PRE-TAGHANIC (LOWER TO LOWER MIDDLE GIVETIAN) BRACHIOPODS FROM MIŁOSZÓW IN THE HOLY CROSS MOUNTAINS (POLAND)

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Abstract: Sixty-eight brachiopod species are reported from the upper part of the Skały Formation at Miłoszów (Łysogóry Region of the Holy Cross Mts., central Poland) on the basis of over 2,200 specimens. The fauna is Early to early Middle Givetian in age (timorensis to rhenanus/varcus conodont zones) and thus predates the Middle Givetian Taghanic Bioevent. One new genus and three new species are described. Leiocyrtia Baliński gen. nov. (type species: Leiocyrtia rara Baliński gen. et sp. nov.; Spiriferida, Cyrtiidae) is characterised by a non-costate shell with prominent sulcus and fold and capillate microornament. Undispirifer sidoniae Halamski and Baliński sp. nov. is characterised by transverse shells and dense ribbing. Moravilla andreae Baliński and Halamski sp. nov. is characterised by relatively coarse radial capillate ornament and is the first representative of the genus outside the type species from the Givetian of Moravia. The most abundant species are: Spinulicosta cf. spinulicosta, Antirhynchonella linguiformis, Pentamerelloides davidsoni, Peratos beyrichi, Plectospira ferita, Spinatrypa wotanica (confirmed to belong to that genus and not to Spinatrypina), Ambothyris sp., and Echinocoelia dorsoplana. 'Spirifer' quadriplicatus Sandberger and Sandberger, 1856, a rare species known from Miłoszów and the Rhenish Massif, is an orthide and belongs to Teichertina. The relationship between Skenidioides polonicus and S. cretus, formerly understood as anagenesis, is re-interpreted as budding cladogenesis. Davidsonia septata is reported as an epizoan on rugosan corals, a relationship never previously observed in representatives of that genus. Brachiopods represent different palaeoecological groupings, from relatively shallow-water taxa (BA3, globetum) to deep-water mud-dwelling ones (BA5, deeper brachiopodetum). The richest beds are M1-IIa (28 brachiopod species), M3-7 (23 species), and M0-9 (22 species). Eighteen species described here were not known previously in the Holy Cross Mountains, so the corrected total number of brachiopod species from the Middle Devonian of the Łysogóry Region is 140.

Key words: Systematics, evolution, palaeoecology, benthic assemblage, biodiversity, brachiopodetum, Devonian, Taghanic Bioevent.

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INTRODUCTION

The Devonian period was the acme of brachiopod diversity (Curry and Brunton, 2007, figs 1912, 1914) and the European Middle Devonian faunas are rich and relatively well understood (Jansen *et al.*, in press). However, Eifelian faunas are better known than the Givetian ones. This discrepancy in knowledge is due to several unrelated causes. In the Eifel, the area that yielded the richest European Middle Devonian brachiopod faunas, marine Givetian strata are largely dolomitised. In the Barrandian area of Bohemia, the Eifelian is marine, whereas the Givetian is mostly terrestrial. In the Holy Cross Mountains, the Skały Formation, spanning

the Eifelian–Givetian boundary, contains an exceptionally rich level in its lower part (Konzentrat-Lagerstätte at Skały; Halamski and Zapalski, 2006; Woźniak *et al.*, 2022), so the Eifelian part of this lithostratigraphic unit is better studied than its Givetian part.

The object of the present paper is the systematic description of the brachiopod fauna from the Givetian part of the Skały Formation (see Racki *et al.*, 2022), cropping out in the Miłoszów Wood, near Nieczulice in the Holy Cross Mountains (central Poland). Out of 68 species described here, 18 were not reported previously from the Devonian of the Holy Cross Mts. Three new species and one new genus, *Leiocyrtia* (Spiriferida, Cyrtiidae) are described.

The present study is part of a larger project, aiming at the reconstruction of the Lower to Middle Givetian ecosystems of Miłoszów (Halamski, 2022) in the context of Middle Devonian bioevents, in particular the Taghanic Biocrisis (e.g., Aboussalam and Becker, 2011; Zambito, 2011; Narkiewicz *et al.*, 2015; but see also Halamski, 2018). The well preserved and abundant Miłoszów fauna was selected as a representative of pre-Taghanic brachiopod assemblages. The general results of the project are summarised in a separate contribution (Halamski *et al.*, 2022b). The reader is referred to this paper for research history, regional geology, and details of local geological setting, including the precise locations of outcrops; only basic data are summarised here.

GEOLOGICAL SETTING

The brachiopods studied in the present paper come from the Skały Formation, a Middle Devonian lithostratigraphic unit in the Łysogóry Region (= northern region of the Holy Cross Mountains, central Poland). The Skały Formation (formerly Skały Beds) was first described in the stratotypic Grzegorzowice-Skały section with focus on its lower, Eifelian part by Pajchlowa (1957) and a formal definition was given by Racki et al. (2022). Miłoszów Wood, situated ca. 3 km westwards from Skały, possesses a few rather poor outcrops of the higher, Givetian part of the Skały Formation. Some brachiopods from the "Miłoszów limestone" (an informal lithostratigraphic unit, never satisfactorily defined) were studied by Biernat (1964, 1966), but the stratigraphy was not considered. The material described in the present paper comes mostly from trenches, dug by or under the supervision of the present authors between 2017 and 2022 (Halamski, 2022; Halamski et al., 2022b) in order to elucidate the stratigraphy and investigate the fauna. Additionally, brachiopods described from Miłoszów by Biernat (1964, 1966) and collected earlier (starting in the 1970s) by Andrzej Piotrowski, Wojciech Kozłowski, Jarosław Musialik, and the present authors, also were used.

The outcrops (Fig. 1D; see also Halamski, 2022, figs 1B, 2) consist of four continuous sections, numbered from M0 (easternmost) to M3 (westernmost), mostly separated by faults. The stratigraphy and correlation between these sections have been possible thanks to the study of conodonts and palynomorphs (Fig. 1C, E; Halamski *et al.*, 2022b). It should be stressed that the numbering was done at the very beginning of the field studies and corresponds to the present-day topography; this numerical order is different from the stratigraphic sequence, with the oldest strata cropping out at M1 and the youngest ones at M0.

The M1 section likely belongs to the lower part of the *Polygnathus timorensis* Zone, whereas the M2–M3 sections (physical continuity between the two could be traced) belong likely to the upper part of the same zone (Fig. 1C; see Halamski *et al.*, 2022b). The youngest sediments crop out in the M0 section, which was dated to the upper part of the *Polygnathus rhenanus / Polygnathus varcus* Zone (early

Polygnathus ansatus Zone cannot be excluded; Halamski *et al.*, 2022b). In terms of palynostratigraphy, all outcrops belong to the "*Geminospora*" *extensa* Zone, with the outcrops M1 and M2–M3 belonging to the Ex1 subzone and the outcrop M0 belonging partly to the Ex1 subzone and partly to the Ex2 subzone (Halamski *et al.*, 2022b). The age of the brachiopods studied here spans thus the Early Givetian and an earlier part of the Middle Givetian.

The Skały Formation corresponds to a carbonate ramp depositional system on an open-marine shaly-carbonate shelf (Halamski *et al.*, 2022b; Pisarzowska *et al.*, 2022; Racki *et al.*, 2022). The area considered here belonged to the southern shelf of Laurussia or, to say it differently, to the northern shore of the Rheic Ocean (see e.g., Golonka *et al.*, 2019 and references therein). Brachiopods studied in the present paper belonged to communities ranging from BA3 (moderate depth) to BA5 (deep), according to Boucot's (1975) terminology of Benthic Assemblages.

MATERIAL AND METHODS

Generalities

The brachiopods described in the present paper come from several levels within four sections at Miłoszów (Fig. 1E), characterised by different lithologies, resulting in the application of different techniques of collecting and study. First of all, it should be stressed that brachiopods are not distributed equally in the investigated sections; three especially rich levels are M1-IIa, M3-7, and M0-9, whereas the remaining beds yielded moderately rich (Fig. 2) to very poor (and in some cases indeed, none) brachiopod faunas. The M1-IIa composite bed is a shale level; brachiopods were collected by sediment washing and sieving in the field and partly in the laboratory (about 100 kg of sediment in total). Bed M3 λ , belonging to composite bed M3-7, and bed M0-9 are limestone beds, so brachiopods were obtained by splitting the rock with hammers. Small samples from shale and marly beds were taken to the laboratory and washed on fine sieves. Finally, phosphatic-shelled brachiopods were obtained from the residues of acid-dissolved limestone (primarily intended for conodont study). The differences in the taxonomic composition of beds and numbers of taxa present in a single bed (see below, subchapter Species pool), thus partly correspond to genuine differences in the fossil content, but their numerical values can be biased by a positive feedback, consisting of a richer bed being sampled more thoroughly.

Location of outcrops, lithology, stratigraphic details, and information on co-occurring fauna are given in Halamski *et al.* (2022b). Brachiopods are the most diversified fossil group at Miłoszów, with 68 species corresponding to about 39% of the total number of 170 animal species (Halamski *et al.*, 2022b, tab. 2). The total number of brachiopod specimens from all four sections at Miłoszów exceeds 2,200.

Repositories

The described material is housed in the Institute of Paleobiology of the Polish Academy of Sciences (Warsaw, Poland) under the collection number ZPAL V.74/Bp



Fig. 1. Geological setting of the studied brachiopods. **A.** Contour map of Poland showing the Palaeozoic core of the Holy Cross Mountains (red) and the location of the area shown in B. **B.** Simplified geological map of the Holy Cross Mountains with the location of Miłoszów (after Halamski *et al.*, 2022b, fig. 1C and ref. therein); HCD – Holy Cross Dislocation. **C.** Conodont and spore zones of the Lower and Middle Givetian with the presumed stratigraphic positions of the studied sections (after Halamski *et al.*, 2022b, figs 7, 8 and ref. therein). **D.** Lidar map (Geoportal, 2023) of the Miłoszów area showing the location of the four studied sections (after Halamski *et al.*, 2022b, fig. 3A and ref. therein). **E.** Lithological columns of the four sections at Miłoszów (Skały Formation, except for bed M0-10 belonging to the Świętomarz beds) with occurrences of brachiopods (after Halamski *et al.*, 2022b, fig. 3B).



Fig. 2. Mass occurrence of *Antirhynchonella linguiformis* Biernat, 1966 in a coquina-like lens (specimen ZPAL V.74/Bp/17/M2/5; outcrop M2, composite bed M2-3, bed M2ɛ; Lower Givetian).

[V – Varia; all fossil groups collected at Miłoszów are kept together; Bp – Brachiopoda]. Following the usage introduced by Halamski (2004b, 2009), inventory numbers consist of three parts separated by slashes, the first one denoting the species (as given below, see subchapter Species pool), the second one the outcrop, and the third one the individual specimen. For example, the holotype of *Undispirifer sidoniae* has the inventory number ZPAL V.74/Bp/50/M0/l, where 50 is the ordinal number of the species, M0 denotes the outcrop, and l is the number of this specimen. The entire collection of this species can be referred to, omitting the last two parts of the inventory number, as ZPAL V.74/Bp/50.

The described material has been collected by the present authors and subordinately by the late Gertruda Biernat (see Halamski and Baliński, 2016), Wojciech Kozłowski, Jarosław Musialik, and the late Andrzej Piotrowski. The specimens collected by W. Kozłowski and J. Musialik can be assigned unequivocally to outcrops M0-M3 as defined by the present authors and are cited under inventory numbers containing the aforementioned outcrop abbreviations. The specimens collected by A. Baliński in the 1970-ies are denoted with reference to his old trenches (MS1 - trench S1, approximately corresponding to M2-M3 herein; MS2 trench S2, approximately corresponding to M1 herein). The specimens collected by A. Piotrowski from beds corresponding approximately to M1-IIa as understood here, have inventory numbers with the abbreviation MP. The specimens collected by G. Biernat are referred to either by published inventory numbers ZPAL Bp (mostly the collection ZPAL Bp VII) or (for unpublished specimens) by MII, MIII, and MIV, referring to the sections Miłoszów II and Miłoszów III (approximately our M3-7) and Miłoszów IV (approximately our M0-9; see Halamski et al., 2022b).

Additional material from the following institutions was also used: Forschungsinstitut Senckenberg, Frankfurt am Main, Hessen, Germany (institutional abbreviation SMF); Museum of Comparative Zoology, Harvard University, Cambridge, Ma., USA (institutional abbreviation MCZ); Museum of Nature of Kharkiv National University, Kharkiv, Ukraine (institutional abbreviation MNKhU); Landesmuseum für Kunst und Natur, Wiesbaden, Hessen, Germany (institutional abbreviation MWNH); Natural History Museum, National Academy of Sciences of Ukraine, Lviv (formerly Dzieduszycki Museum, Lwów), Ukraine (institutional abbreviation L); Université de Strasbourg, Institut des Sciences de la Terre, Strasbourg, France (institutional abbreviation UNISTRA); United States National Museum, Smithsonian Institution, Washington, D.C., USA (institutional abbreviation USNM).

Special taxonomic questions

As in the recently published study of Middle Devonian brachiopods from northern Maïder (Halamski et al., 2022a), a few brachiopod groups are omitted from the present systematic account, pending a detailed revision based on the material from Europe (Holy Cross Mountains, Eifel) and Northern Africa (Morocco). These groups include the uncinuloid rhynchonellides (Kransia, Beckmannia) and the athyridide genus Bifida. These brachiopods are illustrated, but either only a cursory description is given or none at all. The reticulariid spiriferides Ambothyris, Echinocoelia, Warrenella, and Thomasaria are described in detail as far as the Miłoszów material is concerned, but uncertainties concerning the type material of relevant species results in open nomenclature being used or detailed discussions being referred to a further study. Species recently described in detail by the present authors often are illustrated and briefly commented, whereas a complete description is not given; in such cases a bibliographic reference to a description is always quoted.

Images were mostly taken using a Fujifilm Finepix S2 pro camera with a Nikon micro 60 mm lens. Enlargements were photographed under a Nikon SMZ 1500 binocular microscope, equipped with a Nikon D800 digital camera. Specimens were coated with ammonium chloride before being photographed. Some photographs were assembled from a series of frames, using Helicon Focus software.

Internal features of the brachiopods were investigated, using the standard technique of serial sections and acetate peels. The peels were mounted between microscope slides and photographed under a binocular microscope. The photographs were imported to CorelDRAW and internal details were drawn using a digital drawing tablet.

Descriptions are illustrated by means of photographic plates, serial sections, and dispersion diagrams (Figs 3–60).

Calculations were mostly made with PAST (Hammer *et al.*, 2001) and Microsoft Excel software. Measurements of the material studied are given as follows: (a-)b-c(-d) [N], with a – minimum value; b – first quartile; c – third quartile; d – maximum value; N – number of observations. 'Width index' is used for concision to denote the width-to-length ratio.

Synonymies are an essential part of the taxonomic work. However, for species recently described by the present authors, the synonymies are limited to the first description and a recent revision with a more extensive synonymy list (*ubi syn.*, abridged for "*ubi synonymia*", Latin: where synonymy [is to be found]); only omissions are corrected, if needed. For species lacking a recent taxonomic treatment, complete synonymy lists are given. Synonymies are commented upon by means of the signs, proposed by Richter (1948) and Matthews (1973), as used by Halamski (2009, pp. 46–47).

Abbreviations used in the tables of measurements: L - length; 1 - dorsal valve length; Ndc - total number of dorsal ribs; Ndc/5 mm - number of dorsal ribs measured at the commissure per 5 mm length; Nfl - number of ribs per flank; T - thickness; W - width; wt - width of the tongue; ws - with of the sulcus; War - width of the interarea. The sign ~ denotes that a given value is measured approximately or estimated.

SYSTEMATIC PALAEONTOLOGY

Splitting vs. lumping taxonomic treatments

A short comment about splitting vs. lumping styles of taxonomy, as applied to the present study, may be useful. The present authors have not applied any consistently lumping or splitting approach. However, in a few cases (Antirhynchonella, Parapugnax, Undispirifer, Cyrtina; see below), the proposed systematic treatment can probably described as that made by splitters. There is no single reason for that. As explained in more detail in the corresponding descriptions, (some) species within Antirhynchonella and Parapugnax are distinguished by weak characters and it is probable that these taxa represent single biological species. However, owing to problems related to the type material of some of these taxa (small samples that do not allow appreciation of the variability; poor preservation; uncertain stratigraphy precluding ascertaining whether variants are truly coeval), such a conclusion was estimated as probable, but not certain. In such cases, variants are distinguished formally, as less harm seem to be done by separating insignificant variants than by mixing genuinely different units (in other words, oversplit data can always be lumped by future workers, but overlumped data cannot be easily split). Undispirifer sidoniae Halamski and Baliński sp. nov. is described on the basis of a small sample showing weak morphological variation, but distinctly outside that of the previously known species of Undispirifer. A splitting-style of Cyrtina is consistently applied by recent brachiopodologists working on that genus and the present authors conformed to this style of descriptions.

Conversely, the present treatment of *Gruenewaldtia* and *Thomasaria* (see below) may probably be considered as that made by lumpers. In both cases, such an approach is based on analyses of large samples, resulting in a conclusion about continuous intergrading of variants purportedly diagnostic of separate taxonomic units according to other brachiopodologists.

Descriptions

Phylum Brachiopoda Duméril, 1805 Subphylum Linguliformea Williams *et al.*, 1996 Class Lingulata Gorjansky and Popov, 1985 Order Lingulida Waagen, 1885 Superfamily Linguloidea Menke, 1828

Family uncertain Genus *Lingulipora* Girty, 1898

Type species: *Lingula (Lingulipora) Williamsana* Girty, 1898; Upper Devonian; Kentucky, USA.

* 2019 *Lingulipora budili* sp. nov. – Mergl, pp. 173– 174, figs 3, 4.

Material: One shell and almost 50 mainly fragmentary loose valves, isolated from a conodont sample digested in acetic acid.

Description: Shell biconvex, elongate suboval in outline, much longer than wide, width-to-length ratio about 0.55-0.60; lateral margins broadly arched, anterior margin rounded. Ventral valve with angularly tapered posterior region; pseudointerarea well developed, with accentuated growth lines, apsacline, divided into propareas by a well-marked pedicle groove. Dorsal valve with a narrowly rounded posterior margin; pseudointerarea reduced, instead thickened posterior rim present (Fig. 3F); well preserved cup-like first formed shell observed in a single valve (Fig. 3I), measuring 84 µm in width. Shell thin-walled; interior of both valves without recognizable structures, but with sparse circular, cylindrical pores measuring 5 µm in diameter on average; the pores penetrate the entire thickness of the valves, but are covered with an outer shell layer (something like a canopy), which has, more or less centrally, a small external opening up to 1 µm across (Fig. 3J). The shell exterior is weakly ornamented with growth lines.

Remarks: This species is represented in the studied material by shells reaching a length of up to 2.1 mm, nevertheless some fragments indicate a maximal length of about 3 mm. It is included into *Lingulipora* Girty, 1898 on account of the presence of cylindrical pores. Elliptic shell outline and small shell dimensions, as well as the relatively large size of the ventral pseudointerarea and narrow and swollen dorsal posterior margin (Mergl, 2019, fig. 4D, E) are the factual basis of identification of the present material with the Late Eifelian species *L. budili* Mergl, 2019.

It is also noteworthy that both Miłoszów and Koněprusy specimens have a characteristic cup-like first-formed shell (protegular section), observed in the posterior-most region of the dorsal valve. In a single dorsal valve from Miłoszów, this structure reaches a width of 84 μ m, has 14 weak radial ribs, a well-marked subperipheral rim, and an apical circular depression. The same structure was described in *L. budili* from Koněprusy by Mergl (2019).

The morphological features of the first formed shell in *L. budili* generally agree with those described in the Devonian linguloids by Baliński (1997, 2001). The structure of pores also fully agrees with that described in the Frasnian–Famennian *Lingulipora* sp. from Poland (Baliński, 1988). Halamski (2009, pl. 1, fig. 1) reported a single, poorly preserved specimen from outcrop SW-6 (Świętomarz-Śniadka section, Givetian), tentatively identified as Pseudolingulidae gen. et sp. indet.; it is over 12 mm long, so at least four times larger than *Lingulipora budili*, and has subparallel lateral margins.



Occurrence: Miłoszów, M2-3, Lower Givetian. The species was described by Mergl (2019) from the Upper Eifelian of the Koněprusy area (grey crinoidal limestone, *Tortodus kockelianus* Zone and limestone of the upper dark interval, *Polygnathus ensensis* Zone, Jirásek's Quarry).

Superfamily Discinoidea Gray, 1840 Family Discinidae Gray, 1840 Genus *Orbiculoidea* d'Orbigny, 1847

Type species: *Orbicula forbesii* Davidson, 1848; Wenlock (Silurian); West Midlands, England.

Orbiculoidea? sp. Fig. 3R

Material: A single subcomplete shell attached to the internal surface of the ventral valve of *Spinulicosta* cf. *spinulicosta* from outcrop M2-3 at Miłoszów.

Remarks: The only specimen available, with exposed dorsal exterior, measures 5.7 mm in length and 5.3 mm in width, is oval in outline with a slightly narrowing posterior half, lowly conical in lateral view, with the apex situated about 1 mm from the posterior margin. Surface is ornamented with fine concentric fila. It is tentatively identified as representing the widely reported genus *Orbiculoidea* d'Orbigny, 1847. Both possible representatives of this genus reported from the Middle Devonian of the Łysogóry Region (*Orbiculoidea*? sp. 1, Błonia Sierżawskie, SW-2, Middle? Givetian; *Orbiculoidea*? sp. 2, Skały, SK-3, Upper Eifelian; Halamski, 2009, pl. 1, figs 2–3, 14) differ in the apex being situated nearer the centre of the shell.

Order Acrotretida Kuhn, 1949 Superfamily Acrotretoidea Schuchert, 1893 Family Biernatiidae Holmer, 1989

Remarks: The original, incorrect spelling of the family name, 'Biernatidae', is corrected herein. The family is based on the genus *Biernatia* Holmer, 1989, so the radical, on which the name should be built, is Biernati-, not Biernat-.

Genus Opsiconidion Ludvigsen, 1974

Type species: *Opsiconidion arcticon* Ludvigsen, 1974; Michelle Formation, early Emsian, Devonian; northern Yukon Territory, Canada. **Remarks:** The oldest representatives of *Opsiconidion* were revealed from the Upper Ordovician of Estonia (Popov, 1981) and the uppermost Ordovician of Podolia in the Kytayhorod section (unpublished data of AB). On the other hand, Langer (1971) noted some high conical ventral valves, probably representing *Opsiconidion*, from the middle Givetian and Frasnian of Germany. The genus was also reported from the Givetian Gobialtai Formation, Shine Jinst region of southern Mongolia (Arno *et al.*, 2010). The collection described here was found in a single conodont sample, representing *Polygnathus rhenanus/varcus–P. ansatus* conodont zones taken from the dark-grey marly limestone of the M2 outcrop in Miłoszów, and thus represents one of the latest occurrences of the genus.

Mergl (2001) rightly observed that the genus *Opsiconidion* is characterised by long stratigraphical and wide geographical ranges. Such a situation is, however, not unusual among inarticulate brachiopod genera; for example, the craniide *Deliella* Halamski, 2004 is known at least from the Ordovician (Mergl, 2012, p. 42) to the Middle Devonian and possibly to the Carboniferous (Halamski, 2004a).

The gender of the genus name *Opsiconidion* is neuter, insofar as it is assimilated to a Greek diminutive in *-ion* (Ludvigsen, 1974, p. 143), which are always of neuter gender (Smyth, 1920, p. 45). The epithet *arcticon* is a Greekstyle neuter adjective, although for the purposes of the Code it has to be treated as indeclinable (ICZN, Art. 31.2.3). *Opsiconidion* has been incorrectly treated as masculine by Popov (1981), Mergl (1982), Mergl and Ferrová (2009), Mergl *et al.* (2018), and Holmer *et al.* (2020).

Opsiconidion cf. arcticon Ludvigsen, 1974 Fig. 3K–Q

- cf. * 1974 Opsiconidion arcticon n. g. n. sp. Ludvigsen, p. 145, figs 4–5.
- cf. 1979 Opsiconidion arcticon Ludvigsen, 1974 von Bitter and Ludvigsen, p. 707, pl. 90, figs 1–12, pl. 91, figs 1–12.
- cf. 1995 Opsiconidion arcticon Ludvigsen, 1974 Brock et al., p. 111, fig. 4A–P.

Material: Five more or less complete and 3 fragmentary dorsal valves, but all with damaged median septum; one ventral valve. All specimens come from acid-treated residues. **Description:** A single revealed ventral valve about 500 µm high, conical; larval shell conical, about 120 µm high, with

Fig. 3. Givetian inarticulate brachiopods (lingulides and acrotretides) from Miłoszów. **A–J.** *Lingulipora budili* Mergl, 2019; A–C – complete shell ZPAL V.74/Bp/1/M2/1 with slightly displaced valves in dorsal and lateral views, and enlargement of the posterior region; D – exterior of the dorsal valve ZPAL V.74/Bp/1/M2/2; arrows indicate pore openings; E – antero-lateral margin of the shell ZPAL V.74/Bp/1/M2/3 (ventral valve below) showing numerous large pore openings visible on the interior surface of the ventral valve; F.– incomplete dorsal valve ZPAL V.74/Bp/1/M2/4 in interior view; G – dorsal valve ZPAL V.74/Bp/1/M2/5 in interior view; H – interior view of the posterior region of the ventral valve ZPAL V.74/Bp/1/M2/6; I – posterior view of the incomplete dorsal valve ZPAL V.74/Bp/1/M2/7 showing a cup-like first formed shell; J – pore viewed from the interior showing a small external opening (specimen ZPAL V.74/Bp/1/M2/8). **K–Q.** *Opsiconidion* cf. *arcticon* Ludvigsen, 1974; K, L – complete dorsal valve ZPAL V.74/Bp/3/M2/1 in interior and lateral view; M – damaged dorsal valve ZPAL V.74/Bp/3/M2/2 viewed from the interior; N, O – ventral valve ZPAL V.74/Bp/3/M2/3 viewed from the exterior and enlarged apical region; P, Q – complete dorsal valve ZPAL V.74/Bp/3/M2/4 in exterior view and enlargement showing larval shell. **R.** *Orbiculoidea* sp. Shell ZPAL V.74/Bp/2/M2/1 in dorsal view. All specimens from outcrop M2-3.

apical circular pedicle opening of 12 μ m diameter; surface of the larval shell with dense circular pits of two size ranges, larger about 5–7 μ m and smaller 1–1.7 μ m in diameter, the latter rather scarce in distribution.

Dorsal valve up to 930 μ m in width, subtrapezoidal in outline, wider than long, widest in the anterior third of the valve, narrowing posteriorly; lateral margins gently curved, anterior margin nearly straight to gently curved; pseudoint-erarea apsacline, 37–63 μ m high, without a clearly defined median plate; valve surface almost flat with a wide and faint sulcus. Dorsal larval shell discoidal, about 150 μ m in diameter, slightly extended beyond the posterior valve margin, clearly raised above the surface of the postlarval valve, with two broad diverging and elongated swellings; surface of larval shell with dense, overlapping and flat-bottomed round pits of one size, usually 5–7 μ m in diameter.

Interior of the ventral valve apparently smooth, without muscle impressions. Dorsal interior with high median septum reaching at the front about 82-87% of the valve length; top of the septum with more or less flattened, widening anteriorly surmounting plate reaching up to 120 µm in width; limbus 20–30 µm wide recognizable on some dorsal interiors.

Both valves ornamented with fine concentric fila (on average 13 per 100 μ m).

Remarks: Poor material and incompletely preserved dorsal interior makes a better taxonomic assessment of the studied specimens difficult. However, the shape of the dorsal valve and length of the dorsal median septum of the form from Miłoszów shows evident resemblance to Opsiconidion nanum Mergl, 2019, described by Mergl (2019) from the Upper Eifelian Acanthopyge Limestone of Jirásek's Quarry of the Koněprusy area. As Mergl (2019) indicated, his new species is distinguished by small shell size not exceeding 500 µm in width and thick-shelled valves. The species reported here differs in being more expanded in width, thinshelled and about twice as large as the former and in having more arched anterior margin. Opsiconidion decessus Mergl, 2001 from the Eifelian of Bohemia (Mergl, 2001, 2019), O. ephemerum (Mergl, 1982), O. bouceki Mergl et al., 2018 and O. parephemerum Mergl et al., 2018 from the Upper Silurian of Bohemia (Mergl, 1982, 2001; Mergl et al., 2018) and O. aldridgei (Cocks, 1979) from the Llandovery of Great Britain (Cocks, 1979) differ from the present specimens mainly in having more rounded dorsal valve. In comparison with specimens from Miłoszów, O. simplex Mergl, 2001 from the Přidoli of Bohemia (Mergl, 2001) has more angular posterolateral margins of dorsal valve and shorter and lower median septum without surmounting plate. The specimens from Miłoszów are also similar in general appearance and in the presence of a median furrow on the surmounting plate to O. minus Popov, 1981 from the Emsian of Novaya Zemlya (Popov, 1981) and from of the Emsian Ogilvie Formation in Alaska and Yukon Territory, Canada (Holmer et al., 2020). The main difference between them is the less rounded posterolateral margins of the dorsal valve, observed in the Polish form.

The present material is most similar to the type species of the genus, i.e., *O. arcticon* Ludvigsen, 1974 described originally from the lower Emsian of the northern Yukon Territory in Canada (Ludvigsen, 1974). Other occurrences of the species were reported from the Lochkovian to Pragian of Australia (Brock *et al.*, 1995) and from the Emsian– Eifelian of Ontario, Canada (von Bitter and Ludvigsen, 1979). Compared to *O. arcticon*, the species from Miłoszów has very similar outline of the dorsal valve, larval shell size and outline, and similarly developed dorsal pseudointerarea. The main noticeable difference between these forms lies in the degree of development of the surmounting plate, which in the type species is poorly developed, but in the specimens of the present authors, it is well formed and wide. Because of the fragmentary state of the available material, no more detailed taxonomic evaluation is possible. **Occurrence:** Miłoszów, M2-3; Lower Givetian; rare.

Subphylum Rhynchonelliformea Williams, Carlson, Brunton, Holmer and Popov, 1996 Class Strophomenata Williams, Carlson, Brunton, Holmer and Popov, 1996 Order Strophomenida Öpik, 1934 Superfamily Strophomenoidea King, 1846 Family Rafinesquinidae Schuchert, 1893 Subfamily Leptaeninae Hall and Clarke, 1894a Genus *Leptagonia* M'Coy, 1844

Type species: *Producta analoga* Phillips, 1836; lower Visean; probably Bolland, Yorkshire.

- v* 1966 *Leptaena analogaeformis* n. sp. Biernat, pp. 38–42, text-figs 6, 7, pl. 3, figs 1– 16, pl. 4, figs 1–13.
- v. 2009 Leptagonia analogaeformis (Biernat, 1966)
 Halamski, pp. 50–52, text-figs 2, 3, pl. 1,
 figs 16–19, 21–23, 25, pl. 2, figs 1–12, 14,
 15, 17, pl. 16, figs 19–22, 29 [ubi syn.].
- v. 2022b Leptagonia analogaeformis Halamski et al., fig. 27–3.

Material: Four nearly complete and 24 fragmentary specimens, most of them embedded in rock, collection number ZPAL V.74/Bp/4.

Description: See Biernat (1966) and Halamski (2009).

Remarks: The holotype of *L. analogaeformis* is from the Upper Eifelian of Skały (Biernat, 1966; Halamski and Zapalski, 2006), but the species occurs also in the entire Skały Formation (Upper Eifelian to Middle Givetian; Skały, Miłoszów, Świętomarz; Biernat, 1966; Halamski, 2009).

The present material from Miłoszów fully corresponds to specimens, described by Biernat (1966, pl. 4, figs 1–4) from the same locality. It is worth noting that, in comparison with specimens from the Upper Eifelian of Skały, those from the Givetian of Miłoszów have slightly finer concentric rugae. The density of the concentric rugae measured in 10 mm at the anterior region of adult shells of *L. analogaeformis* ranges from 4 to 6 in specimens from Skały, 6–8.5 in Miłoszów, 6–10 in Maïder and 4–5 in Mauritania. As Biernat (1966) and Halamski and Baliński (2013) remarked, the density of



Fig. 4. Givetian strophomenide brachiopods from Miłoszów. **A–C, E–H.** *Parastrophonella anaglypha* (Kayser, 1871) from outcrop M1-IIa at Miłoszów or equivalent strata; A – articulated shell ZPAL V.74/Bp/10/MP/1; B, G – fragmentary dorsal valve ZPAL V.74/Bp/10/MP/3, general view (B) and enlargement of the cardinalia (G); C, H – fragmentary ventral valve ZPAL V.74/Bp/10/MP/3, general view (C) and enlargement of the posteromedian region (H); E, F – fragmentary dorsal valve ZPAL V.74/Bp/10/M1/4, general view (C) and enlargement of the cardinalia (F). **D, I–K, N.** *Leptagonia analogaeformis* (Biernat, 1966); D, I – interior of the ventral valve ZPAL V.74/Bp/4/M3/1 in general (I) and enlarged (D) views; outcrop M3-7; J, N. – dorsal interiors ZPAL V.74/Bp/4/M2/3, 4; outcrop M2; K – ventral valve ZPAL V.74/Bp/4/M3/2 embedded in limestone. Outcrop M3-7. L, M, O, P. *Radiomena irregularis* (Roemer, 1844); L, M–ventral valve ZPAL V.74/Bp/7/M0/1 embedded in limestone; outcrop M0; O, P–dorsal interior ZPAL V.74/Bp/7/MS2/2; trench S2. **Q–U.** *Gibbodouvillina interstrialis* (Phillips, 1841); Q, R, S – ventral valve ZPAL V.74/Bp/5/M1/1 embedded in limestone and enlargement of the ornamentation; outcrop M1-I; T, U – ventral valve ZPAL V.74/Bp/5/M3/2 embedded in limestone in lateral and ventral views; outcrop M3.

concentric rugae is apparently a variable character within this species.

Occurrence: Middle Devonian of the Holy Cross Mountains (outcrops M0 bed 9, M2, M3 in Miłoszów; Skały, Świętomarz), Eifel, Sauerland, Maïder, and Mauritania; possibly also Inner Mongolia and Japan (Chen and Tazawa, 2003).

Family Douvillinidae Caster, 1939| Subfamily Protodouvillininae Harper and Boucot, 1978 Genus *Gibbodouvillina* Jansen, 2014

Type species: *Strophomena taeniolata* Sandberger and Sandberger, 1856; Upper Emsian; Rhenish Slate Mountains (see Jansen, 2014, p. 128 for details).

Gibbodouvillina interstrialis (Phillips, 1841) Fig. 4Q–U

- * 1841 Orthis interstrialis, Leptaena interstrialis Phillips, pp. 61–62, pl. 25, fig. 103a–e.
- v. 2009 *Protodouvillina interstrialis* (Phillips 1841) – Halamski, pp. 53–54, text-fig. 4, pl. 3, figs 1–6, 8–17, 19–20, 30–32 [*ubi syn.*].

Material: A single subcomplete shell, embedded in limestone, ten fragments of articulated shells, one dorsal and one ventral interior, ZPAL V.74/Bp/5/M1; seven shells mostly embedded in limestone, ZPAL V.74/Bp/5/M3.

Description: Shell semi-elliptic in outline, concavo-convex, up to ca. 35 mm in width. Hinge line straight. Ventral interarea apsacline, dorsal one hypercline. Ornament parvicostellate; 3–8 striae between each two costellae, usually 4–8 striae per mm at anterior margin.

Ventral interior: muscle area piriform, medially indented, postero-laterally enclosed by distinct, straight ridges, medially bisected by a low ridge; ventral process strong; a single paradental plate parallel to the hinge line observed.

Dorsal interior: cardinal process bifid, lobes subdichotomous, attachment surface directed posteroventrally; laterally accompanied by a pair of short socket ridges; brachiophores stout, separated from the cardinal process, incurved towards the plane of symmetry; pair of medial septa diverging at an angle of ca. 10° present.

Remarks: The material at hand is not numerous, but the presence of both interiors allows secure identification. The pair of dorsal medial septa (see Biernat, 1966, pl. 5, fig. 11; Halamski, 2009, pl. 3, fig. 32) was observed externally in a decorticated specimen, but not in the single available interior; its absence has already been observed (Halamski, 2009, pl. 3, fig. 31). Only a single paradental plate, a diagnostic feature of *Gibbodouvillina*, was observed (not preserved in the ventral interior figured by Halamski, 2009, pl. 3, fig. 30); this structure is easier to find on internal moulds.

The bilobed cardinal process is postero-ventrally directed (Williams, 1953, fig. 2), a feature insufficiently known in the type species of the genus, *G. taeniolata*, where the direction of the cardinal process was described as posterior on the basis of a single specimen (Jansen, 2014, p. 126).

Distribution: Miłoszów: M1, M3. Other occurrences from the Holy Cross Mts. were discussed by Halamski (2009). *G. interstrialis* was reported from the Devonian of several regions (Brice, 1970; Halamski, 2009 and references therein), but lacks a comprehensive revision; the lectotype of this species is an incomplete articulated shell (Halamski, 2009, pl. 3, fig. 21).

Genus Radiomena Havlíček, 1962

Type species: *Orthis irregularis* Roemer, 1844; Middle Devonian; Gerolstein, Eifel.

Radiomena irregularis (Roemer, 1844) Fig. 4L, M, O, P

- 1844 Orthis irregularis mihi Roemer, p. 75, pl. 4, fig. 1a–c.
- v. 2013 Radiomena irregularis (Roemer, 1844) Halamski and Baliński, p. 252, fig. 4N–V [ubi syn.].

Material: One incomplete articulated shell ZPAL V.74/ Bp/7/M1/1M0/1 and two fragmentary specimens 74/Bp/7/ M1/1, 74/Bp/7/S2/1.

Remarks: A characteristic and widely distributed largeshelled species, revised by Harper *et al.* (1967), Halamski (2009; see especially for other occurrences in the Holy Cross Mts.), and Halamski and Baliński (2013). The best specimen from Miłoszów is about 56 mm wide.

Distribution: Miłoszów: M0 and M1. Europe, northern Africa, and Burma; Middle Devonian (Harper *et al.*, 1967; Halamski, 2009; Halamski and Baliński, 2013).

Genus Parastrophonella Bubličenko, 1956

Type species: *Strophomena anaglypha* Kayser, 1871; Crinoiden-Schicht, Middle Devonian (probably Eifelian); Prüm Syncline, Eifel, Germany.

> Parastrophonella anaglypha (Kayser, 1871) Fig. 4A–C, E–H

- v* 1871 Strophomena anaglypha Kayser, pp. 628– 629, pl. 14, fig. 3 a–f.
- v. 2009 Parastrophonella anaglypha (Kayser 1871) – Halamski, pp. 60–62, text-fig. 7, pl. 5, figs 1–5, 9–13, 16–20, 23–27, 30–47 [ubi syn.].

Material: Six fragmentary shells, ZPAL V.74/Bp/10/M3. **Remarks:** A characteristic and widely distributed species; the occurrences in the Holy Cross Mts. were discussed in detail by Halamski (2009).

Distribution: Miłoszów: M3. Europe, northern Africa; Middle Devonian (Harper and Boucot, 1978; Halamski, 2009, Halamski and Baliński, 2013, and references therein).

Order Productida Sarytcheva and Sokolskaya, 1959 Suborder Chonetidina Muir-Wood, 1955 Family Anopliidae Muir-Wood, 1962 Genus *Devonaria* Biernat, 1966

Type species: Chonetes zeuschneri Sobolew, 1909; Skały Formation, Upper Eifelian; Skały, Holy Cross Mts.

Devonaria zeuschneri (Sobolew, 1909) Fig. 5U

- * 1909 Chonetes Zeuschneri n. sp. Sobolew, pp. 444–446.
- v. 1966 *Eodevonaria* (*Devonaria*) *zeuschneri* (Sobolev, 1909) – Biernat, pp. 77–82, textfigs 24–26, pl. 15, figs 1–17, pl. 16, figs 1–16.
- v. 2009 Devonaria zeuschneri (Sobolew 1909) Halamski, pp. 62–63, text-fig. 8, pl. 2, figs 16, 18–22, pl. 6, figs 12–37 [ubi syn.].

Material: Seven ventral valves embedded in limestone, out of which two subcomplete, two incomplete, and three fragmentary ones, ZPAL V.74/Bp/9.

Description: See Biernat (1966) and Halamski (2009).

Remarks: Species of *Devonaria* differ mainly in ornament density (Halamski *et al.*, 2022a). The sample from Miłoszów with shells 12–15 mm wide and having about 35 ventral ribs falls within the variability of *D. zeuschneri* (Halamski, 2009, text-fig. 8).

Distribution: Miłoszów: M0-9. Skały, outcrop SK-3, Upper Eifelian (type locality), abundant. Świętomarz, outcrop SW-2, (Middle?) Givetian, seldom. Species known solely from the northern region of the Holy Cross Mountains.

Material: Two incomplete ventral valves, embedded in limestone, ZPAL V.74/Bp/61/M3.

Description: Ventral valve semi-elliptic in outline, up to 3 mm long, transverse (width-to-length ratio about 2.3), strongly convex (length-to-thickness ratio about 1.7), but less so laterally. Hinge line straight, spines not observed. Ornament of radial ribs, new ones appearing by bifurcation, about 8 per mm at anterior margin; traces of faint growth lines observed anteriorly. Interior unknown.

Remarks: These brachiopods are tentatively included into the family Anopliidae on account of their very small-sized, strongly convex strophic shells. The material at hand does not allow a more precise identification. In comparison with the three small-sized anopliids reported by Halamski (2009) from the Givetian of the Świętomarz–Śniadka section (*Devonaria* cf. *minutissima* Struve, 1981; *Holynetes* sp. 1; '*Chonetes*' aspera Gürich, 1896), the representatives of this family from Miłoszów are distinctly more transverse. *Devonaria zeuschneri* (Sobolew, 1909) is larger and more equally convex (lateral extremities not flattened; Biernat, 1966; Halamski, 2009).

Distribution: Miłoszów: M3λ.

Family Chonetidae Bronn, 1862 Subfamily Dagnachonetinae Rachebœuf, 1981 Genus *Luanquella* García-Alcalde & Rachebœuf, 1978

Type species: *Luanquella cantabriensis* García-Alcalde & Rachebœuf, 1978; Upper Emsian; Cantabrian Mts., Spain.

Species assigned: See Rachebœuf (1998, pp. 69–70).

Luanquella cf. vanigibbosa (Havlíček, 1978) Fig. 5S, T

cf. * 1978 Chonetes vanigibbosus sp. n. – Havlíček, pp. 64–65, pl. 14, figs 8–12.

Material: Four subcomplete ventral valves, embedded in limestone, ZPAL V.74/Bp/60.

Description: Ventral valve semi-elliptic in outline, up to about 15 mm in length, transverse (width-to-length ratio about 1.6 in the largest specimen, about 1.75 in two shells slightly over 8 mm long). Cardinal margin straight, with single spine bases in two specimens, in each case about 5 mm from the umbo, insertion oblique. Ventral valve moderately convex in umbonal region (length-to-thickness ratio approximately 3–4.5 in the two larger specimens), flattened laterally, with a very shallow U-shaped sulcus developed anteriorly in specimens over 10 mm long.

Ornament of radial ribs covering the entire valve, separated by narrower interspaces, new ones appearing by bifurcation. Ribs of approximately same width for their entire length, 6–8 per 2 mm at 5 mm from the umbo, crossed by numerous well developed, very fine concentric fila, the latter 7–11 per mm.

Traces of a narrow ventral median septum observed in the delaminated posterior fourth of a single valve; otherwise, interior unknown.

Remarks: These brachiopods are included into the subfamily Dagnachonetinae on account of strophic shells with spines inserted solely on the hinge line and ornament consisting of fine ribs (with no thickened median rib) crossed by concentric fila (Rachebœuf, 1998, p. 68; 2000, p. 394). They are further included into the genus *Luanquella* on account of ribs being of the same thickness posteriorly and anteriorly (ribs thinning anteriorly in *Dagnachonetes*; Rachebœuf, 1998, p. 68–69; 2000, p. 394–395).

The sample of the present authors is similar to *Luanquella vanigibbosa* described from the Givetian of Čelechovice in Moravia (Havlíček, 1978) in shell size and ornament density. However, the Moravian species is described as having a ventral sulcus beginning at umbo and slightly less transverse shells (width-to-length ratios quoted 1.45, 1.56). Specimens at our disposal come from two outcrops, the two from the bed 9 at M0 are larger and less transverse, whereas the two from M3 λ are smaller and more transverse. The sample is too small to decide whether any of the above-mentioned differences are of taxonomic value.

The three species of *Luanquella* known from the Upper Emsian of Brittany and Cantabrian Mts. are more different from the present sample (data after Rachebœuf, 1981): *L. henryi* (Rachebœuf, 1981) is smaller (maximum length 9.5 mm in a sample of 93 specimens), *L. alcaldei* (Rachebœuf, 1981) has finer capillae (8–10 per 2 mm), and in *L. cantabriensis* the shell is wider (length-to-width ratio slightly over 2). *Dagnachonetes supragibbosus* (Sobolew, 1909) from the Upper Eifelian of Skały is larger, has a higher shell, and a relatively deep ventral sulcus (Biernat, 1966; Halamski, 2009). *Dagnachonetes bretzii* (Schnur, 1853) and *D. planus* (Schnur, 1853) are difficult to compare because of the insufficiently detailed descriptions.



Fig. 5. Givetian productides and orthotetides from Miłoszów. **A–P.** *Spinulicosta* cf. *spinulicosta* (Hall, 1857); A–E – articulated shell ZPAL V.74/Bp/6/M3/2 in dorsal, ventral, lateral, posterior, and anterior views; F – ventral valve ZPAL V.74/Bp/6/M2/3 embedded in limestone; G–I, J–L, N–P – ventral valves ZPAL V.74/Bp/6/M3/4, 5 and 6/M2/6 embedded in limestone in ventral, lateral, and anterior views; M – dorsal valve ZPAL V.74/Bp/6/M3/7 from outcrop M3-7 embedded in limestone. **Q.** *Iridistrophia* cf. *undifera* (Schnur, 1854 in 1853–54); incomplete ventral valve ZPAL V.74/Bp/8/M2/1 embedded in limestone (specimen figured also in Halamski *et al.*, 2022b, fig. 22DD); outcrop M2-1. **R.** Strophalosioidea fam, gen. et sp. indet. Fragmentary ventral valve ZPAL V.74/Bp/11/M2/1 attached on a ventral valve of *Septalaria gracilis* (Gürich, 1896) from outcrop M2 (compare Fig. 18Q, S). **S, T.** *Luanquella* cf. *vanigibbosa* (Havlíček, 1978); ventral valves ZPAL V.74/Bp/60/M0/1, 2 embedded in limestone; outcrop M0-9. **U.** *Devonaria zeuschneri* (Biernat, 1966); ventral valve ZPAL V.74/Bp/9/M0/1, embedded in limestone; outcrop M0-9. **V.** Anopliidae indet.; ventral valve ZPAL V.74/Bp/61/M0/1 from outcrop M0-9.

Distribution: Miłoszów: M0-9, M3λ. *Luanquella vanigibbosa* is known solely from the Givetian of Čelechovice.

> Suborder Productidina Waagen, 1883 Superfamily Productoidea Gray, 1840 Family Productellidae Schuchert, 1929 Genus *Spinulicosta* Nalivkin, 1937

Type species: *Productus spinulicostæ* Hall, 1857; Hamilton Group, Givetian (Middle Devonian); shores of Cayuga Lake, New York, USA.

Remarks: The original spelling of the type species of *Spinulicosta* is *"Productus spinulicostæ"* (Hall, 1857, p. 173). In a subsequent publication Hall (1867) spelt the name of his species as *"Productella spinulicosta"*, so we treat the original spelling as a *lapsus calami*.

Spinulicosta cf. spinulicosta (Hall, 1857) Figs 5 A-P, 6

- cf. 1857 Productus spinulicostæ (n. s.) Hall, p. 173.
- cf. 1867 *Productella spinulicosta* Hall, p. 160, pl. 23, figs 6–8, 25–34.
- cf. 1960 Spinulicosta spinulicosta (Hall) Muir-Wood and Cooper, pl. 32, figs 1–4.
- cf. 1960 Spinulicosta cf. S. spinulicosta (Hall) Muir-Wood and Cooper, pl. 33, fig 1–5.
- non 1975 Spinulicosta spinulicosta (Hall, 1857) rousmiche, pp. 123–127, pl. 1, figs 4, 5, text-fig. 1.
- non 1983 Spinulicosta spinulicosta (Hall 1857) Rachebœuf, p. 154–156, pl. 3, figs 2–21.
- cf. 2015 Spinulicosta spinulicosta (Hall, 1857) Gourvennec and Hoşgör, p. 585, fig. 5A–H.
- v. 2022b Spinulicosta cf. spinulicosta (Hall, 1857) Halamski et al., fig. 22R.

Material: Nearly a hundred specimens, of varying degrees of incompleteness and decortication, usually embedded in the rock, a few fragments of free shells, collection number ZPAL V.74/Bp/6.

Description: Shell concavo-convex, typically about 15–18 mm wide (maximum recorded width 24.6 mm), wider than long (width-to-length ratio about 1.2–1.4). Ventral valve: short concentric growth lamellae, few rugae posteriorly; scattered spines arising from short spine ridges, the latter in a few rare shells poorly developed. Dorsal valve: spines none, concentric short lamellae and scattered dimples present.

Ventral interior: delicate and small hinge teeth (Fig. 6). Dorsal interior: strong bilobate cardinal process and a low median septum; the cardinal process is separated from the median septum by a shallow, but clear pit.

Remarks: This productide is included into *Spinulicosta* Nalivkin, 1937 on account of the presence of elongate spine bases and short radial ribs, the latter especially well developed anteriorly on several large shells (Fig. 5F, N–P), even if in a few shells the spine ridges are poorly developed, mimicking the ornament of *Productella*. The

most common productide in the Middle Devonian Skały Formation [*Poloniproductus varians* (Biernat, 1966); see Biernat, 1966; Biernat and Lazarev, 1988; Halamski, 2009] differs in having more numerous spines, quincuncially arranged and without spine ridges.

Spinulicosta spinulicosta (Hall, 1857) the type species of the genus, is similar in shape and ornament to the present material but differs in being less transverse: specimens figured by Muir-Wood and Cooper (1960) have width-tolength ratios about 1.1. Spine bases in the Hamilton species seem stronger than in the present shells. Given that no detailed description of the New York species exists on the one hand and the generally unsatisfactory state of preservation of the studied material on the other hand, open nomenclature is used. Gourvennec and Hoşgör (2015) treated *S. spinulicosta* widely, when dealing with brachiopods from the Middle to Upper Devonian boundary beds in Turkey; their specimens seem similarly more transverse (like those from Miłoszów) compared to those from Hamilton.

Another representative of the genus, showing notable similarity to brachiopods from Miłoszów, is *Spinulicosta* sp. described by Brice and Latrèche (1998) from the upper Givetian of Eastern Algerian Sahara. Both forms may be conspecific although the former appears to have less strong radial ribbing.

Other species of *Spinulicosta* are more different. *Spinulicosta navicella* (Hall, 1857) is also less transverse than the specimens from Miłoszów (Muir-Wood and Cooper, 1960, pl. 33, figs 6–17), sometimes even longer than wide (Hall, 1867, pl. 23, figs 9, 10). *S. costatula* (Hall, 1867) is even more elongate (Hall, 1867, pl. 26, figs 9–15). Large shells of *S. arctirostrata* (Hall, 1857) have a median depression in the ventral valve (Hall, 1867, pl. 26, figs 22, 28), a feature altogether absent in the Miłoszów material. *Spinulicosta muirwoodi* Johnson, 1971, *S. stainbrooki* Crickmay, 1960, and *S. prima* Chatterton and Perry, 1978 have stronger ribs or spines.

Spinulicosta hamata Mergl and Massa, 1992 from the Givetian-Frasnian boundary beds of western Libya



Fig. 6. Transverse serial sections of *Spinulicosta* cf. *spinulicosta* (Hall, 1857) through the shell ZPAL V.74/Bp/6/M3/1 from outcrop M3-7. Distances measured in millimetres from the tip of the ventral umbo.

(Mergl and Massa, 1992) differs from the present specimens in the smaller shell size and by having a row of spines in the mid-sector of the ventral valve, which is not observed in the Polish form. *Spinulicosta spinulicosta*, described by Brousmiche (1975) from the upper Givetian–lower Frasnian of Morocco and by Rachebœuf (1983) from the upper Eifelian of the Mid-Armorican Synclinorium (Brittany, France), differ from the specimens studied here in more dense spines, more distinct concentric lamellae and weaker elongated spine bases. Externally, the Moroccan and Armorican specimens seem to represent more the genus *Poloniproductus* Biernat and Lazarev, 1988.

Occurrence: It is fairly common in marly limestone intercalations at the M2 and M3 localities, but is usually represented by fragmented and partially exfoliated specimens.

> Suborder Strophalosiidina Schuchert, 1913 Superfamily Strophalosioidea Schuchert, 1913 Strophalosioidea fam., gen. et sp. indet. Fig. 5R

Material: A single fragmentary ventral valve, attached to the postero-lateral region of the ventral valve of *Septalaria* cf. *descendens* Schmidt, 1975.

Description: Ventral valve about 2.3 mm wide and 2.2 mm long, cemented to the shell of another brachiopod by an extensive cicatrix and a few thin, about 1.5 mm long, rhizoid and radiating spines, with two of them at the hinge line, with a distinct interarea attaining about 0.6 of the total width of the cicatrix. Psudodeltidium and teeth present.

Remarks: This fragmentarily preserved brachiopod is included into the superfamily Strophalosioidea Schuchert, 1913 on account of the presence of the cicatrix and radiating cementing spines. As no complete specimen is available, further identification can be tentative at best. Middle Devonian *Devonalosia* Muir-Wood and Cooper, 1960 and *Auchmerella* Struve, 1964 (family Araksalosiidae Lazarev, 1989) have thicker and more numerous spines and usually are more transverse (García-Alcalde, 1973, 2012; Halamski, 2009). Approximately equidimensional shell and thin spines are suggestive of *Leptalosia* Dunbar and Condra, 1932 belonging to the family Strophalosiidae Schuchert, 1913, which is, however, known to occur only in the Carboniferous (Brunton *et al.*, 2000).

Occurrence: The specimen was found in the M2 (bed 2) outcrop in Miłoszów.

Order Orthotetida Waagen, 1884 Suborder Orthotetidina Waagen, 1884 Superfamily Chilidiopsoidea Boucot, 1959 Family Chilidiopsidae Boucot, 1959 Subfamily Chilidiopsinae Boucot, 1959 Genus *Iridistrophia* Havlíček, 1965

Type species: *Orthis umbella* Barrande, 1848; Lochkovian; Bohemia.

Iridistrophia cf. undifera (Schnur, 1854 in 1853–54) Fig. 5Q

- cf. * 1854 *Orthis undiferus* Schnur, p. 217, pl. 45, fig. 1 a–d.
- v. 2009 Iridistrophia cf. undifera (Schnur 1854 in 1853–54) Halamski, pp. 71–72, pl. 8, figs 1–11, pl. 16, figs 5–7, 11, 12, 16.
- v. 2022b *Iridistrophia* cf. *undifera* (Schnur 1854) Halamski *et al.*, p. 353, fig. 22DD.

Material: Seven fragmentary specimens from M2 α and a single fragmentary one from M0-9, ZPAL V.74/Bp/8.

Description: Shell probably up to at least 60 mm in width (size of the largest preserved fragment ca. 50 mm), strophic, concavo-convex. Ornament of subequal smooth radial ribs, 8–11 per 5 mm. Interior unknown.

Remarks: *Iridistrophia undifera* is a poorly understood species from the Middle Devonian of the Eifel (type material lost; see Halamski, 2009); the identification of the material from SW-2 by Halamski (2009; dorsal interiors partly known) was tentative, and the identification of the material from Miłoszów is in its turn based on similarities with the shells from the nearby Świętomarz–Śniadka section.

Distribution: At Miłoszów, *Iridistrophia* cf. *undifera* is common in a single limestone layer (M2 α) in which it is the most frequent, indeed almost the only brachiopod species present. A single specimen comes from the bed 9 at M0. Other occurrences in the Holy Cross Mts. were listed by Halamski (2009); they include the (Middle?) Givetian of Błonia Sierżawskie near Świętomarz (SW-2) and other localities in the Świętomarz–Śniadka section (beds 5a, 6 *sensu* Sobolew, 1909; material examined, MNKhU Pal-*Sobolew* 688, 699).

Class Rhynchonellata Williams et al., 1996 Order Protorthida Schuchert and Cooper, 1931 Superfamily Skenidioidea Kozłowski, 1929 Family Skenidiidae Kozłowski, 1929 Genus *Skenidioides* Schuchert and Cooper, 1931

Type species: *Skenidioides billingsi* Schuchert and Cooper, 1931; Black River Formation, Sandbian, Upper Ordovician; near the Ottawa River, Québec, Canada.

Remarks: The material of *Skenidioides* from Miłoszów (MI and M2) consists of sixteen measurable specimens and a few fragments. The measurable specimens can be divided into two morphotypes: strongly transverse shells with relatively coarse ornament (ratio of the number of dorsal ribs to shell width 1.87–2.95, mean 2.32, N = 12) and weakly transverse shells with finer ribbing (ratio of the number of dorsal ribs to shell width 3.83–6.80, mean 5.04, N = 4). The two samples are described below as separate species; graphical comparison is given in Figure 8.

Skenidioides cretus was interpreted as an evolutionary descendant of *S. polonicus* (Baliński *et al.*, 2016). However, given that the presumed ancestor, the Upper Eifelian to Givetian *S. polonicus* is present at Miłoszów in stratigraphically younger strata (M2) than the presumed descendant species, the Givetian to Frasnian *S. cretus* (M1), anagenesis can be excluded. The relationship between *S. polonicus* and *S. cretus* corresponds probably rather to the budding cladogenesis model (see, e.g., de Wever *et al.*, 2010, p. 464),

in which a descendant species (*S. cretus*, Lower Givetian to Lower Frasnian) arises from an ancestor species (*S. polonicus*, Upper Eifelian to Middle Givetian), the latter remaining unchanged. There are no data to say if the cladogenesis was gradual or punctual.

Skenidioides cretus Halamski in Baliński et al., 2016 Figs 7K–Y, CC–FF, 8

v* 2016 *Skenidioides cretus* Halamski sp. nov. – Baliński *et al.*, pp. 138–140, text-fig. 6, pl. 6, figs 1–30.

Material: Twelve variously preserved articulated shells, and a few fragments, ZPAL V. 54/Bp/12.

Description: Shell hemipyramidal [thickness-to-length ratio (0.51-)0.69-0.82(-1.05); N = 10], transverse [width-to-length ratio (1.19-)1.36-1.77(-2.25); N = 11], up to about 7 mm in width, typically 4.5–5.9 mm wide, 3.2–4.0 mm long, and 2.2–2.8 mm thick. Hinge line slightly less than or equal to the maximal shell width, postero-later-al extremities mucronate, anterior commissure ventrally deflected. Ventral valve rounded triangular in anterior view; interarea high, apsacline, catacline, or procline, flat or weakly to more seldom markedly concave; delthyrium occupying about one fourth of the interarea width. Dorsal valve nearly flat, medially shallowly grooved; interarea very low, anacline; dorsal valve length-to-total length ratio (0.79-)0.89-1.00 (N = 12).

Ornament of rounded ribs, the number of those on the dorsal valve (11–)12–13(–15) [N = 12]; often a single thickened median dorsal rib with weak median furrow present. Ratio of the number of dorsal ribs to width (1.87–)2.06– 2.60(–2.95) [N = 12].

Ventral interior: Spondylium relatively close to the interarea, extending to about half of the delthyrium length; otherwise not studied. Dorsal interior: Cardinal process and brachiophores visible through the delthyrium; otherwise not studied.

Remarks: These brachiopods are tentatively included in *Skenidioides* on account of their minute, impunctate, hemipyramidal shells with a spondylium and a cardinal process continuous with the median septum. Given their transverse outline, relatively small number of ribs, frequent presence of a strong dorsal median rib, relatively high ventral interarea, and a relatively wide delthyrium, they are identified as *S. cretus*, a species described from the Lower Frasnian of Józefka in the southern Holy Cross Mts. (Baliński *et al.*, 2016). A comparison with *Skenidioides polonicus* (Gürich, 1896) from M1 is given above (Remarks on the genus, Fig. 8).

Skenidioides cretus is interpreted as an evolutionary descendant of *S. polonicus*. The available sample is too small for a formal comparison between the two subsamples coming from levels M1-IIa and M2 β + δ , but a difference in costation can be noted. The three shells from the latter level have 17, 18, and 20 costae, whereas in the former there is a single specimen with 18 costae and ten specimens with 11–15 costae.

Brachiopods from the Eifelian of Inner Mongolia, identified by Zhang (1985) as *S. polonicus* are close to *S. cretus* in having 14–18 ribs and relatively high ventral interareas, but a detailed comparison is not possible.

Distribution: Miłoszów, Ml-IIa, Givetian. Józefka, Lower Frasnian.

- v* 1896 Skenidium polonicum Gürich, pp. 237– 238, pl. 10, figs 3, 14.
- v. 2009 Skenidioides polonicus (Gürich 1896) Halamski, pp. 72–74, text-fig. 10, pl. 10, figs 1–38, pl. 12, fig. 30 [ubi syn.].
- v. 2022a Skenidioides polonicus (Gürich, 1896) Halamski et al., pp. 16–17, figs 8, 9 [ubi syn.].

Material: Three variously preserved articulated shells, a single dorsal valve, and a few fragments, ZPAL V. 54/Bp/62.

Description: Shell lowly hemipyramidal [thickness-tolength ratio 0.48–0.65; N = 3], weakly transverse [widthto-length ratio 1.14–1.47; N = 3], 2.5–4.9 mm wide, 1.7– 4.0 mm long, and 1.1–1.9 mm thick. Hinge line slightly less than or equal to the maximal shell width, postero-lateral extremities auriculate, anterior commissure ventrally deflected. Ventral valve rounded triangular in anterior view; interarea moderately high, apsacline to weakly procline, straight flat or weakly incurved concave. Dorsal valve nearly flat, medially shallowly grooved; interarea very low, anacline [dorsal valve length-to-total length ratio 0.83–1.00; N = 3].

Ornament of fine ribs, the number of those on the dorsal valve 17-20 [N = 4]; in the middle a weak midrib pair starting at some distance from the umbo. Ratio of the number of dorsal ribs to width 3.83–6.80 [N = 4].

Ventral interior unknown. Dorsal interior: Cardinal process continuous with the median septum, the latter occupying about 0.8 of the valve length; brachiophores relatively narrow, divergent; sockets shallow, septalium shallow.

Remarks: These brachiopods are included in *Skenidioides* on account of their minute, impunctate, hemipyramidal shells with a septalium and a cardinal processes that is continuous with the dorsal median septum. They are described as *S. polonicus* on account of their moderately transverse and relatively finely ribbed shells with a dorsal midrib pair.

Distribution: Miłoszów, M2-2 (β + δ), three specimens; M1-IIa, a single specimen; Givetian. Skały, Upper Eifelian (Biernat, 1959). Świętomarz-Śniadka section, (Middle?) Givetian (Halamski, 2009 and references therein). Northern Africa, Maïder and Drâa valley, (Upper Eifelian? to) Givetian (Drot, 1961; Halamski *et al.*, 2022a).

> Order Orthida Schuchert and Cooper, 1931 Suborder Dalmanellidina Moore, 1952 Superfamily Dalmanelloidea Schuchert, 1913 Family Rhipidomellidae Schuchert, 1913 Subfamily Rhipidomellinae Schuchert, 1913 Genus *Aulacella* Schuchert and Cooper, 1931





Comparison of biometric characters of the two spe-Fig. 8. cies of Skenidioides present in the Lower Givetian of Miłoszów. A. Number of dorsal ribs to width. B. Number of dorsal ribs to width-to-length ratio.

Type species: 'Orthis eifeliensis Schnur, 1853' (misspelling for eifliensis; = Orthis prisca Schnur, 1851), Middle Devonian; Eifel, Germany.

Aulacella prisca (Schnur, 1851) Fig. 9K-O

- O[rthis] prisca nob. Schnur, p. 13 v* 1851
- 1959 Aulacella eifeliensis (de Verneuil) - Biernat, v. pp. 26-35, text-figs 9, 10, text-pl. 3, pl. 1, figs 10-15, pl. 2, figs 1-15, pl. 3, figs 9, 10, pl. 12, figs 1, 2.
- Aulacella prisca (Schnur, 1851) Halamski, 2009 v. pp. 74-77, text-fig. 11, pl. 11, figs 1-36, pl. 14, figs 3-10, 13-16, 21-27, 29, 30 [ubi syn.].
- 2013 Aulacella prisca (Schnur, 1851) - Halamski v. and Baliński, pp. 257-258, fig. 7A-M.

Material: Over twenty articulated shells, ZPAL V.74/Bp/14. Remarks: This is the most common species in the Middle Devonian of the northern region of the Holy Cross Mts. Its morphology and variability were described by Biernat (1959) and Halamski (2009).

Distribution: Miłoszów: M1-IIa, M2, M3. Otherwise Eifelian and Givetian of Europe, Africa, and Asia (Halamski and Baliński, 2013 and references therein).

Family Mystrophoridae Schuchert and Cooper, 1931 Genus Mystrophora Kayser, 1871

Type species: Orthis areola Quenstedt, 1871; Middle Devonian; Eifel, Germany. Species assigned: see García-Alcalde (2018, p. 61).

Mystrophora areola (Quenstedt, 1871) Figs 9F-J, 10

- 1871 Orthis areola – Quenstedt, p. 589, pl. 57, fig. 27.
 - 1871 Mystrophora areola Quenstedt - Kayser, pp. 612–614, pl. 13, fig. 5.
 - 1882 Skenidium areola, Quenstedt, sp.? - Davidson, pp. 49-50, pl. 3, figs 11-14.
 - 1885 Skenidium areola Quenst. - Maurer, pp. 141–142, pl. 5, 12–13.
- 1904 Skenidium areola Quenstedt - Sobolew, non p. 63 [= Biernatium fallax; see Sobolew, 1909, p. 455].
 - Scenidium areola Quenstedt Torley, p. 33, 1908 pl. 7, figs 7, 8, pl. 8, fig. 1.
 - 1932 *Mystrophora* areola (Quenstedt) Schuchert and Cooper, pp. 131-132, text-figs 20, 21, pl. 16, figs 1-5.
 - 1934 Skenidium areola (Quenstedt) - Torley, pp. 126-127, pl. 8, fig. 67 [ubi syn.].
 - Mystrophora areola (Quenstedt) Cooper, 1955 pp. 48-50, pl. 11, figs 39-50.
 - 1969 Mystrophora areola (Quenstedt 1871) -Anderson et al., p. 124, pl. 1, figs 18-22.
 - 1969 Mystrophora areola – Boucot et al., pl. 2, figs 1-6.

Material: Nine articulated shells, six of which are complete, and a single dorsal valve, ZPAL V.74/Bp/16.

Description: Shell up to 14.6 mm in width, strongly ventribiconvex, transverse (width-to-length ratio 1.18-1.29, N = 3). Anterior margin medially indented in dorsal view, gently unisulcate in anterior view, sulcation V-shaped. Ventral valve hemipyramidal; interarea concave, apsacline, with a wide open delthyrium (its width being usually over

Fig. 7. Representatives of the protorthide genus Skenidioides from the Givetian of Miłoszów. A-J, Z-BB. Skenidioides polonicus (Gürich, 1896) from outcrop M2-2; A-E, F-J - articulated shells ZPAL V. 54/Bp/62/M2/3, 1 in dorsal, ventral, lateral, posterior, and anterior views; Z-BB - dorsal interior ZPAL V. 54/Bp/62/M2/2, ventral view (BB) and two oblique views. K-Y, CC-FF. Skenidioides cretus Halamski in Baliński et al., 2016 from outcrop MI-IIa or approximately corresponding strata (A. Piotrowski's collection); K-O, U-Y – articulated shells ZPAL V. 54/Bp/12/M1/1 from outcrop M1-IIa and ZPAL V. 54/Bp/12/MP/2 in dorsal, ventral, lateral, posterior, and anterior views; P-T, FF - articulated shell ZPAL V. 54/Bp/12/MP/1 in dorsal, ventral, lateral, posterior, and anterior views, and enlargement of the delthyrium (FF); CC-EE - ZPAL V. 54/Bp/12/M1/2 from outcrop M1-IIa, dorsal and ventral views (DD, EE), and enlargement of the repaired anterior commissure injury (CC).

¹⁄₄ of that of the interarea). Dorsal valve moderately to markedly transverse (width-to-length ratios for the dorsal valves 1.48–1.60); postero-lateral extremities concave; maximum width anteriorly to mid-length; with a median sulcus; interarea low, anacline; notothyrium wide. Ornament of radial ribs, new ones appearing by both bifurcation and intercalation, up to 61 in total on the dorsal valve of the largest shell, slightly less in smaller ones, rib density 13–14 per 5 mm at anterior margin in the largest shell, 17–19 in the smaller ones. Shell substance punctate.

Ventral interior: apical plate over the valve floor visible through the delthyrium in the posterior part of the latter (Fig. 10V, Y); otherwise, interior unknown. Dorsal interior: cardinal process massive, superficially bilobed, filling the apical part of the notothyrium; median septum extending for the entire valve length, incompletely preserved; cruralium incompletely preserved; valve margin entirely denticulate, denticles (2–)3 per mm. Remarks: The type stratum of Mystrophora areola is in the middle part of the Middle Devonian of the Eifel (Kayser, 1871, p. 614). Shells measured by Kayser (1871) are 7-11 mm wide, but in a larger collection from the type area there are larger shells, 9.9-14.1 mm in width, the width-tolength ratios 1.16-1.40 [N = 5], and the ornament density 12-16 ribs per 5 mm at anterior commissure (USNM 123350, 127867, 127868a-c). These values are very similar to those for the largest shell from the Miłoszów sample (see Tab. 1). Smaller shells from Miłoszow have slightly denser ribbing. Cooper (1955, pl. 11, figs 41, 44) figured a specimen from the Eifel over 16 mm wide. The variability of the discussed species is not fully known, but we are inclined to treat it widely. A single shell from the Upper Emsian of Grzegorzowice (Grzegorzowice Formation, leg. Ł. Rakowicz) is externally indistinguishable from M. areola; it is tentatively included to this species. This specimen is figured in Figure 9F-J.



Fig. 9. Givetian orthides from Miłoszów. **A–E.** *Biernatium* cf. *fallax* (Gürich, 1896); articulated shell ZPAL V.74/Bp/58/M2/1 in dorsal, ventral, lateral, posterior, and anterior views; outcrop M2, probably composite bed M2-2. **F–J.** *Mystrophora areola* (Quenstedt, 1871); juvenile articulated shell ZPAL V.74/Bp/16/M1/6 in dorsal, ventral, lateral, posterior, and anterior views; outcrop M1-IIa. **K–O.** *Aulacella prisca* (Schnur, 1851); articulated shell ZPAL V.74/Bp/14/M2/1 in dorsal, ventral, lateral, posterior, and anterior views; outcrop M2, probably composite bed M2-2. **P.** *Schizophoria* (*Schizophoria*) *schnuri* Struve, 1965; incomplete articulated shell ZPAL V.74/Bp/13/M1/1 in dorsal view; outcrop M1.



Fig. 10. Orthide brachiopod *Mystrophora areola* (Quenstedt, 1871) from the Lower and Middle Devonian of the Holy Cross Mountains. A–E, U–W, Y. Juvenile articulated shell ZPAL V.74/Bp/16/M1/4 in dorsal, ventral, lateral, posterior, and anterior views (A–E) and enlargements of the interareas in ventral oblique (U), dorsal oblique (V), and ventral (W, Y) views; Miłoszów, M1-IIa, Givetian. F–J. Articulated shell ZPAL V.74/Bp/16/G/1 in dorsal, ventral, lateral, posterior, and anterior views; Grzegorzowice, upper Emsian. K–O, P–T. Articulated shells ZPAL V.74/Bp/16/M1/2, 1 in dorsal, ventral, lateral, posterior, and anterior views; Miłoszów, M1-IIa, Givetian. X. Dorsal interior ZPAL V.74/Bp/16/M1/2, 1. Miłoszów, M1-IIa, Givetian.

| Specimen data Locality | | Dimensions | W | L | 1 | Т | W/L | W/1 | Ndc | Ndc/ |
|--|--------|--------------------------|------|------|-----|-----|------|------|-----|-------|
| | | Coll. no. | (mm) | | | | | | 5mm | |
| Holy Cross Mts., Miłoszów, M1-IIa, Lower Givetian | | ZPAL V.74 /Bp/16/M1/1 | 11.7 | 9.1 | 7.9 | 5.7 | 1.29 | 1.48 | 61 | 13–14 |
| | | ZPAL V.74/ Bp/16/M1/3 | 14.6 | _ | 9.1 | _ | _ | 1.60 | _ | _ |
| | | ZPAL V.74/ Bp/16/M1/2 | 8.5 | 7.2 | 5.6 | 4.4 | 1.18 | 1.52 | 58 | 17–18 |
| | | ZPAL V.74/ Bp/16/M1/5 | 9.0 | 7.1 | 5.7 | 4.6 | 1.27 | 1.58 | 51 | 17–19 |
| Holy Cross Mts., Grzegorzowice, Upper Emsian | | ZPAL V.74/ Bp/16/G/1 | 8.6 | 7.1 | 5.3 | 4.6 | 1.21 | 1.62 | 56 | 18–19 |
| Eifel, Eifelian | Prüm | USNM 127867 | 14.1 | 10.1 | ? | 6.7 | 1.40 | ? | ? | 12–15 |
| | Kerpen | USNM 127868a | 12.8 | 11.0 | ? | 7.4 | 1.16 | ? | ? | 13–16 |
| | | USNM 127868b | 11.8 | 9.0 | ? | 4.5 | 1.31 | ? | ? | 13 |
| | | USNM 127868c | 12.0 | 10.0 | ? | 6.3 | 1.20 | ? | ? | 11–15 |
| | Pelm | USNM 123350 | 9.9 | 8.4 | ? | 5.2 | 1.18 | ? | ? | 14–15 |

Biometric characteristics of *Mystrophora areola* (Quenstedt, 1871) from the Lower and Middle Devonian of the Eifel and the Holy Cross Mountains.

Biernatium fallax, co-occurring in outcrop M1 with *Mystrophora areola*, is distinguished by the lack of a median indentation of the anterior commissure, a less high ventral valve and, internally, by a slightly longer, narrower cruralium, and absence of the apical plate and of fulcral plates (Williams and Harper, 2000). The latter feature may be difficult to observe (fulcral plates not preserved in the single dorsal valve of *Mystrophora* described here). A representative of *Biernatium* from Skały was misidentified by Sobolew (1904) as *Mystrophora areola* (identification corrected by Sobolew, 1909).

Distribution: At Miłoszów the discussed species was found in the outcrop MI, in the case of specimens collected *in situ* the precise level is MI-IIa; in addition, one juvenile shell was found in M2-2. In the Rhenish Slate Mountains *M. areola* is known both from the Eifelian of the Eifel (Kayser, 1871) and from the Givetian of the Sauerland (Torley, 1934 and references therein; May, 1991). Additional occurrences are from the Givetian of Lummaton, England (Davidson, 1882) and the Eifelian? of Padaupkin, Burma (Anderson *et al.*, 1969).

It is worth noting that this species was often reported as occurring in small numbers: Kayser (1871) says it is "rare", Torley (1908) calls it a "rarity at Iserlohn", the English material (Davidson, 1882) amounts to a single specimen, that from Waldgirmes (Hessen) to two (Maurer, 1885), that from Burma to three (Anderson, Boucot and Johnson, 1969), and the present collection is similarly sparse. Only Torley (1934, p. 126) cited "several" specimens from Bilveringsen (Sauerland).

Single specimens, identified as Mystrophora sp., were reported from the Givetian of the Ardennes (Trois-Fontaines Fm, Godefroid and Mottequin, 2005) and Asturias (Portilla Fm, García-Alcalde, 2018), and from the uppermost Eifelian of the Barrandian (Mergl and Budil, 2019). In each case, it is unclear whether the listed differences with M. areola correspond to genuine taxonomic separateness or might be better explained by taphonomic factors and/or intra-specific variability. There were also citations (without descriptions or illustrations, so impossible to check) of Mystrophora areola (or Mystrophora cf. areola) from the Middle Devonian of Transcaucasia (Mamedov in Dubatolov et al., 1983, p. 124, 128), of Mystrophora? aff. areola from the Middle Devonian of Salair (Yazikov, 2014, fig. 1), and of Mystrophora cf. M. areola from the Middle? Devonian of Nevada (Zen, 1964, p. 32, 37).

For a possible occurrence in the Upper Emsian, see above.

Genus Biernatium Havlíček, 1975

Type species: *Skenidium fallax* Gürich, 1896; Sierżawy beds sensu Gürich (1896) [Nieczulice beds or Skały Formation?], (Middle?) Givetian, Middle Devonian; Śniadka, bed 10 *sensu* Gürich (1896) [Sierżawskie Doły between Świętomarz and Sierżawy = Szerzawy], northern region of the Holy Cross Mountains, Poland.

Remarks: It should be borne in mind that the very long cruralium, purportedly characteristic for *Biernatium* (Williams and Harper, 2000, fig. 5b), is a feature of a sample misidentified by Havlíček (1975) as *Skenidium fallax* Gürich, 1896, the type species of *Biernatium*. The genuine *Biernatium fallax* has a cruralium that extends for approximately half the length of the dorsal valve (Halamski, 2009, pl. 15, figs 22, 33, 34; Baliński *et al.*, 2016, p. 142; Halamski *et al.*, 2022a, p. 23).

Biernatium cf. *fallax* (Gürich, 1896) Fig. 9A–E

cf. * 1896 Skenidium fallax, nov. sp. – Gürich, pp. 236–237, pl. 10, fig. 9.

cf. 2009 *Biernatium fallax* (Gürich 1896) – Halamski, pp. 83–85, text-fig. 16, pl. 14, figs 28, 31, pl. 15, figs 16–34 [*ubi syn.*].

Material: Three incomplete articulated shells and a single fragmentary dorsal valve, ZPAL V.74/Bp/58.

Description: Shell shield-shaped, ventribiconvex, with a wide hinge line. Dorsal valve with a median sulcus. Ventral valve parabolic in anterior view, interarea apsacline. Ornament costellate. Ventral interior unknown. Dorsal interior: cardinal process and brachiophores poorly preserved; the latter supported by anteriorly convergent crural plates thus forming a cruralium of moderate length; cruralium supported by the median septum.

Remarks: These brachiopods are assigned to the genus *Biernatium* on account of the characteristic external form and the presence of a cruralium. The material at hand is insufficient for a precise identification, but the available characters do not differ from those of *Biernatium fallax* described from approximately coeval strata of the Świętomarz-Śniadka section (Gürich, 1896; Halamski, 2009). Open nomenclature is used as a precaution. It should be noted that in the type area the discussed species is rather common, whereas it occurs only rarely at Miłoszów.

Distribution: *Biernatium* cf. *fallax* is present at Miłoszów in levels MI-IIa and M2-2. The species *Biernatium fallax* is known solely from the (Middle?) Givetian of the Świętomarz–Śniadka section. Former reports of this species from the Upper Eifelian of Skały and the Givetian of Moravia are erroneous (see Halamski *et al.*, 2022a and references therein).

Suborder Dalmanellidina Moore, 1952 Superfamily Dalmanelloidea Schuchert, 1913 Family Dicoelosiidae Cloud, 1948 Genus *Teichertina* Veevers, 1959

Type species: *Teichertina fitzroyensis* Veevers, 1959; Sadler Formation, Frasnian; Fitzroy Basin, Western Australia.

Teichertina peregrina Havlíček, 1977 Fig. 11A–H

- * 1977 Teichertina peregrina sp. n. Havlíček, pp. 215–216, pl. 56, figs 22–29.
 - 1978 *Teichertina peregrina* Havlíček, 1977 Ficner and Havlíček, p. 61, pl. 13, figs 1–5.

cf. 2018 Teichertina cf. peregrina Havlíček, 1977 – García-Alcalde, pp. 67–68, fig. 8b.

Material: Four subcomplete articulated shells and a crushed incomplete one, ZPAL V.74/Bp/3.

Description: Shell very small (typically about 4–4.5 mm wide, 2–2.5 mm long, and 1.5–2 mm thick), ventribiconvex to nearly hemipyramidal, transverse, with straight cardinal margin, alate cardinal extremities, and distinctly medially indented anterior commissure. Ventral valve rounded triangular in anterior view; interarea rather high, catacline to apsacline, flat to weakly incurved; delthyrium narrow. Dorsal valve lowly triangular in anterior view, with a flat-bottomed median sulcus. Ornament of strong ribs accompanied by weaker ones, on the dorsal valve the strongest pair is that bordering the sulcus, with four stronger and sometimes a few weaker ribs per flank. Interior unknown.

Remarks: These brachiopods are included in *Teichertina* on account of their cordate outline with alate cardinal extremities and into *T. peregrina* on account of the ornament. As stressed by Havlíček (1977, p. 216), the ornament of *T. peregrina* is markedly different of that of *T. fitzroyensis*, the type species of the genus; it is fascicostellate with imbricate growth lines in the latter, whereas in the former it consists of ribs of subequal size.

At Miłoszów MI-IIa, this species co-occurs with *Teichertina quadriplicata* which is of similar shape and size, and also possesses a radial ornament. The most striking differences are in the form of the anterior commissure and the ornament. The anterior commissure possesses several indentations in *T. quadriplicata*, but only a single median one in *T. peregrina*. The ornament consists of acute opposite ribs in *T. quadriplicata*, but of rounded angular ribs that are partly opposite and partly alternating in *T. peregrina*. Moreover, the cardinal extremities are mucronate in *T. quadriplicata* and alate in *T. peregrina*, whereas the median sulcus is V-shaped in *T. quadriplicata* and flat-bottomed in *T. peregrina*.

Occurrence: Miłoszów, M1-IIa (five specimens). Čelechovice na Hané, Givetian (Havlíček, 1977). Possibly Portilla Formation of León, Spain, middle Givetian (García-Alcalde, 2018).

Teichertina quadriplicata (Sandberger and Sandberger, 1856 in 1850–1856) Fig. 11I–S

v* 1856 Spirifer quadriplicatus Sandb. – Sandberger and Sandberger, pp. 323–324, pl. 32, fig. 9.

Type material: Articulated shell MWNH-DEVO-000262 figured by Sandberger and Sandberger (1856, pl. 32, fig. 9) and herein (Fig. 11N), the only specimen of this species in their collection or mentioned in the original text, so assumed to be the holotype by monotypy.

Type locality and stratum: Lahnstein mine, Weilburg (Lahn Syncline), Hessen, Germany; Roteisenstein, Middle Devonian, Givetian (most probably Upper Givetian, but lowermost Frasnian cannot be excluded, see Heidelberger *et al.*, 2003 and references therein).

Material: Two articulated shells, ZPAL V.74/Bp/63/M1.



Fig. 11. Middle Devonian orthide *Teichertina* Veevers, 1959 from the Holy Cross Mountains and the Rhenish Massif. **A–H.** *Teichertina peregrina* Havlíček, 1977 from Miłoszów; A–E – articulated shell ZPAL V.74/Bp/63/Ml/1 in dorsal, ventral, lateral, posterior, and anterior views; F–H – articulated shell ZPAL V.74/Bp/63/Ml/2 in dorsal, lateral, and anterior views. **I–S.** *Teichertina quadriplicata* (Sandberger and Sandberger, 1856); I–M – articulated shell ZPAL V.74/Bp/67/MP/1 in dorsal, ventral, lateral, posterior, and anterior views; Miłoszów, approximately M1-IIa; N – articulated shell (holotype; figured by Sandberger and Sandberger, 1850–1856, pl. 32, fig. 9) MWNH-DEVO-000262 in dorsal view; Weilburg (Lahn Syncline), probably Upper Givetian; O–S – articulated shell SMF 120233.1 in dorsal, ventral, lateral, posterior, and anterior views; Crinoiden-Schicht (middle part of the Middle Devonian), near Rommersheim (Eifel).

Other material: SMF 120233.1 – Crinoiden-Schicht near Rommersheim, Eifel, Germany.

Description: Shell small (the larger specimen is 6.4 mm wide, 2.9 mm long, and 2.9 mm thick), trapezoidal in outline, transverse, markedly ventribiconvex, maximum width at hinge line, postero-lateral extremities mucronate. Commissure with five to seven rounded and shallow indentations limited by plicae. Ventral valve triangular in anterior view, with a relatively high and incurved interarea, first weak-ly procline, then gradually changing the growth direction and becoming apsacline; delthyrium open. Dorsal valve lowly triangular in anterior view, with a V-shaped median sulcus.

Ornament consisting of angular plications: on the dorsal valve a strong pair bordering the sulcus, another more external strong pair and two pairs of weaker ones, thus four per flank in total; on the ventral valve a median plication and three pairs per flank. Folding opposite. Growth lines sublamellose.

Interior: small cardinal process visible through the delthyrium; otherwise, unknown.

Remarks: This brachiopod was originally interpreted as a spiriferide (Sandberger and Sandberger, 1850–1856). Scupin (1900, p. 212) and Gourvennec (1994b, p. 573) suggested its assignment to the genus *Verneuilia* Hall and Clarke, 1893 (type species: *Spirifer cheiropteryx* d'Archiac & de Verneuil, 1842; Paffrath, Nordrhein–Westfalen, Germany; Frasnian; see Wang *et al.*, 2022). However, the shell substance of the type specimen is punctate, a character allowing its classification as an orthide. Its peculiar shape with a metacarinate margin points to the genus *Teichertina*.

The monograph by Sandberger and Sandberger (1850– 1856) was published in several fascicles over a few years; the pages 233–564, including the pages 323–324 containing the description of *Spirifer quadriplicatus*, were printed in 1856 (Richter and Richter, 1954).

For comparison with *T. peregrina* co-occurring in the same outcrop, see above.

The Zlichovian species *Teichertina polyformis* Havlíček, 1977 is similar to *T. quadriplicata* in overall shape and ornament, but its ribbing seem stronger and denser (material not seen). Drewitz (1985, p. 97, pl. 1, figs 1–3) reported poorly preserved material (impressions and casts) of *Teichertina* from the Ohle Formation (middle part of the Eifelian) of the Attendorf Syncline (Sauerland). These brachiopods were identified as *T. polyformis* Havlíček, 1977, a species known from the Zlichovian (Lower Emsian) of Bohemia (Havlíček, 1977, pp. 213–214). The ornamentation of the only impression shown (Drewitz, 1985, pl. 1, fig. 3) is suggestive of *T. quadriplicata* (material not examined). Another report of *`Teichertina polyformis*' from the Ohle Formation of the Sauerland by Langenstrassen (2008, p. 429) might perhaps also concern *T. quadriplicata* (material not seen).

Distribution: This is a particularly rare brachiopod species, known from five specimens. Two specimens, collected by the late Andrzej Piotrowski, are known from Miłoszów, Ml (probably M1-IIa; one of them illustrated in Fig. 11I-M); no new material was recovered during the fieldwork of the present authors. A single specimen (the holotype; Fig. 11N) comes from the (Upper?) Givetian of the Lahnstein mine near Weilburg (Sandberger and Sandberger, 1850-1856; see also Schöndorf, 1908, p. 58; Heidelberger et al., 2003, p. 60). Two previously unreported specimens come from the Eifel (Crinoiden-Schicht near Rommersheim, coll. Richter 1917; one of them is illustrated in Fig. 11O-S). For possible occurrences in the Ohle Formation (Eifelian), see above. The report of this species from the Lower Devonian (Béclard, 1896, p. 278) is based on erroneous dating of the type locality.

Superfamily Enteletoidea Waagen, 1884 Family Schizophoriidae Schuchert and LeVene, 1929 Genus *Schizophoria* King, 1850

Type species: *Conchyliolithes Anomites resupinatus* Martin, 1809; Lower Carboniferous; Derbyshire, Great Britain.

Subgenus Schizophoria (Schizophoria) King, 1850 Schizophoria (Schizophoria) cf. schnuri Struve, 1965 Fig. 9P

cf. 1959 *Schizophoria striatula* (Schlotheim) – Biernat, pp. 54–63, text-figs 20, 21, text-pl. 6, pl. 7, figs 1–13, pl. 8, figs 1–5, pl. 9, figs 1–6, pl. 11, fig. 3.

- cf. 1965 Schizophoria schnuri n. sp. Struve, pp. 202–208, pl. 19, fig. 4, pl. 20, pl. 21.
- cf. 2009 Schizophoria (Schizophoria) cf. schnuri Struve, 1965 – Halamski, p. 87, text-fig. 17, pl. 14, figs 11, 17, pl. 15, figs 11–15, pl. 16, figs 10, 14, 15, 23, 24 [ubi syn.].
- cf. 2012 Schizophoria (Schizophoria) schnuri Struve, 1965 Halamski, p. 352.

Material: Four fragmentary specimens, ZPAL V.74/Bp/13. **Remarks:** The material consists of incomplete, deformed, or juvenile specimens, neither a formal description nor a species-level identification is feasible. It is, however, likely that the described brachiopods represent the widely distributed Middle Devonian representative of *Schizophoria*, namely *S.* (*S.*) *schnuri* Struve, 1965 known from the Upper Eifelian to Middle Givetian Skały Formation (Skały, Świętomarz; Biernat, 1959; Halamski, 2009).

Occurrence: The species is represented by several subspecies occurring in the Middle Devonian of the Eifel region (Struve, 1965), the Ardennes (Hubert *et al.*, 2007), Moravia (Havlíček, 1977), Holy Cross Mountains (Halamski, 2009, 2012), Burma (Anderson *et al.*, 1969), Transcaucasia (Alekseeva *et al.*, 2018), and Northern Africa (Halamski and Baliński, 2013). The present material comes from outcrops M0 (bed 9), M1N and M2 in Miłoszów.

Order Pentamerida Schuchert and Cooper, 1931 Suborder Pentameridina Schuchert and Cooper, 1931 Superfamily Gypiduloidea Schuchert and LeVene, 1929 Family Gypidulidae Schuchert and LeVene, 1929 Subfamily Gypidulinae Schuchert and LeVene, 1929 Genus *Gypidula* Hall, 1867

Type species: *Gypidula typicalis* Amsden, 1953; Cedar Valley Group, Middle Devonian; Independence, Iowa.

Gypidula biplicata (Schnur, 1851) Fig. 12A–J

1851 P. [Pentamerus] biplicatus, n. sp. – Schnur, p. 8.

- 1853 Pentamerus biplicatus m. Schnur, p. 196, pl. 31, fig. 3.
- 1896 Pentamerus galeatus var. cf. biplicatum Gürich, p. 274
- 1904 Pentamerus galeatus Sobolew, p. 86, pl. 9, fig. 11.
- 1909 *Pentamerus biplicatus* Schnur Sobolew, p. 496.
- 1934 Sieberella biplicata (Schnur) Torley, p. 92; text-fig. 23, pl. 4, figs 67–68 [ubi syn.].
- 1966 *Gypidula* (*Gypidula*) cf. *biplicata* (Schnur, 1854) Biernat, pp. 29–30, pl. 1, fig. 11.
- cf. 2000 *Gypidula* cf. *biplicata* (Schnur, 1854) Sapel'nikov and Mizens, p. 23, pl. 4, figs 8–11.
 - 2013 *Gypidula biplicata* (Schnur, 1851) Halamski and Baliński, pp. 259, 261, pl. 9, figs A–E.



Fig. 12. Givetian pentamerides from Miłoszów. **A–J.** *Gypidula biplicata* (Schnur, 1851); A–E – articulated shell ZPAL V.74/Bp/18/ MS1/1 in dorsal, ventral, lateral, posterior, and anterior views; trench I; F–J – articulated shell ZPAL V.74/Bp/18/M0/1 in dorsal, ventral, lateral, posterior, and anterior views; outcrop M0-9. **K–O, Q–EE.** *Antirhynchonella linguiformis* Biernat, 1966; K–O, Q–U, V–Z – articulated shells ZPAL V.74/Bp/17/M3/1–3 (approximately strato- and topotypic) in dorsal, ventral, lateral, posterior, and anterior views; outcrop M3-7; AA–EE – articulated shell ZPAL V.74/Bp/17/M2/4 in dorsal, ventral, lateral, posterior, and anterior views; outcrop M2-3. **P.** Gypidulidae indet.; incomplete ventral valve ZPAL V.74/Bp/19/M1/1; outcrop M1-Ib.

Material: Three almost complete and one damaged shell and 13 fragmentary shells and ventral valves, ZPAL V.74/ Bp/18. A nearly complete adult shell measures about 16.4 mm in length, 19.3 mm in width and 14.2 mm in thickness. **Description:** Shell rounded pentagonal in outline, wider than long to subequal, up to about 40 mm in width, maximum width anterior to mid-length. Ventral umbo very thick, beak strongly incurved. Anterior commissure plicosulcate, dorsal sulcus with 1(-2) plicae, low ventral fold with 2(-3)plicae, faint lateral plicae sometimes present; plicae, fold and sulcus appear slightly posteriorly to the shell midlength. Shell smooth. Interior not studied.

Remarks: Externally the studied specimens differ from the type material of Gypidula biplicata from the Eifel (Schnur, 1853, pl. 31, fig, 3) in being elongate, whereas the latter are transverse. However, elongate specimens are also present in the type region (SMF collections, Junkerberg-Schichten, Hönselberg-Hzt., Betterberg, Bl. Dollendorf; Rommersheimer Schichten, Schurfgraben Gondelsheim). Variation in the number of plicae was noted by Halamski (2004b). Differences between the single specimen found by Biernat (1966) at Skały (outcrop 81 sensu Pajchlowa, 1957; Upper Eifelian) and the type material are taxonomically insignificant. Occurrence: Middle Devonian: Eifel, Ardennes, Holy Cross Mts. (Eifelian: Skały; Givetian: Sitka, Miłoszów; Givetian?: Cząstków; Halamski, 2004b), Maïder (Halamski and Baliński, 2013). At Miłoszów the species is rare in the M0 and M2 outcrops.

Gypidulidae gen. et sp. indet. Fig. 12P

Material: One incomplete and deformed shell and six fragmentary ventral valves embedded in limestone.

Remarks: This fragmentary material can be attributed to the family Gypidulidae on account of the smooth, strongly convex ventral valve with massive umbo, a strongly incurved beak, low fold, and unisulcate anterior commissure. It differs from *Gypidula biplicata* in the lack of radial ornament. Incomplete preservation and lack of knowledge of interiors preclude any more detailed identification.

Occurrence: This form was found in the M0 and M1 outcrop in Miłoszów.

Superfamily Clorindoidea Rzhonsnitskaya, 1956 Family Clorindidae Rzhonsnitskaya, 1956 Genus Antirhynchonella Œhlert, 1887

Type species: *Atrypa linguifera* Sowerby in Murchison, 1839; Coalbrookdale Fm, Wenlock Limestone, Silurian; Stumps Wood, Malvern hills, Worcestershire, western England.

Antirhynchonella linguiformis Biernat, 1966 Figs 2, 12K–O, Q–EE, 13

- 1896 Pentamerus globus var. c Gürich, pp. 276–277, pl. 7, fig. 9.
- 1904 Pentamerus brilonensis Kayser Sobolew, pp. 88–89, pl. 9, fig. 13.

- 1909 *Pentamerus* cf. *linguifer* Sow. Sobolew, pp. 494–495, pl. 6, figs 4–5.
- v* 1966 Antirhynchonella linguiformis n. sp. Biernat, pp. 35–36, text-fig. 5, pl. 2, figs 2–5.
- v. 2022b Antirhynchonella linguiformis Biernat, 1966 – Halamski et al., pp. 325, 336, 353, fig. 22D–F.

Material: 18 complete to almost complete and about 40 fragments of shells, about 60 fragmentary ventral and 5 dorsal valves, ZPAL V.74/Bp/17.

Type locality and stratum: Given in the original publication (Biernat, 1966, p. 35) as "Miłoszów, exposure 2 (limestone of Miłoszów), Skały beds, Middle Devonian. Miłoszów near Skały, Łysogóry region, Holy Cross Mountains". This corresponds most probably to level M3-7 of the present authors or its equivalent (see Halamski *et al.*, 2022b). This species occurs most abundantly in the bed M3 λ , but it is not certain that the holotype comes from there. The age of this part of the Skały Formation is probably Early Givetian.

Description: Shell usually about 20 mm wide (see Tab. 2), ovoid in outline, strongly ventribiconvex, weakly wider than long to subequal, widest slightly anteriorly to mid-length; cardinal margin short and curved, cardinal extremities, lateral and anterior margins rounded; anterior commissure uniplicate.

Ventral valve strongly convex, regularly parabolic in anterior view; umbo very massive, inflated, high; beak strongly incurved, frequently adpressed to the umbo of the opposite valve; sulcus absent to faint, recognizable near the anterior commissure; tongue short, flat with weakly rounded to almost straight top. Dorsal valve weakly convex, with well-marked umbo; fold weak, originating at mid-length or more anteriorly, well-marked close to anterior margin, with flat to slightly convex top, occupying 0.47–0.53 of the valve width.

Ventral interior with a median septum posteriorly embedded in umbonal thickening, anteriorly high, supporting a narrow and deep spondylium. Interior of dorsal valve with hinge plates lyre-shaped in cross section; inner hinge plates weakly converging basally, but discrete, not joined on the valve floor (Fig. 13).

Table 2

Biometric characteristics of *Antirhynchonella linguiformis* Biernat, 1966 from the Givetian of Miłoszów.

| Cat. No. | L | W | XX7/T | Т | ws | |
|----------------------|------|------|-------|------|------|--|
| ZPAL V.74/ Bp/17/ | (mm) | | W/L | (mm) | | |
| M3/2 | 16.3 | 16.8 | 1.03 | 11.9 | 7.9 | |
| M3/1 | 16.7 | 17.5 | 1.05 | 11.8 | 9.9 | |
| M3/3 | 17.9 | 19.8 | 1.11 | 13.4 | ~9.5 | |
| M3/8 | 18.8 | 21.7 | 1.15 | 12.2 | 11.4 | |
| M3/9 | 19.7 | 22.3 | 1.13 | 14.4 | 12.0 | |
| M2/4 | 23.4 | 23.8 | 1.02 | 16.0 | 12.8 | |
| M3/10 | 23.8 | 25.8 | 1.08 | 15.7 | 15.8 | |

Remarks: Biernat (1966) noted that A. linguiformis is similar to Pentamerus sublinguifer Maurer, 1885 (= Antirhynchonella sublinguifera) from the Middle Devonian of the Rhenish Slate Mountains, and especially to two of four specimens of this species, illustrated by Maurer (1885, pl. 9, figs 8, 10). Indeed, the two specimens of P. sublinguifer mentioned by Biernat (1966, p. 36) are externally similar to the species described from Miłoszów, but they differ in having wider and smaller shells, less thickened ventral umbones and better marked ventral sulci. It should be noted that the other two of Maurer's specimens, one of them representing the typical variety P. sublinguifer (Maurer, 1885, pl. 9, fig. 7) and the second described as P. sublinguifer var. glabra (Maurer, 1885, pl. 9, fig. 9), differ noticeably from A. linguiformis in being extremely narrow or very wide and flat, respectively. The type material of Antirhynchonella sublinguifera (Maurer, 1885) is thus possibly heterogenous,

so it seems more prudent to use the name *A. linguiformis* for the Holy Cross Mts. material until the revision of the German species, even if the two may ultimately prove to be synonymous, as proposed by Halamski and Baliński (2013). The synonymy given above is thus deliberately limited to the occurrences from the Holy Cross Mts.

Occurrence: This is the most numerous species in the M2 (Fig. 2) and M3 outcrops at Miłoszów. It was also reported from the "crinoid limestone" [Skały Formation, uppermost Eifelian–lowermost Givetian] at Skały (Sobolew, 1904) and from a few levels in the Świętomarz-Śniadka section (Gürich, 1896; Sobolew, 1909).

Genus Pentamerelloides García-Alcalde, 2010

Type species: *Spirifer Davidsoni* Schnur, 1853; Middle Devonian; Gerolstein, Eifel, Germany.



Fig. 13. Transverse serial sections of *Antirhynchonella linguiformis* Biernat, 1966 through shells ZPAL V.74/Bp/24/M3/5 (**A**), M3/6 (**B**), and M3/7 (**C**), and M3/8 (**D**) from M3-7. Distances measured in millimetres from the tip of the ventral umbo.

Remarks: *Pentamerelloides* García-Alcalde, 2010 was segregated from *Pentamerella* Hall, 1867 (type species: *Atrypa arata* Conrad, 1841) for rather small brachiopods with wide shells ornamented by 14–16 costae increasing in number by rare bifurcation and intercalation and characterised internally by a carinate cruralium and a long ventral median septum supporting the spondylium. *Pentamerella* s.s. was retained for large-sized brachiopods with elongated shells ornamented by numerous (usually more than 20), frequently bifurcating and intercalating costae, and internally with a sessile cruralium without carinae and by a spondylium supported by a rather short median septum (García-Alcalde, 2010).

Pentamerelloides davidsoni (Schnur, 1853) Figs 14, 15

- * 1853 Sp. [Spirifer] davidsoni n. sp. Schnur, p. 206, pl. 35, fig. 7, pl. 44, fig. 3.
 - 1871 Spirifer davidsoni Schnur Kayser, p. 586.
 - 1900 Spirifer davidsoni Schnur Scupin, p. 77.
 - 1904 Spirifer davidsoni Schnur Sobolew, p. 72, pl. 8, fig. 20.
 - 1909 Spirifer davidsoni Schnur Sobolew, p. 469.
 - 1951 Pentamerella davidsoni (Schnur, 1853) Havlíček, pp. 3–4, pl. 1, figs 7, 9.
 - 1978 *Pentamerella davidsoni* (Schnur, 1853) Ficner and Havlíček, p. 68, pl. 2, figs 18–22.
- ? 1980 Pentamerella cf. davidsoni Johnson et al., p. 81, pl. 1, figs 12–18.
 - 2010 Pentamerelloides davidsoni (Schnur, 1853) García-Alcalde, pp. 427–429, figs 4, 5 [ubi syn.].
- v. 2022b *Pentamerelloides davidsoni* (Schnur, 1853) – Halamski *et al.*, pp. 353, 360, fig. 220–Q.

Material: About 40 complete and 24 damaged shells, two isolated ventral and dorsal valves and about 20 fragmentary specimens, ZPAL V.74/Bp/17/M1.

Description: Shell up to 11.2 mm in width, but typically about 8–9 mm wide, suboval to rounded in outline, weakly ventribiconvex, weakly wider than long with width-to-length ratio about 1.1–1.3 (mean 1.18, N = 13), widest at mid-length (see Tab. 3); cardinal margin narrow to fairly wide and slightly curved; cardinal extremities and lateral margins rounded, anterior margin usually rounded, seldom straight; anterior commissure uniplicate.

Ventral valve more convex than the opposite valve, with a massive umbo and a strongly incurved, stubby beak; sulcus not recognizable posteriorly, anteriorly very shallow, laterally bounded with a pair of strong costae; tongue short, strongly incurved dorsally, in large shells almost perpendicular to the commissural plane; interarea apsacline, rather well discernible, quite high and wide, concave and vertically striated; delthyrium to a large extent open, apically covered by a short and flat deltidium that covers the apical part of the spondylium (Fig. 15G, H); delthyrium laterally bounded by subvertical ridges (faint and narrow deltidial

Biometric characteristics of *Pentamerella davidsoni* (Schnur, 1853) from the Givetian of Miłoszów.

| Cat. No. ZPAL V.74/ | L | W | W/L | Т | Ndc | |
|------------------------|-----|------|------|------|-----|--|
| Bp/20/M1/ | (m | m) | | (mm) | | |
| 5 | 1.1 | 1.2 | 1.09 | 0.4 | 1 | |
| 6 | 2.0 | 2.2 | 1.10 | 0.7 | 3 | |
| 11 | 4.4 | 5.9 | 1.34 | 3.0 | 10 | |
| 16 | 6.1 | 7.5 | 1.23 | 4.7 | 11 | |
| 12 | 6.3 | 6.9 | 1.10 | 4.8 | 11 | |
| 1 | 6.4 | 7.5 | 1.17 | 5.1 | 12 | |
| 15 | 6.6 | 8.2 | 1.20 | 5.2 | 11 | |
| 14 | 6.6 | 7.7 | 1.17 | 5.3 | 11 | |
| 2 | 8.1 | 9.1 | 1.12 | 6.1 | 10 | |
| 10 | 8.2 | 9.8 | 1.13 | 6.7 | 10 | |
| 3 | 8.7 | 9.7 | 1.11 | 6.3 | 11 | |
| 13 | 8.8 | 10.8 | 1.23 | 7.1 | 11 | |
| 4 | 9.5 | 11.2 | 1.18 | 8.5 | 12 | |

plates). Dorsal valve with well marked, slightly protruding umbo; fold originating at some distance from the umbo, becoming well defined anteriorly and high at the commissure, fitting the protruding tongue of the ventral valve.

The ornament consists of strong, usually rounded, sometimes more angular costae increasing in number abaxially by intercalation and bifurcation; on the dorsal valve the first median costa appearing at a distance of about 0.5–1 mm from the umbo (Fig. 15D); successive costae gradually appear laterally to the median costa and then to other existing costae (Fig. 15E); invariably two costae in the sulcus and three costae on the fold; 4–5 costae on each flank in adult shells.

Interior of the ventral valve with a U-shaped spondylium, supported by a high and long median septum; the most apical region of spondylium covered with deltidium, as mentioned above. Dorsal valve with antero-laterally diverging outer hinge plates and subparallel inner hinge plates, the later usually uniting on the dorsal valve floor along the midline or a median ridge, but, less frequently, meeting the valve floor at some distance to each other (Fig. 15A–C, F).

Remarks: The brachiopods from Miłoszów discussed here show complete agreement in external features to *P. davidso-ni* from the Eifel, as described by Schnur (1851, 1853); two shells from the Eifelian of the type area are illustrated in Figure 14 F–J, U–Y for comparison with the material from Miłoszów. Furthermore, they fully agree externally and internally with *P. davidsoni* from the Givetian Portilla Fm of the Cantabrian Mts., as described by García-Alcalde (2010). Internal features of *P. davidsoni* from the type area remain unstudied.

Occurrence: Middle Devonian: Eifel (Eifelian; Schnur, 1853; Kayser, 1871; Scupin, 1900); Moravia (Havlíček, 1951; Ficner and Havlíček, 1978); León, Spain (lower part of the middle Givetian; García-Alcalde, 2010). Johnson *et al.* (1980) reported *P. cf. davidsoni* from the Givetian

Table 3



Fig. 14. *Pentamerelloides davidsoni* (Schnur, 1853) from the Givetian of Miłoszów (A–E, K–T, Z–DD) and the Eifelian of the Eifel (F–J, U–Y). **A–E, K–O, P–T, Z–DD.** Specimens ZPAL V.74/Bp/18/M1/20/1–4 from outcrop M1-IIa. **F–J.** Specimen SMF 88a from locality 880 *sensu* Struve, ca. 900 m NE from Nollenbach on the road Nollenbach–Ahütte, Eifel; Freilingen Formation (Upper Eifelian). **U–Y.** Specimen SMF *s.n.* from locality 633 *sensu* Struve, 135 S from the road Nollenbach–Ahütte, ca. 50 m WSW from the western building of the Kalkwerk Müller, Eifel; Junkerberg Formation (Middle Eifelian). All specimens are articulated shells in dorsal, ventral, lateral, posterior, and anterior views.



Fig. 15. *Pentamerelloides davidsoni* (Schnur, 1853) from the Givetian of Miłoszów. **A**, **C**. Dorsal interior ZPAL V.74/Bp/18/M1/20/8, general view (C) and enlargement of the cardinalia (A). **B**, **F**. Dorsal interior ZPAL V.74/Bp/18/M1/20/9, general view (F) and enlargement of the cardinalia (B). **D**, **E**. Juvenile articulated shells ZPAL V.74/Bp/18/M1/20/5, 6 in dorsal views. **G**, **H**. Fragmentary ventral interior ZPAL V.74/Bp/18/M1/20/7, general view (G) and enlargement of the median region (H). All specimens from outcrop M1-IIa.

(ensensis to lower varcus zones) of central Nevada, unfortunately without description.

In the Holy Cross Mts. *Pentamerelloides davidsoni* was reported from the "crinoid limestone" [uppermost Eifelian or lowermost Givetian] at Skały (Sobolew, 1904, 1909); the present material comes from the trench MIN at Miłoszów (Lower Givetian). The difference between local stratigraphic ranges of this species in different areas is noteworthy.

Order Rhynchonellida Kuhn, 1949 Superfamily Uncinuloidea Rzhonsnitskaya, 1956 Family Hebetoechiidae Havlíček, 1960 Genus *Kransia* Westbroek, 1967

Type species: *Terebratula parallelepipeda* Bronn, 1837 *sensu* Westbroek, 1967.

Kransia (K.) parallelepipeda (Bronn, 1834 in 1834–38 ['1835–37']) Fig. 16K–O

- v*p 1834 Terebratula Wilsoni [parallelepipeda] Bronn, p. 73.
- v. 2013 Kransia parallelepipeda (Bronn, 1834 in 1834–38 ["1835–37"]) – Halamski and Baliński, p. 265, fig. 13K–II.
- v. 2022 *Kransia parallelepipeda* (Bronn, 1834) Halamski *et al.*, figs 22L–N, 27–4.

Material: Over thirty-five specimens, mostly articulated shells that are complete or subcomplete, but often deformed, from outcrop Ml.

Remarks: The description of this material will be given separately in a joint treatment of the European and African Hebetoechiidae.

Kransia (K.) subcordiformis (Schnur, 1853) Fig. 16P–T

- v* 1853 *Terebratula subcordiformis* n. sp. Schnur, p. 186, pl. 25, fig. 6a–k.
- v. 2013 Kransia subcordiformis (Schnur, 1853) Halamski and Baliński, p. 265, fig. 13JJ–NN [ubi syn.].
- v. 2022b Kransia subcordiformis (Schnur, 1853) Halamski et al., p. 353, fig. 22AA–CC.

Material: 57 complete or almost complete and more than 60 damaged articulated shells, often decorticated to varying degrees, from outcrop M0.

Remarks: The description of this material will be given separately in a joint treatment of the European and African Hebetoechiidae.

Genus Beckmannia Mohanti, 1972

Type species: *Uncinulus minor beckmanni* Schmidt, 1951; Middle Devonian (Lower Givetian?); Letmathe, Sauerland, Rhenish Slate Mountains.

> Beckmannia propentagona (Schmidt, 1950) Fig. 16A–E

- v* 1950 Uncinulus pentagonus propentagonus n. ssp. Schmidt, pp. 80–82, text-figs 2, 3.
- v. 2022b *Beckmannia propentagona* (Schmidt, 1950) – Halamski *et al.*, fig. 22G–I.

Material: Over ninety specimens (mostly subcomplete and complete articulated shells), ZPAL V.74/Bp/21.

Remarks: These brachiopods are characterised by a length typically about 10 mm, subangular pentagonal outline,



Fig. 16. Uncinuloid rhynchonellides from the Givetian of Miłoszów. A–E. Beckmannia propentagona (Schmidt, 1950); specimen ZPAL V.74/Bp/23/M2/1 from outcrop M2. F–J. Beckmannia cf. beckmannii (Schmidt, 1951); specimen ZPAL V.74/Bp/59/M0/1 from outcrop M0-9. K–O. Kransia parallelepipeda (Bronn, 1834 in 1834–38 ['1835–37']); specimen ZPAL V.74/Bp/22/M1/1 from outcrop M1-IIa. P–T. Kransia subcordiformis (Schnur, 1853); specimen ZPAL V.74/Bp/23/M0/1 from outcrop M0-9. U–Y. Glosshypothyridina procuboides (Kayser, 1871); specimen ZPAL V.74/Bp/64/M2/1 from outcrop M2-5. All specimens are articulated shells in dorsal, ventral, lateral, posterior, and anterior views.

a low but distinct dorsal fold, a ventral sulcus appearing in the umbonal region, and a high, thin dorsal median septum. A full treatment of this species, described on the basis of a numerically scarce sample from the Eifelian of the Eifel (Schmidt, 1950) as a subspecies of *Beckmannia pentagona* (Kayser, 1871), considered now to represent a separate species, now found to occur abundantly at Miłoszów, will be given separately.

Distribution: Eifel Mts., Eifelian (Schmidt, 1950); Miłoszów, especially common in outcrop M3, but present also in M1, and M2.

> Beckmannia cf. beckmannii (Schmidt, 1951) Fig. 16F–J

cf. * 1951 Uncinulus minor beckmanni n. ssp. – Schmidt, pp. 89–90, pl. 1, figs 1–3.

Material: Three variously preserved articulated shells, ZPAL V.74/Bp/59.

Remarks: These brachiopods are similar to *Beckmannia propentagona* (see above) in general form but can be distinguished by the absence of the fold, a sulcus that is present only in anterior region, and a lower tongue. The sample is insufficient for a more extensive treatment.

Distribution: Miłoszów, outcrop M0. *Beckmannia beckmannii* is known from the Givetian of the Eifel.

Family Hypothyridinidae Rzhonsnitskaya, 1956 Genus *Glosshypothyridina* Rzhonsnitskaya, 1978

Type species: *Rhynchonella procuboides* Kayser, 1871; Eifelian; Eifel, Germany.

Glosshypothyridina procuboides (Kayser, 1871) Fig. 16U–Y

- v* 1871 Rhynchonella procuboides n. sp. Kayser, pp. 513–514, pl. 9, fig. 3.
- v. 2013 Glosshypothyridina procuboides (Kayser, 1871) – Halamski and Baliński, p. 267, fig. 14F-Y [ubi syn.].

Material: One complete articulated shell and 8 fragmentary specimens.

Description: See Halamski and Baliński (2013).

Remarks: This species is easily distinguished thanks to its characteristic shape and fine medially-grooved ribs. **Distribution:** Miłoszów, M2-3, M2-5 and M3-7. Otherwise, Eifel, Maïder; Middle Devonian.

Superfamily Camarotoechioidea Schuchert, 1929 Family Leiorhynchidae Stainbrook, 1945 Genus *Eumetabolotoechia* Sartenaer, 1975

Type species: *Rhynchonella* (?) *Laura* Billings, 1860; Hamilton Group, middle Givetian; Thedford, Ontario, Canada.

Species assigned: see Sartenaer (1975, p. 3; 2014, p. 285), Boucot *et al.* (1983), Mergl and Massa (2000).

Remarks: The diagnostic characters of the family Eumetabolotoechiidae Sartenaer, 2014 are in the opinion

of the present authors insufficient for a family-level distinction, so they follow Savage (2002) in assigning the discussed genus to the Leiorhynchidae Stainbrook, 1945.

Leiorhynchus Hall, 1860 (type species: Orthis quadracostata Vanuxem, 1842; uppermost Givetian) differs in being less flat and having stronger dental plates, Hadrotatorhynchus Sartenaer, 1986 (type species: Leiorhynchus halli Flamand, 1911; uppermost Givetian) in lacking a septalium, Cherryvalleyrostrum Sartenaer, 2004 (type species: Leiorhynchus limitaris Vanuxem, 1842; Eifelian) in having frequently bifurcating costae, and Katabuporhynchus Sartenaer, 2014 (type species; Leiorhynchus mesacostalis, upper Givetian–lower Frasnian) in a stronger median septum.

Sartenaer (2014) proposed an "upper Givetian" [middle *Polygnathus varcus* Zone, so Middle Givetian as understood herein] *Eumetabolotoechia* Zone in eastern North America. The material described here is only slightly older.

Eumetabolotoechia subplicata (Biernat, 1966) Figs 17, 18

- ? 1904 Camarophoria formosa Schnur Sobolew, p. 89, pl. 9, fig. 16.
- ? 1909 Leiorhynchus cf. laura Billings (= multicosta and laura Hall & Clarke) – Sobolew, pp. 500–501.
- v* 1966 *Leiorhynchus subplicatus* n. sp. Biernat, pp. 82–83, pl. 17, figs 1–4, pl. 19, fig. 26.

Material: Holotype ZPAL Bp VII/25 and four newly collected subcomplete shells from the restricted type locality, ZPAL V.74/Bp/24. Biernat (1966) reports ten specimens, on which her description is based, but these could not be found in the collections.

Type locality and stratum: Given in the original publication (Biernat, 1966, p. 35) as "Limestone of Miłoszów, Skały beds, Middle Devonian. Miłoszów near Skały, Łysogóry region, Holy Cross Mountains". This species was found by the present authors solely in bed M0-9, so it is nearly certain that this is the restricted type locality and stratum. The age of this part of the Skały Formation is early Middle Givetian.

Description: Shell rounded pentagonal to ovate in outline, weakly dorsibiconvex, typically 25–28 mm wide, wider than long (width-to-length ratio about 1.1–1.4), maximal width at about the anterior third; cardinal margin obtuse, apical angle attaining 125°–133°, lateral margins rounded, anterior margin truncated to weakly arched; anterior commissure moderately to markedly uniplicate, tongue subtrapezoidal, moderately high, occupying 0.54–0.64 of the shell width.

Ventral valve weakly convex, with incurved beak; sulcus begins near the umbonal region, wide, flat-bottomed, rather shallow. Dorsal valve more convex than the opposite valve, parabolic in lateral and anterior view; fold wide, well-marked, but low, appearing near the umbonal region, with flat to slightly convex top; flanks mildly convex.

Shell ornamented with rounded and rather low costae appearing near the umbonal regions, increasing in number by rare bifurcations and intercalations; costae on fold and in



Fig. 17. Middle Givetian rhynchonellide brachiopod *Eumetabolotoechia subplicata* (Biernat, 1966) from outcrop M0 at Miłoszów. **A–E.** Holotype ZPAL Bp VII/25 (figured by Biernat, 1966, pl. 17, fig. 1); probably about M0, bed 9. **F–J, K–O.** Specimens ZPAL V.74/ Bp/24/M0/1, 2, respectively; outcrop M0, bed 9. All specimens are approximately strato- and topotypic and are articulated shells in dorsal, ventral, lateral, posterior, and anterior views.



Fig. 18. Transverse serial sections of *Eumetabolotoechia subplicata* (Biernat, 1966) through the shell ZPAL V.74/Bp/24/M0/3 from M0-9 (approximately strato- and topotypic). Distances measured in millimetres from the tip of the ventral umbo.

sulcus generally slightly to clearly stronger than costae on flanks; 4–5 costae in sulcus, 5–6 on fold and 9–10 on flanks, parietal portions usually smooth, occasionally with up to three faint costae. Micro-ornament of faint growth lines only.

Interior poorly preserved and recrystallized; dental plates in a single sectioned specimen not revealed, owing to preservation; septalium thin, subhorizontal with narrow inner hinge plates and closely set crural bases; crura fairly long, distally strongly bent postero-ventrally (Fig. 18).

Remarks: The described species is assigned to the genus *Eumetabolotoechia* Sartenaer, 1975 on account of relatively flattish, ovate shells with low fold, shallow sulcus, and straight costae, weaker on the flanks than on the fold or sulcus externally and presence of a septalium internally (Sartenaer, 1975; Savage, 2002). *E. subplicata* is similar externally to the type species *E. laura* in ovate outline and character of the costation (compare Fig. 17 and Sartenaer, 1975, pl. 1). External differences include wider shells, more exposed ventral interareas, and a higher apical angle in *E. subplicata* (80°–120° in *E. laura*). Some internal differences should also be noted, among which the most important is lack of hinge plates in the Polish species (compare Fig. 18,

section 2.85 mm and Sartenaer, 1975, pl. 2; *E. alaura* Sartenaer, 2014 also lacks hinge plates, see Sartenaer, 2014, p. 283). Moreover, the septalium in *E. subplicata* is longer and the crura are more strongly incurved. The present authors are of the opinion that the above-mentioned similarities have greater significance than the differences, so they treat the genus *Eumetabolotoechia* widely.

From *Eumetabolotoechia kelloggi* (Hall, 1867), described from the Givetian of Ohio, USA (Hall, 1867, pl. 57, figs 1–12), the species from Miloszów differs mainly in having stronger and more posteriorly extended shell costation. *Leiorhychus huronensis* Nicholson, 1874 from the Hamilton Group of Ontario, which, according to Sartenaer (1975), should be included within the genus *Eumetabolotoechia*, is distinguished from *E. subplicata* by a strongly elongate and inflated shell.

Terebratula longinqua Beyrich, 1852 from the Devonian sandstone of the Murzuq area (Libya) has a similar shell outline as the species described here but differs in having shallower sulcus and lower fold as well as more frequent bifurcations of costae (see Beyrich, 1852, p. 14, pl. 3, figs 2, 4c, d). Mergl and Massa (2000) reported the species from the Murzuq Basin as *Eumetabolotoechia longinqua*, but their single illustrated specimen is inadequately preserved for a more detailed comparison.

Occurrence: *Eumetabolotoechia subplicata* is known only from bed 9 of M0 outcrop at Miłoszów. A single specimen from the "crinoid limestone" [Skały Formation, uppermost Eifelian or lowermost Givetian] was reported as *Camarophoria formosa* by Sobolew (1904) and as *Leiorhynchus* cf. *laura* by Sobolew (1909); this report may represent *E. subplicata*, but the identification should be checked with the specimen (the figure is in anterior view only).

Family Septalariidae Havlíček, 1960 Genus *Septalaria* Leidhold, 1928

Type species: *Terebratula ascendens* Steininger, 1853; Nohn beds, Eifelian, Middle Devonian; Prüm Syncline, Eifel, Germany.

Septalaria gracilis (Gürich, 1896) Fig. 19K–T

- v* 1896 *Camarophoria gracilis* n. sp. Gürich, pp. 278–279, pl. 7, fig. 3a–g.
- v. 1975 Septalaria descendens n. sp. Schmidt, pp. 93–96, text-figs 2, 6, pl. 3, figs 15–16, pl. 4, figs 17–18 [ubi syn.].
- v. 2013 Septalaria gracilis (Gürich, 1896) Halamski and Baliński, pp. 267–269, figs 15, 16K–O, Q–OO [ubi syn.].
- v. 2022a Septalaria gracilis (Gürich, 1896) Halamski et al., pp. 30–31, figs 17K, Y, 18.

Material: Two complete well-preserved shells and 12 more or less fragmentary specimens, ZPAL V.74/Bp/26 (see Tab. 4).

Description: Shells subpentagonal in outline, profile strongly dorsibiconvex, tongue high with nearly flat top

and subparallel sides. Costae 4–7 in the sulcus, 5–8 on the fold and 6–8 on each flank. The costae are marked from near the umbonal region to slightly posteriorly to shell midlength.

Remarks: Following the taxonomic treatment by Halamski and Baliński (2013) and by Halamski *et al.* (2022a), the shells described here are included within the widely understood species *Septalaria gracilis* (incl. *S. descendens*). The two shells from Miłoszów have a slightly wider, less sharply delineated ventral sulcus than specimens described by these authors; this feature is interpreted as corresponding to intraspecific variation.

A single small and deformed shell, described by Biernat (1966) from Miłoszów as *Septalaria* cf. *subteragona* (Schnur, 1851), may be conspecific with the present material but its poor preservation precludes a close taxonomic evaluation.

Occurrence: Miłoszów, M2-2, M3-7, Givetian.

Genus Nemesa Schmidt, 1941

Type species: Nemesa nemesana Schmidt, 1941; Rommersheimer Beds, Eifelian, Middle Devonian; Gondelsheim, Eifel, Germany.

Nemesa sp. Fig. 19U–DD, 20

1966 Pseudocamarophoria sp. – Biernat, p. 104, pl. 17, fig. 5.

Material: One nearly complete shell, two shells partially damaged and 16 more fragmentary specimens, ZPAL V.74/ Bp/25.

Description: Shell medium in size, attaining up to about 30 mm in width, dorsibiconvex, transversally elliptical in outline, wider than long; lateral margins rounded, anterior margin truncated, anterior commissure uniplicate, nonserrate.

Ventral valve with weakly convex flanks and incurved beak; sulcus appears slightly posteriorly to midlength, wide, with usually single, weak median plica, sometimes bearing poorly visible and wide median furrow; tongue short, trapezoidal and rounded. Dorsal valve with well marked fold appearing slightly posterior to mid-length; fold bearing shallow and wide median furrow resulting in weakly biplicate appearance. Flanks of both valves smooth.

Ventral interior without discernible dental plates; teeth with fossettes. In dorsal valve high median septum present;

Table 4

Biometric characteristics of *Septalaria gracilis* (Gürich, 1896) from the Givetian of Miłoszów.

| Cat. No. | L | W | Т |
|---------------------|------|------|------|
| ZPAL Bp V.74/Bp/26/ | | (mm) | |
| M3/1 | 11.0 | 13.4 | 8.5 |
| M2/1 | 14.1 | 16.7 | 10.7 |



Fig. 19. Givetian rhynchonellides from Miłoszów. A–J. *Isopoma brachyptyctum* (Schnur, 1853); specimens ZPAL V.74/Bp/27/M1/1 from M1-IIa and ZPAL V.74/Bp/27/M0/1 from M0-9. K–T. *Septalaria gracilis* (Gürich, 1896); specimens ZPAL V.74/Bp/26/M3/1 from outcrop M3-7 and ZPAL V.74/Bp/26/M2/1 from outcrop M2-2. In the latter note the epizoan strophalosioid brachiopod shown by a paper arrow glued onto the ventral valve (compare Fig. 5R). U–DD. *Nemesa* sp.; specimens ZPAL V.74/Bp/25/M3/1, 2 from outcrop M3-7. All specimens are articulated shells in dorsal, ventral, lateral, posterior, and anterior views.

septalium short, hinge plates horizontal, divided anterior of septalium (Fig. 20).

Remarks: The specimens studied are assigned to the genus *Nemesa* Schmidt, 1941, mainly on the basis of the similarity of the external appearance of the shell and resemblance in internal structure to the type species of the genus *N. nemesana* Schmidt, 1941 from the Eifelian of the Eifel. The weak median plica in the ventral sulcus and smooth flanks in the majority of specimens from Miłoszów and the Eifel seem to be particularly characteristic. The former differ from the type species mainly by attaining greater shell dimensions and by total absence of weak radial ribs which occur in some specimens of *N. nemesana*. The sections of the shell of *N. nemesana* shown by Schmidt (1941, pl. 7,

figs 22–24) revealed the absence of free, well individualized dental plates. The same situation is observed in the species from Miłoszów (Fig. 20). The cardinal process is not visible on the cross-sections of both *N. nemesana* and the form from Miłoszów, contrary to specimens of *Nemesa hertae* Havlíček, 1961 described by Havlíček (1961, pp. 190–192, pl. 27, figs 13–15, text-figs 85–86) from the Eifelian of the Czech Republic. *Nemesa hertae* also differs from the present specimens in having a smaller and ribbed shell. *Isopoma? ren* Schmidt, 1951 from the Upper Givetian of Germany, which Havlíček (1961) included in the genus *Nemesa*, is externally similar to the specimens from Miłoszów in the outline of the shell and character of the sulcation, but differs in achieving smaller dimensions, having better marked radial



Fig. 20. Transverse serial sections of *Nemesa* sp. through the shell ZPAL V.74/Bp/25/M3/3 from M3-7. Distances measured in millimetres from the tip of the ventral umbo.

ribs and, according to Schmidt's description (1951, p. 88), in absence of a dorsal median septum. The specimens from Miłoszów probably represent a still undescribed species, but the present material is insufficient to provide a basis for a formal description of the species. **Occurrence:** Miłoszów, M3-7, rare.

Superfamily Pugnacoidea Rzhonsnitskaya, 1956 Family Pugnacidae Rzhonsnitskaya, 1956 Genus *Parapugnax* Schmidt, 1964

Type species: *Pugnax pugnus brecciae* Schmidt, 1941; Iberg Limestone, Frasnian; Langenaubach near Haiger, Dill Syncline, Germany.

Remarks: The scarce material from Miłoszów is described here as belonging to two separate species, *Pugnax anisodontus* (Phillips, 1841) and *P. denticulatus* (Maurer, 1885) [for gender of *Parapugnax*, see Halamski *et al.*, 2022a, p. 31]. As explained in the introduction to the systematic part, in such a dubious case a splitting treatment is preferred because of uncertain stratigraphy both in England and at Waldgirmes, absence of intermediary forms in our material, and stratigraphic separation between the two morphotypes. The two taxa are, however, likely to have belonged to a single biological species, as proposed by Höflinger and Jung (2020).

Parapugnax anisodontus (Phillips, 1841) Figs 21F–DD, 22

- * 1841 *Terebratula anisodonta* Phillips, p. 86, pl. 34, fig. 154.
- non 1966 Pugnax cf. anisodonta (Phillips, 1841) Biernat, p. 109, pl. 17, fig. 13, pl. 19, fig. 30 [P. denticulatus].
- ? 2013 Parapugnax? cf. skalensis (Biernat, 1966)
 Halamski and Baliński, p. 269, fig. 16A– J, P.

Material: Five nearly complete and 21 fragmentary and deformed shells, ZPAL V.74/Bp/28/M1.

Additional material examined: Articulated shell SMF 102232, Grube Haina, Waldirmes, Givetian (leg. Müller 1948).

Description: Shell medium-sized, dorsibiconvex, widely subelliptical to subpentagonal in outline, transverse, about 1.5 times wider than long, maximal width at about mid-length or slightly anteriorly; cardinal margin obtuse, apical angle attaining 125°–133° (see Tab. 5), lateral margins rounded with strongly zigzagged commissure, anterior margin truncated, anterior commissure widely uniplicate, strongly serrate.

Ventral valve weakly convex, flanks near lateral margins depressed to weakly concave; sulcus U-shaped, deeply excavated, wide, occupying 63–79% of the valve width, tongue trapezoidal, high, slightly concave, with straight top; umbonal region and beak too poorly preserved to describe. Dorsal valve strongly convex, highly parabolic in anterior view, slightly arched in the lateral profile, but frequently more straight near anterior margin; fold wide, well marked, confined to the anterior part of the valve, with flat to slightly convex top; flanks strongly expanded ventrally.

Shell paucicostate, ornamented with strong costae restricted to the anterior and lateral regions of valves; 3 costae in sulcus, 4 on fold and 3–4 on flanks, parietal portions smooth, occasionally with a single faint costa; costae rounded, gradually more angular to acute-crested approaching the commissure, those on fold and ventral flanks with deflected tips at the margins. Micro-ornament of faint growth lines only, radial striae or capillae not observed.

Ventral interior with well developed, subparallel dental plates and distinct umbonal chambers; muscle filed wide, impressed. Interior of dorsal valve with divided, subhorizontal hinge plates, not supported by median septum; median myophragm well-developed, fairly high, triangular in cross section and wide (Fig. 22).

Remarks: The present specimens have been included in the genus *Parapugnax* on the basis of their characteristic pugnacoid shell form and similarity in the internal shell structure to that of the type species of the genus, i.e., *Parapugnax brecciae* (Schmidt, 1941) expressed in the presence of well-developed dental plates, divided hinge plates and the absence of crural support. The difference between these forms, which should be commented, concerns the dorsal median septum which is absent in specimens from Miłoszów (instead, a strong dorsal myophragm is developed), but was



Fig. 21. Givetian representatives of the rhynchonellide genus *Parapugnax* from Miłoszów in the Holy Cross Mts. and Waldgirmes in the Lahn Syncline. **A–E.** *Parapugnax denticulatus* (Maurer, 1885), specimen ZPAL V.74/Bp/68/M0/1 from outcrop M0-9 at Miłoszów. **F–DD.** *Parapugnax anisodontus* (Phillips, 1841). F–J – specimen SMF 102232 from Waldgirmes; K–Y – specimens ZPAL V.74/Bp/28/M1/1–3 from M1-IIa at Miłoszów; Z–DD – specimen SMF 102231.1 from Waldgirmes. All specimens are articulated shells in dorsal, ventral, lateral, posterior, and anterior views.
Table 5

| Cat. No. ZPAL | L | W | W/L | Т | ws | No. of median | No. of lateral | A |
|----------------|-------|------|-------|------|------|---------------|----------------|--------------|
| Bp V.74/Bp/28/ | (mm) | | W/L | (mm) | | ribs | ribs | Apical angle |
| M1/5 | 10.0 | 15.0 | 1.50 | 8.9 | 9.6 | 3/4 | 4 | 125° |
| M1/1 | ~10.8 | 16.8 | ~1.56 | 9.7 | 11.6 | 3/4 | 3 | 125° |
| M1/2 | 11.0 | 17.5 | 1.59 | 9.3 | 11.0 | 3/4 | 4 | 132° |
| M1/3 | 12.2 | 18.7 | 1.53 | 12.7 | 14.8 | 4/4 | 4 | 133° |

Biometric characteristics of Parapugnax anisodontus (Phillips, 1841) from the Givetian of Miłoszów.

recognized in the type specimens from Germany by Schmidt (1964, 1965). However, as Johnson *et al.* (1969, pp. 1358, 1360) remarked, the supposed median septum, illustrated on Schmidt's (1965, figs 7–11) serial sections of the type species *P. brecciae*, does not extend to the anterior end of the hinge plates and may rather be a myophragm exaggerated by the orientation of sections in relation to the dorsal beak curvature. The present authors are inclined to this point of view.

The two samples from Miłoszów, described here as separate species, differ mainly in the costation: the ribs start in the anterior region in *P. anisodontus* known from M1-IIa, whereas they start in the umbonal region in *P. denticulatus* known from M0-9.

Externally *Parapugnax anisodontus* is similar to '*Pugnax*' bernesgae Mohanti, 1972, described from the Eifelian–Givetian transitional beds of the Cantabrian Mountains (Mohanti, 1972). Both species have similar transverse shell shapes, slightly concave ventral flanks, wide fold and sulcus, strongly zigzagged commissures, and costate anterior regions of the shell. *P. denticulatus* differs in attaining larger size and in the lack of shell geniculation. Internally, '*P.*' bernesgae has a short dorsal median septum supporting hinge plates which is not developed in *P. anisodontus*.

Occurrence: Miłoszów, Ml-IIa; two fragmentary specimens were found in limestone, exposed in pit P-1 representing the Pokrzywianka beds. Lahn Syncline, Givetian (Maurer, 1885).

Parapugnax denticulatus (Maurer, 1885) Fig. 21A–E

- * 1885 *Rhynchonella anisodonta* Phill. var. *denticulata* n. Maurer, pp. 205–206, pl. 8, fig. 32.
 - 1966 *Pugnax* cf. *anisodonta* (Phillips, 1841) Biernat, p. 109, pl. 17, fig. 13, pl. 19, fig. 30.
 - 2022a Parapugnax denticulatus (Maurer, 1885) Halamski et al., pp. 31–34, figs 17Z–II, 19.

Material: A single incomplete articulated shell ZPAL V.74/ Bp/68/M0/1.

Additional material examined: Articulated shell SMF 102231.1, Grube Haina, Waldirmes, Givetian (leg. Müller 1948).

Description: The single incomplete shell available from Miłoszów measures 13.8 mm in length, has a distinct pugnacoid aspect and is similar to the shells, described above as *P. denticulatus*. It differs from the latter in having long



Fig. 22. Transverse serial sections of *Parapugnax anisodontus* (Maurer, 1885) through the shell ZPAL V.74/Bp/28/M1/4 from M1-IIa. Distances measured in millimetres from the tip of the ventral umbo.

costae starting from the umbonal regions of the shell. There are five costae on the fold, four in the sulcus and four on a preserved dorsal flank. The fold is wide, appears slightly posteriorly to mid-length and is flat arched. The ventral valve has weakly concave flanks and weakly trapezoidal and flat tongue.

Remarks: For comparison with *P. anisodontus*, see above. **Occurrence:** England; Germany, Lahn Syncline; Morocco, probably southern Maïder; Miłoszów, M0-9.

Family Aseptirhynchiidae Savage, 1996

Remarks: The subdivision of the superfamily Pugnacoidea proposed by Savage (1996) is followed. The family Isopomatidae Sartenaer and Ebbighausen, 2007 (corrected name for Isopomidae, see Halamski *et al.*, 2022a, p. 34) is not used here.

Genus Isopoma Torley, 1934

Type species: *Terebratula brachyptycta* Schnur, 1853; Freilinger Schichten, Eifelian, Middle Devonian; Blankenheim, Eifel, Germany.

Isopoma brachyptyctum (Schnur, 1853) Figs 19A–J, 23

- 1853 *T.* [*Terebratula*] *brachyptycta* n. sp. Schnur, p. 178, pl. 3, fig. 6a–c.
- p 1966 *Isopoma brachyptyctum* (Schnur, 1853) Biernat, pp. 106–108 (partim), text-fig. 35, pl. 22, figs 1–9.

- 1998 Isopoma brachyptyctum (Schnur, 1853) Mohanti and Brunton, pp. 156–157, figs 1–5, 19.
- 2007 Isopoma brachyptyctum (Schnur, 1853) Sartenaer and Ebbighausen, pp. 49–58, pl. 1, figs 1–35, pl. 2, figs 36–70 [ubi syn.].

Material: Nearly 50 complete or subcomplete shells and 70 more fragmentary shells and single valves, some of them embedded in limestone, ZPAL V.74/Bp/27. Most specimens come from limestone (M0 and M3 outcrops), all others were found in weathered shale of the M1 trench.

Remarks: This species was described from the studied area in detail, including the internal structure of the shell based on serial sections by Biernat (1966, pp. 106-108, pl. 22, figs 1-9, text-fig. 35). Her description was based on specimens originating partly from Miłoszów, the same locality from which the material studied here originates. Here, we show serial sections of one of the recently found shells from Miłoszów (outcrop M0, bed 9; see Fig. 21). The sections show no traces of dental plates, but the presence of strong teeth is noteworthy. In the dorsal valve there are thick, unsupported and inclined outer hinge plates with well marked crural bases. The crura are thick, proximally subparallel, distally becoming divergent and strongly curved ventrally. Although a median ridge is present in both valves, that in the dorsal valve is narrower and more angular. The new material fully agrees with the description of Biernat (1966) as well as with specimens from the type and adjacent area in Germany (Schnur, 1853; Schmidt, 1941; Mohanti and Brunton, 1998; Sartenaer and Ebbighausen, 2007).



Fig. 23. Transverse serial sections of *Isopoma brachyptyctum* (Schnur, 1853) through the shell ZPAL V.74/Bp/27/M9/3 from M0-9. Distances measured in millimetres from the tip of the ventral umbo.

The shells from Miłoszów are characterized by having invariably two costae in the sulcus, three costae in the fold and two-three (rarely four) costae on each flank. The median groove, separating the two costae in the sulcus, is slightly better accentuated than other intercostal grooves but extends posteriorly no further than the midlength. *Isopoma hertae* Mohanti, 1972 described from the Eifelian–Givetian transitional beds of the Portilla Formation of the Cantabrian Mountains has the same pattern of the shell costation, but differs, among other things, in having a longer median groove in the ventral valve starting closer to the umbo.

Occurrence: Mohanti and Brunton (1998) reviewed the stratigraphic and geographic distribution of the species. According to their study Isopoma brachyptyctum ranges from the middle Eifelian to the upper Givetian. More recently, however, Sartenaer and Ebbighausen (2007) made a critical and very detailed review of all occurrences of this species, concluding that it is confined to the Upper Eifelian and thus rejecting all its Givetian records. Although the species had previously been reported from Germany, Poland, Moravia, Russia, Transcaucasia and China, Sartenaer and Ebbighausen (2007) limited its occurrence to the first two countries. At the same time, they remarked that no element allows separation of the Polish specimens of Isopoma brachyptyctum from those of the type area (Sartenaer and Ebbighausen, 2007, p. 58). The present material comes from the Givetian (outcrops M0, M1 and M3) of Miłoszów.

> Order Atrypida Rzhonsnitskaya, 1960 Suborder Atrypidina Moore, 1952 Family Atrypidae Gill, 1871 Subfamily Atrypinae Gill, 1871 Genus *Atrypa* Dalman, 1828

Type species: *Anomia reticularis* Linnaeus, 1758 emend. Alexander, 1949. Lower Hemse beds, Gorstian, Ludlow, Silurian; Hammarudden, Östergarn parish, Gotland, Sweden (see Copper, 2004, p. 37).

Remarks: The distinction between *Atrypa* (*Atrypa*), *A.* (*Planatrypa*), and *Kyrtatrypa* is clear-cut only when type species of the three (sub)genera are concerned. There exist species having intermediate characters, like *A. confusa* (Struve, 1992) (see details in Halamski and Baliński, 2013, p. 273) and *A. subtrigonalis* Biernat, 1964 (see below). The present authors place *A. subtrigonalis* in the genus *Atrypa*, refraining from using any subgeneric subdivision.

Atrypa subtrigonalis Biernat, 1964 Figs 24, 25

- 1896 Atrypa reticularis var. trigonalis Gürich, p. 270 [nomen nudum].
- v* 1964 Atrypa subtrigonalis n. sp. Biernat, pp. 298–303, text-figs 6, 7, 8 (la–c), 9, pl. 2, figs 1–8.
- v. 1966 Atrypa (Kyrtatrypa?) subtrigonalis Biernat – Struve, pp. 135, 136, 137.

- ? 1981 Atrypa subtrigonalis Biernat Łobanowski, p. 253.
- non 1996 Atryparia (Atryparia) subtrigonalis (Biernat) – Alekseeva, pp. 115–117, textfig. 61, pl. 13, figs 6, 7.
- non 2001 *Atrypa (Planatrypa) subtrigonalis* Biernat – Halamski, pl. 1, fig. 1a–b [= *A. depressa* Sobolew, 1904].
- v. 2022b Atrypa subtrigonalis Biernat, 1964 Halamski et al., pp. 353, 363, fig. 22A–C.

Material: Over seventy articulated shells, but infrequently complete, ZPAL V.74/Bp/29.

Description: Shell shield-shaped in outline, strongly dorsibiconvex, up to 19.9 mm in width, typically 14–17 mm long and wide, slightly wider than long or slightly longer than wide [width-to-length ratio (0.91-)0.96-1.03(-1.06); N = 20], rather weakly convex [thickness-to-length ratio (0.47-)0.55-0.62(-0.71); N = 20]. Maximum width posteriorly to mid-length of the shell. Anterior commissure straight to uniplicate; tongue not seldom lacking even in fully grown specimens; if present, relatively narrow [its width making (0.37-)0.42-0.54(-0.59) of that of the shell] and low (never higher than 5 mm, usually much lower), rounded to subtriangular. Ventral valve regularly arched in anterior view; beak appressed to the dorsal valve. Dorsal valve lowly triangular in anterior view.

Ornament of fine radial ribs, (9–)10–11(–15) per 5 mm at anterior margin. New ribs arising mostly by bifurcation on the ventral valve, and by intercalation on the dorsal valve. Frills preserved in three specimens, up to 5 mm long.

Ventral interior: dental nuclei weak, but distinct; teeth stout, bilobed. Dorsal interior: small cardinal pit with the cardinal process; hinge plates relatively thin; long crural bases (Fig. 25); dorsally oriented spiralium, eight whorls observed. **Remarks:** These brachiopods are included into the family Atrypidae, subfamily Atrypinae on account of the presence of undulose ribs, frills, and of a cardinal process, whereas spines or a ventral carina are absent (Copper, 2002). Within the subfamily, they are conventionally placed in the genus Atrypa (see above, remarks on the genus). The material at hand agrees with Atrypa subtrigonalis Biernat, 1964, described from Skały in fine radial ornament with new ribs arising mostly by intercalation on the dorsal and bifurcation on the ventral valve (checked on the original material), lowly subtrigonal ventral valve, maximum width situated posteriorly, and in the presence of relatively large specimens with rectimarginate anterior commissure. The interior is also quite similar to that illustrated by Biernat (1964, text-fig. 6), especially in the bilobed teeth and rather thin hinge plates. The only difference is in smaller size of the present material (in the Skały sample the maximum reported width is 25.3 mm; Biernat, 1964); this is estimated to have no taxonomic significance.

The type locality of *A. subtrigonalis* was given by Biernat (1964, p. 298), as "shales, complex XIII, outcrop 72" at Skały. However, set XIII *sensu* Pajchlowa (1957) consists of organodetritic limestones and the outcrop 72 belongs to set XIV. Investigations of the present authors failed to establish the presence of this species in set XIV (Halamski

and Zapalski, 2006). The preservational aspect of the type material indicates that the shells come from limestone rather than from shale. The type stratum of the discussed species cannot be given at present with certainty; it can be supposed that it belongs to limestone of set XIII or XV, thus Eifelian (probably Upper Eifelian) in age.

Atrypa subtrigonalis Biernat, 1964 is especially similar to *Atrypa (Planatrypa) tirocinia* Copper, 1967 from the Eifel Mts. in the general shell form and size; the Polish form is distinguished by its finer ornament.

Among the representatives of the Atrypidae from the Holy Cross Mts. the species in question can be easily distinguished precisely thanks to its particularly fine ribbing. *Atrypa (Planatrypa) depressa* Sobolew, 1904 from the Upper Eifelian of Skały has moreover a flat ventral valve.

Brachiopods from Siberia, described by Alekseeva (1996) as "*Atryparia (Atryparia) subtrigonalis* (Biernat, 1966)", characterised, in comparison with the Holy Cross specimens, by twice as coarse costellae and somewhat different proportions of the shell, cannot be considered as conspecific. It is uncertain whether *Atrypa subtrigonalis* sensu Łobanowski (1981; neither description nor figure) from the Upper Emsian of Bukowa Góra is conspecific with the genuine *Atrypa subtrigonalis*.

Distribution: Miłoszów: M3-7, Lower Givetian; Skały: most probably (Upper?) Eifelian.

Genus Atryparia Copper, 1966b

Type species: *Atryparia instita* Copper, 1966b; Ahbach Beds, Upper Eifelian (Copper, 1966b); Mühlenberg near Niederehe, Hillesheim Syncline, Eifel, Germany.

Atryparia cf. instita Copper, 1966b Fig. 26G–P

cf. * 1966b *Atryparia instita* n. gen., n. sp. – Copper, pp. 3–5, figs 2, 1–4.

Material: Two articulated shells, ZPAL V.74/Bp/30.

Description: Shell shield-shaped to pentagonal in outline, about 20–24 mm long, longer than wide (width-to-length ratios 0.86–0.96), moderately to markedly dorsibiconvex. Ventral valve lowly triangular in anterior view, umbo fine, beak suberect. Dorsal valve parabolic in anterior view. Anterior commissure straight to uniplicate; tongue, if present, low. Ornament of straight, bifurcating ribs, 3–4 per 5 mm at anterior margin; growth lamellae distinct, relatively widely spaced. Interior not studied.

Remarks: These brachiopods are assigned to *Atryparia* on account of coarse ribs, interrupted by relatively widely spaced growth lines (see Copper, 2002). The present material seems close to the insufficiently known Upper Eifelian species *A. instita*; both have an approximately shield-shaped outline and somewhat flattened coarse ribs; however, *A. instita* is described as having "equally convex valves except in late maturity" (Copper, 1966b). The Middle Eifelian *A. eta* Struve, 1995 has finer ribbing (about 5 per 5 mm). *Atryparia dispersa* (Struve, 1966) is more strongly dorsibiconvex.

Distribution: Miłoszów, M1-I.



Fig. 24. Middle Devonian atrypide brachiopod *Atrypa subtrigonalis* Biernat, 1964 from Miłoszów and Skały. A–E, F–J, K–O, P–T, U–Y. Articulated shells ZPAL V.74/Bp/29/M3/1–5 in dorsal, ventral, lateral, posterior, and anterior views; Miłoszów, M3-7, Givetian.
Z–DD. Holotype, articulated shell ZPAL Bp VI/251 (specimen figured by Biernat, 1964, pl. 2, fig. 3) in dorsal, ventral, lateral, posterior, and anterior views; Skały, Skały Formation, possibly set XIII or XV, thus late Eifelian (see text for discussion).

Subfamily Spinatrypinae Copper, 1978 Genus *Isospinatrypa* Struve, 1966

Type species: *Terebratulites asper* von Schlotheim, 1813; Middle Devonian; Eifel, Germany.

> *Isospinatrypa* sp. Figs 26A–F, 27A

Material: Seven subcomplete to incomplete articulated shells and a few fragments, ZPAL V.74/Bp/31.

Description: Shell subcircular in outline, up to about 18 mm in length, typically 10–13 mm long and wide and 5–7 mm thick. Ventral valve slightly more convex than the dorsal one or both valves of the same convexity. Ventral umbo fine, beak suberect. Anterior commissure approximately straight. Ornament of undulating ribs, 10–14? in total, 2–4 per 5 mm at anterior margin, crossed by strong growth lamellae, thus producing imbricate-like thickenings over ribs at crossings; a slightly stronger midrib pair present on the ventral valve.

Ventral interior with well marked dental nuclei, expanding anteriorly into dental cavities, and slightly divergent dental plates; teeth massive with lateral lobes; deltidial plates small; pedicle callist small. Dorsal interior with deep sockets and low middle socket ridge; cardinal process lining a deep cardinal pit.

Remarks: These brachiopods are included into the family Atrypidae, subfamily Spinatrypinae on account of the nodular surface macroornament and into the genus *Isospinatrypa* on account of small size and nearly biconvex (weakly ventribiconvex) shell (Copper, 2002). *Invertrypa* is strongly ventribiconvex with flattended dorsal valve; here the dorsal valve is convex, although less so than the ventral one.

Among similar species one may note other smallsized Middle Devonian representatives of the genus, like *Isospinatrypa faseleta* Struve, 1992 from the Freilingen or *Isospinatrypa parva* (Li and Jones, 2003) from the Bird Fiord Formation (Eifelian) in Arctic Canada, but the material at hand is insufficient for a species-level identification. *Isopinatrypa asperoides* (Biernat, 1966) from the uppermost Eifelian of Skały has a finer ornament.

Distribution: Miłoszów: M0, bed 9.

Genus Spinatrypa Stainbrook, 1951

Type species: "Atrypa hystrix var. occidentalis Hall" (lapsus calami pro Atrypa aspera var. occidentalis Hall, 1858) sensu Stainbrook, 1945; Cedar Valley Formation, Frasnian; Iowa, USA.

Spinatrypa wotanica Struve, 1964 Figs 27B, 28, 29

- v* 1964 *Spinatrypa aspera wotanica* ssp. n. Struve, pp. 529–530, fig. 2.
- . 1967 Spinatrypina wotanica (Struve 1964) Copper, pp. 517–518, pl. 82, figs 23–28, 83, figs 1–4.

Material: 68 mostly slightly damaged (deformed and compressed diagenetically) articulated shells, about 20



Fig. 25. Transverse serial sections of *Atrypa subtrigonalis* Biernat, 1964 through the shell ZPAL V.74/Bp/29/M3/6 from M3-7. Distances measured in millimetres from the tip of the ventral umbo.

fragmentary specimens and 8 single valves; in addition, several dozen juvenile shells ranging from below 1.0 to 3.5 mm in length, ZPAL V.74/Bp/32.

Description: Shell rounded penta- or hexagonal to rounded in outline, up to 14.4 mm in width, typically about 11–13 mm long and wide, weakly ventribiconvex, rather weakly convex (typically 5–6 mm high, but most specimens are flattened). Anterior commissure uniplicate, tongue broad, rather low. Ventral valve subtriangular in anterior view; interarea orthocline; delthyrium partly closed by deltidial plates, foramen submesothyrid. Dorsal valve lowly rounded to flattened in anterior view.

Ornament of tubular ribs, 19–26 in total on the dorsal valve, new ones appearing by bifurcation, more seldom by intercalation; growth lines moderately strong, producing thickenings on crossings with ribs; spines rarely preserved, but present (Fig. 28).

Internally relatively thick-shelled (Fig. 27B). Ventral interior with dental nuclei and small dental cavities; teeth large with small lateral lobes; deltidial plates present, delicate; pedicle collar not discernible in the sectioned shell. Dorsal interior with wide sockets and weakly developed middle socket ridge; cardinal process lining inner socket ridges and cardinal pit.

Remarks: This species was initially described as a subspecies of '*Spinatrypa*' aspera (now *Isospinatrypa aspera*). Copper (1967) transferred it to *Spinatrypina*, but both the type material of Struve (1964) and the specimens from Miłoszów have spines (Fig. 28), so the assignment to *Spinatrypina* is excluded.

Distribution: Eifel region, Lower Givetian; Miłoszów: Ml-IIa, Lower Givetian.

Subfamily Variatrypinae Copper, 1978 Genus *Desquamatia* Alekseeva, 1960

Type species: *Atrypa (Desquamatia) khavae* Alekseeva, 1960; lower Eifelian; Urals, Russia.

Subgenus Desquamatia (Desquamatia) Alekseeva, 1960

Type species: As for the genus.

Desquamatia (D.) subzonata Biernat, 1964 Fig. 30A–J



Fig. 26. Givetian atrypides from Miłoszów. **A–F.** *Isospinatrypa* sp. from outcrop M0-9; A–E – incomplete articulated shell ZPAL V.74/ Bp/31/M0/1 in dorsal, ventral, lateral, posterior, and anterior views; F – incomplete articulated shell ZPAL V.74/Bp/31/M0/2 in dorsal view. **G–P.** *Atryparia* cf. *instita* Copper, 1966b from trench 2 (leg. A. Baliński, 1970); G–K, L–P – articulated shells ZPAL V.74/Bp/30/ MS2/1–2 in dorsal, ventral, lateral, posterior, and anterior views.



Fig. 27. Transverse serial sections of *Isospinatrypa* sp. through the shell ZPAL V.74/Bp/31/M0/3 from M0-9 (A) and of *Spinatrypa wotanica* Struve, 1964 through the shell ZPAL V.74/Bp/32/M1/7 from M1-IIa (B). Distances measured in millimetres from the tip of the ventral umbo.



Fig. 28. Lower Givetian atrypide brachiopod *Spinatrypa wotanica* Struve, 1964 from outcrop M1-IIa at Miłoszów. A–E, F–J. Articulated shells ZPAL V.74/Bp/32/M1/1, 2 in dorsal, ventral, lateral, posterior, and anterior views. K–O, BB; P–T, CC; U–Y, DD. Articulated shells ZPAL V.74/Bp/32/M1/3–5, respectively, in dorsal, ventral, lateral, posterior, and anterior views and enlargements of the ventral interarea. Z, AA, EE. Incomplete articulated shell ZPAL V.74/Bp/32/M1/6 in dorsal view and enlargements of the ventral interarea and of the median region of the valve with epizoan ascodictyids *Allonema* sp.



Fig. 29. Lower Givetian atrypide brachiopod *Spinatrypa wotanica* Struve, 1964 from the Eifel (A, B, D, E; Nohner Mühle, locality 127 *sensu* Struve, 1964) and of the Holy Cross Mts. (C, F; Miłoszów, outcrop M1-IIa). **A**, **D**. Articulated shell SMF 19090.1 (paratype): dorsal view and enlargement of the spine bases in more inclined view. **B**, **E**. Articulated shell SMF 19090.2 (paratype): dorsal view and enlargement of the spine bases in more inclined view. **C**, **F**. Articulated shell ZPAL V.74/Bp/32/M1/8: dorsal view and inclined dorso-lateral view of partial enlargement showing the spine bases on the left.

- ↓ 1896 Atrypa desquamata Sow. Gürich, p. 271 [excl. var.].
 - 1904 Atrypa desquamata Sow. Sobolew, p. 84, pl. 9, fig. 6.
- p 1909 Atrypa desquamata Sow. Sobolew, p. 487.
- v. 1961 Atrypa zonata Schnur Biernat, pp. 17–27, pl. 1, figs 1–6, pl. 2, fig. 3, pl. 3, figs 1–3, pl. 4, figs 1–3.
- v* 1964 *Desquamatia subzonata* n. sp. Biernat, pp. 319–322, text-figs 3(3), 8(3), 16, 17, pl. 7, fig. 10, pl. 8, figs 1–7, pl. 9, figs 1–8.
- . 1970 *Desquamatia subzonata* Biernat MacKinnon and Biernat, pp. 170–171, fig. 1A.
- cf. 1995 Desquamatia cf. subzonata Biernat Godefroid, p. 110.
 - 2010 *Desquamatia subzonata* Biernat Baliński and Sun, fig. 1C.
- cf. 2022a *Desquamatia* cf. *subzonata* Biernat Halamski *et al.*, p. 42–43, fig. 23G–K, AA.

Material: Two subcomplete adult articulated shells, over 15 juvenile or incomplete ones, ZPAL V.74/Bp/33.

Description: Shell subcircular in outline with weakly angular postero-lateral extremities, moderately dorsibiconvex, up to 20.2 mm wide. Ventral umbo fine, beak almost appressed against the dorsal umbo. Anterior commissure straight. Ornament of tubular ribs, about 10 per 5 mm at anterior margin, interrupted by growth lines; frills seldom preserved. Interior not studied.

Remarks: The described brachiopods are included into *Desquamatia* on account of tubular ribs interrupted by distinct growth lines with frills. Subcircular outline, dorsibic-onvexity, and ribbing density are the same as in *D. subzonata* from the Upper Eifelian of Skały. The Middle Eifelian *Desquamatia microzonata* Struve, 1966 from the Eifel is very similar to *D. subzonata* Biernat, 1964: the shape of the shell is identical, the differences lie in denser ribbing and slightly smaller size of the former species (see also Halamski and Baliński, 2013, pp. 278–279).

Distribution: Miłoszów: Ml, Lower Givetian. Skały: Upper Eifelian (type locality). Błonia Sierżawskie near Świętomarz, (Middle?) Givetian (Halamski, 2004b). *Desquamatia* cf. *subzonata* was reported from the Middle



Fig. 30. Givetian representatives of the atrypide genus *Desquamatia* from Miłoszów. **A–J.** *Desquamatia* (*D.*) *subzonata* Biernat, 1964 from outcrop M1-IIa; A–E, J – articulated shell ZPAL V.74/Bp/33/M1/1 in dorsal, lateral, posterior, and anterior views (A–E) and enlargement of ventral ornamentation (J); F–I – articulated shell ZPAL V.74/Bp/33/M1/2 in dorsal, ventral and anterior views (F–H) and enlargement of ventral ornamentation (I). **K–AA.** *Desquamatia* (*Independatrypa*) *circulareformis* Biernat, 1964 from outcrop M0-9 (specimens probably approximately strato- and topotypic); K–O, P–T – articulated shell ZPAL V.74/Bp/37/M0/1, 2 in dorsal, ventral, lateral, posterior, and anterior views (see also Fig. 34O); U–AA – articulated shell ZPAL V.74/Bp/37/M0/3 in dorsal, ventral, posterior, and lateral views (U–Y); ventral valve with embedding limestone to show frills (Z); enlargement of the median region of the ventral valve to show ornamentation (AA).

Devonian of the Ardennes (Godefroid, 1995) and Maïder (Halamski et al., 2022a).

Subgenus Desquamatia (Independatrypa) Copper, 1973

Type species: *Atrypa independensis* Webster, 1921; Cedar Valley Formation, middle Givetian; Iowa, USA.

Desquamatia (Independatrypa) circulareformis Biernat, 1964 Figs 30K–AA, 31, 34O

- v* 1966 Desquamatia circulareformis n. sp. Biernat, pp. 326–327, pl. 8, fig. 8, pl. 12, figs 2–3.
- v. 2013 Desquamatia (Independatrypa) circulareformis Biernat, 1964 – Halamski and Baliński, pp. 279, 281, fig. 26U–DD.
- v. 2022b Desquamatia (Independatrypa) circulareformis Biernat, 1964 – Halamski et al., pp. 325, 336, 353, figs 22HH–JJ, 27–6.

Material: Eight complete and nine slightly damaged shells, 37 fragmentary specimens, ZPAL V.74/Bp/37.

Type locality and stratum: Given in the original publication (Biernat, 1964, p. 326) as "Lower Givetian (Upper Eifelian?), argil[I]aceous limestone of Miłoszów. Miłoszów, Łysogóry region, Holy Cross Mountains". Most of the present material comes from M0-9, which belongs to the lower Middle Givetian. However, one cannot be entirely certain that this is the type stratum, as a few small specimens come also from M1-I (trench S2).

Description: Shell rounded in outline, up to 44.3 mm in length, weakly wider than long, moderately dorsibiconvex. Maximum width at mid-length of the shell, maximal thickness at $\frac{1}{3}$ of the shell length. Anterior commissure uniplicate, tongue rounded, occupying 0.3–0.4 of the shell width. Ventral valve markedly convex in umbonal region, somewhat flattened laterally and towards the anterior margin, sulcus very shallow and broad. Ventral interarea occupying $\frac{2}{3}$ of the shell width, apsacline, nearly straight, up to 4 mm in height; delthyrium occupying $\frac{1}{3}$ of the width of the

interarea, deltidial plates fused, pedicle foramen large (nearly half of the delthyrium height, submesothyrid). Dorsal valve semi-elliptic in anterior view, fold developed in the immediate proximity of the anterior margin, umbo rather thick, interarea not visible.

Ornament of strong radial ribs, originating in the umbonal region, new ones appearing by both bifurcation and intercalation, 4–5 per 5 mm at anterior margin in fully grown shells. Separating furrows approximately as wide as the ribs. Frills observed up to 15 mm long, ornamented similarly to the shell (Fig. 20Z).

Ventral interior (Fig. 31): Posterolateral regions of the valve relatively thick-shelled; clear dental nuclei expanding anteriorly into prominent large dental cavities and nearly vertical dental plates; teeth moderately sized with lateral lobes; distinctive, strong deltidial plates, in the sectioned shell with a T-shaped median ridge protruding into umbonal cavity; pedicle collar not discernible in the sectioned shell.

Dorsal interior (Fig. 31) with deep sockets and low, wide middle socket ridge; cardinal process wrapped around wide and deep cardinal pit; crural bases triangular in cross section, leading to fibrous crura.

Remarks: These brachiopods are included into *Desquamatia* (*Independatrypa*) on account of subcircular to shield-shaped shells with large tongues, although the latter character is well-marked only in the largest shells.

Distribution: Miłoszów: M0, relatively frequent; M1, seldom; Givetian. Upper Eifelian or Lower to Middle Givetian of Aferdou, southern Maïder, Anti-Atlas, Morocco (Halamski and Baliński, 2013).

Suborder Davidsoniidina Copper, 1996 Superfamily Davidsonioidea King, 1850 Family Davidsoniidae King, 1850 Genus *Davidsonia* Bouchard-Chantereaux, 1849

Type species: *Davidsonia verneuillii* Bouchard-Chantereaux, 1849; Upper Eifelian, Middle Devonian; Eifel, Germany.

> Davidsonia septata Copper, 1996 Fig. 32



Fig. 31. Transverse serial sections of *Desquamatia* (*I.*) *circulareformis* Biernat, 1964 through the shell ZPAL V.74/Bp/37/M0/4 from M0-9 (approximately strato- and topotypic). Distances measured in millimetres from the tip of the ventral umbo.



Fig. 32. The epibiontic atrypide brachiopod *Davidsonia septata* from the Givetian of Miłoszów. All specimens from outcrop MI-IIa or equivalent strata. **A–E.** Articulated shell ZPAL V.74/Bp/34/MP/1 in dorsal, ventral, lateral, posterior, and anterior views. **F, J, L.** Ventral interiors ZPAL V.74/Bp/34/MI/5, 34/MP/3, 4, and 34/MI/5. **G.** Articulated shell ZPAL V.74/Bp/34/MI/6 in dorsal view. **H, I.** Articulated shell ZPAL V.74/Bp/34/MI/6 in dorsal view. **H, I.** Articulated shell ZPAL V.74/Bp/34/MI/6.

- * 1996 Davidsonia septata new species Copper, pp. 596–597, figs 6, 8.1–8.6.
- . 2020 Davidsonia Zatoń and Wrzołek, pp. 3, 4, fig. 5C.
- v. 2022b *Davidsonia septata* Copper, 1996 Halamski *et al.*, p. 353, figs 22J–K, 27-5.

Material: Ten subcomplete articulated shells, four well preserved adult ventral valves, two juvenile ventral valves, and several less complete specimens, ZPAL V.74/Bp/34/M1, 74/ Bp/34/AP; also, specimens in the collection GIUS 422 (see Zatoń and Wrzołek, 2020).

Description: Shell variable in outline, rounded rectangular, elliptic, or semi-elliptic; the largest specimens about 10–11.5

mm wide and 8.5–10 mm long, width-to-length ratio about 1.0–1.3. Ventral valve cemented; interarea apsacline, delthyrium completely covered by markedly convex deltidial plates. Dorsal valve smooth or with strong growth lines. Ventral interior: median septum strong, thick, extending from the muscle area nearly to the anterior margin; spiralial cones with deeply incised grooves, four whorls observed; gonadal pits relatively weak. Dorsal interior with a pair of conical depressions with weakly marked spiralial grooves; a pair of adductor scars deeply indented, separated by median septum, which is thin and sharp umbonally and marked-ly thicker anteriorly; gonadal pits distinct, subperiferal rim well marked.

Remarks: Putting aside Early Frasnian Davidsonia enmerkaris Halamski in Baliński et al., 2016 and Middle Devonian Rugodavidsonia woodwardiana (de Koninck, 1855), two species with costate shells, the classification of smooth-shelled representatives of the genus Davidsonia is based mostly on internal characters of ventral valves. It follows that, strictly speaking, articulated shells cannot be identified with certainty, unless one assumes that all shells in a given sample belong to a single species. The material described herein consists mostly of articulated shells. Among the remaining five ventral valves, four can be identified as Davidsonia septata Copper, 1996 on account of a strong median septum extending from the muscle area to the marginal region of the ventral valve, relatively weak gonadal pits, and subquadrate shells (Fig. 32F, J, L). However, one of these five ventral valves seems morphologically closer to Davidsonia verneuillii Bouchard-Chantereaux, 1849 because of a weaker septum, stronger gonadal pits, and a wider shell (width-to-length ratio >1.4; Fig. 32J). The size criterion given by Copper (1996) does not seem appropriate, as the sample from Jbel Issoumour in Morocco, described by Halamski et al. (2022a), has shape characters of D. verneuillii, but the size given as characteristic of D. septata in the original description.

Davidsonia septata was described from the Banqao section in Yunnan; the type stratum is both underlain and overlain by layers with *Stringocephalus* (Copper, 1996), so undoubtedly Givetian in age (locally dated as late Givetian according to Copper, 1996). Davidsonia verneuillii is known from the Middle Devonian of Europe, Asia, North America, and northern Africa Devonian (Copper, 1996, p. 594; Halamski *et al.*, 2022a, p. 44). A possible interpretation of the known distribution of the two species is thus the origin of *D. septata* from *D. verneuillii* in Europe about the Early–Middle Givetian and its migration to China in the late Givetian. Alternatively, the *D. septata* and *D. verneuillii* could be considered as extreme morphological variants of a single biological species.

In the material investigated here, *Davidsonia septata* is an epizoan of tabulate corals (Fig. 32F, L), large solitary rugose corals (Zatoń and Wrzołek, 2020, fig. 5C), and of small colonial rugosans *Thamnophyllum* (Fig. 32H, I); at its turn, it is sometimes overgrown by hederelloids (Zatoń and Wrzołek, 2020). Platy tabulate corals (*Coenites*, *Roseoporella*, *Alveolites*) were frequently reported as hosts of *Davidsonia* and *Rugodavidsonia* (Mohanti, 1972, p. 150; Racki *et al.*, 1985, pl. 5, fig. 1, pl. 11, fig. 4; Copper, 1996; Baliński *et al.*, 2016, p. 153; Zatoń *et al.*, 2018). According to Copper (1996, p. 592), stromatoporoids are also frequent hosts, whereas less often *Davidsonia* was able to attach to "hardgrounds, rocky grounds, firmgrounds, or shell grounds". To the knowledge of the present authors, rugosans have not been reported previously as hosts of *Davidsonia*.

Occurrence: Banqao, Yunnan, China, Givetian; Miłoszów, Ml-IIa, Lower Givetian.

Family Carinatinidae Rzhonsnitskaya, 1960 Genus *Eifelatrypa* Copper, 1973

Type species: *Atrypa reticularis* var. *plana* Kayser, 1871; Middle Devonian, possibly Freilingen beds, Upper Eifelian; Eifel, Germany (see Copper, 1973).

- v* 1871 Atrypa reticularis var. plana Kayser, pp. 545–546, pl. 10, fig. 3.
 - 1896 Atwrypa plana Kayser Gürich, p. 272.
- non 1909 Atrypa plana Kayser Siemiradzki, p. 85.
- non 1922 Atrypa plana Kayser Siemiradzki, p. 21.
 - 1964 *Carinatina plana* (Kayser, 1871) Biernat, pp. 329–330, pl. 13, figs 10–12.
 - 1973 Eifelatrypa plana (Kayser) Copper, p. 497, pl. 3, figs 1–4.
 - 1978 *Eifelatrypa plana* (Kayser) Copper, fig. 5.
 - 2002 E. [Eifelatrypa] plana (Kayser) Copper, p. 1450, fig. 980.2a–e, 980.2f–h [k Copper, 1978].

Material: Two subcomplete adult and 6 complete juvenile shells, along with 38 fragments, ZPAL V.74/Bp/35.

Description: Shell approximately semi-elliptic in outline, very flat, with straight hinge line. Ventral valve flat with a triangular apsacline interarea, delthyrium partly closed by deltidial plates, foramen large, subhypothyrid (Fig. 33N). Dorsal valve with a median sulcus and a low anacline interarea.

Ornament of tubular ribs, separated by narrower interspaces and increasing in number mainly by intercalations on dorsal and bifurcations on ventral valves. Micro-ornament consisting of very fine concentric filae and flattened pustulose extensions of growth lines (Fig. 330–Q); filae averaging about 14 μ m in thickness (about 70 per mm) and may reflect a roughly diurnal or circadian growth rhythm.

Interior: dorsally oriented spiralia with fimbriae (Fig. 33M), seven whorls observed; otherwise not studied.

Remarks: *Eifelatrypa* can be distinguished from similar *Carinatina* (see e.g., Halamski and Baliński, 2013, fig. 28F–K) in ribs keeping the same width up to the anterior margin (thinning in *Carinatina*), lack of a ventral keel (present in *Carinatina*; Copper, 1973, 2002) and finer ribs. Kayser (1871), Biernat (1964), and Copper (1973) agree in qualifying *E. plana* as a rare species.



Fig. 33. *Eifelatrypa plana* from the outcrop M1-IIa at Miłoszów. A–F. Juvenile articulated shell ZPAL V.74/Bp/35/M1/2 in dorsal, ventral, lateral, posterior, and anterior views, and enlargement of the delthyrium with the pedicle foramen in posterior view. G–J, L. Articulated shell ZPAL V.74/Bp/35/M1/1 in dorsal, ventral, posterior, anterior, and lateral views. K. Decorticated shell ZPAL V.74/Bp/35/M1/2 (M0/3 embedded in limestone, dorsal view. M, N. Ventral valve ZPAL V.74/Bp/35/M1/4 in interior view to show the dorsally oriented spiralia (M) and enlargement of the delthyrium with the pedicle foramen (N). O–Q. Micro-ornamentation on the ventral valves (O, Q) ZPAL V.74/Bp/35/M1/6, 7 and on the dorsal valve ZPAL V.74/Bp/35/M1/5 (P).

Atrypa plana sensu Siemiradzki (1909, 1922) from Lechów (southern region of the Holy Cross Mts.) is a fragmentary ventral valve, keeled, with 5–7 costellae per 5 mm at anterior margin (specimen L PZ-D.740, *olim* 878a), thus not conspecific with the genuine *Eifelatrypa plana*.

Distribution: Miłoszów: M0, M1, Givetian. Otherwise Skały, set XVII (about the Eifelian–Givetian boundary).

Eifel, Upper Eifelian (Copper, 1973). Biernat (1964) and Kayser (1871) agree in qualifying this species as rare; slightly more numerous only in an environment with a strongly laminar current (Copper 1973, p. 497). This is the first uncontested report of this species from the Givetian.

Family Paraferellidae Spriesterbach, 1942 Genus *Gruenewaldtia* Tschernyschew, 1885

Type species: *Terebratula latilinguis* Schnur, 1851; Junkerberg beds, Middle Eifelian; Gerolstein, Eifel, Germany (Struve, 1955; Copper, 1965, p. 289).

Remarks: Copper (1965) was of the opinion that taxonomic distinctions within the discussed genus can be based on internal characters (in particular, the number of septa), whereas external characters were inconclusive for a systematic analysis.

Gruenewaldtia latilinguis (Schnur, 1851) Figs 34A–N, 35

- * 1851 Terebratula latilinguis, n. sp. Schnur, p. 7.
- 1882 Atrypa latilinguis (Schnur) Davidson, p. 41, pl. 2, figs 9, 9a.
- v. 1964 Gruenewaldtia sp. Biernat, p. 332, pl. 12, fig. 4, pl. 14, figs 4, 7.
 - 1969 *Gruenewaldtia latilinguis* (Schnur) Johnson, text-fig. 1A–E, H–I.
 - 2013 Gruenewaldtia latilinguis (Schnur, 1851)
 Halamski and Baliński, pp. 281, 283, figs 21A–E, 29 [ubi syn.].
- v. 2022b *Gruenewaldtia* sp. Halamski *et al.*, p. 353, fig. 22EE–GG.

Material: Nine complete, 14 slightly damaged shells and 45 fragments of shells and valves, 17 of them embedded in limestone. ZPAL V.74/Bp/38.

Description: Shell rounded, weakly ventribiconvex to dorsibiconvex, slightly wider than long, up to about 32 mm in width (estimated), widest at mid-length; anterior commissure straight in juveniles up to about 15 mm in length, to gently uniplicate in larger shells.

Ventral valve regularly convex in anterior view with flattened to slightly concave flanks and inflated posterior region; interarea well-marked, high, nearly flat to moderately concave, apsacline to anacline; wide and shallow sulcus developed only near the anterior commissure. Dorsal valve regularly convex in anterior view, without perceptible fold.

Interior of the ventral valve with dental plates and prominent lateral umbonal chambers; elevated muscle platform supported by two septa.

Dorsal interior with well-marked, high median ridge (Fig. 35A, sections 2.8–3.5 mm; 35B, section 7.1 mm); muscle platform supported by two major septa and additionally by short and weak median septum.

Ornament of uninterrupted radial ribs, 7–10 per 5 mm at anterior margin, increasing by frequent bifurcations on the ventral and intercalations on the dorsal valves.

Remarks: These brachiopods are included in the genus *Gruenewaldtia* on account of their subequally biconvex shell, fine ribbing uninterrupted by growth lamellae, and presence of raised muscle platforms in both valves. The present material was found in the same bed as specimens of *Gruenewaldtia* sp. described by Biernat (1964). She remarked that this species differs from *Gruenewaldtia latilinguis* (Schnur) occurring in the nearby

locality at Skały, mainly in less transverse shell outline, more rounded cardinal angles and slightly more distinct radial ribs. She considered these differences significant, but the lack of material at her disposal prevented her from establishing a new species. The richer and more representative present material from Miłoszów, however, does not show any significant morphological differences with the Schnur species. For this reason, the specimens from Miłoszów were included in *Gruenewaldtia latilinguis*.

The sectioned specimens from Miłoszów show that apart from the two major septa, the dorsal muscle platform is also buttressed by a weaker and shorter middle support. This is consistent with Copper's observation (Copper, 1965, p. 289) that in this species the brachial platform may have a medial support from the remnants of the medial septum.

Distribution: Poland: Miłoszów, M0; Skały, Skaly Formation, set XXI, outcrop 113. Germany: Eifel, Upper Eifelian. England: Chercombe Bridge shales of Devon.

Superfamily Glassioidea Schuchert and LeVene, 1929 Family Glassiidae Schuchert and LeVene, 1929 *Peratos* Copper, 1986

Type species: *Peratos arrectus* Copper, 1986; Freilingen Formation, Upper Eifelian; Eifel, Germany.

Peratos beyrichi (Kayser, 1872) Figs 36, 37

- 1872 Rhynchonella Beyrichi n. sp. Kayser, p. 678, pl. 26, fig. 6.
 - 1908 Glassia Beyrichi Kayser Torley, pp. 21–22, pl. 3, figs 11–19.
- non 1930 Glassia Beyrichi Kayser Nalivkin, pp. 96–97, pl. 7, figs 18, 19.
 - 1934 *Glassia beyrichi* (Kayser) Torley, p. 125, pl. 9, figs 78–79.
- non 1956 *Glassia beyrichi* (Kayser, 1872) Havlíček, pp. 51–52, pl. 5, figs 22–26.
- ? 1962 Glassia beyrichi Kayser 1873 Gunia, p. 511, pl. 47, figs 11–12.
- v. 2022 Peratos beyrichi Kayser 1873 Halamski et al., fig. 22S–T.

Material: 75 complete to slightly damaged shells and nearly 83 more damaged shells, ZPAL V.74/Bp/40.

Description: Shell typically 11–13 mm long (maximum recorded length 14.1 mm), slightly ventribiconvex, rounded subpentagonal to ovoid in outline, slightly longer than wide to about as wide as long, maximal width at about mid-length; cardinal margin obtuse at about 93°–115°, apical angle attaining 111°–140°, postero-lateral margins nearly straight, lateral margins rounded, anterior margin weakly arched, anterior commissure commonly rectimarginate, seldom its gentle deflection indicates a uniplication.

Ventral valve weakly convex; sulcus imperceptible, but slight median flattening near the anterior margin noted in large specimens; interarea quite high, weakly concave,



Fig. 34. Givetian atrypides from Miłoszów. **A–N.** *Gruenewaldtia latilinguis* (Schnur, 1851); A–E, M – articulated shell ZPAL V.74/ Bp/38/M0/1 in dorsal, ventral, lateral, posterior, and anterior views (A–E) and enlargement of the ventral ornamentation (M); F–J – articulated shell ZPAL V.74/Bp/38/M02/ in dorsal, ventral, lateral, posterior, and anterior views; K, L, N – subcomplete articulated shell ZPAL V.74/Bp/38/M0/3 in dorsal and ventral views (K, L) and enlargement of the ventral ornamentation (N). **O.** *Desquamatia (Independatrypa) circulareformis* Biernat, 1964. Enlargement of the ventral ornamentation (compare Fig. 30L).

orthocline anteriorly to anacline posteriorly; beak erect, sometimes with more incurved tip; delthyrium closed with fused deltidial plates, pierced by large apical foramen (Fig. 36AA–CC). Dorsal valve less convex than the opposite valve, parabolic in lateral and anterior view; fold absent.

Shell smooth, with well-marked growth lines, rare posteriorly, becoming crowded and more pronounced in marginal region; micro-ornament rarely preserved, of faint regularly disposed concentric filae, about 24 per millimetre (Fig. 36Z).

Interior with variably developed dental plates (Fig. 37), often poorly separated from thickened umbonal walls, thin and slightly divergent when better developed. Hinge plates thin, slightly concave, weak dorsal median ridge may be present in umbonal chamber; spiralia medially directed (Fig. 37H); internally thick shelled, especially posteriorly. **Remarks:** The present brachiopods are included in the genus *Peratos*, mainly on the basis of their high orthocline ventral interareas with prominent deltidial plates pierced by the apical foramen (Fig. 36AA–CC) and medially directed spiralia. Dental plates, which are a diagnostic feature for the genus (Copper, 1986), are variably developed in the studied specimens. They are often fused with the thickened lateral umbonal walls forming a distinct lining of the pedicle cavity comparable to the condition shown by Copper (1986, fig. 17, sections at 0.4–1.2 mm) in the



Fig. 35. Transverse serial sections of *Gruenewaldtia latilinguis* through the shell ZPAL V.74/Bp/38/M0/4 (\mathbf{A}) and M0/5 (\mathbf{B}) from outcrop M0-9. Distances measured in millimetres from the tip of the ventral umbo.

type species of the genus. However, in some shells from Miłoszów the dental plates are thin and well-separated from lateral walls (Fig. 37F).

The external characteristics of the specimens from Miłoszów agree with *Peratos beyrichi* (Kayser, 1872, p. 678, pl. 16, fig. 6) described from the upper Givetian or possibly lower Frasnian of Germany (see Copper, 1986, p. 858). As Copper noted (1986, p. 858) the serial sections of the topotype material from Brilon showed internal structures, similar to those of the type species *P. arrectus* Copper, 1986.

Gunia (1962) described a single, probably juvenile shell from the lower or middle Frasnian of the Sudetes as *Glassia beyrichi*, but inadequate preservation of the specimen prevents a close taxonomic evaluation. Brachiopods from the Zlíchov limestone (Lower Eifelian) of the Prague region identified by Havlíček (1956) as *G. beyrichi* differ from the type material in having more oval (less pentagonal) and wider outline. *Glassia beyrichi* sensu Nalivkin (1930) from the Middle Devonian of Turkestan differs from the type material in having wider, less biconvex shells and a more often and better developed weak sulcation of the commissure.

Occurrence: *Peratos beyrichi* was originally described from the upper Givetian or lower Frasnian Rotheisenstein at Brilon, Nordrhein–Westfalen, Germany (Kayser, 1872). The

species was also recorded from the Givetian of Waldgirmes (Hessen, Germany), Schleddenhof, and Bilveringsen (both Nordrhein–Westfalen, Germany) (Maurer, 1885; Torley, 1908, 1934). The present material was found at localities M0, M1 and M3 in Miłoszów (common at the two latter ones).

Order Athyridida Boucot, Johnson and Staton, 1964 Suborder Athyrididina Boucot, Johnson and Staton, 1964 Superfamily Athyridoidea Davidson, 1881 Family Athyrididae Davidson, 1881 Subfamily Athyridinae Davidson, 1881 Genus *Athyris* M'Coy, 1844

Type species: *Terebratula concentrica* von Buch, 1834; Eifelian, Middle Devonian; Eifel, Germany.

Athyris sp. Fig. 38A–G

Material: Ten complete to nearly complete, but crushed shells, 9 fragmentary specimens and three incomplete loose valves; in addition, about 20 juvenile shells ranging from 1.8 to 2.7 mm in length; collection number ZPAL V.74/Bp/36.



Fig. 36. Givetian atrypide brachiopod *Peratos beyrichi* (Kayser, 1872) from Miłoszów. **A–E, F–J, K–O, U–Y.** Articulated shells ZPAL V.74/Bp/40/M1/1–4 from outcrop M1-IIa in dorsal, ventral, lateral, posterior, and anterior views. **P–T, BB.** Articulated shell ZPAL V.74/Bp/40/MP/1 in dorsal, ventral, lateral, posterior, and enlargement of the ventral interarea (BB). **Z.** Ventral micro-ornament of the shell from M1-IIb. **AA, CC.** Enlargements of the ventral interareas of the articulated shells ZPAL V.74/Bp/40/M1/5, 6 from outcrop M1-IIa.



Fig. 37. Transverse serial sections of *Peratos beyrichi* (Kayser, 1872) through the shells ZPAL V.74/Bp/40/M1/7, 8 (**A**, **G**) from outcrop M1-IIa and 40/M3/1 (**B**), M3/2 (**C**), M3/3 (**D**), M3/4 (**E**), and M3/5 (**F**) from outcrop M3-7; drawings of serial sections (A–F) and photograph of a polished section showing the disposition of the spiralia (G). Distances measured in millimetres from the tip of the ventral umbo.

Remarks: This poorly preserved collection consists of invariably compressed and deformed specimens; hence, a detailed description is not feasible. Generally, this form attains a rather small size (maximum recorded length 14 mm) and is characterized by elliptic, slightly wider than long shell outline and a narrow, but well marked ventral sulcus that extends from the umbonal region. A single dorsal valve shows the cardinal plate perforated by a fairly large, elongate subtriangular foramen and a long, well marked myophragm (Fig. 38A, G).

The specimens from Miłoszów closely resemble those from Skały, described by Biernat (1966) as *Athyris* cf. *ventrosa* (Schnur, 1853). According to Halamski (2004b), however, the latter differ from typical *Athyris concentrica ventrosa* from the Eifel Mts. in its much smaller shell dimensions. Unfortunately, the inadequate present material from Miłoszów does not allow a more detailed description and comparison.

Occurrence: The present material comes from trench MIN and outcrop M0-1–4 in Miłoszów.

Genus Leptathyris Siehl, 1962

Type species: *Leptathyris gryphis* Siehl, 1962; Eifelian, Middle Devonian; Greifenstein limestone, Dill Syncline, Rhenish Slate Mountains, Germany.

?Leptathyris sp. Figs 39, 42K–O

Material: Four complete to nearly complete shells and six fragmentary specimens, ZPAL V.74/Bp/43.

Description: Shell subcircular in outline, approximately equibiconvex (very weakly ventribiconvex), small-sized

(the largest complete shell is 5.7 mm long, 5.4 mm wide, and 2.9 mm thick). Cardinal margin approximately straight; ventral palintrope apsacline, beak pointed, delthyrium wide, open; dorsal palintrope linear, weakly apsacline (nearly orthocline). Anterior commissure rectimarginate. Shell macroscopically smooth.

Remarks: These subadult brachiopods are tentatively included into the genus *Leptathyris* on account of their small, circular, lens-like, smooth (non-lamellose) shells and interior with dental plates and weakly concave, posteriorly perforated cardinal plate bordered by high inner socket ridges. Owing to the fragmentary nature of the material, a more detailed taxonomic assessment is not attempted. **Occurrence:** Miłoszów, Skały Formation, M3-8.

ccurrence: Minoszow, Skary Formation, MIS-8.

Superfamily Meristelloidea Waagen, 1883 Family Meristidae Hall and Clarke, 1895 Genus *Dicamara* Hall and Clarke, 1893

Type species: *Atrypa plebeia* Sowerby, 1840; Middle Devonian; Mount Wise and Plymouth, England.

Remarks: No specimen of *Atrypa plebeia* from the type region has ever been sectioned. Given that meristid systematics is largely based on features observable solely in sections (like presence or absence of mystrochial plates), the characters of the genus *Dicamara* should be considered as uncertain (see a more detailed comment by Halamski and Baliński, 2013, p. 285). The present analysis is based on the assumption that the type species is present in Germany (Siehl, 1962; Alvarez and Rong, 2002).

Dicamara plebeia (Sowerby, 1840) Figs 38H–R, 40



Fig. 38. Large-sized Givetian athyridides from Miłoszów. **A–G.** *Athyris* sp. Outcrop M1-IIa; A, G – dorsal interior ZPAL V.74/Bp/36/M1/2, general view (A) and enlargement of the cardinalia (G); B–F – crushed articulated shell ZPAL V.74/Bp/36/M1/1 in dorsal, ventral, lateral, posterior, and anterior views. **H–R.** *Dicamara plebeia* (Sowerby, 1840); H – isncomplete articulated shell V.74/Bp/36/M0/1 in dorsal view; outcrop M0-9; I–M, N–R – articulated shells ZPAL V.74/Bp/36/M3/2 from outcrop M3 and V.74/Bp/36/M0/3 from outcrop M0-9 in dorsal, ventral, lateral, posterior, and anterior views.

- * 1840 Atrypa plebeia Sow. Sowerby, pl. 56, figs 12–13.
 - 1962 Dicamara plebeja (Sowerby 1837) Siehl, p. 207, table 5, pl. 32, fig. 1 [errore pro Sowerby, 1840].
 - 1964 Dicamara plebeia (Sowerby 1840, in Sedgwick and Murchison 1840) – Struve, pp. 515–516, text-figs 9–10 (copy of Sowerby 1840), 12.
 - 1966 *Dicamara plebeia* (Sowerby, 1840) Biernat, pp. 138–140, text-fig. 48, pl. 21, fig. 1.
 - 1998 *Dicamara plebeia* (Sowerby, 1840) Alvarez *et al.*, fig. 1–4.

2002 *Dicamara plebeia* (Sowerby) – Alvarez and Rong, fig. 1069–4.

Material: Four nearly complete shells, five slightly damaged and 20 more fragmentary specimens; in addition, one damaged juvenile specimen; ZPAL V.74/Bp/36.

Description: Shell pentagonal in outline, approximately aequibiconvex, maximum width slightly anteriorly to mid-length, typically about 19–22 mm wide, weakly wider than long, relatively high (thickness-to-length ratio about 0.7–0.8). Anterior commissure uniplicate, tongue subtrapezoidal, moderately wide to wide. Ventral valve with a shallow flat-bottomed sulcus anteriorly, umbo thick, beak overhanging that of the dorsal valve. Dorsal valve



Fig. 39. Transverse serial sections of *?Leptathyris* sp. through the shell ZPAL V.74/Bp/43/M3/2 from outcrop M3-7. Distances measured in millimetres from the tip of the ventral umbo.

subtriangular in anterior view, an indistinct flattened fold present in anterior third, umbo thick. Shell smooth.

Ventral interior: shoe-lifter process present; dental plates long, lateral cavities huge; mystrochial plates none; teeth somewhat elongate. Dorsal interior: shoe-lifter process bisected by the median septum; septalium present; spiralium poorly preserved.

Remarks: These shells are included in the genus *Dicamara* on account of smooth shells that are pentagonal in outline and possess characteristic internal structures, revealed either in the sectioned shell (Fig. 40) or thanks to exfoliation

of the specimens (e.g., Fig. 38I). The serial sections show welldeveloped shoe-lifter structures in both valves. The dorsal shoe-lifter is additionally supported by a long median septum, a feature characteristic for *Dicamara* (Alvarez and Rong, 2002). Externally, the studied collection shows great variability in the general shell shape, thickness of the ventral umbo, development of sulcus, fold and uniplication (see Fig. 38H–R).

The studied specimens are identified as *Dicamara* plebeia (Sowerby, 1840) on account of their relatively high and weakly wider than long shells. *Dicamara scal*prum (Roemer, 1844) has a flatter shell and *D. prunulum* (Schnur, 1851) is longer than wide. *Dicamara plebeia* was originally described from the Middle Devonian of England (Sowerby, 1840). Most probably it is present also in the Eifel (Siehl, 1962; Struve, 1964). Records based on examination of external characters only should be treated as unconfirmed.

Occurrence: This is an uncommon species in the M0-9, M1 and M2 localities at Miłoszów. Biernat (1966) also described the species from outcrops 83 and 89 of the Skały Formation at Skały.

Superfamily Retzioidea Waagen, 1883 Family Neoretziidae Dagys, 1972 Genus *Plectospira* Cooper, 1942

Type species: *Terebratula ferita* von Buch, 1834; Eifelian, Middle Devonian; Eifel, Germany.



Fig. 40. Transverse serial sections of *Dicamara plebeia* (Sowerby, 1840) through the shell ZPAL V.74/Bp/36/M3/4 from outcrop M3-7. Distances measured in millimetres from the tip of the ventral umbo.



Fig. 41. *Plectospira ferita* (von Buch, 1834). A–E, F–J. Articulated shells ZPAL V.74/Bp/42/M1/2, 3 in dorsal, ventral, lateral, posterior, and anterior views. K–O, V. Articulated shell ZPAL V.74/Bp/42/M1/1 in dorsal, ventral, lateral, posterior, and anterior views (K–O) and enlargement of the ventral interarea (V). P. Articulated shell ZPAL V.74/Bp/42/M1/4 in dorsal view. Q, R. Articulated shell ZPAL V.74/Bp/42/M1/7 in oblique lateral and anterior views. S. Articulated shell ZPAL V.74/Bp/42/M1/6 in lateral view. T, U. Articulated shell ZPAL V.74/Bp/42/M1/5 in dorsal and ventral views. All specimens from outcrop M1-IIa.

Plectospira ferita (von Buch, 1834) Fig. 41

- * 1834 *Terebratula ferita* n. von Buch, pp. 76– 77, pl. 2, fig. 37.
 - 1841 *Terebratula ferita* Phillips, pp. 89–90, pl. 35, fig. 163.
 - 1851 *T.* [*Terebratula*] *ferita* v. Buch Schnur, p. 6.
- vp 1853 *Terebratula ferita* v. Buch Schnur, pp. 184–185, pl. 25, fig. 4a–d, non 4e–g [= *P. longirostris*].
 - 1853 *T.* [*Terebratula*] *ferita;* v. Buch Steininger, p. 63.
- non 1854 Spirigera ferita v. Buch sp. Sandberger and Sandberger, p. 330, pl. 32, fig. 13 [= P. longirostris].
- non 1864 *Retzia ferita*, Von Buch (sp.) Davidson, p. 21, pl. 4, figs 8–10 [= *P. longirostris*].
 - 1871 Retzia ferita Buch Kayser, p. 557.
 - 1885 *Retzia ferita* Buch Maurer, pp. 174– 175, pl.7, fig. 27.
 - 1893 *Ptychospira ferita* von Buch Hall and Clarke, pp. 112–113, pl. 50, figs 10–11.
 - 1894b *Ptychospira ferita*, von Buch Hall and Clarke, p. 793, text-fig. 360, pl. 36, figs 20–21.
- v. 1966 *Plectospira ferita* (L. v. Buch, 1834) Biernat, pp. 146–147, pl. 28, fig. 1.
- p 1969 *Plectospira ferita* (von Buch 1834) Anderson *et al.*, pp. 143–144, pl. 6, figs 19–23, 26–27, non 24–25.
 - 1978 *Plectospira ferita* (Buch, 1834) Ficner and Havlíček, p. 76, pl. 5, figs 9–10.
- v. 1982 *Plectospira ferita* (v. Buch) Biernat and Baliński, pp. 857–866, text-fig. 1, pl. 92, figs 1–6, pl. 93, figs 1–7, pl. 94, figs 1–7, pl. 95, figs 1–6.
 - 2012 Plectospira ferita (Buch, 1834) Gourvennec and Hoşgör, p. 353, fig. 4F–M.
- v. 2013 *Plectospira ferita* (von Buch, 1834) – Halamski and Baliński, p. 287, fig. 30W–AA.
 - 2020 *Plectospira ferita* (von Buch, 1834) García-Alcalde and El Hassani, pp. 24– 25, figs 11.1–11.4.
- v. 2022a *Plectospira ferita* (von Buch, 1834) Halamski *et al.*, p. 50, fig. 34F–J.

Material: 36 complete to nearly complete shells, 20 damaged ones, and about 50 fragments of shells; specimens frequently deformed or compressed by sediment compaction; collection number ZPAL V.74/Bp/42.

Description: Shell small, the largest specimens in the studied collection attaining up to 6.5 mm in length, subequally biconvex; outline quite variable, subpyriform, rounded

to weakly transversely or weakly longitudinally suboval; hinge line narrow, nearly straight to slightly angular; lateral and anterior commissure strongly undulating to serrate.

Ventral valve with prominent umbo and a straight beak bearing apical, round, mesothyrid foramen; interarea extremely narrow, almost nonexistent, apsacline, delthyrium closed by a flat deltidium. Dorsal valve with a slightly protruding triangular umbo.

Shell ornamented with very strong, high, rounded radial plicae separated by very deep, U-shaped interspaces; ventral valve invariably with three pairs of plicae and a narrow median interspace corresponding to a sulcus; in the anterior region of large specimens the median interspace bears a median pustulose ridge (Fig. 41L, O, R); dorsal valve with three plicae on each flank and a median plica, corresponding to a fold; the latter in adult shells with a shallow median depression anteriorly; distal parts of the ventral and dorsal plicae in large shells higher, strongly protruding externally at the commissure (Fig. 41Q, S). Micro-ornament with faint growth lines, scattered pustules and well visible endopunctation (for more detail see Biernat and Baliński, 1982).

Shell interior not studied.

Ontogeny: The smallest juvenile shells in the present collection attain 2.3–3.6 mm in width (Fig. 41A–E, T, U). At that stage of growth, they already possess the final number of radial plications like in adult forms. The plications are recognizable as early as about 0.4–0.5 mm from the tip of both beaks.

Remarks: Notwithstanding frequent diagenetic deformation of the studied specimens, significant variability of the shape and proportions of the the shell is clearly observed. Although equidimensional or weakly wider than long shells are more common, elongated ones are also present (Fig. 41F–J).

In comparison with representatives of this species from the Eifel, specimens of *P. ferita* from the Skały Formation are distinctly smaller, the typical size being about 5 mm. In the Eifel the typical size is about twice greater and the largest shells are about three times greater than the maximum size from Miłoszów (a specimen from Kerpen: width 19.2 mm, length 18.3 mm, thickness 9.2 mm; a specimen from Gees: width 17.1 mm, length 13.4 mm, thickness 7.2 mm; MCZ collections).

Characteristic shape of the shell, dimensions, and ornament allow its unmistakable attribution to *Plectospira ferita*. Other species may be distinguished on the basis of external features. For example, *Plectospira longirostris* (Kayser, 1871) has a much longer ventral umbo (e.g., Anderson *et al.*, 1969, pl. 6, figs 28–32), whereas *Plectospira multiplicata* Zhang, 1985 from the Eifelian of Inner Mongolia has lower ribs.

Occurrence: The species was recorded in the Middle Devonian of Germany, England, Moravia, Burma, Morocco, and Turkey (see Halamski and Baliński, 2013 and references therein; Halamski *et al.*, 2022a). In the type region of the Eifel, published reports with detailed stratigraphic data are from the Lower Eifelian (Nohn beds; Schulz, 1883, p. 22), Middle Eifelian (Junkerberg beds; Jungheim, 2000, p. 78), and the Upper Eifelian (Freilingen beds; Glinski, 1961, p. 284). The stratigraphic distribution seems therefore

relatively wide (see also Rauff, 1911, p. 27). In the Rhenish Slate Mts., there is a record from the Middle Eifelian (Ohler Schiefer, Sauerland; May, 1993, p. 115). In the Holy Cross Mts., *P. ferita* was described from the Upper Eifelian of Skały (Biernat, 1966; Biernat and Baliński, 1982); the present material comes from the Lower Givetian at Miłoszów (M1-IIa).

Family Anoplothecidae Schuchert, 1894 Genus *Bifida* Davidson, 1882

Type species: *Terebratula lepida* d'Archiac and de Verneuil, 1842; Eifelian; Eifel, Germany.

Bifida sp. Fig. 42A–I

v. 2022b *Bifida* sp. – Halamski *et al.*, pp 353, 360, figs 22U–W, 27–1.

Material: Over forty articulated shells and a few isolated valves, ZPAL V.74/Bp/36/M1-IIb/1–2, 36/M2/1–37, 36/M3/1–14.

Remarks: These brachiopods will be described in a study of all *Bifida* species in the Holy Cross Mountains (in progress). **Distribution:** Miłoszów, M1-IIb (rare), M2 β + δ (frequent), M3 θ - μ (not seldom, material collected from scree, some coming probably from shales θ and some from the overlying limestone).

Family Kayseriidae Boucot, Johnson and Staton, 1964 Genus *Kayseria* Davidson, 1882

Type species: *Orthis lens* Phillips, 1841; Middle Devonian (upper Eifelian?); vicinity of Torquay, Devon, England (see Copper, 1973, p. 131).

Kayseria alvea Copper, 1973 Fig. 42J

- * 1973 *Kayseria alvea* sp. nov. Copper, pp. 134– 136, text-fig. 6, pl. 7, figs 12–22.
- v 2013 *Kayseria alvea* Copper, 1973 Halamski and Baliński, pp. 287–288, fig. 30HH–KK.

Material: A single incomplete ventral valve, embedded in shale, ZPAL V.74/Bp/15/M0/1.

Description: Ventral valve ovate in outline, weakly indented medially, markedly convex, 11.8 mm long and about 8.8 mm wide, maximum width anteriorly. Ornament of numerous straight, rounded ribs, appearing in umbonal region; two stronger ones bordering the median sulcus, three (or four?) weaker ones between them, and at least eight per flank.

Remarks: The single available specimen, although poorly preserved, is included in *Kayseria* Davidson, 1882 on account of relatively small size, median indentation of the commissure, and ornament. It is similar to *K. alvea* Copper, 1973 in being longer than wide and possessing a stout rib pair bordering the median sulcus, markedly stronger than median or lateral ribs. Its convexity is relatively high for a representative of the species, but falls within the variation

interval (compare Copper, 1973, pl. 7, fig. 14). *Kayseria lens* sensu Biernat (1966) from the Upper Eifelian of Skały has more uniform ribs all over the entire shell; most probably it represents a different species [according to Ficner and Havlíček (1978), *Kayseria* described by Biernat (1966) is *K. procera* Ficner and Havlíček, 1978; this should be checked in detail].

Occurrence: *Kayseria alvea* Copper, 1973 was originally described from the Ahbach beds (uppermost Eifelian–lowermost Givetian) of the Eifel Mts., Germany (Copper, 1973). It was further reported from the Middle Devonian (Eifelian?) of southern Maïder, Morocco (Halamski and Baliński, 2013). The single available specimen comes from locality M0 at Miłoszów.

Order Spiriferida Waagen, 1883 Suborder Spiriferidina Waagen, 1883 Superfamily Ambocoelioidea George, 1931 Family Ambocoeliidae George, 1931 Genus *Ambothyris* George, 1931

Type-species: *Spirifera infima* Whidborne, 1893; Givetian, Middle Devonian; Lummaton, Devonshire, England.

Ambothyris sp. Figs 43A–Y, 44

Material: Nearly 180 shells, majority of them complete to nearly complete, some more damaged and crushed. ZPAL V.74/Bp/65.

Description: Shell small, the most often 3–6 mm in length, the largest 7.9 mm long, ventribiconvex, slightly wider than long, rounded to subpentagonal in outline; hinge margin submegathyrid to rarely brachythyrid, cardinal extremities rounded; lateral and anterior margins gently rounded, anterior commissure rectimarginate.

Ventral valve nearly twice as deep as the dorsal one, with inflated umbonal region; interarea moderately high, from rarely nearly catacline to usually apsacline near the hinge, concave, beak slightly incurved, delthyrium open except very small apical thickening visible in some large shells and in the sectioned shell (Fig. 44, sections 0.4 and 0.6 mm); margins of delthyrium accentuated by very low deltidial plates projecting more or less normal to the interarea (Fig. 44, sections 0.8–1.15 mm).

The dorsal valve usually in the outline of a rounded trapezoid, interarea anacline, slightly concave.

Shell surface apparently smooth, on exceptionally well-preserved specimens with a dense cover of very minute spines arising from long ridge-like spine bases.

Interior of ventral valve with dental ridges, without dental plates. Dorsal interior with long crural plates almost converging on the valve floor, anteriorly more clearly separated (Fig. 44, section 1.8 mm); crural bases not sessile, but instead supported well above the valve floor; cardinal process small, knob-like, with longitudinal ridges.

Remarks: The generic affiliation of this species is somewhat doubtful. Externally, it is similar to *Crurithyris* George, 1931 in having a strongly ventribiconvex, submegathyrid shell, but differs essentially from the latter in having



Fig. 42. Small-sized Givetian athyridides from Miłoszów. **A–I.** *Bifida* sp. from outcrop M2-2; A–E – articulated shell ZPAL V.74/ Bp/36/M2/1 in dorsal, ventral, lateral, posterior, and anterior views; F, H – dorsal valve ZPAL V.74/Bp/36/M2/2: general view (F) and enlargement of the cardinalia and of the septum (H); G, I – ventral valve ZPAL V.74/Bp/36/M2/3: general view (G) and enlargement showing median septum (I). **J.** *Kayseria* sp.; ventral valve ZPAL V.74/Bp/15/M0/1 embedded in limestone; outcrop M0, lower part. **K–O.** *?Leptathyris* sp.; articulated shell ZPAL V.74/Bp/43/M3/1 in dorsal, ventral, lateral, posterior, and anterior views; outcrop M3-7.

well-developed crural plates. The presence of a rectimarginate anterior commissure and a convex brachial valve without a median fold preclude the assignment of the studied form to the genus *Crurispina* Goldman and Mitchell, 1990, whose shells possess a uniplicate to parasulcate commissure, flat to weakly convex dorsal valve and weak dorsal fold (Goldman and Mitchell, 1990). The structure of the interior of the studied form, especially the well-developed crural plates and the lack of dental plates as well as small-sized ventribiconvex, submegathyrid shell suggest that it can be assigned to the Givetian–Frasnian genus *Ambothyris* George, 1931. The only difference between the specimens from Miłoszów and *Ambothyris* is that the former has smooth shell and minute spines, whereas the type species of the latter has very fine, radiating striae, although, according to George (1931), this feature was observed on one shell (syntype) only and smooth forms are not excluded.

The present specimens are similar externally and internally to *Ambothyris infima* (Whidborne, 1893), as described by Vandercammen (1956) from the upper Givetian and middle Frasnian of Belgium. The latter, however, differ mainly in having a radial capillate ornament.



Fig. 43. Givetian small smooth spiriferides from Miłoszów. **A–Y.** *Ambothyris* sp.; A–E, F–J, K–O, P–T, U–Y – articulated shells ZPAL V.74/Bp/65/M1/1–5 in dorsal, ventral, lateral, posterior, and anterior views. Outcrop M1-IIa. **Z–II.** *Echinocoelia dorsoplana* (Gürich, 1896); Z–DD, EE–II – articulated shells ZPAL V.74/Bp/45/M3/1 from outcrop M3-8 and V.74/Bp/45/M2/1 from outcrop M2-2 in dorsal, ventral, lateral, posterior, and anterior views.

Fig. 44. Transverse serial sections of *Ambothyris* sp. through the shell ZPAL V.74/Bp/65/M1/6 from outcrop M1-IIa. Distances measured in millimetres from the tip of the ventral umbo.

A. cf. *infima* described by García-Alcalde (2010) from the Givetian of northern Spain differs from our form in more rounded outline, catacline ventral interarea and weakly sulcate dorsal valve. Interestingly, this author remarked that the radial fibrous fabric of shell on exfoliated specimens gives the impression of a capillate micro-ornament (García-Alcalde, 2010, p. 55).

Internally and externally the present specimens are almost identical with *Crurithyris inflata* (Schnur, 1853), described by Biernat (1966) from the Upper Eifelian of the Skały Formation at Skały. The differences are minor and are expressed in the presence of weak sulci on both valves of the specimens from Skały. *Spirifer inflatus* Schnur, 1853 is a taxon that is difficult to interpret, as the types are lost. However, most specimens, identified as such in the collections of the SMF, are much larger, about 1 cm in width, so the present material seems different at least at the species level. Owing to the taxonomic uncertainties among related species, an open nomenclature is used.

Occurrence: Miłoszów: M1-IIa, common.

Subfamily Rhynchospiriferinae Paulus, 1957 Genus Moravilla Havlíček, 1953

Type species: *Moravilla ficneri* Havlíček, 1953; lower Givetian, Middle Devonian; Čelechovice na Hané, Moravia, Czech Republic.

Diagnosis (emended): A representative of the Rhynchospirinae Paulus, 1957, characterised by small- to medium-sized, transverse, ventribiconvex shells with capillate ornament, intercapillar grooves with faint spines; anterior commissure straight or nearly so; ventral interarea catacline to apsacline; delthyrium edge strengthened by short ridges, but true dental plates absent; crural plates joining

along a median line to form a cruralium or touching the valve floor at a small distance from each other.

Remarks: The type species of the genus was described and illustrated by Havlíček (1953, pp. 4–5, pl. 2, figs 1–3; 1959, pp. 183–184, 259, pl. 3, fig. 6, pl. 27, fig. 5) and Ficner and Havlíček (1978, pp. 86–87, pl. 8, figs 1–6). A succinct diagnosis of the genus was given by Johnson and Hou (2006, p. 1744) and an emended diagnosis, including features present in *Moravilla andreae* Baliński and Halamski sp. nov., is given herein. These descriptions are not fully concordant, so a few comments are needed.

The structure located in the median part of the dorsal valve was described as a "cruralium-like structure ('pseudocruralium')" by Havlíček (1953), as "basal plates [that] converge (...) and rest by their inner edges on the bottom of the valve" by Havlíček (1959), as a "cup-like cruralium sedens" formed by converging "massive plates" by Ficner and Havlíček (1978), and as discrete crural plates by Johnson and Hou (2006). The present authors describe the two plates as crural plates, similarly to descriptions of other ambocoeliids (Ilmospirifer Ljaschenko, 1969; Ladjia Veevers, 1959; Johnson and Hou, 2006, p. 1743), and the structure arising from their connection along the median line as a cruralium. In M. andreae the latter may be situated distinctly above the valve floor (Fig. 45O-R), very lowly above the valve floor (Fig. 46V–W), or the crural plates may touch the valve floor at some distance from each other (Fig. 46P–U).

In the ventral valve, the structures connected to the margins of the delthyrium were described as "short and high dental plates" by Havlíček (1959) followed by Johnson and Hou (2006). The same structures were called simply "very short plates" by Ficner and Havlíček (1978). The present authors follow the latter authors in abstaining from qualifying these structures as dental plates; using the term "dental ridges". Under such naming convention, genuine dental plates are absent in *Moravilla*.

Ficner and Havlíček (1978, p. 87) stated that no true microspines were observed in *M. ficneri*. However, rows of faint spines, disposed in the intercapillar grooves, are clearly visible on one of the specimens illustrated by these authors (Ficner and Havlíček, 1978, pl. 8, fig. 6). Similarly distributed faint spines occur on the shells studied here (Fig. 47).

Moravilla andreae Baliński and Halamski sp. nov. Figs 45–47

v. 2022b Moravilla sp. nov. – Halamski et al., p. 353.

Etymology: *andreae* – in honour of the late Andrzej Piotrowski (29.11.1945–5.01.2022), palaeontologist and fossil collector, first finder of specimens of this species at Miłoszów (Latin version of the forename *Andreas*, genitive *Andreae*).

Type material: Holotype: a complete articulated shell ZPAL V.74/Bp/44/M1/1 (Figs 46 M–O, Q, R, 47A, D, E); paratypes: 41 complete or slightly damaged shells, 4 complete dorsal and 2 ventral valves and about 50 fragmentary shells and single valves, collection number ZPAL V.74/Bp/44/M1.



Type locality: Miłoszów, trench M1 (coordinates: 50°54′08.4″N, 21°07′16.2″E), Holy Cross Mountains, Poland.

Type horizon: Skały Formation, marly shales M1-IIa; Lower Givetian.

Diagnosis: *Moravilla* with markedly transverse shell (width-to-length ratio about 2.2–2.6), obtuse ears, catacline to apsacline ventral interarea, and 2–3.5 capillae per mm.

Description: Shell small-sized, complete specimens in the studied collection attaining up to 7.4 mm in width, although a few fragments suggest shells may have attained even twice that size; ventribiconvex, transversely subtrapezoidal to sub-triangular in outline, 2.2–2.6 times wider than long; hinge line wide, almost equal to the maximum shell width; cardinal angles expanded into well marked ears, but with narrowly rounded, obtuse tips; lateral margins straight, anterior margin narrow, weakly rounded to somewhat



Fig. 45. *Moravilla andreae* Baliński and Halamski sp. nov. **A–C.** Articulated shell ZPAL V.74/Bp/44/M1/3 (paratype) in dorsal, lateral, and posterior views. **D–H.** Articulated shell ZPAL V.74/Bp/44/M1/1 (holotype) in dorsal, ventral, lateral, posterior, and anterior views. **I–K.** The largest articulated shell ZPAL V.74/Bp/44/M1/2 (paratype) in dorsal, lateral, and posterior views. **L–N.** Ventral valve ZPAL V.74/Bp/44/M1/4 (paratype) in external, posterior, and internal views. **O–R.** Dorsal valve ZPAL V.74/Bp/44/M1/5 (paratype) in interior views: general views (P, R) and enlargements of the cardinalia (O, Q). All specimens from outcrop M1-IIa.



Fig. 46. *Moravilla andreae* Baliński and Halamski sp. nov. **A.** Fragmentary ventral valve ZPAL V.74/Bp/44/M1/12, enlargement of the umbonal region. **B, C.** Fragmentary ventral valve ZPAL V.74/Bp/44/M1/13, general view (B) and enlargement of the posterior region (C). **D, E.** Juvenile articulated shell ZPAL V.74/Bp/44/M1/14 in dorsal and posterior views. **F, G.** Juvenile articulated shell ZPAL V.74/Bp/44/M1/14 in dorsal and posterior views. **F, G.** Juvenile articulated shell ZPAL V.74/Bp/44/M1/14 in dorsal and posterior views. **F, G.** Juvenile articulated shell ZPAL V.74/Bp/44/M1/15 in dorsal and posterior views. **H–L.** Articulated shell ZPAL V.74/Bp/44/M1/7 in dorsal, ventral, lateral, posterior, and anterior views (see also Fig. 47B, C, F). **M–O, Q, R.** Articulated shell ZPAL V.74/Bp/44/M1/8 in dorsal, lateral, anterior, ventral and posterior views (see also Fig. 47A, D, E). **P, T, U.** Fragmentary dorsal valve ZPAL V.74/Bp/44/M1/9: general view (P) and enlargements of the cardinalia in antero-dorsal (U) views. **S, X, Y.** Subcomplete dorsal valve ZPAL V.74/Bp/44/M1/10: general view (S) and enlargements of the cardinalia in antero-dorsal (X) and dorsal (Y) views. **V, W.** Fragmentary dorsal valve ZPAL V.74/Bp/44/M1/10: general view (S) and enlargements of the cardinalia in antero-dorsal (W) views. All images are SEM micrographs; all specimens are paratypes and are from outcrop M1-IIa.



Fig. 47. *Moravilla andreae* Baliński and Halamski sp. nov. from the Lower Givetian of Miłoszów. **A**, **D**, **E**. Articulated shell ZPAL V.74/ Bp/44/1/8 (paratype; compare Fig. 46M): general view (D) and enlargements of the micro-ornament (A, E). **B**, **C**, **F**. Ventral valve ZPAL V.74/Bp/44/M1/7 (paratype; compare Fig. 46I): general view (C) and enlargements of the micro-ornament (B, F). All specimens are stratoand topotypic paratypes and are from outcrop M1-IIa.

truncated, anterior commissure most often rectimarginate or with almost imperceptible undulation (extremely weak unisulcation).

Ventral valve about twice as convex as the opposite valve, without perceptible sulcus or fold; interarea widely triangular, moderately high, laterally delineated with sharp beak ridges, weakly concave near the hinge margin, curved near the umbo, catacline to apsacline, with growth striation parallel to the hinge line, and sporadically preserved vertical striae; beak suberect to erect; delthyrium high, open, with an apical angle of about 44°–61°.

Dorsal valve gently convex with a broad but prominent umbo and small inclined beak; interarea low, nearly flat, catacline; notothyrium open with cardinal process visible apically, apical angle of about 93°–111°; median fold absent, exceptionally with barely visible median depression resulting in very weak undulation of the anterior commissure.

Shell ornamented with a total of 26–35 (in post-juvenile shells) fine rounded capillae increasing in number by rare bifurcation, separated by narrower interspaces; radial rows of faint spines attaining 16–27 μ m in diameter (Fig. 47A, B, E, F) may form delicate intercapillar spine ridges.

Ventral valve interior with well-marked dental ridges; dental plates absent; apical umbonal cavity occupied by a short, horizontal, slightly convex apical plate lying clearly below the level of the interarea and therefore not limiting the opening of the delthyrium, fused with the inner surface of the interarea laterally from the dental ridges (Fig. 46A–C); muscle scars elongate, divided medially by well marked, thick and rounded myophragm (Fig. 46A–C); hinge margin denticulate (Fig. 45M, N).

Interior of dorsal valve with rather small, knob-like cardinal process; outer hinge plates wide, subvertical; crural plates wide, weakly concave, converging medially with each other and with the valve floor forming a spoon- or cupshaped sessile cruralium, which extends for about one-third of the valve length (Figs 45O–R, 46S–Y); adductor impressions indistinct on the interiors examined, visible only on the cruralium; spiralium not observed, crura running quite low above the bottom of the valve and weakly converging medially.

Ontogeny: The present collection includes several juvenile specimens in the range of 1.5–2.5 mm in width. These specimens differ from adult forms primarily in proportion of the shell outline, which in the smallest specimens is more semicircular and less expanded in width (Fig. 46D, E). In these specimens, the shell is 1.3–1.8 times wider than long, while specimens over 5 mm in width are 2.4–2.7 times wider. Furthermore, the growth lines on larger valves show that the shell accretion is much faster at lateral extremities near hinge margin, resulting in more and more extended ears (e.g., Figs 45D, E, L, 46M, Q).

Remarks: The described brachiopods are included in the genus *Moravilla* Havlíček, 1953 on account of ventribiconvex, transverse shells without fold or sulcus, with capillate ornament and, internally, a simple cardinal process and a cruralium.

Moravilla andreae sp. nov. differs from the type species *Moravilla ficneri* Havlíček, 1953 described from the lower Givetian limestone of Čelechovice na Hané, Moravia (Havlíček, 1953, 1959; Ficner and Havlíček, 1978) in having coarser radial ornament, obtuse tips of cardinal extremities and a proportionally shorter cruralium. The last of these differences deserves a brief comment. Havlíček (1953, 1959) and Ficner and Havlíček (1978) noted that the cruralium in *M. ficneri* reaches the valve midlength. In the species described here, this structure is much shorter, reaching about one-third of the valve length. It seems, however, that the relative length of the cruralium in the Moravian species may have been overstated due to the likely damage of the more delicate valve anterior, resulting in an underestimation of the total length of the valve.

As observed above, the shell of the species described here is distinguished by the coarser ornament, having 26–35 capillae in total, whereas in *M. ficneri* about 70 capillae can be counted in the specimen illustrated by Ficner and Havlíček (1978, pl. 8, fig. 6). Ficner and Havlíček (1978, p. 87) noted that in the type species there are 4–5 capillae per 1 mm, while in *M. andreae* sp. nov. this number is lower, attaining 2–3.5 in adult shells.

Occurrence: The species was found only in Miłoszów in trench MlN at the weathered top of the limestone complex and basal 1.5 m of overlying shale.

Subfamily Ambocoeliinae George, 1931 Genus Echinocoelia Cooper and Williams, 1935

Type species: *Echinocoelia ambocoelioides* Cooper and Williams, 1935; Tully Formation, Givetian; New York, USA.

Echinocoelia dorsoplana (Gürich, 1896) Figs 43Z–II, 48

| * | 1896 | Reticularia dorsoplana nov. nom. – Gürich, p. 260, pl. 9, fig. 3. |
|-------|-------|---|
| v non | 1909 | Reticularia dorsoplana Gürich – Siemi- radzki, p. 84. |
| | 1909 | Spirifer (Reticularia) dorsoplanus Gür. – Sobolew, pp. 472–473. |
| v non | 1922 | Spirifer (Reticularia) dorsoplanus Gür. – Siemiradzki, p. 14. |
| | 1975 | Proreticularia dorsoplana Gürich – Ba- liński, p. 179, pl. 32, fig. 2, pl. 35, fig. 7. |
| v. | 2022a | <i>Echinocoelia dorsoplana</i> (Gürich, 1896) – Halamski <i>et al.</i> , p. 54, fig. 36A–J, Q–R. |
| V. | 2022b | <i>Echinocoelia dorsoplana</i> (Gürich, 1896) – Halamski <i>et al.</i> , p. 360, figs 22X–Z, |

27 - 2.

Material: 80 complete or nearly complete shells with conjoined valves and about a hundred fragmentary shells and single valves, ZPAL V.74/Bp/45.

Description: Shell small, on average 3–4 mm long, the largest up to 5.5 mm in length, slightly wider than long to subequal, subcircular in outline, strongly unequally ventribiconvex with ventral valve attaining 79% of the total thickness on average; hinge line straight, occupying about 44–79% of the shell width; anterior margin weakly rounded, lateral margins and postero-lateral extremities rounded; anterior commissure rectimarginate to widely and weakly unisulcate.

Ventral valve strongly convex with massive umbonal region; sulcus usually absent, occasionally very weak median trough; interarea concave, apsacline, beak suberect to slightly incurved; delthyrium narrowly triangular with an apical angle of 20° - 36° , at one-third to one-half of its height, closed by an apical plate placed below the surface of the interarea (Fig. 48B); delthyrium bordered by low and fragile deltidial plates projecting more or less normal to the interarea. Dorsal valve transversally elliptical in outline, weakly convex, without perceptible sulcus or fold; dorsal interarea low, indistinctly concave, anacline, divided by an open notothyrium with an apical angle of 66° - 86° .

Interior of ventral valve with massively thickened dental ridges converging and thickening markedly posteriorly, then diverging from each other and becoming higher before meeting the floor of the valve, constricting small triangular cavity (Fig. 48B). Dorsal valve with small, knob-like cardinal process occupying apical region of the notothyrium (Fig. 48A).

Shell surface with densely spaced (7–10 per 1 mm) concentric bands of closely spaced spine bases (32–36 per 1 mm width); when preserved minute spines form dense cover (Fig. 48C, D); spines up to 250 μ m long and 10–30 μ m thick.

Remarks: Reticularia dorsoplana Gürich, 1896 was included in the genus Echinocoelia Cooper and Williams, 1935 by Halamski (2004b), who described and illustrated this species from Błonia Sierżawskie (SW-2 locality, then interpreted as belonging to the Skały Formation, but possibly representing the Nieczulice Beds), located about 400 m west of the type locality in the Holy Cross Mountains. The present material from Miłoszów displays a close general similarity and comparable range of variability in shell shape to Gürich's species. The former, however, seems to be generally slightly smaller attaining up to 5.5 mm in length, whereas the largest shells of the latter may reach up to 8.8 mm in length (see Halamski 2004b). This only noticeable difference, however, does not seem significant enough to establish a new species, because the size may have been influenced by environmental factors and transport after death.

Reticularia dorsoplana sensu Siemiradzki (1909, 1922) from Sitka (material examined, L PZ-D.919, *olim* 693) is a fragmentary specimen of *Thomasaria*? cf. *aviceps*.

Occurrence: Holy Cross Mountains: Świętomarz–Śniadka section, probably upper Middle Givetian (Gürich, 1896; Halamski, 2004b); Miłoszów (about 9 km SE from the former locality), shale and marly shale of M2 and M3 outcrops. Anti-Atlas, northern Maïder, upper Eifelian? (Halamski *et al.*, 2022a).



Fig. 48. Internal features and micro-ornament of *Echinocoelia dorsoplana* (Gürich, 1896) from the Givetian of Miłoszów. A. Interior of the dorsal valve ZPAL V.74/Bp/65/Ml/4; outcrop M1-IIa. B. Interior of the ventral valve ZPAL V.74/Bp/65/Ml/5; outcrop M1-IIa. C, D. Ventral micro-ornament of shells ZPAL V.74/Bp/65/M2/1, 2; outcrop M2-2.

Suborder Delthyridina Ivanova, 1972 Superfamily Delthyridoidea Phillips, 1841 Family Delthyrididae Phillips, 1841 Genus *Ivanothyris* Havlíček, 1957

Type species: *Spirifer gibbosus* Barrande, 1879; Lochkovian, Lower Devonian; Czech Republic.

Ivanothyris aculeata (Schnur, 1851) Fig. 49

- * 1851 *Sp[irifer] aculeatus* nob. Schnur, pp. 10–11.
 - 1853 *Sp[irifer] aculeatus* m. Schnur, p. 203, pl. 34, fig. 2.
 - 1963 *Delthyris aculeata* (J. Schnur, 1851) Vandercammen, pp. 112–116, pl. 11, figs 1–8, text-figs 72–74.

- 1997 "Spirifer" aculeatus Schnur 1853 Gourvennec in Boumendjel et al., pp. 109–110.
- 2013 Ivanothyris aculeata (Schnur, 1851) Halamski and Baliński, p. 290, fig. 35A–E.

Material: Six nearly complete shells and 20 mainly small fragments of shells and single valves that can be assignable by the distinctive ornament; 6 dorsal valves embedded in limestone; ZPAL V.74/Bp/47.

Description: Shell subrhomboidal in outline, with a wide hinge line, nearly as long as the maximum width; shell transverse (dimensions of a typical specimen: 17.8 mm wide, 12.7 mm long). Ventral interarea low and concave, ventral beak strongly incurved. The characteristic ornament of the shell consists of very strong and high radial plicae, the number of which on each flank of the ventral valve is three. On the dorsal valve there are a median fold and two



Fig. 49. *Ivanothyris aculeata* (Schnur, 1851) from the Lower Givetian of Miłoszów. **A.** Ventral interior ZPAL V.74/Bp/47/M1/4. **B.** Dorsal interior ZPAL V.74/Bp/47/M1/3. **C–G.** Juvenile articulated shell ZPAL V.74/Bp/47/M1/2 in dorsal, ventral, lateral, posterior, and anterior views. **H–O.** Articulated shell in ZPAL V.74/Bp/47/M1/1 in dorsal, ventral, lateral, posterior, and anterior views. **H–O.** Articulated shell in ZPAL V.74/Bp/47/M1/1 in dorsal, ventral, lateral, posterior, and anterior views (H–L), enlargement of ventral micro-ornamentation (M; inset shown in N), and SEM micrographs (N, O) showing enlarged details of elaborate microspines (N with inset shown in O). All specimens from outcrop MI-IIa.

lateral plicae. The plication of the shell results in strongly zigzagged anterolateral commissure. The micro-ornament consists of distinct concentric growth lamellae, especially pronounced near the anterior commissure, bearing densely packed spine bases at their anterior edges resulting in the fimbriate appearance (Fig. 49M). Some of the better-preserved spines reveal a complex structure (Fig. 49N, O).

Remarks: The overall shell outline and the characteristic strong radial plicae in combination with a fimbriate ornament are the basis of identification of our material as *Spirifer aculeatus* Schnur, 1851. The only adult shell available from Miłoszów differs in having three radial plicae on each flank of the ventral valve whereas two shells illustrated by Schnur (1853, pl 24, fig. 2a–f) possess four plicae. However, in an examined collection of this rare species from the Eifel (UNISTRA.2022.0.54001.1–6) larger specimens have three plicae, and smaller ones have two, so, quite self-evidently, the number of plicae shows some intraspecific variation.

Halamski and Baliński (2013) reported a single specimen from the Middle Devonian of Aferdou and another one from Madène el Mrakib, both from Morocco, and referred them to Ivanothyris aculeata. Earlier, Schnur's species had been attributed either to Spirifer (Scupin, 1900; Maurer, 1885; Holzapfel, 1895), Spiriferina? (Kayser, 1871), Hysterolites (Le Maître, 1944), Delthvris (Vandercammen, 1963), or to "Spirifer" (Gourvennec in Boumendiel et al., 1997). The main difficulty with assigning this species to the genus is the lack of data on the internal structure of the shell, which is partly due to the rare occurrence of this brachiopod. However, in the present collection from Miłoszów there are specimens that shed a little more light on this problem. A single fragment of the dorsal valve reveals the presence of a well-developed striated cardinal process and very short, rudimentary crural plates that coalesce with the base of the former and supporting crural bases just proximally (Fig. 49B). The interior of the ventral valve shows well-developed, extrasinal and divergent anteriorly dental plates (Fig. 49A). There is no distinct ventral median septum in the studied specimens although in some ventral valves a very low, short and rounded median ridge is visible. As Havlíček noted (1959, pp. 135, 244) the ventral median septum in the type species of the genus, Ivanothyris gibbosa (Barrande, 1879) from the Lochkovian Kotýs Limestone, is completely covered with adventitious deposit and visible only in the serial sections. His sections also reveal that between dental plates only a low and rounded median ridge on the bottom of the valve is marked (Havlíček, 1959, fig. 61). On the other hand, Boucot (1962) and Garcia-Alcalde (2001) remarked that in some species of the genus, the median septum may be better marked anteriorly.

Occurrence: As Halamski and Baliński (2013) summarized, *I.? aculeata* is known as quite rare element of the brachiopod fauna from the Eifelian of the Eifel (Schnur, 1853), the Ardennes (Jemelle Formation; Vandercammen, 1963) and from the Middle Devonian of the Maïder (Halamski and Baliński, 2013). Gourvennec (in Boumendjel *et al.*, 1997) reported the species from the uppermost Emsian or Eifelian of the Saoura valley in Algeria. The present material has been revealed in the Skały Formation at Miłoszów (M1 and M0 outcrops).

Superfamily Reticularioidea Waagen, 1883 Family Reticulariidae Waagen, 1883 Subfamily Reticulariinae Waagen, 1883 Genus *Undispirifer* Havlíček, 1957

Type species: *Spirifer undiferus* Roemer, 1844; Middle Devonian; Rhenish Slate Mts. (both Eifel and regions on the right bank of the Rhine), Germany.

Remarks: The original description of Undispirifer undiferus was based on specimens from Refrath region, Bergisches Land (Steinbreche, Lustheide; likely Givetian in age) and the Eifel region (Girzenberg near Sötenich and Gerolstein; probably Eifelian). This material is probably heterogeneous and no data on the origin of the only illustrated specimen (Roemer, 1844, pl. 4, fig. 6) are available. This question was not addressed by either Vandercammen (1957c, 1959), who treated this species very widely, or by Havlíček (1957, 1959). Vandercammen (1959) was of the opinion that Spirifer curvatus var. undulata Roemer, 1844 [according to him, a synonym of Spirifera gerolsteinensis Steininger, 1853; see Struve, 1981 for an opposed view] is a synonym of *Spirifer undiferus*, whereas for Struve (1990) the two species belong to different genera, the former being taken as the type species of Gerolsteinites Struve, 1990. A detailed summary of existing difficulties that could be solved by establishing a neotype of Spirifer undiferus was given by Carter et al. (1994, p. 354), but this has not been done. Following Carter et al. (1994) and Carter and Gourvennec (2006), Undispirifer is treated here widely, i.e., including Gerolsteinites.

Undispirifer sidoniae Halamski and Baliński sp. nov. Figs 50, 51

- ? 1904 *Reticularia* (?) *undifera* F. Roemer Sobolew, p. 74.
- v. 1966 Undispirifer sp. cf. Undispirifer undiferus (Roemer, 1844) – Biernat, pp. 116–117, pl. 28, figs 2–4.
- v. 2022b Undispirifer sp. nov. Halamski et al., p. 353.

Type material: Holotype, complete articulated shell ZPAL V.74/Bp/50/M0/1; paratypes, complete articulated shells ZPAL Bp VII/ 598, Bp 48/64/1/1, incomplete articulated shells ZPAL V.74/Bp/50/M0/4, 6–10 (6 – sectioned), single valves ZPAL V.74/Bp/50/M0/3, 5, and 15 smaller fragments of shells.

Type locality: Outcrop M0, Miłoszów, Łysogóry Region, Holy Cross Mountains, Poland.

Type stratum: Skały Formation, bed M0-9, lower Middle Givetian.

Diagnosis: Undispirifer with markedly transverse brachythyrid shell (width-to-length ratio about 1.4), low ventral interarea, and 9–13 costae per flank.

Derivatio nominis: in honour of Sidonia Hedwig Zäunemann (15.1.1711–11.12.1740), German poet (see Gottschall, 1892), author of a description of mines at Ilmenau (Zäunemann, 1738, pp. 562–587).

Description: Shell rounded in outline, weakly to moderately ventribiconvex, typically slightly over 30 mm wide,



Fig. 50. Undispirifer sidoniae Halamski and Baliński sp. nov. **A–C.** Subcomplete articulated shell ZPAL Bp 48/64/1/1 (paratype) in dorsal, lateral, and posterior views. Limestone lens most probably corresponding to bed M0-9 (erroneously described by Halamski, 2004, p. 226, as coming from outcrop M1). **D.** Ventral valve ZPAL V.74/Bp/50/M0/3 (paratype); outcrop M0-9. **E.** Incomplete articulated shell ZPAL V.74/Bp/50/M0/4 (paratype) in dorsal view. Outcrop M0-9. **F.** Dorsal valve ZPAL V.74/Bp/50/M0/5 (paratype) embedded in limestone. Outcrop M0-9. **G–K.** Articulated shell ZPAL V.74/Bp/50/M0/1 (holotype) in dorsal, ventral, lateral, posterior, and anterior views. Outcrop M0-9. **L–P.** Articulated shell ZPAL Bp VII/598 (paratype) in dorsal, ventral, lateral, posterior, and anterior views. Specimen figured by Biernat (1966, pl. 28, fig. 3); most probably outcrop M0-9.

transverse (width-to-length ratio about 1.4; see Tab. 6); maximum width in the middle third of the dorsal valve; antero-lateral margins rounded; anterior margin truncated, short. Ventral valve with a low, apsacline interarea and a wide, shallow sulcus appearing in umbonal region. Dorsal valve with a rounded fold, the latter flatteded anteriorly. Anterior commissure uniplicate, tongue subtriangular, its width about 0.3–0.4 of that of the shell. Ornament of low, weak, rounded costae, starting at about one-fourth of the valve length, 9–13 per flank, the 2–4 exteriormost ones being rather striae than ribs. Micro-ornament of dense concentric growth lamellae and irregularly distributed spines.

A single sectioned dorsal valve reveals rather small sockets and wide crural bases that do not develop into crural plates (Fig. 51).

Remarks: The studied brachiopods are included in the genus *Undispirifer* s.l. on account of their rounded cardinal extremities, narrow sulcus and fold, and micro-ornament

Table 6

Biometric characteristics of *Undispirifer sidoniae* Halamski and Baliński sp. nov. from the Givetian of Miłoszów.

| Cat. No. | L | W | Т | ws | 1 | NA | |
|-----------------------------------|-------|-------|-------|------|-------|----|--|
| ZPAL | | Nfl | | | | | |
| V.74/Bp/50/ M0/1 Holo- type | 22.0 | 32.0 | 15.6 | 11.7 | 19.4 | 12 | |
| Bp VII/598 | 20.2 | 30.6 | 17.4 | 12.6 | 19.5 | 13 | |
| Bp 48/64/1/1 | 20.5 | ~32 | ~15 | - | 18.0 | 10 | |
| V.74/Bp/50/ M0/7 | ~22.2 | ~27.6 | 14.3 | 12.1 | 18.8 | ~9 | |
| V.74/Bp/50/ M0/8 | ~21.3 | ~31.5 | >14.2 | _ | 18.3 | ~9 | |
| V.74/Bp/50/ M0/9 | 26.1 | 31.7 | 18.0 | 11.5 | >21.6 | 9 | |

(Carter and Gourvennec, 2006). As summarised above, U. undiferus (Roemer, 1844) is in need of revision. Nonetheless, representatives of Undispirifer from Western Europe, including the above-mentioned type species, are characterised by a smaller number of costae than that in the sample from Miłoszów, where it mostly exceeds ten. Undispirifer gerolsteinensis (Steininger, 1853) [the type species of Gerolsteinites] has also 10-12 ribs per flank (Steininger, 1853, p. 76; Schnur, 1853–54, pl. 34, fig. 3g-h), but differs from U. sidoniae sp. nov. in possessing a high, nearly catacline ventral interarea (Struve, 1981, p. 440; 1992, p. 582), maximum width situated at or near the cardinal margin, and more distinct costae (starting at umbo). It follows that the brachiopods from Miłoszów are best described as a new species, despite a rather small number of specimens at hand. The shape of available shells is relatively constant.

The numbers of costae per flank in samples described as *U. undiferus* [s.l.] are 6–8 in the Eifel and/or Rhenish Slate Mountains (Roemer, 1844, p. 73), 5–10 in the Eifelian to Frasnian of the Ardennes (material most probably heterogenous; Vandercammen, 1957c, p. 4), and (5–)6–7(–9) in the Givetian of Boulonnais (Brice and Loones, 2002, p. 96). Other species of *Undispirifer* have similar values: 6–10 in *U. rigauxi* Brice and Loones, 2002, 3–6 in *U. belliloci* Brice and Loones, 2002, 6–9 [after photographs, data not given in the text] in *Undispirifer*? gerolsteinensis grandis Brice and Loones, 2002, 4–5(–7) in *U. givefex* (Struve, 1981; Godefroid, 1995, p. 104).

Undispirifer schemachensis (Sapel'nikov and Sapel'nikova, 1996) from the Eifelian of the western slope of the Middle Urals (at Nizhnyaya Shemakha River), originally described as a subspecies of *U. undiferus*, but out of variation range of that species, has 8–15 costae per flank (Sapel'nikov and Mizens, 2000, p. 123), but differs from the Miłoszów sample in being approximately as long as wide. *Elytha* ex gr. *undifera* sensu Ljaschenko (1959, p. 118, pl. 11, figs 13–14) from the Starooskolskiy horizon (upper part



Fig. 51. Transverse serial sections of *Undispirifer sidoniae* Halamski and Baliński sp. nov. through shells ZPAL V.74/Bp/50/ M0/6 (paratype) from outcrop M0-9. Distances measured in millimetres from the tip of the ventral umbo.

of the Givetian) of the Central Devonian Field has 10–12 costae and width-to-length ratio of 1.4; it may represent the same species, but the sample is insufficient to be certain. **Occurrence:** All specimens, for which detailed data are available, come from bed 9 at locality M0 in Miłoszów.

Subfamily Rhenothyridinae Gourvennec in Carter *et al.*, 1994 Genus *Warrenella* Crickmay, 1953

Type species: *Warrenella eclectea* Crickmay, 1953; Cheviot Formation, Frasnian; Alberta, Canada.

Synonyms: *Minatothyris* Vandercammen, 1957a (type species: *Spirifer euryglossus* Schnur, 1851; Frasnian; Büdesheim, Eifel, Germany); see Pitrat (1965, p. *H*721) and Ludvigsen and Perry (1975, p. 71). *Nordella* Ljaschenko, 1973 (type species: *Elytha orbiculata* Ljaschenko, 1959; Middle Frasnian; southern Timan, Russia); see Oleneva (2013, p. 61).

Subgenus Warrenella (Warrenella) Crickmay, 1953 Warrenella (Warrenella) concentrica (Schnur, 1851) Fig. 52

* 1851 Sp. concentricus nob. – Schnur, p. 11.

р

- 1853 Sp. concentricus m. Schnur, pp. 210– 211, pl. 37, fig. 1a–c, non fig. 1d–f.
 - 1895 Spirifer Gosseleti n. sp. Holzapfel, pp. 256–258. [ubi syn.].
 - 1895 Spirifer Maureri n. sp. Holzapfel, p. 444, pl. 17, figs 1, 2.
 - 1900 *Spirifer Maureri* Holzapfel Scupin, pp. 40–41, pl. 4, figs 3, 4.
- v non 1922 Spirifer (Reticularia) Maureri Holzpf. Siemiradzki, p. 14.
- non 1957b *Minatothyris maureri* (E. Holzapfel, 1896) – Vandercammen, pp. 7–17, pl. 2, figs 1–12, pl. 3, figs 1–13.

- 1966 *Minatothyris maureri* (Holzapfel, 1896) – Biernat, pp. 132–133, non pl. 31, figs 4, 5.
- 1966 Minatothyris sp. cf. Minatothyris concentrica (Schnur, 1854) – Biernat, p. 133, pl. 31, fig. 6.
- 1969 *Minatothyris maureri* (Holzapf.) Filonowicz, p. 34.
- 1970 Minatothyris concentrica (Schnur 1851)
 Struve, pp. 540–541, pl. 12, figs 60, 61, pl. 13, figs 64, 65, pl. 14, fig. 68 [ubi syn.].
- non 1975 *Warrenella* cf. *W. maureri* (Holzapfel) – Ludvigsen and Perry, p. 85, pl. 17, figs 1–10.

Material: Four complete, eight slightly damaged and 29 fragments of shells, ZPAL V.74/Bp/49.

Description: Shell rounded in outline, typically 28–30 mm wide, 25–28 mm long, and 16–18 mm thick in adults, usually weakly transverse, width-to-length ratio (0.95-)1.05-1.11(-1.19) [N = 8] (see Tab. 7); weakly ventribiconvex to subequal; maximum width about mid-length of the shell, maximum thickness slightly posteriorly to mid-length. Cardinal margin gently bent, attaining about 52–59% of the shell width, cardinal extremities rounded; anterior



Fig. 52. *Warrenella concentrica* (Schnur, 1851). A–E, F–J, K–O. Articulated shells ZPAL Bp V.74/Bp/51/M3/1–3 in dorsal, ventral, lateral, posterior, and anterior views. P–R. Fragmentary articulated shell ZPAL V.74/Bp/49/M3/4 in dorsal, lateral, and posterior views. All specimens from outcrop M3-7.

р
commissure uniplicate, tongue rounded, low, typically 12– 15 mm wide, reaching 38–54% of the shell width. Dorsal valve with gentle fold, ventral valve with U-shaped sulcus, both observable from the umbonal regions, not sharply delineated. Ventral umbo thick, incurved; interarea small, concave, apsacline to nearly orthocline. Ornament exceptionally preserved, consisting of fine growth lamellae with very fine marginal spine bases. Interior not studied.

Remarks: Brachiopods from Miłoszów (M2-5 and M3-7) are included into the genus *Warrenella* on account of micro-ornament, weakly transverse medium-sized shells with thick ventral umbo (Ludvigsen and Perry, 1975, p. 69), rounded cardinal margins, poorly expressed but distinct fold and sulcus, and low, usually apsacline ventral interareas (Carter and Gourvennec, 2006, p. 1857). It may be noted that in the description given by Carter and Gourvennec (2006), *Warrenella* is described as having elongate shells, but the illustrated specimens of the type species *W. eclectea* (Carter and Gourvennec, 2006, fig. 2) are weakly transverse. The brachiopods from Miłoszów are further included into the subgenus *W. (Warrenella*) on account of lack of costation.

The present authors follow Struve (1970) in recognising (i) a relatively long-ranging and variable *Warrenella concentrica*, the type of which is from the Eifelian and that includes *W. maureri* (Holzapfel, 1895), the type of which is from the Givetian; (ii) two other narrowly defined species, the Upper Eifelian *W. weigelti* Struve, 1970 and the Givetian *W. torleyi* Struve, 1970. It is not excluded that *W. concentrica* s.l. (as here) may be subdivided into several taxa in the future, but this would require a detailed study of the material from the Rhenish Slate Mountains, which is outside the scope of the present paper.

Two *Warrenella* species present in the Rhenish Slate Mountains, *W. weigelti* and *W. torleyi* are characterised by relatively high, subtrapezoidal tongues, much unlike the low and rounded tongue of the specimens from Miłoszów. On the other hand, the width-to-length ratio of the material studied, mostly about 1.1 (see above), is more like that of *W. weigelti* (1.07–1.13; Struve, 1970) than that of *W. concentrica* from the Eifel (1.12–1.33; Struve, 1970), but there is nonetheless some overlapping of the ranges for Miłoszów and *W. concentrica* from the Eifel. Given the above, the brachiopods from Miłoszów are assigned to *Warrenella concentrica* s.l. Such taxonomic treatment is the best that can be proposed at the moment, although it is not entirely satisfying.

Biernat (1966) treated the representatives of *Minatothyris* (here: *Warrenella*) from the Łysogóry Region as belonging to two species: *M. maureri* (Miłoszów and outcrops 89, 92, 93, 101 at Skały; five specimens) and *Minatothyris* cf. *concentrica* (a single specimen from Miłoszów). Following Struve (1970), the Eifelian–lowermost Givetian brachiopods from Skały (*Minatothyris* cf. *concentrica sensu* Biernat, 1966, or at least the shells illustrated by Biernat, 1966, pl. 31, figs 4, 5) are considered as belonging to *W. weigelti*, the shells of which are higher and more transverse. On the other hand, all the material of Miłoszów (incl. *Minatothyris* cf. *concentrica* sensu Biernat, 1966 and partly *M. maureri sensu* Biernat, 1966) is considered to belong to a single species.

Warrenella maureri was described as *Spirifer Gosseleti* Holzapfel, 1895 in the text of his monograph (Holzapfel, 1895, pp. 256–258). This name is a junior homonym of *Spirifer gosseleti* Béclard, 1887 (now: *Mauispirifer gosseleti*, see Jansen, 2016, p. 76 and Mottequin, 2019, p. 66–69; Lower Devonian); the mistake is corrected and the valid specific name is proposed at the end of the text (Holzapfel, 1895, p. 444) and in the atlas.

Spirifer maureri sensu Siemiradzki (1922) from Skiby (Kielce Region; L PZ-D.363, olim 996; other specimens not found), is costate. *Minatothyris maureri sensu* Vandercammen (1957b) from the Middle and Upper Frasnian of Belgium differs from the specimens studied in having a proportionally wider shell and narrower hinge margin. *Warrenella* cf. *W. maureri sensu* Ludvigsen and Perry (1975) from the Pine Point Formation (Givetian) near Great Slave Lake (Northwest Territories, Canada) is strongly transverse.

From the palaeoecological point of view, it is interesting to note that in bed M3-7 at Miłoszów, *Warrenella concentrica* s.l. co-occurs with *Stringocephalus* sp. Ludvigsen and Perry (1975, p. 69) noted that "*Warrenella* very rarely has been reported with *Stringocephalus*".

Table 7

| Coll. number ZPAL V.74/ | L | W | Т | W | War | W/L | w/W | War/W |
|----------------------------|------|------|------|------|------|------|------|-------|
| Bp/49/M3/ | | | (mm) | W/L | | | | |
| 1 | 22.7 | 24.3 | 13.1 | 9.2 | 14.0 | 1.07 | 0.38 | 0.58 |
| 2 | 25.6 | 24.3 | 15.3 | 12.5 | - | 0.95 | 0.51 | - |
| 3 | 27.6 | 30.4 | 17.8 | 13.5 | - | 1.10 | 0.44 | - |
| 6 | 29.1 | 33.0 | 19.3 | 14.4 | 18.3 | 1.13 | 0.44 | 0.55 |
| 7 | 26.3 | 28.2 | 16.6 | 12.4 | 15.6 | 1.07 | 0.44 | 0.55 |
| 8 | 25.2 | 30.0 | 15.7 | 16.3 | - | 1.19 | 0.54 | - |
| 9 | 25.7 | 26.9 | 16.1 | 12.1 | 14.7 | 1.05 | 0.45 | 0.59 |
| 10 | 26.9 | 28.2 | 17.4 | 15.1 | - | 1.05 | 0.54 | - |

Biometric characteristics of Warrenella (Warrenella) concentrica (Schnur, 1851) from the Givetian of Miłoszów.

Occurrence: Rhenish Slate Mountains, Eifelian of the Eifel (*W. concentrica* s.s.), Middle Eifelian (Ahrdorf Formation) according to Struve (1970); Givetian of Frettertal and other localities (*W. maureri*). Devon, Givetian (according to Holzapfel, 1895; material not checked by the present authors). Holy Cross Mountains, Łysogóry Region: M2-5, seldom; M3-7, common (Lower Givetian).

Family Thomasariidae Cooper and Dutro, 1982 Genus *Thomasaria* Stainbrook, 1945

Type species: *Thomasaria altumbona* Stainbrook, 1945; Independence Shale, Upper Frasnian; Iowa, USA.

Thomasaria ex gr. *simplex* (Phillips, 1841) Figs 53A–O, 54

1966 Pyramidalia cf. simplex (Phillips, 1841) – Biernat, p. 136, pl. 27, fig. 1.

Material: Four complete, five slightly damaged shells and about 30 fragmentary specimens, some of them embedded in limestone, ZPAL V.74/Bp/51.

Remarks: This species is characterized by a fairly small shell size, reaching a width of about 17 mm and a transversely subtrapezoidal outline. The shell is strongly ventribiconvex with the ventral valve about 2.5 times deeper than the opposite one. The ventral procline interarea reaches



Fig. 53. Givetian spiriferides from Miłoszów. **A–O.** *Thomasaria* ex gr. *simplex* (Phillips, 1841); A–E, F–J, K–O – articulated shells ZPAL Bp V.74/Bp/49/MS1/1–3 in dorsal, ventral, lateral, posterior, and anterior views; specimens from trench 1 (1970). **P–Y.** *Thomasaria*? cf. *aviceps* (Scupin, 1900); P–T, U–Y – articulated shells ZPAL Bp V.74/Bp/46/M3/1–2 in dorsal, ventral, lateral, posterior, and anterior views; specimens from outcrop M3-7.

a width of about 0.66 of the total shell width, is highly triangular and flat, with the apical tip slightly inclined dorsally or deflected ventrally. Internally, the described shells reveal typical structures for the genus, such as strongly divergent dental plates and slightly concave crural bases that do not meet the valve floor (Fig. 54). Biernat (1966) described a single incomplete specimen from Miłoszów as *Pyramidalia* cf. *simplex* (Phillips).

External characters of the shells described here strongly suggest their closeness to the Givetian species *Thomasaria simplex* (Phillips, 1841; see Halamski and Baliński, 2019; Halamski *et al.*, 2022a). The material at hand is insufficient for a definitive identification.

Occurrence: Very rare in the marly limestone intercalations in M3 and S1 in Miłoszów.

Thomasaria? cf. aviceps (Kayser, 1871) Figs 53P-Y, 55

- cf. 1871 Spirifer aviceps Kayser, pp. 578–579, pl. 11, fig. 4.
 - 1896 Reticularia aviceps Kays. Gürich, pp. 257– 258, pl. 9. fig. 7.
 - 1904 Reticularia aviceps Kayser Sobolew, p. 72.
 - 1909 Spirifer aviceps Kayser Sobolew, pp. 474–475.
- v 1966 *Eorecticularia aviceps* (Kayser, 1871) Biernat, pp. 128–131, text-figs 45–46, pl. 30, figs 1–12.

Material: Seven nearly complete or slightly damaged shells and 29 fragmentary specimens including 12 shells, 12 ventral and 5 dorsal valves, ZPAL V.74/Bp/46.

Description: Shell medium-sized, 16–20 mm in length on average, the largest attaining about 27 mm in length (see Tab. 8); ventribiconvex, subtrapezoidal to subpentagonal in outline, wider than long, widest near the hinge line; length reaches 60–76% of the width; hinge margin straight, shorter than the greatest shell width; cardinal extremities rounded, lateral margins nearly straight to gently arched, rarely rounded, anterior margin angularly indented, anterior commissure uniplicate.

Ventral valve regularly arched in lateral profile, with fine and pointed umbo; interarea well exposed, triangular, high, catacline to apsacline, rarely weakly procline near the hinge margin, always weakly concave, rather narrow reaching 60-75% of the total shell width, quite well-delimited from flanks in specimens with well-preserved shell matter; beak usually straight to weakly inclined; delthyrium distinctly narrow, usually enclosing an angle of $15^{\circ}-27^{\circ}$, exceptionally wider, apical one-third to one-half closed by apical thickening formed by two coalescent plates deposited on inner sides of the dental plates, placed a little below the surface of the interarea (see detailed drawings in Biernat, 1966, fig. 45); sulcus narrow to medium in width, well-marked, originating at umbo; tongue rather short, concave with rounded top.

Dorsal valve transversally subtrapezoidal in outline, slightly less convex than the opposite valve, regularly and gently convex in anterior view with more inflated umbonal region; fold imperceptible posteriorly, appearing in anterior

Biometric characteristics of *Thomasaria*? cf. *aviceps* (Kayser, 1871) from the Givetian of Miłoszów.

| Cat. No. ZPAL | L | W | L/W | Т | War | War/W |
|----------------|-------|-------|-------|------|------|-------|
| Bp V.74/Bp/46/ | (m | m) | L/ W | (m | m) | warrw |
| M3/1 | 11.0 | 18.3 | 0.60 | 10.0 | 11.2 | 0.61 |
| M3/2 | ~17.5 | 24.4 | 0.66 | 13.1 | 18.1 | 0.69 |
| M3/ | 16.4 | 26.9 | 0.61 | 14.2 | 18.1 | 0.67 |
| M3/ | 17.4 | ~29.4 | ~0.59 | 13.6 | - | - |
| S1/1 | ~26.1 | ~34.3 | ~0.76 | 21.7 | - | - |

region of the valve, poorly delimited from flanks, frequently with faint median through or flattening.

Interior of the ventral valve with strong ventrally divergent dental plates reaching a quarter to one third of the valve length, massive umbonally, markedly thinning anteriorly (Fig. 55). Dorsal valve with socket plates fused with crural bases, nearly vertical posteriorly; anteriorly crural bases concave, more or less parallel to and hanging well above the valve floor, not supported by crural plates; cardinal process striated, slightly raised above the valve floor, stretched between apical portion of the inner socket ridges, anteriorly bilobed in one of the sectioned specimens (Fig. 55A).

Shell surface marked by fine concentric growth lines, each bearing a row of minute spines.

Remarks: Biernat (1966) rightly noticed the great similarity of her specimens from Skały to those described by Kayser (1871) from the Calceola-Kalk and the Crinoiden-Schicht of the Eifel as *Spirifer aviceps*. She included this species in the genus *Eoreticularia* Nalivkin, 1924. The serial sections of specimens from Skały (Biernat, 1966, fig. 46), as well as those of the conspecific material from Miłoszów (Fig. 55) show that, unlike *Eoreticularia*, which possesses crural plates joined with the median septum or ridge, the former have no crural plates at all. For the same reason, the studied form cannot be included in the genus *Reticulariopsis* Frederiks, 1916, which also possesses well defined crural plates (see Gourvennec, 1994a).

Conversely, the internal structure of the studied specimens is similar to that of the Lower Devonian Deltospirifer Wang and Rong, 1986, and especially to the Middle-Upper Devonian Thomasaria Stainbrook, 1945. The present specimens are externally similar to Deltospirifer in terms of the general shell outline and the well-defined sulcus and fold but differ mainly in the absence of radial plications and in having a higher, less curved ventral interarea. The specimens from Miłoszów, in addition to having a similar internal shell structure, are also externally alike Thomasaria. They show a similar shell outline and microornament, rather rounded to feebly angular cardinal extremities, well-defined sulcus and fold, pointed ventral beak, narrow delthyrium and lack of distinct radial plicae. It is worth noting that Sobolew (1909, p. 474) also pointed out the great similarity of S. aviceps from Skały to Thomasaria simplex. The main difference between these forms is in the form of the ventral

Table 8



Fig. 54. Transverse serial sections of *Thomasaria* cf. *simplex* (Phillips, 1841) through the shell ZPAL V.74/Bp/49/M3/4 from outcrop M3-7 (**A**, ventral valve; **B**, dorsal valve). Distances measured in millimetres from the tip of the ventral umbo.

interarea, which in *Thomasaria simplex* is wider, procline to catacline, very high and flat to weakly concave, giving the ventral valve a shape of a pyramid, whereas in the species discussed here the interarea is narrower, less high, more concave, and catacline to more often apsacline.

Internal structures of the type material of *Spirifer aviceps* Kayser, 1871 from the Eifel are unknown, so at present an accurate taxonomic assessment of the specimens studied cannot be effectuated.

Occurrence: Miłoszów, Givetian: M3-7, common; M2-3 and M2-5 rare.

Superfamily Cyrtioidea Frederiks, 1924 Family Cyrtiidae Frederiks, 1924 Subfamily Eospiriferinae Schuchert, 1929 Genus *Leiocyrtia* Baliński gen. nov.

Type species: *Leiocyrtia rara* gen. et sp. nov., as below. **Species assigned:** Type species only.

Diagnosis: Small to medium in size, ventribiconvex, subpentagonal to transversely elliptical in outline, wider than long, with well-developed sulcus and fold originating at the beaks; surface smooth. Ventral interarea concave, apsacline; delthyrium bordered by sub-vertical deltidial plates. Ventral interior with slightly extrasinal dental plates and short and high median myophragm, shorter than the length of the dental plates. Dorsal interior with small cardinal process and narrow, converging crural plates forming U-shaped sessile cruralium. Micro-ornament of dense, flat-topped radial capillae separated by narrow intercapillar grooves.

Etymology: Combination of Greek $\lambda \varepsilon \widetilde{i} \circ \zeta$ (smooth; referring to smooth, noncostate shell) and the genus name *Cyrtia*; the genus name is feminine.

Remarks: The most characteristic features of the described genus are non-costate and non-plicate flanks, rather small to medium-sized shell with a pronounced sulcus and fold originating at the beaks. Internally, it is characterized by having dental plates and a short but distinct median myophragm

inside the ventral valve and a small and low cardinal process and sessile cruralium within the dorsal valve. The characteristic capillate microornament of Myriospirifertype sensu Havlíček (1980) suggests an affinity with the superfamily Cyrtioidea, especially the eospiriferins, which, however, disappear from the fossil record generally by the end of the Lower Devonian (see Johnson and Hou, 2006), and thus clearly before the appearance of the form reported here. Some reports, however, suggest that the upper range of eospiriferins may have been much higher. For example, Havlíček (1980) remarked that a small species of Myriospirifer Havlíček, 1978, M. insidiosus (Barrande, 1879) in Bohemia occurs not only in the Emsian, but it may also occur in the Acanthopyge Limestone (Eifelian; Havlíček, 1980, p. 39). Oleneva (2010, 2016) described small-sized eospiriferins from the Middle to Upper Frasnian of the Russian Platform and assigned them to the new genus Tokmospirifer Oleneva, 2010. This genus is similar in the internal structure to the form from Miłoszów in having dental plates, crural plates and cardinal process. Both forms have the same type of the capillate microornament, although the capillae in the Russian form are markedly thicker (8-10 capillae per 1 mm in the Russian form and 16-24 per 1 mm in the present material). The form described here can be easily distinguished from the latter by its wider shell, much better marked sulcus and fold, and smooth, non-plicate lateral valve flanks. Internally it differs in having a distinct ventral umbonal myophragm.

The cosmopolitan genus Myriospirifer, ranging from the Llandovery to the Emsian, and probably ranging into the Lower Eifelian, is characterized, like the form from Miłoszów, as having an elongate hinge line, a nonplicate shell with a well-developed fold and sulcus and very fine radial capillae separated by narrower interspaces. They also have similarly disposed deltidial plates that border the delthyrium and protrude almost at right angles to the interarea. In addition to external similarity, the form from Miłoszów and Myriospirifer share some important details of the internal structure such as the presence of dental and crural plates. Apart from M. insidiosus (Barrande, 1879), which is the smallest representative of the genus, other species of Myriospirifer differ from Leiocyrtia gen. nov. in usually achieving much larger shell dimensions (up to about 50 mm in width). Internally, Myriospirifer is distinguished primarily by the absence of the ventral myophragm, which in the form from Miłoszow, although short, is quite high, sometimes resembling the median septum (Fig. 57).

Recently, Waterhouse (2016) introduced *Waddingtonia*, a new reticulariid genus with *Reticulariopsis? warreni* Perry, 1984 from the Delorme Formation (Lochkovian and Pragian) of Yukon, Canada, as a type species. This genus differs from *Leiocyrtia* primarily in that it is about twice as large, has a more transverse and more oval outline, narrower sulcus and fold, and more prominent growth lamellae interrupting the radial capillae. Internally, the former genus differs in having much longer dental plates and a ventral and dorsal myophragm, as well as in the absence of a cruralium.

The cosmopolitan genus *Eospirifer* Schuchert, 1913, occurring from the Upper Ordovician to the Lower Devonian (Emsian), differs from *Leiocyrtia* primarily in attaining a



Fig. 55. Transverse serial sections of *Thomasaria*? cf. *aviceps* (Scupin, 1900) through shells ZPAL V.74/Bp/46/M3/3 (A) and M3/4 (B) from outcrop M3-7. Distances measured in millimetres from the tip of the ventral umbo.

much larger shell size, having longer dental plates and a different type of micro-ornament (*Eospirifer*-type, see Havlíček, 1980), and lacking a ventral myophragm and cruralium.

Leiocyrtia rara Baliński gen. et sp. nov. Figs 56, 57

v. 2022b Cyrtiidae gen. et sp. nov. – Halamski *et al.*, p. 353.

Type material: Holotype: a complete articulated shell ZPAL Bp ZPAL V.74/Bp/48/M3/l, figured in Fig. 56F–J; paratypes: five complete or slightly damaged shells, 20 fragments of disarticulated valves and shells, collection number ZPAL V.74/Bp/48.

Etymology: Latin *rara*, rare; on account of rarity of this species in the type outcrop.

Type locality: Miłoszów, M3 outcrop (coordinates: 50°54′9.6″N, 21°07′12″E), Holy Cross Mountains, Poland.

Type horizon: Skały Formation, composite bed M3-7, bed M3 λ ; Lower Givetian, probably upper part of the *Polygnathus timorensis* conodont zone.

Diagnosis: Shell small to medium in size, on average 9– 15 mm in length, subpentagonal to transversely elliptical in outline, wider than long, widest at mid-length, ventribiconvex; lateral margins and postero-lateral extremities rounded; sulcus and fold well-developed, originating at the beaks, accentuated by bordering weak plications (sulcus) and wide furrows (fold), resulting in a weakly parasulcate anterior commissure; ventral interarea concave, apsacline near the cardinal margin; delthyrium open, with an apical angle of about 53°.

Description: Shell small to medium in size, most often about one centimeter in length, the largest specimen (with slightly damaged ventral umbo) about 14.7 mm long (see Tab. 9); wider than long, widest at midlength, subpentagonal to transversely elliptical in outline, ventribiconvex with



Fig. 56. *Leiocyrtia rara* Baliński gen. et sp. nov. from the Lower (to lower Middle?) Givetian of Miłoszów. A–E, F–J. Articulated shells ZPAL V.74/Bp/48/MS2/2 (paratype) from trench II and ZPAL V.74/Bp/48/M3/1 (holotype) from outcrop M3-7 in dorsal, ventral, lateral, posterior, and anterior views. K–O, U. Articulated shell ZPAL V.74/Bp/48/MS2/3 (paratype) from trench II in dorsal, ventral, lateral, posterior, and anterior views with an enlargement of the anterior view to show capillate micro-ornament in the sulcus. P–T. Articulated shell ZPAL V.74/Bp/48/M3/4 (paratype) from outcrop M3-7 in dorsal, ventral, lateral, posterior, and anterior views 2PAL V.74/Bp/48/M3/6 from outcrop M3-7 (V) and V.74/Bp/48/M1/1 from outcrop M1-IIa (W, X). Y, Z. Incomplete articulated shell ZPAL V.74/Bp/48/M3/5 (paratype) from outcrop M3-7 in dorsal and ventral views. All paratypes except the shell ZPAL V.74/Bp/48/M1/1 are strato- and topotypic.



Fig. 57. Transverse serial sections of *Leiocyrtia rara* Baliński gen. et sp. nov. through shells ZPAL V.74/Bp/48/M3/7 (**A**), M3/8 (**B**), M3/9 (**C**), M3/10 (**D**), all four paratypes from outcrop M3-7. Distances measured in millimetres from the tip of the ventral umbo.

ventral valve attaining 61–64% of the total thickness; hinge line straight to slightly angular occupying about 72–93% of the shell width; anterior margin weakly rounded to straight.

Ventral valve strongly convex, with pronounced umbo and incurved beak; sulcus well marked, moderately deep, with faint, barely perceptible median furrow, widely V-shaped in transverse section, originating near the beak, laterally limited by faint rounded plicae; flanks of the valve weakly convex; interarea concave, apsacline near the cardinal margin; delthyrium open, with an apical angle of about 53°, bordered by low and fragile, nearly vertical deltidial plates. Dorsal valve transversally elliptical in outline, less convex than the opposite valve; fold extending from the beak, well marked, rounded, enhanced laterally by wide troughs particularly well-developed in the anterior region of the valve and resulting in weakly parasulcate commissure.

Interior of ventral valve with slightly extrasinal, ventrally divergent dental plates and a short, low to high median

Table 9

Biometric characteristics of *Leiocyrtia rara* Baliński gen. et sp. nov. from the Givetian of Miłoszów.

| Cat. No. ZPAL | L | W | W/L | Т | ws | | | | |
|----------------|-------|-------|-------|------|------|--|--|--|--|
| Bp V.74/Bp/48/ | (m | m) | W/L | (mm) | | | | | |
| M3/12 | 7.8 | 9.7 | 1.24 | 6.0 | 4.0 | | | | |
| M3/1 | 9.3 | 11.3 | 1.22 | 7.6 | 5.6 | | | | |
| M3/4 | 10.1 | 13.0 | 1.29 | 8.2 | ~5.6 | | | | |
| M3/5 | ~10.8 | ~12.6 | ~1.17 | 8.2 | 5.5 | | | | |
| M3/11 | ~14.5 | ~16.7 | ~1.15 | 10.4 | 7.6 | | | | |

ridge or myophragm, the latter shorter than the length of dental plates (Fig. 57A, C); delthyrial plate not developed, but faint delthyrial ridges on the adaxial surface of dental plates partially occlude delthyrium near the apex (Fig. 57C, sections 0.8–1.5). Dorsal valve with small and low cardinal process; dental sockets deep; outer hinge plates wide, apically inclined to converge with the base of cardinal process; crural bases closely set, embedded in a median thickening, anteriorly elevated above the valve floor and supported by narrow converging crural plates, forming U-shaped sessile cruralium (Fig. 57).

Shell smooth, noncostate; micro-ornament consists of dense, flat-topped radial capillae numbering 16–24 per 1 mm, increasing by rare bifurcations; intercapillar grooves much narrower than the capillae; concentric growth lines weak, rarely visible (Fig. 56V–X).

Remarks: The described species resembles externally some other Lower-Middle Devonian smooth spiriferides. The general outline of the shell, a well-marked ventral sulcus emphasized by the faint bounding plications, a dorsal fold limited by weak bordering furrows resulting in a weakly parasulcate anterior commissure, and smooth flanks make the new species similar to brachiopods described from the Eifelian of Padaukpin, Burma by Anderson et al. (1969) as Reticulariopsis eifliensis (Scupin, 1900). The latter are easily distinguishable mainly by its very different micro-ornament in the form of concentrically arranged marginal spines which is characteristic of many reticularioidean spiriferides. It is worth to note that a single shell from the lower Calceolaschichten of the Eifel illustrated by Scupin (1900, pl. 5, fig. 5a-d) as Spirifer robustus var. eifliensis is evidently less convex and has a much shallower sulcus and a lower fold. Leiocyrtia rara differs from the Bohemian Lower Devonian Quadrithyris robusta (Barrande, 1848) in being smaller (shells of the latter are up to 26.2 mm wide), having a less rounded anterior commissure, longer tongue, and deeper sulcus. Internally the new species differs in having a much shorter ventral median septum or myophragm (in Q. robusta it reaches twothirds of the valve length), shorter dental plates, and in possessing crural plates (no crural plates in the Bohemian species).

Occurrence: Type horizon at Miłoszów, M3-7. A few additional specimens were recovered from M1-IIa.

Order Spiriferinida Ivanova, 1972 Family Cyrtinidae Frederiks, 1911 Genus *Cyrtina* Davidson, 1859

Type species: *Calceola heteroclita* Defrance in Blainville, 1824; Néhou, Normandy; Lower Devonian (Pragian or Lower Emsian?).

Remarks: Difficulties in finding a satisfying taxonomic treatment of *Cyrtina* were discussed by Halamski and Baliński (2013, p. 295), Gourvennec (2019, p. 119), and Halamski *et al.* (2022a, p. 61). We adopt here a splitting taxonomy for the reasons given in the latter work.

> Cyrtina sauvagei Rigaux, 1908 Fig. 58F–J, K–O

- ^{*} 1908 Cyrtina Sauvagei Rigaux, p. 6, 20, pl. 1, fig. 8.
 1988 Cyrtina sauvagei Rigaux 1908 Brice, pp. 359–360, pl. 43, figs 11–12.
- v 2013 *Cyrtina sauvagei* Rigaux, 1908 Halamski and Baliński, pp. 295–296, fig. 36BB–FF [*ubi syn*.].
- cf. 2022a *Cyrtina* cf. *sauvagei* Rigaux, 1908 Halamski *et al.*, pp. 61–62, fig. 43CC–GG.

Material: Over thirty specimens, mostly fragmentary, ZPAL V.74/Bp/53.

Description: Shell typically 12–15 mm wide, transverse (width-to-length ratio of the dorsal valve 1.32–1.56), strongly ventribiconvex, maximum width near or at the posterior margin. Ventral valve with a rather shallow V-shaped median sulcus; interarea apsacline, catacline, more seldom weakly procline; delthyrium narrow, closed by a convex pseudodeltidium; foramen not preserved. Dorsal valve with a moderately wide and slightly flattened median fold, and with up to five pairs of rounded, relatively weak ribs per flank; lateral ribs gradually diminishing in size towards lateral margins. Interior not studied.

Remarks: The identification is based mostly on a single very well-preserved shell (Fig. 58K–O) whose shape and ornament agree with those of *C. sauvagei*. The remaining specimens from M3 have low and blunt ribs and are reminding of those from African samples described as *C. evanescens* Gourvennec, 2019 (Tindouf Syncline) or *Cyrtina* cf. *evanescens* (Jbel Issoumour; Halamski *et al.*, 2022a). At Miłoszów the difficulty in observing the ribs is likely to be due to preservation. Specimens from M0 have low but distinct plications and are less transverse. At Jbel Issoumour representatives of the genus described as *Cyrtina* cf. *sauvagei* and *Cyrtina* cf. *evanescens* co-occur in a single outcrop and intermediates exist; it cannot thus be excluded that the two taxa might represent extreme morphological variants of a single biological species.

Occurrence: Miłoszów, M1-IIa, M3-7.

Cyrtina cf. planarea Ficner and Havlíček, 1978 Fig. 58P, Q

cf. * 1978 *Cyrtina planarea* sp. n. – Ficner and Havlíček, pp. 87–89, pl. 10, figs 8–20, 25, pl. 16, fig. 5.



Fig. 58. Representatives of the spiriferinide genus *Cyrtina* from the Givetian of Miłoszów. **A–E.** *Cyrtina* sp. Articulated shell ZPAL V.74/Bp/66/M1/1 in dorsal, ventral, lateral, posterior, and anterior views; outcrop M1. **F–J, K–O**. Articulated shells *Cyrtina sauvagei* Rigaux, 1908. ZPAL V.74/Bp/53/M3/1, 2 in dorsal, ventral, lateral, posterior, and anterior views; outcrop M3. **P**, **Q**. *Cyrtina* cf. *planarea* Ficner & Havlíček, 1978; articulated shell ZPAL V.74/Bp/52/M0/1 in dorsal and ventral views; outcrop M0-4.

Material: ZPAL V.74/Bp/52/M0/1-4.

Description: Shell about 9–12 mm wide, moderately transverse (width-to-length ratio of the dorsal valve 1.20–1.37), strongly ventribiconvex, maximum width at about two-fifths of the dorsal valve length (that is, slightly posteriorly to the mid-length of the valve). Ventral valve with up to five ribs per flank, those bordering the median sulcus stronger, the remaining ones of approximately same size; interarea anacline, nearly flat. Dorsal valve with a wide median fold and three ribs of similar width per flank. Micro-ornament not preserved. Interior not studied.

Remarks: The available material consists of four poorly preserved shells. They can be distinguished from *Cyrtina sauvagei* Rigaux, 1908, thanks to the relatively more elongate (less wide) outline of the dorsal valve and the character of ribs, which are less dissimilar from each other (ribs close to the fold and lateral ribs are more or less alike, whereas in *C. rigauxi* the farther a rib is from the median fold, the smaller it is. Similarities of the present material with *C. planarea* described from the Givetian of Čelechovice (Moravia) include the relatively long dorsal valve, ribs only moderately decreasing in size towards the lateral margins, and straight ventral interarea. Differences include smaller

size and smaller number of ribs in our material; the number of specimens at hand precludes definitive identification. **Occurrence:** Miłoszów, outcrop M0, bed 4. *Cyrtina planarea* is known from the horizon 9 at Čelechovice.

Cyrtina sp. Fig. 58A–E

Material: A single subcomplete shell, ZPAL V.74/Bp/66. **Description:** Shell about 16 mm wide (recorded width 12.6 mm, estimated width ca. 16 mm), strongly ventribiconvex, transverse (width-to-length ratio of the dorsal valve 1.86), maximum width at posterior margin. Ventral valve with two pairs of ribs per flank; interarea procline, incurved; delthyrium at least partially covered (incompletely preserved), septum tichorhini present. Dorsal valve with a wide flattened median plication (0.38–0.41 of the valve width) and another relatively wide rounded rib per flank; another low, faint rib per flank poorly visible. Interior otherwise not studied. Microstructure of the shell punctate, micro-ornament not preserved. **Remarks:** This single shell of *Cyrtina* from MI is distinguished from the remaining representatives of this genus at Miłoszów by the presence of a single wide and exceptionally strong costa on each flank of the dorsal valve. This seems outside the variation range of *C. sauvagei* co-occurring at M1. The Lower Devonian *Cyrtina* (*Hystricocyrtina*) kazi Havlíček, 1956 described from the Pragian Dvorce-Prokop Limestone (Prague Basin; Havlíček, 1956) has also a scantly plicate shell and well-marked growth. The brachiopods from Miłoszów lack, however, the strong spines diagnostic for *C.* (*Hystricocyrtina*) according to Havlíček and Vaněk (1998). It is unclear whether similarities between the present material and *C.* (*H.*) kazi reflect a close relationship or convergence of shape.

Occurrence: Miłoszów, Ml.

Order Terebratulida Waagen, 1883 Suborder Terebratulidina Waagen, 1883 Superfamily Stringocephaloidea King, 1850 Family Stringocephalidae King, 1850 Subfamily Stringocephalinae King, 1850 Genus *Stringocephalus* Defrance in de Blainville, 1827

Type species: *Terebratula Burtini* Defrance in de Blainville, 1825; Middle Devonian, Givetian ("Rodertium"); Chimay sur la Meuse, Dinant synclinorium, Belgium (see discussion by Stehli, 1965, p. *H*748 and Struve, 1992, p. 586).

Stringocephalus sp. Fig. 59

Material: One complete subadult and one adult shells and six small fragments, ZPAL V.74/Bp/54.

Description: Shell subcircular in outline, large (dimensions of the complete adult specimen: 60.4 mm long, 59.9 mm wide, and 39.2 mm thick; the largest fragment ca. 60 mm long, estimated maximum length ca. 70 mm), moderately to markedly ventribiconvex. Anterior commissure straight, neither sulcus nor fold. Ventral interarea relatively high, apsacline, concave. Shell smooth.

Ventral interior: long and thin median septum, starting from the umbonal region of the valve revealed in two shell fragments. Dorsal interior: traces of a median septum and of a pair of long crural plates revealed on the decorticated dorsal valve of the complete specimen.

Remarks: This brachiopod is included into the subfamily Stringocephalinae on account of a large-sized smooth shell with septa in both valves and into the genus *Stringocephalus* on account of a non-sulcate, markedly ventribiconvex shell. Taxonomy of *Stringocephalus* is in a state of flux between lumping and splitting approaches, and a revision appears hardly feasible at present, as the material at hand is usually limited and does not allow appreciation of the populational and ontogenetic variability. Open nomenclature is therefore used. **Occurrence:** M3-7.

Stringocephalinae gen. et sp. indet. Fig. 60H–N

Material: Fragment of the posterior part of a large shell, ZPAL Bp XVI/162.

Description: Shell very large (preserved width 87.8 mm), possibly aequibiconvex. Neither sulcus nor fold visible in

the preserved posterior region. Umbo of ventral valve fine, elongate, beak weakly incurved. Ventral interarea low, apsacline, slightly concave, occupying the entire width of the preserved fragment. Dorsal valve regularly convex, interarea linear, apsacline.

Shell macroscopically smooth. As a result of weathering, concentric bands (ca. 2 mm wide), separated by spaces 3–5 mm wide, beginning 1 mm from the umbo, are visible on a part of the ventral valve.

Ventral interior: median septum over 10 mm high, ca. 2 mm thick, with a median lamella ca. 0.3 mm thick. Dorsal interior: median septum markedly thickened, 8 mm thick and 16 mm high, internal structure poorly visible. Crural plates thin (less than 1 mm), supported by the median septum. Cardinal process anteriorly supported by the septum, bulbous, thick, with maximum width in its central part, proximal part with median ridges on posterior and anterior surfaces; distally embracing the ventral septum.

Remarks: This brachiopod is included in the subfamily Stringocephalinae on account of a large-sized smooth shell with septa in both valves. The anterior region is lacking, so a confident identification is not feasible. Compared to *Stringocephalus* sp. described above, the ventral interarea is proportionally lower and the beak is less protruding, which is suggestive of taxonomic distinctness, so the descriptions are given separately, but ontogenetic variability cannot be excluded either. *Stringocephalus glinskii* Struve, 1992 (see Thormann and Weddige, 2001, pl. 7, fig. 50–51) and *Stringodiscus giganteus* J. de C. Sowerby, 1840 (see Torley, 1934, pl. 6, fig. 14) have similarly shaped ventral interareas.

This specimen comes from an old collection and has two labels, 'Miłoszów' and 'Skały, reef'. On account of personal communication given by the late Gertruda Biernat, it is assumed to have been collected at Miłoszów. The matrix is a limestone with rugose corals, so the specimen might have come either from M1-I or from an outcrop of 'coral limestone' *sensu* Filonowicz (1968) that has now disappeared.

> Subfamily Bornhardtininae Cloud, 1942 Genus *Bornhardtina* Schulz, 1914

Type species: *Bornhardtina uncitoides* Schulz, 1914; Middle Devonian (Givetian?); Gerolstein, Eifel, Germany (see Cloud, 1942, p. 101).

Remarks: Representatives of *Bornhardtina* are common in the Givetian of the Eifel, the Ardennes, and the Urals (Cloud, 1942; Hodalevič and Brejvel', 1972; Godefroid and Mottequin, 2005). In Poland, the only representative of this genus reported previously was *B. skalensis* Biernat, 1953 from the Middle Eifelian of the Grzegorzowice-Skały section (set XI sensu Pajchlowa, 1957; Kowala Formation), which may be the oldest occurrence of the genus. This is the first record of the genus in the Givetian of the Holy Cross Mountains.

Bornhardtina sp. Fig. 60D

Material: One small fragment of ventral valve and three fragmentary dorsal valves with partially preserved cardinalia.

Description: Shell fragments indicative of a length of at least 30 mm, shell thick-shelled, macroscopically smooth, outline unknown. Dorsal interior: hinge plates thick, discrete; diductors scars located in the posterior-most region of

the hinge plates (Fig. 60D), deeply impressed, semi-circular in outline, 10 mm long. Ventral interior not revealed.

Remarks: These fragmentary specimens are included into *Bornhardtina*, owing to the presence of discrete hinge



Fig. 59. *Stringocephalus* sp. from the Givetian of Miłoszów. A–F. Juvenile articulated shell ZPAL V.74/Bp/54/2 in dorsal, ventral, lateral, posterior, and anterior views (A–E), and enlargement of the ventral interatrea in dorsal view (F). Miłoszów, old collection, details unknown. G–K, L–P. Articulated shells ZPAL V.74/Bp/54/M3/1, 3 in dorsal, ventral, lateral, posterior, and anterior views; outcrop M3-7.

plates, the absence of dental plates, cardinal process and median septa in both valves. **Occurrence:** Miłoszów, M1-IIa.

Terebratulidina superfam., fam., gen. et sp. indet. 1 Fig. 60A-C

Material: One fragmentary specimen from bed 9 of M0 outcrop in Miłoszów.

Description: Shell fragmentarily preserved, ventribiconvex, estimated width about 20 mm, estimated length probably slightly less, thickness 7.3 mm; outline possibly transversely elliptical; ventral valve moderately convex, subtriangular in anterior view, with an apsacline ventral interarea; dorsal valve lowly subtriangular in anterior view. Shell substance endopunctate. Internally, long, thin and slightly ventrally convergent dental plates revealed through the broken ventral umbo (Fig. 60C); otherwise, unknown.

Remarks: This specimen is included into the order Terebratulida on account of shell structure and form; it cannot be decided whether it belongs to the superfamily Stringocephaloidea King, 1850 or Cryptonelloidea Thomson, 1926, although the second possibility seems less likely.

Terebratulidina superfam., fam., gen. et sp. indet. 2 Fig. 60E–G

Material: One incomplete shell from Miłoszów (old collection, trench MS2).



Fig. 60. Terebratulides from the Givetian of Miłoszów. **A–C.** Terebratulidina superfam., fam., gen. et sp. indet. 1. Fragmentary articulated shell ZPAL V.74/Bp/56/M0/1 in dorsal, lateral, and posterior views. Outcrop M0-9. **D.** *Bornhardtina* sp.; dorsal valve fragment ZPAL V.74/Bp/55/M1/1 in interior view. Outcrop M1-IIa. **E–G.** Terebratulidina superfam., fam., gen. et sp. indet. 2. Fragmentary articulated shell ZPAL V.74/Bp/57/M/1 in posterior, lateral and dorsal views. Old collection, detailed outcrop unknown, probably corresponding to M2–M3 section. **H–N.** Stringocephalinae gen. et sp. indet. Shell fragment ZPAL Bp XVI/162 cut into parts to show internal structures; H – dorsal view of the posterior region; I – posterior view. **J–M.** Two polished transverse sections, situated ca. 24 mm (J, L) and 29 mm (K, M) from the ventral umbo: small views with legends (L, M) and enlargements (J, K). **N.** Lateral view of the posterior region; cp – cardinal process; cr – crus; dms – dorsal median septum; hp – hinge plate; vms – ventral median septum. Old collection, detailed outcrop unknown (see text).

Description: Shell elliptic in outline, 13.0 mm long, 9.6 mm wide, and 6.8 mm thick, very weakly dorsibiconvex (nearly aequibiconvex); anterior commissure rectimarginate; ventral umbo thick, beak poorly preserved, suberect? Poorly preserved very low, rounded ribs, about 3 per mm, observed on the ventral valve; the dorsal valve is mostly desquamated, so ribbing observed only near the anterior margin. Shell substance endopunctate. Interior not studied.

Remarks: The specimen is so poorly preserved that it is even uncertain whether the observed pattern corresponds to original ribbing or to an artefact. It is included in the order Terebratulida on account of shell structure and form. It might belong either to the Stringocephaloidea King, 1850 or Cryptonelloidea Thomson, 1926. Unknown internal characters prevent a more precise determination of its taxonomic affiliation.

GENERAL CHARACTERISTICS OF THE MIŁOSZÓW BRACHIOPOD FAUNA

Species pool

The three (composite) beds at Miłoszów that yielded the richest brachiopod faunas are MI-IIa with 28 species, M3-7 with 23 species, and M0-9 with 22 species (see Fig. 61 and Tab. 10). These values are evidently higher than those for any Recent environment, but not particularly high for the Middle Devonian. 44 brachiopod species were found in the Upper Eifelian brachiopod shale (Dobruchna Member) at Skały (Halamski and Zapalski, 2006; Woźniak *et al.*, 2022), whereas the Middle Eifelian 'trilobite fields' at Gees (Ahrdorf Formation) yielded over 60 brachiopod species (Struve, 1982).

The numbers of species common to any two out of these three beds are rather low; eight species occur either in both M1-IIa and M3-7, six in both M1-IIa and M0-9, five in both M3-7 and M0-9, and only three (*Isopoma brachyptyctum*, *Peratos beyrichi*, and *Dicamara plebeja*) in all three above-mentioned levels. This means that in any of these three beds over the half of brachiopod species are absent from the other two beds. Therefore, the brachiopod assemblages can be described as rather different from each other (Jaccard similarity coefficients 0.13–0.19; values not very different from those obtained when comparing the total Miłoszów fauna to Upper Eifelian or upper Middle Givetian assemblages, see below).

A further comparison is possible between the Miłoszów brachiopod fauna as a whole and two other brachiopod assemblages from the Łysogóry Region, the Upper Eifelian brachiopod shales from Skały (Halamski and Zapalski, 2006; Woźniak *et al.*, 2022) and the upper Middle Givetian (?) assemblage from Błonia Sierżawskie near Świętomarz (outcrop SW-2 *sensu* Halamski, 2004b, 2009; see also Halamski and Segit, 2006). The former is relatively well-studied and 44 brachiopod species are listed from there by Halamski and Zapalski (2006). The latter is less well-known and its stratigraphic position is not entirely certain (formerly usually considered as belonging to the Skały Formation; a new palynological dating suggests it may belong to the younger Nieczulice beds); a provisory unpublished list of

34 brachiopod species (Halamski, 2004b; modified) is used. The degree of taxonomic uncertainty is relatively high here, owing to brachiopods being described under open nomenclature and lack of up-to-date treatment of the Świętomarz fauna, but the counts are as follows:

- species in common between the Upper Eifelian Dobruchna Member and Lower to lower Middle Givetian Miłoszów fauna as a whole: minimum estimate 14, maximum estimate 18 (see Tab. 10; Jaccard similarity coefficient 0.15–0.20); these include Leptagonia analogaeformis, Gibbodouvillina interstrialis, Skenidioides polonicus, Aulacella prisca, Kransia parallelepipeda, Plectospira ferita, Ivanothyris aculeata;
- species in common between the Lower to lower Middle Givetian Miłoszów fauna as a whole and the younger fauna from Błonia Sierżawskie near Świętomarz (SW-2; upper Middle Givetian?): minimum estimate 12, maximum estimate 19 (see Tab. 10; Jaccard similarity coefficient 0.13–0.23); these include: Leptagonia analogaeformis, Gibbodouvillina interstrialis, Skenidioides polonicus, Aulacella prisca, Kransia parallelepipeda, Echinocoelia dorsoplana.

The numerical values of Jaccard coefficients are neither high nor very different between these two pairs of faunas. Interestingly, the values for the interval spanning the Taghanic Bioevent are not much lower and possibly even higher than those for the Eifelian-Givetian similarities, thus confirming the preliminary observation by Halamski (2018) about the absence of a large-scale brachiopod fauna replacement, similar to that in the Taghanic type area (see Halamski et al., 2022b, pp. 363–365 for a more detailed analysis). The species in common between the Dobruchna and Miłoszów faunas on the one hand and between the Miłoszów and Błonia Sierżawskie faunas on the another hand are often those relatively frequent in at least one of these three localities (Leptagonia analogaeformis, Gibbodouvillina interstrialis, Aulacella prisca, Kransia parallelepipeda; note that these species are present in all the three faunas discussed here), but in at least one case a very rare brachiopod (Ivanothyris aculeata) occurs in the Dobruchna and Miłoszów faunas.

Finally, it is worth noting that at least 18 species (excluding those identified at family level) described here have not been reported heretofore from the Middle Devonian of the Łysogóry Region. The total number of known Middle Devonian brachiopod species in the northern region of the Holy Cross Mountains is thus 140, as compared to 122 species listed by Halamski (2004b, 2008).

Palaeoecology

The palaeoecological analysis of the whole Givetian fauna of Miłoszów, including the brachiopods, especially the ecological interpretation of common species, is given elsewhere (Halamski *et al.*, 2022b, see especially fig. 27). Here the focus is more precisely on brachiopod species synecology. A synecological analysis of Middle Devonian atrypides of the Eifel was given by Copper (1966a). It provides a valuable interpretation key for the Łysogóry Region, but the ecological zones distinguished in the Eifel cannot be uncritically transferred into the Holy Cross Mountains, given the major difference in palaeogeography: in the Eifel most brachiopods are known from an area, corresponding to the sheltered shelf sea (Copper, 1966a, fig. 2: zones 2–6), whereas the area investigated here is located on the external side of the barrier reef, that is, on the middle to outer ramp (Halamski *et al.*, 2022b, figs 10, 27A).

The brachiopods of the shallowest-water settings in the described material are possibly the thick-shelled gypidulids. These may be related to the small reefs (**globetum** *sensu* Struve, 1963; shallow BA3). *Bornhardtina* may have lived in close association with reef-forming species (Jansen *et al.*, in press), although this genus can also be found in association small orthides *Aulacella* or minute athyridides

Table 10

Stratigraphic distribution of brachiopods at Miłoszów. Species present in the Upper Eifelian Dobruchna Member (after Halamski and Zapalski, 2006 and references therein, modified) and in the outcrop SW-2 at Błonia Sierżawskie near Świętomarz (Nieczulice beds?; after Halamski, 2004b, 2009; modified) are also given.

| | | Stratigraphy | Skały | | | | | | | | Mi | łosz | zów | | | | | | | | Święto- marz |
|----------------|--------------|--------------------------------|-------|----|----|-----|-----|---|---|-----|----|------|-----|---|---|-----|---|-----|---|----|-----------------|
| Taxonomy | | | | M1 | | | | | l | M2, | M | 3 | | | | | | | | | |
| Order | Coll. No. | Species | D | Ia | Ib | IIa | IIb | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 1–3 | 4 | 5-8 | 9 | 10 | SW-2 |
| ulida | 1 | Lingulipora budili | | | | | | | | + | | | | | | | | | | | |
| Lingulida | 2 | Orbiculoidea sp. | х | | | | | | | + | | | | | | | | | | | х |
| Ac. | 3 | Opsiconidion cf. arcticon | | | | | | | | + | | | | | | | | | | | |
| ida | 4 | Leptagonia analogaeformis | + | | | | | | | + | | + | | + | | | | | + | | + |
| Strophomenida | 5 | Gibbodouvillina interstrialis | + | | + | + | | | | | | | | + | | | | | | | + |
| phoi | 7 | Radiomena irregularis | + | | + | | | | | | | | | | | | | | + | | |
| Stro | 10 | Parastrophonella anaglypha | + | | | | | | | | | | | + | | | | | | | + |
| | 9 | Devonaria zeuschneri | + | | | | | | | | | | | | | + | | | + | | + |
| ida | 61 | Anopliidae gen. et sp. indet. | | | | | | | | | | | | + | | | | | | | |
| Productida | 60 | Luanquella cf. vanigibbosa | | | | | | | | | | | | + | | | | | + | | |
| Proc | 6 | Spinulicosta cf. spinulicosta | | | | | | | | + | | + | | + | | | | | | | |
| | 11 | Strophalosioidea indet. | | | | | | | + | | | | | | | | | | | | х |
| Or. | 8 | Iridistrophia cf. undifera | | | | | | + | | | | | | | | | | | + | | + |
| Protor. | 12 | Skenidioides cretus | | | | + | | | | | | | | | | | | | | | |
| Prot | 62 | Skenidioides polonicus | + | | | ? | | | + | | | | | | | | | | | | + |
| | 63 | Teichertina peregrina | | | | + | | | | | | | | | | | | | | | |
| | 67 | Teichertina quadriplicata | | | | + | | | | | | | | | | | | | | | |
| nida | 14 | Aulacella prisca | + | | | + | | | + | | | | | + | | | | | | | + |
| Orthida | 16 | Mystrophora areola | | | | + | | | + | | | | | | | | | | | | |
| | 58 | Biernatium cf. fallax | | | | + | | | + | | | | | | | | | | | | х |
| | 13 | Schizophoria schnuri | + | | | + | | | | + | | | | | | | | | + | | + |
| da | 18 | Gypidula biplicata | | | | | | | | | | + | | | | | | | + | | |
| neri | 19 | Gypidulidae gen. et sp. indet. | | | + | | | | | | | | | | | | | | + | | |
| entamerida | 17 | Antirhynchonella linguiformis | | | | | | | | + | | | | + | | | | | | | |
| Pe | 20 | Pentamerelloides davidsoni | | | | + | | | | | | | | | | | | | | | |
| | 22 | Kransia parallelepipeda | + | | | + | | | | | | | | | | | | | | | + |
| lida | 23 | Kransia subcordiformis | | | | | | | | | | | | | | | | | + | | |
| onel | 59 | Beckmannia cf. beckmanni | | | | | | | | | | | | | | | | | + | | |
| nche | 21 | Beckmannia cf. propentagona | | | | + | | | | | | + | | + | | | | | | | ? |
| Rhynchonellida | 24 | Eumetabolotoechia subplicata | | | | | | | | | | | | | | | | | + | | |
| | 26 | Septalaria gracilis | | | | | | | + | | | | | + | | | | | | | |

Table 10 (continued)

| | | Skały Miłoszów | | | | | | | | | | | | | | | Święto- marz | | | | |
|----------------|--------------|----------------------------------|--------------------|----|-------------|-----|-----|---|---|---|---|----------|-----------|----|---|-----|-----------------|-----|----|----|--------------------|
| Taxon | lomy | | | | M1 M2, M3 M | | | | | | | | M0 | | | | | | | | |
| Order | Coll. No. | Species | D | Ia | Ib | IIa | IIb | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 1–3 | 4 | 5-8 | 9 | 10 | SW-2 |
| da | 64 | Glosshypothyridina procuboides | | | | | | | | + | | + | | + | | | | | | | |
| ellia | 25 | Nemesa sp. | | | | | | | | | | | | + | | | | | | | |
| hon | 28 | Parapugnax denticulatus | + | | | | | | | | | | | | | | | | + | | |
| Rhynchonellida | 68 | Parapugnax anisodontus | | | | + | | | | | | | | | | | | | | | |
| RI | 27 | Isopoma brachyptyctum | + | | | + | | | | | | | | + | | | | | + | | |
| | 29 | Atrypa subtrigonalis | ? | | | | | | | | | | | + | | | | | | | |
| | 30 | Atryparia sp. | | + | - | | | | | | | | | | | | | | | | |
| | 31 | Isospinatrypa sp. | | | | | | | | | | | | | | | | | + | | |
| | 32 | Spinatrypa wotanica | | | | + | | | | | | | | | | | | | | | |
| Atrypida | 33 | Desquamatia subzonata | + | | | + | | | | | | | | | | | | | | | + |
| \try | 37 | Desquamatia circulareformis | | | + | | | | | | | | | | | | | | + | | |
| 1 | 34 | Davidsonia septata | | | | + | | | | | | | | | | | | | | | |
| | 35 | Eifelatrypa plana | | | | + | | | | | | | | | | | | | + | | |
| | 38 | Gruenewaldtia latilinguis | | | | | | | | | | | | | | | | | + | | |
| | 40 | Peratos beyrichi | | | | + | | | | | | | | + | | | | | + | | |
| | 39 | Athyris sp. | | | | + | | | | | | | | | | | + | | | | ? |
| 5 | 43 | Leptathyris sp. | | | | | | | | | | | | | + | | | | | | |
| idid | 41 | Dicamara plebeia | | | | + | | | | | | | | + | | | | | + | | |
| Athyridida | 42 | Plectospira ferita | | | | + | | | | | | | | | | | | | | | |
| A | 36 | <i>Bifida</i> sp. | | | | | + | | + | | | | + | + | + | | | | | | х |
| | 15 | Kayseria sp. | х | | | | | | | | | | | | | ? | | | | | |
| | 65 | Ambothyris sp. | | | | + | | | | | | | | | | | | | | | |
| | 44 | Moravilla andreae sp. nov. | | | | + | | | | | | | | | | | | | | | |
| | 45 | Echinocoelia dorsoplana | | | | | | | + | | | | | | + | | | | | | + |
| ida | 47 | Ivanothyris aculeata | + | | | + | | | | | | | | | | | | | + | | |
| piriferida | 50 | Undispirifer sidoniae sp. nov. | | | | | | | | | | | | | | | | | + | | |
| Spir | 49 | Warrenella concentrica | | | | | | | | | | ? | | + | | | | | | | |
| | 51 | Thomasaria ex gr. simplex | | | | | | | | | | | | + | | | | | | | ? |
| | 46 | Thomasaria? cf. aviceps | х | | | | | | | + | | + | | + | | | | | | | |
| | 48 | Leiocyrtia rara gen. et sp. nov. | | | | + | | | | | | | | + | | | | | | | |
| nida | 52 | Cyrtina sauvagei | + | | | + | | | | | | | | + | | | | | | | + |
| Spiriferinida | 53 | Cyrtina cf. planarea | | | | | | | | | | | | | | | + | | | | |
| Spir | 66 | <i>Cyrtina</i> sp. | | | | + | | | | | | | | | | | | | | | |
| da | 54 | Stringocephalus sp. | | ? | , | | | | | | | | | + | | | | | | | |
| atuli | 55 | Bornhardtina sp. | | | | + | | | | | | | | | | | | | | | |
| Terebratulida | 56 | Terebratulidina indet. 1 | | | | | | | | | | | | | | | | | + | | |
| Ter | 57 | Terebratulidina indet. 2 | | | | | | | | | | ? | - | | | | | | | | |
| | | TOTAL | 14 (18) [44] | 0 | 4 | 28 | 1 | 1 | 8 | 9 | 0 | 6 spe | 1 cies | 23 | 3 | 0 | 1 | 0 | 22 | 0 | 12 (19) [34] |

 $\begin{array}{l} \mbox{Explanations: } + - \mbox{species present; x - [used only in the columns D and SW-2], the same species as in Miłoszów possibly present. Merged cells denote uncertainty as to the exact provenance of a specimen. The three totals in the D and SW-2 columns refer to the minimum and maximum (in parentheses) numbers of species in common with the total (aggregated) Miłoszów fauna and to the total numbers of brachiopod species in the Dobruchna Member and Błonia Sierżawskie faunas (in brackets). Abbreviations: Ac. – Acrotretida; D – Dobruchna Member; Or. – Ortothetida; Protor. – Protorthida. \end{array}$

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Fig. 61. Bar graphs showing frequencies of brachiopod species in the fauna studied. **A.** Total fauna of Miłoszów (all outcrops aggregated). 'Other' stands for 43 species, the relative frequencies of which were under 1% of the total (number of specimens less than 22). **B.** Lower Middle Givetian bed M0-9. **C.** Lower Givetian composite bed M1-IIa.

Kayseria (Copper, 1966a, p. 256) having lived in deeper water or in other types of deeper subtidal environments (Skompski and Szulczewski, 1994). Stringocephalids are interpreted as having dwelt in channels or depressions of the reef (Struve, 1982, pp. 250–251). At Jurkowice-Budy and at Dziewki, they are related to stromatroporoid biostromes (Racki, 1993, p. 335).

Other relatively shallow-water species are those related to smaller-sized corals, above all the epizoan *Davidsonia septata* living on branching rugosans and platy tabulates. Following general patterns of correlation of morphologies and lifestyles (Jansen *et al.*, in press, and references therein), strongly ornamented *Pentamerelloides davidsoni* is interpreted also as living in high-energy environments. *Spinatrypa wotanica* is also strongly ornamented, but spines are rather an adaptation to mud-dwelling, so this may have been a species of a slightly deeper or calmer environment. This environment of small corals, crinoids, and brachiopods (marly biostrome M1-IIa and adjoining habitats) would be the **crinoidetum–cespitetum** and **rapetum** sensu Struve (1963) or deeper BA3 sensu Boucot (1975). The *Heliophyllum–Pentamerella* community from the approximately coeval Hamilton Group of New York (Grasso, 1986) might also be an analogue.

Deeper environments are characterised by the near-absence of corals and muddy bottom. Middle-sized brachiopods with functional pedicle, like *Kransia* or *Atrypa subtrigonalis* likely belong to what could be termed the **shallower brachiopodetum** *sensu* Struve (1963), that is the shallower part of the so-called brachiopod meadows, probably corresponding to BA4 *sensu* Boucot (1975). Spinose shells, like that of *Spinulicosta* cf. *spinulicosta* are evidently

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an adaptation to a muddy environment as well. The same may be said about very wide shells, like that of *Moravilla andreae*, or those with large interareas, like *Skenidioides*, *Mystrophora* or *Teichertina*. *Thomasaria* may also belong to this group. The shallower brachiopodetum is thus a relatively highly-diverse brachiopod assemblage, but some of its members may have been more eurytopic and able to dwell also in shallower habitats (Jansen *et al.*, in press). An older example of a rich brachiopod meadow from the Łysogóry Region is that from the Upper Eifelian Dobruchna Member of the Skały Formation at Skały (Woźniak *et al.*, 2022).

Finally, the deepest environments in the studied material are represented by samples characterised by fine-grained sediments and taxonomically poorly-diverse small brachiopod assemblage, consisting solely of two species, Bifida sp. and Echinocoelia dorsoplana (both about 5 mm in length or less). This environment is called here the deeper brachiopodetum and it might correspond to the BA5 sensu Boucot (1975). It should be stressed that in a slightly younger outcrop at Świętomarz (SW-2 sensu Halamski, 2009) Echinocoelia dorsoplana and Bifida sp. (possibly the same species) co-occur with numerous other brachiopod species, both small and middle-sized, but a palaeoecological study of this assemblage has never been conducted. In the Hamilton Group of New York an Ambocoelia-nuculid association is represented on the slope and in the deeper shelf (Baird and Brett, 1983; Grasso, 1986).

All in all, in comparison with the classic area of the Eifel, the knowledge of the environments of the Łysogóry Region is still patchy. Present data on ecological preferences of some brachiopod groups (like stringocephalids) do not constitute a firm basis for a precise palaeoecological synthesis. Moreover, some questions could not be satisfactorily explained during the present study and are left for future research. In particular, these include the genesis of the brachiopod-rich bed M3 λ belonging to the otherwise nearly barren composite bed M3-7 (tempestite? see Brett et al., 1986; for the question of the presence of tempestites at Miłoszów, see Pisarzowska et al., 2022) and a detailed palaeoecological interpretation of bed M0-9 containing brachiopods that presumably lived in very different habitats (Desquamatia circulareformis: relatively shallow-water environment; Eumetabolotoechia: species of this genus are characteristic of dysoxic environments in New York); this might correspond to ecological succession, given the presence of mesophotic tabulates (see Zapalski in Halamski et al., 2022b).

Regional comparison

The brachiopod fauna studied has undeniable Rhenish affinities, as evidenced by the abundance of wellknown species, belonging to the genera like *Leptagonia*, *Gibbodouvillina*, *Parastrophonella*, *Aulacella*, *Kransia*, *Glosshypothyridina*, *Plectospira*, *Ivanothyris* (e.g., Halamski, 2008). Quite unsurprisingly, especial similarities with Givetian faunas of the Rhenish Mountains (e.g., Holzapfel, 1895) and Moravia (Ficner and Havlíček, 1975), can be noted. Species, known solely from the Rhenish Mountains and Miłoszów, include *Spinatrypa wotanica* and *Peratos beyrichi*. Similarities with the fauna of Čelechovice are expressed in the presence of *Moravilla* (genus unknown outside these two localities) and *Luanquella* (known also from Gondwana). A formal palaeobiogeographic analysis is not attempted here.

A few analogies between brachiopod communities of the Givetian part of the Skały Formation and the approximately coeval Hamilton Group of New York are given above. However, generally speaking, a prima facie comparison between the Hamilton and Skały brachiopod communities indicates they are rather different from each other. This is evidenced not only by presence or absence of particular brachiopod taxa (genus-level or higher), but also by more general palaeoecological characteristics, like the ratio of articulated vs. disarticulated brachiopod shells ('leiorhynchids' mostly disarticulated in the Centerfield Mb., Savarese et al., 1986; mostly articulated at Miłoszów) or the contrast between the abundance of bivalves in New York (e.g., Brower and Nye, 1991) and their extreme rarity in the Łysogóry Region (Halamski and Zapalski, 2006; Halamski et al., 2022b).

CONCLUSIONS

A diverse brachiopod fauna (68 species, including one new genus and three new species) is reported from the upper part of the Skały Formation at Miłoszów. The age determination is based on conodonts and spores; the investigated fauna is Early to early Middle Givetian in age and thus predates the Taghanic Bioevent.

Out of these 68 species, at least 18 (excluding those identified at family level) have not been reported previously from the Middle Devonian of the Łysogóry Region. The total number of known Middle Devonian brachiopod species in the northern region of the Holy Cross Mountains is thus 140 (compare Halamski 2004b, 2008 for previous estimates).

Leiocyrtia rara Baliński gen. et sp. nov. (Spiriferida, Cyrtiidae) is characterised by a non-costate shell with prominent sulcus and fold and capillate micro-ornament.

Undispirifer sidoniae Halamski and Baliński sp. nov. is characterised by transverse shells and dense ribbing (up to 13 ribs per flank).

Moravilla andreae Baliński and Halamski sp. nov. is characterised by relatively coarse radial capillate ornament and is the first representative of the genus outside the type species from the Givetian of Moravia.

The type stratum of the brachiopod species, described by Biernat (1964, 1966) from Miłoszów, is given as 'Miłoszów limestone' (an incorrectly defined stratigraphic unit). *Eumetabolotoechia subplicata* (Biernat, 1966) is present solely in M0-9 (lower Middle Givetian), so a restricted type locality and stratum can be given. *Desquamatia* (*Independatrypa*) circulareformis Biernat, 1964 is most common in M0-9, but present also in M1-I (Lower Givetian). *Antirhynchonella linguiformis* Biernat, 1966 is common in M3-7 (Lower Givetian), but present also in other outcrops. In these two cases restricted type localities and strata cannot be given. The type specimen of *Spirifer quadriplicatus* Sandberger and Sandberger, 1856 from Weilburg (Hessen, Germany) has a punctate shell structure and is an orthide. This species belongs to the genus *Teichertina*; it is particularly rare (five specimens are known in total) and occurs at Miłoszów, in the Eifel, and in the Lahn Syncline.

Spinatrypa wotanica Struve, 1964, an atrypide species present at Miłoszów (M1-IIa) and in the Eifel, has spines and belongs thus to *Spinatrypa*, as proposed by Struve (1964) and not to *Spinatrypina*, as proposed by Copper (1967).

The Lower to lower Middle Givetian Miłoszów brachiopod fauna as a whole shows moderate degree of similarity to both Upper Eifelian and upper Middle Givetian brachiopod faunas from the Łysogóry Region (Jaccard similarity coefficients 0.15–0.20 and 0.13–0.23, respectively).

The brachiopod fauna studied has Rhenish affinities and shows especial affinities to Givetian faunas from the Rhenish Slate Mountains and from Moravia.

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