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CENOMANIAN (LATE CRETACEOUS) SILICEOUS SPONGES OF WESTERN UKRAINE – NEW AND SUPPLEMENTARY DATA

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Abstract: Taxonomic research on the early Cenomanian sponges from western Ukraine has been ongoing since the late 19th century. The taxonomic analysis conducted here supplements and extends the authors' research results, presented in 2012 and 2013. A new portion of the studied material (over 500 specimens, mainly from the Petriv Quarry) revealed 26 species belonging to the order Sceptrulophora, 27 species to the order Lychniscosida, and two species of lithistid demosponges to the order Tetractinellida. Six new taxa are proposed: two sceptrulophorans – *Tretodictyum petrivensis* sp. nov. and *Tretodictyum complicatus* sp. nov.; four lychniscosidans – *Khmilevskia papillata* gen. et sp. nov., *Brachiolites elongatus* sp. nov., *Plocoscyphia anastomosa* sp. nov. and *Ophrystoma olehii* sp. nov. Apart from these, 15 hexactinellid species and one lithistid species, previously unknown from the Cretaceous of the study area, are described in detail. The early Cenomanian sponge fauna of western Ukraine consists almost exclusively of hexactinellid sponges and comprises a total of 56 species. This makes it the richest and taxonomically most diverse assemblage of hexactinellid sponges from the Cenomanian in the world. Microfacies and petrographic studies of the material, infilling the sponge skeletons and the surrounding rocks, suggest that the early Cenomanian sponge meadows were located in a deeper part of the shelf. This area was calm, but within reach of material, carried from the mainland (silt-sized quartz from the Ukrainian Land). In many respects, the habitat of these sponges resembles the conditions, prevailing today on the western Canadian continental shelf, where hexactinellid reefs (mounds) have been found.

Key words: Sponges, Sceptrulophora, Lychniscosida, taxonomy, Cenomanian, Upper Cretaceous, western Ukraine.

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INTRODUCTION

Siliceous sponges were an important component of the benthic faunal communities, inhabiting the Late Cretaceous European epicontinental sea. Cenomanian sponge assemblages, containing numerous and taxonomically diversified hexactinellids, are known mainly from England (Hinde, 1883; Reid, 1958a, b, 1961, 1968), France (Moret, 1926; Regnard, 1926), and western Ukraine (Dunikowski, 1889; Khmilevsky, 1969, 1977; Olszewska-Nejbert and Świerczewska-Gładysz, 2013; Świerczewska-Gładysz and Olszewska-Nejbert, 2013). Some Cenomanian hexactinellid species were also described from Belgium (Defretin-Lefranc, 1960), northern Germany (Roemer, 1864; Schrammen, 1912; Wilmsen, 2003; Wilmsen *et al*., 2011), Denmark (Birkelund, 1973), and Moldova (Trest'jan, 1972, 1973). Only one species, *Laocoetis piserai* Vodrážka and Crame, 2011, has been recorded outside Europe, from deposits with an approximated age pointing to the late Albian–late Cenomanian of Antarctica (Vodrážka and Crame, 2011).

Sponges from the present-day western Ukraine were studied for the first time by Dunikowski (1889), and in later years by Bujalski (1918–1919) and Khmilevsky (1969; 1977). From 2009 to 2014, one of the authors (DON) took part in

several scientific expeditions to western Ukraine. During the first two expeditions, in 2009 and 2010, a rich collection of sponge material was gathered in the area around Nezvys'ko and Rakovets'. In the first paper (Olszewska-Nejbert and Świerczewska-Gładysz, 2012), the authors proposed five neotypes for species that had been described by Dunikowski (1889) as new taxa, based on their material (127 specimens), collected from these localities. This material was supplemented during subsequent expeditions in 2011, resulting in a further elaboration of Cenomanian sponges from the Nezvys'ko and Rakovets' area. In the second paper (Olszewska-Nejbert and Świerczewska-Gładysz, 2013), the authors described 294 specimens and distinguished 30 hexactinellid species and one lithistid taxon. The next expedition in 2012 delivered new specimens from Nezvys'ko and Rakovets', and preliminary research was conducted at a new locality in the working quarry near Petriv, about 8 km to the NW from Nezvys'ko and Rakovets' (Fig. 1). The collected material (112 specimens), including also the specimens from Petriv, allowed the authors to propose a new monotypic genus and five new species of hexactinellids from the Cenomanian deposits of western Ukraine in a subsequent paper (Świerczewska-Gładysz and Olszewska-Nejbert, 2013). By that time, a total of 533 specimens had been described, and the taxonomically diverse specimens from western Ukraine probably represent the richest assemblage of Cenomanian hexactinellids described in the literature (Olszewska-Nejbert and Świerczewska-Gładysz, 2012, 2013; Świerczewska-Gładysz and Olszewska-Nejbert, 2013). Moreover, the prospects for finding new material look very promising.

During the expeditions in 2013 and 2014, rich material was obtained from Petriv and less abundant material from Horodenka and other previously examined localities. The new material helped to resolve several problems and establish some species, not yet described from Ukraine. However, some specimens appeared to represent new taxa. The state of preservation of some of these specimens is good, but their abundances are very low in the studied collection.

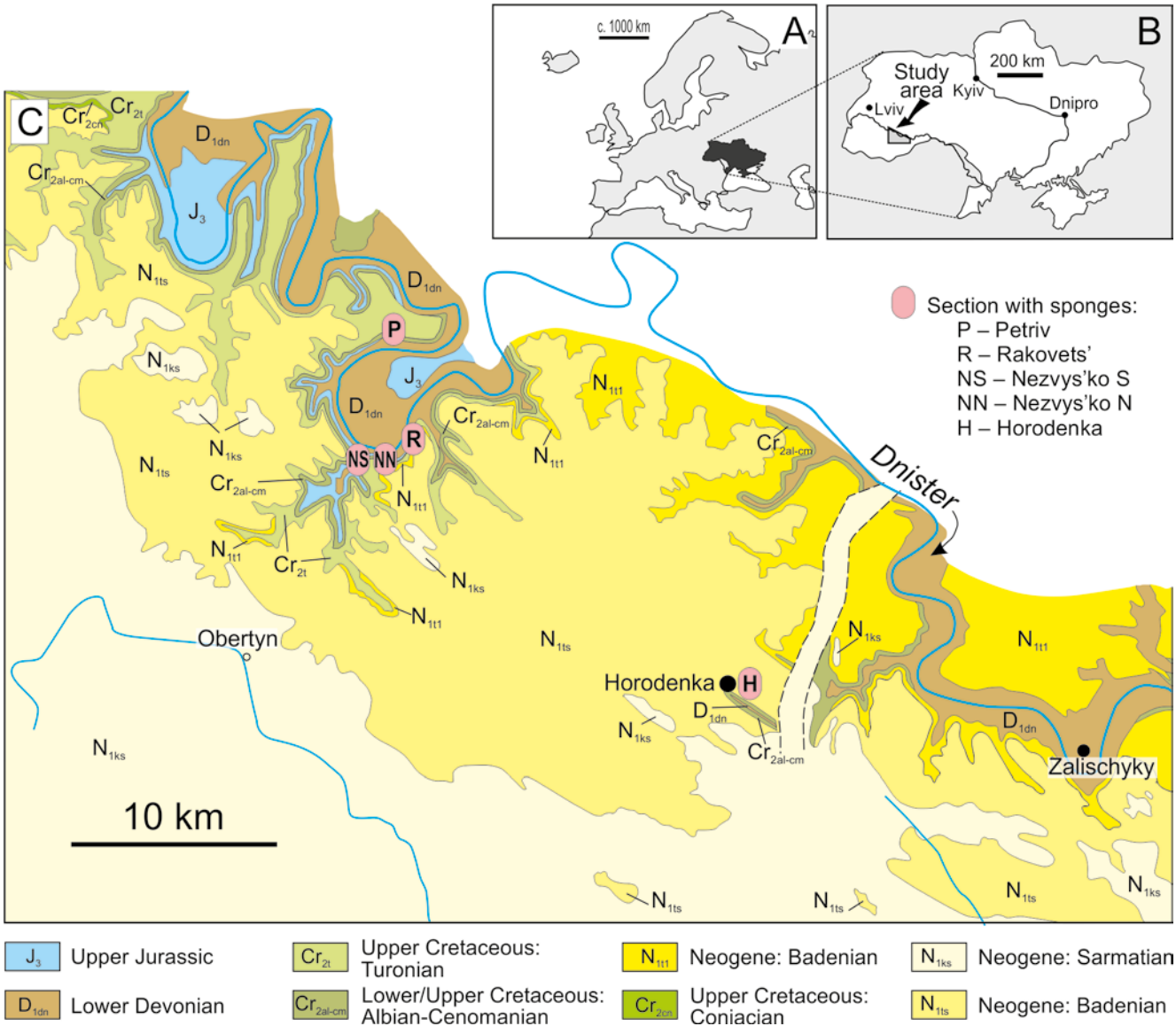


Fig. 1. Geology and locality studied. **A**–**B.** Location of the study area in Europe and Ukraine. **C**. Geological map of western Ukraine with location of the investigated sections (modified and simplified after Bielavskaya and Rastoczynskaya, 1977; extension of Devonian strata, modified after Małkowski *et al*., 2009).

The preservation of other specimens is very poor, and determination of all diagnostic features is not possible, therefore new taxa cannot be proposed. The authors delayed the publication of this new material, hoping for subsequent field expeditions and opportunities to collect new, better preserved reference material. Unfortunately, the unrest in Ukraine (the annexation of Crimea in 2014, the outbreak of the Ukrainian-Russian war in 2022, and the poor prospects for it ending soon) make it very unlikely that a scientific expedition will be organized in the near future. Therefore, the authors have decided to present in this paper the remaining rich, interesting, and spectacular material, especially from Petriv.

This paper can be regarded as the fourth in the series of reports on the phosphatized Cenomanian sponges from western Ukraine. The aim of this paper is to: (1) supplement the previous research, (2) propose new hexactinellid taxa from the Cenomanian, (3) describe their richness and taxonomic variety, and (4) reconstruct the life settings and taphonomic processes of sponges from western Ukraine.

MATERIAL, METHODS AND REPOSITORIES

The new material, presented herein, consists of 605 catalogued specimens and was collected from five exposures: Nezvys'ko S, Nezvys'ko N, Rakovets', Petriv, and Horodenka (Fig. 1; Tabs 1–4). This material supplements and enriches the collection, previously gathered and compiled by 2012 (Tabs 2–4). In the material compiled so far, specimens from Nezvys'ko S, Nezvys'ko N and Rakovets' were given the repository numbers MWG ZI/52/001–476 (Olszewska-Nejbert and Świerczewska-Gładysz, 2012, 2013; Świerczewska-Gładysz and Olszewska-Nejbert, 2013), and the specimens from Petriv – MWG ZI/53/001–068 (Świerczewska-Gładysz and Olszewska-Nejbert, 2013). Subsequently collected material described herein was added to the existing collections and catalogued accordingly. Thus, 78 specimens from Nezvys'ko S, Nezvys'ko N, and Rakovets' described herein are catalogued as MWG ZI/52/477–554, whereas specimens from Petriv and Horodenka – as MWG ZI/53/069–594 (527 specimens – including 514 from Petriv and 13 from Horodenka). All specimens are housed in the Stanisław Józef Thugutt Museum of the Faculty of Geology of the University of Warsaw.

The skeleton structure of sponges was determined on the basis of casts of dissolved spicules. Observations of the details on the casts of the skeletal network and the photographs were made in the Microscope Laboratory of the Department of Invertebrate Zoology and Hydrobiology of Łódź University.

Petrographic studies of thin sections and their photographic documentation were performed at the Microscope Laboratory and Microanalysis Laboratory, University of Warsaw, using a Nikon ECLIPSE E600WPOL optical microscope equipped with a Nikon Digital Sight DS-5Mc camera and NIS-Elements AR software. JMicroVision Software v.1.2.7 (Roduit, 2007) was used to estimate the composition of the phosphatized sponges and deposits underlying, surrounding and overlying the 'sponge bed'. The petrology of the material representing each microfacies distinguished was assessed independently. In the images, each microfacies was characterised on the basis of 300 points, using the point-counting function. Detailed observations of the material infilling the spongocoels, tubes and the interspicular spaces with the skeleton of the sponges were carried out on the phosphatized fragments of sponges at the Laboratory of Electron Microscopy, Microanalysis, and X-Ray Diffraction at the Faculty of Geology, University of Warsaw, on a JEOL JSM-6380LA scanning electron microscope.

GEOLOGICAL SETTING AND STRATIGRAPHY

The study area is situated on the western–southern flank of the East-European Platform and represents part of the Volhyn-Podilla Plate, a tectonic structure, located between the Ukrainian Shield and the Carpathian Fold-and-Thrust Belt. The study sections are located in western Ukraine (Tab. 1; Fig. 1). The oldest deposits, exposed in the study area, are represented by grey and red sandstones of the Old Red Sandstone Facies Formation of Early Devonian age (e.g., Voichyshyn, 2011). In the vicinity of Nezvys'ko S,

Table 1

Location of studied sections with the Cenomanian phosphatized 'sponge bed' in western Ukraine.

Locality	Coordinates	Brief characteristics of locality	Description of sponges
Nezvys'ko S	N48°46′42.3″, E025°15′26.6″, ±3 m	southern slope of a canyon near the Orthodox church, easily accessible outcrop	Dunikowski (1889); Bujalski (1918–1919); Khmilevsky (1977); Olszewska-Nejbert and Świerczewska-Gładysz (2012, 2013); Świerczewska-Gładysz and Olszewska-Nejbert (2013)
Nezvys'ko N	N48°46′40.5″, E025°15′37.6″,±10 m	northern slope of the canyon near the Orthodox church, moderately accessible outcrop	
Rakovets'	N48°47′ 42.4″, E025°17′52.3″, ±3 m	easily accessible outcrop along the road, near Rakovets' village	Olszewska-Nejbert and Świerczewska-Gładysz (2012, 2013)
Petriv	N48°49′50.8″, E025°15′55.9″, ±3 m	large working quarry, located 2 km southwest of Petriv village	Świerczewska-Gładysz and Olszewska-Nejbert (2013)
Horodenka	N48°40′19.8″; E 025°30′32.7″, ±3 m	an old, abandoned and overgrown quarry, difficult to access	Khmilevsky (1969, 1977)

Table 2

Taxonomic composition of sceptrulophoran sponges from the Cenomanian of western Ukraine and the number of specimens representing the species recognized; species described here for the first time in the studied assemblage are in bold; the star indicates the species, known only from localities studied in this paper.

Sceptrulophoran species	Number of specimens described previously	Number of specimens described here				
		Rakovets'	Nezvys'ko S	Nezvys'ko N	Petriv	Horodenka
Aphrocallistes hurcewiczae Trest'jan, 1972	18				7	
Andreaea micropora Lagneau-Hèrenger, 1962	4				1	
****Cribrospongia* sp.**					2	
***Eurete mantelli* Reid, 1958**		2		3	1	2
Eurete meandrina (Regnard, 1926)	20	1			22	
Eurete prolatum Reid, 1958	9			1	15	2
***Guettardiscyphia zitti* Vodrážka, 2017**			1			
**Heterohone boguckii* Świerczewska-Gładysz & Olszewska-Nejbert, 2013	53				23	
****Hexactinella* sp.**					1	
****Hillendia* (?) sp.**					1	
Laocoetis beaumonti (Reuss, 1846)	46	2			28	1
***Laocoetis cancellata* (Roemer, 1864)**		1	1	2	1	
***Laocoetis fittoni* (Mantell, 1822)**		1	2	2	1	
Laocoetis maxima (Dunikowski, 1889)	30	5	2		29	
Leptophragma murchisoni (Goldfuss, 1831)	5				3	
**Mylusia rakovensis* Świerczewska-Gładysz & Olszewska-Nejbert, 2013	12			1	11	
Periphragella plicata (Schrammen, 1902)	22				35	
***Petalope auriformis* Počta, 1883**			1		4	
Pleurostoma (?) *scyphus* Počta, 1883	11		2		3	
Stichmaptyx undulatum (Moret, 1926)	9				7	
****Tretodictum petrivensis* sp. nov.**			2	1	36	1
****Tretodictyum complicatus* sp. nov.**			1		3	
**Verrucocoelia regularis* Świerczewska-Gładysz & Olszewska-Nejbert, 2013	9					
***Verrucocoelia tubulata* (Toulmin Smith, 1848)**		1	3		3	
***Verrucocoelia alpina* Hérenger, 1944**		1	1	1	2	
Verrucocoelia vectensis Hinde, 1883	3	1		1	7	
****Wollemannia* sp.**			1		1	
**Tretochone cretacea* Świerczewska-Gładysz & Olszewska-Nejbert, 2013	4					
28 species	255	297				

the Devonian deposits are covered by a Jurassic carbonate succession, up to 20 m thick (Bieniasz, 1887; Kokoszyńska, 1931; Tokarski, 1931; Senkovsky *et al*., 1989). Jurassic carbonates are most probably late Tithonian to early Berriasian in age (Gutowski *et al*., 2005). In Nezvys'ko S and Horodenka, the Jurassic deposits are capped by Cretaceous deposits (beginning with the Albian), whereas in Nezvys'ko N, Petriv and Rakovets', analogous Cretaceous deposits (Albian) directly overlie the Lower Devonian Old Red Sandstone Facies Formation (Fig. 1; Tokarski, 1931; Khmilevsky, 1969; Senkovsky *et al*., 1989). The Cretaceous deposits are capped by various limestones, marls, sands, and gypsum of Neogene age and Quaternary gravels, sands, and loess (Fig. 1). All of the beds, from the Devonian to the Neogene and Quaternary, lie horizontally or nearly horizontally. A small regional dip of up to 4° to the west and/or south-west (Tokarski, 1931; Senkovsky *et al*., 1989) can be observed.

Table 3

Taxonomic composition of lychniscosidan sponges from the Cenomanian of western Ukraine and the number of specimens, representing the species recognized; description as in Table 2.

Lychniscosidan species	Number of specimens described previously	Number of specimens presented here				
		Rakovets'	Nezvys'ko S	Nezvys'ko N	Petriv	Horodenka
Becksia plicata (Sinzov, 1878)	7			1	1	
**Becksia* sp.	2					
Brachiolites aptiensis (Lagneau-Hérenger, 1942)	6	**1**			**12**	**1**
***Brachiolites elongatus* sp. nov.**		1			1	
**Callodictyonella regularis* (Dunikowski, 1889)	46				53	
Camerospongia fungiformis (Goldfuss, 1831)	1				1	
***Coscinopora macropora* Goldfuss, 1826**		1	1	1		
Diplodictyon heteromorphum (Reuss, 1846)	3					
**Dunikowskiella nezvyskensis* Świerczewska-Gładysz & Olszewska-Nejbert, 2013	25	1	3	2	7	
Exanthesis labrosa (Smith, 1848)	7				20	
***Khmilevskia papillata* gen. and sp. nov**		1				
**Leiostracosia crassa* (Dunikowski, 1889)	25				20	
**Moretiella foliacea* Świerczewska-Gładysz & Olszewska-Nejbert, 2013	9				1	
Ophrystoma micrommata (Roemer, 1864)	5					
***Ophrystoma olehii* sp. nov.**		2	2	1	1	
Orthodiscus fragilis Schrammen, 1924	2				5	
Pleurope lacunosa (Roemer, 1840)	4				7	
***Plocoscyphia anastomosa* sp. nov.**			1		2	
Plocoscyphia communis Moret, 1926	14	3			3	
**Plocoscyphia podolica* Dunikowski, 1889	44	1			26	2
***Rhizopoterion* sp.**		1			-	
Sestrocladia furcata Hinde, 1883	26				40	1
**Sestrocladia* sp.	4					
Sestrodictyon reteformis (Hinde, 1883)	15	4			29	
Sporadoscinia alcynoides (Mantell, 1822)	6	1			1	
Ventriculites chonoides (Mantell, 1815)	4				4	
Trematobolites megastoma (Roemer, 1841)			3			1
**Toulminia polonica* Dunikowski, 1889	17				24	
28 species	272	295				

The Cretaceous succession in the study area begins with transgressive clastic-carbonate Albian deposits (up to 5 m thick). Cenomanian strata include calcareous-glauconitic-quartz sands with irregular horizons of phosphatized sandstones (ca. 0.7 m thick), and moderately cemented grey marls (ca. 0.6 m thick); weakly cemented, dark-grey marls, or clayey marls with phosphatized fossils, mainly sponges (ca. 0.25 m thick), strongly cemented inoceramid limestones with scattered phosphatized fossils at the base (up to 1 m thick), and strongly cemented inoceramid limestones (ca. 7 m thick; e.g., Pasternak *et al*., 1987; Senkovsky *et al*., 1989 and own observations). The Cenomanian inoceramid limestones are overlain by well-cemented, poorly fossiliferous pelitic limestones of early Turonian age (Pasternak *et al*., 1968). All specimens described herein originate from the horizon rich in phosphatized sponges, referred to as the 'sponge beds' (Senkovsky *et al*., 1989), lying directly below and at the base of the strongly cemented, hard inoceramid

Table 4

Taxonomic composition of lithistid sponges and sponges without a rigid skeleton from the Cenomanian of western Ukraine and the number of specimens, representing the species recognized; description as in Table 2.

Lithistid demosponges and siliceous species without rigid skeleton	Number of specimens described previously	Number of specimens presented here				
		Rakovets'	Nezvys'ko S	Nezvys'ko N	Petriv	Horodenka
***Jerea* sp.**		1	1			1
Siphonia pyriformis Goldfuss, 1826	6				3	
unspecified phymatellids	–				4	1
unspecified rhizomorinids	–				1	
unspecified demosponges without rigid skeleton	–				1	
2 lithistid species and a few (3–4?) unspecified taxa	6	13				

limestones (Fig. 2). All sponge specimens are phosphatized. The best-preserved specimens occur in the clayey marls unit. At the base of the inoceramid limestones, the redeposited sponges are rarer, more destroyed and represented by smaller fragments. In addition, at all localities, the phosphatized sponge beds also contain rare, phosphatized bivalve moulds of the genus *Aucellina*, calcite rostra of belemnites *Neohibolites ultimus* (d'Orbigny) as well as fragments of phosphatized wood.

The stratigraphy of the 'sponge bed' studied herein is not very clear, due to the absence of index taxa. Pasternak *et al*. (1966, 1968, 1987) and Senkovsky *et al*. (1989) indicated the age of sponge bed as the late Cenomanian. On the other hand, Khmilevsky (1969) dated the sponges, described by him from Horodenka, as early Cenomanian in age. Dunikowski (1889) noted the presence of the ammonite *Acanthoceras rhotomagense* (Brongniart), which is the index taxon for the lower middle Cenomanian (e.g., Wiedmann *et al*., 1989), *Nautilus elegans* Sowerby, *Inoceramus latus* Mantell, in the sponge bed in Nezvys'ko. Unfortunately, the present authors did not find any index taxa during their field work. The original collection of Dunikowski (1889) has been lost, and it is impossible to confirm the information about the presence of the index ammonite taxon. However, it is worth noting that the authors found the stratigraphically important belemnite *Neohibolites ultimus* (d'Orbigny) as well as phosphatized bivalve moulds of *Aucellina* sp. together with the phosphatized sponges. In western Europe, *N. ultimus* occurs mainly in the lowermost Cenomanian, but it is known also from the middle Cenomanian (Christensen *et al*., 1992; Christensen, 1997; Mitchell, 2005; Wilmsen *et al*., 2010; Machalski *et al*., 2023). The youngest record of *N. ultimus* is from the *Acanthoceras rhotomagense* Zone, *Turrilites acutus* Subzone of northern France (Christensen *et al*., 1992; Christensen, 1997). Mitchell (2005) distinguished several belemnite biohorizons within the Cenomanian deposits of north-western Germany. The *N. ultimus* biohorizon 1 (Belemnite Biohorizon II of Mitchell, 2005) is connected with the occurrence of *Aucellina*. The *N. ultimus* biohorizon 2 (Belemnite Biohorizon III of Mitchell, 2005) is at the base of the First Inoceramid Bed. The *N. ultimus* biohorizon 3 (Belemnite Biohorizon IV of Mitchell, 2005) is connected with the sponge bed (sponges, represented mainly by anastomosing becksiid forms in inoceramid debris). The first two *N. ultimus* biohorizons mentioned above are correlated with the lower Cenomanian *Mantelliceras mantelli* Zone. The third biohorizon corresponds to the middle Cenomanian *M. dixoni* Zone (Wilmsen, 2003). All three elements mentioned above (phosphatized *Aucellina*, inoceramid debris, and numerous phosphatized sponges) co-occur with *N. ultimus* in the study area. Thus, it is very difficult to precisely correlate the stratigraphic position of the Ukrainian 'sponge bed' with any of the *N. ultimus* horizons from north-western Germany, distinguished by Mitchell (2005). However, it is worth mentioning that in north-western Germany the *N. ultimus*/*Aucellina* transgressive event started with the lower Cenomanian Depositional Sequence Ce 1 (Wilmsen, 2003, 2012). Additionally, previous research has shown that the sponge assemblage in western Ukraine is most similar to the lower Cenomanian sponges from England (Olszewska-Nejbert and Świerczewska-Gładysz, 2013 and references therein).

On the basis of the new data presented in this work, the authors believe that the assemblage of phosphatized sponges, non-phosphatized belemnites *N. ultimus*, and phosphatized moulds of *Aucellina* accumulated in unit 4 (Fig. 2) seems to indicate rather the lower Cenomanian (compare with Machalski *et al*., 2023).

The present authors assume a middle Cenomanian age of the inoceramid limestones (unit 5 in Fig. 2), as suggested by Kyselevych and Kovalchuk (2021) for a similar inoceramid limestone, occurring eastward of the study area in the Middle Dnister region. The late Cenomanian age of the inoceramid limestones, noted by the earliest investigators (Pasternak *et al*., 1966, 1968, 1987; Senkovsky *et al*., 1989), was applied, when the Cenomanian was divided into two stages (lower and upper). Kyselevych and Kovalchuk (2021) suggested the subdivision of the Cenomanian into three substages, based on numerous fossil taxa; this subdivision seems to be more precise and appropriate. Only a small number of lower Cenomanian phosphatized sponges and other phosphatized remains were redeposited in the middle Cenomanian inoceramid limestones.

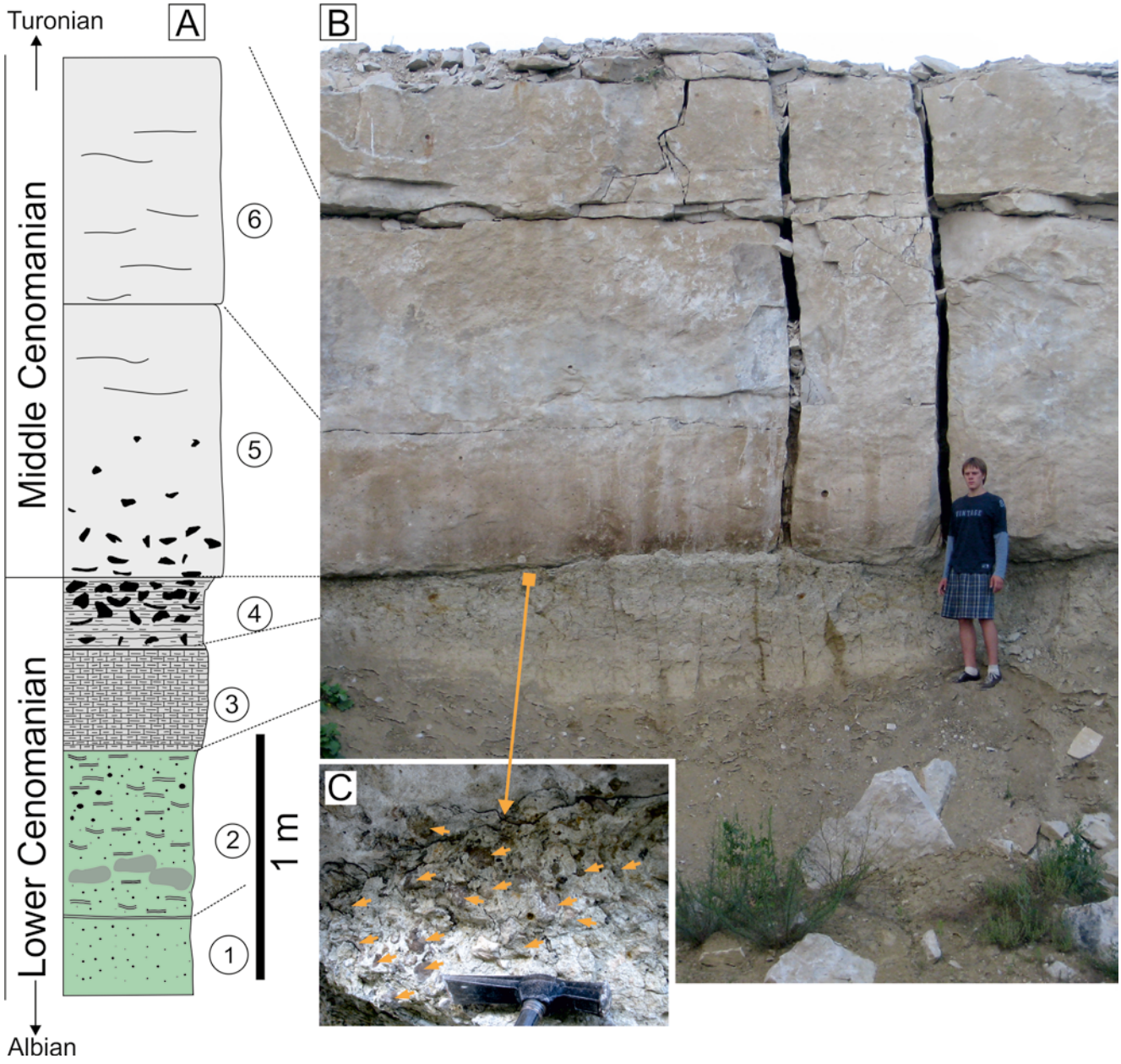


Fig. 2. Lithological column of the Cretaceous succession (stratigraphic terminology after Pasternak *et al*., 1987 and Senkovsky *et al*., 1989; corrected), exposed in the Petriv Quarry. **A.** Geological section of part of the Cretaceous deposits. Units: 1 – quartz sand or weakly cemented quartz sandstone; 2 – quartz-calcareous sand/sandstone with admixture of glauconite and numerous bioturbation traces, scattered lydite grains and irregular parts cemented by phosphatization; 3 – moderately cemented grey marls; 4 – weakly cemented dark grey clayey marls with phosphatized 'sponge bed'; 5 – strongly cemented inoceramid limestones with irregular horizontal streaks and scattered phosphatic fragments, higher amount of fragments (mainly sponges) at the base; 6 – strongly cemented inoceramid limestones with irregular horizontal streaks. **B.** Photograph of a fragment of the quarry wall with 'sponge bed' (unit no. 4), the lowest quarry level; as of 2012. **C.** Enlarged fragment of the 'sponge bed' rich in phosphatized sponges, some sponges arrowed.

LITHOLOGY, PETROGRAPHY AND MICROFACIES OF THE 'SPONGE BED' AND ASSOCIATED DEPOSITS

Deposits directly associated with the 'sponge bed' belong to units 3–5, distinguished in the section (Fig. 2). In stratigraphic order, beds 3 to 5 (Fig. 3) are characterised as follows: grey marls (unit 3), dark grey clayey marls with an accumulation of phosphatized sponges (unit 4), and detrital inoceramid limestones (unit 5) with phosphatized sponges, but not as frequent as in unit 4. Microfacies characteristic for each unit are described in Tables 5 and 6.

Taphonomy

The sponges studied here from the 'sponge bed' represent one taphonomic group. The specimens are dark, almost black, strongly cemented and phosphatized. During the phosphatization processes, the phosphates - carbonate fluorapatite (francolite) – crystallised in the interspicular spaces

Table 5

Results of point-counting [in %] (JMicroVision software) of the different microfacies, distinguished in the lithological samples from units 3–5, connected with the 'sponge bed'. Every column corresponds to data from the image presented in Fig. 3; m.g.m. – moderately grey marls; d.g.c.m. – dark grey clayey marls; at.ph.d. – phosphatized deposit attached to the outer surface of the sponge; o.w.sp. – outer side of phosphatized sponge wall; i.w.sp. – inner side of phosphatized sponge wall (close to spongocoel); ph.d.sp – phosphatized deposit infilling the spongocoel; f.d.l. – fine-detrital limestone; bold font – data from interspicular space of the phosphatized sponges. Microfacies MF M1, MF M2, MF M3, MF AD, MF SP, and MF PA are explained in the text and Table 6.

	Unit 3		Unit 4							Unit 5				
	Figure 11													
	F	G	H			D		E		A		B	C	
	m.g.m	m.g.m.	d.g.c.m.	at.ph.d.	sponge	at.ph.d.	o.w.sp	i.w.sp	ph.d.sp.	f.d.l.	sponge	f.d.l.	at.ph.d.	sponge
Quartz-silt size	38.0	37.6	28.7	17.7	**4.7**	28.3	**5.3**	**2.3**	18.3	3.7	**5.7**	2.3	18.0	**2.3**
Quartz-sand size	–	10.0	2.7	–	**–**	–	**–**	**–**	–	0.3	**–**	3.0	–	**–**
Inoceramian debris	23.3	16.7	10.3	0.5	**–**	–	**–**	**–**	–	74.7	**–**	79.0	–	**–**
glauconite	2.4	2.0	6.0	3.0	**1.7**	3.3	**1.0**	**2.0**	1.7	3.0	**1.0**	2.0	5.7	**1.0**
Phosphates CFA <10 μm	–	–	1.0	78.7	**88.0**	68.4	**93.0**	**91.4**	79.7	–	**93.3**	–	76.3	**96.3**
micrite	36.3	33.7	51.3	–		–		**–**	–	12.3	**–**	13.7	–	**–**
sparite	–	–		–	**5.6**	–	**0.7**	**4.3**	0.3	6.0	**–**	–	–	**0.4**
Acronym of microfacies	MF M1	MF M2	MF M3	MF AD	MF SP	MF AD	MF SP	MF SP	MF AD	MF PA	MF SP	MF PA	MF AD	MF SP

of the sponge skeleton, its canals and the spongocoel. The siliceous skeletons of these sponges were completely dissolved. The space after spicules remained empty, or partially (sometimes completely) filled with francolite or another mineral (e.g., calcite, clay minerals, glauconite). Many sponges have well-preserved morphology, but on the other hand, numerous specimens are destroyed, crushed and with an obliterated external surface. The best-preserved sponges were collected from the weakly cemented dark grey clayey marls of unit 4 (Fig. 2). More damaged sponges occur in the hard detrital limestone in the basal part of unit 5 (Fig. 2); likewise, they are also dark, almost black, strongly cemented and phosphatized. The total size of the broken specimens is usually unknown. The outer surface of the specimens is damaged to a variable degree, whereas the spongocoel is often fully or partially filled with a phosphatized deposit or its surface is covered with a thin layer of phosphatized material. Therefore, in several species, it was not possible to study the morphology and structure of the dictyonal skeleton on the inner surface of the sponges. The siliceous skeleton of the studied specimens is completely dissolved. The casts are empty or filled with carbonate-clay material. Due to diagenetic processes, casts after spicules as well as the skeletal canals may be undistinguishable within the wall. The preserved sponges underwent a process, known as local phosphatization (Föllmi, 1990; Olszewska-Nejbert and Świerczewska-Gładysz, 2009), which resulted in the sponges retaining a fairly accurate shape, similar to that which they had, while alive. It is also worth noting that there are no borings at the surface of the phosphatized sponges, and epibionts (oysters) occur extremely rarely.

A rare, but important component of the phosphatized sponge specimens is detrital quartz within the phosphatized material that filled them. Detrital quartz in the silt fraction was quite common in the environment, where the sponges lived and died. After a sponge died, its skeleton, composed of small meshes in the dictyonal network, formed a barrier for the penetration of quartz, thus only a few silt grains entered the interspicular space and were incorporated into the process of phosphatization (Figs 3C, 4D, 5C). Sponges with larger meshes in the dictyonal network allowed significantly more quartz grains to enter, also of silt size (Figs 3A, D, E, H; 4A-C, 5A, D). Rounded sand-size quartz grains, observed in some specimens from Petriv, are attached to the surface of the spongocoels or the outer surface of the sponge in the phosphatized zone (Fig. 5B). Sand-size quartz grains also have been noted in the canals. Sand-size quartz grains (above 0.1 mm) were too large to enter the interspicular space and are attached only to the outer and inner surfaces of the sponges.

Microfacies characteristics of the beds underlying, surrounding and overlying the sponges

Microfacies of unit 3 are represented by two varieties (MF M1 and MF M2; Tables 5, 6). Microfacies MF M1 (Tab. 5; Fig. 3F) is represented by packstone with common detrital quartz of silt-size (38.0%), common inoceramid debris of silt-size (23.3%), and a moderate amount of clayey-calcareous micrite (36.3%). Microfacies MF M2 is very similar to MF M1 but has an admixture of sand-size detrital quartz (Tab. 5; Fig. 3G). The components are common silt-size detrital quartz (37.6%), detrital sand-size quartz (10%),

Table 6

Lithological units and related microfacies with a generalized interpretation of the sedimentary environment.

Unit	Typical lithology	Microfacies acronym	Microfacies (after Flügel, 2010, also adopted for phosphatic components)	Microfacies – important components	Remarks	Environmental interpretation
Top of unit 3 Figs 2, 3	Grey marls underlying the phosphatized 'sponge bed'	MF M1	Packstone – Fig. 3F	Common silt-sized detrital quartz, 38.0%; silt-size inoceramid debris, 23.3%; glauconite, 2.4%; and a moderate amount of clayey-calcareous micrite, 36.3%	Silt-sized quartz grains, angular and subangular; rare thin-shelled bivalves and foraminifers	Shelf-mud environment situated below the storm-wave base; possibly prodelta deposits
		MF M2	Packstone – Fig. 3G	Same as above, plus 10% sand-sized detrital quartz	Sand-sized detrital quartz grains, subrounded and rounded; rare thin-shelled bivalves and foraminifers	
Unit 4 Figs 2, 3	Dark grey clayey marls surrounding the 'sponge bed'	MF M3	Wackestone passing to packstone – Fig. 3H (upper left corner)	Moderately common silt-sized detrital quartz, 28.7%, rare sand-sized quartz, 2.7%, a small amount of inoceramid debris, 10.3%; glauconite, 6.0%; a large amount of clayey-calcareous micrite, 51.3%	Silt-sized quartz grains, angular and subangular; rare thin-shelled bivalves and foraminifers	Shelf-mud environment situated below the storm-wave base; possibly a calmer environment than that represented above, such as a distal prodelta setting
	Phosphatized sponges	MF SP	Wackestone – Figs 3D, E, 4D; Wackestone passing to packstone – Figs 3H (lower right corner), 4A, C	Phosphates (very fine-grained carbonate fluorapatite – francolite), 88.0–93.0%; a small amount of silt-sized detrital quartz, 2.3–5.3%, glauconite, 1–2%	Silt-sized quartz grains, angular and subangular, absent or dispersed in the interspicular space and more frequent outside the sponges; siliceous spicules and thin calcareous components dissolved	During the life of the sponges: shelf-mud environment situated below the storm-wave base, possibly in calmer parts of the prodelta; early diagenetic setting: rapid local phosphatization of dead sponges covered with sediment
	Deposit infilling the spongocoel and attached to the sponge	MF AD	Wackestone; wackestone passing into packstone – Fig. 3D, E, H (middle part of image)	Phosphates (very fine-grained carbonate fluorapatite – francolite), 68.4–79.7%; moderate amount of silt-sized detrital quartz, 17.7–28.3%; glauconite, 1.7–3.3%		Sedimentary setting: shelf-mud environment, situated below the storm-wave base; possibly in calmer parts of the prodelta; early diagenetic setting: rapid local phosphatization of deposits, attached directly to the sponges or/and infilling the spongocoels
Bottom of unit 5 Figs 2, 3	Phosphatized sponges	MF SP	Wackestone – Fig. 3A, C; Wackestone passing into packstone – Fig. 4	Phosphates (very fine-grained carbonate fluorapatite – francolite), 93.3–96.3%; a small amount of silt-sized detrital quartz, 2.3–5.7%; and glauconite, 1%	As above for unit 4	Same as MF SP in unit 4 (see above)
	Deposit infilling the spongocoel and/or attached to sponge	MF AD	Wackestone passing into packstone – Fig. 11C	Phosphates (very fine-grained carbonate fluorapatite – francolite), 76.3%; a moderate amount of silt-sized detrital quartz, 18.0%; glauconite, 5.7%		Same as MF AD in unit 4 (see above)
	Detrital inoceramid limestone	MF PA	Packstone – Fig. 3A (left side of image), B	Inoceramid debris, 74.7–79.0%; silt-sized quartz, 2.3–3.7%; sand-size quartz, 0.3–3%; glauconite, 2–3%; micrite, 12.3–13.7%; sparite, 0–6.0%	Predominantly strongly crushed inoceramid valves, mostly of fine-sand size; fragments larger than 0.25 mm are rare; detrital sand-sized quartz, subrounded and rounded; rare foraminifers present	Storm reworking of the deposit, probably near the storm-wave base but below the normal wave base, in inner- to middle-shelf settings

silt-size inoceramid debris (16.7%), and a moderate amount of clayey-calcareous micrite (33.7%).

Unit 4 is represented by three microfacies (MF M3, MF SP and MF AD; Tab. 5, Fig. 3H). Microfacies MF M3 (Fig. 3H), directly surrounding the sponges in the 'sponge bed', is represented by wackestone passing to packstone with moderately common silt-sized quartz (28.7%), rare sand-size quartz (2.7%), a low amount of silt-size inoceramid debris (10.3%), and a large amount of clayey-calcareous micrite (51.3%). Microfacies MF SP is represented by wackestone. It is associated with phosphatized sponges, i.e., with the interspicular space of the sponge (Fig. 3D, E, H) and occurs not only in unit 4 but also in the phosphatized sponges from unit 5 (Fig. 3A, C). Because the components of these sponges are similar, their composition is presented here for both units jointly: phosphates represented by carbonate fluorapatite (francolite; 88.0–96.3%) and a small amount of detrital silt-size quartz (2.3–5.7%). Microfacies MF AD (Fig. 3D, E, H), also occurring in unit 5 (Fig. 3C), is connected with the phosphatized deposit attached to outer surface of the sponges or infilling the spongocoel, and is represented by wackestone passing into packstone. Its characteristic components are phosphates, represented by carbonate fluorapatite (francolite; 68.4–79.7%), and a moderate amount of detrital silt-size quartz (17.7–28.3%). It is worth noting that the silt-size quartz content is by an order of magnitude higher in the material surrounding the sponges (17.7–28.3%) than in the sponges themselves (2.3–5.7%), but comparable to the silt-size quartz content in microfacies MF M3 (28.7%), i.e., in the non-phosphatized wackestone passing to packstone surrounding the phosphatized elements (Tab. 5).

Unit 5 is represented by one new microfacies (MF PA; Tab. 5; Fig. 3A, B), and two microfacies described above, i.e., MF SP and MF AD (Tab. 5). The new microfacies MF PA is represented by packstone with a large quantity of sand-size (prevailing) inoceramid debris (74.7–79.0%) and detrital quartz (4.0–5.3%). It is worth noting that there are no larger fragments or well-preserved inoceramids in this microfacies. A small admixture of glauconite (1–6%) appears in every microfacies.

SYSTEMATIC PALAEONTOLOGY

Class Hexactinellida Schmidt, 1870
Order Sceptrulophora Mehl, 1992

Remarks: The species described here represent families that in the traditional palaeontological systematics were assigned to the order Hexactinosida Schrammen, 1903. The studies of living sponges have shown that Hexactinosida is a polyphyletic group and these families now should be assigned to the order Sceptrulophora Mehl, 1992.

Family Euretidae Zittel, 1877

Remarks: Fossil euretid sponges recognized, based on the body form and features of the dictyonal skeleton due to the lack of loose spicules, which are critical for the taxonomy of some recent genera of the Family Euretidae (see Reiswig and Wheeler, 2002).

Genus *Eurete* Semper, 1868
sensu Reid (1958a)

Type species: *Eurete simplicissima* Semper, 1868, p. 30, by monotypy.
Diagnosis: See Reid (1958a).

Eurete mantelli Reid, 1958
Figs 6A, 7A, B

1958a *Eurete mantelli* Reid, pp. 23–25, pl. 3 fig. 3, pl. 4, figs 1, 2.

Material: Two specimens from Rakovets' (MWG ZI/52/510, 511), three specimens from Nezvys'ko S (MWG ZI/52/512–514), one specimen from Petriv (MWG ZI/53/523), and two specimens from Horodenka (MWG ZI/53/524, 525).
Description: Fragmentary preserved sponges, up to 5.5 cm in size, composed of dichotomously divided tubes, 10–23 mm in diameter (Fig. 6A). Some of them are irregularly anastomosing. Peripheral tubes occasionally with slightly narrowed apex. Wall 2–2.5 mm thick, without canals.

Outer surface of tubes is covered by a thick layer of dense network with very small hexactines with thickened beams, and rounded triangular and quadrangular meshes, ca. 0.1–0.2 mm (Fig. 7A). Evenly arranged rounded openings in this network measure 0.5–0.8 mm in size. In places, where the dictyonal cortex is destroyed, an irregular subdermal network with triangular and quadrangular meshes, ca. 0.1–0.3 mm in size, is visible (Fig. 7B). Dictyonal skeleton inside the wall is very poorly preserved and only occasionally observed in transversal sections of the tubes, where the network meshes are triangular and 0.1–0.25 mm in size. The meshes in longitudinal section of the wall are square or rectangular, 0.25–0.35 mm in size. Inner surfaces of tubes are not visible.
Remarks: The specimens studied here, classified as *Eurete mantelli* Reid, 1958, can be distinguished from other Cretaceous species of the genus *Eurete* (including *E. meandrina* (Regnard, 1926) and *E. prolatum* Reid, 1958, also present in the collection from western Ukraine), by the wide, irregularly anastomosing tubes. Tubes in the specimens from western Ukraine reach 20 mm in diameter, whereas the diameter of the tubes of specimens from the Cenomanian of England are up to even 32 mm in diameter. A characteristic feature of the skeleton of *E. mantelli* is the very dense dictyonal cortex on the dermal surface, whose casts are locally well-recognizable on some of the examined specimens.
Occurrence: Western Ukraine (lower Cenomanian); England (Cenomanian).

Genus *Verrucocoelia* Éttalon, 1859

Type species: *Scyphia verrucosa* Goldfuss, 1829, p. 51, pl. 33, figs 8a–c designated by Hinde, 1883, p. 200.
Diagnosis: See Reid (2004a).

Verrucocoelia tubulata (Toulmin Smith, 1848)
Figs 6B, 7C, D

1848 *Brachiolites tubulatus* – Toulmin Smith, pp. 366–367, pl. 15, fig. 7.
2010 *Verrucocoelia tubulata* (Toulmin Smith) – Świerczewska-Gładysz, p. 7, figs 3f, 5c (cum syn.).

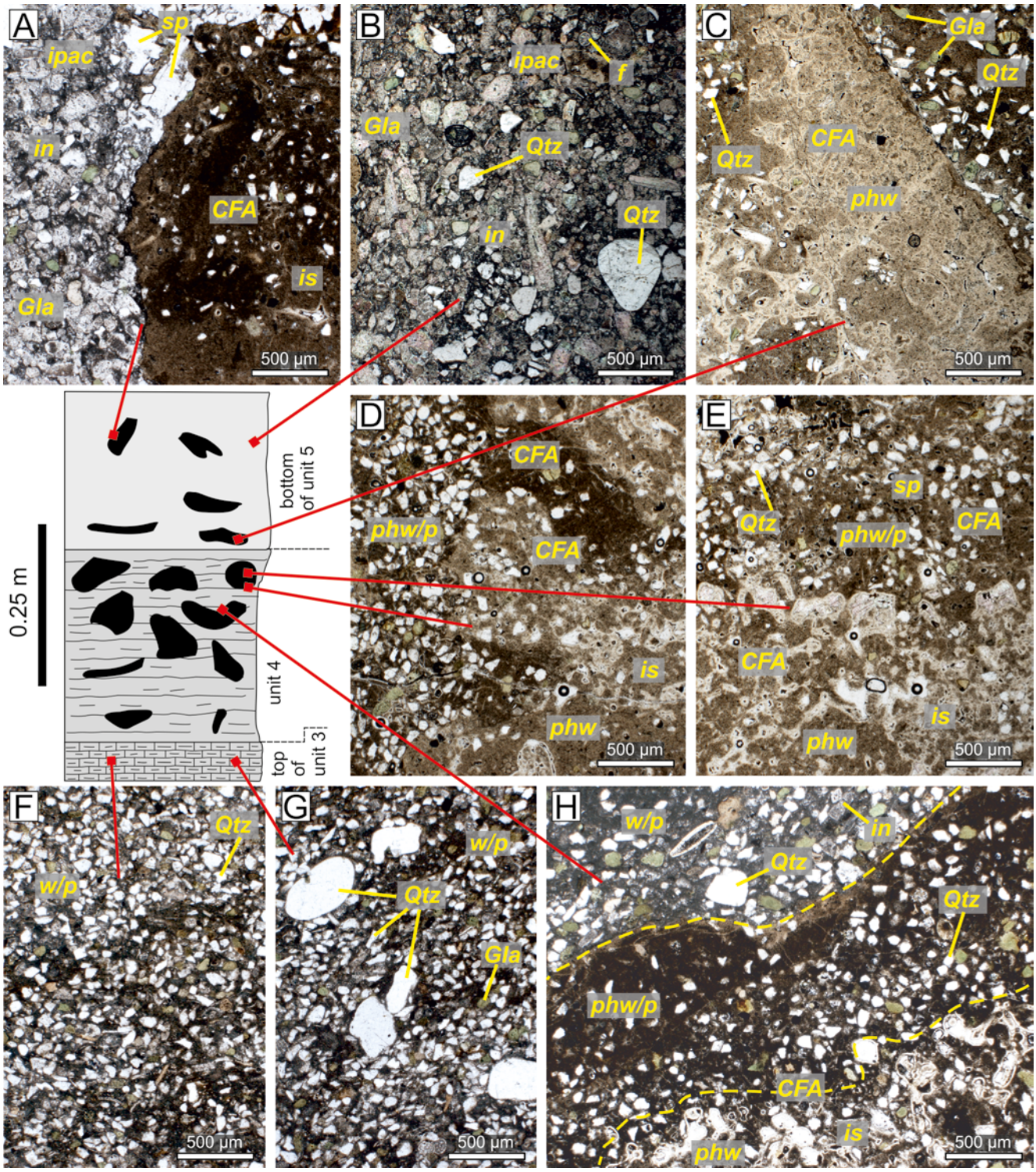


Fig. 3. Fragment of section enriched in phosphatized sponges with underlying, surrounding and overlying deposits – 'sponge bed' with microfacies in thin section (lower/middle Cenomanian boundary). **A.** Phosphatized sponge (brown, phosphatized wackestone MF SP), surrounded by inoceramid packstone MF PA with admixture of detrital quartz grains and glauconite. **B.** Inoceramid packstone MF PA with admixture of detrital quartz grains and glauconite. **C.** Phosphatized rock, composed of phosphatized sponge (phosphatized mudstone/wackestone MF SP) with attached deposit (also phosphatized wackestone MF AD) redeposited into unit 5. **D, E.** Thick-walled *Laocoetis maxima* with phosphatized interspicular space (phosphatized wackestone MF SP), phosphatized deposit, attached to the surface of wall (D), and deposit (E), infilling the spongocoel (phosphatized wackestone/packstone MF AD). **F**. Clayey-calcareous wackestone/packstone MF M1 (marls of unit 3, underlying the phosphatized sponges, note silt-size detrital quartz). **G.** The same as in F with admixture of sand-size detrital quartz in MF M2. **H.** Fragment of phosphatized sponge (phosphatized wackestone MF SP) with attached phosphatized deposit (phosphatized wackestone/packstone MF AD), surrounded by non-phosphatized clayey-calcareous deposits (wackestone/packstone MF M3). A – Nezvys'ko S; B, C, F-H – Nezvys'ko N; D, E – Rakovets'. CFA – carbonate fluorapatite (francolite); Gla – glauconite; in – inoceramid debris; Qtz – quartz; ipac – inoceramid packstone; is – interspicular space; phw – phosphatized wackestone; phw/p – phosphatized wackestone/packstone; sp – spongocoel; w/p – clayey-calcareous wackestone/packstone with silt-size quartz grains.

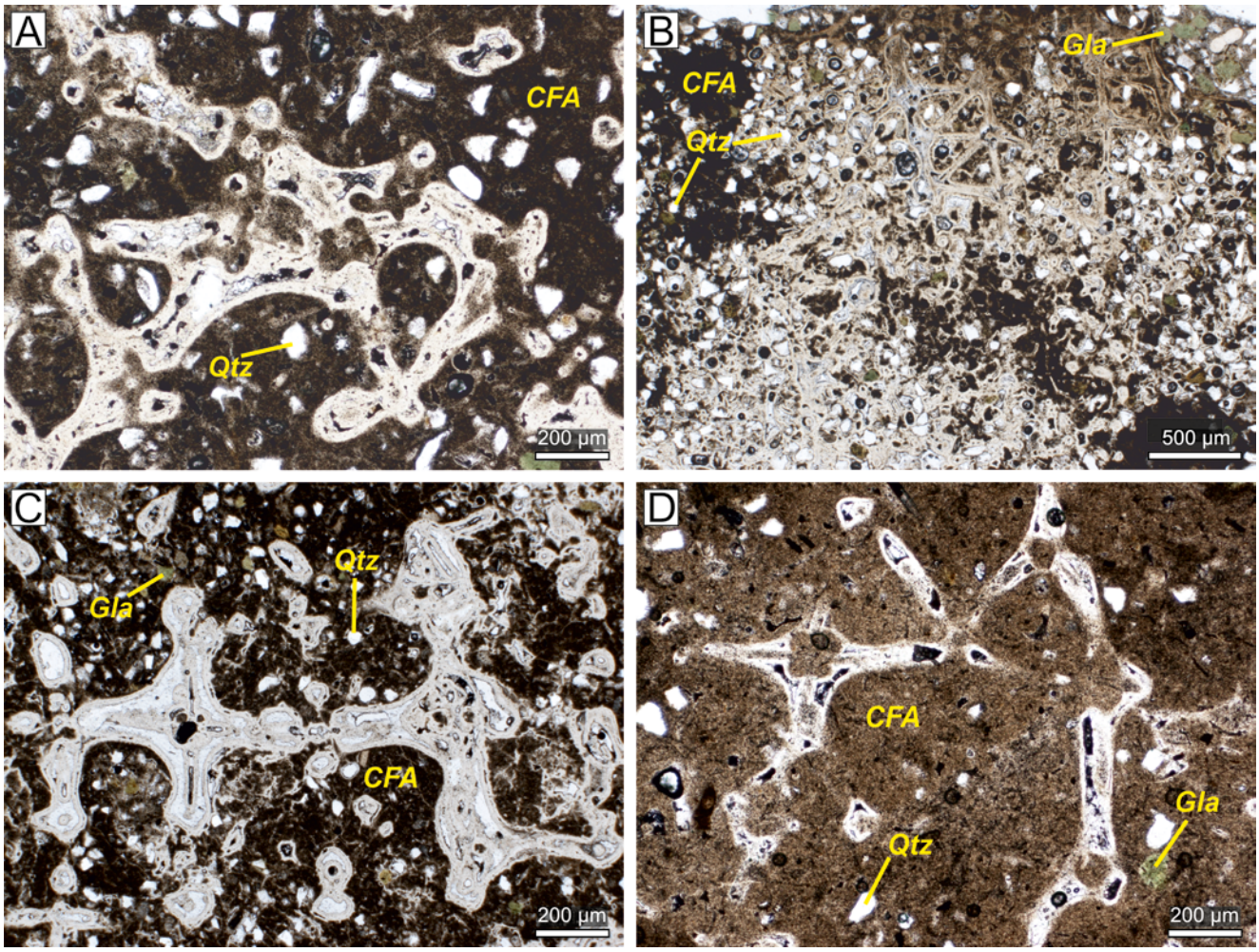


Fig. 4. Examples of phosphatized sponge skeletons in thin section, note the variable occurrence of silt-size detrital quartz. **A.** Quartz grains inside the large meshes in the dictyonal skeleton network of a phosphatized sponge, Nezvys'ko N. **B.** Quartz grains in the subdermal part of the dictyonal skeleton of *Sestrodictyon reteformis* (Hinde, 1883), MWG ZI/52/378, Nezvys'ko S. **C.** Rare quartz grains between the spicules of the phosphatized dictyonal skeleton of *Callodictyonella regularis* (Dunikowski, 1889), (MWG ZI/52/051), Rakovets'. **D.** Rare dispersed quartz grains inside the skeleton of a phosphatized lychniscosid sponge, note the preserved nodal octahedral, Nezvys'ko N. CFA – carbonate fluorapatite (francolite); Gla – glauconite; Qtz – quartz.

Material: One specimen from Rakovets' (MWG ZI/52/515), three specimens from Nezvys'ko S (MWG ZI/52/516–518), and three specimens from Petriv (MWG ZI/53/526–528).
Description: Thin-walled (1–1.5 mm), conical sponges with a deep spongocoel and lateral finger-like outgrowths, usually directed downwards. The best-preserved specimen is 49 mm high and 37 mm wide (Fig. 6B). The largest outgrowths, occurring in the upper part of the specimens, are up to 12–16 mm in diameter and 19 mm long.

Secondary network, covering the dermal surface of tubes, is denser, irregular, with triangular, rarely quadrangular meshes, 0.15–0.3 mm in size, and with sparsely arranged, round pores, ca. 0.5–0.6 mm in diameter (Fig. 7C). Dictyonal skeleton without canals, comprising hexactines forming a regular network (observed in the longitudinal section of the wall) with rectangular meshes, 0.2–0.25 mm × 0.3–0.35 mm in size (Fig. 7D). Occasionally, small (0.15 mm in size) triangular meshes occur, which disturb the network. Skeleton on the gastral surface is not visible.

Remarks: Specimens of *Verrucocoelia tubulata* (Toulmin Smith, 1848) differ from the co-occurring *V. vectensis* Hinde, 1883 by sparsely arranged, blind outgrowths, which in the latter species are more numerous, distributed in clusters, and with summits terminating with round openings. The secondary network on the dermal surface of *V. vectensis* is thicker than in *V. tubulata* and pierced by pit-like openings (see Hinde, 1883; Olszewska-Nejbert and Świerczewska-Gładysz, 2013).
Occurrence: Western Ukraine (lower Cenomanian); Poland (Kraków area: Coniacian and/or Santonian sponges redeposited to Santonian deposits); France (Provence: Albian; Normandy: Cenomanian); Germany (Lower Saxony: Campanian); southern England (Turonian) after Reid (1968).

Verrucocoelia alpina Hérenger, 1944
Figs 6C, 7E, F

1944 *Verrucocoelia alpina* – Hérenger, p. 84, figs 2a–d.

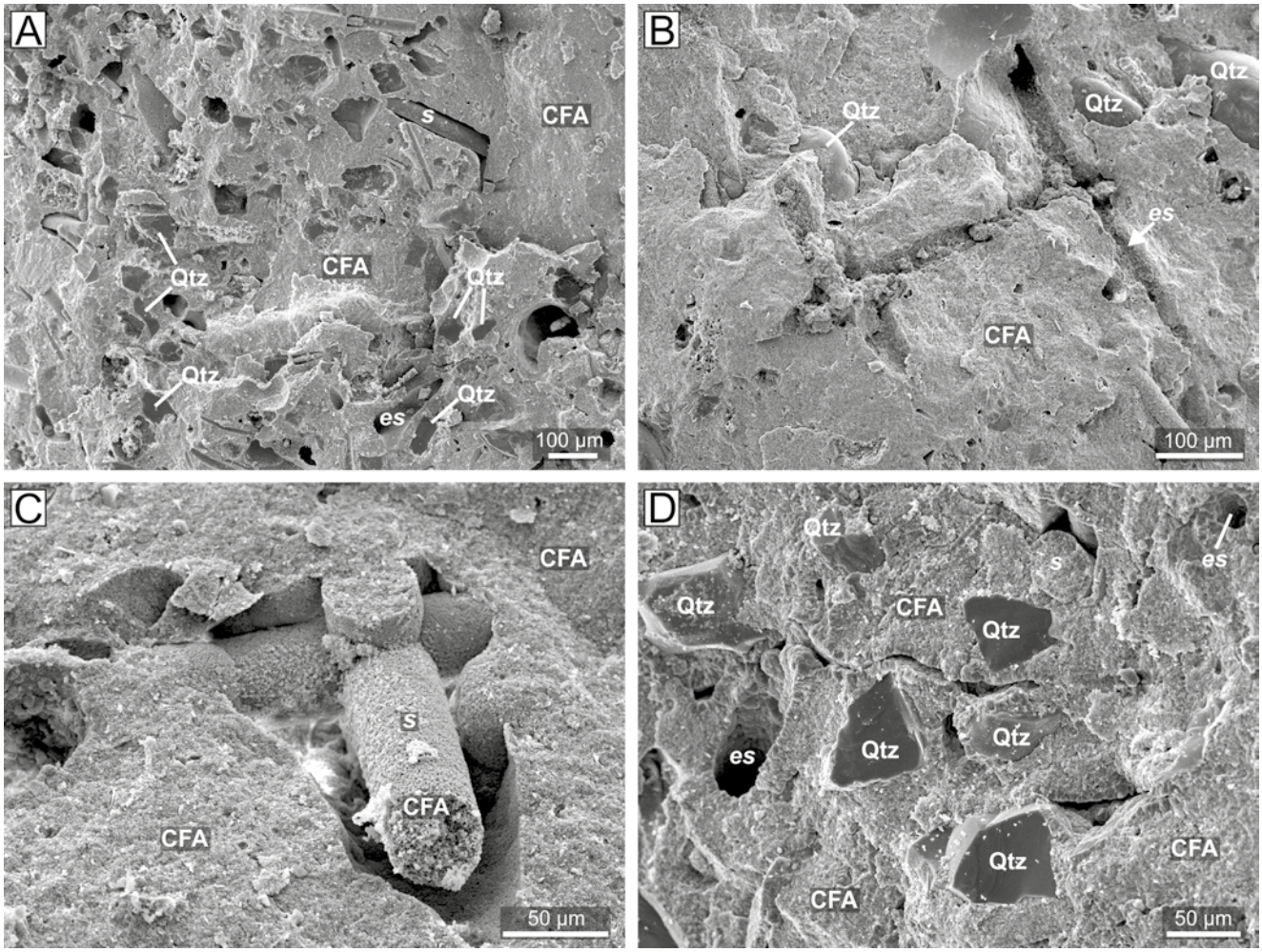


Fig. 5. Examples of SEM photomicrographs of the phosphatized interspicular space of sponges. **A.** Fragment of phosphatized sponge with a moderate amount of angular silt-size quartz grains, Rakovets'. **B.** Fragment of phosphatized sponge with dictyonal skeleton, note the attached, rounded, detrital quartz grains in psammitic size, a rare case, Petriv. **C.** Fragment of phosphatized sceptrulophoran sponge without visible quartz grains, a common case, note the well-preserved hexactin node, Petriv. **D.** Angular and subangular detritic silt-size quartz grains in the skeleton of phosphatized sponges, Rakovets'. CFA – carbonate fluorapatite (francolite); es – empty space after dissolved spicule; Qtz – quartz; s – phosphatized spicule.

1962 *Verrucocoelia alpina* Hérenger – Lagneau-Hérenger, p. 79, pl. 1, fig. 10; text-pl. 12, figs 2a–d.

1980 *Plocoscyphia fenestrata* (Smith) – Małecki, pl. 10, fig. 7a, b.

2010 *Verrucocoelia alpina* Hérenger – Świerczewska-Gładysz, p. 7, fig. 3d, e.

Material: One specimen from Rakovets' (MWG ZI/52/519), one specimen from Nezvys'ko S (MWG ZI/52/520), one specimen from Nezvys'ko N (MWG ZI/52/521), and two specimens from Petriv (MWG ZI/53/529, 530).

Description: Columnar or narrow-conical sponges (Fig. 6C), up to 37 mm in height and 23 mm wide, with a central spongocoel. Wide aperture of spongocoel irregularly undulating. Simple, very short lateral outgrowths, 6–8 mm in diameter, arranged evenly but randomly. Tips of outgrowths rounded with a round or oval osculum, 2–3 mm in diameter. Thin wall of tubes (1.5–2 mm thick) without skeletal canals.

The secondary skeletal network on the dermal surface (occasionally preserved) is very irregular with meshes variable in shape (quadrangular, triangular or pentagonal) and size, ca. 0.1–0.6 mm (Fig. 7E). A similar loose, irregular network occurs on the inner surface (observed near the margin of the aperture). In transverse section of the wall, the dictyonal skeleton is also irregular, with quadrangular, rarely pentagonal or triangular meshes, 0.25–0.45 mm in size (Fig. 7F).

Remarks: The lateral outgrowths of *Verrucocoelia alpina* are similar in shape and size to the outgrowths of *V. regularis* Świerczewska-Gładysz and Olszewska-Nejbert, 2013, but they are distributed randomly, whereas in *V. regularis* they are arranged in 4–5 vertical rows. The secondary network on the dermal surface of *V. regularis* is denser than in *V. alpina*, with triangular meshes and only 0.2 mm in size. Meshes of the main dictyonal network of *V. regularis* are smaller, up to 0.2 mm × 0.3 mm. Moreover, quadrangular meshes dominate in the skeleton of *V. alpina* (Lagneau-Hérenger, 1962, text-pl. 12, fig. 2d), whereas such meshes occur occasionally in *V. regularis*, only in the subdermal part of the skeleton.

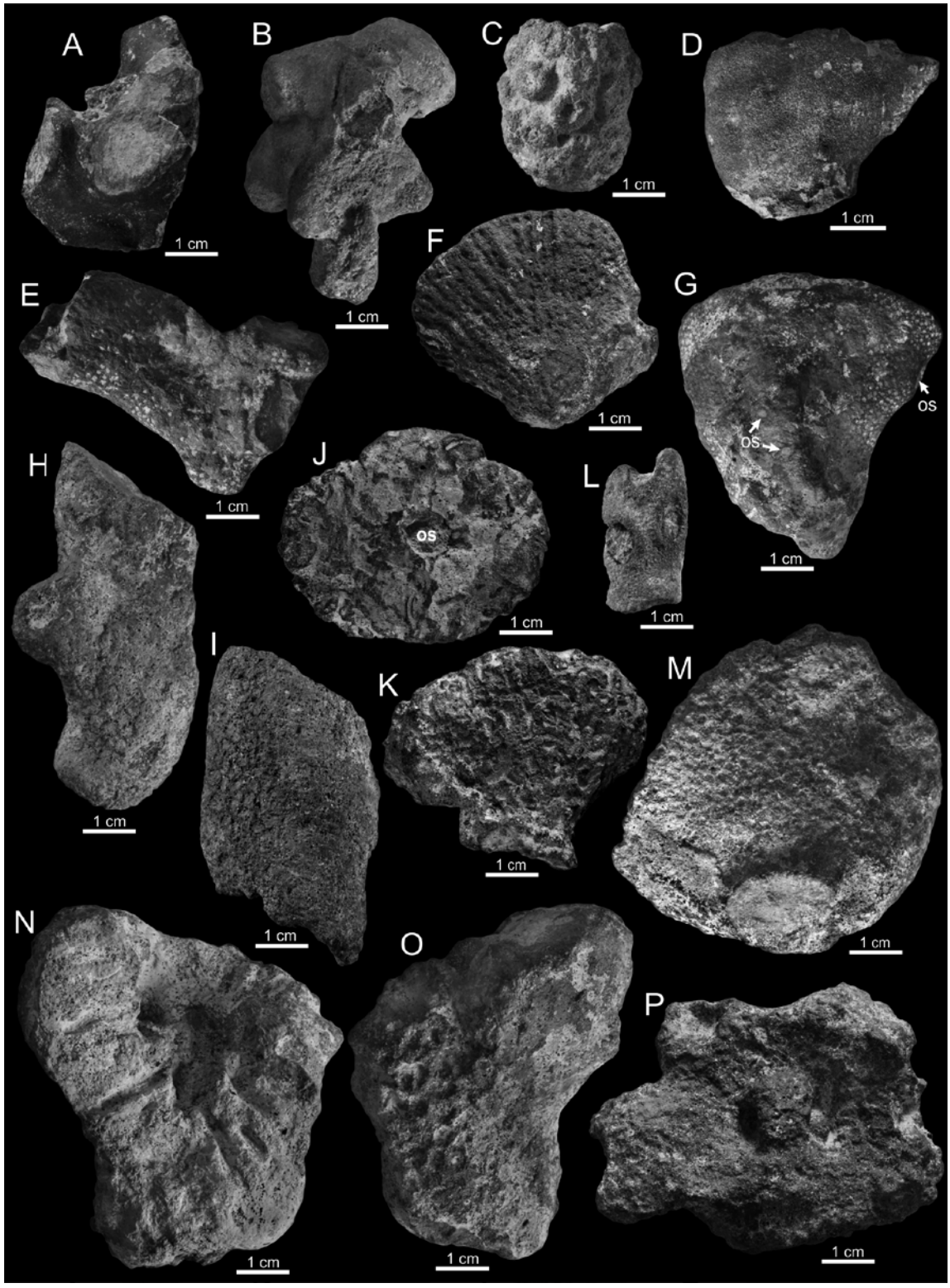


Fig. 6. Specimens of sceptrulophoran species. **A.** *Eurete mantelli* Reid, 1958; lateral view of fragmentarily preserved specimen MWG ZI/53/523, Petriv. **B.** *Verrucocoelia tubulata* (Toulmin Smith, 1848); lateral view of specimen MWG ZI/53/526, Petriv. **C.** *Verrucocoelia alpina* Hérenger, 1944; lateral view of specimen MWG ZI/53/530, Petriv. **D.** *Wollemannia* sp.; lateral view of specimen MWG ZI/52/522, Nezvys'ko S. **E.** *Laocoetis fittoni* (Mantell, 1822); lateral view of specimen MWG ZI/52/526, Nezvys'ko N. **F.** *Laocoetis cancellata* (Roemer, 1864); lateral view of specimen MWG ZI/52/528, Rakovets'. **G.** *Guettardiscyphia zitti* Vodrážka, 2017; lateral view of specimen with visible lateral oscula (os), MWG ZI/52/532, Nezvys'ko S. **H, I.** *Tretodictyum petrivensis* sp. nov.; H – lateral view of holotype; MWG ZI/53/540, Petriv; I – lateral view of paratype MWG ZI/53/542, Petriv. **J, K.** *Hexactinella* sp; J – upper view of specimen with narrow osculum (os), MWG ZI/53/580, Petriv; K – lateral view of the same specimen. **L.** *Hillendia* (?) sp.; lateral view of specimen MWG ZI/53/587, Petriv. **M.** *Petalope auriformis* Počta, 1883; lateral view of specimen MWG ZI/53/536, Petriv. **N, O.** *Cribrospongia* sp.; N – longitudinal section of specimen with wide canals visible, MWG ZI/53/534, Petriv; O – lateral view of the same specimen. **P.** *Tretodictyum complicatus* sp. nov.; lateral view of holotype MWG ZI/53/577, Petriv.

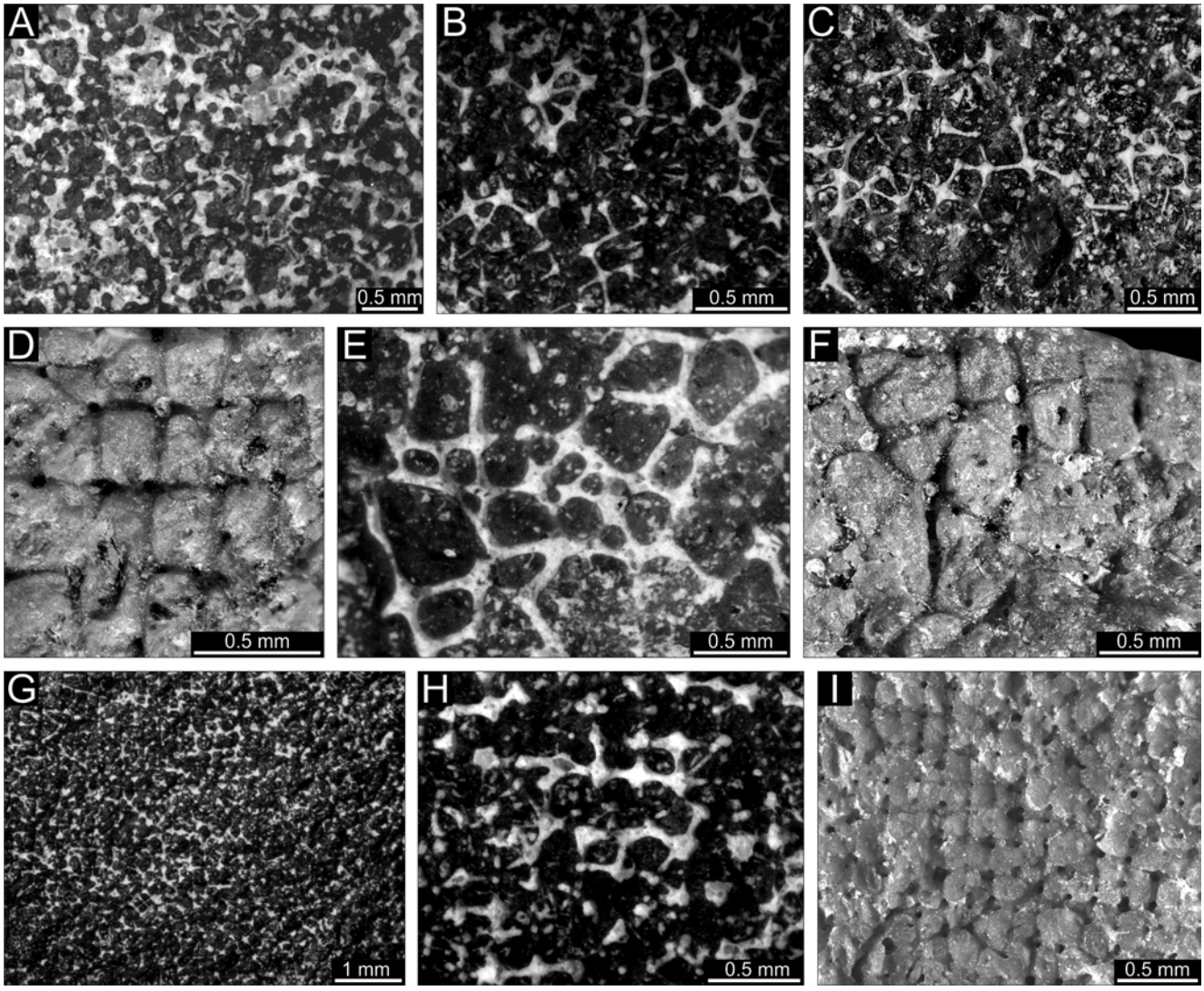


Fig. 7. Skeletons of euretoid (Sceptrulophora) species. **A, B.** *Eurete mantelli* Reid, 1958; MWG ZI/53/523, Petriv; A – dense secondary network on the dermal surface of dictyonal skeleton; B – network in the subdermal part of dictyonal skeleton. **C, D.** *Verrucocoelia tubulata* (Toulmin Smith, 1848); MWG ZI/53/527, Petriv; C – secondary network on the dermal surface of dictyonal skeleton; D – regular dictyonal skeleton, visible in longitudinal section of the wall. **E, F.** *Verrucocoelia alpina* Hérenger, 1944; MWG ZI/53/529, Petriv; E – secondary network on the dermal surface of dictyonal skeleton; F – dictyonal skeleton, visible in transverse section of the wall. **G–I.** *Wollemannia* sp.; G, H – secondary network on the dermal surface of dictyonal skeleton, MWG ZI/52/522, Nezvys'ko S; I – dictyonal skeleton, observed in a section parallel to the outer surface, MWG ZI/53/531, Petriv.

Occurrence: Western Ukraine (lower Cenomanian); Poland (Kraków area: Coniacian or/and Santonian sponges redeposited to Santonian deposits); France (Provence: Valanginian).

Genus *Wollemannia* Schrammen, 1912

Type species: *Wollemannia araneosa* Schrammen, 1912, p. 247, text-pl. 10, figs 4–6, pl. 27, fig. 2, pl. 41, fig. 5, by monotypy.

Wollemannia sp.
Figs 6D, 7G–I

Material: One specimen from Nezvys'ko S (MWG ZI/52/522), and one specimen from Petriv (MWG ZI/53/531),

Description: Cup-shaped sponges without a preserved base and apical part. The larger specimen is 30 mm high and 43 mm wide (Fig. 6D). Wall in the upper part is thin (1.5–2 mm thick), whereas near the base it is up to 5 mm. The secondary network on the dermal surface is thin, but it can reach a thickness of 0.2 mm in the lower parts of the sponges. This network comprises quadrangular or triangular meshes, usually 0.1–0.15 mm in size (Fig. 7G, H). Larger, irregular or rounded meshes, up to 0.2–0.25 mm in diameter, occasionally occur in the lower part of the sponge.

In the regular dictyonal skeleton (observed locally under the secondary network and in a section parallel to the outer surface of the sponge) dominate square, rarely rectangular meshes, 0.15–0.2 mm in size (Fig. 7I). Small triangular meshes occur occasionally. In the transverse section of the wall, there is a dense network with small (up to 0.12 mm in

size) triangular meshes and multiradiate nodes. Gastral surface invisible. Skeletal canals are not developed.
Remarks: The studied specimens were assigned to the genus *Wollemannia* due to the cup-like shape of body, very regular euretoid dictyonal skeleton, and lack of skeletal canals. In contrast to *Wollemannia araneosa*, the type species of this genus, the skeletal meshes of the studied specimens are smaller (in *W. araneosa* up to 0.5–0.6 mm in size – Schrammen, 1912; Ulbrich, 1974; Mehl, 1992; Jahnke and Gasse, 1993; Świerczewska-Gładysz, 2006, 2010; Olszewska-Nejbert and Świerczewska-Gładysz, 2011; Świerczewska-Gładysz *et al*., 2019) and meshes in the secondary network on the dermal surface are more variable in terms of shape and size.
Occurrence: Western Ukraine (lower Cenomanian).

Family Craticulariidae Rauff, 1893
Genus *Laocoetis* Pomel, 1872

Type species. *Laocoetis crassipes* Pomel, 1872, p. 93, pl. 1[ter], fig.1, pl. II, fig. 4, designated by de Laubenfels, 1955, p. 80.
Diagnosis: See Mehl (1992).

Laocoetis fittoni (Mantell, 1822)
Figs 6E, 8A

1822 *Millepora fittoni* – Mantell, p. 106, pl. 15, fig. 10.
2006 *Laocoetis fittoni* (Mantell) – Świerczewska-Gładysz, p. 241, fig. 9i (cum syn.).
2010 *Laocoetis fittoni* (Mantell) – Świerczewska-Gładysz, p. 8–9. fig. 6a, b (with additional syn.).

Material: One specimen from Rakovets' (MWG ZI/52/523), two specimens from Nezvys'ko S (MWG ZI/52/524, 525), two specimens from Nezvys'ko N (MWG ZI/52/526, 527), and one specimen from Petriv (MWG ZI/53/532).
Description: In the studied material, this species is represented by fragments of simple, dichotomously forked or irregularly fused branches (Fig. 6E). The branches are 19–31 mm in diameter with a 3–3.5 mm thick wall. On the outer surfaces the canal openings are round, rarely oval, 1.2–1.5 mm in size. They are distributed in horizontal and vertical rows. This pattern is slightly disrupted in the bifurcation points. Longitudinal and transverse skeletal bands between the canal openings are ca. 1 mm wide. On the gastral surface, only single round canal openings, ca. 1.5 mm in diameter, are visible. Canals straight, perpendicular to the wall.

Dermal surface covered by a dense, fine-porous secondary network. In the subdermal and subgastral part, the network is irregular with triangular or quadrangular meshes, usually 0.2 mm in size. The dictyonal skeleton is visible in the longitudinal section of the wall, regular with square or rectangular meshes, elongated vertically or horizontally, usually 0.25–0.3 mm × 0.3–0.35 mm in size (Fig. 8A).
Remarks: All specimens have a strongly destroyed surface, but canal openings arranged in a quadrunx, which is characteristic for *Laocoetis*, locally are clearly visible. Unforked fragments of *L. fittoni* branches described herein resemble the cylindrical specimens of *L. maxima* (Dunikowski, 1889), also present in the collection from western Ukraine, which Dunikowski (1889) described as the new species *Craticularia cylindriformis* (see Olszewska-Nejbert and Świerczewska-Gładysz, 2012). However, *L. maxima* is characterized by a very thick wall (7–10 mm) and the rectangular canal openings on its outer surface are often transversely elongated (Olszewska-Nejbert and Świerczewska-Gładysz, 2012).

Most of the described and/or illustrated sponges of *Laocoetis fittoni* (in the literature referred to as *Craticularia fittoni* or *Paracraticularia fittoni*) have a body in the form of dichotomous branches (e.g., Mantell, 1822; Hinde, 1833; Pajaud, 1973). In the studied material, the branches of one specimen are fused together similarly to some specimens from the Turonian of France (Defretin-Lefranc, 1960), the Santonian and Campanian of Poland (Świerczewska-Gładysz, 2006, 2010), and specimen no. Pl P 1548 from the Upper Chalk of England, housed in the Natural History Museum, London (2026); https://data.nhm.ac.uk/object/91347eea-c94d-4ba0-88fe-9495e853e1df/1790672485484.
Occurrence: Western Ukraine (lower Cenomanian); Poland (Kraków area: Coniacian or/and Santonian sponges redeposited to Santonian deposits; Middle Vistula valley: upper Campanian–Maastrichtian); France (Provence: Valanginian; Normandy: Cenomanian; northern Paris Basin: Turonian; southern France: Campanian after Hérenger, 1946); Czech Republic (upper Turonian); Spain (Cantabria: Aptian); Germany (Bavaria: lower Turonian; Saxony-Anhalt: lower Campanian); south-eastern England (Aptian–Coniacian, after Reid, 1968).

Laocoetis cancellata (Roemer, 1864)
Figs 6F, 8B, C

1864 *Ocellaria cancellata* – Roemer, p. 17, pl. 7, fig. 2.

Material: One specimen from Rakovets' (MWG ZI/52/528), one specimen from Nezvys'ko S (MWG ZI/52/529), two specimens from Nezvys'ko N (MWG ZI/52/530, 531), and one specimen from Petriv (MWG ZI/53/533).
Description: The material studied comprises a single, thin-walled, wide conical sponge (31 mm in height and ca. 44 mm wide; Fig. 6F) and fragments of the wall, ca. 4 mm thick. The dermal surface is with round, rarely oval canal openings, 0.8–0.9 mm × 0.8–1 mm in size. Canal openings located on the bottom of the furrows are separated by prominent ribs, 1–1.2 mm wide. Horizontal skeletal bands between the canal openings are 0.9–1.2 mm wide. The regular arrangement of the canal openings in the vertical and horizontal rows is often disturbed due to the forking of the ribs. The inner surface has canal openings of a similar size, but less densely distributed in the furrows. Long, straight canals show a craticulariid arrangement.

Both surfaces are with a dense secondary network, consisting of small, variably oriented hexactines (Fig. 8B). Network on the upper margin of the sponges is irregular with rounded, quadrangular, and rarely triangular meshes, 0.18–0.3 mm in size (Fig. 8C). In the subdermal part of the skeleton dominate rounded quadrangular meshes, 0.15–0.3 mm in size, but occasionally small triangular meshes and multiradiate nodes also occur; deeper network is not visible.
Remarks: Reid (2004a) assigned Roemer's species *Ocellaria cancellata* to the genus *Laocoetis* Pomel, 1872, which

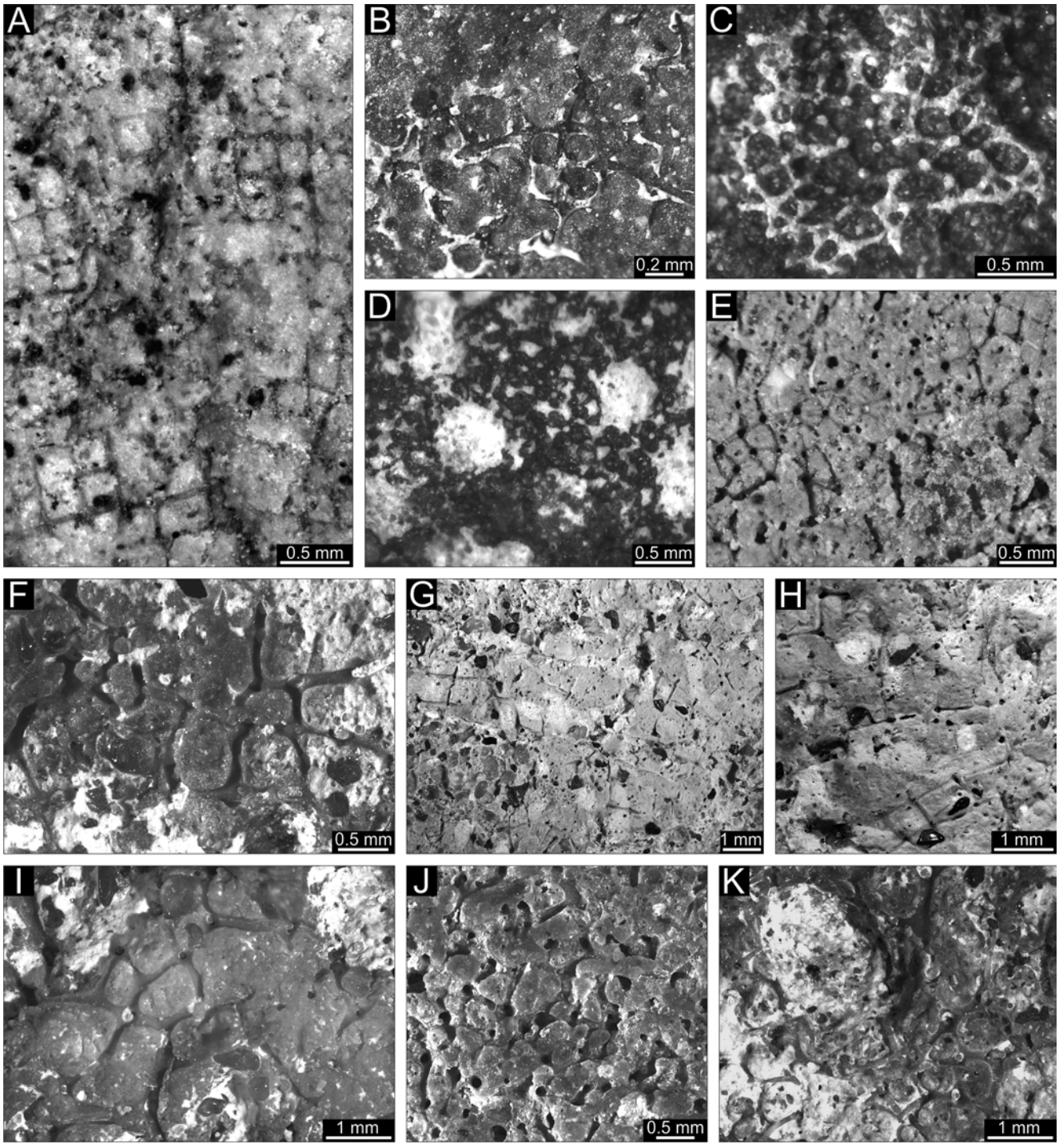


Fig. 8. Skeletons of craticulariid and cribrospongiid (Sceptrulophora) species. **A.** *Laocoetis fittoni* (Mantell, 1822); MWG ZI/52/527, Nezvys'ko N; dictyonal skeleton, visible in longitudinal section of the wall. **B, C.** *Laocoetis cancellata* (Roemer, 1864); B – secondary network on the dermal surface of the dictyonal skeleton, MWG ZI/52/528, Rakovets'; C – dictyonal skeleton, observed on the upper margin, MWG ZI/52/530, Nezvys'ko N. **D.** *Guettardiscyphia zitti* Vodrážka, 2017; secondary network on the dermal surface of the dictyonal skeleton with inhalant canal openings, MWG ZI/52/532, Nezvys'ko S. **E.** *Hillendia* (?) sp.; dictyonal skeleton, observed in transverse section of the wall, MWG ZI/53/587, Petriv. **F**–**H.** *Cribrospongia* sp.; MWG ZI/53/534, Petriv; F– irregular network on the dermal surface; G, H – regular dictyonal skeleton, visible in longitudinal section of the wall. **I**–**K.** *Petalope auriformis* Počta, 1883; MWG ZI/53/537, Petriv; I – irregular dictyonal skeleton, observed in a section parallel to the outer surface; J – irregular dictyonal skeleton, observed in transverse section of the wall; K – irregular network, observed on the inner surface.

is consistent with the views of the present authors. Characteristic features of this rare species are the presence of deep furrows on both surfaces of the sponge. In other representatives of the genus *Laocoetis*, the furrows, if present, occur only on the inner surface.

Occurrence: Western Ukraine (lower Cenomanian); Germany (Lower Saxony: Turonian).

Family: Cribrospongiidae Roemer, 1864
Genus *Guettardiscyphia* de Fromentel, 1860

Type species: *Guettardia stellata* Michelin, 1844, pp. 121–122, pl. 30, figs 1–1l, designated by de Fromentel, 1860, p. 121.

Diagnosis: see Vodrážka (2017).

Guettardiscyphia zitti Vodrážka, 2017
Figs 6G, 8D

1883 *Guettardia trilobata* Roemer – Počta, p. 23, text. fig. 9.

1969 *Guettardiscyphia* aff. *alata* (Pomel) – Khmilevsky, p. 29, pl. 5, fig. 1.

2017 *Guettardiscyphia zitti* – Vodrážka, pp. 634–637, figs 3, 4 (cum syn.).

Material: One specimen from Nezvys'ko S (MWG ZI/52/532).

Description: The only specimen, 51 mm high, is a bilaterally flattened sponge, half bent at an angle of about 120º (Fig. 6G). In the lower part of the convex side of the sponge, there is an elongated prominent rib, which is a poorly developed third lobe. The narrow side of the body is 11 mm wide; the wider side is 49 mm wide in the upper part and 16 mm wide near the broken base. The wall is 3 mm thick. Additional oscula on the narrow margins of the sponge are round or oval, 4–6 mm in diameter. Canal openings on the dermal surface are round, 0.7–1 mm in diameter, and alternately distributed. Canal openings on the gastral surface are of similar size. Canals straight, long and perpendicular to the wall surface.

Dense secondary network covering only the dermal surface (Fig. 8D). Due to phosphatization, small hexactines within this network are only occasionally recognizable. Dictyonal skeleton (visible only in the transverse section of the basal part) with quadrangular or triangular meshes, 0.2–0.3 mm in size.

Remarks: Most representatives of this species, known from the Czech Republic, have three lateral lobes, but occasionally specimens with only two lobes also occur (Vodrážka, 2017). The specimen studied here and the specimen from Horodenka, described by Khmilevsky (1969) as *Guettardiscyphia* aff. *alata* (Pomel), have one poorly developed lobe or an undeveloped lobe, respectively.

Occurrence: Western Ukraine (lower Cenomanian); Czech Republic (Turonian).

Genus *Hillendia* Reid, 1964

Type species: *Hillendia polymorpha* Reid, 1964, pp. 64, 67, text fig. 33a, b, by monotypy.

Diagnosis: See Reid (1964).

Hillendia (?) sp.
Figs 6L, 8E

Material: One specimen from Petriv (MWG ZI/53/587).

Description: The specimen is a fragment of a tubular sponge, 30 mm long and 16 mm in diameter (Fig. 6L). Thickness of wall 2.5–3 mm. The lateral oscula are arranged alternately over the entire surface of the tubes. They are oval, 8–9 mm in size and surrounded by ring-shaped thickenings, 2 mm wide. Rounded canal openings on the outer surface, 0.6–0.8 mm in size, alternately distributed. On the inner surface, the exhalant canal openings are elliptical, 0.6 mm × 1 mm in size. Canals long and perpendicular to the sponge surface. Distribution of exhalant canal openings and canals within the wall is impossible to determine.

Dermal surface is covered by a dense, secondary network with variably oriented hexactines. Meshes of this network are rounded, triangular or quadrangular, 0.1–0.15 mm, rarely 0.2 mm in size. Meshes of the primary dictyonal skeleton, visible in transverse section of the wall, rectangular or triangular, 0.1–0.15 mm in size (Fig. 8E). In longitudinal section of the wall, the meshes are rectangular, 0.2–0.4 mm in size. The gastral surface is not visible.

Remarks: The tube-like shape of the studied specimen with lateral oscula and alternately arranged inhalant canal openings leading to long canals correspond to the characteristics of the genus *Hillendia* Reid, 1964 (Reid, 1964; Vodrážka, 2017). In contrast to the representatives of this genus and other related genera with the lateral oscula, located along the narrower side of the body (e.g., *Guettardiscyphia* de Fromentel, 1860), the oscula in the studied specimens are evenly distributed on the outer surface and the body is not flattened. A similar arrangement of lateral openings is observed in some fossil representatives of *Eurete* Semper, 1868 (e.g., *Eurete lithodendron* Reid, 1961; *Eurete* (?) *setosum* Reid 1961 and *Eurete rauffi* Schrammen, 1910), but in these species such openings are outlets of the reduced lateral branches, and no canals are developed in their wall.

Occurrence: Western Ukraine (lower Cenomanian).

Genus *Cribrospongia* d'Orbigny, 1849
(= *Tremadictyon* Zittel, 1877)

Type species: *Scyphia reticulata* Goldfuss, 1826, p. 10; pl. 4, fig. 1c, by monotypy.

Cribrospongia sp.
Figs 6N, O, 8F–H

Material: Two specimens from Petriv (MWG ZI/53/534, 535).

Description: The better-preserved specimen is a thick-walled (18–19 mm), goblet-like sponge, 63 mm high and 55 mm wide in the upper part, with a thick stalk that is 39 mm wide, without the basal part preserved (Fig. 6N, O). The second specimen is only a fragmentarily preserved massive stalk, 44 mm long and 34 mm wide. The outer

surface of the specimens is covered with polygonal (mainly hexagonal) canal openings that are densely alternately arranged. These canal openings are 2.5–3 mm in size in the upper part and 2–2.5 mm in size on the stalks. The skeletal band between the canal openings is concave and ca. 1 mm wide. The inhalant and exhalant canals are wide and long, perpendicular to the surface of the wall. They have a cribrospongiid arrangement. The distribution of inhalant canal openings on the inner surface is not visible.

The dictyonal skeleton on the outer surface is very irregular, with thickened beams, so that the polygonal (mainly quadrangular) meshes are rounded (Fig. 8F). Their size is very variable from 0.15 to 0.75 mm. The network inside the wall observed in longitudinal section is very regular with transversely elongated, rectangular or trapezoidal meshes, up to 0.7–0.8 mm in size (Fig. 8G, H). The inner surface of the dictyonal skeleton is not visible.

Remarks: Species of *Cribrospongia* (= *Tremadictyon* Zittel, 1877) are known mainly from the Jurassic deposits of Europe (e.g., Mehl, 1992; Pisera, 1997). Specimens described from the Cretaceous as *Cribrospongia* do not have stauractines preserved and according to Mehl (1992) their assignment to this genus is questionable. The specimens studied here also do not have dermal and gastral megascleres preserved, but all other features correspond well to the characteristics of *Cribrospongia*. Their outer surface with large polygonal canal openings resembles the fragmentarily preserved specimens (fragments of the thick wall) from the Albian of southern France described by Lagneau-Hérenger (1962) as *Tremadictyon* aff. *cucullatum* Quenstedt, 1878. In contrast to the latter specimens, the dictyonal skeleton of the sponges from Ukraine consists of larger hexactines.

Occurrence: Western Ukraine (lower Cenomanian).

Genus *Petalope* Počta, 1883

Type species: *Petalope auriformis* Počta, 1883, p. 25, pl. 2. fig. 6a, b, text-fig. 10, designated by de Laubenfels, 1955, p. 82.

Diagnosis: See Reid (2004a).

Remarks: After Reid (2004a), the genus *Petalope* is characterized by radial canals, which are curved; however this shape of canals was noted by Počta (1883) only in *Petalope foveata*, whereas the canals of the type species *Petalope auriformis* were described as straight, which is consistent with the observations of the present authors.

Petalope auriformis Počta, 1883
Figs 6M, 8I–K

1883 *Petalope auriformis* – Počta, p. 25, pl. 2. fig. 6a, b. text-fig. 10.

Material: One specimen from Nezvys'ko S (MWG ZI/52/533), and four specimens from Petriv (MWG ZI/53/536–539).

Description: Asymmetrical bowl-like specimens, up to 52 mm wide and 43 mm high, occasionally preserved with a short stalk and a flat base (Fig. 6M). The wall thickness is usually 6 mm in the upper part of the sponge. Both surfaces are covered by round canal openings, arranged more or less in a quincunx or irregularly. The canal openings are 1.8–2 mm in diameter, separated by skeletal bands that are 1.5–1.8 mm wide. Inhalant canals are long, in upper part perpendicular to the wall surface. Exhalant canals are shorter, pit-like.

The dictyonal skeleton consists of massive, irregularly oriented hexactines, with ca. 0.1 mm thick beams. In section parallel to the outer surface, the meshes are polygonal, 0.5–1.2 mm in size (Fig. 8I). In transverse section the polygonal meshes are smaller, 0.25–0.6 mm in size (Fig. 8J). On both surfaces, the beams are thickened (up to ca. 0.15–0.2 mm) and the rounded meshes do not exceed 0.75 mm in size (Fig. 8K).

Remarks: Specimens of *Petalope auriformis*, occurring in the Cenomanian of the Czech Republic are ear-shaped sponges (Počta, 1883). In the material studied herein, platy-like fragments of the wall predominate, but the shape of a few nearly complete specimens indicates that some of them had a more regular, cup-like body.

Occurrence: Western Ukraine (lower Cenomanian); Czech Republic (Cenomanian).

Family Tretodictyidae Schulze, 1886
Genus *Tretodictyum* Schulze, 1886

Type species: *Hexactinella tubulosa* Schulze, 1886, p. 78, by monotypy.

Diagnosis: see Reid (2004a).

Remarks: The diagnosis of the extant *Tretodictyum* Schulze, 1886 is largely based on the composition of microscleres (Reiswig, 2002a; Reiswig *et al*., 2008), absent from the fossil record. In the case of extinct taxa, the genus is characterized by a schizorhysal canalization and a tube- or branch-shaped body (Reid 2004a), despite the fact that some recent species of *Hexactinella* Carter, 1885 can also have a tubular habitus (e.g., *H. aurea* Reiswig and Kelly, 2011).

Tretodictyum petrivensis sp. nov.
Figs 6H, I, 9A–F

Etymology: The name comes from the village of Petriv; numerous specimens of this species were found in a quarry near Petriv.

Holotype: MWG ZI/53/540 (Figs 6H, 9A).

Paratypes: Thirty-five specimens (MWG ZI/53/541–575).

Other material: Two specimens from Nezvys'ko S (MWG ZI/52/534, 535), one specimen from Nezvys'ko N (MWG ZI/52/536), and one specimen from Horodenka (MWG ZI/53/576).

Type locality and stratigraphic horizon: Petriv (western Ukraine), large working quarry, located 2 km to the southwest of Petriv village. GPS locality: 48°49′50.8″N; 25°15′55.9″E +/–3 m. Clayey marls directly below the base of the inoceramid limestones, lower Cenomanian.

Diagnosis: Tube-like sponges, up to 40 mm wide and 65 mm high, often forked or with a lateral branch. Thick wall with labyrinthine schizorhyses. Schizorhyse openings on the outer surface in the shape of rounded polygons, 2–3 mm in size, irregularly distributed. Inner surface with short crack and small opening. Euretoid skeleton with dictyonal strands

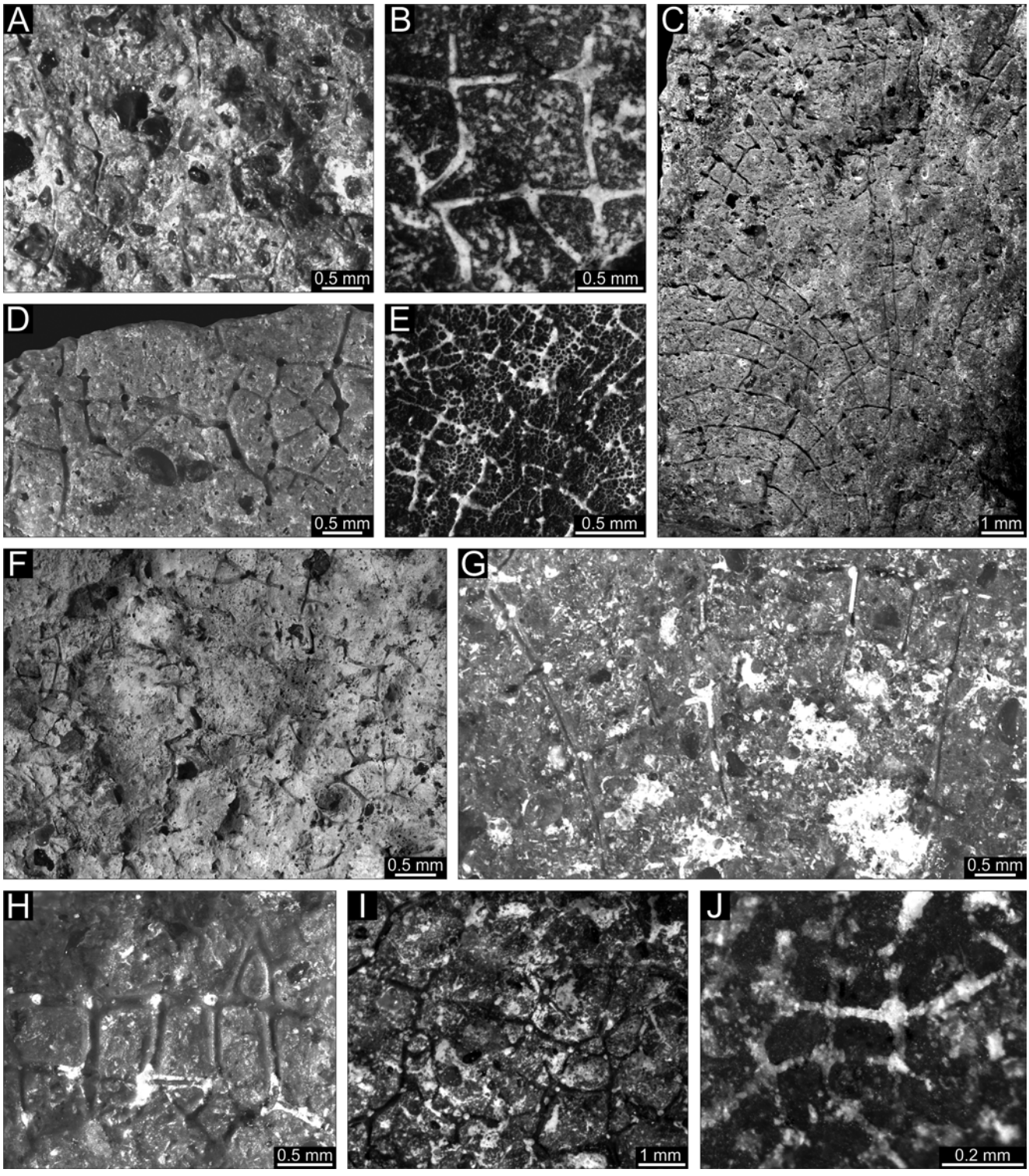


Fig. 9. Skeletons of tretodictyid (Sceptrulophora) species. **A**–**F.** *Tretodictyum petrivensis* sp. nov.; A – network on the dermal surface, holotype MWG ZI/53/540, Petriv; B – fragment of network with curved beams, MWG ZI/53/542, Petriv; C – dictyonal strands, visible in longitudinal section of the wall, MWG ZI/53/54l, Petriv; D – network in transverse section of the wall near the dermal surface (at the top), MWG ZI/53/54l, Petriv; E – basal skeleton with modified hexactines and synapticules, MWG ZI/53/543, Petriv; F – network in transverse section of the wall with schizorhyses, MWG ZI/53/544, Petriv. **G**–**I.** *Tretodictyum complicatus* sp. nov.; holotype MWG ZI/53/577; Petriv; G – dictyonal strands, visible in longitudinal section of the wall; H – network, observed in transverse section of the wall; I – network on the dermal surface. **J.** *Hexactinella* sp.; dictyonal skeleton, observed in transverse section of the wall, MWG ZI/53/580, Petriv.

arranged bilaterally, with more strongly curved strands towards the dermal surface. Beams of network often strongly curved. Meshes of network of various size; the largest being usually quadrangular, up to 0.9–1 mm in size. No secondary layer of network on both surfaces of dictyonal skeleton.

Description: The sponge body consists of thick-walled (0.6–1.1 mm), cylindrical or narrow conical branches, which are simple, forked or with a lateral branch, rarely with small swellings (Fig. 6H, I). The largest, fragmentarily preserved specimens are up to 65 mm high and 40 mm wide. Base (if preserved) is flat or concave, often strongly extended and oblique to the branch axis. Outer surface with rounded polygonal canal openings, 2 mm in size, rarely up to 3 mm, randomly distributed. Skeletal bands between the canal openings are usually 2–3 mm wide. Short, widening crack (ca. 2 mm in size) and small (1–1.5 mm in size), rounded or elongated openings on the inner surface are also irregularly distributed. Inside the wall, the width of the branching canals usually does not exceed 1 mm. In the subdermal part of the dictyonal skeleton (in section parallel to surface), these canals are curved, winding or branched. Additionally, numerous small holes (0.7–1 mm in size) are noted, which are the cross-sections of canals, ending blindly beneath the outer surface.

In longitudinal section, the dictyonal strands show a bilateral and strongly asymmetric arrangement. The bands towards the gastral surface are at an angle of ca. 45°, whereas towards the dermal surface at ca. 90°; in the central part of the wall, the dictyonal strands are nearly parallel to both surfaces. The network is not very regular because the hexactines vary in size and the beams are often curved (Fig. 9B, C). The dominant quadrangular meshes are 0.5–0.9 mm in size; pentagonal, rectangular or triangular meshes also occur. In transverse section of the wall the network is irregular with polygonal and triangular meshes, 0.4–0.7 mm in size (Fig. 9D, F). The irregular network on both surfaces (poorly preserved) is with polygonal or triangular meshes, up to 1 mm. The basal skeleton comprises modified hexactines (pentactines?), connected by synapticular filaments (Fig. 9E).

Remarks: Two species of *Tretodictyum*, i.e., *T. loeschmanni* Schrammen, 1912 and *T. pfaffi* Schrammen, 1912, were described from the Cretaceous. Due to the tubular shape of the body, the proposed new species resembles rather *T. pfaffi*, but the tubes of this species are thin-walled, more branched and their diameter only slightly exceeds 10 mm. Based on Schrammen's (1912) description (irregular network on the outer surface and regular network on the inner surface), it can be concluded that the arrangement of dictyonal strands in *T. pfaffi* is bilateral and asymmetric as in *Tretodictyum petrivensis* sp. nov., but the network meshes of the new species are at least twice as large. A large-meshed and not very regular skeleton occurs in some recent species of *Tretodictyum*, e.g. *T. cocosensis* Reiswig, 2010 and *T. amchitkensis* Reiswig and Stone, 2013.

Tretodictyum complicatus sp. nov.
Figs 6P, 9G–I

Etymology: *Complicatus* (Latin) – complicated. The species name refers to the complicated form of the sponge body.

Holotype: MWG ZI/53/577 (Figs 6P, 9G-I).

Paratypes: Two specimens (MWG ZI/53/578, 579).

Other material: One specimen from Nezvys'ko S (MWG ZI/52/537).

Type locality and stratigraphic horizon: Petriv (western Ukraine), large working quarry located 2 km to the southwest of Petriv village. GPS locality: 48°49′50.8″N; 25°15′55.9″E +/–3 m. Clayey marls directly below the base of the inoceramid limestones, lower Cenomanian.

Diagnosis: Thick-walled, irregular bulbous sponge, comprising convoluted lamellae and short tubes. Both surfaces with variously shaped canal openings that are randomly distributed, up to 4.5 mm in size on the outer surface and 2 mm in size on the inner surface. Choanosomal canalization in the form of labyrinthine schizorhyses. Large hexactines formed inside the wall forming a regular dictyonal network, usually with rectangular meshes, up to 1.0–1.2 mm in size. Dictyonal strands arranged bilaterally. Secondary network not developed on both surfaces of dictyonal skeleton.

Description: Irregular bulbous sponges, up to 70 mm in size, comprising folds and short tubes, 17–30 mm in diameter, which are blind or with an irregular opening (Fig. 6P). Wall thickness is 7–12 mm. Basal part is not preserved. The outer surface contains randomly distributed canal openings. They are usually rounded, oval or irregular, 1.5–3 mm in size, rarely in the shape of short slits, up to 4.5 mm long. Prominent skeletal bands between them are 1–2.5 mm wide. In places, where the outer surface is destroyed, irregularly branched canals or chambers are visible. On the inner surface the canal openings are rounded or oval, 2 mm in size, irregularly distributed, and spaced at 1.5–3.5 mm.

The euretoid type of skeleton contains bilaterally arranged dictyonal strands (due to the damage and folding of the specimen wall, it is not possible to clearly determine at what angle the skeletal bands bend directly next to both surfaces of the sponge). In longitudinal section of the wall, the network meshes are usually rectangular, 0.5–0.6 mm × 0.7–1.2 mm in size (Fig. 9G). In transverse section of the wall, the network consists of quadrangular meshes, 0.5–0.6 mm in size and smaller triangular meshes, up to 0.3 mm in size (Fig. 9H). The network on both surfaces is irregular with polygonal meshes usually 0.5–0.8 mm in size but occasionally reaching up to 1 mm (Fig. 9I). In places, where additionally small hexactines occur, the meshes are triangular, 0.3–0.5 mm in size.

Remarks: In addition to its different body shape, *Tretodictyum complicatus* sp. nov. differs from *Tretodictyum petrivensis* sp. nov. in having larger canal openings on both surfaces and a more regular skeleton within the wall. A body, composed of irregularly connected tubes, resembling the shape of the new species, is characteristic of the Campanian species *T. loeschmanni* Schrammen, 1912, but its tubes are thin-walled. Moreover, the dictyonal skeleton of *T. loeschmanni* contains very small hexactines, and both its surfaces are covered by a dense secondary network (Schrammen, 1912).

Genus *Hexactinella* Carter, 1885

Type species: *Hexactinella ventilabrum* Carter, 1885, p. 397, by monotypy.

Diagnosis: see Reid (2004a).
Remarks: Distinguishing the extant representatives of the genus *Hexactinella* Carter, 1885 from the closely related genus *Tretodictyum* Schulze, 1886 is based on the composition of microscleres, which are not preserved in the fossil record (Reiswig, 2002a; Reiswig *et al*., 2008; Reiswig and Kelly, 2011). Therefore, in the case of fossil specimens, representatives of this genus include cup- or funnel-like sponges with cleftform to labyrinthine schizorhyses and a skeleton without swollen surface dictyonal nodes (Reid, 2004a).

Hexactinella sp.
Figs 6J, K, 9J

Material: One specimen from Petriv (MWG ZI/53/580).
Description: Funnel-like sponge with short stalk (Fig. 6K). The specimen is 43 mm high and 49 mm wide. The spongocoel is very narrow, 9 mm in diameter (Fig. 6J); its surface is not visible. The outer surface has winding fissures, 1.2–2 mm wide, separated by flat skeletal bands, 2 mm wide. Sparsely arranged round canal openings, 1–1.3 mm in diameter, are located on these bands. The thick wall (20 mm) contains labyrinth-like schizorhysis, ca. 2 mm wide, separated by skeletal septa of a similar width.

Dictyonal hexactines (very poorly preserved) in transverse section of the wall form a network with quadrangular, less frequently triangular or pentagonal meshes, 0.1–0.2 mm in size (Fig. 9J). Beams in the surface network (very poorly preserved) are thickened, rounded meshes are very small, up to 0.1 mm in size.
Remarks. The thick-walled cup shape with labyrinthine schizorhyses is typical for *Hexactinella* Carter, 1885 and *Psilocalyx* Ijima, 1927, but in the latter genus the apertures of schizorhyses are wide and rounded (Reiswig, 2002a). Nodes in the external hypersilicified part of the dictyonal skeleton of *Psilocalyx* are swollen, a feature that was not observed in the analysed specimen, and therefore it was assigned to *Hexactinella*. Representatives of the genus *Hexactinella* are known mainly from recent seas, the fossil species being rare (Mehl and Fürsich, 1997; Pisera and Busquets, 2002). Only a few species of *Hexactinella* were described from the Cretaceous, but some of these are currently included in the genus *Polyopesia* Schrammen, 1902 (Reid, 1963). The systematic position of several other species, such as *H. digitata* (Regnard, 1926), *H. alpina* (Lagneau-Hérenger, 1962) and *H. nymphaea* (Defretin-Lefranc, 1960), is unclear. Due to the well-developed labyrinth-like schizorhysis, the specimen studied here resembles rather *Hexactinella* sp. from the Campanian of Poland (Świerczewska-Gładysz, 2006), but in that species there are no fissures on the outer surface, and the canal openings are round or comma-like. Despite these facts, a new species was not proposed, due to the poor state of preservation of the skeleton.

Order Lychniscosida Schrammen, 1903
Family Callodictyonidae Zittel, 1877
Genus *Brachiolites* Toulmin Smith, 1848

Type species: *Brachiolites fenestratus* Toulmin Smith, 1848, pp. 367–368, pl. 16, fig. 3, designated by Reid, 1958b, p. 263.
Diagnosis: See Reid (2004b).
Remarks: The diagnoses of the genera *Brachiolites* Toulmin Smith, 1848 and *Plocoscyphia* Reuss, 1846 are based mainly on macroscopic features. In both genera there are no skeletal canals and no spongocoel, and their tubes are divided dichotomously, but in *Brachiolites*, unlike *Plocoscyphia*, they do not form anastomoses (Reid, 2004b). The main dictyonal skeletons of both genera are similar, but within these genera there are species with an irregular secondary network or synapticular cortex, as also without a special external network on the dermal surface. Thus, a revision of these genera is necessary, but this requires re-examination of the type specimens of all species representing these genera, as they are poorly described in the literature; this, however, is beyond the scope of the present article.

Brachiolites elongatus sp. nov.
Figs 10A, 11A, B

Diagnosis: Sponges composed of dichotomously divided tubes, up to 15 mm in diameter. Tubes, growing from a wide base, initially vertical and densely packed; terminal tubes arranged diagonally. Dictyonal skeleton without a canal, consisting of large lychniscs forming a regular network with rectangular or square meshes up to 0.3–0.4 mm in size. Cortical structures not developed.
Etymology: *Elongatus* (Latin) – elongated. The name refers to the elongated shape of the sponge.
Holotype: MWG ZI/52/538 (Figs 10A, 11A, B).
Other material: One specimen from Petriv (MWG ZI/53/581).
Type locality and stratigraphic horizon: Rakovets' (western Ukraine), exposure near the road. GPS locality: 48°47'42.4"N; 25°17'52.3"E +/–3 m. Clayey marls directly below the base of the inoceramid limestones, lower Cenomanian.
Description: Sponges, up to 62 mm high and ca. 55 mm wide, composed of dichotomously divided tubes, ca. 15 mm in diameter, growing from a wide (ca. 40 mm in size) base (Fig. 10A). Due to the fragmentary preservation of both specimens under study, it is not possible to determine how many tubes grew directly from the base. The tubes in the lower part of the sponges are vertical and densely packed, whereas after the division, the tubes are oriented diagonally. Top of tube is rounded, with a terminal osculum slightly narrower than the tube diameter. Wall is 2 mm thick, without canals.

The dictyonal network contains hexactines with large octahedral nodes and thick beams. The skeleton is regular with square, rectangular or trapezoidal meshes, 0.25–0.3 mm × 0.3–0.4 mm in size (Fig. 11A). On the dermal surface, less regularly oriented hexactines form a network with rounded meshes, 0.3–0.35 mm in size (Fig. 11B). The gastral surface is not visible.
Remarks: The skeletal structure of the new species described here is similar to that of *Brachiolites aptiensis* (Hérenger, 1942), which co-occurs with it in the material from western Ukraine. The latter species also has dichotomous branches, but they are significantly shorter, more densely packed, and are connected by skeletal bridges, resulting in the sponges having a bulbous shape (see Hérenger, 1942; Lagneau-Hérenger,

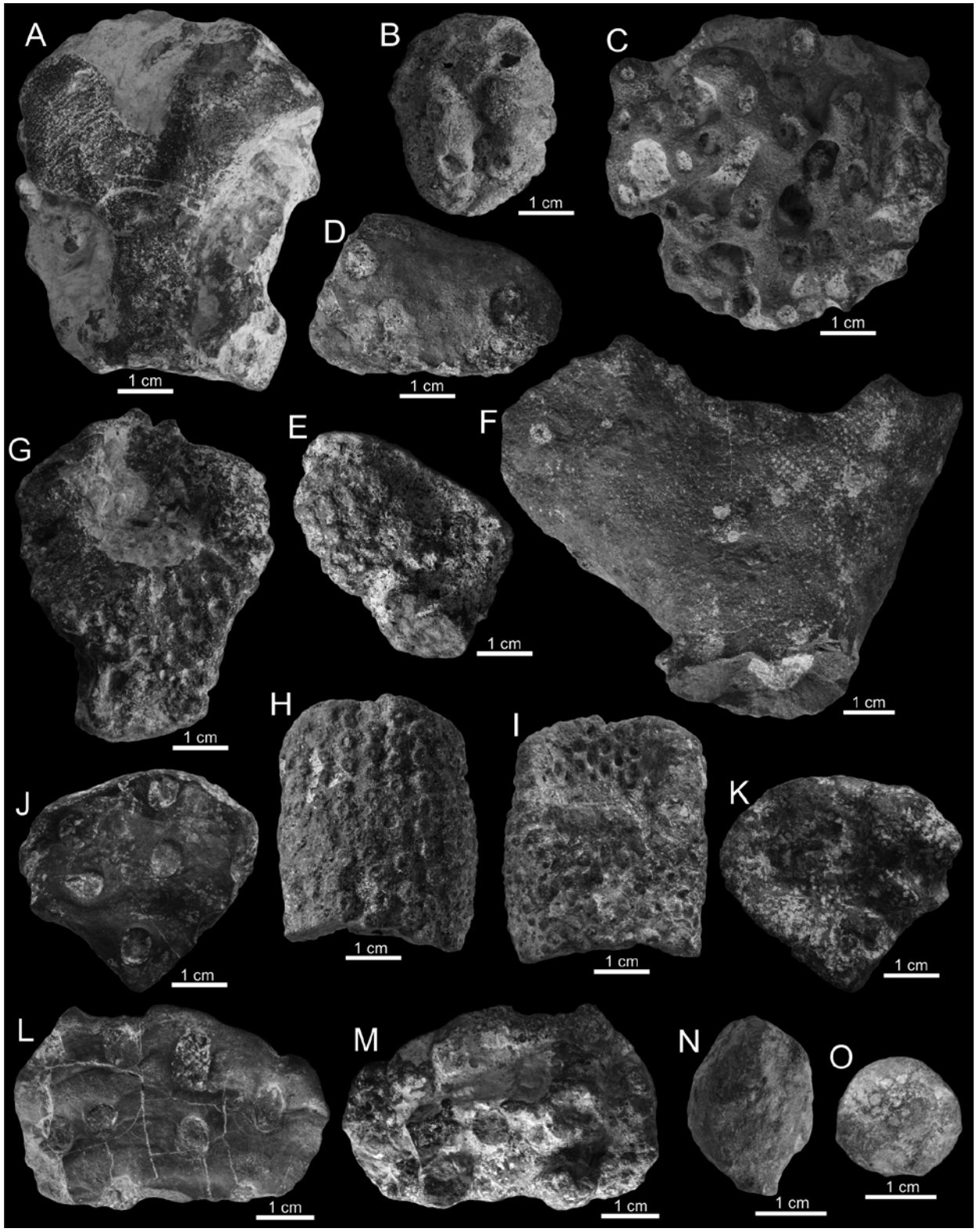


Fig. 10. Specimens of lychniscosidan and lithistid species. **A.** *Brachiolites elongatus* sp. nov.; lateral view of holotype MWG ZI/52/538, Rakovets'. **B, C.** *Plocoscyphia anastomosa* sp. nov.; B – lateral view of paratype MWG ZI/53/583, Petriv; C – lateral view of holotype MWG ZI/53/582, Petriv. **D, E.** *Trematobolites megastoma* (Roemer, 1841); MWG ZI/52/540, Nezvys'ko S; D – upper view of specimen; E – lateral view of the same specimen. **F.** *Coscinopora macropora* Goldfuss, 1826; lateral view of specimen; MWG ZI/52/545, Nezvys'ko S; **G**. *Rhizopoterion* sp.; lateral view of specimen; MWG ZI/52/546, Rakovets'. **H, I.** *Khmilevskia papillata* gen. and sp. nov.; holotype MWG ZI/52/547, Rakovets'; H – lateral view of side with better-preserved papillae; I – lateral view of opposite, destroyed side with exhalant canal openings, visible in the upper part of the inner surface**. J**–**M.** *Ophrystoma olehii* sp. nov.; J – upper surface of specimen MWG ZI/52/550, Rakovets'. K – lower surface of the same specimen; L – upper surface of holotype MWG ZI/52/548, Nezvys'ko S; M – lower surface of holotype. **N, O.** *Jerea* sp.; MWG ZI/52/554, Rakovets'; N – lateral view of specimen, O – upper view with visible exhalant canal openings.

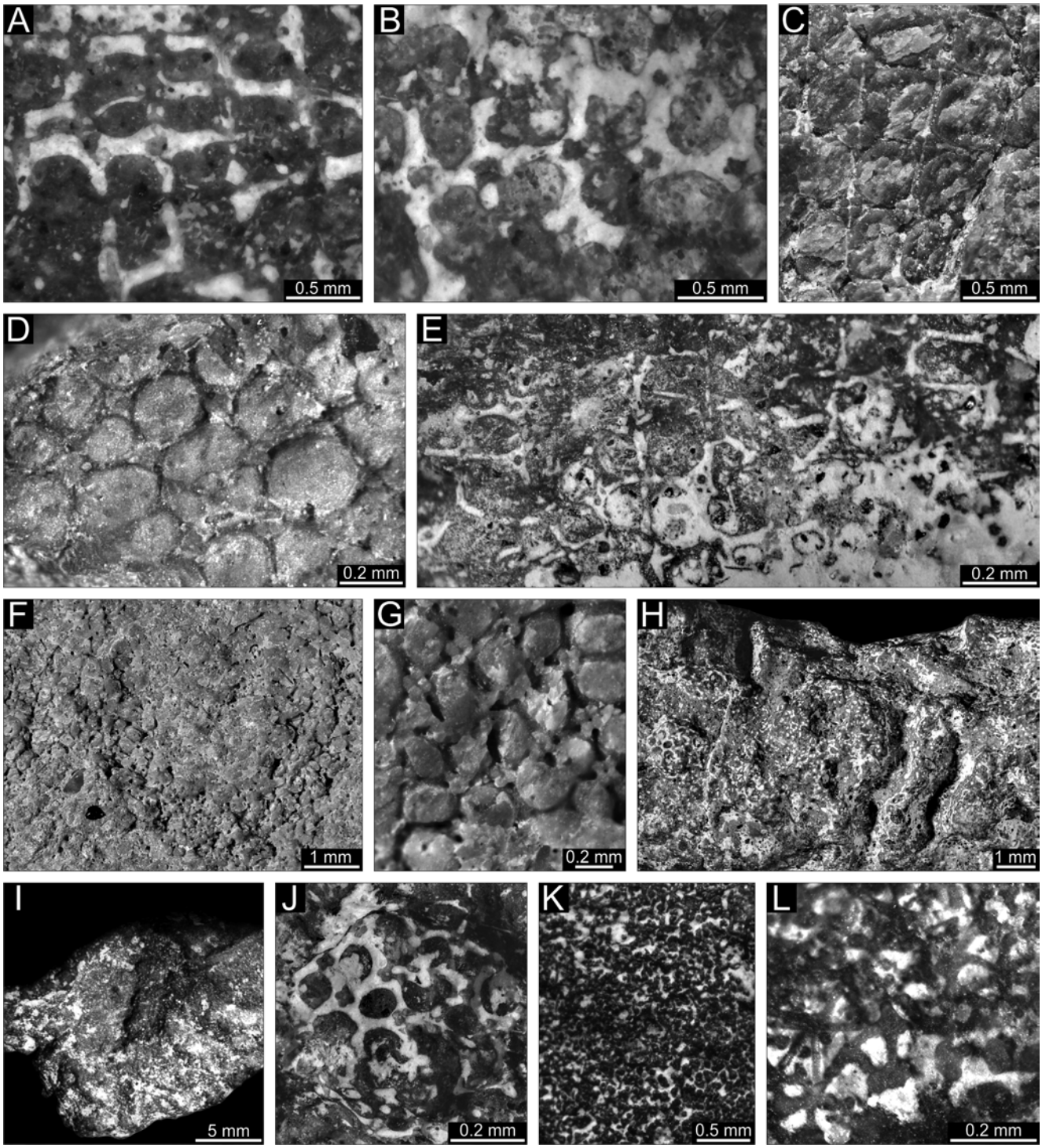


Fig. 11. Skeletons of lychniscosidan species. **A, B**. *Brachiolites elongatus* sp. nov.; holotype MWG ZI/52/538, Rakovets'; A – subdermal part of dictyonal skeleton, B – disturbed network on dermal surface. C–E. *Plocoscyphia anastomosa* sp. nov.; C – dictyonal skeleton, visible in longitudinal section, MWG ZI/52/539, Nezvys'ko S; D – dictyonal skeleton, visible in transverse section, MWG ZI/52/539, Nezvys'ko S; E – disturbed network on the dermal surface, holotype MWG ZI/53/582, Petriv. **F, G.** *Tremabolites megastoma* (Roemer, 1841); MWG ZI/52/540, Nezvys'ko S; F – transverse section of the tube wall; G – detail of dictyonal skeleton, visible in transverse section of the tube wall. **H–L.** *Ophrystoma olehii* sp. nov. H – transverse section of the wall with canals, holotype MWG ZI/52/548, Nezvys'ko S; I – transverse section of the wall with canals and pit-like cavity, MWG ZI/52/550, Rakovets'; J – network on the dermal surface, holotype MWG ZI/52/548, Nezvys'ko S; K, L – dense network on gastral surface with secondary hexactines, holotype MWG ZI/52/548, Nezvys'ko S.

1962; Olszewska-Nejbert and Świerczewska-Gładysz, 2013). The habitus of *Brachiolites elongatus* sp. nov. is also similar to that of *Brachiolites* sp. from the Upper Turonian of the Opole Basin in southern Poland. However, in that species, the dermal surface of the tubes is covered by a loose synapticular cortex with pores up to 0.8 mm in size (Świerczewska-Gładysz *et al*., 2019). Due to the vertical arrangement of the tubes and the lack of central cavities, the specimens described here resemble representatives of the genus *Cavispongia* Quenstedt, 1878, but in this genus, the external branches have short, lateral outgrowths or rounded knobs (Reid, 2004b; Frisone *et al*., 2016).

Genus *Plocoscyphia* Reuss, 1846

Type species: *Scyphia labyrinthica* Reuss, 1844, p. 173, by monotypy.
Diagnosis: See Reid (2004b).

Plocoscyphia anastomosa sp. nov.
Figs 10B, C, 11C–E

Diagnosis: Bulbous sponges, consisting of thin-walled, dichotomously divided tubes, which on the outer surface are connected by skeletal bridges, forming rounded, anastomosing ridges with rounded openings. Ridges separated by elongated or furrow-like cavities. Hexactines with large octahedral nodes forming a regular skeleton, with rounded rectangular or square meshes 0.25–0.4 mm × 0.3–0.5 mm in size. Network on the dermal surface less regular. Skeletal canal not developed.
Etymology: *Anastomosis* (Greek) – anastomosis. The name refers to the habitus of the sponge, characterised by anastomosing ridges on the outer surface.
Holotype: MWG ZI/53/582 (Figs 10C, 11E).
Paratype: One specimen (MWG ZI/53/583).
Other material: One specimen from Nezvys'ko S (MWG ZI/52/539).
Type locality and stratigraphic horizon: Petriv (western Ukraine), large working quarry, located 2 km to the southwest of Petriv village. GPS locality: 48°49′50.8″N; 25°15′55.9″E +/–3 m. Clayey marls directly below the base of the inoceramid limestones, lower Cenomanian.
Description: The largest specimen (holotype) is a fragmentarily preserved bulbous sponge, 55 mm × 60 mm in size (Fig. 10C). Two other specimens are small, 35 mm and 37 mm in length (Fig. 10B). The sponge body consists of dichotomously, thin-walled (1.2–1.5 mm thick), divided tubes. Distal parts of tubes are connected by skeletal bridges, forming anastomosing ridges, 7–10 mm wide. Cavities between the ridges are elongated or furrow-like, similar in width. Openings on the ridges (corresponding to the tube outlets) are rounded or oval, 4–6 mm in size, and spaced at 4–9 mm. Some tubes located near the upper margin of the specimens are unfused and measure 7–8 mm in diameter. Pores on the sponge surface and skeletal canals are not present.

The dictyonal skeleton consists of massive hexactines with large octahedral nodes. Inside the wall, in a section parallel to the surface of the tubes, the skeleton is regular with rounded quadrangular meshes (mainly rectangular, rarely square or trapezoidal), 0.25–0.4 mm × 0.3–0.5 mm in size (Fig. 11C). In the transverse section of the tubes, the lychniscs are more densely packed and the network is less regular with meshes 0.15–0.3 mm in size (Fig. 11D). Network on the dermal surface is locally disturbed with thickened beams and rounded meshes, 0.2–0.3 mm in size (Fig. 11E). Dictyonal cortex is not developed.
Remarks: The feature, which distinguishes the proposed new species from other representatives of the genus *Plocoscyphia*, is the presence of anastomosing ridges with sparsely arranged openings, corresponding to the outlets of the tubes, connected by skeletal bridges. In some species included in *Plocoscyphia*, the tubes can grow together, but in that case they form open meandriform folds (e.g., Hinde, 1883; Leonhard 1897; Schrammen, 1912; Moret, 1926). Fusion of the superficial tubes in a way similar to *Plocoscyphia anastomosa* sp. nov. appears in the representatives of *Beckia* Schlüter, 1868, *Toulminia* Zittel, 1877 and *Rigonia* Frisone, Pisera and Preto, 2016. However, the first two genera have a central cavity and *Toulminia* additionally has an apex with a silica membrane (Reid, 2004b). In turn, *Rigonia* is a sceptrulophoran species (Frisone *et al*., 2016).

Genus *Tremabolites* Zittel, 1877

Type species: *Manon megastoma* Roemer, 1841, p. 3, pl. 1, fig. 9, designation by de Laubenfels, 1955, p. 89.
Diagnosis: See Reid (2004b).

Tremabolites megastoma (Roemer, 1841)
Figs 10D, E, 11F, G

1841 *Manon megastoma* – Roemer, p. 3, pl. 1, fig. 9.
2006 *Tremabolites megastoma* (Roemer) – Świerczewska-Gładysz, pp. 269–270, figs 35c, 36h (cum syn.).
2021 *Tremabolites megastoma* (Roemer) – Pervushov, 114–115, pl. 1 figs 1, 2.

Material: Three specimens from Nezvys'ko S (MWG ZI/52/540–542), 1 specimen from Horodenka (MWG ZI/53/584).
Description: Nodular, usually asymmetrical specimens, up to 70 mm in size, occasionally with a short, thick stalk preserved (Fig. 10E). Sponges consist of thin-walled (ca. 1–1.5 mm) anastomosing tubes, 3–8 mm in diameter. Inlets of tubes are located on a slightly convex dermal side. The gastral side is strongly convex and covered by a thick membrane with a few round or elongated openings, 0.4–0.8 mm in size (Fig. 10D). Openings with protruding margin are distributed irregularly.

Dictyonal skeleton with rounded square or rectangular meshes, 0.25–0.3 mm × 0.25–0.35 mm in size is observed only in transversal section of the stalk (Fig. 11F, G). Canals in choanosomal skeleton not developed.
Remarks. *Tremabolites megastoma* (Roemer, 1841) is a polymorphic species (Mehl, 1992), and the specimens studied here correspond to the morphotype with small tubes, described by Schrammen (1910) as the new species *T. leonhardi*. Specimens of *T. megastoma*, including those in the

studied material, are often asymmetric (Quenstedt, 1878; unpublished observations of EŚG on material from the upper Turonian and lower Coniacian of the Opole Basin, southern Poland), which is probably a feature, related to the habitat (e.g., settling on a hard uneven ground).
Occurrence: Western Ukraine (lower Cenomanian); Poland (Middle Vistula valley: upper Campanian); Opole area: upper Turonian; Kraków area: Santonian); Spain (Catalonia: Aptian); France (south-eastern France: Albian; northern France: Coniacian); Czech Republic (Cenomanian); Russia (Saratov area: Santonian); Germany (Lower Saxony: Turonian–Campanian).

Family Ventriculitidae Toulmin Smith, 1848
Genus *Coscinopora* Goldfuss, 1826

Type species: *Coscinopora infundibuliformis* Goldfuss, 1826, p. 31, pl. 9, fig. 17, by monotypy.
Diagnosis: See Reid (2004b).

Coscinopora macropora Goldfuss, 1826
Figs 10F, 12A, B

1826 *Coscinopora macropora* nobis – Goldfuss, p. 31, pl. 9, fig. 17.
1877 *Coscinopora macropora* Goldfuss – Zittel, p. 49, p. 31, pl. 9, fig. 17.
1912 *Coscinopora macropora* Goldfuss – Schrammen, p. 293.
1960 *Coscinopora macropora* Goldfuss – Defretin-Lefranc, pp. 80–81, pl. 10, figs 1–3, text-fig. 22.

Material: One specimen from Rakovets' (MWG ZI/52/543), one specimen from Nezvys'ko S (MWG ZI/52/544), one specimen from Nezvys'ko N (MWG ZI/52/545).
Description: Wide-conical sponges, up to 70 mm high and 95 mm wide, with a rounded or flat base, sometimes with a short, thick stalk (Fig. 10F). Wall in the upper part is 2–3 mm thick; in the lower part 4 mm thick; in the tube-like part of the stalk 6–9 mm thick. The outer surface is covered by round canal openings, usually 0.5 mm in diameter, occasionally up to 0.7 mm and arranged in a quincunx. The average density of canal openings is 60–80/cm^2. The inner surface is not visible. The canals are straight, long and perpendicular to the wall.

Hexactines with small nodal octahedrals form a very regular dictyonal network (visible in longitudinal and transverse sections of the wall) with small, square and rectangular meshes, 0.2 mm × 0.2–0.3 mm in size (Fig. 12A, B). Only locally the network is disturbed by additional lychniscs (Fig. 12B). In the subdermal part the meshes are square, 0.3 mm in size. The dermal surface is covered by a fine porously synapticular cortex (only locally preserved), consisting of hexactines without nodal octahedrals. Gastral surface not visible.
Remarks: *C. macropora* differs from the very common Cretaceous species *C. infundibuliformis* Goldfuss, 1826, in its larger canal openings (Goldfuss, 1826; Schrammen, 1912; Defretin-Lefranc, 1960). Ventruclitid species often show a large variation in size of the canal openings, and it cannot be ruled out that *C. macropora* is one of the morphotypes of *C. infundibuliformis*, but this hypothesis requires further research, based on more abundant material.

The specimens studied here, in comparison to the known representatives of *Coscinopora macropora* Goldfuss, 1826, show relatively large and sparsely distributed canal openings. According to Schrammen (1912) and Defretin-Lefranc (1960), the density of canal openings in *C. macropora* can reach as many as 100 per 1 cm^2. From this point, the morphology of the outer surface of the specimens from western Ukraine resembles some specimens of *S. alcynoides* from the Turonian of the Opole area (Southern Poland), which are characterized by small canal openings, but in the latter species the inhalant and exhalant canals are interconnected by tangential passages (Świerczewska-Gładysz, 2006, 2012).

C. macropora was previously noted in the Cenomanian of Ukraine by Khmilevsky (1969), but this author did not describe or illustrate the lychniscs in the specimens studied. The lack of visible nodal octahedrals may be due to the poor state of preservation of the specimens, but it cannot be ruled out that these specimens belong to sceptrulophoran species.
Occurrence: Western Ukraine (lower Cenomanian); northern France (Turonian, Coniacian); Germany (Westphalia, Turonian).

Genus *Rhizopoterion* Zittel, 1877

Type species: *Siphonia cervicornis* Goldfuss, 1826, p. 17; pl. 6, fig. 11, by monotypy.
Diagnosis: See Reid (2004b).

Rhizopoterion sp.
Figs 10G, 12C, D

Material: One specimen from Rakovets' (MWG ZI/52/546).
Description: Funnel-like sponge, 54 mm high and 45 mm wide in the upper part, where the wall is 12 mm thick (Fig. 10G). Basal part not preserved. Outer surface with oval canal openings, 2–3 mm × 3–4 mm in size, arranged in quincunx. A flat skeletal band separates the canal openings up to 3 mm wide. On the inner surface, the exhalant canals are round, ca. 2 mm in diameter (their arrangement is impossible to determine). The inhalant and exhalant canals are long, straight and perpendicular to the sponge surfaces. Additional canals run near the outer surface (Fig. 12C).

The dictyonal skeleton (observed in transverse section of the wall) is irregular and consists of hexactines of various size with large octahedral nodes (Fig. 12D). The rounded meshes are usually up to 0.4–0.5 mm in size, occasionally even 0.6 mm in size. Locally, a finely-porous synapticular cortex is preserved on both surfaces of the sponge.
Remarks: The diagnostic feature for *Rhizopoterion* Zittel, 1877 is the presence of canals running beneath the dermal surface that connect with exhalant canals (Reid, 1962a; Świerczewska-Gładysz, 2012). The longitudinal section of the wall of the examined specimen shows subdermal canals, but the state of preservation (numerous wall damages, including cracks) does not allow for tracing their arrangement and connections with the exhalant canals. Representatives of *Rhizopoterion* are often confused with another

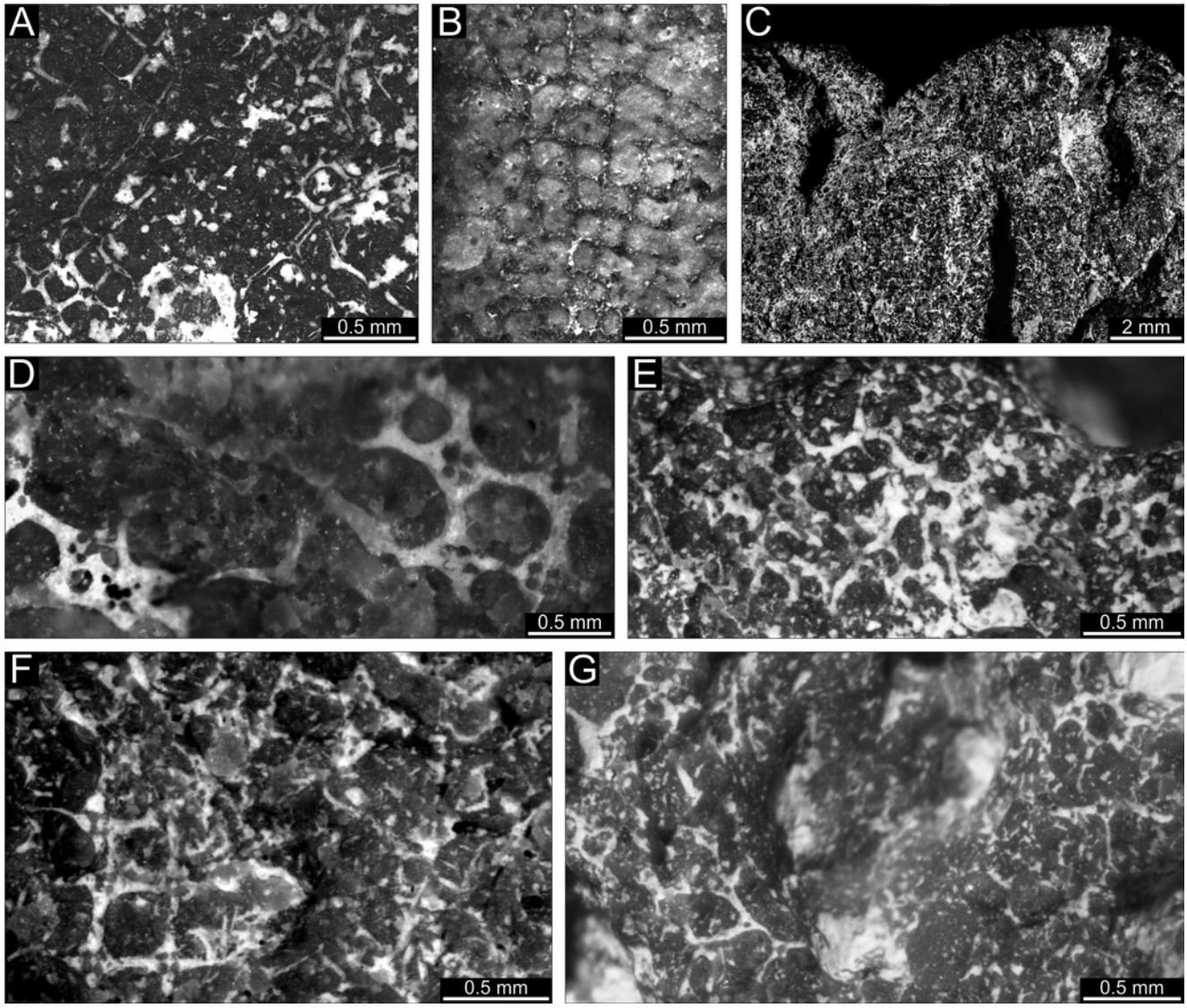


Fig. 12. Skeletons of lychniscosidan species. **A, B**. *Coscinopora macropora* Goldfuss, 1826; A – subdermal part of dictyonal skeleton, MWG ZI/52/544, S; B – dictyonal skeleton, visible in longitudinal section of the wall, MWG ZI/52/545, Nezvys'ko N. **C, D.** *Rhizopoterion* sp., MWG ZI/52/546, Rakovets'; C – transverse section of the wall with canals; D – dictyonal skeleton, visible in transverse section of the wall. **E**–**G**. *Khmilevskia papillata* gen. et sp. nov.; holotype MWG ZI/52/547, Rakovets'; E – irregular network on the surface of the papilla; F – dictyonal skeleton, visible in transverse section of the wall; G – irregular network on the gastral surface.

Cretaceous genus *Ventriculites* Mantell, 1822 (Reid, 1962a). Some poorly described specimens of various species assigned to *Rhizopoterion*, especially from older Cretaceous strata (e.g., Reuss, 1846; Defretin-Lefranc, 1960), where *Ventriculites* sponges are abundant, are questionable. Thus, the specimen described here is the oldest documented representative of this genus.

Occurrence: Western Ukraine (lower Cenomanian).

Genus *Khmilevskia* gen. nov.

Diagnosis: Tubular sponge with the outer surface covered by round inhalant canal openings, located on the top of small papillae, distributed alternately in longitudinal rows. Exhalant canal openings round or elliptically arranged in a quincunx. Inhalant and exhalant canals perpendicular to the sponge surface, distributed in alternating, longitudinal series. In dictyonal skeleton, consisting of lychniscs, dominate square or trapezoidal meshes, ca. 0.25–0.3 mm in size. Dense network with irregularly oriented lychniscs developed only on the dermal surface.

Etymology: Named in honour of Z. I. Khmilevsky, the researcher of Late Cretaceous sponges from Ukraine, including sponges from the Cenomanian of western Ukraine.

Remarks: The genus *Khmilevskia* is assigned to the family Ventriculitidae, due to the presence of a skeleton with lychniscs, the arrangement of canal openings in a quincunx, and the distribution of inhalant and exhalant canals in alternating longitudinal series. The new genus is proposed herein, even though only one specimen of the type species *Khmilevskia papillata* sp. nov. is available, due to its very characteristic feature, which is the presence of inhalant canal openings located on the top of small papillae. Small papillae distributed in vertical rows have been noted in another ventriculitid

genus *Rhytistamnia* Pomel, 1872 (diagnosis after Reid, 2004b). However, in *Rhytistamnia* the apex is covered by a synapticular membrane, the papillae are blind, whereas the openings of the inhalant canals are situated in the grooves between the rows of the papillae (see *Cephalites guttata* in Toulmin Smith, 1848; Reid, 2004b). Papillary tubercles occur on the outer surface of some representatives of *Ventriculites* Mantell, 1815, but these papillae are also blind and are located on the skeletal band between the canal openings (Mantell, 1822; Reid, 1962a; Świerczewska-Gładysz, 2012).

Khmilevskia papillata gen. and sp. nov.
Figs 10H, I, 12E–G

Diagnosis: As for genus.
Etymology: *Papilla* (Latin) – papilla. The name refers to presence of papillae on the outer surface.
Holotype: MWG ZI/52/547 (Figs 10H, I, 12E–G).
Type locality and stratigraphic horizon: Rakovets' (western Ukraine), exposure near the road. GPS locality: 48°47'42.4"N; 25°17'52.3"E. Clayey marls directly below the base of the inoceramid limestones, lower Cenomanian.
Description: The holotype is a tubular fragment of a sponge (without the base), 41 mm high and 32 mm in diameter (Fig. 10H, I). The wide spongocoel narrows towards the bottom and the thickness of wall is 6 mm in the upper part and 10 mm in the lower part. The outer surface is covered by papillae, 3–3.5 mm in diameter, with small (1.5 mm in diameter) canal openings on the top, leading to straight inhalant canals, penetrating ca. 2/3 of the wall thickness. The papillae are arranged alternately in longitudinal rows. The grooves between longitudinal rows are up to 2–2.5 mm wide, whereas the distances between the adjacent papillae in a row are usually shorter and sometimes (especially in the lower part of the specimens) the papillae are connected by narrow skeletal bands. The inner surface is covered by elliptical openings, 2 mm × 2.5–4 mm in size, distributed in a quincunx. They are inlets of long exhalant canals, perpendicular to the sponge surface. Inhalant and exhalant canals are distributed in alternating, longitudinal series.

The dictyonal skeleton in transverse section of the wall is rather regular, with square or trapezoidal meshes, ca. 0.25–0.3 mm in size (Fig. 12F). In the subdermal part and on the gastral surface the skeleton is less regular (Fig. 12G). The dermal surface of the dictyonal skeleton is covered by a dense, irregular network, consisting of lychniscs with shortened, thick beams (Fig. 12E).

Family *incerte sedis*
Genus *Ophrystoma* Zittel, 1877

Type species: *Porospongia micrommata* Roemer, 1864, p. 9, pl. 4, fig. 14, by monotypy.
Diagnosis: See Reid (2004b).

Ophrystoma olehii sp. nov.
Figs 10J–M, 11H–L

Diagnosis: Probably discoidal sponges with densely arranged, anastomosing canals, leading to pit-like cavities with round or oval oscula, 6–11 mm in size, distributed evenly on the upper side. Upper side covered by a compact synapticular membrane supported by small, variably oriented dictyonal hexactines. Lower surface slightly uneven or with prominent bulges, with densely arranged, rounded or irregular inhalant canal openings, 1–1.5 mm wide. Dictyonal skeleton, consisting of massive hexactines with large octahedral nodes, forming irregular network with meshes usually ca. 0.3 mm in size.
Etymology: Named for the Ukrainian soldier, Oleh Tsvihun, a friend of ESG, who died on 7 July 2024, while defending his homeland.
Holotype: MWG ZI/52/548 (Figs 10L, M, 11H, J–L).
Paratypes: One specimen (MWG ZI/52/549).
Other material: Two specimens from Rakovets' (MWG ZI/52/550, 551), one specimen from Nezvys'ko N (MWG ZI/52/552), and one specimen from Petriv (MWG ZI/53/585).
Type locality and stratigraphic horizon: Nezvys'ko S (western Ukraine), southern slope of a canyon near the Orthodox church in the village. GPS locality: 48°46'42.3"N; 25°15'26.6"E. Clayey marls directly below the base of the inoceramid limestones, lower Cenomanian.
Description: The examined specimens are flat fragments, sometimes with preserved arcuate edges, indicating that the sponges were discoidal in shape (Fig. 10J–M). The specimens are large, up to 67 mm in size and 10–12 mm thick. Oscula in a very dense synapticular membrane cover the upper (gastral) side of the sponges and are 6–9 mm in diameter (Fig. 10J, L). Their thickened margin is slightly protruding or bent inwards. Oscula are evenly distributed, at 6–12 mm intervals. The lower (dermal) side is slightly uneven or with prominent irregular or semi-circular bulges (up to 12 mm) separated by wide dimples (Fig. 10K, M). Canal openings on the lower surface are small (1–1.5 mm in diameter), rounded or irregular, and separated by skeletal bands, which are ca. 1 mm wide. Irregularly branched canals, up to 0.4–0.5 mm wide (Fig. 11H, I), lead to deep pit-like cavities, which (if present) are located in the bulges.

The dictyonal skeleton consists of massive hexactines containing large octahedral nodes. The skeletal network is irregular with square, rectangular or triangular meshes, 0.2–0.25 mm, rarely up to 0.4 mm in size (Fig. 11J). Within the dense synapticular membrane occur variously oriented small hexactines, which form an irregular network with triangular, rarely quadrangular meshes, 0.08–0.1 mm in size (Fig. 11K, L). The band between the canal openings on the lower surface is covered by finely porous synapticular cortex (only occasionally preserved).
Remarks: The species described here is assigned to *Ophrystoma* Zittel, 1877, due to the discoidal shape of the body, with densely packed branched canals and the presence of a synapticular membrane with openings, covering the upper side of the sponges, containing small dictyonal hexactines. A discoidal body and a synapticular membrane with large openings occur also in the representatives of the genus *Tremabolites*, but in that case membrane stauractines occur. Moreover, the body of this sponge is composed of anastomosing tubes, the wall of which is devoid of skeletal canals. Until now, only one species of this genus was known, i.e.,

O. micrommata (Roemer, 1864). The proposed new species differs from *O. micrommata*, co-occurring in the Cenomanian of western Ukraine (Olszewska-Nejbert and Świerczewska-Gładysz, 2013), in a significantly larger oscula (in *O. micrommata* their diameter is only up to 3 mm). The lower surface of *O. micrommata* is always flat, without bulges. In *O. micrommata* the membrane on the upper side consists of synapticules, developed between rays of small hexactines, forming a quite regular network with small rectangular meshes. In the specimens described here, small hexactines within the membrane are diversely oriented and triangular meshes dominate. The poor state of preservation of the network on the dermal surface of the studied specimens makes it impossible to determine whether it contains hexactines without nodal octahedrals, similar to *O. micrommata*.

Class Demospongiae Sollas, 1885
Order Tetractinellida Marshall, 1875
Family Phymatellidae Schrammen, 1910
Genus *Jerea* Lamouroux, 1821 *sensu* Schrammen, 1910

Type species: *Jerea pyriformis* Lamouroux, 1821, p. 79, pl. 78, fig. 3, by monotypy.
Diagnosis: See Schrammen (1910).

Jerea sp.
(Figs 10N, O, 13A)

Material: One specimen from Rakovets' (MWG ZI/52/554), one specimen from Nezvys'ko S (MWG ZI/52/553), and one specimen from Horodenka (MWG ZI/53/586).
Description: Spindle-shaped sponges, up to 26 mm high and 23 mm wide (Fig. 10N). A few exhalant canal openings, 1–1.5 mm in diameter, are situated on a flat or slightly rounded top (Fig. 10O). Poorly visible inhalant canal openings are 0.3 mm in diameter. Long, arched exhalant canals running vertically are observed in places, where the surface of the sponges is destroyed.

Casts after tetraclones (preserved occasionally on the outer surface) have smooth, weakly branched clones, reaching 0.4 mm in length (Fig. 13A).
Remarks: Besides the morphology, the characteristic feature of the studied specimens that allows them to be assigned to the genus *Jerea* is the presence of large tetraclones, which distinguishes this genus from the juvenile representatives of the genus *Siphonia* Parkinson, 1822 *sensu* Schrammen (1910), which may not have a developed spongocoel (Schrammen, 1910; Świerczewska-Gładysz and Jurkowska, 2023).
Occurrence: Western Ukraine (lower Cenomanian).

DISCUSSION

Taxonomic composition of Cenomanian sponge assemblage from western Ukraine (B)

The studied Cenomanian sponge assemblage from western Ukraine contains almost exclusively hexactinellid species (their percentage is 98% – Fig. 14). Demospongiae is an accessory group, represented only by a dozen specimens (Fig. 14). Until now, fifteen species of sceptrulophorans (previously classified as hexactinosidans) have been documented from the 'sponge bed', exposed in this region (Dunikowski, 1889; Khmilevsky, 1969; Olszewska-Nejbert and Świerczewska-Gładysz, 2012, 2013; Świerczewska-Gładysz and Olszewska-Nejbert, 2013). In the new portion of material, 13 species were identified that had been described previously (Olszewska-Nejbert and Świerczewska-Gładysz, 2012, 2013; Świerczewska-Gładysz and Olszewska-Nejbert, 2013). Among them, the most abundant species are: *Laocoetis maxima* (Dunikowski, 1889), *Laocoetis beaumonti* (Reuss, 1846), *Heterohone boguckii* Świerczewska-Gładysz and Olszewska-Nejbert, 2013, and *Periphragella plicata* (Schrammen, 1902). A further 13 species are described for the first time from the area (Tab. 2). Two species of the latter group are recognized as new species: *Tretodictyum petrivensis* sp. nov. and *Tretodictyum complicatus* sp. nov. Four very rare taxa, although also seem to represent new species, are recognised only at genus level (*Cribrospongia* sp., *Hexactinella* sp., *Hillendia* (?) sp. and *Wollemannia* sp.), as it was impossible to determine all diagnostic features, due to their poor state of preservation.

The other seven sceptrulophoran species, noted in the analysed material, were also described from the Upper Cretaceous of Europe. Four of these species are known from the Cenomanian stage: *Eurete mantelli* Reid, 1958; *Petalope*

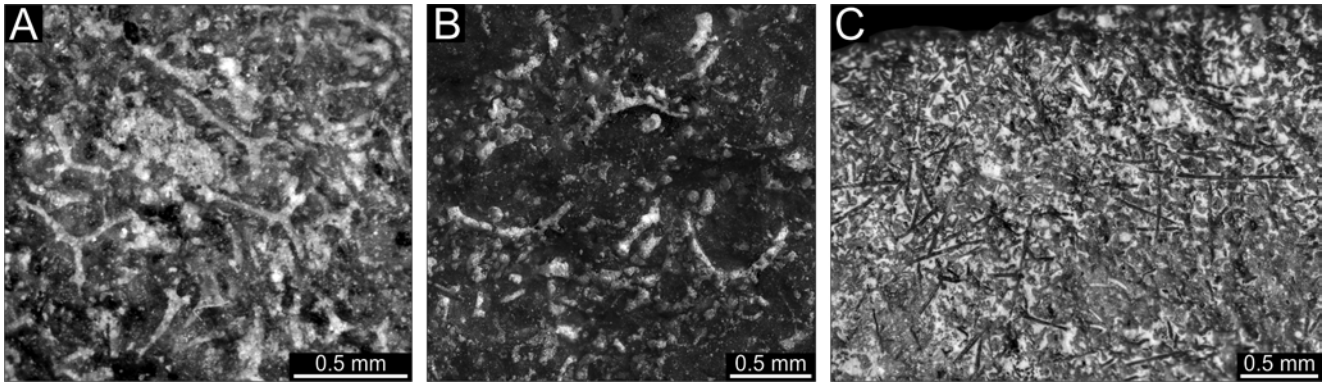


Fig. 13. Skeleton of lithistid demosponges and siliceous sponges without a rigid skeleton. **A.** *Jerea* sp.; choanosomal tetraclones, MWG ZI/52/554, Rakovets'. **B.** Rhizoclones of an indeterminate rhizomorinid species, MWG ZI/53/588, Petriv. **C.** Monaxone megascleres of indeterminate species of non-rigid sponges, MWG ZI/53/589, Petriv.

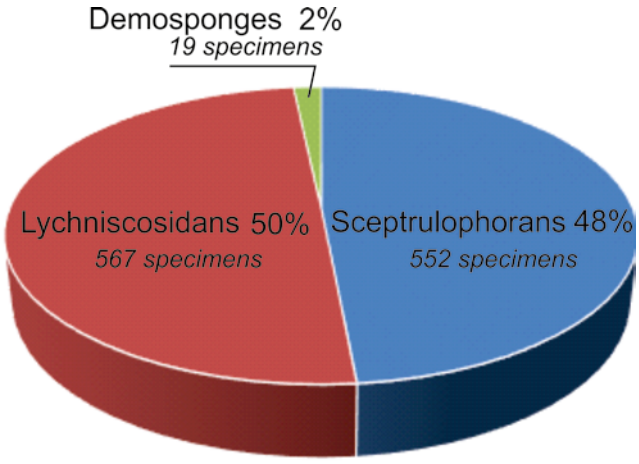


Fig. 14. Percentage content of hexactinellids (sceptrulophorans and lychniscosidans) and demosponges in the Cenomanian assemblage of western Ukraine – pie chart, compiled from all studied outcrops.

auriformis Počta, 1883; *Verrucocoelia tubulata* (Toulmin Smith, 1848); and *Laocoetis fittoni* (Mantell, 1822). The latter two species are also listed from other stages of the Upper Cretaceous. Other sceptrulophoran species, recognized in the Cenomanian of western Ukraine, are known from the Albian (*Verrucocoelia alpina* Hérenger, 1944) or the Turonian (*Laocoetis cancellata* [Roemer, 1864] and *Guettardiscyphia zitti* Vodrážka, 2017). Khmilevsky (1969) reported the presence of the sceptrulophoran species *Guettardiscyphia* aff. *alata* (Pomel, 1872) in the material from Horodenka, but in the opinion of the present authors, the unique specimen described by this author represents *Guettardiscyphia zitti* Vodrážka, 2017.

Cenomanian Lychniscosida sponges also exhibit a high taxonomic diversity and are represented by 28 species in total (Tab. 3). Twenty-one of the lychniscosidan species were presented in previous papers by the authors (Olszewska-Nejbert and Świerczewska-Gładysz, 2012, 2013; Świerczewska-Gładysz and Olszewska-Nejbert, 2013). Most of them (17 species) previously recognized by them were noted in the new portion of the material. Four species (*Callodictyonella regularis*, *Leiostracosia crassa*, *Plocoscyphia podolica* and *Toulminia polonica*) common in the Cenomanian of western Ukraine, which were designated by Dunikowski (1889), were also frequent in the new portion of the material analysed herein (Tab. 3). Seven rare species are described herein for the first time, including one new genus and species (*Khmilevskia papillata* gen. and sp. nov.), three new species (*Brachiolites elongatus* sp. nov., *Ophrystoma olehii* sp. nov., and *Plocoscyphia anastomosa* sp. nov.), and also *Tremabolites megastoma* (Roemer, 1841), *Rhizopoterion* sp. and *Coscinopora macropora* Goldfuss, 1826. Until now, the latter species was unknown from the Cenomanian; it had been noted only in the Turonian and Coniacian of western and central Europe (Schrammen, 1912; Defretin-Lefranc, 1960).

Despite examining a large amount of material, the present authors have still not been able to determine the taxonomic position of the specimens, classified by Dunikowski (1889) as new species of *Plocoscyphia* Reuss, 1846 – i.e., *P. tostum pirum*, *P. baculiformis*, and *P. cerebralis*. The latter species was also mentioned by Khmilevsky (1969). The occurrence of two taxa distinguished by Khmilevsky (1969) in a sponge assemblage from Horodenka, i.e., *Plocoscyphia morchella* (Goldfuss, 1826) and *Coscinopora infundibuliformis* var. *micropora* Schrammen, 1912 is also controversial. All of the above species are poorly described and lack graphic documentation, or the illustrations are of poor quality, therefore the diagnostic features of these specimens are difficult to verify.

Among the 56 Hexactinellida species identified in the analysed sponge assemblage, there are numerous species known from the Late Cretaceous of central and western Europe, especially from the Cenomanian (see also Olszewska-Nejbert and Świerczewska-Gładysz, 2013). However, 23 species have not been recorded outside the Cenomanian of western Ukraine (Tabs 2, 3). These species can hardly be considered endemic, as data on the Late Cretaceous sponges from other regions of eastern Europe are very sparse (Sinzov, 1878; Gerasimov, 1960; Shemjakin, 1965; Pervushov, 2002), and the palaeogeographic and stratigraphic ranges of these taxa remain unknown.

The very rare lithistid sponges in the studied assemblage are represented only by a few specimens of Siphonia pyriformis Goldfuss, 1826 (Olszewska-Nejbert and Świerczewska-Gładysz, 2013), *Jerea* sp. and a few fragments of unidentified phymatellids and rhizomorinids (Fig. 13B; Tab. 4). Lithistids have a high fossilization potential and are a very common fossil in Upper Cretaceous deposits (e.g., Schrammen, 1910; Moret, 1926; Ulbrich, 1974; Kauffman *et al.*, 2000; Świerczewska-Gładysz and Jurkowska, 2023), therefore their low frequency in the studied collection appears to reflect their negligible presence in the Cenomanian sponge assemblage that lived in this area.

Only one fragment of unspecified demosponge without a rigid skeleton was found in the studied material (Fig. 13C; Tab. 4). Skeletons of non-rigid sponges are composed exclusively of loose spicules that disperse into the sediment after the sponge's death and they are very rarely found in Cretaceous sediments as body fossils (Schrammen, 1910; Świerczewska-Gładysz *et al.*, 2019; Jurkowska and Świerczewska-Gładysz, 2022). The loose spicules of non-lithistid demosponges in the upper Albian and Cenomanian deposits of Ukraine were noted by Klymenko (2024). The material studied by her came from outcrops, situated to the east of the areas investigated in this paper, primarily in the region, known as the Middle Dnister Region. Described spicules were isolated from slightly shallower facies (mainly sands) than the material studied here (mainly silts). From the information provided by Klymenko (2024), but unfortunately without any maps, geological sections or any other graphical documentation, it can be surmised that the spicules, listed by her, originated from demosponges, which inhabited the shallow waters of the Tethys Shelf during the episode(s) of marine transgression in the late Albian and early Cenomanian. The sponges, described in the present study, developed during the early Cenomanian transgression, but in a different, deeper part of the shelf and at a slightly later time (see the following sections for descriptions).

Microfacies and environmental analysis

The described characteristics of the identified microfacies allowed for a preliminary interpretation of the sedimentary environment (Tab. 6).

Microfacies MF M1 and MF M2 of unit 3 are represented by packstone, rich in detrital silt-size quartz, common silt-size inoceramid debris, a moderate amount of clayey-calcareous micrite, sometimes with an admixture of detrital sand-size quartz and subtle bioturbation points to a shelf-mud environment, situated below the storm-wave base, in quiet marine water. The detrital material (quartz) was probably supplied from the mainland and was the finest material, transported by the river/rivers far out to the sea, building prodelta deposits (Reineck and Singh, 1980). In the study area, that unit is strongly reduced and only a thin layer has been preserved. The fine detrital 'land' components (quartz) were mixed with 'marine' components, i.e., mainly calcareous fine inoceramid debris. Rare thin-shelled bivalves and rare foraminifers also occur.

Microfacies MF M3 of unit 4, represented by wackestone passing to packstone, is very similar to the microfacies described above, but is poorer in detrital silt-size quartz, but clearly richer in clayey-calcareous micrite (Table 5). Rare thin-shelled bivalves and rare foraminifers also occur. Such features also indicate a shelf-mud environment situated below the storm-wave base, but the setting seems to be even calmer, with less detrital material being supplied, possibly to calmer places (? more distal parts) of the prodelta. The two next microfacies, MF SP and MF AD, are connected with early diagenetic phosphatization episode(s). Microfacies MF SP represented by wackestone which infilled the interspicular space of sponges is poor in detrital silt-size quartz (Table 5). However, the MF AD microfacies (a phosphatized deposit, directly attached to the sponge) represented by wackestone, passing to packstone, is characterised by the presence of a moderate amount of detrital silt-size quartz (Table 5). This microfacies is texturally similar to the non-phosphatized MF M3 microfacies, which suggests a connection between MF M3 and MF AD. The phosphatization of sponges took place in deposits similar to the MF M3 microfacies. That fact may suggest that the sponges, found in unit 4, were buried and phosphatized *in situ*, or almost *in situ*, in the environment where they had lived.

Microfacies MF PA of unit 5, represented by packstone with a prevailing content of sand-size inoceramid debris, points to a major change in the dynamic environment. The deposit was reworked by storms, developing near the storm-wave base, below the fair-weather wave base in middle/distal inner shelf settings. Inoceramid shells were completely crushed and accumulated as thick layers. The terrigenic input is rather low. Microfacies connected with phosphatized rocks, MF SP with a low amount of silt-size quartz, and MF AD with a minor amount of silt-size quartz (Table 5), are clearly connected with unit 4. The clear difference in microfacies between unit 4 and unit 5 (Tables 5, 6; Fig. 3) indicates that the phosphatized sponges were redeposited from unit 4 into unit 5. The phosphatization phenomena took place before that redeposition and all sponges present in unit 5 are phosphatized and composed of microfacies, showing phosphatization, described from unit 4. The phosphatized sponges are also more damaged in unit 5 than in unit 4. Most likely, the redeposition process (due to currents, generated by storms) was responsible for the poorer preservation of the phosphatized sponges. The high dynamics of redeposition is evidenced also by a large content of crushed inoceramid prisms. Moreover, the up-section decreasing size of the sponge fragments and their quantities (Figs 2, 3) additionally indicates the post-storm sedimentation of deposits in that unit.

Stages related to the accumulation of phosphatized sponges

Based on the sedimentological, palaeontological, microfacies and petrographical observations, the following stages connected with the development of the 'sponge bed' in the area of western Ukraine can be distinguished:

Late Albian

At that time, a great transgression took place, similar to that in Western Europe (Pasternak *et al*., 1968; Kyselevych and Kovalchuk, 2021). The Volhyn-Podilla Plate (part of the East European Platform) was entered by a shallow sea, which represented the northern shelf of Tethys (Senkovsky *et al*., 2004). The studied area is located on the shelf, relatively close to the mainland, which comprised the uplifted Ukrainian Shield and Vendian, Silurian, Devonian and Jurassic formations on the south-western margins of the Ukrainian Shield (Senkovsky *et al*., 2004; Kyselevych and Kovalchuk, 2021). During the Albian, siliciclastic-carbonate sands were deposited on that shelf, with a typical coastal and shallow marine fauna (Kyselevych and Kovalchuk, 2021; Klymenko, 2024) and ichnofauna (Author's observation in Albian sections of Rakovets', Petriv and Horodenka). In Petriv, one of the present authors (DON) found late Albian belemnites of the species *Neohibolites minimus* (Miller). Eastward of the studied area in the Middle Dnister region, Kyselevych and Kovalchuk (2021) reported the occurrences of *Neohibolites minimus* in some outcrops with strata also dated to the upper Albian.

Early Cenomanian

During Cenomanian, the transgression progressed. The nature of sedimentation changed from coarse-grained to fine-grained, with siliciclastic-carbonate deposits. The detrital material (silt-size quartz) was probably delivered to the sea by rivers. Subsequently, as a result of progressive transgression, the studied area was located within the inner/middle shelf, clearly below the storm-wave base, probably in the distal parts of the prodelta. The sea floor was colonized by, e.g., thick-shelled bivalves (? inoceramids), thin-shelled bivalves, and benthic foraminifera.

The studied area was located in a specific palaeophysiographic position on the shelf, between the Ukrainian Land and the continental slope (several dozen kilometres from each), behind which stretched the deep Carpathian Basin (northern part of the Tethys). The Ukrainian Land in the Cenomanian is understood here as an emerged land, comprising the Ukrainian Shield and the adjacent pre-Cretaceous

sedimentary cover (Senkovsky *et al*., 2004, their figs 3, 28). A slightly lower content of terrestrial detrital material (silt-size quartz) was delivered to the study area at that time. Generally, the sedimentary settings were calm. The palaeogeographic conditions, i.e., deep basin-shelf-land, generated upwelling (Senkovsky *et al*., 2004; Kyselevych and Kovalchuk, 2021), which lifted cold water from the deep Carpathian Basin onto the shelf. The cold waters rich in Si favoured the development of sceptrulophoran and lychniscosidan sponges with a dictyonal skeleton. Sponges colonized vast areas, forming sponge meadows. These sponges had no rhizoids (outgrowths stabilizing the sponges in the soft sediment) and required a hard substrate to colonize. Sometimes new sponges used dead sponges as a substrate and grew on them. Many other sponges had a concave basal part, as if adapted to the concave-up valves of bivalves. These bivalves have not been preserved in their entirety, or even as larger fragments. In the microfacies abundant very small fragments of inoceramid debris can be observed. Inoceramids, living in deeper shelf settings below the storm-wave base in the early Cenomanian, are described in the literature (Wilmsen *et al*., 2021). Apart from inoceramids, belemnites *Neohibolites ultimus* and small characteristic bivalves *Aucellina* also occur. After death, the sponges were slowly covered with sediment and became centres of local phosphatization. The skeletal network structures of the sponges protected the interspicular spaces from the penetration of detrital quartz grains, and the early phosphatization of the space previously occupied by the soft body of the sponge prevented the penetration of larger quantities of fine quartz grains (Figs 3A, C-E, H, 4, 5). The sponges and the deposits directly attached to the sponges are phosphatized. Upwelling from deeper parts of the basin, in that case, provided the organic matter and phosphorus necessary for the process of phosphatization. Fine carbonate debris was dissolved during the phosphatization. Only the calcitic rostra of belemnites, composed of large calcite crystals, have been preserved. Apart from the sponges, the moulds of *Aucellina*, moulds of gastropoda, and wood fragments were also phosphatized. Thin calcareous shells of bivalves and foraminifera tests were completely dissolved.

Middle Cenomanian

After the phosphatization process, at the boundary between the early and middle Cenomanian, there was an eustatic sea level fluctuation. The sea became shallower (upper mid or/and inner shelf), and *Thalassinoides* isp. burrows appeared (observations from Petriv). The hydrodynamic conditions changed and the studied area was at that time above the storm-wave base. The lower part of the clayey marls with large amounts of buried phosphatized sponges remained untouched by the storm, hence their much better state of preservation. As a result of the storm, some of the already phosphatized sponges that were shallowly buried in the still loose clayey marl sediment or were lying directly on the sea bottom were disturbed. The currents generated by storms eroded the upper part of the vertical burrows, leaving only the lower part of horizontal galleries. The phosphatized sponges in the upper part of the 'sponge bed' were disturbed, locally transported, partially destroyed, and crushed. Scattered phosphatized sponges, as heavy components, were the first deposited from gravity on the seabed supported and surrounded by inoceramid debris. During the storm, all the inoceramid shells were disintegrated into the sand-size fraction. Fragments of phosphatized sponges are found up to ca. 0.5 m (rarely up to 1 m) above the base of the detrital inoceramid layer. Despite intensive field search, with such an abundant accumulation of inoceramid prisms, it was not possible to find larger shell fragments, which may further indicate the high dynamics of the environment redepositing the sponges at the base of the limestones. The almost complete absence of epifauna and borings on redeposited sponges indicates that the reburial was fast. Towards the top of the section, inoceramid detrital limestones pass into (after approx. 7 m) the chalk facies (Turonian), which indicates deepening of the sea (Senkovsky *et al*., 1989).

Occurrence of hexactinellid sponge assemblages in different Cretaceous facies of the European basin

The occurrence of fossil specimens of Cretaceous hexactinellids with a rigid skeleton is connected almost always with the presence of calcareous facies, where they are often the prevailing group of sponges. The rich and taxonomically diverse hexactinellid assemblages are known from limestones and marls (e.g., Schrammen 1912; Moret, 1926; Defretin-Lefranc, 1960; Ulbrich, 1974; Žítt *et al*., 2006; Schneider, *et al*., 2011; Świerczewska-Gładysz, 2012; Świerczewska-Gładysz *et al*., 2019). They are also very numerous in opokas (carbonate-siliceous rocks) with a very low quartz content, deposited in the outer shelf environment (e.g., Khmilevsky, 1974; Świerczewska-Gładysz, 2006; Jurkowska and Świerczewska-Gładysz, 2022). Hexactinellid sponges are noted in chalk, that is, pelagic sediments having insignificant amounts of detrital quartz (e.g., Hinde, 1883; Reid, 1968; Nestler, 1961; Olszewska-Nejbert and Świerczewska-Gładysz, 2011).

Hexactinellid sponges are often found in sandy deposits in form of agglomerates of phosphatic intraclasts (e.g., Rauff, 1933; Poukarová and Bubík, 2012). In contrast to specimens from the Cenomanian of western Ukraine, these reworked fossils most often derived from destroyed carbonate deposits (Vodrážka *et al*., 2009). The material infilling the interspicular spaces, i.e. canals and cavities inside the sponge skeleton, contains a negligible amount of very fine detrital quartz (Świerczewska-Gładysz and Olszewska-Nejbert, 2006; Olszewska-Nejbert and Świerczewska-Gładysz, 2009). The material infilling the sponge skeletons, examined herein, contains small or moderate amounts of fine detrital quartz, which indicates an environment with a significant influx of terrigenous material (see text above). The *in-situ* occurrence of hexactinellids in Cretaceous sediments, rich in detrital material, is rare, known mainly from claystones and mudstones, deposited around the Sudetic Islands (Žitt *et al*., 2006, 2010). The appearance of hexactinellid sponges in these sequences is interpreted as a result of marine deepening and a reduction in terrigenous input (Žitt *et al*., 2006; Schneider *et al*., 2011).

Comparison of the habitat of Cenomanian sponge assemblages from western Ukraine and modern communities on the Western Canadian Continental Shelf

The occurrence of living sceptrulophorans and lychniscosidans is restricted mainly to the bathyal and abyssal zones (Finks and Rigby, 2003) and to deeper parts of the shelf (e.g., Van Soest and Stentoft, 1988; Krautter *et al*., 2001; Finks and Rigby, 2003; Leys *et al*., 2004). The constitution of these sponges and their vital functions are adapted to slow sedimentation rates, low energy conditions, and cold water (Tabachnick, 1988; Krautter, 1997). Therefore, the discovery of sponge mounds (reefs), composed of sceptrulophoran sponges (hexactinellids with a rigid skeleton), in the late 1980s in several places on the Western Canadian Continental Shelf (Fig. 15), was a global phenomenon (Conway *et al*., 1991). Most of the sponge mounds in this area flourished at depths of below 100 m in zones with slow sedimentation rates (0.3–0.9 mm/yr – Leys, 2013). Bioherms, exceeding 21 m in height, and banks (biostromes), extending for tens of kilometres at depths between 140–240 m, were described from the shelf of the Queen Charlotte Basin (QCB; Whitney *et al*., 2005). Several hundred kilometres to the south, in the Georgia Basin (GB), were discovered slightly smaller bioherms, up to 14 m in height (Conway *et al*., 2004). Siliceous sponge reefs, existing on the west coast of Canada are, so far, the only build-ups, composed of almost solely sponges of the order Sceptrulophora (Conway *et al*., 1991; Krautter *et al*., 2001; Whitney *et al*., 2005). These sponges are represented by only three species: *Aphrocallistes vastus* Schulze and *Heterochone calyx* Schulze, and *Farrea occa* Bowerbank. These sponges with a dictyonal skeleton built the main framework of the reefs. Other sponges, associated with reefs, include a rossellid species, *Rhabdocalyptus dawsoni* (Leys and Lauzon, 1998), and rare encrusting non-lithistid demosponges (Law *et al*., 2020). Demosponges without a rigid skeleton are only more numerous in the subtidal zone of some fjords in British Columbia (Ott *et al*., 2024). The discovery of sponge mounds, composed of hexactinellid sponges, opened the possibility of comparing the modern mounds with the extensive band of sponge bioherms, known from the northern shelf of the Tethys Ocean in the Jurassic (Krautter *et al*., 2001). The analogy is very significant, although Jurassic and Early Cretaceous sponge bioherms developed entirely in carbonate settings and contained also microbialites (Trammer, 1991; Leinfelder *et al*., 1996; Pisera, 1997; Leinfelder and Schmid, 2000), a feature that is not characteristic of the modern mounds from the Western Canadian Continental Shelf (Krautter *et al*., 2001). Unlike the modern reefs, the Jurassic and Early Cretaceous sponge mounds contained numerous representatives of lithistid demosponges and lychniscosidans, which are recently a relict group, living mainly in the deep sea (below 200 m, Reiswig, 2002b, c). At the beginning of the Early Cretaceous, sponge mounds with microbial structures began to disappear and during the Late Cretaceous, numerous sceptrulophorans and lychniscosidans occurred within sponge

Table 7

Comparison of ancient sponges (lower Cenomanian) on the northern Tethys shelf near the Ukrainian Land with modern sponges from the Western Canadian Continental Shelf (WCCS). Data about WCCS compiled from: Conway *et al*. (1991, 2004), Krautter *et al*. (2001), Whitney *et al*. (2005), and Austin *et al*. (2007).

	Modern sponges near British Columbia (Canada) on the Pacific shelf, Western Canadian Continental Shelf	Ancient sponges (Cenomanian) near Ukrainian Land on the northern Tethys shelf
Similarities	settlement of the shelf during a marine transgression	
	distance from the land about 50–150 km from shore (Fig. 15)	
	the dominant hexactinellid sponges with a rigid skeleton, rarely other hexactinellids and accessory demosponges	
	the fine silty quartz material derived from land (probably by load of rivers) in detrital material, the fine material is dispersed in the sea and introduced to sponge building	
	the depth below the storm wave base in calm, oligotrophic environment	
	sponges need a hard base to settle	
	a lack of microbial structures	
Differences	sponges build the mounds/reefs or biostromes with a rigid framework	sponges represented in meadows (grounds) and only in rare cases the sponge used the skeleton of dead sponge as a base for growth
	the taxonomic variety of hexactinellids is very poor, composed only of three sceptrulophoran species	the taxonomic variety of hexactinellids is very rich, composed of at least 56 species (28 sceptrulophorans and 28 lychniscosidans)
	the size of single specimens can be very large, up to 3.4 m long x 1.1 m high, x 0.5 m wide	the size of single specimens or parts of specimens are small, up to 13 cm, usually smaller than 10 cm
	siliceous sponge within siliciclastic- dominated settings, rare calcareous components	siliceous sponge within siliciclastic-dominated settings with admixture of carbonate elements (e.g., inoceramid debris)

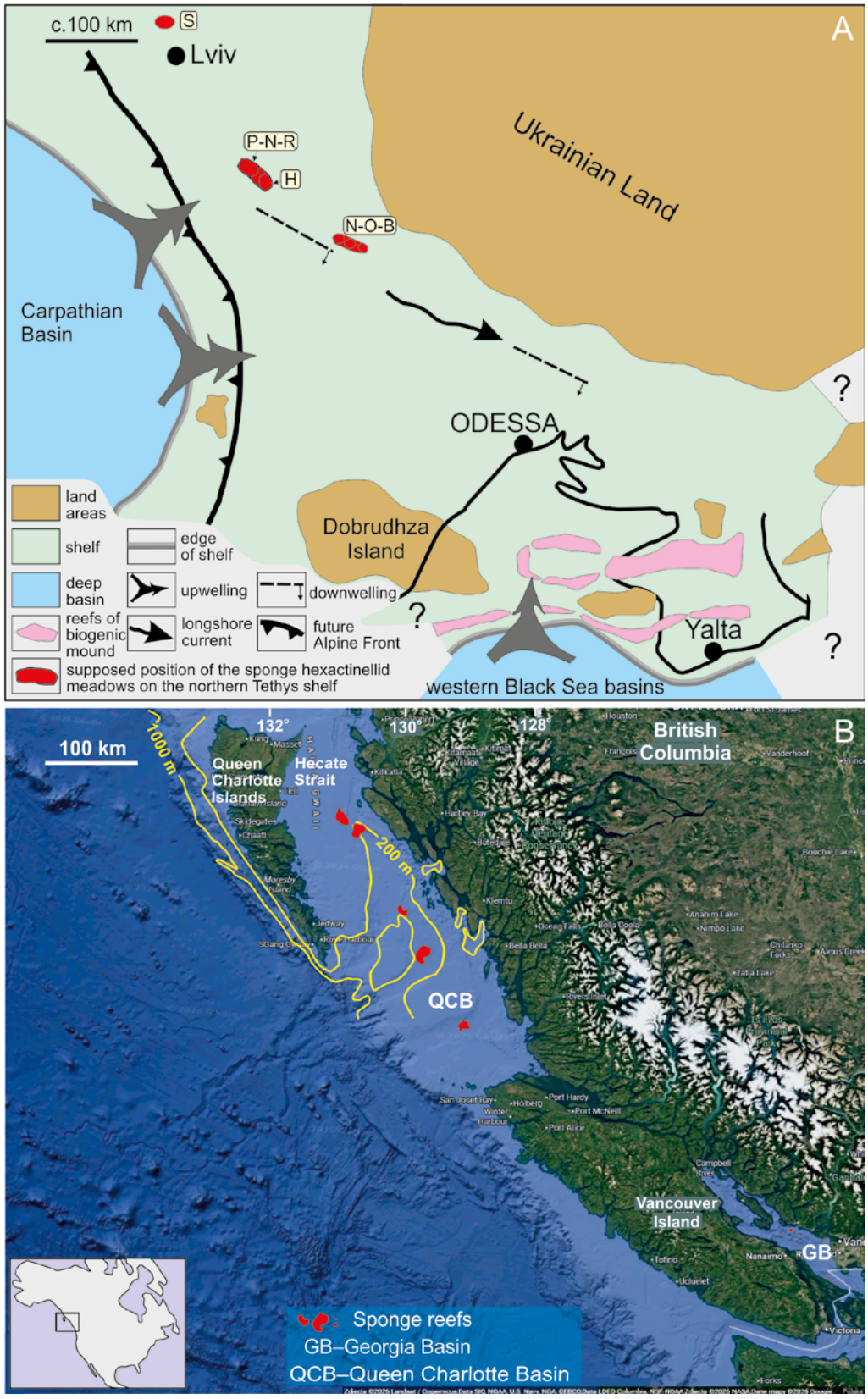


Fig. 15. Palaeogeography of the ancient northern Tethys Ocean shelf in the Early Cenomanian with distribution of siliceous sponge meadows and comparison of it with the recent distribution of sponge mounds/beds in the Queen Charlotte Basin and Georgia Basin on the eastern Pacific shelf. **A.** Approximate positions of sponge meadows (red spots) on the northern shelf of the Tethys Ocean (palaeogeography after Senkovsky *et al*., 2004, simplified) in the early Cenomanian. **B.** Location of the Queen Charlotte Basin and Georgia Basin with distribution of sponge mounds/beds (red spots) on the western Canadian margin (based on the satellite photos, modified from Google, 2026; Conway *et al*., 2004, 2005). P+N+R – Petriv, Nezvys'ko, Rakovets'; H – Horodenka; P+N+R and H consisted of probably one meadow area studied herein; N+O+B – Naslavcea, Otaci, Bronnytsya – supposed meadow area, mostly in Moldova, based on data from Trest'jan (1972, 1973); S – borehole Stoivka, supposed sponge accumulation, following data from Senkovsky *et al*. (1989).

meadows (Leinfelder and Schmidt, 2000; Wiese *et al*., 2004). In the early Cenomanian, sponge meadows developed on the shelf of the Ukrainian Land. The habitat of Cenomanian sponges from this area shows many similarities to the modern sponge mounds (reefs) developed on the Western Canadian Continental Shelf (Tab. 7). Firstly, the modern sceptrulophoran sponge mounds on the Western Canadian Continental Shelf started to develop on the gently dipping shelf during the eustatic sea level rise after the retreat of the Wisconsinan ice-sheet and the restoration of the isostatic equilibrium (Krautter *et al*., 2001). During the rapid transgression (Krautter *et al*., 2001), sponges settled in the iceberg furrows in the glacial substrate, in a hydrodynamically calm environment (Conway *et al*., 1991, 2004) and started to build the mounds probably since c. 10,000 years BP (Whitney *et al*., 2005). Similarly, the development of sponge meadows on the early Cenomanian shelf of the Ukrainian Land could have started during the eustatic sea-level rise and was connected with the Depositional Sequences Ce1-Ce2 (DS Ce1-Ce2), and probably with the early stage of DS Ce3 (compare Wilmsen, 2003, 2012). The Baddeckenstedt Quarry section, in the Salzgitter area, northern Germany, begins with 'sponge beds' overlying inoceramid floatstones rich in the debris of lychniscosidan sponges (Ernst and Rehfeld, 1997; Wilmsen, 2003). The 'sponge bed' in Baddeckenstedt is early Cenomanian in age and began during DS Ce3 (Wilmsen and Niebuhr, 2002; Wilmsen, 2003). In western Ukraine, during the interval following Sequence Boundary Al8 (SB Al8), after the time of the *ultimus*/*Aucellina* transgression (transgression in Depositional Sequence Ce1), sceptrulophoran and lychniscosidan sponges started to form sponge meadows, settling on the calm sea bottom on the gently dipping, homoclinal northern shelf of Tethys (Fig. 15A). It is possible that the Ukrainian sponge meadow corresponds to that from the lower part of DS Ce3, similarly as in the Baddeckenstedt Quarry (compare Wilmsen, 2003). The lower Cenomanian deposits in western Ukraine have very reduced thicknesses and small contents of calcareous components, such as silt-size inoceramid grains. It is possible that those inoceramid grains are the equivalent of DS Ce2, rich in representatives of *'I.' crippsi* from northern Germany (Wilmsen, 2003). The present authors therefore assume that the co-occurrence in one bed of *Neohibolites ultimus* belemnites, phosphatized bivalve moulds of *Aucellina*, inoceramid debris, and phosphatized sponges – of which lychniscosidans account for 50% – corresponds to a composed DS, spanning the DS Ce1 to the lower part of DS Ce3 (compare with data from northern Germany in Wilmsen, 2003, 2012). Secondly, modern reefs in the QCB are located approximately 70–80 km from the mainland and approximately 100 km from the continental slope (Fig. 15B). The sponge meadows, studied herein, developed in a very similar palaeophysiographic location, ca. 60–100 km from the Ukrainian Land and about 100 km from the continental slope passing to the deep Carpathian Basin (Fig. 15A). This palaeophysiographic location was favourable for the development of upwelling processes, which brought refreshing, oligotrophic and cold waters to the shelf area, creating conditions with a low sedimentation rate, favourable for hexactinellids similarly as on the Western Canadian Continental Shelf (Whitney *et al*., 2005). In both sponge assemblages, the demosponges are an accessory component. Thirdly, the petrographic analysis of Cenomanian sediments indicates a sponge environment in a calm hydrodynamic regime, but with a quite high proportion of siliciclastic components, similar to that found in modern sponge mounds of the Western Canadian Continental Shelf (Tab. 8). Fourthly, the extant sponges of the Western Canadian Continental Shelf require a hard surface to settle on. The ancient Cenomanian sceptrulophorans and

Table 8

List and comparison of the size of basic components in ancient shelf deposits of the Cenomanian Ukrainian Land and the Western Canadian Continental Shelf; PC – point-counting (%); Wgh – weight (%); *data from Conway *et al*. (2004).

Western Ukraine			
Microfacies of marly type	**Sand-size**	**Silt-size**	**Clay-size**
MF M1 [PC]	–	63.7	36.3
MF M2 [PC]	10.0	56.3	33.7
MF M3 [PC]	**2.7**	**46.0**	**51.3**
Microfacies of phosphate type			Fine phosphates
MF AD [PC]		**20.0–31.6**	**68.4–79.7**
MF SP [PC]	–	2.3–5.7	88.0–96.3
Microfacies of limestone type			**Micrite**
MF PA [PC]	75.7–80.0	4.3–4.7	12.3–13.7
Western Canadian Continental Shelf*			
Modern locality	**Sand-size**	**Silt-size**	**Clay-size**
Queen Charlotte Basin [Wgh]	18.0	33.0	49.0
Georgia Basin [Wgh]	1.0–2.0	45.0	54.0

lychniscosidans studied herein also required a hard substrate (e.g., bioclasts) to settle (Olszewska-Nejbert and Świerczewska-Gładysz, 2013), although in their later evolution, in the Turonian-Maastrichtian times, they were perfectly adapted to soft-bottom settings by developing rhizoids (e.g., Reid, 1962b; Świerczewska-Gładysz, 2006, 2012). Finally, the microbial structures, known from the famous Jurassic sponge mounds (Leinfelder and Schmid, 2000; Krautter *et al*., 2001), were not found either in modern sceptrulophoran sponges building the mounds or in the Cenomanian sponges, living in sponge meadows.

The petrography of the sediments, connected with the 'sponge bed' in Ukraine, is somewhat similar to that of the QCB sediments and also to that of the GB sediments (Tab. 8). In the deposits from Ukraine, there are more components in the sand-size fraction, similarly as in the QCB shelf (Tab. 8). On the other hand, directly around the phosphatized sponges from unit 4 in Ukraine has a slightly dominant a clay-sized material. A similar proportion of the finest-sized material is found in the GB, where there are the smaller sponge reefs, associated with the calmer environment of the distal parts of the prodelta setting (Tab. 8). Sponges from the Cenomanian of Ukraine represent quite diverse shapes, including plate- or cup-like ones, which indicates their adaptation to living conditions at very slow sedimentation rates, as is the case in the QCB (less than 0.1 mm per year, according to Conway *et al*., 2004). Sponges from the GB are tube-shaped and closely adjacent to each other (Conway *et al*., 2005), which are features, adaptive for a slightly faster sedimentation rate (2 cm per year, according to Conway *et al*., 2004). In the opinion of the present authors, the Cenomanian sponge meadows of Ukraine show adaptive features to the conditions, currently prevailing in the QCB and the GB, although they seem to have been better adapted to open-shelf conditions (Fig. 15), with a slower sedimentation rate as is the case of the QCB shelf. Detrital material delivered from land (silt-sized quartz), probably by rivers, is significantly visible in the petrographic images, hence, one cannot rule out the fact that sponges could have inhabited the distal parts of the prodelta at very calm hydrodynamic conditions similarly as in the GB (Conway *et al*., 2004).

Specimens from western Ukraine are generally smaller than the sponge specimens in the modern reefs, and occasionally up to 13 cm in their largest dimension, with most of the specimens not exceeding 10 cm in size (Dunikowski, 1889; Khmilevsky, 1969; Olszewska-Nejbert and Świerczewska-Gładysz, 2012, 2013). This situation indicates that the present-day Western Canadian Continental Shelf has better conditions for sponge development than those that existed around the Ukrainian mainland in the Cenomanian. However, many of the specimens examined are severely crushed, and their overall size is unknown. Numerous preserved fragments, especially of thick, long stems, suggest that some sponges could have reached much larger sizes (c. 20 cm). The fossilization processes (in this case – phosphatization) of these sponges during early diagenesis were also an important factor preventing the complete preservation of large specimens. The identified phosphatization processes were typically involved in the very thin layers of sediment in near-surface zones, in approximately 20 cm of the sediment column (e.g., Föllmi, 1990; Jarvis *et al*., 1994). Furthermore, these sponges underwent local phosphatization (Föllmi, 1990; Olszewska-Nejbert and Świerczewska-Gładysz, 2009) affecting small objects. All cases of phosphatized sponges from Cretaceous deposits, described to date, are usually small specimens or crushed fragments, rarely exceeding a dozen cm in size (e.g., Hurcewicz, 1988; Świerczewska-Gładysz, 2006; Świerczewska-Gładysz and Olszewska-Nejbert, 2006, 2013; Olszewska-Nejbert and Świerczewska-Gładysz, 2009, 2011, 2012, 2013; Vodrážka *et al*., 2009; Pervushov, 2018).

CONCLUSIONS

1. The present authors describe in detail 21 species of siliceous sponges (13 sceptrulophoran species, 7 lychniscosidan species, and one lithistid species), which have not been described so far from the Cenomanian of western Ukraine. Two new species of Sceptrulophora (*Tretodictyum petrivensis* sp. nov. and *Tretodictyum complicatus* sp. nov.), one new monotypic genus of Lychniscosida (*Khmilevskia papillata* gen. et sp. nov.) and three other new lychniscosidan species (*Brachiolites elongatus* sp. nov., *Ophrystoma olehii* sp. nov., *Plocoscyphia anastomosa* sp. nov.) are proposed.
2. The Cenomanian sponge assemblage of western Ukraine studied is the taxonomically most diverse hexactinellid sponge assemblage of this age. It includes 28 sceptrulophoran species and 28 lychniscosidan species in total. Among them, 23 species are not known from other regions of the Cretaceous epicontinental basin of Europe.
3. Lithistid demosponges (mainly represented by two phymatellid species) and body-preserved demosponges without a rigid skeleton are extremely rare in the studied assemblage.
4. The environmental preferences of contemporary hexactinellids and the type of material infilling the phosphatized sponges indicate that this assemblage inhabited a relatively deep shelf that was located relatively close to the land area (Ukrainian Land), from which fine (silt-size) quartz reached the sea.
5. The life settings of the studied Cenomanian sponges were most similar to those, currently found on the Western Canadian Continental Shelf. However, the key difference is that modern sponges have built mounds (reefs), while the Cenomanian assemblage from western Ukraine occurred as sponge meadows.

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