

Prognathodon (Squamata, Mosasauridae) from the Maastrichtian chalk of Denmark

TOM J. GILTAIJ, JESPER MILÀN, JOHN W.M. JAGT & ANNE S. SCHULP



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

Received 15 September 2020
 Accepted in revised form
 30 April 2021
 Published online
 31 May 2021

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Giltaij, T.J., Milàn, J., Jagt, J.W.M. & Schulp, A.S. 2021: *Prognathodon* (Squamata, Mosasauridae) from the Maastrichtian chalk of Denmark. *Bulletin of the Geological Society of Denmark*, vol. 69, pp. 53–58. ISSN 2245-7070.
<https://doi.org/10.37570/bgds-2021-69-03>

Two mosasaur tooth crowns collected from the Maastrichtian chalk sequences of Stevns Klint and Møns Klint are here assigned to *Prognathodon*, a mosasaur genus hitherto unknown from Denmark. Together with previous records of the mosasaurs *Plioplatecarpus*, *Mosasaurus* and *Carinodens*, these new finds of *Prognathodon* document the coexistence of four mosasaurid genera in the Danish chalk and underscore similarities to coeval assemblages from the Maastrichtian type area in the Netherlands and Belgium.

Keywords: Marine reptiles, northern Europe, Upper Cretaceous, faunal compositions, comparisons.

Tom J. Giltaij [tom.giltaij@live.nl], Faculty of Science, Vrije Universiteit Amsterdam, De Boelelaan 1085, 1081 HV Amsterdam, the Netherlands; also Geologisch Museum Hofland, Hilversumseweg 51, 1251 EW Laren, the Netherlands; and Faculty of Geosciences, Utrecht University, P.O. Box 80115, 3508 TC Utrecht, the Netherlands. Jesper Milàn [jesperm@oesm.dk], Geomuseum Faxe/Østsjælland Museum, Rådhusvej 2, 4640 Faxe, Denmark. John W.M. Jagt [john.jagt@maastricht.nl], Natuurhistorisch Museum Maastricht, De Bosquetplein 6-7, 6211 KJ Maastricht, the Netherlands. Anne S. Schulp [anne.schulp@naturalis.nl], Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, the Netherlands; also Faculty of Science, Vrije Universiteit Amsterdam, Faculty of Geosciences, Utrecht University, and Natuurhistorisch Museum Maastricht.

Corresponding author: Jesper Milàn

Mosasaurs were the apex predators of the Late Cretaceous seas, and their fossil remains have been recorded from all continents (Polcyn *et al.* 2014). In spite of the numerous outcrops of Upper Cretaceous (Maastrichtian) marine sedimentary rocks in northern and eastern Denmark, and the countless hours of dedicated field work by a vibrant community of citizen scientists and professionals alike, the Danish mosasaur record is comparatively poor. Only recently has a third mosasaur taxon, *Carinodens*, been recognised from the Danish Chalk (Milàn *et al.* 2018), and this record is based on a single tooth crown only. Here we describe and illustrate a fourth mosasaur genus from the Maastrichtian of Denmark, *Prognathodon*, on the basis of two isolated tooth crowns.

Material

Institutional abbreviation: NHMD: Natural History Museum of Denmark (Statens Naturhistoriske Museum), Copenhagen, Denmark.

The material consists of two isolated tooth crowns: one from Møns Klint, initially identified as *Mosasaurus hoffmanni* Mantell, 1829 and collected in 2004 by amateur palaeontologist Mette Hofstedt, and another from Mandehoved, Stevns Klint, collected by amateur palaeontologist Peter Bennicke in the spring of 2019. Both specimens have been declared Danekræ (a rare or extremely well-preserved fossil found in Denmark with unique scientific value) with Danekræ numbers DK-740 and DK-1049, respectively, and are now housed

in the collections of the Natural History Museum of Denmark (NHMD-188119 and NHMD-633422, respectively).

Geological setting

The Upper Cretaceous (Maastrichtian) chalk in Denmark is most prominently exposed in the coastal cliffs of Stevns Klint (Stevns peninsula) and Møns Klint (island of Møn, eastern Denmark), and to a lesser degree at inland quarries in the northern part of Jylland (Fig. 1A). The Maastrichtian chalk of Denmark is assigned to the upper portion of the Boesdal Member of the Campanian–Maastrichtian Mandehoved Formation and to the overlying Møns Klint Formation, which is subdivided into four members (Fig. 1B). The lowermost of these is the Hvidskud Member, which stratigraphically spans the lower to middle upper Maastrichtian. This particular unit is exposed in the glacial thrust sheets that form the coastal cliffs at Møns Klint and has also been recognised in the borehole cores Stevns-1 and Stevns-2 (Surlyk *et al.* 2013). The Hvidskud Member is overlain by the Rørdal Member, which is exposed at Rørdal quarry (Ålborg, northern Jylland) and has also been recorded in cores Stevns-1 and Stevns-2, Kalslunde-1 and in boreholes to the south and west of Copenhagen (Surlyk *et al.* 2013). Topping

the Rørdal Member is the Sigerslev Member, which is prominently exposed along the coastal cliffs of Stevns Klint and in boreholes in eastern Sjælland. There are also outcrops of this unit in small quarries south of Ålborg in northern Jylland. The Sigerslev Member is topped by a thick nodular flint band and two incipient hardgrounds, which, in turn, are overlain by a few metres of mounded bryozoan-rich chalk of the uppermost Maastrichtian Højerup Member (Fig. 1). The age of the Højerup Member is difficult to determine precisely because its basal level predates the terminal cooling event at ~200,000 years prior to the Cretaceous/Palaeogene boundary. The base of the member is represented by an incipient hardground, which reflects a hiatus of unknown duration. Due to the complex stratigraphy of Stevns Klint, the top of the Højerup Member is either an erosive surface or is overlain by the Fiskeler Member of the lower Danian Rødvig Formation (Surlyk *et al.* 2006). Based on the average sedimentation rate during the Late Maastrichtian, the Højerup Member must represent a time span of about 50,000 to 60,000 years (Thibault *et al.* 2016; Thibault & Husson 2016). The Cretaceous/Palaeogene (K/Pg) boundary is exposed in the upper part of the cliff where the basal Fiskeler and *Cerithium* Limestone Members of the Rødvig Formation occur in small depressions topped by an erosional hardground and overlain by lower Danian bryozoan limestone mounds of the Stevns Klint Formation (Surlyk *et al.*

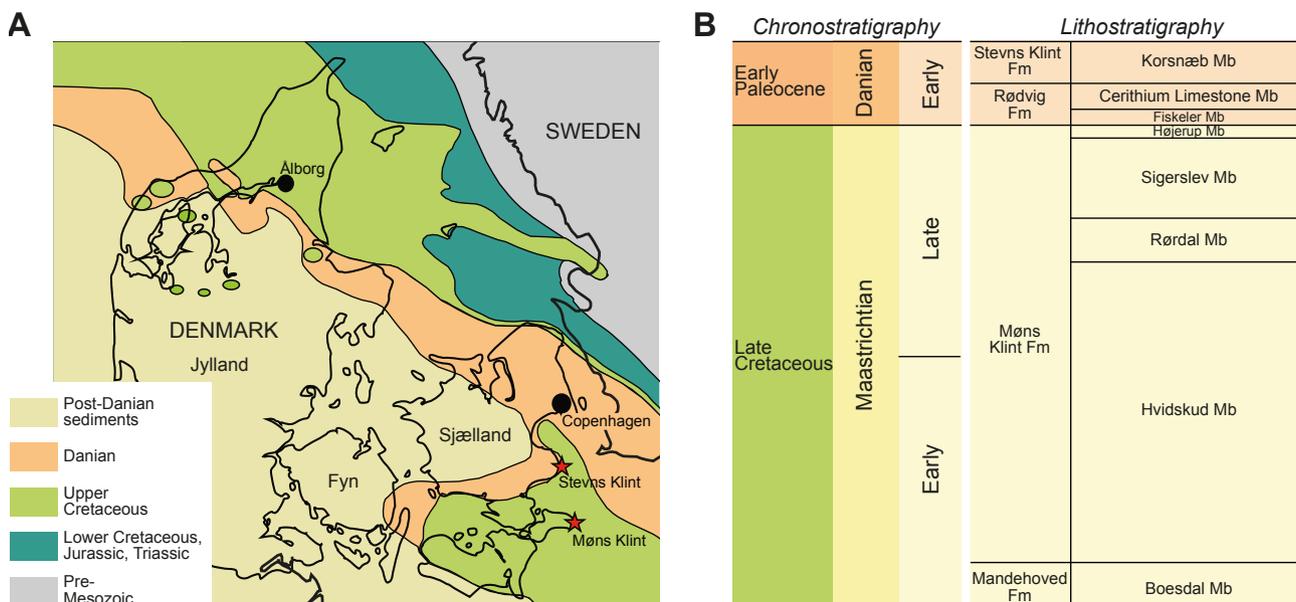


Fig. 1. A: Pre-Quaternary map of Denmark, modified from Thomsen (1995). The mosasaur tooth crowns recorded herein originate from the cliffs at Møns Klint and the UNESCO World Heritage Site of Stevns Klint. **B:** Schematic representation of the Maastrichtian–lower Danian stratigraphy of Denmark, modified from Lauridsen *et al.* (2012) and Surlyk *et al.* (2013). Specimen NHMD 633422 stems from either the Sigerslev or Højerup Member (Møns Klint Formation), while NHMD 188119 is from the Hvidskud Member (Møns Klint Formation).

2006, 2013). The strata at Møns Klint are heavily disturbed by glacial tectonics; they are assigned to the Hvidskud Member (Møns Klint Formation) in their entirety.

Description

Specimen NHMD 188119 (Fig. 2A–D) is a medium-sized tooth crown; as preserved, total crown height is 36 mm. The base measures 25 mm anteroposteriorly and 18 mm labiolingually. There are no conspicuous prisms or fluting on the labial and lingual enamel surfaces. The enamel surface is macroscopically smooth and shows a weak texturing from a microscopic perspective. At about one-third of crown height, posterior recurvature commences, with a near-straight carinal section underneath. The base of the crown is slightly swollen over the root (root not preserved) and elliptical in cross section. Both carinae carry serrations of about 0.2×0.2 mm. The absence of prisms (which are characteristic of *Mosasaurus*), the macroscopically smooth enamel surface, the inconspicuous, yet characteristic inflexion in the posterior carina at about one-third of crown height ('pinched' condition; Bardet *et al.* 2013), the aspect ratio, the serration-carrying carinae and the slightly swollen base all favour assignment of NHMD 188119 to *Prognathodon* (compare Dortangs *et al.* 2002, Bardet *et al.* 2005, 2013; Schulp *et al.* 2008; Grigoriev 2013). On a final note, both *Eremiasaurus* and *Gnathomortis* can be excluded from consideration here, too. In comparison with *Eremiasaurus* (LeBlanc *et al.* 2012), the aspect ratio of NHMD 188119 only leaves anterior teeth of *Eremiasaurus* for consideration, but these lack the posterior curvature seen in the Danish material. The teeth of *Gnathomortis* (Lively 2020) (formerly known as *Prognathodon stadmani*) are wider labiolingually compared to NHMD 188119, the curvature of the posterior carina lacks the characteristic 'pinch' (Bardet *et al.* 2013) with a smooth, continuous curvature instead (pers. obs. AS), and the inflation of the basal tooth crowns is missing (Lively 2020).

Similar considerations apply to the much smaller NHMD 633422 (Fig. 2E–H). Crown height as preserved is 10.5 mm, but only the topmost part is preserved. Anteroposterior dimensions are 7.5 mm as preserved, but a part of the enamel is missing on the lower part on the anterior edge. Labiolingually, the thickest part preserved is 6.1 mm. Enamel thickness increases markedly towards the apex. The tooth has carinae both anteriorly and posteriorly. Posterior recurvature of the preserved section of the crown is similar to NHMD 188119. The sediment adhering to the tooth crown contains abundant bryozoan fragments.

Discussion

Vertebrate palaeobiodiversity

Currently, the Maastrichtian vertebrate fauna of Denmark comprises 31 species of neoselachians, all based on isolated teeth (Adolfsson & Ward 2014), with additional evidence in the form of coprolites (Milàn *et al.* 2015). Teleosteans are represented by at least eight taxa, documented by skeletal remains and otoliths (Bonde *et al.* 2008; Bonde & Leal 2017; Schwarzshans & Milàn 2017). Remains of marine reptiles are comparatively rare; to date, isolated tooth crowns of thoracosaurine crocodylians (Gravesen & Jakobsen 2012), and a single carapace fragment of a chelonioid turtle (Karl & Lindow 2009) have been recorded. Mosasaurs are hitherto known from finds of mainly isolated tooth crowns and isolated elements of the appendicular skeleton of *Mosasaurus hoffmanni*, *Plioplatecarpus* sp. (Lindgren & Jagt 2005) and the durophagous mosasaur *Carinodens minalmamar* Schulp *et al.*, 2010 (Milàn *et al.* 2018). Recognition of *Prognathodon* adds the fourth mosasaur genus to the Danish faunal assemblage and increases the similarity to the mosasaur faunas of the Maastrichtian type area in the south-east Netherlands and north-east Belgium, where representatives of these four genera are known. Based on the dimensions of the two tooth crowns, and the recurvature suggesting a position somewhat posteriorly in the dental ramus, a body length of close to 7.5 and 4 m, respectively, can be extrapolated (Fig. 2I) (compare Giltaij *et al.* 2021).

Stratigraphical age of the specimens

The Danish mosasaur finds are important as they represent some of the stratigraphically youngest mosasaur records worldwide, with both *Mosasaurus* and *Plioplatecarpus* being found within the highest Maastrichtian levels (Lindgren & Jagt 2005). A single find of the durophagous mosasaur *Carinodens* has been assigned to the Højerup Member (Møns Klint Formation), placing it within the latest 50,000 years of the Cretaceous (Milàn *et al.* 2018). The larger tooth crown described here (NHMD 188119) was found loose at Møns Klint, where the Lower–Upper Maastrichtian Hvidskud Member (Møns Klint Formation) is exposed. The exact position within the member is not possible to determine. The small specimen (NHMD 633422) was found loose on the beach in a small rockfall below Mandehoved (Stevns Klint), where the top of the Sigerslev Member and the entire Højerup Member (both Stevns Klint Formation) are exposed. At Mandehoved, the Højerup Member is approximately 1.5 m thick (Surlyk *et al.* 2006). At the locality which yielded NHMD 633422, the Højerup Member is the main cliff-forming unit, together with the overlying Danian Stevns Klint Formation, but as the tooth crown

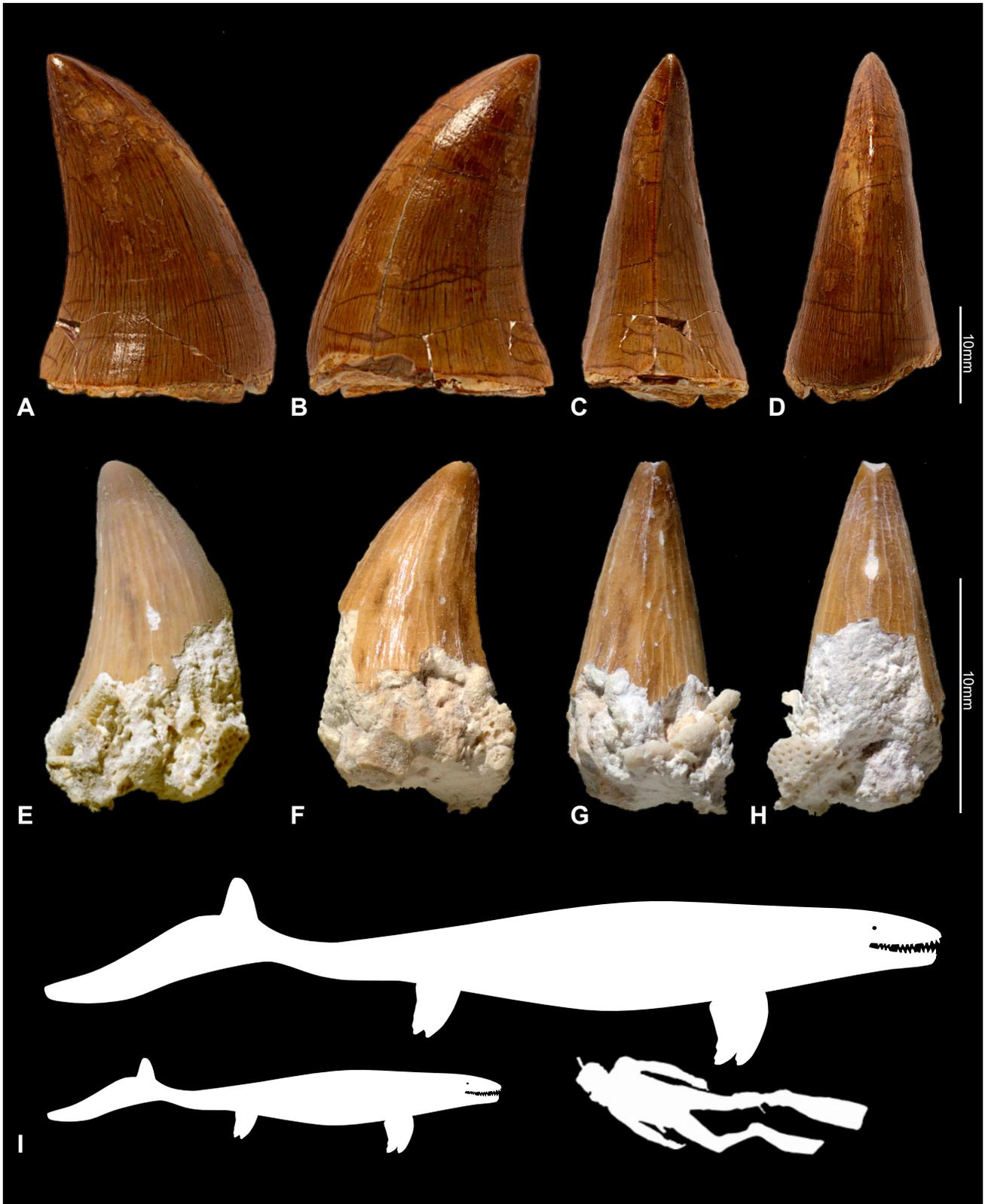


Fig. 2. *Prognathodon* sp.; **A–D:** NHMD 188119, from Møns Klint, in labial, lingual, posterior and anterior views, respectively. **E–H:** NHMD 633422, from Stevns Klint in labial, lingual, posterior and anterior views, respectively. Scale bars equal 10 mm. Note the abundant bryozoan fragments in the sediment below the crown. Photos: Sten Lennart Jakobsen. **I:** Silhouettes of two *Prognathodon* scaled to the approximate overall body size on the basis of the two isolated tooth crowns (Giltaij *et al.* 2021); human diver for scale. Mosasaur silhouettes follow tail flukes as documented by Lindgren *et al.* (2013).

was not found *in situ*, it could also have originated from the uppermost section of the Sigerslev Member. The presence of abundant bryozoan fragments in the sediment below the tooth crown suggests that NHMD 633422 originates from the Højerup Member and thus represents one of the youngest records of *Prognathodon* worldwide.

Conclusions

The presence of *Prognathodon* in the Danish chalk brings the diversity of latest Cretaceous (Maastrichtian) mosasaurs to four genera, which is in accordance with the mosasaur diversity known from the type Maastrichtian. Stratigraphically, the Danish mosasaurs rank amongst the youngest finds, showing a high mosasaur diversity right up to the K/Pg boundary.

Acknowledgements

We are grateful to amateur palaeontologists Mette Hofstedt and Peter Bennicke, who collected the specimens. Bent Lindow (Natural History Museum of Denmark, Copenhagen) kindly gave us access to study the specimens. Sten Lennart Jakobsen (Geomuseum Faxe) provided photographs of the specimens. We appreciate the helpful feedback and suggestions provided by reviewers Eric Mulder and Michael Polcyn.

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