

Danish mosasaurs

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Abstract

Presented are the first formal descriptions of mosasaur remains of Maastrichtian age from the Danish mainland (Jylland, Sjælland); just two taxa are recognised, viz. *Mosasaurus* cf. *hoffmanni* and *Plioplatecarpus* sp. Recent finds include an association of skeletal fragments, inclusive of a single marginal tooth crown, from within 10 metres or so of the K/T boundary near Holtug, Stevns Klint (Sjælland, eastern Denmark), here assigned to *Plioplatecarpus* sp. A brief review of previous records of Danish mosasaurs is added.

Keywords: Cretaceous, Maastrichtian, Denmark, *Mosasaurus*, *Plioplatecarpus*

Introduction

Despite being exceedingly rare, mosasaur remains from the Maastrichtian ‘white chalks’ (Skrivekridt) of Denmark are of considerable biostratigraphic significance, as they represent some of the youngest records to date of Mosasauroida prior to their sudden, end-Cretaceous demise. Until now, the occurrence of mosasaurs in the Upper Cretaceous of Denmark has merely been hinted at, or discussed cursorily, in a small number of popular science publications.

The earliest report is that by Floris (1964, p. 26), who illustrated two isolated tooth crowns from the uppermost Maastrichtian as exposed at the ‘Dania’ quarry near the hamlet of Assens (northern Jylland). Unfortunately, these teeth cannot be traced now in the collections of the Geological Museum (Copenhagen), and may therefore be presumed lost. A third tooth crown (MGUH 27472), collected from (unspecified) Maastrichtian strata in an unnamed chalk pit in the vicinity of Aalborg, was later illustrated by Rasmussen (1966, p. 55). Subsequently, these three teeth have also appeared in papers by

Rasmussen (1967, fig. 121.3) and Bonde (1997a, b). Rasmussen (1967) identified them as belonging to the genus *Mosasaurus*, whereas Bonde (1997a, b) was more specific in his assignment and concluded that at least MGUH 27472 could be assigned to one of the larger mosasaurs of all time, *Mosasaurus hoffmanni*. The most recent contribution to our knowledge of Danish mosasaurs is that by Heinberg (2000), who briefly mentioned the presence of the genus *Mosasaurus* in the Maastrichtian white chalks of Denmark, although what he illustrated as a mosasaur vertebra (Heinberg, 2000, fig. 16) is in fact a selachian or actinopterygian vertebral centrum.

Recently, a few isolated teeth and fragmentary skeletal elements of mosasaurs have been found weathering out of a cliff face near Holtug (Stevns Klint) and in an adjacent limestone quarry (Sjælland, eastern Denmark), from within some 10 metres of the K/T boundary there. The present contribution provides the first description of these mosasaur remains as well as the first formal account of the Aalborg specimen.

Geological setting

The uppermost Cretaceous and lowermost Paleogene of Denmark comprise a thick sequence (>600 m; see Rasmussen, 1967) of chalks and limestones deposited in a vast epicontinental sea at depths between 100 and 250 m (Bromley, 1979). Today, these shelf sediments crop out over large parts of the Danish mainland, although most quarries and natural outcrops are located in northern Jylland and along narrow belts following the eastern coasts of the islands of Fyn and Sjælland. The Maastrichtian grey-white chalks and limestones in Denmark are mainly of pelagic origin, comprising calcareous nanno- (especially coccoliths) and microfossils (foraminifera and dinoflagellate cysts) deposited as low mounds (Bromley, 1979; see also Surlyk et al., 2003). Abundant macrofossils include bryozoans, brachiopods and echinoderms. Numerous flint nodules and flint-filled burrows testify to a palaeoenvironment with oxygenated bottom waters in which a highly diverse benthic fauna thrived. Thin beds of marl, varying from a few to several tens of centimetres in thickness, occur sporadically within the chalk facies (e.g. at 'Dania').

Age assignments rely mainly on coleoid and ammonoid cephalopods (Schulz, 1979; Birkelund, 1993; Christensen, 1996, 1997a, b; Machalski, 1996, work under way), and dinoflagellates (Schjøler & Wilson, 1993). The highest part of the 'white chalk' and the 'grey chalk' (Gråkriddt), as exposed along Stevns Klint, are of latest Maastrichtian age. Elsewhere (e.g. Møn), the sequence comprises older strata, of early Maastrichtian age (Schulz, 1979; Birkelund, 1993).

For more comprehensive descriptions of the formation and petrology of the Upper Cretaceous and lowermost Paleogene of Denmark, reference is made to Surlyk (1984) and Schmitz et al. (1992); localities referred to in the text are shown in Fig. 1.

Systematic palaeontology

Institutional abbreviations – MGUH - Geological Museum, University of Copenhagen, Copenhagen; NHMM - Natuurhistorisch Museum Maastricht, Maastricht; MNHN - Muséum National d'Histoire Naturelle, Paris.

Family Mosasauridae

Subfamily Mosasaurinae

Genus *Mosasaurus* Conybeare, 1822

Mosasaurus cf. hoffmanni Mantell, 1829; Fig. 2

1964 Tand af slangeøgle – Floris, p. 26.

1966 Slangeøgle – Rasmussen, p. 53.

1966 *Mosasaurus* Conybeare – Rasmussen, p. 55.

1967 *Mosasaurus* Conybeare – Rasmussen, p. 142, fig. 121.3.

1997a *Mosasaurus* (?) *hoffmanni* Mantell – Bonde, pp. 29, 30.

1997b *Mosasaurus hoffmanni* Mantell – Bonde, p. 13.

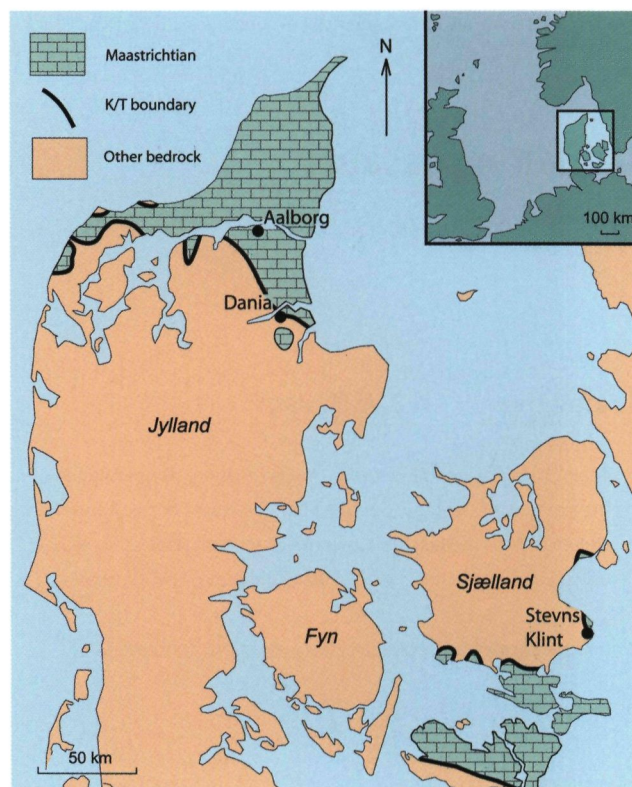


Fig. 1. Simplified map of the Danish mainland, showing the extension of the Maastrichtian white chalks and the localities mentioned in the text.

Material – MGUH 27472; a marginal tooth crown collected from lower? Maastrichtian strata near the town of Aalborg in northern Jylland, Denmark (see Håkansson & Hansen, 1979 for a comprehensive description of the Upper Cretaceous exposed in the Aalborg area).

Description – MGUH 27472 is an isolated, presumably shed, marginal tooth crown of an adult individual assumed to have come from the mesial part of the jaw. As preserved, the sturdy crown measures 42.8 mm in total height (when measured at a right angle to the plane formed at the base of the crown) and 30.1 mm in basal width (in meso-distal direction). The original height is estimated to have been around 45 mm. Sharp and minutely serrated carinae divide the crown into a gently convex labial face and a deeply U-shaped lingual surface. Four flattened facets are present on the labial face, giving this surface a somewhat prismatic appearance, whereas the lingual face is covered by very obscure facets. Most of the apical portion of the crown is broken off, although a shallow and elongated groove on the remaining lingual face indicates that the tip originally was heavily abraded. Another prominent furrow occupies the basal portion of the mesial face of the crown, and, in accordance with the apical one, may have been inflicted through occlusion. In basal view, the crown has a broadly elliptical outline.

Remarks – Regardless of their position in the jaw, marginal teeth of mosasaurine mosasaurs always lack a delicate surface

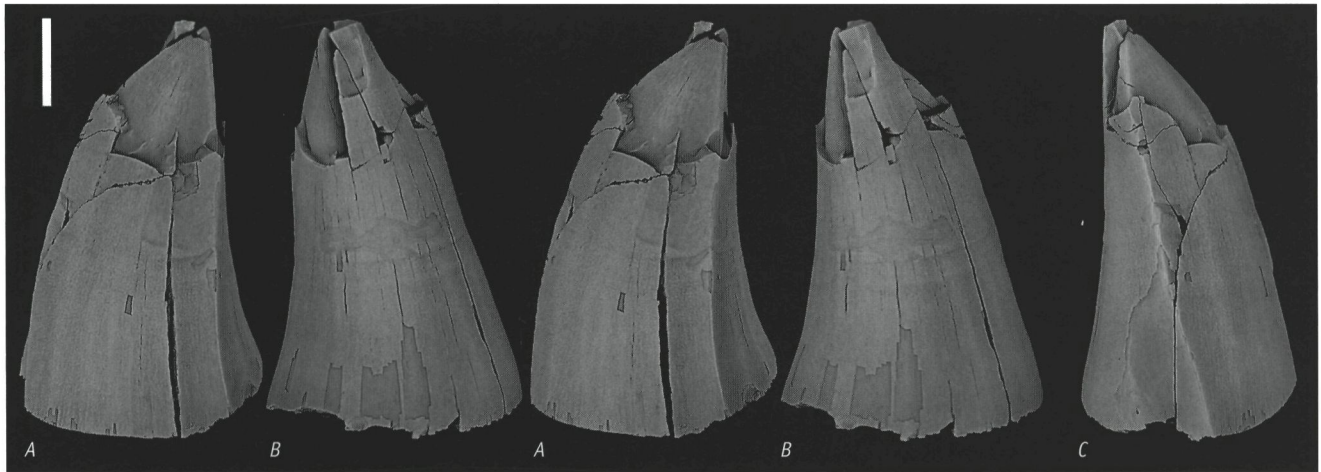


Fig. 2. *Mosasaurus* cf. *hoffmanni* Mantell, 1829 (MGUH 27472) from the lower Maastrichtian of Aalborg (Jylland, Denmark), in labial (A, stereo pair), lingual (B, stereo pair) and mesial (C) view, respectively. Scale bar equals 10 mm.

texture of closely spaced vertical striations on their lingual face, a feature typical of tylosaurines, plioplatecarpines and the enigmatic basal mosasaur *Halisaurus* (see Bell, 1997; Lindgren & Siverson, 2002, 2004). A relatively low number of distinctly flattened facets on the labial face of the crown characterises teeth of the mosasaurine genera *Mosasaurus* and *Clidastes* (see Lindgren & Siverson, 2004). However, apart from a marked difference in maximum size (in adult individuals), laterally situated marginal teeth of *Mosasaurus* can be readily distinguished from those of *Clidastes* by their unequally convex labial and lingual faces (nearly symmetrically bicarinate crowns in, at least, *C. liodontus*; see Lindgren & Siverson, 2004) and finely serrated carinae (the carinae are smooth in *Clidastes*) (see e.g. Lingham-Soliar, 1995, fig. 15; Mulder, 1999, fig. 4; Lindgren & Siverson, 2004, figs. 3, 4).

Currently, four nominal species of *Mosasaurus* from the upper Campanian and Maastrichtian of Europe, North America and North Africa are recognised as valid, namely *M. hoffmanni* (= *M. maximus* and *M. dekayi*), *M. lemonnieri* (= *M. conodon*; but see also Lingham-Soliar, 2000), *M. missouriensis* (= *M. maximiliani*; see Caldwell & Bell, 2005) and *M. beaugei* (see Bardet et al., 2004). Of these species, MGUH 27472 shows the closest similarity to teeth of *M. hoffmanni*, as the crown is large and robust, and possesses flattened facets on its labial face. The moderately large (by mosasaur standards) *M. lemonnieri* and *M. missouriensis* have generally slender and labio-lingually compressed teeth relative to the robust and conical crowns of the giant *M. hoffmanni* (see e.g. Kuypers et al., 1998, pl. 2; Mulder, 1999, fig. 4.3; Machalski et al., 2003, fig. 7).

Moreover, the tooth facets in *M. lemonnieri* are commonly separated by distinct crests, resulting in concave facets, as opposed to the flattened to convex facets on the teeth of *M. hoffmanni* (Meijer, 1984). In *M. lemonnieri*, the facets are of subequal width on both surfaces, while the prisms are fewer and wider on the labial face than they are on the lingual surface on marginal teeth of *M. hoffmanni* (Machalski et al.,

2003). Recently, Bardet et al. (2004) claimed that marginal teeth of *M. beaugei* from the Maastrichtian of Morocco possess three to five labial prisms, whereas those of *M. hoffmanni* merely show two to three. However, as several *M. hoffmanni* teeth examined by us (including those in the type specimen; NMHN AC 9648) have four facets on their labial face, this statement is erroneous. Nevertheless, isolated marginal teeth of at least large individuals of *M. hoffmanni* can be separated from those of *M. beaugei* by their sturdier and labio-lingually less compressed crowns (cf. Arambourg, 1952, pl. 39, figs 13, 14, 19; Lingham-Soliar, 1995, fig. 15). Finally, it should be noted that, occasionally, teeth of *M. hoffmanni* appear to lack facets altogether, as pointed out by Kuypers et al. (1998).

Subfamily Plioplatecarpinae

Genus *Plioplatecarpus* Dollo, 1882

***Plioplatecarpus* sp.; Fig. 3**

Material – MGUH DK 424; an association comprising a marginal tooth crown, an incomplete tooth base, a piece of ?sclerotic ring, and several unidentifiable skeletal fragments, presumably from a single individual, found on the shore below the cliffs near Holtug exposing uppermost Maastrichtian (*Belemnella* (*Neobelemnella*) *kazimiroviensis* Zone) white chalks along Stevns Klint (Sjælland, eastern Denmark).

Description – As preserved, the marginal tooth crown is 21,1 mm tall, and 11,0 mm wide. It is broken transversally across the base, exposing a capacious pulp cavity, which indicates that it probably has not been shed, but instead was detached directly from the jawbone. The tooth is strongly distally curved from about the mid-point of its height, and the enamelled faces are covered with numerous weak facets. Delicate and densely spaced striations reach a few millimetres up the base on both the lingual and labial face of the crown. Conspicuous wear

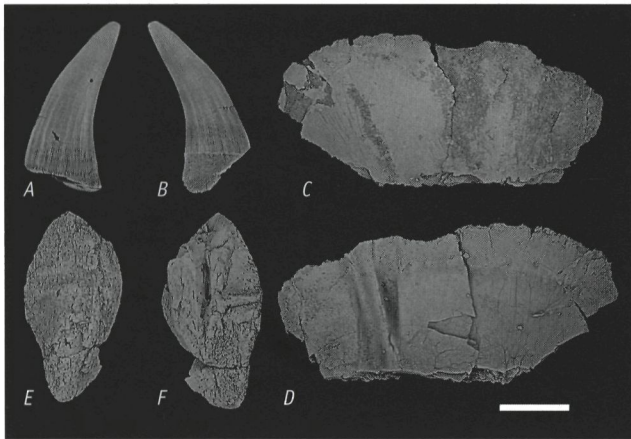


Fig. 3. *Plioplatecarpus* sp. (MGUH DK 424) from uppermost Maastrichtian (*Belemnella* (*Neobelemnella*) *kazimiroviensis* Zone; brachiopod zone 10 sensu Surlyk, 1972) strata near Holtug, Stevns Klint (Sjælland, eastern Denmark); A, B – marginal tooth crown in labial and lingual view, respectively; C, D – fragment of ?sclerotic ring in lateral and medial view, respectively; E, F – incomplete tooth base in lateral and medial view, respectively. Scale bar equals 10 mm.

facets are present at the apex and along the anterior edge of the crown, whereas the posterior carina is intact and lacks serrations.

The inferred partial ?sclerotic ring comprises a very thin sheet of vaulted bone, measuring 50,6 mm in total length and 23,3 mm in maximum width. A few wide, indistinct grooves (and one deep depression) run perpendicular to the longitudinal axis of the bone, thus contributing to a gently undulating surface of the element.

Remarks – Isolated tooth crowns of plioplatecarpine mosasaurs can be distinguished from those of mosasaurines, tylosaurines and *Halisaurus* on the basis of the following character state combination: (1) fine hairline striations are present on, at least, the basal portion of the lingual face of the crowns; (2) the labial and lingual surfaces are faceted, giving the crowns a more or less prismatic appearance; (3) the carinae are prominent but rather blunt and lack serrations; (4) the crowns are more or less abruptly curved distally from about mid-height; (5) in basal view, the crowns are elliptical to subcircular; (6) the labial and lingual surfaces on at least lateral and distal teeth are of subequal convexity; and (7) the crowns are generally rather slender and slightly pointed in lateral aspect (Bengtson & Lindgren, 2005).

The slender and abruptly distally curved nature of the marginal tooth in this new mosasaur assemblage from Stevns Klint allows a definitive generic identification, as teeth of *Plioplatecarpus* show a very characteristic morphology. They strongly resemble those in the dentition of the modern gavia (see Massare, 1987), and hence it is reasonable to assume that *Plioplatecarpus* too was adapted to piscivorous feeding. Moreover, the overall morphology of the teeth in *Plioplatecarpus*

suggests that they had an even more pronounced piercing function than had those in the closely related genera *Platecarpus* and *Ectenosaurus*.

The dental morphology of *Plioplatecarpus* is closer to that of *Platecarpus* and *Ectenosaurus* than it is to any other plioplatecarpine genus, although marginal teeth of *Plioplatecarpus* can normally be separated from those of the two last-named genera by their more acute distal curvature, more delicate form and more pointed tips (see Williston, 1898, pl. 13; Kuypers et al., 1998, pl. 6). Furthermore, these genera are also temporally separated, as *Platecarpus* has been recorded from deposits spanning the middle and/or upper Turonian-lower Campanian interval (Bengtson & Lindgren, 2005), whereas *Plioplatecarpus* is known only from strata post-dating the lower Campanian (*Ectenosaurus* is, so far, known exclusively from the upper Coniacian-lowermost Campanian Smoky Hill Chalk Member of the Niobrara Formation in western Kansas; see Russell, 1967).

Miscellaneous remains and teeth in private collections

In addition to the specimens described above, four fragments of a dorsal(?) mosasaur vertebra (MGUH V2004-348a/d) were found eighteen years ago by the skilled non-professional palaeontologist, Mrs Alice Rasmussen of Fakse, at the same locality from which she recently collected *Plioplatecarpus* remains (MGUH DK 424; see above). Unfortunately, the vertebra is too poorly preserved to be identified beyond family level with confidence.

Moreover, a few isolated mosasaur teeth from the Danish Maastrichtian are retained in private collections. Specimens that we know of include:

- an isolated marginal tooth crown of *Plioplatecarpus* and one pterygoid tooth crown, presumably assignable to *Mosasaurus*, from the uppermost Maastrichtian (*Belemnella kazimiroviensis* Zone; brachiopod zone 10 sensu Surlyk, 1972) at ‘Stevns kridtbrud’, close to Sigerslev. Both specimens are currently housed in the private collection of Alice Rasmussen.
- the upper portion of a fragmentary tooth crown, collected 11 June 2003 by Sylvia Verschueren, from the Thisted Kalkværk quarry, northeast of Thisted (Thy, northern Denmark), found loose on a scree slope, but apparently of late Maastrichtian age. In general habitus, this specimen matches MGUH 27472 well, in showing a deeply U-shaped lingual surface and a serrated carina. Moreover, enamel features and faceting are also comparable.
- recently, a very large marginal tooth, belonging either to *Mosasaurus* or to a tylosaurine, was presented to the Geological Museum (Copenhagen). This specimen was collected from a loose boulder of unknown origin, and is currently being assessed by museum staff.

Discussion

As presently recognised, *Mosasaurus hoffmanni* had a wide geographical distribution during the late Maastrichtian, ranging from present-day Alabama and Missouri (US Gulf Coast) in the southwest (Kiernan, 2002; Gallagher et al., 2005), across north-central Europe and Russia (Nikolov & Westphal, 1976; Yarkov, 1993; Tzankov et al., work under way), to Turkey in the southeast (Bardet & Tunçoğlu, 2002). In accordance with distributional patterns of marine vertebrates in the Western Interior and Gulf Coast of North America during the early Campanian (see Nicholls & Russell, 1990), the range of *M. hoffmanni* may have been linked to palaeolatitudinal gradients (Bardet & Pereda Suberbiola, 1996; Bardet et al., 2004). As observed by the latter authors, occurrences of *M. hoffmanni* are limited mainly to a palaeolatitudinal belt around 30° N, corresponding arbitrarily to the northern margin of the Mediterranean Tethys (but see also Lingham-Soliar, 1991). If correctly identified, MGUH 27472 represents the most northerly occurrence of the species so far (around 45° N), and hence extends the geographical range of that species.

There are very few mosasaur records close to the K/T boundary from anywhere in the world, owing mainly to the general paucity of large-sized vertebrate fossils. Consequently, every single specimen is of interest, as long as reworking can be ruled out. The occurrence of *Plioplatecarpus* sp. in the upper part of the uppermost Maastrichtian *Belemnella* (*Neobelemnella*) *kazimiroviensis* Zone at Stevns Klint demonstrates that this, by all means, was one of the last mosasaurs around prior to the bolide impact event that defines the end of the Cretaceous. The same genus is also the last one to be found in situ in the Maastrichtian type area (the Netherlands; Mulder et al., 1998), and the stratigraphically youngest records comprise two pterygoid tooth crowns of *Plioplatecarpus marshi* (NHMM 2002 003 (leg./don. A. Hofman) and NHMM 2004 155 (leg./don. S. Goolaerts) collected from the higher portion of the Meerssen Member (subunits IVf-5 and f-6, *Belemnella* (*Neobelemnella*) *kazimiroviensis* Zone), between c. 8 and 1 metres below the K/T boundary in the area. Thus the question arises whether mosasaurs as a group were declining in diversity prior to the profound mass extinction at the end of the Cretaceous or not. Hopefully, future in-depth stratigraphical research in Denmark, the Netherlands and other regions with suitable deposits spanning the uppermost Maastrichtian-lowermost Paleogene interval, will reveal the true story behind the disappearance of these mighty marine reptiles.

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