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Frippia labroiformis n. gen. n. sp., a new perciform fish from the Eocene of Pesciara di Bolca, Italy

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KEY WORDS - Perciformes, Percoidei incertae sedis*, new genus and species, Eocene, northern Italy, Pesciara di Bolca.*

ABSTRACT - A new genus and species of percoid fish, Frippia labroiformis *n. gen. n. sp. from the Eocene of Pesciara di Bolca, northern Italy, is described based on three well-preserved specimens characterized by a moderately elongate body and a short and deep caudal peduncle.* Frippia *n. gen. exhibits a unique combination of features, including the following: weak pharyngeal apophysis of the parasphenoid; orbit with sclerotic ossifications; jaws with single series of strong conical teeth; slightly curved preopercle with smooth posterior margin; opercle devoid of spines; six branchiostegal rays; blunt and conical lower pharyngeal teeth; 26 (10+16) vertebrae; caudal skeleton with urostylar complex fused to uroneural and third and fourth hypurals, first and second hypurals fused, fifth hypural and parhypural autogenous, three epurals, autogenous haemal spines of second and third preural vertebrae, and low neural crest on second preural vertebra; caudal fin rounded with 17 principal rays and six to seven upper and five to six lower procurrent rays; predorsal formula 0/0/0+2/1+1/; continuous dorsal fin with nine spines and 14 soft rays; anal fin with three strong spines and 10 rays; pectoral fin with 15 rays; pelvic fin with one spine and five long rays, the longest reaching posteriorly to anal-fin origin; scales relatively large, thin and finely ctenoid on trunk and cycloid on head. Because of its unique combination of features* Frippia *n. gen. cannot be confidently assigned to any of the existing extant or fossil percoid families and it is therefore interpreted herein as* incertae sedis *within the Percoidei.*

RIASSUNTO - [*Frippia labroiformis* n. gen. n. sp., un nuovo percoide nell'Eocene della Pesciara di Bolca, Italia] - Frippia labroiformis *n. gen. n. sp., un nuovo perciforme proveniente dai depositi eocenici della Pesciara di Bolca, Italia settentrionale, viene descritto sulla base di tre esemplari in ottimo stato di conservazione caratterizzati da corpo moderatamente allungato e da un peduncolo caudale breve e alto.* Frippia *n. gen. mostra una combinazione di caratteri molto particolare, che comprende la presenza di un'apofisi faringea del parasfenoide poco sviluppata; orbita con ossificazioni sclerotiche; mascelle dotate di una singola serie di robusti denti conici; preopercolare leggermente curvo e con margine posteriore liscio; opercolare privo di spine; sei raggi branchiostegi; denti faringei inferiori conici non appuntiti; 26 (10+16) vertebre; scheletro caudale con complesso urostilare fuso all'uroneurale e al terzo e quarto ipurali, ipurali primo e secondo fusi a formare un'ampia piastra triangolare ipassiale, quinto ipurale e paraipurale autogeni, tre epurali, spine emali della seconda e terza vertebra preurale autogene e spina neurale della seconda vertebra preurale ridotta ad una cresta poco sviluppata; pinna caudale arrotondata formata da 17 raggi principali e sei-otto raggi procurrenti superiori e cinque-sei raggi procurrenti inferiori; formula predorsale 0/0/0+2/1+1/; pinna dorsale continua e contenente nove spine e 14 raggi; pinna anale formata da tre robuste spine e 10 raggi; pinna pettorale costituita da 15 raggi; pinna pelvica formata da una spina e cinque raggi molto allungati, il più sviluppato dei quali raggiunge posteriormente l'area di inserzione della pinna anale; scaglie piuttosto ampie, sottili e finemente ctenoidi sul tronco e cicloidi a coprire parte del capo. A causa della peculiare combinazione di caratteri non è possibile assegnare il genere* Frippia *n. gen. ad alcuna delle famiglie note di percoidi e pertanto viene considerato* incertae sedis *all'interno di questo eterogeneo sottordine di perciformi.*

INTRODUCTION

Bolca is situated in the eastern part of Monti Lessini, north of Verona, northern Italy. This locality includes many productive sites characterized by different fossil content (see Tang, 2001). The most important of these sites is that of the Pesciara quarry, celebrated since the mid-16th century for the extraordinarily well-preserved fishes (see e.g., Gaudant, 1997). The first comprehensive analysis on the Bolca fish fauna, the *Ittiolitologia veronese*, was published by Abbott Giovanni Serafino Volta (1796). Subsequently, Louis Agassiz (1833-1844) published his milestone of paleoichthyology, the *Recherches sur les poissons fossiles*, largely based on material from Bolca. Regular extensive excavations at this locality, however, started in the mid-19th century, resulting in the extraction of several thousands of fossils (bony and cartilaginous fishes, polychaete worms, jellyfish, cephalopods, crustaceans, insects, and plants) now housed in scientific institutions and private collections around the world (see Blot, 1969).

The deposits of the Pesciara quarry site belong to the so-called 'Calcari Nummulitici', an informal unit of Eocene age widespread in the surroundings of Bolca. According to Papazzoni & Trevisani (2006), the Pesciara quarry stratigraphic section is characterized by alternated laminated micritic limestone with fishes and plants and biocalcarenite/biocalcirudite-bearing benthic fossils. Fishes commonly occur in a finely laminated limestone characterized by a micritic matrix, with sparse pyrite and bitumen. These fishes are usually fully articulated with complete squamation and, in certain cases, preserved pigmentation patterns (e.g., Blot, 1984; Bellwood & Sorbini, 1996; Bannikov, 2004). The excellent preservation of the fossils, absence of bioturbation, laminated style of the deposit, limited number of benthic taxa, and presence of bitumen and pyrite are indicative

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of poorly oxygenated bottoms during the deposition of the micritic limestone. The taphonomic features and ecological spectrum of the fossil assemblage concur to indicate that the Pesciara quarry limestone represents an obrutionary stagnation deposit (Seilacher et al., 1985). According to Landini & Sorbini (1996), the Pesciara paleobiotope was located at a short distance from the coast, many dozens of metres in depth, in a silled depression with restricted circulation on the seafloor. The structure and composition of the fish assemblage indicate that coral reefs and seagrass beds were present in close proximity to the depositional environment, which was also subject to fluvial influences. More recent studies based on facies analysis and foraminiferal paleoecology (Papazzoni & Trevisani, 2006; Schwark et al., 2009), suggested that the fish-bearing layers originated in a subtropical lagoon close to an emerged area, characterized by seasonal changes of water circulation, which affected the oxygen content on the sea bottom. Summarizing, authors cited above (Landini & Sorbini, 1996; Papazzoni & Trevisani, 2006; Schwark et al., 2009) agree that the micritic sedimentation took place in a depressed basin characterized by permanent bottom anoxia and low hydrodynamic energy, close to the coast in a tropical or subtropical context. The age of the ichthyolitiferous micritic limestone was redefined by Papazzoni & Trevisani (2006), who, on the basis of the macroforaminiferans, assigned these deposits to the *A. dainellii* zone. Following the biostratigraphical scheme elaborated by Serra-Kiel et al. (1998), the Pesciara quarry limestone is referred to the SBZ 11 biozone, corresponding to the Middle Cuisian (late Ypresian; about 50 Mya).

The Bolca locality certainly has one of the most important ichthyofaunistic fossil assemblages known. The fish assemblage consists of more than 200 species (see Bannikov, 2010), representing as well the earliest record of a percomorph dominated fish assemblage. The assemblage includes the first representatives of many of the fish groups found on coral reefs today (Patterson, 1993; Bellwood, 1996; Landini & Sorbini, 1996), thereby marking the starting point in the known evolution of most reef fish groups (Bellwood & Wainwright, 2002), and apparently providing evidence of the stability of the morphological characteristics of tropical and subtropical marine ichthyofaunas throughout the Cenozoic era. Despite the broad similarities in the familial composition between the Bolca ichthyofauna and extant reef fish assemblages, however, the numerical abundance of the various families and their taxonomic diversity are notably different (Bellwood, 1996; Bannikov, 2010). Moreover, the Bolca percomorph assemblage includes a number of taxa of problematic affinities either placed in separate families or, most commonly, left *incertae sedis* (e.g., Bannikov & Carnevale, 2007, 2009, 2011) within such a heterogeneous and diverse group.

Among the undescribed percomorph fishes held in the collection of the Museo Civico di Storia Naturale, Verona, there are three specimens of what appears to be a new percomorph fish, figured by Caltran & Zorzin (1998) and considered therein as an extinct representative of the family Embiotocidae. The purpose of this paper is to describe the morphology of this fish in detail and to discuss its possible affinities.

METHODS

The specimens were studied using a stereomicroscope Wild Heerbrugg with attached camera lucida drawing arm. Measurements were taken with a dial calliper, to the nearest 0.1 mm. The specimens required matrix removal before examination in order to allow investigation of their structure in as much detail as possible; matrix removal was achieved using entomological needles. Comparative data were derived mainly from the literature.

Abbreviations

aa, angulo-articular; br, branchiostegal rays; cor, coracoid; d, dentary; ect, ectopterygoid; end, endopterygoid; ep, epural; h, hyomandibula; hb, hyoid bar; HL, head length; hpu, haemal spine of the preural vertebra; hyp, hypural; MCSNV, Museo Civico di Storia Naturale, Verona; mtp, metapterygoid; mx, maxilla; na, nasal; npu2, neural spine of the second preural vertebra; op, opercle; pas, parasphenoid; pcl, postcleithrum; php, parhypural; pmx, premaxilla; pop, preopercle; pu, preural centrum; q, quadrate; rar, retroarticular; sc, sclerotic ring; sca, scapula; scl, supracleithrum; SL, standard length; sym, symplectic; u, ural centrum; uh, urohyal; un, uroneural; v, vomer.

SYSTEMATICS

Subdivision Teleostei *sensu* Patterson & Rosen, 1977
Order Perciformes *sensu* Johnson & Patterson, 1993
Suborder Percoidei Bleeker, 1859
Family *incertae sedis*

Genus *Frippia* n. gen.

Diagnosis - Percoid with moderately elongate body; caudal peduncle short and deep; supraoccipital crest low; pharyngeal apophysis of parasphenoid weak; sclerotic ossifications present; jaws with single series of strong conical teeth; preopercle slightly curved, with smooth posterior margin; opercle spineless; six branchiostegal rays; lower pharyngeal teeth blunt and conical; 26 (10+16) vertebrae; caudal skeleton with urostylar complex fused to uroneural and hypurals third and fourth, first plus second hypurals fused into triangular hypaxial plate, fifth hypural and parhypural autogenous, parhypurapophysis absent, three epurals, autogenous haemal spines of second and third preural vertebrae, and low neural crest on second preural vertebra; caudal fin rounded with 17 principal rays and six to seven upper and five to six lower procurrent rays; predorsal formula 0/0/0+2/1+1/; dorsal fin long-based and continuous, with nine spines gradually increasing in size and fourteen soft rays; anal fin with three strong spines (second and third spines almost equal in length) and ten rays; pectoral fin contains fifteen rays; pelvic fin with one spine and five long rays, longest ray reaching posteriorly to anal-fin origin; scales relatively large, thin and finely ctenoid, forming sheath at base of anal and dorsal fins; head covered with cycloid scales; lateral line gently curved following dorsal border of body until posterior third of soft portion of dorsal fin, where it is interrupted.

Type species - *Frippia labroiformis* n. sp., by monotypy and designation herein.

Etymology - It is our pleasure to name this genus after the British musician and composer Robert Fripp in recognition of his outstanding musical and cultural work.

Frippia labroiformis n. sp.
(Figs 1-5)

1998 Embriotocidae (sic) - Caltran & Zorzin, text-fig. p. 91.

Diagnosis - As for the genus.

Etymology - The species name reflects the superficial similarity in general appearance and caudal skeleton structure of the new taxon with those of labroid fishes.

Holotype - MCSNV T 187, well-preserved complete articulated skeleton in a single plate, 36 mm SL (Fig. 1a).

Paratypes - MCSNV IG 23594/23595, part and counterpart of a partially complete articulated skeleton lacking the anterior part of the head, ca. 37 mm SL (Fig. 1b); MCSNV IG 43395/43396, part and counterpart of a nearly complete articulated skeleton, 27 mm SL (Fig. 1c).

Type locality and horizon - Bolca locality, Pesciara quarry site; Early Eocene, late Ypresian, middle Cuisian, SBZ 11, *A. dainelli* zone (see Papazzoni & Trevisani, 2006).

Measurements (*of the holotype, as percentage of SL*) - Head length = 31; maximum body depth = 36.5; caudal peduncle depth = 20; snout length = 8; orbit diameter = 8; lower jaw length = 13.5; predorsal (spiny dorsal) length = 36; predorsal (soft dorsal) length = 56; preanal length = 71; distance between pelvic and anal fins = 28.5; dorsal-fin base length = 50.5; spinous dorsal-fin base length = 18; anal-fin base length = 23; length of the first dorsal-fin spine = 4; length of the longest dorsal-fin spine = 15; length of the first anal-fin spine = 6; length of the third anal-fin spine = 15.5; length of the pelvic-fin spine = 12; length of the longest caudal-fin ray = 26.

Description - The body is moderately elongate, with a short and deep caudal peduncle (Figs 1-2). The caudal peduncle depth is about 0.55 of the body depth. The head is moderately large, its length is contained approximately 3.25 times in SL. The dorsal and ventral profiles of the body are almost equally convex.

The head is relatively deep, with its depth slightly less than its length. The orbit is moderately developed and apparently characterized by sclerotic ossifications (Fig. 3). The horizontal diameter of the orbit is about 26% of HL. The snout is slightly shorter than the orbit diameter. The mouth is moderately wide and terminal. The lower jaw articulation is situated behind the middle of the orbit.

The neurocranium is moderately deep, with a poorly developed supraoccipital crest (Fig. 3). The osteological structure of the neurocranium cannot be confidently interpreted because of inadequate preservation. The ethmoid region is relatively short. The parasphenoid is rather strong and almost straight, apparently bearing a moderately developed ventral flange; this robust bone is well-exposed along the lower border of the orbit; what appears to be a weak pharyngeal apophysis (Greenwood, 1978; Stiassny & Jensen, 1987; Rosen & Patterson, 1990) is feebly exposed in the holotype. The vomer has a prominent ventral process, which is clearly exposed in the paratype MCSNV IG 43396.

The nasal is short and thin (Fig. 3). What appear to be badly damaged delicate infraorbital bones are partially recognizable in the holotype and paratype MCSNV IG 43396.

The premaxilla has a long and slender ascending process clearly separated from a robust articular process (Fig. 3). A postmaxillary process can be observed in the paratype MCSNV IG 43395/43396. The premaxilla bears a series of rather strong, blunt and curved conical teeth. The maxilla is only partially preserved; its head is concave rostrad. There is no evidence of a supramaxilla. The lower jaw is moderately deep; its length is about 44% of HL. The dentary slightly projects ventrally near the oblique symphysis. The dentary teeth are identical to those of the upper jaw. The dentary is bifurcated posteriorly, forming a relatively deep dentary fossa into which the anterior process of the angulo-articular inserts. There is no gap between the postero-dorsal arm of the dentary and the main body of the angulo-articular. The retroarticular is rather thick.

The hyomandibular shaft is obliquely oriented, with an anteroventrally tilted lower tip. Details of the structure of the hyomandibula are not clear. The quadrate is triangular in outline, with a thickened posteroventral margin (Fig. 3). The symplectic is wedge-shaped. The metapterygoid is only partially preserved. The endopterygoid is flat and relatively elongate. The ectopterygoid is moderately curved. The palatine is poorly preserved and difficult to recognize.

The opercular region is rather broad (Fig. 3). The preopercle is flat and thick, broad ventrally and slightly curved, with a smooth posterior border. The opercle is relatively wide and evidently spineless.

The ceratohyal does not seem to be perforated. The number of branchiostegal rays is unclear, but probably there are six sabre-like elements (Fig. 3). The urohyal has a wide posterior concavity and bears lateral wings along its ventral border; the vertical plate of the urohyal extends posteroventrally so that its ventral margin is longer than its dorsal margin (Fig. 3).

The gill arches are not recognizable in the available specimens, except for the poorly preserved pharyngeal bones in the holotype MCSNV T 187 and paratype MCSNV IG 23594, which bear conical teeth (Fig. 4). It cannot be properly determined whether there is a diarthrosis between the upper pharyngeal jaws and the basicranium, and whether the lower pharyngeal jaws are fused.

The vertebral column consists of 26 (10+16) vertebrae, including the urostyle (Fig. 2). The axis of the vertebral column is slightly sigmoid and anteriorly elevated in a slight kyphotic curve. The vertebral centra are almost rectangular, longer than high, with two longitudinally-developed fossae separated by a median ridge along

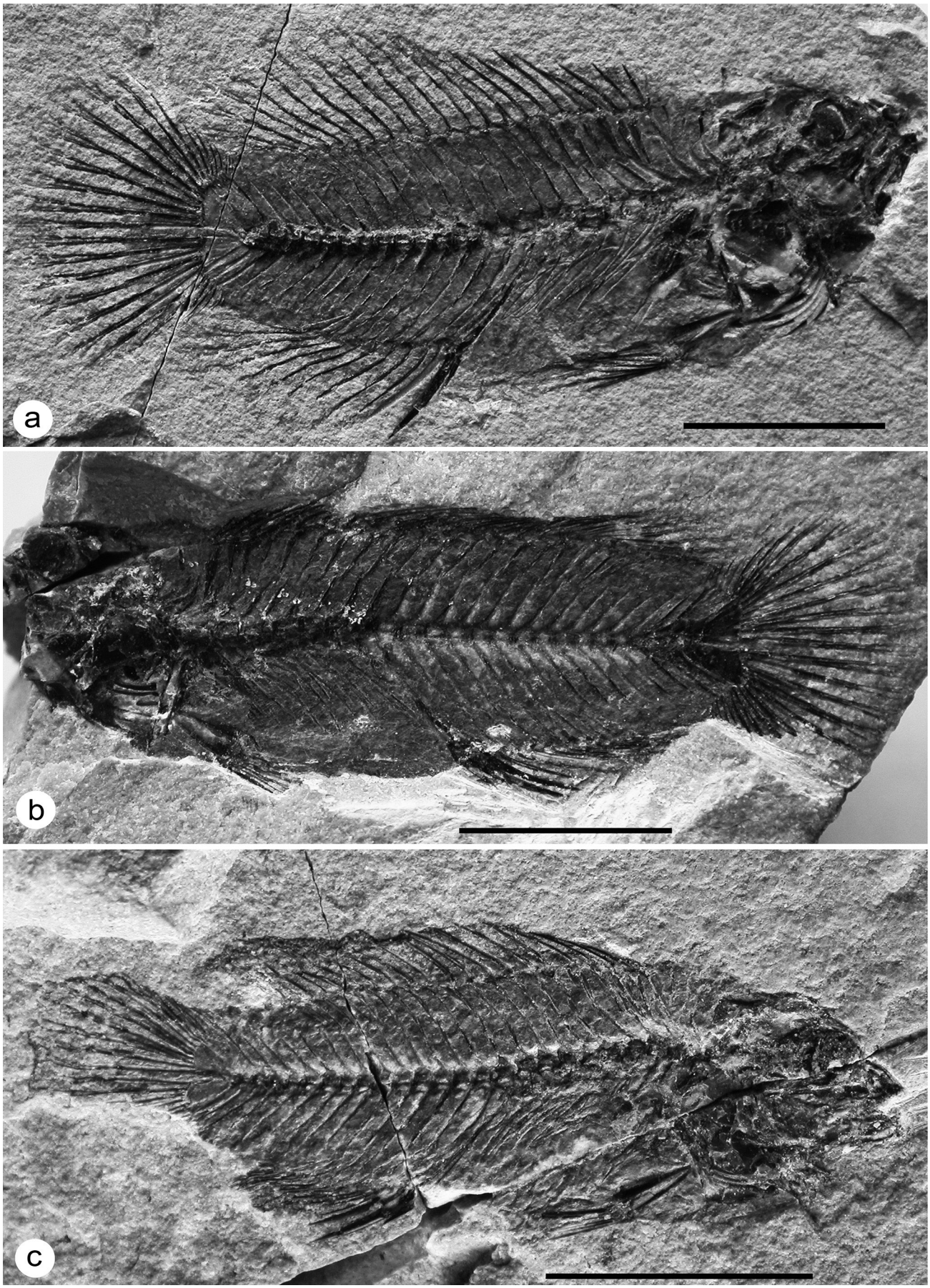

Fig. 1 - *Frippia labroiformis* n. gen. n. sp. from the Eocene of Pesciara di Bolca. a) Holotype, MCSNV T 187, right lateral view; b) paratype, MCSNV IG 23594, left lateral view; c) paratype, MCSNV IG 43396, right lateral view. Scale bar 10 mm.

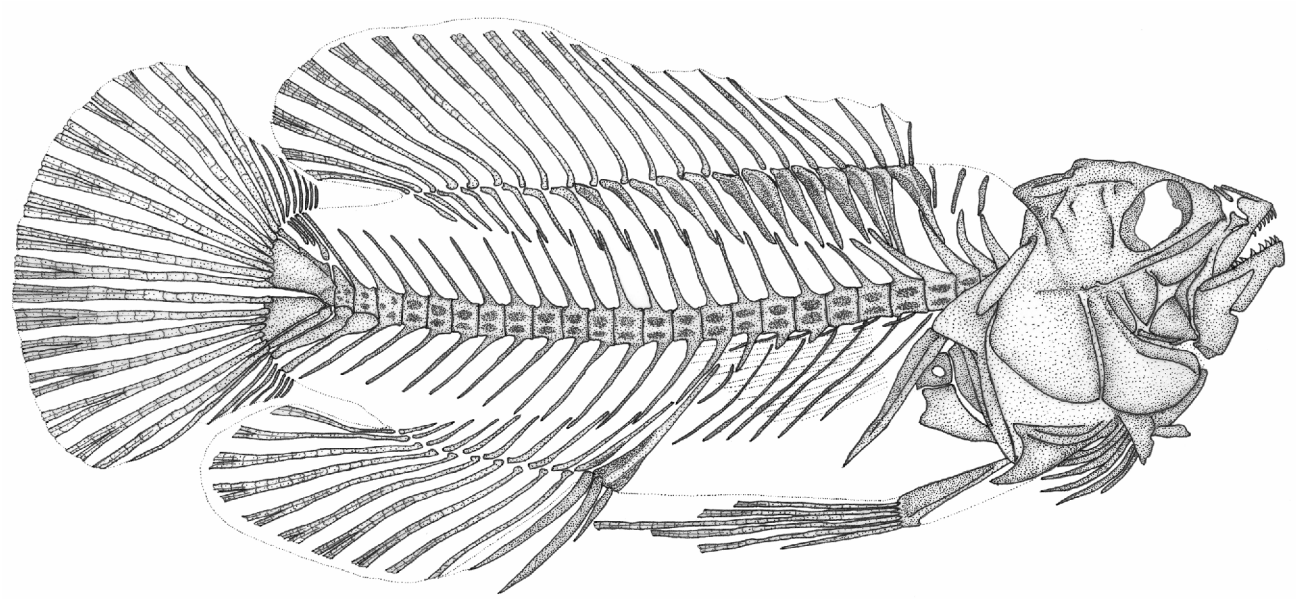

Fig. 2 - *Frippia labroiformis* n. gen. n. sp. from the Eocene of Pesciara di Bolca. Reconstruction of the skeleton, right lateral view; scales omitted.

their lateral sides. The length of the caudal portion of the vertebral column is about 1.6 times greater than that of the abdominal portion. The vertebral spines are relatively short and robust, straight or slightly curved. The neural spines of the five anteriormost vertebrae are more broadly expanded anteroposteriorly with respect to those of the succeeding vertebrae, with the second spine being more curved than the others. The haemal spines of the anterior caudal vertebrae are longer and usually more strongly inclined to the axis of the backbone than the opposite neural spines. Most of the neural spines emerge from the middle of the centra, whereas the anterior haemal spines arise from the anterior half of the centra. The parapophyses are poorly recognizable in the three posteriormost abdominal vertebrae. The pleural ribs are long, slender and strongly inclined posteroventrally. Slender epineurals associated to abdominal vertebrae are recognizable.

The terminal centrum consists of the fused first preural and the first and second ural centra; this centrum is completely fused to the uroneural, forming a solid block ankylosed to the fused hypurals 3 and 4 (Fig. 5). The hypurals 1 and 2 are fused into a roughly triangular hypaxial hypural plate. The reduced fifth hypural ("hypurale minimum"; Monod, 1968) is autogenous. There is a deep hypural diastema between the epaxial and hypaxial plates. The parhypural is autogenous; it apparently lacks a parhypurapophysis. The haemal spines of the second and third preural centra are autogenous and thicker than those of the preceding vertebrae (Fig. 5). The neural spine of the second preural centrum is reduced to a short crest. There are three epurals, of which the first is more developed. The caudal fin is rounded, moderately long and deep. There are seventeen principal rays in the caudal fin (I,8-7,I); there are six to seven upper procurrent rays and five to six lower procurrent rays. There are no indications of the presence of a procurrent spur (Johnson, 1975).

There are three relatively slender supraneurals lacking any apical projection (Fig. 2). The predorsal formula (Ahlstrom et al., 1976; Johnson, 1980, 1984) is 0/0/0+2/1+1/. In the holotype the predorsal configuration is /0/0+0+2/1+1/, with the first supraneural that inserts in the first interneural rather than in the preneural space; we are convinced that this configuration represents a taphonomic artifact produced by a slight post-mortem posterior shift of the supraneural series. The dorsal fin is long-based and continuous (Figs 1-2); it originates over the fourth or fifth vertebra and terminates at the level of the 22nd or 23rd vertebra. The dorsal fin contains nine spines and fourteen soft segmented and branched rays supported by twenty-one pterygiophores. The dorsal-fin spines are relatively slender. The spines gradually increase in length posteriorly. The posteriormost spine is 3.7 times longer than the first spine and 2.3 times longer than the second spine. The first two dorsal-fin spines are supernumerary on the first dorsal-fin pterygiophore; these are rather closely spaced. The longest soft ray of the dorsal fin is 1.4 times longer than the longest dorsal-fin spine. The length of the base of the soft portion of the dorsal fin is 1.7 times longer than the base length of the spiny portion of the dorsal fin. The membrane that connects the dorsal-fin spines and soft rays is preserved as a thin film of dark pigment, with the coloration being more extensive distally in the anterior half of the fin. The first pterygiophore is large and sturdy, anteroposteriorly expanded, and characterized by a longitudinal strengthening ridge; the succeeding pterygiophores become gradually narrow. Posteriorly in the series, the dorsal-fin pterygiophores gradually decrease in length. The interneural spaces underlying the dorsal fin are occupied by the ventral shafts of one (usually in the anterior portion of the series) or two (usually in the posterior portion of the series) pterygiophores.

The anal fin originates under the fourth or fifth caudal vertebra and terminates at the level of the posterior end of the dorsal-fin (Fig. 2). The fin contains three spines and ten soft, segmented and branched rays, supported by eleven anal-fin pterygiophores. The anal-fin spines are strong, with the second and third spines being the longest. The first two spines are supernumerary. The longest anal-fin

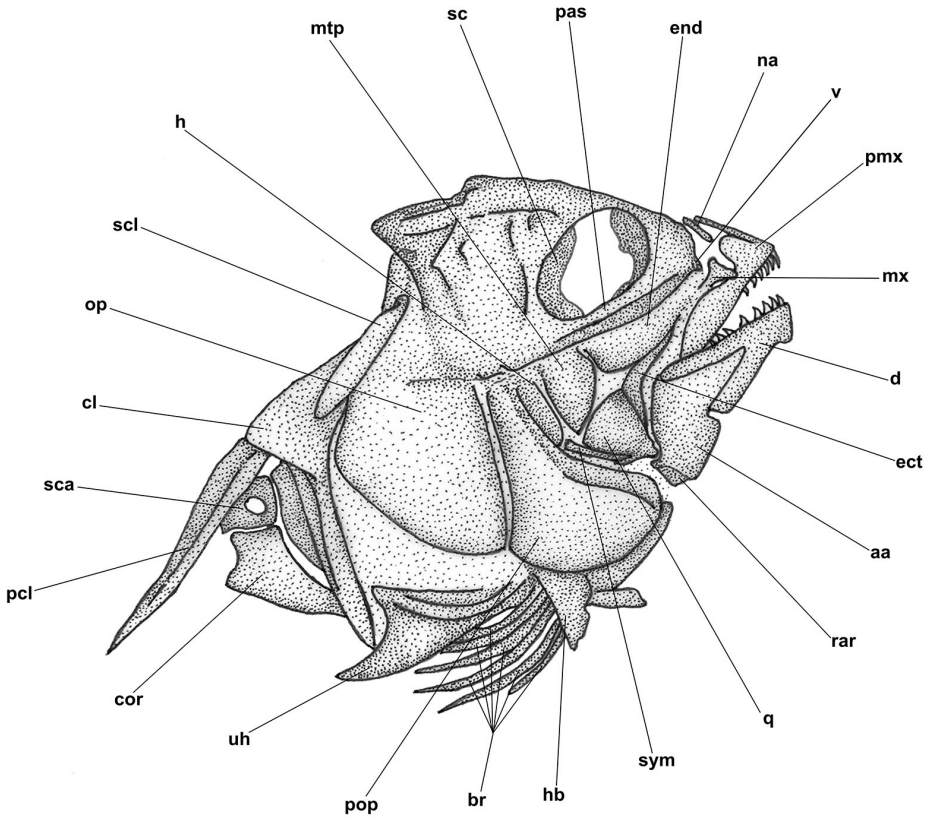

Fig. 3 - *Frippia labroiformis* n. gen. n. sp. from the Eocene of Pesciara di Bolca. Reconstruction of the skull, right lateral view.

spines are only slightly longer than the longest dorsal-fin spine and 2.4 times longer than the first anal-fin spine. The longest anal-fin soft rays are almost as long as the longest dorsal-fin soft rays and 1.4 times longer than the longest anal-fin spine. Like in the dorsal fin, the membrane that connects the anal-fin spines and soft rays is preserved as a thin dark pigmented film. The first anal-fin pterygiophore is very long and sturdy; it is strongly inclined, with an angle of 46-54° relative to the body axis. The succeeding anal-fin pterygiophores are slender; these decrease in size posteriorly in the series.

The posttemporal is not completely preserved above the occiput. The supracleithrum is strong and elongate. The cleithrum is large, with a curved upper part (Fig. 3). The upper portion of the cleithrum is mostly hidden by the second and third vertebrae. The ventral postcleithrum is relatively long, broad and tapered distally. The relatively small coracoid has a narrow ventral projection and a broad postcoracoid process. The scapula is scarcely preserved; it is perforated by an ovoid foramen. The pectoral-fin radials are mostly obscured. The base of the pectoral fin is located under the fifth or sixth vertebra, just below the vertebral column (MCSNV IG 23594/23595; Fig. 1b) or somewhat lower on the flank (in the two other specimens; Figs 1a and 1c). As can be observed in the paratype MCSNV IG 43396 in which it is well-preserved and clearly exposed, the pectoral fin of *Frippia labroiformis* n. gen. n. sp. has fifteen rays.

The basipterygia are moderately elongate and relatively narrow, lacking a postpelvic process (Fig. 2). Each pelvic fin contains a single spine and five soft, branched rays. The pelvic fin is inserted below the pectoral-fin base or just behind it. The pelvic fin is long, its longest ray posteriorly reaches the anal-fin origin. The pelvic-fin spine is relatively slender and much shorter than the pelvic-fin soft rays; it is 1.3 times shorter than the longest dorsal-fin spine.

Large and thin scales cover the entire body and the opercular series as well as the bases of the dorsal, anal and caudal fins (Fig. 1). The trunk scales are finely ctenoid, and each of them bears several radii in the basal field, whereas the head scales are definitely cycloid and lack radii. The lateral line runs very high on the body flank, following the dorsal profile of the body just below the bases of the dorsal-fin rays until the posterior third of the soft portion of the dorsal fin where it is interrupted.

DISCUSSION

As evidenced in the descriptive analysis, the morphology of *Frippia* n. gen. is in some ways reminiscent of that of certain members of the perciform family Labridae and, more generally, of the suborder Labroidei. The resemblance of *Frippia* n. gen. to certain labrid genera is primarily exemplified by the general physiognomy of

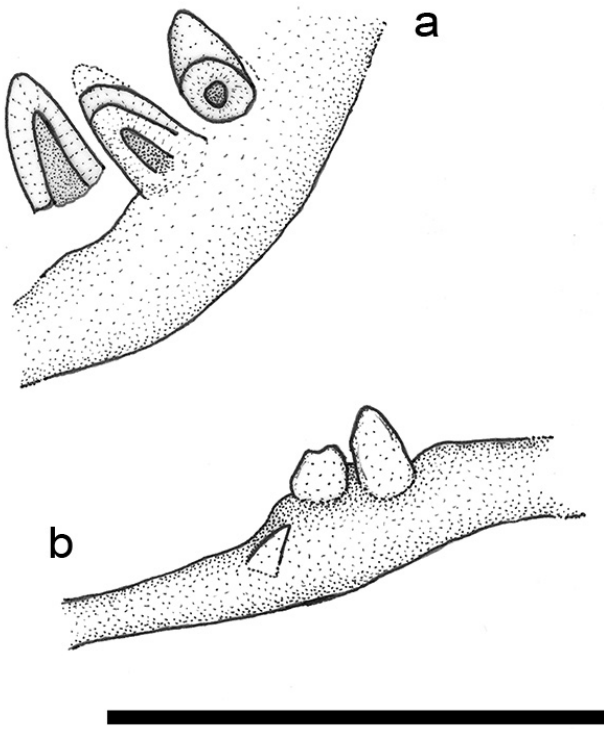

Fig. 4 - *Frippia labroiformis* n. gen. n. sp. from the Eocene of Pesciara di Bolca. Lower pharyngeal teeth. a) Paratype, MCSNV IG 23594; b) holotype, MCSNV T 187. Scale bar 1 mm.

the body and by the degree of consolidation of the caudal skeletal elements, with the urostyle (pu1+u1+u2) fused to the uroneural plus hypurals 3 and 4, and the hypurals 1 and 2 fused into a triangular plate (see Fujita, 1990). Several studies have suggested that the monophyly of the family Labridae is primarily defined by a series of characters of the pharynx and pharyngeal jaw apparatus (e.g., Regan, 1913; Nelson, 1967; Yamaoka, 1978; Liem & Greenwood, 1981; Kaufman & Liem, 1982; Stiassny & Jensen, 1987). Unfortunately, these pharyngeal characters refer to skeletal or muscular structures not preserved or inaccessible in the available specimens of *Frippia* n. gen., such as the epibranchials, pharyngobranchials, pharyngocleithral articulation and pharyngocleithralis and levator posterior muscles (see Kaufman & Liem, 1982). The skeleton of *Frippia* n. gen., however, is characterized by a combination of features that clearly indicates a placement well outside the limits of the family Labridae. In particular, *Frippia* n. gen. is characterized by a premaxilla with separated ascending and articular processes, possession of three supraneurals, ctenoid scales along the trunk, caudal skeleton with three epurals and autogenous haemal spine of the antepenultimate vertebra, and absence of the adductor process of the parasphenoid (see Stiassny & Jensen, 1987; Bannikov & Carnevale, 2010).

The evaluation of the potential labroid affinities of *Frippia* n. gen. is more complex. The limits and composition of this extremely diverse and successful extant group have been relatively unstable, characterized by repeated additions in the last four decades (see Greenwood et al., 1966; Liem & Greenwood, 1981; Kaufman & Liem, 1982). Kaufman & Liem (1982) and, subsequently, Stiassny & Jensen (1987), included four families (Cichlidae, Embiotocidae, Labridae, Pomacentridae) within the Labroidei and provided morphological support for their monophyly exclusively based on gill-arch anatomy. The peculiar pharyngeal jaw apparatus of labroid fishes was proposed to be a significant innovation that promoted the extraordinary evolutionary success and diversity of this group (e.g., Liem, 1973, 1979). A commented list of the gill arch synapomorphic features claimed to corroborate labroid monophyly was recently provided by Wiley & Johnson (2010). Seven of the eight synapomorphies listed by Wiley & Johnson (2010) are related to features poorly exposed or inadequately preserved in the available fossil specimens (blade-like keel on lower pharyngeal jaw correlated with shift in insertion of part to all of transversus ventralis onto the keel. Third subdivision of transversus dorsalis anterior, muscle transversus pharyngobranchialis 2 present; transversus dorsalis anterior and transversus dorsalis posterior do not completely overlie raised articular bony facets of third pharyngobranchial, leaving facets exposed and creating a true diarthrosis; sphincter oesophagi with no subdivision; insertion of levator externus 4 shifted from fourth epibranchial to fifth ceratobranchial; fifth ceratobranchials united to form single unit; first basibranchial elongate, cylindrical and displaced dorsoventrally to lie below basihyal axis). The only potentially valuable labroid synapomorphy (see Stiassny & Jensen, 1987) observed in *Frippia* n. gen. is the weakly developed pharyngeal apophysis apparently arising from the ventral margin of the parasphenoid; however, as pointed out by Rosen & Patterson (1990), the possession of the pharyngeal apophysis is rather ambiguous as a phylogenetically relevant character since it is also present in other perciform groups, including gerreids, haemuloids and sparoids. The Bolca ichthyofauna includes the earliest known record of the Labroidei (Bellwood, 1999), represented by three labrid and two pomacentrid taxa (see Bellwood & Sorbini, 1996; Bannikov & Carnevale, 2010). Moreover, at least two additional Bolca taxa, *Sorbinia* and *Tortonesia*, have been assigned to the Labroidei based on characters of the pharyngeal jaw apparatus (Sorbini et al., 1991; Bellwood, 1995) and another taxon, *Quasicichla*, was interpreted as closely related to the family Cichlidae (Bannikov, 2004). Although long recognized and diagnosed by a series of synapomorphic features, labroid monophyly has been recently reconsidered and extensively discussed by several authors pointing out that it is exclusively supported by a single complex of functionally related characters (e.g., Johnson, 1993; Mabuchi et al., 2007; Wainwright et al., 2012), none of which appears to be unique to labroids. Some morphological studies (e.g., Rosen & Patterson, 1990; Johnson, 1993) and a number of molecular studies (e.g., Streelman & Karl, 1997; Sparks & Smith, 2004; Mabuchi et al., 2007; Alfaro et al., 2009; Santini et al., 2009; Wainwright et al., 2012) have questioned or substantially refuted the possibility of a monophyletic Labroidei. Molecular evidence provides convincing arguments clearly indicating that labroids are polyphyletic (see Wainwright et al., 2012). Moreover, recent studies of functional morphology have concluded that the labroid pharyngeal jaw apparatus is neither behaviourally nor functionally more versatile with respect to that of

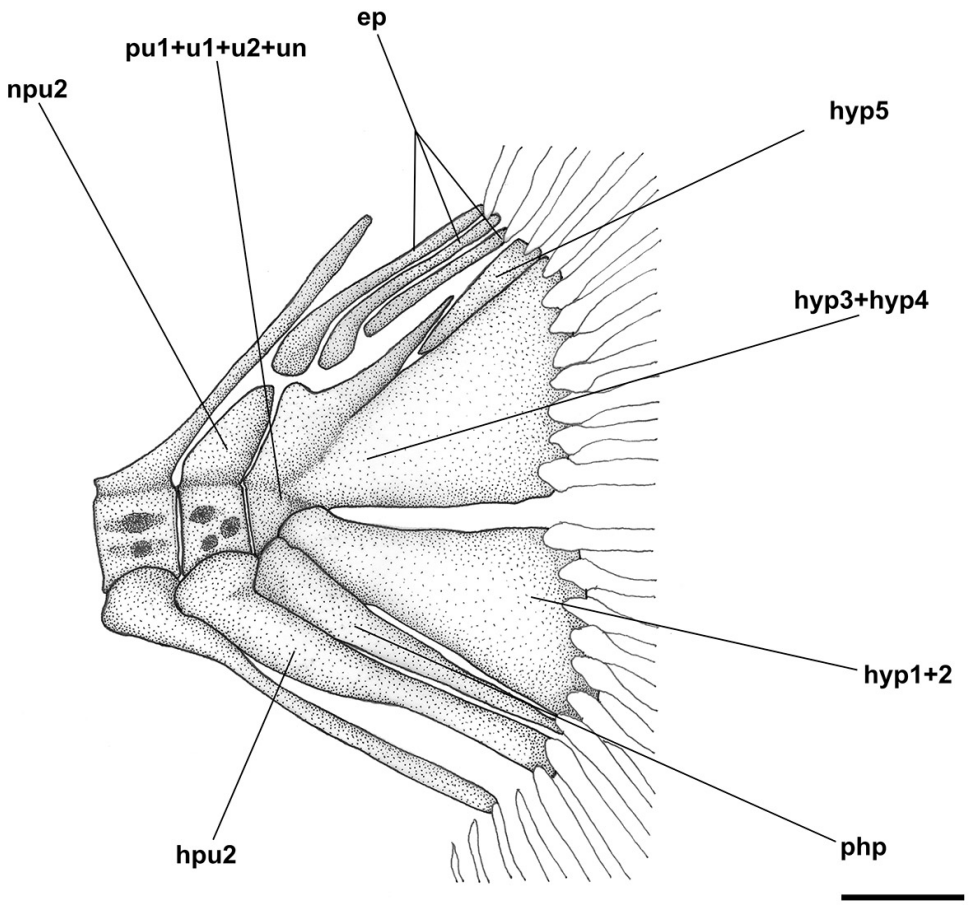

Fig. 5 - *Frippia labroiformis* n. gen. n. sp. from the Eocene of Pesciara di Bolca. Reconstruction of the caudal skeleton based on the paratype MCSNV IG 23594, left lateral view. Scale bar 1 mm.

generalized perciform fishes (Wainwright, 2006), thereby largely reducing its relevance as a major key innovation that facilitated their evolutionary success and diversification. In summary, considering the growing evidence that the Labroidei is not monophyletic, it is reasonable to conclude that the putative relationships of *Frippia* n. gen. to labroids are only due to superficial resemblance and that the labroid affinities of *Quasicichla*, *Sorbinia* and *Tortonesia* should be necessarily reconsidered.

The analysis of the osteological features of *Frippia* n. gen. clearly indicates that it cannot be confidently assigned to any of the perciform suborders (e.g., Johnson, 1993; Nelson, 2006) except for the inadequately defined and possibly non-monophyletic Percoidei. This heterogeneous assemblage is currently defined by several plesiomorphic perciform features and in practice constitutes a convenient repository for those generalized perciform fishes, like *Frippia* n. gen. and many other taxa from Bolca (see Bannikov & Carnevale, 2009), that cannot obviously be placed elsewhere (Johnson, 1984).

Frippia n. gen. is characterized by a unique combination of features that clearly distinguish it from known Recent and fossil percoid taxa. Most of these features are present in their primitive condition, while some others, such as the basic structure of the caudal skeleton, exhibit a derived morphology, which is unique within the Percoidei and, more generally, within percomorphs.

The premaxilla of *Frippia* n. gen. possesses a relatively elongate alveolar process that supports a long ascending process separated from the robust articular process by a deep notch. Such a premaxillary structure is considered primitive for percoids (Rosen & Patterson, 1990) and is characteristic of many basal percoids (see Bannikov & Carnevale, 2007), including the Acropomatidae, Ambassidae, Apogonidae, Centropomidae, Latidae, Lutjanidae, Kuhliidae, Moronidae, Percichthyidae, Percidae, Pomatomidae, Priscacaridae, Serranidae, Sciaenidae, Terapontidae, etc. Within the Percoidei, a derived premaxillary structure appears to be typical of gerreids, haemuloids and sparoids (Johnson, 1980; Rosen & Patterson, 1990), in which the ascending and articular processed are coalesced and, in some cases, the length of the alveolar process is sometimes reduced to about half of the length of the ascending-articular process.

As documented above, the hyoid bar of *Frippia* n. gen. appears to support six branchiostegal rays. The possession of six branchiostegal rays is rather common within the Percoidei, observed in about forty families or *incertae sedis* genera (see Johnson, 1984), including the Ambassidae, Aplodactylidae, Callanthiidae, Centrarchidae, Cepolidae, Chaetodontidae, Cheilodactylidae, Chironemidae, Cirrhitidae, Coracinidae, *Datnioides*, Drepanidae, Ephippidae, Gerreidae, Girellidae, Grammatidae, Kuhliidae, Latrididae, Leptobramidae, Lethrinidae,

Lobotidae, Malacanthidae, Nemipteridae, *Neoscorpis*, Opistognathidae, Percichthyidae, Percidae, Plesiopidae, Pomacanthidae, Priacanthidae, Pseudochromidae, Scatophagidae, Serranidae, Sillaginidae, Sparidae and Terapontidae.

The vertebral column of *Frippia* n. gen. contains 26 (10+16) vertebrae. The possession of twenty-six vertebrae is derived within the Percoidei since the possession of twenty-four (Gosline, 1968, 1971; Johnson, 1984) or, at least, twenty-five (Tominaga, 1986) vertebrae is currently considered the primitive condition for percoids. Percoid families or *incertae sedis* genera characterized by twenty-six vertebrae include the Cirrhitidae, *Dinoperca*, Enoplosidae, Haemulidae, *Howella*, Kyphosidae, Opistognathidae, Ostracoberycidae, Plesiopidae, Pseudochromidae, Scombropidae, Serranidae, and Terapontidae.

The caudal skeleton of *Frippia* n. gen. exhibits a peculiar morphology, with the urostylar complex fused to the single uroneural plus hypurals third and fourth, fused first plus second hypurals, autogenous fifth hypural and parhypural, parhypurapophysis absent, three epurals, autogenous haemal spines of the second and third preural centra, and a low neural crest on the second preural centrum. Such a configuration of the caudal skeleton appears to be unique within the Percoidei (see Johnson, 1984). Considered at a more inclusive taxonomic level, a similar structure of the caudal skeleton has been observed in a few percomorph taxa, including certain pomacentrids and triglids, which, in any case, also possess a well-developed parhypurapophysis (see Fujita, 1990).

Frippia n. gen. possesses the primitive percoid complement of principal caudal-fin rays; the seventeen principal caudal-fin rays (I,8-7,I) are associated with six to seven upper and five to six lower procurrent caudal-fin rays. The complement of principal and procurrent caudal-fin rays observed in *Frippia* n. gen. also occurs in members of several extant percoid families and *incertae sedis* genera (see Johnson, 1984), including the Apogonidae, Bramidae, Caesionidae, Callanthiidae, Centrarchidae, Enoplosidae, Ephippidae, Grammatidae, *Hapalogenys*, Monodactylidae, Pempheridae, Pentacerotidae, Percichthyidae, Plesiopidae, Sciaenidae and *Siniperca*.

Frippia n. gen. possesses three slender supraneurals and exhibits the predorsal formula 0/0/0+2/1+1/; such a condition is considered primitive for the Percoidei and it is extremely common in this group, observed in representatives of many families and *incertae sedis* genera (see Johnson, 1984), including the Acropomatidae, Arripidae, Caesionidae, Centropomidae, Cirrhitidae, Enoplosidae, Epigonidae, Gerreidae, Glaucosomatidae, Grammatidae, *Hemilutjanus*, *Howella*, Kuhliidae, Lactariidae, Lobotidae, Moronidae, Mullidae, Ostracoberycidae, Plesiopidae, *Polyprion*, Pseudochromidae, Scombropidae, Scorpididae, Serranidae, *Siniperca*, and *Stereolepis*.

The continuous dorsal fin of *Frippia* n. gen. consists of nine spines plus fourteen soft rays while the anal fin contains three spines plus ten soft rays. Moreover, the first pterygiophore of both the dorsal and anal fins supports two supernumerary spines, representing the primitive condition for percoid fishes (Johnson, 1984; Patterson, 1992). A similar combination of dorsal- and anal-fin formulae has been observed in certain taxa of a few percoid families (see Johnson, 1984), including the Caesionidae, Gerreidae, Haemulidae, Pentacerotidae, Percichthyidae, Percidae and Plesiopidae.

The pelvic fin of *Frippia* n. gen. is characterized by one spine and five elongate soft rays. According to Johnson (1984), this is the most consistent feature of the Percoidei and also represents the primitive perciform condition. Only a few percoid fishes (*Gadopsis*, Plesiopidae, Pseudochromidae) are characterized by a different pelvic-fin complement, with less than five soft rays.

As far as the squamation is concerned, *Frippia* n. gen. exhibits the co-occurrence of ctenoid and cycloid scales. Ctenoid scales cover the entire body and the bases of the dorsal, anal and caudal fins, while cycloid scales cover part of the head (opercular series). Ctenoid scales are widespread within percoids (Johnson, 1984). The phylogenetic significance of cycloid scales is of problematic evaluation; according to Johnson (1984), the cycloid scales of percoids may represent a plesiomorphic condition or these may be secondarily derived when they only occur in selected taxa of groups mostly characterized by ctenoid scales. The condition of *Frippia* n. gen. is difficult to interpret from a phylogenetic perspective since cycloid scales sporadically occur on the head of a number of percoid taxa.

In conclusion, the comparative analysis of the distribution of the skeletal features of *Frippia* n. gen. clearly reveals that its relationships are rather problematic. The basic osteological configuration apparently did not provide any convincing evidence that would relate *Frippia* n. gen. to any of the known extinct or living percoid families or *incertae sedis* genera. *Frippia* n. gen. shares several morphological (supraneural configuration; disjunct and high lateral line) and meristic (number of vertebrae; dorsal-, anal-, and caudal-fin formulae) features with members of the family Plesiopidae (see Johnson, 1984), from which it notably differs in having a unique structure of the caudal-fin skeleton (see Fujita, 1990; Mooi, 1993), premaxilla with separate ascending and articular processes (see Mooi, 1995), and pelvic fin with five rays (see Mooi, 1993). Therefore, because of the evident difficulties to unambiguously identify the sister-group relationships of *Frippia* n. gen., it is reasonable to place this new Eocene taxon *incertae sedis* among the percoid fishes.

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