Eocene Round Herring from Monte Bolca, Italy

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GIUSEPPE MARRAMÀ and GIORGIO CARNEVALE

Fishes of the subfamily Dussumieriinae, also known as round herrings, are a small subgroup of the family Clupeidae inhabiting tropical and subtropical marine coastal waters. A new genus and species of round herring, *Trollichthys bolcensis* gen. et sp. nov., is described from the lower Eocene micritic limestone of Monte Bolca, northern Italy. This new clupeid taxon is based on seven partially complete articulated skeletons that exhibit a unique combination of features, including: two supramaxillae, edentulous jaw and palate bones, 41–42 preural vertebrae and 22–24 pleural ribs, pleural ribs-preural vertebrae ratio ranging 0.52–0.57, five or six supraneural bones, dorsal-fin origin located at about mid-length of the body, dorsal fin with about 16 rays, two postcleithra, pelvic-fin insertion slightly behind the dorsal-fin origin, and pelvic fin with eight rays. *Trollichthys bolcensis* shares several features with the extant round herring genus *Spratelloides*. However, because of its unique combination of features, *Trollichthys bolcensis* cannot be confidently assigned to any of the extant dussumieriine lineages and present evidence does not favour any particular sister-group relationship.

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Introduction

The ichthyofauna of Monte Bolca represents one of the most important fossil fish assemblages known to date. Because of their excellent preservation, these Eocene fishes have attracted the attention of palaeontologists and zoologists for several centuries. The ichthyofauna consists of more than 250 taxa of sharks, batoids, pycnodontiforms, and teleosts (Blot 1980; Bellwood 1996), representing the earliest record of many reef-fish groups and providing strong evidence of the stability of the tropical and subtropical marine ichthyofaunas throughout the Cenozoic (Bellwood and Wainwright 2002).

Several dozen studies have focused on the taxonomy and systematics of the bony fishes of Monte Bolca in the last 40 years. As a result of these efforts, the diversity of certain groups of teleosts is currently well known, including anguilliforms, atherinomorphs, beryciforms, pleuronectiforms, lophiiforms, tetraodontiforms, acanthuroids, pharyngognaths, scombroids, sparids, as well as of a number of other percomorphs (Blot 1969, 1978; Tyler and Santini 2002; Bannikov and Carnevale 2010; Carnevale and Pietsch 2010, 2012). Clupeid fishes are commonly found in the fish-bearing deposits of Monte Bolca, and certainly represent the most conspicuous group in terms of abundance of specimens. Paradoxically, the morphology and taxonomy of the clupeids from Monte Bolca are nearly unknown and the only available studies date back to the second half of the 19th and beginning of the 20th century (Lioy 1866; Woodward 1901).

The family Clupeidae comprises some of the most abundant fish taxa on Earth, some of which support extremely important commercial fisheries (see Blaxter and Hunter 1982), including several species of herrings, sardines, pilchards, sprats, shads, and round herrings. According to the classification proposed by Grande (1985), the family Clupeidae includes five subfamilies (Alosinae, Clupeinae, Dorosomatinae, Dussumieriinae, Pellonulinae), of which two, Dussumieriinae (round herrings) and Pellonulinae, seem to be monophyletic. Grande (1985) figured part of the pelvic girdle of a single round herring specimen from Monte Bolca housed in the Natural History Museum, London, without describing it in detail. In the course of revision of the abundant clupeoid material from the Eocene of Monte Bolca, additional dussumieriine specimens were identified. The goal of this paper is to describe a new genus and species of round herring from the Eocene of Monte Bolca.

Institutional abbreviations.—MCSNV, Museo Civico di Storia Naturale, Verona, Italy; MSNM, Museo Civico di Storia Naturale, Milano, Italy; NHMUK, Natural History Museum, London, UK.

Other abbreviations.—SL, standard length.

Geological setting

The fossils were collected in the Pesciara quarry site of the Monte Bolca locality, in the eastern part of Monti Lessini, a few kilometres from the village of Bolca, north of Verona, northeastern Italy. The fish-bearing limestone of the Pesciara quarry is the "Calcari nummulitici", an informal unit of Eocene age widely distributed in northeastern Italy (Barbieri and Medizza 1969). The succession of the Pesciara quarry consists of a cyclic alternation of finely laminated micritic limestone, characterized by exquisitely well-preserved fossils (plants, fishes, soft-bodied invertebrates and crustaceans), and biocalcarenite/biocalcirudite rich in molluscs and other benthic fossils. The taphonomic features of the fossils and the sedimentological characteristics of the finely laminated deposits suggest scarcely oxygenated bottom conditions with low hydrodynamic energy. According to the classification proposed by Seilacher et al. (1985), the taphonomic features and ecological spectrum of the fossil assemblage indicate that this is an obrutionary stagnation deposit. Based on their benthic larger foraminiferan content, the fish-bearing limestone of the Pesciara cave site has been referred to the *Alveolina dainelli* Zone (Papazzoni and Trevisani, 2006), or SBZ 11 Biozone (Serra-Kiel et al. 1998), corresponding to the middle Cuisian (late Ypresian; about 50 Myr).

Material and methods

This study is based on seven specimens from the Eocene of Monte Bolca currently housed in the Museo Civico di Storia Naturale, Verona, Italy (MCSNV), Museo Civico di Storia Naturale, Milano, Italy (MSNM), and Natural History Museum, London, UK (NHMUK). The fossils were studied using a stereomicroscope Leica M80 with an attached camera lucida drawing arm. Measurements were taken using a dial caliper, to the nearest 0.1 mm. Counts and measurements were made following Grande (1985) and Whitehead and Teugels (1985). Some of the specimens required matrix removal before examination and were prepared using thin entomological needles. Osteological terminology mainly follows Ridewood (1904) and Grande (1985). Comparative information was derived mainly from the cited literature.

Systematic palaeontology

Subdivision Teleostei sensu Patterson and Rosen, 1977

Superorder Clupeomorpha Greenwood, Rosen, Weitzman, and Myers, 1966

Order Clupeiformes sensu Grande, 1985

Suborder Clupeoidei sensu Grande, 1985

Family Clupeidae Cuvier, 1817

Genus *Trollichthys* nov.

Type species: *Trollichthys bolcensis* sp. nov., by monotypy and designation herein; see below.

Etymology: In honour of the American artist Ray Troll in recognition of his spectacular reconstructions of fossil fishes and other extinct and living animals.

Diagnosis.—Small-sized clupeid (largest specimen measuring 100.1 mm SL) with elongate and compressed body; head length contained approximately four times in SL; snout pointed; mouth terminal with slightly projecting lower jaw; two supramaxillae, anterior small and rod-like, posterior symmetrical and paddle-shaped; teeth absent in jaws and palate; 41–42 preural vertebrae and 22–24 pleural ribs; pleural ribs-preural vertebrae ratio ranging 0.52–0.57; prepelvic and postpelvic scutes absent, except for a single unkeeled W-shaped pelvic scute surrounding the base of the pelvic fins; dorsal scutes absent; five or six supraneurals; caudal fin with eight and nine principal rays in the ventral and dorsal lobes, respectively; dorsal-fin origin at about mid-length of the body; dorsal fin with about 16 rays; two postcleithra; pectoral fin with about 14 rays; pelvic-fin origin below the middle part of the dorsal-fin base; pelvic fin with eight rays.

Remarks.—In the fourth volume of his monumental "Catalogue of Fossil Fishes", Woodward (1901) referred one of the specimens documented herein (NHMUK OR 37227) to *Clupea leptostea* Agassiz, 1835. Grande (1985) provided anatomical evidence of the dussumieriine affinities for this specimen. The species *Clupea leptostea* from the Eocene of Monte Bolca was introduced without a formal description by Agassiz (1835–1844). A few years later, Lioy (1866) made it the type species of the genus *Ptericephalina*. Based on a more careful taxonomic analysis, Eastman (1905) assigned the species *Clupea leptostea* to the otophysan genus *Chanoides*; such opinion was not supported by Patterson (1984), who evidenced its affinities with the genus *Coelogaster*.

Stratigraphic and geographic range.— Ypresian (early Eocene), northeastern Italy.

Trollichthys bolcensis sp. nov.

Figs. 1–5.

1901 *Clupea leptostea* Agassiz, 1835; Woodward 1901: 153 (pro parte).
1985 Dussumieriinae indet.; Grande 1985: 274, text-fig. 17.

Etymology: In reference to the Monte Bolca locality.

Type material: Holotype: MSNM V2890a/b, part and counterpart of a well preserved nearly complete articulated skeleton, 100.1 mm SL (Fig. 1A). Paratypes: NHMUK OR 37227, partially complete articulated skeleton in a single plate, 78.5 mm SL (Fig. 1B); MSNM V235, nearly complete articulated skeleton in a single plate, 84.8 mm SL (Fig. 1C); MCSNV IG.VR.24388, partially complete articulated skeleton in a single plate, 43 mm SL; MCSNV IG.VR.132573/132574, part and counterpart of a partially complete articulated skeleton, 75.3 mm SL (Fig. 2A); MCSNV IG.VR.81999/82000, part and counterpart of a partially complete articulated skeleton, 85.9 mm SL (Fig. 2B, C); MCSNV.IG.VR.82193/82194, part and counterpart of a partially complete articulated skeleton, 24.3 mm SL.

Type locality: Monte Bolca locality, Pesciara quarry site.

Fig. 1. Round herring *Trollichthys bolcensis* gen. et sp. nov., Ypresian (Eocene), Monte Bolca, Italy. **A**. MSNM V2890a (holotype). **B**. NHMUK OR 37227 (paratype). **C**. MSNV V235 (paratype).

Type horizon: Late Ypresian, middle Cuisian, early Eocene, SBZ 11, *Alveolina dainelli* Zone (see Papazzoni and Trevisani 2006).

Diagnosis.—As for the genus.

Description.—Counts and measurements for *Trollichthys bolcensis* are given in Tables 1 and 2. The body is elongate and laterally compressed, its maximum depth contained be-

Table 1. Measurements as percentage of SL of *Trollichthys bolcensis* gen. et sp. nov. from Ypresian (Eocene), Monte Bolca, Italy.

Specimen	Standard length (in mm)	Total length (in mm)	Maximum body depth	Head length	Head depth	Snout length	Orbit diameter	Dorsal fin base length	Anal fin base length	Prepectoral length	Predorsal length	Prepelvic length	Preanal length	Caudal peduncle depth
MSNM V2890	100.1	112.6	?	23.9	14.2	7.2	3.9	?	?	25.2	44.0	53.6	?	7.3
MCSNV IG.VR. 24388	43.0	107.6	?	27.4	19.3	7.6	4.4	12.7	?	25.3	?	62.7	?	8.1
MCSNV IG.VR. 81999/82000	85.9	?	23.8	25.7	17.8	6.6	3.4	10.0	?	28.1	41.2	57.2	74.8	8.0
MCSNV IG.VR. 82193/82194	24.3	117.2	16.8	27.9	13.1	7.4	4.5	9.8	11.9	27.5	40.3	53.4	77.4	8.2
MCSNV IG.VR. 132573/132574	75.3	114.3	21.7	22.8	14.0	5.7	3.5	13.1	8.6	23.9	41.6	50.1	76.0	7.7
MSNM V235	84.8	117.6	24.6	?	16.6	?	4.9	?	9.3	29.3	?	60.9	77.5	8.1
NHMUK OR 37227	78.5	?	24.8	28.6	18.2	?	?	12.7	16.9	26.7	48.0	58.9	78.2	7.5

Table 2. Summary of selected meristic features used to discriminate the round herring genera. Data from Grande (1985), Taverne (2002), Carnevale (2004), DiBattista et al. (2012).

Taxon	Supra-neurals	Branchio-stegal rays	Supra-maxillae	Pleural ribs (pairs)	Preural vertebrae	Pleural ribs-preural vertebrae ratio	Post-cleithra	Pelvic-fin rays	Dorsal-fin pterygiophores	Anal-fin pterygiophores	Epurals
Trollichthys	5–6	?	2	22–24	41–42	0.52–0.57	2	8	14–16	13	?
Dussumieria	21–22	12–17	2	37	55–56	0.67	1	8	19	14	2
Etrumeus	10–12	11–16	1	34–40	49–56	0.70–0.74	2	8–9	19–20	9–11	3
Jenkinsia	6–8	6–7	1	21–26	38–44	0.58–0.61	1	8	11–13	15	1
Spratelloides	9–11	7–8	2	27–32	41–50	0.64–0.68	1	7–8	10–14	10–14	1
Nardoclupea	15	12–14	1	37–39	54–55	0.69–0.71	2	7–8	14–16	6	1

tween four to five times in SL. The belly is fairly rounded and the dorsal profile of the body slightly convex. The head is relatively elongate and slender, its length contained slightly less than four times in SL. The snout is pointed, its length contained between three to four times in head length. The orbit is rounded, its diameter is about 16% of head length. The mouth is small, with slightly projecting lower jaw.

The description of the structure of the neurocranium is primarily based on the holotype MSNM V2890 and the paratype MCSNV IG.VR.81999/82000, in which the head skeleton is partially preserved (Fig. 3). The overall morphology of the neurocranium is consistent with that of other clupeids (Ridewood 1904; Phillips 1942; Chapman 1944). The neurocranium is elongate and shallow, with a nearly straight dorsal profile. The frontals are the largest bones of the skull roof, occupying more than 65% of the total neurocranial length; each of the two contralateral bones tapers anteriorly and is broadly expanded posteriorly; the anterior sector of these bones is characterized by a relatively short and vertically developed median longitudinal flange; what appears to be a small median anterior fontanelle is located approximately in the anterior third of the length of the frontals; the two frontals articulate medially with each other, anteriorly with the mesethmoid, ventromedially with the lateral ethmoid, orbitosphenoid, and pterosphenoid, posteroventrally with the sphenotic, and posteriorly with the parietal; because of inadequate preservation, it is not possible to properly determine the presence of the

posterior cranial fontanelles (see Whitehead 1963), as well as the transverse commissure linking the supraorbital sensory canals. The parietal is oblong and irregular; it articulates anteriorly with the frontal, anteroventrally with the pterotic and posteroventrally with the epioccipital. The temporal foramen and pre-epiotic fossa are large and nearly ovoid in outline. The supraoccipital is only partially traceable; it forms the posteromedial end of the skull roof. Much of the otic region and basicranium are inadequately preserved or inaccessible thereby preventing the proper description of the structure of these portions of the neurocranium. The epioccipital occupies the dorsolateral part of the posterior surface of the neurocranium; in lateral view, this bone appears L-shaped, with the two arms forming an angle of about 55°; it articulates anterodorsally with the parietal and anteriorly with the pterotic. Of the pterotic, the articular facet for the posterior hyomandibular condyle is partially recognizable. The sphenotic meets the pterotic posteriorly and bears an articulatory facet for the anterior hyomandibular condyle along its ventrolateral surface. The dorsal wall of the orbit is formed by the orbitosphenoid, while the basisphenoid and pterosphenoids contribute to its posterior wall. The parasphenoid is long and curved, characterized by a shallow median longitudinal ridge along its dorsal surface. The vomer is short and thick; there is no evidence of vomerine teeth; these were either poorly developed or absent. The mesethmoid is very robust and elongate; it bears short lateral processes for the palatine arising from its anterior portion.
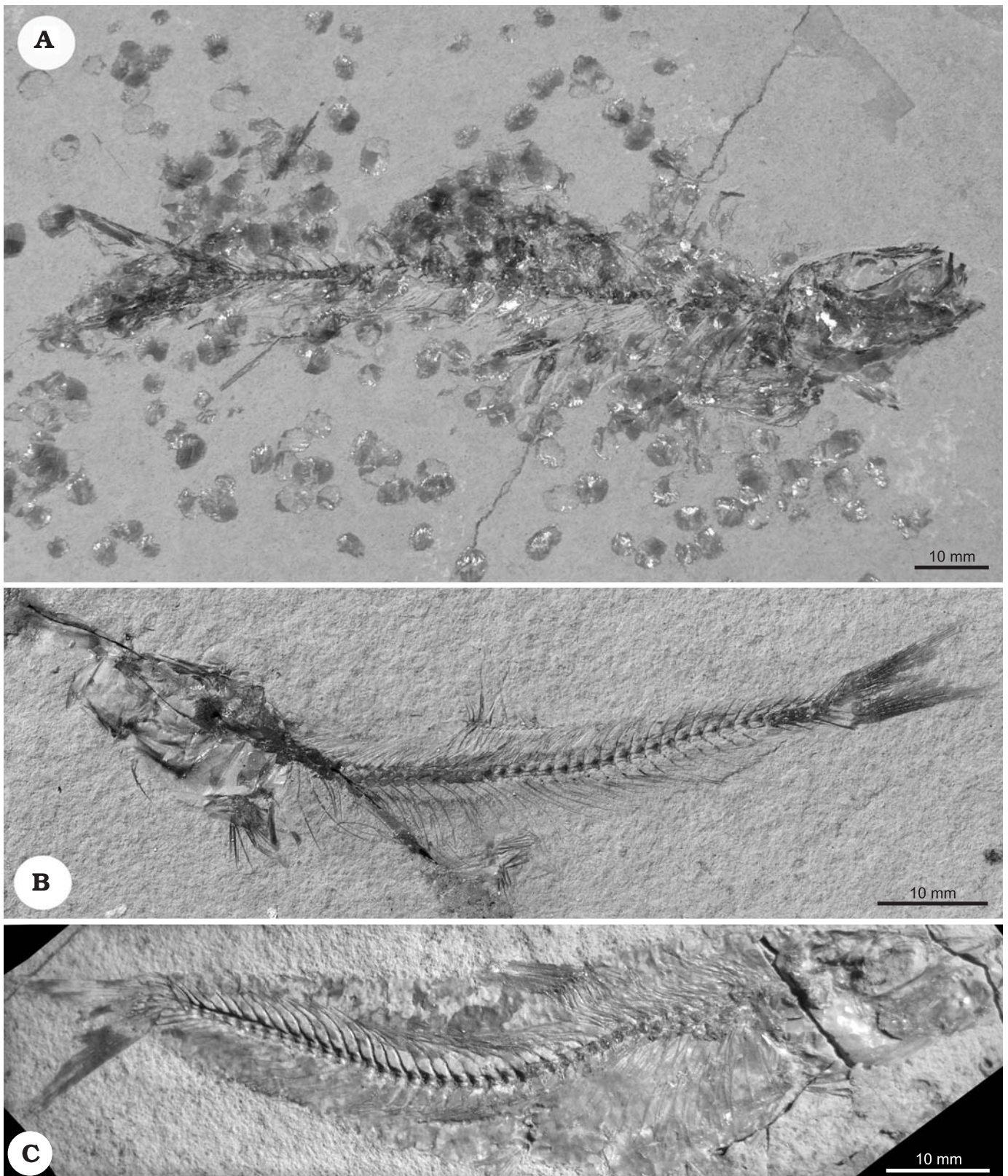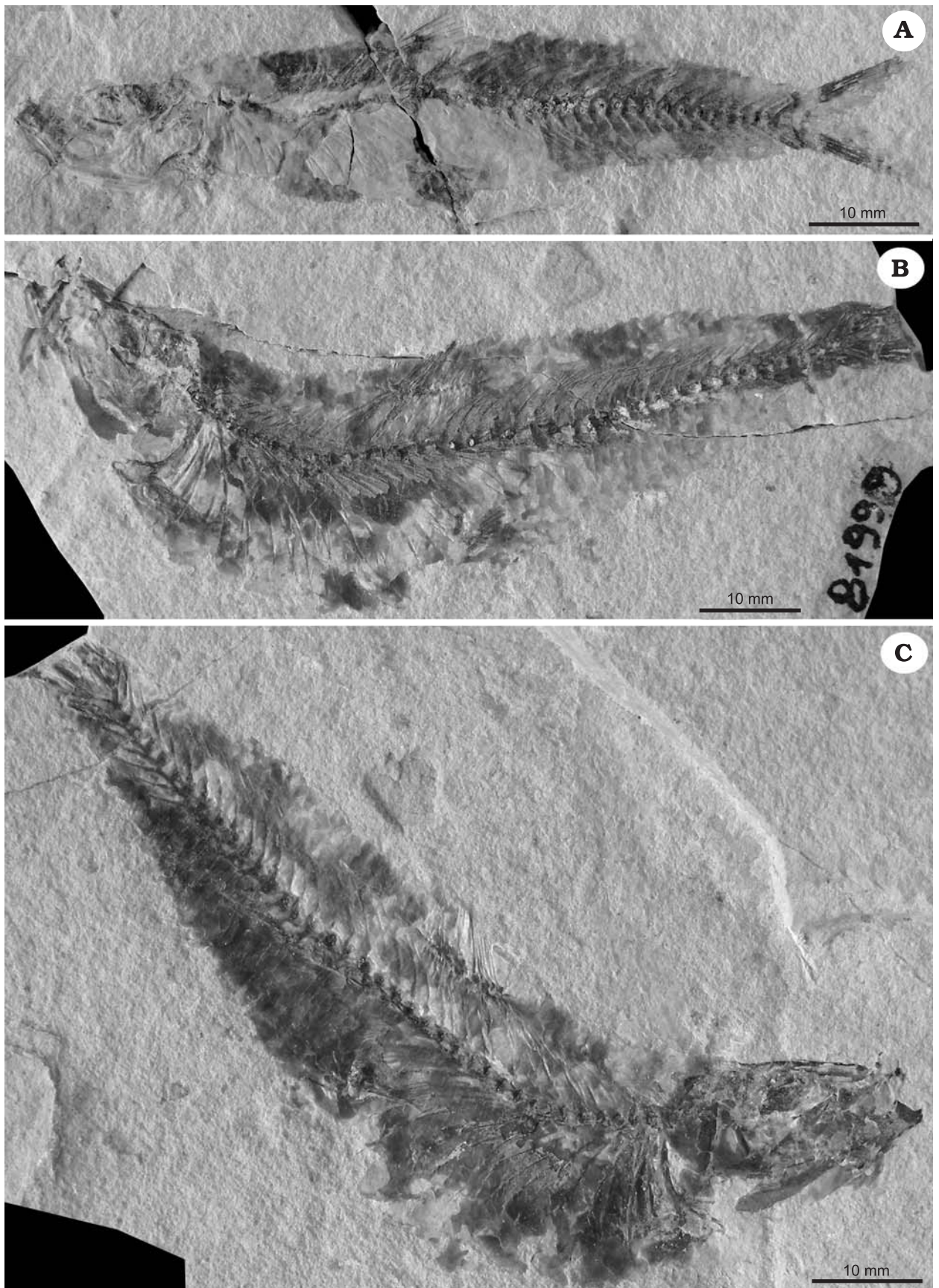
Fig. 2. Round herring *Trollichthys bolcensis* gen. et sp. nov., Ypresian (Eocene), Monte Bolca, Italy. **A**. MCSNV IG.VR. 132573 (paratype). **B**. MCSNV IG.VR.81999 (paratype). **C**. MCSNV IG.VR.82000 (paratype).
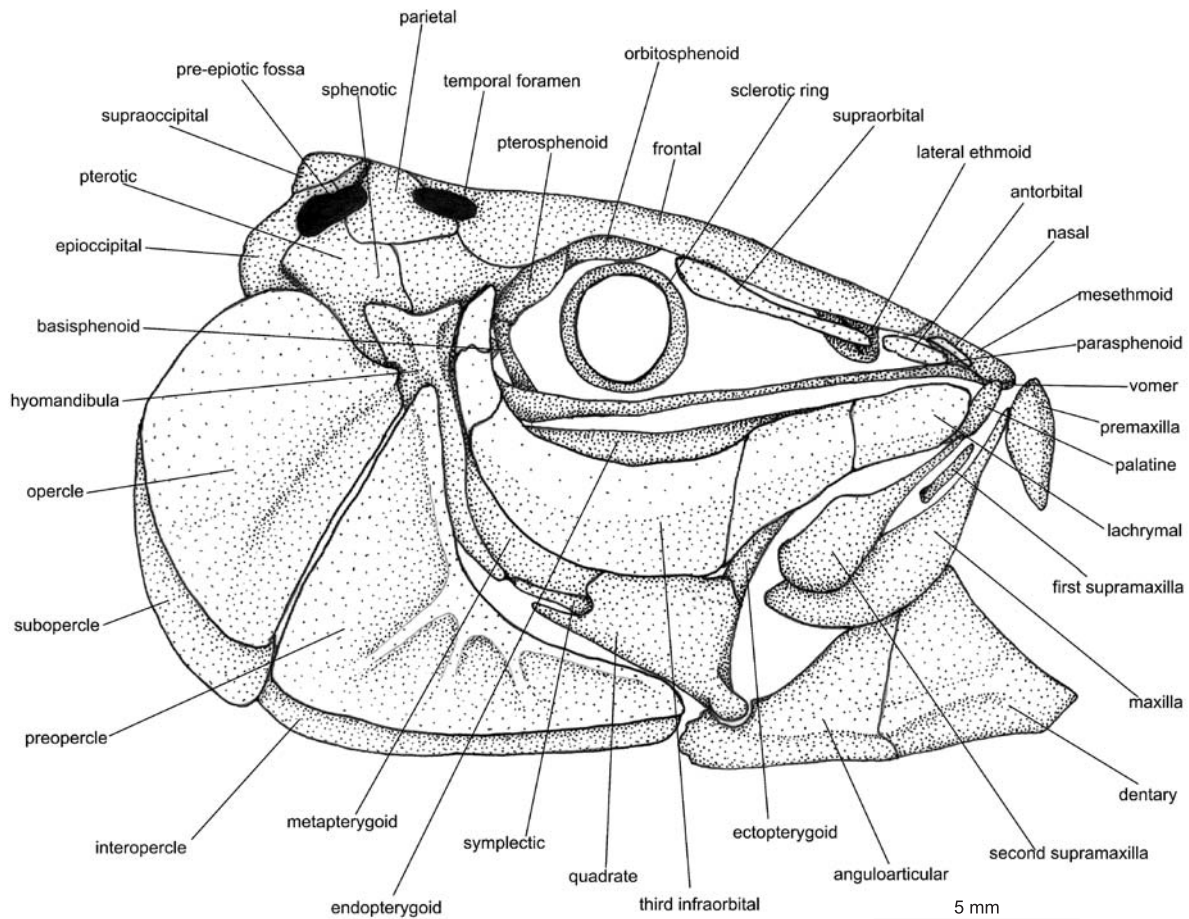
Fig. 3. Round herring *Trollichthys bolcensis* gen. et sp. nov., Ypresian (Eocene), Monte Bolca, Italy. Reconstruction of the skull, right lateral view.

The lateral ethmoid is well ossified and articulates anterodorsally with the frontal.

The nasal is thin and irregular. The bones of the circumorbital series are delicate and often badly damaged. The supraorbital is slender and appears to be partially supported by a lateral expansion of the frontal. The small antorbital is in some way connected to the anterior end of the supraorbital. Five infraorbital bones are clearly recognizable (Fig. 3). The lachrymal is relatively small and subrectangular in outline. The other four infraorbitals are saddle-shaped, the third being the largest element of the series. The identity of the two posterior elements of the infraorbital series is difficult to interpret.

The premaxilla is well ossified and subtriangular in outline (Fig. 3); the oral margin is nearly sigmoid and apparently toothless. The maxilla is slender and laterally compressed, with a moderately robust proximal head and a slightly expanded distal blade; the ventral margin of the distal blade is edentulous. There are two supramaxillae (Fig. 3). The first supramaxilla is thin, rod-like, lying below the anterior process of the second supramaxilla. The second supramaxilla is large and paddle-shaped, being slightly less than three times as long as deep, and its maximum depth is equal to that of the maxilla. The lower jaw is approximately triangular (Fig. 3). The suture between the dentary and anguloarticular is long and oblique. The dentary is massive and edentulous, with a

prominent coronoid process; the ventral margin of the dentary is strongly ossified and bears a flange that covers the mandibular laterosensory canal. The anguloarticular bears a moderately developed condyle for articulation with the head of the quadrate. The retroarticular is not clearly recognizable.

The palatine is small and nearly triangular in shape. The ectopterygoid is slender and gently curved. The endopterygoid is antero-posteriorly elongate. There is no trace of palatine or pterygoid teeth. The metapterygoid is irregular and laminar. The quadrate is large and nearly triangular in shape (Fig. 3). The symplectic is thin and rod-like. The upper part of the hyomandibula is inclined slightly backward; it has two distinct articular condyles, of which the posterior is the larger.

The preopercle is large and crescent shaped, with a very long horizontal arm (Fig. 3). The opercle is laminar and nearly quadrangular in outline; it has rounded posterior and dorsal margins, oblique ventral margin and smooth outer surface. The interopercle is only partially recognizable. The subopercle is small and subtriangular, slightly overlapped by the anteroventral corner of the opercle; the posterior margin of the subopercle is rounded. Based on the morphology of the bones of the opercular series, it is reasonable to hypothesize that the posterior border of the gill opening was gently rounded in origin and possibly characterized by a cleithral lobe (= cleithral flap of Whitehead 1963).

The hyoid and branchial arches are not exposed in the available material, being hidden by the opercular bones in a condition reminiscent to that characteristic of the species of the extant genus *Etrumeus* (see Whitehead 1963).

The vertebral column consists of 41 or 42 vertebrae (Table 2), including the first preural centrum; of these, 19–20 are abdominal and 21–22 are caudal. The vertebral centra are approximately rectangular, longer than high, with a small constriction in the middle. The anterior vertebral centra bear small and posteriorly directed parapophyses. Neural prezygapophyses and neural and haemal postzygapophyses are relatively expanded; the haemal prezygapophyses of the caudal vertebrae are remarkably developed, elongate and pointed; in the anterior portion of the caudal region, the haemal prezygapophyses emerge distally from the anterior margin of the haemal arches; the interzygapophysal articulation (Di Dario 2002) is recognizable in the caudal portion of the vertebral column. There are about 22–24 pairs of pleural ribs, apparently beginning from the third vertebra. Of the intermuscular series, the epineurals and epipleurals are clearly recognizable; these epineurals originate on the bases of the neural arches from the third (or fourth) vertebra and extend posteriorly to vertebrae 22–24; epipleurals are recognizable only in the caudal region.

The caudal skeleton is consistent with that of other clupeid fishes (Fig. 4). Overall, the elements of the caudal skeleton are associated with a single preural centrum and two ural centra. The first preural centrum is fused with the first ural centrum bearing an obliquely oriented elongate neural plate; this centrum articulates with a strongly ossified autogenous parhypural. There are six hypurals; all are autogenous except that the second hypural is fused to the fused first preural and first ural centrum. The first hypural is the largest of the series. There are two uroneurals, the first of which is fused to the first preural centrum. Nothing can be said about the epurals. The caudal fin is deeply forked and contains 17 principal rays. The number of dorsal and ventral procurrent rays is unclear.

There are five or six anteroposteriorly expanded supraneurals (Table 2), each characterized by a median thickened ridge. The dorsal fin originates slightly before the midpoint of the body and contains 14–16 rays supported by 14–16 pterygiophores (Table 2). As in other clupeids, proximal and middle pterygiophores are fused into a single structure (Grande 1985). The distal pterygiophores are small and usually poorly preserved. The first pterygiophore is greatly expanded and approximately triangular in outline. There is a short dorsal-fin stay (sensu Weitzman 1962). The first two dorsal-fin rays are unbranched and considerably shorter that those following.

The anal fin originates approximately at three fourths of the length of the body and includes 13 slender pterygiophores (Table 2). The proximal and middle pterygiophores of the anal fin appear to be fused into a single structure. Distal pterygiophores are not preserved. There is no trace of the anal-fin stay.

The structure of the pectoral girdle is partially recognizable. The posttemporal is subtriangular in outline. The supracleithrum is spatulate and laminar. The cleithrum is the larg-
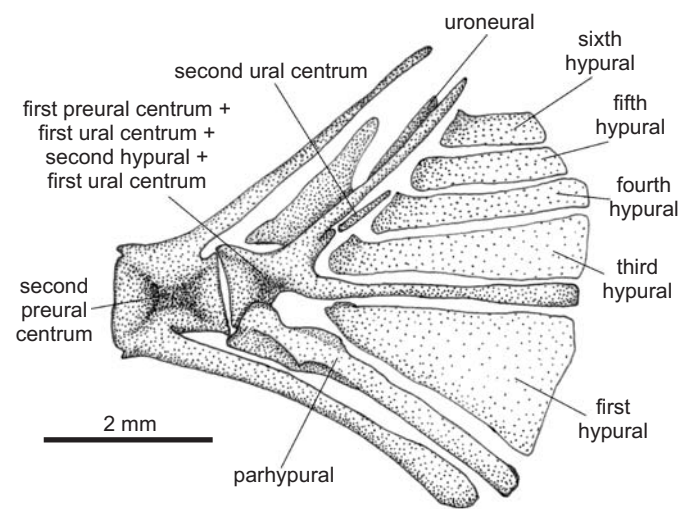

Fig. 4. Round herring *Trollichthys bolcensis* gen. et sp. nov., Ypresian (Eocene), Monte Bolca, Italy. Reconstruction of the caudal skeleton, left lateral view.

est bone of the pectoral girdle; it is approximately sigmoid in shape. There are two rod-like postcleithra. Coracoid, mesocoracoid, scapula and radials are inadequately preserved and difficult to interpret. The pectoral fin contains about 14 rays.

The pelvic fin inserts slightly behind the dorsal-fin origin and contains eight rays, the first of which is unbranched. The triangular basipterygia (Fig. 5) appear to be poorly ossified and characterized by a straight ventral margin.

Pre- and post-pelvic abdominal scutes are absent except for an unkeeled W-shaped element located immediately anterior to the pelvic fins; the arms of this W-shaped scute extend laterally around the base of the pelvic-fin rays (Fig. 5; see also Whitehead 1962, 1963; Grande 1985).

The body is covered by thin deciduous cycloid scales. The scales are often partially disarticulated and scattered around the skeleton. These are subcircular to ovoid and gradually decrease in size posteriorly. The anterior field of the scale has three or four discontinuous vertical striae (five striae, one of which is continuous, in the caudal region), while the posterior field is smooth. The scales are characterized by 15 to 17 delicate circuli.

Discussion

The overall morphology of the body, as well as the presence of certain features of the axial skeleton, including the relatively high pleural rib to preural vertebrae ratio (Table 2), fusion of the first uroneural with the first preural centrum, reduced size of the first ural centrum, separation between parhypural and first preural centrum (Fig. 4), and absence of lateral line scales clearly indicate that *Trollichthys bolcensis* is a clupeoid fish. Moreover, despite the incompleteness of the available material, the taxon possesses two postcleithra, a feature that justifies the assignment of this new taxon to the family Clupeidae (see Grande 1985).
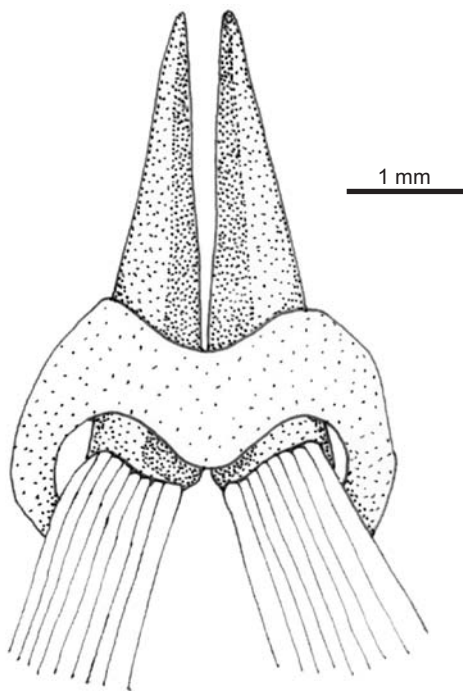
Fig. 5. Round herring *Trollichthys bolcensis* gen. et sp. nov., Ypresian (Eocene), Monte Bolca, Italy. Pelvic girdle and W-shaped pelvic scute, ventral view.

Trollichthys bolcensis lacks abdominal scutes along the midline of the body, with the exception of a single, unkeeled W-shaped pelvic scute immediately anterior to the pelvic-fin insertion (Fig. 5), a character that unquestionably supports its assignment to the Dussumieriinae (Grande 1985).

The dussumieriines are a small group of clupeids broadly distributed in tropical and subtropical waters, primarily in the Indo-Pacific region (Whitehead 1963). Members of this group are characterized by rounded rather than keeled bellies due to the absence of the abdominal scutes typical of other clupeid fishes. Several authors (Jordan and Gilbert 1883; Svetovidov 1952; Grande 1985; Whitehead 1985b) considered the round herrings as a subfamily of Clupeidae, whereas some others have given family status to this group (Bertin 1943; Whitehead 1963). Dussumieriines were traditionally considered as the most primitive group of clupeids, representing the sister group of all other clupeid subgroups (Whitehead 1963; Nelson 1967, 1970) primarily because of the lack of abdominal scutes. However, both Svetovidov (1952) and Grande (1985) suggested that the round herrings should be regarded as a derived group within the clupeoids. Based on the shared possession of a single, unkeeled W-shaped pelvic scute, Grande (1985) included four extant genera (*Dussumieria*, *Etrumeus*, *Jenkinsia*, *Spratelloides*) in the subfamily Dussumieriinae, and recognized two monophyletic subgroups, the Dussumieriini and Spratelloidini. The skeletal anatomy of round herring genera is relatively well known (Ridewood 1904; Hollister 1936; Chapman 1948; Gosline 1960; Whitehead 1963; Monod 1968; Cervigon and Velazquez 1978; Grande 1985; Fujita 1990), and Grande (1985) provided a cladistic analysis of the extant dussumieriine genera based on osteological

characters. Recent molecular studies, however, suggest that this group may not be monophyletic (Lavoué et al. 2007, 2013; Li and Ortí 2007; Wilson et al. 2008).

The fossil record of round herrings includes a number of Jurassic to Miocene fossils (Bertin 1943; Arambourg 1927, 1954, 1967; Misra and Saxena 1954; Bochino 1967; Danil'chenko 1980). In his review of the clupeomorph fossil record, Grande (1985) recognized the presence of the single W-shaped pelvic scute in the Neogene Palaeomediterranean taxa, *Etrumeus boulei* and *Spratelloides lemoinei* (see Arambourg 1927; Carnevale 2004), as well as in the new genus and species from the Eocene of Monte Bolca documented herein. Moreover, Grande (1985) tentatively referred to this group a few other taxa in which the peculiar pelvic scute was not observed, including *Etrumeus hafizi* from the Oligocene of Iran (Arambourg 1967), *Paretrumeus avitus* from the Oligocene of the Caucasus (Danil'chenko 1980), and *Sahelinia gregaria* from the Mediterranean Miocene (Arambourg 1927). Landini and Menesini (1980) referred the latter to the sternoptychid *Maurolicus muelleri*. Therefore, according to Grande (1985) only three taxa can be undoubtedly considered as members of the Dussumieriinae. Subsequently, Gaudant and Busquets (1996) reported the presence of the W-shaped pelvic scute in the middle Eocene *Spratelloides eocaenicus* from the Vallfogona Formation near Borredà, Barcelona Province, Spain. Taverne (2002, 2007) referred to the Dussumieriinae the Late Cretaceous *Nardoclupea grandei* and *Portoselvaggioclupea whiteheadi* from Nardò, southern Italy. The first was described from a number of specimens, and despite the absence of the unkeeled W-shaped pelvic scute, Taverne (2002) listed several features that seem to demonstrate its affinities with the round herrings. On the other hand, it is very difficult to verify the dussumieriine relationships of *Portoselvaggioclupea whiteheadi*, represented only by a largely incomplete caudal skeleton (see Taverne 2007). In summary, only two fossil taxa (*Etrumeus boulei*, *Spratelloides lemoinei*) other than *Trollichthys bolcensis* exhibit the only known synapomorphy of Dussumieriinae, the single, unkeeled W-shaped pelvic scute. As a consequence, taking into account also the middle Eocene and Oligocene taxa (*Etrumeus hafizi*, *Paretrumeus avitus*, *Spratelloides eocaenicus*) putatively included within the Dussumieriinae, *Trollichthys bolcensis* is the earliest unquestionable round herring. However, *Nardoclupea grandei* possesses a combination of features that seem to support its placement within the Dussumieriinae, thereby making this Cretaceous taxon possibly the earliest representative of the group.

The new taxon *Trollichthys* differs from all other dussumieriines in having a small number of supraneurals and pleural rib pairs and a low pleural ribs-preural vertebrae ratio (see Table 2), the latter feature comparable to that typical of certain pellonulines, dorosomatines, alosines and clupeines (see Grande 1985). The overall body shape and small size of *Trollichthys* resemble that of two genera of Spratelloidini, *Jenkinsia* and *Spratelloides*, with which it also shares the possession of an approximately triangular premaxilla, an au-

togenous parhypural, fused first preural and first ural centra, and the reduction of the number of infraorbital bones to five (see Grande 1985). However, *Trollichthys* lacks at least one of the other synapomorphies of Spratelloidini documented by Grande (1985), having an expanded fourth hypural (see Fig. 4). It also differs from the Spratelloidini (in the sense of Grande 1985) in having two postcleithra, a feature shared with *Etrumeus* within the Dussumieriinae (see Grande 1985). The bones of the upper jaw of *Trollichthys* are remarkably similar to those of *Spratelloides*; the premaxillae of *Trollichthys* and *Spratelloides* are edentulous and approximately triangular in shape, and both genera have two supramaxillae, the first of which is small, rod-like and the second paddle-shaped (see Fig. 3). However, *Trollichthys* differs from *Spratelloides* in having an edentulous maxilla and a pelvic-fin insertion located under the dorsal-fin base, exhibiting a pattern very similar to that of *Dussumieria* and *Jenkinsia* (see Whitehead 1963, 1985a).

Inadequate preservation and inaccessibility of certain skeletal structures relevant for the definition of the phylogenetic relationships among the round herrings (see Grande 1985), including the gill and hyoid arches and the upper portion of the caudal skeleton, preclude us from making a definitive assessment of the affinities of *Trollichthys*, for which additional comparative information would be necessary.

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