Campanian (Late Cretaceous) Theonellidae and Phymaraphiniidae (lithistid Demospongiae) from the Miechów and Mogilno-Łódź synclinoria (southern and central Poland): new data and taxonomic revision

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Abstract: Theonellid and phymaraphiniid sponges were described for the first time in assemblages of Campanian lithistid Demospongiae collected from Miocene gravels in the Bełchatów lignite mine (Mogilno-Łódź Synclinorium, central Poland). Here we add an analysis of sponges from museum collections, as well as of newly collected material from Campanian strata in the Miechów Synclinorium. Four phymaraphiniid and 11 theonellid species have been distinguished in these assemblages. Two phymaraphiniid species (Phymaraphinia infundibuliformis and Prokaliapsis janus), and five theonellids (Rhadudinia doederleini, Rhoztrum scytaliforme, Astrocladia laevis, Collossolaxis plicata and Phylodermina antiqua) have not been recorded previously from the Campanian of Poland. With three exceptions, all other theonellids and phymaraphiniids described herein are also known from the Campanian of Subhercynian and/or Lower Saxony basins in Germany. On account of the good preservation of the sponge skeletons, new data on the choanosomal and ectosomal spicules of Cretaceous theonellids and phymaraphiniids can now be presented. Our analysis of the distribution of theonellids and phymaraphiniids in various Cretaceous facies has allowed palaeoenvironmental factors conducive to the settlement of these sponges to be outlined.

Key words: Theonellidae, Phymaraphiniidae, lithistid demosponges, taxonomy, Cretaceous, palaeoecology.

Cretaceous siliceous demosponges described herein can be assigned to the families Theonellidae Lendenfeld, 1903 and Phymaraphiniidae Schrammen, 1910 (Schuster et al. 2015). In traditional palaeontological classification, both these families are characterized by the presence of choanosomal tetraxial desmas (tetracloenes in theonellids and triders in phymaraphiniids), have been placed in the suborder Tetracladina Zittel, 1878 (Pisera 2002; Reid 2004). Ectosomal spicules of these sponges are phyllotriænes and/or discotriænes; microscleres, which are important for the classification of living taxa, are unknown in Cretaceous species (Reid 2004).

Extant theonellids are represented by five genera, comprising 62 species, whereas the family Phymaraphiniidae at present encompasses three genera with only eight species (Pisera & Lévi 2002a,b; Van Soest et al. 2021a,b). During the Cretaceous, however, both families were taxonomically more diverse, with 17 genera of Theonellidae and eight of Phymaraphiniidae distinguished to date (Pisera 2002). The exact number of Cretaceous species representing these genera is difficult to determine because species diagnoses are often imprecise; some may turn out to be junior synonyms of previously described forms.

Extant representatives of both families have a global distribution and occur in both shallow and deep waters (Pisera & Lévi 2002a,b). Similarly to other representatives of the Tetractalinida, Cretaceous theonellid and phymaraphiniid species are known almost exclusively from epicontinental marine strata across Europe. Cretaceous tetractadins are considered to be characteristic of shallow to moderately deep water facies (e.g. Defretin-Lefranc 1960; Wagner 1963; Schneider et al. 2013); however, the palaeoecology of Theonellidae and Phymaraphiniidae has not yet been analysed in detail.

The material presented herein consists of Campanian (Late Cretaceous) material from southern and central Poland (Fig. 1; Table 1). Most of the sponges studied originated from Miocene gravels at the Bełchatów Lignite Mine (Mogilno-Łódź Synclinorium, central Poland). This redeposited assemblage of Cretaceous lithistid sponges ranks among the richest in Europe. To date, from this locality sponges representing only three families (Pleromidae,
Isoraphiniidae and Corallistidae) have been studied in detail (Swierczewska-Gładysz 2016, 2017). Additionally, specimens from the Kraków, Miechów, Pilica and Lełów areas (Miechów Trough, southern Poland) have been studied (Table 1); part of this material is contained in museum collections that were previously described by Bieda (1933) and Hurcewicz (1966). The Polish assemblages are crucial to taxonomic interpretation of fossil theonellids and phymaraphiniids on account of their well-preserved skeletal structures. In most cases the skeletons of Cretaceous sponges are completely dissolved or retain only single desmas. Almost all specimens studied here are partly silicified, which explains why portions of their siliceous skeleton are locally very well preserved. Thus, it is possible to study not only the shape of individual megascleres but also their original organization within the skeleton.

The aim of the present paper is to discuss the results of our taxonomic study of the Theonellidae and Phymaraphiniidae from the Belchatów, Pilica and Lełów areas, and a revision of other material from southern Poland described by Hurcewicz (1966) and Bieda (1933). Our analysis of new and historical material supplements existing information on the skeleton of these sponges and their intraspecies variability. We also wish to refine...
data on the palaeoecological requirements of Cretaceous theonellid and phymaraphinid taxa by including palaeoenvironmental observations outlined in previous studies (Jurkowska et al. 2019a, b; Jurkowska & Swierczewska-Gładysz 2020a, b).

**GEOLOGICAL SETTING**

During the Late Cretaceous, the high sealevel (probably at its peak) led to the breakdown of the shelf margin and a predominance of shielded basins in which carbonate pelagic sedimentation prevailed. These distinctive conditions can be attributed to high rates of sea-floor spreading, particularly in the Atlantic and south-east Pacific. During that time a large part of the present territory of Europe was covered by an extensive epicontinental sea (Fig. 2). The chalk mud accumulating on the sea floor consisted of calcite skeletons of unicellular coccoliths, as well as an insignificant amount of terrigenous material (detrital clays and quartz) (Jurkowska et al. 2019b) forming a soft, porous bottom deposit. Some regions of the European epicontinental sea were strongly influenced by oceanic influxes, which, by dissolved silica (DSi) enrichment, triggered the significant development of sponge meadows (Świeczewska-Gładysz 2006, 2012; Jurkowska & Świeczewska-Gładysz 2020a). Sponge spicules (mainly of non-rigid demosponges) incorporate into sediment were dissolved later and led to the formation of the carbonate–siliceous opoka facies. In contrast, the pelagic environment, which constituted the remaining part of the European Basin, saw deposition of pure carbonate (chalk) (Jurkowska et al. 2019b). Areas adjacent to emerged islands were characterized by a significant influx of terrigenous material, which explains why sandy and marly facies occur in these regions.

Campanian (Upper Cretaceous) marine deposits in the Polish part of the European Basin comprised mainly a thick succession of opoka (carbonate rock with opal-CT as the main component of insoluble residue) with horizons of siliceous nodules (cherts) and marly intercalations. The Campanian sequence in southern Poland, in the Miechów Synclinorium, starts with a thick (up to 30 m; Rutkowski 1965) complex of marls, which passes upwards into opoka with marly intercalations in the lower section followed by sandy opoka and gaize in the uppermost section (Rutkowski 1965; Jurkowska 2016). In the lower part of the Campanian sequence, above the
complex of marls, distinctive horizons of cherts with black flint cores have been documented (Rutkowski 1965; Pozarski 1966; Jurkowska & Święczewska-Gładysz 2020b). Fossils are abundant and consist mainly of siliceous sponges (Bieda 1933; Barczyk 1956; Hurcewicz 1966, 1968; Święczewska-Gładysz 2016, 2017), bivalves, cephalopods and echinoids (Rutkowski 1965; Jurkowska 2016). Lithistid sponges, which are numerous in lower Campanian strata, usually are silicified and often form the black flint core in chert nodules (Jurkowska & Święczewska-Gładysz 2020b). In middle and upper Campanian levels, the hexactinellids predominate, while lithists are rare. Most of the outcrops studied in the Miechów Synclinorium (Table 1; Fig. 1D–E) have been described earlier in terms of stratigraphy, lithology and petrography (Hurcewicz 1966, 1968; Święczewska-Gładysz 2016, 2017; Jurkowska et al. 2019b; Jurkowska & Święczewska-Gładysz 2020b). Some of these localities, as well as natural outcrops, are currently unavailable for research.

Current knowledge of the Campanian sequence in the Mogilno-Łódź Synclinorium, which is bordered to the south by the Miechów Synclinorium (Pozarski 1974), is poor, being known mainly from borehole cores. Like the Miechów Synclinorium, the Campanian strata are represented mainly by opoka with marly intercalations, as well as marly opoka and siliceous nodules of chert with a black flint core documented from the lower part of the succession (Pozarski 1960). Clasts of Campanian opoka and siliceous nodules (often containing lithistid sponges), as well as isolated silicified sponges, are found as redeposited elements in Miocene gravels in the Bełchatów area (Table 1; Fig. 1B–C). The occurrence of Campanian lithistid sponges in the Bełchatów lignite mine of the Mogilno-Łódź Synclinorium has been the subject of previous work (Święczewska-Gładysz 2016, 2017).

**MATERIAL AND METHOD**

The present material originates from seven localities where lower–upper Campanian deposits of the Miechów Synclinorium crop out and from one locality where Miocene gravels
with redeposited Campanian fossils are exposed in the Belchatów lignite mine (Table 1). In all, our material consists of 307 specimens from Belchatów that are housed in the collections of the Geological Museum of the University of Łódź, Poland (collection UL no. XXV). Phymaraphiniid and theonellid sponges from the Lełów, Pilica, Mięchów and Kraków areas, collected previously by H. Hurewicz, and more recently by ourselves, have also been examined. This material, also housed at this institute (collections UL nos II, IIa and IIIb), consists of 15 specimens from Pniaki, 20 from Zbyczynce, eight from Skrajniwa, one from Przesławice, three from Wierzbica, three from Mięchów and seven from Bonarka.

With the exception of some poorly preserved specimens with dissolved skeleton from Mięchów and Przesławice, all sponges studied by us are silicified. Choanosomal skeletons are usually best preserved in the outer, less silicified part of these sponges, while inside the wall desmas are only occasionally recognizable (compare Jurkowska & Świerczewska-Gładysz, 2020a,b). Frequently preserved spots of weathered opoka on the surfaces of specimens from Belchatów indicate that most of these fossils (if not all) derived from opoka. Some specimens commonly have borings and silicified episkeletozoans (epibionts), mainly bryozoans and serpulid polychaetes.

Sponge skeletons from opoka were etched in 10% hydrochloric acid, washed in an ultrasonic cleaner and then examined under scanning electron microscopy—energy dispersive x-ray spectroscopy (SEM-EDS) at the Microscope Laboratory of the University of Warsaw and the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw, as well as at the AGH Laboratory of Phase, Structural, Textural and Geochemical Research.

In general, our sponge classification and terminology follows Boury-Esnault & Rützler (1997), Hooper et al. (2002) and Finks et al. (2003).

SYSTEMATIC PALAEONTOLOGY

Family PHYMARAPHINIIDAE Schrammen, 1910
Genus PHYMARAPHINIA Schrammen, 1901

Type species. Phymaraphinia infundibuliformis Schrammen, 1901 (p. 9, pl. 1, figs 6–7) by monotypy.

Diagnosis. See Reid (2004).

Phymaraphinia infundibuliformis Schrammen, 1901
Figures 3A–G, 4

1910 Phymaraphinia infundibuliformis Schrammen; Schrammen, p. 105, pl. 5 figs 1–2.
1964 Phymaraphinia infundibuliformis Schrammen; Giers, p. 219.
1966 Cycloclema compressa (Hinde); Hurewicz, pp. 70–72 (pars), pl. 21 fig. 2 only.
1993 Phymaraphinia infundibuliformis Schrammen; Jahnke & Gasse, pl. 10 figs 2, 5–6.

Material. 27 specimens from Belchatów Lignite Mine (ULXXV/101/1–27), two from Zbyczynce (ULII/781, 1437), one from Mięchów (ULII/826) and one from Wierzbica (ULIIa/30).

Description. Funnel-shaped or ear-shaped sponges with rounded edges and 4–11-mm-thick wall (Fig. 3A–F); most complete specimen being 55 mm in width and 66 mm in height, but large plate-like fragments of wall indicating that these sponges could grow significantly larger. Preserved stalks usually short and thick (up to 15 mm), but in a few slender, thin-walled specimens, only 5–6 mm in diameter. Outer surface with densely distributed rounded canal openings, usually 0.4–0.8 mm in diameter, occasionally reaching 1 mm in size (Fig. 3G). Canal openings arranged irregularly, in vertical rows or lying on the bottom of fine, shallow furrows. Canal openings on inner surface usually slightly larger and less densely distributed, either randomly or in shallow furrows. Furrows on both surfaces (if present) arranged vertically; occasionally, orientation locally disturbed and furrows run obliquely or even horizontally. Ridges between furrows c. 1 mm wide.

Choanosomal skeleton composed of triders with button-like brachyomes, 80–110 µm in diameter, and clones with ring-like swellings near the centre of desmas (Fig. 4A–B). Swellings and brachyomes strongly granular to nearly smooth. Clones 90–100 µm thick and usually 400–550 µm long, but triders with one or two (rarely with all) shorter clones (c. 250–300 µm long) also occur. Clones simple or forked, ending in strong zygomes forming spherical or slightly elongated zygosis, 300–380 µm in size. In outer parts of choanosomal skeleton zygosis larger and irregular (Fig. 4B). Small tubercles appearing on surface of clones or only on zygomes. Generally, most ornamented triders with protuberant ring-like swellings occur on the surface of the choanosomal skeleton (Fig. 4C), but are often masked by tightly entwined, strongly modified desmas (Fig. 4D–E), forming a very compact network on both surfaces in places with prominent furrows and ridges and on the surface of stalks. Most modified desmas are triders with very small smooth brachyomes and long (up to 600–700 µm), irregularly branched clones. These clones poorly tuberculate or smooth, with or without a small, ring-like swelling. Other rare desmas are irregular tetraclines with four arms. Dense ectosomal layer (preserved mainly on stalks) composed of densely packed branched phyllotriaenes (Fig. 4F). Their clads, 500–750 µm long, usually truncate or with pointed tips. Small (up to c. 150 µm in size), flattened, multangular megascleres filling spaces between phyllotriaenes.

Remarks. Features of all specimens studied fully correspond to the diagnosis of P. infundibuliformis, for which modified desmas that are observed locally on both surfaces of the choanosomal skeleton

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Description. Funnel-shaped or ear-shaped sponges with rounded edges and 4–11-mm-thick wall (Fig. 3A–F); most complete specimen being 55 mm in width and 66 mm in height, but large plate-like fragments of wall indicating that these sponges could grow significantly larger. Preserved stalks usually short and thick (up to 15 mm), but in a few slender, thin-walled specimens, only 5–6 mm in diameter. Outer surface with densely distributed rounded canal openings, usually 0.4–0.8 mm in diameter, occasionally reaching 1 mm in size (Fig. 3G). Canal openings arranged irregularly, in vertical rows or lying on the bottom of fine, shallow furrows. Canal openings on inner surface usually slightly larger and less densely distributed, either randomly or in shallow furrows. Furrows on both surfaces (if present) arranged vertically; occasionally, orientation locally disturbed and furrows run obliquely or even horizontally. Ridges between furrows c. 1 mm wide.

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Remarks. Features of all specimens studied fully correspond to the diagnosis of P. infundibuliformis, for which modified desmas that are observed locally on both surfaces of the choanosomal skeleton
and on the stalk have not been described before. In the present material, a greater variation in desmas ornamentation has also been recognized (compare Jahnke & Gasse 1993; Pisera 2002).

As well as the Campanian deposits of Europe, *Phymaraphinia infundibuliformis* has also been noted from the Albian of northern Spain (Rosales et al. 1995), but because no description of this material was supplied, assignment to this species cannot be proved.

**Occurrence.** Poland (Belchatów area, early Campanian sponges as redeposited elements in Neogene deposits; Lelów and Pilica areas, lower Campanian; Miechów area, upper Campanian); north-west Germany (Lower Saxony, lower and upper Campanian; Westphalia, upper Campanian).

**Genus CYCLOCLEMA Schrammen, 1910**

*Type species:* *Rhadadinia compressa* Hinde, 1883 (p. 82, pl. 19, figs 3, 3a) by subsequent designation (Reid 2004, p. 223).

*Diagnosis.* See Reid (2004).
FIG. 4. A–F, Phymaraphinia infundibuliformis Schrammen, 1901. A, choanosomal skeleton within the wall, showing poorly ornamented triders (ULXXV/10T/4, from Bełchatów). B, network on the inner surface of the choanosomal skeleton of the same specimen. C, network on the outer surface of the choanosomal skeleton showing ornamented triders (ULXXV/10T/3, from Belchatów). D–E, network with modified triders covering the outer surface of the choanosomal skeleton; and locally visible typical, ornamented triders (ULXXV/10T/3, from Belchatów). F, ectsomal skeleton with phyllotriaenes and small flattened megascleres from the outer surface of the specimen (ULXXV/10T/5, from Belchatów). Scale bars represent: 500 µm (A–B, D–F); 200 µm (C).
Cycloclema compressa (Hinde, 1883)

Figures 3H–L, 5

1883 Rhagadinia compressa Hinde, p. 82, pl. 19 figs 3, 3a.
1910 Cycloclema compressa Hinde; Schrammen, pp. 105–106, pl. 5 figs 3–4; text-fig. 72.4.
1926 Cycloclema compressa (Hinde); Moret, p. 192, pl. 16 fig. 9; text-pl. 6 fig. 5.
1960 Cycloclema compressa (Hinde); Defretin-Lefranc, p. 115, pl. 19 figs 2–3; text-fig. 37.
1966 Cycloclema compressa (Hinde); Hurcewicz, pp. 70–72 (?pars), ?pl. 21 fig. 1, non pl. 21 fig. 2; ?text-fig. 20.

Material. 43 specimens from Belchatów Lignite Mine (ULXXV/8T/1–43), ?two from Miechów (ULII/58, 87).

Description. Damaged funnel-like specimens, numerous fragments of crushed wall (4–10 mm thick), isolated stalks or stalks with small pieces of wall and/or broken root-like processes preserved (Fig. 3H–L). Largest specimen (without stalk and uppermost part) 72 mm in height and 86 mm in width (Fig. 3H). Both surfaces smooth, but occasionally vertical or oblique furrows occur on lowermost part. Deep furrows also covering stalks, up to 100 mm in length and 50 mm in diameter (Fig. 3I). Inhalant canal openings round or oval, 1 mm × 1–1.8 mm in size, alternately arranged in vertical rows. Between these, especially in the lower part, there are smaller (0.5–0.8 mm), irregularly distributed openings. Short inhalant canals running slightly obliquely to surface of wall. On inner surface, short canal openings in upper part short, perpendicular to wall surface. In stalk, canals parallel to its axis.

On the outer surface of choanosomal skeleton triders have prominent, button-like brachyomes, 90–100 µm in diameter, covered by granules (Fig. 3A). Clones 100 µm thick with a granulated ring-like swelling, c. 50 µm wide, near the centre. Straight clones usually 450–550 µm long. In places on outer surface (where network very compact), triders have shortened clones (c. 300–400 µm long), smooth or with small tubercles. Particularly dense tubercles cover strong, finger-like zygomes. Zygosus usually rounded or elongated, 200–400 µm in size. Rarely preserved choanosomal skeleton inside wall consisting of triders with small brachyomes and slender clones, 60–70 µm thick and 400–600 µm long. Clones smooth with or without small swelling and small tubercles only on zygomes. Zygosus rounded or irregular, 400 µm in diameter. Network on inner surface less compact than on outer surface, containing triders with clones 70–80 µm thick and reaching 450–600 µm in length (Fig. 3B–D). These clones often with swellings having the shape of incomplete rings. Occasionally, desmas with four clones and no swelling occur also within this network (Fig. 5D). Triders often with arched, branched clones near canal openings. In lower part of sponge, network with elongated triders with poorly developed swellings on both surfaces (Fig. 5E). The longest clones of these triders reach 1400 µm in length. Modified network passing into stalk skeleton, where a linear arrangement of densely packed, elongated desmas is observed (Figs 3K–L). Modified desmas without swellings have small smooth brachyomes and poorly tuberculate, very long zygomes. Single phyllotriaenes, observed on exhalant surface of a few specimens, with branched clads, up to 700–1100 µm long. Tips of clads rounded or truncated.

Remarks. The shape, size and distribution of canal openings on both surfaces of specimens from Belchatów are identical to those of Cycloclema compressa from England, France and Germany (Hinde 1883; Schrammen 1910; Moret 1926; Defretin-Lefranc 1960).

Desmas of Cycloclema compressa illustrated by other authors differ in size and ornamentation. Analysis of the material from Belchatów indicates that the differences are related to the location of desmas in the choanosomal skeleton. The massive, tuberculate triders resembling desmas illustrated by Defretin-Lefranc (1960) occur only on the outer surface of the choanosomal skeleton. Large and slender triders, corresponding to the desmas presented by Hinde (1883), Schrammen (1910) and Moret (1926), are found mainly on the inner surface of the sponge. Choanosomal desmas of the Museum-held specimen are large triders, similar to desmas of Cycloclema compressa, but the ectosomal spicules illustrated by Hurcewicz (1966, text-fig. 20) are plate-like with a slightly jagged edge, in contrast to phyllotriaenes with long, branched clads characteristic of the present species. It is not possible to determine if these ectosomal spicules really stem from this sponge, because the surface of this specimen has been considerably destroyed as a result of chemical preparation, and lacks a clear morphology (Hurcewicz 1966, pl. 21, fig. 1); no ectosomal spicules are preserved in situ. Other specimens from the Lelów area described by Hurcewicz (1966) as C. compressa have no preserved skeleton or show desmas typical for Ph. infundibuliformis (see above) or Prokaliapsis janus (Roemer, 1864) (see below) and the last are considered by us as representatives of these two species.

Occurrence. Poland (Belchatów area, early Campanian sponges as redeposited elements in Neogene deposits; Miechów area, upper Campanian); north-west Germany (Lower Saxony, lower and upper Campanian); France (Paris Basin, Coniacian; Pauvrelay area, Late Cretaceous sponges redeposited into Miocene deposits); England (Upper Chalk, probably upper Turonian or lower Coniacian).

Genus PROKALIAPSIS Schrammen, 1901
(= Procalapis Schrammen, 1910; Lopadoporus Schrammen, 1910; Ulbrich 1974)

Type species. Prokaliapsis cylindrica Schrammen, 1901 (p. 8, pl. 1 fig. 5, pl. 4 fig. 1) by subsequent designation (Laubenfels 1955, p. E59).

Diagnosis. See Reid (2004).

Remarks. Schrammen (1910) and later Lagneau-Hérenger (1962) and Reid (2004) considered the presence of pits, hollow or as
FIG. 5. A–F, Cycloclema compressa (Hinde, 1883). A, outer surface of choanosomal skeleton, showing compact network with ornamented triders (ULXXV/8T/3, from Belchatów). B–D, inner surface of choanosomal skeleton (ULXXV/8T/5, from Belchatów). B, network with canal openings. C–D, detail of network, showing ornamented triders, triders with small swelling (t) and desmas with four arms (d). E–F, choanosomal skeleton with modified desmas (ULXXV/8T/3, from Belchatów). E, network from the lower part of the sponge. F, network from the stalk. Scale bars represent: 200 µm (A, C–D); 500 µm (B, E–F).
shallow depressions, to be a diagnostic feature of the genus \textit{Lopadoporus}. These structures, which do not occur in all specimens of \textit{Lopadoporus janus} (Roemer, 1864), the type species of the genus according to Laubenfels (1955), were interpreted by Ulbrich (1974) as ichnofossils. In addition, Ulbrich (1974) recognized that the species included by Schrammen (1910) in his new genus \textit{Lopadoporus} were in fact representatives of \textit{Prokaliapsis} Schrammen, 1901, as based on the shape and size of the choanosomal desmas, and patterns of canals inside the choanosomal skeleton. Our observations match Ulbrich’s view and we also consider \textit{Lopadoporus} to be a junior synonym of \textit{Prokaliapsis}.

\textbf{Prokaliapsis clavata} (Hinde, 1883)

\textbf{Figures 6A–G, 7}

- 1883 \textit{Rhagadinia clavata} Hinde, p. 84, pl. 19 fig. 4a–c.
- 1901 \textit{Prokaliapsis cylindrica} Schrammen, p. 8, pl. 1 fig. 5, pl. 4 fig. 1.
- 1910 \textit{Prokaliapsis clavata} Hinde; Schrammen, pp. 108–109, pl. 8 figs 9–12; text-pl. 6 fig. 1.
- 1926 \textit{Prokaliapsis clavata} (Hinde); Moret, pp. 193–194, text-fig. 72.2.
- 1966 \textit{Prokaliapsis clavata} (Hinde); Hurewicz, pp. 68–69, pl. 23 figs 2–4, text-fig. 18.
- 1966 \textit{Prokaliapsis clavata} (Hinde); Van Kempen, pp. 259–267, fig. B only.

\textbf{Material.} 17 specimens from Belchatów Lignite Mine (ULXXV/9T/1–17), two from Pniaki (ULII/876, 1030), three from Zbyczycze (ULII/823, 1435, 1481) and one from Wierzbica (ULIIa/36).

\textbf{Description.} Club-like or cylindrical, occasionally with transverse narrowing, some slightly bent or strongly curved near base, often with bulges or traces after longer processes on one side (Fig. 6A–G). Others strongly flattened laterally with apex situated asymmetrically. Large specimens with damaged base and/or apex, up to 50 mm in height and 16–21 mm in width. Rarely, well-preserved apex slightly rounded with a set of 6–12 small (1–1.5 mm in diameter), densely packed exhalant canal openings. Vertical exhalant canal running from apex to base. Outer surface unevenly covered by fine, longitudinal or oblique grooves. In lower part, inhalant canal openings 0.2–0.3 mm in diameter; very sparsely distributed and usually lying on bottom of furrows; in upper part, arranged more densely and up to 0.5 mm in diameter. Short inhalant canals oblique.

Choanosomal skeleton very compact, consisting of small desmas. Triders occurring on outer surface of choanosomal skeleton with prominent granulated button-like brachyome, occasionally with large rounded granule on top (Fig. 7A–B). Short clones, 180–240 µm long and 100 µm thick, branching out just behind granulated swellings in the shape of rings, rarely half-rings. Triders with one or two longer clones (up to 350–380 µm long) occurring occasionally. Large triders especially numerous in area of furrows; long clones running across furrow. Triders with strong zygomes covered by small tubercles. Tubercles occasionally occurring also on longer clones. Zygosia spherical or elongated, 250–500 µm in size. Desmas with four clones, 180–200 µm long; rare on outer surface of skeleton, but more numerous inside wall where, in addition to regular and strongly ornamented triders, triders with or without smooth swellings are frequent (Fig. 7E). Smooth and very irregular branched desmas with long zygomes additionally occur on surface of exhalant canals (Fig. 7C–D). Branched ectosomal phyllotriaenes, with very short rhabdomes and cladomes up to 500–550 µm, forming smooth layer covering grooves and inhalant canal openings. Most phyllotriaenes having wide clads, but slender phyllotriaenes with almost twice narrower clads also occurring.

\textbf{Remarks.} The specimens studied have the shapes and morphology typical of \textit{Prokaliapsis clavata} but also have a greater variation of triders within a single specimen than has been previously known (compare Hinde 1883; Schrammen 1910; Hurewicz 1966). Triders without swellings and desmas with unreduced fourth clones, occurring mainly in the inner part of the skeleton, have until now not been recognized. Brachyomes, swellings and sometimes also long clones of triders of the specimens studied (also those in the Hurewicz Collection) are often covered by minute tubercles. This ornament was not described by previous authors, which is probably due to being viewed at lower magnification.

Triders of fragmentarily preserved sponges from the Santonian of southern France have a brachyome with a conical spike (Moret 1926), which has not been observed in other representatives of \textit{Pr. clavata}. Phyllotriaenes of these specimens are also less indented than the ectosomal spicules of the present species, which indicates that the French material constitutes a different species of \textit{Prokaliapsis}.

In specimens of \textit{Pr. clavata} found as erratics in the Netherlands, Van Kempen (1966, p. 267, figs 3c, d, f) described also dichotriaenes, in addition to phyllotriaenes characteristic of this species. Dichotriaenes do not occur in the representatives of the family Phymaraphiniidae Schrammen, 1901 (Pisera & Lévi 2002b; Reid 2004) and these loose spicules certainly do not come from that sponge.

\textbf{Occurrence.} Poland (Belchatów area, early Campanian sponges as redeposited elements in Neogene deposits; Lelów and Pilica areas, lower Campanian); north-west Germany (Lower Saxony, lower and upper Campanian); southern England (Upper Chalk, probably upper Turonian or lower Conician); the Netherlands (erratics).

\textbf{Prokaliapsis janus} (Roemer, 1864)

\textbf{Figures} 6H–N, 8

- 1864 \textit{Ocdispongia janus} Roemer, p. 48, pl. 16 fig. 12.
- 1889 \textit{Coelocorypha janus} (Roemer); Griepenkerl, p. 17.
- 1910 \textit{Lopadoporus janus} (Roemer); Schrammen, pp. 109–110, pl. 10 fig. 3.
- 1910 \textit{Lopadoporus lacunosus} Schrammen, pp. 110–111, pl. 10 fig. 4; text-pl. 6 fig. 4.
1966  Prokaliapsis arborescens (Michelin); Hurcewicz, pp. 69–70, pl. 223 fig. 1, text-fig. 19.
1974  Prokaliapsis janus (Roemer); Ulbrich, pp. 29–30, pl. 16 fig. 3, text-fig. 11a–d.

Material. 14 specimens from Belchatów Lignite Mine (ULXXV/16T/1–14), two from Pniaki (ULII/1625, 1626) and one from Skrajniwa (ULII/1297).

Description. Small specimens widely conical with shallow depression on top and wide base or thick, short stalk (Fig. 6H–L). Depression usually with smooth surface, occasionally with conical process developed asymmetrically or with numerous small bulges. Large specimens, up to 90 mm in height, cup- or ear-like (Fig. 6M–N), occasionally with stalk. Wall thickness usually 0.7–10 mm, but near base of some robust ones it can reach up to 15 mm. Round canal openings on outer surface, 0.3–0.5 mm in diameter, irregularly arranged, spaced at 1–3 mm intervals. Canal

FIG. 6. A–G, Prokaliapsis clavata (Hinde, 1883). A, lateral view of asymmetrical specimen with well-preserved ectosomal layer (ULXXV/9T/1, from Belchatów). B, lateral view of (ULXXV/9T/2) with base preserved, from Belchatów. C, lateral view of club-like specimen with base preserved (ULXXV/9T/6, from Belchatów). D, lateral view of flattened specimen (ULXXV/9T/6, from Belchatów). E, lateral view of ULXXV/9T/4 with two short processes, from Belchatów. F, lateral view of ULXXV/9T/7 with transversal narrowing (from Belchatów). G, lateral view of asymmetrical specimen with process (ULXXV/9T/8, from Belchatów).
H–N, Prokaliapsis janus (Roemer, 1864). H, lateral view of specimen without ectosomal layer, showing canal openings (ULXXV/16T/1, from Belchatów). I, upper view of the same specimen. J, lateral view of specimen with well-preserved ectosomal layer (ULXXV/16T/3, Belchatów). K, upper view of specimen (ULXXV/16T/4, from Belchatów). L, lateral view of the same specimen with preserved base. M, lateral view of irregular specimen (ULII/1626, from Pniaki) previously assigned to Prokaliapsis arborescens (Michelin, 1840). N, fragment of large specimen with borings on the outer surface (ULXXV/16T/5, from Belchatów). Scale bar represents 1 cm.
openings often lying at end of short (1.5 mm long) grooves, passing into oblique inhalant canals. Differently oriented, longer furrows occurring locally on both surfaces; very thin and occasionally branched and meandering. Canal openings on inner side, 0.8–1 mm in size; irregularly distributed, but more densely packed in central part. Exhalant canals perpendicular or slightly oblique to

**FIG. 7.** A–F, *Prokaliapsis clavata* (Hinde, 1883). A–E, choanosomal skeleton with small triders (ULXXV/9T/5, from Belchatów). A–B, dense network on the outer surface of the choanosomal skeleton. C–D, network with modified desmas on the wall of exhalant canals. E, various ornamented triders. F, ectosomal phyllotriaenes (ULXXV/9T/3, from Belchatów). Scale bars represent: 200 µm (A, C, F); 100 µm (B, D–E).
inner surface and in axial part very long and running vertically towards base.

Outer surface skeleton very compact, consisting of small triders with knob-like, granulated brachyome (Fig. 8A–B); small tubercle on top of brachyome occasionally slightly larger than other ones. Clones, 50–80 µm thick and c. 180–220 mm long, ramifying just behind a large granulated ring-like swelling. Strong zygomes usually with three branches. Zygomes entwining brachyomes of neighbouring desmas forming a rounded zygosis, 200–250 µm in size. Triders with longer (250–320 µm long) tuberculate clones occurring occasionally between small desmas. Less dense network on inner (exhalant) surface of choanosomal skeleton (Fig. 8C) having small, strongly ornamented triders and triders with poorly developed swelling on forked clones of various lengths (250–450 µm). Irregularly branched desmas with flattened, poorly tuberculate clones occur on the bottom of furrows on both surfaces (Fig. 8B). In the central part of the choanosomal skeleton triders with forked clones predominate, 250–300 µm long. Zygosis usually elongated, c. 200–250 × 400 µm in size. Branched phyllotriaenes, present on both sponges surfaces, large, with cladomes 500–700 µm in size (Fig. 8D) and highly variable widths (30–70 µm).

Remarks. Our analysis of early Campanian material from Poland combined with literature data, indicates that Pr. janus (Roemer) is a polymorphic species. Some of our specimens are similar to material of this species from the Santonian and lower Campanian of Germany (Roemer 1864; Schrammen 1910; Ulbrich 1974; Müller 1977, pl. 1 figs 1–13, pl. 2 figs 1–8), whereas the bulbous morphotype known from there is lacking in the present specimens. The shape of the other thin-walled specimens studied corresponds well to the cup-like specimen from the Campanian of Lower Saxony described by Schrammen (1910) as a new species, Lopadoporus lacunosus. Desmas of the single specimen known of L. lacunosus (Schrammen 1910, text-pl. 6, fig. 4) have extremely shortened clones with strong, three-branched zygomes. They are identical to the triders occurring on the surface of the choanosomal skeleton of Pr. janus described herein. In our opinion, the species L. lacunosus should be considered a junior synonym of Pr. janus.
because there are no other features differentiating the two forms. When characterizing L. janus and L. lacunose, Schrammen (1910) focused on the shape and arrangement of the pits that occur on the outer surface and/or upper margin of the specimens studied by him. However, some specimens of Pr. janus from the very rich collection of the lower Campanian of Saxony-Anhalt (Cretaceous Subhercynian Basin) have no pits (Ulbrich 1974, p. 29, text-fig. 11c–d). The pits were considered to be ichnofossils by later researchers (Ulbrich 1974; Müller 1977; Uchman et al. 2018), which is also in agreement with our observations. The slit-like hole, interpreted by Ulbrich (1974) and Uchman et al. (2018) as a trace produced after the post-mortem colonization of sponges by bivalves, has been noted only in a single specimen from Belchatów. Irregular cavities, resembling the pits visible on the specimen illustrated by Schrammen (1910, pl. 10, fig. 4) as L. lacunosus, are more frequent, but they have been noted also in specimens of other species, which suggests that the origin of these bioerosion traces requires additional study.

Hurcewicz (1966) included the thin-walled specimens with slender stalks (i.e. the undescribed morphotype) from the Campanian of the Lełów area in Pr. arborescens (Michelin, 1840), based on a similarity to sponges from France described by Moret (1926). Specimens presented by Michelin (1840, pp. 136–137, pl. 42, fig. 2a–b as Jerea arborescens) and Moret (1926, p. 194, pl. 12, fig. 15, pl. 14, fig. 12) represent only the lowermost part of the sponges (i.e. stalks terminated by strong root-like processes), occasionally with a small fragment of the cup-like body. The triders of Pr. arborescens have simple clones with short zygomes (Moret 1926, text-fig. 72,1), whereas those in the Polish material have forked clones or simple clones with long zygomes. Triders of Pr. arborescens have brachyomes with a conical spike, whereas the present specimens have a granulated brachyome, occasionally with a more prominent apical tubercle. Moreover, the desmas characteristic of Pr. arborescens include also elongated triders occurring in the stalks. A fragment of the slender stalk is present only in a single specimen from the Museum collection that we have studied, but no desmas are preserved. The enigmatic desmas with two clones from the outer surface, illustrated by Hurcewicz (1966, text-fig. 19b), have not been recognized. Based on body shape, slender funnel-like specimens of Pr. janus from the Lełów area are similar to Prokaliapsis cretaceus Schrammen, 1901, but the triders and ectosomal phyllotriaenes of the latter species are significantly larger (Schrammen 1910, text-pl. 6, fig. 2) than the desmas of Pr. janus and other species of the genus Prokaliapsis.

Occurrence. Poland (Belchatów area, early Campanian sponges as redeposited elements in Neogene deposits; Lełów area, lower Campanian); north-west Germany (Saxony-Anhalt, Santonian and lower Campanian; Lower Saxony, lower Campanian).

Family THEONELLIDAE Lendenfeld, 1903
Genus RHAGADINIA Zittel, 1878

Type species. Cupulospongia rimosa Roemer, 1864 (p. 51, pl. 17, fig. 8a–d) by subsequent designation (Zittel 1878, p. 152).

Diagnosis. See Reid (2004).

Rhagadinia rimosa (Roemer, 1864) Figures 9A–F, 10

1864 Cupulospongia rimosa Roemer, p. 51, pl. 17 fig. 8a–d.
1966 Rhagadinia rimosa (Roemer); Hurcewicz, p. 63 (pars), pl. 13 figs 1a–b, text-fig. 16.
2006 Rhagadinia rimosa (Roemer); Świerczewska-Gładysz, p. 279, text-fig. 40c (with additional synonymy).

Material. 113 specimens from Belchatów Lignite Mine (ULXXV/157/1–113), seven from Bonarka (ULII/83, 706–709, 1056, 1239), eight from Pniaki (ULIIa/31, ULII/143, 827, 828, 829a, 1218, 1016, 1057), six from Zbyczyce (105, 829, 830, 1018 1204, 1215), one from Skrajniwa (ULIIa/32) and one from Wierzbica (ULIIa/35).

Description. Asymmetric cup-, bowl- or funnel-like sponges, or in a leaf shape or as irregular lobes, often with edges folded inwards (Fig. 9A–F). Some with a short, thick stalk (in large sponges up to 30–40 mm in diameter), ending in root-like processes (usually broken). Isolated processes, covered by anastomosed furrows, reaching 50 mm in length. In other sponges, massive processes grow at base, but occasionally also appear in higher parts of the sponge body on one side or edge (Fig. 9E). Large specimens up to 120 mm in size. Wall thickness 7–15 mm, occasionally up to 25 mm. On outer surface (Fig. 9A, C, E) round canal openings, 0.6–0.8 mm in diameter, lying on the bottom of thin furrows, usually at 1.5–2.5-mm intervals, occasionally in some large specimens even at 3–3.5 mm. Furrows covering entire outer surface and also rounded margin. Long, poorly branched furrows running longitudinally or obliquely near lateral margin (in asymmetrical specimens), separated by ridges usually 1–2 mm in width, rarely up to 2.5–3 mm in some large sponges. Furrows on one or both surfaces of some specimens or only in the lower part of the outer surface, anastomosed and with net-like arrangement, with polygonal meshes, 1.5–2 mm or 2–3 mm in size, depending on specimen. Branched winding furrows on inner surface (Fig. 9D, F) usually short (up to 9 mm) and variably oriented. Randomly scattered canal openings, 0.8–1.5 mm in diameter, lying at the end of furrows, rarely between these. Occasionally, 5–9 canal openings grouped and surrounded by furrows in a star-like pattern. In some specimens, groups of canal openings are located on small bulges. Inhalant canals run more or less perpendicularly to wall. Exhalant canals irregularly branched; branches differently oriented, with most of the branches arranged parallel to wall surface.

The choanosomal skeleton on both sponge surfaces consists of large, strongly tuberculate tetraclonies (Fig. 10A–D). Oval tubercles, up to 50 µm in size, elongated transversely to axis of clone. Clones, 310–420 mm long, occasionally forked with strong zygomes forming a terminally irregular zygosis. Beside these, bifurcate zygomes may be connected to the lateral sides of clones of neighbouring desmas. Inside wall, zygosis more regular (rounded or elongated), c. 300 x 300–600 µm in size. Tuberculate desmas predominate in this part of skeleton, but between these appear poorly tuberculate tetraclonies or smooth clones with tubercles only on zygomes. Less ornamented tetraclonies...
most numerous near canals (Fig. 10C–D). Single, young tetracolones with smooth short clones (up to 200–220 \(\mu\)m) and poorly developed zygomes occur occasionally.

Overlapping phyllotriaenes form smooth layers, covering both surfaces of the sponge (Fig. 10E–F), usually fragmentarily preserved and often strongly silicified with poorly visible phyllotriaenes (Fig. 10F). Small, irregularly branched spicules rarely noted between phyllotriaenes in less heavily silicified specimens. Strongly indented phyllotriaenes occur on the inner surface with massive clads, c. 100 \(\mu\)m wide and up to 250–300 \(\mu\)m long. Slender phyllotriaenes with (twice) narrower clads predominate on the outer surface, but packets of phyllotriaenes with wide clads are observed locally in some specimens.
Remarks. The diversity of shape and morphology of both surfaces of specimens from Belchatów and the Campanian of southern Poland are consistent with the published descriptions of *Rhagadinia rimosa* (Roemer 1864; Počta 1884; Schrammen 1910; Moret 1926; Bieda 1933; Defretin-Lefranc 1960; Wagner 1963; Hurcewicz 1966; Ulbrich 1974). The wall thickness of

**FIG. 10.** A–F, *Rhagadinia rimosa* (Roemer, 1864). A–B, outer surface of choanosomal skeleton with canal openings (ULXXV/15T/1, from Belchatów). C, inner surface of choanosomal skeleton with furrows (ULXXV/15T/2, from Belchatów). D, tetraclines on the wall of a canal (ULXXV/15T/1, from Belchatów). E, ectosomal phyllothriaenes with wide clads on inner surface (ULXXV/15T/1, from Belchatów). F, ectosomal phyllothriaenes with narrow clads on outer surface (ULXXV/15T/3, from Belchatów). Scale bars represent: 500 µm (A, C); 200 µm (B, D–F).
previously described specimens did not exceed 10–15 mm, whereas numerous fragments of sponges in our collection from Belchatów have a wall thickness up to 25 mm.

The features of choanosomal desmas and ectosomal spicules of all specimens analysed fully correspond to characteristics of *Rh. rimosa* (e.g. Zittel 1878; Schrammen 1910; Defretin-Lefranc 1960; Ulbrich 1974; Pisera 2002). Most of the specimens from Germany and France have no ectosomal spicules preserved on the outer surface and phyllotriaenes with wide clads derived from the gastral surface, which have been presented in the literature. Slender phyllotriaenes of *Rh. rimosa* were described for the first time by Hurcewicz (1966). According to Hurcewicz (1966), this type of phyllotriaene occurs on the outer surface, while massive phyllotriaenes covered only the inner surface. Our research does not confirm this observation, because phyllotriaenes with broad clads are also observed on the outer surface.

**Occurrence.** Poland (Belchatów area, early Campanian sponges as redeposited elements in Miocene deposits; Lełów and Pilica areas, lower Campanian; Miechów area, upper Campanian; Kraków area, lower Campanian and sponges redeposited into Miocene deposit; Middle Vistula River valley, upper Maas- strichtian); north-west Germany (Lower Saxony, lower and upper Campanian; Saxony-Anhalt, lower Campanian); southern Germany (Bavaria, Cenomanian to lower Turonian); the Czech Republic (Cenomanian); France (Ardennes, Cenomanian; Provence, Santonian).

**Genus RHOPTRUM Schrammen, 1910**

**Figures 9G–K, 11**

1910 *Rhogadinia doederleini* Schrammen, p. 101, pl. 7 figs 1–3.

1966 *Rhogadinia rimosa* (Roemer); Hurcewicz, p. 63 (*pars*), pl. 13 figs 1a–b, text-fig. 16.

1966 *Rhogadinia foraminifera* Hurcewicz, pp. 66–67, pl. 12 fig. 1a–c, text-fig. 17.

1993 *Rhogadinia doederleini* Schrammen; Jahnke & Gasse, pl. 13 figs 1, 2.

**Material.** 25 specimens from Belchatów Lignite Mine (ULXXV/12T/1–25), one specimen from Skrajniwa (ULII/284) and seven from Zbyczycze (ULIIa/33, ULII/395, 829, 1009, 1019, 1466, 1612).

**Description.** Leaf-like, irregularly lobate or asymmetrical funnel-like sponges, up to 90 mm in height, with rounded margin covered by furrows and thick, very short stalk with expanded base (Fig. 9G–K). Wall thickness 11–20 mm. Round canal openings on outer surface, 0.4–1 mm in diameter; hidden between meshes of choanosomal skeleton and poorly visible randomly arranged, spaced at c. 1.5–2.5 mm. Inhalant canals short and very narrow. On inner surface, canal openings, 0.8–1.1 mm in diameter, situated on wall of pits, 2–3 mm in diameter and 5 mm deep (Fig. 9H–J). Pits 10–15 mm apart surrounded by radially distributed widening furrows, up to 10–15 mm long. Branched exhalant canals very long, arranged radially around pits.

Compact choanosomal skeleton on outer surface of wall consists of irregular branched tetracolones with clones up to 400–500 µm long and 80–100 µm thick (Fig. 11A). Round, triangular or oval tubercles, up to 50 µm in size, covering clones and their short strong zygomes. On inner surface, skeleton slightly less dense and containing, apart from strongly lumpy tetracolones, rare less tuberculare desmas (Fig. 11B–D). Poorly tuberculare or nearly smooth tetracolones with a clone reducing in thickness (50–60 µm) more numerous inside wall; tetracolones very regular with an articulation similar to that in *Rh. rimosa*. Locally, young smooth desmas with still not fully developed zygosis occurring between adult desmas. Ectosomal skeleton in some specimens completely covering both surfaces. Poorly ramified phyllotriaenes on inner surface massive, with clads up to 250–320 µm long (Fig. 11E). Small irregular spicules, infilling spaces between phyllotriaenes, rare and recognizable only on less strongly silicified specimens. On outer surface strongly incised phyllotriaenes predominating, with narrow clads up to 200–250 µm long (Fig. 10F). Single phyllotriaenes with wider clads preserved only occasionally.

**Remarks.** Until now, *Rhogadinia doederleini* was known only from two specimens from the lower Campanian of Lower Saxony. Our analysis of rich material from Poland has shown that this species is a polymorphic one, as is *Rh. rimosa* (Roemer). According to Schrammen (1910), *Rh. doederleini* differs from the latter species in having a thicker wall (up to 15 mm), a coarsely porous outer surface, and exhalant canal openings arranged in groups that are located in small cavities on the inner surface of the sponges. Some specimens of *Rh. doederleini* from Belchatów are relatively slender, with walls thinner than in the massive specimens of *Rh. rimosa*. Thus, the wall thickness should not be considered as a diagnostic feature for this species.

The tuberculare tetracolones of *Rh. doederleini* are similar to the desmas of *Rh. rimosa* (see also Jahnke & Gasse 1993, pl. 13 figs 1, 2), whereas the phyllotriaenes (not yet illustrated) are less branched. Such phyllotriaenes are visible on two specimens assigned by Hurcewicz (1966) to *Rh. rimosa* and on all specimens of *Rh. foraminifera* Hurcewicz, 1966, mainly on the better preserved inner surface. Features that are characteristic of the latter species (i.e. the lack of furrows on the outer surface and the presence of cavities with canal openings on the inner surface) are compatible with the diagnosis of *Rh. doederleini*. Analysis of the specimens from the Hurcewicz Collection conducted here found no differences between the two species, therefore *Rh. foraminifera* is recognized here as a junior synonym of *Rh. doederleini*.

**Occurrence.** Poland (Belchatów area, early Campanian sponges as redeposited elements in Neogene deposits; Lełów area, lower Campanian); north-west Germany (Lower Saxony, lower Campanian).

**Genus RHOPTRUM Schrammen, 1910**

**Type species.** *Rhoptrum scytaliforme* Schrammen, 1910 (p. 104, pl. 5, figs 5–7; text-pl. 5, fig. 2) by monotypy.

**Diagnosis.** See Reid (2004).
FIG. 11. A–F, Rhagadinia doederleini Schrammen, 1910. A, compact network on outer surface of choanosomal skeleton with tuberculated tetraclones (paratype of *Rhagadinia foraminifera* Hurcewicz, 1966; ULII/1009, from Zbyczyce). B–D, inner surface of choanosomal skeleton with furrows; the various ornamentation of tetraclones is visible (ULXXV/12T/2, from Belchatów). E, ectosomal phyllotriaenes with wide clads on inner surface (paratype of *Rh. foraminifera* Hurcewicz, 1966; ULII/1009, from Zbyczyce). F, ectosomal phyllotriaenes with narrow clads and single phyllotriaene with wide clads (w) on the outer surface (ULXXV/12T/1, from Belchatów). Scale bars represent: 200 µm (A, C–D, F); 500 µm (B, E).
Rhoptrum scytaliforme Schrammen, 1910
Figures 12A–B, 13A–B

1910 *Rhoptrum scytaliforme* Schrammen, p. 104, pl. 5 figs 5–7, text-pl. 5 fig. 2.
1962 *Rhoptrum scytaliforme* Schrammen; Lagneau-Hérenger, pp. 145–146, text-pl. 21 fig. 5.
1993 *Rhoptrum scytaliforme* Schrammen; Jahnke & Gasse, pl. 20, fig. 5.

**Material.** 2 specimens from Belchatów Lignite Mine (ULXXV/21T/1–2).

**Description.** Club-like or cylindrical sponge with slightly narrowed, rounded apex (Fig. 12A–B); lower part not preserved in either of the two specimens. Larger specimen 34 mm in height and 18 mm in width; smaller one 40 mm and 20 mm, respectively. Spongocoel very deep and narrow, 7 mm and 8 mm in diameter, respectively. Exhalant canal openings (visible only in upper part of spongocoel) oval, 1.5 mm in size, leading to short oblique canals. Evenly distributed inhalant canal openings very small, 0.3 mm in diameter, occasionally attaining up to 0.5 mm in diameter. Inhalant canals very short and only slightly wider than meshes of choanosomal skeleton.

Compact skeleton consisting of massive tetraclines with clones 280–420 µm long and 100–160 µm thick (Fig. 13A–B). Surface of clones smooth, wrinkled, or with sparsely distributed tubercles. Terminal zygomes, up to 200 µm long, strongly branched and densely covered by prominent mushroom tubercles, 15–35 µm in diameter. Zygosis very elongated, c. 250–550 µm long. Ectosomal spicules not preserved.

**Remarks.** Body shape, morphology of both surfaces, size and articulation of tetraclines observed in these specimens from Belchatów fully correspond to the characteristics of *Rhoptrum scytaliforme*. In the present specimens, the tetraclines have strongly tuberculate zygomes, whereas the clones are poorly tuberculate to entirely smooth. Such ornamentation of desmas is visible also in the fragment of the network in the specimen from the Schrammen Collection (Jahnke & Gasse 1993). Strongly tuberculate tetraclines, similar to some desmas presented by Schrammen (1910), and tetraclines illustrated by Lagneau-Hérenger (1962), have not been observed in the material noted here.

**Occurrence.** Poland (Belchatów area, early Campanian sponges as redeposited elements in Miocene deposits); north-west Germany (Lower Saxony, lower Campanian); Spain (Catalonia, Aptian).

Genus ASTROCLADIA Zittel, 1878

**Type species.** *Asterospongia laevis* Roemer, 1864 (p. 54, pl. 9, fig. 2) designated by Laubenfels (1955, p. 57).

**Emended diagnosis.** Branched or club-like sponges without spongocoel; groups of exhalant canal openings surrounded by star-like furrows. Exhalant canals running parallel, oblique or perpendicular to sponge surface; inhalant canal openings randomly distributed on sponge surfaces. Inhalant canals short and
perpendicular to sponge surface. Choanosomal desmas small, smooth or spiny or tuberculate tetraclones with strongly branched zygomes. Ectosomal phyllotriaenes small, with wide clads.

Remarks. According to Zittel (1878) and subsequent authors (Schrammen 1910; Reid 2004), the diagnosis of the genus notes that tetraclones are characterized by smooth clones. However, the material from Poland and from Germany (Schrammen Collection, Tübingen University) has smooth and tuberculated tetraclones.

Astrocladia laevis (Roemer, 1864)  
Figures 12C–E, 13C–D

1864  Asterospongia laevis Roemer, p. 54, pl. 9 fig. 2.  
1878  Astrocladia subrnanosa (Roemer); Zittel, p. 84, pl. 9 fig. 9a–b.

non 1884  Astrocladia laevis Roem. sp.; Počta, p. 38, pl. 2 fig. 10; text-fig. 22.

Material. 8 specimens from Belchatów Lignite Mine (XXV/6T/1–8) and one from Pniaki (ULIIa/34).

Description. Best preserved specimen, 75 mm in height and 17 mm in diameter, club-shaped, without spongocoel and flattened apex (Fig. 12E). Other specimens club-like or near-cylindrical fragments, without any remains of lateral branching (Fig. 12C). Inhalant canals straight and perpendicular to sponge surface. Inhalant canal openings 0.2–0.25 mm in diameter, randomly distributed on surface of sponges. Exhalant canal openings 0.3–0.5 mm in diameter, arranged in groups located on lateral sponge surface (Fig. 12C–E), occasionally situated on top of very low papillae. Small groups, consisting of 6–9 canal openings, rounded in outline. Number of canal openings in larger groups with elongated or irregular outline reaching 9–13.
Groups of canal openings surrounded by long, branched furrows (up to 15 mm). Exhalant canals with outlet on periphery of groups running parallel or slightly obliquely to surface; central canals oblique to perpendicular.

Choanosomal skeleton extremely compact, especially on outer surface; composed of small, regular tetraclones (Fig. 13C–D). Smooth clones, 180–250 µm long, usually unbranched, rarely forked in the terminating portion. Longer clones, up to 300 µm, occur in tetraclones near furrows, running across furrows. Clones terminated by long, finger-like zygomes, forming a very elongated zygosis, up to 1 mm long and 200–300 µm wide. Ectosomal spicules not preserved.

Remarks. Roemer (1864) presented two, macroscopically very similar species, namely Asterospongia laevis and A. subramosa. The former was said to differ from the latter in having a smoother surface; this characterization has been considered as enigmatic by later workers (Počta 1884; Schrammen 1910). Asterospongia laevis, designated by Laubenfels (1955) as the type species of the genus Astrocladia, was not described subsequently and the diagnostic features of this species remain unclear. Roemer (1864) did not present the skeleton of either species, but it can be concluded that the characteristics given by him do not refer to the ectosomal skeleton (as suggested by Počta 1884), because the illustrated specimens of both species show star-like furrows, running on the surface of the choanosomal skeleton. Our observations indicate that the choanosomal skeleton of Astrocladia laevis, consisting of tetraclones with smooth clones, is more compact than that of Astrocladia subramosa. For this reason, the surface of specimens of A. laevis, which is devoid of ectosomal spicules, is in actual fact distinctly smoother than that of A. subramosa.

Tetraclones of the Polish material are identical to the desmas of the sponge from the Cretaceous of Ahlten (Lower Saxony) recorded by Zittel (1878, p. 84, pl. 9, fig. 9a–b) as A. subramosa. The latter is characterized by less regular tetraclones with ornamented clones and zygosis (see below). In addition to the ornamentation of the tetraclones, A. laevis differs also from branched specimens of A. subramosa by the club-like or cylindrical shape of the body.

Occurrence. Poland (Belchatów area, early Campanian sponges as redeposited elements in Miocene deposits; Lebów area, lower Campanian); north-west Germany (Lower Saxony, upper Turolian or lower Coniacian, Campanian).

Astrocladia subramosa (Roemer, 1864)

Figures 12F–I, 14

1864  *Asterospongia subramosa* Roemer, p. 54, pl. 9 fig. 3.
1884  *Asterospongia laevis* Roem. sp.; Počta, p. 38, pl. 2 fig. 10; text-fig. 22.
? 1889  *Astrocladia subramosa* (Roemer); Griepenkerl, p. 21.
1910  *Astrocladia subramosa* (Roemer); Schrammen, p. 111, pl. 6 figs 4–5; text-pl. 6 fig. 9.
1924  *Astrocladia subramosa* (Roemer); Moret, pp. 195–196, pl. 10 fig. 10; text-fig. 75.

? 1963  *Astrocladia subramosa* (Roemer); Wagner, p. 186.
1966  *Astrocladia subramosa* (Roemer); Hurcewicz, pp. 67, 68.
? 1974  *Astrocladia subramosa* (Roemer); Ulbrich, p. 27.

Material. 39 specimens from Belchatów Lignite Mine (ULXXV/13T/1–39), one from Przesławice (ULII/30) and one from Pniaki (ULII/160).

Description. The material studied includes fragments of cylindrical or branched twigs, 25–55 mm long (Fig. 12F–I); most of these are 5–8 mm thick and rarely up to 12–15 mm. Occasionally preserved apex slightly rounded. One specimen with preserved fragment of expanded, flat base, 30 mm in size. Inhalant canal openings very small, 0.15–0.25 mm in diameter, scattered on sponge surface at intervals of 0.5–15 mm. Exhalant canal openings, 0.2–0.6 mm in diameter, densely arranged in groups, consisting of several to a dozen canal openings; occasionally located on small protuberances and often surrounded by 1.5–5.5-mm-long radial furrows. Distance between groups of opening on individual specimens very different: from 5 mm to 13 mm. Inhalant canals perpendicular to sponge surface. Exhalant canals with various orientations; canals with outlets in centre of group more or less perpendicular to sponge surface, whereas external channels run obliquely inside sponges.

Dense choanosomal skeleton consisting of small tuberculate tetraclones (Fig. 14A–B). Desmas with smooth clones or with single tubercles occurring occasionally only inside the wall (Fig. 14C). Small, but prominent, conical tubercles with rounded or mushroom-like top sparsely arranged on clones. Summit of mushroom-like tubercles rounded or elongated, usually in the direction transverse to clone. More densely distributed tubercles occurring on zygomes finer, occasionally spine-like. Clones, usually 100–180 µm long, unbranched or forked with moderately branched terminal articulations. Arched, irregularly branched tetraclones appear on canal walls. Zygomes usually not too long, but occasionally reach up to 70–80 µm, forming an elongated zygosis, usually c. 70–80 µm × 150–250 µm in size. Rarely the zygosis is very elongated and can reach a length of 400 µm. Massive ectosomal phyllotriaenes with wide, ragged clads, 80–180 µm long (Fig. 14D). Spaces between ectosomal phyllotriaenes filled with very densely packed, small, flat, irregular spicules.

Remarks. Schrammen (1910) stated that tetraclones of Astrocladia subramosa were smooth with spiny zygomes; however, the clones of desmas presented by him seem to be ornamented (Schrammen 1910, text-pl. 6, fig. 9). Our study of Schrammen’s specimens indicates that tetraclones of this species are tuberculate. Desmas of specimens from Belchatów and also those from the Miechów area have a similar ornamentation, despite the fact that Hurcewicz (1966) described the latter as smooth. Minor differences in the ornamentation of the desmas in individual specimens are related to the diagenetic dissolution of spicules, especially the smallest tubercles and tips of tubercles (Fig. 14A–B). Poorly ornamented desmas of Astrocladia laevis from the Czech Republic, described and illustrated by Počta (1884), are here reassigned to A. subramosa.
The taxonomic position of some Cretaceous specimens described as *A. subramosa* (Griepenkerl 1889; Wagner 1963; Ulbrich 1974) is ambiguous due to insufficient documentation of the desmas.

**Occurrence.** Poland (Belchatów area, early Campanian sponges as redeposited elements in Miocene deposits; Kraków area, middle or upper Campanian); north-west Germany (Lower Saxony, lower and upper Campanian; Saxony-Anhalt, lower Campanian); the Czech Republic (Cenomanian); southern Germany (Bavaria, Cenomanian to lower Turonian).

**Genus COLOSSOLACIS Schrammen, 1910**

*Type species.* *Colossolacis plicata* Schrammen, 1910 (pp. 103–104, pl. 8 fig. 5; pl. 9 figs 1–2; text-pl. 5 fig. 1) by monotypy.

**Diagnosis.** See Reid (2004).

*Colossolacis plicata* Schrammen, 1910

**Figures 15A–C, 16**

1910  *Colossolacis plicata* Schrammen, pp. 103–104, pl. 8 fig. 5, pl. 9 figs 1–2; text-pl. 5, fig. 1.
1974  *Colossolacis plicata* Schrammen; Ulbrich, p. 26.
1993  *Colossolacis plicata* Schrammen; Jahnke & Gasse, pl. 13 figs 3–4, pl. 16 figs 2, 5, 6.
2006  *Colossolacis plicata* Schrammen; Świerczewska-Gładysz, p. 277; text-figs 40d–e, 41d.

*Material.* 7 specimens from Belchatów Lignite Mine (ULXXV/6T/1–7).
Description. Specimens of various shapes (Fig. 15A–C). Small specimens conical with or without short stalk; no lateral lobes or with little bulging in upper part. Large ones with conical lower part and upper part with four irregular lobes arranged radially. Straight or forked furrows occurring in the lower part of the sponges and on the lateral surface of the lobes. Spongocoel of small specimens with 4–5 longitudinal furrows, 2–3 mm wide, resulting in a star-like outlet of spongocoel. Lateral fold of spongocoel within lobes of large specimens very narrow, 1–2 mm wide, occasionally with transverse skeletal bridges dividing folds of spongocoel into smaller, pit-like cavities. Surface of spongocoel containing canal openings that are round, 1–1.5 mm in diameter, or oval, up to 2 mm × 3 mm in size, sparsely distributed in 3–5 mm intervals. Straight or branched exhalant...
canals oriented more or less transversely to sponge wall and ending just below the outer surface. Walls of exhalant canals perforated by large openings, leading to smaller canals penetrating sponge walls transversely to main canals. Outer surface with round or oval inhalant canal openings, 0.6–1.5 mm in size (occasionally up to 2 mm), spaced every 1.5–4 mm, with smallest and most densely arranged openings occurring on the small specimens. Inhalant canals initially running perpendicularly in the wall, but not visible more deeply down.

Choanosomal desmas large tetraclones, with clones 450–580 μm long. Inside wall, tetraclones quite regular with unbranched, usually smooth clones. Terminal zygomes, up to 180 μm long, densely covered by small tubercles, forming spherical or slightly elongated zygosis, c. 200–300 μm in size. Less regular tetraclones, often with clones of different lengths and occasionally forked, appearing in an external part of the wall, perforated by numerous canals (Fig. 16A). Tetraclones with very irregular ramified clones occurring especially on canal walls (Fig. 16B–C). Clones of these tetraclones usually smooth, but sparsely arranged flat tubercles or slight ring-like swellings occasionally appear on the terminal part near zygomes. Prominent tubercles covering zygomes, up to 30 μm in diameter, conical or mushroom-like. Zygosis formed by tips of zygomes, but often strongly branched zygomes of some desmas also connect with the lateral side of clones of neighbouring tetraclones. Zygosis very elongated and reaching 200–250 μm × 600–700 μm in size. Extremely compact network on inner surface of choanosomal skeleton consisting of smooth or ornamented tetraclones with long (up to 300–500 μm long) and very branched zygomes (Fig. 16D). Strongly tuberculate zygomes intertwining with each other but also connecting with the distal, unbranched part of clones of neighbouring desmas. A few, partly damaged phyllotriaenes preserved on the stalks of small specimens and on the lateral surface of lobes of two strongly silicified specimens. Branched, narrow clads (100 μm thick), c. 350–500 μm long. Spaces between phyllotriaenes filled by small, flattened spicules with a ragged margin.

**FIG. 16.** A–D, Colossolacis plicata Schrammen, 1910. A, network from the subsurface of the choanosomal skeleton with smooth and poorly tuberculated tetraclones (ULXXV/22T/3, from Belchatów). B, network surrounding canals with irregular tetraclones (ULXXV/22T/4, from Belchatów). C, detail of skeleton of the same specimen. D, very compact choanosomal network on surface of spongocoel (ULXXV/22T/3, from Belchatów). Scale bars represent: 200 μm (A, C); 500 μm (B); 100 μm (D).
Remarks. Analysis of specimens from Belchatów and of the
descriptions of German material, measuring 25–30 cm in diam-
eter (Schrammen 1910; Ulbrich 1974), indicates that the shape of
Colossolacis plicata changed during individual development.
In the initial growth phase, sponges are conical. Later, radial lobes
develop, which are secondarily folded in mature individuals.
Small specimens with underdeveloped lobes differ from other
theonellid sponges by the star-like spongocoel with a characteris-
tically sparsely arranged, round or oval canal openings that vary
in size.

According to Schrammen (1910) and Ulbrich (1974), the
large tetracolones of C. plicata have smooth clones with strongly
tuberculate zygomes. The regular choanosomal skeleton of one
syntype in the Schrammen Collection presented by Jahnke &
Gasse (1993, pl. 13, figs 3–4) also consists of only smooth teta-
colones with terminal, tuberculate zygomes. Smooth desmas in
the specimens studied are often noted within the poorly pre-
served fragment of the choanosomal skeleton network from the
central part of the wall. Due to significant damage to the surface
of most of the desmas as a result of diagenesis, it cannot be
determined whether they were all smooth or whether some of
them were also ornamented. The dense network of one syntype
from the Schrammen Collection contains irregular desmas char-
acterized by clones that are smooth or contain sparse tubercles
(Jahnke & Gasse 1993, pl. 16, figs 2, 5–6). Such a shape and
sculpture of the tetracolones can be observed in the network from
the outer part of the wall of the specimens from Belchatów.
The weak ornamentation of the desmas was also noted by Świe-
czewska-Gładysz (2006) in a phosphatized specimen from the
Middle Vistula River section, central Poland.

The extremely compact skeleton on the inner surfaces of the
choanosomal skeleton, very well visible also on the inner surface
of the specimen illustrated by Schrammen (1910, pl. 8, fig. 5), is
one of the most characteristic features of the skeleton in this
species.

Occurrence. Poland (Belchatów area, early Campanian spon-
ges as redeposited elements in Miocene deposits; Middle Vistula
River valley, uppermost Maastrichtian); north-west Germany
(Lower Saxony, lower and upper Campanian; Saxony-Anhalt,
lower Campanian).

Genus PHYLLODERMIA Schrammen, 1924

Type species. Discodermia antiqua Schrammen, 1901 (p. 5, pl. 1
figs 2–4, pl. 4 fig. 3) by original designation (Schrammen 1924,
p. 48).

Diagnosis. See Reid (2004).

Phyllodermia antiqua (Schrammen, 1901)
Figures 15D–G, 17A–D

1901 Discodermia antiqua Schrammen, p. 5, pl. 1 figs 2–4,
pl. 4 fig. 3.

2006 Phyllodermia antiqua (Schrammen); Świeczewska-
Gładysz, pp. 278–279, figs 37g, 41a (with additional
synonymy).

Material. 6 specimens from Belchatów Lignite Mine (ULXXV/14T/1–6).

Description. Pearl-like or cylindrical sponges, occasionally with
irregular bulges in the lower part of the body or bulbous with a
short stalk (Fig. 15D–G). Largest specimens up to 100–120 mm
in height (Fig. 15F). Spongocoel narrow and deep; osculum, 8–
22 mm in diameter, centrally or asymetrically on sponge apex.
Outer surface (in places devoid of ectosomal skeleton) smooth
or covered by short widening furrows, differently oriented. Inha-
lant canal openings 0.8–1.5 mm in size, round or elliptical,
spaced at c. 2–3 mm. First sections of ephrhyxes perpendicular or
slightly oblique to sponge surface; unrecognizable deeper. Exha-
lant canals, 1.5–2.2 mm wide, running almost horizontally, very
long and ending right below outer surface. Canal openings not
visible on surface of spongocoel, being masked by overlapping
phyllotriaenes.

Choanosomal skeleton inside wall consisting of regular des-
mas (Fig. 17A). Clones of these tetracolones, 280–420 µm long
and c. 75–80 µm thick, poorly tuberculate or smooth, only with
ornamented terminal unbranched part and/or zygomes. Tuber-
cles, 10–30 µm in diameter, hemispherical or conical with
rounded top. Small tubercles densely covering zygomes most
prominent. Long, branched zygomes forming terminal, rounded
or elongated zygomes, up to 400 µm in size. Choanosomal
skelton around canals not distinguished by greater density, but
only by presence of less regular desmas, often with bent clones.
Tetracolones on outer surface of choanosomal skeleton with mas-
ive clones, up to 90 µm thick and 380–420 µm long (Fig. 17B).
Unbranched part of clones usually 150–200 µm long, but occa-
sionally shortened, measuring only c. 100 µm, covered by round
or elongated tubercles, which often connect with each other,
forming a characteristic half-ring-like swelling. Due to the frag-
mentary preservation of the strongly siliceous euctosomal layer,
phyllotriaenes only locally observed. Some of the phyllotriaenes
have narrow clads (c. 50 µm wide), others have clads c. 100 µm
wide (Fig. 17C–D). Clads of the single phyllotriaene often vari-
ious lengths (longest reaching up to 350–400 µm), poorly rami-
fied and characterized by spatulate terminal branches of same
width, narrowed or less often slightly dilated. Small and
branched spicules, bearing minute granules, co-occurring with
phyllotriaenes.

Remarks. Phyllodermia antiqua is a polymorphic Cretaceous spe-
cies, known from various parts of Europe (e.g. Moret 1926;
Hérenger 1946; Lagneau-Hérenger 1967; Van Kempen 1966;
Gruber 1993). Specimens studied are represented by morpho-
types with a well-developed spongocoel. The features of
choanosomal desmas and euctosomal phyllotriaenes recognized in
specimens from Belchatów fully correspond to the characteristics
of the skeleton of Ph. antiqua listed by other authors (compare
Schrammen 1901, pl. 4, fig. 3; 1910, text-pl. 5, fig. 4; Gruber
1993, p. 41, pl. 8, figs 2–3; Pisera 2002, fig. 21a–b).
FIG. 17. A–D, Phyllodermia antiqua (Schrammen 1901). A, choanosomal skeleton from the central part of the wall (ULXXV/14T/2, from Belchatów). B, network from the outer surface of the choanosomal skeleton (ULXXV/14T/3, from Belchatów). C, ectosomal skeleton mainly showing phyllotriaenes with narrow clads (ULXXV/14T/2, from Belchatów). D, ectosomal skeleton of the same specimens showing phyllotriaenes with wider clads. E–F, Phyllodermia pulchra Hurcewicz, 1966 (holotype, UL II/391, from Skrajniwa). E, tetraclines on the outer surface of the choanosomal skeleton. F, ectosomal skeleton with fragmentarily preserved phyllotriaenes and rare small spicules. Scale bars represent 200 μm.
Phyllotriaenes with narrow clads had not yet been described for the present species, but they are visible in the illustration presented by Pisera (2002, fig. 21b).

Occurrence. Poland (Belchatów area, early Campanian sponges as redeposited elements in Miocene deposits; Middle Vistula River valley, uppermost Maastrichtian); north-west Germany (Lower Saxony, lower and upper Campanian); southern France (Département Department Drôme, Turonian; Beausset area, Santonian; Petites Pyrénées, Campanian); the Netherlands (erratics).

Phyllodermia pulchra Hurcewicz, 1966
Figures 15H–K, 17E–F

1966 *Phyllodermia pulchra* Hurcewicz, pp. 57–58, pl. 12 fig. 2; text-fig. 13.
1966 *Discodermia cf. galloprovincialis* Moret; Hurcewicz, pp. 54–55.

Material. Three specimens from Belchatów Lignite Mine (ULXXV/3T/1–3), one from Zbyczyc (ULII/214) and five from Skrajniwa (ULII/285, 391, 392, 714, 1293).

Description. Club-like to conical sponges with 2–3 large, irregular bulges in upper part, separated by deep furrows or wide shallow depression (Fig. 15H–K). Largest specimen 65 mm in height and 52 mm wide. Spongocoel not developed. Short (up to 10 mm long), winding furrows visible on sponge surface in places devoid of echosomal skeleton, part of these showing star-like arrangement. Openings of inhalant canals, 0.4–0.5 mm in diameter, spaced at c. 1–2 mm. Inhalant canals (recognizable in two specimens) perpendicular to the surface (mainly in the lower part of sponges) or oblique, and initial sections having the form of fine, short grooves (2–4 mm long). Single, larger openings, 1–1.5 mm in diameter, occurring in the upper part of the sponge probably outlets of inhalant canals. Pattern of aporhyses inside sponges impossible to define because only cross-sections of dispersed aporhyses are visible on the broken apex or base.

Poorly visible tetracolones on the outer surface of the choanosomal skeleton, with clones 60–70 mm thick and 300–380 long (Fig. 17E). Strong zygoomes usually half the length of clones. Prominent, mushroom-like, rarely conical tubercules densely covering clones. Tubercule diameter 15–30 µm on the unbranched part of clones and 10–15 µm on zygoomes. Single, noticeably deeper tetracolones ornamented by small (up to 15 µm in diameter) and very sparsely distributed tubercules. Layer of echosomal skeleton covering a large part of the specimens, but phyllotriaenes forming this poorly preserved, with strongly crushed clads (Fig. 17F). Overlapping phyllotriaenes with cladomes up to 700 µm in size and irregularly branched clads. Spatulate terminal part of clads with expanded tips and up to 150–200 µm wide. Rare fragments of small spicules covered by minute granules occurring between phyllotriaenes.

Remarks. On account of the irregular body shape and the lack of the spongocoel, these specimens resemble some representatives of *Phyllodermia antiqua* with a reduced spongocoel (Schrammen 1901, 1910; Świerczewska-Gładysz 2006). *Phyllodermia pulchra* may be distinguished from the latter by a narrower inhalant canal and smaller phyllotriaenes with clearly expanded tips of clads. There are also slight differences in the ornamentation and dimensions of the tetracolones occurring on the surface of the choanosomal skeleton of both species.

These characteristic features of *Ph. pulchra* are also seen in the three specimens from the museum collections described by Hurcewicz (1966) as *Discodermia cf. galloprovincialis*. Irregular bulges in the upper part of the specimens were considered by Hurcewicz (1966, p. 54) as ‘globular individuals with a common base’, which show a broad or reduced spongocoel, replaced by a bundle of aporhyses. Such structures were not found in any of these specimens (compare fig. 14I), and in our opinion the sponges from Poland show no macroscopic resemblance to the colonial specimens of *Discodermia galloprovincialis* from the Santonian of France, which are composed of finger-like individuals with a deep cylindrical spongocoel (see Moret 1926, pp. 176–178, pl. 15, figs 1–2). In contrast to the granulated phyllotriaenes of *D. galloprovincialis* (Moret 1926, pp. 176–178, text-fig. 69,1), the phyllotriaenes of the specimens studied here are smooth, as previously noted by Hurcewicz (1966).

Occurrence. Poland (Belchatów area, early Campanian sponges redeposited into Miocene deposits; Lelów area, lower Campanian).

Genus *Eustrobilus* Schrammen, 1910

Type species. *Eustrobilus callosus* Schrammen, 1910 (p. 103, pl. 8 figs 3–4, pl. 15, fig. 1, pl. 23, fig. 6; text-pl. 4, fig. 12) by monotypy.

*Eustrobilus extraneus* Hurcewicz, 1966
Figures 18A–D, 19A–C

1966 *Eustrobilus extraneus* Hurcewicz, pp. 61–63, pl. 9 fig. 1a–c; text-fig. 15.
1966 *Eustrobilus callosus* Schrammen; Hurcewicz, pp. 59–61 (pars), pl. 10 figs 2–3.

Material. A single specimen from Pniaki (ULII/1617) and another one from Zbyczyc (ULII/726).

Description. Holotype: club-like sponge, 79 mm in height, with narrowed apex, two thick lateral lobes and irregular, partly destroyed bulges situated in the upper part (Fig. 18A–B). Second specimen, significantly damaged by cutting and grinding performed by Hurcewicz: fragment of upper part of a sponge with one large lobe (Fig. 18C–D). Spongocoel in both specimens deep and very narrow (6 mm in diameter). Osculum surrounded by long, forked furrows, up to 1 mm wide. Exhalant canals visible in cross-section of one specimen oblique and upward facing.
Poorly visible canal openings on the surface of spongocoel elliptical, 1 mm in size. Canals opening on outer surface occurring in lower part of sponges round or elongated, 0.4–0.6 mm in size, leading to slightly oblique or nearly perpendicular inhalant canals. In upper part of sponges less densely distributed canal openings strongly elongated or comma-like, up to 0.7 mm wide and 2–3 mm long. Inhalant canals oblique and running mainly upward. Inhalant canals penetrate more than halfway into the sponge wall. Arrangement of inhalant canals on bulges and locally on lobes disturbed; canals differently oriented, with the first section often having the form of short furrows (up to 4–5 mm).

Massive tetraclones on outer surface of choanosomal skeleton having clones 280–360 µm long and 80–100 µm thick (Fig. 19A–B); their short zygomes usually connected with the lateral side of clones of adjacent desmas. Round or elongated tubercules, densely covering clones, very prominent. Apices of large tubercules, up to 50 µm in size, divided by shallow furrows into 2–3 smaller lumps (Fig. 19B). Flattened, irregular desmas with tubercules only on the terminal part occasionally occurring between typical desmas. Tetraclones inside wall slightly larger, with clones unbranched or occasionally irregularly forked. Tubercles, sparsely arranged on the surface of clones, not exceeding 30 µm in diameter. Very variable phyllotriaenes often with clads of various length, the longest reaching 350 µm (Fig. 19C). Some of the phyllotriaenes with wide, spatulate clads with additional small to deep indentations, often showing slightly convex, finely granulated upper side. Other phyllotriaenes with narrow and very deeply indented clads; usually smooth. Irregularly branched spicules (up to 200 µm in size) with small tubercules occurring between overlapping phyllotriaenes.

**Remarks.** *Eustrobilus extraneus* differs from other species of *Eustrobilus* mainly by its club-like body with irregular lobes in the upper part. Hurcewicz (1966) assigned only a single specimen to *E. extraneus*, but the features of another specimen in the museum collection agree with the description of this species. Hurcewicz (1966, p. 60) described this particular specimen, identified by her as *E. callosus* Schrammen, 1910, as ‘consisting of two concrescent individuals’. Indeed, two hollows occur on its upper side, but only one of them is the osculum, while we interpret the second, which leads to an oblique short tunnel without canal openings, to be a boring trace (Fig. 18C). Such, or smaller, borings occur also on the lateral side of this specimen and near the base of the holotype specimen (Fig. 18A).

Unlike *Eustrobilus callosus*, the desmas of both specimens of *E. extraneus* are more massive, with unbranched or only occasionally forked clones (Hurcewicz 1966, pp. 59–63, text-figs. 14–15). The observation of Hurcewicz (1966, p. 62) that both species ‘fundamentally differ in structure of the cortical skeleton’ is incomprehensible. The shape and diversity of phyllotriaenes are similar in *E. extraneus* and *E. callosus* (Fig. 19D). Moreover, in both species some of the phyllotriaenes are characterized by a slightly convex, granulated upper side of the cladomes. These features, visible only on SEM, have not been recorded before in representatives of the genus *Eustrobilus*. 
Occurrence. Poland (Lelów area: lower Campanian).

Genus **PSEUDOJERA** Moret, 1926

Type species. *Pseudojerea massiliensis* Moret, 1926 (p. 181, pl. 4 fig. 7, pl. 6 fig. 2) by subsequent designation (Laubenfels 1955, p. E58).

**Pseudojerea sp.**

Figure 18E

Material. A single specimen from Belchatów Lignite Mine (ULXXV/25T/1).

Description. Fragment of apical part of probably club-like sponge, 66 mm in diameter (Fig. 18E); rounded apex with shallow depression, 20 mm in diameter, surrounded by short, widening furrows. Canal openings in depression round, 2–2.5 mm in diameter and separated by a skeletal band of 0.5–0.7 mm in width. Vertical exhalant canals forming central bundle. Outer surface with small round canal openings, 0.5–0.6 mm in diameter, occasionally up to 1 mm. Inhalant canals not visible due to strong silicification of specimen.

Choanosomal desmas visible mainly on wall of exhalant canals, where strongly tuberculate tetracloones show irregularly branched clones, c. 200 µm long. Poorly preserved tetracloones inside wall with forked or unbranched clones with short terminal zygomes forming small rounded zygosis. Ectosomal spicules not preserved.

Remarks. Despite the lack of ectosomal phyllotriaenes, the specimen from Belchatów is here assigned to *Pseudojerea* on the basis of the characteristic axial bundle of exhalant canals and tuberculate tetracloones. In view of the lack of a well-developed spongoeclet and the shape of the body, this specimen most closely resembles *Ps. massiliensis* Moret, 1926 from the Santonian of Provence (southern France) and *Ps. micropora* Defretin-Lefranc, 1960 from the Cenomanian of northern France. Club-like specimens of both these species are smaller, not exceeding 45 mm in
width. In contrast to the poorly ornamented desmas of "Ps. micropora" (Defretin-Lefranc 1960, pp. 111–112, text-fig. 34), tetraclines of the specimen studied are strongly tuberculate as in "Ps. massiliensis" (Moret 1926, p. 181, pl. 4, fig. 7, pl. 6, fig. 2). Despite the similarities, the specimen cannot be assigned to this species in the absence of ectosomal spicules.

**Occurrence.** Poland (Belchatów area, early Campanian sponges as redeposited elements in into Miocene deposits).

### DISCUSSION

**Taxonomic composition of Campanian phymaraphiniids and theonellids from the Mogilno-Łódź and Miechów synclinoria**

Early Campanian phymaraphiniid sponges are rare in the Mogilno-Łódź and Miechów synclinoria, being represented in both regions by only four species namely *Phymaraphinia infundibuliformis*, *Prokaliapsis clavata*, *Prokaliapsis janus* and *Cycloclema compressa* (Fig. 20).

Theonellid sponges from the Mogilno-Łódź and Miechów synclinoria show variation in terms of species composition and frequency of occurrence (Fig. 20). Nine species of theonellids are distinguished in the assemblage from Belchatów (Mogilno-Łódź Synclinorium): *Rhagadinia rimosa*, *Rh. doederleini*, *Astrocladia subramosa*, *A. laevis*, *Rhoptrum scytaliforme*, *Colossolacis plicata*, *Phylloodermia antiqua*, *Ph. pulchra* and *Pseudejeroa* sp. The commonest theonellid of these is *Rh. rimosa* (Roemer, 1864), which is also the most frequent species of siliceous sponge in the Belchatów gravels. This species also occurs relatively often in opoka and marls in the Lelów and Krakow area (Bieda 1933; Hurcewicz 1966). The remaining eight species are rare in Belchatów and, furthermore, only three of these (*Rh. doederleini*, *Ph. pulchra*, *A. subramosa*) have been found in the Miechów synclinorium.  

![FIG. 20. Stratigraphic and palaeogeographic distribution of phymaraphiniid and theonellid species in the Cretaceous of Europe. Abbreviations: Cz, Czech Republic (after Počta 1884); E, England (after Hinde 1883); F, France (after Moret 1926; Hérenger 1946; Defretin-Lefranc 1960); G, Germany (after Roemer 1864; Schrammen 1910, 1912, 1924; Wagner, 1963; Ulbrich 1974; Schneider et al. 2013); P, Poland (Middle Vistula River valley after Świerzewska-Gładysz 2006); S, Spain (after Lagneau-Hérenger 1962, Rosales et al. 1995); distribution of species in Miechów Synclinorium after Bieda (1933) and Hurcewicz (1966) complemented by data from the present study; species that are here recognized from the Campanian of Poland for the first time are marked with an asterisk.](image-url)
Synclinorium. Additionally, Hurcewicz (1966) described two species of *Eustrobius* (*E. callosus* Schrammen, 1910, a taxon accepted by us, plus *E. extraneus* Hurcewicz, 1966, of which a complementary description is provided here), two species of *Phyllodermia* and one species of *Discodermia* from marly deposits in the Mięchów Synclinorium. Specimens described by Hurcewicz (1966) as *Discodermia cf. galloprovincialis* are here assigned to *Phyllodermia pulchra*. The species affiliation of the unique specimens of *Phyllodermia magna* Hurcewicz, 1966 and the two specimens described by Hurcewicz (1966) as *Phyllodermia costata* (Hinde) subsp. *brevicostata* (Michelin, 1847) are still undecided on account of the strong silicification of these specimens and the very poor preservation of their skeleton.

**Taxonomic remarks**

Classification at the genus level of fossil Theonellidae and Phymaraphiniidae is based on a combination of the shape of the ectosomal triaenes, as well as the shape, size and ornamentation of the choanosomal desmas, in addition to the shape of the sponge body and arrangement of canals in the choanosomal skeleton (Zittel 1878; Schrammen 1910, 1924; Reid 2004). Microscleres important in the taxonomy of Recent sponges are unknown in fossil representatives of both families. Hurcewicz (1966) noted microscleres in almost all species of Theonellidae from the Campanian of southern Poland, although this was not confirmed by us. Loose mega- and microscleres of various demosponges occur abundantly in the Campanian opoka (Moczydowska & Paruch-Kulecycka 1978; Jurkowska et al. 2019b; Jurkowska & Świerczewska-Gładysz 2020a) and the majority of microscleres noted by Hurcewicz (1966) in many lithistid species are most probably derived from such soft demosponges (Świerczewska-Gładysz 2016, 2017). According to Hurcewicz (1966), microscleres in theonellids are mainly globular or elongated spherasters. These microscleres are characteristic only for the family Geodiidae Gray, 1867 (e.g. Uriz 2002; Cárdenas et al. 2011, 2013; Cárdenas 2020) while acanthorhabds, pseudospherasters, microxeas, streptasters and amphistelars characterize extant Theonellidae (Pisera & Lévi 2002a). The supposed spherasters illustrated by Hurcewicz (1966, pl. 9, fig. 1c; pl. 10, fig. 3b; pl. 11 fig. 1b; pl. 12 fig. 1c; pl. 13, fig. 1b) are probably the grains of detrital quartz occurring in marls or/and large opal-CT lepispheres (up to 80–100 μm in size), which infill the foraminiferal chambers, common in Campanian opoka (Jurkowska & Świerczewska-Gładysz 2020b).

The ectosomal triaenes of Recent species of genera *Theonella* Gray, 1868 and *Racodiscula* Zittel, 1878 (family Theonellidae) have a wide variety of shapes (Vacelet & Vasseur 1965; Van Soest & Stentoft 1988; Pisera & Pomponi 2015; Carvalho et al. 2020). The width of the phyllotriaene clads varies considerably in a single species. In some cases, even transitional morphologies from phyllotriaenes to discoctriaenes have also been noted. The occurrence of various types of ectosomal spicules, recorded also in Palaeogene theonellid species (Pisera 2000), has been occasionally documented in Cretaceous theonellids and phymaraphiniids (Schrammen 1910, text-pl. 4, fig. 12; Hérenger 1942; Hurcewicz 1966). Descriptions of Cretaceous species usually lack detailed data on the shapes of the phyllotriaenes or present only one type. In the latter case, such a shape has been considered by subsequent researchers to be diagnostic for that particular species. Our study indicates that the variability of ectosomal phyllotriaenes within a single species was a common situation in the Cretaceous theonellids and phymaraphiniids. According to Hurcewicz (1966), representatives of *Rhagadinia* Zittel, 1878 have massive phyllotriaenes on the inner surface of sponges, and slender ones on their outer side. A similar differentiation of ectosomal desmas on the outer and inner surfaces of sponges is noted in some modern theonellid species (Pisera and Lévi 2002a). Our study, which includes numerous specimens collected during fieldwork, as well as from the Hurcewicz Collection, also noted a high variability of phyllotriaenes in both species of *Rhagadinia*, but could not confirm that the massive phyllotriaenes with broad clads are located only on the inner surface of the sponges. They occasionally also occur, besides slender phyllotriaenes, within the thick ectosomal layer on the outer surface of the *Rhagadinia* sponges. In addition to both species of *Rhagadinia*, a high variability in phyllotriaenes shape was observed in several other species from the Polish material: *Prokaliapsis clavata*, *Pr. janus* (Roemer, 1864), *Phyllodermia antiqua*, *Ph. pulchra*, *Eustrobius extraneus* and *E. callosus* Schrammen, 1910. In all of these species, the less common type of phyllotriaene occurs locally on both surfaces of the sponges.

In extant theonellids cladoles of ectosomal triaenes are usually characterized by the presence of a smooth surface, but in some species of *Theonella* and *Discodermia* du Bocage, 1869 they are covered by small protuberances (e.g. Vacelet & Vasseur 1971; Van Soest & Stentoft 1988; Pisera & Pomponi 2015; Carvalho et al. 2020). In the present material, phyllotriaenes with granulated cladoles have been observed in two species of *Eustrobius*. To date, the only known Cretaceous theonellid species with granulated ectosomal triaenes is *Discodermia galloprovincialis* Moret, 1926 (= *Rhagadinia galloprovincialis*, sensu Hérenger 1942). In all of these fossil species, with the exception of ornamented phyllotriaenes, smooth phyllotriaenes are also present (see also Moret 1926, text-fig. 61.1).
Limited data regarding the euctosomal skeleton of the Cretaceous sponges is the result of the poor preservation of the specimens. The single euctosomal phyllotriaenes are often found scattered in the Upper Cretaceous deposits (e.g. Schönlaub 1973; Moczydlowska & Paruch-Kulczycka 1978; Bless & Felder 1989; Bąk et al. 2015; Okoński et al. 2014), while they are rarely observed in situ on the surface of fossil sponges. They are also not common in the present specimens despite the fact that they have undergone very rapid silification following the burial of dead sponges in the sediment (Jurkowska & Świerczewska-Gładysz 2020b). This is because the euctosomal phyllotriaenes become incorporated in the sediment after the sponge’s death and the decomposition of the soft body but before the sponge is covered completely by sediment. The euctosomal spicules were usually preserved on the surface of the basal part of the studied sponges and root-like outgrowths that were already embedded in the soft sediment in Cretaceous lithistids during their lifetime (Świerczewska-Gładysz, 2006). In the redeposited specimens from Belchatów, euctosomal spicules are preserved mainly on the inner surface of specimens, which was less exposed to mechanical damage during transportation by the river.

Phyllotriaenes occur relatively frequently in situ in some species, indicating that this is related to the structure of their euctosomal skeleton. In representatives of the genera Prokaliapsis, Phyllodermia and Rhagadinia, overlapping phyllotriaenes formed a thick layer that was predisposed to preservation in the fossil record. Moreover, in the last two genera, small subeuctosomal spicules (rhizoclons, sensu Reid 2004), which are present both under and between phyllotriaenes, made the outer skeletal layer extra compact. Subeuctosomal spicules are also important skeletal components of two species of Eustrobilus and of Astrocładia subramosa. In the species of Theonellidae studied, these spicules differ in shape, ornamentation (smooth or tuberculate) and size. With the current state of research, it is difficult to determine whether the morphology of these additional spicules may be helpful in the taxonomy of Cretaceous theonellids. Additional subeuctosomal spicules, unknown in extant lithistid sponges, were noted in many Cretaceous species that are representative of other lithistid groups, such as Phymatellidae Schrammen, 1910 and Corallistidae Sollas, 1888 (Schrammen 1910; Reid 2004; Świerczewska-Gładysz 2016, 2017), but have never been found in fossilized phymaraphiniids.

In the literature, descriptions and illustrations of single choanosomal desmas of Cretaceous theonellids and phymaraphiniids are common, whereas fragments of their skeletal network, with a visible arrangement of desmas, are very rarely documented (Hinde 1883; Moret 1926; Jahanske & Gasse 1993). Moreover, descriptions do not usually contain information regarding from which part of the sponge the illustrated network or singular desmas come. Our analyses showed that in a single specimen the skeletal structure is not identical in different parts of the sponge wall, which is reflected by the variable size, shape, articulation and ornamentation of desmas. This information has not been included in the descriptions of the species. In the theonellid and phymaraphiniid species studied here, the most compact network was observed on the outer and, occasionally, also on the inner surface of the choanosomal skeleton. This network is composed of smaller desmas or desmas with more branched zygomes, compared with the skeleton of the internal part of the wall. In theonellids, the surface of desmas is usually strongly tuberculated, while desmas inside the wall are poorly ornamented or even smooth, which is also observed in some modern Theonellidae (Carvalho et al. 2020). In turn, triders occurring on the outer surface of phymaraphiniids have clones with more prominent ring-like swelling compared with other desmas.

The fossil lithistid sponges often show modification of desmas in the stalk and/or near the base (Pisera 2000; Świerczewska-Gładysz 2016, 2017). Modified tetraclones with very elongated clones and without ring-like swelling occur on the surface of the stalks of Phymaraphinia infundibuliformis and Cycloclema compressa. In the latter species, a choanosomal network with modified desmas sometimes also occurs in the upper part of sponges, where it covers the network with typical small triders.

Some of the Cretaceous genera described here (e.g. Phymaraphinia, Cycloclema, Colossolacis and Rhoprum) are represented by only one or two species. In addition to the characteristic features of its skeleton, the shape of the body is an important attribute for Colossolacis plicata. Our observation indicates that the funnel-like body with an irregularly plicated wall, considered diagnostic of this species, is typical only of adult individuals, while juvenile forms are characterized by an unfolded outer surface and a star-like spongocoel. Other genera (such as Prokaliapsis, Phyllodermia, Rhagadinia) have more species but many of them have been described only on the basis of a single or a few specimens (Schrammen 1901, 1910, 1924; Wagner 1963; Hurcewicz 1966). Some of these species have been distinguished mainly on the basis of criteria that are doubtful in the case of polymorphic species, such as body shape, details of sponge surfaces and the thickness of the wall. The intraspecies variability of body shape, frequently noted in Recent phymaraphiniid and theonellid species (Pisera & Pomponi 2015; Carvalho & Pisera 2019; Carvalho et al. 2020), has been well recognized only in a few common Cretaceous species, such as Prokaliapsis clavata, Phyllodermia antiqua and Rhagadinia rimosa. The analysis presented here of the specimen-rich collection from Poland has enabled the completion of the data regarding intraspecies variability of the above species, along with several others such as Colossolacis plicata, Rhagadinia.
doederleini, Prokaliapsis janus and Phylloidermia pulchra. In turn, Rhagadinia foraminifera appears to be a junior synonym of Rh. doederleini, known so far from only a few specimens from the Campanian of Lower Saxony. This species, similar to Rh. rimosa, has a variety of body shapes and wall thickness (Fig. 8). Most of the specimens of Prokaliapsis janus described from the Santonian and lower Campanian of Goslar and Ilsenburg (north-west Germany) are bulbous or very massive cup-like sponges (Roemer 1864; Schrammen 1910; Ulbrich 1974; Müller 1977). In the material from Poland, thin-walled, funnel-like morphotypes, occasionally with thin stalks, are also present in the fossil record. Schrammen (1910) identified a similar thin-walled specimen from the Campanian of Oberg (north-west Germany) as a new species, Lapadoporus lacunosus, which is recognized here as a junior synonym of Pr. janus. We agree with the opinion expressed by other authors (Ulbrich 1974; Müller 1977; Uchman et al. 2018) that the pits and additional wide canals occurring in some specimens of Pr. janus, as recognized by Schrammen (1910) as diagnostic features for the new genus Lapadoporus, are trace fossils and we accept Ulbrich’s (1974) view that this genus is a junior synonym of the genus Prokaliapsis. In contrast to the material from shallow-water facies of the Campanian of north-west Germany (Ulbrich 1974; Müller 1977; Uchman et al. 2018), borings are rarely noted in specimens of Pr. janus from Poland. The sponges studied lived in the offshore zone of the Late Cretaceous European epicontinental sea, where boring organisms were uncommon.

Spatial and stratigraphical distribution of Cretaceous phymaraphiniid sponges

The phymaraphiniids were a more important component of the sponge fauna during the Cretaceous than they are today (Pisera & Lévi 2002b). However, they were poorly diversified taxonomically and less numerous than other Cretaceous tetracladinid sponges. Phymaraphiniids were reported from only a few Aptian–Campanian assemblages of Europe, while they are not known from Maastrichtian strata.

All phymaraphiniid species described here as originating from Poland have also been noted from Campanian strata of Germany (Fig. 20), where they were recognized in sponge assemblages rich in lithistids and hexactinellids in marls and limestones of early Campanian age in Lower Saxony (Oberg and Misburg areas; Schrammen, 1910). Early Campanian phymaraphiniids from this region are taxonomically more diverse (7 species) than the present assemblages from Poland, but compared with other co-occurring groups of siliceous sponges they are rare. The species Phymaraphinia infundibuliformis, Cycloclema compressa and Prokaliapsis clavata were also found by Schrammen (1910) in the upper Campanian of the Misburg area. This section includes marls, marly limestones and opoka (Wiese et al. 2013) but Schrammen (1910) did not indicate from which lithology the specimens came.

Prokaliapsis janus, which is extremely rare in Lower Saxony, is very common in the nearshore sandy marls of the lower Campanian (Wernigerode area) and Santonian (Sudenberges area) in the Subhercynian Basin (Germany, Saxony-Anhalt) where it co-occurred with representatives of other species of Prokaliapsis, as well as various lithistids (Schrammen 1910; Ulbrich 1974; for lithology and stratigraphy see also Voigt et al. 2006). Specimens of Pr. janus also appear as redeposited clasts with borings in the offshore marly mudstones and marls of the Ilsenburg Formation of the Subhercynian Basin (Uchman et al. 2018). The only representative of Phymaraphiniidae in the Cretaceous Münsterland Basin (western Germany) is Phymaraphinia infundibuliformis, which is noted in offshore marly-carbonate of the lower upper Campanian (Giers 1964; for lithology and stratigraphy see also Kappel 2003).

In addition to the aforementioned deposits of northern and western Germany, Cycloclema compressa and Prokaliapsis clavata were also found by Hinde (1883) in flint nodules from the Upper Chalk of Wiltshire (southern England), probably of late Turonian or early Coniacian age (Woods 2015) (Fig. 20). Moreover, C. compressa was identified in Coniacian chalk of central France (Moret 1926) and Cenomanian gaize of northern France (Defretin-Lefranc 1960) (Fig. 20). The occurrence of Phymaraphinia infundibuliformis in shallow-water Albian marls from northern Spain may constitute the earliest palaeontological record of this species (Rosales et al. 1995), however, the lack of proper documentation of these specimens prevents their taxonomic verification.

Sponge assemblages containing another species of phymaraphiniid are rarely recorded in pre-Campanian deposits of European epicontinental sea species. They are noted in marls and limestones of the Aptian of Catalonia (Spain) (Lagneau-Hérénger 1962; lithology after Moreno 2005), in Cenomanian to lower Turonian siliceous clays and silt with siliceous nodules of the Danubian Basin (Neuburg Kieselerde Member, Bavaria, southern Germany) (Wagner 1963; Schneider et al. 2013), and Santonian nearshore facies of Saint-Cyr (Beausset Basin, south-east France) (Moret 1926). The taxonomic composition of phymaraphiniids from these deposits is completely different from the assemblages of the Campanian of Poland and Germany.

Spatial and stratigraphical distribution of the Cretaceous theonellid sponges

During the Cretaceous period, theonellids constituted an important group of lithistid demosponges that were more
numerous and taxonomically diverse than they are today. However, knowledge of the distribution of these sponges in the European epicontinental sea, as is the case for other lithistids, is incomplete, largely due to post-Maastrichtian erosion of Cretaceous deposits. Data on Maastrichtian theonellids are especially limited. Single specimens of theonellid species (Colossolacis picta, Rhagadinia rimoso and Phyllodermia antiqua) redeposited from Maastrichtian opoka were found in Danian glau-conitic sandstone at Nasiłów (Poland, Middle Vistula River valley) (Świerczewska-Gładysz 2006) (Fig. 20).

In addition to the three species that are known exclusively from the lower Campanian of Poland (Eustrobulus extraneus, Phyllodermia pulchra and Pseudojerea sp.), all others are characteristic fossils of the Santonian and/or Campanian of Germany (Fig. 20). Astrocladia laevis and Rhagadinia rimoso were described from the Santonian of the Subhercynian Basin (Germany, Saxony-Anhalt). The latter, as well as Colossolacis picta, were also noted from lower Campanian marls of the Ilsenburg Formation in the Subhercynian Basin Ulbrich (1974). Theonellids are also common in Campanian littoral facies of this region, but are represented only by two species of Phyllocleris (Griepenkerl 1889; Ulbrich 1974), which are unknown from the Cretaceous of Poland. Specimens of Colossolacis picta and Rhagadinia rimoso, in addition to Rhagadinia doederleini, Astrocladia subrmosa, Rhoptrum scyliforme, Phyllocleris antiqua and Eustrobulus callosus, occur in Campanian marls and limestones of Misburg and Oberg (Germany, Lower Saxony) (Schrammen 1901, 1910, 1924; Gruber 1993). The diversity of early and late Campanian theonellids from Lower Saxony is significantly higher than that of the Polish material, as well as that of other known Cretaceous theonellid assemblages. A number of species and a few genera (Leiophyllum Schrammen, 1924, Mastophorus Schrammen, 1924, Placocystus Schrammen, 1901) were recorded only from these assemblages. The Campanian sponge fauna from pelagic deposits of the Münsterland Basin was dominated by hexactinellids, while rare theonellids are represented by only two species (Gas et al. 1988, 1991).

Some Cretaceous species, including Rhagadinia rimoso, Phyllocleris antiqua, Astrocladia subrmosa and Eustrobulus callosus known from Poland, had long stratigraphic ranges and a wide palaeogeographic distribution (Fig. 20). The first three species, as well as seven other theonellid species, were recorded from a species-rich assemblage from Cenomanian to lower Turonian deposits of the Danubian Basin (Neuburg Kieselerde Member, Bavaria, southern Germany) (Wagner 1963; Schneider et al. 2013). Moreover, Astrocladia subrmosa was known from the Cenomanian of the Czech Republic (Pocta 1884).

Rhagadinia rimoso, Phyllocleris antiqua and some other species of Discodermia and Pseudojerea were noted by Moret (1926) from the Santonian shoreface sandy marly-carbonate facies of Saint-Cyr (Beausset Basin, south-east France). Rhagadinia rimoso, Eustrobulus callosus and representatives of Thamnospongia Hinde, 1883 and Phymatoplecta Hinde, 1883 are known from pelagic Santonian marly-carbonate facies of south-east France (Nice area) (Moret 1926). Species of these last two genera have been found, outside of France, only in siliceous nodules from the Upper Chalk in southern England (Hinde, 1883).

Representatives of various species of Phyllocleris and Rhagadinia were recognized in Turonian marl and limestones from the Eygaliers area (southern France) (Lagneau-Hérenger 1967; lithology after Letourneur & Porthault 1966) and Cenomanian deposits of the AngloParis Basin: in gaise of the Marlemont area (France, Ardenas) (Defretin-Lefranc 1960; lithology after Mégien & Mégien 1980), as well as from some layers (probably malmstones after jeans 1978) of the Upper Greensand from Warminster (England) (Hinde 1883). Moreover, theonellid sponges are represented in Cenomanian and upper Lower Cretaceous sponge assemblages of France and Spain by species of Verrucodesma (Lagneau-Hérenger 1962).

Some reports of Cretaceous Theonellidae from Spain (Rosales et al. 1995), France (Hérenger 1946), the Czech Republic (Pocta 1884) and Nova Scotia, the only locality outside of Europe (Eliu & Levesque 1989), require confirmation.

Palaeogeography of Cretaceous Theonellidae and Phymaraphiniidae

Modern phymaraphiniids live mainly in the tropical zone of the eastern (Carvalho et al. 2015, 2020; Carvalho & Pisera 2019) and western Atlantic (Laubenfels 1936; Pomponi et al. 2001) at depths of 168–1000 m. Most extant theonellids also inhabit deep-sea environments (110–936 m) but occur worldwide (e.g. Van Soest & Stentoff 1988; Pomponi et al. 2001; Schlacher-Hoenlinger et al. 2005; Fromont & Pisera 2011; Van Soest et al. 2014; Carvalho et al. 2015, 2020; Pisera & Pomponi 2015; Schuster et al. 2018). Some representatives of both groups are noted also in shallower water, even at depths below 60 m (Vacelet & Vasseur 1971; Pouliquen 1972; Hoshino 1981; Van Soest & Beglinger 2008; Hall et al. 2014; Rützler et al. 2014; Calcina et al. 2017; Van Soest 2017; Carvalho et al. 2020). The Cretaceous representatives of theonellids and phymaraphiniids lived in European epicontinental sea, while deep-water species were not documented. However, the palaeogeography of Cretaceous theonellids and phymaraphiniids is not well understood, which is due to the fact that palaeoenvironmental
analyses have been performed only for all lithistids or tetractinellids, excluding detailed analysis of the families Theonellidae and Phymaraphiniidae belonging to these groups of sponges (e.g. Moret 1926; Defretin-Lefranc 1960; Wagner 1963). The observation that in Upper Cretaceous successions within the system of European basins, the assemblages that are rich in lithistids and have rare or absent hexactinellid sponges occur in rocks with a significant amount of terrigenous material (e.g. sands, sandy marls, marls and gaizes: siliceous–carbonate rocks with a significant amount of detrital quartz; see Cayeux 1929; Sujkowski 1931), has led to the conclusion that the presence of abundant lithistids in the geological record signifies shallowing sealevel events (e.g. Reid 1962; Świerczewska-Gładysz & Olszewska-Nejbert 2006, Świerczewska-Gładysz & Jurkowska 2013; Żitt et al. 2006). The analysis presented here re-evaluates this view and indicates that the distribution of theonellids and phymaraphiiniids is not restricted mainly to the shallow-water facies of the European epicontinental sea, but reflects a wider palaeoecological spectrum and adaptation to various environments.

Phymaraphiiniids are noted in offshore deposits, such as chalks (Hinde 1883; Moret 1926; Fabricius 2007) and marly-carbonate facies (Schrammen 1901, 1910; Giers 1964; Wise et al. 2013), and are characterized as having a funnel-like shape with a thin wall or small club-like body. The analysis conducted here indicates that phymaraphiiniids with a similar body shape also occur in opoka facies, carbonate–siliceous rocks with a small amount of terrigenous input and marly intercalations. The opoka facies covered a significant part of the Late Cretaceous European Basin and formed under offshore conditions of slow sedimentation and low energy (Jurkowska et al. 2019b). Phymaraphiiniids recovered from open-marine facies differ in species composition and morphology of sponges compared with those known from nearshore deposits, Prokaliapsis clavata, characterized by a small, slender body shape and noted in opoka and chalk facies, is unknown from nearshore sandy marls. In the latter environment, massive species of Prokaliapsis are numerous (Ulbrich 1974), while such are absent or rare in opoka and are represented by thin-walled morphotypes. Theonellid sponges are known from both onshore and offshore facies (see above), but differences in species composition and intraspecific morphotypes are also documented between the assemblages from these two different environments. Two theonellid species (Rhadadinia rimoso and Rh. doederleini) in the collections studied are known from both facies, but the specimens from offshore facies are characterized by thicker walls and less regular body shape than those from the nearshore facies. The occurrence of theonellid sponges in shallow-water sandy marls noted by the previous authors (Griepenkerl 1889; Schrammen 1910, 1924; Moret 1926; Defretin-Lefranc 1960; Ulbrich 1974) refers mostly to representatives of the genus Phyllodermia. Bulbous or irregularly shaped thick-walled species of this genus, which are occasionally recorded from offshore facies (Wagner 1963; Schneider et al. 2013), have not been found in opoka sections of the Mięchów Synclinorium. These sponges are rare in the Belchatów assemblage and are represented only by Ph. antiqua and Ph. pulchra. However, Ph. pulchra and a few other species of Phyllodermia, as well as Eustrebilus, not recorded from pelagic opoka, do occur in lower Campanian marls and marly intercalations in the Mięchów Synclinorium (Hurcewicz 1966). The marly deposits accumulated under open-marine conditions, similar to those governing the formation of opoka (Jurkowska & Świerczewska-Gładysz 2020b). However, the presence of a significant amount of detrital clays (Jurkowska & Świerczewska-Gładysz 2020b), originating from the erosion of emerged submarine swells (Rutkowski 1965; Deconinck et al. 1989; Jurkowska et al. 2019a), indicates that this depositional environment differs from that of opoka in a higher rate of sedimentation as a result of a significant influx of detrital clays (Jurkowska 2022). This distinctive distribution of theonellid sponges is indicative of its association with facies characterized by a high rate of sedimentation (marly deposits) in offshore and onshore zones of the European epicontinental sea. Other parts of the offshore zones of opoka and chalk sedimentation, which were characterized by a lower rate of sedimentation and calm, low-energy conditions, were preferred by other theonellids (e.g. Astrocladia). The fact that both theonellids and phymaraphiiniids have not been documented in onshore sandy deposits indicates that the high-energy environment close to the islands in the European epicontinental sea were not conducive to their development. Most of the extant theonellids and phymaraphiiniids also prefer the calm water conditions of the deeper sea. In the shallow-water environment they often inhabit cavities in coral reefs or submarine caves sheltered from wave action (Vacelet & Vasseur 1971; Pouliquen 1972; Carvalho et al. 2020), but a few species can tolerate higher-energy conditions (Pomponi et al. 2001; Ruiz et al. 2013; Rützler et al. 2014, Samaai et al. 2019).

Present-day theonellids and phymaraphiiniids, as well as other lithistids, settle mainly on the hard bottom substrates (e.g. Pomponi et al. 2001; Kelly 2007; Schuster et al. 2018; Carvalho et al. 2020) and only occasionally do they occur on soft floors (Pulitzer-Finali 1993; Van Soest 2017). During the Cretaceous, when soft muddy sediment prevailed, numerous lithistid sponges colonized the sea floors (Świerczewska-Gładysz 2006, 2017). This adaptation to a soft bottom is also evident in some of the theonellids and phymaraphiiniids studied herein. Funnel- and leaf-like specimens of Phymaraphinia infundibuliformis,
Cycloclema compressa, Rhagadinia rimosa and Rh. doederleini have bases with root-like outgrowths, typical of Cretaceous sponges on soft bottom substrates. In turn, well-preserved specimens of Prokaliapsis janus and Pr. clavata have flat, expanded bases, which suggests that these sponges settled on hard clasts (i.e. molluscan shell, corals or the skeleton of other sponges). The thick outgrowths in the upper part in some specimens of Rh. rimosa and Pr. clavata indicate that these sponges needed additional stabilization during growth.

The distribution of Recent siliceous sponges is largely dependent on dissolved silica (DSi) availability in the seawater (Maldonado et al. 1999, 2005). In modern seas, DSi concentration is the lowest in Earth’s history, which is an unfavourable factor that hinders the development of sponges with hyper-silicified skeletons. Lithistid species with a dense skeleton live in areas of deep and shallow seas that are characterized by elevated DSi concentration (as a result of volcanic eruptions, upwellings and hydrothermal activity or freshwater influx) (e.g. Tréguer et al. 1995; Maldonado et al. 1999; Kelly et al. 2007; Pisera & Gerovasileiou 2021). In other sea regions, where DSi concentration is low, species with less dense skeletons or even underdeveloped desmas (e.g. some species of Theonella species) occur (Hall et al. 2014; Schuster et al. 2021). Moreover, the same lithistid species show intraspecies variability of spicules, which is believed to be due to variations in the DSi concentration in the environment in which they live (Pisera & Gerovasileiou 2021).

In the Late Cretaceous seas, DSi concentration was four orders of magnitude higher than in modern seas (Siever 1991; Racki & Corde 2000), which made this element easily available to siliceous sponges. The studied species have a choanosomal skeleton with large, massive desmas or small but very densely arranged desmas. These types of choanosomal skeleton are similar to skeletons of modern lithistids typical of regions with a high DSi concentration. The presence of additional irregular spicules that fill the space between the ectosomal phyllotriaenes in some species, which does not occur in modern taxa, is related to the DSi concentration being higher than it is today. Although spatial and temporal fluctuations in Si concentration occurred in seawater of the Late Cretaceous European epicontinental sea, which was reflected in the variable lithology (opoka and chalk, Jurkowska & Święczeńska-Gładysz 2020a), the DSi concentration was similar during the formation of opoka, marls and marly intercalations (Jurkowska et al. 2019a; AJ unpub. data). This could also be confirmed by the theonellid and phy- maraphiniids sponges studied here, given that spicules of specimens from the same species from various facies have a similar size, shape and ornamentation.

Of the siliceous sponges that grew over the muddy sea floor of the opoka facies, the non-rigid demosponges (known almost solely from spicules dispersed in deposits) were the most abundant (Jurkowska et al. 2019b). Bodily preserved sponges are represented mainly by slow-growing, deep water Hexactinellida, while theonellids and phymaraphiniids, similar to other lithistids, were less common. This probably resulted from competition for free space on the surface of the sea floor and/or food (e.g. bacterioplankton) between non-rigid and lithistid demosponges. The success of non-rigid demosponges was related to their rapid skeleton growth (Page et al. 2005; Ruiz et al. 2013). The construction of a skeleton with loose spicules in non-rigid demosponges requires less energy than the formation of a rigid, compact skeleton as in lithistids. The rivalry between these sponge types could be confirmed by the observation that in the lower Campanian opoka of the Miechów Synclinorium, in which theonellids and phymaraphiniids are the most abundant, the number of non-rigid demosponges was relatively low in comparison with other parts of the Upper Cretaceous opoka successions in southern Poland (Jurkowska & Święczeńska-Gładysz 2020a). The richest and most taxonomically diverse assemblages of Campanian siliceous sponges, containing theonellids and phymaraphiniids, are known from Lower Saxony in marly-calcareous facies, where non-rigid demosponges are rare (Schrammen 1901, 1910) and the lithistids had no competition.

**CONCLUSION**

Campanian sponge assemblages from Mogilno-Lódź comprise four species of phymaraphiniids (Phymaraphinia infundibuliformis, Prokaliapsis clavata, Pr. janus and Cycloclema compressa) and eight theonellids (Rhagadinia rimosa, Rh. doederleini, Astrocladia laevis, A. subramosa, Rhoptrum scytaliforme, Colossolacis plicata, Phylldermia antiqua and Pseudojerea sp.). Of these, Phymaraphinia infundibuliformis, Prokaliapsis janus (Phymaraphiniidae) and Rhagadinia doederleini, R. scytaliforme, A. laevis, C. plicata and Phylldermia antiqua (Theonellidae) had not been recorded previously from the Campanian of Poland. It should be noted that Campanian phymaraphiniids and theonellids are known only from Poland and Germany. In fact, all phymaraphiniid species and eight theonellids from the Miechów and/or Mogilno-Lódź synclinoria have also been recorded from Campanian strata in Subhercynian and/or Lower Saxonian basins.

With regard to the palaeoenvironmental distribution of Cretaceous phymaraphiniids and theonellids, they were not restricted to the shallow zone of the European epicontinental sea; numerous representatives also settled in offshore zones. All studied phymaraphiniids and theonellids of Campanian age inhabited the calm, offshore water...
of the European epicontinental sea, with the majority (species occurring in opoka) preferring a slow rate of sedimentation. Only a few theonellid species (from marls and marly intercalation) were adapted to a higher rate of sedimentation, as generated by a significant influx of detrital clays.

Late Cretaceous phymaraphiniid and theonellid assemblages from open-marine facies with low rates of sedimentation differ in species composition and sponge morphology from those recorded from levels characterized by high rates of sedimentation. Similar to other lithistids, phymaraphiniids and theonellids are rare in the Campanian opoka. This is probably due to competition with non-rigid demosponges, which occurred in large numbers in regions of the European epicontinental sea, where opoka was deposited.

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