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A new genus and two new species of Monodactylidae (Perciformes s.l.) from the Eocene of northern Italy (Bolca: Monte Postale and Pesciara)

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ABSTRACT

A new genus of monodactylid percoid fish, †*Zaiaichthys* gen. nov., with two new species, †*Z. postalensis* gen. et sp. nov. and †*Z. watersi* gen. et sp. nov., is described based on three skeletons from the Eocene locality of Bolca in northern Italy. This is the second genus of fingerfishes found among the Bolca fish fauna. The group was previously known only by †*Psettopsis* Blot, 1969. Among other characters, †*Zaiaichthys* gen. nov. differs from †*Psettopsis* in having a larger head, serrated preopercle and rounded rather than truncate caudal fin. †*Zaiaichthys postalensis* gen. et sp. nov. is described based on a single skeleton discovered recently at the Monte Postale site, whereas the two available specimens of †*Z. watersi* gen. et sp. nov. are from the Pesciara cave site and were earlier misidentified as belonging to †*Psettopsis subarcuatus* (Blainville). †*Zaiaichthys postalensis* gen. et sp. nov. is twice larger than †*Z. watersi* gen. et sp. nov. and differs from the latter by its strongly ctenoid (vs. cycloid) scales and greater number of soft rays in the dorsal and anal fins (respectively 32 vs. 30 and 26 vs. 24 in †*Z. watersi*).

Key words: Perciformes s.l., Monodactylidae, new genus and species, Eocene, northern Italy, Bolca locality, Pesciara, Monte Postale.

RIASSUNTO

Un nuovo genere di pesci percoidi della famiglia Monodactylidae, †*Zaiaichthys* gen. nov. rappresentato da due nuove specie, †Z. postalensis gen. e sp. nov. e †Z. *watersi* gen. e sp. nov., è descritto sulla base di tre scheletri provenienti dalla località eocenica di Bolca, nel nord Italia. Questo è il secondo genere di pesci luna per la fauna ittica di Bolca. Il gruppo era precedentemente conosciuto solo da †*Psettopsis* Blot, 1969. Tra le altre caratteristiche, †*Zaiaichthys* gen. nov. differisce da †Psettopsis per la testa più grande, un preopercolo seghettato e una pinna caudale arrotondata anziché tronca. †*Zaiaichthys postalensis* gen. e sp. nov. è descritto sulla base di un unico scheletro scoperto di recente presso il sito del Monte Postale, mentre i due esemplari di †*Z. watersi* gen. e sp. nov. rinvenuti al sito della Pesciara sono stati in precedenza erroneamente identificati come appartenenti a †*Psettopsis subarcuatus* (Blainville). †*Zaiaichthys postalensis* gen. e sp. nov. è due volte più grande di †*Z. watersi* gen. e sp. nov. e differisce da quest'ultimo per le sue scaglie fortemente ctenoidi (vs. cicloide) e un maggior numero di raggi molli nella pinna dorsale e anale (rispettivamente 32 vs. 30 e 26 vs. 24 in †Z. watersi).

Parole chiave: Perciformes s.l., Monodactylidae, nuovo genere e specie, Eocene, Italia settentrionale, Bolca, Pesciara, Monte Postale.

INTRODUCTION

The Early Eocene fish fauna of the famous locality Bolca, to the north of Verona in northern Italy, known since the mid-sixteenth century (Sorbini, 1981), is exceptionally rich in marine fishes, especially of the acanthomorphs (Bannikov, 2014; Carnevale *et al.*, 2014; Friedman and Carnevale, 2018, etc.). Fish remains have long been collected from two approximately coeval sites (Pesciara and Monte Postale) of the Bolca locality that are close by each other but which have different fish assemblages and different depositional contexts (Marramà *et al.*, 2016).

One of the Bolca's acanthomorph fishes has been known since the publication of the pioneering monograph on the Bolca fish fauna by Volta (1796: 31, pl. VIII, fig. 1). This relatively large fish was erroneously attributed by Volta to the extant species *Chaetodon arcuatus* L., and subsequently the new species name †*C. subarcuatus* was proposed by de Blainville (1818). That species was transferred from *Chaetodon* to the genus *Pomacanthus* by Agassiz (1833-1844), and this identification was not questioned for the next 125 years (Zigno, 1874; Woodward, 1901; Eastman, 1905; d'Erasmo, 1922), until Blot (1969) showed that the fossil species was not closely related with *Pomacanthus*. Blot erected the new genus †*Psettopsis* for the species *subarcuatus*, and placed this genus to the fingerfish family Monodactylidae. Blot (1969: 293) noted that †*P. subarcuatus* is a very rare species, being represented only by the type specimen from the Muséum National d'Histoire Naturelle (Paris), and perhaps also by two specimens from the museums in Brussels and Budapest. Subsequently, one more well-preserved and especially large specimen was indicated in the collection of Mr. Giuseppe Baja and transferred to the Museo Civico di Storia Naturale di Verona (Sorbini, 1983, pl. I).

Later, a relatively small specimen from the Pesciara di Bolca resembling †*Psettopsis subarcuatus* in general body shape and the structure of the fins was described as a new species, †*P. latellai* (Bannikov, 2005). Recently Bannikov and Zorzin (2019) described the percomorph fish †*Quasinectes durello* from the Monte Postale site as possibly being related with the "stem pleuronectiform" (Friedman, 2008) †*Heteronectes*. This discovery led them to reassess the systematic position of †*Psettopsis latellai*: it was removed from the genus †*Psettopsis* into its own new genus †*Latellopsis* of incertae sedis percomorphs (Bannikov and Zorzin, 2019). At the same time, two specimens of small fishes from the Pesciara cave site were identified as young †*Psettopsis subarcuatus* (Bannikov and Zorzin, 2019: fig. 4). However, a special study of these specimens revealed their difference from †*P. subarcuatus* at the generic level.

During the field excavations executed by the employees of the Museo Civico di Storia Naturale di Verona and the Cerato family (Bolca township) in 2022 at the Monte Postale site of the Bolca locality were discovered, among the other materials, a specimen (in part and counterpart) representing the monodactylid fish somewhat similar to the genus †*Psettopsis*. Being more than twice as large as the above-mentioned small specimens from the Pesciara, and somewhat damaged by fracturing of the matrix layer, the new find clearly represents the same genus, but differs at the species level. The following is a description of a new genus of fingerfishes and two new species.

METHODS

The specimens were examined using a WILD Heerbrugg stereomicroscope with an attached camera lucida drawing arm. Some details of the specimens examined were best seen when the specimens were moistened with alcohol. The specimens were prepared by needles. Measurements were taken with a dial caliper, to the nearest 0.1 mm.

Interneural and interhaemal spaces are numbered based on the vertebra whose neural or haemal spine forms the anterior border of the space, with the first space being between the first and second neural or haemal spines (following Baldwin and Johnson, 1993; Bannikov and Tyler, 1995; Tyler and Bannikov, 1997; etc.).

Abbreviations are as follows:

- *Institutional*:
  MCSNV – Museo Civico di Storia Naturale di Verona;
  MFB – Museo dei Fossili di Bolca;
- *Anatomical*:
  PU – preural vertebra;
  SL – standard length;
  U – ural vertebra.

The dagger symbol (†) indicates extinct taxa.

SYSTEMATIC DESCRIPTION

Order Perciformes *sensu* Nelson, 2006
Suborder Percoidei *sensu* Nelson, 2006
Family Monodactylidae Jordan, 1923
Genus †*Zaiaichthys* gen. nov.

Diagnosis

Body deep, oval and compressed, with short caudal peduncle. Head obtusely conical, relatively large, 38–39% SL. Mouth moderate, lower jaw articulation under anterior border of orbit or slightly behind it. Ascending process of premaxilla very long and slender. Retroarticular process of mandible massive.

Opercle without spines, preopercle serrated posteriorly. Coracoid extends to lower end of cleithrum. Vertebrae 24 (10+14). Neural spines of posterior abdominal vertebrae at least slightly anteriorly curved. Caudal skeleton not consolidated. Ribs short. Supraneurals 3. Single dorsal fin with short spiny portion and extended soft portion, not forming prominent lobe. Dorsal fin with 6 graduated spines and 30–32 soft rays. Fourth to eighth interneural spaces accommodate one pterygiophore each. Anal fin long-based, with 3 spines and 24–26 soft rays, not forming prominent lobe. Single anal pterygiophore precedes first haemal spine, and six or seven pterygiophores located in front of haemal spine of third caudal vertebra. Pectoral fin small and placed relatively low. Pelvic fin short but not reduced, situated under pectoral. Caudal fin slightly rounded, with 17 principal rays. Scales small, ctenoid or cycloid.

Type Species
†*Zaiaichthys postalensis* sp. nov., by designation herein.

Etymology
The genus is named in honor of Mr. Luca Zaia, President of the region Veneto (Italy), who sponsored the inclusion of the Eocene paleontological localities of the Alpone Valley and upper Chiampo Valley into the Italian UNESCO Tentative List, and from the Greek word *ichthys* for fish; gender masculine.

Composition
Type species and †*Z. watersi* sp. nov. from Pesciara di Bolca.

†*Zaiaichthys postalensis* sp. nov.
Figures 1–3

Diagnosis
Body oval, its depth is 0.65 of its length. When mouth closed, head exceptionally obtuse anteriorly. Ascending premaxillary process almost as long as alveolar branch. Lower jaw articulation under anterior border of orbit. Preopercle serrated posteriorly, with stronger serrations at angle. Neural spines of posterior abdominal vertebrae anteriorly moderately curved. Dorsal fin with 6 spines and 32 soft rays. Anal fin with 3 spines and 26 soft rays. Seven anal pterygiophores precede haemal spine of third caudal vertebra. Scales small, ctenoid. Traces of original pigmentation pattern preserved poorly.

Etymology
The species is named after the Monte Postale site of the Bolca locality, where the holotype was found in 2022.

Holotype
MCSNV 22.285/22.286, part and incomplete counterpart, complete skeleton somewhat damaged by oblique fracturing of the matrix layer, ca. 56 mm SL (Fig. 1).

Referred Specimens
None.

Type Locality and Horizon
Bolca locality, Monte Postale site; late Early Eocene, late Ypresian, about 50 ma (see Papazzoni *et al.*, 2014).

Description
The holotype is relatively poorly preserved, being somewhat damaged by oblique fracturing of the matrix layer in postero-ventral portion of the body (Fig. 1), with many details of the caudal skeleton being obscured. The body is deep and oval, evidently compressed laterally, with a very short caudal peduncle. The head is relatively large, its length (tip of snout to anterior edge of upper part of pectoral girdle) is 1.7 times smaller than the maximum body depth. The head length is about 38% SL. When the mouth is closed, the head outline is exceptionally obtuse anteriorly. The dorsal and ventral profiles of the body are almost equally convex.

Head. The head is relatively deep, with its depth much greater than its length. The orbit is as equally long as high, moderately large (0.33 of HL) and placed above the middle of the head depth. Ossifications of the sclerotic are relatively small. The neurocranium is deep. The supraoccipital crest is high and rounded posterodorsally; it overhangs above the orbit and seems to continue into the frontal crest. The supraoccipital crest is sculptured by subvertical grooves (Fig. 2). The parietal crest is well recognizable. The frontals overhang above the ethmoids; the ethmoid region is very short. The parasphenoid is slender and straight; it is exposed along the lowermost portion of the orbit. The limits of the infraorbital bones are poorly recognizable. The mouth is terminal; the lower jaw articulation is situated under the anterior border of the orbit. The ascending process of the premaxilla is very long and slender; it seems to be as long as the alveolar ramus of the

Fig. 1 – †*Zaiaichthys postalensis* gen. et sp. nov., holotype MCSNV 22.285, general view; Lower Eocene of Bolca in northern Italy, Monte Postale. Scale bar: 1 cm.

bone, with which it forms an obtuse angle. Most of the maxilla is not recognizable; only its posterior spatulate portion is evident. The supramaxilla seems to be absent. The mandible is deep and triangular in shape; its length is about 50.5% of the head length. The retroarticular process of the mandible is deep and stout. The limits of the mandibular bones are poorly recognizable; there seems to be no space between the upper portions of the dentary and anguloarticular. The symphyseal portion of the dentary is low and slightly bent; just behind the symphysis the outer surface of the bone is penetrated by the pore. The oral teeth are very small and conical; the lower jaw teeth seem to be smaller than those of the upper jaw. The hyomandibular shaft is moderately inclined. The limits of the pterygoid bones are scarcely distinguishable. The quadrate is relatively narrow and triangular, thickened along its posterior border and with a strong articular condyle. The symplectic is weak, narrow and wedge-shaped. The preopercle is moderately curved and relatively narrow; it is extensively serrated along its posterior border and posteriorly on its lower border. A few larger serrations are present at the angle of the preopercle. The opercle is flat and broad, thickened along the anterior border, and without evident spines. The hyoid bar bones are incompletely preserved; and the total complement of branchiostegal rays is unknown. About six recognizable branchiostegal rays are sabre-like; originally it probably had one more ray. Faint imprint of the urohyal indicates that it was relatively deep. The holotypic counterpart MCSNV 22.286 exhibits densely spaced mineralized gill filaments; pharyngeal dentition is not evident.

Axial skeleton. There are 24 vertebrae, 10 abdominal and 14 caudal. The axis of the vertebral column is gently sygmoid and somewhat elevated anteriorly. The vertebral centra are square or shortened anteroposteriorly. There are indications that at least some centra bear a longitudinal ridge on the lateral surface. The length of the caudal portion of the vertebral column is about 1.6 times greater than the length of the abdominal portion of the vertebral column. The neural and haemal spines of the caudal vertebrae are

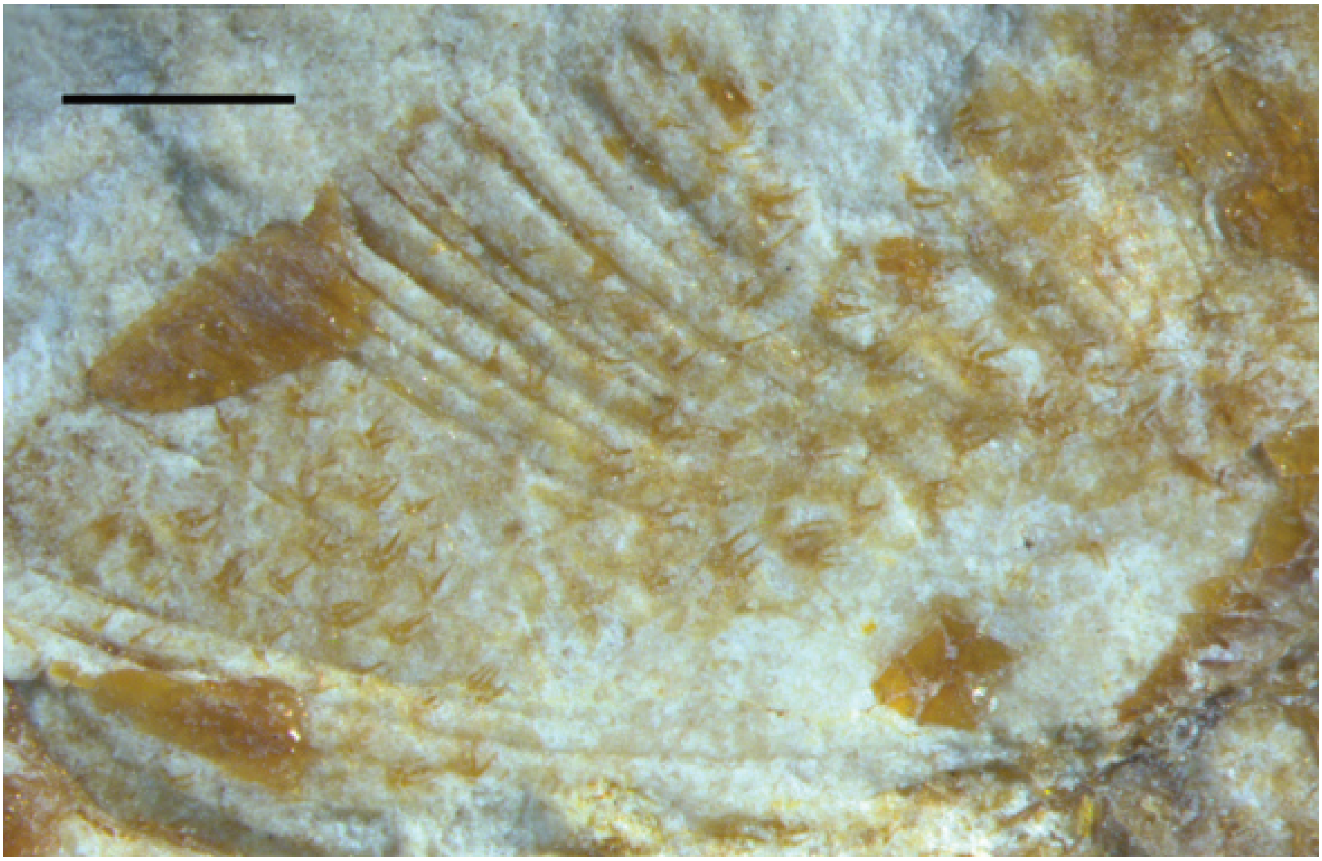

Fig. 2 – †*Zaiaichthys postalensis* gen. et sp. nov., holotype MCSNV 22.285, detail of the skull showing sculpture of the supraoccipital crest and ctenoid scales; Lower Eocene of Bolca in northern Italy, Monte Postale. Scale bar: 1 mm.

straight or slightly curved posteriorly, whereas the neural spines of the four posterior abdominal vertebrae are moderately curved anteriorly. The neural spines of the fifth to eighth vertebrae are distinctively more slender than those of the preceding and succeeding vertebrae. None of the interneural spaces below the dorsal fin is vacant. The haemal spines of the anterior caudal vertebrae are longer than the corresponding neural spines, and they are more strongly inclined to the body axis (the neural spines of the first two caudal vertebrae are relatively vertically oriented). The haemal spines of the four anterior caudal vertebrae are especially stout, and the two posterior of them are anteriorly expanded in their upper third. The approximately five posteriormost abdominal vertebrae bear pointed parapophyses. The pleural ribs are short and very slender; these are strongly inclined posteriorly, thus occupying only the upper half of the abdominal cavity. No epineurals are evident.

Pectoral fin and girdle. The posttemporal is moderately large and forked; the supracleithrum seems to be elongate and relatively small. The cleithrum is a large, robust and elongate bone situated just below the second vertebra; the upper part of its length is curved moderately forward. The posterodorsal flange of the cleithrum is narrow. The ventral postcleithrum is narrow and long, oriented posteroventrally and ends between the posterior process of the basipterygium and the anterior projection of the distal end of the first anal-fin pterygiophore. The dorsal postcleithrum is a relatively large flat bone thickened along its anterior margin and situated above and posterior to the pectoral-fin base. The coracoid is moderately narrow; it extends to the lower end of the cleithrum. The small scapula and pectoral radials are partly recognizable only on the holotypic counterpart; the latter are of increasing size ventrally. The pectoral fin is inserted low on the flank, below the midpoint between the vertebral column and the ventral profile of the

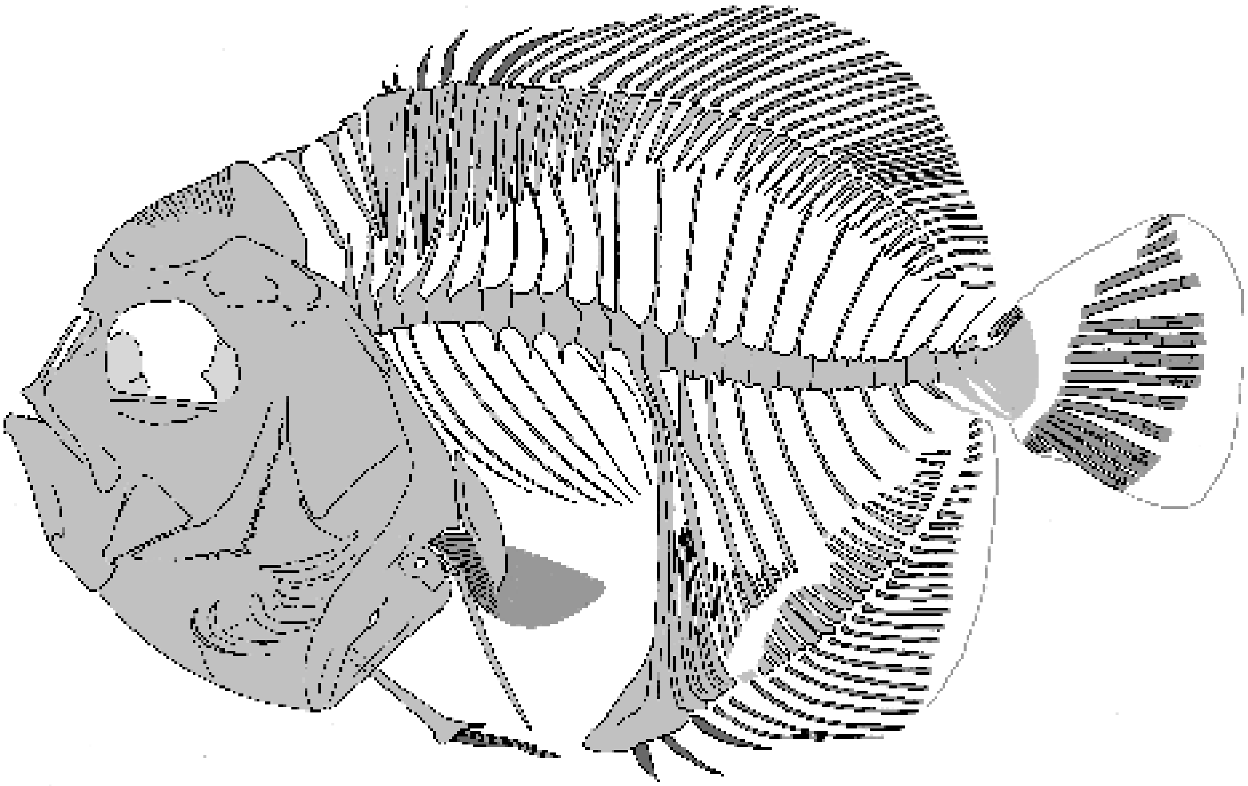

Fig. 3 – †*Zaiaichthys postalensis* gen. et sp. nov., reconstruction of the skeleton based on the holotype.

body. The pectoral fin is relatively poorly preserved; about 18 rather short pectoral-fin rays can be determined.

Pelvic fin and girdle. The pelvic bones are long and narrow; these are oriented posteroventrally from their attachment to the cleithra under the sharp angle to the body axis. The pelvic fin is small; it has a short spine and a few soft rays (their precise number cannot be determined). The pelvic fin is inserted under the pectoral-fin base; it does not reach the anterior projection of the distal end of the first anal-fin pterygiophore.

Supraneurals and dorsal fin. There are three strong supraneurals (predorsal bones) of increasing length posteriorly; each has tapered projections directed anteriorly and posteriorly from the upper end of the bone. The anterior projection of the first supraneural is especially long and slender. The first supraneural precedes the neural spine of the first vertebra, whereas the second and third supraneurals are situated in the second interneural space together with the first dorsal-fin pterygiophore. Thus, the predorsal formula (Ahlstrom et al., 1976; Johnson, 1984) is 0//0+0+2/1+1/1/.

The single dorsal fin has a very long base. The origin of the dorsal fin is at a level above the centrum of the third vertebra. There are six short but robust dorsal-fin spines of increasing length posteriorly; the first spine is greatly reduced in size, being minute but evidently protruding to the exterior beyond the skin. The first two spines are supernumerary on the first dorsal-fin pterygiophore. The dorsal-fin spines are confluent with the segmented rays. The soft portion of the dorsal fin forms a rounded profile, without a lobe anteriorly. The rays are segmented but apparently unbranched. There are 32 soft dorsal-fin rays. The length of the soft portion of the dorsal fin is approximately 4.5 times longer than the length of the spiny portion. The first dorsal-fin pterygiophore penetrates down into the second interneural space; it is expanded medially and bears a longitudinal strengthening ridge. The succeeding pterygiophores become gradually shorter and narrower. Each interneural space above the abdominal vertebrae accommodates the proximal ends of one dorsal-fin pterygiophore, except for the third and ninth spaces accommodating two pterygiophores. Each of the succeeding interneural spaces has two or three pterygiophores present. The longitudinal strengthening ridges of the anteriormost dorsal-fin pterygiophores are only slightly inclined, whereas succeeding pterygiophore shafts become increasingly inclined posteriorly. The medial pterygiophores seem to be fused with the proximal pterygiophores. The dorsal fin ends above the penultimate vertebra.

Anal fin. The anal fin originates approximately under the first caudal vertebra. Two oblique fractures damage the anal fin and its support, but with relatively little bony structure lost in the fractures. There are three robust spines and 26 soft rays in the anal fin. The first two spines are supernumerary on the first anal-fin pterygiophore. The first spine is shortest, twice shorter than the third spine, which is the longest. The length of the longest anal-fin spine equals to the length of the penultimate dorsal-fin spine. The shape of the soft part of the anal fin seems to be similar to that of the soft part of the dorsal fin. The first anal-fin pterygiophore is almost straight, very long and stout; its proximal portion is attached along the anterior edge of the distal portion of the first haemal spine. The ventral end of this pterygiophore is strongly expanded anteriorly. The second and succeeding anal-fin pterygiophores decrease in length posteriorly in the series. The dorsal ends of the three anal pterygiophores enter into the first and second interhaemal spaces above the anal fin; thus, the seven anal pterygiophores precede the haemal spine of the third caudal vertebra. The longitudinal strengthening ridge of the second and third anal-fin pterygiophores are relatively vertically oriented, whereas all the succeeding pterygiophore shafts become increasingly inclined posteriorly.

Caudal fin and skeleton. Two oblique fractures strongly damage the caudal skeleton and basal portion of the caudal fin. The condition of the haemal spines of PU2 and PU3, uroneurals, hypurals and parhypural cannot be determined. There are definitely three epurals. The caudal fin is also preserved incompletely, but it is most probably rounded and has 17 principal rays. The exact number of procurrent rays is unknown.

Squamation. Very small ctenoid scales cover the body, head and median fins. The scales are thin and bear tiny circuli; radii are hardly recognizable. Ctenii are not numerous (usually three to five per scale), and are especially robust on the head (Fig. 2); some of the scales on the head appear to be spinoid (Roberts, 1993). The lateral line is very gently arched low on the flank, just above the vertebral column.

Coloration. Weak traces of the original pigmentation pattern are preserved in some portions of the body, mostly in the abdomen: these represent minute dark spots arranged sparsely.

Measurements of the holotype, in percent of SL (ca. 56 mm), are only approximate because of fracturing of the matrix layer in postero-ventral portion of the body:

- Head length from tip of snout to posterior border of opercle: ca. 38
- Maximum body depth: ca. 65
- Distance between tip of snout and first dorsal-fin spine: ca. 46
- Distance between tip of snout and first dorsal-fin soft ray: ca. 56
- Distance between tip of snout and anal fin: ca. 68
- Distance between pelvic fin and anal fin: ca. 17
- Length of base of dorsal fin: ca. 59
- Length of longest (last) spine of dorsal fin: ca. 10
- Length of longest (last) spine of anal fin: ca. 8
- Length of pectoral fin: ca. 17
- Length of spine of pelvic fin: ca. 6.5
- Preorbital distance: ca. 8
- Horizontal diameter of orbit: ca. 12
- Length of lower jaw: ca. 19

†*Zaiaichthys watersi* sp. nov.

Figures 4–6

†*Psettopsis subarcuatus*: Bannikov and Zorzin, 2019, fig. 4 (misidentification).

Diagnosis

Body oval, its depth is 0.62–0.63 of its length. Head not exceptionally obtuse anteriorly. Ascending premaxillary process clearly shorter than alveolar branch. Lower jaw articulation under anterior border of orbit or slightly behind it. Preopercle serrated posteriorly, with a spinule at angle. Neural spines of posterior abdominal vertebrae anteriorly slightly curved. Dorsal fin with 6 spines and 30 soft rays. Anal fin with 3 spines and 24 soft rays. Six anal pterygiophores precede haemal spine of third caudal vertebra. Scales small, cycloid. Traces of original pigmentation pattern preserved throughout whole body.

Etymology
It is our pleasure to name this species after the famous British musician Roger Waters, co-founder of the progressive rock band "Pink Floyd".

Holotype
MFB IG129669/IG129670, part and counterpart, complete skeleton, 25.5 mm SL (Fig. 4).

Paratype
MCSNV IG126426, single plate, complete skeleton poorly preserved postero-ventrally (Bannikov and Zorzin, 2019: fig. 4B).

Referred specimens
None.

Type Locality and Horizon
Bolca locality, Pesciara cave site; Early Eocene, late Ypresian, middle Cuisian, SBZ 11, *Alveolina dainelli* Zone (see Papazzoni and Trevisani, 2006; Papazzoni *et al.*, 2014).

Description
The holotype is relatively well-preserved, but fracture of the matrix layer makes it difficult to recognize the first spine of the anal fin and part of the pelvic fin (Fig. 4), whereas in the paratype more than half of the postero-ventral portion of the body is very poorly preserved. The body is deep and oval, evidently compressed laterally, with a very short caudal peduncle; its depth is 0.62–0.63 of SL. The head is large; its length (tip of snout to anterior edge of upper part of pectoral girdle) is 1.6 times smaller than the maximum body depth. The head length is 37–39% SL. Both of the specimens available have the mouth open, but it is clear that even with the mouth closed the head is not exceptionally obtuse anteriorly. The dorsal and ventral profiles of the body are almost equally convex.

Head. The head is relatively deep, with its depth greater than its length. The orbit is slightly longer than high, moderately large (0.3 to 0.35 of HL) and placed above the middle of the head depth. Ossifications of the sclerotic are relatively small. Traces of the eyeball are preserved as a thin carbonaceous film. The neurocranium is deep. The supraoccipital crest is high and rounded posterodorsally; it overhangs above the orbit and seems to continue into the frontal crest. The supraoccipital crest lacks subvertical grooves but, rather, is waved in parallel to its upper margin (Fig. 5A). The parietal crest is well recognizable. The frontals overhang above the ethmoids; the ethmoid region is short. The parasphenoid is slender, straight or very slightly curved; it is exposed along the lowermost portion of the orbit. The limits of the infraorbital bones are poorly recognizable. The mouth is terminal; the lower jaw articulation is situated under the anterior border of the orbit or slightly behind it. The ascending process of the premaxilla is very long and slender, but clearly is shorter than the alveolar ramus of the bone. The maxilla is curved anteriorly and spatulate posteriorly. The supramaxilla seems to be absent. The mandible is deep and triangular in shape; its length is about 48–49% of the head length. The retroarticular process of the mandible is deep and stout. The limits of the mandibular bones are poorly recognizable; there seems to be no space between the upper portions of the dentary and angulo-articular. The symphyseal portion of the dentary is relatively low and almost not bent. The oral teeth are very small and conical. The hyomandibular shaft is relatively slightly inclined. The quadrate is relatively narrow and triangular, thickened along its posterior border and with moderate articular condyle. The symplectic is narrow and wedge-shaped. The metapterygoid is poorly recognizable, whereas the entopterygoid is moderately wide and lamellar; it shows characteristic waving: an alternation of weak and narrow ridges and grooves in an antero-posterior direction (Fig. 5B). The ectopterygoid is a narrow bone consisting of the tapered ventral arm and longer anterior shank. The palatine is poorly recognizable. The preopercle is moderately curved and relatively narrow; it is extensively serrated along its posterior and lower border, with the largest spinule present at the angle of the preopercle. The opercle is flat and broad, thickened along the anterior border, without evident spines but with a ridge extended posteriorly from the articular facet. The limits of the subopercle and interopercle are poorly recognizable. The hyoid bar bones are partly preserved on the paratype; both the ceratohyal and epihyal are broad and robust. The ceratohyal is broadest at the posterior and anterior ends, and has a concave ventral margin; it seems to have a "beryciform foramen" (McAllister, 1968). The middle and upper parts of the ceratohyal posteriorly interlocks with the triangular epihyal by means of odontoid processes issuing from both elements. The total complement of branchiostegal rays is not recognizable; the first branchiostegal is narrow, whereas the others are broader and sabre-like in shape. At least one branchiostegal is attached to the epihyal. The holotypic counterpart MCSNV IG129670 exhibits

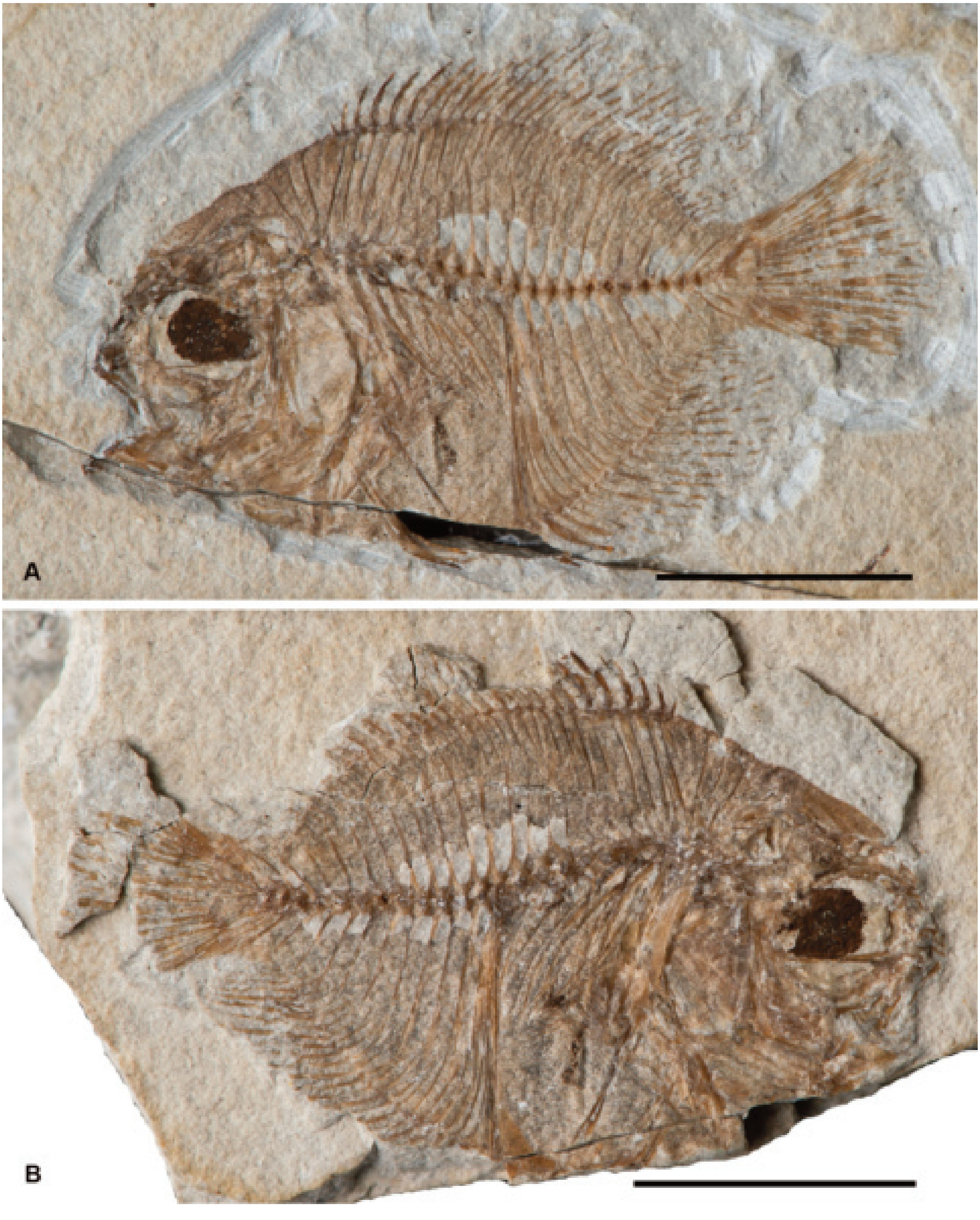

Fig. 4 – †*Zaiaichthys watersi* gen. et sp. nov., holotype; Lower Eocene of Bolca in northern Italy, Pesciara: A – general view of MCSNV IG129669, B – counterpart MCSNV IG129670. Scale bar: 1 cm.

densely spaced mineralized gill filaments, whereas the paratype exhibits several gill rakers; pharyngeal dentition is not evident.

Axial skeleton. There are 24 vertebrae, 10 abdominal and 14 caudal. The axis of the vertebral column is gently sygmoid and elevated anteriorly. The vertebral centra are square or shortened anteroposteriorly. There are indications that at least some centra bear a longitudinal ridge on the lateral surface. The length of the caudal portion of the vertebral column is about 1.55 times greater than the length of the abdominal portion of the vertebral column. The neural and haemal spines of the caudal vertebrae are straight or slightly curved posteriorly, whereas the neural spines of the four posterior abdominal vertebrae are slightly curved anteriorly. The neural spines of the fifth to seventh vertebrae are distinctively more slender than those of the succeeding vertebrae, which are somewhat broadened distally. None of the interneural spaces below the dorsal fin is vacant. The haemal spines of the anterior caudal vertebrae are longer than the corresponding neural spines. The neural spines of the last abdominal and first caudal vertebrae are relatively vertically oriented; the succeeding spines become inclined posteriorly. The haemal spines of the three anterior caudal vertebrae are stouter than the succeeding ones, and the third spine is somewhat anteriorly expanded in its upper third. At least four posteriormost abdominal vertebrae bear parapophyses. The pleural ribs are short and slender; these are rather strongly inclined posteriorly, occupying the upper half of the abdominal cavity. A few epineurals are distinguishable anteriorly in the abdominal cavity just under the vertebral column.

Pectoral fin and girdle. The posttemporal is moderately large and forked; the supracleithrum seems to be elongate and relatively long. The cleithrum is a large, robust and elongate bone situated just below the second or third vertebrae; it is gently sigmoidally curved. The posterodorsal flange of the cleithrum is narrow. The ventral postcleithrum is narrow and long, oriented posteroventrally about in parallel to the basipterygium and almost touches the anterior projection of the distal end of the first anal-fin pterygiophore. The coracoid is moderately narrow; it extends to the lower end of the cleithrum. The dorsal postcleithrum, scapula and pectoral radials are not well recognizable. The pectoral fin is moderately long; it is inserted opposite to the fifth vertebra low on the flank, just below the midpoint between the vertebral column and the ventral profile of the body. The pectoral fin is relatively poorly preserved and the precise number of its rays is unknown; not less than 16 pectoral-fin rays can be determined.

Pelvic fin and girdle. The pelvic bones are long and narrow; these are oriented posteroventrally from their attachment to the cleithra under the angle of about 70° to the body axis. The pelvic fin is small; it has a short spine and a few soft rays (their precise number cannot be determined). The pelvic fin is inserted under the pectoral-fin base; it reaches the anterior projection of the distal end of the first anal-fin pterygiophore.

Supraneurals and dorsal fin. There are three strong supraneurals (predorsal bones); each has tapered projections directed anteriorly and posteriorly from the distal end of the bone. The anterior projection of the first supraneural is especially long. The predorsal formula is 0/0/0+2/1+1/1/.

The single dorsal fin has a very long base. The origin of the dorsal fin is at a level above the centrum of the third or fourth vertebra. There are six short but robust dorsal fin spines of increasing length posteriorly; the first spine is not extremely short. The first two spines are supernumerary on the first dorsal-fin pterygiophore. The dorsal-fin spines are confluent with the segmented rays. The soft portion of the dorsal fin forms a rounded profile, without a lobe anteriorly. The rays are segmented but apparently unbranched. There are 30 soft dorsal-fin rays; the last ray is split to base. The length of the soft portion of the dorsal-fin is approximately 3.9 times longer than the length of the spiny portion. The first dorsal-fin pterygiophore penetrates down into the second interneural space; it is expanded medially and bears a longitudinal strengthening ridge. The succeeding pterygiophores become gradually shorter and narrower. Each interneural space above the abdominal vertebrae accommodates the proximal ends of one dorsal-fin pterygiophore, except for the third and ninth spaces accommodating two pterygiophores. Each of the succeeding interneural spaces has two or three pterygiophores present. The longitudinal strengthening ridges of the anteriormost dorsal-fin pterygiophores are relatively slightly inclined, whereas the succeeding pterygiophore shafts become increasingly inclined posteriorly. The medial pterygiophores seem to be fused with the proximal pterygiophores. The dorsal fin ends above the penultimate vertebra.

Anal fin. The anal fin originates approximately under the first caudal vertebra. There are three robust spines and 24 soft rays in the anal fin. The first two spines are supernumerary on the first anal-fin ptery-

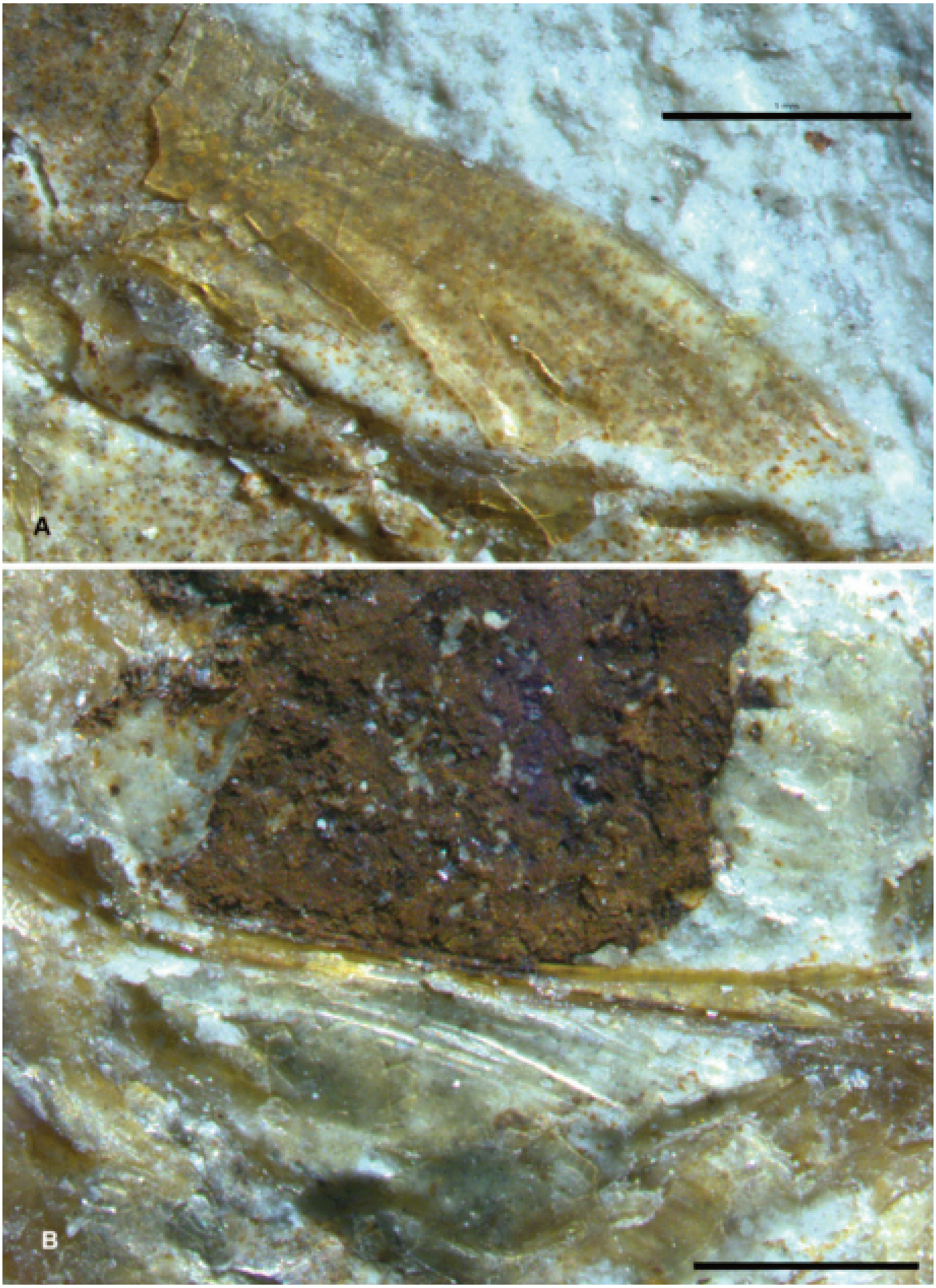

Fig. 5 – †*Zaiaichthys watersi* gen. et sp. nov., holotype MCSNV IG129670: A – detail of the skull showing sculpture of the supraoccipital crest and traces of the original pigmentation pattern; B – detail of the skull showing traces of the eyeball in the orbit and sculpture of the entopterygoid; Lower Eocene of Bolca in northern Italy, Pesciara. Scale bar: 1 mm.

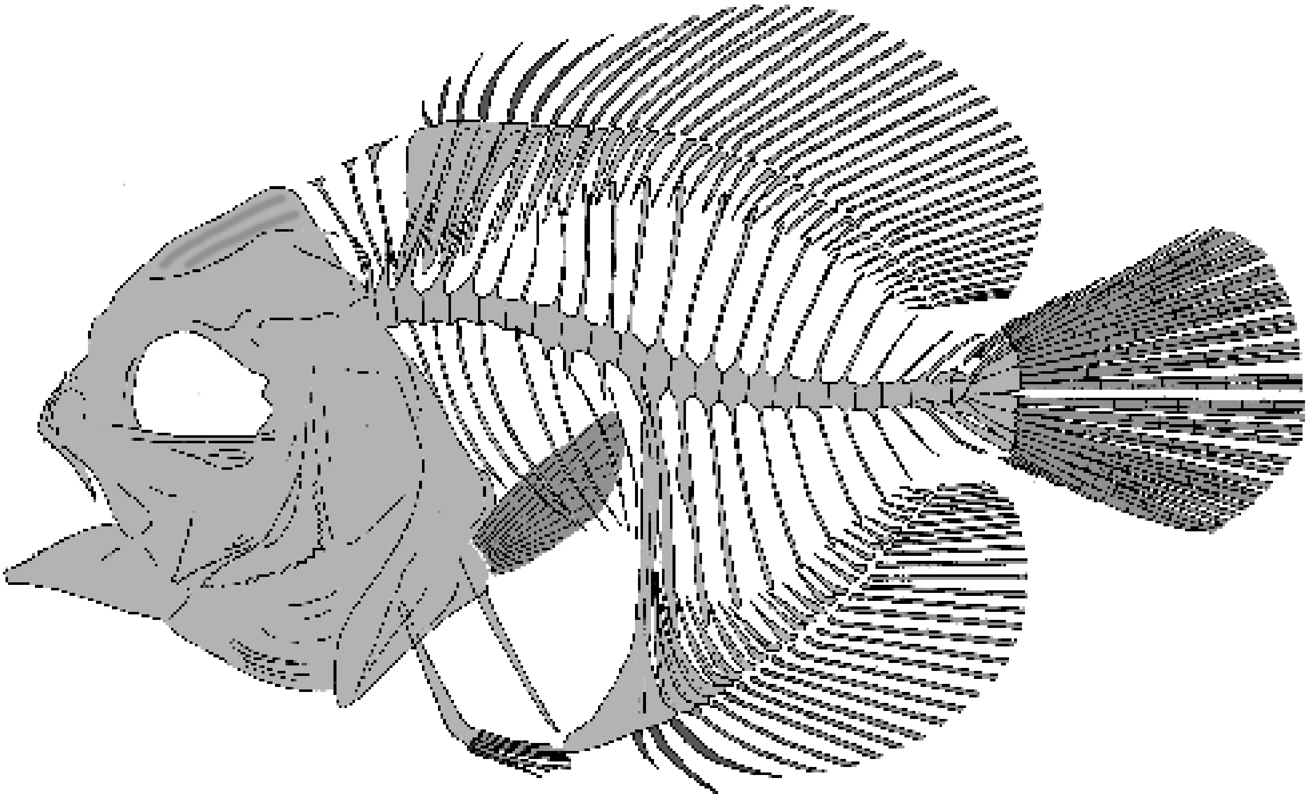

Fig. 6 – †*Zaiaichthys watersi* gen. et sp. nov., reconstruction of the skeleton based on the holotype.

giophore. The first spine is shortest, approximately twice shorter than the third spine, which is the longest. The length of the longest anal-fin spine almost equals to the length of the longest dorsal-fin spine. The shape of the soft part of the anal fin is similar to that of the soft part of the dorsal fin. The first anal-fin pterygiophore is almost straight, very long and stout; its proximal portion is attached along the anterior edge of the distal portion of the first haemal spine. The ventral end of this pterygiophore is strongly expanded anteriorly. The second and succeeding anal-fin pterygiophores decrease in length posteriorly in the series. The dorsal ends of the three anal pterygiophores enter into the first interhaemal space; a total of six anal pterygiophores precede the haemal spine of the third caudal vertebra. The longitudinal strengthening ridge of the second anal-fin pterygiophore is relatively vertically oriented, whereas all the succeeding pterygiophore shafts become increasingly inclined posteriorly.

Caudal fin and skeleton. The caudal skeleton is of the generalized percoid type, showing the fusion of PU1, U1, and U2 in the terminal centrum. The neural spine of PU2 forms a low crest. All five hypurals, the parhypural, and probably the haemal spines of PU2 and PU3 are autogenous. There are three epurals (the last is weak) and a stegural formed by the first pair of uroneurals. The presence of a second pair of uroneurals is also evident. The neural and haemal spines of PU3 are somewhat stronger than those of the preceding vertebra. The caudal fin has 17 principal rays, with 15 branched (I,8-7,I). Branched rays are only once divided. There are about six procurrent rays above and about five rays below, with no procurrent spur (Johnson, 1975). The caudal fin is relatively long and rounded.

Squamation. Very small cycloid scales cover the body, head and median fins. The scales are thin; the limits of individual scales are scarcely recognizable. The lateral line is poorly traceable.

Coloration. Traces of the original pigmentation pattern are preserved throughout the whole body and the dorsal and anal fins: these represent numerous minute dark spots arranged densely.

Measurements of the holotype, in percent of SL (25.5 mm), are as follows:

- Head length from tip of snout to posterior border of opercle: 39
- Maximum body depth: 64
- Depth of caudal peduncle: 15
- Distance between tip of snout and first dorsal-fin spine: 50
- Distance between tip of snout and first dorsal-fin soft ray: 60
- Distance between tip of snout and anal fin: ca. 67
- Distance between pelvic fin and anal fin: ca. 16
- Length of base of dorsal fin: 55
- Length of base of anal fin: ca. 39
- Length of first spine of dorsal fin: 3
- Length of longest (last) spine of dorsal fin: ca. 12
- Length of longest (last) spine of anal fin: ca. 13
- Length of spine of pelvic fin: 8
- Length of longest soft ray of pelvic fin: ca. 14
- Length of longest ray of dorsal fin: ca. 29
- Preorbital distance: 10
- Horizontal diameter of orbit: 13.5
- Length of lower jaw: 18

DISCUSSION

The perciform fishes (*sensu* Nelson, 2006) are the most diverse among the Monte Bolca fishes, and percoids predominate among these perciforms. The order Perciformes has traditionally been considered (Berg, 1940; Greenwood *et al.*, 1966; Nelson, 2006; etc.) the most diverse order of evolutionarily advanced bony fish, the largest of the orders not only of fishes, but of vertebrates in general. Recently, however, the traditional classification of organisms is often replaced by a formal cladistic systematics, built on computer processing of molecular data and often contradicting morphological evidence. In cladistic taxonomy, the order Perciformes is divided into numerous orders, bizarrely grouped into taxa of higher rank (Wiley and Johnson, 2010; Near *et al.*, 2012, 2013; Betancur-R. *et al.*, 2013, 2017; Nelson *et al.*, 2016; etc.). The higher taxa of the cladistic hierarchy are morphologically heterogeneous, which is recognized by the cladists themselves (Miya *et al.*, 2013); usually these taxa cannot be diagnosed by morphological features.

The fingerfish family Monodactylidae has traditionally been placed in the perciform suborder Percoidei, this “largest and most diverse of the perciform suborders is undoubtedly polyphyletic...” (Johnson, 1993, p. 15) and is diagnosed by several plesiomorphic features for the Perciformes; this group includes those of perciforms that cannot be placed in other suborders. Within the Percoidei sometimes Monodactylidae was regarded as part of the so-called “squamipinnes group” (e.g., Nelson, 2006). In molecular taxonomy, Monodactylidae does not have a fixed position: it is placed either in the same clade with Priacanthidae and Acanthuriformes in the clade Percomorpharia (Betancur-R. *et al.*, 2013) or in the same clade with Leiognathidae and Chaetodontidae (Near *et al.*, 2013), or it forms the sister-group of Lobotidae (Ghezelyagh *et al.*, 2022), or it is left *incertae sedis* in the series Eupercaria (Betancur-R. *et al.*, 2017). For this reason, we prefer to adhere to the traditional, natural taxonomy, where the order Perciformes and the suborder Percoidei are considered in a broad sense (e.g., Nelson, 2006), as did, e.g., Heemstra *et al.* (2022).

Most of the features of †*Zaiaichthys* gen. nov. (deep compressed body; 10+14 vertebrae; single extended dorsal and anal fins with numerous rays; small scales covering body, head and median fins; supraoccipital continued forward over the frontals; etc.) indicate that it could be accommodated to the family Monodactylidae, although it has one less dorsal-fin spine (6 vs. 7 to 8) than recorded for the extant fingerfishes, less numerous soft anal-fin rays (see Johnson, 1984: Table 120) and two rather than one spine supernumerary on the first dorsal-fin pterygiophore. Within this family the new genus is most closely related to the Eocene genus †*Psettopsis* Blot from Bolca: both have six dorsal-fin spines, the caudal skeleton unconsolidated, the dorsal and anal fins not forming distinct lobes, and the caudal fin not forked. However, †*Zaiaichthys* gen. nov. differs from †*Psettopsis* in having a larger head, serrated preopercle, and a rounded rather than truncate caudal fin. The coracoid of †*Zaiaichthys* gen. nov. extends to the lower end of the cleithrum [Gosline (1985) regarded this character of monodactylids as being valuable phylogenetically] in contrary to †*Psettopsis*, in which the coracoid is shorter (Blot, 1969). Also, the fourth to eighth interneural spaces of the new genus accommodate one dorsal pterygiophore each, whereas in †*Psettopsis* two pterygiophores enter to the sixth interneural space. Finally, six or seven anal-fin pterygiophores of †*Zaiaichthys* gen. nov. are located in front of the haemal spine of the third caudal vertebra, whereas in †*Psettopsis* at least eight anal-fin pterygiophores precede the haemal spine of the third caudal vertebra.

In addition to the fossils, the family Monodactylidae includes two extant genera, *Monodactylus* and

Schuettea, both with the dorsal and anal fins forming prominent lobes. Unlike in †*Zaiaichthys* gen. nov., in the genus *Monodactylus* Lacepède the pelvic fins are present in juveniles but absent or vestigial in adults (Nelson, 2006; Nelson *et al.*, 2016). *Schuettea* Steindachner differs from the new genus in having 15 caudal vertebrae and three anal-fin pterygiophores inserted in front of the first haemal spine (Tominaga, 1968).

†*Zaiaichthys postalensis* gen. et sp. nov. is twice larger than †*Z. watersi* gen. et sp. nov. and clearly differs from the latter by the characters which are evidently not of an ontogenetic nature: e.g., by strongly ctenoid (vs. cycloid) scales and greater number of soft rays in the dorsal and anal fins (respectively 32 vs. 30 and 26 vs. 24 in †*Z. watersi*). Also, †*Z. postalensis* has a somewhat deeper body, the skull more obtuse anteriorly, longer ascending process of the premaxilla, and less intensive original pigmentation pattern. Finally, †*Z. postalensis* differs from †*Z. watersi* by its predorsal formula (if it is not the result of post-mortem displacement of the second supraneural of the former), somewhat stronger curvature of the neural spines of the posterior abdominal vertebrae, and seven rather than six anal-fin pterygiophores preceding the haemal spine of the third caudal vertebra. Thus, it is evident that the genus †*Zaiaichthys* gen. nov. is represented in Bolca by two different species: †*Z. postalensis* inhabited an emerged coastal area of the Tethys ocean (Marramà *et al.*, 2016) and †*Z. watersi* inhabited an intraplatform basin.

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