The first record of the mosasaur *Clidastes* from Europe and its palaeogeographical implications

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Remains of the mosasaur *Clidastes propython* in marine strata of latest early Campanian age from the Kristianstad Basin, southern Sweden, represent the first record of *Clidastes* outside of North America. The material consists of shed marginal and pterygoid tooth-crowns, and vertebrae (including eleven associated cervicals and dorsals from a juvenile). The majority of the teeth and skeletal elements can be referred to juveniles (mostly in the estimated 2–3 m total body length range), but large, presumably adult individuals (up to an estimated total length of 6 m) are also represented. Available data indicate that the Kristianstad Basin population of *C. propython* represents a short-lived migration, most likely from the Mississippi Embayment in North America. The local extinction of *Clidastes* in southern Sweden, tentatively placed at the early/late Campanian boundary (*sensu germanico*), may coincide with that in the Western Interior Seaway and Gulf Coast of North America. Within the Kristianstad Basin area, *Clidastes* occurs in high-energy, shallow water deposits, where it is the most common mosasaur. This finding is in stark contrast to recent publications suggesting that *Clidastes* inhabited mainly off-shore, deeper waters.

Key words: Reptilia, Mosasauridae, *Clidastes*, teeth, vertebrae, Cretaceous, Campanian, Sweden.

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Introduction

Mosasaurs are extinct Late Cretaceous reptiles comprising one of the most widely distributed groups of marine tetrapods, with reported occurrences from all continents. Fragmentary skeletal remains of this group occur in several Campanian/Maastrichtian biostratigraphical units of southern Sweden (e.g., Persson 1959, 1963; Brotzen 1960; Lindgren and Siverson 2002, 2003). The vast majority of the Swedish mosasaur material originates from the latest early Campanian *Belemnellocamax mammillatus* zone (an informal biozone correlating with the German *Belemnitella mucronata senior*/*Gonioteuthis quadrata gracilis* Zone; Christensen 1975) in the Kristianstad Basin area (Lindgren and Siverson 2002). Persson (1963) listed *Mosasaurus hoffmanni ivoensis* = *Tylosaurus ivoensis* (Persson, 1963); see Lindgren and Siverson (2002) and *Platecarpus somenensis* Thévenin, 1896 from the *B. mammillatus* zone of the Kristianstad Basin. Examination of existing collections in Sweden and extensive sieving of the marine sands at the Åsen locality (see Appendix) have revealed that the mosasaur fauna from this interval is far more diverse than indicated by Persson's work and in fact more diverse than suggested by Lindgren and Siverson (2002; see also Lindgren and Siverson 2003). One of the species that escaped Persson's notice turned out to be the most common mosasaur in the area. Personal examination of specimens from the Niobrara Chalk of Kansas and the Mooreville Chalk of Alabama allow us to identify this species as *Clidastes propython* Cope, 1869.

Comprehensive descriptions of the skeletal anatomy of *Clidastes* Cope, 1868 have been given in papers by, among others, Cope (1870), Williston (1898) and Russell (1967). Unfortunately, its dental characters have not received the same attention, and detailed descriptions of *Clidastes* teeth accompanied by adequate illustrations are absent. As discussed elsewhere (Lindgren and Siverson 2002), this is a common but deplorable situation in mosasaur research, resulting in valuable taxonomic information being overlooked.

The presence of *Clidastes* in early Campanian strata of southern Sweden has been discussed briefly in a number of abstracts (Lindgren 1998, 1999, 2001). The present communication provides an expanded description of the Swedish *Clidastes* remains and includes a detailed comparison of Swedish and North American material.

Geological setting

The Kristianstad Basin is limited to the south-west by the prominent Nävlingeåsen and Linderödsåsen horsts, and the marine Cretaceous reaches its maximum thickness (locally at least 250 m; Erlström and Gabrielson 1992) close to these fault structures. Towards the north the strata thin out and form an irregular boundary with several outliers. The

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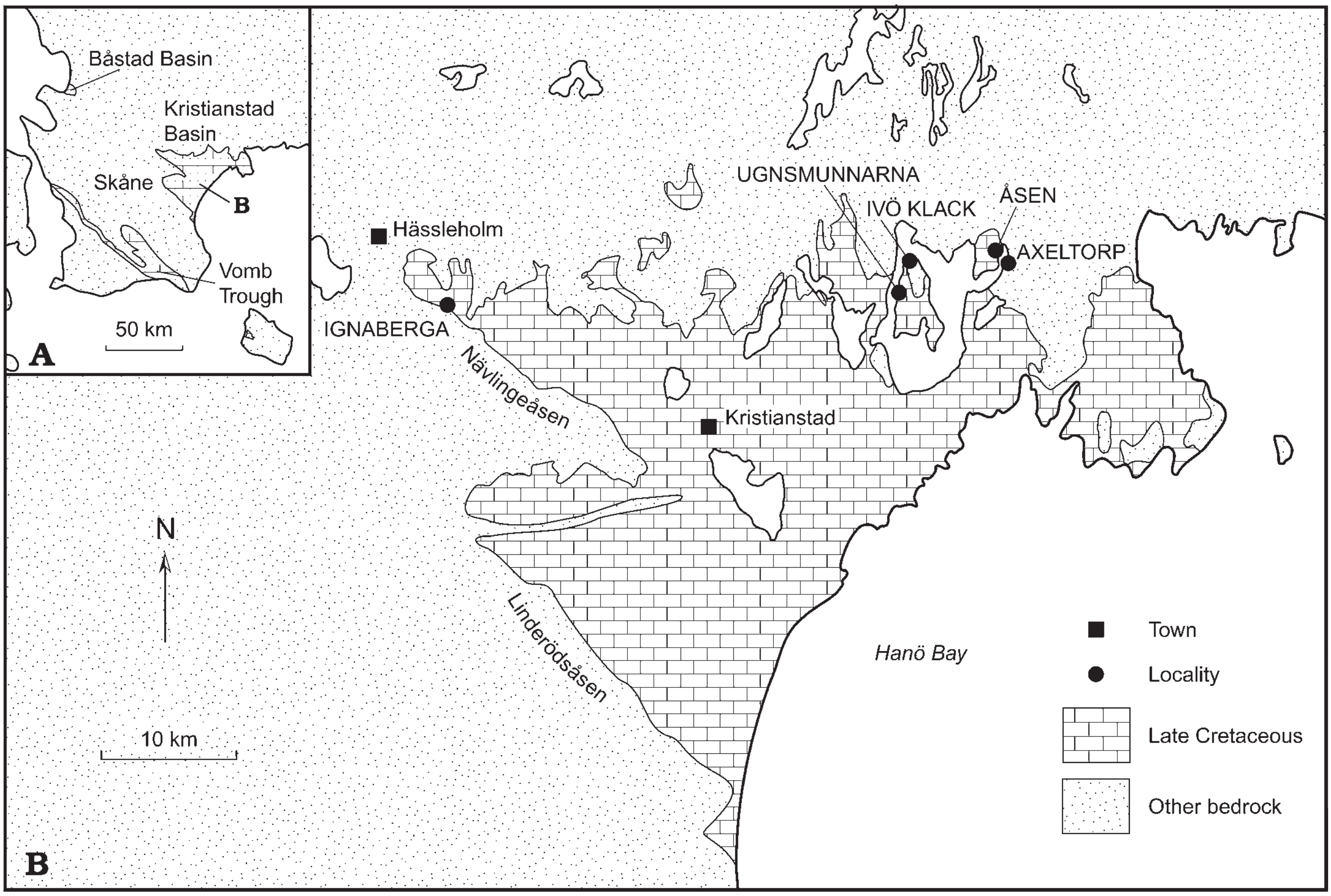

Fig. 1. **A**. Localization of Kristianstad Basin, Southern Sweden. **B**. Map of the Kristianstad Basin with the localities yielding remains of *Clidastes propython* Cope, 1869. The term "other bedrock" refers to both Precambrian and Phanerozoic rocks covered by Quaternary deposits. Slightly modified from Lindgren and Siverson (2002: fig. 1).

south-eastern border of the Kristianstad Basin is arbitrarily drawn along the coastline of the Hanö Bay (see Erlström and Gabrielson 1992: fig. 2), even though the Cretaceous bedrock extends eastward into the Baltic sea (e.g., Norling and Bergström 1987: fig. 4). A warm and humid climate throughout the Rhaetian to Middle Jurassic, and possibly also in the Early Cretaceous, resulted in extensive kaolinization of the principally Precambrian crystalline basement, where weathering resistant heights rose above the surrounding lowland (Lidmar-Bergström 1982). Tectonic block movements in the Early Cretaceous to early Campanian in the Late Cretaceous, formed a basin by tilting the basement towards the Nävlingeåsen and Linderödsåsen horsts (Bergström and Sundquist 1978). The area was flooded repeatedly during the Cretaceous (Christensen 1975; Norling 1981), and an archipelago with small islands and rocky shorelines was developed in the northern part during higher sea-level stands (Bergström and Sundquist 1978; Jensen 2002: 24).

Exposed strata of the latest early Campanian *Belemnellocamax mammillatus* zone comprises sandstones, more or less sandy calcarenites and calcirudites, resting upon either residual kaolin clay, reworked kaolin and quartz sand or directly upon the crystalline basement (Lundegren 1934). Numerous storm generated conglomerates with belemnite guards, coarse shell debris and pebbles of crystalline rocks, attest to a near shore depositional environment (Erlström and Gabrielson 1992). Five localities exposing sediments of latest early Campanian age, i.e. Åsen, Axeltorp, Ignaberga, Ivö Klack and Ugnsmunnarna (Fig. 1), have produced remains of *Clidastes* (for locality data, see Appendix).

Material and methods

The mosasaurian material from the Kristianstad Basin consists mainly of isolated, shed tooth-crowns and vertebral centra; the latter either found as isolated specimens or as natural associations comprising several consecutive vertebrae from a single individual. The generally fragmentary state of mosasaur bones from the Kristianstad Basin is largely a result of a shallow-water, high-energy depositional environment. Tooth-crowns, however, are generally well preserved and none of the bones shows any signs of compaction deformation.

The specimens from Ignaberga, Ugnsmunnarna and Åsen were collected by us and others (see Acknowledgements) over the last 15 years, whereas the material from Axeltorp and Ivö Klack is part of old collections dating back to the beginning of the twentieth century. There is a strong collecting bias towards larger vertebrate fossils in the Ivö Klack collections. This is, for example, the only site from which (the large) teeth of *Tylosaurus ivoensis* are the most common mosasaur fossils. The relatively large number of vertebrae (most of which would be much larger than the teeth from the same animals) from *C. propython* indicates that this species was common in the waters surrounding the Ivö Klack island and yet only a single tooth (RM PZ R1966) of this species is present in the Ivö Klack collections. Likewise, there are several vertebrae of an undescribed *Halisaurus* Marsh, 1869 in the Ivö Klack collections but not a single tooth. The smallish teeth of *Halisaurus* are otherwise relatively common in sieved residues from the *B. mammillatus* zone at Åsen.

Preparations of the teeth and vertebrae included removal of adhering carbonates with buffered acetic acid (see Jeppsson et al. 1999), and hardening by application of polyvinylbutyral in acetone. Illustrated specimens were coated with ammonium chloride prior to being photographed.

Institutional abbreviations.—BMNH, the Natural History Museum, London, England; LO, Department of Geology, Lund University, Lund, Sweden; PMU, Museum of Evolution, Palaeontology Section, Uppsala University, Uppsala, Sweden; RMM, Alabama Collections Center at McWane Center, Birmingham, Alabama, USA (former Red Mountain Museum collection); RM PZ, Swedish Museum of Natural History, Department of Palaeozoology, Stockholm, Sweden; YPM, Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA; YPM-PU, former Princeton University collection, now housed in the Peabody Museum of Natural History, Yale University, New Haven, Connecticut, USA.

Systematic palaeontology

Squamata Oppel, 1811
Mosasauridae Gervais, 1853
Mosasaurinae Gervais, 1853
Clidastes Cope, 1868

Type species: *Clidastes propython* Cope, 1869, from the early Campanian part of the Mooreville Chalk Formation of the Selma Group in west-central Alabama, USA (see Kiernan 1992; ICZN Opinion 1750).

Additional species: *Clidastes liodontus* Merriam, 1894. The (recently) frequently cited *C.* "*moorevillensis*" is unfortunately still a *nomen nudum* (Kiernan 2002). We have examined specimens of the latter from the Mooreville Chalk in Alabama, and they differ dentally from both *C. liodontus* and *C. propython* (see below).

Discussion.—The dental and vertebral morphology of *Clidastes* are closer to those of *Mosasaurus* Conybeare, 1822 than to any other mosasaurine. However, besides a marked difference in the maximum size of the teeth, marginal tooth-crowns of Campanian *Mosasaurus*, e.g., *M. missouriensis* (Harlan, 1834) and *M. conodon* (Cope, 1881) (the two oldest unquestionable *Mosasaurus*), differ from those of *Clidastes* in having a larger number of facets, which are also generally far more distinct than they are in *Clidastes*.

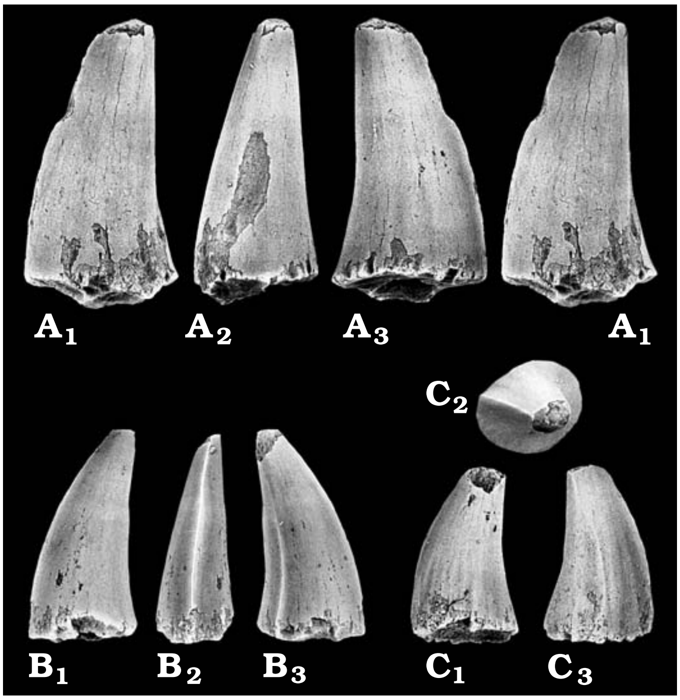

Fig. 2. *Clidastes propython* Cope, 1869, anteriorly situated marginal tooth-crowns of juvenile individuals, *Belemnellocamax mammillatus* zone, Åsen, Kristianstad Basin, southern Sweden; All × 3.5. **A**. RM PZ R1794, first premaxillary or first dentary tooth-crown; buccal (A_1, stereo pair), posterior (A_2), and lingual (A_3) views. Note the absence of a posterior cutting edge. **B**. RM PZ R1795, second premaxillary or second dentary tooth-crown; lingual (B_1), anterior (B_2), and buccal (B_3) views. **C**. RM PZ R1796, first premaxillary or first dentary tooth-crown; lingual (C_1), occlusal (C_2), and buccal (C_3) views.

Cervical vertebrae of *Clidastes* differ from those of *Mosasaurus* by their more elongated shape. The total vertebral length/condyle height relationship is about 2:1 in the juvenile *Clidastes* cervical centra from the Kristianstad Basin. This agrees very well with the data from North American *Clidastes* and sets them apart from the relatively shorter cervical centra of *Mosasaurus* (see Caldwell and Bell 1995).

The bases of the chevrons on caudal vertebrae are laterally compressed in *Mosasaurus* and extend anteriorly further towards the edge of the centrum than they do in *Clidastes* (see Kuypers et al. 1998: pl. 9: 11, and personal observation of *Mosasaurus*; RMM 3037, from the Demopolis Chalk of Alabama). In the latter, the bases of the chevrons are circular in cross-section, rather than antero-posteriorly elongated as they are in *Mosasaurus*.

The teeth from an undescribed mosasaurine in the *B. mammillatus* zone (referred to as a "*Liodon*-like" species by Lindgren and Siverson 2002: 79, and to *Dollosaurus* Yakovlev, 1901 by Lindgren and Siverson 2003) are similar to those of the coexisting *Clidastes* in being more or less symmetrically bicarinate (does not apply to the anteriorly situated teeth in either of the two species) and lacking basal striations. They differ mainly in being much larger (up to about 40 mm high compared to 20 mm for *Clidastes*), strongly recurved, having weakly serrated cutting edges (these are smooth in *Clidastes*) and very poorly developed facets or, more commonly, lacking facets altogether. A fragmentary dentary (RM PZ R1772) with associated teeth of the undescribed mosasaurine from the Maltesholm locality demonstrates that this skeletal element is very robust in this species. In contrast, the dentary is slender in *Clidastes*.

Clidastes propython Cope, 1869

For synonyms.—See Russel (1967).

Material examined (see also Table 1).—Marginal teeth: Åsen 100 teeth (LO 8231t, 8232t and 86 unnumbered, Lund University; RM PZ R1776, 1777, 1794–1803); Ignaberga, three teeth (all unnumbered, Lund University); Ivö Klack, one tooth (RM PZ R1966); Ugnsmunnarna, two teeth (both unnumbered, Lund University). Pterygoid teeth: Åsen, 13 teeth (RM PZ R1804, 1805; 11 unnumbered, Lund University). Jawbones: Ugnsmunnarna, four fragments (of which one is a pterygoid) from a large individual (RM PZ R1790–1793). Cervical vertebrae: Åsen, four vertebrae (RM PZ R1778, 1779, 1782, 1789); Axeltorp, one axis vertebra from a very large individual (RM PZ R1752a–b); Ivö Klack, one vertebra (unnumbered, Department of Geology and Geochemistry, Stockholm University). Dorsal vertebrae: Åsen, two vertebrae (RM PZ R1780, 1781). Cervical/dorsal vertebrae: Åsen, six vertebrae (RM PZ R1783–1788). Terminal caudal vertebrae: Åsen, 11 vertebrae (RM PZ R1806–1816); Ivö Klack, 10 vertebrae (one unnumbered, Lund University; PMU R415, 417, 1255; RM PZ R911, 958, 1015, 1027, 1028, 6081).

Occurrence.—*Clidastes propython* has been recorded in the early Campanian Mooreville Chalk, Alabama (Russell 1967, 1970; Shannon 1977; Bell 1985; Wright 1986a, b; Kiernan 2002); the early Campanian Roxton Limestone, Texas (Echols 1972); the early Campanian lower Pierre Shale, Colorado (Carpenter 1990); the middle Santonian to earliest Campanian part of the Smoky Hill Chalk Member of the Niobrara Formation, Kansas (Everhart 2001); the late early Campanian Sharon Springs Member of the lower Pierre Shale, Kansas and South Dakota (Russell 1967); the earliest Campanian part of the Niobrara Formation, South Dakota, (Russell 1967; Martin et al. 1998), and the late early Campanian part of the Pembina Member of the Pierre Shale, southern Manitoba (Nicholls 1987, 1988).

Description.—*Marginal teeth*. Premaxillary and the most anteriorly situated dentary tooth-crowns are posteriorly curved and more or less oval in basal cross-section (Figs. 2, 3B). The teeth are equipped with a strong anterior carina (Fig. 2B_2) and a weak, often incomplete (may be absent altogether; Fig. 2A_2) bucco-posterior carina (both carinae without serrations). The buccal surface is relatively narrow and gently convex, while the lingual face is strongly U-shaped. The lingual surface lacks distinct facets, whereas two or three buccal facets may be present on teeth from juvenile individuals. There is only one tooth of a large, presumably adult animal from this part of the marginal dentition present in our collection, and it lacks both buccal and lingual facets. The tooth-crowns are up to approximately 17–18 mm high (estimated original height and width of RM PZ R1776, a basally and apically incomplete 11.5 mm high crown).

Maxillary and the corresponding dentary tooth-crowns are up to 19 mm high (estimated original height of RM PZ R1777, a 15 mm high crown with a worn apex and an incomplete base). In lateral view, the tooth-crowns have a triangular outline with an upright (Fig. 4D) to slightly medio-posteriorly curved apex (Fig. 4B). In occlusal view, the prominent

Table 1. Recorded remains (154 specimens) of *Clidastes propython* Cope, 1869 from the *Belemnellocamax mammillatus* zone.

Localities	Marginal teeth	Pterygoid teeth	Cervical vertebrae	Dorsal vertebrae	Cervical/dorsal vertebrae	Terminal caudal vertebrae
Åsen	100	13	4	2	6	11
Axeltorp			1			
Ignaberga	3					
Ivö Klack	1		1			10
Ugnsmunnarna	3					
∑	106	13	6	2	6	21

Fig. 3. *Clidastes propython* Cope, 1869; all × 3.5. **A**. Premaxillary or first or second dentary tooth-crown of YPM 1319, late Santonian to earliest Campanian part of the Smoky Hill Chalk Member of the Niobrara Formation in western Kansas, USA; buccal (A_1, stereo pair), anterior (A_2, stereo pair), and lingual (A_3) views. **B**. RM PZ R1797, second premaxillary or second dentary tooth-crown from a juvenile or sub-adult individual, *Belemnellocamax mammillatus* zone, Åsen, Kristianstad Basin, southern Sweden; anterior (B_1, stereo pair) and buccal (B_2, stereo pair) views. **C**. *Clidastes propython* Cope, 1869, late Santonian to earliest Campanian part of the Smoky Hill Chalk Member of the Niobrara Formation in western Kansas, USA. YPM 1319, buccal (C_1, stereo pair), occlusal (C_2), and lingual (C_3, stereo pair) views; a crown from the mid-portion of the jaw. **D**. *Clidastes liodontus* Merriam, 1894, late Coniacian to earliest Campanian Smoky Hill Chalk Member of the Niobrara Formation in western Kansas, USA. YPM-PU 17249, buccal (D_1, stereo pair), occlusal (D_2), and lingual (D_3, stereo pair) views; the eleventh left dentary tooth.

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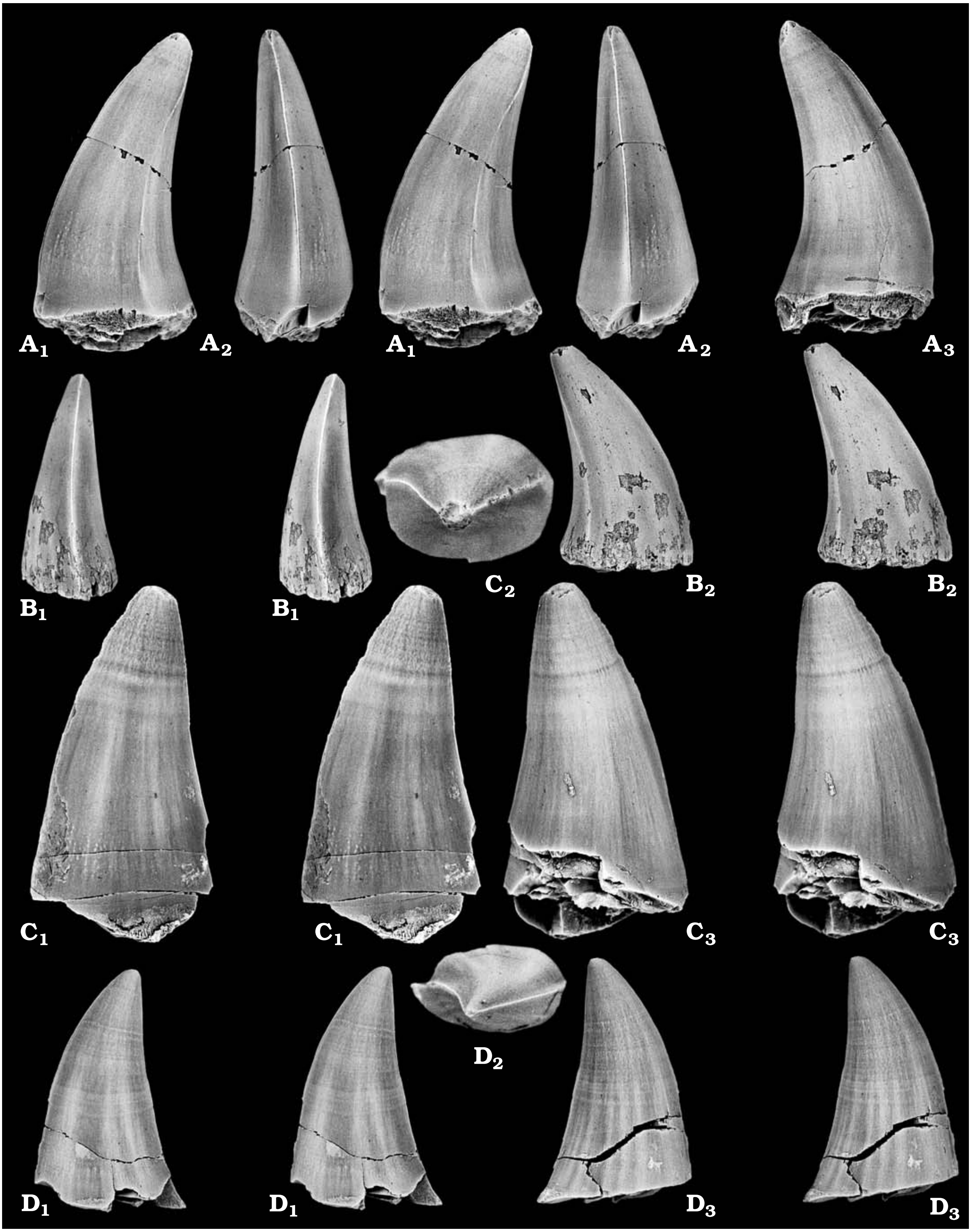
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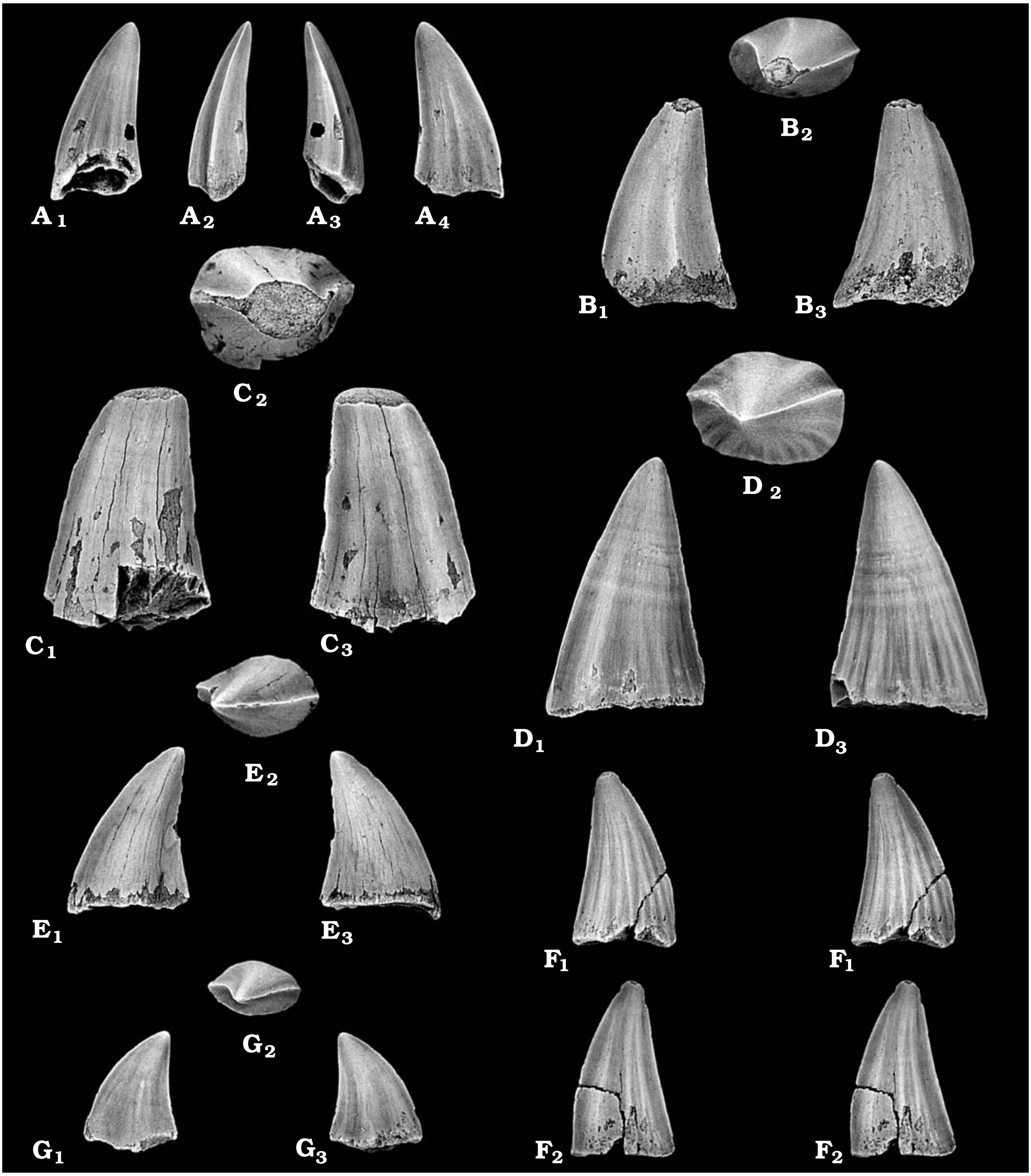

Fig. 4. *Clidastes propython* Cope, 1869, marginal tooth-crowns, *Belemnellocamax mammillatus* zone, Åsen, Kristianstad Basin, southern Sweden; all × 3.5. **A**. LO 8231t, a tooth-crown from a small juvenile; lingual (A_1), anterior (A_2), posterior (A_3), and buccal (A_4) views. **B**. LO 8232t, a crown from the mid-portion of the jaw; buccal (B_1), occlusal (B_2), and lingual (B_3) views. **C**. RM PZ R1799, a large tooth-crown from the anterior part of the mid-portion of the jaw; lingual (C_1), occlusal (C_2), and buccal (C_3) views. **D**. RM PZ R1798, a large crown from the mid-portion of the jaw; buccal (D_1), occlusal (D_2), and lingual (D_3) views. **E**. RM PZ R1801, a crown from the posterior portion of the jaw; buccal (E_1), occlusal (E_2), and lingual (E_3) views. **F**. RM PZ R1800, a juvenile crown from the anterior part of the mid-portion of the jaw; lingual (F_1, stereo pair) and buccal (F_2, stereo pair) views. **G**. RM PZ R1803, a crown from the posterior portion of the jaw; buccal (G_1),occlusal (G_2), and lingual (G_3) views.

anterior and posterior carinae divide the crown into an angular buccal face (does not apply to the most posteriorly situated teeth, in which both sides are gently rounded) and an equally large (the most posteriorly situated teeth; Fig. $4E_2$) to much larger (anteriorly situated teeth; Fig. $4C_2$) lingual face. The lingual surface has a rounded (Fig. $4B_2$) to sub-rectangular (Fig. $4D_2$) basal cross-section. Most teeth have facets; three to four on the buccal face and five to ten, usually less distinct, on the lingual face. The buccal facets are indistinct on most of the larger teeth (e.g., Fig. $4C_3$). The most anteriorly situated maxillary and corresponding dentary teeth are relatively more slender in lateral view (but thicker bucco-lingually) than are teeth from a more posterior position.

Crowns from the posterior part of the maxillae and dentaries are comparatively short and wide, with buccal and lingual surfaces of equal convexity (Fig. 4G). In lateral view, the anterior margin is strongly curved medio-posteriorly, while the posterior margin is straighter. The enamel-covered surfaces are either smooth or obscurely faceted, and are separated from one another by marked anterior and posterior carinae. In basal cross-section, the crowns have a thick oval outline.

Pterygoid teeth.—Pterygoid tooth-crowns (Fig. 5) are up to 8 mm high and 5.5 mm wide at the base. The crowns are strongly distally curved in lateral view. The surface of the enamel is entirely smooth. An indistinct antero-buccal carina and a much stronger posterior cutting edge separate the crown into a flat to gently convex external surface and a strongly convex lingual side. The outline of the basal cross-section has the shape of a swollen ellipse.

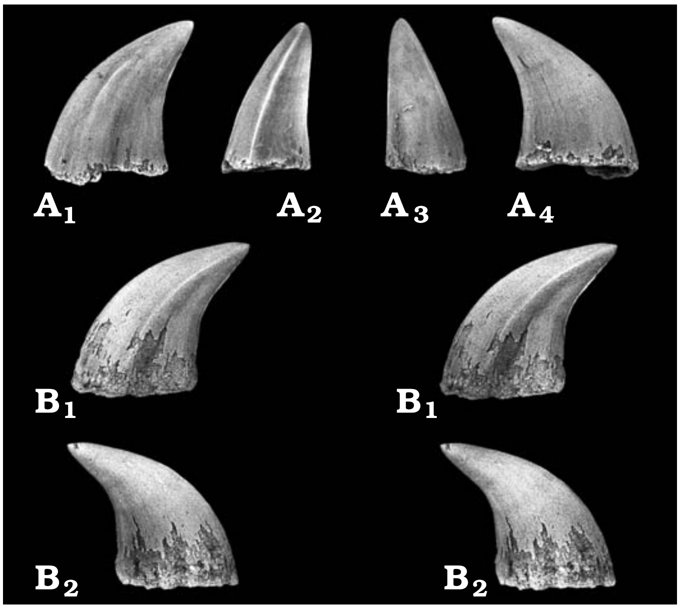

Fig. 5. *Clidastes propython* Cope, 1869. Pterygoid tooth-crowns, *Belemnellocamax mammillatus* zone, Åsen, Kristianstad Basin, southern Sweden; all × 3.5. **A**. RM PZ R1804, buccal (A_1), posterior (A_2), anterior (A_3), and lingual (A_4) views. **B**. RM PZ R1805, buccal (B_1, stereo pair) and lingual (B_2, stereo pair) views.

Cervical vertebrae.—An associated group of eleven fragmentary cervicals and dorsals from Åsen (RM PZ R1778–1788), representing a juvenile individual, are indistinguishable from the corresponding vertebrae in similarly-sized *Clidastes propython* from the upper Smoky Hill Chalk Member, Niobrara Formation, in western Kansas, and the Mooreville Chalk of west-central Alabama. In addition to the former vertebrae, we also refer three isolated cervicals from Ivö Klack (unnumbered, Department of Geology and Geochemistry, Stockholm University), Axeltorp (RM PZ R1752a–b) and Åsen (RM PZ R1789) respectively, to *C. propython*. The three best preserved cervical vertebrae (two from the natural association of juvenile vertebrae from Åsen and a very large axis vertebra from Axeltorp) are described separately below.

RM PZ R1778 (Fig. 6A) is the third, or possibly fourth, cervical from a small juvenile (estimated total length of 2–2.5 m). The condyle articulation is sub-triangular in outline with rounded apices, and is wider than it is tall (12.8 mm wide and 10.4 mm high). Basal remains of the right half of the neural arch indicate that the neural canal was wide (approximately 8 mm at its base). Only the most proximal part of the right synapophysis is preserved, and it is situated on the anterior portion of the lateral surface of the centrum. The hypapophyseal peduncle is large and occupies more than half of the length of the, incomplete, ventral surface of the centrum. The cotyle is very incomplete, and only the most central parts of the surface are preserved. The length of the vertebral centrum is 21.1 mm, as measured between the centres of the interarticular surfaces.

RM PZ R1779 (Fig. 7A) is the sixth or possibly seventh cervical. The condylar articulation surface is kidney-shaped and wider than it is high (14.2 mm and 10.8 mm, respectively). In lateral view, the posterior margin of the right (and only preserved) half of the neural arch is evenly curved and terminates in a slightly abraded but clearly visible posterior zygapophysis. A rudimentary hypapophyseal peduncle occupies the posterior half of the ventral surface of the centrum. As in RM PZ R1778, only the central parts of the cotyle surface are preserved. The length of the centrum (measured between the centres of the interarticular surfaces) is 21.5 mm.

RM PZ R1752 (Fig. 6C) comprises two fragments (1752a and 1752b) of an axis vertebra from a very large individual (estimated total length of 6.0 m). The larger of the two parts (1752a, Fig. $6C_1$, C_3, C_4) includes a well preserved posterior (condyle) articulating surface, a portion of the hypapophyseal peduncle and the posterior edge of both the left and the right synapophysis. The condyle measures 34.9 mm in width and 32.3 mm in height. The hypapophyseal peduncle has an almost straight posterior border and is very wide, measuring 25.5 mm in basal width. Nothing of the anterior surface is preserved on this fragment. The total length of RM PZ R1752a is 56 mm.

The smaller fragment (1752b, Fig. $6C_2$) comprises the upper left portion of the anterior end of the centrum. It includes the anterior edge of the base of the left leg of the neural arch

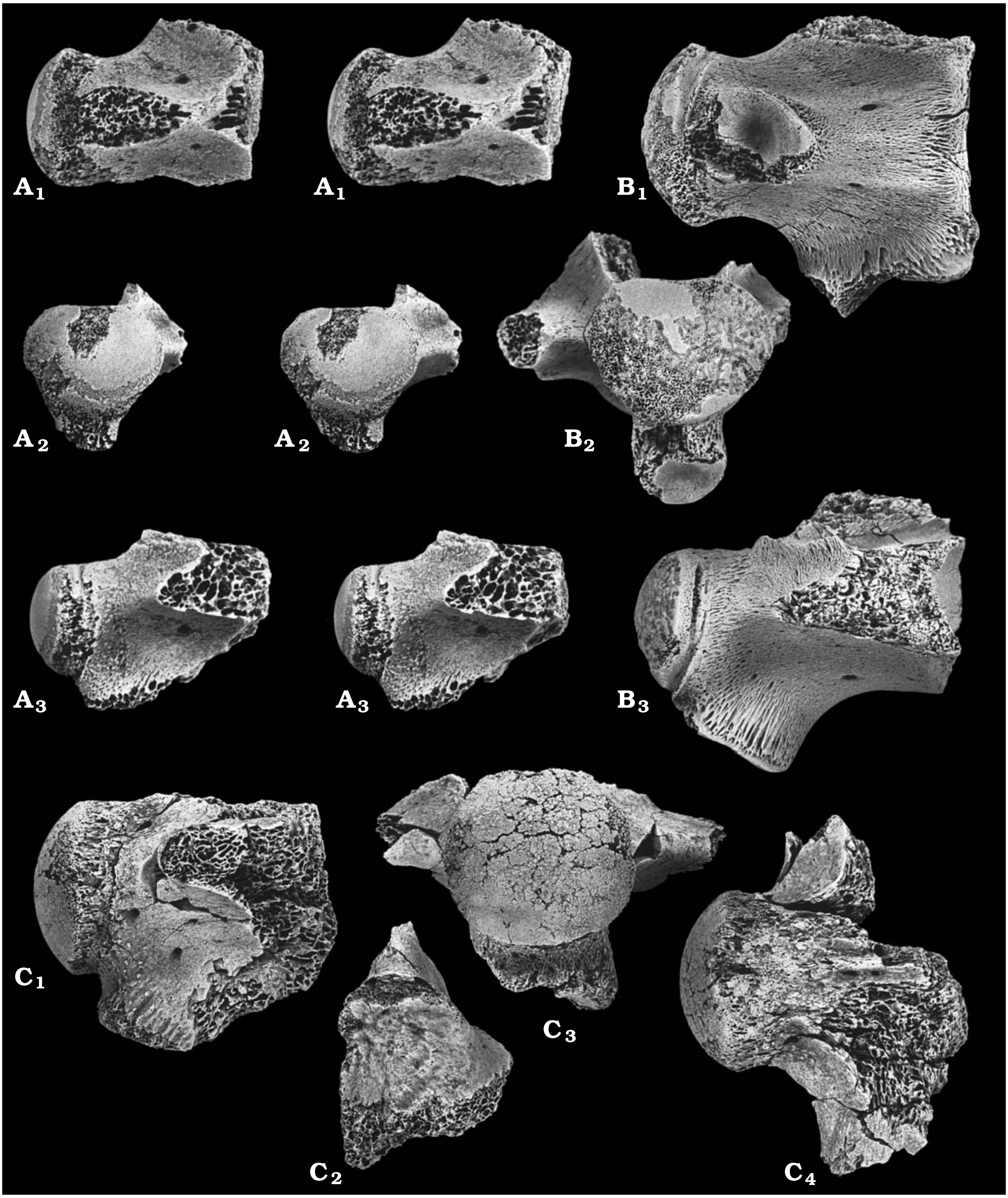

Fig. 6. *Clidastes propython* Cope, 1869. **A**. RM PZ R1778, the third? cervical vertebra from a juvenile individual, *Belemnellocamax mammillatus* zone, Åsen, Kristianstad Basin, southern Sweden, × 2.0; ventral (A_1, stereo pair), posterior (A_2, stereo pair), and lateral (A_3, stereo pair) views. **B**. *Clidastes propython* Cope, 1869, the third? cervical vertebra of YPM 1123, late Santonian part of the Smoky Hill Chalk Member of the Niobrara Formation in western Kansas, USA, × 2.0; ventral (B_1), posterior (B_2), and lateral (B_3) views. **C**. RM PZ R1752, two fragments (R1752a, C_1, C_3, C_4 and R1752b, C_2) of an axis vertebra from a very large individual, *Belemnellocamax mammillatus* zone, Axeltorp, Kristianstad Basin, southern Sweden, × 1.0; lateral (C_1), anterior (C_2), posterior (C_3), and dorsal (C_4) views.

Fig. 7. **A**. *Clidastes propython* Cope, 1869. *Belemnellocamax mammillatus* zone, Åsen, Kristianstad Basin, southern Sweden, × 2.0. RM PZ R1779, most likely the sixth or seventh cervical vertebra (the same animal as RM PZ R1778); ventral (A_1, stereo pair), posterior (A_2, stereo pair), and lateral (A_3, stereo pair) views. **B**. *Clidastes propython* Cope, 1869, earliest Campanian part of the Smoky Hill Chalk Member of the Niobrara Formation in western Kansas, USA, × 2.0. YPM 40354, most likely the sixth or seventh cervical vertebra; ventral (B_1), posterior (B_2), and lateral (B_3) views.

and the upper left corner of the rough anterior surface connecting the vertebra to the atlas.

Dorsal vertebrae.—Two partial vertebral centra (RM PZ R1780–1781) are identified as dorsal vertebrae (these specimens are part of the Åsen association). The specimens possess sub-triangular to kidney-shaped condylar articulations, and are distinguished from cervicals by their lack of a hypapophyseal peduncle. As preserved, the more complete of the two specimens (RM PZ R1780) is 21 mm long and 13.4 mm wide (measured between the centres of the interarticular surfaces and on the condyle, respectively). Basal remains of the neural arch, the posterior edge of the right synapophysis, and the central parts of the cotyle are preserved on the specimen.

Caudal vertebrae.—All caudal vertebral centra of *C. propython* from the *B. mammillatus* zone are terminal caudals. The most proximally situated vertebrae have circular articulations and are considerably shorter (measured between the centres of the central articulations) than the width and height of the condyle and cotyle. Further back, the centra retain a more or less circular articular outline, whereas the relative length of the centra increases, approaching the width and the height of the central articulations. One of the illustrated specimens (RM PZ R1027; Fig. 8A) with this morphology is from a large, presumably adult, individual. The vertebra is 29.0 mm high, 27.5 mm wide and 25.0 mm long (measured on the condyle and between the centres of the central articulations). On some specimens (including RM PZ R1027) a delicate but distinct crest runs along the medial margin of each chevron (Fig. $8A_3$).

The most distally situated terminal caudal vertebrae have vertically oval to barrel-shaped central articulations. The centra are longer than wide, whereas the height is similar to the length. The illustrated specimen (PMU R417; Fig. 8C) in this category is 13.4 mm high, 12.1 mm wide and 13.7 mm long (measured on the condyle and between the centres of the interarticular surfaces). This particular specimen is not as markedly barrel-shaped as some of the other caudals of this group from the Åsen and Ivö Klack localities.

Comparisons.—In addition to a number of skeletal features (see e.g., Russell 1967); *C. propython* can be separated from *C. liodontus* by the morphology of its marginal teeth (personal observations of e.g., BMNH R4547, YPM 1100, 1318, 1319; *C. propython*, YPM 1335, 3996 and YPM-PU 17249; *C. liodontus*). In *C. propython*, tooth-crowns from the mid-portion of the dental ramus have a lingual side usually markedly larger than the buccal one (Figs. $3C_2$ and $4D_2$), approaching the asymmetry seen in marginal teeth of *Mosasaurus*. The corresponding crowns of *C. liodontus* are symmetrically bicarinate (Fig. $3D_2$). Moreover, lateral and posterior tooth-crowns of *C. propython* are generally thicker bucco-lingually than are the rather flattened crowns of *C. liodontus*. We have found no dental differences (neither in juveniles nor in adults) between the Kristianstad Basin population of *C. propython* and those of the Mooreville Chalk of Alabama and uppermost Smoky Hill Chalk of Kansas.

Examination of reasonably complete *Clidastes* skeletons (e.g., RMM 070, 2986) housed at McWane Center (former Red Mountain Museum collection) in Birmingham, Alabama, USA, supports Bell's (1997) conclusion that the Mooreville Chalk contains a third, hitherto undescribed, species of *Clidastes* (informally denominated *C. moorevillensis* by Bell). Besides a marked difference in size (tooth-crowns of *C.* "*moorevillensis*" are considerably larger than are those of similarly sized *C. propython*), marginal teeth from the mid-portion of the jaw in *C. propython* can be separated from those of *C.* "*moorevillensis*" by their moderately recurved crowns. In *C.* "*moorevillensis*", tooth-crowns from a mid-lateral position are strongly distally curved, whereas the corresponding crowns of *C. propython* are more upright. A second distinguishing character might be the development of granulae on the antero-basal part of the buccal face of the crowns. Marginal tooth-crowns of *C. propython* occasionally display a small number of indistinct swellings on the buccal face, whereas the lower half of the external surface is covered with more conspicuous small bumps in those specimens of *C. moorevillensis* that we have examined.

Cervical and anteriorly situated thoracic vertebrae of small individuals of *C. propython* can be distinguished from those of *C. liodontus* by the shape of the central articulations. Small-sized individuals of *C. propython* (e.g., YPM 1123—early juvenile, according to Sheldon 1996, 40354, and see list of material above) have cervical and anteriorly situated thoracic vertebrae with sub-triangular to kidney-shaped central articulations, which are wider than high (Figs. $6B_2$, $7B_2$). In larger (adult) individuals of this species (e.g., YPM 1100, 1316 and RM PZ R1752a-b) the interarticular surfaces have a sub-circular outline (Fig. $6C_3$). In *C. liodontus* (e.g., YPM 3996, 24914, YPM-PU 17249) the cotyle and condyle articulations are more or less circular in both small and large individuals.

In having kidney-shaped central articulations, cervical vertebrae of juvenile *C. propython* somewhat resemble those of *Platecarpus* Cope, 1869 (a genus represented by *P.* cf. *somenensis* and possibly also *Platecarpus*? sp. in the *B. mammillatus* zone of the Kristianstad Basin, see Lindgren and Siverson 2003). However, cervicals of *Platecarpus* are very stout compared to the slender and elongated centra of *C. propython*. They are also significantly shorter relative to their condyle and cotyle widths than are the cervical centra of *Clidastes* (see Caldwell and Bell 1995).

In 1914, Pravoslavlev described a new nominal species of *Mosasaurus*, i.e. *M. donicus*, from the Don Province in Russia. The type specimen comprises an incomplete intermediate caudal vertebra and a marginal tooth-crown (Pravoslavlev 1914: pl. 1), found in strata of late early Campanian age in the Liski River Basin. Subsequently, in a work devoted to the history of mosasaur research in Russia, Yarkov (1993) referred *M. donicus* to *Clidastes*. Judging from the description and illustrations in Pravoslavlev (1914: pl. 1: 1–4), the caudal vertebra has typical mosasaurine proportions and displays fused chevrons of the haemal arch. The tooth-crown is large and robust (45 mm high in lingual view) with smooth enamelled surfaces (Pravoslavlev 1914: pl. 1: 5). In cross-section, the crown has a gently convex buccal face and a deeply U-shaped lingual surface (Pravoslavlev 1914: pl. 1: 6). The large size and overall morphology of the tooth-crown are inconsistent with an assignment to *Clidastes*.

Discussion.—Marginal tooth-crowns of *Clidastes* have been described as displaying smooth enamel by several workers (e.g., Russell 1967; Thurmond and Jones 1981), even though some (e.g., Williston 1898; Bell and Sheldon 1986) have observed facets on teeth of this mosasaur. Recently, Bell (1997) pointed out that marginal teeth in many juvenile and a few

Fig. 8. *Clidastes propython* Cope, 1869. Posteriorly situated terminal caudal vertebrae, *Belemnellocamax mammillatus* zone, Ivö Klack, Kristianstad Basin, southern Sweden; all × 2.0. **A**. RM PZ R1027, a vertebra from a large individual; anterior (A_1), lateral (A_2, stereo pair), ventral (A_3, stereo pair), and posterior (A_4) views. **B**. PMU R415, anterior (B_1), lateral (B_2), and dorsal (B_3, stereo pair) views. **C**. PMU R417, anterior (C_1), lateral (C_2), ventral (C_3), and posterior (C_4) views.

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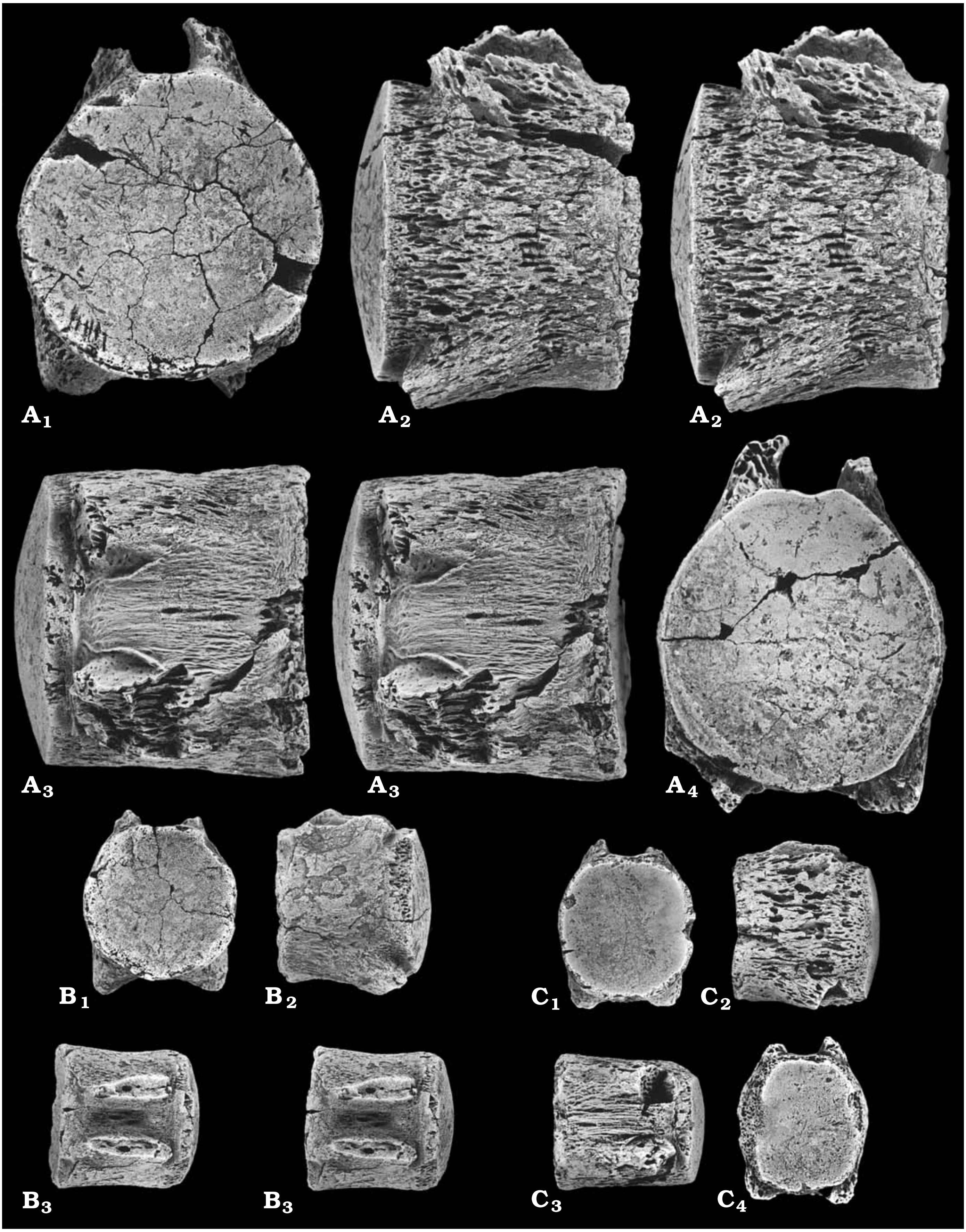
A1
A2
A2
A3
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A4
B1
B2
C1
C2
B3
B3
C3
C4

larger specimens of *Clidastes* possess three distinct facets on the medial [*sic*] face (this is almost certainly a typographical error, as this number of facets is typical for the buccal side of the crown). Our own examination of marginal teeth of Smoky Hill Chalk *C. propython* (BMNH R4547, YPM 1100, 1318, 1319) and *C. liodontus* (YPM 1335, 3996, YPM-PU 17249) largely confirmed Bell's observation, although it is not uncommon with four buccal facets. Facets are usually more distinct on tooth-crowns from small- to moderate-sized (juvenile) individuals (e.g., Fig. 4A, F) than on crowns from large (adult) animals (e.g., Fig. 4C).

Palaeobiogeography

Exposed Cretaceous sediments in the Kristianstad Basin range from the early or middle Santonian to the earliest Maastrichtian (in belemnite terms, see Christensen 1975, 1997). There are several hiatuses in the sedimentation record. Much of the early Campanian (except for its earliest and latest parts) is missing. A minor hiatus marks the early/late Campanian boundary (at Åsen; see below) whereas the earliest Maastrichtian rests disconformably on the early late Campanian. The latter hiatus, spanning the later two thirds of the late Campanian, equals approximately 6 Ma. Very few mosasaur remains have been collected from the early/middle Santonian to earliest Campanian interval. The possibly oldest mosasaur fossil from the Kristianstad Basin is an incomplete tooth-crown (LO 4085) of a "russellosaurine" mosasaur from the Ringeleslätt quarry (see Persson 1963). It originates from an unknown horizon in the quarry. Biostratigraphically, the strata at this locality ranges from the late early Santonian-early middle Santonian *Gonioteuthis westphalica* Zone to the earliest early Campanian *G. granulataquadrata* Zone (Christensen 1975, 1997).

A rich vertebrate assemblage from one of the Ullstorp quarries (Ullstorp 1, conglomerate C *sensu* Erlström and Gabrielson 1986) comprises hundreds of selachian teeth, chimaeroid tooth plates, bones and teeth of teleosts, relatively abundant crocodile remains (*Aigialosuchus* Persson, 1959), a single worn dinosaur tooth (ornithopod), a few plesiosaur teeth, and a fragment of a mosasaur tooth, probably of a *Platecarpus*. Associated belemnites indicate an earliest Campanian age (*Gonioteuthis granulataquadrata* Zone; unpublished data). Notable is the extreme rarity of mosasaurs (and total absence of *Clidastes* and *Halisaurus*, which are the most common mosasaurs in the *B. mammillatus* zone) relative to that of other large predators (i.e. lamniform sharks) that otherwise occur abundantly also in the younger *B. mammillatus* zone.

As the sea flooded the area again in the latest early Campanian, it brought with it one of the most diverse mosasaur faunas known from anywhere in the world. Species identified include *Platecarpus somenensis*, *Platecarpus*? sp. (a very large plioplatecarpine), *Tylosaurus ivoensis*, *Hainosaurus* sp., *Dollosaurus* sp., *Clidastes propython*, *Halisaurus* sp., and possibly yet another mosasaurine (Lindgren and Siverson 2003).

The occurrence of *C. propython* in southern Sweden extends the palaeobiogeographical range of both the species and the genus beyond North America. Previous records of *C. propython* are restricted to the Western Interior of North America and the Gulf Coastal Plain of the USA (e.g., Russell 1967, 1970; Nicholls 1988; Kiernan 2002). The spatial distribution of mosasaurs in the Western Interior Seaway of North America suggests that *Clidastes* was adapted to warm temperate to subtropical environments (Nicholls and Russell 1990), which probably ruled out an arctic migration route across central Canada (see Kauffman 1984: fig. 11). It seems more likely that it spread to north-west Europe via the east coast of North America and perhaps southern Greenland. However, reports of *Clidastes* from the eastern coast of the USA are surprisingly few. In a list of fossils from the late early Campanian Merchantville Formation in New Jersey, Gallagher (1984) included a single tooth identified as *Clidastes* sp. by Miller (1955). As the specimen has neither been formally described nor figured (William B. Gallagher, personal communication 2001), it is at present not possible to determine whether the tooth should be assigned to *Clidastes* or not. Lauginiger (1984) referred isolated mosasaurian teeth from Campanian sediments dredged from the Chesapeake and Delaware canal in Delaware to *Clidastes* cf. sp. The material was recovered from spoil heaps which included sediments from the Mount Laurel, Merchantville, Englishtown and Marshalltown formations. Unfortunately, the meagre description in combination with the lack of precise stratigraphic information complicate an evaluation of Lauginiger's identification. The rarity of reports of *Clidastes* from latest early Campanian sediments along the Atlantic Coastal Plain is somewhat puzzling, considering that this would be a natural route towards Europe for a North American marine reptile adapted to a life in warm temperate to subtropical neritic environments. The absence of *Clidastes* in Niobrara-equivalent strata of southern Sweden indicates that the migration event took place sometime during the early, but not earliest, Campanian.

A major faunal turnover amongst the mosasaurs took place near the early/late Campanian boundary (*sensu germanico*) in the Western Interior Seaway (Russell 1967, 1993), Texas (Echols 1972) and Alabama (Kiernan 2002). *Clidastes*, *Platecarpus* and *Tylosaurus* Marsh, 1872 that dominated Niobrara-age faunas were abruptly replaced by mainly *Mosasaurus*, *Plioplatecarpus* Dollo, 1882, and *Prognathodon* Dollo, 1889. The precise timing of the turnover between the three areas has not been determined but the local extinctions might represent an isochronous event. Correlation is complicated by difficulties applying the detailed ammonite zonation of the Western Interior (for which a three-fold division of the Campanian is employed) to the Gulf Coast. In the Kristianstad Basin (and northern Europe; see Christensen 1996), the end of the early Campanian is marked by the extinction of the belemnite genus *Gonioteuthis* Bayle, 1878.

This datum seems to coincide with the highest occurrence of *Belemnellocamax mammillatus* (Nilsson, 1826). All evidence suggests that the latter species evolved into *B. balsvikensis* (Brotzen, 1960), which is known almost exclusively from southern Sweden (Christensen 1976). The probably oldest population of *B. balsvikensis* is from the basal 0.5 m of the *B. balsvikensis* zone at Åsen (Walter K. Christensen, personal communication 2002). Here, the top of the *B. mammillatus* zone is cut off by an erosional surface with burrows, immediately overlain by a lag deposit comprising reworked *B. mammillatus*. The uppermost 0.5 m of the *B. mammillatus* zone is a highly calcareous sand with numerous, often articulated oysters and abundant *B. mammillatus*. A thorough investigation of the *B. balsvikensis* zone in the Kristianstad Basin, combined with a critical evaluation of North American records of mosasaurs across the early/middle (and early/late, where a two-fold division is used) Campanian boundary, could provide us with a unique opportunity to study an extremely critical interval in mosasaur evolution and directly compare the order of events between two continents. Although several localities expose strata of the *B. balsvikensis* zone, the Åsen locality does probably have the best potential as it is the only locality exposing (after some excavation) the early/late Campanian boundary (*sensu germanico*) in the area and preserves the probably oldest known part of the *B. balsvikensis* zone. The bulk of this local belemnite zone correlates with the *Echinocorys conica/Belemnitella mucronata senior* Zone in the German standard zonation of the late Campanian, although the upper part of the *B. balsvikensis* zone might correlate with the lower part of the *Galeola papillosa basiplana/Trachyscaphites spiniger* Zone (Christensen 1976; see also Schönfeld et al. 1996: fig. 3).

Our preliminary results from limited sampling of the *B. balsvikensis* zone seem to mirror those in North America but more material is needed. First of all, mosasaur remains, and to some extent other vertebrates, are less common in the *B. balsvikensis* zone than they are in the underlying *B. mammillatus* zone. We have collected only three mosasaur teeth from the *B. balsvikensis* zone at Åsen, two *Tylosaurus ivoensis* and one *C. propython*. The colour and state of preservation of the latter indicate reworking from the *B. mammillatus* zone, whereas the *Tylosaurus* teeth are very well preserved and do not appear to be reworked. Although there are only two non-reworked teeth from the basal *B. balsvikensis* zone at Åsen, they tell a story of faunal disintegration. In the underlying *B. mammillatus* zone, there would have been about half a dozen of teeth of *Platecarpus* cf. *somenensis*, a couple of *Dollosaurus*, and 20–30 teeth of both *C. propython* and *Halisaurus* sp. for every two *T. ivoensis*.

A single tooth of *Prognathodon*? sp. has been collected from the lower part of the *B. balsvikensis* zone at Västra Olinge (the strata at this locality were erroneously assigned to the *B. mammillatus* zone by Christensen in 1975, who must have based his opinion on mislabelled material). Again, a totally anomalous occurrence had it been in the *B. mammillatus* zone, as this species does not occur in the latter biozone.

In summary, the very limited material at hand from the basal part of the late Campanian is nonetheless significantly different in composition from that of the *B. mammillatus* zone and indicates an abrupt faunal turnover at the early/late Campanian boundary. The fact that this turnover seems to coincide more or less precisely with that in North America (even in markedly different environments; i.e., nearshore rocky coast, warm temperate waters in the Kristianstad Basin vs. offshore subtropical in Alabama) suggests that an intercontinental event, or a series of events, near the early/late Campanian boundary wiped out a mosasaur community that had been in place for quite some time. It is hard to otherwise explain why a seemingly very healthy and diverse mosasaur fauna abruptly disappears almost entirely at the same time on two separate continents.

Palaeoecology

Williston (1897) remarked that remains of *Clidastes* were restricted to the upper part of the Smoky Hill Chalk in western Kansas, in deposits interpreted by him as representing generally shallower waters than those at the base of the chalk. Russell (1967) examined mosasaurian material from the Smoky Hill Chalk in western Kansas, collected during the Yale expeditions of 1871 and 1874, and noticed that the relative abundance of *Clidastes* increased in the upper levels of the member, in beds also rich in pterodactyls and toothed birds (see Williston 1897). This observation led Russell (1967) to conclude that *Clidastes* inhabited nearshore waters. Martin and Rothschild (1989) suggested that *Clidastes* was a surface dwelling species, as they found no signs of avascular necrosis (a decompression syndrome caused by gas bubbles interrupting the blood supply to a skeletal element) in bones of this mosasaur. Sheldon (1996), on the other hand, pointed out that Hattin (1982) had interpreted the upper beds of the Smoky Hill Chalk as being deposited in deeper water (approaching 300 m) than the lower part of the member. Collection data available at that time indicated that *Clidastes* did not occur in the lower part of the chalk (i.e. below Hattin's marker unit 9, but see Everhart 2001), and hence Sheldon (1996) concluded that there were no verified records of *Clidastes* in nearshore sediments of the Smoky Hill Chalk Member. In a subsequent publication, Sheldon (1997) demonstrated that the ribs of adult *Clidastes* are porous, and suggested that they were filled with significant quantities of lipids in life. Based on comparisons with extant marine vertebrates with similar bone architecture, she stated that the reduced bone density in adult *Clidastes* indicates that it ranged in deeper-water environments. The lack of compression bends in bones of *Clidastes* (see Martin and Rothschild 1989) was explained by the ability of the mosasaur to reduce its lung volume during deep dives, which would have decreased diffusion of gases into the bloodstream (Sheldon

1997). Recently, Kiernan (2002) studied changes in the mosasaur fauna in the Santonian Eutaw Formation and late Santonian–late Maastrichtian Selma Group of western and central Alabama, USA. As the shoreline migrated northeast, the *Tylosaurus* dominated nearshore mosasaurian assemblage of the Tombigbee Sand gave way to an offshore, Mooreville Chalk fauna dominated by *Clidastes*. She did however, wisely as it turned out, emphasize that the offshore habitat of *Clidastes* in Alabama did not automatically mean that such an environment was favoured by populations outside of the Mississippi Embayment.

In the Kristianstad Basin, southern Sweden, remains of *Clidastes* are found in sediments deposited in a shallow water, rocky coast environment. Erlström and Gabrielson (1992) demonstrated that the calcareous deposits at Ignaberga accumulated within the storm wave base to breaker zone interval (the limited material from this locality indicates that *Clidastes* and *Halisaurus* were the most common mosasaurs in this area), and Surlyk and Christensen (1974) showed that the marine strata at Ivö Klack were deposited within the intertidal zone. At the Åsen site, where isolated tooth-crowns of *C. propython* make up approximately 50 per cent of all mosasaur teeth found, the water depth was likewise shallow (above the storm wave base).

The material of *C. propython* from southern Sweden covers the range from small juveniles (some of the teeth from Åsen indicate animals less than 2 m long) to large, presumably adults (an axis vertebra from Axeltorp; RM PZ R1752a–b; Fig. 6C, indicates a total length of approx. 6.0 m). At Åsen, most of the teeth and vertebrae are from juveniles in the estimated 2–3 m range. A smaller number of teeth from this locality represent large individuals, probably ranging from subadult to adult individuals (the largest teeth are slightly larger than the corresponding ones of YPM 1319 with an estimated total length of 4.5 m). Terminal caudal vertebrae representing juvenile (PMU R415; Fig. 8B) to large, presumably adult (RM PZ R1027; Fig. 8A) individuals have been recorded from Ivö Klack. Although recently collected material of *C. propython* from Ugnsmunnarna and Ignaberga is very limited, it does suggests that these areas were populated mainly by sub-adult to adult *C. propython*. This ontogenetic age distribution is markedly different from that at Åsen, where most individuals were juveniles (typically estimated at less than half the length of large adults). The close proximity to a river (a nearby fluviatile system is indicated by the presence of hybodont shark teeth; Rees 1999, and dinosaur remains in the lower part of the *B. mammillatus* zone at Åsen), that almost certainly flowed through the upper part of the (by *B. mammillatus*-time) partly submerged N-S trending Höljedalen valley (formed in pre-Cretaceous times), may have resulted in murky water with poor visibility. This could perhaps have offered some protection for young *C. propython* from predation pressure by the gigantic *T. ivoensis*, which, at an estimated lower jaw length approaching 2 m in large adults, would be the most likely predator on young *Clidastes*.

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Appendix

Åsen.—*Map sheet*: Karlshamn 3E NV (topographical map sheet, 1:50 000); coordinates UTM VC 690 229 (N 56°08'56.1'', E 14°29' 56.0''). *References*: Christensen 1975; Siverson 1992; Rees 1999; Lindgren and Siverson 2002. All *Clidastes* remains included in this study originate from the lower half of the section, which is latest early Campanian (*B. mammillatus* zone) in age.

Axeltorp.—*Map sheet*: Karlshamn 3E NV (topographical map sheet, 1:50 000); coordinates UTM VC 708 229 (N 56°08'57.5'', E 14°31'35.3''). *References*: Grönwall 1915; Lundegren 1934. *Age*: *B. mammillatus* zone (latest early Campanian).

Ignaberga "new quarry" *sensu* Erlström and Gabrielson (1992).—*Map sheet*: Kristianstad 3D SO (topographical map sheet, 1:50 000); coordinates UTM VC 288 195 (N 56°07'00.1'' E 13°50'54.5''). *References*: Lundegren 1934; Surlyk 1973, 1980; Bruun-Petersen 1975; Siverson 1992; Erlström and Gabrielson 1992. *Age*: *B. mammillatus* zone (latest early Campanian).

Ivö Klack.—*Map sheet*: Karshamn 3E SV (topographical map sheet, 1:50 000); coordinates UTM VC 631 222 (N 56°08'21.6'' E 14°24'05.8''). *References*: Grönwall 1915; Lundegren 1934; Skarby 1968; Surlyk and Christensen 1974; Christensen 1975; Siverson 1992. *Age*: *B. mammillatus* zone (latest early Campanian).

Ugnsmunnarna.—*Map sheet*: Karshamn 3E SV (topographical map sheet, 1:50 000); coordinates UTM VC 619 199 (N 56°07'14.3'' E 14°23'14.5''). *References*: Persson 1960; Christenson 1975; Siverson 1992. *Age*: *B. mammillatus* zone (latest early Campanian). The mosasaurian material from this locality originates from the uppermost conglomerate (bed 5 in Persson 1960: fig. 1).