

***Zorzinilabrus furcatus*, a new genus and species of labrid fish (Perciformes) from the Eocene of Bolca in northern Italy**

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ABSTRACT

A new genus and species of labroid fish, *Zorzinilabrus furcatus* (family Labridae) is described based on a single skeleton from the Eocene locality Bolca in northern Italy. *Zorzinilabrus* gen. nov. is characterized by a unique mosaic of characters, including labrid synapomorphies (such as a single supraneural, oligomerization of the caudal skeleton and pharyngognath) and features plesiomorphic for labrids (two supernumerary dorsal-fin spines and forked caudal fin with numerous procurrent rays). In some characters *Zorzinilabrus* gen. nov. differs from the known Labridae, having very slender and flexible unpaired-fin spines (vs. stronger spines in labrids), as few as seven dorsal and two anal-fin spines (vs. not less than eight dorsal and three anal-fin spines in labrids), four anal-fin pterygiophores placed anterior to the second haemal spine (vs. two anal-fin pterygiophores anterior to the second haemal spine in labrids). In these characters *Zorzinilabrus* gen. nov. resembles basal labroids from Monte Bolca such as *Tortonesia* (Tortonesidae). *Zorzinilabrus* appears to represent the earliest branching lineage within the Labridae. A functional interpretation of the morphology of *Zorzinilabrus*, including the unusual forked caudal fin, suggests that *Zorzinilabrus* fed on plankton away from reefs or hardgrounds. This is the earliest record of planktivory within the Labroidei s.s. or Labridae.

Key words: Perciformes, Labroidei, new genus and species, Eocene, northern Italy, Bolca locality.

RIASSUNTO

Un nuovo genere e nuova specie di labroide, *Zorzinilabrus furcatus* (famiglia Labridae) viene descritto sulla base di un singolo scheletro della località eocenica di Bolca, in Italia settentrionale. *Zorzinilabrus* nov. gen. è caratterizzato da un insieme unico di caratteri, che include sinapomorfie dei labridi (come un unico supraneurale, l'oligomerizzazione dello scheletro della pinna caudale e il peculiare apparato faringeo) oltre a caratteri plesiomorfici per i labridi (due spine dorsali supranumerarie e pinna caudale biforcata con numerosi raggi accessori). Per alcuni caratteri *Zorzinilabrus* nov. gen. differisce dai Labridae noti, per avere le spine delle pinne impari allungate e flessibili (vs. spine più robuste nei labridi), sette spine alla pinna dorsale e due alla pinna anale (vs. non meno di otto spine alla pinna dorsale e tre alla pinna anale nei labridi), quattro pterigiofori della pinna anale in posizione anteriore rispetto alla seconda spina emale (vs. due pterigiofori della pinna anale in posizione anteriore rispetto alla seconda spina emale nei labridi). In questi caratteri *Zorzinilabrus* nov. gen. assomiglia ai labroidi basali di Bolca come il genere *Tortonesia* (Tortonesidae). *Zorzinilabrus* sembra rappresentare la prima ramificazione all'interno dei Labridae. Un'interpretazione funzionale della morfologia di *Zorzinilabrus*, inclusa l'insolita pinna caudale biforcata, suggerisce che *Zorzinilabrus* si nutriva di plancton lontano dalla scogliera corallina o dagli hardground. Questo rappresenta la prima testimonianza di planctofagia all'interno dei Labroidei s.s. o Labridae.

Parole chiave: Perciformes, Labroidei, nuovo genere e nuova specie, Eocene, Italia settentrionale, Bolca.

INTRODUCTION

The Early Eocene fish fauna of the famous locality Monte Bolca, to the north of Verona in northern Italy, is exceptionally rich in marine fishes, especially the acanthomorphs. Monte Bolca marks the first fossil record of many groups of fishes found on

modern coral reefs (BELLWOOD, 1996). Some groups of Recent coral reef fishes (e.g., butterflyfishes and gobies) first appeared only in the Oligocene or later in the Eocene (COWMAN and BELLWOOD 2011; NEAR *et al.*, 2013); these were represented in the Bolca assemblage by their extinct ecological analogues (BANNIKOV, 2004a, b). For example, true gobioids are

only represented in Bolca by a single specimen of diminutive fish (BANNIKOV and CARNEVALE, 2016). Of the fishes with pharyngeal jaws, except for discoveries of fragmentary remains (pharyngeal jaws) elsewhere, the Bolca fish fauna establishes the earliest known record of the Pharyngognathi or Labroidei. After an extensive study of the Bolca pharyngognath fishes spanning more than 25 years (BELLWOOD, 1991, 1995, 1999; SORBINI *et al.*, 1991; BANNIKOV and SORBINI, 1991; BELLWOOD and SORBINI, 1996; BANNIKOV, 2004b; BANNIKOV and CARNEVALE, 2010, 2012; BANNIKOV and BELLWOOD, 2014) (see overview in BANNIKOV and BELLWOOD, 2015), the latest lists of the Monte Bolca fishes (BANNIKOV, 2014; CARNEVALE *et al.*, 2014) include nine monotypic pharyngognath taxa: three Labridae (*Phyllopharyngodon* BELLWOOD, 1991, *Eocoris* BANNIKOV et SORBINI, 1991 and *Bellwoodilabrus* BANNIKOV et CARNEVALE, 2010), three Pomacentridae (*Palaeopomacentrus* BELLWOOD et SORBINI, 1996, *Lorenzichthys* BELLWOOD, 1999 and *Sorbinichromis* BANNIKOV et BELLWOOD, 2014), and a number of taxa of *incertae sedis* including *Tortonesia* SORBINI, 1983, *Sorbinia* BELLWOOD, 1995, and *Quasicichla* BANNIKOV, 2004. Most recently BANNIKOV and BELLWOOD (2015) added one more labrid taxon, *Labrobolcus giorgioi*, to the list, bringing the total number of Labridae to four.

Recent molecular evidence indicates that the Pharyngognathi and Labroidei *sensu lato* (following STIASSNY and JENSEN, 1987) is not monophyletic and that the Labroidei *s.l.* incorporates at least two distinct lineages, the Labridae which remains in the Labroidei *sensu stricto*, and the Pomacentridae and Cichlidae (MIYA *et al.*, 2003; WAINWRIGHT *et al.*, 2012). The Bolca deposits thus provide the first clear record of both of these major lineages (lineages that share the common functional development of a pharyngeal apparatus, and are thus described as pharyngognath).

Each labrid and pomacentrid taxon is represented by one (usually) to three specimens, whereas *Tortonesia*, *Sorbinia* and *Quasicichla* are somewhat more commonly collected. All the Bolca pharyngognath fishes were collected at the Pesciara cave site rather than at Monte Postale site. The quantitative and taphonomic analyses of the Pesciara and Monte Postale fish assemblages performed recently (MARRAMÀ *et al.*, 2016a) clearly defined two distinctive paleocommunities and two different depositional settings.

Among the fossil fishes housed in the collection of the MCSNV there is one more specimen from

Monte Bolca, which can be interpreted as belonging to a new genus and species of pharyngognath fish that may be tentatively placed in the Labridae. This fish is described below as a new genus and species *Zorzinilabrus furcatus*.

METHODS

The specimen was studied using a stereomicroscope (Wild Heerbrugg) with an attached camera lucida drawing arm. Some details of the specimen examined were best seen when the specimen was moistened with alcohol. The specimen was prepared by needle.

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

Abbreviations are as follows: *Institutional*: MCSNV - Museo Civico di Storia Naturale di Verona; *Anatomical*: HL - head length; PU - preural vertebra; SL - standard length; U - ural vertebra.

SYSTEMATIC DESCRIPTION

Order Perciformes

Suborder Labroidei

Family Labridae Cuvier, 1817

Genus *Zorzinilabrus* gen. nov.

Diagnosis

Relatively elongated fish with a relatively long caudal peduncle. Head moderately large, 3.2 times in SL. Maximum body depth 1.2 times less than head length. Supraoccipital crest moderate and triangular. Lower jaw articulation under anteriormost portion of orbit. Mouth relatively small. Jaw teeth conical, arranged in a single row; enlarged premaxillary canines absent. Posterior preopercular margin even. Five (?) branchiostegal rays. 25 (10+15) vertebrae. Supraneural single. Dorsal fin continuous, with 7 spines (2 supernumerary) and 13 soft rays. Anal fin with 2 spines and 11 rays. Unpaired-fin spines very slender and flexible. Four anal-fin pterygiophores placed anterior to second haemal spine. 13 pectoral-fin rays; first pectoral ray reduced and not branched. Pelvics inserted just before pectorals, relatively small. Caudal fin forked, with 15 principal rays plus 13 procurent rays both above and below.

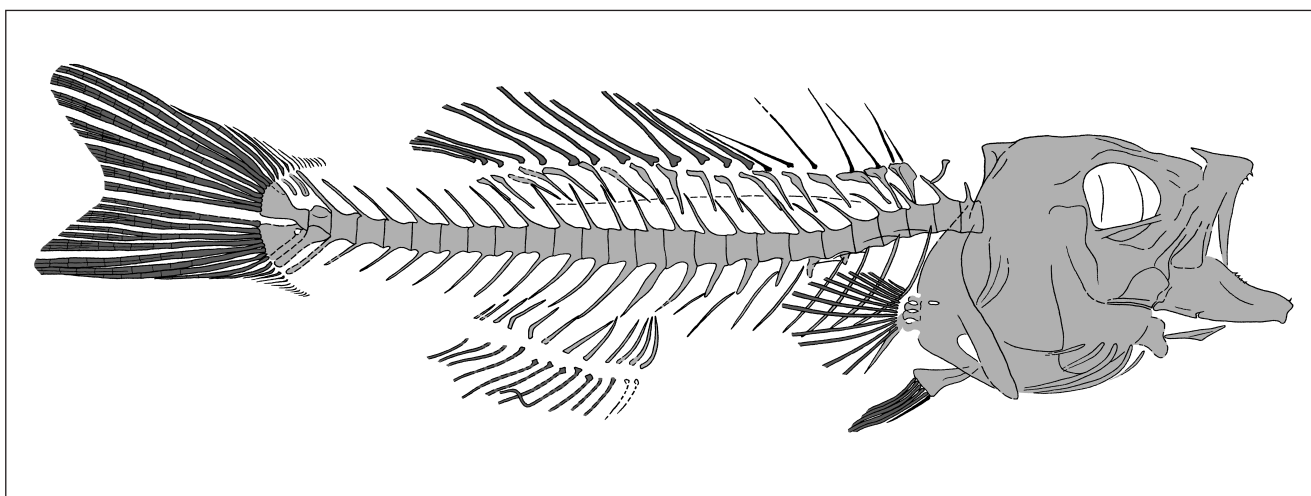
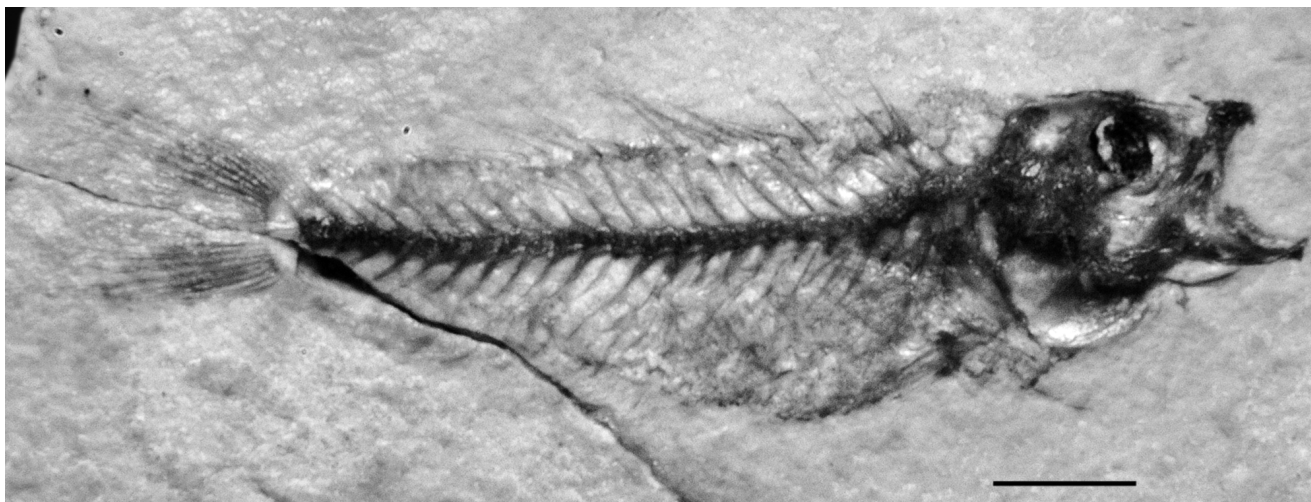


Fig. 1 – *Zorzinilabrus furcatus* gen. et sp. nov., holotype MCSNV T 1042; Lower Eocene of Bolca in northern Italy, Pesciara. Scale bar: 0.5 cm.

Fig. 2 – *Zorzinilabrus furcatus* gen. et sp. nov., reconstruction of the skeleton based on holotype, scales omitted.

Scales thin and cycloid. Lateral line follows dorsal contour of body and interrupted below posterior portion of soft dorsal fin.

Type Species

Zorzinilabrus furcatus sp. nov., by monotypy and designation herein.

Etymology

The genus is named in honour of our friend and colleague Dr. Roberto Zorzin, geologist and curator at the Museo Civico di Storia Naturale di Verona, and the genus *Labrus*; gender masculine.

Composition

Type species only.

Zorzinilabrus furcatus sp. nov.

Figures 1, 2.

Diagnosis

As for the genus.

Etymology

The species is named after the Latin word *furcatus* for forked, referring to the forked caudal fin of the fish.

Holotype

MCSNV T 1042, single plate, complete skeleton, 35.5 mm SL. There is a fracture along the posteroventral portion of the body, from the anal to the caudal fin; therefore, the lower half of the caudal skeleton is missing.

Referred Specimens

None.

Type Locality and Horizon

Monte Bolca locality, Pesciara cave site; Early Eocene, late Ypresian, middle Cuisian, SBZ 11, *Alveolina danelli* Zone (see PAPAZZONI and TREVISANI, 2006).

Description

The body is relatively elongate, perhaps somewhat laterally compressed, with a moderately deep and relatively long caudal peduncle. The dorsal and ventral profiles of the body are almost equally convex. The body depth is contained 3.8 times in SL. The caudal peduncle depth is about 0.54 of the body depth. The head is moderately large, contained 3.2 times in SL. The head is relatively deep, its maximum depth is only slightly less than its length; the snout is moderately elongate and contained 3.1 times in HL. The mouth is terminal, probably nearly horizontal, with a relatively small gape. The lower jaw articulation is situated under the anteriormost portion of the orbit.

Head. The neurocranium is relatively deep and has a moderate and triangular supraoccipital crest. The details of the ethmoid region are not recognizable; the massive lateral ethmoids form the anterior rim of the orbit. It is unclear if the ethmoid-frontal depression (=frontal recess; see GOMON, 1997) is developed or not. The frontals occupy most of the braincase roof above the orbit. The parasphenoid is an almost straight rod; its apophyses are not recognizable. The nasals are barely recognizable. Only faint remains of some infraorbital bones can be recognized. The premaxilla has a moderately high ascending process apparently coalescent with the articular process. The premaxillary alveolar process is much longer than the ascending process. Only few of the premaxillary teeth are preserved, these are relatively small and conical. Anterior teeth are only slightly stronger than others. The maxilla is only partially preserved; it is only moderately expanded distally. The lower jaw is moderately deep; its length is 2.2 times shorter than HL. The dentary is V-shaped and bears deep indentation for the insertion of the angulo-articular. The symphysis of the dentaries is almost vertical and moderately deep. The oral border of the dentary possesses relatively small sharp conical teeth apparently arranged in a single row. Anterior teeth are only slightly (if at all) stronger than others. Tip of tooth crowns is darkened. The angulo-articular is an elongate bone tapered anteriorly. The bones of

the suspensorium are only fragmentary preserved. The shaft of the hyomandibula appears to be only slightly obliquely oriented. The quadrate is subtriangular in outline and very wide, it is thickened from the condyle along the postero-ventral margin. The ectopterygoid seems to be narrow and elongate. The limits of the meta- and endopterygoid are unclear. The opercular region is relatively wide; its bones are not clearly recognizable. The preopercle appears to be moderately curved; there is no evidence of serrations along the posterior and lower margins of this bone. Only five sabre-like branchiostegal rays are recognizable; however, we cannot exclude possibility that one more ray is present but completely hidden. The hyoid bar is indistinctly outlined in its anterior portion; the moderate narrow bone projects anteriorly from the hypohyals. We interpret this bone as the glossohyal. The branchial skeleton is not recognizable, being hidden by the opercular bones. The pharyngeal jaws are certainly hypertrophied, and one of the pharyngeal jaws (perhaps the upper one) is outlined in lateral view as a ridge extended subvertically from the basioccipital to the cleithrum. There is no evidence of a cleithral articular process fossa (perhaps due to inadequate preservation of the holotype). The pharyngeal teeth are not visible, being obscured by the opercular bones.

Axial skeleton. The vertebral column consists of 25 (10+15) vertebrae, including the urostyle. The axis of the vertebral column is very slightly curved and elevated anteriorly. The vertebral centra are rectangular to subrectangular in lateral view. The length of the caudal portion of the vertebral column is one and half times greater than the length of the abdominal portion of the vertebral column. The vertebral spines are relatively short, straight or only slightly curved, and usually slender (anterior few haemal spines are somewhat thickened). The neural spine of the first vertebra is evidently much reduced as in many labrid taxa (see RUSSELL, 1988; GOMON, 1997). Well-developed parapophyses are clearly recognizable in the five posterior abdominal vertebrae. The haemal spines of the anterior caudal vertebrae are somewhat longer than the opposite neural spines. There are eight pairs of slender and relatively short pleural ribs. Few of the short and very thin epineurals are seen on and under the centra of several abdominal vertebrae.

Caudal fin and skeleton. The caudal skeleton is incompletely preserved because of a fracture along the posteroventral portion of the body. The urostyle is characterized by the fusion of the centrum PU1 to

the centra U1 and U2; it seems to be completely fused to the uroneural, forming a solid block ankylosed to the fused hypurals 3 and 4. The hypaxial hypural plate and parhypural are missing in the holotype, as well as most of the haemal spines of PU2 and PU3. The reduced fifth hypural is hardly recognizable. There seems to be a deep hypural diastema between the epaxial and hypaxial plates. The haemal spine of the penultimate vertebra is autogenous, while that of the antepenultimate vertebra is fused to the centrum. The neural spine of the PU2 vertebra seems to represent a short crest. The neural spine of the third preural vertebra is somewhat stronger than that of the preceding vertebra. There appears to be two epurals, the first of which being longest. The caudal fin is moderately large and forked; it consists of 15 principal rays (I,7-6,I), plus as many as 13 procurent rays both above and below.

Supraneural and dorsal fin. There is a single thin somewhat curved supraneural. The supraneural is obliquely oriented, extending antero-dorsally in front of the distal tip of the second neural spine. The dorsal fin is moderately long at the base; its extension is less than half of the body length. The dorsal fin is continuous and originates just above the border between the third and fourth vertebra. The first dorsal-fin pterygiophore is located between the neural spines of the second and third vertebrae, i.e., in the second interneural space. The dorsal fin contains seven very slender and evidently flexible spines and 13 soft segmented rays, supported by 18 pterygiophores. Two first dorsal-fin spines are in supernumerary association on the first dorsal-fin pterygiophore; the first spine is 1.47 times shorter than the second spine. The latter is 1.28 times shorter than the fourth dorsal-fin spine which seems to be the longest (although the fifth spine is not complete distally). The last two spines are almost as equally long as the fourth dorsal-fin spine. The longest dorsal-fin spine is 2.7 times shorter than the maximum body depth. Most of the dorsal-fin soft rays are evidently longer than the spines. The restored predorsal formula (see AHLSTROM *et al.*, 1976) is /0/2/1+1/1/ (the fourth pterygiophore of the holotype is displaced post-mortem). The first dorsal-fin pterygiophore is broad, another pterygiophores of the spiny portion of the dorsal fin are narrower and wedge-shaped, with a longitudinal strengthening ridge laterally; each of these pterygiophores bears a spine in supernumerary association, and sixth pterygiophore additionally bears serially associated first soft ray. The ptery-

giophores of the soft portion of the dorsal fin seem to be narrower than those of the spiny portion of the dorsal fin. The interneural spaces below the dorsal fin have the ventral shafts of one (usually) or two (the third, 11th, 14th and 15th spaces) pterygiophores present. The dorsal fin terminates above the eighth caudal vertebra.

Anal fin. The anal fin originates just below the second caudal vertebra and ends approximately below the end of the dorsal fin. The anal fin is very poorly preserved, partly because of a fracture which crosses along the fin; most of its elements are both incomplete and represented by their imprints on the matrix rather than bony substance. The anal fin is restored to consist of two very slender spines and 11 soft rays, supported by 12 pterygiophores; the first anal-fin spine seems to be supernumerary. The first anal-fin pterygiophore is curved and almost not exceeds the length of the succeeding pterygiophores. Since the haemal spine of the first caudal vertebra is incomplete distally, it is unknown how many anal-fin pterygiophores are placed anterior to it. However, it is clear that the four anal-fin pterygiophores precede the second haemal spine (unlike typical labrid condition of the two anal-fin pterygiophores placed anterior to the second haemal spine). The interhaemal spaces above the anal fin have the ventral shafts of one or two pterygiophores present.

Pectoral fin and girdle. The pectoral girdle is relatively robust. The posttemporal and supracleithrum are poorly preserved. The cleithrum is large and elongate. The upper part of the cleithrum is curved forward and situated below the first and second vertebrae. The ventral postcleithrum is slender and rib-like. The coracoid seems to be relatively narrow; there is a gap between the lowermost portions of the cleithrum and coracoid. The limits of the scapula are hardly recognizable; the bone is pierced by an elongate ovoid foramen. The pectoral radials are hourglass-shaped, these are oriented posteriorly. The four pectoral radials increase in length downward. The base of the pectoral fin is moderately wide and obliquely oriented, located under the fourth vertebra, close to the midpoint between the vertebral column and the ventral profile of the body. The pectoral fin contains 13 relatively short rays. The first ray seems to be very short and not branched.

Pelvic fin and girdle. The basypterygium is a relatively short and wedge-shaped bone. The pelvic fin contains one spine and five soft branched rays. The fin inserts just before the pectoral fin insertion. The pelvic-fin rays appear to be slightly shorter

than the pectoral-fin rays; the pelvic-fin spine is short and slender.

Squamation. Thin and evidently cycloid scales cover the entire body and head. The limits of the individual scales are hardly recognizable. The lateral line has an almost straight contour, nearly parallel to the dorsal body profile; it is interrupted under the posterior portion of the soft dorsal fin.

No pigmentation is traceable.

Measurements. As percentage of SL of holotype: head length = 31; maximum body depth = 26; caudal peduncle depth = 14; snout length = 10; orbit diameter = 7; lower jaw length = 14; distance between tip of the snout and first dorsal-fin spine = 35; distance between tip of the snout and first dorsal-fin ray = 50; distance between tip of the snout and anal fin = 66; distance between pelvic and anal fins = 28; dorsal-fin base length = 43; spinous dorsal-fin base length = 14; anal-fin base length = ca. 18; length of the first dorsal-fin spine = 3.7; length of the second dorsal-fin spine = 6.8; length of the longest dorsal-fin spine = 9.6; length of the pelvic-fin spine = 5; length of the longest caudal-fin ray = 24.

DISCUSSION

Zorzinilabrus gen. nov. is characterized by a unique mosaic of characters. This includes labrid synapomorphies (such as a single supraneural, oligomerization of the caudal skeleton and pharyngognath: following STIASSNY and JENSEN, 1987) and on this basis it is placed within the Labridae. However, it also has a number of features plesiomorphic for labrids (two supernumerary dorsal-fin spines and forked caudal fin with numerous procurrent rays). Furthermore, in some characters *Zorzinilabrus* gen. nov. differs from the known Labridae in having very slender and flexible unpaired-fin spines (vs. stronger spines in labrids), four anal-fin pterygiophores placed anterior to the second haemal spine (vs. two anal-fin pterygiophores anterior to the second haemal spine in labrids), and as few as seven dorsal and two anal-fin spines. According to a list of meristic features of the genera within the Labridae (BANNIKOV and BELLWOOD, 2015, Table 1), wrasses do not have less than eight dorsal and three anal-fin spines. Two anal-fin spines have been recorded only in a single species of the genus *Thalassoma*, *T. lutescens* (LAY et BENNETT, 1839) (MASUDA *et al.*, 1984), although this may be an error as *T. lutescens* usually has three anal spines (e.g. RANDALL *et al.*, 1997). Two anal-fin spines is a synapomorphy of the Pomacentridae but only

if they are in supernumerary association (BELLWOOD and SORBINI, 1996). However, like *Zorzinilabrus*, two anal spines with one in supernumerary association is also found in *Tortonesia* and *Sorbinia* (BELLWOOD and SORBINI, 1996). It appears to be a relatively widespread basal labroid condition.

This complex combination of plesiomorphic and apomorphic characters is similar to the situation seen in the earliest Tetraodontiformes (BANNIKOV *et al.*, 2016) and appears to be a characteristic of the early diversification of these major lineages. Given the combination of character traits in *Zorzinilabrus*, including a number of synapomorphies (especially a single supraneural; a potentially unique, and certainly unreversed synapomorphy), we tentatively place this species in the Labridae (being placed within the Labroidei based on the presence of a pharyngeal jaw). It appears to be an early diverging or basal labrid in that it shares a range of plesiomorphic labroid features with labroid taxa of uncertain affinity, i.e. *Tortonesia* and *Sorbinia*. Given the available evidence, it appears that *Zorzinilabrus* may be the earliest diverging sister taxon to the crown-group within the Labridae. Hopefully further, more complete, material of *Zorzinilabrus* will permit a detailed cladistic analysis of the phylogenetic relationships of the basal labrids and labroids.

Zorzinilabrus also offers interesting insights into the ecology of the Bolca fishes during this early phase of labroid evolution. It has previously been emphasised that the Bolca fish fauna is remarkably well developed in terms of the range of taxa present (BELLWOOD, 1996; BANNIKOV, 2014), their general morphological shape (MARRAMÀ *et al.*, 2016b) and in the wide range of ecological forms represented (BELLWOOD *et al.*, 2014, 2017). There are, for example, early representatives of most major feeding groups seen in high-diversity extant systems such as modern coral reefs, with major groups of predators, durophages and the first records of herbivores, including the specialist turf-feeding grazers (BELLWOOD *et al.*, 2014, 2017). This diversity of ecological forms also applies within lineages and is exemplified by the present description of *Zorzinilabrus* with its unusual forked caudal fin.

Labrid fishes swim primarily by pectoral locomotion, giving rise to the term 'labriform' locomotion (BELLWOOD and WAINWRIGHT, 2001; FULTON and BELLWOOD, 2005). The caudal fin in these fishes is mainly used for sudden acceleration over short distances, e.g. during reproduction, aggression, flight or escape from predators. For these purposes a

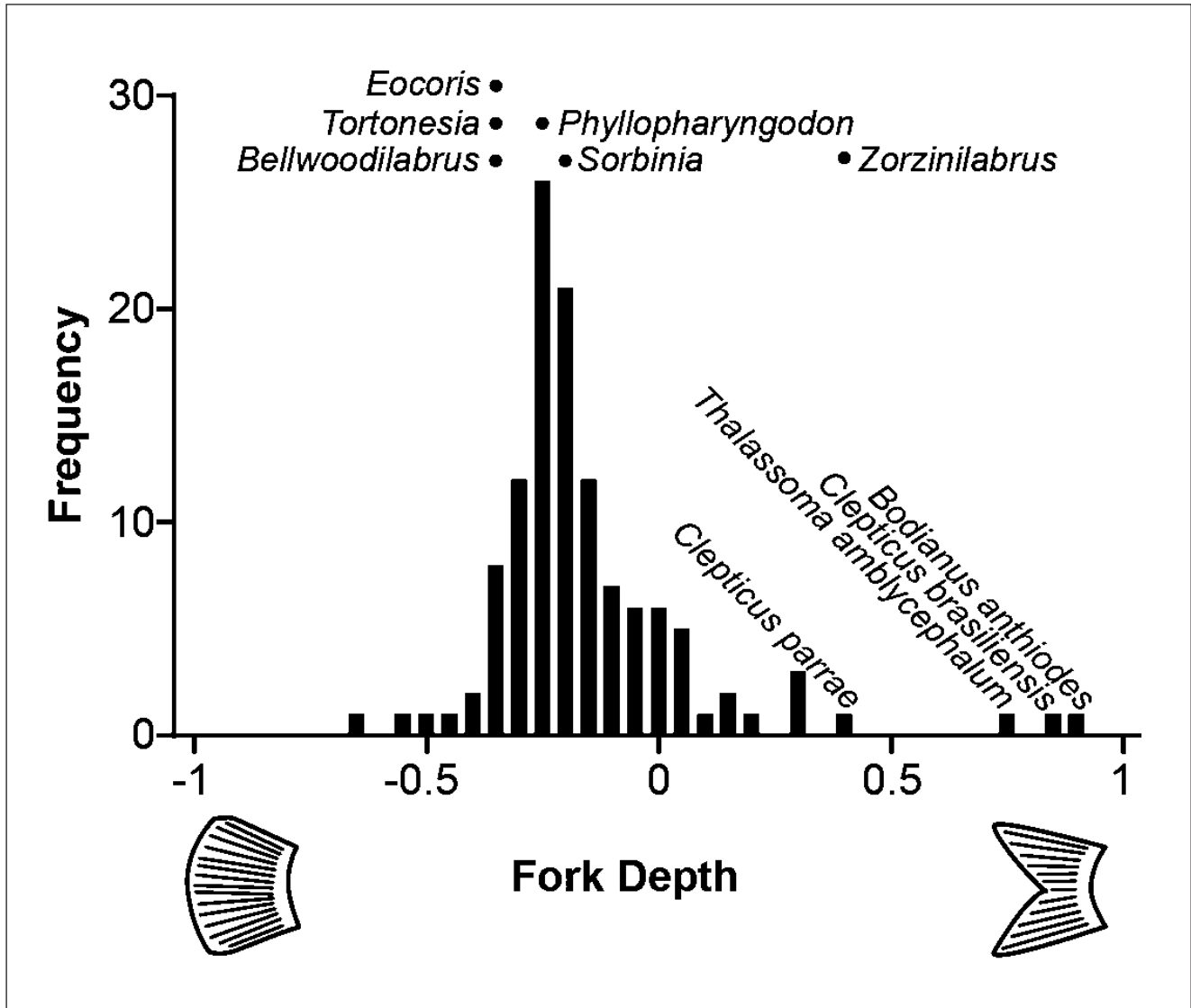


Fig. 3 – The distribution of caudal fin shapes among extant Labridae and Bolca labroids. 120 labrids were examined with representatives from 69 genera. The fork depth is the distance to the right (positive) or left (negative) of a vertical line marking the point of greatest caudal-fin depth. The deviation distance was standardized relative to the length of the caudal length along the midline; thus in *B. anthiodes* the fork depth is slightly smaller than the length of the caudal at the midline.

rounded caudal is ideally suited, as this low-aspect ratio shape is associated with rapid acceleration. A forked caudal fin is indicative of a markedly different pattern of use.

A forked caudal fin is associated with an increased aspect ratio and is indicative of relatively high mobility, if at the expense of less initial acceleration. This increased mobility may reflect early ecological diversification within the Bolca labroids. Although forked caudal fins are represented in a number of pomacentrid lineages (e.g. *Chromis*, *Abudefduf*), they are rare within the Labroidei and Labridae. Indeed,

based on a survey of extant labrid species, the caudal fin shapes are overwhelmingly rounded with a relatively narrow range of variation. Of the 120 species quantified, across 69 extant genera, only three had a deeply forked caudal fin (Fig. 3). The widespread rounded caudal configuration is consistent with all previously described labroids from Bolca. All Bolca labrids and labroids have a rounded caudal fin except *Zorzinilabrus*. What is particularly interesting to note is that the top four extant species with forked caudal fins are all unusual in that they depart from the typical labrid lifestyle (i.e. swimming close to

the reef, BELLWOOD and WAINWRIGHT, 2001) by living away from reefs or hard structures. Three taxa are planktivores feeding in the water column off the reef (*Thalassoma amblycephalum*, *Clepticus braziliensis* and *C. parrae*) while the other species, *Bodianus anthoides*, also spends a lot of time in the water column. This off-reef behaviour is not restricted to forked tailed species, but it is a relatively atypical labrid habitat. Given the distinctly forked caudal fin of *Zorzinilabrus*, it would appear that *Zorzinilabrus* is an early example of a labroid fish that lives away from reefs or hard benthic structures.

This unusual morphology in *Zorzinilabrus* is noteworthy given the restriction of pharyngognath fishes to the Pesciara deposits rather than in Monte Postale. The presence of all labroids, including *Zorzinilabrus*, in Pesciara suggests that a diverse array of habitats were occupied by these labroid fishes, reflecting the diversity of other groups recovered from these deposits (MARRAMÀ *et al.*, 2016a). It is also consistent with the suggestions that the coral-bearing hardgrounds around Bolca were typical of early Eocene reefs, with limited reefal development, reefs at this time being limited to coral growing on outcrops or boulder-sized bioherms (BELLWOOD *et al.*, 2017). All other Bolca labroids have morphological features including low aspect ratio pectoral fins that are indicative of relatively sheltered water and/or a close association with the benthos (BELLWOOD and WAINWRIGHT, 2001; BANNIKOV and BELLWOOD, 2015). *Zorzinilabrus* is one of the first labroids with a caudal fin that is indicative of higher mobility.

This exceptional feature raises the question of the ecology of *Zorzinilabrus*. The lack of large canines suggests that it did not grab large elusive prey or tear off attached robust prey (WAINWRIGHT and BELLWOOD, 2002). Furthermore, the moderate jaw closing lever ratio (0.32) and limited premaxillary ascending process length suggest that this species had a relatively slow-closing jaw (WAINWRIGHT and BELLWOOD, 2002) and limited protrusion (BELLWOOD *et al.*, 2015); it is unlikely therefore to feed on particularly elusive prey. It does, however, have a moderately large gape. Taken together, these morphological features suggest that it probably fed on relatively soft prey of moderate speed, possibly small crustaceans or other small invertebrates. These attributes are highly consistent with those seen in the Atlantic genus *Clepticus*, that feeds on zooplankton in the water column off the reef (RANDALL, 1967). The available evidence therefore strongly suggests that *Zorzinilabrus* was a zooplanktivore feeding in the

water column away from the hard benthos or reefal structures. This is interesting as it represents the first evidence of planktivory in the Labridae or Labroidei s.s. Based on a molecular phylogeny, the origins of planktivory in the Labridae was placed in the early Miocene (COWMAN *et al.*, 2009). A functional analysis of the morphology of *Zorzinilabrus*, however, strongly suggests that this feeding mode, planktivory, was already represented in labroids in the early Eocene. This observation reinforces the suggestion that the fishes of Bolca are in many ways, taxonomically, functionally and ecologically, as diverse as their modern counterparts on coral reefs and in other tropical ecosystems.

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LITERATURE CITED

- AHLSTROM E.H., BUTLER J.L., SUMIDA B.Y., 1976. Pelagic stromateoid fishes (Pisces, Perciformes) of the eastern Pacific: kinds, distributions and early life histories and observations on five of these from the northwest Atlantic. *Bulletin of Marine Science*, 26: 285-402.
- BALDWIN C.C., JOHNSON G.D., 1993. Phylogeny of the Epinephelidae (Teleostei: Serranidae). *Bulletin of Marine Science* 52 (1): 240-283.
- BANNIKOV A.F., 2004a. Eocottidae, a new family of perciform fishes (Teleostei) from the Eocene of northern Italy (Bolca). *Miscellanea Paleontologica n. 7. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 10: 17-35.
- BANNIKOV A.F., 2004b. Fishes from the Eocene of Bolca, northern Italy, previously classified with the

Chaetodontidae (Perciformes). *Miscellanea Paleontologica n. 7. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 10: 55-74.

BANNIKOV A.F., 2014. The systematic composition of the Eocene actinopterygian fish fauna from Monte Bolca, northern Italy, as known to date. *Miscellanea Paleontologica n. 12. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 15: 23-33.

BANNIKOV A.F., BELLWOOD D.R., 2014. A new genus and species of pomacentrid fish (Perciformes) from the Eocene of Bolca in northern Italy. *Miscellanea Paleontologica n. 12. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 15: 7-14.

BANNIKOV A.F., BELLWOOD D.R., 2015. A new genus and species of labrid fish (Perciformes) from the Eocene of Bolca in northern Italy. *Miscellanea Paleontologica n. 13. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 16: 5-16.

BANNIKOV A.F., CARNEVALE G., 2010. *Bellwoodilabrus landinii* n. gen., n. sp., a new genus and species of labrid fish (Teleostei, Perciformes) from the Eocene of Monte Bolca. *Geodiversitas*, 32 (2): 201-220.

BANNIKOV A.F., CARNEVALE G., 2012. *Frippia labroiformis* n. gen. n. sp., a new perciform fish from the Eocene of Pesciara di Bolca, Italy. *Bollettino della Società Paleontologica Italiana*, 51 (3): 155-165.

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 (1): 13-22.

BANNIKOV A.F., SORBINI L., 1990 (1991). *Eocoris bloti*, a new genus and species of labrid fish (Perciformes, Labroidei) from the Eocene of Monte Bolca, Italy. *Miscellanea Paleontologica, Studi e Ricerche sui Giacimenti Terziari di Bolca*, 6: 133-148.

BANNIKOV A.F., TYLER J.C., 1995. Phylogenetic revision of the fish families Luvaridae and †Kushlukidae (Acanthuroidei), with a new genus and two new species of Eocene luvarids. *Smithsonian Contributions to Paleobiology*, 81: 1-45.

BANNIKOV A.F., TYLER J.C., ARCILA D., CARNEVALE G., 2016 (2017). A new family of gymnodont fish (Tetraodontiformes) from the earliest Eocene of the Peri-Tethys (Kabardino-Balkaria, northern Caucasus, Russia). *Journal of Systematic Palaeontology*, 15 (2): 129-146. DOI 10.1080/14772019.2016.1149115.

BELLWOOD D.R., 1990 (1991). A new fossil fish *Phyllopharyngodon longipinnis* gen. et sp. nov. (family Labridae) from the Eocene, Monte Bolca, Italy. *Miscellanea Paleontologica, Studi e Ricerche sui Giacimenti Terziari di Bolca*, 6: 149-160.

BELLWOOD D.R., 1992 (1995). A new Eocene fossil

fish, *Sorbinia caudopunctata* gen. et sp. nov., from Monte Bolca, Italy. *Bollettino del Museo Civico di Storia Naturale di Verona*, 19: 461-474.

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

BELLWOOD D.R., 1999. Fossil pharyngognath fishes from Monte Bolca, Italy, with a description of a new pomacentrid genus and species. *Miscellanea Paleontologica, Studi e Ricerche sui Giacimenti Terziari di Bolca*, 8: 207-217.

BELLWOOD D.R., GOATLEY C.H.R., BELLWOOD O., DELBARRE D.J., FRIEDMAN M., 2015. The rise of jaw protrusion in spiny-rayed fishes closes the gap on elusive prey. *Current Biology*, 25: 2696-2700.

BELLWOOD D.R., GOATLEY C.H.R., BELLWOOD O., 2017. The evolution of fishes and corals on reefs: form, function and interdependence. *Biological Reviews*, 92(2): 878-901. doi: 10.1111/brv.12259.

BELLWOOD D.R., GOATLEY C.H.R., BRANDL S.J., BELLWOOD O., 2014. Fifty million years of herbivory on coral reefs: fossils, fish and functional innovations. *Proceedings of the Royal Society B*, 281: 20133046.

BELLWOOD D.R., SORBINI L., 1996. A review of the fossil record of the Pomacentridae (Pisces: Labroidae) with a description of a new genus and species from the Eocene of Monte Bolca, Italy. *Zoological Journal of the Linnean Society*, 117: 159-174.

BELLWOOD D.R., WAINWRIGHT P.C., 2001. Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. *Coral Reefs*, 20: 139-150.

CARNEVALE G., BANNIKOV A.F., MARRAMÀ G., TYLER J.C., ZORZIN R., 2014. The Pesciara-Monte Postale *Fossil-Lagerstätte*: 2. Fishes and other vertebrates. In: Papazzoni C.A. et al. (Editors), *The Bolca Fossil-Lagerstätten: A window into the Eocene World. Rendiconti della Società Paleontologica Italiana*, 4: 37-63.

COWMAN P.F., BELLWOOD D.R., 2011. Coral reefs as drivers of cladogenesis: expanding coral reefs, cryptic extinction events, and the development of biodiversity hotspots. *Journal of Evolutionary Biology*, 24: 2543-2562.

COWMAN P.F., BELLWOOD D.R., VAN HERWERDEN L., 2009. Dating the evolutionary origins of wrasse lineages (Labridae) and the rise of trophic novelty on coral reefs. *Molecular Phylogenetics and Evolution*, 52: 621-631.

FULTON C.J., BELLWOOD D.R., 2005. Wave-induced water motion and the functional implications for coral reef fish assemblages. *Limnology and Oceanography*, 50: 255-264.

GOMON M.F., 1997. Relationships of fishes of the labrid tribe Hypsigenyini. *Bulletin of Marine Science*, 60 (3): 789-871.

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 palaeoecology and taphonomy of the fish assemblages of the Eocene Bolca Konservat-Lagerstätte, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 454: 228-245.

MARRAMÀ G., GARBELLI C., CARNEVALE G., 2016b. A clade-level morphospace for the Eocene fishes of Bolca: patterns and relationships with modern tropical shallow marine assemblages. *Bollettino della Società Paleontologica Italiana*, 55 (2): 139-156.

MASUDA H., AMAOKA K., ARAGA C., UYENO T., YOSHIRO T. (Eds.), 1984. *The fishes of the Japanese Archipelago*. Tokai University Press, Tokyo: 437 pp.

MIYA M., TAKESHIMA H., ENDO H., ISHIGURO N.B., INOUE J.G., MUKAI T., SATOH T.P., YAMAGUCHI M., KAWAGUCHI A., MABUCHI K., SHIRAI S.M., NISHIDA M., 2003. Major patterns of higher teleostean phylogenies: a new perspective based on 100 complete mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 26: 121-138.

NEAR T.J., DORNBURG A., EYTAN R.I., KECK B.P., SMITH W.L., KUHN K.L., MOORE J.A., PRICE S.A., BURBRINK F.T., FRIEDMAN M., WAINWRIGHT P.C., 2013. Phylogeny and tempo of diversification in the superradiation of spiny-rayed fishes. *Proceedings on the National Academy of Sciences of the United States of America*, 110: 12738-12743.

PAPAZZONI C.A., TREVISANI E., 2006. Facies analysis, palaeoenvironmental reconstruction, and biostratigraphy of the "Pesciara di Bolca" (Verona, northern Italy): An early Eocene *Fossil-Lagerstätte*. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 242: 21-35.

RANDALL J.E., 1967. Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography*, 5: 665-847.

RANDALL J.E., ALLEN G.R., STEENE R.C., 1997. *Fishes of the Great Barrier Reef and Coral Sea*. University of Hawai'i Press, Honolulu: 557 pp.

RUSSELL B.C., 1988. Revision of the fish genus *Pseu-*

dolabrus and allied genera. *Records of the Australian Museum*, Suppl. 9: 1-72.

SORBINI L., BOSCAINI E., BANNIKOV A.F., 1990 (1991). On the morphology and systematics of the Eocene fish genus *Tortonesia* Sorbini from Bolca. *Miscellanea Paleontologica. Studi e Ricerche sui Giacimenti Terziari di Bolca*, 6: 115-132.

STIASSNY M.L.J., JENSEN J.S., 1987. Labroid interrelationships revisited: morphological complexity, key innovations, and the study of comparative diversity. *Bulletin of the Museum of Comparative Zoology*, 151: 269-319.

TYLER J.C., BANNIKOV A.F., 1997. Relationships of the fossil and Recent genera of rabbitfishes (Acanthuroidei: Siganidae). *Smithsonian Contributions to Paleobiology*, 84: 1-35.

WAINWRIGHT P.C., BELLWOOD D.R., 2002. Ecomorphology of feeding in coral reef fishes. In: SALE P.F. (Editor), *Coral reef fishes. Dynamics and diversity in a complex ecosystem*. Academic Press, San Diego: 33-55.

WAINWRIGHT P.C., SMITH W.L., PRICE S.A., TANG K.L., SPARKS J.S., FERRY L.A., KUHN K.L., EYTAN R.I., NEAR T.J., 2012. The evolution of pharyngognath: a phylogenetic and functional appraisal of the pharyngeal jaw key innovation in labroid fishes and beyond. *Systematic Biology*, 61: 1001-1027.

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