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New plesiosaur fossils from the Pliensbachian (Early Jurassic) of Bornholm, including the first juvenile specimen from Denmark

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Plesiosaurs were an extremely successful, globally distributed group that thrived from the Late Triassic to the end of the Cretaceous Period. The Early/Middle Jurassic faunal turnover greatly affected plesiosaur evolution, although it remains poorly understood, partly due to the scarcity of plesiosaur fossils from the Pliensbachian age (192.0–184.2 Ma). This paper describes five fossil plesiosaur skeletal elements found in the Pliensbachian aged Hasle Formation on the Danish island of Bornholm. The five specimens are isolated remains, including a tooth, spinal fragments, a rib and a propodial. The tooth can be assigned to Pliosauridae indet. due to its robust form and ornamentation, and the spinal fragments to Plesiosauria indet. The neural spine is detached and could therefore either be from an osteologically immature individual or show signs of paedomorphism. Lastly, but most importantly, an osteologically immature propodial is described. It is the first of its kind found in Denmark.

Keywords: Plesiosaur, marine reptile, juvenile, Pliensbachian, Denmark, Hasle

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The plesiosaurs (Plesiosauria) were an extremely successful, globally distributed group of Mesozoic marine tetrapods. They thrived over a period of approximately 130 million years, from the Late Triassic (200 Ma) to the end of the Cretaceous Period (66 Ma; Bardet *et al.* 2014). Plesiosauria was the only clade within the superorder Sauropterygia that survived beyond the Triassic Period (Bardet *et al.* 2014) and by the Early Jurassic plesiosaurs had a worldwide distribution. The relationships between and within major plesiosaur clades remain debated, although consensus is increasing in more recent years (Benson & Druckenmiller 2013; Roberts *et al.* 2020; Sachs *et al.* 2024). In addition to long-necked species with small heads in the clade Plesiosauroidea, Plesiosauria include taxa with short necks and larger heads, a body shape that evolved more than once within the two families Rhomaleosauridae and Pliosauridae (Fischer *et al*. 2020).

The Early/Middle Jurassic faunal turnover (*c*. 175 Ma) affected plesiosaur evolution, including a near extinction of the rhomaleosaurids, paving the way for the plesiosaur clades that came to dominate the oceans from the Middle Jurassic until the end-Cretaceous (Fischer *et al.* 2021; Sachs *et al.* 2024). Pliensbachian plesiosaur occurrences preceding the Early/Middle Jurassic faunal turnover are globally sparse and currently only three plesiosaur taxa are formally named: *Westphaliasaurus simensensii* (Schwermann & Sander, 2011), *Cryonectes neustriacus* (Vincent *et al*., 2013) and *Arminisaurus schuberti* (Sachs & Kear, 2018). In addition, Perrson (1963) reported three species from France that are incompletely described, and there are also undiagnostic plesiosaur specimens found in the UK (Storrs 1995; Evans 2003; Forrest 2006; Evans 2012), Spain (Bardet *et al*. 2008), Germany (Sachs 2014) and Australia (Kear 2012; Table 1).

Additionally, plesiosaur fossils from the Pliensbachian have been found in the Hasle Formation on the Danish island of Bornholm (Bonde 1993; Milàn & Bonde 2001; Bonde & Christensen 2003; Smith 2008). Smith (2008) represents the only scientific description and taxonomic assessment of plesiosaur material from Denmark. All specimens described in that contribution were found to be insufficiently diagnostic for referral to genus or species level, contrary to previous suggestions (Milàn & Bonde 2001; Smith 2008). The plesiosaur diversity is nonetheless high in

Table 1. Overview of plesiosaur specimens described from Pliensbachian strata

Specimens	Locality/country	Reference
Westphaliasaurus simonsensii	Germany	Schwermann & Sander 2011
Juvenile plesiosaur	Germany	Sachs 2014
Plesiosaur indet.	Lincoln, England	Forrest 2006
Plesiosaur indet. (LEICT G1.2002)	Gloucestershire, England	Evans 2000
Juvenile plesiosaur (BRSMG Cel17972)	Dorset, England	Storrs 1995
Adult plesiosaur (NHMUK R16330)	Lyme-Regis, England	Evans 2012
Microcleidus cf. *homalospondylus*	France	Perrson 1963
Plesiosaurus cf. *dolichodeirus*	France	Perrson 1963
Sthenarosaurus dawkinsi	France	Perrson 1963
Cryonectes neustriacus (MAE 2007.1.1)	Normandy, France	Vincent, Bardet & Mattioli 2013
Juvenile plesiosaur (MUHA 0518)	Asturias, Spain	Bardet *et al*. 2008
Isolated remains of plesiosaurs (MGUH GM-V-2006-8, MGUH DKV-2002-70 MGUH DKV-2002-149, MGUH DK-2002-69, MGUH DK417, MGUH DK416 MGUH 2002-65, MGUH DKV-2002-74 and MGUH 2003-1720)	Bornholm, Denmark	Smith 2008
Arminisaurus schuberti	Germany	Sachs & Kear 2018
Isolated plesiosaur remains (QM F983-QMF5500)	Australia	Kear 2012

the Hasle Formation with at least three (and possibly six) distinct taxa (Smith 2008). Smith (2008) confirmed the presence of the family Rhomaleosauridae in Europe during the Pliensbachian and thus extended the known range of this family into Scandinavia.

Since Smith (2008) five additional plesiosaur specimens have been found in the Hasle Formation of Bornholm and are described in this contribution. Of particular interest is a small and probably juvenile propodial which is the first of its kind found in Denmark, and only the fourth confirmed juvenile plesiosaur specimen from the Pliensbachian of Europe (Table 1). Description of these specimens is significant as it adds to our understanding of the Pliensbachian marine reptile diversity and distribution at higher latitudes.

Geological setting

Bornholm is located in the Baltic Sea, 169 km southeast of Copenhagen and 37 km southeast of the coast of Sweden. It is a faulted block within the Sorgenfrei–Thornquist Zone, which separates the Danish Basin from the Baltic Shield (Milàn & Surlyk 2015). Sedimentary geology consists of Palaeozoic to Mesozoic sandstones, limestones and shales. The Jurassic of Bornholm consists of four formations: Rønne, Hasle, Sorthat and Bagå, which are all part of the Bornholm Group. The fossils described here originate from the Hasle Formation, an 80–140 m thick sequence of strata located on the southwestern part of the island (Fig. 1). It is of the Lower Pliensbachian Age (192–184 Ma) and has been correlated with the *Uptonia jamesoni* to *Prodactylioceras davoei* ammonite zones (Rees 1998; Donovan & Surlyk 2003). The sediments of this formation consist of hummocky and swaley cross-stratified and siltstones and sandstones with sparse layers of coarse-grained sandstone and gravel, indicating shoreface to offshore depositional environment that was storm influenced (Larsen & Friis 1991; Michelsen *et al.* 2003; Milàn & Surlyk 2015). Near Rønne intercalated clays are also present (Michelsen *et al.* 2003). Numerous fossils have been found in the deposit, including both vertebrate and invertebrate taxa. Ammonoids, belemnites, bivalves, gastropods, and brachiopods all occur within the Hasle Formation

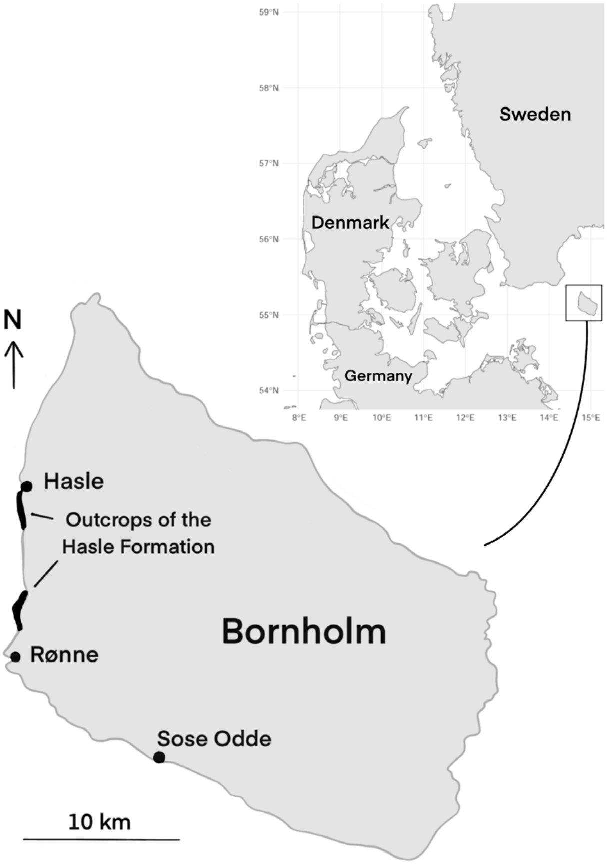

Fig. 1. Map of the Danish island of Bornholm showing the location of the Hasle Formation. Modified from Molin *et al.* (2024).

(Donovan & Surlyk 2003; Vajda & Wigforss-Lange 2009; Milàn & Surlyk 2015) and vertebrate fossil finds are becoming increasingly diverse with dinosaurian remains (Bonde & Christensen 2003; Milàn & Surlyk 2015; Milàn & Mateus 2024), crocodile (Milàn & Mueller 2021), holocephalians (Duffin & Milàn 2017; Duffin & Milàn 2022), a mammal-like cynodont (Molin *et al.* 2024) and a number of plesiosaur bones and teeth (Bonde 1993; Smith 2008). There remains a lack of ichthyosaurs in the formation, which is interesting as this group is commonly found alongside plesiosaurs in other Early Jurassic strata in Europe (Milàn & Bonde 2001).

Methods and materials

The five plesiosaur specimens (Table 2) described here were found in the Hasle Formation between 2009 and 2019 and consists of isolated tooth and skeletal elements, including spinal fragments, a rib and a propodial. They are currently stored within the Danekræ collection of the palaeontological collections at the Natural History Museum Denmark (NHMD) in Copenhagen.

The specimens were photographed using the NHMD photography studio with a Canon EOS RS and EOS Utility Program and measured using an Absolute AOS Digimatic caliper of the model number CD-15AXR.

Comparisons are made with specimens within Rhomaleosauridae, Pliosauridae, Plesiosauridae, and Microcleididae.

Systematic palaeontology

Sauropterygia Owen, 1860

Plesiosauria de Blainville, 1835

Pliosauridae Seeley, 1874

Pliosauridae indet.

Referred specimen. NHMD 625447 (Fig. 2a).

Description. NHMD 625447 is a single tooth in sandstone matrix. The tooth is robust and slightly curved. Its base is 12.3 mm wide and this is also the widest part of the tooth. It narrows to 10.7 mm midway and tapers to 7.8 mm at its tip, which is damaged. As preserved, the crown measures 26.4 mm from base to broken apex. The ornamentation of the tooth consists of longitudinal enamel ridges arranged in an even pattern that runs along the tooth, from the base of the crown to the apex. Thirteen tightly spaced ridges are visible in lateral view. The base of the tooth is smooth compared to the rest of the tooth due to poor preservation, and no root is visible. The cross section of the tooth is circular.

Comparison. Previously described plesiosaur teeth from the Hasle Formation were categorised into three different tooth types A, B, and C based on morphology; the latter including 14 of the 16 described teeth (Smith 2008). Tooth type A is typical for Lower Jurassic Plesiosauroidea as it is slender and has a tightly packed pattern of seven longitudinal ridges in lateral view. The crown of type A is 4.0 mm wide compared to 12.3 mm of NHMD 625447, whereas A is 18.0 mm long and NHMD 625447 is 26.4 mm long. This makes NHMD 625447 significantly larger and more robust than the characteristic slender morphology of Plesiosauroidea.

Tooth type B from the Hasle Formation is most similar to the genus *Rhomaleosaurus* (Smith 2008). It is more robust than tooth type A and has a slight recurved form. Smith (2008) estimated it to be approximately 30 mm long in life, which is similar to NHMD 625447. Type B is sparsely ridged, with only five ridges visible in lateral view that do not extend to the apex. This contrasts with NHMD 625447 where all ridges run the entirety of the tooth.

Type C were identified as Pliosauroidea, a clade comprising pliosaurids and rhomaleosaurids, based on the robust construction and broad bases by Smith (2008), and it has been suggested that they belong to the species *Attenborosaurus conybeari* (Milàn & Bonde 2001), due to the closely striated ornamentation. Type C teeth display a distinct ornamentation of ridges along the whole crown with most extending to the tip. The number of ridges ranges from 9 to 11 in lateral view. These teeth are robust and resemble

Table 2. Plesiosaur material from Bornholm described in this paper

Specimen number	Brief description	Found by	Determined by	Locality and date
NHMD 625145 (DK 610)	Incomplete humerus or femur	Mette Hofstedt	Niels Bonde	Hasle Klint, 4 December 2009
NHMD 625357 (DK 803, 1-2)	Neural arch and spine (1), rib from neck or tail (2)	Mette Hofstedt	Niels Bonde, Adam Smith	Hasle Klint, 4 December 2015
NHMD 625435 (DK 881)	Neural spine	Mette Hofstedt	Niels Bonde	Hasle Klint, 2017
NHMD 625447 (DK 913)	Single tooth in matrix	Mette Hofstedt	Niels Bonde	Hasle Klint, 5 May 2017
NHMD 625503 (DK 976)	Base of spinal process of vertebra	Marianna Nattestad	Bent Lindow	Hasle Klint, 11 September 2019

NHMD numbers: collection numbers of the specimens, DK numbers: numbering system specifically for Danekræ specimens

NHMD 625447 more than type A and B as they share approximately the same amount of ridges in lateral view and have a similar shape and curve. However, NHMD 625447 is longer than any of the type C teeth, even if they vary in size (length 5–20 mm).

The teeth of plesiosaurs are long, slender, curved and have a deeply rooted base with a large pulp cavity (Andrews 1910). Pliosaur teeth tend to be more robust. NHMD 625447 is a robust tooth, and thus different from the long and slender teeth of the basal pliosaur *Cryonectes neustriacus* (Vincent *et al.,* 2013). They are also more robust than *Macroplata tenuiceps* (BMNH R5488) from the Hettangian (Ketchum & Smith 2010), but instead resemble *Thaumatodracon widenrothi* from the Sinemurian (Smith & Araújo 2017).

Plesiosauroid teeth are often sub-circular in cross section (Andrews 1910), whereas some Late Jurassic pliosauroids, e.g. *Pliosaurus* are triangular (Benson *et al*. 2013; Sander 2023). The cross section of NHMD 625447 is circular, similar to most Jurassic plesiosauroids, e.g. *Microcleidus tournemirensis* (Bardet *et al.* 1999; Evans *et al*. 2012), *Macroplata tenuiceps* (Ketchum & Smith 2010), *Seeleyosaurus guilelmiimperatoris* (Sachs *et al*. 2025) and *Thaumatodracon* (Smith & Araújo, 2017), whereas *Cryonectes neustriacus* (Vincent *et al*., 2013) has teeth that are sub-circular in cross section with compressed tips.

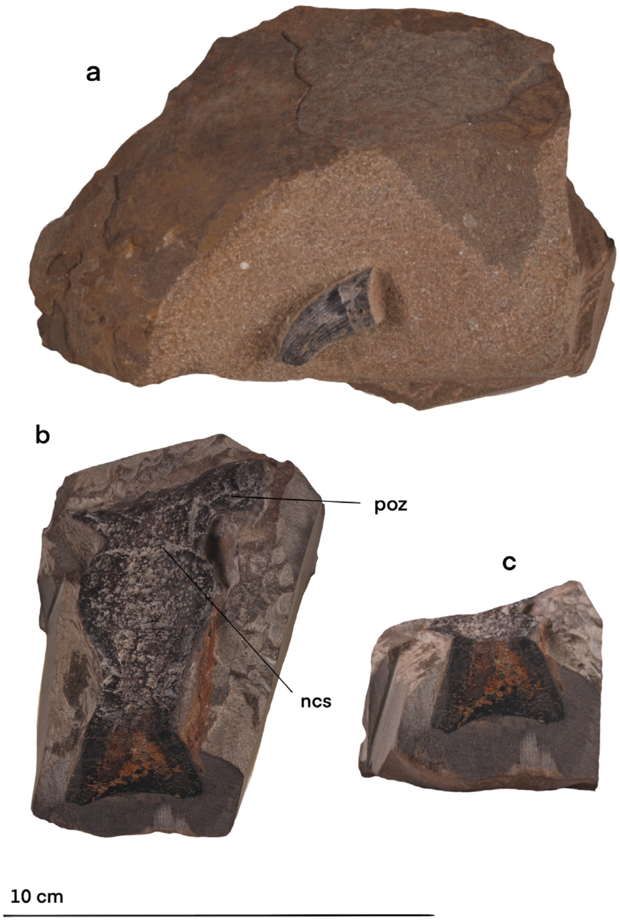

Fig. 2. Tooth in sandstone matrix (NHMD 625447) in a) dorsal view. Partial vertebra (NHMD 625503) in b) partial anterior view c) distal view. poz: postzygapophysis, ncs: neurocentral-suture.

NHMD 625447 is ornamented with longitudinal enamel ridges from the base of the crown to the apex, resembling that of *Microcleidus* (Bardet *et al*. 1999; Evans *et al*. 2012). The ornamentation of *Macroplata tenuiceps* extends from the crown to the apex, however only one or two reaches the very tip (Ketchum & Smith 2010). In *Thaumatodracon wiedenrothi* (Smith & Araújo, 2017), the enamel ridges are tightly spaced, and most reach from the base of the crown to the apex, similar to NHMD 625447. They are thus more closely striated than in *Rhomaleosaurus zetlandicus* (Taylor 1992) and more similar to *Atychodracon megacephalus* (Cruickshank 1994). All ridges of *Rhomaleosaurus zetlandicus* do not extend to the tip, however, making these teeth unlike NHMD 625447.

Compared to the size of the teeth in *Cryonectes neustriacus* (Vincent *et al*., 2013), which are 50 mm in height, NHMD 625447 is significantly smaller. *Microcleidus*, in contrast, had teeth between 31 and 54 mm long (Bardet *et al*. 1999; Evans *et al*. 2012), probably similar to the actual size of NHMD 625447 in life, whereas *Macroplata tenuiceps* was somewhat smaller (Ketchum & Smith 2010). *Thaumatodracon* on average have teeth no larger than 15 mm (Smith & Araújo 2017), whereas *Rhomaleosaurus zetlandicus* (Taylor 1992) and *Atychodracon megacephalus* (Cruickshank 1994) have teeth approximately 25 mm in length, comparable to NHMD 625447.

In summary, NHMD 625447 shares similarities with both pliosaurs, microcleidids and rhomaleosaurians. NHMD 625447 does not resemble the rhomaleosaurid tooth known from the Hasle Formation (MGUH DKV 2002-70), and thus, based on the ornamentation, robustness, shape and size, NHMD 625447 is concluded to be a tooth of an early pliosaurid. Given previous finds on Bornholm, it could be a tooth of *Attenborosaurus*, as the teeth of this species have very closely spaced ridges (Smith 2007), however as this is hard to confirm, the tooth is identified to Pliosauridae indet.

A study on long-term ecological changes in a seaway of the Middle-Late Jurassic focused on the shape and function of marine reptile teeth, dividing the marine reptiles into the pierce, generalist, and cut guilds (Massare 1987; Foffa *et al*. 2018). According to this scheme, NHMD 625447 best coincides with the 'generalist' guild, in which either the 'cut' or 'pierce' subguild could fit. 'Pierce' is most likely, given the shape and the circular cross section of the tooth. This subguild is characterised by large, conical and variably ornamented teeth and mostly includes large Callovian pliosaurs. This indicates that NHMD 625447 is most likely from an early relative of the large Middle Jurassic thalassophonean pliosaurids.

Plesiosauria indet.

Referred specimen. NHMD 625503 (Fig. 2b-c)

Description. NHMD 625503 is a partial vertebra with its neural spine missing. The fossil is encased in a grey sandstone matrix with a rust-coloured surface, evident by the reddish tones present in the distal end of the fossil. The vertebra is presumably preserved in lateral view, showing the neural arch with zygapophyses. The neurocentral suture is visible (fig. 2, b), showing the fusion of the neural arch to the centrum. The preservation of the fossil makes it difficult to fully predict how much of the bone is preserved and the exact orientation within the matrix. The length of the fossil is 71.2 mm.

The neural arch presumably belongs to a posterior cervical or anterior dorsal vertebra, based on the shape of the spinal process and the post-zygapophysis. The preserved part of the neural arch has an irregular, elongate shape that narrows dorsally. The rounded facet on one side of the fossil is likely the right post-zygapophysis, whereas the left is eroded. Collectively the post-zygapophysis and the preserved neural arch have a width of 49.4 mm. The inner bone microstructure is spongious, especially prevalent in the centrum. The cross section of the centrum has a trapezoid shape, and a thick outer layer is present, surrounding a fine spongy structure of secondary trabeculae arranged longitudinally.

Comparison. The preservation of NHMD 625503 makes it difficult to assign taxonomically. The matrix obscures the features in a way that a direct comparison of other vertebrae is difficult. In addition to Plesiosauria, both Dinosauria and Ichthyosauria have been proposed in the original identification reports. The longitudinal pattern of the spongy tissue and the shape of the neural arch lead us to tentatively assign the specimen to Plesiosauria.

Referred specimen. NHMD 625435 (Fig. 3a-d)

Description. NHMD 625435 consists of a well-preserved neural arch and spine with five accompanying sandstone matrix pieces. The neural arch is loose (i.e. not connected to a centrum) and it is three-dimensionally preserved. Measured from one pedicle to the other, the arch measures 56.9 mm in mediolateral width. Both pre- and post-zygapophyses are well preserved, although the specimen exhibits taphonomic surface abrasion. The neural spine is straight and broken anteriorly, measuring 31.1 mm from the apex of the broken part to the neural canal. The neural canal itself is 9.7 mm wide with a length of 11.6 mm. The angle in which the pedicles protrude from the neural canal is wide at 90 degrees, and the shape of the neural canal is almost square. The width between the post-zygapophyses is 32.6 mm. The entirety of the fossil measures 59.6 mm from apex of the broken neural spine to the base of the pedicles. Distally to the robust pedicles is the neurocentral junction and based on the rugged texture of the facets, it appears that the neural arch was not fused to the vertebral centrum. The posterior facets of the pedicles are flat and oval with no rim.

Comparison. This is only the third plesiosaur neural arch recovered from the Hasle Formation, and the first that is not fused to a vertebral centrum. This fea-

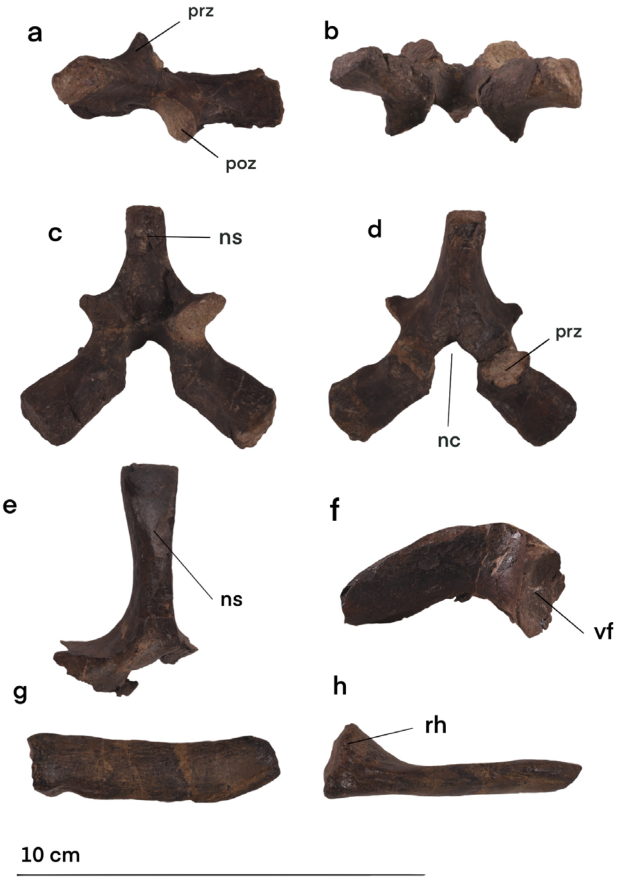

Fig. 3. Neural arch and spine (NHMD 625435) in a) lateral view, b) posterior view, c) posterodorsal view, d), anterodorsal view. Neural spine (NHMD 625357-1) in e) dorsal view, f) lateral view. Complete rib (NHMD 625357-2) in g) lateral view, h) dorsal view. poz: postzygapophyses, prz: prezygapophyses, ns: neural spine, nc: neural canal, vf: vertebral facet, rh: rib head.

ture indicates an osteologically immature individual, and could perhaps belong to a juvenile, however detached arches are also found in presumed adult individuals within Rhomaleosauridae, Pliosauridae, Elasmosauridae, Polycotylidae and Leptocleididae (except *Gronausaurus wegneri*; Araújo & Smith 2023).

As NHMD 625435 does not possess transverse processes, it is not from the dorsal region. The 90-degree angle of the pedicels in NHMD 625435 correlates with either a pectoral vertebra, as in *Stratesaurus taylori* (Benson *et al*., 2015), *Microcleidus tournemirensis* (Bardet *et al*., 1999) and *Plesiopharos moelensis* (Puértolas-Pascual *et al*., 2021), or a sacral vertebra, as in *Colymbosaurus svalbardensis* (Roberts *et al*., 2017), *Microcleidus tournemirensis* (Bardet *et al*., 1999), and an indeterminate plesiosaur vertebra (NHMD 188220/ MGUH 2003-1720) from the Hasle Formation (Smith 2008).

The pectoral vertebrae of *Stratesaurus taylori* possess neural canals that are circular with pedicles nearly horizontal, compared to the 90-degree angle of NHMD 625435 (Benson *et al*. 2015). The vertebrae of *Microcleidus tournemirensis* have very small circular neural canals (Bardet *et al*. 1999), unlike NHMD 625435, whereas *Plesiopharos moelensis* have pectoral vertebrae with larger, square shaped neural canals and straight, posteriorly oriented neural spines (Puértolas-Pascual *et al*. 2021). The neural arches of *Plesiopharos moelensis* resemble the shape of the neural canal and neural spine of NHMD 625435, although as the neural spine of NHMD 625435 is broken the size and shape are difficult to fully estimate. The sacral vertebrae of *Colymbosaurus svalbardensis* has small pedicles with a nearly triangular neural canal and therefore does not correlate very closely with NHMD 625435 (Roberts *et al*. 2017). The neural arch of the sacral vertebra found in the Hasle Formation of Bornholm described by Smith (2008; NHMD 188220/ MGUH 2003-1720) is, unlike NHMD 625435, fused to the centrum body. The neural canal of NHMD 188220 is 10.3 mm long and 9.3 mm wide and thus similar to NHMD 625435 (11.6 mm length, 9.7 mm width), albeit the neural canal of NHMD 625435 is larger. The neural canal of NHMD 188220 has a more pointed shape dorsally, whereas NHMD 625435 is square. The pedicles of NHMD 188220 are wide, measuring 50.8 mm from the outer edges, making it slightly smaller than NHMD 625435 which is 56.9 mm wide.

Many well-preserved plesiosaurian neural arches has been found in the Oxford Clay (Middle Jurassic), e.g. *Muraenosaurus durobrivenis*, *Muraenosaurus platyclis*, *Muraenosaurus leedsi*, *Cryptoclidus oxoniensis*, *Tricleidus seeleyi* and *Picrocleidus beloclis* (Andrews 1910). The anterior cervical vertebra of *M. durobrivenis* has a similar angle of the pedicels, but the neural canal is more oval than NHMD 625435, whereas *Cryptoclidus oxoniensis* has a more rounded neural canal. The thin lateral neural spine resembles that of NHMD 625435. The prezygapophyses of *Cryptoclidus* and *Tricleidus* are quite pointed and oriented parallel to the neural spine in anterior view, compared to the prezygapophyses of NHMD 625435 being angled horizontally. Prezygapophyses of *M. platyclis* are less parallel to the neural spine than in *Cryptoclidus* but still show a more vertical angling than NHMD 625435. Cervical vertebrae of *Picrocleidus beloclis* have quite small prezygapophyses oriented close to the median of the neural spine. The neural canal is square, much like NHMD 625435 (Andrews 1910).

Due to the arch being detached (i.e. unfused to a centrum), NHMD 625435 could be from a rhomaleosaur (Araújo & Smith 2023), however given that other families also experience paedomorphism (such as Pliosauridae), it is not possible to taxonomically assign NHMD 625435 beyond Plesiosauria indet.

Referred specimen. NHMD 625357-1 (Fig. 3e-f)

Description. NHMD 625357-1 is a disarticulated, three-dimensionally preserved neural arch with a complete spine, accompanied by a sandstone impression. In dorsal view, the neural spine is mediolaterally flattened with a width of 13.6 mm. Distally the spine flattens to a square tipped paddle shape and is strongly oriented posteriorly. The entire length of the neural spine and the remaining arch is 57.3 mm. The arch is 32.1 mm wide. The neural arch has been fused to the vertebra centrum, but is broken off, leaving only parts of the neural arch on both sides, with a piece of the centrum preserved on the right side of the specimen. The left base of the neural arch has been broken off, however, the right side is well preserved with a large facet. This facet is oval with a surrounding rim. The pedicles protrude in a strong convex shape on each side of the dorsal spine. Laterally the pedicles are smooth and flat with some cracks dorsoventrally. Part of the neural canal has been preserved.

Comparison. *Microcleidus tournemirensis* has dorsal spines that flare dorsally when seen in lateral view, which is both apparent in cervical and pectoral vertebrae (Bardet *et al*. 1999). In anterior view, they are very narrow and often yielding to one side, unlike NHMD 62357-1 which is straight. NHMD 625357-1 is flattened, but to a much lesser degree: the dorsal spine flares distally in dorsal view, instead of having a narrow tip, which is more common. The pectoral vertebrae of *Stratesaurus taylori* from the Hettangian of England have distally flared neural spines in a rod-like shape (Benson *et al*. 2015), as in NHMD 625357-1, but *Stratesaurus* does not possess the flat, paddle-like shape at the distal end of the neural spine, characteristic of NHMD 625357-1. However, they do share a robust, thick neural spine.

Plesiopharos moelensis from the Sinemurian has well preserved vertebra (Puértolas-Pascual *et al*. 2021). These vertebrae have approximately the same width the entirety of the neural spine length. Only the third pectoral vertebra (fig. 2A:4 (Puértolas-Pascual *et al*. 2021) share a similar pattern to NHMD 625357-1 as it, seen from above, flares distally. Dorsal vertebrae from the Hettangian of Ireland have straight neural spines, both in dorsal and lateral view, in contrast to NHMD 625357-1 that is only straight from above, but curves posteriorly when seen in lateral view (Smith 2010).

The neural spines of *Muraenosaurus duribrivensis* are nearly straight in lateral view and therefore much less posteriorly inclined than NHMD 625357-2, whereas *Muraenosaurus leedsi* has a slight posterior curve. The neural spines of the latter are broken though, so the full shape cannot be compared. The posterior caudal vertebrae of *Cryptoclidus oxoniensis* display a prominent posterior incline in a similar fashion to *Picrocleidus beloclis*, however only *Tricleidus seeleyi* share a robust shape like NHMD 625357-1. None of *Tricleidus* vertebrae display the same strong posterior curve though (Andrews 1910).

A Plesiosauria indet. sacral vertebra (NHMD 188220/MGUH 2003-1720; pers. obs. ZK) from the Pliensbachian of Bornholm, has a neural spine that is equally wide from the base to the tip and that appears to be straight (Smith 2008). NHMD 625357-1 in contrast, flares distally and is curved. Neural spines of *Westphaliasaurus simonsensi* from the Pliensbachian displays the same straight shape laterally, as in NHMD 625357-1, although some of them bend strongly to the side in dorsal view (Schwermann & Sander 2011).

Thus, the shape of the neural spine of NHMD 625357-1 is unusual with its strong posterior curve in lateral view, together with the distal flaring that leads to a paddle shape. The neural spine is also more robust than other compared fossils. For now, it is assigned to Plesiosauria indet.

Referred specimen. NHMD 625357-2 (Fig. 3g-h)

Description. NHMD 625357-2 is a complete rib with a length of 61.7 mm. The rib is mediolaterally compressed and reversely spatulate with the rib head curved in a convex fashion dorsoventrally. The rib head has an irregular oval outline surrounded by a slight rim. The margins of the rib are slightly upwards curling, which are most noticeable posteriorly at the tapered, rounded tip. The base of the rib has a width of 19.6 mm that narrows to 14.3 mm at the tip. Subtle longitudinal ridges span across the entirety of the rib. It has been affected by taphonomy with the posterior side having a longitudinal crack from the tip.

Comparison. Based on its short length, the rib is most likely either a cervical, sacral or caudal rib. It could, however, also be a juvenile. The rib is most likely not a chevron, as these are shown to be proximally expanded and tapering to a narrow point distally, e.g. *Muraenosaurus leedsi* (Andrews 1910).

Cervical ribs of many Lower Jurassic plesiosaurs are often short and hatchet shaped (Andrews 1910), e.g. *Franconiasaurus brevispinus* (Sachs *et al*., 2024), *Stratesaurus taylori* (Benson *et al*., 2015) and *Seeleyosaurus guilelmiimperatoris* (Sachs *et al*., 2025). The form of NHMD 625357-2 is instead spatulate and therefore most likely not a cervical rib.

For sacral ribs a spatulate form is common. Sacral ribs from *Colymbosaurus svalbardensis* shows equally expanded proximal and distal ends (Roberts *et al*. 2017), differing from the spatulate sacral ribs found in *Tatenectes laramiensis* (O'Keefe *et al*. 2011) and *Pantosaurus striatus* (Wilhelm & O'Keefe 2010), which have expanded distal ends. In *Cryptoclidus eurymerus* (Brown, 1981) the proximal end is dorsoventrally thicker than the distal end, similar to *Muraenosaurus durobrivensis* (Andrews 1910). In NHMD 625357-2 the distal end is narrower than the proximal end and the rib itself has a spatulate shape, more similar to *Cryptoclidus*.

The rib may be caudal, based on the nearly flat facet on its distal end, the curved posterior portion, and the circular rib head (Andrews 1910). *Stratesaurus taylori* has caudal ribs that share a similar shape and size as NHMD 625357-2, although the rib head appears larger and more irregular on *Stratesaurus* (Benson *et al*. 2015). Caudal ribs of *Colymbosaurus svalbardensis* have a similar size and shape as NHMD 625357-2, although these ribs display a more curved shape distally, when seen in lateral view (Roberts *et al*. 2017). They do, however, share the same spatulate form as NHMD 625357-2. This is also true for *Muraenosaurus platyclis* and *Muraenosaurus leedsi* (Andrews 1910), as well as *Seeleyosaurus guilelmiimperatoris* (Sachs *et al*. 2025).

Given the size, rib head and overall morphology of NHMD 625357-2, we identify it as a caudal rib, assigned to Plesiosauria indet.

Referred specimen. NHMD 625145 (Fig. 4)

Description. NHMD 625145 consists of an incomplete propodial with a broken off counterpart. Both are partially encased in sandstone matrix with a margin of iron oxidation, limited to one side of the bone. The bone is curved, with the minimum anteroposterior width of 35.6 mm at the proximal end. Distally to this, the bone widens to 40.2 mm mid shaft and flares distally to a maximum width of 47.8 mm. The proximodistal length of the entire element is 117 mm. In dorsoventral view, the anterior margin is slightly convex and curves posteriorly, whereas the posterior margin is more concave, due to the postaxial expansion of the distal end.

Ontogeny. The propodial is juvenile based on its osteologically immature morphology and small size. In dorsal view, the distal end of the limb bone displays a soft, rounded edge, in contrast to the well-defined lines associated with adult plesiosaur limb bones (Araújo & Smith 2023), where the distal end often flares anteroposteriorly. This rounded edge is similar to plesiosaur material found in the Jurassic of Wyoming (Wahl 2006). There are no distinct surfaces for the epipodials or other well-defined anatomical structures, all indicating that this is a juvenile. The specimen does not possess a strong concave postaxial margin as is often characteristic of adult plesiosaurs (Storrs 1997; Bardet *et al*. 1999; O'Keefe 2001).

Fig. 4. Propodial with accompanying sandstone counterpart (NHMD 625145). a) sandstone encased side of propodial, b) sandstone encased counterpart that is broken off, c) propodial, d) broken off counterpart. All shown in dorsal view. e) propodial and its counterpart shown interlocking, left lateral view, f) right lateral view.

The propodial of NHMD 625145 is 117 mm long, which is small compared to adult specimens from the Lower Jurassic, where propodials found in the UK have a measured range from 140 mm (Storrs 1997) to around 350 mm (Smith & Vincent 2009; Ketchum & Smith 2010; Smith 2015), whereas most other finds in Table 3 in general are smaller, ranging from 124 to 290 mm for the mature individuals, except *Meyerasaurus victor* from Germany that has propodials measuring 385 mm (Smith & Vincent 2010).

Taphonomy has affected the bone in which the anterior margin shows obvious signs of poor preservation, where the distal end is partly eroded, showing the fine striations of the outer layer of the bone. A juvenile would probably be more susceptible to being affected by taphonomy because of the less advanced ossification.

Comparison. The comparable juvenile specimens that are preserved with propodials from the same time interval, resemble NHMD 625145 in size given that the length of the propodials are 111 mm (Bardet et al. 2008), 101 mm (humerus) and 122 mm (femur; Vincent 2010). A juvenile specimen from the Cretaceous of Australia has propodials that are 122 mm (Kear 2007). It is worth noting however that *Plesiopharos moelensis*, an adult specimen, has a femur length of only 130 mm and a humerus length of 150 mm (Puértolas-Pascual *et al*. 2021). This is still larger than NHMD 625145 but indicates the wide size range of plesiosaur propodials.

A juvenile specimen of *Rhomaleosauris zetlandicus* described by Smith & Vincent (2009) has propodials with underdeveloped trochanter, which is a juvenile character. These propodials are nearly symmetrical, with the expansion being slightly more postaxial than preaxial (Smith & Vincent 2009). Similar to this, a juvenile plesiosaur from Germany (Vincent 2010) has an almost symmetrical femur with the preaxial border being straight and the postaxial being slightly concave. The propodials of the Cretaceous juvenile specimen from Australia have straight anterior margins with strong concave posterior margins (Kear 2007). The distal flaring of this specimen is more pronounced than the other two specimens mentioned and more similar to the Pliensbachian juvenile specimen from Spain (Bardet *et al.* 2008).

Humeri and femora of plesiosaurs are relatively similar in shape, and it is often hard to differentiate, and this is further complicated by the juvenile stage of NHMD 625145. The humerus of *Atychodracon megacephalus* has a straight shaft and a strongly concave postaxial margin with a distal flare (Smith, 2015) traits which look similar to *Marcoplata tenuiceps* (Ketchum & Smith, 2010) and the isolated humerus that has been found on Bornholm (Smith 2008). Other plesiosaurs like *Plesiopharos moelensis* have

Table 3. Comparison of different propodial lengths of plesiosaurs

Specimen	Length of propodial (mm)	Age	Formation/locality/country	Reference
Macroplata tenuiceps (BMNH R5488)	350	Hettangian	Blue Lias Formation, UK	Smith & Ketchum 2010
Rhomaleosaurus zetlandicus (WM 851.S), possible juvenile	365	Toarcian	Yorkshire, UK	Smith & Vincent 2009
Atychodracon megacephalus (BRSMG Cb 2335)	350	Triassic-Jurassic boundary	Somerset, UK	Smith 2015
Plesiopharos moelensis (ML 2302)	130 (femur) 150 (humerus)	Sinemurian	Coimbra Formation, Portugal	Puértolas-Pascual *et al.* 2021
Unidentified plesiosaur (MGUH DK416)	190	Pliensbachian	Hasle Formation, Denmark	Smith 2008
Juvenile plesiosaur (SMNS 51141)	101 (humerus) 122 (femur)	Toarcian	Posidonia Shale, Germany	Vincent 2010
Franconiasaurus brevispinus (BT 011224.00)	220 (humerus) 240 (femur)	Toarcian	Jurensismergel Fm, Germany	Sachs *et al.* 2024
Juvenile plesiosaur (MUHA 0518)	111	Pliensbachian	Asturias, Spain	Bardet *et al.* 2018
Westphaliasaurus simensensii	290	Pliensbachian	Germany	Schwermann & Sander 2011
Juvenile plesiosaur (SAM P15980)	122	Aptian	Australia	Kear 2007
Meyerasaurus victor (SMNS 12478)	385	Toarcian	Germany	Smith & Vincent 2010
Plesiosaurus dolichodeirus (BMNH 22656); (OXFUM J.10304); (BMNH 36183) (YPM-PU 3352); (NHMN 8592)	190 (humerus) 180 (femur) 210 (humerus) 200 (femur) 210 140 220 (humerus) 190 (femur)	Sinemurian	Lyme Regis, England	Storrs 1997

Unless otherwise stated, the specimens are adult individuals. The list is not all inclusive.

tear-drop shaped humeri with postaxial expansions in the distal region that makes the posterior outline concave with straight anterior expansions. This is a primitive character found in Lower Jurassic plesiosaurs (Puértolas-Pascual *et al.* 2021). In contrast, the femur is almost symmetrical with equal anterior and posterior expansions distally. *Franconiasaurus* shares a similar pattern of having propodials with straight anterior margins that flares distally. It, however, is not as concave as *Plesiopharos*, nor does the humerus and femur differentiate as much in *Franconiasaurus* (Sachs *et al*., 2024). If NHMD 625145 shares the basal characters found in Lower Jurassic plesiosaurs, it is most likely a humerus, as the bone has a somewhat concave postaxial margin that could, if the individual had reached adult age, have evolved a more pronounced shape with distal flaring, characteristic of Lower Jurassic humeri. Assigning NHMD 625145 to a family is difficult as it is an isolated bone and because of its juvenile traits.

Discussion

First juvenile plesiosaurs from Denmark

The propodial and possibly the detached neural arch discussed in this paper represent the first unequivocally juvenile plesiosaur specimens from Denmark. The very small size of the propodial, together with the lack of well-defined anatomical structures and the rounded shape, means that we can confidently conclude that that it is from a juvenile individual.

The juvenile propodial (NHMD 625145) is a unique specimen, as it is one of few juvenile specimens known from the Lower Jurassic (Table 1), particularly from the Pliensbachian. While the two presumably juvenile propodials from Germany and the one of *Rhomaleosaurus zetlandicus* share similarities to NHMD 625145, the juvenile humerus found in Spain (Bardet *et al.* 2008) and the one found in Australia (Kear 2007) displays a shape more similar to adults, with a straight anterior shaft and a distal flare that makes the posterior margin somewhat concave. This indicates that there is considerable variation in juvenile propodial shape, and scope for future research into plesiosaur ontogeny and growth.

It is more uncertain whether the neural arch (NHMD 625357-1) represents a juvenile or is a result of paedomorphism – the retention of juvenile traits in adult individuals, which have been found to be widespread in several plesiosaur clades (Araújo & Smith 2023). Araújo & Smith (2023) explain that this is due to the retention of the plesiomorphic condition of Pistosauria. It is especially worth noting that neural arches remain separated throughout ontogeny in every taxon of the rhomaleosaurid clade. Araújo & Smith (2023) argue that one should be careful to assign a fossil to being a juvenile, unless the traits for this is obvious, as many previously considered juveniles simply may be paedomorphic adults. With regard to the propodial, the size and shape together show that it is clearly a juvenile, whereas this is less clear for the neural arch. Should one instead look at what family is most plausible for the detached neural arch to belong to, it would be the Rhomaleosauridae, given their arches remain detached throughout life, they emerged in the Early Jurassic, and the family have been confirmed on Bornholm (Smith 2008). Pliosauridae would also be plausible as this family existed alongside Rhomaleosauridae during the Pliensbachian. If so, this is the first rhomaleosaurid neural arch from the Hasle Formation.

Conclusion

In this contribution we describe five new plesiosaur specimens from the Pliensbachian (Lower Jurassic) of Bornholm, Denmark. This increases the number of formally described specimens to sixteen, adding to previous work (Smith 2008). It also expands the range of described skeletal elements with neural arches. Plesiosaurs are commonly found only with their centra preserved, because of the fragility of the arches and spines. This hampers a thorough comparison to other taxa, but showcasing new material like in this case are valuable additions to our understanding of plesiosaur anatomy. Most significantly, this contribution increases the ontogenetic diversity of plesiosaurs from the formation by the addition of at least one juvenile specimen.

Even if inconclusive taxonomically, our work supports Smith's (2008) suggestion of the potential presence of rhomaleosaurids in Scandinavia, and in addition, indeterminate plesiosauroids and large pliosaurids. This means that the Pliensbachian seas at Bornholm contained marine ecosystems with both short- and longnecked plesiosaurs, covering most, if not all, ontogenetic stages.

The Pliensbachian was historically considered a poorly sampled interval in plesiosaur evolution, but recent discoveries (Table 1) have significantly improved the record. Nevertheless, disarticulated elements that cannot be assigned to genus or species remain important for understanding the diversity and distribution of plesiosaurs during this stage.

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