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The dentition of Omalodontiformes, the order of unusual Devonian stem-chondrichthyans

La dentición de los Omalodontiformes, el inusual orden de condrictios troncales del Devónico

Michał GINTER

Abstract: The early chondrichthyan order Omalodontiformes from the late Early Devonian through to the Late Devonian is characterised by specific teeth. Unlike in most Devonian sharks, their bases are directed labially or are reduced and devoid of labial or lingual extensions. In this paper the complex history of investigation on the dermal skeleton of omalodontiforms is presented and the validity of the established taxa is revised. The dentition of an Emsian representative of this group, known from a single articulated specimen (NMBG 10127) and several isolated fin spines from Canada and previously, probably incorrectly, attributed to *Doliodus*, is distinctly heterodont. The nature of this heterodonty suggests that the two omalodontiform tooth-based genera described originally from the Middle–Upper Devonian Aztec Siltstone (Antarctica), *viz*. *Portalodus* and *Anareodus*, are in fact congeneric as their teeth represent different parts of the same jaw. Because the teeth of the Canadian specimen differ in important aspects from those of typical *Doliodus* and are generally similar to those of *Portalodus*, it probably should be placed in a new genus. Also, the validity of the distinction between *Portalodus bradshawae* and *P. mannoliniae* is considered questionable.

Resumen: El orden de los condrictios primitivos de los Omalodontiformes, Devónico Inferior tardío a Devónico Superior, se caracteriza por su específica morfología dental. A diferencia de la mayoría de tiburones devónicos, sus bases se desarrollan labialmente, o por el contrario, son bases muy reducidas que carecen de proyecciones labiales o linguales. En este artículo, se presenta la compleja historia de la investigación sobre el esqueleto dérmico de los Omalodontiformes y se revisa la validez de los taxones establecidos. La dentición de un representante emsiense de este grupo, conocido por un único espécimen articulado (NMBG 10127) y varias espinas de aletas aisladas de Canadá, fue atribuido probablemente de forma incorrecta a *Doliodus*. Pero esta dentición es claramente heterodonta, lo que sugiere que los dos géneros basados en dientes omalodontiformes descritos originalmente en el Devónico Medio–Superior en Aztec Siltstone (Antártida), *Portalodus* y *Anareodus*, son de hecho sinónimos, ya que sus dientes representan diferentes partes de la misma mandíbula. Dado que los dientes del espécimen canadiense difieren en aspectos importantes de los típicos de *Doliodus* y son, en general, similares a los de *Portalodus*, probablemente deberían incluirse en un nuevo género. Asimismo, se cuestiona la validez de la distinción entre *Portalodus bradshawae* y *P. mannoliniae*.

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INTRODUCTION

The dentition of the majority of Devonian chondrichthyans is composed of teeth in which the bases form lingual extensions (Ginter *et al*., 2010). Such extensions of subsequent teeth in a tooth family overlap and in this way individual teeth are protected from tearing off by struggling prey. However, there is one order of stem chondrichthyans, the Omalodontiformes Turner, 1997, in which the teeth have broad labial (instead of lingual) basal extensions (Ginter, 2004) or, in posterolateral positions, are devoid of extensions at all (Fig. 1). Instead of mutual protection of subsequent teeth by overlapping bases, the interconnection between them was apparently strengthened by the presence of a highly curved band on which they were situated (Maisey *et al*., 2014).
The other difference between the omalodontiforms and most of primitive chondrichthyans is the presence of pectoral and pelvic fin spines, at least in one genus (Maisey *et al*., 2017; a form intermediate between *Doliodus* and *Portalodus*, see the discussion below). This feature makes them look closer, in spite of their generally 'shark-like' characteristics, to the conventionally understood acanthodians. It was proposed earlier (Susan Turner, pers. comm.; first published mention in

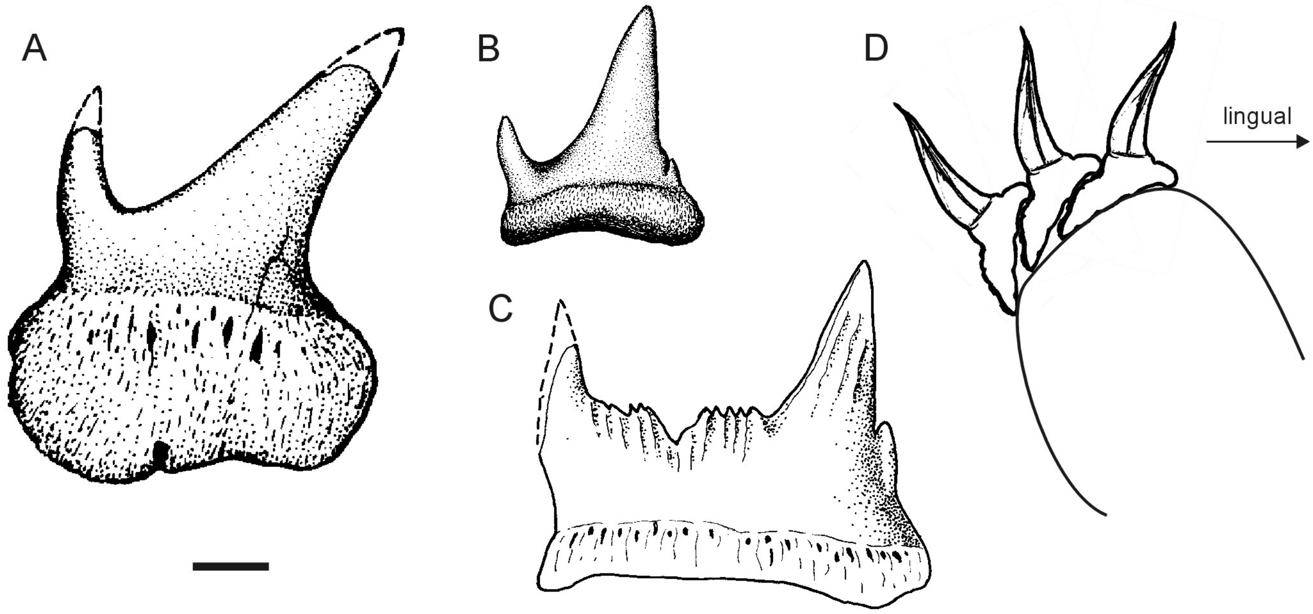

Figure 1. **A**–**C,** Omalodontiform teeth from the Aztec Siltstone, Givetian, Portal Mountains, Antarctica; **A,** *Portalodus bradshawae* Long & Young, 1995, CPC 21224, labial view, with a broad labial extension of the base; probably a lateral tooth; **B,** *Anareodus statei* Long & Young, 1995, WAM 94.2.9, labial view, without a basal extension; probably a posterolateral tooth of *P. bradshawae*; **C,** *Aztecodus harmsenae* Long & Young, 1995, CPC 21229, labial view; **D,** fragment of a hypothetical tooth family to show a typical omalodont overlapping of bases. A, B, from Long and Young (1995); C, from Young (1982); D, outlines of the teeth based on Turner (2004); scale bar = 2 mm.

Wilson *et al*., 2007) that certain fin spines, the asymmetry of which suggested their pectoral position, belonged to *Antarctilamna*, a Devonian shark with a typical diplodont dentition. It seems likely that at least some of such isolated spines, formerly attributed to *Antarctilamna*, may in fact have represented omalodontiforms.

The taxonomic history of the Omalodontiformes is rather complicated, as usually is the case of the groups of vertebrates initially described based on isolated skeletal remains, such as teeth, scales or fin spines. The first tooth of an omalodontiform (currently known as *Doliodus* Traquair, 1893) was described by Woodward (1892a), but the first and thus far the only articulated specimen representing this group was published at the beginning of this millennium (Miller *et al*., 2003). The latter discovery shed much light on the anatomy of omalodontiforms, but added more questions than answers to their taxonomy and phylogeny.

In this paper, the major steps in the history of research on this group are analysed and certain new, considered necessary, taxonomic solutions are proposed.

Institutional abbreviations. AEU, Islamic Azad University, Esfahan, Iran; **AMNH,** American Museum of Natural History, New York, USA; **CPC,** Commonwealth Palaeontological Collection, Canberra, Australia; **CSGN,** Central Siberian Geological Museum, Novosibirsk, Russia; **MB,** Museum für Naturkunde, Berlin, Germany; **MCZ,** Museum of Comparative Zoology, Cambridge, USA; **NHMUK,** The Natural History Museum, London, UK; **NMBG,** New Brunswick Museum, Saint John, Canada; **NYSM,** New York State Museum, Albany, USA; **OSU,** Ohio State University, Columbus, USA; **RSM,** Royal Scottish Museum, Edinburgh, UK; **WAM,** Western Australian Museum, Perth, Australia.

THE HISTORY OF INVESTIGATION ON THE DERMAL SKELETON OF OMALODONTIFORMES

Omalodus

The first teeth which were later attributed to the genus *Omalodus* had been described by Hussakof and Bryant (1918; Fig. 2A). They were found in the so-called Conodont Bed, of the late Givetian to early Frasnian age, North Evans Limestone, Eighteen Mile Creek, New York, USA, and assigned as *Dittodus grabaui*. Then, Wells (1944) described and illustrated two teeth from the Givetian of Kentucky, USA (Fig. 2B), similar to those from the Conodont Bed. He did notice that similarity (Wells, 1944, p. 42–43), but nevertheless he named his newly described teeth *Phoebodus*? *bryanti*. On the one hand, he acknowledged that they were characterised by a phoebodont crown, with three major cusps and a few intermediate cusplets between them (see Ginter *et al*., 2010), but on the other, he saw that “the cusps seem to be inclined strongly forward [= labially] rather than backwards [= lingually] as usual” and that was the reason of the question mark in the name. Of course, as we know now, not the cusps were inclined outward (which would be absurd from the functional point of view), but the base had a labial extension instead of a lingual one.

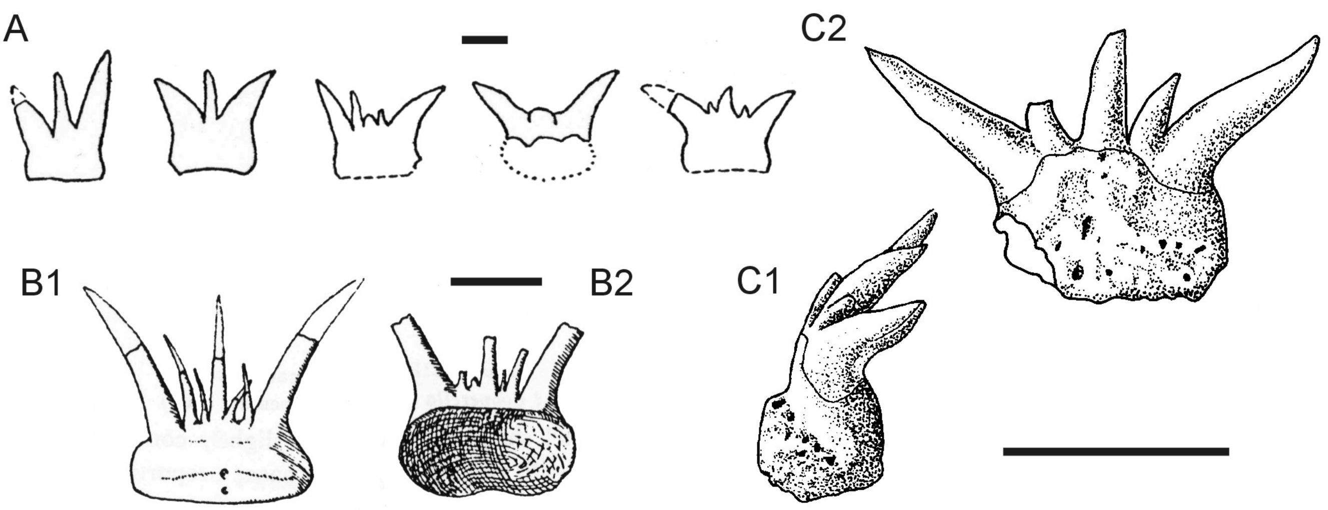

Figure 2. *Omalodus grabaui* (Hussakof & Bryant, 1918). **A,** Outline sketches of teeth from the type collection, North Evans Limestone, late Givetian to early Frasnian, Eighteen Mile Creek, New York, USA; **B,** tooth OSU 19476 (holotype of *Phoebodus*? *bryanti sensu* Wells, 1944) from the Kiddville Bone Bed of Boyle Limestone Fm., Givetian, Kentucky, USA; in labial (**B1**) and lingual (**B2**) views; **C,** tooth MB.f.8620 (holotype of *Omalodus schultzei sensu* Hampe *et al*., 2004), middle Givetian, El Atrous, Morocco; in lateral (**C1**) and labial (**C2**) views. A, from Hussakof and Bryant (1918), B, from Wells (1944), C, from Hampe *et al*. (2004); scale bars = 1 mm.

For the first time this feature was correctly presented by Ginter and Ivanov (1992, p. 62) based on the omalodont material from the upper Givetian of Kuznetsk Basin, Russia. Because of such an important difference in the structure of the base they proposed to separate such teeth from *Phoebodus* and to translate them to a new genus, *Omalodus*. However, because of the phoebodont style of the crown, they decided to retain *Omalodus*, together with *Phoebodus* and *Thrinacodus*, in the family Phoebodontidae. Ginter and Ivanov (1992) had no possibility to examine Hussakof and Bryant's material at the time of their publication and did not know how closely the teeth from the Conodont Bed resembled those from the other collections. Therefore, they proposed the combination *Omalodus bryanti* (Wells, 1944) for all the teeth of this type published by then (*e.g.*, Wells, 1944, pl. 3, figs. 24–27; Gross, 1973, pl. 34, fig. 23, pl. 35, fig. 8; Ginter & Ivanov, 1992, fig. 3I–3M).

Finally, Hussakof and Bryant's material in Buffalo was re-examined by Turner (1997). In her crucial paper, she separated the omalodont teeth from those of other chondrichthyans present in the Conodont Bed samples (*e.g.*, *Wellerodus* and *Phoebodus*), noted that they differ from "*Omalodus bryanti*" "in only small details" (Turner, 1997, p. 111), and proposed a new combination *Omalodus grabaui* (Hussakof & Bryant, 1918). She also erected a new order, Omalodontida (later renamed as Omalodontiformes), but did not establish any family for *Omalodus*. Only a few years later, Ginter *et al*. (2008) published teeth of *O. grabaui* from Givetian *varcus* Zone of the Renanué section in the Aragonian Pyrenees, Spain, and proposed a family name, Omalodontidae, for *Omalodus*, *Portalodus* and *Doliodus*. Hampe *et al*. (2004) named a few omalodont teeth from the Givetian of El Atrous, Morocco, "*Omalodus schultzei*" (Fig. 2C), but their morphology lies within the spectrum of *O. grabaui*, so it seems that at the moment *Omalodus* is a monotypic genus (Ginter *et al*., 2010).

Generally, the dentition of *Omalodus* is relatively homodont. The teeth are small, the maximum size does not exceed 3 mm. The tooth crowns are of phoebodont type, with the median cusp often slightly smaller than the main lateral cusps. Several intermediate cusplets, sometimes asymmetrically placed (unlike in *Phoebodus*), can occur. In many cases these cusplets rise directly from the sides of the main cusps. All the cusps are slender, smooth and rounded in cross section. The base is relatively thin, labially convex and concave lingually. It is directed labially and forms an obtuse angle with the crown. Since *Omalodus* is known only from dispersed teeth, it seems likely that a permanent, mineralised connection between adjacent tooth bases did not exist.

Teeth of *Omalodus* are widely distributed in the Givetian of Northern Hemisphere. It is known from eastern USA, Morocco, Spain, Poland and Russia (Ginter *et al*., 2010).

Doliodus

In a short paper published in Geological Magazine on the fish fauna from Lower Devonian (Emsian) Atholville Beds of the area of Campbellton, New Brunswick, Canada, Woodward (1892a) described and illustrated with a drawing a diplodont tooth with a partial base and called it *Diplodus problematicus*. The tooth (Fig. 3A; see also Burrow & Desbiens, 2023, fig. 1) had two lateral main cusps unequal in size and a much smaller and thinner intermediate, median cusp. A year later, Traquair (1893), based on a much larger collection of teeth from the same locality, proposed for them and

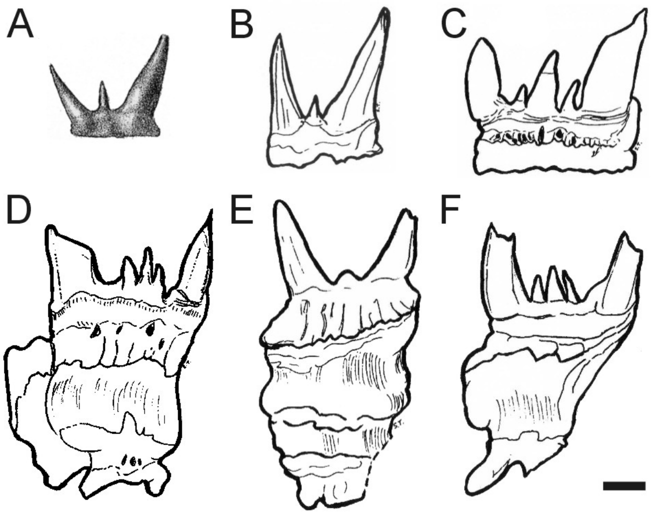

Figure 3. Teeth and tooth families of *Doliodus problematicus* (Woodward, 1892a) from the Emsian, Atholville Beds, Campbellton Fm., Atholville, New Brunswick, Canada. **A,** Holotype, NHMUK P.6540, labial view, from Woodward (1892a); **B**–**F,** Traquair's specimens, from Turner (2004); **B,** RSM1897.51.44.1; **C,** RSM1897.51.47; **D,** RSM1897.51.54; **E,** MCZ 12097; **F,** RSM1897.51.45; scale bar = 1 mm, A not to scale.

Woodward's specimen a new generic name, *Doliodus*, because he saw important differences between the Canadian material and the xenacanthiform teeth described by Agassiz (1837) under the name of *Diplodus*. Traquair (1893, p. 10) noted that the tooth base of *Doliodus* was "a broad thin plate, convex anteriorly [= labially] and above, concave posteriorly [= lingually] and below". Although he did not illustrate his specimens, his description suggested that the base had a labial direction. This was confirmed by Turner (2004) who re-examined Traquair's collection in Edinburgh and provided sketch drawings and photographs of several teeth from that material. She also proposed to place *Doliodus problematicus* (Woodward, 1892a), because of the form of the base, in the order Omalodontiformes, within the Chondrichthyes, despite the earlier suggestions of its acanthodian affinity (see Burrow *et al*., 2017; Burrow, 2021). Actually, she had already signalled the basal similarity of *Doliodus* and *Omalodus*, in her paper on the material from the Conodont Bed in New York (see above; Turner, 1997).

The teeth of *Doliodus* from Traquair's collection (Fig. 3B–3F) have two lateral main cusps usually somewhat unequal in size and, which is important, smaller intermediate cusplets (from 1 to 4) are always present. The bases in a tooth family (composed of up to four teeth) are connected by a curved phosphatised tissue (Fig. 3D–3F) or, according to Burrow and Desbiens (2023), by a curved bony plate. The tooth width is usually between 2 and 5 mm. Similar teeth and tooth-whorls were reported by Burrow and Desbiens (2023) from the Early Devonian of the Gaspé Peninsula, Quebec, Canada.

In addition to the teeth mentioned above, the Lower Devonian at Campbellton yielded an articulated specimen (NBMG 10127) of a chondrichthyan, the anterior portion of a skeleton, with an almost intact dentition (Maisey *et al*., 2014), a set of paired ventral spines (pectoral, pre-pectoral and probable pre-pelvic, Maisey *et al*., 2017; Burrow *et al*., 2017) and remnants of cartilaginous elements. From the very start after its discovery (Miller *et al*., 2003) the specimen was referred to as *Doliodus problematicus*, because of the superficial similarity of the teeth, the structure of tooth whorls, and the locality and horizon in which it was found. However, when the computer tomography was applied to the jaw region and the detailed morphology of the teeth was revealed (Maisey *et al*., 2014; Fig. 4), the situation became less clear. It is certain that the crowns are diplodont, that the main cusps are in most cases, except in the most anterior tooth families, of different sizes; and that most probably the teeth sit on a common curved, phosphatised membrane or some other curved basal plate (Maisey *et al*., 2014, fig. 3). However, two contradicting interpretations as to the results of the ct-scan analysis occur in the literature. The first, presented by Ginter (2022), directly based on the illustrations of the dentition of NBMG 10127 provided by Maisey *et al*. (2014), states that these illustrations are generally correct. If so, it turns out that none of the teeth displays minor, intermediate cusplets, the presence of which is a common feature of all isolated teeth of *D. problematicus* from Campbellton; and that in most cases, except the posterolateral region, the tooth bases are directed labially and overlap (Figs. 4, 6D).

The second interpretation, presented by Burrow and Desbiens (2023, this volume) and supported by Susan Turner (pers. comm., 2022-23) states that the ct-scan images presented by Maisey *et al*. (2014) are incorrect to some extent; that there is no tooth overlap, as all the teeth lack basal extensions and are separated by a thin bony basal plate (and are not just sitting on a phosphatised membrane); and that the tooth crowns are digitally smoothed and that is why the intermediate cusplets are invisible "but visual examination of the specimen indicates that most teeth do have intermediate cusps" (Burrow & Desbiens, 2023, p. 6–7). Unfortunately, the sketch drawing made by Susan Turner and published by Burrow and Desbiens (2023, fig. 3B) as a support for their opinion is rather unconvincing. On the other hand, the scan illustrations provided by Maisey *et al*. (2014; see also Burrow & Desbiens, 2023, fig. 3C) look very natural and it is hard to believe in a serious flaw in the case of so many analysed and illustrated teeth. It is certain that higher resolution scans of the teeth on the articulated fish are necessary to finally resolve this issue, but at the moment the available literature is on the side of the first interpretation and, because of that, in the following descriptions and discussions this interpretation will be adopted.

In the dentition of NBMG 10127 there are three morphotypes of teeth: anterior (three first tooth families

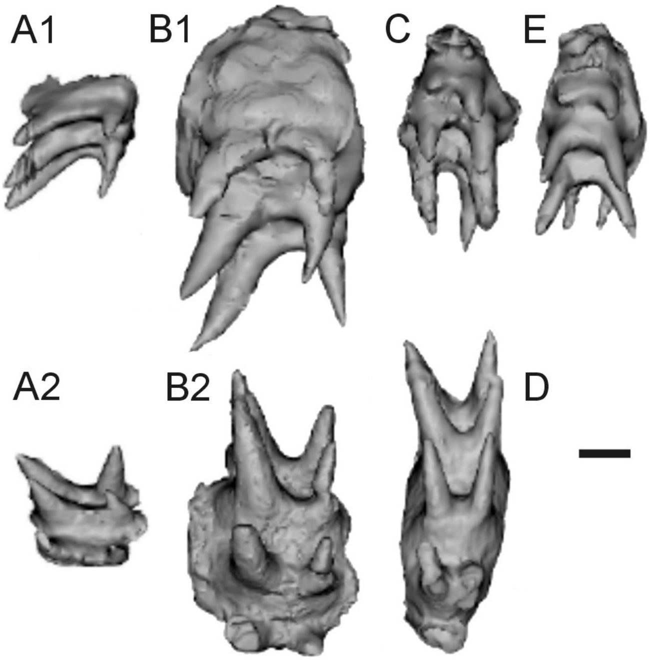

Figure 4. Selected tooth families from the dentition of the articulated specimen of *Portalodus*? *latispinosus* (Whiteaves, 1881) (= *Doliodus problematicus sensu* Miller *et al*., 2003 and Maisey *et al*., 2014), NMBG 10127, from the Emsian, Atholville Beds, Campbellton Fm., Atholville, New Brunswick, Canada. **A,** Posterolateral teeth; **A1,** UR 10; **A2,** LR10; **B,** Lateral teeth; **B1,** UR5, **B2,** LR5; **C,** anterior teeth, UR1; **D,** anterior teeth, LL1; **E,** mesial teeth, UM. Symbols of tooth families: **UR,** upper right; **LR,** lower right; **LL,** lower left; **UM,** upper mesial. From Maisey *et al*. (2014); scale bar = 1 mm.

on each upper jaw ramus, three first tooth families on each lower jaw ramus and an unpaired mesial tooth family on the lower jaw); lateral (families 4 to 9 on each jaw ramus); and posterolateral (families 10 to 12 or 14) (Maisey *et al*., 2014, fig. 4). The anterior teeth (Fig. 4C–4E) are small, virtually symmetrical, their two cusps are only slightly divergent, and they possess a labial extension of the base. The lateral teeth (Fig. 4B) are larger, almost twice as large as the anterior ones, their cusps clearly differ in size (the distal cusp is larger) and the labial extension of the base is present. The posterolateral teeth (Fig. 4A) are again smaller, the cusps are of different size and inclined posteriorly, and they are devoid of any basal extension.

The study on the spines of NBMG 10127 and comparison with older, isolated specimens led Burrow *et al*. (2017) to rename the specimen as *Doliodus latispinosus* (Whiteaves, 1881). The reason for that was the resemblance of the pectoral fin spines of NBMG 10127 to isolated fin spines also from Atholville Beds originally called *Ctenacanthus latispinosus* by Whiteaves (1881) and attributed by him to chondrichthyans. For a long time, since the re-study of these spines by Woodward (1889, 1892b) they were considered to belong to climatiid acanthodians and usually referred to as *Climatius latispinosus* (*e.g.*, Burrow *et al*., 2008; for the long taxonomic story on this subject see Burrow *et al*., 2017). As said above, the latter authors proposed a new combination, *D. latispinosus*, and stated that although the specimen NBMG 10127 “shares numerous endoskeletal features with many other Palaeozoic shark-like fishes in its cranium, jaws, and pectoral region, as well as in its squamation and teeth (...) [it] also possessed climatiid acanthodian type layout of paired pectoral fin spines, prepectoral spines, and prepelvic spines” (Burrow *et al*., 2017, p. 1252). Maisey *et al*. (2019, 2021) adopted this nomenclatural revision and the idea that NBMG 10127 is a transitional fossil between “conventionally defined acanthodians” and “conventionally defined chondrichthyans”.

Siberiodus and *Manberodus*

After the establishment of the Order Omalodontiformes, several tooth-based taxa were placed in it with a greater or lesser certainty. Ivanov and Rodina (2004) described a few asymmetrical, tri- to pentacuspid teeth from the Famennian of Kuznetsk Basin, Russia, under the name of *Siberiodus mirabilis* (Fig. 5A, 5B). The lateral main cusps are of different size, rounded in cross section. The intermediate cusplets (one or three) are much smaller. The base is bar-like with a rather short labial extension. Interestingly, the crown looks very similar to that observed in Traquair’s isolated teeth of *Doliodus problematicus* (compare Fig. 5A and Fig. 3B, Fig. 5B and Fig. 3D). There is a difference in size of the labial basal extension between *D. problematicus* and *S. mirabilis*, as well as a great time difference between their occurrences, but otherwise these two taxa could be synonymised.

Siberiodus was also found in the Famennian of Chariseh section, central Iran (Hairapetian & Ginter, 2009). From the same section, but from its Frasnian part, yet another probable omalodontiform, *Manberodus fortis*, was recovered (Hairapetian *et al*., 2008). Its teeth are more compact than those of *Siberiodus*, with three thick cusps. The lateral cusps somewhat differ in size; the middle cusp is evidently smaller. The labial extension of the base, if present at all, is very short. Among more than 100 teeth extracted from the section, only one (Hairapetian *et al*., 2008, fig. 2E) displayed two intermediate cusplets. Thus far, the geographic range of this species is restricted to the type area.

Portalodus and other omalodonts from Antarctica

At the beginning of 1980s, Gavin Young described remains of a few chondrichthyans from Givetian Aztec Siltstone of south Victoria Land, Antarctica (Young, 1982). Among them, he illustrated two unusual forms which he referred to as *Xenacanthus* sp. and *Mcmurdodus*? cf. *featherensis*. The former was recognised as a xenacanthiform because of its diplodont crown; its cusps are divergent and unequal in size (Fig. 1A), but this also is observed in certain xenacanths, such as *Dicentrodus* or *Lebachacanthus* (see, *e.g.*, Ginter

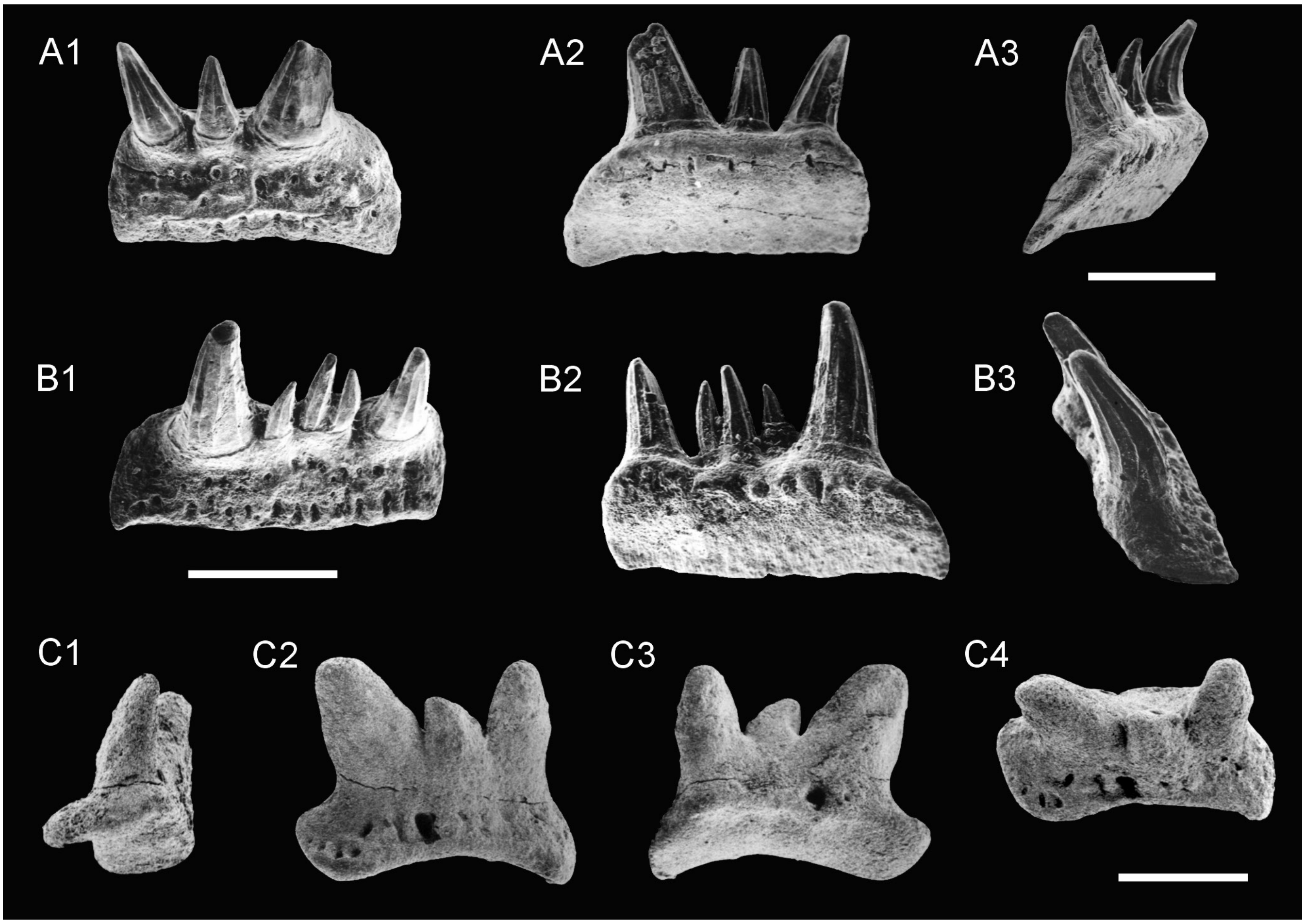

Figure 5. Teeth of *Siberiodus* and *Manberodus*. **A, B,** *Siberiodus mirabilis* Ivanov & Rodina, 2004, Famennian, Kuznetsk Basin, Russia; **A,** CSGN 838/1, in oral/labial (**A1**), aboral/lingual (**A2**) and lateral (**A3**) views; **B,** pentacuspid specimen (CSGN 838/2), in oral/lingual (**B1**), aboral/labial (**B2**) and lateral (**B3**) views; **C,** *Manberodus fortis* Hairapetian & Ginter, 2008 in Hairapetian *et al.* (2008), holotype, AEU 591, in lateral (**C1**), labial (**C2**), lingual (**C3**) and oral (**C4**) views, Frasnian, Chahriseh, central Iran. A–F, from Ivanov & Rodina (2004); J–M, from Hairapetian *et al.* (2008); scale bars = 0.5 mm.

et al., 2010, figs. 38, 40). However, the base of "*Xenacanthus* sp." is a broad flap, directed labially and downward, typically of omalodontiforms, and not xenacanthiforms or other common Devonian sharks with primitive, lingually directed bases. This feature went unnoticed at that time by Young who incorrectly identified sides of the teeth (Young, 1982, fig. 3E–3G), similarly to Wells (1944) in the case of *Omalodus*, despite the evident opposite directions of the base and the curvature of the cusps (Young, 1982, pl. 89, fig. 2). The teeth of "*Mcmurdodus*? cf. *featherensis*" (Fig. 1C; only one tooth was originally found), although also diplodont, are different. The two cusps are widely spaced and there is a kind of crenulation between them. The base is subrectangular and devoid of any extensions. Young's reference to *Mcmurdodus* White, 1968, a strange Devonian shark with neoselachian-like teeth, was only tentative and expressed the unusual nature of the newly found tooth. The teeth of both taxa mentioned in this section are relatively large, reaching almost 10 mm in the largest dimension.

Thirteen years later, Long and Young (1995) revised Young's (1982) identifications based on a much larger Antarctic material. They proposed new names for "*Xenacanthus* sp." (*Portalodus bradshawae*) and "*Mcmurdodus*? cf. *featherensis*" (*Aztecodus harmsenae*) and corrected identification of sides of *Portalodus* teeth. They also added yet another tooth-based species from Aztec Siltstone, *viz*. *Anareodus statei* Long & Young, 1995. The teeth of the latter are on average somewhat smaller than those of *Portalodus* and *Aztecodus*, their crown is very similar to that of the former, but the base is similar to that of the latter, with no extension. Hairapetian *et al.* (2008) understood the similarity of bases in *Aztecodus* and *Anareodus* and a few other resemblances (*e.g.*, crenulation between the cusps observed in some specimens of *Anareodus*) as sufficient for suppressing *Anareodus* and considering *Az. harmsenae* and *An. statei* as conspecific. They also erected a new family, Aztecodontidae, for *Aztecodus* and *Manberodus*, within the Omalodontiformes. In the same volume, Ginter *et al.* (2008) erected the family Omalodontidae for *Omalodus*, *Portalodus* and *Doliodus* (see also Ginter *et al.*, 2010, p. 28–32). *Siberiodus* was left as Omalodontiformes incertae sedis.

For quite a long time, *Portalodus* and the other Antarctic sharks were considered to be endemic to Gondwana. However, Ginter *et al*. (2006) reported two teeth from the Givetian of Cairo Quarry in northern New York state, USA, very similar to those from Victoria Land (Fig. 6B, 6C, 6E). A few years later Potvin-Leduc *et al*. (2015) described a rich collection of *Portalodus* teeth from that locality. Despite a great similarity to the teeth of *P. bradshawae* from Antarctica, a new species name, *viz*. *P. mannoliniae*, was proposed in the latter paper, based mainly on the absence of cristae on the cusps of the latter and their apparent presence in the former (Long & Young, 1995, fig. 7D). I consider this a minor difference, concerning rather the state of preservation of the enameloid than a real morphological disparity, so I do not see the ground for the specific distinction in this case. In the most of teeth illustrated by Potvin-Leduc *et al*. (2015) there is almost no size difference between the cusps (Fig. 6A). However, in the two teeth studied by Ginter *et al*. (2006, 2010), this size difference is comparable to that of the Antarctic material (Fig. 6B, 6C, 6E).

THE HETERODONTY IN OMALODONTIFORMES

The review presented above shows that the degree and mode of heterodonty in the genera referred here to Omalodontiformes vary considerably. In *Manberodus* the heterodonty is virtually nonexistent, all known teeth save for one have the same number and form of cusps (Hairapetian *et al*., 2008, fig. 2A–2K). In *Omalodus* it is restricted to the number and position of intermediate cusplets (compare Wells, 1944, fig. 8a; Gross, 1973, pl. 34, fig. 23 and Hampe *et al*., 2004, fig. 3c), but no general rule can be observed. In *Doliodus sensu* Woodward (1892a), Traquair (1893) and Turner (2004), as well as in *Siberiodus* (Ivanov & Rodina, 2004, fig. 3) there are two types of teeth: one with a single intermediate cusplet and another with three, of which the central one is the highest. In *Doliodus* sometimes, but rarely, an additional, fourth cusplet occurs. It is only a matter of speculation, with no direct proof, that the narrower teeth with fewer cusplets represent anterior portion of a jaw and those with more cusplets occupy lateral positions.

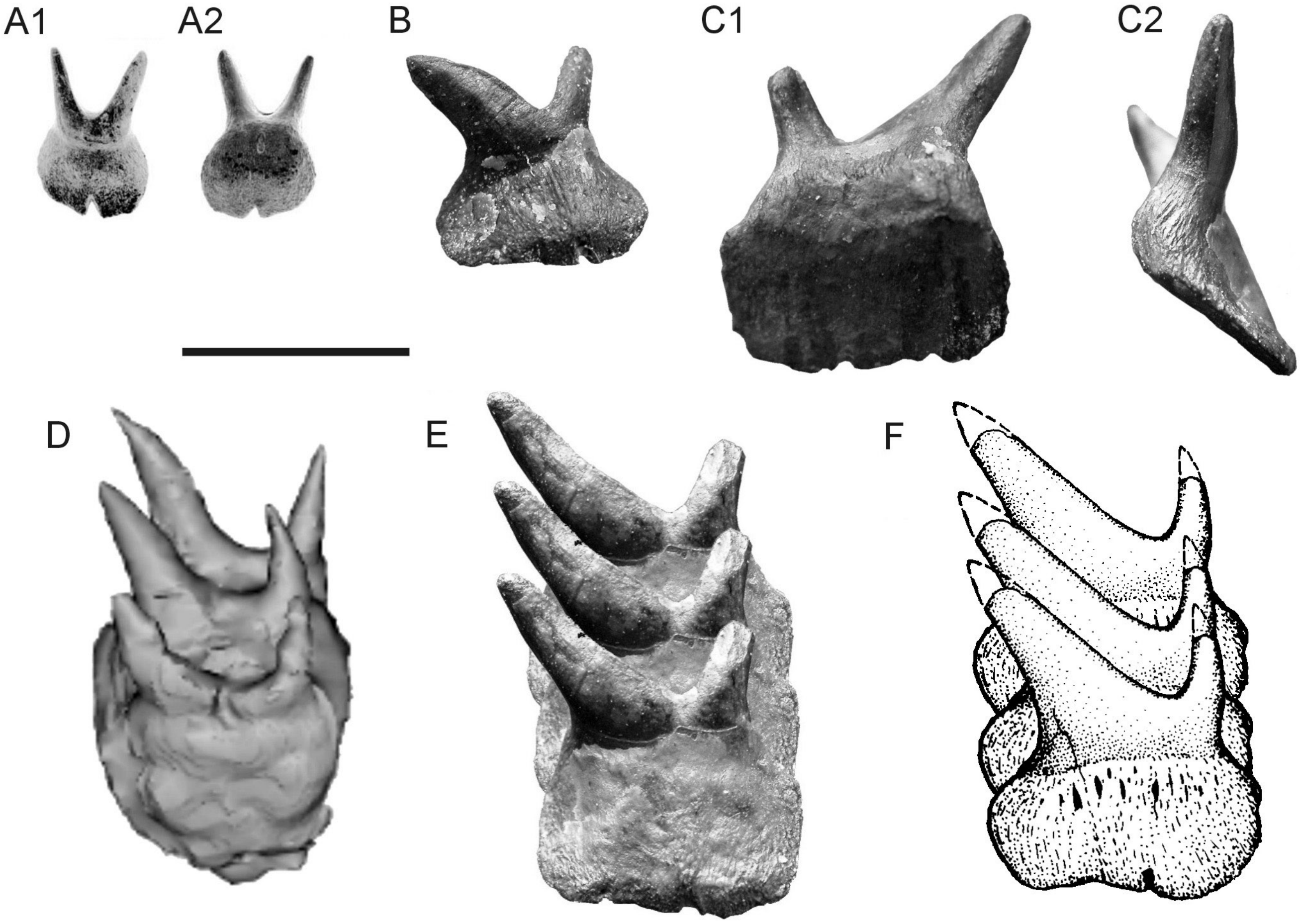

Figure 6. A–**C,** *Portalodus* teeth (attributed to *P. mannoliniae* by Potvin-Leduc *et al*., 2015) from the middle Givetian, Plattekill Fm., Cairo, New York, USA. **A,** Anterior tooth, NYSM 17726, in labial (**A1**) and lingual (**A2**) views; **B**–**C,** lateral teeth, unnumbered specimens deposited at AMNH, in labial (**B**), lingual (**C1**) and lateral (**C2**) views; **D**–**F,** comparison of (**D**) lateral teeth of alleged *Doliodus problematicus* from the Atholville Beds (NMBG 10127, UR 5 tooth family) with the computer-generated tooth families of (**E**) *Portalodus mannoliniae* from Cairo and (**F**) *P. bradshawae* from Antarctica. A, from Potvin-Leduc *et al*. (2015); D, from Maisey *et al*. (2014); F, from Long & Young (1995, modified); scale bar A–C = 10 mm, D–F not to scale.

The heterodonty in the articulated dentition of the Canadian specimen NBMG 10127, with its three general types of teeth (anterior, lateral and posterolateral) was described in the previous section and by Maisey *et al*. (2014). It is very interesting that among the teeth of *Portalodus* from Cairo, New York (*P. mannoliniae sensu* Potvin-Leduc *et al*., 2015) some are comparable to the anterior teeth of NBMG 10127 (compare Figs. 4D and 6A), and the other to its lateral teeth (compare Fig. 6D and 6E). The similarity is striking. It is important to stress that, according to the first interpretation (see section on *Doliodus*), neither in NBMG 10127 nor in *Portalodus* intermediate cusplets were found. Maisey *et al*. (2014, p. 3) admitted that a search for such cusplets was performed, probably in order to confirm the identification of this specimen as *Doliodus*, but “only the largest cusplets [*i.e.*, the lateral main cusps] were revealed by the scan”. On the other hand, the teeth of Antarctic *Anareodus* have much in common with the posterolateral teeth of NBMG 10127, and especially those from the tooth families 9 to 11. In both cases the labial extension of the base is reduced and the crown is “*Portalodus*-like”, with the cusps greatly differing in size and inclined in the same direction (distal in NBMG 10127). Therefore, it is possible that the teeth referred to as *Anareodus* represent in fact the poterolateral region of jaw of *Portalodus*.

To summarise: the diversity of teeth of *Portalodus*, especially with the teeth of *Anareodus* included, corresponds directly to the heterodonty observed in the articulated specimen NBMG 10127, thus far considered to belong to *Doliodus problematicus*. The teeth of NBMG 10127 are significantly different from those of *D. problematicus*. Therefore, a logical conclusion can be drawn that NBMG 10127 actually represents *Portalodus*. However, no remnant of a phosphatised membrane or a curved basal bony plate has ever been found in the association with *Portalodus* teeth. Therefore, it seems rather likely that NBMG 10127 represents an intermediate form (a separate genus?) between *Doliodus sensu stricto* and *Portalodus*. The computer simulation (Fig. 6D–6F) also shows that no important difference can be shown between the lateral tooth families of NBMG 10127, *P. mannoliniae* and *P. bradshawae*.

There is one point which remains unclear, though: the relationship between *Anareodus statei* and *Aztecodus harmsenae*. Certain teeth illustrated by Long and Young (1995, fig. 10B) as *Anareodus* display features similar to *Aztecodus* (form of the base, crenulation on the crown) and because of that Hairapetian *et al*. (2008) synonymised these two genera. Judging from the above discussion, this position seems currently untenable and *Anareodus* should be treated as a morphotype of *Portalodus*, and *Aztecodus* should be left as a separate genus.

CONCLUSIONS

If the reasoning from the previous sections, based on the first interpretation of the dentition of NBMG 10127, is accepted, several taxonomic revisions should be made. First of all, the names *Portalodus mannoliniae* Potvin-Leduc *et al*., 2015 and *Anareodus statei* Long & Young, 1995 should be suppressed and replaced with *Portalodus bradshawae* Long & Young, 1995 (it

Table 1. Taxonomic revision of omalodontiform species.

Species	Former identifications and selected references	Age
Omalodus grabaui (Hussakof & Bryant, 1918)	*Dittodus grabaui* (Hussakof & Bryant, 1918), *Phoebodus* ? *bryanti* (Wells, 1944; Gross, 1973), *Omalodus bryanti* (Ginter & Ivanov, 1992), *Omalodus grabaui* (Turner, 1997; Ginter *et al*., 2008, 2010), *Omalodus schultzei* (Hampe *et al*., 2004)	Givetian - Frasnian?
Doliodus problematicus (Woodward, 1892a)	*Diplodus problematicus* (Woodward, 1892a), *Doliodus problematicus* (Traquair, 1893; Turner, 2004; Ginter *et al*., 2010)	Emsian
Portalodus bradshawae Long & Young, 1995	*Xenacanthus* sp. (Young, 1982), *Portalodus bradshawae* (Long & Young, 1995; Ginter *et al*., 2006, 2010), *Anareodus statei* (Long & Young, 1995), *Portalodus mannoliniae* (Potvin-Leduc *et al*., 2015)	Givetian
Portalodus or a new genus? *latispinosus* comb. nov. (Whiteaves, 1881)	*Ctenacanthus latispinosus* (Whiteaves, 1881), *Climatius latispinosus* (Woodward, 1892b; Burrow *et al*., 2008), *Doliodus problematicus* (Miller *et al*., 2003; Maisey *et al*., 2014, 2017), *Doliodus latispinosus* (Burrow *et al*., 2017; Maisey *et al*., 2019, 2021; Burrow & Desbiens, 2023)	Emsian
Aztecodus harmsenae Long & Young, 1995	*Mcmurdodus* cf. *featherensis* (Young, 1982), *Aztecodus harmsenae* (Long & Young, 1995; Ginter *et al*., 2010)	Givetian
Siberiodus mirabilis Ivanov & Rodina, 2004	*Siberiodus mirabilis* (Ivanov & Rodina, 2004, Hairapetian & Ginter, 2009; Ginter *et al*., 2010)	Famennian
Manberodus fortis Hairapetian & Ginter, 2008	*Manberodus fortis* (Hairapetian *et al*., 2008; Ginter *et al*., 2010)	Frasnian

has a page priority over *Anareodus*). Then, NBMG 10127 should be removed from *Doliodus* and placed in a separate new genus, if not simply in *Portalodus*. The generic name *Doliodus* should be restricted to the teeth of *D. problematicus sensu* Traquair (1893) and Turner (2004). All the established omalodontiform species and their former identifications are presented in the Table 1. Contrary to the opinion expressed by Zangerl (1981) and shared by many palaeoichthyologists from the middle twentieth century, teeth are the most useful diagnostic tools in the taxonomy of Palaeozoic chondrichthyans, particularly at the specific and generic level. They provide links between very rare articulated specimens and, in the absence of more complete fossils, suggest the relationships and evolutionary paths between the better-defined groups. In the case of Omalodontiformes, there is only one species based on an articulated specimen and the rest (six species) are known only from dental elements. Therefore, almost all the analyses of the geographic and stratigraphic distribution of the order depends on the discoveries of these specific teeth. On the other hand, of course, finding of at least partly articulated specimens solve many problems which otherwise are intractable. For a long time, there was an argument among the scientists if the teeth of omalodonts belong to acanthodians or to chondrichthyans. The discovery of NBMG 10127 with fin spines comparable to *Climatius*, *Portalodus*-like teeth in the mouth, and the general chondrichthyan characteristics showed that omalodontiforms are a transitional group and so the points of view of both parties are justified.

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