The Eocene sardine †Bolcaichthys catopygopterus (Woodward, 1901) from Monte Bolca, Italy: Osteology, taxonomy, and paleobiology

Published version:

DOI:10.1080/02724634.2015.1014490

The Eocene sardine †*Bolcaichthys catopygopterus* (Woodward, 1901) from Monte Bolca, Italy: osteology, taxonomy and paleobiology

GIUSEPPE MARRAMÀ[*] and GIORGIO CARNEVALE
Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso, 35, I-10125 Torino, Italia; giuseppe.marrama@unito.it; giorgio.carnevale@unito.it

RH: MARRAMÀ AND CARNEVALE—EOCENE CLUPEID FISH FROM MONTE BOLCA

DOI: 10.1080/02724634.2015.1014490

---

[*] Corresponding author

ABSTRACT—Clupeid fishes are rather abundant in the Eocene fossiliferous limestone of Monte Bolca, representing by far the most common group of this celebrated locality. However, despite of their abundance, the clupeid fishes from Monte Bolca have been scarcely investigated up to date. A broad analysis of about 300 well-preserved clupeid specimens from Monte Bolca housed in several institutions clearly indicates that more than 95% of the available material belongs to different developmental stages of a single taxon traditionally referred to as †*Clupea catopygoptera* Woodward. †*Bolcaichthys*, a new genus of clupeid fish, erected to contain †*Clupea catopygoptera* Woodward from the Eocene of Monte Bolca, Italy, is described and compared with extant and fossil genera of the family Clupeidae. This new genus shows a unique combination of characters (head length contained approximately three to four times in the standard length; skull roof with 10–14 fronto-parietal striae; mouth terminal; two supramaxillae; edentulous jaws and palate; complete series of about 20–22 abdominal keeled scutes with ascending arms; no dorsal scutes; 5–6 branchiostegal rays; eight supraneurals; 40–42 vertebrae and 20–22 pleural ribs; three epurals) that supports its recognition as a new genus of the family Clupeidae. Paleobiological considerations suggest that the presence of a very large number of the schooling clupeids belonging to the genus †*Bolcaichthys* present in all stages of development (larval, juvenile and adult) support the hypothesis that the sediments were deposited close to the coast in a context subject to the ecological influence of the open sea.

INTRODUCTION

Clupeoidei are one of the most abundant and widespread group of teleostean fishes that include over 300 extant species whose first representatives apparently date back to the early Cretaceous (Figueiredo, 2009). The taxon Clupeoidei includes small to medium size fishes like herrings, sardines, shads, sprats, round herrings and anchovies, with a worldwide distribution, from tropical to the cold temperate waters. These fishes form large monotypic schools feeding on zooplankton (Whitehead, 1985) and are one of the fish groups of primary importance to fisheries, representing one-third of total worldwide commercial fishing catch (Blaxter and Hunter, 1982). Diagnostic characters of the Clupeoidei include the fusion of the first uroneural with the first preural centrum, reduction in relative size of the first ural centrum, parhypural separated from first ural centrum, and loss of lateral line scales (Grande, 1985). Fishes of the family Clupeidae differ from others clupeoids in the presence of two long rod-like postcleithra in the pectoral girdle (Grande, 1985). The body of clupeids is moderately elongate and fusiform, herring-like; the mouth is terminal, having usually two supramaxillae; jaw teeth are small or absent; the dorsal fin is short and placed at midpoint of the body; the pelvic fins are just in front of, below or just behind the dorsal fin base, and the anal fin is short and its origin is well behind the last dorsal-fin ray. However, there is a broad intrafamilial morphologic variability, with some species characterized by a strongly compressed or deepened body, scutes sometime reduced or absent, one or both supramaxillae absent, and, sometimes, deciduous scales (Whitehead, 1985).

The taxon Clupeidae is by far the most common group in the Eocene fish assemblage of Monte Bolca (north-eastern Italy) in terms of number of specimens (Landini and Sorbini, 1996) and, at the same time, it is also one of the most scarcely investigated. Because of their abundance in the fish assemblage of Monte Bolca, the clupeids certainly had a relevant ecological role in the original paleobiotope. Unfortunately, the potential paleoenvironmental role of the fishes has been traditionally neglected or underestimated (Bellwood, 1996; Landini and Sorbini, 1996). Despite the large amount of systematic studies carried out on fishes from Monte Bolca in the last decades (e.g., Tyler and Bannikov, 1997; Tyler and Santini, 2002; Day, 2003; Monsch, 2006; Bannikov, 2008; Bannikov and Carnevale, 2009, 2010, 2011, 2012; Carnevale and Pietsch, 2009, 2010, 2011, 2012; Friedman, 2012), the earliest study on clupeid fishes dates back to the second half of the nineteenth century when Lioy (1866) institutes some species belonging to this family, based on inadequate descriptions and without iconographic documentation. In this study we describe a new genus of the Clupeidae, based on material from the Eocene of Monte Bolca, previously referred to the genus *Clupea* (Agassiz, 1833–44; Lioy, 1866; Zigno, 1874; Bassani, 1897; Woodward, 1901; see synonymy below). Paleobiological and paleoenvironmental implications of the family Clupeidae are also discussed. This work is another in a series of papers focused on the Eocene clupeoid fishes from Monte Bolca (e.g., Marramà and Carnevale, in press).

LOCALITY

The material documented herein was collected from the Pesciara Cave and Monte Postale sites of the Monte Bolca locality, in the eastern part of Monti Lessini, approximately 2 km north-east of the Bolca village, not far from Verona, northeastern Italy. The geological features of the fish-bearing limestone exposed at Monte Bolca were investigated by several authors, including Fabiani (1914, 1915), Sorbini (1968), Barbieri and Medizza (1969), Massari and Sorbini (1975) and, more recently, by Papazzoni and Trevisani (2006). The fish-bearing limestone pertains to the 'Calcari Nummulitici', an informal unit of Eocene age widely distributed in northeastern Italy. The succession consists of a cyclic alternations of laminated micritic limestone and biocalcarenite-biocalcirudite, the former characterized by beautifully preserved remains of fishes, invertebrates and plants. According to Seilacher et al. (1985), the taphonomical features and ecological spectrum of the fossil assemblage are indicative of a stagnation deposit with a poorly oxygenated bottom. Based on their benthic large foraminiferan content, the fish-bearing strata of the Pesciara Cave site have been referred to the *Alveolina dainelli* Zone (Trevisani et al., 2005; Papazzoni and Trevisani, 2006) or SBZ 11 Biozone (Serra-Kiel et al., 1998), corresponding to the Middle Cusian (late Ypresian; about 50 Ma). A detailed biostratigraphic study of the fish-bearing layers of the Monte Postale site is not available. The two sites, however, have been traditionally considered as approximately coeval.

MATERIAL AND METHODS

The material examined consists of specimens provisionally referred to the genus ‘*Clupea*’ or to an indeterminate clupeid taxon or, in some cases, assigned to the order Clupeiformes. The present study is based on 287 well-preserved specimens housed in the collections of the Museo Civico di Storia Naturale di Verona, Verona (MCSNV), Museo di Geologia e Paleontologia, Università degli Studi di Padova, Padova (MGPUP), Museo Civico di Storia Naturale di Milano, Milan (MSNM), Museo Regionale di Scienze Naturali, Torino (MRSN), and Natural History Museum, London (NHMUK P). The material was examined using a Leica M80 stereomicroscope equipped with a camera lucida drawing arm. Measurements were made to the nearest 0.1 mm using a dial caliper. All counts and measurements follow Hubbs and Lagler (1958), Grande (1985), Whitehead (1985) and Whitehead and Teugels (1985).

Most of the specimens were mechanically prepared using mounting entomological needles and some were prepared using the transfer method following the procedure proposed by Toombs and Rixon (1956).

Osteological terminology mostly follows Ridewood (1904), Phillips (1942) and Whitehead and Teugels (1985). All extinct taxa are marked with dagger (†) preceding their name.

Least squares regression is used to obtain the relation between the standard length (SL) or head length (HL) and other morphometric features. Alpha was set at 0.05. Data were log-transformed to fit the allometric equation $y = bx^m$ into the linear equation $\log(y) = m*\log(x) + \log(b)$, where y is the variable morphometric character, x is the independent character (standard length or head length), m and b (respectively slope and intercept) are the constant values that could be determined by the least square method. The results of the linear regression analyses are shown in scatterplots. All calculations were conducted using the software PAST (Hammer et al., 2001).

The length at first maturity (L_m), representing the size at which 50% of the specimens was mature, was determined by the empirical equation $\log L_m = - 0.1189 + 0.9157 * \log (L_{max})$, where L_{max} is the largest standard length in the sample (Binohlan and Froese, 2009).

Anatomical Abbreviations—**aa**, anguloarticular; **ao**, antorbital; **bsp**, basisphenoid; **d**, dentary; **ect**, ectopterygoid; **ep**, epural, **epi**, epioccipital; **f**, frontal; **hym**, hyomandibula; **hyp**, hypural; **io**, infraorbital; **iop**, interopercle; **le**, lateral ethmoid; **me**, mesethmoid; **mtp**, metapterygoid; **mx**, maxilla; **na**, nasal; **np**, neural plate; **op**, opercle; **osp**, orbitosphenoid; **pa**, parietal; **pas**, parasphenoid; **phy**, parahypural; **pl**, palatine; **pmx**, premaxilla; **pop**, preopercle; **pto**, pterotic; **pts**, pterosphenoid; **pu**, preural centrum; **q**, quadrate; **ra**, retroarticular; **smx**, supramaxilla; **SL**, standard length; **so**, supraorbital; **soc**, supraoccipital; **sop**, subopercle; **sph**, sphenotic; **sr**, sclerotic ring; **sym**, symplectic; **u**, ural centrum; **un**, uroneural; **vo**, vomer.

SYSTEMATIC PALEONTOLOGY

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 †*BOLCAICHTHYS*, gen. nov.

Type species —†*Bolcaichthys catopygopterus* (Woodward, 1901) by monotypy and designation herein.

Etymology—Named after the locality ‘Bolca’ and from Greek -ichthys ‘fish’.

Diagnosis—Small to medium-sized clupeid (largest specimen measuring 101.1 mm SL) with elongated and tapered body, sardine-like; †*Bolcaichthys* gen. nov. is unique among clupeids in having the following combination of characters: head length contained approximately three to four times in SL; skull roof with 10–14 fronto-parietal striae; mouth terminal; two supramaxillae, anterior small and rod-like, and posterior paddle-shaped; teeth absents in jaws and palate; complete series of abdominal keeled scutes (10–11 pre-pelvic and 10–11 post-pelvic) with ascending arms; dorsal scutes absent; fewer branchiostegal rays (5–6), supraneurals (8), vertebrae (40–42) and pleural ribs (20–22) compared with other genera of clupeids; pleural ribs-preural vertebrae ratio ranging from 0.48 to 0.55; three epurals; deeply forked caudal fin with 19 principal caudal-fin rays; dorsal fin small, inserting at about mid-length of the body with 15–16 rays; about 15–16 anal-fin rays; about 14–18 pectoral-fin rays; pelvic-fin origin slightly in front of or behind the posterior end of the dorsal fin; eight pelvic-fin rays.

Remarks—The species †*Clupea catopygoptera* was created by Louis Agassiz (1835, 1844) without any formal description, figure and indication of the type material. Because of the inadequate taxonomic procedure [designation of the name did not satisfy the stipulation of Article 12 of the ICZN (1999)] followed by Agassiz, this species was considered as nomen nudum. In 1901, Woodward provided the first description of †*Clupea catopygoptera* based on a nearly complete specimen housed in the Natural History Museum, London (NHMUK P.3829a; Fig. 1); for this reason he should be credited for authorship following ICZN Articles 21 and 50. Woodward (1901) assigned the species to the genus *Clupea* Linnaeus, 1758, a common practice followed by most others authors in nineteenth century, when almost all fossils and recent clupeids were referred to this repository genus. Woodward (1901) retained Agassiz's name because the specimen NHMUK P.3829a was labeled by Agassiz and for this reason he (Woodward, 1901: 148) assumed the specimen to be the representative of †*Clupea catopygoptera* Agassiz, 1835. Grande (1985) provided evidence of the incorrect generic placement of this species and claimed about the necessity of a revision of the clupeoid material from Monte Bolca.

†*BOLCAICHTHYS CATOPYGOPTERUS* (Woodward, 1901)

(Figs. 1-10)

†*Clupea catopygoptera* Agassiz, 1835:31 (original occurrence of name, no description or figure).

†*Clupea catopygoptera* Agassiz, 1835: Agassiz, 1843:120 (second occurrence of name, no description or figure).

†*Clupea catopygoptera* Agassiz, 1835: Zigno, 1874:143 (third occurrence of name, no description or figure).

†*Clupea catopygoptera* (Agassiz, 1835, nomen nudum): Woodward, 1901:148, pl. 6, fig. 2.

†*Clupea catopygopterygia* (Agassiz, 1835): Eastman, 1905:357.

†*Clupea catopygoptera* (Agassiz, 1835): Blot, 1980:351.

†‘*Clupea’ catopygoptera* (Agassiz, 1835): Grande, 1985:281, 310-311.

Holotype—NHMUK P.3829a, nearly complete articulated skeleton in single plate (Fig. 1), 57.9 mm SL; late early Eocene, Ypresian, Monte Bolca, Italy.

Referred material—MCSNV IG.VR.57598/57599, part and counterpart (Fig. 2A) of an almost complete articulated skeleton, 56.9 mm SL; MCSNV IG.VR.71407/71408, part and counterpart (Fig. 2B) of a partially articulated skeleton, 39.0 mm SL; MCSNV T.361, almost complete articulated skeleton (Fig. 2C), 52.0 mm SL. Additional 283 additional articulated skeletal remains are listed in Supplementary data 1 and 2.

Locality and horizon—Monte Bolca, Pesciara locality; early Eocene, late Ypresian, middle Cuisian, SBZ 11, *Alveolina dainelli* Zone.

Diagnosis—As for the genus.

DESCRIPTION

Morphometrics and counts are given in Tables 1 and 2. The body is elongate, tapered and sardine-like. The head is about 3.6 times in the SL and the maximum body depth is about 4.4 times in the SL. The mouth is small terminal with slightly projecting lower jaw. The belly is completely armed with keeled scutes with ascending arms in front of and behind the pelvic fins. The description of the skeletal structures and the restoration of the head (Fig. 3) and the axial skeleton (Fig. 4) is primarily based on the specimens MCSNV IG.VR.57598/57599, MCSNV IG.VR.71407/71408 and MCSNV T.361.

Neurocranium—The neurocranium is rather elongate and, laterally, nearly triangular in outline. The paired frontals are the largest bones of the skull roof, occupying about 70% of the total neurocranial length. Each of the frontals articulates anteriorly with the posterior surface of the mesethmoid, ventrally with the orbitosphenoid and lateral ethmoid, medioventrally with the pterosphenoid, posteriorly with the parietal and posteroventrally with the sphenotic. There are 10 to 14 fronto-parietal striae that appear visible only in the posterior portion of each of the frontal, which are observed mostly in larger specimens. The parietal is a scythe-like bone that articulates anteriorly with the frontal, anteroventrally with the sphenotic, posterodorsally with the epioccipital, and posteroventrally with the pterotic. The pre-epiotic fossa is rather small. The supraoccipital forms the posteromedial end of the skull roof and has a rhomboidal shape. The epioccipital marks the postero-dorsal border of the pre-epiotic fossa and articulates anteriorly with the parietal, ventrally with the pterotic and posteriorly with the upper limb of the posttemporal. The pterotic marks the ventral margin of the pre-epiotic fossa; it is antero-posteriorly elongate and articulates anterodorsally with the parietal, posterodorsally with the epioccipital, posteriorly with the exoccipital, and anteriorly with the sphenotic. The sphenotic is a strongly ossified bone, subtriangular in shape, articulating posteriorly with the pterotic and bearing an articulation facet for the anterior hyomandibular condyle. The prootic appears to be rather small. The long orbitosphenoid forms the dorsal wall of the orbit; it bears an anterior process that articulates with the lateral ethmoid and contacts the parasphenoid anteroventrally via a thin and laminar sheet of bone. The pterosphenoid and basisphenoid form the posterior wall of the orbit. The parasphenoid is a long and thin bone, extending for the most of the basicranial length. The vomer is thin and apparently toothless. The mesethmoid is long, slender and anteriorly forked. The lateral ethmoid is small and thin with expanded ventral end characterized by irregular ventral margin.

Circumorbital series—The nasal is short and moderately elongate. The supraorbital is long and slender, antero-posteriorly elongated, supported by the antero-ventral margin of the frontal. The small antorbital is subtriangular in shape, loosely articulated with the anterior end of supraorbital. Six infraorbitals surround the lower margin of the orbit. The first infraorbital is small, subtriangular in shape, and anteriorly pointed. The second and the third infraorbitals, the largest of the series, are approximately trapezoid in shape. The dermosphenotic is small, approximately triangular in shape, dorso-ventrally elongate and lying along the posterior margin of the orbit. The sclerotic ring is formed by two semicircular plates.

Jaws—The premaxilla is well-ossified and triangular in outline, with a slightly curved and toothless oral margin. The maxilla is elongate, and laterally flattened, with a straight and thin anterior head and a convex edentulous oral margin. There are two supramaxillae, the first of which is thin, rod-like and slightly arched, and the second large, paddle-shaped. The dentary is edentulous, robust and deep, trapezoid in shape, with a steep anterior margin; the entire ventral margin bears a flange for the mandibular laterosensory canal; a large ovoid mental foramen lies ventrally in the most anterior part of the dentary. The anguloarticular is rhomboid in shape. A small retroarticular lies ventrally to the articular condyle.

Suspensorium—The palatine is long and slender, with an anterior hook-like maxillary process. The ectopterygoid is long and well-developed, forming an obtuse angle at its mid length. The endopterygoid is antero-posteriorly elongate, posteriorly expanded with a concave dorsal margin; it bears a ridge along its entire length. The metapterygoid is a laminar bone, subtriangular in shape that overlies anteroventrally the quadrate. The quadrate is triangular in shape with a well-developed condyle; its postero-ventral margin bears a thickened elongate and backward directed process. The symplectic is rod-like. The hyomandibula has two condyles in the articular head for the sphenotic and pterotic, respectively; the foramen for facial nerve is clearly recognizable; the opercular process is well-developed.

Opercular series—The preopercle is large, crescent-shaped; the vertical arm of the preopercle is slightly shorter than the horizontal one. The opercle is about two times as deep as broad, ovoid in shape, with a vertical anterior margin; in the dorsal third of the bone, an horizontal concave striation extends forward from the posterior margin, resembling, at least in part, the condition described by Whitehead (1973) in *Pellona flavipinnis*. The subopercle is small and the interopercle is relatively long and slender, slightly broader posteriorly.

Hyoid bar—The paired dorsal hypohyals are small and poorly ossified, L-shaped. The paired ventral hypohyals are long, thin and tubular. The anterior ceratohyal is robust and elongate, slightly constricted in the middle and characterized by an irregular groove for the hyoid artery. There are at least five or six elongate branchiostegal rays.

The gill arches are not clearly recognizable in the available material.

Vertebral column and intermuscular bones—The vertebral column consists of 40–42 vertebrae (usually 41), including the first preural centrum; of these, 23–25 are abdominal and 16–18 are caudal; the vertebral centra are almost quadrangular, with a small constriction in the middle; neural pre- and postzygapophyses are moderately developed throughout the entire length of the vertebral column; the parapophyses are rather small, plate-like; the haemal postzygapophyses occur from the 16th or 17th vertebra backward. There are 20–22 (usually 21) pairs of pleural ribs that articulated with the parapophyses starting from the third vertebra. The epineurals articulate with the base of neural spines from vertebra four or five to the vertebra 20 or 22, becoming separated towards the end of the vertebral column. The epicentrals are very short, curved and articulate along the base of the pleural ribs from the vertebra five or six to the vertebra 23 or 24. The epipleurals are not clearly recognizable in the examined specimens. There are eight slender supraneurals.

Caudal skeleton—The caudal skeleton (Fig. 5) is consistent with that of other clupeoids (see, e.g., Grande, 1985). The first preural centrum is short and subtriangular in shape; dorsally, it bears a laminar, elongate and subrectangular neural plate. The first ural centrum is fused to the second hypural. The second ural centrum is short and tubular. There are six hypurals, all autogenous but the second, which is elongate and slender and fused to the first ural centrum; the first hypural is the largest of the series. The autogenous parhypural is slender. There are three uroneurals, the first of which is the longest, rod-like and fused with the first preural centrum. There are three slender epurals. The caudal fin is deeply forked and contains 19 principal caudal-fin rays, of which the central two show a dorsal and ventral peg, as in most clupeines (Grande, 1985).

Median fins and supports—The dorsal fin is short, approximately triangular in shape originating at about the mid-length of the body, overlying the vertebrae 13 to 15; it seems to contain 15 or 16 rays supported by 15 or 16 pterygiophores. As in other clupeids, each proximal and associated middle pterygiophores appears to be fused into a single structure (e.g. Grande, 1985); the first pterygiophore is the largest of the series and consists of an expanded triangular plate, with rounded edges. The distal pterygiophores are small and subrectangular in shape, decreasing in length posteriorly. There is a long dorsal-fin stay (sensu Weitzman, 1962). The first two dorsal-fin rays are unbranched and much shorter than others.

The anal fin contains 15–16 rays supported by 15 or 16 pterygiophores more or less closely associated with the haemal spines of the vertebrae 28 to 36. As for the dorsal-fin pterygiophores, the proximal and middle anal-fin pterygiophores appear to be fused into a single structure. The length of the proximal-middle pterygiophores slightly decreases posteriorly in the series. The distal pterygiophores are subquadrangular in shape. There is no trace of the anal-fin stay or, alternatively, it was extremely reduced.

Paired fins and girdles—The posttemporal is well-ossified, elongate and subtriangular in outline. The supracleithrum is long, curved and distally expanded. The cleithrum is the largest bone of the pectoral girdle, nearly sigmoid in shape; the ventral arm bears a little flange at its mid length for the articulation with the head of the mesocoracoid; the lower portion of the cleithrum partially covers the anterior portion of the coracoid. There are two long rod-like postcleithra. The scapula is an irregular bone, in which it distinguishes a hollow for insertion of the external hemitrich of the first pectoral-fin ray. The mesocoracoid is small, elongate and subcylindrical in shape; ventrally it articulates to the medial surface of the scapula. The coracoid is robust hatchet-shaped, anteroposteriorly elongated, with a curved antero-ventral margin; some ridges along the medial surface extend from the scapula-coracoid junction to the ventral margin of the coracoid; the posterior edge of the coracoid is pointed with a process extending backward. There are four proximal radials, the first of which is the largest and subtriangular in shape. There are at least 13 short distal radials. The pectoral fin contains 14 to 18 rays, the first of which is the longest.

The pelvic fins originate at the level or slightly behind the posterior end of the dorsal fin and contain eight rays. The basipterygia are elongate and narrow, nearly triangular in shape.

Abdominal scutes—Abdominal scutes form a continuous series extending from the lower end of the cleithrum to approximately the anal-fin origin. There are 10–11 pre-pelvic, one pelvic and 10–11 post-pelvic keeled scutes with ascending arms. The pelvic scute is the largest of the series. Juvenile specimens (until about 52 mm SL, see below) exhibit a lower number of scutes, which appear to be absents in the larval specimens.

Squamation—The squamation consists of cycloid scales covering the entire body, arranged in about 50 transverse and about 10 horizontal scale rows; the lateral line is absent. Given their close association to the body flanks, the scales were probably firmly attached to their pockets in origin. The scales are subcircular in shape and gradually decrease in size posteriorly; each scale shows four to five discontinuous vertical striae and numerous concentric circuli.

Pigmentation—The original pigmentation of the body is represented by small and circular brown spots of pigment showing different degrees of aggregation. In larval and juvenile specimens the pigmentation is mostly restricted to the entire back forming a thin line from the head to the caudal fin. Ontogenetically, this line becomes more expanded dorsoventrally and the spots tend to aggregate. As a consequence, in adult specimens (from 52 mm SL) the pigmentation consists of a strong, uniform and continuous brown band extending from the head back to the caudal fin. In several specimens (e.g. MCSNV IG.VR.57598, Fig. 2A), the eyeball is nearly circular and preserved as a dense carbon film; this organic film possibly consists of an accumulation of melanosome-like microbodies containing molecularly preserved melanin (see Lindgren et al., 2012). In the larval and juvenile specimens the scales are very thin and transparent so that the shape of the pigmented peritoneal membrane is visible. The preserved peritoneal membrane appears to be subtriangular in shape, elongate, lying between the pectoral and anal fins; the peritoneal membrane is rarely visible in the adult specimens because of the thickness of the scales.

Cololites—The cololites, or intestinal fossil contents, are visible in a few specimens (e.g. MCSNV IG.VR.57598, Fig. 2A); they are never coiled and lie in the abdominal region between the 5th or 6th pleural ribs and the anal fin and their distal end possibly terminates in correspondence of the anus. The cololites are relatively short possibly in relation to the zooplanktivorous diet typical of most clupeids (Whitehead, 1985).

Biometrical remarks—The large number of specimens examined allows us to test the homogeneity of the sample and, as a consequence, to confirm its assignment to a single species. Table 3 shows the mean biometrical parameters used for the description of the sample. These parameters allow to determine the specific biometrical data for the examined sample of †*Bolcaichthys catopygopterus*. Size-frequency histograms (Fig. 6) appear to be non-normally distributed and some of the distributions appear to be skewed. The regression lines with a high coefficient of determination (Table 4) indicate a good alignment of the points around the line (Figs. 7 and 8). The analysis of linear regression of the morphometric data confirmed that there was a strong significant relationship between standard length (or head length) and each of the morphometric characters ($p < 0.001$). In addition, high degree of positive correlation between standard length (or head length) and each morphometric character was indicated by high values of determination coefficient (r^2) that ranges from 0.84 to 1.00. The least squares regression suggests that there is a real dependence between the variables x and y; therefore, it is possible to reject the null hypothesis (no correlation between x and y) for each of the relationships between the variables x and y for which the estimated regression of the variables y on the variables x is highly significant.

Because the length at first maturity (L_m) is proportional to the maximum length of the fish (L_{max}) (Beverton, 1963), it is possible to estimate the mean length to discriminate between juvenile and adult specimens. Using the empirical equation for estimating the length at first maturity from the maximum body length (Binohlan and Froese, 2009), it is possible to estimate that †*Bolcaichthys catopygopterus* reached the length at first maturity at about 52 mm SL.

DISCUSSION

Comparison and relationships

The osteological, morphometric and meristic data support the assignment of the examined specimens to a new genus of the family Clupeidae from the Eocene of Monte Bolca. The anatomical analysis of the specimens documented herein has revealed the presence of several clupeomorph characters (Grande, 1985), including the presence of one or more abdominal scutes that crosses the ventral midline of the body, second hypural fused with the first ural centrum, and autogenous first hypural. The fusion of the first uroneural with the first preural centrum, the size reduction of the first ural centrum, as well as the separation of the parhypural from the first ural centrum suggest that the described material belongs to the suborder Clupeoidei. The assignment to the family Clupeidae is clearly supported by the presence of two long, rod-like postcleithra (Grande, 1985).

Due to the overall morphological similarity, the relationship between the clupeid genera is difficult to determine. Within the family Clupeidae, several authors (e.g., Grande, 1985; Whitehead, 1985) recognized five subfamilies (Pellonulinae, Dussumieriinae, Dorosomatinae, Clupeinae and Alosinae), of which only the Dussumieriinae and Pellonulinae are characterized by a diagnosis based on morphological features (Grande, 1985). Recent molecular studies, however, suggest that these groups may not be monophyletic (e.g., Lavoué et al. 2007; Li and Ortí, 2007).

The unique combination of meristic characters observed in †*Bolcaichthys* gen. nov. certainly supports its recognition as a new clupeid genus. †*Bolcaichthys* gen. nov. exhibits a complete series of pre-pelvic and post-pelvic scutes, plus a large pelvic scute between the pelvic fins. For this reason, it cannot be placed within the subfamily Dussumieriinae, whose members are characterized by the absence of pre-pelvic and post-pelvic scutes and the presence of a single W-shaped scute, immediately anterior to the pelvic fins (Grande, 1985; Whitehead, 1985). The placement of †*Bolcaichthys* gen. nov. in the subfamily Pellonulinae can be ruled out as well because the representatives of this group are characterized by the loss of the anterior supramaxilla. The Eocene †*Vectichthys* has two supramaxillae (see Gaudant and Quayle, 1988) but was considered as a pellonuline by Grande (1985) for the presence of separated first preural and first ural centra in the caudal skeleton. The monophyletic status of the three remaining subfamilies, Alosinae, Clupeinae, and Dorosomatinae, has not been demonstrated (Grande, 1985). Several authors (e.g., Regan, 1916, 1917; Miller, 1960; Whitehead, 1962, 1985; Nelson and Rothman, 1973) provided a detailed description of extant representatives of the subfamilies Dorosomatinae, Clupeinae and Alosinae based on external features and soft anatomy (e.g., the digestive tract). The deep-bodied dorosomatinae are characterized by the presence of a single supramaxilla (except for *Dorosoma* and *Signalosa* that possess two supramaxillae), long and filamentous last dorsal-fin ray, inferior mouth, dentary flared outward, and snout usually rounded and projecting. As documented above †*Bolcaichthys* gen. nov. has a body moderately elongate and tapered, mouth terminal, two supramaxillae, small and triangular dorsal fin without long and filamentous rays, and snout almost pointed, a combination of features than can exclude any assignment to the subfamily Dorosomatinae. There are no osteological arguments useful to distinguish the genera of the Alosinae from those of the Clupeinae. The structure of the gill arches could reveal some derived characters useful to distinguish the representatives of these two subfamilies of clupeids (Nelson, 1967; Grande, 1985); however, the preservation of the clupeid fishes from Monte Bolca does not allow the observation of these skeletal structures. According to Whitehead (1973, 1985), the Alosinae can be distinguished from the Clupeinae for the presence of moderate to large or very large body (from 200 to 600 mm SL), dorsal scutes present along back (e.g., *Ethmidium, Ethmalosa* and some species of *Pomolobus*), upper jaw frontally not rounded and characterized by a distinct notch into which the symphysis of the lower jaw fits. Following the diagnosis provided by Whitehead (1985), the assignment of †*Bolcaichthys* gen. nov. to the Alosinae can be excluded because of the absence of dorsal scutes and body size. The average size of the specimens from Monte Bolca is about 40–60 mm SL with the largest specimen that reaches 101 mm SL, evidently shorter than that of most Alosinae. As a consequence, †*Bolcaichthys* gen. nov. is tentatively assigned to the subfamily Clupeinae.

†*Bolcaichthys* gen. nov. differs from the other clupeine genera for its unique combination of meristic features (Table 5). It can be easily separated from *Clupea*, †*Chasmoclupea, Clupeonella, Escualosa, Platanichthys*, †*Primisardinella, Ramnogaster,*

Rhinosardinia, Sardinops, *Sardina*, †*Sarmatella, Sprattus*, and *Strangomera* for its reduced number of supraneurals (8 vs 9–19). †*Bolcaichthys* gen. nov. lacks the dorsal scutes characteristic of †*Gosiutichthys, Harengula, Herklotsichthys* and *Opisthonema*. Moreover, the number of preural vertebrae is useful to separate †*Bolcaichthys* gen. nov. (40 to 42) from *Amblygaster, Clupea*, *Opisthonema, Ramnogaster*, *Strangomera, Sardina*, *Sardinella, Sardinops*, †*Sarmatella*, *Sprattus*, †*Xyne* (43 to 57) and †*Gosiutichthys* (34–36). †*Bolcaichthys* gen. nov. has 15–16 dorsal-fin pterygiophores compared with the 10–13 of †*Chasmoclupea*, †*Gosiutichthys* and *Platanichthys* and 17–20 of *Amblygaster, Clupea, Opisthonema, Ramnogaster, Sardina, Sardinops, Sprattus*, and *Strangomera*. Finally, it has 15–16 anal-fin pterygiophores compared with the 10–14 of †*Gosiutichthys* and 17–22 of *Amblygaster, Clupeonella*, *Escualosa*, *Herklotsichthys*, *Opisthonema*, *Platanichthys, Ramnogaster, Sardinops*, *Sardina*, and *Strangomera*.

Paleobiological notes

Extant clupeids are typical pelagic, marine coastal inshore fishes, inhabiting tropical to cold-waters worldwide from 70°N to about 60°S where they form large monotypic schools that typically feed on zooplankton; some species inhabit the freshwaters of rivers or lakes (Whitehead, 1985).

As in many other fish groups, the larval, juvenile and adult stages of extant clupeids, like sardines and herrings, are very different in appearance from each other. Larval clupeids are elongated, with narrow, slender and transparent body, measuring few millimeters, and entirely lacking scales. After hatching, the journey of the pelagic larvae is primarily at the mercy of the prevailing currents, tides and wind. Not surprisingly, mortality is high during this stage, primarily because of predation or dispersal in habitat not suitable for the survival of the larvae (e.g., Hjort, 1914; Townsend, 1992). During the juvenile stage clupeids are a few dozen of millimeters long, their bodies begin to deepen and flatten, becoming semi-transparent and the scales start to form. The juvenile clupeids migrate shoreward entering shallow bays and inlets, grouping in dense schools near the surface or migrating vertically in the water column in response to light cycles (see Cognetti and Sarà, 1974). Adult marine clupeids migrate over great distances in open sea seasonally to feed and spawn, becoming totally pelagic (Moyle and Cech, 1992).

Because of the large number of available specimens for study, all the three developmental stages have been observed in the clupeine †*Bolcaichthys catopygopterus* (Fig. 9A-C). The larval stage, however, is represented by a single specimen 9.5 mm SL (MCSNV IG.VR.71432/71433). The alevin is elongate with a slender and narrow body. The pigmented peritoneum is strongly visible since the lack of scales makes the body transparent. The pigmentation of the body is localized in the back as a thin line running from the head to the caudal fin.

The mean ratio L_m/L_{max} for †*Bolcaichthys* is equal to 0.52, in agreement with the hypothesis that tropical and subtropical clupeoids reach their sexual maturity before those typical of high latitudes (see Beverton, 1963; Blaxter and Hunter, 1982). The majority (about 58%) of the available specimens ranges from about 15 to 52 mm SL, thereby representing juveniles. Their bodies begin to deepen and flatten, the scales start to cover the semi-transparent to almost completely non-transparent body. For this reason, the pigmented peritoneum becomes gradually less visible during the ontogeny.

The adult stage is represented by about 42% of the studied individuals, which measured from 52 to 101 mm SL. Their body is entirely covered with thick scales that do not allow the observation of the peritoneum and the external pigmentation consists of a strong, uniform and continuous dark band running from the head to the caudal fin progressively increasing latitudinally from the back to the mid-body height.

Moreover, because the size-frequency distribution (Fig. 6) shows that young fishes are not well-represented, as it would be expected in a population in which the young individuals are very abundant (Newbrey and Bozek, 2003). Therefore, it is possible that young †*Bolcaichthys* preferentially lived in other biotopes or, alternatively, that taphonomic biases prevented the preservation of young individuals.

The presence of mass mortality layers characterized by individuals of †*Bolcaichthys catopygopterus* (Woodward, 1901) almost of the same size (Fig. 10A-B) seems to be indicative of discrete mortality events that involved the entire school, thereby suggesting that this Eocene species formed monotypic assemblages with a behavior similar to that of extant marine clupeid fishes (Whitehead, 1985).

Paleoenvironmental remarks

Today, clupeids play a central role in the ecology of tropical and subtropical coastal marine environments (e.g., Longhurst and Pauly, 1987). These primarily zooplanktivorous fishes are extremely abundant in tropical and subtropical seas, where they are prominent converters of zooplankton also representing fundamental prey for higher trophic levels vertebrates. Ecological and trophic relationships of the Monte Bolca ichthyofauna were discussed by many authors who always considered the fish assemblage as the earliest example of a reefal or peri-reefal fish assemblage in the fossil record (e.g., Bellwood, 1996; Landini and Sorbini, 1996).

Considering its abundance in the fish assemblage of Monte Bolca and its consequent relevant ecological role in the original paleobiotope, the potential paleoenvironmental role of †*Bolcaichthys catopygopterus* (Woodward, 1901) has been traditionally neglected or underestimated. The depositional paleoenvironment of Monte Bolca was discussed by a number of authors in the past decades, resulting in a series of interpretative reconstructions, all of which more or less closely related to a coral reef context. Sorbini (1968) and Massari and Sorbini (1975) hypothesized that the fish-bearing micritic limestone was deposited in a tropical coastal lagoon close to coral reefs. According to Landini and Sorbini (1996), the fossiliferous deposits originated in a silled depression parallel to the coast and in proximity to coral reefs, periodically subjected to bottom anoxia. In such a paleoenvironmental scenario, the influence of the open sea is clearly demonstrated by the presence of a large number of pelagic fishes, including clupeoids and scombroids. More recently, based on facies analysis, Papazzoni and Trevisani (2006) suggested that the fossiliferous limestone was deposited in a subtropical lagoon affected by periodical changes of water circulation that influenced the oxygen content on the bottom.

As documented above, during their juvenile phase, clupeids migrate shoreward entering shallow bays and inlets, while adults tend to become totally pelagic (e.g., Blaxter and Hunter, 1982; Munroe, 2000). Although not all the authors agree with the hypothesis of a depositional environment in close proximity with a coral reef system, most of them concur to suggest that the sediments originated in a depressed and moderately deep basin, near to coast and characterized by reduced circulation of water in a tropical or subtropical context. The presence of a large number of both adult and juvenile individuals of the clupeine †*Bolcaichthys catopygopterus* (Woodward, 1901), however, appears to confirm the paleoenvironmental model proposed by Landini and Sorbini (1996), providing further evidence of the reduced distance from the coast line as well as of the remarkable ecological influence of the open sea.

SUMMARY

Osteological, morphometric and meristic analysis of the clupeoid fishes from Monte Bolca revealed that a single taxon, the clupeine †*Bolcaichthys catopygopterus* (Woodward, 1901) is by far the most common clupeoid, and, more generally, the most common taxon, within the Monte Bolca fish assemblage. The presence of marine coastal and schooling clupeids in the fish assemblage of Monte Bolca confirms the hypothesis that the fish-bearing micritic limestone was deposited in a paleoenvironmental context close to the coast, and notably subject to open sea influences.

Because of its abundance, †*Bolcaichthys catopygopterus* (Woodward, 1901) certainly played a key role in the Monte Bolca paleobiotope. Such a relevant ecological role should necessarily be taken into account in future paleoecological and paleoenvironmental studies dealing with this celebrated Fossil-Lagerstätte.

ACKNOWLEDGMENTS

The authors thank A. Vaccari and R. Zorzin (MCSNV), G. Teruzzi (MSNM), M. Fornasiero (MGPUP), D. Ormezzano (MRSN), E. Bernard and M. Richter (both at NHMUK) for access to fossil material under their care. We thank also A. Acquaotta (Università degli Studi di Torino) for her advice in the statistical analysis of data. Thanks are also due to F. Chilese (Verona) for his hospitality during visit to Verona by one of the authors (G. M.) and to S. Giacomel (Toronto) for improvement of the English. This work was supported by grants (ex-60% 2012) to G. C. from the Università degli Studi di Torino.

LITERATURE CITED

Agassiz, L. 1833–44. Recherches sur les poissons fossiles. Petitpierre, Neuchâtel, 1420 pp.

Agassiz, L. 1835. Kritische Revision der in der Ittiologia Veronese abgebildeten fossile Fische. Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefakenkunde, Jahrgang, 1835:290–316.

Bannikov, A. F. 2008. Revision of the atheriniform fish genera *Rhamphognathus* Agassiz and *Mesogaster* Agassiz (Teleostei) from the Eocene of Bolca, northern Italy. Studi e Ricerche sui Giacimenti Terziari di Bolca 9:65–76.

Bannikov, A. F., and G. Carnevale. 2009. A new percoid fish from the Eocene of Monte Bolca, Italy: *Hendrixella grandei* gen. & sp. nov. Swiss Journal of Geosciences 102:481–488.

Bannikov, A. F., and G. Carnevale. 2010. *Bellwoodilabrus landinii*, a new genus and species of labrid fish (Teleostei: Perciformes) from the Eocene of Monte Bolca. Geodiversitas 32:201–220.

Bannikov, A. F., and G. Carnevale. 2011. Enigmatic spiny-rayed fish from the Eocene of Monte Bolca. Geological Journal 46:52–62.

Bannikov, A. F., and G. Carnevale. 2012. *Frippia labroiformis* gen. et sp. nov., a new perciform fish from the Eocene of Pesciara di Bolca, Italy. Bollettino della Società Paleontologica Italiana 51:155–165.

Barbieri, G., and F. Medizza. 1969. Contributo alla conoscenza geologica della regione di Bolca (Monte Lessini). Memorie dell’Istituto di Geologia e Mineralogia dell’Università di Padova 27:1–36.

Bassani, F. 1897. Aggiunte all’ittiofauna eocenica dei Monti Bolca e Postale. Palaeontographia Italica 3:77–88.

Baykina, E. M. 2013. A revision of *Clupea doljeana* Kramberger and *Sarmatella vukotinovici* (Kramberger) (Pisces, Clupeidae) from the Sarmatian of Croatia. Paleontological Journal 47:523–532.

Bellwood, D. R. 1996. The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage. Coral Reefs 15:11–19.

Beverton, R. J. H. 1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. Rapports et procès-verbaux des réunions. Conseil Permanent International pour l'Exploration de la Mer 154:44–67.

Binohlan, C., and R. Froese. 2009. Empirical equation for estimating maximum length from length at first maturity. Journal of Applied Ichthyology 25:611–613.

Blaxter, J. H. S., and J. R. Hunter. 1982. The biology of the clupeoid fishes. Advances in Marine Biology 20:1–223.

Blot, J. 1980. La faune ichthyologique des gisements du Monte Bolca (Province de Verone, Italie). Catalogue systématique présentant l'état actuel des recherches concernant cette faune. Bulletine du Museum d'Histoire Naturelle de Paris 2:339–396.

Carnevale, G., and T. W. Pietsch. 2009. An Eocene frogfish from Monte Bolca, Italy: the earliest skeletal record for the family. Palaeontology 52:745–752.

Carnevale, G., and T. W. Pietsch. 2010. Eocene handfishes from Monte Bolca, with description of a new genus and species, and a phylogeny of the family Brachionichthyidae (Teleostei: Lophiiformes). Zoological Journal of the Linnean Society 160:621–647.

Carnevale, G., and T. W. Pietsch. 2011. Batfishes from the Eocene of Monte Bolca. Geological Magazine 148:461–472.

Carnevale, G., and T. W. Pietsch. 2012. †*Caruso*, a new genus of anglerfishes from the Eocene of Monte Bolca, Italy, with a comparative osteology and phylogeny of the teleost family Lophiidae. Journal of Systematic Palaeontology 10:47–72.

Cognetti, G., and M. Sarà. 1974. Biologia marina. Calderini, Bologna, 440 pp.

Cuvier, G. 1817. Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Les reptiles, les poissons, les mollusques et les annlé1ides. A. Belin, Paris, Vol. 2, 532 pp.

Daniltshenko, P. G. 1968. Fish of the Upper Palaeocene of Turkmenistan. In Ocherki po filogenii i sistematike iskopaemykh ryb i beschelyustnykh. Nauka, Moscow, 113–156. [in Russian]

Day, J. J. 2003. Evolutionary relationships of the Sparidae (Teleostei: Percoidei): integrating fossil and Recent data. Transactions of the Royal Society of Edinburgh: Earth Sciences 93:333–353

Eastman, C. R. 1905. Les types de poissons fossiles du Monte Bolca au Muséum d'Histoire Naturelle de Paris. Mémoires de la Société Géologique de France 3:1–33.

Fabiani, R. 1914. La serie stratigrafica del Monte Bolca e dei suoi dintorni. Memorie dell'Istituto di Geologia della Regia Università di Padova 2:223–235.

Fabiani, R. 1915. Il Paleogene del Veneto. Memorie dell'Istituto di Geologia della Regia Università di Padova 3:1–336.

Figueiredo, F. J. 2009. A new marine clupeoid fish from the Lower Cretaceous of the Sergipe-Alagoas Basin, northeastern Brazil. Zootaxa 2164:21–32.

Friedman, M. 2012. Osteology of †*Heteronectes chaneti* (Acanthomorpha, Pleuronectiformes), an Eocene stem flatfish, with a discussion of flatfish sister-group relationships. Journal of Vertebrate Paleontology 32:735–756.

Gaudant, J., and W. J. Quayle. 1988. New palaeontological studies on the Chapelcorner Fish Bed (Upper Eocene, Isle of Wight). Bulletin of the British Museum, Natural History (Geology) 44:15–39.

Grande, L. 1982a. A revision of the fossil genus †*Diplomystus*, with comments on the interrelationships of Clupeomorph fishes. American Museum Novitates 2728:1–34.

Grande, L. 1982b. A revision of the fossil genus †*Knightia*, with a description of a new genus from Green River Formation (Teleostei, Clupeidae). American Museum Novitates 2731:1–22.

Grande, L. 1985. Recent and fossil clupeomorph fishes with materials for revision of the subgroups of clupeoids. Bulletin of the American Museum of Natural History 181:231–372.

Greenwood, P. H., D. E. Rosen, S. H. Weitzman, and G. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bulletin of the American Museum of Natural History 131:339–456.

Hammer, Ø., D. A. T. Harper, and P. D. Ryan. 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4:1–9. Available at http://folk.uio.no/ohammer/past. Accessed April 03, 2014.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in light of biological research. Rapports et procès-verbaux des réunions. Conseil Permanent International pour l'Exploration de la Mer 20:1–8.

Hubbs, C. L., and K. L. Lagler. 1958. Fishes of the Great Lakes region. Cranbrook Institute of Science Bulletin 26:1–213.

International Code of Zoological Nomenclature. 1999. International Commission of Zoological Nomenclature Fourth Edition [Incorporating Declaration 44, amendment of Article 74.7.3, with effect from 31 December 1999 and the Amendment on e-pubblication, amendment to Articles 8, 9, 10, 21 and 78, with effect from 1 January 2012]. Http://iczn.org/iczn/index.jsp.

Landini, W., and L. Sorbini. 1996. Ecological and trophic relationships of Eocene Monte Bolca (Pesciara) fish fauna. In Cerchi A., ed. Autecology of selected fossil organisms:

achievement and problems. Bollettino della Società Paleontologica Italiana, Special Volume 3:105–112.

Lavoué, S., M. Miya, K. Saitoh, N. B. Ishiguro, and M. Nishida. 2007. Phylogenetic relationships among anchovies, sardines, herrings and their relatives (Clupeiformes), inferred from whole mitogenome sequenze. Molecular Phylogenetics and Evolution 43:1096–1105.

Li, C., and G. Ortí. 2007. Molecular phylogeny of Clupeiformes (Actinopterygii) inferred from nuclear and mitochondrial DNA sequenze. Molecular Phylogenetics and Evolution 44:386–398.

Lindgren, J., P. Uvadl, P. Sjövall, D. E. Nilsson, A. Engdahl, B. P. Schultz, and V. Thiel. 2012. Molecular preservation of the pigment melanin in fossil melanosomes. Nature Communications 3:1–824.

Linnaeus, K. 1758. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata. Holmiae: Laurentii Salvii, 824 pp.

Lioy, P. 1866. Sulle clupee fossili di Bolca. Atti della Società Italiana di Scienze Naturali 8:410–414.

Longhurst, A., and D. Pauly. 1987. Ecology of Tropical Oceans. Academic Press, San Diego, 407 pp.

Marramà, G., and G. Carnevale. In press. Eocene round herring (Teleostei: Clupeidae) from Monte Bolca. Acta Palaeontologica Polonica.

Massari, F., and L. Sorbini. 1975. Aspects sedimentologiques des couches à poissons de l’Eocene de Bolca (Vérone-Nord Italie). In IXe Congrès International de Sedimentologie, Nice, 55–61.

Miller, R. R. 1960. Systematics and biology of the gizzard shad (*Dorosoma cepedianum*) and related fishes. Fishery Bulletin 60:371–392.

Monsch, K. A. 2006. A revision of scombrid fishes (Scombroidei, Perciformes) from the middle Eocene of Monte Bolca, Italy. Palaeontology 49:873–888.

Moyle, P. B., and J. J. Cech. 1992. Fishes, an introduction to Ichthyology, Second Edition. Prentice Hall, New Jersey, 559 pp.

Munroe, T. 2000. An overview of the biology, ecology, and fisheries of the clupeoid fishes occurring in the Gulf of Maine. Northeast Fisheries Science Center Reference Document 00–02:1–226.

Murray, A. M., E. L. Simons, and Y. S. Attia. 2005. A new clupeid fish (Clupeomorpha) from the Oligocene of Fayum, Egypt, with notes on some other fossil clupeomorphs. Journal of Vertebrate Paleontology 25:300–308.

Nelson, G. J. 1967. Gill arches of teleostean fishes of the family Clupeidae. Copeia 2:389–399.

Nelson, G., and M. N. Rothman. 1973. The species of gizzard shads (Dorosomatinae) with particular reference to the Indo-Pacific region. Bulletin of the American Museum of Natural History 150:133–206.

Newbrey M. G., and M. A. Bozek. 2003. Age, growth, and mortality of *Joffrichthys triangulpterus* (Teleostei: Osteoglossidae) from the Paleocene Sentinel Butte Formation, North Dakota, U.S.A. Journal of Vertebrate Paleontology 23:494–500.

Papazzoni, C. A., and E. Trevisani. 2006. Facies analysis, paleoenvironmental reconstruction and biostratigraphy of the ‘Pesciara di Bolca’ (Verona, northern Italy): an early Eocene Fossil-Lagerstätte. Palaeogeography, Palaeoclimatology, Palaeoecology 242:21–35.

Patterson, C., and D. E. Rosen. 1977. Review of the ichthyodectiforms and other Mesozoic teleost fishes and the theory and practice of classifying fossils. Bulletin of the American Museum of Natural History 158:81–172.

Phillips, J. B. 1942. Osteology of the sardine (Sardinops caerulea). Journal of Morphology 70:463–500.

Regan, C. T. 1916. The British fishes of the subfamily Clupeinae and related species in other seas. Annals and Magazine of Natural History 18:1–19.

Regan, C. T. 1917. A revision of the clupeoid fishes of the genera *Pomolobus, Brevoortia* and *Dorosoma* and their allies. Annals and Magazine of Natural History 19:297–316.

Ridewood, W. G. 1904. On the cranial osteology of the clupeoid fishes. Proceeding of the Zoological Society of London 2:448–493.

Seilacher, A., W. -E. Reif, and F. Westphal. 1985. Sedimentological, ecological and temporal patterns of fossil Lagerstätten. Philosophical Transactions of the Royal Society of London B 311:5–24.

Serra-Kiel, J., L. Hottinger, E. Caus, K. Drobne, C. Ferràndez, A. K. Jauhri, G. Less, R. Pavlovec, J. Pignatti, J. M. Samsó, H. Schaub, E. Sirel, A. Strougo, Y. Tambareau, J. Tosquella, and E. Zakrevskaya. 1998. Larger foraminiferal biostratigraphy of the Tethyan Paleocene and Eocene. Bulletin de la Société Géologique de France 169:281–299.

Sorbini, L. 1968. Contributo alla sedimentologia della ‘Pesciara’ di Bolca. Bollettino del Museo Civico di Storia Naturale di Verona 15:213–221.

Toombs, H. A., and A. E. Rixon. 1959. The use of acids in the preparation of vertebrate fossils. Curator 2:304–312.

Townsend, D. 1992. Ecology of larval herring in relation to the oceanography of the Gulf of Maine. Journal of Plankton Research 14:467–493.

Trevisani, E., C. A. Papazzoni, E. Ragazzi, and G. Roghi. 2005. Early Eocene amber from the 'Pesciara di Bolca' (Lessini Mountains, Northern Italy). Palaeogeography, Palaeoclimatology, Palaeoecology 223:260–274.

Tyler, J. C., and A. F. Bannikov. 1997. Relationships of the fossil and Recent genera of rabbitfishes (Acanthuroidei: Siganidae). Smithsonian Contributions to Paleobiology 84:1–35.

Tyler, J. C., and F. Santini. 2002. Review and reconstructions of the tetraodontiform fishes from the Eocene of Monte Bolca, Italy, with comments on related Tertiary taxa. Studi e Ricerche sui giacimenti Terziari di Bolca 9:47–120.

Weitzman, S. H. 1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family. Stanford Ichthyological Bulletin 8:1–77.

Whitehead, P. J. P. 1962. A review of the Indo-Pacific gizzard shad genera *Nematalosa*, *Clupanodon* and *Konosirus* (Pisces: Dorosomatidae). Bulletin of the British Museum, Natural History (Zoology) 9:87–102.

Whitehead, P. J. P. 1973. Clupeoid fishes of the Guianas. Bulletin of the British Museum, Natural History (Zoology), suppl. 5:1–227.

Whitehead, P. J. P. 1985. Clupeoid fishes of the world. (Suborder Clupeoidei). Part.1. Chirocentridae, Clupeidae and Pristigasteridae. FAO Species Catalogue 7:1–303.

Whitehead, P. J. P., and G. G. Teugels. 1985. The West African pygmy herring *Sierrathrissa leonensis*: General features, visceral anatomy and osteology. American Museum Novitates 2835:1–44.

Woodward, A. S. 1901. Catalogue of Fossil Fishes in the British Museum (Natural History), 4: Containing the Actinopterygian Teleostomi of the Suborders Isospondyli (in part), Ostariophysi, Apodes, Percesoces, Hemibranchii, Acanthopterygii and Anacanthini. London, Taylor and Francis, 636 pp.

Zigno, A. De 1874. Catalogo Ragionato dei Pesci Fossili del Calcare Eoceno di M. Bolca e M. Postale. Stabilimento Tipografia Grimaldo e C., Venezia, 215 pp.

Submitted April 05, 2014; accepted January 26, 2015

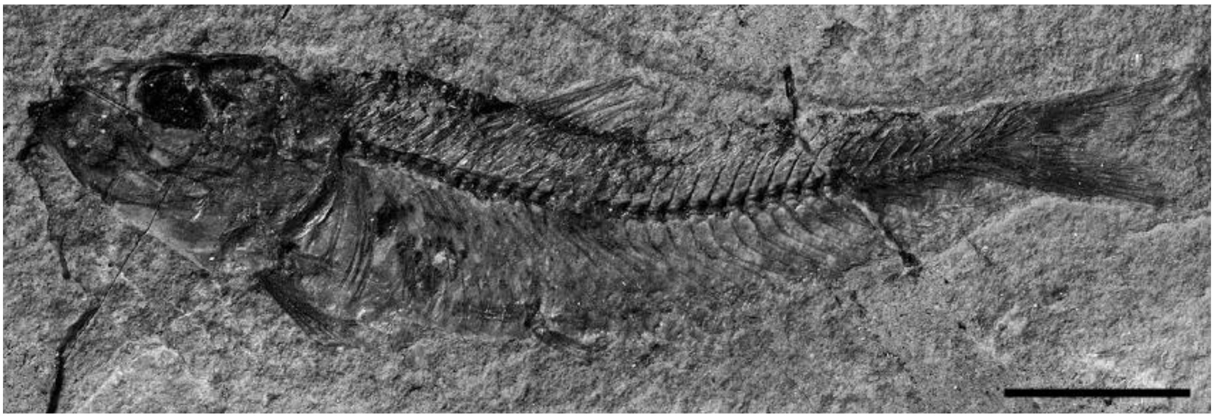


FIGURE 1. †*Bolcaichthys catopygopterus* (Woodward, 1901); holotype, NHMUK P.3829a. Scale bar equals 10 mm.

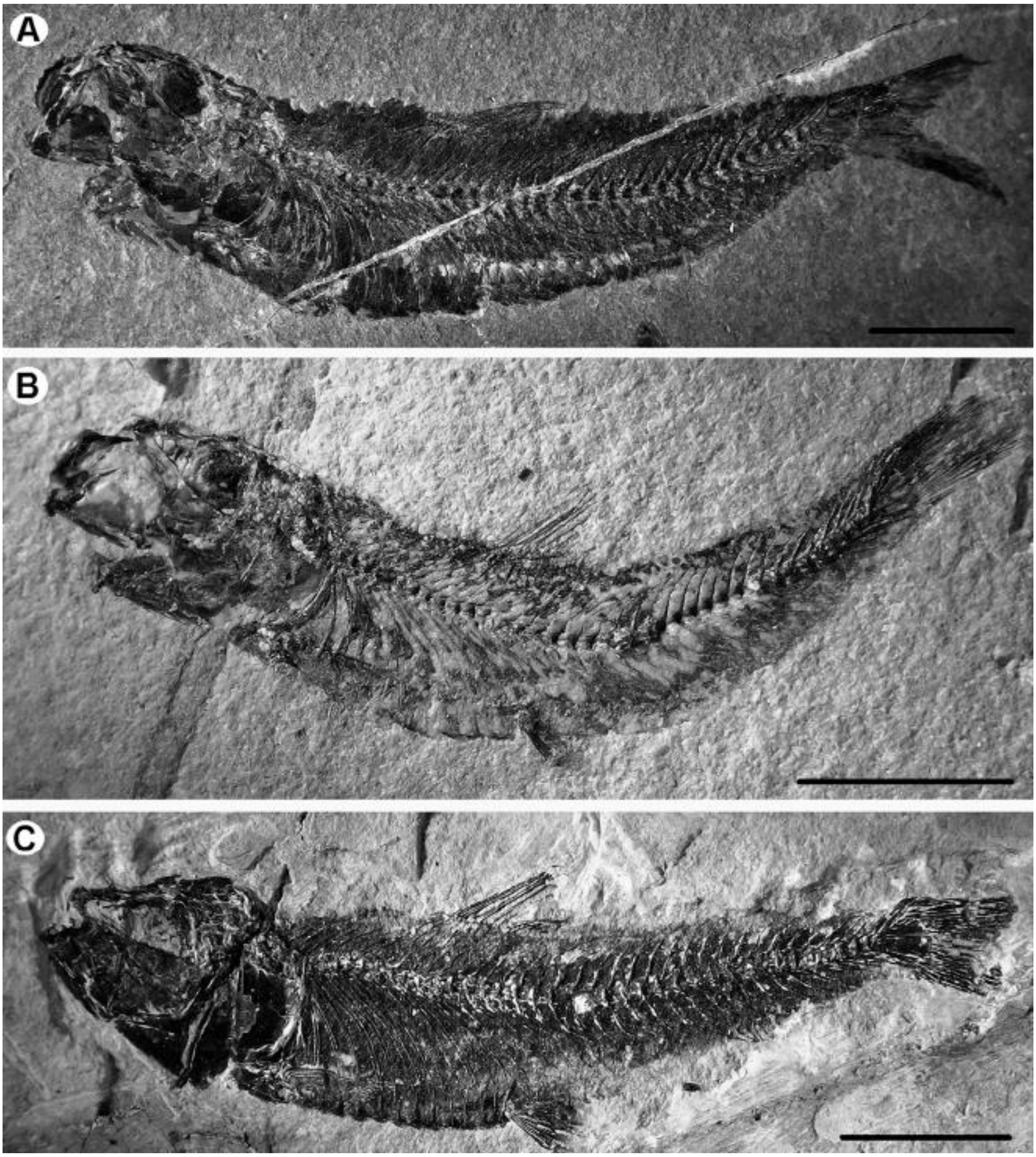


FIGURE 2. †*Bolcaichthys catopygopterus* (Woodward, 1901); A. MCSNV IG.VR.57598; B. MCSNV IG.VR.71407; C. MCSNV T.361. Scale bars equal 10 mm.

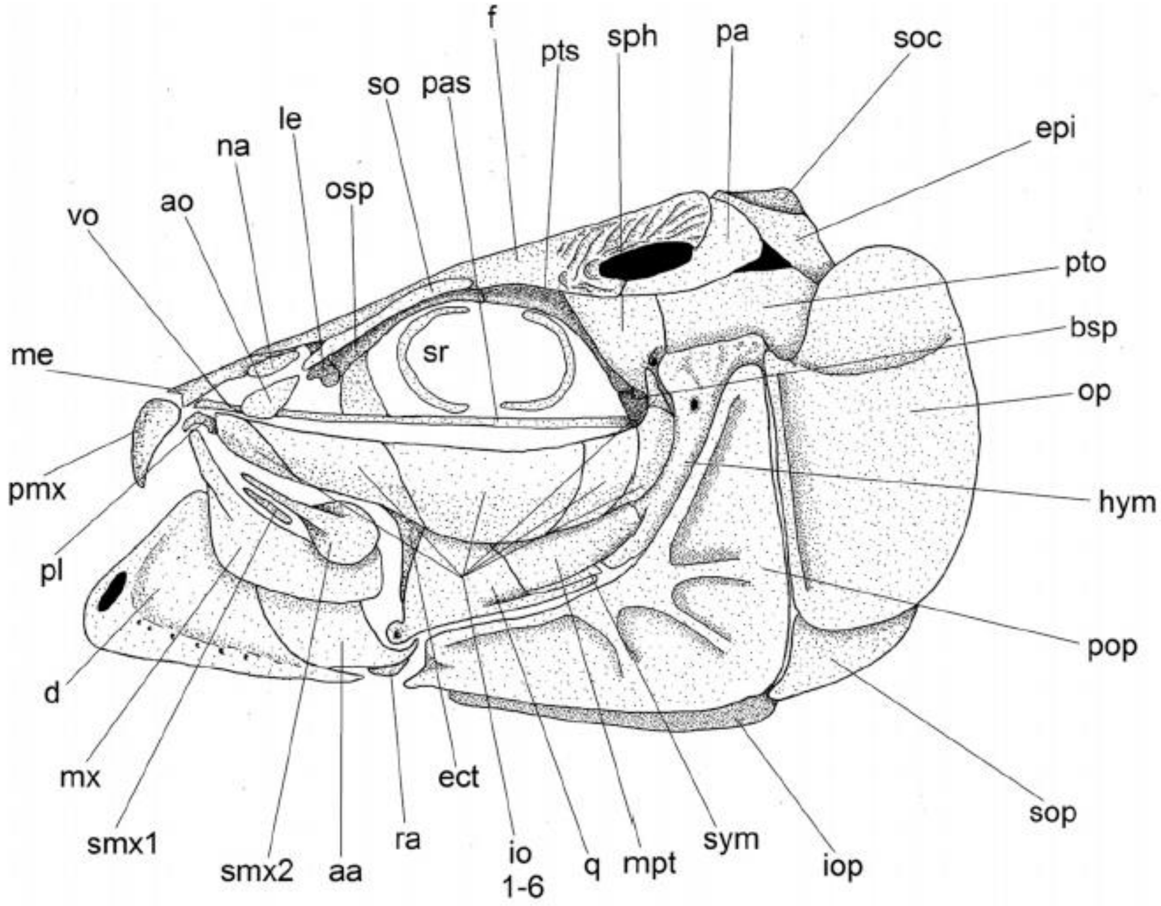


FIGURE 3. †*Bolcaichthys catopygopterus* (Woodward, 1901); reconstruction of the head primarily based on specimens MCSNV IG.37584/37585, MCSNV IG.VR.71407/71408 and MCSNV T.361.

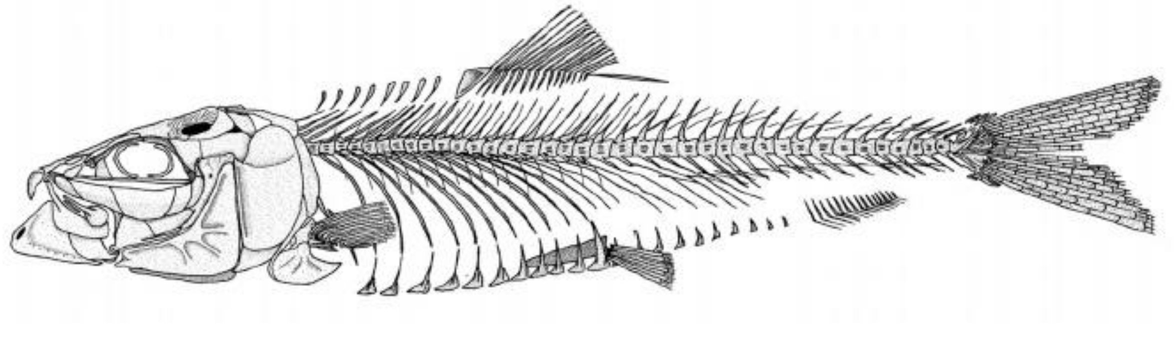


FIGURE 4. †*Bolcaichthys catopygopterus* (Woodward, 1901); reconstruction of the skeleton primarily based on specimens MCSNV IG.37584/37585, MCSNV IG.VR.71407/71408 and MCSNV T.361.

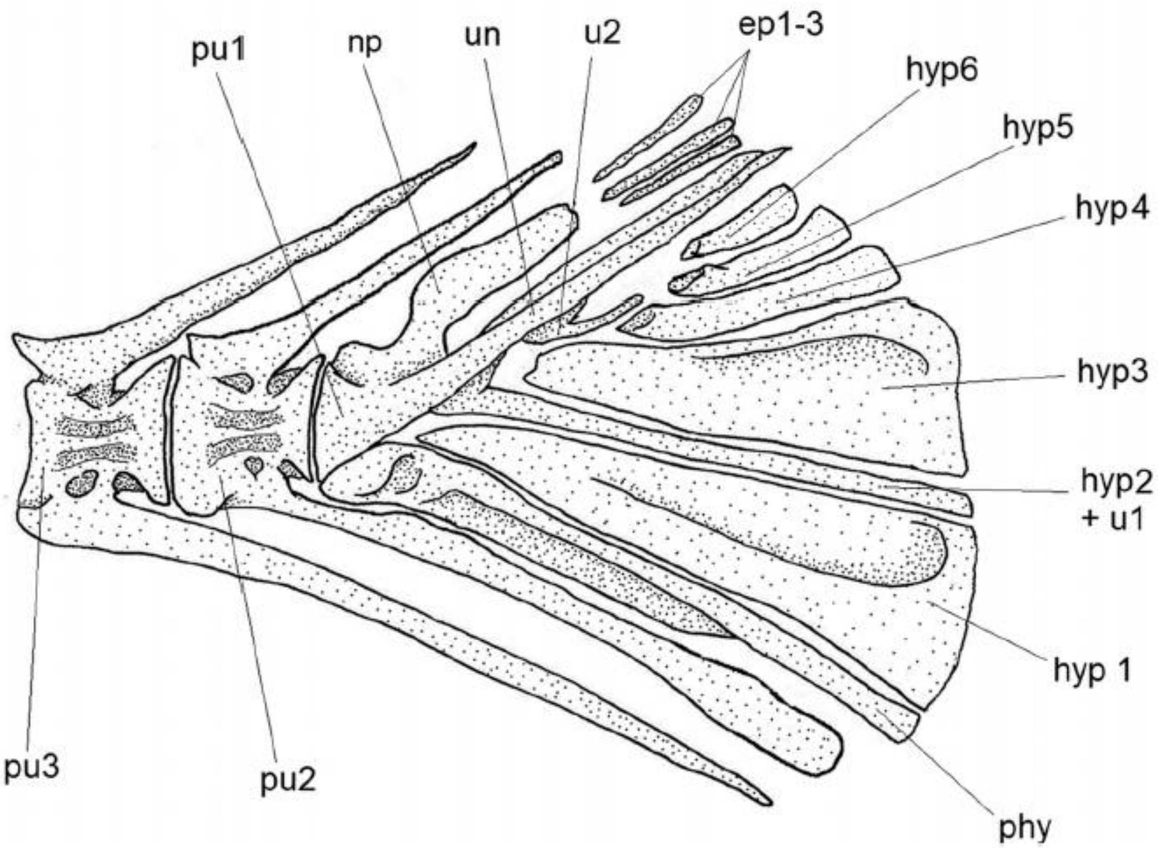


FIGURE 5. †*Bolcaichthys catopygopterus* (Woodward, 1901); reconstruction of the caudal skeleton primarily based on specimens MCSNV IG.37584/37585, MCSNV IG.VR.71407/71408 and MCSNV T.361.

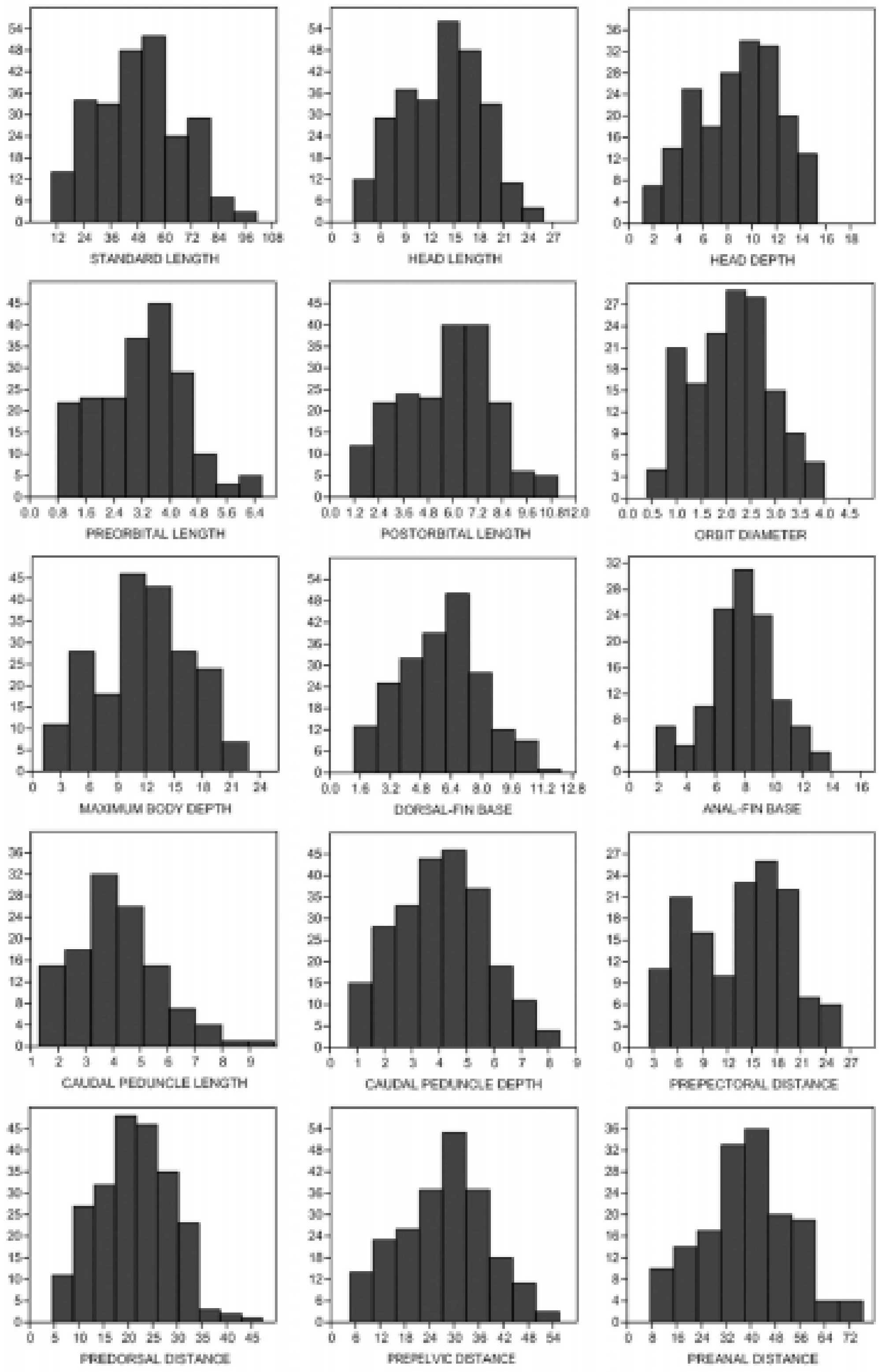


FIGURE 6. Size-frequency distributions for each morphometric character of †*Bolcaichthys catopygopterus* (Woodward, 1901); all measurements in mm and the y-axis represents relative frequency.

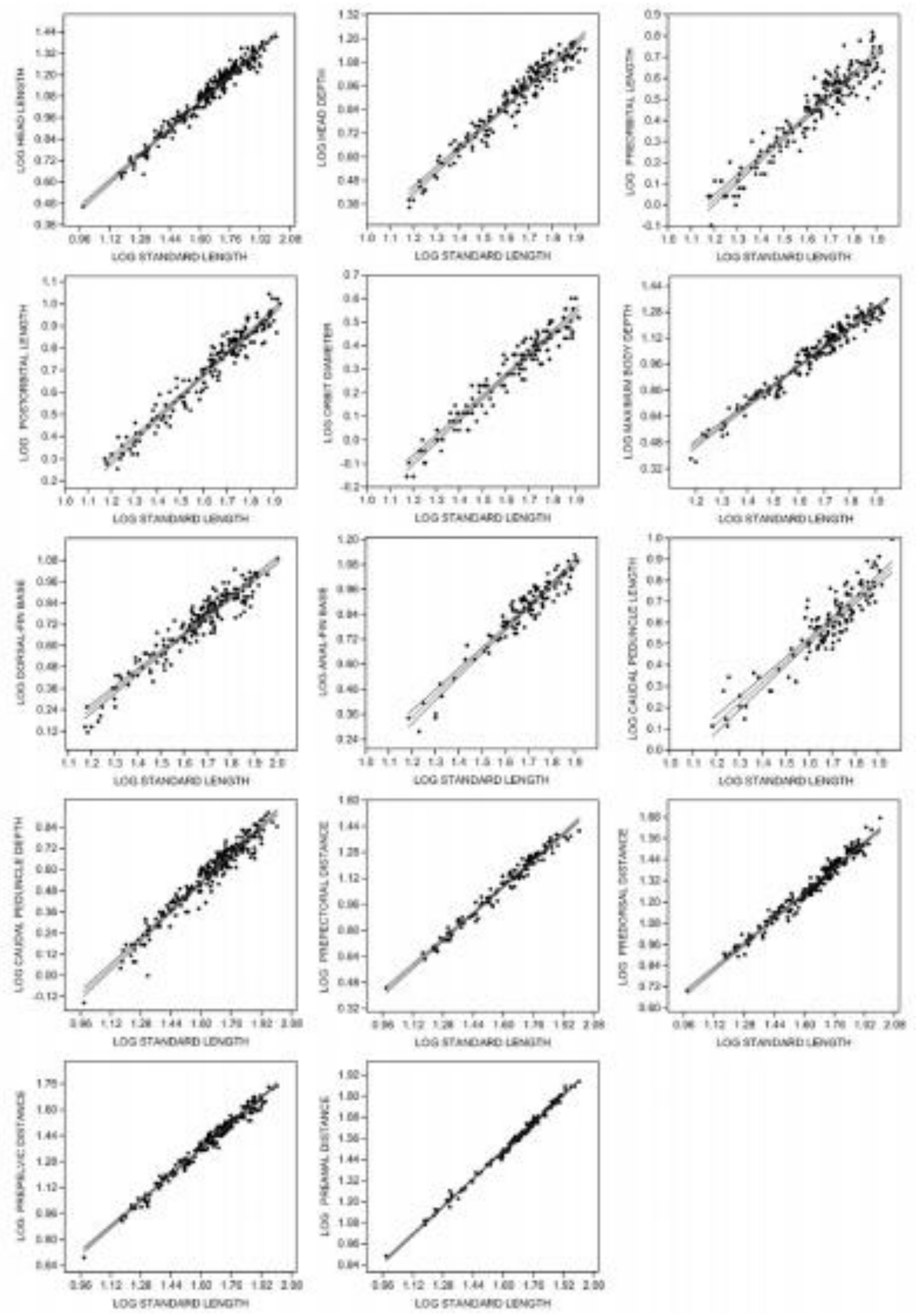


FIGURE 7. Scatterplots and regression lines with 95% confidence bands of the relationships between each morphometric character and the standard length of †*Bolcaichthys catopygopterus* (Woodward, 1901).

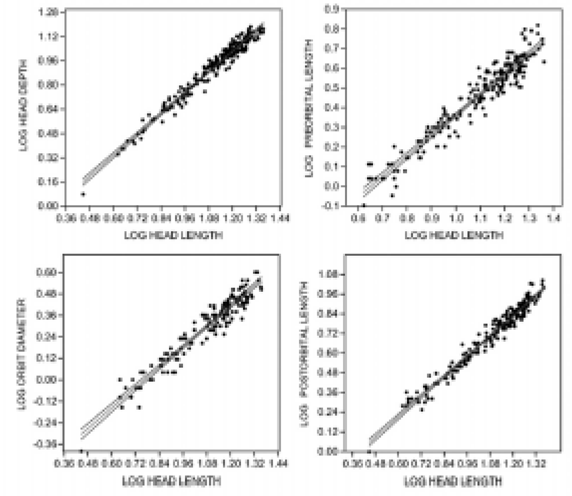


FIGURE 8. Scatterplots and regression lines with 95% confidence bands of the relationships between each morphometric character of the cranium and the head length of †*Bolcaichthys catopygopterus* (Woodward, 1901).

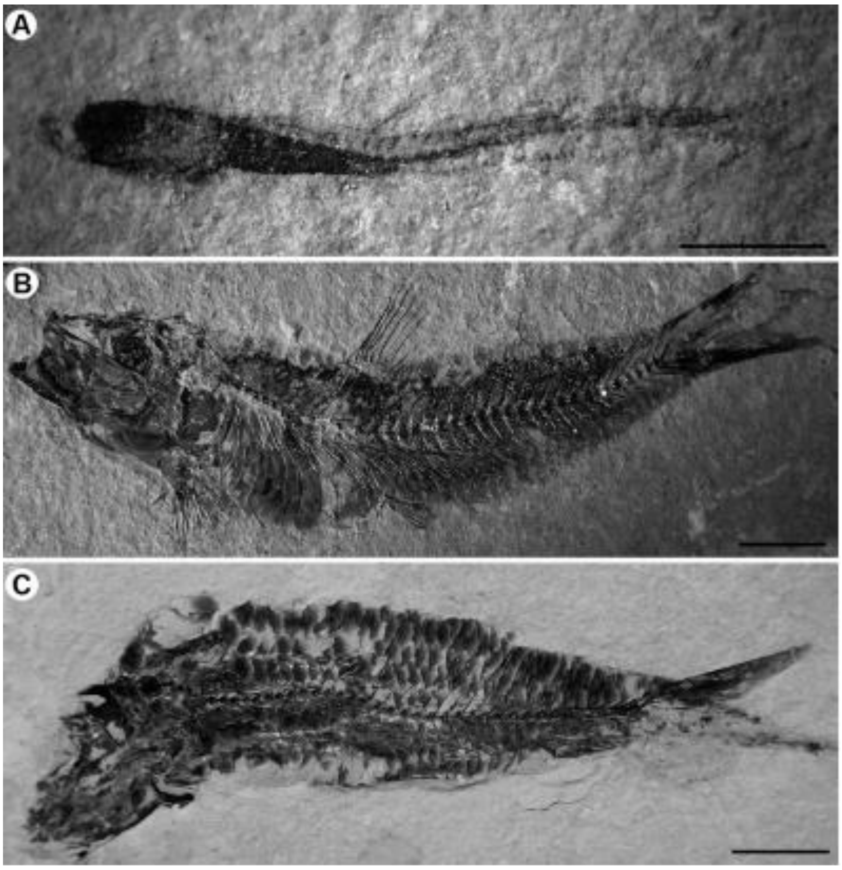


FIGURE 9. Ontogenetic series of †*Bolcaichthys catopygopterus* (Woodward, 1901). **A,** larva, MCSNV IG.VR.71433, scale bar equals 2 mm. **B**, juvenile, MCSNV IG.37584, scale bar equals 5 mm; **C**, adult, MCSNV IG.145058a, scale bar equals 10 mm.

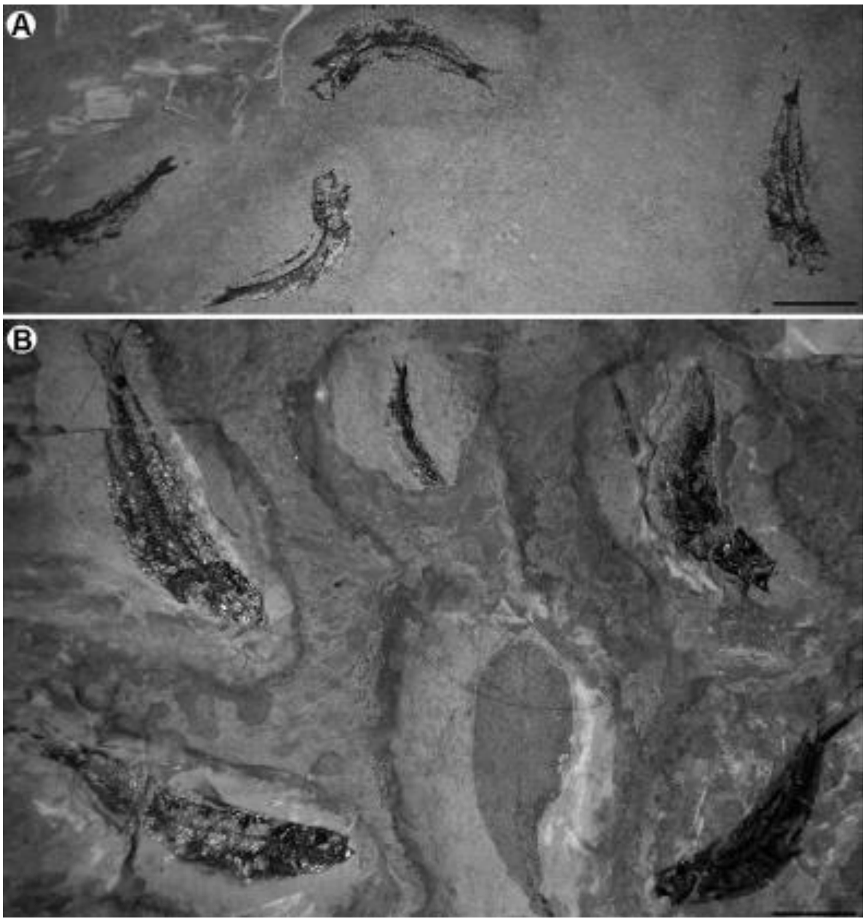
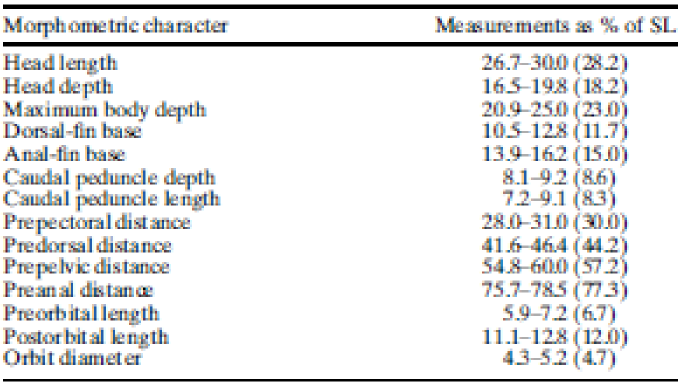
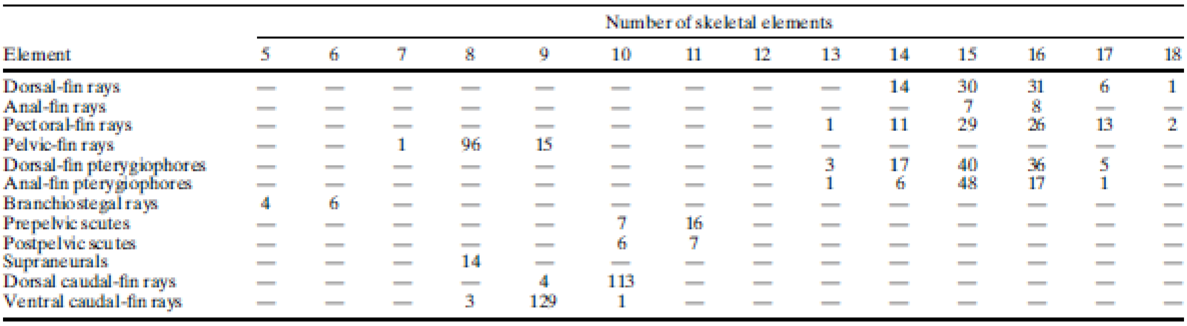


FIGURE 10. Mass mortalities levels involving †*Bolcaichthys catopygopterus* (Woodward, 1901). **A,** MSNM V164; **B**, MSNM V342. Scale bars equal 20 mm.



Morphometric character	Measurements as % of SL
Head length	26.7–30.0 (28.2)
Head depth	16.5–19.8 (18.2)
Maximum body depth	20.9–25.0 (23.0)
Dorsal-fin base	10.5–12.8 (11.7)
Anal-fin base	13.9–16.2 (15.0)
Caudal peduncle depth	8.1–9.2 (8.6)
Caudal peduncle length	7.2–9.1 (8.3)
Prepectoral distance	28.0–31.0 (30.0)
Predorsal distance	41.6–46.4 (44.2)
Prepelvic distance	54.8–60.0 (57.2)
Preanal distance	75.7–78.5 (77.3)
Preorbital length	5.9–7.2 (6.7)
Postorbital length	11.1–12.8 (12.0)
Orbit diameter	4.3–5.2 (4.7)

TABLE 1. Morphometric data (measurements as percentage of SL, mean values in parentheses) for †*Bolcaichthys catopygopterus* (Woodward, 1901).

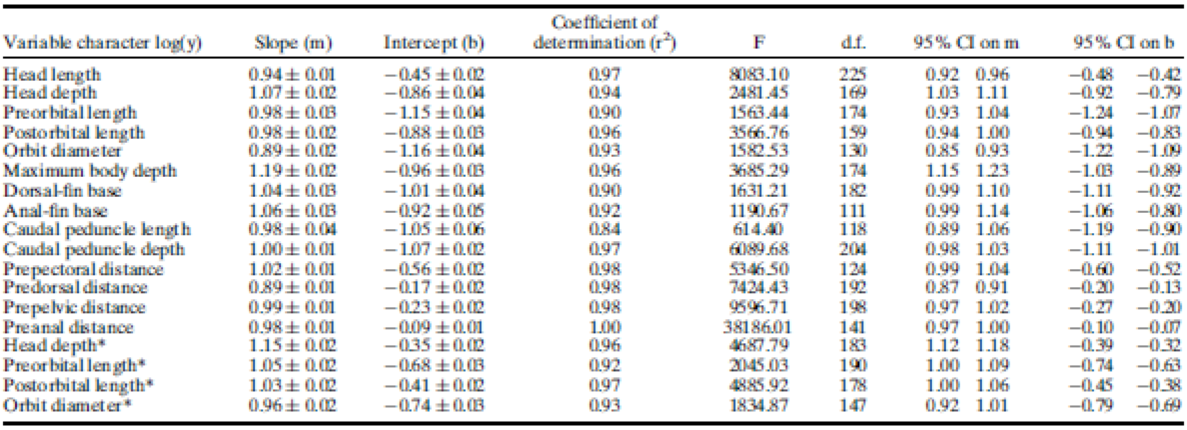


	Number of skeletal elements													
Element	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Dorsal-fin rays	—	—	—	—	—	—	—	—	—	14	30	31	6	1
Anal-fin rays	—	—	—	—	—	—	—	—	—	—	7	8	—	—
Pectoral-fin rays	—	—	—	—	—	—	—	—	1	11	29	26	13	2
Pelvic-fin rays	—	—	1	96	15	—	—	—	—	—	—	—	—	—
Dorsal-fin pterygiophores	—	—	—	—	—	—	—	—	3	17	40	36	5	—
Anal-fin pterygiophores	—	—	—	—	—	—	—	—	1	6	48	17	1	—
Branchiostegal rays	4	6	—	—	—	—	—	—	—	—	—	—	—	—
Prepelvic scutes	—	—	—	—	—	7	16	—	—	—	—	—	—	—
Postpelvic scutes	—	—	—	—	—	6	7	—	—	—	—	—	—	—
Supraneurals	—	—	—	14	—	—	—	—	—	—	—	—	—	—
Dorsal caudal-fin rays	—	—	—	—	4	113	—	—	—	—	—	—	—	—
Ventral caudal-fin rays	—	—	—	3	129	1	—	—	—	—	—	—	—	—

TABLE 2. Meristic information for †*Bolcaichthys catopygopterus* (Woodward, 1901); n is listed for each category, "-" indicates 0 specimens.

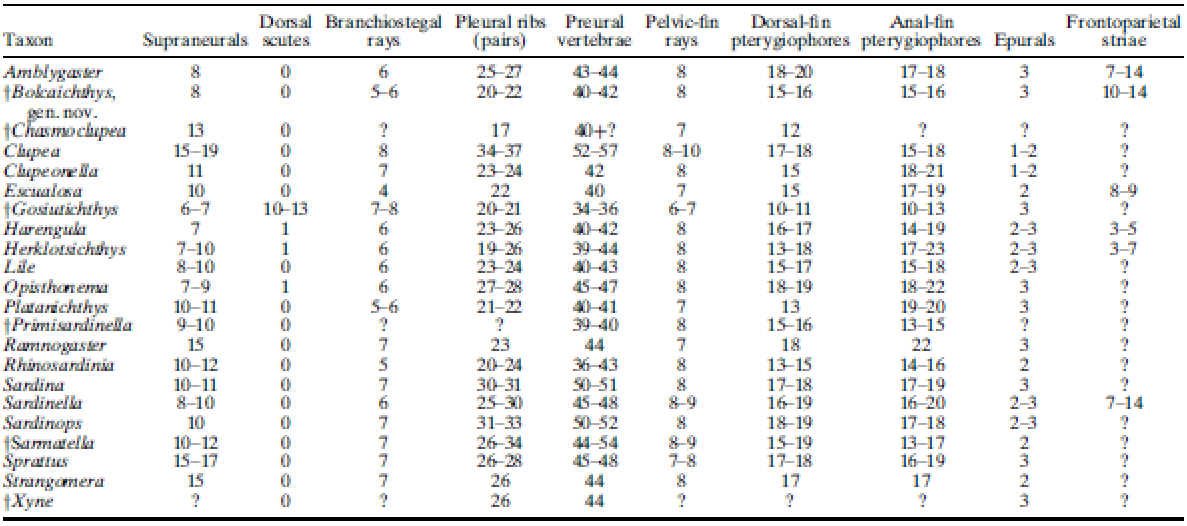
Dimension	Min	Max	Mean	Median	Variance	SD
Standard length	9.5	101.1	48.4	48.1	354.8	18.8
Head length	2.8	25.9	13.5	14.0	23.5	4.9
Head depth	1.2	15.3	8.9	9.2	11.1	3.3
Preorbital length	0.8	6.6	3.2	3.3	1.5	1.2
Postorbital length	1.0	10.6	5.6	5.9	4.8	2.2
Orbit diameter	0.4	4.0	2.1	2.2	0.6	0.8
Maximum body depth	1.2	22.8	11.9	11.9	22.5	4.7
Dorsal-fin base	1.3	12.2	5.9	6.0	4.6	2.1
Anal-fin base	1.9	13.9	7.8	8.0	5.9	2.4
Caudal peduncle length	1.3	9.9	4.2	4.1	2.5	1.6
Caudal peduncle depth	0.7	8.4	4.2	4.2	2.5	1.6
Prepectoral distance	2.5	25.9	13.6	14.5	31.7	5.6
Predorsal distance	4.6	40.6	21.2	21.4	52.2	7.2
Prepelvic distance	4.6	55.6	27.7	28.3	112.9	10.6
Preanal distance	7.4	76.4	39.0	39.2	202.6	14.2

TABLE 3. Mean biometric data for examined specimens of †*Bolcaichthys catopygopterus* (Woodward, 1901).



Variable character log(y)	Slope (m)	Intercept (b)	Coefficient of determination (r^2)	F	d.f.	95% CI on m		95% CI on b	
Head length	0.94 ± 0.01	−0.45 ± 0.02	0.97	8083.10	225	0.92	0.96	−0.48	−0.42
Head depth	1.07 ± 0.02	−0.86 ± 0.04	0.94	2481.45	169	1.03	1.11	−0.92	−0.79
Preorbital length	0.98 ± 0.03	−1.15 ± 0.04	0.90	1563.44	174	0.93	1.04	−1.24	−1.07
Postorbital length	0.98 ± 0.02	−0.88 ± 0.03	0.96	3566.76	159	0.94	1.00	−0.94	−0.83
Orbit diameter	0.89 ± 0.02	−1.16 ± 0.04	0.93	1582.53	130	0.85	0.93	−1.22	−1.09
Maximum body depth	1.19 ± 0.02	−0.96 ± 0.03	0.96	3685.29	174	1.15	1.23	−1.03	−0.89
Dorsal-fin base	1.04 ± 0.03	−1.01 ± 0.04	0.90	1631.21	182	0.99	1.10	−1.11	−0.92
Anal-fin base	1.06 ± 0.03	−0.92 ± 0.05	0.92	1190.67	111	0.99	1.14	−1.06	−0.80
Caudal peduncle length	0.98 ± 0.04	−1.05 ± 0.06	0.84	614.40	118	0.89	1.06	−1.19	−0.90
Caudal peduncle depth	1.00 ± 0.01	−1.07 ± 0.02	0.97	6089.68	204	0.98	1.03	−1.11	−1.01
Prepectoral distance	1.02 ± 0.01	−0.56 ± 0.02	0.98	5346.50	124	0.99	1.04	−0.60	−0.52
Predorsal distance	0.89 ± 0.01	−0.17 ± 0.02	0.98	7424.43	192	0.87	0.91	−0.20	−0.13
Prepelvic distance	0.99 ± 0.01	−0.23 ± 0.02	0.98	9596.71	198	0.97	1.02	−0.27	−0.20
Preanal distance	0.98 ± 0.01	−0.09 ± 0.01	1.00	38186.01	141	0.97	1.00	−0.10	−0.07
Head depth*	1.15 ± 0.02	−0.35 ± 0.02	0.96	4687.79	183	1.12	1.18	−0.39	−0.32
Preorbital length*	1.05 ± 0.02	−0.68 ± 0.03	0.92	2045.03	190	1.00	1.09	−0.74	−0.63
Postorbital length*	1.03 ± 0.02	−0.41 ± 0.02	0.97	4885.92	178	1.00	1.06	−0.45	−0.38
Orbit diameter*	0.96 ± 0.02	−0.74 ± 0.03	0.93	1834.87	147	0.92	1.01	−0.79	−0.69

TABLE 4. Relationships between morphometric characters and standard length or head length (these latter marked with an asterisk *) using least squares regression for †*Bolcaichthys catopygopterus* (Woodward, 1901); all $p < 0.001$.



Taxon	Supraneurals	Dorsal scutes	Branchiostegal rays	Pleural ribs (pairs)	Preural vertebrae	Pelvic-fin rays	Dorsal-fin pterygiophores	Anal-fin pterygiophores	Epurals	Frontoparietal striae
Amblygaster	8	0	6	25–27	43–44	8	18–20	17–18	3	7–14
†*Bolcaichthys*, gen. nov.	8	0	5–6	20–22	40–42	8	15–16	15–16	3	10–14
†*Chasmoclupea*	13	0	?	17	40+?	7	12	?	?	?
Clupea	15–19	0	8	34–37	52–57	8–10	17–18	15–18	1–2	?
Clupeonella	11	0	7	23–24	42	8	15	18–21	1–2	?
Escualosa	10	0	4	22	40	7	15	17–19	2	8–9
†*Gosiutichthys*	6–7	10–13	7–8	20–21	34–36	6–7	10–11	10–13	3	?
Harengula	7	1	6	23–26	40–42	8	16–17	14–19	2–3	3–5
Herklotsichthys	7–10	1	6	19–26	39–44	8	13–18	17–23	2–3	3–7
Lile	8–10	0	6	23–24	40–43	8	15–17	15–18	2–3	?
Opisthonema	7–9	1	6	27–28	45–47	8	18–19	18–22	3	?
Platanichthys	10–11	0	5–6	21–22	40–41	7	13	19–20	3	?
†*Primisardinella*	9–10	0	?	?	39–40	8	15–16	13–15	?	?
Ramnogaster	15	0	7	23	44	7	18	22	3	?
Rhinosardinia	10–12	0	5	20–24	36–43	8	13–15	14–16	2	?
Sardina	10–11	0	7	30–31	50–51	8	17–18	17–19	3	?
Sardinella	8–10	0	6	25–30	45–48	8–9	16–19	16–20	2–3	7–14
Sardinops	10	0	7	31–33	50–52	8	18–19	17–18	2–3	?
†*Sarmatella*	10–12	0	7	26–34	44–54	8–9	15–19	13–17	2	?
Sprattus	15–17	0	7	26–28	45–48	7–8	17–18	16–19	3	?
Strangomera	15	0	7	26	44	8	17	17	2	?
†*Xyne*	?	0	?	26	44	?	?	?	3	?

TABLE 5. Summary of selected morphological features used to discriminate the genera of the subfamily Clupeinae. Data from Daniltshenko (1968); Grande (1982a, 1982b, 1985); Whitehead (1985); Gaudant and Quayle (1988); Murray et al. (2005); Baykina (2013).