

Rapid Communication

Cite this article: Vullo R, Bardet N, Gheerbrant E, and Jalil N-E (2019) Multicuspid tooth morphology in a gigantic Palaeocene pycnodont fish: evolutionary and palaeoecological significance. *Geological Magazine* **156**: 1618–1622.
<https://doi.org/10.1017/S0016756819000736>

Received: 3 April 2019

Revised: 17 May 2019

Accepted: 24 May 2019


First published online: 8 July 2019

Keywords:

Actinopterygii; pycnodontiformes; dentition; trophic specialization; Palaeogene; Morocco

Author for correspondence: Romain Vullo,
 Email: romain.vullo@univ-rennes1.fr

Multicuspid tooth morphology in a gigantic Palaeocene pycnodont fish: evolutionary and palaeoecological significance

Romain Vullo¹ , Nathalie Bardet², Emmanuel Gheerbrant² and Nour-Eddine Jalil^{2,3}

¹Univ Rennes, CNRS, Géosciences Rennes, UMR 6118, 35000 Rennes, France; ²CR2P, UMR 7207, MNHN-CNRS-Sorbonne Université, Muséum National d'Histoire Naturelle, CP38, 75005 Paris, France and ³BioDEcos, Department of Geology, FSSM-UCAM, BP2390, Marrakesh, Morocco

Abstract

A pycnodont premaxilla bearing a large incisiform tooth with an unusual crown morphology is described from the Palaeocene (Thanetian) phosphate deposits of Morocco. This peculiar tooth shows a broad, fan-shaped multicuspid crown with nine cusps, well adapted for benthic macroalgal scraping. This morph, assigned to a new species of *Pycnodus* (*P. multicuspidatus* sp. nov.), emphasizes the phenotypic plasticity of the group and documents an additional trophic specialization among Palaeogene pycnodontiform fishes. In the post-K/Pg boundary marine ecosystem of the Ouled Abdoun Basin, *P. multicuspidatus* sp. nov. may have opportunistically replaced Maastrichtian fish taxa with a similar front dentition and feeding behaviour, such as the putative specialized pycnodontiforms *Stephanodus* and *Hadrodus*.

1. Introduction

Multicuspid teeth are known in various, distantly related groups of both extinct and living fishes and are generally indicative of algivorous/herbivorous diets (e.g. Gibson, 2015; Davis *et al.* 2016). Despite a rich fossil record and a high ecomorphological diversity, no true multicuspid teeth have been clearly reported among pycnodont fishes, a widespread group known from the Upper Triassic to the Eocene. The anterior dentition of pycnodonts usually consists of moncuspid or slightly bifid prehensile teeth, very flattened and fully incisiform in derived taxa (Nursall, 1996; Poyato-Ariza & Wenz, 2002; Kriwet, 2005; Poyato-Ariza, 2005; Poyato-Ariza & Martín-Abad, 2013). Nevertheless, Kriwet (2005: fig. 42e) figured dentary teeth of *Nursallia* with slightly incised crowns. In addition, the possible pycnodontiform genera *Stephanodus* and *Hadrodus* have large, broad incisiform teeth with, respectively, a denticulated occlusal edge (e.g. Zittel, 1888: fig. 310; Cappetta, 1972: pl. 13, figs 1–3) and a bicuspoid crown (e.g. Leidy, 1873: pl. 19, figs 17–20; Bell, 1986: fig. 2.4–6).

The well-known Late Cretaceous (Maastrichtian) and Palaeogene (Danian–Ypresian) phosphate deposits of the Ouled Abdoun Basin (Morocco) have yielded abundant and diverse vertebrate remains, including many marine fish taxa (Arambourg, 1952; Bardet *et al.* 2017). Among them, pycnodont fishes are well represented, with *Phacodus* and *Eoserrasalmimus* in the Maastrichtian, and *Pycnodus* and *Serrasalmimus* in the Palaeogene (Arambourg, 1952; Kriwet, 2005; Vullo *et al.* 2017). In addition, the enigmatic genera *Stephanodus* and *Hadrodus* are two other possible pycnodontiforms present in the Maastrichtian beds of the Ouled Abdoun Basin (Arambourg, 1952, 1964). We describe here two large pycnodontid premaxillae, each with one tooth preserved *in situ*, from the Thanetian of the Ouled Abdoun Basin. Both specimens show a similar incisor-like morphology; however, while the tooth crown of the first specimen (tentatively referred to *Pycnodus* cf. *praecursor*) shows a non-incised occlusal margin, the second specimen is characterized by a multicuspid crown and is assigned to a new species (*Pycnodus multicuspidatus* sp. nov.). These two pycnodont specimens illustrate the evolutionary transition between a typical generalist form and a new, previously undescribed adaptive form. This discovery suggests that the regulatory pathways that govern tooth shape formation and lead to multicuspid teeth in teleostean fishes may also have been present in non-teleost actinopterygians such as pycnodontiforms.

2. Systematic palaeontology

ACTINOPTERYGII Cope, 1887

NEOPTERYGII Regan, 1923

PYCNOTONTIFORMES Berg, 1937

PYCNOTONTIDAE Agassiz, 1833 (*sensu* Nursall, 1996)

Table 1. Measurements of specimens MHNM.KHG229 and MHNM.KHG230

	MHNM.KHG229, left premaxilla of <i>Pycnodus</i> cf. <i>praecursor</i>	MHNM.KHG230, left premaxilla of <i>Pycnodus multicuspidatus</i> sp. nov.
Total height (as preserved) (mm)	50.9	38.1
Tooth width (mm)	15.7	16.6
Tooth height (crown, without tooth neck) (mm)	10.4	10.1
Tooth height (including tooth neck) (mm)	17.8	14.6
Tooth thickness (mm)	6.3	6.2

PYCNODONTINAE Agassiz, 1833 (*sensu* Poyato-Ariza & Wenz, 2002)

Pycnodus cf. *praecursor* Darteville & Casier, 1949

(Fig. 1a–d)

Material. MHNM.KHG229, a left premaxilla with one tooth preserved, housed at the Muséum d'Histoire Naturelle de Marrakech (MHNM).

Locality and horizon. Sidi Daoui area, Ouled Abdoun Basin, Province of Khouribga, Morocco. Upper Phosphorite Bed IIa – base of the Intercalary Bed II/I interval, Thanetian (Palaeocene) in age (Kocsis *et al.* 2014).

Description. MHNM.KHG229 is a nearly complete left premaxilla with one tooth preserved (mesial tooth). A second, lateral tooth, broken at its base, was originally present. The preserved tooth crown is wider than high (see Table 1 for measurements). It is spatulate, typically incisiform in shape, with a markedly convex and asymmetrical occlusal margin in labial view. The occlusal margin is continuous, i.e. not incised. The labial face is convex and shows a dozen slight sub-vertical folds. The lingual face is concave and bears three wear facets. There is a high, well-developed tooth neck. The thick, sub-vertical ascending premaxillary process is broken apically (dorsally). There is no fenestra, but a large mesiolingual olfactory fossa is present; this depression was forming part of the nasal capsule, together with the olfactory fossa of the mesethmoid.

Remarks. Features of the premaxilla (i.e. two teeth originally present, elongated and almost vertical ascending process, large olfactory fossa for the nasal capsule) combined with the typical incisiform shape of the preserved tooth clearly indicate that MHNM.KHG229 belongs to Pycnodontidae (Poyato-Ariza & Wenz, 2002; Kriwet, 2005). The well-developed olfactory fossa is similar in size, shape, and position to the pocket described in the premaxilla of *Hadrodus marshi* (Gregory, 1950: fig. 1a). By its size, MHNM.KHG229 might correspond to the premaxilla of *Pycnodus praecursor*, a large to gigantic nominal species from the Palaeocene of Africa (Angola, Niger) known only from isolated dentitions (Darteville & Casier, 1949; Cappetta, 1972). MHNM.KHG229 is therefore tentatively referred to *Pycnodus* cf. *praecursor*. A large fragmentary prearticular dentition from Palaeocene of Togo, described as *Pycnodus variabilis* var. *togoensis* (Stromer, 1910: fig. 2), might correspond to the same taxon.

It is worth noting that the type species of *Pycnodus* (i.e. *Pycnodus apodus* from the early Eocene Bolca Lagerstätte, Italy), known from complete articulated specimens, is the only well-defined species of the genus (Poyato-Ariza & Wenz, 2002; Poyato-Ariza, 2013; Cawley

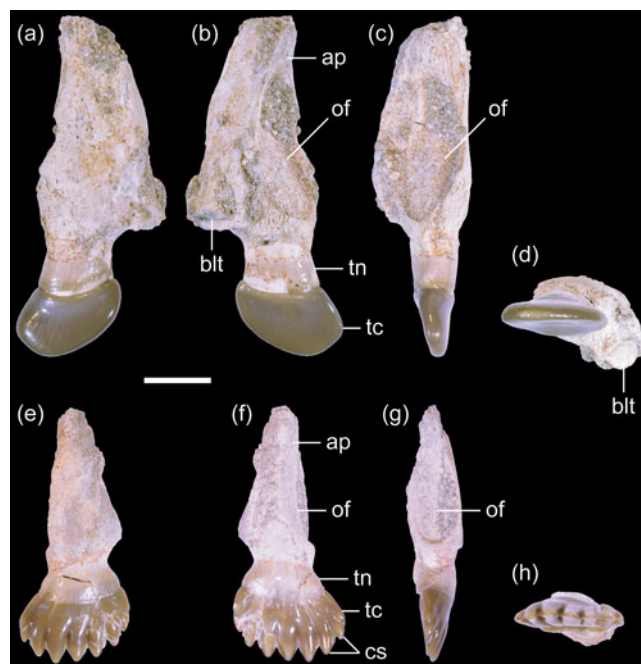


Fig. 1. Left premaxillae of *Pycnodus* cf. *praecursor* (MHNM.KHG229) (a–d) and *P. multicuspidatus* sp. nov. (holotype MHNM.KHG230) (e–h) from the Palaeocene of the Ouled Abdoun Basin, Morocco, in labial (a, e), lingual (b, f), mesial (c, g) and ventral (occlusal) (d, h) views. Abbreviations: ap – ascending process; blt – base of the (missing) lateral tooth; cs – cusps; of – olfactory fossa; tc – tooth crown; tn – tooth neck. Scale bar: 10 mm.

et al. 2018). Most of the numerous Palaeogene nominal species based on isolated dentitions and traditionally referred to the genus *Pycnodus* (e.g. Longbottom, 1984; for a short review, see Cawley *et al.* 2018) need confirmation of their generic placement (Poyato-Ariza, 2013); however, a systematic revision of these tooth-based species is beyond the scope of this paper. Therefore, the two specimens described here are provisionally assigned to *Pycnodus*.

Pycnodus multicuspidatus sp. nov.

(Fig. 1e–h)

Holotype and only known specimen. MHNM.KHG230, a fragmentary left premaxilla with one tooth preserved, housed at the MHNM.

Locality and horizon. Sidi Daoui area, Ouled Abdoun Basin, Province of Khouribga, Morocco. Upper Phosphorite Bed IIa – base of the Intercalary Bed II/I interval, Thanetian (Palaeocene) in age (Kocsis *et al.* 2014).

Diagnosis. Large to gigantic species of *Pycnodus* with incisiform premaxillary teeth characterized by a deeply incised, multicuspoid crown (nine triangular cusps in the mesial tooth).

Description. MHNM.KHG230 is a fragmentary left premaxilla with one tooth preserved (mesial tooth). The lateral part of the bone (originally bearing a second, lateral tooth) is broken and worn. The labiolingually compressed, spatulate tooth crown is wider than high (see Table 1 for measurements). The crown is multicuspoid, with seven well-defined cusps and a pair of poorly defined lateral cusps. The cusps are triangular in shape and equally developed, albeit slightly decreasing in size laterally. The cuspidate occlusal margin is markedly convex in labial view. There is a well-developed, lingually inflated tooth neck. The mesiolingual olfactory fossa can be discerned along the thick, poorly preserved ascending premaxillary process. There is no fenestra.

Remarks. With the exception of the well-preserved tooth, MHNM.KHG230 is less complete and more abraded than

MHNM.KHG229. Although MHNM.KHG230 clearly differs from MHNM.KHG229 by the multicuspidation of the preserved tooth crown, both specimens are similar in size and gross morphology (see Fig. 1; Table 1). Moreover, MHNM.KHG230 and MHNM.KHG229 share some characters (i.e. asymmetry and proportions of the crown, development of the tooth neck, thickness of the ascending premaxillary process, shape of the olfactory fossa; see Fig. 1), indicating that these two specimens belong to distinct but closely related pycnodontid species.

3. Discussion

3.a. Tooth shape development and evolution

Several studies have argued that only simple genetic changes were required for the rise of multicuspid teeth in the evolution of fishes (Streelman *et al.* 2003; Streelman & Albertson, 2006; Jackman *et al.* 2013). In their study on living African cichlids, Albertson *et al.* (2003a) found that interspecific differences in cusp number are determined by approximately one gene, suggesting that this character has the potential to respond to selection extremely quickly. A similar simple genetic basis of evolutionary novelty in the front dentition of pycnodontids can be assumed here, as suggested by the overall resemblance between specimens MHNM.KHG229 and MHNM.KHG230 as well as by the co-occurrence of the ancestral (MHNM.KHG229) and derived (MHNM.KHG230) morphotypes in the Thanetian strata of the Ouled Abdoun Basin. The peculiar tooth morphotype MHNM.KHG230 appears to be directly derived from the plesiomorphic monocuspid tooth morphotype MHNM.KHG229, and this may represent a case of punctuated equilibrium, with speciation between *Pycnodus* cf. *praecursor* and *Pycnodus multicuspidatus* sp. nov. by 'budding cladogenesis' (Wagner, 2000).

Whether multicuspid teeth have arisen during fish evolution either by concrescence, or by differentiation of tooth germs, is still debated (Trapani *et al.* 2005; Jernvall & Thesleff, 2012; Jackman *et al.* 2013). However, this mainly concerns teleost taxa with numerous minute, closely spaced teeth (Trapani *et al.* 2005; Jackman *et al.* 2013). In the fossil record, the oldest evidence of similar increase in cusp number (from mono- or bicuspid to multicuspid small incisiform teeth) is known between two Late Triassic non-teleostean neopterygians, i.e. the dapediids *Sargodon* (Tintori, 1983, 1998) and *Hemicalypterus* (Gibson, 2015, 2016).

In pycnodontiform fishes, the number of premaxillary and dentary teeth never exceeds three and five, respectively (Poyato-Ariza & Wenz, 2002). In *Pycnodus* and other derived pycnodontids, these bones bear two monocuspid incisiform teeth (Nursall, 1996; Poyato-Ariza & Wenz, 2002), except *Polazzodus*, *Sylvienodus* and *Tergestia*, which have a premaxilla bearing a single tooth (Capasso, 2000; Poyato-Ariza, 2010, 2013). Therefore, it is obvious that the nine-cusped tooth of *Pycnodus multicuspidatus* sp. nov. described here arose from complex folding of a single tooth germ (Differentiation Theory) rather than from early fusion of several tooth germs (Concrescence Theory). This interpretation is clearly supported by the equally sized premaxillary tooth MHNM.KHG229, which shows a similar overall morphology and differs only by its simple, non-incised crown contour (ancestral condition).

During the development of mammalian teeth, the folding of the enamel epithelium leading to the formation of multicuspid crowns is regulated by signalling centres called secondary enamel knots (Jernvall *et al.* 1994; Vaatokari *et al.* 1996). The presence of enamel knot-like signalling centres controlling the cusp number in

teleostean fishes has been suggested by several authors (Streelman *et al.* 2003; Fraser *et al.* 2008, 2013; Jernvall & Thesleff, 2012; Atukorala & Franz-Odenaal, 2014; Debiais-Thibaud *et al.* 2015). Recently, Smith *et al.* (2015) showed that the development genes *shh* and *bmp4* operating in the dentition of teleosts are similarly expressed in the dentition of the basal actinopterygian *Polyodon*, thus extending this conserved developmental pattern within the Actinopterygii. Therefore, the evolutionary transition observed between the monocuspid pycnodont tooth MHNM.KHG229 and the multicuspid pycnodont tooth MHNM.KHG230 may be explained by minor genetic changes leading to the formation of secondary enamel knot-like structures in the derived form, as for the difference in cusp number observed today between the adult teeth of two closely related species of cichlid fishes, i.e. *Metriaclima zebra* and *Labeotropheus fuelleborni* (Albertson *et al.* 2003a,b; Streelman *et al.* 2003). The symmetrical formation of four lateral cusps on each side of the central cusp of MHNM.KHG230 could be compared with that of the tricuspid teeth of *Labeotropheus fuelleborni*, which is due to the uniform development of secondary enamel knots (and thus lateral cusps) on both the mesial and distal sides of the central cusp (Streelman *et al.* 2003).

3.b. Feeding habits and palaeoecological implications

The large size of MHNM.KHG230 contrasts with the diminutive size characterizing the multicuspid teeth of many modern fish taxa (Jernvall & Thesleff, 2012). However, the dental morphology observed in MHNM.KHG230 is strikingly similar to that observed in modern algivorous/herbivorous forms, such as the characids *Hemigrammus*, *Hyphessobrycon* and *Phycocharax* (Lima *et al.* 2009; Ohara *et al.* 2017a, b), the acanthurid *Acanthurus nigrofuscus* (Fishelson & Delarea, 2013), the sparid *Crenidens* (Fishelson *et al.* 2014), the terapontid *Helotes* (Davis *et al.* 2016) and the cichlid *Labeotropheus* (Fraser *et al.* 2008). Interestingly, a similar tooth morphology is also found in various groups of herbivorous reptiles, such as pareiasaurs (e.g. Jalil & Janvier, 2005; Tsuji, 2013), ankylosaurian dinosaurs (Ósi *et al.* 2017), the extinct crocodyliform *Simosuchus* (Kley *et al.* 2010) and the algae-eating Galápagos marine iguana *Amblyrhynchus* (Melstrom, 2017). Among mammals, similar fan-shaped multicuspid incisors are present in an extinct macroselidid tentatively referred to *Miorhynchocoyon gariepenensis* (Senut, 2003) and in some hyracoids (De Blieux & Simons, 2002).

Although the vomerine and prearticular dentitions of *Pycnodus multicuspidatus* sp. nov. still remain unknown and may have had a crushing function, all the aforementioned morphological similarities clearly indicate that at least one pycnodontine species has evolved an anterior dentition well suited for benthic macroalgal scraping. *Pycnodus multicuspidatus* sp. nov. was likely able to feed on the heavily calcified macroalga *Halimeda*, a chlorophyte abounding in the shallow marine ramp facies of the Palaeogene formations of the central High Atlas (Dragastan & Herbig, 2007).

The multicuspid incisiform teeth of *Pycnodus multicuspidatus* sp. nov. are rather similar to those of the front dentition of *Stephanodus splendens* and *Hadrodus belinkoi*, two putative pycnodontiform taxa occurring in the underlying Maastrichtian strata of the Ouled Abdoun Basin (Arambourg, 1952, 1964). However, the incisiform teeth of *Stephanodus* and *Hadrodus* can be easily distinguished from those of *Pycnodus multicuspidatus* sp. nov. The incisiform teeth of *Stephanodus* have a lower crown with a recitilinear or slightly concave occlusal margin showing numerous (up to 14), smaller cusps (Zittel, 1888: fig. 310; White, 1934: pl. 10,

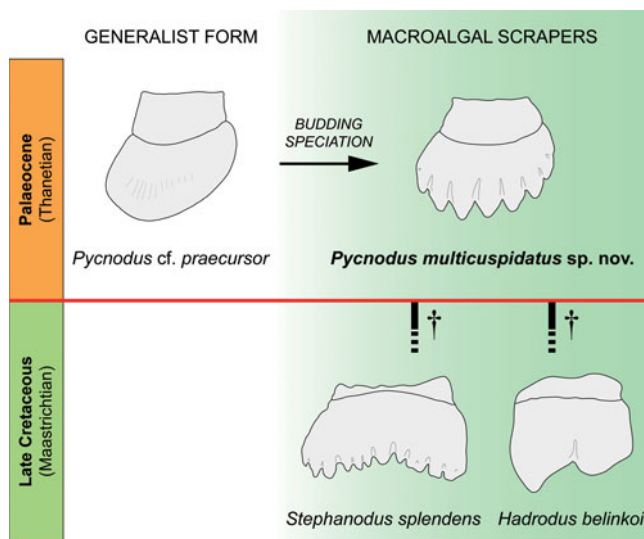



Fig. 2. End-Cretaceous extinction of the macroalgal scrapers *Stephanodus* and *Hadrodus* (?Pycnodontiformes) followed by opportunistic refilling of vacated ecospace by the Palaeocene pycnodontid *Pycnodus multicuspidatus* sp. nov. Line drawings of *Stephanodus* and *Hadrodus* incisiform teeth after Tabaste (1963: pl. 13, fig. 3) and Arambourg (1964: fig. 1a), respectively. Not to scale.

fig. 11; Tabaste, 1963: pl. 13, fig. 3; Cappetta, 1972: pl. 13, figs 1–3). The incisiform teeth of *Hadrodus* are usually bifid, with a crown showing two well-separated and well-developed cusps sometimes flanked by one or two additional cusps in dentary teeth (Arambourg, 1964; Bell, 1986). In pycnodont fishes, premaxillary and dentary teeth may have distinct crown morphologies (e.g. Szabó *et al.* 2016). As suggested by the dignathic heterodonty observed between premaxillary and dentary teeth of *Hadrodus hewletti* (Bell, 1986: fig. 2.4–6), teeth of *Hadrodus belinkoi* and *Stephanodus splendens* may correspond, respectively, to premaxillary and dentary teeth of the same species (with large hook-shaped branchial teeth originally described under the name *Ancistrodon libycus*; Dames, 1883; Arambourg, 1952). A complete systematic revision of this group of putative pycnodonts is clearly needed but is beyond the scope of this paper; therefore, pending further investigation, *Hadrodus belinkoi* and *Stephanodus splendens* are considered here as two distinct taxa.

In the Palaeocene epicontinental seas of Morocco, *Pycnodus multicuspidatus* sp. nov. may have occupied, by opportunistic replacement, the trophic niche filled by *Stephanodus* and *Hadrodus* before the K/Pg boundary and vacated by the end-Cretaceous extinction of these two taxa (Fig. 2). This case of parallelism emphasizes the high morphological plasticity of pycnodont fishes and their ability to adapt to sudden palaeoenvironmental and palaeoecological changes (Poyato-Ariza, 2005). Pycnodont fishes appear to have been trophically diverse in the Ouled Abdoun Basin ecosystem during the Palaeogene, with generalist, shell-crushing forms (*Pycnodus* spp., including *P. cf. praecursor*), a macroalgal scraper (*Pycnodus multicuspidatus* sp. nov.) and a predatory, flesh-eating form (*Serrasalmimus secans*).

Author ORCIDs.  Romain Vullo, 0000-0002-1900-9991

Acknowledgements. We would like to thank Patrick Catto for kindly donating the holotype of the new species described in this paper, and Damien Gendry for his help with the photographs of the specimens. Márton Szabó and an anonymous reviewer provided constructive comments that improved the manuscript. There are no sources of financial support.

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