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THE PRE-TAGHANIC (GIVETIAN, MIDDLE DEVONIAN) ECOSYSTEMS OF MIŁOSZÓW (HOLY CROSS MTS, POLAND)

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Abstract: The middle and upper parts of the Skały Fm, Early to Middle Givetian in age, were investigated in four sections at Miłoszów Wood in the Łysogóry Region (northern region of the Holy Cross Mountains, central Poland). The dating is based on conodonts (*Polygnathus timorensis* Zone to the later part of the *Polygnathus varcus*/*Polygnathus rhenanus* Zone; early *Polygnathus ansatus* Zone cannot be excluded) and spores (Ex1–2 subzones) and, coupled with cartographic analysis and geophysical investigation, allows correlation within the strongly faulted succession. Significant lateral facies variations within the carbonate ramp depositional system in comparison with the better studied Grzegorzowice–Skały section, about 3 km distant, are documented, thanks to conodont-based correlation of both successions. Foraminifers, fungi, sponges, rugose and tabulate corals, medusozoans, microconchids and cornulitids, polychaetes (scolecodonts), molluscs (bivalves, rostroconchs, and gastropods), arthropods (trilobites and ostracods), bryozoans, hederelloids, ascodictyids, brachiopods, echinoderms (mostly crinoids, rare echinoids, holuthurians, and ophiocistoids), conodonts, fish, plants (prasinophytes, chlorophycophytes, and land plant spores), and acritarchs are present. Brachiopods are the most diverse phylum present (68 species), other richly represented groups are bryozoans and echinoderms; in contrast, cephalopods and trilobites are low in diversity and abundance. The muddy, middle to outer ramp biota (200 marine taxa, including 170 species of marine animals, 22 photoautotrophs, 6 forams) represents a mixture of allochthonous shallower-water communities (upper BA3), including storm- and possibly tsunami-affected coral mounds, and autochthonous deep-water soft-bottom brachiopod (e.g., *Bifida–Echinocoelia*) communities (BA 4–5). The richness and diversity of the Miłoszów biota is relatively high, comparable with other approximately coeval pre-Taghanic ecosystems during the Devonian climatic deterioration (cooling). Preliminary data indicate that in the Holy Cross Mountains, no large-scale replacement of brachiopod (and probably many other benthic ones, like crinoids) communities took place between the Early–Middle Givetian and the Early Frasnian, in contrast to the demise of the Hamilton/Upper Tully fauna in the Appalachian Basin. Such a similarity of pre- and post-Taghanic faunas does not exclude the occurrence of environmental perturbations and transient community turnovers, caused by immigrations during the Taghanic Biocrisis, but evidences the successful recovery of the indigenous biota.

Key words: Stratigraphy, palaeoecology, biota, biodiversity, mesophotic, deeper shelf, climate, carbonate.

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INTRODUCTION

General purpose of the present work

The Holy Cross Mountains (central Poland) are the only major area with outcrops of Devonian sedimentary rocks between the classical regions of this system in the Rhenish Mountains (Rhenish Slate Mountains) and the Harz Mountains, in the central part of European Russia, and in the Barrandian of Bohemia (Fig. 1A). In particular, the Łysogóry Region (= northern region of the Holy Cross Mountains) is well-recognised, owing to a long tradition of geological and palaeontological studies. However, up to now, only a single series of outcrops, the Grzegorzowice–Skały section, received comprehensive treatment, so the interplay of local, regional, and global determinants of the observed faunal succession is unclear. The general aim of the present work is thus to provide a similarly detailed geological and palaeontological study of another series of Middle Devonian outcrops, located in the Łysogóry Region, namely the Miłoszów section.

The Givetian of Miłoszów in its local, regional, and world context

The Givetian age of the Middle Devonian epoch witnessed important events in the history of the Earth's biosphere, among which one may note the first trees (Retallack, 1997; Stein *et al.*, 2007), the first ammonoids with complex septal structures and shell ontogenies (Bockwinkel *et al.*,

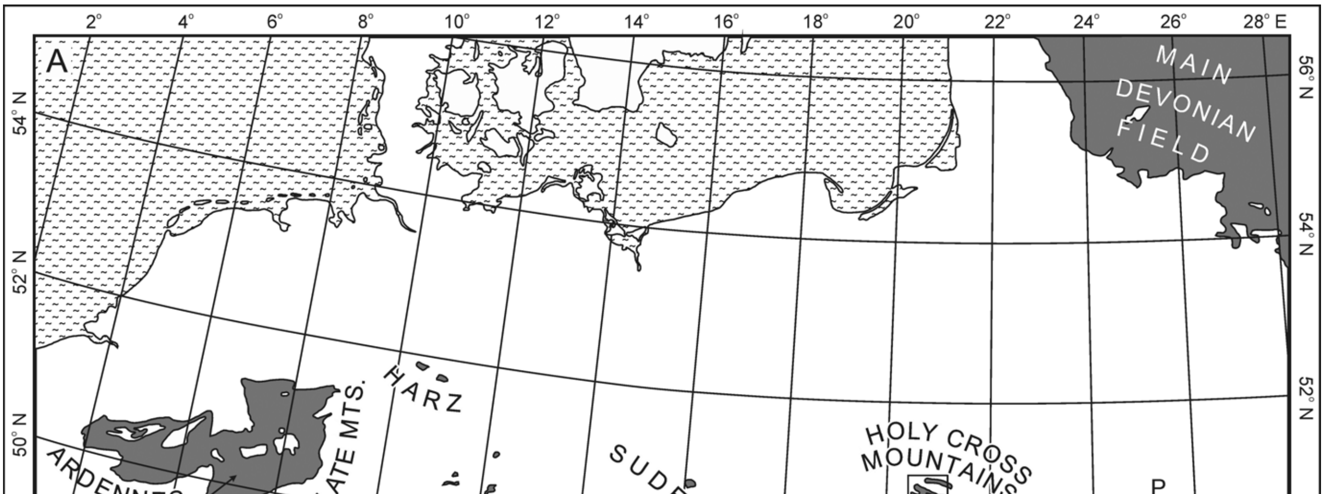

Fig. 1. Regional geological and palaeogeographical setting of the studied biota. **A.** Simplified geological map of Central Europe, showing only areas with Devonian sediments (after Asch, 2005). B – Barrandian area, Bohemia; Č – Čelechovice, Moravia; D – Dębnik Anticline, Małopolska; E – Eifel; S – Saxothuringian Zone; P – Povcha (Pełcza), Volhynia. **B.** Geological map of the Holy Cross Mountains (after Racki *et al.*, 2004). HCD, Holy Cross Dislocation. **C.** Palaeogeography of the Holy Cross Mountains in the Givetian (after Racki, 1993 and Baliński *et al.*, 2016) with the presumed localisation of Miłoszów.

2009), the radiation of the calcareous foraminifers (Givetian revolution *sensu* Vachard *et al.*, 2010), and the expansion and demise of gigantic stringocephalid brachiopods (Struve, 1992; Baranov *et al.*, 2021). Of no less importance were significant extinction events in the mid-Givetian (Taghanic Crisis; House, 1996; Aboussalam, 2003; Aboussalam and Becker, 2011; Ernst, 2013) and at the Givetian/Frasnian boundary (Frasnes Event; House, 1985; Racki, 1993; Walliser, 1996; Becker *et al.*, 2016, 2020). The terrestrial and marine events were arguably interconnected (Algeo and Scheckler, 1998; Bond and Stephenson, 2020).

In several regions of Central Europe, the Givetian marine biotas are less well known than the Eifelian ones. The reasons are varied, including widespread dolomitisation of Givetian sediments in the Eifel (Meyer, 2013) and absence of Devonian sediments younger than Early Givetian in the Barrandian (Chlupáč, 1993). In the Holy Cross Mountains, most palaeontological work on Middle Devonian faunas focused on the lower (Eifelian) part of the Skały Fm, as formally defined in Racki *et al.* (2022), including the brachiopod Konzentrat-Lagerstätte shale deposits (Halamski and Zapalski, 2006 and references therein; erroneously referred to the Givetian by several previous authors; see the historical account in Racki *et al.*, 2022). On the contrary, in the Kielce Region (southern region of the Holy Cross Mts), faunas of the Givetian bank-type carbonate platform are relatively well studied (summary in Racki, 1993). In the Devonian, the area corresponding to the present-day Holy Cross Mountains lay on the southern shelf of Laurussia (see e.g., Golonka *et al.*, 2019 and references therein).

The aims of the research project, the results of which are summarised in the present paper, were: (i) documentation of the stratigraphy and the fossil content of the Givetian part of the Skały Fm at Miłoszów, including in particular (ii) a reconstruction of the palaeoecosystems and (iii) elucidation of the nature of the “Miłoszów Limestone”, a lithostratigraphic unit used by previous authors, but never adequately defined; and (iv) examination of the bearing of the assembled data on the issue of Givetian global events in the Holy Cross Mountains.

History of research

The Devonian outcrops at Miłoszów were first mentioned in print by Samsonowicz (1936). Czarnocki (1950) briefly described the stratigraphy of the area and drew a bedrock map (see also Czarnocki, 1957, abridged version). A cursory survey of existing outcrops and a geological map form the content of an unpublished MSc. thesis, realised under the tutorship of Jan Samsonowicz (Nowicka, 1955).

Moenke (1954) described the representatives of the massive rugosan genus *Hexagonaria* Gürich, 1896 from several Devonian localities of the Holy Cross Mts, including *H. hexagona* (Goldfuss, 1826) from Miłoszów. Tabulate corals from the Skały Fm, including three species from Miłoszów, were dealt with by Stasińska (1958). Middle Devonian brachiopods from the northern part of the Holy Cross Mountains were described by Biernat (1964, 1966), who reported 26 species from the “Miłoszów limestone”. The type material of *Desquamatia circulareformis* Biernat, 1964, *Antirhynchonella linguiformis* Biernat, 1966, and *Leiorhynchus subplicatus* Biernat, 1966 is from Miłoszów. The “Miłoszów limestone” was also mentioned in the explanatory text for the sheet Nowa Słupia of the 1:50,000 Geological Map of Poland by Filonowicz (1968). Wrzołek (2002) gave a detailed description of the siphonophrentid rugosan *Enallophrentis corniformis* (Gürich, 1896) based in part on the material from Miłoszów.

A short description of outcrop M1 was given by Halamski (2004, 2009). On the basis of Halamski (2004) and unpublished information from Wojciech Kozłowski and the late Andrzej Piotrowski, detailed fieldwork under the supervision of AB and ATH started in 2018. Recently, Zatoń and Wrzołek (2020) and Zapalski *et al.* (2021) published two palaeoecological studies, while facies were dealt with in an unpublished MSc. thesis by Kubiszyn (2018; see also Kubiszyn, 2019).

This enumeration, aimed at completeness, shows that the Skały Fm at Miłoszów received little attention, compared to better studied outcrops in the Bodzentyn Syncline (Fig. 1B), i.e., the Świętomarz–Śniadka section (Zeuschner, 1866; Sobolew, 1904; Filonowicz, 1969; Piotrowski, 1977; Dzik, 2002; Halamski and Segit, 2006; Woroncowa-Marcinowska, 2012; Dec, 2020; see also the unpublished reports by Bednarczyk, 1955 and Kłossowski, 1976, 1981) and especially the Grzegorzowice–Skały section (Zeuschner, 1869; Gürich, 1896; Sobolew, 1903–1904, 1909; Siemiradzki, 1909; Kielan, 1953; Pajchlowa, 1957; Dzik, 1981; Malec and Turnau, 1997; Wrzołek, 2002; Halamski and Zapalski, 2006; Zatoń and Krawczyński, 2011; Zapalski *et al.*, 2017; see also unpublished reports by Woźniak, 1992 and Krul, 1995).

Authorship

A. T. Halamski provided introductions to the whole present paper and to its sections. He worked also on brachiopods, sponges, echinoderms and vertebrates, the overview of biota and ecosystems, and the comparison with New York. He contributed also to the description of the outcrops and to the summary of the geological succession. A. Baliński worked on outcrop descriptions and the systematics of brachiopods and medusozoans. Subsections on the carbonate ramp and the perspectives for future research are the work of G. Racki, who also participated in the elaboration of geological and biostratigraphical parts and in the discussion on regional aspects of the Taghanic Event. All matters related to conodonts have been worked upon by K. Narkiewicz (correlation in collaboration with G. Racki). W. Kozłowski described the geological setting. R. Mieszkowski provided geophysical data and interpretation. M. Kondas and P. Filipiak summarised palynostratigraphy and palynofacies, and contributed to the marine microbiota.

In the systematic overview of the biota, the responsabilities of the co-authors are as follows: Z. Dubicka – Foraminifera; M. Zatoń – marine microfossils, hederelloids and ascodictyids, echinoderms, in part also the overview of the biota as a whole; J. Denayer and T. Wrzołek – rugose corals; M. K. Zapalski – tabulates; W. Krawczyński – gastropods; M. R. W. Amler – bivalves and rostroconchs;

M. Basse – trilobites; E. Olempska – ostracods; P. N. Wyse Jackson – bryozoans, hederelloids and ascodictyids.

All authors agreed to the Conclusions of the present paper.

GEOLOGY

Geological setting

The Holy Cross Mountains (HCM), localised in the south-eastern part of central Poland, are a small inlier of Paleozoic rocks at the boundary between the East European Craton and the West European Platform.

The Paleozoic inlier is divided latitudinally by the Holy Cross Dislocation into two contrasting facies-tectonic domains: Kielce in the south and Łysogóry in the north (Czarnocki, 1919; Fig. 1B, C). The Łysogóry (northern) succession includes Cambrian to uppermost Devonian (Famennian) rocks, which were moderately deformed during the Variscan Orogeny inside the Holy Cross Mountains Fold Belt (Konon, 2006), the latter being located in the north-eastern foreland of the Variscan Orogen. The most extensive Variscan geological structure in the Łysogóry Region is the elongated and internally folded Bodzentyn Syncline, composed of Devonian strata.

The Devonian rocks, cropping out in the HCM (for synopsis see Szulczewski, 1995), represent an epicratonic succession of the southern (so-called Fennosarmatian) shelf of the Laurussia (Old Red) palaeocontinent. The major component of the Eifelian–Frasnian succession of the Kielce Region (the southern region of the Holy Cross Mountains) is the Kowala Fm (Narkiewicz *et al.*, 1990), comprising shallow-marine, tropical bank to shoal-rimmed, carbonate platform succession (Szulczewski, 1971; Racki, 1993). In contrast, the Łysogóry Region represents more diversified palaeoenvironments, evolved from a carbonate platform interior (Wojciechowice and Kowala Fm) in the Eifelian (e.g., Skompski and Szulczewski, 1994; Narkiewicz *et al.*, 2015), to a carbonate ramp (Skały Fm; Racki *et al.*, 2022) and an intra-shelf clastic (deltaic; Malec, 2012) clayey-carbonate basin (Świętomarz, Nieczulice, and Kostomłoty beds; sometimes incorrectly termed "formations") in the Givetian and Frasnian (Fig. 2B).

The Devonian succession of the southern limb of the Bodzentyn Syncline in the Łysogóry Region is best exposed along Dobruchna Stream and Pokrzywianka Brook in the Grzegorzowice–Skały section (Zeuschner, 1869; Pajchlowa, 1957). The Devonian succession of the key-profile (lithological sets I–XXVIII *sensu* Pajchlowa, 1957) starts with Emsian terrigenous deposits, representing the Rhenish magnafacies. They are covered by 250-m-thick dolostones of the Wojciechowice Fm, deposited in an inner carbonate platform-lagoon environment (set IX *sensu* Pajchlowa, 1957; Narkiewicz *et al.*, 2015), succeeded by a partly dolomitised limestone set (sets X–XII *sensu* Pajchlowa, 1957; recently classified as belonging to the Kowala Fm by Narkiewicz and Narkiewicz, 2010). The dolostones and dolomitised limestone represent a tide-dominated carbonate platform interior (Skompski and Szulczewski, 1994; Łuczyński, 2008).

The strata, situated near the transition from the Wojciechowice Fm to the Kowala Fm, contain conodonts of the *costatus* Zone (Middle Eifelian). This transition is interpreted as corresponding to the Id (Johnson *et al.*, 1985), that is, the *costatus*/*australis* transgressive event (Narkiewicz and Narkiewicz, 2010). The next characteristic two-step Ie–If transgressive event (Johnson *et al.*, 1985, but see an update in Fig. 7D), starting in the *kockelianus* Zone (identified by Malec and Turnau, 1997), is recognised as a distinct rapid deepening at the base of the Skały Fm (Skompski and Szulczewski, 1994). The Eifelian/Givetian boundary is probably localised at about the middle part of the formation; according to Malec and Turnau (1997), within set XIX *sensu* Pajchlowa (1957; see below).

The Skały Fm is composed of clayey shales, marls, and limestone with diversified and abundant fossils (Pajchlowa, 1957; Halamski, 2005; Halamski and Racki, 2005; Racki *et al.*, 2022). The facies are representative of varied palaeoecologic and palaeobathymetric conditions (from euphotic coral-crinoidal patch reefs to foreramp muddy intrashelf basin) inside the carbonate ramp to clayey-marly foreramp environment. The proportion of the terrigenous (clay-silt) material increases towards the top of the Skały Fm, the latter being in turn succeeded by the clastic-dominated Świętomarz Beds (Kłossowski, 1985; Malec, 2012), representing clastic-influenced intrashelf basin conditions.

The four sections at Miłoszów are situated in the valley of the Pokrzywianka Brook (Halamski, 2022, fig. 1B), which flows along the strike of the Kowala and Skały formations, perpendicular to the tributary Dobruchna Valley, localised 3 km to the east. In the Dobruchna Valley (Halamski, 2022, fig. 1C) both formations are exposed along the dip direction in the classic Grzegorzowice–Skały cross-section (Pajchlowa, 1957). On the lidar image of the Miłoszów area (Fig. 2), two distinct, hard bedrock zones can be observed. They correspond to the more resistant Kowala Fm and Świętomarz Beds and are separated by less resistant mudstone and limestone of the Skały Fm (as in the detailed geological map of Filonowicz, 1968). Despite tectonic complications caused by the presence of a fault network (Fig. 2), the synthetic succession of the Skały Fm in the Grzegorzowice–Skały section (as given by Pajchlowa, 1957) fits well to the geological cross-section of the Miłoszów area (Fig. 2B), even if estimations of the total thickness of the Skały Fm were widely varying, according to different authors (see summary in Racki *et al.*, 2022). According to geometric-lithological correlation and results of the cross-section, the Middle Devonian rocks cropping out or studied in trenches at Miłoszów represent the middle or upper part of the Skały Fm (Pajchlowa, 1957; Malec and Turnau, 1997).

Description of the outcrops

All the outcrops described below are situated in Miłoszów Wood, located near the hamlet of Miłoszów, between Nieczulice, Cząstków, and Pokrzywianka Dolna villages in the Holy Cross Mountains (Figs 2A, 3A). Most of the material comes from trenches, dug by the authors from 2018 to 2021 that have been refilled after study. The description refers to the trenches and to the state of the outcrops before

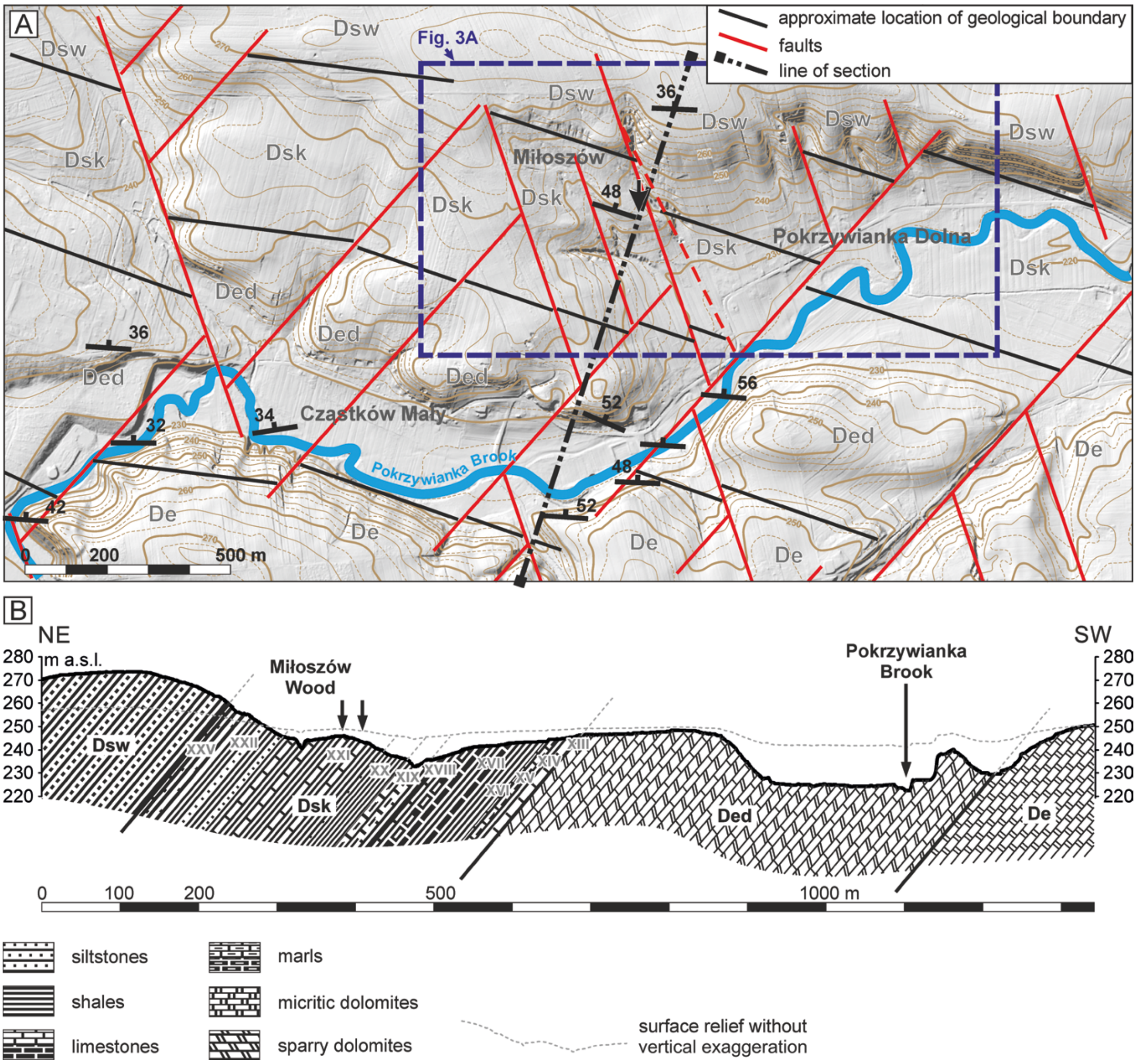

Fig. 2. Local geological context of the studied biota. **A.** Geological (tectonic) sketch of the bedrocks in the Miłoszów area obtained by combination of the (sub)surface geological map by Filonowicz (1968), the lidar image (Geoportal, 2022) and recent field cartographic reambulation. **B.** Geological cross-section across the Miłoszów area along the guideline shown on the tectonic sketch. The Skały Fm succession after Pajchlowa (1957), with lithological sets of the Skały Beds (XIII–XXV); thicknesses approximately as given by Pajchlowa (1957) and Biernat (1964), see text for further discussion. The arrows denote the approximate location of the studied sections (see Fig. 3). De – Wojciechowice Beds; Ded – Kowala Fm; Dsk – Skały Fm; Dsw – Świętomarz Beds.

fieldwork (Halamski, 2004, 2009). Apparently, the situation in the 1950s was much different, with outcrops concentrated in another ravine, situated in the southern part of the wood (Nowicka, 1955; see also the map provided by Czarnocki, 1950); despite a diligent search, the authors were unable to find any trace of those outcrops.

The sections are situated in the eastern part of the wood, in a NNW–SSE-trending ravine and along a forest road, oriented approximatively WNW–ESE (Fig. 3A). They are numbered from east to west, starting from M0 and ending with M3. Note that in some previous publications (Halamski, 2009; Zapalski *et al.*, 2021), symbols relating to sections were written with a hyphen (M-0, M-1, M-2, and M-3).

Section M0 is a fragment of the western wall of the ravine, situated in the eastern part of the wood (Fig. 4A). It probably had been used by local residents as a small quarry; during the present investigation, it was slightly refreshed with use of an excavator. About five metres of limestones and marls can be seen, overlain by shale and contacting with Quaternary sand (Pisarzowska *et al.*, 2022). The presence of a fault in the southern part thus may be inferred. The richest fauna comes from bed 9, including brachiopods, trilobites, and tabulates. The section is considered as the hypostratotype of the upper boundary

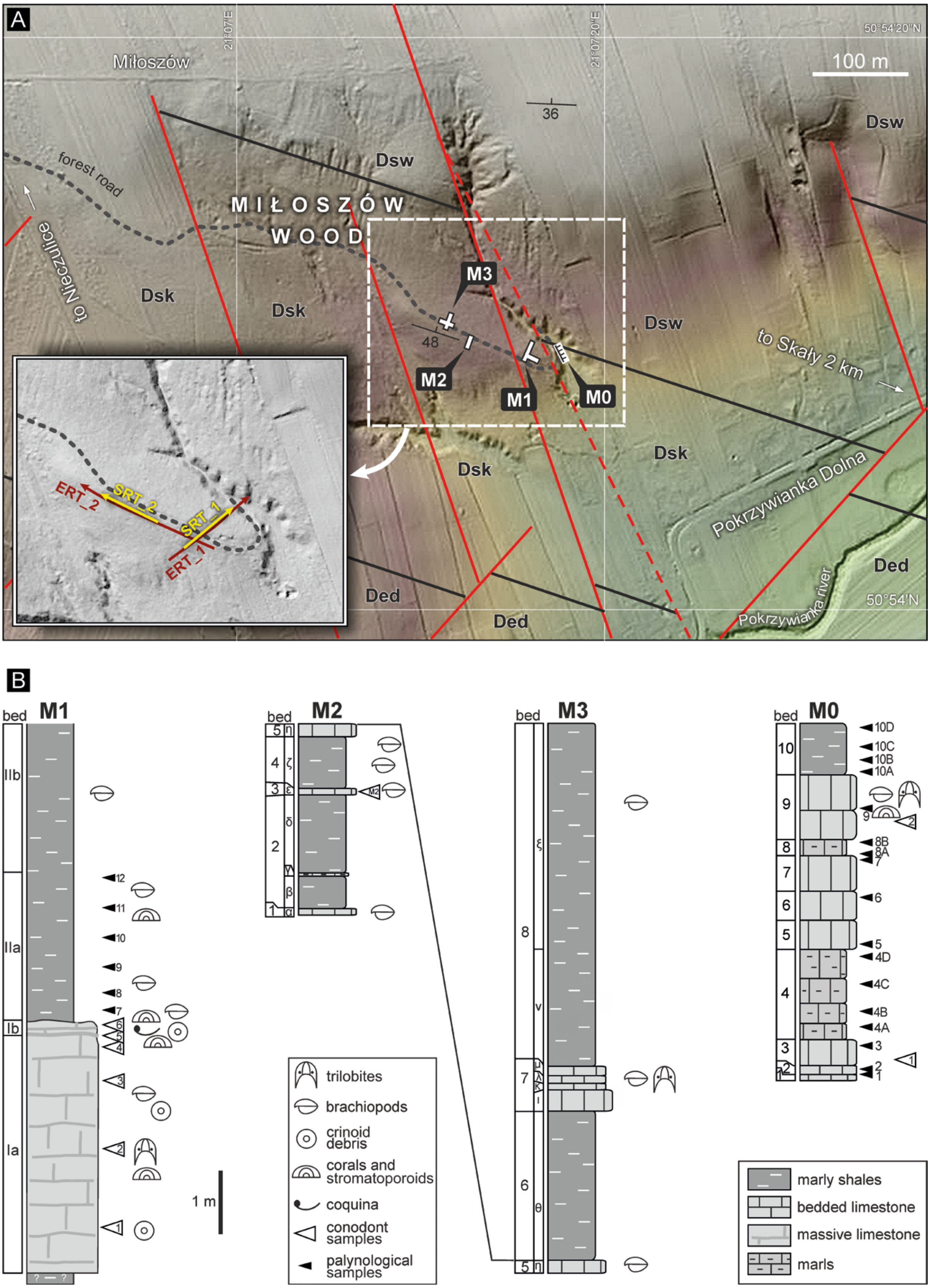

Fig. 3. Location and lithostratigraphy of the studied outcrops. **A.** Lidar image (Geoportal, 2022) of the studied area showing the outcrops M0, M1, M2, and M3 at Miłoszów. The black-and-white map shows the location of the two geophysical transects on the lidar image (Geoportal, 2022) of the studied area. ERT – electrical resistivity tomography; SRT – seismic resistivity tomography. Coordinates according to the Polish 1992 System (EPSG: 2180). **B.** Lithostratigraphic columns of single outcrops at Miłoszów with major occurrences of fossils. See Figure 8 for correlation between outcrops.

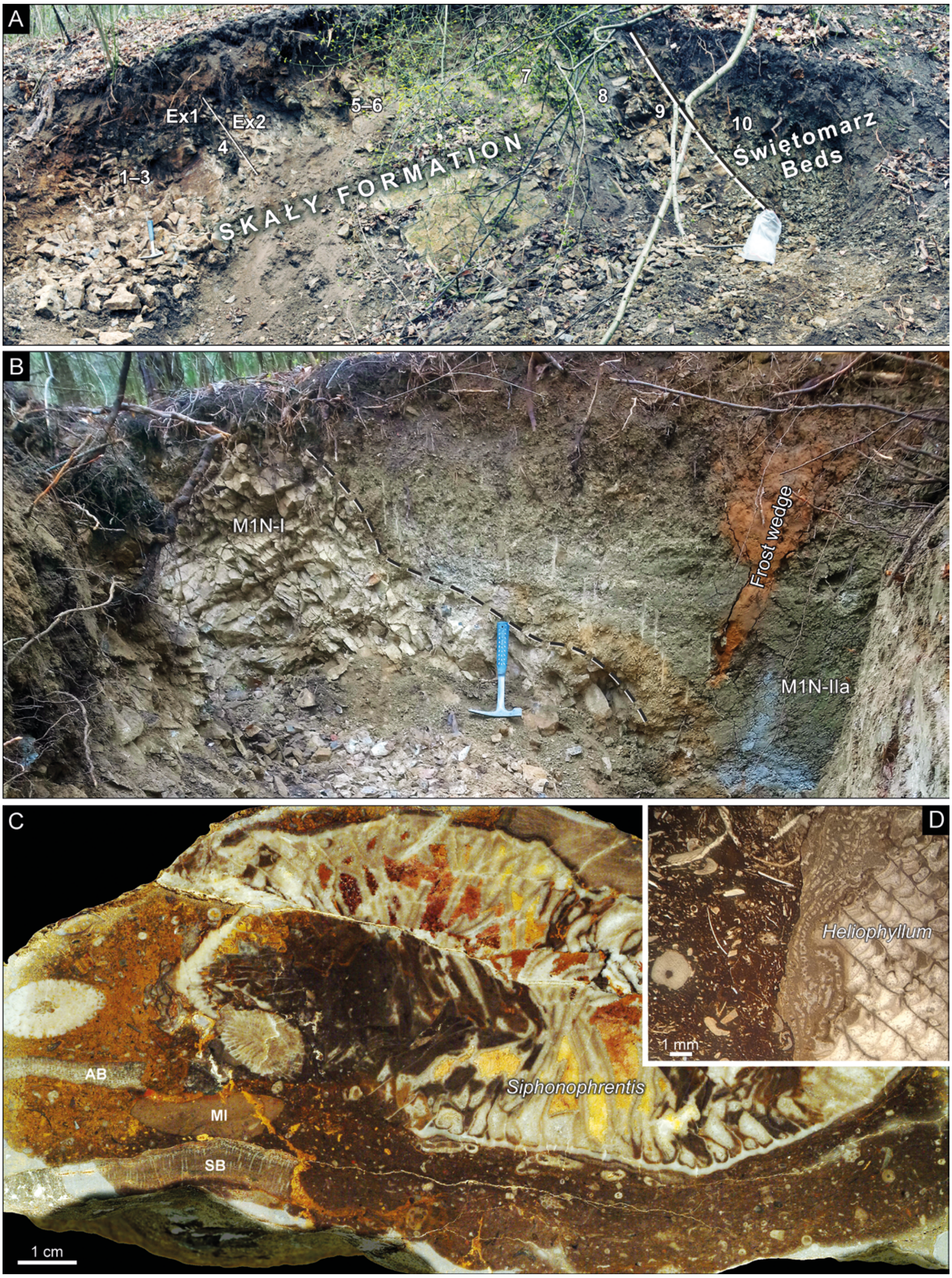

Fig. 4. Outcrops of the Skały Fm in a road escarpment (M0; A) and in a trench (M1N; B) in the Miłoszów Wood; cross-sectioned limestone slab from the top of M1-I unit shown in Figure 4B (C; see also Fig. 13), and microfacies from the same unit (D). **A.** Topmost limestone-marly part of the Skały Fm succession is visible in the locality M0 (for lithology of layers 1–10 see Fig. 3B), succeeded by a clayey set assignable to the basal Świętomarz Beds. The key boundary of Middle Givetian miospore zones Ex1 and Ex2 (Kondas and Filipiak, 2022; see Fig. 9) is marked in the layer 4. **B.** The fractured massive limestone unit (M1N–I) rapidly replaced in the Skały Fm succession by a clayey unit (M1N-2; Fig. 3B; compare Halamski, 2022, fig. 2E). Note the occurrence of a sandy frost wedge in the thick argillaceous weathered cover. **C.** Coral-intraclastic accumulation (biointrarudstone), with the large rugosan *Siphonophrentis* (overgrown by a small alvelitid tabulate colony at the top; cut and slightly displaced along the subhorizontal fracture); fragmented lamellar stromatoporoid (SB) and alveolitid (AB), and flat micritic intraclasts (MI) in crinoid-rich wackestone matrix; unit M1-Ib, sample M1/5 (compare Pisarzowska *et al.*, 2022, fig. 6C). **D**. Rugose coral *Heliophyllum* in tangential section with corallite expansions and a contraction, overgrown *syn vivo* by a stromatoporoid (see Zatoń and Wrzołek, 2020), embedded in the bioturbated crinoid-brachiopod micrite matrix, unit M1-IB; courtesy of T. Wrzołek (his thin section MI w27_3).

of the Skały Fm (between layers 9 and 10; Racki *et al.*, 2022; Fig. 4A).

Section M1 is situated in the immediate proximity of a forest road (northwards from it), approximately 25 m WSW from M0. The presence of a rich fossil fauna in small pits was noted by Halamski (2004). The first trench (M1N; see Halamski, 2022, fig. 2A, B, E) ca. 24 m long and approximately perpendicular to the beds, was dug in 2018 in order to explore the stratigraphy (southern end: 50°54.142′N 21°7.261′E; northern end: 50°54.150′N 21°7.271′E). However, the Devonian bedrock *in situ* occurs in about half the length of the trench. Northward, along with the drop in the hill slope, clay sediments with scattered limestone debris dominate, interpreted as Cenozoic colluvial sediments, including Pleistocene sandy frost wedges (Fig. 4B).

The strongly fractured limestone succession (M1-I; ca 4 m thick) includes presumably unbedded pale grey micritic lithologies with dispersed crinoid detritus; brachiopods are less common (mostly as disarticulated valves), as well as coral-stromatoporoid reef builders. The uppermost 30 cm of the limestone succession (M1-Ib) is distinguished by the richness of the coral assemblage (Fig. 4C) and contains thin irregular brachiopod coquinoid partings. Overlying, shaly deposits (M1-II; 4.7 m thick) were exposed over a considerable length of the trench as *in situ* weathered clayey cover with rock rubble (Fig. 4B). The lower part is characterised by a rock-forming coral fauna (M1-IIa), dominated in terms of specimens by thin branching tabulates (see below). This lithology probably represents marly biostromes, analogous to those from the Laskowa Góra Beds above the *Amphipora* dolomites, well displayed today in the Józefka Quarry, near Górno (Baliński *et al.*, 2016, pl. 2: 5, 6). In the higher part of the shaly succession, the only macrofauna is an infrequently occurring low-diversity brachiopod-crinoid association.

As the lowermost part of the shale, immediately overlying the limestone (M1-IIa), turned out to be the richest in fossil fauna, a second trench ca. 18 m long (M1E; see Halamski, 2022, fig. 2B, E) was dug in 2019, approximately parallel to the layers in order to collect the fauna from the limestone-to-shale contact zone (western end: 50°54.140′N 21°7.264′E; eastern end: 50°54.139′N 21°7.279′E).

The assemblage is the most diversified among those studied herein, including stromatoporoids, rugose and tabulate corals, ostracods, bryozoans, hederelloids, ascodictyids, brachiopods, and echinoderms.

Section M2 is situated approximately 60 m from the western end of M1 in a WNW direction (i.e., along the forest road). Two limestone beds (M2ε, M2η), parallel to the road, crop out in the road itself (Halamski, 2022, fig. 2F); especially the latter, which is thicker, is a good marker that can be followed for several dozen metres along the road. In 2020, a trench 3.5 m long (Fig. 3B; see also Halamski, 2022, fig. 2C) was dug perpendicularly to the beds at 50°54.139′N 21°7.213′E, revealing a limestone bed with brachiopods at the bottom (M2α), shale (M2β), a single layer of marl (M2γ), shale (M2δ), and the limestone at the top (M2ε).

Section M3 is located at 50°54.161′N 21°7.190′E, or at approximately 25 m from M2 further WNW along the road, i.e. about 60 m eastwards from a crossing of forest roads. A trench 3.5 m long was dug in 2020 subparallel to the bedding (Halamski, 2022, fig. 2D). It revealed ca. 35 cm of limestone (M3-7) overlain by shale (M3-8). Another trench was dug perpendicular to the bedding in 2021 in order to find the characteristic bed M2η. The continuity of the section between outcrops M2 and M3 thus may be assured (in other words, M2η = M3η; see Fig. 3B).

Here the fauna comes mostly from the single bed M3λ belonging to the limestone M3-7 (Halamski, 2022, fig. 2D), and consists almost exclusively of brachiopods, accompanied by very rare trilobites. Rare brachiopods were also found in the overlying shale (M3-8).

Geophysical survey

Continuous mapping of the deposits in the study area was performed during geophysical surveys using two methods: electrical resistivity tomography (ERT) and seismic refraction tomography (SRT). The location of the geophysical surveys is presented in Figure 3. A detailed description of the methodology is given in the online Supplementary Material. The investigations included field measurements (see Tab. S1), data processing, and interpretation (see Tab. S2).

Results of the ERT survey. The results of ERT surveys are presented in resistivity profiles (Fig. 5A, B, showing the electrical resistivity of the rock mass). Analysis of ERT profiles allows the recognition of three geoelectrical layers:

1. rocks with low resistivity (< 50 Ωm) – shales;
2. rocks with medium resistivity (50–85 Ωm) – marls;
3. rocks with high resistivity (> 100 Ωm) – limestones.

Potential geological boundaries have been marked by white-and-black dashed lines in the profiles. Vertical contacts of geological layers suggest the occurrence of tectonic discontinuities. Strong variability of resistivity indicates the lithological heterogeneity of the rocks.

Results of the SRT survey. Analysis of the SRT profile allowed recognition of two seismic layers (Fig. 5C, D showing the longitudinal wave velocity distribution):

1. Quaternary sediments – weathering cover (Vp < 1000 m/s);
2. Bedrock (Vp > 1000 m/s).

The distinct anomaly in profile SRT2 in the 20–30-m interval of the profile length points to the presence of a fault in the bedrock. The arched, oblique anomaly of reduced velocities in Figure 5D may indicate the local interbedding of a geological layer in the depth range of about 8–18 m below ground level.

Comments. The lack of a clear correlation between the results of electrical resistivity and seismic measurements (compare Fig. 5A, 5B with Fig. 5C and 5D) results from different measured physical and mechanical parametres of the rocks. The ERT method determines the electrical resistivity, which depends mainly on lithology, content of clay minerals, and humidity. In the seismic method, the density of the rocks is measured. The interpretation of results, obtained using the two methods, is not straightforward.

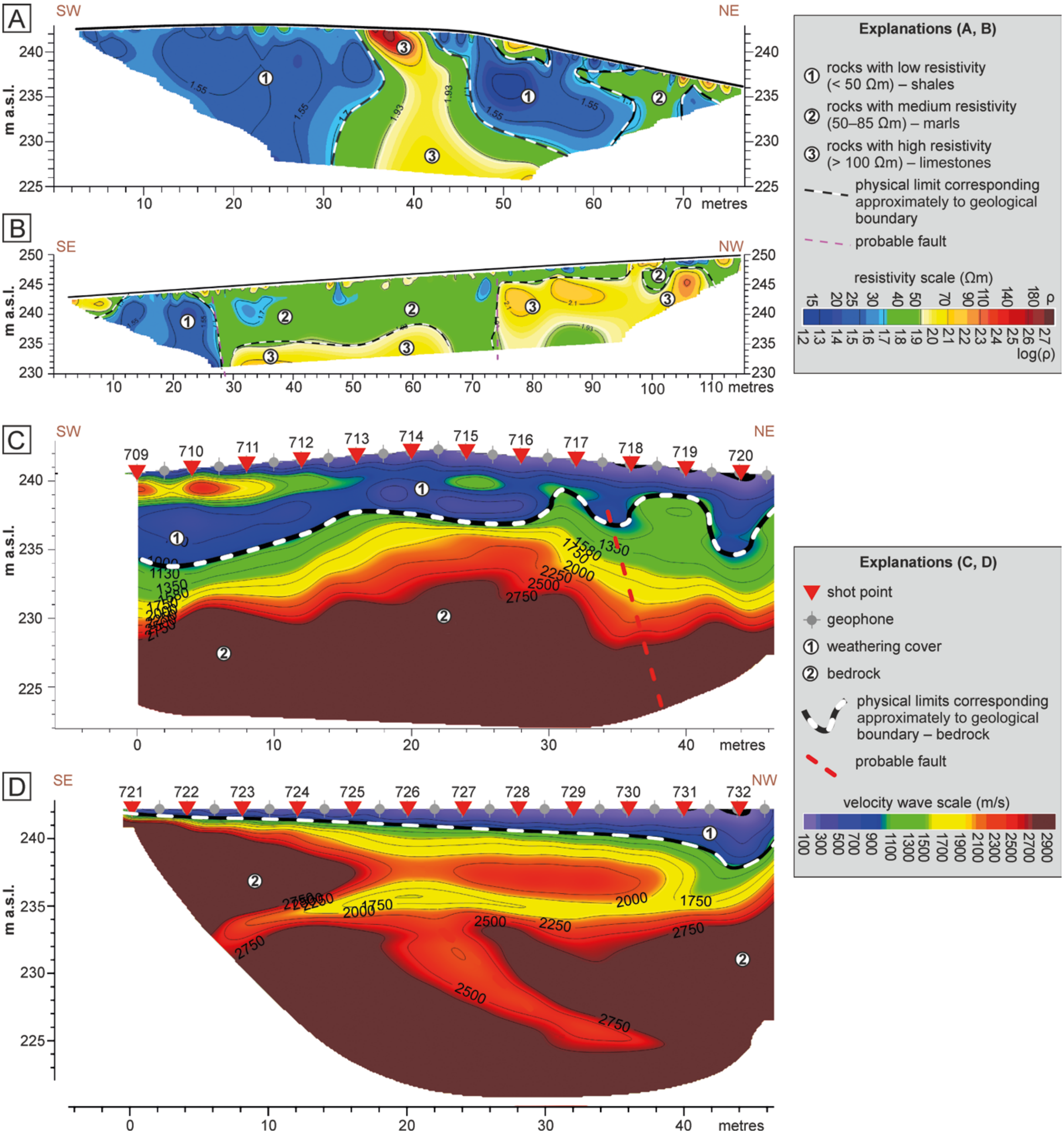

Fig. 5. Geophysical sections across the study area. **A, B.** Electrical resistivity tomography surveys ERT_1 and ERT_2. **C, D.** Seismic resistivity tomography surveys SRT_1 and SRT_2. Detailed locations of the sections given in Figure 4.

BIOSTRATIGRAPHY

Biostratigraphy of the sections investigated herein is based on conodonts and palynomorphs. The results of conodont studies are given first, whereas the systematic description of selected conodont taxa is provided below (Overview of the biota, Conodonts). This is followed by a partial re-interpretation of conodont-based biostratigraphy of the Grzegorzowice–Skały section, constituting a regional standard. A short summary of the palynostratigraphic results published elsewhere follows.

Following Becker *et al.* (2020), in the entire text Eifelian and Givetian substages are spelt with capital letters (Early/Lower Givetian and so on).

Conodont biostratigraphy

The standard Givetian conodont zonation is based on a succession of *Polygnathus* taxa (Clausen *et al.*, 1993; Becker *et al.*, 2016), whereas an alternative zonation is based on *Icriodus* (Bultynck, 1987; Narkiewicz and Bultynck, 2010; Fig. 6). The former subdivision is applicable to open- and

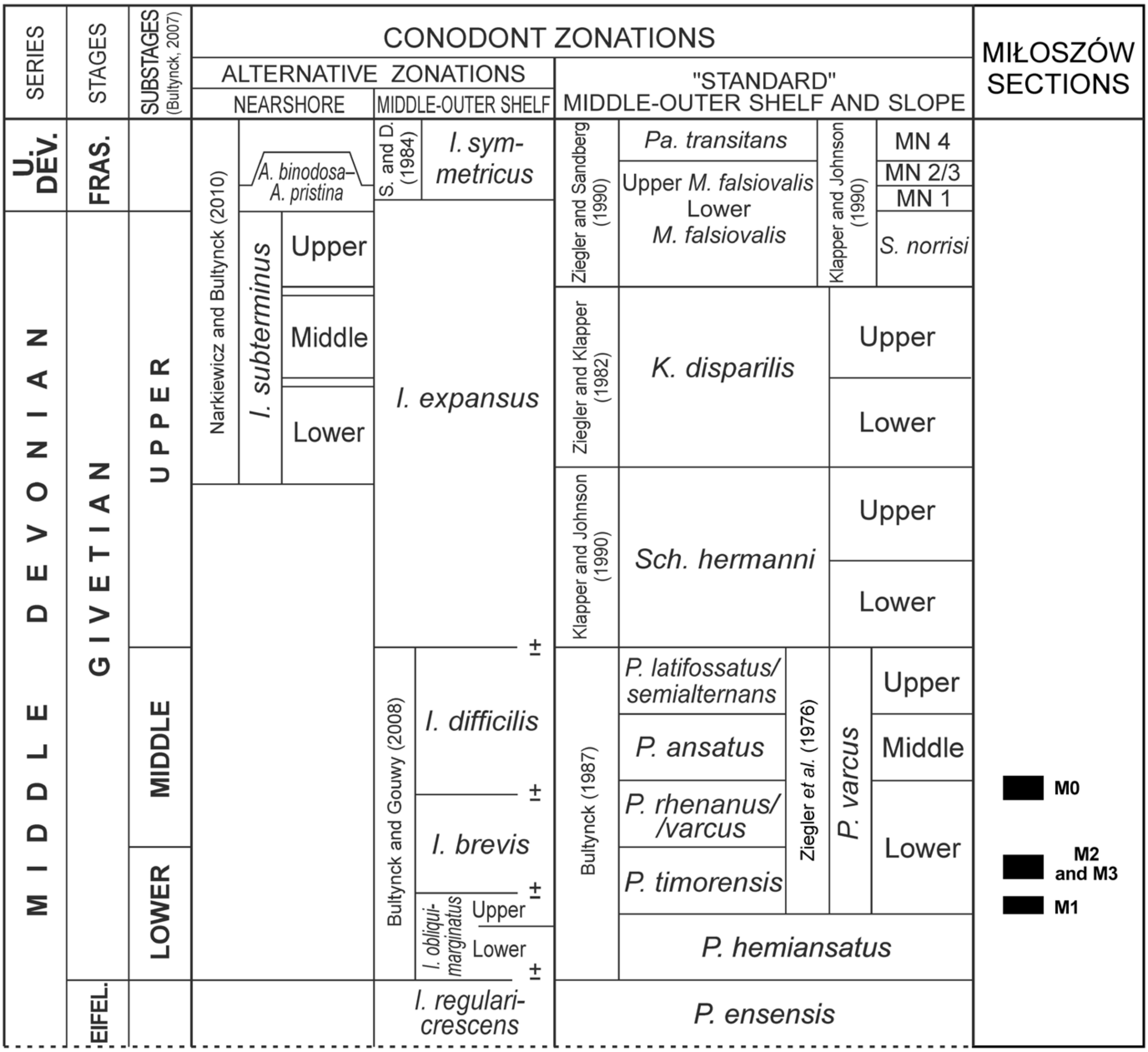

Fig. 6. Conodont zonations of the Givetian after various authors (as given). S and D (1984) = Sandberg and Dreesen (1984).

deeper-marine facies, whereas the latter applies to shallower and/or nearshore sediments. Introduction of the icriodid zonation appeared to be useful, as during the Givetian extensive shallow-water epeiric seas and carbonate platform existed, in which *Polygnathus* was relatively rare. It should be noted that in previously published zonation schemes, the *Icriodus obliquimarginatus* Zone was not subdivided. Here, the author follows Bultynck (1987, p. 151), who introduced a subdivision into lower and upper parts of the zone based on the FAD of *Icriodus lindensis* Weddige, 1977 (see Fig. 6).

In the collected material, both *Icriodus* and *Polygnathus* are represented (Tab. 1), so both zonations are used. The biostratigraphic determinations were based on the total stratigraphic ranges of all elements present in the studied assemblage (see Fig. 7A). The ranges of icriodid elements are based on data from Bultynck (2003), those of other forms on available published sources, cited below in discussions of particular taxa.

Infrequent *Icriodus* elements were found in trenches M1N and M0. In samples M1N-1, -4 and -6, the observed succession of *Icriodus* species allowed the more precise establishment of the age of the assemblages studied. This interval may be assigned to the *obliquimarginatus* Zone, on the basis of the the presence of the nominal species in older samples (see below; Fig. 25A–F; Tab. 1), succeeded in sample M1N-6 by a transitional form *Icriodus lindensis* Weddige, 1977 → *Icriodus brevis* Stauffer, 1940 (see below; Fig. 25G–K; Tab. 1). The occurrence of the transitional form indicates that subunit M1-Ib (Fig. 3B) may be constrained to the upper part of the *obliquimarginatus* Zone i.e., to a lower part of the *timorensis* Zone. The dating was extended down to include the entire 2.5 m-thick interval of unbedded limestones in the M1 succession (set I; Figs 3B, 4B).

This extrapolation is due to the assumed fast rate of deposition in the peri-biohermal environment and the implied short duration of a rubble-like facies (see below).

Table 1

Conodonts, list of taxa.

Conodont zones	lower part of *timorensis*				upper *timorensis*		*rh./v.*–l. *ans.*
	obliquimarginatus				*obliq.–brevis*		*diffic.*
Trenches	M1N				M2		M0
Sample numbers	M1N1	M1N2	M1N4	M1N6	M2	M2A	M0
Weight (kg)	4.65	2.15	4.60	2.45	~3	~3	4.0
I. obliquimarginatus morphotype γ	2		1				
Icriodus lindensis→I. brevis				2			
Icriodus difficilis							4
Icriodus sp.			1	2			
Ozarkodina plana					1		
Ozarkodina cf. *O. plana*					1		
Polygnathus ling. linguiformis γ_{1a}					1		
Polygnathus ling. linguiformis γ_3							1
Polygnatus ling. cf. *P. ling. klapperi*			1				
Pol. timorensis→P. rh. rhenanus					2	1	
Polygnathus sp.				1	1	2	
Belodella sp., S elements	8	3	5	4			2
Neopanderodus aequabilis					1	1	
Neopanderodus sp.	1	4	4	5	9	5	4
Ramiform elements					7	5	
P1 elements	2		3	5	6	3	5
Total number of elements	11	7	12	14	25	14	11

Abbreviations: *diffic.*, *difficilis*; l. *ans.*, lower *ansatus*; *ling.*, *linguiformis; obliq.*, *obliquimarginatus*; *rh./v., rhenanus/varcus.*

The polygnathid assemblage was detected in samples M2 and M2A. Their age may be constrained to an upper part of the *timorensis* Zone on the basis of the presence of forms transitional between *Polygnathus timorensis* Klapper, Philip and Jackson, 1970 and *P. rhenanus rhenanus* Klapper, Philip and Jackson, 1970, in both samples (see below, Fig. 25X–BB; Tab. 1). The age of the M0 assemblage is within the interval between the upper part of the *rhenanus/varcus* Zone, based on the FAD of *Icriodus difficilis* Ziegler and Klapper, 1976 (see below, Figs 7A, 25L–P; Tab. 1), to a lower part of the *ansatus* Zone based on the last appearance of *Polygnathus linguiformis linguiformis* Hinde, 1879 morphotype γ3 Walliser and Bultynck, 2011 (see below, Figs 7A, 25W; Tab. 1). However, the upper range of the latter taxon has been established in a single area and thus is not certain: it might be higher.

Correlation with the Grzegorzowice–Skały section

The Grzegorzowice–Skały section (e.g., Sobolew, 1903–1904, 1909; Pajchlowa, 1957; Malec and Turnau, 1997) is the best-studied Middle Devonian section in the Holy Cross Moutains and serves as a regional reference. It is situated less than 3 km east of the sections at Miłoszów, so a comparison of biostratigraphic data from both sections appeared essential to the present study.

Conodont data from the Grzegorzowice–Skały section are provided in Malec and Turnau (1997), but neither a complete list nor numerical abundances of taxa found in single samples are given. Conodonts in the Skały Fm (= Skały Beds as used by Malec and Turnau, 1997, but without set XIII and subset XXVB) were described only as rare and limited to certain levels (denoted as conodont assemblages CA1 to CA5 in Fig. 8). This is the reason why the comparison of both sections is based solely on the illustrated taxa in Malec and Turnau (1997, pls I–IV), some of which are revised here.

The Skały Fm in the Grzegorzowice–Skały section is divided into three units, comprising 13 sets (units XIII–XXV as used by Malec and Turnau, 1997; sets XIII–XXV herein, for terminology see Racki *et al.*, 2022). Malec and Turnau (1997) assigned the whole succession to the interval from the *kockelianus* Zone of the Upper Eifelian to the Early *varcus* Zone of the Lower Givetian (= present *hemiansatus* and *timorensis* zones; Fig. 6).

Slightly below the Skały Fm base (set XIII, sample K 15, Malec and Turnau, 1997, fig. 4; CA1 in Fig. 8), the species assigned by Malec nad Turnau (1997, pl. I, fig. 1) to *Icriodus regularicrescens* Bultynck, 1970 is included by the present author (KN) in *Icriodus arkonensis walliserianus* Weddige, 1988. In sample 17 from the same set, a stratigraphically important form was identified as *P. linguiformis linguiformis*

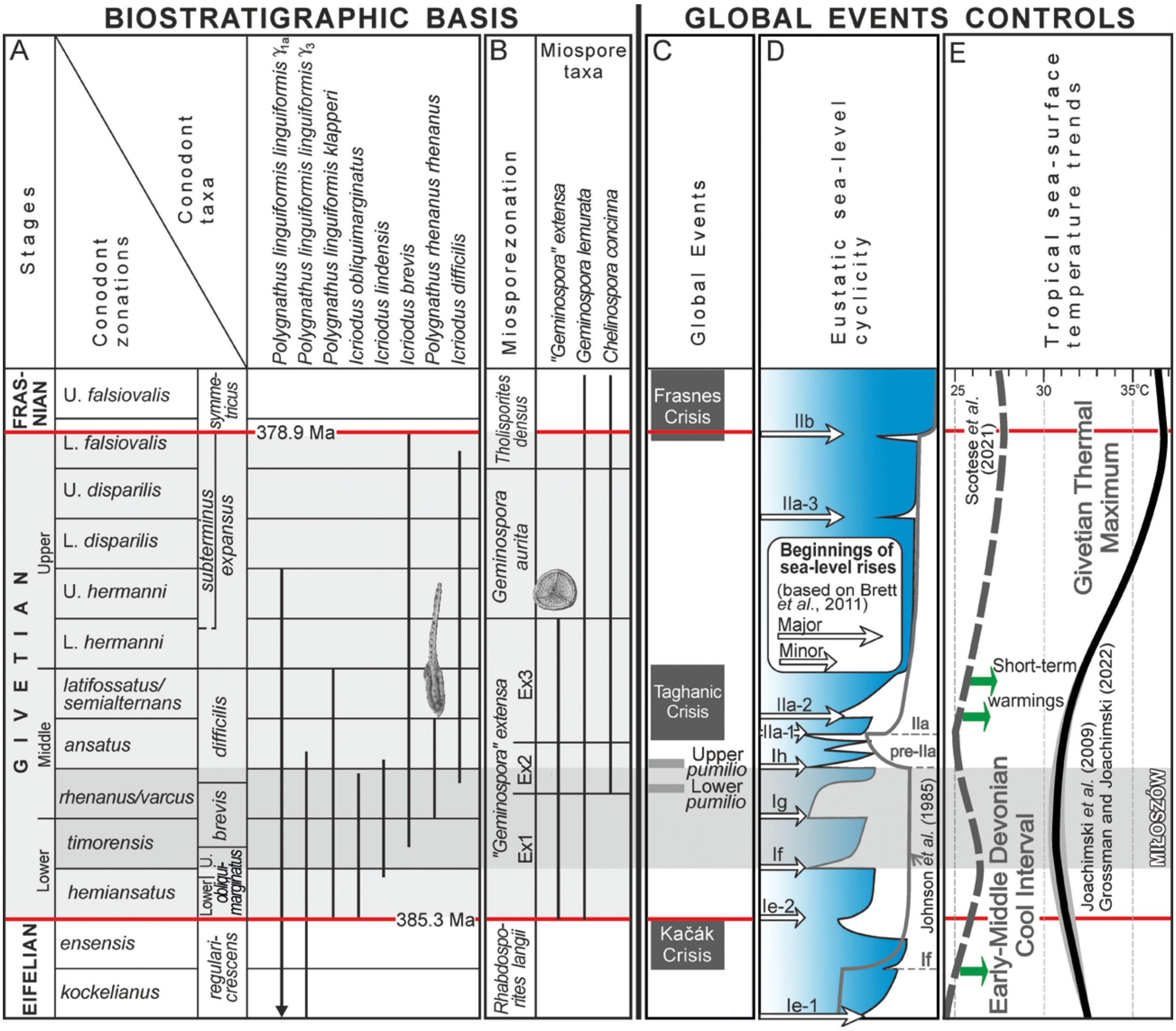

Fig. 7. Biostratigraphic basis for the Givetian succession of the Skały Fm at Miłoszów (A, B), against the global event stratigraphy, and eustatic and climatic settings (C–E). Red lines denote stage boundaries (Bultynck, 2007); absolute datings after Becker *et al.* (2020). **A**. Total ranges of key conodont taxa present in the studied samples, referred to the Eifelian to basal Frasnian polygnathid and icriodid zonation schemes (see Fig. 6), after Bultynck (2003), Gouwy and Bultynck (2003), Benfrika *et al.* (2007), Narkiewicz and Bultynck (2007), Narkiewicz and Königshof (2018). **B**. Total ranges of key miospore taxa present in the studied samples, referred to zonation of Turnau (2011), partly based on figure 4 in Kondas and Filipiak (2022). **C.** Global events, including biotic crises and faunal bloom (pumilio) events, after Becker *et al*. (2016, fig. 1; 2020, fig. 22.11). **D**. The eustatic sea-level changes, mostly based on updated sequence stratigraphy by Brett *et al.* (2011, fig. 21 and Brett, pers. comm., 2022; see also Becker *et al.*, 2020, fig. 22.11), against the standard sea-level curve of Johnson *et al.* (1985). **E**. The first-order tropical sea-surface temperature trend approximated from Joachimski *et al.* (2009, fig. 7) and Grossman and Joachimski (2022, fig. 5), and greenhouse episodes after Brett (pers. comm., 2022) based on oxygen isotope analysis of carbonate and phosphate conodont fossils, compared to the temperature curve (broken line) derived from figure 19 and table 4 in Scotese *et al.* (2021). Two Givetian climatic intervals after Scotese *et al*. (2021).

by Malec and Turnau (1997, pl. IV, fig. 1). According to the present author (KN), however, the illustrated specimen represents *Polygnathus linguiformis* subsp. A Uyeno and Bultynck, 1993. Importantly, the FADs of both revised taxa lie in the *ensensis* Zone. In addition, the stratigraphic range of *P. linguiformis* subsp. A straddles the Eifelian/Givetian boundary, comprising the *ensensis-hemiansatus* zones interval (Uyeno and Bultynck, 1993; Bultynck and Hollevoet, 1999). The updated conodont data imply a probable location of the stage boundary in the lower portion of the Skały Fm (Fig. 8; see further discussion in Racki *et al*., 2022).

In the lower part of the middle unit (Malec and Turnau, 1997: set XX, sample K 8, fig. 5; CA2 in Fig. 8) an assemblage including *Icriodus obliquimarginatus* (Malec and Turnau, 1997, pl. I, fig. 2), *Bipennatus bipennatus bipennatus* Bischoff and Ziegler, 1957 (Malec and Turnau, 1997, pl. II, figs 1–6) and *I. brevis* (pl. I, fig. 4) was found. According to the present author (KN), the identification of the last-named taxon is questionable as the denticles at the extension of the median row are completely removed (erased), thus precluding the straightforward identification of the specimen. Other taxa have a similar stratigraphic range, from

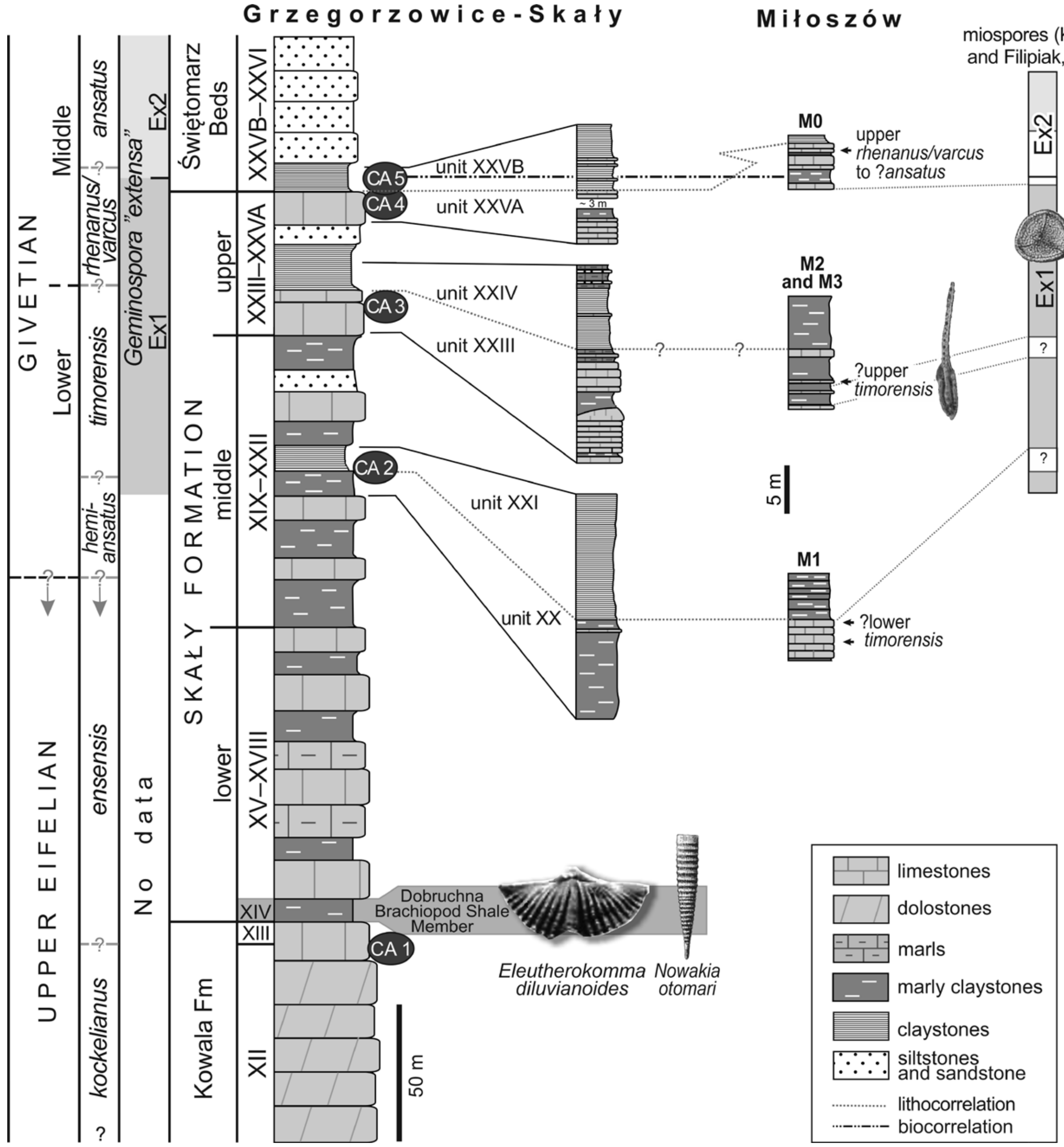

Fig. 8. Correlation of three isolated Miłoszów sections (M0 to M2–M3) with the composite succession of the Grzegorzowice–Skały section (modified fig. 3 of Malec and Turnau, 1997), against lithological subdivision (units mostly after Pajchlowa (1957) and combined updated conodont and miospore dating from Malec and Turnau (1997). Scarce distribution of conodont faunas in the Skały Fm is marked as five assemblages (CA) reported by Malec and Turnau (1997). Note modified boundaries of the formalised lithostratigraphic unit (see Racki *et al.*, 2022), as well as the crucial correlative significance of the Ex1–Ex2 palyno-subzone boundary.

the *hemiansatus* Zone to an upper part of the *timorensis* Zone of the Lower Givetian (Bultynck, 1987). It may be noted that the *I. obliquimarginatus* specimen, figured by Malec and Turnau (1997), is very similar to those from Miłoszów (section M1), assigned to morphotype γ (Tab. 1). The data suggest that the oldest part of the Skały Fm in Miłoszów from trench M1N (samples M1N-1 to -6) can be correlated with the middle part of the middle unit of the Skały Fm (sets XX to XXI) in the Grzegorzowice–Skały section.

At the base of the upper unit (Malec and Turnau, 1997: set XXIII, sample K 57, fig. 6; CA3, Fig. 8), a specimen identified as *Polygnathus timorensis* by Malec and Turnau (1997; pl. III, fig. 1) was found. This is not a typical representative of the species, but rather a transitional form between *P. timorensis* and *P. rhenanus* characterised by a distinctly shortened platform and a pronounced outward bowing of the outer anterior trough margin. Such transitional forms were found at Miłoszów (section M2; Tab. 1). Thus, the Lower Givetian strata assigned to the upper part of the *timorensis* Zone in trench M2 can be correlated with the lowermost part of the upper unit (sets XXIII to XXIV, Fig. 8).

Near the top of the Skały Fm (set XXVA, sample K 28, Malec and Turnau, 1997, fig. 6; CA4 in Fig. 8), the first representative of *Icriodus* cf. *I. difficilis*, can be noted, identified by Malec and Turnau (1997, pl. I, fig. 7) as *Icriodus* sp. Its presence indicates that sample K 28 assemblage cannot be older than the upper part of the *rhenanus/varcus* Zone. Consequently, the age of these deposits is consistent with the Middle Givetian age of the uppermost part of the Skały Fm in the Miłoszów section, studied in trench M0. The youngest sediments at Miłoszów were assigned to the upper part of the *rhenanus/varcus* Zone and, possibly, to the lower part of the *ansatus* Zone (Tab. 1). Malec and Turnau (1997; pl. I, figs 9, 13; CA5 in Fig. 8) reported only *Icriodus eslaensis* from set XXVB, but Narkiewicz in Turnau and Narkiewicz (2011, p. 37) re-identified the specimens as *Icriodus* sp. and *I. arkonensis walliserianus* Weddige, 1988. The latter species ranges from the *ensensis* Zone to the lower part of the *ansatus* Zone.

This correlation of the topmost Skały Fm with the M0 section is supported conclusively by the miospore data (Fig. 8), because the boundary between the subzones Ex1/Ex2 in the higher part of the *rhenanus/varcus* Zone (Fig. 7B) was documented by Malec and Turnau (1997) in the lower part of set XXVB and by Kondas and Filipiak (2022) in the lower interval of the M0 succession (layer 4, Figs 3B, 4A).

Palynostratigraphy

The results of palynological investigations of the Givetian samples from Miłoszów were published separately: a new genus of acritarchs was described by Kondas *et al.* (2021), whereas a complete palynostratigraphic study was given by Kondas and Filipiak (2022). Only a short summary of these results is provided here.

Analyses of the palynological content were conducted for sections M0 (18 samples), M1 (12 samples), and M2 (six samples). Palynomorphs of terrestrial origin, represented mostly by miospores and phytoclasts, strongly predominated. Marine components were limited in number and represented by prasinophytes, acritarchs, and scolecodonts. Only a single sample (M2α) contained chitinozoans. Among the prasinophytes, different-sized *Leiosphaeridia* were the most abundant. Among the acritarchs, the most abundant genera were *Gorgonisphaeridium*, *Micrhystridium, Muraticavea*, *Navifusa*, *Polyedrixium*, and *Teleostomata* (see Kondas *et al.*, 2021).

On the basis of the miospore assemblage, the age of the deposits in the M0 section was established as the Ex Zone *sensu* Turnau (1996, 2007, 2008). Samples 1, 2 and 3 were included into the Ex1 Subzone, owing to the presence of *Geminospora lemurata* and *Aneurospora extensa* combined with the absence of *Chelinospora concinna*. Samples 4B, 4C and 4D contained miospore assemblage characteristic for the Ex2 Subzone, with *Aneurospora extensa*, *Rhabdosporites langii*, *R. streeli* and numerous species belonging to the genus *Ancyrospora* (Turnau, 1996, 2007, 2008). The index taxon *C. concinna* was documented in sample 4B and its presence allowed recognition of this Subzone. *Corystisporites collaris* var. *kalugianus* was documented in samples 8A and 10A. According to Turnau (2011), this miospore taxon disappears within the Ex2 Subzone; as a consequence, its presence indicates Ex2 as the youngest possible subzone for these samples. This result must be treated with caution as samples 8A, 8B, 10B, 10C and 10D contained miospores that strongly resemble *Samarisporites triangulatus,* which is the index taxon for the Ex3 Subzone; moreover, *C. concinna* may range to the Late Givetian (Streel *et al.*, 2021).

On the basis of miospore content, the age of the M1 section was tentatively established as the Ex1 Subzone. Each of the samples contained the index taxon *Aneurospora extensa* (= "*Geminospora*" *extensa*), whereas *Geminospora lemurata* was documented in samples from 8 to 10.

On the basis of the miospore succession, the age of the deposits from all four palynologically positive samples from the M2 section was established as the possible Ex1 Subzone. All samples contained both index taxa: *Aneurospora extensa* and *Geminospora lemurata*. For detailed palynostratigraphical data, see Kondas and Filipiak (2022).

Stratigraphic position of brachiopods described from Miłoszów by Biernat (1964, 1966)

The material from Miłoszów from Gertruda Biernat's collection (partly used in Biernat, 1964, 1966) is kept in ZPAL, but difficult to use, insofar as accompanying information is very scarce and sometimes contradictory (see below). The usual details may have been recorded elsewhere than on the labels, but this could not be verified, so the precise location of outcrops is not known and there are no collector names or dates. The presence of brachiopods, revealed by the present authors to occur only in single levels at Miłoszów, allow identification of "trench IV" with bed M0-9 of the present authors and sections "Miłoszów II" and "Miłoszów 3" with composite bed M3-7. Biernat (1964, 1966) combined all Miłoszów sections under the heading "Miłoszów limestone". The type stratum of *Eumetabolotoechia subplicata* (Biernat, 1966) is bed M0-9. *Desquamatia* (*I.*) *circulareformis* Biernat, 1964 is common in M0-9, but present also in M1-I; *Antirhynchonella linguiformis* Biernat, 1966 is common in bed M3-7, but present also in other outcrops. In the published work only "exposure 2" is mentioned (Biernat, 1966, pp. 35, 99, 104).

The Miłoszów limestone *sensu* Biernat (1964, 1966), a never defined designation, used exclusively to denote the type level of the three brachiopod species described from Miłoszów, corresponds therefore to at least two separate different-aged Lower to lower Middle Givetian limestone layers in localities M0 and M3 (Figs 3B and 9; see also Baliński and Halamski, in press). Such a litostratigraphic unit cannot

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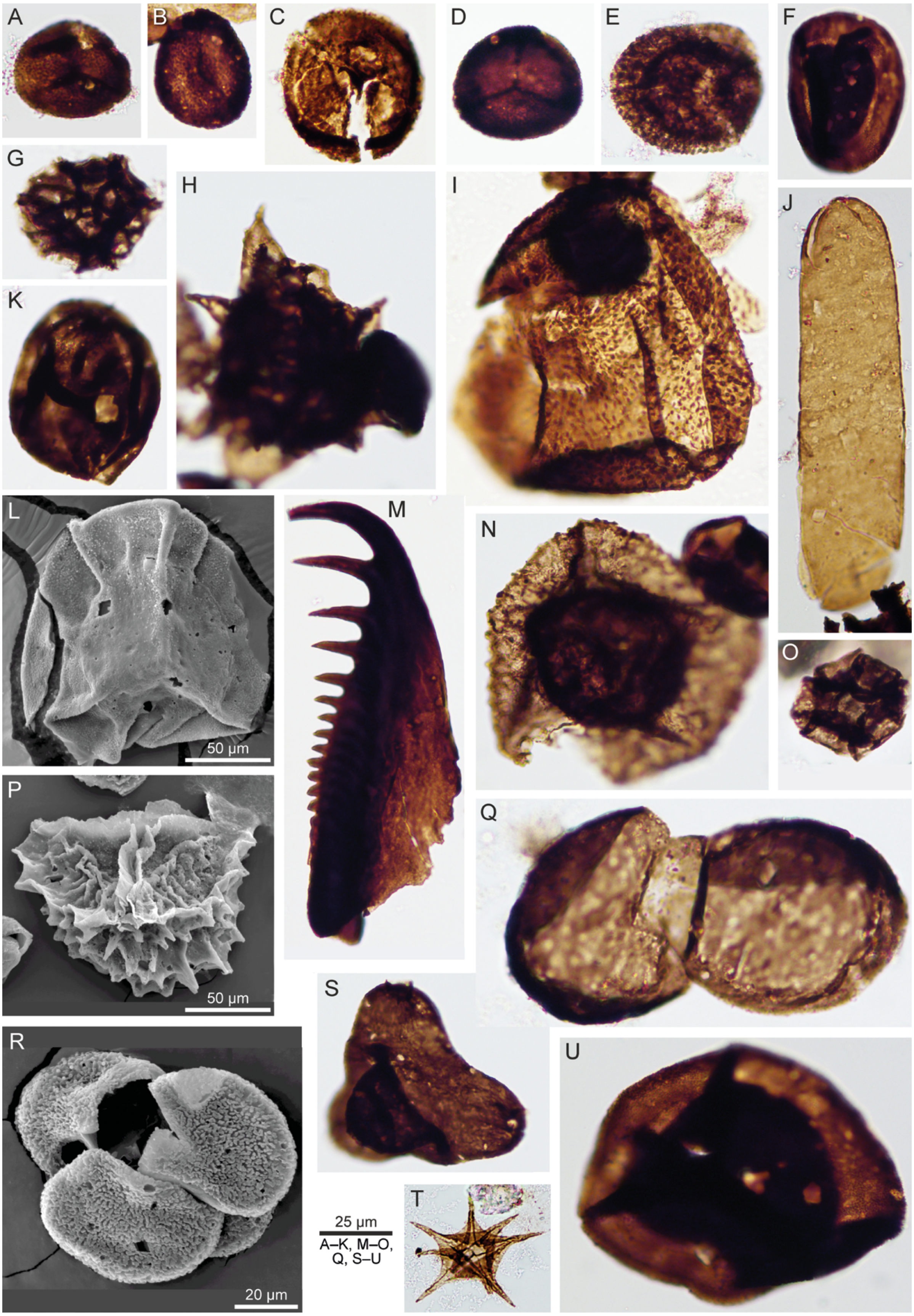
Fig. 9. Selected Givetian ("*Geminospora*" *extensa* Zone) palynomorphs recovered from section M0 at Miłoszów. **A.** *Geminospora tuberculata* (Kedo) Allen, 1965. Sample 10D. **B.** *Aneurospora goensis* Streel, 1964. Sample 8B. **C.** *Geminospora lemurata* Balme emend. Playford, 1983. Sample 10D. **D.** *Aneurospora extensa* (Naumova) Turnau, 1986. Sample 10C. **E.** *Lanatisporites bislimbatus* (Tchibrikova) Arkhangelskaya, 1985. Sample 10D. **F.** *Rhabdosporites streeli* Marshall, 1996. Sample 10C. **G.** *Chelinospora concinna* Allen, 1965. Sample 4B. **H.** *Corystisporites collaris* var. *kalugianus* Arkhangelskaya, 1985. Sample 10A. **I.** *Dibolisporites echinaceus* (Eisenack) Richardson, 1965. Sample 10D. **J.** *Navifusa bacilla* (Deunff, 1961b) Playford, 1977. Sample 10D. **K.** *Leiosphaeridia* sp. Sample 10B.



L, U. *Rhabdosporites langii* (Eisenack) Richardson, 1960. Samples 10D (L) and 10B (U). **M.** Unidentifed scolecodont. Sample 10D. **N.** *Grandispora echiniformis* Kedo, 1955. Sample 10C. **O.** *Polyedrixium skalense* Turnau in Turnau and Racki, 1999. Sample 10B. **P.** *Ancyrospora involucra* Owens, 1971. Sample 8A. **Q.** *Leiosphaeridia* sp. Sample 10A. **R.** Tetrad of miospores. Sample 10D. **S.** *Teleostomata rackii* Kondas, Filipiak and Breuer, 2021. Sample 10D. **T.** *Stellinium micropolygonale* (Stockmans and Willière) Playford, 1977. Sample 10D. Localisation of samples given in Figure 3B.

thus be distinguished. On the other hand, comparison of the Miłoszów brachiopod localities with the middle part of the Skały Fm given by Biernat (1964, p. 282; 1966, fig. 3) is partly confirmed by data of the present authors from the M3 section (Fig. 9).

SUMMARY OF THE GEOLOGICAL SETTING

The four investigated sections in Miłoszów Wood belong to the Skały Fm, an Upper Eifelian to Middle Givetian lithostratigraphic unit of the Bodzentyn Syncline of the Łysogóry Region (Fig. 2B). Note that the newly defined Skały Fm differs slightly from the Skały Beds *sensu* Pajchlowa (1957), as the formerly basal set XIII is included here in the Kowala Fm. Biostratigraphic evidence, paired with correlation with the reference Skały Fm section (Fig. 8), is overall conclusive and allows dating all four outcrops at Miłoszów to the Lower to Middle Givetian.

The M1 to M3 sections probably represent lower "*Geminospora*" *extensa* (Ex1) miospore Zone (Kondas and Filipiak, 2022). The oldest strata studied here are those from section M1. Its lower limestone portion (M1-I; Fig. 3B) most likely belongs to the lower part of the *timorensis* Zone, whereas data on conodonts from the the overlying shaly unit (M1-II) are missing. The mostly limestone strata cropping out in M0 are distinctly younger, belonging to two successive subzones of the "*Geminospora*" *extensa* miospore Zone, Ex1 and Ex2 (Kondas and Filipiak, 2022), corresponding to the upper part of the *rhenanus*/*varcus* Zone, but the presence of the lower part of the *ansatus* Zone cannot be excluded. Data from section M2 indicate the upper part of the *timorensis* Zone. No dating was performed on the mainly shaly strata of the M3 section, which concordantly overlie those of M2.

In summary, the Miłoszów sections represent three small successive fragments of the thick succession of the Skały Fm (ca 250 m; see summary of differing estimates of the total thickness in Racki *et al.*, 2022), as revealed by comparison with the Grzegorzowice–Skały reference section (Fig. 8). The best proved is the time equivalency of section M0 with the transitional interval of the Skały Fm to the Świętomarz Beds (subset XXVB *sensu* Malec and Turnau, 1997), thanks to combined conodont and miospore dating. A diachronous passage from limestone to siliciclastic facies eastward is conclusively shown over a distance of less than 3 km. Lower intervals of the Miłoszów succession are less certainly interrelated with the Grzegorzowice–Skały succession because of the very fragmentary conodont record and the distinct lateral facies change.

It seems therefore that in general more carbonate facies developed westwards, which is also confirmed by the oldest correlated strata (limestone set M1-I versus marly set XX; fig. 5 in Malec and Turnau, 1997; Fig. 8). Chemical data (Pisarzowska *et al.*, 2022) demonstrate the marly character of the shaly units in the Miłoszów sites (above 10% $CaCO_3$), in contrast to the common argillaceous units occurring eastward (note also silty-sandy deposits in the upper XXII and XXIV sets; Pajchlowa, 1957; Malec and Turnau, 1997, fig. 6; Malec, 1999). However, geophysical ERT data (Fig. 5A) point to a limited extent of the wedge-like (?) carbonate lithosome within the shaly strata and set M1-II seems to be a lithostratigraphic equivalent of set XXI (black clayey shales). On the other hand, the same geophysical survey (Fig. 5B) indicates an occurrence of a thicker limestone lithosome below the shaly-dominated M2–M3 succession, thus supporting the assumed correlation with the XXIII/XXIV sets transition (Fig. 8).

As the differently aged Miłoszów sections are located approximately along the strike of the Devonian units (Figs 2A, 3A), the network of transverse and diagonal faults, related to the major Łysogóry Fault (Fig. 1B), is inferred by Czarnocki (1950, pls I, X) and Filonowicz (1963; see also Biernat, 1964, p. 282). In particular, the major fault FI is hypothesised to have separated blocks within sections M1 and M2–M3 and to account for the intense fracturing of the limestone body M1-I (Fig. 4B). However, the main tectonic gap, in the order of 100 m, unexpectedly occurs between the adjacent M1 and M0 localities. Therefore, the presence of a supplementary fault FII is postulated (Fig. 3A), a dislocation delineating the location of the M0 succession within a tectonic trough block. Even smaller displacements between limestone and shale units cannot be ruled out, but, for example, the rapid lithofacies shift in the M1 trench agree well with the expected biofacies succession (see below).

THE GIVETIAN ŁYSOGÓRY CARBONATE RAMP: ENVIRONMENTS AND EVENTS

The Skały Fm has been known as a unique stratigraphic unit in the Holy Cross Mts (see Racki *et al.*, 2022), distinguished by the abundance of diverse fossils and variable lithology from reef limestones to dark *Styliolina* shales (Pajchlowa, 1957; Malec and Turnau, 1997). Initiation of the open marine facies in the Łysogóry Region resulted from the Late Eifelian eustatic sea-level rise (Fig. 7D). The second deepening pulse of the subcycle Ie (Brett *et al.*, 2011; Becker *et al.*, 2020, fig. 22.11; = transgression If in the scheme of Johnson *et al.*, 1985), paired with the global Kačák Event (Walliser, 1996; Narkiewicz *et al.*, 2021), certainly are recorded in the lower Skały Fm, in particular best expressed in the fossiliferous basal Dobruchna Member (set XIV of Pajchlowa, 1957; see also Woźniak *et al.* 2022; Fig. 8).

In a supra-regional context, the Late Eifelian facies turnover was the first of several back-stepping events linked to the consequent shelf drowning that led to restriction of the coral-stromatoporoid reef growth on the vast Laurussian shelf (see Racki *et al.*, 1985; Racki, 1986, 1993; Narkiewicz, 1988; Narkiewicz *et al.*, 2006, 2011; Narkiewicz and Narkiewicz, 2010). Thus, time-equivalent strata in the Kielce undifferentiated (flat-topped) carbonate platform include a lower part of the bank-to-reef complex (Racki, 1993; see also Wolniewicz, 2021), i.e., mostly dolomitised lagoonal-biostromal strata of the *Stringocephalus* Beds in the basal part of the Kowala Fm (Narkiewicz *et al.*, 1990). Notably, the transitional barrier-type deposits between the Kielce and Łysogóry regions are unknown because they were eroded over the Łysogóry Anticline

(Fig. 10). The onset of open shelf sedimentation in the Łysogóry Region was correlated with the transition from sabkha-type dolomitic strata to the bank-type succession in the Kielce Region (Narkiewicz and Narkiewicz, 2010), possibly recorded in the coquinoid-crinoid level with *Rensselandia* at Jurkowice-Budy (Racki, 1993). The top of the Kowala Fm in the Łysogóry Region therefore hypothetically is approximated with the base of Kowala Fm in the Kielce Region, as a record of a peculiar interregional "facies switch" (see fig. 9 in Racki *et al*., 2022).

In the Łysogóry Region, the Kačák Crisis is surprisingly linked to a peak of benthic colonisation and biodiversification climax in oligotrophic habitats (Woźniak *et al*., 2022). As noted above (WK), this corresponds to the initiation of calcareous mud deposition in a ramp setting, which continued northward in the Łysogóry–Radom Basin (Narkiewicz *et al*., 2011; Racki *et al*., 2022). The ramp-style basin model may be assumed, given the general architecture of the evolving carbonate complex, namely the facies shift from an undifferentiated biostromal bank to the more localised Dyminy Reef (Szulczewski, 1971, 1995; Narkiewicz, 1988; Narkiewicz *et al*., 1990; Racki, 1993), as indicated previously for the bryozoan-rich Givetian strata of the Kostomłoty facies zone (Morozova *et al*., 2002) and the Early Frasnian Kadzielnia mud mound setting (Szulczewski and Racki, 1981). This depositional system was characterised by a low-gradient slope and facies belts, which gradually transitioned offshore into deeper-water, low-energy deposits and then into pelagic-basin sediments (homoclinal ramp model of Read, 1985; Fig. 10). The gentle slopes were more effective at suppressing the most violent hydrodynamic effects than the steep slope of a rimmed shelf. This protection is recorded in the general scarcity of coarse-grained sediments, the dominance of mud-supported fabrics, and the subdued massive framebuilding in organic buildups (Wilson, 1975, p. 362; Tucker and Wright, 1990, pp. 47–50; Burchette and Wright, 1992; Flügel, 2010, pp. 664–666, 716–719; see also the T-factory systems in Reijmer, 2021).

The mud-dominated depositional system, evidenced in the disconnected Miłoszów sections (Pisarzowska *et al*., 2022), reveals analogies with the high-latitude Early Givetian Moroccan intrashelf basin (Kaufmann, 1998; see also Wendt *et al*., 1997 and Jakubowicz *et al*., 2019). Despite its location within the equatorial belt, this hindrance is also visible in the coeval fragmentary Miłoszów succession. Only the shallower (middle) ramp, affected by episodic high-energy events in the euphotic zone, and the deeper (outer) ramp, encompassing mostly mesophotic low-energy, maybe also oxygen-depleted habitats (Fig. 10), can be distinguished without doubt. In contrast to common sponge-microbial mud mounds with abundant stromatactis cavities (Wendt *et al*., 1997; Flügel, 2010, p. 196; Jakubowicz *et al*., 2019), only skeletal (stromatoporoid-coral or coral) buildups, partly of mesophotic type, have been observed up to now among Givetian organic buildups in the Łysogóry succession (Malec and Turnau, 1997; Malec, 1999, 2012; Zapalski *et al*., 2017; Zatoń *et al*., 2022). In particular, Filonowicz (1968) reported "coral limestone lenses" (bioherms?) from Miłoszów Wood, and the massive rugosans *Hexagonaria hexagona*, known from the top set XXVA of the Skały Fm (Pajchlowa, 1957), were described by Moenke (1954) from this locality. Two slightly younger Middle Givetian Pokrzywianka stromatoporoid-coral bioherms, mapped by Czarnocki (1950, pl. 10), were 250 to 380 m long and up to ca. 20 m thick (see description of the 9 m thick succession in Zatoń *et al*., 2022).

The Early–Middle Givetian eustatic lowstand and cooling interlude in the Devonian greenhouse climate, involving an estimated temperature drop below 26 ºC or only below 34 ºC in tropical sea-surface temperatures, according to Scotese *et al*., 2021 and Grossman and Joachimski, 2022; respectively (Fig. 7D, E), most likely limited the efficiency of the tropical carbonate factory (see review in Reijmer, 2021). A key depositional role was played by build-ups, colonised by diverse massive and branching corals, stromatoporoids and crinoids (see Fig. 27), with only a small contribution

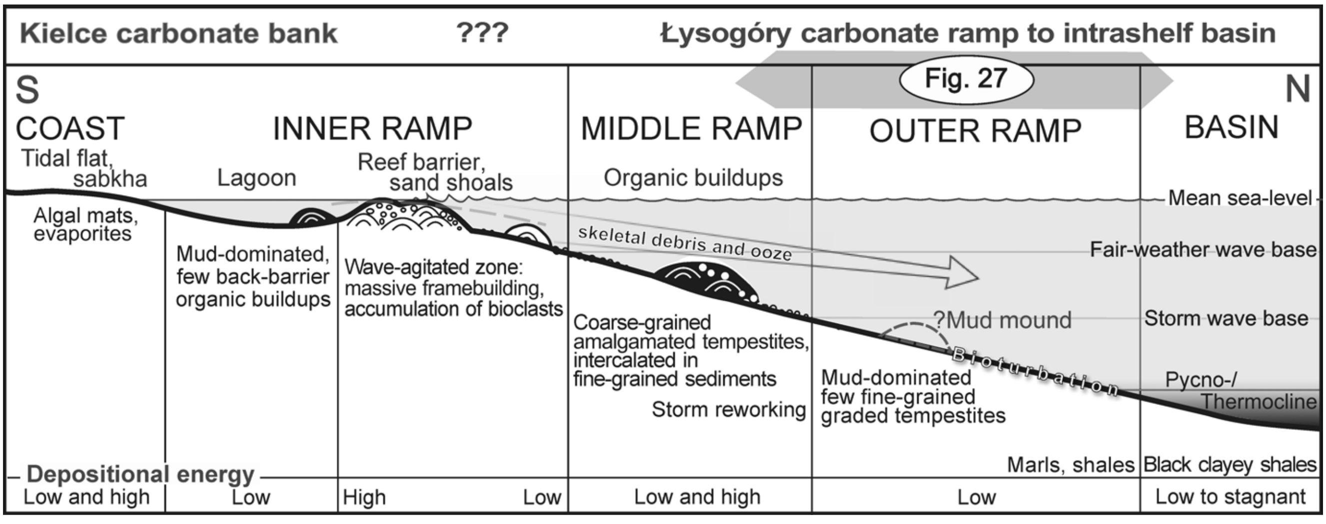


Fig. 10. A generalized framework of the carbonate ramp system (fig. 12 in Pisarzowska *et al.*, 2022; based on Flügel, 2010, figs 2.7 and 14.3, and box 2.4), adapted to the Holy Cross shelf domain by highlighting a depositional role of stromatoporoid-coral skeletal reefs (sensu Riding, 2002). The homoclinal slope profile is greatly exaggerated. Compare also Figure 27.

of microbial communities. The episodically eroded shoals, evidenced by coral intrabiorudites in subset M1-Ib (Fig. 4C, D) could have been affected sporadically by violent storms or tsunamis, evidenced in on-shore deposition of stromatoporoid rubble in the nearby Kielce biostromal bank (Łuczyński, 2022; see further discussion by Pisarzowska *et al.*, 2022).

Platy tabulates (alveolitids and coenitids) in the M0 section (layer 9) represent pioneer colonization by typical mesophotic faunas (Zapalski *et al.*, 2017; see below). A more diverse biota characterised M1-IIa biostromes, including also bulbous and thin branching tabulates, and differentiated rugosans (Zatoń and Wrzołek, 2020). The pioneer reef communities record an arrested ecological succession in the hostile muddy conditions (Copper, 1988; see also Wendt *et al.*, 1997; Jakubowicz *et al.*, 2019). However, no preceding stabilizing carpet by crinoid clusters is observed, as well as the flanking encrinites expected in rubble-like deposits of set M1-I. Similar examples are known as an incipient organic building on the drowned *Stringocephalus* biostromal bank in result of the Middle Givetian Taghanic (IIa) transgression (Fig. 7D). The marly tabulate biostromes occur commonly in the basal Laskowa Góra Beds, that passed laterally into the Kadzielnia-type mounds (Racki *et al.*, 1985; Baliński *et al.*, 2016; Zapalski *et al.*, 2017), but also developed in the Upper Givetian of the Kielce platform (*Alveolitella fecunda* assemblage; Racki 1993, fig. 29). Hence, it is likely that typical mud mounds occur in the Skały Fm. (Fig. 10).

Soft-bottom habitats of the Łysogóry outer ramp were successfully colonised by a variety of mostly low-diversity brachiopod communities of BA 3 and likely BA 4 biofacies of Boucot (1975; Brachiopodetum in Fig. 27B, see below). A rich shelly benthos thrived in niches related to the tabulate biostrome (set M1-IIa, Baliński and Halamski, in press). The bottom-level faunas, along with tiny bryozoan thickets and crinoid clumps, developed probably in generally oxic and eutrophic regimes, as indicated by geochemical proxies and rich mud-feeding infauna (Pisarzowska *et al.*, 2022).

The ramp-type successions graded upward into the margin zone of a medium-sized deltaic system, recorded in the mudstone-sandstone Świętomarz Beds (Malec, 2012; Zatoń *et al.*, 2022; Fig. 8). The Middle Givetian event likely resulted from a tectonic activation (in western Volhynia?; Kuleta and Malec, 2015) and/or climatic change (Czarnocki, 1950; Kłossowski, 1985; Malec, 2012), paired with the pre–IIa sea-level fall (Narkiewicz *et al.*, 2011). However, Brett *et al.* (2011) proposed that sea-level changes in the regressive time interval were more fluctuating (Fig. 7D; compare Turnau and Racki, 1999, fig. 8). The ecological changes in pelagic biota, promoted by the prograding delta front in the Łysogóry Basin, are explained by the occurrence of low-salinity proximal watermasses in the estuarine-type circulation, as proposed for the Givetian Hamilton-Tully biofacies relations in the Appalachian Basin (Brett *et al.*, 2007, 2009; Zambito *et al.*, 2012; see fig. 13 in Pisarzowska *et al.*, 2022).

In summary, the Skały Fm represents an overall stable tropical carbonate factory during the Late Eifelian to Middle Givetian timespan, as manifested also in carbon isotope data (Pisarzowska *et al.*, 2022). More generally, this time interval corresponded to a relatively undisturbed global ecosystem and eco-evolutionary stasis between the Kačák and Taghanic crises (Walliser, 1996; Becker *et al.*, 2016, 2020), marked by regional biodiversification episodes, as visible, among other events, in the Eifel Mts succession (Struve, 1963; May, 1992; see below). Only two somewhat enigmatic acme or mass killing *pumilio* bio-events are referred to this timespan (Fig. 7C; Becker *et al.*, 2020, p. 763), recorded in spectacular brachiopod-styliolinid coquinoid accumulations, reported from Germany, southern France, and Morocco (Lottmann, 1990; Jansen *et al.*, in press). However, similar event horizons have not been found so far in the entire Holy Cross Mts (see a possible styliolinid signature after Woroncowa-Marcinowska, 2012, p. 359). Such an absence can be interpreted as corresponding either to (1) the deposits intersecting not the actual transects M1–M3 and M0, or (2) to the events not affecting this particular local-scale area at all (as for example in time-equivalent Hamilton Group deposits in New York; Brett *et al.*, 2007, 2009; see an expanded summary in Pisarzowska *et al.*, 2022).

OVERVIEW OF THE BIOTA

Generalities

During the investigations of sections M0 to M3 at Miłoszów, the presence of the following groups was noted:

1. Amoebozoa: foraminifers;
2. Fungi (unidentifiable fragments of hyphae of terrestrial fungi);
3. Animals: sponges, rugose and tabulate corals, medusozoans, microconchids and cornulitids, polychaetes (scolecodonts), molluscs, arthropods (trilobites and ostracods), bryozoans, hederelloids, ascodictyids, brachiopods, echinoderms (mostly crinoids, rare echinoids, holothurians, and ophiocistoids), conodonts, and fish;
4. Plants (prasinophytes, chlorophytes, and spores of land plants);
5. Acritarchs (palynomorphs *incertae sedis*) and chitinozoans (microfossils *incertae sedis*; both see below under Marine microbiota).

Of these, selected groups have received detailed taxonomic investigation, either in the present monographic issue (foraminifers: Gajewska, 2022; brachiopods: Baliński and Halamski, in press) or elsewhere (palynomorphs: Kondas and Filipiak, 2022; bryozoans: in progress) and the results of these investigations are only briefly summarised below. Other groups are treated in more detail here, including complete lists of taxa. A few groups (fungi, scolecodonts, chitinozoans) are only noted as present in the sections studied without any detailed investigation.

The institutional abbreviations are: GIUS, Institute of Earth Sciences, University of Silesia in Katowice, Sosnowiec. MWGUW, S. J. Thugutt Geological Museum, Faculty of Geology, University of Warsaw. ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Foraminifera

Foraminifers are protists belonging to the supergroup (Kingdom) Rhizaria (Pawlowski, 2014) that have an exceptionally good fossil record (e.g., Loeblich and Tappan, 1964). At Miłoszów, they have been revealed in beds 4, 5, 7, 8, and 9 of section M0 and, subordinately, in the lower part of the shales in the M1 section (M1-IIa). They are described in detail in a separate paper (Gajewska, 2022).

Foraminifers and foraminifer-like fossils are represented by: (i) true calcareous plurilocular biserial and fan-shaped members of the Semitextulariidae Pokorný, 1956 [*Semitextularia thomasi* Miller and Carmer, 1933; *S. oscoliensis* Bykova, 1952; *Cremsia proboscidea* (Cushman and Stainbrook, 1943); and *Pseudopalmula palmuloides* Cushman and Stainbrook, 1943; Fig. 11]; (ii) bilocular and tubular forms of the family Moravamminidae Pokorný, 1951a (*Moravammina segmentata* Pokorný, 1951a; *Vasicekia moravica* Pokorný, 1951a and *Vasicekia* sp.); and (iii) foraminifer-like forms of uncertain affinities representing at least six taxa. These foraminifer-like forms are the dominant group in the microfossil assemblages studied, whereas the species *M. segmentata* and *S. thomasi* are the most common taxa among the (fossil) foraminiferal communities. Despite minor quantitative differences throughout section M0 analysed in detail, the microfossil assemblages studied appear to be rather stable, without any significant quantitative or qualitative changes.

The microfossil record of the M0 and M1 sections is unique, insofar as it yielded an exceptionally well-preserved mid-Devonian foraminiferal community, rarely described from elsewhere, which provides a valuable insight into a significant evolutionary event, termed the foraminiferal "Givetian Revolution" (Vachard *et al.*, 2010; Vachard, 2016). The mid-Devonian is regarded as one of the most important phases of the evolutionary history of foraminifers. It comprises the origin of true calcareous plurilocular forms and was probably linked with the evolutionary development of the main Recent foraminiferal clades (Pawlowski *et al.*, 2003, 2013; Dubicka and Gorzelak, 2017), as well as of some extinct groups of Foraminifera (Dubicka *et al.*, 2021a).

The Eifelian–Givetian radiation might have been linked with the development of foraminiferal symbiosis with microalgae or by sequestering plastids (kleptoplasts) of digested algae, what enabled foraminifera to stay photosynthetically active and largely benefit from the photosynthetic process (Dubicka *et al.*, 2021b). Such behaviour is a significant advantage for continued growth, the survival of the hosts, and the enhancement of foraminiferal calcification (Prazeres and Renema, 2019).

The Mid-Devonian multichambered foraminifera settled in carbonate platforms that developed in shallow, warm, and high calcium carbonate precipitation environments, namely in stromatoporoid-coral build-ups, that constituted a unique ecosystem in geological history (Racki and Soboń-Podgórska, 1993; Vachard *et al.*, 2010). The strong connection between the foraminifera and the environment they inhabited is confirmed by their joint disappearance during the Frasnian–Famennian biotic crisis (Ross and Ross, 1991; Vachard *et al.*, 2010; Dubicka, 2017).

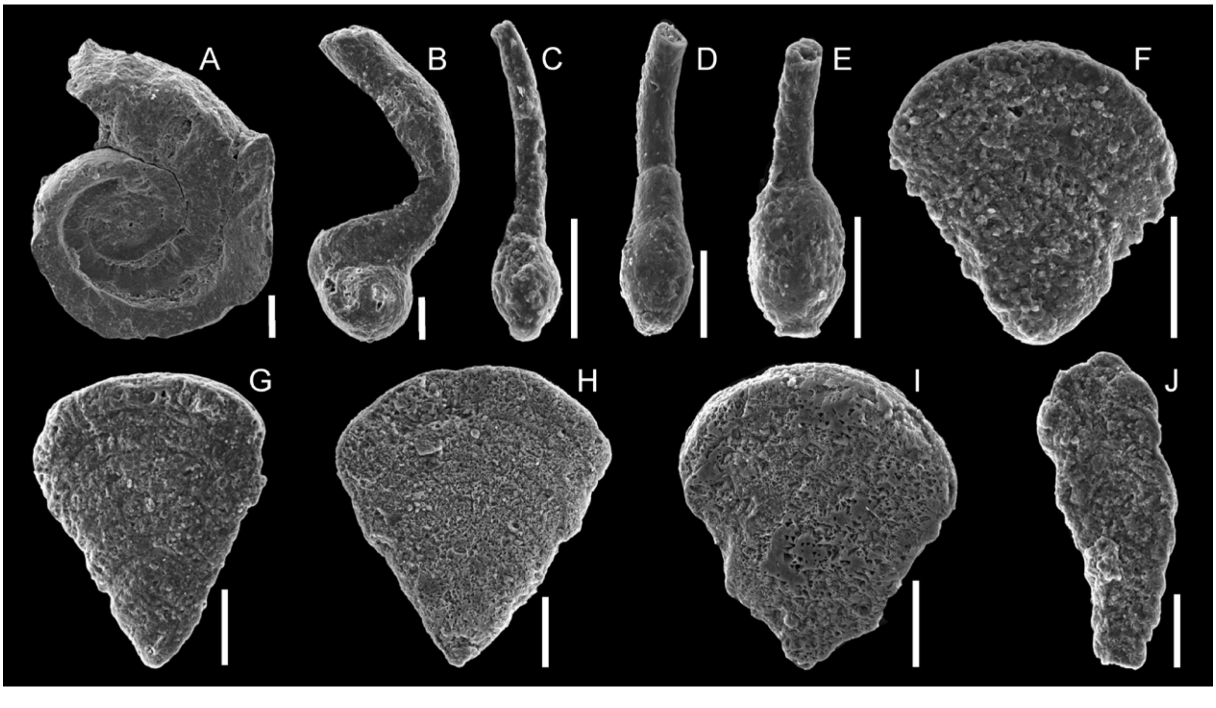


Fig. 11. Selected Givetian Foraminifera from section M0 at Miłoszów. **A, B.** *Moravammina segmentata* Pokorný, 1951. Specimens MWGUW ZI/67/83.02 (A), ZI/67/83.15 (B). **C–E.** *Vasicekia moravica* Pokorný, 1951. Specimens MWGUW ZI/67/83.20 (C), ZI/67/83.01 (D), ZI/67/83.17 (E). **F.** *Semitextularia oscoliensis* Bykova, 1952. Specimen MWGUW ZI/67/83.07. **G–I.** *Semitextularia thomasi* Miller and Carmer, 1933. Specimens MWGUW ZI/67/83.05 (G), ZI/67/83.21 (H), ZI/67/83.22 (I). **J.** *Cremsia proboscidea* (Cushman and Stainbrook, 1943). Specimen MWGUW ZI/67/83.04. All figures are SEM images. All scale bars 100 µm.

Marine microbiota (*Rothpletzella*, phytoplankton, chitinozoans, and scolecodonts)

Representatives of *Rothpletzella* Wood, 1948 are encrusting microfossils, known from the Silurian to the Devonian, which used to be interpreted either as cyanobacteria (Wood, 1948), algae (Johnson, 1964), or microproblematica (Riding and Soja, 1993). Recently, it was proposed that *Rothpletzella* likely belonged to the chlorophycophytan order Bryopsidales (Zatoń and Jarochowska, 2020). They were revealed as epibionts on rugose corals from the M1 section (Zatoń and Wrzołek, 2020).

All samples contained diversified assemblages of marine palynomorphs; 21 phytoplankton species were documented, the most abundant genera being *Gorgonisphaeridium* Staplin, Jansonius and Pocock, 1965 (4 species) and *Polyedrixium* Deunff ex Deunff, 1961a (5 species; Fig. 9O). The former genus belongs to the acritarchs (organic microfossils *incertae sedis*), whereas the other is a prasinophyte (paraphyletic group of planktonic unicellular chlorophytes, i.e., green algae excluding streptophytes). A new genus and species of acritarchs, *Teleostomata rackii* Kondas, Filipiak and Breuer, 2021, was described from the M2 and M0 sections (Fig. 9S). A full treatment of palynomorphs is given elsewhere (Kondas and Filipiak, 2022); note that numbers of beds in the M2 section are different in that paper.

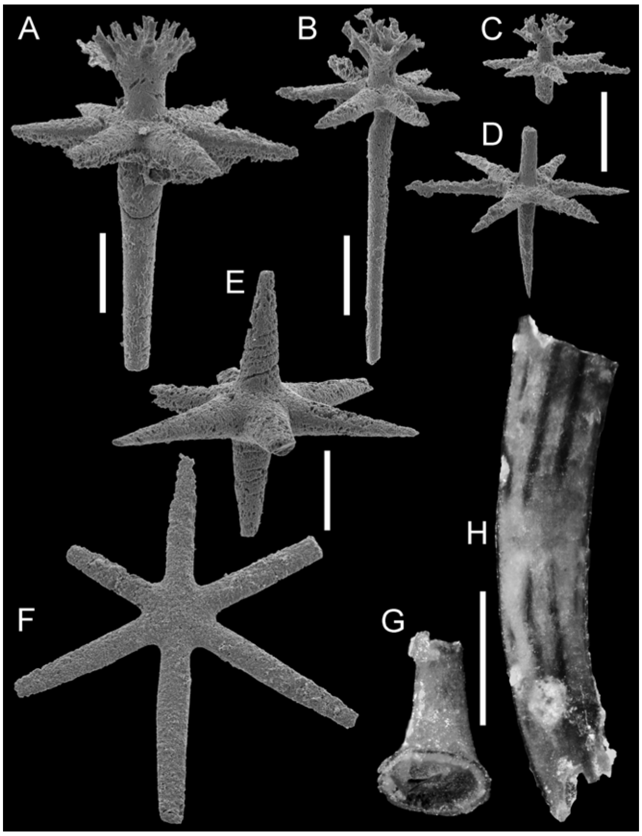


Fig. 12. Metazoan-related microfossils from limestone intercalations within the Skały Fm at Miłoszów. **A–F.** Isolated octactinellid sponge spicules; M0 outcrop. **G, H.** Phosphatic tubes of the medusozoan cnidarian *Sphenothallus* sp.; M2 outcrop; G – proximal (basal) part of the tube; H – partly translucent tube revealing internal septa-like structures (darker lines); M2 outcrop. Scale bars 500 µm.

Chitinozoans are organic-walled marine microfossils of uncertain affinities, the most frequently cited hypotheses being metazoan eggs (e.g., Gabbott *et al.*, 1998) and protists (e.g., Liang *et al.*, 2019). Chitinozoans belonging to the families Desmochitinidae Eisenack, 1931 and Lagenochitinidae Eisenack, 1931 are present in sample M2α. This is the first report of the group from the Givetian of Poland.

Scolecodonts are the jaws of polychaete annelids. Their infrequent presence (Fig. 9M) was noted in each studied sample except M2δ.

Terrestrial palynomorphs

Plant microfossils, representing terrestrial vegetation, were recovered from sections M0, M1 and M2. They represent a taxonomically differentiated assemblage, 57 taxa in total. As a whole, the assemblage is similar to those reported from the Givetian of central and east Europe (see Avkhimovitsch *et al.*, 1993; Turnau and Racki, 1999; Telnova, 2007). Among the terrestrial palynomorphs, the lycophyte spore genus *Ancyrospora* Richardson, 1960 (10 species; Fig. 9P), as well as the progymnosperm spore genera *Aneurospora* Streel, 1964 (3 species; Fig. 9B, D), *Geminospora* Balme, 1962 (9 species; Fig. 9A, C) and *Rhabdosporites* Richardson, 1960 (2 species; Fig. 9L, U) are the most common. Plant cuticles and tracheids are also present but restricted in number. For the complete characteristics of the palynomorph assemblage see Kondas and Filipiak (2022); note that numbers of beds in the M2 section are different in that paper.

The Middle Devonian terrestrial vegetation is difficult to characterise in brief, as strong regional and local variation occurred (Retallack and Huang, 2011). Trees existed already in the Givetian (Stein *et al.*, 2012) and large areas of land started to be covered by plant communities, but this may not have applied to highlands or drier habitats (Cleal, 2021). The study of land vegetation is beyond the scope of the present paper.

Sponges

Sponges are known from the M1 section as epibiontic stromatoporoids and as isolated spicules of octactinellides. Neither has been investigated in detail.

Solitary rugosans recovered from the shaly part of outcrop M1 (M1-IIa) are overgrown by epibiontic, laminar stromatoporoids (Zatoń and Wrzołek, 2020).

In the same strata, rare astrose spicules (octactines) were recovered from the limestone residues dissolved for conodonts. This morphology is diagnostic for the order Octactinellida Hinde, 1887 (pers. comm. A. Pisera, 2021), belonging to the extinct class Heteractinida de Laubenfels, 1955 (see Termier *et al.*, 1978; Pickett, 2002; Rigby, 2003; Finks and Rigby, 2004; Hooper *et al.*, 2011). Three morphotypes of probably originally calcitic spicules may be distinguished:

1. Octactines with secondary rays on the distal ray (Fig. 12A–C), similar to those found in *Ensiferites;*
2. Octactines with a simple distal ray (Fig. 12D, E);

3. Octactines lacking both proximal and distal rays (Fig. 12F).

It is unclear how many species these morphotypes may represent (see e.g., Kučera, 1993). Similar spicules were reported from the Givetian and Frasnian of the Holy Cross Mountains and adjacent areas by Hurcewicz (1993), according to whom a "prolific development of calcareous octactinellids was typical of the vast Late Givetian to Early Frasnian sea-shelf of the Holy Cross Mountains" (Hurcewicz, 1993, p. 294).

Rugose corals

Rugose corals were recovered almost solely from the M1 section, where several hundred specimens representing 10 species were collected. The systematic treatment of the material will be published separately. Two poorly preserved small solitary rugosans were recovered from the M3 section.

Within the M1 section, corals were recovered from the upper part of the limestone unit (M1-Ib) and from the lower part of the overlying shales (M1-IIa). The M1 assemblage contains:

– few massive colonies of *Cyathophyllum tabulatum* Quenstedt, 1878 (Fig. 13A);
– abundant *Heliophyllum* sp. (Fig. 13F), solitary, but numerous specimens with offsets;
– dendroid colonies of *Thamnophyllum skalense* Różkowska, 1956 – including many isolated broken branches (Fig. 13 J, K);
– and the solitary *Stringophyllum buechelense* (Schlüter, 1889; Fig. 13B), *S. acanthicum* (Frech, 1885; Fig. 13C), *Acantophyllum* ex gr. *radiatum* (Wedekind, 1924), *A. concavum* (Walther, 1928; Fig. 13G), *Cystiphylloides macrocystis* (Schlüter, 1889; Fig. 13I), *C. secundus* (Goldfuss, 1826; Fig. 13H), *Mesophyllum* ex gr. *maximum-cristatum* (Frech, 1885; Fig. 13D), and ?*Ceratophyllum* cf. *typus* (Gürich, 1896; Fig. 13E).

The rugose corals of these two assemblages can be classified within 6 morphological groups:

1. Cystimorphs (*Cystiphylloides, Mesophyllum*), characterised by the underdevelopment of the septal apparatus but a variable diameter, and complexity of internal structure;
2. Solitary forms with long septa and wide and complex dissepimentarium (*Acanthophyllum, Heliophyllum*), commonly of large diameter;
3. Small ceratoid or cerato-cylindrical solitary forms with thickened septal apparatus (*Stringophyllum*);
4. Solitary cylindrical forms with relatively wide tabularium (*?Ceratophyllum*);
5. Dendroid colonial form (*Thamnophyllum*), and
6. Massive colonial form (*Cyathophyllum*).

The first two categories represent about one-third of the assemblage each and dominate both in number of specimens and in taxonomic diversity. It has to be noted that the proportions given here are significantly different from those reported by Zatoń and Wrzołek (2020) as the latter counted isolated fragments of *Thamnophyllum* colonies as separate specimens.

The morphological groups listed above reflect various ecological strategies of growth and adaptations to different micro-environments. Colonial *Heliophyllum* and massive colonies of *Cyathophyllum* indicate optimum conditions for coral development, constant supply of food particles and moderate to high wave activity in clear-water settings. On the other hand, one of the three *Cyathophyllum* colonies collected displays distal contraction of numerous corallites, thus indicating mud fouling, possibly resulting from seasonal or occasional influx of fine-grained sediment. The large solitary corals (solitary *Heliophyllum*, *Acanthophyllum*) indicate a slightly deeper setting, still with abundant food, but with weak water movement. The typically straight-conical shape of coral skeletons, including smaller solitary corals, such as *Stringophyllum*, is noteworthy, indicating undisturbed growth on the seafloor; curved corallites are rare. Cystimorph rugosans (*Cystiphylloides* and *Mesophyllum*) most likely preferred quiet and often muddy environment, though they are ubiquitous and may also occur in more dynamic environments (Pedder, 1999). The dendroid phillipsastraeid, *Thamnophyllum*, indicates quiet conditions, but the abundance of broken branches and corallites possibly reflects fragmentation of colonies during occasional hydrodynamic events (storms). Nevertheless, there are no traces of extensive abrasion on the fragments.

The co-occurrence of these micro-environments in the same beds and lack of traces of abrasion indicate a (limited) post-mortem transportation of the corals and/or time-averaging of the assemblage. The idea of some mixing of faunal components has been confirmed by M. Rakociński (pers. comm., 2021), who noted differences between the sediment, filling the internal voids in fossils, and the rock matrix in some coral-bearing samples from M1-Ib. Hence, corals, which initially grew on a shallow platform were redeposited into slightly deeper settings, where micrite dominated.

The absence of representatives of the *Cyathaxonia*-fauna corals at M1 is noteworthy. They are small, undissepimented solitary forms, predominating in turbid or deeper offshore settings (Wrzołek, 1999).

The studied corals represent mostly the widely distributed Old World coral fauna; on the other hand, the siphonophrentids, noted in an earlier study of Miłoszów rugosans (Wrzołek, 2002), but also zaphrentids *Heliophyllum*, indicate invasion of elements of Eastern North America Realm (Oliver and Pedder, 1989) into the Old World Realm, in particular into the Holy Cross Mts. Jamart and Denayer (2020) interpreted this arrival of exotic fauna as marking the Kačák biotic Event. The occurrence of eastern North American rugosan taxa at Miłoszów is an argument for the horizon studied being not older than the Late Eifelian Kačák Event (*ensensis* conodont Zone, directly below the Eifelian–Givetian boundary).

Tabulates

Tabulates were recovered from the M0 and M1 sections; they are absent in the M2 and M3 sections. They are discussed briefly below in chronological order. Species reported from Miłoszów by Stasińska (1958, p. 169) probably represent a mixed assemblage, corresponding to M1-I and M1-IIa of the present authors.

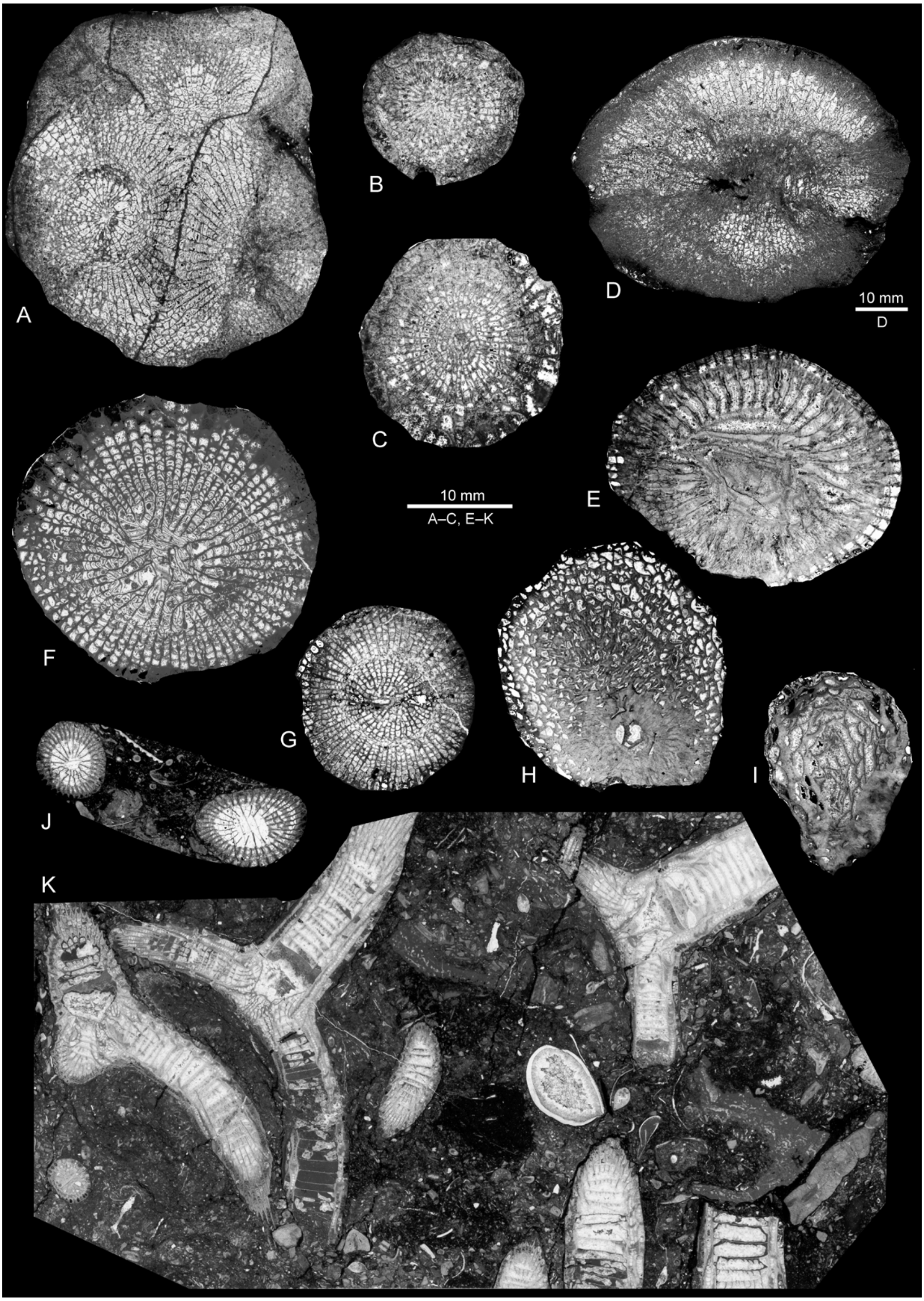


Fig. 13. Givetian rugose corals from section M1 at Miłoszów (A: M1-Ib; B–K: M1-IIa; see also Fig. 4C, D). **A.** *Cyathophyllum tabulatum* Quenstedt, 1878, specimen GIUS 422 MI w08, cut at the base of the colony. **B.** *Stringophyllum buechelense* (Schlüter, 1889), GIUS 422 MI w01. **C.** *Stringophyllum acanthicum* (Frech, 1885), GIUS 422 MI z17. **D.** *Mesophyllum* ex. gr. *maximum-cristatum* (Frech, 1885), GIUS 422 MI w15. **E.** ?*Ceratophylum* cf. *typus* (Gürich, 1896), GIUS 422 MI z55. **F.** *Heliophyllum* sp., GIUS 422 MI w06 (note that this specimen has offsets in its distal parts). **G.** *Acanthophyllum concavum* (Walther, 1928), GIUS 422 MI z26. **H.** *Cystiphylloides secundus* (Goldfuss, 1826), GIUS 422 MIz108. **I.** *Cystiphylloides macrocystis* (Schlüter, 1889), GIUS 422 MI z43. **J, K.** *Thamnophyllum skalense* Różkowska, 1956, GIUS 422 MI w06 (J); GIUS 422 MI w13_2 (K).

The M1-I assemblage consists of rare, moderately large (~ 15 cm) massive colonies of *Favosites*. The presence of such massive forms, combined with lack of platy, foliose and branching corals, may indicate very shallow environments (Hallock and Schlager, 1986; Król *et al.*, 2018). The apparent lack of any other forms makes it different from other known shallow-water coral assemblages of that age (Król *et al.*, 2021; Zapalski *et al.*, 2021).

The M1-IIa assemblage is represented by small (up to 3.8 cm, usually smaller), bulbous *Favosites goldfussi* d'Orbigny, 1850, which most likely were autorotative colonies (coralliths; Zapalski *et al.*, 2022). These anthozoans are interpreted as having lived in a relatively deep, fore-reef environment; a modern analogue from a reef channel 28 m deep was found (Zapalski *et al.*, 2021). Small, platy alveolitids are also present, together with thin branching pachyporids (*Striatopora*) and coenitids (*Coenites*). Both the upper and lower surfaces of platy tabulates are overgrown by epibiont-auloporid tabulates and bryozoans. Tabulates encrust also solitary rugose corals – these epibionts include representatives of the genera *Alveolites* and *Aulopora*. This assemblage is somewhat different from the typical Devonian mesophotic assemblages that usually lack autorotative forms and are strongly dominated by platy and branching corals (Zapalski *et al.*, 2017; Majchrzyk *et al.*, 2022).

The M0 assemblage (mostly recovered from bed 9) consists of platy alveolitids and coenitids, mostly representatives of *Alveolites, Roseoporella* and *Platyaxum* (Fig. 14). These colonies exclusively show proportions exceeding 1:4 (length-to-thickness) ratio, and nearly all observed fragments possibly exceed 1:10; the preserved fragments exceed 10 cm in length. Other morphologies of colonies are absent. Such dominance of platy corals is also unusual for the Devonian mesophotic coral ecosystems (MCEs; Zapalski *et al.*, 2017), where branching forms also are common, but it is similar to Silurian MCEs, known from the Baltica shelf (Zapalski and Berkowski, 2019), where branching forms may be nearly absent in some places.

In both the M1-IIa and M0 assemblages, the diversity of platy corals is low, indicating that they lived in the lower euphotic zone (for discussion see Zapalski *et al.*, 2017). While both represent typically mesophotic faunas (Kahng *et al.*, 2012; Zapalski *et al.*, 2017; Zapalski and Berkowski, 2019), they might differ in bathymetry, owing to differences in the optical quality of water (Kahng *et al.*, 2010). This is also emphasised by the presence of autorotatory forms, linked with strong bottom currents, in M1-IIa (Zapalski *et al.*, 2021), whereas such forms are absent in M0. The coral assemblages indicate that they both represent habitats marginal for reef development (see Renema, 2019 for discussion), and potential bathymetric difference cannot be inferred from analysis of the coral assemblage. Coral assemblages with mesophotic features are known both from very shallow, turbid environments (Santodomingo *et al.*, 2016; Zapalski *et al.*, 2021), and very deep, clear-water habitats (e.g., Kahng *et al.*, 2010; Renema, 2019; Muir and Pichon, 2019), yet the shallow water faunas usually contain also other growth forms (Zapalski *et al.*, 2021; Król *et al.*, 2021; Huang *et al.*, 2020). Thus, the situation at Miłoszów rather may correspond to deep-water "blue mesophotic" environments than to relatively shallow-water "brown mesophotic". The collected material, however, does not allow a clear distinction between the two.

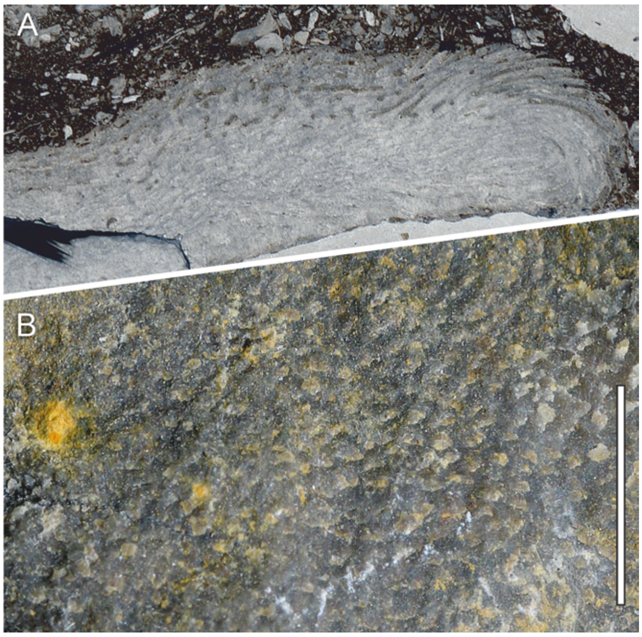


Fig. 14. Givetian mesophotic tabulate coral *Roseoporella* sp. from bed M0-9 at Miłoszów. **A.** Thin section. **B.** Corallum surface with corallites visible. Scale bar (both photographs) 5 mm.

Medusozoan cnidarians

Phosphatic tubes of the medusozoan cnidarian *Sphenothallus* Hall, 1847 were recovered from outcrop M0 (Fig. 12G, H). Although *Sphenothallus* has been reported from rocks ranging from the Early Cambrian (Muscente and Xiao, 2015) to the Late Carboniferous (Lerner and Lucas, 2011) in age, its internal septa-like structures were revealed only recently on the basis of specimens coming from Ordovician, Silurian and Early Devonian strata (Dzik *et al.*, 2017). Here the authors document the occurrence of the Givetian *Sphenothallus*, with clearly visible septa-like structures in partly translucent proximal regions of the tubes. As in the Ordovician representatives of the genus, these septa are arranged in rows, oblique to the tube axis (Fig. 12H).

Gastropods

Gastropods occur mostly in the upper (shaly) part of outcrop M1 (M1-II). This rather low-diversity gastropod association (collection number: ZPAL V.74/Ga/1–8) comprises eight taxa. A single specimen of *Platyceras* sp. was found in limestone M3-7.

The material from the shale M1-IIa consists of internal moulds (86 specimens); given that gastropod taxonomy is based largely on shell characters, moulds are specifically unrecognizable and are described below under informal morphotype names:

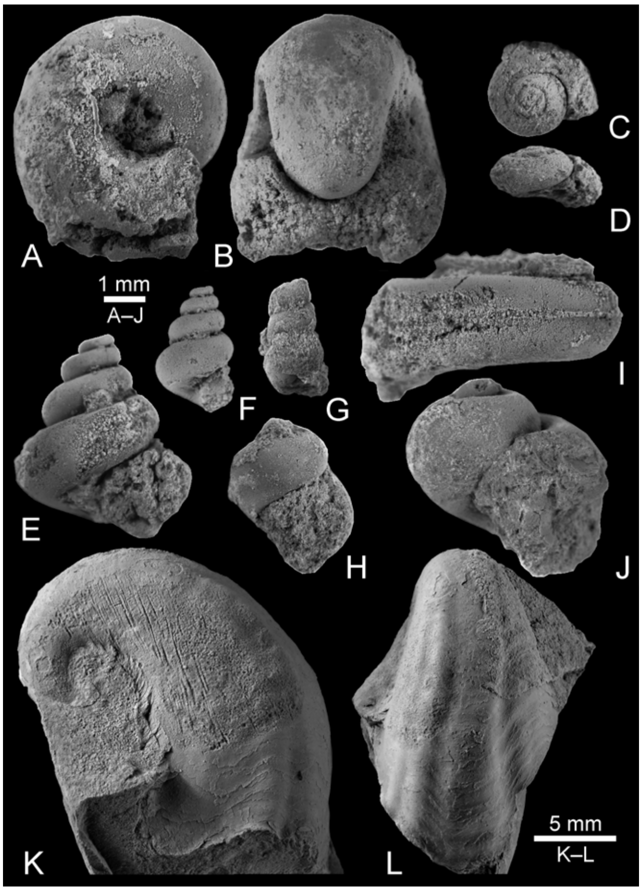


Fig. 15. Internal moulds of Givetian gastropods from Miłoszów (A–J, M1-IIa; K–L, M3-7). **A, B.** Lateral (A) and apertural (B) views of a bellerophontid (ZPAL V.74/Ga/6/1). **C, D.** Apical (C) and apertural (D) views of rotelliform morphotype (ZPAL V.74/Ga/3/1). **E.** Apertural view of trochiform morphotype (ZPAL V.74/Ga/4/1). **F.** Apertural view of turbiniform morphotype (ZPAL V.74/Ga/1/1). **G.** Fragment of a spire of turriculate morphotype (ZPAL V.74/Ga/8/1). **H.** Apertural view of fusiform morphotype (ZPAL V.74/Ga/5/1). **I.** Lateral view of discoidal morphotype (ZPAL V.74/Ga/7/1). **J.** Apertural view of naticiform morphotype (ZPAL V.74/Ga/2/1). **K, L.** *Platyceras* sp., ZPAL V.74/Ga/9/1, apical (K) and lateral (L) views. All specimens coated with ammonium chloride.

- turbiniform morphotype, the most common (26 specimens, 26/86 ≈ 30%), with a clearly rounded base of shell, the height of which reaches 3 mm (ZPAL V.74/Ga/1/1–26; Fig. 15D);
- naticiform morphotype, also relatively numerous (19 specimens, 19/86 ≈ 22%), with spherical shells up to 8 mm high, probably belonging to the cosmopolitan naticopsids (ZPAL V.74/Ga/2/1–19; Fig. 15H);
- rotelliform morphotype (13 specimens; ZPAL V.74/Ga/3/1–13; Fig. 15B) having lenticular shells up to 3 mm wide;
- trochiform morphotype (11 specimens; ZPAL V.74/Ga/4/1–11; Fig. 15C), the shells of which measure up to 7 mm, high have a slightly more flattened base of shell;
- fusiform morphotype (7 specimens; ZPAL V.74/Ga/5/1–7; Fig. 15F), with poorly preserved internal moulds, mostly without spires;
- planispiral moulds of bellerophontids (5 specimens; ZPAL V.74/Ga/6/1–5; Fig. 15A) characterised by symmetrical involute shells up to 7 mm high;
- discoidal morphotype (3 specimens; ZPAL V.74/Ga/7/1–3; Fig. 15G) with a pronounced keel at the periphery of the whorl, probably belonging to the euomphalids; and
- turriculate morphotype (2 specimens; ZPAL V.74/Ga/8/1–2; Fig. 15E), represented only by spire fragments.

A single shell of *Platyceras* sp. (Fig. 15K, L) was revealed from limestone in the M3 section (M3-7). Representatives of this characteristic gastropod genus are most probably crinoid parasites (Bowsher, 1955; Baumiller, 2003).

No Givetian gastropods of the Łysogóry Region of the Holy Cross Mountains were described up to now. Middle Devonian gastropods, represented by two species [*Raphistoma bronnii* (Goldfuss, 1844) and "*Turbo*" *scalensis* Sobolew, 1904 in 1903–1904], were described only from the Eifelian deposits of the Skały section (Sobolew, 1903–1904; Halamski, 2002, pl. 1, fig. 5). However, they occur as accompanying fauna in Givetian carbonate rocks of the Kielce Region. The most diverse gastropod association (10 taxa) is found at Jurkowice-Budy. In three other sites, the taxonomic diversity is clearly low (Góra Zamkowa – 3 taxa, Wymysłów – 2, and Jaźwica – 2; Karczewski, 1989; Krawczyński, 1999; Krawczyński *et al.*, 2003). Givetian gastropods were also described from Dębnik, near Kraków (12 taxa; Gürich, 1903; see also Krawczyński *et al.*, 2003).

Rich Givetian gastropod associations were described from the Rhenish Mountains. The gastropod association, characterised by the highest diversity, is from Hahnstätten (see Heidelberger, 2001) and includes 55 taxa representing the reef environment and 15 lagoon-dwelling taxa. Highly diverse associations were also identified at Frettertal (41 taxa; Heidelberger, 2008), Villmar (36 taxa; Heidelberger, 2001), and Sötenich (35 taxa; Heidelberger, 2001, 2007). A low-diversity gastropod association was described from Elbingerode in the Harz Mountains (8 taxa; Krawczyński, 2001). Given the state of preservation of the material described here, no comparison other than that of the numbers of taxa present is feasible.

Middle Devonian gastropods were relatively highly diversified, mainly in reef environments. They were also present, even if in smaller numbers of taxa, in lagoon and open marine environments. From the taxonomic point of view, they mostly belong to extinct orders. The most frequent lifestyle among Middle Devonian gastropods was probably herbivorous and benthic.

Bivalves and rostroconchs

The upper (shaly) part of outcrop M1 (M1-II) yielded also a small sample of bivalves and rostroconchs. This collection was lost in transit after preliminary photographs were made and the study was completed, but before the preparation of definitive photographs. The Figures 16, 17 are thus given on the basis of preliminary (uncoated) images.

Bivalves, generalities. The bivalve assemblage is of very low diversity and composed of few nuculoid Palaeotaxodonta and one specimen of probable heterodont assignment. If compared with other contemporaneous assemblages from the southern Laurussian shelf, they are remarkably underrepresented. Although several studies focussed on Palaeozoic palaeotaxodonts, taxonomy and systematics are still unsolved, mostly because of the lack of well-preserved material. Many taxa are devoid of characteristic external morphology; modern nuculid taxa can be identified only by analysis of the periostracum, not preserved in fossil specimens.

Material and preservation. Nine specimens only were sampled from the Miłoszów section, most of which are preserved as steinkerns in a bivalved condition.

Morphology and taxonomy. Conventionally, smooth, triangular Devonian nuculids are assigned to the genus *Nuculoidea* Williams and Breger, 1916. *Nuculoidea lirata* (Conrad, 1842) is one of the most cited nuculoid species of the Devonian, but generic and species concepts are variable and imprecise. Post-Devonian taxa are classed with *Nuculopsis* Girty, 1911 (see also discussion in Johnston and Goodbody 1988, p. 340 and Amler, 1996, 2004, p. 157). The only substantial difference between the genera concerns the micropectination on the inner shell margin and a different curvature of the umbo, although overlap within certain species may occur. *Nuculopsis* rarely has been used for Devonian nuculids, except for *Nuculopsis gibbosa* Yang in Pojeta, Zhang and Yang, 1986 (Pojeta *et al.*, p. 62). This name, however, is a junior homonym of *Nuculopsis gibbosa* (Fleming, 1828) from the Early Carboniferous of western Europe and, thus, invalid. Specimens Bi-1, Bi-4, Bi-5, Bi-6, Bi-7 are attributed to nuculoid taxa (Fig. 16A–D).

More or less transversely oval palaeotaxodonts are assigned to the genus *Palaeoneilo* Hall and Whitfield, 1869. Although some species included are remarkably commarginally ribbed, others are relatively smooth. In addition, the characteristic sinus in the posterior margin may be developed rather shallow and, thus, unpronounced. Specimen Bi–3 may be assigned to *Palaeoneilo* (Fig. 16E).

Only one possibly heterodont specimen (Bi-8) in steinkern preservation is present in the small assemblage. The pronounced post-umbonal morphology allows assignment to a heterodont or anomalodesmatan taxon (Fig. 16F).

Life habits and palaeoecology. The bivalve assemblage, though probably incompletely known, agrees well in its composition, life habits and trophic structure with the sedimentological data. The fauna is small in size, thin-shelled and weakly ornamented. Most specimens are preserved articulated; no large, thick-shelled and roughly ornamented epifauna has been found, the latter normally indicative of agitated water conditions and unstable sedimentary environments yielding coarse-grained deposits. Accordingly, the (relatively) high percentage of deposit-feeders correlates with sediment grain size. The Palaeotaxodonta (*Nuculoidea*, *Palaeoneilo*) are commonly regarded as non-byssate, infaunal deposit-feeders, partly siphonate (*Palaeoneilo* sp.), partly non-siphonate (*Nuculoidea* sp.; see Bradshaw, 1999; Amler, 1996, 2004). By analogy with modern protobranchs, they probably ingested organic particles from the sediment with the aid of palp proboscides. In summary, a rather calm, mid-shelf environment is indicated from the bivalve assemblage. The only probable heterodont specimen may have been an infaunal or semi-infaunal suspension feeder and fits into the presumed facies conditions.

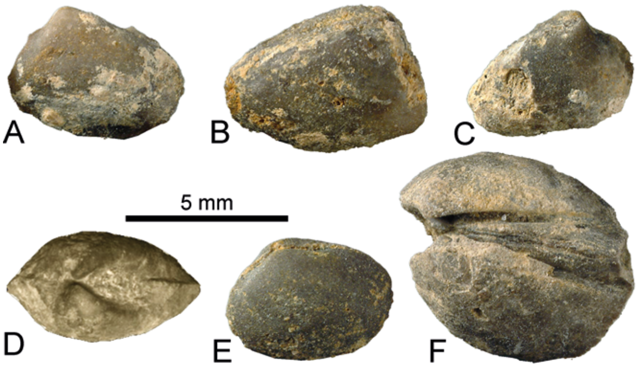


Fig. 16. Givetian bivalves from section M1-IIa at Miłoszów (uncoated specimens, material lost). **A.** *Nuculoidea*? sp., specimen Bi-4, right lateral view. **B.** *Nuculoidea*? sp., specimen Bi-6, left lateral view. **C.** *Nuculoidea*? sp., specimen Bi-1, left lateral view; **D.** *Nuculoidea*? sp., specimen Bi-7, dorsal view; **E.** *Palaeoneilo*? sp., specimen Bi-3, left lateral view. **F.** Heterodont? bivalve, specimen Bi-8, posterodorsal view.

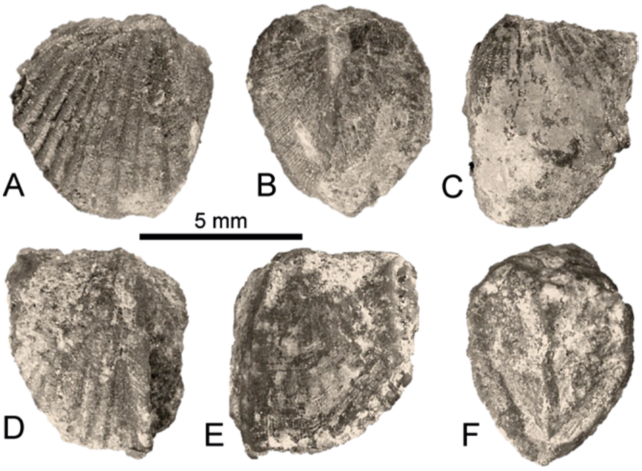


Fig. 17. Givetian rostroconch *Bieberiana* cf. *pugnans* (Whidborne, 1892) from section M1-IIa at Miłoszów (uncoated specimens, material lost). **A, B.** Specimen Ro-9, left lateral (A) and posterior (B) views. **C.** Specimen Ro-10, right lateral view. **D–F.** Specimen Ro-12, left lateral (D), right lateral (E) and posterior (F) views. Note preservation of hood in D–F and reticulate external shell layer in B, E; anterior snout damaged; rostrum broken off.

Rostroconchia, generalities. Rostroconchs are generally a very small component of fossil assemblages but may add useful information to palaeoenvironmental reconstructions, if preserved rather autochthonous. The Miłoszów fauna yields 4 specimens, all of which are fragments.

Material and preservation. Preservation of rostroconchs is quite variable and mostly controlled by shell mineralogy, host rock matrix and permeability, diagenetic processes, etc. Similar to brachiopods, most rostroconchs are preserved with both halves of their conch in the original position and in contact because of the continuous dorsal shell layer (for details see Rogalla *et al.*, 2003; Schröder-Rogalla, 2005; Amler and Rogalla, 2007). Fragile parts of the shell are mostly fragmented; distal parts of the hood, the most anterior portion of the snout as well as the rostrum are often broken off or damaged (Fig. 17A–F), owing to post-mortem transportation. Pre-depositional, syn- and post-diagenetic processes have altered the external shell surface morphology, thus, the four specimens display different modes of preservation.

Nevertheless, reconstruction of the morphology allows their identification at least at the generic level. If compared with the basic morphological characters (see Schröder-Rogalla, 2005; Amler and Rogalla, 2007, 2013; Amler, 2016), the partition into (1) the anterior prolonged snout with the snout gape, (2) the globose, often triangular central body posteriorly truncated, and (3) the flattened posterior rostral area with the tubular rostrum is clearly visible. The additional presence of a hood (French: éventail; German: Schleppe), composed of one shell layer only, which surrounds the rostral area, is preserved in specimens Ro-9 and Ro-12. Specimens Ro-10 and Ro-11 are severely damaged and distorted.

Morphology and taxonomy. Specimens Ro-9, Ro-10 and Ro-12 show the central body of the conch, the transition to the snout, which is broken off, and the rostral area. The rostrum is broken off at its base in all specimens. In all four specimens, the middle shell layer is exposed, showing coarse radial ribs. Additionally, a few parts of the middle layer are covered by the finely reticulate cover of the external shell layer, which is also visible on the rostral area and the fragments of the hood in Ro-12. Specimens Ro-9 and Ro-12 also clearly show that the rostral area occupies almost 100 per cent of the total height of the conch (hippocardiin condition according to Rogalla and Amler, 2006b, p. 347; Fig. 17).

On the basis of the presence of a hood, the specimens are members of the superfamily Hippocardioidea Pojeta and Runnegar, 1976 (but see reservations of Amler and Pfennings, 2019). According to the subdivision of the superfamily into families and subfamilies by Schröder-Rogalla (2005) and Rogalla and Amler (2006a, b), the four specimens can be identified as *Bieberiana* cf. *pugnans* (Whidborne, 1892). At present, only the type species *Bieberiana pugnans* (Whidborne) is known, but includes several nominal taxa as subjective synonyms, such as *Conocardium confusum* Beushausen, 1895 and *Conocardium eifeliense* Beushausen, 1895, and thus is widely distributed in the Givetian of southern Laurussia (central and western Europe; Rogalla and Amler, 2006a, p. 253).

Life habits and palaeoecology. The facies distribution of conocardiid rostroconchs was controlled by various factors, e.g., facies stability, salinity, sediment grain size, oxygen content, water temperature, nutrient supply, etc., but only few of them are as yet directly identifiable. On the basis of the morphological variation in anatomical characters and palaeobiological constraints, derived from the basic molluscan body plan, several life styles were realised (summarised in Amler and Rogalla, 2007, 2013; Amler, 2016) for occupation of various niches, e.g., reef margins, soupy muds or unstable sands. The morphology of *Bieberiana* sp. reflects its life habit; on the basis of the presence of a hood and an overall rather compact conch, an immobile semi-endobenthic sediment-sticking life position is inferred. Owing to the function of the hood, the water depth should not have exceeded 80 to 100 metres and water agitation was rather low, without remarkable currents below the storm wave base.

Trilobites

The trilobites discussed here (Figs 18, 19) were recovered from sections M0 (most of the material, coming either from the bed 9 or from a lens presumably corresponding to this bed), M1 (a single specimen), and M3 (a few specimens from the lithological set M3-7).

In the M0 section, a low-diversity assemblage with three species is present. Most of the material consists of internal moulds of cephala and pygidia of a representative of the subfamily Phacopinae Hawle and Corda, 1847. Phacopine taxonomy is based also on the sculpture of the dorsal exoskeleton of the cephalon; since the latter is rather thick in most species, internal moulds differ strongly from the calcified exoskeleton and thus comparison of the present material with taxa described on the basis of better preserved specimens from the Late Eifelian to Early Givetian beds of the Rhenohercynian Zone (Belgian Ardennes; German Eifel Synclines and western Sauerland region; e.g., van Viersen, 2007; Basse, 1998, 2006), is unfeasible. The remaining features are in good agreement with the "forme grande" [*sensu* Kielan, 1954; Fig. 18D, E, H–Q; an undescribed new species different from the name-bearing "forme petite" of *Phacops schlotheimi skalensis* Kielan, 1954 = *Nyterops skalensis* (Kielan, 1954)]. The following identification of the most common species under open nomenclature thus appears to be appropriate: *Hypsipariops* sp. cf. "forme grande" of *Phacops* (*Phacops*) *schlotheimi skalensis* Kielan, 1954 (= *Hypsipariops* sp. nov.). In the Ardenno-Rhenish massifs, representatives of *Hypsipariops* Struve, 1982 have hitherto been reported from the Late Eifelian to the Early Givetian.

Moreover, section M0 yielded two representatives of the family Scutelluidae Richter and Richter, 1955, less numerous in terms of specimens. Both are referable to the genus *Goldius* de Koninck, 1841 and differ in the segmentation of their pygidia (*Goldius* sp. 1 has narrow rib furrows and *Goldius* sp. 2 has wide rib furrows). A single cranidium of *Goldius* was found separately (Fig. 18B), so it cannot be decided, which of the two species it represents.

A single fragmentary pygidium with one thoracic segment attached from section M3 belongs to *Scabriscutellum* sp. nov. (Fig. 18G), another scutelluine genus, which is characterised by partial bifurcation of the median rib of the pygidium, whereas in *Goldius* it is not. Interestingly, that pygidium has rib furrows with longitudinal rows of hemispherical swellings, hitherto unknown in scabriscutelluines and thus justifying its assignment to a new species. This is the first report of a pygidium of this genus from Poland and the third Givetian occurrence worldwide (for overview, see Basse and Müller, 2004). A cranidium of *Scabriscutellum* from the 'Couvinian' (Upper Emsian or lowermost Eifelian) of Wydryszów (Łysogóry Region of the Holy Cross Mts, Poland) was reported by Osmólska (1957, pl. 2, fig. 6) but erroneously assigned to the scutelluine *Paralejurus* Hawle and Corda, 1847.

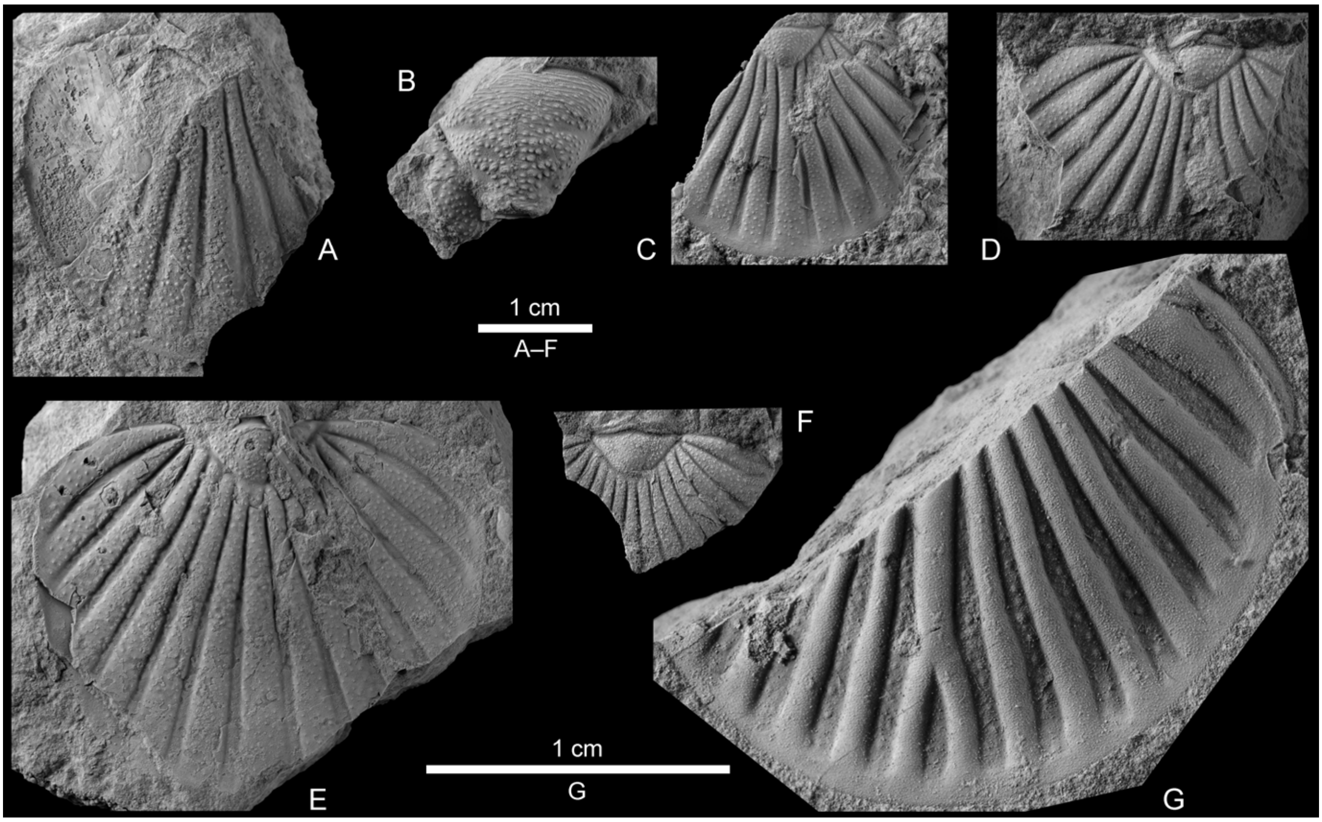


Fig. 18. Givetian scutelluine trilobites from Miłoszów (A: M1; B–F: M0; G: M3). **A, C–E.** *Goldius* sp. 2; A – incomplete pygidium ZPAL V.74/Tr/M1/1. M1-Ib; C – incomplete pygidium MWGUW ZI/105/3. M0, lens probably corresponding to the bed 9; D – fragmentary pygidium MWGUW ZI/105/4. M0, lens probably corresponding to the bed 9; E – incomplete pygidium MWGUW ZI/105/5. M0, lens probably corresponding to the bed 9. **B.** *Goldius* sp. 1 vel sp. 2. Fragmentary cranidium MWGUW ZI/105/2. M0, lens probably corresponding to the bed 9. **F.** *Goldius* sp. 1. Fragmentary pygidium MWGUW ZI/105/1. M0, lens probably corresponding to the bed 9. **G.** *Scabriscutellum* sp. nov. Incomplete pygidium ZPAL V.74/Tr/M3/1. M3-7.

Section M3 also yielded a single pygidium of cornuproetine gen. indet., sp. 2 (Fig. 19C). It differs from "*Otarion* (*Otarion*) sp." of Kielan (1954, pl. 2, fig. 12 = cornuproetine gen. indet., sp. 1) from the Upper Eifelian part of the Skały Fm at Skały (wrongly dated to the Givetian by Kielan, 1954) by having less deep pleural furrows and 5 + 1 pygidial axial rings (*vs*. 4 + 1 in sp. 1). These two species are the only cornuproetines described from the Middle Devonian of Poland.

Ostracods

The Early Givetian ostracod assemblage (Fig. 20) from the Miłoszów M1 section (samples M1, M1-B, M1-C, M1-N from the contact interval M1-Ib/M1-IIa) include nine species numerically strongly predominated by two species: palaeocopid species *Kozlowskiella kozlowskii* (Přibyl, 1953) and podocopine species *Tubulibairdia fecunda* (Přibyl and Šnajdr, 1950). The entire ostracod assemblage includes only marine, benthic forms.

Ostracods are preserved as articulated carapaces, so a study of internal features was not feasible. The ostracods represent mostly adult forms.

Kozlowskiella kozlowskii (Fig. 20A–C) so far was known in the Holy Cross Mts from the fossiliferous brachiopod shale (set XIV of Pajchlowa, 1957), the Grzegorzowice–Skały section (Přibyl, 1953; Adamczak, 1958, 1976), and the Late Eifelian part of the Skały Fm (Malec and Turnau, 1997). Recorded also from the Early Givetian of N-Eifel region (Becker, 1964) and from the Late Eifelian of the Rhenish Mountains (Groos, 1969).

Palaeozoic Eridostracines, ostracods with moult retention, are represented at Miłoszów (M1-IIa) by one species *Eridoconcha papillosa* Zagora, 1966 (Fig. 20D, E). In the Holy Cross Mountains, it also occurs in the Skały Fm, at Skały (Adamczak, 1961).

Metacopines are represented by two poorly preserved specimens of *Polyzygia* cf. *trigonata* (Gürich, 1900); it is limited to the Eifelian and Givetian of Palaeotethys (e.g., Crasquin-Soleau *et al*., 1994); *Bufina* sp. aff. *Bufina unicornuta* Adamczak, 1976 also known from the Skały Fm, and *Ropolonellus* cf. *kettneri* (Pokorný, 1951b), known from the Skały Fm (Adamczak, 1976).

Podocopines are most abundant in terms of the number of specimens. The most abundant is up to 3 mm long and thick-shelled *Tubulibairdia fecunda*; *Bairdiocypris* cf. *eifliensis* (Kegel, 1928) *sensu* Adamczak (1976), which also occurs in the Skały Fm; *Haeldianella* sp.; *Bairdia* (*Rectobairdia*) *paffrathensis* Kummerow, 1953 ranging from the Late Eifelian to the Middle Frasnian (e.g., Casier and Préat, 1991; Olempska, 1979); and one specimen, probably belonging to the *Acratia*? sp. indet.

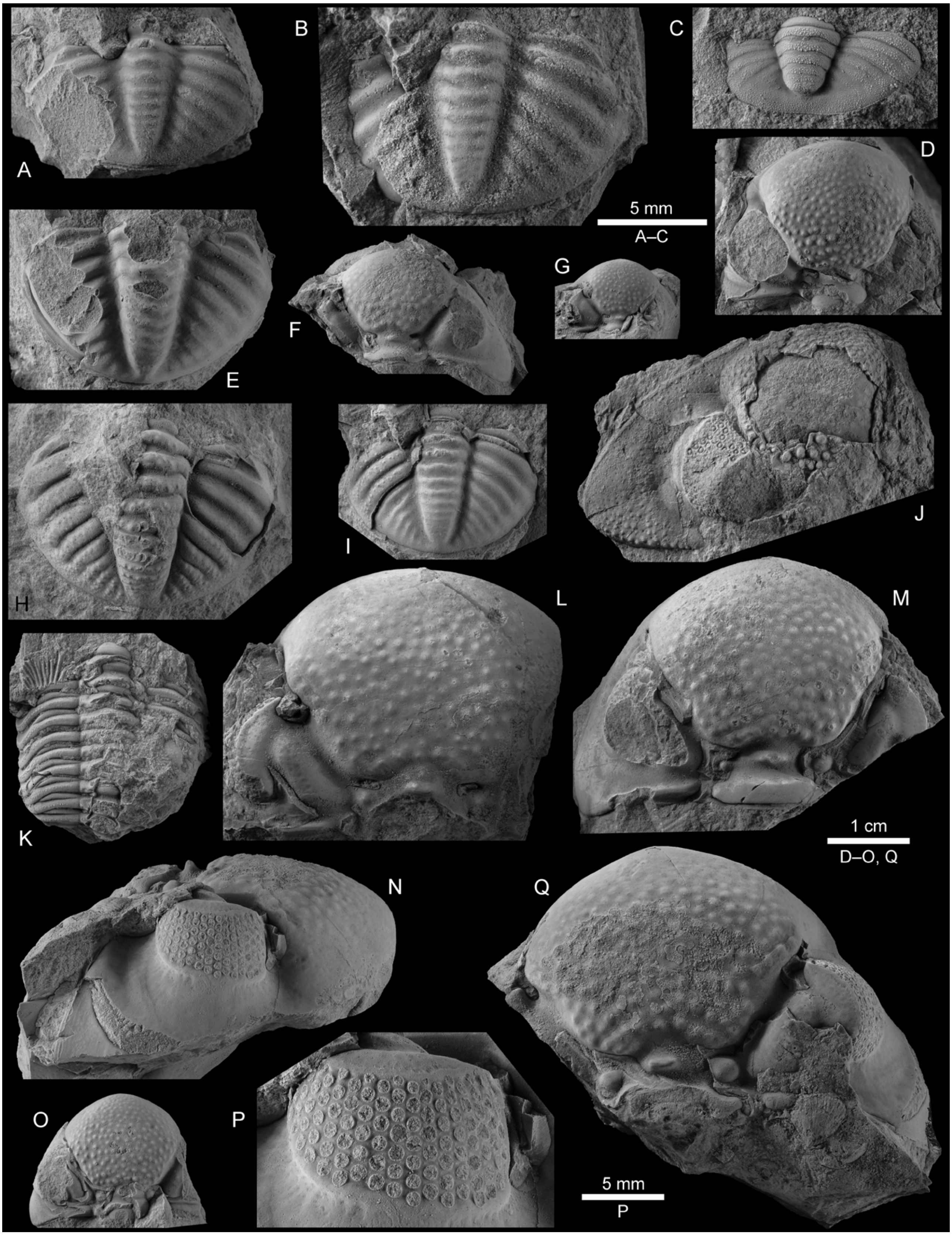


Fig. 19. Givetian phacopid (A, B, D–Q) and cornuproetid (C) trilobites from Miłoszów (A–C, F, G: M3; D, E, H–R: M0). **A, B.** Phacopid pygidia ZPAL V.74/Tr/M3/5, 6. M3-7. **C.** Cornuproetine gen. indet., sp. 2. Pygidium ZPAL V.74/Tr/M3/2. M3-7. **D, E, H–Q.** *Hypsipariops* sp. nov. M0; D, J, O – cephala ZPAL V.74/Tr/M0/2, 3, 8. M0, bed 9; L, M – cephala MWGUW ZI/105/6, 7. M0, lens probably corresponding to the bed 9; E – pygidium ZPAL V.74/Tr/M0/1. M0, bed 9; H, I – pygidia MWGUW ZI/105/8, 9. M0, lens probably corresponding to the bed 9; K – thorax MWGUW ZI/105/6, 7. M0, lens probably corresponding to the bed 9; N, P, Q – cephalon MWGUW ZI/105/10: dorsal view (Q), lateral view (N), and enlargement of the eye (P). M0, lens probably corresponding to the bed 9. **F, G.** Phacopid cephala ZPAL V.74/Tr/M3/3, 4. M3-7.

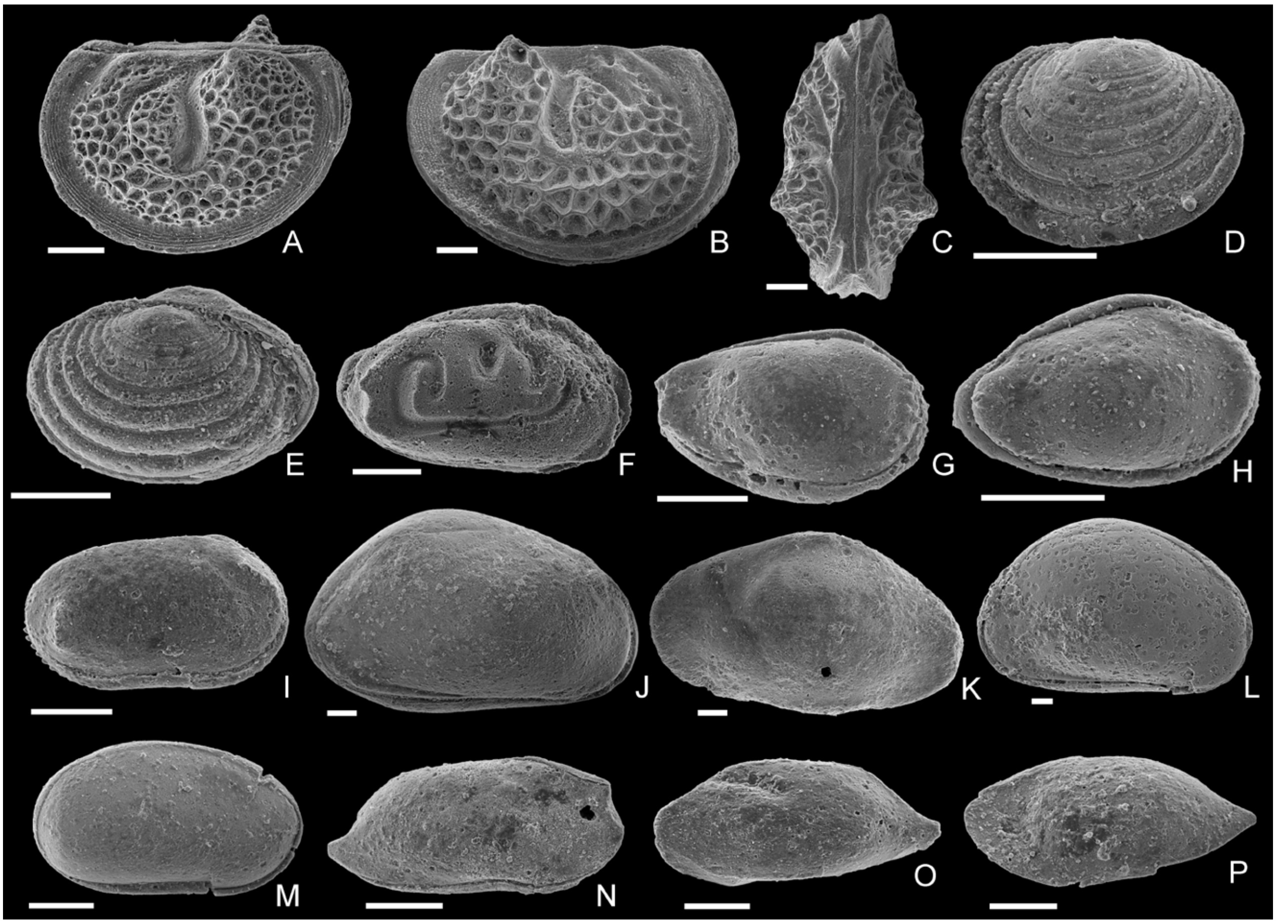


Fig. 20. Givetian ostracods from section M1 at Miłoszów. **A–C**. *Kozlowskiella kozlowskii* (Přibyl, 1953); A – carapace ZPAL V.74/O./01 in left lateral view; B – carapace ZPAL V.74/O./02 in right lateral view; C – carapace ZPAL V.74/O./03in dorsal view. **D–E**. *Eridoconcha papillosa* Zagora, 1966; D – carapace ZPAL V.74/O./04 in external view; E – carapace ZPAL V.74/O./05 in external wiev. **F**. *Polyzygia* cf. *trigonata* (Gürich, 1900), carapace ZPAL V.74/O./06 in right lateral view. **G–H**. *Ropolonellus* cf. *kettneri* (Pokorný, 1951b); G – carapace ZPAL V.74/O./07 in right lateral view; H – carapace ZPAL V.74/O./08 in right lateral view. **I**. *Bufina* sp. aff. *Bufina unicornuta* Adamczak, 1976; carapace ZPAL V.74/O./09 in right lateral view. **J–K**. *Tubulibairdia fecunda* (Přibyl and Šnajdr, 1950); J – carapace ZPAL V.74/O./10 in right lateral view; K – left valve ZPAL V.74/O./11 in lateral view. **L**. *Bairdiocypris* cf. *eifliensis* (Kegel, 1928) *sensu* Adamczak (1976); carapace ZPAL V.74/O./12 in right lateral view. **M**. *Healdianella* sp., carapace ZPAL V.74/O./13 in right lateral view. **N–O**. *Bairdia* (*Rectobairdia*) *paffrathensis* Kummerow, 1953; N – carapace ZPAL V.74/O./14 in right lateral view; O – left valve ZPAL V.74/O./15 in lateral view. **P**. ?*Acratia* sp. indet., left valve ZPAL V.74/O./16 in lateral view.

In the Holy Cross Mountains, *Tubulibairdia fecunda* has been found in the Grzegorzowice–Skały section (levels 9–14 of Adamczak, 1976), the Late Eifelian part of the Skały Fm, as well as in the Givetian of Pokrzywianka and Nieczulice beds in the same section (Malec and Turnau, 1997). It is also known from the Late Givetian of Jaźwica Member, Kowala Fm, Marzysz and Posłowice, Kielce Region, SW part of HCM (Malec and Racki, 1993) and also from the Late Givetian of Pomerania, NW Poland (Żbikowska, 1983). The species was also recorded from the upper part of the Hlubočepy Beds, the uppermost part of the Choteč Limestone (Eifelian), Central Bohemia Region, Czech Republic (Přibyl and Šnajdr, 1950; Přibyl, 1954).

The ostracod assemblage from the Miłoszów section, albeit of lower diversity, section shows a close relationship to that from the Eifelian to Givetian of the Skały Fm (Adamczak, 1976). The association of marine benthic ostracods, found in the Miłoszów section, belongs to the Eifelian Mega-Assemblage, indicative of a well-oxygenated shallow-marine environment (e.g., Becker in Bandel and Becker, 1975; Casier, 2004). In this Mega-Assemblage, four assemblages are recognised: 0, I, II, III (e.g., Maillet *et al.*, 2016). Assemblage 0, with dominance of Leperditicopid ostracods indicates lagoonal environment; assemblage I, dominated by palaeocopids, platycopids and eridostracines, indicating semi-restricted environment; assemblage II, with predominant thick-shelled podocopines, e.g., *Tubulibairdia* and *Bairdiocypris*, indicating agitated marine environments above the fair-weather wave base; and assemblage III, with a high diversity of metacopins, podocopids, palaeocopids and platycopids points to open marine environment below the fair-weather wave base.

In most samples from the Miłoszów section, the low-species-diversity assemblage occurs and thick shelled taxa, such as podocopid *Tubulibairdia*, *Bairdiocypris* and palaeocopid *Kozlowskiella* individuals, are dominant. They are representative of the Eifelian Mega-Assemblage II, indicating a shallow environment with agitated waters.

The well-diversified palaeocopid, metacopid and podocopid taxa (more than 50 species) found in the Grzegorzowice–Skały and Śniadka sections (Adamczak, 1968, 1976) are representatives of the Eifelian Mega-Assemblage III. The ecological drivers of why ostracods are abundant and well diversified in the Skały Fm in the Skały and Śniadka sections, while a decline of diversity can be observed at Miłoszów, remain unclear. This may be due to the method of sampling, in particular sediment sample size (volume). The volume of fossil samples collected in 1953–1956 (Adamczak, 1968, 1976) from several trenches located close to Grzegorzowice and Skały villages was very large. The decline of diversity may also be related to the periodically very agitated waters, transport and sorting specimens by currents, oxygen content of the bottom waters, or other factors.

Bryozoans

Bryozoans were extracted from samples taken from the contact interval M1-Ib/M1-IIa (M1-C, M1-N) and from samples M1-7–10. A preliminary examination of the external features of bryozoan zoaria has revealed that as many as 20 genera are present. Bryozoans, with the exception of the Cyclostomata, are represented in each of the stenolaemate orders: Cystoporata: *Eridopora* (Fig. 21B), *Fistulipora* (Fig. 21A), *Sulcoretepora* (Fig. 21C); Trepostomata: *Anomalotoechus*, *Eostenopora*, *Leioclema* (Fig. 21H), *Microcampylus*; Cryptostomata: *Acanthoclema* (Fig. 21E), *Nematopora*, *Orthopora*, *Rhombopora*?, *Streblotrypella*, cryptostome bases, small undetermined cryptostomes; Fenestrata (Phylloporinidae): Undetermined taxon; Fenestrata (Fenestellidae): *Dissotrypa*?, *Hemitrypa* spp., *Polypora*

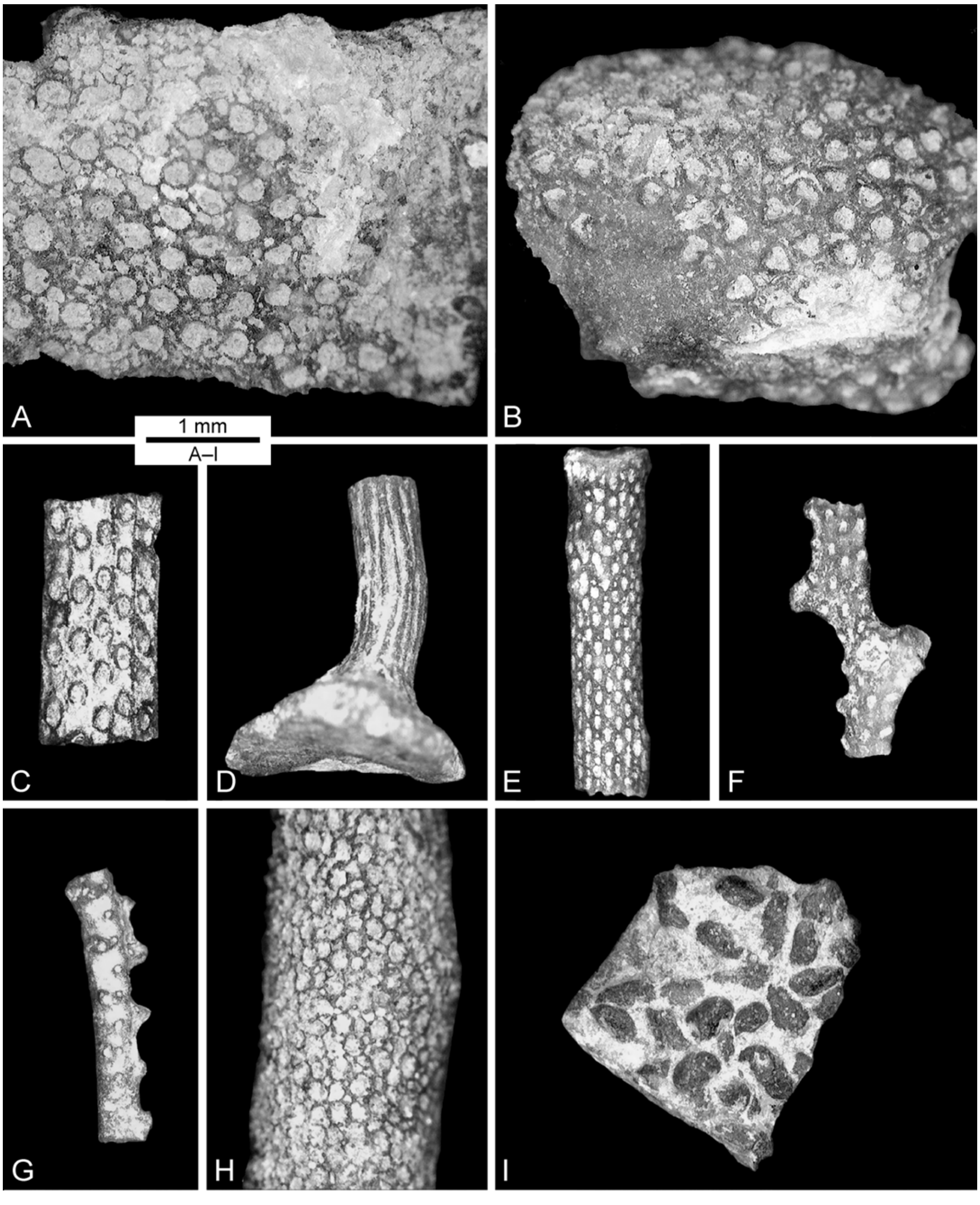


Fig. 21. Selected Givetian bryozoans and ascodictyids from section M1 at Miłoszów. **A.** *Fistulipora* sp. **B.** *Eridopora* sp. **C.** *Sulcoretepora* sp. **D.** Cryptostome base. **E.** *Acanthoclema* sp. **F.** *Polypora* sp., fragment with circular ovicell. **G.** *Penniretepora* sp. **H.** *Leioclema* sp. **I.** *Allonema moniliforme*. Scale bar 1 mm.; B – sample M1N; A, D, F – sample M1N/7; C, E, G, H, I – sample M1N/8.

(Fig. 21F), *Semicoscinium*, *Spinofenestella*; Fenestrata (Acanthocladiidae): *Diploporaria*, *Penniretepora* spp. (Fig. 21G).

Each of the horizons sampled at M1 show subtle differences: trepostomes are most common at M1-Ib/M1-IIa (sample M1C); large cystoporate colonies, some tiny fenestellid fragments and narrow cryptostomes at M1-7; small pinnate acanthocladiid fenestrates at M1-9; and delicate cryptostomes and small fenestrates at M1-10.

Encrusting bases of cryptostomes and possibly some trepostomes form small circular expansions, from which erect dendroid or ramose cylindrical branches developed rapidly above the encrusting disc. Such bases have previously been reported as epiphytically attached to corals (Zatoń and Wrzołek, 2020) and here two are attached to a brachiopod, but most are isolated.

The fauna at Miłoszów shows some similarities to those reported from the Givetian of the Holy Cross Mountains (Morozova *et al.*, 2002), and to Germany (Ernst, 2008a, b; Ernst and Schroeder, 2007) and Spain (Ernst *et al.*, 2011). The pre-Taghanic fauna represented here is rich; the Taghanic Event resulted in the disappearance of forty Devonian bryozoan genera globally (Ernst, 2013, tab. 2).

A comprehensive assessment will be undertaken in due course, in which both external and internal features are characterised through SEM and thin-section studies; this will provide a comprehensive and authoritative taxonomic listing.

Hederelloids and ascodictyids

In addition to previously mentioned bryozoans, such encrusters as *Allonema moniliforme* (Fig. 21I), *Ascodictyon sparsiforme* (treated as *Eliasopora sparsiformis* by Olempska and Rakowicz, 2014), *A. vinelliforme*, and *A. venustum*, previously regarded as ctenostome bryozoans by Kiepura (1965) but considered to represent entirely different, microproblematica (Wilson and Taylor, 2014), and Foraminifera-like (Jarochowska and Munnecke, 2014; Olempska and Rakowicz, 2014) organisms referred to as the ascodictyids (Olempska and Rakowicz, 2014), commonly encrust rugose corals (Zatoń and Wrzołek, 2020). *Allonema moniliforme aggregatum* Ulrich and Bassler, 1904 (see Kiepura, 1965) also encrusts the reverse surface of an undetermined fenestrate.

Previously considered as cyclostome bryozoans by Kiepura (1973), problematic colonial metazoans, known as hederelloids (Taylor and Wilson, 2008), are also a common constituent of encrusting assemblages on rugose corals (Zatoń and Wrzołek, 2020).

Brachiopods

Brachiopods are the most frequent group of macrofauna at Miłoszów. The 68 taxa represent 43% of the total number of animal species (see below). They are thus taxonomically diversified (belonging to 14 out of 17 orders known from the Devonian worldwide; Curry and Brunton, 2007), present in all four sections studied, and numerically abundant. A full taxonomic treatment of the material consisting of several hundred specimens is given elsewhere (Baliński and Halamski, in press; see especially table 1 providing data on stratigraphic distribution of all taxa). A summary of the major brachiopod assemblages is given below.

There are three rich polydominant assemblages, one from the shales M1-IIa (27 species; Fig. 22J–Q) and two from limestone beds, M3-7 (23 species; Fig. 22A–I, R–T) and M0-9 (22 species; Fig. 22EE–JJ). Eight beds yielded distinctly poorer assemblages, consisting of 1–9 species; such paucity can perhaps be partly explained by sampling artefacts (limestone beds M2-3 and M2-5), but in many cases corresponds to a real phenomenon (especially the nearly monospecific assemblage from M2-1 (Fig. 22DD); also the poorly diversified faunas in shales M1-IIb and M3-8 (Fig. 22U–Z). Finally, six stratigraphic levels (out of a total of 17) yielded no brachiopods at all; once again, the absence partly can be explained by sampling and counting artefacts (dubious presences disregarded), but significant differences with the above-mentioned rich assemblages are real (see numerical data in Baliński and Halamski, in press).

The three rich assemblages are relatively dissimilar to each other, insofar as the numerically dominant taxa are different in each of them. Characteristic species (either numerically dominant in a level and absent or rare elsewhere, or rare but present exclusively in single levels) include: *Pentamerelloides davidsoni*, *Spinatrypa wotanica*, *Davidsonia septata*, *Plectospira ferita*, and *Moravilla* sp. nov. in M1-IIa; *Kransia subcordiformis*, *Beckmannia beckmannii*, *Eumetabolotoechia subplicata*, *Desquamatia circulareformis*, *Gruenewaldtia latilinguis*, and *Undispirifer* sp. nov. in M0-9; *Antirhynchonella linguiformis*, *Beckmannia pentagona*, *Atrypa subtrigonalis*, and Cyrtiidae gen. et sp. nov. in M3-7.

A single brachiopod species, *Iridistrophia* cf. *undifera*, was recovered from limestone at M2-1 (bed M2α). It certainly represents a peculiar ecological setting, insofar as this is the only bed to yield chitinozoans. A precise interpretation is unclear.

Brachiopods from shales M2-2 (bed M2δ) and M3-8 predominantly include very small (under 5 mm) forms belonging to the athyridide genus *Bifida* and the ambocoeliid *Echinocoelia* (see below for interpretation). The bed M2ε is the only outcrop having yielded phosphate-shelled brachiopods (“inarticulates”), among which minute (< 1 mm) acrotretides *Opsiconidion* cf. *arcticon*.

In summary, several relatively distinctive brachiopod assemblages may be distinguished. Such a situation is suggestive of a high beta diversity, but differences in age between the assemblages and the mixed character of at least the richest assemblage M1-IIa impede any detailed analysis (see Roden *et al.*, 2020, and references therein). The palaeoecological interpretation of the assemblages is given below (see the chapters The Givetian ecosystems at Miłoszów, Brachiopod assemblages and communities).

On an inter-regional scale, the assemblage as a whole is most similar to that from the Eifel in Germany, like the already known Middle Devonian brachiopod assemblages from the Holy Cross Mts (Halamski, 2008). The genus *Moravilla* was known previously from a single species occurring in a single region (Moravia); it is interesting to note the presence of *Moravilla* sp. nov. at Miłoszów.

Echinoderms

Echinoderms were revealed mostly from the upper (shaly) part of outcrop M1 (basal M1-IIa) and additionally from outcrops M0 and M2 (shales M2-2). Crinoids (Fig. 23A, B, D–J, M–Q) form the overwhelming majority of the collection and are represented mostly by stem elements, more rarely by fragments of arms and calyces. Moreover, the presence of echinoids (Fig. 23K, L; Fig. 24C, D, F, G), holothurians (Fig. 24A, B, E), and ophiocistoids (Fig. 23C) was noted.

In general, the collection of crinoid remains from Miłoszów is typical for Givetian assemblages (see e.g., Głuchowski, 1993 and references therein). No systematic treatment is intended here; the following overview is based on information, obtained from W. Ausich, J. Bohatý, and P. Gorzelak (pers. comm., 2022). The assemblage from M0 contains, among others, *Halocrinites*, *Storthingocrinus* (Fig. 23G), and cf. *Salairocrinus* (col.). *Cupressocrinites elegans* is a common species in the M1-IIa sample, which contains also, among others, taxa preliminarily identified as *Cupressocrinites hieroglyphicus* (Fig. 23I), *Halocrinites schlotheimii* (Fig. 23J), *H. minor* (Fig. 23F), cf. *Codiacrinus* (Fig. 23H), cf. *Mediocrinus* (col.), cf. *Noctuicrinus*? (col.) (Fig. 23E), cf. *Laudonomphalus* (col.), cf. *Lageniocrinus* (Fig. 23D), *Platycrinites*, *Ammonicrinus* (Fig. 23Q; see also Kongiel, 1958; Piotrowski, 1977; Bohatý, 2011). The assemblage from M2-2 contains, among others, *Haplocrinites* (Fig. 23A). Several other columnal taxa (denoted here by the abbreviation 'col.') may be distinguished, using the parataxonomic columnal taxonomy of Moore and Jeffords (1968).

Crinoid holdfasts have been noted on the rugose corals (M1-IIa) by Zatoń and Wrzołek (2020). Interestingly, in some cases the holdfasts evidently were oriented upward and downward with respect to the corallite growth, indicating their growth during the life (*syn vivo*) of the coral hosts.

Moreover, a few echinoid, holothurian, and ophiocistoid sclerites were found. Echinoid pedicellariae from M0 (Fig. 24C, D, F, G) are similar to those reported from Givetian to Frasnian deposits of the Holy Cross Mountains (Boczarowski, 2001, pl. 12, fig. 3; pl. 13, figs 9, 15). Echinoid spines, teeth, and a single rotula also were noted in samples from M1-IIa. At M0 the authors also noted the presence of well-preserved anal teeth of dendrochirotide holothurians belonging to the genus *Devonothyonites* Langer, 1991 (Fig. 24A, B, E), possibly representing *D. avis* Boczarowski, 2001, known from mid-Givetian to mid-Frasnian (Boczarowski, 2001, p. 123). A single ophiocistoid goniodont was noted at M1-IIa.

To sum up, there are at least 15 taxa of crinoids, as well as single biological species of echinoids, holothurians, and ophiocistoids. Abrasion traces and strong disarticulation of crinoid remains points to this material having been partly subjected to transport. The crinoid assemblage as a whole probably consists of a mixture of autochthonous and allochthonous elements (pers. comm., P. Gorzelak, 2022).

Conodonts

Conodonts (Pander, 1856) are tooth-like elements of an extinct group of animals, the systematic position of which is still debated (e.g., Briggs *et al.*, 1983; Blieck *et al.*, 2010; Turner *et al.*, 2010; Murdock *et al.*, 2013). The conodont study is based on four samples from trench M1N (M1N-1, M1N-2, M1N-4, M1N-6), two samples from the trench M2 (M2 and M2A) and a single one from trench M0 (see Fig. 3B for localisation of samples). In total, 7 samples were investigated, each weighing from 2 to nearly 5 kg, yielding 16 nominal taxa (see Tab. 1). The rock samples were dissolved in 15% formic acid, and the residue was enriched in the heavy fraction using the sodium metatungstate solution. The total number of conodont elements extracted is 94, including 24 P_1 elements useful for biostratigraphy (Tab. 1). Relatively most frequent, present in all samples studied, are coniform elements (Barrick, 1977; Sweet, 1981) attributable to the genera *Belodella* and *Neopanderodus*.

The overall preservation state of microfossils may be described as moderate. Many specimens are broken, fractured, covered with sediment particles or crystal overgrowths, precluding closer identification. Corroded surfaces and mineral overgrowths evidence the activity of mineralised

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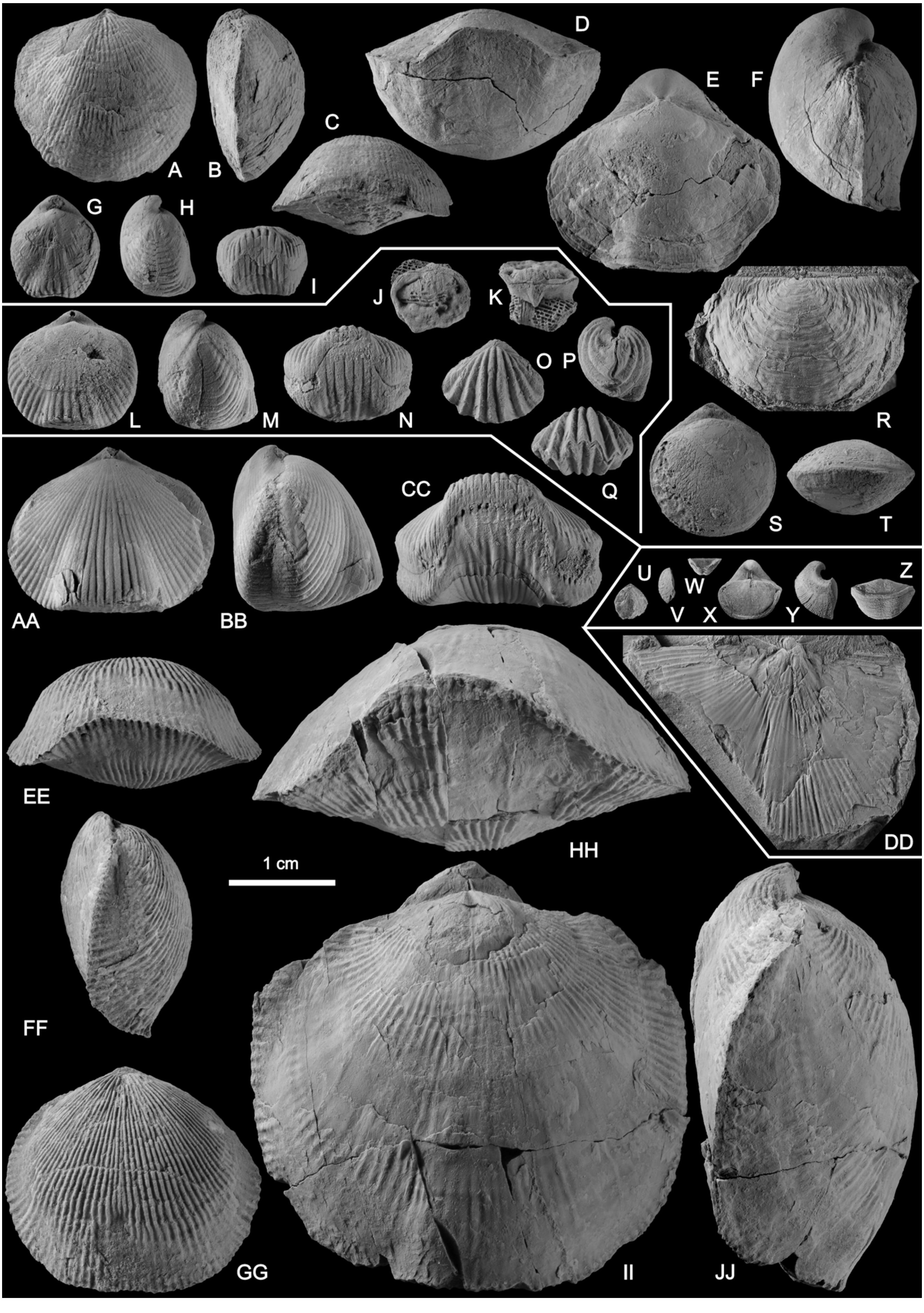
Fig. 22. Selected Givetian brachiopods from Miłoszów, all figured twice natural size to show ecological differences between assemblages. White lines separate assemblages (A–I, R–T: M3-7; J–Q: M1-IIa; U–Z: shales; AA–CC, EE–JJ: M0-9; DD: M2-1; see text for further explanations). **A–C.** *Atrypa subtrigonalis* Biernat, 1964. Articulated shell ZPAL V.74/Bp/29/M3/5 in dorsal, lateral, and anterior views. **D–F.** *Antirhynchonella linguiformis* Biernat, 1966. Articulated shell ZPAL V.74/Bp/17/*M3/9 in anterior, lateral, and dorsal views. **G–I.** *Beckmannia propentagona* (Schmidt, 1950). Articulated shell ZPAL V.74/Bp/21/M3/1 in dorsal, lateral, and anterior views. **J, K.** *Davidsonia septata* Copper, 1996. Incomplete shell V.74/Bp/34/M1/8 overgrowing a rugosan coral in dorsal and posterior views. **L–N.** *Kransia parallelepipeda* (Bronn, 1834). Articulated shell ZPAL V.74/Bp/22/M1/2 in dorsal, lateral, and anterior views. **O–Q.** *Pentamerelloides davidsoni* (Schnur, 1853). Articulated shell ZPAL V.74/Bp/20/M1/10 in dorsal, lateral, and anterior views. **R.** *Spinulicosta* cf. *spinulicosta* (Hall, 1857). Ventral valve ZPAL V.74/Bp/6/M3/8 embedded in limestone. **S, T.** *Peratos beyrichi* (Kayser, 1872). Articulated shell ZPAL V.74/Bp/40/M3/1 in dorsal and anterior views. Note this species is present in several assemblages. **U–W.** *Bifida* sp. Articulated shell ZPAL V.74/Bp/36/M2/4 in dorsal, lateral, and anterior views. M2-2 (bed δ). **X–Z.** *Echinocoelia dorsoplana* (Gürich, 1896). Articulated shell ZPAL V.74/Bp/45/M3/1 in dorsal, lateral, and anterior views. M3-8. **AA–CC.** *Kransia subcordiformis* (Schnur, 1853). Articulated shell ZPAL V.74/Bp/32/M0/2 in dorsal, lateral, and anterior views. **DD.** *Iridistrophia* cf. *undifera* (Schnur, 1854). Ventral valve ZPAL V.74/Bp/8/M2/1 embedded in limestone. **EE–GG.** *Gruenewaldtia* sp. Articulated shell V.74/Bp/38/M0/5 in anterior, lateral, and dorsal views. **HH–JJ.** *Desquamatia* (*Independatrypa*) *circulareformis* Biernat, 1964. Articulated shell ZPAL V.74/Bp/37/M0/5 in anterior, dorsal, and lateral views.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fluids. The damage of specimens could have resulted from their transportation in a sedimentary basin and/or from tectonic processes. The palaeothermal index varies from the conodont CAI 2.5 (for delicate and/or juvenile forms) to CAI 3 (for large and/or mature individuals), which points to heating of the host rocks to temperatures in the order of 110–200°C (Epstein *et al.*, 1977). This data generally confirm the previously established pattern of thermal maturity in the Devonian strata north of the Holy Cross Fault zone (Bełka, 1990; Narkiewicz and Malec, 2005).

In this study, formal conodont taxonomy is applied, based mainly on P_1 elements (Sweet, 1988; Purnel *et al.*, 2000). The genera *Polygnathus*, *Icriodus*, *Ozarkodina* were identified based on P_1 elements whereas *Belodella* and *Neopanderodus* mainly on S elements (Barrick, 1977; Klapper and Barrick, 1983). Although neopanderodontid elements were partly described at the species level, their recognition is still insufficient to provide a reliable synonymy. This is related to the observation that some of the existing form species may have belonged to the same apparatus (Klapper and Barrick, 1983). Therefore, in this study, they were the subject of neither taxonomic nor biostratigraphic analysis.

Icriodus lindensis Weddige, 1977 → *Icriodus brevis*
Stauffer, 1940
Fig. 25G–K

Remarks: *Icriodus brevis* has no formal diagnosis, merely a description based on early juvenile forms, which was detailed by Klapper (in Ziegler, 1975) and Ziegler and Klapper (in Ziegler *et al.*, 1976).

Bultynck (1987) noticed that the species *Icriodus brevis*, *I. lindensis*, and *I. eslaensis* Van Adrichem Boogaert, 1976, display an identical denticle pattern on the spindle. Although he discriminated the above named species on the basis of the posterior extension of the middle row denticles behind the spindle, their identification still poses problems. Diagnostic features, facilitating the discrimination of the three species, are therefore listed below.

Icriodus brevis: Denticles on the posterior extension are not markedly higher than those on the spindle, the outline of the extension is fan-shaped. A cusp is inclined and usually wider than other denticles on the extension.

Icriodus lindensis: The spindle is slightly biconvex. Denticles on the posterior extension increase regularly in height. The cusp is inconspicuously higher and wider, and slightly or strongly reclined. The posterior extension is slightly curved in the upper view.

Icriodus eslaensis: First 2–4 denticles of the posterior extension are relatively small, whereas the cusp on the posterior end is distinctly higher and wider.

From the above description, it appears that the Miłoszów specimens have a narrow, slightly biconvex spindle, whereas the specimen shown in the Figure 25K also displays a strongly reclined cusp. Such features are characteristic for typical forms of *I. lindensis*. Nevertheless, the denticles on a posterior extension, which are slightly higher than those on the spindle, as well as the fan-like posterior extension particularly conspicuous in the illustrated specimen (Fig. 25K) also indicate affinity to *I. brevis*.

Polygnathus timorensis Klapper, Philip and Jackson, 1970
→ *Polygnathus rhenanus rhenanus* Klapper,
Philip and Jackson, 1970
Fig. 25X–BB

Remarks: Representative specimens of *Polygnathus rhenanus rhenanus* have a markedly asymmetrical, short platform (Klapper *et al.*, 1970, p. 654) and the more pronounced outward bowing of the outer anterior trough margin, in comparison to *Polygnathus timorensis* Klapper, Philip and Jackson, 1970 (Bultynck, 1987).

Neither of the specimens illustrated is a typical representative of *Polygnathus rhenanus rhenanus*. The specimens figured in Fig. 25X and 25Z have a relatively narrow, elongated platform, sharply pointed at the posterior end. Geniculation points are slightly displaced relative to each other, the outer point is located more anteriorwards than the inner one. The above named features indicate a similarity to *P. timorensis*. In the specimen figured in Figure 25BB, one may notice a tendency to shortening of the platform and an opposite location of the geniculation points. The blade is too short, however, only 1.5 times the platform length. All the illustrated specimens display a pronounced outward bowing of the outer anterior trough margin and the basal cavity is much displaced anteriorwards, features characteristic for *Polygnathus rhenanus rhenanus*.

Vertebrates

A few poorly preserved vertebrate fragments were recovered from sample M2-3 and from a preliminary sample from outcrop M0. According to M. Ginter (pers. comm., 2022), they represent ctenacanth shark scales, possibly also a single placoderm scale, and bone fragments (heterostracans or placoderms).

THE GIVETIAN ECOSYSTEMS AT MIŁOSZÓW

Introduction to the palaeoecological analysis

Conodont analyses performed at Miłoszów provide datings, ranging from the *Polygnathus timorensis* Zone to at the most the earlier part of the *Polygnathus ansatus* Zone (Figs 7A, 8; Tab. 1). In other words, the sections studied extend from the Lower to the lower Middle Givetian, or, in terms of absolute ages, from ca. 384.2 Ma to ca. 381.7 Ma (Becker *et al.*, 2020, p. 752), that is, maximally for 2.5 million years. It should, however, be noted that no conodont dating was performed either in the upper (shaly) part of the M1 section (M1-II) or in the M3 section; the latter is certainly younger than the strata in M2, dated to the later part of the *Polygnathus timorensis* Zone, but it is not known how much younger. The biota dealt with here is thus younger than that of the Late Eifelian Konzentrat-Lagerstätte of Skały (Halamski and Zapalski, 2006 and references therein; Woźniak *et al.*, 2022), but older than that known from the brachiopod-rich outcrop at Błonia Sierżawskie near Świętomarz (SW-2; Halamski and Segit, 2006; dated to the Ex3 Subzone, M. Kondas and P. Filipiak, unpublished data).

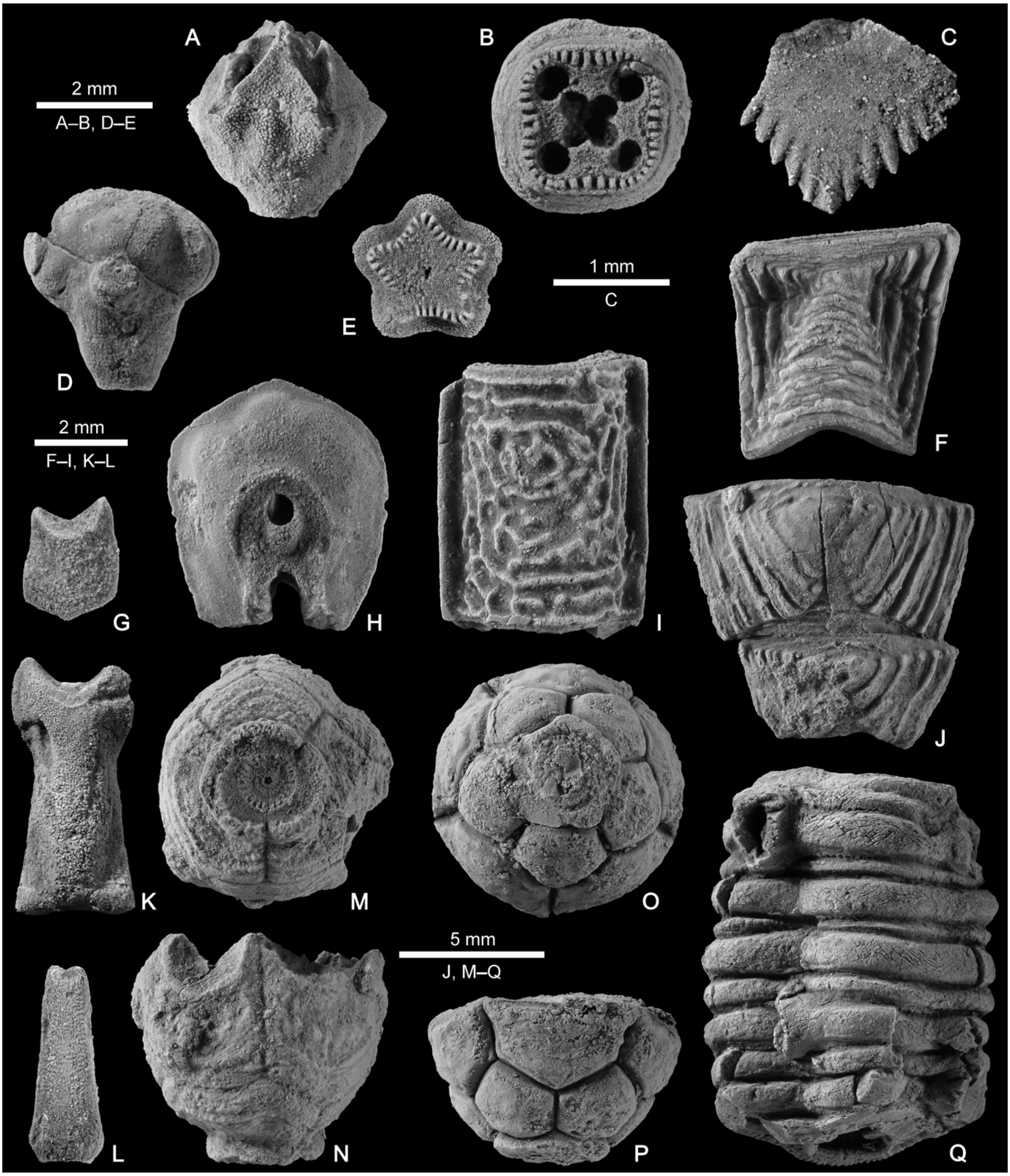

Fig. 23. Givetian echinoderm (A, B, D–J, M–Q, crinoids; C – ophiocistoid; K, L – echinoids) macrorests from Miłoszów (A–M2; G, L–M0; otherwise M1-IIa). **A.** *Haplocrinites* sp., calyx in lateral view. **B.** Cupressocrinitid, gasterocomoid, or rhapalocrinitid crinoid columnal (articular facet view). **C.** Unidentified incomplete ophiocistoid goniodont (inner view). **D.** cf. *Lageniocrinus* sp., calyx in lateral view. **E.** cf. *Noctuicrinus*? sp. (col.), articular facet of columnal. **F.** *Halocrinites minor* (Schultze, 1866), isolated brachial in lateral view. **G.** *Storthingocrinus* sp., radial plate (lateral view). **H.** cf. *Codiacrinus* sp., radial plate (lateral view). **I.** *Cupressocrinites hieroglyphicus* (Schultze, 1866), isolated brachial in lateral view. **J.** *Halocrinites schlotheimii* Steininger, 1831, brachials in lateral view. **K.** Unidentified echinoid rotula (lateral view). **L.** Unidentified echinoid spine (lateral view). **M, N.** Incomplete calyx of a monobathrid camerate or a disparid crinoid in aboral (M) and lateral (N) views. **O, P.** Calyx of eucladid crinoid in aboral (O) and lateral (P) views. **Q.** *Ammonicrinus* sp., stem fragment (lateral view).

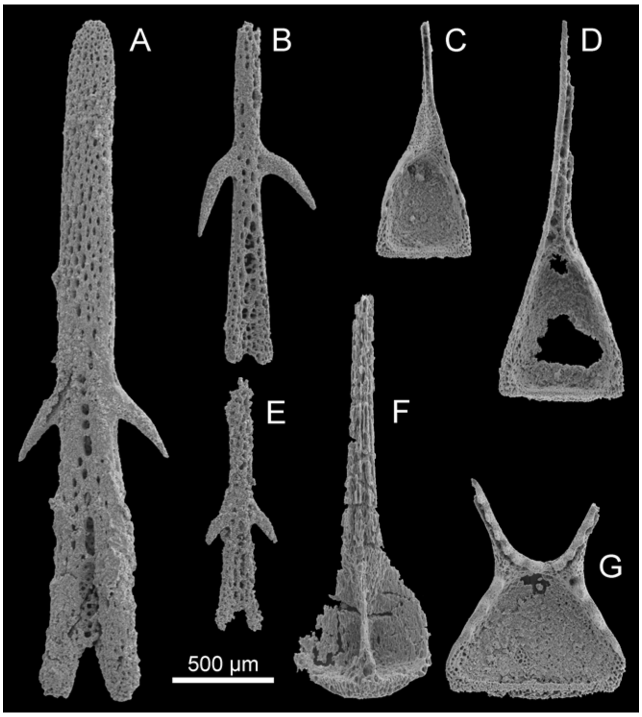

Fig. 24. Givetian echinoid and holothurian sclerites, obtained from a limestone sample dissolved in acid (outcrop M0 at Miłoszów). **A, B, E.** Anal teeth of the dendrochirotide holothurian *Devonothyonites* sp. **C, D, F, G.** Unidentified echinoid pedicellariae. All images are SEM photographs.

On the basis of the available conodonts, the entire studied biota thus pre-dates the Taghanic Event (Fig. 8C), the latter having occurred in a later part of the *ansatus* Zone and in the *semialternans* Zone (Aboussalam and Becker, 2011, p. 137; Becker *et al.*, 2016).

The palaeoecological analysis is based on brachiopod autecology and synecology (especially in terms of Benthic Assemblages *sensu* Boucot, 1975; see also Jansen *et al.*, in press), conodont palaeoecology, and the presence and/ or absence of particular morphotypes of rugose and tabulate corals. To a lesser extent, the authors used foraminifer-, sponge-, bivalve-, and rostroconch-related data.

Conodont palaeoecology

The application of conodonts for palaeoenvironmental interpretation of described sediments from Miłoszów is difficult, owing to the low frequency of the studied microfossils, precluding their quantitative evaluation. The reason for the general scarcity of conodonts may be connected with the high sedimentation rates, typical for the Łysogóry–Radom Basin (Narkiewicz, K., 2011; Narkiewicz, M., 2011) and emphasised also above for Miłoszów peri-biohermal facies (unit M1-I). Moreover, the lack of juvenile forms and a poor preservation state of many elements may evidence their reworking and redeposition from neighbouring (shallower?) facies settings.

The studied collection, seen as a whole, is indicative of a range of conodont biofacies with a variable proportion of polygnathids and icriodids. These P_1 elements are regarded as representing deep/offshore and shallow/nearshore Givetian shelf-settings, respectively (for a review see Narkiewicz *et al.*, 2016). It may be noted that *Icriodus* occurs in closely located trenches M1N and M0, and is lacking in trench M2, in which only *Polygnathus* has been found.

Notably, there is a relatively large proportion of the coniform elements belonging to *Belodella* and *Neopanderodus* in all the conodont assemblages investigated (Tab. 1). Large, well-preserved *Belodella* elements seem to dominate in the lower part of the M1N trench section, contrasting with a few icriodids displaying distinctly corroded surfaces. This could attest to redeposition of icriodids and the autochthonous nature of belodellids. In other assemblages, the proportions of *Belodella* and *Neopanderodus* are more equal, except for the M2 assemblage in which *Belodella* is lacking, whereas *Neopanderodus* attains its maximum frequency.

Belodella is a rare genus, generally attaining a low percentages in conodont assemblages of the Middle to Upper Devonian. Schumacher (1976) noted its presence together with *Panderodus* in nearshore, low-energy facies. On the other hand, Sparling (1983, 1984) placed *Belodella* in the most nearshore part of the shelf, with elevated salinity and temperature. In the Polish carbonate shelf, in the interval of the initial Taghanic transgressive phase (Middle Givetian *ansatus* Zone) *Belodella* is found in a nearshore zone, as well. Its presence is controlled both by the distance from a shore and water clarity, and its abundance diminishes with increasing terrigenous admixture (Narkiewicz *et al.*, 2016, fig. 9a). The latter is consistent with previous observations by Dzik (2002, p. 609), regarding Frasnian *Belodella*. This genus is found preferentially in conodont faunas, characteristic for the Frasnian mudmound and reef environments, composing from 1 to 50 % of a single assemblage in the sample (Sobstel *et al.*, 2006; see also Sandberg *et al.*, 1992). In the samples from Miłoszów, *Belodella* occurs most often in talus-like limestones of the unit M1-I (Tab. 1).

The habitat of panderodids (*Panderodus* and *Neopanderodus*) has not been investigated in detail and their position in shelf environments has not been determined unambiguously. According to Chatterton (1974, fig. 4), in the Middle Devonian they inhabited shallow-shelf settings, with low to medium water-energy, slightly elevated salinity and temperature, and protection from open-marine basin conditions. On the other hand, Sweet (1981, p. W88) and Sandberg and Dreesen (1984, fig. 4) regarded them as pelagic forms. Such interpretation may be confirmed by their occurrence in a deeper-shelf zone of the Middle Givetian in Morocco (Narkiewicz *et al.*, 2016, fig. 9b).

The distribution of *Belodella* and *Neopanderodus* in the Miłoszów area may indicate the presence of local environmental fluctuations. The relatively larger abundance of *Belodella* near the bottom of the Skały Fm is associated with shallow-water carbonate facies of an open-marine character, with sparse conodont and coral fauna and clear seawater. The subsequent drop in the abundance of *Belodella* and the appearance of *Neopanderodus* may have been caused by a gradual change in environmental conditions resulting from the increase in terrigenous influx from the NE (Narkiewicz *et al.*, 2011). The maximum influx may have

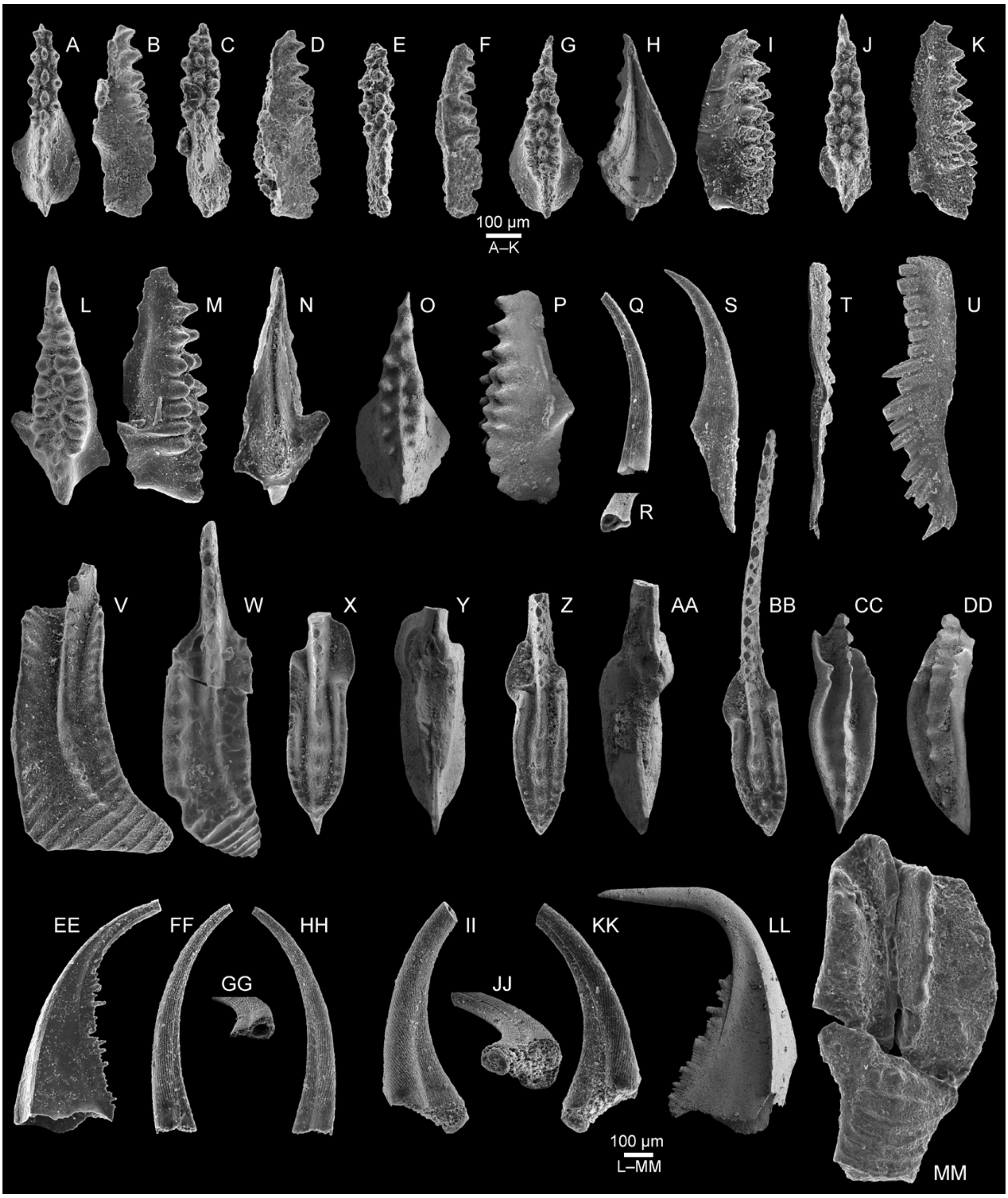

Fig. 25. Selected conodont elements from sections M0, M1, and M2 at Miłoszów. **A–F.** *Icriodus obliquimarginatus* Bischoff and Ziegler, 1957 – morphotype γ *sensu* Walliser and Bultynck, 2011; A–D – sample M1N 1; E–F – sample M1N 4; A, C, E – upper views; B, D, F – lateral views. **G–K.** *Icriodus lindensis* Weddige, 1977→*I. brevis* Stauffer, 1940. Sample M1N 6; G, J – upper views; H – lower view; I, K – lateral views. **L–P.** *Icriodus difficilis* Ziegler, Klapper and Johnson, 1976. Sample M0; L, O – upper views; M, P – lateral views; N – lower view. **Q–R, FF–KK.** *Neopanderodus* sp.; Q–R – Sa element, sample M0; Q – obverse view; R – cross-sectional view; FF–HH – Sa element, sample M1N 4; FF – obverse view; GG – cross-sectional view; HH – reverse view; II–KK – S element, sample M2. II, reverse view; JJ – cross-sectional view; KK – obverse view. **S.** *Neopanderodus aequabilis* Telford, 1975; reverse view of element M? Sample M2. **T, U.** *Ozarkodina plana* (Bischoff and Ziegler, 1957). Sample M2; T – lower view; U – lateral view. **V.** *Polygnathus linguiformis linguiformis* Hinde, 1879 morphotype γ1a *sensu* Walliser and Bultynck, 2011; Upper view; Sample M2. **W.** *Polygnathus linguiformis linguiformis* Hinde, 1879 morphotype γ3 *sensu* Walliser and Bultynck, 2011; Upper view; Sample M0. **X–BB.** *Polygnathus timorensis* Klapper, Philip and Jackson, 1970→*P. rhenanus rhenanus* Klapper, Philip and Jackson, 1970; X–Y – Sample M2A; X – upper view; Y – lower view; Z–BB – Sample M2; Z, BB – upper views; AA – lower view. **CC, DD.** *Polygnathus* sp. Sample M2; CC – upper view; DD – lateral view. **EE, LL.** *Belodella* sp.; EE – Sb element, outer view; Sample M1N 1; LL – Sc element, inner view. Sample M0. **MM.** *Polygnathus linguiformis* cf. *klapperi* Clausen, Leuteritz and Ziegler, 1979; Upper view; Sample M1N 4. All images are SEM photographs.

led to the disappearance of *Belodella* to be replaced by *Neopanderodus*, as observed in the M2 trench. The latter species co-occurs with narrow-platform polygnathids and ramiform elements, which were found in M2 and M2A samples only. Their presence points to deeper-shelf and low-energy habitats.

Brachiopod assemblages and communities

The deposits, studied at Miłoszów, contain quite different brachiopod assemblages (see above; see also Baliński and Halamski, in press). Here, the question of whether these assemblages represent (or not) Devonian brachiopod communities will be addressed. The framework of Benthic Communities proposed by Boucot (1975) is used.

The M1-IIa assemblage is quite heterogeneous. The most abundant species, such as *Pentamerelloides davidsoni*, *Spinatrypa wotanica*, and *Plectospira ferita* have small and strongly ornamented shells. Such a morphology is usually interpreted as being related to relatively high-energy environments. On the contrary, *Skenidioides* and *Cyrtina* with their remarkably high ventral interareas, as well as the wide-shelled *Moravilla*, seem rather adapted to soft-bottom conditions (Fürsich and Hurst, 1974; but *Cyrtina* may also be epibiontic, see Ivanova, 1962). This heterogeneity is present also in other faunal groups, with ostracods (Eifelian Assemblage II) pointing to agitated water, and bivalves and rostroconchs, especially the (semi-)infaunal species being clearly indicative of soft-bottom condition. The M1-IIa assemblage is preserved in shales and thus best interpreted as a mixture of (i) an autochthonous soft-bottom community (BA 4?) and (ii) a numerically dominant parautochthonous high-energy community (BA3). The conclusion about the mixed character of the assemblage was also obtained on the basis of the crinoid assemblage.

The M0-9 assemblage is characterised by the presence of a large-sized representative of *Desquamatia* (*Independatrypa*) (compare Webb and Schneider, 2013). This bed also yielded several large colonies of platy (mesophotic) tabulate corals. On the other hand, the uncinuloids *Kransia* and *Beckmannia* are often interpreted as having been adapted to turbid waters, their commissural spines acting as additional protection during filter-feeding. It might thus be hypothesised that this fauna is indicative of a shallow, turbid environment (the so-called brown mesophotic; see above, Tabulates). However, *Gruenewaldtia* has been interpreted as claricolous (Jansen, 2019, p. 740). The environmental setting of *Eumetabolotoechia subplicata* is unclear. In the Givetian of the eastern United States *Eumetabolotoechia* often is found in deep-water shales (Bartholomew and Brett, 2007, p. 111); it is uncertain whether the Polish species had the same environmental preferences. Environmental interpretation of *Undispirifer* is similarly unclear. It follows that a part of the M0-9 assemblage may be tentatively interpreted as a shallow turbid-water-related community, but it is unknown if all the species present in this assemblage belong to the community.

The M3-7 assemblage differs from the two previously discussed ones in the near absence of corals. This seems to indicate greater depth, which is concordant with the conodont data. *Antirhynchonella* with a functional pedicle, at least in the earlier stages of growth, and *Atrypa* with more or less flat ventral valves seem to represent a soft-bottom community. This community could belong to a deeper variant of the BA 3, as proposed by Boucot (1975) for the gypidulinid community.

A recurrent association of the very small species *Bifida* sp. and *Echinocoelia dorsoplana* occurs in shaly beds M1-IIb, M2-2 and M3-8. The former was interpreted by Copper (1973) as having preferentially lived on a calcareous muddy bottom in relatively quiet to slightly disturbed waters. *Echinocoelia* indicates the Devonian Ambocoeliid Community, which appears to occur in relatively deeper-water position, seaward to reef-like bodies in BA 4 to possibly BA 5 (Boucot, 1975). Fürsich and Hurst (1974) and Boucot (1975) note that quiet-water taxa are generally smaller than rough-water taxa. *Bifida* sp. and *E. dorsoplana* co-occur also in a younger outcrop at Błonia Sierżawskie, near Świętomarz (outcrop SW-2; Halamski, 2004), but there they are associated with a rich fauna of brachiopods and of other groups; a detailed analysis of this assemblage is not available.

The Givetian assemblages discussed here are entirely different from the Late Eifelian productide-dominated assemblages, recognised in the upper part of the brachiopod shales of the Dobruchna Mbr. (Woźniak *et al.*, 2022).

Biota as a whole

Generalities. From a (palaeo)ecological point of view, Phanerozoic biocoenoses (biotic parts of ecosystems) consist of three main categories of living organisms (Lindeman, 1942): producers, consumers, and decomposers (microconsumers *sensu* Odum, 1971). Consumers can be further subdivided into several categories, according to the vertical tiering, motility, and feeding mechanism (Bush *et al.*, 2007).

The reconstruction of past biocoenoses is usually incomplete on account of biases in the fossil record. In terms of biomass, producers are always the dominant trophic level (e.g., Ager, 1963, p. 218–220 and references therein), whereas at Miłoszów the record of primary producers is limited to microscopic organisms. There is no fossil record of decomposers.

Quantitative data for the assemblages from Miłoszów are only partly available. Rarefaction analyses have been performed for the gastropods and brachiopods from the richest layer M1-IIa and for the total (aggregated) sample of brachiopods from Miłoszów. Calculations were made, using the PAST software (Hammer *et al.*, 2001). The gastropod assemblage (Fig. 26A, $N = 86$, $S = 8$) is of moderate diversity (Simpson index $1–D \approx 0.81$, Shannon index $H \approx 1.86$, Margalef index $K \approx 1.57$) and appears as saturated. The brachiopod assemblage from M1-IIa (Fig. 26B, $N = 1008$, $S = 28$) is weakly unsaturated and of rather high alpha diversity (Simpson index $1–D \approx 0.91$, Shannon index $H \approx 2.74$, Margalef index $K \approx 3.90$). The diversity of the aggregated brachiopod assemblage (Fig. 26B, $N = 2263$, $S = 68$) is high (Simpson index $1–D \approx 0.96$, Shannon index $H \approx 3.48$, Margalef index $K \approx 8.51$) and the assemblage appears as clearly unsaturated.

Primary producers. The only photosynthetic groups, confirmed in the fossil record at Miłoszów, are planktonic prasinophytes and acritarchs, as well as the benthic *Rothpletzella* (see above). The presence of benthic macroalgae is not verified, but likely, as they are commonly present in Givetian deposits globally (Roux, 1991, p. 363). *Jansaella* was reported as commonly occurring in the Upper Givetian of the Southern Region of the Holy Cross Mountains (Racki and Soboń-Podgórska, 1993). The foraminifer *Semitextularia* is interpreted as having possessed photosymbionts, as well (Dubicka *et al.*, 2021b).

Consumers. In present-day ecosystems, consumers include a variety of microscopic organisms (‘zooplankton’) and (larger) animals. The former have either no fossil record (e.g., most ciliates; Dunthorn *et al.*, 2015), appeared after the Devonian (e.g., planktic foraminiferans; Rigby and Milsom, 2000 and references therein), or have not been found in the material studied (radiolarians). Nektic animals, apart from conodonts and rare fish, have no fossil record at Miłoszów, but the presence of other pelagic predators (cephalopods), should be assumed on the basis of their remains found in the approximately coeval deposits of the neighbouring Świętomarz–Śniadka section (Sobolew, 1909; Dzik, 2002, p. 576–577, fig. 3; see also Dec, 2020) and other localities in the region (Liszkowski and Racki, 1993). However, the present part deals solely with benthic animals, for which direct data are available at Miłoszów.

Summing the data given in the present contribution, at least 170 animal species are recorded in the four sections at Miłoszów (Tab. 2). This is a minimum estimation, given that two abundantly represented groups, namely bryozoans and crinoids, have not received detailed treatment. Brachiopods are clearly dominant, accounting for about two fifths of the total number of animal species (68; 39%). They are followed by bryozoans with at least 20 species (12%), echinoderms with at least 18 species (11%), and corals (tabulates and rugosans together, 17 species, 10%). Another relatively diversified group is ostracods (10 species, 6%).

The fauna thus is clearly dominated by suspension feeders (brachiopods, bryozoans, ostracods, crinoids), whereas herbivores (gastropods), detritivores (palaeotaxodont bivalves, trilobites), and predators (conodonts?, fish) are less numerous. In terms of tiering, surficial (brachiopods) and erect (crinoids, corals) animals are abundantly represented, pelagic ones are infrequent, even on regional scale, whereas (semi-)infaunal animals are rare (rostroconchs and bivalves, *Lingulipora*). All palaeotaxodont bivalves are mobile, infaunal detritus feeders; they indicate aerated conditions of the substrate, but a reasonable amount of organic detritus for feeding. Usually, the nuculoids live in the uppermost 10 cm of the substrate. Numerous other, likely soft-bodied bioturbators may have been present (Pisarzowska *et al.*, 2022), but their body fossils are not preserved. In general, the abundance of suspension feeders and predominance of erect and surficial tiers are characteristic for Palaeozoic ecosystems, as opposed to post-Palaeozoic ones, where, for example, the erect tier is much less represented, whereas the (semi-)infaunal tiers are more strongly so (Bottjer, 2016 and references therein).

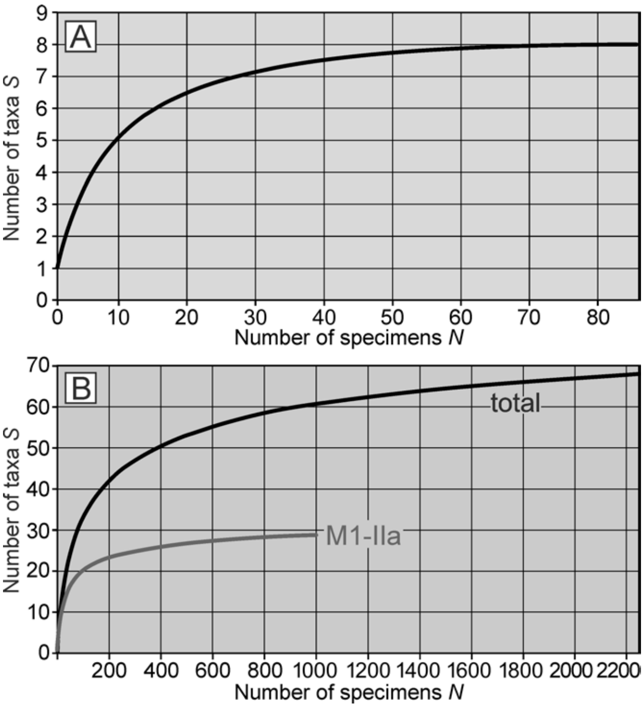

Fig. 26. Rarefaction curves of the gastropod assemblage from the layer M1-IIa (A) and of the brachiopod assemblages (B) from the layer M1-IIa and total (aggregated from all layers).

However, the tiering recorded on secondary hard substrates, like rugose corals (see Zatoń and Wrzołek, 2020), is different. Such palaeocommunities consist mainly of small-sized encrusters and borers (e.g., Taylor and Wilson, 2003), which are not suitable for living on the surrounding soft-bottom. On the rugose corals, the lowest tier (ground layer, 0–2 mm above surface, see Palmer, 1982) was occupied by majority of animals. Suspension-feeders (and probable suspension-feeders) were represented by dominating microconchids and sheet-like bryozoans, foraminifers and subordinate sheet-like stromatoporoids and cornulitids. Feeding strategies of ascodictyids and hederelloids occupying that level are uncertain; however, a suspension-feeding mode is quite probable for them. Primary producers were represented solely by *Rothpletzella*. Carnivorous cnidarians, occupying the ground layer, belonged to tabulate auloporids. The next field layer (2–10 mm above surface) was occupied by suspension-feeding *Davidsonia* brachiopods and such carnivorous cnidarians as rugose corals and tabulates (favositids). The higher scrub layer (10–40 mm above the surface) was solely occupied by suspension-feeding, arborescent bryozoans, whereas the highest canopy layer (> 40 mm) by pelmatozoan crinoids.

Comparisons of the animal species pool at Miłoszów and elsewhere. The minimum total number of species reported from Miłoszów (Tab. 2) is 257, including 200 representatives of the marine biota and 57 land plant spores. For the Devonian, 200 is already a somewhat elevated number, representing, however, a sum of taxa revealed from several levels belonging to four sections and using different techniques (surface searching, rock splitting with hammer, washing, dissolution in acids). A compilation of animal and foraminifer

Table 2

Summary of occurrences of fossil groups within outcrops.

Fossil group		locality M1		localities M2–M3				locality M0		Minimum number of taxa	
		unit I (limestones)	unit II (shales)	layer 1	layers 2–6	layer 7	layer 8	layers 1–8	layer 9		
Foraminifera								+++	+++	6	6
Fungi			+					+	+	1	1
Animals	Stromatoporoids	+	+							1	170
	Octactinellid sponges		+						+	1	
	Rugose corals	++	+++				+			10	
	Tabulate corals	+	++						++	7	
	Medusozoans				+					1	
	Microconchids and cornulitids		+							2	
	Polychaetes		+					+	+	1	
	Molluscs		+							13	
	Trilobites	+				+			++	5	
	Ostracods		++					+		10	
	Bryozoans, hederellids, and ascodictyids		+++							25	
	Brachiopods	+	+++	++	++	+++	+	+	++	68	
	Echinoderms	+	+++					+		18	
	Conodonts	+			+			+		8	
	Fish				+					2	
Photo-autotrophs	*Rothpletzella*		+							1	22
	Green algae		+	++	++			+	+	8	
	Acritarchs		+		+			++	+++	13	
	Land plant spores		++	+	++			+	+	57	57
Chitinozoans				+				+	+	1	1
TOTAL		*7* [4]	*17* [27]	*4* [1]	*7* [17]	*2* [23]	*2* [2]	*12* [2]	*10* [22]	**200** 257	

Explanations: +, present; ++, frequent; +++, exceptionally frequent. Imprecisely located occurrences mostly omitted. Total (last line) stands for the number of groups (*in italics*) confirmed within a given stratigraphic unit (layer or group of layers), but not all levels have been studied at the same level of detail; the number of brachiopod species (in square brackets) is given as an approximation of species-level richness. In the last column, the total minimum number of species present in all studied localities is given (marine species in bold typeface, both marine and terrestrial in Roman typeface). Note that species numbers are minimum estimates, for some groups most probably are rather close to the actual diversity (brachiopods), for some groups grossly underestimated (echinoderms); some levels (M0-1–8, M1-I) may also be underestimated compared to better-studied ones (M1-II).

taxa from a single Upper Eifelian Konzentrat-Lagerstätte level in the Skały Fm by Halamski and Zapalski (2006) listed 144 species; the corresponding value here (animals and foraminifers) is 176. Values for Konservat-Lagerstätten may evidently be significantly higher, like for example, about 400 species for the Lower Devonian Hunsrück Slate (Selden and Nudds, 2012, p. 73 and references therein), but one should keep in mind that such values are usually given per formation (Roden *et al.*, 2019, p. 93 and references therein), whereas here only parts of the Skały Fm are concerned.

The richest horizon is clearly the lower part of the shales at M1 (M1-IIa), although giving a precise number of taxa is not evident, insofar as in some cases it is difficult to decide whether a specimen comes from the weathered uppermost part of the limestone M1-Ib or from the lowermost part of the shale M1-IIa. A tentative account gives the value of 108 species, which means that about 64% (108/170) of animal species at Miłoszów is revealed from that single level. When compared with coeval assemblages from single beds, like those from the Givetian of the Hamilton Group in New York, USA (Baird and Brett, 1983), the Miłoszów assemblage is of comparable richness. The value of 108 animal species is higher than that for the Bay View Coral Bed, containing some 60 taxa, but lower than that for the Fall Brook

Coral Bed with some 120 taxa, both being dominated by brachiopods, bivalves and bryozoans (Moscow Fm; Baird and Brett, 1983, appendices 2A, 2B). These two beds were described as containing "faunas which are among the most diverse and varied in the North American Paleozoic" (Baird and Brett, 1983, p. 417). The assemblage from M1-IIa can thus also be described as relatively rich, which is partly explained by its heterogeneity.

The relatively high number of brachiopod species, which are the most diversified animal group at Miłoszów (68/170 ≈ 39%), is a usual situation in the Devonian (see, e.g., species numbers per region, quoted by Halamski, 2008, p. 87, 88; Halamski *et al.*, 2022, p. 65–69). It may, however, be observed that in the single richest horizon (M1-IIa), the number of brachiopod species (28/108 ≈ 25%) is nearly equal to that of bryozoans s.l. (25/108 ≈ 23%). Conversely, trilobites, cephalopods, and bivalves are clearly less diverse at Miłoszów, compared to rich coeval assemblages reported from elsewhere.

Ecosystems

To sum up, the four sections at Miłoszów yielded evidence of five bottom-level communities dominated by filter-feeders (Fig. 27):

- a shallower-water high-energy claricolous community with numerous rugosans, tabulates, and small strongly ornamented brachiopods (shallow BA 3);
- a community, related to shallow and turbid waters, with platy tabulates (rugosans absent) and uncinuloids;
- a deeper-water soft-bottom community with *Antirhynchonella* and *Atrypa subtrigonalis* and nearly no corals (deep BA 3);
- a rich soft-bottom community with *Skenidioides*, *Cyrtina*, *Moravilla*, and bivalves (BA 4?);
- a deep-water soft-bottom community with *Bifida* and *Echinocoelia* (BA 4, 5).

These five communities appear to have co-existed within a close spatial range (compare Boucot, 1981, p. 240), as evidenced by (i) and (iv) being preserved as a single mixed assemblage (M1-IIa). Faults hamper any precise estimation of the distances between the original locations of these ecosystems. In general, however, in the Early to Middle Givetian, the Łysogóry Basin near the present-day Miłoszów possessed a more complicated structure than usually is assumed, with swells and troughs occupied by different faunas.

The relatively rich biota recorded here is comparable in that respect to other pre-Taghanic ecosystems, as shown, for example, by the general faunistic similarity of rugosans, trilobites, ostracods, and brachiopods with the assemblages, described from the Rhenish Slate Mountains. Detailed comparisons show that differences exist as well: for example, in eastern North America *Echinocoelia* is a representative of the so-called Tully Fauna, the incursion of which is taken as the first step of the Taghanic Biocrisis in the type area (Zambito *et al.*, 2012). In the Holy Cross Mts, *Echinocoelia* is a common element of pre-Taghanic brachiopod communities (M2-2, M3-8). The same may be true for North Africa (Halamski *et al.*, 2022), although in Jbel Issoumour, the stratigraphic control is unsatisfactory.

EVOLUTIONARY *VS.* ECOLOGICAL RECORDS OF THE TAGHANIC CRISIS

The Taghanic Event in the Holy Cross Mountains and in New York

Given the available data on the distribution of fossils in the Miłoszów sections (and to some extent even in the whole Skały Fm) and the investigated carbon isotope trends (Pisarzowska *et al.*, 2022), it is obvious that a post-Kačák interval of optimum conditions and environmental stability developed contemporaneously in the areas, corresponding at present to Central Europe and Eastern North America. The latter is recorded in the Hamilton Fauna, an exceptionally rich ecological-evolutionary subunit, with more than 250 faunal taxa present (complete data not available, Brett *et al.*, 2009, p. 19; see also Brett *et al.*, 2007; Zambito *et al.*, 2012).

An impoverishment trend within the Skały section was shown by Adamczak (1976) for ostracods and for brachiopods by Biernat (1966). Single brachiopod faunas at Miłoszów are indeed less diverse than that from the Dobruchna Member (maximally 21–28 species for each of the former, over 40 for the latter; see Halamski and Zapalski, 2006; Woźniak *et al.*, 2022), but, generally speaking, the entire Early to early Middle Givetian biota from Miłoszów are rich (see above). The pattern is partly influenced by lateral biofacies variation toward more carbonate-rich succession westwards (see above, Fig. 8; Pisarzowska *et al.*, 2022). On the other hand, significant similarities between the brachiopod faunas from the Skały Fm and those from the Lower Frasnian of Józefka were noted in a preliminary communication by Halamski (2018; see also below).

Thus, the question arises, as to whether an eco-evolutionary turnover took place in the Holy Cross Mountains, corresponding to the major and nearly worldwide-recognised Taghanic Crisis. This initially was defined on the basis of the demise of brachiopod provinciality (Johnson, 1970) and major taxonomic turnover among cephalopods (House, 1985, 2002), and now is understood as being marked by an abrupt deepening pulse, expanding anoxia, and disturbed carbon cycle that led to a biogeographical turnover (see Baird and Brett, 2008; Aboussalam and Becker, 2011; Maillet *et al.*, 2013) and extinctions (Zambito *et al.*, 2016) during three discrete bioevents (Zambito *et al.*, 2012; MacGhee *et al.*, 2013). The main eustatic sea-level rise (IIa in Fig. 7D) was clearly recorded in the Holy Cross shelf domain, along with the collapse of the Świętomarz deltaic system (see above), paired with the drowning of the NW part of the Kielce carbonate platform, leading to the development of the Kostomłoty Zone basin, initially with rich benthic life (Racki *et al.*, 1985; Racki, 1986, 1993; Morozova *et al.*, 2002; Zapalski *et al.*, 2017; see above).

The search is hindered by the absence of detailed studies of the post-Taghanic recovery biota. The already preliminarily investigated diverse Late Givetian brachiopod faunas of the Laskowa Góra Beds (mostly *hermanni*? to *disparilis* zones) from the Laskowa and Józefka quarries of the Kostomłoty facies zone (Racki *et al.*, 1985; Baliński *et al.*, 2016), as well as those from poorly known basal Nieczulice

Beds (Pokrzywianka-Włochy section; Turnau and Racki, 1996, 1999; Halamski *et al.*, 2020), are currently under study. A state-of-the-art taxonomic treatment will enable a more relevant comparison of the brachiopod fauna from the Early to Middle Givetian of Miłoszów with that of the Early Frasnian of Józefka, near Górno (Baliński *et al.*, 2016).

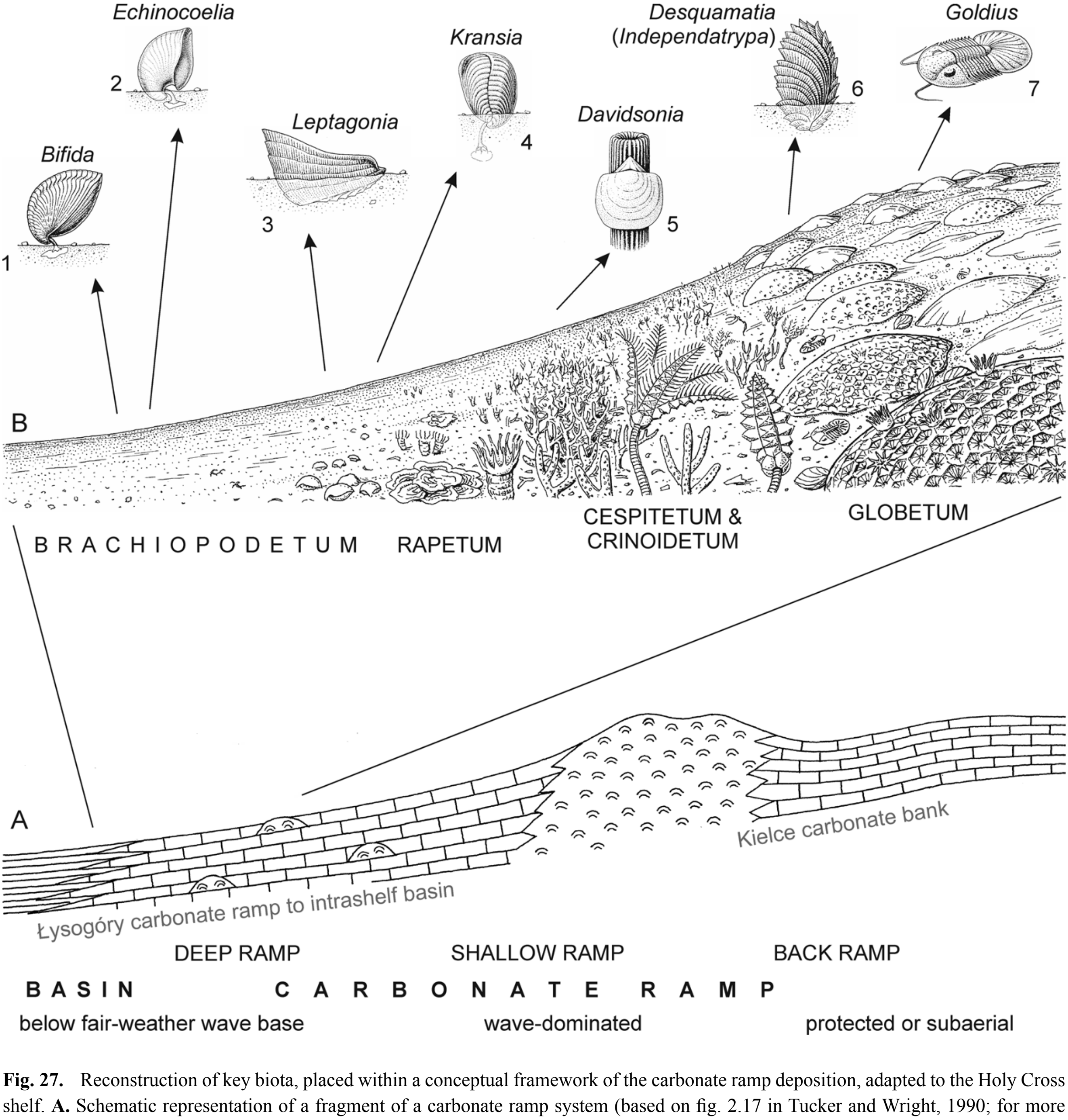

Fig. 27. Reconstruction of key biota, placed within a conceptual framework of the carbonate ramp deposition, adapted to the Holy Cross shelf. **A.** Schematic representation of a fragment of a carbonate ramp system (based on fig. 2.17 in Tucker and Wright, 1990; for more detail and references see Fig. 10). **B.** An idealised palaeoecological transect of the Miłoszów area (inspired after Jungheim, 2022) roughly referred to the palaeoassociation types within the Middle Devonian coral sea of the Eifel Mountains as proposed by Struve (1961) and corresponding to two-fold major biofacies differentiation recognisable in the Early to Middle Givetian succession in the Miłoszów localities (coral mound based on the coeval *Mesophyllum*-Alveolitidae assemblage in Nose *et al.*, 2017, fig. 8; compare also Dubicka *et al.*, 2021b, fig. 5). **1, 2.** Representatives of the deep-water *Bifida–Echinocoelia* Community (BA4–5): 1 – *in vivo* reconstructions of *Bifida* sp.; 2 – *Echinocoelia dorsoplana* (compare Zambito and Schemm-Gregory, 2013, fig. 7). **3, 4.** Representatives of the less deep mud-dwelling brachiopods (lower BA3): 3 – *in vivo* reconstructions of *Leptagonia analogaeformis;* 4 – *Kransia parallelepipeda* (based on Westbroek *et al.*, 1975, fig. 4). **5–7.** Representatives of a shallower-water benthic community (upper BA3) with coral mud-mounds, crinoids, brachiopods, and trilobites: 5 – *Davidsonia septata* as an epizoan on a rugose coral (compare Fig. 22J, K); 6 – *in vivo* reconstruction of *Desquamatia* (*Independatrypa*) *circulareformis* (based on Fenton and Fenton, 1932, figs 1, 2); 7 – schematic representation of *Goldius* sp.

Brachiopod faunas around the Taghanic Crisis

Preliminary results, summarised by Halamski (2018), indicate the persistence of several brachiopod lineages in the northern and central parts of the Holy Cross Mts (Łysogóry-Kostomłoty Domain) from the Middle to the lower Upper Devonian. According to these calculations, 26 species out of 46 present in the Lower Frasnian fauna (57%) represent lineages evolving in place, whereas the migrant lineages (20/46 ≈ 43%) are minoritary. Those evolving in place may be exemplified by the protorthide *Skenidioides* (*S. polonicus*, *S. cretus*; Baliński *et al.*, 2016) and the orthide *Schizophoria schnuri* (successive subspecies from the Late Eifelian to the Early Frasnian; Halamski, 2012).

A *prima facie* comparison of Middle and early Late Devonian brachiopod faunas in the Łysogóry-Kostomłoty Domain results therefore in a picture significantly different with respect to the analogous collation, established for the Eastern North America. There the early phase of the Taghanic Event corresponds to the incursion of warm-water taxa, the so-called Lower Tully fauna (Brett *et al.*, 2009, p. 20). In the Holy Cross Mountains, such a diversified thermophilic assemblage, distinctly different from earlier, Early to early Middle Givetian faunas, is not known to date. Conversely, the Taghanic Event might be recorded in the Holy Cross Mountains by stress-related faunas, characterised by small-sized chonetidine brachiopods at Pokrzywianka (see below). The subsequent two bioevents in the Appalachian Basin consist in the return of a Hamilton-type fauna (Upper Tully fauna; Brett *et al.*, 2009), followed by its demise and replacement by the Geneseo fauna (Zambito *et al.*, 2012, especially fig. 2). In the Holy Cross Mountains, several brachiopod lineages belonging to the 'Hamilton-type' Skały fauna do continue into the Early Frasnian (Halamski, 2018).

Accordingly, it should be stressed that the long-term persistence of the lineages shown above does not preclude the occurrence of possibly radical and short-term ecological-migrational events. These would correspond, above all, to intra-regional migrations and to a lesser extent (as evidenced by the global similarity of Middle Devonian and Lower Frasnian faunas) to a hypothetical invasion of cosmopolitan biota during the Taghanic (IIa) eustatic rise, the latter being in agreement with the well-known biotic pattern in the Appalachian Basin (Brett *et al.*, 2009; Zambito *et al.*, 2012).

Other faunas

Absence of a large-scale turnover is indicated by the tabulate coral faunas of Laskowa, where 7 among 12 taxa, such as *Coenites* aff. *variabilis* (= *Coenites* ex gr. *laminosa sensu* Racki *et al.*, 1985; see Zapalski, 2012), *Platyaxum escharoides* and *Thamnopora micropora*, presumably were allied with the Skały biota (see tabl. 1 and 2 in Zapalski *et al.*, 2017 and Stasińska, 1958). On the other hand, the heliolitid tabulate corals, still present in the upper part of the Skały Fm (Pajchlowa, 1957), went globally extinct during the Givetian (Król *et al.*, 2021 and references therein). The disappearance of a high-rank (order or subclass) group, widespread in the Early Givetian reef environments, even though poorly diverse (five genera globally in the Middle Devonian; Król *et al.*, 2021), is of major significance for the tabulate faunas overall (see also Bridge *et al.*, 2022).

Only preliminary estimates are available for ostracods, but in the species list of the survival-related Middle Givetian microfauna from the Pokrzywianka Beds and lower Nieczulice Beds of Malec and Turnau (1997), 11 species out of 19 quoted occur also in the Skały Fm [e.g., *Amphissites perfectus*, *Roundyella calceolae*, *Polyzygia symmetrica* (Gürich, 1896)]. A similar diversity trend is indicated by unpublished data of Żbikowska (in Turnau and Racki, 1996), not only for the survival phase (the basal Nieczulice Beds; 6 from 7 species are known from the Skały Fm), but also for the recovered ostracod assemblage higher in the Nieczulice Beds (Włochy-studnia site; 4 persisting species among 6 identified). Note that Adamczak (1976) recorded 54 benthic ostracod taxa from the Skały Fm and the appearance of pelagic entomozoids on a regional scale was promoted by the Taghanic transgression (Malec and Turnau, 1997). The Taghanic Crisis is remarkably documented as a reduction in provincialism among the benthic ostracod microfaunas in the historical Givetian type area in the Ardennes (Maillet *et al.*, 2013).

The best documented is the evolutionary continuity of crinoid faunas, elaborated in detail in parataxonomical terms by Głuchowski (1993, fig. 22). In the association from the Laskowa Góra Beds, 22 'species' out of 37, including 3 stem 'species' of *Cupressocrinites*, occur also in the Skały Fm and the Świętomarz Beds, and the Taghanic extinction rate can be estimated as at most 37%.

Perspectives for future research

The new data from the Łysogóry–Kostomłoty domain emerge as a promising agenda for future research around the horizon of the Taghanic transgression. This can be exemplified by two challenging problems:

The Pokrzywianka Beds bioherm assemblage evidently represents a unique record of a reefal community, developed during the high-stress conditions of the environmental shift from deltaic to hemipelagic basin settings (Malec, 2012). A peculiar low-diversity community of mesophotic coral encrusters (Zatoń *et al.*, 2022) can reflect the crisis setting, but a more comprehensive study, especially of bioherm-builders, is needed.

At least, the successions at the Laskowa Quarry (Racki *et al.*, 1985) and in the Pokrzywianka–Włochy area (the latter sampled in trench Po and pit Wł-st; Turnau and Racki, 1996, 1999, fig. 3) provide a still undescribed record of the Taghanic survival and recovery faunas, exemplified by the transition from faunas, dominated by either minute chonetidines (Pokrzywianka) or similarly very small-sized protorthides *Skenidioides* (Laskowa), to a diverse benthic biota with atrypides (coral biostromes at Laskowa) and *Bifida* (deep hemipelagic basin at Włochy) in a main role (see Racki *et al.*, 1985; Halamski and Baliński, 2018). A similar eco-evolutionary pattern might occur in the Świętomarz–Śniadka succession, as evidenced by the *Bifida* faunas of

Gürich (1896) and Sobolew (1909) at Błonia Sierżawskie (SW-2 *sensu* Halamski, 2009; see also Halamski and Segit, 2006; re-dated recently as the Nieczulice Beds; M. Kondas and P. Filipiak, unpublished data).

CONCLUSIONS

The Middle Devonian strata, cropping out in the Miłoszów Wood between Nieczulice and Pokrzywianka Dolna in the Łysogóry Region (northern region of the Holy Cross Mountains, Central Poland), belong to the middle and topmost part of the Skały Fm and are Early to Middle Givetian in age. The conodont datings extend from the *Polygnathus timorensis* Zone to the *Polygnathus rhenanus*/*varcus* Zone but the lower part of the *Polygnathus ansatus* Zone cannot be exluded; the palynostratigraphic datings are referable to the "*Geminospora*" *extensa* Zone (subzones Ex1 and Ex2).

The biota recorded at Miłoszów is rich, as often is the case for Middle Devonian ecosystems pre-dating the Taghanic event. In total, 170 animal species, 21 marine palynomorphs, and 6 foram species are reported. Moreover, the sections studied yielded also 57 palynomorphs of terrestrial origin. Adding single fungal and chitinozoan taxa, the minimum total number of taxa present is 257, including 200 marine species and 57 land plant spores.

Brachiopods (68 species) are the major faunal group in all sections. Brachiopod assemblages vary in the different layers and correspond to several shallow- and deep-water communities, such as dominated by small ornamented taxa (*Pentamerella*) in high-energy environments (shallowest) and *Bifida–Echinocelia* in muddy habitats (deepest).

Other richly represented groups include bryozoans (20 genera) and echinoderms (minimum estimation: 18 taxa, including 15 crinoid taxa). In contrast, bivalves, cephalopods and trilobites are clearly underrepresented compared to coeval assemblages from other regions.

Palaeoecological contrasts existed in the Middle Givetian Łysogóry muddy middle-to outer-ramp biota, representing a mixture of allochthonous shallower-water benthic communities (upper BA3), including storm/tsunami-affected coral-mud mounds, and autochthonous deep-water soft-bottom communities, dominated by small-sized brachiopods (BA 4–5).

The richness and diversity of the Miłoszów biota are comparable with those of other approximately coeval pre-Taghanic ecosystems during the climatic deterioration (cooling) and sea-level lowstand interval, especially in the Rhenish domain. The single richest level (M1-IIa) contains about 108 animal species, a relatively high number by Devonian standards.

A state-of-the-art taxonomic treatment of the Late Givetian brachiopod faunas of the Holy Cross Mts is lacking, thus hampering any definitive conclusion on the Taghanic Event in the area. Preliminary data indicate that no large-scale replacement of faunas took place in the Holy Cross Mts between the Early Givetian and the Early Frasnian, in contrast to brachiopod assemblages of the Appalachian Basin (final demise of the Hamilton/Upper Tully fauna). This 'stasis' probably characterised many other benthic groups and at present is best evidenced in crinoids. This does not preclude any short environmental perturbations and transient community turnovers caused by immigration; in other words, the crisis may have occurred in a similar manner to that of other regions, but the faunal recovery was more successful than that in eastern North America.

The problem of the regional record of survival and recovery processes from the Taghanic Crisis and of the enigmatic *pumilio* events are challenges for future studies in the Holy Cross Mountains.

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