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Diversity of fish scales in Late Triassic deposits of Krasiejów (SW Poland)

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Abstract. Taxonomy of extinct fishes is mostly based on the shapes of their bodies, teeth and skeletons and sometimes the coverage of the body. Analysis of modern fishes shows that sometimes even single-scale morphology can also be used as a taxonomic tool. In spite of the fact that variation in scales character in one species can be broad, some specific features distinguish species of the same genus. Analysis of the fossilized scales of fishes found in the Late Triassic deposits of Krasiejów (SW Poland) shows that the microstructure of the external surface of scales can also be considered as a taxonomic tool in the fossil record. Description of the ornamentation pattern of several scales of fishes from the same group shows diversity of the sculpture, which might be assigned to variation in morphology between several genera or species. Among the scales from Krasiejów there occur the oldest known ctenoid scales (*sensu stricto*) belonging to acanthopterygians.

Key words: Actinopterygii, ctenoid, cycloid, Dipnoi, ganoid, ornamentation

Introduction

Dermal bones are formed without a chondral stage; they are near to the body surface, being elements of the external (dermal) or internal (skull bones, pectoral girdle) skeleton. Dermal bones are often used as a taxonomic tool, e.g. the osteoderms of aetosaurs (Desojo *et al.*, 2013). Dermal elements of the vertebrate skeleton, in particular the microstructure of bone ornamentation, may be useful even when the fossil material is poorly preserved or incomplete and effectively hard to determine macroscopically. Fish scales are also treated as dermal bones, because they are also formed without a chondral stage and their external surface is highly mineralized. This material can be referred to as the bony layer (Zhu *et al.*, 2011). Such a construction increases the preservation potential of the scales. Despite this, scales are not often used as a taxonomic tool at the species level (Patterson *et al.*, 2002; Kaur and Dua, 2004; Esmaeili and Gholami, 2011; Kemp, 2012). Palaeontologists do not use single scales for this purpose at all. The aim of this paper is to define differences of single scales from sediments from Krasiejów and describe the number of possible fish species at the site.

Locality

Krasiejów is a village near Opole city. Geologically the study area is located in the southeastern edge of the Fore-Sudetic Homocline (Upper Silesia, SW Poland) (Bodzioch and Kowal-Linka, 2012) (Figure 1). Late Triassic fine-grained sedimentary rocks (mudstones and claystones with sandstone and limestone intercalations) are exposed there in a post-mining outcrop (Gruszka and Zieliński, 2008). At the Krasiejów 'Trias' site, two bone-bearing horizons occur (Figure 1). The deposits were previously dated as Carnian (Dzik and Sulej, 2007) but now are considered to be Norian (Racki and Szulc, 2015; Szulc *et al.*, 2015).

In the lower-bone bearing horizon many remains of Temnospondyli (*Metoposaurus* and *Cyclotosaurus*) were found as well as *Stagonolepis* (Aetosauria) and *Paleorhinus* (Phytosauria) fossils. From the upper bone-bearing horizon, the remains of *Polonosuchus* (Rauisuchia) and *Silesaurus* (Dinosauriformes?) have been described (Dzik and Sulej, 2007). Fish scales were collected from the lower bone-bearing horizon.

Material and methods

Referred material consists of 50 fragments of fish

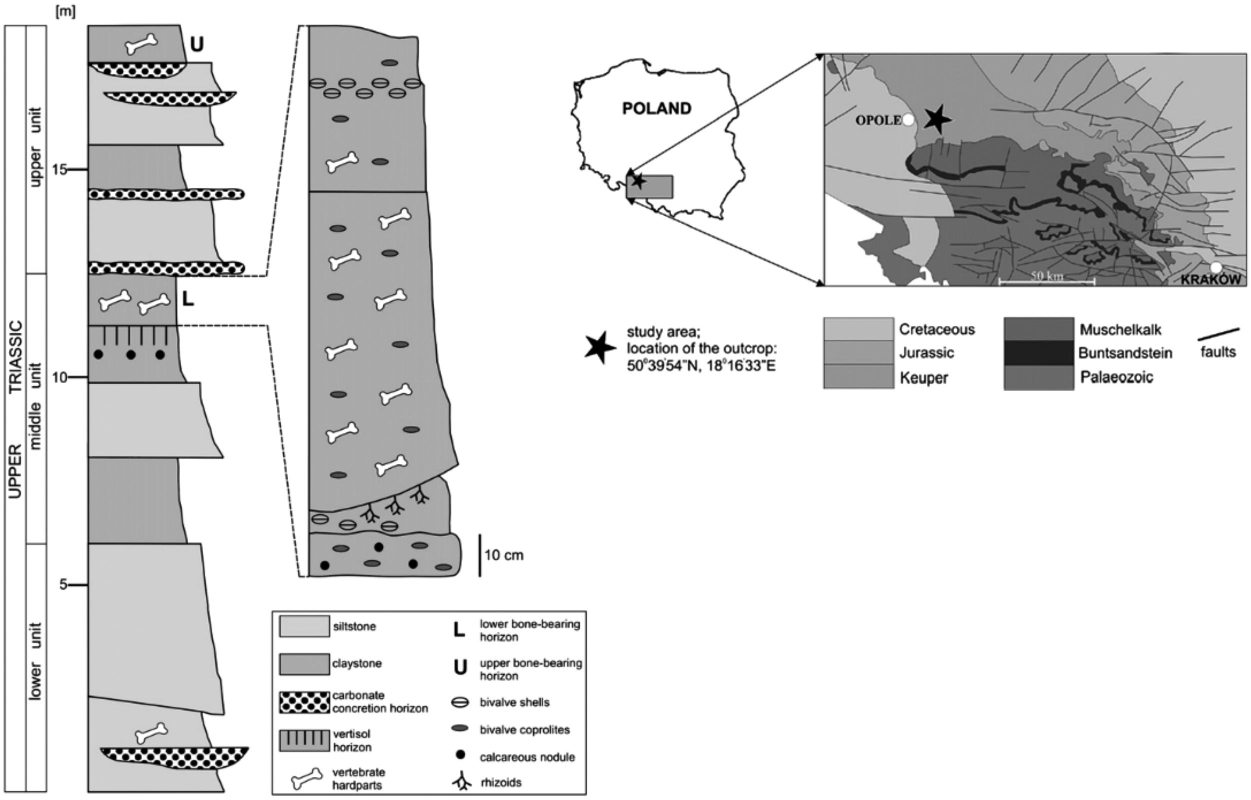

Figure 1. Geological setting and profile of the sediments with enlarged lower bone-bearing horizon.

scales from the Late Triassic deposits of Krasiejów deposited at the Opole University collection (UOPB1032–1082). Material was collected during excavation camps in Krasiejów in the years 2008–2013.

Among the many discoveries and detailed descriptions of terrestrial tetrapods from Krasiejów, fishes have been only briefly described (Dzik and Sulej, 2007), except for dipnoan teeth (Skrzycki, 2011, 2015). Lack of complete fossils and skeletons impedes the description of the Krasiejów ichthyofauna. Most of the fish remains are separated single scales, often incomplete, fragmentary and poorly preserved. Also the very small thickness and fragility of the scales makes preparation difficult.

Analyzed scales were prepared manually and chemically with use of a 30% solution of H_2O_2 and if covered by limestone with 1% HCl. After preparation, scales were analyzed under the Zeiss SteREO Discovery V20 microscope fitted with a Canon EOS 70D camera, and several samples were examined by Scanning Electron Microscope Hitachi S3000N in a high vacuum.

Problem in conclusions—different genus, sex, age or place on the body?

Analyses of the modern Cyprinidae *Puntius binotatus* revealed that individual variation and sexual differences also occur. Scales may possess different shapes in spite of the location on the body (Ganzon *et al*., 2012). The number of first-order radii, which e.g. in *Puntius binotatus* ranges from 10 to 25, may also be different. The reason of such variety is not attributed to the species or the sex of the specimen, but the environment (Johal *et al*., 2006). A higher number of radii is correlated with better nutritional conditions. It also increases the flexibility of the scales (Esmaeili and Gholami, 2007; Ganzon *et al.*, 2012).

Other features, however, like the location of the focus might be considered as species-specific. The focus as the ontogenetically oldest part of the scale does not change its position and is located in the same place irrespective of the location of the scale on the fish body (Patterson *et al*., 2002; Jawad, 2005; Ganzon *et al*., 2012). Taxonomically useful are also: character of the circuli, lepidonts, anterior field covered by the preceding scale, location and shape of chromatophores (Kaur and Dua, 2004).

A separate problem is the fragmentariness and fragility of the scales. Specific parts of one scale are different, especially the anterior and posterior fields, which is the reason why only the same fragments (fields) of particular scales can be compared.

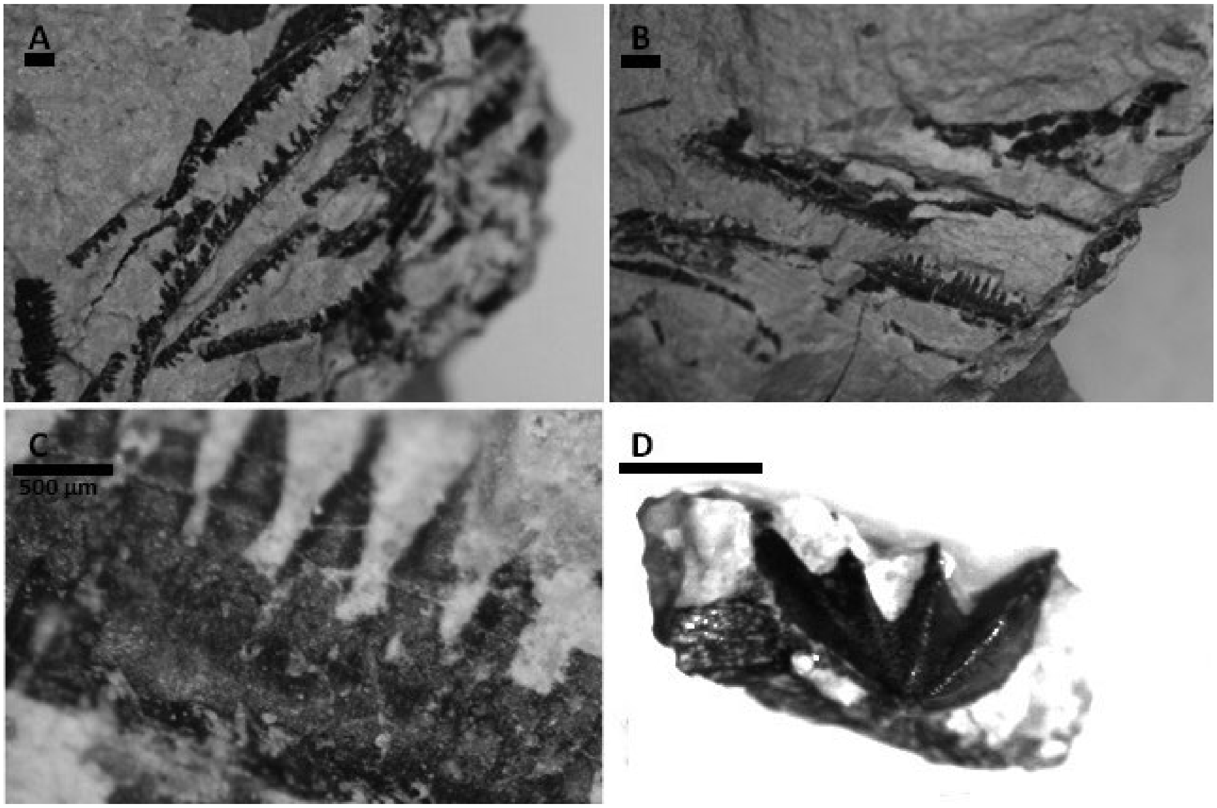

Figure 2. Evidences of fish occurrences in Krasiejów beside scales. **A–C,** gill rakers of the branchial arcs of Actinopterygii; A, UOPB1072; B, C, UOPB1074; **D,** dipnoan toothplate (unnumbered specimen in OU collection). Scale bar 2 mm if not mentioned.

Main groups

Fish scales found at the 'Trias' site in Krasiejów may be divided into three groups: ganoid, cycloid and ctenoid scales. Cycloid scales belong to lungfishes (Dipnoi) while ganoid and ctenoid scales belong to ray-finned fishes (Actinopterygii) (Agassiz, 1884; Benton, 2005). Occurrence of these two groups in the Late Triassic deposits of Krasiejów can be documented by other findings: dipnoan tooth plates of *Ptychoceratodus* (Skrzycki, 2011) and actinopterygian gill rakers of the branchial arcs (Figure 2).

Observations

Ganoid scales

Ganoid scales belong to ray-finned fish (e.g. Acipenseridae: Chondrostei) as well as evolutionarily older groups of Osteichthyes (Benton, 2005). They may cover the whole or part of the fish body. They are relatively heavy and inflexible (Brylińska, 2000; Kardong, 2002).

Differentiation of the ganoid scales from Krasiejów is not obvious. Some of the morphological differences may be the effect of incompleteness of the specimens and the degree of preservation. Nevertheless, it is possible to describe differences in certain characters. The surface of the scales is smooth (Figure 3J) or covered in delicate tubercules (Figure 3E), while scales are rhomboidal (Figure 3A, B) or sigmoidal (Figure 3G) in shape. Cracks in some of the specimens (Figure 3B, H) may be an effect of the compaction process. Ganoid scales differ in the occurrence of additional elements: broad edge of the scale (Figure 3A–C) or indentation (socket) and thin ridge (peg) at the internal surface (Figure 3F–I).

Cycloid scales

Lungfish scales are isopedine, cycloid scales, thin and flexible, and imbricately arranged to decrease water resistance (Brylińska, 2000; Kardong, 2002). They grow together as the fish body grows and are mostly characterized by a large size (over 10 mm), oval shape and, according to Skrzycki (2011), straight posterior edge. Due to their specific construction: mineralized plates (squamulae) at the layer of elasmodin (Kemp, 2012), their surface is cracked and divided into small fragments (e.g. UOPB1035, 1078). Squamulae of dipnoan scales are flat, polygonal, overlapping plates of mineralized tissue (Zylberger, 1988), which appear after the start of calcification

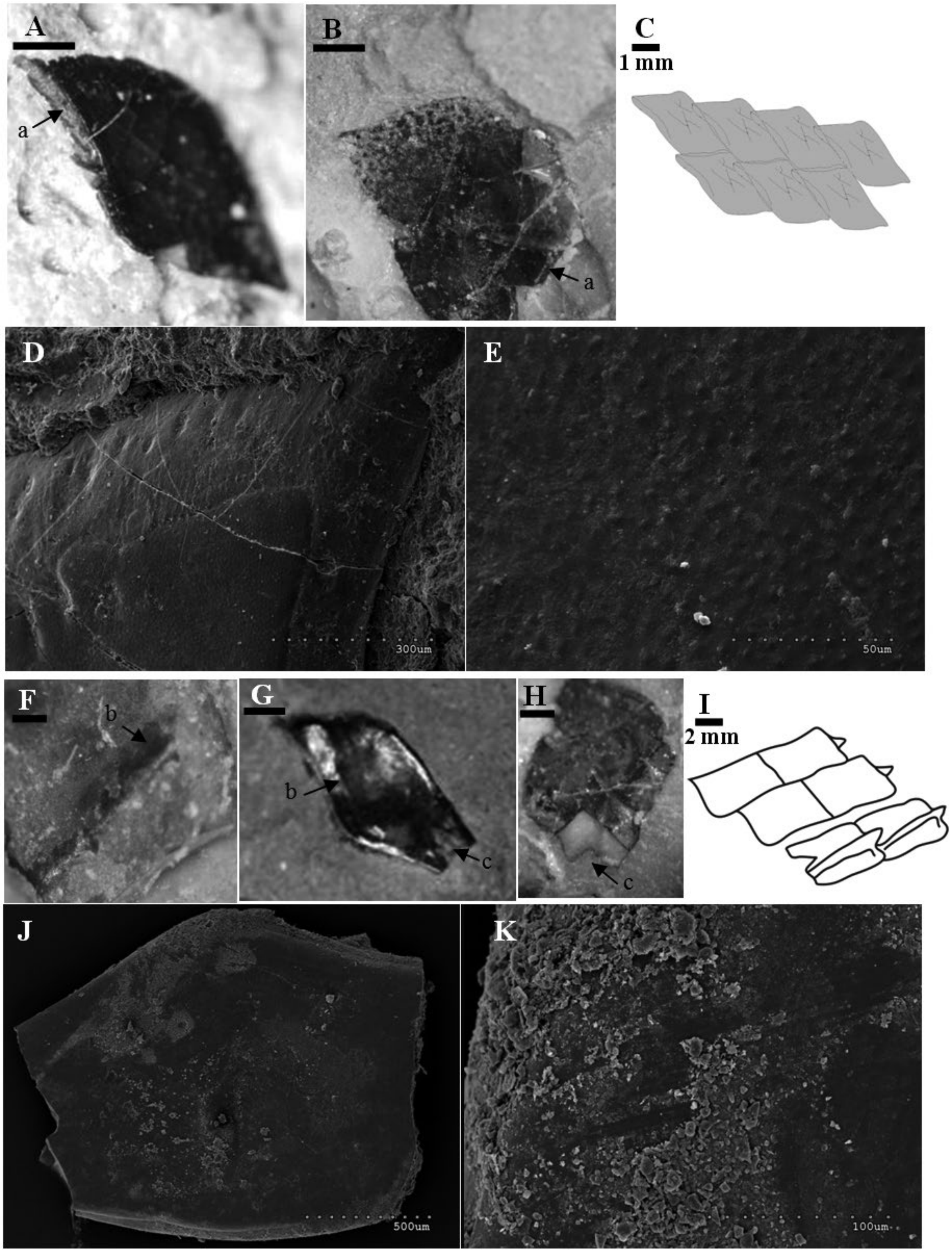

Figure 3. Ganoid scales morphotypes. **A–E,** morphotype 1; A, UOPB1041_1; B, UOPB1042; C, articulation of scales along the edge; D, E, SEM photographs of UOPB1054 showing tuberculate surface; **F–K,** morphotype 2; F, UOPB1061; G, UOPB1052; H, UOPB1081; I, peg and socket articulation of scales; J, K, SEM photographs of UOPB1052 showing smooth surface. a, wide edge serving as connection with adjacent scale in morphotype 1; b, peg; c, socket serving as connection with adjacent scale in morphotype 2.

processes (Kemp, 2012).

Squamulae in the fossil record are separate from each other because in the taphonomic process the internal layer, on which the squamulae are placed, dissolves completely or partially. Preserved elements are the most external and most strongly mineralized layers of the scale (Cavin *et al*., 2007).

Therefore, except for the previously described features shared by all groups of scales, particular scales of lungfishes may also differ in the shape of the squamulae and their ornamentation (Kemp, 2012; Kerr, 1955; Zylberger, 1988).

Cycloid scales from Krasiejów site are divided into small squamulae, thus they are described here as dipnoan scales.

The first squamulae appear in the center of the scale, near the focus. Later they grow along the edges of the scale. The focus divides the scale into anterior, posterior and two lateral fields.

Posterior Field.—Area uncovered by adjacent scales. In the referred material posterior fields represent the pattern of ridges and grooves spreading from the center of the scale to its edge (Figure 4), radiating or nearly parallel. Sets of these ridges and grooves are separated by wider grooves and form elongated squamulae.

At the posterior fields concentric growth rings (circuli/annuli) are clearly visible. These rings are oval in shape without undulations (e.g. UOPB1074, 1078_2) (Figure 4L, M, N) or undulate distinctly (e.g. UOPB1035, 1076, 1063) (Figure 4I, J, K). Specimen UOPB1065 possesses one straight undulation along the posterior edge of the scale (Figure 4O).

Under the electron microscope some additional structures, tooth-like thickenings, are visible. They are distinct, high and closely spaced (e.g. UOPB1063) (Figure 4I’, J’, K’) or lower (less distinct) and arranged more widely apart (e.g. UOPB1047) (Figure 4L’). One of the specimens possesses clearly the most distinct thickenings (UOPB1065) (Figure 4O’).

Anterior field.—Fragments covered by the preceding scale (Figures 4, 5). Fragments of scales representing the anterior fields shows different, more unified ornamentation (Figure 4H). Ridges similar to those from the posterior field can be seen, but they are more compact and intersecting circuli are not visible.

Center.—In the center of some specimens the network of very thin strips is visible (Figure 4F). In UOPB1035 a narrow elongated element is distinct (Figure 4E).

Lateral field.—They consists of smaller, rhomboidal squamulae with strong ornamentation near the edge of the scale, and more anterior-field-like structure near the focus. Differences do not depend on the field or squamulae size. The bigger fields of UOPB1035 possess more delicate ornamentation than the small fragment of UOPB1056 (Figure 4A, B). The sculpture of the lateral fields is more dense than the sculpture of the anterior field, but in some specimens is more delicate (e.g. UOPB1035, 1065), while in others intersecting ridges are massive and more dense (e.g. UOPB1056, 1062) (Figure 4A–D).

Ctenoid scales

Ctenoid scales, like cycloid scales, are imbricately (overlappingly) arranged, which gives the fish greater flexibility than in species with cosmoid and ganoid scales. They are also formed by lamellar bone (Kardong, 2002) and characterized by circular growth. Circuli, however, might not be clearly marked as well as the division into fields.

Ctenoid scales belong to adult (Mookerjee, 1948) advanced actinopterygian fishes: Teleostei (Roberts, 1993; Benton, 2005). The anterior part of the scale is embedded in the fish body, while the posterior, covered with spines or tooth-like structures (cteni), is uncovered and remains in constant contact with water. Cteni reduces hydrodynamic resistance (Kapoor and Khana, 2004) and they may increase the flexibility of the scales (Mookerjee, 1948). Three types of ctenoid scales *sensu lato* can be distinguished (Roberts, 1993):

Crenate.—Scales with large irregular posterior portion of the scale. Additional outgrowths in this part form crenae (Figure 6A). Crenate scales appear in early teleosts, Elopomorpha (Roberts, 1993).

Spinoid.—Scales with spines pointed posteriorly, less common laterally. During ontogeny the first spines get longer and new spines appear along the margin (Figure 6A). They occur e.g. in Ostariophysi (Roberts, 1993).

Ctenoid sensu stricto.—Scales with a more complicated structure than the first two types. They possess spines that are formed as separate ossifications (Figure 6A). Cteni may be formed as ‘transforming cteni’: full spines arranged in two or three alternate marginal rows transforming with time into submarginal truncated spines, or ‘peripheral cteni’: full spines arranged in one row along the posterior margin of the scales. They occur in advanced teleosts, Acanthopterygii such as Perciformes (Roberts, 1993).

With the growth of the scale around the focus new growth rings (circuli) appears, but in the posterior field its continuity is broken by forming cteni (singular: ctenus). Number of spines probably depends on the amount of space between broken circuli. First ctenus appears after the fish reaches an adequate size. In adult forms they are well developed, although with the age of the fish the number of cteni still grows along with the number of circuli. Cteni form along the posterior margin from its center to lateral margins while the whole scale grows (Sire and

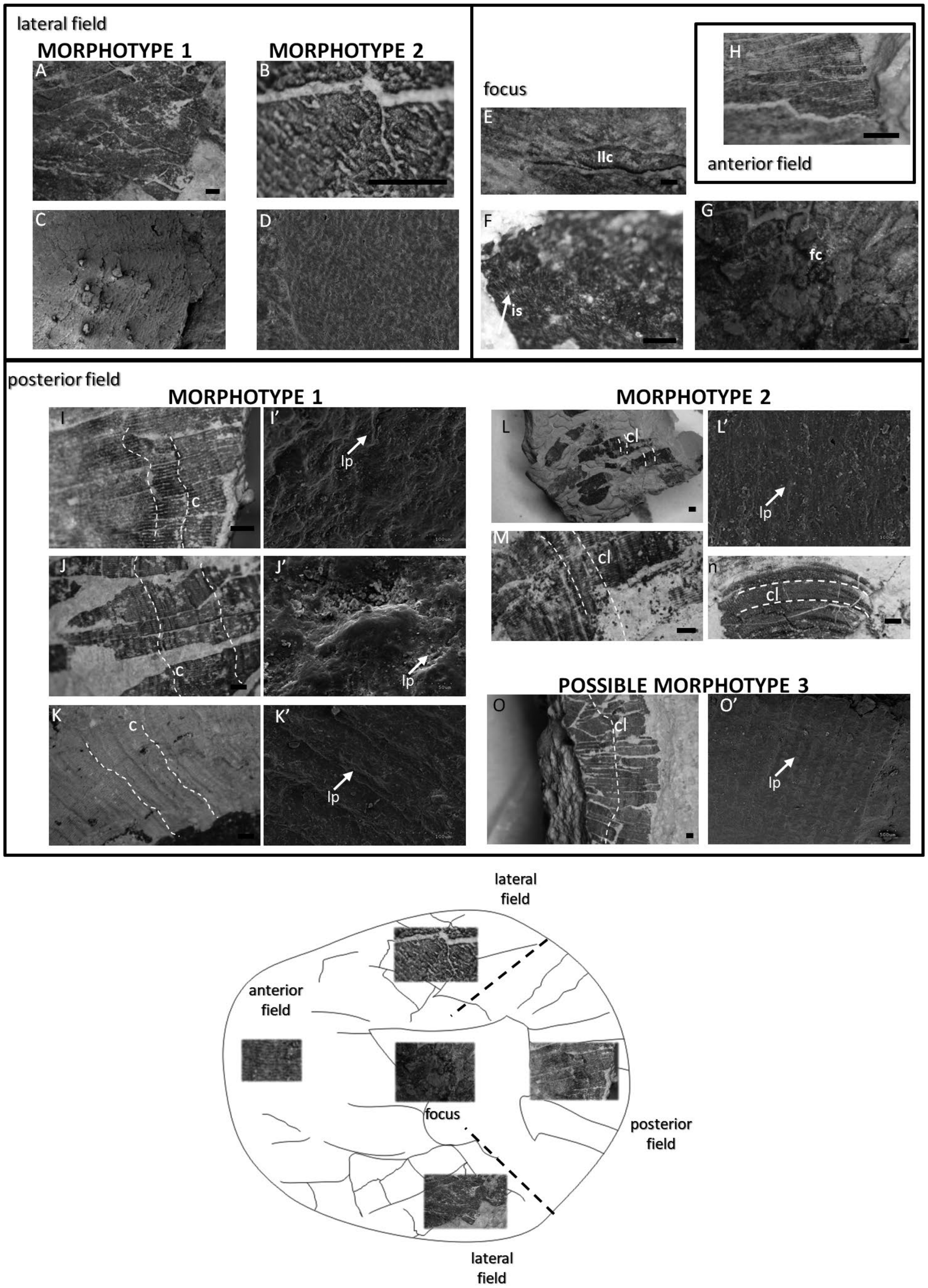

Figure 4. Reconstruction of the Krasiejów Dipnoi scale. **A,** fine ornamentation of lateral field in UOPB1047; **B,** coarse ornamentation of lateral field in UOPB1072; **C,** fine ornamentation of lateral field in UOPB1043; **D,** coarse ornamentation of lateral field in UOPB1056; **E,** center of UOPB1035 with lateral line canal; **F,** focus with concentric squamulae uncovered by isopedine fibres in UOPB1074_2; **G,** focus covered with isopedine fibres in UOPB1075; **H,** delicate ornament of anterior field in UOPB1074; **I–K,** undulating circuli in the posterior field of UOPB1035, 1076, 1063; **I’–K’,** high ‘lepidonts’ with small spacing in UOPB1077, 1076, 1063; **L–N,** straight circuli in UOPB1047, 1078_2, 1048; **L’,** small lepidonts with large spacing in UOPB1047; **O,** circuli with singular straight undulation to the margin of the scale in UOPB1065; **O’,** very large ‘lepidonts’ in UOPB1065. Abbreviations: c, circuli (growth rings); fc, focus with concentric squamulae; is, isopedine fibres; llc, lateral line canal; lp, “lepidonts”. Scale bar 500 µm.

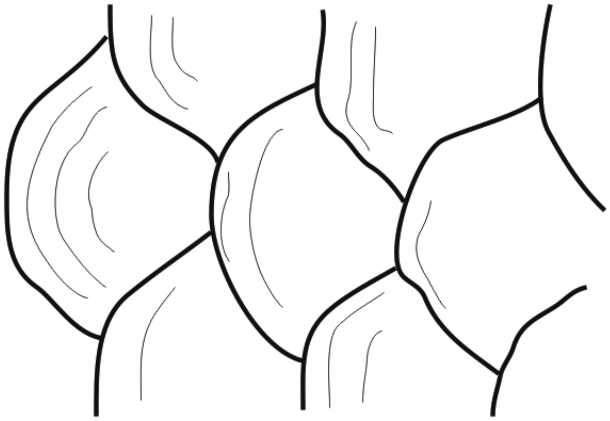

Figure 5. Arrangement of the scales in modern *Neoceratodus forsterii* and fossil Dipnoi from Krasiejów.

Arnulf, 2000). Cteni in ctenoid scales *sensu stricto* at first are long and similar to spines of spinoid scales. When more cteni are formed the transverse cuts appear and later each ctenus is separated from the base. Then the base margin becomes round and thinner, dividing the ctenus into two separate structures (Mookerjee, 1948).

Two of the analyzed specimens possess distinct spines in the posterior parts. Both are small (~2–3 mm). The UOPB1037 specimen is incomplete, however its imprint reveals its oval shape. Surface is relatively smooth and along the posterior margin three equally large spines are visible. Wide, triangular spines occupy almost the whole posterior margin and they correspond to 1/6 of the scale length (Figure 6C). Specimen UOPB1046 is rectangular in shape and slightly larger. Surface is smooth. Posterior margin is occupied by four large spines corresponding to 1/7 of the scale length. At the base spines are cut off and slightly displaced in relation to the base. In half of their length spines are clearly narrowed (Figure 6B).

Results

Ganoid scales

Described additional elements served as the connection between adjacent scales. Thus, two types of the scales' connection into a consistent body coverage occur: overlapping of adjacent scales by the broad edge or 'peg and socket' articulation (Schultze, 1996; Giordano *et al.*, 2016).

As the mentioned differences occur in two sets of features, two distinct morphotypes of ganoid scales can be distinguished:

Morphotype 1.—Scales possess a broad overlapping edge, are usually more sigmoidal and their surface is covered with delicate tubercules (Figure 3; UPB1054, UOPB1041_1, 1066, 1042).

Morphotype 2.—Scales possess a 'peg and socket' articulation system, are usually more rhomboidal and their surface is smooth (Figure 3; UOPB1052, 1061).

Overlapping edges and tubercules on the surface of the ganoine have been observed in Mesozoic and recent holostean and polypterid fishes (Märss, 2006; Schultze, 2016). Although representatives of both of these groups could have lived in the Krasiejów environment, holostean fishes are the more probable candidate, as Polypteriformes are not known from the Triassic.

The earliest known example of a peg and socket articulation system is found in the Carboniferous ray-finned *Amblupterus striatus* (Woodward, 1885). The shape of the scales referred to as morphotype 2 and the relative position of peg and socket resemble Lepisosteiformes (Siemionotiformes) (Schultze, 1996, 2016).

Cycloid scales

In Krasiejów cycloid scales, the anterior field is the biggest. The focus is located at 2/3 length of the scale. Ridges described in the posterior fields probably served as trails for collagen fibers (Figure 4I), which covered this fragment of the scale (Skrzycki, 2011). Typical of cycloid scales, growth rings (circuli) well developed in the posterior field are often seen as concentric grooves instead of ridges, because most of the specimens are imprints of the actual scales. Mentioned tooth-like thickenings (Figure 4I', J', L') are structures similar to lepidonts described on the circuli of modern fishes. Elongated squamulae of anterior and posterior fields (in relation to lateral fields) suggest that at the beginning of ontogenetical growth all fields are equal in size and the scale is round, while later the posterior and anterior fields grow faster than the lateral fields (Figure 4A). Thin strips in the centre of some scales are isopedine fibres (Figure 4F), which improve scale flexibility. The UOPB1035 (Figure 4E) with distinct elongated element in the centre is probably one of the scales of the lateral line, and the central element is the canal, under which neuromasts are located. At the ends of this canal there are foramina for contact of neuromasts with the environment.

Based on the fragments of the scales preserved in different specimens it is possible to reconstruct the whole scale. Proportions of the particular fields allow also to reconstruct the pattern of the scale distribution on the fish body. This pattern is much more the same as in modern *Neoceratodus forsterii* (Figure 5). Krasiejów lungfishes are its close relatives.

From seven Palaeozoic families of lungfishes, only two survived the end-Permian extinction. The mentioned similarity to *Neoceratodus* and the tooth plates described by Skrzycki (2011, 2015) indicate the Ceratodontidae fam-

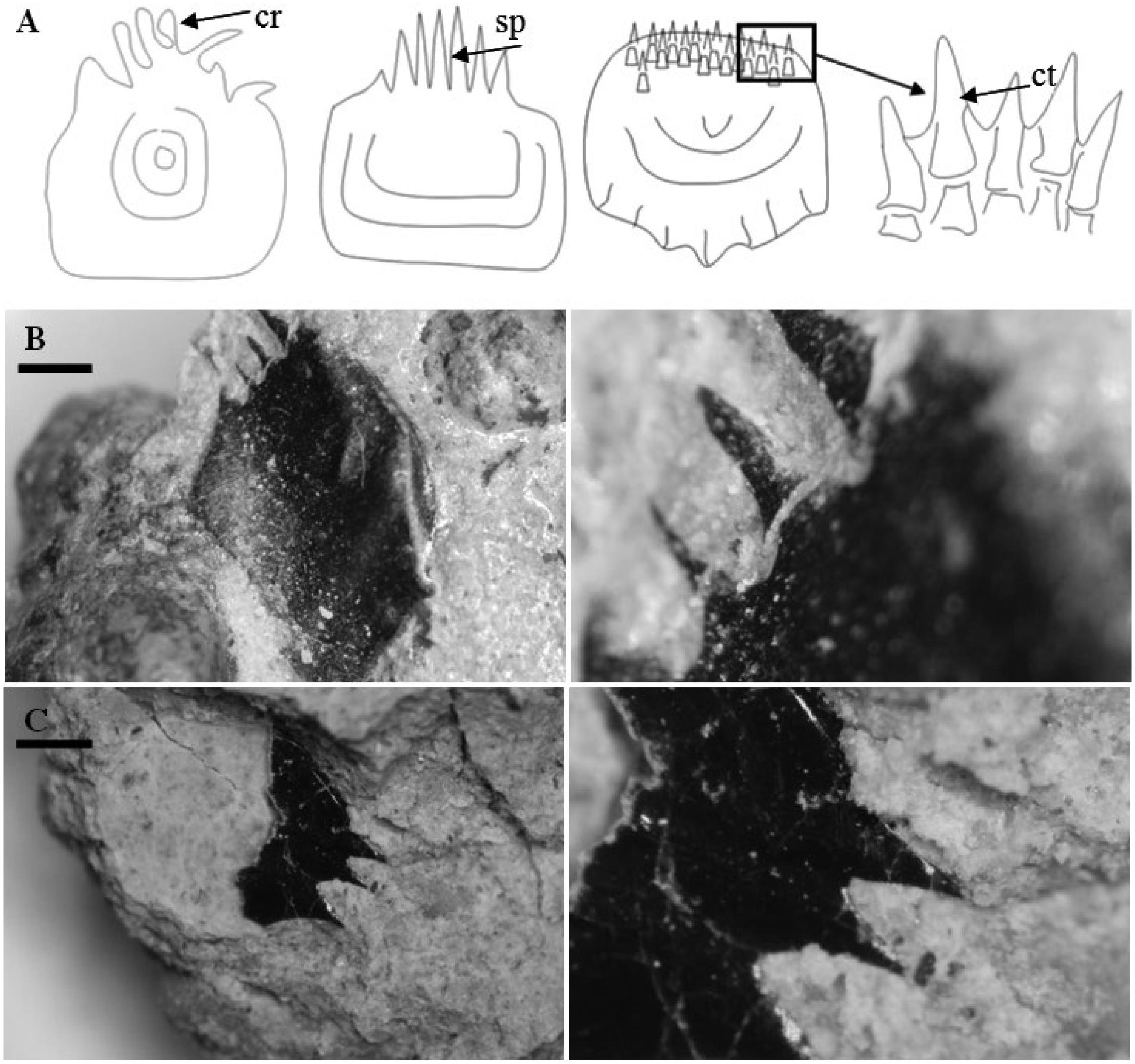

Figure 6. Ctenoid scales. **A,** types of ctenoid scales; **B,** UOPB1037; **C,** UOPB1046. Abbreviations: cr, crenae; ct, cteni *sensu stricto*; sp, spines. Scale bar 500 µm.

ily. However, the described morphotypes might be closely related species within one genus or several subspecies of *Ptychoceratodus*. There are currently several species and subspecies of lungfishes in Central Africa lakes: three species of *Protopterus* and three subspecies of *Protopterus aethiopicus*. Such diversity possibly reflects slightly different environments of several Krasiejów reservoirs (Szulc *et al*., 2015).

Variety of the material is reflected in dimorphism of growth rings shape and in the sculpture of the rhomboidal squamulae of the lateral fields. Additional differences: size and arrangements of 'lepidonts' are visible under the electron microscope. These features are connected with each other. Certain sets of features occur, which allows one to describe at least two morphotypes of the lungfishes scales from Krasiejów deposits (Figure 4).

Morphotype 1.—Undulating circuli in the posterior area, more dense and thick sculpture of the lateral fields, higher 'lepidonts', smaller spacing of the 'lepidonts'.

Morphotype 2.—Oval circuli in the posterior field, thinner sculpture of the lateral fields, lower 'lepidonts', larger spacing of the 'lepidonts'.

Possible morphotype 3.—Straight undulation of circuli along the posterior edge of the scale pointed towards the edge, oval posterior edge, very large 'lepidonts'.

Possible morphotype 4.—According to Skrzycki (2011), straight undulation of circuli along the posterior edge of the scale pointed towards the focus, parallel to the indentation in the posterior edge.

Ctenoid scales

Distinct spines suggest that both specimens can be described as ctenoid scales which are characteristic for relatively advanced fishes and definitely belong to two species. UOPB1037 possesses the characters of spinoidal scales. Spinoidal scales can be divided into several types. One of these types is characterized by an oval scale without visible division into fields with a few massive spines along the posterior (or lateral) margin (Roberts, 1993). The UOPB1046 specimen probably represents an early stage of ctenoid scales with 'transforming cteni', because the scale is rectangular and spines are narrowed and displaced.

Ctenoid scales are not common in the Triassic deposits. Transforming cteni were not previously described from this period, as they are known from Acanthopterygii. Acanthopterygian fossils are known from Cretaceous deposits, but molecular analysis suggests their Jurassic or even Triassic origin (Chen *et al.*, 2014). The oldest acanthomorph fossil otoliths, assigned to the "genus *Acanthomorphorum*," date from the early Aptian (Maestrazgo, Castellon Province, Early Cretaceous, 124–122 Ma) (Nolf, 2004). Findings from Krasiejów shows that acanthopterygians are over 80 Ma older.

Spinoid scales first appeared in Euteleostei (Roberts, 1993). Occurrence of two types of ctenoid scales at Krasiejów site shows that the ichthyofauna diversity was great and some evolutionarily young groups of fishes already occurred, including the oldest known Acanthopterygii.

Conclusions

Fragments of the scales found in the lower bone-bearing horizon in fine-grained Late Triassic deposits of Krasiejów can be divided into ganoid, cycloid and ctenoid scales.

Within ganoid scales, based on the external surface features two morphotypes can be distinguished. Different connection of adjacent scales and surface character can be related to occurrence of two different fish species (genera) of Lepisosteiformes (Siemionotiformes) and possibly Polypteriformes.

Based on the particular fragments of large cycloid dipnoan scales it is possible to reconstruct the whole scale surface and to describe the character of particular fields: anterior, posterior and lateral. Anterior and posterior fields consists of elongated (relative to lateral fields) squamulae, which suggest its faster growth. Based on the micro- and nanostructures it is possible to distinguish at least two morphotypes related to two possibly closely related species. Specimen UOPB1065 and the general scale description of Skrzycki (2011), who observed that in the posterior field circuli can possess a singular indentation parallel to the indentation in the posterior edge of the scale, suggests the possible occurrence of two more morphotypes. These four morphotypes represent four closely related species of the Ceratodontidae family or possibly some subspecies of *Ptychoceratodus*.

Besides ganoid and cycloid scales, some ctenoid (spinoid and ctenoid with transforming cteni) scales occur that belong to evolutionarily young groups of fishes, like Euteleostei and Acanthopterygii, which were not previously known from Triassic deposits (Roberts, 1993).

In modern fish it can be easily proved that there is a differentiation in scale ornamentation at the species level, because the source of the material is known. In fossil record this is not possible, and thus the species cannot be named, but the number of different species from several groups of fishes can be assumed, including the oldest known occurrence of acanthopterygians (80 Ma older than previously known oldest acanthomorphs (Nolf, 2004).

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