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The oldest holocephalan (Chondrichthyes) from the Middle Devonian of the Boulonnais (Pas-de-Calais, France)

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Abstract

The Couderousse Member of the Blacourt Formation in the Banc-Noir quarry, Ferques inlier, Boulonnais (Pas-de-Calais, France) has yielded a tooth plate whose morphology is similar to that of *Synthetodus*, which is considered a holocephalan. Its histology is made of an outer enameloid-like tissue, and an inner trabecular dentine. Its occlusal surface shows a bean-shaped bulge. This tooth plate was prepared from a limestone that is dated from the Middle–Upper *varcus* Conodont Zone, that is lower upper Givetian. This limestone has also yielded a *Pokorninella bricae–Rothpletzella–Tentaculites* assemblage, which is indicative of an environment of the inner to middle marine platform boundary. This specimen appears to be the oldest confirmed holocephalan ('bradyodont') tooth plate for which the name *Melanodus loonesi* nov. gen. et sp. is erected. ***To cite this article: L. Darras et al., C. R. Palevol 7 (2008).***

Résumé

Le plus ancien holocéphale (Chondrichthyes) dans le Dévonien moyen du Boulonnais (Pas-de-Calais, France). Au sein du massif de Ferques (Boulonnais, Pas-de-Calais, France), le membre de Couderousse de la formation de Blacourt dans la carrière du Banc-Noir a fourni un pavé dentaire dont la morphologie est proche de celle de *Synthetodus*, qui est considéré comme un holocéphale. Son histologie présente une couche externe de type émailloïde et une couche interne de dentine trabéculaire. Sa surface occlusale porte une protubérance en forme de haricot. Ce pavé dentaire a été dégagé d'un calcaire qui est daté de la zone de conodonte moyenne à supérieure à *varcus*, c'est-à-dire de la partie inférieure du Givétien supérieur. Ce calcaire a également produit un assemblage de microfossiles calcaires à *Pokorninella bricae–Rothpletzella–Tentaculites*, qui indique un environnement en limite de plate-forme marine interne et moyenne. Ce spécimen apparaît comme étant le plus ancien holocéphale (« bradyodonte ») confirmé. Il est attribué à *Melanodus loonesi* nov. gen. et sp. ***Pour citer cet article : L. Darras et al., C. R. Palevol 7 (2008).***

Keywords: Banc-Noir quarry; Ferques inlier; Blacourt Formation; Givetian; Trabecular dentine; New genus and species; France

Mots clés : Carrière du Banc-Noir ; Massif de Ferques ; Formation de Blacourt ; Givétien ; Dentine trabéculaire ; Nouveau genre et nouvelle espèce ; France

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Nomenclatorial foreword

As one of the referees of this paper said, the vernacular English name of the Superorder Holocephali (*sensu* [29]) is generally written 'holocephalans' (see, e.g., http://www.wordreference.com/enfr/holocephalan) rather than 'holocephalians'. However, the latter is more and more often found in literature (e.g., [13,29] and http://www.thefreedictionary.com/holocephalian). Here, we use 'holocephalans', except when, in references, authors have written 'holocephalians'.

1. Introduction

The holocephalan fishes are chondrichthyans, characterized, among other characters, by the slow growth of their teeth; thus they are often referred to as 'bradyodonts'. For instance, chimaeroids do not shed tooth plates that are growing from their lingual surface [26]. Palaeozoic holocephalans are mostly known from isolated teeth or tooth plates. Their remains are quite common and diversified in the Carboniferous, with a few taxa represented during the Late Devonian [29]. Some of the teeth or tooth plates of Devonian age show an already typical holocephalan histology, including orthotrabeculine, trabecular dentine, and a lamellar basal layer [29]. Here, we show evidence of a holocephalan occurrence in the Middle Devonian of the Boulonnais, northern France. However, its histology differs from the typical holocephalan one.

In northern France and Belgium, many holocephalan remains, mostly represented by tooth plates, are Carboniferous in age [7]. Only one doubtful mention concerns a cochliodont tooth from the Middle Devonian [9,10], hence the interest of our discovery. We first briefly review the pre-Carboniferous holocephalans worldwide in order to settle our discovery in its global context.

After the review by B. Stahl [29] and subsequent publications, Late Devonian holocephalans include the following taxa:

a) Helodontiformes: *Helodus clivulus*, *H. devonicus*, *H. incipiens* and *H. rowleyi* Branson 1914, uppermost Devonian, Grassy Creek Shales, Missouri, USA; *H. subtuberatus* Lambe 1913, ?Upper Devonian, Alberta, Canada; *H. gibberulus* Agassiz 1838, Upper Devonian, Pennsylvania, USA. However, *Helodus* sp. figured by B. Stahl [29, fig. 56] from the Upper Devonian (Famennian) Teddy Mount Formation of Queensland, Australia, is in fact of Early Carboniferous age (after S. Turner in [13]);

b) Cochliodontiformes: *Sandalodus minor* Davis 1884, Upper Famennian, lower Chaffee Formation, Colorado, USA; *Thoralodus cabrieri* Lehman 1952, Famennian, Cabrières, Montagne Noire, southern France; *Psephodus* cf. *magnus* Agassiz 1838, middle Famennian, Kowala quarry, Holy Cross mountains, Poland [13]; and a record of *Cochliodus* sp. from Sort Tepe, Hakkari province, southeastern Turkey (Zap fauna in [17], pl. 2 : 4) whose age is not clear: the Zap fauna comes from the basal Köprülü Formation – not the Yiginli Formation as erroneously indicated in [17]: P. Janvier, pers. comm. 1984 – which is considered latest Famennian in age, but the cochliodont specimen has been collected from an isolated block of a reefal limestone, higher in the Köprülü Formation, which is dated from the Tournaisian [17 (p. 162)]. Specimens referred with question to *Psephodus* from the Upper Devonian of Australia are mentioned by B. Stahl [29] after S. Turner [30]; in fact, this is based on the following information: "teeth which might belong to this genus have been found in the Late Devonian of Western Australia (J.A. Long, pers. comm.)" [30], and this record has still to be considered as doubtful;

c) Psammodontiformes: *Psammodus* sp., uppermost Devonian, central Alborz, Iran ;

d) Copodontiformes: *Acmoniodus clarkei* Hussakof & Bryant 1918, lower Frasnian, Lower Genesee, New York, USA; *Synthetodus trisulcatus* Eastman 1896 and *S. calvini* Eastman 1908, lower Frasnian, Iowa, USA ;

e) in the Upper Devonian (probably Famennian), Witpoort Formation of eastern Cape Province, South Africa, Anderson et al. [1] have interpreted a series of connected skeletal elements "as the earliest known whole-bodied holocephalian"; however, the neurocranium and palatoquadrate of this fish are not fused, and no teeth or tooth plates are preserved, thus it is not considered an holocephalan [29];

Only few remains referred to as holocephalans have been recorded from the Middle Devonian, but they are considered as questionable [29]:

i) *Psammodus antiquus* Newberry 1857 (Eifelian, Ohio, USA), based on a specimen that is incompletely described and not figured;

ii) a small spine "associated with the *Psephaspis* dorsal disc on [the specimen] PF 5675" (Middle Devonian, Idaho, USA), and considered as menaspid-like by R. Denison [6];

iii) a number of "peculiar symmetrical endoskeletal elements" described as *Pucapampella rodrigae* [16],

from the Givetian of Bolivia, have been originally interpreted as holocephalan synarcuals, though they might as well have belonged to non-holocephalan batoid-like chondrichthyans [29]; since its discovery, new specimens of this taxon have been collected; the cranial morphology of *Pucapampella* includes characters that are absent in other chondrichthyans, thus it is now considered "as a cladistically basal member" of the chondrichthyans [21].

Additionally, Dormal [9,10] has mentioned, but did not figure a cochliodont tooth (referred to as "*Cochliodon*: Dent" in [9]; "*Cochliodonte*: Dent" in [10]) from the Alvaux limestone of the Namur Synclinorium, Belgium. This limestone was considered Eifelian in age at that time [7]. This mention is not confirmed, and the age of the Alvaux limestone is Givetian, not Eifelian (now the Alvaux Member of the Bois de Bordeaux Formation [3,4]).

Therefore, the tooth plate that is presented here is assumed to represent the earliest confirmed representative of the Holocephali *sensu* [29]. It is also the oldest chondrichthyan remain from the Boulonnais [8], except for a very doubtful *Petrodus* [5]. To be sure of the age of the new tooth plate, thin sections have been made in its limestone matrix in order to prepare microfossils for independent biochronologic evidence.

2. Stratigraphy and environment

The sample where the specimen comes from is a hard, grey ochreous limestone, with granular patches due to bioturbations. It has been collected by Mr. Christian Loones, an amateur palaeontologist who works with the Natural History Museum of Lille (Nord, France). It

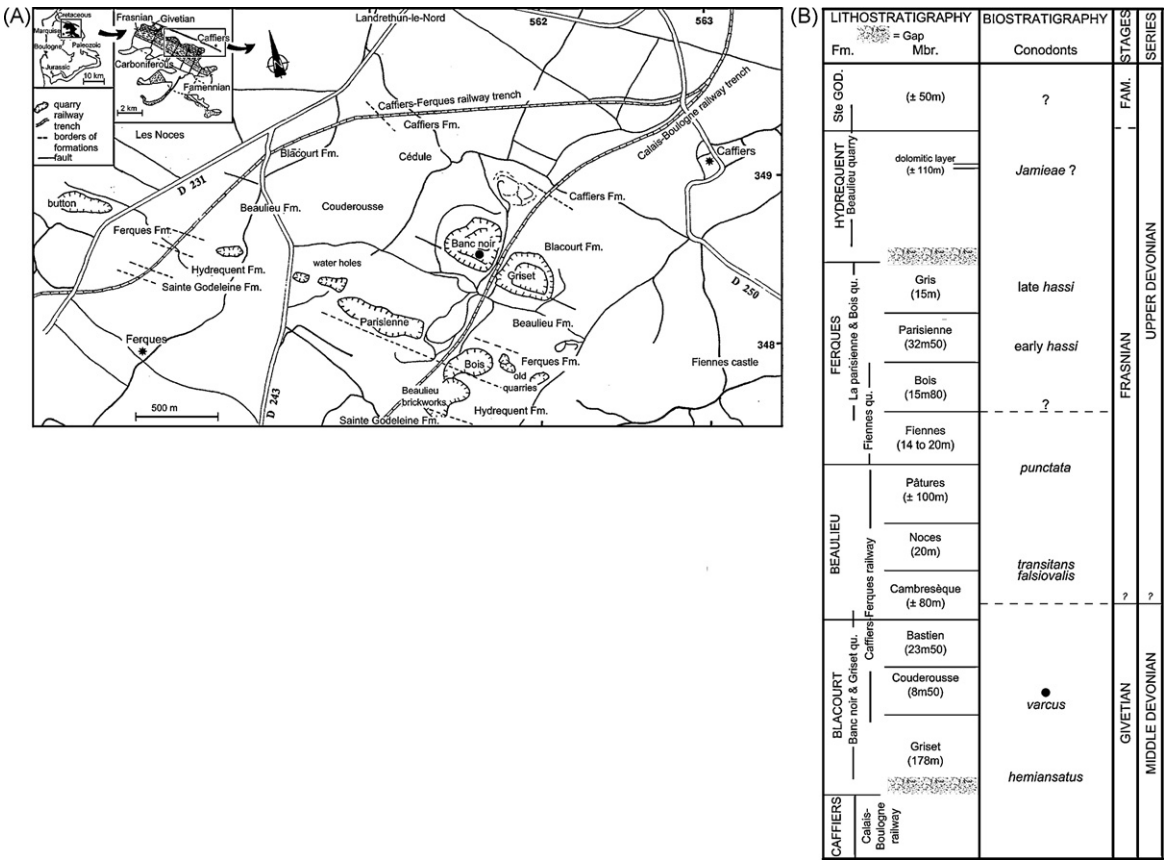
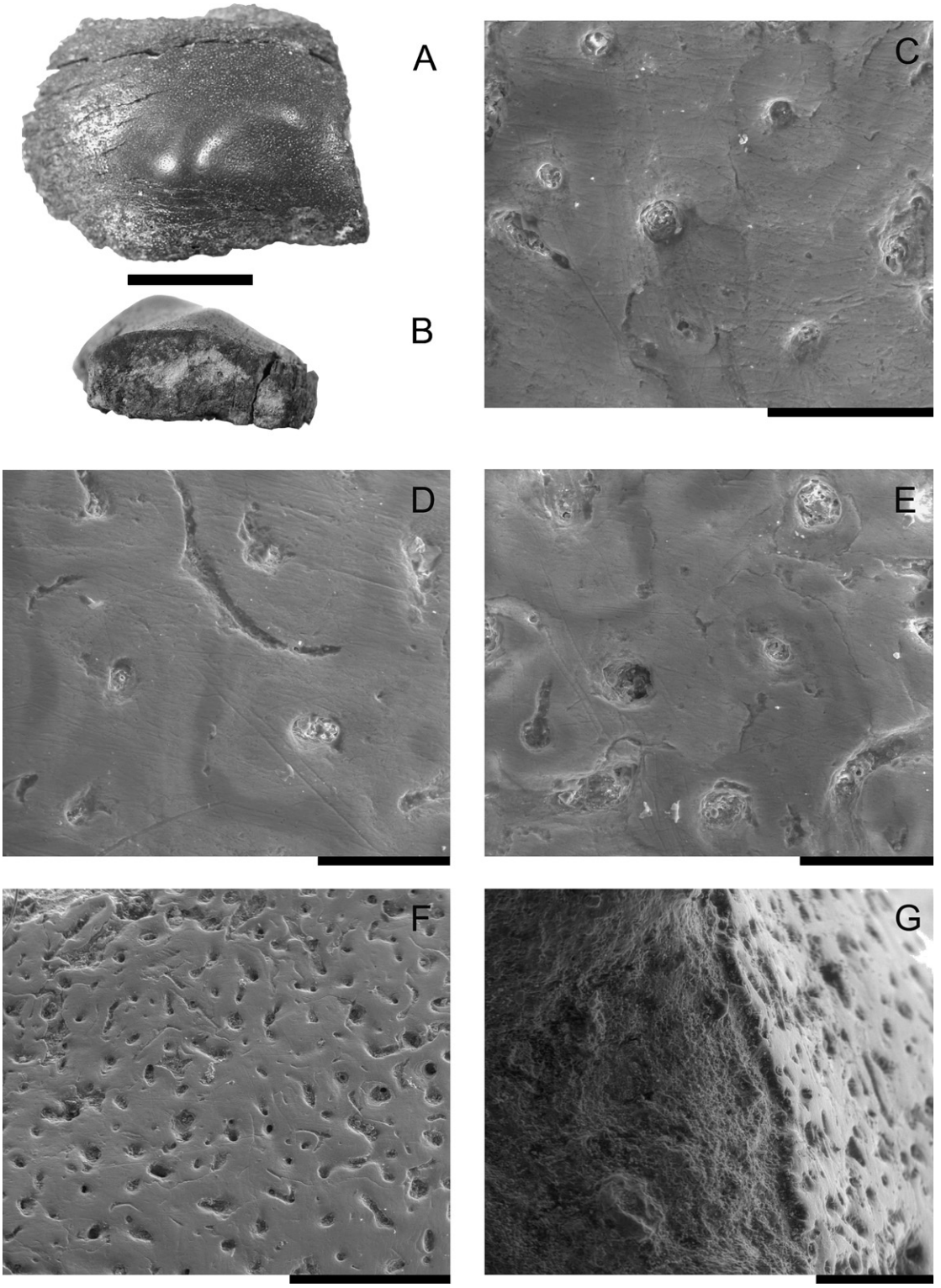


Fig. 1. Geographical (**A**) and stratigraphical (**B**) location of the studied material, indicated by a black dot, with extension of the various field sections logged in quarries and railway trenches. Abbreviations: FAM., Famennian, Fm., Formation, Mbr., Member, qu., quarry, Ste GOD., Ste Godeleine (modified after [2]).

Fig. 1. Localisation géographique (**A**) et stratigraphique (**B**) du matériel étudié, indiquée par une pastille noire, avec extension des diverses coupes de terrain qui ont été levées en carrière et le long des tranchées de chemin de fer. Abréviations : FAM, Famennien, Fm, formation, Mbr., membre, qu., carrière, Ste GOD., Sainte-Godeleine (modifié d'après [2]).


A
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comes from the Banc-Noir quarry (Ferques inlier, Pas-de-Calais), in the Couderousse Member, upper part of the Blacourt Formation (Fig. 1). This member is dated from the Middle-Upper *varcus* Conodont Zone, i.e. lower upper Givetian [2]. The Blacourt Formation has been interpreted as a lagoon-like restricted environment, as suggested by the low density of chitinozoan, acritarch and prasinophycean assemblages [18,24]. Ostracodes suggest that the environment was either lagoon-like or marine, but of shallow water [22].

Thin sections have been made in the matrix of the holocephalan specimen in order to control the age of the limestone, and obtain additional palaeoenvironmental information. The microfacies revealed by these thin sections shows patches of bioclastic bioturbated packstone, in a sandy micritic mudstone. It bears numerous and rather diversified metazoan fragments, dominated by ostracodes and indicative of a relatively deep environment, such as rather common crinoids; relatively abundant ostracodes with rare *Cryptophyllus* sp.; rare bivalve elements with a microperforated periphery belonging to cortoid grain (*sensu* [12]); rare and strongly abraded bryozoans; rare brachiopod shells, with very rare Reticulariacea and *Productella* spines; relatively common but broken fragments of *Tentaculites* sp.; rare to relatively common trilobite elements; very rare phosphatic remains (fish); palaechinid radioles and minute fragments of the cyanobacteria *Rothpletzella* (=*Sphaerocodium* auct.) sp. and of *Pokorninella bricae* [31]. This assemblage is suggestive of an environment from the inner to middle platform boundary, a little below the FWWB (fair-weather waves base), that is at more or less 25 to 50 m of depth.

The co-occurrence of *Pokorninella bricae* Vachard 1988 (synonym: *Moravammina* sp. *sensu* Poncet 1988) [27], *Rothpletzella* and *Tentaculites* regionally dates the middle–upper Givetian. In the Boulonnais, this assemblage has been originally described in the Griset Member of the Blacourt Formation (Lower to Middle *varcus* Conodont Zone) [31]. So, the occurrence of this assemblage in the Couderousse Member (middle–upper *varcus* Conodont Zone, i.e. lower Upper Givetian), which is stratigraphically just above the Griset Member, extends its range slightly higher in the local stratigraphic sequence.

3. Systematics

Class Chondrichthyes Huxley 1880
Subclass Subterbranchialia Zangerl 1979
Superorder Holocephali Bonaparte 1832–41
Order Copodontiformes Obruchev 1953
Family Copodontidae Davis 1883
Copodontidae *incertae sedis*
Melanodus nov. gen.

Derivatio nominis: From '*melan*' black and '*odus*' tooth.

Type and only species: Melanodus loonesi nov. gen. et sp.

Diagnosis: As for the type species.

Melanodus loonesi nov. gen. et sp.

Derivatio nominis: Dedicated to Mr. Christian Loones, an amateur palaeontologist working with the Natural History Museum of Lille, who discovered the specimen.

Holotype and only specimen: MGL 1244 in the collections of geology ('Musée Gosselet') of the Natural History Museum of Lille (Nord, France) (Fig. 2).

Occurrence: Banc-Noir quarry, Ferques, Pas-de-Calais, France; Blacourt Formation, Couderousse Member; lower upper Givetian (Middle-Upper *varcus* Conodont Zone, *Pokorninella bricae-Rothpletzella-Tentaculites* Assemblage).

Diagnosis: A holocephalan incomplete tooth plate; mostly rectangular in outline, with regularly curved mesial-distal margins in occlusal view; 18 mm wide, and ca. 30 mm long (evaluation); the occlusal surface of the crown shows a typical bean-shaped bulge; the crown is

Fig. 2. *Melanodus loonesi* nov. gen. et sp., holotype MGL 1244 (Natural History Museum of Lille, France); Banc-Noir quarry, Ferques inlier, Pas-de-Calais, France; Couderousse Member, Blacourt Formation; lower Upper Givetian (Middle–Upper *varcus* Conodont Zone; *Pokorninella bricae–Rothpletzella–Tentaculites* assemblage). **A, B**: occlusal (**A**) and mesial or distal (**B**) views of the tooth plate. **C–G**: SEM micrographs of the occlusal surface and edge of the tooth plate. **C–E**: details showing the superficial striations due to possible microwear. **F**: detail of interconnected foramina. **G**: detail of one of the broken edges showing the outer enameloid-like layer. **A**, **B**: scale bar = 1 cm; **C**, **D**, **E**: scale bar = 200 μm; F: scale bar = 1 mm; G: scale bar = 500 μm.

Fig. 2. *Melanodus loonesi* nov. gen. et sp., holotype MGL 1244 (Muséum d'Histoire Naturelle de Lille, France) ; carrière du Banc-Noir, massif de Ferques, Pas-de-Calais, France ; membre de Couderousse, formation de Blacourt ; base du Givétien supérieur (zone de conodonte moyenne et supérieure à *varcus* ; assemblage à *Pokorninella bricae–Rothpletzella–Tentaculites*). **A, B** : vues occlusale (**A**) et mésiale ou distale (**B**) du pavé dentaire. **C–G** : photographies au MEB de la surface occlusale et du bord du pavé dentaire. **C–E** : détails montrant les stries superficielles dues à de possibles micro-usures du vivant de l'animal. **F** : détail des foramens interconnectés. **G** : détail d'un bord cassé montrant la couche externe de type émailloïde. **A**, **B** : échelle = 1 cm; **C**, **D**, **E** : échelle = 200 μm; **F**: échelle = 1 mm; **G**: échelle = 500 μm.

made of two mineralized tissues, i.e., an outer irregularly punctuated enameloid-like layer and an inner trabecular dentine (osteodentine) layer.

3.1. Description

The specimen MGL 1244 is a single isolated tooth plate, with a low, mesio-distally elongated crown, corresponding to a crushing tooth. It is 18 mm wide and 24 mm long, 2.5 to 10 mm high. Its mesial or distal side (right side on Fig. 2A) is broken while the others are eroded. The occlusal surface is characterized by an inclined bean-shaped bulge that represents nearly 10% of the surface. Its highest point is not centrally located (Fig. 2A). The whole surface of the specimen is punctuated with small irregular holes. These foramina are often smaller on the bulge than on its lateral parts. They are often fused and interconnected (Fig. 2D and E). The surface seems to be covered by a thick layer of an enameloid-like tissue (Fig. 2G), which otherwise is considered as diagnostic for the Copodontiformes [29]. The basal part is strongly eroded, and reveals a histological structure interpreted as trabecular dentine (osteodentine). However, the basal lamellar layer present in ancient holocephalans is absent from our specimen. Because our specimen is unique, we did not proceed with thin sections of the tooth plate, and the histology has not been studied in detail.

When observed in a SEM, crossed linear striations are seen all over the occlusal surface of the tooth plate (Fig. 2C–F). Two main orientations can be detected, and their density seems to be higher on the bulge (Fig. 2D and F) than on the other parts of the specimen. Furthermore, some are not linear and other are deeper, corresponding to the most recent ones. All those striations may be related to the animal diet (grinding of benthic shells) and/or to the occurrence of sand grains from the substrate where their benthic preys were living [32]. This has been quantitatively evaluated for the stickleback fish *Gaterosteus aculeatus* [28]. However, in the latter case, the microwear concerned the pointed teeth on a living fish, which is different from our tooth plate that has been subject to *post-mortem* transportation (see [15]).

3.2. Discussion

This new specimen of a "bradyodont" tooth plate is morphologically similar to some of the tooth plates of *Synthetodus trisulcatus* from the Lower Frasnian of Iowa, USA, which also have a bean-shaped bulge [29 (fig. 91C and D)]. However, *S. trisulcatus* shows asymmetrical or bilaterally symmetrical teeth [11], a feature that cannot be seen on our single, broken tooth plate. The sizes of *Melanodus loonesi* nov. gen. et sp. and of *Synthetodus* are very similar as well (24 mm and 23–26 mm respectively). However, regarding its thickness, *Melanodus loonesi* nov. gen. et sp. is more mesio-distally elongated than the corresponding teeth of *Synthetodus*. It is also different from all the other tooth plates of holocephalans reviewed by B. Stahl [29].

As to the wear surface, we compared the tooth from the Boulonnais with both *Synthetodus calvini* and *S. trisulcatus*. This kind of tooth was first attributed to the Ctenodipterini dipnoans (including *Dipterus*) by C. Eastman [11], because it corresponds to large and worn tritorial plates. However, Hussakof and Bryant [14] advocated three reasons for excluding *Synthetodus* from the dipnoans; i.e. (1) its teeth present no ridges nor tubercles, (2) they are bilaterally symmetrical, and (3) they are covered with a shiny enamel sprinkled with small punctae. They proposed to include *Synthetodus* within the Cochliodontidae. Later, C. Patterson [25] considered *Synthetodus* as a typical copodont, with a single cusp and a bilaterally symmetrical tooth. This author, however, thinks that the Copodontiformes have a doubtful phylogenetic relationship to other holocephalans. We do agree with this opinion because the histology of *Synthetodus* does not fit exactly the usual holocephalan one, i.e., with orthotrabeculine, trabecular dentine (osteodentine) and a lamellar layer. The histology is not the only clue for taxonomy because it may be a convergent feature as suggested for tubular dentine (after Radinsky 1961 in [25]). Our tooth plate shows trabecular dentine (osteodentine) covered with an enameloid-like tissue punctuated by irregularly spaced foramina, instead of regularly spaced foramina, as usually seen on orthotrabeculine. An attribution of our tooth plate to dipnoans is unjustified, because there is no ascending vascular canal existing in dipnoan teeth as compared with holocephalan teeth (e.g., *Griphognathus* in [23]). Furthermore, the presence of enameloid is characteristic for Copodontiformes [29 (p. 90)], as it is for our specimen.

We consider the superficial wear features of *Melanodus loonesi* nov. gen. et sp. as nearer to the ones of *Synthetodus* than to any other described tooth plate [29]. However, the central bulge of the tooth plate of *Melanodus loonesi* nov. gen. et sp. does not occupy the whole surface of the plate, contrary to all the teeth of *Synthetodus* published by C. Eastman [11].

We also compare *Melanodus loonesi* nov. gen. et sp. with *Thoralodus cabrieri* from the middle Famennian of Cabrières, Montagne Noire, southern France [19]. Both taxa are the only Devonian holocephalans known in France. *T. cabrieri* is represented by a single specimen, the holotype (specimen MNHN-DSF 4 of the palaeon-

tology collection of the National Museum of Natural History, Earth Sciences Department, Paris), which was poorly figured in the original publication [19 (Fig. 1 and pl. 1: 3)]. It has been figured again by Lelièvre et al. ([20] (pl. 5: A–C)), but without histological information. The crown of *Thoralodus* has a convex occlusal surface, but it does not show any bulge. Furthermore, the tooth plate of *Thoralodus* is much bigger than the one of *Melanodus loonesi* nov. gen. et sp.: they are 40 mm and 18 mm wide, respectively. Due to the fact that both are incomplete, and after tentative restoration of their original size, *Thoralodus* may have been at least 90 mm long, although *Melanodus loonesi* nov. gen. et sp. was ca. 30 mm long only. Additionally, the histology of *Thoralodus* shows orthotrabeculine, which is visible mesio-distally. A thin section of this specimen has been made [19], but could not be recovered in the Paris collections. Nevertheless, the histology of *Thoralodus*, as seen directly from its holotype, is different from the one of *Melanodus* nov. gen.

From this comparison, we decide to erect a new taxon name for this tooth plate for two main reasons: (a) it appears that our specimen is clearly different from all other known Devonian holocephalan tooth plates, and (b) it also appears to be the oldest confirmed holocephalan.

4. Conclusion

After comparison with the already known holocephalan tooth plates, it appears that the new specimen from the Devonian of Boulonnais, for which we propose the name *Melanodus loonesi* nov. gen. et sp., is a holocephalan, except in the lack of orthotrabeculine and of a basal lamellar structure; the latter part is surely abraded as it has already been noticed for, e.g., *Thoralodus cabrieri* [29]. It is mostly comparable with *Synthetodus trisulcatus*. However, the shape of *M. loonesi* is more elongate than that of the tooth plates of *S. trisulcatus*. Furthermore, the surface occupied by the bulge and the irregularly spaced foramina on *M. loonesi* is less developed than on *S. trisulcatus*. Additionally, it appears that *M. loonesi*, which is early late Givetian in age and is attributed here to the Copodontiformes, would be the oldest confirmed Devonian holocephalan, if Copodontidae *incertae sedis* are confirmed to be holocephalans.

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