

Neotype designation for *Eurysomus soloduchi*
Minich, 1992 and evidence of durophagy
in the East European Platysomidae
(Actinopterygii, Bobasatraniiformes)

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Neotype designation for *Eurysomus soloduchi* Minich, 1992 and evidence of durophagy in the East European Platysomidae (Actinopterygii, Bobasatraniiformes)

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ABSTRACT

Eurysomus soloduchi Minich, 1992 is a deep-bodied actinopterygian from the Middle Permian (Roadian) of European Russia, described by D. N. Esin. Unfortunately, the type specimen is lost. We nominate a second known skeleton of *E. soloduchi* from the type locality as a neotype of this species. Some features not previously identified in the species are described, and the dentition is described in detail for the first time. The morphology of *E. soloduchi* indicates an intermediate phylogenetic placement among species of paraphyletic genus *Platysomus* Agassiz, 1833 because it has features of both 'Platysomidae' Young, 1866 (*P. superbus* Traquair, 1881, *P. parvulus* Williamson, 1849, *P. striatus* Agassiz, 1833) and 'Bobasatraniidae' Stensiö, 1932 (*P. gibbosus* (Blainville, 1818), *P. biarmicus* Eichwald, 1857, *P. swaffordae* Mickle & Bader, 2009, *P. schultzei* Zidek, 1992). The lower jaw is deep and bears molariform teeth with apical cusps. All teeth have traces of *in-vivo* wear. The jaw anatomy and dentition indicates that *E. soloduchi* was adapted to a durophagous feeding habit, but we assume that it was a generalist feeder that could consume hard prey.

RÉSUMÉ

Désignation de néotype pour *Eurysomus soloduchi* Minich, 1992 et certaines preuves de durophagie chez les Platysomidae (Actinopterygii, Bobasatraniiformes) d'Europe de l'Est.

Eurysomus soloduchi Minich, 1992 est un actinoptérygien au corps haut du Permien moyen de la Russie européenne, décrit par D. N. Esin. Malheureusement, les spécimens types sont perdus. Nous nommons le deuxième squelette connu d'*E. soloduchi* de la localité type comme néotype de cette espèce. Certaines caractéristiques non identifiées auparavant dans l'espèce sont décrites, et la dentition est décrite en détail pour la première fois. La morphologie d'*E. soloduchi* indique une position phylogénétique intermédiaire parmi les espèces du genre paraphylétique *Platysomus* Agassiz, 1833 car il présente des caractéristiques des 'Platysomidae' Young, 1866 (*P. superbus* Traquair, 1881, *P. parvulus* Williamson, 1849, *P. striatus* Agassiz, 1833) et des 'Bobasatraniidae' Stensiö, 1932 (*P. gibbosus* (Blainville, 1818), *P. biarmicus* Eichwald, 1857, *P. swaffordae* Mickle & Bader, 2009, *P. schultzei* Zidek, 1992). La mâchoire inférieure est haute et porte des dents molariformes à cuspides apicales. Toutes les dents présentent des traces d'usure *in vivo*. L'analyse de l'anatomie et de la dentition de la mâchoire indique qu'*E. soloduchi* était adapté à une habitude alimentaire durophage, mais nous supposons qu'il avait un régime alimentaire généraliste avec un fort élément de durophagie.

KEY WORDS

Actinopterygii,
durophagy,
Permian,
East Europe,
Bobasatraniiformes,
Platysomidae.

MOTS CLÉS

Actinopterygii,
durophagie,
Permien,
Europe de l'Est,
Bobasatraniiformes,
Platysomidae.

INTRODUCTION

In 1947, two actinopterygian skeletons were found in Upper Kazanian deposits on the right bank of the Volga River near the Pechishchi village in the Republic of Tatarstan (Russia). These specimens were originally defined as *Platysomus* cf. *biarmicus* Eichwald, 1857 (Solodukho 1951). In 1992, M. G. Minikh (1992), described a new species, *Platysomus soloduchi* Minich, 1992, based on the best preserved specimen of these two (KFU PP/49). One year later D. N. Esin independently described (Esin 1993) the same specimen as the holotype of a new species, but he considered it to belong to *Eurysomus* Young, 1866, as *Eurysomus soloduchoi* Esin, 1993. This article seems (Esin 1993) to have been submitted for publication before the publication of M. G. Minikh's work (Minikh 1992). Both of the specimens discovered by Solodukho have features of the genus *Eurysomus*, and thus, we accept Esin's interpretation that these fossils belong in the genus *Eurysomus*. However, the holotype PP/49 is missing from the KFU collection. For this reason, the second surviving specimen from the type locality (KFU B-682) is designated here as a neotype for *Eurysomus soloduchi*. Fortunately, sufficiently high-quality photographs of the holotype KFU PP/29 taken by D.N. Esin have been preserved, and are used to refine the earlier description.

Eurysomus macrurus was described (originally as part of *Platysomus* Agassiz, 1833) and separated into a separate genus in the 19th century because *Eurysomus* Young, 1866 differ from all species of *Platysomus* in bearing clavate teeth on a peduncle with a constricted neck (Young 1866). Esin (1993) added several features: *Eurysomus* differs from *Platysomus* in the more elongated and less tall head and body; the anal and dorsal fins with a shorter base (relative to the body length) and shifted closer to the caudal fin; larger caudal fin (significantly more than half the height of the body). One feature that distinguishes *Eurysomus* from most Bobasatraniiformes is the presence of robust, bluntly rounded marginal teeth (Schaumburg 1977; Haubold & Schaumburg 1985). Similar teeth are present in both specimens of *Eurysomus soloduchi*. In addition, *E. macrurus* and *E. soloduchi* are similar in body and head shape; large caudal fin; shorter based, caudally shifted unpaired fins (Esin 1993); and short spines on ridge scales. However, the teeth of *E. soloduchi* differ from the type species *E. macrurus* (see below). *Kargalichthys* Minich, 1992 is the only known bobasatraniiform apart from *Eurysomus* that bears bluntly rounded marginal teeth. However, some diagnostic features of *Kargalichthys*, including a fundamentally different pattern of ornamentation on scales and dermal bones do not allow us to attribute the specimens (KFU PP/29 and KFU B-682) discovered by M. G. Minikh to this genus (Minikh A. & Minikh 2009).

Eurysomus has recently been recognized as a junior synonym of *Globulodus* Münster, 1842 (Mesolepididae Young, 1866) (Schultze *et al.* 2021). However, the type species *Globulodus* (*G. elegans* Münster, 1842) is represented by a single fragment of the left jaw bearing teeth similar to *E. macrurus*.

The holotype (whereabouts unknown) of *G. elegans* is too poorly described and illustrated (Münster 1842: pl. XV, fig. 7) for a detail comparison with *E. macrurus*, and the jaw bone fragment is very thin in comparison to *E. macrurus* and, especially, to *E. soloduchi*. In addition, *Mesolepis* Young (the type species of Mesolepididae) morphologically differ from *Eurysomus* (see Discussion). Thus, we consider that there is no reliable evidence for interpreting *Eurysomus* as a junior synonym of *Globulodus*, at least until a better description of the holotype of *G. elegans* is obtained.

Proliferation of durophagy among actinopterygians seems to have occurred in the Triassic and post-Triassic time (Vermeij 1977; Bellwood 2003; Böttcher 2014). However, durophagy among ray-finned fish appears in early Carboniferous (Friedman *et al.* 2018), and appears independently in several Carboniferous and Permian groups of Actinopterygii Cope, 1887. Among these, bobasatraniiformes Berg, 1940 are a prominent example (Johnson & Zidek 1981; Fracasso & Hovorka 1987; Zidek 1992; Sallan & Coates 2013). D. N. Esin (1997) attributed *Eurysomus* to sclerophages (synonym of durophages *sensu* Esin) based on the dental morphology. However, the study of modern teleosts has shown that the tooth shape alone cannot be solid evidence of durophagy, and even representatives of different populations of the same species can differ significantly in the degree of dietary specialization (Purnell & Darras 2015).

Kazanian (Roadian) deposits contain isolated teeth that are morphologically very similar to the teeth of the neotype of *Eurysomus soloduchi* at different stratigraphic horizons. We nominally attribute these teeth to *Eurysomus soloduchi*. All teeth have traces of in-vivo wear of varying degree, allowing a more complete characterization of the trophic specialization of this fish.

MATERIAL AND METHODS

Our work is based on a complete skeleton (*Eurysomus soloduchi* Minichneotype, KFU B-682) originating from the Shikhovochirki locality, as well as 30 isolated teeth originating from the Sentyak locality. The neotype of *Eurysomus soloduchi* Esin was photographed with a Canon EOS 650D camera with a Canon EF 100mm f/2.8 Macro USM lens. Micrographs of the neotype structure, as well as isolated teeth, were obtained using scanning electron microscopes TESCAN VEGA-II XMU and TESCAN VEGA-III XMU at PIN.

Traditionally, the two paired bones in the actinopterygian skull roof are identified using the terms frontal and parietal, like in the skull roofs of sarcopterygians. However, the tetrapod frontal and parietal are not homologous with the bones in actinopterygians that are given the same names (Schultze 2008). This may not cause problems when actinopterygians are compared to actinopterygians, or sarcopterygians to sarcopterygians, but problems may arise when actinopterygians are compared to sarcopterygians (Mickle & Bader 2009). Here we follow Mickle & Bader (2009) and the skull roof will be referred to as the frontal (parietal) and the parietal

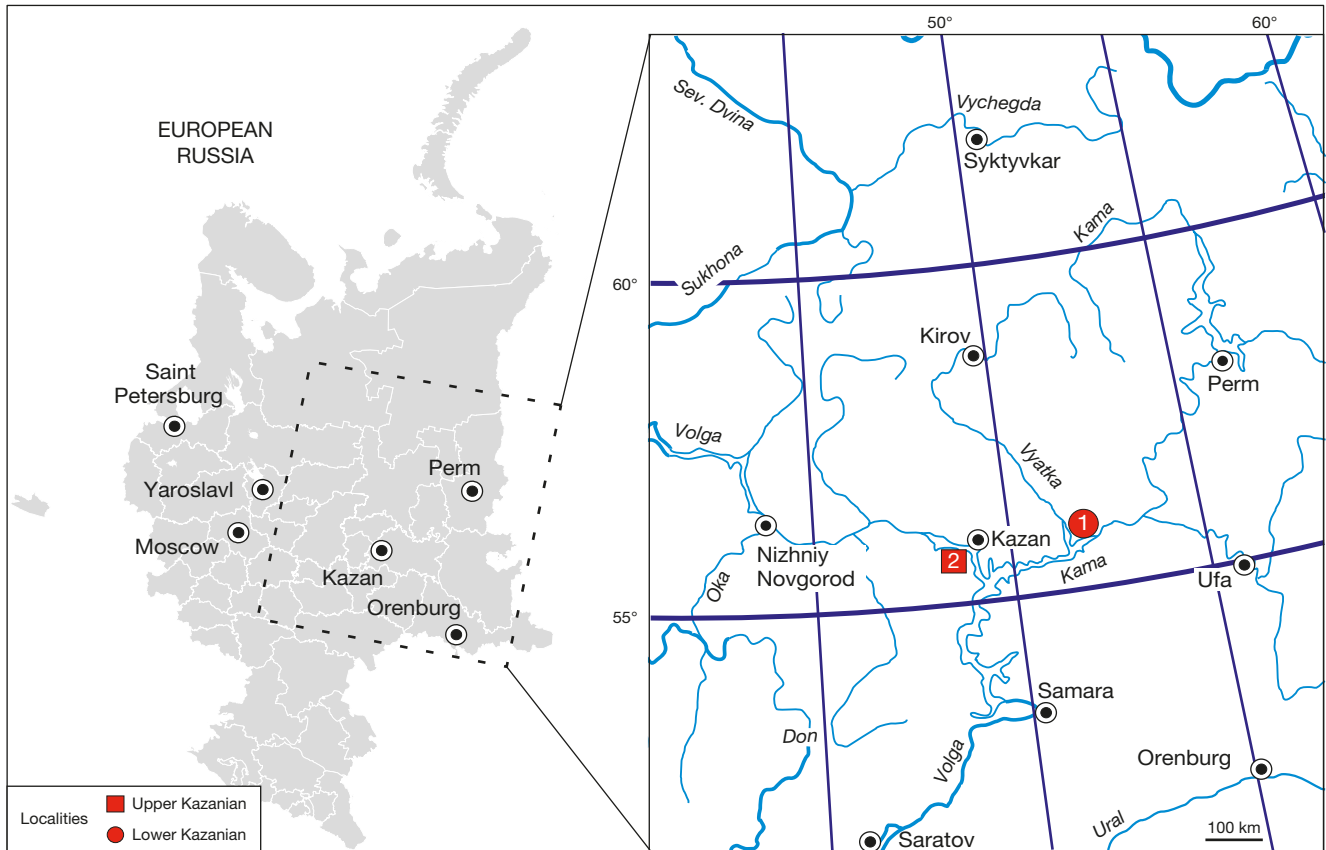


FIG. 1. — Geographic distribution of localities and species of *Euryosomus soloduchi* Minich, 1992 discussed in this paper within the Permian of European Russia. Numbers refer to the following localities: 1, Sentyak; 2, Pechishchi.

(postparietal). Here we are using the terms based on homology and will refer to the bone traditionally referred to as the frontal as the parietal and the bone traditionally referred to as the parietal as the postparietal.

ABBREVIATIONS OF INSTITUTIONS

PIN Borissiak Paleontological Institute, Russian Academy of Sciences, Moscow;
KFU Kazan Federal University, Kazan.

GEOLOGICAL SETTING

Middle Permian deposits are distributed over a significant part of the east and north of the East European Platform. The best outcrops are located along the banks of large rivers: the Kama, Volga, Ural and their tributaries (Fig. 1). During the middle Permian, the East European Platform was located north from equator, in a semiarid paleoclimatic zone. Most of the middle Permian deposits are formed by red-bed terrigenous rocks, predominantly fluvial and lacustrine (i.e., terrigenous) origin, the thickness of which can reach 500 m (Tverdokhlebov *et al.* 2005). Red-bed sediments are mainly composed of red, reddish-brown mudstones, siltstones and fine-grained argillaceous sandstones deposited in river floodplains. Lenses of cross-bedded alluvial sandstones and conglomerates are widespread in these sequences.

Carbonates are usually rare and are represented by gray or reddish-gray limestones and marls formed in lacustrine conditions (Tverdokhlebov *et al.* 2005).

However, the Kazanian (Fig. 2) is partially composed of marine carbonate deposits. In the eastern part of the East European Platform, only the lower part consists of alternating lagoonal and lagoonal-marine carbonates. Continental red-beds of the Belebey Formation overlap carbonate deposits of the area (Tverdokhlebov *et al.* 2005). The thickness of the Belebey Formation gradually decreases to the west, and near Kazan (i.e., in the study area), Kazanian deposits are completely composed of marine carbonates (Silantiev *et al.* 2015a). Local Kazanian deposits are divided into two substages, which are divided into seven successive units (“Beds with geographical names” (Silantiev *et al.* 2015c)). The studied material was collected from the lagoonal Kamyshla (isolated teeth) and marine Pechishchi (complete skeleton) beds. (Fig. 2).

SENTYAK

Republic of Tatarstan, Yelabuga region. Right bank of the Kama River, 0.5 km upstream from the Sentyak village, 5 km downstream from the outskirts of Nizhnekamsk.

Bone-bearing level

Bed S5\6-8. Gray limestone. Thickness 0.6 m (Silantiev *et al.* 2015b).

SGCS			RSICS			SRCS	Central Volga and Lower Kama region lithostratigraphic units	Localities			
System	Series	Stage	Series	Stage	Substage	Horizon					
Permian	Lopingian	Changhsingian	Tatarian	Vyatkian	Upper	Zhukovian	Fifth Fm	2			
		Wuchiapingian			Lower	Bykovian					
		Capitanian			Upper	Putyatnian			Fourth Fm		
					Lower	Sukhonian					
		Wordian			Urzhumian	Urzhumian			Urzhumian	Isheevo Fm	Second Fm
										Sulitsa Fm	First Fm
	Roadian	Biarmian	Kazanian	Upper	Morkvashi Beds	1					
					Verkhnyi Ulson Beds						
					Pechishchi Beds						
					Prikazan Beds						
					Krasnyi Yar Beds						
					Kamyshla Beds						
Baitugan Beds											

FIG. 2. — Stratigraphic distribution of finding localities (based on Silantiev *et al.* 2015a; Schneider *et al.* 2020; with changes). Abbreviations: **RSICS**, Russian Standard Interregional Chronostratigraphic Scale; **SGCS**, Standard Global Chronostratigraphic Scale. Localities: 1, Sentyak; 2, Pechishchi.

Faunal assemblage

Fishes *Alilepis esini* A. Minich, 2006, *Kazanichthys golyushermensis* Esin, 1995, *Palaeoniscum freiselebeni* Blainville, 1818, *P. kasanense* Geinitz et Vetter, 1880, *Platysomus biarmicus* Eichwald, 1857, *Koinichthys ivachnenkoi* Esin, 1995, *Acropholis stensioei* Aldinger, 1937, bivalves *Schizodus rossicus* Verneuill, 1845, *Permophorus simplex* (Keyserling, 1846), *Liebea* (?) sp.; amphibian bone fragments (Silantiev *et al.* 2015b).

Stratigraphic level

Middle Permian (Biarmian) Serie, Kazanian (Roadian) Stage, Lower Kazanian Substage, Kamyshla Beds (Silantiev *et al.* 2015b).

PECHISHCHI

Republic of Tatarstan, Verkhneulonsky district. The right bank of the Volga River opposite the Kazan city, 2 km upstream from the Pechishchi village, near the mouth of the Pologiy Ravine (Solodukho 1951; Silantiev *et al.* 2015c).

Bone-bearing level

Bed no. 16. (K1/16) Nizhniy Mylnik (“Lower Soapstone”). Pale yellow dolostone, thin-bedded, argillaceous; with small ovoid nodules of secondary calcite. Thickness 2.50 m (Silantiev *et al.* 2015c).

Faunal assemblage

Fishes *Euryosomus soloduchi* Minich, 1992; bivalves *Netschajewia* sp., *Pseudomonotis* sp.

Stratigraphic level

Middle Permian (Biarmian) Series, Kazanian (Roadian) Stage, Upper Kazanian Substage, Pechishchi Beds, Podboi Member (Silantiev *et al.* 2015c).

SYSTEMATICS

Superclass OSTEICHTHYES Huxley, 1880
 Class ACTINOPTERYGII Cope, 1887
 Order BOBASATRANIIFORMES Berg, 1940
 Family PLATYSOMIDAE Young, 1866
 Genus *Euryosomus* Young, 1866

Euryosomus soloduchi Minich, 1992

Platysomus sp. Solodukho, 1951: 158-159.

Platysomus soloduchi Minikh, 1992: 138, table 1.

Euryosomus soloduchoi Esin, 1993: 129, fig. 1a-c.

MATERIAL EXAMINED. — **Neotype**. KFU B-682, complete fish skeleton, poorly preserved; Republic of Tatarstan, Verkhneulonsky district, Pechishchi locality; middle Permian (Biarmian) Series, Kazanian (Roadian) Stage, Upper Kazanian Substage, Pechishchi Beds, Podboi Member.

MATERIAL. — Complete fish skeleton and thirty isolated teeth; preserved photographs of the holotype (KFU PP/29).

DIAGNOSIS. — Deep-bodied fish. The head and pectoral girdle are slightly more than one-third of the standard length. The body is more rectangular than circular. The operculum is high and rectangular, with rounded corners; the ventral margin of the operculum is abruptly convex and sits within the concave margin of the suboperculum; the suboperculum is lower and wider than the operculum; the dorsal margin of the suboperculum is slightly concave anteriorly (J-shaped); one pair of extrascapular bones; the lower jaw is deep and stout; jaws bears one row of molariform teeth with apical cusps; phylodont tooth plates absent; the majority of bones and scales are ornamented with subvertical cylindrical ridges; the squamation consists of 40 scale rows; ventral and dorsal ridge scales are extended into short spines; pectoral fins are relatively large; pelvic fins are well developed. At the anterior ends of the dorsal and anal fins, the upper and lower margins are angulated. The dorsal and anal fins are moderately (ratio dorsal fin/standard length is 1:5) long-based and reach all the way down to the narrow caudal peduncle.

DESCRIPTION

Both the lost holotype and the neotype are not well preserved. In the holotype, dermal bones of the skull roof, cheek, and pectoral girdle are preserved as impressions

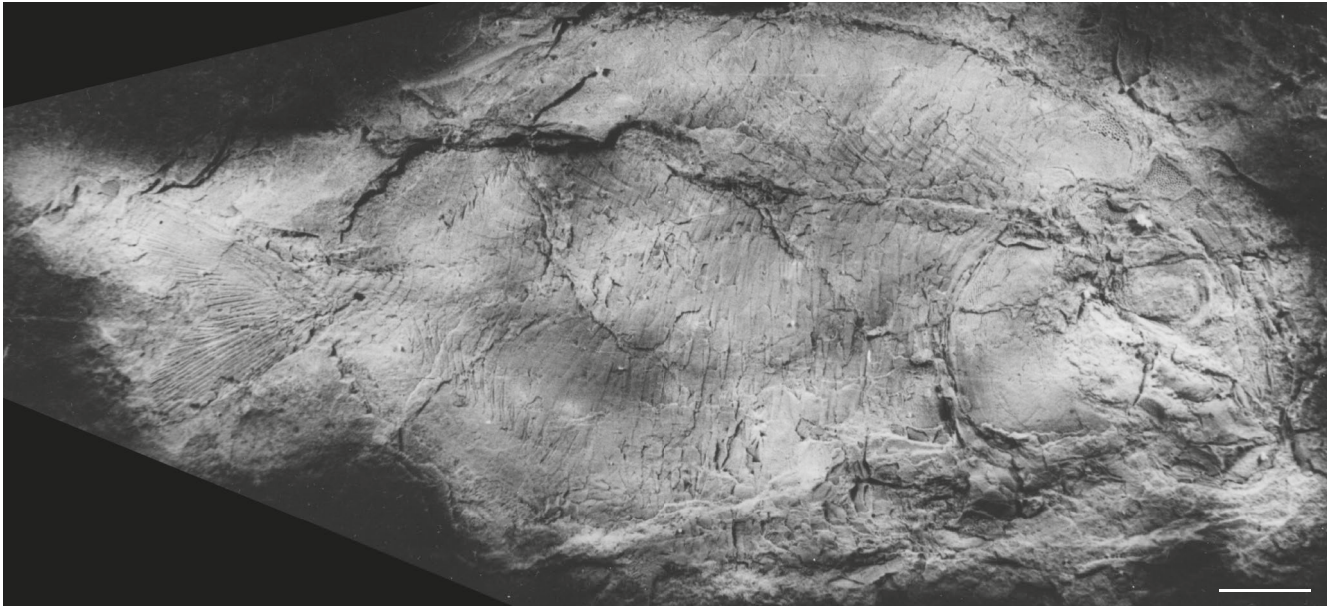


FIG. 3. — Lost holotype of *Eurysomus soloduchi* Minich, 1992 (KFU PP/49), lateral view. Scale bar: 1 cm.

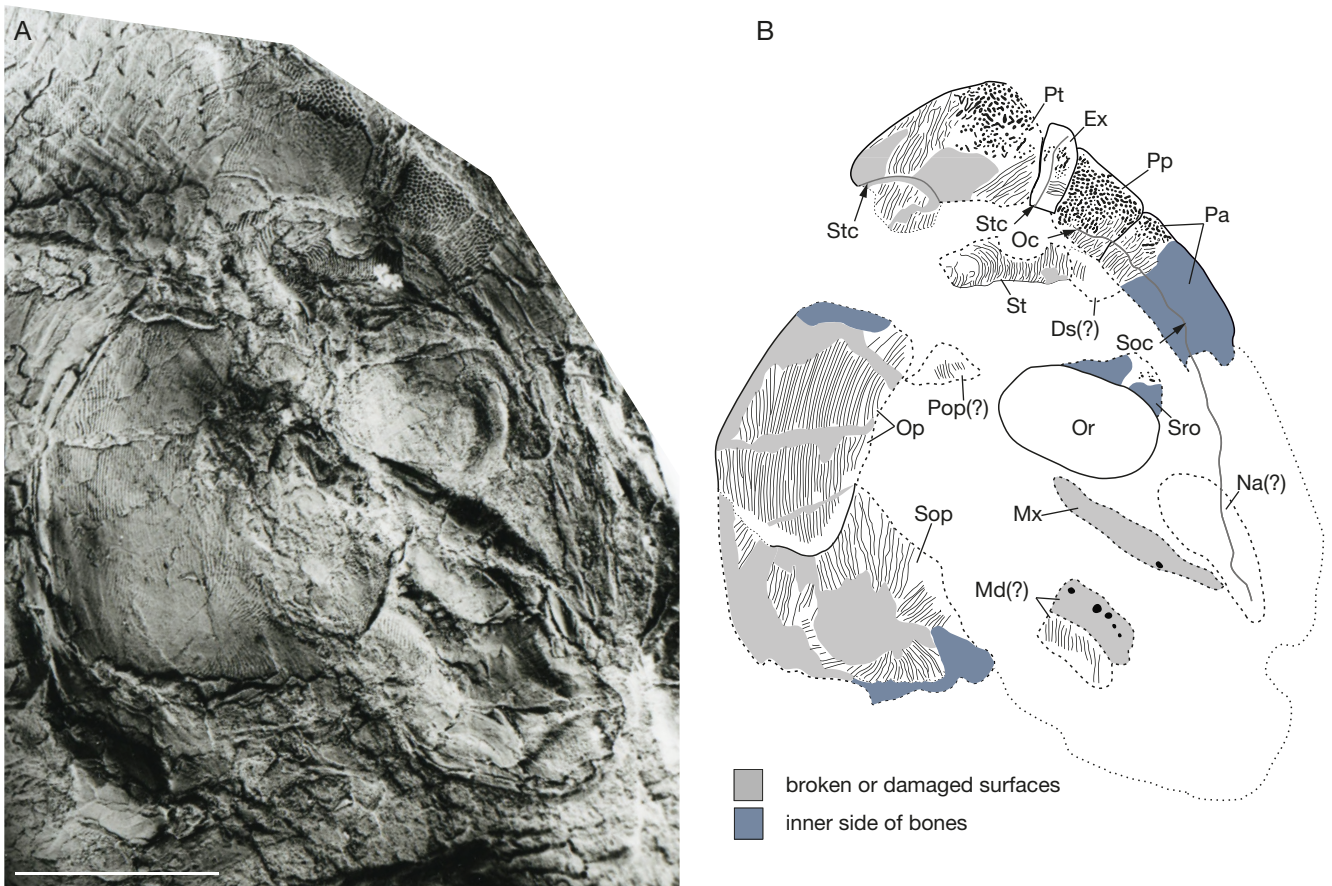


FIG. 4. — Lost holotype of *Eurysomus soloduchi* Minich, 1992 (KFU PP/49): **A**, close-up of the left side of the skull in lateral view; **B**, reconstruction of the lateral side of the head. Abbreviations: **Ds**, dermosphenotic; **Ex**, extrascapulars; **Md**, mandible; **Mx**, maxilla; **Na**, nasal bone; **Oc**, otic canal; **Op**, operculum; **Or**, orbit; **Pa**, parietal bone; **Pop**, preoperculum; **Pp**, postparietal bone; **Pt**, posttemporal; **Soc**, supraorbital canal; **Sop**, suboperculum; **St**, supratemporotabular; **Stc**, supratemporal canal; **Sro**, supraorbital. Scale bar: 1 cm.

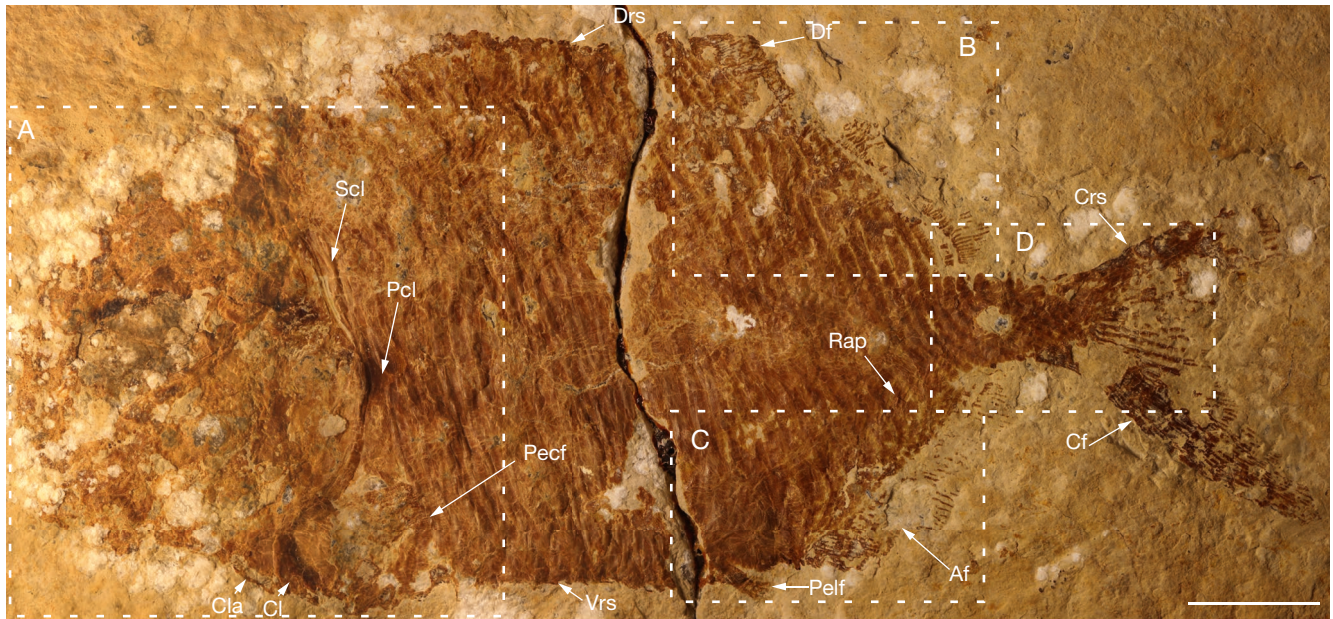


FIG. 5. — Neotype *Eurysomus soloduchi* Minich, 1992 (KFU B-682), lateral view. Abbreviations: **Af**, anal fin; **Cf**, caudal fin; **Cl**, cleithrum; **Cla**, clavicle; **Crs**, caudal ridge scales; **Df**, dorsal fin; **Drs**, dorsal ridge scales; **Pcl**, postcleithrum; **Pecf**, pectoral fin; **Pelf**, pelvic fin; **RAP**, proximal anal fin radials (axonosts); **Scl**, supra cleithrum; **Vrs**, ventral ridge scales. Scale bar: 1 cm.

(Figs 3; 4). The boundaries of individual bones of the neotype are almost indistinguishable (Figs 5; 6). The head and pectoral girdle are slightly more than one-third of the standard length, and the body from the posterior border of the cleithrum to the anterior border of the caudal peduncle is slightly longer than deep. The body is more rectangular than circular. The upper and lower margins of the body at the beginning of the unpaired fins are almost straight and only slightly convex (the height of this part of the body increases very slowly from front to back). At the beginning of the dorsal and anal fins, the upper and lower margins form pronounced dorsal and ventral angles, respectively (Figs 5; 6).

Skull

The post-temporal is relatively well preserved in the lost holotype, but poorly preserved in the neotype. Only the ventral margin of the post-temporal is not well preserved. There is a clear section of the supratemporal canal preserved on the ventral part of the bone (Fig. 4A, B). The ornament consists of subvertical cylindrical ridges in the lower half and anterior and posterior parts, ridges broken into rows of tubercles in the center and upper part, and chaotically placed wide tubercles in the upper third portion of the bone. The posterior and upper margins are concave. The single extrascapular is rectangular, relatively wide and bears a vertical supratemporal canal. The anterior suture with the postparietal is straight. The ornament consists of sub-horizontal cylindrical ridges in the lower half and randomly distributed tubercles in the upper half. Minikh (1992) noted that there is an extrascapular series of five small, rounded bones (Fig. 4A, B). However, our observations do not confirm this because there is only one extrascapular bone.

The postparietal is square with rounded corners. The parietal is rectangular (Fig. 4A, B). The postparietal is half the size of the parietal. A horizontal supraorbital canal goes through both bones. The ornament consists of subvertical cylindrical ridges in the anteroventral third and randomly distributed tubercles in the rest of the bone surface. Suture between the parietal and postparietal is straight. The ventral margins of both bones are not well preserved. Two bones preserved ventral to the skull-roof are presumably the dermosphenotic and supratemporotabular. Both bones are heavily damaged, making their true shapes indistinguishable. However, the position and ornamentation of preserved remains/imprints are allowing to identify these bones. The dermosphenotic and supratemporotabular are ornamented with undulating cylindrical ridges. Another heavily damaged bone, presumably the supraorbital, is preserved above the orbit (Fig. 4A, B).

The opercular series consists of an operculum, suboperculum, and possibly preoperculum (Fig. 4A, B). The operculum is high (approximately two times deeper than wide) and rectangular with rounded corners. The posterior margin is slightly convex. The dorsal and anterior margins of the operculum are not well preserved, so its exact height remains. The ventral margin is strongly convex and sits within the concave margin of the suboperculum. It bears an unornamented area where the suboperculum would have overlapped the operculum. This became observable, apparently, due to the postmortem dislocation of these bones. The ornament consists of long subvertical cylindrical ridges. The suboperculum is large, wider (but two times lower) than the operculum. The anterior and ventral margins are damaged, but overall, the shape of this bone is preserved. The dorsal margin of the suboperculum is slightly concave in its anterior half (J-shaped). The anterior portion of the suboperculum is wider than the posterior

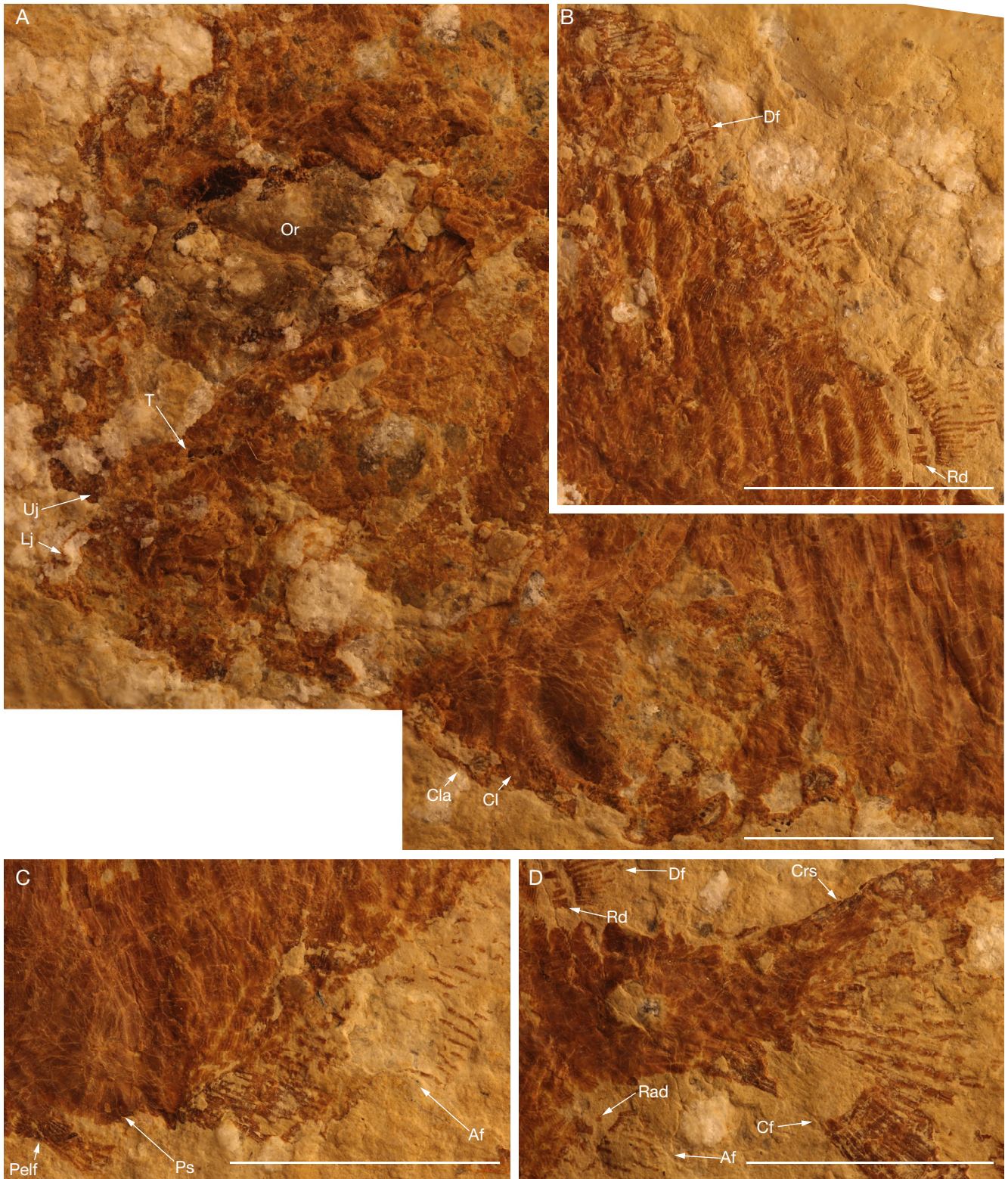


FIG. 6. — Details of neotype *Eurysomus soloduchi* Minich, 1992 (KFU B-682): **A**, head and pectoral fin; **B**, dorsal fin; **C**, pelvic and anal fins; **D**, caudal fin. Abbreviations: **Af**, anal fin; **Cf**, caudal fin; **Cl**, cleithrum; **Cla**, clavicle; **Crs**, caudal ridge scales; **Df**, dorsal fin; **Lj**, lower jaw; **Or**, orbit; **Pelf**, pelvic fin; **Ps**, preanal scute; **Rad**, distal anal fin radials (baseosts); **Rd**, dorsal fin radials (baseosts); **T**, teeth; **Uj**, upper jaw. Scale bars: 1 cm.

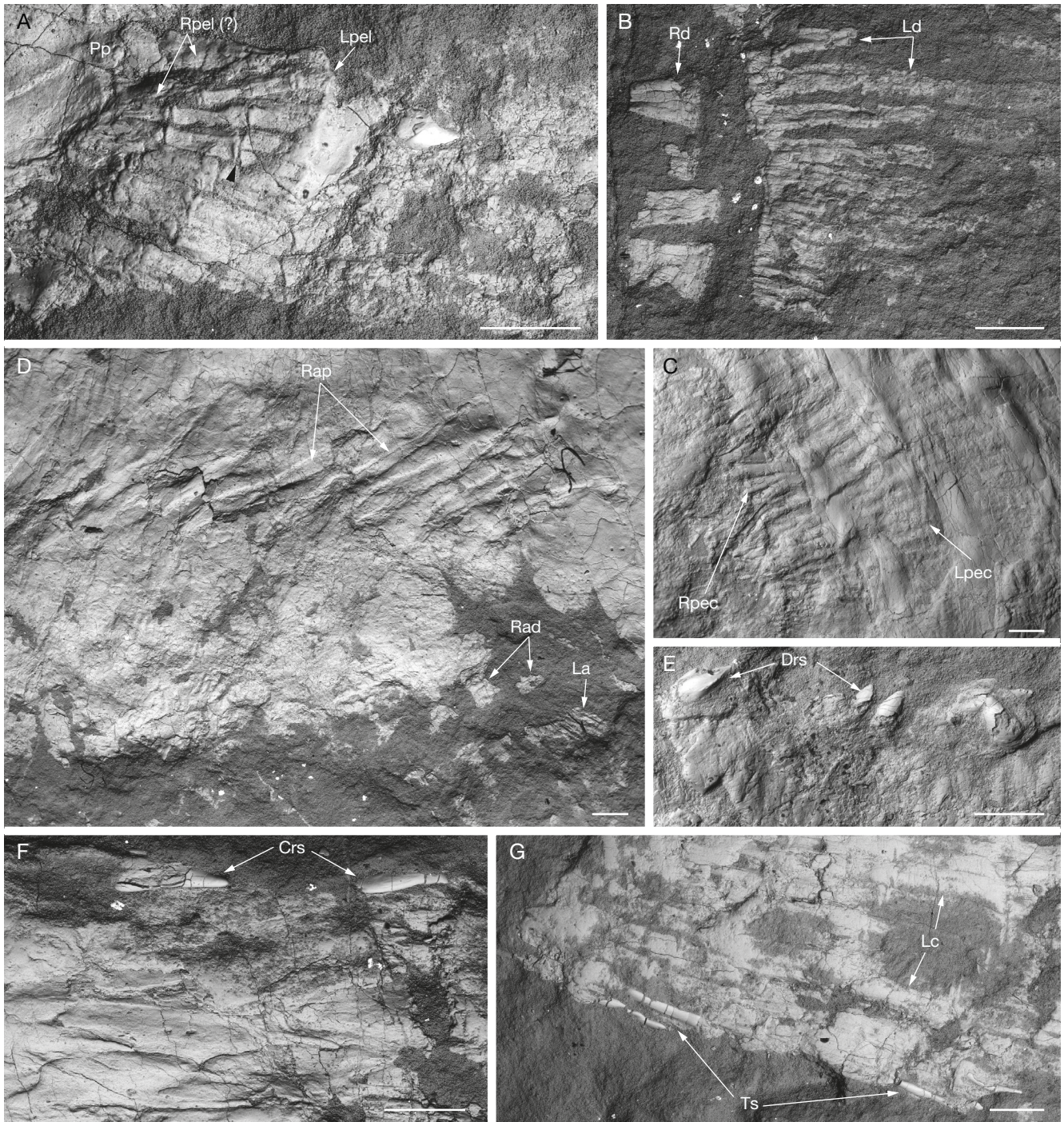


Fig. 7. — Fins and scales of neotype (KFU B-682) *Eurysomus soloduchi* Minich, 1992 under SEM: **A**, pelvic fin; **B**, the most posterior part of dorsal fin; **C**, pectoral fin; **D**, anal fin; **E**, dorsal ridge scales; **F**, dorsal lobe of caudal fin; **G**, ventral lobe of caudal fin; **black arrow** indicate bifurcation of lepidotrichia. Abbreviations: **Drs**, dorsal ridge scales; **Crs**, caudal ridge scales; **La**, anal fin lepidotrichia; **Lc**, caudal fin lepidotrichia; **Ld**, dorsal fin lepidotrichia; **Lpec**, pectoral fin lepidotrichia; **Lpel**, pelvic fin lepidotrichia; **Pp**, pelvic plate; **Rd**, dorsal fin radials (baseosts); **Rad**, distal anal fin radials (baseosts); **Rap**, proximal anal fin radials (axonosts); **Rpec**, pectoral fin radials; **Rpel**, pelvic fin radials; **Ts**, tapered distal segments. Scale bars: A, G, 500 μ m; B-F, 100 μ m.

portion. The ornament consists of radiating cylindrical ridges in anterior part and parallel to posterior margin sub-horizontal cylindrical ridges in the posterior portion. The radial ridges probably diverged from the center of ossification. Between the operculum and the orbit lies a highly damaged bone that we interpreted as remains of a preoperculum. The ornament consists of subvertical cylindrical ridges. Esin (1993) argued

that the suboperculum is much higher than the operculum, which has an almost square shape. We suggest this is a misinterpretation caused by a horizontal crack through the operculum.

The snout is more poorly preserved than other parts of the skull (Fig. 4A, B). In addition to the heavily damaged maxilla and mandible, only the general outline of an indeterminate bone is apparent around the maxilla/mandible remains.

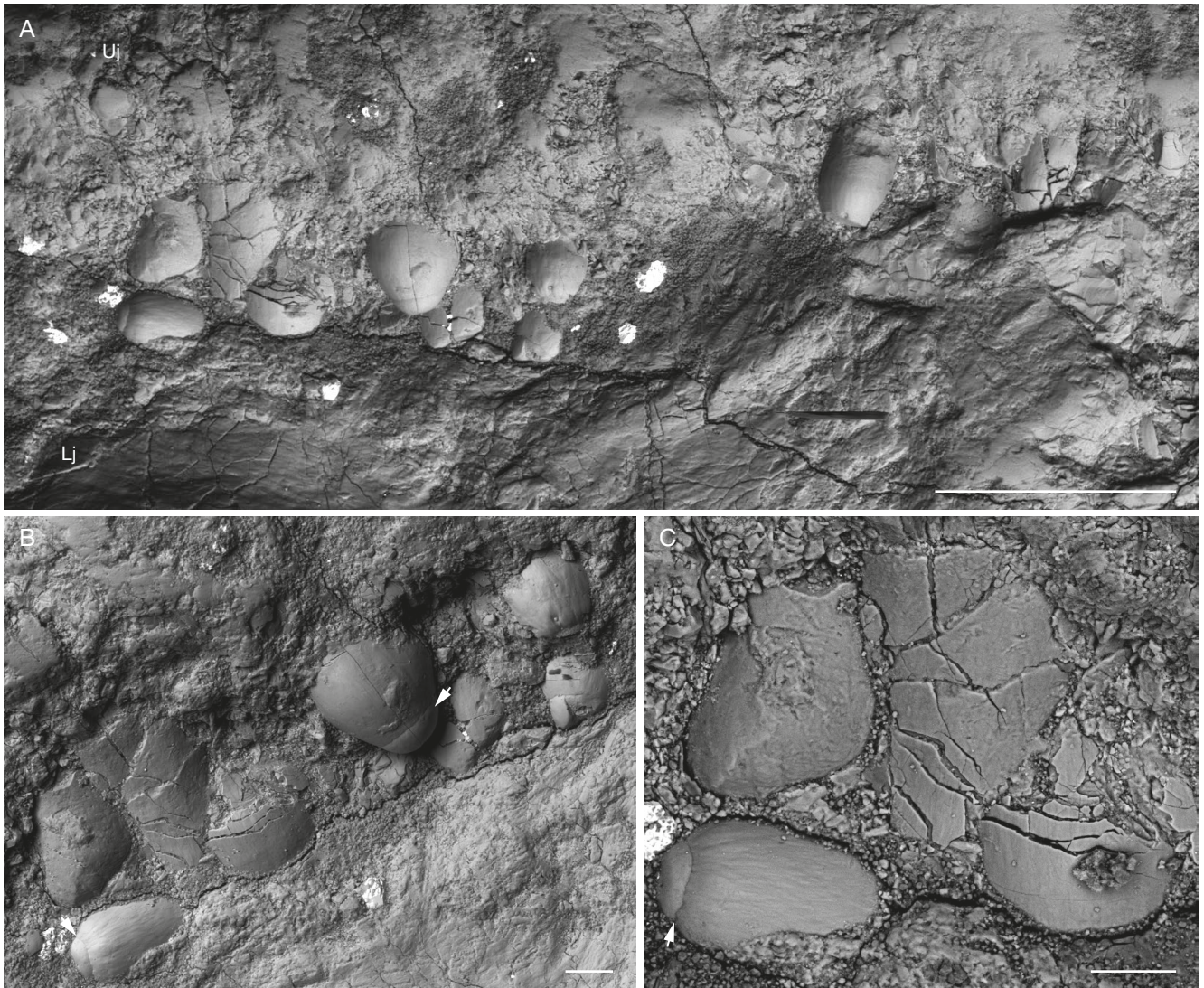


FIG. 8. — Teeth of neotype (KFU B-682) *Eurysomus soloduchi* Esin, 1993 under SEM: **A**, general view; **B**, **C**, same under high magnification. **Arrows** indicate acroclin cap. Abbreviations: **Lj**, lower jaw; **Uj**, upper jaw. Scale bars: **A**, 500 μm ; **B**, **C**, 100 μm .

The preserved supraorbital canal indicates that it may be the outline of the nasal bone. The mouth is terminal. The maxilla is damaged and bears only one tooth. The mandible has five teeth. Its lateral surface is ornamented with cylindrical ridges.

Postcranium

The endoskeletal pectoral girdle consists of the clavicle, cleithrum, supracleithrum, and postcleithrum. All bones are present in the neotype, but observable only from the inner side (Figs 5; 6A). Therefore, the ornamentation of the outer side remains unknown. The clavicle is a triangular bone ventral to the cheek region. The cleithrum consists of a high and slender dorsal part that extends up to about the middle portion of the operculum and a triangular, sigmoidal curved ventral part. There is a clear embayment on the posterior margin of the ventral portion to accommodate the pectoral fin. The supracleithrum is slender, but its precise shape remains unclear. The postcleithrum is crescent-shaped and slender, with a posteriorly directed bony plate on the posterior margin. The bony plate is covered with scales.

All fins are present in the neotype (Figs 5-7). The pectoral and pelvic fins are relatively well developed. There is no evidence of fulcra associated with the pectoral and pelvic fins. The pectoral fin is quite large but relatively poorly preserved (Figs 6A; 7C). Some individual rays can be distinguished, but their exact number cannot be counted. At the base of the rays, elongated bones have been preserved, which may be radials or elongated basal hemisegments (Fig. 7C). The pelvic fin is well preserved and situated a short distance in front of the ventral angle of the ventral trunk margin (Figs 6C; 7A). There is a fairly large plate at the base of the fin, and several small bones, probably radials, are attached to it (apparently, some of them were lost). The posteriormost bone in the row is much larger and could potentially represent the metapterygial axis, like in *Moythomasia* Gross, 1950 (Gardiner 1984). Distal radials (like in *Polypterus* Lacepède, 1803, Molnar *et al.* 2016) are absent. The basal hemisegments of lepidotrichia are large, and the lepidotrichia themselves divide at the border of the basal and following hemisegments (Fig. 7A, small

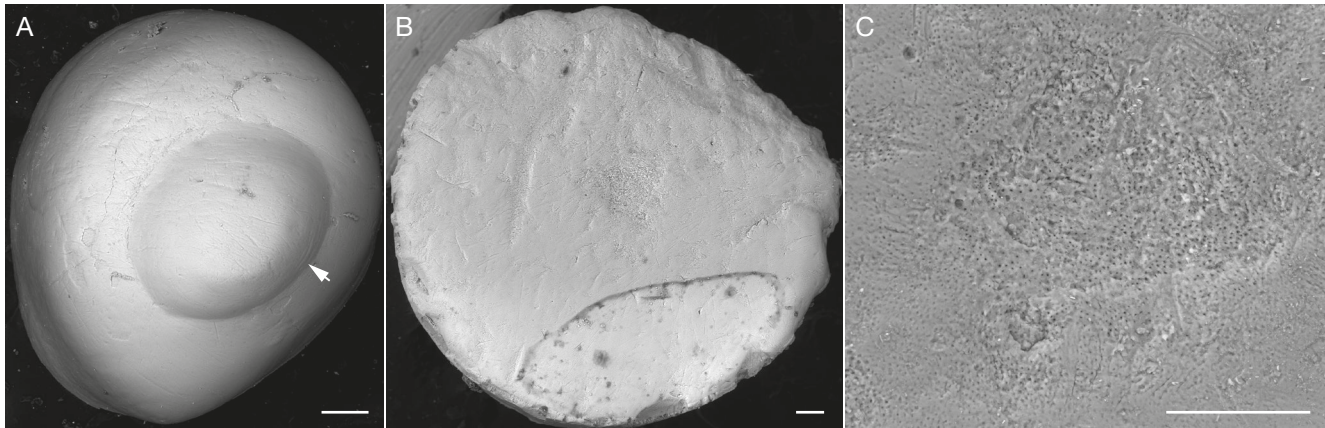


FIG. 9. — Isolated teeth from the Kamyshla Beds, Kazanian (Roadian) of the Sentyak locality (S5/6-8), Tatarstan, Russia: **A**, PIN 5799/19, little worn teeth, crown view; **B**, PIN 5799/19, heavy worn teeth, crown view; **C**, same under high magnification. **Arrow** indicate acrodin cap. Scale bars: 100 μ m.

black arrow). The total number of lepidotrichia reaches nine. There is a large, circular preanal scute between the pectoral and anal fins (Fig. 6C).

The dorsal fin is not very long based but extends all the way down to the caudal peduncle (Figs 6B, D; 7B). Part of the lepidotrichia has been lost, which makes it impossible to establish their total number. The observed rays do not branch. The caudalmost fin rays are the shortest and the most delicate. Apparently, the radials (baseosts *sensu* Stensiö 1932) were hourglass shaped (Fig. 7B). The anal fin is very similar to the dorsal fin in terms of shape, but it has a slightly shorter base (Figs 6C, D; 7D). Part of the lepidotrichia is also missing, and the preserved rays indicate that their total number was not less than 40. These preserved distal radialis were also hourglass shaped. Above the distal radialis there are several obliquely oriented, hourglass shaped bones (inclined backwards) that are tapered in the middle and expanded at the ends (Fig. 7D). We assume that these are proximal radials (axonosts *sensu* Stensiö 1932). The bones are not associated with the vertebral column and, apparently, were unpaired (the observer sees only the bones of the right side of the body). Two rows of large radials are characteristic of some early ray-finned fishes, for example, for *Pteronisculus* White, 1933 (Nielsen 1942). However, the unpaired fins of *E. soloduchoi* are better compared to those of *Bobasatrania groenlandica* Stensiö, 1932, and consist of the same elements (Stensiö 1932). Neotype of *E. soloduchoi* differs from *B. groenlandica* in the absence of dorsal fin axonosts, but this is due to the poor preservation of the specimen. The caudal fin is heterocercal but equilobate (Figs 5; 6D). Some of the lepidotrichia are damaged, the unpreserved rays indicate that there were at least 35 of them. The fin rays gradually shorten toward the center of the fin and branch distally. The lowermost ray of the ventral lobe is much shorter than the successive rays and have tapered, spine-like distal segments (Fig. 7G). Caudal ridge scales (“fulcra” *sensu* Zidek 1992) form the ridge of the caudal lobe and have tapered, spine-like distal projections (Figs 6D; 7F). Their exact number cannot be determined due to poor preservation.

Squamation

The squamation consists of 40 scale rows between the postcleithrum and the end of the caudal peduncle (Fig. 5). Body rows are nearly vertical, with body scale rows only slightly anteriorly inclined, while rows on caudal peduncle are strongly decline posteriorly. The flank scales are rectangular (Fig. 5), low along the ventral and dorsal margins of the body and caudal peduncle and tall otherwise. Pegs for articulations between scales are triangular, tall and well developed. Antero-dorsal and postero-dorsal corners are not pronounced because they are merged with the very wide base of the dorsal peg. The free field consists of cylindrical, nearly parallel, vertical or subvertical ridges. The ridge scales (Fig. 7E) are triangular in lateral projection and bear presumably ganoin-covered denticles (as indicated by ultrasculpture of thin, vertically stretched microtubercles).

Dentition

The teeth of the neotype are partly embedded in the rock, but are better preserved (Fig. 8). The teeth are wide in the lower part and cylindrical in cross section. The maximum width of the tooth is approximately equal to the width of the base. The apex is domed. The apex of the tooth is crowned by a cusp (i.e., acrodin cap), which can be distinguished by translucency relative to the rest of the tooth. The cusp is separated by a sharp angulate inflection. The cusp has the shape of a slightly pointed dome, and together with the tooth forms a compound dome. The surface of the cusp is smooth, but the rest of the tooth bears delicate longitudinal striations. Slightly worn isolated teeth (Fig. 9A) have a slightly pointed cusp, while most of the teeth in the neotype have markedly flattened cusps (Fig. 8B, C), which may indicate some tooth wear. Most of the teeth in the sample are quite heavily worn, and their upper surface is covered with numerous scratches. Some teeth have been worn down to form a flat surface with openings for dentine tubules visible on the surface (Fig. 9B, C). Minikh (1992) noted that the maxilla and the dentary were edentulous, and only the palatine bones bear rod-shaped teeth. However, our observations do not confirm this.

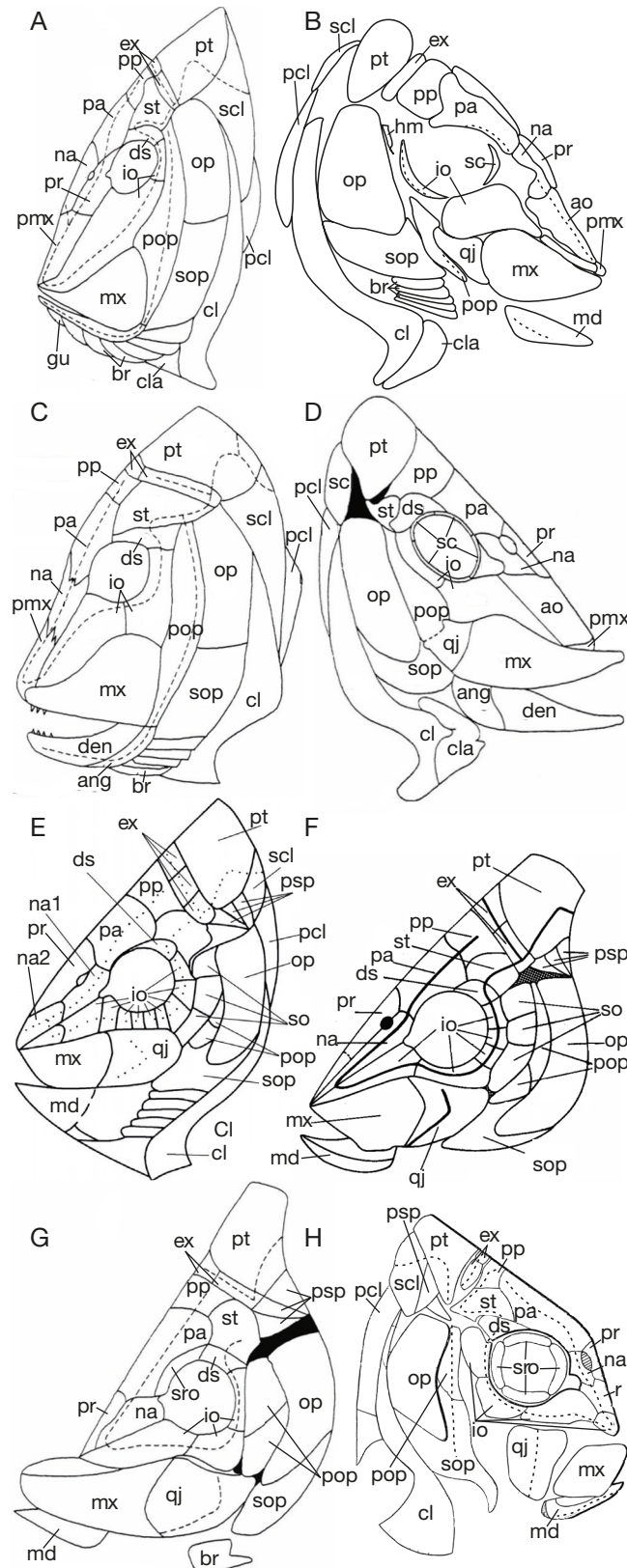


FIG. 10. — Restorations of the head of: **A**, *Platysomus superbus* Traquair, 1881 (from Moy-Thomas & Dyne 1938); **B**, *Platysomus swaffordae* Mickle & Bader, 2009; **C**, *Platysomus striatus* Agassiz, 1833 (from Haubold & Schaumberg 1985); **D**, *Platysomus schultzei* Zidek, 1992 (from Zidek 1992); **E**, *Platysomus biarmicus* Von Eichwald, 1861 (from Minikh & Minikh 2009); **F**, *Platysomus gibbosus* (Blainville, 1818) (from Campbell & Phuoc 1983); **G**, *Ebonaqua ritchiei* Campbell & Duy Phuoc, 1983 (from Campbell & Phuoc 1983); **H**, *Bobasatrania mahavavica* White, 1932 (from Lehman 1956). Abbreviations: **ao**, antorbital; **br**, branchiostegal rays; **cl**, cleithrum; **cla**, clavicle; **ex**, extrascapulars; **hy**, hyomandibula; **io**, infraorbital bones; **md**, mandible; **mx**, maxilla; **na**, nasal bone; **op**, operculum; **pa**, parietal bone; **pp**, postparietal bone; **pcl**, postcleithrum; **pmx**, premaxilla; **pop**, preoperculum; **pr**, postrostral; **pt**, posttemporal; **qj**, quadratojugal; **sc**, sclerotic; **scl**, supracleithrum; **sop**, suboperculum.

REMARKS

The jaws of *E. soloduchi* are less protruding than in *E. macrurus*. *Eurysomus soloduchi* is a much smaller species that also has a smaller caudal fin and narrower caudal peduncle in relation to the body size and the pelvic fin is located much closer to the anal. *E. macrurus* has two rows of clavate teeth with a flattened grinding surface and constricted neck (King 1850; Young 1866; Schaumberg 1976; Haubold & Schaumberg 1985) and an acrodin cap that is wide and flat, and circumscribed by a fine sulcus (King 1850; Geinitz 1861; Schaumberg 1976: abb. 31; Haubold & Schaumberg 1985: abb. 107), whereas *E. soloduchi* has teeth that are cylindrical in cross section and crowned by a slightly pointed dome-shaped acrodin cap. Differences in tooth structure appear to reflect slightly different foraging strategies in these species.

DISCUSSION

SYSTEMATIC IMPLICATIONS

The taxonomy of Paleozoic deep-bodied actinopterygians is difficult and controversial. There is currently no satisfactory classification of the “platysomids” *sensu lato*. Multiple sources have stated “platysomids” (especially *Platysomus*) are in need of revision (Campbell & Phuoc 1983; Zidek 1992; Mickle & Bader 2009; Sallan & Coates 2013; Wilson *et al.* 2021). It is worth noting that many groups of deep-bodied fishes have been extracted from “platysomids” and placed into Eurynotiformes (Sallan & Coates 2013; Friedman *et al.* 2018; e.g. styracopterids, eurynotids, amphicentrids). A phylogenetic analysis did not resolve eurynotiforms and “platysomids” (here taken as including *Platysomus*, *Bobasatrania*, *Ebenaqua*, *Mesolepis*, and closely related taxa) as sister lineages (Giles *et al.* 2017). And the “platysomids” themselves were divided into two or three lineages: “higher” and “lower” (Zidek 1992) or Platysomidae (“lower platysomids” *sensu* Zidek), Bobasatraniiidae Stensiö, 1932 (“higher platysomids” *sensu* Zidek) and Mesolepididae (Schultze *et al.* 2021). Different species of the genus “*Platysomus*” are assigned to different families Platysomidae (*P. superbus*, *P. parvulus* Williamson, *P. striatus* Agassiz) and Bobasatraniiidae (*Platysomus swaffordae* Mickle, Bader, *P. schultzei* Zidek, *P. biarmicus*, *P. gibbosus* Blainville, *P. circularis* Newberry and Worthen). A comprehensive phylogenetic analysis of “platysomids” has not been done; with only a few deep-bodied taxa being included in some analyses (see Wilson *et al.* 2021). However, our phylogenetic analysis did not resolve “platysomids” as a monophyletic group and divided Platysomidae (*Platysomus superbus* Traquair, 1881) and Bobasatraniiidae (*Bobasatrania groenlandica* Stensiö, 1932 and *Ebenaqua ritchiei* Campbell & Phuoc, 1983) into different clades (Giles *et al.* 2017). Unfortunately, Mesolepididae has not been included in any phylogenetic analysis.

The main problem of “platysomids” systematic is that most genera and species are too poorly described (even if entire skeletons have been preserved, like *Platysomus tenuistriatus* Traquair; see Wilson *et al.* 2021: fig. 2a) for useful comparisons and phylogenetic analysis. Only a few fishes were

described in detail, like *Bobasatrania mahavavica* (White 1932), *B. groenlandica* (Stensiö, 1932), *Platysomus schultzei* (Zidek 1992; Hodnett & Lucas 2021, *P. swaffordae* (Mickle & Bader 2009), *Ebenaqua ritchiei* (Campbell & Phuoc 1983). Thus, redescriptions based on undescribed specimens or new investigations of known specimens are important, especially for poorly known taxa. The designation of new neotypes, investigations into morphological characters that have not yet been described are important and help to set the stage for phylogenetic investigations that are necessary to form a better understanding of these fishes. Due to ‘*Platysomus*’ being considered a paraphyletic taxa, we will compare *E. soloduchi* with specific well known ‘*Platysomus*’ species.

The type species *Eurysomus macrurus* (Agassiz, 1833) is one of the rarest fish in the upper Permian of the Central Europe and Western Europe – Kupferschiefer and Marl Slate (Münster 1842; King 1850; Diedrich 2009) Despite this, almost complete skeletons have been found (King 1850). However, *Eurysomus* has not been revised since that time and thus lacks a sufficiently detailed description. In particular, the skull of the most complete specimen is damaged and described very briefly (King 1850: table 26). However, the complex of features of *E. macrurus* presented in various articles makes it possible to reliably distinguish it from *E. soloduchi* (see Remarks). *E. macrurus* and *E. soloduchi* differ from each other and may even belong to different genera. In order to examine this possibility, a sufficiently detailed description of the skull of *E. macrurus* would be necessary and this is beyond the scope of this study. *E. soloduchi* is not sufficiently well preserved to permit detailed comparison with other platysomids, and many significant characters – especially those relating to the cranium – cannot be considered. However, the height operculum with the rounded, convex ventral margin, which sits within the concave margin of the suboperculum, and low, wide, J-shaped suboperculum are much closer to what is seen in Bobasatraniiidae (*sensu* Schultze *et al.* 2021), *Platysomus swaffordae* Mickle & Bader, 2009 (Fig. 10B), *P. schultzei* Zidek, 1992 (Fig. 10D), *P. biarmicus* (Fig. 10E), *P. gibbosus* (Blainville 1818) (Fig. 10F), *P. circularis* Newberry & Worthen, 1870 (Eastman 1903), *Ebenaqua ritchiei* (Fig. 10G), *Bobasatrania mahavavica* White, 1932 (Fig. 10H), *Ecrinesomus dixonii* Woodward, 1910 (Lehman, 1956) than in Platysomidae (*sensu* Schultze *et al.* 2021), *P. superbus* (Moy-Thomas & Dyne 1938), *P. parvulus* Williamson, 1849 (Moy-Thomas & Miles 1971), *P. striatus* Agassiz, 1833 (Haubold & Schaumberg 1985) and Mesolepididae (*sensu* Schultze *et al.*, 2021) *Mesolepis micropterus* Traquair, 1879 (Traquair 1879). The skull bones sculpture of *E. soloduchi*, which is defined by the upper part of the skull roof covered with separate randomly distributed tubercles, which below turn into vertical or subvertical cylindrical ridges, is very similar to *P. schultzei* (Zidek 1992), *P. swaffordae* (Mickle & Bader 2009), *Ebenaqua ritchiei* (Campbell & Phuoc 1983). Even the details of the suboperculum having sculpture of subvertical crests in the posterior part and radial crests in the anterior part are similar among these taxa. The scale morphology (shape, sculpture, etc.) is very similar to most other platysomids, for which these

features are described: all members of *Platysomus* (Sallan & Coates 2013; Wilson *et al.* 2021), *Bobasatrania groenlandica* (Stensiö, 1932) and *Ebenaqua ritchiei* (Campbell & Phuoc 1983). Only *Kargalichthys* (*Palaeoniscimorpha inserte sedis* in Schultze *et al.* 2021) has a sharply different sculpture (Minikh 1992; A. Minikh & Minikh 2009; Bakaev 2022). In particular, the scale sculpture of *E. soloduchi* is almost indistinguishable from that of other “platysomids”, and consists of vertical or subvertical cylindrical ridges, (Aldinger 1937; Ivanov *et al.* 2021; Stensiö 1932). *Eurysomus* has no guard scales (scales, which runs parallel to the base of the dorsal and anal fins), like some Carboniferous platysomids (Wilson *et al.* 2021). *E. soloduchi* has both dorsal and ventral ridge scales on body margins anteriorly by dorsal and anal fins respectively, unlike Mesolepididae *M. micropterus* Traquair (Traquair 1879) and some Platysomidae *Paramesolepis rhombus* (Traquair) (Moy-Thomas & Dyne 1938). There are spines on the ridge scales of *Bobasatrania*, *Ebenaqua*, and *Platysomus gibbosus* (Stensiö 1932; Campbell & Phuoc 1983), but it is not entirely clear how similar they actually are to those of the ridge scales of *Eurysomus*. Apparently, the spines of *Eurysomus* are shorter and not bent back, unlike these other platysomids.

Eurysomus had no phyllodont tooth plates (Johnson & Zidek 1981; Fracasso & Hovorka 1987; Zidek 1992; Böttcher 2014), which are characteristic for the *Platysomus schultzei*, *Schaefferichthys leuderensis* and all *Bobasatrania* spp. (platysomid-bobasatraniid lineage) (Zidek 1992; Böttcher 2014). A phyllodont tooth plate consists of several layers of superimposed, rounded teeth. Apparently, the ability to eat hard food was achieved independently. At the same time, the presence of marginal teeth is similar to *P. striatus*, (Zidek 1992), *P. superbus*, *Paramesolepis rhombus* (Moy-Thomas & Dyne 1938), and *Mesolepis micropterus* (Traquair 1879). However, tooth morphology is distinctly different. The pelvic fins are present in *Ebenaqua ritchiei*, *P. gibbosus* (Campbell & Phuoc 1983), *P. biarmicus* (Minikh A. & Minikh 2009), and the “lower” platysomid *P. superbus* (Moy-Thomas & Dyne 1938), and in *P. parvulus* (Young 1866), *Eurysomus*. The pelvic fins of *P. biarmicus* are very small and were found after publication of Zidek (1992), which incorrectly indicates their absence. Thus, the pelvic fins cannot be used to classify *Eurysomus* exactly. As a result, it can be concluded that *Eurysomus* can't be exactly classified with the current state of our understanding of platysomids, and until more detailed descriptions of the of *E. macrurus* and/or *E. soloduchi* new specimens are published. But *Eurysomus* distinctly differ from *Mesolepis micropterus*, *E. soloduchi* could be placed at an intermediate position between Platysomidae and Bobasatraniidae, because it has features of both Platysomidae (*P. superbus*, *P. parvulus*, *P. striatus*) and Bobasatraniidae (*Platysomus swaffordae*, *P. schultzei*, *P. biarmicus*, *P. gibbosus*, *P. circularis*).

FUNCTIONAL CONSIDERATIONS

Esin (1997) previously classified *Eurysomus* as a specialized durophage. However, it is quite difficult to prove strict durophagy (see above Purnell & Darras 2015), and it is much more correct to speak of the ability to process hard prey.

For example, even such “established” durophagous actinopterygians as pycnodonts were actually more ecologically plastic, and were mainly generalists (and in some cases predators, see Vullo *et al.* 2017) capable of feeding on hard prey, rather than specialized durophages (Poyato-Ariza 2005; Cooper & Martill 2020). Several features support the potential for durophagy in *Eurysomus*.

In particular, low lever ratios (and relative jaw size) are a crude correlate with durophagy. Lower mechanical advantage (Barel 1982) has been applied to investigate contrasts in feeding modes (Bellwood 2003). In addition, lower jaws of *Eurysomus* can be compared directly to the recent material (Bellwood 2003; Bellwood & Hoey 2004). Unfortunately, the preservation of *Eurysomus* skeletons does not allow an accurate calculation of the lower jaw mechanical advantage, as was done for other actinopterygians (Smithwick 2015; Friedman *et al.* 2018). However, the general proportions of the neotype skull and the position of the teeth (apparently reflecting the border of the upper and lower jaw) suggest that the jaw was short and high. Apparently, the lower jaw lever ratio of *Eurysomus* is equal to, or greater than, that of *Eurynotus crenatus* Agassiz, 1835 (Friedman *et al.* 2018), but was inferior to *Dapedium* Leach, 1822 (Smithwick 2015).

The second main morphological indicators for durophagy are teeth. Our understanding of tooth morphology and function has improved markedly in the last couple of decades and tooth morphologies can now be evaluated in a whole-dentition biomechanical context.

In many ray-finned durophagous fishes, molariform teeth form broad dental surfaces (e.g. several rows of closely packed teeth or, in some cases, coalescence of non-shedding teeth). They are located on the inner dental arcade of upper and lower jaws: vomer and coronoids or prearticular in pycnodonts (Kriwet 2005; Vullo *et al.* 2017); dermopalatines and coronoids or prearticular in eurynotiforms (Friedman *et al.* 2018), dapediids (Smithwick 2015), some semionotiforms (López-Arbarello & Sferco 2011) and lepisosteiforms (Leuzinger *et al.* 2020). However, in some durophagous actinopterygians broad dental surfaces are located on the outer dental arcade: premaxilla and dentary in gymnodont tetraodontiforms (Tyler 1980), sparids (Elgendy *et al.* 2016; Germain & Meunier 2020), and scarine wrasses (Viviani 2019). Some taxa bear broad dental surfaces on the pharyngeal jaw, like in durophagous cichlids (Purnell & Darras 2015). Broad dental surfaces consisting of phyllodont tooth plates, are seen in some platysomids (see above) and Cretaceous phyllodontids (Estes 1969) and lingual dental plates formed by several superimposed layers of closely packed teeth, with the external crushing surface forming a smooth surface are found in some Osteoglossomorpha (Meunier *et al.* 2013). Molariform teeth of *Eurysomus* are located on the outer dental arcade of the maxilla and dentary. This variant is closest to modern sparids, but there is an important difference in that the maxilla bears molariform teeth in *Eurysomus* whereas it is the premaxilla in sparids. The exact number of tooth rows in *Eurysomus* is unknown but it may be that there are two rows in *E. macrurus* and one in *E. soloduchi*. With either one or

two rows found in *Euryosomus*, the teeth do not form broad dental surfaces, which sharply distinguishes this genus from all the durophagous actinopterygians listed above. However, there are durophagous vertebrates with one row of molariform teeth, not among actinopterygians, but among lizards. For example, *Dracaena* Daudin, 1802 (Lacertilia, Teiidae) has one row of teeth and feeds on gastropods (Dalrymple 1979). Thus, the distribution pattern of molariform teeth in the jaws of *Euryosomus* does not necessarily confirm the possibility of durophagy, but does not reject it either.

Some fishes have incisiform teeth in the anterior part of the jaws, and molariform teeth in the back. Pycnodonts (Kriwet 2005; Poyato-Ariza 2005), dapediids (Smithwick 2015), sparids (Elgendy *et al.* 2016; Germain & Meunier 2020) have such heterodont arrangement. As noted for sparids, heterodonty allows for easier switching between different types of prey (i.e., promotes a more generalized type of feeding), and this species demonstrates a generalist feeding ecology, but with a strong element of durophagy (Vandewalle *et al.* 1995). *Euryosomus soloduchi* does not bear heterodont dentition, which limits its trophic possibilities. For example, this excludes piscivory, which has been shown for *Dapedium* (Smithwick 2015), but does not exclude feeding on small, soft-bodied organisms, as has been shown for some sparids (Potter *et al.* 2022).

Molariform teeth bearing an apical cusp are best for crushing hard prey (Crofts & Summers 2014). The cusp concentrates forces and increases stress on the prey item, thereby reducing the load needed to crush the shell. The unworn teeth of *Euryosomus* approximately correspond to models H 3, 4 and R 3, 4 Crofts & Summers (2014). A taller cusp would have made it possible to break shells even more effectively (models H 5 and R 5). However, this does not happen, because “[...] here is likely some trade-off between reducing the load needed to break the prey item and dissipating the load safely so the tooth does not fail.” (Crofts & Summers 2014: 8). In addition, the toothplates of Carboniferous *Eurynotus crenatus* and *Amphicentrum granulosum* Young, 1866 (Friedman *et al.* 2018) and some Devonian lungfishes (Cui *et al.* 2022) bear cusps with acute tips, which are arranged in rows. The teeth of recent sparid *Diplodus sargus* Linnaeus, 1758 bear cusps with acute tips too (Vandewalle *et al.* 1995). In this case unworn molariform teeth of *Diplodus sargus* are extremely similar to the apparently worn teeth of some specimens of *Euryosomus macrurus* (Schaumberg 1977: abb. 32). This strange situation requires further consideration.

The final evidence of durophagy in *Euryosomus* is severe tooth wear, but which indicates how the tooth was actively used (Purnell & Darras 2015). Teeth of the neotype *E. soloduchi* show slight traces of wear. We suggest *E. soloduchi* was just as selective in food as some modern sparids (Potter *et al.* 2022), and ate more mechanically challenging food (for example, the hardest prey). Bivalves were found together with *E. soloduchi*, and might have made up part of its diet. However, there is a possibility that animals with a less resistant skeleton but lower preservation potential (e.g. crustaceans or thin-shelled gastropods) were preferred.

Thus, we conclude that *E. soloduchi* was able to feed on hard prey, but also fed on softer organisms, making it a generalist feeder with a strong element of durophagy.

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