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THE EOCENE SARDINE |BOLCAICHTHYS CATOPYGOPTERUS (WOODWARD, 1901) FROM MONTE BOLCA, ITALY: OSTEOLOGY, TAXONOMY, AND PALEOBIOLOGY

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ABSTRACT—Clupeid fishes are abundant in the Eocene fossiliferous limestone of Monte Bolca, representing by far the most common group from this celebrated locality. However, despite of their abundance, the clupeid fishes from Monte Bolca have seldom been investigated. An 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 approximately one third to one quarter standard length; skull roof with 10–14 frontoparietal striae; mouth terminal; two supramaxillae; edentulous jaws and palate; complete series of about 20–22 abdominal keeled scutes with ascending arms; no dorsal scutes; five or six branchiostegal rays; eight supraneurals; 40–42 vertebrae and 20–22 pleural ribs; three epurals) supporting its recognition as a new genus of the family Clupeidae. Paleobiological considerations suggest that the presence of a very large number of schooling clupeids belonging to the genus |Bolcaichthys| at 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.

http://zoobank.org/urn:lsid:zoobank.org:pub:9B9A5490-D543-4ECC-9A74-1305BDC2F764

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

Clupeoidei is one of the most abundant and widespread groups of teleostean fishes, and includes over 300 extant species whose first representatives apparently date back to the early Cretaceous (Figueiredo, 2009). The Clupeoidei includes small- to medium-sized fishes such as herrings, sardines, shads, sprats, round herrings, and anchovies, with a worldwide distribution from tropical to cold temperate waters. These fishes form large monotypic schools feeding on zooplankton (Whitehead, 1985) and form one of the groups of primary importance to fisheries, representing one-third of the total worldwide commercial fishing catch (Blaxter and Hunter, 1982). Diagnostic characters of the Clupeoidei include 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 other 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, usually with two supramaxillae; jaw teeth are small or absent; the dorsal fin is short and placed at the 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 well behind the last dorsal-fin ray. However, there is a broad intraspecific morphological 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).

Clupeidae is by far the most common group in the Eocene fish assemblage of Monte Bolca (northeastern Italy) in terms of number of specimens (Landini and Sorbini, 1996), and, at the same time, it is also one of the least investigated. Because of their abundance in the fish assemblage of Monte Bolca, 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 number of systematic studies carried out on fishes from Monte Bolca in recent 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 last study focused on clupeid fishes dates back to the second half of the 19th century when Liou (1866) identified some species belonging to this family, based on inadequate descriptions and without illustrations. In this study, we describe a new genus of Clupeidae based on material from the Eocene of Monte Bolca, previously referred to the genus |Clupea| (Agassiz, 1833–1844; Liou, 1866; Zigno, 1874; Bassani, 1897; Woodward, 1901; see Systematic Paleontology below). Paleobiological and paleoenvironmental implications are also discussed. This work is one in a series of papers focused on the Eocene clupeoid fishes from Monte Bolca (e.g., Marramà and Carnevale, 2015a, b).
LOCALITY
The material documented herein was collected from the Pescria Cave and Monte Postale sites of the Bolca locality, in the eastern part of Monti Lessini, approximately 2 km northeast of Bolca village, not far from Verona, northeastern Italy. The geological features of the fish-bearing limestone exposed at Monte Bolca have been investigated by several authors, including Fabiani (1914, 1915), Sorbini (1968), Barbieri and Medizza (1969), Massari and Sorbini (1975), and, more recently, Papazzoni and Trevisani (2006). The fish-bearing limestone belongs to the ‘Calcari Nummulitici,’ an informal unit of Eocene age widely distributed in northeastern Italy. The succession consists of cyclic alternations of laminated micritic limestone and biocalcarenite-biocalcicrudite, the former characterized by beautifully preserved remains of fishes, invertebrates, and plants. According to Sei-lacher et al. (1985), the taphonomic features and ecological spectrum of the fossil assemblage are indicative of a stagnation deposit with a poorly oxygenated bottom. Based on their larger 

MATERIALS 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, Padua (MGPUP), Museo Civico di Storia Naturale di Milano, Milan (MSNM), Museo Regionale di Scienze Naturali, Turin (MRSN), and Natural History Museum, London (NHMUK P). The material was examined using a Leica M80 stereomicroscope equipped with a camera lucida drawing attachment. Measurements were made to the nearest 0.1 mm using dial calipers. 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 entomological mounting 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 a dagger (†) preceding their name.

The relationships between length and various morphometric features were analyzed for statistical outliers, which deviate more than 3 standard deviations from the mean. The presence of statistical outliers will indicate specimens of possible additional taxa and require additional scrutiny for differentiation. Least squares regression is used to obtain the relation between 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 \( \log(y) = m \times \log(x) + b \), where \( y \) is the variable morphometric character, \( x \) is the independent character (standard length or head length), and \( m \) and \( b \) (respectively slope and intercept) are the constants to be determined. 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 were mature, was determined by the empirical equation \( L_m = -0.1189 + 0.9157 \times \log(L_{\text{max}}) \), where \( L_{\text{max}} \) is the largest standard length in the sample (Binohlan and Froese, 2009).

Anatomical Abbreviations
- aa, angular orbital; ao, antorbital;
- bsp, basisphenoid; d, dentary; ect, ectopterygoid; ep, epiplacodontid; f, frontal; hym, hyomandibula; hyp, hypural; io, infraorbital; le, lateral ethmoid; me, mesethmoid;
- mp, metapterygoid; mx, maxilla; na, nasal; np, neural plate; op, opercle; osp, orbitosphenoid; pa, parietal; pas, parasphenoid; phy, parhypural; pl, palatine; pmx, premaxilla; pop, preopercle; pto, pterotic; pts, pterosphenoid; pu, preural centrum; q, quadrato; ra, retroarticular; smx, supramaxilla; so, supraorbital; sop, supraoperculum; sp, sphenotic; sr, sclerotic ring; sym, symplectic; u, ural centrum; un, urobrideal; vo, vomer.

SYSTEMATIC PALEONTOLOGY
Subdivision TELEOSTEI sensu Patterson and Rosen, 1977
Superorder CLUPEIFORMES 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 ‘ichthus,’ ‘fish.’

Diagnosis—Small- to medium-sized clupeid (largest specimen measuring 101.1 mm SL) with elongated and tapered body, sarcidine-like; ‘Bolcaichthys’, gen. nov., is unique among clupeids in having the following combination of characters: head length approximately one third to one quarter SL; skull roof with 10–14 frontoparietal striae; mouth terminal; two supramaxillae, anterior small and rod-like, and posterior paddle-shaped; teeth absent in jaws and palate; complete series of abdominal keeled scutes (10–11 prepelvic and 10 or 11 postpelvic) with ascending arms; dorsal scutes absent; fewer branchiostegal rays (5 or 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 or 16 rays; about 15 or 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 catopygopterus’ was created by Louis Agassiz (1835, 1844) without any formal description, figure, and indication of type material. Because of the inadequate taxonomic procedure (designation of the name did not satisfy the stipulation of Article 12 of the International Commission on Zoological Nomenclature [ICZN; 1999]) followed by Agassiz, this species was considered a 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 with authorship following ICZN Articles 21 and 50. Blot (1980) erroneously indicated Sigmo (1874) as the author. Woodward (1901) assigned the species to the genus Clupea Linnaeus, 1758, a common practice followed by most other 19th century authors, when almost all fossil 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 stated the necessity of a revision of the clupeoid material from Monte Bolca.

*BOLCAICHTHYS CATOPYGOPTERUS* (Woodward, 1901) (Figs. 1–10)

*Clypea catopygoptera* Woodward, 1901: Agassiz, 1835:31 (nomen nudum; original occurrence of name, no description or figure).

*Clypea catopygoptera* Woodward, 1901: Agassiz, 1843:120 (second occurrence of name, no description or figure).

*Clypea catopygoptera* Woodward, 1901: Zigno, 1874:143 (third occurrence of name, no figure).

*Clypea catopygoptera* Woodward, 1901: Eastman, 1911:357.

*Clypea catopterygia* Woodward, 1901: Eastman, 1911:357.

*Clypea catopygoptera* Woodward, 1901: Blot, 1980:351.

*Clypea’ catopygoptera* Woodward, 1901: Grande, 1985:281, 310–311.

**Holotype**—NHMUK P.3829a, nearly complete articulated skeleton on a 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; MGSNV IG.VR.71407/71408, part and counterpart (Fig. 2A) of an almost complete articulated skeleton, 56.9 mm SL.
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 daianelli 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. Standard length is about 3.6 times head length and about 4.4 times maximum body depth. The mouth is small, terminal, with a slightly projecting lower jaw. The belly is completely armored, with keeled scutes with ascending arms in front of and behind the pelvic fins. The description of skeletal structures and the restoration of the head (Fig. 3) and axial skeleton (Fig. 4) are primarily based on specimens MCSNV IG.VR.57598/57599, MCSNV IG.VR.71407/71408, and MCSNV T.361.

**Neurocranium**—The neurocranium is rather elongate and nearly triangular in lateral outline. The paired frontals are the largest bones of the skull roof, occupying about 70% of total neurocranium 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 posterodorsally with the sphenotic. There are 10 to 14 frontoparietal striae that appear visible only in the posterior parts of the frontals, as observed mostly in larger specimens. The parietal is a scythe-like bone that articulates anteriorly with the frontal, anterodorsally with the sphenotic, posteroventrally with the epiparietal, and posteroventrally with the pterotic. The pre-epiptial fossa is rather small. The supraepiptial forms the posteroartial end of the skull roof and is rhomboidal in shape. The epiparietal marks the posterodorsal border of the pre-epiparietal 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-epiptial fossa; it is anteroposteriorly elongate and articulates anterodorsally with the parietal, posterodorsally with the epiparietal, posteriorly with the exoepiptial, and anteriorly with the sphenotic. The sphenotic is a heavily ossified bone, subtriangular in shape, articulating posteriorly with the pterotic, and bearing an articular facet for the anterior hyomandibular condyle. The prootic appears to be rather small. The long orbitosphenoids forms the dorsal wall of the orbit; it bears an anterior process that articulates with the lateral ethmoid and contacts the paraphysioden anterogradually via a thin, laminar sheet of bone. The pterosphenoid and basiphenoid form the posterior wall of the orbit. The paraphysioden is a long and thin bone, extending for the most of the basioccipital length. The vomer is thin and apparently toothless. The mesethmoid is long, slender, and anteriorly forked. The lateral ethmoid is small and thin with an expanded ventral end characterized by an irregular ventral margin.

**Circumorbital Series**—The nasals is short and moderately elongated. The supraorbital is long and slender, anteroposteriorly elongated, and supported by the anterotemporal margin of the frontal. The small antorbital is subtriangular in shape and loosely articulated with the anterior end of supraorbital. Six infraorbital 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, dorsoventrally elongate, and lying along the posterior margin of the orbit. The splanchnocran 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 supra-maxillae, the first of which is thin, rod-like, and slightly arched, and the second large and paddle-shaped. The dentary is edentulous, robust, and deep. It is trapezoid in shape, with a steep anterior margin. The entire ventral margin bears a flange for the mandibular laterosensory canal and 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 in the most anterior part of the frontals, as

**TABLE 1. Morphometric data (measurements as percentage of SL; mean values in parentheses) for <i>Bolcaichthys catopygopterus</i> (Woodward, 1901).**

| 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)          |
| Preorbital distance    | 28.0–31.0 (30.0)       |
| Predorsal distance     | 41.6–46.4 (44.2)       |
| Prepelvic distance     | 54.8–60.0 (57.2)       |
| Preanale distance      | 75.7–78.5 (77.3)       |
| Prepectoral distance   | 5.9–7.2 (6.7)          |
| Preorbital length      | 11.1–12.8 (12.0)       |
| Orbit diameter         | 4.3–5.2 (4.7)          |

**TABLE 2. Meristic information for <i>Bolcaichthys catopygopterus</i> (Woodward, 1901).**

| Element                        | Number of skeletal elements |
|--------------------------------|-----------------------------|
| 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                | 3 17 40 36 5 1             |
| Dorsal-fin pterygiophores      | 1 6 48 17 1               |
| Anal-fin pterygiophores        | 7 16                        |
| Branchiostegal rays            | 6 7                         |
| Prepelvic scutes               | 4 14                        |
| Postpelvic scutes              | 129                        |
| Supraneurals                   | 3                           |
| Dorsal caudal-fin rays         |                            |
| Ventral caudal-fin rays        |                            |
**Suspensorium**—The palatine is long and slender, with an anterio hook-like maxillary process. The ectopterygoid is long and well developed, forming an obtuse angle at its mid-length. The endopterygoid is anteroposteriorly elongate, posteriorly expanded and with a concave dorsal margin; it bears a ridge along its entire length. The metapterygoid is a laminar bone, subtriangular in shape, that overlies the quadrate anteroventrally. The quadrate is triangular in shape with a well-developed condyle; its posteroventral margin bears a thickened, elongate and backwardly 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 the facial nerve is clearly recognizable; the opercular process is well developed.

**Opercular Series**—The preopercle is large and crescent-shaped; the vertical arm of the preopercle is slightly shorter than the horizontal one. The opercle is about twice as deep as broad, and ovoid in shape with a vertical anterior margin; in the dorsal third of the bone, a 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, slender, and slightly broader posteriorly.

**Hyoid Bar**—The paired dorsal hypohyal strands are poorly ossified, and L-shaped. The paired ventral hypohyal rays are long, thin, and tubular. The anterior ceratohyal is robust and elongated, 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 and plate-like; 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 the neural spines from vertebra 4 or 5 to vertebra 20 or 22, becoming separated towards the end of the vertebral column. The epicentra are very short, curved, and articulate along the base of the pleural ribs from vertebra 5 or 6 to 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

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**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.
bears a laminar, elongate, and subrectangular neural plate. The first urocentrum is fused to the second hypural. The second urocentrum is short and tubular. There are six hypurals, all autogenous but the second, which is elongate and slender and fused to the first urocentrum; 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 a 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, and overlying vertebrae 13–15; it seems to contain 15 or 16 rays supported by 15 or 16 pterygiophores. As in other clupeids, proximal and associated middle pterygiophores appear 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. They decrease 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 the others.

The anal fin contains 15 or 16 rays supported by 15 or 16 pterygiophores more or less closely associated with the haemal spines of vertebrae 28–36. The proximal and middle anal-fin pterygiophores appear to be fused into a single structure. The length of the proximal-middle pterygiophores decreases slightly 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 robust, hatchet-shaped, anteroposteriorly elongated, and with a curved anteroventral 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 14–18 rays, the first of which is the longest.

**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 or 11 prepelvic, one pelvic, and 10 or 11 postpelvic keeled scutes with ascending arms. The pelvic scute is the largest of the series. Juvenile specimens (up to about 52 mm SL; see below) have a lower number of scutes, which appear to be absent in 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. 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, circular brown spots of pigment showing different degrees of aggregation. In larval and juvenile specimens, the pigmentation is mostly restricted to the 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.

**FIGURE 5.** Bolcaichthys catopygopterus (Woodward, 1901); reconstruction of the caudal skeleton primarily based on specimens MCSNV IG.37586/37585, MCSNV IG. VR.71407/71408, and MCSNV T.361.
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 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 adult specimens because of the thickness of the scales.

Cololites—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 fifth or sixth pleural ribs and the anal fin, and their distal end possibly terminates in correspondence with the anus. The cololites are relatively short, possibly related to the zooplanktivorous diet typical of most clupeids (Whitehead, 1985).

Remarks on Biometry—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 biometric parameters used for the
A description of the sample. These parameters allow us to determine the specific biometric data of 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, 8). Linear regression analysis of the morphometric data confirmed that there was a significant relationship between standard length (or head length) and each of the morphometric characters ($P < 0.001$). In addition, a high degree of positive correlation between standard length (or head length), and each morphometric character was indicated by high values of the coefficient of determination ($r^2$), ranging 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 $y$ on $x$ is highly significant. No specimens fell more than 3 standard deviations from the mean, indicating homogeneous datasets.

Because the length at first maturity ($L_m$) is proportional to the maximum length of the fish ($L_{\text{max}}$) (Beverton, 1963), it is possible to estimate the mean length discriminating between juvenile and adult specimens. Using the empirical equation for estimating length at first maturity from maximum body length (BinoHlan and Froese, 2009), it is possible to estimate that *Bolcaichthys catopygopterus* reached 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 cross the ventral midline of the body, a second hypural fused with the first ural centrum, and an 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. Assignment to the family Clupeidae is clearly supported by the presence of two long, rod-like postcleithra (Grande, 1985).

Due to their overall morphological similarity, relationships between clupeid genera are difficult to determine. Within the family Clupeidae, several authors (e.g., Grande, 1985; Whitehead, 1985) recognize 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 \( \text{Bolcaichthys} \), gen. nov., certainly supports its recognition as a

![FIGURE 8](image8.png)

**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 \( \text{Bolcaichthys catopygopterus} \) (Woodward, 1901).

![FIGURE 9](image9.png)

**FIGURE 9.** Ontogenetic series of \( \text{Bolcaichthys catopygopterus} \) (Woodward, 1901). A, larva, MCSNV IG.YR.71433; B, juvenile, MCSNV IG.37584; C, adult, MCSNV IG.145058. Scale bars equal 2 mm (A), 5 mm (B), and 10 mm (C).
new clupeid genus. *Bolcaichthys*, gen. nov., exhibits a complete series of prepelvic and postpelvic scutes, plus a large pelvic scute between the pelvic fins. For this reason, it cannot be placed in the subfamily Dussumieriinae, whose members are characterized by the absence of prepelvic and postpelvic scutes and the presence of a single ‘W’-shaped scute, immediately anterior to the pelvic fins (Grande, 1985; Whitehead, 1985). 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) due to the presence of separated first preural and first ural centra in the caudal skeleton. The monophyletic status of the

| 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     | 10.6|
| 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|
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) provide a detailed description of extant representatives of the subfamilies Dorosomatinae, Clupeinae, and Alosinae based on external features and soft anatomy (e.g., digestive tract). The deep-bodied Dorosomatinae are characterized by the presence of a single supramaxilla (except for *Dorosoma* and *Signalos*), which 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 moderately elongate and tapered body, terminal mouth, two supramaxillae, small and triangular dorsal fin without long and filamentous rays, and almost pointed snout, a combination of features that excludes any assignment to the subfamily Dorosomatinae. There are no osteological arguments useful for distinguishing the genera of the Alosinae from those of the Clupeinae. The structure of the gill arches might include some derived characters useful in distinguishing 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 in the presence of moderate to large or very large body (from 200 to 600 mm SL), dorsal scutes present along back (e.g., *Ethmi*um, *Ethmalaosa*, and some species of *Pomolobus*), and 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 smaller body size. The average size of the specimens from Monte Bolca is about 40–60 mm SL, with the largest specimen reaching 110 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 in its unique combination of meristic features (Table 5). It can be easily separated from *Clupea*, *Chasmoclupea*, *Clupeonella*, *Escualosa*, *Platichthys*, *Primisdardinella*, *Rhinosardinia*, *Sardinops*, *Sardina*, *Sarmatella*, *Sprattus*, and *Strangomera* in its reduced number of supraneurals (8 vs. 9–19).

Moreover, the number of prevembral vertebrae is useful for separating *Bolcaichthys*, gen. nov. (40–42), from *Amblygaster*, *Clupea*, *Opisthionema*, *Rannogaster*, *Strangomera*, *Sardina*, *Sardinella*, *Sardinops*, *Sarmatella*, *Sprattus*, *Xyne* (43–57), and *Gosiutichthys* (34–36). *Bolcaichthys*, gen. nov., has 15 or 16 dorsal-fin pterygiophores compared with the 10–13 of *Chasmoclupea*, *Gosiutichthys*, and *Platichthys* and 17–20 of *Amblygaster*, *Clupea*, *Opisthionema*, *Rannogaster*, *Sardina*, *Sardinops*, *Sprattus*, and *Strangomera*. Finally, it has 15 or 16 anal-fin pterygiophores compared with the 10–14 of *Gosiutichthys* and 17–22 of *Amblygaster*, *Clupeonella*, *Escualosa*, *Herklotsichthys*, *Opisthionema*, *Platichthys*, *Rannogaster*, *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 a narrow, slender, and transparent body, measuring a 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 to habitats not suitable for the survival of the larvae (e.g., Hjort, 1914; Townsend, 1992). During the juvenile stage, clupeids are a few tens of mm long, their bodies begin to deepen and flatten, becoming semitransparent, and the scales start to form. 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 seasonally or over great distances in open sea, to feed and spawn, becoming totally pelagic (Moyle and Cech, 1992). Because of the large number of specimens available for study, all three developmental stages have been observed in the clupeine *Bolcaichthys catopygopterus* (Fig. 9A–C). The larval stage is represented by a single specimen of 9.5 mm SL (MCSNV IG.VR.71432/71433). The alevin is elongate, with a slender and narrow body. The pigmented peritoneum is clearly visible.

| Variable character | log(y) | Slope (m) | Intercept (b) | Coefficient of determination (r²) | F | d.f. | 95% CI on m | 95% CI on b |
|--------------------|--------|-----------|---------------|----------------------------------|---|------|-------------|-------------|
| Head length        | 0.94   | 0.01      | -0.45         | 0.97                             | 225| 0.92 | -0.48       | -0.42       |
| Head depth         | 1.07   | 0.02      | -0.86         | 0.94                             | 169| 1.03 | -0.92       | -0.79       |
| Preorbital length  | 0.98   | 0.03      | -1.15         | 0.90                             | 1563.44| 174| 0.93 | -1.24       | -1.07       |
| Postorbital length | 0.98   | 0.02      | -0.88         | 0.96                             | 3566.76| 159| 0.94 | -0.94       | -0.83       |
| Orbit diameter*    | 0.89   | 0.02      | -1.16         | 0.93                             | 1582.53| 130| 0.85 | -1.22       | -1.09       |
| Maximum body depth | 1.19   | 0.02      | -0.96         | 0.96                             | 3685.29| 174| 1.15 | -1.03       | -0.89       |
| Dorsal-fin base    | 1.04   | 0.03      | -1.01         | 0.90                             | 1631.21| 182| 0.99 | -1.11       | -0.92       |
| Anal-fin base      | 1.06   | 0.03      | -0.92         | 0.92                             | 1190.77| 111| 0.99 | -1.06       | -0.80       |
| Caudal peduncle length | 0.98  | 0.04      | -1.05         | 0.84                             | 614.40| 118| 0.89 | -1.19       | -0.90       |
| Caudal peduncle depth | 1.00  | 0.01      | -1.07         | 0.97                             | 6089.68| 204| 0.98 | -1.11       | -1.01       |
| Prepectoral distance | 1.02  | 0.01      | -0.56         | 0.98                             | 5346.50| 124| 0.99 | -1.06       | -0.52       |
| Predorsal distance | 0.89   | 0.01      | -0.17         | 0.98                             | 7424.43| 192| 0.87 | -0.20       | -0.13       |
| Prepelvic distance | 0.99   | 0.01      | -0.23         | 0.98                             | 9596.71| 198| 0.97 | -0.27       | -0.20       |
| Preanal distance   | 0.98   | 0.01      | -0.09         | 1.00                             | 3818.61| 141| 0.97 | -0.10       | -0.07       |
| Head length*       | 1.15   | 0.02      | -0.35         | 0.96                             | 4687.79| 183| 1.12 | -0.39       | -0.32       |
| Preorbital length* | 1.05   | 0.02      | -0.68         | 0.92                             | 2045.03| 190| 1.00 | -0.74       | -0.63       |
| Postorbital length*| 1.03   | 0.02      | -0.41         | 0.97                             | 4885.92| 178| 1.00 | -0.45       | -0.38       |
| Orbit diameter*    | 0.96   | 0.02      | -0.74         | 0.93                             | 1834.87| 147| 0.92 | -0.79       | -0.69       |

All P < 0.001.
because the lack of scales makes the body transparent. The pigmentation of the body is localized to the back as a thin line running from the head to the caudal fin.

The mean ratio Lm/Lmax for †Bolcaichthys is 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 range from about 15 to 52 mm SL, thereby representing juveniles. Their bodies begin to deepen and flatten; the scales start to cover the semitransparent to almost completely nontransparent body. For this reason, the pigmented peritoneum becomes gradually less visible during ontogeny.

The adult stage is represented by about 42% of the individuals studied. These measured from 52 to 101 mm SL. Their body is entirely covered with thick scales that do not allow observation of the peritoneum. 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.

The size-frequency distribution (Fig. 6) shows that young fishes are not well represented, contrary to what might be expected in a population in which young individuals should be the most abundant (Newbrey and Bozek, 2003). It is therefore 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) of nearly equal 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 and also fundamental prey for higher trophic level vertebrates. Ecological and trophic relationships of the Monte Bolca ichthyofauna have been discussed by many authors, who always considered the fish assemblage to be the earliest example of a reefal or peri-reefal fish assemblage in the fossil record (e.g., Bellwood, 1996; Landini and Sordini, 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 neglected or underestimated. The depositional paleoenvironment of Monte Bolca has been discussed by a number of authors in the past decades, resulting in a series of interpretative reconstructions, all of which are more or less closely related to a coral reef context. Sordini (1968) and Massari and Sordini (1975) hypothesized that the fish-bearing micritic limestone was deposited in a tropical coastal lagoon close to coral reefs. According to Landini and Sordini (1996), the fossiliferous deposits originated in a silled depression parallel to the coast and in proximity to coral reefs where it was 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 periodic 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, whereas adults tend to become totally pelagic (e.g., Blaxter and Hunter, 1982; Munroe, 2000). Although not all authors agree with the hypothesis of a depositional environment in close proximity with a coral reef system, most concur in suggesting that the sediments originated in a depressed and moderately deep basin close to the coast and characterized by reduced water circulation in a tropical 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 Sordini (1996),...
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providing further evidence for the reduced distance from the coast line as well as the considerable 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 coat, and notably subject to open sea influence.

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

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