

Tylosaurus ivoensis: a giant mosasaur from the early Campanian of Sweden

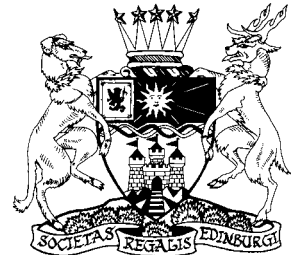
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ABSTRACT: The nominal species *Mosasaurus ivoensis* from the latest early Campanian of the Kristianstad Basin in southern Sweden, is redescribed and assigned to the tylosaurine genus *Tylosaurus* on the basis of its dental and vertebral morphology. A partial skeleton (KUVF 1024) from the late Coniacian to earliest Campanian Smoky Hill Chalk Member of the Niobrara Formation in western Kansas, USA, was previously referred to '*M.* *ivoensis*'. Nevertheless, its marginal teeth are markedly different, both in size and morphology, from those of topotypic *T. ivoensis*.

Examination of type specimens and topotypic material of the nominal tylosaurines *Hainosaurus peminensis* from the late early Campanian of Manitoba, Canada, *H. gaudryi* from the late Santonian or early Campanian of northwestern France, and *H. lonzeensis* from the Coniacian or Santonian of Belgium, indicates that all three may be *Tylosaurus*.

The utility of isolated tooth-crowns in mosasaur taxonomy has been hampered by the often poor quality of the published illustrations of these fossils in combination with poor stratigraphic control. All Swedish remains of *T. ivoensis*, including 172 marginal teeth, 6 pterygoid teeth, several jawbone fragments and 12 vertebrae, were collected from a narrow stratigraphic interval corresponding to the highest biozone in the German eight-fold division of the early Campanian, providing the first good insight into the intraspecific dental variation in a tylosaurine mosasaur.

KEY WORDS: Cretaceous, *Hainosaurus*, Kristianstad, Mosasauridae, *Mosasaurus*, Skåne, teeth, vertebrae.



Mosasaurians are a group of extinct reptiles that inhabited epicontinental seas in a brief 25 million year period of the Cretaceous. The earliest record of mosasaurians is in strata of middle Turonian age (Martin & Stewart 1977; Stewart & Bell 1989; Lingham-Soliar 1994a), and, together with several other animal groups, they perished by the end of the Maastrichtian stage (Russell 1967; Lingham-Soliar 1994b). Mosasaurians had a world-wide distribution and their remains have been found on all continents, including Antarctica (see e.g. Hector 1874; Russell 1967; Chatterjee *et al.* 1984; Suzuki 1985; Lingham-Soliar 1991, 1992; Caldwell & Bell 1995).

Marine strata of Campanian and earliest Maastrichtian age in southern Sweden have yielded a considerable number of isolated tooth-crowns, vertebrae and other, fragmentary skeletal remains of mosasaurians. The bulk of the Swedish material has been collected in quarries and two natural outcrops (Balsberg and Ugnsmunnarna; Fig. 1B) within the Kristianstad Basin area, exposing sediments of the informal *Belemnelloxammammillatus* zone. Christensen (1975) correlated this local biozone with the latest early Campanian *Belemnitella mucronata senior*/*Goniatoteuthis quadrata gracilis* Zone in northwestern Germany.

The invertebrate fauna of the *B. mammillatus* zone is representative of a shallow-water, inner-shelf community (Surlyk & Christensen 1974; Bruun-Petersen 1975; Erlström & Gabrielson 1992). Abundant macro-fossils include echinoids, bryozoans, molluscs (especially oysters and belemnites), brachiopods and calcareous algae. Vertebrate remains are mainly represented by isolated, shed selachian teeth (Davis 1890; Siverson 1992a, b, 1993a, 1995; Rees 1999), but the deposits have also yielded tooth-plates and fin-spines of chimaeroids (Davis 1890), teeth, vertebrae and scales of bony fishes (Davis 1890), skeletal remains of marine turtles (Persson 1959), plesiosaurians

(Persson 1954, 1959, 1962, 1963, 1967, 1990, 1996), mosasaurians (see the historical review below), a crocodile (Persson 1959), and four teeth from ornithischian dinosaurs (undescribed). The report of three teeth from carnivorous dinosaurs from the Ivö Klack site (Blaksudden in older literature) in Persson 1959 (p. 474, pl. 20, fig. 4) is incorrect. The material comprises teeth of teleosts (pers. obs.).

Despite the rather extensive studies of the Late Cretaceous vertebrate faunas from southern Sweden, the mosasaurians are still poorly known. The present communication marks the beginning of a systematic, in-depth study of Swedish mosasaurians. Its main aim is to revise the nominal '*Mosasaurus ivoensis*' Persson 1963, previously known solely from its marginal tooth-crowns. The emended diagnosis of this taxon, presented below, is expanded by also including pterygoid tooth-crowns and caudal vertebrae.

1. Historical review of Swedish mosasaurians

The study of mosasaurians from southern Sweden was commenced in the early nineteenth century by Nilsson (1836). Reptile remains were briefly mentioned by him as early as 1827, but the fragmentary bones presented in this work are neither sufficiently described nor illustrated. We have been unable to locate the material and, based upon Nilsson's inadequate description, it is not possible positively to identify the specimens as mosasaurian. Better-preserved and more complete material was described by Nilsson in 1836 (pl. 4, pl. 5, fig. 1) and included an incomplete mosasaur skull (LO 167 Ta–b) found in Campanian or possibly Maastrichtian strata near the hamlet of Stora Köpinge in the Vomb Trough in southern Skåne (Fig. 1A). Nilsson demonstrated that the

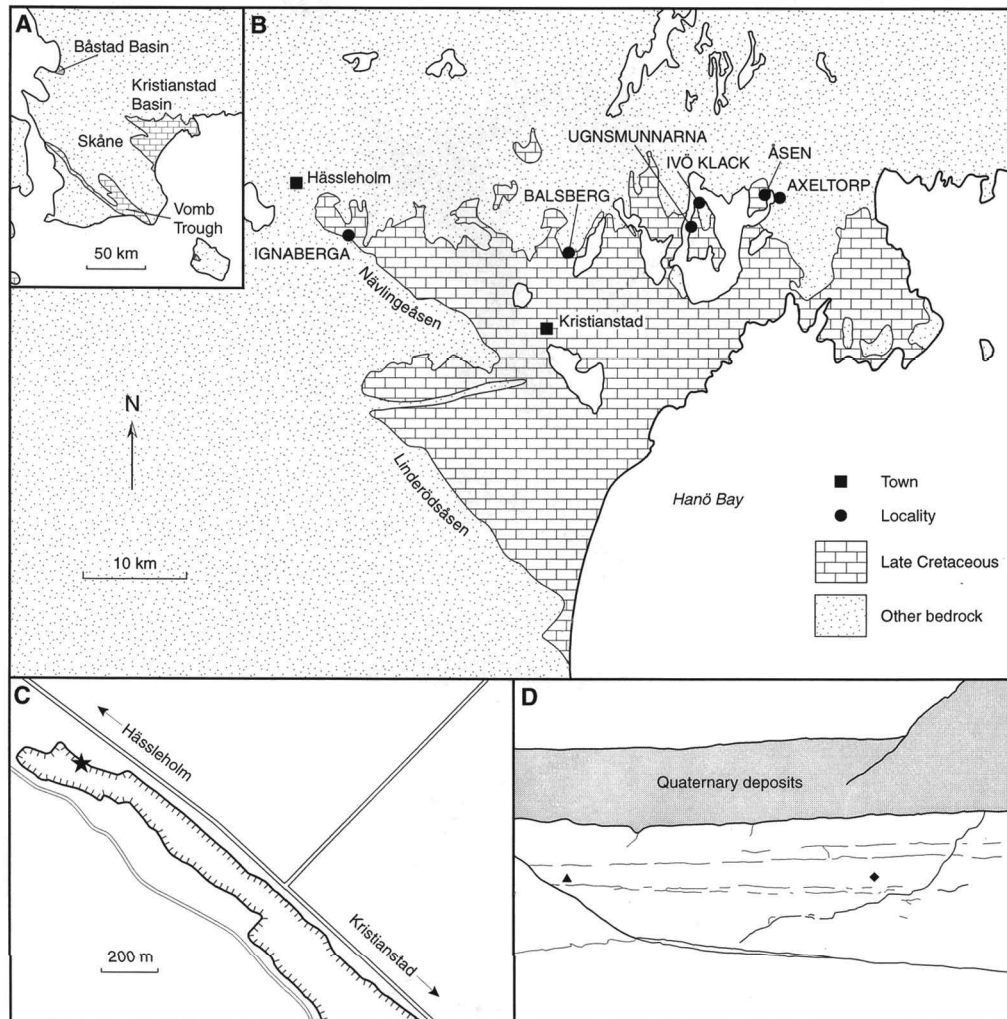


Figure 1 (A) Map of southern Sweden showing the location of the Kristianstad Basin, the Båstad Basin and the Vomb Trough. (B) Map of the Kristianstad Basin with the localities yielding remains of *Tylosaurus ivoensis* (Persson 1963) (based in part on fig. 1 in Siverson 1993b). The term 'other bedrock' refers to both Precambrian and Phanerozoic rocks covered by Quaternary deposits. (C) Close-up map of Ignaberga 'new quarry' sensu Erlström & Gabrielson (1992). The section yielding the vertebrae LO 8229 t and LO 8230 t (Fig. 9) is marked with a star (based on aerial photograph number 914 1D 9f:31, taken 9 May 1991 by Lantmäteriverket). (D) Close-up map of the section yielding LO 8229 t and LO 8230 t (based on a photograph taken in 1986). The location of LO 8229 t is marked with a rhombus and the location of LO 8230 t is marked with a triangle.

specimen was related to modern lizards, but erroneously concluded that it was from a plesiosaurian. In addition, Nilsson (1836, pl. 5, figs 5–6) illustrated two isolated mosasaur tooth-crowns (LO 169 T and LO 170 T) from the Campanian of Oppmanna and the Ivö island (probably the Ugnsmunnarna site) respectively. Nilsson considered these teeth to be from ichthyosaurs, one of few ancient reptiles known to him at that time.

In an all-embracing work devoted to the fossil fauna and flora of Sweden, Hisinger (1837, pl. a, fig. 2a–b, pl. b) re-described and refigured the material examined by Nilsson (1836). Hisinger shared the opinion that the partial skull was from a plesiosaurian but considered the tooth-crowns from Oppmanna (LO 169 T) and the Ivö island (LO 170 T) as being mosasaurian. Hisinger identified the latter tooth as *Mosasauri stenodontis* (*Mosasaurus stenodon* Charlesworth 1846 [= *Liodon anceps* (Owen 1845)]), a species originally identified from the Upper Chalk in Essex, England (see Lingham-Soliar 1993 but note that *Leiodon* Owen 1841 is preoccupied by *Leiodon* Swainson 1839, a nominal genus of bony fish. Agassiz [1846] replaced *Leiodon* Owen 1841 with *Liodon*).

Subsequently, Nilsson (1857) came to a similar conclusion, as he referred LO 169 T to *Mosasaurus hofmanni* [sic] Mantell 1829 and LO 170 T to *M. stenodon*.

The next paper on mosasaurs from southern Sweden was produced by Angelin (1877) and included findings of isolated teeth and vertebrae from the Campanian of the Ivö island, Ivetofta, Oppmanna, Ignaberga and Köpinge. Unfortunately, Angelin did not describe or illustrate any of the referred specimens, which were assigned by him to *Mosasaurus* Conybeare 1822.

Apart from a brief report of an isolated vertebra from Vedhygge (Moberg 1884), no further contributions were made until 1885, when Schröder issued the first comprehensive discussion and review of Swedish mosasaurs. He pointed out that the partial skull from Stora Köpinge (LO 167 Ta–b) could not be from a plesiosaurian but instead was mosasaurian. According to Schröder, the specimen represented a new species which he named *Mosasaurus scanicus* after the province of Skåne. In the same work, Schröder also discussed the teeth from Oppmanna and the Ivö island, referring them to *Mosasaurus* sp. I (LO 169 T) and *Mosasaurus* sp. II (LO 170 T).

Moreover, on the basis of a single tooth-crown (LO 784 T) from the Campanian (see Christensen 1986) of Köpings (not Balsberg, as asserted by Schröder; see Hennig 1911, p. 671 and discussion below), Schröder (1885, pp. 329–31, pl. 17, fig. 3) erected the new nominal species *Leiodon* (= *Liodon*) *lundgreni*. Schröder also reported two isolated teeth (LO 782 t and LO 783 t) from the Köpings area, which he assigned to *Mosasaurus camperi* Meyer 1832 (= *M. hoffmanni*).

Lundgren (1888a, b, 1889) and Nathorst (1894) briefly discussed, illustrated or listed the species previously established by Schröder (1885).

During the first half of the twentieth century only minor contributions to the cognisance of the Swedish mosasaur faunas were published. Törnebohm & Hennig (1904) reported the occurrence of *Mosasaurus* and *Leiodon* [*sic*] in the Late Cretaceous deposits of southern Sweden, while Hennig (1911) listed the reptile faunas formerly described by Schröder (1885). Kuhn (1939) also listed the mosasaur taxa identified by Schröder (1885), with the noteworthy difference that the isolated tooth-crown LO 784 T was referred to as '*Mosasaurus*' *lundgreni*. A few additional findings from the Kristianstad Basin were reported and illustrated in papers by Voigt (1929, pl. 8, fig. 1 and 1931, pl. 1, fig. 1), Lundegren (1934) and Troedsson (1954, fig. 26.2–3), while Zdansky (1935) noted the extensive mosasaurian material from southern Sweden kept at Uppsala University.

In the most comprehensive study on Swedish Cretaceous reptiles conducted so far, Persson (1959, fig. 10, pl. 15, figs 1–7) identified *M. cf. hoffmanni* and *Platecarpus cf. somenensis* Thevenin 1896 (material referred to this taxon included LO 170 T, previously referred to *Mosasaurostenodontis* by Hisinger [1837] and *Mosasaurosp. II* by Schröder [1885]) from strata of latest early Campanian age in the Kristianstad Basin, and *Plioplatecarpus?* sp. and *Leiodon* [*sic*] cf. *anceps* from strata of middle late Campanian age (see Christensen 1993) in the Båstad Basin (Fig. 1A). Persson (1959, figs 11–13, pl. 16) also redescribed and refigured the incomplete skull from Stora Köpings (LO 167 Ta–b), and concluded that it was generically indeterminable. The tooth-crowns LO 169 T and LO 784 T from Oppmanna and Köpings were also considered indeterminable, as were a number of isolated mosasaurian jawbone fragments and vertebrae. Persson provisionally referred 42 isolated tooth-crowns to *Mosasaurus* sp.

The occurrence of mosasaurian remains in strata of earliest Maastrichtian age (*Belemnella lanceolata* Zone but see Christensen *et al.* 2000) at the Balsvik quarry was briefly reported in an excursion guide by Brotzen (1960). According to him, most of the bones found at the locality could be assigned to *Mosasaurus*.

Persson (1962) described a single tooth-crown (LO 4077 t) from early late Campanian (*Belemnitella mucronata* Zone, see Christensen 1975) strata in the Hanaskog quarry in the Kristianstad Basin. He provisionally referred the specimen to *Leiodon* [*sic*] sp.

In 1963, Persson refined his provisional determinations published in 1959, and listed *Leiodon* [*sic*] *anceps* and *Plioplatecarpus* sp. from the middle late Campanian of the Båstad Basin. Based on isolated tooth-crowns from the informal *Belemnello-camax mammillatus* zone in the Kristianstad Basin, Persson erected a new subspecies, denominated *Mosasaurus hoffmanni ivoensis* (the material included specimens assigned to *M. cf. hoffmanni* and *M. sp.* by Persson in 1959). The tooth-crowns from the *B. mammillatus* zone previously (Persson 1959) referred to as *Platecarpus cf. somenensis* were now listed as *P. somenensis*. The incomplete skull from Stora Köpings (LO 167 Ta–b) was provisionally assigned to *Platecarpus?* sp., and a single mosasaurian tooth-crown (LO 4085) was reported

from the early Santonian to earliest Campanian calcarenites at the Ringeleslätt quarry (see Christensen 1975 for a discussion of the belemnites from this locality).

Russell (1967) assigned KUV 1024 (comprising a partial skull, the atlas and axis vertebrae, a coracoid [see Williston 1902] and a fragmentary forelimb) from the late Coniacian–earliest Campanian Smoky Hill Chalk Member (probably upper half) of the Niobrara Formation in western Kansas, USA, to *Mosasaurus ivoensis*, and consequently gave Persson's *M. hoffmanni ivoensis* species rank. He also listed (Russell 1967, chart 7), in stratigraphical order, mosasaur taxa from various regions of the world, including Sweden. The systematics of the Swedish mosasaurs followed that of Persson (1963), with the sole exception that Russell used the correct spelling *Liodon* instead of *Leiodon* for *L. anceps*.

In a contribution to the understanding of the function of conodont elements, Jeppsson (1979, fig. 5a) illustrated a mosasaurian tooth-crown (LO 3879 t) previously identified as *Mosasaurus camperi* by Nathorst (1894, p. 195) and *M. cf. hoffmanni* by Persson (1959, fig. 10, pl. 15, fig. 2). In addition, Jeppsson (1979, figs 5h, 7b) illustrated two teeth (LO 3885 t and LO 3882 t), assigned by Persson (1963) to *Leiodon* [*sic*] *anceps* and *Plioplatecarpus* sp. respectively.

Lingham-Soliar (1991) stated that it is inadvisable to erect nominal mosasaurian species based on tooth morphology alone, and consequently questioned the validity of a few taxa, including '*Mosasaurus*' *ivoensis*. Nevertheless, in 1993 Lingham-Soliar diagnosed his new mosasaur tribe Leiodontini, a taxon ultimately based on a fragment of a dentary (BMNH 41639) with two teeth broken off at the base.

Recently, Bardet & Pereda Suberbiola (1996) 'noted' the occurrence of mosasaurs attributable to the genera *Mosasaurosp.*, *Leiodon* [*sic*] and *Platecarpus* in strata of Campanian age in the province of Skåne.

2. Geological setting

The northern demarcation of the Kristianstad Basin *sensu* Erlström & Gabrielson (1992) constitutes an irregular boundary with several outliers of Cretaceous deposits (Fig. 1B), whereas the Linderödsåsen and Nävlingeåsen horsts confine the basin to the SW.

Calcareous, glauconitic sands yielding Barremian, Aptian–Albian and Cenomanian foraminifera constitute the oldest known sediments in the area, and were recorded from a cored subsurface section (U1B) at Härlöv (see Norling & Skoglund 1977; Bergström & Sundquist 1978; Norling 1981).

Numerous quarries and a few natural outcrops, most of which are more or less covered by scree and vegetation, expose/exposed calcarenites, calcisiltites and calcirudites of latest early and early late Campanian age. Earliest Maastrichtian deposits (*Belemnella lanceolata* Zone, which may actually be of very latest Campanian age if the FAD of *Pachydiscus neubergicus* Hauer 1858 is taken to define the base of the Maastrichtian [see Christensen *et al.* 2000]), comprising calcisiltites and fine-grained calcarenites, are known from a few localities (Siverson 1993a, b). Tertiary strata are not known to be present in the Kristianstad Basin area, although loose blocks of Palaeocene age have been found near Maglehem, at the southern tip of the basin (Sandegren 1914).

Poorly consolidated, sandy calcarenites and calcirudites are the dominant marine lithologies in the latest early Campanian *B. mammillatus* zone. Terrigenous material in conglomerates and boulder beds indicates that nearby land functioned as important source areas, especially along the basin margins (Christensen 1975). The marine deposits may overlie residual

kaolin clay and quartz sand (e.g. Ivö Klack), fluviatile clays and sands (e.g. Åsen), or rest directly upon the crystalline basement (e.g. Balsberg). 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 basin's southwestern extension and to the SE. Erlström & Gabrielson (1992) estimated that the *B. mammillatus* zone is approximately 20 m thick in the Ignaberga 'new quarry' and it is at least 23 m thick in the Ullstorp 1 (*sensu* Erlström & Gabrielson 1986) quarry (conglomerate C and the strata below are of pre-*B. mammillatus* zone age). Both localities are located along the Nävlingeåsen fault. The biozone is at least 50 m thick in the Åhus boring (Christensen 1975).

3. Localities

3.1. Åsen

The Åsen site (Fig. 1B; N 56°08'56.1", E 14°29'56.0") is a clay pit, presently used as a refuse dump. It is by far the most productive locality for Cretaceous vertebrate fossils in Sweden. Up to 3.5 m of glacially tectonised, unconsolidated, marine sands overlie fluviatile clays and sands of late Santonian and/or early Campanian age (Friis & Skarby 1981; Siverson 1992a). The lower half of the sequence yields *Belemnellocamax mammillatus* (Nilsson 1826), *Belemnitella mucronata* (Link 1807) and *Goniot euthis quadrata scaniensis* Christensen 1975, indicating a latest early Campanian age (see Christensen 1975). The upper half yields *Belemnellocamax* aff. *B. balsvikensis* (Brotzen 1960) and *Belemnitella mucronata* (belemnites currently under study by Walter Kegel Christensen). The boundary between the two biostratigraphic units is marked by a discontinuity surface overlain by a conglomerate comprising reworked *B. mammillatus*.

Numerous reptile remains have been recovered in recent years from the lower half of the marine sand (with typical *Belemnellocamax mammillatus*). The upper half is poor in reptile material. All mosasaur remains from Åsen included in this study are from the *B. mammillatus* zone and thus of latest early Campanian age. [Map sheet: Karlshamn 3E NV, coordinates: UTM VC 690 229]

3.2. Axeltorp

The abandoned and overgrown limestone pit at Axeltorp (Fig. 1B; N 56°08'57.5", E 14°31'35.3") exposed an approximately 3.5 m thick section of calcareous strata of latest early Campanian age. References: Grönwall 1915; Lundegren 1934; Christensen 1975. [Map sheet: Karlshamn 3E NV, coordinates: UTM VC 708 229]

3.3. Balsberg

The Balsberg site (Fig. 1B; N 56°06'10.2", E 14°11'55.6") is a natural cave situated on the southwestern slope of the Balsberget hill, W of the Råbelövsvjön lake. The exposed strata in the cave consist of calcarenites of latest early Campanian age, partly conglomeratic with abundant crystalline pebbles. References: De Geer 1886; Lundegren 1934; Christensen 1975. [Map sheet: Karlshamn 3E SV, coordinates: UTM VC 504 178]

3.4. Ignaberga

Ignaberga (Fig. 1B; N 56°06'50", E 13°51'24") is a collective name for a number of limestone quarries situated near a small hamlet with the same name, SE of the town of Hässleholm. References: Christensen 1975; Erlström & Gabrielson 1992. [Map sheet: Kristianstad 3D SO, coordinates: UTM VC 288 195]

3.5. Ivö Klack

The kaolin and limestone quarry at Ivö Klack (Blaksudden in older literature) is situated on the northern slope of the Ivö Klack hill on the Ivö island (Fig. 1B; N 56°08'34", E 14°24'25"). Nowadays mining has ceased and only minor limestone remnants are accessible. References: Grönwall 1915; Lundegren 1934; Skarby 1968; Surlyk & Christensen 1974; Christensen 1975. [Map sheet: Karlshamn 3E SV, coordinates: UTM VC 631 222]

3.6. Ugnsmunnarna

The locality is a natural cliff-section, situated on the western shore of the Ivö island (Fig. 1B; N 56°07'14", E 14°23'14"). The exposed strata have a thickness of 2–5 m and a lateral extension of about 130 m. The section comprises a very sandy calcarenite (up to 50% quartz sand) with five conglomeratic beds. The mosasaur material dealt with herein was collected from the uppermost conglomerate of latest early Campanian age (bed 5 in Persson 1960, fig. 1). References: Persson 1960; Christensen 1975; Siverson 1992a. [Map sheet: Karlshamn 3E SV, coordinates: UTM VC 619 199]

4. Material and methods

As a result of being deposited in a high-energy, nearshore environment with strong currents and abundant scavengers, vertebrates are not found as articulated skeletons in the Kristianstad Basin area. Instead, the material is comprised of isolated teeth and bones (mainly vertebrae), and, in exceptional cases, of disarticulated portions of the skeleton of single individuals. Most teeth at hand are isolated, shed tooth-crowns, although a few specimens also include the bony base (Fig. 5.2). On rare occasions, teeth have been found in association with fragments of jawbones.

The majority of the specimens described and illustrated in this paper were collected at the Ivö Klack site by quarry workers in the early twentieth century. These remains constitute the bulk of the mosasaur material housed in the Swedish Museum of Natural History, Department of Palaeozoology, Stockholm; the Department of Geology and Geochemistry, Stockholm University, Stockholm; the Museum of Evolution, Palaeontology section, Uppsala University, Uppsala; and the Geological Survey of Sweden, Uppsala.

The fossils were treated with buffered acetic acid (pH above 4.0; see Jeppsson *et al.* 1985), which dissolved adhering carbonates, and then hardened with polyvinylbutural. They were coated with ammonium chloride prior to being photographed.

The terminology is based mainly on that of Russell (1967), and systematics follows that of Lingham-Soliar (1992). For descriptive terms used in the text, see Figures 2 and 3.

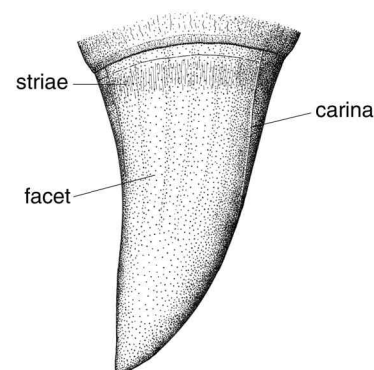


Figure 2 Drawing of a generalised tylosaurine marginal tooth in buccal view, showing the dental terminology used in the text.

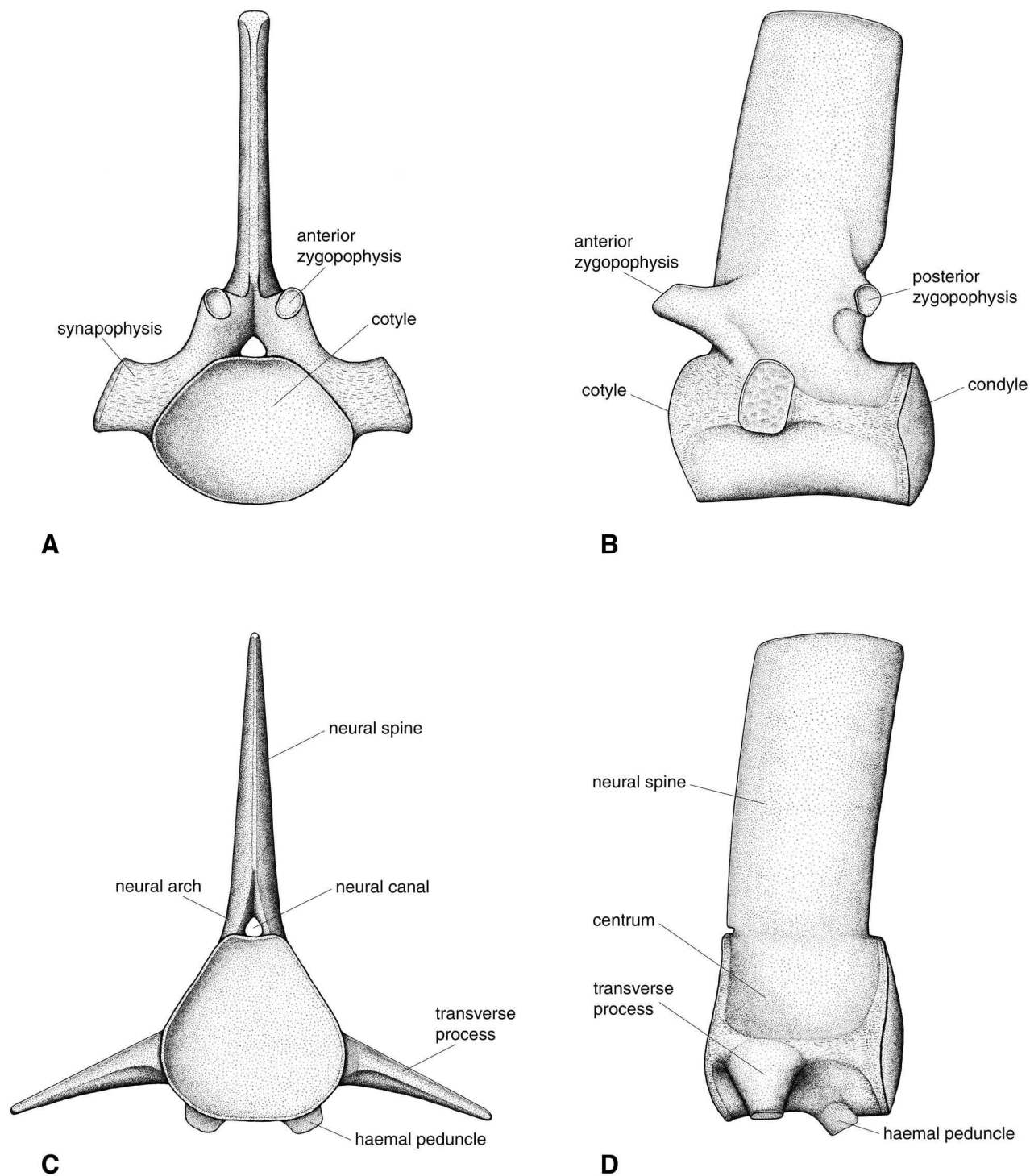


Figure 3 (A–D) Drawings of generalised tylosaurine vertebrae showing descriptive terms: (A–B) dorsal vertebra in (A) anterior and (B) lateral views; (C–D) anteriorly situated intermediate caudal vertebra in (C) anterior and (D) lateral views.

Additional mosasaurian material housed in museums and institutions in Europe and North America has been carefully examined, with particular focus on dental and vertebral characters.

4.1. Repositories

BMNH: The Natural History Museum, London, UK; FFHM: Fick Fossil and Historical Museum, Oakley, Kansas, USA; FHSM: Sternberg Museum of Natural History, Fort Hays State University, Hays, Kansas, USA; IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium;

KrMG: Regionmuseet i Skåne, Kristianstad, Sweden; KUIP: Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, Kansas, USA; LO, LR: Department of Geology, Lund University, Lund, Sweden; MDM: Morden and District Museum, Morden, Manitoba, Canada; MNHN: Muséum National d'Histoire Naturelle, Paris, France; MT: Miami Museum, Municipality of Thompson, Miami, Manitoba, Canada; PMU: Museum of Evolution, Palaeontology Section, Uppsala University, Uppsala, Sweden; RM PZ: Swedish Museum of Natural History, Department of Palaeozoology, Stockholm, Sweden; SGU: Geological Survey

of Sweden, Uppsala, Sweden; YPM: Yale Peabody Museum, Department of Vertebrate Paleontology, Yale University, New Haven, Connecticut, USA.

5. Systematic palaeontology

5.1. The utility of isolated teeth in mosasaur taxonomy

With few exceptions, dental characters have received little attention in taxonomic studies of mosasaurs. Detailed descriptions of mosasaurian teeth supported by adequate illustrations are exceedingly rare. More frequently, teeth have been vaguely described using an uninformative terminology, which has seriously hampered comparisons between different taxa. This is unfortunate, as tooth morphology yields valuable taxonomic information.

Naturally, differences due to ontogeny and the normal range of variation within a species must be taken into consideration when comparing teeth of different mosasaur species. Moreover, the morphology of the tooth-crowns changes along the jaw (see e.g. Thevenin 1896, fig. 3). The extent of this variation differs from one genus to another. For instance, marginal teeth are well differentiated in *Clidastes* Cope 1868 and *Liodon* (Russell 1967; Lingham-Soliar 1993; pers. obs.), while the teeth are more uniform in *Platecarpus* Cope 1869a (Russell 1967; pers. obs.).

Diagnosable mosasaurian species may be based on isolated tooth-crowns, provided that: (1) the number of teeth available is sufficiently large for an appreciation of the heterodonty and intraspecific variation; (2) the diagnosis is accompanied by high-quality illustrations; (3) the material on which the species is based originates from a narrow stratigraphic interval.

Much of what we know about mosasaurs in general is based on more-or-less complete and articulated skeletons collected from the Smoky Hill Chalk Member of the Niobrara Formation in western Kansas, USA. Unfortunately, the poor stratigraphic data for most mosasaur specimens collected from the Smoky Hill Chalk Member prior to the publication of Hattin's (1982) detailed study and identification of useful marker units, continue to plague students trying to sort out the phylogeny of Niobraran mosasaurs. The entire member spans the late Coniacian to earliest Campanian interval, which amounts to approximately 5 Ma (see Kauffman *et al.* 1994). By comparison, the early Campanian mosasaur material from the Kristianstad Basin is very fragmentary (although always preserved undistorted by compaction, unlike material from the lower part of the Smoky Hill Chalk Member) but has reliable stratigraphic data. The local *Belemnellocamax mammillatus* zone is a lateral equivalent to the German *Belemnitella mucronata senior/Gonoteuthis quadrata gracilis* Zone (see Christensen 1975), which (assuming a constant and continuous sedimentation rate in the Lägerdorf quarry [see Schönfeld *et al.* 1996, fig. 2] and a duration of 3 Ma for the early Campanian [see Obradovich 1994]) comprises 0–33 Ma.

5.2. Taxonomy of '*Mosasaurus*' *ivoensis* Persson 1963

Order Squamata Oppel 1811

Family Mosasauridae Gervais 1853

Subfamily Tylosaurinae Williston 1897

Diagnosis. See Russell (1967).

Remarks. Persson (1959) assigned 31 isolated marginal teeth from the latest early Campanian of the Kristianstad Basin in southern Sweden to *Mosasaurus* cf. *hoffmanni*. He refrained from referring them with confidence to *M. hoffmanni* because of their larger number of facets compared to those on the holo-

type of *M. hoffmanni*. In a later review of the Late Cretaceous marine reptiles from southern Sweden, Persson (1963) erected the subspecies *Mosasaurus hoffmanni ivoensis* for the material from the Kristianstad Basin, previously (1959) referred by him to *M. cf. hoffmanni* and *Mosasaurus* sp. He pointed out that not only are facets more numerous on tooth-crowns of the Campanian (nominal) subspecies, but they are also more concave than are the rather flat facets on crowns from *M. hoffmanni hoffmanni*. Russell (1967) gave the nominal *M. hoffmanni ivoensis* species rank, a taxonomic emendation with which we concur, although his diagnosis of the nominal *M. ivoensis* is based almost exclusively on a partial skeleton from the Niobrara Formation of western Kansas, USA, which, as shown below, is not conspecific with Persson's *M. hoffmanni ivoensis*.

Persson (1959) mentioned the presence of basal striae on the lingual side of the teeth from the Kristianstad Basin but did not fully realise the taxonomic significance of this character. Striations are generally present at the base of the lingual face of the crown in species of *Tylosaurus* Marsh 1872 and *Hainosaurus* Dollo 1885, as well as in plioplatecarpines, such as *Platecarpus*, *Plioplatecarpus* Dollo 1882 and *Ectenosaurus* Russell 1967 (see Williston 1898, pl. 29, fig. 1; Dollo 1913, pl. 25, fig. 2; Chitoku 1994, fig. 2, pl. 1, figs 2–5; Bardet *et al.* 1998, pl. 6, figs 3, 8, 10, 11). We have not observed distinct lingual striae on any of the nominal *Mosasaurus* that we have examined, including *M. hoffmanni*, *M. maximus* Cope 1869a and *M. lemnierii* Dollo 1889a. There is no overlap in tooth-crown morphology between '*M. ivoensis*' and the three species of *Mosasaurus* examined by us, whereas '*M. ivoensis*' does overlap in tooth-crown morphology with several tylosaurines, including *Tylosaurus proriger* (Cope 1869b), *Hainosaurus peminensis* Nicholls 1988 and *Hainosaurus gaudryi* (Thevenin 1896). The marginal tooth-crowns of '*M. ivoensis*' differ from those of plioplatecarpines by their larger size, stouter proportions and very unequally convex buccal and lingual surfaces.

Pterygoid teeth of tylosaurine mosasaurs are markedly different from those of the type species of *Mosasaurus*. Two indistinct, lateral carinae divide the crown of pterygoid teeth of *Tylosaurus* and *Hainosaurus* into an anterior and a posterior surface of sub-equal convexity (with the exception of *H. gaudryi*; see below). The anterior face is smooth or slightly faceted, while the posterior face is lined with closely spaced striae (Cope 1870, p. 204; pers. obs.). Corresponding tooth-crowns of *Mosasaurus* lack striations, but possess a distinct and sharp posterior carina and a very weakly developed outer one (pers. obs. of e.g. MNHN AC 9648 [type of *M. hoffmanni*]). Several pterygoid teeth (Fig. 8) from the *B. mammillatus* zone of the Kristianstad Basin correspond perfectly with those of tylosaurine mosasaurs (e.g. *Tylosaurus proriger*). In contrast, no pterygoid teeth matching those of adult *Mosasaurus* have ever been found in these strata. Small-sized mosasaurine pterygoid tooth-crowns are occasionally found at the Åsen locality, but the associated mosasaurine marginal crowns found in the same deposit show that this taxon is not *Mosasaurus*.

We have identified a total of four different 'caudal vertebrae species' of mosasaurs from the *B. mammillatus* zone in the Kristianstad Basin. These correspond to the four 'tooth-crown species' found in the same deposits. Two of the 'caudal vertebrae species' have articulated chevrons, while one has fused haemal arches. The fourth species is represented by an imperfectly preserved posteriorly situated intermediate caudal vertebra and a partial terminal caudal vertebra that probably had fused chevrons, but this cannot be confirmed at this stage. Better-preserved material is needed. The species with fused chevrons (the overall shape of its terminal caudals is very different from that of the fourth species, which probably also had fused chevrons) is of rather small size and is perfectly

matched by a large number of small-sized tooth-crowns (up to 15 mm high) with a typical mosasaurine morphology. Articulated skeletons found elsewhere strongly indicate that these tooth-crowns and vertebrae belong to the same species. The collections from the *B. mammillatus* zone include 24 caudal vertebrae with peduncles for articulation with a free haemal arch. Thirteen of these (two intermediates and 11 terminals [seven of the latter possibly from a single individual]) are of *Platecarpus*-type, while the remaining 11 caudals (seven anteriorly situated intermediates [four of which are possibly from a single individual] and four posteriorly situated terminals) have a typical tylosaurine morphology. Anteriorly situated intermediate caudal vertebrae of tylosaurine mosasaurs are recognised by the marked triangular appearance of the central articulations. The corresponding caudals of *Platecarpus* have interarticular surfaces where the dorsal apex is much wider. Posteriorly situated terminal caudals of tylosaurines are separated from those of *Platecarpus* by the comparatively short length of the vertebral centrum relative to the height of the interarticular surfaces (see Williston 1898, pl 72; pers. obs.). In *Platecarpus* the height of the central articulations generally equals or is less than the length of the centrum. Moreover, vertebral centra from a given area along the vertebral column of adult individuals are usually much larger in tylosaurines such as *Hainosaurus* and *Tylosaurus* than they are in the more medium-sized individuals of *Platecarpus*. This is also the case with the material from the Kristianstad Basin, where the tylosaurine-type caudals are almost twice as large as the corresponding *Platecarpus*-type caudals. The *Platecarpus*-type caudals are well matched by a total of 140 marginal teeth of a large-toothed *Platecarpus* close to or identical with *P. some-nensis* (see Persson 1959, 1963).

Excluding the *Platecarpus* and the small, undescribed mosasaurine, the collections thus include 11 large to very large tylosaurine-type caudals plus two smaller caudals that probably (based on the breakage surfaces) had fused chevrons. These two types of caudal vertebrae correspond to 172 marginal and six pterygoid teeth of '*M.* *ivoensis*' (Table 1) plus 60 teeth (including fragmentary jawbones with eight associated teeth from a single individual) from a mosasaur dentally similar to *Liodon*. The *Liodon*-like tooth-crowns differ markedly from those of tylosaurine mosasaurs in several aspects. The anterior and posterior carinae divide the tooth into two halves of equal convexity. In '*M.* *ivoensis*' the buccal face of the crown is gently convex in cross-section, while the lingual face is deeply U-shaped. The enamel is smooth on the *Liodon*-like teeth, whereas basal striae characterise the lingual side of the tooth-crowns in '*M.* *ivoensis*'. The faceted crowns of the latter species are in contrast to the *Liodon*-like crowns, which either lack facets or have very poorly developed ones. Moreover, the heterodonty in the *Liodon*-like species is strong (as it is in *Liodon*), while it is relatively weak in '*M.* *ivoensis*' (as in *Tylosaurus* and *Hainosaurus*; pers. obs.).

In summary, all evidence indicates a tylosaurine affinity for '*M.* *ivoensis*'. The marginal teeth correspond well to those of tylosaurines (and overlap to some extent with Santonian–Campanian species, including *Tylosaurus proriger*, *Hainosaurus gaudryi* and *H. peminensis*), while they differ from those of *Mosasaurus* in several aspects, including having marked basal striae on the lingual and sometimes also on the buccal face. Pterygoid teeth indistinguishable from those of tylosaurines have been found in the *B. mammillatus* zone, whereas no pterygoid teeth of *Mosasaurus* have ever been collected from these deposits. The tylosaurine tooth-crown morphology of '*M.* *ivoensis*' is nicely matched by large caudal vertebrae with typical tylosaurine proportions and with peduncles for articulation with the chevrons. '*Mosasaurus*' *ivoensis* is the only one of the four 'tooth-crown species' from the *B. mammillatus* zone to which the tylosaurine vertebrae can be matched.

Genus *Tylosaurus* Marsh 1872

Type species. *Tylosaurus proriger* (Cope 1869b), from the Smoky Hill Chalk Member of the Niobrara Formation in western Kansas, USA.

Diagnosis. See Russell (1967).

Comparisons. The subfamily Tylosaurine comprises three genera: *Hainosaurus*, which occurs in Europe and North America (see e.g. Nicholls 1988; Lingham-Soliar 1992); *Tylosaurus*, with occurrences in Asia, Africa and North America (see e.g. Russell 1967; Lingham-Soliar 1992; Chitoku 1994); and *Taniwhasaurus* Hector 1874, which so far has only been identified from New Zealand (see e.g. Welles & Gregg 1971).

Several features, including the length of the external nares relative to the length of the skull, the buttressing of the premaxillary suture, the size of the infrastapedial process on the quadrate and the number of vertebrae between the cranium and the chevron-bearing caudals, have been used to distinguish *Hainosaurus* from *Tylosaurus* (see e.g. Williston 1898; Russell 1967; Nicholls 1988; Lingham-Soliar 1992). Some of these characters appear to be inadequate for separating these two genera. Lingham-Soliar (1992) regarded a double buttressed premaxillary suture to be diagnostic for species of *Hainosaurus*. Nevertheless, this feature is also occasionally present in *Tylosaurus* (e.g. YPM 3974, a *T. nepaeolicus* [Cope 1874]) from the Smoky Hill Chalk Member of the Niobrara Formation in Kansas, and thus cannot be used to distinguish *Hainosaurus* from *Tylosaurus*. Nicholls (1988) noted that the relative length of the external nares is greater in *H. bernardi* and *H. peminensis* than it is in *Tylosaurus*, and stated that the elongated nares is a definitive character of *Hainosaurus*. However, judging from cranial reconstructions of *T. proriger* (see Russell 1967, fig. 92) and *H. bernardi* (see Lingham-Soliar 1992, fig. 3b), the difference in relative length of the external nares seems rather insignificant.

Table 1 Recorded remains of *Tylosaurus ivoensis* (Persson 1963) from the *Belemnellocamax mammillatus* zone.

Localities	Marginal teeth	Pterygoid teeth	Dorsal vertebrae	Intermediate caudal vertebrae	Terminal caudal vertebrae
Åsen	7				
Axeltorp	1				
Balsberg	1				
Ignaberga	11	1	1	2	
Ivö Klack	150	5		5	4
Ugnsmunnarna	2				
Σ	172	6	1	7	4

There are, nonetheless, a number of dental and skeletal characters that separate *Hainosaurus* (i.e. *H. bernardi*, as described by Lingham-Soliar [1992] and pers. obs. of IRSNB R23 and IRSNB 3672) from *Tylosaurus* (i.e. *T. proriger*, as described by Russell [1967] and pers. obs. of e.g. FFHM 1997.10 and FHSM VP-3). These differences include: (1) the marginal tooth-crowns are more compressed bucco-lingually in *Hainosaurus* than they are in *Tylosaurus*; (2) the carinae are more developed on marginal tooth-crowns of *Hainosaurus* than they are on crowns of *Tylosaurus*; (3) the carinae on the pterygoid teeth have minute serrae in *Hainosaurus*, whereas the carinae lack serrations in *Tylosaurus*; (4) the suprastapedial process on the quadrate is small in *Hainosaurus*, while it is relatively large in *Tylosaurus*; (5) the infrastapedial process on the quadrate is virtually absent in *Hainosaurus*, whereas it is well developed in *Tylosaurus*; (6) in lateral view, the quadrate has the shape of a vertical rectangle in *Hainosaurus*, whereas it is more circular in outline in *Tylosaurus*; (7) the femur is longer than the humerus in *Hainosaurus*, while the two elements are more or less equal in length in *Tylosaurus*; (8) there is a larger number of vertebrae between the cranium and the chevron-bearing caudals in *Hainosaurus* than there is in *Tylosaurus* (49+ in *Hainosaurus* vs. 35–37 in *Tylosaurus*); (9) anteriorly situated intermediate caudal vertebral centra are wider and shorter in *Hainosaurus* than they are in *Tylosaurus*.

More or less detailed descriptions of tylosaurine teeth have been given in papers by, among others, Cope (1875), Dollo (1885), Thevenin (1896), Russell (1967), Nicholls (1988), Lingham-Soliar (1992) and Chitoku (1994). Unfortunately, these descriptions are too generalised, and cannot be used to separate *Hainosaurus* from *Tylosaurus* from a dental point of view. We have examined marginal teeth of *H. bernardi* (IRSNB R23, IRSNB 3672) and *T. proriger* (FFHM 1997.10, FHSM VP-3, YPM 1302, YPM 3987, YPM 4002), the type species of *Haino-*

saurus and *Tylosaurus* respectively, and compared these with those of '*M. ivoensis*'. The only significant differences that we detected between the tooth-crowns of *T. proriger* and those of the Swedish tylosaurid concerned the development of facets and carinae. The buccal surface is generally faceted in teeth of the Swedish tylosaurid (Figs 4A–B, 5, 6, 7.2), while teeth of *T. proriger* often have indistinct facets (Fig. 4D). Furthermore, the carinae are generally less pronounced on crowns of *T. proriger* than they are on crowns of '*M. ivoensis*'. Marginal teeth of *H. bernardi*, on the other hand, differ markedly from those of the Swedish tylosaurid. The lingual surface of the crown is deeply U-shaped in '*M. ivoensis*', giving the crown a distinctly asymmetric appearance in teeth with both an anterior and a posterior carina. In contrast, the lingual and buccal surfaces are nearly equally developed in laterally and posteriorly situated crowns of *H. bernardi*. Moreover, the crowns of *H. bernardi* are more compressed bucco-lingually than are the crowns of '*M. ivoensis*'.

Marginal teeth of *Taniwhasaurus* (i.e. *T. oweni* Hector 1874), a tylosaurine from mid and/or late Campanian strata (see Roncaglia *et al.* 1999) of the Conway Siltstone at Haumuri Bluff on the South Island of New Zealand, have been described by Hector (1874, p. 354) as being 'finely striated, only slightly compressed, and without any well-marked ridge'. Recently, Bell *et al.* (1999) synonymised *Tylosaurus haumuriensis* (Hector 1874), another nominal tylosaurine from the same locality, with *Taniwhasaurus*. They also noted similarities between *Hainosaurus* and *Taniwhasaurus*, but did not specify which characters these two genera have in common.

In the absence of complete skeletons of '*M. ivoensis*', our generic assignment of the species within the Tylosaurinae is based on the morphology of the marginal and pterygoid tooth-crowns, the shape of the interarticular surfaces on the anteriorly situated intermediate caudal vertebrae and the

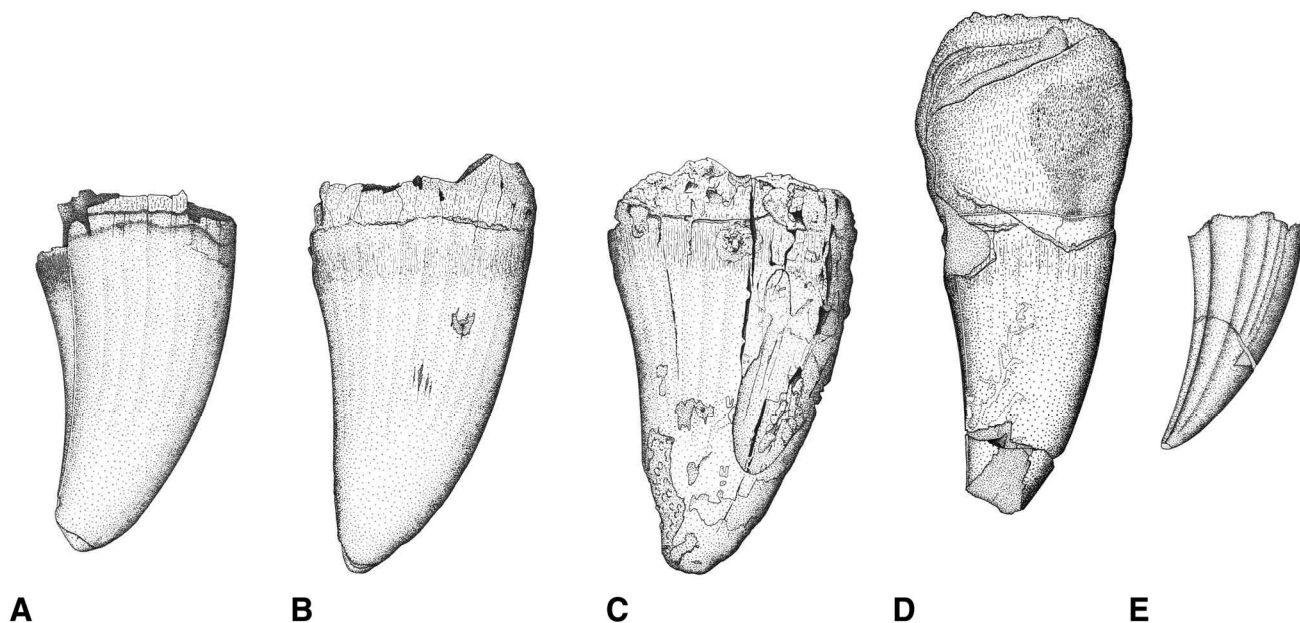


Figure 4 Drawings of marginal teeth (in buccal view) of (A–B) *Tylosaurus ivoensis* (Persson 1963), (C) *Hainosaurus pembinensis* Nicholls 1988, (D) *Tylosaurus proriger* (Cope 1869b) and (E) KUVP 1024: (A) RM PZ R1292, the holotype of *T. ivoensis* from strata of latest early Campanian age at Ivö Klack, Kristianstad Basin, southern Sweden, $\times 0.9$. (B) RM PZ R1180, an isolated tooth-crown of *T. ivoensis* from strata of latest early Campanian age at Ivö Klack, Kristianstad Basin, southern Sweden, $\times 0.9$. (C) MDM M99.03.0X, an isolated tooth-crown of *H. pembinensis* from the late early Campanian part of the Pembina Member of the Pierre Shale in southern Manitoba, Canada, $\times 0.9$. (D) mirror image of YPM 1302, a marginal tooth of *T. proriger* from the upper part (late Santonian–earliest Campanian) of the Smoky Hill Chalk Member of the Niobrara Formation in western Kansas, USA, $\times 0.9$. (E) The eighth, right maxillary tooth of KUVP 1024 from the Smoky Hill Chalk Member (probably upper part) of the Niobrara Formation in western Kansas, USA, $\times 0.9$.

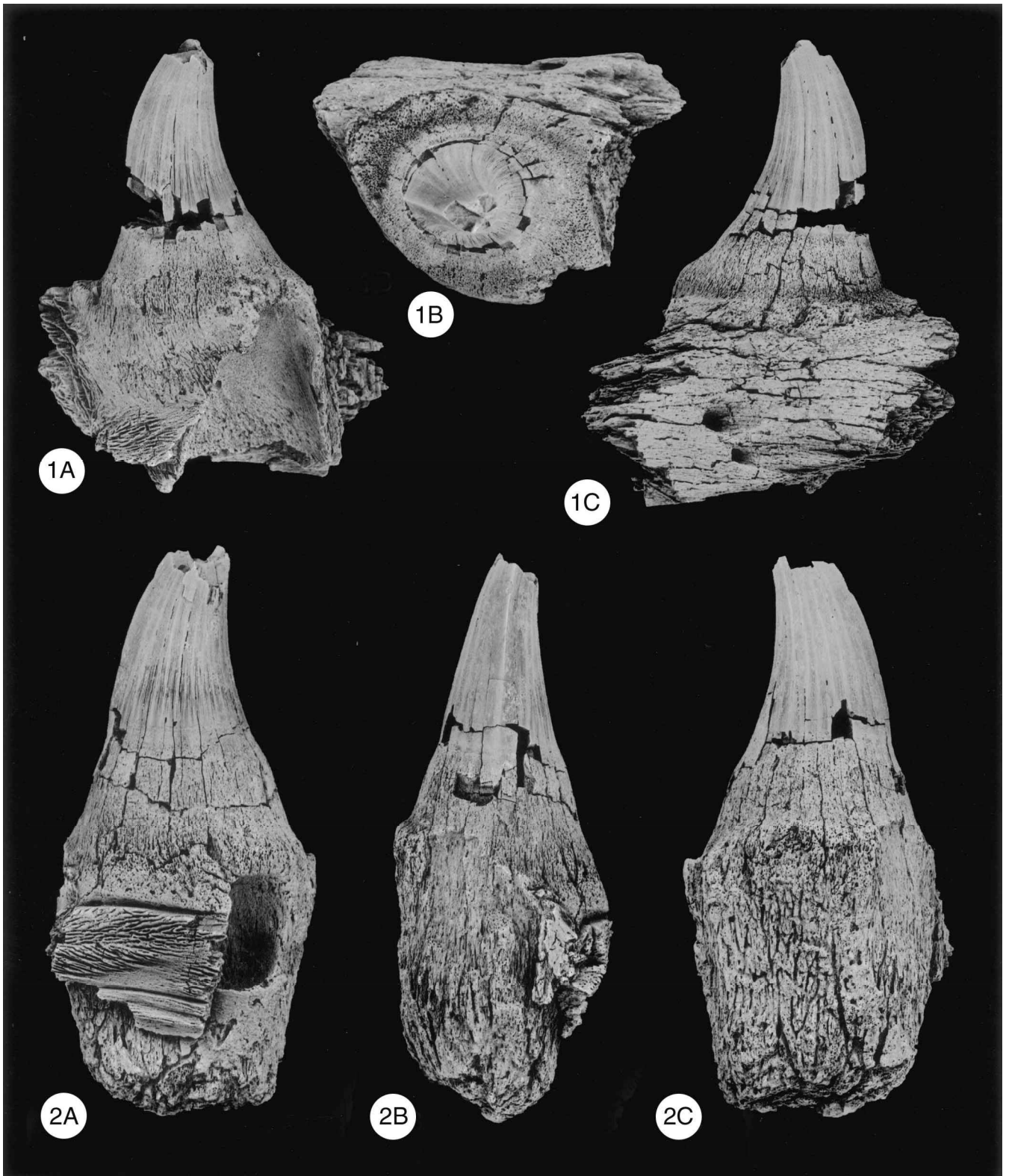


Figure 5 *Tylosaurus ivoensis* (Persson 1963). Premaxillary or the most anteriorly situated dentary teeth from a single individual, *Belemnellocamax mammillatus* zone, Ivö Klack, Kristianstad Basin, southern Sweden, natural size: (1) PMU R421a, lingual (A), occlusal (B) and buccal (C) views. (2) PMU R421b, lingual (A), anterior (B) and buccal (C) views. Prior to preparation, the two teeth were attached to each other, in a natural position, by a few millimetres thick cement of calcarenite. The specimen PMU R421a was situated anterior to PMU R421b. The development of facets and striations is representative of the average morphology in our material of *T. ivoensis*.

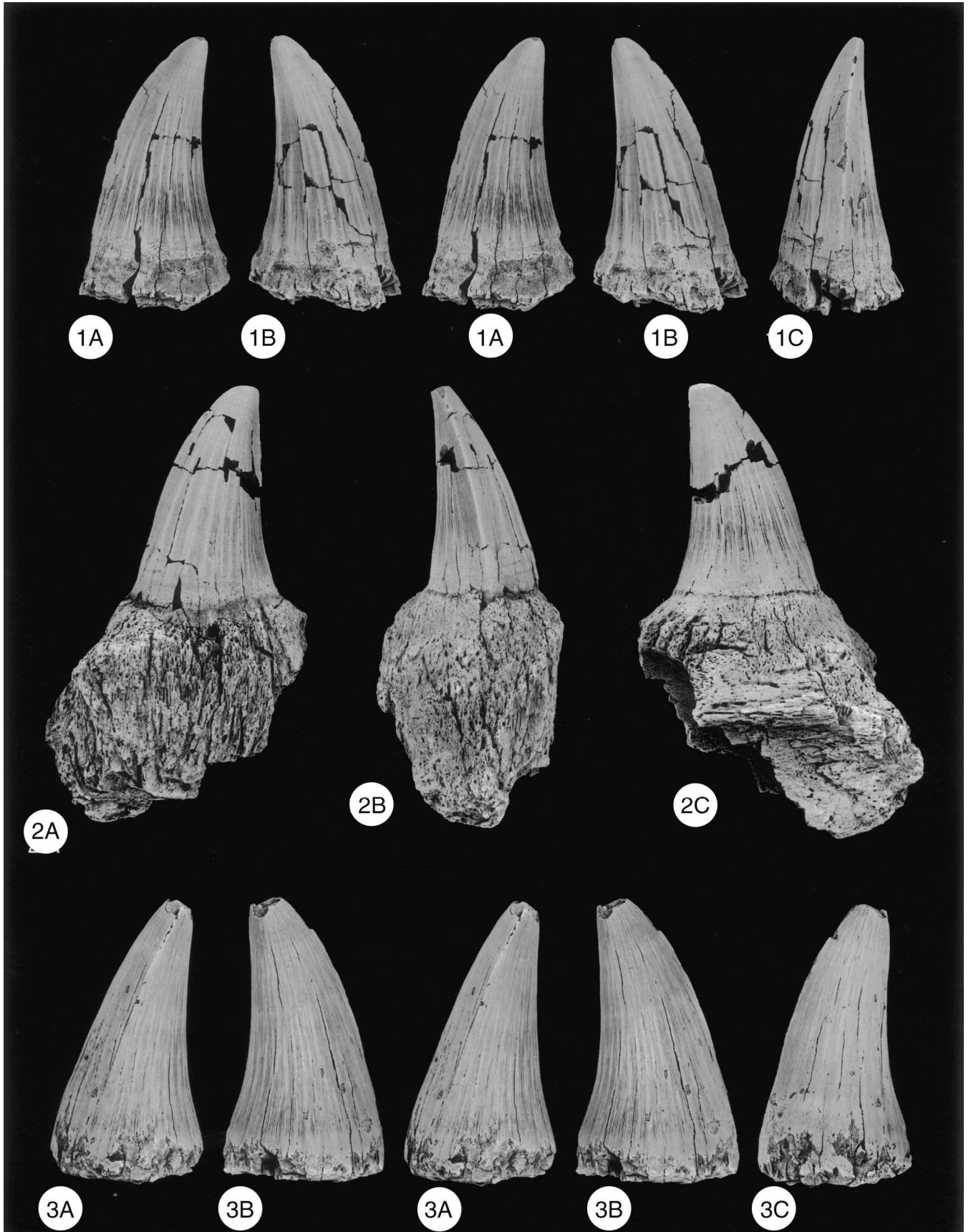


Figure 6 *Tylosaurus ivoensis* (Persson 1963), *Belemnellocamax mammillatus* zone, Ivö Klack, Kristianstad Basin, southern Sweden, natural size: (1) PMU R1251, lingual (A, stereo pair), buccal (B, stereo pair) and anterior (C) views; anterior crown with markedly stronger facets than the average morphology. (2) PMU R423, buccal (A), anterior (B) and lingual (C) views; latero-posterior tooth with somewhat stronger facets than average. (3) RM PZ R1175, posterior (A, stereo pair), lingual (B, stereo pair) and buccal (C) views; anterior crown with weaker facets than average.

relative proportions of these vertebrae. The marginal teeth in *Taniwhasaurus* are much too poorly illustrated to allow a meaningful comparison with those of '*M. ivoensis*, and the morphology of the caudal vertebrae in *Taniwhasaurus* has not been described in the literature. The great distance between what is now New Zealand and southern Sweden makes it somewhat unlikely that '*M. ivoensis* is a *Taniwhasaurus*.

In having a relatively poorly differentiated marginal dentition with conical rather than bucco-lingually flattened crowns, '*M. ivoensis* is dentally closer to the type species of *Tylosaurus* than it is to the type species of *Hainosaurus*. Pterygoid teeth are virtually identical in *T. proriger* and '*M. ivoensis*, whereas pterygoid teeth of *Hainosaurus bernardi* are equipped with finely serrated carinae. Centra of anteriorly situated intermediate caudal vertebrae of *Tylosaurus* are indistinguishable from those of the Swedish tylosaurid, while the corresponding centra in *Hainosaurus* are both shorter and wider than are those of '*M. ivoensis*. The Swedish tylosaurine is therefore referred to *Tylosaurus*.

Tylosaurus ivoensis (Persson 1963) nov. comb.
(Figs 4A–B, 5, 6, 7.2, 8–11)

- ?1836 *Ichthyosaurus*; Nilsson, p. 139, pl. 5, fig. 5.
 ?1837 Mosasauri; Hisinger, p. 7.
 ?1837 Ichthyosauri; Hisinger, pl. a, fig. 2b.
 ?1857 *Mosasaurus hofmanni* [sic]; Nilsson, p. 47.
 ?1885 *Mosasaurus camperi*; Schröder, p. 326.
 ?1885 *Mosasaurus* sp. I; Schröder, p. 327.
 ?1885 *Leiodon* [sic] *lundgreni*; Schröder, pp. 329–331, pl. 17, fig. 3.
 ?1888a *Mosasaurus camperi*; Lundgren, p. 19 (list of fossils).
 ?1888a *Mosasaurus* sp. I; Lundgren, p. 19 (list of fossils).
 ?1888a *Leiodon* [sic] *lundgreni*; Lundgren, p. 19 (list of fossils).
 1894 *Mosasaurus camperi*; Nathorst, p. 195.
 ?1894 *Leiodon* [sic]; Nathorst, p. 195.
 ?1911 *Mosasaurus* sp. I; Hennig, p. 671 (list of fossils).
 ?1911 *Mosasaurus camperi*; Hennig, p. 671 (list of fossils).
 ?1911 *Leiodon* [sic] *lundgreni*; Hennig, p. 671 (list of fossils).
 ?1939 *Mosasaurus giganteus*; Kuhn, p. 67 (list of fossils).
 ?1939 '*Mosasaurus* *lundgreni*'; Kuhn, p. 70 (list of fossils).
 ?1939 Mosasauridae gen. indet. [*partim*]; Kuhn, p. 81 (list of fossils).
 1954 Mosasurie [sic]; Troedsson, fig. 26.2–3.
 1959 *Mosasaurus* cf. *hoffmanni*; Persson, pp. 462–3, 475, fig. 10; pl. 15, figs 1–2.
 1959 *Mosasaurus* sp.; Persson, pp. 463, 475.
 ?1959 Undeterminable mosasaurian tooth-crown I; Persson, p. 470.
 ?1959 Undeterminable mosasaurian tooth-crown II; Persson, p. 470.
 1963 *Mosasaurus hofmanni ivoensis*; Persson, pp. 5–6.
 1967 *Mosasaurus ivoensis*; Russell, pp. 135–6 and chart 7 on p. 237.
 1979 *Mosasaurus* cf. *hoffmanni*; Jeppsson, fig. 5a.
 1991 *Mosasaurus lemonnieri*; Lingham-Soliar, p. 665.
 1996 *Mosasaurus*; Bardet & Pereda Suberbiola, p. 96.
 1998 *Hainosaurus?* *ivoensis*; Lindgren, p. 41.
 1999 *Tylosaurus?* *ivoensis*; Lindgren, p. 16.

Holotype. RM PZ R1292, a marginal tooth-crown from the latest early Campanian *B. mammillatus* zone at Ivö Klack, illustrated by Persson (1959, pl. 15, fig. 1); Fig. 4A herein.

Additional material. *Marginal teeth:* Åsen seven teeth (all unnumbered, Lund University); Axeltorp one tooth (unnumbered, Swedish Museum of Natural History); Balsberg one tooth (LO 3879 t); Ignaberga 11 teeth (LR 1 and one

unnumbered, Lund University; RM PZ R1188, 1232–1234, 1284, 1285 and three unnumbered, Swedish Museum of Natural History); Ivö Klack 149 teeth (KrMG 441; LO 3880, 3881 and one unnumbered, Lund University; PMU R387, 391, 421b, 423, 1251, RP 42 and 65 unnumbered, Museum of Evolution; RM PZ R1112, 1115, 1117, 1130, 1137, 1150–1152, 1154, 1162, 1172–1176, 1179, 1180, 1209, 1214–1217, 1230, 1246, 1247, 1249, 1252, 1255, 1286, 1287, 1289–1291, 1293, 1294, 1310, 1311, 1316, 1318, 1320, 1323, 1324, 1334, 1335, 1377–1380, 1383, 1387, 1388, 1391, 1399, 1400, 1408, 1412, 1417, 1424–1425, 6080 [this label includes four teeth which are, based on colour and state of preservation, probably from Ivö Klack], 6080a–b and six unnumbered, Swedish Museum of Natural History; SGU 3442 Ve 00003, 00004 [these tooth-crowns lack locality data but their colour and state of preservation indicate that they were collected from the Ivö Klack site]; one unnumbered, Department of Geology and Geochemistry, Stockholm University [this tooth-crown also lacks locality data but its colour and state of preservation suggests Ivö Klack]); Ugnsmunnarna two teeth (unnumbered, Lund University).

Pterygoid teeth: Ignaberga one tooth (LR 2); Ivö Klack five teeth (RM PZ R1187, 1314, 1319; two unnumbered, Museum of Evolution).

Partial jawbones: Ivö Klack 18 separate fragments (PMU R421a and 16 unnumbered specimens [some of which are associated with remains of marginal teeth], Museum of Evolution; one unnumbered fragment, Swedish Museum of Natural History).

Dorsal vertebra: Ignaberga 'new quarry' (*sensu* Erlström & Gabrielson 1992) one vertebra (LO 8229 t).

Intermediate caudal vertebrae: Ignaberga 'new quarry' two vertebrae (LO 8230 t, LR 3); Ivö Klack five vertebrae (PMU R409, 410, 1252 and one unnumbered, Museum of Evolution; RM PZ R1013).

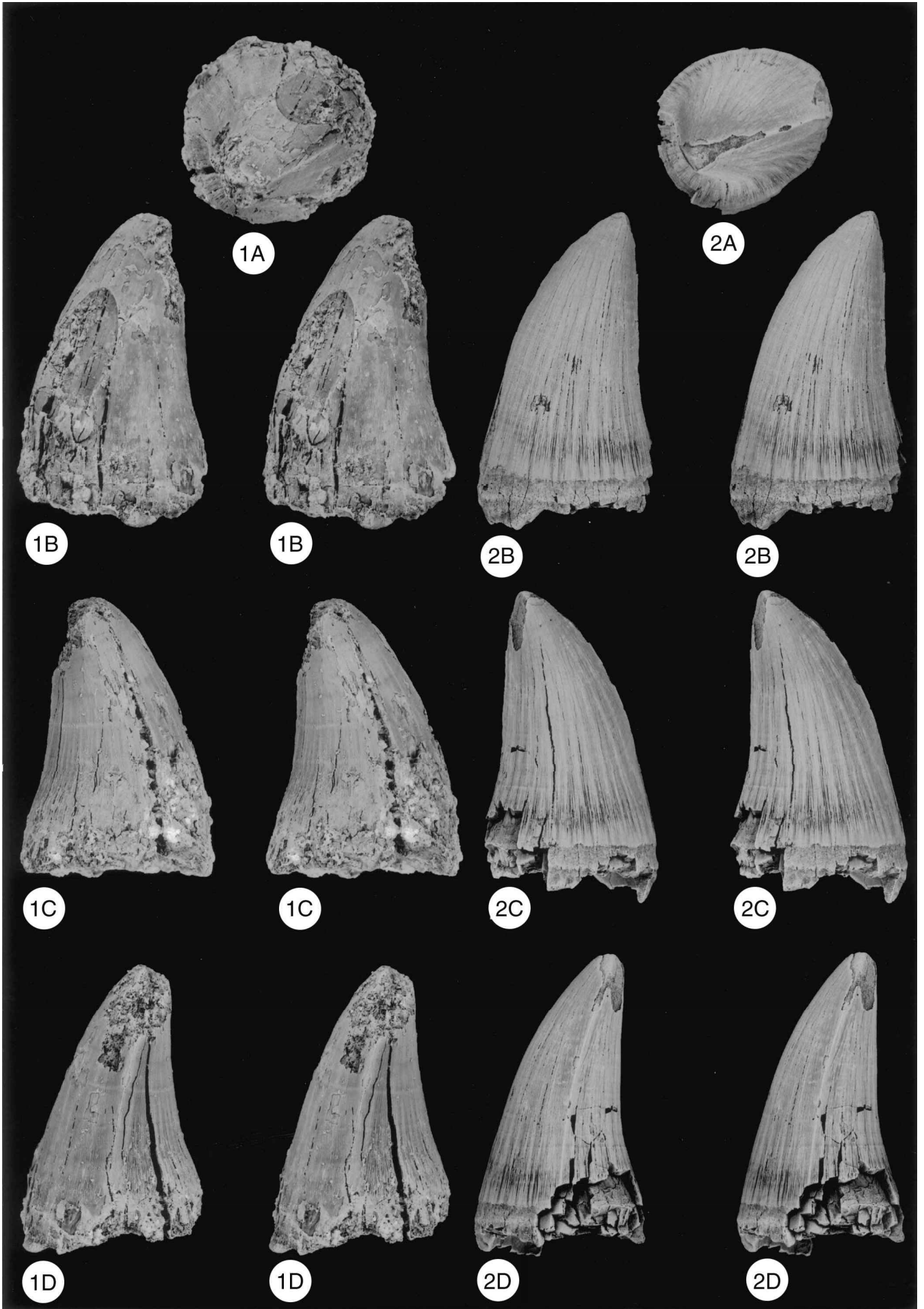
Terminal caudal vertebrae: Ivö Klack four vertebrae (PMU R412; RM PZ R916, 1030; one unnumbered, Stockholm University).

Emended diagnosis. Marginal tooth-crowns are sturdy and very large in adult individuals, occasionally measuring more than 60 mm in height. Medium-sized crowns are moderately curved medio-posteriorly, whereas large crowns are more upright. An anterior and a slightly less prominent posterior carina, both equipped with minute serrations, divide the crowns of all but the most anteriorly situated teeth into a slightly to moderately convex buccal face and a U-shaped lingual face. Premaxillary and/or the most anteriorly situated dentary teeth possess an anterior carina only. Most teeth have numerous, slightly concave facets on both the lingual and buccal sides. Delicate striations are present on the basal portion of the lingual surface of the crown, and occasionally also on the buccal face.

Pterygoid teeth are robust, strongly recurved and sub-circular in cross-section. Lateral carinae on either side of the crown separate it into an anterior and a posterior surface of sub-equal convexity. The enamel on the anterior face is smooth or weakly faceted, and occasionally has basal striations, while the posterior face is lined with closely spaced striae.

The cotyle and condyle articulations in anteriorly situated intermediate caudal vertebrae are shaped as sub-equilateral triangles, with markedly rounded basal apices. The centrum of posteriorly situated terminal caudal vertebrae is shorter than it is high, and exhibits vertically oval to barrel-shaped interarticular surfaces.

Description. *Marginal teeth.* Shed, marginal tooth-crowns range in size from 27 mm to 60 mm in height (measured at a right angle to the plane formed by the base of the crown).



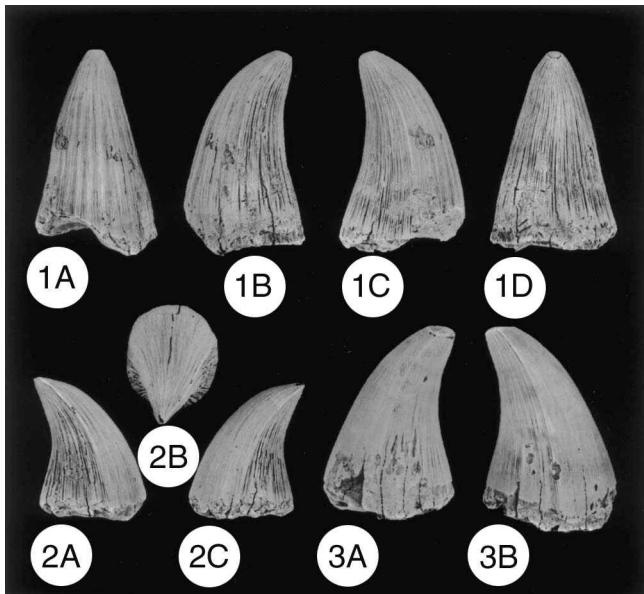


Figure 8 *Tylosaurus ivoensis* (Persson 1963). Pterygoid tooth-crowns, *Belemnellocamax mammillatus* zone, Ivö Klack, Kristianstad Basin, southern Sweden, natural size: (1) RM PZ R1187, anterior (A), lateral (B), lateral (C) and posterior (D) views. (2) RM PZ R1314, lateral (A), occlusal (B) and lateral (C) views. (3) RM PZ R1319, lateral (A) and lateral (B) views.

The largest crown recorded is LR 1, a 60 mm high (estimated original height is 62 mm) and 35 mm wide (at the base) specimen with a worn apex. The buccal surface of anteriorly situated maxillary and dentary teeth is slightly convex and relatively narrow, whereas the lingual face is deeply U-shaped (Fig. 6.1). Posteriorly along the dental ramus the buccal surface widens at the expense of the lingual face and becomes more convex, while the lingual face becomes less markedly U-shaped (Fig. 6.2). The basal face of the crowns is slightly oval to sub-circular. Most teeth have well-developed facets, although the enamel is nearly smooth in a few specimens. Except for the small percentage of teeth with a more or less smooth enamel, the buccal surface has 4–18 facets, whereas the lingual face exhibits 6–20 facets. Delicate, closely spaced and slightly undulating and anastomosing striae cover the lower part of the lingual surface of the crown, and occasionally also the lower portion of the buccal face (Fig. 7.2). The bony base of the teeth is large and barrel-shaped (Fig. 5.2).

Pterygoid teeth. The crowns are up to 28 mm high and 20 mm wide at the base (estimated original height and width of LR 2, a 27 mm high [measured from the base to the apex at a right angle to the plane formed by the base of the crown] and 19 mm wide crown with an incomplete base). The anterior and posterior surfaces are almost equal in convexity and are separated from each other by two indistinct lateral carinae situated on either side of the crown. The enamel on the upper portion of the anterior face is either smooth (as in LR 2) or divided by minute ridges into shallow facets (Fig. 8.1), while

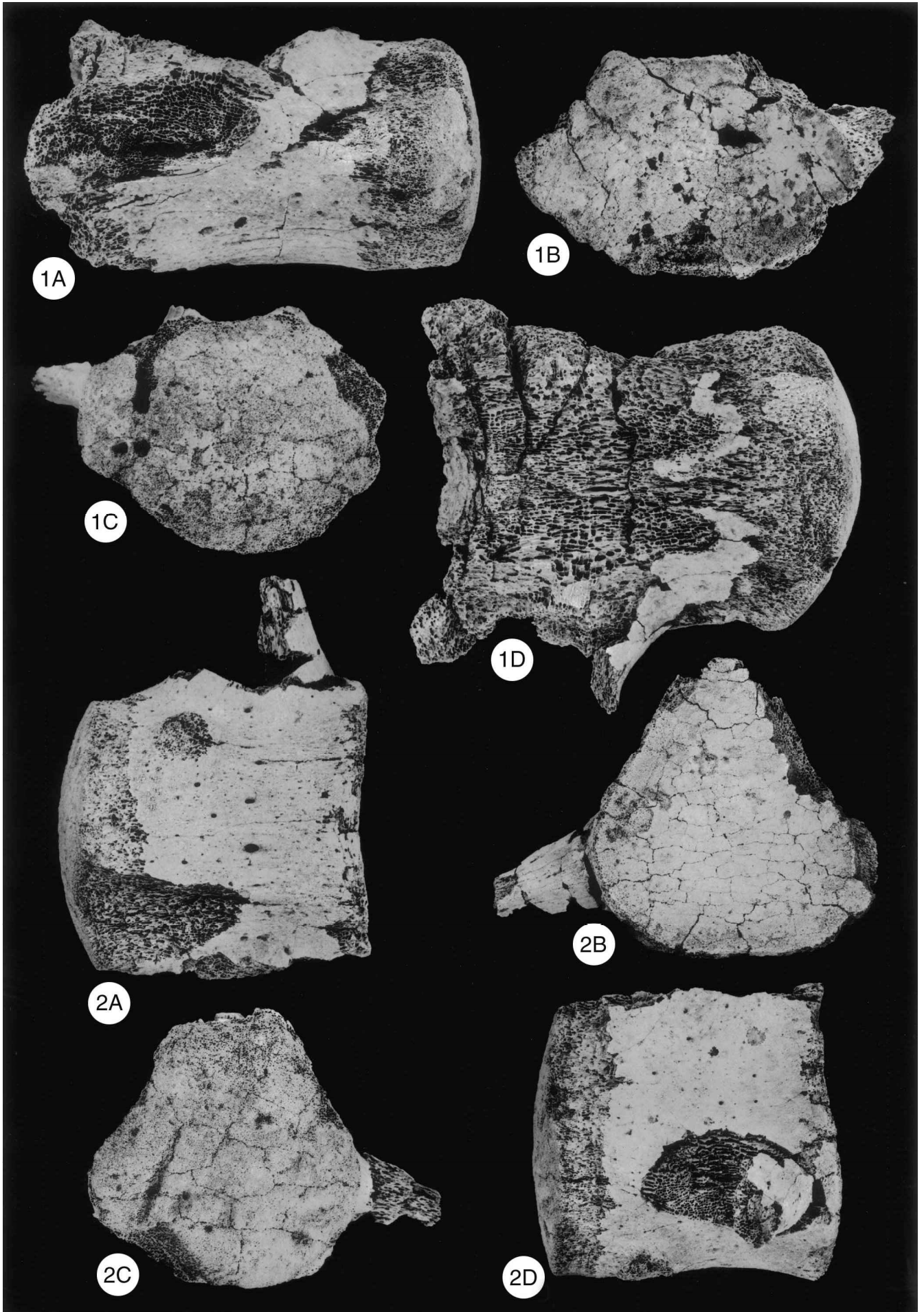
the lower part of the crown displays weak facets and fine, slightly undulating and anastomosing striations. In most teeth the entire posterior surface is lined with striae (Fig. 8.1–2). The morphology of RM PZ R1319 (Fig. 8.3) and LR 2 differs from that of the other four specimens in that the striae on the posterior surface do not reach all the way to the apex of the crown. In RM PZ R1319 the striae reach approximately 5 mm up the base, while the rest of the posterior surface is nearly smooth, with the exception of a few shallow, vertical grooves.

Jawbones. There are a number of separate fragments of jawbones that we refer to *T. ivoensis*. Generally, only the very basal portion of the teeth is preserved, in which case the referral of the material to *T. ivoensis*, rather than to one of the other three mosasaur species present in the *B. mammillatus* zone, is based on the large size of the tooth-bases and their slightly oval to sub-circular cross-section. One fragment of a premaxilla or an anterior portion of a dentary (PMU R421a) includes a functional, nearly complete tooth still attached to the jawbone (Fig. 5.1). Judging from the very fragmentary material at hand, the jawbones in *T. ivoensis* were heavy and powerfully built.

Vertebrae. One incomplete dorsal vertebra, LO 8229 t (Fig. 9.1), is referred to *T. ivoensis*. The maximum length of the centrum (measured between the centres of the interarticular surfaces) is 104 mm. The height of the condyle is 65 mm, and its maximum width is 86 mm. As the specimen is abraded it is difficult to estimate the original outline of the central articulations, although they were clearly markedly wider than high (Fig. 9.1B–C). A fractured synapophysis occupies the antero-dorsal portion of the left lateral surface, and basal remains of the neural arch are visible in dorsal view (Fig. 9.1D). An anteriorly situated intermediate caudal vertebra (LO 8230 t) with a typical tylosaurine morphology, was found some 20 m away from LO 8229 t, in the same horizon in the northern section of Ignabergera ‘new quarry’ (Fig. 1C–D). Based on the colour, state of preservation, matching size and the fact that mosasaur remains are extremely rare at this site, it is possible that the two vertebrae belong to a single individual.

In anteriorly situated intermediate caudal vertebrae the central articulations have the shape of sub-equilateral triangles with markedly rounded basal apices (Fig. 9.2B). A fragmentary, large transverse process occupies the ventro-anterior portion on the right side of LO 8230 t, and slopes at about 20° to the horizontal vertebral axis (Fig. 9.2B). Only one poorly preserved and relatively small peduncle for articulation with a chevron of the haemal arch is preserved in LO 8230 t. The peduncle is situated on the posterior half of the ventral surface of the centrum (Fig. 9.2A). The overall length of LO 8230 t roughly equals the maximum height and width of its interarticular surfaces. At an estimated maximum cotyle width of about 80 mm, the vertebra is approximately 84 mm high (measured on the cotyle) and 75 mm long (measured between the centres of the interarticular surfaces). Centra from a somewhat more posterior portion of the intermediate region of the tail are proportionally shorter, and possess larger, slightly posteriorly inclined haemal peduncles on the

Figure 7 (1) *Hainosaurus peminensis* Nicholls 1988, late early Campanian part of the Pembina Member of the Pierre Shale in southern Manitoba, Canada, natural size. MDM M99.03.0X, occlusal (A), buccal (B, stereo pair), lingual (C, stereo pair), and posterior (D, stereo pair) views; a large, latero-posterior crown. The swollen appearance is partly a result of secondary gypsum growth. (2) *Tylosaurus ivoensis* (Persson 1963), *Belemnellocamax mammillatus* zone, Ivö Klack, Kristianstad Basin, southern Sweden, natural size. RM PZ R1180, occlusal (A), buccal (B, stereo pair), lingual (C, stereo pair), and posterior (D, stereo pair) views; a latero-posterior tooth-crown. This is one of the largest crowns of *T. ivoensis* that we have examined. The facets are of average development, whereas the striae on the buccal face are stronger than average.



ventral surface (Fig. 10.1D and 2C). In anterior view, the base of the neural canal is broad and flattened or slightly concave.

Centra of posteriorly situated terminal caudal vertebrae are markedly high relative to their width and length (Fig. 11). The cotyle and condyle articulations are vertically oval to barrel-shaped in outline, and the height of the surfaces exceeds the width by 18–33%. In anterior and posterior views, the base of the neural canal is nearly flat to slightly concave. Large and deeply pitted peduncles for articulation of the haemal arch are set a few millimetres apart on the ventral surface of the centra (Fig. 11.1D and 2E). The largest posteriorly situated terminal caudal vertebra at hand (PMU R412) is approximately 56 mm high, 43 mm wide and 34 mm long (measured on the cotyle and between the centres of the interarticular surfaces, respectively).

Comparisons. Even though both the pterygoid teeth and the caudal vertebrae of *T. ivoensis* are indistinguishable from those of *T. proriger* from the Smoky Hill Chalk Member of the Niobrara Formation in Kansas, the two species can be separated by the morphology of their marginal teeth. In *T. ivoensis*, the buccal surface of the crowns have generally well-marked facets, whereas tooth-crowns of *T. proriger* often have poorly developed facets. Moreover, the carinae are not as pronounced on crowns of *T. proriger* as they are on crowns of *T. ivoensis*. In addition to a significant difference in maximum tooth-size between *T. proriger* and the gigantic *T. ivoensis*, large tooth-crowns of the latter are stouter than are those of *T. proriger*.

In the original description of the late Coniacian to early Santonian *T. nepaeolicus*, Cope (1874, p. 37) stated that the marginal teeth are not faceted, although ‘the enamel is finely striate-grooved, especially toward the base’. Cope also noted a slight differentiation of the teeth along the jaws, where the anteriorly situated crowns have a narrower buccal face than have more posteriorly situated ones. Differences between *T. nepaeolicus* (we have examined FHSM VP-2209 and YPM 3970) and *T. ivoensis* include: (1) the crowns are tolerably slender in *T. nepaeolicus* relative to the robust crowns of *T. ivoensis*; (2) the carinae are less well developed on the teeth of *T. nepaeolicus* than they are on crowns of *T. ivoensis*; (3) the enamelled surfaces on the teeth of *T. nepaeolicus* are either smooth or obscurely faceted, while the crowns of *T. ivoensis* are generally distinctly faceted; (4) the striations reach somewhat higher up on the crowns of *T. nepaeolicus* than they do on crowns of *T. ivoensis*.

In addition to the distinguishing character state combination of *T. nepaeolicus*, there is a highly significant difference in maximum size between the tooth-crowns of this species and those of *T. ivoensis*. This distinction reflects the moderate adult size of *T. nepaeolicus* relative to the gigantic proportions of *T. ivoensis* (as indicated by its very large tooth-crowns and vertebral centra).

Apart from *T. proriger* and *T. nepaeolicus*, two additional nominal species of *Tylosaurus* are presently recognised as diagnosable (see e.g. Russell 1967; Lingham-Soliar 1992; Kiernan 2002). These include *T. capensis* Broom 1912 from the middle Santonian of Pondoland, South Africa and *T. iembeensis* (Antunes 1964) from the late Turonian of northwestern Angola. The marginal teeth of *T. iembeensis* have been

described as ‘striated (not prismatic)’ by Lingham-Soliar (1992, p. 182) and are in this regard different from those of *T. ivoensis*, as tooth-crowns of the latter are generally faceted, giving the enamelled surfaces a somewhat prismatic appearance. The type material of *T. capensis* does not include marginal teeth (Lingham-Soliar 1992).

Although features characterising *Tylosaurus* predominate in *T. ivoensis*, it is sufficiently similar in tooth-crown and vertebral morphology to *Hainosaurus bernardi* to warrant a detailed comparison with this species, as well as with other nominal *Hainosaurus*. In the original study of *H. bernardi* from the late Maastrichtian of Belgium, Dollo (1885) identified three types of marginal teeth in the type specimen (IRSNB R23): (1) tooth-crowns with a circular cross-section, which are equipped with an anterior carina only; (2) teeth displaying tall and bucco-lingually compressed crowns, where the enamelled surfaces are separated from one another by both anterior and posterior carinae; (3) teeth similar to those of the second category but with a lower crown. Subsequently, Dollo (1889b, pl. 9, fig. 3) illustrated the skull of IRSNB R23 with faceted marginal teeth. More recently, Lingham-Soliar (1992) described teeth of another specimen of *H. bernardi* (IRSNB 3672) as having faint facets and being equipped with an anterior carina only (anteriorly situated teeth), or with both anterior and posterior carinae (more posteriorly situated teeth). By examining both IRSNB R23 and IRSNB 3672, we identified the following differences between *H. bernardi* and *T. ivoensis*: (1) the marginal tooth-crowns are markedly more compressed bucco-lingually in *H. bernardi* than they are in *T. ivoensis*; (2) laterally and posteriorly situated marginal crowns are nearly symmetrically bicarinate in *H. bernardi*, whereas the buccal and lingual surfaces are very unequal in convexity in corresponding crowns of *T. ivoensis*; (3) marginal teeth of *H. bernardi* display numerous but weakly developed shallow facets. In *T. ivoensis* the facets are better developed and more deeply concave; (4) the carinae on the pterygoid teeth are minutely serrated in *H. bernardi*, whereas the carinae lack serrations in *T. ivoensis*; (5) anteriorly situated intermediate caudal vertebral centra are both longer and taller in *T. ivoensis* than they are in *H. bernardi*.

The marginal tooth-crowns of the nominal *H. peminensis* from the late early Campanian part of the Pembina Member of the Pierre Shale in southern Manitoba, Canada, are large and robust with a gently convex buccal surface and a U-shaped lingual face (Fig. 7.1). They are faceted, and basal striae are present on the lingual surface and occasionally also on the buccal face. The teeth are seemingly indistinguishable from similarly sized ones of the coeval *T. ivoensis*, although our dental comparison between the two nominal species is based on a rather small number of imperfectly preserved teeth of *H. peminensis*. We cannot rule out the possibility that a larger sample of teeth (including small to medium-sized specimens) of the Canadian mosasaur would allow it to be separated from *T. ivoensis*. The pterygoid teeth of *H. peminensis* are very similar to those of *T. ivoensis* and *T. proriger*. The two lateral apices of the interarticular surfaces on anteriorly situated intermediate caudal vertebrae are somewhat more angular in *H. peminensis* than they are in *T. ivoensis*, whereas the posteriorly situated terminal caudal centra are virtually identical in the two nominal species.

Figure 9 *Tylosaurus ivoensis* (Persson 1963). Dorsal and anteriorly situated intermediate caudal vertebrae, possibly from a single individual, *Belemnellocamax mammillatus* zone, Ignaberga ‘new quarry’ *sensu* Erlström & Gabrielson (1992), Kristianstad Basin, southern Sweden, $\times 0.7$: (1) LO 8229 t, lateral (A), anterior (B), posterior (C) and dorsal (D) views; an incomplete dorsal vertebra. (2) LO 8230 t, ventral (A), anterior (B), posterior (C) and lateral (D) views; an incomplete, anteriorly situated intermediate caudal vertebra.

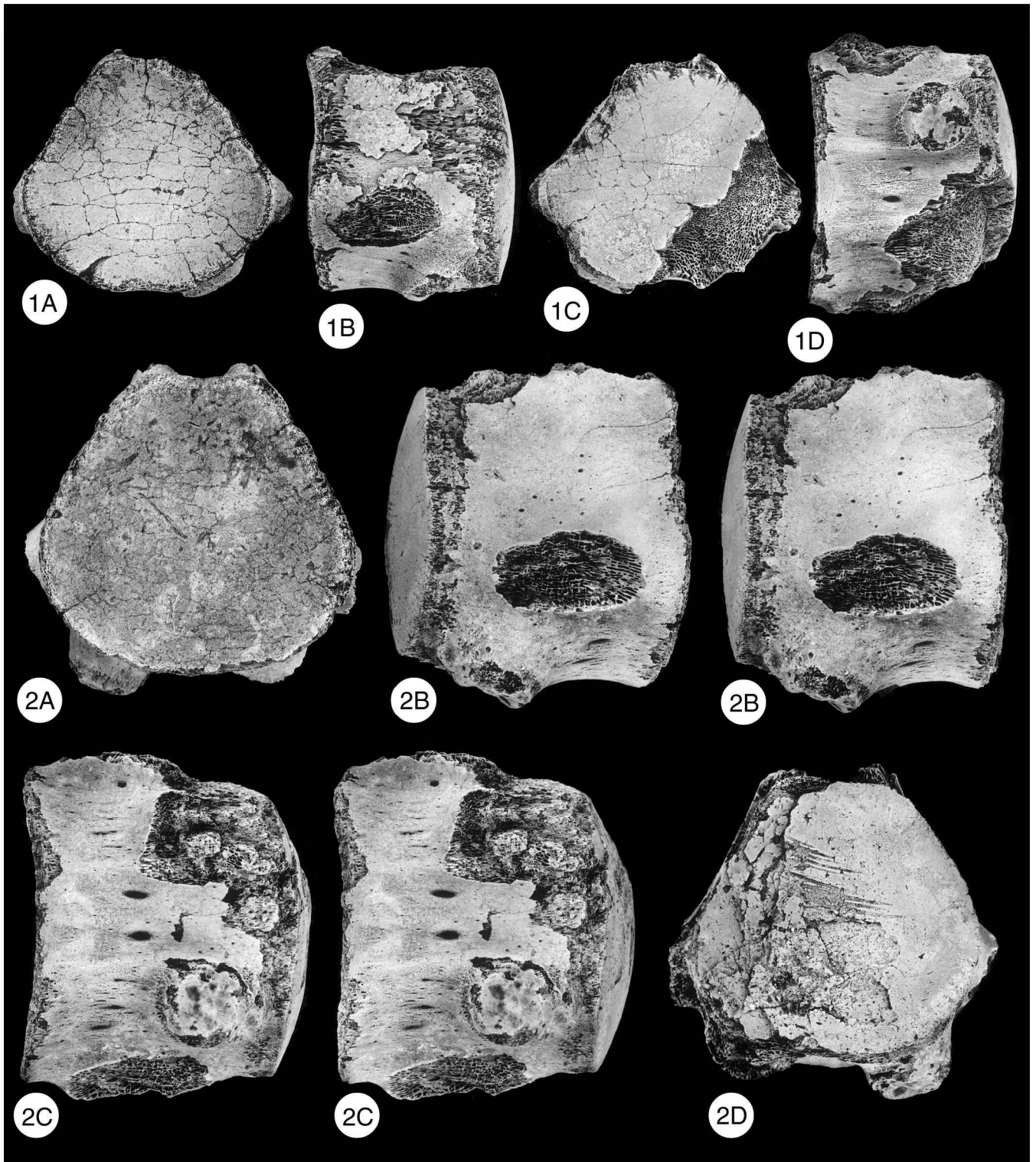


Figure 10 *Tylosaurus ivoensis* (Persson 1963). Anteriorly situated intermediate caudal vertebrae, *Belemnello-camax mammillatus* zone, Ivö Klack, Kristianstad Basin, southern Sweden, $\times 0.7$: (1) RM PZ R1013, anterior (A), lateral (B), posterior (C) and ventral (D) views; a comparatively small vertebra from a young individual. (2) PMU R1252, anterior (A), lateral (B, stereo pair), ventral (C, stereo pair) and posterior (D) views.

When Nicholls (1988) referred her new nominal species *pembinensis* to *Hainosaurus*, she based this assignment on a number of skeletal features, including the large number of vertebrae between the cranium and the chevron-bearing caudals, the small size of the infrastapedial process on the quadrate, the considerable length of the external nares relative to the length of the skull and the great length of the femur relative to the length of the humerus. We have examined most of the

material assigned to *H. pembinensis* (e.g. MDM M74.06.06, MT 2) and found a number of elements in these skeletons with a morphology intermediate between that of *Tylosaurus* (i.e. *T. proriger*) and *Hainosaurus* (i.e. *H. bernardi*). Nicholls (1988) observed that the infrastapedial process on the quadrate is reduced to a small bulge in *H. pembinensis*, and concluded that this character is consistent with an assignment of the species to *Hainosaurus*. Our own examination of the quadrate

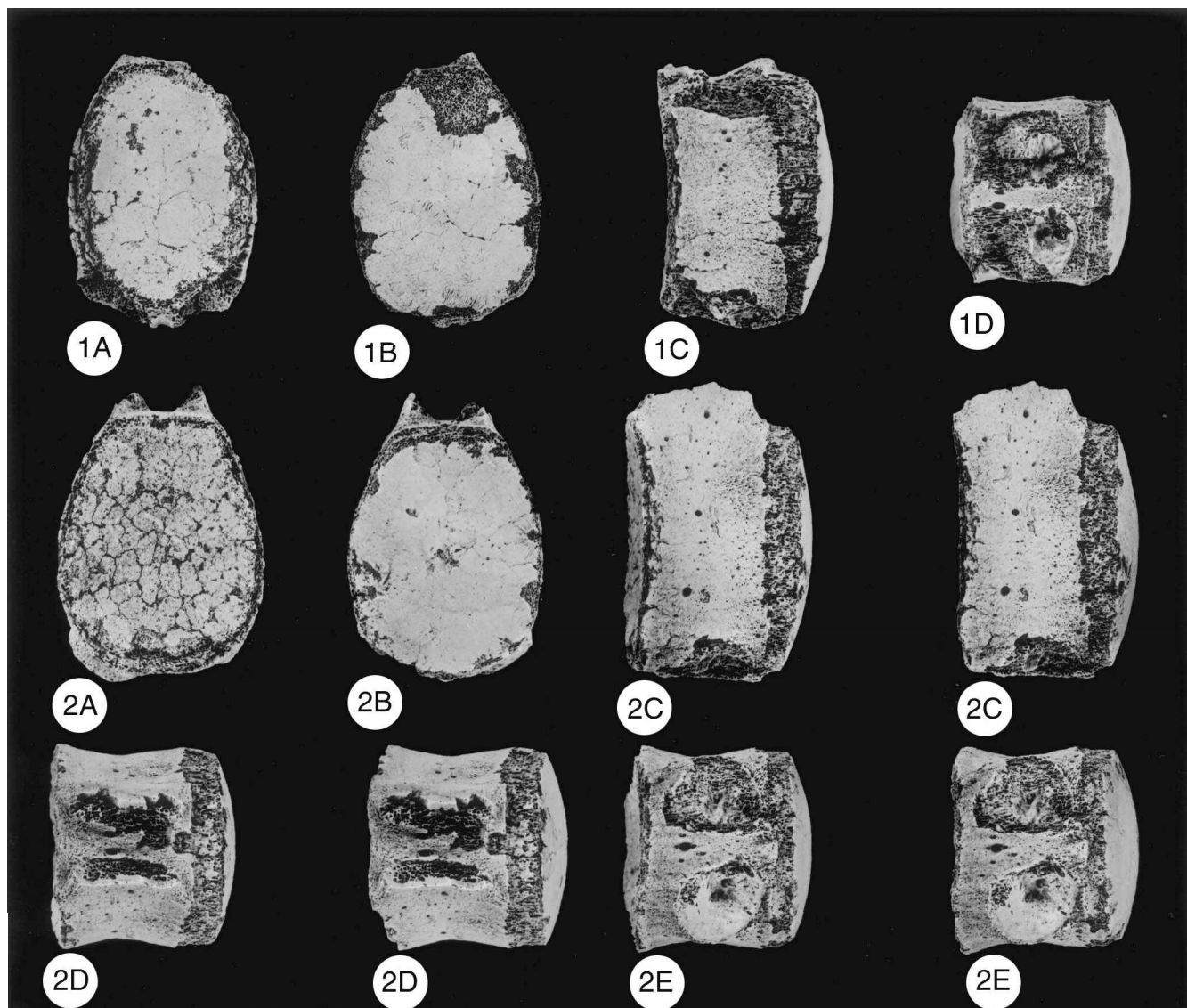


Figure 11 *Tylosaurus ivoensis* (Persson 1963). Posteriorly situated terminal caudal vertebrae, *Belemnellocamax mammillatus* zone, Ivö Klack, Kristianstad Basin, southern Sweden, $\times 0.7$: (1) RM PZ R1030, anterior (A), posterior (B), lateral (C) and ventral (D) views. (2) PMU R412, anterior (A), posterior (B), lateral (C, stereo pair), dorsal (D, stereo pair) and ventral (E, stereo pair) views.

in the type of *H. peminensis* (MT 2) revealed that the infra-stapedial process is in fact somewhat smaller (although not as small as indicated by fig. 6b in Nicholls 1988) than it is in *T. proriger* (e.g. YPM 1304, YPM 3989). Nevertheless, the overall morphology of the quadrate in MT 2 is more similar to that of *T. proriger* than it is to that of *H. bernardi* (e.g. the supra-stapedial process is fairly large in MT 2 and *T. proriger*, while it is relatively small in *H. bernardi*).

According to Nicholls (1988), the vertebral column in the type specimen of *H. peminensis* (MT 2) is almost complete (137 or 138 vertebrae), lacking only the atlas, axis and third cervical vertebrae. However, when examining MT 2 we got the impression that the vertebral series is composed of vertebrae belonging to two different individuals. Based on the colour, size and state of preservation, we associate about 120 vertebrae with the skull and limb elements, and about 15–20 additional vertebrae to another, much smaller individual.

The Morden tylosaurine specimens, assigned by Nicholls (1988) to *Hainosaurus peminensis*, exhibit characters more or less intermediate between those of *Tylosaurus* and *Hainosaurus*. The morphology of the tooth-crowns, intermediate caudal

vertebral centra and quadrate indicate that they are *Tylosaurus*, whereas the large number of vertebrae between the cranium and the chevron-bearing caudals would suggest that they are *Hainosaurus*. Nicholls' generic assignment of this species is thus questionable. Further complicating the matter is the fact that the vertebral centra and tooth-crowns of the Morden tylosaurine are very similar to those of large *T. ivoensis*. If the two names *T. ivoensis* and *H. peminensis* turn out to be synonymous, the former takes priority by 25 years.

The marginal teeth of the late Santonian or early Campanian (N. Bardet pers. comm. 2000) type (and only known) specimen of *H. gaudryi* (MNHN 1896–15) from Eclusier Vaux near Péronne (Somme), France, overlap in morphology with those of *T. ivoensis* (see Thevenin 1896, figs 1–2, pl. 29, figs 1–3; Lingham-Soliar 1992, pl. 7, figs a and b). Nevertheless, the only preserved pterygoid tooth in MNHN 1896–15 is conspicuously different from those of *T. ivoensis*. It displays striations and faint facets as in the Swedish tylosaurine. However, contrary to pterygoid teeth of *T. ivoensis*, the crown is markedly compressed laterally (see Thevenin 1896, fig. 4) and exhibits salient carinae which are situated anteriorly and posteriorly

(Thevenin 1896, fig. 4; pers. obs.), not laterally as in *T. ivoensis* (Fig. 8.1B–C, 2A, C, 3A–B). The incomplete skull comprising MNHM 1896-15 has been assigned to *Hainosaurus* on the basis of a number of characters, which have generally been considered as diagnostic for the genus, including the exclusion of the frontal from the upper margin of the orbit by a prefrontal–postorbitofrontal contact, the great length of the external nares relative to the length of the skull and the double buttressed premaxillary suture (Bardet 1990; Lingham-Soliar 1992). The frontal is, however, also excluded from the dorsal margin of the orbit by a contact of the prefrontal and postorbitofrontal in *Tylosaurus* (Russell 1967), and, as demonstrated above, a double buttressed premaxillary suture is not exclusive to *Hainosaurus*. The large length ratio (0.38) of the external nares/skull (measured from the end of the rostrum to the parietal foramen) given by Bardet (1990) seems somewhat exaggerated. Our own measurements indicate a more moderate ratio of 0.25–0.27, which is more in accordance with that of *T. proriger* (0.26). Hence, the assignment of MNHN 1896-15 to *Hainosaurus* is questionable. Bardet (1990) referred MNHN 1896-15 to *H. bernardi*, whilst Lingham-Soliar 1992 regarded the nominal *H. gaudryi* as a diagnosable species, distinct from *H. bernardi*. The differences in the marginal dentition between *H. gaudryi* and *H. bernardi* are basically the same as between *T. ivoensis* and *H. bernardi*. As outlined above the pterygoid teeth of the three species are all different from each other.

Lingham-Soliar (1992, p. 181) emphasised the significance of the comparatively short rostrum of the premaxilla of *H. gaudryi*. Even though the rostrum seems to be somewhat shorter in MNHN 1896-15 relative to that of *T. proriger*, *H. bernardi* and *H. peminensis* (see Thevenin 1896, pl. 29, figs 1 and 3; Lingham-Soliar 1992, fig. 11, pl. 7, fig. b), the apex is transversally broken and/or pathologically deformed. Consequently, it is difficult to estimate the original length and form of the premaxillary prow of MNHN 1896-15.

The poorly known Coniacian or Santonian (see Malchus *et al.* 1996) *H. lonzeensis* Dollo 1904, from Loncée in the province of Namur, near Gembloux, Belgium, is based on a partial premaxilla and two terminal caudal vertebrae (IRSNB, no catalogue number; see also Dollo 1909). This nominal species has been considered as a *nomen dubium* by Nicholls (1988) and Lingham-Soliar (1992). While the type material in itself seems to be inadequate for a meaningful diagnosis, nearly 50 tylosaurine marginal tooth-crowns (IRSNB, no catalogue numbers) collected from the same locality indicate a species dentally very similar to *T. proriger* (pers. obs.).

Three marginal teeth are preserved in KUVF 1024, an incomplete mosasaur skeleton from the Smoky Hill Chalk Member (probably upper half) of the Niobrara Formation in western Kansas, USA. The tooth-crowns are fairly large (up to 35 mm high and 17 mm wide at the base), and markedly curved in a medio-posterior direction (Fig. 4E). Anterior and posterior carinae are present, both of which are strong. The buccal surface is divided by four to five prominent and smoothly rounded ridges into gently concave facets (a 'fluted' morphology; Bell 1997). Unfortunately, the lingual side of the teeth is obscured by sediment and can therefore not be observed. Based on tooth-crown morphology, Russell (1967) assigned KUVF 1024 to Persson's (1963) nominal *Mosasaurus hoffmanni ivoensis* and gave the subspecies species rank. However, when comparing the marginal teeth in KUVF 1024 with the holotype tooth-crown and additional topotypic tooth-crowns of *T. ivoensis*, it is evident that KUVF 1024 and the Swedish mosasaur represent different species (Fig. 4A, B, E). The facets are significantly more distinct on the teeth of KUVF 1024 than they are on teeth of topotypic *T. ivoensis*. In addition to a very noticeable difference in size (assuming

KUVF 1024 represents an adult individual), tooth-crowns of the Niobraran specimen are more distally curved than are those of *T. ivoensis*.

Remarks. Persson (1959) stated that teeth of *M. cf. hoffmanni* and *Mosasaurus* sp. (both included here in *T. ivoensis*) had been obtained from several localities in the Kristianstad Basin, including Balsberg, Balsvik, Ignaberga, Ivö Klack and Maltesholm. The occurrence of *T. ivoensis* at Balsberg, Ignaberga and Ivö Klack (in addition to the new material from Åsen, Axeltoorp and Ugnsmunnarna) has been confirmed in this study, while no tylosaurine remains from Maltesholm have been located. One tylosaurine tooth (RM PZ R1236) from the Balsvik quarry is similar to the marginal teeth of *T. ivoensis*, although the crown is fairly compressed buccolingually. There is no accompanying note indicating the horizon from which the specimen was collected. This is problematic, as the strata at the Balsvik quarry span the earliest late Campanian through the earliest Maastrichtian (in belemnite terms).

The incomplete tooth-crown LO 169 T (identified as *M. hoffmanni* [sic] in Nilsson [1857, p. 47] and *Mosasaurus* sp. I in Schröder [1885, p. 327]) has a somewhat swollen appearance, and is approximately 36 mm high and 29 mm wide at the base (see Nilsson 1836, pl. 5, fig. 5; Hisinger 1837, pl. a, fig. 2b). In cross-section, the buccal face is slightly convex, while the lingual surface is deeply U-shaped. Both surfaces have numerous obscure facets, and faint striations are present on the basal portion of the internal side of the crown. The tooth-crown resembles marginal teeth of *T. ivoensis*, although it is somewhat more thickset and the facets and striae are indistinct. The stocky appearance and marked curvature may reflect a posterior position on the dental ramus. The specimen was collected in the Oppmanna area, NE of Lake Oppmannasjön in the Kristianstad Basin. Unfortunately, the precise provenance of LO 169 T is not known. Temporarily exposed sediments in the area have yielded belemnites transitional between the latest early Campanian *B. mammillatus* and the earliest late Campanian *B. balsvikensis*, indicating that the stratum from which LO 169 T was collected may be slightly younger than those that accumulated during *B. mammillatus* time (for a more extensive discussion regarding the taxonomy and the biostratigraphy of the belemnites from the Kristianstad Basin, see Christensen 1975). The slightly deviating morphology and probably younger age of LO 169 T prevent us from assigning it to *T. ivoensis* with confidence.

As mentioned in the historical review section above, Schröder's nominal species *L. lundgreni* is based on a mosasaurian tooth-crown (LO 784 T; see Schröder 1885, pl. 17, fig. 3). The specimen is strongly recurved, and is divided by indistinct lateral carinae into an anterior and a posterior surface of subequal convexity. The crown is covered by smooth enamel on the anterior face, while the posterior surface is lined with striations. The striae are closely spaced and well developed on the lower two-thirds of the crown, but weaken gradually towards the apex. The tooth measures approximately 30 mm in height and 21 mm in maximum width. Over the years the provenance of LO 784 T has been a matter of dispute. In the original description, Schröder (1885, p. 329) stated that the tooth was collected at Balsberg, an assertion that subsequently was contested by Hennig (1911). Instead, the latter author (Hennig 1911, p. 671) claimed that LO 784 T had been found near the hamlet of Köpinge in the Vomb Trough (Fig. 1A). Only one tooth-crown (LO 3879 t) from the Balsberg cave is present in the *T. ivoensis* material at our disposal. Its colour and state of preservation differ markedly from those of LO 784 T, and consequently it is unlikely that the two specimens originate from the same locality. We have currently no reason to doubt

Hennig's view that the tooth was collected in the Köpings area. Two belemnite assemblages were recorded by Christensen (1986) from the Köpings sandstone; an older one with *Belemnellocamax mammillatus* and *Belemnitella mucronata*, indicating a latest early Campanian age, and a younger assemblage with *Belemnitella* aff. *B. langei* Jeletzky 1948 and *B. mucronata*, indicating a middle late Campanian age. Ammonites from the Köpings district indicate an early late Campanian age (Kennedy & Christensen 1997).

The morphology and size of LO 784 T agree well with those of pterygoid teeth of *T. ivoensis*, even though the crown has a somewhat more laterally flattened appearance. Because 'L'. *lundgreni* is based on an isolated pterygoid tooth only, the nominal species is here considered as a *nomen dubium*, as tylosaurine pterygoid teeth may not allow separation at species level or even at the generic level. As pointed out above, we found no differences in the morphology of pterygoid teeth between *T. ivoensis* and *T. proriger*. Moreover, as the precise provenance and age of LO 784 T are uncertain, it is currently not possible to collect additional material of this taxon which could otherwise have clarified its taxonomic status.

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