

The first description of coelacanth remains from the Upper Triassic of Krasiejów, Poland

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Coelacanth fishes are nowadays represented by only two species; however, in the Paleozoic and Mesozoic eras, they were common elements of freshwater and marine ecosystems. Their remains are known from several Upper Triassic locations worldwide, but to date, they were not known from the famous site of Krasiejów (Opole area, SW Poland). Here, we describe sarcopterygian isolated scales and tooth-bearing elements. Both scales and teeth have typical sarcopterygian features and bear numerous similarities with fossil and modern coelacanths. The scales, from their characteristic ornamentation pattern, can be described in considerable detail and defined as *Diplurus* sp., being the first occurrence of the *Diplurus* genus outside the Newark Supergroup, showing that Triassic coelacanths lived on opposite margins of the large epicontinental sea located between modern North America and Europe.

Key words: Coelacanthiformes, Sarcopterygii, scales, teeth, microfossils, Triassic.

INTRODUCTION

Abundant fossils of temnospondyl amphibians (Sulej and Majer, 2005; Sulej, 2007; Gruntmejer et al., 2016; Konietzko-Meier et al., 2018; Antczak and Bodzioch, 2018a; Teschner et al., 2018), archosaurs (e.g., Brusatte et al., 2009; Bronowicz, 2009; Fostowicz-Frelik and Sulej, 2010; Sulej, 2010; Antczak, 2016; Dzik and Sulej, 2016) and diverse ichthyofaunal remains have been found in the fine-grained deposits of Krasiejów (SW Poland) of Upper Triassic age (Carnian according to e.g., Lucas, 2015; Dzik and Sulej, 2016; or Norian according to e.g., Szulc et al., 2007, 2015; Jewuła et al., 2019). To date, only a few papers have focused on the Late Triassic fishes from Krasiejów (Skrzycki, 2015; Antczak and Bodzioch, 2018b; Kowalski et al., 2019), specifically on isolated teeth and scales, mostly as microfossils. Nevertheless, different taxa have been reported from the locality, including sharks (Hybodontidae), several families of ray-finned fish (Actinopterygii), and lungfish (Dipnoi) (Antczak and Bodzioch, 2018b; Kowalski et al., 2019). New findings allow us to add another taxon to the list: coelacanths.

In the mudstone/claystone of Krasiejów two main bone-bearing horizons have been described (Dzik and Sulej, 2007; Bodzioch and Kowal-Linka, 2012; Fig. 1), although vertebrate remains can be found also between them, especially micro-vertebrate fossils. Fish scales were found in the lower bone-bearing horizon, which is the layer most abundant in fossil material, and microscopic teeth were found in one of the irregular lenses of coarser-grained deposits. Vertebrate fossil material from the lower bone-bearing horizon is probably at least partially allochthonous (Konieczna et al., 2015) (re)deposited after a flash flood (Bodzioch and Kowal-Linka, 2012). Surface runoff might have occurred in the Late Triassic environment of Krasiejów due to the subtropical climate with dry and rainy seasons in the environment, similar to modern-day Queensland, Australia with its 'Gilgai relief' including ephemeral lakes and streams (Jewuła et al., 2019).

The Coelacanthiformes are represented by only two extant species, but the fossil diversity of this clade is much higher, comprising over 100 species (Cloutier and Forey, 1991; Forey, 1998; Toriño et al., 2021). The oldest representatives are known from Devonian deposits (e.g., Szrek, 2007). In the Carboniferous they were most diverse, adapting to many different environments, including as freshwater biota (Szrek, 2012). Coelacanths were considered extinct following the end-Cretaceous mass extinction, until the famous discovery of a living representative in 1938. For many years they were labeled as 'living fossils', but recent studies show that their genotype is changing significantly (Cavin and Guinot, 2014). The fossil record also reveals that, in the past, morphological and anatomical variations within the group were higher than previously as-

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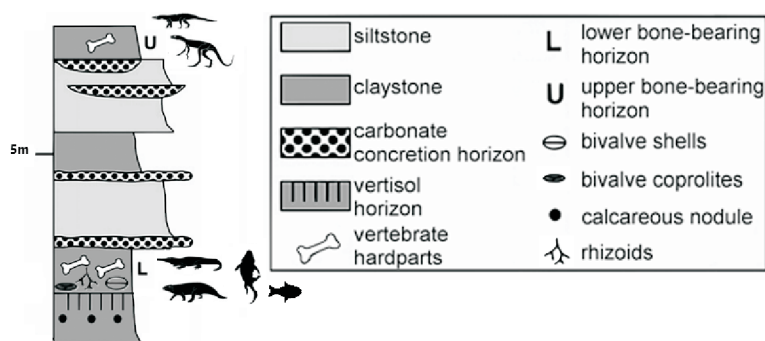


Fig. 1. Schematic section of the strata exposed in the Krasiejów excavation site (after Bodzioch and Kowal-Linka, 2012)

sumed (Casane and Laurenti, 2013; Cavin et al., 2017; Mondéjar-Fernández et al., 2021). The closest relatives of coelacanths are lungfish (Dipnoi) (Amemiya et al., 2013). Here we report several occurrences in the Upper Triassic deposits of Krasiejów of isolated coelacanth scales and tooth-bearing bone elements with a high degree of affinity to this group. Although the teeth can be only putatively attributed to coelacanth fishes, the size and combination pattern of tubercles and ridges on the exposed areas of isolated scales allow us to describe them as belonging to indeterminate species of the genus *Diplurus*.

MATERIAL AND METHODS

Six coelacanth fish scales (~1–1.5 cm in diameter) have been collected from the field so far (Table 1). The scales were prepared manually using mechanical tools. During excavation, 5 tons of rock were collected from the layer containing accumulations of vertebrate microfossils. The material was rinsed with water and hydrogen peroxide, sieved several times, and dried. As a result, ~250 kg of sieved sediment were obtained and in total over 5000 microfossil specimens were curated in the University of Opole collection. The microfossils were hand-picked under binocular microscopes (as described in Kowalski et al., 2019). Among this collection, six tooth-bearing fragments were assigned to coelacanths.

For general taxonomic description, the scale specimens were observed using an Optika SZN-3 stereoscopic microscope. Photographs of scales and teeth were made using a

Leica M205 A microscope at MCBR UO (International Research and Development Center of the University of Opole).

Specimen UOPB3467 was analysed and scanned using a Scanning Electron Microscope Hitachi TM 3000 under high vacuum with EDS (Energy Dispersive X-ray Spectroscopy) for chemical analysis.

Institutional Abbreviations — UOPB, University of Opole, Department of Palaeobiology

RESULTS

SCALES

SYSTEMATIC PALAEONTOLOGY

Class Sarcopterygii Romer, 1955
Order Coelacanthiformes Berg, 1937
Family Mawsoniidae Schultze, 1993
Diplurus sp. Newberry, 1878

M a t e r i a l. – Six scales in the University of Opole collection from the Upper Triassic Krasiejów site (SW Poland), housed at the Institute of Biology. Three scales are well-preserved allowing description of their ornamentation: UOPB 3465, 3466, 3467, and three others are missing half of the scale (UOPB 3559), or the central region (UOPB 35560), or have ornamentation partially damaged (UOPB 3558).

L o c a l i t y. – Upper Triassic site in Krasiejów, SW Poland, Grabowa Variegated Mudstone-Carbonate Formation, Patoka Marly Mudstone-Sandstone Member, Krasiejów bone-breccia level.

D i a g n o s i s. – Scales characterized by 15–16 ridges with the central ridge being the largest and two adjacent lateral ridges reaching the scale's posterior margin. From basal (pre-Triassic) Coelacanthiformes representatives, it differs in having scale ornamentation in the form of elongated ridges instead of small tubercles. From Triassic taxa, it differs in the number (e.g., *Ganbergia* with 50 ridges) of ridges and not having a prominent single central ridge (i.e. *Heptanema*, *Ticinepomis*). From *Diplurus newarki* and *D. longicaudatus* it differs in the number of ridges, with two first lateral ridges (closest to the central ridge) reaching the scale margin. While central ridges are parallel to the scale's anterior-posterior axis, ridges of the external row are slightly oblique.

D e s c r i p t i o n. – The scales are rounded with a slightly elongated anterior-posterior axis. The posterior edge is rounded and wavy. This sinusoidal margin is also seen on growth rings (circuli, according to Mahé et al., 2021, representing annual/periodic scale growth). All specimens possess a series of slender and more or less parallel and hollow ridges (tubes – which can be determined on the eroded surface of scales where broken ridges can be seen, especially on UOPB 3465; Fig. 2I) on the posterior field, which is the part not covered by adjacent scales (= free surface on the external side of the scale). Three of the scales (UOPB 3455–3467) are described in detail as well-preserved specimens. Ornamentation occupies approximately two-fifths of the area of the scale. The ridges are parallel or slightly directed to the centre of the scale. The medial ones are larger than the lateral ones. Some extend to the scale margin, while others are shorter and end midway. In such cases, another ridge emerges immediately after (or is slightly displaced with re-

Table 1

Coelacanth scales: specimen characteristics

Specimen	Length [mm]	Width [mm]	Number of ridges
UOPB 3465	15	12	16
UOPB 3466	16	~13	15
UOPB 3467	~9	11	>12
UOPB 3558	16	11	?
UOPB 3559	?	14	>9
UOPB 3560	15	12	?

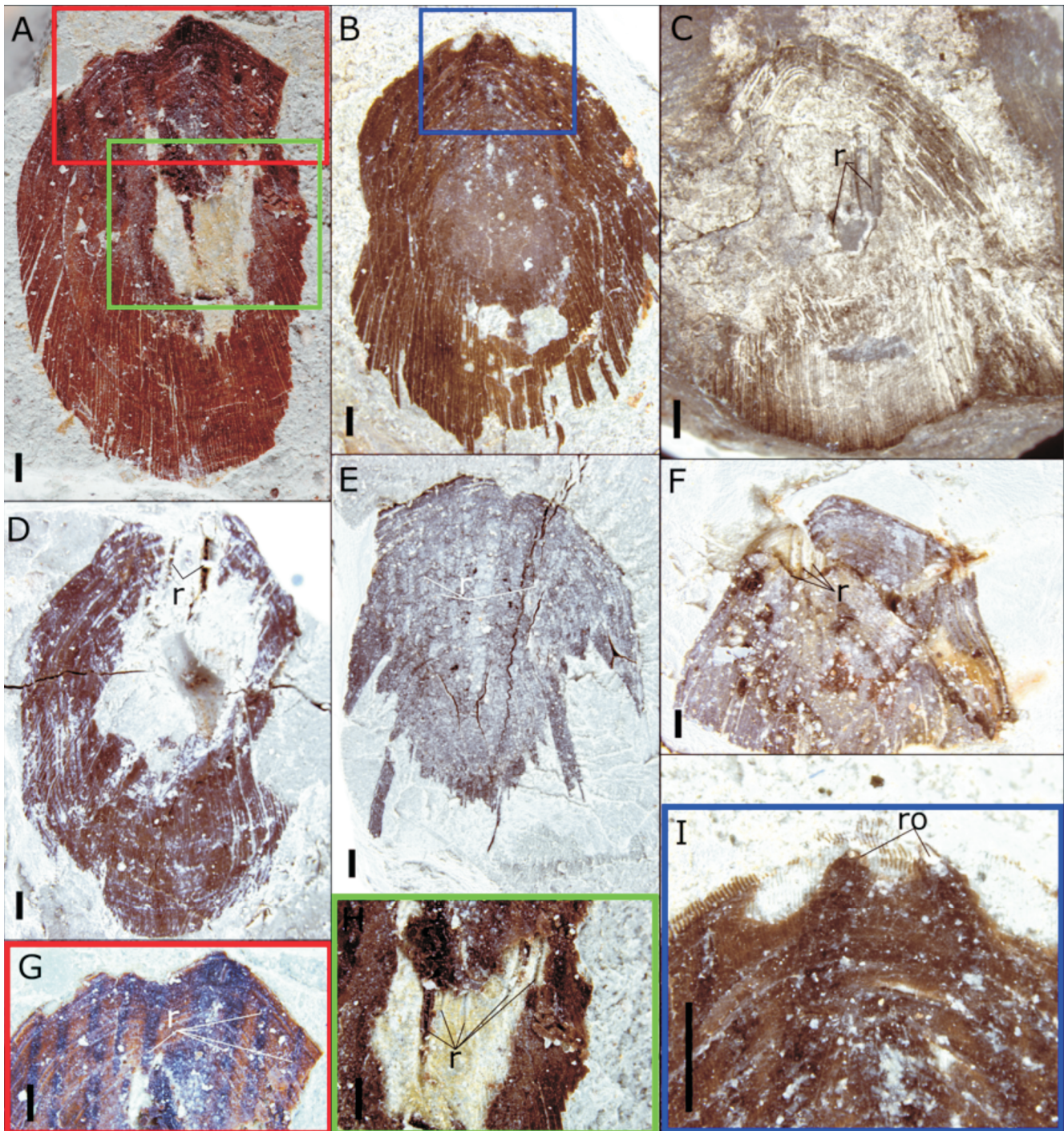


Fig. 2. Coelacanth scales from Krasiejów

A, G, H – UOPB 3466; **B, I** – UOPB 3465; **C** – UOPB 3467; **D** – UOPB 3560; **E** – UOPB 3558; **F** – UOPB 3559. **r** – ornamentation ridges (black – ridges or imprints seen on the broken parts of the scales, white – ridges seen through partially transparent scales on the internal surfaces); **ro** – ridge opening; scale bars 1 mm

spect to) the end of the previous one. The internal sides of the scales are exposed (Fig. 2). However, impressions of several large central ridges can be seen (where the part of the central and posterior fields is missing). According to their spacing and size, it can be estimated that all specimens possess more than a dozen ridges. In UOPB 3665 the tip of the two ridges (adjacent to the central ridge) extends up to the scale margin.

In the covered part of the scale (overlapped by adjacent scales), both lateral and anterior fields are ornamented with fine striae radiating from the centre-posterior part of the scale. Around the focal point of the scale, numerous distinct concentric rings (circuli) can be observed. Specimen UOPB 3465 has a well-preserved central area. The focal point in this scale is a round structure without distinct sculpturing. The anterior and lat-

eral field (parts covered by adjacent scales) has a feather-like appearance of radiating fine striation (crossing the growth rings).

The posterior field reveals a distinct colouring pattern most clearly seen on the scale UOPB 3466 (internal surface). Longitudinal dark stripes extend from the centre of the scale to the edge. Colouration (dark imprints on the lighter brown scale) overlaps the sculpturing. While darker stripes extend along the ridges, which makes estimation of the number of ridges easier. The centre of the scale is also of a darker colour.

EDS observation shows a chemical composition typical for such material. The scales are made of bony material: calcium phosphate, $\text{Ca}_3(\text{PO}_4)_2$. No additional mineralogical signals were found.

TEETH

SYSTEMATIC PALAEONTOLOGY

Class Sarcopterygii Romer, 1955
Order Coelacanthiformes indet. Berg, 1937

Material. – six tooth-bearing elements (UOPB 3481–3486)

Locality. – Upper Triassic site in Krasiejów, SW Poland, Grabowa Variegated Mudstone-Carbonate Formation, Patoka Marly Mudstone-Sandstone Member, Krasiejów bone-breccia level.

Diagnosis. – Grasping teeth are conical, elongated, and curved backwards with visible striations (enamel wrinkles) present at least on the lower part of the crown. The apical part of the crown is not translucent (as in actinopterygians). At the base of the grasping teeth, there are numerous, low, pyramidal and conical additional teeth without wrinkles on the enamel surface. Palatal teeth are flattened, bulbous, and low, arranged in longitudinal rows with enamel wrinkles. The gill teeth are curved, conical, and sharp, arranged in a configuration of three or five teeth with enamel striations per toothplate.

Description. – Fragments of the tooth-bearing bones with dentition tentatively attributed to coelacanth can be divided into three morphotypes (Fig. 3).

The first morphotype (Fig. 3A–F) includes fragments of bone with attached characteristic dentition. The labial surface of the bone lacks additional teeth and its wall is high and vertical. The main row of teeth consists of prominent and massive crowns arranged in a single line (3 in specimen UOPB 3481; only one can be seen in incomplete specimen UOPB 3482, though there are visible circular bases of broken additional teeth in the row). Tooth size increases distally in specimen UOPB 3481. Teeth are attached to the bone surface with widened bases. The tooth bases are round in occlusal view and the crowns are not flattened in the apical part. The crowns from the main row are pointed, elongated, and strongly curved backwards. The apices of the crowns are worn and blunted, which is particularly visible in the case of the last, largest tooth in the row (UOPB 3481). On their entire surfaces, the teeth from the main row have clear striations formed by relatively few wrinkles running by the longitudinal axis of the crown. Numerous and irregularly arranged additional teeth are visible on the entire surface of the bone from the lingual side. They are very small and do not exceed half the height of the lowest tooth in the main row. Their apices are rounded and not very sharp. These additional teeth are very slightly curved backwards and do not have striations on their surface. Both in the case of large teeth and small additional teeth, the apices of the crowns do not possess acrodin

caps, the semi-transparent enamel characteristic of ray-finned fish (Actinopterygii).

Specimens assigned to the second morphotype (Fig. 3G–K) are flat, elongated bone fragments with numerous bulbous teeth arranged in irregular rows. Unfortunately, almost the entire surface of the specimens (UOPB 3483 and 3484) is covered with heavily cemented sediment, the removal of which would most likely damage the fragile fossil. Only the apical parts of the tooth crowns are visible, which are low and circular in occlusal view, and have poorly marked apices. Laterally the individual teeth are strongly inclined, with elongated bases and a rounded upper surface of the crown. On the surface of the teeth, visible wrinkles converge towards the apex. The teeth are of different sizes and the largest of them are located in the dental row lying at one of the edges of the bone element. On the edge of UOPB 3483, there are also traces of broken teeth. The specimens described are undoubtedly parts of larger bone elements.

Specimens assigned to the third morphotype (UOPB 3485 and 3486; Fig. 3L–Q) are flat bone plates with several developed teeth. The elements described are not fragments of larger elements since, apart from small defects at the edges, the bone plates are complete. Each base is slightly convex and smooth. In occlusal view, the plate is oval. On its upper surface, there are three (UOPB 3485) or five (UOPB 3486) teeth attached to the bone surface with strongly widened bases. There is no visible boundary between the base of the tooth crowns and the bone plate. The teeth in occlusal view are arranged in the shape of a triangle (UOPB 3485) or two parallel rows (UOPB 3486). Most of the crowns are missing (broken), and only a few are complete. In occlusal view, the bases of the teeth are circular and the crowns do not flatten in the upper part. The completely preserved crowns are massive and their upper sections are curved. On its entire surface, each tooth has developed ornamentation formed by prominent wrinkles running along the longitudinal axis of the tooth. In the basal part, the ornamentation is barely visible. On the tooth crowns that are broken, the wrinkles of enamel are visible.

DISCUSSION

SCALES

All specimens bear ornamentation consisting of longitudinal hollow ridges covering two-fifths of the scale, as typical for coelacanth, e.g., *Miguashaia bureaui* (Mondéjar-Fernández et al., 2021: fig. 2). Paleozoic coelacanth scale ornamentation is characterized by numerous small and densely packed tubercles and ridges, while Mesozoic and Cenozoic taxa possess rather fewer, but larger, elements (Mondéjar-Fernández et al., 2021: fig. 11).

Thus, the material described differs distinctly from pre-Triassic taxa. From *Rhabdoderma* it differs in having central ridges, the largest with lateral ridges being distinctly smaller. From *Caridosuctor* it differs with the ovate shape of the scale, with a rounded posterior margin and the central-largest ridge not reaching the scale margin.

Triassic taxa also possess distinctly different ornament than seen on the scales from Krasiejów. *Ganbergia* possesses over 50 densely-packed ridges (Yabumoto and Newman, 2004: figs. 1–3). In *Heptanema* each scale bears a stout, prominent median ridge ending posteriorly in a pointed spine that extends beyond the posterior margin of the scale (Renesto and Stockar, 2018: fig. 12B). *Ticinepomis* possesses oval scales orna-

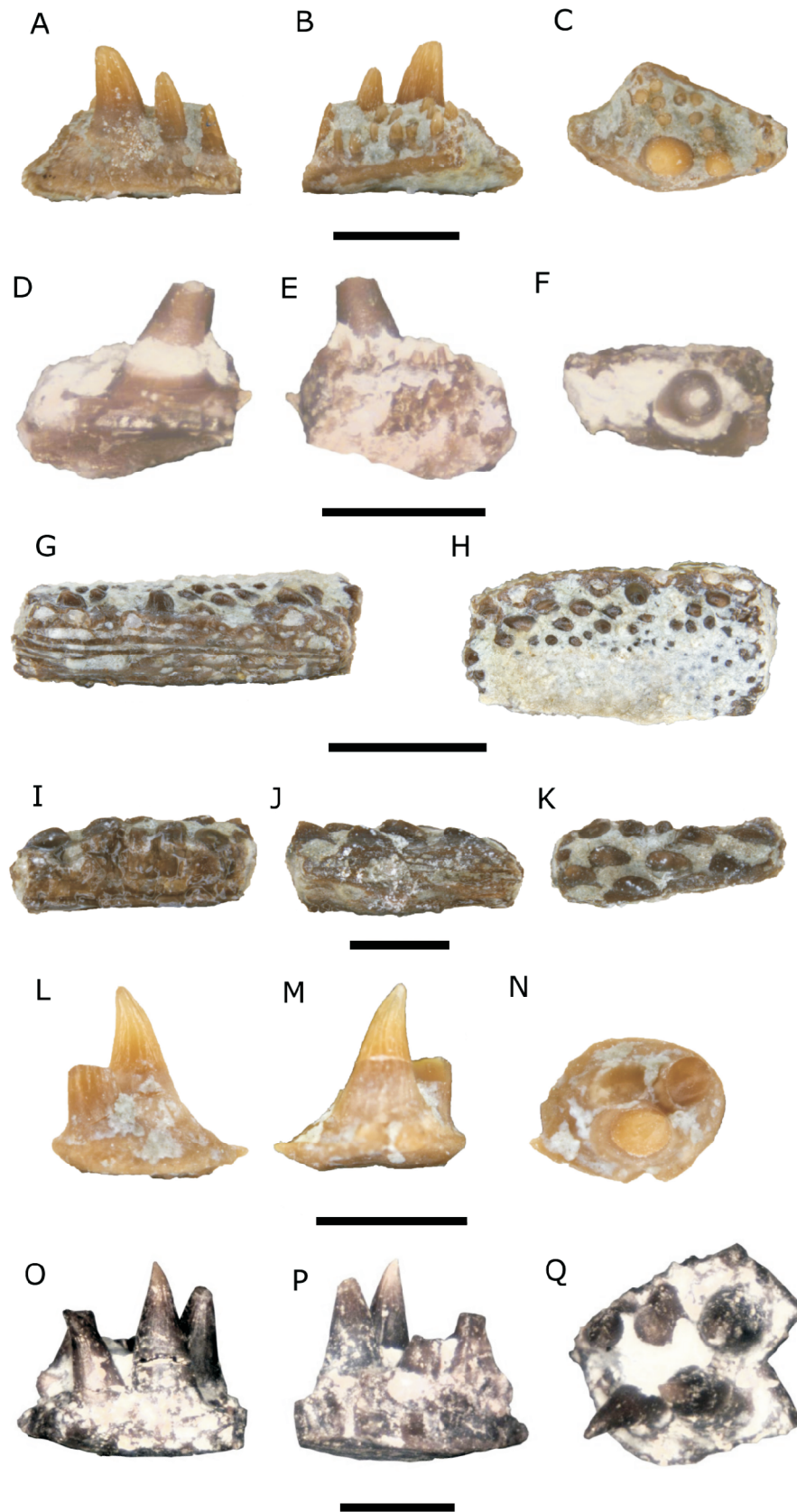


Fig. 3. Coelacanth teeth from Krasiejów

A–F – morphotype 1 (A–C – UOPB 3481; D–F – UOPB 3482); G–K – morphotype 2 (G, H – UOPB 3483, I–K – UOPB 3484); L–Q – morphotype 3 (L–N – UOPB 3485, O–Q – UOPB 3486); scale bars 1 mm

mented with a cluster of elongated ridges surrounding a median larger ridge (Ferrante et al., 2023: fig. 15H). Some basal Coelacanthiformes possess more sparse ornament (e.g., *Coelacanthus harlemensis* from Jurassic deposits of Solnhofen has 5–12 ridges – Lamber, 1991: figs. 8, 11), but their elongated tubercles/ridges are located rather randomly with no distinct difference in their length. The ornamentation pattern, with the largest ridge located in the centre of the posterior field of the scale with laterally distributed smaller ridges, is considered a possible derived character of the Mawsoniidae (Mondéjar-Fernández et al., 2021).

Species closely related to Mawsoniidae from the Middle Triassic Guanling Formation possess a significantly lower number of ridges (i.e., *Yunnancoelacanthus* 3–7 ridges) or tuberculate ornamentation rather than extended ridges, i.e., *Luopingcoelacanthus* (Wen et al., 2013: fig. 6).

The Krasiejów specimens also differ from Cretaceous *Axelrodichthys* by possessing only one central ridge which is distinctly larger than the others and by having a more organized ridge location in two rows as well as a rounded posterior margin. It differs from Jurassic *Lualabaea* by having a rounded posterior margin and the central largest ridge not reaching the margin (Forey, 1998; Mondéjar-Fernández et al., 2021: fig. 11).

The scales described from Krasiejów most closely resemble those of *Diplurus*.

Taxonomic identification of the isolated scales is difficult because scale ornamentation varies significantly between various regions of the fish body (Roberts, 1993). According to Schaeffer's description of the *Diplurus newarki* (Schaeffer, 1952: fig. 12), the pattern of a large ridge in the middle, and smaller ridges (vaguely pointing to the centre) in the lateral parts is typical of lateral-dorsal scales. Scales from other regions possess fewer ridges with no larger ridge in the centre. Thus, the coelacanth scales from the Krasiejów site can be described as scales from the lateral-dorsal part of the body.

The ridges' estimated pattern (according to size, orientation, and number of exposed ridges) is most similar to that of *Diplurus newarki* from the Triassic deposits of the Newark Supergroup (eastern coast of USA) (which has up to 13 ridges). Another described species, *Diplurus longicaudatus* from the Lower Jurassic of North America (Newberry, 1878) possesses up to 27 ridges in the same 'mawsoniid-like' pattern (Wen et al., 2013). Similar in general characteristics and size (~2 cm) are also scales reported as *Diplurus* sp. from the Upper Triassic of Virginia (Weems and Kimmel, 1993) and scales of the Upper Triassic *Chinlea* (Schaeffer, 1967), but they both possess up to 40 ridges at the posterior field.

The character and orientation of ridges in the posterior field allow for assignment to *Diplurus* sp. The number of ridges (15–16) is different than in known species (up to 13 in *D. newarki* and up to 27 in *D. longicaudatus*), unusual is also the condition of two lateral ridges (closest to the central ridge) reaching the scale margin. Ridges in the external row are also slightly oblique with respect to the inner row, while in *D. newarki* they form a direct (straight-line) continuation.

The ornamentation pattern forms on the scale a kind of colour pattern. This resembles the colour pattern in modern striped bass (*Morone saxatilis*), where the elevated part of the posterior field of a single scale is darker than the rest of the lateral fields (Zhu et al., 2013). The fact that the stripes are visible only on posterior fields also suggests that the ornamentation resembles scale colouration in part, and that the stripes visible on the fossil scales are not a result of depositional processes that would include the whole scale.

Colouration preservation examples are known for many taxonomic groups of invertebrates and vertebrates across the fos-

sil record from the early Paleozoic onwards (e.g., Turek, 2009; Baliński, 2010; Kaplan, 2010). The oldest known example of fish with preserved colouration is *Elonichthys* from Permo-Carboniferous strata of Kansas (USA). That specimen shows evidence of countershading but also possesses lateral stripes to break up the outline of the body (Gottfried, 1989). This kind of pattern is also known from more recent fossils of actinopterygians from the Eocene of Monte Bolca, Italy (Vinther, 2015). However, no evidence of chromatophores were noted in the material described. Stripes are visible on the scales with the inner surface preserved, being most probably ridges from the outer surface visible through a partially transparent scale. The darker colour of the stripes is caused by their increased thickness and such a pattern of isolated scales may not correspond to the general colouration pattern for the fish body.

The supposed environment would nevertheless favour disruptive patterns of colouration rather than countershading or multi-coloured designs. Disruptive colouration is useful for a species living in more turbid, murky water with less conspicuous countershading (Fig. 4; Vinther, 2015). A 'swampy' environment was also interpreted by Schaeffer (1952) as the environment where *Diplurus newarki* was the most abundant (for *D. longicaudatus* streams were proposed as the probable habitat). The Krasiejów palaeoenvironment is inferred to be ephemeral lakes, swamps, and meandering rivers (Gruszka and Zieliński, 2008; Bodzioch and Kowal-Link, 2012; Kowalski et al., 2019; Jewuła et al., 2019).

TEETH

The microfossil specimens described closely resemble the dentition of predatory representatives of the Sarcopterygians. The dentition of coelacanth and their closest relatives is characterized by a varied morphology depending on the location of the tooth-bearing elements. The grasping teeth are straight or slightly recurved, tapering markedly from the base toward the apex. The tooth crowns do not flatten towards the apex and remain circular or slightly oval in occlusal view along their entire length (Fig. 3). A characteristic feature of this dentition is the presence of radial ornamentation formed by a relatively few, but most often very distinct, wrinkles in the enamel running parallel to the longitudinal axis of the tooth crown (Fig. 3). These wrinkles in the cross-section of the tooth penetrate internally and form a plicidentine structure. This is a feature that developed in Sarcopterygia dentition as early as the Devonian and, as a primary, plesiomorphic feature, was preserved in later representatives of this group (Szrek, 2012). The grasping dentition in coelacanth, unlike the teeth of amphibians known from the Krasiejów site, does not have developed edges, and the apical part is not flattened. To the tip, the occlusal shape of the crowns of teeth interpreted as belonging to lobed-finned fish is circular or very slightly oval. In the case of specimens representing the presumed lobe-finned dentition, the grasping teeth are always surrounded on at least one side by a dense mosaic of very low and slightly pinnate teeth (Fig. 3). The accessory teeth surrounding the main grasping teeth are low, massive, pyramidal and the apices of their crowns are not so pointed and sharp. They also lack longitudinal ornamentation and their surface is smooth (Clément, 2005; Meunier et al., 2015; Maan et al., 2017). The dentition described, however, is very similar to specimens from a few other palaeontological sites, being most similar to the dentition of the genus *Swenzia* (the ectopterygoid of the holotype specimen MNHN JRE 47) from the Oxfordian (Jurassic) deposits of the Levigny site in France (Clément, 2005). They also share many features with specimens from the Snyder

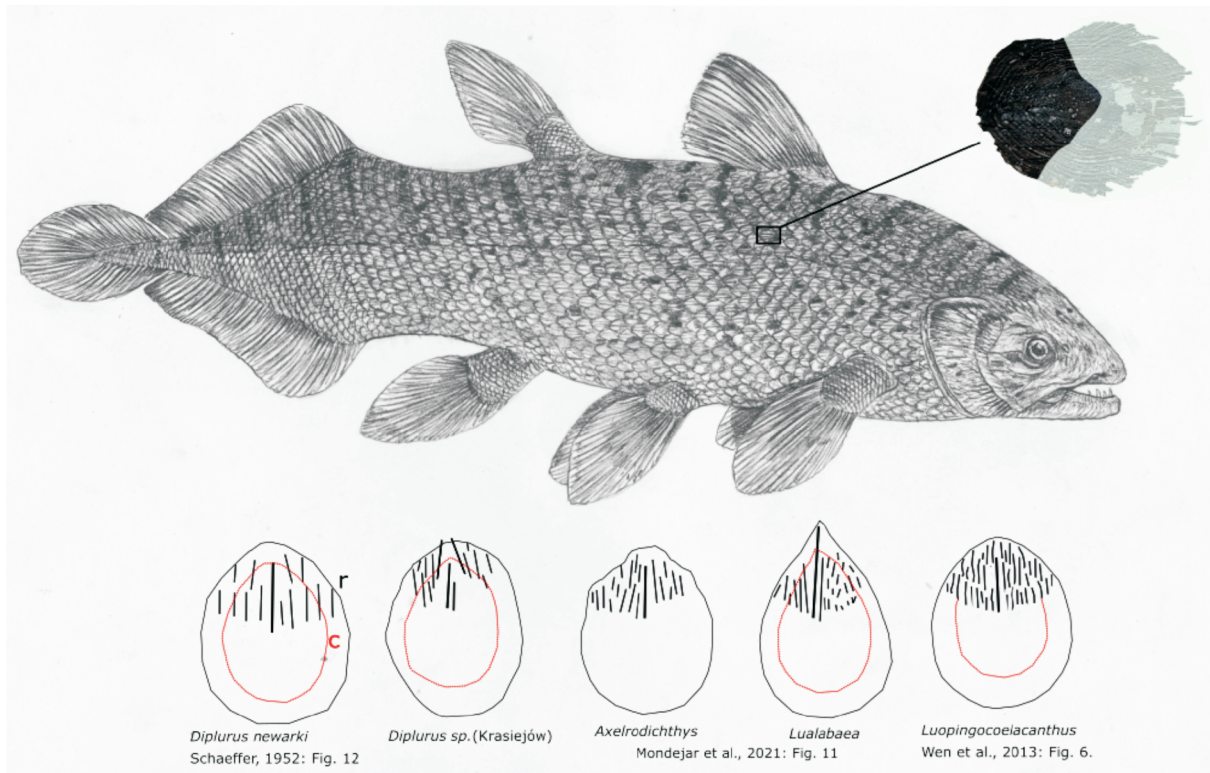


Fig. 4. Reconstruction of the coelacanth fish with striped scales, showing possible placement of one of the scales

Shaded parts of the scale were covered by adjacent scales; C – circulli, r – ornamentation ridges; reconstructions of the scales of chosen mawsoniids and Latimerioidei (author J. Kowalski)

Quarry site in New Mexico (Heckert and Jenkins, 2005) identified as coelacanth tooth plates. More triangular teeth arranged on plano-convex plates included in the third morphotype are probably gill teeth (Isokawa et al., 1968).

To sum up, the first morphotype could be considered as representing buccal grasping toothplates, the second morphotype as a fragment of larger denticulate plates (pterygoid, prearticular, parasphenoid, etc.), and the third morphotype as isolated toothplates covering the gill arches.

PALAEOGEOGRAPHY

The occurrence of *Diplurus* in southern Poland shows that this coelacanth genus was possibly widespread across the epicontinental sea between the modern eastern part of North America and Europe (see north-central part of Pangea in the Late Triassic – Fig. 5A). Coelacanths have not previously been noted from the Triassic deposits of Krasiejów. How freshwater taxa came to occur on opposite sides of the sea cannot be determined based on the present material. Their ancestor might have lived in these areas before the opening of the sea in the Early Triassic, or perhaps they migrated along the coast (see sites with *Diplurus* on the coast of North America – Fig. 5B). The other possibility is that the newly opened shallow sea was brackish, bordered by an ocean with significant freshwater input from the continent, allowing the migration of euryhaline species.

CONCLUSIONS

Different groups of fish have previously been known from the fine-grained Upper Triassic deposits of Krasiejów (southern Poland), including sharks, dipnoans and actinopterygians. These new discoveries of isolated scales and teeth add coelacanths to the list.

The preserved coelacanth scales possess ornamentation of delicate ridges at the posterior field. The pattern of ridges resembles that of the Mawsoniid coelacanths and the number of ridges is similar to the scale ornamentation of the Mesozoic genus *Diplurus*, with some differences to the previously known species *D. newarki* from the Triassic and *D. longicaudatus* from the Jurassic, both of North America. This new material from Poland is here assigned to *Diplurus* sp. Moreover, this is the first occurrence of *Diplurus* outside the Newark Group of the eastern part of North America.

The dentition interpreted here as belonging to coelacanths is distinctly different from that of common temnospondyl and actinopterygian fossils. The most characteristic features are: the type of implantation, longitudinal wrinkles of enamel, and the general arrangement of teeth. In terms of structure and arrangement, this is most similar to the different types of dentition that can be found in the buccal, palatal, and branchial regions of coelacanths described from other fossil sites and observed on the extant coelacanth *Latimeria* (Millot and Anthony, 1958).

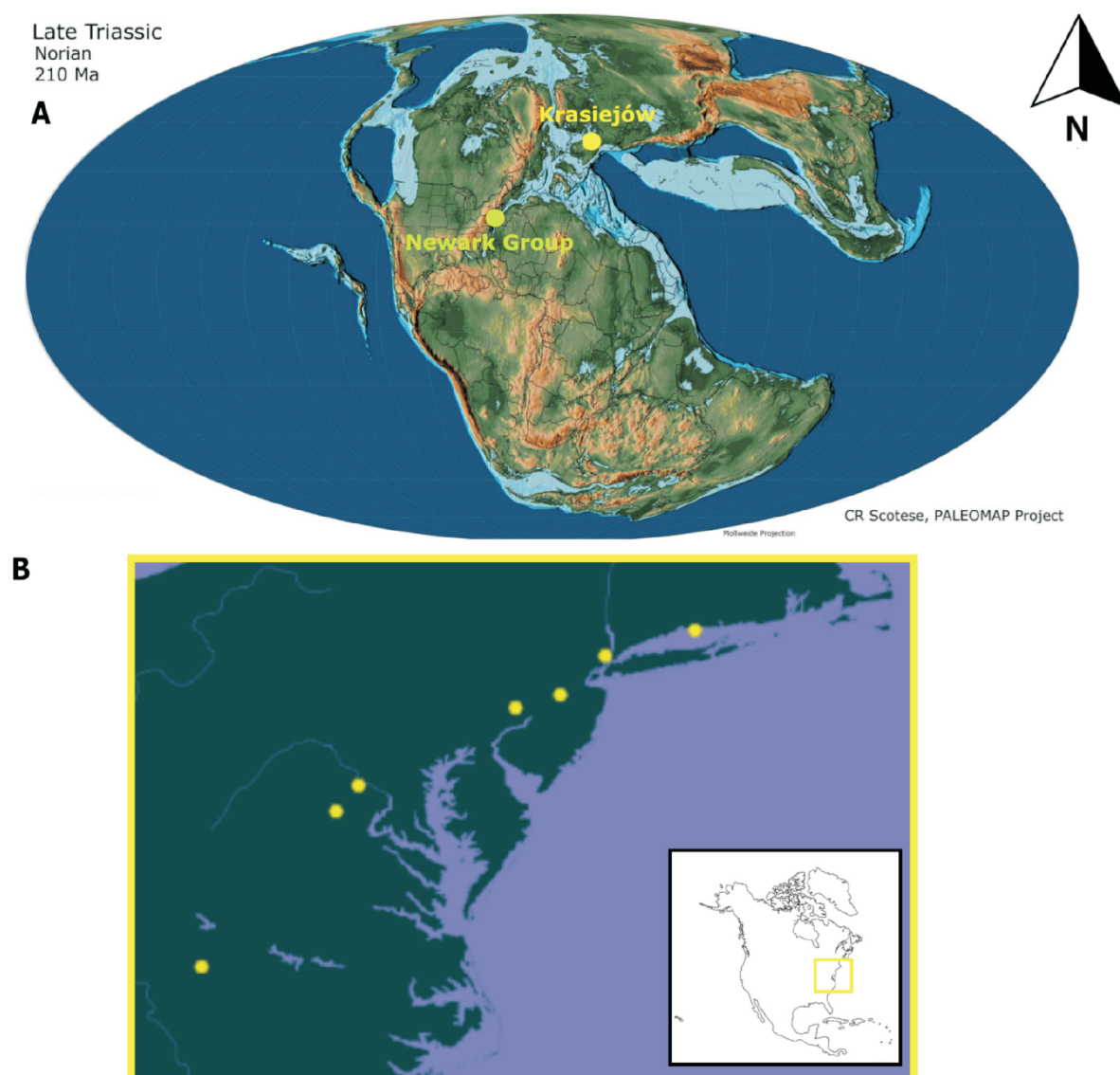


Fig. 5. Location of *Diplurus* finds

A – Pangea in the Late Triassic with *Diplurus* localities (modified after Scotese, 2014); B – records of *Diplurus* in North America (<https://www.gbif.org/species/8328305>)

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The authors report there are no competing interests to declare. The authors confirm that the data supporting the findings of this study are available within the article. The specimens described are housed at the University of Opole and available for research upon request.

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