

TAXONOMY AND PALAEOECOLOGY OF THE LATE CRETACEOUS (CAMPANIAN) PHYMATELLIDAE (LITHISTID DEMOSPONGES) FROM THE MIECHÓW AND MOGILNO-ŁÓDŹ SYNCLINORIA (SOUTHERN AND CENTRAL POLAND)

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Abstract: Phymatellid demosponges are common fossils in the Campanian deposits of central Europe. In Poland, the Campanian phymatellids were known mostly from the opoka facies of the Miechów Synclinorium (southern Poland), where they occur mainly in the characteristic horizons of siliceous nodules in the lower Campanian opoka succession. Similarly preserved early Campanian phymatellids were identified in a redeposited lithistid assemblage in the Neogene gravels, exposed in the Bełchatów Lignite Mine (Mogilno-Łódź Synclinorium, central Poland). Rare phymatellids were noted for the first time in the upper Campanian gaize of the Miechów Synclinorium. The taxonomic descriptions of 16 phymatellid species presented here, including one new species, *Kalpinella fragilis*, completes existing knowledge of the taxonomic diversity of these sponges in the Late Cretaceous basins of central Europe. The present study also supplements the data on the stratigraphic ranges and spatial distribution of these species. The palaeoecology of Cretaceous phymatellids is discussed on the basis of their occurrence in the various facies.

Key words: Fossil sponges, lithistid demosponges, facies, Cretaceous, palaeoenvironment.

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INTRODUCTION

The Cretaceous siliceous demosponges described here belong to the family Phymatellidae Schrammen, 1910 of the order Tetractinellida Marshall, 1876 (see Schuster *et al.*, 2015). This family of lithistid demosponges, characterised by the presence of a rigid choanosomal skeleton, composed of tetractones (tetraxial desmas) and smooth ectosomal dichotriaenes, traditionally has been placed in the suborder Tetracladina Zittel, 1878 (Pisera, 2002; Reid, 2004). According to Reid (2004), the tetractones of the Phymatellidae are smooth and some genera (e.g., *Acrochordonia* Schrammen, 1901) with tuberculated tetractones and ectosomal dichotriaenes, were assigned by this author to the Theonellidae Lendenfeld, 1903, although the latter family is characterised by ectosomal discotriaenes or phyllotriaenes (Pisera and Lévi, 2002a). The view of Reid (2004) is in contradiction to the opinion accepted here of Pisera and Lévi (2002b) on various types of ornamentation

of the desmas of the phymatellids, which comprised mostly tetractones with smooth clones and rarely poorly ornamented to heavily tuberculated desmas. In Cretaceous species, the microscleres, which are important for the classification of living taxa, have not been documented (Reid, 2004).

Extant phymatellids are represented by only three genera (*Neoaulaxinia* Pisera and Lévi, 2002b, *Neosiphonia* Sollas, 1888 and *Reidispongia* Lévi and Lévi, 1988), comprising a total of ten species (de Voogd *et al.*, 2021). With the exception of one phymatellid species, living in dark, anchialine caves in Mexico (Gómez and Calderón-Gutiérrez, 2020), all others are found at deep-water environments. They are known mainly from the western Pacific (the archipelagos of the Philippines, New Zealand and New Caledonia, and also from seamounts along the Norfolk Ridge), where they are noted as occurring at depths of 236–1680 m (Sollas, 1888; Wilson, 1925; Lévi and Lévi, 1988; Schlacher-Hoenlinger *et*

al., 2005; Kelly, 2007). Moreover, one species (*Neosiphonia schmidtii*) was found in the Gulf of Mexico at depths of 145–1470 m (Sollas, 1888).

During the Late Cretaceous, phymatellids were much more abundant and taxonomically diverse than today and were represented by ca. 20 genera (Pisera, 2002). The Late Cretaceous phymatellid taxa are known almost exclusively from deposits of the epicontinental European Basin. However, their palaeoecological requirements, palaeogeographical distribution and stratigraphic range are not fully recognized. The presence of the Phymatellidae in Cretaceous faunas outside of Europe is poorly known. A few species were noted in the Cariblanco Formation of Puerto Rico (Howell, 1966) and Trinidad (Thomas, 1935), but skeletons of these specimens, considered to be phymatellids, are not well documented. In turn, the sponges described as *Siphonia* by Chapman (1914) from Australia have been shown to be pyrite concretions of inorganic origin (Pickett, 1983).

The studied specimens originated in the Miocene gravels at the Bełchatów Lignite Mine (Fig. 1A, C, D; Tab. 1), rich in Campanian (Late Cretaceous) silicified lithistid demosponges. To date, sponges from that locality, representing five other lithistid families (Pleromidae, Isoraphiniidae, Corallistidae, Theonellidae and Phymarinidae), have been studied in detail (Świerczewska-Gładysz, 2016, 2017; Świerczewska-Gładysz and Jurkowska, 2022). Additionally, a collection of sponges from the Campanian of the Miechów Trough (southern Poland) has been analysed (Fig. 1A, B; Tab. 1). Most of this material are museum specimens from

the Lelów, Miechów and Kraków areas, which were collected and previously described by Hurcewicz (1966) and Bieda (1933). The material of the present authors from the Lelów and Jędrzejów areas was additionally examined.

This paper presents the results of taxonomical studies of the Campanian phymatellids, occurring among the re-deposited sponges in the Bełchatów Lignite Mine and the Miechów Trough, supplemented by the taxonomic revision of the representatives of this family, housed in the museum collection of H. Hurcewicz and F. Bieda. The analysis of new and museum material by the present authors enriches existing knowledge about the skeleton of phymatellid sponges and their intraspecific variability. The analysis of the literature, supplemented by the observations of the present authors, complements the data about the spatial and stratigraphical distribution and the palaeoecology of the Cretaceous phymatellid taxa.

GEOLOGICAL SETTINGS

The Campanian–Maastrichtian succession of the Miechów Synclinorium is well known in terms of lithology and stratigraphy (Kowalski, 1948; Rutkowski, 1965; Jurkowska, 2016, 2022). The lower Campanian deposits start with a complex of marls of variable thickness (0–20 m), which passes upwards into the opoka facies (a carbonate-siliceous rock with a significant amount of opal-CT and insignificant amounts of detrital mineralogical components; Jurkowska, 2022) with marly intercalations and horizons of

Table 1

Sections studied, showing data on stratigraphy, lithology and pertinent items of literature.

Geologic area	Geographic region	Location	Stratigraphy	Lithology from which the studied material originate	Authors
Mogilno-Lódź Syn.	Bełchatów area	Bełchatów Lignite Mine	lower Campanian	cherts with flint cores	Požaryski, 1960; Świerczewska-Gładysz, 2016, 2017
Miechów Synclinorium	Lelów area	Pniaki abandoned quarry	lower Campanian	opoka and chert nodules with flint cores	Hurcewicz, 1966; Jurkowska <i>et al.</i> , 2015; Jurkowska and Świerczewska-Gładysz, 2020
		Zbyczyce abandoned quarry	lower Campanian	chert nodules with flint cores	Hurcewicz 1966; Jurkowska <i>et al.</i> , 2015
		Skrajniwa natural outcrop	lower Campanian	siliceous nodules (probably cherts with flint cores)	Różycki, 1938; Hurcewicz, 1966; Pożaryski, 1966
	Miechów area	Miechów (named as Strzeżów 1) abandoned quarry	upper Campanian	gaize	Hurcewicz, 1966; Jurkowska, 2016, 2022
	Proszowice area	Gnatowice	upper Campanian	opoka	Hurcewicz, 1966; Jurkowska, 2014
	Jędrzejów	Jędrzejów	upper Campanian	gaize	Świerczewska-Gładysz and Jurkowska, 2013; Jurkowska, 2016

chert nodules with flint cores (for a detailed description of the mineralogy see: Jurkowska and Świerczewska-Gładysz, 2020b) in the lower part of lower Campanian (*quadrata-papilosa* zones; Barczyk, 1956; Rutkowski 1965; Pożaryski, 1966; Jurkowska, 2016; Fig. 2A). In the middle Campanian, the horizons of chert nodules decrease in number and the upper Campanian opoka facies passes into gaize (a carbonate-siliceous rock with an opal-CT rock framework and a significant amount of detrital quartz; Cayenux, 1929; Jurkowska, 2022), which continues into the Maastrichtian (Fig. 2A).

The Campanian opoka facies in the studied sections (Tab. 1) is microscopically represented by wackestone/packstone with spicules (mainly of non-rigid demosponges, visible as voids left after their dissolution) and foraminifers (Fig. 2B). In the Campanian succession, abundant fossils of bivalves, cephalopods, echinoids and hexactinellid sponges occur. Lithistid sponges appear mainly in the horizons of cherts with flint cores, while in the opoka facies and chert horizons they are rare.

The upper Campanian gaize, which microscopically is a packstone with small detrital quartz grains (< 100 µm in size) and numerous spicules of non-rigid demosponges (Fig. 2C), is also very fossiliferous. The proportions of lithistids and hexactinellids in the assemblage from the lower part of the upper Campanian gaize are similar to those in the lower Campanian opoka. In the upper part of the upper Campanian gaize, changes in the composition of the sponges are noticeable: hexactinellids become rare, while the number of lithistid sponges (representing mainly the family *Rhizomorina* Zittel, 1878) increases (Świerczewska-Gładysz and Jurkowska, 2013; and unpublished data).

At the Campanian–Maastrichtian boundary, a thick horizon with glauconite and lithified carbonate clasts with glauconitic coatings or a complex of marls with abundant oysters have been documented (Rutkowski, 1965; Jurkowska, 2016). The lower Maastrichtian succession is composed of gaize, which differs from the Campanian gaize below, in the occurrence of larger quartz grains (100–200 µm in size) and uncommon fossils, which mostly comprise deeply burrowing bivalves of *Lucinia* sp. and ichnofossils (Jurkowska, 2016). The Maastrichtian gaize is a bioclastic wackestone/packstone with spicules and quartz grains (Fig. 2D). In this gaize, no sponges with rigid skeletons had been found, while the voids left by the loose spicules of non-rigid demosponges are abundant.

The lithology and distribution of the Campanian facies in the Mogilno-Łódź Synclinorium is poorly recognized and known mostly from borehole cores. In general, the Campanian deposits are represented by monotonous carbonate marine sedimentation of opoka facies, with marly intercalations and horizons of chert nodules, including characteristic horizons of cherts with black flint cores, occurring in the lower part of lower Campanian (Pożaryski, 1960). At the Belchatów Lignite Mine, the Upper Cretaceous deposits crop out in the southern slope of excavation (Zapałowicz-Bilan, 1999), but its lithology and stratigraphy are poorly known. The siliceous sponges have been found as redeposited components in gravels (Świerczewska-Gładysz, 2016; 2017; Świerczewska-Gładysz and Jurkowska, 2022), occurring in

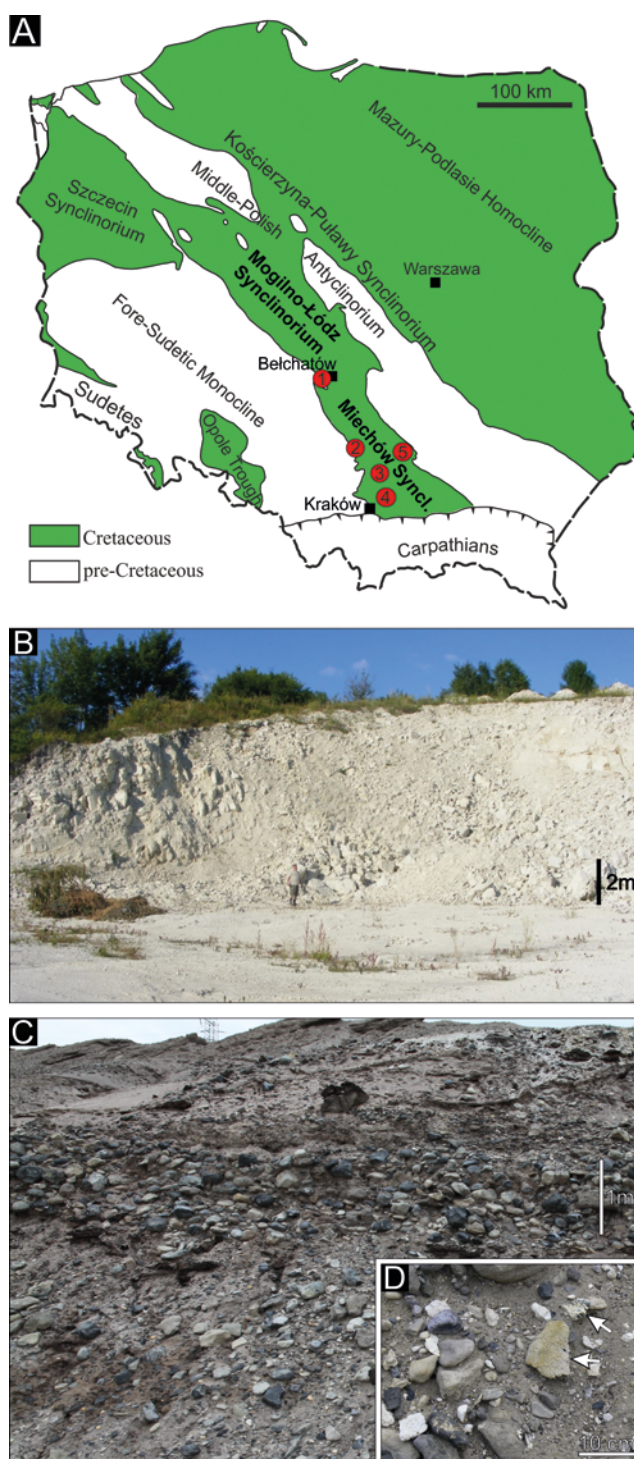


Fig. 1. Localities of studied Campanian sponges in Poland. **A.** Tectonic sketch map of Poland (without the Cenozoic cover; after Pożaryski, 1974 and Żelaźniewicz *et al.*, 2011; simplified) with localities studied: 1 – Belchatów area (Belchatów Lignite Mine); 2 – Lelów area (Pniaki, Zbyczyce, Skrajniwa); 3 – Miechów area (Strzeżów 1); 4 – Proszowice area (Gnatowice); 5 – Jędrzejów area. **B.** Upper Campanian gaize of Strzeżów 1 section. **C, D.** Miocene section of the Belchatów Lignite Mine (sixth exploitation level); **C** – Miocene clayey-sandy deposits with the layers of alluvial gravel; **D** – the gravel contains redeposited siliceous nodules and silicified early Campanian phymatellid sponges (arrow).

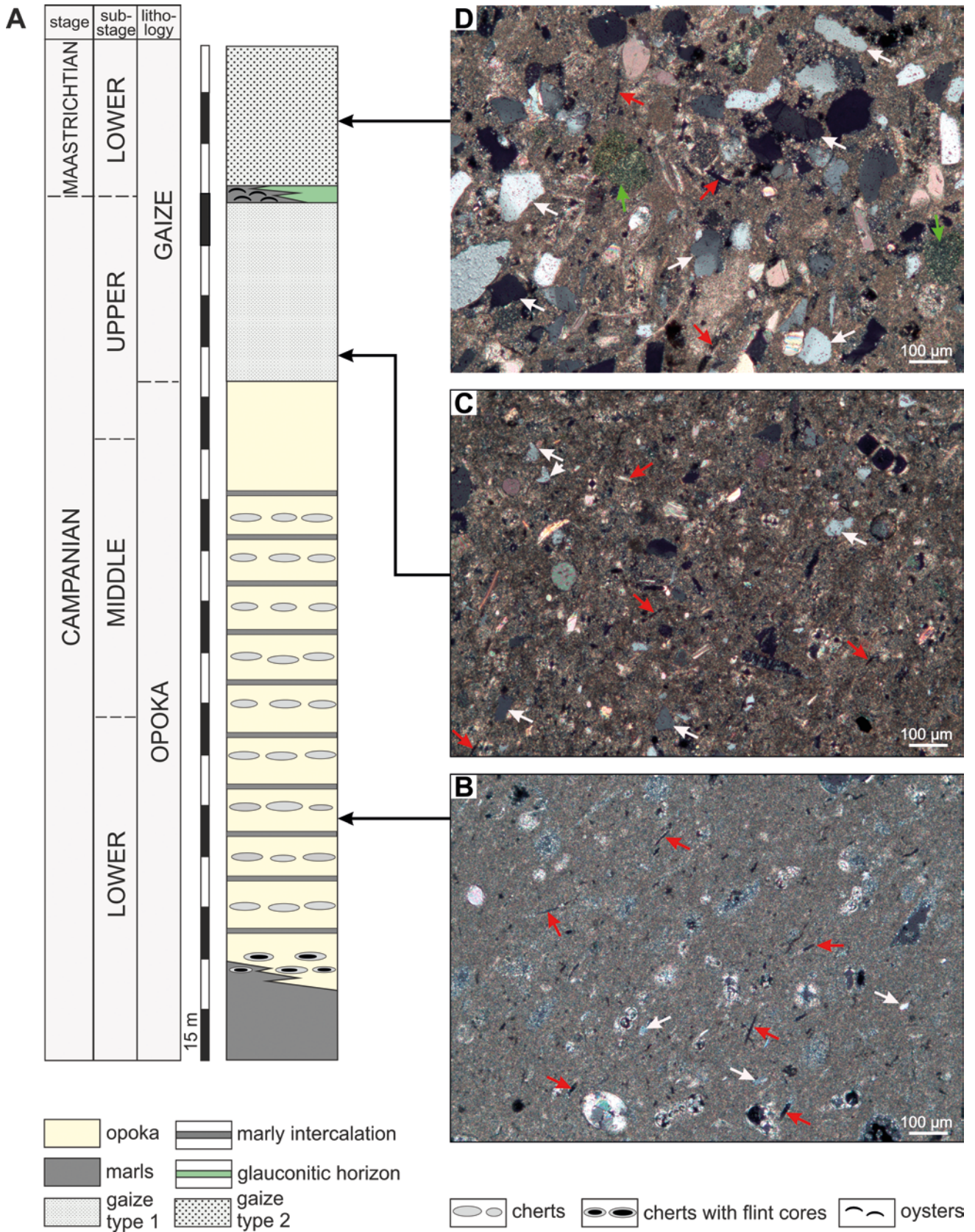


Fig. 2 The Campanian–Maastrichtian succession of Miechów Synclinorium. **A.** The simplified lithological column of thick Campanian–Maastrichtian succession of Miechów Synclinorium (after Jurkowska, 2016; changed). **B.** Wackestone with spicules (red arrows) and foraminifers with rare quartz grains (white arrows) of the Campanian opoka. **C.** The upper Campanian gaize as packstone with detrital quartz grains of sizes below $< 100 \mu\text{m}$ (white arrows). **D.** Wackestone with large detrital quartz grains ($100\text{--}200 \mu\text{m}$; white arrows) and glauconite grains (green arrow) of the lower Maastrichtian gaize.

the lower part of Neogene fluvial sand (Upper Gravels in the lithostratigraphic subdivision after Krzyszkowski and Szuchnik, 1995). The foraminiferal analysis of material infilling the skeletons of sponges determines their age as early Campanian, foraminiferal *Gavelinella clementiana* Zone (Świerczewska-Gładysz, 2016).

Except for various siliceous sponges, these gravels also contain other Late Cretaceous silicified fossils: echinoids, mainly *Micraster* sp., *Offaster pilula* (Lamarck), bivalves and calcareous sponge *Porosphaera globularis* (Phillips, 1829). The borings and silicified epibionts (mainly bryozoans and serpulids), common in some other Campanian lithistids taxa from the Miechów and Mogilno-Łódź synclinoria (Świerczewska-Gładysz, 2016, 2017; Świerczewska-Gładysz and Jurkowska, 2022), are rarely observed in the phymatellid specimens studied here.

MATERIAL AND METHODS

The material described here comprises 266 specimens of phymatellid demosponges. The collection from the Bełchatów Lignite Mine, consisting of 209 specimens, is housed in the Geological Museum of the Faculty of Geographical Sciences, University of Łódź, Poland (collection UL no. XXV). The material from southern Poland, collected by H. Hurcewicz and by the authors, includes of 11 specimens from Pniaki, 11 specimens from Zbyszycze, 24 specimens from Skrajniwa, 5 specimens from Gnatowice, 3 specimens from Strzeżów 1 and 3 from Jędrzejów, and also is housed in this institution (collections UL no. II, IIa and IIb).

The samples of secondarily silicified skeletons were washed in an ultrasonic cleaner to remove clay minerals and quartz grains. The skeleton specimens from the opoka and gaize were etched in 10% hydrochloric acid. Skeletons of all sponges were examined under SEM in the AGH Laboratory of Phase, Structural, Textural and Geochemical Research Microscope Laboratory of the University of Warsaw and in the Institute of Paleobiology of the Polish Academy of Sciences in Warsaw.

Samples of rock were examined in the Clay Minerals Research Group of the Polish Academy of Science in Krakow (XRD quantitative and qualitative mineralogical composition analysis) and at the AGH Faculty Laboratories (XRD qualitative mineralogical composition analysis).

The classification and terminology of sponges were adopted from Boury-Esnault and Rützler (1997), Hooper *et al.* (2002), Finks *et al.* (2003) and Schuster *et al.* (2015). Following Ogg and Hinnov (2012), the tripartite subdivision of the Campanian Stage is applied here (see also Jurkowska, 2016).

STATE OF PRESERVATION AND MINERALOGY OF THE STUDIED FOSSIL SPONGES IN THE DIFFERENT FACIES

The studied fossils of sponges originated from variable lithologies, comprising chert nodules with flint cores, opoka facies and gaize (Tab. 1). Specimens occurring in cherts have been omitted from this study, owing to their

unsuitability for taxonomic research. Below, detailed studies of the state of sponge preservation as well as the mineralogy of the silica minerals infilling the sponge skeletons are presented.

Sponges within cherts nodules with flint cores

The detailed SEM examination of the fragments of the rocks, which are adjacent to the sponge fossils from Bełchatów Lignite Mine, reveals the characteristic microtexture of opal-CT (dense, compact siliceous masses composed of fused blades of opal-CT), which is similar to that observed in cherts nodules with flint cores from the lower Campanian horizons of the Miechów Synclinorium (Jurkowska and Świerczewska-Gładysz, 2020b, fig. 8). This indicates that the studied sponges from the Mogilno-Łódź and Miechów synclinoria originated from the characteristic horizons of cherts with flint cores, which are documented in both areas in the lower part of the lower Campanian (Barczyk, 1956; Pożaryski, 1960, 1966; Rutkowski 1965; Jurkowska, 2016). The flint cores, which are silicified sponges (mainly lithistids), were described in detail by Jurkowska and Świerczewska-Gładysz (2020b). Most of phymatellid specimens presented in the systematic part, especially those from the Bełchatów gravels, are the flint cores, which were separated from the chert nodules surrounding them by mechanical weathering.

In the inner part of the sponge walls (flints) are composed of flints, nano- α -quartz + moganite which form a homogeneous siliceous mass, while desmas are often completely dissolved and rarely preserved as smooth silica (opal-A/CT; Fig. 3A). In the outer part of the wall, choanosomal desmas usually occur more frequently. A smooth silica, which is a different type of silica polymorph (opal-A/CT), builds these spicules, which are cemented by porous silica (see also figs 6, 7 in Jurkowska and Świerczewska-Gładysz, 2020a). The large spaces (spongocoels and wide canals) within the sponge are usually completely infilled by cherts composed of large (20–30 μm) lepispheres of opal-CT. The brown to black colour of the flint cores is caused by the organic matter, which is visible under SEM as an irregular lumps (Fig. 3B).

Moreover, in some of the specimens from the Bełchatów Lignite Mine, which originated from the horizons of cherts with flint cores, the signs of more advanced secondary diagenetic transformations of smooth silica into opal-CT/opal-C (Fig. 3C, D) were documented. The opal-CT/opal-C blades, which cover the sponge skeletons, reorganize to form a triangular structure, which resembles authigenic quartz crystals. This kind of transformation of opal-CT into more stable forms has not been observed in specimens from the Miechów Synclinorium nor in chert nodules and is probably triggered by the long-time weathering of those sponges.

Sponges within opoka and gaize deposits

Specimens from the gaize and opoka, on the basis of macroscopic observation are orange to red in colour and are usually described as limonitized. They are often brittle and disintegrate during extraction of them from the rock.

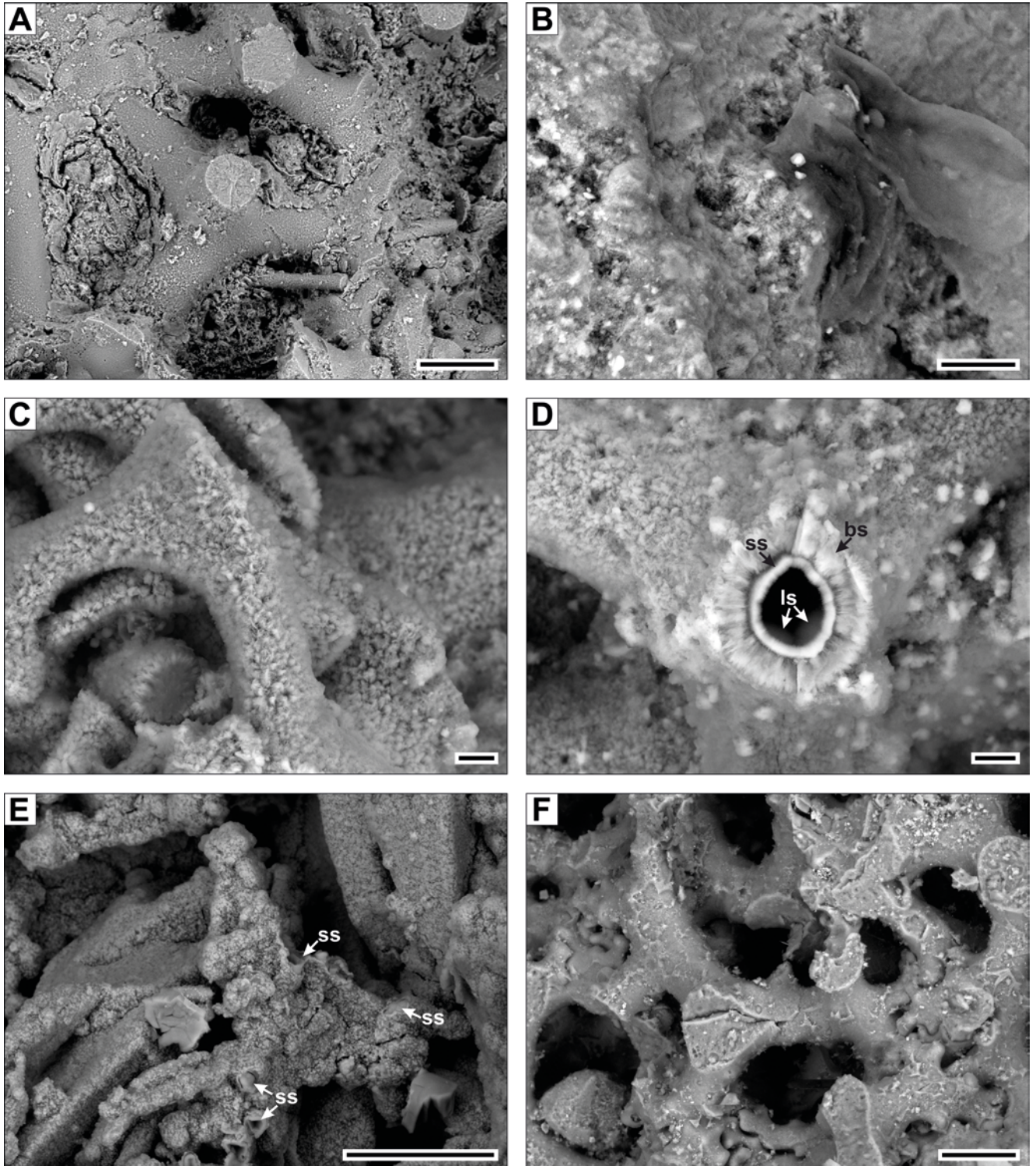


Fig. 3. The state of siliceous sponge preservation. **A.** The inner part of sponge wall with spicules of nano- α -quartz + moganite; specimen from the horizon of cherts with flint core, Pniaki-1.12ch. **B.** The lump of organic matter (on right) within the inner part of sponge wall; specimen from the horizon of cherts with flint core, Pniaki-1.12ch. **C.** The covering of sponge desmas of opal-CT blades which transformed into more stable opal-C, with visible triangular structures; specimen preserved as flint, Bełchatów-sp003. **D.** The partly dissolved desma; in cross section visible: dissolved axial part of desma, layer of large opal-CT lepispheres (ls), layer smooth silica (ss) covered by the opal-CT blades which undergoes transformation (bs); specimen preserved as flint, Bełchatów-sp003. **E.** The fragment of siliceous desmas of smooth silica (ss) densely covered by the mixture of hydrated iron oxides and hydroxides; specimen from gaize, Jędrzejów-sp002. **F.** The siliceous skeleton of smooth silica covered by a mixture of authigenic clays and hydrated iron oxides and hydroxides; specimen from opoka, Gnatowice-sp007. Scale bars represent 100 μ m (A), 50 μ m (E, F) and 10 μ m (B–D).

Their siliceous skeleton are usually dissolved and voids after spicules are poorly visible, which makes taxonomic identification impossible.

Detailed SEM examination of the rarely preserved siliceous skeletons indicated that they are composed of smooth silica (opal-A/CT) covered by minerals, which are a mixture of hydrated ion oxides and hydroxides (Fig. 3E). Only the siliceous skeletons of specimens from Gnatowice are covered by a mixture of authigenic clays and minerals of hydrated iron oxides and hydroxides (Fig. 3F).

SYSTEMATIC PALAEOONTOLOGY

Class Demospongiae Sollas, 1885
Order Tetractinellida Marshall, 1876
“Lithistids” *sensu* Schmidt, 1870
Family Phymatellidae Schrammen, 1910
Genus *Turonia* Michelin, 1847

Type species: *Turonia variabilis* Michelin, 1847, p. 125, pl. 35, figs 1–8, by monotypy.

Turonia variabilis Michelin, 1847
Figs 4A–C, 5A, B

- 1847 *Turonia variabilis* – Michelin, p. 125, pl. 35, figs 1–8.
1966 *Turonia variabilis* Michelin – Hurcewicz, p. 42, pl. 8, fig. 1a, b.
1966 *Turonia variabilis* aff. *variabilis* Michelin – Hurcewicz, p. 43, pl. 8, fig. 2. text-fig. 10.
2006 *Turonia variabilis* Michelin – Świerczewska-Gładysz, p. 274, figs 37a, b, 38a, b [cum syn.].

Material: 5 specimens from Bełchatów (ULXXV/5T/1–5), 2 from Pniaki (ULII/381, 1681), 3 from Strzeżów 1 (ULII/128,129, ULIIb/30), 2 from Jędrzejów (ULIIa/25, 26).

Description: Fusiform sponges, without central spongo-coel, up 67 mm high and 65 mm wide (Fig. 4A, B). Upper surface convex, covered by irregular furrows or flattened with prominent conical apex located centrally. Lower part of sponges usually wide, conical, rarely semi-circular, often with concentric small wrinkles. A few protrusions and/or broken root-like outgrowths, 4–6 mm in diameter, often occurring on the lower part, mainly near the base. Inhalant canal openings (recognizable only on the upper surface of the less silicified specimen from Pniaki), round, 0.6–0.8 mm in diameter. Inhalant canals straight and short. A few exhalant canal openings on top of sponges, rounded, 3–4 mm wide. Exhalant canal running parallel in apical part; deeper becoming oblique and irregularly branched.

Choanosomal skeleton, comprising regular tetracloes with smooth, unbranched clones, 320–450 µm long and 60–70 µm thick (Fig. 5A). Poorly tuberculated zygomes, forming rounded or elongated zygos, 250 µm x 250–450 µm in size. Near the inhalant canals, less regular skeletal network containing tetracloes with clones of various length and occasionally branched. Tetracloes on wall of exhalant canals having poorly developed zygomes and one

or two long clones (up to 600 µm) arranged parallel to canal axis. Compact layer of ectosomal skeleton, ca. 1–1.5 mm thick, covering lower part of sponge and root-like outgrowths. Narrow band of ectosomal layer occasionally occurring near edge of the upper side of specimens, often hiding beneath choanosomal network of expanded apex (Fig. 5B). Ectosomal skeleton consisting of dichotriaenes with thin, pointed clads, 200–600 µm long. Deuteroclads, about twice longer than protoclads, dividing at 70–80°. Flattened, irregular spicules (rhizoclonids, *sensu* Reid, 2004), up to 400 µm in size, occurring under and between overlapping dichotriaenes.

Remarks: *Turonia variabilis* is a common Late Cretaceous species, known from various regions of Europe. In Poland, it is very numerous in the upper Maastrichtian of the Middle Vistula River section (Świerczewska-Gładysz, 2006), while in the Campanian sponge assemblages of Miechów, Lelów and Bełchatów areas it is rare and represented only by small specimens.

Turonia variabilis displays very high intraspecific variability (e.g., Michelin, 1847; Hinde, 1883; Schrammen, 1910; Moret, 1926; Gruber, 1993; Świerczewska-Gładysz, 2006). The shape of the studied specimens is most similar to that of the sponges presented by Michelin (1847, pl. 35, fig. 1a, b), Hinde (1883, pl. 18, fig. 1) and Moret (1926, pl. 12, fig. 10). Small specimens with a poorly developed conical apex resemble to some extent the representatives of *Callopegma acuale* Zittel 1878 (Schrammen, 1910, pl. 4, fig 4; Świerczewska-Gładysz, 2006, fig. 73d, e). In contrast to the latter species, their ectosomal skeleton on the lower surface of the sponges is very thick and except for dichotriaenes contains also flattened irregular spicules.

Distribution: Poland (Bełchatów area: early Campanian sponges as redeposited elements in Neogene deposits, Lelów area: lower Campanian, Miechów area: upper Campanian, Jędrzejów area: upper Campanian, middle Vistula River valley: upper Campanian to upper Maastrichtian); France (Saumur area: Turonian, Paris Basin: Coniacian); Germany (Lower Saxony: lower and upper Campanian); England (Flamborough: Upper Chalk, Campanian; unknown localities from southern England: Upper Chalk, probably Santonian–Maastrichtian).

Genus *Aulaxinia* Zittel, 1878

Type species: *Siphonocoelia sulcifera* Roemer, 1864, p. 30, pl. 11, fig. 7, by monotypy.

Aulaxinia sulcifera (Roemer, 1864)
Figs 4D–F, 5C, D

- 1864 *Siphonocoelia sulcifera* – Roemer, p. 30, pl. 11, fig. 7.
partim 1966 *Aulaxinia sulcifera* (Roemer) – Hurcewicz, p. 35, pl. 3, fig. 3 [non fig. 2].
2006 *Aulaxinia sulcifera* (Roemer) – Świerczewska-Gładysz, pp. 272–274, fig. 38c–e [cum syn.].
2012 *Aulaxinia sulcifera* (Roemer) – Świerczewska-Gładysz, text-fig. 6a.



Fig. 4. Specimens of phymatellid species. **A–C.** *Turonia variabilis* Michelin, 1847; **A** – lateral view of specimen with well-preserved lower part covered by thick layer of ectosomal skeleton (**e**) and small irregularly distributed protrusions (**p**); ULII/1681, Pniaki; **B** – lateral view of specimen with lower part covered by ectosomal skeleton (**e**) and small protrusions (**p**) near base; exhalant canals (**c**) visible on the partly destroyed top; ULXXV/5T/1, Belchatów; **C** – upper view of the same specimen with ectosomal skeleton (**e**) near the margin and exhalant canal openings located centrally on the top. **D–F.** *Aulaxinia sulcifera* (Roemer, 1864); **D** – lateral view of cylindrical specimen; ULXXV/17T/3, Belchatów; **E** – lateral view of small specimen with fragment of other individual and fragmentarily preserved ectosomal skeleton (**e**); ULXXV/17T/2, Belchatów; **F** – lateral view of fusiform specimen; ULXXV/17T/4, Belchatów. **G–I.** *Phymoracia verrucosa* (Roemer, 1864); **G** – lateral view of cosh-like specimen with exhalant canals openings located on the top of poorly developed papillae; ULXXV/1T/3, Belchatów; **H** – lateral view of fragmentarily preserved specimens; visible side without exhalant canal openings; ULXXV/1T/4, Belchatów; **I** – lateral view of the same specimen; visible side with exhalant canal openings located on the top of well-developed papillae. **J–L.** *Craterella auricula* Schrammen, 1910; **J** – outer side of fragmentarily preserved specimen; ULXXV/18T/1, Belchatów; **K** – inner side of the same specimen; **L** – lateral view of specimen with broken root-like outgrowths (**r**); ULXXV/18T/2, Belchatów. Scale bars represent 1 cm.

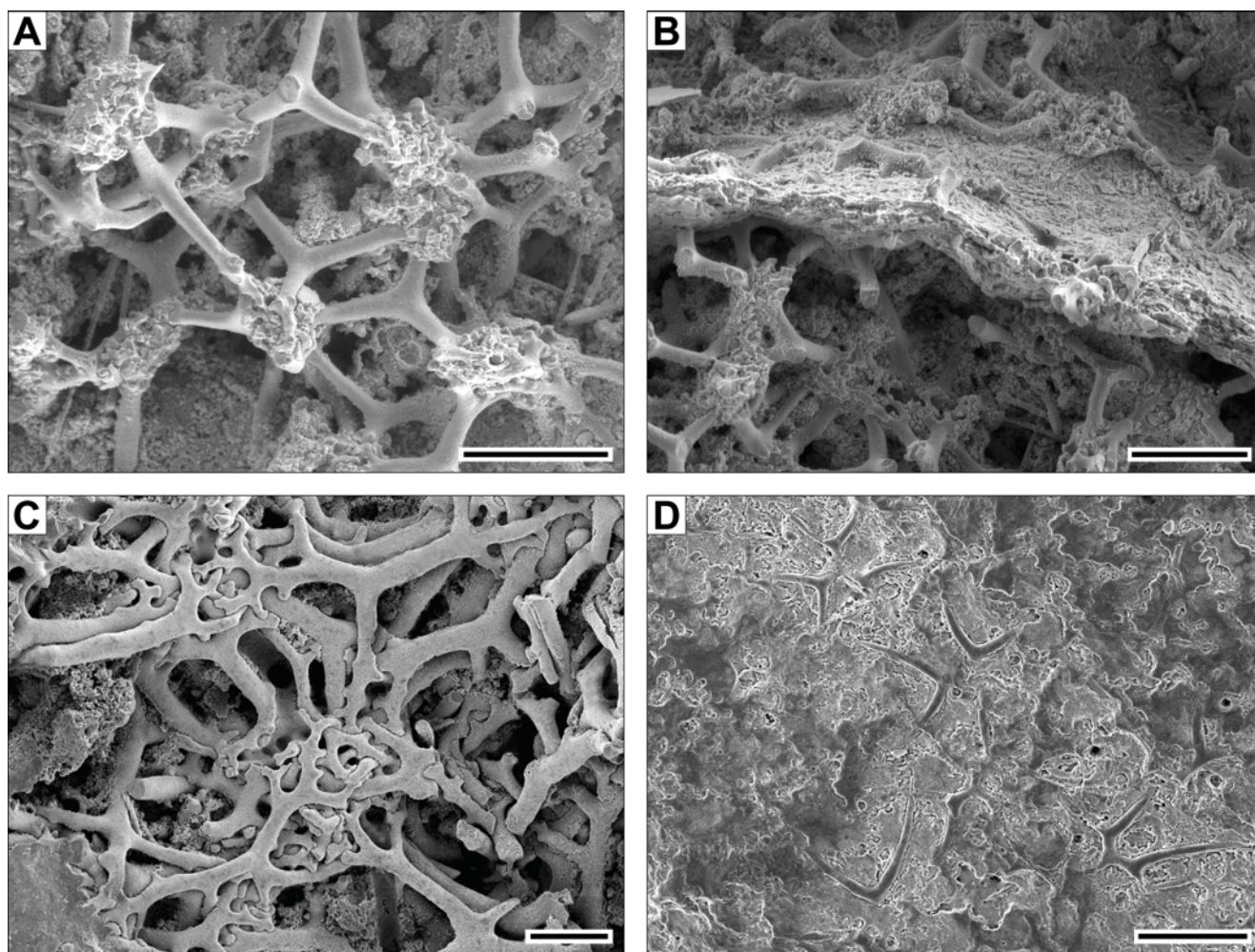


Fig. 5. Skeletons of phymatellid species. **A, B.** *Turonia variabilis* Michelin, 1847; ULXXV/5T/2, Belchatów; A – choanosomal skeleton; B – choanosomal skeleton (below) and thick layer of ectosomal skeleton (centre) covered by desmas of expanding apex (above). **C, D.** *Aulaxinia sulcifera* (Roemer, 1864); C – desmas on the wall of exhalant canal; ULXXV/17T/1, Belchatów; D – ectosomal skeleton with dichotriaenes and irregular, flattened spicules; ULXXV/17T/2, Belchatów. Scale bars represent 500 μm (A, B) and 200 μm (C, D).

Material: 7 specimens from Belchatów (ULXXV/17T/1–7), 2 from Gnatowice (ULII/20, 713).

Description: The studied material consists of cylindrical or fusiform sponges with rounded or flat apex (Fig. 4D–F), and very thin (0.7 mm in diameter), loose stalks. The largest specimen has a broken lower part, is 63 mm in height and 36 mm in diameter. One small specimen without stalk has an irregular basal part with a fragment of another individual (Fig. 4E). Lateral surface of sponges covered with longitudinal slightly undulating furrows, 1.5–2 mm wide. Furrows very regularly distributed, separated by flat ridge, up to 3–4.5 mm wide. Furrows and ridges continue on the stalk, where ridges become narrower, ca. 2 mm wide. Round inhalant canal openings located on ridges and also on furrow bottoms. Canal openings on ridges, 0.6–1 mm in diameter, arranged fairly regularly in longitudinal rows, spaced at 0.3–0.8 mm. Inhalant canal openings in furrows slightly smaller and denser, less regularly distributed. On stalk inhalant canal openings round or oval, 0.3–0.5 mm in diameter. Inhalant canals short and radial. Spongocoel usually deep, rarely reduced to shallow depression on top. Elliptical canal openings in large specimens on surface of spongocoel

up to 9 mm in diameter. Arched to nearly straight exhalant canals, 1–2 mm wide, running along sponge, a few occurring also in axial upper part of the stalk.

Choanosomal desmas are smooth regular tetraclones. Clones, usually 300 μm long and 50–60 μm thick, undivided or dichotomously branched just before their termination. Zygomes of several desmas forming spherical zygoes, ca. 300 μm in diameter. Large tetraclones, with more branched clones, up to 500 μm long, occurring in network around furrows (Fig. 5C). Choanosomal skeleton of stalk very dense; tetraclones with two long clones (up to 400–800 μm long) arranged in parallel to the axis of stalk occurring on a surface of ridges; their third, short clone directed across the furrow. In lowermost part of stalks, choanosomal network covers furrows, which in these places have the form of canals running just below the surface. Small, flattened spicules with jagged edges forming dense layer with occasionally preserved ectosomal dichotriaenes (observed only on one small specimen) (Fig. 4E). Dichotriaenes with thin clads and cladome up to 500 μm (Fig. 5D). Deuteroclads, three or four times longer than protoclads, slightly arched and arranged at ca. 85–100°.

Remarks: *Aulaxinia sulcifera* is one of the most common Cretaceous phymatellid species occurring in various calcareous facies (Roemer, 1864; Hinde, 1883 – as *Aulaxinia costata* sp. nov.; Griepenkerl, 1889; Schrammen, 1910; Nestler, 1961; Lagneau-Héranger, 1962; Ulbrich, 1974; Gruber, 1993; Heinberg, 2000 – as *Aulaxinia costata*; Świerczewska-Gładysz, 2006, 2012), particularly abundant in the Campanian. The choanosomal skeleton of this species was very well documented by earlier authors, although ectosomal megascleres have not been illustrated and described in detail before.

According to some researchers, *A. sulcifera* sponges have a poorly developed spongocoel in the juvenile stage (Schrammen, 1910; Nestler, 1961; Ulbrich, 1974). This is not confirmed in the material from the Middle Vistula River section, because very large specimens, up to 200 mm long, often also have a very low spongocoel (Świerczewska-Gładysz, 2006, 2012, text-fig. 6a). A few small specimens from Bełchatów, not exceeding 30 mm in size, have a very deep spongocoel.

The cylindrical specimen (no. ULII/004 from Przesławice), assigned by Hurcewicz (1966, pl. 3, fig. 2) to this species, has a surface covered by thin irregularly distributed furrows but its choanosomal desmas are small, tuberculated tetraclones. The taxonomic position of this specimen is impossible to determine, owing to its poor state of preservation (destroyed basal and apical portions of sponge and lack of ectosomal spicules).

Distribution: Poland (Bełchatów: early Campanian sponges as redeposited elements in Neogene deposits, Proszowice area: upper Campanian, middle Vistula River valley: upper Campanian and lower Maastrichtian); Spain (Catalonia: Aptian); France (Nice and Saint Cyr area: Santonian, Paris Basin: Coniacian); Germany (Lower Saxony: lower and upper Campanian, Isle of Rügen: lower Maastrichtian); Denmark: Maastrichtian; England (unknown localities: Upper Chalk, ?Turonian–Maastrichtian; Gloucestershire: as glacial erratics).

Genus *Phymoracia* Pomel, 1872 (= *Myrmeciophytum* Schrammen, 1910)

Type species: *Stellispongia verrucosa* Roemer, 1864, p. 50, pl. 17, fig. 5, by monotypy.

Phymoracia verrucosa (Roemer, 1864)
Figs 4G–I, 6A–D

1864 *Stellispongia verrucosa* – Roemer, p. 50, pl. 17, fig. 5.

1910 *Myrmeciophytum verrucosum* (Roemer) – Schrammen, p. 81, pl. 4, fig. 1, text-pl. 4, fig. 3.

1966 *Myrmeciophytum verrucosum* (Roemer) – Hurcewicz, pp. 32–34, pl. 3, fig. 1, text-fig. 7.

Material: 9 specimens from Bełchatów (ULXXV/IT/1–9) and 1 from Zbyszycze (ULII/1471).

Description: Cylindrical sponges with slightly narrowing apex and without spongocoel (Fig. 4G–I). Largest, nearly complete specimen is 85 mm in height and 24 mm in width

(Fig. 4G). Other specimens, devoid of terminal and basal parts, are 24–80 mm in height and 12–38 mm in width. Lateral surface of specimens with shallow pits, ca. 1–1.8 mm in diameter, usually situated on top of small papillae. Papillae, spaced at 4–14 mm apart, often concentrated on one side of sponges. Surface of papillae smooth or covered by stellate arranged furrows. Six to eight exhalant canal openings situated in a pit, round or elliptical, 1.2–1.5 mm in diameter. Exhalant canals, arranged radially around the pit, running obliquely or in parallel to sponges' surface. Inhalant canal openings, 0.5–1 mm in diameter, randomly and densely arranged on surface of sponges. Inhalant canals long and perpendicular to surface of sponge.

Choanosomal skeleton inside the wall composed of tetraclones with smooth clones, 40–50 μm thick and 200–400 μm long, rarely up to 450 μm (Fig. 6A). Poorly branched zygomes with sparsely arranged small nodules forming terminal elongated zygoses, 100–150 μm x 250–450 μm in size. Tetraclones on surface of choanosomal skeleton more massive, with clones that are 50–60 μm thick; clones simple or forked, with zygomes occasionally connected to the unbranched part of clones of an adjacent desma (Fig. 6B, C). Within the network around furrows and exhalant canals, tetraclones with one long clone (up to 500 μm length) directed across furrow (Fig. 6B, D). These tetraclones interlocked by long zygoses arranged in parallel to furrows. Ectosomal spicules not preserved.

Remarks: *Phymoracia verrucosa* is a very rare fossil species, known only from the lower Campanian of Germany and Poland. All previously described specimens of *P. verrucosa* are only cylindrical fragments of sponges, therefore Schrammen (1910) and later Reid (2004) supposed that their body may have been branched. However, there are no remnants after lateral branches in the more abundant and better-preserved material from Bełchatów described here.

The canal openings, grouped on the top of papillae and surrounded by radial furrows, are recognised as characteristic features of *Phymoracia verrucosa* (Roemer, 1864; Schrammen, 1910; Hurcewicz, 1966). In the specimens studied, exhalant canal openings open on the wall of the shallow pit, usually situated on the top of the papillae, but sometimes the papillae are not developed (Fig. 4G). Star-like furrows are also not always visible, where canals run under the surface of the sponges.

Schrammen (1910) did not observe inhalant canals. Likewise, Hurcewicz (1966), possessing only one specimen, suggested that the inhalant canals are short and indistinct in the skeleton, because they are narrower than the skeletal meshes. In the specimens studied from Bełchatów the inhalant canals are narrow, but clearly recognizable in the choanosomal network.

Ectosomal spicules of *Phymoracia verrucosa* are unknown (Reid, 2004). Although Hurcewicz (1966) noted the prodichotriaenes and orthodichotriaenes in this species, but ectosomal spicules preserved *in situ* on the surface of the specimens from her collection were not found.

Distribution: Poland (Bełchatów: early Campanian sponges as redeposited elements in Neogene deposits, Lelów area: lower Campanian); Germany (Lower Saxony: lower Campanian).

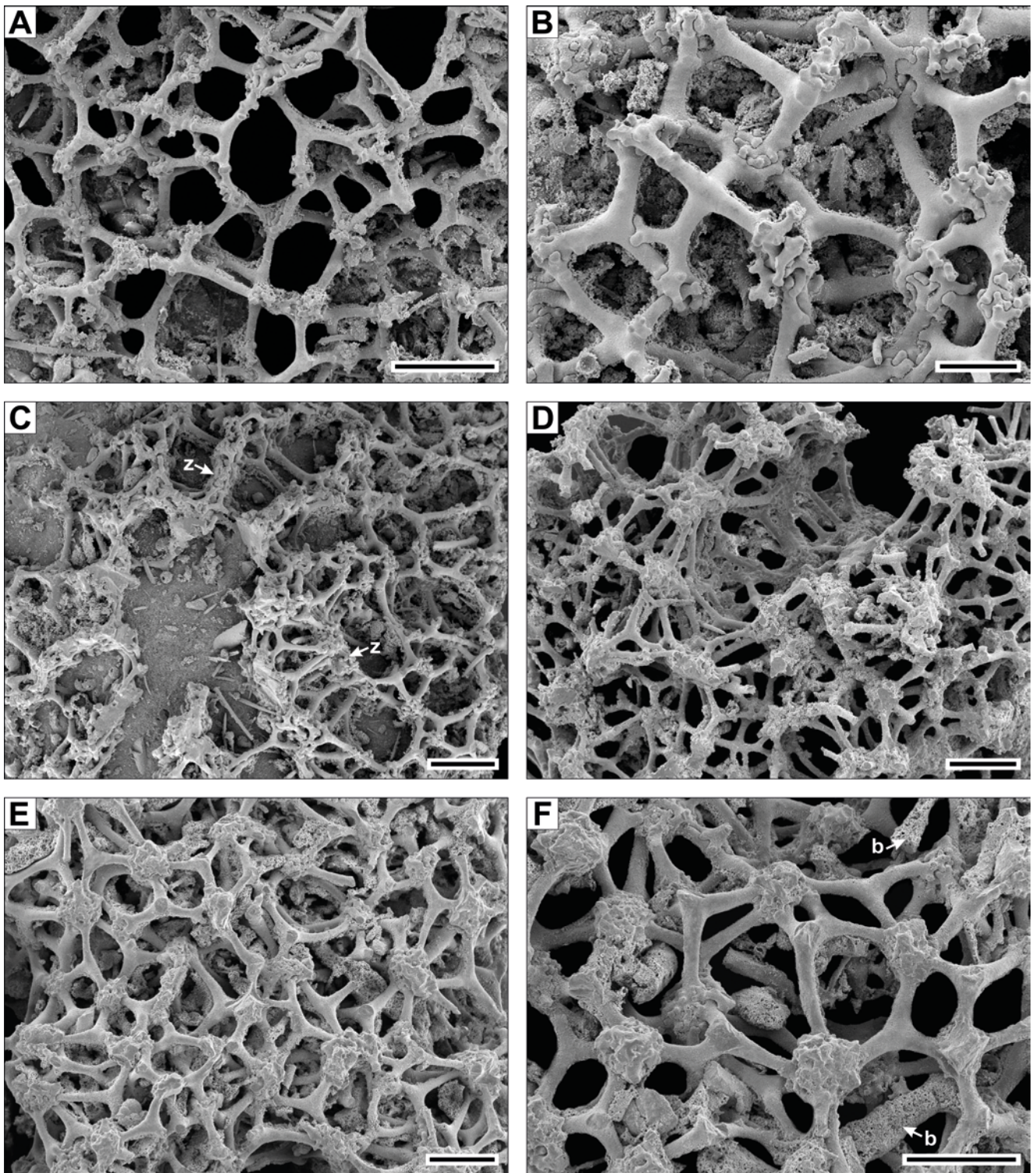


Fig. 6. Skeletons of phymatellid species. **A–D.** *Phymoracia verrucosa* (Roemer, 1864); A – choanosomal skeleton inside the specimen; ULXXV/IT/2, Bełchatów; B – choanosomal skeleton on outer surface with massive tetraclones; ULXXV/IT/2, Bełchatów; C – choanosomal skeleton on surface papilla and surrounding it furrows; very elongated zygoses (z) visible in skeletal band of separated furrows; ULXXV/IT/1, Bełchatów; D – choanosomal network inside the specimen and on the surface of the exhalant canal; ULXXV/IT/1, Bełchatów. **E, F.** *Craterella auricula* Schrammen, 1910; choanosomal skeleton inside the wall; visible silicified material infilling the burrows (b), running in network meshes; ULXXV/18T/1, Bełchatów. Scale bars represent 500 μm (A–C, D, E) and 200 μm (B).

Genus *Craterella* Schrammen, 1901
(= *Carterella* Laubenfels, 1955)

Type species: *Craterella tuberosa* Schrammen, 1901, p. 80, pl. 11, figs 6, 7, by monotypy.

Craterella auricula Schrammen, 1910
Figs 4J–L, 6E, F

- 1910 *Craterella auricula* – Schrammen, p. 80, pl. 11, figs 6, 7.
1926 *Craterella auricula* Schrammen – Moret, pp. 148–149, pl. 13, figs 2, 3; text-pl. 60, fig. 2.
1962 *Craterella auricula* Schrammen – Lagneau-Hérenger, p. 126.

Material: 6 specimens from Bełchatów (ULXXV/18T/1–6), 1 specimen from Jędrzejów (ULIIa/37a).

Description: The material studied consists of two almost complete cup-like specimens, ca. 100 mm in diameter and a height of at least 85 mm (Fig. 4L), and 5 fragments of crushed wall, 10–14 mm thick (Fig. 4J, K). A few broken thick root-like outgrowths occurring near rounded base. On outer surface, round or oval inhalant canal openings, 0.9–1.8 mm in size, irregularly arranged in 1–3 mm intervals. Straight inhalant canals perpendicular or slightly oblique to surface of a sponge. On inner side exhalant canal openings of similar size but loosely distributed, spaced at 3–5 mm. Exhalant canals divided; some branches running obliquely or nearly in parallel to sponge surface, others penetrate deep into the wall.

Dense choanosomal skeleton containing large tetracloones with smooth clones, 350–620 µm long and 70–90 µm thick (Fig. 6E, F). Clones straight, rarely slightly curved. Exceptionally one clone forked, usually roughly in half of its length. Poorly branched zygomes covered by rounded, relatively large tubercles (they are often invisible due to diagenetic changes). Terminal zygoses spherical, 300–380 µm in diameter. Small fragments of strongly silicified layer with irregular flattened spicules, 100–150 µm in size, and crushed dichotriaenes locally preserved. Cladomes of dichotriaenes 450–600 µm in diameter. Thin deutero-clads 2.5–3 times longer than proto-clads and positioned at ca. 75° to each other.

Remarks: The outer surface of specimens of *Craterella auricula* is usually covered by short furrows (Schrammen, 1910; Moret, 1926). The furrows are invisible in the specimens studied because their outer surface is poorly preserved, which is related to the destruction of specimens from Bełchatów during river transport or limonitization of the specimen from Jędrzejów. All other features, observed in the specimens studied, fully correspond to the description of this species.

Distribution: Poland (Bełchatów: early Campanian sponges as redeposited elements in Neogene deposits); Germany (Lower Saxony: lower and upper Campanian), Spain (Catalonia: Aptian), France (Saint Cyr area: Santonian, Paris Basin: Coniacian).

Genus *Kalpinella* Hinde, 1883

Type species: *Kalpinella pateraeformis* Hinde, 1883, p. 77, pl. 18, fig. 4, pl. 19, fig. 1, designated by Laubenfels, 1955, p. 55.

Kalpinella fragilis sp. nov.
Figs 7A–F, 8A–F

Etymology: *Fragilis* (Latin) – fragile. The species name refers to the thin, fragile wall of the sponges.

Holotype: ULXXV/23T/1; Fig. 7C, D.

Type locality and level: The holotype specimen was found in the north-western part of the Bełchatów Lignite Mine (51°14'N, 19°14'E); Miocene (?Pannonian) lag gravel with Campanian fossils, distinguished in the local lithostratigraphic scheme as the Upper Gravels, occurring in the basal part of the Clayey-Sandy Unit of the Bełchatów section.

Material: 9 specimens from Bełchatów (ULXXV/23T/1–9).

Diagnosis: Fan- or plate-like sponges with thin, often irregularly folded wall. Both surfaces of sponges with densely arranged small, round or irregular canal openings. Long epirhyses and aporhyses perpendicular to the surfaces of sponges. Slender choanosomal tetracloones with clones of various length, 200 µm to 550 µm long, terminated by poorly branched zygomes. In ectosomal layer dichotriaenes, with clads up to 280 µm in length, co-occurring with flattened, jagged spicules, up to 150 µm in size.

Description: The studied specimens are fan-like with short stalk or plate-like (Fig. 7A–F). Wall, 3–5 mm thick, irregularly folded and/or with flat thickenings. The folds often stick together and hollows or irregular cavities form between them. The best-preserved specimen (holotype) is 46 mm high and 40 mm wide. The largest fragment is 58 mm in size. Round or irregular canal openings, very densely arranged on both surfaces without any pattern; usually 0.5–0.8 mm, rarely up to 1 mm in size. Straight inhalant and exhalant canals perpendicular to both surfaces of a sponge; they are occasionally oblique only in places, where folds fuse together. Canals long, ending just below the opposite surface.

Choanosomal skeleton composed of slender tetracloones with clones 30–40 µm thick and length varying from 200 to 550 µm. Clones smooth, usually straight, but arched, sometimes irregular ramified also occur, especially on both surfaces of a sponge (Fig. 8A–D). Long, poorly branched zygomes with short, conical or tubular outgrowths, 5–30 µm long. Zygoses in very variable shape and size. They are almost spherical to strongly elongated, 100–150 µm x 150–400 µm in size. Besides them, long, arched zygoses appear, mainly near the canal openings. Ectosomal skeleton (strongly silicified and fragmentarily preserved only on two specimens) consisting of overlapping dichotriaenes having clads up to 280 µm in length. Straight deutero-clads arranged at angle 85–95°. Small, flattened spicules with a jagged edges, ca. 80–150 µm in size, densely packed on surface of choanosomal skeleton and also occurring between the dichotriaenes.

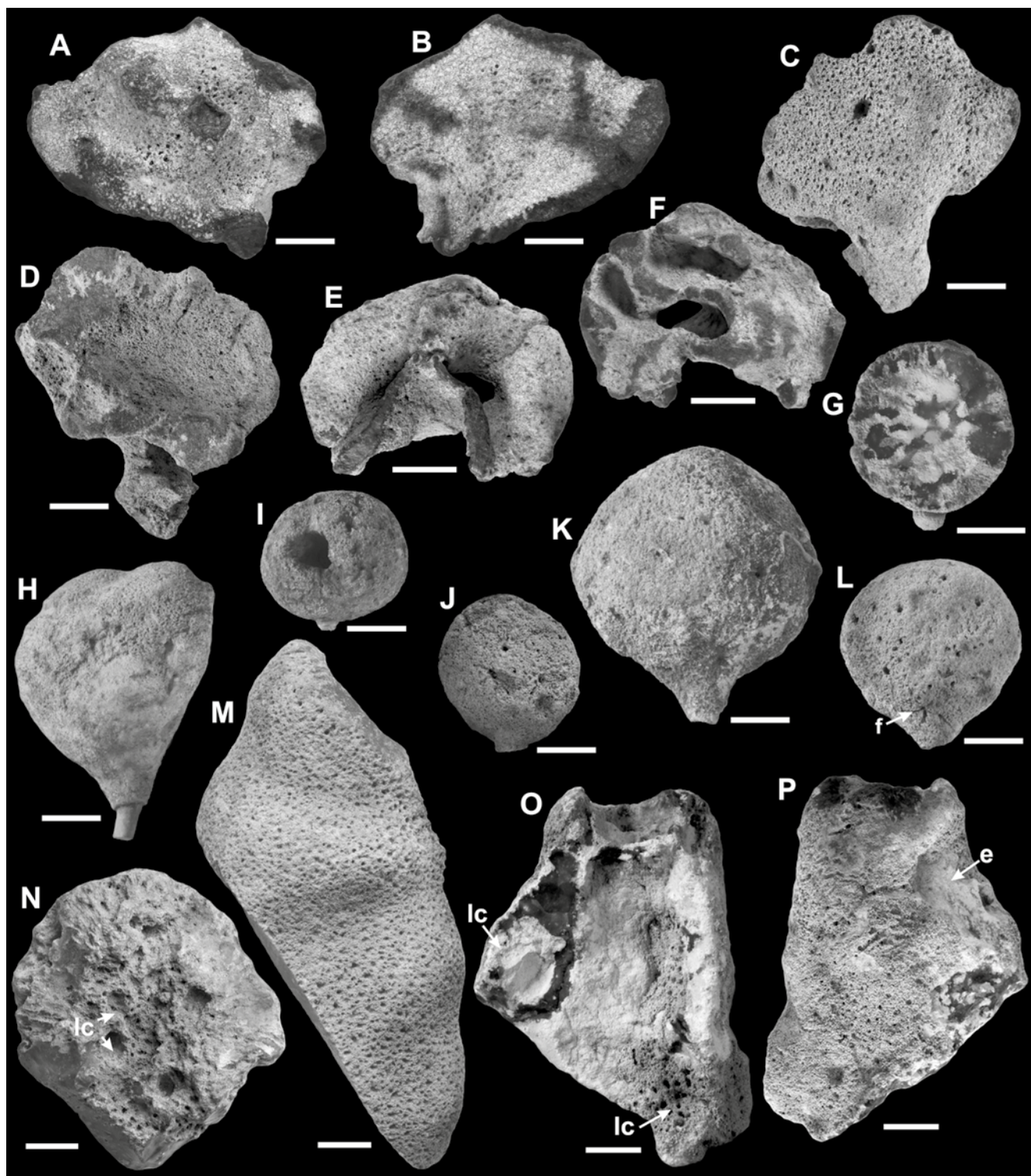


Fig. 7. Specimens of phymatellid species. **A–F.** *Kalpinella fragilis* sp. nov.; **A** – outer side of platy-like paratype with flat thickenings; ULXXV/23T/3, Belchatów; **B** – inner side of the same specimen; **C** – outer side of fan-like holotype; ULXXV/23T/1, Belchatów; **D** – inner side of holotype; **E** – inner side of paratype with irregularly folded wall; ULXXV/23T/4, Belchatów; **F** – outer side of the same specimen. **G–L.** *Bolospongia globata* Hinde, 1883; **G** – cross-section of specimen; ULXXV/19T/2, Belchatów; **H** – lateral view of specimen previously assigned to *Callopegma ficoideum* Hinde, 1883; UL II/1446, Zbyszce; **I** – lateral view of specimen with cylindrical boring, previously assigned to *Siphonia pyriformis* Goldfuss, 1826; UL II/1236, Skrajniwa; **J** – lateral view of specimen; ULXXV/19T/3, Belchatów; **K** – lateral view of largest specimen; ULXXV/19T/4, Belchatów; **L** – lateral view of specimen; one exhalant canal opening surrounded by radial furrow (f); ULXXV/19T/5, Belchatów. **M, N.** *Phymatella tuberosa* (Quenstedt, 1878); **M** – outer surface of specimen; ULXXV/4T/2, Belchatów; **N** – inner surface of specimen fragment; outlets of lateral cavities (lc) visible on surface of spongocoel; ULXXV/4T/3, Belchatów. **O, P.** *Phymatella bulbosa* Zittel, 1878; **O** – inner view of specimen; visible lateral cavities of spongocoel (lc); ULXXV/4T/1, Belchatów; **P** – outer view of the same specimen with fragments of ectosomal skeleton (e) preserved mainly in depressions. Scale bars represent 1 cm.

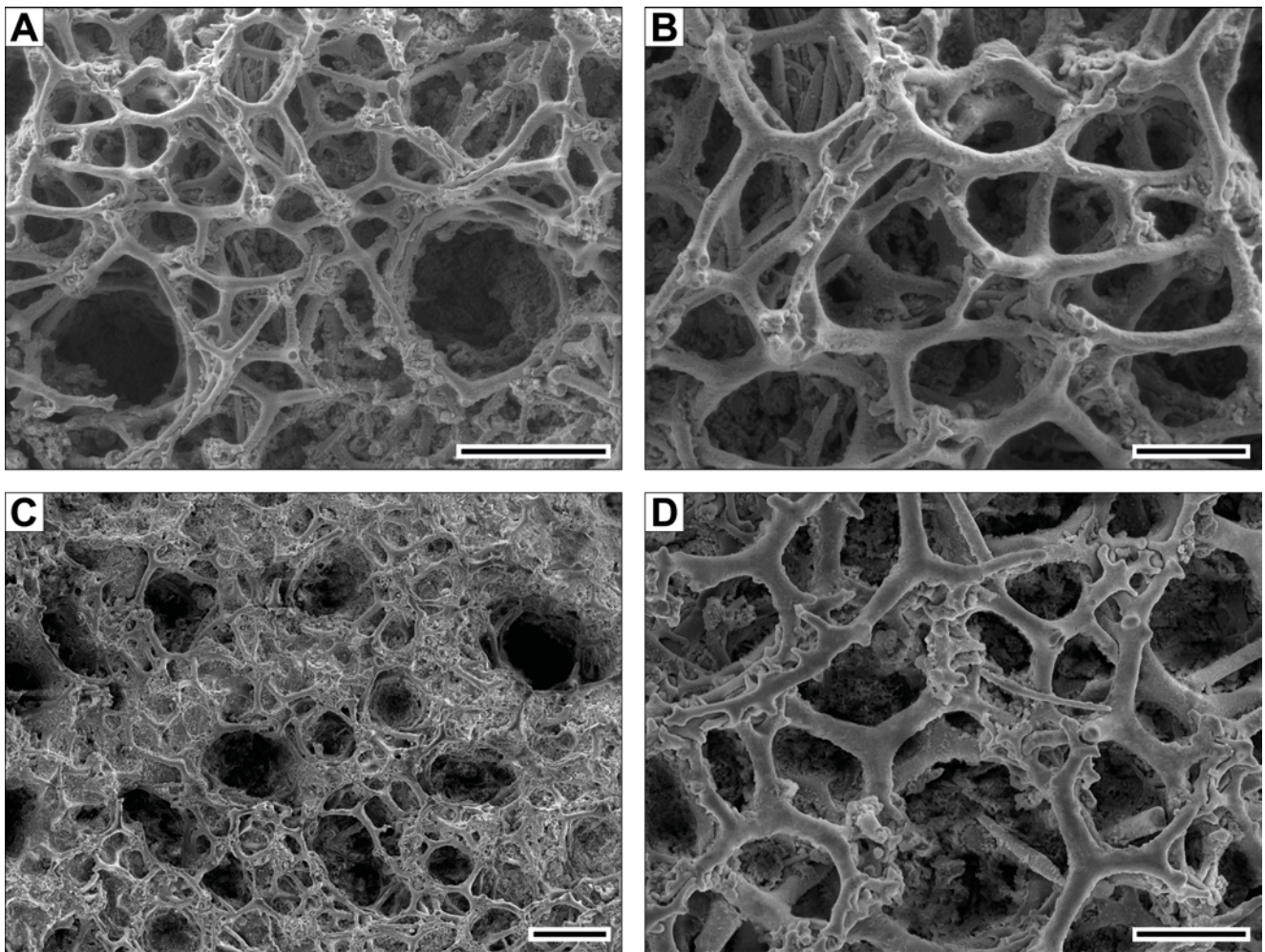


Fig. 8. Skeleton of *Kalpinella fragilis* sp. nov.; paratype ULXXV/23T/2, Belchatów. **A, B.** Choanosomal skeleton on inner surface of specimen. **C, D.** Choanosomal skeleton on outer surface of specimen. Scale bars represent 500 μ m (A, C) and 200 μ m (B, D).

Remarks: The loose structure of the choanosomal skeleton and dense canalization of the wall with canal openings distributed similarly on both surfaces allow inclusion of the proposed new species in the genus *Kalpinella* Hinde, 1883.

Kalpinella fragilis sp. nov. differs from other representatives of *Kalpinella* by a thin, irregularly folded wall. Other cup- or platy-like species of *Kalpinella* have a smooth, thick (ca. 9–35 mm) wall (see Hinde, 1883; Moret, 1926; Defretin-Lefranc, 1960; Lagneau-Hérengrer, 1962; Wagner, 1963; Świerczewska-Gładysz *et al.*, 2019). A folded wall was observed only in *K. rugosa* Hinde, 1883 from the Upper Greensand Formation of southern England, but the folds in that species occur merely in the upper portion of the regular cup- or funnel-like body (Hinde, 1883). Canals in *Kalpinella* run perpendicularly or obliquely to the surface and may also be sinuous. In the studied specimens, the canals are straight and mainly perpendicular. A characteristic feature of the choanosomal skeleton of *K. fragilis* sp. nov. includes slender tetracloes with poorly branched zygomeres. Tetracloes of other species of *Kalpinella* are more massive with strong, tuberculate zygomeres (e.g., Hinde, 1883; Moret, 1926; Defretin-Lefranc, 1960). Ectosomal spicules of *Kalpinella* have not been described so far. Dichotriaenes

found in *K. fragilis* sp. nov. confirm the affiliation of this genus to the Phymatellidae.

Pisera and Lévi (2002b) pointed out that the extant, monotypic genus *Reidispungia* Lévi and Lévi, 1988 resemble the Mesozoic genus, *Kalpinella*. Among known representatives of *Kalpinella*, described here *K. fragilis* sp. nov. is the most similar to *Reidispungia coerulata* Lévi and Lévi, 1988 owing to cup or fan-like body with thin, undulating wall. Desmas of *K. fragilis* sp. nov. are also alike to tetracloes of *R. coerulata*, but they are less branched. Owing to lack of microscleres in described species, the relationship between these taxa remains unclear.

Distribution: Poland (Belchatów: early Campanian sponges as redeposited elements in Neogene deposits).

Genus *Bolospongia* Hinde, 1883

Type species: *Bolospongia globata* Hinde, 1883, p. 74, pl. 17, fig. 1, 1a, b, designated by Laubenfels, 1955, p. 56.

Remarks: Reid (2004) suggested that the genus *Bolospongia* is probably allied to *Phymatella* Zittel, 1878. This is in agreement with observations of the present authors. The genus *Bolospongia* is distinguished by the lack

of spongocoel, but the choanosomal skeleton of the type species of *Bolospongia* and representatives of *Phymatella* observed in longitudinal section show similar skeletal bands with very elongated zygomes (Schrammen 1910, pl. 1 fig. 8, pl. 3, fig. 1; Moret, 1926, pl. 13, fig. 7'). These skeletal bands are distributed radially in *B. globata*, while in *Phymatella* they have a nearly horizontal arrangement (perpendicular or slightly oblique to the spongocoel).

Bolospongia globata Hinde, 1883

Figs 7G–L, 9A, B

- 1883 *Bolospongia globata* – Hinde, p. 74, pl. 17, fig. 1, la, b.
 partim 1968 *Callopegma ficoideum* Hinde – Hurcewicz, pp. 40–42, pl. 1, figs 3, 4.
 partim 1968 *Siphonia pyriformis* Goldfuss – Hurcewicz, pp. 49–50 [non pl. 4, fig. 5].
 partim 1968 *Siphonia tulipa* Zittel – Hurcewicz, pp. 47–49 [non pl. 4, fig. 4].

Material: 18 specimens from Bełchatów (ULXXV/19T/1–18), 6 specimens from Pniaki (ULII/1236, ULIIa/20–24), 1 specimen from Zbuczycze (ULII/1446), 17 specimens from Skrajniwa (ULII/221, 238, 324, 660, 662, 1236, 1240, 1242, 1245, 1246, 1249, 1261, 1269, 1271, 1279, 1280, 1287).

Description: Spherical, rarely hemispherical, bulbous or fig-like sponges, without central spongocoel, not exceeding 50 mm in diameter (Fig. 7G–L). Outer surface smooth, rarely with shallow depressions. Most of specimens with preserved small fragment of stalk, usually 4–5 mm in diameter. Exhalant canal openings round, 1.2–2 mm in diameter, occasionally surrounded by short, thin furrows. Exhalant canal openings irregularly distributed on the entire surface of sponges, usually at ca. 5–8 mm, rarely 9–11 mm intervals. Branched exhalant canals inside the sponges forming a system of irregular cavities, 2–4 mm wide (Fig. 7G). Round inhalant canal openings, 0.4–0.6 mm in diameter, irregularly arranged on surface of sponges, spaced at every 1.5–2 mm. Radial inhalant canals short and very narrow.

Choanosomal skeleton on outer surface composed of regular tetrachlores, with smooth usually unforked clones, 60–80 µm thick and 300–400 µm long (Fig. 9A). Clones terminated by tuberculated zygomes forming spherical or elongated zygomes, 300 µm x 300–500 µm in diameter. In longitudinal section of specimens, choanosomal network with radially arranged skeletal bands (Fig. 9B). They contain irregular tetrachlores with strongly branched zygomes, which intertwine into very elongated zygomes, 500 µm to even 2 mm long. Tetrachlores, with clones of different lengths (up to 450 µm) occurring also on the wall of exhalant canals. Modified desmas in stalk having two long clones (up to 500 µm) parallel to axis of stalk. Strongly silicified ectosomal layer consisting of very small, irregular branched spicules and fragments of ectosomal dichotriaenes, with clads ca. 200 µm long. Protoclads of dichotriaenes twice shorter than deuteroclads.

Remarks: *Bolospongia globata* Hinde, 1883 was previously known only from the Upper Chalk of England. These specimens are subspherical with an uneven surface, while

specimens from Poland mainly have a smooth surface. In specimens from England, inhalant canals were not observed, but these sponges are poorly preserved within flint nodules. In some well-preserved specimens from Bełchatów, very small inhalant canal openings and poorly developed inhalant canals are noted. The exhalant canal system, shape, size and arrangement of tetrachlores in the choanosomal skeleton of the specimens from Poland and England are identical. Hinde (1883) mentioned the presence of an external layer, but without preserved ectosomal spicules. In the specimens studied the ectosomal layer is preserved only on the surface of some stalks and consists of irregular flattened spicules and small dichotriaenes. However, the size of these dichotriaenes cannot be considered as diagnostic for the species, since the ectosomal megascleres on the stalks of phymatellids are often smaller than those on their main body part.

Bolospongia globata is a common species in the lower Campanian opoka of Poland. Macroscopically this species is distinguished by the lack of the central spongocoel and the presence of exhalant canal openings, sparsely distributed on the surface of the sponge (in poorly preserved specimens which are secondarily siliceous or calcified, these openings may be poorly visible). Numerous specimens from the museum collection, recognized here as *B. globata*, were assigned by Hurcewicz (1966) to *Callopegma ficoideum* Hinde, 1883, but these sponges have no axial exhalant canals, typical for *Callopegma* (Fig. 6H) and their tetrachlores are smaller than in *Callopegma*. Ten specimens of *B. globata*, owing to the lack of spongocoel, were previously considered as juvenile individuals of *Siphonia tulipa* Zittel, 1878 (Hurcewicz, 1966). Two others, described by Hurcewicz (1966) as *Siphonia pyriformis* Goldfuss, 1826, have borings, which were incorrectly recognized as the spongocoel. These borings are variably oriented in relation to the axis of the sponges and in the specimen with a destroyed surface, the cylindrical borings pass through the entire body of the sponge (Fig. 6I). Similar borings are common in skeletons of the calcareous sponge, *Porosphaera globularis* (Phillips, 1829), co-occurring with *B. globata* in the Campanian of Poland (Jurkowska *et al.*, 2015), and they are interpreted as the mobile domicile of sipunculan worms (Neumann *et al.*, 2008). In contrast to the representatives of *Siphonia*, the choanosomal network of the specimens mentioned above contains larger, regular tetrachlores with strong zygomes.

Distribution: Poland (Bełchatów: early Campanian sponges as redeposited elements in Neogene deposits, Lelów area: lower Campanian), eastern England (Flamborough: Upper Chalk, Campanian).

Genus *Phymatella* Zittel 1878

Type species: *Eudea intumescens* Roemer, 1864, p. 26, pl. 11, fig. 1, designated by Laubenfels, 1955, p. 56.

Phymatella bulbosa Zittel, 1878

Fig. 6O, P

- 1878 *Phymatella bulbosa* Zittel – Zittel, p. 74, pl. 2, fig. 1.

- non 1966 *Phymatella bulbosa* Zittel – Hurcewicz, p. 29, text-fig. 5, pl. 3, fig. 7.
- 2006 *Phymatella bulbosa* Zittel – Świerczewska-Gładysz, pp. 271–272, figs 37h, i, 38f [cum syn.].

Material: 2 specimens from Bełchatów (XXV/27T/1, 2), 1 specimen from Gnatowice (UŁ II/31).

Description: The largest specimen (Fig. 6O, P) is a fragment of a pear-like sponge, measuring 71 mm in height (without the lower part). Outer surface with shallow depressions and poorly developed bulges, occasionally covered by short grooves. Tube-like spongocoel of this specimen, 15 mm wide, with large irregular cavities (Fig. 6O). Smaller fragments, derived from the lower part of sponges, with prominent bulges. Canal openings on outer surface round, 0.4–1 mm in diameter, spaced at 1–2 mm. Canal openings on surface of spongocoel 1–1.5 mm in size, arranged at ca. 2–2.5 mm intervals. Close to the surfaces of the sponge, inhalant and exhalant canals straight and perpendicular (deeper canals not visible due to silicification of the specimens).

Choanosomal skeleton on both surfaces comprising tetrachloes with smooth clones of variable length (200–300 µm long), terminating with irregularly branched zygomes. Inside the wall clones slightly longer, up to 350 µm long, occasionally forked. Zygomes with sparsely arranged small tubercles, forming irregular zygoses, 300–400 x 500 µm in size, or elongated, 100–200 µm x 400–500 µm. In skeletal bands between inhalant canals most of the elongated zygoses arranged parallel to the canals. Locally preserved, small patches of ectosomal layer composed of small, flattened spicules, 100–150 µm in size, and dichotriaenes with cladomes up to 550–650 µm in diameter. Long deuteroclads straight or slightly arched, dividing at 85–90°.

Remarks: The specimens of *Phymatella bulbosa* differ from other species of *Phymatella*, including *P. tuberosa* co-occurring in the material from Bełchatów, in a spongocoel with irregular, branched cavities and irregular bulges on the outer surface (e.g., Schrammen, 1901, 1910; Ulbrich, 1974; Świerczewska-Gładysz, 2006). The bulges on the outer surface of the largest specimen studied are poorly developed, but this specimen has a damaged lower part, where the bulges are most prominent in this species (Schrammen, 1901, 1910; Ulbrich, 1974; Moret, 1926).

The specimen from the Miechów Synclinorium, described by Hurcewicz (1966, p. 29, pl. 3, fig. 7, text-fig. 5) as *P. bulbosa*, has skeleton consists of rhizoclones (genus and species undetermined due to the poor state of preservation of the specimen). Desmas described and illustrated by Hurcewicz (1966) as tetrachloes of *P. bulbosa* come from a fragment of a phymatellid individual, on which the rhizomorphine sponge grew.

Distribution: Poland (Bełchatów: early Campanian sponges as redeposited elements in Neogene deposits, Proszowice area: lower Campanian, middle Vistula River valley: upper Maastrichtian) Germany (Saxony-Anhalt: lower Campanian, Lower Saxony: lower and upper Campanian, Rügen: lower Maastrichtian).

Phymatella tuberosa (Quenstedt, 1878)
Figs 7M, N, 9C, D

- 1878 *Scyphia tuberosa* – Quenstedt, p. 388, pl. 133, figs 18–20.
- 1878 *Phymatella tuberosa* (Quenstedt) – Zittel, p. 76.
- 1878 *Phymatella heteropora* Roemer – Zittel, p. 76, pl. 8, fig. 2.
- 1910 *Phymatella tuberosa* (Quenstedt) – Schrammen, p. 77.
- 1910 *Phymatella heteropora* Zittel (non Roemer) – Schrammen, p. 76, pl. 3, fig. 1.
- 1974 *Phymatella tuberosa* (Quenstedt) – Ulbrich, p. 17–18, pl. 1, figs 1–3.

Material: 17 specimens from Bełchatów (ULXXV/4T/1–17).

Description: The studied fragments are derived from large, pearl-like to near cylindrical sponges. The largest specimens, without the lower and apical parts, are 85–100 mm in height and 50–60 mm in width (Fig. 7M). Outer surface of specimens smooth, with transverse narrowings or slight bulges and shallow concavities. Tubular spongocoel deep and up to 15–18 mm wide. Surface of spongocoel with round or oval openings, 5 mm x 5–6 mm in size (Fig. 7N); uppermost part of spongocoel of large specimens often without openings. Neighbouring openings connected by spiral canals, 5–7 mm wide, running inside wall. Inhalant canal openings, very densely arranged on outer surface, having various shapes and sizes; being round and small, ca. 0.5–0.7 mm in diameter, while large, up to 1.6 mm, round or irregular. Exhalant canal openings on the surface of spongocoel longitudinally oval, 1–1.5 mm x 1.5–2 mm in size. Inhalant and exhalant canals straight and perpendicular to the outer surface of sponge or surface of spongocoel, respectively.

Choanosomal skeleton inside wall consisting of tetrachloes with smooth, occasionally forked clones (Fig. 9C, D). Clones often of variable length, 250–450 µm long and 25–50 µm thick, terminated by poorly branched zygomes. Zygomes elongated or irregular, usually 300–400 µm in size. Very elongated zygomes, up to 800–900 µm long, occurring in skeletal bands separating the inhalant canals. These zygomes extend in direction parallel to canals. Dense network on outer surface and on surface of spongocoel with smaller tetrachloes, whose clones range up to 250–350 µm in length. Ectosomal skeleton not preserved.

Remarks: Representatives of *Phymatella tuberosa* usually have deep transverse narrowings and rounded bulge/bulges in the lower part of their body (Quenstedt, 1878; Schrammen, 1910; Ulbrich, 1974), but specimens with an almost smooth surface, similar to some specimens from Bełchatów, have also been noted (Schrammen, 1910). These latter specimens are macroscopically identical to the representatives of *Phymatella heteropora* Zittel, 1878, co-occurring with *P. tuberosa* in the Campanian of Lower Saxony (Zittel, 1878; Schrammen, 1910). A characteristic feature of both species, apart from the variable size of the canal openings on the outer surface, is a spongocoel with large openings leading to spiral canals inside the wall. Schrammen (1910) suggested that the choanosomal skeleton of *P. heteropora*

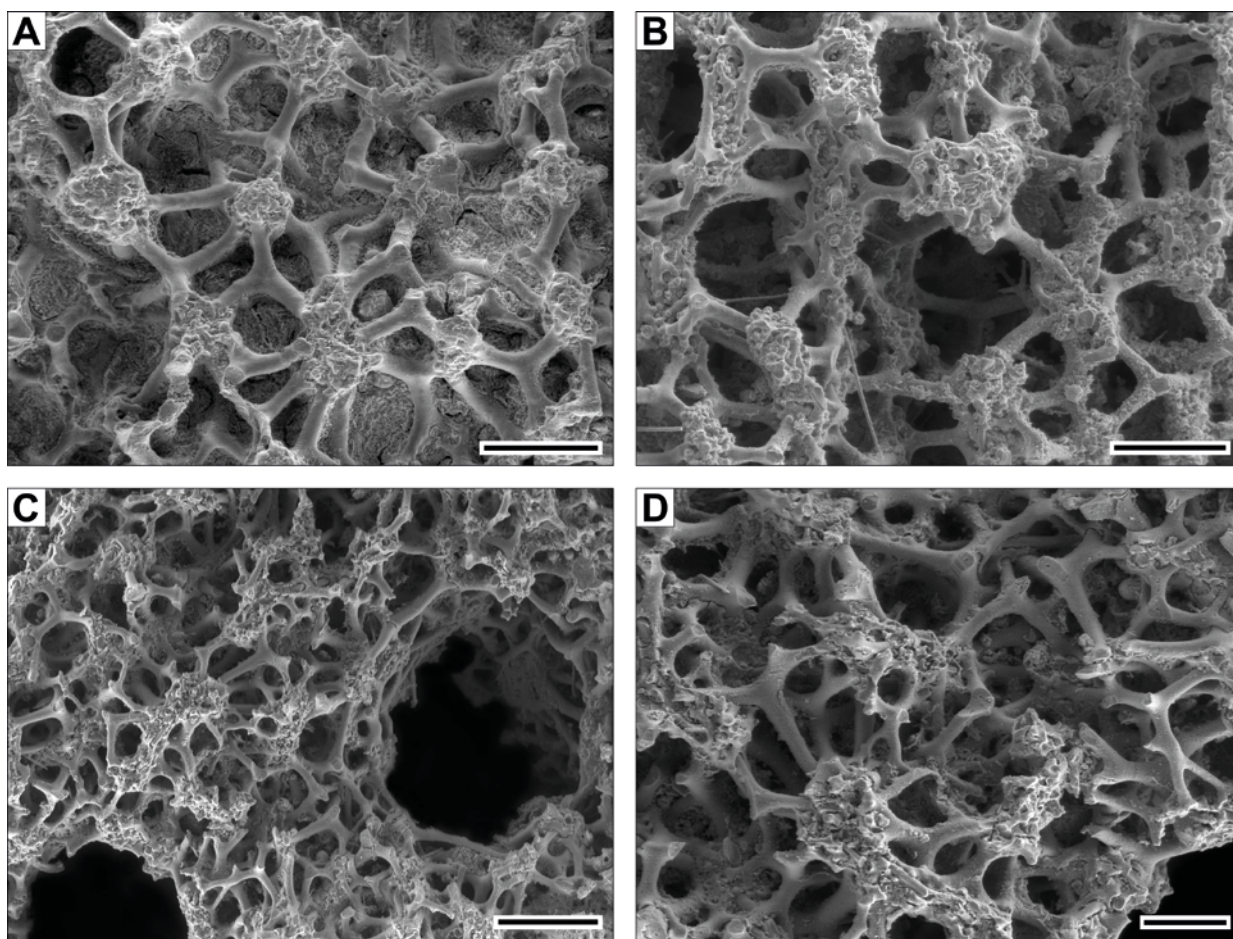


Fig. 9. Skeletons of phymatellid species. **A, B.** *Bolospongia globata* Hinde, 1883; ULXXV/19T/1, Bełchatów; A – choanosomal skeleton on outer surface of specimen; B – choanosomal skeleton with long zygoses, visible in longitudinal section of specimen. **C, D.** *Phymatella tuberosa* (Quenstedt, 1878); choanosomal skeleton with exhalant canals, observed in cross-section of the wall parallel to spongocoel; ULXXV/4T/1, Bełchatów. Scale bars represent 500 μm (A–C) and 200 μm (D).

is slightly denser than in *P. tuberosa*, but other descriptions of the desmas of both species (Zittel, 1878; Ulbrich, 1974) and measurements by the present authors do not confirm this assumption. Thus, the authors propose to include the discussed specimens of *P. heteropora* in *P. tuberosa*.

Distribution: Poland (Bełchatów: early Campanian sponges as redeposited elements in Neogene deposits); Germany (Saxony-Anhalt: lower Campanian, Lower Saxony: lower and upper Campanian).

Genus *Jerea* Lamouroux, 1821 sensu Schrammen, 1910

Type species: *Jerea pyriformis* Lamouroux, 1821, p. 79, pl. 78, fig. 3, by monotypy.

Remarks: Reid (2004) accepted the diagnosis of the genus given by Zittel (1878), assuming that the absence of the spongocoel is a diagnostic feature of this genus, distinguishing it from the genus of *Siphonia* Parkinson, 1822. Our observation is in agreement with Schrammen (1910), who indicated that the presence or lack of a spongocoel in both genera may be associated with their ontogenetic development, therefore the size of the spicules is a more important diagnostic feature. Choanosomal tetracloes and ectosomal dichotriaenes of *Jerea* are significantly larger than in *Siphonia*.

Jerea pyriformis Lamouroux, 1821

Fig. 10A–C

- 1821 *Jerea pyriformis* – Lamouroux, p. 79, pl. 78, fig. 3.
- 1937 *Jerea pyriformis* Lamouroux – Lehner, p. 159, pl. 16, figs 1–3.
- 1960 *Jerea pyriformis* Lamouroux – Defretin-Lefranc, pp. 103–104, pl. 16, figs 5, 6 [cum syn.].
- 1963 *Jerea pyriformis* Lamouroux – Wagner, pp. 177–178.
- non 1966 *Jerea pyriformis* Lamouroux – Hurcewicz, pp. 46–47, pl. 4, fig. 1–3 [= *Siphonia* sp.].
- 1967 *Jerea pyriformis* Lamouroux – Lagneau-Hérenger, p. 86, pl. 2, fig. 9a, b.
- 1993 *Jerea pyriformis* Lamouroux – Gruber, p. 38, pl. 21, figs 1, 2.
- 2013 *Jerea pyriformis* Lamouroux – Vodrážka, in Schneider *et al.*, text-fig. 7h.

Material: 6 specimens from Bełchatów (ULXXV/7T/1–6).

Descriptions: Sponges ovoid or egg-like, up to 78 cm in height and 52 cm in diameter (Fig. 10A–C). Two specimens with remnant of thin stalk. Apex of sponges flat or rounded with densely distributed exhalant canal openings, 1–1.5 mm in diameter. Thin, undulating furrows occurring in upper part of some specimens. Round, sparsely arranged inhalant canal openings, 0.5–1.1 mm in diameter. Inhalant canals in outer part of sponges straight; in deeper parts of a sponge body invisible. Wide exhalant canals in axial part of a sponge straight and running vertically, while peripheral canals bending towards lateral surface of a sponge. Some of them forked and ending just below the surface (in places where outer surface has been damaged, the terminal section of these canals in longitudinal or cross section have shapes of furrows or large round holes, respectively).

Preserved very small fragments of choanosomal skeleton consisting of tetracloes with smooth clones, 50–60 µm thick and 250–340 µm long. Due to secondary silicification of the specimens, shape and ornamentation of zygomes not recognized. Zygotes ellipsoidal or irregular, usually 200 µm x 300–400 µm in size. On wall of exhalant canals, clones sometimes forked, up to 420 µm long. Zygotes in this compact network more elongated (200–300 µm x 400–550 µm) and usually extending transversely to the canal. Ectosomal skeleton not preserved.

Remarks: *Jerea pyriformis* is a common species in the Cenomanian and Turonian of western Europe (Lamouroux, 1821; Lehner, 1937; Moret, 1926; Defretin-Lefranc, 1960; Wagner, 1963; Lagneau-Hérenger, 1967; Schneider *et al.*, 2013). It was listed in the Campanian strata only by Hurcewicz (1966), but three specimens from the Miechów Trough included by her in *J. pyriformis* were recognized by the present authors as *Siphonia* sp. due to the presence of small tetracloes (see below). The size of desmas and all other characteristics of the specimens from Belchatów correspond well with the previous descriptions of *J. pyriformis*. This species differs from some fig-shaped juvenile specimens of *Jerea quenstedti* without a developed spongocoel (co-occurring in the collected material) mainly by slightly smaller tetracloes and large, well-developed zygotes.

Distribution: Poland (Belchatów: early Campanian sponges as redeposited elements in Neogene deposits); France (Normandy and Ardennes: Cenomanian, Department Drôme: Turonian, Paris Basin: Coniacian); Germany (Bavaria: lower Turonian).

Jerea quenstedti Zittel, 1878

Figs 10D–J, 11A–E

- 1878 *Jerea quenstedti* – Zittel, p. 145, pl. 10, fig. 2.
 1910 *Jerea quenstedti* Zittel – Schrammen, p. 81, pl. 2, figs 1–4, text-pl. 4, fig. 2 [with previous synonyms].
 1966 *Siphonia tubulosa* (Roemer) – Hurcewicz, pp. 51–53, pl. 5, figs 1, 2, pl. 4, figs 1, 2, text-fig. 1.
 1966 *Thecosiphonia gracilis* sp. nov. – Hurcewicz, pp. 34–35, pl. 9, fig. 2, text-fig. 8.
 1966 *Aulaxinia ventricosa* Schrammen – Hurcewicz, pp. 38–39, pl. 3, fig. 4, pl. 24, fig. 1.

Material: 74 specimens from Belchatów (ULXXV/2T/1–74), 7 specimens from Zbyszycze (ULII/257b, 670, 1565; ULIIb/39–42), 7 specimens from Skrajniwa (UL/257a, 275, 386; ULIIb/35–38).

Description: Tubular, ovoid, pear-like or conical sponges (Fig. 10E, F, I, J). Tubular specimens often asymmetrically curved. Largest, crushed specimens up to 190 mm high. In adult sponges with thick wall (usually 20–30 mm, occasionally even 50–55 mm thick), deep spongocoel cylindrical or narrow conical. In a few juvenile specimens (not exceeding 65 mm in height), spongocoel not developed and only a shallow depression occurring on their apex (Fig. 10D, G). Some specimens with remains of thin stalk (ca. 20 mm in diameter). Isolated short fragments of stalk terminated by thick, root-like outgrows (Fig. 10H). Broken root-like outgrows with a diameter of up to 18–20 mm, being also observed in the lower part of the body of large sponges (Fig. 10F). Short, straight or winding furrows, in some cases occurring around osculum, in lower part of sponges and also on root-like outgrows. Outer surface covered by round or elongated inhalant canal openings, 0.7–2 mm in size. Two (rarely three) small openings located close to each other leading to one inhalant canal (thin skeletal band between these canal openings often destroyed and openings seem to be large, irregular or comma-like). Straight or widening inhalant canals running perpendicularly or slightly obliquely. In lowermost part of the sponge body, on the stalks and on entire surface of the smallest specimens round or oval inhalant canal openings are smaller (0.7–1 mm in diameter), leading to straight, perpendicular or slightly oblique inhalant canals. Exhalant canal openings elliptical, rarely round, 1.2–2.8 mm in size, arranged very irregularly on the surface of the spongocoel, spaced at 2.5–5 mm. Long exhalant canals straight or arched, occasionally forked, running obliquely to surface of spongocoel. Canals opening on the bottom of spongocoel are arranged vertically. Several of them continue inside the stalk.

Poorly preserved choanosomal skeleton inside the wall consisting of tetracloes with straight or arched clones, often irregularly branched (Fig. 11A, E). Some tetracloes with rounded knob or short process, which correspond to reduced clone or are laterally branched. Smooth clones, 250–480 µm long and 60–70 µm thick, with terminal and also lateral zygotes. Short, poorly branched zygotes covered by small, sparsely arranged tubercles. Weak, elongated or irregular zygotes, 200–250 µm in size. On surface of choanosomal skeleton desmas slightly smaller, with clones 250–400 µm long and 60–80 µm thick, arranged more densely (Fig. 11B). Very compact network on wall of exhalant canals with large openings (200–400 µm in diameter), surrounded by tetracloes with curved and strongly branched clones (Fig. 11C). Ectosomal skeleton (Fig. 11D) rarely preserved, mainly on the surface of stalk and root-like outgrows. Dichotriaenes with cladomes 350–550 µm in size. Protoclads extremely shortened, while long and thin deuteroclads, usually slightly curved and arranged at 70–95°. Occasionally, one deuteroclad may be distorted and longer than the others. Flattened spicules with jagged edges, usually 150–200 µm in size occurring under and occasionally between overlapping dichotriaenes.

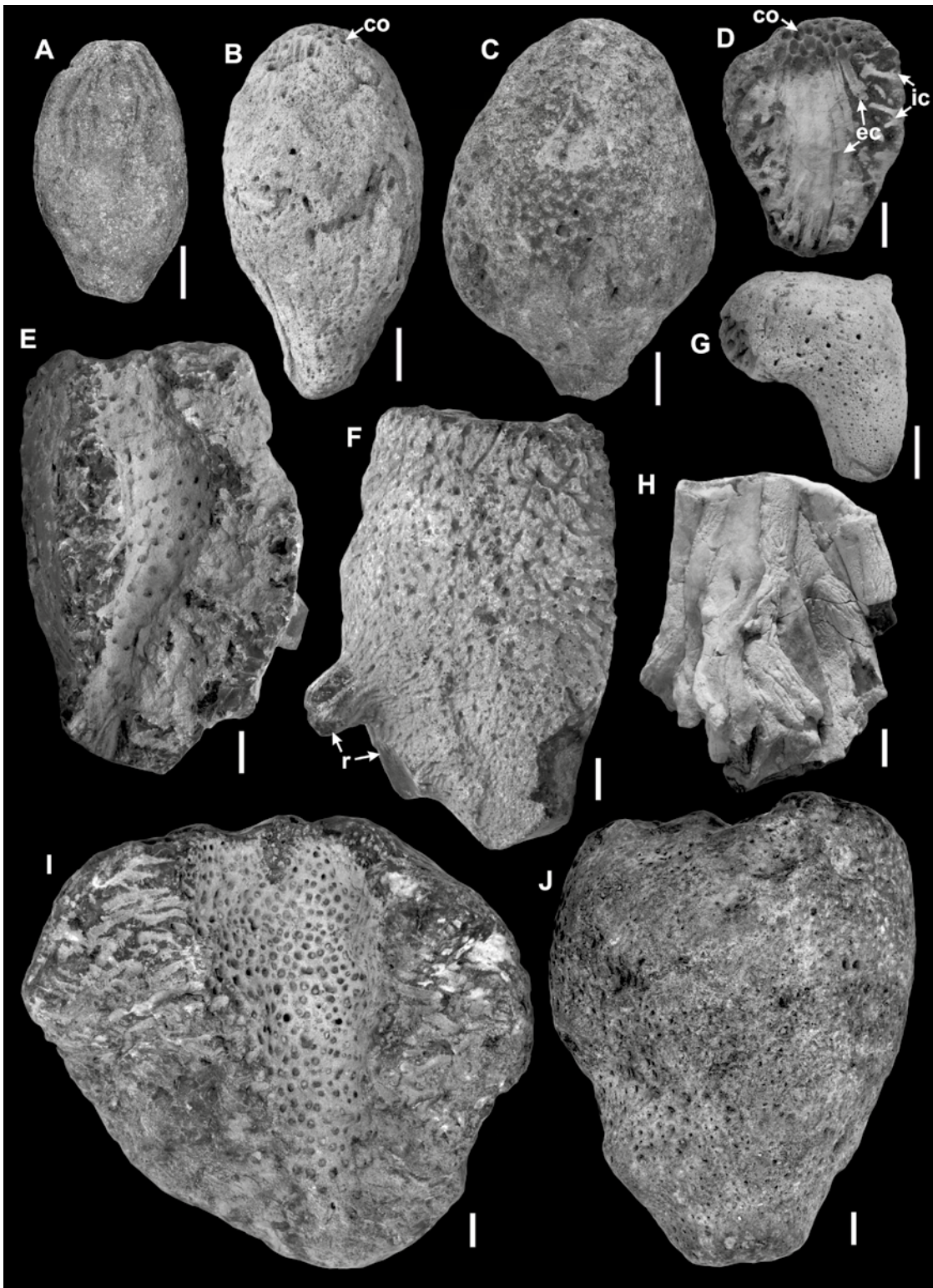


Fig. 10. Specimens of phymatellid species. **A–C.** *Jerea pyriformis* Lamouroux, 1821; **A** – lateral view of specimen with furrows in upper part; ULXXV/7T/1, Bełchatów; **B** – lateral view of specimen; exhalant canal openings visible on the top; ULXXV/7T/2, Bełchatów; **C** – lateral view of specimen; ULXXV/7T/3, Bełchatów. **D–J.** *Jerea quenstedti* Zittel, 1878; **D** – cross-section of juvenile specimen with shallow spongocoel on the top; visible inhalant canals (ic), exhalant canals (ec) and their openings (co) on the surface of spongocoel; ULXXV/2T/1, Bełchatów; **E** – cross-section of cylindrical specimen with sparsely arranged canal openings on surface of deep spongocoel; ULII/670, Skrajniwa; **F** – lateral view of the same specimen with broken root-like outgrowths (r); **G** – juvenile, curved specimen with bowl-like spongocoel on the top; ULXXV/2T/2, Bełchatów; **H** – root-like outgrowths; specimen previously recognized as holotype of *Thecosiphonia gracilis* Hurcewicz, 1966; ULII/1565, Zbyszycze; **I** – cross-section of wide specimen with densely arranged canal openings on surface of deep spongocoel; ULXXV/2T/5, Bełchatów; **J** – lateral view of conical specimen; ULXXV/2T/6, Bełchatów. Scale bars represent 1 cm.

Remarks: Hurcewicz (1966) included numerous specimens of *Jerea quenstedti* from the Lelów area to *Siphonia tubulosa* (Roemer, 1841). Both species are macroscopically very similar but differ in the size of choanosomal and ectosomal spicules (Zittel, 1878; Schrammen, 1910). Schrammen's

specimen of *S. tubulosa* studied by the authors shows small tetraclones with clones that are only 200–300 µm long (Fig. 11F). Hurcewicz (1966) admitted that the specimens described by her have massive tetraclones with clones of just this length, but the illustrated tetraclones are broken,

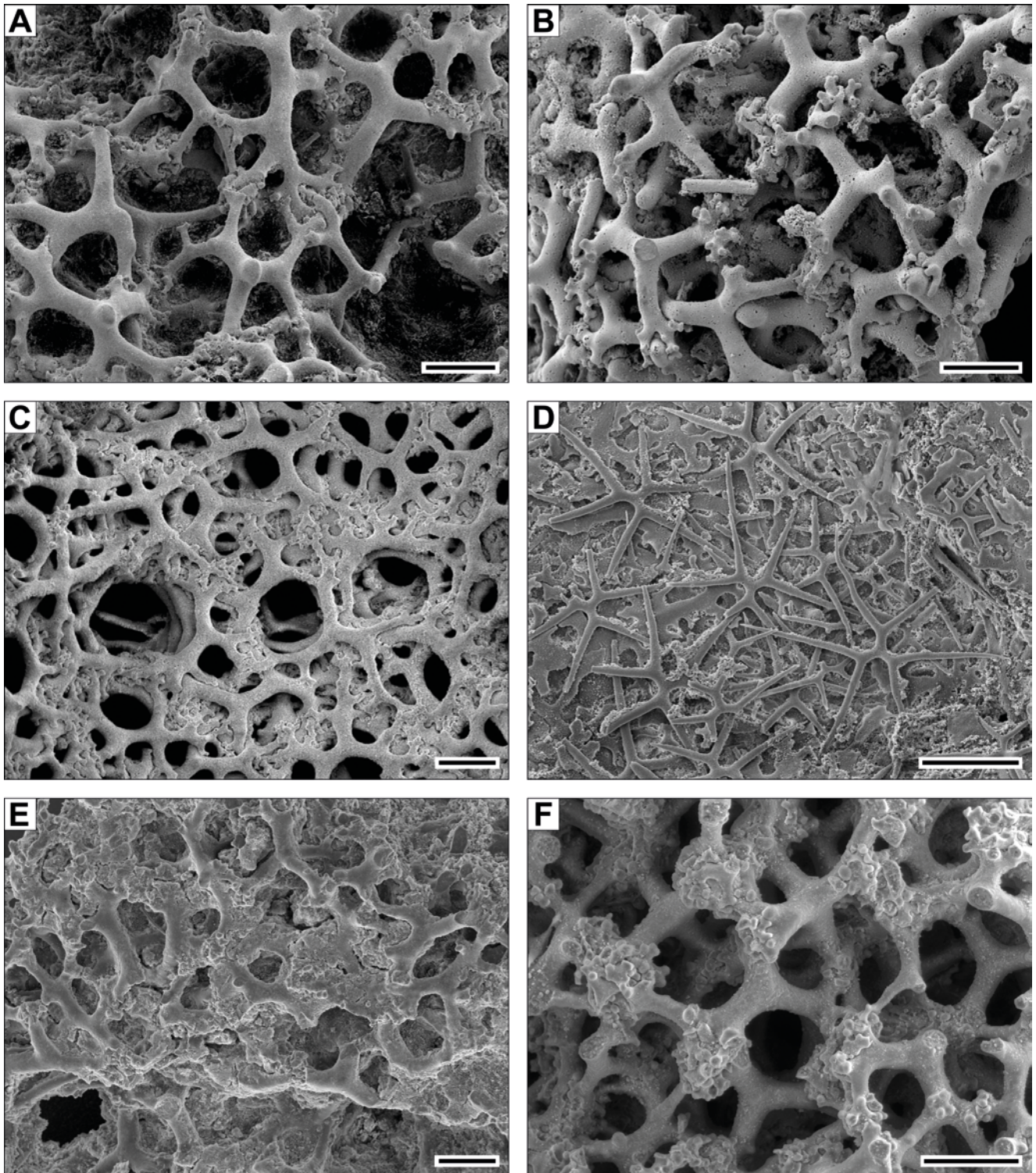


Fig. 11. Skeletons of phymatellid species. A–E. *Jerea quenstedti* Zittel, 1878. A – choanosomal skeleton inside the wall; ULXXV/2T/3, Bełchatów; B – choanosomal skeleton on outer surface of specimen; ULXXV/2T/3, Bełchatów; C – choanosomal network on the surface of exhalant canals; ULXXV/2T/3, Bełchatów; D – ectosomal skeleton consists of dichotriaenes and irregular, flattened spicules; ULXXV/2T/4, Bełchatów; E – poorly preserved desmas of specimen previously described as the holotype of *Thecosiphonia gracilis* Hurcewicz, 1966; ULII/1565, Zbyszycze. F. Choanosomal skeleton of Schrammen's specimen of *Siphonia tubulosa*, housed in the Palaeontological Collection of the University of Tübingen (1854/41). Scale bars represent 200 µm.

without the branched part of clones. In fact, the desmas of these specimens are significantly larger and, similarly as in the specimens of *J. quenstedti* from the Bełchatów area and Germany, have irregularly branched clones reaching a length of up to 400–480 µm.

The group of root-like outgrowths of *J. quenstedti*, with a well-preserved ectosomal skeleton (Fig. 10H), was described by Hurcewicz (1966) as the only representative of the new species *Thecosiphonia gracilis*. These outgrowths, recognized as a group of fine branches fused together, have no axial canals typical for the specimens of the genus *Thecosiphonia* Zittel, 1878 (= *Polyjerea* Fromentel, 1860). Unlike the choanosomal skeleton of *Thecosiphonia* with regular tetracloones forming large, rounded zygoes (see Zittel, 1878, pl. 10 fig. 3), its strongly silicified skeleton (Fig. 11E) consists of large, irregular branched tetracloones connected by poorly developed zygoes (which contradicts the diagnosis and description of *T. gracilis* given by Hurcewicz, 1966). All features of the destroyed specimen, classified by Hurcewicz (1966) as *Aulaxinia ventricosa* Schrammen, 1910, also fully correspond to the characteristics of *J. quenstedti*.

Distribution: Poland (Lelów area: lower Campanian, Bełchatów: early Campanian sponges as redeposited elements in Neogene deposits); Germany (Lower Saxony: lower and upper Campanian).

Genus *Siphonia* Parkinson, 1822 *sensu* Schrammen, 1910
(= *Hallirchoa* Lamouroux, 1821)

Type species: *Siphonia pyriformis* Goldfuss, 1826, p. 16, pl. 6, fig. 7a, designated by Hinde, 1883, p. 63.

Remarks: In this paper, Schrammen's (1910) diagnosis of the genus *Siphonia* is accepted, according to which this phymatellid genus is characterised by small tetracloones, while the depth of spongocoel is variable. According to Schrammen (1910), the tetracloones of *Siphonia* are smooth, but the desmas of one *Siphonia* species illustrated by him (see Schrammen, 1910, text-pl. 4, fig. 10) are poorly tuberculated. Also observations of the present authors indicate that beside smooth tetracloones, weakly ornamented desmas occur in some species of *Siphonia*.

Representatives of *Hallirchoa* Lamouroux, 1821 differ from *Siphonia* only by possessing a body with lateral ribs, and this taxon is often recognized as the subgenus or even synonym of *Siphonia* (e.g., Schrammen, 1910; Moret, 1926; Reid, 2004); the second view was accepted here.

Many researchers of Cretaceous sponges, on the basis of Zittel's (1878) diagnosis of *Siphonia*, considered that the most characteristic feature of this genus is the deep spongocoel while features of the desmas were omitted. In effect, a large number of specimens representing quite different groups of sponges (e.g., the Theonellidae or Rhizomorina) were classified as species of *Siphonia*.

Siphonia costata (Lamouroux, 1821)
Fig. 12A, B

1821 *Hallirchoa costata* – Lamouroux, p. 72, pl. 78, fig. 1.

1960 *Siphonia (Hallirchoa) costata* Lamouroux – Defretin-Lefranc, pp. 109–110, pl. 18, fig. 3 [cum syn.].

Material: 1 specimen from Bełchatów (ULXXXV/28/1).

Description: The strongly silicified specimen is a fragment of a large sponge, over 180 mm in height and ca. 120 mm in diameter, with a slightly narrowing apex (Fig. 12A, B). Lateral surface with preserved four longitudinal lobes (probably there were 6–7 lobes on the whole sponge). Inhalant canal openings polygonal, 1.2–1.8 mm in size, densely distributed on outer surface, at ca. 1 mm intervals. In outer part of choanosomal skeleton inhalant canals straight and perpendicular to the surface; deeper invisible. Deep, tube-like spongocoel, 19 mm in diameter, with surface covered by oval exhalant canal openings, 2–2.5 mm in size, arranged more or less alternately. Wide exhalant canals, up to 3 mm in diameter, running obliquely.

Choanosomal skeleton almost completely dissolved. Single, poorly visible tetracloones on the outer surface of sponge having smooth clones, 150–200 µm long. Rare tetracloones preserved on surface of spongocoel slightly larger, with clones up to 250–300 µm in length. No ectosomal megascleres preserved.

Remarks: *Siphonia costata* is a polymorphic species (e.g., Michelin, 1847; Hinde, 1883; Moret, 1926; Defretin-Lefranc, 1960), especially common in the Cenomanian of western Europe. So far, it was not known neither from the Campanian nor from Poland.

The shape of the body of the specimen described here and also other known representatives of *S. costata* clearly differ from the two Campanian species of *Siphonia* with lateral ribs, described in the literature also as *Hallirchoa*, e.g., *S. sexplicata* (Roemer, 1864) and *S. fusiformis* (Schrammen, 1910). Both these species are characterised by a very elongated body and narrow angular ribs (Roemer, 1864; Griepenkerl, 1889; Schrammen, 1910).

Distribution: Poland (Bełchatów area: early Campanian sponges as redeposited elements in Neogene deposits); France (Normandy: Cenomanian, ?Paris Basin: Coniacian); England (Warminster: Upper Green Sand, Cenomanian; Norfolk: Red Chalk, Albian).

Siphonia micropora Schrammen, 1910
Figs 12C, 13A–C

1910 *Siphonia micropora* – Schrammen, pl. 2, figs 9, 10, text-pl. 4, fig. 10.

1966 *Aulaxinia fallax* Schrammen – Hurcewicz, pp. 37–38.

Material: 1 specimen from Bełchatów (ULXXV/29/1) and 2 specimens from Gnatowice (ULII/2, 20).

Description: The largest club-like specimen, without a basal part and with a destroyed apex, is 74 long and 48 in diameter (Fig. 12C). Locally, outer surface with shallow variously oriented grooves. Round canal openings, 0.3–0.8 mm in diameter, are spaced at 0.8–2 mm intervals. Straight inhalant canals perpendicular or oblique to the surface of a sponge. Straight exhalant canals, 0.5–1 mm wide, loosely arranged

and parallel to axis of a sponge. Exhalant canal openings (visible only on the bottom of spongocoel of one destroyed specimen) of similar size and spaced at 1.5–2 mm.

Very dense choanosomal network on the surface of specimens consisting of small tetracloones with irregular branched clones, 150–250 µm long (occasionally up to 300 µm long) and 50–60 µm thick (Fig. 13A, B). Sparsely arranged flattened tubercles, up to 30 µm in size, sometimes occurring on clones. Short, tuberculated zygomeres form irregular zygomeres, usually 160–200 µm wide and 200–500 µm long. Tetracloones with smooth clones and tuberculated zygomeres dominating in deeper, poorly preserved part of choanosomal skeleton. Small remains of compact layer covering the choanosomal skeleton containing flattened, irregular branched spicules, up to 100–150 µm in size, and rare crushed dichotriaenes (Fig. 13C). Dichotriaenes small with clads up to 100 µm in length. Protoclads, ca. 25 µm wide, slightly shorter than deuteroclads.

Remarks: The important features that distinguish this species from *Siphonia tubulosa* indicated by Schrammen (1910) are the smaller size of inhalant and exhalant canal openings,

which are less densely distributed. Analysis of the skeletons of specimens of both species carried out here shows that the tubercles sometimes occur on the unbranched part of clones of *S. micropora*, while clones in *S. tubulosa* are always smooth.

Specimens with destroyed basal and apical part from the Miechów Synclinorium, included here to *Siphonia micropora*, were previously described by Hurcewicz (1966) as *Aulaxinia fallax* Schrammen. In contrast to the latter, the tetracloones of the discussed specimens are small with branched clones.

Distribution: Poland (Proszowice area: upper Campanian, Belchatów: early Campanian sponges as redeposited elements in Neogene deposits); Germany (Lower Saxony: lower Campanian).

Siphonia sp.

Figs 12D–F, 13D

1966 *Jerea pyriformis* Lamouroux – Hurcewicz, pp. 46–47, pl. 4, figs 1–3.

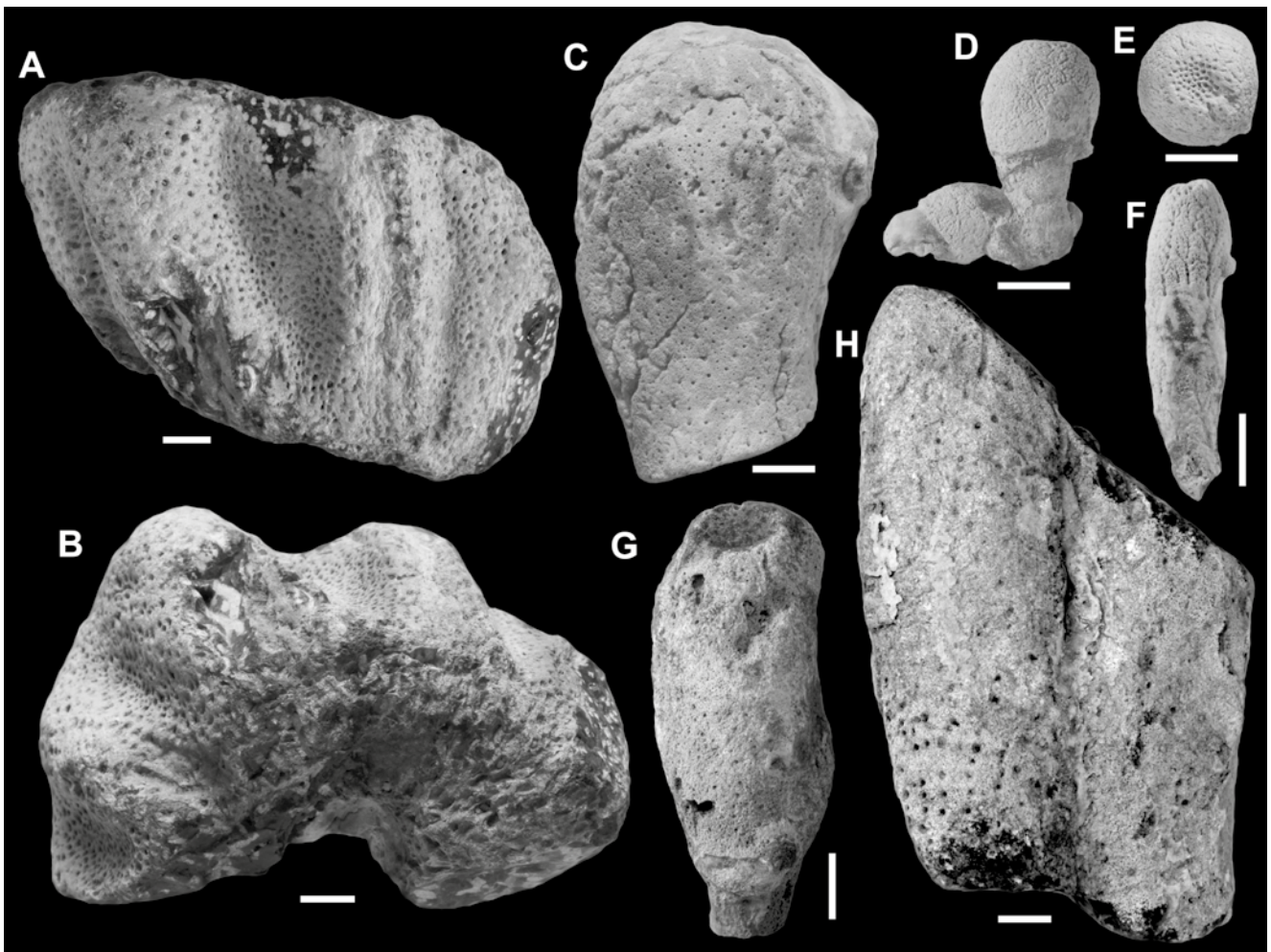


Fig. 12. Specimens of phymatellid species. **A, B.** *Siphonia costata* (Lamouroux, 1821); A – lateral view of specimen; ULXXV/2T/1, Belchatów; B – upper view of the same specimen. **C.** *Siphonia micropora* Schrammen, 1910; lateral view of specimen previously described as *Aulaxinia fallax* Schrammen, 1910; ULII/2, Gnatowice. **D–F.** *Siphonia* sp.; specimens previously described as *Jerea pyriformis* Lamouroux, 1821; D – lateral view of specimen ULII/1624, Pniaki; E – upper view of the same specimen; F – lateral view of elongated specimen; ULII/382, Pniaki. **G, H.** *Polyiera torgeri* (Schrammen, 1910); G – lateral view of single specimen; ULXXV/24T/3, Belchatów; H – fragment of specimen consisting of two individuals ULXXV/24T/2, Belchatów. Scale bars represent 1 cm.

Material: 3 specimens from Pniaki (II/373, 382, 1624).

Description: Small, club-like or near cylindrical sponges, not exceeding 45 mm in height (Fig. 11D–F). Numerous exhalant canals, 0.3–0.4 mm in diameter, densely packed in very shallow depression at the top of the sponge, which is

surrounded by short furrows. Lateral surface with irregularly arranged shallow grooves and sparsely distributed inhalant canals, 0.2–0.3 mm in diameter.

Choanosomal skeleton (preserved only in outer part of specimens) very compact, consisting of small tetracles,

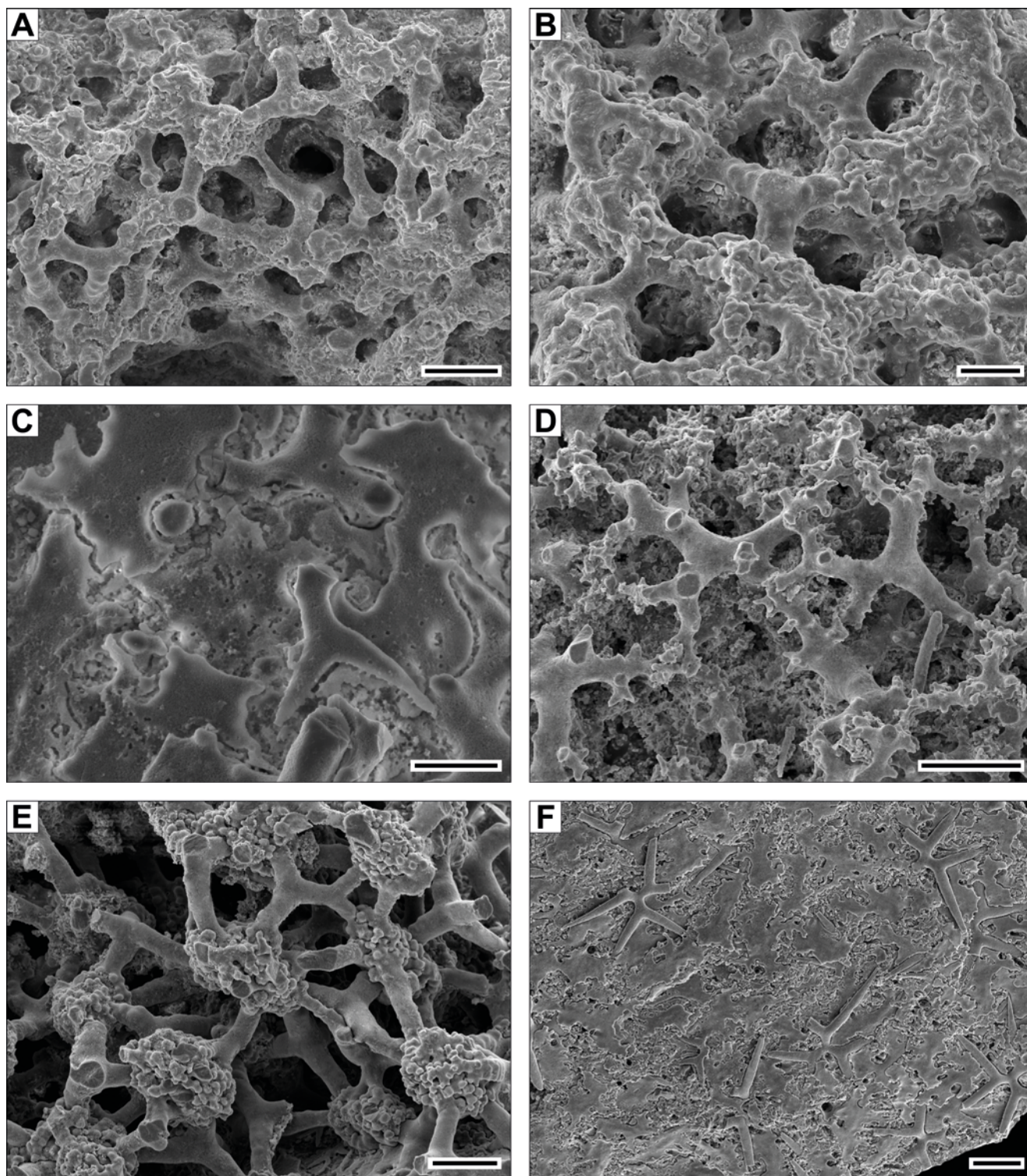


Fig. 13. Skeletons of phymatellid species. **A–C.** *Siphonia micropora* Schrammen, 1910; specimen previously described as *Aulaxinia fallax* Schrammen, 1910; ULII/20, Gnatowice; **A, B** – choanosomal skeleton; **C** – ectosomal skeleton with crushed dichotriaenes and irregular flat spicules. **D.** *Siphonia* sp.; choanosomal skeleton of specimen previously described as *Jerea pyriformis* Lamouroux, 1821; ULII/1624, Pniaki. **E, F.** *Polyierea torgeri* (Schrammen, 1910); **E** – choanosomal skeleton; ULXXV/24T/1, Bełchatów; **F** – ectosomal skeleton with dichotriaenes and irregular, flattened spicules; ULXXV/24T/1, Bełchatów. Scale bars represent 200 μm (**A, D–F**), 100 μm (**B**) and 50 μm (**C**).

with irregularly forked clones, 150–300 µm long and 60 µm thick (Fig. 13D). Short, poorly branched zygomes with small conical outgrowths, occasionally appearing also on the distal part of the clones. Ectosomal skeleton consisting of dichotriaenes with cladomes 250–300 µm in diameter. Deuteroclads, slightly longer than protoclads, diverge at 92–94°. Densely packed small, flattened spicules, occurring under and between dichotriaenes, usually 150–250 µm in size.

Remarks: The specimens from the Lelów area presented here were previously described by Hurcewicz (1966) as *Jerea pyriformis* Lamouroux. In contrast to that species co-occurring in the material studied, they show very narrow exhalant canals and very small, irregular tetracles. The sizes of choanosomal and ectosomal spicules and all others features of these specimens fully correspond to the genus *Siphonia* (see Schrammen, 1910). These specimens are distinguished from other known species of this genus by tetracles with small conical outgrowths. A new species was not proposed, owing to the small number of specimens that may be juvenile individuals, as indicated by the undeveloped spongocoel and very small size of sponges.

Distribution: Poland (Lelów area: lower Campanian).

Genus *Polyierea* Fromentel, 1860 (= *Polyjerea* Pomel, 1847; *Thecosiphonia* Zittel, 1878)

Type species: *Jerea gregarea* Michelin, 1847, p. 134, pl. 38, fig. 1, designated by Fromentel, 1860, p. 33.

Remarks: Schrammen (1910) pointed out that the differences between *Polyjerea* Pomel, 1847 and *Thecosiphonia* Zittel, 1878 are negligible, and distinguishing both genera is problematic. In the opinion of the present authors, the features distinguishing them indicated by Moret (1926), i.e., the presence of a shallow bow-like spongocoel and a thicker ectosomal layer in *Thecosiphonia*, are not significant enough to justify the distinctiveness of these genera. Therefore, the authors share Reid's (2004) view and consider *Thecosiphonia* as a synonym for *Polyjerea*.

Polyierea torgeri (Schrammen, 1910)

Figs 12G, H, 13E, F

- 1910 *Thecosiphonia torgeri* – Schrammen, pp. 83–84.
 1963 *Thecosiphonia torgeri* Schrammen – Wagner, p. 180, pl. 25, figs 3, 4.
 1967 *Thecosiphonia torgeri* Schrammen – Lagneau-Hérenger, pp. 84–86, pl. 1, fig. 4.
 1993 *Thecosiphonia togeri* Schrammen – Jahnke and Gasse, pl. 5, fig. 2

Material: 8 specimens from Bełchatów (ULXXV/24T/1–8).

Description: Specimens cylindrical or club-like, with destroyed base (Fig. 12G). They reach 40 mm in diameter and 92 mm in length. The largest fragment consists of two individuals, 38 mm and 104 mm long, respectively, joined together laterally (Fig. 12H). Apex (preserved only in one specimen) slightly rounded with a group of ca. 20 exhalant canal openings, 1.3–2.2 mm in diameter. Vertical exhalant canals running towards the base. Inhalant canal openings,

0.5–1 mm in diameter, irregularly distributed, but in lower part of a few specimens arranged in indistinct vertical rows. Short inhalant canals perpendicular or slightly oblique to the outer surface of sponge.

Choanosomal tetracles with smooth, straight or slightly arched clones, 220–330 µm long and 60–90 µm thick (Fig. 13E). Occasionally clones forked and up to 350 µm in length. Poorly branched zygomes with small, prominent tubercles. Terminal zygoses ellipsoidal or elongated, 180–200 µm x 350–420 µm in size. On the wall of exhalant canals, very compact network consisting of large tetracles with clones up to 480 µm long, articulated by large (up to 800 µm in size) irregular zygoses. Fragmentarily preserved thick and smooth ectosomal layer is visible in various places on the outer surface of the sponges, except for their apical part. This layer continues between two fused individuals. Ectosomal dichotriaenes with clads 400–420 µm long, occurring among densely packed flattened spicules (up to 400 µm in size) with heavily indented border (Fig. 13F). Deuteroclads of dichotriaenes much longer than protoclads and diverge at 90–100°.

Remarks: Exhalant canal openings, noted in representatives of *Polyierea torgeri*, are 1–1.5 mm in diameter (Schrammen, 1910; Wagner, 1963), while in the largest specimen described here, they reach 2.2 mm in diameter. The known specimens of *P. torgeri* usually consist of two or more fused together individuals growing out of a joint base, but solitary specimens are also noted (Schrammen, 1910; Wagner, 1963; Lagneau-Hérenger, 1967). In the material studied only one specimen comprises two fused individuals. In others the basal part is destroyed and it is impossible to determine whether they grew singly or in groups. It is also impossible to unequivocally state whether the lack of the ectosomal layer in the upper part of the specimens is the result of its damage, or whether this layer was not developed in this part, as in the specimens from Germany and France. The skeleton of *P. torgeri* has not been illustrated so far, but the features of the ectosomal and choanosomal spicules observed in the material studied correspond to descriptions of the megascleres of this species from Germany (Schrammen, 1910; Wagner, 1963).

Owing to the shape of the body and the arrangement of exhalant canals, single specimens of *P. torgeri* from Bełchatów are similar to specimens of *Jerea clavata* Počta, 1892 described by Defretin-Lefranc (1960, pp. 104–105, pl. 17, fig. 1) or to some juvenile individuals of *J. quenstedtii* Zittel, 1878 with a poorly developed spongocoel (Schrammen, 1910, pl. 2, fig. 4). In contrast to the representatives of *Jerea*, the specimens studied show a thicker ectosomal layer, more regular choanosomal tetracles and well-developed terminal zygoses.

Distribution: Poland (Bełchatów: early Campanian sponges as redeposited elements in Neogene deposits); Germany (Bavaria: lower Turonian, Saxony-Anhalt: Turonian), France (Department Drôme: Turonian).

Genus *Acrochordonia* Schrammen, 1910

Type species: *Acrochordonia ramosa* Schrammen, 1901, p. 7, pl. 1, fig. 8, pl. 5, fig. 1, by monotypy.

Remarks: Reid (2004) included the genus *Acrochordonia* to the family Theonellidae, because of the ornamentation tetracles. However, the presence of ectosomal dichotriaenes proves assignment of it to the family Phymatellidae (Pisera, 2002; Pisera and Lévi, 2002b).

Acrochordonia ramosa Schrammen, 1901

Figs 14A–D, 15A, B

- 1901 *Acrochordonia ramosa* – Schrammen, p. 7, pl. 1, fig. 8, pl. 5, fig. 1.
 1910 *Acrochordonia ramosa* Schrammen – Schrammen, p. 96, pl. 4, figs 5, 6, text-pl. 6, fig. 10.
 1926 *Acrochordonia ramosa* Schrammen – Moret, p. 175, pl. 16, fig. 10, text-fig. 68.
 1993 *Acrochordonia ramosa* Schrammen – Gruber, p. 32, pl. 4, figs 6, 7.
 2006 *Acrochordonia ramosa* Schrammen – Świerczewska-Gładysz, p. 277, fig. 40f.

Material: 15 specimens from Bełchatów (ULXXV/11T/1–15).

Description: Irregularly branched sponges, up to 62 mm in height (Fig. 14A–D). Lateral branches, 11–33 mm wide, cylindrical, club-like, bulbous or leaf-like with truncated

or rounded edge. Inhalant canal openings, 0.5–0.7 mm in size, are evenly distributed on all surfaces at 1.2–1.6 mm intervals. Inhalant canals perpendicular to the surface of the sponge, but may be oblique near bifurcation. Exhalant canal openings, 1–1.2 mm in diameter, arranged in groups of ca. 40–50, which lie in very shallow to deep, bowl-like depressions, 9–15 mm in size. These groups located on the lateral surface of branches, usually near bifurcation or their apex (Fig. 14A, B, D). Canal openings, located on the periphery of the group leading to canals oblique or almost parallel to the surface. Others exhalant canals running deeply into the branches.

Choanosomal skeleton comprising tetracles with irregularly branched clones, 250–430 μm long and 45–75 μm thick, covered by mushroom-like tubercles, up to 45 μm in diameter (Fig. 15A, B). Short zygomeres interlocking with tubercles on the lateral and upper side of the clones of neighbouring desmas. Desmas on surface of choanosomal skeleton, especially in lower part of sponges, more massive (up to 90–110 μm thick) with larger (up to 60 μm in diameter) and more densely arranged tubercles. Ectosomal dichotriaenes with cladomes up to 650 μm long.

Remarks: All the features of the specimens from Bełchatów described here fully correspond to the diagnosis of *Acrochordonia ramosa*. This species, known

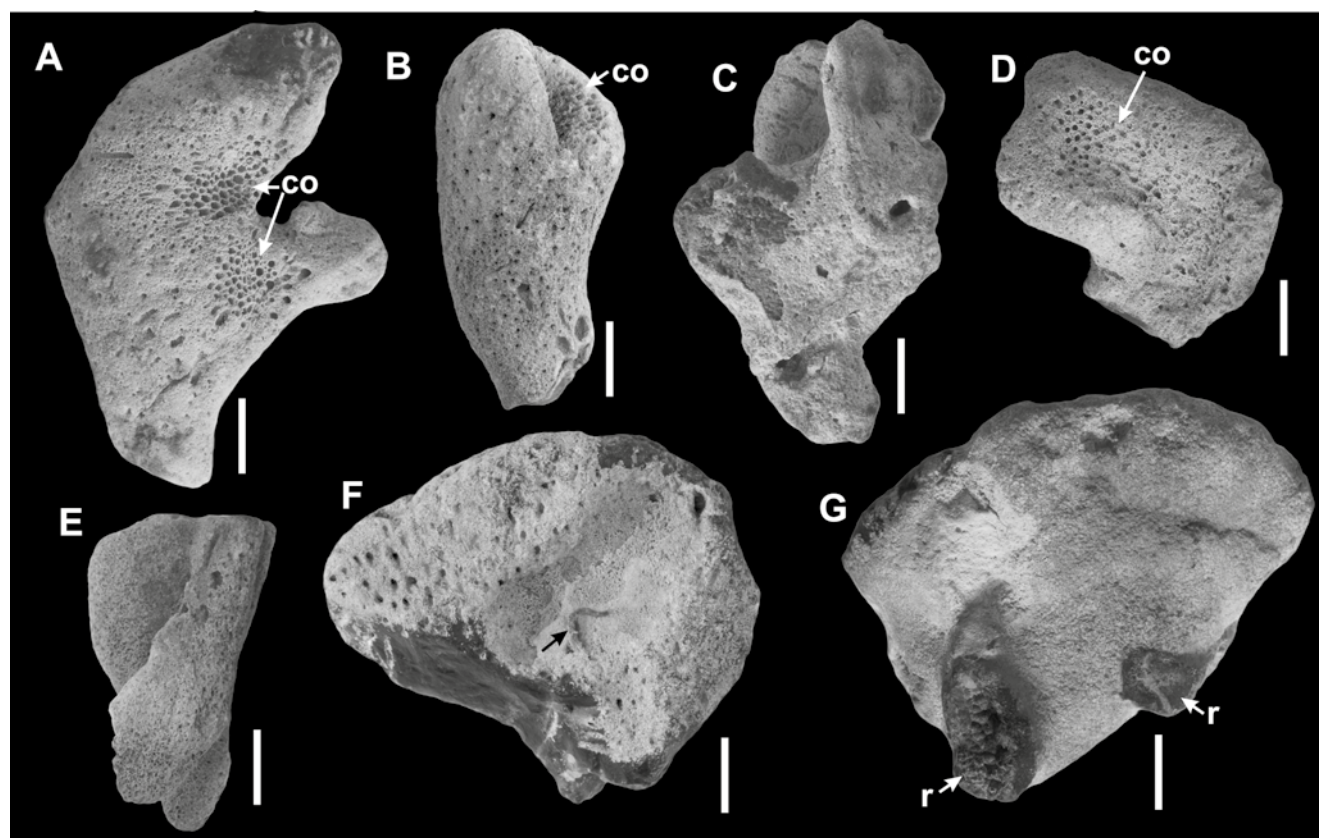


Fig. 14. Specimens of phymatellid species. A–D. *Acrochordonia ramosa* Schrammen, 1901; A – lateral view of sponge with two groups of exhalant canal openings; ULXXV/11T/2, Bełchatów; B – branch with group of exhalant canal openings situated in depression near top; ULXXV/11T/3, Bełchatów; C – lateral view of specimens; ULXXV/11T/4, Bełchatów; D – inner side of leaf-like branch with exhalant canal openings; ULXXV/11T/5, Bełchatów. E–G. *Procorallistes polymorphus* Schrammen, 1901; E – fragment of thin-walled sponge; ULXXV/27T/5, Bełchatów; F – fragment of thick-walled sponge with attached *Serpula* (black arrow); exhalant canal openings visible in places without ectosomal skeleton; ULXXV/20T/3, Bełchatów; G – lateral view of specimen with broken thick outgrowths (r); ULXXV/20T/1, Bełchatów. Scale bars represent 1 cm.

from the Maastrichtian of the middle Vistula River valley, has not been recorded yet in the Campanian of Poland. Hurcewicz (1966, pp. 106–107) described a dichotomously branched specimen from the Miechów Synclinorium as

Acrochordonia cf. *ramosa*, but the skeleton characteristics of this species indicate that it represents a corallistid sponge (possibly a root-like outgrow of *Schrammeniella scytali-forme* – compare Świerczewska-Gładysz, 2017, fig. 10E).

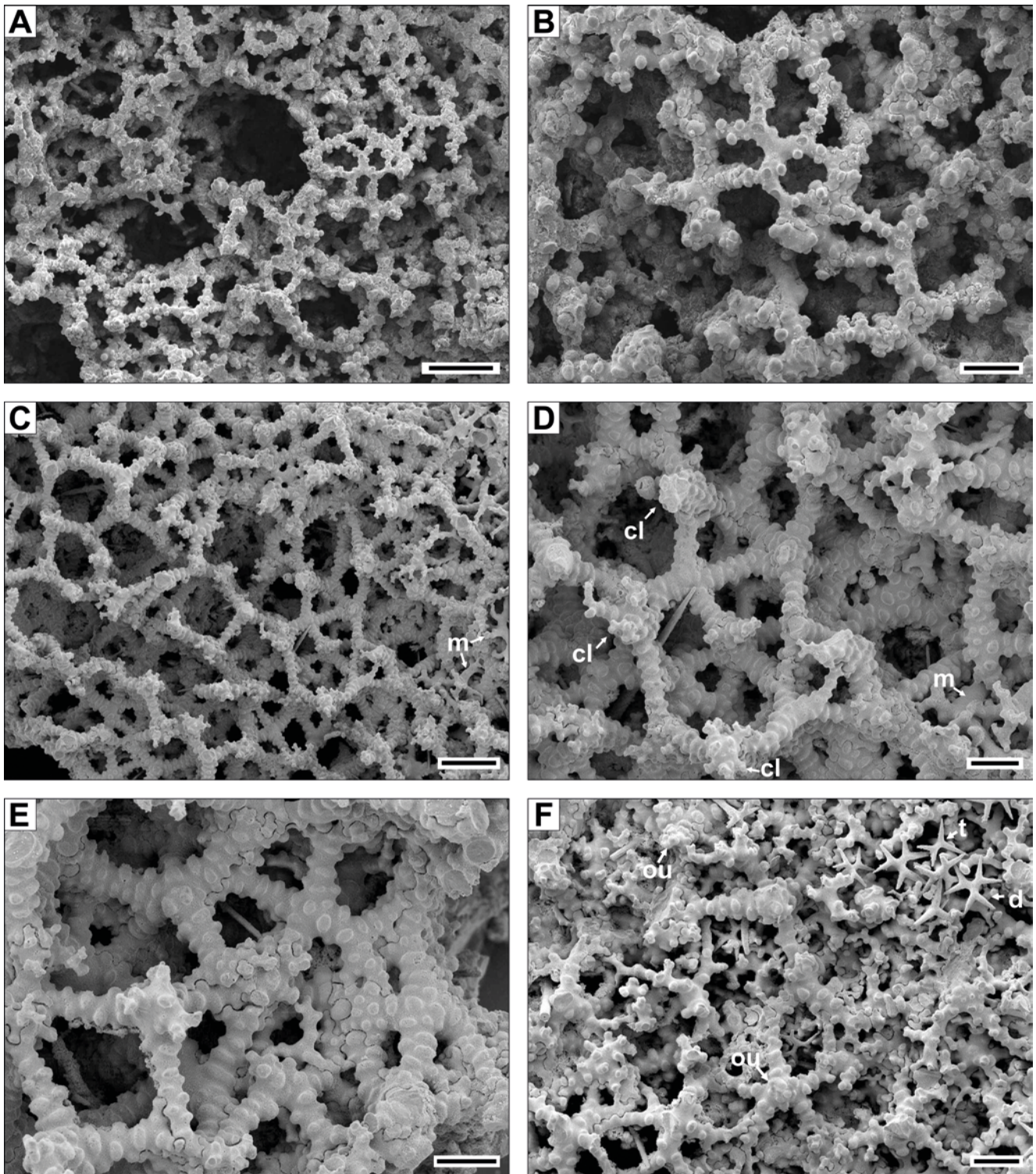


Fig. 15. Skeletons of phymatellid species. **A, B.** *Acrochordonia ramosa* Schrammen, 1901; ULXXV/11T/1, Bełchatów; A – choanosomal skeleton on outer surface of specimen with inhalant canal openings; B – detail of choanosomal skeleton. **C–F.** *Procorallistes polymorphus* Schrammen, 1901; C, D – inner surface of choanosomal skeleton consisting of massive tetraclones with one long clone (cl) directed outwards, and rare smooth or poorly tuberculated megascleres (m); ULXXV/20T/4, Bełchatów; E – choanosomal tetraclones within central part of wall; ULXXV/20T/4, Bełchatów; F – choanosomal desmas, often with one clone reduced to tuberculate outgrow (ou) and ectosomal regular dichotriaenes (d) and few modified triaenes (t) preserved on inhalant surface of sponge; ULXXV/20T/2, Bełchatów. Scale bars represent 500 μm (A, C), 200 μm (B, D–F).

Distribution: Poland (Bełchatów area: early Campanian sponges as redeposited elements in Neogene deposits, middle Vistula River valley: uppermost Maastrichtian); Germany (Lower Saxony: Campanian); France (Saint Cyr areas: Santonian).

Genus *Procorallistes* Schrammen, 1901

Type species: *Procorallistes polymorphus* Schrammen, 1901, p. 15, pl. 1, fig. 10, pl. 5, fig. 8; designated by Laubenfels, 1955, p. 45.

Remarks: Schrammen (1901, 1910) and subsequent researchers placed the genus *Procorallistes* into the family Corallistida Sollas, 1888, characterised by choanosomal skeleton consisting of dicranoclones (tuberculate monaxial desmas), while desmas of the specimens of the type species *Procorallistes polymorphus* from the Schrammen Collection are tuberculate tetracloes (pers. comm. A. Pisera, 2017). The presence of dichotriaenes in *Procorallistes* indicates its assignment to the family Phymatellidae.

Procorallistes polymorphus Schrammen, 1901

Figs 14E–G, 15C–F

- 1901 *Procorallistes polymorphus* – Schrammen, p. 15, pl. 1, fig. 10, pl. 5, fig. 8.
- 1901 *Procorallistes tuberosus* sp. nov. – Schrammen, p. 15, pl. 1, fig. 11.
- 1910 *Procorallistes polymorphus* Schrammen – Schrammen, p. 69, pl. 20, figs 1, 2; text-pl. 3, fig. 3.
- 1926 *Procorallistes polymorphus* Schrammen – Moret, p. 113, text-fig. 41.
- non 1960 *Procorallistes polymorphus* Schrammen – Defretin-Lefranc, p. 120, text-fig. 40.
- 1963 *Procorallistes polymorphus* Schrammen – Wagner, p. 202.
- 1993 *Procorallistes polymorphus* Schrammen – Jahnke and Gasse, pl. 8, fig. 6, pl. 9, fig. 1. 2002 *Procorallistes polymorphus* Schrammen – Pisera, fig. 8b.

Material: 14 specimens from Bełchatów (ULXXV/20T/1–14) and 2 from Zbuczycze (ULIIB/33, 34).

Description: Cup-like or irregularly folded plate-like sponges (Fig. 14E–G). The most complete specimen, 58 mm high and 66 mm wide, has remains after broken massive root-like outgrowths in the lower and middle part of the sponge (Fig. 14G). Wall thickness varies widely among individual specimens, from 6 mm to 20 mm. In the most robust sponges, locally the wall is thickened, up to 25 mm thick (Fig. 14F). Canal openings on both surfaces of the choanosomal skeleton small, 1–1.5 mm in diameter, distributed randomly without clear patterns. They are often invisible, masked by a well-preserved piece of the ectosomal skeleton. Inhalant and exhalant canals are long, straight or slightly arched, perpendicular to the wall or slightly oblique.

Choanosomal tetracloes having clones, 100–180 μm thick and 200–500 μm long (Fig. 15E). They are terminated

by short, strong zygomies, which clasp clones of adjacent desmas. Clones heavily ornamented with smooth mushroom-shaped tubercles. Round or elongated heads of the tubercles measure 50–70 μm in diameter; long axis of large, elongated tubercles up to 90 μm . Desmas on inner surface of choanosomal skeleton often having one long clone directed outwards (Fig. 15C, D). Dense network on outer surfaces of the choanosomal skeleton consists of smaller tetracloes (average 500 μm in size) with irregularly branched clones (Fig. 15F). Occasionally, tetracloes having one clone reduced to short, tuberculate outgrow, up to 150 μm long. Thin, irregularly branched spicules, up to 1000 μm in length, smooth or poorly tuberculated, occurring between tetracloes (Fig. 15C, D). Smooth dichotriaenes have cladomes up to 280–300 μm in size (Fig. 15F). Deuteroclads are about twice as long as the protoclads. Occasionally occur modified dichotriaenes without one ray or triaenes with undivided rays (Fig. 15F). Conical rhabds short, not exceeding 400 μm in length in large dichotriaenes.

Remarks: Specimens of *Procorallistes polymorphus* from various stages of the Cretaceous in Europe are characterised by a great diversity of shape and wall thickness. Thin-walled, irregular specimens, similar to some crushed specimens from Poland, were described by Moret (1926) from the Santonian of France. The wall thickness of cup-like or ear-like specimens from Germany is 6–10 mm (Schrammen, 1910) or 12–14 mm (Wagner, 1963). Such specimens are the most common in the material studied, whereas the wall of three crushed specimens from Bełchatów is extremely thick and measures 20–25 mm.

The size, shape and ornamentation of the desmas of *P. polymorphus* are diversified. Our observations have shown that unmodified tetracloes (see Moret, 1926; Jahnke and Gasse, 1993) occur in the central part of the sponge wall. Desmas with a long outgrow (see Schrammen, 1910), being modified clones, were noted only on the inner surface of the choanosomal skeleton. They have often remains after reduced zygomies, which have not been documented so far. In turn, small desmas with short outgrowths (see Schrammen, 1910) were recognized on the outer surface.

Defretin-Lefranc (1960) described one specimen from the Turonian of France as *P. polymorphus*. This poorly preserved specimen has no ectosomal megascleres and its poorly tuberculated desmas are very regular tetracloes, twice smaller than the desmas of *P. polymorphus*. Contrary to the lateral zygomies occurring in the skeletal network of *P. polymorphus*, these tetracloes form regular, spherical zygomies situated terminally. Therefore, in the opinion of the present authors, the assignment of the discussed specimen to *P. polymorphus* is not correct.

P. polymorphus has not been noted previously from Poland, however among the material of F. Bieda, containing Campanian sponges from the Kraków area, one specimen (no. A-I-1/34/14) from Podgórze (at present a district of Kraków) figured in the museum collection as the pleromid species *Heterostinia obliqua* (Benett, 1831) shows all features characteristic for *P. polymorphus* Schrammen, 1910.

Distribution: Poland (Bełchatów: early Campanian sponges as redeposited elements in Neogene deposits, Lelów area: lower Campanian, Kraków area: sponges redeposited into

Neogene deposits); Germany (Bavaria: lower Turonian, Lower Saxony: Turonian, Campanian); France (Nice and Saint Cyr areas: Santonian); Spain (Cantabria: lower Albian).

TAXONOMIC COMPOSITION OF CAMPAIAN PHYMATELLIDS FROM MIECHÓW AND MOGILNO-ŁÓDŹ SYNCLINORIA

In the material studied from the Campanian of the Miechów and Mogilno-Łódź synclinoria, 17 species, included one new *Kalpinella fragilis* sp. nov., were distinguished (Tab. 2). Among them, 8 species such as *Craterella auricula* Schrammen, 1910, *Bolospongia globata* Hinde,

1883, *Phymatella tuberosa* (Quenstedt, 1878), *Jerea quenstedti* Zittel, 1878, *Siphonia costata* (Lamouroux, 1821), *Siphonia micropora* Schrammen, 1910, *Polyjerea torgeri* (Schrammen, 1910) and *Procorallistes polymorphus* Schrammen, 1901, were reported from Cretaceous of Poland for the first time.

Hurcewicz (1966) in material from the Campanian of Miechów Synclinorium distinguished 17 phymatellid species, but a review of this collection indicates the presence of only eight species, wherein the taxonomic position of some museum specimens, especially derived from the Skrajniwa section, has not been determined, owing to their poor preservation. All strongly silicified specimens included by Hurcewicz (1966) to *Siphonia tulipa* Zittel, 1878 have desmas preserved only on surface of deep spongocoel, which are rhizoclones and they were incorrectly classified into

Table 2

Stratigraphic and palaeogeographic distribution of phymatellid species studied here in the Cretaceous of Europe.

Phymatellid species	Aptian	Albian	Cenom.	Turon.	Coniac.	Santon.	Campan.	Maastr.
<i>Acrochordonia ramosa</i> Schrammen, 1910						F	G	P
<i>Aulaxinia sulcifera</i> (Roemer, 1864)	S			?E	F, ?E	F, ?E	?EG	G, D, P, ?E
<i>Bolospongia globata</i> Hinde, 1883							E	
<i>Craterella auricula</i> Schrammen, 1910	S				F	F	G	
<i>Jerea pyriformis</i> Lamouroux, 1821			F	FG	F			
<i>Jerea quenstedti</i> Zittel, 1878							G	
<i>Kalpinella fragilis</i> sp. nov.								
<i>Kozłowskispongia bulbosa</i> Hurcewicz, 1966								
<i>Phymatella bulbosa</i> Zittel, 1878						F	G	G, P
<i>Phymatella tuberosa</i> (Quenstedt, 1878)							G	
<i>Phymoracia verrucosa</i> (Roemer, 1864)							G	
<i>Polyjerea torgeri</i> Schrammen, 1910				FG				
<i>Procorallistes polymorphus</i> Schrammen, 1901		S		G		F	G	
<i>Siphonia costata</i> (Lamouroux, 1821)		E	F, E		F			
<i>Siphonia micropora</i> Schrammen, 1910							G	
<i>Siphonia</i> sp.								
<i>Turononia variabilis</i> Michelin, 1847				F	F	?E	G, E	?E, P

■ occurrence in the European Basin

▨ occurrence in the Mogilno-Łódź and Miechów synclinoria

▨ occurrence only in the Miechów Synclinorium

▨ occurrence only in the Mogilno-Łódź Synclinorium

E – England (after Hinde, 1883); F – France (after Moret, 1926; Defretin-Lefranc, 1960; Lagneau-Hérenger, 1967); G – Germany (after Roemer, 1864; Schrammen 1910, 1924; Nestler, 1961; Wagner, 1963; Ulbrich, 1974; Schneider *et al.*, 2013); P – Poland, middle Vistula River valley (after Świerczewska-Gładysz, 2006); S – Spain (after Lagneau-Hérenger, 1962); distribution of species in the Miechów Synclinorium after Bieda (1933) and Hurcewicz (1966) complemented by data from the present study.

Phymatellidae. In the opinion of the present authors, they are juvenile individuals of *Aulosoma radiciformis* (Phillips, 1829) and/or *Scyrtalia turbinata* Roemer, 1864. A single specimen described by Hurcewicz (1966) as *Phymatella bulbosa* Zittel, 1878, also turned out to be a representative of the *Rhizomorina* Zittel, 1878.

The analysis of the details of skeletons of some other specimens, included by Hurcewicz (1966) in various species, *Siphonia tubulosa* (Roemer, 1840), *Aulaxinia ventricosa* Schrammen, 1910 and new species *Tecosiphonia gracilis*, indicated that their megascleres are identical with other phymatellids species *Jerea quenstedti*. All other features of these discussed specimens also correspond to the diagnosis of *Jerea quenstedti*, which allows to include them in this species and recognize *Tecosiphonia gracilis* as its junior synonym. Part of specimens described by Hurcewicz (1966) as *Siphonia pyriformis* Goldfuss, 1833 and *Callopegma ficoideum* Hinde, 1883 were classified here as *Bolospongia globata*, while all specimens of *Aulaxinia falax* Schrammen, 1910 as *Siphonia micropora* Schrammen, 1910. In turn, *Phymatella irregularis* Hurcewicz, 1966 appears to be a junior synonym of *Phymatella bulbosa* (Świerczewska-Gładysz, 2006). The present authors accepted the new genus and new species *Kozłowskispongia bulbosa* proposed by Hurcewicz (1966), but this taxon was not found in the material collected by them. The verification of museum collection of F. Bieda from the Kraków area showed that only one phymatellid species in this material is *Procorallistes polymorphus*, represented by only one previously undescribed specimen.

Among 8 species distinguished by the authors in material from the lower Campanian of Miechów Synclinorium, 7 are also noted in lower Campanian sponge assemblage from Miocene gravels, where additionally 7 other phymatellid species were recognized (Tab. 2). Greater taxonomic diversity of early Campanian phymatellids from Bełchatów than the Miechów Synclinorium may be the result of noticeably larger numbers of specimens collected from the gravels, which are recently more accessible to the research than the outcrop of the lower Campanian in the Miechów Trough. In the upper Campanian of Miechów Synclinorium only 5 phymatellid species were noted. Except mentioned above *Kozłowskispongia bulbosa*, all others are known also from early Campanian assemblages (Tab. 2).

Two species: *Phymoracia verrucosa* (Roemer, 1864) and *Bolospongia globata* Hinde, 1883, occurring in phymatellid sponge assemblages from the Campanian of Poland, were known so far only from a few specimens. Stratigraphic range of these species and also *Phymatella tuberosa* and *Jerea quenstedti* is very narrow and limited to the Campanian (Tab. 2). Most of the other phymatellids species described here are known mainly from Campanian of western Europe, especially from the Lower Saxony (Schrammen 1910, 1924), but they are also noted in other Cretaceous sections (Tab. 2). Only *Polyjerea torgeri* (Schrammen, 1910) and *Siphonia costata* (Lamouroux, 1821) were known hitherto exclusively from older stages of the Upper Cretaceous, from the Turonian of Bavaria and Saxonia-Anhalt, and the Cenomanian of France and southern England, respectively (Tab. 2).

FACIES-RELATED DISTRIBUTION OF PHYMATELLIDS IN CRETACEOUS DEPOSITS OF EUROPEAN EPICONTINENTAL SEA

The authors of the present account present a review of the literature data, which is supplemented by observations concentrating on the distribution of phymatellid sponges in different Cretaceous facies. The better recognition of these facies of the European Basin through petrographic studies, which was realized in a few last years enables the determination of the palaeoenvironmental conditions during sedimentation (Faÿ-Gomord *et al.*, 2016; Jurkowska *et al.*, 2019; Saïag *et al.*, 2019; Jurkowska and Świerczewska-Gładysz, 2020b). The compilation of the occurrence of Cretaceous phymatellids within variable lithologies will enable the analysis of their palaeoecological requirements and bathymetric distribution.

The number of phymatellid species listed below have not been determined with the accuracy because a lot of taxa requires revision, especially those described at 19th and early 20th century. Moreover, the frequency of phymatellids in some of the discussed deposits is unknown. Some reports about distribution of phymatellid sponges in the Cretaceous of Europe have not been included in the following considerations, because: 1) the taxonomic position of some described specimens, classified as phymatellid species, is doubtful due to their poor preservation and/or lack of well documented skeletons; 2) specimens described as phymatellids were recognized by us as representatives of other group of lithistids (e.g., skeleton of “Siphoniid sponges” presented by Bert and Breton, 2017, figs 5, 6 contains rhizoclonal, desmas typical of *Rhizomorina*); 3) the lithology is uncertain or there are no data, from which facies specimens originated (e.g., redeposited Upper Cretaceous specimens from Paris Basin – Moret, 1926; redeposited specimens from the Cenomanian of western Ukraine – Świerczewska-Gładysz and Olszewska-Nejbert, 2013).

Occurrence of phymatellids in carbonate-siliceous deposits

Cretaceous phymatellids are known from two carbonate-siliceous facies: opoka and gaize. Until now, phymatellids from gaize were described only from the Cenomanian of France, mainly from Ardennes and Normandy (Moret, 1926; Defretin-Lefranc, 1960). In these sponges assemblage, dominated by lithistids, 11 species of seven phymatellid genera (*Jerea*, *Phymatella*, *Kalpinella*, *Craterella*, *Polyjerea*, *Siphonia* and *Turonina*) are noted. Actually, rare phymatellids (*Turonina variabilis* and unidentified taxa) are recognized also from the upper Campanian gaize of Miechów Synclinorium, where also lithistid sponges are more numerous than hexactinellid sponges (Świerczewska-Gładysz and Jurkowska, 2013).

Phymatellids from opoka facies (opoka and opoka with marly layers or intercalations) are known only from the Campanian and Maastrichtian of Poland. In the Miechów and Mogilno-Łódź synclinoria, phymatellids are the most

numerous and taxonomically diverse in early Campanian sponge assemblages, which are also rich in other lithistid demosponges (Hurcewicz, 1966, 1968; Świerczewska-Gładysz, 2016, 2017; Świerczewska-Gładysz and Jurkowska, 2022). From younger layer of the Campanian opoka of Miechów Synclinorium, hexactinellid sponges were dominated, such as *Phymatella bulbosa*, *Siphonia micropora* and *Aulaxinia sulcifera*.

Phymatellid sponges, occurring in the upper Campanian and Maastrichtian opoka from the middle Vistula River valley (southern Poland), are also rare in comparison to hexactinellid sponges (Świerczewska-Gładysz, 2006, 2012). The most common phymatellid species in all these opoka sequences is *T. variabilis*. Except this, *A. sulcifera* and *Callopegma acuallis* Zittel, 1878 are noted in the upper Campanian and lower Maastrichtian, while *Phymatella bulbosa* in the uppermost Maastrichtian. A few other species, e.g., *Siphonia tubulosa*, *Acrochordonia ramosa* and *Jerea* sp., were recognized among the redeposited Maastrichtian faunal assemblages occurring in the Danian glauconitic sandstone, covering the top of Maastrichtian opoka (Świerczewska-Gładysz, 2006).

Occurrence of phymatellids in chalk deposits

The phymatellids, like other lithistids demosponges, are rare fossils in chalk (Hinde, 1883; Moret 1926; Nestler, 1961; Reid 1962) and their numerous occurrences have been documented only in some layers (e.g., Campanian Flamborough Sponge Beds – Whitham, 1993). Moreover, the specimens observed in chalk are limonitized, usually without preserved siliceous spicules. Therefore, most of described phymatellids from chalk sections are derived from horizon of flint nodules, where portions of sponge skeletons were preserved as silicified.

The low phymatellids occurrence in chalk facies as well as their poor state of preservation caused the situation that they are not well taxonomically recognized. Only five species, represented by four genera: *Turonia*, *Aulaxinia*, *Callopegma* and *Siphonia* were described from the lower Maastrichtian of Rügen (Germany; Nestler, 1961; Reich and Frenzel, 2002). Species of *Aulaxinia* are noted also from the lower Maastrichtian of Helgoland (Denmark; Stühmer *et al.*, 1986). Except for the taxa mentioned above, representatives of *Bolospongia*, *Phymatella* and *Polyjerea* were recognized in the chalk of England (Hinde, 1883). Hinde (1833) distinguished over a dozen phymatellid species, but according to the authors of the present article this number is overestimated. Some new species proposed by Hinde (1883) are synonymous with earlier described species from Germany (Świerczewska-Gładysz, 2006), while a few others, without documented ectosomal skeleton, need revision, as they may be sponges from the family Theonellidae.

Phymatellids from the chalk of France are poorly recognized. Rare specimens of *Turonia variabilis* and *Thecosiphonia nobilis* (= *Polyjerea nobilis*) were noted in the Turonian chalk of southern part of Paris Basin (Moret, 1926). Moreover, a few species of *Jerea*, *Polyjerea* and *Siphonia* were noted from the lower Campanian chalk of

Charentes (northern Aquitania, France; Lachasse, 1943; lithology after Neumann *et al.*, 1983; Villier *et al.*, 1997).

Occurrence of phymatellids in marly-calcareous deposits

Early Cretaceous phymatellids occurring in marls and limestones are well documented only in the Aptian of Catalonia (Spain) by Lagneau-Hérenger, 1962 (lithology after Moreno, 2005) as three new species (*Callopegma plana*, *Jerea striata* and *Acrochordonia stellate*).

Late Cenomanian phymatellids, described by Počta (1884) from marly limestones of the southern part of the Bohemian Basin (Czech Republic) rich in lithistids, require revision, but the illustrated skeleton of some of these specimens indicate that at least some of them do indeed represent this group of sponges.

The sponge assemblage from Turonian marls and limestones of the Synclinal d'Eygalières (Drôme department, southern France) contains representatives of 6 genera: *Phymatella Aulaxinia*, *Thecosiphonia* (= *Polyjerea*), *Jerea*, *Siphonia* and *Calymmatina* Zittel, 1878 (Lagneau-Hérenger, 1967; lithology after Letourneur and Porthault, 1966). Turonian phymatellids are also important component of sponge fauna occurring in fossil-bearing marly facies of the Subhercynian Basin (Saxony-Anhalt, Germany; Schrammen, 1910; lithology after Voigt *et al.*, 2006). Characteristic taxa for this assemblage are various species of *Turonia*, *Phymatella*, *Thecosiphonia* and *Jerea* (especially *J. quenstedti*).

In the sponge assemblage from the upper Turonian–lower Coniacian marly-calcareous deposits exposed in the Opole Trough (southern Poland), phymatellids are subordinate elements, similar to other lithistids. The phymatellid species most often described from this section is *Thecosiphonia nobilis* Roemer, 1840 (Roemer, 1840–41; Schrammen, 1910; Tarkowski, 1991; Świerczewska-Gładysz *et al.*, 2019), but they occur only in a few marl layers of the uppermost Turonian and the lower Coniacian (unpublished data of EŚG). Except it, only extremely rare specimens of *Phymatella intumescens* Roemer, 1864 (described also as *Spongites plicatus* by Quenstadt, 1878 and *Phymatella plicata* by Leonhard, 1897) and unique specimen of *Kalpinella pateraeformis* Hinde, 1883 was known from the upper Turonian of Opole (Świerczewska-Gładysz *et al.*, 2019). In the upper Turonian marly-calcareous facies (Teplice Fm) of the Bohemian Basin (Czech Republic) also hexactinellid sponges dominated and only a few phymatellids species were described from these deposits (Počta, 1884, 1903; Zahálka, 1887), but they need taxonomic revision.

Taxonomic diverse phymatellids (12 genera with ca. 17 species) are known from Santonian marly-limestones of Saint-Cyr and/or Nice areas (southern France; Moret, 1926). Except abundant *Siphonia koenigi* Mantell, 1822 and *Calymmatina niecensis* Moret, 1926 all others species of are rare. Moreover, a few species of *Jerea*, *Polyjerea* and *Siphonia* were noted from the lower Campanian marly chalky limestone of Charentes (northern Aquitania, France) (Lachasse, 1943; lithology after Neumann *et al.*, 1983; Villier *et al.*, 1997).

Ulbrich (1974) described from lower Campanian marls of the Subhercynian Basin two new species of phymatellids (*Craterella rhizophyta* and *Paraspelaum labyrinthicum*) and also *Aulaxinia sulcifera*, *Callopegma acuale* and four species of *Phymatella*. Also, lower and upper Campanian marl/marly limestones of the Lower Saxony are rich in phymatellids sponges (Schrammen, 1901, 1910, 1924). It is the most taxonomic diverse Cretaceous phymatellid fauna and contains representatives of ca. 32 species of 15 genera, including two genera *Astrolemma* Schrammen, 1924 and *Paraspelaum* Schrammen, 1924 unknown from other localities outside of the Lower Saxony.

Occurrence of phymatellids in sandy, clayey and silty deposits

Phymatellids are an important group of sponges among the abundant lithistids and hexactinellids fauna from the Cenomanian–lower Turonian siliceous clays and silts of the Danubian Basin (southern Germany; Wagner, 1963; Schneider *et al.*, 2013). These phymatellids are represented by 10 species of 6 genera (*Jerea*, *Siphonia*, *Thecosiphonia*, *Turonia*, *Kalpinella* and *Acrochordonia*). In the Danubian Basin, representatives of *Jerea* and *Siphonia* are also main component of siliceous sponge biostromes located within middle Cenomanian fine-grained, poorly glauconitic sandstones (Kauffman *et al.*, 2000; Wilmsen *et al.*, 2010). The lithistid fauna contains also representatives of these two genera, which are known from the Albian greensands of Warminster (southern England; Reid, 1962; Jeans, 1978).

Early Turonian phymatellids (mainly *Siphonia* and *Jerea* species) were recognized in sponge assemblages occurring in clayey and silty deposits exposed in a few stages from Chtrníki and Plaňany areas, Bohemian Basin (Žitt *et al.*, 2006, 2015). Phymatellids were also described from Turonian glauconitic sandstone of the Münsterland Basin (western Germany; Rauff, 1933). These deposits contain mainly numerous phosphatized specimens of hexactinellids, while not phosphatized specimens of phymatellids are rare and represented by two genera, *Jerea* and *Bolojerea* Rauff, 1933, with four species.

Abundant lithistid sponges, including also phymatellids, are distributed in Santonian and/or lower Campanian sandy-marl facies from the Subhercynian Basin (Griepenkerl, 1889; Schrammen, 1910, 1924; Ulbrich, 1974). Owing to very numerous occurrences of *Siphonia griepenkerli* Schrammen, 1910 in the middle Santonian sandy marl (at the base of the Sudenberg Formation), this layer is called *Siphonia* Marl (e.g., Mortimore, 2018). The early Campanian phymatellids from this region are also numerous and poorly taxonomically diversified. They are probably represented by only four species (*Siphonia tubulosa*, *Siphonia griepenkerli*, *Phymatella bulbosa* and *Turonia constricta* Zittel, 1878), because some other specimens described by Griepenkerl (1889) as *Siphonia* or *Polyjerea* were considered by Schrammen (1910) and/or Ulbrich (1974) as *Phyllocladia* species (family Theonellidae).

REMARKS ON PALAEOECOLOGY AND PALAEOENVIRONMENT

The palaeoecological requirements of the Cretaceous phymatellids are poorly understood. One of the reasons is due to fact that their distribution and palaeoenvironmental requirements were analysed together with those of other Tetracladina groups. The present study indicates, that proposed previously connection of Tetracladina with neritic siliceous facies (Defretin-Lefranc, 1960) or their occurrence in the upper neritic zone (Wagner, 1963) are not universal patterns of distribution of all Cretaceous phymatellids. Moreover, the various terms used in the literature for describing the marine provinces within the Cretaceous basins makes a bathymetric analysis of phymatellids occurrence difficult (e.g., the various meaning of the inner, middle and outer shelf, littoral, neritic, offshore). For clarification, in this chapter, the terminology for the marine provinces will be followed after Jong *et al.* (2020).

The occurrence of Cretaceous phymatellids in deep-water basins has been recognized only on the basis of rare loose megascleres (Bağ *et al.*, 2015). All others are known from Cretaceous deposits of the European epicontinental sea, which indicates that most of Cretaceous phymatellids lived in shallower depths comparing to the recent taxa.

Cretaceous phymatellids are mainly noted in chalk, opoka, gaize and marly-calcareous facies deposited in offshore settings of European epicontinental sea (e.g., Schrammen 1910, 1924; Moret, 1926; Lachasse, 1943; Nestler, 1961; Reid, 1962; Wagner, 1963; Ulbrich, 1974; Villier *et al.*, 1997; Reich and Frenzel, 2002; Voigt *et al.*, 2006; Schneider *et al.*, 2013; Wiese *et al.*, 2013; Wilmsen and Niebuhr, 2017). Rarely they are documented in nearshore deposition zone, below storm wave base of sandy, clayey and silty facies (Reid, 1962; Ulbrich, 1974; Voigt *et al.*, 2006; Žitt *et al.*, 2006, 2015; Schneider *et al.*, 2013). At smaller depths, between storm wave base and fair-weather, they were known only from the Danubian basin (Kauffman *et al.*, 2000; Wilmsen *et al.*, 2010) and probably from Cenomanian limestone of the Bohemian Basin (Počta, 1884; Valečka, 2020). The distribution of phymatellids indicates that most of the Cretaceous phymatellids preferred calm water of the outer shelf. The shallower zones were inhabited only by some species, mainly of *Jerea* and *Siphonia*, but representatives of these genera cannot be treated as an indicators of shallow depths because they are also known from pelagic facies.

This considerable bathymetric span of phymatellids indicates that other palaeoecological and palaeoenvironmental factors controlled its distribution within the basin. Among the factors essential for sponge development is the availability of nutrients. This could be confirmed by the low occurrence of phymatellids as well as other lithistids in chalk facies, which was triggered by the oligotrophy of bottom waters. The observed episodes of increases of nutrient availability in the bottom water of the chalk-sea (Vancoppenolle *et al.*, 2022) probably triggered sponge development. Thus, the abundant occurrence of phymatellids as well as their higher species diversity noted only in certain layers of chalk succession is linked to events of higher local nutrient flux in the sea bottom zone. The higher availability of nutrients in

opoka than in chalk causes the situation that phymatellids sponges are slightly more numerous and more taxonomically diversified in the first one (Jurkowska and Barski, 2017; Jurkowska *et al.*, 2019). Moreover, in opoka facies, owing to the abundant occurrences of non-lithistid demosponges, the food competition was very high, which probably also negatively affected lithistid development (Świerczewska-Gładysz and Jurkowska, 2022). The occurrence of phymatellids in horizons of cherts with flint cores, which records events of increased oceanic DSi (= dissolved silicon) influxes and correlates with higher nutrient availability (Jurkowska and Świerczewska-Gładysz, 2020b).

The influence of oligotrophic conditions on the diminishing frequency of sponges is clearly visible in the Late Cretaceous Circum Sudetic-Trap Basins. In the outer shelf marls/limestones of the Turonian and lower Coniacian of the Opole Basin and the upper Turonian (Teplice Fm) of the Bohemian Basin, they are very rare because the facies accumulated under oligotrophic conditions (Kędzierski and Uchman, 2001; Wise *et al.*, 2004; Jurkowska *et al.*, 2018; Świerczewska-Gładysz *et al.*, 2019).

The other palaeoecological factors, which were significant for phymatellid distribution, are the sedimentation rate and terrigenous input. The high rate of sedimentation limited the development of phymatellids in a nearshore environment. The formation of Cenomanian biostromes in shallow settings represents a special case and the development of the sponges was probably triggered by the low terrigenous input noted in that interval (Kauffman *et al.*, 2000). Similarly, in the gaize of Miechów Synclinorium, which is characterised by a high rate of detrital quartz input, the phymatellids are rare or absent.

CONCLUSIONS

Phymatellids are generally rare in the Campanian opoka facies and gaize of Poland. They are more numerous only in the lower Campanian horizons of cherts with flint cores.

Sixteen species of Phymatellidae were distinguished in the lithistid sponge assemblages of the Campanian of the Miechów and Mogilno-Łódź synclinoria. In addition, a new species, *Kalpinella fragilis* sp. nov., is described here.

Eight species, *Craterella auricula* Schrammen, 1910, *Bolospongia globata* Hinde, 1883, *Phymatella tuberosa* (Quenstedt, 1878), *Jerea quenstedti* Zittel, 1878, *Siphonia costata* (Lamouroux, 1821), *Siphonia micropora* Schrammen, 1910, *Polyierea torgeri* (Schrammen, 1910) and *Procorallistes polymorphus* Schrammen, 1901, are reported from the Cretaceous of Poland for the first time.

Ten species described here are known also from the Campanian of Lower Saxony, while *Bolospongia globata* until now was noted only in the Campanian chalk of England.

In the Cretaceous epicontinental European Basin, phymatellids lived mainly in offshore settings, rarely inhabited nearshore zone, below storm wave, while in the shallower zone (above storm wave) they were extremely rare.

The important palaeoecological factors that limited the development of Cretaceous phymatellids are nutrient

deficiency in bottom waters, rapid sedimentation rates, and high terrigenous input. For this reason, phymatellids occur in the opoka succession in large numbers only in some horizons (cherts with flint core), which are a record of nutrient availability. In the gaize facies, characterised by high terrigenous input, the phymatellids are rare or absent.

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