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A first record of late Middle Permian actinopterygian fish from Anatolia, Turkey

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ABSTRACT:

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The Middle–Upper Permian of the Gomaniibrik Formation, of the Tanin Group, in south-east Anatolia, close to the Iraq border, yielded moderately preserved fish remains. Two species, *Palaeoniscum freieslebeni* and *Pygopterus* cf. *nielseni*, known so far only from the Upper Permian deposits of the Zechstein Basin in western Central Europe, were recognised. This late Middle Permian Anatolian record significantly widens the geographical range of these actinopterygians into the equatorial Palaeotethys Realm.

Keywords: Actinopterygians; late Middle Permian; SE Turkey; Palaeotethys.

INTRODUCTION

Fossils have proved to be useful tools in solving problems related to long distance correlation of rock sequences and depositional environments. Fossil fishes have been increasingly used for geological and biostratigraphic correlation in western and central Europe (e.g. Poplin and Lund 2002), which in turn may offer valuable constraints on palaeogeographic interpretations. Of specific interest are the palaeonisciform fishes, described originally from the Late Permian Zechstein Basin in Germany, eastern England and Greenland (e.g. Schaumberg 1977). In the mid-1950s, Permian deposits were discovered in south-east Turkey, north of the Arabian Peninsula (Text-fig. 1A), in Hakkari-Cukurca (Altınlı 1954), near Diyarbakır-Hazro (Kellog 1960), and in Sırnak-Harbol in the Cudi Mountains (Schmidt 1964). Because of the oil prospects in these areas, Permian deposits were studied in considerable detail, with their biostratigraphy based on foraminifers (e.g. Köylüoğlu and Altıner 1989) and palynology (e.g Yahsiman and Ergönül 1959; Stolle 2007). Recently, the senior author carried out detailed stratigraphical work on the Late Palaeozoic successions (Gourvennec and Hoşgör 2012; Hosgör *et al*. 2012; Daneyer and Hoşgör 2014) in the Hakkari-Cukurca area and came across some fish remains in the Permian Tanin Group. Only Devonian–Carboniferous fish remains (actinopterygians, placoderms and lungfish) were reported hitherto (Janvier *et al*. 1984) from south-east Anatolia. Actinopterygian remains are very abundant as isolated bones and scales in the Upper Devonian and Lower Carboniferous sediments (Janvier *et al*. 1984). The only dermal bones of the snout from the Lower Carboniferous are classified as the genus *Canobius*, and a maxilla with dentition belongs to the Amblypteridae. Abundant isolated scales and dermal bones of various types cannot be referred to any particular taxon, but suggest the presence of more numerous taxa of actinopterygians (Janvier *et al*. 1984). Moreover, they are so far the first finds from the eastern Mediterranean area.

The focus of this study is the taxonomic analysis of actinopterygian fishes discovered in the lower part of the Gomaniibrik Formation of south-eastern Turkey and their constraints on the Middle–Late Permian palaeogeography.

GEOLOGICAL SETTING

The Southeast Anatolian Autochthon, south-east Turkey, represents the northern edge of the Arabian Plate and contains more or less continuous Palaeozoic successions (e.g. Göncüoğlu *et al*. 1997). The stratigraphy and structure of the Palaeozoic rocks have been studied in detail along measured sections in the Hazro, Harbol and Hakkari-Cukurca areas as well as in a number of borehole cores (e.g. Yılmaz and Duran 1997) (Text-fig. 1A). Overall, the Lower Palaeozoic of south-east Anatolia is characterized by Cambrian to Silurian siliciclastic rocks with carbonates in the Devonian (e.g. Bozdoğan *et al*. 1996; Göncüoğlu and Kozlu 2000). The Carboniferous is composed mainly of limestones. The Permian deposits rest unconformably on the Carboniferous and are referred to the Tanin Group (Perincek 1990). The group is divided into the Kas Formation (Bozdoğan *et al*. 1987; Bozdoğan and Ertuğ 1997) and the Gomaniibrik Formation (Schmidt 1964). In the west, in the Hazro area, the Kas Formation is siliciclastic, consisting of an alternation of sandstone, organic material-rich shales and marls (Text-fig. 1). Numerous coal layers intercalated with coaly silt- and mudstones characterize the Kas Formation in south-east Anatolia. Based on the spore-pollen assemblages it is suggested that the Kas Formation is of Wordian age (Stolle 2007).

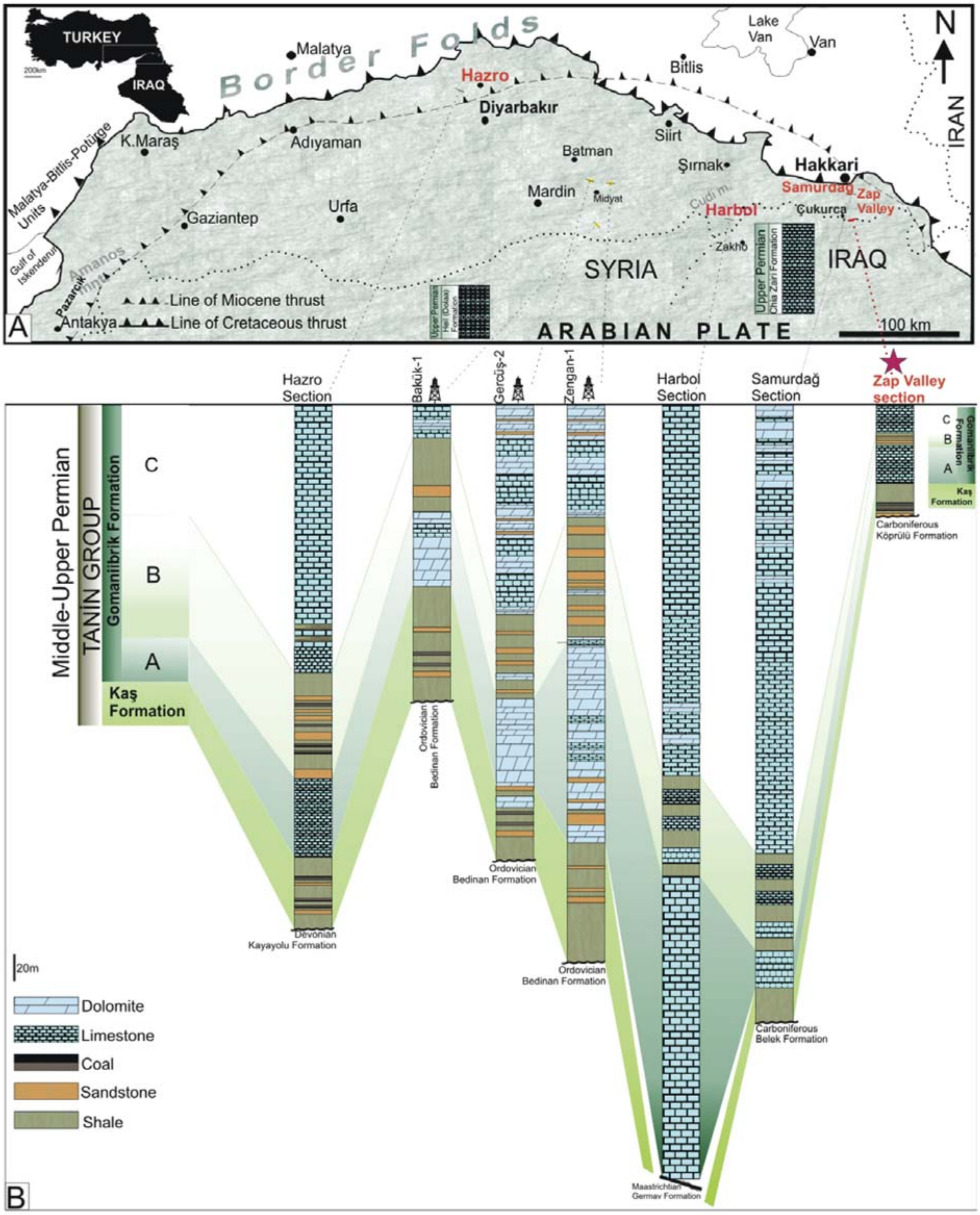
In the Hazro area, the conformably overlying Gomaniibrik Formation comprises three informal members; A, B and C (Text-fig. 1 B). Members A and C are composed of carbonates, whereas member B is made up of siltstones and sandstones with a few coal layers (Yılmaz and Duran 1997), and is similar to the underlying Kas Formation. Towards the east, Permian platform-type carbonate-dominated successions crop out within the Harbol and Cukurca anticlines (Text-fig. 1B). In the Cukurca Anticline, Schmidt (1964) used the name Harbol Limestone (=Gomaniibrik Formation) for the predominantly carbonate rocks with subordinate siliciclastics. Farther to the east, in the Cukurca Anticline (Text-fig. 1B and 2), the Permian unconformably overlies the Carboniferous limestones.

Based on palynomorphs, the Gomaniibrik Formation was previously assigned to the Upper Permian (Tatarian) (Bozdoğan *et al*. 1987). Detailed biostratigraphic study of this formation in the Hakkari area (Köylüoglu and Altıner 1989) allowed the identification of four zones based on foraminiferal taxa (Fusulinina and Miliolina) and a wide range of Late Permian (Murgabhian to Dorashamian) ages was assigned to the formation in the sense of the former twofold classification of the Permian period. Stolle (2007) reviewed the age of the Gomaniibrik Formation. Supported by new palynological data, he assigned the lower and middle parts of the formation to the late Middle Permian (Capitanian), and suggested that its upper part reached up to the Changhsingian. The sedimentological features of the formation together with its fossil content suggest shallow marine conditions (Bozdoğan and Ertuğ 1997).

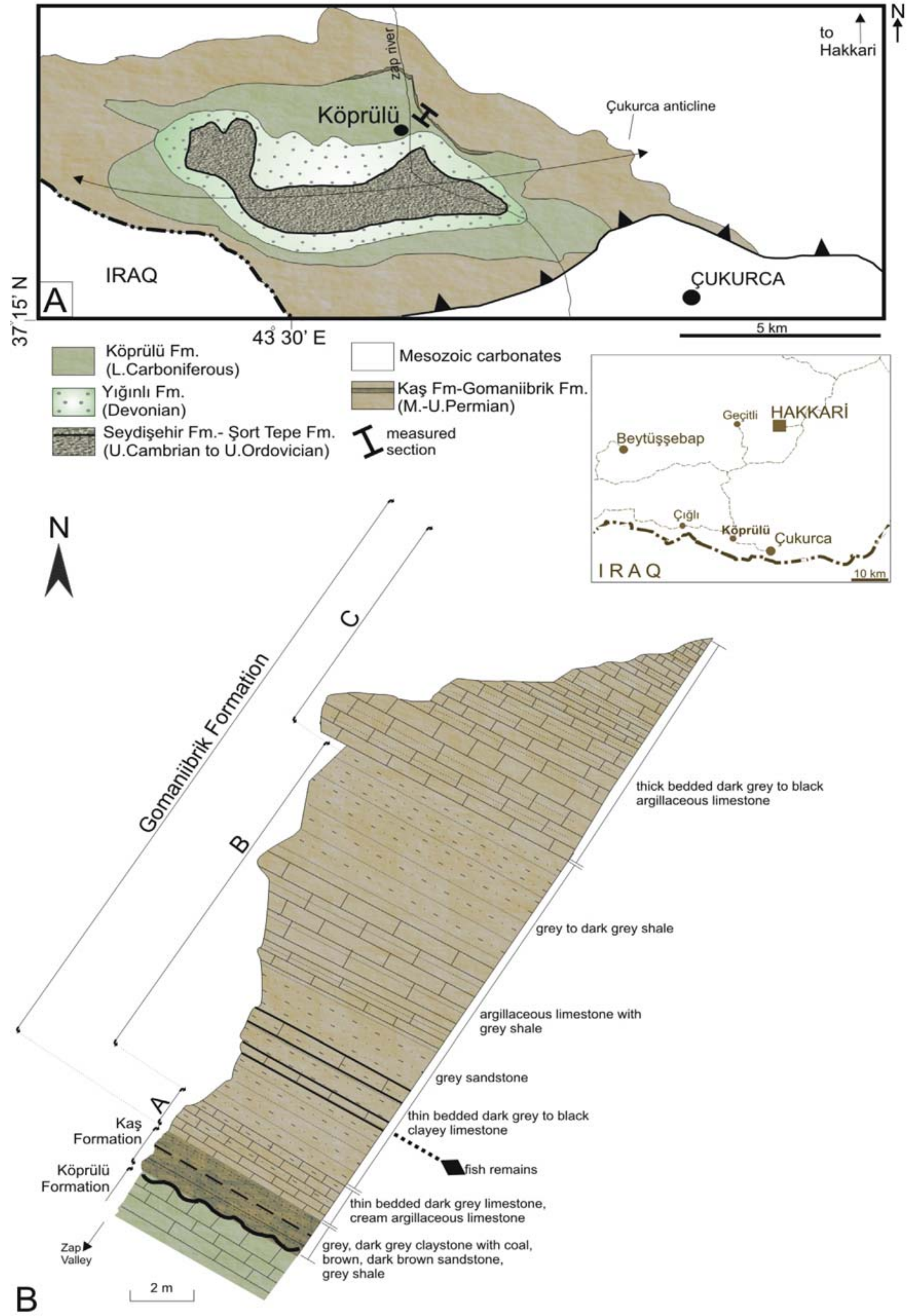
Towards the south in northern Syria and Iraq, Upper Permian sequences corresponding to the Tanin Group in south-eastern Anatolia are shown on Text-fig. 1A, B. The lithostratigaphic and palaeontological correlations between the Gomaniibrik Formation and the upper part of the Chia Zairi Formation in northern Iraq and Heil (Dolaa) Formation in north-east Syria are almost perfect (Schmidt 1964; Ala and Moss 1979; Koehrer *et al*. 2010).

STRATIGRAPHY OF THE FOSSIL LOCATION AND AGE

Several Palaeozoic sections in the Cukurca Anticline were systematically sampled in 2009 and 2010 for geological and palaeontological investigations by the senior author (Gourvennec and Hoşgör 2012; Hoşgör *et al*. 2012; Daneyer and Hoşgör 2014). The measured section of the Gomaniibrik Formation is located south-east of the village of Köprülü in the Zap Valley, 5 km north-west of Cukurca (Text-fig. 2A). In the lower part of this section in the Zap Valley, a thick succession of Cambro-Ordovician siliciclastic rocks (Seydişehir and Şort Tepe formations) crops out. They are unconformably overlain by the siliciclastics of the Devonian Yiginli Formation, which terminates with dolomites. The overlying Upper Devonian–Lower Carboniferous Köprülü Formation is represented in its lower part by a fining-upwards clastic sequence that grades upwards into a thick package of shallow-marine limestones (Text-fig. 2B). In the previous studies (Köylüoğlu 1982) the name Harbol Limestone was applied to the bulk of the unconformably overlying Permian rocks. To avoid confusion, the regional lithostratigraphic name, Tanin Group, will be used for the Middle–Upper Permian rocks in this area. In its lower part, the Tanin Group comprises a thin succession of



Text-fig. 1. **A** – Location map of the study area. **B** – The Middle–Upper Permian lithostratigraphic columns of the northern margin of the Arabian plate (Kellog 1960; Schmidt 1964; Ala and Moss 1979; Köylüoglu and Altıner 1989; Gümüş *et al*. 1992; Tekinli and Eseller 1992; Yılmaz and Duran 1997)



Text-fig. 2. **A** – Geological map of the Cukurca Anticline in the Zap Valley with the location of the measured section (Janvier *et al*. 1984; Gourvennec and Hoşgör 2012; Hosgör *et al.* 2012). **B** – The lithostratigraphy of the studied columnar section with the position of the fish remains conglomeratic sandstones, which is known as the Kas Formation in the Cukurca area (e.g. Köylüoğlu and Altıner 1989). In the studied section, the main body of the formation is represented by an alternation of dark brown sandstones and organic-rich dark grey shales with thin coal layers. Towards the top dark grey claystones dominate. The Kas Formation is conformably overlain by a dark grey, thin-bedded limestone interspersed with cream coloured argillaceous limestone. This first limestone package is referred to Member A of the Gomaniibrik Formation. The conformably overlying Member B starts with grey sandstones and siltstones and includes two ca 5–10 cm-thick layers of thin-bedded dark grey to black clayey limestone, c. 3 m above its base (Text-fig. 2B). These layers are under- and overlain by thin (1–2 cm) carbonaceous black shales, in which the fish remains were discovered. The higher limestone interval within the grey to dark grey siliciclastics in the middle part of Member B is represented by argillaceous dark grey limestones and marls with grey shale interlayers. The upper part of the member is again composed of grey to dark grey shales. Member C is represented by a thick package of thick-bedded, dark grey to black limestones that form the steep cliffs in the Zap Valley.

Member B of the Gomaniibrik Formation is included in the "unite biostratigraphique II", which is described as the "Zone á Chusenella" in the detailed foraminiferal studies by Köylüoğlu and Altiner (1989) and dated as Midian. The fish remains are in the lower third of the formation and can be dated as early to middle Midian, corresponding mainly to the Capitanian, in the new threefold classification. This age assignment is confirmed by Stolle (2007).

SYSTEMATIC PALAEONTOLOGY

Subclass Actinopterygii Cope, 1887
Family Palaeoniscidae Vogt, 1852
Genus *Palaeoniscum* Blainville, 1818

Palaeoniscum freieslebeni Blainville, 1818
(Text-figs 3–5)

REMARKS: Species characters are based on Agassiz (1833), Aldinger (1937), Westoll (1934) and Hauboldt and Schaumberg (1985).

EMENDED DIAGNOSIS AS COMBINATION OF CHARACTERS: The parietals of square shape. The frontals large, posteriorly narrower than anteriorly. Distinct lateral process in the middle of the frontal length. Interfrontal suture curved. Small epitemporal between the dermosphenotic and infraorbital. The opercular large, twice as high as long. Antopercular missing. The subopercular markedly lower anteriorly than posteriorly. The branchiostegal rays number approximately ten or eleven. Only one series of small teeth on the maxillary. Dentary bears a large number of teeth of two sizes but without specially prominent laniaries. Lepidotrichia of the pectoral fin are segmented from their base. One or more large scales in front of the base of the dorsal fin. The scales are ornamented in the anterior area of their surface with short grooves parallel to the ventral border of the scales, the central area of their surface bears small holes, and the scales are posteriorly denticulated. There are 68–70 transverse rows between the supracleithrum and the caudal fin.

MATERIAL: Single specimen MTA-TTM 2014-744 deposited in the General Directorate of Mineral Research and Exploration-Natural History Museum, Ankara,Turkey.

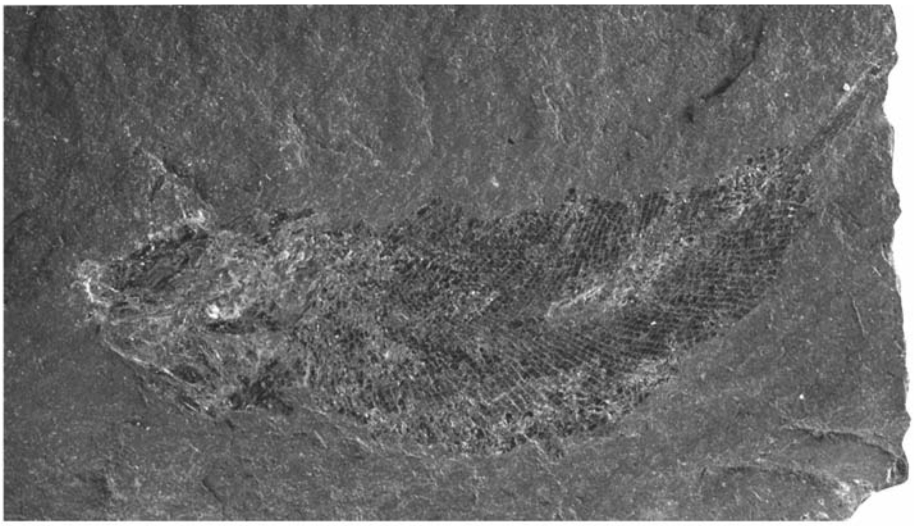
SOURCE HORIZON: Gomaniibrik Formation (late Middle Permian)

SOURCE LOCALITY: Zap Valley, near Hakkari.

DESCRIPTION: The studied specimen is considerably deformed and compressed dorsoventrally. It represents partially preserved skull roof bones and cheek bones, including fragments of the jaws and bones of the opercular apparatus. The trunk exposes the scales including their sculpture, ridge scales in front of the dorsal fin, and the ridge scales covering the caudal peduncle. Paired and unpaired fins are missing apart from the piece of the dorsal lobe of the caudal fin. Total length of the whole specimen is 120 mm (Text-fig. 3).

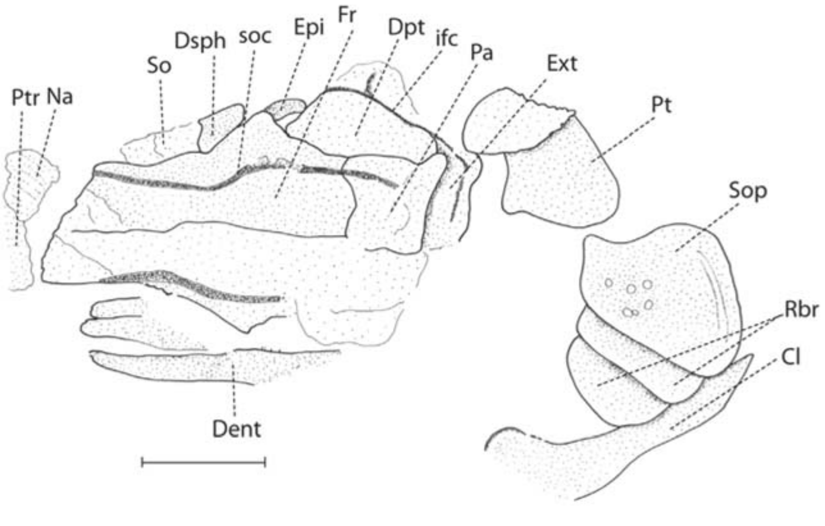
The skull roof (Text-fig. 4) comprises paired frontal, parietal, dermosphenotic, dermopterotic, epitemporal and extrascapulars. The frontal is very narrow and long, with a length/width ratio of 2.9, and it narrows anteriorly. The interfrontal suture is nearly straight, not undulating. The lateral margin of the frontal forms a process in the posterior third of the length of the bone. The supraorbital sensory canal continues anteroposteriorly from the anterior margin of the frontal, and it passes to the parietal posteriorly. The supraorbital sensory canal is not straight, but follows a curved course near the lateral margin on both the right and left bones. The parietal is a relatively small, square-shaped bone, with its length being one third of the frontal length. The supraorbital sensory canal is conspicuous in the anterior third of the bone, but the pit lines cannot be seen. The dermosphenotic is a very small anteroposteriorly elongated bone bordering the frontal laterally. It lies anteriorly from the lateral process of the frontal.

In contrast, the dermopterotic is a large bone elongated anteroposteriorly bordering the parietal and posterior part of the frontal. The dermopterotic narrows anteriorly, and it forms a small process following the lateral margin of the frontal. A very small bone, the epitemporal (see Aldinger 1937), squeezes in the space between the lateral process of the frontal, the dermosphenotic anteriorly and the dermopterotic posteriorly. Extrascapular bones occupy the area posterior to the parietal, but the number of these bones cannot be determined. The infraorbital sensory canal passes along the lateral margin of the dermopterotic, traverses to the extrascapulars, and it is connected with the supratemporal commissure. Traces of the interconnection of the infraorbital and preopercular canals can be observed in the anterior third of the lateral margin of the dermopterotic.



Text-fig. 3. *Palaeoniscum freieslebeni* Blainville, 1818. Zap Valley, SE Turkey. MTA-TTM 2014-744; × 0.9

The cheek bones are vague, without distinct outlines. Only the preopercular, with a long and slightly elevated anterior part and a narrow ventroposterior part, is preserved. Conspicuous inclination of the preopercular anteriorly is an outstanding feature. The posterior margin of the anterior and ventroposterior parts forms a 140 degree angle. The preopercular canal follows near the dorsal and posterior margins of the bone, and is curved in the same angle as the preopercular. The same angle of the preopercular is seen in the reconstruction of *P. freieslebeni* of Westoll (1934), published by Aldinger (1937, fig. 25B). The same or nearly the same angle of the bend of the preopercular has also been described in other Permo-Carboniferous actinopterygians.

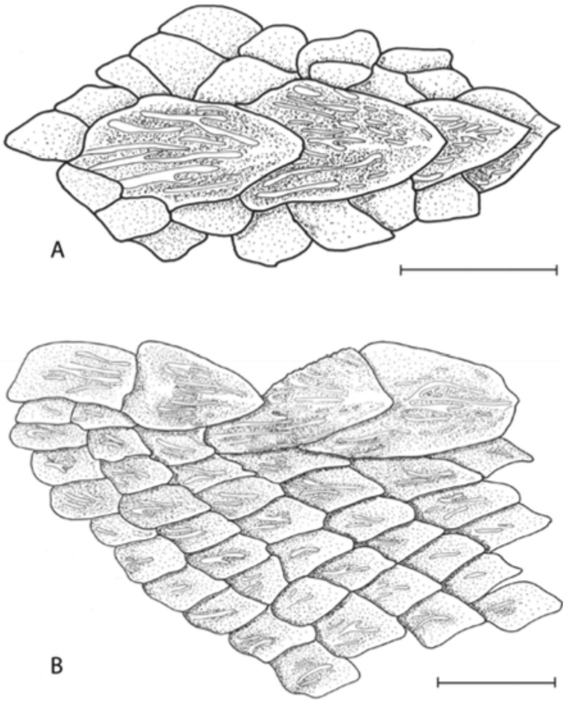


Text-fig. 4. *Palaeoniscum freieslebeni* Blainville, 1818. Interpretive drawing of the skull roof in dorsal view, fragments of the jaw and the bones of the opercular apparatus. MTA-TTM 2014-744. Scale bar represents 5 mm. Dpt – dermopterotic; Dsph – dermosphenotic; Epi – epitemporal; Ext – extrascapular; Fr – frontal; Dent – lower jaw; ifc – infraorbital sensory canal; Na – nasal; Pa – parietal; Pt – posttemporal; Ptr – postrostral; Rbr – branchiostegal rays; Scl – supracleithrum; So – supraorbital; soc – supraorbital sensory canal; Sop – subopercular

The jaws are somewhat crushed, but the large posterior plate of the anterioposteriorly elongate maxillary is obvious. The lower jaw is weak with partly preserved small, slender and sharply pointed teeth.

A clearly identifiable subopercular and two branchiostegal rays are preserved from the dermal bones of the opercular apparatus (Text-fig. 4). The opercular and remaining branchiostegal rays are not preserved. The square-shaped subopercular is twice as low anteriorly as posteriorly, and it exhibits a small process dorsoanteriorly. The subopercular has a concave dorsal margin and convex ventral and posterior margins. The sculpture on the bone is restricted to several inconspicuous flat tubercles. Two branchiostegal rays ventrally from the subopercular are incompletely preserved.

Squamation is present nearly throughout the considerably deformed trunk. The scales are small with peg and socket articulation. They are denticulated posteriorly, but the denticulation is only poorly preserved. The surface of the scales is ornamented with one or more ridges which pass anteroposteriorly across the scale (Text-fig. 5B). These ridges branch in a few cases but are usually simple. Anteriorly located scales bear four or five ridges, the number of ridges decreases posteriorly to one up to three. The scales are relatively small and numerous. There are 33 scale rows from the head to the beginning of the dorsal fin, and 53 scale rows from the head to the first ridge scale covering the caudal peduncle. There were probably more scale rows before the deformation of the specimen. There are four large ridge scales in front of the dorsal fin (Text-fig. 5A). Conspicuous parallel anterioposterior ridges form the sculpture on these ridge scales and also on the ridge scales covering the caudal peduncle (Text-fig. 5B).



Text-fig. 5. *Palaeoniscum freieslebeni* Blainville, 1818. MTA-TTM 2014-744. A – Drawing of ridge scales from the beginning of the dorsal fin. Scale bar represents 2 mm. B – Drawing of scales and ridge scales from the beginning of the caudal peduncle. Scale bar represents 2 mm

DISCUSSION: The configuration of the skull roof bones is characteristic of *Palaeoniscum freieslebeni* as presented by Westoll (1934) and Aldinger (1937). The relationship and shape of the frontal, dermopterotic, dermosphenotic and the presence of the small epitemporal are especially important. In contrast to the reconstructions in Westoll (1934) and Aldinger (1937), the interfrontal suture in the studied specimen is nearly straight. Nevertheless Aldinger (1937) described a not undulating, but only slightly curved interfrontal suture in *P. freieslebeni* from Greenland. Interconnection of the infraorbital and preopercular canal is also observable. Such a connection as present in *P. freieslebeni* was described Poplin and Véran (1996) in *Coccocephalus wildi* Watson, 1925, by Lund and Poplin (1997) in *Wendichthys dicksoni* Lund and Poplin, 1997 and by Nielsen (1942) in the Triassic *Boreosomus piveteaui* Nielsen, 1942. However the direct interconnection of the infraorbital and preopercular canals is not usually observable in the bones of the Permo-Carboniferous actinopterygians (Gardiner 1963, 1984; Poplin and Lund 2002; Schindler 1993, etc.).

The lower jaw of the studied specimen bears small, slender and sharply pointed teeth only. Large laniary teeth, which are known for example in *Pygopterus nielseni* Aldinger, 1937, *Rhabdolepis macropterus* (Bronn, 1829) see Gardiner (1963), *Progyrolepis heyleri* Poplin, 1999, *Letovichthys tuberculatus* Štamberg, 2007 and some other taxa, are not developed.

The subopercular of our specimen is in shape very close to the subopercular of *P. freieslebeni* of Westoll (1934) figured by Aldinger (1937, fig. 25B), but differs from that of *P. freieslebeni* from Greenland figured by Aldinger (1937, fig. 26). The shape of the suboperculars of some other actinopterygians (e.g. *Pygopterus nielseni* Aldinger 1937; *Zaborichthys fragmentalis* Štamberg 1991; *Coccocephalus wildi* Watson, 1925 – see Poplin and Véran 1996; *Mesonichthys aitkeni* (Traquair 1886) – see Gardiner 1963) partly conforms to the subopercular of our specimen. The operculars are mostly lower anteriorly than posteriorly, with a process dorsoanteriorly, however they are usually not convex but concave ventrally, and they have a smaller or larger process ventroanteriorly. *Pygopterus nielseni,* according to the reconstruction of Aldinger (1937, fig. 39), possesses a similar type of subopercular, but it is relatively high anteriorly. The subopercular of *Mesonichthys aitkeni* (see Gardiner 1963) and the incompletely preserved subopercular of *Coccocephalus wildi* (see Poplin and Véran 1996), are more consistent with our specimen.

The size of the scales and the number of scale rows is similar to those described by Traquair (1877, pl. 1, fig. 1) in *P. freieslebeni* from the Zechstein of Germany and by Aldinger (1937, fig. 26) in the same species from Greenland. Both authors indicate a greater number of scale rows (40 between the head and the beginning of the dorsal fin, 68–70 between the head and the beginning of the caudal fin). This difference may have been caused by the deformation of our specimen. It is obvious that our specimen entirely differs in this respect from *Pygopterus nielseni* as described by Aldinger (1937, fig. 37), which has very small scales, and 135 scale rows between the head and the beginning of the caudal fin.

A summary of the results of the study of the preserved features of our specimen, and comparison with the diagnosis, indicate an assignment to *Palaeoniscum freieslebeni* Blainville, 1818, this assignment being supported by the following characters: (1) Formation of the skull roof; (2) Shape of the frontal; (3) Presence of the epitemporal; (4) Shape of the subopercular; (5) Type of dentition on the lower jaw; (6) Shape of the scales and their sculpture; and (7) Number of scale rows.

Family Pygopteridae Aldinger, 1937
Genus *Pygopterus* Agassiz, 1833
Pygopterus cf. *nielseni* Aldinger, 1937
(Text-figs 6–7)

REMARKS: Characters of the genus *Pygopterus* follow Aldinger (1937).

EMENDED DIAGNOSIS AS A COMBINATION OF CHARACTERS: The maxilla and dentary bear teeth in two series – inner row of well spaced large laniaries and outer row of numerous, much smaller, closely arranged teeth. The opercular is distinctly dorsoventrally elongated, more than three times higher than long with the antero-dorsal corner bevelled to admit the antopercular. The subopercular higher anteriorly than posteriorly. More than fifteen branchiostegal rays. The lepidotrichia of the pectoral fin unsegmented in the proximal third of their length. Scales are ornamented with ridges which pass diagonally across the scale. There are 135–140 transverse scale rows between the supracleithrum and the caudal fin.

MATERIAL: Single specimen MTA-TTM 2014-745 deposited in the General Directorate of Mineral Research and Exploration-Natural History Museum, Ankara,Turkey.

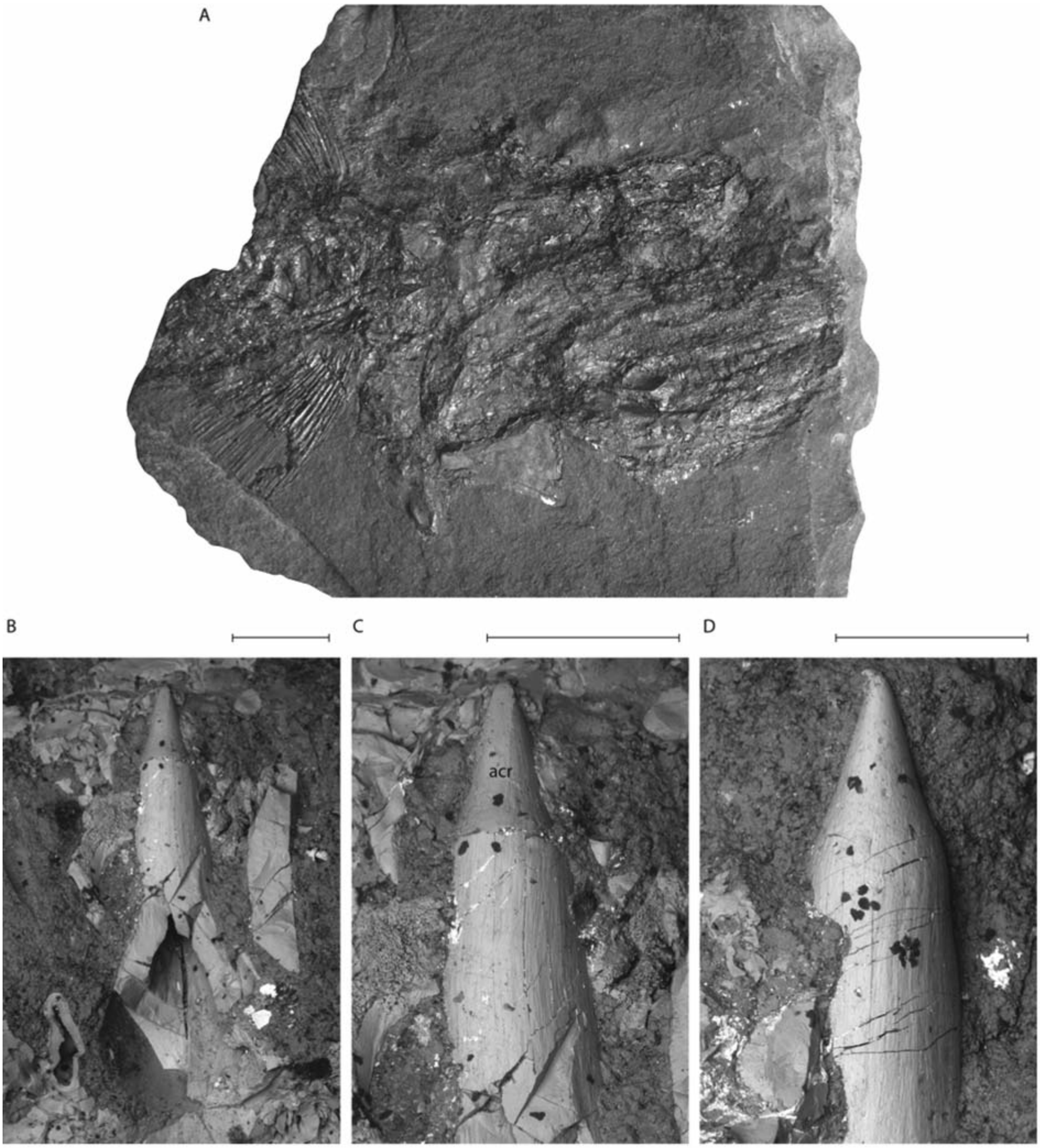
SOURCE HORIZON: Gomaniibrik Formation (late Middle Permian)

SOURCE LOCALITY: Zap Valley, near Hakkari.

DESCRIPTION: The studied specimen is represented by a crushed head and pectoral fins, and is much bigger than the other specimen treated herein (Text-fig. 6A). Total length of the actual fragment of the specimen is 128 mm, but the total length of the complete specimen probably exceeded 300 mm.

Fragments of the upper and lower jaws are preserved. The postorbital plate of the maxillary is ornamented with parallel ridges which pass obliquely downwards. The lower jaw is stout, posteriorly ornamented by oblique ridges. The dentition consists of two types of teeth in the labial and lingual rows. The teeth in the labial row are very small, not exceeding 0.5 mm. The few large laniary teeth in the lingual row are 2–2.5 mm long. Only fine striae on the periphery and acrodin cap are observable (Text-fig. 6B, C, D). The large laniary teeth are relatively slender with a wide base (Text-fig. 6B), equally tapered distally. The last 0.4 mm long section of the teeth is formed with an acrodin cap that is noticeably tapered to a cone (Text-fig. 6C, D). The same type of laniary teeth was described by Aldinger (1937, p. 153) in *Pygopterus nielseni*. A fragment of the subopercular is positioned posterior to the jaws.

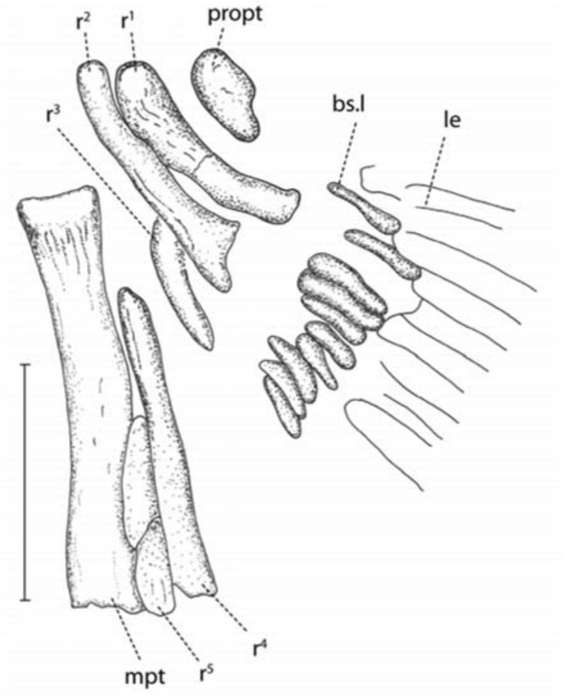
Proximal regions of the right and left pectoral fin including the endoskeleton of the right pectoral fin are preserved (Text-fig. 7). The endoskeleton of the right pectoral fin consists of a series of several ossifications arranged in one row. The first anteriorly positioned ossification is stout with a short propterygium. Subsequent ossifications, radials 1 to 3, become longer: they are stout and rod-like in shape, and are slightly bent. The long and slender radial 4 and the much smaller radial 5 are connected to the stout metapterygium. The posterior metapterygium is 12 mm long, twice as long as radial 1 and four times as long as the propterygium. The distal radials, if they exist, were not observed.



Text-fig. 6. *Pygopterus* cf. *nielseni* Aldinger, 1937. Zap Valley, SE Turkey. MTA-TTM 2014-745. A – Head and pectoral fins, × 0.9. B – Laniary tooth from the middle part of the lower jaw. Tooth is slender with wide base. Scale bar represents 0.5 mm. C – Tooth from Fig. 6B demonstrates in detail fine striae on periphery and an acrodin cap (acr) noticeably tapered to a cone. Scale bar represents 0.5 mm. D – Another laniary tooth from the posterior part of the lower jaw. Scale bar represents 0.5 mm

A row of narrow basal segments of the lepidotrichia follows distally to the radials. It is impossible to determine the exact number of the lepidotrichia because of bad preservation. The anteriorly positioned leading lepidotrichium is not segmented, and it carries on the leading edge small and numerous fringing fulcral scales. Subsequent lepidotrichia are transversely fissured in a way that is reminiscent of segmentation, but the lepidotrichia are actually proximally not segmented apart from the first proximal basal segments (Text-fig. 7).

DISCUSSION: Similar sculpture on the postorbital



Text-fig. 7. *Pygopterus* cf. *nielseni* Aldinger, 1937. Endoskeleton of the right pectoral fin in dorsal view. MTA-TTM 2014-745. Scale bar represents 5 mm. bs.l – basal segments of lepidotrichia; le – lepidotrichia; mpt – metapterygium; propt – propterygium; r $^{1-5}$ – radials

plate of the maxillary as on our specimen is described by Aldinger (1937, p. 152) on *Pygopterus nielseni*, and is also common in *Cosmoptychius*, *Nematoptychius*, etc. (see Traquair 1877, pl. 1, fig. 2, pl. 3, fig. 3). The ossifications of the pectoral fin in the specimen correspond to the base of the pectoral fin of *Mimia toombsi* Gardiner and Bartram, where the metapterygium supports three radials (Gardiner 1984, Fig. 137). A similar structure of the base of the pectoral fin as in *P.* cf. *nielseni* is possible to find in *Palaeoniscum*, or *Pteronisculus* (Jessen 1972, pl. 21, fig. 3, pl. 22, figs 1, 2).

The well preserved endoskeleton of the pectoral fin differs from that in *Cosmoptychius striatus* (Agassiz 1835) presented by Gardiner (1963, fig. 3), which has four radial elements. The formation of the endoskeleton of the pectoral fin on the aeduellid fish *Neslovicella rzehaki* Štamberg, 2007 is also quite distinct: the posteriorly placed radials are the shortest, while the stoutest and longest radials are found anteriorly or in the middle of the row (Štamberg 2007, fig. 26). Movement of the pectoral fin dorsally to the lateral position and changing its orientation in aeduellid fishes is certainly the fundamental reason for the difference between the radial endoskeleton of the pectoral fin of the palaeoniscid and aeduellid fishes.

The two actinopterygian specimens described herein show significant differences. They differ not only in size but mainly in the type of dentition. It is obvious that in possessing large laniary teeth the second specimen belongs not to *Palaeoniscum freieslebeni* but to another taxon. The dentition, with two types of teeth and laniary teeth with a conspicuously tapered apical portion, is reminiscent of the genus *Pygopterus* Agassiz 1833. The determination of the above-described specimen is open to question in the absence of several key features and is based on a combination of characters mentioned in the diagnosis such as the unsegmented proximal portion of the lepidotrichia of the pectoral fin and the shape of the laniary teeth.

An assignment to *Pygopterus* was determined mainly on the following characters:

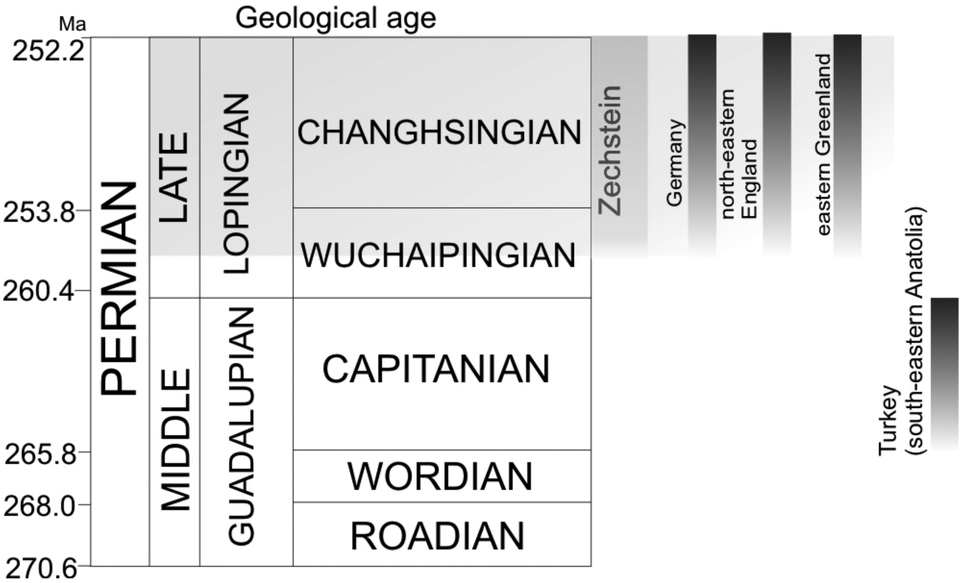
Two rows of teeth with slender laniary teeth in the inner row, with an acrodin cap noticeably tapered to a cone.

Lepidotrichia of the pectoral fin are not segmented in their proximal part.

In view of the occurrence of the genus *Pygopterus* in the sediments together with *Palaeoniscum freieslebeni,* we can expect the species *Pygopterus nielseni* Aldinger, 1937 to be present. The features enumerated above do not enable a positive determination but are sufficient to allow an open nomenclature assignment of the specimen under discussion to *Pygopterus* cf. *nielseni*.

DISCUSSION AND CONCLUSIONS

The taxonomic study of the two newly discovered actinopterygian specimens indicate the occurrence of *Palaeoniscum freieslebeni* and *Pygopterus* cf. *nielseni* in the upper Middle Permian strata of the Cukurca Anticline, in present day south-east Turkey. Both *Palaeoniscum freieslebeni* and *Pygopterus nielseni* are long known from localities in Germany, north-eastern England and eastern Greenland (Text-fig. 8), and they belong to the marine fauna of the Late Permian Zechstein Sea. It is suggested that the Zechstein Sea invaded from the north (Vaughan *et al.* 1989) onto the territory of what is now eastern Greenland, the North Sea, north-eastern England, the Netherlands, Germany, Poland and Lithuania. This marine transgression invaded an area that had been for a very long time dry land with arid and semiarid conditions (Vaughan *et al.* 1989). The transgression was very rapid, and a period of only ten years is proposed from the commencement of the Zechstein transgression until its greatest extension (Glennie and Buller 1983;



Text-fig. 8. The Middle-Late Permian chronostratigraphy with stratigraphic ranges and geographic distribution of the *Palaeoniscum freieslebeni* Blainville, 1818 and *Pygopterus* cf. *nielseni* Aldinger, 1937 (Traquair 1877; Aldinger 1937; Ogg *et al*. 2008 and this study)

Vaughan *et al.* 1989). In the Cukurca Anticline, the fossiliferous layers are in the lower third of Member B of the Gomaniibrik Formation, which is Late Guadalupian (Capitanian) in age. The age of the Capitanian is 265–260 Ma according to the GSSP Table of the International Commission on Stratigraphy and Ogg *et al* (2008). On this basis, the actinopterygian finds from the Cukurca Anticline are older than the Late Permian finds from the European Zechstein Basin and may suggest a later migration from the Palaeotethys to the Zechstein Sea.

Plate tectonic reconstructions (e.g. Gaetani *et al.* 2000; Ziegler *et al*. 1979; Şengör and Atayman 2009) suggest that during the Middle and Late Permian what is today south-east Turkey was located on the southern margin of the Palaeotethys, where a rift system related to the opening of the Bitlis-Zagros branch of the Neotethys between the Gondwanan Arabian Peninsula and the Anatolian-Persian microcontinent commenced (Göncüoğlu *et al*. 1997). The presence of *Palaeoniscum freieslebeni* and *Pygopterus* cf. *nielseni* in the upper Middle Permian marine sediments of the Cukurca Anticline in south-east Turkey documents the migration of these taxa for several thousands of kilometres and a considerable expansion of the environment suitable for their life.

The migration of the actinopterygians through these troughs may have been also controlled by the repeated sea-level changes during the late Middle Permian, evidenced by the transgressions onto the Arabian Peninsula and southern Anatolia (e.g. Leven 1993; Altıner 1999; Vachard *et al*. 2002). In either case, these newly discovered actinopterygian-bearing deposits have provided important new information on the diversity of the group, and demonstrate the potential of new fossil localities.

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