Ray-finned fishes (Osteichthyes, Actinopterygii) from the type Maastrichtian, the Netherlands and Belgium

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Ray-finned fishes are a diverse, but understudied, component of the Maastrichtian marine fauna of the southeast Netherlands (Limburg) and northeast Belgium (Liège-Limburg). The most extensive reviews of fishes from these uppermost Cretaceous deposits were made in the early and mid-Twentieth Century, but little research on this important assemblage has been executed since. The present paper provides figures and brief descriptions of fishes from the Maastrichtian type area as an aid for field identification of fossil discoveries. A simple key to common Maastrichtian fish teeth from this area is also included. All convincing records of ray-finned fishes from the Maastrichtian of the Netherlands and Belgium, inclusive of the Mons Basin, are teleosts, and include both stem- and crown-group members. Higher teleost clades reported here are: Pycnodontiformes (Pycnodontidae), Pachycormiformes (Pachycormidae), Aspidorhynchidiformes (Aspidorhynchidae), Ichthyodectiformes (Saurodontidae), Pachyrhizodontoidei (Pachyrhizodontidae), Aulopiformes (Apateopholidae, Cimolichthyidae, Dercetidae, Enchodontidae), Polymixiiformes (Polymixiidae), Trachichthyiformes (family *incertae sedis*) and Tetraodontiformes (family *incertae sedis*).

Contents

Introduction

Most work on the ray-finned fishes from strata of Maastrichtian age in northeast and southern Belgium, and the southeast Netherlands took place during the late Nineteenth and early Twentieth centuries (Davies, 1878; Forir, 1887, 1889; Woodward, 1891a; Dollo, 1889, 1892, 1893; Kruizinga, 1924; Leriche, 1929). Individual components of the assemblage have since been revisited (Kruizinga, 1952; Goody, 1968, 1969), but few new taxa have been recorded, and subsequent reviews of the fish fauna have been limited in both scope and detail (Albers & Weiler, 1964; Lambers, 1998; Gallagher *et al.*, 2004). As a consequence, the bony fishes represent the component of the Maastrichtian assemblage where future study and collecting are most likely to lead to important new

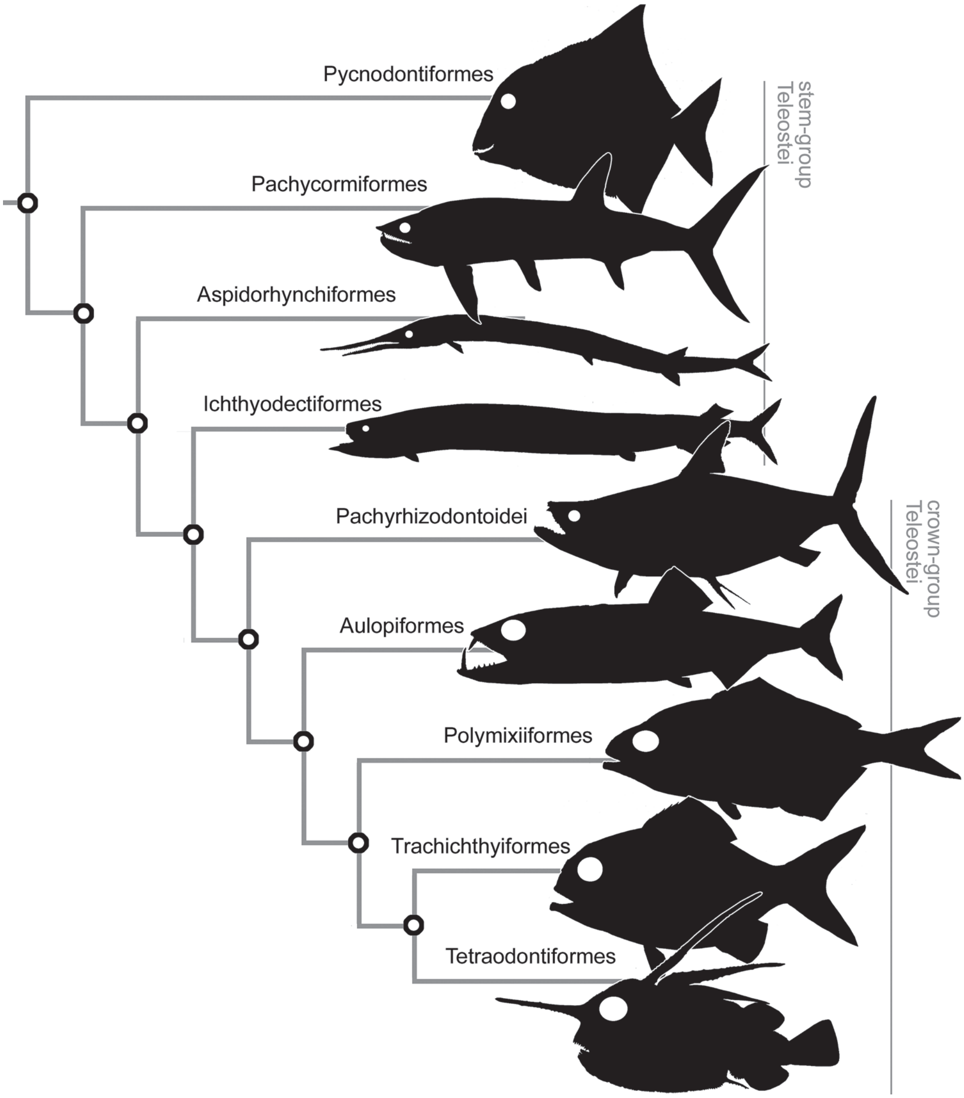


Fig. 1. Phylogenetic relationships of the major groups of ray-finned fishes found in Maastrichtian deposits of the southeast Netherlands and northeast Belgium, plus the Mons Basin (southern Belgium). The cladogram is a composite of the hypotheses presented by Patterson (1977), Johnson & Patterson (1993), Gardiner *et al.* (1996) and Cavin (2001b). Silhouettes of stem-group and crown-group teleosts are offset from each other.

discoveries. Indeed, the recent efforts of amateurs have yielded a diversity of fish remains, some of which belong to groups previously unknown from these deposits (see Lambers, 1998). This has resulted in a considerable expansion of faunal lists in comparison to previous efforts, and the present note introduces several major groups new to the Maastrichtian of Belgium and the Netherlands (Dercetidae, Polymixiidae and

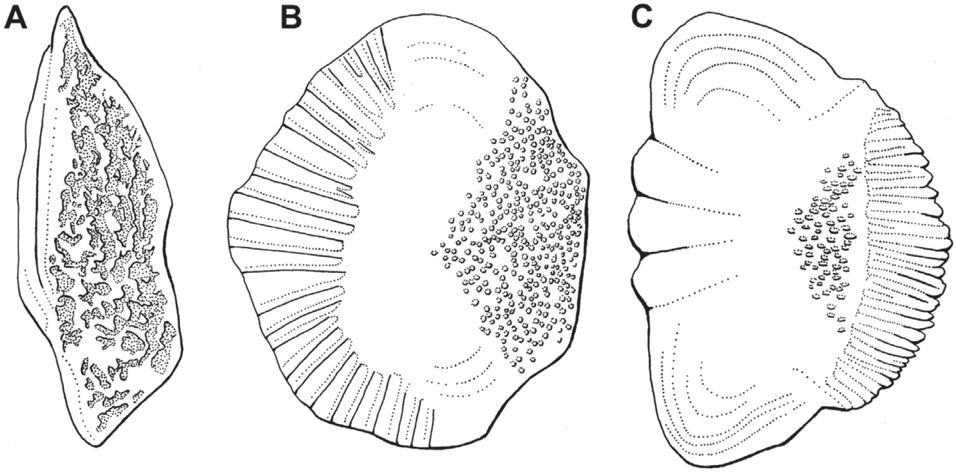


Fig. 2. The three major kinds of bony fish scales, shown in external view with anterior to the left. (A) Ganoid scale of the pycnodont *Anomoeodus* (this class of scale is also found in aspidorhynchids, but differs in exact form from that shown here). (B) Cycloid scale of an ichthyodectidiform (this class of scale is also found in pachyrhizodontids, but differs in exact form from that shown here). (C) Ctenoid scale of a spiny-finned teleost (*Hoplopteryx*). Images not to scale and based on illustrations in Woodward (1902-1912).

Tetraodontiformes). None of these new forms have been formally described or subjected to detailed study, so the identifications given here must be considered provisional pending further analysis. Previously reported fishes have been placed within the existing taxonomic framework, with the acknowledgement that this might be subject to change upon future revision. However, most uncertainties concern old species-level assignments and it is unlikely that most genus-level attributions cited here will change substantially upon further review.

The Maastrichtian fish fauna of Belgium and the Netherlands is particularly important for understanding patterns of turnover associated with the Cretaceous/Paleogene (K/Pg) extinction (Cavin, 2001a; Friedman, 2009, 2010). This assemblage bears a close resemblance to those from older marine sequences in North America (Russell, 1988; Everhart, 2005; Shimada & Fielitz, 2006) and elsewhere in Europe (Woodward, 1902-1912; Ekrt *et al.*, 2008), as well as contemporaneous deposits of the Middle East (Chalifa & Lewy, 1991; Kadummi, 2006), and the east and west coasts of the United States (Fowler, 1911; David, 1946; Gallagher, 2003; Gallagher *et al.*, 2004). These deposits preserve a diverse array of teleosts and teleost relatives, many of which belong to extinct groups (Fig. 1). The remains of large, predatory fishes are the commonest finds, presumably because of the size and robustness of their bones and teeth. The Maastrichtian strata of the type area of that stage record some of the last reliable occurrences of these predators, which appear to have been devastated during the end-Cretaceous extinction (Cavin, 2001a; Friedman, 2009). While articulated or associated fish remains are known, these are comparatively rare; isolated teeth or portions of jaw, scales (Fig. 2) and vertebral centra are more likely discoveries. Of these, teeth or fragments of tooth-bearing bones are the most likely to be diagnostic, so many descriptions included here place an emphasis on details of the dentition. A simple key is given as an Appendix at the end of this paper to aid in the identification of the commonest types of teeth found in Maastrichtian deposits. As this contribution is intended as a field guide, anatomical accounts provided below are intentionally brief and avoid technical language.

The most important collections of fishes from the Maastrichtian of the Netherlands and Belgium, inclusive of the Mons Basin, are housed at The Natural History Museum, London (NHM), the Nederlands Centrum voor Biodiversiteit Naturalis, Leiden (RGM-NCB), the Natuurhistorisch Museum Maastricht, Maastricht (NHMM), Teylers Museum, Haarlem, and the Institut Royal des Sciences Naturelles de Belgique, Brussels (IRScNB). All material described herein is deposited in one of these museums and the final three institutions exhibit Maastrichtian fishes in their public displays at the time of publication. Throughout, I follow the stratigraphic framework for the Cretaceous of Belgium and the Netherlands outlined in Robaszynski *et al.* (2002), Robaszynski (2006) and Jagt & Jagt-Yazykova (2012). In the Maastrichtian type area (southeast Netherlands and northeast Belgium), the most important fish-bearing units of Maastrichtian age are the Vijlen and Lanaye members of the Gulpen Formation, and all members of the Maastricht Formation. For comparison, both coeval and slightly older assemblages from the Mons Basin in southern Belgium are included here; these stem from the Ciply-Malogne Phosphatic Chalk Formation, of early Maastrichtian age.

Systematic palaeontology

Taxa reviewed in the present contribution are limited to material that I examined first hand and to published occurrences that can be corroborated on the basis of illustrations or detailed descriptions. I have been unable to confirm records of three nominal actinopterygian genera included in a previous faunal list, namely *Lepisosteus*, a garpike; *Paralbula*, a bonefish, and *Stephanodus*, a form taxon that has been associated with a number of fish groups (compare Gallagher, 2003), but for which there is no further documentation. The form taxon *Cylindracanthus* (not illustrated) is not included below, although it does occur in both the Ciply-Malogne Phosphatic Chalk (NHM P5838; compare Woodward, 1891b; Leriche, 1929) and Maastricht (NHMM K 2411) formations. Remains attributed to *Cylindricanthus* comprise long, cylindrical rods terminating distally in a pointed tip and ornamented with longitudinal ridges separated by grooves. Internal canals, either median or paired, extend for the length of the structure, and are often visible in transverse breaks. *Cylindracanthus* has endured a tumultuous systematic history, being variously associated with chimaeroids (chondrichthyans related to sharks and rays), tetraodontiforms, billfishes (see summary in Schultz, 1987) and, most recently, sturgeons (Parris *et al.*, 2001). This taxonomic uncertainty is complemented by diverging morphological interpretations; *Cylindracanthus* remains have been described as either fin spines or rostra. None of these interpretations is altogether satisfactory and no specimen of *Cylindracanthus* has ever been found associated with additional skeletal remains that provide further clues to either its systematic position or anatomical identity.

Class Osteichthyes Huxley, 1880 (*sensu* Friedman & Brazeau, 2010)
Subclass Actinopterygii Woodward, 1891b
Teleostei Müller, 1844 (*sensu* de Pinna, 1996)

Remarks – The bony fishes include two major divisions. Living sarcopterygians comprise the lobe-finned coelacanth and lungfishes, and, perhaps unexpectedly, the terrestrial vertebrates or tetrapods. Actinopterygians, or ray-fins, include the vast majority of vertebrates conventionally thought of as 'fish.' Most modern ray-fins are teleosts, the only exceptions being garpikes, bowfins, bichirs, sturgeons and paddlefishes, which together constitute fewer than 50 living species in comparison to over 26,800 extant teleosts (Nelson, 2006).

The Maastrichtian deposits of Belgium and the Netherlands have yielded the remains of several extinct groups that are more closely related to teleosts than any other extant ray-fins, but cannot be placed within the radiation defined by living teleosts, which is known as the teleost crown group. These fossil forms are said to belong to the teleost stem group (Fig. 1). They are listed here by increasing phylogenetic proximity to the extant teleosts, based on a synthesis of the systematic arrangements proposed by Patterson (1977) and Gardiner *et al.* (1996).

Order Pycnodontiformes Berg, 1937

Remarks – Pycnodontiforms are a morphologically diverse radiation of deep-bodied, stem-group teleosts that superficially resemble modern reef fishes (Fig. 1) and probably occupied similar ecological roles. The most distinctive feature of pycnodontiforms is their crushing dentition, which comprises a series of stout teeth borne on the median vomer of the palate and paired lower crushing surfaces formed by similar dentition on the prearticulars of the lower jaw. These robust dentitions are by far the most frequently encountered pycnodontiform remains in the fossil record, and the only material of this group known from the Maastrichtian of Belgium and the Netherlands. Although common during the Mesozoic, pycnodontiforms appear to have been ecologically supplanted by spiny-finned teleosts in the Cenozoic (Friedman, 2010; Goatley *et al.*, 2010), with the latest surviving examples known from the middle Eocene (Poyato-Ariza & Wenz, 2002).

Family Pycnodontidae Agassiz, 1833 *sensu* Poyato-Ariza & Wenz, 2002
Genus *Anomoeodus* Forir, 1887

Remarks – Three species of *Anomoeodus* are known from the Maastrichtian of Belgium and the Netherlands, of which *A. subclavatus* is the commonest and most widely distributed (Jagt & Dols, 2010). Features used to differentiate these species concern subtle details of the lower jaw dentition (Leriche, 1929). The reliability of phylogenetic placements of pycnodonts based on dental features alone has been questioned (Poyato-Ariza, 2003) and it is possible that taxonomic revision of Maastrichtian *Anomoeodus* will result in changes to the historical classification scheme presented herein. Upper crushing surfaces are also known (Fig. 3A), but since these have not been found in association with diagnostic lower dentitions, Maastrichtian pycnodont vomers from the

Netherlands and Belgium cannot be identified more precisely than *Anomoeodus* sp. *Anomoeodus* is restricted to the Mesozoic (J.A. Kriwet, pers. comm., September 2011; *contra* Kriwet, 2002), with the most complete remains from the Lower Cretaceous of Spain (Kriwet, 1999), and the Upper Cretaceous of England (Woodward, 1902-1912; Kriwet, 2002) and Bohemia (figured as *Pycnodus cretaceous* by Fritsch, 1878, pl. 2, figs 1-4). These specimens indicate that *Anomoeodus* – unlike most other fishes known from the Maastrichtian of Belgium and the Netherlands – bore a partial coat of rhombic ganoid scales of the sort primitive for bony fishes (Friedman & Brazeau, 2010). These ganoid scales assume a lozenge-like shape in *Anomoeodus*, with a narrow dorsal peg, and are ornamented on their external surface with an irregular network of ridges (Fig. 2A). Such scales have yet to be reported from the Maastrichtian of Belgium and the Netherlands, and it is possible that these latest Cretaceous examples of *Anomoeodus* were naked.

Anomoeodus foriri Leriche, 1929

Fig. 3B.

Description – The main row of the prearticular dentition is composed of oval-shaped teeth with their long axes oriented obliquely to the long axis of the underlying bone. The anterior margins of these principal teeth are convex to slightly concave. Successive principal teeth are similar in size, giving this row mesial and lateral edges that are nearly parallel. Irregularly spaced circular teeth flank this primary row both laterally and mesially.

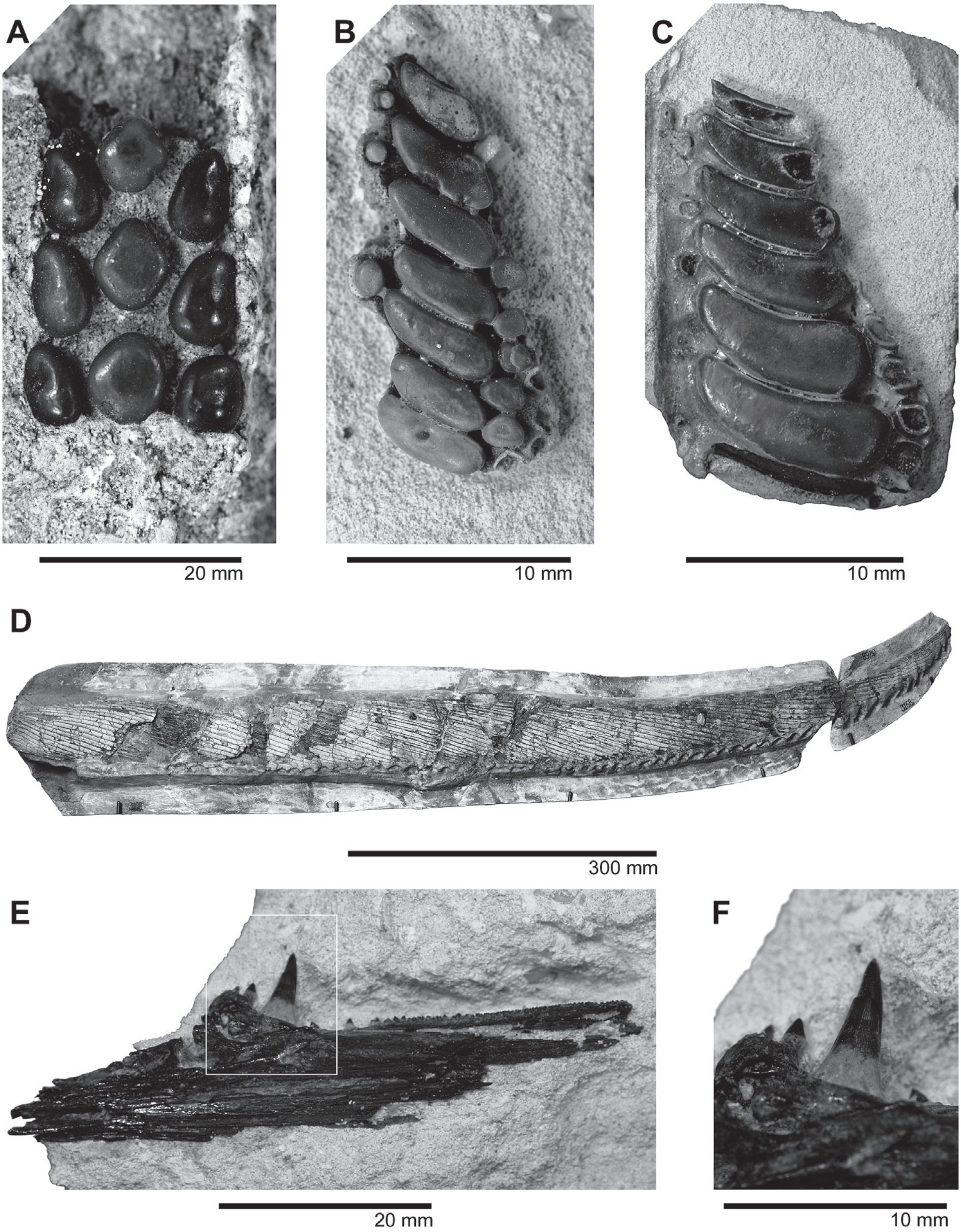
Occurrence – All known specimens of *Anomoeodus foriri* are from unspecified levels within the Maastricht Formation in the St Pietersberg area, south of Maastricht, the Netherlands (Leriche, 1929, p. 269), with the exception of NHMM 001284 (see Fig. 3B), which is from the upper part of the Nekum Member.

Remarks – Teeth attributed to *A. foriri* differ only subtly from those assigned to the type species of the genus, *A. subclavatus*, which also occurs in the Maastrichtian type

►

Fig. 3. Stem-group teleosts from the Maastrichtian of the southeast Netherlands and northeast Belgium, and the Mons Basin (southern Belgium): Pycnodontidae, Pachycormidae and Aspidorhynchidae. (A) *Anomoeodus* sp., vomerine dentition (NHMM 003888), Maastricht Formation, unspecified level (probably Emael or Nekum Member), southern Limburg (locality details lacking), the Netherlands, shown in ventral (occlusal) view. (B) *Anomoeodus foriri* Leriche, 1929, right prearticular dentition (NHMM 001284), Maastricht Formation, upper Nekum Member, St Pietersberg, Maastricht, the Netherlands, shown in dorsal (occlusal) view. (C) *Anomoeodus subclavatus* (Agassiz, 1833), right prearticular dentition (NHMM 001283), Maastricht Formation, unspecified level (probably Emael or Nekum Member), Valkenburg aan de Geul, the Netherlands, shown in dorsal (occlusal) view. (D) *Protosphyraena ferox*, pectoral fin (IRScNB P 8781), Ciply-Malogne Phosphatic Chalk Formation, Mons Basin, southern Belgium, shown with leading edge facing bottom. (E, F) *Belonostomus* sp., probable mandibular fragment (NHMM 2011 051, leg. Tom Veldkamp), Maastricht Formation, basal Emael Member, Eben-Emael (Liège), northeast Belgium. (E) Lateral view; (F) close-up of large tooth framed by box in (E), showing differentiated acrodin cap and striated shaft.

area (see below). I have maintained *A. foriri* as a distinct taxon here in order to reflect current taxonomies, but it is possible that this nominal species simply reflects end-member variation within *A. subclavatus*. A quantitative survey of *Anomoeodus* from the Maastricht Formation is necessary to select between these two alternative interpretations.



Anomoeodus fraiponti **Forir, 1889**

Description – Prearticular dentition with a main row consisting of a few oblong teeth posteriorly and bead-shaped teeth anteriorly. This primary row is flanked laterally by multiple rows of small, subcircular teeth.

Occurrence – The type specimen of *Anomoeodus fraiponti* originates from an unspecified level (?Emael Member) within the Maastricht Formation at Sibbe, near Valkenburg aan de Geul, the Netherlands (Forir, 1889, p. 450 [86]). No recent finds are known.

Anomoeodus subclavatus **(Agassiz, 1833)**

Fig. 3C.

Description – The prearticular dentition comprises a main row of kidney-shaped teeth with their concave faces oriented anteriorly. The width of successive teeth in the principal row increases from anterior to posterior, giving this dental series strongly divergent lateral and medial margins. The principal row is flanked mesially by a row of small, subcircular teeth and laterally by multiple rows of teeth that decrease in size towards the outer margin of the tooth plate.

Occurrence – *Anomoeodus subclavatus* is the most commonly encountered species of this genus in the Maastrichtian of northeast Belgium and the southeast Netherlands (Jagt & Dols, 2010). It is known from various levels within the Maastricht Formation (Gronsveld, Emael, Nekum and Meerssen members) in the St Pietersberg area, from Bemelen, Berg en Terblijt, Geulhem and Valkenburg aan de Geul in the Netherlands, and Vroenhoven and Kanne in Belgian Limburg. Finds in southern Belgium (Mons Basin) and Brabant derive from the Ciply-Malogne Phosphatic Chalk Formation, and the base of the Saint-Symphorien Calcarenite Formation at Ciply and Spiennes, and the Jauche Member at Jandrain, Jauche and Folx-les-Caves (see Leriche, 1929, p. 267).

Order Pachycormiformes Berg, 1937

Remarks – Pachycormiforms are a group of extinct teleosts found in marine deposits ranging in age from the Early Jurassic to the Late Cretaceous. Most pachycormiforms appear to have been fast-swimming, open-water fishes, ecologically similar to modern-day tunas and swordfishes (Lambers, 1992; see Fig. 1). In addition to these moderately sized predators, this group also contains a long-lived radiation of large-bodied suspension feeders (Friedman, in press) including the Jurassic *Leedsichthys* (Liston, 2008) and Cretaceous *Bonnerichthys* (Friedman *et al.*, 2010).

Family Pachycormidae Woodward, 1895

Genus *Protosphyraena* Leidy, 1857

Protosphyraena ferox **Leidy, 1857**

Fig. 3D.

Description – Large, laterally compressed teeth with convex, unserrated cutting edges on posterior and anterior margins. Teeth are typically set within shallow sockets, although they can be fused to the underlying bone. There is a long, pointed rostrum with rounded cross section and irregular external ornament. Pectoral fins are narrow and scythe-shaped, composed of tightly appressed fin rays that do not segment or bifurcate. The leading edge of the pectoral fin is distinctively scalloped.

Occurrence – To date, Maastrichtian material of *Protosphyraena* from the study area is known exclusively from the Ciply-Malogne Phosphatic Chalk Formation at Ciply (Mons Basin). Stratigraphically older Belgian remains of this genus, in the form of isolated teeth, have been recorded from the late Campanian Spiennes Chalk Formation at Lonzée and the early Campanian Folx-les-Caves Member in Brabant (Leriche, 1929, p. 273).

Remarks – The Maastrichtian *Protosphyraena* material from Belgium comprises an anatomically distinctive pectoral fin (Dollo, 1893; Leriche, 1929; see Fig. 3D). Other aspects of the anatomy of this genus, based on more complete remains from the USA and England, have been reviewed above to aid in the identification of future finds. Dollo (1893) assigned Belgian material to *Protosphyraena ferox*, the type species of the genus that is known from the English Chalk (Woodward, 1902-1912). The Belgian fossil shares with *P. ferox* a precisely crenulated anterior margin of the pectoral fin, but similar scalloping also characterises the North American *P. perniciosa* (Stewart, 1988) and the nominal Australian genus *Australopachycormus* (pers. obs., uncatalogued specimen at NHM). The taxonomy of *Protosphyraena* is in a confused state (Lambers, 1992), so Dollo's species-level attribution of the Ciply material should be treated cautiously. The Belgian fossil represents the youngest occurrence of this swordfish-like genus, which first appears in the Albian (Dineley & Metcalf, 1999). Maastrichtian material from the Moreno Formation of California attributed to *Protosphyraena* by David (1946) appears to belong instead to the suspension-feeding pachycormiform *Bonnerichthys* (pers. obs., Natural History Museum of Los Angeles County collections, LACM [CIT] 10125).

Order Aspidorhynchiformes Berg, 1937

Remarks – Aspidorhynchiforms are a group of superficially garpike-like stem teleosts that range in age from the Middle Jurassic to the end of the Cretaceous (Brito, 1997). The needle-like jaws of aspidorhynchidiforms bear a key character of the group: the predentary bone, a mid-line ossification that articulates with the lower jaw at the symphysis. Aspidorhynchidiforms bear rhombic scales that in some (but not all, such as *Aspidorhynchus* (Schultze, 1966)), taxa are coated with a shiny layer of enamel (often referred to as ganoine in ray-finned fishes; Friedman & Brazeau, 2010). These can be divided into two major morphological types: diamond-shaped scales of the form typically found in 'ganoid' fishes and tall, narrow flank scales that have a greatly extended dorsoventral axis.

Family Aspidorhynchidae Nicholson & Lydekker, 1889

Genus *Belonostomus* Agassiz, 1834b

Belonostomus sp.

Fig. 3E, F.

Description **–** Large teeth are ornamented with longitudinal ridges along the shaft and fluting near their bases, where they are fused to the underlying bone. Tips of teeth bear light-coloured acrodin caps that are compositionally distinct from the rest of the tooth. The predentary makes an oblique articulation with the dentary and bears a series of large teeth on its dorsal surface that are set within a median gutter (Taverne, 1998).

Occurrence – The Maastricht Formation yields remains of *Belonostomus* (Taverne, 1998), with records from the lower Emael Member. In southern Belgium, older material of this genus is known from the mid-Late Cretaceous Lonzée Member (Glauconie de Lonzée) near Gembloux, Namur (Leriche, 1929, p. 274).

Remarks **–** The teeth of *Belonostomus* bear two notable similarities to those of gars: ridged bases and acrodin caps. Gars are typically associated with freshwater depositional environments in the latest Cretaceous (e.g., Estes, 1964), so it is possible that reports of *Lepisosteus* from the Maastrichtian of Belgium and the Netherlands (e.g., Gallagher *et al.*, 2004) represent misidentified specimens of *Belonostomus*. The earliest fossils of *Belonostomus* are Late Jurassic (Kimmeridgian) in age (Brito, 1997; Forey *et al.*, 2003), making this genus, as currently defined, exceptionally long lived. An oblique, bevelled articulation between the predentary and dentary is characteristic of Albian and younger specimens of *Belonostomus* (including the Maastricht Formation material; Taverne, 1998). This has led to the suggestion that these species represent a distinct group that merits generic separation from stratigraphically older forms lacking this derived feature (Forey *et al.*, 2003). The Maastrichtian remains have not been identified to the species level, although Taverne (1998) noted similarities to the Turonian *B. cinctus* from the English Chalk (Woodward, 1902-1912).

Order Ichthyodectiformes Bardack & Sprinkle, 1969

Remarks – Ichthyodectiforms are an order of predatory stem teleosts that range in age from Middle Jurassic to Late Cretaceous. The most famous member of this clade is *Xiphactinus*, a giant (*c*. 5 m) genus known from numerous complete specimens from Upper Cretaceous deposits of the Western Interior Seaway of North America. Some of these individuals contain gut contents comprising other large fishes that were apparently swallowed whole (Everhart, 2005).

Family Saurodontidae Cope, 1870

Remarks – Within ichthyodectiforms, a set of three specialised Late Cretaceous genera, *Prosaurodon*, *Saurocephalus* and *Saurodon*, are united in the family Saurodontidae (= subfamily Saurodontinae, *sensu* Taverne & Chanet, 2000; see Fig. 1). These taxa differ from other ichthyodectiforms in several features, most notably the presence of a predentary bone in the lower jaw (Bardack & Sprinkle, 1969; Stewart, 1999). This edentulous ossification is triangular in saurodontids and is not homologous with the bone of the same name found in aspidorhynchidiforms such as *Belonostomus*.

Genus *Saurocephalus* Harlan, 1824
Saurocephalus woodwardii Davies, 1878
Fig. 4A-C.

Description – Teeth have small, triangular crowns bearing cutting edges on the anterior and posterior margins, which can be serrated. All teeth have long roots that insert into deep alveoli. Teeth are closely spaced and increase gradually in size towards the posterior end of the mandible. Vertebrae are cylindrical, with a diameter roughly equal to their length. The lateral face of each vertebral centrum bears two large, elliptical pits.

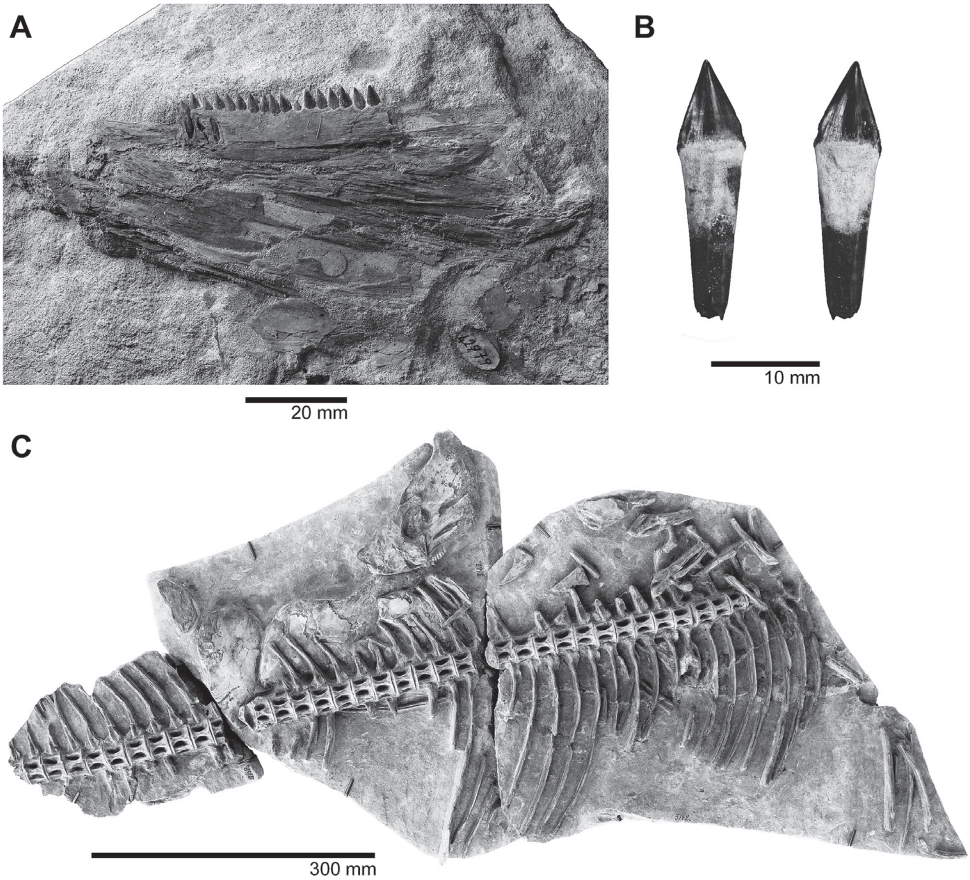


Fig. 4. Stem-group teleosts from the Maastrichtian of the southeast Netherlands and northeast Belgium, and from the Mons Basin (southern Belgium): Saurodontidae. (A) *Saurocephalus woodwardii* Davies, 1878 (holotype, NHM 42979), incomplete right mandible, Maastricht Formation, ?Maastricht area, the Netherlands, shown with anterior to left. (B) *Saurocephalus woodwardii* Davies, 1878, isolated tooth (NHMM K 3646), Maastricht Formation, basal Emael Member, Eben Emael (Liège), Belgium, showing both inner and outer surfaces. (C) ?*Saurocephalus woodwardii* Davies, 1878, cranial remains plus vertebral column with associated neural and haemal spines (IScNRB 8782), Ciply-Malogne Phosphatic Chalk Formation, Mons Basin, southern Belgium, shown in lateral view, with anterior to the right.

Occurrence – The type specimen of *Saurocephalus woodwardii* is from an unspecified level within the Maastricht Formation at Maastricht, the Netherlands. Additional saurodontid material material from the Ciply-Malogne Phosphatic Chalk Formation at Ciply (Dollo, 1892; Leriche, 1929) might also belong to this taxon.

Remarks – Some uncertainty surrounds the taxonomy of the saurodontid material from the Netherlands and Belgium. Bardack & Sprinkle (1969) drew attention to the close correspondence between figured material of *S. woodwardii* from the Maastricht Formation and the type species of the genus, *S. lanciformis*, from the Campanian of the Western Interior and Gulf Coast (Bardack & Sprinkle, 1969; Stewart, 1999), and the Maastrichtian of the Atlantic Coastal Plain (Fowler, 1911) in the USA. These authors tentatively maintained the assignment of the Limburg material to a second species on the basis of geographic separation, but it is possible that taxonomic revision will synonymise these two, in which case *S. lanciformis* has priority. I have attributed the Belgian saurodontid to *S. woodwardii* here, but note that this articulated material has never been subjected to detailed study and has endured a tortuous taxonomic history. These fossils were first mentioned by Dollo (1889, p. 272), who considered them most similar to *Daptinus* (= *Saurodon*) *intermedius* from the English Chalk, but later revised his identification to *Saurocephalus*. Leriche (1929, pp. 275, 286) subsequently attributed the Belgian remains to *Saurodon*. Dollo (1889, p. 272) also recorded additional remains he thought resembled those of another English Chalk ichthyodectiform, *Portheus* (= *Xiphactinus*) *mantelli*. However, he later concluded that these remains were not those of an ichthyodectiform and that the material could only be properly identified after preparation (Dollo, 1892, pp. 182, 183).

Incerti ordinis
Family Pachyrhizodontidae Cope, 1872

Remarks – Pachyrhizodontids are a small radiation of extinct marine teleosts containing fusiform, predatory fishes that range in length from about 200 mm (*Rhacolepis*) to nearly 2 m (*Pachyrhizodus*). Along with *Notelops* and *Elopopsis*, pachyrhizodontids are placed within the suborder Pachyrhizodontoidei. The relationships of pachyrhizodontoids to other fishes have been an area of some uncertainty (Forey, 1977), but it seems clear that they nest within the living teleost radiation (Cavin, 2001b).

Genus *Pachyrhizodus* Dixon, 1850
Pachyrhizodus sp.
Fig. 5A, B.

Description – Stout, conical teeth which lack cutting edges and are subcircular in cross section. Teeth are fused to the underlying bone, with a conspicuously swollen bony collar near their bases. Depressions on the inner surfaces of jaw bones occupy the broad gaps between successive teeth.

Occurrence – *Pachyrhizodus* occurs in both the Maastricht (e.g., NHM 42978a) and Ciply-Malogne Phosphatic Chalk (Dollo, 1892; Leriche, 1929) formations, although the precise level within the former unit cannot be indicated.

Remarks – With their expanded bony bases, the conical and widely spaced teeth of *Pachyrhizodus* can be easily confused with those of marine reptiles. Fragmentary fossils of *Pachyrhizodus* were misinterpreted as the oldest mosasaur remains known from North America before these specimens were correctly identified more than half a century after their initial description (Stewart & Bell, 1994). Along with fossils from the United States (David, 1946), Belgian and Dutch material of *Pachyrhizodus* marks the last occurrence of this genus, which first appears in the Albian of Australia and England (Forey, 1977).

Section Eurypterygii Rosen, 1973
Order Aulopiformes Rosen, 1973

Remarks – The most frequently encountered bony fish fossils in the Maastrichtian chalks are isolated, fang-like teeth of aulopiforms. Modern aulopiforms are an ecologically diverse group, found in environments ranging from coastal estuaries to the abyssal plain (Nelson, 2006). Many fang-like aulopiform teeth in old museum collections are indiscriminately labelled as *Enchodus* (Enchodontidae), but there are two other genera with similar, but readily distinguished, teeth from these deposits: *Apateodus* (Apateopholidae) and *Cimolichthys* (Cimolichthyidae). Dercetids are another group of aulopiforms found in the Maastrichtian, but these somewhat eel-like fishes are not easily confused with *Enchodus*, *Apateodus* or *Cimolichthys* (see below). Rostral teeth of sclerorhynchid sawfishes are relatively common finds in the Maastrichtian of Belgium and the Netherlands (Albers & Weiler, 1964; Herman, 1977), and fragmentary or eroded examples can be mistaken for aulopiform remains. However, complete sclerorhynchid teeth are distinctively kinked and bear a thickened, collar-like base often marked by fluting, making them easy to differentiate from aulopiform fangs.

Family Enchodontidae Woodward, 1901

Remarks – An extinct group of aulopiforms commonly found in Upper Cretaceous marine strata, enchodontids appear to be most closely related to living omosudids (hammerjaws) and alepisaurids (lancetfishes) (Fielitz, 2004), two families of predatory fishes that are today confined to the deep sea. Enchodontids bear an immense fang near the anterior tip of each mandible (Figs. 1, 5C, D, F). These symphysial fangs are so long that they are accommodated by a pair of fenestrations in the snout and their distal tips emerge the dorsal surface of the rostrum when the jaws are closed. The mandibular fangs of enchodontids are complemented by two enlarged palatal fangs, one on each palatine bone (Figs. 1, 5E).

Genus *Enchodus* Agassiz, 1835
Enchodus faujasi Agassiz, 1844

Fig. 5C-F.

Description – The lower jaw bears an enormous fang on the dentary bone, near the symphysis, that has only a single-bladed edge. The dentary fang, along with a near-homodont series of shorter teeth that follow it, are inset from the outer margin of the jaw. A series of smaller accessory teeth flank this primary row laterally. All teeth are fused to the underlying bone. The ventral margin of the jaw is marked by a series of finger-like projections, immediately below the dentary fang. The bulbous palatine bone of the palate bears a large fang complementing that on the lower jaw. The palatine fang differs from that of the dentary in having two cutting edges. Both fangs have a distinctive, sigmoidal profile and sometimes bear striations. There are approximately five, widely spaced, ectopterygoid teeth that decrease in size posteriorly. All teeth are unserrated.

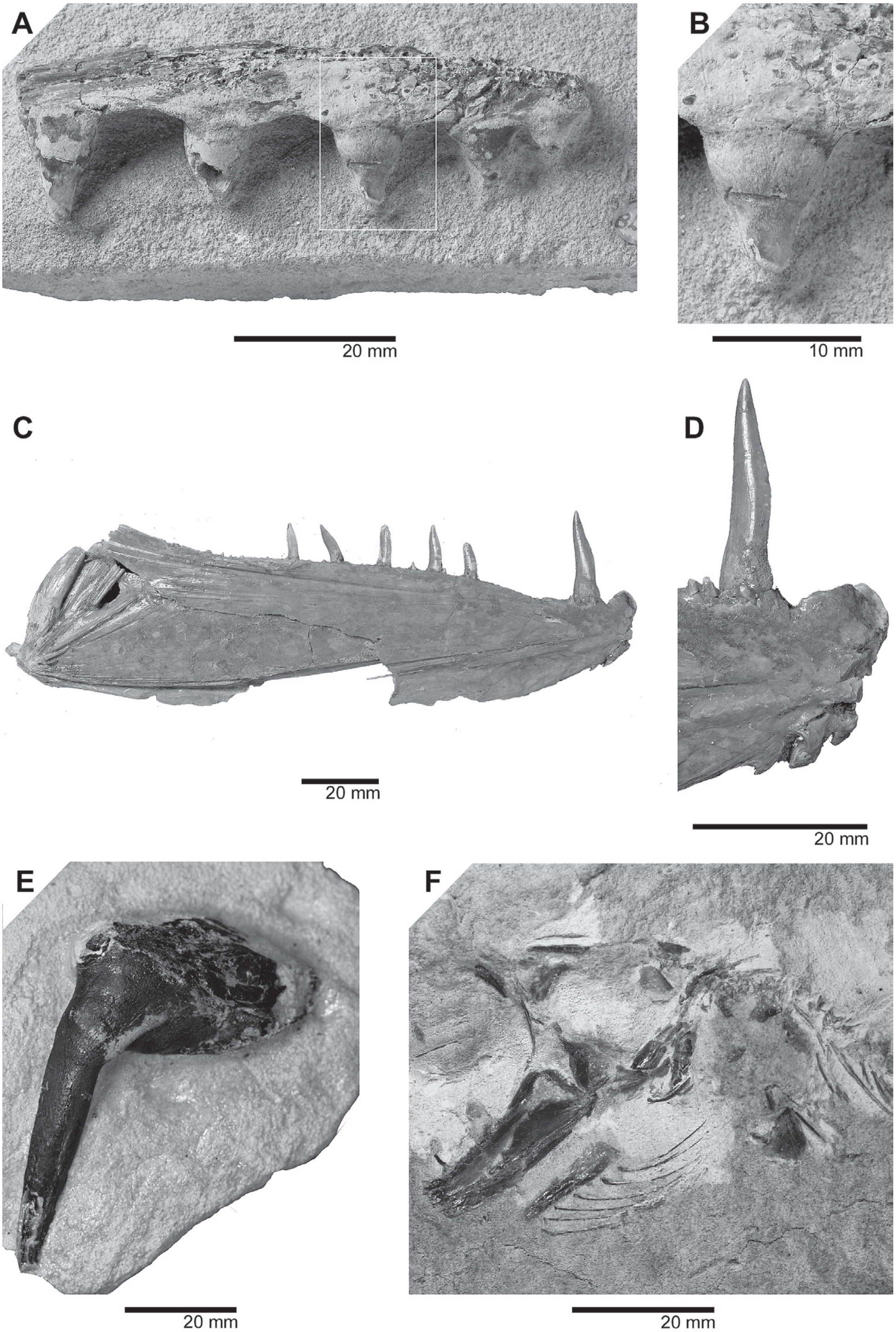
Occurrence – The Gulpen (Vijlen and Lanaye members), Maastricht (all members) and Ciply-Malogne Phosphatic Chalk formations yield fossils of *Enchodus* (Dollo, 1892; Leriche, 1929; Lambers, 1998). Stratigraphically older Belgian material attributed to this genus, mostly in the form of isolated teeth, comes from the mid-Late Cretaceous (Coniacian-Santonian) Lonzée Member of Namur, and the Turonian and Cenomanian of Hainaut (Leriche, 1929).

Remarks – Dollo (1892) considered that the Maastrichtian *Enchodus* material from Belgium and the Netherlands could be divided into two species: *E. faujasi*, from the Maastricht Formation, and *E. lemonnieri*, from the Ciply-Malogne Phosphatic Chalk Formation. In erecting *E. lemonnieri*, Dollo (1892) noted a series of features differentiating his Mons Basin material from Maastricht Formation specimens of *Enchodus*, most significant of which were the morphology of the dentary fang and the number of dentary teeth. However, Goody (1976) considered these dental traits to be variable within species of *Enchodus* and attributed both sets of fossils to a single species, *E. faujasi*. I have maintained this assignment here. Along with *Apateodus* (see below), *E. faujasi* is one of the few fishes from the type Maastrichtian that has been described in detail (on the basis of an acid-prepared skull, NHM 42976; compare Goody, 1968).

Species of *Enchodus* represented by articulated material are known to bear a series of mid-line scutes extending along the dorsal ridge of the body between the back of the skull and the dorsal fin. Unlike some other aulopiforms, *Enchodus* does not bear expanded flank scutes (Goody, 1969). When present, the ridge scutes are bilaterally symmetrical and typically oval in shape, meaning that isolated specimens are unlikely to be confused with the paired, often angular, flank scutes of *Cimolichthys* or dercetids (see below).

Fig. 5. Crown-group teleosts from the Maastrichtian of the southeast Netherlands and northeast Belgium: Pachyrhizodontidae and Enchodontidae. (A, B) *Pachyrhizodus* sp., incomplete ?maxilla (NHM 42978a), Maastricht Formation, ?Maastricht area, the Netherlands. (A) Lateral view; (B) close-up of tooth enclosed by frame in (A). (C, D) *Enchodus faujasi* Agassiz, 1844, right mandible (NHM 42976), Maastricht Formation, ?Maastricht area, the Netherlands. (C) Lateral view; (D) close-up of symphysial region of (C), showing detail of enlarged dentary fang characteristic of *Enchodus*. (E) *Enchodus faujasi* Agassiz, 1844, left palatine and fang (NHMM 1980 144), Lanaye Member (> flint level 22), Gulpen Formation, Petit Lanaye (Liège), Belgium, shown in lateral view. (F) *Enchodus faujasi* Agassiz, 1844, articulated skull (NHMM BL 0858), Gulpen Formation, Lanaye Member, flint levels 15-16, locality unknown, probably St Pietersberg area, south of Maastricht, the Netherlands, shown in lateral view with anterior facing left.

►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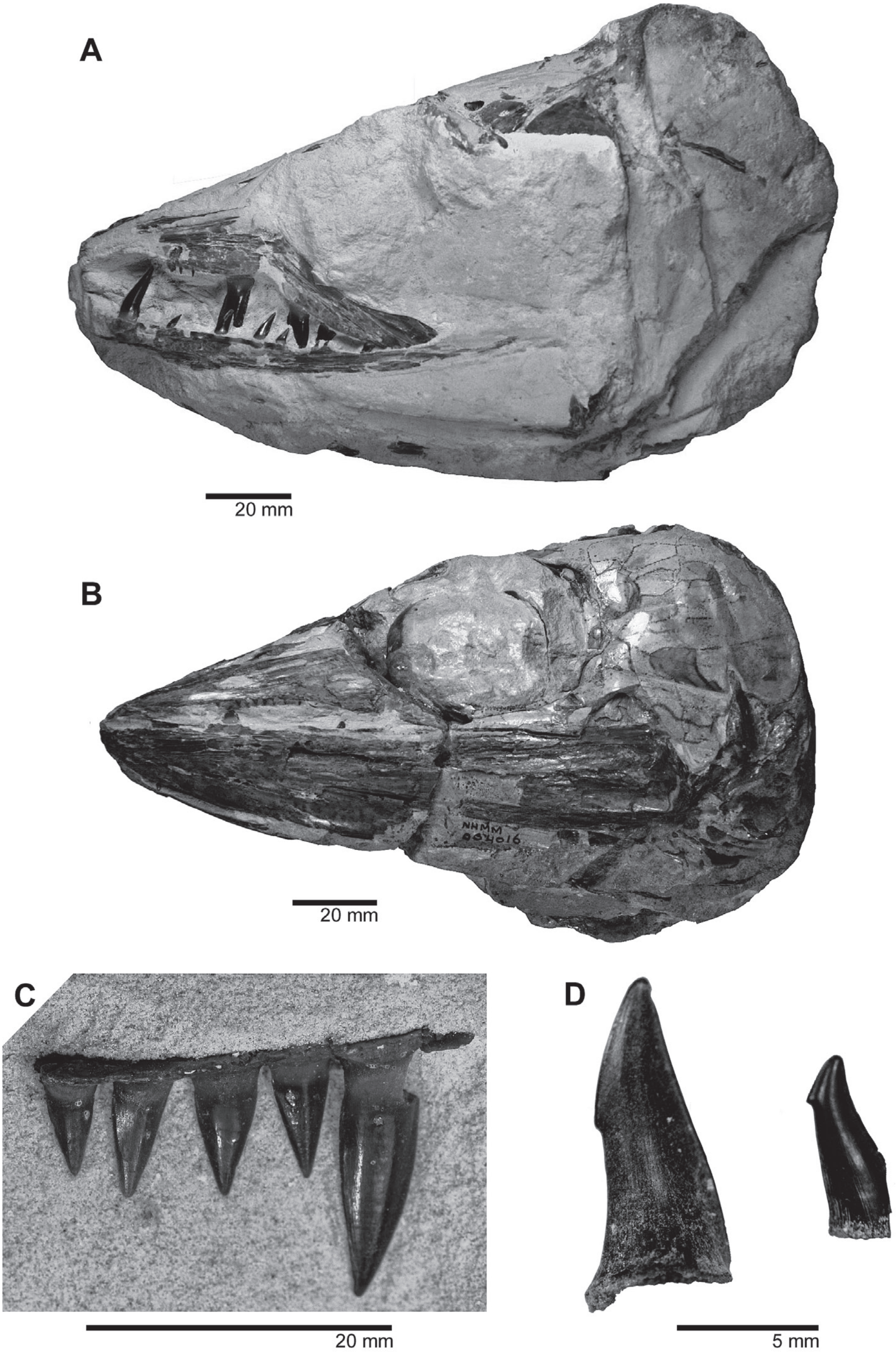
Family Ichthyotringidae Jordan, 1905
Genus *Apateodus* Woodward, 1901
Apateodus corneti (Forir, 1887)
Fig. 6A-C.

Description – Teeth are strongly compressed with anterior and posterior cutting edges that bear fine serrations, and are separated from the fused base of the tooth by a collar-like constriction. Pronounced striations often ornament this basal region. The palatine bears a single, large fang. The mandible is long and narrow, with only a single row of teeth. Tooth rows are strongly heterodont; ectopterygoid teeth are closely spaced and decrease in size posteriorly, while the lower jaw bears two large fangs that are flanked posteriorly by somewhat smaller teeth and anteriorly by a series of diminutive ones.

Occurrence – Remains of *Apateodus* are found at various levels within the Gulpen and Maastricht formations (Lanaye, Valkenburg, Gronsveld, Emael and Nekum members) throughout the study area, and occur also in more or less articulated state (skulls) in the Kunrade limestone facies of the Maastricht Formation in the Heerlen-Kunrade area (southern Limburg, the Netherlands).

Remarks – The Maastrichtian *Apateodus* material was first described by Forir (1887) as a new species of *Enchodus*, *E. corneti*. This taxon was reassigned to *Apateodus* by Kruizinga (1924) in a detailed anatomical account based on several skulls housed in the IRScNB collections. Goody (1969) concluded that the Maastrichtian *Apateodus* was synonymous with *A. striatus* from the English Chalk, but species-level distinction is tentatively maintained here based on the number of fangs borne on the palatines (one in *A. corneti*, two in *A. striatus*). The large fangs of *Apateodus* can be mistaken for the teeth of *Protosphyraena*, but the serrated teeth of the former are always fused to underlying bone (see above), while the unserrated teeth of the latter are typically implanted in sockets. The Maastricht Formation specimens of *Apateodus* represent the youngest convincing remains of this widely distributed (Fielitz & Shimada, 2009) and long-lived genus, which first appears in the Lower Cretaceous (Albian) Gault Clay of the England (Woodward, 1901; Goody, 1969).

Fig. 6. Crown-group teleosts from the Maastrichtian of the southeast Netherlands and northeast Belgium: Apateopholidae and Cimolichthyidae. (A) *Apateodus corneti* (Forir, 1887), articulated skull (NHMM 2011 052), Maastricht Formation, precise level unknown, probably Valkenburg aan de Geul area, the Netherlands, shown in left lateral view. (B) *Apateodus corneti* (Forir, 1887), articulated skull (NHMM 004016), Maastricht Formation, former Schunck quarry (Kunrade), the Netherlands, shown in left lateral view. (C) *Apateodus corneti* (Forir, 1887), left ectopterygoid (NHMM 1983 133), Maastricht Formation, probably Nekum Member, St Pietersberg area, Maastricht, the Netherlands, shown in internal (lingual) view with anterior facing right. (D) *Cimolichthys* sp., entopterygoid or palatine teeth (NHMM K 3618), Maastricht Formation, basal Emael Member, Eben Emael (Liège), Belgium, shown with anterior facing right. ▶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Family Cimolichthyidae Goody, 1969
Genus *Cimolichthys* Leidy, 1857
Cimolichthys sp.
Fig. 6D.

Description – Sigmoidal teeth with a complete cutting edge along the anterior margin and a distally restricted cutting edge along the posterior margin that forms a distinctive post-apical barb. Teeth bear fine serrations along their bladed margins.

Occurrence – Leriche (1929, p. 276) reported that Maastrichtian remains of *Cimolichthys* in Belgium and the Netherlands were limited to the 'Craie phosphatée de Ciply' (now Ciply-Malogne Phosphatic Chalk Formation), but this genus also occurs at various levels within the Maastricht Formation (Albers & Weiler, 1964). In Belgium, stratigraphically older remains of *Cimolichthys* are known from the Campanian Obourg Chalk Formation (Leriche, 1929, p. 276).

Remarks – *Cimolichthys* is known only on the basis of isolated teeth from the Maastrichtian of Belgium and the Netherlands. Barbed teeth are characteristic of this genus, but these are limited to bones of the palate (palatine, ectopterygoid; Goody, 1969, 1970), so it is possible that smaller teeth attributed to other aulopiforms might actually belong to *Cimolichthys*. Mandibular remains have yet to be reported, but should be easily distinguishable from those of other Maastrichtian aulopiforms. *Cimolichthys* has three rows of teeth on its lower jaws, whereas *Enchodus* has two and *Apateodus* only one. In *Cimolichthys*, these rows consist of an outer series of needle-like teeth, a middle row of somewhat larger teeth and an inner set of widely spaced fangs. Like dercetids (see below), *Cimolichthys* has multiple rows of flank scutes. *Cimolichthys* scutes have not been reported from the Maastrichtian of the Netherlands and Belgium, but the scutes of stratigraphically younger specimens from Europe and North America resemble elongated hexagons that bear strengthened ridges that extend across their long and short axes in addition to irregular tuberculate ornament. Along with remains from Niger (Cappetta, 1972), fossils of *Cimolichthys* from the study area represent the youngest occurrence of this genus, which is represented by articulated material from the English Chalk (Woodward, 1909-1912; Goody, 1969), and Niobrara and Sharon Springs formations of the Western Interior Seaway of North America (Goody, 1970).

Family Dercetidae Pictet, 1850

Remarks – Dercetids are a group of extinct marine fishes characterised by long, eel-like bodies, slender skulls, narrow vertebrae and well-developed flank scutes. These scutes are modified scales that form one or more rows along the side of the body (Fig. 7B). Isolated scutes are not uncommon in the Maastrichtian chalks (Fig. 7C), but it is premature to assign these to the species or even genus level until the more complete dercetid remains from these deposits have been properly evaluated. Dercetid scutes typically assume a heart-shaped or triradiate form, unlike the hexagonal and rounded plates characteristic of *Cimolichthys* and *Enchodus*, respectively. The vertebrae of many bony fishes are difficult to identify, but those of most dercetids are easily recognised by two key features: an elongate, hourglass-like profile and well-developed transverse processes, which often exceed the length of the centrum itself.

At first glance, worm burrows lined with fish debris can be mistaken for the narrow scute-covered bodies of dercetids. Historically known to quarrymen as 'petrified eels' (Davies, 1879, p. 145), such burrows were described by Mantell (1822) and Agassiz (1833-1844) as elongate fishes, the latter author attributing English Chalk specimens to *Dercetis* (Davies, 1879; Bather, 1911). Such burrows are common in Cretaceous chalks and limestones, and can easily be distinguished from articulated body fossils in their disordered arrangement of scales and bones, often belonging to different kinds of fishes and typically limited to the periphery of the tube, as examples from the lower Maastricht Formation show (Valkenburg and Gronsveld members) (J.W.M. Jagt, pers. comm., September 2011).

Genus *Dercetis* Münster & Agassiz *in* Agassiz, 1834b

?*Dercetis* sp.

Fig. 7A.

Description – Skull and jaws are not greatly elongated. The dentition consists of multiple rows of hollow, needle-like teeth that are implanted in a series of tightly packed alveoli located on the inner surface of the jaw bones.

Occurrence – Remains of ?*Dercetis* sp. are known in particular from lower levels within the Maastricht Formation (Valkenburg, Gronsveld and Emael members), but there is also a record from interval 6 of the Vijlen Member (Gulpen Formation).

Remarks – Very incomplete dercetid cranial material from both the Vijlen Member (Gulpen Formation) and the Maastricht Formation, comprising lower jaws and a partial skull roof, appears most similar to *Dercetis*. This genus is unusual among members of the family in having a comparatively short rostrum with an anteriorly bifid mesethmoid and is considered to be the sister taxon of all remaining dercetids (Chalifa, 1989; Gallo *et al.*, 2005; Taverne, 2006). Incomplete postcrania might also belong to the same taxon as these skull remains, but there is no positive evidence at present to associate these isolated materials. Once a 'waste-bin' taxon, *Dercetis* has recently been revised by Taverne (2005), who recognised only two species within the genus: the Turonian *D. elongatus* from the English Chalk and the Santonian *D. triqueter* from Sahel Alma, Lebanon. Some material once assigned to *Dercetis* has been removed without assignment to other genera ('*D.*' *reussi*, '*D.*' *latiscutatus* and '*D.*' *maximus*), while additional species have been placed in *Benthiskyme* (Santonian of Lebanon; Campanian of Germany) and *Scaniadercetis* (Danian of southern Sweden). The latter taxon represents the stratigraphically youngest dercetid, and the only member of this family known from the Cenozoic. More definitive placement of the 'short-snouted' Maastrichtian decetid awaits the discovery of better-preserved material.

Genus *Ophidercetis* Taverne, 2005

?*Ophidercetis* sp.

Fig. 7D-F.

Description – The snout is produced as a long, slender rostrum. The greatly elongated body bears multiple rows of overlapping, triangular scutes ornamented with small, irregularly arranged tubercles.

Occurrence – The present form is known from a few levels within the Maastricht Formation, notably from the Gronsveld, Schiepersberg and Emael members.

Remarks – Similarities between the specimen illustrated and *Ophidecertis* include: an exceptionally long, sinuous body; an elongated, needle-like rostrum; and multiple overlapping series of scutes covering the flank (Fig. 7F). While these features are found individually in other dercetid taxa (see Taverne, 2006, for a summary), they are only known to co-occur in *Ophidercetis* from the Campanian-Maastrichtian of Nardò, Italy (Taverne, 2005; the Cenomanian *Cyranichthys* and Turonian '*Dercetis*' *latiscutatus* share some of these traits, but others cannot be checked owing to incompleteness of material; Woodward, 1902-1912; Taverne, 1987). However, characters unique to *Ophidercetis* (e.g., very long dorsal-fin insertion) cannot be detected in NHMM 1993 119 and further study will be necessary before more confident statements about its taxonomic placement can be made.

Sept Acanthomorpha Rosen, 1973

Remarks – The spiny-finned teleosts (Acanthomorpha) are so named because the anterior portions of their dorsal, anal and, in many taxa, pelvic fins are supported by hard, unpaired spines rather than flexible, paired rays of the sort found in most other fishes. Acanthomorphs are the largest living group of teleosts, comprising about 280 families with members as anatomically disparate as anglerfishes, flounders and seahorses (Nelson, 2006). Much of this morphological (Friedman, 2010) and taxonomic (Patterson, 1993a, b) diversity appears to have been generated during the early Cenozoic, and acanthomorphs are neither abundant nor diverse in the Maastrichtian strata of Belgium and the Netherlands. The most likely acanthomorph finds in these deposits are isolated fin spines or distinctive ctenoid scales, in which a comb-like series of serrations (called ctenii) are found on the posterior margin of the scale (Fig. 2C). The acanthomorph fauna of the Maastrichtian is poorly known and isolated remains such as these are unlikely to be diagnostic at even the family level. More precise identifications will require articulated material.

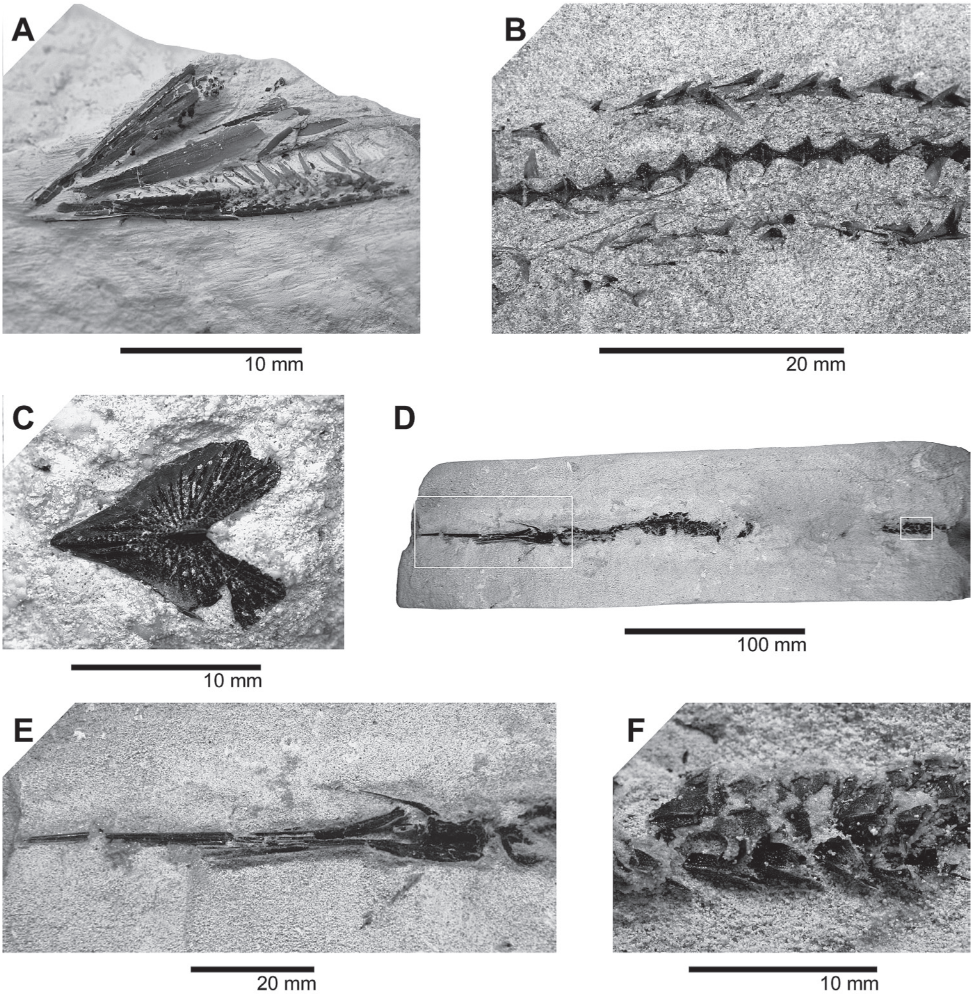

Fig. 7. Crown-group teleosts from the Maastrichtian of the southeast Netherlands and northeast Belgium: Dercetidae. (A) ?*Dercetis* sp., incomplete skull (NHMM K 565), Gulpen Formation, Vijlen Member (interval 6), former CPL SA quarry, Haccourt (Liège), Belgium, shown in dorsal view with anterior facing left. (B) Dercetidae indet., articulated postcranium with flank scutes (NHMM 1998 027/1, 2), Maastricht Formation, upper Valkenburg Member, ENCI-Heidelberg Cement Group quarry, Maastricht, the Netherlands, shown with anterior facing left. (C) Dercetidae indet., isolated flank scute (NHMM K 3272), Maastricht Formation, basal Emael Member, Eben Emael (Liège), Belgium, shown in lateral view with anterior facing left. (D-F) ?*Ophidercetis* sp., incomplete skeleton (NHMM 1993 119), unknown level within the Maastricht Formation, locality unknown, but probably St Pietersberg area, Maastricht, the Netherlands. (D) Lateral view with anterior facing left; (E) close-up of region enclosed by left frame in (D), showing neurocranium and rostrum; (F) close-up of region enclosed by right frame in (D), showing overlapping series of flank scutes encasing the body.

Order Polymixiiformes Rosen & Patterson, 1969
Family Polymixiidae Gill, 1872
Genus *Omosoma* Costa, 1857
?*Omosoma* sp.
Fig. 8A.

Description – A small, fusiform acanthomorph, with small circular scales lacking ctenii. Posterior margin of operculum convex, lacking an embayment. A well-developed supraoccipital crest occurs along the top of the skull, bearing a strengthened ridge. Epipleurals (rod-like bones overlying the ribs) are present.

Occurrence – The present taxon is known exclusively from the Gulpen Formation (Vijlen Member) of the St Pietersberg area, the Netherlands, where it is represented by a single, articulated specimen.

Remarks – Polymixiids are among the most morphologically primitive acanthomorphs (Johnson & Patterson, 1993). Although represented today by a single living genus (*Polymixia*), polymixiids were moderately diverse during the Late Cretaceous, with seven described genera (*Berycopsia*, *Berycopsis*, *Dalmatichthys*, *Homonotichthys*, *Omosoma*, *Omosomopsis* and *Pycnosterinx*; Patterson, 1993a). While *Omosoma* and the Maastrichtian polymixiid resemble the living *Polymixia* in gross body form, some extinct polymixiids diverged from this morphology and were instead characterised by comparatively deep bodies. The interrelationships of these anatomically diverse fossil polymixiids are unclear, having never been subjected to formal analysis.

Order Beryciformes Günther, 1880 (*sensu* Johnson & Patterson, 1993)
Incertae familiae
Genus *Hoplopteryx* Agassiz, 1838
Hoplopteryx sp.
Figs. 2C, 8B.

Description – An acanthomorph with large, rounded scales with well-developed ctenii along their posterior margins and broad scalloping along their anterior margins. The opercle is rhombic and bears a distinct posterior embayment, which defines the ventral margin of a posteriorly oriented spine. Small villiform teeth are borne on a broad band on the dentaries and premaxillae.

Occurrence – *Hoplopteryx* has been reported previously from the Ciply-Malogne Phosphatic Chalk Formation of Belgium (Leriche, 1929, p. 277), but articulated material that appears attributable to this genus is also known from the Maastricht Formation (NHMM K 3067).

Remarks – *Hoplopteryx* is a common acanthomorph in Upper Cretaceous deposits and is known from several localities worldwide (England, Germany, Lebanon, Slovenia, the Czech Republic, Texas and Russia; Patterson, 1964; Stewart, 1996; Forey *et al.*, 2003; Ekrt *et al.*, 2008). This genus has been associated traditionally with extant trachichthyids, or 'slimeheads', a group which includes the modern orange roughy (*Hoploste-*

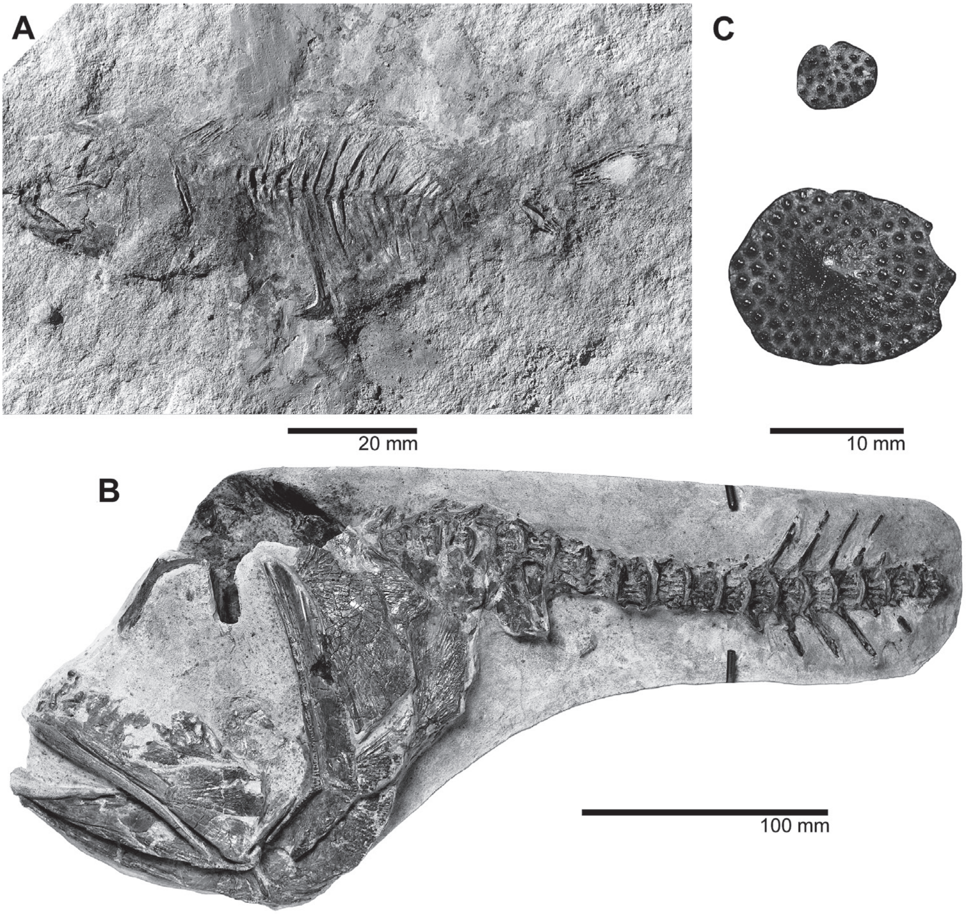

Fig. 8. Crown-group teleosts from the Maastrichtian of the southeast Netherlands and northeast Belgium, and the Mons Basin (southern Belgium): Acanthomorpha. (A) Polymixiidae, ?*Omosoma* sp., articulated specimen (NHMM 2006 025), Gulpen Formation, Vijlen Member, ENCI-Heidelberg Cement Group quarry, the Netherlands, shown in lateral view with anterior facing left. (B) *Hoplopteryx* sp., skull and partial vertebral column (IRScNB P 8783), Ciply-Malogne Phosphatic Chalk Formation, Mons Basin, southern Belgium, shown in lateral view with anterior facing left. (C) Tetraodontiformes *incertae sedis*, dermal scutes (top: NHMM 1994 672/38c, Houthem Formation, Geulhem Member, former Ankerpoort-Curfs quarry, Geulhem; bottom: NHMM K 4029, Maastricht Formation, Meerssen Member, former Blom quarry, Berg en Terblijt, the Netherlands, shown in external view.

thus). Slimeheads are so named because of the large mucus-filled cavities found on the top of the head that represent greatly expanded sensory canals. Similar depressions, separated by ornamented ridges, have been noted for specimens of *Hoplopteryx* from other localities, most notably the English Chalk (Woodward, 1902-1912; Patterson, 1964). However, other aspects of anatomy indicate that this genus probably falls just outside the group containing slimeheads and their nearest living relatives (crown-group trachichthyoids; see Moore, 1993).

Order Tetraodontiformes Regan, 1929

Remarks – Tetraodontiformes (pufferfishes and their allies) are an unusual order of acanthomorph fishes that assume a wide range of morphologies and sizes (Santini & Tyler, 2003; Nelson, 2006). More familiar members of this diverse radiation include triggerfishes, boxfishes and the giant ocean sunfishes. Outside Belgium and the Netherlands, Cretaceous tetraodontiforms are known from three putative stem-group members (Tyler & Sorbini, 1996; Santini & Tyler, 2003), plus a single crown-clade representative assigned to the extant family Diodontidae (porcupinefishes; Gallo *et al.*, 2009). Putative tetraodontiform remains have also been reported from the Maastrichtian-Paleocene intertrappean beds of India (Gayet *et al.*, 1984) and from the lower Paleocene Geulhem Member (Houthem Formation) in the study area (see below), but these are poorly documented (Patterson, 1993b).

Incertae familiae
tetraodontiform gen. et sp. indet.

Fig. 8C.

Description – Polygonal bony plates with a smooth, concave inner face, and ornamented with numerous enamel-bearing pustules on their concave outer face. Intact plates bear a large central boss on their external surface.

Occurrence – Tetraodontiform scale plates are known from a few levels within the Maastricht Formation (Emael, Nekum and Meerssen members), as well as from the lower Paleocene (Houthem Formation, Geulhem Member).

Remarks – Modern boxfishes (families Ostraciidae and Aracanidae) bear a carapace composed of tubercle-bearing, polygonal plates similar to those known from the Maastricht and Houthem formations. Scale plates like these are common finds in Paleogene deposits (Tyler & Gregorová, 1991; Weems, 1998) and are often assigned to the extant genus *Ostracion*. However, genus-level attribution of isolated scutes is unwarranted given the great diversity of fossil tetraodontiforms known to possess anatomically similar plates (Tyler & Sorbini, 1996; Tyler & Santini, 2002; for an insightful discussion, see Tyler & Gregorová, 1991, pp. 1, 2). This basic scute morphology occurs in both stem (Plectocretacicidae; Tyler & Sorbini, 1996) and crown (Bolcabalistidae, Eospinidae, Spinacanthidae, Protobalistidae, Aracanidae and Ostraciidae; Tyler & Santini, 2002; Santini & Tyler, 2003) tetraodontiforms, meaning that it is not possible to tell whether the present material belongs either within or outside the living radiation, or if these fossils derive from one or more taxa. More precise identification of the tetraodontiform specimens from the study area must await the discovery of diagnostic skeletal remains.

Acknowledgements

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Appendix

Key to the identification of ray-finned fish teeth from the Maastrichtian type area

1.	Crushing tooth pavement	*2*
	Pointed or fang-shaped tooth	*3*
2.	Largest teeth kidney-shaped, with concave border facing anteriorly	*Anomoeodus subclavatus*
	Largest teeth oval-shaped, with no concave borders	*8*
3.	Teeth set within sockets	*4*
	Teeth fused to underlying bone	*5*
4.	Teeth with long root and short-bladed crown, set in deep alveoli	*Saurocephalus woodwardii*
	Teeth with high crown with convex anterior and posterior cutting edges that do not bear serrations	*Protosphyraena ferox*
5.	Teeth long and narrow, and bearing sharp cutting edge or edges	*6*
	Teeth conical, with no or poorly developed cutting edges	*9*
6.	Teeth bear a conspicuous post-apical barb	*Cimolichthys* sp.
	Teeth lack post-apical barb	*7*
7.	Teeth with convex anterior and posterior cutting edges, base constricted and striated	*Apateodus corneti*
	Teeth sigmoidal, may or may not have two cutting edges	*Enchodus faujasi*
8.	Oblong teeth with long axes perpendicular to long axis of tooth plate	*Anomoeodus fraiponti*
	Oblong teeth with long axes oblique to long axis of tooth plate	*Anomoeodus foriri*
9.	Teeth with thick, bony collar around base	*Pachyrhizodus* sp.
	Teeth bearing longitudinal groove, with light-coloured apical cap composed of acrodin	*Belonostomus* sp.