



NEW MATERIAL OF THE PUFFER FISH *ARCHAEOTETRAODON WINTERBOTTOMI* TYLER ET BANNIKOV, 1994 (TETRAODONTIDAE) FROM THE OLIGOCENE OF THE EASTERN PARATETHYS

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Abstract: A new specimen of the fossil puffer fish *Archaeotetraodon winterbottomi* (Tetraodontidae) is described from the lower Oligocene deposits of the Sheshory locality, Ukraine. The specimen reveals a number of characters, some of which are diagnostic and others which were recognized herein for first time, such as the possession of a relatively narrow neurocranium in the supraorbital region, smooth frontals, eight abdominal and nine caudal vertebrae, and long and slender postcleithrum.

Key words: Teleostei, Tetraodontiformes, Tetraodontidae, Menilite Series, fossil fish

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Introduction

Puffers (family Tetraodontidae) are a group of primarily marine fishes, with some species inhabiting brackish and fresh waters (Tyler 1980, Nelson et al. 2016 and references therein). The family consists of 26 extant genera traditionally arranged within two subfamilies (Tetraodontinae and Canthigasterinae) and includes the species used in the production of the celebrated and potentially lethal Japanese delicacy “fugu” (the generic name *Fugu* ABE, 1952 is a junior synonym of *Takifugu* ABE, 1949; Matsuura 1990) – for details see Nelson et al. (2016). The family Tetraodontidae is represented in the fossil record mostly by isolated jaws, but rarely also by articulated skeletal remains – for details see Bannikov (2010) and Carnevale and Tyler (2010, 2015). The extinct genus *Archaeotetraodon* TYLER et BANNIKOV, 1994 is currently known from Oligocene and Miocene marine deposits of Europe. The genus includes six species: *A. bannikovi* CARNEVALE et TYLER, 2010, *A. cerrinaferoni* CARNEVALE et SANTINI, 2006, *A. dicarloi* CARNEVALE et TYLER, 2010, *A. jamestyleri* (BANNIKOV, 1990), *A. zafaranai* CARNEVALE et TYLER, 2010, and *A. winterbottomi* TYLER et BANNIKOV, 1994.

The aim of the present study is to describe a new specimen of the latter species from the Oligocene of western Ukraine and briefly document additional and previously unknown morphological details.

Material and geological notes

The material investigated in this study is represented by a single specimen housed in the Department of Palaeontology at the National Museum of Natural History, National Academy of Sciences of Ukraine (NMNHU-P). The specimen was collected (and tentatively identified as a member of the genus *Diodon* LINNAEUS, 1758) by I. Kiselev in 1978 from a natural outcrop at the Sheshory locality. It is situated near the eponymous village in the Ivano-Frankivsk region, western Ukraine, 48.325808 N, 24.981806 E. According to Vialov et al. (1987b), the Sheshory sequence includes green non-calcareous mudstones with interbeds of gray siltstones (upper part of Bystrytsia Formation, upper Eocene) overlapped by mudstones and sandstones. The fossiliferous layers from which the specimen described herein was collected belong to the Rybnytsia Member,

representing the lowermost part of the Menilite Series. These fossiliferous deposits provided a large number of fish specimens assigned to the following taxa: *Maicopiella longimana*, *Pomolobus curtus*, *Pomolobus* sp., Clupeidae indet., *Oligonemichthys photophorae*, *Palaeotroctes strictus*, *Scopeloides glarisianus*, *Oligophus moravicus*, *Eomyctophum* sp., *Palaeogadus intergerinus*, *Palaeogadus* sp., *Gephyroberyx robustus*, *Oliganodon budensis*, *Oliganodon comparabilis*, *Priacanthus spinosus*, *Archaeus* sp., *Repropca* sp., *Palimphytes* sp., *Anenichelum* sp., *Auxides cernegurae*, *Sarda* sp., *Scomber voitestii*, Scombridae indet., *Palaeorhynchus* sp., *Propercarina* cf. *P. rebeli*, and Pleuronectiformes indet. The fish fauna of the Sheshory locality dates back to the early Rupelian (33–32 Ma). The Rybnytsia Member (earlier known as “under-flint” or “upper part of Sheshory horizon”) was formally defined by Vialov et al. (1987a, b, 1988). The nannoplankton assemblage obtained from these deposits is indicative of the NP 22 Biozone (Vialov et al. 1988, Romaniv 1991), being characterized by the presence of *Coccolithus eopelagicus*, *Cyclicargolithus floridanus*, *Helicopontosphaera reticulata*, *H. compacta*, *Isthmolithus recurvus*, *Reticulofenestra bisecta*, *R. dictyoda*, and *R. umbilica*.

In addition, there is a partially complete articulated skeleton (NMNHU-P PI 1678) from the geographically close and probably coeval Pistyn locality (Kovalchuk et al. 2020). This fossil unquestionably belongs to the genus



Text-fig. 1. Iosif Vasilievich Kiselev in the later years of life. The figure from the archive of the Institute of Geography, National Academy of Sciences of Ukraine.

Archaeotetraodon but its identification at the species level is problematic due to inadequate preservation.

Since I. V. Kiselev was practically unknown to a large part of the scientific community, we briefly present a biographic sketch of this scholar, who significantly expanded our knowledge about the fossil fish fauna of Ukraine. Iosif Vasilievich Kiselev (Text-fig. 1) was born on 31 October 1919 in the village Seroglazka, Astrakhan region, Russia. He graduated from a secondary school in Astrakhan in 1938 and entered the ichthyological faculty of the Moscow Technical Institute of Fishery in the same year.

On 25 September 1941, I. Kiselev was mobilized to the Soviet Army. Until 28 March 1942, he served in spare parts and subsequently reached the Bryansk front. Iosif Kiselev took part in the battles of the Central and Fourth Ukrainian fronts. At the end of the war, he participated to the liberation of Prague from German invaders as a guard petty officer. Being demobilized in October 1945, I. Kiselev returned to the Institute, from which he graduated in July 1947 with the title of ichthyologist-fish farmer. The State Commission sent him to the Ukrainian Research Institute of Fisheries as a junior researcher. In November 1953, I. Kiselev started his doctoral studies at the Institute of Hydrobiology of the Academy of Sciences of the Ukrainian SSR. He defended his dissertation and was awarded the degree of Candidate of Biological Sciences in October 1958.

From December 1973 until his death (late 1980s, actual date unknown), I. Kiselev worked as a senior researcher in the Geography Section of the Academy of Sciences of the Ukrainian SSR. Fulfilling departmental topics in the 1970 to 1980s, he was also engaged in collecting fish fossils from sediments of different age. In particular, he collected a large and diverse number of bony fishes from Oligocene localities of the Ivano-Frankivsk region (including the specimen described herein) and donated it to the Central Museum of Natural History (now the National Museum of Natural History, National Academy of Sciences of Ukraine). A small part of this collection was studied in detail much later, becoming the basis for several publications (Přikryl et al. 2017, Kovalchuk et al. 2020, Barkaszi and Kovalchuk 2021, Kovalchuk and Barkaszi 2021, Kovalchuk et al. 2022, Hyžný et al. 2022).

Standard length (SL) is used throughout the text.

Systematic palaeontology

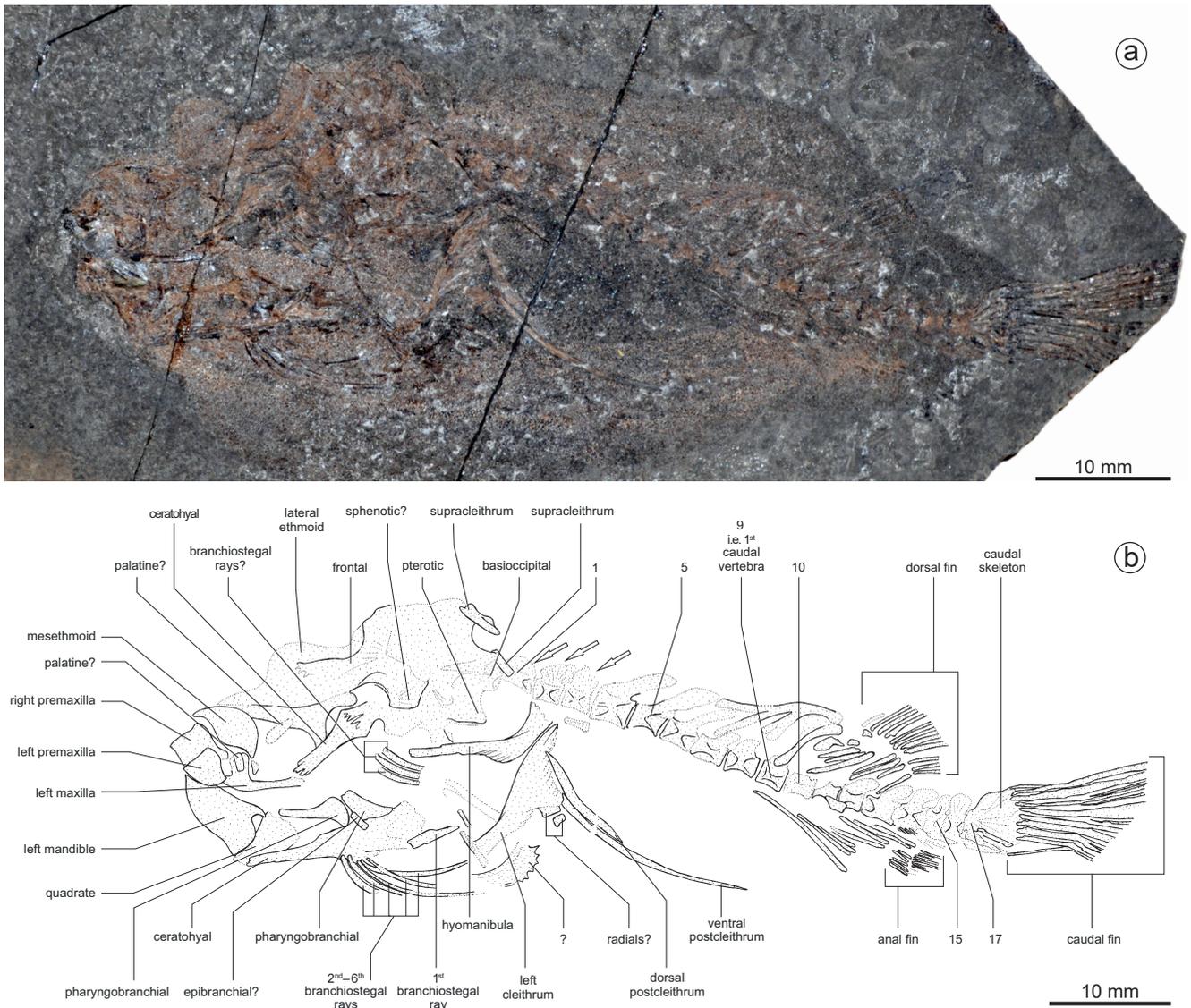
Family Tetraodontidae BONAPARTE, 1832 sensu Tyler 1980

Genus *Archaeotetraodon* TYLER et BANNIKOV, 1994

Archaeotetraodon winterbottomi TYLER et BANNIKOV, 1994 Text-figs 2–3

- 1994 *Archaeotetraodon winterbottomi* new species; Tyler and Bannikov, p. 103, figs 1–4.
2010 *Archaeotetraodon winterbottomi* TYLER et BANNIKOV, 1994; Bannikov, p. 170, pl. XXIX, fig. 3.
2010 *Archaeotetraodon winterbottomi* TYLER and BANNIKOV, 1994; Carnevale and Tyler, p. 295, fig. 13.

Material. The specimen NMNHU-P PI 1995 is deposited in the Department of Palaeontology of the



Text-fig. 2. *Archaeotetraodon winterbottomi*. Specimen NMNHU-P PI 1995. Sheshory locality, Ukraine (Rybnysia Member, lowermost part of the Menilite Series, Oligocene). a: photo of the specimen; b: interpretative drawing of the (a).

National Museum of Natural History, National Academy of Sciences of Ukraine in Kyiv.

Description. The specimen is preserved in left lateral view (Text-fig. 2), with the neurocranium exposed in dorso-lateral view.

The skull roof is almost hourglass-shaped. Although the anterior portion of the neurocranium is not completely clear, it is possible to recognize the crescent-shaped mesethmoid posteriorly articulated with the poorly preserved lateral ethmoids. The frontals have concave lateral margins, widened posteriorly and contact the sphenotics posterolaterally. The outline of the pterotic is partially recognizable. The ventral part of the neurocranium is extensively fragmented and partially covered by overlying bones.

The beak-like jaws are massive. The premaxillae are more or less triangular. Remains of the left maxilla suggest the presence of a relatively large, dorsally oriented process forming a right angle with the main shaft of the bone. The left mandible is triangular in outline and antero-posteriorly elongate; the bone in its postero-ventral corner

is articulated with the quadrate. There is a distinctive notch with a rounded profile along the posterior margin of the mandible. Bony fragments located just below the ethmoid region of the skull probably represent what remains of the palatine.

The ceratohyal is rod-like anteriorly and broadly expanded posteriorly. Along the ventral margin of its expanded portion, it is possible to observe five partially complete branchiostegal rays, possibly representing the second to sixth rays of the series. The first ray was probably enlarged, as in other tetraodontids, and it is poorly preserved, displaced behind the hyoid arch. Remains of three other contralateral branchiostegal rays are preserved below the neurocranium. The left hyomandibula is displaced from its original position; it has a straight vertical shaft and a gently concave anterior margin.

Several isolated fragments of the branchial skeleton (pharyngobranchials and, possibly, a portion of an epibranchial) are disarticulated and dispersed above the ceratohyal.

The cleithrum is sigmoid in outline and bears a posterodorsally-directed spine and a relatively large posterior lamina, partially covering the remains of a single pectoral-fin radial, while a second one is exposed just below it. The supracleithra are extensively fragmented. There are two well-developed postcleithra, of which the ventral one is thin, rib-like and slightly bent. Its length slightly exceeds 20% of SL, while the dorsal one is slightly more massive than the ventral one and its length is about half of the ventral one. Remains of the scapula, coracoid and pectoral fins are not recognizable.

The vertebral column consists of 17 vertebrae (eight abdominal plus nine caudal). The first three abdominal vertebrae bear shortened neural spines. Neural spines of the three successive vertebrae are much longer and posteriorly inclined. The neural spines of the seventh to eleventh vertebrae are not completely recognizable, while the twelfth to penultimate vertebrae have wide and relatively short neural spines. The first centrum seems to be slightly thinner compared to the following ones, but that part of the fossil is not completely preserved, suggesting that this condition may represent a preservation artifact. The subsequent centra are rectangular in outline, longer than high. The terminal section of the vertebral column comprises anteroposteriorly compact centra. Ribs and intermuscular bones are not present.

The caudal skeleton is characterized by an autogenous parhypural and haemal spine of the second preural vertebra fused to the centrum. The hypural plate and the dorsal portion of the caudal skeleton is not completely clear. The truncate caudal fin is only partially preserved; its preserved portion is characterized by nine or ten elongated rays (preserved portion represent 18.3% of SL).

The dorsal fin is located in the posterior third of the body (predorsal length represents 79.9% of SL) and consists of about ten rays. Its endoskeleton is partially preserved, but clearly shows relatively large pterygiophores with the anterior-most one, the so-called “rayless pterygiophore”, that inserts in the fifth interneural space.

The anal fin is not completely preserved, having at least six preserved rays. The anal fin is located just below the posterior part of the dorsal fin and was probably supported by eight pterygiophores, of which the anterior is the longest.

The body is covered with bifid spinules (Text-fig. 3). The spinules apparently lack stellate basal plates.

Measurements. Standard length: 71.2 mm; total measurable length: 86.2 mm; head length (from premaxilla to posterior wall of the basioccipital): 27.1 mm (38.1% of SL); height/length ratio of the posteriormost abdominal centrum 0.63; rayless pterygiophore length: 12 mm (18% of SL); predorsal length: 56.9 mm (79.9% of SL); measurable caudal fin: 13 mm (18.3% of SL); ventral postcleithrum length: 15.1 mm (21.2% of SL).

Discussion and conclusions

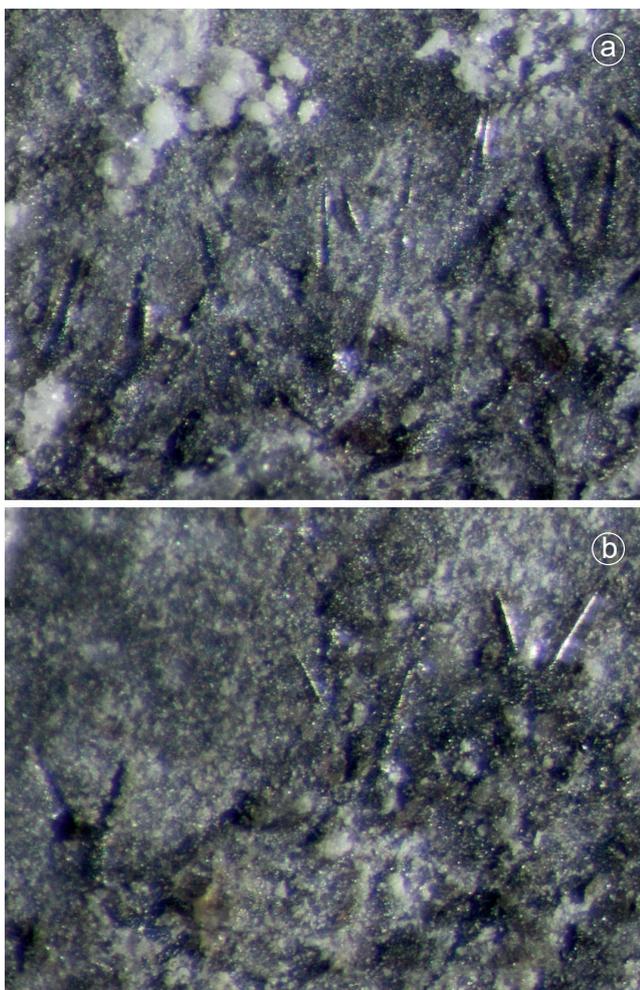
The specimen described herein can be referred to the family Tetraodontidae because of the presence of beak-like jaws characterized by four strong teeth (two above and two below); dorsal and anal fins located far posteriorly; caudal fin truncate; pelvic fins absent; and scales absent, but part of the body is covered by spinules (Matsuura 2015).

The specimen shows three diagnostic characters of the genus *Archaeotetraodon*, including the presence of bifid scale spinules, haemal spine of the penultimate vertebra fused to the centrum and anal fin origin located under the base of the dorsal fin (for details see Carnevale and Tyler 2010). Therefore, the specimen can confidently be attributed to this genus. The total number of vertebrae is slightly lower than that considered as diagnostic for the genus (18–22 vs. 17), although eight abdominal vertebrae are within the diagnosed range known for *Archaeotetraodon* (7–9; see Carnevale and Tyler 2010).

There are six known species of the genus *Archaeotetraodon*. The specimen reported herein resembles *A. winterbottomi* and *A. jamestyleri* by having a neurocranium that is narrowed in the supraorbital region, a reduced number of vertebrae, and a slender ventral postcleithrum. In addition, the specimen shares with the Oligocene species *A. winterbottomi* a similar physiognomy of the body, eight abdominal vertebrae, and a long rod-like rayless pterygiophore of the dorsal fin. Due to these characters, the specimen is referred to the species *A. winterbottomi*. Although some characters differ from the originally described condition, such as the presence of 18 vertebrae, and elongated spinules on the top of the head (some of them are not bifid), these are considered in the range of the species variability and none of them support the creation of a new species.

Previously described species clearly differ from the new specimen of *A. winterbottomi* as follows (only comparable features are listed, following Carnevale and Tyler 2010):

- *A. bannikovi* from the Late Miocene of the Mediterranean differs from the specimen described herein by having a moderately elongate body, enlarged frontals in the supraorbital region, 20 (9+11) vertebrae (vs. 8+9), broadly expanded ventral postcleithrum, and scale spinules with large stellate basal plates;
- *A. dicarloi* from the Middle Miocene of the Mediterranean differs from the fossil described herein by having frontals extensively ornamented and laterally expanded in the supraorbital region; scales ornamented with thick bifid spinules;
- *A. zafaranai* from the Late Miocene of the Mediterranean differs from the specimen described herein by having a very slender and elongated body, frontals broad above the orbits, sculptured surface of the neurocranial bones, straight vertebral column with 22 (7+15) vertebrae, and moderately expanded ventral postcleithrum;
- *A. jamestyleri* from the Middle Miocene of the Eastern Paratethys differs from the fossil described herein by having 18 (7+11) vertebrae, extremely short vertebral centra, bifid spinules developed in the middle of the body and simple spinules in the other parts of the body;
- *A. cerrinaferoni* from the Late Miocene of the Mediterranean differs from the specimen described herein by having a broadly expanded ventral postcleithrum, moderately elongate rayless pterygiophore, extremely elongated centra, and elongated bifid spinules.



Text-fig. 3. *Archaeotetraodon winterbottomi*. Specimen NMN-HU-P PI 1995. Details of dermal bifid spinules.

Carnevale and Tyler (2010) suggested that the diverse body shape of representatives of the genus *Archaeotetraodon* reflects, at least in part, different lifestyles. Therefore, *A. bannikovi*, *A. jamestyleri*, and *A. winterbottomi* were probably more demersal compared to other species that are characterized by a more slender body. A similar lifestyle can be also supported as suggested by the associated fish fauna of the Sheshory locality, which suggests deep-water conditions.

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