

A NEW MOORISH IDOL (TELEOSTEI, ZANCLIDAE) FROM THE EOCENE OF BOLCA, ITALY

GIORGIO CARNEVALE^{1*} & JAMES C. TYLER²

^{1*}Corresponding author. Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso, 35 I-1025 Torino, Italy. E.mail: giorgio.carnevale@unito.it

²National Museum of Natural History, Smithsonian Institution, Washington, DC 20052, USA. E- mail: tylerj@si.edu

Associate Editor: Cristina Lombardo.

To cite this article: Carnevale G: & Tyler J. C. (2024) - A new moorish idol (Teleostei, Zanclidae) from the Eocene of Bolca, Italy. *Riv. It. Paleontol. Strat.*, 130(1): 19-33.

Keywords: *Angiolinia mirabilis* n. gen. et sp.; Acanthuroidei; Pesciara site; Ypresian; phylogenetic relationships.

Abstract. The acanthuriform family Zanclidae, whose members are commonly known as moorish idols, has until now been comprised of two species, the extant *Zanclus cornutus* and the Eocene *Eozanclus brevirostris*. Herein, a new moorish idol, *Angiolinia mirabilis* n. gen. et sp., is described based on three specimens from the Eocene Pesciara site of the Bolca locality, northern Italy.

Morphologically, *Angiolinia mirabilis* n. gen. et sp. appears to be intermediate between *Eozanclus brevirostris* and *Zanclus cornutus* and differs from them by having the following features: body depth 85–87% SL; head length 38.3–39.2% SL; third dorsal-fin spine reaching about 50% SL; pectoral disc width 23.2% SL; dorsal fin containing 31 or 32 rays; anal fin containing 26 or 27 rays; pectoral fin with 11 or 12 moderately elongate rays and caudal fin truncate.

A comparative osteological analysis suggests that the family Zanclidae is defined by two morphological features, namely the presence of a broadly expanded and anteroventrally convex cleithrum forming the so-called pectoral disc together with the coracoid and having a large number of dorsal- and anal-fin rays. The Eocene acanthuriform *Massalongius gazolai* from Bolca represents the sister group to the Zanclidae. Within the zanclids, *Eozanclus brevirostris* represents the sister group to the pair formed by *Angiolinia mirabilis* n. gen. et sp. and *Zanclus cornutus*. This clade is supported by the shared possession of a single supernumerary spine on the first dorsal-fin pterygiophore, a single uroneural in the caudal skeleton, and all but the first two dorsal-fin spines distally filamentous.

INTRODUCTION

The Eocene fish fauna of Bolca certainly represents one of the most celebrated fossil ichthyofaunal assemblages. This is mostly due to the extraordinary preservation of the fossils (e.g., Carnevale et al. 2014; Friedman & Carnevale 2018; Rossi

et al. 2022), as well as to their outstanding diversity (e.g., Carnevale et al. 2014; Marramà et al. 2016b, c), making this assemblage the most diverse of all the Cenozoic marine ichthyofaunas and, at the same time, one of the most diverse fossil vertebrate assemblages known to date on record. Blot (1969) estimated that several thousand fish specimens had been collected at Bolca during more than four centuries, representing more than 250 taxa (Bannikov 2014; Carnevale et al. 2014; Friedman & Carnevale 2018). Because of the very high taxonomic diversity

and the tropical marine shallow-water environment in which they were preserved, the Bolca fish fauna is commonly regarded as the earliest evidence of a modern coral reef fish assemblage (e.g., Bellwood 1996; Carnevale 2006; Friedman & Carnevale 2018; Marramà et al. 2022), documenting the first occurrence of numerous families today associated with coral reefs (e.g., Blot 1980; Blot & Tyler 1990; Bellwood 1996; Carnevale & Pietsch 2009; Bannikov & Carnevale 2010, 2016) and providing evidence of substantial stability of the morphological characteristics of tropical marine fish faunas throughout the Cenozoic.

One of the most iconic fish families today associated with coral reefs and documented in the Bolca assemblage is the Zanclidae, commonly known as moorish idols. This family of derived percomorph fishes is represented in the Bolca assemblage by *Eozanclus brevirostris* (Agassiz, 1835), which was described for the first time by Volta (1796) based on a single specimen and was subsequently revisited by Agassiz (1833–1844). Blot & Voruz (1970, 1975) included three additional specimens in their detailed revision of *Eozanclus brevirostris*, two of which are pre-juvenile individuals showing peculiar morphological features (e.g., one supernumerary spine on the first dorsal-fin pterygiophore versus two in the type specimen) that suggest a separate taxonomic status. More recently, a nicely preserved adult individual exhibiting a similar set of morphological characters has been found in the collection of the Museo della Famiglia Cerato, Bolca (CMC). The goal of this paper is to describe this new zanclid taxon and to discuss its affinities.

The family Zanclidae comprises a single extant species, *Zanclus cornutus* (Linnaeus, 1758), that occurs throughout the Indo-Pacific, including the Eastern Pacific seaboard (e.g., Randall 1955; Winterbottom & McLennan 1993; Kuitert & Debelius 2001). Moorish idols are omnivorous, feeding primarily on sponges and other benthic invertebrates and algae. Young moorish idols are specialized for a prolonged pelagic existence (Strasburg 1962; Johnson & Washington 1987).

GEOLOGICAL SETTING

The specimens described herein were collected from the fossiliferous strata of the Pesciara site

of the Bolca locality, in the eastern portion of the Monti Lessini, Verona Province, northeastern Italy. The Pesciara site has been celebrated for centuries for its exquisitely preserved fossils, especially for the articulated skeletal remains of bony and cartilaginous fishes. To this date, more than 250 fish taxa have been identified from Bolca (Carnevale et al. 2014).

The shallow water Lower Eocene carbonates of the Pesciara site accumulated on the Lessini Shelf, a paleogeographic unit of the Southern Alps (see Bosellini 1989). The Eocene carbonate deposits of the Lessini Shelf have been traditionally referred to as the “Calcarei Nummulitici.” The succession exposed at the Pesciara site consists of about 20 m of alternated finely laminated micritic limestone and coarse-grained biocalcarene/biocalcirudite containing abundant remains of benthic invertebrates deposited during the late Ypresian. Exquisitely well-preserved fishes, plants and soft-bodied invertebrates derive from the inframillimetrically laminated micritic limestone of the Pesciara succession (Friedman & Carnevale 2018). Large size benthic foraminiferans and calcareous nannoplankton indicate that the Pesciara site succession dates back to the middle Cuisian, corresponding to the uppermost part of SBZ 11 and the lower part of the NP 14 and CNE 6, between 48.96 and 48.5 Ma (see Papazzoni et al. 2017).

According to Marramà et al. (2016a), sedimentological and taphonomic features suggest that the fossiliferous laminated micritic limestone originated in a peri-reefal coastal setting, in which local anoxic or dysoxic conditions at the bottom fostered development of a biofilm that promoted the remarkable preservation of the fossils. A paleoecological analysis carried out by Marramà et al. (2016a) evidenced a sharp oligarchic structure in the Pesciara fish assemblage, which is dominated by zooplanktivorous fishes, primarily represented by the sardine *Bolcaichthys catopygopterus* (Marramà & Carnevale 2015).

MATERIALS AND METHODS

The present study is based on three specimens, one of which (the holotype) is housed in the Museo della Famiglia Cerato, Bolca (CMC), and the other two are in the collection of the Museo Civico di Storia Naturale di Verona (MCSNV). Additional Eocene zanclids and acanthurids from Bolca in the collections of the Museo di Geologia e Paleontologia, Università degli Studi di Padova (MG-

PUP), Muséum National d'Histoire Naturelle, Paris (MNHN) and Carnegie Museum of Natural History, Pittsburgh (CMNH) were studied for comparative purposes. Extant comparative materials in the collection of the National Museum of Natural History, Smithsonian Institution, Washington (USNM) were also examined. The specimens were studied primarily using a Leica M80 stereomicroscope equipped with a camera lucida drawing arm. During examination, the fossils were moistened with alcohol to enhance details of the skeletal anatomy. Measurements were taken with a dial caliper to the nearest 0.1 mm. Standard length (SL) is used throughout. Counts and measurements were made mostly following Randall (1955); anatomical terminology primarily follows Tyler et al. (1989).

SYSTEMATICS

Order Acanthuriformes Jordan, 1923

Family Zanclidae Bleeker, 1876

Emended diagnosis: Triangular, peak-like supraoccipital crest with a thickened anterior edge; suborbital shelf present; teeth numerous, setiform, elongate, with smooth edges; five (1+4) branchiostegal rays; 22 (9+13) vertebrae; one supraneural; median locking flanges on the first three dorsal-fin spines; seven dorsal-fin spines; third interneural space vacant; median locking flanges on the first one or two anal-fin spines; cleithrum greatly expanded, remarkably convex anteroventrally; pelvic fin with a single spine and five rays; 16 (I, 7+7, D) principal caudal-fin rays; body covered with scale plates with a rough texture, bearing a serrate vertical ridge.

Type Genus: *Zanclus* Cuvier & Valenciennes, 1831.

Composition: Three genera, the extant *Zanclus* (with a single species), and the Eocene monotypic genera *Angiolinia* gen. nov. and *Eozanclus* Blot & Voruz, 1970.

Genus *Angiolinia* n. gen.

Diagnosis: Body deep, discoid in outline, laterally compressed; body depth 85–87% SL; head length 38.3–39.2% SL; snout length 22–24.7% SL; a single uroneural; first dorsal-fin pterygiophore bears a single supernumerary spine; all but the first two dorsal-fin spines are distally filamentous; third dorsal-fin spine much longer than the others, reaching about 50% SL; 31 or 32 dorsal-fin rays; 26 or 27 anal-fin rays; median locking flanges on the first two anal-fin spines; pectoral fin with 11 or 12 moderately elongate rays; caudal fin truncate; basipterygium depth/length ratio 25–28.1% SL; two postcleithra; pectoral disc expanded, with a width measuring 23.3% SL.

Type species: *Angiolinia mirabilis* sp. nov., by monotypy and designation herein.

Etymology: In honour of Professor Lucia Angiolini in recognition of her outstanding contributions to paleontology.

Angiolinia mirabilis n. sp.

Figs. 1–6

1970 *Eozanclus brevisrostris* Blot & Voruz, 1970, p. 33 (pro parte).

1975 *Eozanclus brevisrostris* Blot & Voruz, 1970 — Blot & Voruz, p. 235, pls. III, IV.

Holotype: CMC 39, a nearly complete articulated skeleton; 117.7 mm SL, 131.4 mm total length (Fig. 1A).

Diagnosis: As for the genus.

Etymology: The name is derived from the Latin *mirabilis*, meaning marvelous or wonderful, in reference to the attractive appearance of this species.

Paratypes: MCSNV I.C. 2-3, a partially complete articulated skeleton belonging to a pre-juvenile individual (Fig. 2A, B), in part and counterpart; 31.3 mm SL, 35.8 mm estimated total length. MCSNV I.C. 5, a partially complete articulated skeleton belonging to a pre-juvenile individual (Fig. 2C); 46.1 mm SL, 58.8 mm total length.

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

Description. Counts and measurements for *Angiolinia mirabilis*, n. gen. et sp., are summarized in Tabs. 1 and 2. The body is notably deep, nearly discoid in outline and laterally compressed, with a maximum body depth reaching 87% SL (Figs. 1, 2). The head is rather large, its length is contained more than two times in SL. The snout is elongate, wide and tubular, its length is contained slightly more than four times in SL. The mouth is terminal, relatively small but conspicuous, and placed below the body axis. The orbit is large and rounded in outline. The abdominal cavity is rather compact. The caudal peduncle is short and compressed, its depth is contained slightly more than five times in SL. The predorsal distance ranges between 61.5 and 65% SL. The dorsal fin is long-based and continuous, with a moderate indentation between the sixth spine and the second ray (thereby involving the relatively short seventh spine and first ray). The dorsal-fin spines abruptly increase in height from the second to the third, which is by far the longest of the series, and then gradually decrease posteriorly. The dorsal-fin rays gradually decrease in height posteriorly from the third, which is the longest. The anal-fin base is relatively long, its length is contained about two times in SL. Of the three anal-fin spines, the third is the best developed, with a length more than two times that of the preceding spine. The anal-fin rays gradually increase in height up to the seventh and then decrease, resulting in an almost vertically oriented posterior portion of the fin. The pectoral fin inserts in the upper portion of the lower half of the body flank.

The pelvic fin originates just below the pectoral-fin insertion. The pelvic-fin rays gradually decrease in length medially. The caudal fin is truncate, extending well beyond the posterior margins of both the dorsal and anal fins.

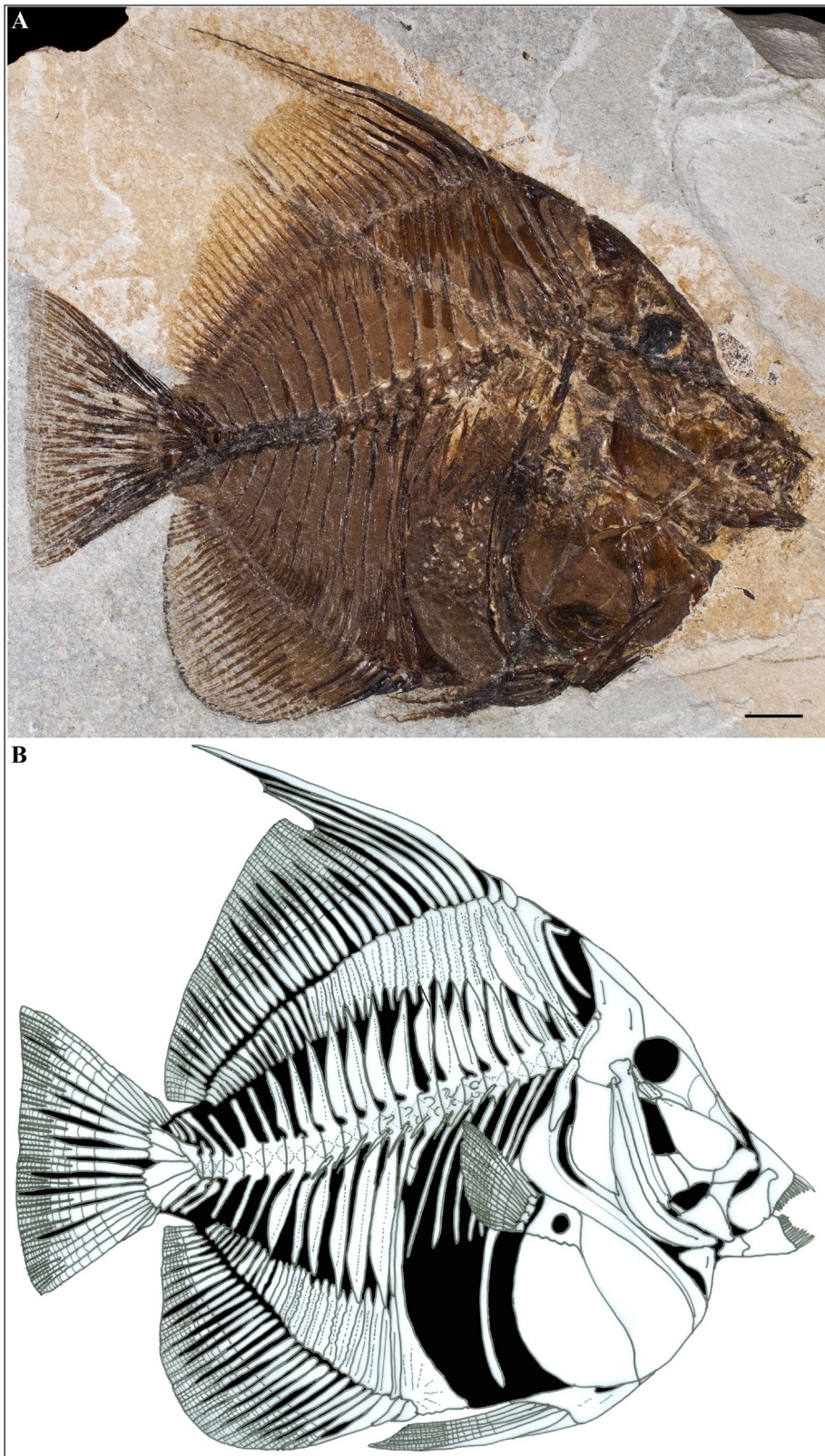


Fig. 1 - *Angiolinia mirabilis* n. gen. et sp. from the Eocene of Bolca. A) holotype, CMC 39, right lateral view; scale bar 20 mm. B) reconstruction of the skeleton of CMC 39.

The neurocranium is deep and triangular in lateral view, with a gently convex anterior profile (Fig. 3). Most of the otic and occipital regions of the neurocranium are poorly preserved in the examined specimens, thereby preventing the obser-

vation and description of their morphological features. The ethmoid region is relatively elongate in the holotype but less developed in the two prejuvenile specimens (MCSNV I.C. 2-3, MCSNV I.C. 5), suggesting a positive ontogenetic allometry for this

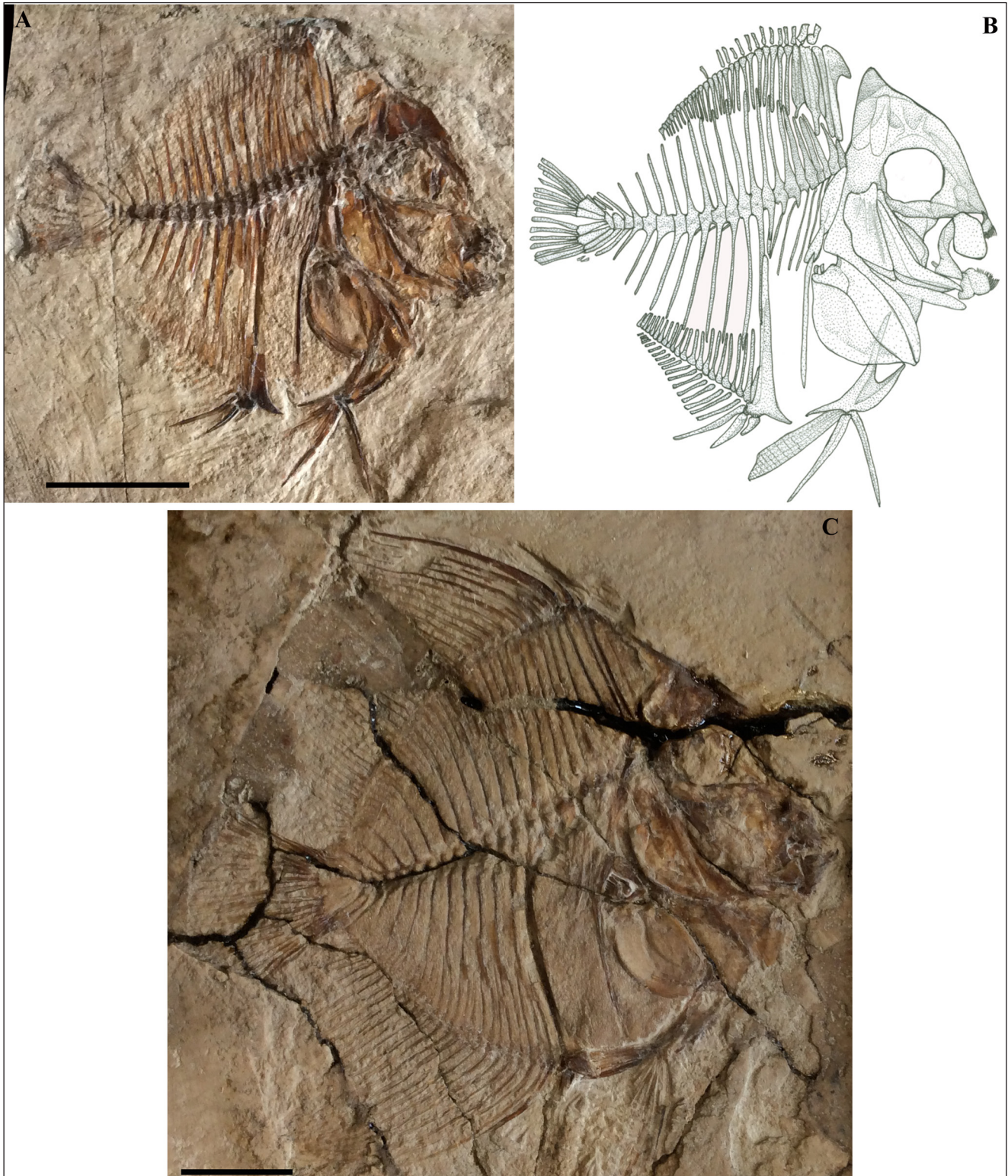


Fig. 2 - *Angiolinia mirabilis* n. gen. et sp. from the Eocene of Bolca. A) paratype, MCSNV I.C. 3, right lateral view. B) reconstruction of the skeleton of MCSNV I.C. 3. C) paratype, MCSNV I.C. 5, right lateral view. Scale bars 10 mm.

portion of the neurocranium. Like in other zanclids (Tyler et al. 1989), the supraoccipital crest is very high, peak-like, with a thickened anterior edge. The frontals are large and laterally expanded, forming a large part of the dorsal and anterior wall of the

orbit. A small bump is present on each frontal near the anterodorsal margin of the orbit; this bump is only observable in the holotype, and it appears to be absent in the pre-juvenile specimens. Part of the supraorbital lateral-line canal can be recognized in

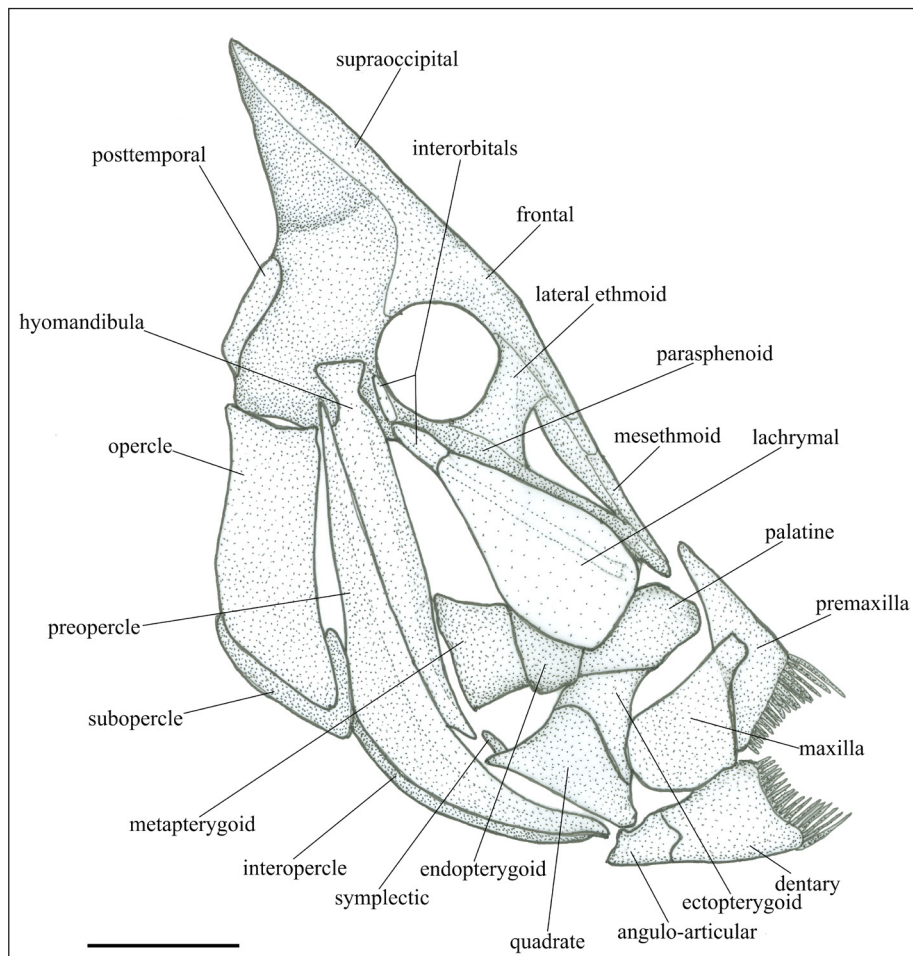


Fig. 3 - *Angiolinia mirabilis* n. gen. et sp. from the Eocene of Bolca. Interpretative reconstruction of the skull, right lateral view. Scale bar 10 mm.

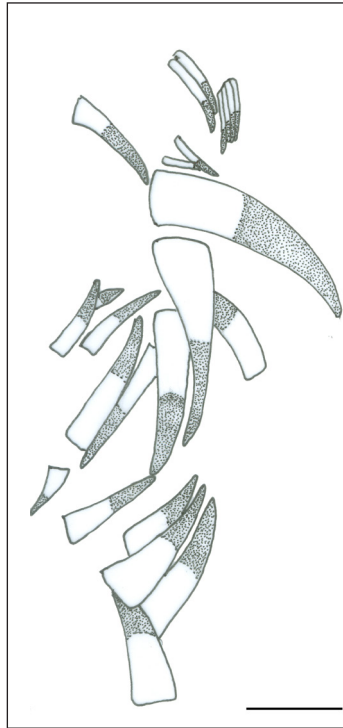
the holotype. The outer surfaces of the supraoccipital and frontals are extensively sculptured with shallow, narrow furrows that alternate with ridges, displaying an overall cancellous texture; the thick external bony layer of these bones is spongy and was probably fat filled in origin. The parietals cannot be recognized due to inadequate preservation. The lateral ethmoid is stout and columnar, forming the anterior wall of the orbit. The mesethmoid is elongate and distally pointed. The parasphenoid is thick and partially exposed in the ethmoid region and under the orbit. The parasphenoid apophysis is hidden by bones of the suspensorium and infraorbital series.

The lachrymal is large and oblong, drop-like, with a rounded anteroventral margin; it is placed along the snout, well forward with respect to the anterior margin of the orbit, and does not articulate with the lateral ethmoid (Fig. 3). The second and third infraorbitals are partially recognizable in the holotype; these bones are relatively small and tubular, and the third infraorbital bears what appears to be a rudimentary subocular shelf.

The mouth is larger than those of the other moorish idols, *Eozanclus brevirostris* and *Zanclus cornutus* (see, e.g., Blot & Voruz 1975; Tyler et al. 1989). The premaxilla bears an elongate ascending process, whose length slightly exceeds that of the alveolar process (Fig. 3). There are numerous setiform, elongate and apparently only slightly movable teeth, with smooth edges and a circular base. The teeth exhibit different sizes, those inserting in the anterior portion of the alveolar process being longer and thicker (Fig. 4). The maxilla is notably expanded distally and bound together with the premaxilla. There is no supramaxilla. The overall configuration of the upper jaws seems to indicate a very limited protrusibility. The mandible is rather elongate in the holotype (Fig. 3); its length is contained about eight times in SL. The dentary is distinctly larger and longer than the anguloarticular. The dentary teeth are identical to their opposite elements of the premaxilla.

The hyomandibula has a straight and elongate shaft bearing an anterior flange that extends for most of its length (Fig. 3). The articular head is broad, with a linear dorsal margin. The quadrate is

Fig. 4 - *Angiolinia mirabilis* n. gen. et sp. from the Eocene of Bolca. Holotype, CMC 39, jaw teeth. Scale bar 2 mm.



triangular in outline. The symplectic is straight, slender and cylindrical. The palatine is rather large and lies forward of the lateral ethmoid. There are no teeth on the palatine. The pterygoids are rather thin and laminar. The ectopterygoid is nearly triangular in outline, whereas the metapterygoid and endopterygoid are quadrangular.

The preopercle is crescent shaped and has smooth posterior and ventral margins (Fig. 3). The opercle is subrectangular, with straight anterior and ventral margins, a gently curved posterior margin and a slightly concave dorsal margin. The dilator process at the posterodorsal corner of the opercle is poorly developed. The morphology of the interopercle and subopercle is consistent with that of other zanclids. The interopercle is greatly elongate and narrow anteriorly but broad posteriorly.

The hyoid apparatus and the branchial skeleton are not preserved in the examined specimens, with the exception of the urohyal. The urohyal is triangular in outline, with a slightly concave posterior margin and a thickened ventral ridge (Fig. 1B).

The vertebral column is slightly sigmoid and consists of 22 (9+13) vertebrae (Fig. 1). The centra are thick, anteroposteriorly compressed, sub-rectangular in outline, and higher than long. The lateral surface of the centra is ornamented with irregular pits and ridges. The neural spine of the first verte-

bra is relatively slender, fused to its centrum, and interdigitates with the lower ends of the two anterior dorsal-fin pterygiophores. The neural spines of both the third and fourth vertebrae are situated between the third and fourth dorsal-fin pterygiophores, thereby implying that the third interneural space is vacant. The neural spines of the successive abdominal vertebrae and of the anterior seven caudal vertebrae are expanded anteroposteriorly due to the presence of laminar flanges with rounded profiles. These flanges originate along the posterior margin of the main axis of the neural spines. The neural spines of the posterior caudal vertebrae are slender and obliquely oriented. The haemal spines are similar to their neural counterparts, although slightly longer. Dorsal prezygapophyses are well developed along the entire vertebral column. Parapophyses of gradually increased size are present in the four posterior abdominal vertebrae. The parapophyses of the posteriormost abdominal vertebra is enlarged, resembling the condition observed in *Zanclus* (see Tyler et al. 1989) and *Eozanclus* [erroneously interpreted by Blot & Voruz (1975) as a laterally expanded rib forming what they called a "pseudobassin"]. Moderately slender ribs extending ventrally for most of the upper half of the abdominal cavity are present on the third to eighth abdominal vertebrae. Thin epineurals are associated with the posterior five abdominal and anterior five caudal vertebrae (Fig. 1B).

The caudal skeleton of *Angiolinia* is similar to that of *Zanclus* and consists of five autogenous hypurals, an autogenous parhypural, a single uroneural articulated with the compound centrum, and three epurals (Fig. 5). The neural spine of the second preural vertebra is short, reduced to a low crest with irregular profile. The haemal spines of the second and third preural vertebrae are autogenous. The neural and haemal spines of the fourth preural vertebra are slightly expanded and spatulate. The caudal fin contains 16 (I, 7+7, I) principal rays plus three upper and three lower procurrent rays.

There is a single supraneural (Fig. 6). The vertical main shaft of this bone is rather thick and inserts in the preneural space together with the first dorsal-fin pterygiophore.

The dorsal fin consists of seven spines plus 31 or 32 rays, supported by 36 or 37 pterygiophores (Tab. 2). The first two spines are rather short and distally pointed (Fig. 6), whereas the third is the

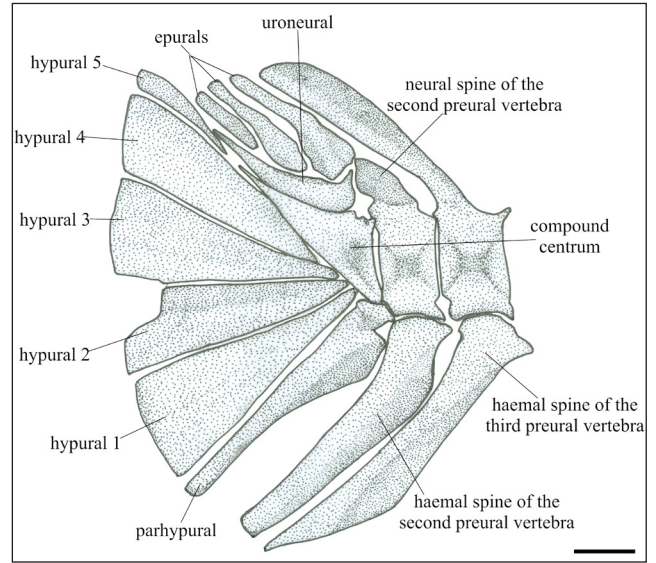


Fig. 5 - *Angiolinia mirabilis* n. gen. et sp. from the Eocene of Bolca. Interpretative reconstruction of the caudal skeleton, right lateral view. Scale bar 2 mm.

longest of the series, with its length contained about two times in SL. All but the two anterior dorsal-fin spines are filamentous distally. The first dorsal-fin spine is in supernumerary association on the first dorsal-fin pterygiophore (Fig. 6). In the two pre-juvenile individuals, the lateral surfaces of the dorsal-fin spines are characterized by shallow furrows. The first three dorsal-fin pterygiophores bear a ribbed and semicircular median flange around which the first three dorsal-fin spines likely rotated and locked (Fig. 6). The anterior 19 or 20 dorsal-fin pterygiophores contact each other, being also partially interdigitated. The dorsal-fin rays bear small spinules along their lateral margins.

The anal fin consists of three spines and 26 or 27 rays, supported by 25–28 pterygiophores (Tab. 2). The first two spines are supernumerary on the enlarged first anal-fin pterygiophore. The first anal-fin pterygiophore has a vertically oriented main shaft, which is expanded anteroventrally in front of the first anal-fin spine, resulting in a gently concave anterior profile; in addition, there are two ribbed median flanges around which the supernumerary spines probably rotated and locked.

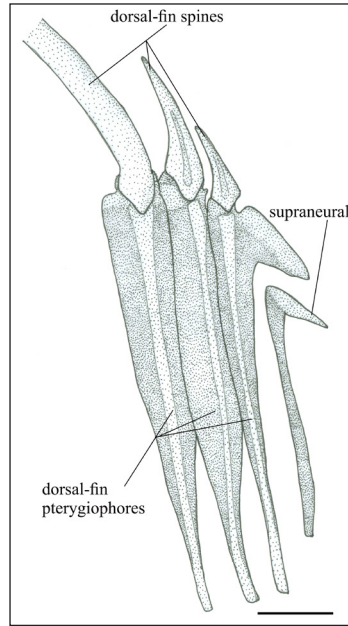
The anterior 15–17 anal-fin pterygiophores are closely associated, in some cases partially interdigitating with each other. Small spinules can be observed along the lateral margins of the anal-fin rays.

The posttemporal and an incomplete extrascapular are partially exposed in the holotype (Fig.

	Total length (mm)	Standard length (mm)	Head length	Body depth	Head depth	Snout length	Orbit diameter	Caudal peduncle length	Caudal peduncle depth	Mandible length	Predorsal length	Preadanal length	Prepectoral length	Prepelvic length
CMC 39	131.4	111.7	38.3	87.0	56.0	23.5	7.9	5.6	17.4	?	61.5	70.9	44.4	52.2
MCSNV I.C. 5	58.8	46.1	38.3	85.2	63.9	24.7	11.9	6.2	19.9	9.7	65.0	66.8	39.6	58.7
MCSNV I.C. 2-3	35.8	31.3	39.2	85.9	52.3	22.0	10.2	?	?	6.7	?	65.4	40.5	48.5
	Spiny dorsal-fin base length	Soft dorsal-fin base length	Anal-fin base length	First dorsal-fin spine length	Second dorsal-fin spine length	Longest dorsal-fin spine length	Longest dorsal-fin ray length	First anal-fin spine	Second anal-fin spine	Third anal-fin spine	Longest anal-fin ray	Pelvic-fin spine length	Basipterygium depth/length (not in % SL)	Pectoral disc width
CMC 39	13.1	44.3	44.1	3.6	5.9	(3rd) 50.6	(3rd) 23.6	3.9	6.6	14.0	(7th) 20.8	15.5	25.0	23.3
MCSNV I.C. 5	?	?	52.4	6.0	9.9	(4th) 45.1	?	?	?	22.1	(4th) 46.2	22.9	?	20.1
MCSNV I.C. 2-3	?	?	?	?	?	?	?	8.9	13.0	19.4	?	24.6	28.1	21.6

Tab. 1 - Measurements of *Angiolinia mirabilis* n. gen. et sp. Values are given as percentage of SL.

Fig. 6 - *Angiolinia mirabilis* n. gen. et sp. from the Eocene of Bolca. MCSNV I.C. 5, supraneural and anterior dorsal-fin pterygiophores, right lateral view. Scale bar 2 mm.



1B). The supracleithrum is narrow, with an irregular anterior profile. The supracleithrum lateral-line canal appears to be absent. The cleithrum is greatly expanded ventrally and is characterized by a remarkably convex anterior profile. The coracoid is expanded, exhibits a rounded profile, and is devoid of a postcoracoid process. Owing to considerable expansion of the lower portion of the cleithrum and of the coracoid, like in other zanclids, the lower half of the pectoral girdle of *Angiolinia* forms a large discoid structure, herein referred to as the pectoral disc, whose width ranges from 20.1 to 23.3% SL. The scapula is subquadrangular in outline and centrally pierced by a rounded scapular foramen. The coracoid, scapula and ventral portion of the cleithrum form a large discoid structure whose width is contained between four and five times in SL. There are two postcleithra (Figs. 1B, 2B), of which the dorsal one is short and oblong and the ventral one is rather thick and vertically oriented, almost reaching the ventral wall of the abdominal cavity. The pectoral fin is obliquely oriented and has at least 12 rays, supported by four small pectoral-fin radials.

The basipterygium is large and bears large iliac (anterior) and ischiac (posterior) processes and a prominent pubic (ascending) process (Figs. 1, 2). The area between the iliac and pubic processes is distinctly concave. The greatest depth-to-length ratio of the basipterygium ranges between 25 to slightly more than 28%. The pelvic fin consists of a single thick and pointed spine plus five rays extending posteriorly to the level of the third anal-fin spine. The relative length of the pelvic-fin spine decreases during ontogeny, reaching about 15% SL in adults.

The entire body, including head and the median-fin bases, is continuously covered with polygonal or dorso-ventrally elongate scale plates bearing upright spinules (Fig. 1A). The upright spinules are especially numerous (20 or more) on the dorso-ventrally elongate scale plates. Small spinules occur laterally along the rays of the median and paired fins.

The scales of the lateral-line series are evident in the epaxial region from the upper portion of the neural spine of the first caudal vertebra, and then curving down on the side until the level of the centrum of the eighth caudal vertebra, after which they can no longer be seen.

The only traces of original pigmentation are short and irregular bands of dark pigment in the abdominal region of the holotype, just below the vertebral centra.

COMPARISON AND RELATIONSHIPS

Within percomorphs, zanclids form a well-defined clade, the acanthuriforms, together with the Acanthuridae and Luvaridae. Morphological and molecular evidences concur to suggest a sister-group relationship between acanthurids and zanclids within the acanthuriforms (e.g., Tyler 1970; Mok 1977; Leis & Richards 1984; Johnson & Washington 1987; Tyler et al. 1989; Winterbottom 1993;

	Vertebrae	Dorsal-fin formula	Anal-fin formula	Pectoral-fin rays	Pelvic-fin formula	Dorsal-fin pterygiophore formula	Anal-fin pterygiophore formula
CMC 39	9+13	VII+31	III+27	12?	I, 5	1/1/1/1/1/1/1/1/1/3/2/4/2/4/3/3/3	1/2/3/2/3/3/4/4/3/3
MCSNV I.C. 5	9+13	VII+32?	III+26	11/12?	I, 5	1/1/1/1/1/1/1/1/1/3/2/3/2/3/3/4/3/4/2	1/2/2/3/3/2/4/3/3/2
MCSNV I.C. 2-3	9+13	?	III+?	?	I, 5	1/1/1/1/1/1/1/2/2/3/3/3/4/3/?	1/2/3/2/4/3/4/?

Tab. 2 - Counts for *Angiolinia mirabilis* n. gen. et sp.

Winterbottom & McLennan 1993; Tang et al. 1999; Holcroft & Wiley 2008; Sorenson et al. 2013; Gill & Leis 2019). Tyler (1970) evidenced the remarkable osteological similarity between zancids and acanthurids and pointed out that there may be merit in recognizing zancids as a lineage within the acanthurids, rather than a separate family. In any case, zancids and acanthurids share at least two synapomorphies (Tyler et al. 1989; Gill & Leis 2019): third interneural space vacant; and first dorsal- and anal-fin pterygiophores bearing a semicircular and ribbed median flange for locking the anterior spines, which can be easily recognized also in fossil material.

Interestingly, both of these features are shared by the Eocene moorish idols *Angiolinia mirabilis* and *Eozanclus brevirostris*, as well as by another extinct acanthuriform, *Massalongius gazolai* (Massalongo, 1859), which was redescribed by Tyler & Bannikov (2005) based on a single specimen collected from the Pesciara site, Bolca. The phylogenetic analysis carried out by Tyler & Bannikov (2005) indicated that this Eocene acanthuriform is the sole member of the family Massalongiidae, which represents the sister group to the Zancidae. All the zancid species, both extant and fossil, share a unique set of features with *Massalongius* (Tyler & Bannikov 2005), namely a very high and triangular supraoccipital crest, three ribbed median pterygiophore locking flanges for the anterior dorsal-fin spines, high spinous portion of the dorsal fin (with spines exceeding 40% SL), and teeth slender, smooth, delicate, and forming a setiform or villiform band.

As documented by Tyler & Bannikov (2005), *Massalongius* exhibits a number of autapomorphies that clearly separate it from the zancid taxa.

The definition of the Zancidae provided by Tyler et al. (1989) was, in large part, based on the extant genus *Zanclus*, with only a few of the recognized apomorphic features also shared by the Eocene *Eozanclus*. The morphological analysis of *Angiolinia* reported above indicates that all three currently known zancid genera share at least two unambiguous features that unquestionably support the monophyletic status of this family (see Tyler & Bannikov 2005): high number of dorsal- (31–43) and anal-fin (26–38) rays; and anterior margin of the cleithrum expanded and remarkably convex below the level of the post-cleithrum, forming a discoid structure (pectoral disc) in conjunction with the coracoid. *Angiolinia* differs from other zancids in having fewer dorsal- (31 or

32 vs 38–43) and anal-fin rays (26 or 27 vs 30–38; see also Tab. 2). *Massalongius* has 20 rays in both the dorsal and anal fins (Tyler & Bannikov 2005), and the vast majority of other acanthuriforms are characterized by fewer than 30 dorsal-fin rays and 26 or fewer anal-fin rays (see Kuitert & Debelius 2001). Furthermore, all the other acanthuriforms exhibit a non-expanded anteroventral portion of the cleithrum with a nearly straight or slightly curved anterior profile.

Within the zancids, *Eozanclus* clearly differs from *Angiolinia* and *Zanclus* by having two supernumerary spines (and, consequently, two ribbed locking flanges) on the first dorsal-fin pterygiophore (Blot & Voruz 1975) and by having two uroneurals in the caudal skeleton (Fig. 7A). Both of these features represent the plesiomorphic acanthuriform condition. Two supernumerary spines on the first dorsal-fin pterygiophore are present in *Massalongius* and in the other acanthuriforms (see Johnson & Washington 1987; Tyler et al. 1989; Tyler & Bannikov 2005), suggesting that the single supernumerary spine shared by *Angiolinia* and *Zanclus* represents a derived condition. Similarly, the presence of two uroneurals in the caudal skeleton is shared with *Massalongius* and extinct surgeonfishes (Tyler 2005a, 2005b; Tyler & Bannikov 2005), including the primitive *Gazolaichthys vestenanae* Blot & Tyler, 1990 and *Padovathurus gaudryi* (Zigno, 1887) (Fig. 7). These features support the basal position of *Eozanclus* within the Zancidae.

Eozanclus further differs from both *Angiolinia* and *Zanclus* by having remarkably expanded parapophyses on the ninth abdominal vertebra. These expanded parapophyses were erroneously interpreted as a modified pair of ribs by Blot & Voruz (1975), who referred to them as “pseudobassin.” In addition, *Eozanclus* is unique within the zancids in having the fourth dorsal-fin spine as the longest of the series, reaching about 50% of SL.

The overall physiognomy and skeletal morphology of *Angiolinia* appear to be intermediate between those of *Eozanclus* and *Zanclus*. The body is almost discoid in outline, with body depth between 85.2 and 87.0% SL (Tab. 3), which is deeper than that of *Eozanclus* (81.8–82.3% SL) but less extreme compared with *Zanclus*, in which body depth is almost comparable to SL (Tab. 3). A similar pattern, with *Angiolinia* showing values intermediate between those of *Eozanclus* and *Zanclus*, can be observed for other body proportions (Tab. 3), including head length, snout length, predorsal length, preanal length and pectoral disc width.

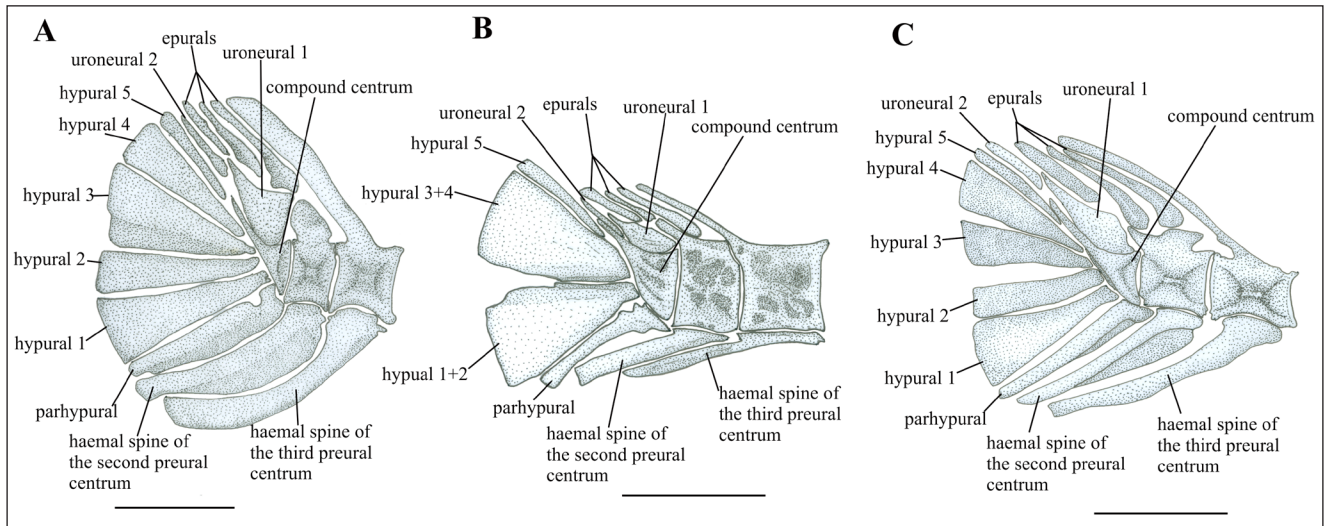


Fig. 7 - Interpretative reconstructions of the caudal skeleton of A) the zanclid *Eozanclus brevirostris* (Agassiz, 1835), MNHN Bol 4, holotype; B) the acanthurid *Gazolaiichthys vestenanovae* Blot & Tyler, 1990, MCSNV B.65.14, holotype; and C) the acanthurid *Padovathurus gaudryi* (Zigno, 1887), MGPUP 11406, holotype. Scale bars 5 mm.

With respect to skeletal morphology, *Angiolinia* and *Zanclus* share the presence of a single uroneural in the caudal skeleton (Fig. 5), a single supernumerary spine on the first dorsal-fin pterygiophore (Fig. 6), and a series (all but the first two) of distally filamentous dorsal-fin spines. *Angiolinia* retains, however, the plesiomorphic condition of two median ribbed flanges in the first anal-fin pterygiophore and two separate postcleithra (Fig. 1), which are also found in *Eozanclus* (Fig. 8A; see Blot & Voruz 1975). Two separate postcleithra are also present in *Massalongius* (Fig. 8B), whereas *Zanclus* has two separate postcleithra while a larva, but they fuse into a single element during ontogeny (Johnson & Washington 1987; Tyler et al. 1989). Within acanthuriforms, *Luarus* also exhibits an ontogenetic fusion of the postcleithra, whereas acanthurids, including the fossil taxa, have a single postcleithrum. Both Johnson & Washington (1987) and Tyler et al. (1989) interpreted the presence of a single postcleithrum as a synapomorphy shared by luvarids, zanclids and acanthurids. The condition observed in fossil zanclids and *Massalongius* suggests that the possession of a single postcleithrum in *Luarus*, *Zanclus* and acanthurids should be regarded as a separate character, thereby representing an autapomorphy for *Zanclus*. Given that acanthurids have a single postcleithrum during ontogeny (Johnson & Washington 1987), this feature possibly represents a synapomorphy for the family.

In addition to the presence of a single postcleithrum, *Zanclus* is characterized by a unique mor-

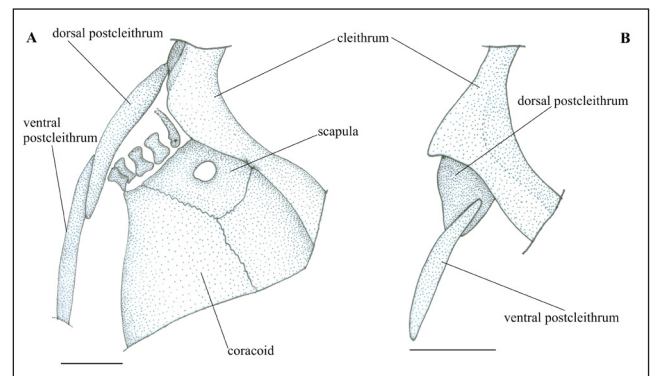


Fig. 8 - Right lateral view of the central region of the pectoral girdle of A) *Eozanclus brevirostris* (Agassiz, 1835) and B) *Massalongius gazolai* (Massalongio, 1859). Scale bars 5 mm.

phology, namely a very deep and discoid body (body depth reaching 98% SL), a tubular snout, a conical protuberance on each frontal close to the anterodorsal margin of the orbit (Tyler et al. 1989), and the presence of a retrorse spine on the lachrymal (see Tyler 1970).

Summarizing the comparative discussion above, the Eocene acanthuriform *Massalongius gazolai* represents the sister group to the Zanclidae, and the latter can be primarily defined by two morphological features (Fig. 9): cleithrum broadly expanded and convex anteroventrally, and together with the coracoid forming the pectoral disc; and presence of a large number of dorsal- and anal-fin rays. Within the zanclids, *Eozanclus* occupies a basal position, thereby representing the sister group to the pair formed by

Angiolinia and *Zanclus*. This derived clade is supported by the shared possession of a single supernumerary spine on the first dorsal-fin pterygiophore, a single uroneural in the caudal skeleton, and all but the first two dorsal-fin spines distally filamentous (Fig. 9).

Acknowledgments. We thank Roberto Zorzin (MCSNV), Massimo Cerato (CMC), Mariagabriella Fornasiero (MGPUP), Alan Pradel and Monette V éran (MNHN), and Amy Henrici (CMNH) for permission to examine the fossil material under their care and for logistic support. At the Smithsonian Institution we thank Ai Nonaka and G. David Johnson for access to their specimens of early life history stages of *Zanclus*, James Di Loreto for photographic services, and Kathy Hollis for facilitating our loans of specimens. The National Science Foundation funded the participation of GC and JCT [grant DEB-1541552]. The research of GC was also supported by grants [ex-60% 2022 and 2023] from the Università degli Studi di Torino. We thank Diane M. Tyler for editing the manuscript.

APPENDIX - DIAGNOSES OF THE OTHER MOORISH IDOL GENERA

Genus *Eozanclus* Blot & Voruz, 1970

Emended diagnosis: Body deep, rhomboid in outline, laterally compressed; body depth approximately 82% SL; head length about one-third (31.7–34.3%) of SL; snout length 20–21.9% SL; parapophysis of the ninth abdominal vertebra expanded; two uroneurals; first dorsal-fin pterygiophore bears two supernumerary spines; median locking flanges on the first three dorsal-fin spines; fourth dorsal-fin spine much longer than the others, reaching about 50% SL; 38 dorsal-fin rays; median locking flanges on the first two anal-fin spines; 30 or 31 anal-fin rays; pectoral fin with 14 moderately elongate rays; caudal peduncle short, measuring about 4% SL; caudal fin slightly rounded; basipterygium depth/length ratio 24.7% SL; two postcleithra; pectoral disc oblong, measuring 16.8–18.6% SL.

Type species: *Zanclus brevirostris* Agassiz 1835.

Composition: Type species only.

Genus *Zanclus* Cuvier & Valenciennes, 1831

Emended diagnosis: Body discoid, laterally compressed, very deep; body depth between 94 to 98.6% SL; snout tubular, elongate, horizontally developed, its length reaching one-fourth (24.4–25.3) of SL; adults with a bony projection on the frontals situated in front of each eye; retrorse spine on the lachrymal; a single uroneural; first dorsal-fin pterygiophore bears a single supernumerary spine; median locking flanges on the first two dorsal-fin spines; all but the first two dorsal-fin spines distally filamentous; third dorsal-fin spine extremely elongate, usually much longer than the body (104.6–115.4% SL); first dorsal-fin ray considerably elongate, reaching 90% SL; 38–43 dorsal-fin rays; median locking flange on the first anal-fin spine; 31–38 anal-fin rays; pectoral fin with 18 or 19 elongate rays; caudal fin slightly emarginated; basipterygium depth/length ratio 18.2–20.1% SL; single postcleithrum (ontogenetic fusion); pectoral disc broad, measuring 26.5–34% SL.

Type species: *Chaetodon cornutus* Linnaeus, 1758.

Composition: Type species only.

	Head length	Body depth	Head depth	Snout length	Orbit diameter	Caudal peduncle length	Caudal peduncle depth	Mandible length	Predorsal length	Prenal length	Prepectoral length	Prepelvic length	Spiny dorsal-fin base length
<i>Angiolinia mirabilis</i> n. gen. et sp.	38.3–39.2	85.2–87.0	52.3–63.9	22.0–24.7	7.9–11.9	5.6–6.2	17.4–19.9	6.7–9.7	61.5–65.0	65.4–70.9	39.6–44.4	48.5–58.7	13.1
<i>Eozanclus brevirostris</i> (Agassiz, 1835)	31.7–34.3	81.8–82.3	52.9–59.3	20.0–21.9	7.6–8.1	4.1–4.3	15.3–15.9	11.8	57.8–60.7	63.5–64.8	37.4–40.6	42.5	11.4–12.2
<i>Zanclus cornutus</i> (Linnaeus, 1758)	36.3–40.3	94.0–98.6	57.7–61.4	24.4–25.3	9.9–11.7	5.0–5.8	13.5–14.7	6.7–7.3	64.3–67.3	73.1–77.4	33.8–40.3	52.3–55.2	7.4–12.1
	Soft dorsal-fin base length	Anal-fin base length	First dorsal-fin spine length	Second dorsal-fin spine length	Longest dorsal-fin spine length	Longest dorsal-fin ray length	First anal-fin spine	Second anal-fin spine	Third anal-fin spine	Longest anal-fin ray	Pelvic-fin spine length	Basipterygium depth/length ratio (not in % SL)	Pectoral disc width
<i>Angiolinia mirabilis</i> n. gen. et sp.	44.3	44.1–52.4	3.6–6.0	5.9–9.9	45.1–50.6	23.6	3.9–8.9	6.6–13.0	14.0–22.1	20.8–46.2	15.5–24.6	25.0–28.1	20.1–23.3
<i>Eozanclus brevirostris</i> (Agassiz, 1835)	53.5–58.0	48.6–53.0	2.2–3.4	4.0–4.4	51.0–51.7	31.6–51.7	5.1	7.2	12.9	15.3–19.5	22.1	24.7	16.8–18.6
<i>Zanclus cornutus</i> (Linnaeus, 1758)	52.1–65.0	47.3–52.0	2.8–4.8	4.4–6.7	104.6–115.4	60.2–90.0	4.2–4.9	6.4–7.5	20.5–21.2	36.6–37.2	20.9–22.6	18.2–20.1	26.5–34.0

Tab. 3 - Summary of morphometric features of fossil and extant moorish idols. Morphometric data of *Angiolinia mirabilis* n. gen. et sp. based on CMC 39 (holotype), MCSNV I.C. 2-3 (paratype), and MCSNV I.C. 5 (paratype). Morphometric data of *Eozanclus brevirostris* (Agassiz, 1835) based on MNHN Bol 4-5 (holotype) and CMNH 4415-5306. Morphometric data of *Zanclus cornutus* (Linnaeus, 1758) based on USNM 428906 and USNM 52506a-b. Values are given as percentage of SL.

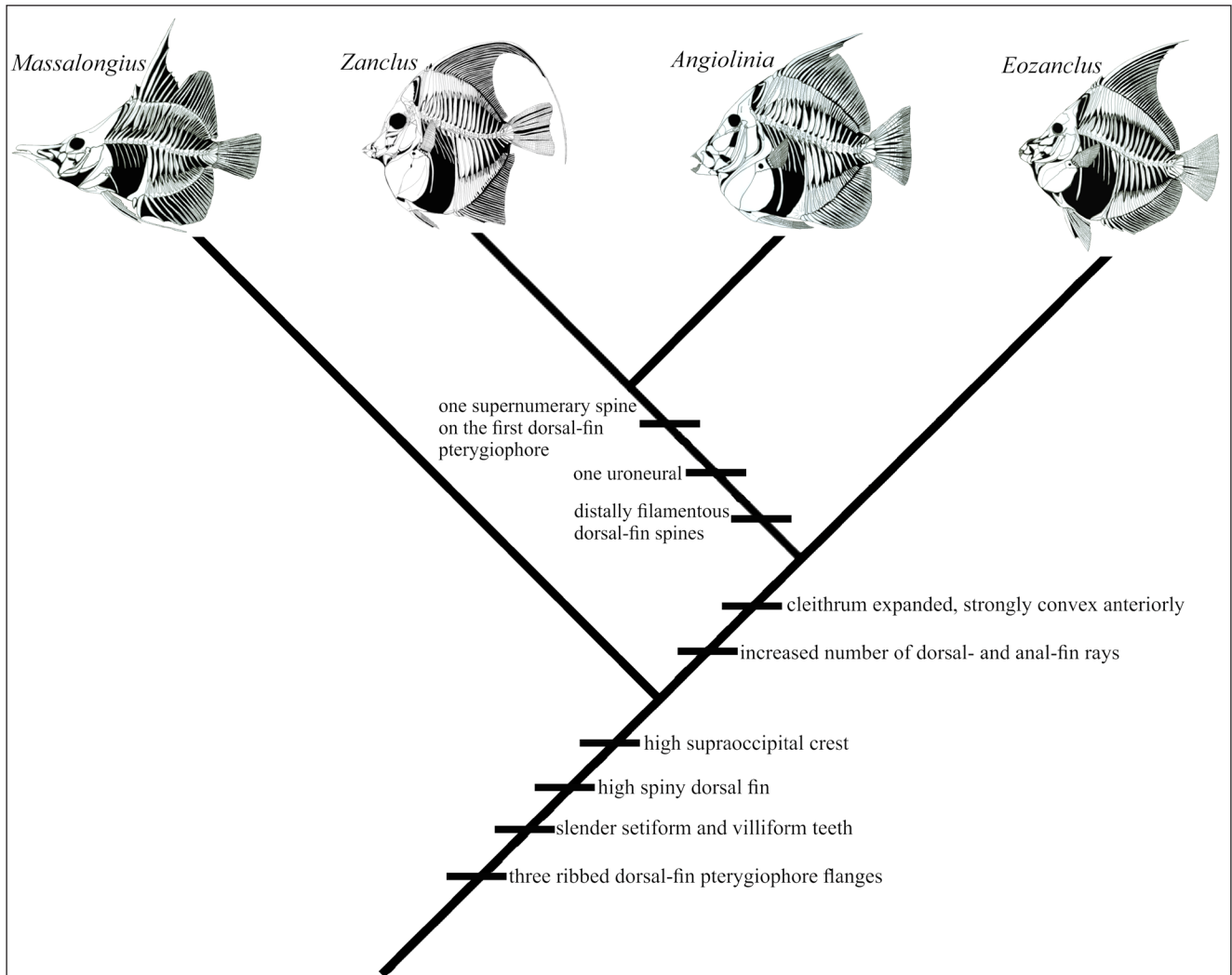


Fig. 9 - Cladogram showing hypothetical relationships of *Angiolinia* n. gen. within the Zanclidae.

REFERENCES

- Agassiz L. (1833-1844) - Recherches sur les poissons fossiles. Petitpierre, Neuchatel (four volumes, text and plates), 1420 pp.
- Agassiz L. (1835) - Kritische revision der Ittiolitologia Veronese abgebildeten fossilen Fische. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde*, 1835: 290-316.
- Bannikov A.F. (2014) - The systematic composition of the Eocene actinopterygian fish fauna from Monte Bolca, northern Italy, as known to date. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 15: 23-34.
- Bannikov A.F. & Carnevale G. (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. & Carnevale G. (2016) †*Carlomonnius quasigobius* gen. et sp. nov.: The first gobioid fish from the Eocene of Monte Bolca, Italy. *Bulletin of Geosciences*, 91: 13-22.
- Bellwood D.R. (1996) - The Eocene fishes of Monte Bolca: The earliest coral reef fish assemblage. *Coral Reefs*, 15: 11-19.
- Bleeker P. (1876) - Systema Percarum revisum. Pars II. *Archives Néerlandaises des Sciences Exactes et Naturelles*, Haarlem, 11: 289-340.
- Blot J. (1969) - Les poissons fossiles du Monte Bolca classés jusqu'ici dans les familles des Carangidae, Menidae, Ephippidae, Scatophagidae. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 1: 1-525.
- Blot J. (1980) - La faune ichthyologique des gisements du Monte Bolca (Province de Verone, Italie). Catalogue systématique présentant l'état actuel des 160 recherches concernant cette faune. *Bulletin du Muséum national d'histoire naturelle Paris*, 2: 339-396.
- Blot J. & Tyler J.C. (1990) - New genera and species of fossil surgeon fishes and their relatives (Acanthuroidei, Teleostei) from the Eocene of Monte Bolca, Italy, with application of the Blot formula to both fossil and Recent forms. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 6: 13-92.
- Blot J. & Voruz C. (1970) - Les poissons fossiles du Monte Bolca. La famille des Zanclidae. *Memorie del Museo Civico di Storia Naturale di Verona*, 18: 31-42.
- Blot J. & Voruz C. (1975) - La famille des Zanclidae. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 2: 233-271.

- Bosellini A. (1989) - Dynamics of Tethyan carbonate platform. In: Crevello P.D., Wilson J.L. & Read J.F. (Eds.) - Controls on Carbonate Platform and Basin Platform. *SEPM Special Publications*, 44: 3-13.
- Carnevale G. (2006) - Morphology and biology of the Miocene butterflyfish *Chaetodon fischeuri* (Teleostei: Chaetodontidae). *Zoological Journal of the Linnean Society*, 146: 251-267.
- Carnevale G., Bannikov A.F., Marramà G., Tyler J.C. & Zorzin R. (2014) - The Pesciara-Monte Postale Fossil-Lagerstätte, 2: Fishes and other vertebrates. *Rendiconti della Società Paleontologica Italiana*, 4: 37-63.
- Carnevale G. & Pietsch T.W. (2009) - An Eocene frogfish from Monte Bolca, Italy: The earliest skeletal record for the family. *Palaeontology*, 52: 745-752.
- Cuvier G. & Valenciennes A. (1831) - Histoire naturelle des poissons. Tome septième. Livre septième: Des Squamipennes; Livre huitième: Des poissons à pharyngiens labryrinthiformes. P. Bertrand Editeur, Paris, 531 pp.
- Friedman M. & Carnevale G. (2018) - The Bolca Lagerstätten: Shallow marine life in the Eocene. *Journal of the Geological Society*, 175: 569-579.
- Gill A.C. & Leis J.M. (2019) - Phylogenetic position of the fish genera *Lobotes*, *Datnioides* and *Hapalogenys*, with a reappraisal of acanthuriform composition and relationships based on adult and larval morphology. *Zootaxa*, 4680: 1-81.
- Holcroft N.I. & Wiley E.O. (2008) - Acanthuroid relationships revisited: A new nuclear gene-based analysis that incorporates tetraodontiform representatives. *Ichthyological Research*, 55: 274-283.
- Johnson G.D. & Washington B.B. (1987) - Larvae of the moorish idol, *Zanclus cornutus*, including a comparison with other larval acanthuroids. *Bulletin of Marine Science*, 40: 494-511.
- Jordan D.S. (1923) - A classification of fishes, including families and genera as far as known. *Stanford University Publications, University Series, Biological Sciences*, 3: 77-243.
- Kuiter R.H. & Debelius H. (2001) - Surgeonfishes, Rabbitfishes and Their Relatives: A Comprehensive Guide to Acanthuroidei. TMC Publishing, Chorleywood, 208 pp.
- Leis J.M. & Richards W.J. (1984) - Acanthuroidei: Development and relationships. In: Moser H.G., Richards W.J., Cohen D.M., Fahay M.P., Kendall Jr. A.W. & Richardson S.L. (Eds.) - Ontogeny and Systematics of Fishes. *American Society of Ichthyologists and Herpetologists, Special Publication*, 1: 547-551.
- Linnaeus C. (1758) - Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Holmiae, 824 pp.
- Marramà G., Bannikov A.F., Tyler J.C., Zorzin R. & Carnevale G. (2016a) - Controlled excavations in the Pesciara and Monte Postale sites provide new insights about the paleoecology and taphonomy of the fish assemblages of the Eocene Bolca Konservat-Lagerstätte, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 454: 228-245.
- Marramà G. & Carnevale G. (2015) - The Eocene sardine †*Bolcaichthys catopygopterus* (Woodward, 1901) from Monte Bolca, Italy: Osteology, taxonomy and paleobiology. *Journal of Vertebrate Paleontology*, 35: e1014490.
- Marramà G., Garbelli C. & Carnevale G. (2016b) - A morphospace for the Eocene fish assemblage of Bolca, Italy: A window into the diversification and ecological rise to dominance of modern tropical marine fishes. *Bollettino della Società Paleontologica Italiana*, 55: 11-21.
- Marramà G., Garbelli C. & Carnevale G. (2016c) - A clade-level morphospace for the Eocene fishes of Bolca: Patterns and relationships with modern tropical marine fish assemblages. *Bollettino della Società Paleontologica Italiana*, 55: 139-156.
- Marramà G., Giusberti L. & Carnevale G. (2022) - A Rupelian coral reef fish assemblage from the Venetian Southern Alps (Berici Hills, NE Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 128: 469-513.
- Massalongo A. (1859) - Specimen photographicum animalium quorundam plantarumque fossilium Agri Veronensis. Vicentini-Franchini, Verona, 101 pp.
- Mok H.-K. (1977) - Gut patterns of the Acanthuridae and Zanclidae. *Japanese Journal of Ichthyology*, 23: 215-219.
- Papazzoni C., Fornaciari E., Giusberti L., Vescogni A. & Fornaciari B. (2017) - Integrating shallow benthic and calcareous nannofossil zones: The Lower Eocene of the Monte Postale section (Northern Italy). *Palaios*, 32: 1-12.
- Randall J.E. (1955) - Fishes of the Gilbert Islands. *Atoll Research Bulletin*, 47: 1-249.
- Rossi V., Unitt R., McNamara M., Zorzin R. & Carnevale G. (2022) - Skin patterning and internal anatomy in a fossil moonfish from the Eocene Bolca Lagerstätte illuminate the ecology of ancient reef fish communities. *Palaeontology*, 65: e12600.
- Sorenson L., Santini F., Carnevale G. & Alfaro M.E. (2013) - A multi-locus timetree of surgeonfishes (Acanthuridae, Percomorpha), with a revised taxonomy of the family. *Molecular Phylogenetics and Evolution*, 68: 150-160.
- Strasburg D.W. (1962) - Pelagic stages of *Zanclus canescens* from Hawaii. *Copeia*, 1962: 844-845.
- Tang K.L., Berendzen P.B., Wiley E.O., Morissey J.F., Winterbottom R. & Johnson G.D. (1999) - The phylogenetic relationships of the suborder Acanthuroidei (Teleostei: Perciformes) based on molecular and morphological evidence. *Molecular Phylogenetics and Evolution*, 11: 415-425.
- Tyler J.C. (1970) - Osteological aspects of interrelationships of surgeon fish genera (Acanthuridae). *Proceedings of the Academy of Natural Sciences of Philadelphia*, 122: 87-124.
- Tyler J.C. (2005a) - Redescription and basal phylogenetic placement of the acanthurid surgeon fish *Gazolaichthys vestenanovae* from the Eocene of Monte Bolca, Italy (Perciformes; Acanthuroidea). *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 11: 97-117.
- Tyler J.C. (2005b) - A new genus for the surgeon fish *Acanthurus gaudryi* De Zigno, 1887 from the Eocene of Monte Bolca, Italy, a morphologically primitive basal taxon of Acanthuridae (Acanthuroidea, Perciformes). *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 11: 149-163.
- Tyler J.C. & Bannikov A.F. (2005) - *Massalongius*, gen. & fam. nov., a new clade of acanthuroid fishes (Perciformes, Acanthuroidea) from the Eocene of Monte Bolca, Italy, related to the Zanclidae. *Studi e Ricerche sui Giacimenti Terziari di Bolca*, 11: 75-95.
- Tyler J.C., Johnson G.D., Nakamura I. & Collette B.B. (1989) - Morphology of *Luvarus imperialis* (Luvaridae), with a phylogenetic analysis of the Acanthuroidei (Pisces). *Smithsonian Contributions to Zoology*, 485: 1-78.

- Volta G.S. (1796) - Ittiolitologia Veronese del Museo Bozziano ora annesso a quello del Conte Giovambattista Gazola e di altri gabinetti fossili veronesi. Stamperia Giuliani, Verona, 323 pp.
- Winterbottom R. (1993) - Myological evidence for the phylogeny of Recent genera of surgeonfishes (Percomorpha, Acanthuridae), with comments on the Acanthuroidei. *Copeia*, 1993: 21-39.
- Winterbottom R. & McLennan D.A. (1993) - Cladogram versatility: Evolution and biogeography of acanthuroid fishes. *Evolution*, 47: 1557-1571.
- Zigno A. De (1887) - Nuove aggiunte alla ittiofauna dell'epoca Eocena. *Memorie dell'Istituto Veneto di Scienze, Lettere ed Arti*, 23: 9-33.

