

The different taxonomic combinations (also introduced by outstanding experts in Palaeozoic microfossils and to our knowledge without studying the Russian type-material) clearly expressing the continuing uncertainty. This is also evident from the differing interpretations concerning the biogenic nature, from unilocular foraminifera, algae (algae *incertae sedis*, Dasycladales, Thaumatoporellaceans *sensu* DE CASTRO), microproblematicum, and non-biogenic in the case of *Uslonia* (see Tab. 3).

Here we pick up again the idea (or hypothesis) already expressed by VACHARD & CLEMENT (1993, p. 301, translated): "*In conclusion it might therefore be appropriate to add false Palaeozoic foraminifera,* Bisphaera *and* Cribrosphaeroides, *to the Mesozoic Thaumatoporellales*" (although before, e.g., VACHARD, 1991 and later again, e.g., VACHARD et al., 2010, *Bisphaera* was considered as representing a unilocular foraminifer). Shortly afterwards, this view was further specified by VACHARD (1994, p. 34) as follows: "*The genus* Cribrosphaeroides *is morphologically closest to* Thaumatoporella, *and daughter-colonies seem to be figured by* CHUVASHOV (1965)". To comprehend this hypothesis, it is re-illustrated here and compared to similar internal structures observed from Cretaceous "*Micritosphaera*" (SCOTT, 1978) (Fig. 2).

Excluding the genus *Vermiporella*, *Thaumatoporella* represents thus the oldest available name for the group of *Bisphaera-Cribrosphaeroides*-type microfossils that, due to their appearance as various morphotypes, were ascribed to different genera (see discussion) (see Fig. 3). This conclusion follows the interpretation of *Bisphaera* as a cyst stage of a possible *Thaumatoporella* species (Pl. 3). Concerning the stratigraphy reported to date in the literature, only slightly dif-

Table 3: Different views of the nature (biogenic/abiogenic) of the group *Bisphaera-Cribrosphaeroides-Uslonia-Vermiporella myna* according to literature data supplemented by our new interpretation.

Bisphaera BIRINA	*Cribrosphaeroides* REITLINGER	*Uslonia* ANTROPOV	*Vermiporella myna* WRAY
unilocular foraminifer (BIRINA, 1948; FLÜGEL & HÖTZL, 1971; LOEBLICH & TAPPAN, 1987; VACHARD, 1991; EDGELL, 2004; VACHARD et al., 2010) incertae sedis (TOOMEY & MAMET, 1979) thaumatoporellacean alga (VACHARD & CLEMENT, 1993) free stage of a psammobiontic, deformed taxon, namely *Irregularina* (VACHARD, 1994) radiolaria, namely *Trochodiscus* HAECKEL (AFANASIEVA & AMON, 2011)	unilocular foraminifer (REITLINGER, 1959; FLÜGEL & HÖTZL, 1971; LOEBLICH & TAPPAN, 1987; VACHARD, 1991; MAY, 1994) alga (TOOMEY & MAMET,1979) thaumatoporellacean alga (VACHARD, 1994)	unilocular foraminifer (ANTROPOV, 1959; LOEBLICH & TAPPAN, 1987) incertae sedis (TOOMEY & MAMET, 1979) non-biogenic, irregular sparitic debris (cortoids) (VACHARD, 1994)	dasycladale alga (WRAY, 1967; FLÜGEL & HÖTZL, 1971) ulvophycean alga (FENG et al., 2010) thaumatoporellacean alga (VACHARD, 1994: *Cribrosphaeroides myna*)
This work			
free cyst stage of a thaumatoporellacean (incertae sedis), possibly *Thaumatoporella* PIA	*thaumatoporellacean* (incertae sedis), possibly *Thaumatoporella* PIA		

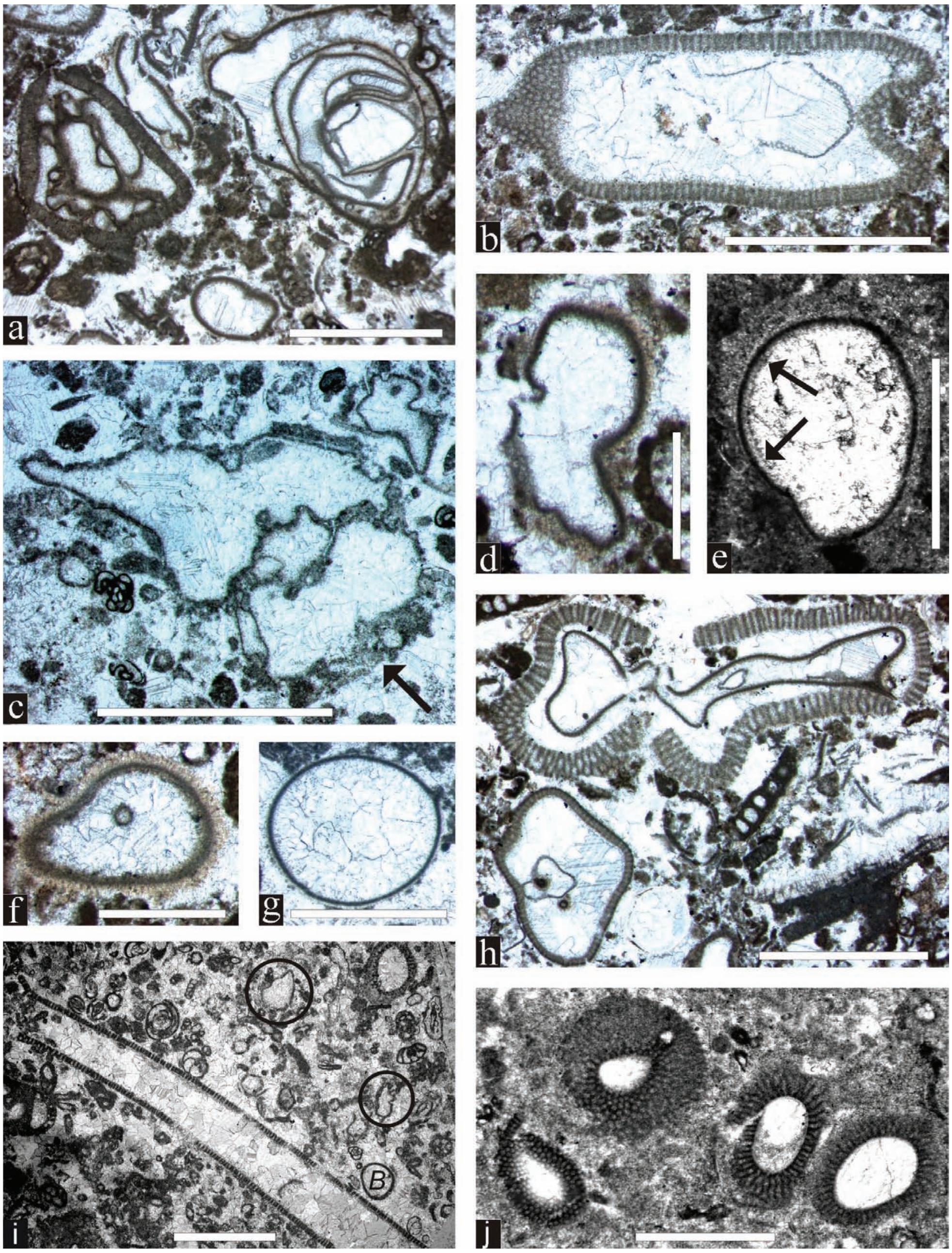


PLATE II

Morphological variability of *Thaumatoporella parvovesiculifera* (RAINERI) from the Liassic (Late Sinemurian) of Albania (a-d, f, h), Lower Cretaceous (Aptian) of Italy (e), Middle Jurassic (Late Aalenian) (g) and the Upper Cretaceous (Coniacian) of Slovenia (i) and Croatia (j).

- **a** *Thaumatoporellaceans* as microfacies dominating biogens. Note the nesting doll-like "bodies" placed one inside the others (daughter-colonies *sensu* DE CASTRO, 1988 or ontogenetic stages sensu FLÜGEL, 1983). Rhapsha-Tamara, NW-Albania, thin-section A 3639.
- **b** Tube-like morphotype with a handle (left) and constriction (right). Note the thin-walled internal "body" (compare to a). Rhapsha-Tamara, NW-Albania, thin-section A 3639.
- **c** Irregular-shaped morphotype exhibiting thin walls, interpreted as psammobiontic forms winnowed from a packstone (see remains of original matrix around the two specimens in the centre). Rhapsha-Tamara, NW-Albania, thin-section A 3644.
- **d, f** Irregular rounded specimens exhibiting constrictions. This morphotype compares to specimens of the Palaeozoic *Bisphaera*. Rhapsha-Tamara, NW-Albania, thin-section A 3639.
- **e** Same as d and f. Note the inner fibrous calcitic layer (arrows). Aptian of Sorrento Peninsula, S-Italy (see RASPINI, 2011).
- **g** Spherical morphotype exhibiting a thin wall without detectable pores. This morphotype compares to specimens of the Palaeozoic *Bisphaera*. Mount Biokovo, Croatia, thin-section BST 8-1.
- **h** Specimens with internal "bodies" (compare to a). Note that the latter display thinner walls and completely mimic the shape of the external wall (specimen above). Rhapsha-Tamara, NW-Albania, thin-section A 3639.
- **i** Grainstone with benthic foraminifera (mainly miliolids) and variously-shaped thaumatoporellaceans: cylindrical, lobate to bizarre-shaped ("*Irregularina*"-type, circles) and globose ("*Bisphaera*"-type, *B*). Coniacian-Santonian of SW Slovenia (see JEŽ et al., 2011: Fig. 7d).
- **j** Thick-walled specimens (*Thaumatoporella* wackestone). Coniacian of Mljet Island, Croatia. Thin-section MRS 3-1.

Scale bars 1 mm for a-d, h-i; 0.5 mm for e-g, j.

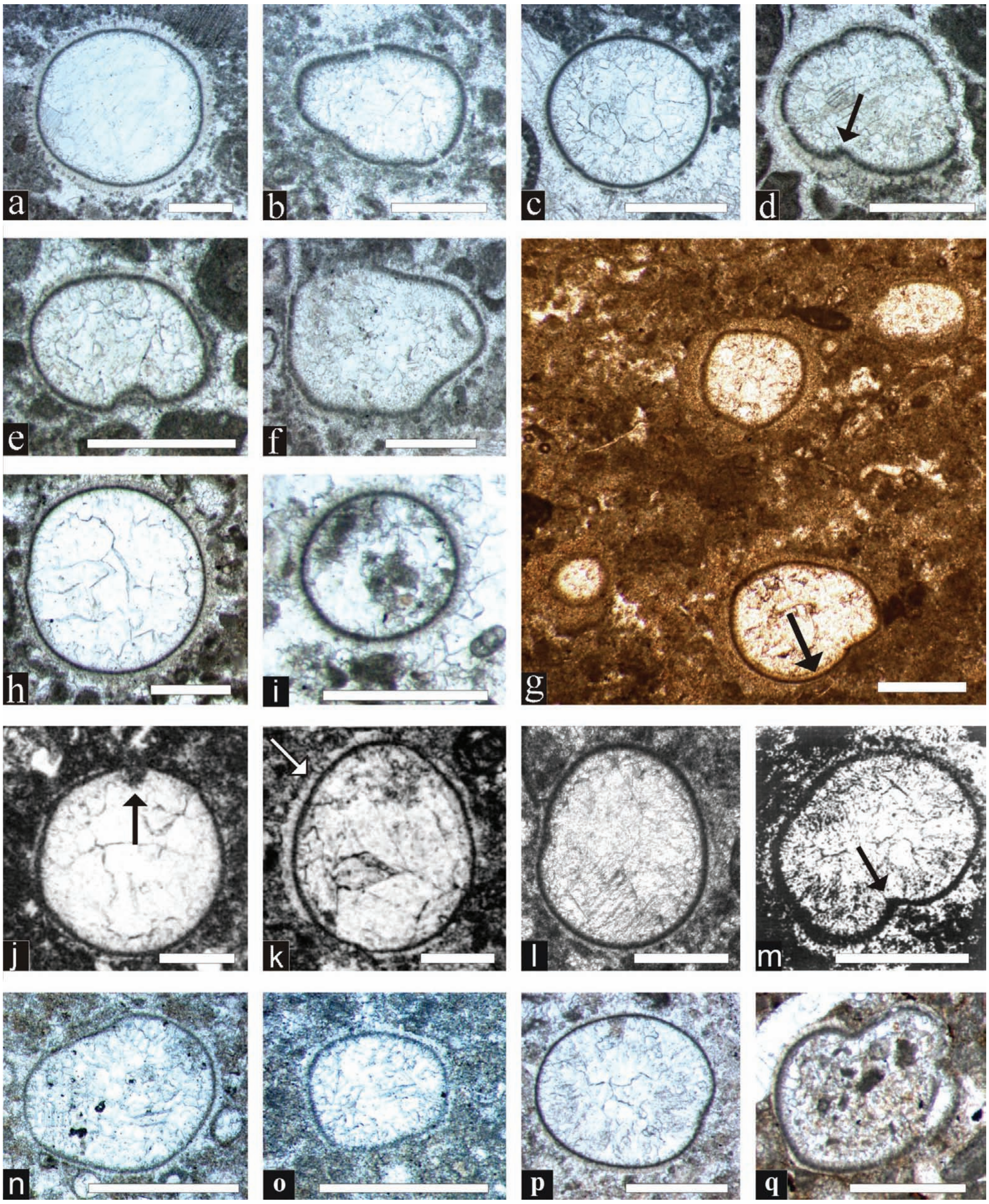


PLATE III

Spheroidal thaumatoporellaceans interpreted as cyst stages: *Thaumatoporella parvovesiculifera* (RAINER) (a-n) and *Thaumatoporella*? *malevkensis* (BIRINA) nov. comb. (m-q).

a Pliensbachian of Croatia, thin-section VE 514-2 (leg. I. GUSIČ).
b Pliensbachian of Croatia, thin-section VE 514-3 (leg. I. GUSIČ).
c Late Aalenian-Early Bajocian of Croatia, thin-section BST 8-1 (leg. I. VELIĆ).
d-e Note the slight constriction (arrow). Compare with example (m). Late Aalenian-Early Bajocian of Croatia, thin-section SL 4a (leg. I. VELIĆ).
f Late Aalenian-Early Bajocian of Croatia, thin-section SL 5B (leg. I. VELIĆ).
g Late Aptian of Italy. Note the inner inner fibrous layer (arrow) (leg. A. RASPINI).
h-i Late Cenomanian of Serbia, thin-section RR 6145 (leg. R. RADOIČIĆ).
j-k Modified from SCOTT (1978: Fig. 1A and 1D), figured as *Micritosphaera ovalis*. Note the wall interruption (interpreted as aperture in the original description) in (arrow in 10) and the outer cement fringe in (arrow in 11). Thin-sections 9015-19 and 9019-19.
l Norian-Rhaetian of Austria, thin-section OK W 530-1 (leg. O. KRISCHE).
m *"Bisphaera variabilis"* CONIL & LYS, modified from EDGELL (2004: Pl. 1, Fig. 1); Devonian of Australia. Note the slight constriction (arrow).
n Devonian of Czech Republic, thin-section HL 234.
o Devonian of Czech Republic, thin-section HL 259.
p Devonian of Germany, thin-section K 41.
q Devonian of Germany, thin-section K 44.
Scale bars 0.3 mm.

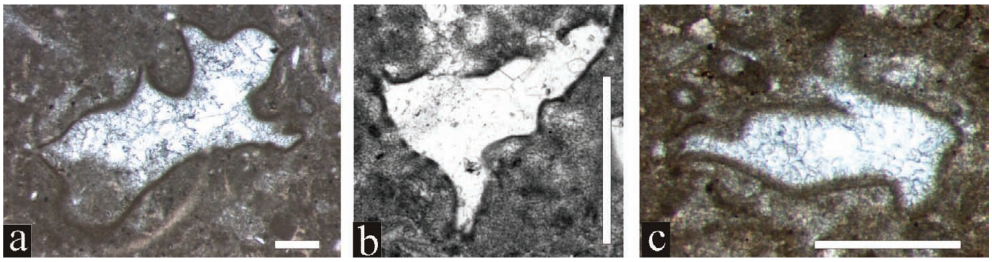


Figure 4: Irregular shaped Palaeozoic *Irregularina* (a) and Mesozoic thaumatoporellaceans (b-c) assumed to have a psammobiontic way of life (SCHLAGINTWEIT et al., 2013, for details). **a** *Irregularina* without discernible pores. The laterally arising prolongations were described as "apertural nozzles" of *Irregularina karlensis* VISSARIONOVA. Givetian of Germany, thin-section SB 16. **b** *Thaumatoporella* exhibiting perforate wall. Upper Cretaceous ("Senonian") of Albania, thin-section Kru 1b. **c** Specimen without discernible pores. Liassic of Albania, thin-section A 3642.

fering ranges have been defined and these can therefore not be considered as a strong argument against this interpretation.

Bisphaera: Early Devonian (VACHARD, 1994) up to the upper part of the Tournaisian (REITLINGER et al., 1996; KULAGINA, 2013) [but with the possibility of emerging since the Late Ordovician (cf. the thin sectioned objects from Uggwa Limestone, Carnic Alps – KREUTZER, 1992, pl. 3, fig. 4); or even Early Ordovician (SABIROV & GUSHCHIN, 2006, Tajikistan) though the latter was considered dubious by VACHARD et al., 2010, p. 220].

Irregularina: Givetian – Tournaisian (VACHARD, 1994) [possibly from Silurian–Devonian (JUYAL et al., 2009, determined by I. Premoli Silva) and also Ordovician (KREUTZER, op. et loc. cit., figured)].

Cribrosphaeroides: Givetian (VACHARD, 1994) up to the upper part of the Tournaisian (KULAGINA, 2013) [possibly Silurian–Devonian (JUYAL et al., op. cit.), and, possibly since the Late Ordovician (BYKOVA, 1961, Kazakhstan)].

However, one must be aware that shifts in these ranges are always possible bearing in mind the evolving knowledge base on the stratigraphic distribution of Mesozoic *Thaumatoporella* as indicated in the introduction of this paper.

Concerning the genus *Irregularina* BYKOVA, 1955, the possible transfer to thaumatoporellacens is problematic as no "internal bodies" (= daughter-colonies *sensu* DE CASTRO) or perforations in the wall were observed in our material (see SCHLAGINTWEIT et al., 2013, for details) (Fig. 4a). The morphology, however, is well known from Mesozoic *Thaumatoporella* (SCHLAGINTWEIT et al., 2013, for details) including forms with (Fig. 4b) and without detectable pores (Fig. 4c). It is worth mentioning that *Irregularina longa* described by KONOPLINA (1959) is said to possess a perforated wall. In fact, this form most likely corresponds to irregular tubiform morphotypes of the species described as *Vermiporella myna* by WRAY (1967) (see details in the discussion) (e.g., Pl. 4m). Further remarks on all aspects and interpretations are given in "remarks and discussion" below the systematic description.

3.4. Systematic micropaleontology

The suprageneric taxonomy used here partly follows the suggestion of DE CASTRO (1988, 1990). While accepting the family name, however, we consider the algal nature as doubtful.

Incertae sedis
Family Thaumatoporellaceae DE CASTRO, 1988
Genus *Thaumatoporella* PIA, 1927

(Assumed) synonyms: *Bisphaera* BIRINA, *Cribrosphaeroides* REITLINGER, ? *Irregularina* BYKOVA, *Uslonia* ANTROPOV.

***Thaumatoporella*? *malevkensis* (BIRINA, 1948) nov. comb.**

(Fig. 4a?, Fig. 5, Fig. 6a, Figs. 7a–b, Pl. 3m–q, Pls. 4–8)

*1948a. *Bisphaera malevkensis* n. gen., n. sp.– BIRINA, p. 159, Pl. 2, fig. 9.

1954. *Cribrosphaera simplex* n. gen., n. sp.– REITLINGER, p. 65, Pl. 18, fig. 7, Pl. 19, figs. 9-10, ? Pl. 21, fig. 1 (Remark: possibly a fixed specimen).

1959. *Cribrosphaeroides simplex* (REITLINGER) – REITLINGER in RAUZER-CHERNOUSOVA & FURSENKO, p. 174, fig. 70.

1959. *Uslonia permira* n. gen., n. sp.– ANTROPOV, p. 28, Pl. 1, figs. 1–2.

1967. *Vermiporella myna* n. sp.– WRAY, p. 31, text-fig. 12, Pl. 6, figs. 6–8, Pl. 7, figs. 1–2.

Description: The Devonian specimens display a wide variability with respect to shape, biometric data (size, pore diameter, wall thickness) and wall preservation (Figs. 8-9). The shape ranges from spherical, ovoid with or without constrictions, irregular to bent tubes displaying irregular constrictions and swellings. Concerning the circular sections (Pl. 4f), these may result either from spherical specimens, or represent the transverse sections of tubes. In tangential sections of the wall, a honey-comb-like pattern is discernible (Pl. 4c). Specimens with a round outline exhibiting more or less equal wall thickness throughout, and poorly detectable pores, can be assigned to spheroidal morphotypes (= *Bisphaera*-type) (Fig. 5b, Pl. 5d, Pl. 8h). Such sections may be more or less completely round (Pl. 5d), ovoid (Pl. 8h), with one to several constrictions (e.g., = type "*Bisphaera elegans*", Pl. 5h). One shallow constriction in a slightly elliptical form may result in a virtual "two-chambered" bipartition along a central symmetry plane (= type "*Bisphaera malevkensis*", Pl. 7d).

Tubes may be more or less straight (Pl. 8c) to slightly curved (Pl. 4m, Pl. 5b, Pl. 7j, Pl. 8c) or irregular serpentine to sigmoidally curved (Pl. 4l, Pl. 8b, d). More rarely specimens show irregular branching or bifurcation (Fig. 6a). Such shapes were illustrated for both "*Vermiporella myna*" (WRAY, 1967: Pl. 6, fig. 7) and "*Uslonia permira*" (ANTROPOV, 1959: Pl. 1, figs. 1-2). In rare cases, tubes exhibit irregular club-shaped swellings (Pl. 7c). The interior of the polymorphic specimens is usually filled with sparry calcite. Sometimes, partial damage may have resulted in the intrusion of sediment grains from the surrounding matrix (e.g., Pl. 5b). Rather common, various shaped "internal bodies" with thin micritic walls, with poorly preserved to non detectable pores, thus appearing imperforate, can be observed. These may be rather small compared to the outer enclosing tube or other morphology, thus seemingly floating in its interior (e.g., Pl. 6a). More rarely these structures are comparatively large, almost entirely filling the interior and thus in part closely attached to the surrounding wall (Pl. 6e). In exceptional cases, there are several "bodies" stacked one in another (Pl. 8e). These structures were previously illustrated from "*Cribrosphaeroides permirus*" by CHUVASHOV (1965) or from "*Bisphaera* sp." by VACHARD & CLEMENT (1994). They are in our opinion slightly recognizable in the two specimens of "*Uslonia permira*" illustrated in the work of ANTROPOV (1959: Pl. 1, figs. 1-2). These two specimens resemble the one illustrated here on Plate 5j.

The wall of *Thaumatoporella*? *malevkensis* (BIRINA) is composed of dark micrite, appearing either homogeneous (without detectable pores) or transsected by close-set pores that in tangential sections appear as a typical honey-comb pattern (Pl. 4c, Pl. 7k, Pl. 8j). It is common, for a hyaline fibrous outer zone to be present, mostly in *Bisphaera*-type specimens with comparatively thin walls without detectable pores (e.g., Pl. 5b, e, i) (compare Liassic *Thaumatoporella* specimens in Pl. 2d, f-g). Another type of preservation is represented by a less dense outer zone (microsparite?) that due to its poorly recognizable pores does not seem to represent a precipitated cement but likewise a part of the former organism wall. Such an alteration phenomenon is also reported from Mesozoic *Thaumatoporella* (e.g., DE CASTRO, 1991, Pl. 3, fig. 4).

Dimensions: (see also Figs. 8-9)
Diameter of (subcircular) sections: 0.28 to 0.55 mm
Diameter of ovoid sections: up to 0.7 mm
Maximum length of tubiform morphotype: 2.25 mm
Thickness of tubiform morphotype: 0.25 to 0.4 mm
Thickness of wall: 15 to 50 µm
Diameter of pores: 8 to 31 µm

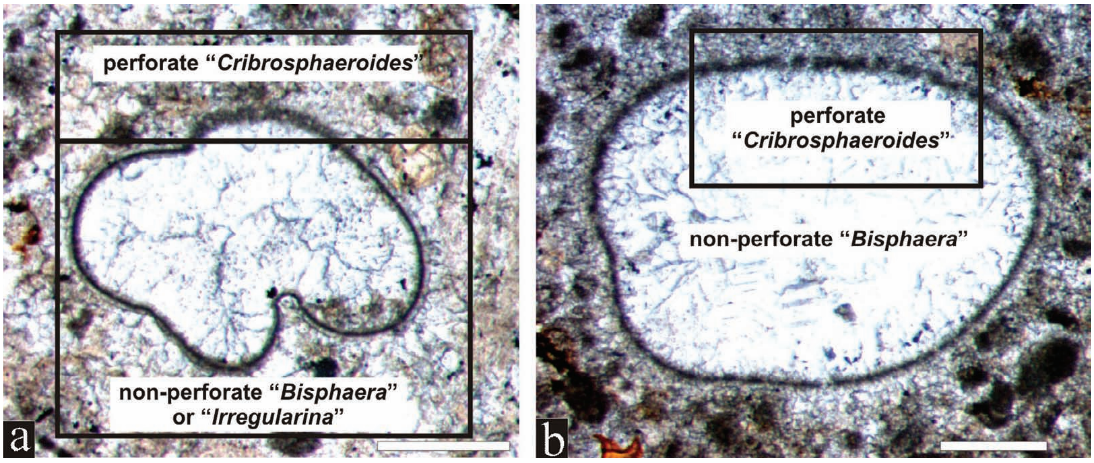


Figure 5: "Two in one" aspect of specimens lacking visible pores in the lower part (genus "*Bisphaera*") and displaying a perforate wall in the upper part (genus "*Cribrosphaeroides*"). The lobate outline may be present in both "*Bisphaera*" (or deeply multilobate in *Irregularina*) and "*Cribropshaeroides*". **a)** Thin-section K 39 **b)** K 56. Devonian (upper Eifelian) of the Hillesheim Syncline, Germany. Scale bars 0.2 mm.

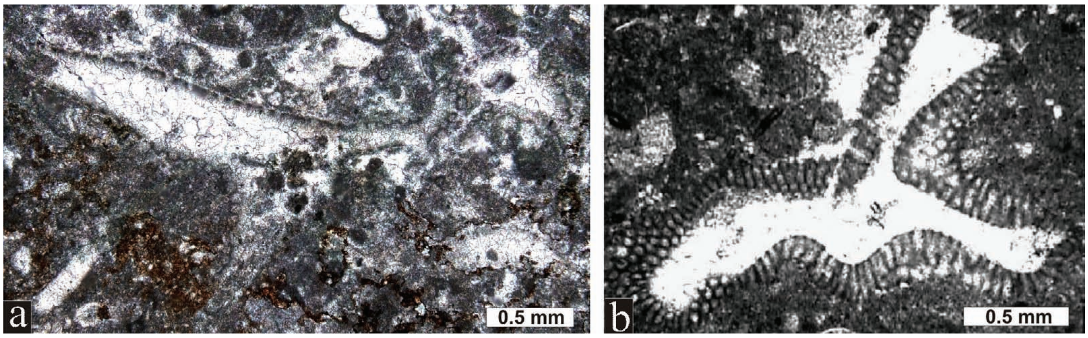


Figure 6: "Branching" specimens of *Thaumatoporella*. a) *Thaumatoporella*? *malevkensis* (BIRINA) nov. comb., Middle-Upper Givetian of Ostravice NP-824 well, Czech Republic (see ZUKALOVA, 2004: *Vermiporella* sp., Pl. 13, fig. 3). b) *Thaumatoporella parvovesiculifera* (RAINERI), Upper Cretaceous (Coniacian-Campanian interval) of south Italy (see CHECCONI et al., 2008: Pl. 1, fig. 18).

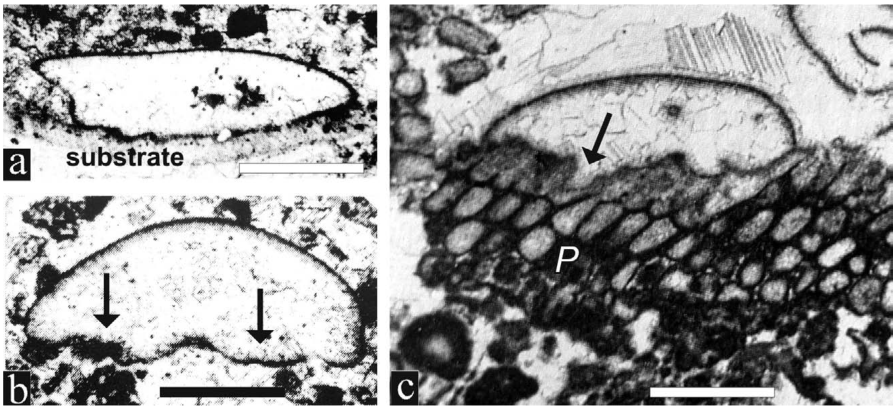


Figure 7: Attaching specimens of *Thaumatoporella*? *malevkensis* (BIRINA) nov. comb. (a-b), Devonian (Famennian) of Luxembourg (from CONIL in BOUCKAERT et al., 1977: Pl. 3, Figs. 57-58) and *Thaumatoporella parvovesiculifera* (RAINERI) (c), Liassic of Italy (modified from DE CASTRO, 1997: Pl. 24, fig. 1). Arrows in b indicate the attached side. The Liassic specimen attaches to the main axis of the dasycladale *Palaeodasycladus mediterraneus* PIA (P). Note the basal protrusion (arrow). Morphologically, these Palaeozoic and Mesozoic forms cannot be distinguished from each other (details in the text).

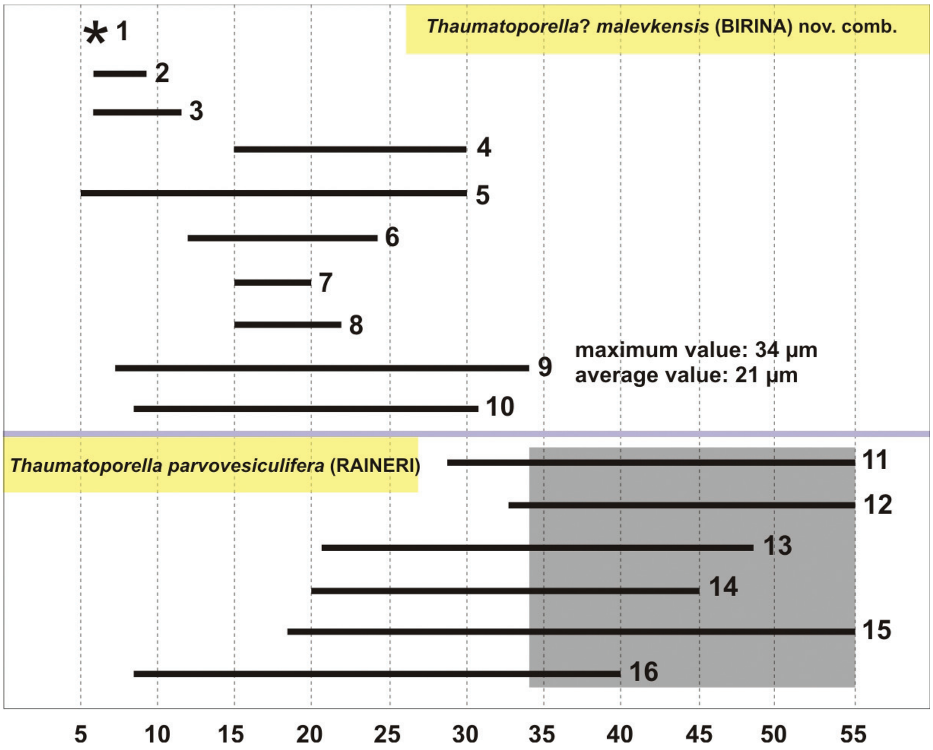


Figure 8: Pore diameter (in µm) of *Thaumatoporella*? *malevkensis* (BIRINA) nov. comb. (1-10) against *Thaumatoporella parvovesiculifera* (Pia) (11-16). 1-4 for *Cribrosphaeroides simplex*, 5 for *Uslonia permira* 6-9 for *Vermiporella myna*. 1: REITLINGER (1954) 2: CHUVASHOV (1965) 3: POYARKOV (1969) 4: VACHARD (1994) 5: ANTROPOV (1959) 6: FLÜGEL & HÖTZL (1971) 7: MAY (1994) 8: WRAY (1967) 9: TOOMEY et al. (1970) 10: This work, Givetian-Frasnian of Germany and Czech Republik 11: PIA (1938, Upper Cretaceous of Greece) 12: IMAIZUMI (1965, Upper Jurassic of Japan) 13: SARTONI & CRESCENTI (1959, Liassic and Upper Cretaceous of Italy) 14: FLÜGEL (1983, Upper Triassic of Greece) 15: JOHNSON & KASKA (1965, Upper Cretaceous of Guatemala) 16: This work, Liassic (Late Sinemurian) of Albania.

Remarks: From the pore diameters given in the literature, the range of "*Uslonia permira*"-"*Cribrosphaeroides myna*" is well present in *Thaumatoporella parvovesiculifera* but the latter also comprises specimens with distinctly greater values (Fig. 8). In contrast, also at the lower end of pore range, the Devonian representatives often exhibit smaller diameters. An equivalent observation is obtained from the wall thickness comparing Palaeozoic and Mesozoic forms (Fig. 9). Again, the measurements of the Palaeozoic forms correspond well with Mesozoic *Thaumatoporella* but the latter also exhibits distinctly thicker walls (or "cell length" in the older literature, e.g., JOHNSON & KASKA, 1965). The highly evolved Late Cretaceous representatives of *Thaumatoporella parvovesiculifera* may reach wall thicknesses of up to 230 µm as measured from DE CASTRO (1990, Pl. 4, fig. 3) (see Pl. 2j). The wall thickness of the Liassic assemblages

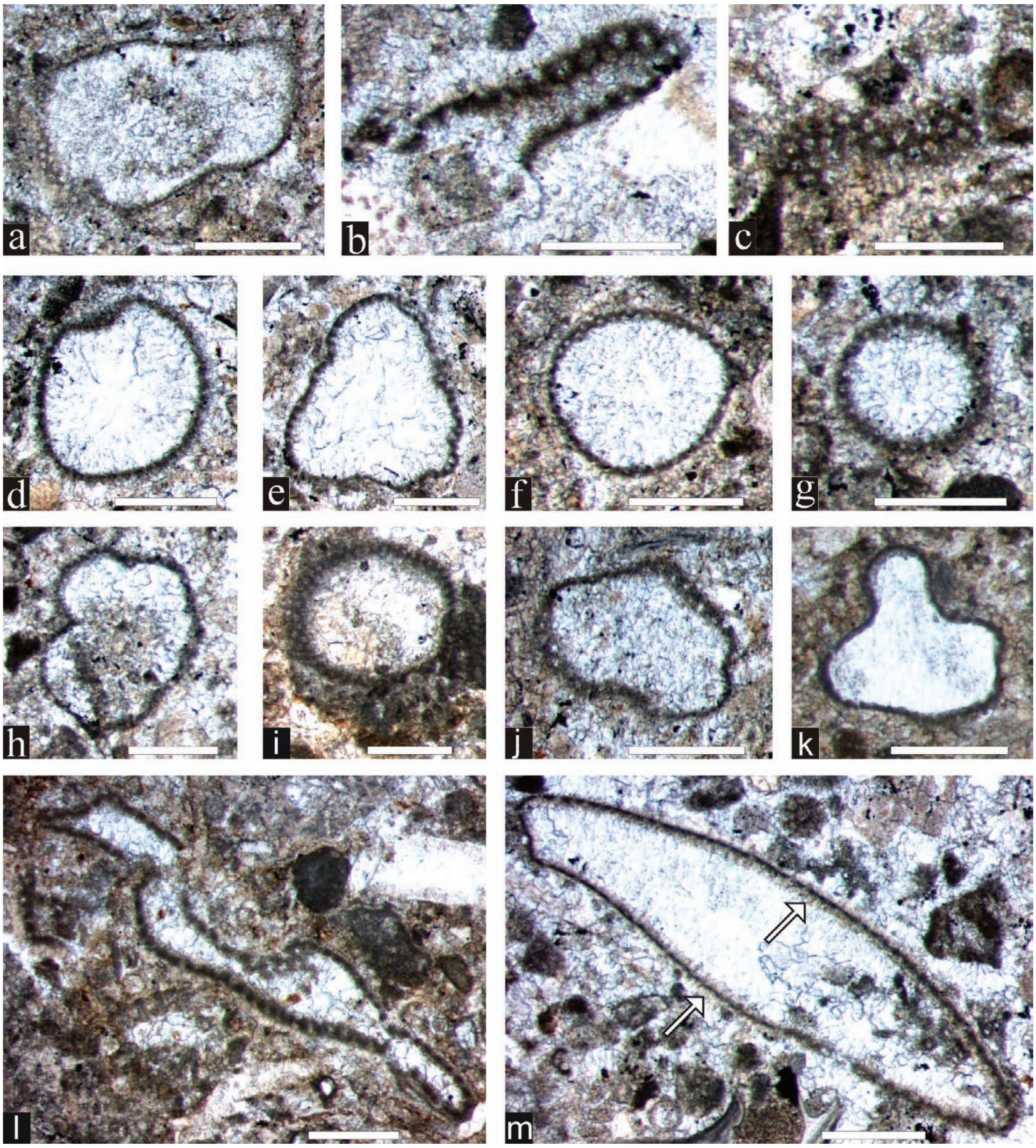


PLATE IV

Thaumatoporella*? *malevkensis (BIRINA) nov. comb. from the Devonian (upper Eifelian) of the Hillesheim Syncline, Eifel hills, Germany.

a Oblique section showing pores on the left side. Thin-section K 39.
b-c Tangential sections showing honey-comb-like pore pattern. Thin-section K 39.
d-e Slightly lobate thalli with barely visible pores, e.g., right below in e. Thin-section K 39.
f-g,i Transverse sections of spherical or cylindrical thalli showing perforate wall. Thin-section K 39.
j-k Lobate specimens with (j) and without visible pores (k). Thin-sections K 39 and K 41b.
l Longitudinal section of an irregular bended tubiform thallus with well discernible pores. Thin-section K 41b.
m Longitudinal section of a slightly bended tubiform thallus. Note the yellowish calcitic inner and outer rim (arrows). Thin-section K 39.
Scale bars 0.25 mm

shown in Plate 2a-h, ranges from ~15 to 160 µm, the pore diameters from ~8 to 40 µm. The extreme upper values of the Mesozoic forms, never reached even roughly by the Palaeozoic specimens, is here taken as evidence that we are dealing with two different taxa, interpreted as specific characteristics: *Thaumatoporella*? *malevkensis* (BIRINA) nov. comb. and *Thaumatoporella parvovesiculifera* (RAINERI). The wide range of pore diameter on the other hand, cannot be taken as a clearly defined criterion to separate "coarsely perforate" forms like "*Cribrosphaeroides*" from finely perforate forms such as some specimens of "*Bisphaera*".

Furthermore it can be stated that the overall morphological variability of the Devonian specimens is slightly reduced compared to *Thaumatoporella parvovesiculifera* (RAINERI), such as the lack of highly constricted, partitioned morphotypes in the latter.

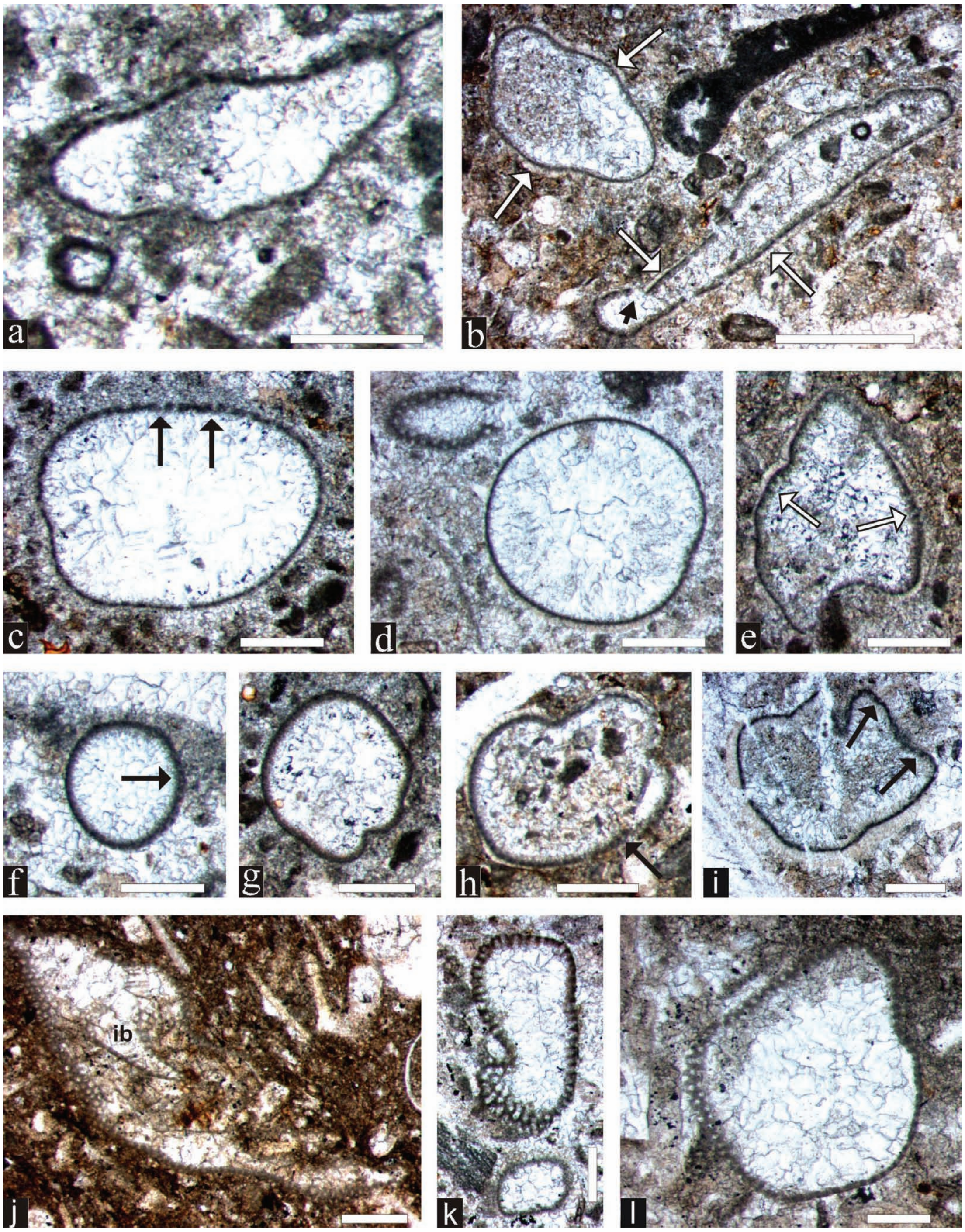


PLATE V

Thaumatoporella? malevkensis (BIRINA) nov. comb. from the upper Eifelian to lower Givetian of the Hillesheim and Sötenich synclines, Eifel hills, Germany.

a Irregular tubiform thallus. Thin-section K 56.

b Ovoid-lobate specimen without discernible pores (typus "*Bisphaera grandis-elegans*", left above, see also Fig. **4a)** and irregular cylindrical specimen showing perforate wall. Both exhibit a thin outer cement crust (white arrows). Partial breakage of the wall (black arrow) may have resulted in the intrusion of sediment grains of the surrounding matrix.Thin-section K41b.

c Ovoid specimen showing slightly lobate appearance (on the left, typus *Bisphaera*) and partly with visible pores (arrows). Thin-section K 56.

d Almost circular section with thin wall. Pores are not visible. Thin-section K 44b.

e Lobate specimen with visible pores (arrows). Thin-section K 56.

f Circular sections with pores (arrow). Thin-section K 44b.

g-h Lobate morphotypes (type "*Bisphaera malevkensis*"), partly with visible pores (arrow in h). Thin-sections K 56, K 41b.

i Lobate form with a deep-reaching constriction (above) and partly visible pores (arrow). Note the rather thick outer rim of yellowish calcite. Thin-section K44b.

j Irregular tubiform morphotype with "internal body" (ib). Thin-section SB 15.

k-l Oblique sections. Thin-section K 39 and MP 2/3.

Scale bars 0.2 mm for a, c-l, 0.5 mm for b

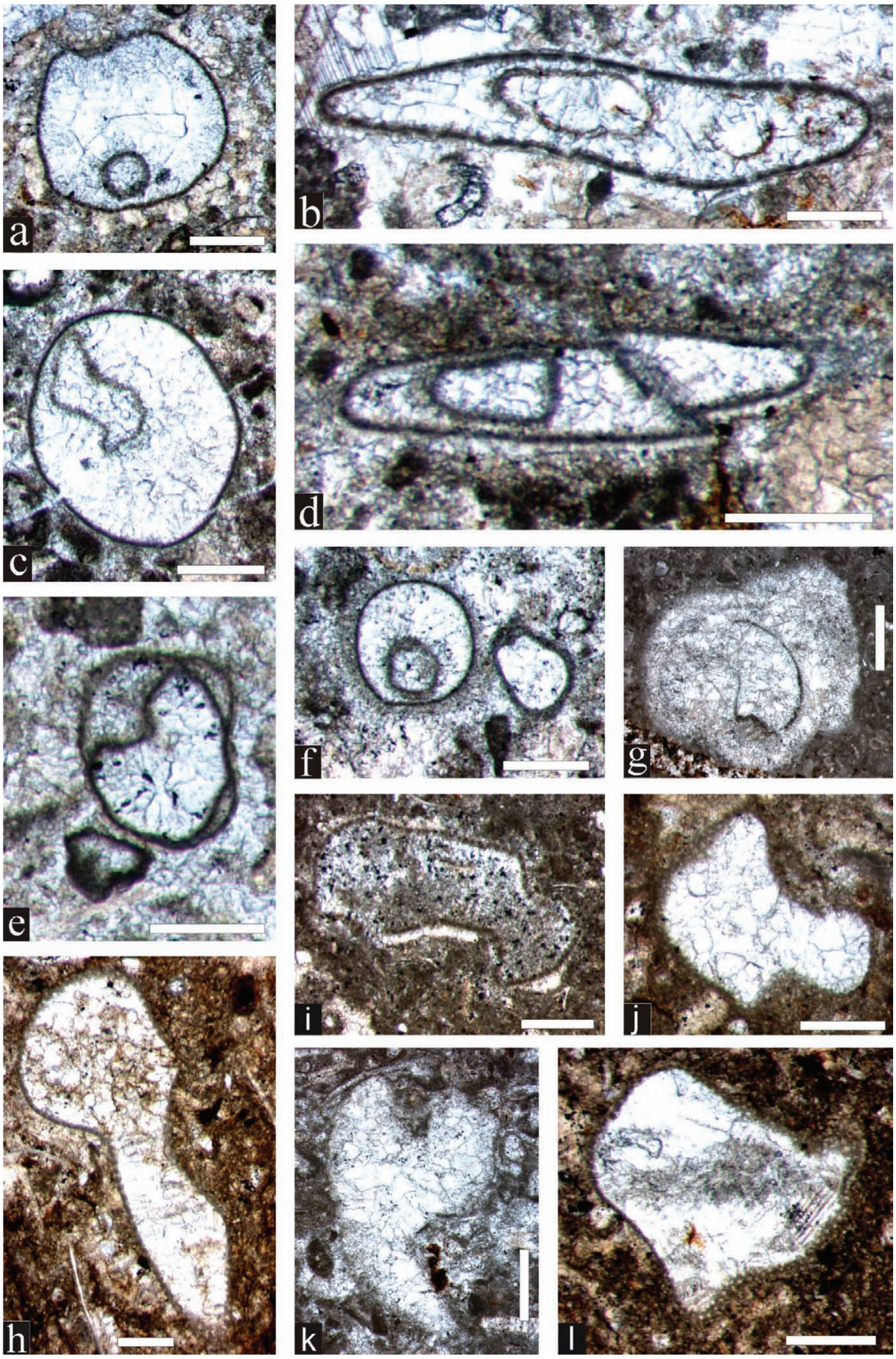


PLATE VI

Thaumatoporella? malevkensis (BIRINA) nov. comb. from the upper Eifelian to Givetian of the Hillesheim and Sötenich synclines, Eifel hills, Germany.

a-g Different sections of specimens exhibiting internal "bodies". These may be of similar (e.g., a, f) or different shape (e.g., c, e) than the external outline. Thin-sections K 39 (a, e), K 42 (b), K 56 (c-d), SH2-2 (f) and SB 16 (g).

h Irregular club-shaped specimen. Thin-section SB 15.

i-j Irregular lobate specimen showing pores and outer calcitic rim in i. Thin-sections SB 16 and SB 9.

k Multilobate specimen with obliterated and barely visible wall. Thin-section SB 5.

l Multilobate specimen exhibiting pores. Thin-section SB 15.

Scale bars 0.2 mm for a-f, h-j, l, 0.5 mm for g, k

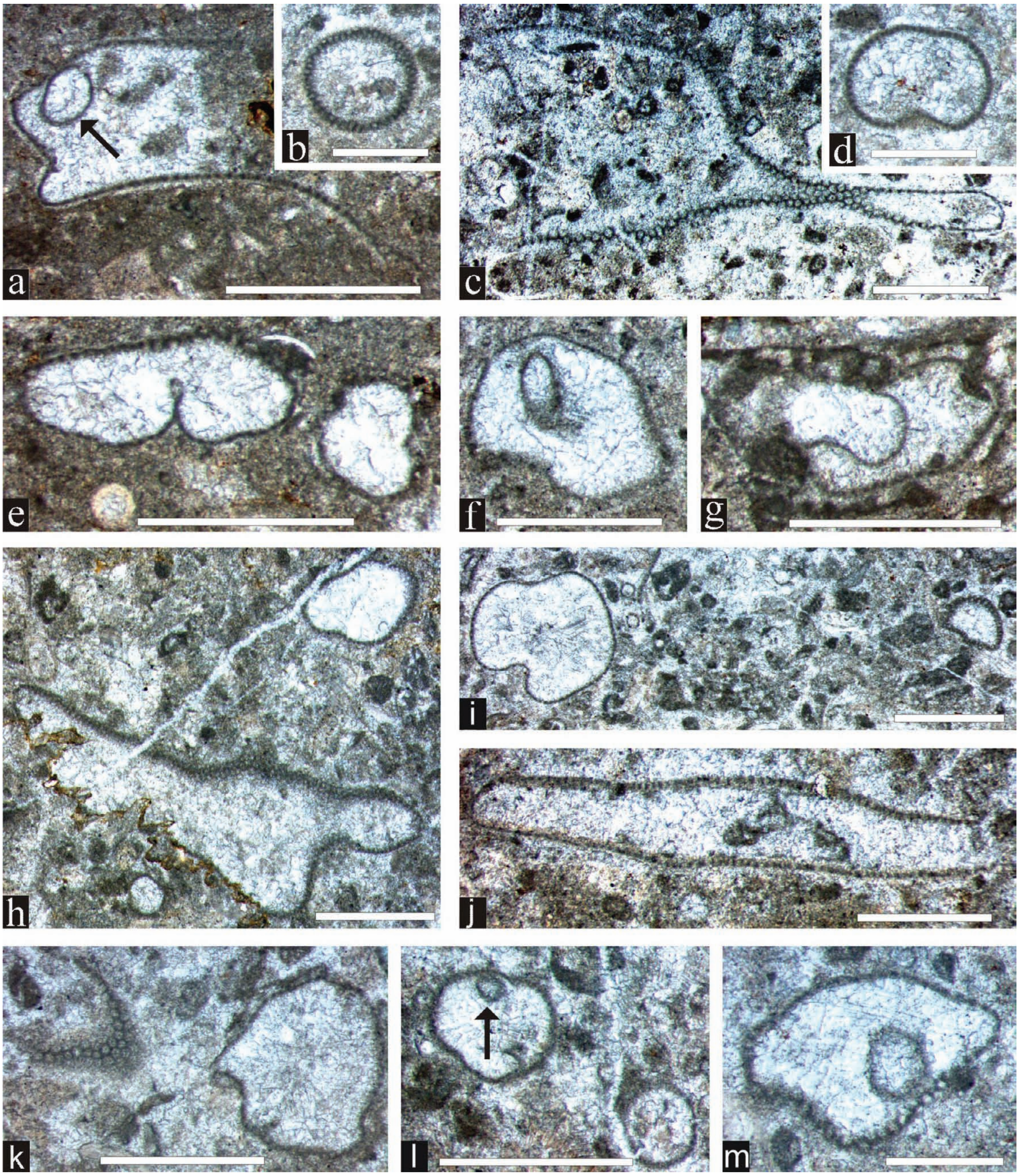


PLATE VII

Thaumatoporella? malevkensis (BIRINA) nov. comb. from the lower Givetian of the Dollendorf (b, d, e, h, i, k-m) and Sötenich (a, c, f-g, j) Synclines, Germany.

a Specimen with internal "body" (arrow). Thin-section 524.
b Transverse section of a "*Cribrosphaeroides*"-type finely perforate cylindrical or spheroidal specimen. Thin-section KBK 68.
c Club-shaped specimen (compare Liassic specimen on Pl. 1, fig. b). Thin-section B 14.
d Kidney-shaped specimen of "*Bisphaera*" type. Thin-section KBK 68.
e Irregular lobate specimens. Thin-section KBK 68.
f-g Lobate specimens exhibiting internal "bodies". Thin-sections B 14 and 524.
h Irregular lobate to subglobular (right above) specimens. The larger specimen (below) partially shows features of pressure solution (stylolites). Thin-section KBK 68-1.
i Lobate thin-walled and finely perforate "*Bisphaera*"-type specimen on the left side and thicker-walled perforate "*Cribrosphaeroides*"-type specimen on the right. Thin-section KBK 68.
j Irregular cylindrical specimen. Thin-section B 14.
k Various sections of two specimens. Thin-section KBK 68.
l-m Various sections of specimens exhibiting internal "bodies" (arrow). Thin-sections KBK 68 and KBK 69.
Scale bars 0.5 mm, except b, d = 0.3 mm.

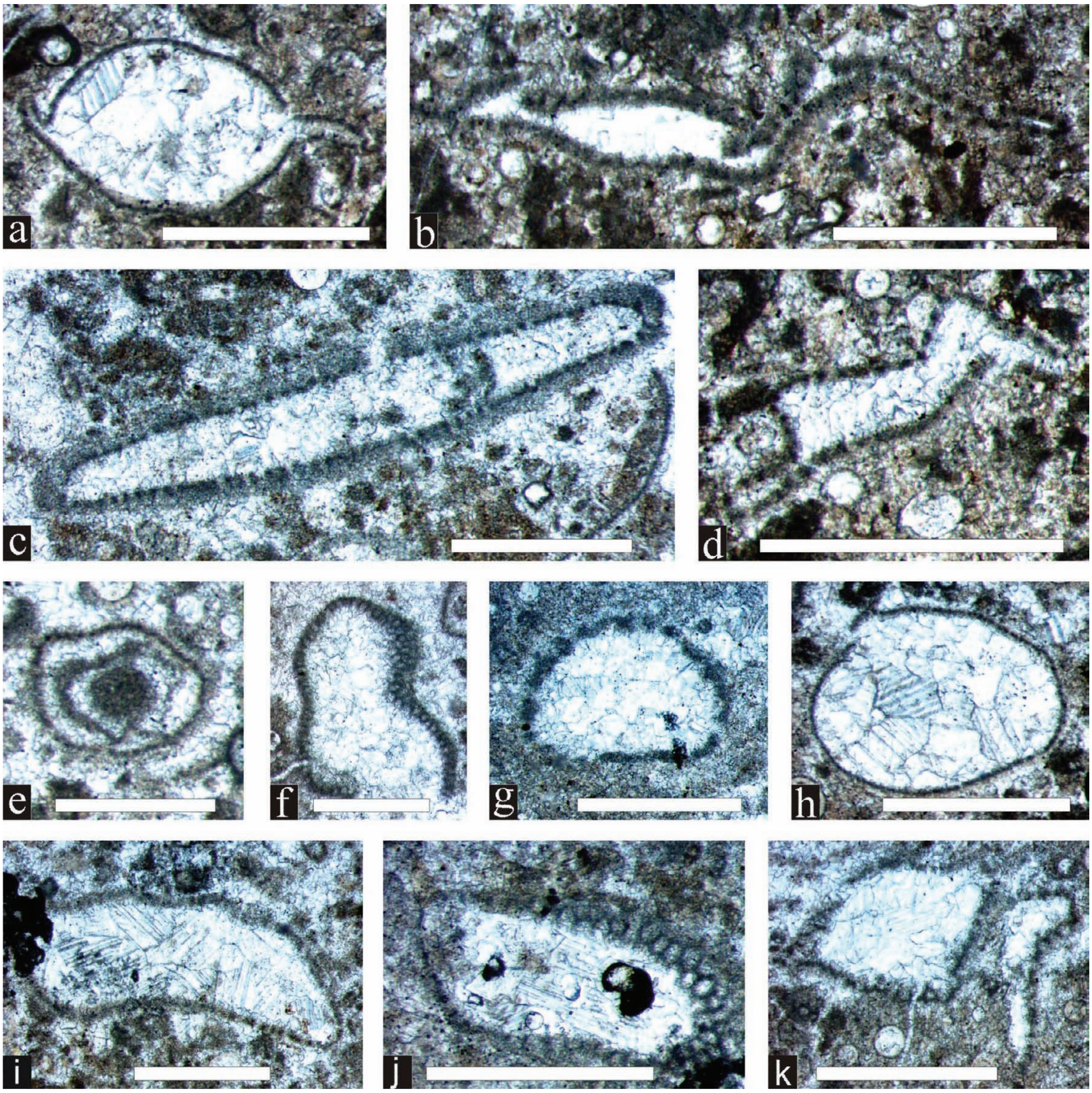


PLATE VIII

Thaumatoporella? malevkensis (BIRINA) nov. comb. from the Frasnian of the Skalka quarry near Ochoz, Czech Republic.

a Specimen showing two appendages. Thin-section Och 224.

b, d, i-k Irregular bent "*Vermiporella myna*"-type specimens showing well discernible perforate character of wall. Thin-section Och 225 (b, d), Och 223 (i-k).

c Cylindrical specimen, length 1.85 mm (compare Upper Cretaceous *Thaumatoporella* shown in Pl. 1, Fig. i). Note the zonation of the wall with a bright, less dense distal zone with poorly recognizable pores, a phenomen also reported from Mesozoic *Thaumatoporella* (e.g., DE CASTRO, 1990: Pl. 3, fig. 4). Thin-section Och 234.

e Specimen showing telescope-like stacked "internal bodies". Compare Liassic specimens shown in Pl. 1, fig. a. Thin-section Och 227.

f Section showing longitudinal (left) and oblique sections of pores (compare text-figure 12 of "*Vermiporella myna*" in WRAY, 1967). Thin-section Och 230.

g Specimen exhibiting semicircular outline and well discernible pores. Morphologically it corresponds to "*Cribrosphaera pertusa*" BYKOVA (1961: Pl. 22, fig. 10). Thin-section Och 253.

h Globular "*Bisphaera*"-type specimen showing thin wall with fines pores only dimly recognizable in some parts. Thin-section Och 227.

Scale bars 0.5 mm, except e = 0.3 mm.

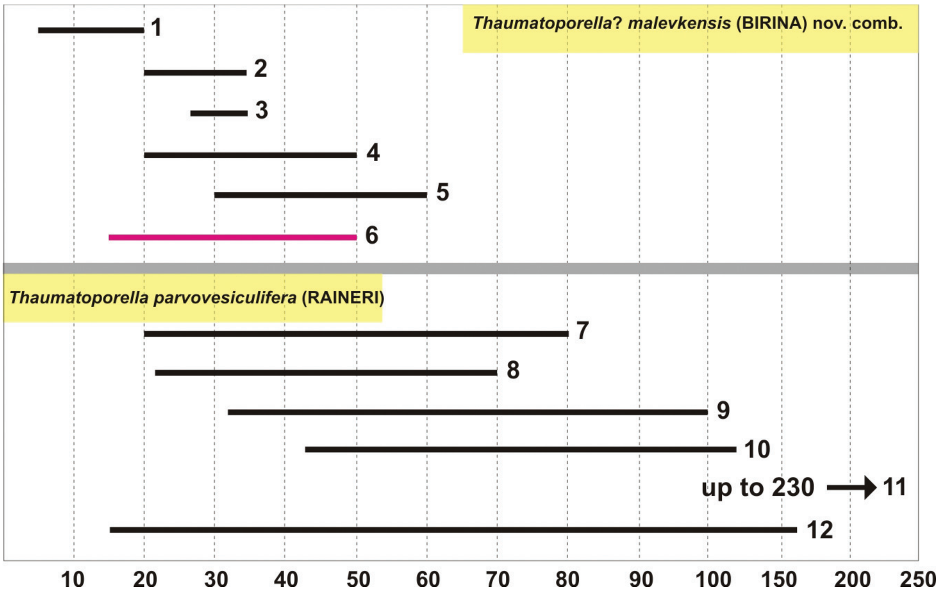


Figure 9: Wall thickness (in µm) of *Thaumatoporella*? *malevkensis* (BIRINA) nov. comb. (1-6) and *Thaumatoporella parvovesiculifera* (RAINERI) (7-12). 1: ANTROPOV (1959: *Uslonia permira*, Upper Frasnian of Russia) 2: TOOMEY et al. (1970: *Vermiporella* sp., Frasnian of Canada) 3: WRAY (1967: Frasnian of Australia) 4: MAY (1994: *Vermiporella myna*, Givetian to Frasnian of Germany) 5: FLÜGEL & HÖTZL (1971: *Vermiporella* cf. *myna*, Givetian of Germany) 6: This work. 7: FLÜGEL (1983, Upper Triassic of Greece)

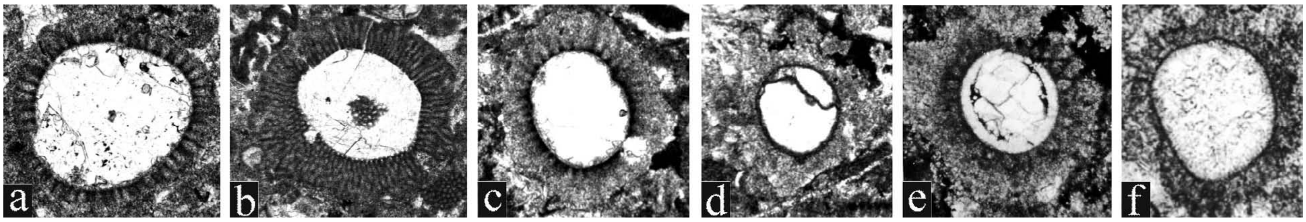


Figure 10: Preservational aspects of Upper Cretaceous ("Senonian") *Thaumatoporella* PIA (a-d) compared to Upper Devonian *Eovolvox* (from KAŹMIERCZAK, 1976: Pl. 22, fig. 1, partly) (e) and Middle Devonian *Cribraurоria* (from VACHARD, 1994: Pl. 4, fig. 7) (f). Without scale. The intention of the example selection is only to show similar diagenetic phenomena without implication of any taxonomic connection.

The assumed cyst stages of both *Thaumatoporella*? *malevkensis* (BIRINA) nov. comb. and *Thaumatoporella parvovesiculifera* (RAINERI) cannot be distinguished, neither on aspects of morphology, size, wall thickness nor preservational modes (Pl. 3).

Referring to the Middle Devonian (Eifelian) to Early Carboniferous (Tournaisian) occurrences of *Thaumatoporella*? *malevkensis* (REITLINGER), the huge gap of roughly more than 100 my until the appearance of *Thaumatoporella parvovesiculifera* (PIA) in the Middle Triassic can also be taken as evidence that these are different taxa. Alternatively, our data are currently insufficient to provide a comprehensible explanation, whether we are dealing with a real reappearance of the same genus (Lazarus taxon or effect; JABLONSKI, 1986; WIGNALL & BENTON, 1999; FARA, 2001), a case of morphological convergence (e.g., ?functional convergence: psammobiontic *Irregularina*-type forms) of two different genera, or incompleteness of the fossil record perhaps in a period of generally low proliferation of thaumatoporellacens. In the latter case, thaumatoporellacenas might have survived the end-Permian mass-extinction (e.g., KNOLL et al., 2007; BOTTJER et al., 2008; SAHNEY & BENTON, 2008) and could then be considered as a long-term refugia species (e.g., HARRIES et al., 1996). Maybe the Upper Carboniferous to Early Triassic gap of any *Thaumatoporella* (or microfossils that could possibly be synonymised with the latter) record is just an apparent one. For example, a lobed form was described recently as *Bisphaera*? *improvisa* from the Middle Permian of Texas by NESTELL et al. (2006). Not mentioned by the authors, *B.*? *improvisa* can morphologically barely be distinguished from the Devonian *Irregularina lobata* REITLINGER, 1954 or other "*Bisphaera*" species (VACHARD, 1994: Fig. 15.1). The generic uncertainty was only "because of the long stratigraphic gap" (NESTELL et al., 2006: p. 170). If "*Cribrosphaera pertusa*" described by BYKOVA (1961) from the Late Ordovician of Kazakhstan or *Bisphaera eomalevkensis* described recently by SABIROV & GUSHCHIN (2006) from the Early Ordovician of Tajikistan, are also included, the stratigraphic range of thaumatoporellaceans (as interpreted here) would enlarge even more. The latter age however was doubted by VACHARD et al. (2010, p. 220) who instead assumed a Devonian age.

Discussion: As already repeatedly stated, the high morphological variability of Mesozoic *Thaumatoporella* repre-

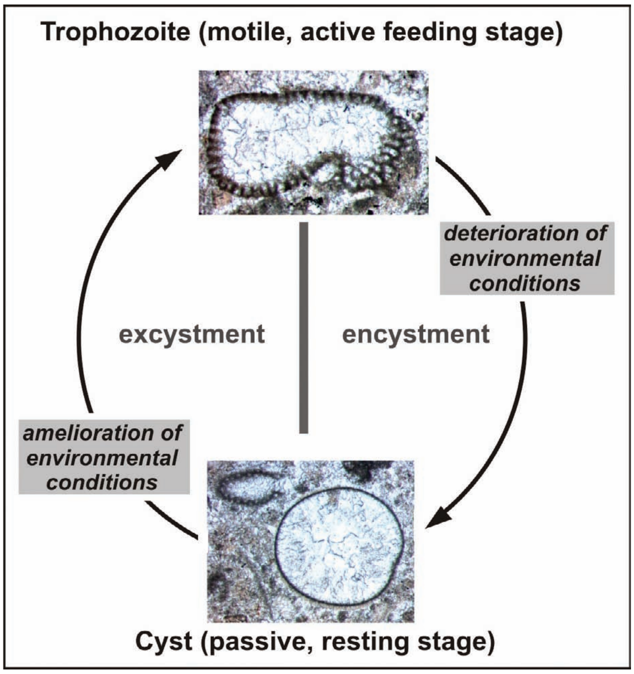


Figure 11: Hypothetical model of "*Cribrosphaeroides-Bisphaera*" life-cycle with interpretation as trophozoite and cyst stages respectively. Examples from the (upper Eifelian) of the Hillesheim Syncline, Eifel hills, Germany; thin-section K 39-9 (above) and K 44b (below).

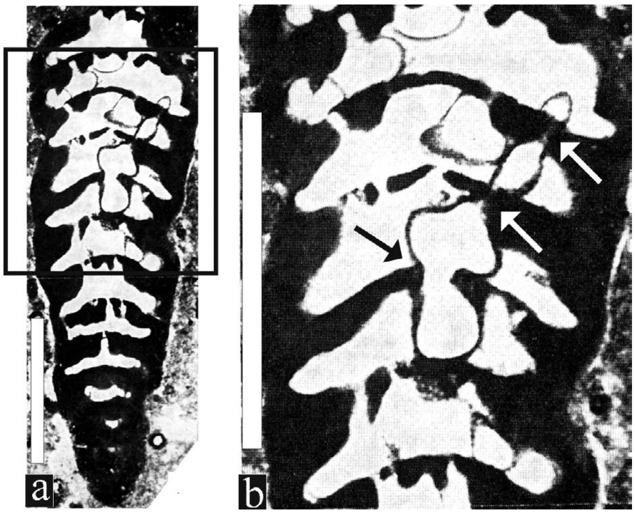


Figure 12: Cryptoendolithic specimen of *Thaumatoporella* inside the test of a large-sized miliolid (modified from DE CASTRO, 1971, pl. 9, fig. 1). The stretching of the thaumatoporellacean body through the foraminiferan septal perforations (arrows) would not have been possible if the membrane was originally heavily calcified. Here the impression of a tube under pressure that can be squeezed through small passages is evident (see SCHLAGINTWEIT & VELIĆ, 2012, for details). Scale bars 1 mm.

sentatives is considered to be the clue and the base for the interpretation of the Palaeozoic material. In the Liassic material from Albania (e.g., Pl. 2, fig. 1) there are transitional types of variously shaped and sized specimens with thick and thin walls, with pores and without detectable pores etc. Apart from a narrower range of wall thickness, the same observations can be applied to the studied Palaeozoic microfossils, i.e. representatives of parathuramminid foraminifera and algae *incertae sedis*, possibly also to some unusual large calcisphaerids for instance. One common feature of these "foraminifera" in question is their single-chambered (monothalamous) test without internal partitions, combined with an obvious lack of any aperture. The aperture is the "ultimate opening of the last chamber cavity into the ambient environment" (HOTTINGER, 2006) from "which protoplasma (pseudopodia) protrudes" to "assist in locomotion, capturing of food, and removal of waste products" (FLÜGEL, 2004, p. 453). It is also strange that the lack of this functional feature has not hindered these forms being assigned to foraminiferans and the establishment of a taxonomic concept including families and subfamilies that, though modified in some details, has also been adopted by LOEBLICH & TAPPAN (1987). Some of these families were grouped together within the order Parathuramminida MIKHALEVICH by VACHARD (1994). For the taxa in question, it can be stated that most of them were established in times where it was the general consensus to describe new taxa with little illustrations (e.g., two in *Uslonia permira*) insufficient to demonstrate the natural morphological variability. This was certainly one of the reasons that many different "species" have been established on the basis of morphology and size that should differ from already known taxa. For example, VACHARD (1994: Fig. 15/1) nicely demonstrated that there are all types of gradual transitions from more or less spherical "tests" with one single slight constriction (e.g., *Bisphaera malevkensis*) to highly constricted forms (e.g., *Bisphaera* div. sp. and genus *Irregularina*). So these morphological variations were used in the past as a stay of knowledge not only to delimit different "species" but also to differentiate independent genera. Besides real morphological intergradations, the effect of different planes of cutting creates highly variable aspects in random thin-sections. This aspect of consideration was stressed by RACKI & SOBÓN-PODGÓRSKA (1993). Another criterion of high taxonomic value in benthic foraminifera is the wall structure (LOEBLICH & TAPPAN, 1987; VACHARD et al., 2010) and without any doubt the presence or absence of pores in the wall and its microstructure are prime criteria of suprageneric importance (e.g., KAMINSKI, 2004). In the Devonian material there are not only specimens with and without detectable pores, but also ovoid- to egg-shaped forms that display both within the same specimen. According to systematic consensus, those parts without apparent pores are referred to *Bisphaera* BIRINA, the perforate parts to *Cribrosphaeroides* REITLINGER (Fig. 5). This "two in one" aspect, however, clearly evidences that in finely perforated walls this feature can be masked and be lost through diagenesis. Let us remember that REITLINGER (1954, p. 65, translated) in the diagnosis of *Cribrosphaera* (later renamed as *Cribrosphaeroides*) remarks that "the test has an irregular shape, similar in type to the Irregulariinas and Bisphaeras".

The diagnosis of *Bisphaera* BIRINA was given by LOEBLICH & TAPPAN (1987, p. 195) as follows: "Test subglobular to pyriform, may have constriction suggesting a tendency to divide; wall single layered, of finely granular calcite, perforate; no aperture observed". An enlarged diagnosis is presented by VACHARD (1994, p. 34–35, translated): "Test free (?), unilocular, sometimes slightly subdivided appearance by constrictions of the wall. Dark, segregated wall, comparatively thin, finely perforate, sometimes double-layered with an internal fibrous layer". As VACHARD correctly remarked, the inner fibrous layer may be present or absent as is also the case in Mesozoic *Thaumatoporella* (Pl. 2d versus Pl. 2e, Pl. 3g).

As the denoted bipartition of the "test" is not always visible in thin-section specimens (whether primary or due to the effect of sectioning) the genus name *Bisphaera* might be misleading. The fibrous inner layer is in our opinion not recognizable in the original figurations of BIRINA (1948a). The figures look like a filling of coarse-grained blocky calcite with crystals attached to the microcrystalline wall. As our examples shown in Fig. 5 and Pl. 5c, we also have the impression that the holotypes of both *Bisphaera malevkensis* and *B. irregularis* exhibit tiny pores. Furthermore, TOOMEY et al. (1970, p. 972) reported the observation that "a few specimens (Remark: of *Bisphaera*) in which the test wall microstructure could be observed closely, showed slight indications of what may possibly be a perforated wall".

As has been shown by DE CASTRO (1990) for *Thaumatoporella parvovesiculifera*, the wall structure is controlled by diagenesis, leading to different preservational modes (Fig. 10). Similar preservational types (or preservational history) as observed in *Thaumatoporella* were described in detail from Devonian volvocacean algae (KAŹMIERCZAK, 1976) and acritarchs (KAŹMIERCZAK & KREMER, 2005), e.g., post-mortem bacterial decomposition of a mucilaginous envelope and resulting cement precipitation. Whether or not this observation is of taxonomic importance is unknown.

Although not diagnostic *per se*, it should be mentioned that a honey-comb pore pattern in tangential section of "*Uslonia*" was indicated by ANTROPOV (1959) and has also been observed several times for *Thaumatoporella* (e.g., RADOIČIĆ, 1960: p. 137; IMAIZUMI, 1965: p. 53).

From Mesozoic strata, (sub)spherical to ovoid shaped thaumatoporellaceans with or without one (rarely more than one) slight depression (constriction?) are well known (see for example isolated specimens in DE CASTRO (1990, pl. 6 therein, "forma globosa") (Pl. 3). In the literature they were also named *Thaumatoporella* sp. (e.g., DI STEFANO & RUBERTI, 2000: Pl. 29, Fig. 3; FABBI & SANTANTONIO, 2012: Fig. 7f) or "primitive *Thaumatoporella* sp." (RUBERTI et al., 2013: Fig. 5c). The outer diameter of these spheroids ranges from about 0.25 mm up to 0.9 mm (often values between 0.4 and 0.6 mm). The micritic membrane is typically thin (~15 to ~18 µm) and appears mostly imperforate. Occasionally, fine pores are dimly recognizable. The micritic membrane may be surrounded externally by a thin rim of slightly yellowish calcite (thickness ~30 to ~65 µm). The interior of the bodies is filled with sparry calcite or sometimes with an inner fibrous layer (Pl. 3g), which sometimes is also observed in Palaeozoic "*Bisphaera*" specimens (VACHARD, 1994, p. 35, "...parfois double d´une couche interne fibreuse"). The spheroidal forms may co-occur with other thaumatoporellacean morphotypes or dominate the assemblage in micropaleontologically impoverished microbialitic layers. From Cretaceous strata, SCOTT (1978) described such forms (spheroidal *incertae sedis*) as *Micritosphaera ovalis* (see Pl. 3j-k), interpreted to represent a junior synonym of *Thaumatoporella* PIA recently by SCHLAGINTWEIT & VELIĆ (2012). The specimen showing an "interior ring" (SCOTT, 1978, fig. 1g, refigured here in Fig. 2b) and external wall "invaginations" was interpreted in this context as representing structures assigned to mother- and daughter-colonies sensu DE CASTRO (1990). Another specimen shown by SCOTT (1978, fig. 1f) is fixed to a foraminiferan. Interestingly, SCOTT (1978) compared *Micritosphaera* with the Devonian *Bisphaera*. Both the Mesozoic spheroids and their Palaeozoic equivalents (Pl. 3) are here interpreted as representing resting cyst stages as known for example from taxonomically different groups of protozoans (e.g., SLEIGH, 1989; PRESCOTT et al., 2002; FUNATANI et al., 2010) or algae (e.g., MOCZYDLOWSKA, 2010). The function of a resting cysts (or dormant stage) in the life cycle may be the protection against unfavourable environmental conditions (e.g., VERNI & ROSATI, 2011; SMIRNOV, 2008). The reversible process of encystation is called excystment taking place by a return to favourable conditions. The metabolically active protozoan growth (or feeding) stage is called trophozoite (e.g., KHUNKITTI et al., 1998) (Fig. 11). It is dominant in favorable environmental conditions. Encystment goes along with the shape of the body morphology. Generally, a spherical shape is approached by the cysts.

As for the acritarchs (e.g., KAŹMIERCZAK & KREMER, 2005), we believe that the wall of *Thaumatoporella*? *malevkensis* (BIRINA) nov. comb. was originally organic and flexible and became calcified early post-mortem. This assumption would also allow the transformation from variously shaped morphotypes to imotile sphaeroidal cysts. For *Micritosphaera*, SCOTT (1978, p. 509–510) remarked that "the variably shaped and arranged invaginations and protuberances in many specimens indicate that originally the wall was pliable; perhaps it was a combination of micritic and organic layers". It is also worth mentioning that only recently *Irregularina*, due to an assumed psammobiontic way of life and thereby the inferred possibility for movement and changeable morphology (requiring a flexible body wall), was compared to amoeboid protists (SCHLAGINTWEIT et al., 2013). Cryptoendolithic thaumatoporellaceans often display body compression (as in a flexible tube) under pressure in order to squeeze into or through small openings of host skeletons (Fig. 12). These body contractions would not be possible if thaumatoporellaceans possessed a rigid heavily calcified wall during their life-time. This observation was interpreted as an indication of a protozoan rather than algal nature for the thaumatoporellaceans (SCHLAGINTWEIT & VELIĆ, 2012; SCHLAGINTWEIT et al., 2013).

It should be mentioned that DE CASTRO also discussed the adaptation of the globose morphotypes to environmental conditions such as hydrodynamic energy. It should then result from a rolling movement. In our material the spheroidal morphotype is always associated with other different morphotypes. This observation can either reflect mixing or an indication that the globose shape is not the result of hydrodynamism. But there are also examples illustrated in the literature of spheroidal morphotypes in paleoenvironments of reduced water energy. For example, GRAZIANO (2013: Fig. 16) illustrated abundant thaumtoporellaceans in clotted microbial crusts from the Early Aptian of southern Italy. SPALLUTO (2011: Fig. 5d) illustrated similar microfacies from the Albian/Cenomanian of Apulia, S-Italy. There are also further examples where these spheroidal thaumatoporellaceans occur associated with microbial laminites: Gargasian (RUBERTI et al., 2013: Fig. 5e) and Upper Cretaceous of S-Italy (BORGOMANO, 2000) or Upper Cretaceous of Croatia (GUŠIĆ & JELASKA, 1990: Pl. 6, Fig. 3). These peculiarities could have been linked to the preponderance of special mesotrophic to oligotrophic (nutrient-deficient) conditions as discussed, e.g., for the Early Jurassic (FUGAGNOLI, 2004), an acme period of thaumatoporellaceans (see SARTONI & CRESCENTI, 1959, 1963). The cyst interpretation model would fit the observed dominance of spheroidal thaumatoporellaceans in microbial intervals that reflect some kind of environmental changes or disturbances. ROMANO & BARATTOLO (2005) discussed the bioevents that followed the Triassic-Jurassic boundary mass extinction among the typical low-diversity lowermost Liassic *Thaumatoporella* assemblage in terms of palaeoenvironmental conditions. Considering *Thaumatoporella* to be an r-strategy organism, they conclude that it represents a disaster taxon. Generally, r-strategy organisms possess the ability for rapid reproduction and are thus predominat in times of unstable environments (e.g., REZNICK et al., 2002, for discussion). A cross-reference to the dominance of a low diversity thaumatoporellacean assemblage in the aftermath of the Triassic–Jurassic boundary event might be the preponderance of *Bisphaera* (over *Cribrosphaeroides* and others) in the lower Tournaisian (basalmost Carboniferous), e.g., "*Bisphaera* Beds" (BIRINA, 1948b; MAMET & BELFORD, 1968; SANDO et al., 1969; KALVODA, 1986, 1990, 2002; MAKHLINA et al., 1993; REITLINGER et al., 1996; in contemporary literature named as upper Gumerovian and Malevkian, cf. KULAGINA, 2013). This assemblage follows the terminal Famennian mass-extinction (Hangenberg Event; e.g., WALLISER, 1984; KAISER, 2005).

The occurrence of microbialites with abundant thaumatoporellacens (mostly spheroidal forms) during oceanic anoxic events (OAEs) seems to be another interesting topic for further study (e.g., GRAZIANO, 2013: OAE 1a, KORBAR et al., 2012: OAE 2). A cross-reference is hereby given to the "out-of-balance" facies rich in microbial ("bacinellid") crusts and other structures assumed to be coeval to the Early Aptian OAE 1a (e.g., IMMENHAUSER et al., 2005; RAMEIL et al., 2010). Also the increased abundance of Devonian thaumatoporallecean-like forms corresponds to dysoxic episodes and events, e.g., in the Upper Givetian, basal Frasnian or with the Middle Frasnian, e.g., in the *Pa. punctata* Zone (HLADIL et al., 2009). It is very likely that both the major and medium-magnitude Palaeozoic events which caused proliferation of microbially dominated benthic communities and organomineralization of sediment in the post-crisis period (BOURQUE et al., 2004) led to the right setting for production and release of the cysts. This is particularly true for the Early Tournaisian times when plenty of them are locally preserved in the sedimentary rocks (see "*Bisphaera* Beds" above).

An interesting observation, emphasized by D. VACHARD in his review to our paper, relates to the calcification of cysts and formation of carbonate cements: The Palaeozoic forms frequently show an inner, isopachous, radial-fibrous to bladed 'light' layer that is often continued by centripetal growth of drusic cement, but is not so frequent in the Mesozoic. However, there are many exceptions. For example, MAKHLINA et al. (1993, Pl. 1) or KULAGINA (2013, Fig. 6A, D and E) show *Bisphaera* sections where an inner 'light' layer is absent or very irregular, and HANCE et al. (2011, p. 243, Pl. 2/6) illustrated a *Bisphaera* where the 'light' layer is absent on the inner side, but is greatly developed on the outer side of the 'dark' calcified wall – just inside out; here, in addition, the inner drusic cement is only at the very base of a geopetal fill. According to comparison of the very tiny and coarsely porous honeycombed membranes, e.g., between the Palaeozoic *Bisphaera* and *Cribrosphaeroides*, or Palaeozoic vs. Mesozoic forms, we have found that the formation of an inner vs. outer cement layers reflect mainly the early diagenetic permeability of the calcified and coated membrane. The fine porous fabrics of *Bisphaera* type were rapidly quasi-hermetically sealed and crystallization proceeded in the same way as in any closed microcavities (e.g. ostracods with firmly closed valves). However, the coarsely porous structures exchanged fluids with ambient pore waters for longer periods of time, and the outer cement layers gradually came to be predominant in volume (as for any porous bioclasts covered by cements). The latter may, but not necessarily, also contain a thin fibrous layer. Consequently, the problem of a bilayered "*Bisphaera* wall" and the regular presence of its fibrous inner part is possibly more complex than previously thought (VACHARD et al., 2010; RICHARDSON, 2012). In addition, the extracellular precipitation on an organic template (*in vivo*) can also be mistaken for early diagenetic, microbially-mediated fibrous crusts, as the latter are particularly common in the periods coming after the carbonate productivity crises and/or major regressions; the indicators of this, although not directly connected to the *Thaumatoporella* facies, are cements in microbialites (RIDING, 2005) or "stromatactis" (e.g., HLADIL et al., 2007, 2008; AUBRECHT et al., 2009). Eventually, secular variations in overall marine cementation intensities and morphologies might also have played a role. According to KIESSLING (2002), the amount of reef cements vary through time with medium to high amounts in the Palaeozoic and Lower/Middle Triassic as compared to the usually low mean cement content in Jurassic to Cenozoic times (see also FLÜGEL, 2004). Although *Thaumatoporella* is not restricted to reef facies and also thrives in inter- to subtidal inner platform environments (often still peri-reefal), different conditions for marine cement precipitation in the Palaeozoic should be also taken into account.

It is well known that protozoan cysts may be round or irregular shaped, displaying single- or double-layered, thin or thick walls with a structure being different from the non-cyst stage (e.g., SMIRNOV, 2008). Within the protozoa, a considerable variation in the cyst wall microstructure is present (LAYBOURN-PARRY, 1984, for details). Sometimes, different cyst wall layers are named ectocyst (outermost layer) and endocyst (inner layer/s) (e.g., KIDA & MATSUOKA, 2006). This ectocyst is typically a dense layer. From the Upper Cretaceous isolated specimens DE CASTRO (1990) noted an external coating, (different to the dense microgranular membrane), assigned to the peripherical parts of the wall. It could represent the yellowish radial-fibrous calcitic outer rim observable in the thin-section specimens. An interpretation as a calcified mucilaginous substance known to envelop resting cysts ("mucoid layer") as reported from other organisms (e.g., VERNI & ROSATI, 2011: Fig. 1f) seems possible. In some forms (Pl. 3a), this outer rim exhibits a finely jagged outline that could be compared to the finger-like protrusions covering the entire cyst surface and produced during the final step in cyst formation of some protozoans (e.g., VERNI & ROSATI, 2011, Fig. 1e). The formation of a dense ectocyst layer could be a hypothesis for the thin and usually imperforate character of "*Bisphaera*", contrasting the perforate non-cyst stage inferred for "*Cribrosphaeroides*". The formation of the dense cyst wall layer during the encystment process might be evidenced by the specimens showing the "two in one aspect", parts with discernible fine pores and others without (Fig. 5).

Concerning the size, the cysts of the giant amoebozoa *Chaos* LINNAEUS attain a medium size of 0.25 mm (GOODKOV et al., 1999) but may be up to 0.6 mm. For Givetian "*Bisphaera*" specimens from W-Germany, FLÜGEL & HÖTZL (1971: p. 365) indicate diameters from 0.1 to 0.525 mm exhibiting wall thicknesses of 0.01 to 0.03 mm. The cyst wall of modern protozoans is distinctly thinner, often less than 1 µm, up to some microns only (e.g., KIDA & MATSUOKA, 2006; VERNI & ROSATI, 2011). The holotype of the type-species *Bisphaera malevkensis* BIRINA has a diameter of 0.53 mm and other representatives of the genus range up to 0.65 mm. From Tournaisian strata, *Bisphaera* specimens of up to 1.1 mm are known (J. KALVODA, pers. comm.). In Early Jurassic to Upper Cretaceous spheroidal *Thaumatoporella*, the outer diameter ranges from about 0.25 mm up to 0.9 mm (often values between 0.4 and 0.6 mm). For "*Micritisphaera*" (that we interpret as a synonym of *Thaumatoporella*), SCOTT (1978) indicates diameters from 0.49 mm to 1.18 mm.

A further cross-reference of the studied Devonian specimens to Mesozoic *Thaumatoporella* is given also by forms that were likely attached to hard substrates. Such specimens of "*Bisphaera*" were illustrated by CONIL in BOUCKAERT et al. (1977: figs. 57-58) (Figs. 7a-b). They are characterized by thin walls without detectable pores. The part of the wall attached to the substrate closely follows its morphology, and may result in a wavy outline whereas the non-attached part displays a smooth convex outline. For the purpose of completeness, it must be mentioned that VACHARD (1994: p. 30) is not convinced that the mentioned *Bisphaera* specimens were in fact attached forms. He favoured an interpretation as test deformations resulting from a possible psammobiontic way of life not from substrate irregularities. We do not follow this view and want to draw attention to fig. 58 of CONIL in BOUCKAERT et al. (1977), refigured here in Fig. 7a where in our opinion a basal substrate (concave upper side pelecypod shell?) is dimly recognizable. Anyway, homeomorphic attaching specimens are well known from Mesozoic thaumatoporellaceans (e.g., DE CASTRO, 1997: Pl. 24, fig. 1) (Fig. 7c). In the original description of "*Uslonia permira*", ANTROPOV (1959) also indicated that the test was most likely attaching. In this respect it must be mentioned, that REITLINGER (1954: Pl. 21, fig. 1) illustrated an elongated specimen of *Cribrosphaera*? sp. showing constrictions with a thin micritic perforated wall that we interpret to have been fixed to a bioclast.

Last but not least, both the Palaeozoic and Mesozoic specimens exhibit internal structures or bodies that were interpreted as *Thaumatoporella* daughter-colonies by DE CASTRO (1990). For some Palaeozoic "Usloniidae", VACHARD (1994: p. 37) and VACHARD & CLEMENT (1994: p. 300) already stated the resemblances to Mesozoic thaumatoporellaceans. They compare internal bodies observed in *Bisphaera* and *Cribrosphaeroides* with the thaumatoporellacean daughter-colonies *sensu* DE CASTRO (1990). Interestingly, *Messopotamella angulata* described by DRAGASTAN et al. (1985) from the Upper Triassic of Greece was compared morphologically by the authors with *Uslonia* ANTROPOV. *Messopotamella* is considered a *Thaumatoporella* with thin walls without detectable pores where some specimens may exhibit tapering ("angular") ends (see also DE CASTRO, 1990). Considering the two illustrations (though of not good quality) of *Uslonia permira* presented by ANTROPOV (1959), we infer that both exhibit barely recognizable thin-walled "internal bodies". Such structural details inside the "test" of *Uslonia* however were not mentioned in the original description. In this point, we disagree with the assumption of VACHARD (1994) of an abiogenic nature for *Uslonia* representing "sparitic, large and irregular debris" or cortoids.

Due to our assumptions and interpretations, the foraminiferan family Usloniidae in the sense of LOEBLICH & TAPPAN (1987) needs a taxonomic reconsideration. With the assumed synonymization of *Uslonia* ANTROPOV, 1959 with *Thaumatoporella* PIA, 1927, the family-group name Usloniidae loses the reference to a type genus (Article 35, International Code of Zoological Nomenclature ICZN). Normally, however, the "validity of family-group names" is "not affected"…."when the name of a type genus of a nominal family-group taxon is considered to be a junior synonym of the name of another nominal genus" and "the family-group name is not to be replaced on that account alone" (Article 40 ICZN). Besides "*Uslonia*", the family Usloniidae contains two other genera *Bisphaera* BIRINA and *Parphia* MIKLUKHO-MAKLAY. *Bisphaera* is also considered here as representing a thaumatoporellacean-like microfossil and for the rather large spherical "bodies" of *Parphia* with its finely perforated micritic wall a possible algal origin is more likely than representing a unilocular foraminifer. The situation becomes even more complex as the family Thaumatoporellaceae was created in 1988 by DE CASTRO, the Usloniidae by MIKLUKHO-MAKLAY in 1963 and finally the Irregularininae (as a subfamily of the Parathuramminidae) by ZADOROZHNYY & YUFEREV in 1984. So just from the date of publication, the Usloniidae would have priority.

4. CONCLUSIONS

The long-term practice of establishing different taxa of Palaeozoic parathuramminids/*incertae sedis* on the basis of differences in morphology and size (mainly in random thin-sections) is as equally problematic as taking into account the different aspects of the wall structures. These might represent either true original differences or just expressions of various preservational (e.g., alteration, recrystallization, cement fringes) or developmental stages (phases of life cycles). In Mesozoic *Thaumatoporella*, it is the consensus to accept comparable to equivalent taphonomic aspects, as preservational modes of a single taxon and not different genera.

The widely accepted concept of polymorphism of Mesozoic-Early Cenozoic *Thaumatoporella* is discussed for some seemingly homeomorphic Palaeozoic taxa leading in our interpretation to a rather radical synonymization. With *Thaumatoporella* having priority, *Bisphaera* BIRINA, *Cribrosphaeroides* REITLINGER, *Uslonia* ANTROPOV and *Vermiporella myna* WRAY (not the genus *Vermiporella* STOLLEY) are here interpreted as possible junior synonyms. The aforementioned genera and their species were already treated as highly controversial among micropalaeontologists concerning both their possible synonymies and biogenic nature. Also from the Mesozoic, a lot of genera and species are considered to represent synonyms of a single taxon, *Thaumatoporella* PIA (or species of it): *Polygonella* ELLIOTT, *Micritosphaera* SCOTT, *Messopotamella* DRAGASTAN et al., *Lithoporella elliotti* (EMBERGER) and *Vermiporella crisiae* DRAGASTAN et al. *Irregularina* BYKOVA also might represent thaumatoporellaceans, respectively psammobiontic forms.

In analogy to Mesozoic homeomorphs, *Bisphaera* is proposed as representing a possible *Thaumatoporella* resting cyst stage. The interpretation of *Bisphaera*-type spheroids is compatible with the lack of any aperture, an observation that always made the attribution of these forms to monothalamous foraminifera problematic. Mesozoic equivalents were described as *Micritosphaera* SCOTT or "primitive thaumatoporellaceans", "*Thaumatoporella* sp." in the literature. The assumed cyst stages of both *Thaumatoporella*? *malevkensis* (BIRINA) nov. comb. and *Thaumatoporella parvovesiculifera* (RAINERI) are almost identical with respect to morphology, size, wall thickness, both exhibiting also various aspects of preservation.

The possible Palaeozoic record of thaumatoporellaceans would suggest that they represent long-living and morphologically rather conservative microorganisms. The assumed ability to change morphology during their life-time and motility, the optional occurrence in completely shaded habitats and the inferred formation of resting cysts challenges the attribution of thaumatoporelaceans to algae. These aspects instead are compatible with a protozoan nature.

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