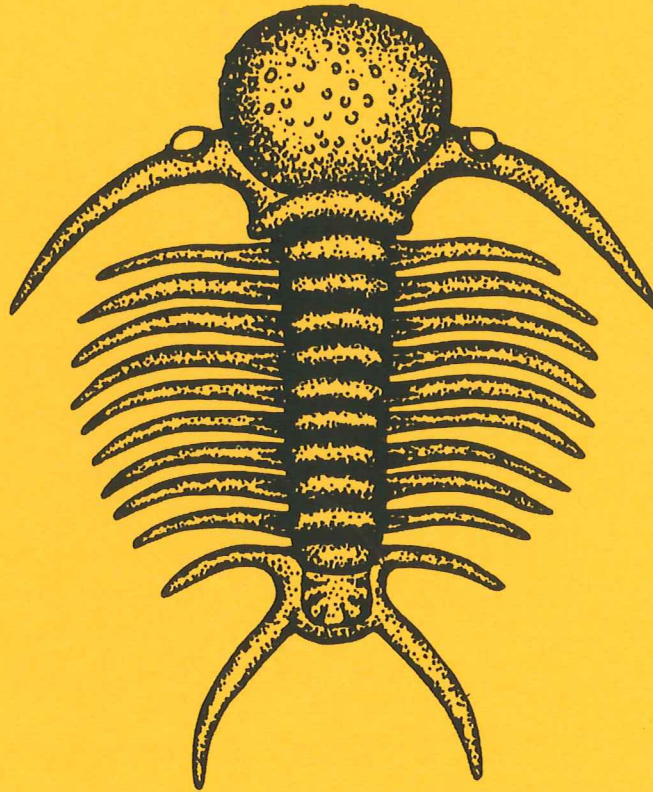


EXAMENSARBETE I GEOLOGI VID LUNDS UNIVERSITET

Historisk geologi och Paleontologi



**Early Campanian mosasaurs (Reptilia; Mosasauridae)
from the Kristianstad Basin, southern Sweden**

Johan Lindgren

per

Lunds univ. Geobiblioteket



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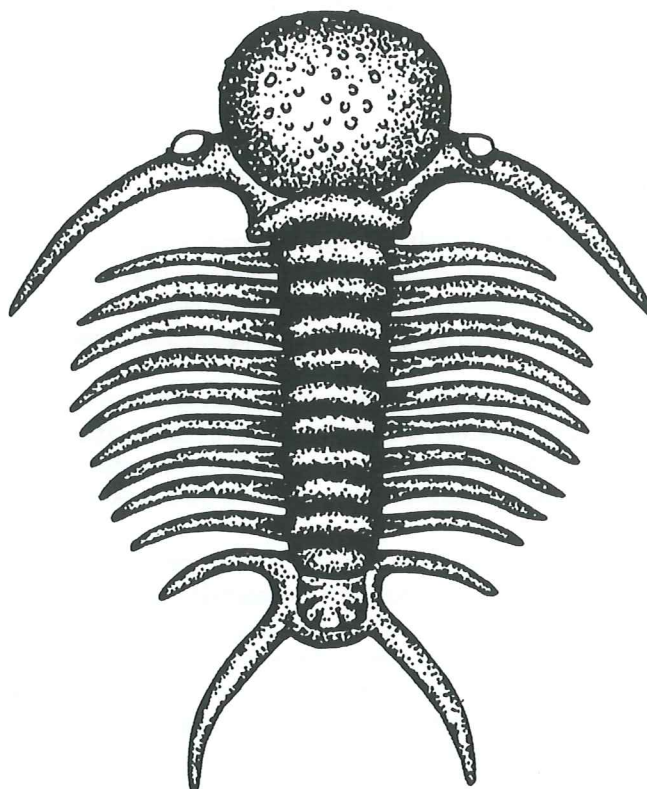
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Nr 95

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Abstract: Marine strata of latest early Campanian age from the Kristianstad Basin in Skåne, southern Sweden, have yielded a diverse mosasaur fauna comprising four taxa: *Clidastes?* sp., *Platecarpus* cf. *somenensis*, *Hainosaurus?* *ivoensis* and Mosasauridae sp. The material consists primarily of isolated tooth-crowns, although a number of incomplete vertebrae and cranial elements have been recorded as well.

Based on the collections of mosasaur remains from four localities, i.e. Åsen, Ignaberga, Maltesholm and Ugnsmunarna, some differences in the distribution of mosasaur taxa within the Kristianstad Basin have been observed. *Clidastes?* sp. is the predominant mosasaur in the near-shore deposits at Åsen, whereas the Ugnsmunarna site, with a more open water environment, has yielded mainly *Platecarpus* cf. *somenensis*.

The assemblage is similar in composition to approximately coeval mosasaur faunas in the Upper Chalk deposits in Norfolk, Sussex and Hampshire, England, the Lower Pierre Shale in South Dakota, USA and the Pembina Member of the Pierre Shale in Manitoba, Canada.

Hainosaurus? *ivoensis* was formerly believed to be a *Mosasaurus* (i.e. *M.* cf. *hoffmanni*, *M. hoffmanni ivoensis* and *M. ivoensis* of previous writers).

Tooth-crowns of Mosasauridae sp. are fairly large, strongly recurved and covered by smooth enamel. As this combination appears to be unique, Mosasauridae sp. may represent a new genus.

Keywords: Mosasauridae, *Clidastes*, *Platecarpus*, *Hainosaurus*, mosasaur, Cretaceous, Campanian, Kristianstad, Skåne, Sweden

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The study of mosasaurs was introduced in the early nineteenth century, as a consequence of the discovery of an excellent preserved specimen (later named *Mosasauros hoffmanni* Mantell 1829), by some quarrymen 30 metres below the surface of Mount St. Peters, Maastricht in Holland. The finding itself and the unusual circumstances surrounding it, attracted much attention and the discovery was soon followed by others. Mosasaur remains have over the years been collected on all continents, with recent findings in Antarctica (Chatterjee et al. 1984) and New Zealand (Wiffen 1990). For a more comprehensive historical review, see Russell (1967).

Generally, mosasauroids (mosasaurs, aigialosaurs and coniasaurs) are considered to be true lizards, closely related to extant varanoids, like the Komodo dragon, *Varanus komodoensis* Ouwens 1912. As demonstrated by Russell (1967), several features, particularly in the skull, indicate a close relationship between these groups. However, this classification has not been universally accepted and other opinions about the affinity exist. Caldwell et al. (1995) concluded that mosasauroids is a monophyletic assemblage, distinct from varanoids. A recent study of an early Cenomanian, marine snake, *Pachyrachis problematicus* Haas 1980, supports an old theory about a mosasauroid-snake affinity (Caldwell & Lee 1997).

Based on differences in certain skeletal elements, mainly in the skull and, to a lesser extent, in the postcranial region, the family Mosasauridae is subdivided into three subfamilies; Mosasaurinae, Plioplatecarpinae and Tylosaurinae (Russell 1967).

Mosasaurs inhabited shallow, temperated to subtropical seas, in a brief 25 million years, during the later half of the Cretaceous period (Russell 1967). The first record of the group is in strata of Turonian age and

together with several other animal groups they disappeared by the end of the Maastrichtian (Lingham-Soliar 1994a).

The anguilliform, slender body-shape and flipper-shaped extremities (Figs. 1, 5, 10 and 14) indicate that mosasaurs swam by lateral undulations of the posterior portion of the body and tail, while the flippers primarily functioned as steering devices (Russell 1967). However, based on the large pectoral girdle and comparatively short thorax in *Plioplatecarpus* Dollo 1882, Lingham-Soliar (1992a) proposed subaqueous flight as a mode of locomotion for mosasaurs of this genus. Living primarily as active carnivores, mosasaurs hunted in near-surface water with the help of a good sense of sight and excellent subaqueous hearing (Russell 1967). Medium-sized fish seems to have been the preponderant element in the diet, even though fossilised stomach-contents include prey, as different as cephalopods, sharks, turtles, birds and even other mosasaurs. The majority of the mosasaurs had a dentition where the individual tooth primarily had a cutting function (Massare 1987), although a few (i.e. *Globidens* Gilmore 1912, *Igdamanosaurus* Lingham-Soliar 1991 and *Carinodens* Thurmond 1969) had spherical teeth, probably as an adaptation to a diet of shelled molluscs and echinoids (Russell 1967; Massare 1987; Lingham-Soliar & Nolf 1989; Lingham-Soliar 1991).

Adult animals ranged in length from 2 to 17 metres. The 17 metres long *Hainosaurus bernardi* Dollo 1885 is one of the largest known marine reptiles of all time (Russell 1967; Lingham-Soliar 1992b).

Late Cretaceous strata in southern Sweden have yielded one of the most diverse mosasaur faunas known. Commercial exploitation of calcareous rocks in the Kristianstad Basin has revealed numerous teeth, vertebrae and other fragmentary bones, while quarrying in

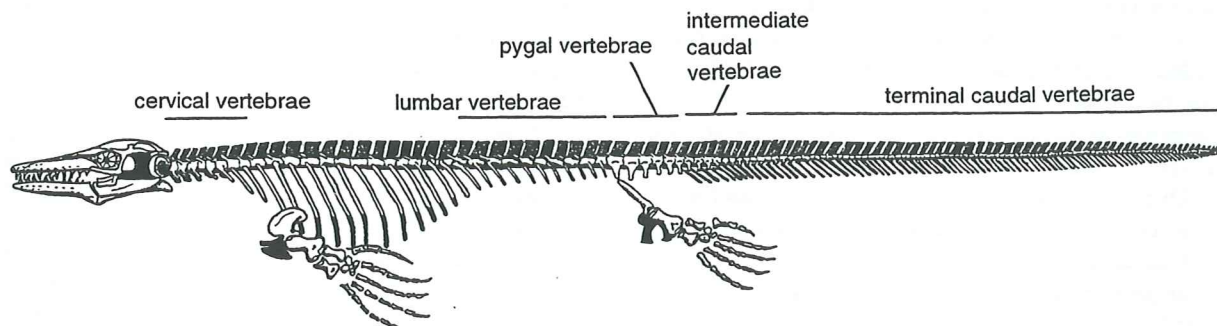


Fig. 1. Schematic drawing of a mosasaur skeleton to illustrate the anguilliform body-shape, the flipper-shaped extremities and the position of the vertebrae (based on Russell 1967, plate I, figs. 1-3, plate II, figs. 1-2).

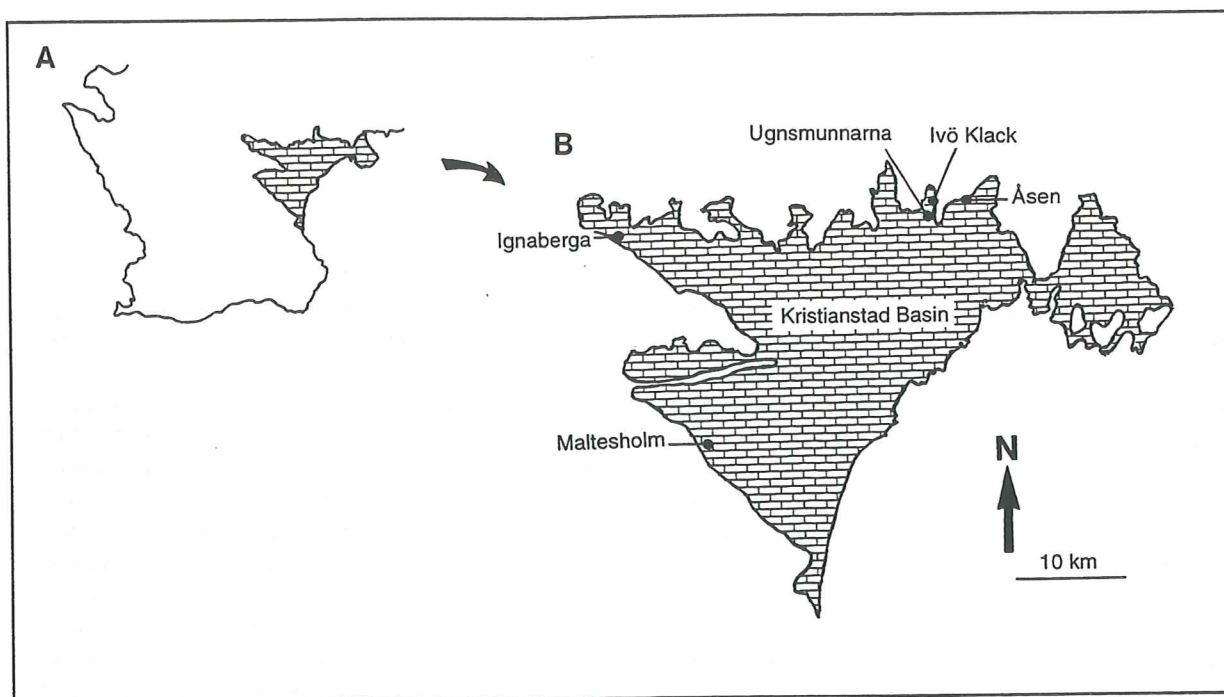


Fig. 2 A. Map of southern Sweden showing the location of the Kristianstad Basin in the north-eastern corner of Skåne. B. Close up map of the Kristianstad Basin with the localities yielding mosasaur remains marked (redrawn from Erlström & Gabrielson 1992).

the Båstad Basin and the Vomb Trough has provided some isolated teeth and an incomplete skull-roof. Previous investigations of Swedish marine reptiles have been conducted by, among others, Nilsson (1835, 1856), Schröder (1885), Troedsson (1954) and Persson (1954, 1959, 1963). Nilsson (1835) described and illustrated an incomplete skull-roof found at Köpinge Mölla, a specimen which in his opinion was of a plesiosaurian. Later, Nilsson (1856) described a tooth from Oppmanna, which he referred to *Mosasaurus hoffmanni*. In a more extensive work Schröder (1885) demonstrated that the skull-roof from Köpinge Mölla could not be of a plesiosaurian, but instead had mosasaurian affinity. Schröder was of the opinion that the fossil represented a new species, which he named *Mosasaurus scanicus* after the province of Skåne. In the same paper, Schröder also described and figured some mosasaur teeth from Oppmanna and Balsberg, which he assigned to *Mosasaurus* sp. I, *Mosasaurus* sp. II and his new nominal species *Leiodon lundgreni*. In the most comprehensive work on Swedish Cretaceous reptiles published so far, Persson (1959) identified two mosasaur taxa (*Platecarpus* cf. *somenensis* Thevenin 1896 and *Mosasaurus* cf. *hoffmanni*) from strata of latest early Campanian age and two taxa (*Leiodon* cf. *anceps* Owen 1851 and *Plioplatecarpus* sp.) from strata of early late Campanian age in southern Sweden.

During the last ten years, additional material has been collected in quarries and cliff-sections (i.e. Ugnsmunnarna) exposing sediments of the informal *Belemnellocamax mammillatus* zone. Christensen (1975) referred this biozone to latest early Campanian and the period has been defined by the contemporary occurrence of the belemnites *Belemnellocamax m. mammillatus*

(Nilsson 1826), *Belemnitella m. mucronata* (Link 1807) and *Goniteuthis quadrata scaniensis* Christensen 1975. This paper deals with the new material mentioned above, including remains of two genera previously not known from Sweden. New findings have also shown that some taxonomic conclusions made by Nilsson (1856), Schröder (1885) and Persson (1959, 1963) have to be reassessed.

Geological setting and localities

The Kristianstad Basin is situated in the north-eastern corner of the province of Skåne in southern Sweden, extending from the Hanö Bay in the east, to the town of Hässleholm in the west. The Linderödsåsen and Nävlingeåsen ridges confine the basin to the southwest, while the northern demarcation forms an erosional boundary with several outliers (Fig. 2 A, B).

A warm and moist climate in the Jurassic and/or Early Cretaceous, resulted in extensive weathering of the crystalline basement in the area. Widespread kaolinization created an uneven topography, where weathering-resistant parts of the basement rose above the surrounding lowland (Christensen 1975). Tectonic block movements in the Early Cretaceous lowered the basin by tilting against the adjacent Nävlingeåsen ridge (Bergström & Sundquist 1978, fig. 31). The area became thereby within reach of several transgressive pulses of the Late Cretaceous sea. Transgressions in the pre-Cenomanian, Cenomanian, early Santonian, mid-Campanian and early Maastrichtian resulted in the formation of an archipelago with low islands and peninsulas (Christensen 1975). As suggested by Christensen (1975), depths generally appear to have been less than 40 metres.

Poorly consolidated skeletal calcirudites, calcarenites and calcisiltites are the dominant marine lithologies, while glauconitic sands occur more sporadically (Christensen 1975). Several flint layers are interbedded in strata of early late Campanian and earliest Maastrichtian age (Siverson 1992a). Clastic terrigenous material in conglomerate layers and boulder beds indicates that nearby land functioned as important source areas, especially along the basin margins (Christensen 1975). The marine deposits may overlay kaolin clay, residual quartz-sand and fluviatile clays and sands, or rest directly upon the crystalline basement. The fossil fauna has a shallow marine composition characteristic of an inner shelf community (Erlström & Gabrielson 1992). Abundant macro-fossils include echinoids, bryozoans, molluscs, brachiopods and calcareous algae (Christensen 1975).

All quarries and outcrops dealt with in this paper are situated along the periphery of the basin (Fig. 2B). Quarrying and natural weathering have exposed sediments of latest early Campanian age (i.e. the informal *B. mammillatus* zone, see Christensen 1975) at several localities, of which the following have produced mosasaur remains:

Åsen. - The Åsen site is an abandoned clay pit, nowadays serving as a refuse dump. The locality is situated approximately three kilometres south of the town of Näsrum and approximately one and a half kilometre west of route 116 between the towns of Bromölla and Näsrum. Up to three metres of unconsolidated, marine greensand, with interbedded "oyster banks" and abundant belemnites, overlies fluviatile clays and sands of late Santonian/early Campanian age (Friis & Skarby 1981).

Numerous reptile remains have been collected in the easily wet-sieved greensand unit. Vertebrate remains occur scattered throughout the marine section, even though an increased frequency has been noted near the base of the greensand, in a bed composed of coarse quartz-sand, fragmented belemnite guards and oysters. *Map sheet*. - Näsrum 3E 5d, Ed. 1 Apr. 1975 (economic map, 1:10 000), coordinates 622519 141873 [Swedish National Grid 2.5 gon V system].

Ignaberga "new quarry". - In the area southeast of the hamlet of Ignaberga there are four quarries and the locality is one of a few being regularly worked at in the Kristianstad Basin. Ignaberga "new quarry" is situated in a NW-SE direction, along route 21 between the towns of Hässleholm and Kristianstad. The name "new quarry" refers to the time when only two quarries existed (i.e. Ignaberga "old quarry" and Ignaberga "new quarry", see Christensen 1975; Erlström & Gabrielson 1992; Siverson 1992a), but since two new quarries have been opened in 1995 and 1996, the name is nowadays somewhat misleading.

The quarry is situated along the faultline of the nearby Nävlingeåsen ridge and the beds dip 5-10° in a

NE direction (Erlström & Gabrielson 1992). The exposed limestone consists of calcirudites and calcarenites, interbedded by thin conglomerates (Erlström & Gabrielson 1992), with abundant fragments of molluscs, bryozoans, echinoderms and algae (Christensen 1975). *Map sheet*. - Kristianstad 3D SO, coordinates: UTM VC 288 195.

Maltesholm. - This abandoned quarry is situated approximately four kilometres south-southwest of the town of Östra Vram, alongside the northern margin of the Linderödsåsen ridge. The sediment consists of coarse to fine grained calcirudites and calcarenites, with interbedded conglomerates. The macro-fossil content includes rudists, calcareous algae, belemnites and, more scarcely, brachiopods (Sandström 1994).

Map sheet. - Tomelilla 2D NO/Simrishamn 2E NV, coordinates: UTM VB 955 382.

Ugnsmunnarna. - The locality is a cliff-section with natural caves, situated on the western shore of the Ivö island. The exposed strata have a thickness of two to five metres and a lateral extension of about 130 metres (Persson 1960). The section comprises biocalcarenites and five conglomeratic beds. Large fragments, or complete shells of oysters, together with belemnites and crystalline pebbles, are the main constituents of the conglomeratic horizons (Christensen 1975), while the biocalcarenite is more homogenous, containing smaller shell-fragments and crystalline gravel. The material dealt with herein has been collected from the uppermost conglomeratic bed.

Map sheet. - Karlshamn 3E SV, coordinates: UTM VC 619 199.

Material and methods

The material was obtained by surface-collecting isolated specimens and by sieving the deposits at Åsen and Ugnsmunnarna through a 2,5 mm sieve. The greater part of the fossils has been collected by Dr Mikael Siverson and Mr Peter Cederström, during numerous fieldtrips to the Kristianstad area. The localities dealt with here have also produced numerous remains from other vertebrates, mainly shark teeth (Siverson 1992a, 1992b, 1995), but also tooth-plates and fin-spines of chimaeroids, teeth and vertebrae of bony fishes, bones of turtles, teeth and bones of plesiosaurs [i.e. *Scanisaurus* cf. *nazarowi* (Bogolubov 1911) and *Elasmosaurus? gigas* (Schröder 1885), see Persson (1959)], teeth of a pliosaur [Polycotylidae?, see Persson (1959)] and even a few teeth of herbivorous dinosaurs.

The fossils were cleaned with buffered acetic acid (pH above 3,5, Jeppsson et al. 1985), which desolved adhering carbonates, and hardened with ethylene butyrate. The most representative specimens are illustrated herein. They were coated with ammonium chloride before being photographed. Additional mosasaurian

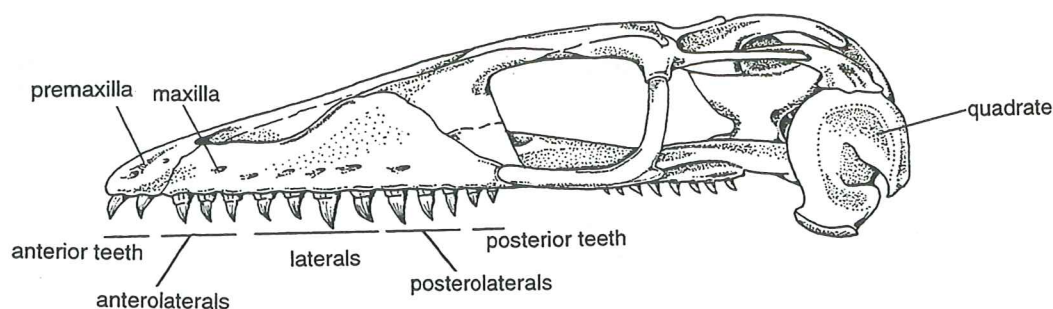


Fig. 3. Schematic drawing of a mosasaurian skull in lateral view, showing the marginal dentition (based on Holmes 1996, figs. 2, 8).

material was examined in the collections from Ivö Klack (Blacksudden) and Ignaberga, housed at the Department of Historical Geology and Palaeontology in Lund and at the Department of Palaeozoology, Swedish Museum of Natural History in Stockholm.

Systematic palaeontology

Systematic position. - Superorder SQUAMATA; Order SAURIA (=LACERTILIA); Family MOSASAURIDAE Gervais 1853

Subfamily MOSASAURINAE (Gervais 1853) Williston 1897

Diagnosis. - see Russell (1967)

Remarks. - Terminal caudal vertebrae found at the Åsen site are displaying fused chevrons of the haemal arches, a feature characteristic to genera within the subfamily Mosasaurinae (Russell 1967) and *Prognathodon* Dollo 1889 within the subfamily Plioplatecarpinae (Lingham-Soliar & Nolf 1989). Most teeth obtained from the same locality are small and bucco-lingually flattened. There are striking similarities between these tooth-crowns from the Åsen site and those in the marginal dentition of *Clidastes*, a mosasaurid mosasaur (Russell 1967).

Genus CLIDASTES? Cope 1868

Type species. - *Clidastes iguanavus* Cope 1868

Diagnosis. - see Russell (1967)

Remarks. - Teeth from the Kristianstad Basin are fairly small, mono or bicarinate and strongly bucco-lingually flattened. The tooth-crowns closely resemble those in the marginal dentition of *Clidastes* (see Russell 1967).

Partial caudal vertebrae from the Åsen site have fused haemal arches. Although abraded, the most complete chevron slopes ventero-medially at an angle of about 35-40° to the horizontal vertebral axis. As demonstrated by Russell (1967) and Milner (1987), the inclination of the haemal arch is uniformly 40° in caudal vertebrae of *Clidastes*.

Clidastes? sp.

Figs. 5, 6 A-O, 8 A-D, 9 A-E

Referred material. - Fiftythree teeth from Åsen; fourteen anterior teeth (JL001-JL014), eight antero-laterals (JL015-JL022), twentythree laterals (JL023-JL045), six latero-posteriors (JL046-JL051) and two posterior teeth (JL052, JL053). One lateral tooth (JL054) discovered at Ignaberga. Eleven partial vertebrae, probably from one individual, from Åsen, including one lumbar? vertebra (JL055) and ten terminal caudals (JL056-JL065).

Description. - Anterior teeth (Figs. 3, 4 and 6 A-C) exhibit a poorly developed posterior carina or completely lack cutting edges. The teeth are up to 10 mm high, displaying a slender crown, with the tip strongly curved medio-posteriorly. In cross-section, the crowns are nearly circular or has the shape of a swollen ellipse. The surface of the enamel is either smooth or has weak facets.

Antero-laterals (Figs. 3, 6 D-F) are up to 10 mm high, displaying a slender crown, with the apex moderately curved posteriorly. Anterior and posterior carinae are present, although the latter is less prominent. The crowns are triangular or droplet-shaped in cross-section. The surface of the enamel is smooth, without ridges or facets.

Laterals (Figs. 3, 6 G-I) are strongly bucco-lingually compressed and somewhat flattened in cross-section. The teeth are up to 15 mm high and 8 mm wide at the base. The buccal and lingual faces are almost subequal in convexity and are separated from each other by

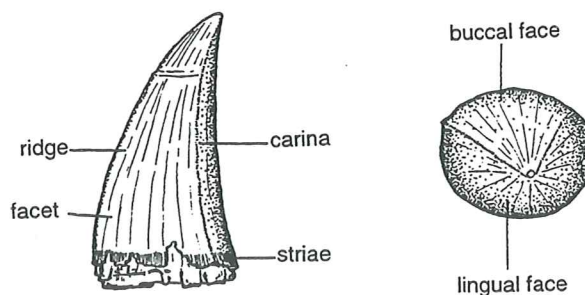


Fig. 4. Schematic drawing of a mosasaurian tooth-crown.

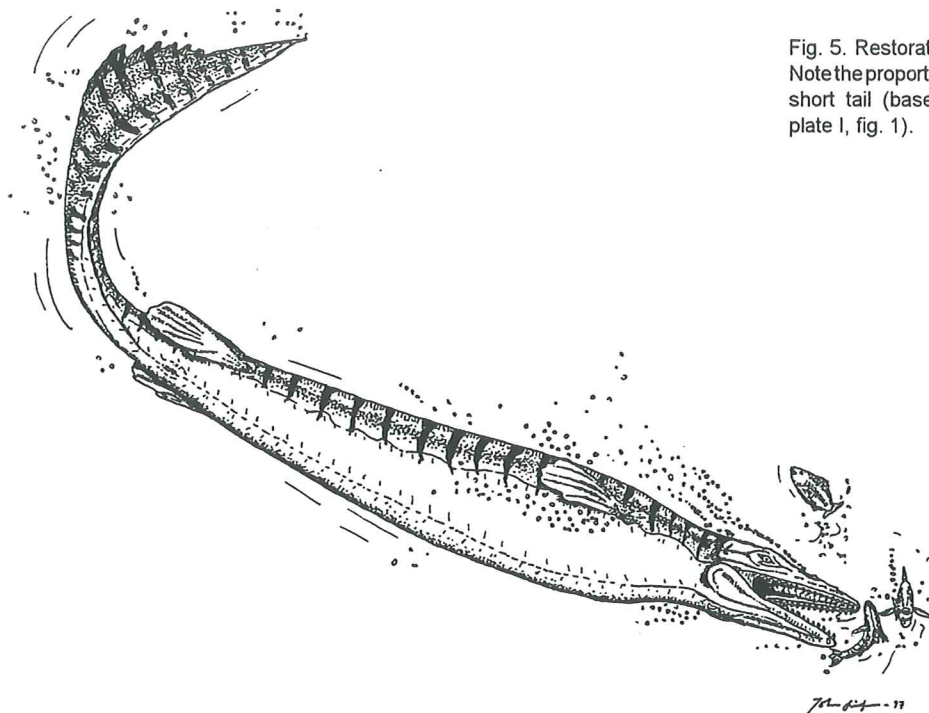


Fig. 5. Restoration of *Clidastes?* sp. Note the proportionately long body and short tail (based on Russell 1967, plate I, fig. 1).

anterior and posterior carinae. The enamel is either smooth or lined with vertical crests, approximately two on the buccal face and four on the lingual face, which are separated from each other by flattened facets.

Latero-posteriors (Figs. 3, 6 J-L) are stout and triangular in lateral aspect. The height of the crowns is up to 8 mm, while the maximum width is about the same, or slightly less, as the height. Due to a relative increase in bucco-lingual thickness, latero-posteriors are more oval in cross-section than laterals. The surface of the enamel is smooth, without ridges or facets.

In what I interpret to be posterior teeth (Figs. 3, 6 M-O), only a posterior carina is present. The tooth-crowns have strongly recurved tips and are covered by a slightly

faceted enamel. In cross-section, the buccal surface is flattened at the base, while the lingual face is U-shaped. The height of the tooth-crowns (measured from the anterior base of the enamel to the apex) is about 8 mm.

Among postcranial elements, a number of associated, incomplete terminal caudal vertebrae (JL056-JL065) are present in the Lund collection. A posterior fragment of what may be a lumbar vertebra (JL055) is also included in the material. The general state of preservation is poor and several specimens are badly abraded. Still, partial fused chevrons and basal parts of neural arches are visible. Based on the outline of the condyle and cotyle articulations (Figs. 7, 8 A, D and 9 A, B), I have divided the caudal vertebrae into four groups;

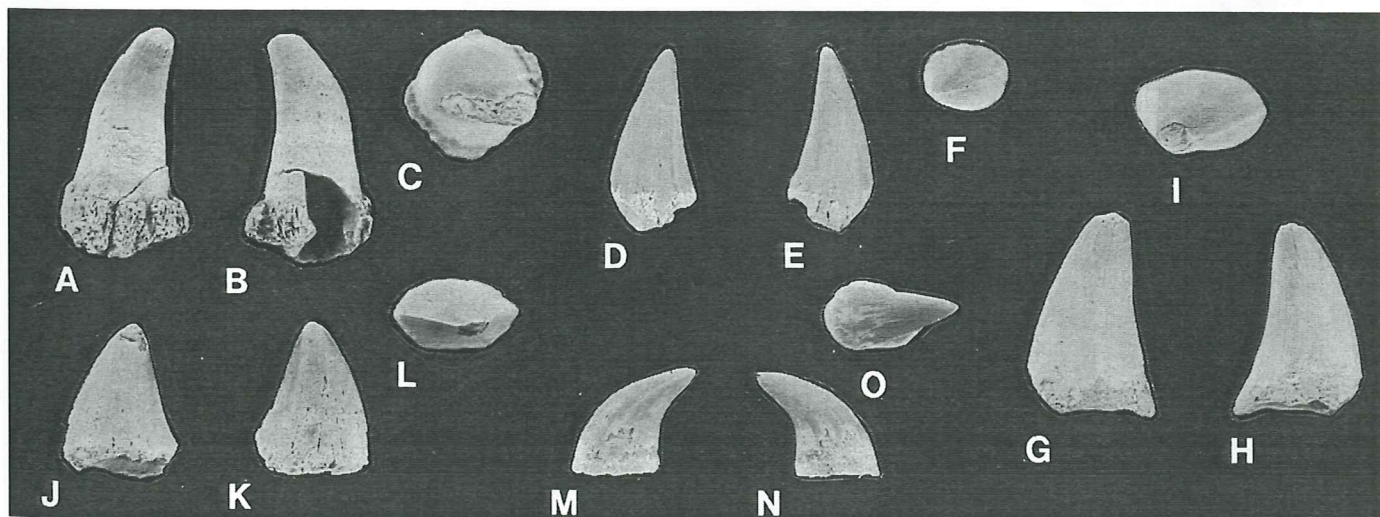
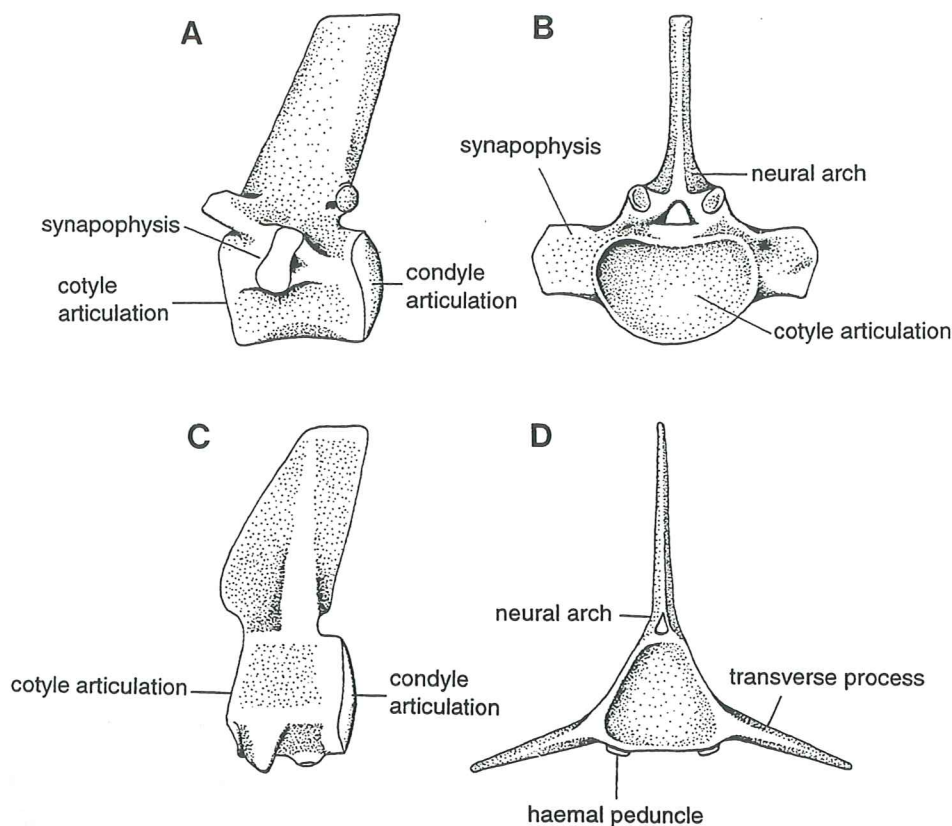


Fig. 6 A-O. Tooth-crowns of *Clidastes?* sp., x2.5. A-C. JL001: Anterior tooth-crown from Åsen; A. lingual view, B. buccal view and C. occlusal view. D-F. JL015: Antero-lateral from Åsen; D. buccal view, E. lingual view and F. occlusal view. G-I. JL023: Lateral tooth-crown from Åsen; G. buccal view, H. lingual view and I. occlusal view. J-L. JL046: Latero-posterior tooth-crown from Åsen; J. lingual view, K. buccal view and L. occlusal view. M-O. JL052: Posterior tooth-crown from Åsen; M. buccal view, N. lingual view and O. occlusal view.

Fig. 7 A, B. Schematic drawing of a dorsal vertebra; A. lateral view and B. anterior view. C, D. Schematic drawing of an intermediate caudal vertebra; C. lateral view and D. anterior view (based on Holmes 1996, figs. 10, 12).



vertebrae with sub-hexagonal central articulations, vertebrae with circular or nearly circular central articulations, vertebrae with vertically oval central articulations and vertebrae with horizontally oval central articulations. The radius of curvature of the central articulations is greater in the lumbar vertebra than in the caudal vertebrae (Figs. 8 A, D, 9 A, B).

A supposed lumbar vertebra (JL055) is badly eroded and consists of little more than a fragmentary condyle articulation. Although incomplete, the relatively high radius of curvature is clearly visible. The height of the remaining surface is 12 mm, while the maximum width is about 16 mm.

Only one vertebra with a sub-hexagonal articulation surface (JL056) is present in the material. The specimen is poorly preserved, with only the posterior half intact. The height of the condyle articulation is 25 mm, while the maximal width is about the same as the height. The length of the centrum is about 20 mm.

The second group comprises caudal vertebrae where the outline of the central articulations is circular or nearly circular (Fig. 8 A-D). Two vertebrae possessing this feature are included in the group (JL057-JL058). The height of the centra equals the width and is about 17 and 22 mm respectively, while the length, measured from the most lateral portion of the anterior surface to the most lateral portion of the posterior surface, is about 17 and 18 mm respectively.

Two incomplete vertebrae (JL059-JL060) and fragments of yet another two (JL061-JL062) are displaying

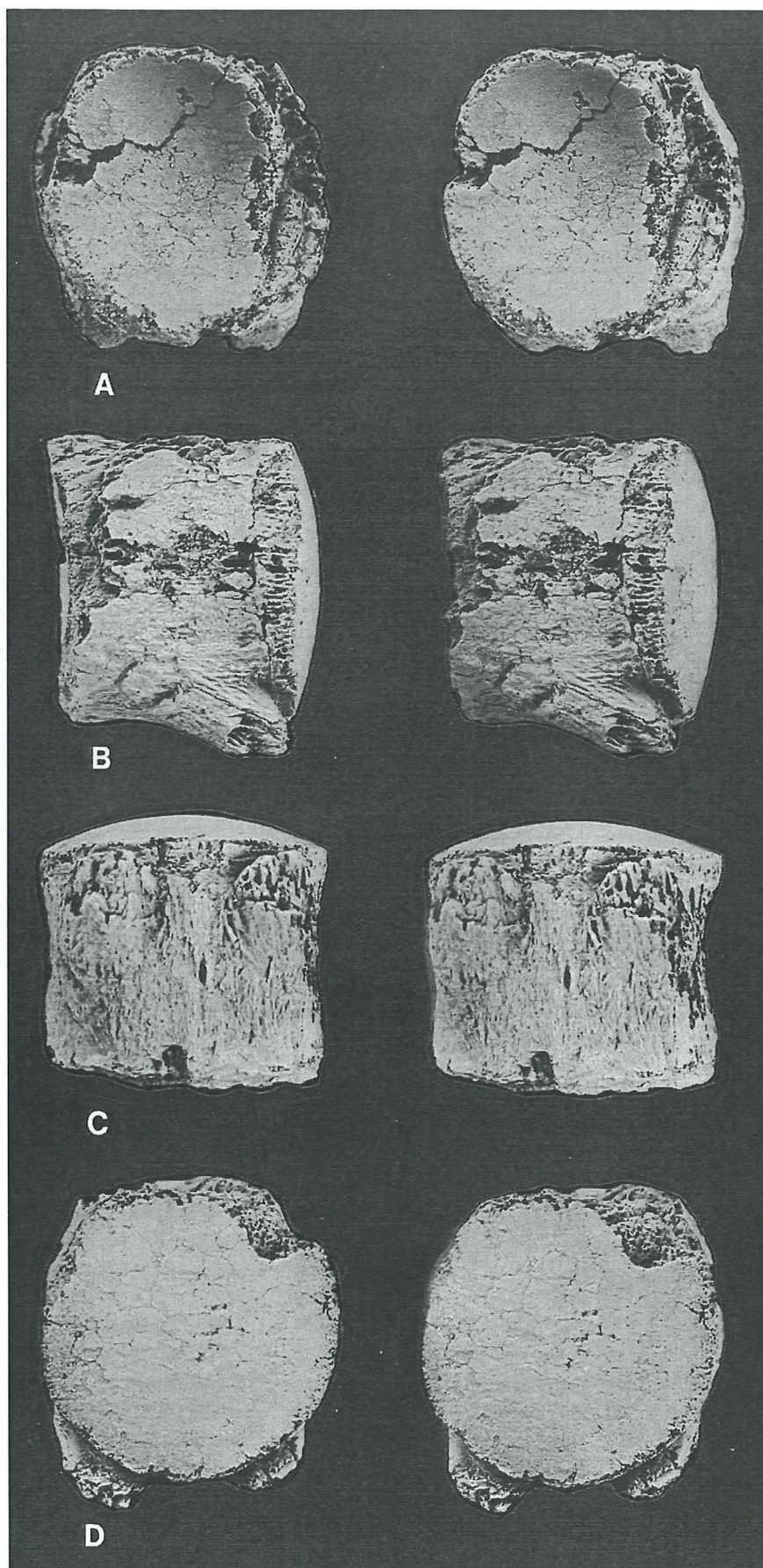
vertically oval central articulations (Fig. 9 A-E). These specimens form the third group. The height of the condyle articulations (measured on the two most complete vertebrae) is 16 and 17 mm respectively, while the maximum width is slightly less at about 13 and 14 mm respectively. The length of the centra is 13 and 12 mm respectively. Fused chevrons of the haemal arch slope ventero-medially at an angle of about 35 to 40° to the horizontal vertebral axis.

The fourth group consists of caudal vertebrae where the outline of the condyle and cotyle articulations is horizontally oval. Only one vertebra displaying this feature has been recorded (JL063). The height of the centrum is 12 mm, while the maximum width and length is about 14 mm and 10 mm respectively.

Due to a very poor state of preservation, two caudal vertebrae (JL064 and JL065) could not be referred to any of the above mentioned groups.

Comparisons. - At least six nominal species of *Clidastes* have been identified from the late Coniacian to earliest Campanian Smoky Hill Member of the Niobrara Formation in Kansas, USA and from the mid-Campanian Mooreville Chalk of the Selma Formation in Alabama, USA. Three of these (i.e. *C. propython* Cope 1869, *C. sternbergi* Wiman 1920 and *C. liodontus* Merriam 1894) are based on sufficient material (Russell 1967, 1970; Wright 1988). Based on the figures in Russell (1967, figs. 71, 73, 74) and Wright (1988, fig. 1A), the tooth-crowns described in this work closely

Fig. 8 A-D. JL057: Terminal caudal vertebra of *Clidastes?* sp. from Åsen, x2,5; A. anterior view, stereo pair, B. lateral view, stereo pair, C. ventral view, stereo pair and D. posterior view, stereo pair.



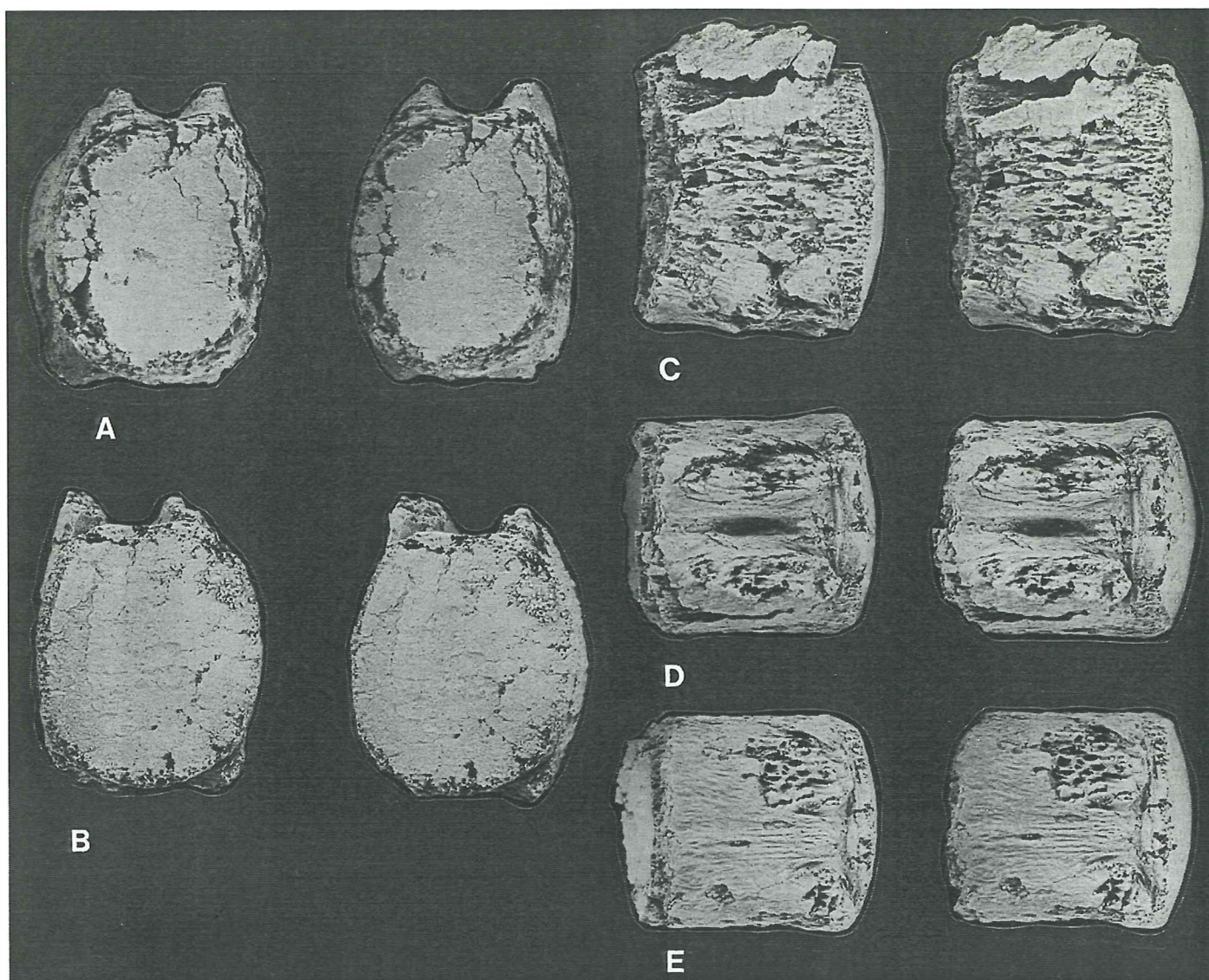


Fig. 9 A-E. JL059: Terminal caudal vertebra of *Clidastes?* sp. from Åsen, x2,5; A. anterior view, stereo pair, B. posterior view, stereo pair, C. lateral view, stereo pair, D. dorsal view, stereo pair and E. ventral view, stereo pair.

resemble those in the dentitions of *C. liodontus* and *C. sternbergi* ("*Halisaurus*" *sternbergi*, see Russell 1970, p. 371), while the marginal teeth in *C. propython* are somewhat more slender.

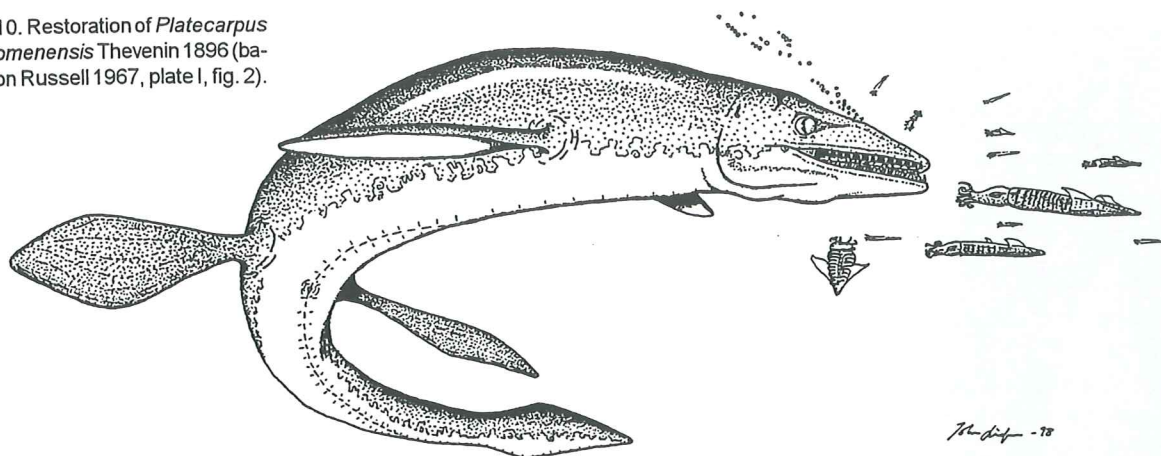
Based on the size of JL057 (Fig. 8 A-D) and a skeletal reconstruction of *Clidastes* (Russell 1967, plate I, fig. 1), I have estimated the maximum total length of *Clidastes?* sp. to approximately 3,8 metres. Russell (1967) estimated the total length of *C. liodontus* to approximately 3,5 metres and the total length of *C. sternbergi* to approximately 2,7 metres. However, *C. liodontus* is recorded from strata assigned to the late Santonian? (Russell 1967) and the earliest Campanian (Wright 1988) and may have been replaced by *C. propython* by the time of latest early Campanian (Russell 1967).

Recently, seven cervical and dorsal vertebrae from a single individual have been found at the Åsen site by the author. Contrary to cervical vertebrae assigned to *C. liodontus* (see Russell 1967), the vertebrae from Åsen

exhibit "kidney"-shaped central articular surfaces, where the width/height ratio is approximately 1,5:1. Cervical vertebrae referred to *Clidastes?* (*Halisaurus?*) *sternbergi* have horizontally oval to "kidney"-shaped central articulations and the width of the surfaces is about twice the height (Russell 1967, 1970). This may indicate that the Swedish mosasaur represents a new, previously undescribed species of *Clidastes* or *Halisaurus*. However, more well-preserved material is required, as well as detailed comparisons with the type specimens of *C. liodontus* and *Clidastes?* (*Halisaurus?*) *sternbergi*.

Remarks. - The outline of the central articulations is sub-hexagonal in mosasaur vertebrae behind the pygal series (Figs. 1, 7 C, D) and tend to become vertically oval posteriorly to the dilated portion of the tail (Russell 1967). As shown above, the largest caudal vertebra recorded has a sub-hexagonal central articulation surface. The specimen probably originates from the base of the tail, near the pygal series. The smaller vertebrae,

Fig. 10. Restoration of *Platecarpus* cf. *somenensis* Thevenin 1896 (based on Russell 1967, plate I, fig. 2).



displaying vertically oval central articulations, probably originate from a position behind the dilated portion of the tail.

The caudal series from Åsen is obviously very incomplete. Russell (1967) estimated the total number of caudal vertebrae in *Clidastes* to 76-79, including 4-7 pygals, 26 intermediate caudals and 46 terminal caudals.

Subfamily PLIOPLATECARPINAЕ (Dollo 1884) Wiliston 1897

Diagnosis. - see Russell (1967)

Remarks. - Fairly large isolated tooth-crowns from the Kristianstad Basin are slender, strongly faceted and delicately striated. Most genera within the Plioplatecarpinae exhibit slender and faceted teeth (Russell 1967; Lingham-Soliar 1994a, 1994b), whereas most genera within the Mosasaurinae or Tylosaurinae have teeth lacking these features.

Genus PLATECARPUS Cope 1869

Type species. - *Platecarpus tympaniticus* Cope 1869

Diagnosis. - see Russell (1967)

Remarks. - Holmes (1996) assigned *Platecarpus somenensis* to *Plioplatecarpus*. However, judging by the figures and the descriptions given by Persson (1959), Russell (1967) and Lingham-Soliar (1994b), teeth assigned to *Plioplatecarpus* differ from teeth referred to *P. somenensis*. Tooth-crowns of *Plioplatecarpus* are generally slender and abruptly curved posteriorly, whereas teeth of *P. somenensis* are somewhat more robust, faceted and only slightly curved medio-posteriorly.

Platecarpus cf. *somenensis* Thevenin 1896

Figs. 10, 11 A-L, 13 A-H

Synonymy. - 1885 *Mosasaurus* sp. II Schröder, p. 327, pl. 17, fig 2. 1959 *Platecarpus* cf. *somenensis* Persson,

pp. 463-464, pl. 15 figs. 3a-3c. 1963 *Platecarpus somenensis* Persson, p. 6.

Referred material. - Åsen, five teeth (JL066-JL070); Ignaberga, one tooth (JL071); Maltesholm, one tooth (JL072); Ugnsmunnsarna, six teeth (JL073-JL078) and fragments of one? jaw-bone (JL079-JL082).

Additional occurrence. - In the mid-Campanian lower portion of the Pierre Formation in the USA (Russell 1967); in "Craie Phosphate de la Picardie" (the Phosphatic Chalk at Picardie) in France (Russell 1967).

Diagnosis. - see Russell (1967)

Description. - Marginal teeth: Of the thirteen marginal teeth at hand, five are reasonably well preserved and described separately below.

JL073, Fig. 11 A-C: A fairly large antero-lateral? tooth displaying a tall and slender crown (about 33 mm high and 17 mm wide), with the apex curved medio-posteriorly. The tooth is nearly circular in cross-section at the base and becomes moderately bucco-lingually flattened as the apex of the crown is approached. Anterior and posterior carinae are present. The buccal and lingual surfaces are almost subequal in convexity and are divided by crests into flattened or gently concave facets. There are nine facets on the buccal face and seven facets on the lingual face. Delicate striations reach a short distance up the base on the lingual surface.

JL072, Fig. 11 D-F: This lateral tooth is 30 mm high and 16 mm wide. The crown is slightly oval in cross-section at the base, while the upper two-thirds are strongly bucco-lingually flattened. The buccal and lingual surfaces are almost equally convex and are separated from each other by prominent anterior and posterior carinae, both of which are showing minute serrations. The buccal surface is divided by crests into nine facets, while the lingual face is lined with small, vertical ridges. Delicate striations reach a short distance up the base, particularly on the lingual surface.

JL074, Fig. 11 G-I: A fairly robust lateral tooth, with a tall and flattened crown. The apex is slightly curved

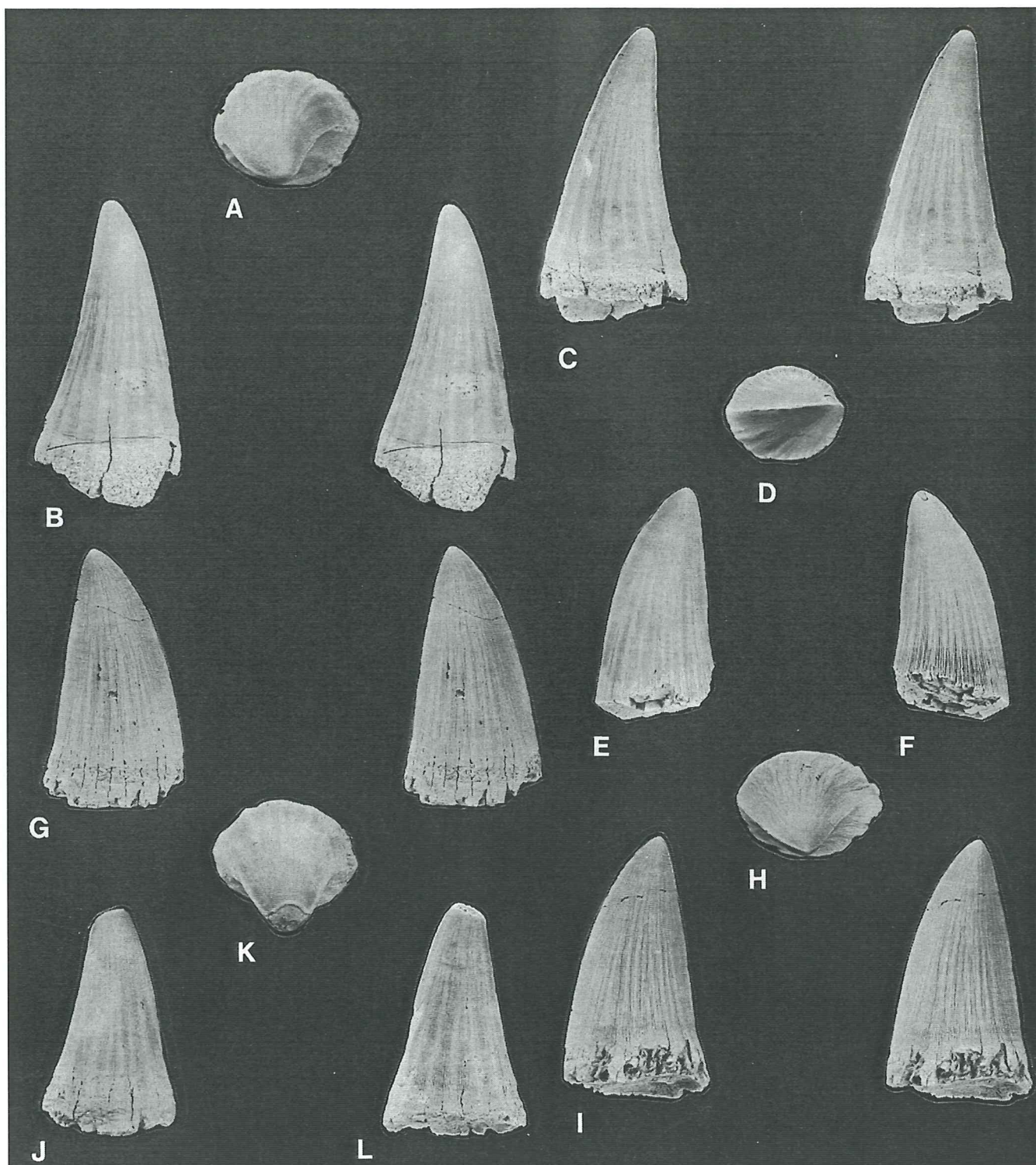


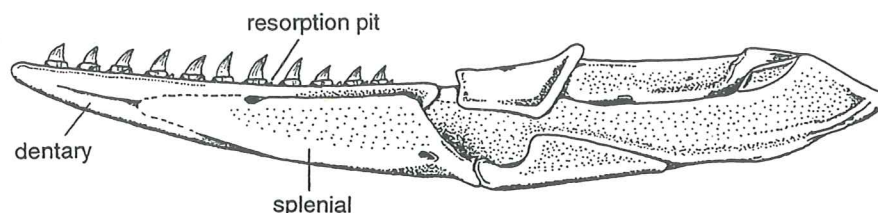
Fig. 11 A-L. Tooth-crowns of *Platecarpus* cf. *somenensis* Thevenin 1896, x1,3. A-C. JL073: Antero-lateral from Ugnsmunna; A. occlusal view, B. buccal view, stereo pair and C. lingual view, stereo pair. D-F. JL072: Lateral tooth-crown from Maltesholm; D. occlusal view, E. buccal view and F. lingual view. G-I. JL074: Lateral tooth-crown from Ugnsmunna; G. buccal view, stereo pair, H. occlusal view and I. lingual view, stereo pair. J-L. JL075: Lateral? tooth-crown from Ugnsmunna; J. buccal view, K. occlusal view and L. lingual view.

medio-posteriorly. The height of the crown is 31 mm, while the maximum width is about 18 mm. In cross-section, the tooth is oval at the base, but becomes strongly bucco-lingually flattened in its upper two-thirds. Pronounced anterior and posterior carinae divide the crown into a buccal and a lingual surface of almost equal size. The buccal face of the tooth is

strongly faceted (nine facets), while the lingual face has numerous vertical crests. Delicate striations reach approximately seven millimetres up the base on the lingual surface.

JL075, Fig. 11 J-L: This abraded lateral? tooth lacks the tip of the crown. The crown is moderately curved medio-posteriorly. The height of the tooth is 28 mm,

Fig. 12. Schematic drawing of a mosasaurian lower jaw in medial view.



while the maximum width is about 17 mm. The base is oval in cross-section, while the upper half of the tooth is somewhat flattened. The crown displays eight facets on the buccal face and eight facets on the lingual face. Delicate striations reach a short distance up the base on the lingual surface.

JL066: A somewhat stout latero-posterior? tooth, displaying a moderately stout crown. The height of the specimen is 23 mm, while the maximum width at the base is about 14 mm. Anterior and posterior carinae divide the crown into a buccal and a lingual surface of almost equal size. Eight facets are present on the buccal face, while the lingual face is diffusely faceted. Delicate striae are present at the base of the lingual face.

Four separate fragments of a maxilla (Fig. 3) or a dentary (Fig. 12) from a single individual, collected at the Ugnsmunnarna site, are also included in the material (JL079-JL082). However, as the specimens are badly abraded, it is impossible to determine their original position in the jaw. Each fragment is described separately below.

JL079, Figs. 12, 13 A-B: The abraded fossil is broken both anteriorly and posteriorly through an alveoli. No teeth are present, only five sockets. In dorsal aspect, the posteriorly located sockets exhibit droplet-shaped elevations. Inside each elevation is a shallow cavity, with a bucco-lingually flattened pit in its centre. The maximum length of the cavities is 15-16 mm, while the maximum width is about 8-11 mm. One anteriorly situated socket shows a bony plate, with a cone-shaped, bucco-lingually compressed pit in its centre. The tooth-base is completely surrounded by an oval groove. The length of the bony plate is about 20 mm and the maximum width is 15 mm. A circular resorption pit is located medio-posteriorly to each socket. These pits extend anteriorly into the central cavities of the next tooth-base. The surface of the bone is only partially preserved on the medial face. The overall length of the specimen is 124 mm, while the maximum width is about 24 mm.

JL080, Fig. 13 C-D: This poorly preserved fossil is displaying a partial tooth-crown. The tooth completely

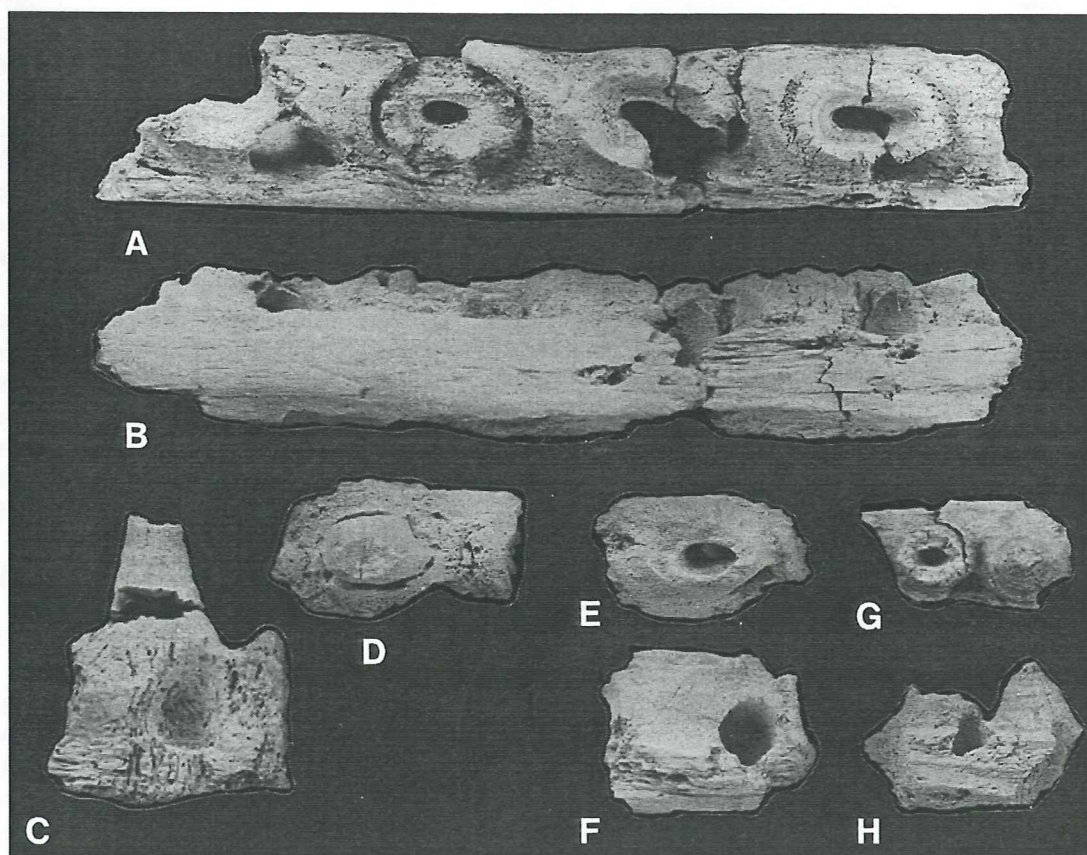


Fig. 13 A-H. One? jaw-bone of *Platecarpus* cf. *somenensis* Thevenin 1896, natural size. A, B. JL079; A. dorsal? view and B. medial view. C, D. JL080; C. medial view and D. dorsal? view. E, F. JL081; E. dorsal? view and F. medial view. G, H. JL082; G. dorsal? view and H. medial view.

lacks enamel and resembles a bluntly terminated and somewhat bucco-lingually flattened cone. A posterior carina is present, giving the tooth a droplet-shape in basal cross-section. The height of the incomplete crown is about 16 mm, while maximum width is about 14 mm. A resorption pit is located medio-posteriorly to the tooth. The pit extends deeply into the bony base of the tooth in front. The jaw-fragment is terminated posteriorly by a vertically oval articulation surface. The total length of the specimen is 34 mm, while the maximum height is about 36 mm.

JL081, Fig. 13 E-F: This small and narrow fragment shows one empty alveoli. In lateral aspect, the socket is moderately elevated above the surrounding bone. Dorsally, the oval shape of the central cavity is visible. A resorption pit is located medio-posteriorly to the socket, but no replacement tooth is present. The alveoli extends deeply into the bony base of the tooth in front. The overall length of the specimen is 28 mm, while the maximum height is about 23 mm.

JL082, Fig. 13 G-H: The fragment is 30 mm long and includes fragmentary remains of two tooth-crowns. Like the specimens described above, the fossil is abraded and has resorption pits medio-posteriorly to each tooth-base.

Remarks. - According to Persson (1959, p. 464), the tooth-crowns from the Kristianstad Basin resemble marginal teeth in the holotype of *P. somenensis*, except that the facets show "... a somewhat wider range of variation with regard to their number". This condition, however, can be expected, as the description of *P. somenensis* is based on a single individual, whereas the teeth from southern Sweden belong to several individuals (Persson 1959).

The teeth in *Platecarpus* are poorly differentiated along the jaw margins. The only variation within the marginal dentition seems to be that anterior and posterior teeth are somewhat smaller than lateral teeth and that the teeth in the maxillae are slightly larger than the teeth in the dentaries (see Russell 1967). The former is also true for the teeth described in this work. A slender crown, with weakly developed cutting edges, is concluded to be from an antero-lateral tooth, while a strongly flattened tooth, with prominent anterior and posterior carinae indicates a lateral position in the jaw. A fairly small and stout tooth-crown indicates in the same way a latero-posterior position.

Subfamily TYLOSAURINAE (Williston 1895) Williston 1897

Diagnosis. - see Russell (1967)

Remarks. - Large intermediate caudal vertebrae from Ignaberga (Figs. 1, 18 A-E, 19 A-C and 20) exhibit peduncles for articulation with chevrons of the haemal arches, a feature characteristic to most genera within the subfamilies Tylosaurinae and Plioplatecarpinae. Genera within the subfamily Mosasaurinae, on the

other hand, are characterised by having fused haemal arches.

The size of the vertebrae and the tooth-crowns described below indicates very large mosasaurs, probably with total lengths of nine metres or more. While both *Tylosaurus* Marsh 1872 and *Hainosaurus* Dollo 1885 (the genera included in the subfamily Tylosaurinae) are known to have been large (Russell 1967; Lingham-Soliar 1992b), only species of *Prognathodon* within the subfamily Plioplatecarpinae exceeded nine metres in length (see Russell 1967; Lingham-Soliar & Nolf 1989). However, in a study of *Prognathodon* from the Ciply Phosphatic Chalk in Belgium, Lingham-Soliar & Nolf (1989) observed that fused haemal arches are present uniformly in all known species of the genus.

The scarce material from Skåne also exhibits several other features that indicate an affinity to the subfamily Tylosaurinae. One of these features is the angle at which the transverse processes project from the caudal centra (Figs. 7 C, D, 18 A-E). Only one fragmentary process is preserved in the material. The process slopes at about 20° to the horizontal vertebral axis. According to Russell (1967), transverse processes slope at about 20° in caudal vertebrae of *Tylosaurus*, a tylosaurid mosasaur, whereas the processes slope at about 30° in caudal vertebrae of *Platecarpus*, a plioplatecarpid mosasaur. The tylosaurid teeth from the Kristianstad Basin are large, stout, faceted and slightly curved medio-posteriorly. They closely resemble those of the genera within the subfamily Tylosaurinae (see Russell 1967).

Genus HAINOSAURUS? Dollo 1885

Type species. - *Hainosaurus bernardi* Dollo 1885

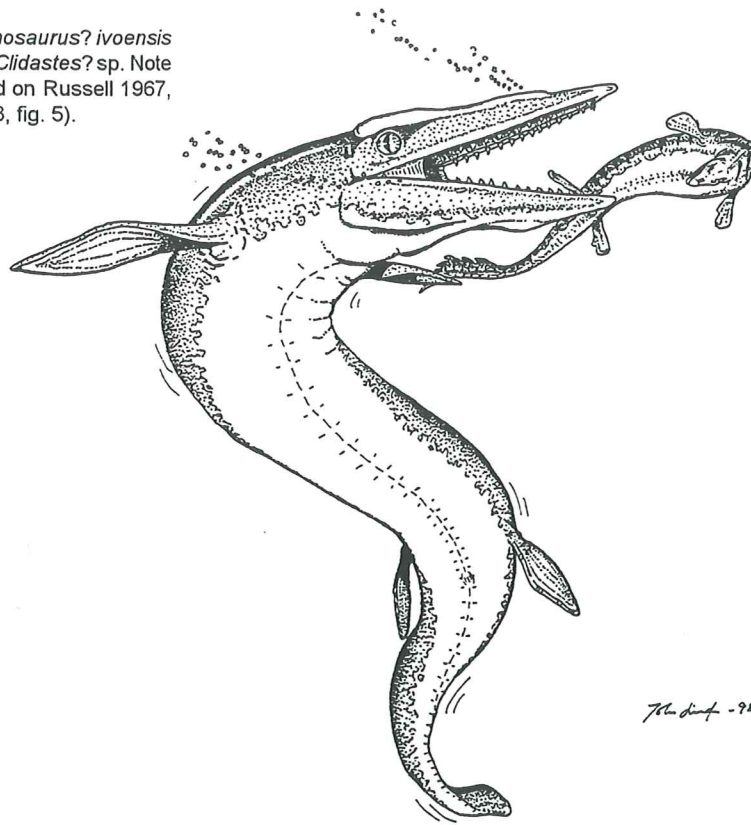
Diagnosis. - see Lingham-Soliar (1992)

Remarks. - Several features, including the length of the external nares relative to the length of the skull, the buttressing of the premaxillary suture, the length of the femur relative to the length of the humerus and the number of presacral vertebrae, are commonly used to distinguish *Hainosaurus* from *Tylosaurus* (Russell 1967; Nicholls 1988; Lingham-Soliar 1992b). However, as the material from Sweden only comprises teeth and incomplete vertebrae, none of the distinguishing features mentioned above can be used to establish the generic identity of the Kristianstad Basin tylosaurid. Size cannot normally be considered to be a good character, but it may, in this case, be of importance and will therefore be briefly discussed below.

Based on the size of the most complete postpygal vertebra from Ignaberga (JL088, Fig. 18 A-E) and a skeletal reconstruction of a *Hainosaurus* (see Nicholls 1988, fig. 5), I have estimated the length of the animal, to which the specimen belonged, to between 9 and 9.5 metres.

Remains of *Tylosaurus* and *Hainosaurus* in strata of early Campanian age are previously known from North America. A moderately large *Tylosaurus* (i.e. *T. prori-*

Fig. 14. Restoration of *Hainosaurus? ivoensis* (Russell 1967) attacking a *Clidastes? sp.* Note the size differences (based on Russell 1967, plate I, fig. 1; Nicholls 1988, fig. 5).



ger Cope 1869) has been obtained from the lower portion of the Pierre Shale in South Dakota, USA (see Russell 1967, 1970). Nicholls (1988) identified a giant *Hainosaurus* (i.e. *H. pembinensis* Nicholls 1988), found in the the Pembina Member of the Pierre Shale in Manitoba, Canada. According to Russell (1967), Lingham-Soliar (1992b) and figures in Nicholls (1988, figs. 3, 5) the size of a *Tylosaurus* is approximately two-thirds of the size of a *Hainosaurus*. While the largest complete *T. proriger* measured about 8,8 metres (Russell 1967), Nicholls (1988) estimated the total length of adult *H. pembinensis* to between 12 and 15 metres.

Based on size alone, it is likely that the mosasaur under discussion is a *Hainosaurus*, even though a relationship with *Tylosaurus*, or some undescribed tylosaurid can not be ruled out. More well-preserved material is required, as well as comparisons with material from Canada and the USA, in order to determine the relation of this Swedish mosasaur to *Tylosaurus* and *Hainosaurus*.

Hainosaurus? ivoensis (Russell 1967)

Figs. 14, 15 A-F, 16 A-C, 17 A-B, 18 A-E, 19 A-C, 20

Synonymy. - 1856 *Mosasaurus hoffmanni* Nilsson, p. 47. 1885 *Leiodon lundgreni* Schröder, p. 329-333, pl. 17, fig 3. 1959 *Mosasaurus cf. hoffmanni* Persson, pp. 461-462, pl. 15, figs 1-2. 1959 *Mosasaurus sp.* Persson, p. 463. 1963 *Mosasaurus hoffmanni ivoensis* Persson, pp. 5-6. 1967 *Mosasaurus ivoensis* Russell, p. 135-136, fig 79. 1991 *Mosasaurus lemonnieri* Lingham-Soliar, p. 665.

Referred material. - Four tooth-crowns; one from Åsen (JL083), one from Ignaberga (JL084) and two from Ugnsmunarna (JL085, JL086). Three vertebrae from Ignaberga, probably from one individual; one lumbar (JL087) and two postpygals (JL088, JL089).

Additional occurrence. - Possibly in the early Campanian Pembina Member of the Pierre Formation in Manitoba, Canada (Nicholls 1988) and the earliest Campanian Niobrara Chalk in Kansas, USA (Russell 1967).

Diagnosis. - Marginal teeth are very robust, stout, faceted and moderately recurved. Anterior and posterior carinae, both with minute serrations, divide the crown into a flattened buccal surface and a deeply U-shaped lingual surface. Delicate striae are present on the basal portion of the crown, particularly on the lingual surface.

The transverse processes slope at about 20° to the horizontal vertebral axis on intermediate caudals. Chevrons are not fused to caudal centra.

Description. - Marginal teeth are very robust and stout, with the apex moderately curved medio-posteriorly (Fig. 15 A-F). The crowns are triangular in lateral aspect and are up to 60 mm high and 35 mm wide. Anterior and posterior carinae are present, although the anterior carina is stronger. Both cutting edges display minute serrations. In cross-section, the buccal face is flattened or gently convex and the lingual surface is deeply U-shaped. The enamel exhibits vertical ridges or crests, which are separated from each other by flattened

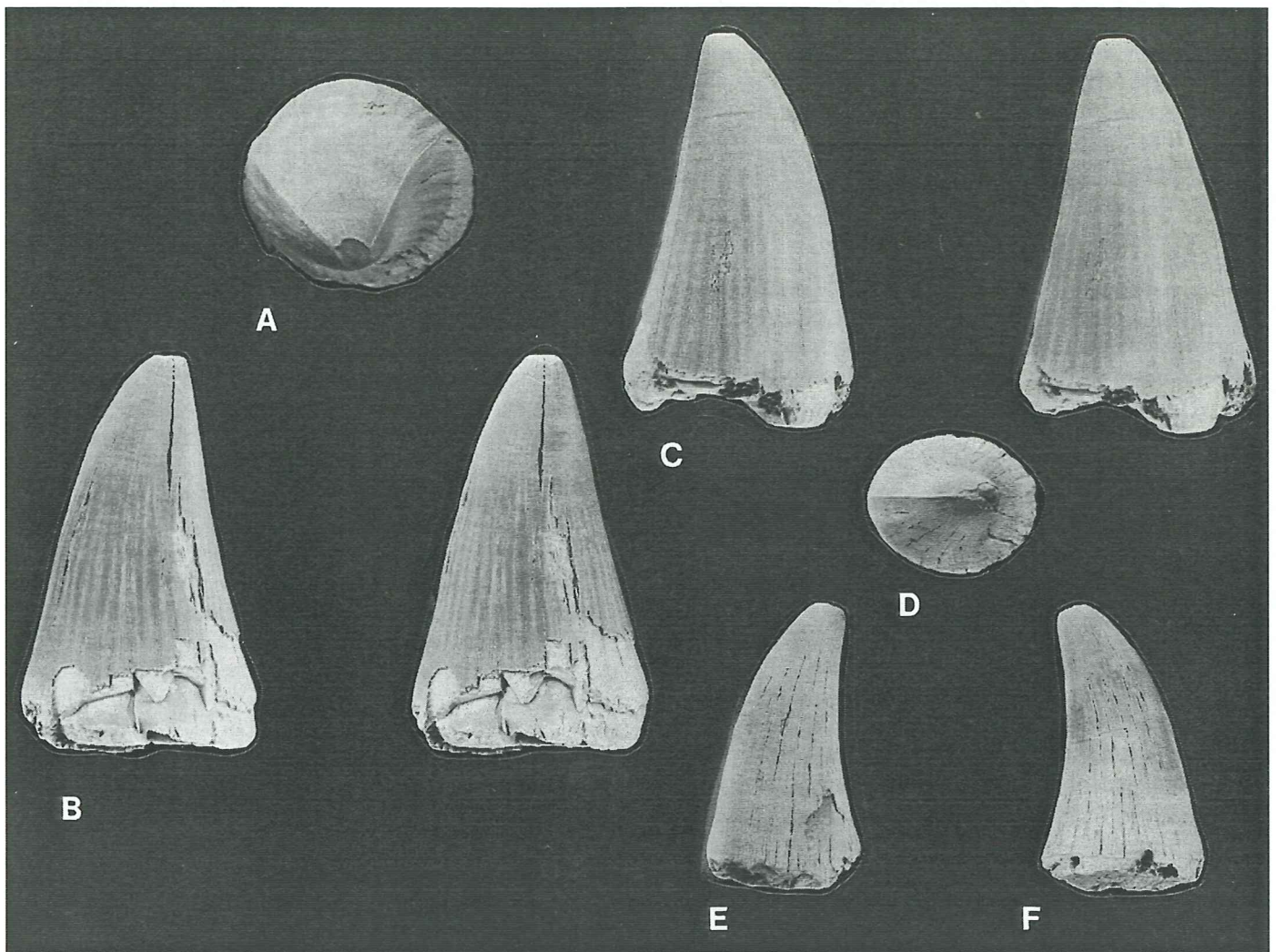


Fig. 15 A-F. Tooth-crowns of *Hainosaurus? ivoensis* (Russell 1967), natural size. A-C. JL084: Antero-lateral? from Ignaberga; A. occlusal view, B. lingual view, stereo pair and C. buccal view, stereo pair. D-F. JL083: Lateral tooth-crown from Åsen; D. occlusal view, E. buccal view and F. lingual view.

or gently concave facets. The buccal surface has 7 to 9 facets, whereas the lingual surface has 15 to 16 facets. Delicate striations reach a short distance up the base, particularly on the lingual surface.

One incomplete dorsal vertebra (JL087) has been recorded (Figs. 1, 7 A, B, 16 A-C and 17 A, B). Although abraded, the outline of the condyle and cotyle articulations, a fragment of the left synapophysis and basal fragments of the neural arch are clearly visible. The maximum length of the specimen is 102 mm. The height of the cotyle articulation is 60 mm and maximum width is about 88 mm. The outline of the inter-articular surfaces is horizontally oval and the surfaces show a high radius of curvature. A basal, posterior part of the left synapophysis is present. The outgrowth is somewhat dorso-ventrally flattened and occupies the dorsal portion at the centre of the lateral surface.

One incomplete, intermediate caudal vertebra (JL088) is present in the material (Figs. 1, 7 C, D and 18 A-E). The length of the partial centrum is 74 mm, while the height is 75 mm and maximum width about the same as the height (the height and the width are

measured on the posterior articulation surface). The outline of the central articulations is sub-triangular and the surfaces show a low radius of curvature. An anterior part of a right transverse process occupies the ventero-anterior portion of the lateral surface and slopes at about 20° to the horizontal vertebral axis. One incomplete peduncle for articulation with a chevron of the haemal arch is present. It occupies the posterior corner of the ventral surface. A broad, shallow and about 30 mm long groove (possibly a bite mark, see under "Palaeoecology" below) extends diagonally on the ventral portion of the posterior central articulation surface (Fig. 18 B).

A partial second postpygal vertebra (JL089) consists of a fragmentary condyle and the posterior parts of the left peduncle for articulation with the haemal arch (Fig. 19 A-C). The flattened surface of what is interpreted to be the central pit (see Russell 1967, p. 82) is visible in ventral view (Fig. 20).

Comparisons. - Teeth similar to those from the Kristianstad Basin have been described from the early Campanian Pembina member of the Pierre Formation in

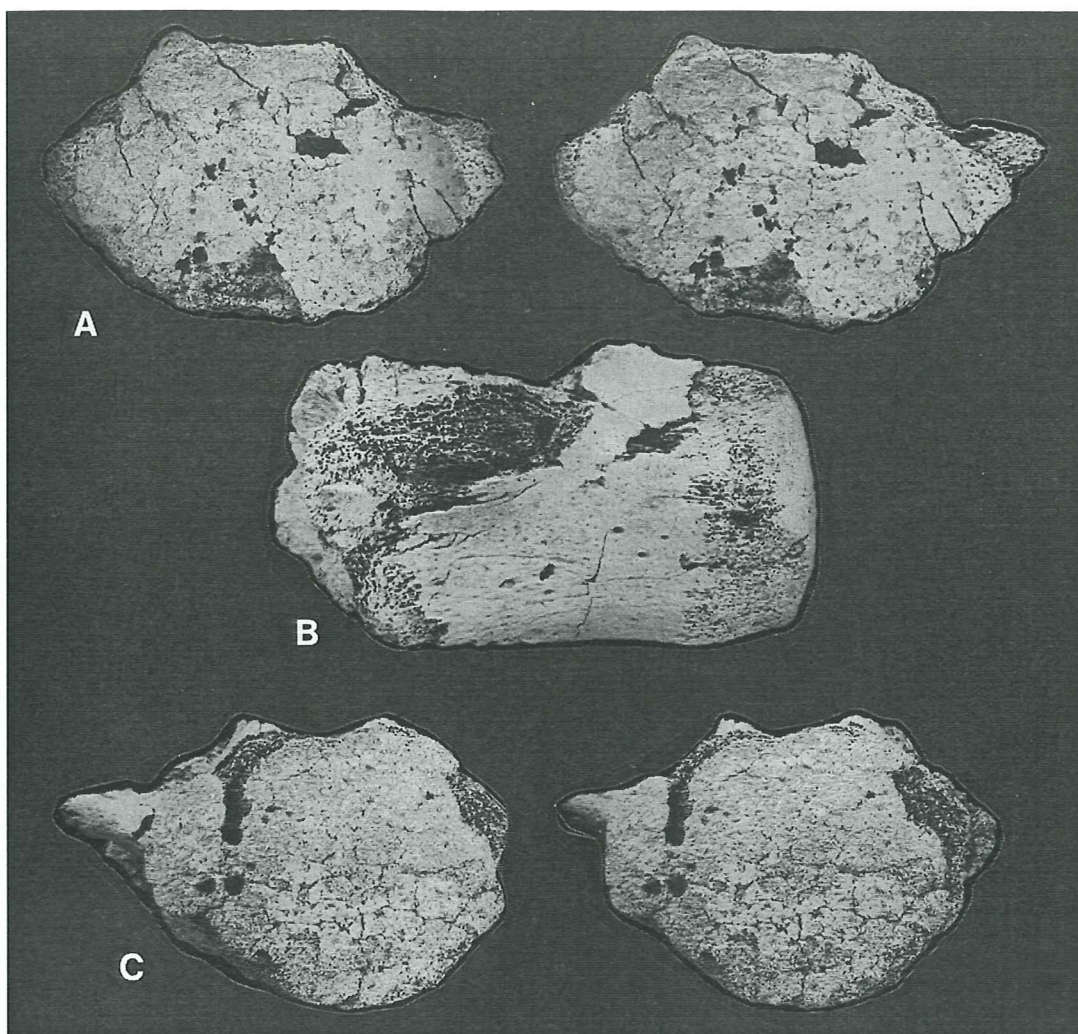


Fig. 16A-C. JL087: Lumbar? vertebra of *Hainosaurus? ivoensis* (Russell 1967) from Ignaberga, x0,58; A. anterior view, stereo pair, B. lateral view and C. posterior view, stereo pair.

Canada (Nicholls 1988). Several reasonably well preserved skeletons of *Hainosaurus peminensis*, discovered near the town of Morden in Manitoba, exhibit stout and striated teeth, where both the anterior and posterior carinae show minute serrations. The estimated adult size of *H. peminensis* is 12 to 15 metres (Nicholls 1988) and fits well with the estimated size of *H? ivoensis*. However, Nicholls' description of the teeth and vertebrae is incomplete and does not allow a detailed comparison between *H. peminensis* and *H? ivoensis*.

Russell (1967) referred a partial muzzle, a lower jaw and a fragmentary forelimb (KU 1024), found in earliest Campanian strata of the Niobrara Chalk in Kansas, USA, to "*Mosasaurus ivoensis*". The identification was based on an abbreviated rostrum of the premaxilla, a feature characteristic to most genera within the subfamily Mosasaurinae (Russell 1967). While the mosasaur may be a new member of *Mosasaurus*, the specimen includes bones with conflicting features that need to be addressed. According to Russell (1967), the shape of the pterygoid and the ectopterygoid is not typical *Mosasaurus*, but "... may be of a *Tylosaurus*". Another peculiar

feature of KU 1024 is the weakly developed ventero-posterior process of the jugal. A weak process is not characteristic to other species of *Mosasaurus*, but rather to species of *Tylosaurus* (Russell 1967, p. 24).

Remarks. - The tooth-crown from Ignaberga (JL084, Fig. 15 A-C) is nearly circular in cross-section and has a moderately strong anterior carina and a poorly developed posterior carina. In cross-section, the crown from Ugnsmunnarna (JL085) has the shape of a swollen ellipse and exhibits more pronounced cutting edges, with the anterior carina being somewhat stronger. The tooth from Åsen (JL083, Fig. 15 D-F) is oval in basal cross-section and has continuous cutting edges. It resembles the tooth from Ugnsmunnarna. These different morphologies probably reflect different positions in the jaws. Generally, antero-laterals are nearly circular in cross-section and exhibit an anterior carina only, while laterals are oval in cross-section and show continuous cutting edges (Russell 1967). Judging from the limited material at hand, the number of facets on both the buccal and the lingual face, appears to increase with increased tooth size (from 7 and 15 facets, on the buccal and

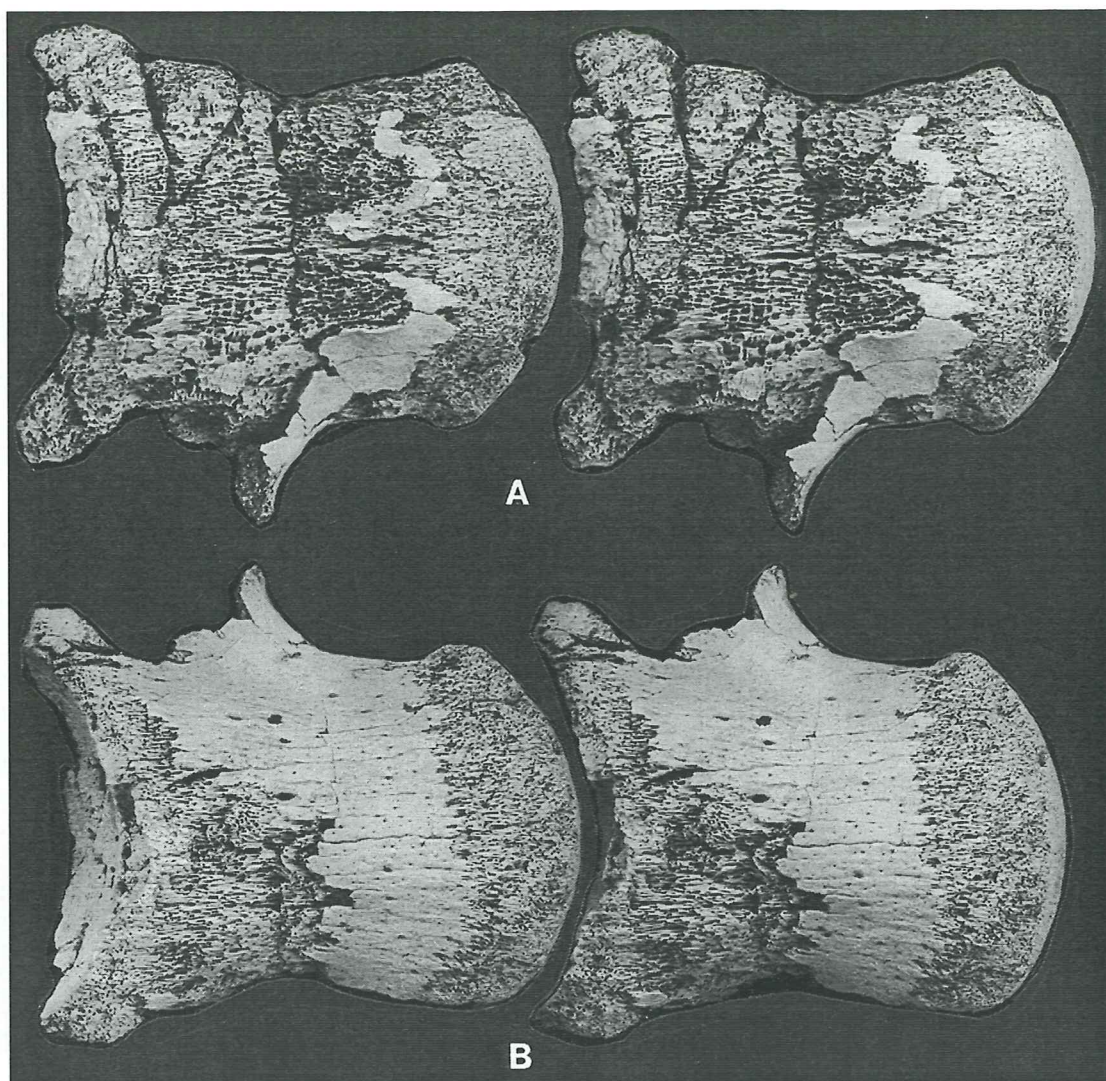


Fig. 17 A, B. JL087: Lumbar? vertebra of *Hainosaurus? ivoensis* (Russell 1967) from Ignaberga, x0,58; A. dorsal view, stereo pair and B. ventral view, stereo pair.

lingual faces respectively, on the surface of a 40 mm high tooth-crown, to 9 and 16 facets, on the buccal and lingual faces respectively, on the surface of a 60 mm high tooth-crown).

In a paper devoted to *Plioplatecarpus primaevus* Russell 1967, Holmes (1996, figs. 9-12) figured vertebrae from various parts of the vertebral column. Based on the dorso-ventrally flattened appearance of the synapophysis and the high radius of curvature of the condyle and cotyle articulations (see Russell 1967), the dorsal centrum described in this work is considered to be from the lumbar portion of the vertebral column.

The two incomplete vertebrae discussed above were found some twenty metres apart in a thin conglomerate in the northern section of Ignaberga "new quarry" (Siverson pers. comm.). The third specimen, a fragment of a second caudal vertebra, was found in a heap of calcarenite piled up near the section where the two other vertebrae were found. Based on the colour, state of preservation, matching size and the fact that mosasaur remains are extremely rare at the site, it is reasonable to

assume that all three vertebrae belong to a single individual.

Judging by the collection of mosasaur vertebrae from the Ivö Klack site, stored at the Museum of Natural History in Stockholm and the collection from Ignaberga, all large caudal vertebrae show peduncles for articulation with chevrons of the haemal arches. This indicates that the larger mosasaurs in the Kristianstad Basin were either tylosaurinae mosasaurs or plioplatecarpinae mosasaurs, as caudal vertebrae in mosasaurinae mosasaurs possess fused haemal arches.

Mosasauridae sp.

Figs. 21 A-H, 22 A-J, 23 A-F

Referred material. - Åsen, one tooth (JL090); Maltesholm, eight broken off teeth (JL091-JL098), a partial dentary? (JL099-JL102), fragments of a splenial? (JL100, JL103) and fragments of a maxilla? (JL104-JL106), all from one individual.

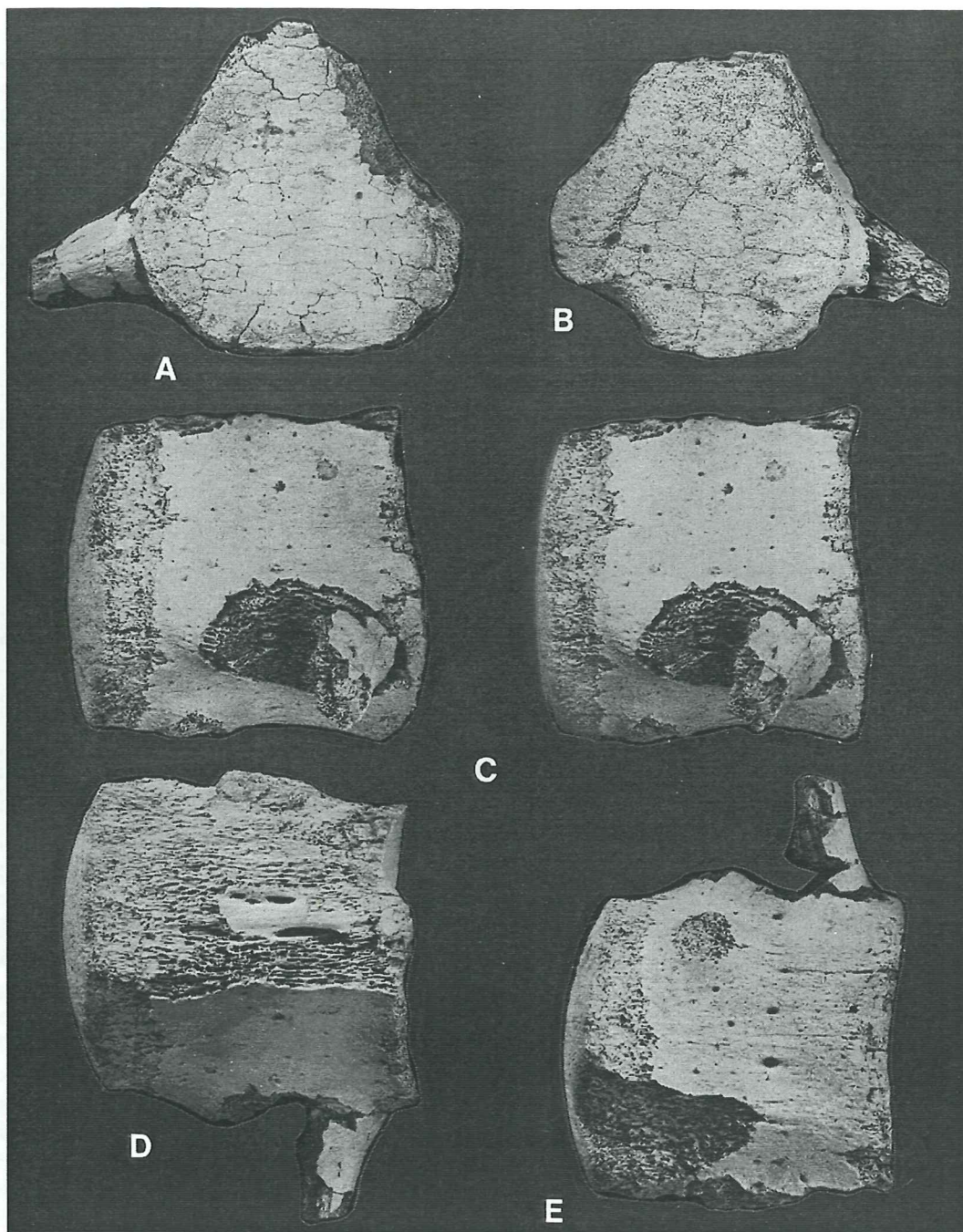


Fig.18 A-E. JL088: Intermediate caudal vertebra of *Hainosaurus? ivoensis* (Russell 1967) from Ignaberga, x0,58; A. anterior view, B. posterior view, C. lateral view, stereo pair, D. dorsal view and E. ventral view.

Description. - Marginal teeth: The crowns are strongly curved medio-posteriorly, slightly bucco-lingually compressed and symmetrically bicarinate (Fig. 21 A-H). The enamel-covered surfaces are smooth and shining. The height of the tooth-crowns is up to 35 mm, while the maximum width is about two-thirds, or slightly less, of the height.

Dentary? (Figs. 12, 22 A-J): Four separate fragments of a partial right? dentary? (JL099-JL102) are included in the material. The dentary is relatively powerfully built (compare with the *Platecarpus* dentary? from Ugnsmunnarna, Fig. 13 A-H) and narrows anteriorly. All that remains of the teeth are five vacant

alveoli. The tooth-bases rise a few mm above the surrounding bone and slope somewhat antero-laterally in relation to the dorsal surface of the bone. The bases display oval cavities, deeply excavated into the bone of the dentary. The cavities are up to about 15 mm in cross-section and set at a slight medio-lateral angle to the antero-posterior axis of the dentary. Alveoli of antero-lateral teeth are also deeply excavated into the bone, but are nearly circular in cross-section. Resorption pits, 10 to 15 mm in cross-section, erupt medio-posteriorly to each tooth-base. No replacement teeth are preserved.

Splenia? (Figs. 12, 22 D, E): Two fragments of a right? splenia? are present, one separate (JL103) and

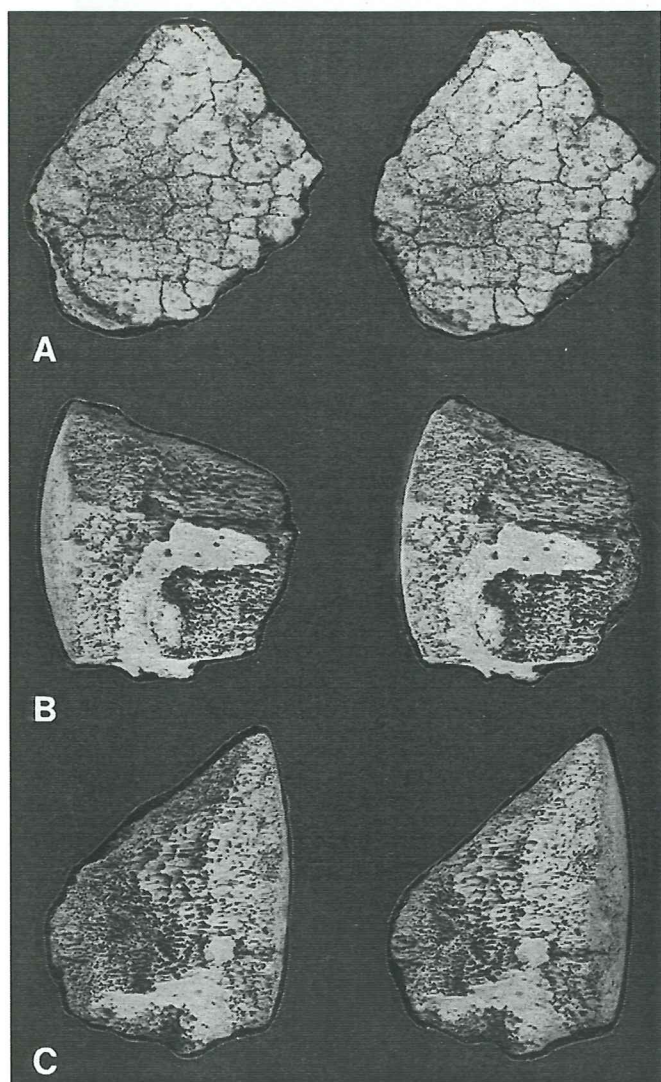


Fig. 19 A-C. JL089: Postpygal vertebra of *Hainosaurus? ivoensis* (Russell 1967) from Ignaberga, x0,58; A. posterior view, stereo pair, B. ventral view, stereo pair and C. lateral view, stereo pair.

one in contact with a part of the partial dentary (JL100). The alae are up to 10 mm wide and exhibit one roughened medial? surface and one smooth lateral? surface.

Maxilla? (Figs. 3, 23 A-F): Three abraded fragments (JL104-JL106), displaying one oval tooth-base and one resorption pit each, have the sockets reversed in relation to the tooth-bases on the dentary and may thus be parts of the right maxilla. As the inner structure of the bone does not resemble the structure of the dentary, the fragments are tentatively considered to be from the right maxilla, rather than from the left dentary.

Comparisons. - Smooth enamel, in combination with a strong curvature of the crown, seem to be a highly unusual combination in a mosasaur tooth. Several genera possess a dentition where the individual tooth-crown displays smooth enamel (i.e. *Clidastes*, *Leiodon* Owen 1841, *Rikisaurus* Wiffen 1990 and *Prognathodon*), but the tooth-crowns in these genera are nearly straight or only moderately curved medio-posteriorly

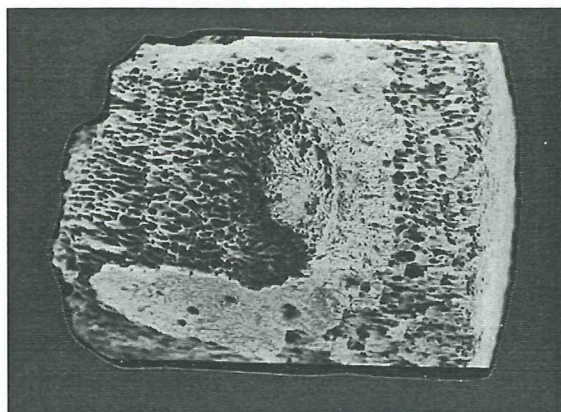


Fig. 20. Peduncle for articulation with a chevron of the haemal arch on a caudal vertebra (JL089) of *Hainosaurus? ivoensis* Russell (1967) from Ignaberga; ventral view, x1,5.

(see Russell 1967; Lingham-Soliar & Nolf 1989; Wiffen 1990). A strong curvature is present only in teeth of *Plioplatecarpus* (see Russell 1967; Lingham-Soliar 1994b; Holmes 1996), which has strongly faceted crowns. Thus, the tooth-crown from Åsen and the material from Maltesholm may belong to a new, previously undescribed genus.

Remarks. - With all four separate fragments lined up, the partial dentary is about 300 mm long. Together, the fragments include five vacant alveoli, with another four tooth-bases probably present originally. Based on the size of the partial, reassembled dentary and reconstructions of various mosasaurs, the total length of the Maltesholm specimen has been estimated. Based on a reconstruction of a mosasaurid mosasaur (i.e. *Clidastes*, see Russell 1967, plate I, fig. 1.), the estimated length of the Maltesholm specimen is approximately 8,2 m. However, based on skeletal reconstructions of plioplatecarpid mosasaurs (i.e. *Platecarpus* and *Prognathodon*, see Russell 1967, plate I, fig. 2; Lingham-Soliar & Nolf 1989, fig. 20 and plate 5B), the total length of the animal does not exceed 6,5 metres. As the tooth-crown from the Åsen site (JL090) is approximately 30-50% larger than the largest tooth-crown from Maltesholm, the Åsen specimen probably represents a much larger individual. Thus it seems the Swedish mosasaur fauna contained at least two giant mosasaurs.

Palaeoecology

Large orbits, calcified tympanic alae of the quadrates (Fig. 3) and a lack of pressure-protective devices suggest that mosasaurs hunted in near-surface water, with the help of a good sense of sight and good subaqueous hearing (Russell 1967). Like the majority of modern marine mammals, most ancient marine reptiles seem to have preferred pelagic prey (Massare 1987). Generally, the crown of an individual mosasaur tooth displays anterior and posterior carinae, is robust and slightly

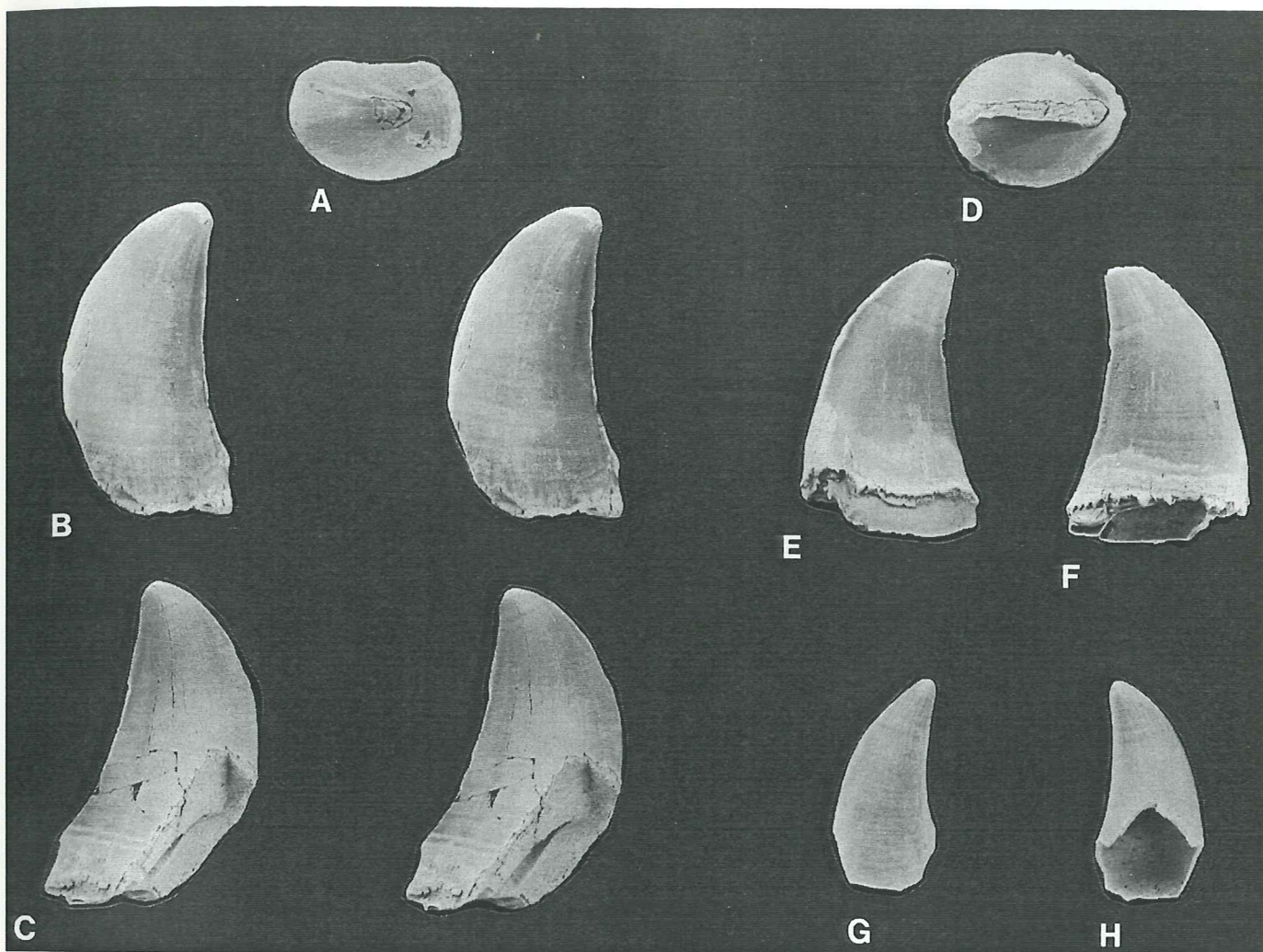


Fig. 21 A-H. Tooth-crowns of *Mosasauridae* sp., x1,3. A-C. JL090: Lateral? tooth-crown from Åsen; A. occlusal view, B. buccal view, stereo pair and C. lingual view, stereo pair. D-F. JL091: Lateral? tooth-crown from Maltesholm; D. occlusal view, E. lingual view and F. buccal view. G, H. JL092: Antero-lateral? from Maltesholm; G. buccal and H. lingual view.

bucco-lingually compressed. Based on the characters of the dentition, Massare (1987) has shown that the teeth primarily had a cutting function. Preserved stomach-contents have shown that the dominant element in the diet was small and medium-sized fish, even though the larger mosasaurs were probably capable of eating just about anything they encountered (Russell 1967; Massare 1987).

According to Russell (1967), the jaws of *Clidastes* were long and slender as an adaptation to a rapid biting. In the same paper, Russell (1967) also demonstrated that the elongated body and the small flippers made *Clidastes* less agile than some other mosasaurs. Russell (1967) was of the opinion that the small flippers and the development of a caudal fin indicate that *Clidastes* was a relatively rapid swimmer, adapted to catching swift fishes, which were relatively incapable of sudden evasive movements.

In contrast to *Clidastes*, the body of *Platecarpus* was short, while the flippers were long and well-developed. *Platecarpus* was probably a relatively slow swimmer,

but must have been able to make abrupt turns (Russell 1967). Small and medium-sized fish have been found inside the body cavity of a *Platecarpus* discovered in Gove County, Kansas (Williston 1899, pp. 40-41), even though Russell (1970) has proposed belemnites as a dominant element in the diet of this mosasaur (Fig. 10).

In the Niobrara Formation, Kansas, USA, *Platecarpus* is the most common mosasaur in lower parts of the unit. The number of *Clidastes* specimens increases upwards. As fossils of birds and pterodactyls are restricted to an upper unit near the top of the formation, this may indicate shallowing water conditions in the upper parts of the strata (Russell 1967). Based on fossil evidence, Russell (1967) stated that *Platecarpus* preferred off-shore waters.

In a work devoted to tylosaurid mosasaurs from Europe and Africa, Lingham-Soliar (1992b) suggested that *Hainosaurus* was not a very fast swimmer, but instead patrolled by stealth. The statement is based on the observations that the bones in tylosaurid mosasaurs are highly cancellous and that the paddles as well as the

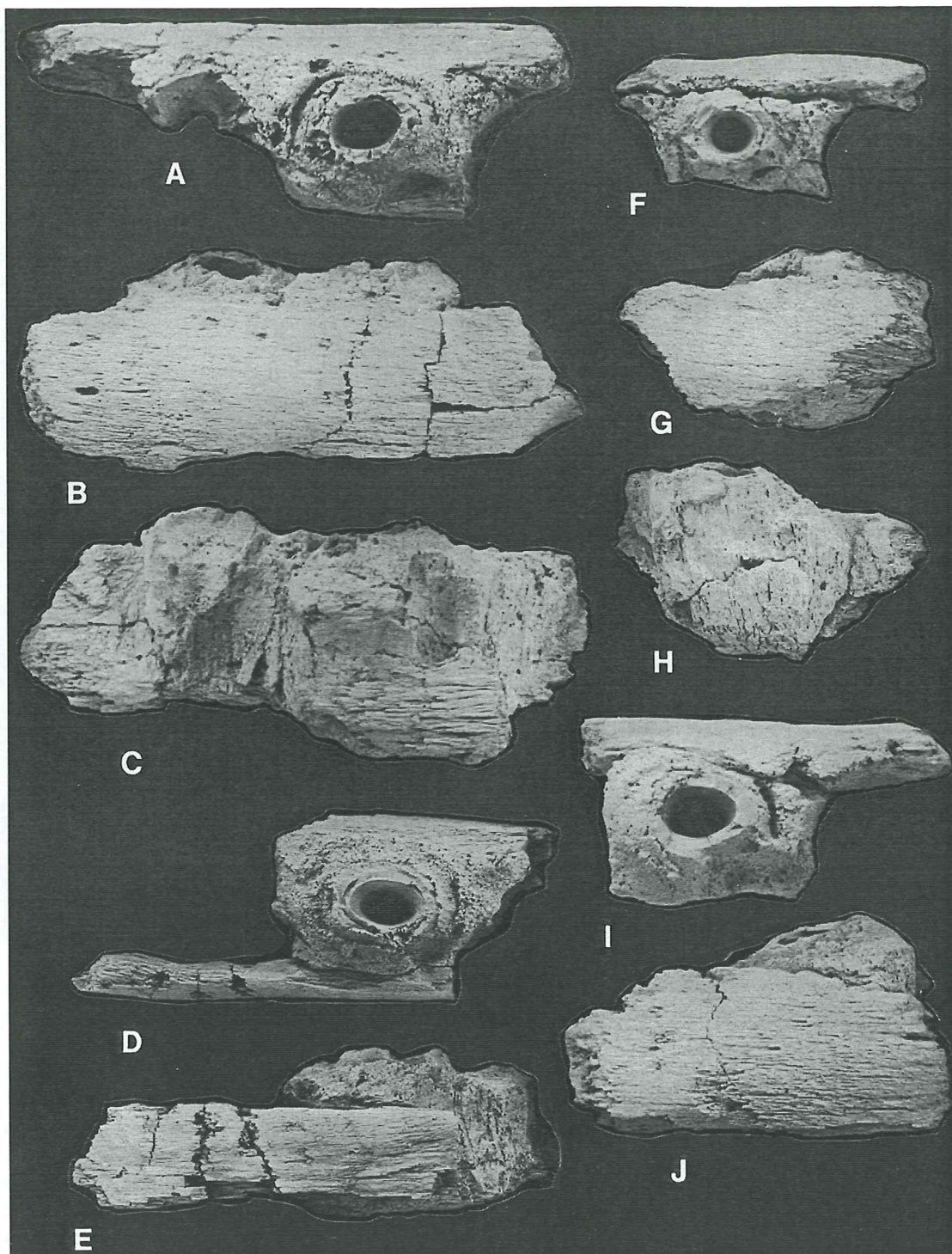
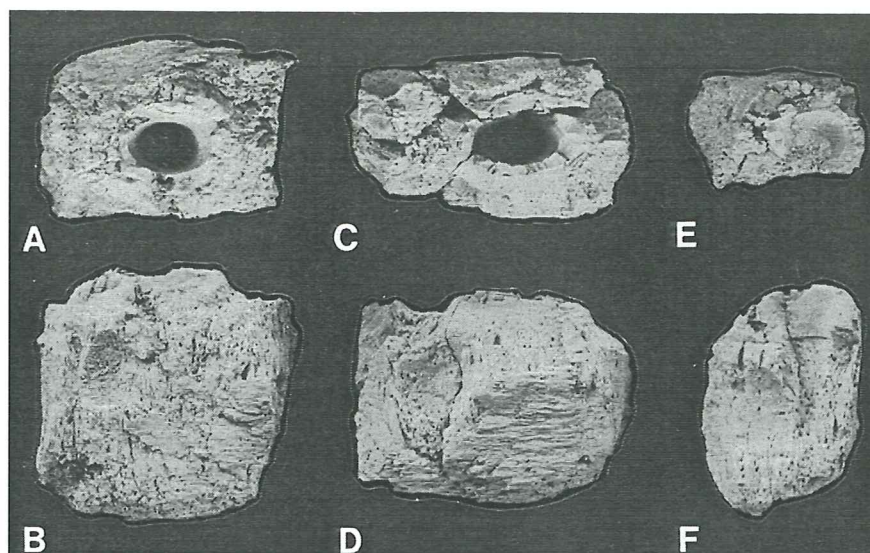


Fig. 22 A-J. Dentary? and splenial? from a single individual of *Mosasauridae* sp. from Maltesholm, x0.8. A-C. JL099; A. dorsal view, B. lateral view and C. medial view. D, E. JL100; D. dorsal view and E. medial view. F-H. JL102; F. dorsal view, G. lateral view and H. medial view. I, J. JL101; I. dorsal view and J. lateral view.

pectoral and pelvic girdles are highly reduced. The resulting reduction in body weight increased buoyancy, allowing tylosaurid mosasaurs to conserve energy. As proposed by Lingham-Soliar (1992b), *Hainosaurus* hunted over fairly large areas, ambushing its prey by a burst of acceleration, assisted by the large tail. Together with the large selachian *Cretoxyrhina mantelli* (Agassiz 1843) (see Siverson 1992a), *H. ivoensis* and *Mosasauridae* sp. were undoubtedly the top predators in the

shallow sea covering the Kristianstad Basin during the *B. mammillatus* time. Remains of a small mosasaur, a shark and some bones of a flightless bird have been found inside the body cavity of a *Tylosaurus*, recovered from the Gammon Ferruginous Member of the Pierre Shale in South Dakota (Martin & Bjork 1987) and some turtle bones have been found in association with a *Hainosaurus* in Belgium (Dollo 1887, cited in Russell 1967, p. 69).

Fig. 23 A-F. Maxilla? from a single individual of Mosasauridae sp. from Maltesholm, x0.8. A, B. JL104; A. ventral view and B. medial view. C, D. JL105; C. ventral view and D. medial view. E, F. JL106; E. ventral view and F. medial view.



Based on the collections of mosasaur remains from Åsen, Ignaberga, Maltesholm and Ugnsmunnarna, some differences in the distribution of mosasaur taxa within the Kristianstad Basin has been observed. As seen in Table 1., the material obtained from the Åsen site comprises mainly *Clidastes?* sp., although remains of all four mosasaur taxa included in this paper have been recorded from the locality. The Ignaberga "new quarry" has yielded one tooth-crown referred to *H?* *ivoensis*, one crown assigned to *P.* cf. *somenensis* and one crown referred to *Clidastes?* sp. Maltesholm has only produced one tooth assigned to *P.* cf. *somenensis* and the associated remains of a single individual of Mosasauridae sp., while the Ugnsmunnarna site has provided several teeth of *P.* cf. *somenensis* and two tooth-crowns referred to *H?* *ivoensis*. As discussed above, *Platecarpus* probably preferred somewhat deeper waters further away from the coast than did *Clidastes*. Teeth of juvenile sharks are more common at the Åsen site than at the other three sites (Siverson pers. comm.). This indicates a shallow, protected environment. *Hainosaurus?* *ivoensis* may well have included *Clidastes?* sp. in its diet (Fig. 14). As *H?* *ivoensis*, like *Platecarpus*, probably patrolled more open waters [a large number of shed teeth of *H?* *ivoensis* has been recorded from the Ivö Klack site (see Persson 1959), a small island during the *B. mammillatus* time], the shallow water conditions at Åsen probably offered some protection for *Clidastes?* sp., partly explaining the abundance of shed teeth assigned to *Clidastes?* sp. from this site.

A broad and shallow groove on the condyle articulation in an intermediate caudal vertebra assigned to *H?* *ivoensis*, may be a bite mark (Fig. 18 B). The location of the mark and the size of the vertebra suggest that the mark is a result of scavenging rather than predation. Scavenging by the Late Cretaceous selachian *Squalicorax* has previously been reported by Schwimmer et al. (1997). However, the trace differs from bite marks made by this shark in that the trace is shallow and broad. The width and size of the trace suggest that it may have been inflicted by another mosasaur. Tooth marks, possibly inflicted by mosasaurs, have previously been found on a *Tylosaurus* skull (Massare 1987).

Palaeobiogeography

The assemblage from the Kristianstad Basin is similar in composition to approximately coeval mosasaur faunas in the Upper Chalk deposits in Norfolk, Sussex and Hampshire, England, the lower portion of the Pierre Shale in South Dakota, USA and the Pembina Member of the Pierre Shale in Manitoba, Canada (see Russell 1967, 1970; Milner 1987; Nicholls 1988). It is important to note that the similarity is not at a species level, but rather in the general composition, as each assemblage comprises one, or possibly two, giant tylosaurid mosasaurs, one or several plioplatecarpid mosasaurs of moderate size (generally *Platecarpus*) and one or two smaller mosasaurid mosasaurs (generally *Clidastes*).

Table 1. Number and localities yielding tooth-crowns of *Clidastes?* sp., *Platecarpus* cf. *somenensis* Thevenin 1896, *Hainosaurus?* *ivoensis* (Russell 1967) and Mosasauridae sp. *From one individual.

	<i>Clidastes?</i> sp.	<i>Platecarpus</i> cf. <i>somenensis</i>	<i>Hainosaurus?</i> <i>ivoensis</i>	Mosasauridae sp.
Åsen	53	5	1	1
Ignaberga	1	1	1	
Maltesholm		1		8*
Ugnsmunnarna		6	2	
total	54	13	4	9

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