Geological Quarterly, 2024, 68: 12
DOI: http://dx.doi.org/10.7306/gq.1741

A new early Permian actinopterygian assemblage shows environmental controls on the distribution of *Paramblypterus* (Intra-Sudetic Basin, Poland)

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Pawlak, W., Ploch, I., Štamberg, S., Raczyński, P., Kiersnowski, H., 2024. A new early Permian actinopterygian assemblage shows environmental controls on the distribution of *Paramblypterus* (Intra-Sudetic Basin, Poland). Geological Quarterly, 68: 12; https://doi.org/10.7306/gq.1741

Amblypteridae are ray-finned fish particularly common in late Carboniferous and early Permian vertebrate assemblages. We describe a rich new fish assemblage from the Poland-Czechia borderland, composed of only one species of amblypterid: *Paramblypterus rohani*. The analysis of articulation and completeness of the individuals unearthed shows that most of them underwent two, strongly different taphonomic histories. The first is represented by highly articulated and complete specimens buried close to their death site. Their decomposition took place mainly at the bottom of a deep lake with low hypolimnic temperature and bottom hypoxia. The second is represented by highly disarticulated and incomplete specimens, for which the bloat and float mechanism appears to be the main driver of decomposition. The results obtained suggest that thermal conditions in the former reservoir were seasonally varying. Moreover, the mass occurrence of amblypterids in environments largely touched by hypoxia shows that they were efficient open-water predators, which contrasts with previous ecomorphological studies of this group. The stratigraphic position of the assemblage studied remains unclear due to conflicting biostratigraphic and field data. The most parsimonious resolution of this ambiguity comes through considering the occurrence of various amblypterid species in the Intra-Sudetic Basin as controlled by environmental factors rather than by evolution.

Key words: palaeontology, fish fossils, Sudetes, Upper Paleozoic.

INTRODUCTION

Amblypterids are among the most common fish fossils occurring in the upper Carboniferous to lower Permian freshwater strata of Europe. They are components of most fish assemblages recognized from this interval in the belt stretching today from Spain in the west to Czechia in the east (Soler-Gijon and Moratalla, 2001; Štamberg, 2013a). They are fusiform to slightly hump-backed, relatively small actinopterygians, usually reaching up to twenty centimetres in length. Species belonging to this group show a limited interspecific diversity, seen mainly as variations in cranial bone shape and scale ornamentation (Dietze, 2000; Štamberg, 2021). All are regarded as planktivorous, though some ontogenetic shifts in dietary preferences are inferred as their dentition varied with age (Štamberg, 2020). Amblypterids usually occur in lacustrine facies together with other vertebrates, such as acanthodians, chondrichthyans, sarcopterygians, amphibians and other actinopterygians (Zajíc and Štamberg, 2004; Štamberg, 2021). They dominate some vertebrate assemblages. An example of an amblypterid-rich deposit is the lower Permian (Asselian) succession of the Saar-Nahe Basin, comprising several lacustrine levels from which hundreds of amblypterid individuals had been recovered (Dietze, 1999). Because of their abundance, studies on amblypterid diversity, palaeobiology and ecological preferences are pivotally important for the understanding of late Carboniferous to early Permian freshwater ecosystems.

Three species of amblypterids from Europe have well-recognized anatomy. The best studied is *Paramblypterus duvernoyi* for which the material collected allowed for three-dimensional body reconstructions, functional interpretations and studies on intraspecific variability (Dietze, 1999, 2001), mainly

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Received: July 03, 2023; accepted: February 11, 2024; first published online: July 4, 2024

known mainly from the Saar-Nahe Basin in western Germany. Two other species come from the Intra-Sudetic Basin in Czechia and Poland: *P. rohani* and *P. vratislaviensis*. *Paramblypterus rohani* occurs also in the Krkonoše-Piedmont Basin in Czechia.

In the species from the Intra-Sudetic Basin, the body reconstructions are less comprehensive though still based on numerous specimens (Štamberg, 2021, 2022). A peculiar pattern of distribution occurs with *P. rohani* and *P. vratislaviensis* in the Intra-Sudetic Basin. *Paramblypterus vratislaviensis* occurs in the Ruprechtice lake deposits, accompanied by abundant fossils of other vertebrates, such as xenacanthids, temnospondyls and seymouriamorphs, though no other amblypterids (Štamberg, 2021). By contrast, *P. rohani* occurs in the Otovice lake deposits, constituting a strongly dominant component; other vertebrates are significantly less frequent. These deposits include xenacanthids, aeduellid actinopterygians and rare *P. vratislaviensis* specimens (Štamberg, 2022). Besides the Intra-Sudetic Basin, *P. vratislaviensis* has been reported from the North-Sudetic Basin (Roemer, 1857; Becker, 1869; Weiss, 1879); however, these occurrences require reinvestigation in the light of the recent revision of this species (see Štamberg, 2021).

Here, we describe a new vertebrate assemblage from the Intra-Sudetic Basin composed exclusively of amblypterids. Their utter dominance suggests that the assemblage relates to an environment strongly favourable for these animals. We use sedimentological and taphomical data from this assemblage to recognize the controls on these amblypterids' apparent abundance and to reconstruct the conditions preferred by these fishes.

GEOLOGICAL SETTING

The Intra-Sudetic Basin represents one of the large late- to post-Variscan intramontane troughs of Europe. It is situated at the northern margin of the Bohemian Massif, as a fault-bounded synclinorial structure. During the latest Carboniferous and earliest Permian the basin was filled with dominantly fine-grained deposits of alluvial to lacustrine origin accompanied by volcanic rocks. The Lower Rotliegend – Krajanów Formation (Bečkov Member) and Słupiec Formation (Broumov Formation) are interpreted as two successive, fining-upwards megacyclothems consisting, from base to top, of alluvial fan, fluvial and lacustrine deposits (e.g., Dziedzic, 1961; Wojewoda and Mastalerz, 1989; Kurowski, 2004; Kowalski and Furca, 2023). The double lithostratigraphic terminology results from the independent history of research in the Czech and Polish parts of the basin. The sedimentation of the Słupiec (Broumov) Formation was influenced by volcanic activity entailing emplacement of subvolcanic intrusions, lavas and widespread ignimbrites (Awdankiewicz, 1999; Awdankiewicz et al., 2003) and has been interpreted as an alluvial fan fringing central playa-like, shallow lakes (Kurowski, 2001, 2004). The extent of the lake deposits in the basin centre fluctuated, probably as a result of cyclical climate changes, as well as from possible tectonic controls (Dziedzic, 1961; Wołkowicz, 1988; Wojewoda and Mastalerz, 1989; Kurowski, 2004). These processes led to several levels of lacustrine deposits, two of which in the Czech part of the Basin have been distinguished as the Ruprechtice and Otovice horizons (Tásler et al., 1979). The former was deposited earlier and is separated from the Otovice horizon by a package of volcanogenic rocks. In the Polish part, all lacustrine deposits are usually assigned to the *Walchia* shales, being regarded as a subdivision of the Słupiec Formation, roughly equivalent to the Olivětín Member (Awdankiewicz et al., 2003).

The new fish assemblage comes from an exposure of the Słupiec (Broumov) Formation in the vicinity of Janików, being part of the Tłumaczów village. The exposure is located close to the Polish-Czech border, on the southern bank of the Bożanowicki stream, in the central part of the Intra-Sudetic Basin (Fig. 1A). The section (Fig. 1B, C) starts with 1.5 m of dark to brown tuffs, conspicuously laminated. This is overlain by the fish-bearing fossiliferous interval composed of microlaminated, bituminous marlstone, ~60-cm-thick. Mineralogically, it comprises mainly microsparitic calcite with numerous embedded automorphic crystals of dolomite, probably late diagenetic in origin (Fig. 1D). The horizontal lamination of the rock reflects enrichment in iron oxides and organic matter, intercalated in the carbonate matrix. Beside the fish, this package is also rich in plant remains dominated by *Lobatopteris*, *Nemeicopteris* and *Dicksoniites* (Šimůnek and Ploch, 2022). No invertebrates were found. The fossiliferous shale, as well as underlying tuffs, are locally strongly silicified and contain chalcedonic lenses. The fossiliferous layer is overlain by a ~10-cm-thick layer of bituminous mudstone. It terminates with a sharp erosional boundary, above which is a ~1-m-thick package of a coarse-grained, cream-coloured tuff. In nearby exposures, the fossiliferous sequence is succeeded by shales with ripplemarks and poorly-preserved tetrapod tracks.

MATERIALS AND METHODS

The actinopterygian material studied from Janików comprises 100 specimens, listed in the systematic palaeontology section. The majority of these specimens were unearthed during fieldwork we conducted in 2018–2022. An exception is MGUWr 6417s collected by Anna Górecka-Nowak in 1980. Most of the specimens excavated were prepared via mechanical methods using manual and pneumatic needles. In some cases, the rock matrix was softened using a diluted solution of acetic acid (~10% w/w).

The comparative material comprises amblypterids, aeduellids, trissolepidids and paleoniscids from the Czech part of the Intra-Sudetic Basin, Krkonoše Piedmont Basin, Boskovice Basin, and western Bohemia basins housed in the Museum of Eastern Bohemia in Hrádec Kralove (*Neslovicella rzehaki*, *N. elongata*, Aeduellidae indet., *Aeduella* sp. *Bourbonella hirsuta*) and the National Museum in Prague (*Paramblypterus rohani*, *P. vratislaviensis*, *P. ziedleri*, *P. kablikae*, *Sceletophorus biserialis*, *Sphaerolepis kounovensis*, *Pyritocephalus sculptus*), as well as the amblypterids from the Saar-Nahe Basin housed in the collection of the Geoskop Urweltmuseum in Thallichtenberg (unnumbered, about two hundred specimens of undetermined *Paramblypterus* specimens). The anatomical terminology of skull roof and rostral bones follows Štamberg (2022), however several terminologies can be found in the amblypterid literature. To retain consistency with previous work, alternative names of ossifications used in the studies of Dietze (2001) and Štamberg (2021) are placed in brackets in the text.

Estimations of the articulation and completeness of specimens follow the method described by Beardmore et al. (2012) and Beardmore and Furrer (2016) though with modifications. The fish body was divided to nine regions, separately scored for completeness and articulation: skull, pectoral girdle, pectoral fins, pelvic fins, dorsal fin, anal fin, caudal fin, trunk anterior to the dorsal fin edge, and trunk posterior to the dorsal fin edge. Both parameters were scored using a four-level scale. Consecutive levels of articulation correspond to the following states: (0) complete disconnection of the elements belonging to the region, (1) connection between at least part of the elements be-

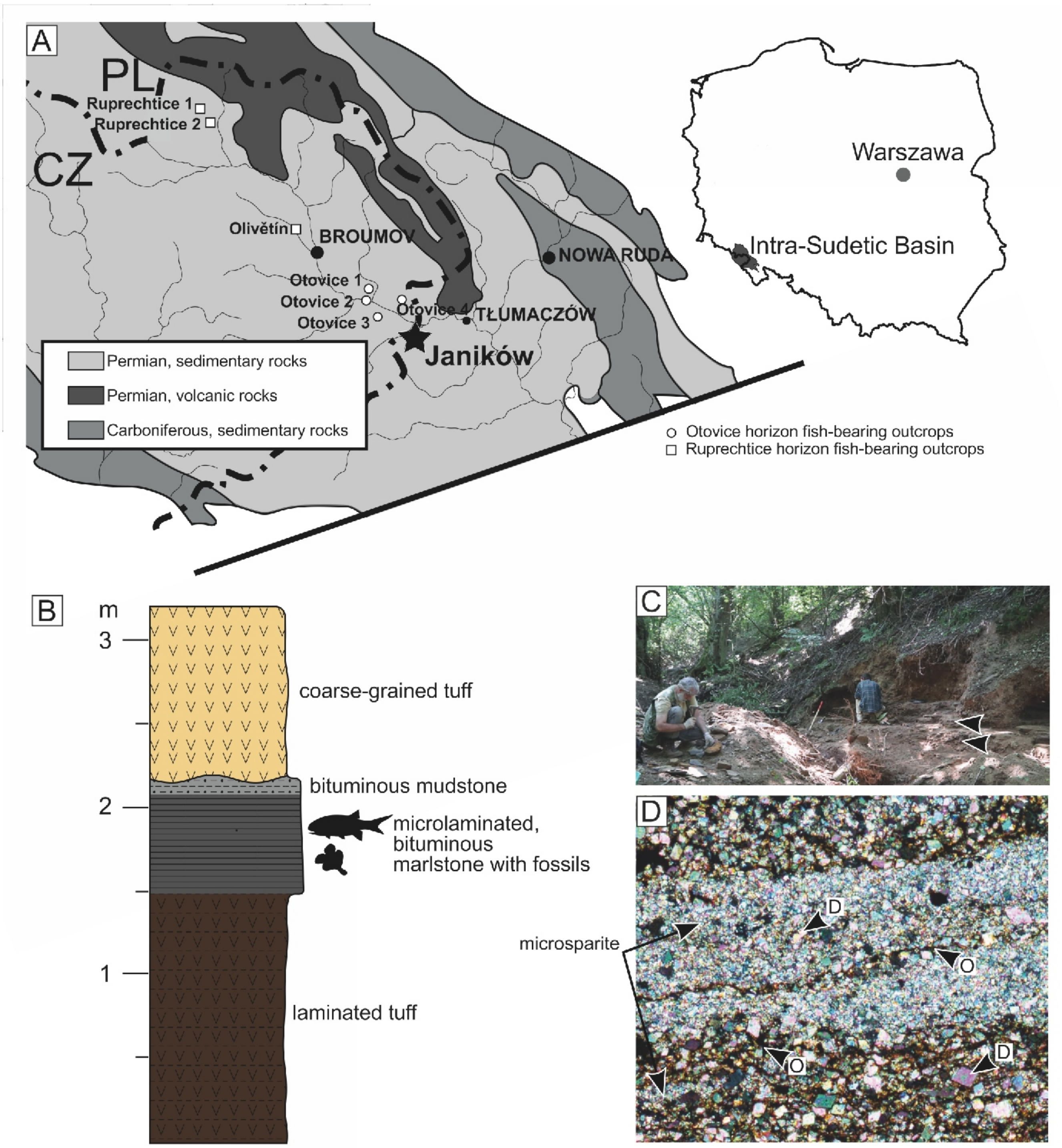

Fig. 1. Study site

A – map of the Intra-Sudetic Basin with fish-bearing localities of the Słupiec (Bromov) Formation marked; **B** – geological section of the Janików exposure; **C** – authors (P.R and W.P) at field work at the Janików site; arrows indicate the fish-bearing part of the section; **D** – thin section of a fish-bearing marlstone (crossed polars) from Janików; abbreviations: D – dolomite automorphic crystals, O – accumulations of organic matter and iron oxides longing to the region with each other, (2) dislocation of the elements with preservation of their general position within the skeleton, disconnection of less than 5% of the elements, (3) full anatomical articulation. For completeness: (0) the complete lack of the region, (1) presence of at least part of the elements belonging to the region, (2) lack of up to 5% of the elements, (3) presence of all elements. Obviously, estimation of the parameters is not possible for all specimens collected due to damage incurred during excavation or rock weathering. In such cases, the parameters were not scored. In case of slight incompleteness of the region resulting from non-taphonomic causes, we assumed that the part lacking represented a state similar to the part present. For every individual studied, the average completeness and average articulation scores were calculated on the basis of nine scores estimated for each body region. Statistical analysis was performed using *PAST 4.10* software.

To estimate frequencies of the modes of preservation, we studied all specimens housed in the MGUWr and specimens collected in the field, subsequently housed in the ZPAL. The latter were unearthed from a volume of the fossiliferous shale via separation of particular laminae, and collection of all fish remains found. Specimens too weathered for reliable scoring were excluded from analysis. Concerning the MGUWr collection, small (1–2 cm^2) rock slabs containing fish remains were excluded from analysis to avoid bias resulting from the collection of fragmented slabs, possibly containing more complete individual before their desintegration. The excavations revealed that isolated scales or bones are extremely rare in the Janików site while disarticulated specimens with scattered scalation are relatively frequent, which justifies the exclusion applied. In all, 29 specimens were used in the analysis, 26 housed in ZPAL and 3 in MGUWr.

INSTITUTIONAL ABBREVIATIONS

ZPAL – Institute of Paleobiology of the Polish Academy of Sciences, Warsaw

MGUWr – Geological Museum of the Institute of Geological Sciences of Wrocław University

RESULTS

SYSTEMATIC PALAEONTOLOGY

Class: Osteichthyes Huxley, 1880
Subclass: Actinopterygii Cope, 1887
Family: Amblypteridae Romer, 1945
Paramblypterus rohani (Heckel & Kner, 1861)

Referred material. – ZPAL V.81/001-044, 046-047, MGUWr 5822s, 5824s, 5826s-5828s, 5830s, 5833s-5836s, 5839s, 5840s, 5843s-5849s, 6305s, 6416s, 6417s, 6530s, 6536s, 6540s, 6545s, 6549s.

Locality and age. – Janików, bituminous marlstone, Asselian.

Description. – Numerous actinopterygian specimens from Janików represent complete individuals with well-preserved skeletons except skulls. All specimens represent a fusiform silhouette with slightly convex back between the skull and dorsal fin (Fig. 2). Some specimens (e.g. MGUWr 6305s, ZPAL V.81/042) appear to have a deepened body compared to other individuals, though this results from dorsolateral compaction.

The cranial anatomy is provided by five individuals: MGUWr 6305s, MGUWr 6417s, ZPAL V.81/042, ZPAL V.81/046, and two isolated bones: ZPAL V.81/013 and ZPAL V.81/020. The jaws and circumorbital series are the best-preserved parts of the skull in MGUWr 6417s (Fig. 3A). The maxilla is divided into an elongated anterior part and deep posterior field. Most of the anterior part is overlapped, postmortem, by the infraorbital inferior and jugal. It bears dozens of tiny, conical teeth. The posterior field is fragmented and eroded. However, its roughly oval shape, slightly elongated anteroposteriorly, is visible. Only the anteriormost part of the posterior field appears to be tooth-bearing. The dorsal margin between the anterior and posterior fields is steep. The lower jaw is narrow, thickening posteriorly. In the anterior part, openings for the mandibular sensory line are visible. The posterior part is abraded and partially covered by the posterior field of the maxilla. The jugal is a robust bone with conspicuous ascending and anterior processes. Its posteroventral edge is convex, revealing the shape of the suture with the maxilla. The anterior process is elongated, and reaches far into the anteroventral side of the orbit. It articulates with the narrow, small and only partially preserved infraorbital inferior (lacrimal *sensu* Dietze, 2001 and Štamberg, 2021). The ascending process articulates with the infraorbital posterior located posteriorly to the orbit (second jugal *sensu* Dietze, 2001; infraorbital *sensu* Štamberg, 2021). This infraorbital posterior has roughly the same anteroposterior width as the jugal in the widest section. It bears two openings of the infraorbital sensory line. This bone appears to have been formerly fused with the jugal in the specimen studied, then fractured post-mortem, though the state of preservation does not allow this to be established with certainty. The posterodorsal side of the orbit is bordered by the crescent-shaped dermosphenotic (second dermosphenotic *sensu* Dietze, 2001; infraorbital superior *sensu* Štamberg, 2021), bearing numerous openings of the infraorbital sensory line. Its posteroventral ending is crushed, and a fragment of the bone is dislocated within the orbit.

The skull roof in MGUWr 6417s is almost completely disarticulated and strongly abraded due to recent surface erosion. The best preserved portion of the roofing in this specimen is the anteriormost region, absent in other individuals. It shows a rectangular ossification being the antorbital. Its lateral edge is slightly convex, forming the anterodorsal border of the orbit. The anterior edge is concave in the medial section and convex in the lateral part. MGUWr 6417s comprises a poorly preserved parietal which shows anteroposterior elongation. Complementary information about the medial series of the skull roof is shown by MGUWr 6305s, revealing the arrangement of its posterior part (Fig. 3B, C). Only the posterior portion of the left parietal is present in this specimen. Its posterior margin forms a sinus on the medial side, a convexity in the central section, and another sinus on the lateral side. It is ornamented with concentric ridges, and bears a sensory line canal running anteroposteriorly through the bone and ending close to the tip of the posterior convexity. Posteriorly to the parietal, the medial and left extrascapulars are preserved. Both are roughly rectangular, but the medial one forms a wide-based posterior process. Bone fragments located between the parietal and the extrascapulars are difficult to determine, likely representing the eroded left postparietal. Such an interpretation is supported by the presence of sensory canals spreading in three directions from their shared origin. The elements of the lateral series of the skull roof are preserved in MGUWr 6417s, MGUWr 6305s, and ZPAL V.81/020. In MGUWr 6417s, the intertemporal (first dermosphenotic *sensu* Dietze, 2001; dermosphenotic *sensu* Štamberg, 2021) is located ventrally to the parietals, partially covered by the left one. It is significantly elongated anteropo-

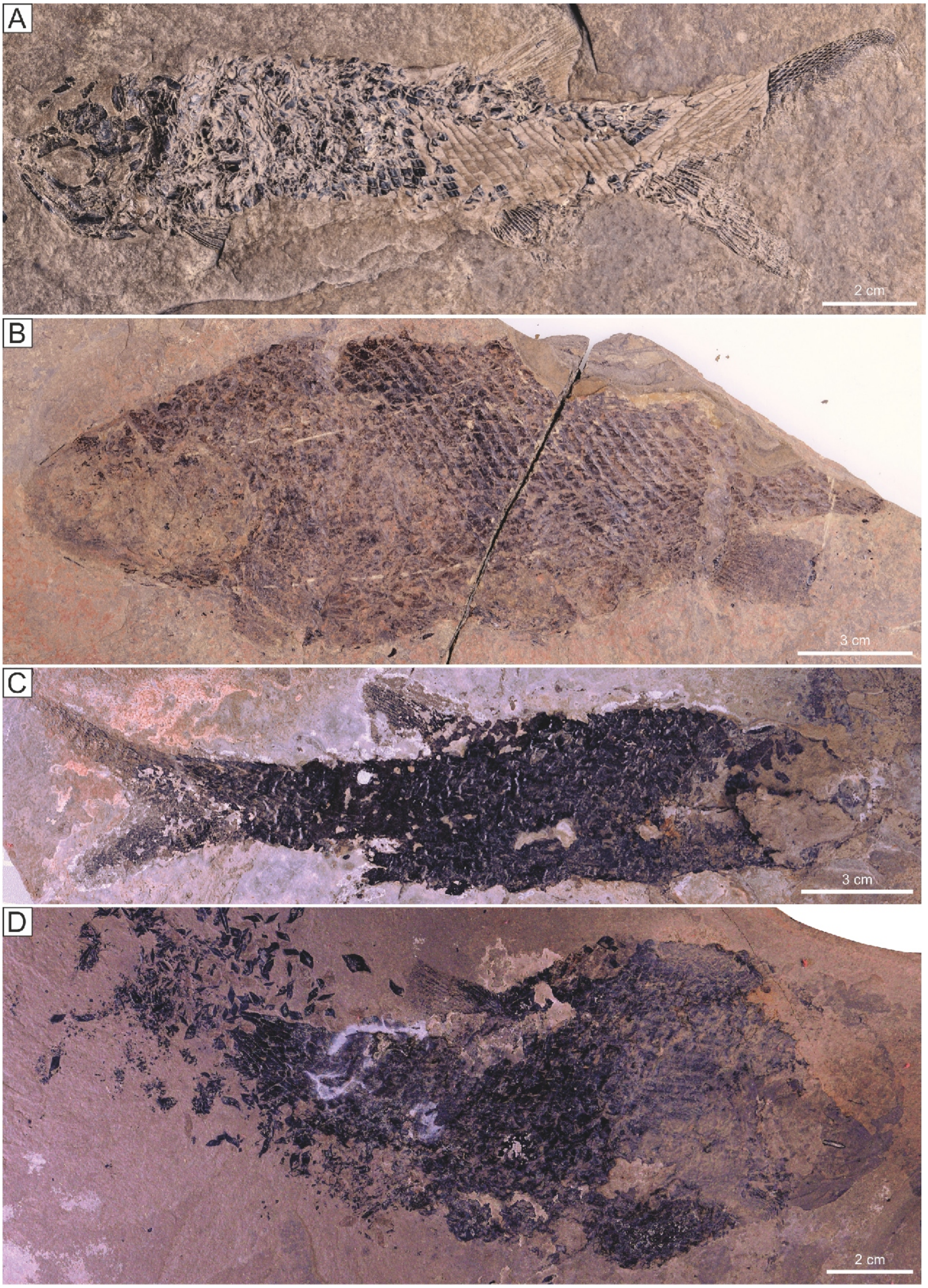

Fig. 2. ***Paramblypterus rohani*** **from the Janików locality**

A – MGUWr 6417s; **B** – MGUWr 6305s; **C** – ZPAL V.81/042; **D**– ZPAL V.81/046

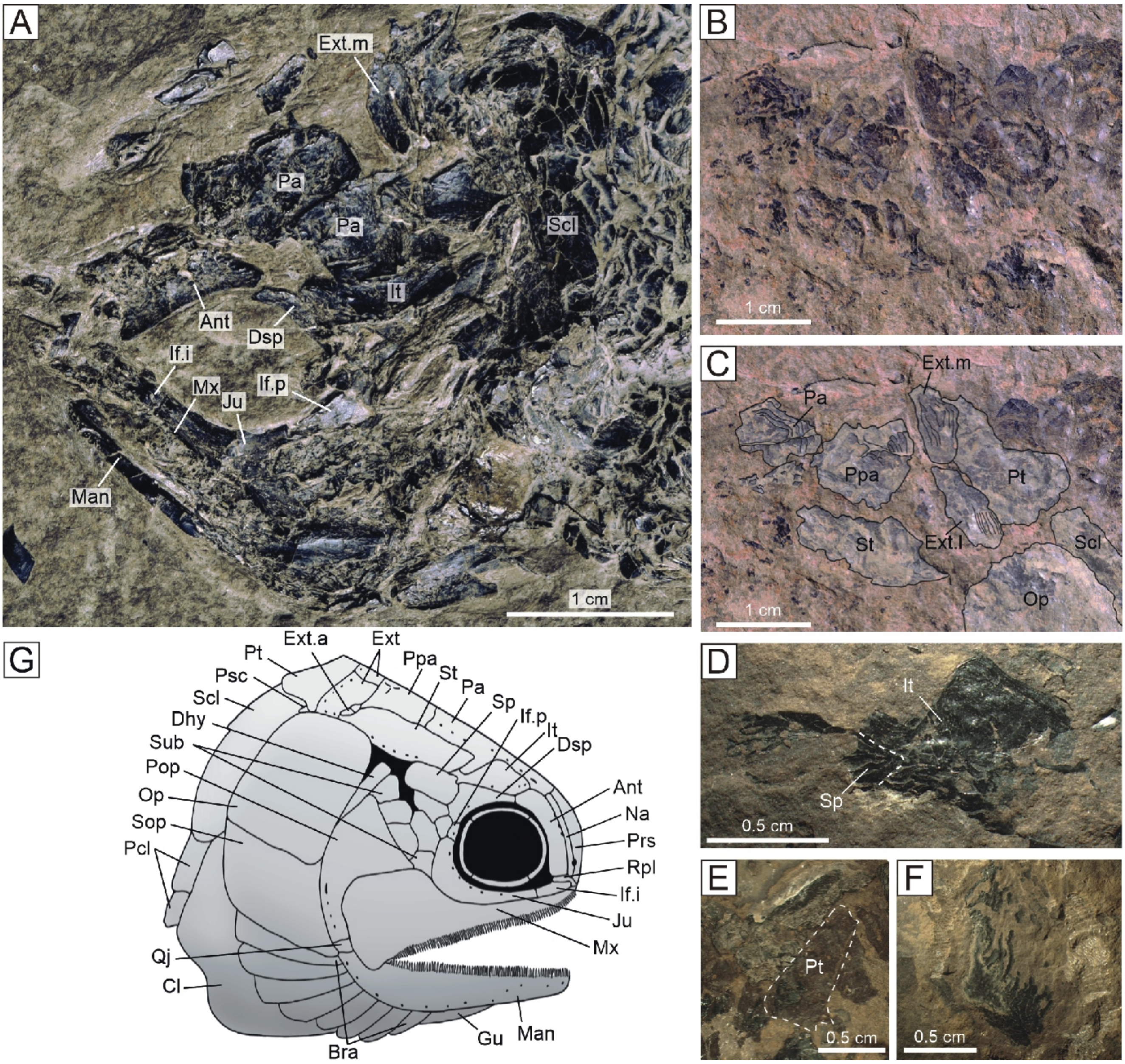

Fig. 3. Cranial features of *Paramblypterus rohani* from the Janików locality

A – skull of the individual MGUWr 6417s; **B** – skull roof of individual MGUWr 6305s; **C** – interpretative drawing of the skull roof of individual MGUWr 6305s; **D** – ZPAL V.81/020; **E** – dorsal region of pectoral girdle of the individual ZPAL V.81/042; **F** – ZPAL V.81/013; **G** – reconstruction of the skull of *Paramblypterus rohani* from Janików; abbreviations: Ant – antorbital, Bra – branchiostegal rays, Cl – cleithrum, Dhy – dermohyal, Dsp – dermosphenotic, Ext – extrascapula, Ext.a – accessory extrascapula, Ext.l – extrascapula lateral, Ext.m – extrascapula median, Gu – gular, If.i – infraorbital inferior, If.p – infraorbital posterior, It – intertemporal, Ju – jugal, Man – mandible, Mx – maxilla, Na – nasal, Op – operculum, Pa – parietal, Pcl – postcleithra, Pop – preoperculum, Ppa – postparietal, Prs – postrostral, Psc – presupracleithrum, Pt – posttemporal, Qj – quadratojugal, Rpl – rostro-premaxillo-lacrimal, Scl – supraclaithrum, Sop – suboperculum, Sp – spiracular, St – supratemporal, Sub – suborbitals

steriorly, with openings of the temporal sensory line distributed along the ventral edge. The dorsalmost section of the anterior edge forms a process, formerly inclined between the parietal and the dermosphenotic. The ventral section of the anterior edge has a visible suture facet for the overlapping dermosphenotic. ZPAL V.81/020 shows the right intertemporal in lateral aspect (Fig. 3D) with an attached rudiment of the spiracular. The anterior portion of the intertemporal forms two triangular processes directed anteriorly and medially. Both have wide bases confluent with the main body of the bone. Between the processes, the bone margin is slightly concave. Posteriorly to the medial process, the bone margin forms a deep, triangular incision for the parietal. The posteromedial process is located more posteriorly. It has a damaged tip, but the preserved part has a constant width. The posterior margin of the intertemporal forms an incision for the spiracular, which is about two times narrower than the incision for the parietal. The lateral margin of intertemporal is partially covered by matrix, except the anteriormost section which runs obliquely and forms the lateral margin of the anterior process. The ornament is preserved only in the medial and posterior part of the bone. It consists of merging ridges, running anteroposteriorly. In the middle of the bone length, close to the lateral margin, an opening of the sensory line is present. A small part of the spiracular attaches to the intertemporal posterior margin and matches with the posterior incision. It is covered by a similar rugous ornamentation. The supratemporal (dermopterotic *sensu* Štamberg, 2021) is strongly abraded in MGUWr 6417s but retains its former shape, appearing to be elongated anterposteriorly, about two times longer than wide. The dorsal edge is sinusoidal with deep incisions for the postparietal and/or parietal; the anterior edge is convex, whereas the ventral is roughly straight. The posterior part of bone forms a short process directed posteroventrally. The supratemporal is better preserved in MGUWr 6305s. It has a similar general shape to this in MGUWr 6417s but additionally a gradual narrowing toward the anterior edge is visible. Its dorsal and ventral edges are roughly straight, while the anterior one is convex with the dorsal section slightly extended anteriorly. The posterior edge forms the conspicuous posterior process.

The opercular apparatus and gular region are partially preserved in MGUWr 6305s. The operculum is a rectangular bone which appears to occupy a larger part of the gill cover than the suboperculum. However, the original proportions appear to be distorted by compaction. In the ventral part of the skull MGUWr 6305s shows imprints of three, relatively wide branchiostegal rays and a delta-shaped gular. They are accompanied by the imprint of the proximal section of the lower jaw.

The pectoral girdle elements are preserved in MGUWr 6305s, MGUWr 6417s, ZPAL V.81/013, and ZPAL V.81/042. The posttemporals occur posteriorly to the extrascapulars in MGUWr 6305s. They are poorly preserved and slightly dislocated, thus only the general outline of the right posttemporal is readable. It is an anteroposteriorly elongated bone with a rounded posteroventral margin. The right posttemporal is preserved also in ZPAL V.81/042 (Fig. 3E). It has a mediolaterally elongated shape, widening laterally. All margins of this bone are roughly straight, except for the posteroventral one which is conspicuously rounded. The ventral half of the anterior margin is probably broken but the preserved part suggests the presence of an anteriorly oriented convexity. The ganoin cover of the bone is exfoliated and dislocated towards the posterodorsal direction. It shows conspicuous circuli parallel to the bone edges. In MGUWr 6417s the supracleithrum is clearly elongated dorsoventrally and has a heavy ornamentation composed of wide ridges and tubercles. ZPAL V.81/013 is an isolated, posteroventral part of the right cleithrum exposed in the lateral aspect (Fig. 3F). It shows a conspicuous ornamentation composed of dorsoventrally running ridges which cover the lateral surface of the lateral lamina. The ventralmost part of the bone forms a slight, laterally directed ridge, the ventral surface of which is ornament-free. Only the posterior and ventral margins of ZPAL V.81/013 are well preserved. Both are straight, but the posterior margin forms two convexities, one close to the dorsal edge of the specimen, and the second at the junction with the ventral margin.

Scales are devoid of ornamentation in most of the specimens studied. In MGUWr 6305s about seven anteriormost rows of the flank scales display serration of the posterior margin, gradually fading away in more posterior rows (Fig. 4A). Counts of scales are difficult to perform, since most specimens have a more or less weathered scale cover, with poorly preserved anterior scale rows or absent fins. ZPAL V.81/006 has the best preserved postcranium, allowing for counts for all fins except the caudal one. Based on this specimen: 27, 12 and 20 scale rows are located between the beginning of the lateral line and the dorsal, pelvic and anal fin, respectively. There are 37 preserved scales in the lateral line. Based on other specimens (ZPAL V.81/003, 011, 042 and MGUWr 6305s) with well-preserved postcrania, we estimate the total number of scales in the lateral line at 40-45. In numerous specimens (MGUWr 6417s, ZPAL V.81/006, 011, 003, 042) the relative position of the dorsal and anal fin is clearly readable and the distance between their anterior edges equals 5–8 vertical scale rows. The dorsal keel scales are well-exposed in ZPAL V.81/046 and MGUWr 5848s (Fig. 4H). The dorsal fin is preceded by four enlarged scutes devoid of ornamentation. The anteriormost scute is rectangular, while the rest have an ovoid shape. There are three, minute, tear-shaped dorsal scutes located directly behind the dorsal fin. They are followed by three rows of paired scales, posteriorly to which the unpaired scutes continue. This second series of unpaired scutes is composed of four scales, significantly larger than those located directly behind the dorsal fin, pentagonal to triangular in shape. They are followed by a series of strongly elongated, paired basal fulcra of the caudal fin. The anal fin is preceded by three scutes surrounding the cloacal opening. The large unpaired scute is followed by a pair of symmetrical scutes located posterolaterally to it. The latter are poorly preserved in all specimens studied. In ZPAL V.81/011 the preanal area is well exposed but disarticulated. It shows a conspicuous serration of the posterior margins of the preanal scutes (Fig. 4I).

The number of rays in the paired fin is difficult to determine due to their folding and relatively high degree of disarticulation in the sample studied. Based on ZPAL V.81/042 and 046, the number of fin rays is at least 12 and 13 in the pectoral and pelvic fin. The dorsal and anal fins are similar in shape and size, located vis-à-vis each other (Fig. 4C, D). Both are composed of about 30 segmented lepidotrichia (based on ZPAL V.81/006 and 011). The anterior edges of all paired, dorsal and anal fins are margined by the fringing fulcra and tip segments of the lepidotrichia. In all these fins, the lepidotrichia are regularly segmented, and they start to bifurcate approximately in the middle of their proximodistal length. The basalmost segments are usually more robust and elongated than the more distal ones. The ratios of lepidotrichia segments vary within and between individuals. In the pectoral fin, the segments tend be strongly elongated, being up to six times longer than wide (Fig. 4G). In other fins they are usually about two times longer than wide. However, in some specimens, the shortened segments of lepidotrichia occur together with the elongated ones in the median fins. The ratio of anteroposterior width to proximodistal length of the most shortened lepidotrichia reaches about 1.5 in MGUWr 6305s and 0,9 in ZPAL V.81/006 and 011. The shortened segments tend to occur close to the fin base and the posterior and anterior edges (Fig. 4F). Moreover, the shortened segments are prone to having more complicated, sinusoidal intersegmental joints, in contrast to the straight joints occurring between the elongated segments (Fig. 4E–G). Besides their variation in shape, the lepidotrichia show two different patterns of ornamentation: a smooth surface and ornamentation composed of numerous, minute, proximodistal ridges (Fig. 4E). We interpret this variability as intraspecific, possibly related with late ontogenetic changes and complication of the lepidotrichia morphology with age. Fields covered by relatively small, rhomboidal scales occur at the bases of the pelvic, dorsal, and anal fins. The caudal fin is composed of about 65 bifurcating and regularly segmented lepidotrichia (Fig. 4J). The length to width ratios of the lepidotrichia segments appear to be relatively stable and equal about 2. Dorsal and ventral margins of the caudal fin are margined by the fringing fulcra, and (rarely) distalmost segments of the lepidotrichia.

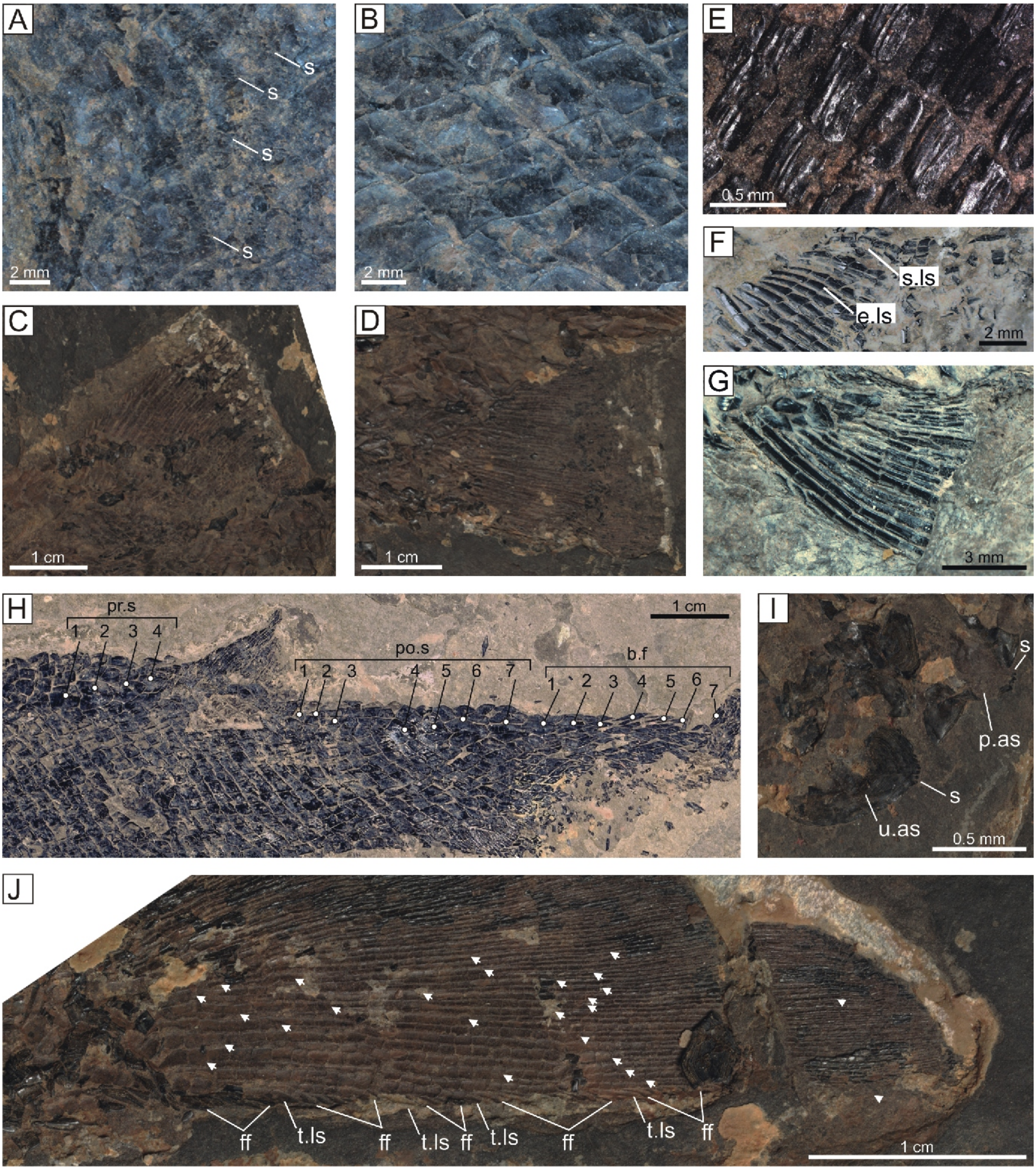

Fig. 4. Postcranial features of *Paramblypterus rohani* from the Janików locality

A – serrated scales in the anterior part of the trunk (MGUWr 6305s); **B** – scales in the posterior part of the trunk (MGUWr 6305s); **C** – dorsal fin (ZPAL V.81/011a); **D** – anal fin (ZPAL V.81/011a); **E** – magnification of segments of lepidotrichia with the ornamentation composed of proximodistal ridges in the dorsal fin of ZPAL V.81/42; **F** – morphological variation of the segments of lepidotrichia and the intersegmental joints in the anal fin of MGUWr 6417s; **G** – pectoral fin (MGUWr 6417s); **H** – dorsal ridge scalation pattern (MGUWr 5848s); **I** – anal scutes (ZPAL V.81/011a); **J** – ventral lobe of the caudal fin (ZPAL V.81/011a). Arrows indicate the bifurcation spots in the eight ventralmost lepidotrichia. Abbreviations: b.f – paired basal fulcra of the caudal fin, e.ls – elongated segments of lepidotrichia, ff – paired fringing fulcra of the caudal fin, p.as – paired anal scute, po.s – postdorsal unpaired scutes, pr.s – predorsal unpaired scutes, s – serration, s.ls – shortened segments of lepidotrichia, t.ls – terminal segments of lepidotrichia of the caudal fin, u.as – unpaired anal scute

Remarks. – The actinopterygian from Janików shows clear affinities to *Paramblypterus* with regard to skull bone arrangement (Fig. 3G) and ornamentation, fin position and structure, body proportions, scale morphology and counts. While some individuals show serration in the anteriormost rows of the scales, the generally smooth appearance of the scales precludes a relationship with heavily ornamented species of amblypterids. Unornamented scales with occasional serration are present in two species known from the Intra-Sudetic and Krkonoše Piedmont Basins: *P. vratislaviensis* and *P. rohani* (Štamberg, 2021). They differ from each other in the morphology of skull bones, which is rather poorly recognized in the material examined. However, among the prominent features of *P. vratislaviensis* are a bar-like intertemporal and supratemporal devoid of a posterior process, which contrasts with the specimens from Janików. The relatively robust intertemporal and the supratemporal with the conspicuous posterior process strongly suggest that the population studied belongs to *P. rohani*. An additional feature is the ornamentation of the intertemporal, composed of vermicular ridges, whereas in *P. vratislaviensis* the skull roof tends to be ornamented with isolated tubercles. The validity of *P. rohani* remains unsure due to its strong similarity to *P. duvernoyi* (Dietze, 2000; Štamberg, 2022); however, until more detailed comparisons will be performed, we conservatively assign the material described to *P. rohani*.

ZPAL V.81/006 and 011 differ from other specimens in more complex joints between segments of lepidotrichia in the unpaired fins. While they are nearly straight in most specimens described, in these two individuals the distal margins of the segments form a conspicuous sinus. Such sinusoidal courses of the intersegmental joints occur widely in aeduellids in which the postcranial skeletons can be very similar to those of amblypterids. However, the scale counts of ZPAL V.81/006 and 011 are consistent with those observed in other specimens from Janików. Additionally, the relative position of dorsal and anal fins is typical for amblypterids and differs from that in aeduellids. In the latter, the anal fin is usually shifted more posteriorly than the dorsal, while in the specimens discussed both fins are positioned roughly against each other. Because the skulls of both specimens are basically unpreserved, the postcranial features only help determine their affinity. ZPAL V.81/006 and 011 may represent an unknown species of amblypterid, but at this point we interpret them as representing morphological variability, possibly related to an advanced ontogenetic age of these individuals.

TAPHONOMY

All fish specimens from Janików share a strong compaction and dark coloration of the bone and enamel. The latter points to at least partial carbonization of the remains after burial. A more excessive carbonization, visible in some specimens (e.g., ZPAL V.81/016, 042), results from the recent weathering of the soft, fossil-bearing shale. The weathering strongly affected the quality of detail preserved in these specimens, especially in the skull and pectoral girdle regions but in some cases also the scale cover (ZPAL V.81/042). The signs of weathering are lesser in specimens preserved in silicified slabs, which provided the most informative specimens (e.g., MGUWr 6417s, ZPAL V.81/046).

A large part of the specimens collected from the Janików site represents almost intact individuals at the time of burial. All articulated skeletons are compacted laterally with the exception of several specimens showing slightly ventrolateral or dorsolateral flattening (e.g., MGUWr 6305s, ZPAL V.81/046). Moreover, all fairly complete specimens have a straightened body without signs of bending. Despite the high proportion of complete individuals, more or less disarticulated specimens are also frequent in Janików. The sample studied for articulation and completeness displays a bimodal distribution of the average scores for both parameters (Fig. 5B). The non-normal distribution is supported by the Shapiro-Wilk test for normality ($p<0.01$ for average articulation, $p<0.001$ for average completeness). The bimodality is more stark for the completeness. The most frequent are individuals showing very high (2–3) and very low (below 0.5) avarage scores of the completeness and articulation.

DISCUSSION

TAPHONOMY OF THE ACTINOPTERYGIANS

The decomposition of the fish skeleton results from the influence of various factors, such as predation, scavenging, microbial decay and water movement. Each of these factors results in different patterns of articulation, completeness, and arrangement of disarticulated elements, as was demonstrated on modern examples (Elder, 1985; Elder and Smith, 1984, 1988; Smith et al., 1985; Chidami and Amyot, 2008; Iniesto et al., 2013) as well as in fossil fish assemblages (Wilson, 1988; Viohl, 1994; Ferber and Wells, 1995; Burrow, 1996; Wilson and Barton, 1996; Bieńkowska, 2004; Barton and Wilson, 2005, Bieńkowska-Wasiluk, 2010). Predation tends to leave little trace in the fossil record, since the entire prey or its significant part is usually digested. The exception are bromalites, being direct evidence for consumed matter. Moreover, predator-caused damage can be subsequently overprinted by other taphonomic processes (Wilson, 1987). A possible way to infer that remains are predated are bite-marks (Randle and Sandom, 2019) or unusual patterns of fragmentation (Spiekman and Mujal, 2023). Scavenging occurs mainly on the bottom of the water body and results in the more or less extensive disarticulation of the skeleton followed by a reduction in its completeness, and eventually may lead to the complete removal of the body. Scavengers tend to attack the fish head first, then other parts of the body, and to move disarticulated elements in all directions (Elder, 1985). Exposure of the fish body to the forces generated by water flow is usually related to its flotation. It occurs when a body gains positive buoyancy following production of post-mortem gases in the body cavity by microbes (Elder, 1985; Elder and Smith, 1988). Two types of flotation can be distinguished. In the case of the full flotation, the body is raised to the water surface, where it experiences wave action and surface currents. Depending on the duration of full flotation, this tends to lead to significant disarticulation and incompleteness of the entire skeleton (including the skull and pectoral girdle), which loses the poorly attached elements when it sinks and hits the bottom (Elder, 1985; Elder and Smith, 1988). In the case of partial flotation, the gases accumulated in a body are not sufficient to lift it to the surface. This results in the posterior part of a body floating above the bottom, subject to intensified disarticulation, while the anterior part of the body is still attached to the ground (Elder, 1985; Elder and Smith, 1988). The skeletal elements are dropped in the proximity of the body, and tend to show a preferred orientation if bottom currents are active. When a body resides on the bottom, microbial decay can be the main factor leading to decomposition. In contrast to the previously mentioned mechanisms, this rarely leads to loss of skeleton completeness, apart from some possible disarticulation (Elder, 1985; Elder and Smith, 1988).

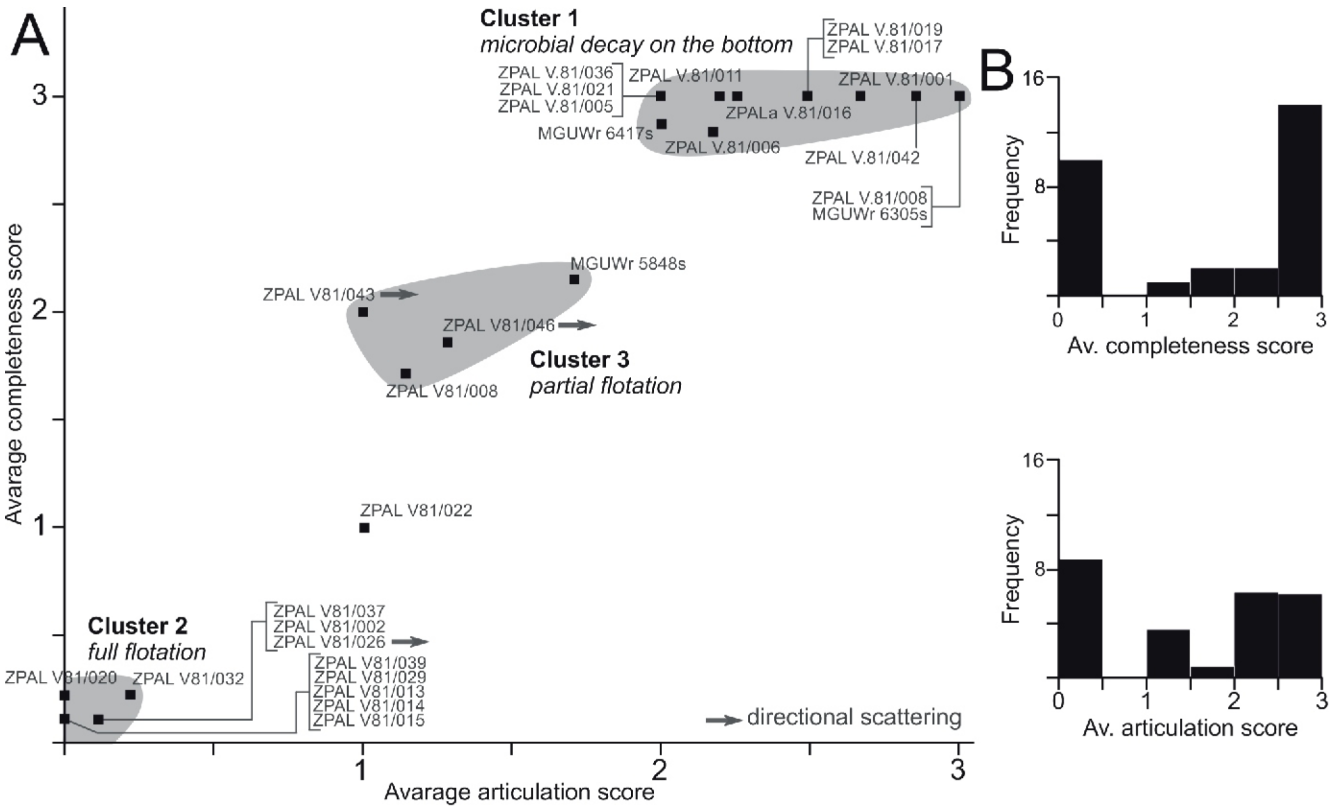

Fig. 5. Taphonomic analysis of actinopterygian fossils from the Janików locality

A – scatterplot of the average articulation versus the average completeness scores in the sample studied; **B** – frequency distributions of the average completeness and articulation scores in the sample studied

The analysis of completeness and articulation allowed recognition of three main types of fish preservation in the Janików site. The first taphonomic type (T1, cluster 1 in Fig. 5A) is represented by carcasses displaying high levels of completeness and moderate disarticulation. The latter is expressed mainly by slight dislocation of elements (mainly scales or lepidotrichia, occasionally skull bones) remaining in contact with anatomically neighbouring ossifications. In rare cases, singular elements are strongly shifted outside the body outline. Despite the partial disarticulation, most individuals belonging to this group preserve fully complete skeletons. This indicates that they did not experience flotation and decay took place entirely on the bottom. This also suggests that scavengers were not present. The disarticulation pattern is consistent with calm microbial decay with simultaneous burial.

The second taphonomic type (T2, cluster 2 in Fig. 5A) is represented by strongly incomplete carcasses, being usually assemblages of flank and ridge scales as well as fin elements (lepidotrichia, fringing fulcra). Only one isolated bone was found during the excavations (cleithrum, ZPAL V.81/013). Since the preservation mode represented by T1 as described above shows a lack of scavenger activity in the section studied, the low disarticulation and completeness most probably result from the full flotation of the bodies, which lost most of their elements during prolonged exposure at the surface and on subsequent sinking. This is supported by the preferred orientation of some individuals, which suggests current activity in the water body.

The third taphonomic type (T3, cluster 3 in Fig. 5A) is characterized by intermediate scores of completeness and articulation between the first and second type. Individuals belonging to this group share a preferred orientation of the disarticulated elements, as well as the lower completeness and articulation scores in the posterior part of the body. The best preserved specimen is ZPAL V.81/046 which shows an exploded abdominal cavity and strong disarticulation of the posterior and posteroventral regions of the skeleton, while posterodorsal and anterior regions remain almost intact. We interpret this type of preservation as resulting from partial flotation, since the higher articulation of the anterior region is consistent with the common pattern of flotation with bottom-oriented head.

ZPAL V.81/022 and 008 represent atypical patterns of preservation for the Janików site, possibly representing rare taphonomic histories. ZPAL V.81/022 is a cluster of firmly articulated flank scales, separated from any other remains. If being the product of flotation they are expected to be at least partially disarticulated or dislocated, as well as possibly surrounded by some other skeletal elements. We regard this specimen as a possible leftover from a predated individual, although the flotation scenario cannot be excluded. ZPAL V.81/008 is a fairly complete individual but lacking the skull, the only example of such a pattern in the Janików site. The skull disarticulation may be referred to the activity of scavengers at some phase of the body's decay. However, in this case also we cannot exclude atypical disarticulation via flotation; the specimen is strongly weathered, hampering detailed observations.

PALAEOENVIRONMENT OF THE JANIKÓW FISH-BEARING LAYERS

The Janików section is dominated by dark-coloured, rhythmic, microlaminated strata, typical of lacustrine deposits. Undisturbed horizontal lamination in the fossiliferous interval, devoid of ripplemarks or storm deposits, suggests that it formed in

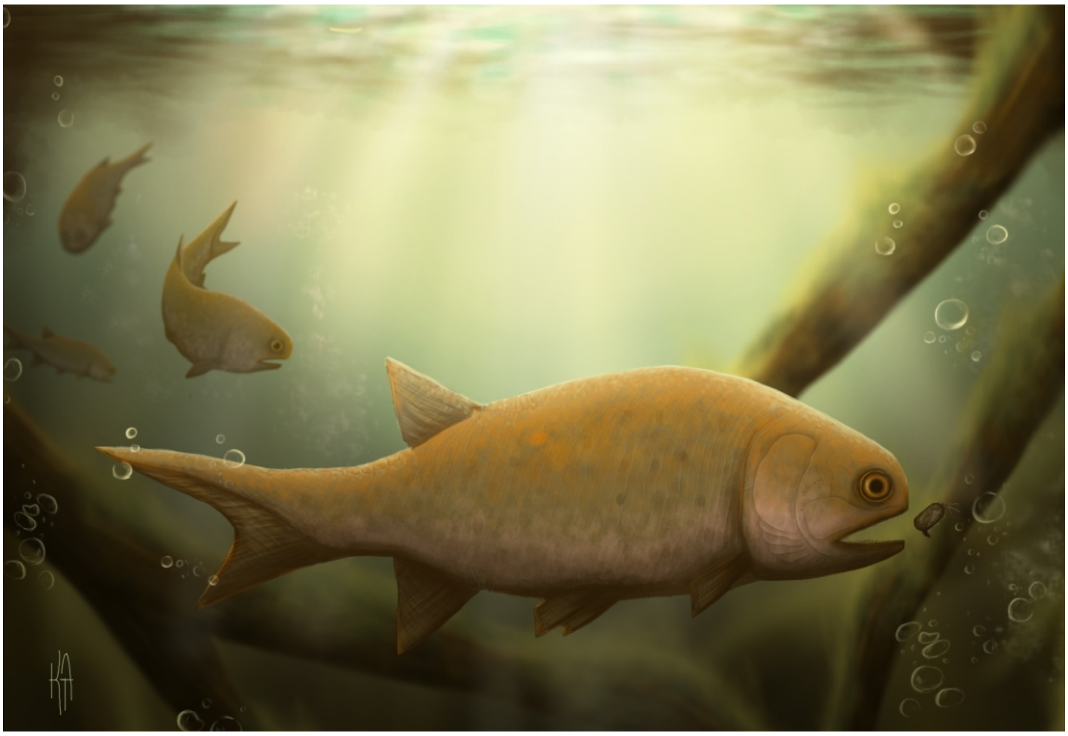

Fig. 6. Reconstruction of *Paramblypterus rohani* in life predating on a conchostracan in the pelagic zone of the Janików lake (artwork by Tetiana Kozyk)

the offshore region of the lacustrine basin, below storm wave base. This interpretation is also supported by the domination of carbonate sedimentation over deposition of terrigenous material, as well as by the mode of preservation of plant remains, which occur commonly in the fish-bearing layers. These are represented mainly by strongly fragmented debris, indicating a relatively large distance from the shore (Šimůnek and Ploch, 2022). Bedding planes rich in ripplemarks and with occasional traces of tetrapods occur immediately above the fish-bearing interval, showing a shallowing tendency in the lake's evolution. The high content of organic matter, as well as lack of bioturbation, clearly point to hypoxic conditions in the lake sediment and possibly in the hypolimnion. This is supported by the results of our taphonomic analysis, indicating conditions allowing calm decay on a bottom dominated by microbial activity, uninterrupted by scavengers needing aerobic conditions.

The flotation of fish carcasses is closely controlled by water pressure and temperature, that relate too water depth. On the basis of features specific for the offshore zone in this instance, it can be inferred that the Janików fish-bearing layers formed at the depth of 30 m or more. This can be regarded as a relatively deep water body, sufficient to prevent fish carcass flotation via a stable, low hypoliminic temperature and high water pressure. In the case of shallow lakes, the low pressure and rise in temperature through the entire water column are strongly favourable factors for flotation. The presence of individuals clearly stagnating on the bottom during their entire decay (T1) supports the deep lake scenario. Moreover, the lack of abruptions in their abdominal regions suggest that the decay took place in relatively cool hypolimnic water (possibly 5-8°C), which slowed the metabolism of bacteria and allowed slow degassing of the carcasses.

Nevertheless, the taphonomic analysis shows that more or less intact individuals represent only part of the fish sample studied. A very similar number of specimens represents highly disintegrated skeletons (T3) which have undergone full flotation, while a minority represents partially floating individuals (T2). This means that at least at times, the hypolimnic temperature was high enough for the full flotation of carcasses, and at some points only for the partial rise of the body and flotation at the bottom. Our quantitative comparison shows that the assemblage displays a bimodal distribution of the preservation modes (Fig. 5B). This suggests that two temperature regimes alternated during the formation of the assemblage, possibly reflecting seasonal decreases of the lake stratification, related to a temporary increases in bottom water temperature. The fluctuations of the hypolimnic temperature may have been related to the preferred orientation of some fish specimens which experienced partial or full flotation, suggesting the presence of weak currents, and possibly indicating mixing of the water masses.

MODE OF LIFE OF AMBLYPTERIDS

The morphological diversity of amblypterids is relatively narrow, thus it can be assumed that all exhibited a similar lifestyle, limited by their body plan. All species share a similar body shape, fin position, scale cover, dentition, and skull arrangement (Dietze, 2000; Štamberg, 2013b, 2020). The silhouette of amblypterids is fusiform, flattened from the ventral side and convex in the dorsal aspect, making their outline slightly hump-backed. The anal and dorsal fins are shifted toward the tail and positioned vis-à-vis each other, displaying a pattern sometimes called a 'second tail' arrangement (Weihs, 1989). The caudal fin is moderately incised. On the base of body shape and fin arrangement, Dietze (2001) regarded *P. duvernoyi* a moderately fast swimmer, adapted to rapid acceleration and a demersal lifestyle. There is some diversity related to the relative size of the fins, which in *Amblypterus* tend to have a larger surface area relative to body size than in *Paramblypterus* (see Štamberg, 2013b), most probably influencing the locomotion of these fishes. In most species scales are rhomboidal, with smooth external surfaces and no to slight serration of the posterior margins. If it occurs, the serration is present in several scale rows at the deepest point of body, between the pectoral and pelvic fins (cf. Dietze, 2001; Štamberg, 2021), indicating their function as turbulators in fast swimming (Fletcher et al., 2014). In some cases (e.g., *P. decorus, P. gelberti*), the serration of scales is more extensively distributed over the body (Dietze, 2000). Such diversity in scale ornamentation suggests differences between species in swimming velocity or exposition to water currents. The dentition of amblypterids is significantly different from that of other actinopterygians, except for the Aeduellidae (Schultze et al., 2021). The teeth located on the jaw margins are strongly elongated and narrow, having a "tubular" morphology and forming together a brush-like structure. The teeth of the second type are located on the coronoid and palatoquadrate. They are low, conical with wide bases. These dental characters were described for the first time in *P. decorus* by Blot and Heyler (1963), and later in *P. duvernoyi* by Dietze (2001), *Paramblypterus*. cf. *rohani* and *Paramblypterus* sp. by Štamberg (2020). The dentition of amblypterids appears to be specialized to feed on small benthic or planktonic invertebrates as suggested by Dietze (2001), for example on conchostracans (Štamberg, 2020). Feeding on larger organisms (such as small fish) seems unlikely, since no teeth display the shape typical for seizing such prey, or the inclined orientation hampering its escape.

The new occurrence of *Paramblypterus rohani* in Janików shows that it was well-adapted to live in the pelagic zone, contrastingly to the previous interpretation of amblypterids as bottom-dwellers (Fig. 6; cf. Dietze, 2001). The comparative taphonomic study shows that deep parts of the lake were incapable of sustaining benthic or hyperbenthic fauna. At the same time, the mode of fish preservation excludes distant transportation for most of the buried carcasses. Therefore, the main source of food for the amblypterids unearthed was open-water plankton. Moreover, *P. rohani* appears to be by far the most dominant fish in the Janików assemblage, suggesting that it was strongly competitive against other planktivorous species. In the light of the current results, amblypterids appear to be effective open-water predators, though this does not contradict previous inferences about their demersal lifestyle. We rather lean to the interpretation that amblypterids were strongly opportunistic fish adapted to various conditions, which partially explains their success in the late Carboniferous and early Permian.

STRATIGRAPHIC POSITION OF THE JANIKÓW SITE

The relation between the Janików fossil-bearing section and the two lacustrine packages usually distinguished in the Słupiec (Broumov) Formation – Ruprechtice and Otovice – is a fundamental question from the stratigraphic perspective. Usually, the classic fossil-bearing deposits of the Ruprechtice Horizon are represented by pale cream to pink limestones with reddish to dark brown fish fossils. Meanwhile, the fossil-bearing deposits of the Otovice Horizon, recognized near Janików, are represented by dark marls with black fish remains similar to the previously known Otovice Horizon outcrops. Šimůnek and Ploch (2022) assigned the Janików section to the Ruprechtice Horizon, on the basis of mapping by Tásler (1966), in which the Ruprechtice and Olivětín limestones are represented by a similar lithology in the Otovice and Janików area. In fact, the composition of fish assemblage from Janików resembles those known from the Otovice Horizon due to the strong dominance of *P. rohani* (see Štamberg, 2021). Therefore, the faunal data contradicts the results of Tásler (1966) as noted by Šimůnek and Ploch (2022). If the outcrop in Janików truly represents the Ruprechtice Horizon it is the first assemblage from this stratum dominated by *P. rohani* intead of *P. vratislaviensis*. The occurence of both species may be controlled by yet unknown environmental factors.

CONCLUSIONS

The Janików fish-bearing beds belonging to the Słupiec (Broumov) Formation formed in an lacustrine offshore zone. Preservation of the fish fossils can be attributed to bottom hypoxia, which prevented scavenging. The main factors responsible for decomposition of the fish bodies was flotation and microbial decay at the bottom of the reservoir. The assemblage comprises a nearly equal ratio of fully articulated and highly complete individuals versus ones that are strongly incomplete and disarticulated. Such a bimodal taphonomic composition suggests variations in water temperature, being intermittently warm enough to induce flotation of fish carcasses. The only species identified in the assemblage is *P. rohani*. The taphonomic history and sedimentary features suggest that this species was an effective pelagic predator, despite its morphological features clearly indicating adaptations to bottom-dwelling. Contradictory data on the stratigraphic position of these strata in Janików suggest that the occurrence of amblypterids in the Intra-Sudetic Basin was controlled by environmental factors.

Acknowledgements. We are grateful to J. Białek, U. Kosarewicz, A. Setlik (MGUWr), B. Ekrt (National Museum in Prague), S. Voigt and J. Fischer (Geoskop Urweltmuseum in Thallichtenberg) for their hospitality and help during the visits and examination of the collections. We thank M. Tałanda (University of Warsaw) for valuable comments to the manuscript. The research was funded by the Polish National Science Centre (grant 2017/26/M/ST10/00646).

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Cataluge number	skull		pectoral girdle		pectoral fins		pelvic fins		dorsal fin		anal fin		caudal fin		scales anterior		scales posterior	
	A	C	A	C	A	C	A	C	A	C	A	C	A	C	A	C	A	C
ZPAL V.81/046	3	3	-	-	2	3	-	-	2	3	0	1	1	1	0	1	1	1
ZPAL V.81/001	-	-	-	-	-	-	-	-	3	3	-	-	3	3	2	3	-	-
ZPAL V.81/002	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
ZPAL V.81/003	-	-	-	-	-	-	-	-	3	3	3	3	3	3	3	3	3	3
ZPAL V.81/005	-	-	-	-	-	-	-	-	-	-	-	-	2	3	-	-	2	3
ZPAL V.81/006	-	-	-	-	3	3	1	2	2	3	2	3	-	-	2	3	3	3
ZPAL V.81/008	0	0	0	0	0	0	-	-	2	3	2	3	-	-	2	3	2	3
ZPAL V.81/011	-	-	-	-	-	-	-	-	2	3	2	3	3	3	2	3	2	3
ZPAL V.81/013	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ZPAL V.81/014	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
ZPAL V.81/015	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
ZPAL V.81/016	-	-	-	-	-	-	2	3	-	-	3	3	-	-	2	3	2	3
ZPAL V.81/017	-	-	-	-	-	-	-	-	3	3	-	-	-	-	2	3	-	-
ZPAL V.81/018	-	-	-	-	-	-	-	-	-	-	3	3	3	3	-	-	3	3
ZPAL V.81/019	-	-	-	-	-	-	-	-	-	-	3	3	-	-	-	-	2	3
ZPAL V.81/020	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
ZPAL V.81/021	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	3	-	-
ZPAL V.81/022	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1
ZPAL V.81/026	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
ZPAL V.81/029	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
ZPAL V.81/032	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1
ZPAL V.81/036	-	-	-	-	-	-	-	-	-	-	2	3	2	3	-	-	2	3
ZPAL V.81/037	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
ZPAL V.81/039	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
ZPAL V.81/042	-	-	2	3	-	-	3	3	3	3	3	3	3	3	3	3	3	3
ZPAL V.81/043	-	-	-	-	-	-	-	-	-	-	-	-	1	2	-	-	1	2
MGUWr 5848	-	-	-	-	2	3	1	1	3	3	1	1	1	1	2	3	2	3
MGUWr 6305	3	3	3	3	3	3	-	-	-	-	3	3	-	-	3	3	3	3
MGUWr 6417	1	3	2	3	3	3	-	-	3	3	1	2	2	3	2	3	2	3

A - articulation C - completeness