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SHORT COMMUNICATION

PLESIOSAURS FROM THE PLIENSBACHIAN (LOWER JURASSIC) OF BORNHOLM, DENMARK

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The Danish island of Bornholm has yielded a number of isolated plesiosaur specimens. These are derived from the Hasle Formation, a sandstone/siltstone unit of Pliensbachian age, a time period from which little plesiosaur material has been collected. The fossil remains from Bornholm therefore serve to fill a hiatus in our understanding of plesiosaur diversity, often called the 'Pliensbachian gap' (M. Evans pers. comm. 2003).

The earliest mention of plesiosaurs in the Hasle Formation was given by Malling (1911) who noted the presence of plesiosaur teeth and rib bones from the cliffs near Hasle harbour. Rees and Bonde (1999) reported briefly on the fossil plesiosaurs from Bornholm and identified a fauna consisting of three taxa. These findings were based on the wide diversity of plesiosaurian tooth morphologies present within the Hasle Formation. Bonde (1993), Milàn and Bonde (2001) and Bonde and Christiansen (2003) also outlined some of the plesiosaur remains from the Hasle Formation but no thorough systematic descriptions were provided. This paper gives an inventory and detailed description of the plesiosaur material from the Hasle Formation of Bornholm held in the Geologisk Museum, Copenhagen, and comments on the assemblage derived from the unit.

Institutional Abbreviations: **LEICT**, New Walk Museum, Leicester, UK; **MGUH**, Geologisk Museum, Copenhagen, Denmark; **TCD**, Trinity College, Dublin, Ireland.

GEOLOGICAL AND PALEONTOLOGICAL SETTING

The Danish island of Bornholm is situated in the Baltic Sea approximately 150 km from the east coast of mainland Denmark and 40km from the southern coast of Sweden (Fig. 1). All of the fossils described here originate from the Hasle Formation, an 80-140m thick sequence of strata that outcrop sporadically on the southwestern part of the island (Donovan and Surlyk, 2003). The most notable exposures are found at the type locality on the Western coast of Bornholm, a 1km stretch of low coastal cliff face immediately south of the town of Hasle. This is the source location of nearly all of the fossils described below with one exception, specimen DK416 (Rees and Bonde, 1999) was discovered in the poorly exposed Hasle Formation along the coastal cliffs on the south of the island, just west of the spit at Sose Odde (Fig. 1).

The Hasle Formation comprises a series of cross-stratified fine-grained sandstones and coarse-grained siltstones (Surlyk and Noe-Nygard, 1986). Based on the fossil ammonites within the unit, the formation has been correlated with lower Pliensbachian strata (Jamesoni to Davoei ammonite zones) (Gravesen et al., 1982). The depositional environment is regarded as a near-shore, shallow, open-marine shelf, with sediment deposited between depths of 10-40 metres, probably within two kilometres from the coastline (Surlyk and Noe Nygard, 1986). Underlying the Pliensbachian strata of the Hasle Formation are Hettangian and Sinemurian rocks belonging to the Rønne Formation. These strata represent a transgressive sequence from lacustrine to fluvial to tidal flat deposits (Surlyk and Noe Nygard, 1986); thus the Hasle Formation represents a continuation of this transgressive trend into shallow marine waters. Unconformably overlying the Pliensbachian strata are Bajocian and Bathonian age coal-bearing clays and sands of the Baga Formation. Rocks of Toarcian and Aalenian age are absent on Bornholm (Surlyk and Noe Nygard, 1986).

The most abundant and diverse vertebrate remains that have been collected from within the Hasle Formation are selachian fish teeth—at least three hybodont shark species and three neoselachian species have been recorded (Rees, 1998). With the exception of plesiosaur fossils no other fossil vertebrate remains have yet been reported from the Hasle Formation. Eleven plesiosaur specimens from the Hasle Formation are held within the Geologisk Museum, Copenhagen, all representing isolated elements (in the case of some tooth fossils, several are included under a single specimen number) (Table). This material includes teeth, a possible jaw fragment and postcranial elements. None of these remains can be conclusively associated.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903
SAUROPTERYGIA Owen, 1860
PLESIOSAURIA de Blainville, 1835
PLESIOSAUROIDEA Gray, 1825
Indeterminate
(Fig. 2A)

Material—MGUH GM-V-2006-8, plesiosauroid tooth in sandstone matrix, tooth type A (Fig. 2A).

Description—Tooth type A is very slender and only slightly recurved. The crown is elongate (18mm long, 4mm wide at base of crown) and subtly sigmoidally shaped in lateral view (Fig. 2A). Only one tooth in the collection belongs to type A—part of the root of MGUH GM-V-2006-8 is preserved but is broken off 5mm from the base of the tooth crown. The ornamentation consists of closely and evenly spaced longitudinal ridges of which there are seven in lateral view. All of the ridges run the whole length of the tooth crown from the apex to the base, with the exception of a single ridge, which is truncated so as not to reach the base of the crown.

Discussion—The slender morphology of tooth type A and the tightly packed pattern of longitudinal ridges are diagnostic among Lower Jurassic plesiosaurs restricted to Plesiosauroidea.

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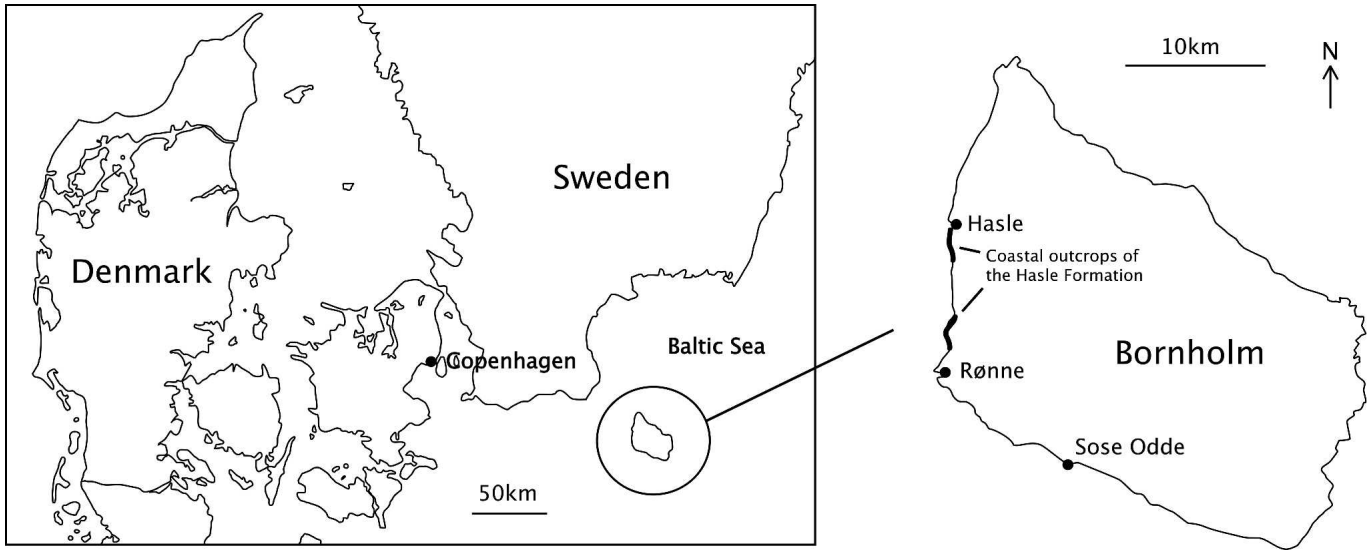

FIGURE 1. Locality map to show the Danish island of Bornholm in the Baltic Sea: the Hasle Formation outcrops sporadically on the west and southwest coast.

PLIOSAUROIDEA Seeley, 1874
RHOMALEOSAURIDAE (Nopsca, 1928) Kuhn 1961
(Fig. 2B, D)

Material—MGUH DKV 2002-70 a single plesiosaur tooth Type B (Fig. 2B).

Description—Tooth type B is of robust form and only slightly recurved (Fig. 2B). The single tooth crown is 26mm long as preserved but would be approximately 30mm long when restored making this the largest type of tooth from the Hasle Formation. The crown is sparsely ridged, about 5 ridges can be seen in lateral view but none of the ridges extend to the tooth apex. There are many longitudinal cracks in the enamel.

Discussion—The sparse pattern of ridges is most similar to that observed by Taylor (1992) in the genus *Rhomaleosaurus* and the large size of the tooth is also consistent with this diagnosis.

Material—MGUH DKV-2002-69, a complete tibia (Fig. 2D).

Description—MGUH DKV-2002-69 is an isolated flattened rectangular epipodial bone, 50 mm long and 41 mm wide. The preaxial margin is almost straight and the postaxial margin is concave indicating the presence of a large interosseal space. The postaxial margin is much shorter than the preaxial margin so that the humerus facet and mesopodial facet converge posteriorly and endow the bone with a wedge-like appearance in dorsal/ventral view (Fig. 2D). There is a distinct angle on the distal margin of the epipodial delineating a short facet for articulation with the astragalus.

Discussion—In the epipodial row of Lower Jurassic plesiosaurs the preaxial element (i.e., the radius in the forelimb and the tibia in the hind limb) can be distinguished from the postaxial element (i.e., the ulna in the forelimb and the fibula in the hind limb), based on its more angular appearance. On this basis MGUH DKV 2002-69 may be regarded as either a radius or tibia. Amongst Lower Jurassic plesiosaurs the tibia is always shorter relative to distal width than is the more slender radius (pers. obs); MGUH DKV 2002-69 thus can be identified as a probable tibia based on its proportions. Furthermore, there is a distinct discrepancy between the epipodial proportions in Lower Jurassic plesiosaurs. The radius/tibia is always far longer than it is wide in plesiosauroids; in contrast, the epipodials are much stouter in Toarcian pliosauroid forms, most notably in *Rhomaleosaurus propinquus* (Watson, 1910). MGUH DKV 2002-69 exhibits proportions almost identical to *Rhomaleosaurus* and is also united to this genus (to the exclusion of other Lower Jurassic plesiosaurs) by the shared possession of a distinct postero-distal facet. Indeed, the confirmed presence of rhomaleosaurid teeth in these deposits (see below) lends credence to this inference.

PLIOSAUROIDEA Seeley, 1874
Indeterminate
(Fig. 2C)

Material—MGUH DKV-2002-149, fourteen isolated plesiosaur teeth belonging to tooth type C (Fig. 2C).

Description—Tooth type C ranges in size from about 5mm to 20mm long (Fig. 2C). There is a distinct ornament of ridges around the whole tooth crown and most of the ridges continue to the tip (although in many teeth this area has been damaged or broken off during taphonomy). The number of ridges ranges from 9 to 11 in lateral view.

Discussion—Rees and Bonde (1993) and Milàn and Bonde (2001) regarded the morphology of tooth type C to approximate *Attenborosaurus conybeari* from the Lower Lias of Charmouth. However, this cannot be corroborated because the holotype of

TABLE. Plesiosaur material from Bornholm.

Specimen number	Brief description
MGUH DK416	Complete humerus (Fig. 2F)
MGUH DK417	Complete ischium (Fig. 2E)
MGUH DKV-2002-74	Sacral rib (Fig. 2H)
MGUH DKV-2002-75	Fragment of dorsal/pectoral rib
MGUH GM-V-2002-65	Complete ulna/fibula (Fig. 2G)
MGUH GM-V-2002-69	Complete tibia (Fig. 2D)
MGUH GM-V-1.2002	Jaw fragment with 11 alveoli
MGUH GM-V-2006-8	Single plesiosauroid tooth ('Type A') (Fig. 2A)
MGUH GM-V-2002-70	Single rhomaleosaurid plesiosaur tooth ('Type B') (Fig. 2B)
MGUH GM-V-2002-149	Fourteen loose plesiosaur teeth ('Type C') (Fig. 2C)
MGUH GM-V-2003-1720	Vertebra in sandstone matrix (Fig. 2I, J)

Attenborosaurus was one of many marine reptiles destroyed during an air raid on the Bristol City Museum in 1940 (Taylor, 1994). Close personal observation of a surviving cast (TCD.47763) provided no further information due to lack of surface detail. These teeth can therefore only be identified to the level of Pliosauroidoidea based on their robust construction and broad bases (Brown, 1981).

PLESIOSAURIA de Blainville, 1835
Indeterminate
(Figs. 2E–J)

Material—MGUH DK417, complete right ischium (Fig 2E).

Description—The total length of this specimen is 93 mm and the distance from the tip of the anterior process to the posterior

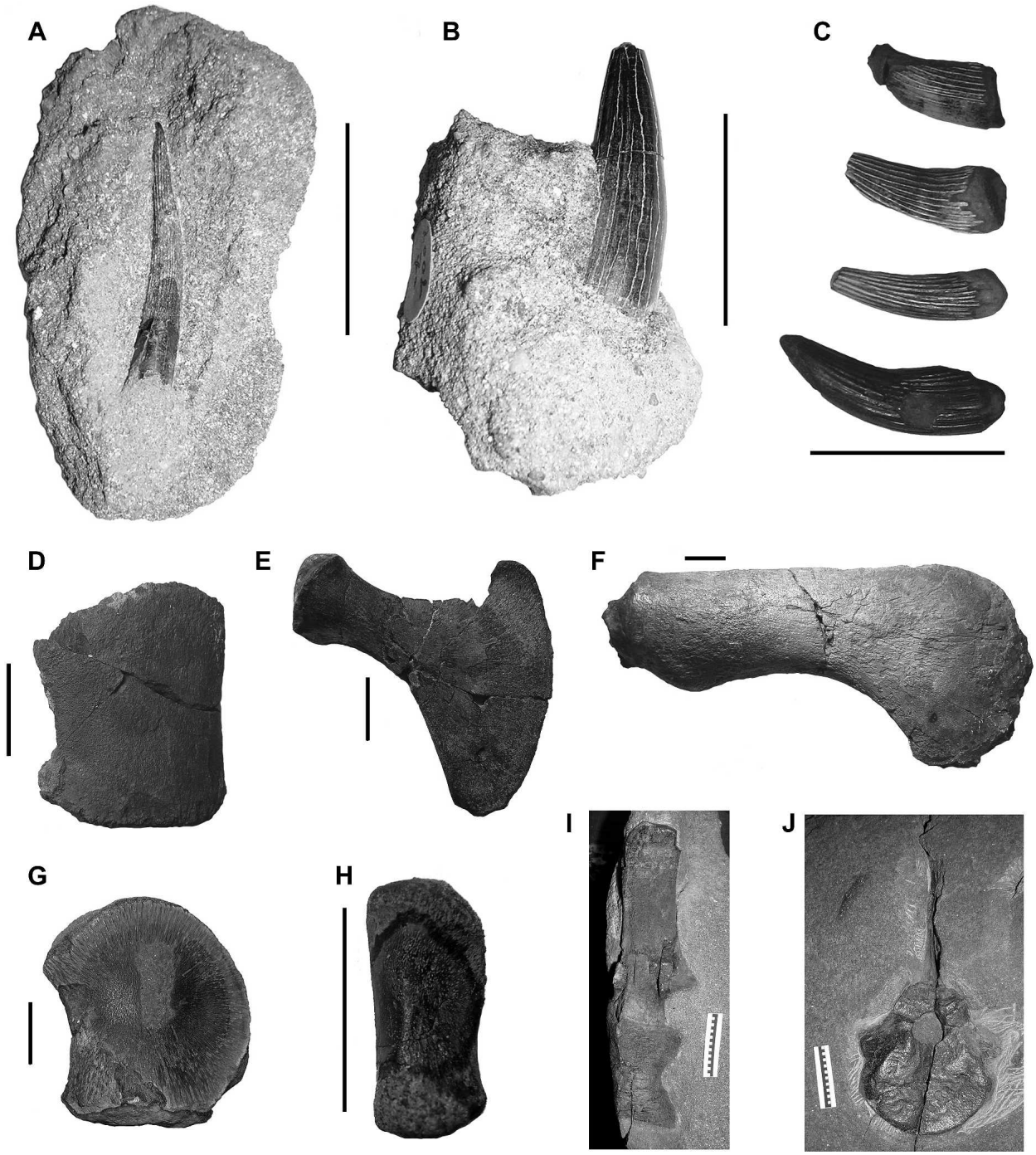

FIGURE. 2. Plesiosaur remains from the Lower Jurassic (Pliensbachian) of Bornholm, Denmark. **A**, indeterminate plesiosauroid tooth (type A) (MGUH V-2006-8) in sandstone matrix. **B**, plesiosaur tooth (Type B) (MGUH 2002-70) referred to cf. *Rhomaleosaurus zetlandicus*. **C**, four representative pliosauroid teeth (type C) (MGUH DKV-2002-149) out of a collection of fourteen teeth. **D**, plesiosaur tibia (MGUH DK-2002-69) referred to cf. *Rhomaleosaurus*. **E**, indeterminate plesiosaur ischium (MGUH DK417). **F**, indeterminate plesiosaur humerus (MGUH DK 416). **G**, indeterminate plesiosaur ulna/fibula (MGUH 2002-65). **H**, indeterminate plesiosaur sacral rib (MGUH DKV-2002-74,). **I, J**, indeterminate plesiosaur vertebra (MGUH 2003-1720) in (**J**) anterior view and (**I**) lateral view along a longitudinal break through the centrum just left of the midline. Scale bars equal 20 mm.

tip is 81 mm. The distance from the acetabulum to the medial margin (as measured along the axis of the shaft of the lateral process) is 90 mm, thus the length and width of the ischium are subequal. The lateral process is very slender measuring 19 mm wide. The anterior process curves ventrally slightly, and the thickest part of the medial symphysial surface is situated just behind this area, behind which the symphysis tapers at a very shallow angle. In ventral view the posterior process tapers gradually to a broad rounded tip (Fig. 2E). The lateral margin is notably concave but there is a sharp natural angle at the posterolateral tip.

Discussion—The elongate narrow lateral shaft immediately distinguishes MGUH DK417 from *Plesiosaurus,* and the posterior process is also much broader in *Plesiosaurus* (see Storrs, 1997, Figure 12). *Eretmosaurus* is distinguished from MGUH DK417 by an elongate posterior process that does not taper posteriorly (see Owen, 1865, Tab XIV). The ischium of *Attenborosaurus* is distinct, with a much straighter posterolateral margin (Pers. obs. and Sollas, 1881 Plate XXIII). In *Rhomaleosaurus thorntoni* (Andrews, 1922) and *R. victor (*Fraas, 1910) the posterior process is also very much broader and generally more robust. The posterior process of the ischia of *Sthenarosaurus* are very much truncated relative to all other plesiosaurs (Watson, 1909, Fig. VI), including MGUH DK 417. There is apparently a considerable amount of variation in the structure of the ischia in *Microcleidus* (Watson, 1909), a feature attributed to sexual dimorphism by Watson (1909). However, In MGUH DK417 the proportions of the posterior process are intermediate between the two types of *Microcleidus*. Among Lower Jurassic plesiosaurs with known ischia, *Occitanosaurus* shows the greatest similarity to MGUH DK417—both share similar proportions (the posterior process of MGUH DK417 is slightly broader) and both possess a sharp angle on the distal posterolateral tip.

Material—MGUH DK416, a complete isolated humerus (Fig. 2F).

Description—This bone is 190 mm long and flares distally to a maximum width of 90 mm. The preaxial margin is straight (there is no preaxial flare) whereas the postaxial margin is strongly concave and significantly flared distally (Fig. 2F). At the posterodistal corner of the humerus there is a straight facet that runs parallel to the preaxial margin, this is positioned at a sharp angle to the rest of the distal facets. The minimum width (48 mm) of the humerus is situated exactly half way along the shaft and at the proximal part of the shaft is a strong posterior flange. There is a small arterial foramina positioned exactly half way along the shaft on the postaxial border. The distal facets curve gently toward the postaxial border.

Discussion—The straight shaft and straight anterior margin of MGUH DK416 differentiates it from the convex anterior humerus border in *Plesiosaurus dolichodeirus* (Storrs, 1997, Figure 10), *Microcleidus* (Watson, 1911, Fig. 2), *Attenborosaurus* (Sollas, 1881, Plate XXIII), *Rhomaleosaurus victor* (Fraas, 1910, Taf. VIII*)* and *Rhomaleosaurus megacephalus* (pers. obs.); and the slightly concave anterior border in *Rhomaleosaurus zetlandicus* (pers. obs.) and *Rhomaleosaurus cramptoni* (pers. obs.). The distinct posterodistal facet distinguishes MGUH DK416 from *Thalassiodracon* (pers. obs.), *Seeleysaurus guilelmiimperatoris* (Dames, 1895, Taf. I) and *Sthenarosaurus* (Watson, 1911, Fig. IV). *Eretmosaurus* (Owen, 1865) and *Occitanosaurus* (Bardet *et al.,* 1999) possess two distinct epipodial facets whereas in MGUH DK416 the facets are not positioned at sharp angles. In general outline and morphology MGUH DK416 shows the closest similarity amongst Lower Jurassic plesiosaurs with *Archaeonectrus* (Owen, 1865, Tab. IX).

Material—MGUH DKV-2002-65, complete ulna/fibula (Fig. 2G).

Description—MGUH DKV-2002-65 is an isolated flattened lunate epipodial bone, 71 mm long and 66 mm wide.

Discussion—The lunate shape of MGUH DKV-2002-65 immediately distinguishes it as a postaxial epipodial and the bone is therefore either an ulna or fibula. Unfortunately there is not enough variation between these two bones in most Lower Jurassic plesiosaur taxa to determine which MGUH DKV-2002-65 represents.

Material—MGUH 1.2002, fragment of jaw with eleven alveoli.

Description—This specimen suffers from pyrite overgrowth but contains eleven visible individual alveoli that decrease in size posteriorly (see Milàn and Bonde, 2001; Figure 9). The bone is 135mm long and the thecodont tooth implantation suggests a plesiosaurian affinity.

Material—MGUH DKV-2003-1720, a complete vertebra from the sacral region in sandstone matrix (Figs. 2I, J).

Description—The vertebra is preserved in anterior view, however, a vertical crack runs longitudinally through the middle of the centrum and along the left border of the neural spine affording a lateral view of the vertebra. The neural spine is approximately 44 mm high and situated directly above the centrum. The centrum is wider than it is long, 29 mm high (to the neural canal) and 43 mm wide. The neural canal is 10 high and 10 mm wide. The neural arch is fused to the centrum body— indicative of osteological maturity. The facets for the sacral ribs are clear in anterior view, each 17mm high and indented 'V'-shaped. The centrum is notably amphiocoelus, as seen in longitudinal cross section. It is not possible to identify this sacral vertebra beyond plesiosauria indet.

Additional Nondiagnostic Material—MGUH DKV-2002-74, small sacral rib (Fig. 2H); MGUH DKV– 2002-75, Single fragment of rib.

DISCUSSION

The record of marine reptile fossils from the Pliensbachian (Early Jurassic) is very poorly known. At present, three diagnostic ichthyosaur taxa have been recorded from this interval: the holotype of *Leptonectes moorei* from England (McGowan and Milner, 1999); *Leptonectes tenuirostris* from Switzerland (Maisch and Reisdorf, 2006); and *Temnodontosaurus* from strata in Germany (Hungerbühler and Sachs, 1996). There are currently no definitively named plesiosaur taxa.

Existing Pliensbachian plesiosaur material is restricted to isolated elements, with all articulated or associated remains currently considered indeterminate or undescribed. Examples include: a partial postcranium attributed to *Plesiosaurus* sp. from Charmouth, Dorset, England (Storrs, 1995); undescribed articulated specimens from Gloucestershire (LEICT G1.2002, M. Evans pers. comm.) and Lincolnshire (R. Forrest pers. comm.), England; a partial skeleton including the skull from Normandy, France (Vincent, 2004); and a partial skeleton of a plesiosauroid from Asturias, Spain (Bardet et al., 2008). The remains presented here are therefore particularly important in helping to elucidate the diversity and abundance of plesiosaurs during this time. Further, they represent the only plesiosaur material described from Denmark. The presence of Rhomaleosaurid fossil remains within this assemblage (Figs. 2B and D) confirms the presence of this Family in Europe during Pliensbachian times and extends the known range of rhomaleosaurids into Scandinavia.

Plesiosaur diversity in the Hasle Formation is particularly high—at least three taxa are present based on tooth morphology alone (Fig. 2A–C). Tooth 'type A' belongs to a plesiosauroid; 'type B' belongs to a large rhomaleosaurid, and 'type C' belongs to a pliosauroid sharing similarities with *Attenborosaurus*. The postcranial material also indicates three types of plesiosaur, of the determined remains the ischium appears to belong to a plesiosauroid sharing similarity with *Occitanosaurus*, the humerus appears to belong to a pliosauroid sharing similarity with *Archaeonectrus*, and the radius/tibia is tentatively identified as a

rhomaleosaurid. Therefore, at least three taxa (and a possible maximum of six taxa) can be confirmed within the Hasle Formation.

The apparently high abundance and diversity of plesiosaurs relative to other marine reptiles in this small sample from the Hasle Formation is intriguing, because ichthyosaurs and crocodiles are typically more abundant than plesiosaurs in Lower Jurassic marine deposits (Benton and Taylor, 1983; Benton and Spencer, 1995); ichthyosaurs in particular are usually dominant in Pliensbachian strata (see Maisch and Reisdorf, 2006). However, it is possible that this represents an artefact of the small data set and it would be premature to make any conclusions regarding this apparent pattern.

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