

Late Permian ichthyofauna from the North-Sudetic Basin, SW Poland

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The late Permian time was a transformative period before the most severe mass extinction known. Even though fishes constitute a key component of marine ecosystems since the Silurian, their biogeographic patterns during the late Permian are currently insufficiently known. The new ichthyofaunal material described here comes from the southeastern part of the Zechstein Basin, from the calcareous storm sediments alternating with marls, which were deposited in less energetic conditions. Chondrichthyans and osteichthyans are reported here for the first time from the Nowy Kościół quarry in the SW Poland. The assemblage consists of various euselachian dermal denticles, actinopterygian scales and teeth, and isolated hybodontoid tooth putatively assigned as extremely rare *?Gansuselache* sp. from the Permian. The diverse actinopterygian tooth shapes show significant ecological differentiation of fishes exploring sclerophagous, durophagous, and herbivory modes of feeding in the given part of the Zechstein Basin suggesting the presence of complex ecosystems even in hyper-saline conditions of an epicontinental sea.

Key words: Euselachii, Actinopterygii, teeth, scales, trophic groups, Permian, Zechstein, Poland.

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Introduction

Ever since the Carboniferous, Osteichthyes and Chondrichthyes have been the most successful marine vertebrates (Near et al. 2012; Pindakiewicz et al. 2020). Late Permian fish fossils are widely distributed in the marine and freshwater ecosystems around Pangea (Koot 2013; Romano et al. 2016) including saline, semi-enclosed, lagoon or the playa-like Zechstein Sea in NW Europe. Fish fossils from this basin are known from Germany (Diedrich 2009), England (King 1850), East Greenland (Nielsen 1952), Latvia (Dankina et al. 2020) and Lithuania (Dankina et al. 2017).

Until now only very rare and taxonomically low diversity occurrences of the fish remains were found in the southeastern part of the Zechstein successions. Kaźmierczak (1967) putatively assigned some teeth and scales as Palaeoniscidae in the Zechstein sequences at the Kajetanów quarry in the Holy Cross Mountains, central Poland. Incomplete *Platysomus* sp. trunks were also found from the copper-bearing Zechstein layers and *Palaeoniscus* sp. trunks from the Lubin

mine in SW Poland, which are stored at the University of Wrocław.

The current study represents the first record of the ichthyofaunal assemblage from a new paleoichthyological locality—the Nowy Kościół quarry in the SW Poland. The paleoenvironmental and ecological changes in the eastern Zechstein Sea ecosystems are discussed in connection to the ecomorphological features of described teeth assemblages. The described ichthyofaunal assemblage patterns from the SW Poland shed new light on the dispersal patterns and palaeobiogeography of fishes in the Zechstein Sea.

Institutional abbreviations.—VU-ICH-NK, Geological Museum at the Institute of Geosciences of Vilnius University, Vilnius, Lithuania.

Geological setting

The Zechstein Basin in Poland is a result of widespread cyclic carbonate and evaporite sediments (Poszytek and

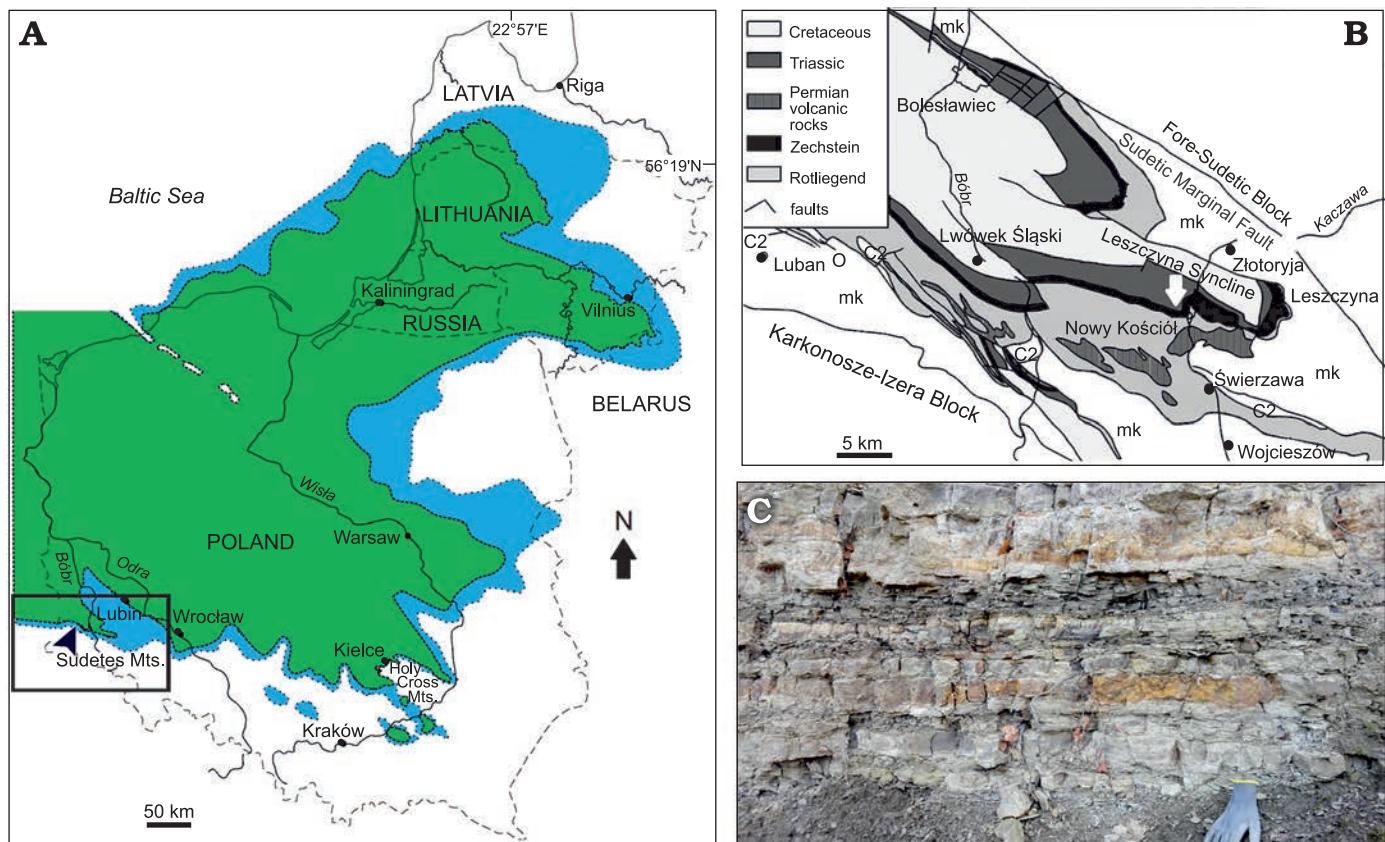


Fig. 1. Location of the late Permian fish-bearing site in SW Poland. A. Map of the Eastern Europe with position of Nowy Kościół (blue, the original distribution of the eastern margin of Zechstein Limestone; green, current distribution of Zechstein sediments in Poland, Russia, Lithuania, and Latvia; Raczyński and Biernacka 2014). B. The geological map of the North-Sudetic Basin showing location of studied site (white arrow) (after Biernacka et al. 2005). C. Photograph of the middle Zechstein limestone sequences of the Nowy Kościół section from 2016. mk, Kaczawa metamorphic rock; C2, Upper Carboniferous.

Suchan 2016). The studied sites of the first Zechstein cycle in SW Polish suggested an existence of a narrow zone of upper Permian sediments in the outer part of the North-Sudetic Basin (Gunia and Milewicz 1962; Raczyński 1997; Biernacka et al. 2005; Fig. 1A). The Nowy Kościół area is located in the Leszczyna Syncline in the southeastern, marginal part of the Zechstein Basin (Biernacka et al. 2005; Fig. 1B). Scupin (1933) proposed lithostratigraphic division of the upper Permian association in this part of the Zechstein Basin. According to Scupin's (1933) division, the limestone-marl association is subdivided into three main units: spotted marl, copper-bearing marl, and lead-bearing marl (Biernacka et al. 2005).

The limestone-marl sequence with the underlying Basal Limestone (micritic limestone) and overlying middle Zechstein (micro-oncolitic limestone) are equivalent to the carbonate rocks of the first evaporitic cyclothem assigned as Zechstein Limestone (Cal) (Peryt 1978; Raczyński 1997; Biernacka et al. 2005). The duration of sedimentation of the entire first evaporitic cyclothem did not exceed two million years (Menning 1995; Biernacka et al. 2005). The upper Permian limestone-marl association was deposited in the ~20–30 km width and ~100 km length zone along the WNW-ESE stretching lagoon (Biernacka et al. 2005; Fig. 1B).

Material and methods

The studied material was collected in the Nowy Kościół quarry in SW Poland ($51^{\circ}5'19.654''N$, $15^{\circ}52'43.613''E$) (Fig. 1). Sediments are mostly carbonates consisting of marl and limestone layers. In total eleven samples were collected. Two samples were taken from the Basal Limestone; three samples from copper-bearing marl; three samples from lead-bearing marl; three samples from Middle Zechstein Limestone (Fig. 2). The total weight of the collected samples reached ~128.4 kg. The average mass of each sample was ~14 kg.

The fossil-bearing samples were chemically prepared using standard chemical dissolution technique in buffered formic acid described by Jeppsson et al. (1999). The residues were dried at room temperature and sieved from 0.2 to 0.063 mm sieves in order to more effectively optically spot and pick microremains under the binocular microscope under fixed magnification. Scanning electron microscope (SEM) imaging of the selected fish remains was conducted at the Nature Research Centre (Vilnius, Lithuania).

The collected samples yielded 112 isolated chondrichthyan and osteichthyan fish microremains. The collection is housed in the Geological Museum at the Institute of Geosciences of Vilnius University (VU-ICH-NK).

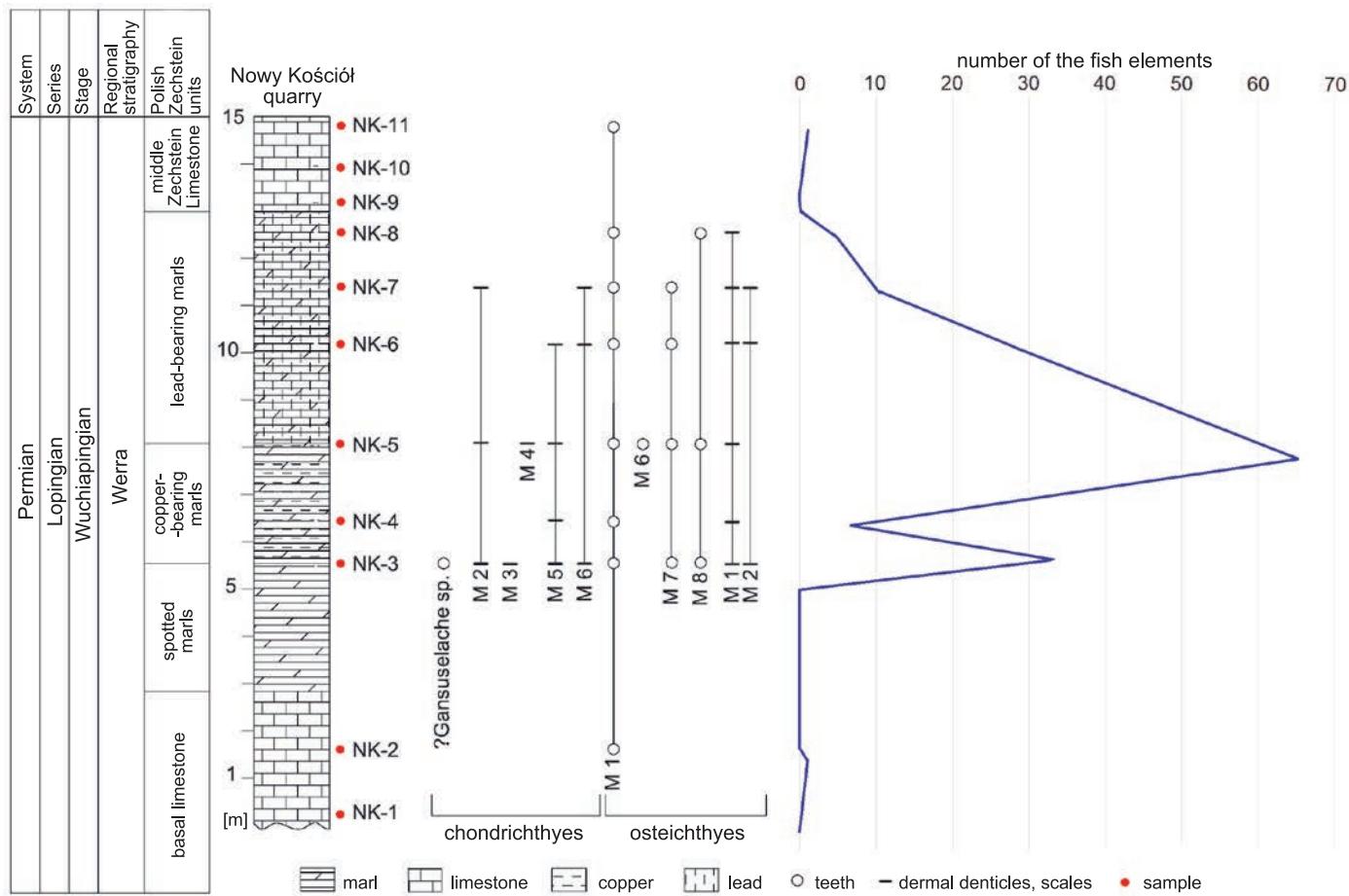


Fig. 2. Stratigraphical profile of the Nowy Kościół quarry with an indication of the late Permian fish assemblage, stratigraphic repartition of the chondrichthyan and osteichthyan taxa based on isolated teeth, dermal denticles and scales; and its vertical distribution. M, morphotype.

Systematic palaeontology

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Order Hybodontiformes Patterson, 1966

Superfamily Hybodontoidea Owen, 1846

Family Lonchidiidae Herman, 1977

Genus *Gansuselache* Wang, Zhang, Zhu, and Zhao, 2009

Type species: *Gansuselache tungshensi* Wang, Zhang, Zhu, and Zhao, 2009; Mazongshan Mountain, Gansu Province, north-western China; Fangshankou Formation, late Permian.

?*Gansuselache* sp.

Fig. 3A.

Material.—Single isolated tooth (VU-ICH-NK-001) from the upper Permian of the Nowy Kościół Quarry, Leszczyna Syncline, SW Poland.

Description.—The tooth is mesiodistally elongate (slightly less than 3 mm in length), labiolingually compressed, low-crowned, slightly inclined lingually and near-symmetrical. The tooth crown is multicuspous; its central cusp is higher

and wider than two pairs of low lateral cusplets. The cusplets are ornamented separately with two or three vertical strong ridges that continue to the root in labial and lingual face of the tooth. The tooth root is massive, higher in labial face than in the lingual one. It has some enlarged and irregular foramina on both lingual and lateral faces, which are filled by sediments. The tooth base is oval and deeply concave.

Remarks.—The teeth of ?*Gansuselache* sp. are rare in late Permian material. However, the analysed tooth here is assigned to ?*Gansuselache* sp. as it matches the following diagnosed characters: multicuspous crown, with central high cusp and lower two pairs of cusplets which are covered by vertical strong ridges. Similar teeth were found in the late Permian material of the Fangshankou Formation in north-western China (Wang et al. 2009: fig. 7C).

Cohort Euselachii Hay, 1902

Euselachii indet.

Fig. 3B–R.

Material.—44 isolated dermal denticles were found from the upper Permian of the Nowy Kościół Quarry, Leszczyna Syncline, SW Poland. The dermal denticles are represented

Table 1. The different morphotypes distribution of late Permian fish remains in Latvia, Lithuania, and Poland.

	Morphotype	Poland (Nowy Kościół)	Lithuania (Karpėnai)	Latvia (Kūmas)
Euselachii dermal denticles	M1	—	—	+
	M2	+	+	+
	M3	+	+	+
	M4	+	+	+
	M5	+	+	+
	M6	+	+	+
Actinopterygii teeth	M1	+	+	+
	M2	—	—	+
	M3	—	+	+
	M4	—	+	+
	M5	—	—	+
	M6	—	+	+
	M7	+	—	—
	M8	+	—	—
Actinopterygii scales	M1	+	+	+
	M2	+	—	+
	M3	—	—	+
	M4	—	+	+
	M5	—	—	+
	M6	—	—	+

Table 2. The main characteristics of the different morphotypes of Euselachii dermal denticles. M1–6, morphotype 1–6.

Morphotype	Crown ridges	Crown symmetry	Horizontal crown	Visible neck	Roots foramina
M1	no	yes	yes	yes	yes
M2	yes	yes	yes	yes	no
M3	partly	yes	partly	yes	yes
M4	yes	no	yes	partly	no
M5	partly	partly	no	no	no
M6	yes	partly	no	no	no

here by SEM microphotographs of microremains VU-ICH-NK-002–018.

Description.—The microremains are identified as euselachian-type dermal denticles based on resembling material from the middle Permian of the Apache Mountains in West Texas, USA (Ivanov et al. 2013); Permian of the Kanin Peninsula in Russia (Ivanov and Lebedev 2014); Lower Triassic of Oman (Koot et al. 2015); Carboniferous of Oklahoma, USA (Ivanov et al. 2017); upper Permian of Lithuania (Dankina et al. 2017), and Latvia (Dankina et al. 2020); and are divided into morphotypes based on the morphological differences between their crown, neck, and base.

The morphotype numeration and description in this study is taken from previous studies of late Permian euselachian material from southern Latvia (Dankina et al. 2020; Tables 1, 2).

Morphotype 2: Seven dermal denticles from this morphotype were found in the Nowy Kościół quarry (Fig. 3B–D). The denticles have a trident or nearly trident crown with a high, slender, and narrow neck (Fig. 3B), hidden under the crown in apical view (Fig. 3C, D). The crown sits horizontally or slightly obliquely up on the neck. The exterior of the crown is sculptured with numerous gentle convex ridges and furrows originating at the longitudinal crest and reaching 0.1–0.4 mm length. The base has a rhomboid surface and one roundish canal opening in proximal view. The denticle reaches 0.3–0.4 mm height, and 0.4–0.5 mm crowns length and width.

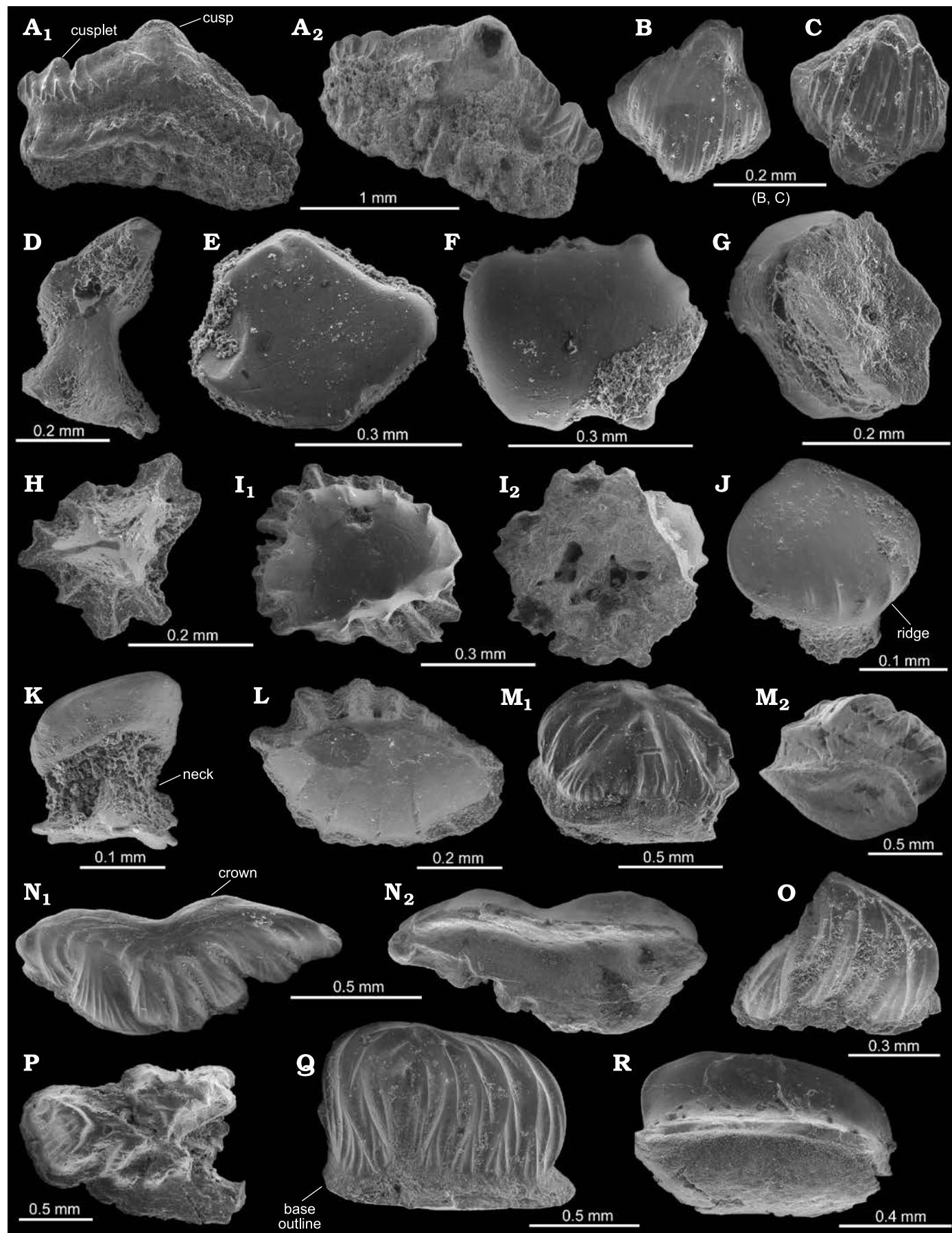
Morphotype 3: Four dermal denticles from this morphotype were found in the Nowy Kościół quarry (Fig. 3E–G). The roundish crown is smooth, thick, without ornamentation (Fig. 3E, F). The crown sits horizontally on the neck and reaches around 0.4–0.8 mm in diameter. The neck is wide and massive. The wide base is slightly curved, multipetaloid in shape, and with concave canal opening in the proximal view (Fig. 3G).

Morphotype 4: Two dermal denticles from this morphotype were found in the Nowy Kościół quarry (Fig. 3H, I). The denticle has a curved outline of the crown; strongly convex, with three continuous ridges joined on the top of the surface (Fig. 3H). Sometimes, the crown is flat, thick, without ornament, has a serrated margin (Fig. 3I₁). The crown is placed horizontally on the slender neck. The neck is short and narrow. The base has an indeterminate sinuous shape with deep vertical grooves along base outline. Dermal denticles reach 0.3–0.6 mm in length and 0.5–0.6 mm in width.

Morphotype 5: 21 dermal denticles from this morphotype were found in the Nowy Kościół quarry (Fig. 3J–L). The denticles have an anteriorly-inclined crown ornamented by some short ridges (4–5 ridges) on the anterior side (Fig. 3J, L). This type of denticles have a smooth, drop-like crown margin surface, which sits evidently obliquely up on the wide low neck (Fig. 3K). The crown reaches 0.4–0.5 mm length. The neck and crown widths are almost identical and approximately equal 0.3–0.4 mm (Fig. 3J). The base is flat, sinuous, multipetaloid in shape (Fig. 3L) with concave canal openings in the proximal view.

Morphotype 6: 10 dermal denticles from this morphotype were found in the Nowy Kościół quarry (Fig. 3M–

Fig. 3. Euselachian dermal denticles and hybodontoid tooth from the upper Permian of the Nowy Kościół quarry, Poland. A. ?*Gansuselache* sp. tooth → VU-ICH-NK-001, labial (A₁) and lingual (A₂) views. B–D. Euselachian-type dermal denticles of morphotype 1. B. VU-ICH-NK-002, crown view. C. VU-ICH-NK-003, crown view. D. VU-ICH-NK-004, lateral view. E–G. Euselachian-type dermal denticles of morphotype 2. E. VU-ICH-NK-005, crown view. F. VU-ICH-NK-006, crown view. G. VU-ICH-NK-007, basal view. H, I. Euselachian-type dermal denticles of morphotype 3. H. VU-ICH-NK-008, apex crown view. I. VU-ICH-NK-008, apex crown (I₁) and basal (I₂) views. J–L. Euselachian-type dermal denticles of morphotype 4. J. VU-ICH-NK-010, crown view. K. VU-ICH-NK-011, lateral view. L. VU-ICH-NK-012, apex crown. M–R. Euselachian-type dermal denticles of morphotype 5. M. VU-ICH-NK-013, lateral crown (M₁) and lateral basal (M₂) views. N. VU-ICH-NK-014, apex crown (N₁) and basal (N₂) views. O. VU-ICH-NK-015, lateral crown view. P. VU-ICH-NK-016, crown view. Q. VU-ICH-NK-017, lateral crown view. R. VU-ICH-NK-018, lateral basal view.



R). The denticles have a complex crown shape, from very narrow, subparallel with straight ridges (Fig. 3O, Q) to wide triangular being striated by curved, branched ridges (Fig. 3P). The neck is poorly developed. The base is low and flat. Its profile has a rhomboid (Fig. 3M₂) or polygonal outline (Fig. 3N₂), with a slightly convex basal surface (Fig. 3M₂) and without any foramina (Fig. 3R). These dermal denticles could reach 0.7–2.0 mm in length and 0.5–0.8 mm in height.

Remarks.—Complex shape of the morphotype 2 denticles is morphologically similar to Carboniferous chondrichthyan scales of Oklahoma, USA (Ivanov et al. 2017). Also, this morphotype is similar to Devonian–early Carboniferous ctenacanthid scales in Belarus (Ivanov and Plax 2018); Carboniferous in Lublin area, SE Poland (Ginter and Skompski 2019); and Devonian of the Holy Cross Mountains (Liszowski and Racki 1992). The identical dermal denticles of morphotype 3 have been found and described as late Permian euselachian-type dermal denticles from Naujoji Akmenė Formation in Lithuania (Dankina et al. 2017) and Latvia (Dankina et al. 2020). A roundish denticle of morphotype 4 was interpreted as being a ?hybodont/synechodontiform scale from the Lower Triassic in Oman (Koot et al. 2015). Similar denticles but with different neck have been found and described as late Permian euselachian-type denticles from the Naujoji Akmenė Formation in Lithuania (Dankina et al. 2017) and Latvia (Dankina et al. 2020). The morphological similarities of the morphotype 5 dermal denticles (shape of the crown, roots, slender neck) have been found and described as Triassic Hybodontidae dermal denticles in Spitsbergen (Reif 1978) and as late Permian euselachian-type denticles from the Naujoji Akmenė Formation in Lithuania (Dankina et al. 2017) and Latvia (Dankina et al. 2020). The morphotype 6 denticles with similar features (shape of the crown, ornament, base) were identified as

hybodontiform scales from the Upper Triassic in Germany (Reif 1978) and Middle Triassic in Spain (Manzanares et al. 2014). Also, the denticles with morphological similarities (size, trident crown, ornament) have been found and described as late Permian euselachian-type dermal denticles from the Naujoji Akmenė Formation in Lithuania (Dankina et al. 2017) and Latvia (Dankina et al. 2020).

Superclass Osteichthyes Huxley, 1880

Class Actinopterygii Cope, 1887

Actinopterygii indet. (teeth)

Fig. 4A–L.

Material.—38 isolated teeth (Fig. 4A–L) from the upper Permian of the Nowy Kościół Quarry, Leszczyna Syncline, SW Poland. The teeth are represented here by SEM microphotographs of microremains VU-ICH-NK-019–030.

Description.—The teeth divided into three morphotypes based on their different shape and enameloid microstructure. The morphotype numeration and description in this study is continued on from previous studies of the late Permian actinopterygian material from southern Latvia (Dankina et al. 2020; Tables 1, 3).

Morphotype 1: 26 teeth from this morphotype were found in the Nowy Kościół quarry (Fig. 4A–E). The canine-like teeth are conical, straight (Fig. 4A, B) or curved characterised by the “horn-like” shape (Fig. 4C), thin (Fig. 4A) or wide and convex in the central part (Fig. 4E), with an acrodin cap. Tooth surface is smooth, with no distinct visible ornament, although the microtubercles are well-developed (Fig. 4D₂). The microtubercles are proximo-distally elongated, narrow and blend together in oblique rows (Fig. 4D₂). Morphotype 1 teeth reach 0.4–1.2 mm in width and 0.6–1.9 mm in length.

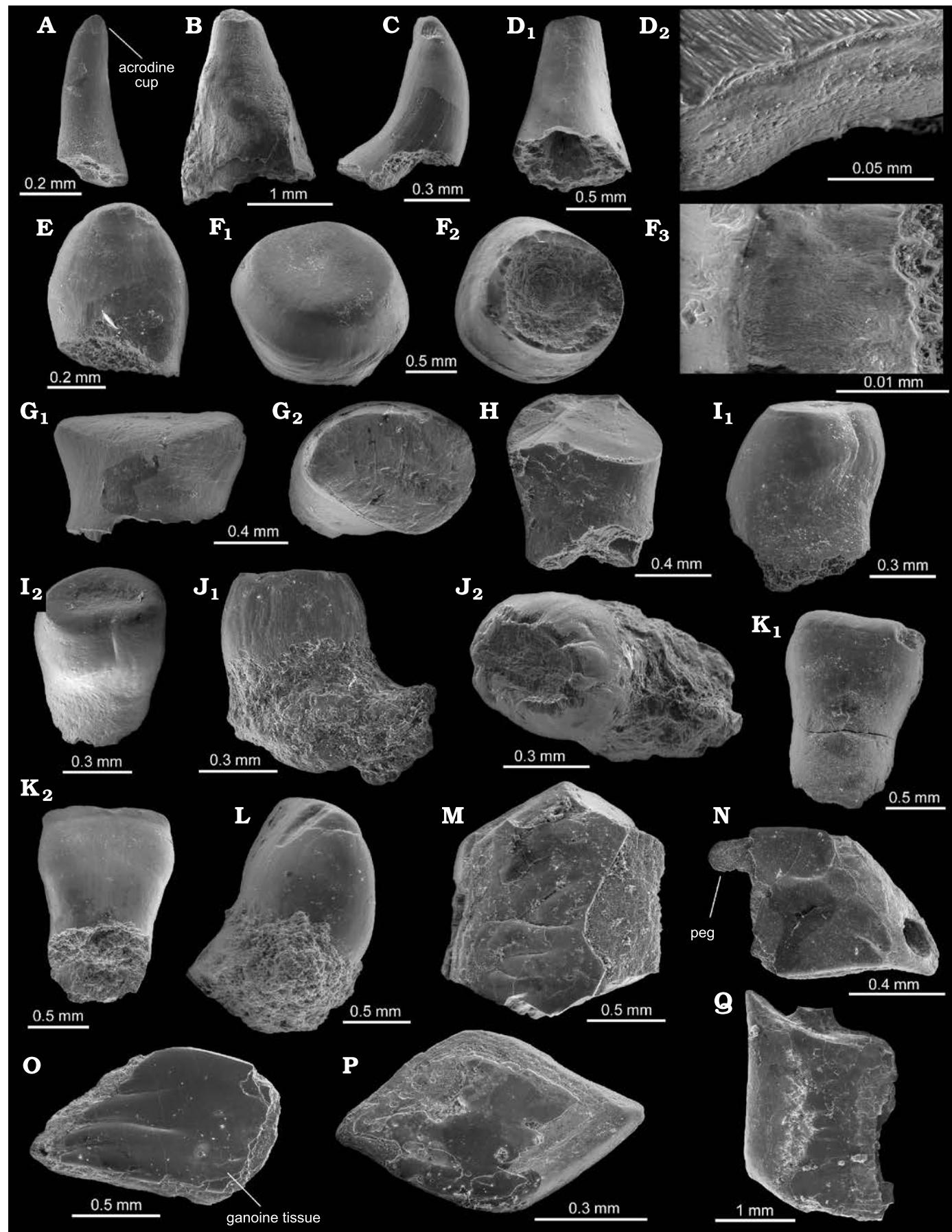
Morphotype 7: Five teeth from this morphotype were found in the Nowy Kościół quarry (Fig. 4F–I). The molar teeth are roundish (Fig. 4F), short, slightly depressed in labial-lingual face (Fig. 4G), cylindrical in shape (Fig. 4H), and with convex outline in lateral view (Fig. 4I). The surface of these teeth is smooth with a slightly concave central part (Fig. 4F₁, I₁). Some teeth have well-developed, vertically elongated, narrow microtubercles (Fig. 4G₁). These teeth reach a maximum of 0.2–0.6 mm in width, 0.6–1.2 mm in length and 0.4–1.0 mm in height.

Morphotype 8: Five teeth from this morphotype were found in the Nowy Kościół quarry (Fig. 4J–L). The teeth are straight, wide, and narrow (depressed in labial-lingual face) and with well-developed, vertically elongated, narrow

Table 3. The main characteristics of the different morphotypes of Actinopterygii teeth. M1–8, morphotype 1–8.

Morpho-type	Surface ornament	Flat crown top	Visible roots	Tooth symmetry	Micro-tubercles
M1	no	no	partly	yes	yes
M2	yes	yes	partly	yes	yes
M3	yes	partly	no	partly	yes
M4	no	partly	partly	yes	yes
M5	no	yes	no	yes	yes
M6	yes	partly	no	partly	yes
M7	no	partly	no	partly	partly
M8	no	no	partly	yes	partly

Fig. 4. Actinopterygian remains from the upper Permian of the Nowy Kościół quarry, Poland. **A–E.** Actinopterygian teeth of morphotype 1. **A.** VU-ICH-NK-019, lateral view. **B.** VU-ICH-NK-02-20, lateral view. **C.** VU-ICH-NK-021, lateral view. **D.** VU-ICH-NK-022, lateral view (D₁), microtubercles structure (D₂). **E.** VU-ICH-NK-023, lateral view. **F–I.** Actinopterygian teeth of morphotype 3. **F.** VU-ICH-NK-024, extero-lateral (F₁) and basal (F₂) views, detailed tissue pattern (F₃). **G.** VU-ICH-NK-025, lateral (G₁) and external (G₂) views. **H.** VU-ICH-NK-026, lateral view. **I.** VU-ICH-NK-027, lateral (I₁) and extero-lateral (I₂) views. **J–L.** Actinopterygian teeth of morphotype 4. **J.** VU-ICH-NK-028, lingo-lateral (J₁) and labio-lateral (J₂) views. **K.** VU-ICH-NK-029, lingual (K₁) and labial (K₂) views. **L.** VU-ICH-NK-030, lateral view. **M–P.** Actinopterygian scales of morphotype 1, VU-ICH-NK-031–034, all external view. **Q.** Actinopterygian scale of morphotype 2, VU-ICH-NK-035, external view.



microtubercles (Fig. 4J). Some teeth consist of the three layers: upper layer is dark grey; middle, light grey; lower, medium grey; according to the SEM picture (Fig. 4K, L) while under microscope the tooth's upper part has the light amber acrodin (almost white); middle part is dark brown; and lower part—mid-amber colour. Rarely the tooth has concave top of the central part (Fig. 4K₂, L). The surface is smooth, without any ornament (Fig. 4K, L), sometimes with preserved sediments in the lower part of the tooth (Fig. 4L). These teeth reach 0.7 mm in width and 1.2 mm in height.

Remarks.—Similar Actinopterygii teeth of the morphotype 1 are known from Permian fish assemblages in Argentina (Cione et al. 2010), Latvia (Dankina et al. 2020) and Lithuania (Dankina et al. 2017). Moreover, the *Gyrolepis albertainii* conical teeth with transparent acrodin cup are known from the Upper Triassic of the Westbury Formation in southwest Britain (Landon et al. 2017: fig. 6A).

Actinopterygii indet. (scales)

Fig. 4M–Q.

Material.—29 scales (Fig. 4M–Q) from the upper Permian of the Nowy Kościół Quarry, Leszczyna Syncline, SW Poland. The scales are represented here by SEM microphotographs of microremains VU-ICH-NK-031–035.

Description.—The scales divided into two morphotypes relatively based on their different shape and ganoine layer characteristics. The morphotype numeration and description in this study is taken from previous studies of late Permian euselachian material from southern Latvia (Dankina et al. 2020; Tables 1, 4).

Morphotype 1: 26 scales from this morphotype were found in the Nowy Kościół quarry (Fig. 4M–P). The scales are rhombic-shaped, thick, massive and gently convex in their central part. Scales have numerous small, roundish-shaped microtubercles in the outer ganoine-covered field part (Fig. 4M–P). The surface is covered by smooth ganoine tissue (Fig. 4P), with some fine, slightly diagonally oriented, short ridges, which are separated by narrow grooves (Fig. 4O). In rare cases, scales have a well-preserved peg articulation and significantly wide anterior entry of the lateral line canal (Fig. 4N). Scales reach 0.6–1.0 mm in length and 0.4–0.6 mm in width.

Morphotype 2: Three scales from this morphotype were found in the Nowy Kościół quarry (Fig. 4Q). Elongated

Table 4. The main characteristics of the different morphotypes of Actinopterygii scales. M1–6, morphotype 1–6.

Morpho-type	Ganoine top	Scale symmetry	Surface ridges	Surface grooves	Micro-tubercles	Canal openings
M1	yes	yes	no	partly	yes	yes
M2	yes	partly	no	yes	no	no
M3	yes	no	no	partly	yes	yes
M4	yes	no	yes	no	yes	no
M5	yes	no	no	no	yes	yes
M6	yes	partly	no	partly	yes	yes

rhombic-shaped scale with almost right-angled (~90°) all four corners. The base is thick and convex in the central part. The scale has preserved a fragment of the peg articulation. The ganoine-covered field is smooth without any ornament. The scale reaches 2.3 mm length and 1.4 mm width.

Remarks.—The scales collection of morphotype 1 with similar morphological characteristics (rhombic shape and ganoine pattern) was found in late Permian actinopterygian scales from Lithuania (Dankina et al. 2017) and Latvia (Dankina et al. 2020). Also, rhomboidal scales are known from the middle Permian of the Apache Mountains in West Texas, USA (Ivanov et al. 2013); Permian in England (King 1850); and Permian in Argentina (Cione et al. 2010). The morphotype 2 scale seems to be similar to the Middle Triassic *Gyrolepis* sp. rhomboidal scales from the North-Sudetic Basin in Poland (Chrząstek 2013).

Discussion

The hybodontoids are one of the best-known groups of fossil sharks and their teeth, spines and scales are common fossils in several Mesozoic rock formations (Wang et al. 2009). The new material (isolated chondrichthyan tooth) described herein is attributed to the family Lonchidiidae. This tooth has the most morphological similarities (elongate shape, low-crowned, higher central cusp and two pairs of low lateral cusplets, ornament, deep root, with irregular, numerous foramina) to the teeth of *Gansuselache* from the upper Permian of north-western China (Wang et al. 2009). Although *Lissodus* teeth are similarly shaped (Ginter et al. 2010), the main differences between them and the described tooth are blunt cusps and an absence of the coarse vertical ridge ornamentation, which descends from the tip of the cusp downwards. Additionally, no obvious labial peg was observed, which is typical for *Lissodus*. On the other hand, the geographic distribution of the genus *Gansuselache* Wang et al. (2009) first described from the late Permian deposits in north-western China, is poorly known. However, the Lonchidiidae remains are more widely distributed and known from the Permian of the Kanin Peninsula, Arkhangelsk Region in Russia (Ivanov and Lebedev 2014); lower Permian of Germany (Hampe 1996); and middle Permian of central Japan (Yamagishi and Fujimoto 2011).

Herein, actinopterygian teeth are divided into three different morphotypes based on the various shapes. The tooth form is mainly determined by the different types of food ray-finned fishes consume. Every trophic group is characterised by a certain mode of feeding, suited type of diet, and specific morphofunctional adaptations of jaws and teeth (Esin 1997). According to Esin (1997) who described major trophic groups of fish, “morphotype 1” with a small canine-like shape suggests “specialised sclerophagous”

and “small predator” diets. The small predatory teeth are conical with acute terminations (Fig. 4A, B). Sometimes this morphotype of teeth are high, conic, slightly turned back into the mouth (Fig. 4C) and high-conic with blunt top shapes (Fig. 4E). Smaller teeth (presumably of juvenile individuals) of this type are covered with numerous acute microtubercles (Fig. 4D). Fishes with similar teeth shape mostly fed on crustaceans with hard shells and also on aquatic insects (Esin 1997). The earliest aquatic insects are known from the early Permian (Sinitshenkova 2003). This type of feeding could be compared to that of modern chubs or perch, which diets include arthropods, small fishes and vegetation (Esin 1997). The Permian genera, such as *Acropholis*, *Acrolepsis*, *Palaeoniscum*, *Elonichthys*, *Varialepis* are characterised by this tooth ecomorphotype (Esin 1997). *Acropholis* remains are known from the Permian of Greenland (Aldinger 1937) and Russia (Nurgaliev et al. 2015); *Acrolepsis* was found in Permian sequences of Germany (Diedrich 2009), the United Kingdom (King 1850) and Russia (Nurgaliev et al. 2015); Permian *Palaeoniscum* was found in United Kingdom (King 1850); Germany (Diedrich 2009), Russia (Nurgaliev et al. 2015), Turkey (Hoşgör and Şämberg 2014); Permian *Elonichthys* are known from Greenland (Aldinger 1937) and Russia (Nurgaliev et al. 2015); while Permian *Varialepis* was found in Russia (Tverdokhlebov et al. 2005; Nurgaliev et al. 2015), and USA (Ivanov et al. 2013).

Morphotype 7 teeth suggest durophagous-type mode of feeding. These teeth are rod-shaped or slightly depressed cylinders with rounded and almost rounded flat or concave apex (Fig. 4F–I). These teeth most likely were used for crushing and grinding of hard external skeletons, such as shells (Purnell and Darras 2015) of molluscs or brachiopods as well as possibly soft-bodied invertebrates (polychaetes) (Esin 1997). Productid brachiopods, and many species of bivalves were common in the Zechstein strata and are known from the Holy Cross Mountains, Poland (Kaźmierczak 1967), England (Ramsay 1878), and Lithuania (Suveizdis 1975). Also, polychaetes are known from the upper Permian of Poland (Szaniawski 1968). This type of teeth can be compared to the modern breams in their mode of life (Esin 1997). Morphotype 8 teeth are interpreted here to represent a “grazing” trophic mode (Fig. 4J–L). These teeth come in a variety of different shapes, others are characterised by the saw-edge or even are fused into the “beak”, like in modern parrotfishes. The wide and thin teeth are adapted for feeding on water vegetation, apparently used for cutting thin threadlike algae (Esin 1997). This morphotype of teeth is characterised by the herbivorous diet, which is very similar to Recent freshwater teleosts, such as characiforms and cichlids (Pindakiewicz et al. 2020).

The morphotype diversity of fish teeth from the upper Permian in the SW Poland indicates that ray-finned fishes already started wide exploration of different feeding modes before the onset of the Mesozoic.

Conclusions

The micropaleontological study of the late Permian fish assemblages from the distal storm deposits of the Nowy Kościół quarry revealed assemblages that are composed of non-abundant but relatively diverse isolated microremains of different fish taxa, including euselachian dermal denticles, diverse actinopterygians scales and teeth, and *?Gansuselache* sp. tooth. The finding of the later taxon significantly extends the known geographic distribution of this hyodontiform genus (or closely related forms), which was previously known only from China.

The stratigraphic distribution of fish remains and in particular their abundance in Nowy Kościół site shows high congruence with the Werra marine transgression. This transgression created the favourable conditions for flourishing of fish fauna in the Zechstein Basin. The highest abundance of fish microremains and their diversity was found at the boundary between copper-bearing and lead-bearing marl sequences in Nowy Kościół quarry. The association of transgression with higher abundance of ichthyofauna could be explained by two-fold effect. Transgression should have positively affected abundance by increasing runoff of nutrients from surrounding terrain in a warmer climate, and diluting hyper-saline waters. On other hand warmer climates, which accompany transgressions, should have promoted effectiveness of biomass transfer to the higher trophic levels occupied by fishes by physiologically reinvigorating predation efficiency (Britten and Sibert 2020).

The diverse morphology of actinopterygian denticulation demonstrates the prevalence of three trophic groups in the eastern Zechstein Sea margin. Those groups are inferred based on the three ecomorphotypes, which dominate the assemblages: (i) morphotype 1, teeth of specialised sclerophagous and small predators; (ii) morphotype 7, the crushing and grinding teeth of durophagous-type; (iii) morphotype 8, peg-like teeth adapted for herbivory or general grazing. The actinopterygian teeth material indicates that small generalized predators dominated among the recorded ichthyofauna. The diversity of different types of teeth indicates an onset of active ecomorphological specialization among the fish taxa, which further strengthens the case that the roots of Mesozoic Marine Revolution were set in Palaeozoic.

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