

Tylosaurine mosasaurs (Squamata) from the Late Cretaceous of northern Germany

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Abstract

Two genera of tylosaurine mosasaurs, *Tylosaurus* and *Hainosaurus*, are recorded for the first time from Germany. *Tylosaurus* sp. is represented by two isolated tooth crowns, originally described as *Mosasaurus? alseni* (here considered a *nomen dubium*) from the latest Santonian–Early Campanian, which are very similar to *T. ivoensis* and *T. gaudryi*. The material of *Hainosaurus* sp. comprises a maxillary with associated postorbitofrontal, two pterygoid teeth and several indeterminate cranial fragments. The specimen from the Late Campanian is slightly less derived than *H. bernardi* from the Maastrichtian in retaining labiolingually less compressed anterior maxillary teeth and unserrated pterygoid teeth with only very weak carinae. Despite only minor skeletal differences, the genus *Hainosaurus* is considered to be distinct from *Tylosaurus* because of its significant modification of the dental apparatus compared to the plesiomorphic condition in the latter. This dental morphology suggests a phylogenetic trend from a generalised-piercing marginal dentition in *Tylosaurus* towards the increasingly labiolingually compressed, symmetrical, strongly bicarinate cutting marginal teeth in *Hainosaurus* spp. from the Early through Late Campanian and Maastrichtian. A similar trend is also present in pterygoid teeth with very indistinct unserrated carinae in the Campanian *Hainosaurus* sp. towards serrated ones in the Maastrichtian *H. bernardi*. A short review indicates the presence of *Hainosaurus* in northern, central and western Europe (Sweden to Spain) since the Early Campanian, and the occurrence of *Tylosaurus* spp. in the same area until the Late Campanian. *Hainosaurus* persisted until the end of the Maastrichtian; outside Europe it may have been present in the Late Campanian of the USA and the Maastrichtian of the Democratic Republic of Congo. Judging from a simple, uni- to bicarinate, stoutly conical tooth morphology in aigialosaurs and very basal mosasaurs as well as phylogenetic patterns, the development of blade-like cutting tooth crowns appears to have been convergent in several clades of large-bodied Campanian–Maastrichtian mosasauroids. These include both mosasauroines (*‘Leiodon’ mosasauroides*, *Prognathodon? sectorius*, *Prognathodon? kianda*, *Eremiasaurus heterodontus*) and tylosaurines (*Hainosaurus* spp.).

Keywords: Mosasauridae, Tylosaurinae, *Tylosaurus*, *Hainosaurus*, Campanian, evolution

Introduction

Mosasaurs (Mosasauridae Gervais, 1853) were large, pelagic, predatory squamates with a global distribution during the Late Cretaceous. Among these some of the largest known individuals belong to species of the subfamily Tylosaurinae Williston, 1895, especially the genus *Hainosaurus* Dollo, 1885a, which attained body lengths of >15 m (Lingham-Soliar, 1992). While this subfamily is particularly well represented in the early Late Cretaceous of North America (e.g. Russell, 1967; Everhart, 2005) and reached

a near-cosmopolitan distribution during Santonian–Campanian times (e.g. Caldwell et al., 2008), its record from Europe is comparatively rare and much more poorly known. Apart from *Hainosaurus bernardi* Dollo, 1885a, of which a near-complete skeleton and several crania from the Early Maastrichtian of southern Belgium are known (Dollo, 1885a,b, 1888; Lingham-Soliar, 1992), only scattered finds – mostly of tooth crowns – are widely distributed from the Santonian/Early Campanian through the Late Maastrichtian for localities in southern Sweden (Lindgren, 2005), Belgium (Jagt, 2005), Poland (Jagt et al., 2005),

England (Jagt et al., 2005), France (Bardet, 1990, 2012) and Spain (Bardet et al., 1997, 2006).

These findings are supplemented by so far misidentified material from the Campanian of northern Germany (Fig. 1). Two tooth crowns, described by Stolley (1892) from the latest Santonian or Early Campanian of Schleswig-Holstein as *Mosasaurus? alseni*, are restudied and found to share great similarities with *Tylosaurus ivoensis* (Persson, 1963). They are re-identified as *Tylosaurus* sp. and represent the first record of this genus from Germany.

Another tylosaurine is represented by a large maxillary with teeth and associated fragments. The specimen was collected in April 1908 from sediments of Campanian age near Haldem (now Stenwede-Haldem), eastern North-Rhine Westphalia. It was firstly described by Pompeckj (1910) and is housed today in the collections of the Geoscience Centre, University of Göttingen (GZG), Lower Saxony. This material constitutes the most comprehensive cranial material known from any mosasaur in Germany (see Sachs et al., 2014, for a historical review, also, for example, Sachs, 2000, 2006; Diedrich & Mulder, 2004; Caldwell & Diedrich, 2005; Hornung & Reich, 2006; Jagt et al., 2006 for more recent records). This particular specimen sparked a detailed discussion on mosasaur palaeobiology and phylogeny by Pompeckj (1910). For a review of its historical significance reference is made to Sachs et al. (2014). Previously, this material was identified as belonging to the genus *Mosasaurus* Conybeare in Parkinson, 1822 or to *Liodon* Agassiz, 1846 (= *Leiodon* Owen, 1841 in Owen 1840–45, praeocc.). It is shown below that this specimen can be referred to the genus *Hainosaurus*, thus constituting the first record of this genus from Germany and the most comprehensive material from Europe outside the type locality of *H. bernardi* in southern Belgium.

Recently, the validity and content of the genus *Hainosaurus* have been challenged, and it has been proposed that it should be synonymised with *Tylosaurus* Marsh, 1872 (e.g. see Bullard &

Caldwell, 2010). However, for the reasons outlined below, we prefer to retain these genera as distinct.

Earlier, Jagt et al. (2006) indicated that a now lost tooth from the Early Maastrichtian of Blandow (Isle of Rügen, Western Pomerania, northeastern Germany, see Sachs et al. (2014) for a more detailed account) in the former Friedrich von Hagenow collection might be referred to *Hainosaurus* 'sp. 2' (*sensu* Jagt et al., 2005). This view was based on the partial reproduction of an unpublished figure of this tooth produced by von Hagenow (Reich & Frenzel, 2002: pl. 2, fig. 4). However, this figure by von Hagenow in its entirety, here reproduced in Fig. 2, reveals the markedly asymmetric D-shaped cross-section of the lower crown (and apparently of the crown-base) with a strongly convex lingual face and a near-flat labial face. Although the pattern of facets is similar to that of *Hainosaurus* 'sp. 2' there is no indication of any basal tertiary striations that are typical of tylosaurine teeth. However, the teeth of derived species of *Mosasaurus* show variation in the intensity of faceting, also dependant on the ontogenetic stage (Mulder et al., 2004), and typically also a D-shaped cross-section, especially in rostral marginal teeth (e.g. Lingham-Soliar, 1995; Kuypers et al., 1998; pers. obs.). We therefore here refer to this specimen as *Mosasaurus* cf. *hoffmanni* Mantell, 1829, which closely matches the original identification by von Hagenow.



Fig. 1. Map of northern Germany with mosasaur-bearing localities (green) and repositories (grey) mentioned in the text.



Fig. 2. Unpublished drawing by Friedrich von Hagenow from the 1830s/1840s depicting a mosasaur tooth from the Early Maastrichtian chalk facies of Blandow, Isle of Rügen. Jagt et al. (2006) noted that this specimen (now lost) could possibly represent *Hainosaurus* 'sp. 2', but it is considered here to be assignable to *Mosasaurus* cf. *hoffmanni* Mantell, 1829 on account of its strongly asymmetric cross-section (lower figure). This sketch represents the first record of a mosasaur from Germany (see Sachs et al., 2014).

Terminology

The analysis of dental morphology for the identification of mosasaur species has gained increasing importance in recent years (e.g. see Lindgren & Siverson, 2002, 2004; Lindgren, 2005, for extensive application), although it has also encountered scepticism (e.g. Caldwell & Diedrich, 2005). Features of the tooth enamel have been described on the basis of varying terms, although their use is not always consistent, sometimes semantically incorrect, or the terminologies adopted are not always unambiguously defined. Here we propose the following definitions for the three-dimensional, apicobasal, linear enamel features which serve to describe the material here considered (Fig. 3).

Circular cross-sections and striations

Striae (singular *stria*) are thin, apicobasally striking, linear enamel ridges covering the surface of the tooth crown. On the basis of size and strength, three orders, i.e. primary, secondary and tertiary striae, can commonly be distinguished (Fig. 3a). *Secondary striae* are less prominent than *primary striae* and may be intercalated between the former (Fig. 3a/1) or branch off from these (Figs 3a/2 and 3a/4–5). *Tertiary striae* are much fainter and mostly much denser than primary and secondary ones. Dense tertiary striae are a common feature in teeth of tylosaurines (Lindgren & Siverson, 2002). In cases where secondary or even primary striae are missing, tertiary striae may nevertheless be present and should be classified as such in order to denote clearly the size difference to the primary striae (Fig. 3a/3). Still finer, short, irregular, not necessarily continuous enamel ridges, often with a patchy distribution across the tooth crown, are *wrinkles*. Tooth crowns with a continuously

curved surface, simply covered in striae, are *striated* (Fig. 3b), spaces between the striae being referred to as *inters-trial areas*. Striae may *bifurcate* (Fig. 3a/2), *converge* adaptically (Fig. 3a/4) or *anastomose* (Fig. 3a/5). Wrinkles commonly anastomose.

Polygonal cross-sections and concave linear features

In many cases, mosasaur teeth are characterised by polygonal horizontal cross-sections. The sides of these polygons may be flat, concave or convex, and the edges separating them may be marked by primary striae. These features have been described by various terms in the past, such as prisms, facets and flutes. Basically, a tooth with a polygonal cross-section can be described as *prismatic* (Figs 3c–g). The polygon faces can be characterised as *prism faces*, which may be *flat* (Fig. 3c) or *convex* (Fig. 3d). The term ‘prism’ for these faces (e.g. see Lingham-Soliar, 1995) is incorrect semantically because, in geometrical terms, a prism is a three-dimensional body, not a face of this body. When bordered by primary striae the faces are *facets* (syn. flutes). Facets may be superimposed on wider prism faces (Fig. 3e), which is an important reason for the terminological discrimination between these two features. Facets may be *concave* (Fig. 3f) or *flat-bottomed* (Fig. 3g). When the delimiting striae are densely spaced, facets and simple striation may be difficult to discern.

Dental functional morphology and trophic guilds

Massare (1987) defined seven trophic guilds for marine reptiles on the basis of a qualitative placement of tooth morphologies in a ternary system spreading between (1) slender, pointed, piercing teeth, (2) blunt, robust teeth, increasingly suitable for

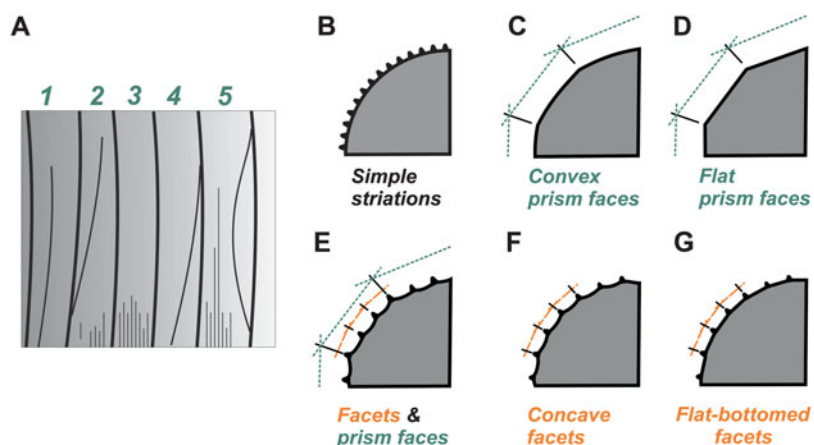


Fig. 3. Terminology of enamel structures and tooth crown geometries adopted in this paper. A, Striation hierarchy and patterns (on a schematic enamel surface): 1, primary and secondary striae; 2, primary stria bifurcating adaptically into secondary stria, tertiary striae at the base; 3, primary and tertiary striae; 4, primary stria converging adaptically with secondary stria; 5, primary stria anastomosing into secondary stria, tertiary striae at the base. B–G, Polygonal cross-sections and concave linear features (schematic cross sectional quadrant of tooth crown): B, simple striations; C, convex prism faces; D, flat prism faces; E, concave facets superimposed to prism faces; F, concave facets; G, flat-bottomed facets.

crushing, and (3) sharp, robust cutting teeth. While widely adopted also for mosasaurs (Massare, 1987; Schulp et al., 2006; Ross, 2009), this scheme has some drawbacks with regard to strongly labiolingually compressed tooth crown morphologies. Inclusion of all degrees of tooth crown compression in bicarinate, ‘robust’ teeth in the ‘cutting’ guild will result in poor functional resolution for many mosasaur taxa (e.g. Schulp et al., 2006: fig. 8). Thus, we here propose to modify the scheme by introduction of an eighth guild, ‘cut II’, in which the teeth are characterised by strong labiolingual compression (Fig. 4A). ‘Cut’ (*sensu* Massare, 1987) is here renamed to ‘cut I’ and typical examples, such as marginal teeth of *Mosasaurus* spp., are shifted towards the ‘crunch’ side on the ‘crunching–cutting’ axis for the labiolingual expansion. In this model, the

‘piercing–cutting’ axis is defined mostly by a mesiodistal expansion and acquisition of serrated carinae from ‘pierce I’ towards ‘cut II’.

Systematic palaeontology

Institutional abbreviations

CAUK – Institut für Geowissenschaften der Christian-Albrechts-Universität, Kiel, Germany; GZG.V. – Vertebrate collection, Geowissenschaftliches Zentrum der Universität Göttingen, Germany; IRSNB – Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MNHN – Muséum Nationale d’Histoire Naturelle, Paris, France.

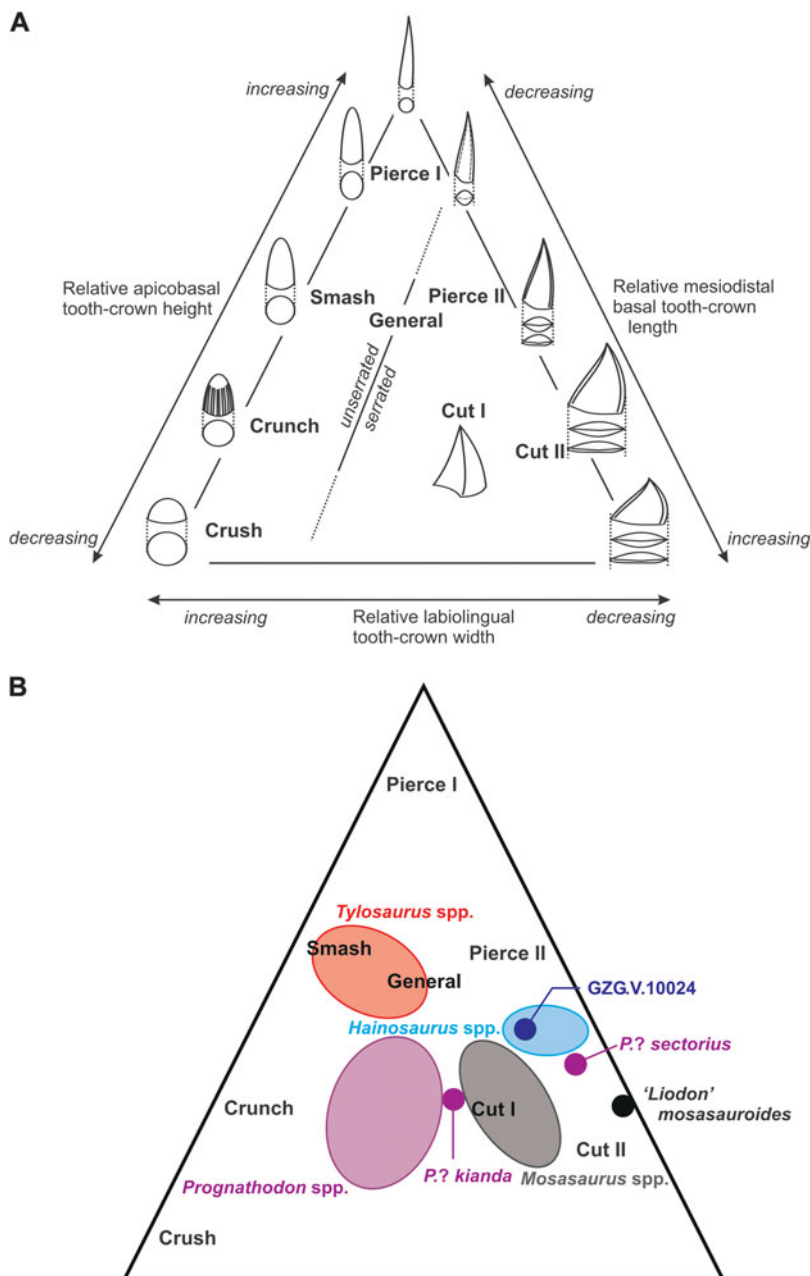


Fig. 4. Classification of trophic guilds in mosasaurs, based on Massare (1987) and Schulp et al. (2006), modified to represent morphological trends in tooth crown shape. The ternary system is defined by height/length and height/width ratios of the tooth crowns. This results in the proposal of a new ‘cut II’ guild for laterally strongly compressed, blade-shaped teeth, while ‘cut I’ (= ‘cut’ in Massare, 1987) retains a labiolingually expanded crown with cutting carinae. A, Modified ternary diagram with qualitative definition of guilds and typical representatives of shapes, based on Schulp et al. (2006). The occlusal view of the teeth on the right side is shown to include symmetrical and asymmetrical cross-sections. B, approximate position attained by various mosasaur taxa discussed in the text within the modified Massare classification (data from Gaudry, 1892; Massare, 1987; Schulp et al., 2006; pers. obs.). Note the shift in trophic guild assignment from ‘smash/general’ in *Tylosaurus* spp. towards ‘pierce II/cut II’ in *Hainosaurus* spp.. P.?: *Prognathodon*?

Reptilia Laurenti, 1768
 Squamata Oppel, 1811
 Platynota Camp, 1923
 Pythonomorpha Cope, 1869
 (emend. Lee & Caldwell, 2000)
 Family Mosasauridae Gervais, 1853
 Subfamily Tylosaurinae Williston, 1895
 Genus *Tylosaurus* Marsh, 1872
***Tylosaurus* sp.**
 (Fig. 5)

- v 1892 *Mosasaurus? alseni* sp. n. – Stolley: p. 223, pl. VII, fig. 1. (*nomen dubium*)
- v 1929 *Mosas. (?) alseni* St. – Klähn: p. 59.
- v 2014 *Mosasaurus? alseni* Stolley, 1892 – Sachs et al. doi: 10.1017/njg.2014.16, fig. 5B.

Material

Syntypes of *Mosasaurus? alseni* Stolley, 1892: CAUK G-K-588, a marginal tooth crown; CAUK without number, marginal tooth crown. From the 'Quadratenkreide' (Stolley, 1892), which in current terminology would correspond to the Lägerdorf Formation, latest Santonian to latest Early Campanian (*Goniot euthis granulata* to *G. quadrata gracilis/Belemnitella mucronata* belemnite zones; Niebuhr, 2010) of the Alsen chalk-pit near Lägerdorf, Schleswig-Holstein, northern Germany.

Marginal tooth crowns

CAUK G-K-588 (Fig. 5A–F) is a shed, gently postero-lingually recurved tooth crown, with an ovate cross-section, highly asymmetrically divided into a gently convex labial and a deeply convex (U-shaped) lingual side by mesial and distal carinae. The mesial carina extends from the apex to the base of the tooth crown and bears minute serrations. The distal carina is distinct only in the apical third of the crown, curves labially and is adorned with much coarser serrations than the mesial carina. In the basal two-thirds of the tooth crown it effaces, becoming a faint, unserrated stria. Due to the asymmetry of the cross-section, the labial face corresponds only to about one-third of the basal circumference of the crown. In the basal third of this face about 8–10 narrow concave facets are present, separated by primary striae. Apically this number is reduced to four or five concave facets due to the fact that striae efface in between and the apical third of the labial face is smooth. The lingual face exhibits c. 17 narrow concave facets with the separating primary striae, occasionally bifurcating into, or converging with, short secondary striae along their length. Striation and faceting efface apically and the apical third of the tooth crown is nearly smooth, except for faint tertiary striae. Those are numerous and often anastomose near the base but decrease strongly in density apically.

The second, unnumbered CAUK tooth crown (Fig. 5G–K) is slightly less asymmetric in cross-section than CAUK G-K-588,

although the lingual face still is much more convex than the labial one, occupying about 60% of the basal circumference. The tooth crown is recurved lingually, and lingual and labial faces are separated by carinae. Both carinae are finely serrated and the mesial carina extends along the whole apicobasal height of the crown, while the distal one effaces at mid-height from the apex into a faint, unserrated stria. The basal half of the labial face bears six to eight shallow and narrow facets, separated by primary striae, effacing towards a nearly smooth apex. Additionally, the labial face is very gently prismatic, with about three prism faces onto which the narrow facets are superimposed. The lingual face is covered in its basal half by 13–15 shallow facets, smoothing towards the apex, and by numerous partially anastomosing tertiary striae, which decrease in density but persist to the apex. A part of the labial face is covered by a patch of glue.

Comparisons and remarks

Both tooth crowns show characters which have been considered diagnostic for the genus *Tylosaurus* (see Lindgren & Siverson, 2002), such as the stout morphology, weak recurvature, ovate cross-section with convex lingual and labial faces, occupying highly unequal sectors of the circumference, presence of relatively shallow, yet numerous, facets and distinct, fine tertiary striations, especially near the crown base. In fact, morphologically, they are nearly indistinguishable from the marginal teeth of *Tylosaurus ivoensis* (Persson, 1963) and *T. gaudryi* (Thevenin, 1896) from the late Early Campanian of Sweden and the Late Santonian–Early Campanian of France, respectively (Lindgren & Siverson, 2002). The only differences appear to be the coarser serrations on the distal carina of CAUK G-K-588, the persistence of tertiary striae apically to mid-height and the weak prismatic appearance of the labial face in the second, unnumbered CAUK specimen (although the latter seems to be present also in some teeth of *T. ivoensis*, compare Lindgren & Siverson, 2002: fig. 7/1a). Other differences, also between the present tooth crowns, can either be ascribed to their respective position in the jaws or are within the range of morphology exhibited by the much larger Swedish sample (Lindgren & Siverson, 2002).

The posterolingual recurvature and discontinuous distal carina on CAUK G-K-588 suggests a rostral position in the dentary or premaxillary. The second CAUK tooth apparently had a more posterior position.

Stolley (1892) described both tooth crowns as syntypes of a new species, *Mosasaurus? alseni*. He provided a detailed and comprehensive description, although he treated both specimens as if they were identical. Additionally, he supplied an illustration of CAUK G-K-588 (Stolley, 1892: pl. VII, fig. 1). In his discussion he compared the teeth mostly to those of *Mosasaurus* and '*Leiodon*', noting the circular cross-section and the striated and faceted surface as main distinguishing features, respectively. He also stated that the teeth are different from 'Zähnen amerikanischer Pythonomorphen' ('teeth of American pythonomorphs')

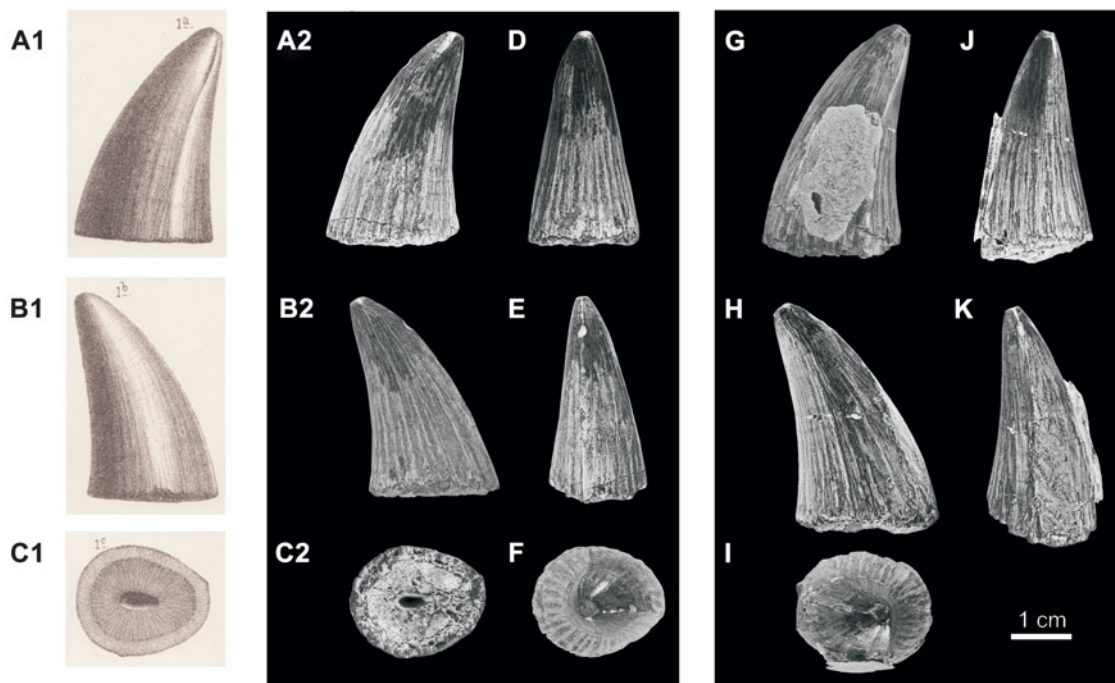


Fig. 5. *Tylosaurus* sp. (= *Mosasaurus? alseni* Stolley, 1892), lateral tooth crowns, Lägerdorf Formation, latest Santonian to Early Campanian of Lägerdorf, Schleswig-Holstein, northern Germany. A–F, CAUK G-K-588 in (A) labial, (B) lingual, (C) basal, (D) distal, (E) mesial. (F) occlusal aspects; A1–C1: original figure of the specimen by Stolley (1892: pl. VII, fig. 1a–c) for comparison. G–K, CAUK unnumbered specimen in (G) labial, (H) lingual, (I) occlusal, (J) distal, (K) mesial aspect.

as well as from those of the ‘neuerdings von Dollo beschriebenen Mosasauriden’ (‘mosasaurids recently described by Dollo’), referring to Dollo (1882, 1885a,b, 1889, 1890), although he did not provide a rationale for this claim. On the other hand, he did find similarities to an unnamed, fragmentary tooth from the Chalk Group of Norwich, England, figured and described by Owen (1850: 385, pl. XXXVII, fig. 14). He concluded that the specimens represent a new species, hesitatingly referring it to the genus *Mosasaurus*, yet he failed to give an explicit diagnosis of this new form.

Despite this, Stolley’s nomenclatural act is fully valid under the regulations of the ICZN (1999). In fact, it might be argued that – in view of the large overlap in dental morphology – *Mosasaurus? alseni* Stolley, 1892 constitutes a senior synonym of *Mosasaurus gaudryi* Thevenin, 1896 (now *Tylosaurus gaudryi*) and of *Mosasaurus hoffmanni ivoensis* Persson, 1963 (now *Tylosaurus ivoensis*), taking precedence. However, the taxonomic resolution of dental features below the genus level in *Tylosaurus* is not straightforward and should be only based on large samples. For a striking example, Lindgren & Siverson (2002) reported that the lateral dentition of *T. ivoensis* and *T. gaudryi* overlap morphologically, although their pterygoid teeth are clearly distinct. Therefore, with the scant material at hand, we cannot determine safely whether ‘*M.? alseni*’ was a taxon different from *T. ivoensis* or *T. gaudryi*. In the light of the small database for ‘*M.? alseni*’, it is considered to be a *nomen dubium*, and the syntypes are referred herein to *Tylosaurus* sp., awaiting the discovery of further specimens.

Genus *Hainosaurus* Dollo, 1885a

***Hainosaurus* sp.**

(Figs. 6–9)

- v 1910 *Mosasaurus* cf. *mosasauroides* (Gaudry) – Pompeckj: 126, pl. 4.
- v (partim) 1993 *Leiodon mosasauroides* Gaudry, 1892 – Lingham-Soliar: 453.
- v 2000 *Leiodon* cf. *mosasauroides* Gaudry, 1892 – Sachs: 37, fig. 2.
- ? 2003 *Plioplatecarpinae* sp. A – Machalski et al.: 405, fig. 9B.
- v 2005 Oberkiefer (*Leiodon*) ... – Reich et al.: fig. 12c.
- ? 2005 *Hainosaurus* sp. 1 – Jagt et al.: 303, 304, fig. 1.
- ? 2005 *Hainosaurus* sp. – Lindgren: 1159, fig. 2.
- v 2006 *Hainosaurus* sp. – Hornung & Reich: 40.
- v 2014 Oberkiefer (*Hainosaurus*) – Frenzel et al.: fig. 5c.
- v 2014 Cranial remains of a mosasaur – Sachs et al. doi: 10.1017/njg.2014.16, fig. 6B.

Material

GZG.V.10024 (Pompeckj, 1910; Sachs, 2000; Figs 6–9), a fragmentary right maxillary with associated fragmentary left post-orbitofrontal, indeterminate cranial fragments, two pterygoid

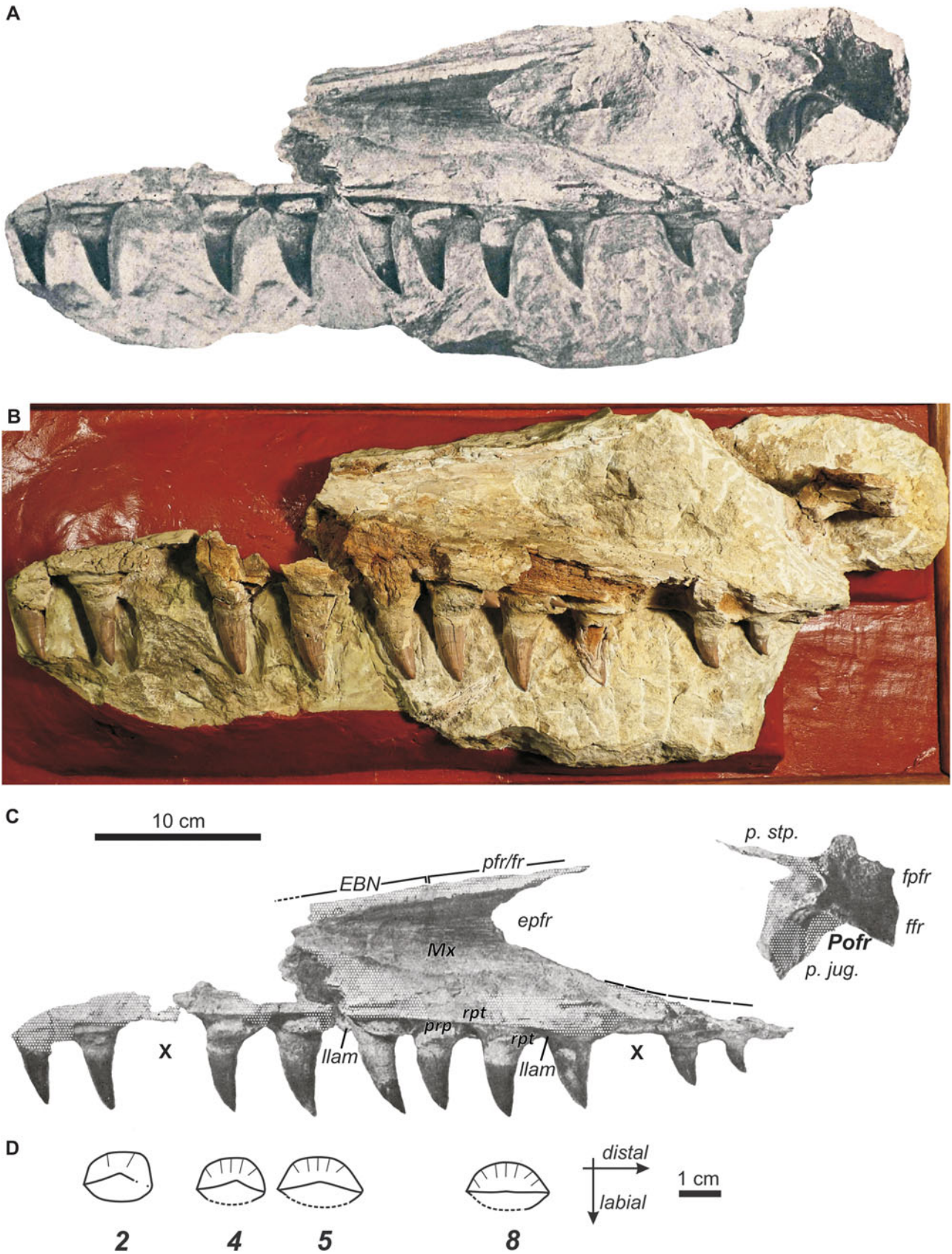


Fig. 6. *Hainosaurus* sp., GZG.V.10024, associated cranial elements, Haldem Member, Stemwede Formation, Late Campanian of Stemwede-Haldem, North-Rhine Westphalia, northwestern Germany: A, as figured by Pompeckj (1910: pl. IV); B, as presently preserved; C, interpretative sketch based on the figure by Pompeckj (1910); D, schematic occlusal aspect of teeth (tooth positions 2, 4, 5 and 8). EBN, Position of external bony naris; epfr, caudal embayment for the rostral wing

teeth, plus a fragmentary cervical vertebra (lost) and rib fragments (lost) of a single individual from the latest Campanian (*Bostrychoceras polyplacum* ammonite zone, Pompeckj, 1910), in current terminology the Haldem Member, Stenwede Formation (Dölling et al., 2006, 2010) at the Stenweder Berg, vicinity of Stenwede-Haldem, near Lemförde, northeastern North-Rhine Westphalia, northwestern Germany.

The same locality has yielded some ribs and postcranial fragments of an indeterminate mosasaur, now housed in the collections of the Aquazoo Museum, Düsseldorf (Sachs, 2000).

The specimen is mounted on a block of matrix and can almost exclusively be observed from the medial/lingual side (Fig. 6). However, some of the teeth are more or less freed from the surrounding matrix and allow at least a partial assessment of their labial side and cross-section. During conservation work a few years ago, the postorbitofrontal was in part removed from the matrix, but was subsequently refitted to the mount. The pterygoid tooth and a few small indeterminate bone scraps have been kept isolated. The poorly preserved cervical vertebra and rib fragments, mentioned by Pompeckj (1910: 122), are now missing from the material. Judging from Pompeckj (1910: pl. IV) the specimen has suffered from some damage since its discovery, especially in the dorsal and rostral regions of the maxillary and along the dental shelf (Fig. 6C).

Maxillary

The right maxillary (Fig. 6) is only fragmentarily preserved. Most of the rostral part is missing and the dorsal and caudal margins are damaged to some degree. The oral margin posterior to tooth position 5 is damaged now, but was originally preserved (Pompeckj, 1910). A slightly thickened, rounded dorsal margin, extending from above tooth positions 5 to 7, probably represents the lateral margin of the external naris. At the level of tooth position 7 it slightly bulges posteriorly and while now damaged and almost inconspicuous, the illustration by Pompeckj (1910) clearly shows a longitudinal groove stretching along the margin to the caudal end of the processus nasalis of the maxillary. This groove is considered to represent the contact to either the frontal or the processus nasalis of the prefrontal, depending on the configuration of the skull roof (Russell, 1967; Lingham-Soliar, 1992). The external bony naris would therefore have extended caudally to a level between tooth positions 7 and 8.

The caudal part shows a deep, rounded-triangular excavation, opening caudally and reaching to tooth position 8 rostrally. The margin of this excavation appears to be intact for most of its length and not to result from damage (contra Pompeckj, 1910).

It is nearly smooth, although showing slight serrations in places, and represents the contact with the triangular rostralateral 'wing' of the prefrontal.

As is common in mosasaurids, the tooth row is situated on a robust ventromedian shelf ('buttress' *sensu* Russell, 1967). This shelf bears a slight ventral emargination medially to the teeth (preserved above tooth position 7, 'parapet' *sensu* Russell, 1967) and also one laterally to the tooth row (Pompeckj, 1910), although the latter is almost entirely missing due to damage or is otherwise obscured. Above tooth positions 4 to 5 it shows a medial vertical sutural surface for the contact with the vomer, which passes caudally into a horizontal groove (no longer preserved) above tooth position 6. The main body of the maxillary forms an almost right angle with the tooth-bearing shelf. The oral margin of the maxillary is very gently concave. The general proportions of what is preserved from the maxillary suggest a gently tapering, low muzzle with proportionally large teeth.

Postorbitofrontal

Most of the left postorbitofrontal (Fig. 7) is preserved together with the right maxillary of GZG.V.10024, turned by about 180° in position relatively to the latter element. The postorbitofrontal was correctly identified by Pompeckj (1910), but referred to as a possible pterygoid by Sachs (2000). It consists of a subpentagonally outlined plate of bone from which a robust, mediolaterally broad, distally tapering processus jugalis projects ventrally and an elongate processus supratemporalis caudally. Most of the distal and lateral processus jugalis is broken away and its base is pierced posteromedially by a small (1.5 mm diameter) foramen. The processus supratemporalis is a thin, narrow strap of bone, extending from the dorsocaudal margin of the processus jugalis with a medial and ventral off-set relative to the lateral margin of the bone. It is incomplete caudally and longitudinally twisted by about 50°. Its lateral and medial margins are damaged or covered by matrix, respectively. The thinness of the bone suggests that it overlapped the rostral process of the squamosal for most of its length but the ventrally facing contact surface is obscured by matrix.

The dorsal surface of the postorbitofrontal is damaged and the thin substantia compacta lost, revealing a highly cancellous substantia spongiosa. The anteromedial and medial margins of the postorbitofrontal show two separate sutural faces, the rostral one of which is the best preserved. It forms a transverse, deeply excavated, locally vertically striated, horizontal notch

of the prefrontal; ffr, facet for contact with frontal; fpfr, facet for contact with prefrontal; llam, ventrolabial lamina on the maxillary; Mx, right maxillary; p. jug., processus jugalis; pfr/fr, medial contact to the prefrontal or frontal; Pofr, left postorbitofrontal; prp, medial parapet on the maxillary shelf; p. stp., processus supratemporalis; rpt, replacement teeth; X, position of missing teeth; white dotted area, damage to the specimen since 1910.

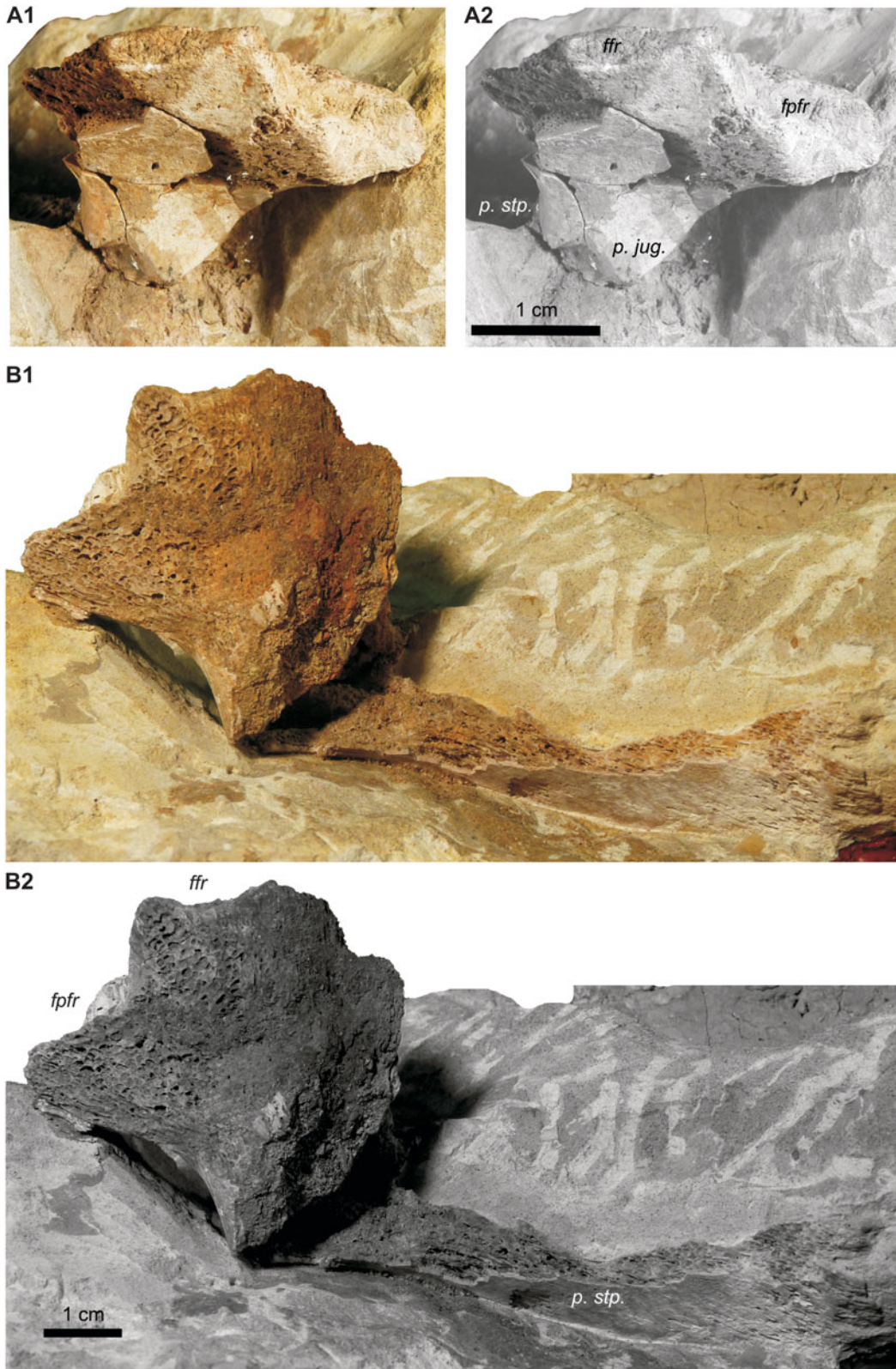


Fig. 7. *Hainosaurus* sp., GZG.V.10024, fragmentary left postorbitofrontal: A, medial aspect; B, dorsal aspect; for abbreviations see Fig. 6.

in the slightly dorsoventrally thickened rim of the bone. The second, situated at the medial margin of the postorbitofrontal, is slightly concave. The margin of the bone is not thickened. The caudomedially located contact to the parietal is damaged.

The number and configuration of the anteromedial and medial sutural faces in GZG.V.10024 show close similarities to that in *Hainosaurus bernardi* as described by Lingham-Soliar (1992: figs. 6 and 7). This implies that the rostralmost face received

the caudoventral process of the prefrontal, which met the post-orbitalfrontal caudally to exclude the frontal from the dorsolateral margin of the orbit. This interpretation is supported by the deep excavation and separation of the rostral sutural contact from the medial one. In taxa where the prefrontal and postorbitofrontal are separated by the frontal (e.g. *Clidastes* spp., compare Russell, 1967), the rostral contact of the postorbitofrontal to the frontal is smooth and tapers laterally, passing continuously into the medial contact. The medial sutural face contacted the ventrolateral margin of the frontal. Because of poor preservation it is not clear whether there was a processus prefrontalis, overlapping dorsally onto the prefrontal as in other tylosaurines (Russell, 1967; Lingham-Soliar, 1992; Lindgren, 2005), or not.

Maxillary dentition

The maxillary of GZG.V.10024 bears at least 12 tooth positions, 10 of which preserve the teeth. The designation of the first tooth as position 1 is conjectural as nothing of the premaxillaries is preserved. Yet, based on the overall morphology of the tooth row and maxillary it appears improbable that the total number of teeth in the maxillary exceeded 12. Tooth positions 3 and 10 are empty and tooth 9 is very poorly preserved. For most teeth only the lingual surface is observable.

The tooth morphology (Figs 6D and 8A–E) varies slightly along the tooth row. The rostral teeth (1–4) are gently labiolingually compressed, oval and decreasingly asymmetrical in cross-section with a more convex lingual side. More caudally the teeth first become more strongly compressed (5–7) and then again more oval in cross-section towards the end of the maxillary (8–12) and obtain a nearly symmetric cross-section. All teeth bear a mesial carina, extending from the base to the apex of the tooth crown. A weak distal carina is present on tooth 2, where it extends from the apex to about mid-height of the crown and a well-developed distal carina, running from the apex to the base of the tooth, is present on teeth 4–12. All carinae are minutely, weakly and irregularly serrated, the serrations are generally being slightly more conspicuous on the distal carinae. On teeth 1 and 2 the distal carina is substituted near the base by a rounded edge, separating the lingual from the labial side. All teeth are weakly prismatic, teeth 1–9 exhibit six to eight flat-bottomed facets on the lingual side, separated by weak primary striae. Each facet bears five to eight very faint secondary striae. Teeth 11 and 12 show three facets on the lingual side, also with seven to eight faint primary to secondary striae on each facet. In most teeth primary and secondary striae extend to about 50–60% of the crown height before effacing into a smooth apex. Only the lingual side of tooth 12 is covered for about 80% of its height in a dense array of secondary striae. A tertiary order of striation is present as very fine non-anastomosing striae, extending from

the base to about 40–50% of crown height in teeth 1, 2 and 12, and to about 20% in the other teeth on the lingual side.

The labial surface of tooth 2 is the only one that can be sufficiently observed; it appears to bear a similar number of facets to the lingual side, with slightly more pronounced primary striae. All tooth crowns are caudally recurved with an increasing degree of recurvature towards the distal end of the tooth row. Additionally tooth crowns 1 to 5 are slightly curved medially. The enamel shows a slight transverse light-and-darker colour banding, with bands c. 1–2 mm in width. The tooth bases are slender, cylindrical and have a slight constriction at the base of the enamelled crown. They contain replacement teeth in a posteromedially located socket. Replacement teeth are preserved at the bases of teeth 7 and 8 (Fig. 8F). Their smooth apices point caudoventrally, forming an angle of 15–25° to the horizontal plane.

Pterygoid dentition

Two fragmentary pterygoid tooth crowns are preserved. The pterygoid teeth are small in comparison to the marginal dentition (i.e. the tooth crown height of the better-preserved specimen is 17 mm, but may actually have been 19–20 mm when complete). The larger one (Fig. 8G and H) is better preserved, while the smaller one is split parasagittally, with only a sector of the labial side still available for examination. The tooth crowns are slightly compressed and symmetrically oval in cross-section, short, with a slightly inflated base, tapering rapidly to a strongly distally and slightly lingually recurved apex. The enamel is covered by fine yet distinctive secondary striae (0.5–1 per mm) that are intercalated by thin tertiary striae (2–3 per mm). On the smaller tooth about the apical third is smooth; in spite of this the ornament is uniform around the whole circumference in both teeth. The larger tooth possesses an unserrated weak mesial carina and a very short, vestigial, unserrated labial carina near the apex. The preserved labial face of the smaller tooth shows a very indistinct, smooth, edge-like lateral carina. The bony base is only preserved to some extent on the larger tooth; it is short and stoutly conical, passing continuously into the enamelled crown.

Comparisons and remarks

GZG.V.10024 was originally assigned by Pompeckj (1910), with some reservation, to the poorly known mosasaurine *Liodon mosasauroides* Gaudry, 1892, from the Maastrichtian of the French Pyrenees. Lingham-Soliar's (1993) synonymy list included GZG.V.10024 under *L. mosasauroides*, although that author did not further discuss this specimen. Sachs (2000) followed Pompeckj (1910) in being more cautious in identifying the specimen as *L. cf. mosasauroides*.

There are several issues surrounding these identifications. The holotype of '*L.*' *mosasauroides* consists of a large snout



Fig. 8. *Hainosaurus* sp., GZG.V.10024, details of dentition: A–C, second maxillary tooth; A, mesial aspect; B, lingual aspect; C, occlusal/lingual aspect. D–E, fourth maxillary tooth; D, mesiolingual aspect; E, lingual aspect; F, replacement tooth in position 8. G, H, pterygoid tooth; G, labial aspect; H, mesial aspect; lc, vestigial labial carina; mc, weak mesial carina. Scale bars: 10 mm in A–E, 5 mm in F–H.

section, comprising an articulated fused premaxillary, maxillaries and dentaries (MNHM 1891-14; see Lingham-Soliar, 1993; Bardet, 2012) with a distinctive, highly trenchant dentition. Actually '*L.*' *mosasauroides* has exceptionally strongly labiolingually compressed, but asymmetrically cross-sectioned tooth crowns, broadly triangular in lateral aspect, with smooth enamel, and a higher number of maxillary teeth (13) than GZG.V.10024 (Gaudry, 1892; Lingham-Soliar, 1993; Bardet, 2012). On the basis of these differences the latter cannot be assigned to '*L.*' *mosasauroides*.

However, moderately recurved to upright tooth crowns with subequal lingual and labial faces, a subovate to moderately labiolingually compressed cross-section, several orders of striae commonly vanishing towards the apex and dense tertiary striae near the crown base are features generally held typical of members of the subfamily Tylosaurinae (Russell, 1967; Bardet, 1990;

Lingham-Soliar, 1992; Lindgren & Siverson, 2002; Lindgren, 2004, 2005; Jagt et al., 2005).

Within this subfamily GZG.V.10024 shares the following dental characters with the genus *Hainosaurus* (see Lindgren & Siverson, 2002; Lindgren, 2005): caudolateral teeth bicarinate with serrated carinae, labiolingually compressed with subequal lingual and labial faces, seven or eight weak facets on the lingual face, non-anastomosing second- and third-order striae at the base of the crown. In this genus, two nominal species are currently recognised (Lindgren & Siverson, 2002; Lindgren, 2005; Martin, 2007, but see Bullard & Caldwell, 2010), the type species *H. bernardi* and *H. neumilleri* Martin, 2007, from the Late Campanian of South Dakota, USA. In addition to these, further material, potentially at least partially representing unnamed species, has been referred to this genus (Lindgren, 2005; Jagt et al., 2005, 2006). Most characters of GZG.V.10024 are

consistent with those described by Lingham-Soliar (1992) and Lindgren (2005) for *H. bernardi*. It is distinguished, however, from the type species in that the distal carina is missing from the first two maxillary teeth. Additionally, the anterolateral tooth crowns are slightly more inflated lingually and more asymmetrical than in *H. bernardi*. The most important differences are presented by the pterygoid teeth. GZG.V.10024 shows, at least on some pterygoid teeth, an indistinct, unserrated, mesial carina and a very weak, incompletely developed, unserrated, lateral (labial) carina. The ornament on the pterygoid teeth is uniform along the entire circumference and the teeth are slightly recurved medially. In *H. bernardi* and *Tylosaurus* spp. (with the exception of *T. gaudryi*), the pterygoid teeth bear two distinct lateral carinae, which are serrated in *H. bernardi* and have separate, differently ornamented, rostral and caudal sides (Lindgren & Siverson, 2002; Lindgren, 2005). Mesial and distal carinae are present in *T. gaudryi* (see Thevenin, 1896; Lindgren, 2005). Finally, the ventrally and slightly laterally arched supratemporal bar is different from *H. bernardi*, in which the corresponding element is straight (Lingham-Soliar, 1992). GZG.V.10024 differs from *H. neumilleri* by the presence of more distinctively prismatic lateral teeth and probably more flattened labial faces in the marginal teeth of the latter (Martin, 2007).

Another character supporting assignment of GZG.V.10024 to the Tylosaurinae is the deep triangular embayment of the caudal margin of the maxillary, receiving the rostral triangular wing of the prefrontal. This feature was not depicted in the skull reconstruction of *H. bernardi* by Lingham-Soliar (1992) but can be seen in the holotype (IRSNB R23 [1564], Lingham-Soliar, 1992: pl. I, fig. A) and in the reconstruction by Dollo (1888: pl. I, fig. 2). Although the prefrontal wing is absent from IRSNB R23, the caudal margin of the maxillary seems to be largely intact, a view supported by the configuration of the prefrontal-maxillary contact in the genus *Tylosaurus* (e.g. see Russell, 1967; Everhart, 2005).

GZG.V.10024 probably represents a still undescribed species of *Hainosaurus* (Fig. 9), but the paucity of the material leads us to refrain from the introduction of a new nominal taxon until better-preserved material becomes available.

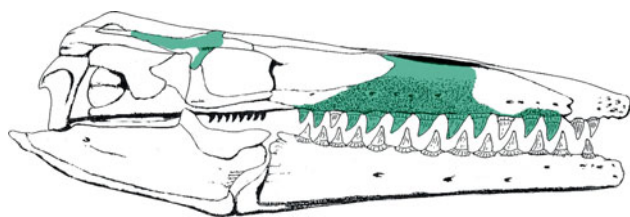


Fig. 9. *Hainosaurus* sp. from the Late Campanian of Stemwede-Haldem, reconstruction based upon *H. bernardi* Dollo, 1885a (after Lingham-Soliar 1992, modified). Preserved parts in green, left postorbitofrontal mirrored to the right side.

Isolated teeth referred to *Hainosaurus* 'sp. 1' from the Late Campanian of Poland (Machalski et al., 2003; Jagt et al., 2005) and the Early Campanian of Sweden (Lindgren, 2005) show a close resemblance to the posterolateral teeth of GZG.V.10024, despite a lower number of facets on the lingual face (three to nine rather than nine to twelve) in the latter. However, the teeth from Poland and Sweden are significantly smaller than those of GZG.V.10024. This fact, coupled with the observation that a decrease in the number of facets during ontogeny has been proposed earlier for the genus *Mosasaurus* by Mulder et al. (2004) let it appear reasonable that the former represent juvenile or subadult specimens of the same species as GZG.V.10024 (compare Lindgren, 2005).

Discussion

The validity of Hainosaurus Dollo, 1885a

The distinction between the closely related genera *Tylosaurus* and *Hainosaurus* has been based on relatively few cranial, dental and vertebral characters (Dollo, 1885a,b; Lingham-Soliar, 1992; Lindgren & Siverson, 2002; Lindgren, 2005). Lindgren & Siverson (2002) reduced the supposed differences between both genera to (1) labio-lingually compressed lateral teeth with (2) minutely serrated mesial and distal carinae in *Hainosaurus*, while they are ovate in cross-section, asymmetric and with unserrated carinae in *Tylosaurus*; (3) pterygoid teeth with serrated carinae in *Hainosaurus*, while they are unserrated in *Tylosaurus*; (4) a small suprapedial process of the quadrate in *Hainosaurus*, while it is large in *Tylosaurus*; (5) a large infrastapedial process of the quadrate in *Hainosaurus*, while it is larger in *Tylosaurus*; (6) a quadrangular outline of the quadrate in lateral aspect in *Hainosaurus*, whereas it is more circular in *Tylosaurus*; (7) the femur in *Hainosaurus* is longer than the humerus, while being subequal in length in *Tylosaurus*; (8) a larger number of vertebrae between the cranium and the chevron-bearing caudals in *Hainosaurus* than in *Tylosaurus*; and (9) anteriorly situated intermediate caudal centra in *Hainosaurus* that are wider and shorter than in *Tylosaurus*.

However, following a revision of North American material previously referred to *Hainosaurus*, Bullard & Caldwell (2010) suggested that most of the cranial and postcranial features were ambiguously dispersed among the two genera and not suitable to distinguish between them, leading to the conclusion that *Hainosaurus* might be a junior synonym of *Tylosaurus* (see also Jimenez-Huidobro & Caldwell, 2012).

While we are not prone herein to present a complete reassessment of *Hainosaurus bernardi*, the Belgian type species of the genus (Dollo, 1885a), we opt to retain *Hainosaurus* as a valid genus for several reasons. Most important is the strong modification of the lateral and pterygoid dentition, which is clearly linked to a change in the choice of prey and probably also of feeding behaviour (see also Lingham-Soliar, 1992; Fig. 4B).

During the Campanian, the plesiomorphic condition (relative to *Hainosaurus*) of robust caudolateral, conical, laterally only slightly compressed, asymmetric, unserrated tooth crowns in *Tylosaurus* spp., which belong functionally to the ‘general’ guild (*sensu* Massare, 1987; Fig. 4), to the almost symmetrical, laterally strongly compressed, nearly blade-like posterior marginal tooth crowns in *Hainosaurus*, functionally referable to the ‘cut II’ guild (Fig. 4). Similar changes occurred in the pterygoid teeth, which became more recurved (caudomedially) and in some species of *Hainosaurus* also serrated. This character is plesiomorphic in GZG.V.10024, which lacks serrations on the pterygoid teeth at all, as well as distinct carinae, suggesting that the modification of the pterygoid dentition occurred phylogenetically later than that of the lateral dentition. Another character probably connected to these major changes of the dental apparatus is the presence of a thin bony lamina protruding ventrally and labially to the dentigerous buttress from the maxillary to form a straight oral margin of the maxillary. Such a lamina, although delicate and easily damaged, is present in the type and referred material of *H. bernardi* (see Lingham-Soliar, 1992; Martin, 2007: figs. 3e and f), as well as in GZG.V.10024. In *Tylosaurus*, the oral margin of the maxillary is more or less confluent with the labially bulging tooth bases, leaving laterally open interdental reception grooves for occlusion with the dentary teeth (e.g. Everhart, 2005).

While differentiation in the dentition may be regarded a minor character in contrast to the extensive overlap of osteological characters between both genera, we consider them important enough to warrant distinction between *Tylosaurus* (*sensu stricto*) and derived forms with a trenchant dentition. The hierarchical level of such a distinction may be a matter of discussion. Nonetheless we propose *Hainosaurus* to be retained as a valid genus (instead of, for example, a more informal specialised ‘species group’ of *Tylosaurus*) because it appears – despite the scarce remains – that tylosaurine mosasaurs with a trenchant dentition form a clade of several species which also show some degree of phylogenetic trend, increasing the pronouncement of typical characters of the genus from the Early Campanian through the Late Maastrichtian (Jagt et al., 2005, and discussion below). For similar reasons we propose to consider *H. neumilleri* at least tentatively as valid because its holotype, the incomplete remains of a tylosaurine, is undoubtedly associated with lateral teeth characteristic of *Hainosaurus* (but not of *H. bernardi*, see Martin, 2007). We are also aware that there might be the caveat that remains of *Tylosaurus*-like tylosaurines which do not include teeth (e.g. *Tylosaurus capensis* Broom, 1912, see Lingham-Soliar, 1992) may not be identifiable at genus level.

As has been recently shown, for example by Young & Andrade (2009) and Young et al. (2012) for marine crocodylians and Knutsen (2012) for pliosauurs, niche-partitioning by developing a variety of tooth morphologies linked to different feeding habits strongly augments the diversification of marine reptile

clades, which show otherwise relatively little variation in the skeletal bauplan. It also provides an explanation for the sympatricity of a wealth of large-bodied, generally similar mosasaurs in the Late Cretaceous (see also Ross, 2009). We therefore support the call by Lindgren & Siverson (2002, 2004) and Lindgren (2004, 2005) to value the dental morphology of derived mosasaurs as a taxonomic tool at low systematic levels, given their stringent analysis and description of more complete types for reference.

The history of tylosaurines in Europe

Teeth of *Tylosaurus* sp. from the Coniacian/Santonian of Lonzeé, Belgium (Lindgren & Siverson, 2002) may represent the oldest tylosaurines in Europe. Very poorly preserved and undiagnostic remains from the same stratum and locality have been described as *Hainosaurus lonzeensis* Dollo, 1904, but this taxon has unequivocally been considered a *nomen dubium* (Nicholls, 1988; Lingham-Soliar, 1992; Lindgren & Siverson, 2002).

The Early Campanian saw some diversification of the genus *Tylosaurus* across Europe, with the slightly better known *T. gaudryi* from northeastern France and *T. ivoensis* from southern Sweden (Lindgren & Siverson, 2002; Bardet, 2012). *Tylosaurus* sp. from northern Germany (Stolley, 1892; the present paper) also falls into this temporal range. During the Early Campanian, *Hainosaurus* appeared for the first time with *H.* sp. from southern Sweden (Lindgren, 2005) and northeastern Belgium (Jagt, 2005). It may have also been present in northern Spain (Bardet et al., 1997: fig. 3/1 [as *Mosasaurus lemonnieri* Dollo, 1889]).

The stratigraphically youngest European occurrence of *Tylosaurus* sp. was recorded from the Late Campanian of northern Spain (Bardet et al., 2006). Widespread, albeit scanty remains of *Hainosaurus* sp. are known from the Late Campanian of France, England, northwestern Germany and Poland (Jagt et al., 2005; Bardet, 2012; the present paper), and possibly of northern Spain (Bardet et al., 1997: fig. 3/4 [as *Mosasaurus* sp.]). Mulder & Mai (1999) referred a partial parietal (von Meyer, 1860) from the early Late Campanian of Belgium to *H.* cf. *bernardi*, citing it as the potentially oldest occurrence of the species. However, the absence of teeth in that material makes such an identification slightly ambiguous.

The best record of *Hainosaurus* to date is from the Early Maastrichtian Cibly Phosphatic Chalk Formation of Belgium with *H. bernardi*. In the Late Maastrichtian *H.* ‘sp. 2’ is known from central Poland (Dollo, 1885a; Lingham-Soliar, 1992; Jagt et al., 2005).

Outside Europe, *H. neumilleri* may represent the genus in the Late Campanian of North America (but see Bullard & Caldwell, 2010, for an opposing view). Lingham-Soliar (1994: 262, fig. 1i and j) referred to at least two teeth from the Maastrichtian of Manzadi, Bas Congo, western Democratic Republic of Congo, as cf. *Mosasaurus lemonnieri*. They exhibit a strong labiolingual, subsymmetrical compression, shallow concave facets

(c. six labially and 12–14 lingually) and well-developed mesial and distal carinae. These characters are congruent with those of the genus *Hainosaurus* and may indicate the presence of this genus in the Maastrichtian of central Africa.

Comments on species previously referred to the genus *Liodon* Agassiz, 1846

GZG.V.10024 was originally tentatively assigned to the problematic species '*Liodon*' *mosasauroides* Gaudry, 1892 by Pompeckj (1910), although he referred the species to the genus *Mosasaurus*, following Dollo (1893). The main reason for this assignment was the labiolingually compressed, blade-like shape of the 'smooth' lateral teeth (Pompeckj, 1910: 126). While these similarities are only superficial (see above), the status of the genus *Liodon* has not yet been resolved satisfactorily. It was created as *Leiodon* by Owen (1841, in Owen, 1840–1845) for its type species *L. anceps*, based on several teeth and associated jaw fragments from the Campanian of England. The genus name was preoccupied and substituted by the junior synonym *Liodon* Agassiz, 1846. While Owen saw the most important difference in the smooth enamel in contrast to the faceted enamel of *Mosasaurus*, Dollo (1893) was the first to reject the validity of '*Leiodon*', proposing synonymy with *Mosasaurus*. In the meantime a number of species have been referred to this genus, in part erroneously. Lingham-Soliar (1993) revised it and proposed four species to be valid, namely *L. anceps*, *L. compressidens* (Gaudry, 1892), *L. sectorius* Cope, 1871, and *L. mosasauroides*, forming a phylogenetic series of increasingly trenchant, smooth marginal teeth. However, doubts were expressed over the recognition of the type material of *L. anceps*, and recently Schulp et al. (2008) have proposed to transfer diagnosable species of the poorly known genus '*Liodon*' to *Prognathodon* Dollo, 1889. Although this would appear an elegant approach in order to deal with the numerous problems surrounding the taxonomy of '*Liodon*', caution is called for when considering that species with a strongly labiolingually compressed dentition should be indifferently included in the genus *Prognathodon*, which is generally characterised by conical, massive, more or less swollen or only slightly compressed, symmetrically cross-sectioned lateral teeth and procumbent premaxillary teeth in several species (see also Konishi et al., 2011).

'Liodon' *sectorius*, based on fragmentary remains from the Maastrichtian of New Jersey, USA, northeastern Belgium and possibly northern Spain (Cope, 1871; Russell, 1967; Kuypers et al., 1998; Bardet et al., 2012) shows dental characters that are clearly similar to those of *Prognathodon* spp., especially the swollen tooth bases and vestigial anastomosing wrinkles on otherwise smooth enamel. The labiolingually compressed, symmetrical cross-section of lateral tooth crowns is closely similar to that of *P. kianda* Schulp, Polcyn, Mateus, Jacobs & Morais, 2008, from the Maastrichtian of Angola. However, it should be noted that *P. kianda* was found to be located outside

of and more basal to a monophyletic genus *Prognathodon* in recent analyses (LeBlanc et al., 2012; Grigoriev, 2013). It may therefore form a sister-taxon to '*L. sectorius*' in a still unnamed genus.

'Liodon' *compressidens* Gaudry, 1892 from the Early Campanian of France (Bardet, 2012) was assigned to '*Liodon*' by Lingham-Soliar (1993) and to *Prognathodon* by Schulp et al. (2008) and Bardet (2012). However, the holotype and sole specimen known, MNHM AC 1878-575, is the rostral part of a skull which appears to show cranial and dental features that are more consistent with assignment to the Mosasaurini Gervais, 1853, than to *Prognathodon*. These include the narrow, tapering jaws, the presence of low and long maxillaries (which are generally shorter and taller in lateral aspect in *Prognathodon* spp., see, for example, Lingham-Soliar & Nolf, 1990; Schulp, 2006: fig. 4; Konishi et al., 2011), and the presence of a small but distinct premaxillary rostrum, which is absent or very indistinct in most species of *Prognathodon*. Although Lingham-Soliar (1993) claimed that the degree of lateral compression shown in the cross-sections of the marginal teeth figured by Gaudry (1892: pl. I) was exaggerated, his own illustration (Lingham-Soliar, 1993: fig. 3) confirms the labiolingual compression and more importantly a slightly asymmetric cross-section of the bicarinate tooth crowns, with a more convex lingual face and weak faceting of both sides, lacking a swollen base. The overall cranial and dental morphology appears similar to that of the genus *Clidastes* Cope, 1868 (see Russell, 1967; Lindgren & Siverson, 2004), although the size is much larger than is common in this genus, approaching the dimensions attained by *Mosasaurus*. Pending a revision of this material, inclusion of '*Liodon*' *compressidens* into the Mosasaurini should be considered at least probable.

LeBlanc et al. (2012) also expressed doubt over the assignment of '*L. mosasauroides*' to *Prognathodon* and proposed a closer relationship of the former with *Mosasaurus*. In our view this is also supported by the dental morphology of the holotype, which exhibits a marked asymmetry between a near-flat labial and a gently to rostrally increasingly convex lingual side (Gaudry, 1892: pl. II). At least the rostralmost dentary teeth have a distinct D-shaped cross-section, which is very similar to that in *Mosasaurus* spp. Although clearly highly derived, the dentition is still most close in morphology to and clearly derivative from that in *Mosasaurus*. The double row of vascular foramina on the maxillary and the presence of a small premaxillary rostrum also underscores a close relationship to the latter. '*Liodon*' *mosasauroides* may therefore either be considered a highly derived species of *Mosasaurus* or belong to a still unnamed genus that probably evolved from the latter.

Conclusions

Two genera of tylosaurine mosasaurs, *Tylosaurus* and *Hainosaurus*, are recorded for the first time from the Campanian of

Germany. *Tylosaurus* sp. is represented by two isolated tooth crowns, originally described as *Mosasaurus? alseni* (here considered a *nomen dubium*), which exhibit a close similarity to *T. ivoensis* and *T. gaudryi*.

The genus *Hainosaurus* is considered valid and distinct from *Tylosaurus*, despite minor osteological differences, for its significant modification in the dental apparatus in comparison to the plesiomorphic condition in the latter. The development of a cutting dentition from the generalised-piercing dentition of *Tylosaurus* was probably linked to major shifts in prey preference and feeding behaviour.

The material of *Hainosaurus* sp. from Germany comprises a maxillary with associated postorbitofrontal, two pterygoid teeth and several indeterminate cranial fragments. The specimen from the Late Campanian is slightly less derived than *H. bernardi* from the Early Maastrichtian in retaining less labiolingually compressed anterior maxillary teeth and unserrated pterygoid teeth with only very weak carinae. A short review indicates the presence of *Hainosaurus* in northern, central and western Europe (Sweden to Spain) ever since the Early Campanian, and the occurrence of *Tylosaurus* spp. in the same area up to the Late Campanian. *Hainosaurus* persisted until the end of the Maastrichtian and outside Europe it may have been present in the Late Campanian of the USA and the Maastrichtian of the Democratic Republic of Congo. The dental morphology of this genus shows some morphological modification throughout its existence, suggesting a phylogenetic trend in the marginal dentition of European tylosaurines from the robust, 'generalised' teeth of *Tylosaurus gaudryi* and *T. ivoensis* from the Campanian (Massare, 1987; Lindgren & Siverson, 2002; Lindgren, 2005) towards the increasingly labiolingually compressed, symmetrical, strongly bicarinate, trenchant teeth of *Hainosaurus* sp. from the Early through Late Campanian and *H. bernardi* from the Early Maastrichtian (Dollo, 1885a,b; Lingham-Soliar, 1992; Lindgren, 2005). This morphocline may be extended into the Upper Maastrichtian with *H. 'sp. 2'* (*sensu* Jagt et al., 2005) from Poland, with marginal teeth that are strongly labiolingually compressed and have well developed denticles on the mesial and distal carinae. A similar trend is also present in the pterygoid teeth with very indistinct, unserrated carinae in the Campanian *Hainosaurus* sp. towards serrated carinae in the Maastrichtian *H. bernardi*.

Judging from a simple, uni- to bicarinate, stoutly conical tooth morphology in aigialosaurs and basal mosasaurs (Polcyn et al., 1999; Dutchak & Caldwell, 2009), providing a grasping and piercing function, and phylogenetic patterns, the development of highly trenchant ('cut II') dentitions seem to have been acquired convergently in several clades of large-bodied Campanian–Maastrichtian mosasauroids. These include mosasauroines (*'L.'* *mosasauroides*, *Prognathodon? sectorius*, *Prognathodon? kianda*, *Eremiasaurus heterodontus* LeBlanc, Caldwell & Bardet, 2012) as well as tylosaurines (*Hainosaurus* spp.).

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