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A NEW FOSSIL CLARIFIES THE ANATOMY AND PHYLOGENETIC RELATIONSHIPS OF THE EOCENE GYMNODONT FISH †*ZIGNOICHTHYS OBLONGUS* (ZIGNO, 1874)

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Abstract: The Eocene tetraodontiform fish †*Zignoichthys oblongus* (Zigno, 1874) from the Bolca Konservat-Lagerstätte, northeastern Italy, is redescribed in detail based upon new material. This taxon exhibits a combination of features (parasphenoid shaft-like and bearing a ventral flange; non-protractile upper jaw; teeth incorporated into beak-like jaws; premaxilla without ascending process; palatine massive and firmly connected to the ethmo-vomerine region; supracleithrum distinctly oblique) that clearly supports its assignment to the gymnodonts, suborder Tetraodontoidei. The analysis of this new material also demonstrates that the previous apparent absence of plesiomorphic characters (e.g., spiny dorsal fin) was the result of taphonomic biases. †*Zignoichthys* shares a number of features (basisphenoid, urohyal, beryciform foramen perforating the anterior ceratohyal, ribs, more than 20 vertebrae, epineurals, 12 principal caudal-fin rays, procurrent caudal-fin rays, unfused hypurals, autogenous haemal arch and spine of the third preural vertebra, dorsal-fin spines, scapular foramen entirely enclosed by the scapula) with the extant *Triodon,* which support their sister-group relationship and their basal position within the Tetraodontoidei. An analysis of the skeletal morphology of †*Zignoichthys* is presented and compared with that of other gymnodonts. We also compare our phylogenetic results with previous hypotheses about Tetraodontoidei relationships.

INTRODUCTION

Tetraodontiform fishes are a monophyletic group of teleosts comprising more than 350 extant species assigned to ten families, showing a variety of forms and extraordinary anatomical diversity (Tyler 1980). Tetraodontiform families have been traditionally arranged into two lineages, the scleroderms and the gymnodonts (Cuvier 1817; Tyler 1980). Scleroderms are characterized by having separate individual jaw teeth and body covered by thick scales or carapace plates, whereas gymnodonts (today referred as the suborder Tetraodontoidei) include those tetraodontiforms with teeth incorporated into beak-like jaws and scales commonly modified into prickly spines. The origin of tetraodontiforms seems to be deeply rooted into the Cretaceous (e.g., Tyler & Sorbini 1996; Arcila et al. 2015; Close et al. 2016; Bannikov et al. 2017), but its diversification took place mostly in the aftermath of the K/Pg extinction (e.g., Arcila & Tyler 2017). The fossil

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record of tetraodontiform fishes has been extensively explored in the past few decades, with the description of several new taxa and the redefinition of many others (e.g., Tyler & Santini 2002; Tyler et al. 2006; Close et al. 2016; Bannikov et al. 2017). The oldests fossil gymnodonts have been reported from the early Ypresian, with taxa known from Bolca, the London Clay Formation, and Kabardino-Balkaria (Tyler & Patterson 1991; Tyler & Santini 2002; Close et al. 2016; Bannikov et al. 2017), although an isolated dental plate belonging to a porcupinefish (family Diodontidae) discovered in a museum collection has been tentatively referred to the Upper Cretaceous (Maastrichtian) Gramane Formation of the Paraíba Basin, Brazil (Gallo et al. 2009). The ambiguous criteria used to support the Cretaceous age of this specimen have led some authors to question the reliability of the provenance and age of this occurrence (e.g., Dornburg et al. 2014, Bannikov et al. 2017). Consequently, the species †*Balkaria histiopterygia* described by Bannikov et al. (2017) currently represents the earliest unquestionable gymnodont.

Due to their excellent preservation and taxonomic diversity, the Ypresian tetraodontiforms from Bolca represent the most important source of information about the early Cenozoic evolutionary history of these fishes. Five of the ten extant families (Aracanidae, Diodontidae, Ostraciidae, Tetraodontidae, Triacanthidae) are represented in the Bolca fish assemblage, along with taxa of extinct lineages (Bannikov 2014; Carnevale et al. 2014). Examples of extinct gymnodonts from Bolca include †*Eoplectus bloti* Tyler, 1973 and †*Zignoichthys oblongus* (Zigno, 1874). †*Eoplectus bloti* is known from two specimens, one of which is poorly preserved, and is characterized by unfused premaxillae and dentaries, basisphenoid absent, 20 (9+11) vertebrae, six dorsal-fin spines, 12 principal caudal-fin rays, well-developed pelvic fins and girdle, ribs and intermuscular bones absent, and caudal skeleton with five autogenous hypurals (Tyler 1973; Tyler & Santini 2002). †*Zignoichthys oblongus* has been known from two specimens, of which the holotype is largely incomplete and poorly preserved (Tyler 1973, 1980), whereas the second specimen is partially complete and moderately well preserved (Tyler & Santini, 2002). Although †*Eoplectus* has been recurrently recovered as basal to all other gymnodonts, the phylogenetic position of †*Zignoichthys* appears to be unstable (Winterbottom 1974; Tyler 1980; Santini & Tyler 2003; Close et al. 2016; Arcila & Tyler 2017; Bannikov et al. 2017). Recently, an additional well-preserved and nearly complete specimen of †*Zignoichthys oblongus* has been discovered in the collection of the Museo dei Fossili della Famiglia Cerato. This new †*Zignoichthys oblongus* specimen exhibits several previously unrecognized morphological features that can help to clarify its phylogenetic relationships. We describe this fossil in detail and assess the phylogenetic relationships of †*Zignoichthys oblongus* within the gymnodonts.

LOCALITY AND STRATIGRAPHY

The material described herein was collected from the Pesciara site of the Bolca locality, which is located in the eastern portion of Monti Lessini, Verona Province, in northeastern Italy (Fig. 1). Bolca has been celebrated for centuries for its spectacularly preserved fossils (Friedman & Carnevale 2018; Rossi et al. 2022; Romano & Carnevale 2023), especially for the abundant articulated skeletal remains of bony and cartilaginous fishes, among which more than 250 species-level taxa have been identified (Bannikov 2014; Carnevale et al. 2014). Because of the very high taxonomic diversity and the tropical shallow-water environment in which they were preserved, the Bolca fish fauna is regarded as the earliest available evidence of a modern coral reef fish assemblage (e.g., Bellwood 1996; Carnevale 2006; Marramà et al. 2022). Furthermore, the Bolca locality documents the stability of the main structural features of tropical marine fish faunas throughout the Cenozoic Era. The fish assemblage includes the first occurrences of numerous fish lineages that today are associated with coral reefs (e.g., Blot & Tyler 1990; Bellwood 1996; Carnevale & Pietsch 2009; Bannikov & Carnevale 2010, 2016).

The Pesciara site consists of a carbonatic olistolith packed into volcanic deposits. The shallow water Lower Eocene carbonates of the Pesciara accumulated on the Lessini Shelf, a paleogeographic unit of the Southern Alps (Bosellini 1989). The Eocene carbonate deposits of the Lessini Shelf have been traditionally referred to as the “Calcari Nummulitici.” The succession exposed at the Pesciara site consists of about 20 m of alternated finely laminated micritic limestone and coarse-grained biocalcarenite/biocalcirudite containing abundant

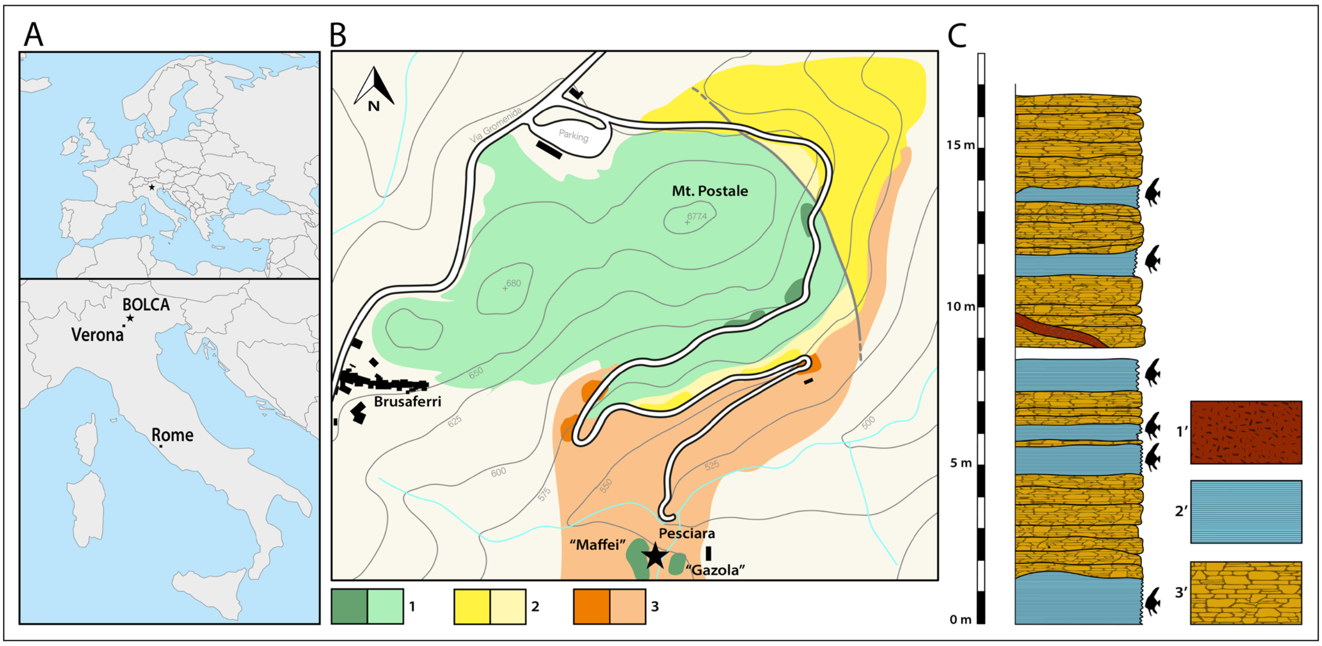

Fig. 1 - Location and geological map of the Pesciara site of the Bolca Lagerstätte. (A) Location of Bolca in northern Italy. (B) Geological map of the area near the village of Bolca; numbers indicate the following lithologic units: 1, bedded/laminated limestone; 2, massive limestone; 3, volcanics; intensity of colours indicates either rock exposed in outcrop (dark) or inferred (light). (C) stratigraphic section of the Pesciara sequence; numbers indicate the following lithotypes: 1´, volcanics; 2´, laminated micritic limestone with fish and plant remains; 3', biocalcarenite-biocalcirudite with benthic fauna. Modified from Papazzoni & Trevisani (2006) and Trevisani (2015).

remains of larger benthic foraminiferans and molluscs deposited during the late Ypresian. Exquisitely well-preserved fishes, plants, and soft-bodied invertebrates derive from the inframillimetrically laminated micritic limestone of the Pesciara succession (Friedman & Carnevale 2018). Calcareous nannoplankton and larger benthic foraminiferans indicate that the Pesciara site succession dates back to the middle Cuisian, corresponding to the uppermost part of SBZ 11 and the lower part of NP 14 and CNE 6, between 48.96 and 48.5 Ma (see Papazzoni et al. 2017).

Taphonomic and sedimentological observations indicate that the fossiliferous limestone accumulated in an intraplatform peri-reefal setting, characterized by local anoxic or dysoxic conditions at the bottom that fostered the development of a microbial film that promoted the remarkable preservation of the fossils (Schwark et al. 2009; Marramà et al. 2016). The paleoecological analysis proposed by Marramà et al. (2016) revealed an oligarchic structure in the Pesciara fish assemblage, which was dominated by planktivorous fishes, especially by the sardine †*Bolcaichthys catopygopterus* (Marramà & Carnevale 2015).

Materials and methods

The present study is based primarily upon a newly collected specimen of †*Zignoichthys oblongus* (CMC 40) belonging to the fossil collection currently housed in the Museo dei Fossili della Famiglia Cerato, Bolca. The skeletal anatomy of †*Zignoichthys oblongus* is described herein in detail to illustrate the osteological features of the taxon. The fossil was examined using a Leica M80 stereomicroscope equipped with a camera lucida drawing arm. Measurements were taken to the nearest 0.1 mm using a dial caliper. Standard length (SL) is used throughout. Anatomical terminology mainly follows Tyler (1980). Extinct taxa are marked with a dagger (†) preceding their name.

To infer the taxonomic position of †*Zignoichthys* within the gymnodonts (i.e., suborder Tetraodontoidei), we performed a phylogenetic analysis. The character matrix consists of 25 taxa (14 extinct) and 114 morphological characters (see Appendix). The taxa include two outgroups (*Antigonia capros,* an eupercarian non-tetraodontiform; and *Triacanthodes anomalus,* a triacanthodid) and 21 Tetraodontoidei as the ingroup (†*Archaeotetraodon jamestyleri,* †*Archaeo-*

tetraodon winterbottomi, Canthigaster rostrata, Chilomycterus schoepfi, Diodon holocanthus, †*Eomola bimaxillaria,* †*Eoplectus bloti,* †*Eotetraodon pygmaeus,* †*Heptadiodon echinus, Lagocephalus laevigatus, Mola mola,* †*Prodiodon erinaceus,* †*Prodiodon tenuispinus,* †*Pshekhadiodon parini, Ranzania laevis,* †*Sphoeroides hyperostosus, Sphoeroides maculatus, Triodon macropterus,* †*Triodon antiquus,* †*Zignodon fornasieroae,* †*Zignoichthys oblongus*) taken from Santini & Tyler (2003) plus †*Ctenoplectus williamsi* and †*Balkaria histiopterygia,* recently described by Close et al. (2016) and Bannikov et al. (2017), respectively. For new data on *Triodon macropterus* and dewlap fan flaring see Bemis et al. (2023). The 114 characters were selected from the original 210 characters of the database published by Santini & Tyler (2003), based upon their reliability in elucidating the relationships of the taxa used for their analysis (see Supporting Information). The characters used in this study are denoted by "ch." preceding the character number followed by the character state in brackets. The matrix (Supporting Information, Table S1) was compiled in MESQUITE v.3.03 (Maddison & Maddison 2008), and the phylogenetic analysis was performed in TNT 1.6 (Goloboff & Morales 2023) using traditional search with 1000 replicates, 100 random seeds, tree bisection and reconnection with ten trees saved per replication and collapsing trees after search. All characters are unordered and given equal weight. Tree length, consistency (CI), and retention (RI) indices were calculated for the 50% majority-rule tree.

Institutional abbreviations: CMC, Museo dei Fossili della Famiglia Cerato, Bolca; MCSNV, Museo Civico di Storia Naturale, Verona; MGPPD, Sezione di Geologia e Paleontologia del Museo della Natura e dell'Uomo dell'Università di Padova, Padova.

SYSTEMATIC PALEONTOLOGY

Order **Tetraodontiformes** *sensu* Santini & Tyler (2003)
Suborder **Tetraodontoidei** (Gymnodontes) *sensu* Santini & Tyler (2003)
Family †Zignoichthyidae Winterbottom, 1974
Genus †*Zignoichthys* Tyler, 1973

Type species: †*Zignoichthys oblongus* (Zigno, 1874), by monotypy and original designation.

Diagnosis: A tetraodontoid genus unique in having the following combination of features: basisphenoid present; jaws massive and beak-like, with the outer surface of the biting edges characterized by subhorizontal bands; upper jaw with separated left and right premaxillae and lower jaw with fused left and right dentaries; urohyal; beryciform foramen present; 21 (10+11) vertebrae; ribs and epineurals present; caudal fin with 12 principal rays and five upper and four lower procurrent rays; caudal skeleton with five autogenous hypurals and a parhypural, parhypurapophysis absent, a single uroneural, a single epural, haemal arches and spines of the second and third preural vertebra autogenous; dorsal fin with two short and stout spines; second dorsal fin containing 14 rays; anal fin containing 12 rays; scapular foramen entirely enclosed within the scapula; pelvic fins and girdle absent; body densely covered with thick scales with rounded bases bearing three to nine upright spines of variable thickness.

Remarks. In establishing the genus †*Zignoichthys,* Tyler (1973) assigned it to the triacanthodid subfamily †Eoplectinae, together with the better known †*Eoplectus.* Such a placement was extremely tentative because of the evident gymnodont affinities of †*Zignoichthys.* Winterbottom (1974) considered †*Zignoichthys* to be a gymnodont and created the family †Zignoichthyidae for it.

†*Zignoichthys oblongus* (Zigno, 1874)

Figs. 2–8

1874a †*Ostracion oblongus* Zigno, 1874, p. 294, pl. X, fig. 3.
1874b †*Ostracion oblongus* Zigno, 1874 — Zigno, p. 161.
1901 †*Ostracion oblongus* Zigno, 1874 — Woodward, p. 569.
1973 †*Zignoichthys oblongus* (Zigno, 1874) — Tyler, p. 146–148, pl. IV.
1980 †*Zignoichthys oblongus* (Zigno, 1874) — Tyler, p. 65, fig. 18.
1995 †*Zignoichthys oblongus* (Zigno, 1874) — Frickhinger, p. 931.
2002 †*Zignoichthys oblongus* (Zigno, 1874) — Tyler & Santini, p. 91–94, figs. 23, 24.
2017 †*Zignoichthys oblongus* (Zigno, 1874) — Arcila & Tyler, table S4.

Holotype: MGPPD 6789, a poorly preserved articulated skeleton, showing the lower jaw and the median fins; ~161 mm SL (Fig. 2).

Diagnosis: As for the genus.

Referred specimens: MCSNV T370/MCSNV IG24510, a partially complete articulated skeleton, in part and counterpart; 132 mm SL, 160.1 mm total length (see Tyler & Santini 2002) (Fig. 3); CMC 40, a well-preserved partially complete articulated skeleton; 113 mm SL, 141 mm total length (Fig. 4).

Type locality and horizon: Pesciara site, Bolca Lagerstätte, northeastern Italy; late early Eocene, late Ypresian, middle Cuisian, between 48.96 and 48.5 Ma (see Friedman & Carnevale 2018).

Description

Measurements for the two referred specimens of †*Zignoichthys oblongus* (Zigno, 1874), are reported in Table 1.

The following description is based upon the newly available, well-preserved referred specimen, CMC 40. The overall morphology of the body can be observed in Figs. 2–5. The body is deep and ovoid. The maximum body depth is contained

Tab. 1 - Measurements as % of standard length of CMC 40 and MCSNV T370/MCSNV IG24510 of †*Zignoichthys oblongus* (Zigno, 1874) from the Eocene of Bolca Lagerstätte. The incompleteness and poor preservation of the holotype, MGPPD 6789, does not allow the recording of reliable measurements.

	Total length (mm)	Standard length (mm)	Head length	Body depth	Head depth	Snout length	Orbit diameter	Caudal peduncle length	Caudal peduncle depth
CMC 40	141	113	38.5	62.4	50.9	12.5	12.3	15.1	14.7
MCSNV T 370-MCSNV IG 24510	160.1	132	50.8	64.8	54.7	13.4	16.2	18.0	16.7

	Predorsal length (spinous)	Predorsal length (soft)	Distance between spinous and soft dorsal fins	Preanal length	Soft dorsal-fin base length	Anal-fin base length	First dorsal-fin spine length	Longest dorsal-fin ray length	Longest anal-fin ray length
CMC 40	41	79.3	12	83.8	21.1	13.3	5.6	18.4	15.3
MCSNV T 370-MCSNV IG. 24510	?	94.5	?	105.9	24.1	16.1	?	12.6	12.3

slightly less than two times in SL. The caudal peduncle is short (comprising five vertebrae) and relatively thick. The head is deep and relatively large, contained slightly less than 2.5 times in SL. The head depth is comparable to its length. The orbit is large; its diameter represents about one-third of the head length. The snout is gently curved anteroventrally; its length is contained slightly less than three times in head length. The beak-like mouth is terminal, with a horizontal gape.

Neurocranium. The neurocranium is robust, moderately elongate, and thick. It is exposed in lateral view, revealing part of the original configuration of the bones (Fig. 6). Based upon the recognizable morphology, it is reasonable to assume that the neurocranium was moderately expanded laterally and, thus, substantially different from other gymnodonts (e.g., diodontids and several tetraodontids possess a very thick and laterally expanded frontal bone that makes this portion of the skull rather wide; Tyler 1980). The bones of the dorsal surface of the skull exhibit a fibrous texture and are characterized by a relatively linear outer profile. Most of the otic and occipital regions of the neurocranium are inadequately preserved or not exposed, hidden by other cranial bones. The frontals appear to be almost triangular in outline, comprising the largest bones of the skull roof; each frontal articulates anteriorly with the mesethmoid, anteroventrally with the lateral ethmoid, posteriorly with the supraoccipital, and latero-ventrally with the sphenotic and pterotic. The mesethmoid is robust and thick; its gently convex dorsal margin is posteriorly continuous with the frontal and forms the anterior and dorsal walls of the nasal capsule; it articulates posterodorsally with the frontals, posteroventrally with the lateral ethmoid, ventrally with the parasphenoid, and anteriorly with the vomer. The lateral ethmoid is well developed and columnar; it articulates anterodorsally with the mesethmoid, posterodorsally with the frontal, and ventrally with the parasphenoid; the anterior margin of the lateral ethmoid forms the posterior wall of the nasal capsule, whereas its posterior margin defines the anterior wall of the orbit. The vomer is small and sub-triangular; it articulates dorsally with the mesethmoid and posteriorly with the anterior end of the parasphenoid. The parasphenoid is a robust and elongated shaft that occupies the vast majority of the basicranial length and bears a short median flange emerging along its ventral margin. The pterosphenoid is thick and follows the curve of the posterodorsal region of the orbit; it articulates dorsally with the frontal, posterodorsally with the sphenotic, posteroventrally and ventrally with other bones of the otic region, most likely the pterotic. The basisphenoid is in the posteroventral portion of the orbit, where it articulates ventrally with the parasphenoid. The sphenotic can be observed immediately posterior to the pterosphenoid; it is almost round in outline and articulates anteriorly with the pterosphenoid, dorsally with the frontal, and posteriorly and posteroventrally with the pterotic. The pterotic is large but poorly preserved and is only partially recognizable; it articulates with the sphenotic anteriorly and the prootic ventrally. The morphology of the prootic cannot be properly recognized because of inadequate preservation. The basioccipital forms the posteroventral corner of the neurocranium where it articulates with the first vertebra. The supraoccipital is only partially recognizable; the supraoccipital crest is expanded backward, extending posteriorly to the distal tip of the third neural spine.

There is no evidence of the bones of the circumorbital series.

Jaws. The beak-like jaws are thick and massive. The right and left premaxillae seem to be separated, whereas the two contralateral dentaries appear

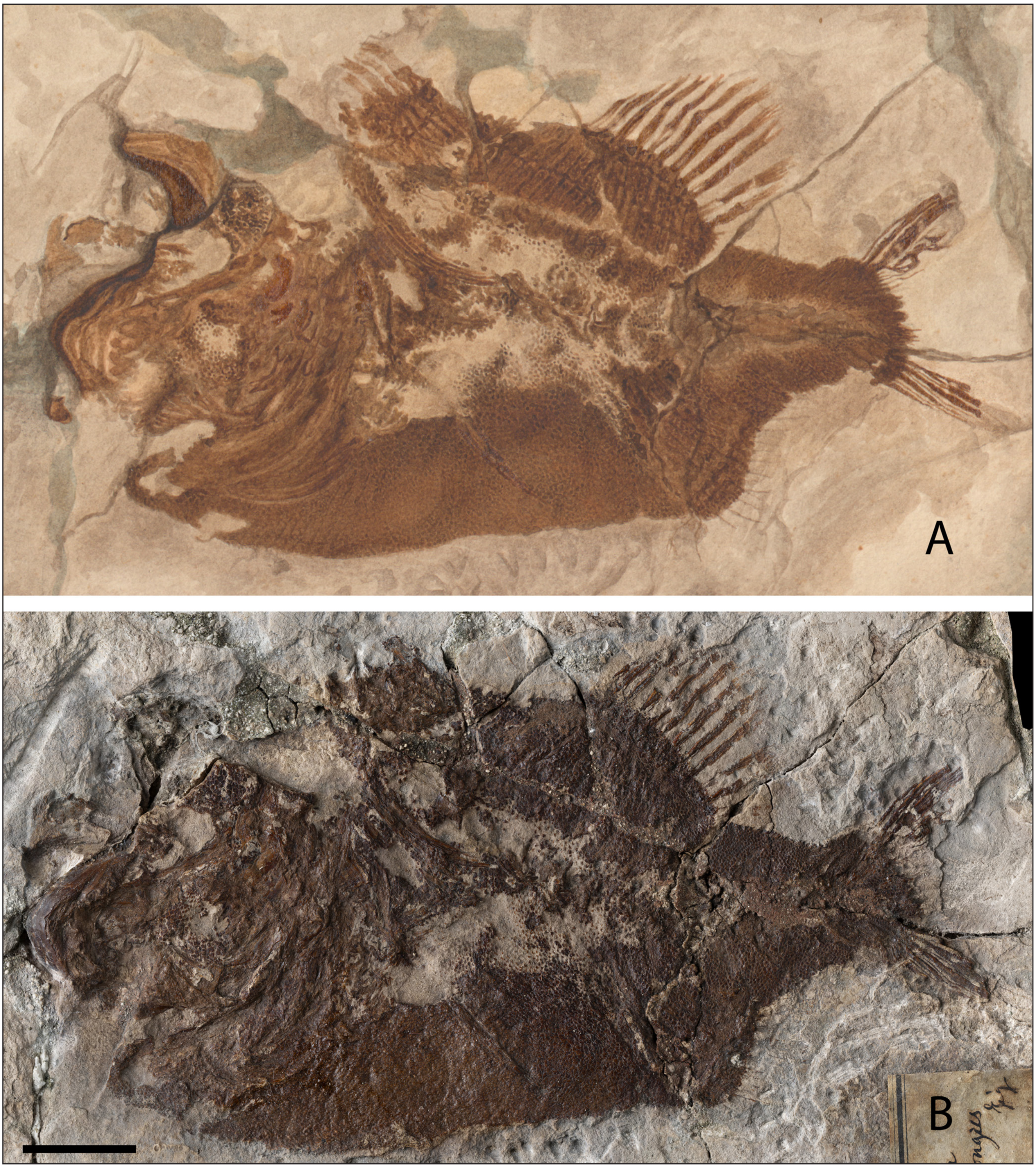

Fig. 2 - †*Zignoichthys oblongus* (Zigno, 1874) from the Eocene of Bolca Lagerstätte. (A) Original unpublished drawing of the holotype, MGPPD 6789, by Achille De Zigno; photo: courtesy of Luca Giusberti (Dipartimento di Geoscienze, Università di Padova) and Dipartimento di Geoscienze of the Università di Padova; (B) the holotype, MGPPD 6789. Scale bar 20 mm.

to be fused, as also reported by Tyler (1973) and Tyler & Santini (2002). The outer surface of the biting edges of the jaws exhibits at least 15 subhorizontal bands, consistent with the lamellae of the pufferfish jaws described by Tyler (1980); these bands resemble the dentine replacement bands described by Fraser et al. (2012) in tetraodontids. Medial to these bands, separate dental units seem to be recognizable and are coalescent within a thick and robust matrix, likely formed by osteodentine (see Tyler 1980; Andreucci et al. 1982; Britski et al. 1985; Bannikov et al. 2017). It is not possible to determine whether

Fig. 3 - †*Zignoichthys oblongus* (Zigno, 1874) from the Eocene of Bolca Lagerstätte. (A) MCSNV T370; (B) MCSNV IG24510; specimen in part and counterpart. Scale bars 20 mm.

trituration plates are present or not. The maxilla is large, curved, and distally expanded, with a concave posterior margin; throughout its length, it tightly articulates with the posterior border of the premaxilla, thereby suggesting that the upper jaw was non-protractile in life. The anguloarticular is sub-triangular in shape and notably compact anteroposteriorly. A small quadrangular retroarticular can be recognized in the posteroventral corner of the lower jaw.

Suspensorium. Most of the suspensorium is exposed in medial view, except for the palatine and the preserved portion of the hyomandibula. Overall, the bones forming the suspensorium are notably robust and firmly connected to each other. The quadrate is triangular in outline and has a very thick ventral margin. The symplectic is rod-like. The hyomandibula is robust, with a rather large articular head that tapers ventrally into a thick shaft. The hyomandibula articulates with the preopercle along its posterior margin and bears a thick and short opercular process. The ectopterygoid is compact and has a slightly curved anteroventral border. The endopterygoid is broad and laminar. The metapterygoid is quadrangular in outline, with a gently rounded ventral margin. The palatine is large and remarkably thickened, with a finely sculptured outer surface. The palatine firmly articulates with the ethmo-vomerine region of the neurocranium.

Fig. 4 - †*Zignoichthys oblongus* (Zigno, 1874) from the Eocene of Bolca Lagerstätte; the referred specimen CMC 40. Scale bar 20 mm.

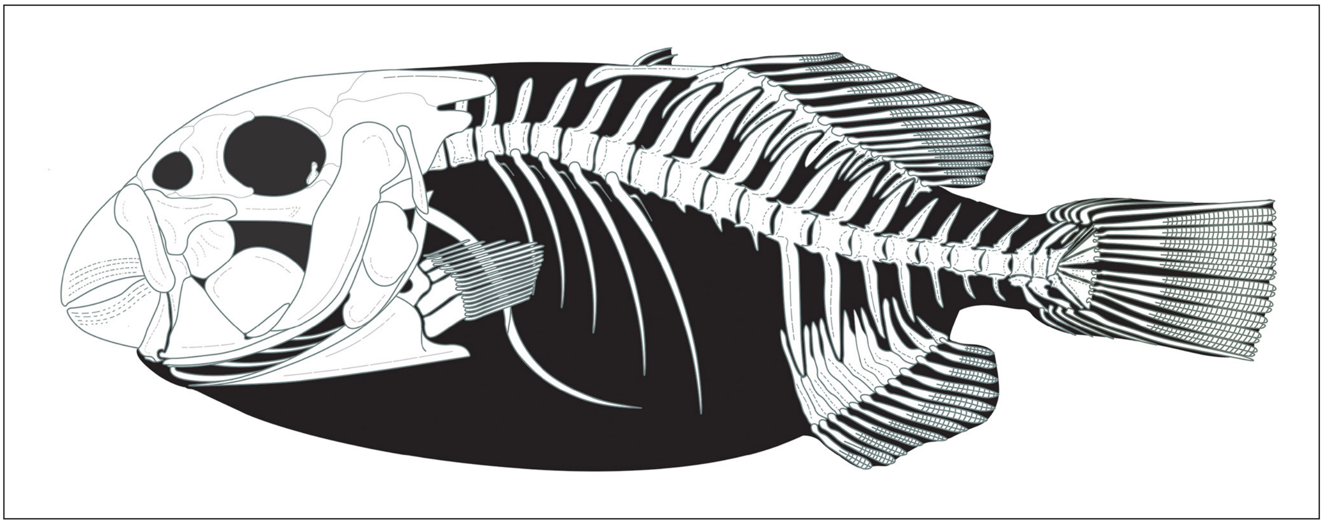

Fig. 5 - Interpretative reconstruction of the whole skeleton of †*Zignoichthys oblongus* (Zigno, 1874) from the Eocene of Bolca Lagerstätte.

Opercular series. The bones of the opercular series are only partially exposed. The preopercle is elongate and crescent-shaped; its upper limb articulates with the vertical shaft of the hyomandibula. The interopercle is partially exposed along the posterior border of the preopercle. The opercle is incomplete and solely represented by its thickened proximal portion. The subopercle is poorly preserved.

Hyoid apparatus and branchial skeleton. The hyoid arch is rather thick and robust, showing a constriction at its midlength and along its anterior margin at the level of the articulation between the dorsal and ventral hypohyals. The hypohyals are quadrangular in outline. The anterior ceratohyal is large and quandrangular in outline; it is pierced by a small and oblong beryciform foramen. The posterior ceratohyal is almost triangular in outline and apparently not fused to the anterior one. Four sabre-like branchiostegal rays can be recognized, of which the first one is moderately expanded. Part of the urohyal can be recognized anterodorsally to the hyoid bar.

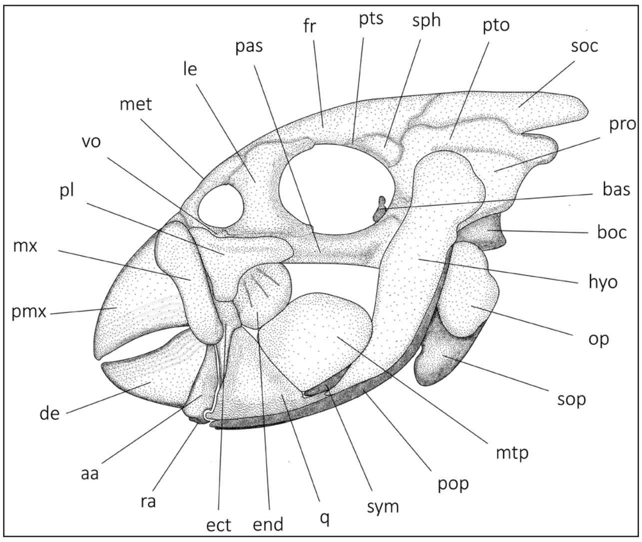

Fig. 6 - Interpretative reconstruction of the head of †*Zignoichthys oblongus* (Zigno, 1874) from the Eocene of Bolca Lagerstätte. Abbreviations: aa, anguloarticular; bas, basisphenoid; boc, basioccipital; de, dentary; ect, ectopterygoid; end, endopterygoid; fr, frontal; hyo, hyomandibula; le, lateral ethmoid; met, mesethmoid; mtp, metapterygoid; mx, maxilla; op, opercle; pas, parasphenoid; pl, palatine; pmx, premaxilla; pop, preopercle; pro, prootic; pto, pterotic; pts, pterosphenoid; q, quadrate; ra, retroarticular; soc, supraoccipital; sop, subopercle; sph, sphenotic; sym, symplectic; vo, vomer.

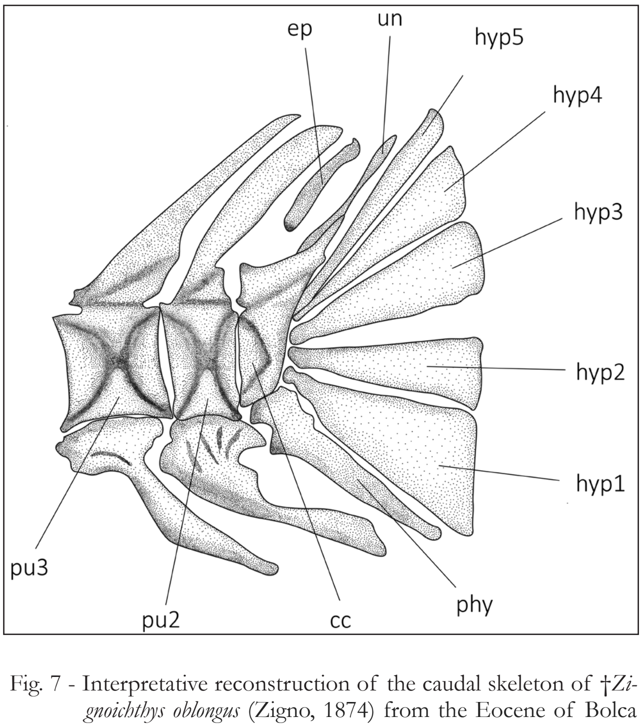

Fig. 7 - Interpretative reconstruction of the caudal skeleton of †*Zignoichthys oblongus* (Zigno, 1874) from the Eocene of Bolca Lagerstätte. Abbreviations: cc, compound centrum; ep, epural; hyp, hypurals; phy, parhypural; pu, preural vertebrae; un, uroneural.

The branchial skeleton is represented by fragments of elongate, rod-like bones, most likely the ceratobranchials.

Vertebral column. The vertebral column is robust and forms a kyphotic curve in the anterior part of the abdominal region; it consists of 21 (10+11) vertebrae (Figs. 2–5). The morphology of the vertebrae changes throughout the length of the column; the anterior abdominal centra are anteroposteriorly compressed, higher than long, whereas those in the central portion of the abdominal region are almost quadrate, gradually becoming subrectangular and longer than high in the remaining part of the vertebral column. Dorsal and ventral pre- and post-zygapophyses are poorly to moderately developed. The neural spines are large, anteroposteriorly expanded, and distally spatulate. The first haemal spine is massive and articulates with the second anal-fin pterygiophore along its posterior margin. The morphology of the haemal spines is similar to that of the opposite neural spines. Large and distally pointed parapophyses, which gradually increase in size posteriorly, occur in the three posteriormost abdominal vertebrae. Thick ribs extend ventrally down to the level of the lower third of the abdomen and articulate with the ventral portion of the centra of the third through seventh vertebrae. Epineurals articulate with the proximal portion of the ribs.

Median fins and supports. The caudal fin is moderately rounded and contains 12 principal caudal-fin rays (I, 5+5, I), plus five upper and four lower procurrent rays. The caudal skeleton (Fig. 7) is only partially exposed. The compound centrum is compact. There are five autogenous hypurals, plus an autogenous parhypural. The parhypurapophysis seems to be absent. There is a single poorly preserved uroneural and a single epural. The haemal spines of the second and third preural centra are autogenous.

There are two separate dorsal fins. The first dorsal fin (Figs. 5, 8A) inserts above the eighth abdominal vertebra and contains at least two short and slender spines of which the second is preserved as an impression only. The two spines, one of which is in supernumerary association, are supported by a thick pterygiophore that runs parallel to the dorsal profile of the body. The two dorsal spines do not interdigitate with the underlying neural spines, and they are anteriorly expanded at the level of the articulation between the sixth and seventh abdominal vertebrae. Dense and thick scales covering the region make it impossible to determine if there is a

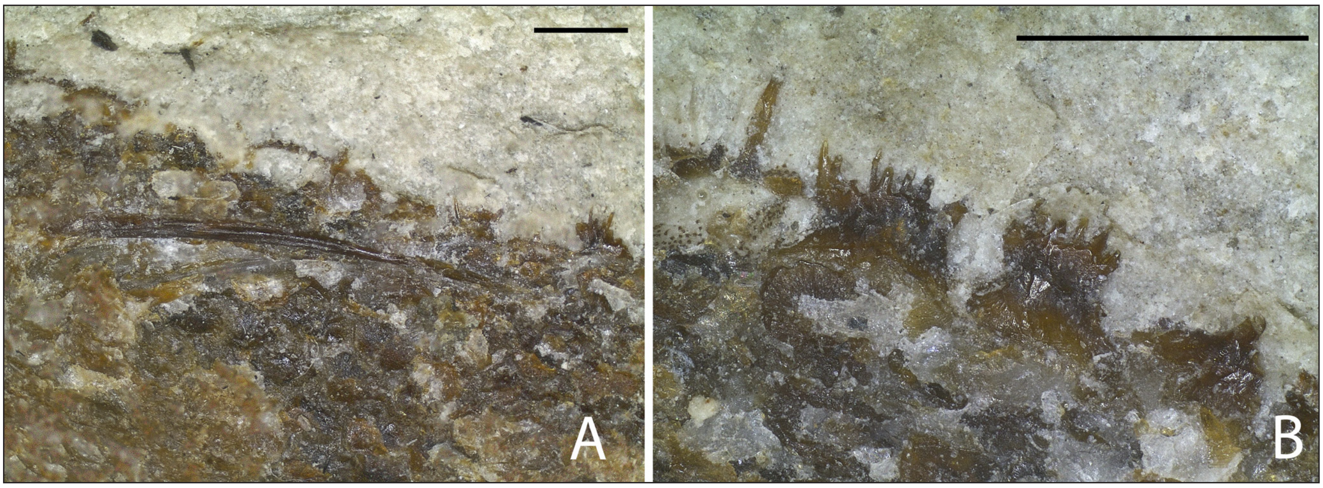

Fig. 8 - †*Zignoichthys oblongus* (Zigno, 1874) from the Eocene of Bolca Lagerstätte. (A) Close-up of the dorsal-fin spines of specimen CMC 40; (B) close-up of some scales of specimen CMC 40. Scale bars 10 mm.

connection between the pterygiophore supporting the dorsal-fin spines and the first pterygiophore of the soft dorsal fin.

The second dorsal fin consists of 14 rays that increase in length to the seventh ray, which is the longest. The dorsal-fin rays are supported by 14 thick and rod-like pterygiophores that have slightly expanded distal ends. The first dorsal-fin pterygiophore inserts in the interneural space between the seventh and eighth abdominal vertebrae. The second dorsal-fin pterygiophore is slightly displaced from its original position, and we suggest that it was located in the interneural space between the eighth and ninth vertebrae. Overall, the pterygiophore formula of the soft dorsal fin is 1/1/2/2/2/3/2/1.

The anal fin originates at the level of the fourth caudal vertebra and consists of 12 rays supported by 11 thick pterygiophores. The first anal-fin ray appears to be supernumerary on the first anal-fin pterygiophore. The anal-fin rays gradually increase in length to the seventh ray, which is the longest. The first anal-fin pterygiophore inserts just before the first haemal spine. The second anal-fin pterygiophore articulates with the distal tip of the first haemal spine. The anal-fin pterygiophore formula is 1/4/3/2/1.

Paired fins and girdles. The pectoral fin is poorly preserved and only fragments of two rays can be recognized just above the scapula, thereby suggesting that the insertion of this fin was placed along the flanks close to the midheight of the body (Figs. 2–5).

The bones of the pectoral girdle are remarkably thick and robust. Inadequate preservation makes it impossible to determine if a posttemporal was originally present. The ventral portion of the supracleithrum articulates with the cleithrum, almost overlying the proximal portion of the dorsal postcleithrum. The cleithrum is elongate and arcuate, ending anteroventrally as a slender prolongation under the anterior region of the quadrate. The coracoid is approximately triangular and is characterized by a straight ventral margin that bears a short postcoracoid process. The scapula is polygonal in outline and contains a circular scapular foramen. The dorsal and ventral postcleithra are well exposed and form a sigmoid outline; the dorsal postcleithrum is gently curved and laterally flattened, exhibiting a convex ventral profile. Conversely, the moderately curved ventral postcleithrum has a convex dorsal margin. Four pectoral-fin radials are scarcely recognizable. There is no evidence of the pelvic fins and girdle.

Squamation. The body, including the entire head, is completely covered with dense, thick scales. The scales vary in size, but the diameter of their rounded bases never exceeds 0.7 mm (Fig. 8B). The basal plate of each scale bears a cluster of three to nine upright spines of variable thickness. The scale cover is less dense in the abdominal area, suggesting an increased dermal flexibility of this sector of the body. In addition, just before the anal-fin insertion the scale cover is less conspicuous and the basal plates of the scales are separated from each other, possibly indicating the location of the cloacal area.

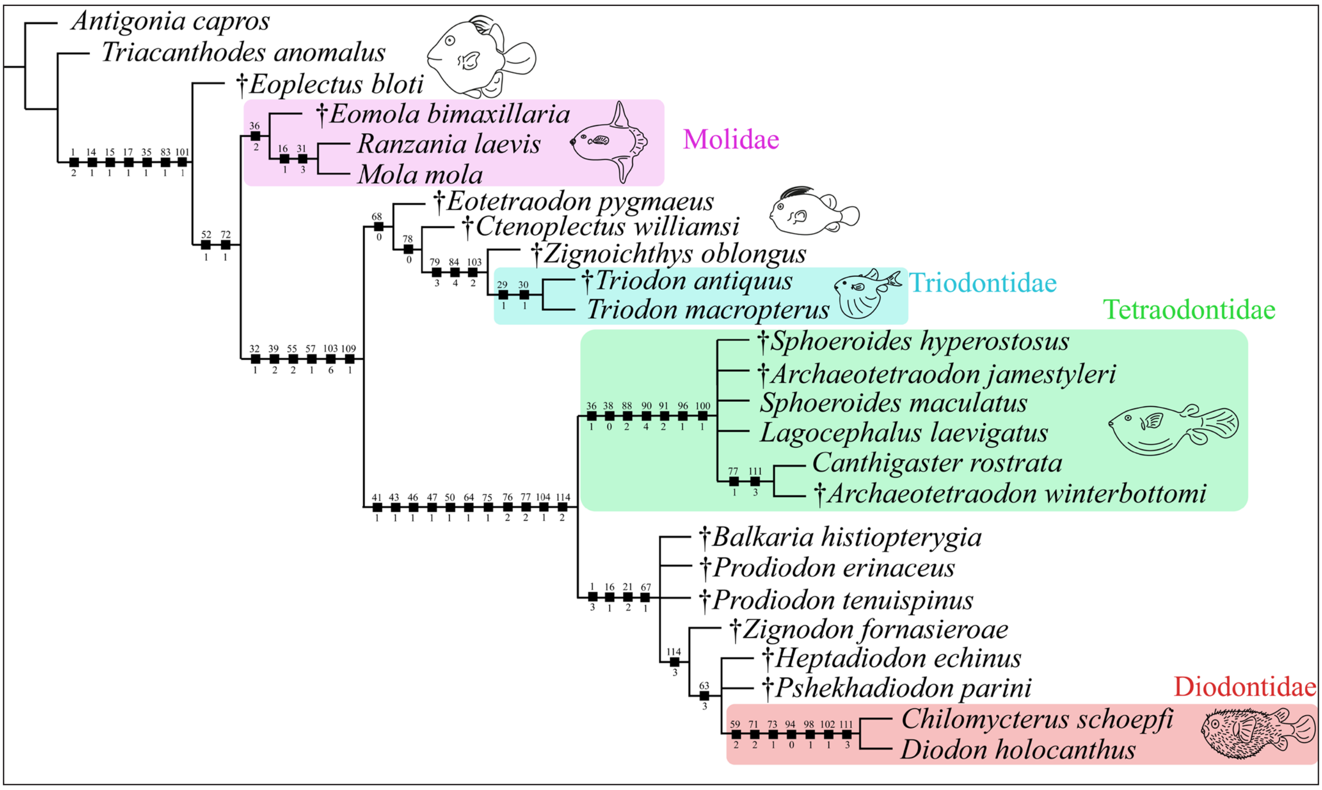

Fig. 9 - The 50% majority-rule tree retrieved in TNT based upon 114 characters and 25 taxa, showing the hypothetical phylogenetic relationship of †*Zignoichthys oblongus* (Zigno, 1874) within the Tetraodontoidei. Synapomorphies supporting the clades are indicated as nodes represented by black squares whose character numbers and states are placed above and below the node, respectively.

Phylogenetic analysis

The analysis of 114 morphological characters coded for 25 taxa yielded 308 equally parsimonious trees that were used to build the 50% majority-rule tree shown in Fig. 9, having a tree length of 241 steps, CI of 0.668, and RI of 0.748 (strict consensus tree in Supporting Information, Fig. S1). The tree appears to be almost completely resolved, with the families Molidae, Triodontidae, Diodontidae, and Tetraodontidae representing monophyletic groups, although the intrarelationships of the Tetraodontidae are not fully resolved. †*Eoplectus bloti* is the sister taxon to all other gymnodonts, with the monophyly of the suborder strongly supported herein by seven characters: parasphenoid shaft-like, with a ventral flange deeper than the shaft (ch. 1 [2]); premaxillary ascending process absent (ch. 14 [1]); immovable and interdigitated articulation of the premaxilla with the maxilla (ch. 15 [1]); maxilla slightly indented dorsolaterally for articulation with the anterior end of the palatine (ch. 17 [1]); teeth in jaws not protruding, incorporated in the matrix of the beak-like jaw bones (ch. 35 [1]); spines associated with the first pterygiophore with shallow grooves (ch. 83 [1]); and uroneurals absent (ch. 101 [1]).

The family Molidae is the sister group to the remaining gymnodonts, and its monophyly is supported by a single synapomorphy: individual teeth indistinguishable and fused into a parrot-like beak (ch. 36 [2]).

The clade comprising all remaining Tetraodontoidei is supported by six characters: ventral prong of the interopercular present (ch. 32 [1]); first branchiostegal ray with dorsomedial edge enlarged and inturned (ch. 39 [2]); uppermost pectoral-fin ray about one-half or less the length of the first caudal vertebral centrum (ch. 55 [2]); anterior edge of cleithrum strongly concave, with a long forward extension beyond its contact with the coracoid (ch. 57 [1]); body scales having multiradiate bases with a single protruding spiny process (ch. 103 [6]); and pectoral-fin rays numbering between 16 and 19 (ch. 109 [1]).

†*Eotetraodon* and †*Ctenoplectus* are successive sister taxa to the pair †*Zignoichthys* plus the Triodontidae, with this latter sister-group relationship being supported by three characters: first spiny dorsal pterygiophore a horizontal shaft not connected to the head, without median flanges, and not modified into a carina (ch. 79 [3]); no spiny dorsal-fin

pterygiophore anterior to the neural spine of the fourth abdominal vertebra (ch. 84 [4]); body scales with thin, irregular to rounded basal plates bearing one or more nonarticulated upright spinules (ch. 103 [2]).

The relationship between Tetraodontidae and Diodontidae is strongly supported by 11 synapomorphies: interhyal absent (ch. 41 [1]); teeth on first pharyngobranchial (ch. 43 [1]); fourth pharyngobranchial absent (ch. 46 [1]); gill rakers along the posterior edge of the fourth arch absent (ch. 47 [1]); no gill slit between the fourth and fifth arches (ch. 50 [1]); three or more neural spines of abdominal vertebrae with bifid processes to either side of the midline (ch. 64 [1]); haemal spine of PU3 short to moderate, about equal to or less than the depth of the centrum (ch. 75 [1]); PU2 and PU3 far removed from the caudal fin and not directly supporting it (ch. 76 [2]; ch. 77 [2]); inflatable diverticulum of gut present (ch. 104 [1]); 11 principal caudal-fin rays (ch. 114 [2]; note, it has recently been documented by Bemis et al. (2023) that inflation is also present in *Triodon macropterus*).

Taxa of the family Tetraodontidae form a large polytomy, but the monophyly of the clade is supported by seven characters: teeth shaped as elongated rods fused into a parrot-like beak (ch. 36 [1]); internal teeth in lower jaw absent as individual units or as trituration teeth (ch. 38 [0]); at least some anal-fin pterygiophores sutured at both the distal rounded articular heads and along the edges of the median flanges, at least for some portion distally (ch. 88 [2]); rayless pterygiophore preceding the soft dorsal fin present as a long, slender, rod-like, horizontal bone (ch. 90 [4]); soft dorsal-fin pterygiophores sutured at both the distal rounded articular heads and along the median flange edges, at least for some portions distally (ch. 91 [2]); two unbranched principal rays present in the lower half of the caudal fin (ch. 96 [1]); first epural sutured to the caudal skeleton (ch. 100 [1]).

Interestingly, †*Balkaria,* †*Prodiodon,* † *Zignodon,* †*Heptadiodon,* and †*Pshekhadiodon* were recovered as stem-Diodontidae because they share with *Chilomycterus* and *Diodon* the following four characters: parasphenoid shaft-like and expanded anterolaterally (ch. 1 [3]); premaxilla fused to its opposite member in the midline (ch. 16 [1]); jaws thick, massive, wide, and long, about one-half the length of the skull (ch. 21 [2]); neural spines of vertebrae supporting the basal pterygiophores of the soft dorsal-fin being short and broad, not slender shafts and not penetrating the interspaces between the pterygiophores (ch. 67 [1]).

The few polytomies and the high consistency and retention indices recovered suggest that characters employed in our TNT analysis are quite robust and the arrangement very stable.

DISCUSSION

Comparative discussion

The fossil documented herein (CMC 40) represents the third known specimen that can be referred to the extinct gymnodont †*Zignoichthys oblongus*. The poorly preserved holotype, MGPPD 6789, was described for the first time by Zigno (1874a) and was re-examined subsequently by Tyler (1973). A better preserved second specimen, in part and counterpart (MCSNV T370/MCSNV IG24510), was cursorily described by Tyler & Santini (2002).

The three known fossils of †*Zignoichthys oblongus* exhibit comparable sizes. CMC 40 has a SL of 113 mm, MCSNV T370/MCSNV IG24510 has a SL of 132 mm, and MGPPD 6789, the largest individual, has a SL of 161 mm. All three specimens have a similar body outline and a dense covering of small-sized scale plates bearing three to nine upright spinules. The skull of the holotype is exposed in dorsoventral view, and only the consolidated lower jaws are well recognizable, thereby preventing any possible detailed comparative analysis with the other two known specimens. The overall morphology of the head, neurocranium (e.g., position of the orbit and nasal capsule, relative size of the basicranium), jaws, and suspensorium and the presence of four branchiostegal rays of MCSNV T370/MCSNV IG24510 are consistent with that of CMC 40. Both MCSNV T370/MCSNV IG24510 and CMC 40 exhibit 21 (10+11) vertebrae; the vertebral number cannot be determined in the holotype because of inadequate preservation. Tyler & Santini (2002) described the moderately preserved caudal skeleton of MCSNV T370 as having fused first and second hypurals, fused third and fourth hypurals, and three upper and four lower procurrent rays; however, the recent reexamination of MCSNV T370/MCSNV IG24510 revealed the presence of a caudal skeleton fully consistent with that of CMC 40, including five autogenous hypurals, five upper and four lower procurrent rays, plus a single epural and a scarcely recognizable uroneural. The caudal skeleton is not exposed in the holotype. The spinous portion of the dorsal fin is not preserved in MCSNV T370/MCSNV IG24510. Tyler (1973) suggested that a spinous dorsal fin of unknown size was likely present in the holotype based on the occurrence of fragments of dorsal-fin pterygiophores and scattered putative spines. The soft dorsal fin of MCSNV T370/MCSNV IG24510 is consistent with that of CMC 40. The incompleteness of the anal fin in MCSNV T370 prevents any detailed comparison with CMC 40, and, likewise, a detailed comparison is impossible for the pectoral fin and girdle, except for the well-developed ventral postcleithra whose morphology is very similar in MCSNV T370/MCSNV IG24510 and CMC 40.

Gymnodonts form a diverse and heterogeneous assemblage within tetraodontiforms and are currently represented by the extant families Diodontidae, Molidae, Tetraodontidae, and Triodontidae, plus the extinct families †Balkariidae, †Eoplectidae, and †Zignoichthyidae, and the enigmatic †*Ctenoplectus williamsi*. All gymnodonts share a series of synapomorphic features (Santini & Tyler 2003; Tyler et al. 2006; Bannikov et al. 2017; Arcila & Tyler, 2017), many of which can be easily recognized in †*Zignoichthys oblongus,* including the following: parasphenoid shaft-like and bearing a ventral flange; non-protractile upper jaw; teeth incorporated into beak-like jaws; premaxilla without an ascending process; palatine massive and firmly connected to the ethmo-vomerine region; and supracleithrum distinctly oblique. The relationships of gymnodont lineages have been extensively discussed (e.g., Tyler 1973, 1980; Winterbottom 1974; Santini & Tyler 2003; Tyler et al. 2006; Close et al. 2016; Arcila & Tyler, 2017; Bannikov et al., 2017), and all the studies concur to indicate the Eocene eoplectids as basal to all the other gymnodonts.

As discussed above, gymnodonts are primarily known for their peculiar jaws that superficially resemble the beak of a parrot. The shared possession of beak-like jaws may reflect common gene expression patterns for jaw development (Bannikov et al. 2017). The structure of the beak-like jaws exhibits broad variation among gymnodonts because of the possible fusion of the opposite premaxillae or dentaries (see Tyler 1980; Bannikov et al. 2017). The plesiomorphic condition consists of four dental units, two in the upper jaw and two in the lower jaw, extending laterally from the midline (Tyler 1980). The premaxillae and dentaries are separate in the Tetraodontidae and the Eocene †Eoplectidae; fused dentaries are characteristic of triodontids and zignoichthyids, whereas fusion of both the premaxillae and dentaries occurs in diodontids, molids, and the Eocene †*Balkaria* and †*Ctenoplectus*. The phylogenetic significance of the fusion of the opposite premaxillae or dentaries, however, is difficult to interpret, and it cannot be regarded as evidence of a close relationship between taxa because the possible combinations may have arisen independently in gymnodont lineages (e.g., Tyler & Bannikov 1992). †*Zignoichthys* shows a condition similar to that of *Triodon* (Tyler 1973, 1980; Tyler & Santini 2002), with fused dentaries and interdigitated premaxillae. Moreover, gymnodont beaks also differ in their patterns of tooth-unit coalescence (Bannikov et al. 2017; Close et al. 2016).

We do not discuss herein the Eocene gymnodont †*Avitoplectus molaris* from India (Bemis et al. 2017) because its relationships are uncertain given that it is known only from a lower jaw. The jaw is fused along the midline and bears unique rounded molariform inner teeth.

†*Zignoichthys* retains a series of plesiomorphic features that characterize its peculiar body plan and play a relevant role in defining its phylogenetic position within the gymnodonts (Tab. 1). These plesiomorphies include the presence of a basisphenoid, a urohyal, a beryciform foramen perforating the anterior ceratohyal, more than 20 vertebrae, ribs and intermuscular bones, 12 principal caudal-fin rays and nine procurrent caudal-fin rays, five autogenous hypurals in the caudal skeleton, an autogenous haemal arch and spine of the third preural vertebra, a spinous dorsal fin, a scapular foramen entirely enclosed within the scapula, and the lack of a dewlap of expansible skin and scales in front of the anal region.

The presence of a basisphenoid seems to be one of the most salient plesiomorphic features observed in †*Zignoichthys*. Within gymnodonts, a basisphenoid has also been observed in †*Balkaria* (Bannikov et al. 2017) and in *Triodon macropterus* (Tyler 1980) (unknown in †*T. antiquus*), whereas its occurrence in †*Ctenoplectus* cannot be determined because of the incompleteness of the fossil. A basisphenoid has also been reported in the Molidae, although according to Britz & Johnson (2012) it could be interpreted as a highly modified pterosphenoid. The urohyal is absent in gymnodonts except *Triodon* and †*Zignoichthys,* in which it is relatively small and dorsoventrally depressed. Conversely, a well-developed urohyal is present in triacanthoids and balistoids, and a highly reduced urohyal is characteristic of ostraciontoids (Tyler 1962, 1968, 1980). Along with *Triodon,* †*Zignoichthys* is the only tetraodontiform possessing a beryciform foramen that perforates the anterior ceratohyal. As pointed out by Britz & Johnson (2012), this feature is common in basal acanthomorphs and occurs sporadically among percomorphs. †*Zignoichthys* has 21 (10+11) vertebrae, *Triodon* has 20 (9+11) vertebrae, and the other gymnodonts, both extant and fossil, exhibit a reduction in the number of vertebrae to 16 to 18 (Tyler 1980). Ribs are present in †*Zignoichthys* and also in †*Ctenoplectus,* †*Eoplectus,* †*Eotetraodon,* and *Triodon* (Tyler 1962, 1973, 1980; Close et al. 2016); ribs are not exposed in †*Iraniplectus* because of the thick cover of scale plates (Tyler et al. 2006), and for this reason their original presence cannot be excluded. The occurrence of epineurals in †*Iraniplectus* is also considered to be a plesiomorphy, being solely observed in *Triodon* and †*Zignoichthys*; in †*Ctenoplectus* and †*Balkaria* the area of the abdominal vertebrae is poorly preserved, making it impossible to determine whether or not the intermuscular bones were originally present. †*Zignoichthys* has 12 principal caudal-fin rays, a condition exclusively observed in it and *Triodon* among gymnodonts. A similar complement of caudal-fin rays is present in triacanthoids and balistoids (Tyler 1962). Caudal procurrent rays are commonly absent in tetraodontiforms, except for *Triodon* and the fossil gymnodonts †*Balkaria,* †*Eotetraodon,* †*Iraniplectus,* and †*Zignoichthys* (Tyler 1962, 1980; Tyler et al. 2006; Tyler & Bannikov 2012). The fusion of the hypurals is considered to be a derived feature within gymnodonts and is characteristic of †*Balkaria,* Tetraodontidae, and Diodontidae; *Triodon* and all fossil gymnodonts except †*Ctenoplectus,* for which the condition is unknown because the caudal portion of the body is not preserved, have unfused hypurals. Tyler (1970, 1980) noted that *Triodon* is the only tetraodontiform with an autogenous haemal arch and spine of the third preural vertebra, a condition now documented herein as also occurring in †*Zignoichthys*. †*Ctenoplectus* and †*Balkaria* have a well-developed spinous dorsal fin that extends anteriorly over the head. This condition is similar to that of typical lophiiforms, which are commonly recognized as the sister group to the tetraodontiforms (e.g., Near et al. 2013; Arcila & Tyler 2017). The spinous dorsal fin is not present in †*Eotetraodon* and †*Iraniplectus*. †*Zignoichthys* and *Triodon* have two stout but short dorsal-fin spines (Tyler 1962, 1967, 1980). Dorsal-fin spines are absent in Diodontidae, Molidae, and Tetraodontidae, although the presence of a large rayless pterygiophore is characteristic of the tetraodontids (Tyler 1980). Finally, the scapula of †*Zignoichthys* completely encloses the scapular foramen, a condition previously observed exclusively in *Triodon* within the gymnodonts; in other gymnodonts the scapular foramen is closed anteriorly by the cleithrum (Tyler 1962, 1980).

Despite this long list of plesiomorphies, †*Zignoichthys* does exhibit some derived features, including the loss of the pelvic fins and girdle and the presence of subhorizontal bands on the biting edges of the jaws, which are similar to the dentine replacement bands of tetraodontid pufferfishes (Fraser et al. 2012). The basipterygia are usually absent in gymnodonts, except for *Triodon* and the extinct †*Ctenoplectus* and †*Eoplectus,* thereby suggesting that the condition observed in †*Zignoichthys* is derived. †*Eoplectus* is the only known gymnodont characterized by the presence of pelvic fins (Tyler 1973, 1980). The beak-like jaws of several gymnodonts, including *Triodon,* are formed through the coalescence of a number of separate tooth units within a matrix. The condition observed on the outer surface of the jaws of †*Zignoichthys* is, in many ways, similar to that of tetraodontid pufferfishes, with the biting edges characterized by subhorizontal bands formed by incorporated teeth.

The simplified but highly heterogeneous skeleton of gymnodonts shows an extreme mosaicism of primitive and derived characters, and the evolutionary history of this group of fishes is characterized by repeated independent losses of skeletal structures, possibly related to their modular organization (Bannikov et al. 2017). In this context, †*Zignoichthys* is unique in having a remarkable suite of plesiomorphies (presence of a basisphenoid, urohyal, beryciform foramen perforating the anterior ceratohyal, ribs, more than 20 vertebrae, epineurals, 12 principal caudal-fin rays, procurrent caudal-fin rays, unfused hypurals, autogenous haemal arch and

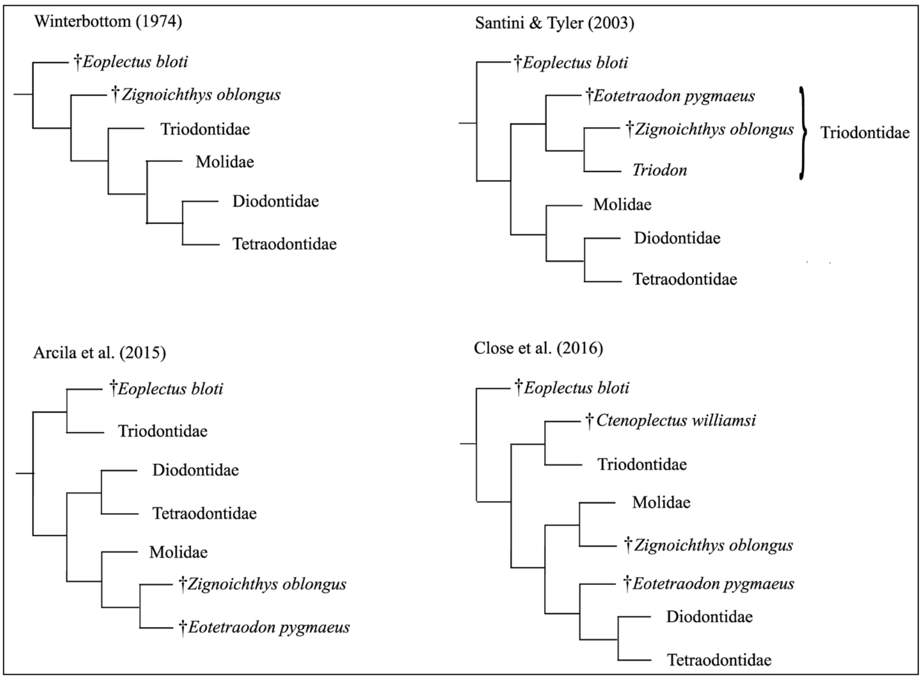

Fig. 10 - Selected cladograms depicting previous hypotheses on phylogenetic relationships among gymnodonts.

spine of the third preural vertebra, dorsal-fin spines, scapular foramen entirely enclosed by the scapula) associated with derived features (absence of pelvic fins and girdle, and teeth incorporated into the matrix of the biting edges of the jaws into subhorizontal slender bands). As discussed above, all the plesiomorphic features that define the peculiar body plan of †*Zignoichthys* are shared with *Triodon*. Although shared plesiomorphies should not be used to interpret their phylogenetic affinities, at the same time it is also difficult to believe that the retention of this complex set of characters occurred independently in the genera *Triodon* and †*Zignoichthys,* especially considering that these two genera also share a similar structure of the beak-like jaws, with fused dentaries and interdigitated premaxillae.

Relationships

Several studies have examined the phylogenetic relationships of the gymnodonts and, more generally, of the Tetraodontiformes, and they have recurrently recovered these clades as monophyletic (e.g., Tyler 1980; Santini & Tyler 2003; Holcroft 2005; Yamanoue et al. 2008; Santini et al. 2013; Arcila et al. 2015; Arcila & Tyler 2017), although the taxonomy of some taxa and the intrarelationships within certain groups are still debated (Fig. 10). The first cladistic attempt to analyze the phylogenetic relationships of the Tetraodontiformes was provided by Winterbottom (1974) and was based upon myology. He recovered the gymnodonts (his superfamily Tetraodontoidea) as monophyletic and sister to the clade formed by Ostraciidae+(Balisitidae+Spinacanthidae). Tyler (1973) placed †*Zignoichthys oblongus* within the family †Eoplectidae, whereas Winterbottom (1974) established the new monotypic family †Zignoichthyidae and divided the gymnodonts into six families with †Eoplectidae, †Zignoichthyidae, Triodontidae, and Molidae as successive sisters to the pair formed by Tetraodontidae and Diodontidae (Fig. 10). Winterbottom (1974) assumed that †*Zignoichthys* was one of the basalmost gymnodonts. A few years later, Tyler (1980) did not consider the family †Zignoichthyidae as valid and placed †*Zignoichthys* and †*Eoplectus* in the non-gymnodont family Triacanthodidae, subfamily †Eoplectinae, based on the morphology of the caudal fin, caudal peduncle, and dorsal fin. Subsequently, Santini & Tyler (2003) carried out a phylogenetic analysis of tetraodontiforms using a matrix that included 56 taxa and 210 morphological characters. Their analysis provided the first robust phylogenetic evidence of the monophyletic status of the suborder Tetraodontoidei that was based on solid morphological characters; however, the tree topology that they recoved is quite different from our result. Santini & Tyler (2003) recovered †*Eoplectus* as basal to all other tetraodontoidei, as in our study; it showed †*Zignoichthys* as a member of the family Triodontidae along with †*Eotetraodon* and *Triodon* (very close to *Triodon*); and it revealed the Molidae as the sister-group to the clade formed by Diodontidae plus Tetraodontidae (Fig. 10). The inclusion in our analysis of †*Ctenoplectus* and †*Balkaria* may be why we recovered a different arrangement in which †*Eoplectus,* Molidae, and the clade formed by †*Eotetraodon,* †*Ctenoplectus,* and †*Zignoichthys* as stem Triodontidae, are successive sister taxa to the dichotomy formed by Tetraodontidae and Diodontidae.

The *incertae sedis* Oligocene gymnodont †*Iraniplectus bakhtiari* was placed by Tyler et al. (2006) close to the family †Zignoichthyidae despite the limited anatomical information available about its skeletal anatomy, which is mostly inaccessible because of the very dense and thick scale cover. For this reason, †*Iraniplectus* was not included in the phylogenetic analysis presented herein. In the phylogenetic analysis of Arcila et al (2015), †*Zignoichthys* is still close to †*Eotetraodon,* and both are close to Molidae rather than to *Triodon* (Fig. 10). Bannikov et al. (2017) recovered, under a Bayesian tip-dating analysis, a tree topology similar to that of Santini & Tyler (2003) in which †*Zignoichthys* is close to †*Eotetraodon* and both are close to *Triodon*. Conversely, Close et al. (2016) produced a tree topology (Fig. 10) in which †*Zignoichthys* is the sister taxon to the Molidae, and both are sister to the clade formed by [†*Eotetraodon pygmaeus* + (Diodontidae+Tetraodontidae)].

Data Availability Statement

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

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Appendix

Character list

The following character list used for this parsimony analysis was taken directly from Santini & Tyler (2003). The original matrix was created for the study of all the Tetraodontiformes. We have reduced it by selecting only those characters that are useful for the phylogenetic analysis of our target group, the Tetraodontoidei (= gymnodonts). We have also added an additional character state (indicated by an asterisk) to characters 1, 65, 79, and 80. The characters are arranged by anatomical regions based upon the scheme used by Santini & Tyler (2003). The original numbers used by Santini & Tyler (2003) are included as ST in parentheses.

Cranial

1. (ST1) Parasphenoid: shaft-like, with either no ventral flange or a narrow flange that is no deeper than the shaft [0]; plate-like, expanded both dorsally and ventrally (relative to level of vomer and base of cranium) into the orbital septum and/or in the region anterior to the orbit, with or without a strengthening ridge along its dorsal edge [1]; shaft-like, with a ventral flange deeper than the shaft [2]; shaft-like and expanded anterolaterally [3]; shaft-like and expanded anterolaterally, with a ventral flange deeper than the shaft [4*].

2. (ST5) Parasphenoid, anterior end of: variously thin and wide or deep in the region of articulation with the vomer, but not an expanded cone-like structure with an empty cavity [0]; becoming expanded into a wide, deeply concave cone-like structure, the concavity not being a place for the articulation of other bones [1].

3. (ST7) Lateral ethmoid, size: large, extending from the frontal ventrally to the level of the parasphenoid and vomer, to moderate, extending down only about one-half the distance between the frontal and the parasphenoid [0]; small, a thin plate, broadly sutured to the overlaying frontal and not extending ventral to it [1].

4. (ST9) Bony canal for the nerves and blood vessels running from the orbit to the nasal region: incomplete, surrounded by the lateral ethmoid laterally, above, and below, but not medially [0]; partially complete, surrounded nearly entirely by the lateral ethmoid in adults, with the upper and lower regions of the medial edge of the lateral ethmoid coming in close contact but not fusing, so the bony substance is not continuous medially [1]; no trace of a canal evident, the lateral ethmoid reduced and sutured to the frontal [2]; fully complete, entirely surrounded by the continuous substance of the lateral ethmoid [3].

5. (ST11) Frontal, in posterior orbital region: not in contact with the prootic, separated from it by the sphenotic and pterosphenoid [0]; in contact with the prootic [1].

6. (ST14) Supraoccipital, shape of dorsal surface of: flat [0]; dome-like [1].

7. (ST16) Supraoccipital, posterior crest of: present [0]; absent [1].

8. (ST17) Supraoccipital, posterior crest shape: laterally compressed and mainly in a vertical plane, although its dorsal edge may be somewhat thicker than the ventral plate [0]; dorsoventrally compressed, and entirely in a horizontal plane, wider than deep throughout its length [1]; not applicable [–].

9. (ST18) Exoccipital: with a condyle and in contact with the first vertebra, which articulates anteriorly with both the exoccipital and basioccipital [0]; without a condyle and in contact with the first vertebra, which articulates anteriorly with either both the exoccipital and basioccipital, or mostly with the exoccipital [1]; without a condyle and not in contact with the first vertebra, which articulates anteriorly only with the basioccipital [2].

10. (ST19) Basioccipital: not prolonged dorsally to exclude the exoccipital from bordering the foramen magnum [0]; prolonged dorsally behind the exoccipital to border the foramen magnum to the exclusion of the exoccipital [1].

11. (ST22) Endopterygoid: in contact with the ectopterygoid [0]; not in contact [1]; not applicable [–].

12. (ST23) Ectopterygoid: with a substantial part of its length extending dorsally or posterodorsally above its contact with the quadrate [0]; in contact with the quadrate for nearly all of its length, and not extending much dorsally or posterodorsally to it [1]; in contact with the quadrate for nearly all of its length, and with a substantial portion of the bone extending dorsally to the level of the upper end of the quadrate [2].

13. (ST26) Basisphenoid: a small rod placed far posteriorly in the interorbital septum and articulated with the anterior edge of the dorsal roof of the myodome [0]; absent [1]; present as a large plate in the interorbital septum [2].

14. (ST27) Premaxilla, ascending process of: present [0]; absent [1].

15. (ST29) Premaxilla, articulation with maxilla: movable [0]; interdigitated and immovable [1].

16. (ST30) Premaxilla: not fused to its opposite member in the midline [0]; fused [1].

17. (ST32) Maxilla: moderately to deeply indented 35 [0]; only slightly indented [1].

18. (ST33) Maxilla, lateral surface: relatively flat [0]; deeply indented between the anterior and posterior ridges, sometimes with a lateral flange on the posterior ridge [1].

19. (ST36) Dentary: not fused to its opposite member in the midline [0]; fused [1].

20. (ST38) Sesamoid articular: present [0]; absent [1].

21. (ST40) Upper and lower jaws: bones not especially thick, massive, and wide, length of the upper jaw about one-third or less of the length of the skull [0]; jaws not thick, massive, and wide, but long, about one-half the length of the skull [1]; jaws thick, massive, wide, and long, about one-half the length of the skull [2].

22. (ST41) Upper jaw: moderately to highly protractile [0]; only slightly protractile [1]; non-protractile [2].

23. (ST44) Palatine: not in contact with the frontal [0]; in contact and sutured to the frontal [1].

24. (ST46) Ethmoid: evenly convex upper surface, without a laterally expanded dorsolateral region and usually no wider dorsally than ventrally [0]; expanded dorsolaterally, at least anteriorly, and never narrower dorsally than ventrally [1]; a flat to curving dorsolateral expansion, which is moderate to broad but not much wider dorsally than ventrally [2]; greatly reduced in size to a thin plate and perhaps combined with the vomer [3].

25. (ST47) Sphenotic, size and position: relatively large and not confined to the posterior wall of the orbit, being present on the lateral and/or dorsal surface of the skull [0]; relatively small and confined to the posterior wall of the orbit, not reaching the lateral and/or dorsal surface of the skull [1].

26. (ST48) Sphenotic, anterior region of: either flat or with a broad lateral or anterolateral process [0]; with a long slender laterally directed sturdy prong [1].

27. (ST50) Epioccipital: without a prominent posterior prolongation beyond the level of the rear of the skull [0]; with a large broad-based tapering posterior prolongation beyond the rear of the skull [1]; with a basally restricted narrow prolongation to the rear of the skull or beyond [2].

28. (ST52) Pterotic, posterior region of: relatively flat and not extending beyond the rest of the skull or, if moderately prolonged posteriorly beyond the level of the basioccipital, a stout bone, about as long as wide [0]; prominently prolonged posteriorly beyond the level of the basioccipital as a thinner bone, much longer (two times or more) than wide [1].

29. (ST56) Hyomandibula: more or less elongate and shaft-like throughout most of its length, sometimes expanded at either its dorsal or ventral end [0]; broad flat plate expanded throughout much of its length [1].

30. (ST58) Hyomandibula, horizontal crest of: absent [0]; present [1].

31. (ST60) Interopercle: long, deep, and laterally compressed, extending posteriorly well behind the junction of the epihyal and interhyal [0]; short, rod-like, not extending posteriorly beyond the junction of the epi- and interhyal [1]; slender, rod-like, with a short to long posterior shaft behind the epi-interhyal junction [2]; a very slender sesamoid bone, of moderate size [3].

32. (ST61) Interopercle, ventral prong at the level of the epi-interhyal junction: absent [0]; present [1].

33. (ST63) Subopercle, anterodorsal region of: without a prominent discrete anteriorly directed prong [0]; with a prominent discrete anteriorly directed prong reaching under the rear edge of the preopercle [1].

34. (ST64) Posttemporal: present [0]; absent [1].

35. (ST68) Teeth in jaws: discrete units, protruding out of sockets in the jaws [0]; not protruding, incorporated in the matrix of the beak-like jaw bones [1]; absent [2].

36. (ST70) Teeth, when fused into a parrot-like beak: small, more or less rounded individual units [0]; mostly elongated rods [1]; individual units indistinguishable [2]; not applicable [–].

37. (ST71) Teeth internal to the major outer series or band in the upper jaw, either as individual units or as trituration teeth: absent [0]; present [1].

38. (ST72) Teeth internal to the major outer series or band in the lower jaw, either as individual units or as trituration teeth: absent [0]; present [1].

Branchial apparatus

39. (ST77) First branchiostegal ray: with the dorsomedial edge not modified and inturned [0]; anteriorly slightly enlarged, but not inturned [1]; with the dorsomedial edge enlarged and inturned [2].

40. (ST80) Dorsal hypohyal: large size, its greatest dimension five or fewer times the length of the ceratohyal [0]; small size, its greatest dimension nine or more times the length of the ceratohyal [1]; absent [2].

41. (ST83) Interhyal: present [0]; absent [1].

42. (ST86) First pharyngobranchial: present [0]; absent [1].

43. (ST87) First pharyngobranchial, teeth: absent [0]; present [1]; not applicable [–].

44. (ST88) Second pharyngobranchial, teeth: well developed [0]; minute or absent [1].

45. (ST89) Third pharyngobranchial, teeth: well developed [0]; minute or absent [1].

46. (ST90) Fourth pharyngobranchial: present [0]; absent [1].

47. (ST92) Fourth arch, gill rakers along the posterior edge of: present [0]; absent [1].

48. (ST93) Fifth arch (ceratobranchial), gill rakers along the anterior edge of: present [0]; absent [1].

49. (ST94) Gill rakers along the anterior edge of the first gill slit: absent [0]; present [1].

50. (ST96) Gill slit between the fourth and fifth arches: present [0]; no slit between the fourth and fifth arches [1].

51. (ST98) Gills: not greatly expanded dorsally above and beyond the supporting arches [0]; greatly expanded dorsally above and beyond the supporting arches [1].

Paired fin girdles

52. (ST99) Pelvis: present [0]; absent [1].

53. (ST103) Dewlap of skin with modified scales in front of the anal region: absent, and pelvis (if present) not rotatable in life around its anterior articulation with the cleithra or absent [0]; present, associated in extant taxa (and presumably also in fossil species) with the pelvis being rotatable around its articulation with the cleithra [1].

54. (ST109) Pelvis, ventrolateral region at the base of the pelvic-fin spine: side of pelvis and the base of the pelvic spine both with a foramen, forming a ring-link articulation [0]; without a foramen in the side of the pelvis, and the pelvic spine without a foramen through its base, and thus no ring-link articulation [1]; not applicable, when pelvic spine is absent [–].

55. (ST110) Uppermost pectoral-fin ray: three times or more the length of the first caudal vertebral centrum [0]; one to two times the length of the first caudal vertebral centrum [1]; about one-half or less the length of the first caudal vertebral centrum [2].

56. (ST111) Pectoral- fin radials: not sutured to the scapula or coracoid or to each other, except sometimes basally [0]; immovably sutured to the scapula or coracoid and to each other along most of their length [1]; slightly sutured to each other basally, and sometimes distally, the first two often sutured to the scapula but none of them sutured to the coracoid [2].

57. (ST115) Cleithrum, shape of anterior edge of: relatively straight, or only slightly concave to convex [0]; strongly concave, with a long forward extension beyond its contact with the coracoid [1].

58. (ST118) Cleithrum, percentage of contact with the supracleithrum: one-third to one-half of the inner surface of the supracleithrum free from contact [0]; most of the inner surface of the supracleithrum in contact with the outer surface of the cleithrum [1].

59. (ST119) Coracoid: narrower ventrally than dorsally and without a lateral flange, or with only a narrow flange [0]; large (as deep as the cleithrum below the level of the scapula) and expanded ventrally, as wide or wider there than dorsally, with a prominent broad lateral flange along its anterior edge [1]; small (much less deep than the cleithrum below the level of the scapula) and expanded ventrally, as wide or wider there than dorsally, without a broad flange along its posterior edge [2]; large (as deep as the cleithrum below the level of the scapula) and expanded ventrally, as wide or wider there than dorsally, without a broad flange along its anterior edge [3].

60. (ST120) Coracoid, upper region of posterior edge: with a distinct posterior prong below the lower radia, or with a short process of the posterodorsal edge sutured to the lowermost radial [0]; without a posterodorsal prong below the lower radial and not connected to the lowermost radial [1].

61. (ST121) Supracleithrum: not very elongate, only its extreme proximal end articulated directly with the pterotic region [0]; extremely elongate, broadly articulated over the anterior one-third to one-half of its length with the pterotic region [1].

62. (ST123) Postcleithrum, number of separate bony elements: one [0]; two [1].

63. (ST124) Postcleithrum complex, ventral half of (whether one piece or two): a long oblique posteroventrally directed strut, slender or stout, extending well below or behind the pectoral-fin base [0]; expanded into a thin plate, always much larger than the upper part of the postcleithrum complex [1]; expanded into a thin plate, always much smaller than the upper part of the postcleithrum complex [2]; short, oblique [3]; bifurcated distally just below the level of the pectoral-fin base, with the anterior ramus alongside the pectoral actinosts [4]; expanded into a plate of about the same size as the upper part of the postcleithrum complex [5].

64. (ST131) Neural spines of abdominal vertebrae: non-bifid, single, in the midline (with possible exception of first neural spine, or composite first fused vertebral elements in ostracioids attached to skull) [0]; three or more with bifid processes to either side of the midline [1].

65. (ST132) Neural spines of abdominal vertebrae, when bifid processes are present on either side of the midline: first three or four vertebrae bifid [0]; ten or more vertebrae bifid, all those anterior to the first dorsal pterygiophore [1]; six vertebrae bifid (all but the last abdominal vertebra bifid) [2*]; not applicable [–].

66. (ST133) Number of neural spines anterior to first pterygiophore of soft dorsal fin: 7–9 [0]; 4–6 [1]; 10–12 [2].

67. (ST134) Neural spines of vertebrae supporting the basal pterygiophores of the soft dorsal fin: normal, long, slender shafts, penetrating the interspaces between the pterygiophores [0]; short and broad, not slender shafts and not penetrating the interspaces between the pterygiophores [1].

68. (ST135) Ribs: present [0]; absent [1].

69. (ST136) Epineurals: present [0]; absent [1].

70. (ST139) Haemal spines of second and immediately following caudal vertebrae: long, shaft-like, length two or more times that of the vertebral centra [0]; short, stout, ventrally orientated, length between 1.5 times to equal to that of the vertebral centra [1]; essentially absent [2]; short, slender, posteroventrally orientated shaft, length about equal to that of the vertebral centra [3]; short, slender to stout, posteriorly orientated under the length of the centra [4]; very short, thin but broad, irregularly emarginated distally, length less than that of the vertebral centra [5].

71. (ST140) Haemal spines of posterior abdominal vertebrae, and of the caudal vertebrae anterior to the one or two vertebrae supporting the last pterygiophore of the anal fin: relatively well developed [0]; absent [1]; if arches and spines incomplete, then with broad ventrolateral parapophyses [2].

72. (ST142) Haemal canal, posterior extension: penetrating the last vertebral complex to exit between the parhypural and lower hypural or at the foramen between the consolidated parhypural and lower hypural region [0]; not extending posterior to the front of the last vertebra, not penetrating the last vertebral complex [1]; not applicable [–].

73. (ST143) Centra of vertebrae preceding the hypural centrum: none especially anteroposteriorly compressed relative to the immediately preceding centra [0]; at least one centrum much compressed [1].

74. (ST144) Haemal spine of antipenultimate vertebra (PU3): autogenous [0]; nonautogenous [1].

75. (ST145) Haemal spine of PU3: long, one and half or more times the depth of the centrum [0]; short to moderate, about equal to or less than the depth of the centrum [1].

76. (ST146) First vertebra in caudal peduncle with a neural spine modified for caudal fin support: PU3 [0]; PU2 [1]; PU2 and PU3 far removed from the caudal fin and not directly supporting it [2].

77. (ST147) First vertebra in caudal peduncle with a haemal spine modified for caudal fin support: PU3 [0]; PU2 [1]; PU2 and PU3 far removed from the caudal fin and not directly supporting it [2].

Dorsal, anal, and caudal fins

78. (ST148) Spiny dorsal fin: present [0]; absent [1].

79. (ST153) First spiny dorsal pterygiophore: long ventral shaft with only narrow median flanges anteriorly and posteriorly except sometimes at its distal end where flanges may be about as wide as the shaft [0]; long ventral shaft with broad median flanges anteriorly and posteriorly (flanges several times wider than the shaft) [1]; shaft very short or absent, without thin median flanges, distal part of the pterygiophore modified into a carina [2]; a horizontal shaft not connected to the head, without median flanges, and pterygiophore not modified into a carina [3]; long, thick, robust, horizontal shaft attached (sutured) along midline of the middle region of the top of the skull from about the levels of the anterior end of the orbit to the posterior end of the sphenotic [4*]; not applicable [–].

80. (ST155) Second spiny dorsal pterygiophore, ventral shaft of: long, deeply inserted between the neural spines [0]; short, does not reach the neural spines, to intermediate length, barely reaches tips of the neural spines [1]; ventral shaft posteriorly to posteroventrally oriented and closely attached to the dorsal surface of the skull from either over or behind the orbit [2*]; not applicable [–].

81. (ST157) Spiny dorsal pterygiophores, distal suturing: the first three or more sutured [0]; none sutured [1]; the first two sutured [2]; not applicable [–].

82. (ST158) Spiny dorsal-fin origin: well behind the rear edge of the head [0]; about at the rear edge of the head [1]; in front of the rear edge of the head [2]; not applicable [–].

83. (ST160) Spine, or at least one of the two spines, associated with the first pterygiophore: deep grooves [0]; shallow grooves [1]; grooves absent [2]; not applicable [–].

84. (ST162) Spiny dorsal-fin pterygiophores anterior to the neural spine of the fourth abdominal vertebra: three [0]; two [1]; four [2]; one [3]; none [4]; not applicable [–].

85. (ST164) First anal pterygiophore, position of: along the front edge of the haemal spine of the first caudal vertebra, in the prehaemal space [0]; along the rear edge of the haemal spine of the first caudal vertebra, in the first interhaemal space [1]; not applicable [–].

86. (ST166) Anal pterygiophores in the first interhaemal space: five [0]; one [1]; two [2]; three [3]; four [4]; none [5]; not applicable [–].

87. (ST167) Anal pterygiophores anterior to the haemal spine of the third caudal vertebra: seven or more [0]; three or less [1]; four [2]; five to six [3]; not applicable [–].

88. (ST168) Anal pterygiophore articulation: pterygiophores not sutured to one another in any region, except sometimes the first two distally [0]; pterygiophores sutured along the edges of the anterior and posterior median flanges but not between the distal rounded articular heads just below the rays [1]; at least some pterygiophores sutured at both the distal rounded articular heads and along the edges of the median flanges, at least for some portion distally [2]; pterygiophores sutured at distal rounded articular heads but not along the edges of the median flanges [3].

89. (ST170) Dorsal-, anal-, caudal- (pseudocaudal), and pectoral-fin rays: with many cross-striations, these not confined to only the distal end of the rays in adults [0]; with extremely few cross-striations, those present only at the extreme distal end of the rays in adults [1].

90. (ST171) Rayless pterygiophore preceding soft dorsal fin: absent

[0]; very long horizontal bone, four times or more the length of the vertebral centra, with a broadly expanded dorsal edge along the dorsal profile [1]; short horizontal bone, between one and two times the length of the vertebral centra, with a broadly expanded dorsal edge along the dorsal profile [2]; oblique strut between the rear of the spiny dorsal fin and an abdominal neural spine [3]; long slender rod-like horizontal bone along the dorsal profile [4]; two elements, the first short and the second long [5]; extremely long slender rod as an anterior extension of the first pterygiophore, contacting the posterior crest of the supraoccipital [6].

91. (ST172) Soft dorsal-fin pterygiophore articulation: pterygiophores not sutured to one another in any region [0]; pterygiophores sutured along the edges of the anterior and posterior median flanges but not between the distal rounded articular heads just below the rays [1]; pterygiophores sutured at both the distal rounded articular heads and along the median flange edges, at least for some portions distally [2]; pterygiophores sutured at the distal rounded articular heads but not along the edges of the median flanges, except for sometimes the last few [3].

92. (ST173) Dorsal- and anal-fin rays: not widely separated from their basal pterygial supports by a large block of cartilage [0]; widely separated from their basal pterygial supports by a large block of cartilage [1].

93. (ST174) Caudal fin: present [0]; absent, replaced by a pseudocaudal fin [1].

[Note that both †*Balkaria histiopterygia* and †*Zignoichthys oblongus* exhibit state 0, whereas in †*Ctenoplectus williamsi* the character was not observable.]

94. (ST176) Number of caudal peduncle vertebrae (those behind the last vertebra whose haemal spine supports an anal-fin pterygiophore): three or four [0]; five [1]; six [2]; seven [3]; not applicable [–].

95. (ST178) Caudal fin, procurrent rays: present [0]; absent [1]; not applicable [–].

96. (ST179) Caudal fin, number of unbranched principal rays in lower half of fin: one [0]; two [1]; not applicable [–].

97. (ST180) Hypurals 1–4: not fused, and free from each other and from the last vertebra [0]; 1+2 and 3+4 forming plates, these two plates fused to each other and to the last vertebra, and in some cases may be fused also to hypural 5 and/or to parhypural [1]; 1+2 and 3+4 forming two plates, but these plates are separate from one other and from the last vertebra [2]; 1+2 forming a plate, and this plate is fused to the last vertebra, 3+4 forming an autogenous plate [3]; 1+2 and 3+4 forming two plates, but these two plates separate from one another until the point of fusion to the last vertebra [4]; absent [5].

98. (ST181) Last centrum and hypurals, horizontal lateral flange: absent [0]; present [1]; not applicable [–].

99. (ST182) Epurals: two or more, free [0]; one, either free or fully sutured or fused to the urostylar region [1]; absent [2].

100. (ST183) First epural: a free element, not sutured to the caudal skeleton [0]; sutured to the caudal skeleton [1]; fully fused to the urostylar region of the caudal skeleton [2]; fully fused to the posterior end of NPU2 [3]; not applicable [–].

101. (ST184) Uroneurals: one or more pairs present [0]; absent [1].

102. (ST185) Parhypural: autogenous [0]; non-autogenous [1]; absent [2].

Epidermis

103. (ST187) Scales, on most of body: normal spiny ctenoid to relatively cycloid [0]; thick enlarged hexagonal sutured plates [1]; thin, irregular to rounded basal plates bearing one or more nonarticulated upright spinules [2]; thick basal plates ornamented with a cruciform ridge or a series of vertical ridges [3]; thick, hexagonal to rounded basal plates bearing a central spine [4]; thick, small to moderate overlapping rectilinear basal plates with low ornamentation such as granulations [5]; small to large multiradiate bases with a single protruding spiny process [6]; thick large irregular plates with low granular ornamentation (7); small moderately thick basal plates, irregularly angular to hexagonal and without upraised spinules (8).

Miscellaneous

104. (ST197) Inflatable diverticulum of gut: absent [0]; present [1].

105. (ST198) Peritoneum: pale silvery [0]; dark, tending to black [1].

106. (ST199) Air bladder: present and well developed [0]; absent, at least in adults [1].

Meristics

107. (ST200) Branchiostegal rays: six [0]; seven [1]; five or fewer [2].

108. (ST202) Pectoral-fin radials, number: four [0]; three [1].

109. (ST203) Pectoral-fin rays: 15 or less [0]; 16–19 [1]; 21 or more [2].

110. (ST204) Abdominal vertebrae: 10–11 [0]; 8–9 [1]; 12–13 [2]; 6–7 [3].

111. (ST205) Caudal vertebrae: 11–12 [0]; 19–21 [1]; 13–14 [2]; eight to 10 [3].

112. (ST208) Soft dorsal rays: 20 or more [0]; 15–19 [1]; 10–14 [2]; nine or fewer [3].

113. (ST209) Soft anal rays: 20 or more [0]; 15–19 [1]; 10–14 [2]; nine or fewer [3].

114. (ST210) Caudal fin, number of principal rays: 12 [0]; 13 or more [1]; 11 [2]; 10 or less [3]; not applicable [–].

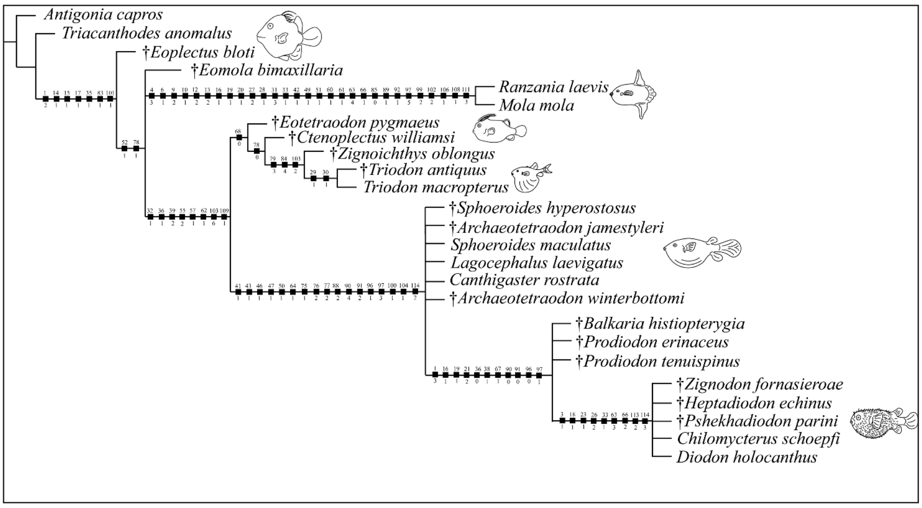

Fig. S1 - The strict consensus tree retrieved in TNT based on 114 characters and 25 taxa, showing the hypothetical phylogenetic relationship of †*Zignoichthys oblongus* (Zigno, 1874) within the Tetraodontoidei. Synapomorphies supporting the clades are indicated as nodes represented by black squares whose character numbers and states are placed above and below the node, respectively.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
Antigonia capros	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0
Triacanthodes anomalus	0	0	0	0	0	0	1	-	0	0	1	1	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	-	1	1	0	0
Triodon macropterus	2	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	2	0	2	1	0	0	0	1	1	2	1	1	0	1	0	1	1	2	0
†*Triodon antiquus*	?	?	0	?	?	0	0	0	?	?	?	?	?	1	?	0	?	?	1	?	0	2	0	2	1	0	0	0	1	1	?	?	1	?	1	0	?	?	?	?
†*Eoplectus bloti*	2	0	0	?	?	?	?	?	?	?	?	?	1	1	1	0	1	0	0	?	2	2	?	?	?	?	?	?	0	?	?	?	?	?	1	0	?	?	?	?
†*Zignoichthys oblongus*	0	0	0	?	?	0	0	0	?	?	0	0	0	1	1	0	1	0	1	?	0	2	0	?	1	0	?	?	0	0	?	?	?	?	1	0	?	?	1	1
Lagocephalus laevigatus	2	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	2	0	2	0	0	0	0	0	0	2	1	0	1	1	1	1	0	2	1
Sphoeroides maculatus	2	0	0	0	0	0	0	0	0	0	0	2	1	1	1	0	1	0	0	0	0	2	0	2	0	0	0	0	0	0	2	1	0	1	1	1	1	0	2	1
Canthigaster rostrata	2	0	0	0	0	0	0	0	0	0	0	2	1	1	1	0	1	0	0	0	0	2	0	1	0	0	0	0	0	0	2	1	0	1	1	1	0	0	2	2
†*Eotetraodon pygmaeus*	0	0	0	?	?	?	?	?	?	?	?	?	1	?	?	0	?	?	0	?	0	2	?	?	?	?	0	0	0	?	?	?	?	?	1	1	?	?	2	?
†*Archaeotetraodon winterbottomi*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	0	?	0	2	?	?	?	?	0	?	?	?	?	?	?	?	1	?	1	0	?	?
†*Archaeotetraodon jamestyleri*	?	0	0	?	?	0	0	0	?	?	?	?	1	1	1	0	1	0	0	?	0	2	0	?	0	0	0	0	0	?	?	?	?	?	1	?	?	?	2	?
†*Sphoeroides hyperostosus*	2	0	0	?	0	0	0	0	?	?	?	?	1	1	1	0	1	0	0	?	0	2	0	2	0	0	0	0	0	0	?	?	0	?	1	1	1	0	2	?
Diodon holocanthus	3	1	1	2	1	0	0	1	0	0	0	0	1	1	1	1	1	1	1	0	2	2	1	3	0	1	0	0	0	0	2	1	1	1	1	0	1	1	2	1
Chilomycterus schoepfi	3	1	1	2	1	0	0	1	0	0	0	0	1	1	1	1	1	1	1	0	2	2	1	3	0	1	0	0	0	0	2	1	1	1	1	0	1	1	2	1
†*Pshekhadiodon parini*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	?	2	2	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	1	2	?
†*Prodiodon tenuispinus*	3	1	?	?	?	0	?	?	?	?	?	?	?	?	?	1	?	?	1	?	2	2	?	?	?	?	0	?	?	?	?	?	?	?	1	0	1	1	2	?
†*Prodiodon erinaceus*	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	1	?	?	1	?	2	2	?	?	?	?	0	?	?	?	?	?	?	?	1	0	1	1	2	?
†*Heptadiodon echinus*	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	1	?	?	1	?	2	2	?	?	?	?	0	?	?	?	?	?	?	?	1	0	1	1	2	?
†*Zignodon fornasieroae*	?	?	?	?	?	0	?	?	?	?	?	?	?	?	?	1	?	?	1	?	2	2	?	?	?	?	0	?	?	?	?	?	?	?	1	0	?	?	?	?
Mola mola	2	0	0	3	0	1	1	-	2	1	0	2	2	1	1	1	1	0	1	1	0	2	0	2	0	0	2	1	0	0	3	0	1	1	1	2	1	1	0	0
Ranzania laevis	2	0	0	3	0	1	0	0	2	1	0	2	2	1	1	1	1	0	1	1	0	2	0	2	0	0	2	1	0	0	3	0	1	1	1	2	1	1	0	0
†*Eomola bimaxillaria*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	0	?	?	?	2	?	?	?	?	?	?	?	?	2	?	?	?	1	2	1	?	?	?
†*Balkaria histiopterygia*	4	0	0	?	?	0	1	-	?	?	0	0	0	1	1	1	1	0	1	?	2	2	0	0	0	0	0	0	0	0	?	?	0	?	1	0	?	?	?	?
†*Ctenoplectus williamsi*	?	?	0	?	?	?	?	?	?	?	?	?	?	1	1	1	0	0	1	?	0	2	0	?	?	?	?	?	?	?	?	?	0	0	1	0	0	0	?	?

	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80
Antigonia capros	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triacanthodes anomalus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	-	0	0	1	0	0	0	0	0	1	0	1	1	0	1	0
Triodon macropterus	0	0	0	0	0	0	0	1	0	0	0	0	1	-	2	0	1	0	0	0	0	1	0	0	-	0	0	0	0	3	0	0	0	0	0	1	1	0	3	-
†*Triodon antiquus*	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Eoplectus bloti*	?	?	?	?	?	?	?	?	?	?	?	0	0	?	?	?	?	?	?	?	?	?	?	0	-	0	0	1	?	0	0	?	0	1	0	1	1	0	0	0
†*Zignoichthys oblongus*	?	?	?	?	?	?	?	?	?	?	?	1	1	-	?	?	1	0	0	0	?	1	0	0	-	0	0	0	0	0	0	?	0	0	0	1	0	0	3	?
Lagocephalus laevigatus	0	0	0	0	0	1	1	1	0	1	0	1	0	-	2	2	1	0	0	0	0	1	0	1	0	0	0	1	1	4	0	0	0	1	1	2	2	1	-	-
Sphoeroides maculatus	1	0	1	0	0	1	1	1	0	1	0	1	0	-	2	2	1	0	0	0	0	1	0	1	0	0	0	1	1	4	0	0	0	1	1	2	2	1	-	-
Canthigaster rostrata	1	0	1	0	0	1	1	1	0	1	0	1	0	-	1	2	1	0	0	0	0	1	0	1	0	0	0	1	1	1	0	0	0	1	1	2	1	1	-	-
†*Eotetraodon pygmaeus*	?	?	?	?	?	?	?	?	?	?	?	1	0	-	?	2	1	?	?	?	?	1	0	?	?	2	0	0	?	0	0	?	0	1	0	1	1	1	-	-
†*Archaeotetraodon winterbottomi*	?	?	?	?	?	?	?	?	?	?	?	1	0	-	?	?	?	?	?	?	0	?	0	1	0	0	0	1	?	?	0	?	0	1	1	2	1	1	-	-
†*Archaeotetraodon jamestyleri*	?	?	?	?	?	?	?	?	?	?	?	1	0	-	?	2	?	?	?	?	0	?	0	1	0	0	0	1	?	?	0	?	0	1	1	2	2	1	-	-
†*Sphoeroides hyperostosus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	0	?	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Diodon holocanthus	1	0	1	1	1	1	1	1	0	1	0	1	0	-	2	2	1	0	2	0	0	0	3	1	1	2	1	1	1	5	2	1	1	1	1	2	2	1	-	-
Chilomycterus schoepfi	1	0	1	1	1	1	1	1	0	1	0	1	0	-	1	2	1	0	2	0	0	0	3	1	1	2	1	1	1	5	2	1	1	1	1	2	2	1	-	-
†*Pshekhadiodon parini*	?	?	?	?	?	?	?	?	?	?	?	1	0	-	?	?	0	?	0	1	?	0	3	?	?	1	?	1	?	?	0	?	0	1	1	2	2	1	-	-
†*Prodiodon tenuispinus*	?	?	?	?	?	?	?	?	?	?	?	1	0	-	?	?	?	?	?	?	?	?	0	?	?	?	?	1	?	?	?	?	0	1	1	1	1	1	-	-
†*Prodiodon erinaceus*	?	?	?	?	?	?	?	?	?	?	?	1	0	-	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	0	?	?	?	?	1	-	-
†*Heptadiodon echinus*	?	?	?	?	?	?	?	?	?	?	?	1	0	-	?	?	?	?	?	?	?	?	?	?	?	?	?	1	?	?	?	?	?	?	?	?	?	1	-	-
†*Zignodon fornasieroae*	?	?	?	?	?	?	?	?	?	?	?	1	0	-	?	?	?	?	?	?	?	?	0	?	?	?	?	1	?	?	?	?	0	?	?	?	?	1	-	-
Mola mola	0	1	-	0	0	0	0	0	1	0	1	1	0	-	1	2	0	0	0	1	1	0	4	0	-	1	0	1	1	0	0	-	0	1	0	1	1	1	-	-
Ranzania laevis	0	1	-	0	0	0	0	0	1	0	1	1	0	-	1	2	0	0	0	1	1	0	4	0	-	1	0	1	1	0	0	-	0	1	0	1	1	1	-	-
†*Eomola bimaxillaria*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Balkaria histiopterygia*	?	?	?	?	?	?	?	?	?	?	?	?	0	?	?	2	1	0	0	1	0	?	0	1	2	0	1	1	1	1	0	?	1	1	0	2	2	0	5	2
†*Ctenoplectus williamsi*	?	?	?	?	?	?	?	?	?	?	?	0	?	?	?	2	1	0	0	0	0	1	0	?	-	?	?	0	?	?	?	?	?	?	?	?	?	0	0	-

	81	82	83	84	85	86	87	88	89	90	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114
Antigonia capros	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Triacanthodes anomalus	0	1	0	1	1	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	2	0	1	0	0	0	0	1	0	1	2	0
Triodon macropterus	0	0	2	4	1	3	3	0	0	0	0	0	0	2	0	0	0	0	1	0	0	0	2	0	0	0	0	0	1	1	0	2	2	0
†*Triodon antiquus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?
†*Eoplectus bloti*	0	0	1	1	1	1	1	?	0	0	?	0	0	1	1	0	0	0	1	0	1	?	2	?	?	?	?	?	?	1	0	1	1	0
†*Zignoichthys oblongus*	?	0	?	4	0	4	3	0	0	0	0	0	0	2	0	0	0	0	1	0	0	?	2	?	?	?	2	?	?	0	0	2	2	0
Lagocephalus laevigatus	-	-	-	-	1	1	1	2	0	4	2	0	0	1	1	1	3	0	1	1	1	0	6	1	0	0	0	0	1	1	0	1	2	2
Sphoeroides maculatus	-	-	-	-	1	1	1	2	0	4	2	0	0	2	1	1	3	0	1	1	1	0	6	1	0	0	0	0	1	1	0	3	3	2
Canthigaster rostrata	-	-	-	-	1	1	3	2	0	4	2	0	0	2	1	1	3	0	1	1	1	0	6	1	0	0	0	0	1	1	3	2	3	2
†*Eotetraodon pygmaeus*	-	-	-	-	1	2	1	?	?	?	?	0	0	2	1	?	0	0	1	0	?	0	6	?	?	?	0	0	?	0	0	2	2	0
†*Archaeotetraodon winterbottomi*	-	-	-	-	?	1	1	?	?	4	?	0	0	2	1	1	3	0	1	?	1	0	6	?	?	?	?	?	?	1	3	3	3	2
†*Archaeotetraodon jamestyleri*	-	-	-	-	?	?	?	?	?	?	?	0	0	?	1	?	3	0	?	?	?	0	6	?	?	?	?	0	0	3	0	?	?	2
†*Sphoeroides hyperostosus*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Diodon holocanthus	-	-	-	-	1	1	3	0	0	0	0	0	0	0	1	0	1	1	1	3	1	1	6	1	0	0	0	0	2	2	3	1	2	3
Chilomycterus schoepfi	-	-	-	-	1	1	3	0	0	0	0	0	0	0	1	0	1	1	1	3	1	1	6	1	0	0	0	0	2	(12)	3	2	2	3
†*Pshekhadiodon parini*	-	-	-	-	?	?	?	?	?	0	?	0	0	1	1	0	1	0	1	?	1	0	6	?	?	?	?	?	?	1	0	2	2	3
†*Prodiodon tenuispinus*	-	-	-	-	?	?	?	?	?	?	?	?	0	1	1	0	1	?	?	?	?	?	6	?	?	?	0	?	?	?	?	?	?	2
†*Prodiodon erinaceus*	-	-	-	-	?	?	?	?	?	?	?	?	0	?	1	0	1	?	?	?	?	?	6	?	?	?	?	?	?	?	?	3	3	2
†*Heptadiodon echinus*	-	-	-	-	?	?	?	?	?	?	?	?	0	?	1	?	?	?	?	?	?	?	6	?	?	?	?	?	?	?	?	?	?	3
†*Zignodon fornasieroae*	-	-	-	-	?	?	?	?	?	?	?	?	0	?	1	?	?	?	?	?	?	?	6	?	?	?	?	?	?	?	?	?	?	3
Mola mola	-	-	-	-	0	5	1	0	1	5	0	1	1	-	-	-	5	-	2	-	1	2	2	0	0	1	0	1	0	1	3	0	0	-
Ranzania laevis	-	-	-	-	0	5	1	2	1	6	2	1	1	-	-	-	5	-	2	-	1	2	8	0	0	1	2	1	0	1	3	0	0	-
†*Eomola bimaxillaria*	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
†*Balkaria histiopterygia*	0	2	1	2	?	?	?	?	0	0	0	0	0	?	0	0	1	0	1	0	1	?	6	?	?	?	?	0	?	3	0	2	?	2
†*Ctenoplectus williamsi*	0	2	2	2	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	6	?	?	?	?	?	?	?	?	?	?	?

Tab. S1 - Data matrix used in the phylogenetic analysis.