

Non-pollen palynomorphs from the Devonian (Givetian/Frasnian) of south-central Poland

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ISSN (imprimé / print): 1631-0683/ ISSN (électronique / electronic): 1777-571X

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Submitted on 24 January 2024 | Accepted on 21 May 2025 | Published on 17 September 2025

[urn:lsid:zoobank.org:pub:3C1864A2-9623-4E23-8364-427D30ECCBDB](https://doi.org/10.5852/cr-palevol2025v24a22)

Kondas M., Camina S. C., Filipiak P. & Tonarová P. 2025. — Non-pollen palynomorphs from the Devonian (Givetian/Frasnian) of south-central Poland. *Comptes Rendus Palevol* 24 (22): 425–447. <https://doi.org/10.5852/cr-palevol2025v24a22>

ABSTRACT

The first report of the Devonian non-pollen palynomorphs (NPP) from the Givetian/Frasnian of Poland reveals diverse assemblages that contain chitinozoans, scolecodonts, organic tentaculitoids, animal remains, phytoplankton, plant debris, nematophytes and fungi. Analysed material provided the first documentation of chitinozoans from this time interval in Poland and the world oldest occurrence of organic tentaculitoids. These palynomorphs hold significant palaeoenvironmental value. The differentiated palynomorph assemblage indicates a deposition in a shallow water-marine environment with high terrestrial input. The age of the analysed deposits was established as “*Geminospora*” *extensa* (Ex) Miospore Zone to *Geminospora aurita* (Aur) Miospore Zone (conodont zones *hemiansatus* to lower *falsiovalis*).

RÉSUMÉ

Palynomorphes non-polliniques du Dévonien (Givétien/Frasnien) du centre-sud de la Pologne.

Le premier rapport sur les palynomorphes non polliniques (NPP) du Dévonien du Givétien/Frasnien de Pologne révèle des assemblages diversifiés contenant des chitinozoaires, des scolecodontes, des tentaculitoïdes organiques, des restes d'animaux, du phytoplancton, des débris végétaux, des nématophytes et des champignons. Le matériau analysé a fourni la première documentation sur les chitinozoaires de cette période en Pologne et la plus ancienne occurrence des tentaculites organiques au monde. Ces palynomorphes ont une valeur paléoenvironnementale significative. L'assemblage palynomorphique différencié indique un dépôt dans un environnement marin peu profond avec un apport terrestre important. L'âge des dépôts analysés a été établi entre la zone à miospores « *Geminospora* » *extensa* (Ex) et la zone à miospores *Geminospora aurita* (Aur) (zones à conodontes *hemiansatus* à *falsiovalis* inférieur).

KEY WORDS

Non-pollen
palynomorphs,
Devonian,
chitinozoans,
tentaculitoids,
Poland.

MOTS CLÉS

Palynomorphes non-
polliniques,
Dévonien,
chitinozoaires,
tentaculites,
Pologne.

INTRODUCTION

Non-pollen palynomorphs (NPP) have been found in marine and lacustrine deposits throughout most of the geological time. This group comprises a variety of organisms, including prokaryotes as well as unicellular eukaryotes and some specimens of multicellular structure (Agić & Cohen 2021; Waller *et al.* 2023). NPPs show the complex evolution of eukaryotic life, making them particularly significant especially for the Precambrian and Cambrian (see Agić & Cohen 2021; Slater & Bohlin 2022; Waller *et al.* 2023 and references therein). Organic microfossils contain the oldest body fossil evidence for a number of key metazoan clades (Slater & Bohlin 2022). However, they also provide valuable environmental information for Devonian deposits from both Laurussia (e.g. Le Hérisse *et al.* 2009; Wicander & Playford 2022) and Gondwana (e.g. Grahn *et al.* 2016; Noetinger & di Pasquo 2011).

Middle and Late Devonian (Givetian and Frasnian) deposits from south-central Poland (Łysogóry-Radom and Lublin Basins) have never been subjected to detailed palynological investigations involving microfossils other than miospores (e.g. Turnau 1985, 1986, 2011; Narkiewicz *et al.* 2011; Kondas & Filipiak 2022a, b). Both basins were object of studies focused on biostratigraphy disregarding the complexity of Givetian/Frasnian biocenosis (e.g. Malec & Turnau 1997; Kondas & Filipiak 2022a, b).

The Łysogóry-Radom Basin (LRB) has been the topic of numerous palynological studies, covering sediments from boreholes (e.g. Turnau 1985, 1986; Turnau & Jakubowska 1989; Kondas & Filipiak 2022b) and exposed sections (e.g. Malec & Turnau 1997; Turnau & Racki 1999; Kondas & Filipiak 2022a). Compared to the LRB, the palynology of the Lublin Basin (LB) is less well-known. The latest palynological studies in this area were conducted by Turnau (2011), Turnau & Narkiewicz (2011) and Kondas & Filipiak (2022b). In addition, Turnau (2014) addressed the Taghanic Event, discussing the palynological aspects of the entire region. However, none of these papers present the full spectrum of the palynomorphs occurring in the analysed time interval.

The samples, collected from multiple boreholes and exposures scattered across the study regions (Fig. 1) and different miospore horizons, exhibit diverse organic matter content in terms of palynomorph quality and abundance. Samples from the Miłoszów outcrop and four drill cores (Szwejk IG-3, Niesiołowice IG-1, Giełczew PIG 5, Krowie Bagno IG-1) yielded chitinozoans, scolecodont specimens, animal remains, organic tentaculitoids, phytoplankton, a diverse assemblage of plant remains, nematophytes, coenobial algae, and fungi. Notably, Middle and Upper Devonian chitinozoans have never been identified in Poland before. The youngest specimens, obtained by Wrona (1980), were from the Silurian-Devonian boundary (boreholes Ciepeliów IG-1, Białopole IG-1, Strzelce IG-1, Strzelce IG-2). Papers discussing nematophytes from Poland are also scarce. Previously, they were investigated by Filipiak & Zatoń (2011) in the Lower Devonian of southern Poland. The organic tentaculitoids from the studied area were for the first time documented by Wood *et al.* (2004)

and later by Kondas & Filipiak (2021). Other NPPs from the Devonian of Poland were briefly characterised by Filipiak *et al.* (2022), who described a complex palynomorph assemblage from the Emsian of Holy Cross Mountains and Turnau & Racki (1999), who described phytoplankton from Givetian of Holy Cross Mountains (HCM). The most intense studies of NPPs from Poland have focused on Late Devonian phytoplankton from HCM (acritarchs and prasinophytes; e.g. Filipiak 2002, 2005, 2011).

A detailed list of NPP type and taxa is provided in Appendices 1, 2.

GEOLOGICAL SETTING

The investigated area covers the region of the Łysogóry-Radom Basin and Lublin Basin. During the Devonian, south-eastern Poland was part of the south-facing outer shelf of the Laurussia palaeocontinent (Narkiewicz & Dadlez 2008; Narkiewicz *et al.* 2011). The LB developed on a cratonic basement of the East European Platform, which is overlain by Neoproterozoic to Lower Palaeozoic deposits. The south-west margin of LB is limited by LRB, which is developed on Łysogóry terrane that accreted to the craton no later than the Early Devonian (Narkiewicz *et al.* 2011). The Holy Cross Mountains Fault zone limits the basin from the south. Simplified geological structural schemes are shown in Figure 1. Within the LRB, four sections are identified: two Miłoszów outcrops, Szwejk IG-3, and Niesiołowice IG-1. In the LB, two sections are identified: Giełczew PIG 5 and Krowie Bagno IG-1.

MIŁOSZÓW SECTIONS

The outcrop is located in the vicinity of the Miłoszów village (Fig. 1). Two sections have been investigated for NPPs: the M0 section (50°54.07'N, 21°07.18'E) and the M2 section (perpendicular to the beds at 50°54.139'N, 21°7.213'E). The studied interval belongs to the Skały Beds, which consist of mixed limestone and shale and are rich in fossils (e.g. Malec & Turnau 1997; Halamski 2004, 2005; Zatoń & Wrzosek 2020). The Skały Beds are underlain by the Kowala and Wojciechowice Formations (Skompski & Szulczewski 1994; Halamski & Racki 2005) and it is overlain by Świętomarz Beds, which consists of shales and sandstone (Fig. 2; Halamski 2005; Halamski *et al.* 2022).

SZWEJKI IG-3 AND NIESIOŁOWICE IG-2 SECTIONS

The Szwejk IG-3 borehole is located in Kaleń settlement (51°42.451'N, 20°32.34'E), and the Niesiołowice IG-1 is placed in Rybitwy (51°01.52'N, 21°50.06'E). The analysed interval involves the Givetian Bąkowa Formation (with the Łaziska Member included), and consists mostly of siliciclastic and carbonate rocks. The Bąkowa Formation is overlain by the fully carbonate Szwejk Formation, which is subsequently overlain by the siliciclastic-carbonate Iłzanka Formation. Both the Szwejk and Iłzanka formations are Givetian/Frasnian in age (Fig. 2). This lithostratigraphic division follows the scheme proposed by Narkiewicz *et al.* (2011). The Emsian

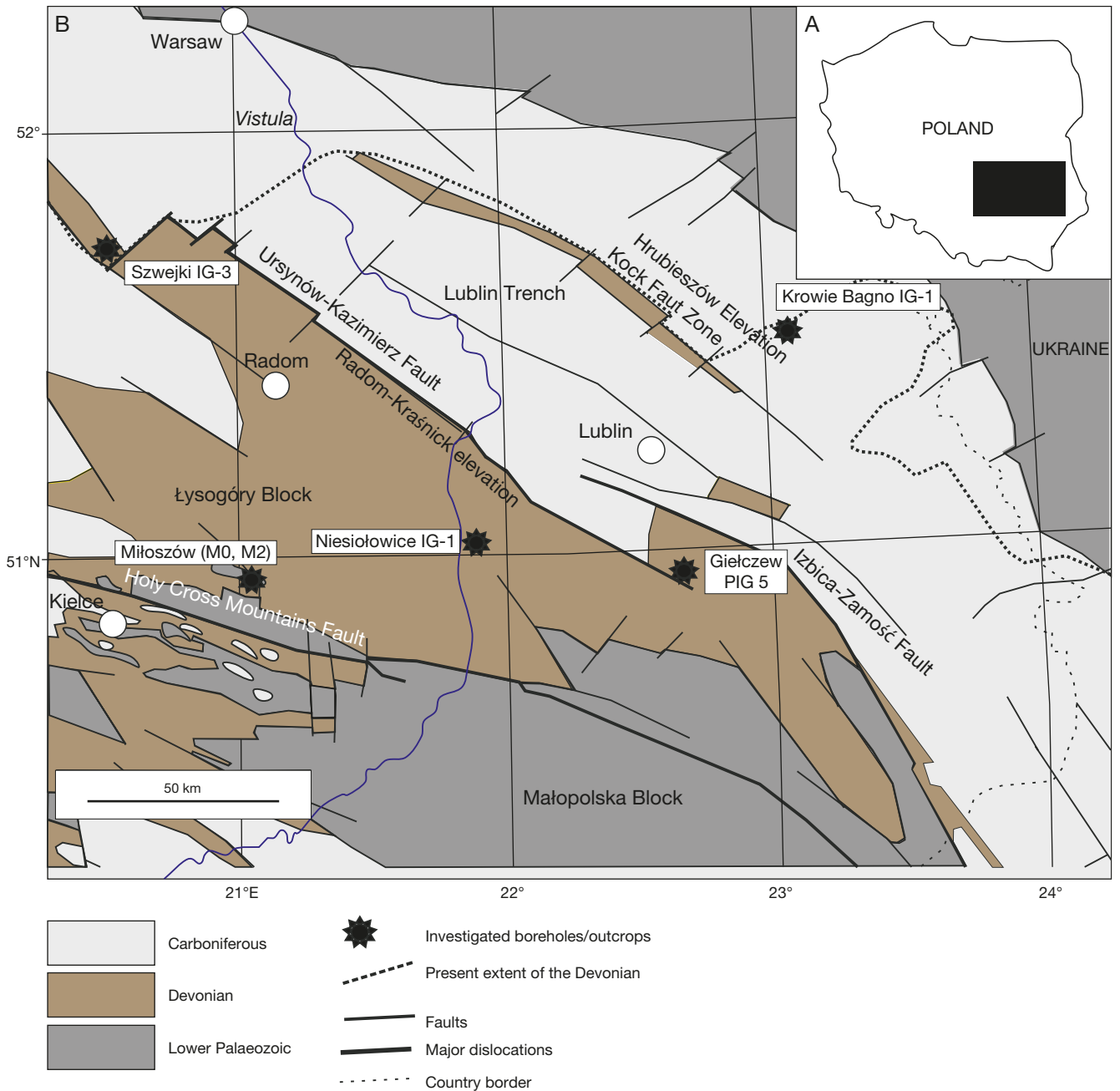


FIG. 1. — Location of the investigated boreholes and outcrops relative to selected geological structures in the area of Łysogóry-Radom and Lublin basins: **A**, simplified map of Poland showing the investigated area; **B**, the investigated area in detail (modified after Narkiewicz *et al.* (2011) and references therein).

to Early Frasnian deposits of the LBR are the result of the rapid sedimentation caused by basement block subsidence (Narkiewicz *et al.* 2011).

GIELCZEW PIG 5 AND KROWIE BAGNO IG-1 SECTIONS

Gielczew PIG 5 is located in the town of Gielczew ($50^{\circ}56.391'N$, $22^{\circ}40.35'E$), and the Krowie Bagno IG-1 borehole is placed in the Pieszowola village ($51^{\circ}30.03'N$, $23^{\circ}09.06'E$). According to lithostratigraphy, the studied interval belongs to the Telatyń Formation and underlies the Modryń Formation (Fig. 2). The Telatyń Formation is characterised by marly dolomites, breccias, and sandstones in its lower part, and carbonate deposits

in its upper part (Narkiewicz *et al.* 2011). The Telatyń Formation represents a carbonate platform and shallow, restricted shelf, while the Modryń Formation represents a carbonate shelf (Narkiewicz *et al.* 2011).

MATERIAL AND METHODS

The 5.3 metres thick M0 section provided 18 samples that contained palynomorphs. Six samples were taken from the 2 metres thick M2 section. The preservation varied: shales contained a well-preserved material, while palynomorphs from

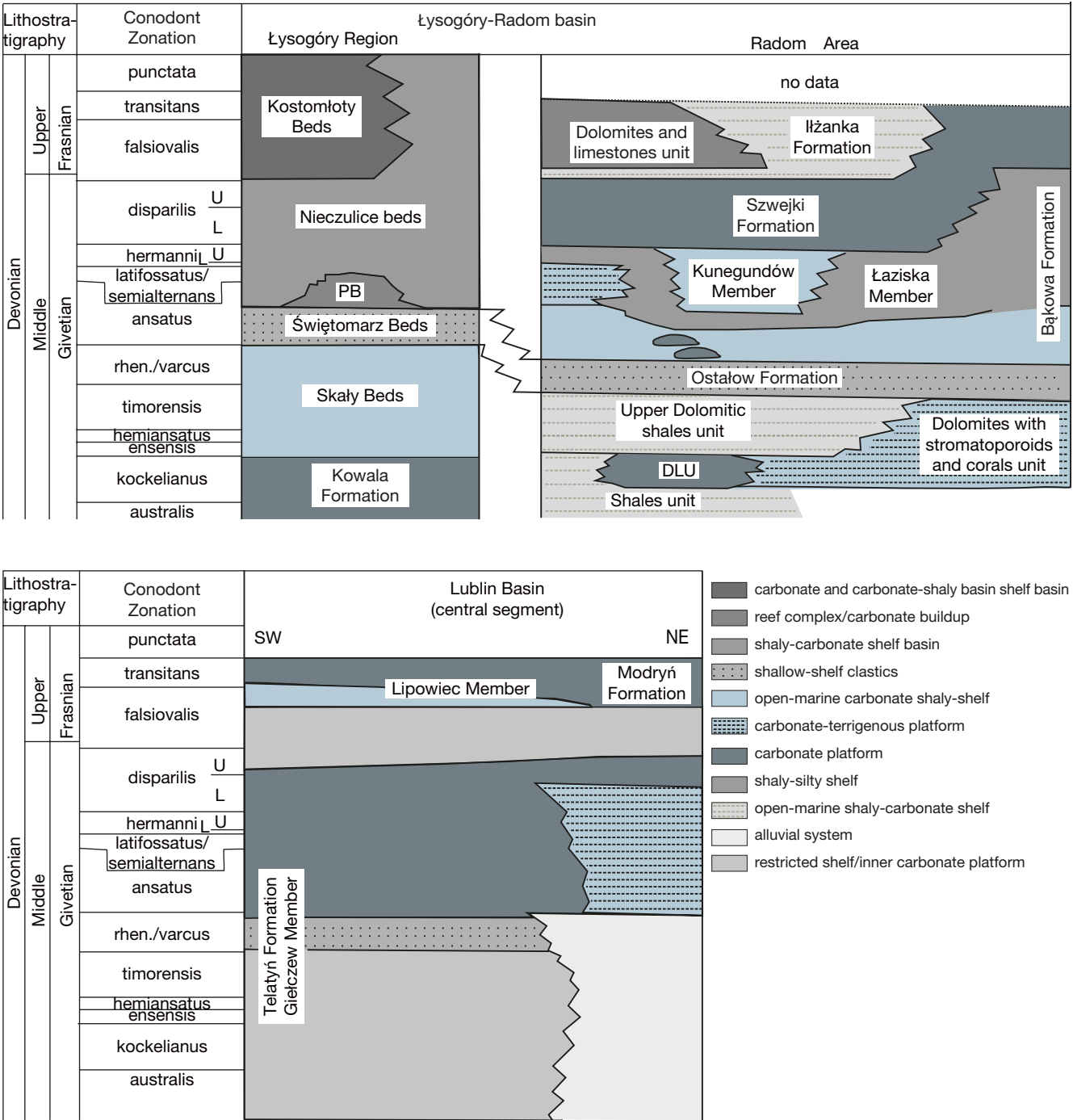


FIG. 2. — Lithostratigraphical diagram of the Givetian-Frasnian deposits in the Łysogóry-Radom and Lublin basins area. Abbreviations: **DLU**, Dolomitic Limestone Unit; **L**, Lower; **PB**, Pokrzywna beds; **U**, Upper (modified after Narkiewicz *et al.* 2011).

limestone were thermally altered (8.0-9.5 on the Spore Color Index scale; see Fischer *et al.* 1981; Suárez-Ruiz *et al.* 2012). Thirty-nine samples were taken from the 720 metres thick section Szwejk IG-3. The preservation was very good, with no signs of thermal changes. Twenty-seven samples were obtained from the 220 metres thick drill core Niesiołowice IG-1; the shale intervals provided well-preserved palynomorphs, but the organic material obtained from the limestone was corroded. Twenty-nine samples were taken from the Giełczew

FIG 5 section, all of which showed very good preservation of the organic matter. Section Krowie Bagno IG-1 (130 metres thick) provided 13 samples with recognisable palynomorphs. All samples are marked in Figure 3. Samples were macerated using the standard palynological procedure (Wood *et al.* 1996; Riding 2021). HCl acid was used to remove the carbonates, followed by 40% HF acid to remove silicates. Any remaining carbonates were eliminated with a second application of HCl. For the samples that were dominated by amorphous

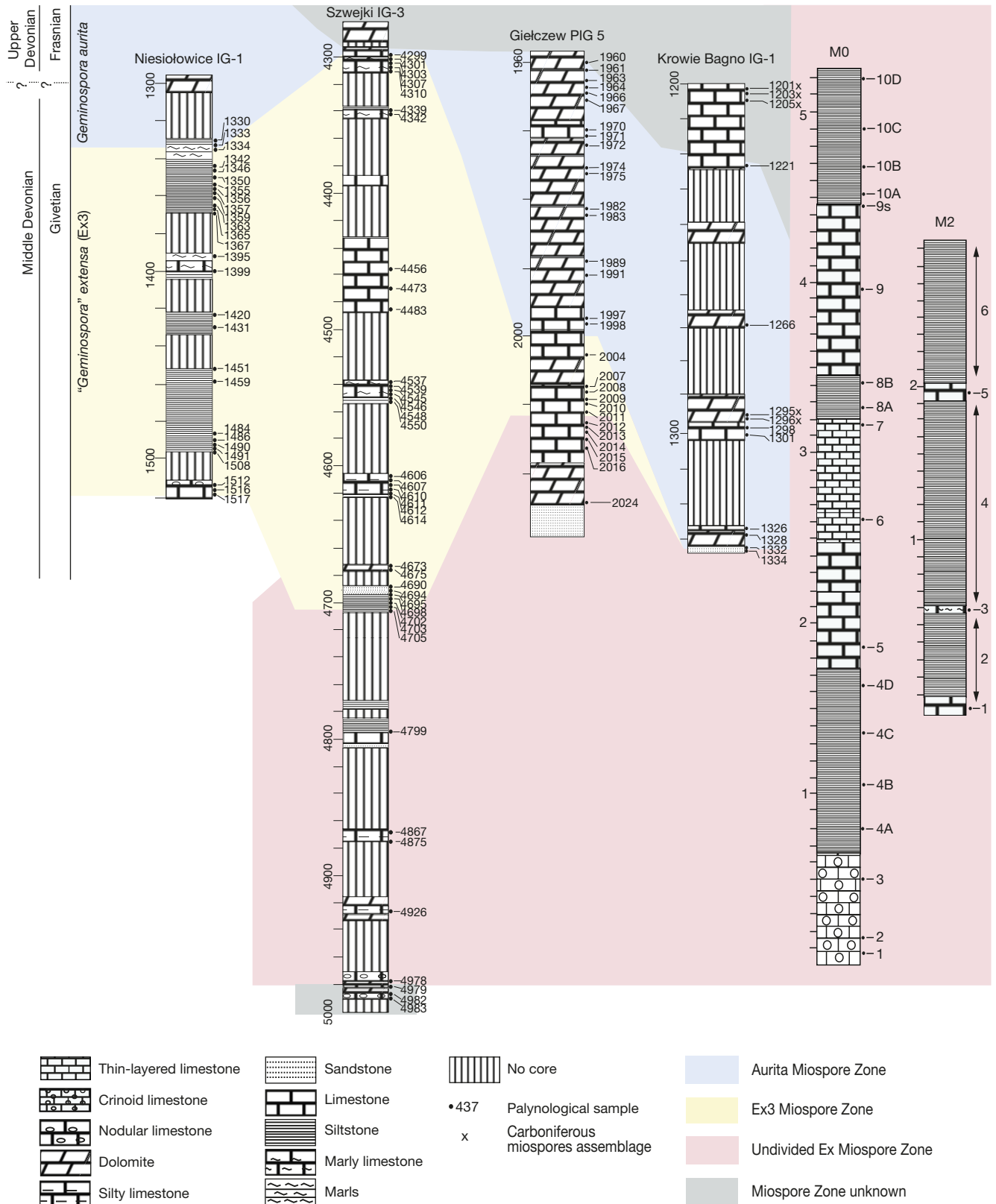


FIG. 3. — Palynostratigraphical correlations between sections Szwejki IG-3, Niesiolowice IG-1, M0, M2 (Łysogóry-Radom Basin) and Gielczew PIG 5, Krowie Bagno IG-1 (Lublin Basin).

TABLE 1. — Morphological features of phytoclasts from section M0 (Miłoszów). Frequency of particular groups is given as the total number.

Sample	Color			Outline			Shape				
	Dark brown-black	Yellow-brown	Light-yellow-colorless	Sharp	Corroded	Frayed	Lath	Equant	Planar	Irregular	Acicular
10D	66	23	11	72	1	27	43	41	12	4	0
10C	72	27	1	79	1	20	47	43	10	0	0
10B	68	29	3	74	0	26	46	38	2	1	1
10A	76	19	5	74	3	23	58	41	12	0	1
9s	83	11	6	64	10	26	32	35	16	12	4
9	86	14	0	66	11	23	33	39	19	9	1
8B	96	4	0	89	8	3	47	37	13	0	3
8A	73	26	1	87	1	12	44	53	2	1	0
7	71	27	2	64	26	10	51	47	0	1	0
6	64	32	4	63	6	31	57	41	0	2	0
5	68	31	1	72	7	21	51	46	3	0	0
4D	87	13	0	88	3	9	97	3	0	0	0
4C	85	15	0	86	5	9	91	4	3	0	2
4B	85	13	2	86	0	14	92	6	1	1	0
4A	87	12	1	84	1	15	93	7	0	0	0
3	74	24	2	78	3	19	57	39	1	1	2
2	89	9	2	91	0	9	64	31	4	1	0
1	67	29	4	68	5	27	67	32	0	1	0

organic matter (AOM) 100% nitric fuming acid was also applied. The obtained organic residue was sieved using 18 µm nylon mesh. Two palynological slides were prepared for each sample. Petropoxy 154 was used as the mounting agent, and Cellosize was applied as a dispersal agent to prevent organic clumping. Palynological analysis was carried out using Optika B-510BF and Nikon Eclipse 50i transmitted light microscopes with NIS Elements-D software and NIK-Cam Pro-1 camera. The chitinozoans and scolecodonts were documented under the scanning electron microscope (SEM) Philips XL 30. All slides and organic residue are housed at the Faculty of Natural Sciences, Institute of Earth Sciences in Sosnowiec. England Finder coordinates were used to establish the location of palynomorphs on the slides. The number of counted phytoclasts is limited due to their total low number, comprising no more than 20% of the total palynomorphs assemblage (see Kondas & Filipiak 2022b). Phytoclasts, as defined by Bostick (1971), include all clay- or fine-sand-sized particles derived from higher plants. Phytoclasts were counted up to 100 specimens in each sample to establish the relative percentage of opaque/translucent particles. Phytoclasts were classified according to the different systems (see Whitaker 1984; Boulter & Riddick 1986; Whitaker *et al.* 1992). In this paper, phytoclasts were divided into cuticles, tracheids and *other*. An additional division was made based on their main morphological features: colour, outline and shape (Tables 1-6). The results are shown as total amounts for each category.

PALYNOSTRATIGRAPHY

In order to determine the age of the investigated deposits, the local stratigraphic scheme proposed by Turnau (2007, 2008) was applied. The microflora of Poland shares many similarities with both Western and Eastern European assemblages (for comparison see Richardson & McGregor (1986) and

Avkhimovitch *et al.* (1993)). For detailed palynostratigraphical analysis of the currently investigated sections, see Kondas & Filipiak (2022a, b).

The age of the analysed deposits ranges from Ex1 Subzone of the “*Geminospora*” *extensa* (Ex) Miospore Zone to *Geminospora aurita* (Aur) Miospore Zone by Turnau (2007, 2008). This corresponds to the conodont zones from *hemiansatus* to lower *falsiovalis* (lowermost Givetian up to lowermost Frasnian). The age correlation between all sections is shown in Figure 3.

RESULTS

CHITINOZOANS

Chitinozoa Eisenack, 1931 is a group of organic-walled microfossils found in marine sediments. Since their biological affinity is still uncertain, these organisms are classified based on their highly variable morphological features (Paris *et al.* 2000). Even though chitinozoans are a widespread group of fossils ranging from Early Ordovician up to the latest Devonian, they have not been previously described from the Middle and Late Devonian of Poland. The recovered specimens are relatively well-preserved, allowing the identification of four confidently assigned species and one species left in open nomenclature (Fig. 4). Exclusively preserved specimens of *Eisenackitina* cf. *spongiosa* Swire, 1990 were found in the Miłoszów section. *Eisenackitina spongiosa* Swire, 1990 shows a variation in length and shape of the vesicle chamber, which can also be observed in specimens from the Miłoszów section. The original description of the species mentions that the reticulate ornamentation covers entirely the vesicle surface, meanwhile, in *E. cf. spongiosa* some glabrous spaces are present on the surface. However, this could be due to the preservation of the material rather than a morphological feature. Another fact to take into account is that *Eisenackitina spongiosa* Swire, 1990, is the

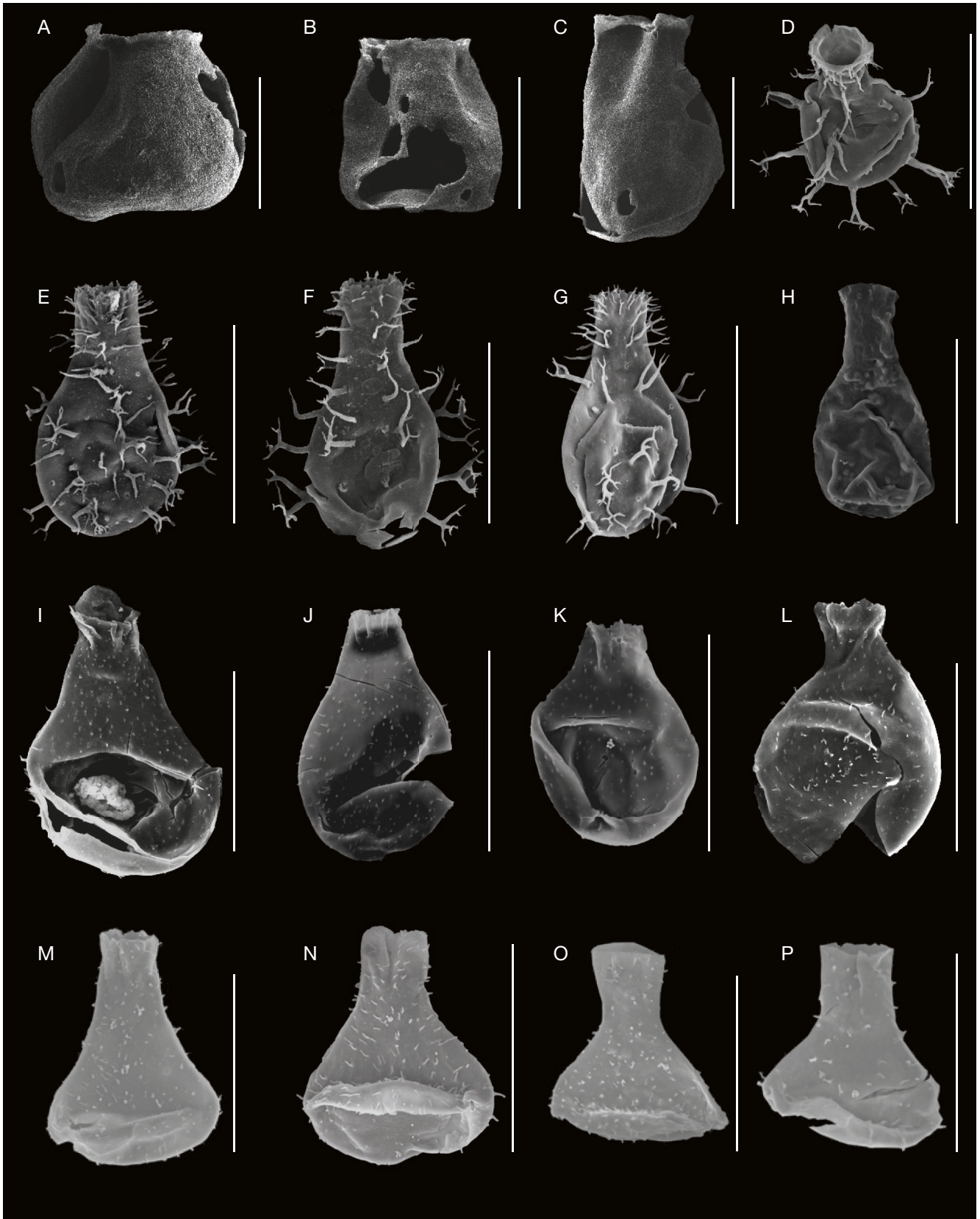


FIG. 4. — Chitinozoans documented from Łysogóry-Radom and Lublin basins: **A-C**, *Eisenackitina* cf. *spongiosa*, section M2, sample 4; **D-G**, *Ramochitina ramosi* Sommer & van Boekel, 1964, section Szwejkki IG-3, depth: 4607 m; **H**, *Lagenochitina crassa* Grignani & Mantovani, 1964, section Szwejkki IG-3, depth: 4703; **I-L**, *Angochitina capillata* Eisenack, 1937, section Niesiołowice IG-1, depth: 1346 m; **M-P**, *Fungochitina pilosa* (Collinson & Scott, 1958), section Gielczew PIG 5, depth: 1966 m. Scale bars, 100 μ m.

TABLE 2. — Morphological features of phytoclasts from section M2 (Miłoszów). Frequency of particular groups is given as the total number.

Sample	Color			Outline			Shape				
	Dark brown-black	Yellow-brown	Light-yellow-colorless	Sharp	Corroded	Frayed	Lath	Equant	Planar	Irregular	Acicular
6	67	32	1	81	17	22	56	41	2	1	0
4	69	25	6	80	20	0	59	39	2	0	0
3	63	34	3	86	12	2	60	38	1	0	1
2	0	0	0	0	0	0	0	0	0	0	0

TABLE 3. — Morphological features of phytoclasts from section Szwejki IG-3. Frequency of particular groups is given as the total number.

Sample	Color			Outline			Shape				
	Dark brown-black	Yellow-brown	Light-yellow-colorless	Sharp	Corroded	Frayed	Lath	Equant	Planar	Irregular	Acicular
4299	31	54	15	78	1	21	66	32	2	0	0
4301	33	58	9	83	2	15	56	39	2	1	2
4303	31	57	12	91	0	9	55	39	1	0	5
4307	28	44	28	89	1	10	54	41	2	1	3
4310	19	79	2	79	7	14	58	42	0	0	0
4339	21	77	2	83	2	15	43	52	1	1	3
4342	46	53	1	86	0	14	47	49	1	2	1
4456	32	63	5	88	0	12	53	44	3	0	0
4537	18	77	5	87	0	13	57	43	0	0	0
4539	21	78	1	88	2	10	61	37	0	0	2
4545	32	65	3	85	3	12	63	34	3	0	0
4548	28	66	6	90	0	10	66	34	0	0	0
4560	35	62	3	91	0	9	67	29	3	0	1
4606	82	18	0	93	0	7	71	26	1	1	1
4607	39	54	7	93	1	6	73	23	2	0	2
4610	52	45	3	96	0	4	75	25	0	0	0
4611	49	47	4	89	2	9	78	17	5	0	0
4612	55	41	4	90	6	4	80	18	1	1	0
4614	41	45	14	93	2	5	65	29	5	0	1
4673	47	41	12	96	0	4	63	33	0	0	4
4675	39	60	1	90	4	6	77	15	5	0	3
4690	40	58	2	92	3	5	46	54	0	0	0
4694	42	51	7	89	0	11	48	51	1	0	0
4695	39	56	5	91	1	8	41	59	0	0	0
4698	43	50	7	93	0	7	45	51	4	0	0
4702	49	45	6	100	0	0	55	45	0	0	0
4703	44	43	13	100	0	0	58	38	3	0	1
4705	0	0	0	0	0	0	0	0	0	0	0
4867	72	28	0	87	0	13	59	39	2	0	0
4875	0	0	0	0	0	0	0	0	0	0	0
4978	53	29	18	71	6	23	58	31	7	3	1
4979	45	33	22	65	9	26	54	36	8	0	1

index species of the *E. spongiosa* regional interval Biozone described by Loydell *et al.* (2010), and is restricted to the Sheinwoodian-Homerian-Wenlock. The Miłoszów section has been assigned to the Givetian (Kondas & Filipiak 2022a), and the difference in stratigraphical range between *E. spongiosa* and *E. cf. spongiosa* could indicate two separate species. The middle part of the Szwejki IG-3 borehole yielded one specimen of *Lagenochitina crassa* Grignani & Mantovani, 1964, and several specimens of *Ramochitina ramosi* Sommer & van Boekel, 1964. It is worth noting that this is the first record of *R. ramosi* outside Western Gondwana (see Camina *et al.* 2025). The lowest and highest siltstones from the Niesiołowice IG-1 borehole provided specimens of *Angochitina capillata* Eisenack, 1937. The middle and

upper part of the Giełczew PIG 5 section yielded several specimens of *Fungochitina pilosa* (Collinson & Scott, 1958).

SCOLECODONTS

Scolecodonts are common zoomorphs occurring from the Cambrian to Recent, but they are most common in the Lower Palaeozoic (Kielan-Jaworowska 1966; Szaniawski 1996; Eriksson *et al.* 2004). They are dispersed elements of proboscidian jaw apparatuses of the polychaete annelids. Only a single paper described Frasnian scolecodonts from Poland (Szaniawski & Wrona 1973). In the current study, the number of scolecodonts is limited as they were only a by-product of the maceration. Many of the specimens are fragmented, with the best-preserved ones presented in Figure 5.



FIG. 5. — Scolecodonts and organic tentaculitoids from Łysogóry-Radom and Lublin basins: **A**, Paulinitid? maxilla, section Gielczew PIG 5, depth: 1966 m; **B**, *Atraktopirion* sp., right first maxilla, section Niesiołowice IG-1, depth: 1459 m; **C**, Paulinitid second maxilla, section Niesiołowice IG-1, depth: 1491 m; **D**, *Mochtyella*? sp., section Krowie Bagno IG-1, depth: 1298 m, EF: O17/2; **E**, Paulinitid first maxilla; section Gielczew PIG 5, depth: 2008 m, EF: K19/2; **F**, Polychaetaspid? maxilla, section Gielczew PIG 5, depth: 2008 m, EF: J11/3; **G**, *Mochtyella* sp., left MI, similar to *Mochtyella* sp. 1 *sensu* Tonarová *et al.* 2016, Miłoszów, section M0, sample 10A; **H**, *Kielanopirion* sp., first maxilla, section Gielczew PIG 5, depth: 2007 m, EF: K18; **I**, anterior teeth, placognatha, section Gielczew PIG 5, depth: 2008 m, EF: F23/2; **J, K, M, O, Q**, organic tentaculitoids, Dacryoconarida, section Szwejki IG-3, depth: 4979 m: **J**, EF: L14/2; **K**, EF: S19/3; **M**, EF: R15/2; **O**, EF: N9/1; **Q**, EF: R23/3; **L, N**, organic tentaculitoids, Dacryoconarida, section Szwejki IG-3, depth: 4705 m: **L**, EF: F21/4; **N**, EF: O14/2. Scale bars: A, 20 μ m; B, D-Q, 50 μ m; C, 100 μ m.

TABLE 4. — Morphological features of phytoclasts from section Niesiolowice IG-1. Frequency of particular groups is given as the total number.

Sample	Color			Outline			Shape				
	Dark brown-black	Yellow-brown	Light-yellow-colorless	Sharp	Corroded	Frayed	Lath	Equant	Planar	Irregular	Acicular
1330	71	27	2	78	3	19	65	33	2	0	0
1333	55	45	0	82	17	1	58	36	4	0	2
1334	61	38	1	82	18	0	54	45	1	0	0
1342	43	54	3	86	14	0	54	33	9	2	2
1346	98	2	0	88	1	11	47	50	2	0	1
1357	46	51	3	79	3	18	46	45	8	0	1
1359	82	16	2	85	0	15	44	56	0	0	0
1363	84	16	0	89	0	11	58	39	1	2	0
1365	61	35	4	90	0	10	48	47	4	0	1
1367	60	40	0	87	0	13	55	37	7	0	1
1395	72	22	6	92	1	7	47	53	0	0	0
1399	56	44	0	90	1	9	53	34	11	0	2
1431	81	11	8	95	0	5	49	31	18	0	2
1459	76	24	0	97	0	3	56	32	9	0	3
1484	65	27	8	100	0	0	63	35	1	1	0
1486	65	34	1	96	0	4	41	56	1	1	1
1490	49	47	4	98	0	2	63	28	10	0	0
1491	55	45	0	100	0	0	68	31	1	0	0
1508	63	22	15	96	0	4	58	40	1	0	1
1512	64	32	4	100	0	0	39	57	3	1	0
1415	54	45	1	97	0	3	72	28	0	0	0
1517	47	49	4	89	0	11	33	49	15	0	3

The jawed polychaete fauna from the Givetian-Frasnian of Radom-Lublin area has a similar composition as other coeval faunas. At least five families are present, i.e., Paulinitidae Lange, 1947, Kielanoprionidae Szaniawski, 1968, Mochtyellidae Kielan-Jaworowska, 1966, Atraktoprionidae Kielan-Jaworowska, 1966, and Polychaetaspidae Kielan-Jaworowska, 1966. Determining the genus and species level is rather difficult due to the small collection size, as proper determination typically requires at least the left and right first maxillae. However, the genera *Atraktoprion* Kielan-Jaworowska, 1962 (Fig. 5B), *Kielanoprion* Szaniawski, 1968 (Fig. 5H), and *Mochtyella* Kielan-Jaworowska, 1961 (Fig. 5D, G) can be determined with certainty. Additionally, there are several anterior teeth probably belonging to placognath taxa.

ORGANIC TENTACULITOIDS

The six specimens of organic tentaculitoids were previously briefly mentioned from the Szwejki IG-3 section (depths 4 979 and 4 705 meters; see Kondas & Filipiak 2022b). Considering the conical, tapering shell shape and bulbous embryonic chamber, they are classified within the Dacryoconarida. Although all specimens were fragmented, they exhibited noticeable annular thickenings forming ribs. The length of the two most complete specimens varied from *c.* 142 μm up to *c.* 155.10 μm . The striation displays a regular, sigmoidal pattern (Fig. 5).

REMAINS OF EURYPTERID RESPIRATORY ORGANS

Eurypterid respiratory organs were found only in the Niesiolowice IG-1 section. They are preserved as fragments only. The surface of the spinules is covered by a hexagonal pattern (9 $\times$ 9 μm) formed by thin projections, *c.* 9–11 μm in length and *c.* 3–4 μm in width (Fig. 6D). Often these appa-

tuses are terminated with a solid spine (Manning & Dunlop 1995), which was not observed in the analysed material. Similar to spineless forms described by Filipiak & Zatoń (2011) from the Early Devonian of Holy Cross Mountains, the currently observed distinctive cuticles are interpreted as eurypterid respiratory organs (“gill tracts” or *Kiemenplatten*; e.g. Manning & Dunlop 1995; Filipiak & Zatoń 2011).

OTHER ARTHROPOD REMAINS

Arthropod remains were recorded in small quantities in the studied samples (Fig. 6). They mainly occurred individually in the boreholes Szwejki IG-3 (4 537 m) and Niesiolowice IG-1 (1 365 m). They are relatively large (e.g. 280 $\times$ 180 μm) in the form of more or less rectangular, bent cuticles. Other remnants preserve the conical shape (425 $\times$ 215 μm) with the characteristic two oval holes measuring 25 $\times$ 15 and 24 $\times$ 30 μm . Additionally, another category of residues consists of remains of tubular forms with a characteristic external ornamentation resembling “rings” fitted into one another. The diameter of these tubes varies between 110 and 160 μm , while the width of the individual “rings” is more or less constant at *c.* 23 μm .

ACRITARCHS AND PRASINOPHYTES

Phytoplankton, including prasinophytes and acritarchs, were present in all sections, though both groups were limited in number (see details in Kondas & Filipiak 2022a, b). The acritarch assemblage was dominated by *Micrhystridium*, *Multiplicisphaeridium* and *Verhachium* genera. The prasinophytes were mainly represented by thin-walled, folded phycmata of different sizes (*Leiosphaeridia* spp.). Individual, but well-preserved taxa were documented on plates 3 and 4 in Kondas & Filipiak 2022b).

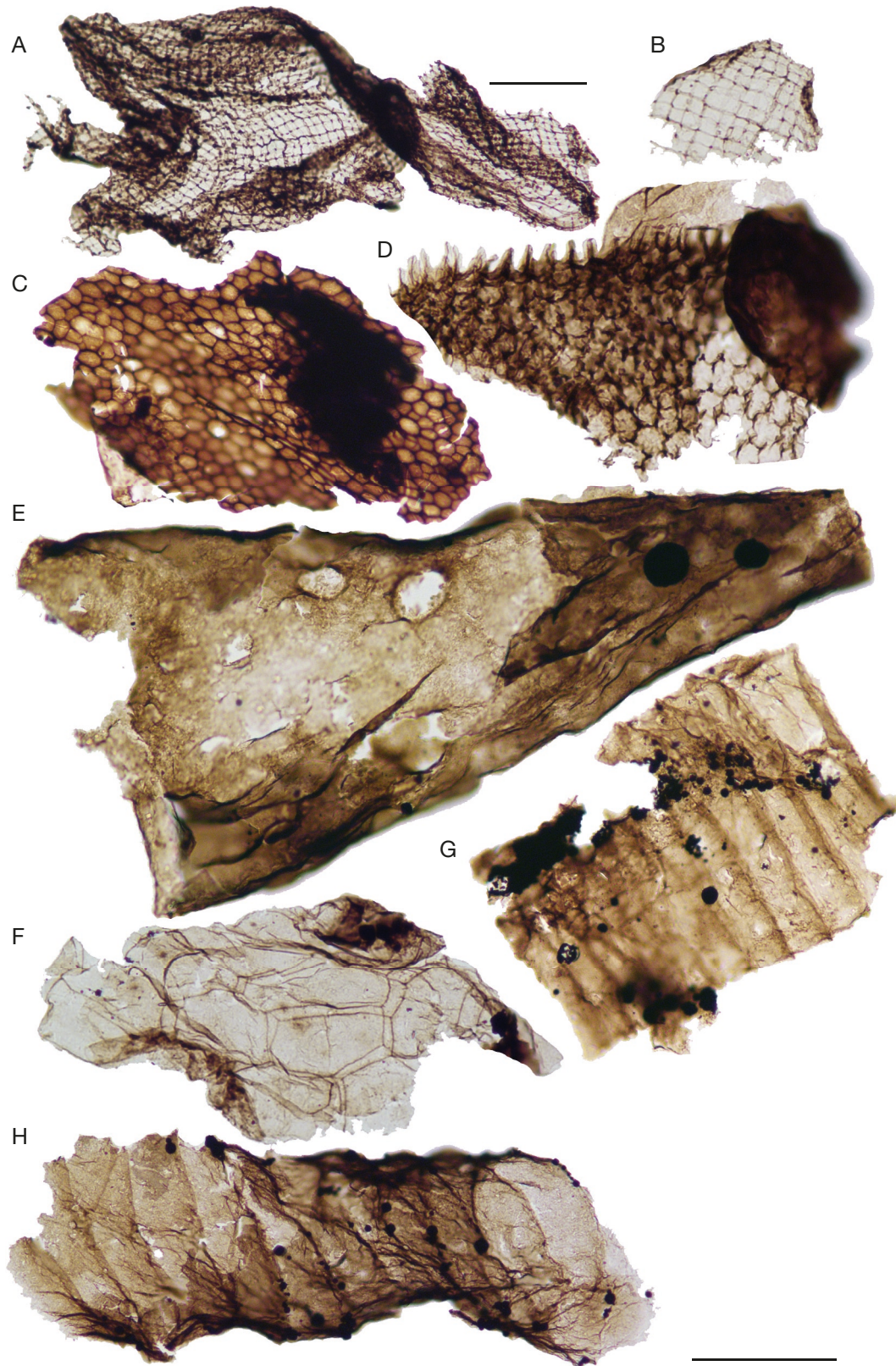


FIG. 6. — Plant and animal debris from Łysogóry-Radom and Lublin basins: **A, B**, *Mussivum gradzinskii* Wood & Turnau, 2001, section Niesiołowice IG-1, depth: 1491 m; **A**, EF: S16/4; **B**, EF: H29/3; **C**, *Nematothallus* sp., section Niesiołowice IG-1, depth: 1491 m, EF: F30; **D**, eurypterid respiratory organ, section Niesiołowice IG-1, depth: 1491 m, EF: U25/4; **E**, Arthropod remain, section, Szwejki IG-3; depth: 4537 m, EF: K35; **F**, thin cuticle, section Niesiołowice IG-1; depth: 1491 m, EF: K32/3; **G, H**, remains of ribbed animal (?) pipes: **G**, section Szwejki IG-3, depth: 4537 m, EF: E49/4; **H**, section Niesiołowice IG-1, depth: 1491 m, EF: C18/3. Scale bars: **A**, 100 μ m; **B-H**, 50 μ m.

TABLE 5. — Morphological features of phytoclasts from section Gielczew PIG 5. Frequency of particular groups is given as the total number.

Sample	Color			Outline			Shape				
	Dark brown-black	Yellow-brown	Light-yellow-colorless	Sharp	Corroded	Frayed	Lath	Equant	Planar	Irregular	Acicular
1960	91	9	0	88	0	12	52	45	2	0	1
1961	88	6	6	92	0	8	47	43	1	2	7
1963	89	11	0	95	1	4	64	28	5	2	1
1964	0	0	0	0	0	0	0	0	0	0	0
1966	96	4	0	92	0	8	66	33	1	0	0
1967	79	18	3	91	1	8	78	19	2	0	1
1970	79	7	14	90	2	8	69	22	6	1	2
1971	88	3	9	93	0	7	49	51	0	0	0
1972	0	0	0	0	0	0	0	0	0	0	0
1974	98	2	0	97	0	3	47	49	3	0	1
1975	90	8	2	97	1	2	44	55	0	1	0
1982	69	30	1	93	2	5	49	48	3	0	0
1983	0	0	0	0	0	0	0	0	0	0	0
1989	89	11	0	89	9	2	66	29	5	0	0
1997	91	9	0	83	0	7	88	12	0	0	0
1998	86	14	0	91	0	9	79	19	1	1	0
2004	84	15	1	90	2	8	66	33	1	0	0
2007	63	35	7	89	4	7	33	65	1	0	1
2008	32	47	21	99	0	1	49	51	0	0	0
2009	39	57	4	94	2	4	52	44	1	1	2
2010	43	48	9	100	0	0	50	39	7	4	0
2011	0	0	0	0	0	0	0	0	0	0	0
2012	0	0	0	0	0	0	0	0	0	0	0
2013	99	1	0	71	25	4	29	69	1	1	0
2014	97	3	0	68	31	1	31	69	0	0	0
2015	99	1	0	57	42	1	22	71	6	1	0
2024	96	4	0	66	32	2	29	66	3	1	1

TABLE 6. — Morphological features of phytoclasts from section Krowie Bagno IG-1. Frequency of particular groups is given as the total number.

Sample	Color			Outline			Shape				
	Dark brown-black	Yellow-brown	Light-yellow-colorless	Sharp	Corroded	Frayed	Lath	Equant	Planar	Irregular	Acicular
1221	76	12	12	87	0	13	95	5	0	0	0
1298	77	21	4	90	1	9	96	3	1	0	0
1301	82	17	1	87	2	11	87	12	1	0	0
1326	88	10	2	100	0	0	65	25	0	0	10
1328	91	7	2	100	0	0	53	45	0	0	2
1332	65	29	6	98	0	2	51	43	2	0	4

PLANT DEBRIS

Some authors consider the phytodebris to be an assemblage of plant and fungal remains (see Wellman & Ball 2021). However, in this paper, fungal remains are separated from the phytodebris. All analysed sections contained plant remains consisting of cuticles, cuticle-like sheets, tracheids, tracheids-like structures, and other particles with no recognisable structures. All sections provided plant debris as the most numerous types of NPPs. Examples of plant-derived clasts are shown in Figure 7.

Land plants are a significant source of microfossils with high fossilization potential due to their composition (Tyson 1995). The resistance of the plant microfossils allows them to be transported over long distances, usually by wind or water, providing valuable information about rock facies and depositional conditions (Tyson 1995). Usually, fragmented plants are preserved as spores, megaspores, pollen or seeds, or

disarticulated fragments (tracheids, cuticles, other plant fragments). Plant remains that could be classified taxonomically were described in detail in Kondas & Filipiak (2022a, b).

Currently described plant remains occur in two groups: opaque and translucent ones with the dominance of the latter group (Appendix 3A-F).

All opaque cuticles ranged from pale brown to brown, and exhibited visible cellular patterns (see Tables 1-6). Most of them presented sharp outlines and some were slightly irregular showing the undegraded preservation (see Tables 1-6; Fig. 7). Each section also contained tracheids, which displayed internal annular and spiral thickenings (Fig. 7; Appendix 3A-F). The ratio of opaque and translucent particles varied across sections. Sections M2, Szwejki IG-3 and Krowie Bagno IG-1 showed the lowest content of opaque remains (Appendix 3B, C, F), while sections M0, Niesiołowice IG-1 were characterised by



FIG. 7. — Phytoclasts from Łysogóry-Radom and Lublin basins: **A**, lath shaped, striated phytoclast, section Szwejki IG-3, depth: 4695 m, EF: K12; **B**, lath shaped, striated phytoclast, section M2, sample 2, EF: L10/1; **C**, unregular-shaped phytoclast, section Krowie Bagno IG-1, depth: 1298 m, EF: J10/1; **D**, sheet, folded phytoclast, section Gielczew PIG 5, depth: 2009 m, EF: H1/3; **E**, striated and pitted phytoclasts, section Szwejki IG-3, depth: 4695 m, EF: 15X; **F**, pale yellow, sheet phytoclast, section Gielczew PIG 5, depth: 2004 m, EF: 21F; **G**, dark coloured tracheid, section M2, sample 4, EF: K10/3; **H**, tracheids, section Szwejki IG-3, depth: 4695 m, EF: M18; **I**, dark-brown tracheid, section Szwejki IG-3, depth: 4560 m, EF: P22/1; **J**, dark coloured, corroded phytoclast, section Gielczew PIG 5, depth: 2009 m, EF: F11/4; **K**, opaque, lath phytoclasts, section M2, sample 2, EF: J21/2; **L**, opaque phytoclasts, section M2, sample 2, EF: W3; **M**, opaque tracheid, section M2, sample 2, EF: D3/4. Scale bar: 50 μ m.

a high amount of opaque phytoclasts (Appendix 3A, D). The highest presence of black and opaque clasts, mostly with sharp outline and no internal structure, was documented in section Gielczew PIG 5 (Table 5; Appendix 3E). The morphological features of phytoclasts were similar across all sections. In each section, the assemblage was dominated by dark brown and brown particles, except in section Szwejki IG-3, where the assemblage consisted mostly of brown to yellow particles (Tables 1–6). The phytoclasts are predominantly sharp in outline, with lath and equant shapes being the most dominant (Tables 1–6).

NEMATOPHYTES

The nematophytes are an enigmatic group of organisms, whose origin remains uncertain (Taylor & Wellman 2009). Some recognised cuticles possess a reticulate pattern with a smooth outer surface without stomata, those were reported from Szwejki IG-3, Niesiołowice IG-1 and Gielczew PIG 5

sections (Fig. 6). These cuticles have been assigned to the genus *Nematothallus*. The inner surface is covered with a reticulum of flanges separating more or less polygonal cell-like fields, most of which are solid, though some possess natural perforation. The size of the largest cuticle is $150 \times 150 \mu\text{m}$, but a single reticulate field is $c. 10 \times 6 \mu\text{m}$. *Nematothallus* is considered to be the organism that shows the features of both plants and animals (Gensel *et al.* 1990; Edwards *et al.* 2013). These organisms consist of a peripheral cortex covered by a cuticle, above a palisade zone of wider hyphae, and a basal zone comprising wefts of smaller hyphae (Edwards *et al.* 2013).

ALGAE REMAINS

Coenobial sheets are preserved in relatively large sets (e.g. $c. 290 \times 135 \mu\text{m}$), often folded and bent (Fig. 6A, B). They are represented by one species: *Mussivum gradzinskii* Wood

& Turnau, 2001, and its presence was documented in Niesiołowice IG-1 section (depth 1 491 m; Fig. 6A, B). They are uni-layered and planar, with thin-walled square individual cells. The aggregation of 16 cells is enveloped by a slightly thicker, more distinct wall. Each cell measures $5 \times 5 \mu\text{m}$, with a wall height of *c.* 1.5–1.8 μm . According to Wood & Turnau (2001), who first described these taxa from the Devonian of Poland, *Mussivum* belongs to the coenobial Chlorococcales (hydrodictyacean) fresh-water algae.

FUNGI AND FUNGI-LIKE FILAMENTS

Observed taxa were assigned to fungi and fungi-like filaments on the basis of their size, surface ornament and branching pattern (Fig. 8). The *Tortotubus*-like filaments were documented from Szwejki IG-3 borehole (depth 4 342 m). Two specimens (A and B, Fig. 8A, B) of different widths were observed. They have a complex structure with an internal tube usually surrounded by a fragmentarily preserved very thin envelope.

The specimen A possesses an elongate filament with a width of 22.3–33.6 (mean 28) μm , and specimen B is narrower [15.9–24.7 (mean 19.9)] μm . The internal structure of specimen A measures 8.7 to 22.8 μm (mean 16.7 μm) in width, and for specimen B, it measures 7.7 to 10 μm (mean 9.4 μm). The A specimen is 530 μm long and has a branch length of 250 μm , whereas specimen B is a curved tube with a length of 450 μm . Both specimens are incompletely preserved. The surface of the external sheath is sometimes covered with fine ornamentation of clustered grana mixture (*c.* 1 μm diameter) but is mostly smooth or with very single distributed ornamentation. Within the envelope, the presence of single crystals of pyrite was detected. Considering the set of features outlined above, the specimens from the Szwejki IG-3 borehole resemble *Tortotubus* Smith, 2016, described from the Ludfordian (Silurian) of Sweden (Gotland; Smith 2016; see also further discussion about this taxon in Auxier *et al.* 2016).

Two specimens of *Laevitubulus frondifera* Wellman, 1995 were identified from the section Niesiołowice IG-1 (depth 1 459 m; Fig. 8D, E). The first specimen with a length of *c.* 295 μm and the second *c.* 214 μm . Their diameters are similar, averaging 6.4 μm and 5.4 μm for the second specimen. Parallel tubes are interconnected by perpendicular branches forming H-patterns. The surfaces of the filaments are smooth and not covered with any ornamentation. Comparing *Tortotubus*-like filaments, specimens from Niesiołowice IG-1 borehole (1 459 m) have smaller filament diameters and no external envelope.

The presence of *Laevitubulus plicatus* Burgess & Edwards, 1991 was observed in the Szwejki IG-3 borehole (depths 4 299 m, 4 342 m) and Giełczew PIG 5 borehole (depths 1 966 m and 1 982 m). This species includes all individual tubes with a folded wall (Fig. 8K). It is difficult to determine their total length because they have been preserved in fragments. Nevertheless, the measured specimens range between 210 and 600 μm in length, and their width is between 20 and 35 μm and *c.* 40 μm . Only one specimen possesses natural terminations in a form of a tapering ending.

The unbranched tubes with consistent diameter (7 or 12 μm) and opaque walls occurred in the Szwejki IG-3 borehole at depth of 4 310 m (Fig. 8C). It is difficult to determine whether these tubes belong to *Laevitubulus tenuis* or *Laevitubulus crassus* without seeing the thickness of the wall, which is the diagnostic feature of these species (Burgess & Edwards 1991). Thus they were classified as *Laevitubulus* sp. Burgess & Edwards, 1991.

The specimens of *Porcatitubulus cf. spiralis* Burgess & Edwards, 1991, found in Niesiołowice (depth 1 486 m) have an unspecified complete length of *c.* 250 μm and 28 μm in width. At one end there is a visible natural ending forming a thicker lip (the width of the thickening is *c.* 2.5 μm). A characteristic feature of these specimens is the very fine ornamentation consisting of a dense internal spiral less than 0.5 μm thick (Fig. 8L). This specimen differs from *P. spiralis* Burgess & Edwards, 1991 by having much finer internal ornamentation and a characteristic thickening at the end, which was not determined by Burgess & Edwards (1991).

Not all organic remains can be associated with the previously described taxa. Some lack all the necessary taxonomic characteristics, particularly the fungal remains (?) preserved as organic mats (Fig. 8F, G). The specimen shown in Figure 8F is similar to *Ornatifilum* Burges & Edwards, 1991 (see figs 55–60) but lacks the granulated external ornamentation. These mats are smooth, non-banded, with relatively small diameter (6–8 μm). The fibers are of various lengths, broken, without natural ends. The thickness of the walls varies, with some being translucent and others almost black. They are usually branched, and septa are rarely observed; some filaments possess long constructions (Fig. 8F).

DISCUSSION

The main objectives of this paper are to document the relationship of NPPs to the palaeoenvironment and to complete the palynological study by Kondas & Filipiak (2022a, b) conducted on the same sections.

The detailed observation of the NPPs obtained from the studied sections show the complexity of the Givetian and earliest Frasnian biocoenosis of Łysogóry-Radom and Lublin basins. To some extent, the taxonomical composition of the studied group shows similarities with NPP assemblages recorded worldwide. Each section presents a limited number of chitinozoans and scolecodonts combined with other animal remains, acritarchs and prasinophytes with massive land-derived input, mostly phytoclasts. This suggests a shallow marine setting; moreover, the presence of animal remains, if they are not transported, indicates oxic conditions. Some of the arthropod remains are interpreted as respiratory organs of eurypterids, and their presence is characteristic of marine environments, however this issue remains an open problem for further discussion (Laurin 2024 and references therein).

The chitinozoan assemblage shows low taxonomic richness, with some species being problematic, such as *E. cf. spongiosa* (see discussion above). However, they support the



FIG. 8. — Tubes: various tubular remains: **A, B**, *Tortotubus*-like filaments, section Szwejk IG-3, depth: 4342 m: **A**, EF: K12; **B**, EF: N20. **Arrows** indicate a thin partly preserved envelope about the main filament; in **A** the **arrow** is positioned in the pustule area; **C**, *Laevitubulus* sp. section Szwejk IG-3, depth: 4310 m, EF: W32; **D, E**, *Laevitubulus frondifera* Wellman, 1995, section Niesiolowice IG-1, depth: 1459 m; **D**, EF: J13/3; **E**, EF: P18. Both specimens possess characteristic H-branching connections; **F, G**, clusters of branching filaments; section Niesiolowice IG-1, depth: 1491 m; **F**, EF: J29/1; **G**, EF: F17. Most branches at obtuse angles (**white arrows**). **F**, some filaments have long constrictions (**black arrow**); **H-K**, *Laevitubulus plicatus* Burgess & Edwards, 1991: **H**, section Szwejk IG-3, depth: 4299 m, EF: S29; **K**, depth: 4342 m, EF: C25/2; **I**, section Gielczew PIG 5, depth: 1966 m EF: O29/1; **J**, depth: 1982 m, EF: H18/4. **White arrow** in **H** indicates natural ending; **L**, *Porcatitubulus* cf. *spiralis*, Niesiolowice IG-1, depth: 1486 m, EF: O29. **Black arrow** indicates the delicate internal spiral ornamentation. Scale bar: 50 μ m.

Givetian and earliest Frasnian age for the studied sections. Three taxa were documented from the Radom part of LRB. *Lagenochitina crassa* Grignani & Mantovani, 1964 observed in Szwejki IG-3 section, has so far only been recorded by Grignani & Mantovani (1964) in the Middle-Late Devonian of Morocco. Another specimen from that section, *Ramochitina ramosi* Sommer & van Boekel, 1964 is a common species from the Eifelian to the middle Givetian of Brazil (Sommer & van Boekel 1964; Lange 1967a, b; Quadros 1982; Grahn *et al.* 2000; 2003; 2008; 2010 and Grahn & Melo 2005). It has also been registered from the early-middle Givetian of central and south Bolivia (Grahn 2002), and from the early Givetian of east Paraguay (Grahn *et al.* 2002). This species has been synonymised with *Ramochitina boliviensis* Grahn, 2002, extending the records of the species to northwestern Argentina (Camina *et al.* 2025). Previously restricted to Western Gondwana, this record marks the first occurrence outside that region. *Angochitina capillata* Eisenack, 1937 documented in Niesiołowice IG-1 borehole, first appears in the Middle Ordovician and ranges into the Famennian; however, some authors have suggested that Devonian specimens could possibly be a different species (Winchester-Seeto 1993). The specimens from Niesiołowice IG-1 section resemble those *A. capillata* described by Urban & Newport (1973) from the Middle Devonian of Iowa, and Askew & Russell (2019) from the Middle Devonian of northern Spain. Long-ranging taxon of *Fungochitina pilosa* (Collinson & Scott, 1958), was documented from LB, Giełczew PIG 5 section. *Fungochitina pilosa* has been well reported worldwide from the late Silurian to the late Frasnian, nonetheless, it is a common species within the biozones for the middle and late Givetian (Paris *et al.* 2000; Grahn 2005).

Scolecodonts were preserved in very limited number, but it can be noticed that very similar scolecodont assemblages were reported from Eifelian-Frasnian from the following localities: Middle to Upper Devonian of United States: New York (Eller 1934, 1936, 1941), Missouri (Sylvester 1959), Frasnian of Iowa (Eller 1963; Hogancamp 2017); Ontario, Lake Erie district (Stauffer 1939; Eller 1964); Eifelian of the Eifel Mountains, Germany (Tonarová *et al.* 2016); Givetian of France (Taugourdeau 1970); Frasnian of France (Taugourdeau 1971); Devonian of Egypt (El Shamma *et al.* 2011, 2019; Makled *et al.* 2021); Upper Devonian of Poland (Szaniawski & Wrona 1973) and Devonian of the Prague Basin (Tonarová *et al.* 2017, and unpublished collection). It can be summarised that the Middle and Late Devonian jawed polychaetes were cosmopolitan. Other zoomorphs were present as single specimens; however they showed exceptional diversity compared to other Middle Devonian NPPs associations (e.g. Bosetti *et al.* 2010; Noetinger & di Pasquo 2011; Grahn *et al.* 2016). The organic tentaculitoids classified as Dacryoconarida found in Szwejki IG-3 section were an extremely small group of NPPs. Previously, there were only four world records of organic tentaculitoids; twice from the Frasnian deposits of Poland (Wood *et al.* 2004; Filipiak & Jarzynka 2009), and twice from the Famennian of Russia (Marshall & Tel'nova 2012, 2017). Considering the deposits' age established as the Ex

Miospore Zone, the tentaculitoids from Szwejki IG-3 section are the oldest documented specimens of these palynomorphs. Another diversified group of NPPs were fungi, which occur as hyphae, hyphal structures and thick-walled spores (Shumilovskikh *et al.* 2021). Fungi show a broad range of ecological tolerances, thus their presence may indicate a variety of palaeoenvironments, from terrestrial, through freshwater to proximal marine close to the fluvio-deltaic source areas (e.g. deltaic, estuarine, lagoonal facies; Tyson 1995; Mendonça Filho *et al.* 2011; Nuñez Otaño *et al.* 2021). Interwoven mats of smooth filaments, similar to specimen shown in Figure 8F, have been documented from the early Silurian of Virginia (United States; Pratt *et al.* 1978: pl. IV, 10) and lately from the Lower Devonian of Bukowa Góra Quarry (Filipiak *et al.* 2022: pl. V, 1, 5). Sections Szwejki IG-3, Niesiołowice IG-1, Giełczew PIG 5 and Krowie Bagno IG-1 were enriched in presence of nematophytes, fungi and fungal-like filaments confirming the proximal, near-shore environment area of deposition. Especially well-preserved, unfragmented specimens of hydrodictyacean chlorococcalean algae *Musivum gradzinskii* confirm a low energy environment and indicate the relatively short transportation. These algae have been reported from Ordovician to Frasnian in a few localities worldwide, always representing proximal settings (e.g. Filipiak 2011; Marshall *et al.* 2017; Navidi Izad *et al.* 2020; Filipiak *et al.* 2022).

Regarding the above-discussed taxonomically classified groups, the massive part of the assemblage that cannot be classified taxonomically constitutes a significant portion of the entire NPPs assemblage found in the analysed sections. The phytoclasts provide vital information about the depositional environment. The abundance of land-origin material in distal facies decreases with distance (Tyson 1995). The terrestrial organic remains are usually deposited in prodelta facies or trapped in estuaries in a great number, with a relatively small number of particles escaping to be deposited in distal environments (Tyson 1995; Mendonça Filho *et al.* 2011). With increasing distance, less resistant remains are selectively destroyed. The opaque and non-opaque phytoclasts ratio increases because the non-opaque material is lost (Tyson 1995). Since the NPPs assemblage indicates a more proximal environment of deposition the translucency in the analysed samples is more likely related to the thermal alteration (Appendix 3A-F; see also Kondas & Filipiak 2022a, b). According to Gorin & Steffen (1991) the number of lath-shapes phytoclasts decreased offshore, while equant particles are typical for proximal facies. It is worth noting that the relation between the equant and lath phytoclasts depends on their size and the same on their fragmentation (Tyson 1995). The dominance of equant and lath phytoclasts supports the shallow marine environmental diagnosis (Tables 1-6). Plant debris assemblages contain notable amounts of cuticles, which are considered to be the most buoyant type of land-derived organic matter type, with high concentration in nearshore environments (Tyson 1995). Similarly, the well-preserved tracheids with their visible structures suggest the deposition close to the source land area.

A significant change in phytoclasts composition was observed in Giełczew PIG 5 section. Within the entire section, a strong concentration of opaque particles was documented. The opaque phytoclasts are often considered as a result of terrestrial post-depositional alteration, indicating the seasonal fluctuations in the water column and oxidation during transport (Tyson 1995). The black material has a high preservation potential, as it has no nutritional value. It becomes more fragmented towards the distal basin, but once produced, it persists in the environment (Tyson 1995). Its presence corresponds with the visible cyclicity of terrestrial material input (see Kondas & Filipiak 2022b: fig. 11). The intervals enriched in land material are the ones enriched in opaque particles.

The palynofacies analysis had already been carried out on the studied sections by Kondas & Filipiak (2022a, b), revealing pulses of shallowing and deepening depositional environments in both basins. The currently studied material completed and confirmed the previous diagnosis regarding the depositional conditions ranging from intra-shelf to a proximal shelf with significant terrigenous input. In a local context, Turnau & Racki (1999) described the Givetian palynofacies (Świętomarz and Nieczulice Beds) from Holy Cross Mountains (Łysogóry Region, Poland). The main difference was a high number of leiospheres and tasmanitids and a more diversified assemblage of acritarchs. According to the authors, the increased number of prasinophytes reflects the increased pulses of terrigenous input and may be related to surface water eutrophication (Turnau & Racki 1999). Meanwhile, palynofacies and NPPs presence from Łysogóry-Radom and Lublin basins confirmed the high terrestrial input. The level of eutrophication in the currently studied samples might be estimated as moderate to low (see Tappan 1980; Tyson 1995). Detailed NPPs study confirmed palynofacies differences in NPPs assemblage within the Łysogóry-Radom Basin. The palynofacies shifts reflect the complex nature of the depositional environment influenced by sea-level changes and climate changes (see discussion in Kondas & Filipiak 2022a).

SUMMARY

1. The Givetian and early Frasnian deposits from the HCM and Radom-Lublin areas of Poland reveal an abundant and diversified assemblage of non-pollen palynomorphs. Analysed samples provided chitinozoans, scolecodonts, organic tentaculitoids, phytoplankton, animal remains, plant debris, nematophytes, fungi, fungi-like filaments and coenobial algae. Based on this composition and previous palynofacies studies (Kondas & Filipiak 2022a, b) the current investigation confirms that the deposition took place in an environment ranging from intra- to proximal shelf.
2. For the first time, the chitinozoans from the Givetian of Poland were described. They were represented by genera *Angochitina*, *Eisenackitina*, *Fungochitina*, *Lagenochitina* and *Ramochitina*.
3. The oldest known assemblage of organic tentaculitoids (Dacryoconarida) was documented from the middle Givetian (Ex Miospore Zone; Szwejki IG-3).

Acknowledgements

We would like to thank Adam Halamski from Polish Academy of Science (Institute of Palaeobiology) and Agnieszka Pisarzowska (University of Silesia in Katowice, Faculty of Natural Sciences) for helping us during field work and providing rock samples from Miłoszów sections. We also would like to thank two anonymous reviewers, the associated editor, Anaïs Boura, and the editor-in-chief, Michel Laurin, for all notes and comments that allowed us to improve this manuscript.

Funding

This work was financially supported by NCN grant no. 2017/27/N/ST10/01699 (for M. Kondas, University of Silesia in Katowice), NCN grant no. 2016/23/B/ST10/02744 (for A. Baliński, Polish Academy of Sciences), Czech Science Foundation grant No 23-05944K (for P. Tonarová) and internal projects of the Czech Geological Survey No. 311410 and 311650 (to P. Tonarová).

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Submitted on 24 January 2024;
accepted on 21 May 2025;
published on 17 September 2025.

APPENDICES

APPENDIX 1. — List of taxa.

Chitinozoans:

- Eisenackitina* cf. *spongiosa* Swire, 1990
Lagenochitina crassa Grignani & Mantovani, 1964
Ramochitina ramosi Sommer & van Boekel, 1964
Angochitina capillata Eisenack, 1937
Fungochitina pilosa (Collinson & Scott, 1958)

Scolecodonts:

- Atraktoprion* sp.
Kielanoprion sp.
Mochtyella sp.

Acritarchs:

- Micrhystridium* sp.
Multiplicisphaeridium sp.
Veryhachium sp.

Prasinophytes:

- Leiosphaeridia* sp.

Nematophytes:

- Nematothallus* sp.

Coenobial algae:

- Mussivum gradzinskii* Wood & Turnau, 2001

Fungi:

- Laevitubulus frondifera* Wellman, 1995
Laevitubulus plicatus Burgess & Edwards, 1991
Laevitubulus sp.
Porcatitubulus cf. *spiralis* Burgess & Edwards, 1991

APPENDIX 2. — Types of NPPs documented in studied sections.

Sample	Phytoclasts	Acritarchs	Chitinozoans	Nematophytes	Fungal hyphae	Tubes	Scolecodonts	Animal remains	Tentaculitoids
Section M0									
1	X	X					X	X	
2	X	X					X	X	
3	X	X					X	X	
4A	X						X	X	
4B	X						X	X	
4C	X						X	X	
4D	X						X	X	
5	X	X					X	X	
6	X	X					X	X	
7	X	X					X	X	
8A	X	X					X	X	
8B	X	X					X	X	
9	X	X					X	X	
9s	X	X					X	X	
10A	X	X					X	X	
10B	X	X					X	X	
10C	X	X					X	X	
10D	X	X					X	X	
Section M2									
2	X	X					X	X	
3	X						X	X	
4	X	X	X				X	X	
6	X	X						X	
Section Szwejki IG-3									
4299	X				X	X	X	X	
4301	X								
4303	X						X	X	
4307	X				X		X	X	
4310	X				X	X	X		
4339	X	X			X		X	X	
4342	X				X	X	X	X	
4456	X				X		X	X	
4537	X							X	X
4539	X				X			X	
4545	X			X	X			X	
4548	X		X		X			X	
4560	X								
4606	X						X		
4607	X		X					X	
4610	X	X			X			X	
4611	X				X		X	X	
4612	X								
4614	X				X			X	
4673	X								
4675	X								
4690	X						X		
4694	X								
4695	X						X		
4698	X								
4702	X				X		X	X	
4703	X	X	X	X	X			X	
4705		X							X
4867									
4875									
4978	X								
4979	X					X			X
Section Niesiołowice IG-1									
1330	X	X	X				X	X	
1333	X								
1334									
1342									
1346	X	X	X		X			X	
1357									
1359	X		X					X	
1363	X				X			X	

APPENDIX 2. — Continuation.

Sample	Phytoclasts	Acritarchs	Chitinozoans	Nematophytes	Fungal hyphae	Tubes	Scolecodonts	Animal remains	Tentaculitoids
1365	X		X		X				
1367			X		X			X	
1395	X							X	
1399	X								
1431	X				X		X		
1459	X		X		X	X	X		
1484	X								
1486					X	X			
1490	X	X			X		X	X	
1491	X	X		X	X	X	X	X	
1508	X								
1512	X								
1415	X						X		
1517	X								
Section Gielczew PIG 5									
1960	X					X			
1961	X								
1963	X				X			X	
1964	X				X				
1966		X	X		X	X	X		
1967					X				
1970	X						X	X	
1971	X				X		X	X	
1972								X	
1974								X	
1975	X				X				
1982			X		X		X		
1983						X		X	
1989					X				
1997	X								
1998	X								
2004	X								
2007	X			X		X		X	
2008	X					X			
2009									
2010					X			X	
2011									
2012									
2013	X				X			X	
2014	X								
2015	X					X		X	
2024	X					X			
Section Krowie Bagno IG-1									
1221	X				X	X		X	
1298					X	X	X		
1301					X	X	X	X	
1326	X								
1328		X			X				
1332						X			

APPENDIX 3. — Types of phytoclasts documented in studied sections: **A**, types of phytoclasts in M0 (Miłoszów) section; **B**, types of phytoclasts in M2 (Miłoszów) section. The **crossed circle** indicates the sample with the number of phytoclasts lower than 100; **C**, types of phytoclasts in Szwejki IG-3 section. The **crossed circles** indicate the sample with the number of phytoclasts lower than 100. G/F – Givetian/Frasnian, DLU- Dolomitic Limestone Unit. **D**, types of phytoclasts in Niesiolowice IG-1 section; **E**, types of phytoclasts in Gielczew PIG 5 section. The **crossed circles** indicate the sample with the number of phytoclasts lower than 100; **F**, types of phytoclasts in Krowie Bagno IG-1 section: https://doi.org/10.5852/cr-palevol2025v24a22_s1