

Dental and vertebral morphology of the enigmatic mosasaur *Dollosaurus* (Reptilia, Mosasauridae) from the lower Campanian (Upper Cretaceous) of southern Sweden

JOHAN LINDGREN



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Teeth, jawbone fragments and vertebrae of an unusual mosasaurine mosasaur, *Dollosaurus*, have been collected from marine strata of latest early Campanian age in the Kristianstad Basin, southern Sweden. This material enables a detailed analysis of dental and vertebral characters, which, in turn, are used to tentatively distinguish *Dollosaurus* from the closely related globidensine *Prognathodon*. However, the evidence is contradictory, and two evolutionary scenarios are possible: (1) the two genera represent separate offshoots of a single lineage; or (2) *Dollosaurus* represents the most basal ‘*Prognathodon*-like’ taxon known so far.

Key words: Campanian, Cretaceous, Mosasauridae, *Dollosaurus*, *Prognathodon*, Sweden, teeth, vertebrae.

Johan Lindgren [johan.lindgren@geol.lu.se], Geological Museum, University of Copenhagen, Øster Voldgade 5–7, DK-1350 København K, Denmark, and Department of Geology, GeoBiosphere Science Centre, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden.

The squamate family Mosasauridae comprises medium-sized to giant (about 3–13 m long) aquatic lizards that inhabited epicontinental seas and coastal areas during the last 24 million years of the Cretaceous. Shallow-marine strata of Campanian age in southern Sweden have yielded diverse mosasaur faunas, especially from the uppermost lower Campanian. Here, this interval is characterised by the co-occurrence of the belemnites *Belemnellocamax mammillatus* (Nilsson, 1827), *Belemnitella mucronata* (von Schlottheim, 1813) and *Gonioteuthis quadrata scanienensis* Christensen, 1975. Together, strata containing these cephalopods form the local (and informal) *B. mammillatus* zone, a lateral equivalent of the NW European *Belemnitella mucronata senior*/*Gonioteuthis quadrata gracilis* Zone (Christensen 1975). Assuming a constant and continuous sedimentation rate at the Lägerdorf quarry (northern Germany; see Schönfeld *et al.* 1996, fig. 2) and a duration of 3 Ma for the lower Campanian (Obradovich 1994), this biozone spans approximately 330,000 years (Lindgren & Siverson 2002).

The most prolific mosasaur-bearing strata in Sweden are found within the Kristianstad Basin, a graben in northeast Skåne (Fig. 1). During the latest early Campanian, the basin formed a large-scale archipelago with low islands and rocky shorelines (e.g. Surllyk & Christensen 1974). Mosasaurs seemingly occurred in great numbers in the coastal waters along the southern margin of the Fennoscandian Shield, and previously identified taxa include *Tylosaurus ivoensis* (Persson, 1963), *Clidastes propyhton* Cope, 1869, *Halisaurus sternbergi* (Wiman, 1920), *Platecarpus cf. somenensis* Thévenin, 1896, *Hainosaurus* sp., *Platecarpus?* sp., and Mosasaurinae indet. (Lindgren & Siverson 2002, 2003, 2004). In addition to these taxa, several dozens of marginal teeth, two pterygoid teeth, fragments of jawbones with eight associated teeth, and three isolated caudal vertebrae from the *B. mammillatus* zone are here referred to an eighth taxon, *Dollosaurus* sp. As the taxonomic status of *Dollosaurus* Yakovlev, 1901 is somewhat unclear (it was synonymised with *Prognathodon* Dollo, 1889 by Lingham-Soliar & Nolf (1990)), the present note also includes

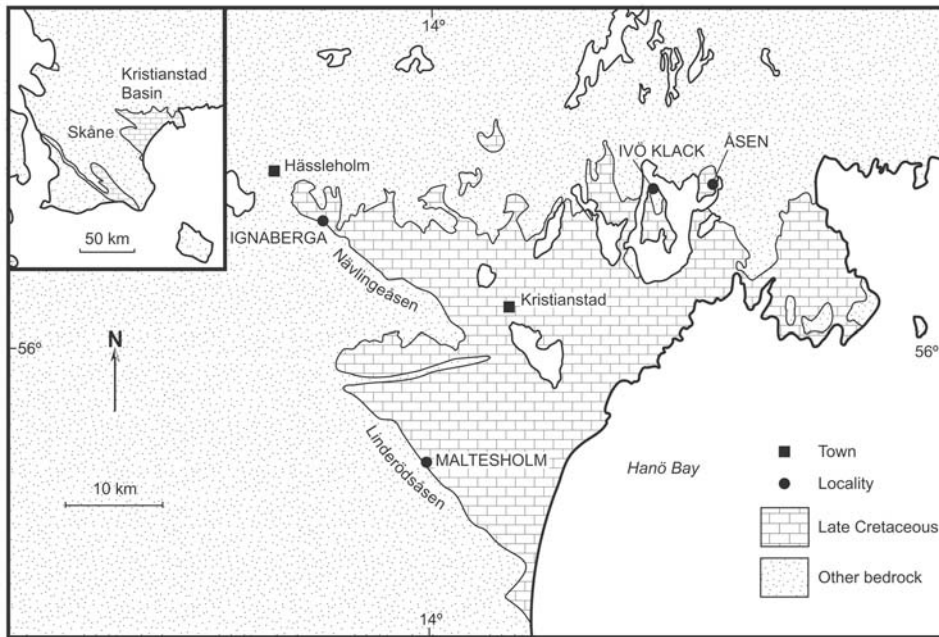


Fig. 1. Sketch-map of southern Sweden showing the Kristianstad Basin and outcrops referred to in the text.

a discussion of a number of contradictory skeletal characteristics which, unfortunately, prevent settling the systematic affinities of *Dollosaurus*.

Geological setting

The geology of Skåne (southernmost Sweden) is strongly affected by large-scale, rift-induced block faulting. These faults lie within the NW–SE trending Fennoscandian Border Zone, a horst and graben system that separates the Fennoscandian Shield to the northeast from the Danish-Polish Trough to the southwest (Kumpas 1980; Norling & Bergström 1987). In the southwest, the Linderödsåsen and Nāvlingeåsen horsts confine the Kristianstad Basin *sensu* Erlström & Gabrielson (1992; Fig. 1). The northern demarcation of the basin constitutes an irregular boundary with several outliers of Cretaceous sediments. These outliers are usually preserved in depressions in the crystalline basement, formed during the latest Triassic to Early Cretaceous when the basement was exposed and subject to extensive weathering, which resulted in a highly uneven topography (Bergström & Sundquist 1978; Lidmar-Bergström 1982).

Poorly consolidated, sandy marine calcarenites and calcirudites are the dominant lithologies in the uppermost lower Campanian *Belemnellocamax mammillatus* belemnite zone. Terrigenous material in conglomerates and boulder beds indicates that nearby land served as an important source area, especially

along the basin margins (Christensen 1975). The marine deposits may overlie residual kaolin clay and quartz sand (e.g. at Ivö Klack), fluvial clays and sands (e.g. at Åsen), or rest unconformably upon the crystalline basement. The thickness of the *B. mammillatus* zone is highly variable. The biozone is locally rather thin or absent in the northern part of the basin (e.g. 1.5–2.0 m at Åsen), whereas much greater thicknesses have been recorded along the two faults demarcating the southwesterly extension of the basin and towards the southeast (Erlström & Gabrielson 1986, 1992). Four localities (Fig. 1) exposing sediments of latest early Campanian age, i.e. Åsen, Ignabergera, Ivö Klack and Maltesholm, have produced remains of *Dollosaurus* (for locality data, see Appendix).

Material and methods

In order to remove the adhering carbonate matrix, specimens described and illustrated herein were treated with an acetate-buffered acetic acid solution (see Jeppsson *et al.* 1999 for details). The fossils were hardened by application of polyvinylbutyral in acetone. Bright coloured specimens were painted with a graphite solution and then coated with ammonium chloride prior to photography. Dark coloured specimens were merely coated with ammonium chloride prior to photography.

Institutional abbreviations. BMNH, the Natural

History Museum, London; CNIGR, Geological Museum, Sankt Petersburg, Russia; HUJ, Hebrew University of Jerusalem, Jerusalem, Israel; IRScNB, Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; NHMM, Natuurhistorisch Museum Maastricht, Maastricht, The Netherlands; PMU, Museum of Evolution, Palaeontology Section, Uppsala University, Uppsala, Sweden; RM PZ, Swedish Museum of Natural History, Department of Palaeozoology, Stockholm, Sweden; SDSMT, Museum of Geology, South Dakota School of Mines and Technology, Rapid City, USA; SGU, Geological Survey of Sweden, Uppsala, Sweden.

Systematic palaeontology

Order Squamata Oppel, 1811
Family Mosasauridae Gervais, 1853
Subfamily Mosasaurinae Gervais, 1853

Genus *Dollosaurus* Yakovlev, 1901

Type species. *Dollosaurus lutugini* Yakovlev, 1901, from the upper Campanian ('*Belemnitella mucronata* Zone') of the Voroshilovgrad region in the Ukraine.

Dollosaurus sp.
Figs 2–3

- 2002 '*Liodon*' (Owen) – Lindgren & Siverson, p. 79.
2003 *Dollosaurus* sp. – Lindgren & Siverson, p. 107.
2004 *Dollosaurus* sp. – Lindgren & Siverson, pp. 230–231.
2004 *Prognathodon?* sp. – Lindgren & Siverson, p. 231.
2004 *Dollosaurus* sp. – Lindgren, fig. 6.

Referred material. Marginal teeth: Åsen, seven teeth (all unnumbered, Lund University), Ignaberga, one tooth (unnumbered, Lund University), Ivö Klack, 58 teeth (one unnumbered, Lund University; PMU R1258, 1259, 1261–1263 and 29 unnumbered, Museum of Evolution; RM PZ R1114, 1124, 1131, 1155, 1161–1163, 1210, 1211, 1226, 1228, 1249, 1251, 1283, 1312, 1388, 1393, 1401, 1403, 1407, and two unnumbered, Swedish Museum of Natural History; SGU 03442 Ve12). Pterygoid teeth: Ivö Klack, three teeth (PMU R1260, 1264; RM PZ R1321). Jawbones: Maltesholm, eight associated fragments with detached teeth (RM PZ R1772). Vertebrae: Ivö Klack, one intermediate caudal (unnumbered, Stockholm University) and two terminal caudals (RM PZ R921 and 1260).

Additionally, two isolated marginal tooth crowns

(unnumbered, Lund University) have been collected from lowermost upper Campanian strata (informal *Belemnelloccamax balsvikensis* zone) at Västra Olinge and Balsvik, respectively (for locality data; see Christensen 1975), although at least one of them (from Balsvik) is probably reworked from underlying deposits.

Description. As reconstructed herein, the marginal dentition of this mosasaurine is well differentiated by mosasaur standards, approaching the heterodonty seen in *Clidastes* Cope, 1868, *Mosasaurus* Conybeare, 1822 and *Liodon* (Owen, 1841).

Premaxillary and the most anteriorly situated dentary teeth are strongly medio-distally curved and subcircular in cross section (Fig. 2A–D). The tooth crowns are equipped with a prominent, unserrated mesial carina that extends the full length of the crown and a weak, often incomplete (i.e. restricted to the apical portion of the crown) distal one. The cutting edges asymmetrically divide the crowns into a convex labial surface and a deeply U-shaped lingual face. The enamelled surfaces are smooth, with the exception of faint anastomosing hairline striations at the apex and a small number of indistinct bumps near the base of the labial face on a few crowns. The teeth are up to 29 mm high and 15 mm wide at the base (estimated original height of PMU R1259, a 26,5 mm high crown with a worn apex).

Anteriorly situated maxillary teeth and antero-laterally positioned dentary teeth are tall, moderately (Fig. 2E–G) to strongly (Fig. 2H–J) distally curved, and divided by sharp yet unserrated carinae into labial and lingual surfaces of subequal convexity. In basal cross section, the teeth range from being subcircular to markedly elliptical in outline. The enamel-covered surfaces are either smooth or (rarely) weakly faceted. In some cases, the lower half of the external surface exhibits a number of indistinct granulae, while the apical portion of the crown may be covered with faint undulating striations. Available specimens range in height from 29 to 35 mm.

Posteriorly along the dental ramus the crowns gradually become more upright and stoutly built, forming an almost blade-like lateral profile with a rounded tip (Fig. 2K–M). Apically inclined serrations are spread irregularly over the carinae, especially along the posterior one (although the serrations on the mesial carina may have been worn off by occlusion). A rough surface texture of undulating striae is present on the apical portion of the crowns, whereas the lower part is more or less smooth with the exception of weak elevations on the basal portion of the labial face. The teeth are up to 39 mm tall and 21 mm wide at the base (estimated original height of

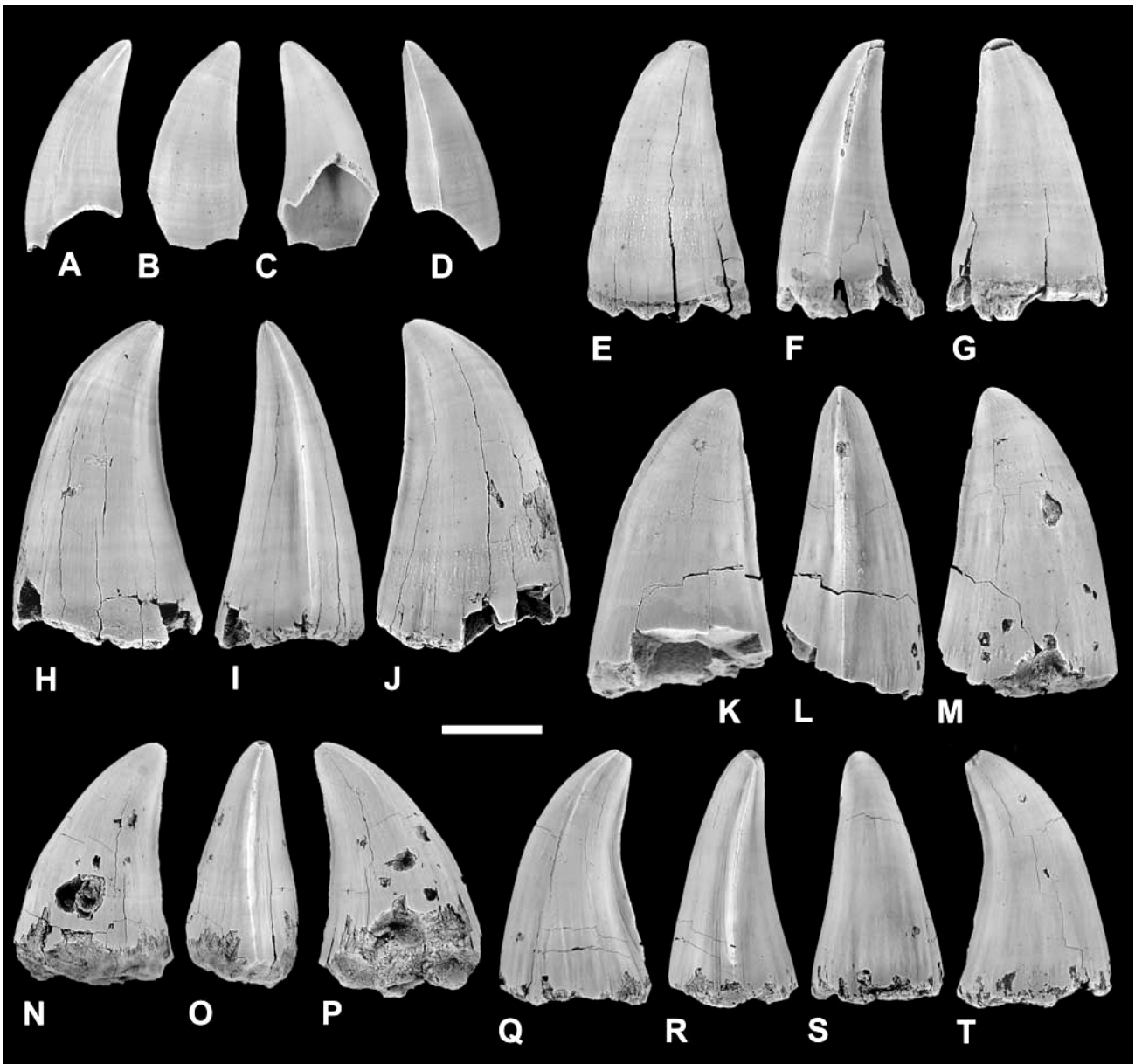


Fig. 2. Marginal and pterygoid tooth crowns of *Dollosaurus* sp. from the uppermost lower Campanian *Belemnellocamax mammillatus* zone of the Kristianstad Basin, southern Sweden. Scale bar 10 mm. A–D. Germ crown of a premaxillary tooth or one of the anteriormost dentary teeth, RM PZ R1772, from Maltesholm in A. distal, B. labial, C. lingual and D. mesial views. Note prominent mesial carina and incomplete posterior cutting edge. E–G. Antero-laterally situated marginal crown, PMU R1262, from Ivö Klack in E. labial, F. distal and G. lingual views. Note distinct pattern of granulae on basal portion of labial face. H–J. Antero-lateral marginal crown, PMU R1261, from Ivö Klack in H. lingual, I. distal and J. labial views. Note strong distal curvature of apex and granulae on the lower half of the labial face of the crown. K–M. Posteriorly situated marginal tooth crown, PMU R1259, from Ivö Klack in K. lingual, L. distal and M. labial views. Note serrations on the distal carina and crenulations at the apex. N–P. Posteriorly situated pterygoid tooth crown, PMU R1260, from Ivö Klack in N. medial, O. distal and P. lateral views. Note incomplete lateral carina. Q–T. Anteriorly situated pterygoid tooth crown, PMU R1264, from Ivö Klack in Q. lateral, R. distal, S. mesial and T. medial views. Note conspicuously serrated distal carina.

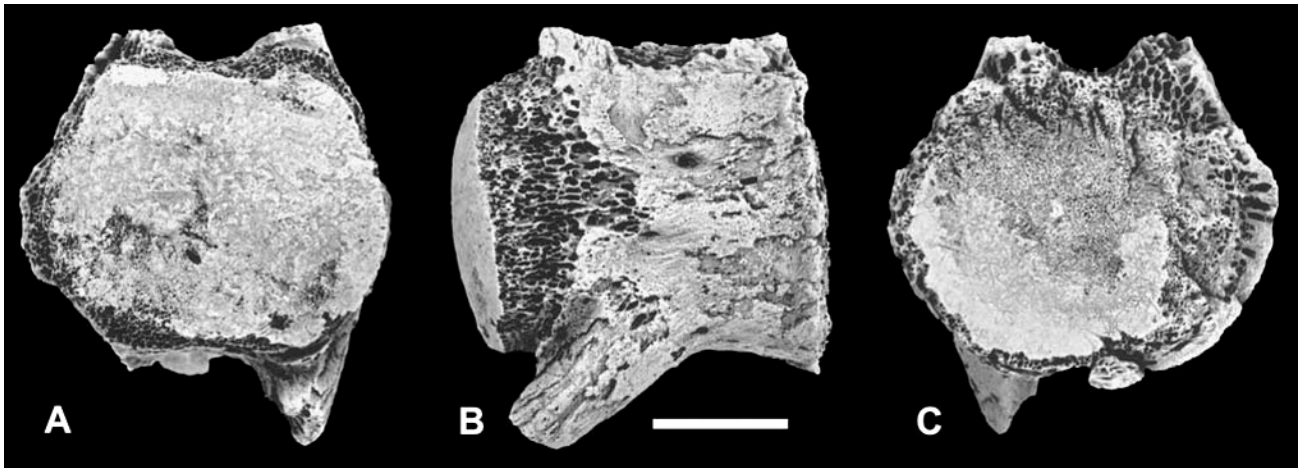


Fig. 3. RM PZ R921, terminal caudal vertebra of *Dollosaurus* sp. from the *Belemnellocamax mammillatus* zone at Ivö Klack, Kristianstad Basin, southern Sweden, in A. caudal, B. lateral and C. rostral views. Scale bar 10 mm.

PMU R1263, a 35 mm tall crown with an abraded tip).

Pterygoid teeth have a similar morphology as the marginal tooth crowns, although they possess a marked (serrated) posterior carina and an incomplete (i.e. apically restricted), less pronounced mesio-lateral one (Fig. 2N–T). The height of the larger of the two pterygoid crowns is 22 mm.

As demonstrated by the eight associated fragments at hand (RM PZ R1772), the jawbone is of massive proportions, with a great depth and width. Circular to slightly oval pits originally housing germ teeth (but now empty) are located on the medio-distal side of the tooth bases. Although all functional crowns are nowadays broken off, basal remains still attached to the jawbone indicate that the teeth were not situated upon tall pedicles, but instead probably emerged almost immediately above the dorsal and ventral margins of the dentaries and maxillae.

The lateral faces of the three caudal centra are markedly angular, contributing to a subhexagonal outline of the articulating surfaces (Fig. 3A, C) and a slight hourglass shape of the centra in dorsal and ventral views. Moreover, the lateral surfaces have one or more large foramina located midway between the condyle and cotyle (Fig. 3B). The chevrons of the haemal arches are fused to the ventral face of the centra. The largest vertebra collected, RM PZ R921, is 25 mm long (measured between the centres of the interarticular surfaces), 25 mm high and 30 mm wide (estimated original height and width of the cotyle).

Discussion. With their markedly angular lateral faces, subhexagonal interarticular surfaces, and large foramina located midway between the condyle and

cotyle, the three vertebrae described above (Fig. 3) are identical to caudals of *Dollosaurus lutugini* (see Yakovlev 1901, pl. 5, fig. 5a–b; personal observation of CNIGR 818 = holotype of *D. lutugini*). Unfortunately, the marginal teeth in CNIGR 818 are painted with varnish and partly obscured by plaster. Hence it has not been possible to conduct a detailed dental examination of the holotype of *D. lutugini*. It has, nevertheless, been possible to conclude that the marginal crowns in CNIGR 818 are unusually large relative to the caudal vertebrae, and that the pterygoid teeth are almost as large as the marginal teeth and armed with a distinct distal carina and a faint lateral one (Yakovlev 1901, pl. 5, fig. 1a–c). Based on these similarities, the Swedish mosasaurine is referred to as *Dollosaurus* sp.

As demonstrated by the fused haemal arches on the caudal vertebrae and lack of basal striae near the base of the lingual face of the marginal crowns, CNIGR 818, and hence also the Swedish material belongs to the subfamily Mosasaurinae (Lingham-Soliar & Nolf 1990). Moreover, the tooth crowns under discussion display weak granulae on their labial face, a feature also present on marginal teeth of the mosasaurines *Clidastes* and *Mosasaurus*, whereas ‘russellosaurines’ *sensu* Bell (1997) apparently lack this character (Lindgren 2004; Lindgren & Siverson 2004).

The taxonomic status of *Dollosaurus* is currently somewhat unclear. Originally, *Dollosaurus* was erected upon an incomplete skull and skeleton (CNIGR 818) collected from upper Campanian strata (*‘Belemnitella mucronata* Zone’) near the town of Krymskoié in the Voroshilovgrad region of the Ukraine (Storrs *et al.* 2000). Yakovlev (1901) considered the combination of functional accessory articulations (zy-

gosphenes and zygantra) and large pterygoid teeth to be distinct to his new taxon, which he dubbed *Dollosaurus* in honour of the contemporary French palaeontologist Louis Dollo. Recently, however, Lingham-Soliar & Nolf (1990) invalidated these characters as being unique to *Dollosaurus* and instead synonymised this nominal taxon with *Prognathodon*. Judging from the gently curved ventral margin of the dentaries (Lingham-Soliar & Nolf 1990, figs 20, 51; Storrs *et al.* 2000, fig. 11.5) and the conspicuously large pterygoid teeth in CNIGR 818 and *P. solvayi* Dollo, 1889 (the type species of *Prognathodon*), there are indeed a number of dental and osteological features to postulate a close relationship between *Dollosaurus* and *Prognathodon*. On the other hand, the markedly angular and laterally pitted caudal vertebrae in *Dollosaurus* suggest a more distant affinity. To complicate matters further, species referred to *Prognathodon* display a wide spectrum of dental morphotypes, and whether this diversity reflects a broad adaptive range or simply phylogenetic artefacts remains to be resolved.

Often, robust and conical tooth crowns with blunt, serrated carinae and smooth enamel (except for a dense pattern of raised crenulations near the apex) are routinely assigned to *Prognathodon* (e.g. Bardet *et al.* 1997, 2000; Kuypers *et al.* 1998; Machalski *et al.* 2003; Lindgren 2004). However, this morphology is only in part in accordance with that found in the type species of the genus. In *P. solvayi*, the marginal teeth deviate from the above description in being markedly labio-lingually compressed and gently faceted (a 'fluted' morphology, as opposed to the generally more deeply concave facets on teeth of 'russellosaurines' *sensu* Bell (1997) and angular facets on teeth of the mosasaurines *Clidastes* and *Mosasaurus*). A distinct pattern of undulating hairline striations is present near the apex of the crowns, however, and the minutely serrated carinae are unsharpened (Lingham-Soliar & Nolf 1990, figs 20, 27; personal observation of IRScNB R33, 4565). Moreover, the crowns are set upon tall pedicles and thus are raised well above the ventral and dorsal margins of the maxillae and dentaries (Lingham-Soliar & Nolf 1990, figs 20, 27). This is also the case in *P. giganteus* Dollo, 1904, *P. overtoni* (Williston, 1897) (i.e. SDSMT 3393) and *P. saturator* Dortangs *et al.*, 2002, but not in '*P.*' *currii* Christiansen & Bonde, 2002 (personal observation of IRScNB R106 = type of *P. giganteus*, NHMM 1998141 = type of *P. saturator*, and HUI OR 100 = type of '*P.*' *currii*). In the latter, the broadly domed marginal crowns are unconstricted at the base, and there are no pedicles to speak of (contrary to what was claimed by Christiansen & Bonde (2002); personal observation of HUI OR 100). Dental morphology and tooth

development of '*P.*' *currii* somewhat resemble those of *Igdamanosaurus* Lingham-Soliar, 1991, a peculiar and little-known globidensine mosasaur from the lower Maastrichtian of western Niger (Lingham-Soliar 1991, fig. 5; Bell personal communication 2004; personal observation of BMNH R11898 = type of *Igdamanosaurus aegyptiacus* (Zdansky, 1935)). Perhaps the gross resemblance between the dentitions of '*P.*' *currii* and *Igdamanosaurus* advocates a closer relationship than previously assumed, or adaptation towards similar ecological niches.

Controversy also surrounds the phylogeny of *Prognathodon*. For instance, Russell (1967) considered the North American forms '*P.*' *crassartus* (Cope, 1872), *P. overtoni* and *P. rapax* (Hay, 1902) to represent an evolutionary lineage, a view subsequently challenged by Bell (1997), who instead concluded that *Prognathodon* is a paraphyletic taxon. Recently, however, Christiansen & Bonde (2002) performed a renewed cladistic analysis based upon a corrected version of Bell's (1997) data set and again found *Prognathodon* to be monophyletic.

In the light of the divergent opinions surrounding the taxonomic status and phylogeny of both *Dollosaurus* and *Prognathodon*, the identification of the Kristianstad Basin mosasaurine must be considered tentative. Judging from dental characters alone, *Dollosaurus* may represent a basal '*Prognathodon*-like' taxon, with a dentition somewhat similar to that of other primitive mosasaurines, such as *Clidastes* (Lindgren & Siverson 2004, figs 2–4). Presumably emergent (derived) features are seen in the undulating pattern of hairline striations near the apex and in the presence of minute serrations on the carinae on a few teeth. Stratigraphically, the mosasaurine from Sweden represents one of the oldest '*Prognathodon*-like' taxa from anywhere in the world, other early occurrences being from the upper lower Campanian of France (Bardet *et al.* 1997) and the lower Campanian of Alabama, USA (Russell 1970). It is reasonable to assume that *Dollosaurus/Prognathodon*, one of few survivors of the mid-Campanian marine crisis that occurred in North America (Russell 1994) and northern Europe (Lindgren 2004), took advantage of the event and soon filled niches left vacant by other taxa. This would explain the rapid dental evolution and broad range of morphotypes in *Prognathodon* by late Campanian/early Maastrichtian time, although it requires a partial retrogression in several species towards a more homodont stage. This interpretation supports Christiansen & Bonde's (2002) view of monophyletic *Prognathodon*.

On the other hand, the caudal vertebrae in *Dollosaurus* are markedly different from those of *Prognathodon*, or any other mosasaur for that matter. The

caudal vertebrae are not angular in *P. giganteus* and *P. saturator* and there are no foramina on the lateral surfaces (unfortunately, the caudals are distorted by compaction in the type of *P. solwayi*). Moreover, the interarticular surfaces are either subcircular or subtriangular, as opposed to the subhexagonal central articulations in *Dollosaurus*. Together with the strong heterodonty and lack of prominent dental peduncles, the highly characteristic vertebrae of *Dollosaurus* suggest a more distant relationship to *Prognathodon*. Perhaps a common ancestor to *Dollosaurus* and *Prognathodon* should be sought for in the early history of the Mosasauridae, an interpretation that would support Bell's (1997) opinion of paraphyletic *Prognathodon*. Hopefully, future in-depth research will help clarify the current ambiguities surrounding the phylogeny of *Dollosaurus* and *Prognathodon*.

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Appendix

Åsen

Map sheet. Karlshamn 3E NV (topographical map sheet, 1:50 000); co-ordinates UTM VC 690 229 (N 56°08'56.1", E 14°29' 56.0"). All *Dollosaurus* remains included in this study originate from the lower half of the section. See also Christensen (1975), Siverson (1992) and Lindgren & Siverson (2002).

Age. *B. mammillatus* zone (latest early Campanian).

Ignaberga 'new quarry' *sensu* Erlström & Gabrielson (1992)

Map sheet. Kristianstad 3D SO (topographical map sheet, 1:50 000); co-ordinates UTM VC 288 195 (N 56°07'00.1" E 13°50'54.5"). See also Lundegren (1934), Siverson (1992) and Erlström & Gabrielson (1992).

Age. *B. mammillatus* zone (latest early Campanian).

Ivö Klack

Map sheet. Karshamn 3E SV (topographical map sheet, 1:50 000); co-ordinates UTM VC 631 222

(N 56°08'21.6" E 14°24'05.8"). See also Lundegren (1934), Surlyk & Christensen (1974), Christensen (1975), and Siverson (1992).

Age. *B. mammillatus* zone (latest early Campanian).

Maltesholm

Map sheet. Tomelilla 2D NO/Simrishamn 2E NV (topographical map sheet, 1:50 000); co-ordinates UTM VB 955 382 (N 55° 54' 00" E 14° 01' 00"). See also Siverson (1992) and Sandström (2001).

Age. *B. mammillatus* zone (latest early Campanian).