

A new percid fish from the Eocene of Monte Bolca, Italy: *Hendrixella grandei* gen. & sp. nov.

ALEXANDRE F. BANNIKOV¹ & GIORGIO CARNEVALE^{2,3,*}

Key words: Teleostei; Percoidei; *Hendrixella grandei*; Eocene; Monte Bolca; Italy.

ABSTRACT

A new genus and species of percid fish, *Hendrixella grandei* gen. & sp. nov. is described from the upper Ypresian limestone of Monte Bolca, Italy. It is based on four well-preserved specimens that show an elongate and slender body and a unique combination of features, including possession of 11 + 13 vertebrae, two series of intermuscular bones, fused haemal spine of third preural centrum, caudal fin with 17 principal rays and 11 upper and eight lower procurrent rays, predorsal formula 0/0/1 + 1/1/, two separated dorsal fins with rayless pterygiophore in-between, and a single supernumerary spine in both dorsal

and anal fins. Due to this unique combination of features, *Hendrixella* cannot be placed within any existing fossil or extant percid families and it is placed *incertae sedis* in the Percoidei. The possession of two series of intermuscular bones represents an unambiguous autapomorphy of *Hendrixella*. A comparative analysis of the distribution of intermusculars among percomorph fishes indicates that the intermuscular bones of the upper series can be homologized with the epineurals and those of the lower series are the homologs of the epicontrals of non-acanthomorphs.

Introduction

The suborder Percoidei is the largest and most diverse of the order Perciformes and contains more than 75 extant families, a number of *incertae sedis* genera, approximately 3200 living species, and an indefinite number of fossil species (Nelson 2006). Despite the extraordinary diversity exhibited by Recent taxa, the evolutionary history of the group is largely unknown and poorly defined. Percoid fishes are highly represented in shallow marine environments forming a significant component of the reef assemblages of tropical and subtropical seas. A few groups of percoids are primarily epi- and mesopelagic and some families are restricted to freshwater. The early radiation of the group occurred in the Cretaceous, documented by rare but well-preserved articulated skeletal remains from India (Arratia et al. 2004) and Italy (Sorbini & Bannikov 1991), as well as by otoliths (see e.g., Sieber & Weinfurter 1967; Nolf & Stringer 1996; Schwarzhan 1996; Nolf 2003). The diversity of percoid fishes was remarkably high at least since the Eocene, documented by an enormous number of records from several marine and freshwater localities of Europe, Africa, Asia, and North and South America.

The renowned Eocene locality of Monte Bolca, Italy, largely contributed to our knowledge of the past diversity of percoid fishes (see e.g., Bannikov 1999, 2008; Bannikov & Zorzini 2004; Bannikov & Carnevale 2007). The highly diverse assemblage from Monte Bolca (see Landini & Sorbini 1996) includes representatives of almost all of the fish families found on coral reefs today, suggesting that it represents the earliest modern coral reef fish assemblage (Bellwood 1996, 1998). The rich fish-bearing micritic limestone of Monte Bolca originated in a shallow marine basin characterized by restricted circulation on the seafloor, exposed to pelagic, seagrass and coral reef biotic influences (Landini & Sorbini 1996).

The initial impetus for this paper was the discovery of a new fossil percoid fish during the examination of a collection of fishes from Monte Bolca housed in the Field Museum of Natural History, Chicago by the senior author. While the osteological description was being prepared, both authors performed a careful analysis of the extraordinary collection of fishes from Monte Bolca of the Museo Civico di Storia Naturale, Verona, which revealed the existence of three additional specimens among the indeterminate material of the collection. Such specimens provided new, previously unrecog-

¹ Borisyak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya 123, Moscow 117997, Russia.

² Dipartimento di Scienze della Terra, Università di Pisa, Via Santa Maria, 53 I-56126 Pisa, Italia.

³ Museo di Storia Naturale e del Territorio, Università di Pisa, Via Roma, 79 I-56011 Calci (PI), Italia.

*Corresponding author: Giorgio Carnevale, E-mail: carnevale@dst.unipi.it

nized features that allowed a substantial improvement of the knowledge of the morphology of this new percoid taxon. A detailed systematic study of the osteology of these fossils suggests unequivocally that such a new taxon cannot be placed within any existing family of percoid fishes. This paper therefore has two goals: the description of this new Eocene fish from Monte Bolca and the discussion of its affinities within the Percoidei.

Materials and methods

The specimens required matrix removal before examination in order to allow investigations of their skeletal structures in as much detail as possible; they were prepared using thin needles. The fossils were studied using a stereomicroscope with attached camera lucida drawing arm. Some details were best seen when the specimens were moistened with alcohol during microscopic examination. Measurements were taken using a dial caliper, to the nearest 0.1 mm. Comparative information was derived mainly from the literature.

Abbreviations – br, branchiostegal rays; cl, cleithrum; co, coracoid; cth, anterior ceratohyal; d, dentary; ec, epicentral; en, epineural; ep, epural; f, frontal; FMNH, Field Museum, Chicago; h, hyomandibula; hyp, hypural; MCSNV, Museo Civico di Storia Naturale, Verona; pcl, postcleithrum; php, parhypural; pmx, premaxilla; pop, preopercle; pr, pleural rib; pu, preural centrum; q, quadrate; scl, supracleithrum; SL, standard length; sn, supra-neural; u, ural centrum; un, uroneural; v, vertebra; vhh, ventral hypohyal.

Systematic palaeontology

Subdivision Teleostei *sensu* Patterson & Rosen, 1977
Order Perciformes *sensu* Johnson & Patterson, 1993
Suborder Percoidei Bleeker, 1859
Family indeterminate
Genus *Hendrixella* nov.

Diagnosis: Percoid with elongate and slender body; head pointed; jaw teeth sharp and posteriorly recurved; seven branchiostegal rays; 11 + 13 vertebrae; two series of intermuscular bones; caudal skeleton with five autogenous hypurals, three epurals, two uroneurals; haemal spine of third preural centrum fused; caudal fin with 17 principal rays and 11 upper and eight lower procurrent rays; predorsal formula 0/0/1 + 1/1/1; two separated dorsal fins with a rayless pterygiophore in-between; first dorsal fin contains nine slender, flexible spines; first dorsal-fin spine supernumerary; second dorsal fin contains one spine and eight soft rays; anal fin with two spines (one supernumerary) and eight soft rays; anal fin opposed and nearly symmetrical to second dorsal fin; pectoral fin narrow; scales moderately large and weakly ctenoid.

Type species: *Hendrixella grandei* gen. & sp. nov., by monotypy and designation herein.

Etymology: Genus named in honour of the musician and composer James Marshall Hendrix.

Hendrixella grandei sp. nov. (Figs. 1–5)

Diagnosis: As for the genus.

Etymology: Species named in honour of the distinguished paleoichthyologist Dr. Lance Grande.

Holotype: FMNH PF 3456, single plate, complete skeleton, 101.5 mm SL; Upper Ypresian (uppermost Lower or lowermost Middle Eocene), *Alveolina dainelli* Zone (Papazzoni & Trevisani 2006); Monte Bolca locality, Pesciara cave site.

Paratypes: MCSNV T 424, single plate, complete skeleton, 83.5 mm SL; MCSNV I.G. 186677, single plate, complete skeleton, 72 mm SL.

Referred specimen: MCSNV T 426, single plate, incomplete skeleton, estimated SL 73 mm.

Measurements (of the holotype): SL of the holotype: 101.5 mm. Other measurements as percentage of SL: Head length: 26; maximum body depth: 15; caudal peduncle depth: 8; predorsal (1st fin) distance: 40; predorsal (2nd fin) distance: 67.5; preanal distance: 70.5; distance between pelvic and anal fins: 37.5; 1st dorsal-fin base length: 20; 2nd dorsal-fin base length: 12; distance between 1st and 2nd dorsal fins: 8; anal-fin base length: 13; longest dorsal-fin spine: 11; longest dorsal-fin ray: 14; longest caudal fin ray: 19.

Description: The body is elongate and slender, with a relatively long caudal peduncle (Figs. 1–2). The caudal peduncle depth is about 53% of maximum body depth. The head is long and pointed, and its length is contained approximately four times in SL. The orbit seems to be located approximately in the middle of the head length. The mouth is terminal and horizontal. The gape of the mouth is wide, apparently reaching almost to the half of the orbit (Figs. 1–3). The body probably was subcylindrical.

The neurocranium is oblong and moderately wide (Fig. 2); it is preserved dorso-ventrally in all four specimens available. The frontals are rather large (Fig. 3); these bones appear only moderately narrowed between the orbits. The ethmoid and otic sectors of the neurocranium are damaged and poorly preserved.

The bones of the infraorbital series are difficult to recognize.

The alveolar process of the premaxilla is narrow. The ascending process of the premaxilla is relatively short and oblique, whereas the articular process is broad. Premaxillary teeth are of moderate size, sharp, conical, slender, and the anteriormost posteriorly recurved (Fig. 3). The lower jaw is very narrow. The dentary is extremely shallow in the symphyseal region. The retroarticular process of the mandible is slightly expanded posteriorly. The mandibular teeth are sharp, conical and moderate in size (Fig. 3).

The bones of the suspensorium cannot be distinguished from each other (Fig. 3). Although the hyomandibula is not completely preserved, it is evident that its shaft is

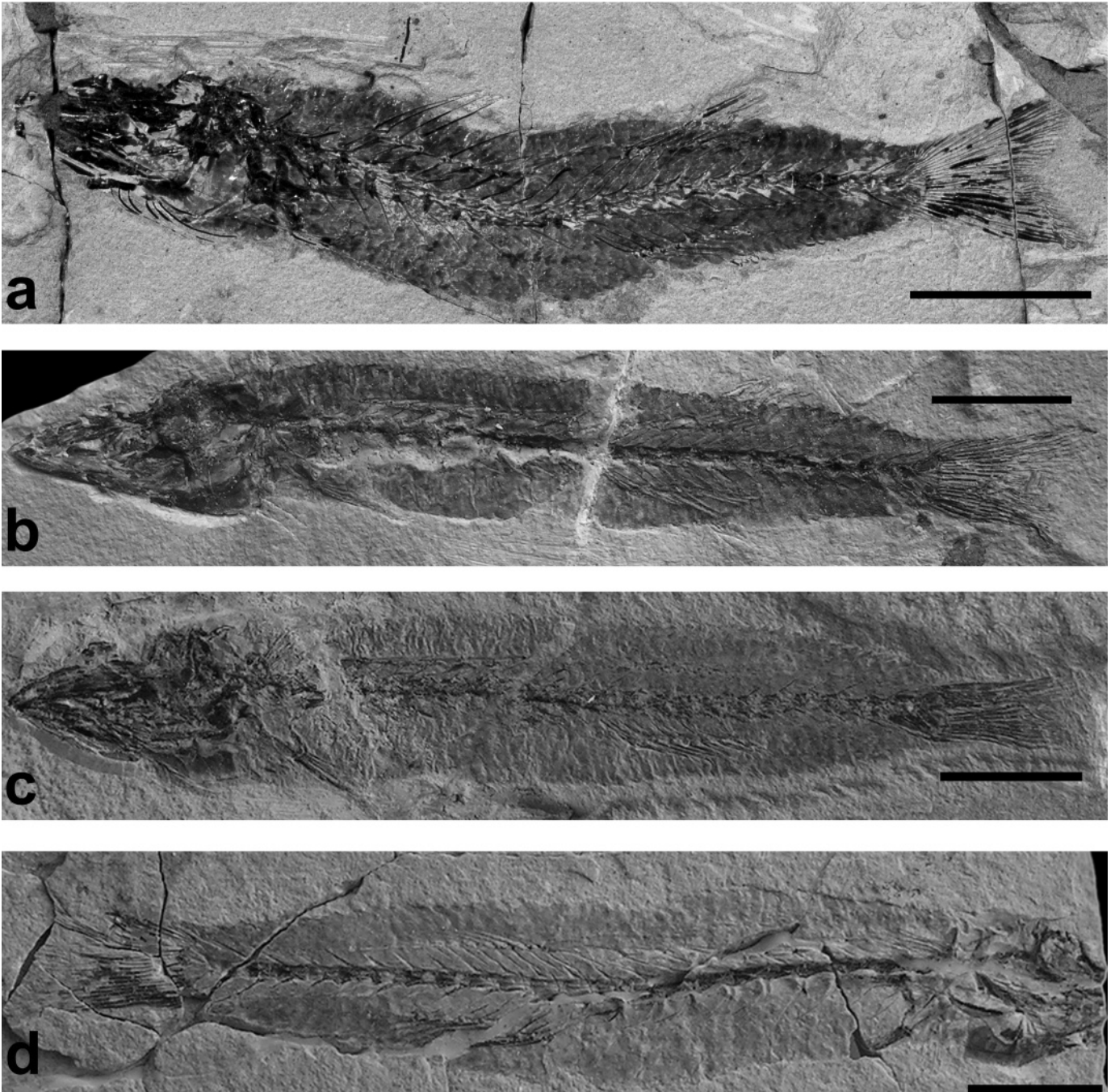


Fig. 1. *Hendrixella grandei* gen. & sp. nov. from the Ypresian of Monte Bolca, Italy: a) FMNH PF 3456, holotype, left side, lateral view, scale bar 20 mm. b) MCSNV I.G. 186677, paratype, left side, lateral view, scale bar 10 mm. c) MCSNV T424, paratype, left side, lateral view, scale bar 10 mm. d) MCSNV T426, right side, lateral view, scale bar 10 mm.

anteroventrally inclined, and its articular head appears to be relatively broad. The articular process of the quadrate is small.

The preopercle is robust, crescent-shaped, with a smooth posterior margin (Fig. 3). The posterior portion of the opercle is not evident.

The hyoid bar is slender and elongate. The anterior ceratohyal possesses a distinct anteroventral process that supports the ventral hypohyal. There are seven sabre-like branchiostegal rays (Fig. 3).

The vertebral column consists of 24 vertebrae, 11 abdominal and 13 caudal, including the urostyle (Fig. 2). The length of

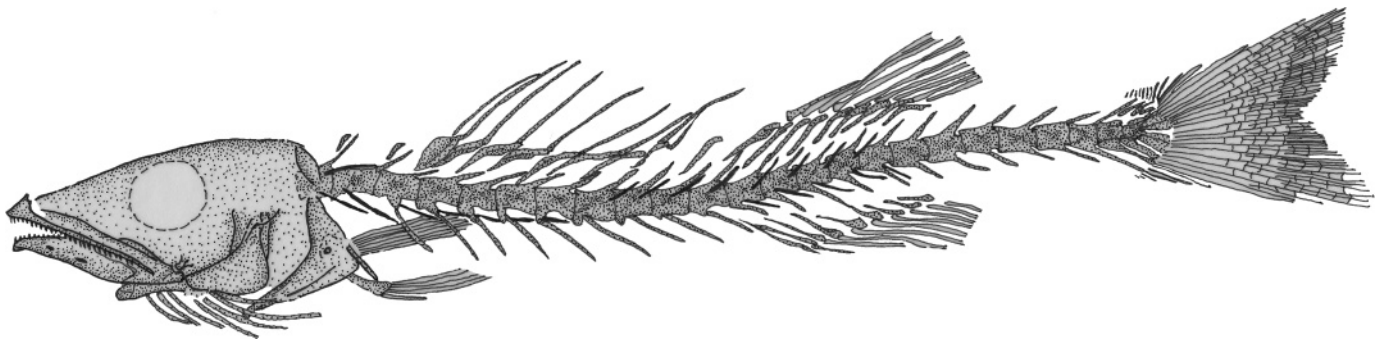


Fig. 2. *Hendrixella grandei* gen. & sp. nov.: reconstruction of the skeleton, left side, lateral view; scales omitted.

Table 1. Distribution of pleural ribs and intermuscular bones in *Hendrixella grandei* gen. & sp. nov.

VERTEBRAE	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17–24
<i>Epineurals</i>		x							x	x	x	x	x	x	x	x	
<i>Epicentrals</i>	x	x	x	x	x	x	x						x	x	x	x	x
<i>Pleural ribs</i>			x	x	x	x	x	x	x	x	x						

the caudal portion of the vertebral column is about 1.05 times greater than the length of the abdominal portion. The vertebral centra are rectangular, longer than high. The first vertebra appears to be fore shortened. The neural spines are short and slender; these arise obliquely from the posterior half of the centrum. The haemal spines are short and relatively slender. The vertebrae 3 through 11 bear robust parapophyses. Thin, slender pleural ribs insert along the posterior margin of the parapophyses. There are two series of intermuscular bones (Figs. 2, 4), which are well exposed in the holotype. Based on their relative position, the bones of the two series are interpreted herein as being epineurals and epicentrals respectively (Tab. 1). The epineurals insert just below or slightly posterior to the bases of the neural arches of vertebrae 1 and 8 through 15 (Figs. 2, 4). The epicentrals of the first two vertebrae originate close to the ventral margin of the centra, those of vertebrae 3 through 7 insert along the posterior margin of the parapophyses, and those of vertebrae 12 through 16 insert just behind the bases of the haemal arches.

The caudal skeleton and fin are relatively well preserved in the material examined (Fig. 5). The terminal centrum is characterized by the fusion of the first preural centrum with one or two ural centra. The five hypurals, parhypural and haemal spine of the second preural centrum are autogenous. The parhypural bears a long and thick parhypurapophysis. There is a reduced diastema between the epaxial and hypaxial hypurals. The neural and haemal spines of the third preural centrum are evidently longer than those of the preceding vertebrae, and the haemal spine appears to be fused to the centrum. The neural spine of the second preural centrum is extremely reduced. There are three epurals; the ventral portion of the second epural is widely enlarged with a rounded profile. There are two uroneurals, the

first forming the stegural. The caudal fin is relatively small and forked. The caudal fin consists of 17 principal rays, 15 of which are branched, and 11 upper and eight lower procurent rays.

There are two small supraneurals; the first supraneural precedes the neural spine of the first vertebra, while the second one lies anterior to the neural spine of the second vertebra. The predorsal formula is 0/0/1 + 1/1/ (Fig. 2). There are two dorsal fins separated by a broad gap, roughly corresponding to the length of 2.5 vertebrae. The first dorsal fin originates above the fourth vertebra and terminates at the level of the 11th vertebra. The first dorsal fin contains nine slender and flexible spines. The first spine, which is in supernumerary association with the first dorsal-fin pterygiophore is 1.15 times shorter than the second. The second and third spines are approximately equal in length, whereas the succeeding spines progressively decrease in size. The first two pterygiophores interdigitate with the second and third neural spines, and the space between the fourth and fifth neural spines accommodates the fifth and sixth pterygiophores. The pterygiophores of the first dorsal fin are strongly inclined posteriorly and are characterized by longitudinal thickened ridges. The ninth pterygiophore is rayless, located in the interneural space between the eighth and ninth vertebrae. The second dorsal fin originates above the border between the 13th and 14th vertebrae and terminates over the 18th vertebra. It consists of one spine and eight soft rays supported by nine pterygiophores. The first soft ray seems to be unbranched. The rays progressively decrease in length posteriorly in the series. The length of the longest soft rays exceeds the length of the longest spines of the first dorsal fin. The proximal and middle radials of the pterygiophores appear to be fused. The four anterior pterygiophores of the second dorsal fin penetrate into the interneural spaces, whereas the proximal shaft of the posterior five do not reach the tips of the neural spines.

The anal fin is opposite and approximately symmetric to the second dorsal fin. The anal fin comprises two short, slender spines and eight soft rays, supported by nine pterygiophores. The first anal-fin spine is supernumerary. The anal-fin pterygiophores are slender, markedly inclined posteriorly, and they decrease in length posteriorly in the series.

The posttemporal is difficult to recognize, whereas the flat, elongate supracleithrum is clearly exposed. The cleithrum and

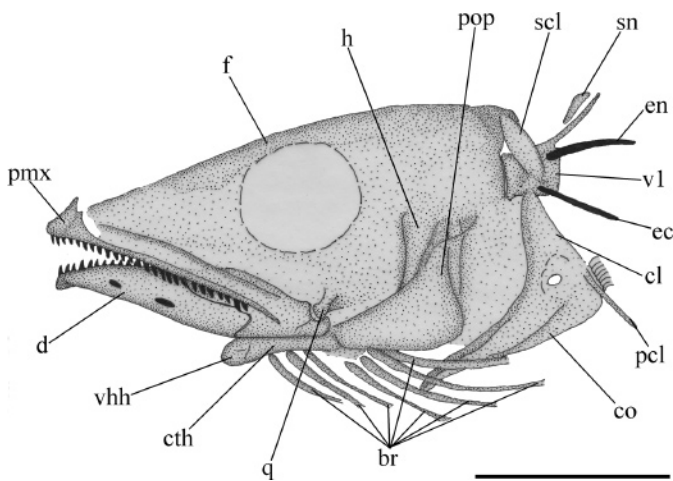


Fig. 3. *Hendrixella grandei* gen. & sp. nov.: reconstruction of the head based on the holotype FMNH PF 3456, left side, lateral view. Scale bar is 10 mm.

coracoid are primarily preserved as impression. The cleithrum is elongate, relatively large, sigmoid in shape (Fig. 3). The coracoid is narrow and wedge-shaped. A small scapular foramen is also present. There is a single slender and relatively short postcleithrum. There is no evidence of preserved pectoral radials. The pectoral fin inserts on the lower half of the body. The original complement of pectoral-fin rays cannot be estimated due to inadequate preservation; however, there are not fewer than nine rays.

The pelvic fin (Fig. 2) inserts behind the pectoral-fin base and contains a short and slender spine and five soft rays. The basipterygium is rather small and poorly ossified.

The entire body and head are covered by thin and moderately large scales. A number of scales exhibit up to 10 delicate basal radii. These scales also show multiple circuli on the surface and minute tubercles on the apical field. Delicate transforming ctenii are also visible. The posterior portion of the lateral line series is preserved in the holotype; due to taphonomic processes, this appears to be displaced below the caudal part of the vertebral column.

Comparison and discussion

A general overview of the morphology of *Hendrixella grandei* gen. & sp. nov. clearly support its alignment with perciform fishes. In particular, the characteristics of the unpaired fins, which contain true dorsal- and anal-fin spines, in combination with completely ossified supraneurals, absence of a free second ural centrum, presence of five autogenous hypurals, presence of a free uroneural, haemal arch and spine of the second preural centrum autogenous, possession of transforming ctenoid scales, caudal fin with 17 principal rays, pelvic fin with one spine and five rays, supracleithrum developed, and anterior neural spines thin and slender unquestionably indicate that it is a member of the highly diverse order Perciformes (see Fujita 1990; Johnson & Patterson 1993; Parenti 1993; Stiassny 1993; Tyler et al. 2003).

Within the Perciformes, *Hendrixella* lacks the features that define all perciform suborders except the Percoidei, the largest group of the order (see Bannikov & Carnevale 2007). Like the order Perciformes, the suborder Percoidei has not been adequately defined and there is no evidence that it represents a monophyletic assemblage (Johnson 1993). In general, the Percoidei has been commonly considered as a convenient repository for those perciforms that cannot be placed elsewhere (see Johnson 1984). For this reason, Percoidei is uniquely diagnosed by several plesiomorphic perciform characters.

Hendrixella possesses a combination of derived features that is unique within percoid fishes, although some of these features can be found in various combination in a few of the percoid groups. The combination of the vertebral number, structure of median fins (including the caudal one), dorsal and anal fins with a single supernumerary spine, predorsal formula, caudal skeleton with fused haemal spine of the third preural centrum, and intermuscular bones complement, as well as general physiognomy clearly distinguish *Hendrixella* from the known representatives of Recent and fossil percoid families and *incertae sedis* genera. Therefore, *Hendrixella* cannot be accommodated in any existing group of percoid fishes. However, the position of *Hendrixella* within the Percoidei is rather problematic to define, even with a detailed comparative analysis of the distribution of its derived features.

As described above, the vertebral column of *Hendrixella* consists of 24 vertebrae; although the possession of 24 vertebrae is considered the primitive condition for percoids (see Gosline 1968, 1971), their relative complement of abdominal (11) and caudal (13) vertebrae is quite unusual, observed only in selected members of the families Carangidae, Chaetodontidae, Lobotidae, and Serranidae (see Johnson 1984).

Hendrixella possesses two externally separated dorsal fins with a spineless pterygiophore that continue beneath such an external gap. A similar arrangement of the dorsal fin also has been observed in the Acropomatidae, Ambassidae, Apogonidae, Emmelichthyidae, Enoplosidae, Epigonidae and Quasimullidae (Johnson 1984; Bannikov 1999).

The dorsal fin of *Hendrixella* contains 10 spines plus eight soft rays; even though the presence of 10 spines is considered as the primitive condition for percoids (see Springer et al. 1977), shared by many families (Acropomatidae, Callanthiidae, Centrarchidae, Coracinidae, Gerreidae, Haemulidae, Kuhliidae, Kyphosidae, Lethrinidae, Lutjanidae, Malacanthidae, Microcanthidae, Moronidae, Nemipteridae, Percichthyidae, Priscacaridae, Sciaenidae, Scorpidae, Sillaginidae, Sparidae, etc.) and *incertae sedis* genera (e.g., *Jimtylerius*, *Hemilutjanus*), the concurrent occurrence of as few as eight soft rays is rather uncommon and only certain members of the families Callanthiidae, Pentacerotidae, Percichthyidae and Plesiopidae exhibit the same dorsal-fin formula.

The first dorsal-fin pterygiophore of *Hendrixella* supports two spines and only one of these is supernumerary. As pointed out by Patterson (1992), the possession of two supernumerary spines is the primitive condition in percoids (and more gener-

ally in perciforms) and the presence of a single spine is relatively uncommon within percoid groups.

The anal fin of *Hendrixella* consists of two spines and eight soft rays. A similar anal-fin formula also has been observed in certain members of the families Acropomatidae, Apogonidae, Centrarchidae, Epigonidae, Mullidae, Pentacerotidae, Percidae, Sciaenidae, and Serranidae. However, only one of the two anal spines is supernumerary. According to Johnson (1984), the same condition is typical of apogonids, resulting from the evolutionary loss of a primitive anteriormost spine. As documented above, the anal fin of *Hendrixella* is opposite to the second dorsal fin; this could be probably interpreted as the primitive percoid condition, given that the symmetrical position of these anatomical units seems to be coordinated in shared myomeres through a common developmental mechanism (Mabee et al. 2002).

Hendrixella possesses two thin and short supraneurals; the presence of two supraneurals represents a derived condition for percoids (Johnson 1984), which is shared by several groups (e.g., Acanthoclinidae, Ambassidae, Banjosidae, Callanthiidae, Centrogenysidae, Chaetodontidae, Cheilodactylidae, Chironemidae, Congrogadidae, Ephippidae, Eocottidae, Giganthiidae, Girellidae, Inermiidae, Latrididae, Malacanthidae, Mullidae, Nemipteridae, Opistognathidae, Oplegnathidae, Pentacerotidae, Plesiopidae, Pomacanthidae, Pseudochromidae, Scatophagidae, Serranidae, Sillaginidae, Toxotidae). The predorsal formula (Ahlstrom et al. 1976) of *Hendrixella* is 0/0/1 + 1/1. Based on the hypothesis proposed by Johnson (1984), this is a derived condition, which also has been observed in certain taxa of the family Ambassidae; however, such a convergence in the predorsal arrangement is clearly homoplastic, since the convergence in identical patterns of the predorsal configuration has arisen independently many times during the evolutionary history of percoid fishes (see Johnson 1984).

The basic structure of the caudal skeleton of *Hendrixella* is similar to that of many percoids, except for the presence of a fused haemal spine of the third preural centrum. It consists of five autogenous hypurals, a parhypural with a strong hypurapophysis, two uroneurals, three epurals and second preural centrum with reduced neural spine and free haemal arch and spine. Although a fused haemal spine of the third preural centrum is typical of some families within the Percoidei (e.g., Ambassidae, Apogonidae, Callanthiidae, Echeneididae, Nandidae, Opistognathidae, Pentacerotidae, Plesiopidae, Pseudochromidae), a similar structure of the whole caudal complex is extremely rare and also has been observed in certain members of the families Eocottidae and Malacanthidae (Johnson 1984; Bannikov 2004).

The caudal fin of *Hendrixella* contains 17 principal rays, plus 11 dorsal and eight ventral procurrent rays. Although the possession of 17 principal caudal fin rays is extremely common within the Percoidei, representing the plesiomorphic condition (see Patterson 1968), the total (principal + procurrent) complement of caudal-fin rays of *Hendrixella* only occurs in certain percoids (see Johnson 1984), including the Ambassidae, Caran-

gidae, Centropomidae, Echeneididae, Girellidae, Haemulidae, Lutjanidae, Malacanthidae, Nemipteridae, Sparidae and Terapontidae.

The possession of two distinct series of intermuscular bones appears to be unique within the Percoidei, representing an unambiguous autapomorphy of *Hendrixella*. According to Patterson & Johnson (1995), a single series of intermuscular bones characterizes percomorph fishes, and more generally all acanthomorphs except for certain polymixiiforms, beryciforms, and lampridiforms.

In summary, the analysis of the distribution of selected derived features of *Hendrixella* clearly indicates that its relationships are rather difficult to define. Such a comparative discussion has not provided any convincing evidence that would unite *Hendrixella* to any previously known percoid family or *incertae sedis* genera. Although *Hendrixella* shares certain morphological features (fused haemal spine of the third preural centrum; median fin distribution) and meristic (dorsal-, anal- and caudal-fin formulae, etc.) features with some members of the families Ambassidae, Apogonidae, and Eocottidae, it differs from the members of these families in having a different jaw dentition, 11 + 13 vertebrae, and two series of intermuscular bones. *Hendrixella* possesses a unique combination of features among percoids and it cannot easily be accommodated within any of the known familial categories. However, even considering that the possession of two distinct series of intermuscular bones is unique among percoids, the difficulties in unambiguously identifying the sister-group relationships of *Hendrixella* strongly support its placement as *incertae sedis* among the Percoidei.

Comments on intermuscular bones

As pointed out in the previous section, one of the most interesting morphological features of *Hendrixella* is the possession of two distinct series of intermuscular bones (Figs. 2, 4; Tab. 1). This represents an unambiguous autapomorphy of *Hendrixella* that, together with the other diagnostic features discussed above, strongly supports its separate status as a new previously unrecognized genus of percoid fish.

The interpretation of these bones is not immediate, and some problems emerged during the attempts to homologize them. Among extant vertebrates, the intermuscular bones are unique to teleost fishes, representing segmental and serially homologous ossifications located in the myosepta (Patterson & Johnson 1995). A number of names have been used for these bones, primarily based on their topographic position along the axial skeleton (see e.g., Monod 1963). Owen (1846, 1866) created the terms epineural, epicentral and epipleural, which are currently used in morphological studies, in order to indicate the three series of intermuscular bones that attach to the axial skeleton of teleost fishes. An extensive survey on intermusculars was realized by Patterson & Johnson (1995), who discussed in great detail the homology of these structures by studying their ontogeny, distribution and systematic value among the major groups of teleost fishes. A relevant part of such a study was

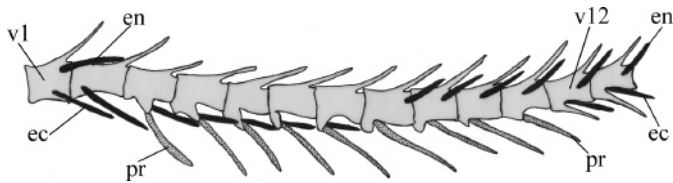


Fig. 4. *Hendrixella grandei* gen. & sp. nov.: first 13 vertebrae and attached intermuscular bones and pleural ribs, based on the holotype FMNH PF 3456 (101.5 mm SL) and supported by the paratypes MCSNV T424 (83.5 mm SL) and MCSNV I.G. 186677 (72 mm SL); left side, lateral view.

devoted to the intermusculars of acanthomorph fishes. Patterson & Johnson (1995) concluded that the single bony series of intermusculars typical of acanthomorph fishes cannot be homologized with the epipleural series of lower teleosts as was commonly thought. The plesiomorphic configuration of intermusculars (bones or ligaments) in acanthomorphs is characterized by epineurals in the epaxial myoseptum, epicentrals in the horizontal septum, and epipleurals in the hypaxial myoseptum (Gemballa & Britz 1998). According to Patterson & Johnson (1995), acanthomorphs lack epipleurals (except polymixiiforms, lampridiforms, and certain holocentroid fishes; see also Johnson & Patterson 1993; Forey et al. 2003) and the single bony series typical of higher acanthomorphs represents the homolog of the epineural series of lower teleosts that is shifted ventrally into the horizontal septum. The shift of the epineurals into the horizontal septum has taken place in three steps, eventually resulting in the ventral displacement of all the elements, a synapomorphy of percomorph fishes (Johnson & Patterson 1993). Patterson & Johnson (1995) also documented the presence of a series of ligaments, in the position of the epineural series of lower teleosts, in several percomorph families, including the ammodotyids, carangids, echeneidids, gerreids, haemulids, kuhliids, labrids, lethrinids, lutjanids, mullids, polynemids, pomacentrids, sciaenids, sparids, and terapontids. Such ligaments are ossified in the pleuronectiform families Bothidae and Samaridae. Since they referred to ventrally displaced epineurals, Patterson & Johnson (1995) interpreted these tendons or bones as neomorphic structures nonhomologous with anything in lower acanthomorphs and non-acanthomorphs, and called them neoneurals. In a successive study, Gemballa & Britz (1998) contradicted the hypothesis proposed by Patterson & Johnson (1995) and homologized the single intermuscular series of higher acanthomorphs with epicentrals of lower teleosts and considered superfluous the concept of neoneurals, which they considered as true epineurals. Later, Johnson & Patterson (2001) published a detailed reply to the paper by Gemballa & Britz (1998) and reiterated the arguments for interpreting the bones of the single series of intermusculars of most acanthomorphs as being epineurals. The cogent debate about the homology of intermusculars in acanthomorph fishes makes it very difficult to interpret the intermuscular bones of *Hendrixella*. The evolutionary scenario hypothesized by Patterson & Johnson (1995) and Johnson & Patterson (2001) is based on careful and detailed observations on hundreds of specimens;

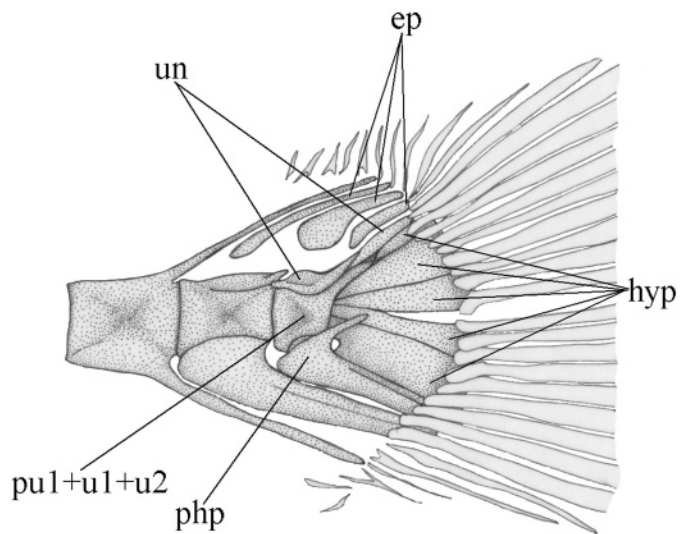


Fig. 5. *Hendrixella grandei* gen. & sp. nov.: reconstruction of the caudal skeleton based on the holotype FMNH PF 3456. Scale bar is 2 mm.

however, several exceptions to their model emerged in last few years (e.g., Gago 1998; Carnevale 2006, 2007). The evidence presented by Gemballa & Britz (1998) that the single series of intermuscular bones of percomorphs is the homolog of the epicentral series of non-acanthomorphs is consistent with the configuration observed in *Hendrixella*. In our opinion, the intermuscular bones of the upper series should be interpreted as being epineurals because their insertion points are located at the base of the neural arches near the junctions with the centra (Figs. 2–4); this is the typical position occupied by the first two intermuscular bones in most acanthomorph fishes. The co-occurrence of two intermuscular bones on the first vertebra (Figs. 2–4) is crucial for the homologization of the two series; the topographical position of the two overlapping bones on the first and following vertebrae provides a convincing evidence that those of the upper series are epineurals whereas those of the lower series are the homologs of the epicentrals of lower teleosts. Moreover, we can exclude that the elements of one of the intermuscular bony series of *Hendrixella* can be interpreted as myorhabdoi, since the latter are “unattached” bones that develop in the uppermost and lowermost forward flexures of the myosepta, respectively (Patterson & Johnson 1995).

Acknowledgements

We wish to thank Walter Landini (Dipartimento di Scienze della Terra, Università di Pisa, Pisa) for his suggestions and critical review of an earlier draft of the text. Lance Grande and William Simpson (FMNH) and Roberto Zorzin and Anna Vaccari (MCSNV) are thanked for permission to examine material under their care and for logistic support. Thanks are also due to Federica Giudice for the improvement of the English. Matt Friedman and Francesco Sorbini kindly made photographs of the specimens in FMNH and MCSNV, respectively. We thank G. David Johnson (National Museum of Natural History, Smithsonian Institution, Washington) and Jürgen Kriwet (Staatliches Museum für Naturkunde, Stuttgart) for careful reviews of the manuscript. Visit of AFB

to Chicago was made possible by a grant of the Borg-Warner Robert O. Bass Visiting Scientist Fund. We are grateful to Dr. Alessandra Aspes, Director of the MCSNV, for providing funding for travel of AFB in February 2009 to Verona. Research of AFB was supported by the Russian Foundation for Basic Research, grants nos. 08-05-00654 and 09-05-00170. The names of the authors are in alphabetical order since each made a substantial contribution to this manuscript.

REFERENCES

- Ahlstrom, E.H., Butler, R.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.
- Arratia, G., López-Arbarelo, A., Prasad, G.V.R., Parmar, V. & Kriwet, J. 2004: Late Cretaceous-Paleocene percomorphs (Teleostei) from India – Early radiation of Perciformes. In: Arratia, G., Wilson, M.V.H. & Cloutier, R. (Eds.): Recent advances in the origin and early radiation of vertebrates. Verlag Dr. Friedrich Pfeil, München, 635–663.
- Bannikov, A.F. 1999: Unusual new percoid fish from the Eocene of Bolca. *Studi e Ricerche sui Giacimenti Terziari di Bolca* 8, 117–128.
- Bannikov, A.F. 2004: Eocottidae, a new family of perciform fishes (Teleostei) from the Eocene of northern Italy (Bolca). *Studi e Ricerche sui Giacimenti Terziari di Bolca* 10, 17–35.
- Bannikov, A.F. 2008: Two new genera for long known percoid fishes (Perciformes) from the Eocene of Bolca, Italy. *Studi e Ricerche sui Giacimenti Terziari di Bolca* 12, 29–44.
- Bannikov, A.F. & Carnevale, G. 2007: The Eocene “*Dules*” *temnopterus* Agassiz, 1836 from Monte Bolca, and the problem of classifying fossil percoid fishes. *Palaeontographia Italica* 91, 69–84.
- Bannikov, A.F. & Zorzin, R. 2004: A new genus and species of percoid fish (Perciformes) from the Eocene of Bolca, Northern Italy. *Studi e Ricerche sui Giacimenti Terziari di Bolca* 10, 7–16.
- Bellwood, D.R. 1996: The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage. *Coral Reefs* 15, 11–19.
- Bellwood, D.R. 1998: What are reef fishes? – Comments on the report by D.R. Robertson: Do coral-reef fish faunas have a distinctive taxonomic structure? *Coral Reefs* 17, 187–189.
- Bleeker, P. 1859: Enumeratio specierum piscium hucusque in Archipelago indico observatarum, adjectis habitationibus citationibusque, ubi descriptiones earum recentiores reperiuntur, nec non speciebus Musei Bleekeriani Bengalensibus, Japonicis, Capensibus Tasmanicisque. *Acta Societas Scientiarum Indo-Neerlandais* 6, 276 pp.
- Carnevale, G. 2006: A new snake mackerel from the Miocene of Algeria. *Palaeontology* 49, 391–403.
- Carnevale, G. 2007: New gadiform fishes (Teleostei, Gadiformes) from the Miocene of Algeria. *Journal of African Earth Sciences* 47, 95–111.
- Forey, P.L., Yi, L., Patterson, C. & Davies, C.E. 2003: Fossil fishes from the Cenomanian (Upper Cretaceous) of Namoura, Lebanon. *Journal of Systematic Palaeontology* 1, 227–330.
- Fujita, K. 1990: The caudal skeleton of teleostean fishes. Tokai University Press, Tokyo, 897 pp.
- Gago, F.J. 1998: Osteology and phylogeny of the cutlassfishes (Scombroidei: Trichiuridae). *Contributions in Science, Natural History Museum of Los Angeles County* 476, 1–79.
- Gemballa, S. & Britz, R. 1998: Homology of intermuscular bones in acanthomorph fishes. *American Museum Novitates* 3241, 1–25.
- Gosline, W.A. 1968: The suborders of perciform fishes. *Proceedings of the United States National Museum* 124, 1–78.
- Gosline, W.A. 1971: Functional morphology and classification of teleostean fishes. University of Hawaii Press, Honolulu, 208 pp.
- Johnson, G.D. 1984: Percoidae: 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, 464–498.
- Johnson, G.D. 1993: Percomorph phylogeny: progress and problems. *Bulletin of Marine Science* 52, 3–28.
- Johnson, G.D. & Patterson, C. 1993: Percomorph phylogeny: a survey of acanthomorphs and a new proposal. *Bulletin of Marine Science* 52, 554–626.
- Johnson, G.D. & Patterson, C. 2001: The intermuscular system of acanthomorph fishes: a commentary. *American Museum Novitates* 3312, 1–24.
- Landini, W. & Sorbini, L. 1996: Ecological and trophic relationships of Eocene Monte Bolca (Pesciara) fish fauna. In: Cerchi, A. (Ed.): *Autecology of selected fossil organisms: Achievements and problems*. Bollettino della Società Paleontologica Italiana, Special Volume 3, 105–112.
- Mabee, P.M., Crotwell, P.L., Bird, N.C. & Burke, A.C. 2002: Evolution of median fin modules in the axial skeleton of fishes. *Journal of Experimental Zoology (Molecular and Developmental Evolution)* 294, 77–90.
- Monod, T. 1963: Sur quelques points de l’anatomie de *Gonorhynchus gonorhynchus* (Linné 1766). *Mémoires de l’Institut Français d’Afrique Noire* 68, 255–313.
- Nelson, J.S. 2006: *Fishes of the World*. Fourth Edition. John Wiley & Sons, Hoboken NJ, 601 pp.
- Nolf, D. 2003: Fish otoliths from the Santonian of the Pyrenean faunal province, and an overview of all otolith-dominated North Atlantic Late Cretaceous teleosts. *Bulletin de l’Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 73, 155–173.
- Nolf, D. & Stringer, G. 1996: Cretaceous fish otoliths – a synthesis of the North American record. In: Arratia, G. & Viohl, G. (Eds.): *Mesozoic fishes – Systematics and Paleoecology*. Verlag Dr. Friedrich Pfeil, München, 433–459.
- Owen, R. 1846: *Lectures on the comparative anatomy and physiology of the vertebrate animals, Part 1: Fishes*. Longman, Brown, Green and Longmans, London, 308 pp.
- Owen, R. 1866: *The anatomy of vertebrates, Vol. 1: Fishes and reptiles*. Longmans, Green & Co., London, 600 pp.
- 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.
- Parenti, L. 1993: Relationships of atherinomorph fishes (Teleostei). *Bulletin of Marine Science* 52, 170–196.
- Patterson, C. 1968: The caudal skeleton in Mesozoic acanthopterygian fishes. *Bulletin of the British Museum (Natural History), Geology* 17, 47–102.
- Patterson, C. 1992: Supernumerary median fin-rays in teleostean fishes. *Zoological Journal of the Linnean Society* 106, 147–161.
- Patterson, C. & Johnson, G.D. 1995: The intermuscular bones and ligaments of teleostean fishes. *Smithsonian Contributions to Zoology* 559, 1–78.
- Patterson, C. & Rosen, D.E. 1977: Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bulletin of the American Museum of Natural History* 158, 81–172.
- Schwarzshans, W. 1996: Otoliths from the Maastrichtian of Bavaria and their evolutionary significance. In: Arratia, G. & Viohl, G. (Eds.): *Mesozoic fishes – Systematics and Paleoecology*. Verlag Dr. Friedrich Pfeil, München, 417–431.
- Sieber, R. & Weinfurter, E. 1967: Otolithen aus tiefen Gosauschichten Österreichs. *Annalen des Naturhistorisches Museum Wien* 71, 353–361.
- Sorbini, L. & Bannikov, A.F. 1991: The Cretaceous fishes of Nardò. 2°. An enigmatic spiny-rayed fish. *Bollettino della Società Paleontologica Italiana* 30, 239–249.
- Springer, V.G., Smith, C.L. & Fraser, T.H. 1977: New species of protogynous hermaphroditic fish, and synonymy of Anisochromidae, Pseudoplesiopiidae, and Pseudochromidae. *Smithsonian Contributions to Zoology* 252, 1–15.
- Stiassny, M.L.J. 1993: What are grey mullets? *Bulletin of Marine Science* 52, 197–219.
- Tyler, J.C., O’Toole, B. & Winterbottom, R. 2003: Phylogeny of the genera and families of zeiform fishes, with comments on their relationships with tetraodontiforms and caproids. *Smithsonian Contributions to Zoology* 618, 1–110.

Manuscript received March 3, 2009

Manuscript accepted September 29, 2009

Published Online first November 14, 2009

Editorial Handling: Michael J. Benton & Daniel Marty