

Hexactinellid sponge assemblages across the Campanian–Maastrichtian boundary in the Middle Vistula River section, central Poland

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ABSTRACT:

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The sponge fauna from the Upper Campanian–lowermost Maastrichtian succession of the Middle Vistula River valley (central Poland) is represented mainly by dictyid hexactinellid sponges (Hexactinosida and Lychniscosida). Their greatest abundance and taxonomic variability is noted in the “*Inoceramus*” *inkermanensis* Zone (Upper Campanian), and they are less diverse in the overlying (Upper Campanian) *Trochoceramus costaecus* Zone and lower “*Inoceramus*” *redbirdensis* Zone. In the upper “*Inoceramus*” *redbirdensis* Zone (basal Maastrichtian in the sense of the Tercis rather than the Boreal definition) they are extremely rare. With the beginning of the Maastrichtian the number of dictyid sponges gradually increases.

The observed changes in the abundance and taxonomic variability of the dictyid sponges indicate environmental changes in the latest Campanian–earliest Maastrichtian sea in the area. It seems that changes in basin bathymetry, confined to eustatic sea-level changes in the latest Campanian and early Maastrichtian, were the most important factor. Progressive shallowing of the basin in the latest Campanian drastically restricted the development of dictyids. In the peak regression, the sea level could have fallen to only several tens of metres. The gradual recovery of the sponge assemblages correlates with subsequent deepening of the basin with the start of the Maastrichtian.

Key word: Sponges, Hexactinosida; Lychniscosida; Ecology; Upper Cretaceous; Campanian–Maastrichtian boundary; Southern Poland.

INTRODUCTION

During the Late Campanian–Early Maastrichtian (Late Cretaceous), the siliceous sponges were one of the most common organisms of the epicontinental seas of Central Europe. They were represented by lithistids (class Demospongiae Sollas, 1885, with a rigid skeleton) and dictyids (class Hexactinellida Schmidt, 1870, with a dictyonal skeleton, including representatives of the orders Hexactinosida Schrammen, 1903 and Ly-

chniscosida Schrammen, 1903). Unfortunately, localities with Campanian and Maastrichtian sponges preserved as body fossils are relatively rare in Poland (a few localities in southern Poland; Aleksandrowicz 1954; Barczyk 1956; Bieda 1933; Cieśliński and Jaskowiak 1973; Hurcewicz 1966, 1968; Hurcewicz 1966, 1968; Różycki 1938; Świerczewska-Gładysz 2006). The Upper Cretaceous Middle Vistula section (see Marcinowski and Radwański 1983), with a rich and extensive sponge record is thus of particular in-

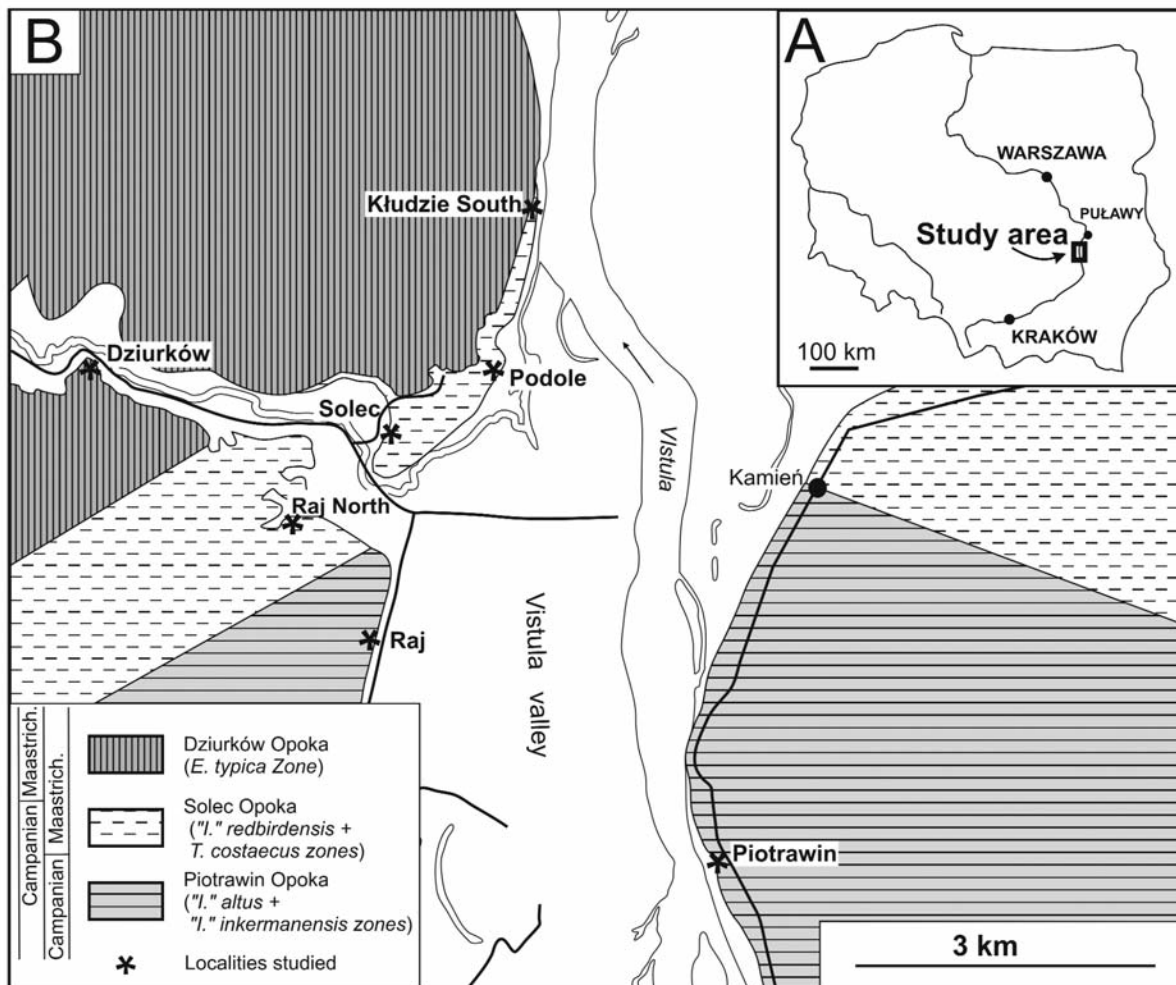
terest. Sponges were first mentioned from this area by Pusch (1837) and reported subsequently by Sujkowski (1931), Pożaryski (1938) and Putzer (1942). The first taxonomic descriptions of sponges from selected intervals were published by Hurcewicz (1966, 1968).

A taxonomic revision of the Late Campanian–Maastrichtian sponges from the Middle Vistula valley was recently published by Świerczewska-Gładysz (2006). Unfortunately, the Campanian–Maastrichtian boundary interval was rather poorly represented in the material presented. Moreover, the stratigraphic interpretation adopted in the paper of the boundary interval in the area (after Błaszkiwicz 1980 and Abdel-Gawad 1986), was out of date and required revision (see Walaszczyk 2004, and this issue). Consequently, new fieldwork and collecting was undertaken in the same area. The present paper concentrates on these new collections, with particular reference to the changes in the sponge assemblages across the Campanian–Maastrichtian boundary succession, as currently interpreted. Environmental interpre-

tations based on the sponges are the main focus of this paper.

GEOLOGICAL SETTING

The Upper Campanian–lowermost Maastrichtian succession exposed between the villages of Piotrawin and Kłudzie, around the town of Solec nad Wisłą (Text-fig. 1A, B), forms a part of the classic Middle Albian–Upper Cretaceous succession of the Middle Vistula River section (see e.g. Marcinowski and Radwański 1983; Walaszczyk, this issue). The succession is composed of monotonous, poorly bedded siliceous chalk (opoka), subdivided into three local lithostratigraphic units (Walaszczyk 2004, and this issue): Piotrawin Opoka, Solec Opoka and Dziurków Opoka (Text-fig. 2). The chronostratigraphic interpretation of the succession and the location of the Campanian/Maastrichtian boundary (the Tercis definition) is based on inoceramid bivalves (Walaszczyk 2004, and



Text-fig. 1 A. Location of study area on the general map of Poland; B. Geological sketch-map with the Upper Campanian and Lower Maastrichtian of the Middle Vistula section (after Walaszczyk 2004)

this issue) and confirmed, based on belemnites (Remin 2007 and this issue; Keutgen *et al.* this issue) and ammonites (Machalski 2012). The Piotrawin and Solec opokas are of Late Campanian age, and the Dziurków Opoka is of earliest Maastrichtian age. The Campanian/Maastrichtian boundary is placed at the ‘boundary marl’ (Walaszczyk 2004), a thin marly unit, at the boundary between the Solec and Dziurków opokas (Text-fig. 2).

THE BOUNDARY SUCCESSION

The oldest strata studied herein are exposed in an abandoned quarry, located c. 500 m to the south of the village of Piotrawin (Text-fig. 1). The light-yellow Piotrawin Opoka, exposed there is extremely fossiliferous, yielding sponges, bivalves, gastropods, ammonites, nautiloids and belemnites, as well as echinoids, brachiopods and solitary corals. The SiO₂ content in these deposits reaches 42%. There is also an insignificant admixture of detritic material and glauconite. Most of the sponge spicules are dissolved, albeit opal spicules are relatively common (Text-fig. 2A–D). Some voids after spicules are filled with calcite or opaque minerals. Oxeas of different sizes (0.05–1.4 mm) predominate (Text-fig. 2A–B). Several triaenes are also present (Text-fig. 2C). Current lineation of spicules is observed locally in the upper part of the succession (Text-fig. 2D). The upper part of the Piotrawin Opoka is accessible in the small quarry located south of the village of Raj (Text-fig. 1).

Walaszczyk (2004) referred the lower part of the succession to the “*Inoceramus*” *altus* inoceramid Zone, and the middle and upper parts to the “*Inoceramus*” *inkermanensis* inoceramid Zone.

The overlying Solec Opoka is exposed in the small, active quarry Raj North, in the abandoned quarry of Solec, as well as in the Vistula River escarpments in Podole and in Kłudzie, in close proximity of the ferry stop (Text-fig. 1). The Solec Opoka is characterized by a higher content of SiO₂ than in the underlying Piotrawin Opoka, reaching 47.5%. The admixture of detritic material is still very low. Voids after sponge spicules (oxeas and triaenes) are very common (Text-fig. 2E, F). Some of them are filled with microcrystalline quartz. A current lineation of spicules is observed (Text-fig. 2E). Belemnites are relatively common, as are bivalves, brachiopods, and solitary corals in the upper part of the succession.

Walaszczyk (2004) referred the lower part of the Solec Opoka to the *Trochoceramus costaecus* Zone, and its upper part to the “*Inoceramus*” *redbirdensis*

Zone. The top of the Solec Opoka is placed at the level of the ‘boundary marl’, which is well exposed in Kłudzie and Podole (Walaszczyk 2004). Deposits situated above the “boundary marl” are referred already to the Dziurków Opoka (Walaszczyk 2004), which spans the uppermost “*Inoceramus*” *redbirdensis* Zone (basal Maastrichtian) and the overlying *Endocostea typica* Zone. In belemnite terms, the Solec Opoka is assigned to the (Lower Campanian) *Belemnella lanceolata* Zone *sensu* Remin (Remin 2007, and this issue), or to the *Belemnella lanceolata* and *Belemnella pseudobtusa* Zone *sensu* Schultz (Keutgen *et al.* this issue).

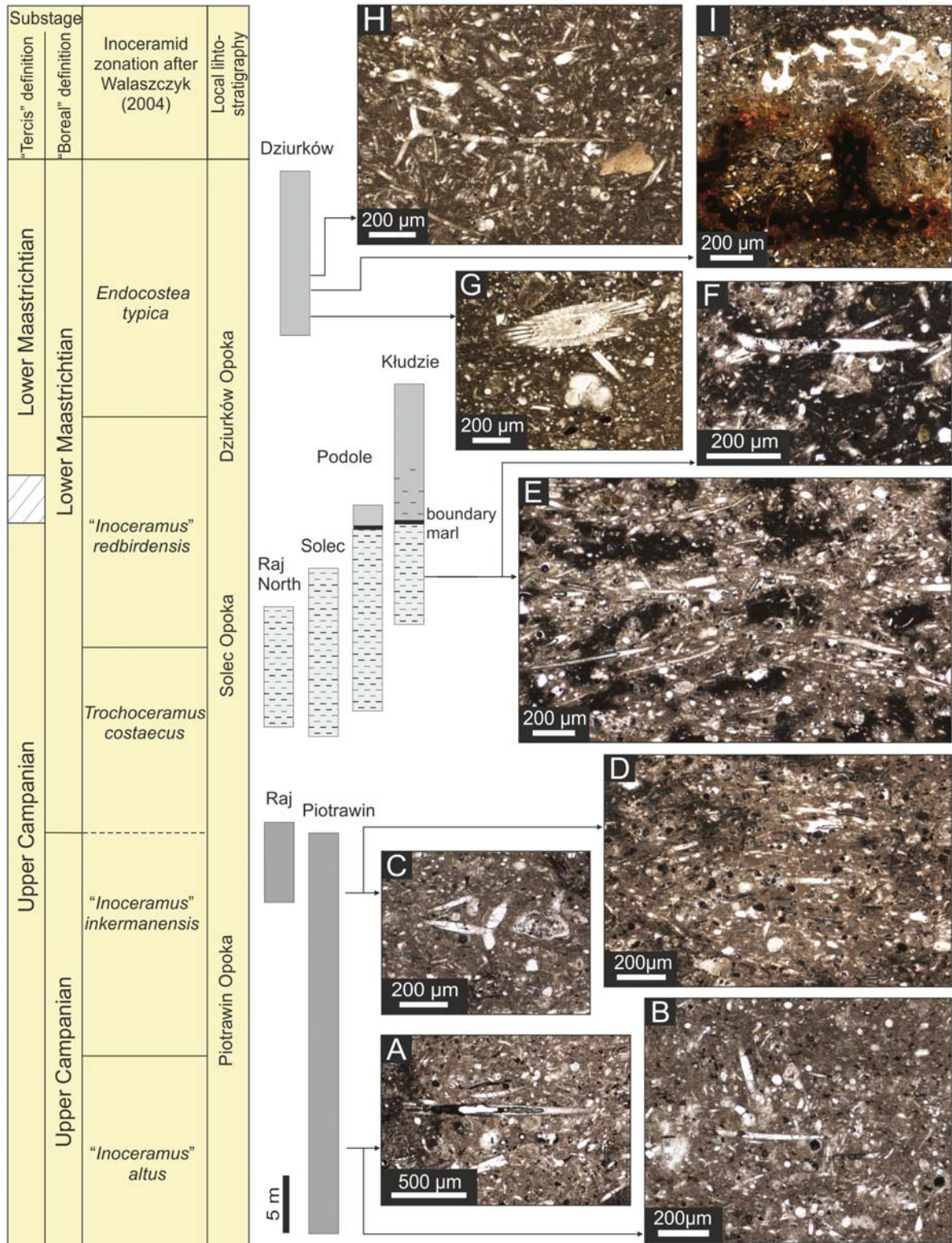
The pale cream coloured, brittle Dziurków Opoka is macroscopically similar to the Piotrawin Opoka. It also contains a very abundant macrofauna. The silica content drops to 36.25%; it additionally contains rare detritic material and glauconite. Numerous, variably oriented voids after sponge spicules (oxeas and rare triaenes) are sporadically filled with fine-crystalline quartz (Text-fig. 2I). Most of the sponges from the Dziurków Opoka were collected in an active quarry located near the eastern part of the village of Dziurków (Text-fig. 1). Walaszczyk (2004) refers the unit (other than its basal part) to the *Endocostea typica* inoceramid Zone. In belemnite terms, it is assigned to the basal Lower Maastrichtian *Belemnella obtusa* Zone by Remin (2007, and this issue) and to the *Belemnella pseudobtusa* and *B. obtusa* zones by Keutgen *et al.* (this issue).

MATERIAL AND METHODS OF STUDY

The studies are based on the author’s archive collections, housed at the Geological Faculty of Łódź University (collection no. UŁ XX), and on the author’s new collections from selected localities. Altogether, the studied material comprises: 369 specimens from Piotrawin; 77 specimens from Raj; 47 from Raj North; 20 from Solec; 17 from Podole; 44 from Kłudzie South; 12 from a series of former small exposures located c. 50–200 m to the south of Kłudzie South; and 131 from Dziurków.

The specimens from the Piotrawin Opoka are strongly limonitized. Due to this fact the course of canals in the wall as well as the distribution of canal openings on its surface are poorly visible or even completely obliterated, which hampers determination at species level. The siliceous skeleton is usually completely dissolved. Preserved fragments of the skeleton are sporadically present in the lower part of the sponges.

Due to the presence of amorphous silica in the siliceous chalk, the specimens were subjected to etch-



Text-fig. 2. Schematic stratigraphic log and thin-section photographs of the uppermost Campanian and lowermost Maastrichtian of the Middle Vistula River valley section. A–D – Piotrawin Opoka; A – partly dissolved opal oxeas; B – variable oriented opal oxeas and voids after spicules; C – void after triane and foraminifera; D – current lineation of voids after spicules; E, F – Solec Opoka; E – current lineation of voids after spicules; F – void after triaene. G–I – Dziurków Opoka; G – foraminifera and fragment of echinoderm; H – void after triaene and variable oriented voids after oxeas; I – void after dictyonal skeleton of *Aphrocallistes cylindrodactylus* Schrammen, 1912, partly filled with limonite

	Local lithostratigraphy	Piotrawin Opoka		Solec Opoka		Dziurków Opoka	
		P	P, R	RN, S, Po	S, Po, K	K	D
	Inoceramid zonation	“Inoceramus” altus	“Inoceramus” inkermanensis	Trochoceramus costaeus	“Inoceramus” redbirdensis	“Inoceramus” redbirdensis	“Endocostea” typica
	Sponge taxa						
HEXACTINOSIDA	<i>Aphrocallistes cylindrodactylus</i> Schrammen, 1912	+++	+++	++	+	++	+++
	<i>Leptophragma micropora</i> Schrammen, 1912	+++	+++	++	^	+	++
	<i>Leptophragma murchisoni</i> (Goldfuss, 1831)	++	++	+	^	^	+
	<i>Eurete formosum</i> Reid, 1959	++	++	^	^	^	++
	<i>Pleurostoma dichotoma</i> (Schrammen, 1902)	^	^	^	^	+	++
	<i>Wollemannia araneosa</i> Schrammen, 1912	++	++	^		^	+
	<i>Hapalopogon meandrina</i> Schrammen, 1912	^	^	^		^	^
	<i>Polyopesia leavis</i> (Schrammen, 1912)	+	++	^			+
	<i>Aphrocallistes alveolites</i> (Roemer, 1841)	^	^	^		^	+
	<i>Aphrocallistes caliciformis</i> Świerczewska-Gładysz, 2006	+	++				
	<i>Eubrochis cribrorum</i> (Reid, 1964)		^				+
	<i>Laocoetis fittoni</i> (Mantell, 1822)		^				
	<i>Chonodictyon</i> (?) cf. <i>sewerbyensis</i> Reid, 1959		^				
	<i>Aphrocallistes</i> sp.		^				
	<i>Hexactinella</i> sp.		^				
<i>Oxyrhizium</i> cf. <i>eximium</i> Schrammen, 1912			^				
LYCHNISCOSIDA	<i>Rhizopoterion cribrorum</i> (Phillips, 1829)	+	++	+	+	+	+
	<i>Rhizopoterion solidum</i> Schrammen, 1912	+	+	^	^	^	+
	<i>Leiostracosia punctata</i> Schrammen, 1902	+	++	^			+
	<i>Coeloptychium seebachi</i> Zittel, 1876	+	++	^			
	<i>Cyclostigma acinosa</i> (Schrammen, 1902)	+	++				^
	<i>Cyclostigma maeandrina</i> Schrammen, 1912	+	++				^
	<i>Leiostracosia robusta</i> (Schrammen, 1902)	+	+				+
	<i>Sporadoscinia decheni</i> (Goldfuss, 1831)	^	^			^	^
	<i>Lepidospongia rugosa</i> Schlüter, 1870	^	^				
	<i>Tremabolites megastoma</i> (Roemer, 1841)		^				

Table 1. Distribution of sponge species in the studied succession (P – Piotrawin, R – Raj, RN – Raj North, S – Solec, Po – Podgórz, K – Kłodzie, D – Dziurków).

^ – <5 specimens, + – 6–10 specimens, ++ – 11–20 specimens, +++ – >20 specimens

ing by hydrofluoric acid (for method see Świerczewska-Gładysz 2006). Voids after dissolved spicules, often filled with iron compounds, were viewed under the microscope.

Specimens from the Solec Opoka are not or only slightly limonitized. In a few cases, fragments of the siliceous skeleton are also present but, due to the high content of silica in the rock, attempts at isolating the skeletal elements were not successful. Due to this fact, studies of the skeletal structures were restricted to microscopic observations of the spicules exposed

on the surface of some specimens. Data on the skeletal structure of these sponges, indispensable for specific assignment, came from voids after dissolved spicules, which are well represented in the studied material.

Sponges from the Dziurków Opoka are strongly limonitized, like those from the Piotrawin Opoka (Text-fig. 2H). Siliceous spicules are almost absent in the material.

Loose spicules (or their voids) dispersed in the rock have been analysed in thin sections.

DISTRIBUTION OF SPONGES IN THE STUDIED SUCCESSION

Piotrawin

Dictyid sponges are very common in this locality (Table 1), particularly in the “*I.* *inkermanensis* Zone part of the succession (Text-fig. 2). Throughout the succession, lump-shaped sponges, and most of the smaller, conical and cup-like sponges not exceeding 10 cm in height, are preserved in life positions (see also Świerczewska-Gładysz 2006). Several specimens possess additional rhizoidal processes growing out of the lower parts of their body, c. 2–3 cm above the main rhizoidal processes. Large conical, cup-like and cylindrical sponges lie on one side. Their bent or broken stalks terminate in rhizoidal processes. In the large specimens of *Coeloptychium seebachi* Zittel, 1876 and *Leiostracosia punctata* Schrammen, 1902, their disc-like upper parts are broken off, but can usually be found close to the discs. Crushed fragments of different specimens have been found only within several detritic accumulations in the upper part of the section.

The dictyid sponges represent a high-diversity, heterogeneous assemblage, with a very low dominance index; no species exceeds 5% of the assemblage. The most numerous are Hexactinosida (181 specimens), represented by fourteen species (see Table 1). Less frequent are Lychniscosida (106 specimens), represented by ten species (Table 1; and Text-figs 5C, D, G).

Some of the dictyids are characterized by very large sizes. Specimens of the genus *Leptophragma* and *Wollemannia araneosa* Schrammen, 1912 attain up to 20 cm. Cup- or funnel-shaped specimens of the genus *Rhizopoterion* are 20–25 cm in height, with the largest exceeding 30 cm. The umbrella-like specimens of *Leiostracosia* and mushroom-like *Coeloptychium seebachi* are 15 cm in height and c. 30 cm in diameter.

The most common lithistid species (more than half of all lithistid collected) is *Callopegma acaule* Zittel, 1878 (Text-fig. 6E), noted exclusively in the uppermost part of the succession (the highest five to six metres). Other lithistids occurring throughout the succession are rare, represented by *Homalodora plana* Schrammen, 1910, *Verruculina miliaris* (Reuss, 1846), *Verruculina tenuis* (Roemer, 1841) and *Aulaxinia sulcifera* (Roemer, 1864) (Text-fig. 6A), as well as single specimens of *Plinthosella squamosa* Zittel, 1878, *Turronia variabilis* Michelin, 1847 and *Ophiraphidites infundibuliformis* Schrammen, 1899. The species *Homalodora ficus* Schrammen, 1910 and *Pachycothon giganteum* (Roemer, 1864), also known from single specimens, have been noted exclusively in the “*Inoceramus*” *inkermanensis* Zone.

Raj

Hexactinosid and lychniscosid sponges are very common and evenly distributed throughout the succession (Table 1). Specimens observed *in situ* do not bear traces of *post-mortem* destruction. The taxonomic composition of the dictyid sponges is very similar to that of the sponges from Piotrawin (Text-figs 3E, 4C), with the exception of seven rare species and *Lepidospongia rugosa* Schlüter, 1870. Also noted was a single specimen of *Eubrochis cribrosum* (Reid, 1964) (Text-fig. 4F). The lithistids are dominated by *Callopegma acaule* (Text-fig. 6D) and *Homalodora plana*, as in the upper part of the Piotrawin section.

Raj North

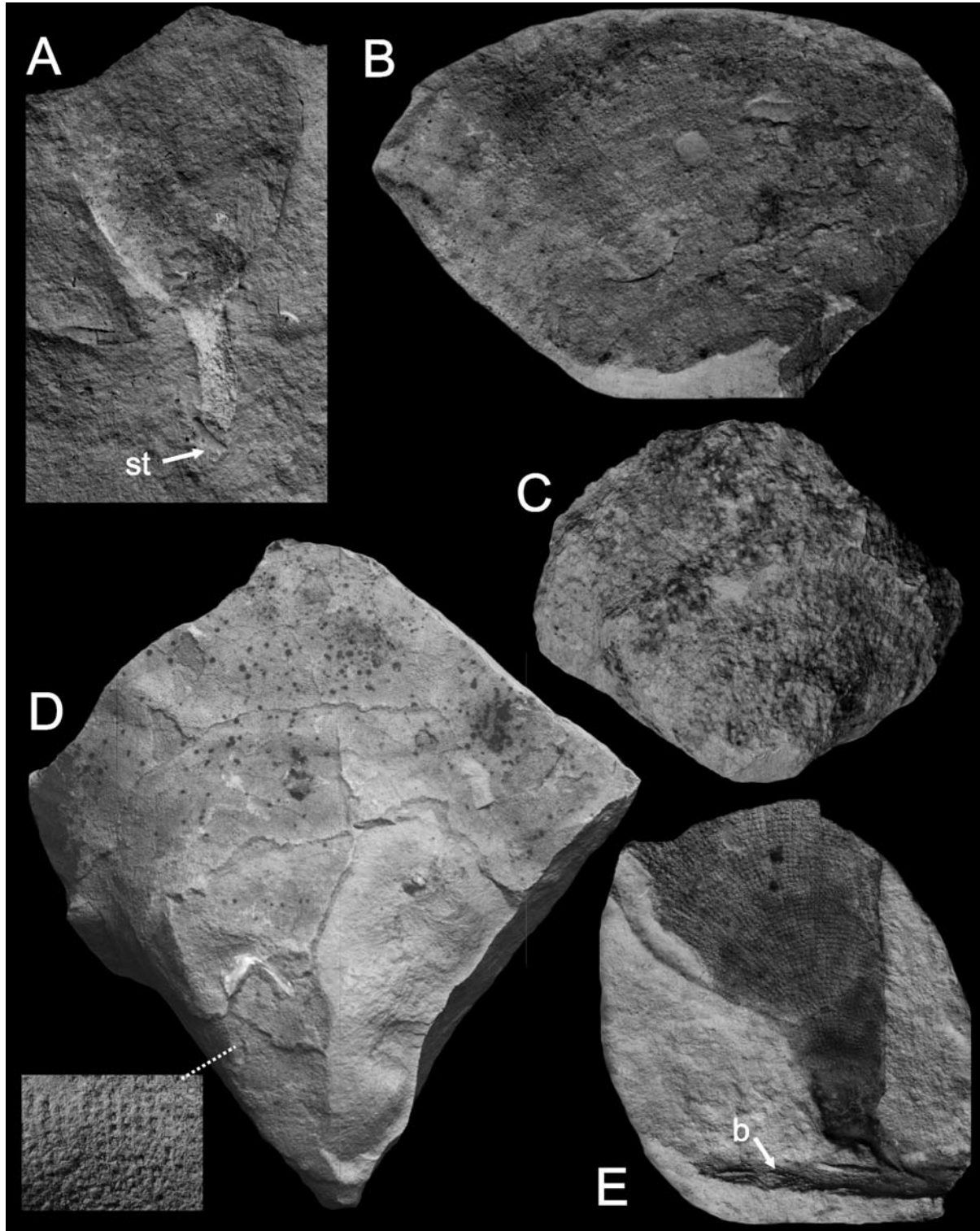
Dictyid sponges are very rare (Table 1). Most of them are preserved in life position or lie on one side but with rhizoidal processes preserved. A serpulid tube was noted on one of the specimens (Text-fig. 3A). Small sponge fragments (probably representing the genus *Leptophragma*) have been found in the biodetritus accumulations. The collected specimens come from the lower part of the succession, most probably from the *Trochoceramus costaecus* Zone. Like in the Piotrawin Opoka, the most common are Hexactinosida. They are dominated by *Aphrocallistes cylindrodactylus* Schrammen, 1912 (Text-fig. 4H), *Leptophragma micropora* Schrammen, 1912 (Text-fig. 3A) and *L. purchisoni* (Goldfuss, 1831). The remaining species (Table 1; and Text-fig. 4A) are rare. Individuals of *L. micropora* and *Wollemannia araneosa* do not exceed 10 cm in height (due to the regular, cup shape of these sponges their height can be estimated despite the damage) and are on average one-third smaller than specimens from Piotrawin and Raj. Lychniscosida are rare and of low diversity (Table 1). A few specimens of *Rhizopoterion cribrosum* (Phillips, 1829) and single specimens of *R. solidum* Schrammen, 1912 and *Leiostracosia punctata* were found. Lithistid sponges are represented by *Aulaxinia sulcifera*, *Homalodora plana*, *Plinthosella squamosa* and fragments of poorly preserved tetractinelid sponges.

Solec

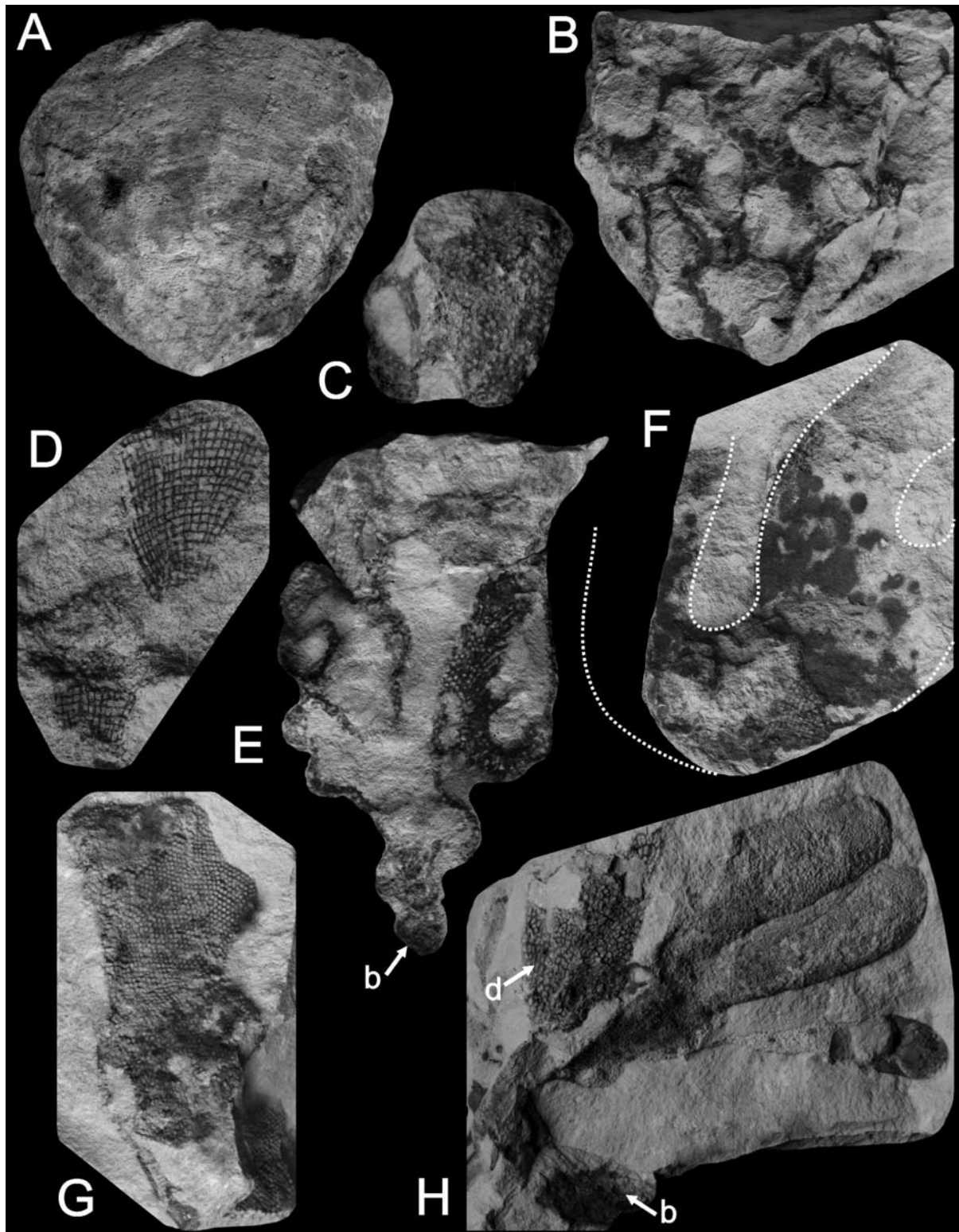
Dictyids are very rare (Table 1). *Aphrocallistes cylindrodactylus*, *Leptophragma micropora*, *L. purchisoni* and *Rhizopoterion cribrosum* have been noted throughout the succession, and *Pleurostoma dichotoma* was found in the upper part of the section. A single specimen of *Oxyrhizium cf. eximium*

Schrammen, 1912 (hexactinosid species) and one specimen of *Rhizopoterion solidum* were found in the

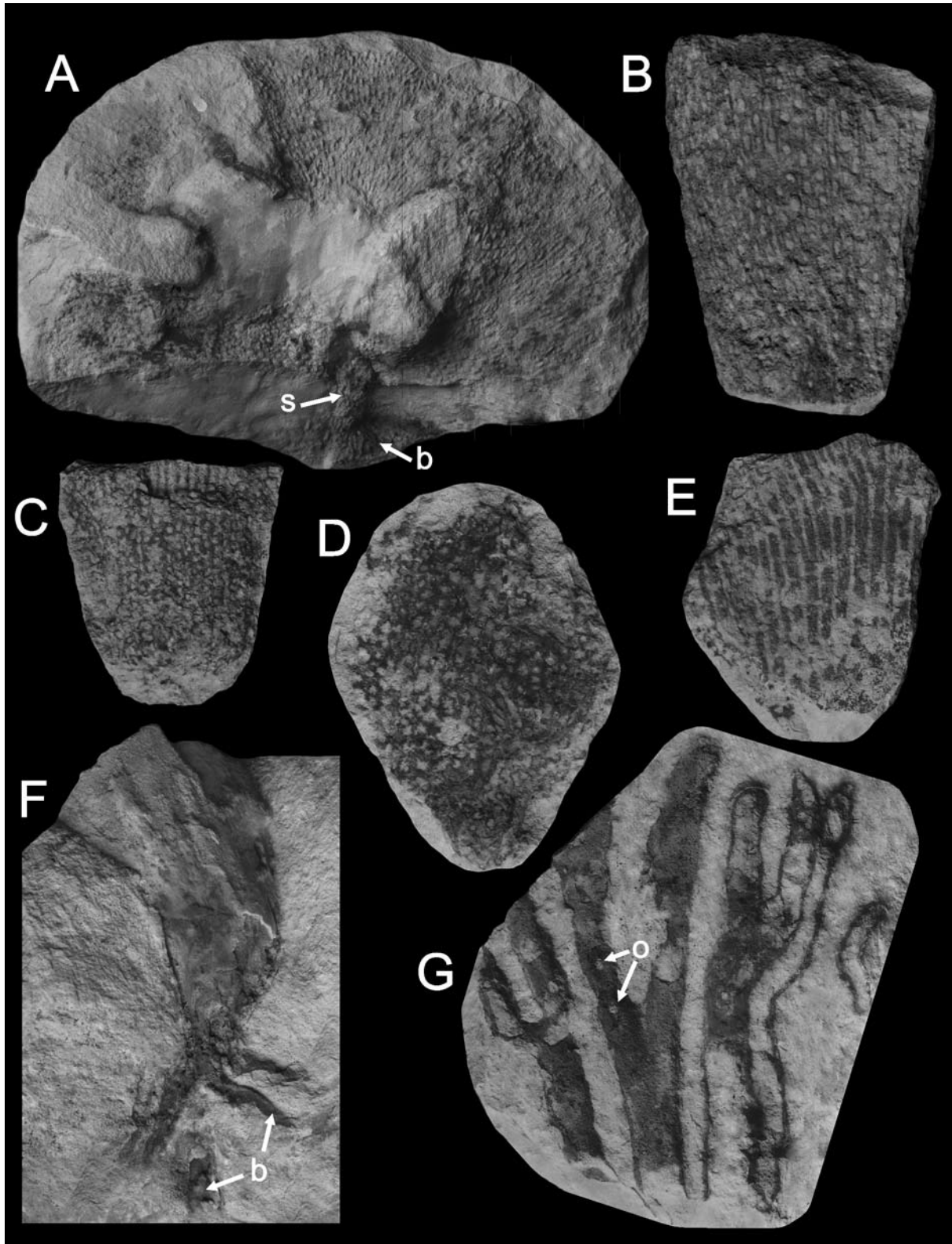
lowermost, at present inaccessible part of the succession (*T. costaeus* Zone). Also found were single



Text-fig. 3. Hexactinosida. **A, B** – *Leptophragma micropora* Schrammen, 1912. **A** – RN9/31, Raj North, $\times 1$; **B** – D9/34, Dziurków, $\times 1$; **C** – *Polyopesia leavis* (Schrammen, 1912); ULXX 2/12, Dziurków, $\times 0.7$; **D** – *Leptophragma munchisoni* (Goldfuss, 1831); ULXX 1/158, Piotrawin, $\times 0.55$, fragment of dermal surface $\times 1.2$; **E** – *Pleurostoma dichotoma* (Schrammen, 1912), R 9/30, lower part of specimen; Raj, $\times 0.90$; st = serpulid tube; basal skeleton



Text-fig. 4. Hexactinosida. A – *Wollemannia araneosa* Schrammen, 1912; RN9/36, Raj North, $\times 1$; B – *Eurete formosum* Reid, 1959; D9/5, Dziurków, $\times 0.90$; C, E – *Aphrocallistes caliciformis* Świerczewska-Gładysz, 2006, C – R9/71, Raj, $\times 10$; E – ULXX 7/49, Piotrawin, $\times 0.55$. D – *Hapalopegma meandrina* Schrammen, 1912; KŁ9/12, Kłudzie, $\times 1$. F – *Eubrochis cribrosum* (Reid, 1964); R 9/17, Raj, $\times 1$. G – *Aphrocallistes alveolites* (Roemer, 1841); P 3/84, Piotrawin, $\times 1$. H – *Aphrocallistes cylindrodactylus* Schrammen, 1912; RN 9/1, Raj North, $\times 0.70$; b = basal skeleton; sp = sieve plate

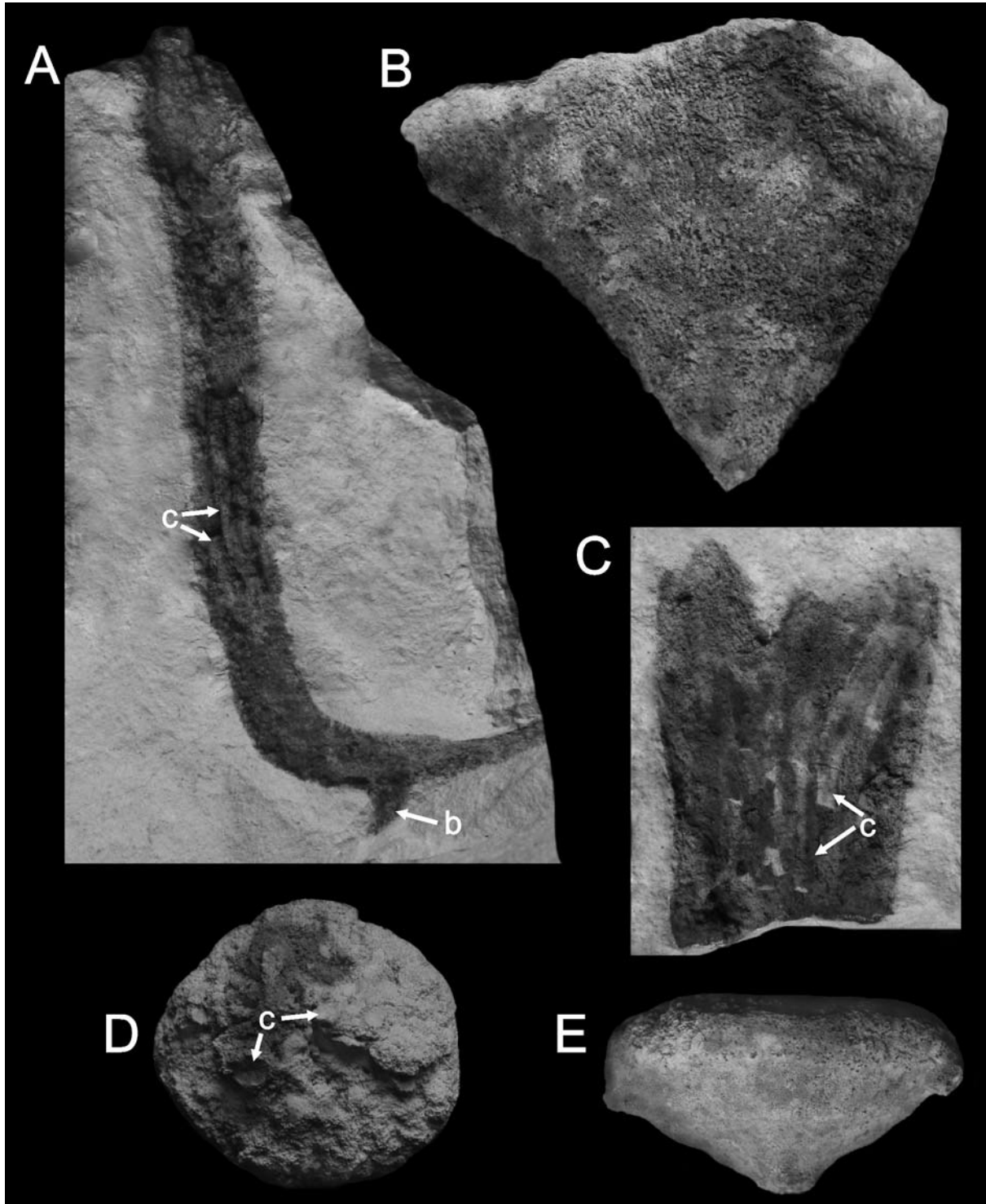


Text-fig. 5. Lychniscosida. **A** – *Rhizopoterion cribrosum* (Phillips, 1829), D 9/40, Dziurków, $\times 0.60$; **B** – *Rhizopoterion solidum* Schrammen, 1912, KL9/24, Kłudzie, $\times 0.75$; **C** – *Leiostracosia punctata* Schrammen, 1902, ULXX 3/44, Piotrawin, $\times 0.8$; **D**, **E** – *Leiostracosia robusta* (Schrammen, 1902), D – ULXX 6/41, Piotrawin, $\times 0.60$; E – ULXX 6/43, Dziurków, $\times 0.6$. **F**, **G** – *Coeloptychium seebachi* Zittel, 1876, F – PO9/6, Podole, $\times 0.8$; G – ULXX 3/46 Piotrawin, $\times 0.8$; s = stalk; b = basal skeleton; o = oscula

specimens of the lithistids *Aulaxinia sulcifera*, *Homalodora plana* and *Plinthosella squamosa*. Other lithistids were too poorly preserved to be determined specifically.

Podole

The very rare dictyids are dominated by hexactinoid sponges, represented by *Aphrocallistes cylindro-*



Text-fig. 6. Lithistida. A – *Aulaxinia sulcifera* (Roemer, 1864); ULXX 3/39, Piotrawin, $\times 1$; B – *Verruculina tenuis* (Roemer, 1841); D9/41, Dziurków, $\times 1$; C – *Homalodora plana* Schrammen, 1910; upper part of specimen; KL3/28, Kłodzie, $\times 1.2$; D, E – *Callopegma acaule* Zittel, 1878; D – upper view; R9/70, Raj, $\times 1.5$; E – upper view; ULXX 1/148, Piotrawin, $\times 1$; b = basal skeleton; c = canals

dactylus, *Leptophragma micropora*, *L. murchisoni* and *Eurete formosum* Reid, 1959 (Table 1). Single specimens of *Hapalopegma meandrina* Schrammen, 1912 and *Wollemannia araneosa* come from the lower part of the section. Also found in this part were three lychniscosid species, *Rhizopoterion solidum*, *R. cribrosum*, and *Coeloptychium seebachi* (see Text-fig. 5F). Higher in the section, the only representative of lychniscosid sponges is *R. cribrosum*. Lithistids are represented by strongly damaged specimens of *Homalodora plana*, *Ophiraphidites infundibuliformis* and some specifically undeterminable fragments of tetractinellids.

Kłudzie

In the Solec Opoka, dictyid sponges are very rare (Table 1), represented by *Aphrocallistes cylindrodactylus*, *Leptophragma micropora*, *L. murchisoni*, *Eurete formosum* and *Pleurostoma dichotoma*. Lychniscosida are represented by *Rhizopoterion cribrosum* and *R. solidum* (Text-fig. 5B). Dictyids were not found in the highest two metres of the Solec Opoka, but they reappear above the “boundary marl” and their frequency gradually increases upwards. In the uppermost part of the section, which represents the Dziurków Opoka, they are relatively numerous. Beside the species occurring in the lower part of the section, three other hexactinosid species (*Aphrocallistes alveolites* (Roemer, 1841), *Wollemannia araneosa*, and *Hapalopegma meandrina*, see Text-fig. 4D) and one lychniscosid species, *Sporadoscina decheni* (Goldfuss, 1831) were found. Poorly preserved fragments of undeterminable lithistids and single specimens of *Aulaxinia sulcifera*, *Plinthosella squamosa* and *Homalodora plana* are also noted (see Text-fig. 6C).

Dziurków

The dictyid sponges are numerous (Table 1), preserved in life position or lying on one side (Text-fig. 5A). Their dimensions are similar to those of specimens from the Piotrawin Opoka. The specific composition of the sponge assemblage is the same throughout the succession. The most numerous and diverse group is the Hexactinosida. *Aphrocallistes cylindrodactylus* is extremely common, representing 17 % of the dictyids in this locality (lower, in the “I.” *redbirdensis* Zone it reaches 26–28%). Also common are *Leptophragma micropora* (Text-fig. 3B), *Eurete formosum* (Text-fig. 4B) and *Pleurostoma dichotoma*. Rarer are *L. murchisoni*, *Wollemannia araneosa*, *Eubrochis cribrosum*, *Aphrocallistes alveolites*, *Polyopesia leavis* Schrammen, 1912 (Text-fig. 3C) and *Hapalopegma meandrina*. Apart

from single specimens of *Cyclostigma acinosa* (Schrammen, 1902) and *C. maeandrina*, the other Lychniscosida are represented solely by the family Ventriculitidae Smith, 1848 (Table 1 and Text-fig. 5A, E). Lithistid sponges are rare but rather diverse. The locality yielded *Aulaxinia sulcifera*, *Homalodora plana*, *Plinthosella squamosa*, *Turonia variabilis* and *Verruculina tenuis* (Text-fig. 6B).

DISCUSSION

The dictyids are most abundant and diverse in the Piotrawin Opoka. Ten hexactinosid and nine lychniscosid species were found in the “I.” *altus* Zone, and five other hexactinosid and one lychniscosid species appear additionally in the succeeding “I.” *inkermanensis* Zone. Most of the sponges from the Piotrawin Opoka attain large body sizes (>30 cm). The growth rate of Recent hexactinellids reaches 0–7 cm/year (Leys and Lauzon 1998; Krautter *et al.* 2001), with a maximum 10 cm/year (Austin *et al.* 2007). The age of the studied sponges may thus be estimated at several to over a dozen years. These observations indicate that the environmental conditions were favourable for the development of dictyids during that time.

A drop in abundance and taxonomic diversity of the dictyid sponges is noted in the Solec Opoka. In the *T. costaeus* Zone there are ten hexactinosids (including nine species known from the Piotrawin Opoka) but only four lychniscosids. In the lower part of the “I.” *redbirdensis* Zone, the dictyid sponges are extremely rare and represented by only a few species; Hexactinosida by five species and Lychniscosida by two. Changes in the sponge assemblages observed in the Solec Opoka indicate a gradual deterioration of life conditions in the latest Campanian. Most probably this was also the cause of the smaller sizes of the sponges. Dictyids are apparently absent from the uppermost part of the Solec Opoka (c. 2 m below the “boundary marl”). It thus seems that the largest crisis in the sponge fauna took place during latest Campanian times.

Above the “boundary marl” in the topmost “I.” *redbirdensis* Zone, the dictyids gradually reappear. Like in the lower part of the “I.” *redbirdensis* Zone, there is a distinct dominance of hexactinosids, represented by eight species, over the lychniscosid sponges, represented by three species. Dictyid sponges become even more common in the succeeding *E. typica* Zone, where ten hexactinosids and six lychniscosid species were documented. This trend clearly indicates the gradual improvement of the environment. All the species are also known from the Piotrawin Opoka, albeit the number of

species recognised in the Dziurków Opoka is lower.

Lithistid sponges are also observed in the studied sections, but changes in their abundance and taxonomic composition are difficult to determine. Due to the poor state of preservation, the number of collected and taxonomically determinable specimens is greatly underestimated in relation to their actual abundance. The occurrence of lithistid sponges in deposits of the Cretaceous European epicontinental seas indicates that these sponges inhabited both the littoral as well as the neritic zone (e.g. Ulbrich 1974; Žitt *et al.* 2006; Wilmsen *et al.* 2011). Also, the Recent lithistids live both in deep-water and shallower environments (e.g. Kelly *et al.* 2007; Schlacher-Hoenlinger *et al.* 2005), tolerating a wider range of environmental parameters (e.g. faster sedimentation rate, higher turbulence) than the hexactinellids (Pisera 1997; Krautter 1997, 1998; Leinfelder *et al.* 1996). Consequently, lithistids are less useful for palaeoenvironmental interpretations than dictyid sponges.

Assessment of the possible role of various environmental parameters on the restriction of the dictyid sponges noted in the study area during the latest Campanian is not easy. Their development depends on various, often interconnected factors (Krautter 1997, 1998; Pisera 1997; Duarte *et al.* 2001; Whitney *et al.* 2005), some of which (e.g. reproduction rate) are difficult to evaluate in the fossil material.

Content of silica

The content of silica in sea water plays the key role in the development of all siliceous sponges (Maldonado *et al.* 1999; Gammon *et al.* 2000; Whitney *et al.* 2005). Enzymes indispensable for the formation of opal spicules are not activated at low silica concentrations (Krasko *et al.* 2000). The main component of the Late Campanian and Early Maastrichtian opokas are loose spicules of soft demosponges, probably from the order Astrophorida Sollas, 1888 (compare Hooper and Van Soest 2002; Pisera *et al.* 2006). The presence of these spicules proves that some groups of siliceous sponges lived in the depositional environments of the opokas, indicating that the silica concentrations were rather high and could not have restricted the development of the hexactinellids co-occurring with them.

Voids after loose spicules of soft demosponges and rigid skeletons of dictyids and lithistids preserved in the opokas indicate that the dissolution of biogenic silica took place mainly in a partly lithified deposit, as in the case of the Upper Maastrichtian opokas (compare Michniak 1979). Spicules of deceased sponges do not undergo corrosion for several years in certain specific

conditions (Krautter *et al.* 2006); however, in this case the process of spicule disintegration began in the freshly deposited sediment (compare Rützler and Macintyre 1978). Precipitation of calcium carbonate points to the low pH of the environment, which obviously favoured the dissolution of spicules. Due to this fact, the pore waters and the overlying marine waters were additionally enriched in silica, which was reintroduced to the environment (Gammon *et al.* 2000).

Bathymetry

Recent Lychniscosida are represented by only three species (Mehl 1992), which generally inhabit the bathyal zone (Ijima 1927; Van Soest and Stenfort 1988). The smallest depth at which they were noted was c. 80 m (Finks and Rigby 2004). Similarly, the Hexactinosida live at present in the bathyal to abyssal zones (Koltun 1967; Vacelet 1969; Tabachnick 1988; Maldonado and Young 1996; Duplessis and Reiswig 2004; McClintock *et al.* 2005; Janussen and Tendal 2007). They are extremely rare in shallower seas (Finks and Rigby 2004), mainly in the peripheral deeper parts of the shelves (Van Soest and Stenfort 1988). The largest shelf assemblage of hexactinosid sponges has been reported from offshore British Columbia (Krautter *et al.* 2001, 2006; Conway *et al.* 2004, 2007; Cook *et al.* 2008), where specific conditions, such as slow sedimentation, low energy, cold water and oligotrophic conditions, are known to occur (Leys *et al.* 2004; Whitney *et al.* 2005; Yahel *et al.* 2007). In this area the hexactinellid sponges (including three species of Hexactinosida) build the only known Recent sponge reef. The largest reef complex occurs at a depth of c. 140–240 m, whereas smaller ones have been reported within a range of 100–140 m (Conway *et al.* 2007; Cook *et al.* 2008). The presence of Recent hexactinosid sponges in shallower zones (less than 100 m) is very rare. Such cases are known from the fjords of British Columbia, where sponges were reported even at 25 m (Leys *et al.* 2004). However, in most fjords the hexactinosids concentrate at depths of 120–160 m, where they reach larger sizes than sponges living in shallower conditions (Leys *et al.* 2004). Some hexactinosid sponges were found at a depth of several metres off the coast of Borneo (Ijima 1927), but they probably came from a deeper zone (Reid 1968).

Late Cretaceous hexactinellids appeared in the neritic zone more often than their Recent counterparts. However, the assemblages of dictyid sponges in the North European province occur almost exclusively in calcareous to marly successions of the deeper parts of epicontinental seas (e.g. Defretin-Lefranc 1960; Nestler 1961; Reid 1968; Termier and Termier 1981; Wiese *et*

al. 2004, Žižt *et al.* 2006). In the shallow-water Cretaceous deposits calcareous and lithistid sponges appear (Finks and Rigby 2004), while dictyids are absent or very rare. For example, a few dictyids are found in the rich siliceous sponge assemblage from the uppermost Lower Campanian deposits in the Subhercynian Cretaceous Basin in front of the Harz Mountains, which were deposited during a regressive phase (Ulbrich 1974). The occurrence of Late Cretaceous dictyids in shallower-water environments is related to specific conditions, e.g. a very low sedimentation rate and/or upwelling of cold oceanic waters from the Tethys Ocean (compare e.g., Mehl and Huschke 1995; Mehl and Niebuhr 1995). Only a few species of hexactinosid and lychniscosid sponges have been noted in the Upper Cretaceous shallow-water deposits (see Schrammen 1912; Reid 1968; Ulbrich 1974; Mehl and Niebuhr 1995; Vodrážka *et al.* 2009). Out of the numerous Cretaceous dictyids, similarly to recent hexactinellids, only some species could tolerate shallower-water conditions. It can also be excluded that some broken specimens of dictyids from shallow-water deposits, especially in conglomerates, were not *in situ*. Redeposited sponges are usually crushed (Wilmsen *et al.* 2011) and/or phosphatized (e.g. Vodrážka *et al.* 2009; Świerczewska-Gładysz and Olszewska-Nejbert 2006; Olszewska-Nejbert and Świerczewska-Gładysz 2009, 2011), but sometimes nearly complete sponges with a siliceous skeleton and an undestroyed surface are found even in glacial deposits (undescribed specimens collected by P. Czubla from Małkolice near Piotrków Trybunalski, Central Poland).

The preference of Recent hexactinellids for a deeper environment, and the distribution pattern of Cretaceous dictyid sponges in the North European Province, suggest that the impoverishment of sponge assemblages observed in the Solec Opoka was caused by sea-level fall in the latest Campanian. Precise determination of the basin bathymetry based on the species recognized is not possible due to the lack of present-day analogues. Representatives of only two of the described genera (*Aphrocallistes* Gray, 1858 and *Eurete* Semper, 1868) live at present and they have a wide bathymetric range (Koltun 1967, 1970; Reid 1968; Finks and Rigby 2004; Leys *et al.* 2004; Reiswig and Wheeler 2004).

The presence of spicules of soft demosponges in the Solec Opoka evidences that these sponges developed in conditions that were unfavourable for sponges belonging to other groups. Recent soft demosponges have very wide bathymetric ranges (Hooper and Van Soest 2002). Accumulations of their spicules are known at present mainly from deep water settings (Conway *et al.* 1991), but under certain specific conditions they could

have also formed in shallow marine environments (Gammon *et al.* 2000). Pisera *et al.* (2006) evaluated the depth of the Miocene sea during the sedimentation of the Mem Monitz Marls (Portugal) at several tens of metres to c. 100 m or more, based on an assemblage dominated by soft sponges with the co-occurrence of lithistids and dictyids. These values also seem appropriate for the depth of the sea during the sedimentation of the Solec Opoka in the study area.

According to the existing interpretations of bathymetric conditions based on molluscs (Pożaryski 1960a; Abdel-Gawad 1986) and sponges (Świerczewska-Gładysz 2006), the Late Cretaceous sea in the study area was deepest during Late Campanian times and shallowest in the terminal Maastrichtian. Although the sea shallowed progressively throughout the Maastrichtian, a short-term deepening took place during the deposition of the lower Upper Maastrichtian marls (see Pożaryski 1960a; Hakenberg and Świdrowska 2001). The observed impoverishment of the dictyid sponge fauna in the Solec Opoka succession evidences that yet another eustatic event took place at the Campanian–Maastrichtian boundary. Despite the shallowing, the content of terrigenous material is negligible in the Solec Opoka. The spiculitic opoka of the Ahlten Formation in northern Germany, which reflects the late Late Campanian *polyplacum* regression, is also characterized by a lower terrigenous input of <10% (Niebuhr *et al.* 1997; Niebuhr 2005).

The bathymetric changes indicated in the study area correspond to global sea-level changes (Haq *et al.* 1988; Miller *et al.* 2003). In the Late Campanian, the sea level was c. 140 m higher than at present (Haq *et al.* 1988), which correlates with the peak of diversity of siliceous sponges in other areas of the epicontinental basin of Europe (Wiedenmayer 1994). Fast sea-level fall by c. 50 m at the end of the Campanian (Haq *et al.* 1988) was noted both in the Tethys Ocean and in the Boreal epicontinental seas of Europe (Jarvis *et al.* 2002; Skupien and Mohamed 2008; Niebuhr *et al.* 2011). In inner to middle shelf deposits, this shallowing is marked by the presence of shallow marine facies or unconformity surfaces with stratigraphic gaps (Pożaryski 1960b; Olszewska 1990; Bless *et al.* 1991; Niebuhr and Ernst 1991).

Water energy

Hexactinellid sponges are characterized by a thin wall and a very delicate, brittle skeleton. Such a structure does not allow them to exist in turbulent environments, therefore hexactinellid remains are considered as indicative of low-energy conditions (e.g. Krautter 1997,

1998; Pisera 1997; Duarte *et al.* 2001), especially calm deeper-water environments below the storm wave base (Žitt *et al.* 2010; Schneider *et al.* 2011). The presence of hexactinellids in the succession studied indicates that these deposits were deposited in low-energy environments. There are no traces of *post-mortem* destruction of the specimens that could be linked with short-term episodes of increased water energy. The sea bottom colonized by sponges was thus below the wave-base even during the maximum shallowing in the terminal Campanian.

Currents

The distribution of sponges is often linked with the circulation of sea currents (Krautter 1998). For example, the development of Recent hexactinellid sponges in offshore British Columbia is largely possible due to currents, which hamper the accumulation of the sediment unfavourable for sponges and supply oceanic water rich in silica and nutrients (Leys *et al.* 2004; Whitney *et al.* 2005). A good sea current circulation was most probably responsible for the peak diversity of the sponge fauna during the deposition of the upper part of the Piotrawin Opoka (Świerczewska-Gładysz 2006). Detritus accumulations (see also Walaszczyk 2004) and the current lineation of spicules in the Solec Opoka indicate the presence of weak sea currents also during the deposition of these sediments. In the latest Campanian, sea currents were most probably responsible for the preservation of a small sponge population in the shallowing basin.

Sedimentation rate

A fast sedimentation rate significantly restricts the occurrence of hexactinellid sponges (e.g. Mehl and Niebuhr 1995; Krautter 1997, 1998; Pisera 1997; Duarte *et al.* 2001; Leys *et al.* 2004). Due to their shape (funnel, cup, cone, etc.), these organisms act as traps for the sediment, which may cause the death of the organism. Sponges which are only sporadically present in environments with slightly faster sedimentation rates protect themselves by narrowing the osculum (Conway *et al.* 2004; Cook *et al.* 2008). Such an adaptation was also reported in the fossil sponges from the Santonian of the Cracow area (Świerczewska-Gładysz 1997). In the present material, morphotypes with shapes pointing to fast sedimentation were not observed. However, many of the specimens from the Solec Opoka are damaged as a result of weathering and it is therefore not possible to compare the shapes of these sponges with those from other parts of the succession.

The location of rhizoids in a small number of specimens from Piotrawin indicates partial burial of the living sponge in the sediment (Świerczewska-Gładysz 2006). Burial of sponges probably took place during local accumulations of sediment resulting, for example, from the sea-bottom relief, and not as a result of an increased sedimentation rate in the basin. There is no evidence either confirming or precluding an increased sedimentation rate in the studied stratigraphic interval.

Food

It was previously assumed that hexactinellid sponges feed on colloidal matter (Reiswig 1990), which controls their occurrence in deep water habitats (Krautter 1997, 1998; Pisera 1997). Recent studies have shown, however, that hexactinellids feed mainly on ultraplankton comprising non-photosynthetic bacteria and nanoplanktonic protists (Pile and Young 2006; Yahel *et al.* 2006, 2007). Demosponges feed on the same sources below the photic zone, whereas in shallower water they also feed on fine phytoplankton <10 µm in size (Pile *et al.* 2003; Yahel *et al.* 2003). According to Yahel *et al.* (2006), in laboratory conditions hexactinellids are also capable of feeding on phytoplankton, and therefore their presence in deeper habitats is not a result of their food preferences. In the photic zone, the plankton is dominated by large phytoplanktonic cells and the largest compounds consumed by the hexactinellids do not exceed 5 µm (Pile and Young 2006). Moreover, in shallower water ultraplankton is used by other, more efficient suspension feeders, including the demosponges (Pile *et al.* 2003; Pile and Young 2006). In the same conditions and at the same ultraplankton composition, the retention efficiencies of the demosponges reach 95–99%, whereas those of the hexactinellids are only up to 47–54% (Pile and Young 2006). Most probably the hexactinellids occur below the photic zone because other filtering organisms are rare there, whereas the concentration of ultraplankton is relatively high (compare Pile and Young 2006).

Substrate

Recent hexactinellid sponges dwell on hard substrates such as rocks, pebbles or skeletons of dead sponges (Krautter *et al.* 2006). This restricts their occurrence to places where such substrates are available due to a low sedimentation rate or the removal of loose deposit by currents (Whitney *et al.* 2005). In contrast to Recent sponges, most Cretaceous species were adapted to live on loose substrates (e.g. Helm and Kosma 2006;

Świerczewska-Gładysz 2006) and only some of them were able to attach to hard substrates by means of a basal plate (Wiese and Wood 2001; Vodrážka *et al.* 2009). In the studied succession are present species that developed rhizoidal or additional processes used for fixing the sponge in loose sediment (see Świerczewska-Gładysz 2006). Thus, the type of substrate did not determine the distribution and abundance of sponges in particular conditions.

Temperature

According to Manconi and Serusi (2008), the cooling phases in the Plio-Pleistocene times restricted the occurrence of lithistids in the Mediterranean Sea, where at present they are very rare. A rapid, global climatic cooling took place at the Campanian–Maastrichtian boundary (Kauffman 1986; Miller *et al.* 2003; Linnert and Mutterlose 2009). Recent lychniscosid and hexactinosid sponges live in warm seas but at the greater depths at which they occur the sea water is cool, with temperatures at c. 10–15°C (Ijima 1927; Reid 1968; Van Soest and Stenotft 1988; Finks and Rigby 2004). Some hexactinellid genera are also known from polar seas (Koltun 1970; McClintock *et al.* 2005; Janussen and Tendal 2007). In British Columbia, water temperature in fjords inhabited by hexactinosid sponges is on average c. 9–10°C (Leys *et al.* 2004), whereas near the reef complex it is only 5.5–7.3°C (Whitney *et al.* 2005). These data indicate that a slight decrease in sea-water temperature (c. 2°C in the surface waters; see Friedrich *et al.* 2005) in the epicontinental basin of Europe at the Campanian–Maastrichtian boundary could not have significantly influenced the populations of the sponges studied. Global climatic changes in the Late Cretaceous correlate with eustatic sea-level changes (Miller *et al.* 2003), therefore the cooling causing sea-level fall could probably have indirectly influenced the sponge fauna.

Oxygen content

Hexactinellids live preferably in well-oxygenated waters (Leys *et al.* 2004), but at the same time they are more capable than other organisms of withstanding seasonal, intense falls of the oxygen content (Whitney *et al.* 2005). In the deep-marine setting typical of Recent sponges, the oxygen content may reach 30 µM (Whitney *et al.* 2005). Changes in the sponge fauna in the Middle Vistula succession were obviously not caused by low oxygen supply. The sedimentary features also indicate good oxygenation of the bottom waters.

CONCLUSIONS

The sponge fauna from the Upper Campanian and Lower Maastrichtian of the Middle Vistula River section (central Poland) is mainly represented by hexactinellid sponges belonging to the suborders Hexactinosida and Lychniscosida. The abundance and taxonomic variability of these sponges vary throughout the succession.

It seems that the most important factor controlling the hexactinellid sponge populations was basin bathymetry. The optimum conditions for the development of the sponges were during “I.” *inkermanensis* Zone time (Piotrawin Opoka). The abundance and specific variability of sponges from that unit indicate calm deeper water conditions (below the maximum storm wave base). In the latest Campanian (*T. costaeus* and “I.” *redbirdensis* zones) (Solec Opoka), progressive shallowing of the basin drastically hampered the development of hexactinellids. Precise determination of the basin depth at the end of the Campanian is not possible, but it seems that the water depth at the peak of the regression could have dropped to several tens of metres, with the sea-bottom colonized by hexactinellid sponges remaining below the normal wave-base and below the photic zone.

Starting with the beginning of the Maastrichtian, gradual deepening of the sea allowed re-establishment of the sponge fauna. Some of the species known from the “I.” *inkermanensis* Zone re-colonized the study area in the *Endocostea typica* Zone.

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