Studi e ricerche sui giacimenti terziari di Bolca, XVI - Miscellanea Paleontologica, 13, 2015: 17 - 26

Pietschellidae fam. nov., a new family of miniature percomorph fishes from the Eocene of Bolca, with the description of a new genus and species

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Abstract

A new genus and species of percomorph fish, Nickcaves pterygocephalus *gen. et sp. nov., is described from the Eocene (Ypresian) deposits of the Monte Postale site of the Bolca locality, north-eastern Italy. This new percomorph fish is based on a single, very small, well-preserved and nearly complete specimen that exhibits a unique combination of features. This new genus closely resembles another percomorph described from the same locality,* Pietschellus aenigmaticus *Bannikov & Carnevale, 2011. These two taxa share a number of features, such as the possession of a sail-like dorsal fin originating over the neurocranium, and are included herein in the new family Pietschellidae, placed* incertae sedis *with the percomorph fishes. The overall morphology of the pietschellid taxa suggests that these fishes were characterized by a benthic lifestyle. The very small body size of both these taxa as well as the shared possession of a suite of reductive characters concur to indicate that the Pietschellidae can be considered as miniature fishes.*
Key words: *Percomorpha* incertae sedis*, new family, genus and species, Eocene, north-eastern Italy, Bolca locality.*

Riassunto

Nickcaves pterygocephalus gen. et sp. nov., un nuovo percomorfo proviente dai depositi carbonatici eocenici (Ypresiano) del sito di Monte Postale, nel territorio della località di Bolca, Italia nord-orientale, viene descritto sulla base di un esemplare parzialmente completo di dimensioni estremamente ridotte e caratterizzato da una combinazione di caratteri peculiare. *Nickcaves pterygocephalus* mostra una spiccata somiglianza ad un altro percomorfo rinvenuto nel medesimo sito, *Pietschellus aenigmaticus* Bannikov & Carnevale, 2011. Questi due taxa condividono numerosi caratteri, tra cui una pinna dorsale a forma di vela la cui origine è localizzata lungo il margine dorsale del neurocranio, e vengono inseriti all'interno della famiglia Pietschellidae fam. nov., considerata *incertae sedis* tra i Percomorpha. Nel complesso, la morfologia corporea dei taxa della famiglia Pietschellidae suggerisce uno stile di vita bentonico. La ridottissima taglia corporea di entrambe le specie, che condividono inoltre una serie di semplificazioni scheletriche, suggerisce che i membri della famiglia Pietschellidae possano essere considerati come taxa miniaturizzati.
Parole chiave: Percomorpha *incertae sedis*, nuova famiglia, nuovo genere e nuova specie, Eocene, Italia nordorientale, località di Bolca.

Introduction

The Eocene fossiliferous locality of Bolca, about 25 km NE of Verona, north-eastern Italy, is known worldwide for the beautiful and exquisitely well-preserved fishes, probably representing the most famous Italian *Fossil-Lagerstätte* and certainly being one of the most important paleoichthyofaunistic assemblages. Fossil fishes from Bolca are known since the sixteenth century and have been regularly excavated since the mid-nineteenth century, resulting in the extraction of a huge number of specimens currently disseminated in the museums, research institutions and private collections around the world (e.g., Blot, 1969). Fish skeletal remains are remarkably abundant in the productive sites making this locality as the most diverse of all the Cenozoic marine fish assemblages, with more than 240 documented taxa (see Carnevale et al., 2014; Bannikov, 2014). Overall, the fish assemblage of Bolca consists of sharks, batoids, pycnodontiforms and teleosts, representing one of the earliest record of a spiny-rayed fishes dominated ichthyofauna, with a diversity foreshadowing that of today (Patterson, 1993).

Most of the fish specimens from Bolca have been collected from the Pesciara cave site, but a relevant number of skeletons has been also extracted over the years from another extremely productive site, that of Monte Postale, located a few hundreds metres from the Pesciara cave site. The geology of this site was described in detail by Fabiani (1914, 1915). The Eocene strata were considered of Lutetian or late Ypresian age by Malaroda

(1954) and Hottinger (1960), respectively. However, an updated biozonal assignment of the fossiliferous layers remains elusive, even if these are currently regarded as approximately coeval of those of the Pesciara site, dating back to the late Ypresian, slightly less than 50 Ma (Papazzoni et al., 2014a; Trevisani, 2015).

The taxonomic composition of the fish fauna of the Monte Postale site has been traditionally considered as very similar to that of the Pesciara site (Bannikov and Zorzin, 2004). Controlled excavations at this site in the 2000s led to the accumulation of a large collection of fishes, invertebrates and plant remains, including several new previously undescribed taxa. The goal of this paper is therefore to describe a small acanthomorph fish known by a single individual and collected at the Monte Postale site in 2003. The fossil closely resembles the only known specimen of *Pietschellus aenigmaticus* also collected at the Monte Postale site in 2003 and described by Bannikov and Carnevale (2011). The detailed morphological and comparative analysis of the new specimen revealed that these two fossils are the sole members of the new family Pietschellidae fam. nov. introduced herein.

Material and methods

The specimen documented herein was found among the undescribed material collected at the Monte Postale site during summer 2003 and housed in the Museo Civico di Storia Naturale di Verona (MCSNV). The fossil consists of a relatively well-preserved complete articulated skeleton (with fragmentary counterpart) preserved on the surface of inframillimetrically laminated micritic limestone. The specimen was examined using a Wild Heerbrugg stereomicroscope equipped with a camera lucida drawing arm and measurements were taken with a dial caliper to the nearest 0.1 mm. Standard length (SL) is used throughout.

Some details of the specimen examined were best seen when the specimen was moistened with alcohol. The specimen was prepared by needle.

Systematic paleontology

Subdivision Teleostei sensu Patterson & Rosen, 1977
Percomorphacea Wiley & Johnson, 2010
Family Pietschellidae fam. nov.

Type genus
Pietschellus Bannikov & Carnevale, 2011.

Diagnosis
A percomorph family unique in having the following combination of characters: body moderately elongate with shortened abdominal region; neurocranium deep, with nearly smooth dorsal surface; premaxilla with distinct ascending and articular processes; jaws with small conical teeth; vertebrae 25 (8+17); ribs and intermuscular bones absent; caudal skeleton with parhypural plus hypurals 1-4 fused with terminal centrum; two epurals; hypurapophysis absent; haemal spine of the penultimate vertebra thick and fused to the centrum; caudal fin rounded with 11 or 12 unbranched principal rays and two upper and two lower procurrent rays; supraneural absent; sail-like dorsal fin with origin shifted forward over the neurocranium; 5 or 6 dorsal-fin spines; anal fin with a spine and 11 to 12 rays; terminal dorsal- and anal-fin pterygiophores support two rays; dorsal- and anal-fin stays absent; anal-fin pterygiophores and vertebrae in one-to-one relationship; body covered with sparse unicuspid dermal scale spinules.

Composition
Type genus plus *Nickcaves* gen. nov.

Remarks
Several osteological features clearly demonstrate that the members of the family Pietschellidae pertain to the percomorph clade, including possession of dorsal- and anal-fin spines, absence of the second ural centrum, reduced number of hypurals, and caudal fin with less than 17 principal rays (see Johnson and Patterson, 1993; Wiley and Johnson, 2010). Within percomorphs, pietschellids exhibit a unique combination of features that strongly support their separate status (Bannikov and Carnevale, 2011). However, some of the salient features characteristic of these fishes are reductive or occur homoplasiously in several unrelated percomorphs groups; some of the reductive features are probably associated with the benthic lifestyle of pietschellids (highly consolidated caudal skeleton; caudal fin rounded; substantial one-to-one relationship between pterygiophores and vertebrae) or to the relative body elongation, being the product of convergent evolution (e.g., Gosline, 1963; Gill and Mooi, 1993). Consequently, it is not possible for the moment to provide any unambiguous hypothesis of a sister group relationship with the known percomorphs and, for this reason, the Pietschellidae should be placed as incertae sedis within the highly diverse percomorph clade.

Genus *Pietschellus* Bannikov & Carnevale, 2011.

Pietschellus: Bannikov and Carnevale, 2011: 53.

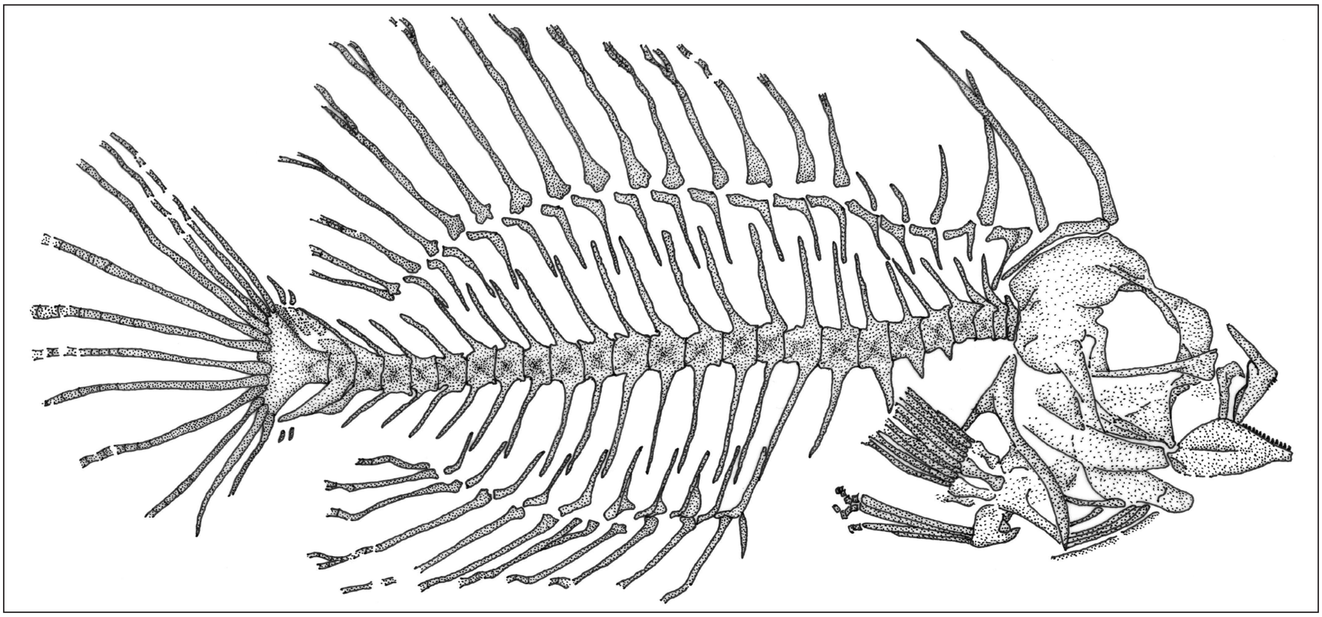

Fig. 1 – *Pietschellus aenigmaticus* Bannikov & Carnevale, 2011. Reconstruction of the skeleton, right side, lateral view [from Bannikov and Carnevale (2011, fig. 2), reversed]. Scale spinules omitted.

Type Species
Pietschellus aenigmaticus Bannikov & Carnevale, 2011 from the Monte Postale site, Bolca locality, north-eastern Italy; late early Eocene (Fig. 1).

Emended Diagnosis
A member of the family Pietschellidae unique in having the following combination of characters: basisphenoid present; neural spine of the first abdominal vertebrae greatly shortened; abdominal vertebrae five to eight with triangular thickened parapophyses of progressively increasing length; caudal fin rounded with 12 (6+6) unbranched rays and two upper and two lower procurrent rays; caudal-fin skeleton with a short autogenous fifth hypural; neural arch of the penultimate vertebra reduced to a low crest; dorsal fin notched and continuous with six spines and 15 rays; vacant interneural space between neural spines of sixth and seventh vertebrae; dorsal- and anal-fin rays distally branched; anal fin contains a short spine and 11 rays; first anal-fin pterygiophore slender; basipterygium short and massive with an anteriorly directed spur; pelvic fin contains one spine and three segmented rays.

Composition
Type species only.

Remarks
Pietschellus aenigmaticus was described by Bannikov and Carnevale (2011) based on a single specimen measuring 18 mm SL (see Table 1). Like the new specimen described herein and representing the holotype of a new genus and species, the single available individual of *Pietschellus aenigmaticus* (MCSNV I.G. VR. 66741) was collected at the Monte Postale site during the 2003 excavation led by the Museo Civico di Storia Naturale di Verona. The fossil consists of a nearly complete and well-preserved articulated skeleton. Measurements for *Pietschellus aenigmaticus* are summarized in Table 1.

Genus *Nickcaves* gen. nov.

Type Species
Nickcaves pterygocephalus gen. et sp. nov. from the Monte Postale site, Bolca locality, north-eastern Italy; late early Eocene.

Diagnosis
A member of the family Pietschellidae unique in having the following combination of characters: neural spines of the three anterior abdominal vertebrae well-developed and anteroposterioly expanded; abdominal vertebrae three to eight with triangular thickened parapophyses of progressively increasing length; neural spine of the penultimate vertebra remarkably enlarged with lobate profile; caudal fin rounded with 11 (5+6) unbranched rays and two upper and two lower procurrent rays; dorsal fin continuous with five spines and 17 rays; height of dorsal-fin spines gradually decreasing posteriorly; first dorsal-fin spine massive and strongly

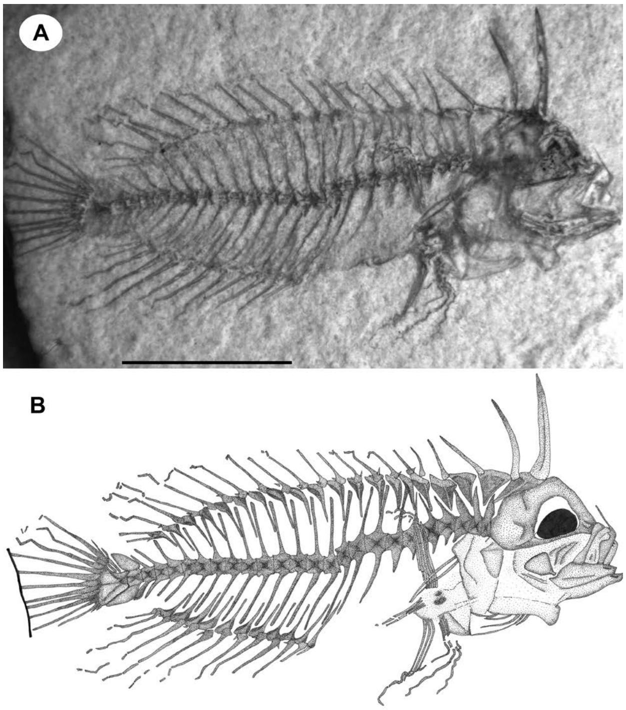

Fig. 2 – *Nickcaves pterygocephalus* gen. et sp. nov.: **A** - holotype, MCSNV I.G. VR. 66660 (wet with alcohol to improve contrast), scale bar 5 mm; **B** - reconstruction of the skeleton, right side, lateral view; body scale spinules omitted.

ossified; vacant interneural space between neural spines of fifth and sixth vertebrae; dorsal- and anal-fin rays unbranched; pterygiophores of the spinous portion of the dorsal fin greatly expanded, nearly triangular in outline; anal fin contains a short spine and 12 rays; a series of unicuspid dermal scale spinules associated with the bases of the dorsal- and anal-fin rays.

Composition
Type species only.

Etymology
The genus is named in honour of the Australian artist Nicholas Edward Cave, better known as Nick Cave; gender masculine.

Nickcaves pterygocephalus gen. et sp. nov.

Figure 2

Holotype
MCSNV I.G. VR. 66660, nearly complete well-preserved articulated skeleton in part and counterpart [counterpart (MCSNV I.G. VR. 666601) highly fragmentary]; 16.5 mm SL (Fig. 2A).

Type Locality and Horizon
North-eastern Italy, Bolca locality, Monte Postale site; late early Eocene, late Ypresian, about 50 Ma (Papazzoni et al., 2014b).

Diagnosis
As for the genus.

Etymology
After the Greek words πτερόν (for wing) and κεφαλή (for skull).

Description
Measurements for *Nickcaves pterygocephalus* are summarized in Table 1. The body is relatively elongate and nearly cylindrical, with a short and deep caudal peduncle (Fig. 2). The head is moderately large; its length is contained more that three times in SL. The snout is short and compact. The orbit is relatively large. The mouth is terminal and characterized by a moderately developed gape. The continuous dorsal fin is extremely elongate, occupying more than three fourths of the SL; the dorsal-fin spines gradually decrease in height posteriorly in the series, with the posterior one being approximately of the same length with the anteriormost dorsal-fin ray. The three posterior dorsal-fin rays of both the dorsal and anal fins are shorter than the preceding ones, producing an almost vertical posterior margin of these fins. Overall, the dorsal-fin rays are shorter than the opposite anal-fin elements. The inadequate preservation of both pectoral and pelvic fins and girdles do not allow to properly define their mutual position along the body axis. The caudal fin appears to be rounded.

The neurocranium is short and rather deep, reaching its maximum height in the orbital region and gradually sloping in the otic and occipital regions (Fig. 2B). The outer surface of the neurocranial bones seems to be smooth. The ethmoid region is stout and strongly ossified. The post-orbital portion of the neurocranium is antero-posteriorly compressed and laterally expanded. The limits and morphology of the neurocranial bones is difficult to recognize because of inadequate preservation. The only neurocranial bone that is clearly identifiable is the nearly straight parasphenoid, which occupies more than half of the basicranial length. There is no evidence of a supraoccipital crest.

The infraorbital bones are not preserved.

The premaxilla bears a very long and slender ascending process separated from a reduced articular process; a well-developed postmaxillary process characterized by a gently rounded dorsal profile is also present; the alveolar process appears to be robust and characterized by an almost straight ventral margin bearing a few small and conical teeth (Fig. 2B). The maxilla is large with a stout articular head. The mandible is relatively short, its length is contained more than seven times in SL; it is nearly quadrangular in outline, being remarkably low in the symphyseal region.

The suspensorium (Fig. 2B) is poorly preserved and most of its elements but the quadrate cannot be properly recognized. The main shaft of the hyomandibula is almost vertically oriented. The quadrate is subtriangular in outline, fan-like, with a stout and short articular head. The bones of the pterygoid series are thin and laminar. The ectopterygoid appears to be rather elongate.

Due to inadequate preservation, the opercular bones are difficult to interpret. What appears to be the crescent-shaped anterior profile of the preopercle is recognizable. The opercle is roughly triangular in outline, with a stout posterior spine representing the distal tip of an horizontal thickened ridge located in the upper fourth of the bone.

The hyoid bar is large, thick and well ossified (Fig. 2B). Not less than five branchiostegal rays seem to be present. The branchial skeleton is not exposed in the specimen.

The vertebral column consists of 25 vertebrae, eight abdominal plus 17 caudal (Fig. 2B). The abdominal portion of the vertebral column is contained slightly more than two times in the length of the caudal portion. All the centra, except for the terminal urostylar one are amphicoelus and midlaterally constricted. The first two centra are shorter than the remaining ones, which are approximately equal in length. With exception of the first two, all the centra are subrectangular, longer than high. The neural spines of the three anterior vertebrae are notably expanded anteroposteriorly. Most of the neural spines are inclined posteriorly, whereas several posterior abdominal and anterior caudal vertebrae have the neural spines anteriorly inclined. The distal tips of the neural spines of the anterior six vertebrae are pointed, whereas those of the following vertebrae are blunt. The haemal spines are similar to their opposite neural spines but somewhat stronger inclined. All the abdominal vertebrae except for the anterior two bear strong parapophyses of progressively increasing size. The parapophysis of the posterior abdominal vertebra is extremely developed and closely resembles the haemal spine of the first caudal vertebra; however, based on its anatomical position and the absence of direct relationships with the anal-fin endoskeleton, it is reasonable to interpret it as a greatly developed parapophysis (see also Bannikov and Carnevale, 2011). There is no evidence of ribs and intermuscular bones. The terminal urostylar vertebra constitutes a single fused element (first preural plus first and second ural centra). The configuration of the caudal skeleton (Fig. 2B) is difficult to interpret, and more particularly the upper portion of what appears to be a fan-like structure possibly produced by the coalescence of the hypurals and the parhypural; however, it is not possible to conclusively define the morphology of such a structure for which additional better preserved material would be necessary. There is no evidence of a parhypurapophysis. Two rod-like epurals can be recognized. The penultimate vertebra bears a very large neural spine with a nearly lobate profile. The haemal spine of the penultimate vertebra is remarkably expanded anteroposteriorly and appears to be fused to the centrum. The haemal spine of the antepenultimate vertebra is thicker than those of the preceding vertebrae of the caudal peduncle. The caudal fin contains five upper and six lower unbranched principal rays, plus two pointed dorsal and ventral procurrent rays.

The sail-like dorsal fin inserts above the top of the head, at the level of the second half of the orbit. It consists of five spines plus 17 soft segmented but unbranched rays (Fig. 2B; dorsal-fin formula: II/I/I/I/1//1/1/1/1/1/1/1/1/1/1/1/1/1/1/2), supported by 20 pterygiophores. There are no supraneurals. The dorsal-fin spines are pointed, heavily ossified and gradually decrease in length backward. The first spine is especially massive and stout, measuring about three times the length of the fifth one; it is in supernumerary association with the first dorsal-fin pterygiophore. The height of the dorsal-fin rays gradually increases posteriorly up to the 14^{th} element of the series. The longest dorsal fin ray (14^{th}) is slightly shorter than the first dorsal-fin spine. The first pterygiophore is bent forward over the posterodorsal portion of the neurocranium. The pterygiophores of the spinous portion of the dorsal fin are greatly enlarged and subtriangular in shape. The two terminal dorsal-fin rays are supported by the posteriormost pterygiophore. The first dorsal-fin pterygiophore lies between the rear of the neurocranium and the neural spine of the first vertebra. With exception of the space between the neural spines of the fifth and sixth vertebrae that is vacant, all the dorsal-fin pterygophores exhibit a one-to-one relationship with the underlying vertebrae.

The anal fin inserts below the fourth caudal vertebra and includes a single short and pointed spine plus 12 soft unbranched rays (Fig. 2B; anal-fin formula: /I+1/1/1/1/1/1/1/1/1/1/2/) supported by 1 1 pterygiophores. The anal-fin spine is in supernumerary association with the first pterygiophore. The morphology of the anal-fin pterygiophores is similar to that of the opposite dorsal-fin pterygiophores. The first anal-fin pterygiophore is longest and situated behind the haemal spine of the first caudal vertebra. The two terminal anal-fin rays are supported by the posteriormost pterygiophore. The latter inserts in the space between the 11th and 12th haemal spines, being opposite to the penultimate dorsal-fin pterygiophore. The anal-fin pterygiophores show a one-to-one relationship with the overlying vertebrae. There is no evidence of dorsal- and anal-fin stays (in the sense of Weitzman, 1962).

The pectoral girdle is poorly preserved and only a few bones are at least partially recognizable (Fig. 2B). The cleithrum appears to be slender and elongate. Both the contralateral postcleithra are clearly exposed in the specimen; these are elongate, slender and distally pointed. What appear to be the pectoral-fin rays are elongate and insert low on the flank at the level of the fifth abdominal vertebra.

The pelvic girdle cannot be determined. The pelvic fin appears to originate approximately at the same level of the pectoral fin. The pelvic-fin rays are elongate. It is not possible to define the original complements of pectoral and pelvic-fin rays; all of them are definitely unbranched.

The body is uniformly covered by small, pointed dermal scale spinules lacking a basal plate. A series of these spinules is associated with the bases of dorsal- and anal-fin rays (Fig. 2B).

Taxonomic discussion

As pointed out above, several features concur to demonstrate that the family Pietschellidae pertains to the highly diverse and morphologically heterogeneous percomorph clade. However, within the percomorphs the relationships of the members of this Eocene family remain elusive. Looking for the possible relatives, Bannikov and Carnevale (2011) surveyed several groups and concluded that most of the features shared with blennioids, callionymoids, cottoids, lophiiforms, pterygocephalids, scorpaenoids, and trachinoids are probably associated to their similar lifestyle or represent the product of convergent or parallel evolution. As a consequence, these enigmatic fishes characterized by a remarkable forward shift of the dorsal-fin origin over the head were placed as *incertae sedis* within the percomorphs. The peculiar set of morphological features exhibited by *Nickcaves*, the new pietschellid genus described herein, definitely confirms the hypotheses provided by Bannikov and Carnevale (2011) based on the genus *Pietschellus* alone. The skeletal anatomy of the new genus suggests that the overall osteological structure of the new Eocene family was rather conservative. Despite *Nickcaves* differs from *Pietschellus* in many respects, they share a clearly recognizable body plan that can be easily separated from that of all the other percomorphs. The differences between these genera concern morphometric, meristic and skeletal features.

Most of the morphometric peculiarities of *Nickcaves* are related to its relative elongation of the body and the extension of the dorsal fin and its portions. In particular, as evidenced in Table 1, *Nickcaves* differs from *Pietschellus* in having a less deep body, a shorter snout, a much slender and elongate mandible, more anterior insertion of median fins, and longer dorsal fin. The overall design of the dorsal fin of *Nickcaves* is remarkably different from that of *Pietschellus* in having a gradual backward decrease of the height of the spines and a subsequent gradual increase of the height of the soft rays up to the 14th element of the series rather than a notched profile of its anterior region due to a steep decrease of the height of the posterior three dorsal-fin spines.

The composition of the median fins of the two pietschellid genera is clearly different. The caudal fin of *Nickcaves* has five upper and six lower principal rays whereas that of *Pietschellus* contains six upper and six lower principal rays. The dorsal fin of *Nickcaves* contains five spines plus 17 soft rays whereas that of *Pietschellus* has six spines plus 15 soft rays. Consequently, the insertion pattern of the dorsal-fin pterygiophores in the interneural spaces reflects these compositional differences. *Nickcaves* exhibits a vacant space between the neural spines of the fifth and sixth vertebrae and the anteriormost pterygiophore inserts in the space between the rear of the neurocranium and the neural spine of the first vertebra. The anteriormost dorsal-fin pterygiophore of *Pietschellus* inserts in the first interneural space (between the neural spines of the first and second vertebrae), and the vacant space is located between the neural spines of the sixth and the seventh vertebrae. Moreover, the two posterior dorsal-fin pterygiophores of *Pietschellus* insert in a single interneural space, whereas there is a substantial one-to-one relationship between dorsal-fin pterygiophores and underlying vertebrae in *Nickcaves*. The anal fin of *Nickcaves* contains a single spine plus 12 soft rays whereas that of *Pietschellus* has a single spine plus 11 soft rays.

Finally, the skeleton of *Nickcaves* includes a series of unique features that reinforce the morphometric and meristic evidences discussed above. The ascending process of the premaxilla of *Nickcaves* is extremely thin and slender, whereas it is stout and robust in *Pietschellus* (see Figs. 1-2). Some of the unique features of *Nickcaves* pertain to the anterior abdominal vertebrae. The neural spine of the anterior abdominal vertebra is well-developed and expanded in *Nickcaves* and very short in *Piet-*

schellus. The neural spines of the two following abdominal vertebrae are notably expanded anteroposteriorly in *Nickcaves*, whereas these are slender and relatively thin in *Pietschellus*. The third and fourth abdominal vertebrae of *Nickcaves* bear strong parapophyses, which are absent in *Pietschellus*. Another difference between these two pietschellid genera can be easily observed in the penultimate vertebra that is characterized by a very large neural spine with lobate profile in *Nickcaves* and by a low crest-like neural arch in *Pietschellus*. The dorsal- and anal-fin pterygiophores of *Nickcaves* are remarkably enlarged compared to the thin and slender elements characteristic of *Pietschellus*; in particular, the pterygiophores of the spinous portion of the dorsal fin of *Nickcaves* are broadly expanded and nearly triangular in outline, whereas those of *Pietschellus* are delicate and approximately L-shaped. The distal ends of most dorsal- and anal-fin rays are bifurcated in *Pietschellus*, whereas these are always unbranched in *Nickcaves*. Moreover, the bases of the dorsal- and anal-fin rays of *Nickcaves* are associated with one or two pointed dermal scale spinules similar to those that cover part of the body; this association was not observed in *Pietschellus* (Bannikov and Carnevale, 2011).

Concluding remarks

One of the most striking features of *Nickcaves* and *Pietschellus* is their very small body size. Body size is one of the most obvious features of an animal with a number of prominent ecological and evolutionary implications (e.g., Peters, 1983; Hanken and Wake, 1993). As documented above, both the pietschellid taxa are known from individuals measuring less than 20 mm SL. However, despite their very small size, the head and axial skeleton of both genera are robust, solidly ossified and completely developed, suggesting that the available specimens represent adult individuals. The tendency towards very small body size is relatively common among fishes, in both marine and freshwater environments. Numerous examples of marine fishes exhibiting a very small body size have been documented (e.g., Tyler, 1970; Johnson and Brothers, 1989; Carnevale, 2008), particularly among tropical gobies (e.g., Lachner and Karnella, 1980; Winterbottom and Emery, 1981; Jewett and Lachner, 1983; Winterbottom, 1990). Several ecological hypotheses were proposed to explain the existence of very small-sized fishes, including life-history strategies (Marzluff and Dial, 1991), resource partitioning allowing coexistence with larger competitors (Schoener, 1974), and behaviour and habitat associations that reduce predation (Werner, 1984). Small-sized species are usually short lived, exhibiting early maturity and high reproductive output (see Begon et al., 1996). According to Hutchinson (1959), small size permits a deeper specialization to small and diversified elements of the environmental mosaic. In particular, small-sized fish species appear to be able to utilize the fine-grain aspects of the environment, being more specialized in terms of habitat use than large species (e.g., Munday and Jones, 1998). This is particularly true in the tropical shallow-water benthic biotopes that offer a complex mosaic of habitat at a fine spatial scale. Overall, small-sized fish species tend to occupy restricted and sheltered habitats and microhabitats not available to the larger taxa (e.g., holes and crevices in reefs, branches of corals, surface of sponges, symbiotic relationships with anemones and echinoderms, and so on; see e.g., Tyler and Böhlke, 1972; Greenfield and Johnson, 1990; Fautin and Allen, 1992; Clarke, 1994; Patton, 1994; Randall et al., 1997). The skeletal configuration of *Pietschellus* led us (Bannikov and Carnevale, 2011) to hypothesize that it was characterized by a benthic lifestyle. A similar lifestyle can be therefore suggested for *Nickcaves*, which exhibits a very similar morphology. The ecological specialization of pietschellid fishes is extremely problematic to define based exclusively on their morphology. However, the overall aspect of these Eocene benthic fishes characterized by a sail-like dorsal fin is in some ways reminiscent of that of certain extant blennioid fishes that use the well-developed dorsal, anal and pelvic fins for flagging or other display behaviour patterns (see Smith et al., 1998).

The comparative osteological analysis of *Nickcaves* confirms the presence of a suite of reductive features (cranial bones not ornamented; absence of ribs, intermuscular bones and supraneurals, reduced number of caudal-fin rays; unbranched median-fin rays) also observed in *Pietschellus* (see Bannikov and Carnevale, 2011), thereby representing some of the distinctive characters defining the new family Pietschellidae. The presence of these reductive features is clearly indicative of the overall structural simplification of certain character complexes in the two pietschellid genera, primarily in the axial skeleton. According to Weitzman and Vari (1988), a diminutive size of less than 25-26 mm SL associated to the presence of reductive morphological features and to an overall tendency to structural simplification are characteristic of miniature fishes. The use of these criteria strongly supports the conclusion than *Nickcaves* and *Pietschellus* are miniature taxa. The anatomical consequences of miniaturization are problematic to quantify. Miniaturized taxa may be dwarfed images of their larger relatives, or may closely resemble an early developmental stage of them (Britz and Kottelat, 2003), or, in many cases, may exhibit one of the various intermediate stages in between these extremes. The presence of reductive features associated with the very small size are often considered as indicative of progenesis, an evolutionary process resulting in paedomorphic phenotypes in which a truncated development with an accelerated maturation produces dwarfed adults characterized by the larval features (see Gould, 1977). Extreme and less extreme cases of developmentally truncated larval-like marine fishes are known primarily among gobioids (e.g., Springer, 1983, 1988; Johnson and Brothers, 1993). Despite the presence of several reductive features, the robust skeletal structure of pietschellid fishes does not exhibit the typical traits of larval-like fishes characterized by progenetic expression (e.g., Springer, 1983; Johnson and Brothers, 1993). Therefore, the osteology of both *Nickcaves* and *Pietschellus* seems to indicate that miniaturization does not always involve the emergence of extreme developmental truncation (see also Johnson and Brothers, 1989). Conversely, these Eocene benthic percomorphs should be regarded as "proportioned dwarfs" (in the sense of Gould, 1971), in which the miniaturization is associated to a general simplification of certain axial skeletal structures. As a final note, it is necessary to take into account that miniaturization is not only associated with reduction of features but also with the emergence of morphological novelties (Hanken, 1993). The sail-like dorsal fin, the spinulose dermal cover and at least some of the reductive characters typical of pietschellid fishes might be also interpreted as morphological novelties, representing some of the final products of miniaturization.

Acknowledgements

We are very grateful to Giuseppe Minciotti, Director of the MCSNV for providing funding for the travel of AFB in 2015 to Verona to engage in this and other studies. We also thank Roberto Zorzin and Anna Vaccari at the MCSNV for their continuing help in facilitating our research on the fishes of Bolca. Thanks are also due to Federica Giudice for the improvement of the English. The research of GC was supported by grants (ex-60% 2013 and 2014) from the Università degli Studi di Torino. AFB was supported by the Russian Foundation for Basic Research, project no. 14-04-00005. The photograph is courtesy of Leonardo Latella (MCSNV).

Table 1. Synopsis of morphometric values of pietschellid taxa. Standard length in mm. All other measurements are as percentage of SL.

	Nickcaves pterygocephalus	*Pietschellus aenigmaticus*
Standard length	16.5	18.0
Head length	28.4	25.9
Maximum body depth	30.0	34.9
Snout length	7.7	10.1
Orbit diameter	7.7	7.7
Mandible length	13.4	12.5
Caudal peduncle depth	10.9	12.8
Predorsal length	16.9	22.9
Predorsal (soft dorsal) length	40.4	46.5
Preanal length	62.3	54.5
Prepelvic length	~37	22.4
Dorsal-fin base length	76.5	72.4
Spinous dorsal-fin base length	23.5	30.6
Soft dorsal-fin base length	51.9	46.8
Anal-fin base length	30.6	31.6
First dorsal-fin spine length	21.0	24.8
Last dorsal-fin spine length	6.2 (fifth spine)	4.0 (sixth spine)
Longest dorsal-fin ray length	~18	24.2
Anal-fin spine length	3.0	4.4
Longest anal-fin ray length	~21	19.5
Longest caudal-fin ray length	~18	26.3

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