

A reappraisal of the Eocene priacanthid fish *Pristigenys substriata* (Blainville, 1818) from Monte Bolca, Italy

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Abstract.—Priacanthids are a small family of percomorph fishes comprising fewer than 20 extant species currently assigned to four genera. One of these, *Pristigenys*, was established by Louis Agassiz (1835) to include the Eocene species *Pristigenys substriata* from Monte Bolca, and is usually regarded as a subjective senior synonym of *Pseudopriacanthus*. Consequently, *Pristigenys* currently comprises five extant species plus the fossil *Pristigenys substriata*. The osteology of the type species of this genus, however, is poorly known, and this makes it difficult to provide an adequate comprehensive definition of the taxonomy of the whole family. *Pristigenys substriata* is redescribed in detail based on five well-preserved articulated skeletons. *Pristigenys substriata* can be easily distinguished from other priacanthids based on its unique combination of characters. Morphological analysis of the fossil specimens reveals that there is substantial evidence to justify recognition of both *Pristigenys* and *Pseudopriacanthus* as valid genera, with extant species previously assigned to *Pristigenys* now referred to *Pseudopriacanthus*. Within the Priacanthidae, *Pristigenys* and *Pseudopriacanthus* form sister taxa and this pair can be considered as the sister-group to all remaining extant priacanthid genera (*Cookeolus* + [*Heteropriacanthus* + *Priacanthus*]).

Introduction

Fishes of the family Priacanthidae constitute a small group of predatory percomorphs occurring circumtropically with greatest diversity in the Indo-Pacific region (Starnes, 1988). Priacanthids exhibit deep bodies, remarkably large eyes, and rough spinous scales. Because of their large eyes, cryptic habits, and night-time angling results, these fishes are usually regarded as nocturnal, even though evidence from stomach contents seems to indicate that they are also active during the day (see Hiatt and Strasburg, 1960). Larval and prejuvenile priacanthids are pelagic in the upper layers of the water column (Caldwell, 1962a, 1962b), whereas juveniles and adults (standard length >70 mm; Caldwell, 1962a) are bottom dwellers with a preference for coral reefs and rocky areas. They are very secretive (Caldwell, 1962a) and usually considered solitary, although some species occasionally occur in loose and undirected aggregations around coral reefs and rock piles (Caldwell and Bullis, 1971). Some species are characterized by a sound-producing mechanism in large part based on extrinsic swimbladder muscles (Salmon and Winn, 1966).

The phylogenetic position of the Priacanthidae within percomorphs is unclear. These fishes have been traditionally aligned with the Percoidei (e.g., Johnson, 1984; Nelson, 2006), but recent large-scale molecular studies hypothesized a close affinity with the Monodactylidae and acanthuriforms

(Betancur et al., 2013), or, alternatively, with the Cepolidae, Siganidae, and Scatophagidae (Near et al., 2013). However, support for the latter hypotheses is somewhat weak and new detailed focused studies are needed to test such phylogenetic interpretations.

The fossil record of the Priacanthidae is relatively rich, documented by several Eocene, Oligocene, and Neogene articulated skeletal remains and otoliths, primarily from Europe (see Fitch and Crooke, 1984; Starnes, 1988; Bannikov, 2010; Nolf, 2013). The earliest articulated skeletal remains of the group consist of a few well-preserved specimens belonging to the species *Pristigenys substriata* from the lower Eocene limestone of Monte Bolca, northeastern Italy. The Eocene occurrence of priacanthids documents the remarkable increase of diversity of nocturnal feeders that took place during the earliest part of the Paleogene (see Goatley et al., 2010; Carnevale et al., 2014).

Overall, the family Priacanthidae currently includes 19 extant species in four genera, *Cookeolus*, *Heteropriacanthus*, *Priacanthus*, and *Pristigenys* (Starnes, 1988; Iwatsuki et al., 2012). The nomenclatural history of *Pristigenys* has been controversial (e.g., White, 1936; Myers, 1958; Caldwell, 1962a; Fitch and Lavenberg, 1975; Fritzsche, 1978; Fritzsche and Johnson, 1981; Fitch and Crooke, 1984; Taverne, 1988). In his comprehensive worldwide revision of the family, Starnes (1988) allied

species formerly referred to *Pseudopriacanthus* to the fossil genus *Pristigenys* based on a few morphological and meristic features, confirming the hypothesis proposed by White (1936) and subsequently reiterated by Myers (1958), Fritzsche and Johnson (1981), and Taverne (1988). However, the skeletal morphology of the type species of the genus *Pristigenys*—the Eocene *P. substriata* from Monte Bolca—has never been examined in detail in order to conclusively demonstrate its affinity to the extant species formerly referred to *Pseudopriacanthus*. The goal of this paper is therefore to describe the osteology of *Pristigenys substriata* in more detail, and to discuss its relationships with the extant members of the Priacanthidae.

Stratigraphy

The celebrated locality of Monte Bolca lies in the eastern part of Monti Lessini, near Verona, northeastern Italy. This locality includes several productive sites, two of which, the Pesciara and Monte Postale, have provided one of the most important and well-known fossil fish assemblages of the world (see Carnevale et al., 2014). The best known of these sites is that of the Pesciara, which is characterized by abundant and exquisitely preserved fossils, particularly fishes (Marramà et al., 2016). The fish-bearing deposits of the Pesciara site pertain to the so-called ‘Calcarei Nummulitici’, an informal Eocene unit widespread in the surroundings of Monte Bolca, and consist of finely laminated micritic limestone. According to Marramà et al. (2016), the fossiliferous deposits of the Pesciara site accumulated in a shallow intraplateau basin in which anoxic conditions at the bottom and the development of a biofilm promoted the high-quality preservation of its fossils.

The age of the fish-bearing laminated limestone of the Pesciara site has been defined on the basis of their large benthic Foraminifera. These deposits have been referred to the *Alveolina dainelli* Zone, or to the SBZ 11 Biozone, corresponding to the late Cuisian (late Ypresian, slightly less than 50 Ma; Papazzoni et al., 2014).

Materials and methods

The fossil material documented herein consists of five well-preserved complete to nearly complete articulated skeletons preserved on the surface of laminated micritic limestone. The preservation quality of the examined specimens, as well as the lithology of the associated sediment, suggest that skeletal material belonging to *Pristigenys substriata* documented herein derive from the excavations carried out at the Pesciara site (see Marramà et al., 2016). The material was examined using Wild M5A and Leica M80 stereomicroscopes equipped with camera lucida. Measurements were taken using a dial caliper, to the nearest 0.1 mm. During examination, the specimens were moistened with alcohol to enhance some details of their skeletal anatomy.

Repositories and institutional abbreviations.—The fossils are housed in the collections of the Natural History Museum, London (NHM) and the Museum National d’Histoire Naturelle, Paris (MNHN).

Anatomical abbreviations.—ach, anterior ceratohyal; ap1, first anal-fin pterygiophore; br, branchiostegals; bsp, basisphenoid; dhh, dorsal hypohyal; dp1, first dorsal-fin pterygiophore; ep, epural; f, frontal; hpu2, haemal spine of the second preural vertebra; hpu3, haemal spine of the third preural vertebra; hs1, first haemal spine; hyp, hypural; io3, third infraorbital bone; lac, lacrimal; le, lateral ethmoid; me, mesethmoid; npu2, neural spine of the second preural vertebra; pas, parasphenoid; pch, posterior ceratohyal; phy, parhypural; pop, preopercle; pp, postpelvic process; SL, standard length; sn, supraneural; soc, supraoccipital; ss, subocular shelf; uh, urohyal; un, uroneural; v, vomer; vhh, ventral hypohyal; vk, ventral keel of the basiptyergium.

Systematic paleontology

Percomorphacea sensu Wiley and Johnson, 2010
Family Priacanthidae Gill, 1872
Genus *Pristigenys* Agassiz, 1835

Type species.—*Chaetodon substriatus* Blainville, 1818.

Included species.—Type species, by monotypy.

Diagnosis.—A deep-bodied priacanthid unique in having the following combination of character-states: orbit moderately large (orbit diameter 14.1–19.6% SL); caudal peduncle short (9.1–11.9% SL) and deep (17.3–20.1% SL); sagittal crest (apparently) present; frontal with smooth supraorbital margin; shelf overlying the preopercular sensory canal smooth; preopercular spine stout; anterior and posterior ceratohyal joined by narrow suture; first haemal spine greatly enlarged and closely associated with anterior anal-fin pterygiophores; single supraneural; dorsal fin containing ten strong and deeply striated spines plus nine to 12 soft rays; dorsal-fin spines and soft rays well developed (longest spine 26.1–32.7% SL; longest ray 27.1–35.6% SL); anal fin containing three strong and deeply striated spines plus nine to 12 rays; anal-fin rays considerably elongate (longest ray 19.7–37.9% SL); pelvic fins remarkably elongate (49.7–57.7% SL); postpelvic processes of basiptyergia expanded into lobes; ventral keel of basiptyergia narrow; black marginal pigmented band on soft portion of dorsal, anal, caudal, and pelvic fins; caudal fin rounded, with three upper and three lower procurrent rays; spinules absent in all fins; body scales with about 15–25 stout spinules on posterior margin.

Occurrence.—As for *Pristigenys substriata*, the type and only known species.

Pristigenys substriata (Blainville, 1818)
Figures 1–6

1796 *Chaetodon striatus* Volta, p. 92, pl. 20, fig. 2.

1818 *Chaetodon substriatus* Blainville, p. 352.

1835 *Pristigenys macrophthalmus* Agassiz, p. 313.

1839 *Pristigenys macrophthalmus* Agassiz, p. 136, pl. 18, fig. 2.

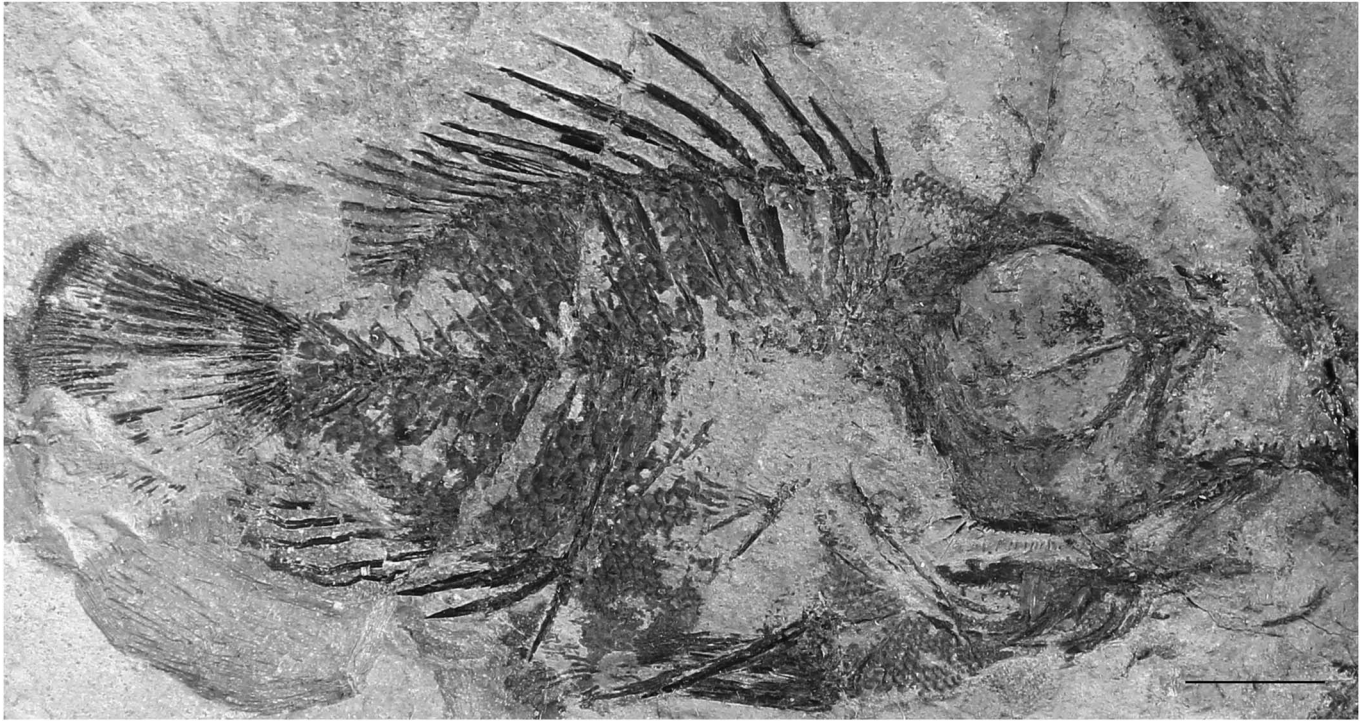


Figure 1. *Pristigenys substriata* (Blainville, 1818) from the Eocene of Monte Bolca, Italy: holotype, MNHN F.Bol529, right lateral view. Scale bar represents 10 mm.

- 1874 *Pristigenys macrophthalmus* de Zigno, p. 61.
 1901 *Pristigenys macrophthalmus* Woodward, p. 415.
 1905 *Pristigenys substriatus* Eastman, p. 21, pl. 3, fig. 3.
 1936 *Pristigenys substriatus* White, p. 49, text-figs. 2, 3.
 1958 *Pristigenys substriata* Myers, p. 41.
 1980 *Pristigenys substriata* Blot, p. 368.
 1981 *Pristigenys substriata* Fritzsche and Johnson, p. 490, text-fig. 1.
 1984 *Pristigenys substriata* Fitch and Crooke, p. 311, text-fig. 11.
 1988 *Pristigenys substriata* Taverne, p. 171, text-figs. 1, 2.
 2000 *Lates gracilis* Edwards and Rosen, backcover.
 2010 *Pristigenys substriata* Taverne and Nolf, p. 187, text-figs. 1, 37.

Holotype.—MNHN F.Bol529, partially complete, relatively well-preserved articulated skeleton, 54 mm SL (Fig. 1).

Referred material.—NHM P.9941, nearly complete, well-preserved articulated skeleton, in part and counterpart (NHM P.14540), 50.4 mm SL (Fig. 2.1, 2.2); NHM P.15370, nearly complete, well-preserved articulated skeleton, in part and counterpart (NHM P.15371), 73.3 mm SL (Fig. 2.3, 2.4), figured in Edwards and Rosen (2000) and erroneously assigned to *Lates gracilis*; NHM P.16127, nearly complete, well-preserved articulated skeleton, in part and counterpart (NHM P.16370), 83.4 mm SL (Fig. 2.5, 2.6); NHM P.19057, nearly complete and relatively well-preserved articulated skeleton, 60.5 mm SL.

Diagnosis.—As for the genus.

Occurrence.—Monte Bolca locality, Pesciara site, NE Italy, late early Eocene, late Ypresian, late Cuisian, ca. 50 Ma (see Papazzoni et al., 2014).

Description

General morphology.—Measurements for *Pristigenys substriata* are summarized in Table 1. The body is ovoid and deep, its maximum depth contained between 1.69 and 1.85 times SL. The head is moderately large, its length less than a third of SL. The head is characterized by a nearly straight dorsal profile. The snout is relatively blunt, its length contained between 3.1 and 3.8 times in head length. The orbit is rounded and relatively large, its diameter between a fifth and sixth SL. The eyeball is very large and preserved as a thick and conspicuous carbon film. The considerable thickness of this carbon film is likely due to the original remarkable size of the tapetum lucidum in the choroid; the possession of a very large ocular tapetum lucidum consisting of several rows of reflecting cells that underlie the entire retina (e.g., Nicol et al., 1973; Wang et al., 1980) is currently regarded as a priacanthid synapomorphy (Starnes, 1988). The mouth is terminal with an oblique and moderately large gape. The mandible length is contained between 1.5 and 1.7 times in head length. The caudal peduncle is short (caudal peduncle length contained up to more than ten times in SL) and very deep (caudal peduncle depth contained about five times in SL). The dorsal-fin origin is located above the occipital region of the neurocranium. The predorsal length is contained between 2.2 and 2.6 times in SL. The sail-like dorsal fin is continuous with spines that rapidly increase in size posteriorly up to the fifth element; the length of the spines gradually decreases posteriorly in the series. The length of the first spine is

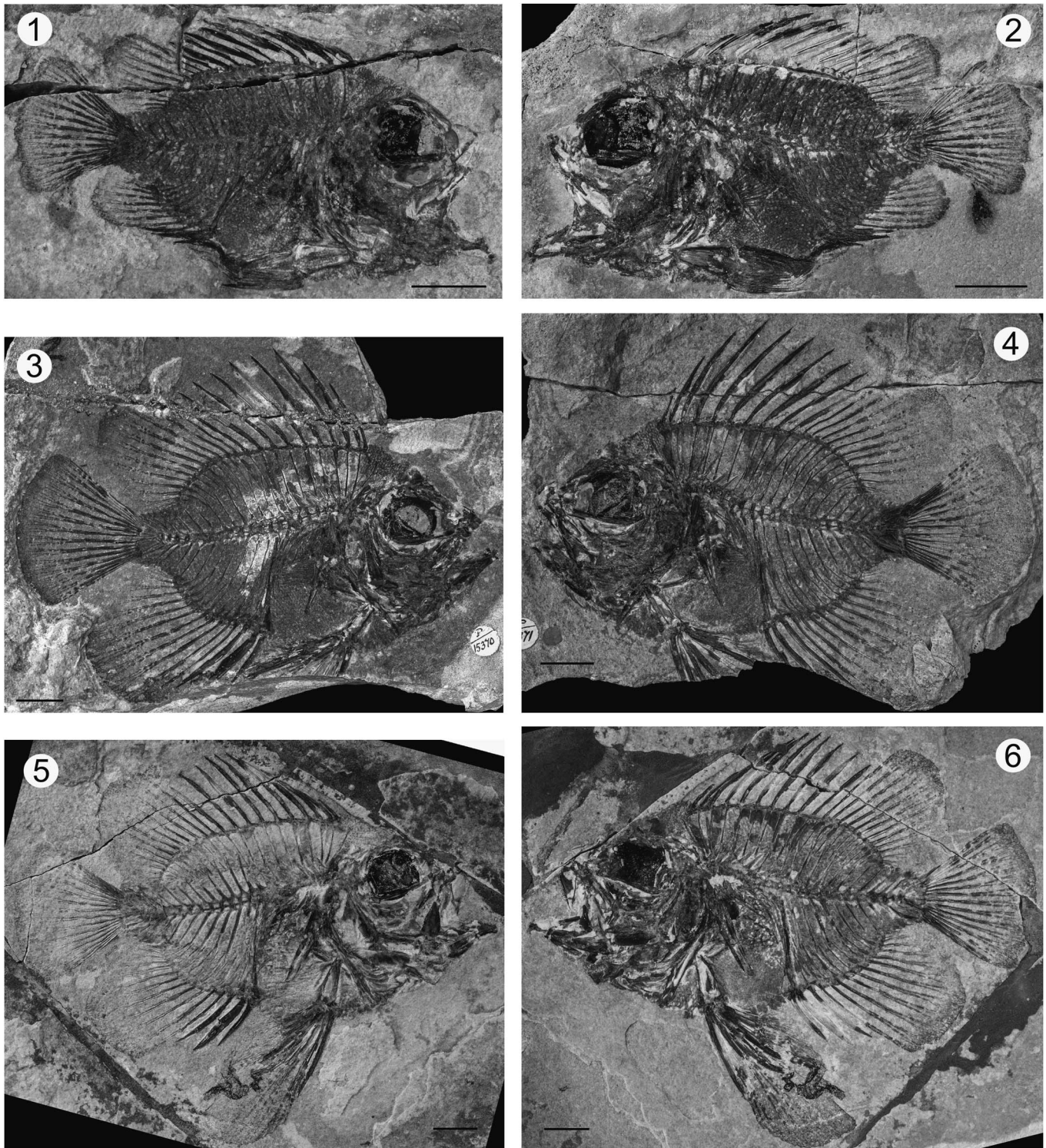


Figure 2. *Pristigenys substriata* (Blainville, 1818) from the Eocene of Monte Bolca, Italy: (1) NHM P.9941, right lateral view; (2) NHM P.14540 (counterpart of the specimen in 1), left lateral view; (3) NHM P.15370, right lateral view; (4) NHM P.15371 (counterpart of the specimen in 3), left lateral view; (5) NHM P.16127, right lateral view; (6) NHM P.16370 (counterpart of the specimen in 5), left lateral view. All scale bars represent 10 mm.

contained about three times in that of the fifth spine. The dorsal-fin soft rays are distally bifurcated and gradually increase in length up to the third element, after which their length rapidly decreases posteriorly in the series. The third dorsal-fin soft ray is slightly shorter or slightly longer than the fifth dorsal-fin spine.

Overall, both the spinous and soft portions of the dorsal fin have a rounded profile. The anal-fin origin is usually placed below the second caudal vertebra. The preanal length is contained about 1.5 times in SL. The anal-fin spines gradually increase in length posteriorly. The length of the first anal-fin spine is contained

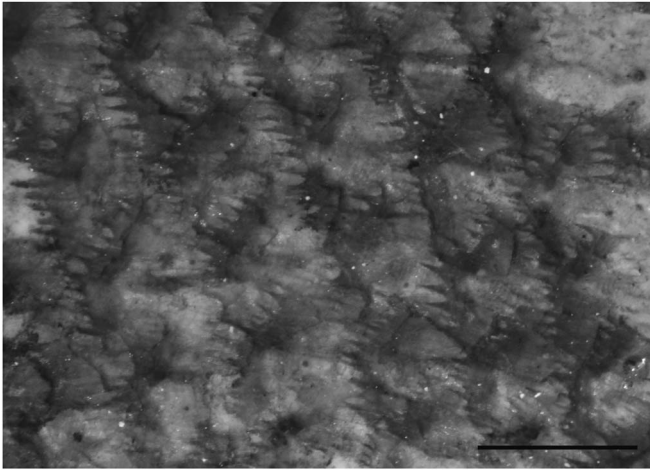


Figure 3. *Pristigenys substriata* (Blainville, 1818) from the Eocene of Monte Bolca, Italy: MNHN F.Bol529, abdominal scales. Scale bar represents 1 mm.

between 1.4 and 1.6 times in that of the third spine. The longest (third) anal-fin soft ray is remarkably longer than the longest anal-fin spine. The soft portion of the anal fin has a gently rounded outer profile. The caudal fin is rounded, and its length is contained about four times in SL. The pectoral fins are incomplete in all examined specimens; however, they appear to be rather short. The pelvic fin insertion is located beneath the pectoral-fin base. The prepelvic distance is contained between 1.75 and 2.5 times in SL. The pelvic fin is adnate and remarkably elongate (pelvic-fin length less than half SL), extending posteriorly well beyond the anal-fin insertion (Fig. 2.5, 2.6). The rays of the dorsal, anal, caudal, and pelvic fins are characterized by a remarkably well-preserved black marginal band (Figs. 1,2).

Squamation.—The body is covered by thick, adherent spinoid scales (type 1 of Roberts, 1993) (Fig. 3). The scales are polygonal in outline with a nearly straight anterior margin and a weakly pointed or convex posterior margin. The spines are stout, variable in size, their number ranging from 15 to ~25. The scales appear to be smaller, irregularly arranged, and structurally modified on the nape, top of the head, gular (including the branchiostegals) and prepectoral areas, opercle, chin, and cheek; although their precise morphology is unclear, at least those of the cheek and some of those of the chin seem to bear spines emerging from their outer surfaces. The circuli of the body scales are characterized by a rough texture, ostensibly related to the presence of microscopic denticles (Starnes, 1988). The lateral line runs very high on the body flank, following the dorsal profile of the body up to the posterior end of the caudal peduncle. The lateral-line scales bear a single tube.

Neurocranium.—Overall, the skeletal morphology is consistent with that of other priacanthid fishes (see Starnes, 1988; Taverne and Nolf, 2010). The skeletal structure of the skull is only partially recognizable due to the extensive fragmentation of most of the bones. The neurocranium is robust, compact, and relatively deep, about 1.5 times as long as deep (Fig. 4.1). Due to the presence of a large orbit, both the ethmoid and postorbital portions of the neurocranium are anteroposteriorly compressed.

The outer margin of the skull roof is nearly straight, whereas that of the ethmoid region appears to be convex. The frontals are the largest bones of the skull roof. A low sagittal crest appears to be present. The supraorbital margin of the frontal is smooth. The mesethmoid is rather thick. The lateral ethmoids are characterized by a large laminar lateral flange with a rounded outer margin. The supraoccipital crest is relatively large, reaching its maximum height just above the midlength of the orbit. The parasphenoid is robust and nearly straight for most of its length, forming a shallow angle at the level of the posterior orbital wall. The basisphenoid is columnar and nearly perpendicular to the parasphenoid.

Infraorbital series.—The bones of the infraorbital series are in general moderately well preserved (Fig. 4.2). A partially preserved and articulated series is exposed in the holotype. The lacrimal has a serrated ventral margin with a large stout spine emerging from its midlength. The third infraorbital is characterized by a relatively large subocular shelf (see Smith and Bailey, 1962). The fourth, fifth, and sixth infraorbitals are preserved in specimen NHM P.15371; their ventral margin is serrated (Fig. 4.2). The nasal and supratemporal bones are not recognizable in the examined material.

Jaws.—The premaxilla has robust ascending and articular processes. A postmaxillary process is not preserved, although it was possibly present originally. The alveolar process is elongate and rather thick, bearing numerous irregularly arranged small conical teeth with slightly recurved tips. The maxilla has an expanded and spatulate distal end. The lower jaw is upturned and projects strongly. The craniomandibular articulation is located just below the anterior margin of the orbit. The dentary is stout and very thick at the symphysis, where it bears a short ventral process. There are numerous teeth along the dorsal margin of this bone, very similar to those of the premaxilla. The anguloarticular and retroarticular are very robust.

Suspensorium.—The morphology of the bones of the suspensorium is consistent with that of other priacanthid fishes (Starnes, 1988). The endopterygoid and ectopterygoid are well preserved in specimens NHM P.16370 and NHM P.14540. The endopterygoid is large and ovoid in outline. The palatine bears a strong finger-like maxillary process, which is well exposed in specimen NHM P.16127. The quadrate is fan-shaped. The symplectic is relatively short. The hyomandibular is always fragmented and inadequately preserved.

Opercular series.—The bones of the opercular series are poorly preserved due to their extensive fragmentation. The crescent-shaped preopercle has finely serrated posterior and ventral margins, and a moderately developed, finely serrated spine at the posteroventral angle (Fig. 4.3). The bony shelf overlying the preopercular sensory canal is smooth. The interopercle is partially preserved in the specimen NHM P.16127; it is oblong with a pointed anterior end and a finely serrated ventral margin.

Hyoid apparatus and gill arches.—The hyoid bar is robust and strongly ossified (Fig. 4.3). The dorsal and ventral hypohyals are

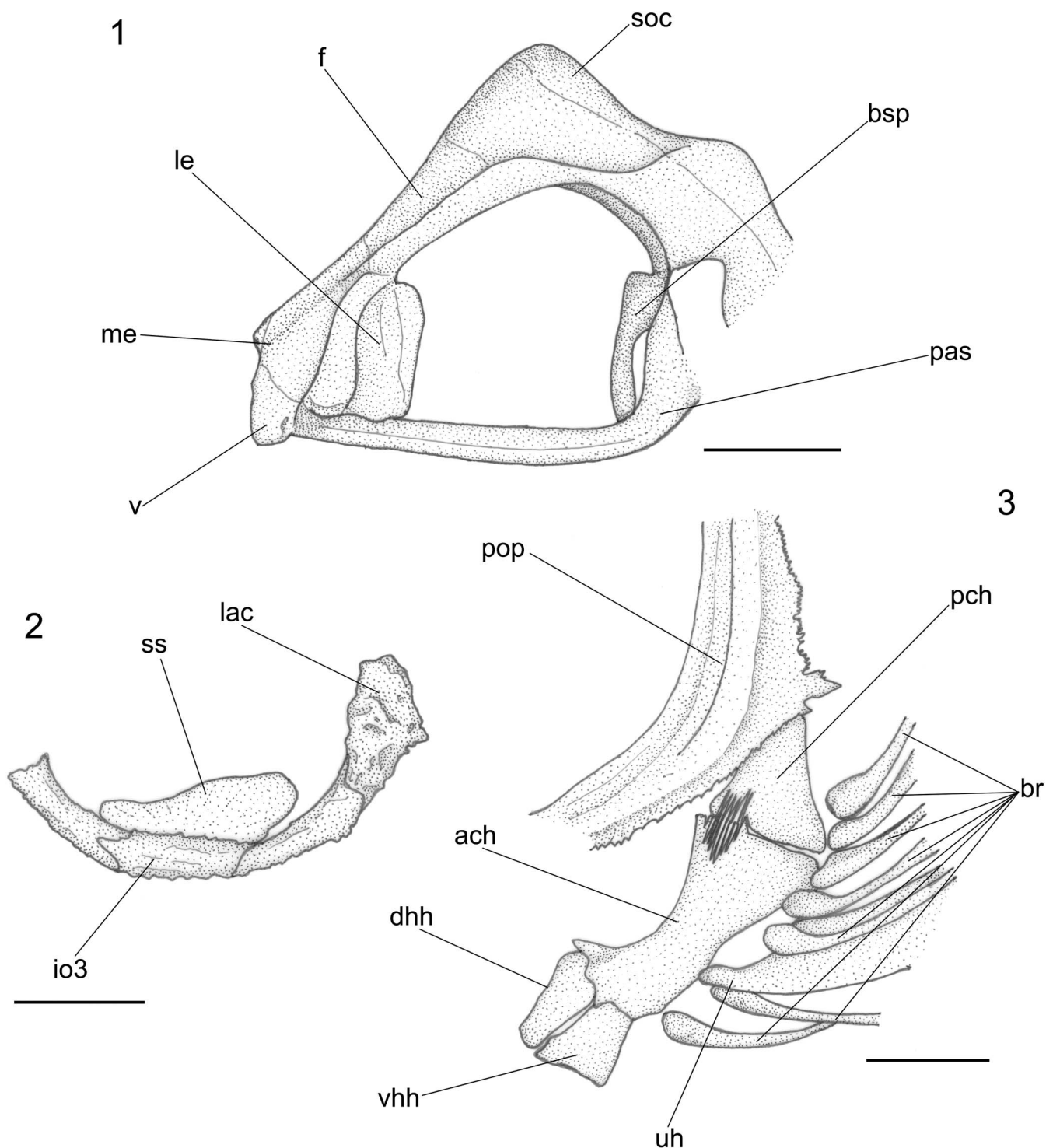


Figure 4. *Pristigenys substriata* (Blainville, 1818) from the Eocene of Monte Bolca, Italy: (1) NHM P.15371, reconstruction of the neurocranium, left lateral view; (2) NHM P.16127, reconstruction of the anterior part of the infraorbital series, right lateral view; (3) NHM P.16370, reconstruction of the preopercle and hyoid bar, left lateral view. All scale bars represent 5 mm. See materials and methods section of text for anatomical abbreviations.

subquadrangular. The anterior and posterior ceratohyals are sutured to each other by a narrow suture formed by deep longitudinal interdigitations. The anterior ceratohyal is constricted at its midlength; a vertical process emerges at its anterodorsal corner; there is no beryciform foramen. The posterior ceratohyal is approximately triangular in outline. There are six strong and relatively short saber-like branchiostegals, of which the posterior

two articulate with the posterior ceratohyal. Fragments of the urohyal are recognizable in specimen NHM P.16370.

The gill-arch skeleton and pharyngeal teeth are not exposed in the available specimens.

Vertebral column.—The vertebral column is compact and contains 23 (10+13) vertebrae, including the urostylar element.

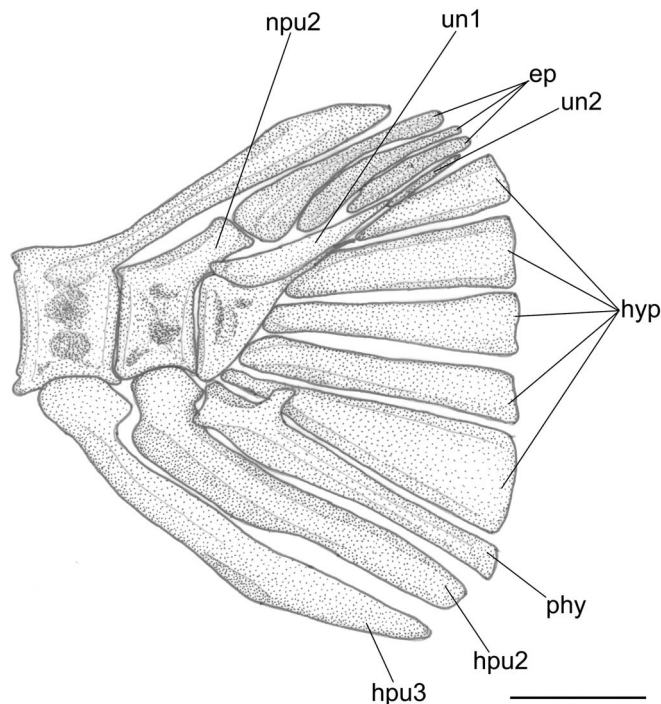


Figure 5. *Pristigenys substriata* (Blainville, 1818) from the Eocene of Monte Bolca, Italy: NHM P.15371, reconstruction of the caudal skeleton, left lateral view. Scale bar represents 2 mm. See materials and methods section of text for anatomical abbreviations.

The abdominal portion of the vertebral column is arched with the concave side oriented toward the venter of the fish, whereas the caudal portion is linear. Except for the first five that are anteroposteriorly compressed, the centra are subrectangular and longer than high. The structure of the first neural arch and spine is difficult to interpret. The neural spines of the second to seventh vertebrae are relatively short, anteroposteriorly expanded, and obliquely oriented. Those of the successive abdominal vertebrae are more elongate, slender, and nearly vertical. The first haemal spine is strong and anteroposteriorly expanded. Most of the centra bear deep and large lateral fossae. The dorsal prezygapophyses are well developed. In the caudal region, the neural spines and their haemal antimeres emerge from the anterior half of the vertebrae and are thick and distally pointed. There are eight pairs of thick ribs articulating with the third to tenth vertebrae. Epineural fragments can be recognized.

Median fins and support.—The caudal skeleton is consistent with that of other priacanthids (Fujita, 1990; Fig. 5). The urostylel vertebra consists of fused first and second ural and first preural centra. There are five nearly triangular autogenous hypurals. The autogenous parhypural is very thick and bears a well-developed parhypurapophysis. There are two uroneurals and three epurals. The neural spine of the second preural vertebra is very short and reduced to a spatulate crest. The haemal spines of the second and third preural vertebrae are autogenous. The caudal fin consists of 16 principal rays (I,7-7,I) plus three upper and three lower procurrent rays; there is no procurrent spur.

There is a single thin, slightly curved, and obliquely oriented supraneural. This slender and delicate bone extends parallel to the anterior margin of the first dorsal-fin pterygiophore and its dorsal end does not reach the dorsal border of the body (Fig. 6.1). The predorsal formula (Ahlstrom et al., 1976) is /0 + 2/1/1/1. The dorsal fin contains 10 spines plus nine to 12 distally branched rays, supported by 17–20 pterygiophores. The spines are strong and pointed, ornamented with numerous deep striations throughout their length (Fig. 6.1). The membrane that connected the dorsal-fin spines is preserved as a very thin, marginal dark band. The first two dorsal-fin spines are in supernumerary association with the first dorsal-fin pterygiophore (Fig. 6.1). The dorsal-fin pterygiophores basically consist of a long and narrow main shaft supporting anterior and posterior laterally flattened bony laminae. The pterygiophores of the soft portion of the dorsal fin are distally bent. The interneural spaces underlying the dorsal fin are occupied by the vertical shafts of one (in the spiny and anteriormost soft portion of the series) or two (in most of the soft portion of the series) pterygiophores.

The anal fin consists of three strong, pointed, and deeply striated spines plus nine to 12 soft rays supported by 10–13 pterygiophores. The first two anal-fin spines are in supernumerary association with the first anal-fin pterygiophore (Fig. 6.2). The large first anal-fin pterygiophore inserts in front of the first haemal spine, to which it appears to be closely bound together with the second anal-fin pterygiophore, which inserts posterior to that haemal spine (Fig. 6.2). The interhaemal spaces overlying the anal fin are occupied by the shafts of two anal-fin pterygiophores. The overall structure and orientation of the anal-fin pterygiophores are similar to those of their dorsal counterparts. Their size gradually decreases posteriorly in the series. There are no spinules along the anterolateral surfaces of the dorsal- and anal-fin spines and rays.

Paired fins and girdles.—The pectoral girdle is difficult to interpret due to inadequate preservation in all the available specimens. What appears to be a strongly fragmented post-temporal is recognizable in specimen NHM P.16370. The supracleithrum is oblong, laminar, and apparently devoid of the dorsal posterior process typical of most extant members of the Priacanthidae. The cleithrum is elongate and slightly curved. The coracoid has a thick and nearly horizontal ventral process that, together with the posteroventral margin of the cleithrum, bounds a large fenestra. There is a single postcleithrum characterized by a moderately expanded posterodorsal lobe. Four pectoral-fin radials appear to be present. The exact number of pectoral-fin rays is difficult to evaluate. About 12 rays are recognizable in the specimen NHM P.14540; a similar count was provided by White (1936).

The basipterygia are approximately triangular and characterized by a narrow ventral keel. The postpelvic processes are rather elongate and expanded laterally into lobes (Fig. 6.3). The pelvic fin consists of a single strong, pointed and laterally striated spine plus five remarkably elongate rays.

Discussion

In his description of the holotype included in the fourth volume of the “Recherches sur les Poissons Fossiles,” Agassiz (1839)

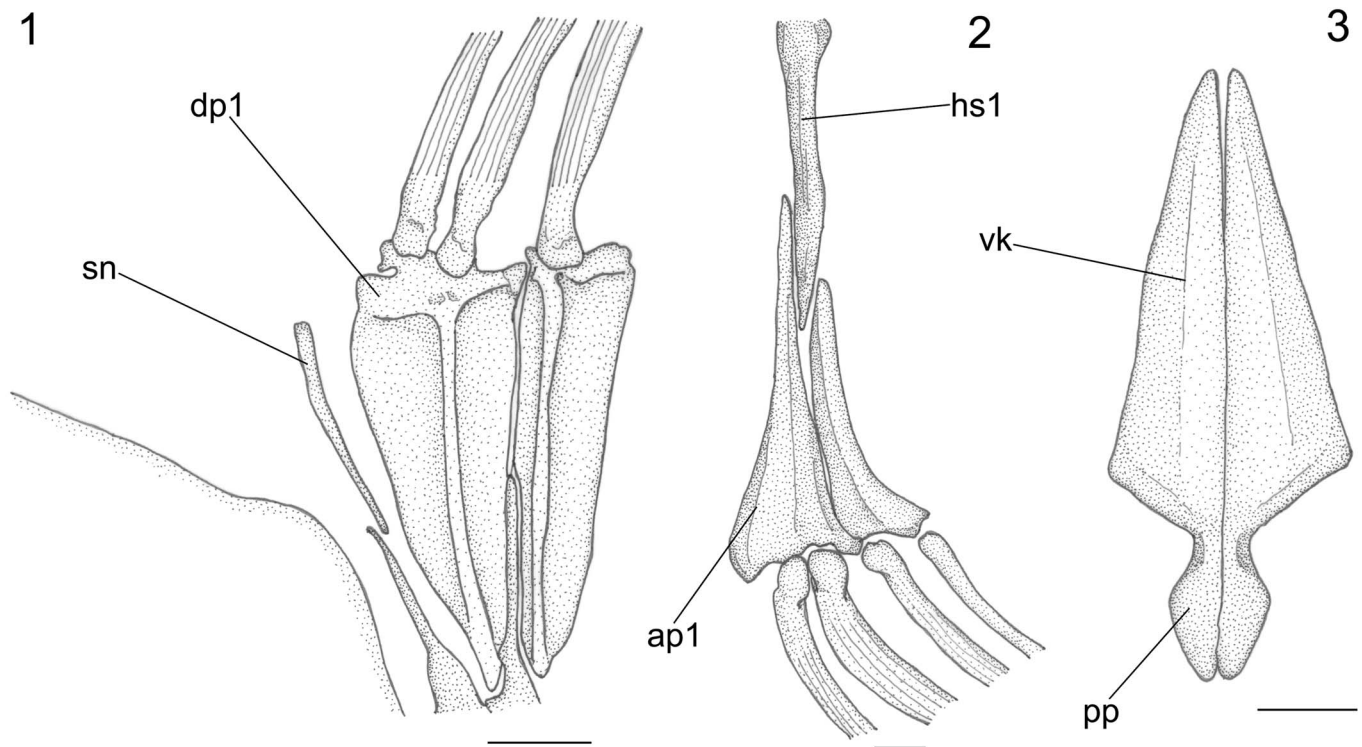


Figure 6. *Pristigenys substriata* (Blainville, 1818) from the Eocene of Monte Bolca, Italy: (1) NHM P.15371, reconstruction of the nuchal region showing the supraneural and the two anterior dorsal-fin pterygiophores, left lateral view; (2) NHM P.16370, reconstruction of the first haemal spine and anterior anal-fin pterygiophores, left lateral view; (3) NHM P.14540, reconstruction of the pelvic girdle, ventral view. All scale bars represent 2 mm. See materials and methods section of text for anatomical abbreviations.

considered *Pristigenys* a close relative of *Beryx*, reinterpreting the identification by Volta (1796) and Blainville (1818) who considered it a member of the butterflyfish genus *Chaetodon*. It is interesting to note, however, that Agassiz (1839) convincingly pointed out the similarities between *Pristigenys* and the Oligocene *Acanus*, the latter currently regarded as a subjective junior synonym of *Priacanthus* (Bannikov, 2010). Based on Agassiz's comments, Woodward (1901) listed *Pristigenys* among the fossil representatives of the Berycidae, an opinion subsequently followed by Eastman (1905). Finally, White (1936) described new specimens in the collection of the British Museum (Natural History) (now The Natural History Museum, London) and, for the first time, referred this Eocene taxon to the family Priacanthidae, a placement supported by our morphological analysis. Numerous features, other than overall physiognomy of the head and body, unquestionably demonstrate that *Pristigenys substriata* is a priacanthid (Fitch and Crooke, 1984; Starnes, 1988), including spinoid scales, scales covering the branchiostegals, infraorbital bones with serrated ventral margins, vertebrae 23 (10 + 13), principal caudal-fin rays 16 (8 + 8), fin spines deeply striated, single postcleithrum, and adnate pelvic fins. The relationships of *Pristigenys substriata* within the Priacanthidae were discussed by White (1936), who considered it almost indistinguishable from *Pseudopriacanthus*, pointing out that the differences between the Eocene and extant genera are inadequate to justify a separation above the species level. Myers (1958) reiterated the arguments discussed by White (1936) and indicated the correct generic name for Eocene and extant species would be *Pristigenys*. Since the publication by

White (1936), the skeletal morphology of Eocene priacanthids from Monte Bolca has been examined only superficially (Fritzsche and Johnson, 1981; Taverne, 1988), primarily to corroborate White's conclusion that *Pristigenys* is the subjective senior synonym of *Pseudopriacanthus*. Although the synonymy of *Pristigenys* and *Pseudopriacanthus* has been accepted by many authors (e.g., Smith, 1966; Fritzsche and Johnson, 1981; Starnes, 1988; Taverne, 1988; Taverne and Nolf, 2010; Iwatsuki et al., 2012), several studies noted that there is no substantial evidence to support such a taxonomic assessment, suggesting that both genera should be retained as valid (e.g., Caldwell, 1962a, 1962b; Fritzsche, 1978; Fitch and Crooke, 1984). A close affinity between *Pristigenys substriata* and its (presumed) extant congeners is supported by several shared features, including a deep, robust body (Figs. 1, 2), anterior and posterior ceratohyals joined by a narrow suture (Fig. 4.3), three upper plus three lower procurrent caudal-fin rays, a single supraneural (Fig. 6.1), an oblong supracleithrum, postpelvic process of the basipterygium expanded into a lobe (Fig. 6.3), a narrow ventral keel of the basipterygium (Fig. 6.3), and a black marginal band on the soft portions of the dorsal, anal, pelvic, and caudal fins (Fig. 2). However, the Eocene taxon exhibits a unique set of features that have not been observed in any of the extant or fossil species currently referred to *Pristigenys* (Starnes, 1988), suggesting generic separation. In particular, *Pristigenys substriata* is characterized by having a moderately developed orbit (Tables 1, 2), a short, deep caudal peduncle (Tables 1, 2), very elongate dorsal, anal, and pelvic fins (Table 1), spinules completely absent on median and paired fins

Table 1. Measurements for *Pristigenys substriata* (Blainville, 1818) from the Eocene of Monte Bolea, Italy. Values are as percentage of SL.

	Standard length (mm)	Body depth	Head length	Head depth	Orbit diameter	Snout length	Caudal peduncle length	Caudal peduncle depth	Mandible length	Pre-dorsal length	Dorsal fin base length	Pre-anal length	Anal-fin base length	Pre-pectoral length	Pre-pelvic length	First dorsal-fin spine length	Longest dorsal-fin spine length (5th)	Longest dorsal-fin ray length (3rd)	First anal-fin spine length	Longest anal-fin spine length (3rd)	Longest anal-fin ray length (3rd)	Pelvic-fin length
MNHN F. 14540	52.6	53.8	37.6	46.9	18.2	11.0	11.9	?	?	38.0	52.6	65.5	24.3	?	38.0	8.1	29.4	19.5	10.0	16.9	19.7	?
NHM P.16127-16370	83.4	55.7	36.6	43.2	14.1	11.0	9.1	17.3	23.6	38.2	52.8	69.0	32.2	51.1	55.5	9.3	26.1	29.1	15.3	22.3	30.9	49.7
NHM P.19057	60.5	53.2	37.1	41.6	16.8	11.4	11.4	19.3	21.8	44.9	50.7	65.4	28.9	?	48.2	?	30.0	27.1	13.2	?	21.8	?
NHM P.15370-15371	73.3	59.0	39.9	46.6	17.8	12.6	10.6	20.1	24.1	37.3	53.8	68.2	31.9	50.3	52.3	11.7	32.7	35.6	?	27.8	37.9	57.7
NHM P.9941-14540	50.4	56.7	42.0	49.2	19.6	10.9	11.7	18.4	24.2	37.3	51.9	71.8	22.4	47.0	57.1	10.1	?	27.3	11.9	17.6	21.8	?

(Figs. 1, 2), soft portions of dorsal and anal fins gently rounded with nine to 12 rays (Tables 1, 2), frontals bearing a shallow sagittal crest and smooth supraorbital margins (Fig. 4.1), a stout spine at the posteroventral angle of the preopercle (Fig. 4.3), a scaleless preopercular shelf (Figs. 1, 2), and a strong and expanded first haemal spine closely bound to the two anterior anal-fin pterygiophores (Fig. 6.2). We believe that these features (Starnes, 1988; Kon and Yoshino, 1997) provide substantial morphological evidence to justify the retention of *Pristigenys* and *Pseudopriacanthus* as valid genera. Some of the features shared by these two genera are not plesiomorphic, and thus may be considered as evidence for their sister-group relationship, e.g., the reduction of the number of procurrent caudal-fin rays, and presence of a black marginal band on dorsal, anal, pelvic and caudal fins (Johnson, 1984; Starnes, 1988). In particular, the possession of three procurrent caudal-fin rays in these genera is regarded as derived, considering that other priacanthids have four or five elements (Johnson, 1984; Starnes, 1988) and the primitive number of procurrent caudal-fin rays is higher in percid percomorphs (see Johnson, 1984).

Summarizing, the detailed reinterpretation of the skeletal morphology of *Pristigenys substriata* suggests that this Eocene taxon forms a clade with the extant *Pseudopriacanthus*, and that this grouping can be considered the sister-group to all remaining extant priacanthid genera (*Cookeolus*, *Heteropriacanthus*, *Priacanthus*) (Fig. 7). According to Starnes (1988), *Cookeolus* represents the sister-group to *Heteropriacanthus* plus *Priacanthus*. As a final remark, we note that the skeletal morphology of *Pristigenys substriata* and its putative sister-group relationship indicate that the evolutionary significance of certain phylogenetically relevant features used by Starnes (1988) should be reconsidered. In particular, the median sagittal crest of the frontals and the massive anterior haemal spines closely associated with robust anal-fin pterygiophores, which were interpreted as derived in *Cookeolus*, *Heteropriacanthus*, and *Priacanthus* by Starnes (1988), should be regarded as plesiomorphic for the family and their absence in *Pseudopriacanthus* as derived.

A number of Eocene, Oligocene, and Miocene priacanthid species have been referred to the genus *Pristigenys* (e.g., Arambourg, 1967; Danil'chenko, 1980; Fitch and Crooke, 1984; Pharissat, 1991; Micklich and Parin, 1996; Taverne and Nolf, 2010; Prokofiev, 2013). Of these, the Oligocene and Miocene species are currently assigned to *Priacanthus* (Bannikov, 2010), or, in certain cases (e.g., *Pristigenys macropus*; Arambourg, 1967), cannot be assigned to the family Priacanthidae (Prokofiev, 2013). As for the other Eocene taxa, they are exclusively based on partially articulated or isolated bones from Belgium and England, representing two species, *Pristigenys rutoti* and *P. hermani* (Stinton, 1980; Taverne and Nolf, 2010). As discussed above, many of the diagnostic features of the genus *Pristigenys* refer to the overall physiognomy and proportions of the body, meristics, and pigmentation, all features that cannot be observed in partially articulated or isolated skeletal remains (including otoliths; Taverne and Nolf, 2010). Furthermore, *Pristigenys substriata* differs from these two species from Belgium and England in having a shallow (vs. absent) sagittal crest on the frontals, smooth (vs. serrate) shelf overlying the preopercular sensory canal, a single stout spine at the posteroventral angle of the preopercle (vs. spine absent in

Table 2. Synopsis of selected morphometric (as percentage of SL) and meristic values of fossil and extant species of the family Priacanthidae. Includes new data and data from Starnes (1988) and Iwatsuki et al. (2012).

	Body depth	Head length	Head depth	Orbit diameter	Snout length	Caudal Peduncle length	Caudal peduncle depth	Mandible length	Longest dorsal-fin spine length	Longest dorsal-fin ray length	Longest anal-fin ray length	Pelvic-fin length	Dorsal-fin formula	Anal-fin formula
<i>Pristigenys substriata</i>	53.2–59.0	36.6–42	41.6–49.2	14.1–19.6	10.9–12.6	9.1–11.9	17.3–20.1	21.8–24.2	26.1–32.7	27.1–35.6	19.7–37.9	49.7–57.7	X, 9–12	III, 9–12
<i>Pseudopriacanthus altus</i>	48.4–63.0	35.7–40.5	41.0–41.5	19.7–21.8	9.0–10.4	14.0–17.4	11.1–12.9	21.6–25.8	16.9–25.2	21.9–25.5	20.9–24.4	28.0–44.7	X, 10–12	III, 10
<i>Pseudopriacanthus meyeri</i>	54.2–55.5	39.1–41.3	51.3–53.3	23.1–23.2	10.6–11.5	13.9–14.9	12.1–12.2	26.6–26.9	19.8–21.5	20.0–23.1	22.6–25.1	34.2–34.8	X, 12	III, 11
<i>Pseudopriacanthus niphonia</i>	52.9–61.2	35.9–38.8	47.3–60.6	18.4–22.1	8.4–10.4	14.8–17.0	12.2–12.9	23.8–26.6	18.1–22.4	19.5–24.1	20.6–23.9	31.6–38.6	X, 10–12	III, 10
<i>Pseudopriacanthus refulgens</i>	44.5–65.0	38.0–49.8	?	19.3–25.0	8.8–12.8	11.4–17.7	10.6–16.0	22.8–27.7	17.4–25.0	20.1–25.8	19.8–26.1	28.4–39.9	X, 10–12	III, 10
<i>Pseudopriacanthus serrula</i>	50.7–58.5	35.3–40.2	44.4–51.4	17.0–20.7	8.8–11.1	15.3–17.5	11.7–13.7	22.5–25.4	15.7–23.8	17.0–25.4	18.9–25.4	28.8–46.9	X, 10–11	III, 10
<i>Cookeolus japonicus</i>	33.9–55.7	25.2–41.2	30.5–47.9	10.1–17.3	7.2–17.2	14.0–24.7	7.7–13.9	9.2–26.4	10.2–26.1	14.2–40.7	12.8–38.0	21.3–63.8	X, 12–14	III, 12–14
<i>Heteropriacanthus cruentatus</i>	37.8–44.6	30.5–34.1	24.9–38.1	13.3–16.5	8.9–10.5	12.8–16.5	8.7–10.1	18.5–21.3	9.9–14.5	12.4–17.4	11.2–16.3	17.2–24.2	X, 12–13	III, 13–14
<i>Priacanthus alalaua</i>	36.7–43.5	30.5–38.7	33.6–40.9	13.8–20.6	8.5–11.5	12.6–15.3	7.2–8.9	17.8–23.0	11.9–16.8	15.1–21.2	12.1–19.9	25.3–31.7	X, 12–13	III, 13–14
<i>Priacanthus arenatus</i>	12.7–17.4	28.0–34.6	28.4–34.6	12.4–17.0	7.9–10.0	12.8–16.1	6.8–12.2	17.2–21.0	12.3–15.9	9.9–19.5	9.4–17.5	21.9–32.3	X–XI, 13–15	III, 14–16
<i>Priacanthus blochii</i>	34.0–38.3	30.0–34.3	28.6–36.8	12.9–16.7	8.5–10.2	12.5–14.9	8.0–9.2	19.1–21.5	12.3–17.0	16.0–20.8	16.3–20.8	27.7–32.1	X, 12–14	III, 13–15
<i>Priacanthus fitchi</i>	28.6–35.0	29.5–35.2	26.5–33.1	13.6–17.1	7.5–8.8	12.5–16.1	6.3–7.6	17.2–20.4	11.3–14.3	11.6–16.9	9.5–15.3	23.1–28.3	X, 13	III, 13–14
<i>Priacanthus hamrur</i>	33.2–42.2	27.9–33.7	29.3–36.1	11.3–16.0	7.6–13.3	13.4–15.9	6.8–9.9	17.1–21.0	10.9–16.8	14.3–20.5	10.9–20.7	26.0–32.2	IX–X, 13–15	III, 13–16
<i>Priacanthus macracanthus</i>	32.7–37.0	28.9–33.9	28.4–32.5	13.4–16.8	6.4–10.2	12.4–16.4	6.7–8.0	17.5–20.5	11.2–17.1	11.7–16.6	12.4–15.6	25.6–29.8	X, 12–14	III, 13–14
<i>Priacanthus meeki</i>	32.9–43.4	27.4–32.7	28.8–36.9	12.1–16.1	8.0–9.6	11.9–14.9	6.8–8.9	16.5–20.6	12.5–17.1	12.9–17.2	12.9–19.2	17.5–31.3	X, 14–15	III, 14–16
<i>Priacanthus nasca</i>	36.7–40.8	30.2–34.6	32.2–36.5	12.1–17.0	8.0–9.5	13.2–15.9	7.9–8.3	17.1–20.0	13.3–16.2	15.3–17.7	13.8–16.7	26.9–32.0	X, 13	III, 14
<i>Priacanthus prolixus</i>	28.9–34.3	29.4–30.5	26.4–30.5	11.3–14.1	7.1–9.1	12.1–15.7	?	15.1–19.4	11.5–18.2	12.1–19.7	11.9–16.5	24.8–30.2	X, 13–14	III, 14–15
<i>Priacanthus sagittarius</i>	38.1–43.2	27.3–35.2	33.6–38.4	13.9–16.7	8.8–10.9	12.4–16.7	8.4–10.4	20.0–22.5	14.6–19.1	19.4–27.3	18.5–26.0	30.4–36.1	X, 13–14	III, 13–15
<i>Priacanthus tayenus</i>	31.9–39.6	31.6–35.4	29.4–34.0	14.7–17.5	7.7–9.8	13.8–17.5	8.5–9.9	19.1–23.3	12.5–15.9	16.9–29.7	16.1–22.0	25.2–34.4	X, 11–13	III, 12–14
<i>Priacanthus zaisarae</i>	37.3–40.9	30.0–33.5	33.7–36.9	15.2–17.3	7.8–10.1	14.8–16.4	7.7–8.9	19.4–21.3	13.9–16.4	16.1–19.5	15.1–17.9	25.4–27.8	X, 13	III, 13–14

Pristigenys *Pseudopriacanthus* *Cookeolus* *Heteropriacanthus* *Priacanthus*

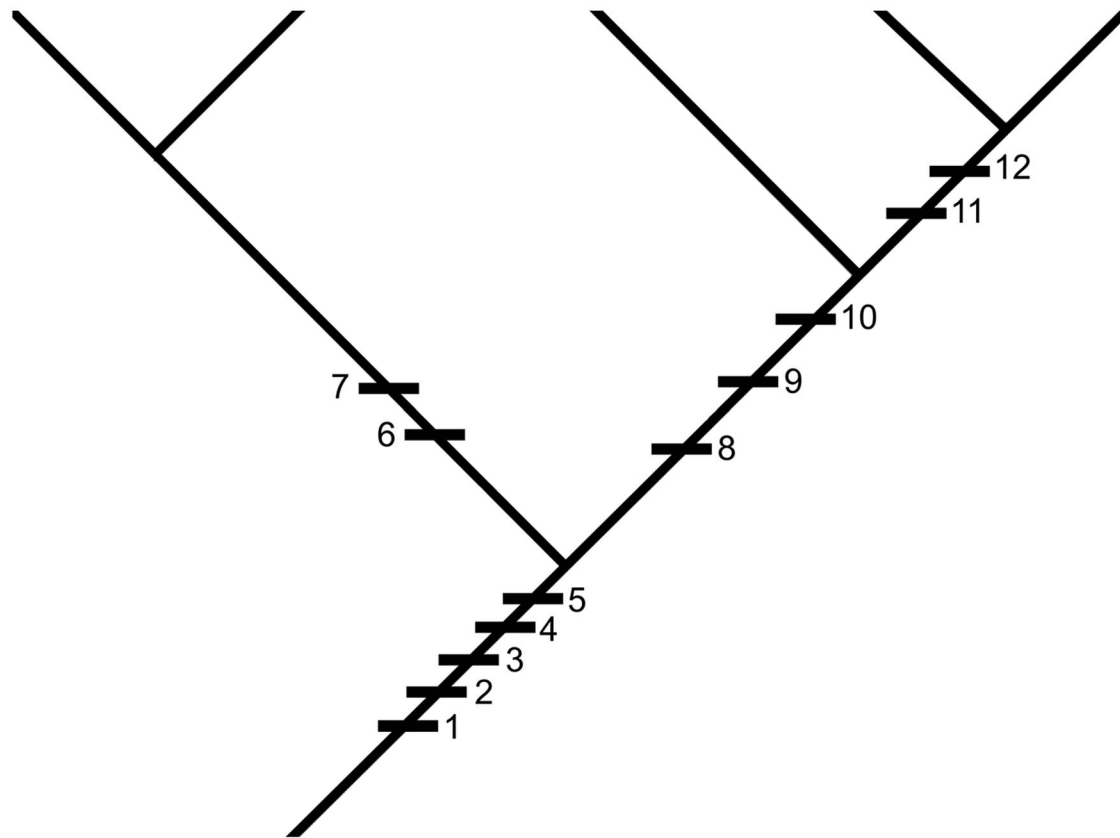


Figure 7. Cladogram showing hypothetical relationships of *Pristigenys* within the Priacanthidae. Character states are: (1) 16 (8+8) principal caudal-fin rays; (2) 23 (10+13) vertebrae; (3) scales on branchiostegals; (4) adnate pelvic fins; (5) single supraneural; (6) black marginal fin bands; (7) 3+3 procurrent rays; (8) supraneural absent; (9) broad suturing of ceratohyals; (10) enlarged ventral keel of the basipterygium; (11) lateral foramina at the base of the haemal spines; and (12) prominent anterior interradial projections on scales (see Starnes [1988] for a detailed explanation).

P. rutoti and two spines present in *P. hermani*) and spinules absent on all fin rays. Accordingly, these two Eocene species cannot be assigned to the genus *Pristigenys*.

Slightly fewer than ten otolith-based species are currently included within the genus *Pristigenys* (see Taverne and Nolf, 2010; Nolf, 2013). However, as previously pointed out by Fitch and Crooke (1984), because there are no otoliths associated with the skeletal remains of *Pristigenys substriata*, there is no robust support for the generic assignment of these otolith-based species.

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References

- Agassiz, L., 1835, Kritische Revision der in der Ittiolitologia Veronese abgebildeten fossilen Fische: Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde, v. 1835, p. 290–316.
- Agassiz, L., 1839, Recherches sur les Poissons Fossiles. Volume 4, Neuchâtel, Petitpierre, 314 p.
- Ahlstrom, E.H., Butler, J.L., and Sumida, B.Y., 1976, Pelagic stromateoid fishes (Pisces, Perciformes) off the eastern Pacific: kinds, distribution and early life histories and observations on five of these from northwest Atlantic: Bulletin of Marine Science, v. 26, p. 285–402.
- Arambourg, C., 1967, Résultats scientifiques de la Mission C. Arambourg en Syrie et en Iran (1938–1939). II. Les poissons oligocènes de l'Iran: Notes et Mémoires du Moyen-Orient, v. 8, p. 1–210.
- Bannikov, A.F., 2010, [Fossil vertebrates of Russia and Adjacent Countries: Fossil Acanthopterygian Fishes (Teleostei, Acanthopterygii)]: Moscow, GEOS, 244 p. [in Russian].
- Betancur, R., Broughton, R.E., Wiley, E.O., Carpenter, K., López, J.A., Li, C., Holcroft, N.I., Arcila, D., Sanciangco, M., Cureton, J.C., Zhang, F., Buser, T., Campbell, M.A., Ballesteros, J.A., Roa-Varon, A., Willis, A., Borden, W.C., Rowley, T., Reneau, P.C., Hough, D.J., Lu, G., Grande, T., Arratia, G., and Ortí, G., 2013, The tree of life and a new classification of bony fishes: PLOS Currents Tree of Life, 2013 Apr 18 [last modified: 2013 Jun 3]. Edition 1. doi: 10.1371/currents.tol.53ba26640df0cc aee75bb165c8c26288.

- Blainville, H.D. de, 1818, Des Ichthyolites du Monte Bolca, ou Vestena Nuova dans le Veronais, in *Nouveau Dictionnaire d'Histoire Naturelle appliquée aux Arts, à l'Agriculture, à l'Economie rurale et domestique, à la Médecine, etc.*, par une Société de Naturalistes et d'Agriculteurs. 27, Paris, Déterville, ed., p. 334–361.
- Blot, J., 1980, La faune ichthyologique des gisements du Monte Bolca (Province de Vérone, Italie). Catalogue systématique présentant l'état actuel des recherches concernant cette faune: Bulletin du Muséum National d'Histoire Naturelle, Paris, 4^e sér, 2, section C, v. 4, p. 339–396.
- Caldwell, D.K., 1962a, Development and distribution of the short bigeye *Pseudopriacanthus altus* (Gill) in the Western North Atlantic: Fishery Bulletin, v. 62, p. 103–150.
- Caldwell, D.K., 1962b, Western Atlantic fishes of the family Priacanthidae: Copeia, v. 1962, p. 417–424.
- Caldwell, D.K., and Bullis, H.R. Jr., 1971, An unusually large aggregation of prejuvenile bigeyes, *Priacanthus arenatus*, in the West Indies: Copeia, v. 1971, p. 176.
- Carnevale, G., Bannikov, A.F., Marramà, G., Tyler, J.C., and Zorzin, R., 2014, The Pesciara-Monte Postale Fossil-Lagerstätte: 2. Fishes and other vertebrates, in Papazzoni, C.A., Giusberti, L., Carnevale, G., Roghi, G., Bassi, D., and Zorzin, R., eds., The Bolca Fossil-Lagerstätte: A Window into the Eocene World: Rendiconti della Società Paleontologica Italiana, v. 4, p. 37–63.
- Daniil'chenko, P.G., 1980, Otryad Perciformes, in Novitskaya, L.I., ed., *Iskopyayemye kostyite ryby SSSR: Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR*, v. 178, p. 115–169. [in Russian].
- Eastman, C.R., 1905, Les types de poissons fossiles du Monte-Bolca au Muséum d'Histoire Naturelle de Paris: Mémoires de la Société Géologique de France, Paléontologie, v. 34, p. 1–33.
- Edwards, K., and Rosen, B.R., 2000, From the Beginning: London, The Natural History Museum, 72 p.
- Fitch, J.E., and Crooke, S.J., 1984, Revision of Eastern Pacific catalufas (Pisces: Priacanthidae) with description of a new genus and discussion of the fossil record: Proceedings of the California Academy of Sciences, v. 43, p. 301–315.
- Fitch, J.E., and Lavenberg, R.J., 1975, Tidepool and Nearshore Fishes of California: Berkeley, University of California Press, 156 p.
- Fritzsche, R.A., 1978, The first eastern Pacific records of bulleye, *Cookeolus boops* (Bloch and Schneider, 1801), (Pisces, Priacanthidae): California Fish and Game, v. 64, p. 219–221.
- Fritzsche, R.A., and Johnson, G.D., 1981, *Pseudopriacanthus* Bleeker, a synonym of the priacanthid genus *Pristigenys* Agassiz: Copeia, v. 1981, p. 490–492.
- Fujita, K., 1990, The Caudal Skeleton of Teleostean Fishes: Tokyo, Tokai University Press, 897 p.
- Gill, T.N., 1872, Arrangement of the families of fishes, or classes Pisces, Marsipobranchi and Leptocardii: Smithsonian Miscellaneous Collection, v. 11, p. 1–49.
- Goatley, C.H.R., Bellwood, D.R., and Bellwood, O., 2010, Fishes on coral reefs: changing roles over the past 240 million years: Paleobiology, v. 36, p. 415–427.
- Hiatt, R.W., and Strasburg, D.W., 1960, Ecological relationships of the fish fauna on coral reefs of the Marshall Islands: Ecological Monographs, v. 30, p. 65–127.
- Iwatsuki, Y., Matsuda, T., Starnes, W.C., Nakabo, T., and Yoshino, T., 2012, A valid priacanthid species, *Pristigenys refulgens* (Valenciennes 1862), and a redescription of *P. nipponia* (Cuvier in Cuvier & Valenciennes 1829) in the Indo-West Pacific (Perciformes: Priacanthidae): Zootaxa, v. 3206, p. 41–57.
- Johnson, G.D., 1984, Percoidei: development and relationships, in Moser, H.G., Richards, W.J., Cohen, D.M., Fahay, M.P., Kendall, A.W., Jr., and Richardson, S.L., eds., *Ontogeny and Systematics of Fishes: American Society of Ichthyologists and Herpetologists, Special Publication*, v. 1, p. 464–498.
- Kon, T., and Yoshino, T., 1997, *Cookeolus spinolacrymatus* sp. nov., a Late Pliocene priacanthid fish from Okinawa, Japan: Ichthyological Research, v. 44, p. 347–356.
- Marramà, G., Bannikov, A.F., Tyler, J.C., Zorzin, R., and Carnevale, G., 2016, 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, v. 454, p. 228–245.
- Micklich, N., and Parin, N.N., 1996, The fishfauna of Frauenweiler (middle Oligocene, Rupelian; Germany): first results of a review: *Publicaciones Especiales, Instituto Español de Oceanografía*, v. 21, p. 129–148.
- Myers, G.S., 1958, The priacanthid fish genus *Pristigenys*: Stanford Ichthyological Bulletin, v. 7, p. 40–42.
- 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., and Wainwright, P.C., 2013, Phylogeny and tempo of diversification in the superradiation of spiny-rayed fishes: Proceedings of the National Academy of Sciences of the United States of America, v. 110, p. 12738–12743.
- Nelson, J.S., 2006, *Fishes of the World, Fourth Edition.*, Hoboken, Wiley & Sons, 601 p.
- Nicol, J.A.C., Arnott, H.J., and Best, A.C.G., 1973, Tapeta lucida in bony fishes (Actinopterygii): a survey: Canadian Journal of Zoology, v. 51, p. 69–81.
- Nolf, D., 2013, The Diversity of Fish Otoliths, Past and Present: Bruxelles, Royal Belgian Institute of Natural Sciences, 222 p.
- Papazzoni, C.A., Carnevale, G., Fornaciari, E., Giusberti, L., and Trevisani, E., 2014, The Pesciara-Monte Postale Fossil-Lagerstätte: 1. Biostratigraphy, sedimentology and depositional model, in Papazzoni, C.A., Giusberti, L., Carnevale, G., Roghi, G., Bassi, D., and Zorzin, R., eds., The Bolca Fossil-Lagerstätte: A Window into the Eocene World: Rendiconti della Società Paleontologica Italiana, v. 4, p. 29–36.
- Pharisat, A., 1991, La paléoichthyofaune du Rupélien marin de Froidefontaine (Territoire de Belfort). Taxinomie et populations, genèse du gisement, implications paléobiogéographiques: Annales Scientifiques de l'Université de Franche-Comté, Besançon, v. 11, p. 13–97.
- Prokofiev, A.M., 2013, Two new species of families Priacanthidae and Reprocridae (Perciformes) from the Upper Part of Lower Oligocene of the Northern Caucasus: Journal of Ichthyology, v. 53, p. 245–251.
- Roberts, C.D., 1993, Comparative morphology of spined scales and their phylogenetic significance in the Teleostei: Bulletin of Marine Science, v. 52, p. 60–113.
- Salmon, J.M., and Winn, H.E., 1966, Sound production by priacanthid fishes: Copeia, v. 1966, p. 869–872.
- Smith, C.L., and Bailey, R.M., 1962, The subocular shelf in fishes: Journal of Morphology, v. 110, p. 1–17.
- Smith, J.L.B., 1966, The rare big-eye, *Pristigenys nipponia* (C & V), in South Africa: Occasional Papers of the Department of Ichthyology, Rhodes University, v. 9, p. 97–102.
- Starnes, W.C., 1988, Revision, phylogeny and biogeographic comments on the circumtropical marine percoid fish family Priacanthidae: Bulletin of Marine Science, v. 43, p. 117–203.
- Stinton, F.C., 1980, Fish otoliths from the English Eocene, Part 4: Palaeontographical Society Monographs, v. 558, p. 191–258.
- Taverne, L., 1988, On the synonymy of the priacanthid genera *Pristigenys* Agassiz, 1835 and *Pseudopriacanthus* Bleeker, 1869 (Teleostei, Percoidei): Cybium, v. 12, p. 171–172.
- Taverne, L., and Nolf, D., 2010, Les Priacanthidae (Teleostei, Perciformes) des Sables de Ledé (Éocène moyen, Belgique): ostéologie et otolithes: Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, v. 80, p. 187–243.
- Volta, G.S., 1796, Ittiolitologia Veronese del Museo Bozziano Ora Annesso a Quello del Conte Giovambattista Gazola e di Altri Gabinetti di Fossili Veronesi: Verona, Stamperia Giuliani, 323 p.
- Wang, R.T., Nicol, J.A.C., Thurston, E.L., and McCants, M., 1980, Studies on the eyes of bigeyes (Teleostei Priacanthidae) with special reference to the tapetum lucidum: Proceedings of the Royal Society of London B, v. 210, p. 499–512.
- White, E.I., 1936, On certain Eocene percoid fishes: Annals and Magazine of Natural History, ser. 10, v. 18, p. 43–54.
- Wiley, E.O., and Johnson, G.D., 2010, A teleost classification based on monophyletic groups, in Nelson, J.S., Schultze, H.-P., and Wilson, M.H.V., eds., *Origin and Phylogenetic Interrelationships of Teleosts*: Munich, Verlag Dr. Friedrich Pfeil, p. 123–182.
- Woodward, A.S., 1901, Catalogue of Fossil Fishes in the British Museum (Natural History), v. Volume 4: London, Trustees of the British Museum, v. 636, p. 1–215.
- de Zigno, A., 1874, Catalogo Ragionato dei Pesci Fossili del Calcare Eoceno di M. Bolca e M. Postale: Venezia, Stabilimento Tipografico Grimaldo e C., 215 p.

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