Taxonomy of *Platypterygius campylodon* and the diversity of the last ichthyosaurs (#9040)

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Taxonomy of *Platypterygius campylodon* and the diversity of the last ichthyosaurs

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A complex and confusing taxonomy has concealed the diversity dynamics of Cretaceous ichthyosaurs (Reptilia, Ichthyosauria) for decades. The near totality of Albian-Cenomanian remains from Eurasia has been assigned, by default, to the loosely defined entity *Platypterygius campylodon*. The holotype of this taxon was supposed to be lost. By thoroughly examining the Cenomanian ichthyosaur collections from the UK, I redescribe the syntypic series of *Ichthyosaurus/Platypterygius campylodon*. This material, along with a handful of other coeval remains, is diagnostic and seemingly differs from the vast majority of Cretaceous remains assigned to this taxon. An holotype for *Ichthyosaurus campylodon* is designated and I reassign this species to *Pervushovisaurus campylodon* nov. comb. To further stabilise the taxonomy of Cretaceous ichthyosaurs, it is here proposed to resurrect the genus *Myopterygius*, with well-known Australian species *Myopterygius australis* as its type species. Ecological and taxonomic diversity patterns of the last ichthyosaurs are updated and conform to the scenario of an early Cenomanian diversity drop prior to the latest Cenomanian final extinction.

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Abstract

A complex and confusing taxonomy has concealed the diversity dynamics of Cretaceous ichthyosaurs (Reptilia, Ichthyosauria) for decades. The near totality of Albian-Cenomanian remains from Eurasia has been assigned, by default, to the loosely defined entity *Platypterygius campylodon*. The holotype of this taxon was supposed to be lost. By thoroughly examining the Cenomanian ichthyosaur collections from the UK, I redescribe the syntypic series of *Ichthyosaurus*/*Platypterygius campylodon*. This material, along with a handful of other coeval remains, is diagnostic and seemingly differs from the vast majority of Cretaceous remains assigned to this taxon. An holotype for *Ichthyosaurus campylodon* is designated and I reassign this species to *Pervushovisaurus campylodon* nov. comb. To further stabilise the taxonomy of Cretaceous ichthyosaurs, it is here proposed to resurrect the genus *Myopterygius*, with well-known Australian species *Myopterygius australis* as its type species. Ecological and taxonomic diversity patterns of the last ichthyosaurs are updated and conform to the scenario of an early Cenomanian diversity drop prior to the latest Cenomanian final extinction.

INTRODUCTION

Ichthyosaurs are iconic reptiles of the Mesozoic marine ecosystems, that disappeared quite abruptly at the beginning of the Late Cretaceous (Bardet, 1992; Fischer et al., 2016). Understanding of the final chapter of their extensive evolutionary history (Olenekian-Cenomanian, about 157 million years (Bardet, 1992; Motani et al., 2015)) has been impaired by a complex and confusing taxonomy, especially at the supra-specific level. The genus *Platypterygius* is by far the most problematic, with no valid definition, no diagnostic features and a biozone spanning the Barremian (‘*Platypterygius*’ *sachicarum*) to the Late Cenomanian (‘*Platypterygius*’ *campylodon*, ‘*Platypterygius kiprijanoffi*’), i.e. 35 million years (Fischer, 2012; Fischer et al., 2014a). Recent phylogenetic analyses have found the species currently referred to *Platypterygius* species to be widely scattered, sometimes within a ophthalmosaurid subfamily, Platypterygiinae (Druckenmiller & Maxwell, 2010; Fischer et al., 2012, 2016; Zverkov et al., 2015). The type species of the genus, *Platypterygius platydactylus*, is phylogenetically isolated from other species currently to as *Platypterygius* and most of the species of this genus are tightly clustered within one or two ecomorphs (Fischer et al., 2016). As a taxonomic entity, *Platypterygius* might thus be biased by ecological convergence of distinct platypterygiine lineages rather than be the product a single Cretaceous radiation. Thus, the diversity of Cretaceous ichthyosaurs cannot be approximated using currently valid genera; the taxonomy of each species needs to critically assessed in isolation and the use of the genus *Platypterygius* should be motivated with respect to the morphology of the time species. Other genus-group names have been used in the past but have since been discarded, notably *Myopterygius* Huene, 1922, *Tenuirostria* Arkhangelsky, 1998, and *Longirostria* Arkhangelsky, 1998 (Huene, 1922; Arkhangelsky, 1998), adding to the confusion.

Another persisting issue in quantifying the diversity and extinction tempo of the last ichthyosaurs is *Ichthyosaurus campylodon* Carter, 1846, which has been used since its creation (Carter, 1846a,b) as a bin for nearly all Cretaceous ichthyosaur remains from Eurasia, regardless of their morphology or stratigraphic position. In this brief contribution, I: (i) evaluate the availability of the genus-group taxon *Myopterygius* Huene, 1922 and propose to resurrect it, with the well-known species *Myopterygius* (‘*Platypterygius*’) *australis* as its type species; (ii) review the status and morphology of the syntypic material of *Ichthyosaurus campylodon* and other remains from the Cenomanian deposits of the United Kingdom; (iii) rediagnose and designate an holotype *I. campylodon*, and transfer it to *Pervushovisaurus campylodon* nov. comb; (iv) provide an updated assessment of the ecological and taxonomic diversity of the last ichthyosaurs.

MATERIAL AND METHODS

Institutional abbreviations–CAMSM: Sedgwick Museum of Earth Sciences, Cambridge University, Cambridge, UK; RBINS/IRSNB: Royal Belgian Institute of Natural Sciences, Brussels, Belgium; NHMUK: Natural History Museum, London, UK.

Specimen list–I surveyed the entire Cenomanian collections of the CAMSM, the RBINS and the NHMUK, but only important specimens are listed here (Table 1). Unlisted remains include centra, undeterminable skeletal fragments and poorly preserved isolated teeth. Specimens from Cambridge Greensand Member (i.e. the base of the West Melbury Marly Chalk Formation, Grey Chalk Subgroup (Hopson, 2005) have been published elsewhere (Fischer et al., 2012, 2014b) and are not listed here.

Specimen	Material	Assignation	Locality

CAMSM B20643	Tooth	Platypterygiinae indet. (holotype of *I. angustidens* = nomina nuda (Fischer et al., 2014b))	Hunstanton
CAMSM B20644	Tooth	*Pervushovisaurus campylodon* (syntype, Carter's series)	Cambridge area
CAMSM B20645	Tooth	Platypterygiinae indet. (syntype, Carter's series)	Cambridge area
CAMSM B20646	Tooth	*Pervushovisaurus campylodon* (syntype, Carter's series)	Cambridge area
CAMSM B20647	Tooth	*Pervushovisaurus campylodon* (syntype, Carter's series)	Cambridge area
CAMSM B20648	Tooth	*Pervushovisaurus campylodon* (syntype, Carter's series)	Cambridge area
CAMSM B20649	Tooth	*Pervushovisaurus campylodon* (syntype, Carter's series)	Cambridge area
CAMSM B20650	Tooth	*Pervushovisaurus campylodon* (syntype, Carter's series)	Cambridge area

CAMSM B20651	Tooth	*Pervushovisaurus campylodon* (syntype, Carter's series)	Cambridge area
CAMSM B20652	Tooth	*Pervushovisaurus campylodon* (syntype, Carter's series)	Cambridge area
CAMSM B20653	Tooth	*Pervushovisaurus campylodon* (syntype, Carter's series)	Cambridge area
CAMSM B20654	Tooth	*Pervushovisaurus campylodon* (syntype, Carter's series)	Cambridge area
CAMSM B20655	Tooth	*Pervushovisaurus campylodon* (syntype, Carter's series)	Cambridge area
CAMSM B20656	Tooth	*Pervushovisaurus campylodon* (syntype, Carter's series)	Cambridge area
CAMSM B20657	Tooth	*Pervushovisaurus campylodon* (syntype, Carter's series)	Cambridge area
CAMSM B20658	Tooth	*Pervushovisaurus campylodon* (syntype, Carter's series)	Cambridge area

CAMSM B20659	Partial rostrum	*Pervushovisaurus campylodon* (syntype, Carter's series)	Cambridge area
CAMSM B20671a	Rostrum	*Pervushovisaurus campylodon*	Barrington
CAMSM B75736	Atlas-axis	Ichthyosauria indet.	Cambridge area
CAMSM B42257	Centrum	Ichthyosauria indet.	Hunstanton
CAMSM TN282	Rostrum	*Pervushovisaurus campylodon*	(chalky part of the Cambridge Greensand Member, Cambridge area)
CAMSM TN283	Rostrum	Platypterygiinae indet.	(chalky part of the Cambridge Greensand Member, Cambridge area)
CAMSM unnumbered	Humerus (HM1 morphotype of Fischer et al. (2014b)	Platypterygiinae indet.	Cambridge area
NHMUK 5648	Teeth	Platypterygiinae indet.	?
NHMUK 33294 partim	Teeth	Platypterygiinae indet.	Isleham, Cambridgeshire

NHMUK 41367	Anterior tip of rostrum	Platypterygiinae indet.	?
NHMUK 41895	Anterior tip of rostrum	Platypterygiinae indet.	?
NHMUK R13	Teeth	Platypterygiinae indet.	?
NHMUK R49	Teeth	Platypterygiinae indet.	Lyden Spout, Folkestone
NHMUK R2335	Rostrum	Platypterygiinae indet.	?
NHMUK R2385	Fragmentary rostrum	Platypterygiinae indet.	?

Table 1. Important Grey Chalk Subgroup (minus most specimens from the Cambridge Greensand Member) specimens studied here.

Late Cretaceous ichthyosaur feeding guilds–The ecological dataset of Fischer et al. (2016) is updated by addition of novel data on the symphysis of '*Platypterygius*' *sachicarum* (E. Maxwell pers. com. 31/03/2016) and correction of erroneous value regarding the symphysis of the '*Platypterygius*' *hercynicus*. The updated dataset is provided in the Supplementary Information. As in the original publication, I submitted this data set to a cluster analysis in R using the Ward method. Data were scaled to have equal variances and transformed to a Euclidean distance matrix before clustering. Because the data is restricted to ecologically relevant measurements and with a strong emphasis on Cretaceous forms, the resulting dataset is small and contain a non-negligible proportion of missing values (39%), which renders usual bootstrapping methods inadequate. To cope with this issue, I assessed the statistical support of our cluster using the “Approximately Unbiased P-value” method of the pvclust v2.0–0 package (Suzuki & Shimodaira, 2015) in R. This method employs multiscaled bootstrapping: instead of simply bootstrapping the dataset, it creates multiple datasets that are smaller, equal and larger than the original dataset. I ran it from 0.5 times to 5 times the size of the original dataset, with 0.1 increments and 10,000 bootstrap per increment.

Nomenclatural acts–The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank,

STATE OF THE ART

Carter (1846a) established the name *Ichthyosaurus campylodon* in a conference abstract. His initial description is based on an articulated rostrum with numerous teeth that he described in a paper the same year (Carter, 1846b). In that paper, he figured two teeth and made clear that his collection contained several specimens, coming from both the Cambridge Greensand Member (which mixes earliest Cenomanian specimens with reworked fossils from the Late Albian of the underlying Gault Formation (Hopson, 2005; Fischer et al., 2014b) and the overlying chalk (i.e. the Grey Chalk Subgroup (Hopson, 2005)). It is therefore difficult to know which particular specimen was used to establish the species in its conference abstract, but relevant information can be extracted from the specimens from his collection, which are now housed in the Sedgwick Museum of the University of Cambridge, UK (CAMSM).

Huene (1922) assigned this species to the genus *Myopterygius* Huene, 1922 and created another genus, *Platypterygius* Huene, 1922 for reception of a single species from the Lower Aptian of Germany, *Platypterygius platydactylus* (Broili, 1907). McGowan (1972) then transferred all species belonging to *Myopterygius* to *Platypterygius*. He choose *Platypterygius* over *Myopterygius* as the single valid Cretaceous ichthyosaur genus "*Because* platydactylus *is the best known species, the genus* Platypterygius *is the most appropriate*" (McGowan, 1972: 18). Since Carter's and McGowan's publications, an overwhelming amount of Cretaceous ichthyosaur remain from Eurasia has been referred to *Platypterygius campylodon*, mostly by default (e.g. Kiprijanoff, 1881, 1883; Sauvage, 1882; Buffetaut, 1977; Buffetaut et al., 1981; Buffetaut, Tomasson & Tong, 2003). Some remains were referred to the species *Platypterygius kiprijanoffi* (Romer, 1968; Bardet, 1989), but these were subsequently assigned to as *Platypterygius campylodon* by McGowan & Motani (2003).

At the current state of our knowledge, *Platypterygius campylodon* is a vague entity with no clear-cut morphology nor any valid diagnostic feature, itself included in a poorly defined genus. As a matter of fact, the only diagnostic feature proposed by McGowan & Motani (2003) for *Platypterygius campylodon* is the probable presence of an "*External longitudinal groove*" (=fossa praemaxillaris/dentalis); such sulcus is actually present in all neoichthyosaurians I have examined so far. With no holotypic or syntypic material clearly identified as such and no diagnostic feature, this species had to be considered as a numen dubium.

McGowan & Motani (2003) attempted to solve this issue. They regarded the specimen SMC B20644 (=CAMSM B20644), "a 60-cm rostral fragment", as the presumed holotype for *Ichthyosaurus campylodon*, mainly because its size matched the length given by Carter ("*more than 2 feet*", p7 in (Carter, 1846b)). But there are several problems with that decision. Firstly, CAMSM B20644 is not a 2 feet-long rostrum but an isolated tooth listed as a syntype of *Ichthyosaurus campylodon* from Carter's collection; this tooth actually seems to be the tooth figured by Carter (p6, Figure a in (Carter, 1846b); see Figure 1). McGowan & Motani (McGowan & Motani, 2003: 120) actually figured a portion of another specimen, CAMSM B20671. CAMSM B20671 is actually more complete than figured in McGowan & Motani (2003) and has diagnostic features (see below), but that specimen is 790 mm, i.e. 2.59 feet long. CAMSM B20671 preserves the tip of both the rostrum and the mandible, whereas Carter clearly stated that the specimen he described lacked these parts (p7 in (Carter, 1846b)). Moreover, CAMSM B20671 is from Barrington quarry and the date written on the specimen is 1881, 35 years after Carter's original descriptions. While this date may be the acquisition date by the museum, all specimens from Carter's collection have a green label glued on them containing "*Presented by J. Carter Fsq.ES.G*"; CAMSM B20671 lacks such a label. Actually, there is not a single 2 feet long rostrum in the CAMSM that bears such label.

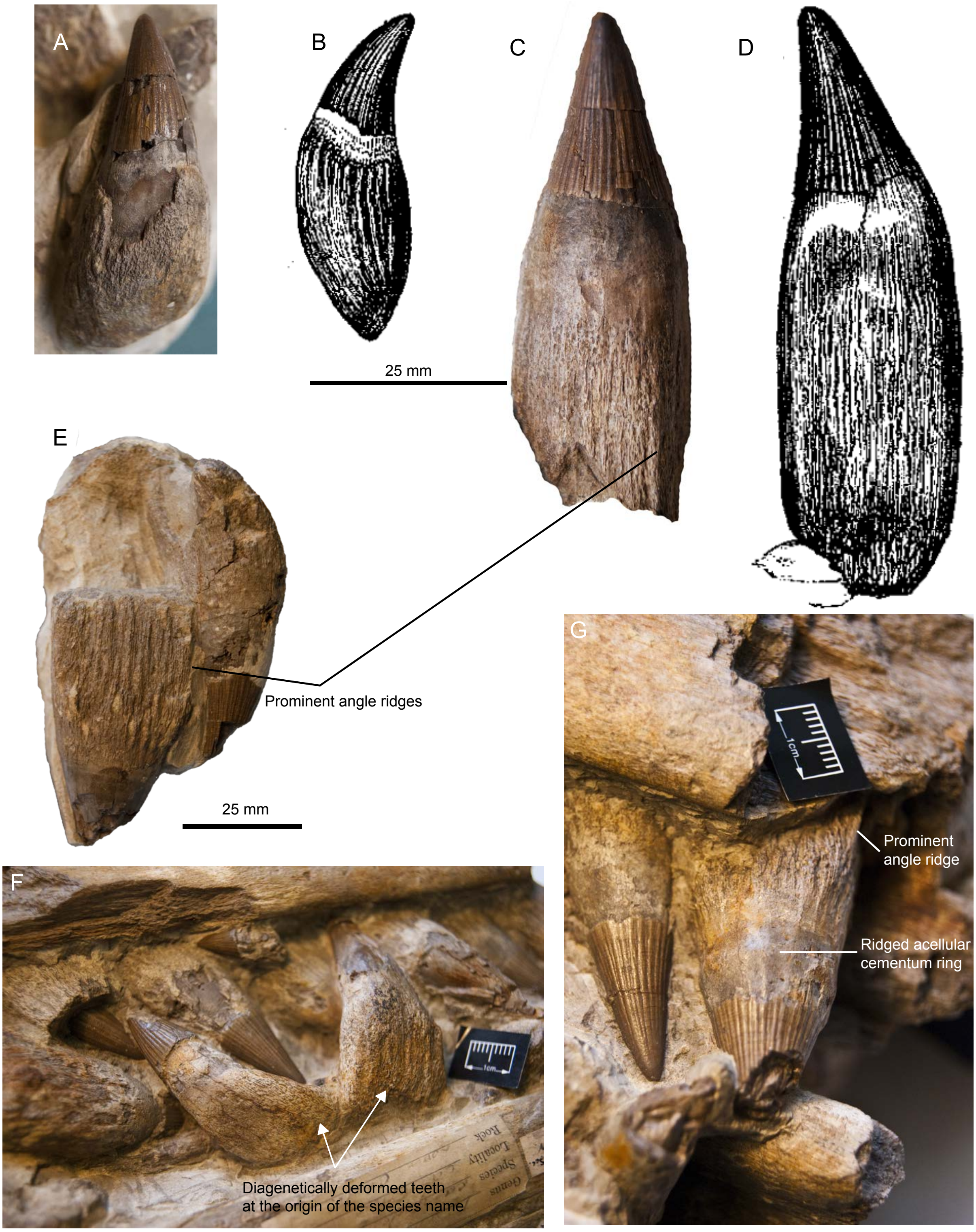

Figure 1. Syntypic material of *Pervushovisaurus campylodon* (Carter, 1846). (A) CAMSM B20645 a posterior tooth likely to be the one figured by Carter (1846b; (B)). This tooth cannot be unambiguously referred to *I. campylodon* and is regarded as Platypterygiinae

indet. (C) CAMSM B20644, a large mid-snout tooth, likely to be the one figured by Carter (1846b; (D). (E_G) CAMSM B20659, a partial rostrum; this specimen was figured by Owen (1851) (Pl. XXV). Note the markedly curved teeth of the lower jaw, considered by Carter (1846b) (and subsequent authors) as a diagnostic feature. This feature is doubtful and appears to be of diagenetic origin. (E) Small posterior tooth from CAMSM B20659. (F) Mid-snout dentary teeth from CAMSM B20659. (G) Mid-snout premaxillary teeth from CAMSM B20659.

There are other large rostra lacking the anterior tip in the CAMSM, but these lack most of their teeth, so these do not match Carter's description either. However, a fragmentary rostrum identified as belonging to Carter's collection (CAMSM B20659) possesses markedly curved teeth (Figures 1, 2). This is probably the material used by Carter to define the species (*campylodon* meaning 'bent tooth'), as the mandibular teeth appear markedly recurved compared to the (pre)maxillary teeth, matching Carter's description. Owen (Pl. XXV in (1851)) figured this specimen, which seemed to include a much longer portion of the rostrum at that time, thus possibly extending up to two feet. In the absence of better evidence, the holotype of *Ichthyosaurus campylodon* should indeed be considered as lost. However, there is an abundant material from the Grey Chalk Subgroup from Carter's Collection, and some specimens are clearly identified as being "*syntypes*": CAMSM B20659 and a series of teeth CAMSM B20644_58, containing the ones likely figured by Carter (1846b) (Figures 1, 2). This material can thus serve as a nucleus to redefine *Ichthyosaurus campylodon,* assess its supraspecific attribution and evaluate the diversity of the last European ichthyosaurs.

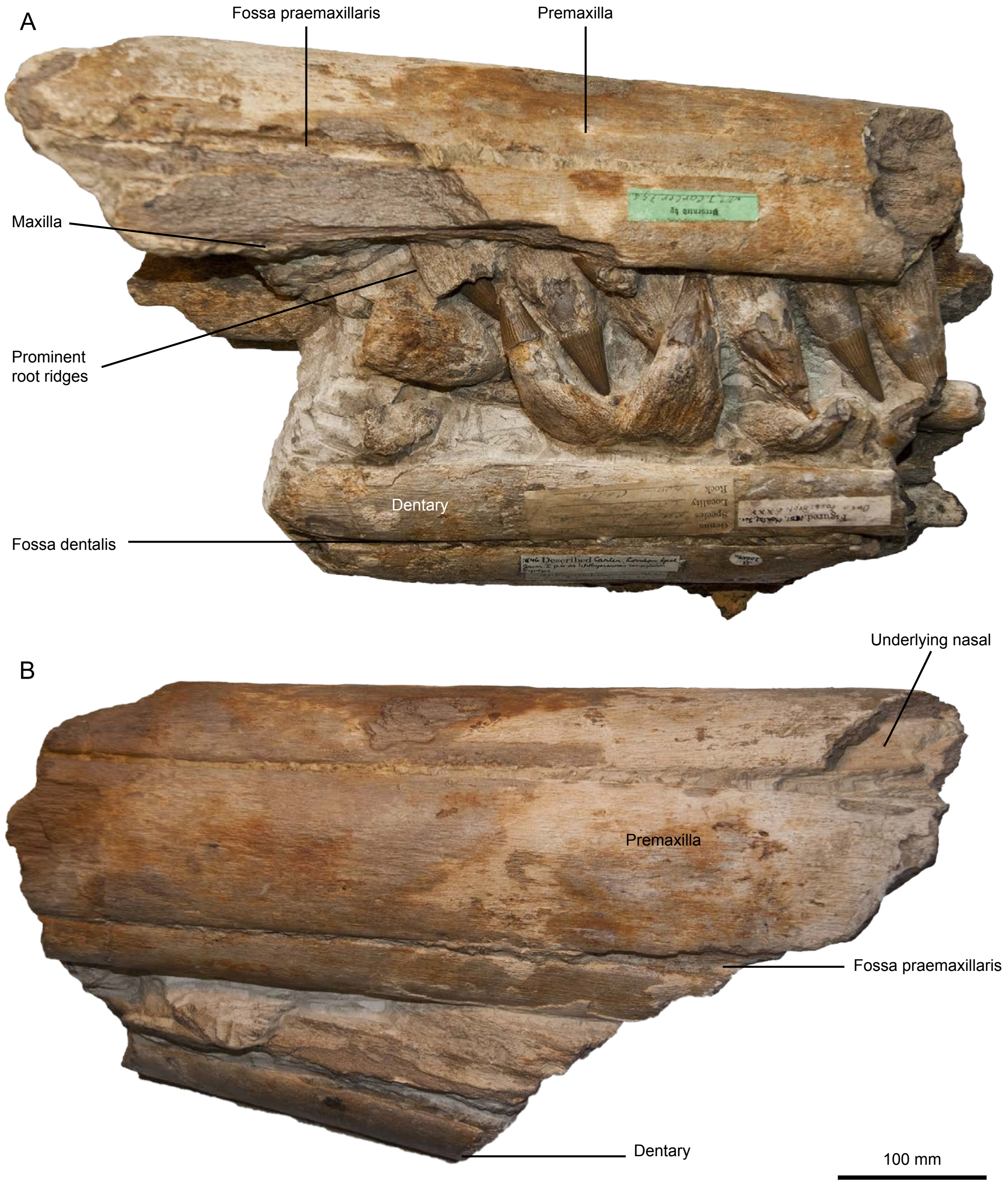

Figure 2. Designated holotype for *Pervushovisaurus campylodon* (Carter, 1846), CAMSM B20659. (A) Mid-snout fragment in right lateral view, showing the diagenetically deformed dentary teeth. (B) Same fragment in dorsolateral view.

SYSTEMATIC PALAEONTOLOGY

ICHTHYOSAURIA Blainville, 1835

THUNNOSAURIA Motani, 1999

OPHTHALMOSAURIDAE Baur, 1987

PLATYPTERYGIINAE Arkhangelsky, 2001 (sensu Fischer et al., 2012)

MYOPTERYGIUS Huene, 1922

Type species–*Ichthyosaurus australis* M'Coy, 1867

Diagnosis–Same as the type and only species. See Zammit (2010), Zammit et al. (2010) and Kear & Zammit (2014) for recent reviews of this species.

Stratigraphic range–Middle-Late Albian (Kear, 2003).

Geographic range–Australia~~,~~ (Kear, 2003).

PERVUSHOVISAURUS Arkhangelsky, 1998

Type species–*Pervushovisaurus bannovkensis* Arkhangelsky, 1998

Additional included species–*Pervushovisaurus campylodon* (Carter, 1846) nov. comb.

Emended diagnosis–(from Fischer et al., 2014a) Platypterygiine ophthalmosaurid characterized by the following autapomorphies (those marked by an asterisk cannot be assessed in the material referred to as *Pervushovisaurus campylodon*): presence of foramina along the ventral premaxillary–maxillary suture*; presence of a semi-oval foramen on the lateral surface of the premaxilla, anteroventral to the external naris*; presence of lateral ridges on the maxilla*; presence of wide supranarial 'wing' of the nasal (a similar structure, although much smaller, is present in *Myopterygius australis* and *Acamptonectes densus*)* (see Kear, 2005; Fischer et al., 2012, respectively); robust splenial markedly protruding from the external surface of the mandible; root with quadrangular cross-section, with the cementum forming prominent 90° angles.

Pervushovisaurus is also characterized by the following unique combination of features: secondarily closed naris surrounded by foramina* (as in '*Platypterygius*' *sachicarum* and *Myopterygius australis* (see Paramo, 1997; Kear, 2005, respectively), and in *Simbirskiasaurus birjukovi*, although the 'anterior' naris is still present in this taxon (Maisch & Matzke, 2000; Fischer et al., 2014a)); elongated anterior process of the maxilla, reaching anteriorly the level of the nasal (unlike in *Aegirosaurus leptospondylus*, *Sveltonectes insolitus* and *Muiscasaurus catheti*) (Bardet & Fernández, 2000; Fischer et al., 2011a; Maxwell et al., 2015, respectively); rostrum straight (unlike in '*Platypterygius*' *americanus*, '*Platypterygius*' *sachicarum*, *Myopterygius australis* and possibly *Muiscasaurus catheti*, where it is slightly curved anteroventrally (Romer, 1968; Paramo, 1997; Kear, 2005; Maxwell et al., 2015, respectively); straight, non-recurved tooth crowns (unlike in *Sveltonectes insolitus*, *Muiscasaurus catheti)* (Fischer et al., 2011a; Maxwell et al., 2015, respectively).

Stratigraphic range–Early-middle Cenomanian, Late Cretaceous.

Geographic range–Europe–western Russia.

PERVUSHOVISAURUS CAMPYLODON (Carter, 1846) nov. comb.

Figures 1–3

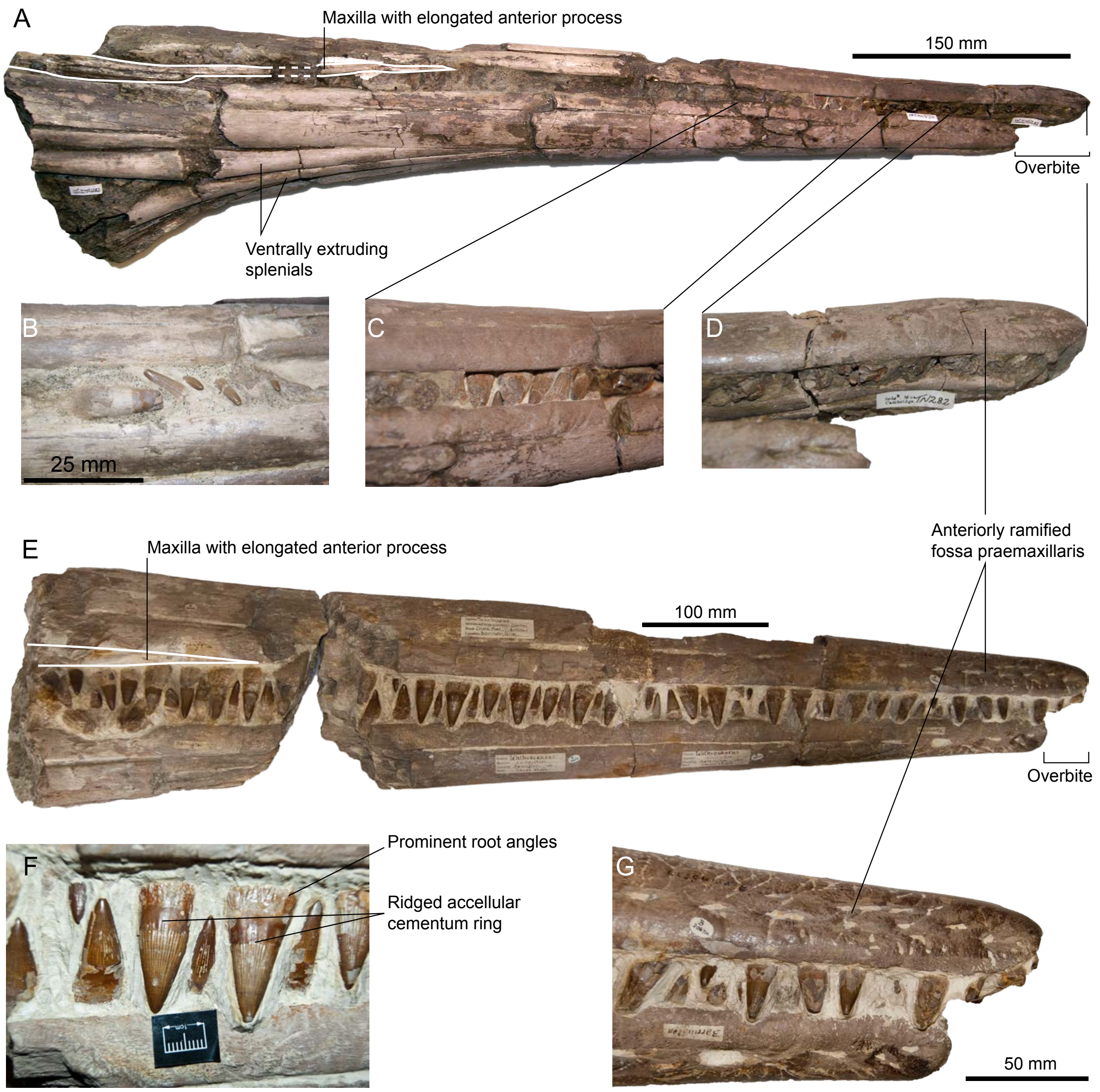

Figure 3. Rostra referred to *Pervushovisaurus campylodon* (Carter, 1846). (A_D) CAMSM TN282, a partial rostrum possibly from a juvenile specimen. (A) Ventrolateral view. (B_C) Details of the teeth. (D) Detail of the premaxillary overbite. (E_F) CAMSM B20671a,

a partial rostrum of a large specimen. (E) Lateral view. (F) detail of the mid-snout teeth. (G) Detail of the premaxillary overbite.

Syntype series and holotype–CAMSM B20644 to CAMSM B20658, a series of teeth (including two teeth likely figured in Carter 1846b; of these, CAMSM B20645 does not exhibit the diagnostic features of *Pervushovisaurus* and *Pervushovisaurus campylodon* and is referred as Platypterygiinae indet.); CAMSM B20659, a partial rostrum, all from the West Melbury Marly Chalk Formation (Early Cenomanian), Cambridgeshire, UK. CAMSM B20659 is here formally designated as the holotype.

Referred specimens–CAMSM B20671a and CAMSM TN282, two partial rostra from the upper (chalky) part of the Cambridge Greensand Member (earliest Cenomanian), Cambridgeshire, UK (the specific locality of CAMSM B20671a is recorded: Barrington); NHMUK 33294 partim, a nearly complete tooth lacking the apex and the distal part of the root, from the Grey Chalk Subgroup at Isleham, Cambridgeshire, UK; NHMUK R49, a series of articulated teeth from the Grey Chalk Subgroup at Lydden Spout, Folkestone, UK.

Emended diagnosis–*Pervushovisaurus campylodon* characterized by the following autapomorphy: slight overbite (3–4 cm). *Pervushovisaurus campylodon* is also characterized by the following unique combination of features: crown with rugose texture (shared with *Aegirosaurus* sp., '*Platypterygius*' *hercynicus* and '*Platypterygius*' sp. specimens from France and UK (Fischer et al., 2011b, 2014b; Fischer, 2012); acellular cementum ring possess shallow apicobasal ridges and furrows (shared with *Myopterygius australis*) (Maxwell, Caldwell & Lamoureux, 2011).

Type horizon and locality–Lower Cenomanian of the Grey Chalk Subgroup, Upper Cretaceous. Cambridge area, Cambridgeshire, UK.

Remarks–The designated holotype (CAMSM B20659), many teeth from rest of the syntypic series (CAMSM B20644_58) and the referred rostra (CAMSM B20671a, CAMSM TN282) each exhibit diagnostic features (Table 2). This material can be combined into a morphologically and spatiotemporally homogenous series that is distinguishable from the other ophthalmosaurid ichthyosaurs for which rostral and dental feature have been reported.

CAMSM TN283, a large rostrum also originating from the Grey Chalk Subgroup, Cambridgeshire, closely resembles CAMSM B20671a and CAMSM TN282, but the autapomorphies of *Pervushovisaurus campylodon* cannot be evaluated unambiguously in this specimen; it is thus referred to as Platypterygiinae indet. A series of teeth and tooth bearing elements from the Grey Chalk Subgroup collections of the NHMUK (NHMUK R1916, NHMUK R2335, NHMUK R2339, NHMUK 41895, NHMUK 47233, NHMUK 49911, NHMUK 52819) are, similarly, compatible with *Pervushovisaurus campylodon* in terms of tooth crown shape and size, maxilla anterior extension but cannot be unambiguously referred to as *Pervushovisaurus campylodon*; these are thus referred to as Platypterygiinae indet. as well.

Osteological feature	Carter's teeth (CAMSM B20644_56)	Syntypic rostrum (CAMSM B20659)	Referred rostra (CAMSM B20671a, CAMSM TN282)
Long maxilla	?	V	V

Prominent root angles	V	V	V
Rugose enamel	V	V	V
Ridged acellular cementum ring	V	V	V
Thickened splenial	?	?	V
Straight rostrum	?	?	V
Overbite	?	?	V

Table 2. Distribution of the diagnostic features of *Pervushovisaurus campylodon* nov. comb. among the available specimens.

DESCRIPTION AND COMPARISON OF *PERVUSHOVISAURUS CAMPYLODON*

Premaxilla (CAMSM B20659; CAMSM B20671a; CAMSM TN282; Figures 2,3)– The premaxilla is markedly elongated and has a semi-circular cross-section. Fossa praemaxillaris is a deep and continuous sulcus that is segmented anteriorly in a series of aligned foramina. As in some other Cretaceous ichthyosaurs, a complex network of the shallow grooves radiates from these foramina and textures the lateral surface of the premaxilla. In the anterior third of the rostrum, the dental groove is constricted between functional teeth, forming subtle pseudo-alveoli. The labial wall of the dental groove then becomes straight and thickens posteriorly. The premaxilla forms a slight overbite (4–5 cm), a unique feature among ophthalmosaurids. This overbite is genuine because premaxillary and dentary teeth are still tightly interlocked in the anterior part of the rostrum in these specimens (CAMSM TN282, CAMSM B20671a).

Maxilla (CAMSM B20659; CAMSM B20671a; CAMSM TN282; Figures 2,3)– The anterior process of the maxilla is elongated and its external extent reaches the level of emergence of the nasal, as in many platypterygiines, except *Aegirosaurus* and *Sveltonectes* (Romer, 1968; Kirton, 1983; Bardet & Fernández, 2000; Sirotti & Papazzoni, 2002; Fischer et al., 2011a,b) (note that Sirotti & Papazzoni (2002) interpreted the rostrum upside-down).

Dentary (CAMSM B20659; CAMSM B20671a; CAMSM TN282; Figure 3)–The dentary is elongated, semi-circular and slightly deeper than the premaxilla. Fossa dentalis is narrow and ends anteriorly as a series of aligned foramina. Like in the premaxilla, the labial wall of the dental groove is constricted between functional teeth in the anterior third of the dentary. It is straight, unlike in some other platypterygiines (‘*Platypterygius*’ *australis*, ‘*Platypterygius*’ *americanus* and ‘*Platypterygius*’ *sachicarum*(Romer, 1948; Paramo, 1997; Kear, 2005)). The dentary is reduced anteriorly, creating an overbite.

Splenial (CAMSM B20671a; CAMSM TN282; Figure 3)–The symphysis is 535 mm long in CAMSM TN282. The splenials are markedly thickened ventrally near the end of the symphysis, similar to the condition seen in *Pervushovisaurus bannovkensis* and regarded as one of the autapomorphies of this taxon (Fischer et al., 2014a).

Dentition (CAMSM B 20644_58; CAMSM B20659; CAMSM B20671a; CAMSM TN282; Figures 1–3)–The crown is conical, robust, and covered by rugose enamel (as in *Aegirosaurus* sp., ‘*Platypterygius*’ *hercynicus* and *Platypterygius* sp. (Fischer et al., 2011b, 2014b; Fischer, 2012). Smaller specimens like CAMSM TN282 tend to have slenderer teeth. The acellular cementum ring is ridged on large teeth, but only apically, as in ‘*Platypterygius*’ *australis* (Maxwell, Caldwell & Lamoureu[illegible]2011). The root possesses markedly flattened surfaces (mostly anterior and posterior ones); the root cement forms protruding ridges in between these facets, forming prominent and sharp ridges with a 90° angle cross-section, as in *Pervushovisaurus bannovkensis* (see Fischer et al., 2014a). This marks a sharp increase of the 'diameter' of the tooth, unlike in '*Platypterygius*' *hercynicus* and many other isolated teeth from the Cambridge Greensand Member (Kuhn, 1946; Fischer et al., 2014b), where the diameter increase gradually. Numerous apicobasal ridges texture the labial and lingual surfaces of the root. The dentary teeth of Carter's syntype (CAMSM B20659) are markedly bent inwardly, which lead Carter to propose the name "*campylodon*" for reception of this material. However, slightly bent teeth are commonly encountered in many ichthyosaur specimens (Sollas, 1916; McGowan & Motani, 2003). While the dental grooves of the dentary appear indeed slightly oblique with respect to the sagittal plane, the strong bent appears here to result from diagenetic compression. We consider this feature as poorly diagnostic, and only very few isolated teeth exhibit a similar curvature of the root.

CLUSTER DENDROGRAM RESULTS

The introduction of a relative symphysis value for '*Platypterygius*' *sachicarum* and correction of a miscoded value for '*Platypterygius*' *hercynicus* resulted in a displacement of '*Platypterygius*' *hercynicus* and '*Platypterygius*' *americanus*, two taxa with absolutely small crowns to the Generalist guild, from the Apex Predator guild (Figure 4). In the Apex Predator guild, *Brachypterygius extremus* and *Pervushovisaurus bannovkensis* now form a cluster; all other relationships are unchanged from Fischer et al. (2016). Confidence values are slightly increased in the new version of the cluster dendrogram, with an average bootstrap of 0.143 (vs 0.122 in Fischer et al. (2016)) and an average approximate unbiased *P* value of 0.988 (vs 0.982 in Fischer et al. (2016)). This change further supports the claim for the presence of diversified ichthyosaur ecomorphs during the Early/earliest Cenomanian, as '*Platypterygius*' *americanus* carries the Generalist guild up to the Early Cenomanian. The ecological diversity drop from 3 to 1 guild documented previously is still located in the Early Cenomanian but its timing remains imprecise, as discussed in Fischer et al. (2016).

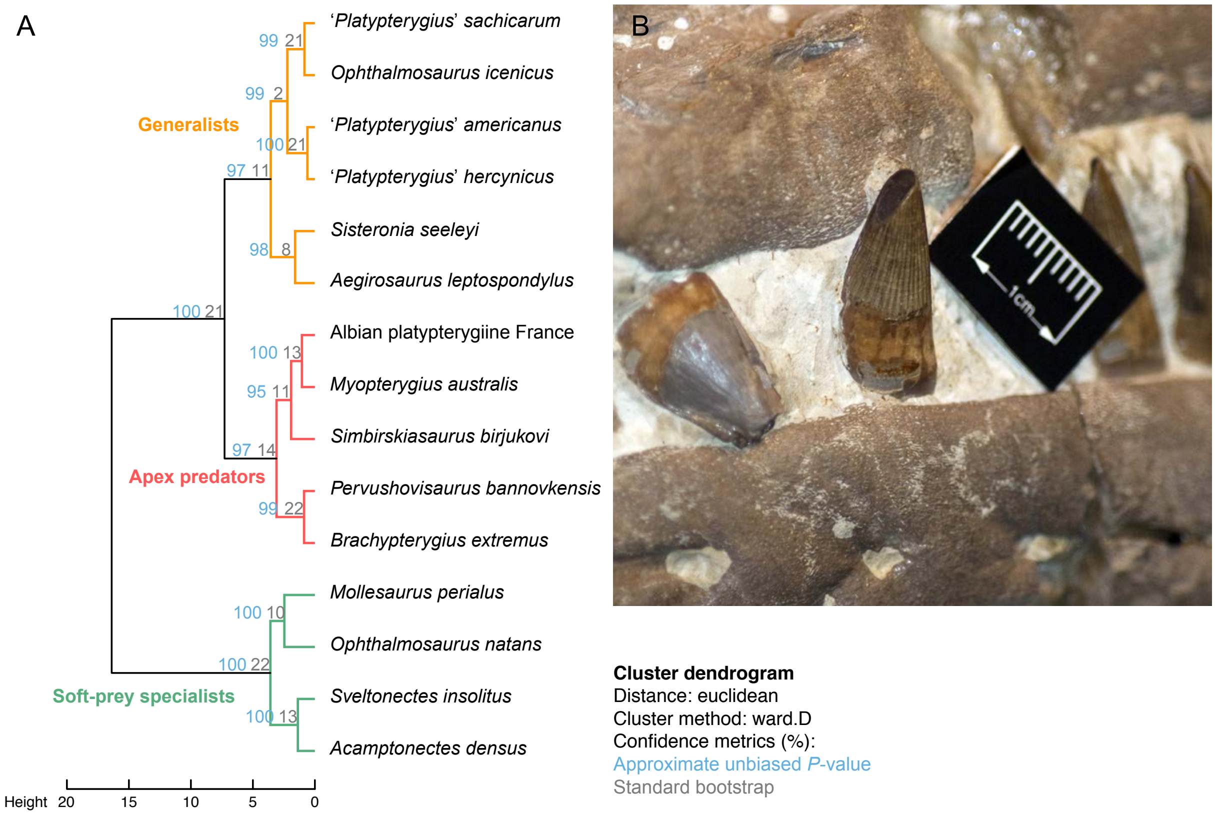

Figure 4. Feeding ecology of the last ichthyosaurs. (A) Cluster dendrogram resulting from the analysis of the updated ecological data set and showing separation of three main guilds. (B) Detail of spalled and subsequently polished apex in CAMSM TN283 (Platypterygiinae indet., closely resembling *Pervushovisaurus campylodon*).

DISCUSSION

Generic attribution of large Albian-Cenomanian platypterygiines–Because *Platypterygius* as traditionally conceived is a wastebasket taxon, incorporating taxa distantly related to the Aptian type species *Platypterygius platydactylus*, assigning Cretaceous specimen to this genus, by default is not advisable (Fischer et al., 2016). However, the genus-group name *Myopterygius* Huene, 1922 is available. It was erected for a series of species: *Ichthyosaurus campylodon*, *Ichthyosaurus strombecki* (=nomen dubium (Fischer et al., 2016)), *Ichthyosaurus hildesiensis* (=nomen dubium (Fischer et al., 2016)), *Ichthyosaurus kokeni* (here regarded as Ophthalmosaurinae indet. ; see Supplementary Information), *Ichthyosaurus indicus* (=nomen dubium (Fischer et al., 2016)) and *Ichthyosaurus marathonensis* (= *Ichthyosaurus australis* (see Zammit, 2010)). The species *campylodon* is the first one on the list. Before proposing the name *Myopterygius*, Huene (1922: 98) refers to the aforementioned species as the "Campylodongruppe" of Lydekker, reinforcing the idea that he probably intended *Ichthyosaurus campylodon* to be the equivalent of a type species for the genus *Myopterygius*. Resurrecting *Myopterygius* for reception of *Ichthyosaurs campylodon* would thus match the original interpretation of Huene, in a binomial that is still largely found in several museum collections across Europe. Yet, there are no systematic rules regarding the designation of originally included nominal type species. The ICZN lists the following rules and best practices in Recommendations 69A.1–10 (reproduced in the Supplementary Information of this paper).

There are thus two candidates for the type species of *Myopterygius*: *I. campylodon* and *I. marathonensis* (=*'Platypterygius*' (*Ichthyosaurus*) *australis*). The species '*Platypterygius*' *australis* is now known by abundant, excellently preserved material (Wade, 1984, 1990; Kear, 2005; Zammit, Norris & Kear, 2010) while *Ichthyosaurus campylodon* better represents the original intention of Huene and matches recommendations 69A.7, 69A.8, 69A.9, 69A.10 of the ICZN code, because *I. marathonensis* was poorly known when Huene published his work. Currently, the number of specimens referred to as '*Platypterygius*' *campylodon* is much larger than those referred to as '*Platypterygius*' *australis*, but the novel features found in the syntypic series of '*Platypterygius*' *campylodon* might result in a smaller number of specimens referable to this species. Nevertheless, because of the abundant quality material available for '*Platypterygius*' australis and because Fischer et al. (2016) found that '*Platypterygius*' australis is distantly related to *Platypterygius platydactylus*, I hereby proposed the resurrect the genus-group name *Myopterygius* and make *Ichthyosaurus* australis as its type species.

The type material of *Platypterygius platydactylus* and *Ichthyosaurus campylodon* are barely overlapping, precluding a referral to that genus. At the current state of knowledge, '*Platypterygius*' *australis* and '*Platypterygius*' *campylodon* do not share apomorphies; their rostral and dental similarities are plesiomorphic for platypterygiinae (Fischer et al., 2012). Most importantly, two peculiar features of *Ichthyosaurus campylodon* are shared with *Pervushovisaurus bannovkensis*: the prominent ridges forming 90° angles formed by the root cement in middle jaw/snout teeth and the ventrally protruding splenials. The type and only specimen *Pervushovisaurus bannovkensis* also exhibit an overbite (Fischer et al., 2014a), but the absence of teeth in situ precludes an unambiguous assessment of this feature in that taxon. Other differences between *Pervushovisaurus bannovkensis* and the syntypic material of *Ichthyosaurus campylodon* are the relatively smaller teeth in *Pervushovisaurus bannovkensis*. The presence or absence of the other autapomorphic features of *Pervushovisaurus bannovkensis* cannot be assessed on material presently available of *I. campylodon*. Because of the similarities between *Pervushovisaurus bannovkensis* and *I. campylodon*, I propose to refer the species *I. campylodon* to the genus *Pervushovisaurus*. While additional specimens are certainly required to better assess whether *Pervushovisaurus campylodon* and *Pervushovisaurus bannovkensis* are conspecific or not, this is another important step in the clarification of Cretaceous ichthyosaur taxonomy.

The diversity of the last European ichthyosaurs–Numerous other ichthyosaur specimens are present in the Grey Chalk Subgroup collections of the CAMSM and NHMUK (excluding the Cambridge Greensand member). These remains – mainly isolated teeth, centra and some basicranial bones – are compatible with derived platypterygiines and resemble ‘*Platypterygius*’ *hercynicus* (Kuhn, 1946; Kolb & Sander, 2009; Fischer, 2012) and the specimen of ‘*Platypterygius*’ cf. *kiprijanoffi* described by Bardet (1989) from the Cenomanian of northwestern France. I have been unable to find other specimens that unambiguously possessed the unique dental features of *Pervushovisaurus campylodon* in the CAMSM, NHMUK and RBINS collections. There are two non-mutually exclusive reasons for this: (i) the prominent root ridges might be restricted to a small region of the snout and (ii) two weakly divergent platypterygiine species might be present in the Grey Chalk Subgroup. This latter possibility is exemplified by NHMUK 41367, a partial rostrum that lacks an overbite (Figure 5), thus differing from the material hereby assigned to *Pervushovisaurus campylodon*. However, the overbite appears more strongly expressed in the smallest rostrum (CAMSM TN283) than in the largest (CAMSM B20671a) and might thus vary with ontogeny in *Pervushovisaurus campylodon*. If present, any additional ichthyosaur species in the Grey Chalk Subgroup appear generally similar to *Pervushovisaurus campylodon* in terms of general tooth shape and inferred ecological niche. These taxa would fall within the ‘Apex predator’ niche, having absolutely large teeth and robust, relatively large, and heavily worn crowns (apex broken and polished; wear stage 3 in (Fischer et al., 2016)). An example of intense wear can be seen on the rostrum CAMSM TN283 referred to as *Pervushovisaurus campylodon* (Figure 4): one of the crown has a significant portion of its apex spalled obliquely and polished. This is a rare wear stage for ichthyosaurs but common in so-called hypercarnivorous forms like the geosaurine metriorhynchid *Dakosaurus maximus* (Young et al., 2012) or tyranosaurid theropods (Schubert & Ungar, 2005). This suggests that *Pervushovisaurus* spp., one of the last ichthyosaurs, occupied an apex predatory niche of large size, as indicated by isolated large centra and humeri in the CAMSM and NHMUK collections. The Cenomanian ichthyosaur record from the Grey Chalk Subgroup thus conforms to the global pattern of a two-step decline, ichthyosaurs being restricted to a single morphotype and ecological guild from the Early Cenomanian onwards: a large and long-snouted predator with robust teeth.

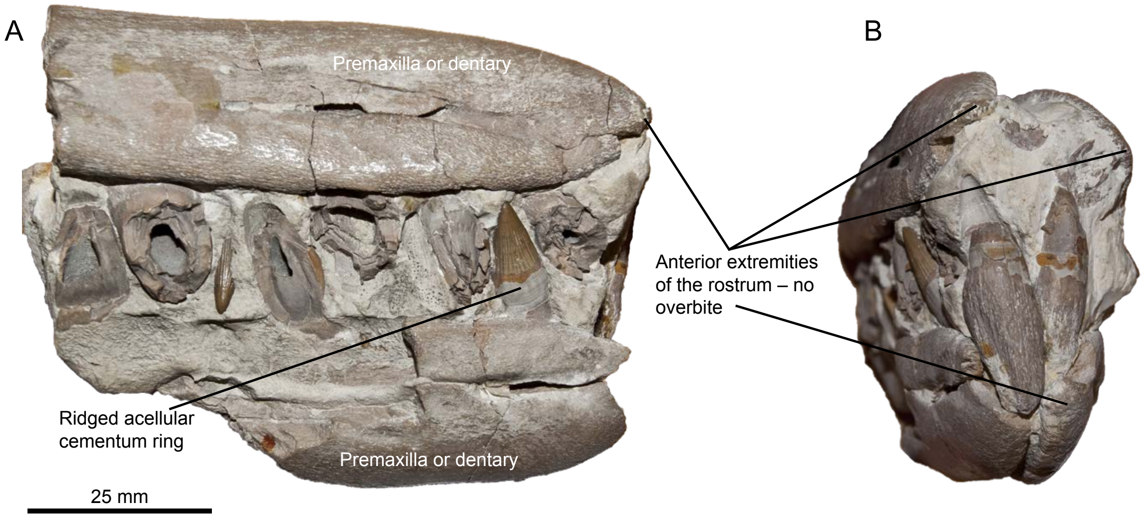

Figure 5. Possible second taxon in the Grey Chalk Subgroup. (A) Right lateral view. (B) Anterolateral view. Note the lack of a premaxillary overbite, as opposed to *Pervushovisaurus campylodon*, but the otherwise very similar teeth and rostrum shape, suggesting a similar ecological niche.

Yet, the small overbite in *Pervushovisaurus campylodon* raises questions regarding its function. Moderate to large overbite evolved among leptonectid ichthyosaurs during the Early Jurassic (Huene, 1951; McGowan, 1986, 1989, 2003; Lomax, 2016). Overbite is not recorded in ichthyosaur after the Toarcian and this feature re-evolved in *Pervushovisaurus campylodon*, after a 73 million years hiatus. A series of hypothetical functions of this feature have been made in the past (McGowan, 1979; Riess, 1986), including predatory (like a swordfish) and tactile (like a narwhal) functions (reviewed in Fischer et. al (2011)). Leptonectids and *Pervushovisaurus campylodon* exhibit complex network of shallow grooves radiating from the anterior part of the fossa praemaxillaris, but such structure is also present in taxa with no overbite, such as *Suevoleviathan* (Maisch, 2001) and yet undescribed forms from France (VF, pers. obs.). These groove probably housed blood vessels, but their concentration in the rostral tip might also be linked to a sensory function, as in *Rhynchops* birds, which feed under low light conditions (Racicot et al., 2014) and the recently described fossil phocoenid porpoise *Semirostrum cerutti*, which likely used its dentary overbite to probe the sediment (Racicot et al., 2014). While not a structural requisite, a slight overbite might ease such probing and might have evolved convergently between leptonectids, *Pervushovisaurus campylodon* (premaxillary overbite) and *Rhynchops* and *Semirostrum* (dentary overbite). However, *Pervushovisaurus campylodon* clearly differ from the aforementioned taxa in having much stouter and larger rostrum and teeth; thus probably consuming a wide range of prey types.

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