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A new species of the fossil pufferfish genus †*Archaeotetraodon* (Tetraodontidae) from the Middle Miocene of the North Caucasus, Russia

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Abstract

The fossil puffer fish genus †*Archaeotetraodon* Tyler & Bannikov, 1994 is unique among the Tetraodontidae in having the upright central spinule of the dermal scale plates bifid rather than singular and undivided. Six species of this genus have previously been described variously from the Oligocene and Miocene of Russia, Italy, Algeria, and Ukraine. Described herein is a seventh species of this genus, †*Archaeotetraodon bemisae* sp. nov., based upon two specimens from the Pshekha River, Krasnodar Region, North Caucasus, Russia. These Maikopian specimens are no less than 15 mya, in the basal-most Middle Miocene. The new species is distinguished from the other six species in the genus by the following combination of characters: thick, sturdy, and smooth bifid spinules; frontal width broad over the orbit; 18 vertebrae; slender ventral postcleithrum; a moderately long rayless pterygiophore; height/length ratio of the posteriormost abdominal centrum being 0.78–0.79; 10 dorsal-fin rays; 9 anal-fin rays; and 14 pectoral-fin rays.

Key words: †*Archaeotetraodon bemisae*, Maikopian, basal-most Middle Miocene, Krasnodar Region, Pshekha River, Tetraodontiformes

Introduction

Pufferfishes are characterized by a suite of unique morphological and functional features, including the following: a remarkably simplified skeletal structure (see Tyler 1980); an inflatable body (see Wainwright & Turingan 1997); and a peculiar steady swimming mode with the simultaneous use of median and pectoral fins (Gordon *et al.* 1996). The Tetraodontidae includes more than 25 extant genera and three exclusively fossil genera that are known from variously intact skeletal remains. The fossil genera include the monotypic †*Leithaodon* from the Middle Miocene of Austria (Carnevale & Tyler 2015); †*Eotetraodon,* with three species (Tyler 1980; Bannikov & Tyler 2008; Tyler & Bannikov 2012) from the Eocene of Monte Bolca (Italy) and the Kuma Horizon (North Caucasus, Russia); and †*Archaeotetraodon,* with six species from the Oligocene of Russia and Ukraine and the Miocene of Russia, Italy, and Algeria (see Tyler & Bannikov 1994; Carnevale 2007; Carnevale & Tyler 2010; Bannikov 2010; Přikryl *et al.* 2022). The fossil record of the Tetraodontidae also includes a few disarticulated remains assigned to the species †*Sphoeroides hyperostosus* from the Pliocene of North Carolina (Tyler *et al.* 1992), as well as numerous isolated and systematically uninformative jaw bones (beaks), which are relatively common in Neogene marine and freshwater deposits throughout the world (for details see Carnevale & Tyler 2010, 2015).

†*Archaeotetraodon* is distinguished from all other tetraodontid genera in having bifid upright spinules protruding from the basal scale plates on at least the middle of the body (Bannikov 1990; Tyler & Bannikov 1994; Carnevale & Santini 2006; Bannikov 2010; Carnevale & Tyler 2010) and in the fusion of the haemal spine of the penultimate vertebra to the centrum (Bannikov 2010; Carnevale & Tyler 2010). Recently, two specimens of a new pufferfish were found during field excavations conducted by the Borissiak Paleontological Institute (PIN) of the Russian Academy of Sciences (RAS) at the locality of the most recent Maikopian fishes in the north-west of the Caucasus (Krasnodar Region, Pshekha River). The presence of bifid upright spinules protruding from the basal scale plates in

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the middle of the body clearly indicates that these two specimens belong to the genus †*Archaeotetraodon*. During previous excavations, †*A. jamestyleri* (Bannikov, 1990) had been found somewhat higher up in this geological section, within deposits of the Tarkhanian Regional Stage (Bannikov 2020). Popov *et al.* (2022, 2023) correlated the Tarkhanian Regional Stage with the Middle Langhian. The two new specimens of pufferfish from the most recent Maikopian are of early Middle Miocene age, making them somewhat older than †*A. jamestyleri,* and they differ from the latter by some morphological details. Therefore, we describe below a new species, †*Archaeotetraodon bemisae* sp. nov., for this late Maikopian Caucasian pufferfish.

Materials and methods

The materials for this research are the imprints of two complete fish skeletons from gray silky clays of the uppermost part of the Maikop Group (Beluzhenko 2002; Popov *et al.* 2022, 2023, etc.), collected on the left bank of the Pshekha River (Krasnodar Region), upstream of Shirvanskaya settlement, and just downstream from the local bridge. The skeletons have a standard body length (SL) of 24.5 and 50 mm.

The specimens were studied using a Leica M165C binocular microscope, as well as a TESCAN VEGA scanning electron microscope at PIN RAS. Specimens of previously described fossil species of pufferfishes were used as comparative material, as were osteological collections and X-ray photographs of the skeletons of extant pufferfishes listed by Carnevale & Tyler (2010, 2015).

The dagger symbol (†) indicates extinct taxa.

Systematic Paleontology

Subdivision TELEOSTEI sensu Patterson & Rosen, 1977

Order TETRAODONTIFORMES sensu Santini & Tyler, 2003 and Arcila & Tyler, 2017

Family TETRAODONTIDAE Bonaparte, 1832

Genus †*Archaeotetraodon* Tyler & Bannikov, 1994

†*Archaeotetraodon bemisae* sp. nov.

Figures 1–5

Holotype. PIN 5917/1, a single, relatively well preserved, nearly complete, articulated skeleton with incomplete counterpart; SL 50 mm (Figs. 1–4).

Paratype. PIN 5917/2, a relatively poorly preserved, nearly complete, articulated skeleton with fragment of counterpart; SL 24.5 mm (Fig. 5).

Horizon and locality. Left bank of the Pshekha River, upstream of Shirvanskaya settlement, and just downstream from the local bridge (Krasnodar Region, SW Russia; 44.367936 N, 39.795570 E); uppermost part of the Maikop Group (correlated with the basal Langhian), basal-most Middle Miocene (not less than 15 mya; Popov *et al.* 2022, 2023).

Diagnosis. An †*Archaeotetraodon* species defined by the following combination of characters: frontal width relatively broad over the orbit; 18 vertebrae, of which eight are abdominal; ventral postcleithrum slender; rayless pterygiophore moderately long; height/length ratio of the posteriormost abdominal centrum 0.78–0.79; pectoral fin with 14 rays; dorsal fin with 10 rays; anal fin with 9 rays; scales on most of the body with smooth bifid spinules, whereas posteriorly at least many of the scales have single undivided spinules; bifid spinules pointed, thick, and sturdy.

Description. In both specimens, the body is preserved in lateral view, whereas the neurocranium is in dorsal view in the part but is in ventral view in the counterpart. The body is moderately elongated, with a large and wide head. The dorsal- and anal-fin bases are moderately long and almost opposite each other (Figs. 1 and 5).

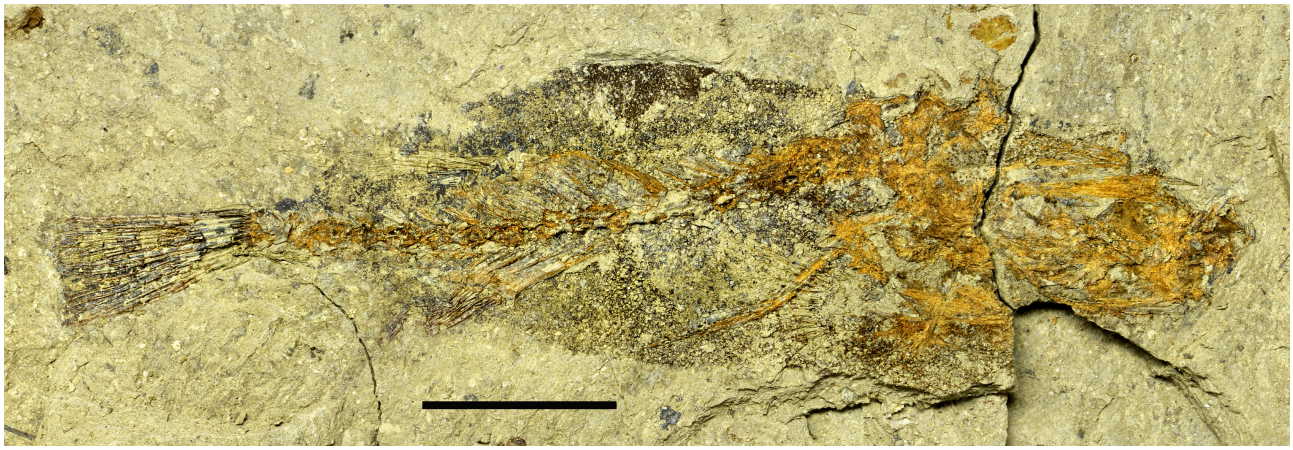

FIGURE 1. Holotype of †*Archaeotetraodon bemisae* sp. nov., PIN 5917/1, 50 mm SL; uppermost Maikopian (basal Middle Miocene) of North Caucasus (Pshekha River). Scale bar 1 cm.

The neurocranium is poorly preserved, with very few details recognizable. It is wider at the level of the sphenotics than at the level of the pterotics. Although most of the bony substance of the frontals is missing, it is evident that the frontal width is relatively broad over the orbit, about half the length of the neurocranium (without ethmoids). The limits of the bones of the neurocranium and ethmoid region are unclear. The size of the orbit is not evident; no sclerotic ossifications are present. The parasphenoid is robust, long, and thickened anteriorly in dorsal view.

The upper- and lower-jaw bones are only partially preserved (Fig. 2). The beak-like premaxilla has an almost straight biting edge. The smooth inner surface of the left premaxilla is exposed in the holotype and reveals two large, elongate trituration teeth and the sockets of three additional, smaller teeth; teeth are set in a longitudinal row just lateral to the premaxillary medial edge. Two large, elongate trituration teeth are also evident in the paratype, although the jaw region is less well preserved than in the holotype. The medial edge of the premaxilla is thick and has prominent interdigitations for articulation with the opposite premaxilla. The maxillae are too incompletely preserved to be described. The right mandible of the holotype is exposed in lateral view; the dentary has a smooth and sturdy beak-like anterodorsal portion. The posteroventral portion of the lower jaw is relatively poorly preserved; however, what we interpret to be the detached angulo-articular is present just anterior to the beak formed by the upper and lower jaws. The angulo-articular is ovoid in shape and thin, except for the thickened oval articular condyle located posteriorly.

The bones of the suspensorium, opercular series, and hyoid apparatus are incompletely preserved and not easily recognizable. The quadrate is relatively narrow, triangular, with a distinct articular condyle. The preopercle is long and strongly inclined anteriorly, with a somewhat concave and thickened dorsal margin. Its width is not evident, but it seems to be rather narrow. Only the anterior margin of the opercle is recognizable; it is long, inclined posteriorly, significantly thickened, and terminates dorsally with a concave articular facet. The hyoid bar is not clear; some saber-like branchiostegal rays are partly recognizable (including the enlarged flattened ray characteristic for puffers), but their precise number cannot be determined.

The vertebral column is very slightly concave dorso-ventrally and consists of 18 (8+10) vertebrae. The vertebral centra are somewhat elongate, rectangular, and longer than high. The length of the abdominal portion of the holotypic vertebral column is 1.4 times shorter than its caudal portion. The first three vertebrae possess relatively broad, rather high, and presumably bifid neural spines. The neural spine of the fourth vertebra is broad, presumably bifid anteriorly, and extends postero-dorsally to a tapering confluent spine. The subsequent neural spines are definitely single and posteriorly inclined; these are broad but very gradually become slender to the 13th vertebra, whose neural spine is the thinnest. The neural spines of the 14th to 17th vertebrae are shorter but broader distally. The haemal spines of the caudal vertebrae supporting the anal-fin pterygiophores are extremely short. These spines posterior to the anal-fin base are shorter than their corresponding neural spines and appear to become increasingly broad.

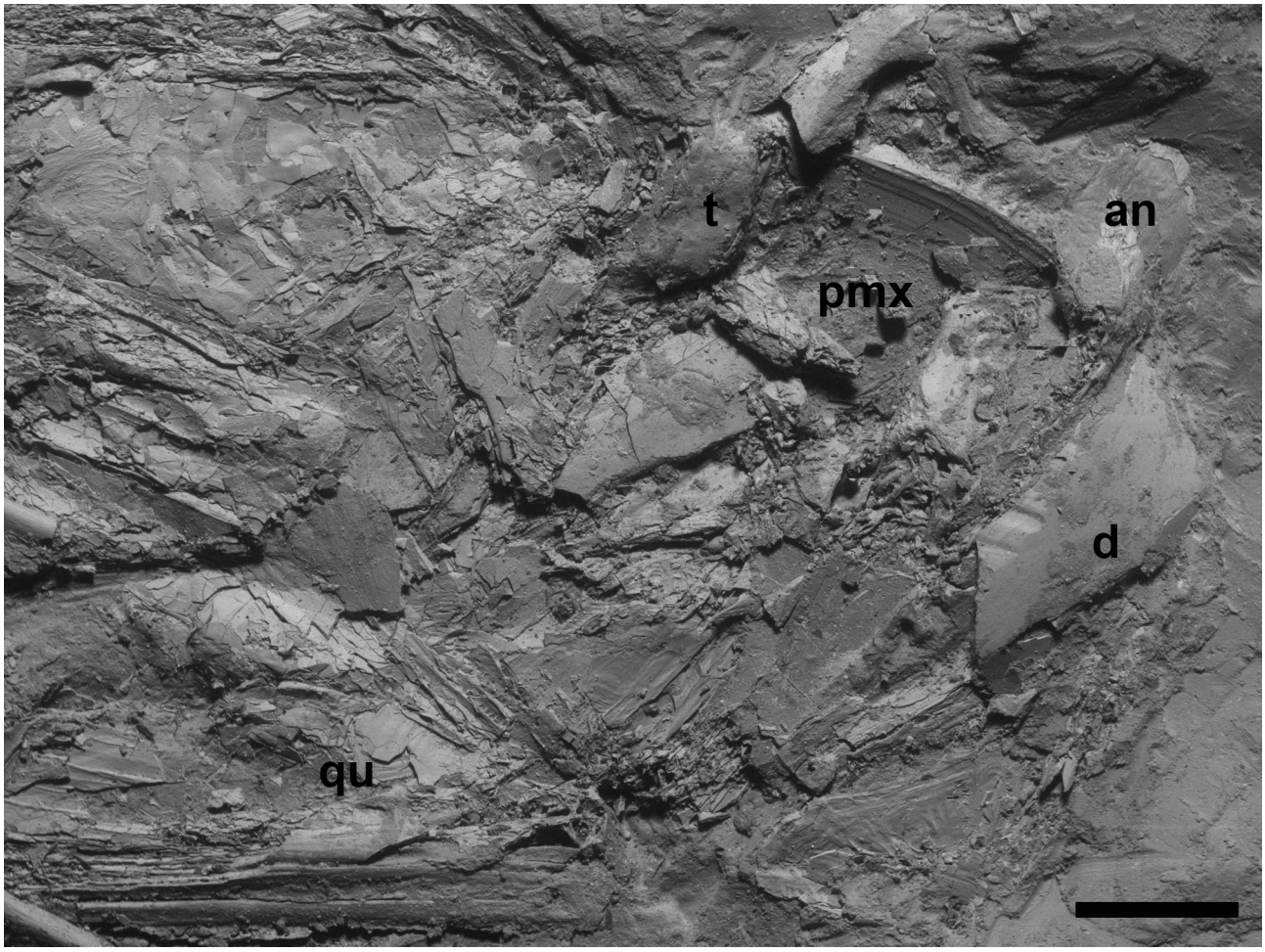

FIGURE 2. Holotype of †*Archaeotetraodon bemisae* sp. nov., PIN 5917/1, scanning electron microscope image of mouth region. Abbreviations: an, angulo-articular; d, dentary; pmx, premaxilla; qu, quadrate; t, trituration teeth. Scale bar 1 mm.

The caudal skeleton is relatively poorly preserved; it has the typical tetraodontid morphology of consolidated hypurals, with the hypaxial plate fused to the terminal centrum and the epaxial hypurals forming an autogenous triangular plate. The parhypural is evidently autogenous; the epural is not recognizable in the holotype, but it is indistinctly visible in the paratype. It is unclear if the haemal spine of the penultimate vertebra is fused to the centrum. The caudal fin is elongate; it consists of eight branched rays and two or three unbranched rays (one ray above and one or two below).

The eight dorsal-fin pterygiophores are located between the neural spines of the seventh to 12th vertebrae; the first pterygiophore seems to be the longest and the second the broadest. The first dorsal-fin pterygiophore forms an anterior prong to which a moderately long (corresponding to the length of two opposite vertebrae) and slender rayless pterygiophore articulates. The dorsal fin originates above the 11th or 12th vertebra. The dorsal fin is moderately long; it consists of 10 soft, segmented, and branched rays. The bases of the dorsal-fin rays form a spiky head (Fig. 3A).

The anal fin originates below the dorsal-fin origin or slightly behind it. There are six anal-fin pterygiophores; the first pterygiophore is especially long, thick, and very strongly inclined. The subsequent anal-fin pterygiophores rapidly decrease in length posteriorly in the series (Fig. 3B). The anal fin is moderately long; it consists of nine soft, segmented, and branched rays. The posterior anal-fin rays are shifted forward post-mortem in the holotype (Fig. 3B). The bases of the anal-fin rays are similar to those of the dorsal-fin rays, and they also form a spiky head.

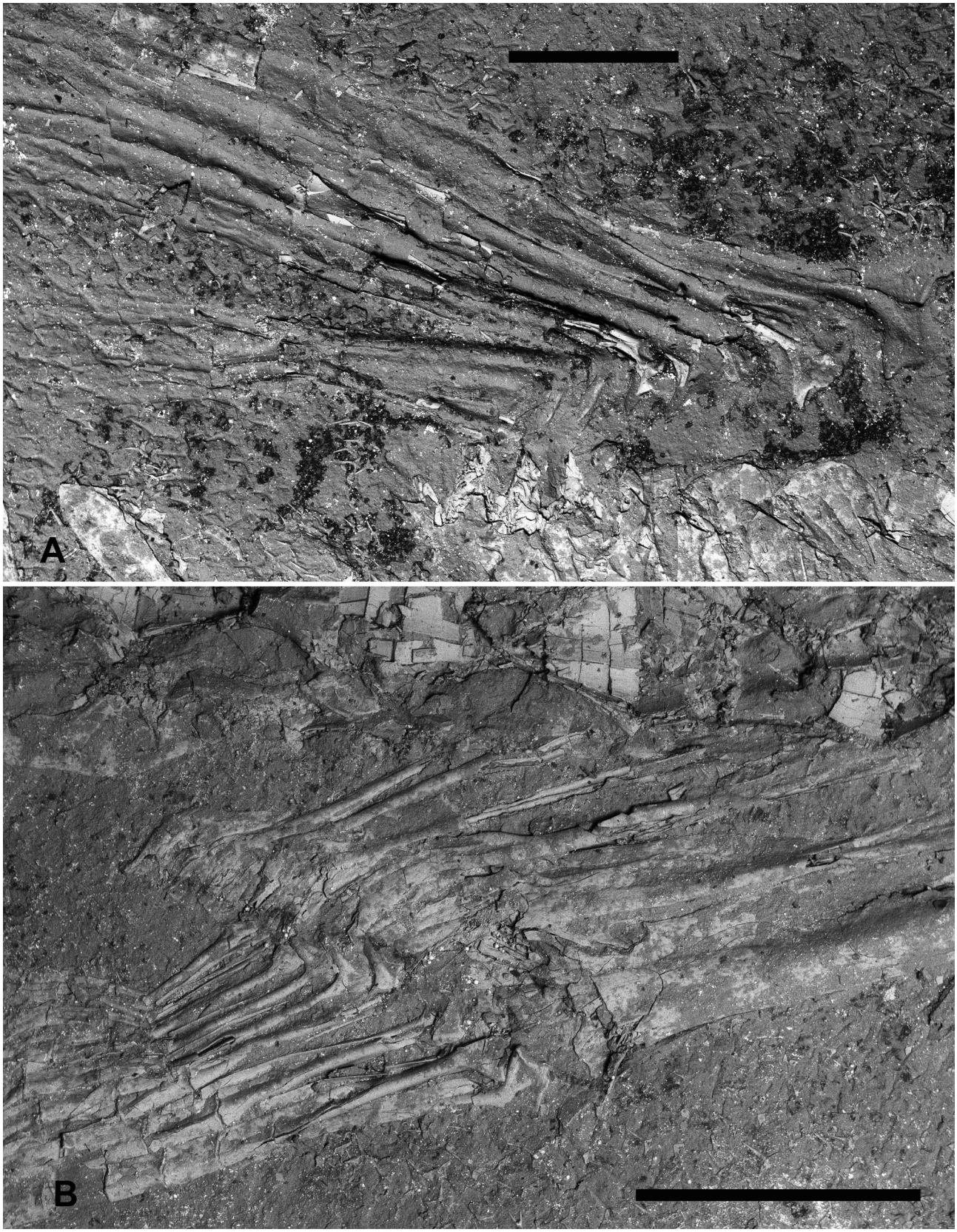

FIGURE 3. Holotype of †*Archaeotetraodon bemisae* sp. nov., PIN 5917/1, scanning electron microscope images. A, dorsal fin, scale bar 1 mm. B, anal fin, scale bar 2 mm.

Among the pectoral girdle bones, the cleithrum, coracoid, and scapula are difficult to recognize (best indicated in the holotypic counterpart). The supracleithrum is elongate and narrow anteriorly where it forms the rounded condyle for articulation with the pterotic. The postcleithrum forms a long, narrow, somewhat curved bar; the ventral and dorsal postcleithra of the holotype are disarticulated post-mortem. Greatest width of the ventral postcleithrum is about 20 times in length. The pectoral radials are rather large; the second and third radials are constricted in the middle, creating an hourglass shape. The fourth radial is concave on the side toward the third radial. The first pectoral radial is reduced to a wedge between the distal regions of the scapula and the second radial. The pectoral fin consists of 14 rays, which are preserved only basally in both specimens. The base of the pectoral fin is relatively wide and sub-vertically oriented.

The entire body is covered with small spinulose scales. Most of these scales have a stellate basal plate from which arise rather thick and sturdy spinules that are bifurcate from the base and divergent distally (Fig. 4). The width of the basal region of the scale at the level of the bottom of its bifurcation is 2.7 to 3 times into the length of the scale spine from this same basal region to the distal end of the scale spine. Many of the scales located posteriorly on the body have single rather than bifid spinules.

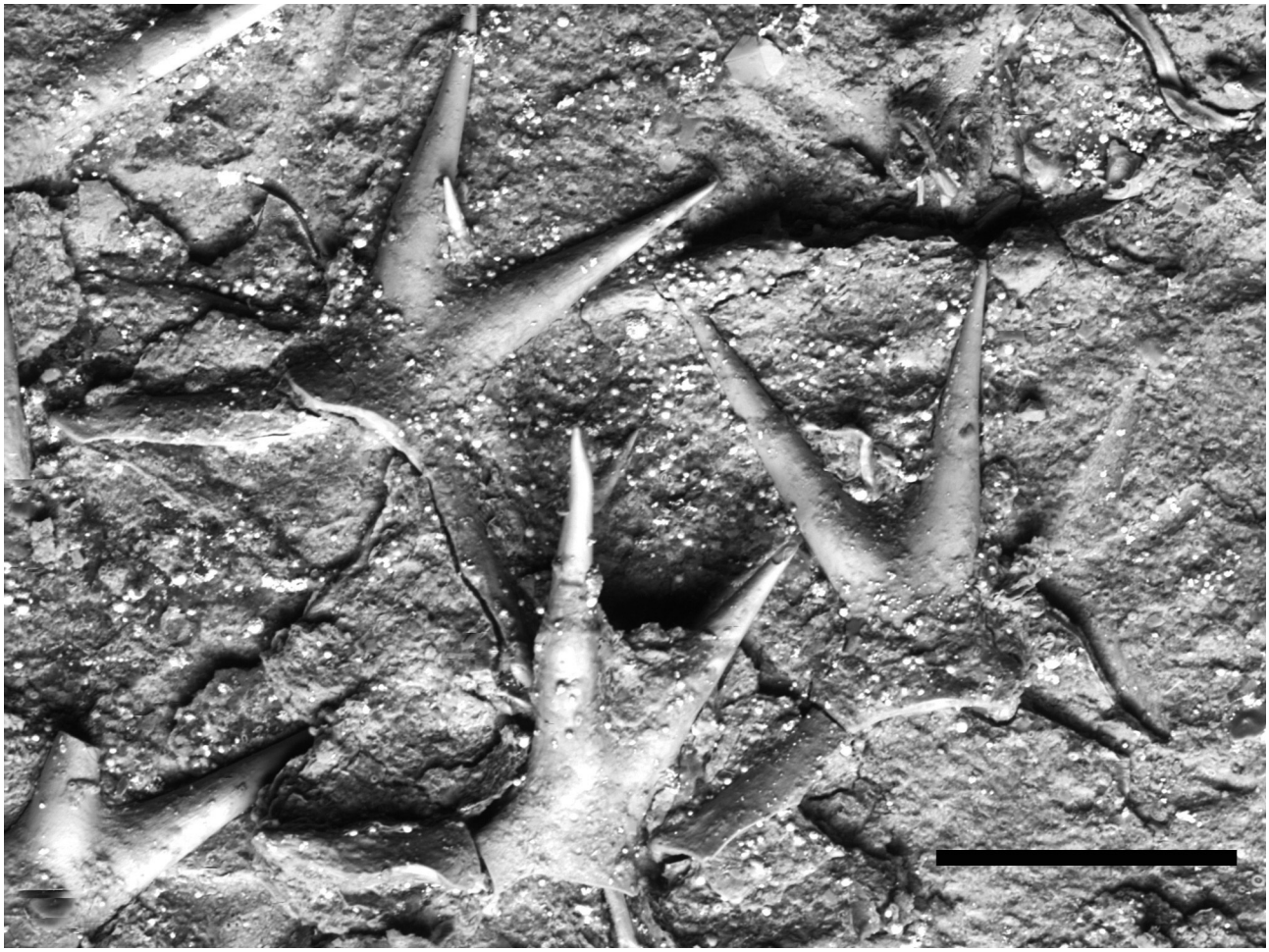

FIGURE 4. Holotype of †*Archaeotetraodon bemisae* sp. nov., PIN 5917/1, scanning electron microscope image of scale spinules. Scale bar 0.2 mm.

Measurements. Measurements are given as percent SL, with the value for the holotype given first followed by that of the paratype in parentheses. Anal-fin-base length: 5.3 (5.4); anal-fin height: ca. 13.5 (9); bifid spinule length from point of bifurcation: 0.4 (?); bifid spinule width at the base: 0.1 (?); body depth: ca. 30 (ca. 30); caudal-fin length: 21 (?); caudal peduncle depth: 6 (6); distance between pectoral and anal fins: 32 (30); dorsal-fin-base length: 6 (5.8); dorsal-fin height: ca. 15.5 (ca. 10.5); first anal-fin pterygiophore length: 12.7 (11.4); head length (premaxilla to posterior end of basioccipital): 38 (46); long trituration teeth length: ca. 2 (?); neurocranium width between sphenotics: ca.18.8 (?); opercle, anterior margin length: ca. 12 (?); predorsal distance: 74 (74.5); preopercle length:

ca. 22 (?); supracleithrum length: ca. 9.8 (?); ventral postcleithrum length: ca. 23.6 (ca. 17); ventral postcleithrum width: 1.0 (ca. 0.7); vertebral centra (middle vertebrae) length: 3.8 (ca. 3).

Etymology. Named in honor of Katherine E. Bemis of the National Systematics Laboratory, National Marine Fisheries Service, located at the National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A., in recognition of her excellent studies of tetraodontiform fishes and of her extensive field work to collect specimens of them.

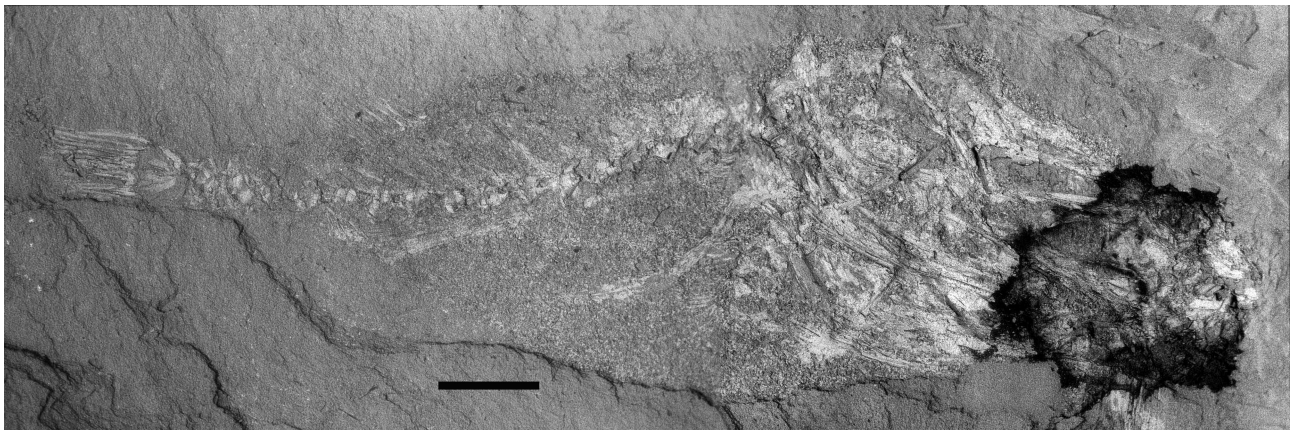

FIGURE 5. Paratype of †*Archaeotetraodon bemisae* sp. nov., PIN 5917/2, 24.5 mm SL, scanning electron microscope image; uppermost Maikopian (basal Middle Miocene) of North Caucasus (Pshekha River). Scale bar 2 mm.

Discussion

The skeletal structure of the new species described above is typical of fossil and extant members of the family Tetraodontidae. Presently, three exclusively fossil genera of tetraodontids are known: †*Eotetraodon,* from the Eocene of the Tethys, and †*Archaeotetraodon* and †*Leithaodon,* from the Oligo-Miocene of the Paratethys and Mediterranean. †*Eotetraodon* is defined by such plesiomorphic features as the presence of pleural ribs, unconsolidated hypurals, and 12 caudal-fin rays (Tyler 1980; Bannikov & Tyler 2008; Tyler & Bannikov 2012). †*Archaeotetraodon* is distinguished from all other tetraodontid genera, including †*Leithaodon,* in having bifid upright spinules protruding from the basal scale plates (Bannikov 1990; Tyler & Bannikov 1994; Carnevale & Santini 2006; Carnevale 2007; Bannikov 2010; Carnevale & Tyler 2010, 2015). Bifid upright spinules cover the body of the late Maikopian pufferfish described above; therefore, it is attributed herein to the genus †*Archaeotetraodon*.

†*Archaeotetraodon* is the most speciose exclusively fossil genus of tetraodontiforms, with the species being based upon relatively complete skeletal remains. Until now, six Oligocene to Miocene species of †*Archaeotetraodon* had been described (Carnevale & Tyler 2010). The new species, †*Archaeotetraodon bemisae,* is the seventh. It differs from †*A. dicarloi* Carnevale & Tyler, 2010 (known from an incomplete specimen from the Serravallian of central Italy) in having smooth scale spinules, whereas in †*A. dicarloi* the scales are ornamented (see Carnevale & Tyler 2010). Thick and sturdy spinules (Fig. 3) distinguish †*A. bemisae* sp. nov. from four other †*Archaeotetraodon* species (Upper Miocene †*A. bannikovi* Carnevale & Tyler, 2010 and †*A. zafaranai* Carnevale & Tyler, 2010 from Italy; Messinian †*A. cerrinaferoni* Carnevale & Santini, 2006 from Algeria; and Oligocene †*A. winterbottomi* Tyler & Bannikov, 1994 from the Caucasus and Carpathians), which have slender and elongate spinules (see Carnevale & Tyler 2010: fig. 1). The new species differs from †*A. jamestyleri* (Bannikov 1990), known from the Tarkhanian of the Crimea and North Caucasus, in having broader frontals and more numerous dorsal- and anal-fin rays. Also, the slender ventral postcleithrum distinguishes †*A. bemisae* sp. nov. from †*A. bannikovi,* †*A. zafaranai,* and †*A. cerrinaferoni,* which have an expanded ventral postcleithrum. †*Archaeotetraodon bemisae* sp. nov. is further distinguished from †*A. zafaranai* by having fewer vertebrae (18 vs. 22) and dorsal-fin rays (10 vs. 14 or 15).

Paleoecology

Although †*Archaeotetraodon jamestyleri* and †*A. bemisae* sp. nov. were found in the same North Caucasian basin, the environmental conditions in which they lived would have been significantly different. †*Archaeotetraodon bemisae* sp. nov. was found in the uppermost Maikopian locality, which is dominated by pipefishes, indicating an inshore or coastal environment. In contrast, †*A. jamestyleri* was found in the Tarkhanian of the Pshekha locality, which is dominated by the lightfish †*Vinciguerria merklini* Danilchenko, indicating the area was then a relatively deep basin and †*A. jamestyleri* most likely inhabited the upper layers of the deep basin.

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