Earth and Environmental Science Transactions of the Royal Society of Edinburgh, **114**, 65–74, 2023

The first Late Permian fish fossils from Leszczyna quarry in South-West Poland

Darja DANKINA[1,2]*, Andrej SPIRIDONOV[2], Paweł RACZYŃSKI[3], Sigitas RADZEVIČIUS[2] and Mateusz ANTCZAK[4]

[1] European Centre of Palaeontology, University of Opole, Oleska st. 48, 45-052, Opole, Poland
[2] Department of Geology and Mineralogy, Vilnius University, M. K. Čiurlionio st. 21/27, LT03101, Vilnius, Lithuania
[3] Institute of Geological Sciences, University of Wrocław, Cybulskiego st. 30, 50-205, Wrocław, Poland
[4] Institute of Biology, University of Opole, Oleska st. 22, 45-052, Opole, Poland
*Corresponding author. E-mail: darja.dankina@gmail.com

ABSTRACT: Permian fishes and their isolated microremains are known from many localities in the Zechstein Basin. However, up to date the vertebrates have never been revealed in the southeasternmost part of this ancient sea. The new material consists of euselachian-type dermal denticles,?*Listracanthus* sp. dermal denticle,?*Omanoselache* sp. tooth, actinopterygian scales and actinopterygian teeth. Here, the detailed study of euselachian and actinopterygian remains, their stratigraphic distribution and geographical contexts is presented. Based on the qualitative analysis of teeth shapes several ecomorphotypes were described as well as the probable dietary preferences of fishes were reconstructed. These finds confirmed existence of small predators who fed on soft bodied prey as well as durophagous forms which were feeding on small shelly crustaceans or molluscs. The analysis of stratigraphic distribution of microremains, and their comparison with neighbouring sections revealed a spatially correlatable trend in increasing abundance of fishes in the more clayey parts of sections, interpreted to be positively associated with a sea level transgression event.

KEY WORDS: Chondrichthyes, dermal denticles, Osteichthyes, scales, teeth, trophic groups, Zechstein Basin.

During the Late Permian the semi-enclosed Zechstein Sea was connected to open ocean through the modern territory of Norway and Greenland – a seaway in the northern Pangea (Maystrenko *et al.* 2008) (Fig. 1a). The palaeogeographical distribution of this epicontinental sea extended from the eastern part of England and Greenland through the northern part of Denmark, Netherlands and Germany into Poland up to the western part of Lithuania and the southern part of Latvia (Van Wees *et al.* 2000; Weissflog *et al.* 2008; Raczyński & Biernacka 2014) (Fig. 1a). The Zechstein Sea reached its widest area during the first carbonate–evaporite cycle (Werra transgression) (Raczyński & Biernacka 2014). The sea water rapidly flooded a depression and due to prevalence of the arid climate, in total seven carbonate–evaporite cycles were deposited there (Peryt *et al.* 2010).

Osteichthyes and Chondrichthyes were the most common vertebrates in the late Palaeozoic marine communities (Vázquez & Clapham 2017). Late Permian fossils of fishes are widely known from marine and freshwater ecosystems of Pangea (Koot 2013; Romano *et al.* 2016) including the Zechstein Sea (King 1850; Nielsen 1952; Diedrich 2009; Dankina *et al.* 2017, 2021a, b).

In this study, we report new chondrichthyans and osteichthyans remains (teeth, dermal denticles and scales) collected from the south-eastern part of the Zechstein Basin in Leszczyna quarry, South-West Poland (Fig. 1b, Table 1). These ichthyofaunal remains are the first record of vertebrates here. However, these fossils are not attributed to any fish genus or species with an exception for two specimens, which were taxonomically identified as ?*Listracanthus* sp. dermal denticle and ?*Omanoselache* sp. tooth. According to this reason, we divided the new material into several morphotypes based on their morphological characteristics. The same division of the ichthyofaunal remains referred to the previous works based on the Late Permian fish material from the Nowy Kościół in South-West Poland (Dankina *et al.* 2021a), Karpėnai quarry in Lithuania (Dankina *et al.* 2017) and Kūmas localities in Latvia (Dankina *et al.* 2021b). Here, we continue using the numeration of morphotypes (M1–M8) which was determined and described in the works mentioned above (Table 2). Thus, a detailed studied fish assemblage increases its distribution and diversity, partly differing from the previously found assemblage in Nowy Kościół locality which was farther offshore of the Zechstein Basin. The quantitative data of found fish fossils in these two localities (Leszczyna and Nowy Kościół quarries) do not show a significant difference. Nevertheless, according to the palaeogeographical location and palaeoenvironmental conditions of studied deposits, the new fish remains reported here add important information especially for the understanding of the relationship between Late Permian sharks' finds from the north-eastern and south-eastern offshore of Zechstein Basin. Additionally, we tried to find a connection between the ecomorphology of Late Permian ray-finned fish teeth and the relation to their diets. Most actinopterygian

 doi:10.1017/S1755691023000051

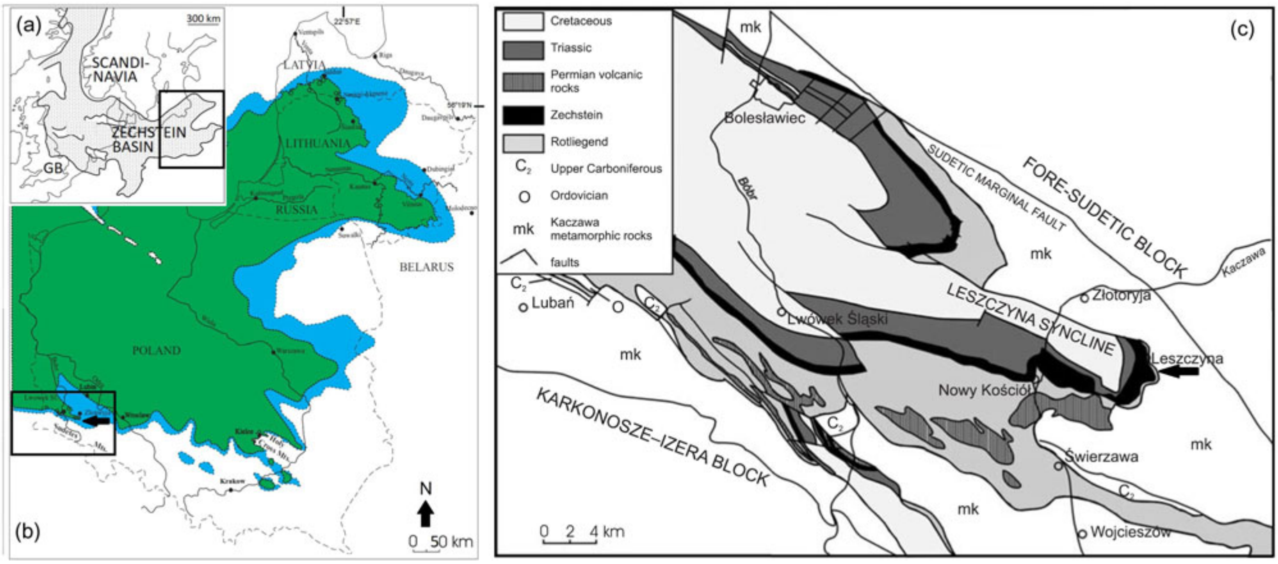

Figure 1 (a) Palaeogeography of the European Zechstein Basin (Becker & Bechstaedt 2006). (b) The map of Eastern Europe showing Leszczyna locality (black arrow). A blue colour represents the original distribution of Zechstein sediments and green is current distribution of Zechstein sediments in Poland, Russia, Lithuania and Latvia (Raczyński & Biernacka 2014). (c) The geological map of North-Sudetic Basin showing location of the studied site (black arrow) (after Biernacka *et al.* 2005).

teeth can be classified as belonging to small predators of soft bodied prey, which fed on small animals (both invertebrates and vertebrates, for example, fish larvae, conodonts, etc.). Rare finds of some actinopterygian teeth may belong to a specialised durophagous forms, which fed on shells and molluscs (Esin 1997; Purnell & Darras 2015).

1. Geological settings

The Zechstein strata formed a relatively narrow zone in the outer part of the North-Sudetic Basin in Poland. The studied Leszczyna section is situated in the Leszczyna syncline (Fig. 1c). It is represented by a minor tectonic unit formed during the Late Cretaceous (Biernacka *et al.* 2005). This section is limited by the Kaczawa Metamorphic Unit from the north, east and south directions while from the west it connects to the North-Sudetic Basin. As a result, it has the shape of an elongated ‘pan’ (Fig. 1c).

The Zechstein marine deposits of the Upper Permian in South-West Poland are famous, in terms of the occurrence of ore-bearing deposits and exploitation of the copper metal. For example, an open-air museum of mining and metallurgy presents here facies of the limestone-marl alternations’ deposits which are exposed in an abandoned quarry in the Leszczyna village (Biernacka *et al.* 2005; Hara *et al.* 2013; Kaczawskie Association 2019). The studied profile from this locality can be divided into two parts. The lower part of this profile is exposed at the base of the quarry in a narrow trench while the upper part could be described as the profile with an extensively cropping outwall. In the lower part of the Leszczyna profile the alternating grey limestone and brown-grey marl can be observed. Within this so-called mottled (spotted) marl gold enriched (0.3 g t^{-1}) deposits were discovered. Also, the high content of copper occurred in the form of malachite and azurite coating there. The amount of copper in these rocks exceeds 1% (Kaczawskie Association 2019). The first stage of ore formation occurred during the sedimentation based on the equilibrium law principle in the aqueous solutions (Serkies *et al.* 1967). The mottled (spotted) marls are covered by thicker layers of limestone with the thinner intercalations of copper-bearing and lead-bearing marls (Kaczawskie Association 2019) (Fig. 2). The local designation of the three units mentioned above has been in use for almost 100 years (Scupin 1931), although, this designation can only reflect the ore content and does not reflect the sedimentological character of the rocks (Biernacka *et al.* 2005). However, these rocks can be described as distal tempestite (Hara *et al.* 2013). The marls were formed on the bottom of the Zechstein Sea without any effect of waves. On the other hand, limestones were deposited with crushed mollusc shells in the lower part of layers as the result of the bottom currents (bearing a washed-out material from the sea coast) (Kaczawskie Association 2019). The complete and incomplete fossils of molluscs, brachiopods,

Table 1 A quantitative (vertical) distribution of fish remains through the studied samples collected from the Leszczyna quarry in South-West Poland.

	Sample (number)	Chondrichthyes’ dermal denticles	Chondrichthyes’ teeth	Osteichthyes’ scales	Osteichthyes’ teeth
	LCZ-11	0	0	0	0
	LCZ-10	0	0	0	0
	LCZ-9	0	0	0	0
	LCZ-8	0	0	0	0
	LCZ-7	0	0	1	0
	LCZ-6	0	0	8	3
	LCZ-5	0	0	0	2
	LCZ-4	0	0	0	0
	LCZ-3	33	1	30	28
	LCZ-2	0	0	0	0
	LCZ-1	0	0	0	0
Total:	11	33	1	39	33

https://doi.org/10.1017/S1755691023000051 Published online by Cambridge University Press

Table 2 A short description of Late Permian fish remains' morphotypes (M) and their distribution in Poland, Lithuania and Latvia.

	Locality	South-West Poland	South-West Poland	Northern Lithuania	P Latvia	Short description of morphotypes
		(present study)	(Dankina *et al.* 2021b)	(Dankina *et al.* 2017)	(Dankina *et al.* 2021a)	
	Morphotype	Leszczyna quarry	Nowy Kościół quarry	Kūmas quarry	Karpėnai quarry	
Euselachii dermal denticles	M1	–	–	+	–	Crown is blunt, 'horn' shaped, elongated, slightly compressed in lateral view
	M2	+	+	+	+	Trident or nearly trident crown with a low, slender and narrow neck
	M3	+	+	+	+	Roundish/semi–roundish denticles with a slightly elongated blunt cusp
	M4	–	+	+	+	'Tripod boomerang' shaped denticles
	M5	+	+	+	+	Drop-like crown margin surface is smooth, with some short ridges on the anterior
	M6	+	+	+	+	Complex crown shape (from narrow, subparallel till wide, triangular)
Actinopterygii teeth	M1	+	+	+	+	Slender, smooth, with no distinct visible sculpture, with microtubercles
	M2	–	–	+	–	Rodshaped, short, cylindrical shape with a flat apex
	M3	–	–	+	+	Semispherical, convex and with a circular surface shaped in the apical view
	M4	–	–	+	+	Globular/circular-rod shaped in the lateral view, with convex, tiny acrodine cap
	M5	–	–	+	–	Spherical or styliform shaped in the lateral view with flat, smooth crown tip
	M6	–	–	+	+	Conical in shape, covered with microtubercles
	M7	+	+	–	–	Roundish, short, slightly depressed in labial-lingual face, cylindrical in shape
	M8	–	+	–	–	Straight, wide, and narrow with vertically elongated, narrow microtubercles
Actinopterygii scales	M1	+	+	+	+	Rhombic or diamond shaped, sometimes gently convex in their central part
	M2	–	+	+	–	Elongated rhombic-shaped scale with right-angles at all four corners
	M3	+	–	+	–	Elongated/square shaped thick, with a slightly twisted posterior corner
	M4	–	–	+	+	Small, elongated/ellipsoid shaped, with an acute angle of the posterior corner
	M5	–	–	+	–	Small, thick and rod-like with an extremely elongated shape, flat surface
	M6	–	–	+	–	Dorsal, ventral, anterior margins are straight, the posterior is pectinated

ostracods and bryozoans (mostly fenestellids) were previously found in the Leszczyna locality (Raczyński 1997; Hara *et al.* 2013). Remains of the vertebrates have not been described in the studied area.

2. Material and methods

The studied samples were collected from three outcrops located in the Leszczyna quarry of South-West Poland [51°5′29.65″N, 15°58′42.55″E; 51°5′47.93″N, 15°58′31.69″E; 51°5′55.11″N, 15°58′24.66″E]. The samples were each taken 1.5–2.0 m throughout a vertical cross-section of these outcrops. Three samples were collected from Lower Zechstein (LCZ-1, LCZ-2 and LCZ-3) and eight samples from Middle Zechstein (LCZ-4–LCZ-11) strata. The total weight of 11 samples from the Leszczyna quarry reached 111.8 kg of carbonate material.

The microfossils were chemically extracted from collected samples using the carbonate dissolution in formic acid technique described by Jeppsson *et al.* (1999). The sample preparation was done in the Micropalaeontological laboratory (Vilnius University) by mixing 23.3 l of 60% formic acid and 116.7 l of tap water in a 70 l vessel. The vessel with a chemical solution and a sample were left for about 48 h till the reaction stopped. The laboratory procedure for one sample was repeated till the carbonate material was totally dissolved. The undissolved residue was dried at room temperature and sieved using the dry sieving technique (Green 2001) for the size range between 0.063 and 3.0 mm to extract it. Later, sorted micromaterial was studied using a binocular microscope.

In total, 106 isolated fish remains were found in the collected samples. The counting was done for each sample and presented in Table 1 for further comparative analyses with the Nowy Kościół quarry section in South-West Poland. All ichthyofaunal finds were divided into four groups (Chondrichthyes dermal denticles, Chondrichthyes teeth, Osteichthyan teeth and Ostichthyes scales) based on the various fossilised remains. These groups were divided into 6–8 morphotypes (M1–M8) according to their morphological characteristics for more detailed studies,

https://doi.org/10.1017/S1755691023000051 Published online by Cambridge University Press

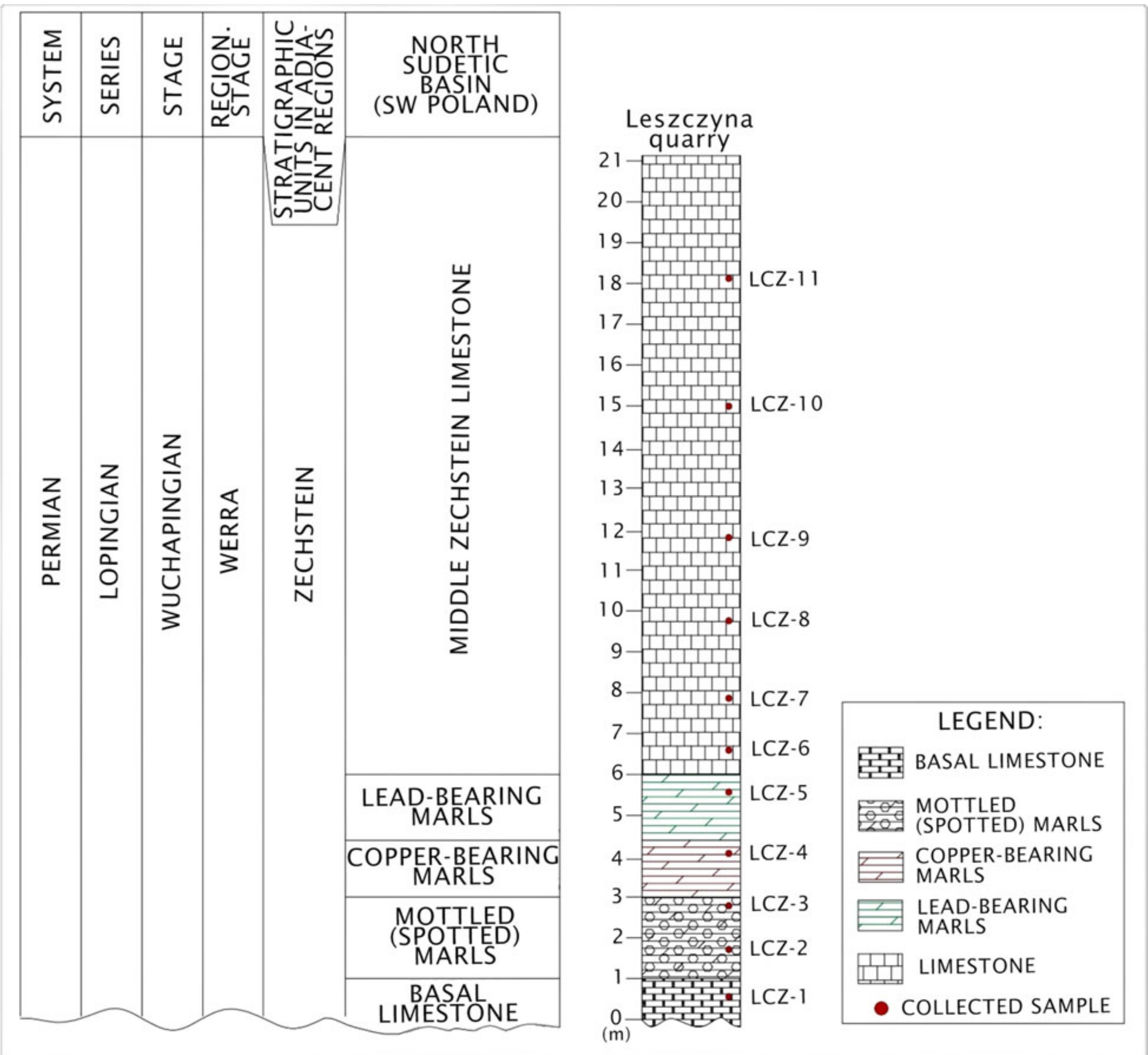

Figure 2 The lithostratigraphic profile of Upper Permian strata in the Leszczyna area.

with an exception of the Chondrichthyes teeth group, since only a single specimen was found. This concept of division of the ichthyofaunal material into morphotype groups follows our previous works based on the Upper Permian materials from the Nowy Kościół quarry in South-West Poland (Dankina *et al.* 2021a), Kūmas quarry in southern Latvia (Dankina *et al.* 2021b) and Karpėnai quarry in northern Lithuania (Dankina *et al.* 2017). In this study, we continue the use of the morphotypes' numeration which was determined and described in the works mentioned above (Table 2).

Figures 2 and 3 were done using AutoCAD software to visualise lithological columns, Adobe Photoshop for adding textual information and Microsoft Excel for a quantitative distribution of fish fossils in the studied outcrops. These fossils were micrographed using a FEI Quanta 250 scanning electron microscope (SEM) at the Nature Research Centre (Vilnius, Lithuania) and presented in Figs 4, 5. The ichthyofaunal material described here is housed in the Geological Museum at the Institute of Geosciences of Vilnius University (Vilnius, Lithuania).

3. Systematic palaeontology

Class Chondrichthyes Huxley (1880)
Subclass Elasmobranchii Bonaparte (1832)
Order Hybodontiformes Patterson (1966)
incertae familiae
Genus *Omanoselache* Koot *et al.* (2013)
?Omanoselache sp.
(Fig. 4a)

Material

Incomplete tooth [UO-ICH-LCZ-01].

Description

The shape of tooth is robust, elongated and slightly but clearly asymmetrical (Fig. 4a1). It reaches 1.6 mm mesio-distal, 0.7 mm labio-lingual and 1.0 mm in height. The central transverse part of the crown has a moderate main cusp with rounded apex (Fig. 4a2). A small labial peg is indented (Fig. 4a1). The crown surface is smooth without any ornamentation. The neck is massive and broad, with some canal openings filled by sediment (Fig. 4a2). The basal plate is elliptical in shape.

Remarks

Similar morphological features (asymmetrical crown, smooth surface with the rounded blunt apex of the main cusp, small labial intended peg and the base with randomly located foramina) were found for a comparison with an elongate tooth three times bigger in size from the Knuff Formation of Middle

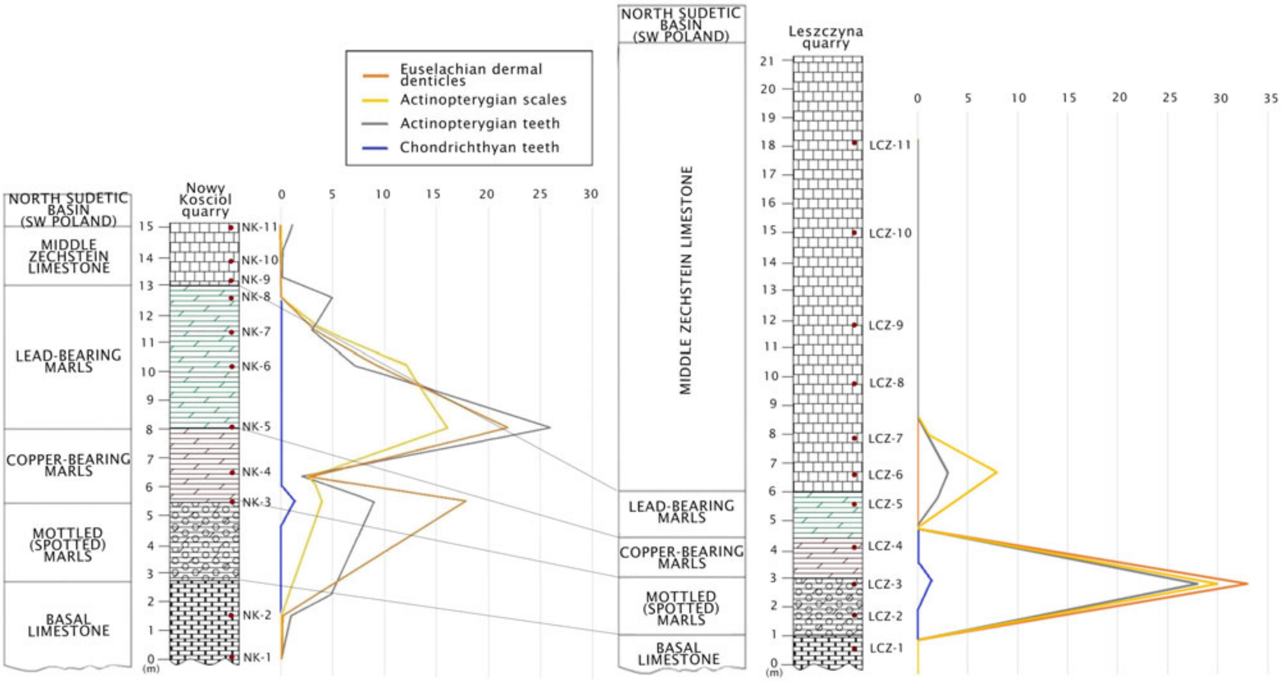

Figure 3 The lithostratigraphic correlation of Upper Permian strata between Nowy Kościół and Leszczyna quarries in South-West Poland with a quantitative (vertical) distribution of fish remains.

Permian in the Oman (Koot *et al.* 2013). Moreover, the analogous specimen with similar parameters, shape and size, was previously found in the Naujoji Akmenė Formation from Upper Permian of the southern Latvia (Dankina *et al.* 2021b).

Subclass Elasmobranchii Bonaparte (1838)
Order *incertae sedis*
Family Listracanthidae Martill *et al.* (2013)
Genus *Listracanthus* Newberry & Worthen (1866)
?Listracanthus sp.
(Fig. 4b)

Material

Incomplete dermal denticle [UO-ICH-LCZ-02].

Description

The stud-like crown is compound, elongate, flattened, and posteriorly recurved. It is covered by vertical ridges along the whole specimen. The crown is perpendicularly attached to the narrow and flat base (Fig. 4b).

Remarks

A similar dermal denticle referred to '*Listracanthus*' type denticles which are know from Early Permian of the Middle and South Ural (Ivanov 2005). The highly notable ridges are incompletely preserved in the studied material. However, these ridges are easy recognisable on the lower part of denticle which are attached to the base.

Cohort Euselachii Hay (1902)
Euselachii indet.
(Fig. 4c–j)

Material

Isolated euselachian dermal denticles were found in the Leszczyna quarry in South-West Poland (Fig. 4c–j). These fossils were divided into four morphotypes (M2, M3, M5 and M6) based on their morphological characteristics, such as shape of the crown and its ornament. The dermal denticles are represented here by SEM micrographs of remains UO-ICH-LCZ-03–UO-ICH-LCZ-010.

Description

The dermal denticles of morphotype 2 [UO-ICH-LCZ-03] have a trident or nearly trident shape of the crown with a low, slender and narrow neck, hidden under the crown in apical view (Fig. 4c). The exterior part of the crown is smooth without any ornamentation. The crown is obtained to be slightly obliquely up from the neck. The shape of base is poorly-preserved. The crown of the denticle is 0.3–0.4 mm in length and width, respectively. The dermal denticles of morphotype 3 [UO-ICH-LCZ-04–UO-ICH-LCZ-05] have a roundish (Fig. 4d) and semi-roundish shape of the crown (Fig. 4e). This type of denticle has a slightly elongated blunt cusp in the posterior margin of the crown (Fig. 4d). The crown surface is smooth without any ornamentation. It has some short ridges and furrows on the anterior margin (Fig. 4d, e). The crown is placed horizontally or evidently obliquely up from the neck. The neck is relatively high. The shape of the base is incompletely preserved. The crown is 0.3–0.4 mm in width and length, respectively. The dermal denticles of morphotype 5 [UO-ICH-LCZ-06–UO-ICH-LCZ-08] have an outline of drop-like crown of different width (Fig. 4f). The crown surface is smooth with some short ridges on the anterior margin (Fig. 4g) or one long furrow in the central part of the crown (Fig. 4h). The crown is placed horizontally or evidently obliquely up from the neck. The outline of the base is curved, multipetaloid in shape, with some concave canal openings in the proximal view (Fig. 4f). The denticles are 0.3–0.5 mm in width and length, respectively. The dermal denticles of morphotype 6 [UO-ICH-LCZ-09–UOICH-LCZ-10] have a vertical oriented compound shape (Fig. 4i, j). The crown is smooth and covered by short, narrow ridges along the posterior part of the denticle. The central part of the crown is strongly concave (Fig. 4j). The neck is poorly developed. The base is flat and low. The denticles are 0.4–1.0 mm in width and 0.8–1.2 mm in length.

Remarks

Dermal denticles of the morphotype 2 have strong morphological similarities (shape of the crown, the neck features and size of the fossils) to other euselachian-type dermal denticles which have already been described from the Upper Permian in

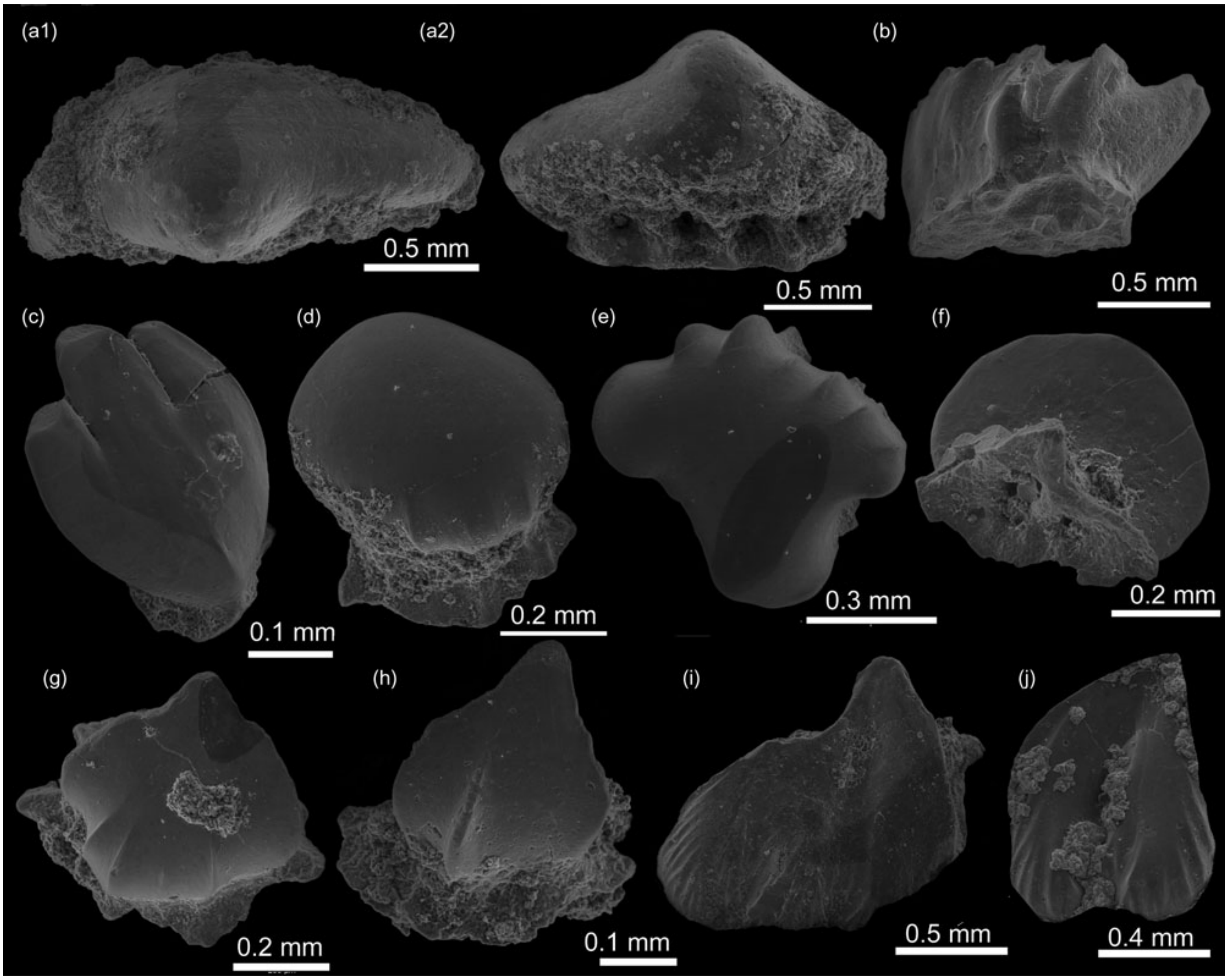

Figure 4 Scanning electron microscope photomicrographs of the Late Permian chondrichthyan remains from the Leszczyna quarry. (a) ?*Omanoselache* sp. tooth: (a1) in occlusal view, (a2) in lateral view [UOICH-LCZ-01]. (b) '*Listracanthus*' type dermal denticles in crown view [UO-ICH-LCZ-02]. (c) Euselachian type dermal denticles of morphotype 2 in crown view [UO-ICH-LCZ-03]. (d) In crown view [UO-ICH-LCZ-04]. (e) In crown view [UO-ICH-LCZ-05]. (f–h) Euselachian type dermal denticles of morphotype 5. (f) In basal view [UO-ICH-LCZ-06]. (g) In crown view [UO-ICH-LCZ-07]. (h) In crown view [UO-ICH-LCZ-08]. (i, j) Euselachian type dermal denticles of morphotype 6. (i) In crown view [UO-ICH-LCZ-09]. (j) In crown view [UO-ICH-LCZ-010]. Abbreviation: DE = euselachian type dermal denticles of morphotype 3.

Lithuania (Dankina *et al.* 2017), Latvia (Dankina *et al.* 2021b) and Poland (Dankina *et al.* 2021a). The main difference between a new material described here and material which already has been found is the absence of crown ornamentation. Dermal denticles of the morphotype 3 are referred to euselachian-like dermal denticles which were found in Permian strata of Russia (Ivanov & Lebedev 2014) and euselachian dermal denticles in Upper Permian strata of Latvia (Dankina *et al.* 2021b). Dermal denticles of the morphotype 5 resemble euselachian-type denticles from the Upper Permian in Lithuania (Dankina *et al.* 2017), Latvia (Dankina *et al.* 2021b) and Poland (Dankina *et al.* 2021a). Also, morphologically similar euselachian denticles are known from Permian strata of Russia (Ivanov & Lebedev 2014). Moreover, these denticles have similarities to hybodontiform scales from Upper Triassic strata of Germany (Reif 1978) and Middle Triassic strata of Spain (Manzanares *et al.* 2014). Dermal denticles of the morphotype 6 have strong similarities (shape of the crown and its ornament) to euselachian-type denticles which are known from Upper Permian strata of Poland (Dankina *et al.* 2021a). Furthermore, similar euselachian dermal denticles to the studied M2, M3, M5 and M6 here were found in Middle Permian strata of the United States (Ivanov *et al.* 2021).

Superclass Osteichthyes Huxley (1880)
Class Actinopterygii Cope (1887)
(Fig. 5)

3.1. Teeth

Material

Isolated actinopterygian teeth were found in the Leszczyna quarry in South-West Poland (Fig. 5a–d). These fossil remains were divided into two morphotypes (M1 and M7) based on their morphological characteristics of teeth shape. The teeth are represented here by SEM micrographs of the remains of UO-ICH-LCZ-11–UO-ICH-LCZ-014.

Description

The teeth of morphotype 1 [UO-ICH-LCZ-11–UO-ICH-LCZ-13] have a conical, thin, straight (Fig. 5a1, b) or slightly curved shape (Fig. 5c1). These teeth have an acrodin cap (Fig. 5c2) or lack of it in some fossils because of poorly-preserved material (Fig. 5b). Teeth surface is smooth with no distinct visible ornament (Fig. 5a–c) but with well-developed microtubercles for some teeth (Fig. 5a2). The microtubercles are proximo-distally elongated, narrow and blend together in oblique rows. These teeth are 0.3–1.1 mm in length. The teeth

https://doi.org/10.1017/S1755691023000051 Published online by Cambridge University Press

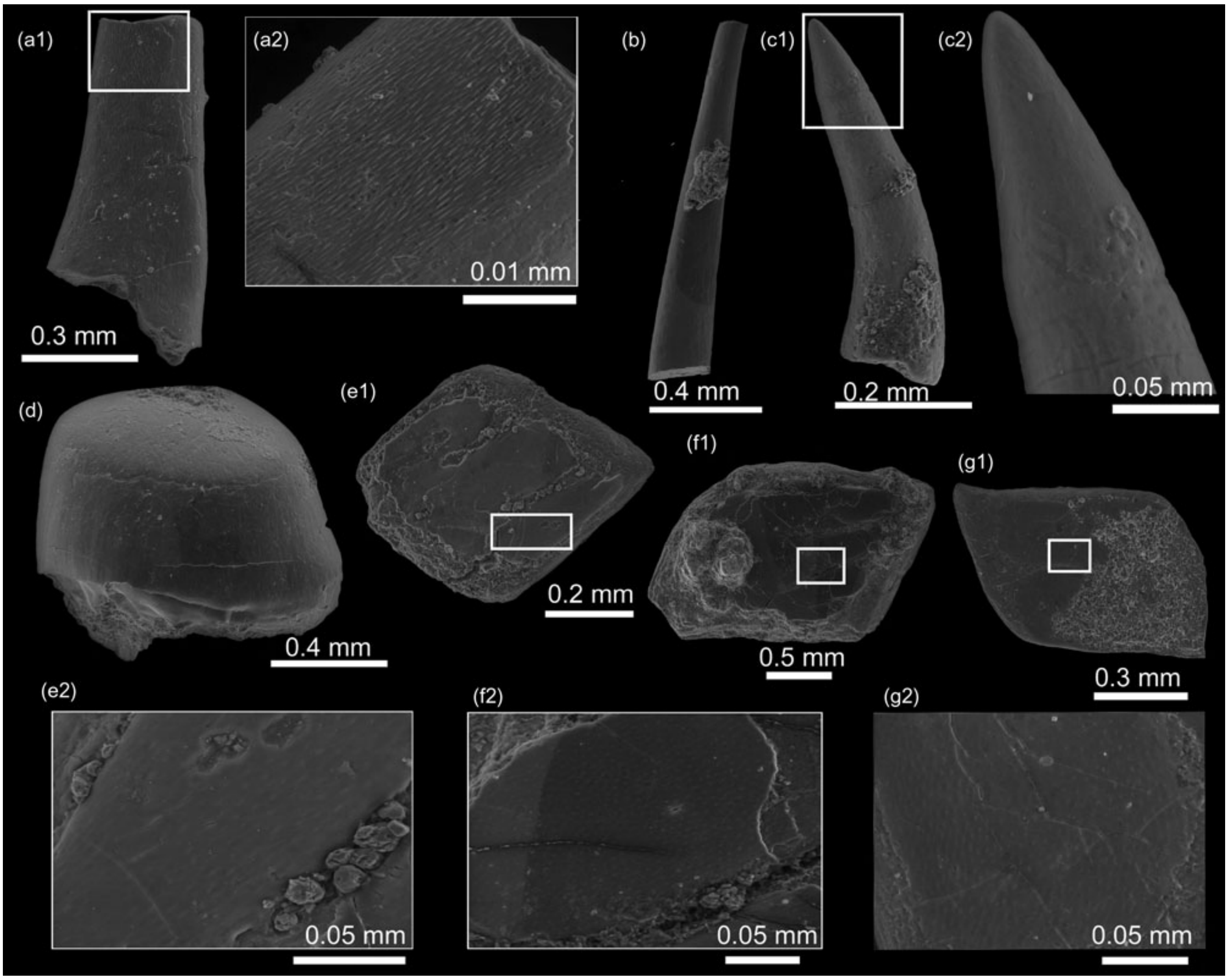

Figure 5 Scanning electron microscope photomicrographs of the Late Permian actinopterygian remains from the Leszczyna quarry. (a–c) Actinopterygian teeth of morphotype 1: (a1) in lateral view [UO-ICHLCZ-011], (a2) the elongated proximo-distally microtubercles. (b) In lateral view [UO-ICHLCZ-012]. (c1) In lateral view [UO-ICH-LCZ-013], (c2) the distinct acrodin apex. (d) Actinopterygian teeth of morphotype 7 in lateral view [UO-ICH-LCZ-014]. (e, f) Actinopterygian scales of morphotype 1: (e1) in external view [UO-ICH-LCZ-015], (e2) the roundish-shaped microtubercles: (f1) in external view [UO-ICH-LCZ-016], (f2) the roundish-shaped microtubercles. (g) Actinopterygian scales of morphotype 3: (g1) in external view [UOICH-LCZ-017], (g2) the roundish-shaped microtubercles.

of morphotype 7 [UOICH-LCZ-14] are roundish in the lateral outline, short and slightly convex in the central part (Fig. 5d). The surface of these teeth is smooth without any ornament. These teeth are about 1.2 mm in width/length and 0.6–0.8 mm in height.

Remarks

The strongly resembling teeth material of morphotype 1 is known from Upper Permian strata of Lithuania (Dankina *et al.* 2017), Latvia (Dankina *et al.* 2021b) and Poland (Dankina *et al.* 2021a). Also, the teeth of this morphotype have similarities (shape of the tooth and its microstructure) to *Elonichthys* sp. teeth from Upper Carboniferous strata of the Czech Republic (Štamberg 2016). The analogous teeth of morphotype 7 are previously described and are known from Upper Permian strata of Poland (Dankina *et al.* 2021a).

3.2. Scales

Material

Isolated actinopterygian scales were found in the Leszczyna quarry in South-West Poland (Fig. 5e–g). These fossils were divided into two morphotypes (M1 and M3) based on their morphological characteristics of the scales' shape. The scales are represented here by SEM micrographs of the microremains of UO-ICH-LCZ-15–UO-ICH-LCZ-017.

Description

The scales of morphotype 1 [UO-ICH-LCZ-15–UO-ICH-LCZ-16] are thick and rhombic-shaped (Fig. 5e1, f1). These scales have numerous small, roundish-shaped microtubercles in the outer ganoine-covered field (Fig. 5e2, f2). The surface is smooth and flat. It has some fine and slightly diagonally oriented ridges which were developed in the posterior parts. These ridges are separated by narrow grooves (Fig. 4e1, f1). Scales are 0.6–1.8 mm in anteroposterior and 0.5–1.0 mm in dorsoventral profile. The scales of morphotype 3 [UO-ICH-LCZ-17] are thick, square-shaped, with a slightly twisted posterior corner (Fig. 5g1). The ganoine tissue is represented here by roundish-shaped and rise-shaped microtubercles in the anteroposterior direction (Fig. 5g2). Scales of this morphotype are about 0.7 mm in anteroposterior profile and about 0.4 mm in dorsoventral profile.

Remarks

The strongly resembling scales collection is known from Upper Permian strata of Lithuania (Dankina *et al.* 2017), Latvia (Dankina *et al.* 2021b) and Poland (Dankina *et al.* 2021a).

4. Discussion

A new fossil fishes' assemblage from the Lower and Middle Zechstein sequences of the Leszczyna quarry in South-West Poland and comprised low abundance microremains of isolated material from Chondrichthyes and Osteichthyes (Fig. 3). The chondrichthyan remains are taxonomically described as euselachian-type dermal denticles, including identification of single specimens of ?*Listracanthus* sp. Dermal denticle and ?*Omanoselache* sp. Tooth while osteichthyan remains are represented by actinopterygian teeth and scales. Genus *Listracanthus* is extremely rare throughout the entire Permian and has never been found in the Zechstein Basin before. However, the *Listracanthus* denticles are known from the Early Permian strata of the Urals (Ivanov 2005). A new specimen has strong morphological affinities to this genus, such as a compound crown with vertical ridges which 'appeared' from the small and flat base. *Omanoselache* taxon is rare in the Palaeozoic fossil record. Although, this genus was discovered comparatively recently by Koot *et al*. (2013) based on the new ichthyofaunal finds from the Late Permian of Oman, it apparently had a wider distribution in the Triassic, ranging from Oman (Koot *et al*. 2015), China (Chen *et al*. 2007), to Spain (Manzanares *et al*. 2018). Nevertheless, a morphologically similar ?*Omanoselache* sp. Tooth was previously found in the north-eastern part of the Zechstein Basin (Dankina *et al*. 2021b). A similar Late Permian ichthyofaunal assemblage with the various morphotypes of euselachian-type dermal denticles, actinopterygian teeth and scales is already known from the eastern part of the Zechstein Basin (Dankina *et al*. 2017, 2021a, b).

A detailed comparison of the Late Permian fossils of fishes between the previously studied Nowy Kościół quarry (Dankina *et al*. 2021a) and new material described here revealed a slight difference (Table 2). In the Nowy Kościół quarry section five morphotypes of euselachian type dermal denticles (M2–M6) were found and described while only four morphotypes of euselachian type denticles (M2, M3, M5 and M6) were found in the Leszczyna quarry. Also, the actinopterygian scales of M1 and M2 were previously described in the Nowy Kościół quarry section, while M1 and M3 were found in the Leszczyna quarry. Moreover, three morphotypes of actinopterygian teeth (M1, M7 and M8) are known from the Nowy Kościół quarry section, while only M1 and M7 were found in the Leszczyna quarry (Table 2). Overall the faunal similarity is evident, and the differences could be partially explained by possible failure of sampling of common taxa because of low absolute abundances of microremains in comparatively large rock samples (low density of finds per unit mass of a bulk sample). The correlation of lithological profiles including quantitative distribution of microremains of fishes between the Nowy Kościół and Leszczyna localities revealed marls as the richest fossils bed (Fig. 3). It is possibly related to formation of marls in the Zechstein Basin where sediments accumulated on the bottom of the basin during a calm state of the water (without any effect of waves) (Kaczawskie Association 2019) which suggest transgressive conditions, milder climate, runoff of nutrients from highlands and possibly greater productivity of marine ecosystems. A minor difference in the diversity of apparent morphotypes of fishes between the Nowy Kościół and Leszczyna quarry sections is possibly related to the palaeogeographical location of the studied area, which was much closer to the shoreline than the Nowy Kościół locality, which was further offshore (Fig. 1c). Therefore, the taxonomic differences at least partially could be accounted for by differences in the position of localities with respect to a major environmental (depth) gradient.

Omanoselache finds from the Leszczyna (South-West Poland) and Kūmas (Latvia) localities in the eastern part of the Zechstein Basin point out to the occurrence of normal marine conditions at a given area, probably facilitated by the input of fresh waters from the surrounding terrains (Dankina *et al*. 2021b). This pattern of higher abundance and diversity of fishes in near-shore settings was determined earlier based on the stratigraphic and geographical comparison of distribution of fish micoremains in nearby Zechstein sections from north Lithuania and south Latvia (Dankina *et al*. 2021b). *Acrodus* and *Helodus* teeth were previously reported in the north-eastern part of the Zechstein Basin (Dankina *et al*. 2017, 2021b) where a coastal zone was much wider compared with the south-eastern part of this basin in South-West Poland (Raczyński & Biernacka 2014). Here, the lithological profile shows prevalence of limestones and dolostone pointing to the shallow marine shoreline nature of the sequence of the Zechstein Sea, which appearance was caused by the first and the strongest transgression which formed the overall successions of the basin (Raczyński & Biernacka 2014; Dankina *et al*. 2017, 2021b).

Two morphotypes (M1 and M7) of Late Permian actinopterygian teeth were found and described in the Leszczyna quarry section. Their morphology revealed that ray-finned fishes occurring in the southeasternmost part of the Zechstein Sea had less different feeding modes than in the nearby areas of Poland (Dankina *et al*. 2021a). Esin (1997) described major trophic groups of fishes based on their teeth shape. Moreover, other scientific works are known based on actinopterygian jaw apparatus (lower jaw) which related to a feeding mode of herbivory and grazing in the marine palaeoenvironment (Bellwood 2003) as well as the earliest discovered durophagous among actinopterygians according to new information about jaws including their palate and dentition (Sallan & Coates 2013; Friedman *et al*. 2019). Durophagy among ray-finned fish appears in the early Carboniferous (Friedman *et al*. 2019), and appears independently in several Carboniferous and Permian groups of Actinopterygii (Fracasso & Hovorka 1987; Zidek 1992; Sallan & Coates 2013). In this study, the morphotype 1 is represented by canine-like shape teeth and their holders should have had feeding styles of small predators, while morphotype 7 is described as rounded teeth in lateral outline and their holders should have belonged to specialised durophagous forms. Fish with teeth shape of morphotype 1 could have fed on the soft-bodied invertebrates (fish larvae and polychaetes) and vertebrates (conodonts). Conodonts are common fossils in the Zechstein deposits of Werra cyclothem from Poland (Szaniawski 1969) and England (Swift 1986). Also, soft-bodied invertebrates such as polychaetes are known from the Upper Permian strata of Poland (Szaniawski 1969). Rare finds of teeth from morphotype 7 point out that their holders processed tough-solid food items, including shelled crustaceans and molluscs (Esin 1997; Purnell & Darras 2015). The foraminifera and ostracods are known from and widely distributed in the Zechstein marine deposits of the Upper Permian in Poland (Woszczynska 1987).

5. Conclusion

Late Permian chondrichthyan and osteichthyan material from the Leszczyna quarry section in South-West Poland presented here add new data to the scarce ichthyofaunal fossil record in the eastern margin of the Zechstein Basin.

The palaeontological study of Zechstein carbonates in the Leszczyna quarry discovered the relatively diverse but low abundance of isolated remains identified and described as four morphotypes of euselachian dermal denticles, two morphotypes of actinopterygian teeth, two morphotypes of actinopterygian scales, ?*Omanoselache* sp. tooth, and ?*Listracanthus* sp. dermal denticle. Previously *Omanoselache* was known from Middle

Permian strata of Oman and Upper Permian strata of Latvia while *Listracanthus* was only known from Lower Permian strata of the Ural Mountains. Thus, the new findings of the latter two genera are significantly extended in their palaeogeographical distributions at the end of the Paleozoic.

The correlation of lithological profiles and comparison of ichthyofaunal assemblage from the Leszczyna and Nowy Kościół quarries show that marly layer is the richest fossils bed in this area. The probable reason for increase in diversity was the prevalence of a more humid climate and runoff of nutrients to the basin.

The teeth of ray-finned fishes demonstrate the prevalence of taxa with two predatory lifestyles in the studied area. The conical teeth of morphotype 1 belonged to the small predators of soft-bodied prey, such as small vertebrates and invertebrates, while crushing teeth of morphotype 7 belonged to durophagous forms who fed on shell-encased prey. The analysis of actinopterygian teeth indicates that, in the eastern part of the Zechstein Sea, this taxon was represented mostly by small pelagic and epibenthic predators.

6. Acknowledgements

The authors thank Dr Alexandr Bakaev (Faculty Member at Russian Academy of Science) for significantly improving the manuscript and sharing important literature. Also, we thank an anonymous reviewer for a useful critique which helped to generate better ideas for this manuscript. Moreover, we thank Vaida Kirkliauskaitė (Vilnius University) and Marijus Ravickas, who helped safely transport samples. Many thanks to Laurynas Šiliauskas (Nature Research Center, Lithuania) for the scanning electron microscope micrographs.

7. Financial support

This research was carried out by the Open Access to the research infrastructure of the Nature Research Centre (Vilnius) under the Lithuanian open access network initiative. The fieldwork to Poland was partly financed by Sepkoski Grant 2018 of Paleontological Society (PaISIRP). Professor Dr Sigitas Radzevičius (co-author) thanks the Polish National Agency for Academic Exchange (NAWA PPN/ULM/2020/1/00306). Besides which, this research was supported by the project S-MIP-21-9 'The role of spatial structuring in major transitions in microevolution'.

8. Competing interests

None.

9. References

Becker, F. & Bechstaedt, T. 2006. Sequence stratigraphy of a carbonate–evaporite succession (Zechstein 1, Hessian Basin, Germany). *Sedimentology* **53**, 1083–120.

Bellwood, D. R. 2003. Origins and escalation of herbivory in fishes: a functional perspective. *Paleobiology* **29**, 71–83.

Biernacka, J., Borysiuk, K. & Raczyński, P. 2005. Zechstein (Ca1) limestone-marl alternations from the North-Sudetic Basin, Poland: depositional or diagenetic rhythms? *Geological Quarterly* **49**, 1–14.

Bonaparte, C. L. J. L. 1838. Selachorum tabula analytica [Analytical table of *Selachus*]. *Nuovi Annali delle Scienze Naturali* **1**, 195–214. [In Latin.]

Chen, L., Cuny, G. & Wang, X. 2007. The chondrichthyan fauna from the Middle–Late Triassic of Guanling (Guizhou province, SW China). *Historical Biology* **19**, 291–300.

Cope, E. D. 1887. Zittel's manual of paleontology. *American Naturalist* **17**, 1014–9.

Dankina, D., Chahud, A., Radzevičius, S. & Spiridonov, A. 2017. The first microfossil record of ichthyofauna from the Naujoji Akmenė Formation (Lopingian), Karpėnai Quarry, North Lithuania. *Geological Quarterly* **61**, 602–10.

Dankina, D., Spiridonov, A., Raczyński, P. & Radzevičius, S. 2021a. Late Permian ichthyofauna from the North-Sudetic Basin, SW Poland. *Acta Palaeontologica Polonica* **66**, s047–57.

Dankina, D., Spiridonov, A., Stinkulis, Ģ, Manzanares, E. & Radzevičius, S. 2021b. A late Permian ichthyofauna from the Zechstein Basin, Lithuanian–Latvian Region. *Journal of Iberian Geology* **47**, 461–81.

Diedrich, C. G. 2009. A coelacanthid-rich site at Hasbergen (NW Germany): taphonomy and palaeoenvironment of a first systematic excavation in the Kupferschiefer (Upper Permian, Lopingian). *Palaeobiodiversity and Palaeoenvironments* **89**, 67–94.

Esin, D. N. 1997. Peculiarities of trophic orientation changes in palaeoniscoid assemblages from the upper Permian of the European part of Russia. *Modern Geology* **21**, 185–96.

Fracasso, M. A. & Hovorka, S. D. 1987. First occurrence of a phyllodont tooth plate (Osteichthyes, Platysomidae) from the Permian San Andres Formation, subsurface, Texas Panhandle. *Journal of Palaeontology* **61**, 375–9.

Friedman, M., Pierce, S. E., Coates, M. I. & Giles, S. 2019. Feeding structures in the ray-finned fish *Eurynotus crenatus* (Actinopterygii: Eurynotiformes): implications for trophic diversification among Carboniferous actinopterygians. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **109**, 33–47.

Green, O. R. 2001. *A Manual of Practical Laboratory and Field Techniques in Palaeobiology.* Berlin: Springer-Science. p. 552.

Hara, U., Słowakiewicz, M. & Raczyński, P. 2013. Bryozoans (trepostomes and fenestellids) in the Zechstein Lime stone (Wuchiapingian) of the North Sudetic Basin (SW Poland): palaeoecological implications. *Geological Quarterly* **57**, 417–432.

Hay, O. P. 1902. Bibliography and catalogue of the fossil vertebrata of North America. *Bulletin of the United States Geological Survey* **179**, 1–868.

Huxley, T. H. 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. *Proceedings of the Zoological Society of London* **43**, 649–62.

Ivanov, A. 2005. Early Permian chondrichthyans of the middle and south Urals. *Revista Brasileira de Paleontologia* **8**, 127–38.

Ivanov, A. O., Bakaev, A. S., Nestell, M. K. & Nestell, G. P. 2021. Fish microremains from the Cutoff Formation (Roadian, Middle Permian) of the Guadalupe Mountains, West Texas, USA. *Micropaleontology* **67**, 365–40.

Ivanov, A. O. & Lebedev, O. A. 2014. Permian chondrichthyans of the Kanin Peninsula, Russia. *Paleontological Journal* **48**, 1030–43.

Jeppsson, L., Anehus, R. & Fredholm, D. 1999. The optimal acetate buffered acetic acid technique for extracting phosphatic fossils. *Journal of Paleontology* **73**, 964–72.

Kaczawskie Association 2019. *Poznaj moc Ziemi Przewodnik po Geoparku Krainy Wygasłych Wulkanów w 30 geopunktach* [Meet the Earth's Power. A guide to the Geopark of the Land of extinct volcanoes in 30 geopoints]. *Printed with EU subsidy.* Poland: Kaczawskie Association. [In Polish.]

King, W. 1850. *The Permian fossils of England*. London, UK: Monograph of the Palaeontographical Society. pp. 1–253.

Koot, M. B. 2013. *Effects of the Late Permian mass extinction on chondrichthyan palaeobiodiversity and distribution patterns.* PhD Dissertation, University of Plymouth, Plymouth, UK. p. 859.

Koot, M. B., Cuny, G., Tintori, A., & Twitchett, R. J. 2013. A new diverse shark fauna from the Wordian (Middle Permian) Khuff Formation in the interior Haushi–Huqf area, Sultanate of Oman. *Palaeontology* **56**, 303–343.

Koot, M. B., Gilles, C., Orchard, M. J., Richoz, S., Hart, M. B. & Twitchett, R. J. 2015. New hybodontiform and neoselachian sharks from the Lower Triassic of Oman. *Journal of Systematic Palaeontology* **13**, 891–917.

Manzanares, E., Plá, C., Ferrón, H. G. & Botella, H. 2018. Middle–Late Triassic chondrichthyans remains from the Betic Range (Spain). *Journal of Iberian Geology* **44**, 129–38.

Manzanares, E., Plá, C., Martínez-Pérez, C., Rasskin, D. & Botella, H. 2014. The enameloid microstructure of euselachian (Chondrichthyes) scales. *Paleontological Journal* **48**, 1060–6.

Martill, D. M., Del Strother, P. J. & Gallien, F. 2013. *Acanthorhachis*, a new genus of shark from the Carboniferous (Westphalian) of Yorkshire, England. *Geological Magazine* **151**, 517–33.

Maystrenko, Y., Bayer, U., Brink, H. J. & Littke, R. 2008. The central European basin system – an overview. In Littke, R., Bayer, U., Gajewski, D. & Nelskamp, S. (eds) *Dynamics of Complex Intracontinental Basins,* 16–34. Berlin, Heidelberg: Springer.

Newberry, J. S. & Worthen, A. H. 1866. Descriptions of vertebrates. *Geological Survey of Illinois* **2**, 11–141.

Nielsen, E. 1952. *On new or little known Edestidae from the Permian and Triassic of East Greenland*. København: De danske ekspeditioner til Ostgronland. p. 55.

Patterson, C. 1966. British Wealden Sharks. *Bulletin of the British Museum (Natural History)* **11**, 283–350.

Peryt, T. M., Geluk, M. C., Mathiesen, A., Paul, J., Smith, K., Doornenbal, J. C. & Stevenson, A. G. 2010. Zechstein. In Doornenbal, J. & Stevenson, A. (eds) *Petroleum geological atlas of the Southern Permian Basin area*, 123–47. Houten, The Netherlands: EAGE Publications bv Houten.

Purnell, M. A. & Darras, L. P. 2015. 3D tooth microwear texture analysis in fishes as a test of dietary hypotheses of durophagy. *Surface Topography: Metrology and Properties* **4**, 014006.

Raczyński, P. 1997. Depositional conditions and paleoenvironments of the Zechstein deposits in the North Sudetic Basin, SW Poland. *Przegląd Geologiczny* **45**, 693–9 [In Polish with English summary.]

Raczyński, P. & Biernacka, J. 2014. Zechstein in Lithuanian–Latvian Border Region. *Geologija (Vilnius)* **56**, 57–62.

Romano, C., Koot, M. B., Kogan, I., Brayard, A., Minikh, A. V., Brinkmann, W., Bucher, H. & Kriwet, J. 2016. Permian Triassic Osteichthyes (bony fishes): diversity dynamics and body size evolution. *Biological Reviews* **91**, 106–47.

Sallan, L. C. & Coates, M. I. 2013. Styracopterid (Actinopterygii) ontogeny and the multiple origins of post-Hangenberg deep-bodied fishes. *Zoological Journal of the Linnean Society* **169**, 156–99.

Scupin, H. 1931. Die Nordsudetische Dyas. Eine stratigraphisch-paläogeographische Untersuchung [The North Sudetic Dyas. A stratigraphic–palaeogeographical study]. *Fortschritte der Geologie und Paläontologie* **27**, 123–234. [In German.]

Serkies, J. I., Oberc, J. & Idzikowski, A. 1967. Deposits in Southwest Poland as exemplified by the studies of the Zechstein of the Leszczyna Syncline. *Chemical Geology* **2**, 217–32.

Štamberg, S. 2016. Actinopterygians of the Stephanian sediments of the Krkonoše Piedmont Basin (Bohemian Massif) and their palaeobiogeographic relationship. *Bulletin of Geosciences* **91**, 169–86.

Swift, A. 1986. The conodont *Merrillina divergens* (Bender & Stoppel) from the Upper Permian of England. In Harwood, G. M. & Smith, D. B. (eds) *The English Zechstein and Related Topics. Geological Society Special Publication No. 22*, 55–62. London: The Geological Society of London.

Szaniawski, H. 1969. Conodonts of the upper Permian of Poland. *Acta Palaeontologica Polonica* **14**, 325–37.

Van Wees, J. D., Stephenson, R. A., Ziegler, P. A., Bayer, U., McCann, T., Dadlez, R., Gaupp, R., Narkiewicz, M., Bitzer, F. & Scheck, M. 2000. On the origin of the southern Permian Basin, Central Europe. *Marine and Petroleum Geology* **17**, 43–59.

Vázquez, P. & Clapham, M. E. 2017. Extinction selectivity among marine fishes during multistressor global change in the end-Permian and end-Triassic crises. *Geology* **45**, 395–8.

Weissflog, L., Elansky, N. F., Kotte, K., Keppler, F., Pfennigsdorff, A., Lange, C. A., Putz, E. & Lisitsyna, L. V. 2008. Late Permian changes in conditions of the atmosphere and environments caused by halogenated gases. *Doklady. Earth Sciences* **425**, 291–5.

Woszczynska, S. 1987. Foraminifera and ostracods from the carbonate sediments of the Polish Zechstein. *Acta Palaeontologica Polonica* **32**, 115–205.

Zidek, J. 1992. Late Pennsylvanian Chondrichthyes, Acanthodii, and deep-bodied Actinopterygii from the Kinney Quarry, Manzanita Mountains, New Mexico. *New Mexico Bureau of Mines and Minerals Resources Bulletin* **138**, 145–82.

MS received 26 April 2022. Accepted for publication 2 February 2023. First published online 23 February 2023