

The dercetid fishes (Teleostei, Aulopiformes) from the Maastrichtian (Late Cretaceous) of Belgium and The Netherlands

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ABSTRACT. Several partial skeletons from the marine Maastrichtian deposits of Belgium and the Netherlands allow to recognize four species of Dercetidae, two of which are new: *Dercetis triqueter*, *Ophidercetis italiensis*, *Cyranichthys jagti* sp. nov. and *Apuliadercetis indeherbergei* sp. nov. This newly studied material greatly enlarges the stratigraphic and paleogeographic ranges of the four concerned dercetid genera.

KEYWORDS: Teleostei, Dercetidae, osteology, relationships, type Maastrichtian, new species.

1. Introduction

Dercetidae (Aulopiformes, Enchodontoidei) are a family of highly specialized Late Cretaceous marine teleost fishes, characterized by a snout forming a long pointed rostrum and by an eel-shaped body that is partially or totally covered with rows of scutes. Fifteen dercetid genera are currently known. Their earliest record dates back to the Cenomanian and their youngest to the Danian. They are found all over the world, with records from Europe, North, Central and South America, Africa, Middle and Far East (Taverne, 1987, 2005; Blanco & Alvarado-Ortega, 2006). Several phylogenetic studies have already been carried out (Taverne, 1987, 1991, 2006b; Chalifa, 1989; Gallo et al., 2005).

Dercetidae were unknown from the Late Cretaceous of Belgium and The Netherlands (Leriche, 1929) until Friedman (2012) briefly described remains of four specimens from the Late Maastrichtian of the Liège-Maastricht basin, which were tentatively identified to the generic level. More recently, two discoveries were made, which shed new light on the presence of the Dercetidae in the Maastrichtian type-area. The first is a block of flint from the eluvium of the CBR Lixhe quarry at Lixhe (Belgium, Fig. 1), which contains a series of vertebrae in anatomical connection, and parts of the fins and the skull. The second was found in the ENCI quarry (The Netherlands, Fig. 1), and contains some skull bones and scutes.

All the above mentioned material is described in detail hereafter and its relationships are discussed.

2. Material and methods

The studied material belongs to the collections of the "Natuurhistorisch Museum Maastricht", Maastricht, The

Netherlands (specimens with prefix NHMM), of the Royal Belgian Institute of Natural Sciences, Brussels, Belgium (prefix IRSNB), and of the Royal Museum for Central Africa, Tervuren, Belgium (prefix MRAC).

These specimens have been studied with a stereomicroscope Wild M5. The drawings of the figures were made by the first author (L. T.) with a *camera lucida*.

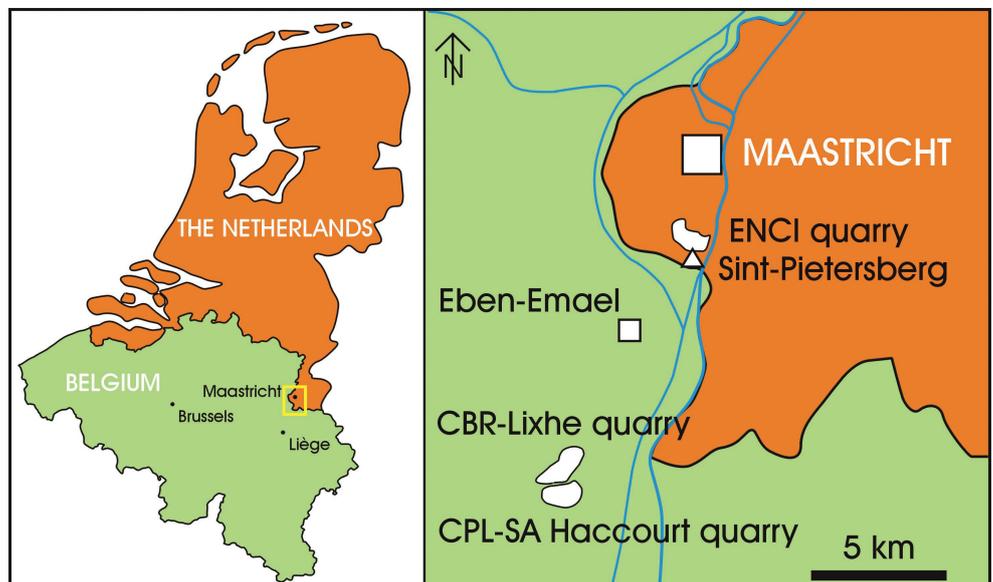
3. Stratigraphy

All specimens originate from a thick series of Upper Maastrichtian (Late Cretaceous) shallow marine deposits. The lower part represents the Gulpen Formation (Vijlen (pars), Lixhe 1-3 and Lanaye Members) and the upper part the Maastricht Formation (Valkenburg, Gronsveld, Schiepersberg, Emael, Nekum and Meerssen Members). The Gulpen Formation also extends down in the stratigraphy (Lower Maastrichtian and Campanian), but have not yielded dercetid remains. A good overview of the litho-, bio- and chronostratigraphy of the type Maastrichtian can be found in Felder (1996) and Jagt (1999). Figure 2 details the stratigraphic position of the four taxa described hereafter.

4. Systematic paleontology

Division Teleostei Müller, 1844
 Cohort Clupeocephala Patterson & Rosen, 1977
 Subcohort Euteleostei Greenwood et al., 1967
 Order Aulopiformes Rosen, 1973
 Suborder Enchodontoidei Berg, 1937
 Family Dercetidae Pictet, 1850

Figure 1. Map of the area.



DISTRIBUTION OF DERCETIDAE						
CHRONOSTRATIGRAPHY			<i>D. triquetra</i>	<i>O. italiensis</i>	<i>C. jagti</i>	
LITHOSTRATIGRAPHY						
UPPER MAASTRICHTIAN	MAASTRICHT FM	MEERSSEN				
		NEKUM				
		EMAEL		⊗	⊗	
		SCHIEPERSBERG				
		GRONSVELD			?	
		VALKENBURG	⊗			
	GULPEN FM	LANAYE				⊗
		LIXHE 3				
		LIXHE 2				
		LIXHE 1				
		VIJLEN	⊗			

Figure 2. Stratigraphic position of the Dercetidae within the Upper Maastrichtian of Belgium and The Netherlands. Note that only the upper part (= interval 6) of the Vijlen Member belongs to the Upper Maastrichtian.

Genus *Dercetis* Agassiz, 1834

Type species: *Dercetis elongatus* Agassiz, 1837 (cf. Taverne, 2005).

Dercetis triquetra Pictet, 1850
(Figs 3-7)

2012 ? *Dercetis* sp. – Friedman: fig. 7 A

2012 Dercetidae indet. – Friedman: fig. 7 B

Material. Specimen NHMM K 565, upper part of a rostrum, from the Vijlen Member (interval 6) of the Gulpen Formation, former CPL SA quarry, Haccourt, Liège, Belgium (Fig. 3).

Specimen NHMM 1998 027- 1, 2, part and counterpart of a partial body comprising 48 complete or fragmentary vertebrae and a few dorsal and ventral scutes, from the upper Valkenburg Member of the Maastricht Formation, ENCI-Heidelberg, Cement Group quarry, Maastricht, The Netherlands (Fig. 4).

Osteology

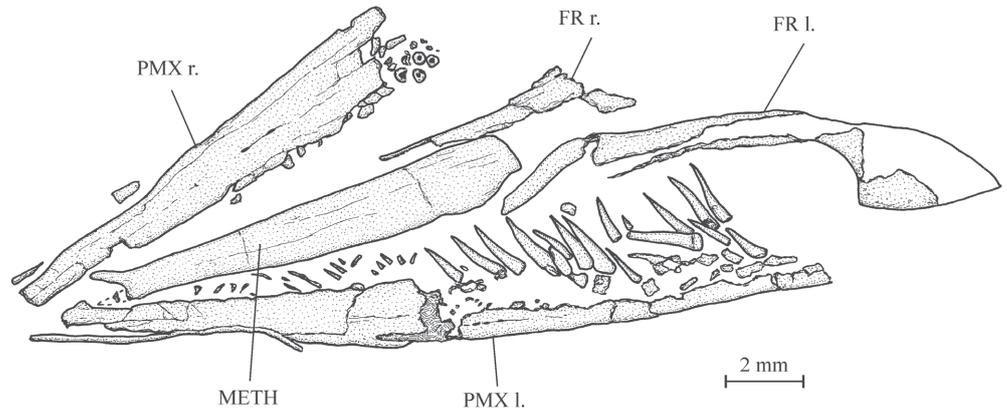
The skull (Fig. 5). Only a small portion of the skull is preserved on specimen NHMM K 565. The mesethmoid is long, narrow and with a bifid anterior extremity. It is surrounded by a pair of very elongated toothed premaxillae. The teeth are numerous, thin, pointed and irregularly ranged. Those on the anterior part of the bone are small but the teeth of the posterior half of the premaxilla

Figure 3. *Dercetis triquetra* Pictet, 1850. Specimen NHMM K 565, an isolated upper part of a rostrum.



Figure 4. *Dercetis triquetra* Pictet, 1850. Specimen NHMM 1998 027- 1, 2, the two faces of a partial body.

Figure 5. *Dercetis triqueter* Pictet, 1850. Rostral region of specimen NHMM K 565.



are very large. Fragments of the two frontals are preserved. The orbital and preorbital portion of the frontal is rather short for a dercetid fish.

The girdles. The pectoral girdle is not preserved. The pelvic girdle is visible on the two faces of specimen NHMM 1998 027-1, 2. The pelvic bones are large and triangular in shape. Each of them bears one strong but short spine following by 5 longer rays.

The axial skeleton (Fig. 6). A great part of the 48 preserved vertebrae on specimen NHMM 1998 027-1, 2 belongs to the abdominal region of the body. The haemal arch is as long as the corresponding centrum. Each haemal arch bears only one pair of long haemapophyses. Some fragments of intermuscular bones are also present.

The squamation (Fig. 7). Some scutes of the dorsal and the ventral rows are visible on specimen NHMM 1998 027-1, 2.

They are triradiate, with a smooth surface. The anterior extension is more or less long and strengthened by a small median crest. The two divergent posterior extensions of the scute are very dissymmetric. The point forming the dorsal and the ventral margin of the body is short, while that directed towards the middle of the flank is much longer.

Genus *Ophidercetus* Taverne, 2005

Type species *Ophidercetus italiensis* Taverne, 2005

Ophidercetus italiensis Taverne, 2005

(Figs 8-10)

Material. Specimen NHMM JJ 15294a, a few skull bones and some scutes, from the Emael Member of the Maastricht Formation (IVd-3), northwest corner of the ENCI quarry, Maastricht, The Netherlands (Fig. 8).

Figure 6. *Dercetis triqueter* Pictet, 1850. Specimen NHMM 1998 027- 2. A few vertebrae, each bearing only one pair of haemapophyses.

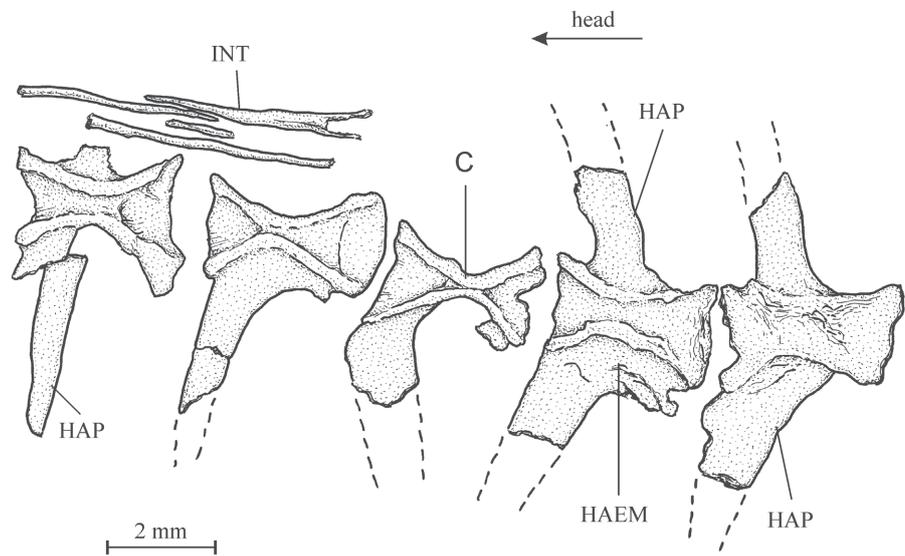


Figure 7. *Dercetis triqueter* Pictet, 1850. Specimen NHMM 1998 027- 2. A few dorsal or ventral scutes.

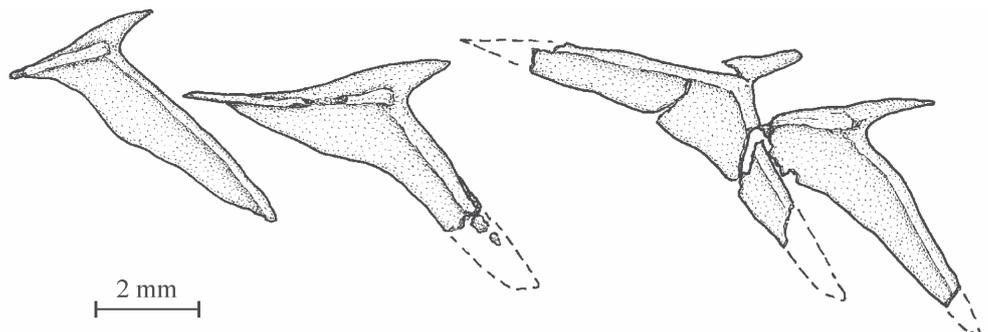
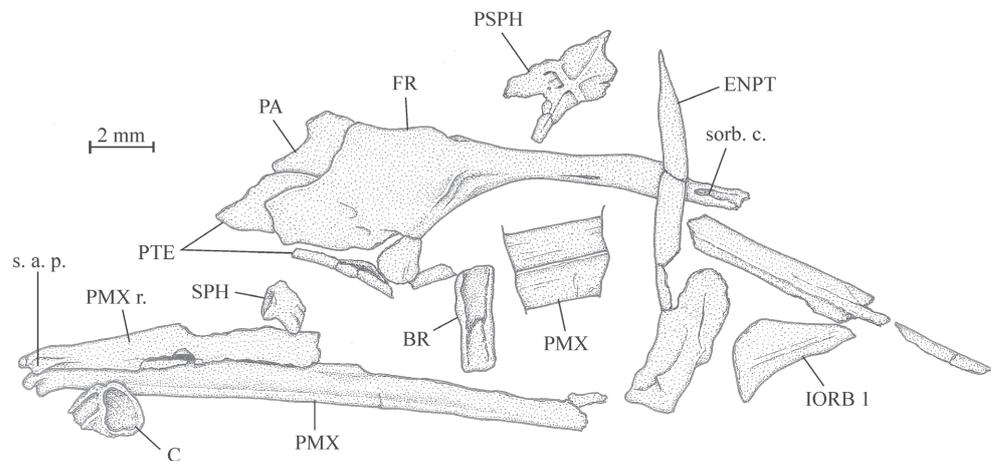


Figure 8. *Ophidercetus italiensis* Taverne, 2005. Specimen NHMM JJ 15294a, a few skull bones and some scutes.



Figure 9. *Ophidercetus italiensis* Taverne, 2005. Skull of specimen NHMM JJ 15294a.

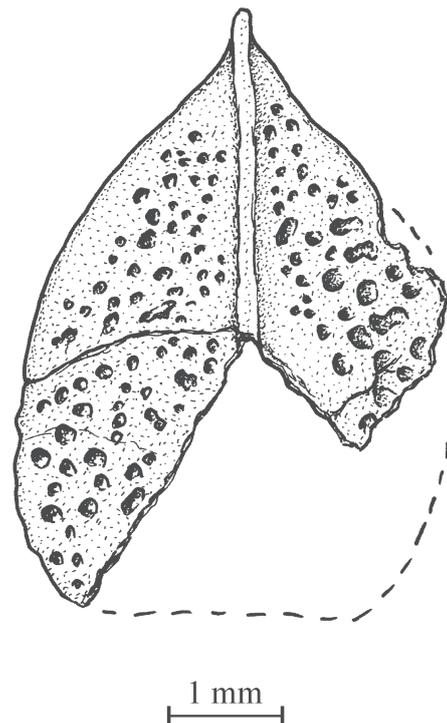


Osteology

The skull (Fig. 9). Only the left part of the skull roof, seen by its internal face, and the anterior region of the rostrum are preserved. The other cranial fragments are too crushed to allow the identification. The rostrum is elongated and formed by the two long and narrow premaxillae placed the one against the other. The premaxilla bears a small symphyseal knob-like ascending process at its anterior extremity. No tooth is visible on the premaxilla. The mesethmoid is not preserved. The frontal is broad in the postorbital region and very narrow and elongated at the level of the orbit and more anteriorly. A short portion of the supraorbital sensory canal is visible. Behind and laterally to the frontal, fragments of the pterotic are preserved, showing that the temporal (= posttemporal) fossa was roofed. The parietal reaches the mid-line of the skull roof, forming a medio-parietal skull. The small left sphenotic and the broad pleurosphenoid are separated from the skull, due to the fossilisation. The supraoccipital and the epiotics are lost. A toothless entopterygoid, a large triangular first infraorbital and a branchial bone are also visible.

The axial skeleton. Some fragments of vertebrae are present but the arches are not preserved.

The squamation (Fig. 10). The scutes are large, lanceolate in shape, and ornamented with numerous small pits and a thin median crest.



Genus *Cyranichthys* Taverne, 1987

Type species: *Cyranichthys ornatissimus* (Casier, 1965)

Figure 10. *Ophidercetus italiensis* Taverne, 2005. Scute of specimen NHMM JJ 15294a.

Cyranichthys jagti sp. nov.
(Figs 11-15)

2012 ? *Ophidercetes* sp. – Friedman: fig. 7 D-F.

Etymology. The name of the new species is dedicated to Dr. John W. M. Jagt, palaeontologist and curator of the “Natuurhistorisch Museum of Maastricht”, Maastricht, The Netherlands.

Holotype. Specimen NHMM 1993 119, a sample with a partial skull, some vertebrae and some scutes, from an unknown level in the Maastrichtian and an unknown locality, but probably Sint-Pietersberg area, Maastricht, the Netherlands (Fig. 11).

Paratype. Specimen NHMM K 3272, an isolated flank scute from the basal Emael Member of the Maastricht Formation, Eben Emael, near Liège, Belgium.

Osteology

The skull (Figs 12, 13). The elongated and very thin upper rostrum is formed for its major part by a pair of very long, narrow and toothless premaxillae firmly sutured together. The mesethmoid is rod-like, not very long for a dercetid fish and located far from the tip of the rostrum. The bone is surrounded by the posterior extremities of the premaxillae and by the anterior extremities of the frontals. A part of a very long toothless bone is visible against the left premaxilla and the parasphenoid. That bone could be a maxilla, a pterygoid bone or even a dentary. The mandible is not preserved and, thus, we do not know if the lower part of the rostrum was as long as the upper region or shorter. A small part of the right frontal and a larger part of the left frontal are preserved. The anterior region of the frontal participates in the rostrum for less than its half. One parietal is partly preserved, the other parietal being lost. It is located before the supraoccipital. Such a position indicates that the skull was medio-parietal. Indeed, the parietals are located on each side



Figure 11. *Cyranichthys jagti* sp. nov. Specimen NHMM 1993 119.



Figure 12. *Cyranichthys jagti* sp. nov. Head region of specimen NHMM 1993 119.

Figure 13. *Cyranichthys jagti* sp. nov. Skull of specimen NHMM 1993 119.

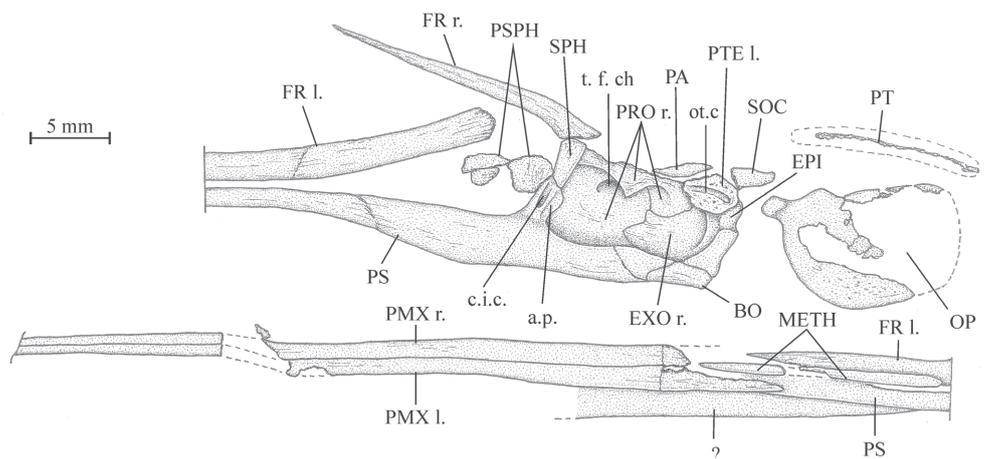


Figure 14. *Cyranichthys jagti* sp. nov. A few scutes of specimen NHMM 1993 119.

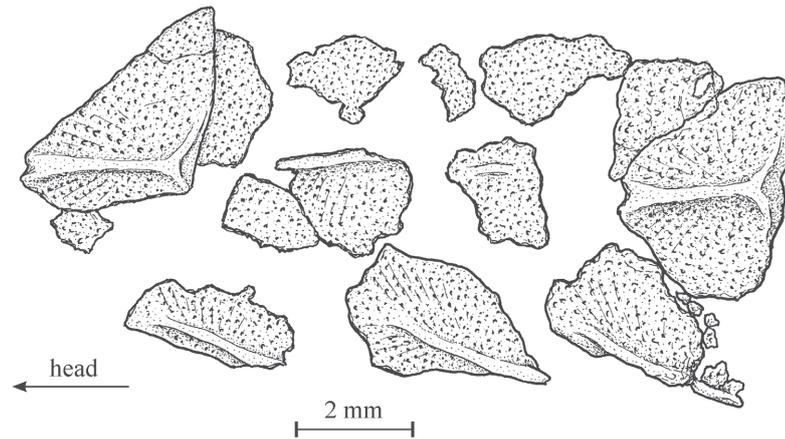
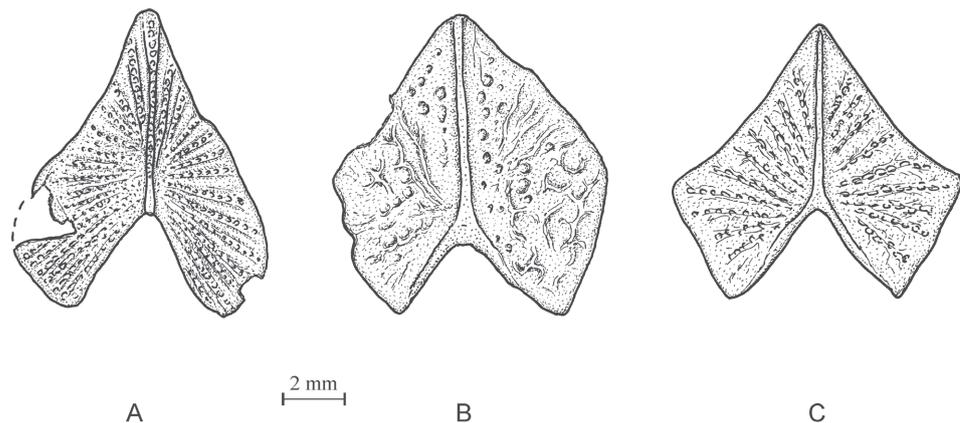


Figure 15. (A) *Cyranichthys jagti* sp. nov. Scute of specimen NHMM K 3272. (B) and (C) *Cyranichthys ornatissimus* (Casier, 1965). (B) Scute of specimen MRAC RG 10.971, from Kipala (Kwango, Democratic Republic of Congo), outcrop 53f, black argillite. (C) Scute of specimen MRAC RG 10.970, from Kipala, pit III, black argillite.



of the supraoccipital in the dercetid fishes with a latero-parietal skull. The supraoccipital bears a small median crest.

The braincase has lost its left wall and the right wall is seen in internal view. The sphenotic, a part of the right pterotic, the posterior portion of the left pterotic with the otic sensory canal, the right prootic, the right exoccipital, a part of the left exoccipital, the parasphenoid and the basioccipital are visible. The fragment of the left pterotic partly covered the epiotic (=epioccipital) and is seen from its external face. This left pterotic is slightly ornamented. That indicates the presence of the dermic component (=dermopterotic) of the bone and also that the temporal (=posttemporal) fossa was roofed. It is always the case in the dercetid genera that possess a dermopterotic. A hollow is visible on the upper margin of the prootic, just at the suture with the pterotic. That is very probably the inner portion of the trigemino-facial chamber. The parasphenoid is a large toothless bone. Its very long trabecular region reaches at least the mesethmoid level and so participates to the upper rostrum. Its ascending process joins the sphenotic and bears a small canal for the internal carotid. Fragments of an ovoid opercle are present behind the braincase. Its anterior dorsal corner forms a sort of articular knob.

The girdles (Fig. 13). Small crushed fragments of a long and horizontally oriented posttemporal are visible above the opercle. No other elements of the pectoral girdle or the pelvic girdle are preserved.

The axial skeleton. A few vertebrae are preserved behind the skull, but the neural and haemal arches are lost. Those vertebrae are longer than deep but not excessively elongated. Some fragments of epineurals and epipleurals are also visible.

The squamation (Figs 14, 15). The body is covered with large arrow head-shaped scutes that seem ranged in three connected rows. These scutes are ornamented with minute tubercles and a strong horizontal crest. The scutes occupying the middle of the flanks are the larger. They are a little deeper than long, with the

median crest posteriorly bifurcated along the posterior margin of the scute. In the upper and lower rows, the horizontal crest is present but located near the margin of the scute.

Paratype NHMM K 3272 is an isolated scute from the flank of a much bigger specimen than the holotype. The ornamentation is more marked and the tubercles are more regularly ranged, forming a series of radiating ridges that surrounds the median crest. The posterior margin is deeply concave.

Genus *Apuliadercetes* Taverne, 2006

Type species: *Apuliadercetes tyleri* Taverne, 2006.

Apuliadercetes indeherbergei sp. nov.

(Figs 16-22)

Etymology. The name of the new species is dedicated to Ludo Indeherberge of the "Werkgroep Krijt en Vuursteen" who has discovered the specimen hereafter described.

Holotype. Specimen IRSNB P9316, a skull roof, parts of the pectoral and the pelvic girdles, fragments of sixteen vertebrae, intermuscular bones and some scutes (Fig. 16). The specimen sits in a block of flint, which was found in the eluvium in the western corner of the CBR Lische quarry during autumn 2013. Due to the peculiarities of the flint, it must have originated from the Lanaye Member, Gulpen Formation, from above flint level 16, probably from the interval 16 to 20.

Osteology

The skull (Figs 17, 18). The skull roof is seen in dorsal view. The posterior region of the rostrum is also preserved. The jaws, the mesethmoid and the other bones of the endocranium and of the suspensorium are lost due to the fossilisation. The frontals are elongated and much broader in the postorbital region than at the orbital and preorbital level. They form the posterior part of the long rostrum. The parietals are large bones meeting in the mid-line (medio-parietal skull). The two temporal (=

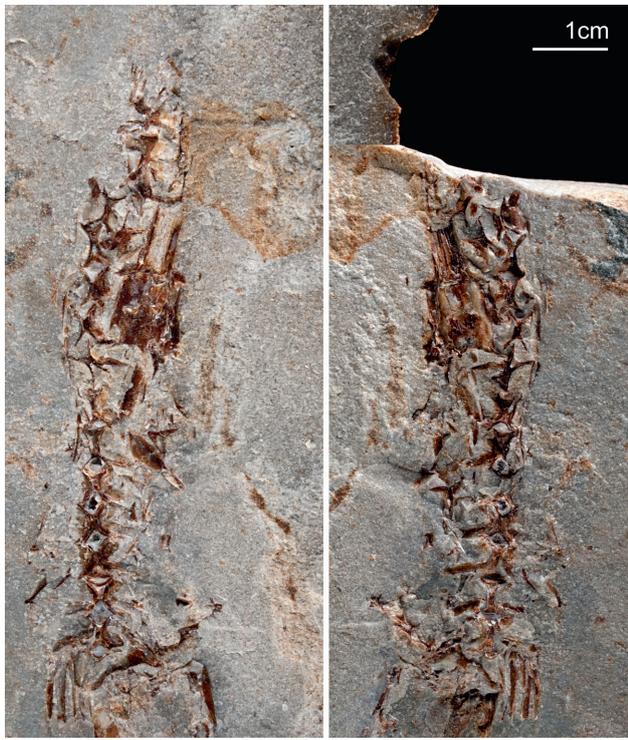
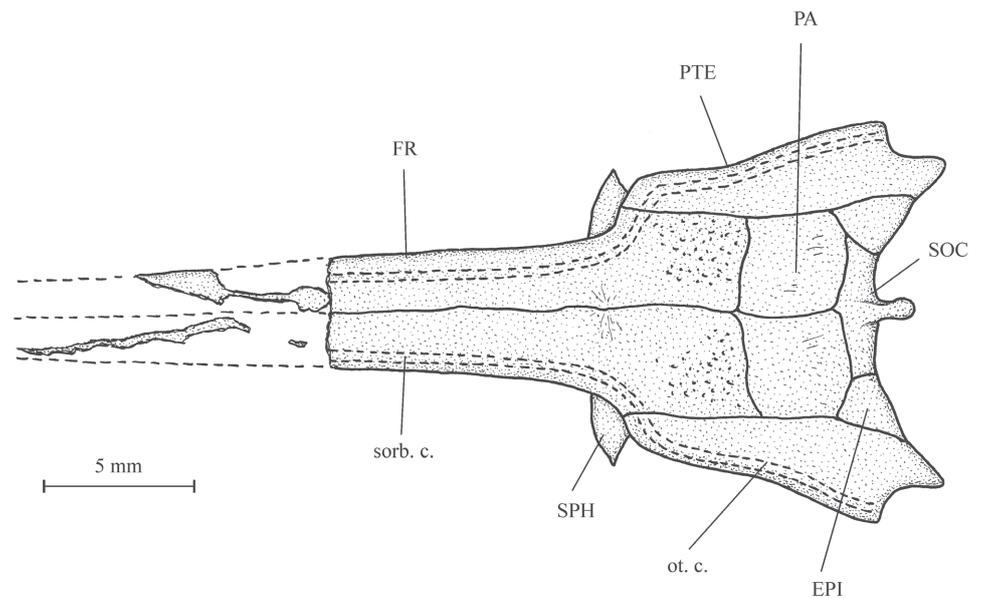


Figure 16. *Apuliadercetis indeherbergei* sp. nov. Both sides of the split holotype IRSNB P9316.



Figure 17. *Apuliadercetis indeherbergei* sp. nov. Both sides of the skull of the holotype IRSNB P9316.

Figure 18. *Apuliadercetis indeherbergei* sp. nov. Reconstruction of the skull roof based on the two faces of holotype IRSNB P9316.



posttemporal) fossae are roofed by the pterotics. A small more or less triangular supratemporal is present behind the pterotic and above the temporal fossa. The postorbital process of the sphenotic forms a pointed spur on each side of the skull, just before the pterotic. The two large epiotics (= epioccipitals) surround the broad supraoccipital. The occipital crest is weakly developed. The supraorbital sensory canal is visible on the frontal and the pterotic.

The girdles (Figs 19, 20). Only two elements of the pectoral girdle are preserved, the posttemporal and the hypercleithrum (= supracleithrum). The posttemporal is elongated, narrow and horizontally oriented. The hypercleithrum is short but rather broad. The pelvic girdle is well developed and located in the abdominal region, far from the head. Indeed, fourteen vertebrae are present before the girdle level. There is only one large ovoid pelvic bone on which at least 5 big rays are articulated.

The axial skeleton (Fig. 21). All the preserved vertebrae belong to the abdominal region. The vertebrae are longer than deep. The neural spines are short. The haemal arch is large and as long as the centrum. Each haemal arch bears at its ventral anterior margin a pair of elongated haemapophyses (= parapophyses). Posteriorly, the haemal arch develops another pair of rounded haemapophyses that are feebly marked. The epineurals and epipleurals are abundant and strongly developed.

The squamation (Fig. 22). The scales are absent but there is at least one row of large triradiate scutes on the flanks. Some smaller scutes are also present. They are shaped as a ridge-tile and probably belong to the ventral keel, the dorsal ridge or the lateral line row.

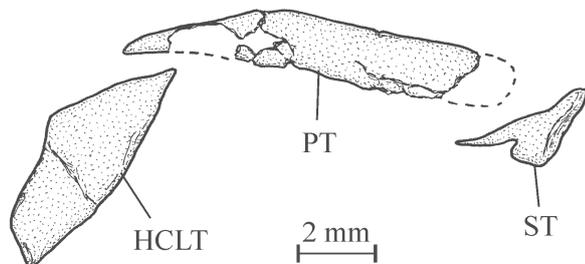


Figure 19. *Apuliadercetus indeherbergei* sp. nov. Upper part of the pectoral girdle of holotype IRSNB P9316.

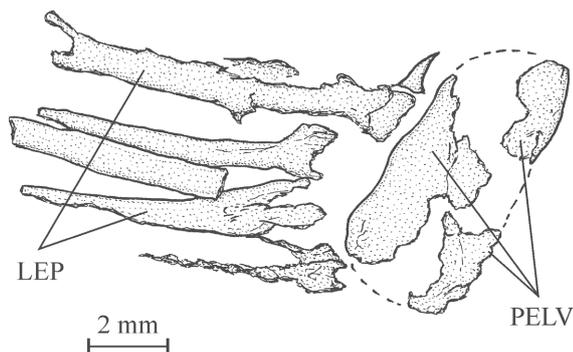


Figure 20. *Apuliadercetus indeherbergei* sp. nov. Pelvic girdle of holotype IRSNB P9316.

5. Discussion

In the comments hereafter, we use the characters chosen in the most detailed phylogenetic hypothesis proposed until now (Taverne, 2006b).

5.1. The case of *Dercetis triqueter*

Three characters allow a very precise determination of the concerned skull fragment: (1) the mesethmoid exhibits a bifid anterior extremity, (2) the rostral part of the frontal is rather short and (3) the premaxilla bears not only small teeth but also a series of very large teeth.

Character (1) is typical of the genus *Dercetis*. No other dercetid genus has an anteriorly bifid mesethmoid. Two species are validly known in that genus: *Dercetis elongatus* from the Turonian and Senonian of England, the type-species, and *Dercetis triqueter* from the Santonian of Lebanon (Taverne, 2005). Characters (2) and (3) correspond to *Dercetis triqueter* (Taverne, 2005). In *Dercetis elongatus*, the rostral part of the frontal is much longer and all the premaxillary teeth are small (Davis & Hitchin, 1996; Taverne, 2005).

The vertebrae of specimen NHMM 1998 027-1, 2 with only one pair of long haemapophyses on the haemal arch are typical not only of the genus *Dercetis* (Taverne, 2005) but also of the genera *Cyranichthys* (Casier, 1965), *Benthesikyme* (Taverne, 2005) and *Scandiadercetis* Taverne, 2005 (Davis, 1890).

The very peculiar shape of some dorsal and ventral scutes in specimen NHMM 1998 027-1, 2 is another apomorphy of *Dercetis triqueter* (Pictet & Humbert, 1866). The attribution of specimens NHMM K 565 and 1998 027-1, 2 to the species *Dercetis triqueter* seems thus totally justified.

5.2. The case of *Ophidercetus italiensis*

The concerned specimen exhibits (1) a medio-parietal skull, (2) a roofed temporal fossa and (3) a small ascending process on the premaxilla.

Characters (1) and (2) are known in the more primitive members of the family, a group including the genera *Dercetis*,

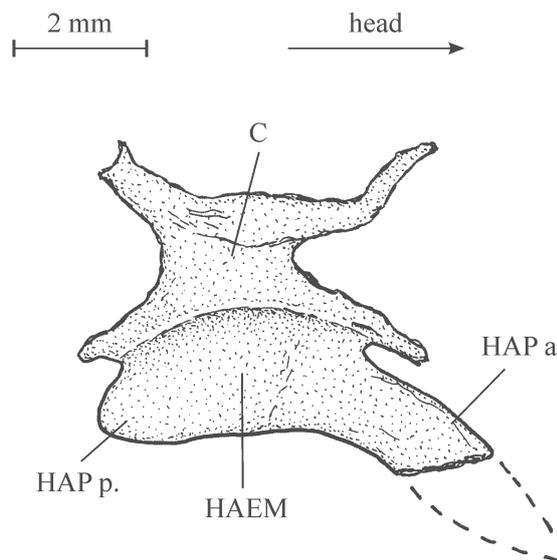


Figure 21. *Apuliadercetus indeherbergei* sp. nov. One abdominal vertebra of holotype IRSNB P9316.

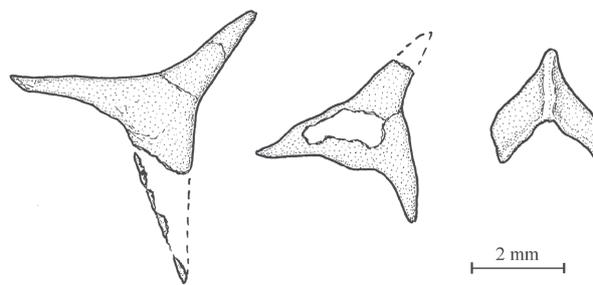


Figure 22. *Apuliadercetus indeherbergei* sp. nov. Three scutes of holotype IRSNB P9316.

Ophidercetus, *Cyranichthys*, *Benthesikyme* White & Moy-Thomas, 1940, *Scandiadercetis* and *Apuliadercetus*. Character (3) is only present in two of those six genera, *Dercetis* and *Ophidercetus*. In all the other known Dercetidae, the symphyseal process is lost. In *Dercetis*, the ascending process is pointed (Davis & Hitchin, 1996; Taverne, 2005), whereas it is smaller and knob-like in *Ophidercetus* (Taverne, 2005). The small knob-like process present on its premaxilla clearly places specimen NHMM JJ 15294a in the genus *Ophidercetus*. The shape and the ornamentation of the scutes on specimen NHMM JJ 15294a are also almost identical to those of the scutes in *Ophidercetus* (Taverne, 2005), confirming so the generic determination of that specimen.

The preserved parts of specimen NHMM JJ 15294a do not differ from the corresponding bones in *Ophidercetus italiensis* from the Maastrichtian of southern Italy. However, the Italian specimens bear teeth on their premaxilla and entopterygoid (Taverne, 2005), whereas the Dutch sample seems toothless. The presence of teeth in some specimens of a peculiar fossil fish species and the absence of teeth in other specimens of the same species is not exceptional (see for instance Taverne, 2002, 2011). Such a difference could be due to a loss during the fossilisation or to seasonal and even sexual variations. The ornamentation of the scutes is also a little different. In the Italian fishes, the pits are less numerous and the median crest is much broader (Taverne, 2005) than in the Dutch specimen. But, once again, those differences can be the result of an individual variation. We range thus provisionally specimen NHMM JJ 15294a in the species *O. italiensis*, but new material could eventually led in the future to the erection of a new species.

5.3. The case of *Cyranichthys jagti* sp. nov.

The systematic position of specimen NHMM 1993 119 proposed hereafter is based on six characters: (1) the skull is medio-parietal, (2) the temporal fossa is roofed, (3) the mesethmoid is rod-like, (4) the very elongated upper rostrum is formed by the two very narrow premaxillae firmly sutured together, (5) the posttemporal is elongated and horizontally oriented and (6) the body is completely covered by large arrow head-shaped scutes.

Character (6) is known in only three dercetid genera, *Cyranichthys*, *Ophidercetus* and *Pelargorhynchus* von der Marck, 1858. However, characters (1), (2) and (3) allow to exclude *Pelargorhynchus* from a close relationship with specimen NHMM 1993 119. Indeed, that genus possesses a latero-parietal skull, an unroofed temporal fossa and a V-shaped mesethmoid forming the tip of the upper rostrum (Goody, 1969). Moreover, its body is covered not only by some rows of scutes but also by numerous very small scales (von der Marck, 1863), thus a very different pattern of scale morphology and distribution.

Ophidercetus and *Cyranichthys* share characters (1), (2), (3) and (6) with specimen NHMM 1993 119. But *Ophidercetus* differs from the concerned specimen by characters (4) and (5). Its rostrum is not so thin and the two premaxillae are juxtaposed but not so firmly sutured together, and its posttemporal is triangular (Taverne, 2005). Its scutes are always longer than deep, ornamented with small irregularly ranged pits, not with tubercles, and the posterior margin is less deeply concave or not concave at all (Taverne, 2005).

Cyranichthys exhibits character (4) (Taverne, 1987), also shared by specimen NHMM 1993 119. The posttemporal is unknown in *Cyranichthys*. The scutes of the Congolese dercetid genus have the same size and shape as in the Belgian specimen. They are strongly ornamented, with small tubercles that sometimes are regularly ranged in rows, a few pits, some ridges, a median crest posteriorly bifurcated and a deeply concave posterior margin (Fig. 15 B, C).

Considering all those resemblances, specimen NHMM 1993 119 can be referred confidently to the genus *Cyranichthys*. However, *Cyranichthys ornatissimus* differs from it by the shape of its opercle that is triangular (Taverne, 1987). The Belgian sample deserves thus its peculiar specific status.

5.4. The case of *Apuliadercetus indeherbergei* sp. nov.

Six characters can be used to assign the exact place of that fossil specimen within the dercetid phylogeny: (1) the skull is medio-parietal, (2) the temporal fossa is roofed, (3) the posttemporal is long, narrow and horizontally oriented, (4) the well-developed pelvic girdle contains only one ovoid pelvic bone, (5) the haemal arches of the abdominal vertebrae bear paired well-developed anterior haemapophyses but the posterior haemapophyses are only feebly marked and (6) large triradiate scutes are present on the body as well as smaller arrow head-shaped scutes.

Character (1) places the sample within the primitive dercetid fishes, a group comprising the genera *Dercetis*, *Ophidercetus*, *Cyranichthys*, *Benthesikyme*, *Scandiadercetus*, *Apuliadercetus* and *Brazilodercetus* De Figueiredo & Gallo, 2006. Character (2) confirms this positioning but allows the exclusion of *Brazilodercetus* from a direct relationship. Indeed, that genus has an unroofed temporal fossa (De Figueiredo & Gallo, 2006). Character (3) is an apomorphy that appears at the level of *Apuliadercetus* and the more evolved genera but that is not yet present in *Dercetis*, *Ophidercetus*, *Cyranichthys*, *Benthesikyme* and *Scandiadercetus*. Character (4) is known in *Ophidercetus* (Taverne, 2005) and *Apuliadercetus* (Taverne, 2006a). However, in *Ophidercetus*, the pelvic girdle is greatly reduced and located near the head (Taverne, 2005). The position and the shape of the pelvic girdle in specimen IRSNB P9316 totally corresponds to the case of *Apuliadercetus*. Character (5) is also typical of *Apuliadercetus* and of no other dercetid genus. Character (6) occurs in *Apuliadercetus* (Taverne, 2006a) and in a few other dercetid genera. The conclusion is thus clear. Specimen IRSNB P9316 belongs to the genus *Apuliadercetus*.

Nevertheless, this specimen differs from *Apuliadercetus tyleri* Taverne, 2006, the type-species and, until now, the only species known in the genus, by at least a few minor osteological characters. *A. tyleri* has a long supraoccipital crest, proportionally broader pterotics and small epiotics not reaching the parietals (Taverne, 2006a). Thus, specimen IRSNB P9316 deserves its peculiar specific status.

5.5. Chronological and geographical implications

The present study allows to greatly enlarge the stratigraphic and paleogeographic ranges of the concerned species and genera. For example, *Dercetis triqueter* was until now known only from the Santonian of Lebanon. The genus *Apuliadercetus* and the species *Ophidercetus italiensis* were until today known only in the Campanian-Maastrichtian of southern Italy.

Much more surprising was the discovery of *Cyranichthys* in the type-area of the Maastrichtian. Until now, the genus was considered to be endemic of the marine Cenomanian of Kipala (Kwango), in the Democratic Republic of Congo. However, close relationships between the Kipala fish fauna and the Mesogean ichthyofauna of the Eurafican realm have already been emphasized by Taverne (1976). These could have been established through a connection via the Benoue Trough (Nigeria), which was a periodical seaway during the Late Cretaceous, known to have played a major role in the dispersal of many fish groups (Vullo & Courville, 2014).

The newly described occurrences of Dercetidae in the type-area of the Maastrichtian clearly demonstrate that our knowledge of the distribution of the Dercetidae, although greatly enlarged over the past decades, is still limited and mostly related to a few isolated finds.

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7. Alphabetic list of abbreviations used in figures

BO: basioccipital; BR: branchial bone; C: vertebral centrum; EPI: epiotic (= epioccipital); EXO: exoccipital; ENPT: entopterygoid; FR: frontal; HCLT: hypercleithrum (= supracleithrum); HAEM: haemal arch; HAP (a., p.): haemapophysis (anterior, posterior); INT: intermuscular bones (= epineurals, epipleurals); IORB 1: infraorbital 1; LEP: fin ray; METH: mesethmoid; OP: opercle; PA: parietal; PELV: pelvic bone; PMX: premaxilla; PRO: prootic; PS: parasphenoid; PSPH: pleurosphenoid; PT: posttemporal; PTE: pterotic; SOC: supraoccipital; SPH: sphenotic; ST: supratemporal (= extrascapular, scale bone).

a. p.: ascending process of the parasphenoid; c. i. c.: canal for the internal carotid; l.: left; ot. c.: otic (= postorbital) sensory canal; r.: right; s. a. p.: symphyseal ascending process of the premaxilla; sorb. c.: supraorbital sensory canal; t. f. ch.: trigemino-facial chamber.

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