# A new myriacanthid holocephalian from the Early Jurassic of Denmark

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A new myriacanthid holocephalian is described from the Hasle Formation (probably the *Uptonia jamesoni* subzone to the *Acanthopleuroceras valdani* subzone, Early Pliensbachian, Early Jurassic) of Bornholm, Denmark, on the basis of isolated upper posterior (palatine) and lower posterior (mandibular) tooth plates. *Oblidens bornholmensis* gen. et sp. nov. differs from all other myriacanthids for which the same dental elements are known, in the distribution of the hypermineralised tissue covering the occlusal surfaces of the tooth plates, and the arrangement of the ridges transecting the tooth plate surface and so varying their surface relief. *Oblidens* is the first myriacanthid holocephalian to be recorded both from the Pliensbachian and from Denmark. The presence of a further, undetermined myriacanthid tooth plate is noted from the same locality.

*Keywords*: Bornholm, tooth plate, Holocephali, Myriacanthidae, Pliensbachian, Early Jurassic, new genus.

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The holocephalians are a group of cartilaginous fishes ranging from the Devonian to Recent. Although clearly closely related to sharks and rays, their evolutionary origin remained obscure until the recent description of an uncrushed braincase with chimaeroid specialisations and belonging to the symmoriiform *Dwykaselachus oosthuizeni* from the Devonian of South Africa (Coates *et al.* 2017).

The Mesozoic record of the chimaeriforms comprises three suborders: the Squalorajoidei (containing *Squaloraja* only and restricted to Hettangian and Sinemurian rocks of the Early Jurassic of Europe); the Myriacanthoidei, with two families (Myriacanthidae and Chimaeropsidae) ranging from Rhaetian, Late Triassic to Tithonian, Late Jurassic of Europe; and the Chimaeroidei, with three families.

As with all chondrichthyans, the relatively high organic content of the cartilaginous endoskeleton reduces its preservation potential when compared to more heavily mineralised tissues like bone, dentine and enamel. This means that articulated, full-bodied chondrichthyan fossils showing high fidelity preservation are generally limited to conservation lagerstätten such as the Early Jurassic (Sinemurian and Toarcian) black shale deposits of Lyme Regis (UK), Osteno (Italy) and Holzmaden (Germany), or the Late Jurassic Plattenkalk of Solnhofen (Germany). Specimens from deposits like these provide anatomical information which is crucial for the elucidation of the evolutionary history of the group. Tooth plates and dorsal fin spines, made up of more densely calcified tissues, are more common as isolated fossil finds; their robust and taphonomically more resilient nature means that they can be preserved in a range of sedimentary environments where the preservation of more delicate skeletal components is compromised. Although limited in terms of the information which they provide, these isolated finds are important indicators of the palaeodiversity shown by the holocephalian chondrichthyans. This paper presents the first myriacanthid remains recorded both from the Pliensbachian and from Denmark.

# Material and methods

Two complete myriacanthid holocephalian tooth plates were collected in 2016 and declared Danekræ DK-865a and DK-865b. Danekræ are fossils, minerals or meteorites of exceptional scientific or exhibitional value, for which the finder is rewarded by the Danish state. One partial tooth plate was collected in 2005 and previously illustrated as *Myriacanthus* sp. (Bonde *et al.* 2008) and declared Danekræ DK-148. All the specimens are now part of the collections of the Natural History Museum of Denmark (NHMD), Østervoldgade 5–7, DK-1350 Copenhagen K (NHMD 117400–117402).

# Geological setting

The Danish island of Bornholm is located in the Baltic Sea just south of Sweden (Fig. 1A). Bornholm is a complex fault block situated adjacent to the NW–SE trending Sorgenfrei–Tornquist Zone, which separates the Danish Basin from the Baltic Shield (Surlyk & Noe-Nygaard 1986). Mesozoic sedimentation was strongly influenced by the movements of the Sorgenfrei–Tornquist Zone, and the eastern border of the fault is located a short distance inland from the west coast of Bornholm (Fig. 1B).

The type section for the Hasle Formation (Fig. 1C) is located just south of the town of Hasle (Fig. 1B), about 1 km to the west of the fault which controlled the location of the coastline during the time of deposition of the Hasle Formation (Surlyk & Noe-Nygaard 1986; Milàn & Surlyk 2015). The Hasle Formation is a reddish-brown fine-grained sandstone to coarse-grained siltstone with hummocky and swaley cross-stratification (Fig. 1C). Single horizons show trough cross-bedding or planar lamination, and at the base of these the individual swales are draped with a fossiliferous conglomeratic layer of clasts of basement rocks (Surlyk & Noe-Nygaard 1986; Larsen & Friis 1991).

The Hasle Formation contains a diverse invertebrate fauna including a rich Early Pliensbachian ammonite



**Fig. 1**. Bornholm and the Hasle Formation. **A**: Location map showing the position of Bornholm in the Baltic Sea. **B**: Outline geological map of Bornholm, showing the location of Hasle. **C**: Photograph of the coastal outcrop of the Hasle Formation (Early Pliensbachian, Lower Jurassic) at Hasle. The cliff face is approximately 4 m high. Notice the prominent trough crosslaminations below the iron-rich concretion layer. fauna comprising 11 species, and several species of bivalves, scaphopods and belemnites (Malling & Grönwall 1909; Malling 1911, 1914, 1920; Höhne 1933; Donovan & Surlyk 2003). Selachians are the most common vertebrate fossil from the Hasle Formation, and so far three species of hybodont sharks and three neoselachians have been recognised (Rees 1998), together with abundant isolated undetermined fish scales. Plesiosaurs are represented by at least three taxa, distinguished by their tooth morphology, of both plesiosauroids and pliosauroids (Milàn & Bonde 2001; Smith 2008). Recent finds of a small theropod footprint in the lower part of the exposed succession demonstrate that parts of the formation were, at least partly, subaerially exposed during deposition (Milàn & Surlyk 2015).

# Myriacanthid holocephalians

The Myriacanthidae is a family of holocephalian chondrichthyan fishes raised by Arthur Smith Woodward in 1889 as part of his bid to rationalise the rather chaotic contemporary classification of the group (Woodward 1889; Duffin 2016). As currently defined, the family embraces nine species belonging to seven genera (Stahl 1999; Table 1), and is exclusively Late Triassic to Early Jurassic in age, ranging from Rhaetian to Toarcian marine strata of north-western Europe. Three genera (plus some additional specimens which remain in open nomenclature) are known from parts of the cartilaginous endoskeleton (*Myriacanthus*, *Metopacanthus* and *Acanthorhina*), whilst two species are known from dorsal fin spines only. Elements of the dentition are known in seven genera.

The myriacanthid dentition comprises a single pair of large tooth plates, the lower or mandibular tooth plates, plus a single medial symphyseal tooth plate anteriorly in the lower jaws, and up to three pairs of tooth plates in the upper dentition. The latter includes an upper posterior or palatine tooth plate pair and a pair of upper anterior or vomerine tooth plates. The occlusal surfaces of all tooth plates are covered, to a greater or lesser extent, with a specialised hypermineralised tissue, usually referred to as pleromin or pleromic hard tissue, which sits upon a lamellar tissue forming the tooth plate base. The dentition has primarily a crushing function, but varying degrees of sectorial action are achieved through topographic variation of the occlusal surface of the plates provided by a series of surface ridges with intervening depressions. Taxonomically important features include the shapes of the various tooth plates, the distribution of the hypermineralised tissue over the occlusal surface and the presence and distribution of any ridges crossing the crushing surfaces.

A guide to the descriptive terminology used in this paper, originally developed by Duffin (1984), subsequently modified by Patterson (1992), and now in general use (Stahl, 1999) is given in Fig. 2.

 Table 1. Stratigraphic distribution and known skeletal elements of myriacanthid holocephalians

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Genus	Species	Main reference	Age	Locality	Material					
					Mandibular	Symphyseal	Palatine	Vomerine	Fin spine	Cartilages
Agkistracanthus	A. mitgelensis	Duffin & Furrer 1981	Rhaetian to Hettangian	Switzerland, UK	х	х	Х		Х	
Alethodontus	A. bavariensis	Duffin 1983b	Hettangian	Germany	х					
Recurvacanthus	R. uniserialis	Duffin 1981	Sinemurian	UK					Х	
Halonodon	H. warneri	Duffin 1984	Sinemurian	Belgium	Х	Х	Х	Х		
	H. luxembourgensis	Duffin & Delsate 1993	Hettangian	Luxembourg	х					
Myriacanthus	M. paradoxus	Patterson 1965	Sinemurian	UK	х	Х	Х	Х	Х	Х
Metopacanthus	M. granulatus	Patterson 1965	Sinemurian	UK	х	Х	Х	Х	Х	Х
	M. bollensis	Duffin 1983a	Toarcian	Germany					х	
Acanthorhina	A. jaekeli	Duffin 1983a	Toarcian	Germany	х	Х	Х	Х	х	Х



**Fig. 2**. Diagram showing the technical descriptive terms used in the text. **A**: NHMD 11740, a right upper posterior (palatine) tooth plate of *Oblidens bornholmensis* in occlusal view. **B**: NHMD 117401, a left lower (mandibular) tooth plate of *Oblidens bornholmensis* in occlusal view.

## Systematic Palaeontology

Class Chondrichthyes Huxley 1880

Superorder Holocephali Bonaparte 1832–1841

Order Chimaeriformes Obruchev 1953

Suborder Myriacanthoidei Patterson 1965

#### Family Myriacanthidae Woodward 1889

#### Genus indet.

Fig. 3F

2008 *Myriacanthus* sp.; Bonde *et al.*, p. 22. *Stratum*: Hasle Formation. *Age*: 'Carixian', Early Pliensbachian, Early Jurassic

(probably the *Uptonia jamesoni* subzone to the *Acan-thopleuroceras valdani* subzone).

*Locality*: Cliff section 100 m south of Hasle, Bornholm, Denmark; 55°10′44.18″N, 14°42′08.58″E.

*Specimen*: NHMD 117402 (ex DK-148), an isolated tooth plate exposed in occlusal view, but still partly embedded in the matrix (Fig. 3F). The exact identity of the tooth plate and its position in the dentition are not clear.

*Comments*: NHMD 117402 clearly belongs to a myriacanthid. It may transpire that this specimen belongs

to *Oblidens bornholmensis* gen. et sp. nov. described below.

#### Genus Oblidens gen. nov.

*Type species by monotypy: Oblidens bornholmensis. Derivation of name*: Latin oblido = to crush; Latin dens = tooth.

*Diagnosis*: Myriacanthid genus known from isolated palatine (upper posterior) and mandibular (lower) tooth plates only. The palatine tooth plate is covered with pleromin (no tritoral areas) and possesses a prominent central ridge which expands lingually, and a weak ridge flanking the labial margin. The mandibular tooth plate is elongate mesio-distally; the occlusal surface is covered with pleromin (no tritoral areas) and transected by a convex central ridge running from the labial angle to the lingual angle, giving way laterally to flattened labial and lingual fields.

#### Oblidens bornholmensis sp. nov.

#### Figures 3A–E

*Derivation of name*: from Bornholm, where the type material was found.

*Holotype*: NHMD 117400 (ex DK-865a), an isolated right upper posterior (palatine) tooth plate exposed in occlusal view, but still embedded in matrix (Fig. 3A). *Paratype*: NHMD 117401 (ex DK-865b), an isolated left lower posterior (mandibular) tooth plate exposed in occlusal view (Fig. 3B–E).

*Type Stratum*: Hasle Formation.

*Age*: 'Carixian', Early Pliensbachian, Early Jurassic (probably the *Uptonia jamesoni* subzone to the *Acan*-

*thopleuroceras valdani* subzone on the basis of the Hasle Formation ammonite fauna collected from inland quarries; Donovan & Surlyk 2003). No ammonites have been described from the coastal exposures. *Type locality*: Cliff section 100 m south of Hasle, Bornholm, Denmark; 55°10′44.18″N, 14°42′08.58″E. *Diagnosis*: as for genus.



Fig. 3. The tooth plates of Oblidens bornholmensis gen. et sp. nov. A: NHMD 117400, the holotype, an isolated right upper posterior (palatine) tooth plate exposed in occlusal view and still embedded in matrix. B: NHMD 117401, an isolated left lower posterior (mandibular) tooth plate exposed in occlusal view before isolation from the matrix. C: NHMD 117401 in basal view. D: NHMD 117401 in labial view. E: NHMD 117401 in mesial view. F: NHMD 117402, a tooth plate of uncertain position in the mouth and from an undetermined myriacanthid, in occlusal view. Scale bar = 5 mm throughout.

Description of the upper tooth plate. The holotype, NHMD 117400, is an isolated right upper posterior (palatine) tooth plate exposed in occlusal view with its base still embedded in matrix (Fig. 3A). The specimen is roughly triangular in outline and measures 15.3 mm diagonally from the mesial angle to the distal angle. The symphyseal margin is straight for the posterior two thirds of its length, diverging laterally from the symphyseal axis toward the mesial angle anteriorly. The total length of the symphyseal margin is 11.3 mm. The gently arcuate labial margin extends from the mesial to the distal angle and measures 15 mm in length. The lingual margin, which represents the growing region of the tooth plate, connects the distal angle with the posteriormost point of the symphyseal margin and is 11 mm long.

The occlusal surface of the tooth plate is formed by a continuous cover of hypermineralised tissue or pleromin, which is not organised into tritoral areas. The 'spotty' appearance of the tooth plate surface is a product of the exposure by antemorteam wear of vertical dentine pillars, with their central vascular canals (expressed as the black centre of each 'spot'), and intervening hypermineralised matrix (which appears white). It is clear that there must be some variation in trajectory of the dentine pillars as they rise from the boundary layer between the superficial pleromin and the lamellar tissue of the base to the occlusal surface. This is indicated by the shapes of the 'spots' on the occlusal surface, which vary from circular to elliptical. Furthermore, complex associations between adjacent and tightly packed dentine pillars must account for the more elongate, ridge-like dentinal patterns closer to the lingual margin of the tooth plate.

Some variation in topography is developed over the occlusal surface of the tooth plate. A prominent central ridge first develops close to the mesial angle and then expands lingually, occupying the central region of the tooth plate. The ridge is convex in lateral view and forms the highest part of the tooth plate surface. It is flanked labially and symphyseally by topographic lows. A weakly developed labial ridge forms the posterior two thirds of the labial margin of the specimen.

Description of the lower tooth plate. NHMD 117401 is an isolated left lower posterior (mandibular) tooth plate originally exposed in occlusal view (Fig. 3B), but now isolated from the enclosing matrix, and has the overall shape of an elongate trapezoid. The mesial angle is missing, but its original outline can be inferred from the surface of the embedding matrix (Fig. 3B). When complete, the diagonal from the mesial angle to the distal angle would have been approximately 25.5 mm long. The symphyseal margin has a slightly

wavy outline and measures 12.5 mm in length (to the inferred tip of the mesial angle). The lingual margin sweeps postero-laterally away from its junction with the symphyseal margin for approximately 10 mm, and is then deflected laterally through an obtuse angle at the lingual angle to form the 5 mm long, straight growing margin of the tooth plate. The approximately 28 mm long labial margin is bowed laterally for the posterior 80% of its length. The anterior section of the labial margin consists of a scalloped labial indentation terminating laterally at a prominent bulge, designated here as the labial angle (Fig. 2B).

Once again, hypermineralised tissue covers the whole of the occlusal surface of the tooth plate. A prominent ridge forms the central high region of the occlusal surface, crossing the tooth plate diagonally



Fig. 4. Reconstructions of the dentitions of various myriacanthid genera, viewed from the front with the mouth open. A: *Oblidens bornholmensis* gen. et sp. nov. (Pliensbachian, Bornholm, Denmark). B: Acanthorhina jaekeli (Toarcian of Germany, after Duffin 1983a). C: *Halonodon warneri* (Sinemurian of Belgium, after Duffin 1984). D: *Myriacanthus paradoxus* (Sinemurian of the UK, after Patterson 1965). Broken lines indicate inferred boundaries. Diagrams not to the same scale.

from the labial angle to the lingual angle (Fig. 3B). The labial margin of the ridge is deepest anteriorly (Fig. 3D), close to the labial angle, shallowing posteriorly such that the flat labial surface of the tooth plate, here designated the labial field (Figs 2B, 3E), rises relatively gently to the ridge crest closer to the distal angle. Similarly, the relatively flat lingual surface of the tooth plate (the lingual field; Fig. 2B) shallows posteriorly.

As in the upper tooth plate, the hypermineralised dentine pillars which make up the crushing tissue of the occlusal surface of the tooth plate show considerable variation in upward trajectory toward the worn surface as reflected in their outlines; those near the labial angle, for example, are closely packed and strongly ellipsoidal, whilst those in the middle, highest part of the central ridge are relatively widely spaced and circular in outline. Complex associations and coalescence of adjacent pillars gives rise to dentinal ridges posteriorly. These dentinal ridges are better developed and more concentrated on the postero-labial flanks of the central ridge and have a complex arrangement; they sometimes bifurcate and anastomose, sweeping in an arc-like fashion from the labial surface of the ridge anteriorly along the junction between the labial field and the central ridge flanks.

The occlusal surface of the tooth plate is gently convex mesio-distally, and the basal surface is gently concave in the same direction (Fig. 3C–E).

A reconstruction of the dentition of *Oblidens bornholmensis* is given in Fig. 4A, based on the two specimens described above. The positions and inferred outlines of other, as yet undiscovered elements of the dentition are represented by dotted lines.

# Comparison with other myriacanthids

*Upper posterior (palatine) tooth plate.* The upper posterior (palatine) tooth plate of Oblidens gen. nov. described above is distinct from those of all other myriacanthid genera for which this dental element is known (Table 1) in that the whole of the occlusal surface is covered with a carpet of hypermineralised tissue, and a central ridge transects the tooth from the mesial angle toward the lingual margin. The upper posterior tooth plates of Myriacanthus paradoxus (Rhaetian to Sinemurian) are also covered with pleromin, but the plates themselves are much more elongate than the rather triangular specimens of Oblidens, and their occlusal surface is crossed by two diagonal ridges, each of which arises from the labial margin and then sweeps lingually across the crushing surface, sometimes with a rather sinusoidal trajectory (Fig. 4D). The upper posterior tooth plates of *Halonodon* (Sinemurian), by contrast, are much more robust than those of *Oblidens* gen. nov., have a somewhat stubby trapezoid outline and have the hypermineralised tissue concentrated in several tritoral areas: a symphyseal area, a lateral area and a posterior area occupying the lingual section of the tooth plate, sometimes coalescing with the former two in worn specimens (Fig. 4C).

The upper dentition in *Acanthorhina jaekeli* (Toarcian of Germany) is unusual in possessing three paired tooth plates, the occlusal surfaces of the central and anterior items of which are the only ones available for study (Duffin 1983a; Fig. 4B). The central upper tooth plate differs from *Oblidens* gen. nov. in that the hypermineralised tissue does not cover the entire occlusal surface but is confined to two triangular areas, one sited anteriorly toward the mesial angle and the other posteriorly, with an intervening triangular area devoid of pleromin situated centrally and arising from the labial margin (Duffin 1983a, p. 9; Fig. 4B).

Material of Agkistracanthius mitgelensis from the Rhaetian to Hettangian of Switzerland and Austria includes what has been interpreted as an upper posterior tooth plate, but details of the occlusal surface are lacking (Duffin & Furrer 1981, p. 818). Material of Agkistracanthus from the Rhaetian of Britain, however, includes a well preserved upper posterior tooth plate. This contrasts with the equivalent plate in Oblidens gen. nov. in having a very short symphyseal margin; hypermineralised tissue covers the occlusal surface with the exception of an oval wear facet located close to the junction of the symphyseal and lingual margins of the tooth plate (Duffin 1994, fig. 5b). This wear facet seems to be absent in the tooth plates of juveniles (Duffin 1994, p.8, fig. 6). Also, a labial ridge is present along the anterior part of the labial margin of the UK material (Duffin 1994, fig. 5b).

*Lower posterior (mandibular) tooth plate.* The lower posterior (mandibular) tooth plate in *Oblidens* gen. nov. is quite distinctive and clearly differs from that in other myriacanthids where this particular dental element is known (Table 1; Fig. 5). Whilst the occlusal surface of *Myriacanthus paradoxus* is covered with hypermineralised tissue, as in *Oblidens* gen. nov., the distribution of diagonal ridges differs between the two taxa. In *Myriacanthus*, three ridges cross the tooth plate surface (compared to only one in *Oblidens* gen. nov.), all arising from the labial border: a symphyseal, central and posterior ridge (Figs 5D, 5B). As a result, the labial margin of the plate is much more sinuous in *Myriacanthus* than in *Oblidens* gen. nov.

In *Halonodon*, the robust lower posterior tooth possesses four tritoral areas surmounting diagonal ridges on the occlusal surface (Figs 4C, 5C, 5D); an

outer elongate labial tritoral area, an elongate symphyseal tritoral area; a central elongate tritoral area may be present on the central diagonal ridge; a posterior tritor occupies the central posterior part of the plate and part of the lingual margin and may contact the symphyseal and central diagonal tritors depending on ante-mortem wear. This contrasts strongly with the single ridge and complete cover of hypermineralised tissue in *Oblidens* gen. nov.

The lower posterior tooth plates of *Acanthorhina* are much more elongate than those of *Oblidens* gen. nov. Furthermore, two diagonal ridges arise from the labial margin just lateral to the mesial angle and converge lingually, enclosing a triangular area which lacks hypermineralised tissue (Figs 4B, 5G); a third diagonal ridge runs from the posterior part of the labial border to the distal angle, in contrast to the condition in *Oblidens* gen. nov.

In *Agkistracanthus*, a convex ridge crosses the occlusal surface diagonally from the labial angle to the



Fig. 5. Comparison of the right lower posterior (mandibular) tooth plates in a range of myriacanthid genera. A: *Oblidens bornholmensis* gen. et sp. nov. (Pliensbachian of Denmark). B: *Myriacanthus paradoxus* (Rhaetian to Sinemurian, UK). C: *Halonodon luxembourgensis* (Hettangian, Luxembourg). D: *Halonodon warneri* (Sinemurian of Belgium). E: *Metopacanthus granulatus* (Sinemurian, UK). F: *Agkistracanthus mitgelensis* (Rhaetian to Hettangian of Switzerland and the UK). G: *Acanthorhina jaekeli* (Toarcian of Germany). H: *Alethodontus bavariensis* (Hettangian of Germany). After Duffin & Delsate (1993). Scale bar =10 mm throughout.

lingual angle, dividing the surface into two (Duffin & Furrer 1981, p1.2, fig. la; Fig. 5F). This ridge is proportionally much narrower in *Agkistracanthus* than its equivalent in *Oblidens* gen. nov., and the tooth plate as a whole is less elongate, more robust and trapezoid in outline. The lower posterior tooth plate of *Metopacanthus* also possesses a single diagonal ridge, this time arising from part way along the labial border passing across the occlusal surface toward the lingual angle, but the form of the tooth plate is much more elongate and slender than *Oblidens* gen. nov. (Fig. 5E).

Alethodontus bavariensis from the Hettangian of Germany (Duffin 1983b) is based upon an isolated external mould of a lower posterior tooth plate whose occlusal surface is transected by two diagonal ridges arising from a common origin on the labial border of the plate; the ridges diverge posteriorly, with one directed toward the lingual angle and the other toward the distal angle of the tooth plate (Fig. 5H).

#### Discussion

To date, there have been only two records of holocephalians from the Pliensbachian of north-western Europe, and both belong to true chimaeroids rather than myriacanthoids – *Eomanodon simmsi* Ward & Duffin (1989) from the *margaritatus* zone of Gloucestershire, UK, and *Brachymylus latus* Duffin (1996) from the *Amaltheus* Shale (*Pleuroceras spinatum* zone, Late Pliensbachian) of Bavaria, Germany. The tooth plates of these two genera clearly differ from those of the Bornholm taxon because the hypermineralised tissue is restricted to discrete units called tritors and does not cover the occlusal surface.

Like other holocephalians, *Oblidens* gen. nov. was probably an opportunistic feeder able to take a range of invertebrate prey; the mode of action of the occlusal surface of the tooth plates would have been predominantly crushing, enhanced by the presence of ridges transecting the tooth plate surface, a feature which may have lent an additional sectorial action to the bite.

# Conclusions

The isolated holocephalian tooth plates described here clearly belong to a myriacanthid on the basis of the widespread distribution of hypermineralised tissue over the whole surface of both palatine and mandibular dental elements. Comparison of the structure of the tooth plates with those of other myriacanthid genera indicates that the Bornholm material should be placed in a new taxon, *Oblidens bornholmensis* gen. et sp. nov. This record increases the known palaeodiversity of the myriacanthid holocephalians and represents the first member of the family to be described from Pliensbachian deposits.

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