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A new species of the surgeonfish genus †*Caprovesposus* (Acanthuridae) from the Lower to Middle Miocene of the North Caucasus, Russia

ALEXANDRE F. BANNIKOV[1], JAMES C. TYLER[2*] & DIANE M. TYLER[2]
[1]*Borissiak Paleontological Institute of the Russian Academy of Sciences, Profsoyuznaya 123, Moscow 117647, Russia*
aban@paleo.ru; *https://orcid.org/0000-0003-2022-4944*
[2]*Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560 USA*
tylerj@si.edu; *https://orcid.org/0000-0003-3202-080X*
tyler.diane@yahoo.com; *https://orcid.org/0000-0002-2928-7039*
**Corresponding author*

Abstract

A new species of fossil surgeonfish, †*Caprovesposus daniltshenkoi* **sp. nov.**, is described based upon two specimens from the terminal Maikopian (upper Lower to lower Middle Miocene; not less than 15 mya) in the northwestern Caucasus. The specimens were excavated from brownish gray clays in the bank of the Pshekha River in the Krasnodar Region of Apsheronsk District, Russia. Both specimens are in the acronurus presettlement stage of development and are placed within the formerly monotypic genus †*Caprovesposus* based upon their possession of vertically elongated, needle-like scales on the body. They differ from the Oligocene †*Caprovesposus parvus* Daniltshenko, 1960 in (1) lacking serrations on the frontal, mesethmoid, preopercle, and basipterygium; and (2) having the vertically elongated, needle-like scales only on the anterior and middle portions of the body, rather than on the entire body. Three additional, previously collected specimens from the Caucasus and Crimea are referred to the new species.

Key words: †*Caprovesposus daniltshenkoi,* acronurus presettlement stage, Maikopian, upper Lower to lower Middle Miocene, Krasnodar Region, Pshekha River, surgeonfish

Introduction

The monotypic genus †*Caprovesposus,* characterized by vertically elongated, needle-like scales on the body, was described by Danil'chenko (1960) for the Early Oligocene species †*C. parvus* from the Lower Maikopian of the Caucasus (Abkhazia and southwestern Russia). He placed the genus in the family Caproidae and proposed that "*Caprovesposus* possibly occupies an intermediate position between Caproidae and Grammicolepididae" and "possibly should be promoted into a family of the Order Zeiformes" (Danil'chenko 1967: 100). Bannikov & Fedotov (1984) established the new monotypic perciform family †Caprovesposidae; they were uncertain whether to attribute this family to the Percoidei or to the Acanthuroidei, so they placed it *incertae sedis* in the Perciformes. Subsequently, Bannikov (1991) placed the †Caprovesposidae in the Acanthuroidei.

Bannikov & Tyler (1992) conducted a revision of the material of †*Caprovesposus* that had been found from localities of various ages and that were housed within the collections of the Borissiak Paleontological Institute, Moscow. †*Caprovesposus* was shown to be the acronurus presettlement stage of an acanthurid. It has such derived features of the acanthurids as highly lobate teeth and a complex locking mechanism of the first two dorsal- and anal-fin spines.

Smirnov (1936) published a monograph on the fishes he collected from a rich locality in the North Caucasus, southwestern Russia (Chernaya Rechka near Vladikavkaz) (see Berezovsky *et al*. 2023). He dated this location to the Lower Oligocene, but later the age was changed to the Early Miocene by Danil'chenko (1960), who attributed the Chernaya Rechka locality to the Zuramakent Horizon of the Upper Maikopian. Smirnov (1939) added to the ichthyofauna of Chernaya Rechka a squamipinne fish that he identified as "*Chaetodon* (*Heptodon* sp. n.)." Danil'chenko (1980) erroneously named Smirnov's find as †*Chaetodon haplodon* Smirnov, 1939. Smirnov's

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material is lost; however, judging by his drawing (Smirnov 1939: text-fig. on page 140), the fossil fish does not belong to the butterflyfish genus *Chaetodon,* but, rather, to the genus †*Caprovesposus* (see Bannikov & Parin 1997; Bannikov 2010). It is worth noting, however, that Smirnov (1939) did not indicate the presence of needle-like scales on the body of the specimen in either his text or his drawing.

The species of Smirnov discussed above cannot be considered valid. Enclosed in parentheses and capitalized, the name *Heptodon* could be construed to be a subgenus, but then it would be a younger synonym of the genus of fossil tapirs *Heptodon* Cope, 1882. Even if Smirnov meant the species *heptodon,* he did not designate a type specimen. Also, the apparent loss of this specimen and the absence of even a photograph of it make it impossible to validate the Smirnov species.

Bannikov & Tyler (1992) referred two incomplete specimens from Upper Maikopian deposits to †*Caprovesposus* sp. The deposits are of the same age as the Chernaya Rechka locality; one is from the Belaya River (North Caucasus), and the other is from Cape Tarkhan (eastern Crimea).

In addition to the Maikop Group, †*Caprovesposus* sp. has been reported from the Eocene of the northern Caucasus (Bannikov & Tyler 1992) and the Middle Miocene of Egypt (Gaudant & Rouchy 1986). The report of †*Caprovesposus* sp. in the Miocene of Romania (Macarovici 1970) was based upon misidentified specimens (Bannikov & Fedotov 1989; Bannikov & Tyler 1992), whereas a specimen from the Oligocene (or more probably Middle to Upper Eocene; Haghipour & Brants 1971) of Iran and referred to by Arambourg (1967: 180, pl. XVII, fig. 3) as “incertae sedis” is most probably †*Caprovesposus* (Bannikov & Tyler 1992).

As a result of the first author’s field excavations in 2024, two specimens of the genus †*Caprovesposus* were found at a locality of the terminal Maikopian (upper Lower to lower Middle Miocene) in the northwestern Caucasus (Krasnodar Region, Pshekha River). Study of these finds has revealed that they represent a new species of †*Caprovesposus,* the second valid species of the genus.

Materials and methods

The material of the new species of †*Caprovesposus* is in the collection of the Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN RAS). The two specimens come from the left bank of the Pshekha River, upstream of Shirvanskaya settlement, and just downstream from the local bridge (Krasnodar Region, Apsheronsk District, southwestern Russia; 44.367936°N, 39.795570°E). They were collected from thin, laminated, brownish gray, silky clays of the Clayish-Siderite Formation of the terminal Maikopian (lowermost Middle Miocene, correlated with the basal Langhian; Beluzhenko 2010; Popov *et al*. 2022, 2023). The specimens have a standard length (SL) of 18 and 28 mm. They were prepared using a bayonet-shaped medical probe and subsequently were examined using a Leica M165C binocular microscope and a TESCAN VEGA scanning electron microscope (SEM) at the PIN RAS.

Abbreviations and symbols: mya = million years ago; ns = neural spines; PU = preural vertebra; U = ural vertebra.

The dagger symbol (†) indicates fossil taxa. The approximate symbol (~) is used when precise measurements are not possible because of poor preservation or obscured features. All measurements are in millimeters (mm).

Systematic paleontology

Family ACANTHURIDAE Bleeker, 1859

Genus †*Caprovesposus* Daniltshenko, 1960

†*Caprovesposus daniltshenkoi* sp. nov.

Figures 1–4

Chaetodon (*Heptodon* sp. n.) Smirnov, 1939: 139, text-fig. on p. 140.
Chaetodon haplodon Smirnov, 1939 (lapsus calami).—Danil’chenko, 1980: 140.
Caprovesposus sp. Bannikov & Tyler, 1992: 816.
Caprovesposus sp. 2. Bannikov, 2010: 125.

Holotype. PIN 5917/6, a relatively well preserved, nearly complete, articulated skeleton with counterpart; SL 28 mm (Figs. 1–4).

Horizon and locality. Left bank of the Pshekha River, upstream of Shirvanskaya settlement, and just downstream from the local bridge (Krasnodar Region, Apsheronsk District, southwestern Russia; 44.367936°N, 39.795570°E; Popov *et al*. 2023: fig. 36); uppermost part of the Maikop Group (correlated with the basal Langhian), basal-most Middle Miocene (not less than 15 mya; Popov *et al*. 2023).

FIGURE 1. Holotype of †*Caprovesposus daniltshenkoi* **sp. nov.**, PIN 5917/6, 28 mm SL; uppermost Maikopian (basal Middle Miocene) of North Caucasus (Pshekha River). A, lateral view. B, lateral view of counterpart. Scale bars 5 mm.

Referred specimens. PIN 5917/7, a relatively well preserved, nearly complete, articulated skeleton in a single plate; SL 18 mm; from the type locality. The following incomplete specimens, mentioned by Bannikov & Tyler (1992: 816) from the upper Maikopian, also likely belong to the new species: PIN 3363/102, Belaya River, Adygea, North Caucasus; PIN 3974/9, Kerch Peninsula, Crimea.

Diagnosis. A †*Caprovesposus* species that differs from †*C. parvus* Daniltshenko, 1960 by the following combination of characters: (1) no serrations on the frontal, mesethmoid, preopercle, and basipterygium; and (2) needle-like elongate scales present only on the anterior and middle parts of the body (versus on the entire body), whereas closer to the caudal peduncle the scales become rounded.

Description. Measurements of the holotype as percent of SL are as follows: body depth 53.0; caudal peduncle depth 10.0; length of head 33.8; least distance between anterior edge of orbit and profile (approximately medial edge of frontal) 4.7; length of first dorsal-fin spine 6.1; length of second dorsal-fin spine 13.6; length of last dorsal-fin spine 15.0; length of spiny dorsal-fin base 27.7; length of entire dorsal-fin base 60.5; pre-anal distance 56.3; length of first anal-fin spine 5.9; length of second anal-fin spine 12.2; length of third anal-fin spine 13.8; length of entire anal-fin base 43.2; length of pelvic-fin spine 13.1; length of caudal fin 24.9.

The body is deep, ovoid in shape, with the dorsal profile slightly more convex than the ventral profile, apparently laterally compressed; the caudal peduncle is short and shallow. The maximum body depth is at the anal-fin origin. The eyes are relatively large and located above the middle of the head; the horizontal diameter of the orbit is ~3 times less than the head length.

Most of the head bones are poorly preserved. The head is deeper than long. The neurocranium is relatively deep. The parasphenoid projects along the lower border of the orbit; it is strong, almost straight, and has a ventrally directed longitudinal ridge. The supraoccipital is a low triangular dome above the deep braincase. The frontal is large; it forms most of the oblique antero-dorsal border of the head. The lateral ethmoid forms the anterior border of the orbit. The cheek region is covered by dense scales; therefore, the bones of the suspensorium are poorly distinguishable (Fig. 2A). The mouth is small, terminal, and apparently not protractile. The mandibular joint is located in front of the orbit. The teeth are large, few in number, and apparently uniserial. The teeth of the right and left sides of the jaws are superimposed upon each other, so their exact number is unknown, but there are approximately six to eight teeth in a single row in both the upper and lower jaws (Fig. 2). The teeth are highly lobate; the few completely preserved teeth have 9–12 lobes (Fig. 2B). The symphyseal border of the lower jaw is deep and oblique, and a single pore of the lateral line sensory canal is visible behind it (Fig. 2A); the dentary of the referred specimen PIN 5917/7 bears at least two prominent serrations along its lower edge. The shaft of the hyomandibula is strong and inclined anteroventrally. The opercular region is deep and narrow, but the limits of its individual bones are unclear. The preopercle is only slightly curved along its anterior edge, and no serrations are evident along its posterior and ventral edges. The bones of the hyoid and branchial arches are too poorly preserved to be described.

The vertebral column is almost straight and consists of 22 (9+13) vertebrae. Most of the vertebral centra are somewhat elongate, rectangular, and longer than high. A few of the anteriormost centra are shortened. The length of the abdominal portion of the vertebral column of the holotype is 1.9 times shorter than its caudal portion. The neural spines are stout; most of them are broadened antero-posteriorly. The neural spines of the anterior caudal vertebrae are the longest; they become shorter and somewhat narrower posteriorly in the series. Most of the neural spines are only slightly inclined posteriorly; those of the caudal peduncle are the shortest and are strongly inclined. The neural spine of PU3 is broad and pointed (as evident in the holotypic counterpart; Fig. 1B), whereas that of PU2 is a short crest. The anterior haemal spines are broad antero-posteriorly and almost vertical; they are longer than their corresponding neural spines. The haemal spines of PU2 and PU3 seem to be autogenous. Parapophyses are not evident. There are apparently seven pairs of ribs, which are moderately long and only slightly inclined; epineurals are not evident.

The caudal skeleton is characterized by the fusion of PU1, U1, and U2 into the terminal centrum; the parhypural and the five hypurals are separate. The large uroneural forms the stegural (as evident in the holotypic counterpart and referred specimen PIN 5917/7); the number of epurals is unclear. The caudal fin is moderately large and truncated; there are 16 principal rays (I,7-7,I) plus about six upper and about five lower procurrent rays.

There are no supraneurals. The single dorsal fin is long at the base; its spinous portion is shorter than its soft portion. There are nine spines and 20 or 21 soft rays in the dorsal fin; each spine has a prominent groove along its length. The two anteriormost dorsal-fin spines are supernumerary on the first pterygiophore; the first spine is the shortest, being less than half the length of the second spine; the second to ninth dorsal-fin spines of the holotype are

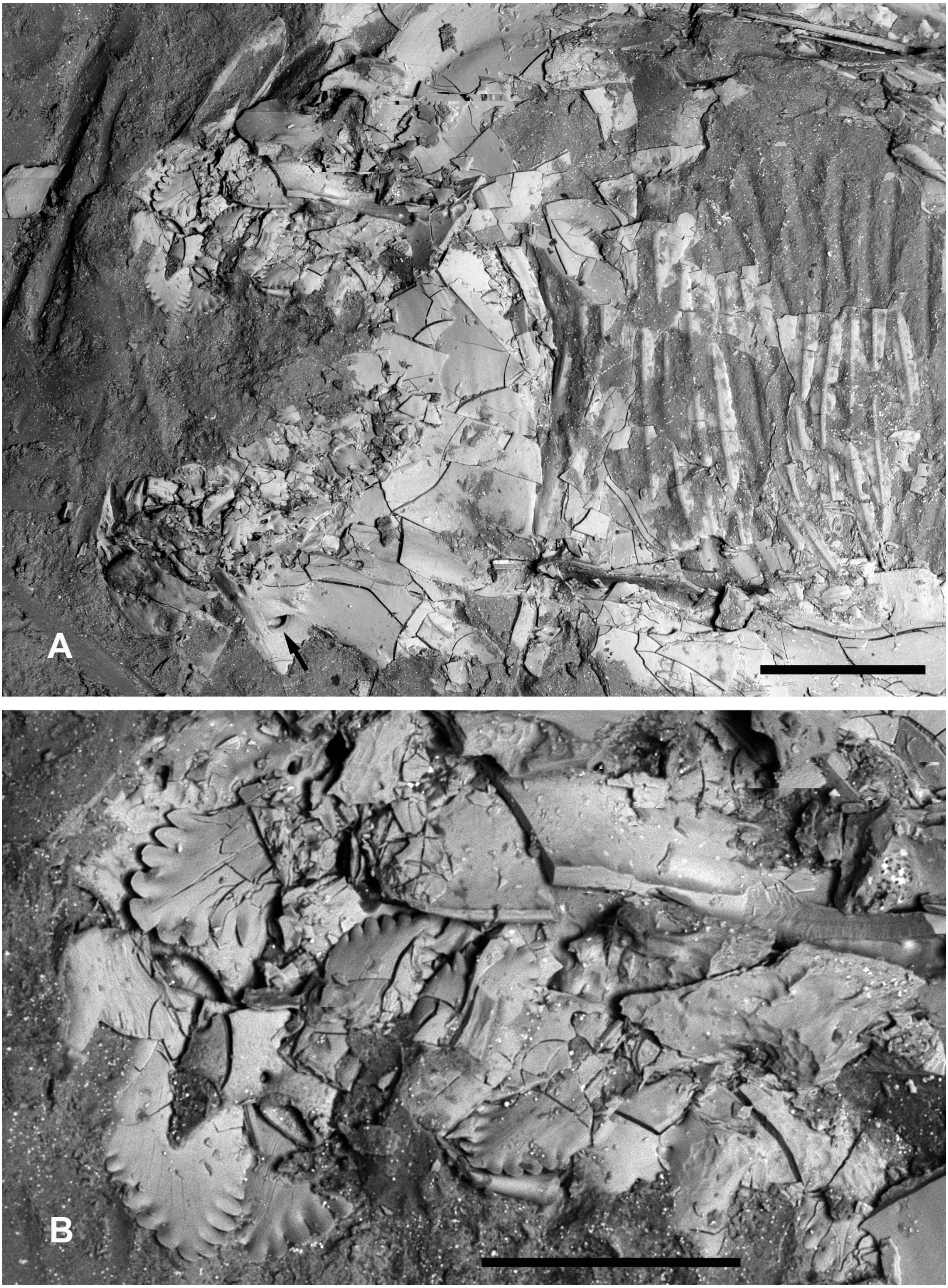

FIGURE 2. Holotype of †*Caprovesposus daniltshenkoi* **sp. nov.**, PIN 5917/6, scanning electron microscope images. A, mouth and cheek region; arrow points to the single lateral line pore; scale bar 1 mm. B, upper jaw; scale bar 0.5 mm.

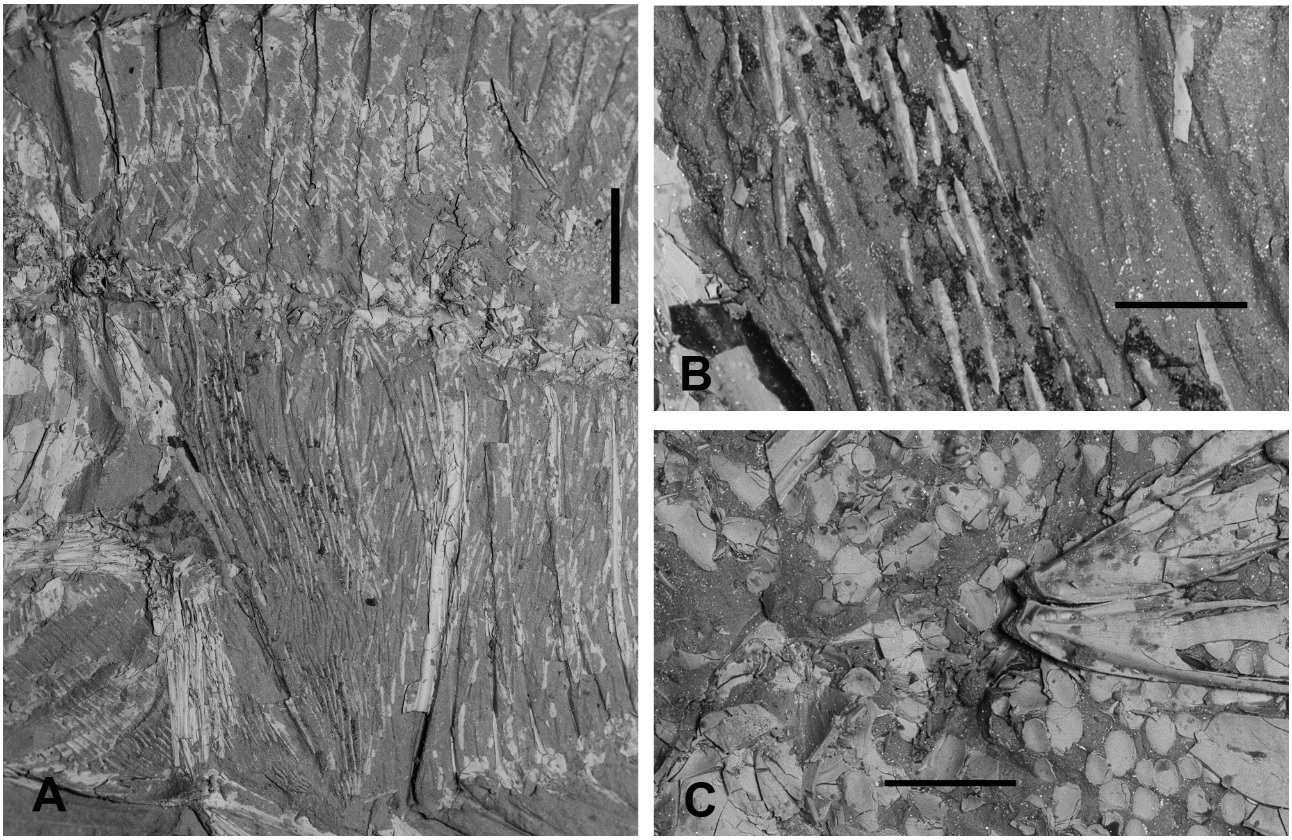

FIGURE 3. Holotype of †*Caprovesposus daniltshenkoi* **sp. nov.**, PIN 5917/6, scanning electron microscope images. A, middle portion of body; scale bar 2 mm. B, upper portion of abdomen; scale bar 0.5 mm. C, caudal peduncle region; scale bar 0.5 mm.

almost equal in length, whereas in the much smaller referred specimen PIN 5917/7, the second spine is significantly longer than the subsequent spines. Several anterior soft dorsal-fin rays are equal in length to the posterior dorsal-fin spines, but subsequent rays become gradually shorter. The first dorsal-fin pterygiophore is long and wide antero-posteriorly; it contacts the occipital region of the skull and the neural spine of the first vertebra (located in a preneural space). Anterior to the second dorsal-fin spine, the upper portion of the pterygiophore forms a rounded flange and has a deep indentation in front of it, thereby creating a complex locking mechanism of the first two dorsal-fin spines. The succeeding dorsal-fin-spine pterygiophores become gradually shorter and narrower; each of them occupies a single interneural space, except for the third interneural space (between the third and fourth neural spines), which is vacant. The pterygiophores of the soft dorsal-fin rays are moderately narrow; usually two of them are located in each interneural space.

The anal fin is long along the base; it has 3 spines and 20 soft rays; each spine has a prominent groove along its length. The first two anal-fin spines are supernumerary on the first pterygiophore. The first spine is the shortest, being less than half the length of the second spine. The second anal-fin spine of the holotype is somewhat shorter than the third spine, whereas in the much smaller referred specimen PIN 5917/7, the second spine is somewhat longer than the third. In the holotype, several anterior soft anal-fin rays are longer than the third anal-fin spine; subsequently, the rays become gradually shorter. The first anal-fin pterygiophore is very long and stout; anteriorly, it is in close contact with the first haemal spine. The lower end of this pterygiophore is widened antero-posteriorly and forms a complex locking mechanism similar to that of the first two dorsal-fin spines. The second and succeeding anal-fin pterygiophores are similar to those of the soft dorsal fin , although the more anterior ones are somewhat longer. The interhaemal spaces above the anal fin usually accommodate two anal-fin pterygiophores.

The posttemporal and supracleithrum are poorly preserved. The cleithrum is large and stout; its anterior margin is gently sigmoid. The strongly expanded coracoid and the posteroventral portion of the cleithrum form a very broad basin for muscle attachment. The scapula and pectoral radials are poorly preserved. The ventral postcleithrum is very long, almost straight, stout, and terminates distally close to the expanded anteroventral end of the first anal-fin pterygiophore. The pectoral fins are moderately large; they are positioned under the fourth vertebra and approximately midway between the vertebral column and the ventral edge of the body. The number of pectoral-fin rays is unclear in the holotype; at least 15 rays are recognizable in referred specimen PIN 5917/7.

The basipterygium is very long, has a low ventral ridge, and is attached to the cleithrum well above its ventral edge. The pelvic bone has a narrow posterior process behind the level of the base of the rays; this process terminates close to the distal end of the postcleithrum. The pelvic fin has a single spine and about five short soft rays. The pelvic-fin spine is similar to the second and third anal-fin spines in shape and length.

The entire body and the cheek region of the head are covered with scales. Anteriorly and mid-body the scales are narrow and strongly vertically elongate, have smooth edges, lack surface ornamentation, and have rounded distal edges (Fig. 3A,B). Toward the posterior of the body, the individual scales become shorter (Fig. 4), and those of the caudal peduncle are ovoid or even rounded rather than elongate (Fig. 3C). No evidence of caudal peduncle armature is recognizable. The lateral line is also not evident, except for a single pore posterior to the symphyseal border of the lower jaw.

Etymology. Named in honor of Dr. Pavel Georgiyevich Danil'chenko (1903–1993), a prominent Russian ichthyologist and paleontologist at the Borissiak Paleontological Institute of the Academy of Sciences, Moscow, who worked to advance the knowledge of the fossil fish fauna of Russia and surrounding areas.

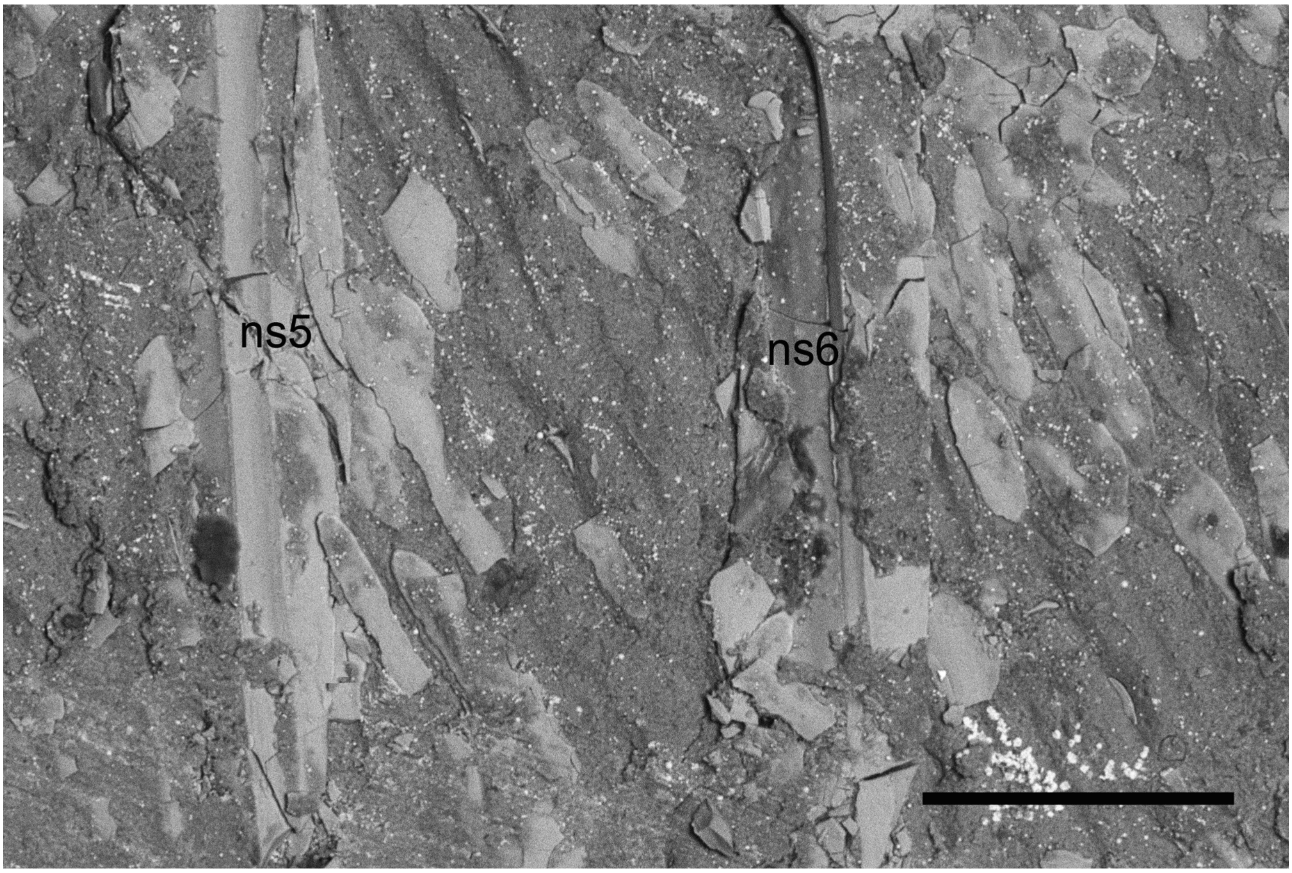

FIGURE 4. Holotype of †*Caprovesposus daniltshenkoi* **sp. nov.**, PIN 5917/6, scanning electron microscope image of middle portion of caudal region above the vertebral column. Abbreviations: ns5, ns6, neural spines of the fifth and sixth caudal vertebrae, respectively. Scale bar 0.5 mm.

Discussion

The skeletal structure of †*Caprovesposus daniltshenkoi* **sp. nov.**, described above, is typical of the acronurus presettlement stage of fossil and extant members of the Acanthuridae. Presently, two exclusively fossil genera of surgeonfishes are based solely upon their acronurus presettlement stage: †*Caprovesposus* Daniltshenko, 1960 from the Middle Eocene to the Lower Miocene of the Caucasus region (Bannikov & Tyler 1992); and †*Tauichthys* Tyler, 1999 from the Lower Eocene of the Bolca locality, northern Italy (Tyler 1999; Tyler & Bannikov 2000). The latter genus is characterized by the reduction in number of dorsal-fin spines to only four, which strongly differs from the nine spines in †*Caprovesposus*.

A number of specimens belonging to †*Caprovesposus* have been discovered from the Middle Eocene and the Lower Miocene, but to date, only the Oligocene Caucasian type species †*C. parvus* had been formally described (Danil'chenko 1960, 1980; Bannikov & Tyler 1992; Bannikov 2010). †*Caprovesposus daniltshenkoi* **sp. nov.**, described herein, differs from †*C. parvus* in having no serrations on the frontal, mesethmoid, preopercle, and basipterygium (versus serrations present on these structures in †*C. parvus*); and in having needle-like elongate scales covering only the anterior and middle parts of the body, with the scales becoming rounded close to the caudal peduncle (versus needle-like elongate scales covering the entire body in †*C. parvus*).

Paleoecology

The pelagic acronurus presettlement stages of the surgeonfishes †*Caprovesposus parvus* and †*C. daniltshenkoi* **sp. nov.** are known from several localities, but no adult specimens of these species are known from those localities. The high quality of preservation of fishes and other marine organisms at the Caucasian localities was the result of their deposition during anoxic episodes characteristic of the Maikopian deposits (Popov *et al.* 2022, 2023). Extant adult surgeonfishes tend to be bottom feeders, and it is reasonable to extrapolate that their fossil anticedents likely were bottom feeders too. Thus, they would have been very susceptible to an anoxic event. Clearly, the habitat of the acronurus presettlement stages of †*C. parvus* and †*C. daniltshenkoi* **sp. nov.** must have been different from that of the adults of these surgeonfishes.

Interestingly, the famous fish fauna of the Middle Eocene Bolca locality in northern Italy is characterized by an unusually high diversity of surgeonfishes (Blot & Tyler 1991; Bannikov 2014; etc.). The rich fossil deposits at Bolca are also thought to be the result of anoxic conditions: "The current taphonomic model for fishes invokes rapid accumulation of corpses on an anoxic bottom, where a well-developed microbial biofilm delayed their decomposition, protected them from scavengers and bottom currents, and promoted rapid mineralization" (Friedman & Carnevale 2018: 573). Adult surgeonfishes and acronurus presettlement stages have been found in the same deposits at Bolca; however, the acronurus presettlement stages of the genus †*Tauichthys* cannot be correlated with any of the genera of Bolca surgeonfishes that are known based on adult specimens from the same habitat.

Acknowledgments

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