# Further holocephalian remains from the Hasle Formation (Early Jurassic) of Denmark

CHRISTOPHER J. DUFFIN & JESPER MILÀN

Geological Society of Denmark
https://2dgf.dk

Received 26 August 2022
Accepted in revised form
12 November 2022
Published online
30 November 2022



Duffin, C.J. & Milàn, J. 2022: Further holocephalian remains from the Hasle Formation (Early Jurassic) of Denmark. Bulletin of the Geological Society of Denmark, Vol. 70, pp. 139–149. ISSN 2245-7070. https://doi.org/10.37570/bgsd-2022-70-10

*Oblidens bornholmensis*, known from isolated upper posterior (palatine) and lower posterior (mandibular) tooth plates, was the first myriacanthid holocephalian to be described from the Hasle Formation (Pliensbachian, Early Jurassic) of Bornholm (Denmark). Further collecting in the Hasle Formation has yielded seven more specimens of myriacanthid tooth plates. Two mandibular tooth plates are assigned to *Myriacanthus paradoxus*, thereby extending both the geographical and stratigraphic range of the genus. In addition to new material of *Oblidens bornholmensis*, some distinctive myriacanthid palatine and mandibular tooth plates are described and left in open nomenclature. The Early Pliensbachian deposits of Bornholm preserve the most diverse myriacanthid fauna known to date.

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

*Christopher J. Duffin [cduffin@blueyonder.co.uk], Earth Sciences Department, The Natural History Museum, Cromwell Road, London SW7 5BD, UK and 146, Church Hill Road, Cheam, Sutton, Surrey SM3 8NF, UK. Jesper Milàn [jesperm@oesm.dk], Geomuseum Faxe/Østsjællands Museum, Østervej 2, DK-4640 Faxe, Denmark.*

Remains of holocephalians are much rarer in the fossil record than those of elasmobranchs, their chondrichthyan sister-group. Unlike elasmobranchs, in which the teeth are shed from the crest of the jaw continuously throughout life in a conveyor belt-like fashion, holocephalian teeth grow from their lingual surface throughout the life of the individual and are not shed. This means that a tooth plate specimen represents the death of an individual in holocephalians, whereas an isolated shark's tooth might represent loss during a single feeding episode.

Mesozoic holocephalians all belong to the Order Chimaeriformes, and can be classified into three suborders: the squalorajoids are represented only by the type genus (*Squaloraja*; Hettangian to Sinemurian of Europe); myriacanthoids range from the Rhaetian (Late Triassic) to the Tithonian (Late Jurassic) of Europe; true chimaeroids, whose oldest known representatives are *Eomanodon simmsi* and *Brachymylus latus* from the Pliensbachian of England and Germany respectively (Ward & Duffin 1989; Duffin 1996). The discovery of tooth plates of *Oblidens bornholmensis*, a myriacanthid, on Bornholm (Duffin & Milàn 2017) marked the first record of the group in Pliensbachian deposits and the earliest point in the overlap of the ranges of the myriacanthoids and chimaeroids. Myriacanthoid remains seem to dominate the holocephalian fossil record in the Early Jurassic, but chimaeroid remains are more abundant and diverse by the Late Jurassic and Early Cretaceous.

Further specimens of myriacanthid holocephalian tooth plates have come to light since the initial work of Duffin & Milàn (2017). The purpose of the present paper is to describe and discuss this additional material and highlight holocephalian diversity in the Pliensbachian Hasle Formation.

## Geological Setting

Bornholm (Fig. 1), a Danish island located south of Sweden in the Baltic Sea, is an upstanding, fault-bounded block. It is situated adjacent to the NW–SEtrending Sorgenfrei-Tornquist Zone, separating the Danish Basin from the Baltic Shield, and whose movements had direct consequences for Mesozoic sediment supply and pulses of sedimentation. The type section for the Hasle Formation is exposed just south of Hasle town (Fig. 1B), approximately 1 km west of a fault line which controlled the shoreline geography during the deposition of the formation (Surlyk & Noe-Nygaard 1986; Milàn & Surlyk 2015). The formation is dominated by arenaceous deposits; reddish-brown, hummocky cross-stratified sandstones and swaley cross-stratified siltstones are interbedded with very fine sandstones (Duffin & Milàn 2017, fig. 1C). Most of the vertebrate remains come from a fossiliferous conglomerate where they are mixed with basement rock clasts draping the bases of individual swales (Surlyk & Noe-Nygaard 1986; Larsen & Friis 2001).

The Hasle Formation is dated to the Early Pliensbachian based on its ammonite fauna, which places the formation within the lower Pliensbachian *Uptonia jamesoni* zone together with the *Acanthopleuroceras valdani* subzone of the overlying *Tragophylloceras ibex* zone (Donovan & Surlyk 2003). Other invertebrates include several species of bivalves, scaphopods and belemnites (Malling & Grönwall 1909; Malling 1911, 1914, 1920; Höhne 1933; Donovan & Surlyk 2003). The Hasle Formation further yields a diverse vertebrate fauna comprising hybodont and neoselachian sharks (Rees 1998), isolated scales of as yet undetermined actinopterygians, and at least three plesiosaurian taxa (Milàn & Bonde 2001; Smith 2008). Recently remains of terrestrial animals have been described in the form of dinosaurian bone fragments and a mammalian tooth (Molin 2021), an osteoderm from a thallatosuchian crocodile (Milàn & Mueller-Töwe 2021), and a single, small theropod footprint (Milàn & Surlyk 2015).

## Material and Methods

Six virtually complete holocephalian tooth plates were collected in 2019 and 2020 by Marianne Nattestad, and one specimen by Anton Wulff Jensen from the out-

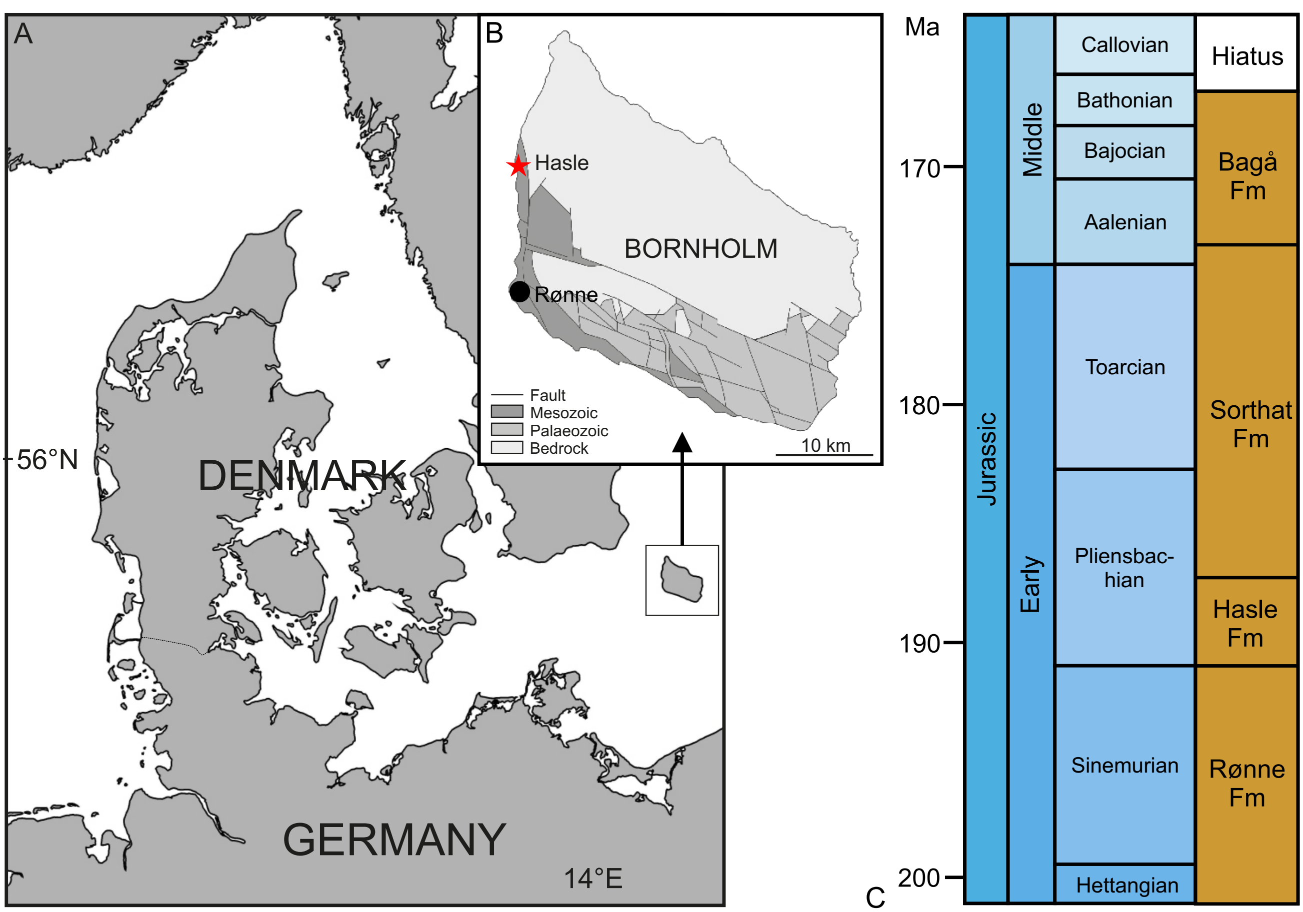


**Fig. 1.** Bornholm and the Hasle Formation. **A**: Location map showing the position of Bornholm in the Baltic Sea. **B:** Outline geological map of Bornholm, showing the location of Hasle. **C:** Late to Middle Jurassic stratigraphy of Bornholm, modified after Sandersen *et al.* (2014).

crop of Hasle sandstone just south of Hasle harbour, Bornholm. The specimens are declared Danekrae NHMD 633649–633653, NHMD 633654 and NHMD 873668. Danekræ are fossils, minerals or meteorites of exceptional scientific merit or value as items for exhibition purposes; the discoverer is rewarded for the material by the Danish state. All the specimens are now part of the collections of the Natural History Museum of Denmark (NHMD), Øster Voldgade 5-7, DK-1350 Copenhagen. The tooth plates were removed from the surrounding matrix by mechanical preparation using an air scribe.

Other institutional abbreviations used in this paper are as follows: NHMUK PV – Fossil Fish section, Earth Science Faculty, The Natural History Museum, Cromwell Road, South Kensington, London SW7 5BD, UK; SMNS – Staatliches Museum für Naturkunde in Stuttgart, Rosenstein 1-3, 70191 Stuttgart, Germany.

## Myriacanthid holocephalians

Ranging in age from the Late Triassic (Rhaetian) to the Early Jurassic (Toarcian; Patterson 1965; Stahl 1999), members of the chimaeriform Family Myriacanthidae are characterised by the presence of a specialised hypermineralised tissue covering the greater part of the occlusal surfaces of the single pair of upper (palatine) tooth plates and the single pair of lower (mandibular) tooth plates. Anterior to the palatine tooth plates, the paired vomerine tooth plates usually have the hypermineralised tissue arranged in distinct units or tritors. There is also a single medial tooth plate, the symphyseal tooth plate, anterior to the mandibular tooth plate pair. The hypermineralised dentine pillars sit upon a base of lamellar tissue. The occlusal surface of the tooth plate is often transected by a series of ridges with intervening depressions. These give rise to sufficient variation in occlusal surface topography to permit development of a sectorial component to the largely crushing function of the tooth plates. Recent work on the histology of the tooth plates of extant chimaeroids (Smith *et al.* 2019; Lijima & Ishiyama 2020; Johanson *et al.* 2021) has demonstrated that the phosphate mineral phase forming the dentinal pillars in the dental hypermineralised tissue of holocephalians is whitlockite (a magnesium and iron-rich calcium phosphate) rather than apatite. This has prompted the use of the term 'whitlockin' for the hypermineralised tissue formerly known as pleromin. Whilst the mineralogy of myriacanthid tooth plates has not yet been checked directly it is most likely to be identical to that of the chimaeroids. However, in the absence of definitive clarification of the chemical composition of the phosphate minerals forming the

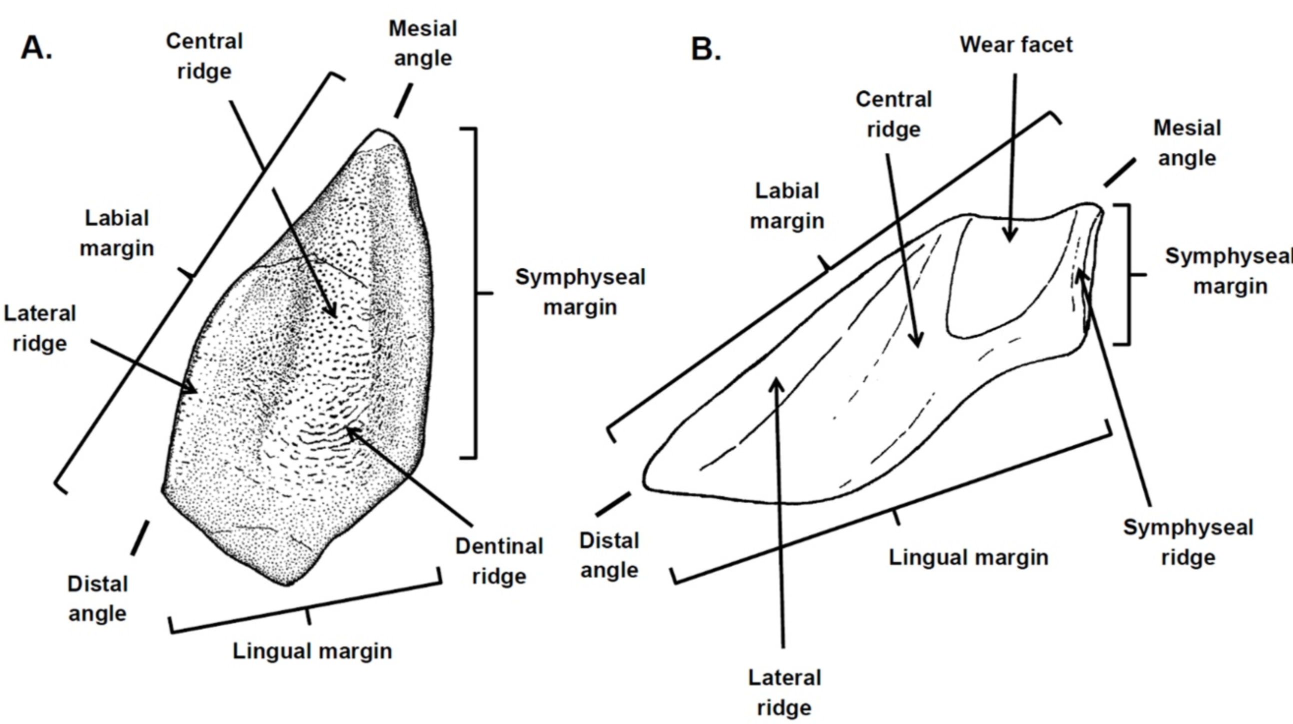


**Fig. 2.** Diagram showing the technical descriptive terms used in the text: **A:** NHMD 11740, a right upper posterior (palatine) tooth plate of *Oblidens bornholmensis* in occlusal view. **B:** NHMD 633652, a left lower posterior (mandibular) tooth plate of *Myriacanthus paradoxus* in occlusal view.

hypermineralised tissue of the tooth plates described here, the term ‘pleromin’ is the name retained here.

The most common myriacanthid fossils are isolated tooth plates whose robust structure favours preservation. Unlike the teeth of sharks, holocephalians do not shed their teeth during life, so the discovery of a tooth plate represents the death of an individual fish. Like their elasmobranch sister group within the chondrichthyans, holocephalians possess cartilaginous skeletons with a high organic content, and consequently low preservation potential. A few specimens preserving parts of the endoskeleton in varying degrees of articulation are known from certain conservation lagerstätten (*Myriacanthus* and *Metopacanthus* from the Hettangian to Sinemurian ‘Lower Lias’ of Lyme Regis in the UK, and *Acanthorhina* from the Toarcian Posidonienschiefer of SW Germany; Patterson 1965; Duffin 1983a). Dorsal fin spines are also commonly preserved as isolated elements. The Myriacanthidae currently contains 10 species distributed amongst eight genera, plus some material which remains in open nomenclature (Stahl 1999; Duffin & Milàn 2017).

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.

## Systematic Palaeontology

### Class Chondrichthyes Huxley, 1880

### Superorder Holocephali Bonaparte, 1832–1841

### Order Chimaeriformes Obruchev, 1953

### Suborder Myriacanthoidei Patterson, 1965

### Family Myriacanthidae Woodward, 1889

#### Genus *Myriacanthus* Agassiz, 1836

*Type species by monotypy. Myriacanthus paradoxus* Agassiz, 1836, ‘Lower Lias’, Sinemurian (Early Jurassic) of Lyme Regis, Dorset, UK.

#### *Myriacanthus paradoxus* Agassiz, 1836

Fig. 3A, B

1822 “External defensive organ” De la Beche, vol. 1, p. 44, pl. 5 figs 1, 2.
1836 *Myriacanthus paradoxus* Agassiz, vol. 3, pl. 6.
1837 *Myriacanthus paradoxus* Agassiz, vol. 3, p. 38.
1837 *Myriacanthus retrorsus* Agassiz, vol. 3, 39.
1838 *Myriacanthus retrorsus* Agassiz, vol. 3, pl. 8a figs 14, 15.
1855 *Chimaera (Ischyodon) johnsoni* Terquem, p. 241, pl. 14 fig. 1.
1872 *Prognathodus guentheri* Egerton, p. 233, pl. 8.
1891 *Myriacanthus paradoxus* Woodward, p. 44, pl. 2 figs 1–3.
1906 *Myriacanthus paradoxus* Woodward, p. 2, pl. 1 figs 1–5.
1906 *Myriacanthus paradoxus* Dean, p. 143, text-figs 119, 119A, 142.
1965 *Myriacanthus paradoxus* Patterson, p. 128, text-figs 13-19, pl. 22 fig. 46, pl. 25 fig. 59, pl. 26 fig. 60, pl. 28 fig. 67.
1992 *Myriacanthus paradoxus* Patterson, p. 45, figs 7A–C.
1993 *Myriacanthus paradoxus* Duffin & Delsate, text-fig. 5f.
1994 *Myriacanthus paradoxus* Duffin, p. 12, figs 8a-b.
1995 *Myriacanthus paradoxus* Duffin & Delsate, p. 4, text-figs 3a, 4, pl. 1. figs a–b.
1999 *Myriacanthus paradoxus* Stahl, p. 120, figs 117C, 120-122, 123F.
1999 *Myriacanthus paradoxus* Duffin, p. 211, text-figs 23A–B.
2016 *Myriacanthus paradoxus* Duffin, p. 12, figs 8a.
2017 *Myriacanthus paradoxus* Duffin & Milàn, figs 4D, 5B.

*Holotype*. NHMUK PV P 6095, a dorsal fin spine (Agassiz, 1836 pl. 6 figs 1–2) from the Lower Lias (?Sinemurian, Early Jurassic) of Lyme Regis, Dorset, England.

*Bornholm material*. NHMD 633652, an isolated left lower posterior (mandibular) tooth plate freed from the matrix (Fig. 3A); NHMD 873668, an isolated right lower posterior (mandibular) tooth plate (Fig. 3B).

*Horizon*. Hasle Formation.

*Age*. ‘Carixian’, Early Pliensbachian, Early Jurassic (probably *Uptonia jamesoni* subzone to *Acanthopleuroceras valdani* subzone based on the Hasle Formation ammonite fauna collected from inland quarries; Donovan & Surlyk, 2003). No ammonites have been described from the coastal exposures.

*Locality*. Cliff section 100 m south of Hasle, Bornholm, Denmark; 55°10′44.18″N, 14°42′8.58″E.

*Description of the Bornholm material.* NHMD 633652 is an isolated left mandibular (lower) tooth plate measuring 27.5 mm across the diagonal from the mesial angle to the distal angle (Fig. 3A). The symphyseal margin is short (7.5 mm long) and straight, 4 mm deep and D-shaped in symphyseal view. It is marked


**Fig. 3.** The tooth plates of *Myriacanthus paradoxus* from the Hasle Formation (Early Pliensbachian) of Bornholm, Denmark. **A:** NHMD 633652 in occlusal and basal views. **B:** NHMD 873668 in occlusal and basal views. **C:** Left lower posterior (mandibular) tooth plate of *Myriacanthus paradoxus* (NHMUK PV P.477) from the Lower Lias (Sinemurian) of Lyme Regis, Dorset, UK, in occlusal view. The specimens are reproduced to the same scale.

by a slight symphyseal ridge. The occlusal surface of the tooth plate is completely covered with a carpet of hypermineralised hard tissue with the exception of a triangular wear facet with broad (6.5 mm long) edge lying along the labial border adjacent to the mesial angle. The straight distal margin of the triangular wear facet is parallel to the symphyseal margin of the tooth plate while the gently curved lingual margin sweeps toward the mesial angle from the wear facet apex. A long, well-developed longitudinal ridge defines the labial border of the tooth plate, widens distally, and has its origin adjacent to the distal limit of the wear facet on the labial border. A second ridge, the central ridge, arises from this same point of origin, flanks the distal margin of the wear facet and crosses the central part of the tooth plate toward the lingual margin. The labial and central ridges diverge at approximately 35° to each other from their common point of origin and are separated by a deep groove. The mesiolabial and mesiolingual borders of the tooth plate are subparallel to each other for a distance of approximately 7 mm.

In basal view it is clear that the mesial angle is sharply defined with fairly deep labial and symphyseal walls. The mesial angle itself is underlain by a deep circular pit. Vascular canals can be seen perforating the basal tissue of the root at low angles of entry.

NHMD 873668 is an isolated right mandibular tooth plate whose overall morphology agrees well with that of the holotype. Rather smaller, it measures 13.4 mm diagonally from the mesial angle to the (incomplete) distal angle (Fig. 3B). Like the holotype, it has a straight symphyseal margin, D-shaped in symphyseal view. The symphyseal margin is 6 mm long. The occlusal surface is covered with pleromin, except for the triangular or V-shaped wear facet occupying the mesiolabial portion of the tooth plate. A lateral ridge follows the labial margin of the plate, strengthening distally and is separated by means of a groove from the broad central ridge which crosses the tooth plate diagonally. The lateral and central ridges have closely adjacent points of origin at a point on the labial margin distal to the mesial angle and diverge from each other at an angle of approximately 30°. Growth lines are visible in the body of the tooth plate lingual to the wear facet.

Although trapezoid in shape, NHMD 873668 is much less gracile and rather broader labio-lingually than NHMD 633652. Also, the lateral ridge along the labial border is not as well developed as in NHMD 633652.

*Comparisons.* NHMD 633652 and NHMD 873668 clearly belong to the same taxon, based on their closely similar morphologies. The comparatively slender, elongate shape of the holotype is similar to that in *Alethodontus bavariensis* (Duffin 1983b) and *Acanthorhina jaekeli* (Duffin 1983a); the mandibular tooth plates of *Halonodon* and *Agkistracanthus* are much broader labio-lingually (Duffin 1984; Duffin & Furrer 1981).

Several myriacanthid genera show topographic variation in the form of distinct ridges which either cross or border the occlusal surface. The specimens described above are similar to the mandibular tooth plate in *Alethodontus* in that the central and lateral ridges meet at a common point of origin on the labial border and diverge lingually from each other at an angle of 30°-35°. *Alethodontus* does not show any sign of a triangular wear facet, however. The type and only specimen of *Alethodontus bavariensis* (SMNS 51956) probably belongs to a juvenile, based on the sharply defined ridges and lack of any significant antemortem wear (Duffin 1983a).

*Acanthorhina* possesses a similar wear facet to that shown in the Bornholm material, but in the Toarcian specimen, two diagonal ridges arise from the labial margin just lateral to the mesial angle, converging lingually (Duffin 1983a).

*Myriacanthus* and *Metopacanthus* both have a fairly simple arrangement with a symphyseal, central and lateral ridge. The latter lacks the distinctive V-shaped wear facet shown in NHMD 633652 and NHMD 873668 (Stahl 1999, fig. 118). In the case of mandibular tooth plates of *Myriacanthus paradoxus*, however, some specimens show the development of a comparable wear facet. NHMUK PV P.477 consists of associated symphyseal, palatine and mandibular tooth plates (Fig. 3C). The mandibular tooth plate in this specimen is an excellent match for the Danish specimens described above, in spite of being much larger (measuring 80 mm across the diagonal from the mesial angle to the distal angle) and less slender in outline. The Bornholm specimens can therefore be attributed to *M. paradoxus*, thereby extending (1) the geographical range of the genus from the UK (Patterson 1965), France (Terquem 1855) and Belgium (Duffin & Delsate 1995) to Denmark, and (2) the stratigraphical range of the genus from the Rhaetian (Duffin 1994) and Sinemurian (Patterson 1965) into the Pliensbachian. The comparatively diminutive size of the Bornholm specimens in comparison to the Lyme Regis material suggests either that (1) the Danish tooth plates are both from juveniles, or (2) that a reduction in body size took place from Sinemurian to Pliensbachian times. Note also the differences in sedimentary facies at the two localities; the 'Lower Lias' consists of an interbedded sequence of marine near- and off-shore calcareous and organic-rich mudstones, whilst the arenite-dominated Bornholm sequence represents a higher energy nearshore environment with greater terrigenous clastic input.

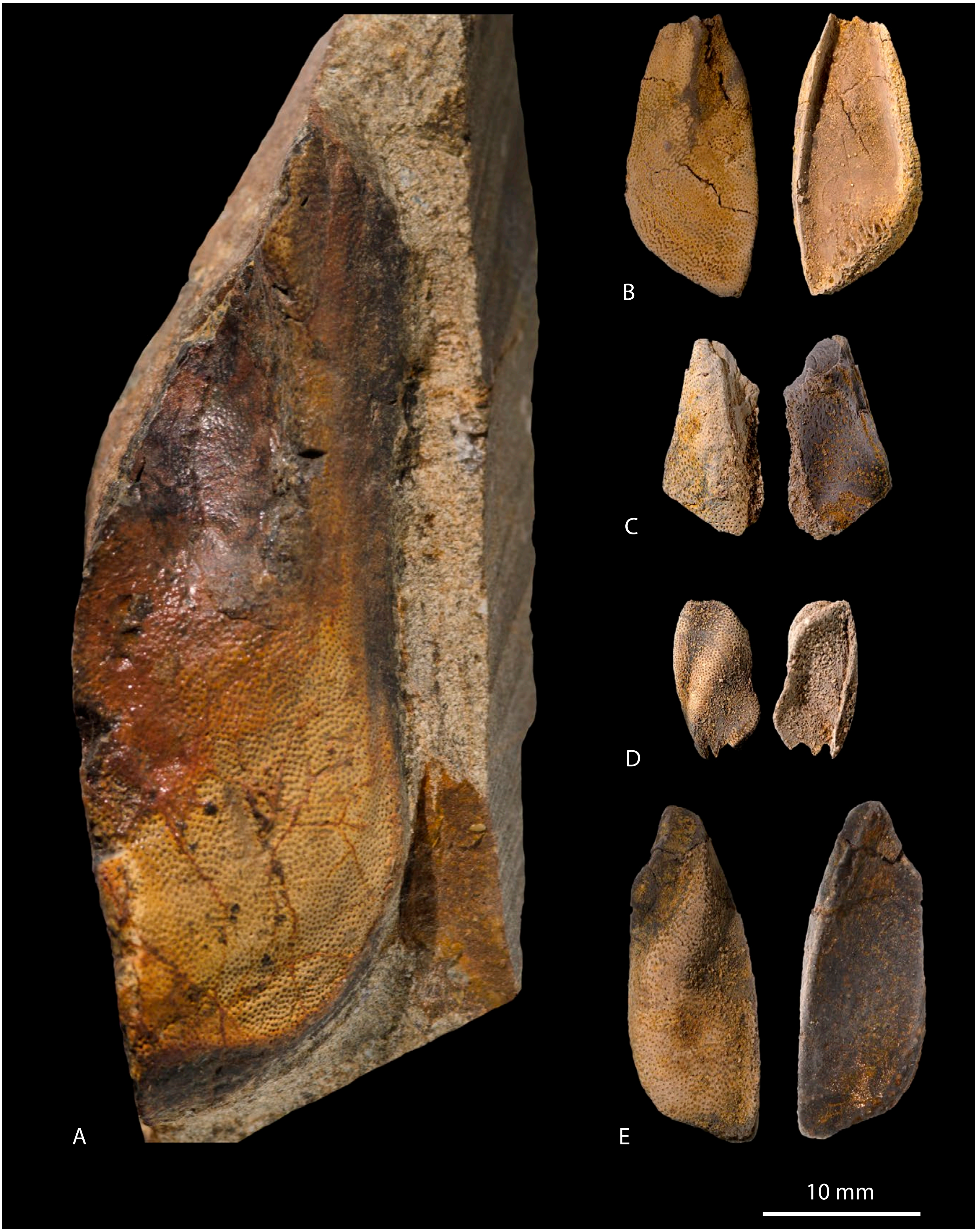


**Fig. 4.** Myriacanthid holocephalian tooth plates from the Hasle Formation (Early Pliensbachian) of Bornholm, Denmark. **A:** NHMD 633649 (note the left side is eroded) in occlusal view. **B:** NHMD 633651: left upper posterior (palatine) tooth plate of *Oblidens bornholmensis* in occlusal and basal views. **C:** NHMD 633650: probably a left upper posterior (palatine) tooth plate of *Oblidens bornholmensis* in occlusal and basal views. **D:** NHMD 633654: right lower posterior (mandibular) tooth plate of an undetermined myriacanthid holocephalian in occlusal and basal views. **E:** NHMD 633653: left upper posterior (palatine) tooth plate of an undetermined myriacanthid holocephalian in occlusal and basal views. The specimens are reproduced to same scale.

The mandibular tooth plates of *M. paradoxus* can be clearly distinguished from those of the coeval *Oblidens bornholmensis* on the basis of overall shape, and the fact that the latter species has only a single ridge which crosses the tooth plate in a central position (Duffin & Milàn 2017).

## Genus *Oblidens* Duffin & Milàn, 2017

*Type species. Oblidens bornholmensis* Duffin & Milàn, 2017

*Revised 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 in juveniles and terminates in the central region of the tooth plate in mature individuals. A weak ridge flanks the labial margin of the palatine tooth plate, and a deep ovoid wear facet is developed on the mesio-labial flanks of the central ridge in mature individuals. 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*

2017 *Oblidens bornholmensis* Duffin & Milàn, 2017; Duffin & Milàn, p. 164, figs 3A-E.

Fig. 4A-C

*Material.* NHMD 633649, an isolated partial right (?) palatine tooth plate (Fig. 4A); NHMD 633650, an isolated left palatine tooth plate (Fig. 4C); NHMD 633651, an isolated fragment of a left palatine tooth plate (Fig. 4B).

*Stratigraphical position*. Hasle Formation.

Age: 'Carixian', Early Pliensbachian, Early Jurassic (probably *Uptonia jamesoni* subzone to *Acanthopleuroceras valdani* subzone).

*Locality.* Cliff section 100m south of Hasle harbour, Bornholm, Denmark; 55°10′44.18″N, 14°42′8.58″E.

*Description*. NHMD 633651 is the best preserved and most complete of the new specimens which can be assigned to *Oblidens bornholmensis* (Fig. 4B). Missing only the mesial angle, the specimen has been completely freed from the matrix and is a left palatine (upper posterior) tooth plate whose preserved diagonal length is 17 mm. The preserved length of the straight symphyseal margin is 11 mm and that of the arcuate labial margin is 16 mm. These dimensions mean that it is slightly larger than the holotype (NHMD 117400). NHMD 633651 conforms well with the overall form of previously described palatine tooth plates belonging to the genus. The central ridge is clearly developed and extends around halfway toward the lingual margin of the plate from the broken mesial angle. A few dentinal ridges are developed on the symphyseal flanks of the central ridge centrally. The overall shape of the tooth plate is rather more oval than that of the holotype; the labial margin curves rather more gently toward the lingual angle and has a barely developed ridge, in contrast to the holotype. NHMD 633651 probably comes from an older individual than NHMD 11740. A shallow sub-oval wear facet has started to develop on the labial flanks of the central ridge but is still floored with hypermineralised tissue. This wear facet has limited the central expansion of the central ridge toward the center of the occlusal surface of the tooth plate. In basal view, the narrow labial wall and the slightly thicker symphyseal wall of the tooth plate can be clearly discerned. Longitudinal vascular canals enter the lingual underside of the root tissues at a shallow angle.

NHMD 633649 is another palatine tooth plate, this time from the right side (Fig. 4A). In overall morphology it agrees well with NHMD 633651. Still attached to matrix by its basal surface, the tooth plate has a broken labial margin. 66 mm long across the diagonal from the mesial angle to the point on the lingual margin closest to the position of the distal angle (now lost), the occlusal surface is completely covered with hypermineralised tissue. The central ridge is well developed and, as in NHMD 633649, extends to about the mid-point of the tooth plate. Dentinal ridges are missing in this specimen, all the individual pillars of pleromin being normal to the biting surface. The ovoid wear facet flanking the mesio-labial border of the central ridge forms a deeply excavated concavity. The symphyseal border of the tooth plate is not as straight as in the holotype and NHMD 633649, being slightly sinuous along its length. By far the largest of the specimens assigned to *Oblidens bornholmensis*, this example probably comes from a mature individual on the basis of both its size and the development of the wear facet.

NHMD 633650 is probably a fragmentary left palatine tooth plate of *Oblidens bornholmensis* (Fig. 4C). Triangular in shape in occlusal view, the pleromin-covered occlusal surface shows no sign of either a symphyseal or a labial ridge. The maximum preserved diagonal is 14 mm long and there is faint evidence of a short length of central ridge present near the mesial angle. The symphyseal margin is straight and measures 11.6 mm in length. No dentinal ridges are present.

### Undetermined myriacanthid remains

NHMD 633654 is an isolated right mandibular tooth plate which is trapezoid in shape measuring 10 mm across the diagonal from the mesial angle to the distal angle (Fig. 4D). The symphyseal margin of the tooth plate is incomplete but the preserved portion is straight and does not seem to be D-shaped in symphyseal view. The symphyseal ridge is weak to moderate. Pleromin covers the whole of the occlusal surface and no differentiated dentine ridges are present. A lateral ridge is present along the labial margin, getting stronger distally. Broader than in NHMD 633652, it is better developed than in NHMD 633653. A central ridge crosses the occlusal surface of the tooth plate diagonally, expanding distally. The lateral ridge and central ridge are separated from each other by a shallow groove mesially, and the two ridges do not meet or have a common origin anywhere on the labial margin. No wear facets are present on the tooth plate. In basal view, the tooth plate clearly possesses a deep labial wall, but details of the vascularisation are obscure.

This tooth plate is much less gracile and much broader labio-lingually than the mandibular tooth plates of *A. bavariensis*, *Acanthorhina* and *Metopacanthus*. The more robust tooth plate shape in NHMD 633654 is more reminiscent of that in *Myriacanthus, Halonodon* and *Akgistracanthus*, although the details of the wear facets and distribution of the pleromin on the occlusal surface is significantly different compared to these three genera. The outline of NHMD 633654 is markedly different to the situation in mandibular tooth plates of *Oblidens bornholmensis*.

NHMD 633653 is an isolated left palatine tooth plate, somewhat tear-dropped in shape, measuring 22 mm across the diagonal (Fig. 4E). The symphyseal margin is slightly concave, measures 5.4 mm in length, is not D-shaped in symphyseal view and is surmounted by a very weak symphyseal ridge. Similarly, a very weak lateral ridge marks the labial margin of the plate, becoming slightly stronger toward the distal angle. An increasingly broad central ridge crosses the tooth plate diagonally but does not meet the lateral ridge on the labial border of the tooth plate. No dentinal ridges are developed and no distinctive wear facets are visible in the pleromin, which covers the occlusal surface of the specimen. Basal view reveals a weak to moderately deep labial wall.

In terms of overall shape, NHMD 633653 is similar to NHMD 633651 (*O. bornholmensis*). In the latter specimen, however, the central ridge is developed differently being limited to the mesial half of the occlusal surface and confined to the mid-line of the tooth plate (rather than crossing it diagonally). NHMD 633653 therefore does not belong to *O. bornholmensis*. Furthermore, the specimen does not pertain to *Myriacanthus paradoxus*, in which the occlusal surface is crossed by two diagonal ridges, or *Halonodon*, which has hypermineralised tissue concentrated in several tritoral areas. In *Acanthorhina jaekeli*, occlusal pleromin is restricted to two triangular areas (Duffin 1983a, p.9), whilst details of the occlusal surface of the palatine tooth plate of *Agkistracanthus mitgelensis* (Rhaetian to Hettangian of Switzerland) are lacking (Duffin & Furrer 1981, p. 818). The material of *A. mitgelensis* described from the British Rhaetian (Duffin 1994) is more oval in shape than the Danish specimen and shows the development of an oval wear facet in larger specimens (Duffin 1994, fig. 5).

NHMD 633654 and NHMD 633653 are left in open nomenclature for the moment, awaiting clarification from further discoveries before their potential relationships can be reassessed.

## Conclusions

It used to be that the Pliensbachian marked a stage in the Early Jurassic where our knowledge of myriacanthid holocephalians was negligible. Indeed, the only known holocephalian taxa from the Pleinsbachian were the earliest true chimaeroids, represented by *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 recent discoveries of myriacanthid tooth plates in the Early Pliensbachian of the cliff sections near Hasle on the Danish island of Bornholm (Duffin & Milàn 2017) have changed this situation dramatically; indeed, although only a relatively small number of tooth plates have been discovered in the succession, they now represent the greatest diversity of Jurassic holocephalians known to date.

The most recent finds of myriacanthid holocephalian tooth plates on Bornholm present a number of problems of interpretation. The mandibular tooth plates can clearly be separated into two groups based upon overall tooth plate shape, wear facet development and ridge development on the occlusal surface. Every myriacanthid taxon is based upon only a small number of specimens which means that there is only limited appreciation of tooth plate variation and ontogeny in the population; this somewhat restricts meaningful comparison and suggests that the discovery of further material may require revision of the conclusions presented here. One of the two groups of mandibular tooth plates is here assigned to *Myriacanthus paradoxus*, previously known from the Rhaetian and Sinemurian of the UK, and the Sinemurian of France and Belgium. The other group of mandibular tooth plates is left in open nomenclature.

The newly discovered palatine tooth plates from Bornholm also fall into two groups – those belonging to *O. bornholmensis* and a further specimen currently left in open nomenclature.

## Acknowledgements

We are extremely grateful to the amateur geologists Marianne Nattestad and Anton Wulff Jensen who found the holocephalian teeth in Hasle, brought them to our attention and donated them to the NHMD. Mette Agersnap Grejsen Hofstedt kindly prepared the teeth for us and Sten Lennart Jakobsen provided photographs of the specimens. We are very grateful to the two referees, Dr. David Ward (NHMUK) and Dr. Evgeny Popov (Saratov) for their helpful and constructive comments at the review stage.

## References

Agassiz, J.L.R. 1833–1843. Recherches sur les Poissons Fossiles. Petitpierre, Neuchâtel. https://doi.org/10.5962/bhl.title.4275

Beche, H.T. de la. 1822. Remarks on the geology of the south coast of England, from Bridport Harbour, Dorset, to Babbacombe Bay, Devon. Transactions of the Geological Society of London series 2, 1, 40–47. https://doi.org/10.1144/transgslb.1.1.40

Bonaparte, C.L.J.L. 1832–1841: Iconografia della Fauna Italica per le Quattro classi degli animali vertebrati di Carlo L. Bonaparte, principe de Canino. V. iii. Pesci. Rome: Salviucci. https://doi.org/10.5962/bhl.title.70395

Dean, B. 1906. Chimaeroid fishes and their development. Publications of the Carnegie Institution 32, 1–194.

Donovan, D.T. & Surlyk, F. 2003: Lower Jurassic (Pliensbachian) ammonites from Bornholm, Baltic Sea, Denmark. In: Ineson, J.R. & Surlyk, F. (eds): The Jurassic of Denmark and Greenland. Geological Survey of Denmark and Greenland Bulletin 1, 555–583. https://doi.org/10.34194/geusb.v1.4684

Duffin, C.J. 1983a: Holocephalans in the Staatliches Museum fur Naturkunde in Stuttgart. 1. Myriacanthoids and Squalorajoids. Stuttgarter Beitrage zur Naturkunde B97, 1–41.

Duffin, C.J. 1983b: Holocephalans in the Staatliches Museum fur Naturkunde in Stuttgart. 2. A myriacanthid tooth plate from the Hettangian (Lower Jurassic) of Bavaria. Stuttgarter Beitrage zur Naturkunde B98, 1–7.

Duffin, C.J. 1984: A new myriacanthid holocephalan from the Sinemurian (Lower Jurassic) of Belgium. Zoological Journal of the Linnean Society 82 (1), 55–71. https://doi.org/10.1111/j.1096-3642.1984.tb00535.x

Duffin, C.J. 1994: Myriacanthid holocephalans (Chondrichthyes) from the British Late Triassic. Neues Jahrbuch *für* Geologie und Paläontologie Abhandlungen 192 (1), 1–16. https://doi.org/10.1127/njgpm/1993/1993/669

Duffin, C.J. 1996: Holocephalans in the Staatliches Museum für Naturkunde in Stuttgart. 4. The earliest German chimaeroid. Stuttgarter Beitrage zur Naturkunde B 240, 1–10.

Duffin, C.J. 1999. Fish, 191–222, In: Swift, A. & Martill, D.M. (eds): Fossils of the Rhaetian Penarth Group. Cambridge: Palaeontological Society.

Duffin, C.J. & Delsate, D. 1993: A new myriacanthid Holocephalan (Chondrichthyes) from the Early Jurassic of Luxembourg. Neues Jahrbuch für Geologie und Paläontologie Monatshefte 1993 (11), 669–680. https://doi.org/10.1127/njgpm/1993/1993/669

Duffin, C.J. 2016: Cochliodonts and chimaeroids: A.S. Woodward and the Holocephalians. In: Johanson, Z., Barrett, P. M., Richter, M. & Smith, M. (eds): Arthur Smith Woodward: His life and influence on modern vertebrate palaeontology. Geological Society, London, Special Publications 430, 137–154. https://doi.org/10.1144/sp430.9

Duffin, C.J. & Delsate, D. 1995: New record of the Early Jurassic myriacanthid holocephalan *Myriacanthus paradoxus* AGASSIZ, 1836 from Belgium. Belgian Geological Survey. Professional Paper 278, 1–9. https://doi.org/10.1127/njgpm/1993/1993/669

Duffin, C.J. & Furrer, H. 1981: Myriacanthid holocephalan remains from the Rhaetian (Upper Triassic) and Hettangian (Lower Jurassic) of Graubünden (Switzerland). Ecolgae Geologicae Helvetiae 74 (3), 803–829.

Duffin, C.J. & Milàn, J. 2017: A new myriacanthid holocephalian from the Early Jurassic of Denmark. Bulletin of the Geological Society of Denmark 65, 161–170. https://doi.org/10.37570/bgsd-2017-65-10

Egerton, P. de M.G. 1872: On *Prognathodus guentheri* Egerton, a new genus of fossil fish from the Lias of Lyme Regis. Quarterly Journal of the Geological Society of London 28, 233–238. https://doi.org/10.1144/gsl.jgs.1872.028.01-02.35

Höhne, R. 1933: Beiträge zur Stratigraphie, Tektonik und Paläogeographie des südbaltischen Rhät-Lias, insbesondere auf Bornholm. Abhandlungen aus dem Geologisch-Paläontologischen Institut der Universität Greifswald 12, 1–105.

Huxley, T.H. 1880: On the application of the laws of evolution to the arrangement of the vertebrata, and more particularly of the mammalia. Proceedings of the Zoological Society of London 1880, 649–662.

Iijima, M. & Ishiyama, M. 2020: A unique mineralization mode of hypermineralized pleromin in the tooth plate of Chimaera phantasma contributes to its microhardness. Scientific Reports 10, 18591. https:// doi.org/10.1038/s4159 8-020-75545-0.

Johanson, Z., Manzanares, E., Underwood, C., Clark, B., Fernandez, V. & Smith, M. 2021: Ontogenetic development of the holocephalan dentition: Morphological transitions of dentine in the absence of teeth. Journal of Anatomy 239 (3): 704–719. https://doi.org/10.1111/joa.13445

Larsen, O. & Friis, H. 1991: Petrography, diagenesis and pore-water evolution of a shallow marine sandstone (Hasle Formation, Lower Jurassic, Bornholm, Denmark). Sedimentary Geology 72, 269–284. https://doi.org/10.1016/0037-0738(91)90015-6

Malling, C. 1911: Hasle-Sandstenens alder. Meddelelser fra Dansk Geologisk Forening 3, 629–631.

Malling, C. 1914: De Jespersenske Buelag i Lias paa Bornholm. Meddelelser fra Dansk Geologisk Forening 4, 265–270.

Malling, C. 1920: Den marine Lias og Wealden-Aflejringer paa Bornholm. Meddelelser fra Dansk Geologisk Forening 5, 55–57.

Malling, C. & Grönwall, K.A. 1909: En Fauna i Bornholms Lias. Meddelelser fra Dansk Geologisk Forening 3, 271–316.

Milàn, J. & Bonde, N. 2001: Svaneøgler, nye fund fra Bornholm. Varv 2001, 3–8.

Milàn, J. & Mueller-Töwe, I. 2021: En havkrokodille fra Hasles fjerne fortid. Natur På Bornholm 2021, 14–16.

Milàn, J. & Surlyk, F. 2015: An enigmatic, diminutive theropod footprint in the shallow marine Pliensbachian Hasle Formation, Bornholm, Denmark. Lethaia 48, 429–435. https://doi.org/10.1111/let.12115

Molin, E. 2021: Rare terrestrial vertebrate remains from the Pliensbachian (Lower Jurassic) Hasle Formation on the island of Bornholm, Denmark. Dissertations in Geology at Lund University 612, 39 pp

Obruchev, D.M. 1953: Edestid researches in the works of A.P. Karpinskii. Trudy Paleozoologicheskogo Instituta. Akademiya Nauk SSSR 45, 1–85. [In Russian]

Patterson, C. 1965: The phylogeny of the Chimaeroids. Philosophical Transactions of the Royal Society of London B249, 101–219.

Patterson, C. 1992: Interpretation of the tooth plates of chimaeroid fishes. Zoological Journal of the Linnean Society 106, 33–61. https://doi.org/10.1111/j.1096-3642.1992.tb01239.x

Rees, J. 1998: Early Jurassic selachians from the Hasle Formation on Bornholm, Denmark. Acta Palaeontologica Polonica 43, 439–452.

Sandersen, P.B.E., Rasmussen, E.S., Bjerager, M., Jensen, J.B., Schovsbo, N. & Vosgerau, H. 2014: Skitser til opbygningen af en national 3D geologisk model for Danmark, Forslag til legende for den danske del af den nationale 3D geologiske model. Internal GEUS working paper, Rapport 2, 47 pp. https://doi.org/10.34194/raekke2.v78.6867

Smith, A.S. 2008: Plesiosaurs from the Pliensbachien (Lower Jurassic) of Bornholm, Denmark. Journal of Vertebrate Paleontology 28, 1213–1217. https://doi.org/10.1671/0272-4634-28.4.1213

Smith, M.M., Underwood, C., Goral, T., Healy, C. & Johanson, Z. 2019: Growth and mineralogy in dental plates of the holocephalan *Harriotta raleighana* (Chondrichthyes): Novel dentine and conserved patterning combine to create a unique chondrichthyan dentition. Zoology Letters, 5, 11. https://doi.org/10.1186/s40851-019-0125-3

Stahl, B.J. 1999: Chondrichthyes III. Holocephali. In: Schultze, H.-P. (ed.): Handbook of Paleoichthyology, 164 pp. München: Verlag Dr. Friedrich Pfeil.

Surlyk, F. & Noe-Nygaard, N. 1986: Hummocky cross-stratification from the Lower Jurassic Hasle Formation of Bornholm, Denmark. Sedimentary Geology 46, 259–273. https://doi.org/10.1016/0037-0738(86)90062-x

Terquem, O. 1855: Paléontologie de l'étage inférieur de la formation liasique de la province de Luxembourg d 'Hettange. Mémoires de la Société Géologique de France (2) 5, 219–343. https://doi.org/10.5962/bhl.title.11874

Ward, D.J. & Duffin, C.J. 1989: Mesozoic chimaeroids. 1. A new chimaeroid from the Early Jurassic of Gloucestershire, England. Mesozoic Research 2 (2), 45–51.

Woodward, A.S. 1889: On the Myriacanthidae – an extinct family of Chimaeroid Fishes. Annals and Magazine of Natural History, Series 6, 4, 275–280. https://doi.org/10.1080/00222938909460526

Woodward, A.S. 1891: Catalogue of the fossil fishes in the British Museum (Natural History), II. London: British Museum (Natural History). https://doi.org/10.5962/bhl.title.162355

Woodward, A.S. 1906: On a new specimen of the chimaeroid fish, *Myriacanthus paradoxus*, from the Lower Lias near Lyme Regis, Dorset. Quarterly Journal of the Geological Society of London 62, 1–4. https://doi.org/10.1144/gsl.jgs.1906.062.01-04.03