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A NEW GENUS AND SPECIES OF BASAL ACTINOPTERYGIAN FISH (OSTEICHTHYES) FROM THE PERMIAN OF EUROPEAN RUSSIA

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Abstract. A new basal ray-finned fish, *Karabalyk esini* gen. et sp. nov., is described based on the occurrence of two incomplete skeletons from Kargaly copper mines (Orenburg Region, Russia; Urzhumian (=Wordian) Stage). Additionally, varieties of isolated scales from the Urzhumian (=Wordian) and Severodvinian (=Capitanian) deposits are referred to *K. esini* on the basis of comparisons with the articulated specimens. *Uranichthys pretoriensis* Minich 2009 was described in a succinct description on a single poorly-preserved specimen from Urzhumian (=Wordian) deposits of the same Orenburg Region. *U. pretoriensis* is considered a *nomen dubium* due to the extremely poor preservation of the holotype (systematically important features absent). Most of *U. pretoriensis* specimens can confidently be assigned to *K. esini* gen. et sp. nov.

Introduction

E.I. Eichwald was one of the first scientists who, in the 19th century, studied Permian fishes in the Russian Empire (Esin 1991; Bakae 2022). He gathered an extensive collection from copper mines that exploited the copper sandstones of the Urals (Fig. 1A) and described several new fish genera and species. However, some specimens have never been identified and described. Part of E.I. Eichwald's collection is housed in the St. Petersburg Mining Museum (SPMM). During a survey of the museum collection, the first author discovered an incomplete fish skeleton (Bx-XIII-245) from the Kargaly copper mines (Urzhumian (=Wordian) Stage) without identification, which had not been previously mentioned in any source.

In addition, during examination of the storage facilities in the Borissiak Paleontological Institu-

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te, Russian Academy of Sciences (PIN), the first author found the specimen V 268/17, which belongs to the RAS Vernadsky State Geological Museum, Russian Academy of Sciences (GGM). Earlier, we reported that it was not possible to locate in the GGM collection (Esin & Bakaev 2022). The specimen V 268/17 has been returned to the owner, in the GGM collection. This is a large fragment of a fish trunk, also coming from the Kargaly copper mines (Esin 1995). Specimens SPMM Bx-XIII-245 and GGM V 268/17 are identical in the morphological features of the scale cover. Based on GGM V 268/17, Esin (1995) described a new species of *Paramblypterus* (*P. kucenkoi* Esin) in his unpublished Ph.D thesis. However, a description of this species has not been published elsewhere, and in accordance with Articles 8.1.3.1, 9.12 of the fourth edition of the International Code of Zoological Nomenclature (International … 1999), a PhD thesis is not considered to be a published work. Thus, *P. kucenkoi* is not valid and has the status of a *nomen nudum*.

Species of *Paramblypterus* Blot, 1966, belong to the most abundant ray-finned fishes in the non-marine Upper Carboniferous and Lower Permian sedimentary basins of Central and Western Europe (Dietze 1999, 2000; Štamberg 2013, 2022). Specimens SPMM Bx-XIII-245 and GGM V 268/17 distinctly differ from all *Paramblypterus* species in the scale morphology and are therefore transferred to a new genus and species – *Karabalyk esini* gen. et sp. nov.

Scales from the same Urzhumian–Severodvinian (Wordian–Capitanian) interval similar to SPMM Bx-XIII-245 and GGM V 268/17 were previously attributed to *Uranichthys pretoriensis* A. Minich, 2009 (Minikh & Minikh 2009). The holotype of *U. pretoriensis* (Saratov State University, 104-B/3062) from the Kichkass locality (one of Kargaly copper mines) is a scale with a seriously damaged free field, broken posterior and ventral margins, anterodorsal and posteroventral corners (Minikh 2009, tab. 1, fig. 5). Because of the poor preservation state of this scale, which does not exhibit sufficiently systematically significant features characteristic of ganoid scales, we deem it inappropriate to be a holotype. Therefore, *Uranichthys pretoriensis* is considered a *nomen dubium*. Most of the scales previously identified as *Uranichthys pretoriensis* A. Minich, 2009 (Minich, & Minich 2009, tab. 23, Figs. 6–9) can be attributed to *Karabalyk esini* gen. et sp. nov.

Geological setting

Extensive Guadalupian deposits cover the eastern part of the East European Platform, from the Barents Sea in the north to the Caspian Depression in the south. The most significant geological outcrops are located along the banks of major rivers, including the Volga, Ural, and Severnaya Dvina, as well as their respective tributaries (fig. 1A).

During the Guadalupian epoch, significant quantities of terrigenous red-bed sediments were deposited in present-day European Russia, resulting in the formation of units that can reach thicknesses of up to 1500 meters. These sedimentary deposits primarily consist of fluvial and lacustrine origins (Tverdokhlebov et al. 2005). The predominant lithology includes subhorizontally bedded mudstones, siltstones, and fine-grained muddy sandstones, characterized by hues of red, reddish-yellow, or reddish-brownish-yellow, which were formed in floodplain environments. The deposits frequently contain lenses of cross-bedded alluvial sandstones and conglomerates, which are indicative of river channel formations. Additionally, the occurrence of rare carbonates, characterized by grey and purple-grey limestones and marls, provides evidence of shallow lacustrine environments (Tverdokhlebov et al. 2005; Silantiev et al. 2018).

Fish remains are typically found within the grey limestone units and sandstone lenses, whereas fossils are comparatively less prevalent in the red-bed mudstones. Notably, remains of *Karabalyk esini* gen. et sp. nov. have been discovered in three regions of Russia: the Mari El Republic, the Republic of Tatarstan, and, presumably, the Orenburg Region. Specimen SPMM Bx-XIII-245 (Fig. 2) is the posterior half of a trunk with well-preserved unpaired fins and scale cover. Specimen GGM RAS V 268/17 (Fig. 3) is an anterior trunk fragment with scale cover preserved. Collector and exact finding locality of both specimens are unknown. However, they are similar in preservation and most likely derive from the Urzhumian Kargaly copper mines, which is located in the southern Ural Mountains, within the borders of the Orenburg Region, close to the boundary of the present-day Republic of Bashkortostan (see details in Naugolnykh 2002; Naugolnykh et al. 2022) (Fig. 1A). The Permian copper-bearing deposits extend in a broad belt from modern Perm Krai in the north to Orenburg Region in the south

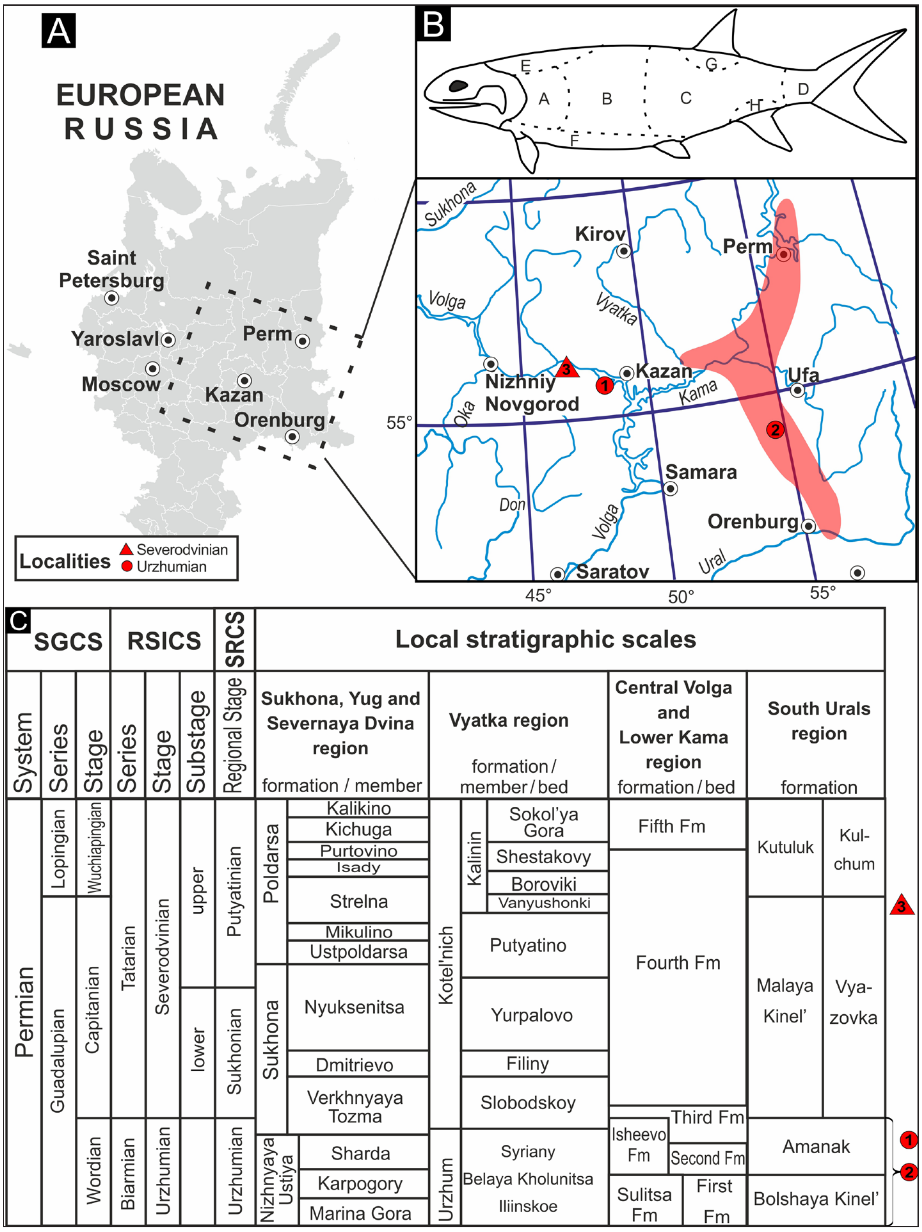

Fig. 1 - Geographic (A) and stratigraphic (C) distribution of finding localities of *Karabalyk esini* gen. et sp. nov., and a general scheme of the topological variability of scales according to body areas (B) according to Esin (1990). Numbers refer to the following localities: 1 – Cheremushka-1, 2 – Kargaly copper mines, 3 – Sundyr-1. The area highlighted marks the distribution of copper sandstones (after Efremov, 1954). Abbreviations: SGCS, Standard Global Chronostratigraphic Scale; SRCS, Standart Regional Chronostratigraphic Scale; RSICS, Russian Standard Interregional Chronostratigraphic Scale.

through eastern Udmurt Republic and Republic of Tatarstan, southern Kirov Region and western Republic of Bashkortostan, and the Kargaly copper mines were designed to be mining copper-bearing sandstones. The Kargaly ore field encompasses an extensive oval area measuring approximately 50 kilometers in length and 10 kilometers in width. Archaeological evidence suggests that open-pit copper mining in the Kargaly ore field, located within the Kargaly copper mining-metallurgical district of the Western Urals, likely commenced during the early Bronze Age, specifically at the onset of the 3rd millennium BCE (Chernykh & Isto 2002). The Kargaly region is characterized by a significant number of operational mines, which exhibit a broad chronological spectrum spanning from Bronze Age to the 18th and 19th centuries (Naugolnykh et al. 2022). During the 19th century, a large amount of various fossils were extracted from the Kargaly copper mines: plants, bivalves, insects, fish, tetrapods, etc. (Efremov 1954; Minikh & Minikh 2009; Aristov et al. 2013; Gomankov 2020; Naugolnykh et al. 2022). The biostratigraphic data obtained from this indicate that in some mines, the copper deposits belong to the Bolshekinelskaya Formation (Kluchevsky Mine-1, Ruzminsky mine), while in others they belong to the Amanak Formation (Yugovsky mine, Kichkass) (Ivakhnenko et al. 1997). Thus, all Kargaly mines are Urzhumian (= Wordian) in age (Naugolnykh et al. 2022).

Additional remains of *Karabalyk esini* gen. et sp. nov. investigated herein come from two localities of European Russia: Cheremushka-1 (Urzhumian) and Sundyr-1 (Severodvinian).

The Cheremushka-1 locality (P07/112) is a ravine on the right Volga bank, 2 km upstream of Pechishche village (Verkhneuslonsky District, Republic of Tatarstan, Russia) (Silantiev et al. 2018). The white, loosely cemented limestone of the bed P07/112 [Urzhumian (= Wordian) Stage, Urzhumian Regional Stage, Isheevo Formation, "Crimson Shale" Member] are exposed in this section (see details in Silantiev et al. 2018). A diverse fossil fauna including actinopterygians *Karabalyk esini* gen. et sp. nov., *Strelnia insolita* (Esin) *in* Esin & Mashin 1996, *Varialepis bergi* A. Minikh *in* Minikh & Minikh 1990, *Kargalichthys efremovi* Minikh *in* Minikh & Minikh 2009, *Platysomus biarmicus* Eichwald, 1857, *Samarichthys luxus* A. Minikh *in* Minikh & Minikh 1990, *Discordichthys spinifer* A. Minich, 1998, *Burguklia minichorum* Bakaev & Kogan, 2020, *Kichkassia furcae* A. Minikh *in* Minikh & Minikh 1990, *Palaeostrugia rhombifera* (Eichwald, 1857), and chondrichthyans Sphenacanthidae gen. indet., "*Lissodus*" cf. *zideki* Johnson, 1981, "*Polyacrodus*" sp., *Desinia radiata* Ivanov et al. 2022; tetrapods *Leptoropha* sp. (Silantiev et al. 2018; Ivanov et al. 2022; Bakaev & Kogan 2020; Bulanov 2020; Bakaev 2024).

The Sundyr-1 locality is situated on the southern bank of the Cheboksary Reservoir (right bank of the Volga River), near the mouth of the Sundyr River (Gornomariysky District, Mari El Republic, Russia). An abundant and diverse fossil fauna including actinopterygians *Karabalyk esini*, *Strelnia insolita*, *Kargalichthys efremovi*, *Platysomus biarmicus*, *P. bashkirus*, *Isadia suchonensis*, *Kichkassia furcae*, *Lapkosubia* sp., *Geryonichthys longus*, *Mutovinia stella*, *Varialepis* sp. (Bakaev 2024); chondrichthyans *Desinia radiata* (Ivanov et al. 2022), tetrapods *Suchonica vladimiri*, *Dvinosaurus* aff. *primus*, *Microphon exiguus*, *Leptoropha* sp., *Enosuchus alveolatus*, *Parasuminia ivakhnenkoi*, *Julognathus crudelis*, *Gorynychus sundyrensis*, Ulemosauridae gen. indet. (Golubev & Bulanov 2018; Suchkova & Golubev 2019a, 2019b) were reported from the yellow conglomerate with pebbles of clayey and carbonate rocks with interbeds of silts and clays of bed 2 [Severodvinian (= Capitanian)] Stage, Upper Severodvinian Substage, Lower Putyatinian Subhorizon, Sundyrian Beds; see details in Golubev & Bulanov 2018; Golubev et al. 2024).

Materials And Methods

The fish remains from Cheremushka-1 and Sundyr-1 localities are housed in the PIN under collection numbers 5844 and 5788 respectively. Micrographs of the scales were taken in the PIN Analytic Instrument Department on TESCAN VEGA-II XMU and TESCAN VEGA-III XMU microanalyzers, with or without gold-palladium coating. Thin sections have been prepared at the Geological Institute of the TU Bergakademie Freiberg (TU BAF), and were studied at TU BAF under a ZEISS AxioLab.A1. Study of the vascular system was performed by photographing scales immersed in an anise oil. This method has been successfully used earlier when studying internal structures of palaeoniscoid-type scales (e.g. Bakaev & Kogan 2022). The material has been photographed at the PIN Analytic Instrument Department using a Leica MZ16 microscope with a camera mounted. Scale morphology is described using the terminology of Schultze (1966) and Esin (1990, 1995) with modifocations by Bakaev & Kogan (2020, 2022). Note that only scales from body areas A and B (Fig. 1B) are diagnostic as to species. Scale ultrastructure is described following the terminology of Märss (2006).

Systematic Palaeontology

Class **OSTEICHTHYES** Huxley, 1880
Subclass **ACTINOPTERYGII** Cope, 1887 (sensu Goodrich 1930)
Superorder **Palaeoniscimorpha** Lund, Poplin et Mccarthy, 1995
Family Gonatodidae Gardiner, 1967
Genus *Karabalyk* gen. nov.

2009 *Uranichthys* – A. Minich, p. 137.
2009 *Uranichthys* – A. Minich & Minikh, p. 104.

Type Species: *Karabalyk esini* sp. nov., by monotypy and designation herein.

Diagnosis: Body deeply fusiform; dorsal and anal fins triangular and approximately equal in size, the first one situated behind the middle of the back, in advance of the second. Unpaired fins with minute fulcra along their leading edge. Caudal peduncle short and deep (Fig. 2A). Scales of area A and B rectangular. Anteroventral and posteroventral scale corners oblique. Peg and anterodorsal corner well-developed, pointed, of approximately equal height. Depressed field narrow. Anterior third of the free field dissected by thin grooves into many flat ridges varying in length and number. Posterior part of the free field smooth with irregularly arranged pores. Posterior

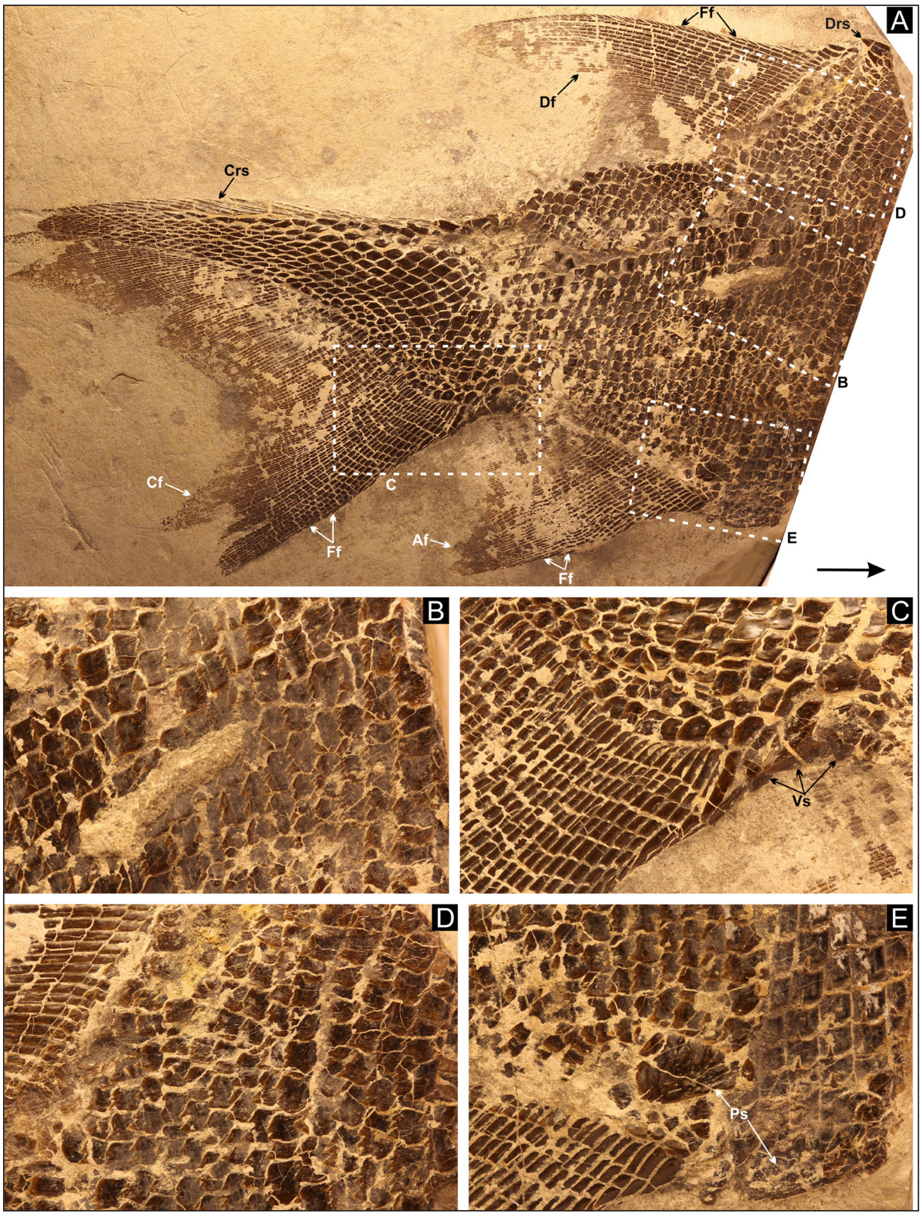

Fig. 2 - Holotype of *Karabalyk esini* gen. et sp. nov. (SPMM Bx-XIII-245) from the Kargaly copper mines, Orenburg Region, Russia; Urzhumian Horizon, Urzhumian (= Wordian) Stage, Guadalupian (Biarmian) Series. A) general view; B–E) details at higher magnification. Abbreviations: Af – anal fin; Cf – caudal fin; Crs – caudal ridge scales; Df – dorsal fin; Drs – dorsal ridge scales; Ff – fringing fulcra; Ps – preanal scutes; Vs – ventral scutes. Scale bar = 1 mm.

margin and the oblique posterior part of the ventral scale margin with few (up to seven) coarse, long and wide-based denticles (Figs. 3 and 5). Vascular system of scales consisting of irregular canals in the central part and a more regular network in the posterior and ventral parts of the free field (Figs. 4C and 6G, H).

Etymology: Karabalyk (bash. **Карабалыҡ**) is the term used for tench (*Tinca tinca*) in Bashkir language.

Composition: Type species only.

Remarks. When GGM V 268/17 was first described, it was assigned to the genus *Paramblypterus* (Esin, 1995). However, the thinner scales of *Paramblypterus* have delicate serration on their posterior edge and a generally smooth free field (the leading margin is not dissected by grooves) with rare minute pores (Dietze, 1999, 2000; Štamberg, 2013, 2021, 2022; Pawlak et al., 2024). Their vascular system consists of individual canals, which are mostly not connected to each other. There is no horizontal network of vascular canals (Aldinger, 1937). Scales referred to *Karabalyk* differ from those of *Paramblypterus* in the more numerous and large pores, the pronounced surface sculpture, the dissected anterior margin of the free field, the presence of the coarsely serrated posterior margin and the more complex and regular vascular system. Thus, *Karabalyk* seems closer to Gonatodidae than to Amblypteridae.

Karabalyk esini sp. nov.

Figs. 2–6

1995 *Paramblypterus kucenkoi* – Esin, p. 120–121, text- fig. 1, pl. 4, fig. 1, in litt.

2009 *Uranichthys pretoriensis* – A. Minich, p. 139, text- fig. 1, pl. 5, figs. 1d, e.

2009 *Uranichthys pretoriensis* – A. Minich & Minikh, p. 105, text- fig. 23, pls. 6-9, figs. 9.

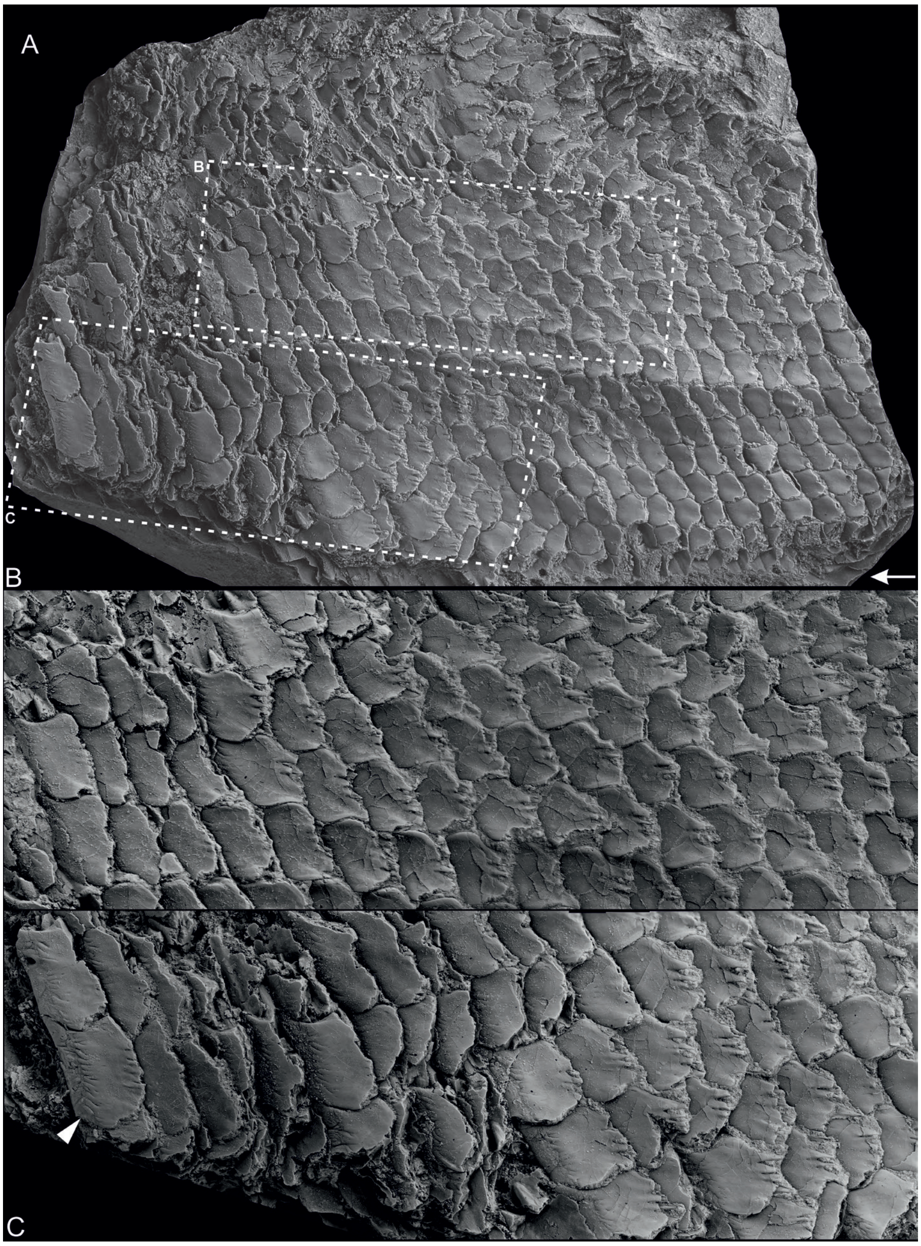

Fig. 3 - Paratype of *Karabalyk esini* gen. et sp. nov. (GGM RAS V 268/17) from the Kargaly copper mines, Orenburg Region, Russia; Urzhumian Horizon, Urzhumian (= Wordian) Stage, Guadalupian (Biarmian) Series. A) general view; B–C) details at higher magnification. White arrowhead indicate scale, redraw in Fig. 4A. Scale bar = 1 mm.

Holotype: SPMM Bx-XIII-245, a posterior body half with well-preserved unpaired fins and scale cover.

Paratype: GGM RAS V 268/17, a scale cover fragment.

Diagnosis: As for the genus.

Etymology: The species is named in honor of the paleoichthyologist Dmitry N. Esin (1964–2003).

Type Locality and Horizon: Kargaly copper mines, Orenburg Region, Russia; Urzhumian Horizon, Urzhumian (= Wordian) Stage, Biarmian and Tatarian (= Guadalupian).

Description

Postcranium. The body is deeply fusiform. The dorsal fin is triangular (Fig. 2A), and situated at a position anterior of the level of the anal fin. The leading edge bears unpaired fringing fulcra. Part of the lepidotrichia have been lost, but their total number was ca. 35. Fin rays consist of short segments (about 30 in the longest ones) and bifurcate in their distal third. The caudalmost fin rays are the shortest and the most delicate. In the holotype SPMM Bx-XIII-245 (Fig. 2A), three preserved ridge scales precede the dorsal fin. The smaller anal fin is very similar to the dorsal fin in shape (Fig. 2A, E), and situated close to the caudal fin. The origin of the anal fin lies approximately on the same vertical line as the posteriormost rays of the dorsal fin insert. Part of the lepidotrichia is also missing, but the preserved rays indicate that their total number was no less than 35. The lepidotrichia are also segmented and branch distally. The anal fin is preceded by at least one pair of large ventral scutes.

The caudal peduncle is very short and thick. The caudal fin is heterocercal, inequilobate, with a triangular ventral hypochordal lobe (Fig. 2A). There

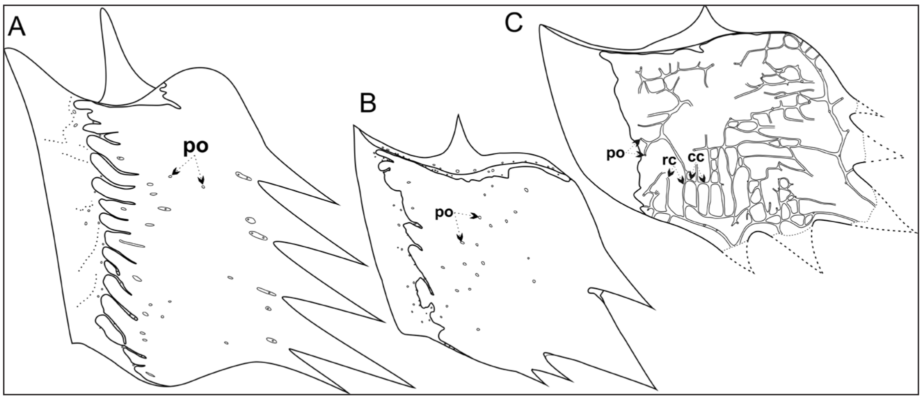

Fig. 4 - *Karabalyk esini* gen. et sp. nov., interpretive drawings of the scales. A) area A scale from Fig. 4C (white arrowhead), paratype, GGM RAS V 268/1; B) area C scale from Figs. 5A; C) area C scale from Fig. 6G with indication of the vascular system. Abbreviation: cc – concentric canals; po – pores; rc – radial canals. Not to scale.

is a smooth reversal in scale-row direction at the base of the notochordal mass of the tail. Some of the lepidotrichia are damaged, and the preserved rays indicate that their total number was no less than 80 (most in chordal lobe). The fin rays gradually shorten toward the dorsal end of the fin. They consist of short segments and branch distally (Fig. 2A). Caudal ridge scales (= "axial fringing fulcra" sensu Sallan & Coates 2013) originate from the base of the caudal peduncle and have tapered, spine-like distal projections (Fig. 2A). Their exact number cannot be determined due to poor preservation. There are three ventral ridge scales (= "caudal basal fulcra" sensu Sallan & Coates, 2013) anterior to the ventral lobe of the caudal fin that overlap each other (Fig. 2A, C). Prominent fringing fulcra line the entire ventral margin of the caudal fin.

Squamation. The holotype SPMM Bx-XIII-245 preserves over 35 vertical scale rows before the caudal inversion. About 30 scale rows are preserved on paratype GGM RAS V 268/17.

Area A (Figs. 3, 4A, 5F, H, J): Rectangular scales, twice higher than long. The anterior and posterior margins are straight. Ventral margin strongly convex; dorsal margin strongly concave. Anterodorsal corner well-developed, with a pointed tip. Anteroventral and posteroventral corners strongly and almost symmetrically oblique (occupying up to 1/3 of scale height), the transition to the anterior margin smoothly rounded; the transition to the posterior margin forms an obtuse angle. Peg high (equal to the anterodorsal corner) and triangular, directed dorsally, with a pointed tip. Socket deep. Keel narrow, located somewhat anterior to peg and socket.

Anterior depressed field narrow, accounting for about 1/6 of the scale length. Dorsal depressed field extremely narrow or absent. There are small pores on the depressed field along the anterior and dorsal margins of the free field. Lobate projections of the free field rounded or pointed. The anterior margin of the free field consists of subvertically or diagonally aligned ridges of varying number, flattened-roundish in cross-section. Grooves separating the ridges short and narrow. The posterior part of the free field smooth with irregularly arranged pores. Posterior margin with 5–7 coarse (long and wide-based) pectinate denticles. Several denticles are also located on the posterior, oblique part of the lower margin.

Area B (Figs. 3C, 5G, K, L): Scale length slightly inferior or equal to height. Anterior margin of the free field straight or undulating. Sculpture of the anterior margin of the free field less pronounced than in area A scales. Posterior margin with 3–4 coarse pectinate denticles. Remaining features as in area A.

Area C (Figs. 3C, 4B, 5A, B, E): Rhombic scales, 1.2–1.5 times longer than high. Anterodorsal corner low and blunt. Peg and socket small. Posterior margin with three or less coarse pectinate denticles. Remaining features as in area B.

Area D (Figs. 5D, M): Scale length exceeding their height twice. Peg and socket absent. Keel indistinct or absent. Depressed field developed as narrow stripes along the anterior and the dorsal margins of the scale. Anterodorsal corner weakly developed, with a rounded tip. Free field ornamented as in area C.

Area F (Fig. 5C): Elongated scales with a well-developed depressed field. Anterodorsal corner weakly developed. Peg and socket small. Keel indistinct or absent. The size of area F scales somewhat decreases towards the ventral midline, and the keel, peg and socket disappear. Free field ornamented as in area C.

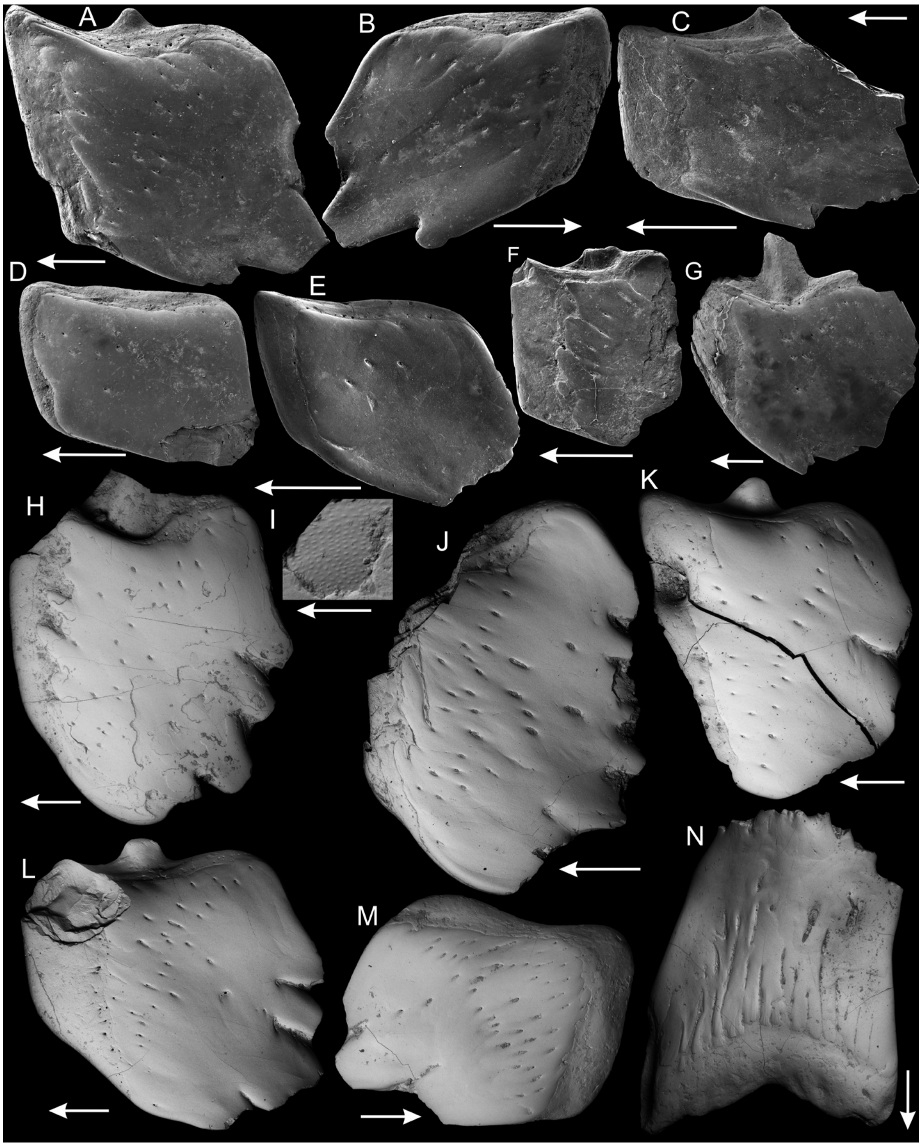

Fig. 5 - Squamation of *Karabalyk esini* gen. et sp. nov., in crown view. Sundyr-1 locality, Gornomariiskii District, Mari El Republic, Russia; lower Putyatinian subhorizon, upper Severodvinian substage, Severodvinian Stage, Guadalupian (Biarmian) Series. A) area B–C scale, PIN 5788/16; B) area C scale, PIN 5788/12; C) area B–F scale, PIN 5788/13; D) area D scale, PIN 5788/61; E) area C–D scale, PIN 5788/14; F) area A–B scale, PIN 5788/15; G) area B–C scale, PIN 5788/62; H) area A–B scale, PIN 5788/63, and I, close-ups of H; J) area A scale, PIN 5788/64; K) area B scale from the lateral line, PIN 5788/65; L) area B–C scale, PIN 5788/66; M) area C–D scale, PIN 5788/67; N) ridge scale, PIN 5788/68. Scale bars equal 100 μm in I and 1 mm in the remaining figures.

Ridge scales (Fig. 5N): Specimen PIN 5788/68 was most likely located in front of the dorsal fin. It is a large, symmetrical, ovoid scale, with a semicircular notch at the anterior end. Depressed field is well-developed, rounded-concave (due to the notch). Anterior part of the free field ornamented with thin, branching grooves into many of very flat ridges of various lengths and approximately equal widths. The surface of the free field is smooth and has pores. The posterior margin bears numerous coarse pectinate denticles.

Ultrasculpture (Fig. 5I): The ganoine surface is covered by microtubercles (normally less than 10 μm in cross section), circular in the central part and elongated towards scale margins and on the sculptural ridges, similar to the pattern seen in most basal ray-finned fishes.

Vascular system (Figs. 4C, 6G, H): Vascular canals can be seen on scales photographed in immersive fluid (Fig. 6). They form an irregular ("torn") horizontal mesh. Horizontal canals (Fig. 6, hc) occur around the bone/dentine boundary, and vertically and subvertically oriented canals pass through the lowermost layer of bone (Fig. 6, dc). Canals of both the depressed and the free field open to the surface through irregularly distributed pores. Radial canals begin at the posterior and ventral margin of the scale and converge towards the centre of the scale, whereby their lumen decreases. They are connected between each other by irregular concentric canals. These short concentric canals do not repeat the whole scale outline, but are also interconnected through irregular radial canals, which end with a row of pores on the scale margins. Canals do not follow a regular pattern in the central part of the scale. Thus, a flat network with regular "combs" formed by the concentric and radial canals occurs only in the ventral and posterior regions of the free field.

Histology: Ganoine, dentine and bone layers are well-developed. The ganoine layer is a markedly thick and multilayered. It is much thicker in the middle scale part due to the higher number of superimposed layers especially in the anterodorsal part of the free field, where it may lies directly on the bone. Rodlike structures are conspicuously in cross-polarized light (Fig. 6I, O). The layers of ganoine are inserted within or between odontodes (Fig. 6I, L, N).

The dentine layer is thin or lack in the central part of the scales, but much more pronounced in the ventral and posterior parts (Fig. 6A, D). It is formed by several concentric odontodes, which fuse into odontocomplexes. The network of thin horizontal canals is located at the base of the odontodes. It is completely embedded in dentine (Fig. 6L, N). There are rare resorption lines between odontode generations (Fig. 6L). Thin, numerous, dichotomizing fan-shaped canaliculi pierce the dentine from the lumen of horizontal canal network. The longer canaliculi are upwardly directed, while the shorter canaliculi can also point into different directions (Fig. 6I, L, N).

The bone layer is a markedly thick and divided into two layers. A woven-fibered bone layer contains chaotically diffuse large osteocytes with long, branching canaliculi (Fig. 6J, L). The layer of parallel-fibered bone is thicker than the ganoine and especially dentine layers. Sharpey's fibers pierce the bone layer along the ventral and dorsal scale margin (Fig. 6D) and through the keel (Fig. 6A, K). They are directed towards the center of the scale. Growth arrest lines (LAG) are well-visible in the bone (Fig. 6K, L, M). The fusiform-flattened osteocyte lacunae are concentrated at LAGs. Their canaliculi are not observable because they lie in the same plane as the LAG.

Descending canals are completely embedded in bone layer (Fig. 6D, M, O). These vascular canals are oriented mainly subvertical, but sometimes almost horizontal (Fig. 6J). There are no traces 'satellite cells'. The centripetally depositioned bone is brighter in polarized light than the surrounding bone and thus reminiscent of primary osteons in cross-section (Fig. 6J, M). The centripetal bone layer of vascular canals is relatively thin and does not enclose cells.

Remarks. *Karabalyk esini* gen. et sp. nov. differs from all other Gonatodidae in the less numerous coarse (long and wide-based) pectinate denticles as well as by the presence of denticles not just on the posterior, but also on the lower margin (on the oblique posterior part) of the scale.

Additionally, *Karabalyk esini* gen. et sp. nov. differs from species of *Gonatodus* and *Novogonatodus* in the nearly smooth free field, the lack of distinct ridges; from species of *Usolia* in the less curvature of dorsal and ventral margins of the scale; from species of *Plotnikovichthys* in the more numerous pores.

Geological age and geographical distribution. Guadalupian, Urzhumian (= Wordian) and Severodvinian (= Capitanian; up to middle part of Mikulino Member, Poldarsa Formation, Sukhona River basin). Republic of Tatarstan; Mari El Republic; Orenburg, Kirov, and Vologda Regions.

Occurrence. Numerous localities on the East European Platform. Urzhumian: Kargaly copper mines, Klyuchevskoy Mine-1; Kuzminsky; Monastery Ravine-1, -3, -D, -9, -10; Cheremushka-1, -2; Gremyachka; Vozdvizhenka B; Yugovsky Mine; Kichkass; Povoyska; Alatay. Severodvinian: Monastery Ravine-11; Yashkino-1-C; Verkhnyaya Tozma; Dmitrievo-2; Bezvodovka; Pleshanovo; Poldarsa-2; Sundyr-1, -2.

Discussion

K. esini gen. et sp. nov. possesses a squamation characterized by rhomboid scales of the palaeoniscoid type, similar to those of the majority of Palaeozoic actinopterygians (for details see: Aldinger 1937; Schultze 2016, 2018; Bakaev & Kogan 2022). The histological structure of the scales and the associated vascular system have been documented exclusively for a limited number of species within the Gonatodidae family.

Gonatodidae Gardiner, 1967 is a family of basal actinopterygians, fairly widespread in the Carboniferous of Europe and Central Asia (Gardiner 1967; Kazantseva-Selezneva 1981; Long 1988; Elliott 2018). Gardiner (1967, p. 146) noted that members of this family are characterised by the following features: "Trunk deeply fusiform; dorsal fin situated behind the middle of the back, more posterior in position than in Elonichthys Giebel…. Dorsal contour arched in advance of dorsal fin. Paired fins large, pelvic pair midway between pectorals and anal. All fins with minute fulcra anteriorly and with rays closely articulated, so as to impart scale-like appearance to individual joints; all rays distally bifurcated. Skull with suspensorium somewhat inclined, not so near vertical as in *Amblypterus*, moderately over hanging rostrum and relatively stout sclerotic ring. Opercular more than twice as deep as subopercular; suborbital series and dermohyal present. Branchiostegal rays numerous, skull roofing bones coarsely striated. Teeth closely set, of moderate size and in one series. Scales large with distinct peg and socket articulation, and ornamented with fine, oblique striae."

Karabalyk esini gen. et sp. nov. is based on fragments of the headless trunk, which prevents a more detailed comparison (including cladistic) with other representatives of Gonatodidae. Therefore, we use the features of body shape, unpaired fins, and scale structure.

In a recent handbook, Gonatodidae is rejected, because they are based upon few, hardly significant features (Schultze et al. 2021). However, this family has noit been revised for a long time, and we do not reject the existence of Gonatodidae until proven otherwise. Currently, Gonatodidae, comprise nine genera from Carboniferous and Permian deposits of the Northern hemisphere. Seven genera are known from skeletal remains: *Gonatodus* Traquair, *Pseudogonatodus* Gardiner*, Drydenius* Gardiner, *Paragonatodus* Kazantseva-Selezneva, *Paradrydenius* Kazantseva-Selezneva*, Brachypareion* Kazantseva-Selezneva, *Novogonatodus* Long (Gardiner 1967; Kazantseva-Selezneva 1981; Long 1988; Elliott 2018).

The systematics of Gonatodidae remains largely underexplored within the framework of cladistics. To date, the majority of the taxa previously mentioned have not been incorporated into any cladistic analyses. Notably, only one study includ some Gonatodidae species (*Gonatodus punctatus*, *Pseudogonatodus aurulentum*, and *P. parvidens*) within a cladistic analysis (Elliott 2018). However, the results of this analysis were insufficient to elucidate their phylogenetic relationships. In cladistic analyses, the genera *Gonatodus* and *Novogonatodus* are frequently cited due to their comprehensive descriptions. However, the outcomes of these analyses have yielded contradictory results across various studies. For example, *Gonatodus* appears as sister genus of *Nematoptychius* + (*Gardineria* + (*Karaoungaria* + *Cylindrichthys*)) + (*Eigilia* + (*Uydenia* + (*Uydenichthys* + (*Kenderlichthys* + (*Akanolepis* + '*Phanerosteon*')) + (*Aeduella* + (*Boreosomus* + *Ptycholepis*))))) in Dietze (2000). The phylogenetic relationships of *Gonatodus* are unresolved in Elliott (2018). The phylogenetic placement of *Novogonatodus*, which is more frequently included in phylogenetic analyses than other Gonatodidae, also remains controversial (Henderson et al. 2022). *Novogonatodus* is placed in a clade composed *of Tegeolepis, Pteronisculus, Mansfieldiscus, Coccocephalus*, for which a consensus tree resulted in many taxa recovered in a large polytomy (Holland et al. 2006). *Novogonatodus* appears as sister of clades: (*Cuneognathus gardineri* + *Limnomis delaynei*) (Choo 2015); (*Kentuckia hlavini* + *Wendyichthys dicksoni*) (Choo et al., 2018); ((*Cuneognathus gardineri* + *Limnomis delayni*) + (*Krasnoyarichthys jesseni* + (*Kentuckia deani* +*Stegotrachelus finlayi*))) (Giles et al. 2015); (*Kentuckia deani* + (*Stegotrachelus finlayi* +*Kentuckia hlavini*)) (Giles et al. 2023). Despite the differences in details, all phylogenetic analyses demonstrate the rather basal position of *Novogonatodus* among ray-finned fishes. It should be noted that the sample of taxa and the set of features used in the analyses including *Gonatodus* and *Novogonatodus* differ significantly, which additionally complicates the reconstruction of their phylogenetic relationships.

Fig. 6 - Histological sections of scales of *Karabalyk esini* gen. et sp. nov. A-F, I-O) Sundyr-1 locality, Gornomariiskii District, Mari El Republic, Russia; lower Putyatinian Regional substage, Putyatinian Regional Stage, upper Severodvinian substage, Severodvinian Stage, Guadalupian (Biarmian) Series. G, H) Cheremushka-1 locality, Verkhneuslonskii District, Republic of Tatarstan, Russia; bed 07/112, Crimson Shale Member, Isheevo Formation, Urzhumian Regional Stage, Guadalupian (Biarmian) Series. A–C, J–N) area C scale PIN 5788/19: A–B) horizontal section of in linearly polarized light (A) and in cross-polarized light (B); C) crown view of scale before sectioning, with indication of the cutting plane; I) magnified fragment of B; J–N) magnified fragments of A; D–F, O) area C–D scale PIN 5788/18: D–E) vertical section of in linearly polarized light (D) and in cross-polarized light (E); F) crown view of scale before sectioning, with indication of the cutting plane; O) magnified fragment of E; G) area C scale PIN 5788/17, immersed in anise oil, in crown view; H) area C–F scale PIN 5788/69, immersed in anise oil, in crown view. Large white arrowheads point to osteocyte lacunae, small arrows indicate incremental lines (lines of von Ebner?). Abbreviations: cp – centripetal bone; dc – descending canals; dt – canaliculi (dentinal tubules); gl – ganoine layers; hc – horizontal canals; LAG – line of arrested growth, lp – lateral pores; od – odontodes; pb – parallel-fibered bone; po – primary osteon; sh – Sharpey's fibers. Scale bars equal 500 μm in A and B and 100 μm in the remaining figures.

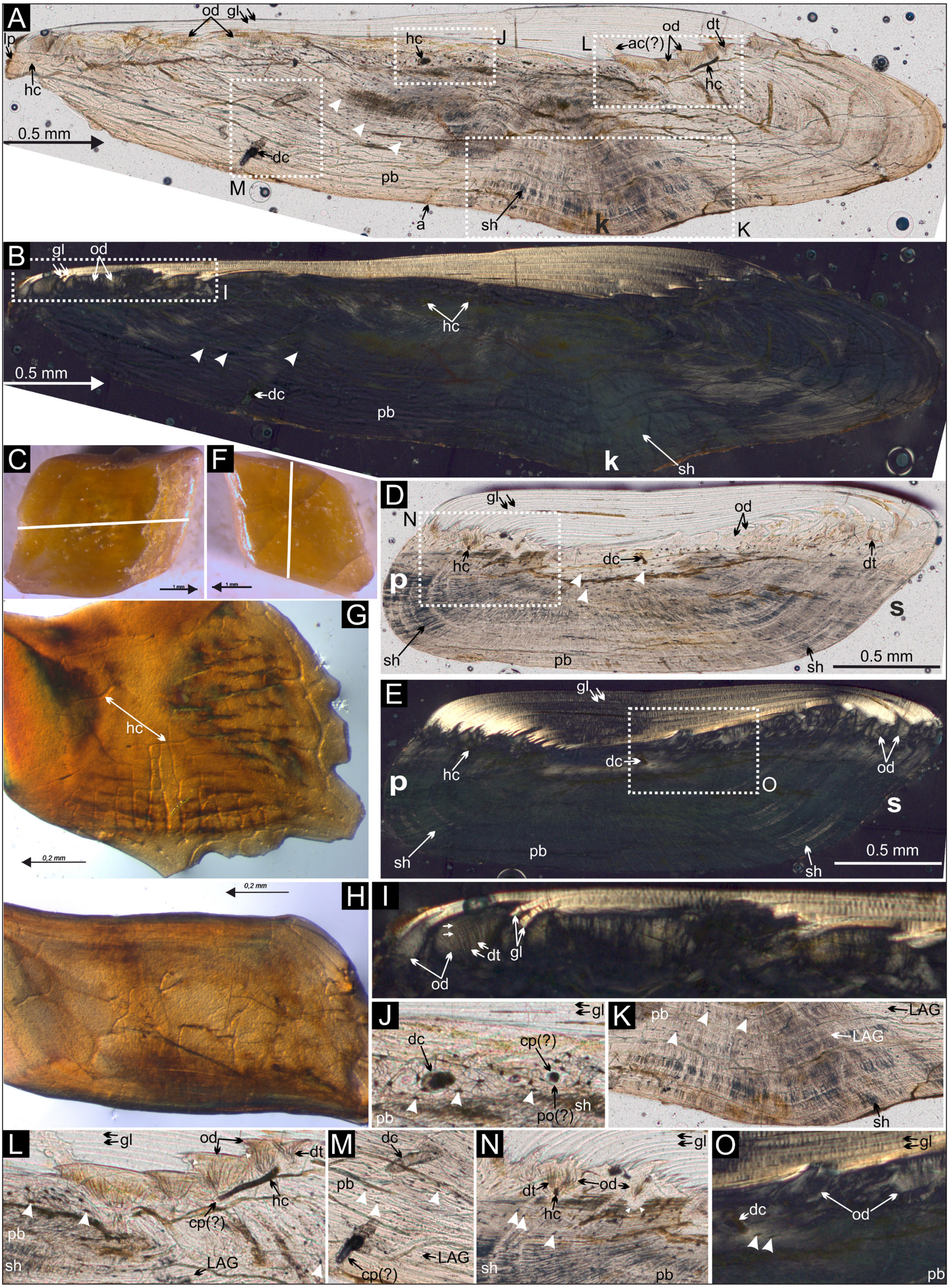
A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
0.5 mm
0,2 mm
od
gl
hc
dc
dt
pb
sh
LAG
cp(?)
po(?)
ac(?)
lp
p
s
k
a

Figure 6

All these taxa are characterized by - excluding cranial features - a deeply fusiform trunk; large, triangular and approximately the same size dorsal and anal fins; dorsal fin anterior (and partly opposite) to anal fin; anal fin close to caudal fin; arched dorsal contour; fins with minute fulcra anteriorly (Gardiner 1967). Additionally, two genera (*Usolia* Yankevich and *Plotnikovichthys* A. Minich) were described based on isolated scales (Minikh & Minikh 2009). With these two genera in consideration, Gonatodid scales can be characterized as follows: scales large with distinct peg and socket; free field of the scales bearing pores and fine, oblique delicate striae ornament or nearly smooth; there is serration on their posterior edge. All those morphological features shared by *Karabalyk* and the other Gonatodidae.

A similar body shape (deeply tapered with a short caudal peduncle) and fins (large unpaired fins shifted towards the tail, dorsal fin shifted forward relative to the anal fin) are typical for Amblypteridae (Dietze 2000) and Aeduellidae (Štamberg 2013). However, the morphology of the scales of these fish differs significantly from that of Gonatodidae: the scales are much thinner, the free field is smooth or sculptured with low concentric ridges and slightly pointed tubercles, with a continuous, straight front edge, bearing few small pores or almost devoid of them; the posterior edge is almost smooth or bears a few small denticles (Štamberg 2007, 2010, 2013, 2016, 2018, 2020, 2022; Štamberg & Werneburg 2023).

Karabalyk esini gen. et sp. nov. has been found in a large number of localities and is geographically and stratigraphically widespread within the East European Platform, which makes it a potentially significant species for the stratigraphy of the region. It first appears in the lower part of the Urzhumian (= Wordian) Stage (Monastery Ravine -1 and -2; I and II formations, respectively; Mouraviev et al. 2018) and it is found in all significant localities of the Urzhumian-lower Severodvinian interval. The last appearance datums of *Karabalyk esini* is in the middle part of the upper Severodvinian substage, at the level of the Mikulino mamber on the Sukhona River, and at the same level in the Sundyr-1, -2, (Golubev & Bulanov 2018) and Poldarsa-2 (Arefiev et al. 2015). The tetrapod remains of the Sundyr faunal assemblage (*Suchonica vladimiri* zone; Golubev, Bulanov 2018; Suchkova & Golubev 2019a, b) have been found at these sites. The Sundyr subcomplex is the last dinocephalian tetrapod fauna in Eastern Europe (Sennikov & Golubev 2017; Schneider et al. 2020). *Suchonica vladimiri* zone has been biostratigraphically correlated with the South African *Diictodon-Styracocephalus* subzone (*Tapinocephalus* zone), which is confirmed by the similarity of faunal complexes (despite differences in some details). In both cases, the upper boundary is marked by the disappearance of dinocephalians (in particular, large tapinocephalids) and some of the tetrapods associated with them (Day et al., 2015a, b; Sennikov, Golubev, 2017; Day, Smith, 2020; Day, Rubidge, 2021). According to current estimates (Day, Rubidge, 2021), the end of the Tapinocephalus zone corresponds to the first step of the initial phase of Capitanian mass extinction, which can be traced not only among terrestrial tetrapods, but also in marine ecosystems (Bond et al. 2010, 2020). Thus, *Karabalyk esini* gen. et sp. nov. became extinct during this extinction event.

Conclusion

Two incomplete skeletons and numerous isolated scales form the base for the description of the new taxon *Karabalyk esini* gen. et sp. nov. as a result of a careful revision of the palaeoichthyological collections at hand. Scales of the new species considerably differ from other previously described scales of Gonatodidae species. The new genus and new species adds new data on the taxonomic composition of the Guadalupian palaeoichthyological assemblages of the East European Platform and the Urals of Russia.

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Data Availability Statement. The data supporting the results of this research are available upon request. Interested researchers may contact the corresponding Author to obtain access.

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