

Bryozoans (trepostomes and fenestellids) in the Zechstein Limestone (Wuchiapingian) of the North Sudetic Basin (SW Poland): palaeoecological implications

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Hara U., Słowakiewicz M. and Raczyński P. (2013) Bryozoans (trepostomes and fenestellids) in the Zechstein Limestone (Wuchiapingian) of the North Sudetic Basin (SW Poland): palaeoecological implications. *Geological Quarterly*, 57 (3): 417–432, doi: 10.7306/gq.1103



A recently investigated Zechstein Limestone (Ca1, Wuchiapingian) bryozoan fauna from the Polish part of the Southern Permian Basin (SW Poland) is dominated volumetrically and taxonomically by fenestellids. In total six species from five genera are recognized, comprising two species of trepostomes belonging to *Dyscritella* Girty, 1911 and four fenestellids attributed to *Kingopora* Morozova, 1970, *Kalvariella* Morozova, 1970, *Acanthocladia* King, 1849 and *Spinofenestella* Termier and Termier, 1971. The greatest biodiversity of the bryozoans in the Ca1 profiles studied is within the slope facies where large, fan-shaped and funnel-shaped reticulate fenestellid colonies up to 10 cm high dominate. In contrast, bryozoans in the marginal (proximal) parts of the basin mostly comprise trepostomes, represented by encrusting plate-like or coil-shaped colonies of *Dyscritella* Girty, and commonly broken branched colonies of *Acanthocladia* King. The changes in the biotic composition of the bryozoans and the presence of a dominant colony growth form in the stratigraphical profile of the Ca1 reflect the depositional environment and water energy. These factors stimulate the successive stages of the development of the biota and their settlement, marked by the rich productid-fenestellid assemblages typical of the offshore setting, with the maximum depth in the middle part of the Ca1 in the Grodziec Syncline. The proximal tempestites and foreshore facies of the upper part of the Ca1 (Leszczyna Syncline) terminate the sedimentary cycle of the Ca1, with the remnant, broken bryozoans of *Acanthocladia* and fenestellids. The relationship between the taxonomic composition, colony growth-patterns, associated biota, and sedimentary structures points to slow sedimentation rate on slope and basin floor of the Ca1 carbonate platform. The fenestellids which are dominated in the studied biota by the reticulate and pinnate colonies of *Spinofenestella*, *Kingopora*, *Kalvariella* and *Acanthocladia* mark a close palaeogeographical link with the Zechstein (Ca1) bryozoans of Great Britain, Germany and the southern Baltic region.

Key words: bryozoans, Late Permian, Zechstein, taxonomy, ecology.

INTRODUCTION

Permian bryozoan faunas are, in terms of overall composition, rather similar to those of the Carboniferous, a time when bryozoan abundance and diversity were dominated by steno-laemates of the order Trepostomida Ulrich and Fenestellida Astrova and Morozova. Due to their abundance, taxonomical and morphological differentiation, bryozoans were important components of shallow-marine Zechstein carbonate environments before the end-Permian global mass extinction (Gilmour and Morozova, 1999).

Zechstein bryozoans were first studied systematically in the 19th century in Germany and NE England by Schlotheim (1820) and King (1850), respectively. Later work was undertaken by Korn (1930), Dreyer (1961), Taylor (1980, 1985), Southwood (1985, 1990) and Ernst (2001a, b). The very first record of Zechstein faunas from Lower Silesia (Fig. 1) was reported by Geinitz (1861–1862) and Langenham (1899). In addition, the earliest references to the occurrence of bryozoans in the North Sudetic Basin are those of Riedel (1917), Gunia (1962), Morozova (1970) and Raczyński (1996). The most extensive systematic works on Polish Zechstein bryozoans were published by Kłapciński (1971) and Kłapciński and Karwowski (1981) from western Poland who described eight species dominated by fenestellids.

The great majority of the Zechstein species come from Germany where 17 species belonging to nine genera of trepostomes and fenestellids and one cyclostome were described by Ernst (2001a). Nevertheless, Late Permian (Zechstein) faunas appear to be not very rich compared to the Early Permian counterparts described from the Arctic (Morozova and Krutshchina,

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1986; Nakrem, 1994), and the United States (Zimmerman and Cuffey, 1987), where more than 160 taxa have been recorded (Gilmour and Morozova, 1999).

This paper gives the detailed description of the bryozoan fauna from the Zechstein Limestone (Ca1) of SW Poland (Fig. 1A) and discusses the palaeoecological importance and distribution of trepostomes such as cosmopolitan genera of *Dyscritella* Girty and fenestellids *Spinofenestella* Termier and Termier, endemic *Kalvariella* Morozova, as well as *Kingopora* Morozova restricted to the Northern Hemisphere and polyphyletic *Acanthocladia* King.

GEOLOGICAL SETTING AND STRATIGRAPHY

The study area is located in the North Sudetic Basin (SW Poland) where Zechstein Limestone (Ca1) deposits are exposed in several abandoned quarries at Leszczyna, Kondratów, Grodziec and Nowy Kościół (Fig. 1B, C). Some specimens were also collected in the southwestern part of the North Sudetic Basin in the Lwówek Śląski Syncline, from the lower part of the Ca1 (Gościszów, Nawojów Śląski and Żarska Wieś; Fig. 1B). Marine waters of the Zechstein Sea rapidly transgressed over the present day North Sea in Late Permian into the Northern Permian Basin and Southern Permian Basin through a strait located between Scandinavia and Greenland ca. 258,5 Ma ago (Gradstein et al., 2012; Kiersnowski 2013), resulting in the deposition of thick (<1800 m) evaporite-carbonate sequences. At present the Lower Zechstein outcrops in Poland are only located at the margins of the SPB, in its southwestern and southern parts. The Lower Zechstein rocks cropping out in SW Poland form a relatively narrow zone in the outer part of the North Sudetic Basin, a remnant of a Late Paleozoic intramontane trough formed as a result of the Variscan orogeny and subsequently tectonically reactivated in the Late Cretaceous when several local synclines were formed (e.g., Raczyński, 2010). Zechstein deposits within the Polish part of the SPB overlie Upper Rotliegend conglomerates and sandstones mostly consisting of fluvial, fan and minor aeolian deposits (Kiersnowski et al., 2010). The Zechstein section within the North Sudetic Basin is condensed and formed by deposits of the first (PZ1 = 50 to 120 m thick) and third (PZ3 <15 m thick) Zechstein cycles (Table 1; Peryt, 1978). The lowest part of the PZ1 cycle is represented by facies similar to those of the shallow-water copper-bearing claystones of the Kupferschiefer, which commonly contain continental plant remains in addition to marine bivalves and the inarticulate brachiopod *Lingula*. This facies represents the lower part of Ca1 deposits (Birnacka et al., 2005). All Ca1 deposits are usually 20 to 40 m thick and were deposited in a narrow (20–30 km) and long (~100 km), WNW–ESE striking lagoon also associated with tidal flat and oolitic-oncolitic shoal environments (Raczyński, 1997). The PZ1 deposits are overlain by PZ3 Platy Dolomite (Ca3) carbonates (10–15 m thick) which consist of shallow-water facies containing *Calcinema* together with bivalves and gastropods. The carbonates are overlain by heterolithic deposits of the Permian to Triassic transitional series which form the youngest Zechstein deposits in the study area.

The Ca1 sections consist of ca. 10–40 m thick limestone-marl sequences (Fig. 2). The overall facies associations in the study area are given in Table 2 and these are: basal conglomerate, basal limestone, mottled marls, copper- and lead-bearing marls, massive limestones with claystones, and sandstones. Of note is a considerable part of the Ca1 succession formed of tempestite deposits (Figs. 2 and 3), which represent the near-shore part of the carbonate platform. The tempestites in the lower part of the Ca1 are distal, whereas those higher in the

succession are proximal (Table 1). Most of the studied bryozoan fauna derives from mottled, lead-bearing and copper-bearing marls of the Grodziec section (Fig. 2), and is dominated by the reticulate fenestellid bryozoans *Kingopora baderi* Ernst (Figs. 4J–M, 5A and 6) and *Spinofenestella geinitzi* (d'Orbigny) (Figs. 5H–L and 7). The family Acanthocladidae Zittel is also well-represented by *Kalvariella typica* Morozova (Fig. 5B, C) and *Acanthocladia anceps* (Schlothheim) (Figs. 5D–G, 8 and 9C). Trepostomes belonging to the family Dyscritellidae are represented by *Dyscritella tubulosa* Morozova (Figs. 4A–F and 9A) and *D. microstoma* Ernst (Figs. 3, 4G–I and 9B1, B2).

Although the distribution of the bryozoans in the marly calcareous series (mottled, copper- and lead-bearing marls) of the Ca1 is patchy this group is accompanied by a rich shallow-water biota represented by molluscs, gastropods, brachiopods, foraminifers and ostracods (Raczyński, 1996), which aid interpretation of the palaeoecology of the bryozoans (Mastalerz and Raczyński, 1993; Raczyński, 1996).

MATERIAL AND METHODS

The Zechstein bryozoan material was collected during 1990–1996 from seven localities spread over a distance of ca. 150 km within the North Sudetic Basin of SW Poland: Grodziec, Gościszów, Nawojów Śląski, Żarska Wieś, Leszczyna, Nowy Kościół and Lwówek Śląski (Fig. 1B). The Grodziec locality yielded the richest bryozoan faunas. Of total 300 samples, forty-one were selected from three outcrops of the Zechstein Limestone (Ca1) for detailed taxonomical bryozoan studies. The twenty-four investigated samples were taken from the lower and upper part of the Ca1, of the Grodziec Syncline, which forms the most axial part of the North Sudetic Basin (Fig. 1C), from mottled marls through copper-bearing marls to the lead-bearing beds (Table 1 and Fig. 2). Six investigated samples were collected in the Leszczyna Syncline (Leszczyna and Leszczyna-Kondratów) from the upper part of the Ca1, and 3 samples from the lower part of the Ca1 (mottled marls, Nowy Kościół). Eight samples were collected from the lower part of the Ca1 (unseparated equivalent of marl-limestone section of the Ca1 profile, between mottled-lead bearing marls) in the Lwówek Śląski Syncline (localities: Gościszów, Nawojów Śląski and Żarska Wieś; Fig. 1C).

Most of the investigated bryozoans are embedded in well-cemented matrix, but some samples expose large and well-preserved colonies on bedding planes that also allow to study of their external morphology. Internal morphology was studied in thin sections made from twenty-five oriented polished surfaces.

Some of the specimens were investigated using a *Philips XL-20* SEM. These were coated with the pure platinum and imaged with secondary electrons. All specimens were examined with a *Wild M10* binocular microscope equipped with planochromatic objective 1.0x. Measurements of all features (Tables 2–7) were made using an eyepiece micrometer affixed to the microscope. Five to thirty measurements of each feature were taken in most of the specimens.

Holotype and lectotype materials are deposited in the following institutions: Senckenberg Museum, Frankfurt; Paleontological Institute of the Academy of Sciences, Moscow; and Museum for Natural Sciences, Central Institute of the Humboldt-University, Berlin.

Described and illustrated material which derived from the samples of the numbers ING Uwr PR/Z/Bry/Ca1/1–41 is archived by the Wrocław University Museum, Institute of Geological Sciences.

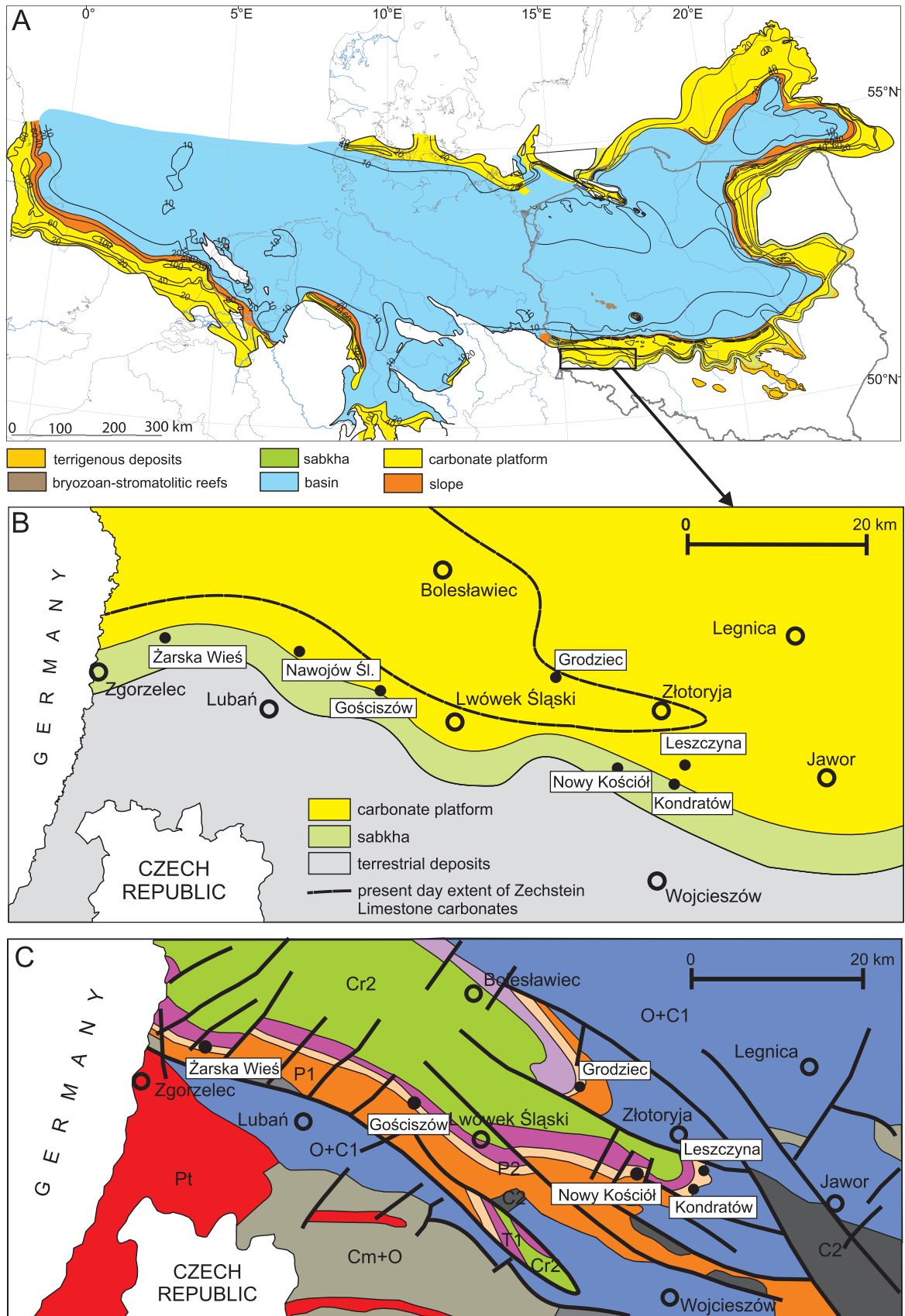


Fig. 1. Location (A) and a close-up view (B) of the study area: facies distribution of the Zechstein Limestone in the Southern Permian Basin (updated after [Buniak et al., 2007](#); [Peryt et al., 2010](#)); C – simplified geological map of the North Sudetic Basin with the Zechstein Limestone sections studied (rectangles)

C – Pt – Proterozoic, Cm+O – Cambrian + Ordovician, O+C1 – Ordovician + Lower Carboniferous, C2 – Carboniferous, P1 – Lower Permian, P2 – Upper Permian (Zechstein), T1 – Lower Triassic, Cr2 – Upper Cretaceous; black solid lines are main faults

Table 1

Lithostratigraphy of the Zechstein in the study area (modified after Raczyński, 2010)

Lithostratigraphy		Lithology	Depositional environment	
Zechstein cycle	Local series			
PZ 4-PZt	sandy-muddy-clayey series	red muddy sediments with thin beds of sandstone and clay; 5–15 m thick	muddy lagoon, coastal zone	
PZ 3	Platy Dolomite	white and grey dolomite, micritic, granular and oolitic; 2–12 m thick	shallow shelf, nearshore carbonate platform	
PZ1	A1	septarian shales	red clayey-muddy sediments with thin beds of sandstones and limestone concretions; 8–15 m thick	muddy lagoon, coastal zone
		sandstones	red and yellow clayey-muddy sediments, with thin beds of fine-grained sandstone; ripple cross-laminated sandstone; 3–30 m thick	shallow water, beach, coast
	massive limestones with claystones	sandy limestones	yellow and grey, thinly and medium bedded sandy limestone and calcareous sandstone; 6 m thick	nearshore lagoon
		claystones with limestones	red and yellow clayey-muddy sediments with thin beds of limestone; 3 m thick	nearshore lagoon, deeper part
		oolitic limestones	laminated light grey oolitic and oncolitic lime packstone and grainstone, oncoids <0.5 cm in diameter in the upper part, lower part contains ooids, carbonate intraclasts, laminae composed of quartz grains also occur, planar and cross-bedding, bioclasts (bivalves, gastropods); 1.5 m thick	nearshore oolitic shoal
		massive limestones	sandy limestone, horizontally and hummocky-crossed stratified, bioclastic packstone: abundant foraminifera, brachiopods, echinoids, bryozoans (in the middle part: fragments of <i>Acanthocladia</i> and fenestellids) and bivalves, bioclasts are represented predominantly by a <i>Bakevellia</i> , <i>Schizodus</i> and <i>Permophorus</i> assemblage, tempestites; 6 m thick	proximal tempestite, shallow water: between normal and storm wave base (HCS – hummocky cross-stratification) and above normal wave base
	Ca1	lead-bearing marls	grey marly lime mudstone with intercalations of dark marls, passing upward into sandy limestone which are horizontally and hummocky-cross stratified; in general, the fauna is represented by abundant foraminifera, brachiopods, echinoids, bryozoans (<i>Dyscritella</i> , <i>Acanthocladia</i> , <i>Spinofenestella</i>), and bivalves (<i>Bakevellia</i> , <i>Permophorus</i>), some fossils are mineralized with copper, lead and/or zinc sulphides; 2.8 m thick	distal tempestite (limestone, marls), shelf (mudstone); below storm wave base
	copper-bearing marls	grey and dark grey clayey marls and marly limestones, rare bioclasts of bivalves <i>Bakevellia</i> and <i>Permophorus</i> , bryozoans (<i>Dyscritella</i> , <i>Acanthocladia</i>) and brachiopods all commonly mineralized with copper sulphides; 1.5 m thick	distal tempestite (limestone, marls), shelf (mudstone); below storm wave base	
	mottled marls	dark grey marls and limestones, mottling associated with red patches (up to 40% of total bed thickness), coquinas: brachiopods, bryozoans (in the lower part: <i>Dyscritella</i> , <i>Kingopora</i> , <i>Kalvariella</i> , <i>Acanthocladia</i> , ostracods, gastropods, foraminifera and bivalves such as <i>Bakevellia</i> , <i>Schizodus</i> and <i>Permophorus</i> ; in upper part 0.4m lime packstones rich in <i>Horridonia</i> , bryozoans: <i>Spinofenestella</i> , <i>Kingopora</i> ; 0.5 m thick; thickness of the horizon <4 m	open shelf; below storm wave base distal tempestite (limestone, marls), shelf (mudstone); below storm wave base	
	basal limestone	grey and purple lime mudstone, medium and thickly bedded, massive, rare fossils, horizontal and wavy bedding, locally interbedded with oolitic limestone; <1 m thick	closed lagoon	
S1	pink and grey polymictic conglomerate, medium and thickly bedded, rare sandstone and conglomerate sandstone with fossils, indistinct normal and parallel bedding, locally in conglomerates are pebbles of quartz, porphyry and schists; 1 m thick	Rotliegend conglomerates reworked during transgression of the Zechstein Sea		
Upper Rotliegend		red and pink polymictic conglomerate, medium and thickly bedded, indistinct normal and parallel bedding, pebbles of quartz, porphyry and schists, locally carbonate cementation caliche-type; >10 m thick	fluvial, alluvial fan	

Informal subunit of massive limestones and claystones is proposed herein as a substitute for Middle Zechstein limestones; PZ 1, 3, 4 – Zechstein cycle 1, 3, 4; A1 – Werra Anhydrite; Ca1 – Zechstein Limestone, S1 – basal conglomerate, PZt – transitional series







SYSTEMATIC DESCRIPTIONS










Type species: *Dyscritella robusta* Girty, 1911;
Lower Carboniferous; North America

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order TREPOSTOMIDA Ulrich, 1882
Family DYSCRITELLIDAE Dunaeva and Morozova, 1967

Dyscritella Girty, 1911

D i a g n o s i s. – Dendroid and encrusting colonies with abundant acanthostyles and exilazooecia. Autozooecia parallel to longitudinal direction of the colony in endozone; gradually arching outwardly in exozone. Diaphragms in autozooecia absent or very rare; absent in exilazooecia. Exilazooecia circular to angular in cross-section and separated from the autozooecia

-  marl
-  claystone
-  conglomerate
-  limestone
-  mudstone
-  sandstone

-  horizontal bedding
-  erosional troughs
-  trough cross-bedding
-  cross bedding
-  ripple lamination
-  ooids
-  oncoids
-  intraclasts
-  desiccation cracks

-  algal laminae
-  position of shells
-  *Dyscritella tubulosa* Morozova
-  *Kingopora baderi* Ernst
-  *Acanthocladia anceps* (Schlotheim)
-  *Dyscritella microstoma* Ernst
-  *Kalvariella typica* Morozova
-  *Spinofenestella geinitzi* (d'Orbigny)
-  sampling points:
41 samples collected
-  1, 2

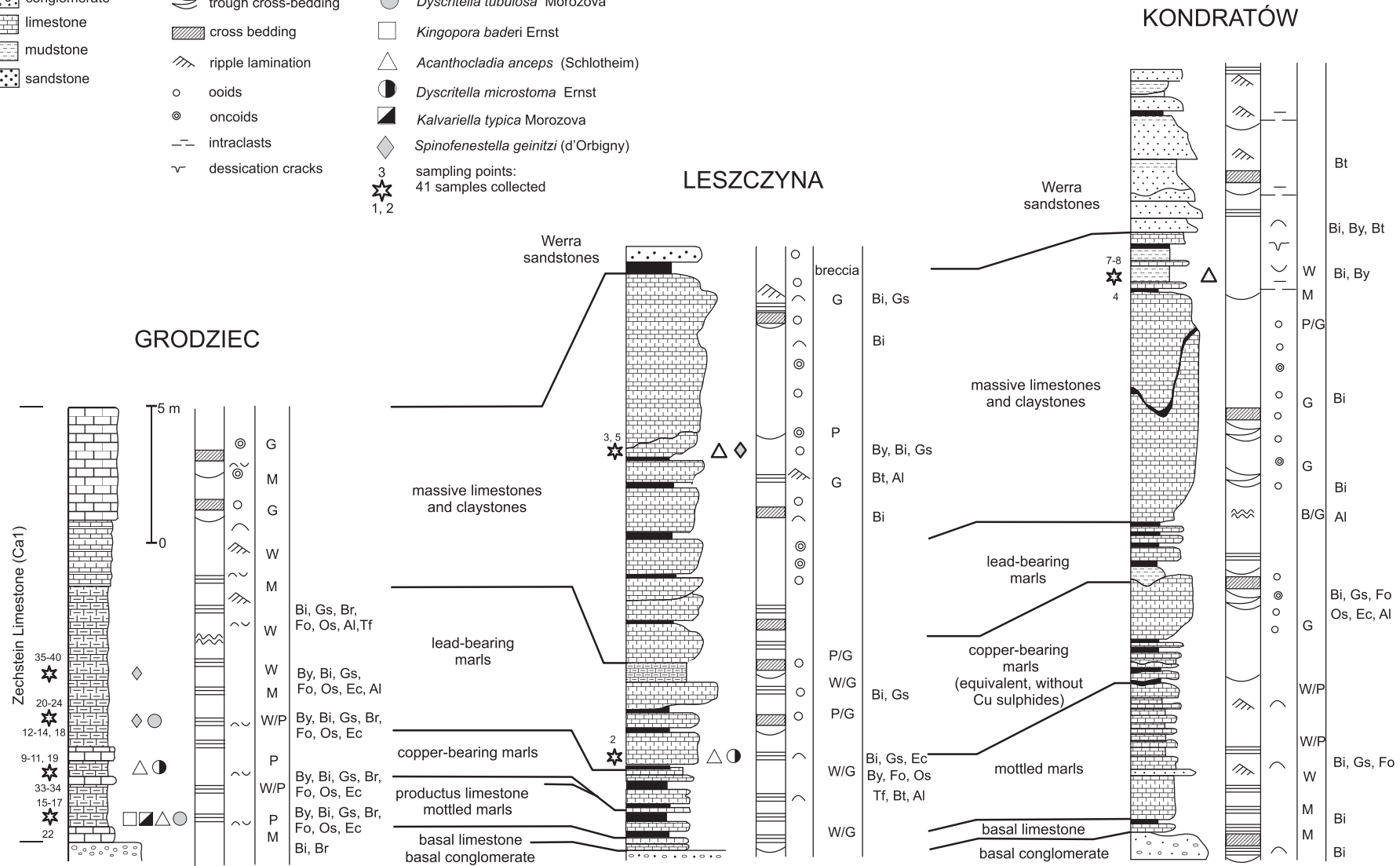


Fig. 2. Sedimentary logs of Zechstein Limestone deposits from SW Poland

Textural types of limestones: B – boundstone, G – grainstone, M – mudstone, P – packstone, W – wackestone; fossils: Al – algae, Bi – bivalves, Br – brachiopods, Bt – bioturbations, By – bryozoans, Ec – echinoderms, Fo – foraminifera, Gs – gastropods, Os – ostracods, Tf – trace fossils

and from each other by thick walls. Two sizes of acanthostyles may be present: large with few per autozoecia, and small with several around each autozoecium. Zoecial walls thin in endozone, rapidly thickening in the exozone.

Comparison. – *Dyscritella* Girty, 1911 differs from *Dyscritellina* Morozova, 1967 by the rarity or absence of diaphragms and less differentiated acanthostyles.

Occurrence. – Carboniferous to Triassic; cosmopolitan.

Dyscritella tubulosa Morozova, 1970
Figs. 4A–F, 9A and Table 2

1970 *Dyscritella tubulosa* Morozova – Morozova (1970), p. 121, pl. 19, fig. 1.
2001 *Dyscritella tubulosa* Morozova, 1970 – Ernst (2001a), p. 139, pl. 1, figs. 1, 2.

Holotype. – No. 2343/122; Paleontological Institute of the Academy of Sciences, Moscow; Upper Permian, Zechstein; Lithuania.

Material examined. – Grodziec (Grodziec Syncline) samples numbered ING UWrPR/Z/Bry/Ca1/15, 24 and Lwówek Śląski Syncline ING UWrPR/Z/Bry/Ca1/30; thin-sections of the samples ING UWrPR/Z/Bry/Ca1/15, 24.

Description. – Encrusting colonies, 0.48–0.66 mm thick. Autozoecial apertures polygonal, 7–9 per 2 mm (in each direction) and 12–18 apertures per 1 mm² at the colony surface. Diaphragms absent both in autozoecia and exilazoecia. Walls in the endozone 0.01–0.015 mm thick, fibrous, in the exozone 0.02–0.04 mm thick and obliquely laminated. Acanthostyles large, abundant, with distinct calcite cores. Cores are 0.015–0.025 mm in diameter and run throughout the exozone. Usually 1–5 acanthostyles surround each autozoecial aperture, 18–40 spaced per 1 mm² at colony surface, often inflecting into the autozoecia. Exilazoecia short, polygonal in cross-section, rare, or absent. Maculae consisting of larger autozoecia.

Comparison. – *Discritella tubulosa* is closely related to *D. incrustata* Morozova, 1970 and *D. microstoma* Ernst, 2001. It differs from *D. incrustata* (Morozova, 1970) by the smaller and weakly differentiated acanthostyles in the latter, and from *D. microstoma* which has larger and more loosely arranged apertures and fewer acanthostyles.

Occurrence. – Ca1, Upper Permian, Grodziec and Lwówek Śląski synclines, North Sudetic Basin, SW Poland; Thuringia (Germany; Ernst, 2001a) and Lithuania (Morozova, 1970).

Dyscritella microstoma Ernst, 2001
Figs. 3, 4G–I, 9B and Table 3

2001 *Dyscritella microstoma* Ernst – Ernst (2001a), p. 139, pl. 1, figs. 3–5.

Holotype. – SMF 1601; Senckenberg Museum, Frankfurt (Main).

Material examined. – Grodziec (Grodziec Syncline) samples numbered ING UWrPR/Z/Bry/Ca1/11, 19, 23 and Lwówek Śląski Syncline samples ING UWrPR/Z/Bry/Ca1/25, and Nowy Kościół samples ING UWrPR/Z/Bry/Ca1/41; the thin sections of the samples ING UWrPR/Z/Bry/Ca1/19, 23, 41.

Description. – Encrusting colonies 0.24 to 0.31 mm thick. Autozoecial apertures polygonal in cross-section, 7–12 apertures per 2 mm (in each direction) and 21–27 apertures in 1 mm² at colony surface. Walls in the endozone 0.01 mm thick and structureless, in the exozone 0.01–0.025 mm thick and obliquely laminated. Exilazoecia polygonal in cross-section, rare, or absent. Diaphragms in autozoecia rare. Acanthostyles large, abundant, with distinct, 0.01–0.025 mm wide calcite

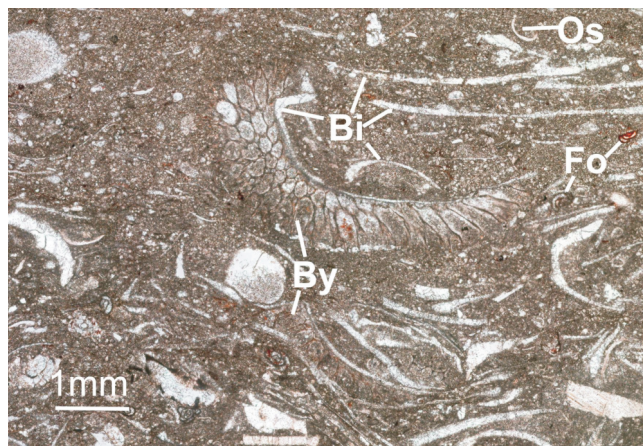


Fig. 3. Bioclastic packstone (distal tempestites) showing an association of the *Dyscritella* bryozoan colony (By) encrusting bivalve shells (Bi), ostracods (Os), and foraminifers (Fo); mottled marls, ING UWrPR/Z/Bry/Ca1/41, Leszczyna Syncline, North Sudetic Basin

cores in cross-section, 50–52 spaced per 1 mm² on colony surface, often deeply inflecting autozoecia. Acanthostyle cores present throughout the exozone, 4–7 acanthostyles surround each aperture.

Comparison. – *Dyscritella microstoma* Ernst, 2001 differs from *D. tubulosa* in having smaller autozoecia, thinner walls as well as smaller and more abundant acanthostyles.

Occurrence. – Ca1, Upper Permian, Grodziec (lower and upper part of Ca1), Lwówek Śląski synclines (lower part of Ca1), Leszczyna Syncline (lower part of Ca1), North Sudetic Basin, SW Poland. This species was originally described from the Ca1 of Germany (Ernst, 2001a). *Dyscritella microstoma* has been recorded from the Zechstein Main Dolomite (Ca2) in the NE part of Germany (Rugen Island) and the western and northern parts of Poland (Pogorzela 2 well, Fore-Sudetic Monocline; as well as Unisław IG 2 in Pomerania; Hara et al., 2009). Recorded also from Thuringia and Hessen and Lithuania (Germany; Ernst, 2001a).

Order FENESTELLIDA Astrova and Morozova, 1956
Suborder FENESTELLINA Astrova and Morozova, 1956
Family Acanthocliadiidae Zittel, 1880
Kingopora Morozova, 1970

Type species: *Gorgonia ehrenbergi* Geinitz 1846,
Upper Permian, Zechstein, Thuringia

Comparison. – *Kingopora* differs from *Reteporida* Nickles and Bassler, 1900 in having fewer rows of autozoecia on the branches joining through anastomoses rather than by dissepiments.

Occurrence. – Lower Permian of the Arctic [*K. micropora* (Stuckenberg, 1895), *K. exigua* Krutchinina, 1986 in Morozova and Krutchinina, 1986]; Middle Permian (Kazanian) of the Russian Plate *K. parvifenestrata* Morozova, 1970; Upper Permian of North America, Germany and England [*K. ehrenbergi* (Geinitz, 1861)].

Kingopora baderi Ernst, 2001
Figs. 4J–M, 5A, 6 and Table 4

2001 *Kingopora baderi* Ernst – Ernst (2001a), p. 144, pl. 4, fig. 6, pl. 5, figs. 1–4.

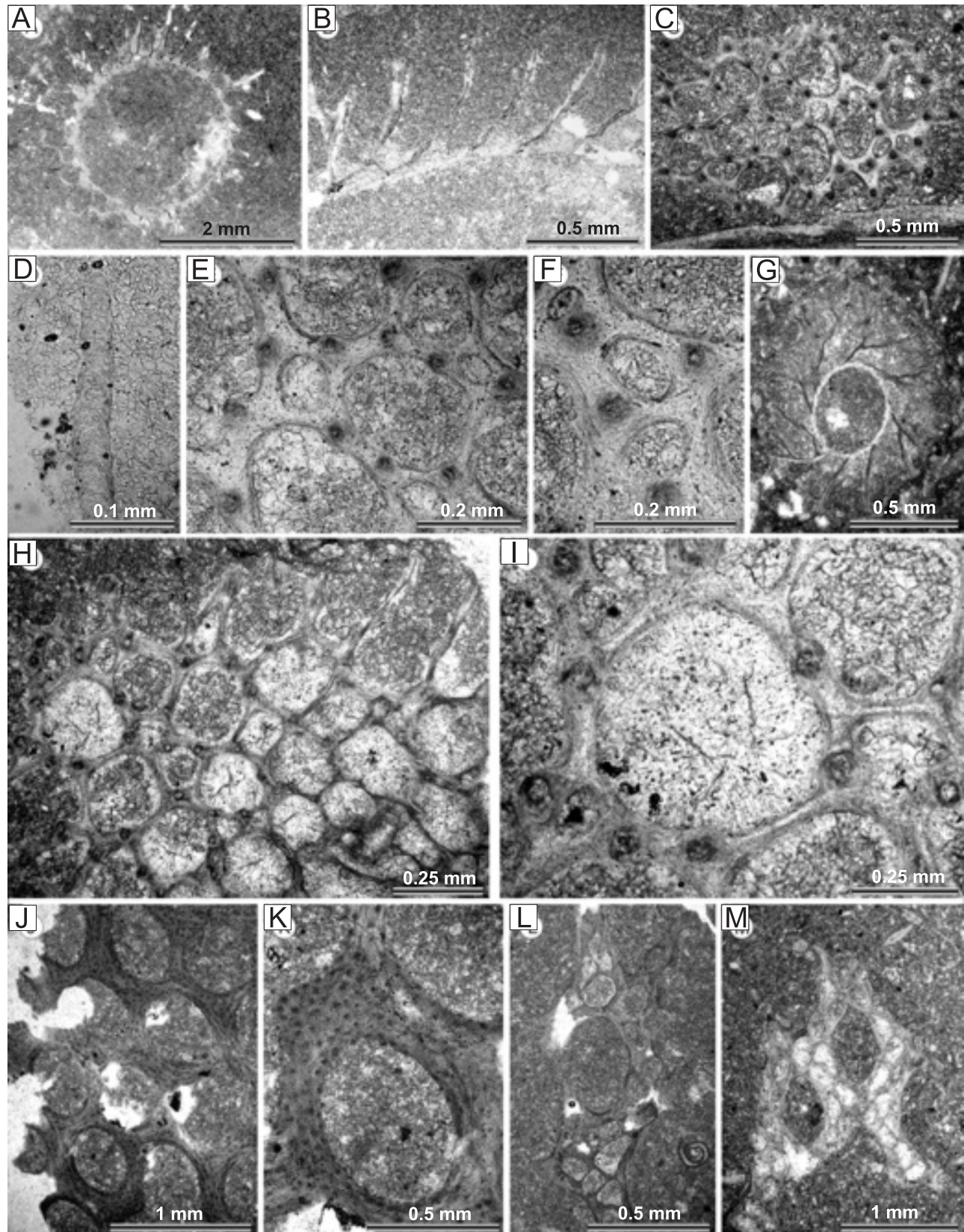


Fig. 4A–F – *Dyscritella tubulosa* Morozova, 1970 (A – cross-section of the tubular colony; B – longitudinal section of the colony; C – tangential section of the colony; D – longitudinal section of the colony displaying wall structure in exozone; E, F – tangential section of the colony, displaying autozooeical apertures, acanthostyles and exilazooecia; A, B, D – specimen ING UWr PR/Z/Bry/Ca1/24, lead-bearing marls; C, E, F – specimen ING UWr/PR/Z/Bry/Ca1/15, mottled marls); G–I – *Dyscritella microstoma* Ernst, 2001 (G – cross-section of an encrusting colony; H, I – tangential section of the colony; G–I specimen ING UWr/PR/Z/Bry/Ca1/19, lower part of the Ca1, copper-bearing marls); J–M – *Kingopora baderi* Ernst, 2001 (J – reverse side of the colony; K – reverse side of the colony, displaying microacanthostyles; L, M – tangential section of the colony displaying apertures and autozooeical chambers; J–M – specimen ING UWr PR/Z/Bry/Ca1/15, mottled marls); A–M – Grodziec (Grodziec Syncline)

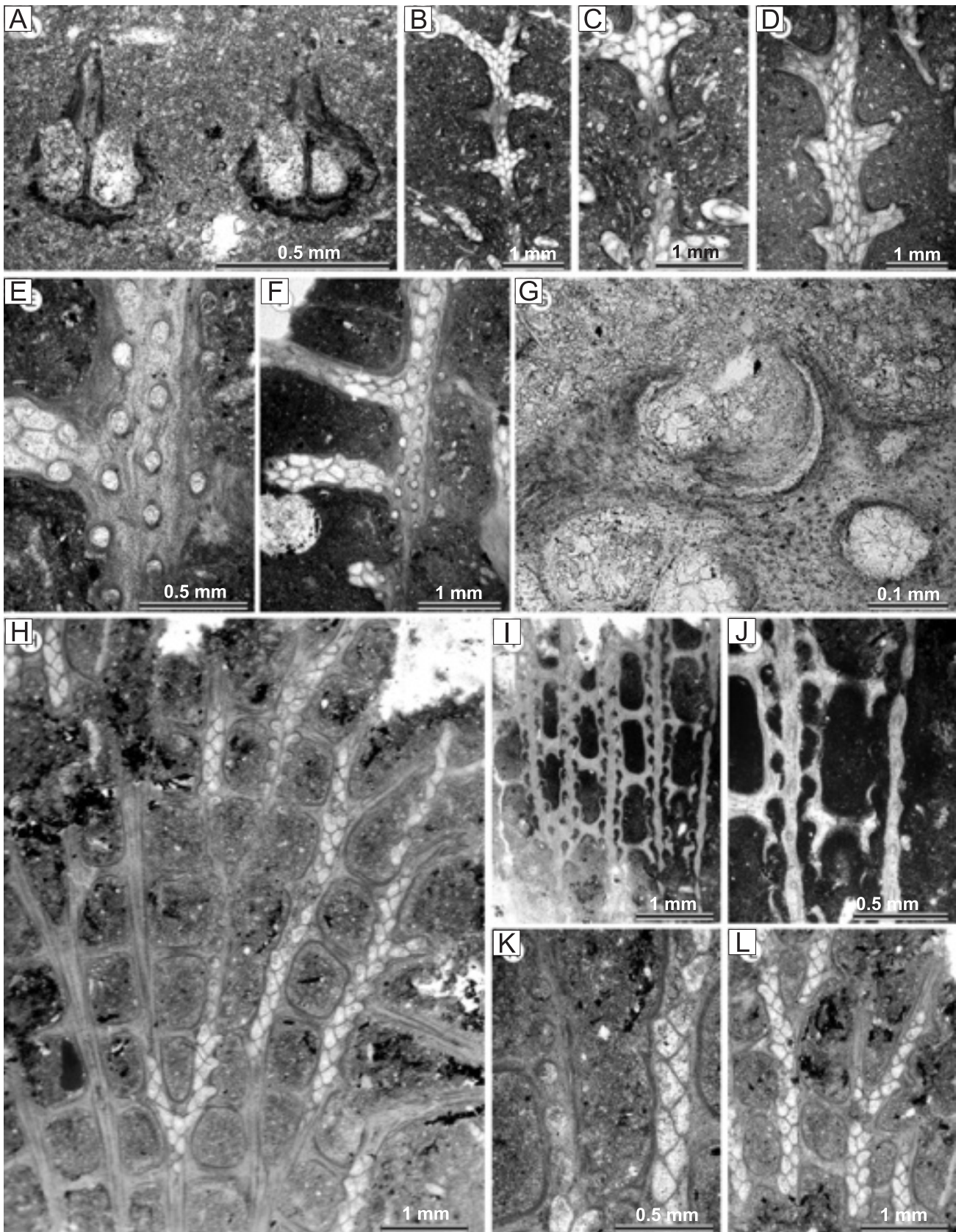


Fig. 5A – *Kingopora baderi* Ernst, 2001, cross-section of the branches; B, C – *Kalvariella typica* Morozova, 1970, tangential thin section of the branch; D–G – *Acanthocladia anceps* (Schlotheim, 1820) (D – deep tangential section of the branch; A–D – specimen ING UWr/PR/Z/Bry/Ca1/15, mottled marls; E – tangential section of the branch; F – tangential section of the branch; E, F – specimen ING UWr PR/Z/Bry/Ca1/38, copper-bearing marls; G – polymorph zooid with ovicell chamber, specimen ING UWr/PR/Z/Bry/Ca1/15, mottled marls); H–L – *Spinofenestella geinitzi* (d’Orbigny, 1850) (H – fragment of the colony, tangential thin section; I, J – tangential thin section, specimen ING UWr PR/Z/Bry/Ca1/13, lower part of the lead-bearing marls; K, L – tangential thin section; H, K, L – specimen ING UWr PR/Z/Bry/Ca1/24, lead-bearing marls); A–L – Grodziec (Grodziec Syncline)

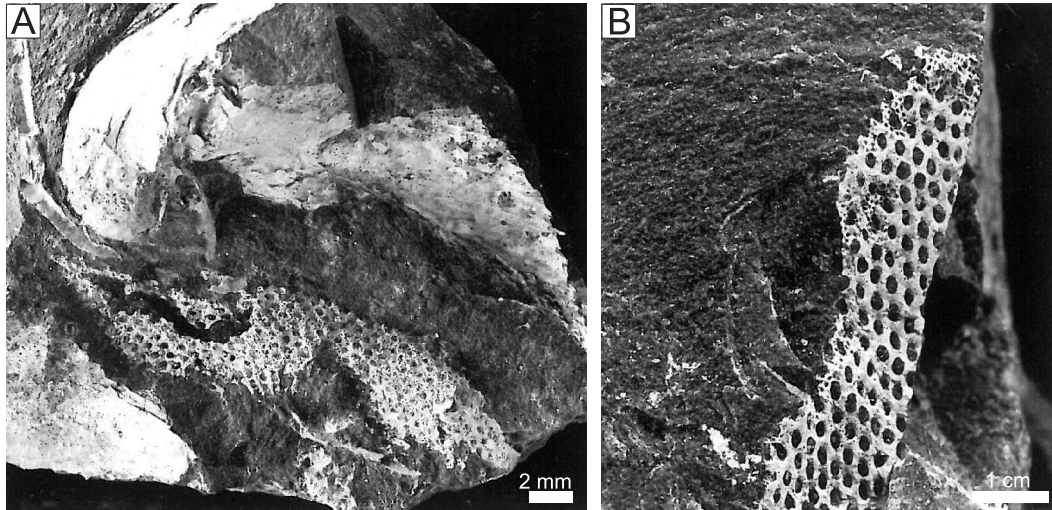


Fig. 6A – *Kingopora baderi* Ernst; A – part of the funnel-shaped retoporiform colony embedded into a sediment in the interior of the large brachiopod shell of *Horridonia horrida* (Sowerby), ING UWr/PR/Z/Ca-1/Bry/30, Źarska Wieś, Lwówek Śląski Syncline; B – part of the retiform colony, showing the oval fenestrules, ING UWr/PR/Z/Ca1/Bry/15, mottled marls (Grodzic, Grodzic Syncline)

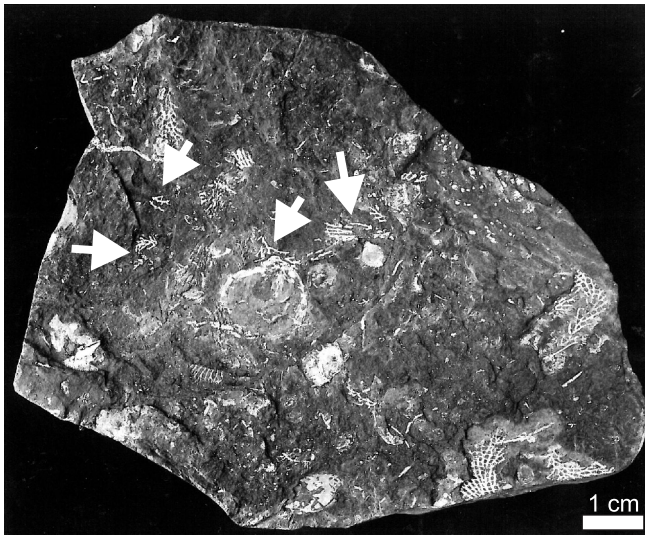


Fig. 7. Weathered fracture in the dark, lead-bearing marls showing the broken reticulated zoaria of *Spinofenestella geinitzi* (d'Orbigny), accompanied by small fragmented branches of acanthocliads (arrows), ING UWr/PR/Z/Ca1/Bry/23, lead-bearing horizon (Grodzic, Grodzic Syncline)

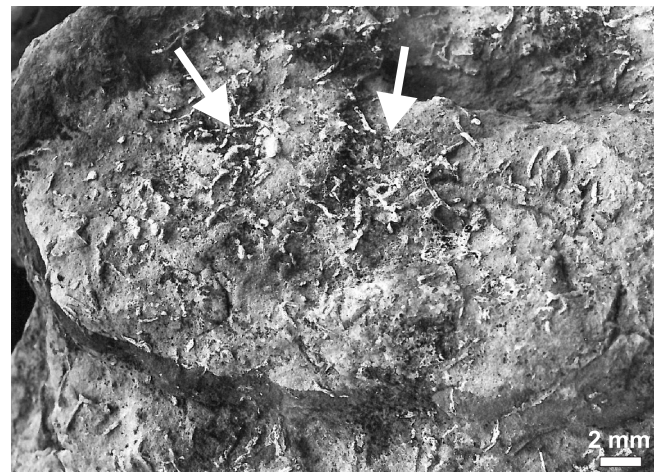


Fig. 8. A weathered top surface of sandy limestones with the broken fragments of the numerous colonies of *Acanthocliadia anceps* (arrows), accompanied by a few zoaria of fenestellids, ING UWr/PR/Z/Ca1/Bry/3, upper part of the Ca1 (Leszczyna, Leszczyna Syncline)

H o l o t y p e. – SMF 1609b; Senckenberg Museum, Frankfurt.

M a t e r i a l e x a m i n e d. – Grodzic (Grodzic Syncline), Zechstein Limestone: sample ING UWr/PR/Z/Bry/Ca-1/15; a thin section of the sample ING UWr/PR/Z/Bry/Ca1/15, mottled marls.

D e s c r i p t i o n. – Small funnel-shaped colony up to 2 cm high. Apertures open on outer side of the colony surface. Branches undulose and joined mostly by dissepiments, oval shaped in cross-section. Fenestrules oval and often extremely narrow. Autozoecia arranged in 2, 3 rows on the branches, the third row usually developed proximal to bifurcations. Dissepiments usually without autozoecia. Autozoecial apertures 3, 4 per fenestrule length, circular to oval with low peristomes. Low keel with long spines between apertures. Microacanthostyles irregularly spaced over the entire surface of the colony,

0.015–0.035 mm in diameter, growing from the granular layer and passing through the outer laminar skeleton to the colony surface. Outer laminar skeleton weakly developed.

I n t e r i o r d e s c r i p t i o n. – Autozoecia box-shaped, short, high, having polygonal shape in the mid tangential section, elongate parallel to branch length; aperture positioned at distal to distal-abaxial end of chamber. Vestibule usually short. Both superior and inferior hemisepta absent.

C o m p a r i s o n. – This species differs from all species of the genus *Kingopora* in the closely spaced autozoecia in two rows on the branches, smaller dimensions of the colony and long spines on the keel.

O c c u r r e n c e. – Ca1, Upper Permian, Grodzic (Grodzic Syncline), North Sudetic Basin, SW Poland. Recorded from the bedded facies of the Zechstein Limestone of Thuringia and Lower Saxony (Germany) (Ernst, 2001a).

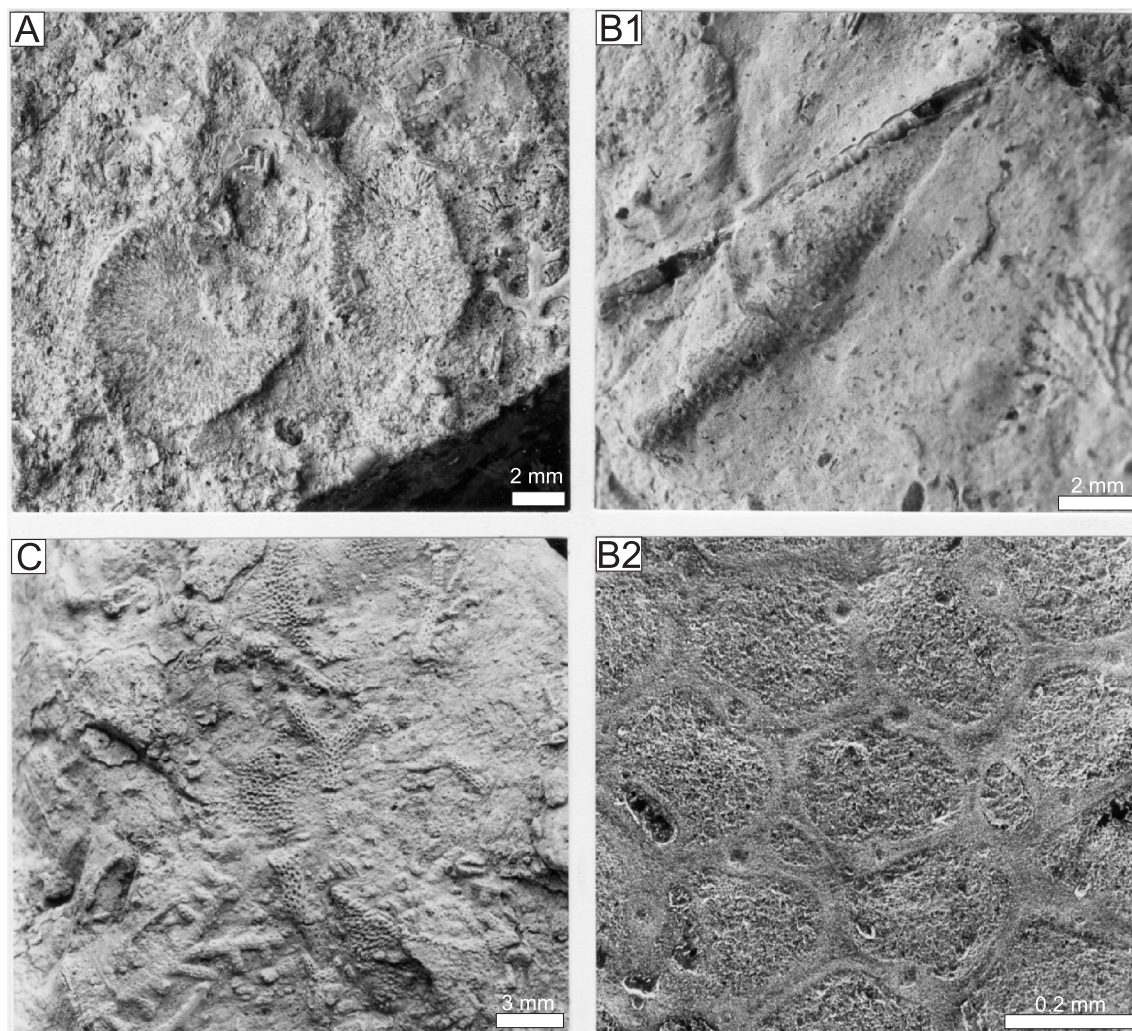


Fig. 9A – cup-shaped colonies of the genus *Dyscritella tubulosa* Morozova, with the accompanying colony of acanthoclaidiid on the right; in the background the shelly remains of the brachiopods are seen, lower part of the Ca1, ING UW/r/PR/Z/Ca1/Bry/30, Żarska Wieś (Lwówek Śląski Syncline); **B1** – encrusting colony of the *Dyscritella microstoma* Ernst overgrowing the long spines of a brachiopod of *Horridonia horrida* (Sowerby); **B2** – SEM image of the zoarial surface of the same colony showing the irregularly-shaped polygonal autozoecia surrounded by 1 to 5 acanthostyles, ING UW/r/PR/Z/Ca1/Bry/11, lower part of the Ca1 (copper-bearing marls), Grodziec (Grodziec Syncline); **C** – broken colonies of the *Acanthocladia anceps* showing mostly the distal parts of the colonies resting on the substratum, ING UW/r/PR/Z/Ca1/Bry/31, Żarska Wieś, lower part of the Ca1 (Lwówek Śląski Syncline)

Table 2

Measurements of *Dyscritella tubulosa* Morozova (two colonies)

	N	X	SD	CV	MIN	MAX
Aperture width	29	0.202	0.0215	10.6624	0.168	0.240
Acanthostyle diameter	30	0.045	0.0051	11.1930	0.035	0.055
Exilazooecia width	16	0.060	0.0244	40.7113	0.025	0.125
Acanthostyles per aperture	25	3.440	1.1576	33.6507	1.000	5.000
Exozonal wall thickness	10	0.028	0.0071	25.0477	0.020	0.040

N – total number of measurements, X – arithmetic mean, SD – standard deviation, CV – coefficient of variance, MIN – smallest measurement, MAX – largest measurement; measurements in mm, except for quantitative parameters

Subfamily Acanthoclaudiinae Zittel, 1880
Kalvariella Morozova, 1970

1930 *Pinnatopora waltheri* (pars Korn) – Korn (1930), p. 371, 372 [partim].
1970 *Kalvariella* Morozova – Morozova (1970), p. 242.
2001 *Kalvariella* Morozova, 1970 – Ernst (2001a), p. 145, 146.
2001 *Kalvariella* Morozova, 1970 – Morozova (2001), p. 78, 79.

Type species. – *Kalvariella typica* Morozova, 1970. Upper Permian, Lithuania.

Diagnosis. – Colonies containing main branches and secondary branches. Autozoecia arranged in two rows on the main branch and in 3–4 rows on secondary branches. Keel on the main branch (Morozova, 1970).

Comparison. – *Kalvariella* differs from *Acanthocladia* in having two rows of autozoecia on the main branches.

Occurrence. – Upper Permian, Zechstein of Germany, England, Poland.

Table 3

Measurements of *Dyscritella microstoma* Ernst (three colonies)

	N	X	SD	CV	MIN	MAX
Aperture width	15	0.167	0.0270	16.1550	0.120	0.204
Acanthostyle diameter	15	0.043	0.0096	22.3235	0.030	0.055
Exilazooecia width	10	0.055	0.0151	27.4406	0.035	0.075
Acanthostyles per aperture	10	5.500	0.8498	15.4516	4.000	7.000
Exozonal wall thickness	10	0.019	0.0047	25.6401	0.010	0.025

For explanations see Table 2

***Kalvariella typica* Morozova, 1970**
Fig. 5B, C and Table 5

1930 *Pinnatopora waltheri* (pars) Korn – Korn (1930), p. 372, 373, pl. 35, fig. 18.
 1970 *Kalvariella typica* Morozova, 1970 – Morozova (1970), p. 242, 243, pl. 58, fig. 6.

2001 *Kalvariella typica* Morozova, 1970 – Ernst (2001a), p. 146, pl. 6, figs. 1–4.

H o l o t y p e. – 2343/7; Paleontological Institute, Moscow. Upper Permian, Zechstein, Lithuania.

M a t e r i a l s t u d i e d. – Grodziec (Grodziec Syncline), single specimen in the sample numbered ING UWrp-R/Z/Bry/Ca1/15, mottled marls.

D e s c r i p t i o n. – Pinnate colony consisting of straight main branch with secondary branches. Main branch 0.44–0.49 mm wide, secondary branches 0.36–0.54 mm wide, diverging at angles of 63–86° (average 76.8°) from the main branch, 3–4 spaced per 5 mm along the main branch on each side. Autozoecia arranged on the main branch in two and on the secondary branches in 3–4 rows. Apertures circular to oval, 18 spaced per 5 mm of the branch length. Wide keel with small elliptical nodes between the rows of autozoecial apertures on the main branch. Abundant microstyles, 0.005–0.015 mm in di-

ameter, regularly spaced at distances of 0.005–0.02 mm. Polymorphs comprising inferred brooding zooids with ovicells at the distal end of the vestibule. The ovicells are 0.18–0.216 mm in diameter.

I n t e r i o r d e s c r i p t i o n. – *Autozoecia* rectangular on the main branch and hexagonal on the secondary branches in mid tangential section; elongate parallel to branch length; aperture positioned at distal to distal-abaxial end of chamber. Superior hemisepta weakly developed; interior hemisepta absent.

O c c u r r e n c e. – Zechstein Limestone, Upper Permian, Grodziec (Grodziec Syncline), North Sudetic Basin, SW Poland. Recorded by Ernst (2001a) from the Zechstein of Germany, as well as from England and Lithuania (Morozova, 2001).

***Acanthocladia* King, 1849**

1850 *Acanthocladia* King, 1849, p. 48.

1861 *Acanthocladia* King, 1849 – Geinitz (1861), p. 119.

1930 *Acanthocladia* King, 1849 – Korn (1930), p. 369.

1930 *Thamniscus* King, 1849 – Korn (1930), p. 364, 365 [partim].

1961 *Acanthocladia* King, 1849 – Dreyer (1961), p. 21, 22.

1970 *Acanthocladia* King, 1849 – Morozova (1970), p. 239.

2001 *Acanthocladia* King, 1849 – Ernst (2001a), p. 146.

2001 *Acanthocladia* King, 1849 – Morozova (2001), 77, 78.

T y p e s p e c i e s. – *Keratophytes anceps* Schlotheim 1820; Upper Permian, Thuringia, Glücksbrunn.

D i a g n o s i s. – Colonies consisting of main branches with secondary branches. Autozoecia arranged in three or more rows both on main and secondary branches, rectangular to hexagonal in mid tangential section. Superior hemisepta weakly developed; inferior hemisepta absent. Apparent reproductive polymorphs in form of isolated zoecia with enlarged proximal endozonal chambers are common.

O c c u r r e n c e. – Upper Permian, lower part of the Ca1 (reefal facies) in Germany, England, Poland, Lithuania and Russia.

***Acanthocladia anceps* (Schlotheim, 1820)**
Figs. 5D–G, 8, 9C and Table 6

1820 *Keratophytes anceps* Schlotheim – Schlotheim (1820), p.341, 342.

1848 *Fenestella anceps* (Schlotheim 1820) – Geinitz (1848), p. 18, pl. 7, figs. 22, 23, [non figs. 19–21].

Table 4

Measurements of *Kingopora baderi* Ernst (two colonies)

	N	X	SD	CV	MIN	MAX
Branch width	10	0.295	0.0434	14.7025	0.240	0.350
Dissepiment width	8	0.378	0.0740	19.5696	0.276	0.528
Fenestrule length	10	0.611	0.0384	6.2909	0.550	0.690
Fenestrule width	10	0.409	0.0618	15.1089	0.336	0.528
Distance between dissepiment centres	10	0.918	0.0839	9.1399	0.780	1.020
Distance between branch centres	10	0.705	0.0495	7.0209	0.600	0.750
Aperture width	7	0.103	0.0117	11.3855	0.084	0.120
Node diameter	10	0.070	0.0113	16.1416	0.054	0.084
Distance between node centres	6	0.354	0.0367	10.3684	0.310	0.420
Autozoecial chamber depth	7	0.168	0.0227	13.5029	0.130	0.200
Branch thickness	10	0.324	0.0310	9.5547	0.290	0.360
Maximal autozoecial chamber width	10	0.129	0.0095	7.3541	0.120	0.144
Vestibule length	5	0.132	0.0306	23.1774	0.096	0.180
Microacanthostyle diameter	10	0.025	0.0058	23.0940	0.015	0.035

For explanations see Table 2

Table 5

Measurements of *Kalvariella typica* Morozova (single colony)

	N	X	SD	CV	MIN	MAX
Aperture width	10	0.090	0.0087	9.6864	0.072	0.096
Distance between aperture centres along branches	10	0.293	0.0180	6.1475	0.264	0.324
Distance between aperture centres across branches	10	0.266	0.0221	8.2907	0.216	0.288
Node diameter	10	0.044	0.0068	15.6808	0.035	0.055
Distance between node centres	6	0.220	0.0561	25.5064	0.156	0.300
Maximal autozooeical chamber width	10	0.122	0.0095	7.7881	0.100	0.135

For explanations see Table 2

Table 6

Measurements of *Acanthocladia anceps* (Schlotheim) (three colonies)

	N	X	SD	CV	MIN	MAX
Main branch width	10	0.645	0.0778	12.0592	0.570	0.840
Secondary branch width	7	0.439	0.0508	11.5856	0.384	0.540
Distance between centres of secondary branches	10	1.254	0.2279	18.1776	1.050	1.800
Aperture width	20	0.077	0.0058	7.5031	0.072	0.084
Distance between aperture centres along branches	20	0.293	0.0256	8.7598	0.252	0.336
Distance between aperture centres across branches	20	0.248	0.0199	8.0073	0.228	0.300
Node diameter	8	0.048	0.0080	16.8797	0.035	0.060
Maximal autozooeical chamber width	10	0.121	0.0066	5.4403	0.110	0.130

For explanations see Table 2

1850 *Acanthocladia anceps* (Schlotheim, 1820) – King (1850), p. 48, 49 [partim], pl. 5, figs. 13–18.

1861 *Acanthocladia anceps* (Schlotheim, 1820) – Geinitz (1861), p. 119, 120 [partim], pl. 22, ?fig. 7.

1930 *Acanthocladia anceps* (Schlotheim, 1820) – Korn (1930), p. 369, 370, pl. 35, figs. 8, 9.

1961 *Acanthocladia anceps* (Schlotheim, 1820) – Dreyer (1961), p. 21, 22, pl. 9, figs. 2–5.

1970 *Acanthocladia anceps* (Schlotheim, 1820) – Morozova (1970), p. 240, pl. 57, figs. 2, 3.

2001 *Acanthocladia anceps* (Schlotheim, 1820) – Ernst (2001a), p. 147, 148, pl. 6, fig. 5, pl. 7, figs. 1–4.

L e c t o t y p e. – *Keratophytes anceps* Schlotheim, 1820; K. 57-1. Museum for Natural Sciences, Central Institute of the Humboldt-University, Berlin.

M a t e r i a l e x a m i n e d. – Grodziec (Grodziec Syncline) samples numbered ING UWrPR/Z/Bry/Ca1/15, 23, 35, 38; Lwówek Śląski Syncline ING UWrPR/Z/Bry/Ca1/31; Leszczyna Syncline samples numbered ING UWrPR/Z/Bry/Ca1/3; thin-sections of the samples ING UWrPR/Z/Bry/Ca1/15, mottled marls, ING UWrPR/Z/Bry/Ca1/35, and ING UWrPR/Z/Bry/Ca1/38.

D e s c r i p t i o n. – Colony consisting of straight main branch with secondary branches. Secondary branches diverging at angles of 77 to 79°, 4 spaced per 5 mm along the main branch on each side. New branches developed by transformation of secondary branches into main branch or by dichotomy of main branches. Dissepiments or anastomoses absent. Apertures arranged in three alternating rows on main branches and secondary branches. Some secondary branches carry at their beginning only two rows of autozoecia. A short distance after diverging they develop three rows. On main and secondary branches four rows of the autozoecia may infrequently appear. Apertures circular to oval. Autozoecia spaced usually

more closely on the secondary branches than on the main branch. Low keels with small nodes between rows of autozoecia. Apparent reproductive polymorphs in form of isolated zoecia with enlarged proximal endozonal chambers common: endozonal chambers 0.144–0.168 mm in diameter.

I n t e r i o r d e s c r i p t i o n. – Autozoecia relatively short, deep, with a long vestibule; rectangular to hexagonal in mid tangential section; elongate parallel to branch length; aperture positioned at distal to distal-abaxial end of chamber. Short superior hemisepta present; inferior hemisepta absent.

C o m p a r i s o n. – *Acanthocladia anceps* (Schlotheim, 1820) differs from *A. laxa* Korn, 1930 in generally having thinner branches, and the arrangement of autozoecia on the branches in 3 rows. *A. minor* possesses thicker branches as well as larger lateral branch angles.

O c c u r r e n c e. – Upper Permian, Ca1, Grodziec (Grodziec Syncline), Leszczyna-Kondratów, Nowy Kościół (Leszczyna Syncline), the upper part of the Ca1; lower part of the Ca1 in Żarska Wieś (Lwówek Śląski Syncline); *Acanthocladia anceps* was also recorded in the boreholes of the Fore-Sudetic Monocline (Kłapciński, 1971); and the Zechstein of Germany, England, and Lithuania (Korn, 1930; Dreyer, 1961; Morozova, 1970; Ernst, 2001a).

Family FENESTELLIDAE King, 1849
Spinofenestella Termier and Termier, 1971

T y p e s p e c i e s. – *Fenestella spinosa* Condra, 1902; Lower Permian, Wolfcampian; North America.

D i a g n o s i s. – Reticulate, fan-shaped as well as funnel-shaped colonies with relatively wide and thick branches and

relatively thin dissepiments. Autozoecia arranged in two rows on the branches. Autozoecia triangular in mid tangential section, triangular to pentagonal proximal to bifurcations. Narrow keel with single row of nodes developed.

C o m p a r i s o n. – *Spinofenestella* Termier and Termier, 1971 differs from *Rectifenestella* Morozova, 1974 in the triangular shape of the autozoecia in mid-tangential section.

O c c u r r e n c e. – Lower Devonian to Upper Permian.

Spinofenestella geinitzi (d'Orbigny, 1850)

Figs. 5H–L, 7 and Table 7

1850 *Fenestella geinitzi* d'Orbigny, 1850 – d'Orbigny (1850), p. 168.
 1861 *Fenestella geinitzi* d'Orbigny, 1850 – Geinitz (1861), p. 116, pl. 22, fig. 2.
 1930 *Fenestella geinitzi* d'Orbigny, 1850 – Korn (1930), p. 355, pl. 1, fig. 6; text-fig. 1.
 1930 *Fenestella retiformis* (Schlotheim, 1820) – Korn (1930), p. 354, pl. 1, fig. 3.
 1961 *Fenestella geinitzi* d'Orbigny, 1850 – Dreyer (1961), p. 13, pl. 4, figs. 2, 3.
 2001 *Spinofenestella geinitzi* (d'Orbigny, 1850) – Ernst (2001a), p. 152, 153, pl. 9, fig. 6, pl. 10, figs. 1–5.

H o l o t y p e. – The location of the type material is unknown.

M a t e r i a l e x a m i n e d. – Grodziec (Grodziec Syncline) samples numbered ING UWrPR/Z/Bry/Ca1/11, 13, 23, 24; Leszczyna samples ING UWrPR/Z/Bry/Ca1/1-8; thin sections of the samples ING UWrPR/Z/Bry/Ca1/13 and ING UWrPR/Z/Bry/Ca1/24.

D e s c r i p t i o n. – Micrometric formula: 14–18.5 (branches per 10 mm), 12.5–14 (fenestrules per 10 mm), 18–24 (apertures per 10 mm along the branch). Fan-shaped colony with regular meshwork. Autozoecia arranged on the branches in two alternating rows. Additional autozoecium occurring at branch bifurcations. Dissepiments thin, fenestrules elongated-oval to rectangular with rounded corners, with 3–4 autozoecial apertures per length of a fenestrule. Autozoecial apertures suboctagonal, with eight thin septa in the high peristome. Septa disappear in deeper tangential sections. Narrow keel with a single row of closely spaced nodes present between the rows of the apertures. Nodes long, 4–5 spaced per 1 mm along the branch. Root-like holdfasts common. Reverse side of the colony strongly ribbed. Internal granular layer well-developed,

continuous with obverse keel, nodes, peristomes and across dissepiments. Long and thin rods extend from the inner granular skeleton and reach the reverse side as microstyles. The microstyles are 0.01–0.015 mm in diameter and regularly spaced. Outer lamellar skeleton moderately thick, usually thickening on the reverse side in the proximal parts of colonies. Heterozoecia absent.

I n t e r i o r d e s c r i p t i o n. – Autozoecia triangular to pentagonal in mid tangential section, relatively high and short, with long vestibule; elongate parallel to branch length; aperture positioned at distal to distal-abaxial end of chamber. Superior hemisepta weakly developed; inferior hemisepta absent.

C o m p a r i s o n. – *Spinofenestella geinitzi* (d'Orbigny, 1850) differs from the other species of the genus in its smaller elements of the meshwork. It differs from *S. minuta* (Korn, 1930) in its wider and longer fenestrules and in the fan-shaped growth-form compared with the funnel-shaped colony of *S. minuta*.

O c c u r r e n c e. – Ca1, Upper Permian, Grodziec (Grodziec Syncline), Leszczyna Syncline, North Sudetic Basin, Fore-Sudetic Monocline (subsurface) (Kłapciński, 1971), SW Poland; Upper Permian (Zechstein) of Germany and England (Ernst, 2001a).

INTERPRETATION

The distributional pattern of the bryozoans in the study area is patchy, and associated with a shallow-water biota, forming a biocenoses dominated by bryozoans, brachiopods, and molluscs in distinct horizons usually at the base of the marly calcareous series of the Zechstein Limestone.

The highest bryozoan diversity in the studied profiles occurs in bedded facies, where the fauna is dominated by large, fan-shaped or funnel-shaped colonies of *Spinofenestella geinitzi*, which indicate a low energy environment and moderate or slow sedimentation rates (Raczyński, 1996) typical of offshore or mid- to outer shelf settings on the Ca1 slope and basin floor and soft substrates (Reid, 2010),

Table 7

Measurements of *Spinofenestella geinitzi* (d'Orbigny) (two colonies)

	N	X	SD	CV	MIN	MAX
Branch width	15	0.309	0.0250	8.1071	0.276	0.360
Dissepiment width	15	0.113	0.0076	6.7283	0.096	0.120
Fenestrule length	15	0.635	0.0405	6.3752	0.540	0.690
Fenestrule width	15	0.362	0.0723	19.9541	0.264	0.492
Distance between dissepiment centres	15	0.730	0.0334	4.5727	0.690	0.780
Distance between branch centres	15	0.610	0.0658	10.7856	0.510	0.720
Aperture width	15	0.080	0.0054	6.7480	0.072	0.084
Distance between aperture centres along branches	15	0.239	0.0140	5.8340	0.216	0.264
Distance between aperture centres across branches	15	0.210	0.0231	10.9637	0.180	0.264
Node diameter	10	0.047	0.0054	11.4358	0.040	0.055
Distance between node centres	10	0.240	0.0271	11.3039	0.216	0.288
Maximal autozoecial chamber width	15	0.122	0.0175	14.3815	0.108	0.168
Branches per 10 mm	5	15.790	1.7587	11.1380	14.000	18.500
Fenestrules per 10 mm	6	13.130	0.5745	4.3751	12.500	14.000
Apertures per 5 mm along the branch	6	21.933	2.0539	9.3645	18.000	24.000

For explanations see Table 2

Three types of the colony growth-forms – membraniporiform, reteporiform and vinculariiform – can be distinguished among the bryozoans in the North Sudetic Basin. The dominant colony growth-form (reteporiform) in the Grodziec Syncline belongs to the reticulate fenestellids. In general, the majority of fenestellid colonies occur mostly in the upper part of the Zechstein Limestone, where they are often accompanied by the pinnate colonies of acanthocladids. Trepostome species, which exhibit an encrusting growth form (membraniporiform) may indicate a shallow depth, moderate to high water energy environment, with low sedimentation rate (cf. Nelson et al., 1988; Reid, 2010) and occur mostly in the marginal parts of the SPB, where reefal/biohermal structures existed during the Ca1 (Leszczyna Syncline). Moreover, they are also abundant and diverse in the lower part of the Ca1 in the western part of the North Sudetic Basin (Lwówek Śląski Syncline) being accompanied by the productid of *Horridonia horrida* and occurring in a low-energy and low sedimentation accumulation rates if sediment input is low or is trapped onshore.

Bryozoans may have been well-adapted to different, often extreme, ecological settings caused by frequent fluctuations of sea level, sedimentation and distribution of microbial mats (Raczyński, 1996; Peryt et al., 2012). In the study area, bryozoans are a good palaeoecological proxy, clearly reacting to small environmental changes. This is well-observed in the tempestite facies characterized by the highest taxonomic diversity and number of bryozoans. Likewise, bryozoans help to distinguish shelf deposits with no storm beds, thus recording maximum depth and extent of the basin – maximum transgression (Grodziec Syncline).

The recognized bryozoan-bearing strata in SW Poland usually occur at the base of the marly-calcareous series of the Ca1 succession (Table 2 and Fig. 2). Here, they are accompanied by a rich shallow-water biota that includes productid brachiopods (*Horridonia horrida*), molluscs, benthic foraminifers and fish remains (Fig. 2). The well-marked bryozoan-bearing horizon in the Lwówek Śląski Syncline is mostly confined to the lower part of the Ca1, in contrast to the bryozoans of the Leszczyna Syncline, which occur mostly in the upper part of the Ca1 (Fig. 3) but also in the lower part of the Ca1 (at the base of the mottled limestones, Nowy Kościół locality; Fig. 3). The presence of the transitional and horizontal sedimentary changes in the different parts of the relatively shallow-water North Sudetic Basin, and frequent oscillations of sea level, are clearly indicated in the profiles studied (Fig. 2) by the occurrence of differentiated biotic assemblages and the composition of the bryozoan fauna.

DISCUSSION

Permian bryozoans, like their modern counterparts, have different growth-forms. Analysis of bryozoan morphotypes has proven to be a valuable tool for palaeoecological interpretation (Stach, 1936; Schopf, 1969; Kelly and Horowitz, 1987; A.M. Smith, 1995; Hageman et al., 1997). Within the North Sudetic Basin these include erect (vinculariiform), fenestellid (reteporiform), and encrusting (membraniporiform) habits. The taxonomically richest bryozoan assemblage occurs in the axial part of the North Sudetic Basin (Grodziec Syncline; Figs. 4–7), where the fauna is dominated by the erect colonies which reveal the reteporiform growth-form and zoaria are composed of large fan-shaped or funnel-shaped colonies of fenestellids with a maximum height of 10 cm. The water energy or turbulence is the primary control on the bryozoans occurrence (Reid, 2010),

therefore, we may assume that erect-rigid fenestellids prefer the low energy environment co-occurring with the productid brachiopods which are common in offshore setting with the moderate or slow sedimentation rate and a soft substrate on the slope of the Ca1 carbonate platform and basin floor (see also Reid, 2010). Colonies of *Spinofenestella geinitzi* (d'Orbigny) are usually heavily calcified and are a common element of the Ca1 (Figs. 5H–L, 7 and 9B1). They can be used as an efficient indicator of the current system with the ability of forming differently shaped colonies from planar or lobate to fan-shaped or conical-shaped zoaria, probably in response of the water current (Figs. 5H–L and 7). Generally, in the lower part of the Grodziec Syncline profile, where the stormy conditions were calmer, the *in situ* bryozoans show planar to fan-shaped zoaria, and they attain larger sizes, contrary to the upper part of the profile where the currents were stronger and the colonies achieved smaller sizes forming mostly the funnel-shaped zoaria. The overall shape of a bryozoan colony is interpreted as an adaptation to an exterior current flow that both increased the physical stability of the colonies and allowed zooids to generate local currents and filter efficiently nutrients from the water (Cowen and Rider, 1971; McKinney, 1977). According to McKinney and Jackson (1989), reticulate fenestellids are less vulnerable to currents and sedimentation rate, and are able to colonize more exposed sites, of the high to low sedimentation rates and shallow to deep water, but they mostly occur in moderately energetic to relatively quiet environments or microenvironments, either near or below the normal waterbase or in sheltered areas (McKinney and Gault, 1980; Nelson et al., 1988). The majority of reteporiform colonies in the material studied from the Grodziec Syncline form funnel-shaped colonies with the zoecia arranged on the outside of the colony, and some possess well-developed supporting roots; however, smaller cone or funnel-shaped colonies also occur (Figs. 5A, H–L, 6 and 7; cf. Ernst, 2001a). The most delicate, erect-rigid colonies from the marly-calcareous sediments of the Grodziec Syncline are pinnate colonies of *Kalvariella typica* (Fig. 5B, C), found at the base of the mottled marls of the Ca1, and they usually colonize a very quiet sedimentary environment far from turbulent areas and with very little terrigenous influx (in the bryozoan life time scale).

The zoaria of fenestellids and acanthocladids together are more common in the upper part of the Ca1 in the Leszczyna Syncline – where they show considerable fragmentation of the colonies, with proximal parts (bases) broken, suggesting high-energy setting, together with the sedimentary features such as the bed bases, graded bedding, as well as a presence of the mollusc coquinas and their connection with the reefal/biohermal structures in the marginal part of the Leszczyna Syncline (Figs. 3 and 8; Raczyński, 1996; Biernacka et al., 2005). Fragments of *Acanthocladia anceps* colonies recognized in Kondratów locality (Leszczyna Syncline) show their higher stratigraphical and sedimentary cycle position in the studied profile (Table 2 and Fig. 2). They occur in the massive limestones which are evidently connected with the regressive event which terminated the occurrence of the bryozoans in the Ca1.

A very common biofacies in the Grodziec Syncline is composed of *Agathammina–Spinofenestella–Horridonia* which may indicate a low-energy environment (Fig. 3). The *Acanthocladia–Bakevella–Schizodus* is common at Leszczyna (Leszczyna Syncline) and the bryozoans occur there in the upper part of the Ca1, which at that time comprised shallow lagoons separated from a deeper shelf by barriers composed of numerous broken colonies of *Acanthocladia* (Figs. 1B, C, 2 and 8; Raczyński, 1996). In the lower part of the Ca1 in the Lwówek Śląski Syncline *Dyscritella* dominates: it forms encrusting zoaria, colonized often a perished algal substrate (Fig. 9A). Cup-shaped,

encrusting colonies favour soft-bottoms supported by algae, either using a hard substrate provided by brachiopod shells of *Horridonia horrida* or echinoid spines (Fig. 9B1). Colonies with a membraniporiform morphotype prefer a low energy, shallow-water, subtidal or lagoonal environment (Lagaaij and Gautier, 1965). It may be suggested that the Lwówek Śląski Syncline deposits originated in a near-shore environment, where the biocenoses of *Acanthocladia–Liebea* are very common, accompanied by a rich productid-brachiopod and microbial mat association and should be referred to the onshore transgressive-regressive facies in the lower part of the Ca1 (Fig. 2; Raczyński, 1996).

Throughout the Phanerozoic bryozoans have been major sources of carbonate sediment (Taylor and Allison, 1998). During Zechstein Limestone time shallow-water conditions favoured the development of microbial-bryozoan reefal facies, prevailing in the SPB from England (e.g., Smith, 1995) and Germany (Paul, 2010 with references therein), to the eastern part of the basin in Poland (Dyjażczynski et al., 2001) and Lithuania (Morozova, 1970). The common constructors of those reefs are also sessile foraminifers (Peryt et al., 2012).

Ernst's (2001a) study showed that within the SPB in Zechstein time, bryozoans of the order Fenestellida were common to ubiquitous inhabitants of small carbonate bioherms composed of reticulate and pinnate colonies of the following genera: *Rectifenestella*, *Penniretepora*, *Acanthocladia*, *Thamniscus*, *Kingopora*, *Kalvariella* and *Synocladia*. Cosmopolitan genera such as *Rectifenestella* and *Dyscritella* and the endemic genus *Kalvariella*, are common among German and Polish Zechstein Limestone faunas.

Among the eight species identified from boreholes in Lithuania and the Kaliningrad district (Russia) five (*Fenestella retiformis*, *Kingopora ehrenbergi*, *Acanthocladia laxa*, *A. anceps* and *Kalvariella typica*) are distributed in the deposits of NW Europe and only a few are common in Poland (Suveizdis, 1975). Moreover, Kłapciński (1971) showed a certain similarity in existence of the same bryozoan-mollusc-brachiopod associations between the Zechstein Limestone and those of the Permian basins located in Pre-Uralian (Russia) and Salt Range of the Himalaya region (Pakistan).

Considering the northwards palaeobiogeographical connection between the Late Permian Northern Permian Basin fauna of NW Europe and the Arctic Boreal Ocean faunas, it should be mentioned that there are a few taxa in common with eastern North Greenland and Svalbard, such as *Dyscritella*, *Stenopora*, *Fenestella* and *Kingopora* (Sørensen et al., 2007).

CONCLUSIONS

In the studied bryozoan fauna from the Zechstein Limestone of the North Sudetic Basin six species belonging to the trepostomids and fenestellids were found. Fenestellids which were likely to have been very common in the marly sections of the Ca1, particularly in the lead-bearing series, occur during the maximum flooding in the axial part of the North Sudetic Basin i.e. Grodziec Syncline.

Factors which contributed to the richness of bryozoans in the North Sudetic Basin included the high availability and abundance of substrates (either hard or soft). Two other important factors such as the favourable current systems and slow or moderate sedimentation rates allowed sufficient time for the colonization of the substrata by the bryozoan biota in the North Sudetic Basin during the Ca1 sedimentation.

The highest faunal taxonomic diversity, including within bryozoans, occurs in the upper part of distal tempestites. This could be interpreted as the effect of improving ecological conditions on the sea-floor and in the bottom waters. This would have allowed a short but intensive development of the sea-floor ecosystem. Analysis of the dominant colony growth-forms in conjunction with the depositional conditions of the Zechstein Limestone marly-calcareous series (mottled, copper- and lead bearing marls) shows that these factors could be correlated with various physical environmental parameters such as current strength, water depth, rate of sedimentation and substrate type.

Acknowledgements. This research was supported by the Polish Geological Institute – Research National Institute (internal projects no. 6.20.9231.00.0 and no. 61.1201.1101.00.0) and by a “Mobility Plus” Programme postdoctoral fellowship of the Ministry of Science and Higher Education of Poland (M.S.). Many thanks are given to J. Błaszcyk for a kind assistance during the SEM sessions, and to Z. Strąg (both from Institute of Paleobiology, PAS) for making the thin-sections. This work benefited from the discussion and kind assistance of A. Ernst during his stay at the PGI-NRI (Warszawa, Poland) as well as from his review of the paper. The authors are very grateful to C.M. Reid, P. Wyse Jackson, H. Arne Nakrem and T. Amund Svånå for their constructive remarks which improved the paper. Many thanks are extended to P.D. Taylor for reading this paper at its early stage and improving the English text. T.M. Peryt is thanked for the critical and editorial remarks of the manuscript.

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