

The Tylosaurine Mosasaurs (Reptilia, Mosasauridae) from the Upper Cretaceous of Europe and Africa

by THEAGARTEN LINGHAM-SOLIAR

Abstract

This study represents the first relatively extensive description of the genus *Hainosaurus* DOLLO, 1885. The description of *H. bernardi* DOLLO, 1885 is based on the holotype and on a previously undescribed specimen. A new specimen of *H. gaudryi* (THEVENIN, 1896) from France is also described. *Mosasaurus iembeensis* TELLES-ANTUNES, 1964, from the Turonian of Angola is reassigned to the genus *Tylosaurus* MARSH, 1872. The only other tylosaurine species from Africa, *T. capensis* (BROOM, 1912) is also briefly described.

The biomechanics of the skull of tylosaurines is examined primarily because of the hypothesis that the large rostrum was used in ramming prey (RUSSELL, 1967). Various other aspects of tylosaurine predatory behaviour are also mentioned.

Key-words: *Hainosaurus*, *Tylosaurus*, *Leiodon*, ramming, ambush-predation, diving

Résumé

Cette étude constitue la première description relativement approfondie du genre *Hainosaurus* DOLLO, 1885. La description d'*H. bernardi* DOLLO, 1885 se base sur l'holotype et sur un spécimen non décrit jusqu'à ce jour. Un nouvel exemplaire d'*H. gaudryi* (THEVENIN, 1896) provenant de France, est également décrit. *Mosasaurus iembeensis* TELLES-ANTUNES, 1964, du Turonien d'Angola, est attribué au genre *Tylosaurus* MARSH, 1872. Les seul autre tylosaurien africain, *T. capensis* (BROOM, 1912) est brièvement décrit.

La biomécanique du crâne des tylosauriens est examinée principalement suite à l'hypothèse selon laquelle le grand rostre servait à attaquer les proies (RUSSELL, 1967). Divers autres aspects du comportement prédateur des tylosauriens sont aussi mentionnés.

Mots-clefs: *Hainosaurus*, *Tylosaurus*, *Leiodon*, prédation, plongée.

Introduction

The gigantic tylosaurine *Hainosaurus bernardi* DOLLO, 1885 was the first mosasaur to be discovered in Belgium. Almost the entire skeleton was found intact, although considerably abraded, in the Ciplu Phosphatic Chalk in a region known as "La Malogne" (Fig.1). It was subsequently described in several papers by DOLLO (1885a, c; 1889; see LINGHAM-SOLIAR & NOLF, 1989 for the geological setting).

Considerable confusion surrounds the tylosaurine mosasaurs and the genus *Leiodon*. It originated with COPE's (1869-1870, p. 200) misappropriation of the name *Leiodon* (and corruption to *Liodon*) to the genus *Tylosaurus*. COPE (1870) realized that he had made a mistake in naming a mosasaur from the White Rotten Limestone of Alabama, as *Mosasaurus brumbyi*. He was satisfied of the error by the presence of free haemal

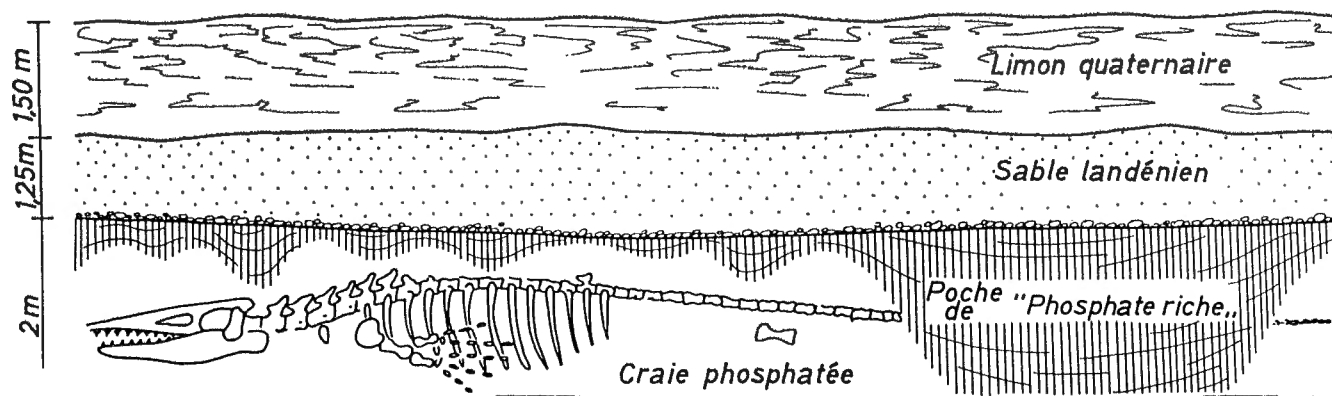


Fig. 1 — Discovery of *Hainosaurus bernardi* IRSNB R23 in La Malogne, near Mesvin in Belgium (after LECLERCQ & BOUKO, 1985)

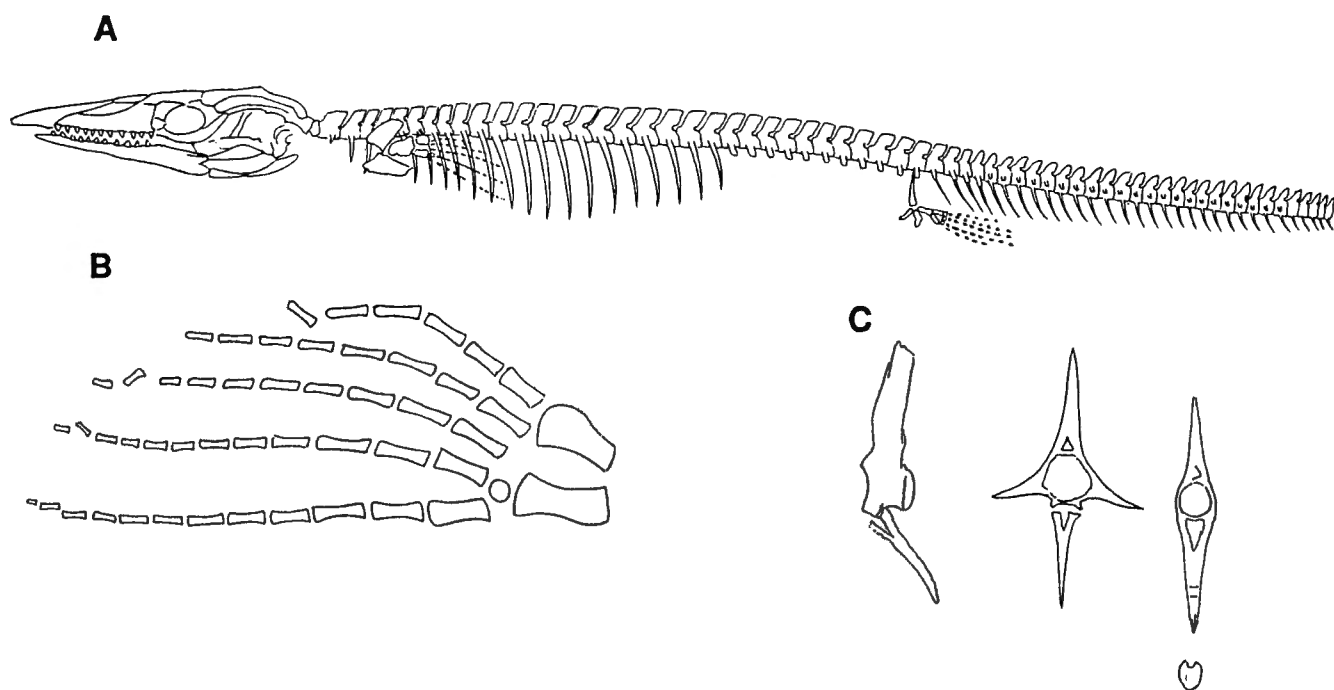


Fig. 2 — Reconstruction of *Tylosaurus* incorrectly assigned to *Leiodon* by Owen 1879, (modified from Owen, 1880)

arches (fused in *Mosasaurus*) and concluded that the specimen had to belong to *Leiodon* (COPE's "*Liodon*") for which there were no vertebral descriptions. OWEN (1879, 1880) himself was guilty of a similar error and added to the confusion that surrounds *Leiodon* to the present day. For instance he (OWEN, 1879) also assigned postcranial remains of *Tylosaurus* (= ?*Macrosaurus*) to *Leiodon*. Indeed his reconstruction of *Leiodon* (OWEN, 1879; Fig.2) is evidently the same as *Tylosaurus* (note also the massive premaxillary rostrum). These errors were based on a simple premise. The postcranial skeleton of *Tylosaurus* resembled neither that of *Mosasaurus hoffmanni* nor *M. missouriensis*, and both COPE (1870) and OWEN (1879, 1880) mistakenly concluded that it therefore had to belong to the only other large recognizable taxon at the time, *Leiodon*. Nor was the genus *Hainosaurus* exempt from this confusion. DÉPÉRET & RUSSO (1925, p.340) and PERSSON (1959, p.465) have suggested that the tylosaurine *Hainosaurus DOLLO*, might prove to be congeneric with *Leiodon anceps*. RUSSELL (1967, p.142) on the other hand was in no doubt that *Leiodon compressidens* and *L. mosasauroides* are generically distinct from *Hainosaurus* but he was uncertain about *L. anceps*. It is clear though that if the latter species was found to be identical to *Hainosaurus* then because of *Leiodon*'s priority (OWEN, 1840-1845) the name *Hainosaurus* would have to be abandoned and all the remaining *Leiodon* species placed in a new genus. Fortunately this is not the case, for the most curious aspect of DÉPÉRET & RUSSO's (1925) and PERSSON's (1959) suggestions that these two forms may be congeneric lies in the fact that there were no diagnos-

tically identifiable teeth for *Hainosaurus* at the time (identifications on *Leiodon* are essentially based on its unique tooth morphology). Exceedingly poor preservation of the few available fragmentary teeth in the holotype of *Hainosaurus bernardi* and IRSNB 3672 makes this kind of judgement dubious. The conditions that are discernible are, an absence of ribbing on either side of the carina and lack of lateral compression in the posterior teeth - presence of either condition is highly diagnostic for *Leiodon*. Recent evidence from a new species *Hainosaurus gaudryi*, discussed in the taxonomic section, conclusively indicates that *Leiodon anceps* and *Hainosaurus* are generically distinct.

Abbreviations & Addresses

BMNH	British Museum (Natural History). Department of Palaeontology. Cromwell Road. London S.W.7 5BD. U.K.
IRSNB	Institut Royal des Sciences Naturelles de Belgique. Rue Vautier 29. B-1040 Brussels. Belgium
MNHN	Museum National d'Histoire Naturelle (Dept. of Palaeontology). 43 Rue Cuvier. 75231 Paris. VI. France
MMMN	Manitoba Museum of Man and Nature, Winnipeg, Manitoba, Canada
SGMA	Servicos de Geologia e Minas de Angola

USTL BUG (coll. Lab. Paléo) Bugarach

SL Saint-Louis

JOU La Jouane.

Systematic palaeontology

Order SQUAMATA OPPEL, 1811

Family MOSASAURIDAE GERVAIS, 1853

Subfamily TYLOSAURINAE WILLISTON, 1895

WILLISTON 1897

Tylosauridae MARSH, 1876: 59, *nomen nudum*.

"Mososaurinés megarhynques" DOLLO, 1890: 163.

Tylosauridae WILLISTON, 1895: 169.

Tylosaurinae WILLISTON, 1897: 177.

DIAGNOSIS

(see RUSSELL, 1967).

Hainosaurus DOLLO, 1885

Hainosaure DOLLO, 1885a: 285.

Hainosaurus DOLLO, 1885a: 288.

Hainosaurus POMPECKJ, 1910: 125.

Hainosaurus DOLLO, 1913: 612.

?*Leiodon* DEPERET RUSSO, 1925: 340.

?*Leiodon* PERSSON, 1959: 465.

Generic type

Hainosaurus bernardi DOLLO, 1885

DIAGNOSIS

Double buttressed premaxillary suture. Twelve to thirteen teeth in maxilla. Supraorbital wing of prefrontal covered dorsally by frontal; prefrontal forms part of posterolateral margin of external nares. Prominent median dorsal ridge on frontal; frontal not emarginate above orbits. Margins of parietal straight as far as posterior diverging suspensorial rami, forming rectangular field medially on parietal. Squamosal wing to parietal moderately developed. Large otosphenoidal crest on prootic covers exits for cranial nerves VII and IX. Broad projection on dentary anterior to first dentary tooth. Ten to eleven teeth on pterygoid.

Articulating surfaces of cervical and anterior dorsal vertebrae nearly circular (except for the atlas which is elliptical); synapophysis located in centre of lateral surface of cervical centra, occupies anterodorsal portion of lateral surface of dorsal vertebra. Ventral border of anteroventral extension of synapophysis not strongly developed on cervicals and anterior dorsals, does not reach level of undersurface of centrum; anterior zygapophyses of cervicals and dorsals connected by sharp ram-rod straight crest posteroventrally to synapophysis, zygosphene-zygantrum rudimentary. Anterior base of atlas neural arch arises directly above condylar facet,

atlas synapophysis small and flattened or rudimentary, hypapophyseal peduncle located posteriorly on ventral surface of cervical centra, articulation for hypapophysis circular with central excavation, five hypapophyses-bearing cervicals, two or three more with rudimentary peduncles, transverse process of pygal vertebrae relatively short, neural spines of caudal, longest and vertical on postsacrals 38-40.

Scapula relatively the smallest in the Mososauridae; much smaller than coracoid. Superior border of scapula strongly convex. Coracoid does not expand medially to point behind glenoid articulation. Distal and proximal ends of slender humerus only slightly expanded, distal end more expanded than proximal; internal trochanter of average proportions and located medially from head; radial process absent, facets for articulation with other elements and sites of muscle attachment not well differentiated. Radius very elongate, proximal end very slightly expanded, shaft narrow, distal end very slightly expanded. Ulnare and fourth carpal, present, lack articulating surfaces. Metacarpal one equal to metacarpal two in length.

Vertebral formula: 40 presacral vertebrae, 9+ pygals, 30-35 intermediate caudals, terminals 33+ (See DOLLO 1885a, c).

Hainosaurus bernardi DOLLO, 1885

Figs. 1, 3, 4, 5, 6, 7, 9, 10, 12; Pls. 1, 2, 3, 4, 5, 6

Hainosaurus bernardi DOLLO, 1885a: 288.

Hainosaurus bernardi DOLLO, 1885b: 31.

Hainosaurus bernardi DOLLO, 1889: pls 9, 10.

Hainosaurus bernardi DOLLO, 1904: 207.

Hainosaurus bernardi DOLLO, 1909: 103.

Hainosaurus bernardi [sic!] Pompeckj, 1910: 139.

Hainosaurus bernardi DOLLO, 1924: 172.

?*Leiodon anceps* DEPERET and RUSSO, 1925: 340.

?*Leiodon anceps* PERSSON, 1959: 465.

Hainosaurus bernardi LINGHAM-SOLIAR, 1991c: 174-175, fig. 5.

HOLOTYPE

IRSNB R23 (old no. R1564), almost complete poorly preserved cranial and postcranial remains.

HORIZON AND LOCALITY

Ciply Phosphatic Chalk, Upper Maastrichtian, in "La Malogne", near the town of Mesvin, Belgium.

REFERRED MATERIAL

IRSNB 3672, almost complete skull and large number of vertebrae. From the Maastrichtian Phosphatic Chalk of Baudoir, Belgium.

DIAGNOSIS

Premaxilla with long ventral process that extends posteriorly to approximately the second maxillary tooth. External nares large - 28-31% of skull length. Parietal

foramen small, located on the fronto-parietal suture. Ventromedial process of postorbitofrontal forms shallow excavation to receive distal process of the vertical arm of the jugal, probably ligamentous; POF wing to parietal deeply invades posterior frontal border either side of parietal foramen. Ventroposterior process on jugal absent. Tympanic ala of quadrate thin. Stapedial pit rectangular in form. Dentary long, thirteen teeth present. Angular widely separated medially from coronoid. Retroarticular process of articular posterodorsally rounded, ventrally straight. Teeth - anterior and posterior carina extend full length of crown; internal and external striae fairly well developed.

DESCRIPTIONS AND COMPARISONS

SKULL

The skull is massive with a prominent anterior rostrum as in other members of the Tylosaurinae (Fig.3; Pls. 1 & 2). Comparisons are made with the North American species *Hainosaurus pembinensis* (as described by NICHOLLS, 1988) and the genus *Tylosaurus proriger* and *T. napaolicus* (as described by RUSSELL, 1967).

PREMAXILLA

The premaxilla in the holotype specimen is poorly preserved with fine detail very much obscured. The large premaxillary rostrum is characteristic of the Tylosauri-

nae although in the holotype the dorsal outline is more rectangular than in IRSNB 3672 and the fragmentary specimen of *Hainosaurus "lonzeensis"* (no specimen number; DOLLO, 1904). Ventrally a long process on either side of the premaxilla extends posteriorly to the second maxillary tooth (Fig.4). The premaxillary suture in IRSNB 3672 is highly unusual forming a double pointed buttress with the maxilla (Figs. 3A, 4A, Pl. 2A). In the holotype it is just distinguishable on the right side despite poor preservation. The suture then rises gently from this point to the posterior margin of the external nares and instead of descending as in *Tylosaurus* (RUSSELL, 1967, p.177) continues in a gentler gradient to the dorsal termination. Unfortunately the posterior sutural contact with the prefrontal is not preserved in either the holotype or IRSNB 3672.

The internarial bar extends deep into the frontal to approximately a third its length (Fig.3B) very much as in *Tylosaurus proriger* (RUSSELL, 1967, p.172, fig.92). In *Hainosaurus pembinensis* MMMN V95, however, it extends to well over half the length of the frontal (observed from photographs, Elizabeth NICHOLLS, pers. comm.)

DISCUSSION

DOLLO (1904, p.213) erected the new species *H. lonzeensis* on the basis of the differences in shape between

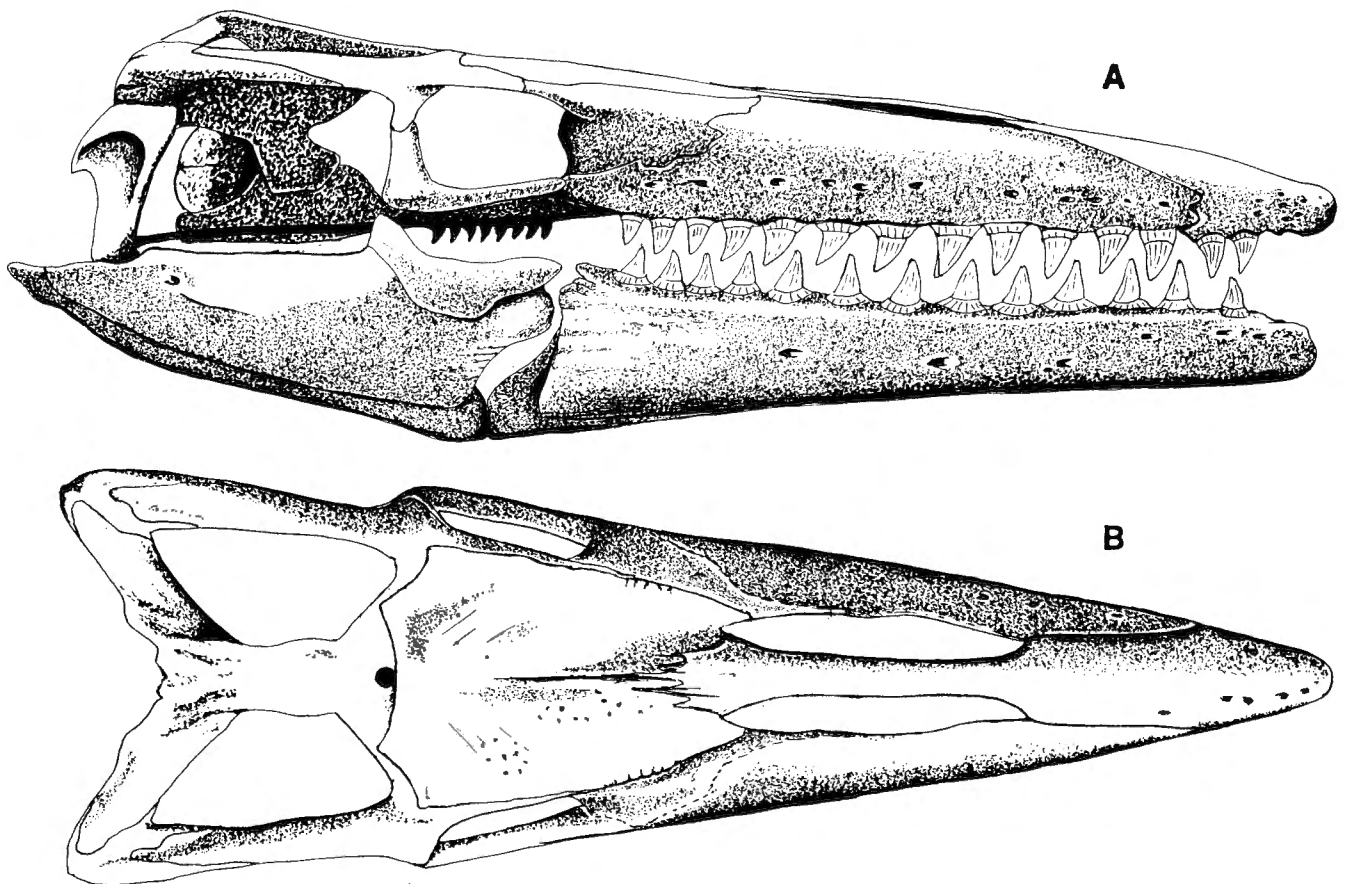


Fig. 3 — *Hainosaurus bernardi* (IRSNB 3672). Restored skull. A, lateral view; B, dorsal view.

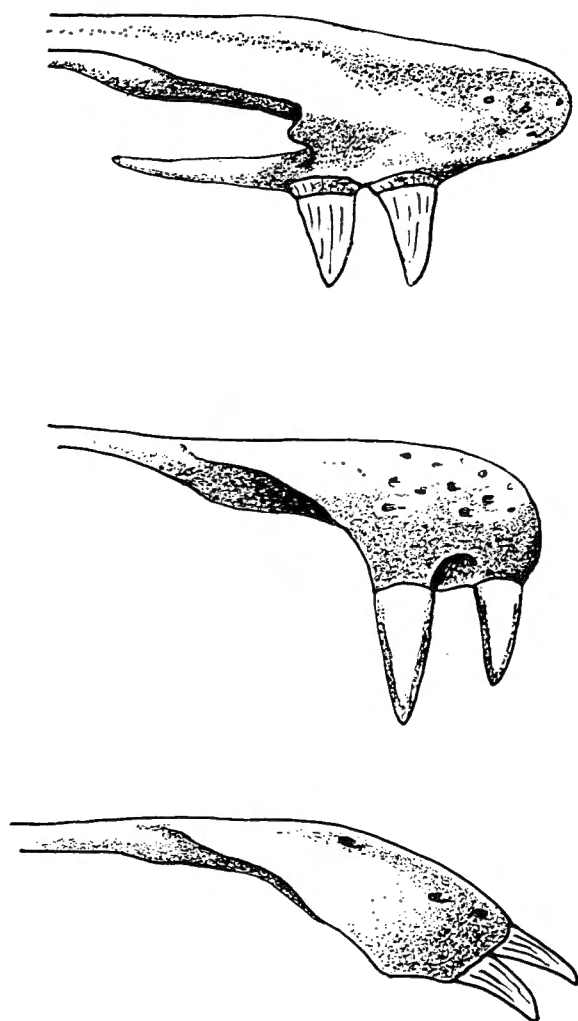


Fig. 4 Premaxillae of three mosasaur taxa showing marked variation. A, *Hainosaurus bernardi* demonstrates a large prow and double buttresses premaxillary/maxillary suture; B, *Goronyosaurus nigeriensis* - the second pair of premaxillary teeth is, uniquely in mosasaurs, the longest in the dental battery; C, *Prognathodon solvayi* with prognathous premaxillary teeth (not to scale).

the premaxillary rostrum in the holotype of *Hainosaurus bernardi* and that of the premaxillary fragment from the Glauconie de Lonzeé "...par son rostre plus conique et à face supérieure plus arrondie, et par ses dimensions moindres". However, the apparent difference is almost certainly the result of poor preservation in the holotype material. NICHOLLS (1988, p.1566, fig.3A) also described a pronounced rectangular premaxillary rostrum of *H. peminensis*. Perhaps the highly gypsiferous nature of the specimen (NICHOLLS, pers. comm.) could account for the apparent rectangular configuration. Certainly in *Hainosaurus "lonzeensis"* the apparent difference in the shape of the rostrum with that of *H. bernardi* is insufficient to warrant the erection of a new

species and I have therefore assigned it as *Hainosaurus* sp.

The ventral projections in the premaxilla of *Hainosaurus bernardi* IRSNB R23 have not previously been described in the Tylosaurinae. They are apparently a more robust counterpart of slender extensions that I have seen on the ventral surface of the premaxilla of *Mosasaurus hoffmanni*.

The diagnostic importance of the double buttressed premaxillary suture in *Hainosaurus* can not be overstated as the condition is certainly not found in *Tylosaurus* (cf. RUSSELL, 1967, p.177, fig.95). For instance the large premaxillary rostrum in "*Mosasaurus*" *gaudryi* (THEVENIN, 1896) makes the material clearly referable to the Tylosaurinae but the presence of the double buttressed premaxillary suture enables a more specific assignment to *Hainosaurus* (functional significance discussed further on).

MAXILLA

Preservation of the maxilla of specimen IRSNB R23 is poor but fortunately it is much better in IRSNB 3672 (Fig.5A). The maxilla is stout and generally consistent with the element in other taxa in the Tylosaurinae. The right maxilla has just two fragmentary tooth crowns preserved and one in the left maxilla. Tooth bases indicate that there were 12 teeth in life.

FRONTAL

The frontal in *Hainosaurus bernardi* IRSNB R23 (Figs.3B, 6A,B) is quite poorly preserved although there are several notable characters. The fronto-parietal suture is narrower in the holotype compared to the condition in *H. peminensis* (NICHOLLS, 1988) and *Tylosaurus* (RUSSELL, 1967, fig.92). The posterior boundary with the postorbitofrontal is also somewhat more concave. Lateral margins above the orbits are straight to slightly convex which is consistent with the condition in *H. peminensis* (photographs, NICHOLLS, pers. comm.) but differs from the somewhat concave orbital margin of *Tylosaurus proriger* (RUSSELL, 1967, p.172). The prefrontal and postorbitofrontal bones exclude the frontal from the orbital border. A pronounced crest extends along three quarters of the length of the bone along the midline although this is a variable condition in *Tylosaurus* (RUSSELL, 1967, p.171).

The ventral surface of the frontal, despite poor preservation, presents several interesting features. The prefrontals underlie the frontals, extending almost to the fronto-parietal suture and they are tightly sutured to the frontal in a relatively deep excavation (Fig.6, Pl.3B). The excavation for the olfactory lobes are apparently shallow. The postorbitofrontal is quite broad and the prefrontal wing extends to the midpoint of the lateral margin of the frontal. Dorsally a narrow process extends from the postorbitofrontal and is sutured into a deep narrow excavation in the prefrontal. The description of the frontal is very similar in the Paris specimen of *Hainosaurus* (described later).

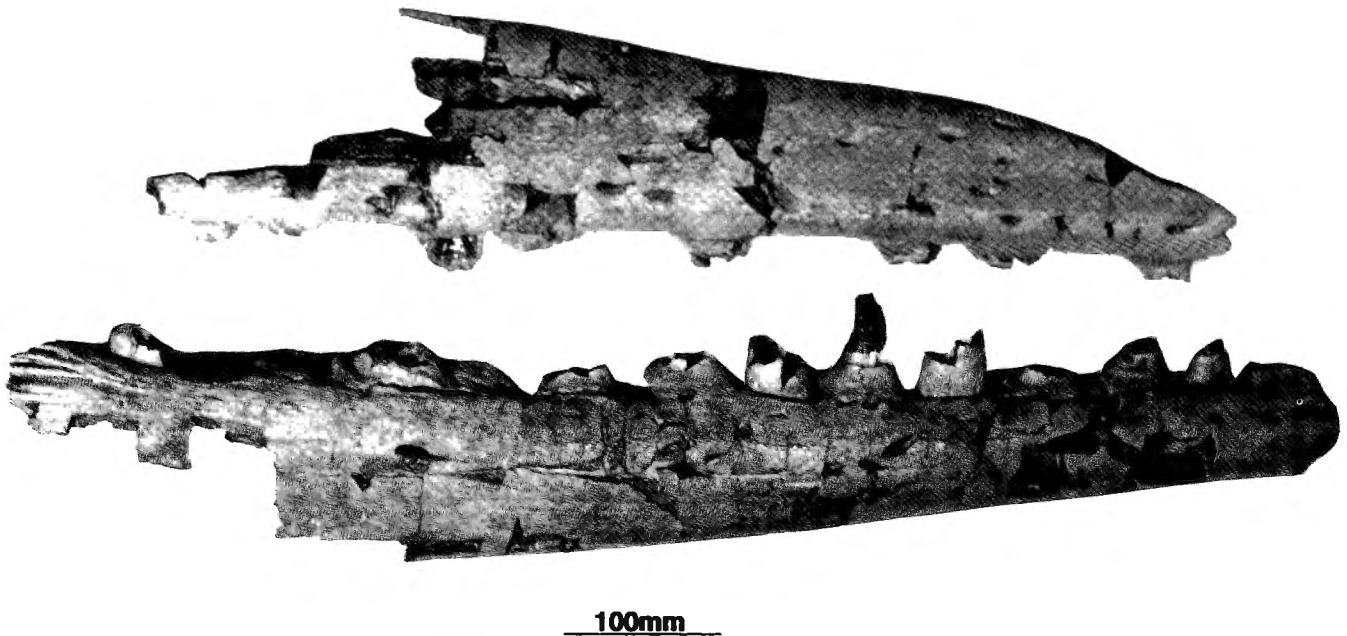


Fig. 5 — *Hainosaurus bernardi* (IRSNB 3672). Right maxilla and dentary.

LACHRYMAL

The lachrymal is well preserved in the holotype of *Hainosaurus bernardi* IRSNB 1564. It is quite broad but is characteristically an arrow-head shaped bone as in other mosasaurs (Pl.1A).

PREFRONTAL

The prefrontal is very poorly preserved in both the holotype and IRSNB 3672. It is nevertheless apparent from the available fragment and from the borders with the frontals and maxilla that it is quite similar to the element in *Tylosaurus proriger* (RUSSELL, 1967, p.172) and *Hainosaurus pembinensis*. However, unlike in

Tylosaurus, a narrow tongue of the prefrontal forms a part of the narial border.

POSTORBITOFRONTAL

The postorbitofrontal of IRSNB 3672, although fragmentary, was clearly a rather robust bone (Pl.3A). The supratemporal wing is long extending to the posterolateral corner of the squamosal. The wing to the jugal is substantial, although incompletely preserved. The wings to the parietal and prefrontal are absent. The large ventral wing to the frontal has, however, already been described in the holotype specimen.

JUGAL

The jugal in the holotype, although incomplete, is evidently similar to that of *Tylosaurus proriger* (RUSSELL, 1967, p.177, fig.95) with a fairly broad ala-like process at the junction of the vertical and horizontal axes. There is no evidence of a postero-ventral process.

SQUAMOSAL

The squamosal is poorly preserved in the holotype and in IRSNB 3672. Anteriorly the squamosal wing extends as far as the jugal wing of the postorbitofrontal.

NASALS

Quite unusually the nasals are preserved in IRSNB 3672 (Pl.2B), fused to the internarial bar. They are known in the literature in three other specimens, the type specimen of *Plotosaurus bennisoni* (CAMP, 1942, pp. 27-28, fig. 14.), in *Tylosaurus* (HUENE, 1910, p.303, fig.5) and in *Clidastes sternbergi* (WIMAN, 1920, p.15, fig.4). I have observed well preserved nasals in a *Tylosaurus* sp.

Fig. 6 — Ventral view of the frontal of *Hainosaurus bernardi* (IRSNB R23) showing prefrontal process deeply sutured close to the fronto-parietal suture.

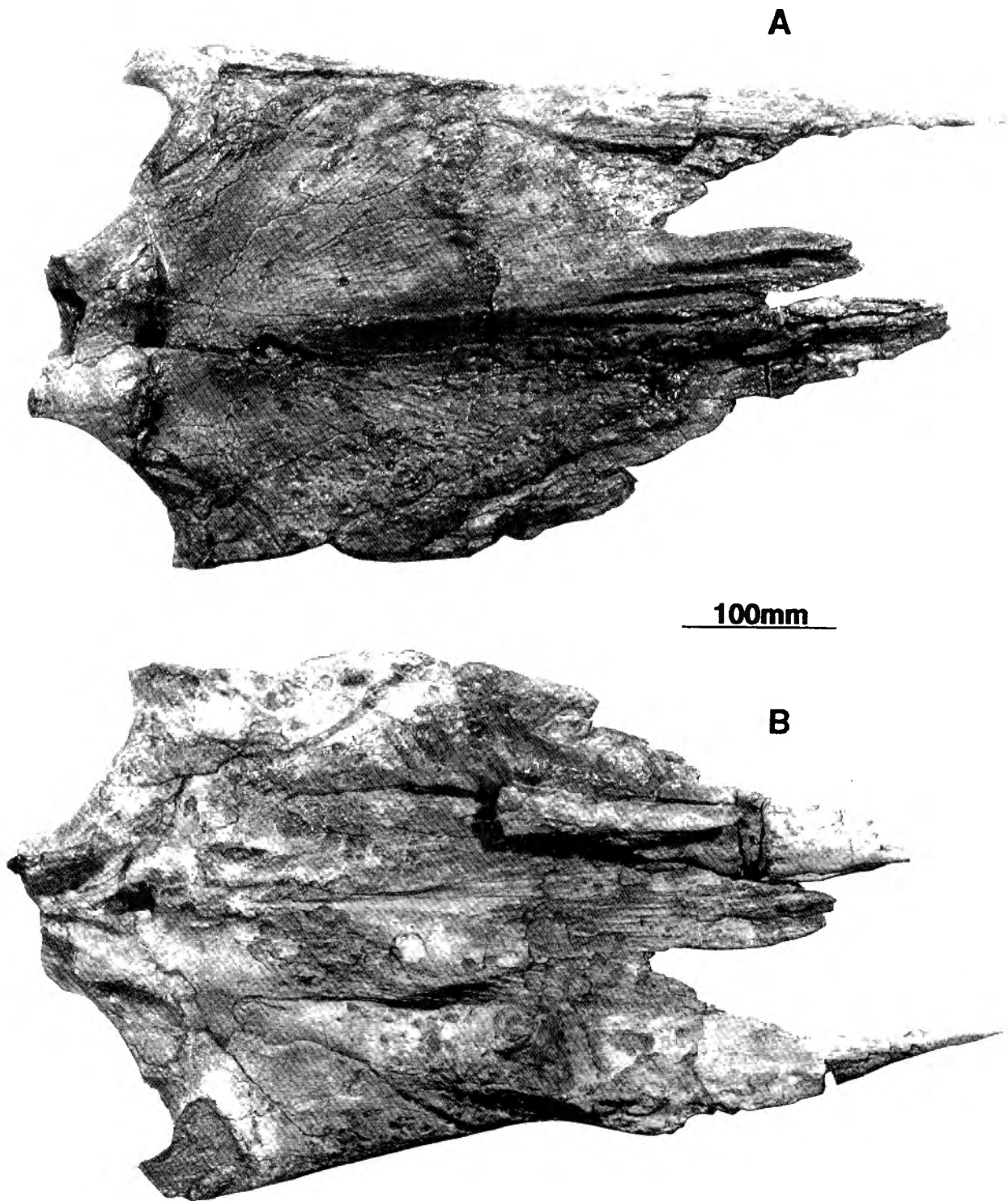


Fig. 7 — *Hainosaurus bernardi* (IRSNB R23) Frontal. A, dorsal view; B, ventral view.

BMNH 3625 (Fig.8) in which they are clearly paired and were either free or lightly sutured to the premaxilla. An apparently tighter fusion of the nasals to the premaxilla in IRSNB 3672 may be the result of preservation.

DISCUSSION

In lepidosauromorphs, nasals are almost uniformly pai-

red (ESTES *et al.*, 1988, p.143). Among squamates, *Lanthanotus* and *Varanus* have fused nasals and the condition also occurs in some chamaeleodontids, some gekkonids and pygopodids, some scolecophidians and some *Leptotyphlops* (ESTES *et al.* 1988, p. 143). ESTES *et al.* (1988, p.143) regarded nasal fusion as synapomorphies within various taxa. I have done likewise and

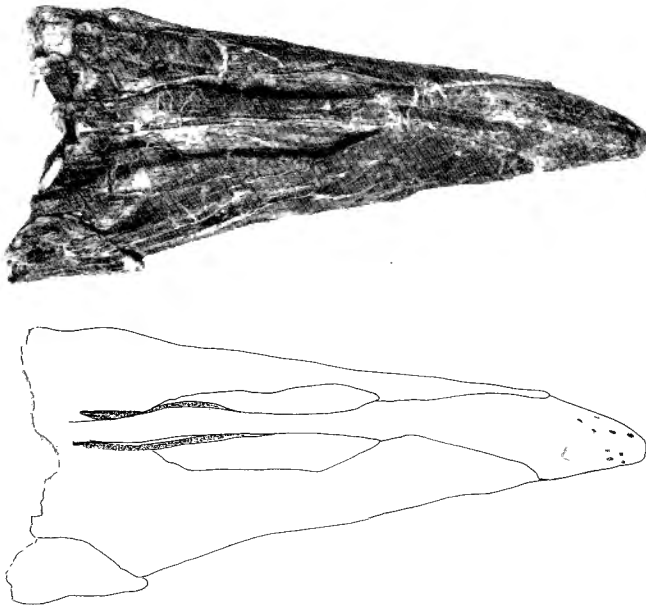


Fig. 8 — *Tylosaurus* (BMNH R3625) showing rarely observed nasals.

regard the presence of free nasals in the Tylosaurinae as a plesiomorphy of the subfamily and possibly of the Mosasauridae. The condition of paired nasals in at least the Tylosaurinae (unknown in other mosasaurs) and fused nasals in *Lanhanotus* and *Varanus* also serves to add to the dubiousness of MCDOWELL & BOGERT'S (1954, p.57) suggestion that the "precise affinities" of *Lanhanotus* are with "the aigialosaur-dolichosaur-mososaur complex rather than with the varanids or *Heloderma*". This view was also previously questioned on a number of other points in a powerful critique by UNDERWOOD (1957).

VOMERS

Relatively well preserved vomers are present in IRSNB 3672 (Pl. 3B, C). Distinct ligamentous surfaces, medially along most of the length of the vomers makes it clear that they were sutured to each at the cranial midline and free only at their anterior terminations. The Jacobson's organs extend from approximately the midpoint of the fourth to just past the fifth maxillary tooth. In *Tylosaurus* they lie opposite the fourth maxillary tooth (RUSSELL, 1967, p. 26). Judging from the shallow groove on the vomer the estimated size of the Jacobson's organ is approximately 76mm by 14mm. The lateral surface of the vomers reveals a large somewhat concave sutural surface anteriorly and a convex sutural surface posteriorly.

PARIETAL

The parietal is characteristically tylosaurine. The parietal foramen is small and of similar proportions to that of *Tylosaurus proriger*, situated on the fronto-parietal suture with perhaps a small part within the frontal.

RUSSELL (1967, p.172, fig.92) indicates that the parietal foramen in *T. proriger* is situated just posterior to the fronto-parietal suture whereas in *Tylosaurus nepaeolicus* it is set well into the parietal.

Descending wings of the parietal are preserved only in IRSNB 3672 where they are rather short.

OCCIPITAL UNIT

The occipital is very poorly preserved in the holotype but somewhat better preserved in IRSNB 3672 (Pl.4). The passage for cranial nerve VII is obscured by the large otosphenoidal crest. Unusually, for the Tylosaurinae, there appear to be two foramina for cranial nerves X, XI and XII. The basioccipital condyle is moderately large although both the basal tuber and basisphenoid are poorly developed.

PTERYGOID

The pterygoid in the holotype is poorly preserved but almost complete, forming approximately 44% of the skull length. The tooth row in the holotype which is probably complete supports nine to ten teeth. Despite the fragmentary nature of the pterygoids in IRSNB 3673 (Pl. 3E) the tooth counts confirm those of the holotype.

QUADRATE

The quadrate in the holotype is poorly preserved and distorted. The suprastapedial and infrastapedial processes are very small (Fig.9A, B, C). Medially the stapedial pit is a rather pinched vertical ellipse. In IRSNB 3672 (Fig.9D, E, F) the suprastapedial process is somewhat better preserved and despite absence of an apparently small fragment confirms the rather small size of the holotype. A fairly delicate tympanic ala indicates that the quadratic tympanum was rather thin. The basal condyle is convex and expanded from side to side.

DISCUSSION

The quadrate is essentially consistent with descriptions of this element in other members of the Tylosaurinae although the suprastapedial process appears somewhat larger in *Hainosaurus peminensis* and *Tylosaurus proriger* (RUSSELL, 1967). Generally in *H. peminensis* (judging from photographs, NICHOLLS, pers. comm.) it seems that the quadrate is more robust compared to the element in *H. bernardi*.

DENTARY

The dentaries in the holotype of *Hainosaurus bernardi* are very poorly preserved (Pl. 1A). The tooth row comprises 14 teeth either very poorly preserved or consisting solely of tooth bases. The dentaries in IRSNB 3672 (Fig. 5B) although rather fragmentary, have much better surface preservation. They are almost identical in shape to those of *Tylosaurus nepaeolicus* (RUSSELL, 1967, p.177, fig.95). The edentulous process anteriorly is as large with a similar, somewhat pinched crest almost at the dorsal termination of the bone. Ventral and dorsal margins of the bone are relatively straight in IRSNB

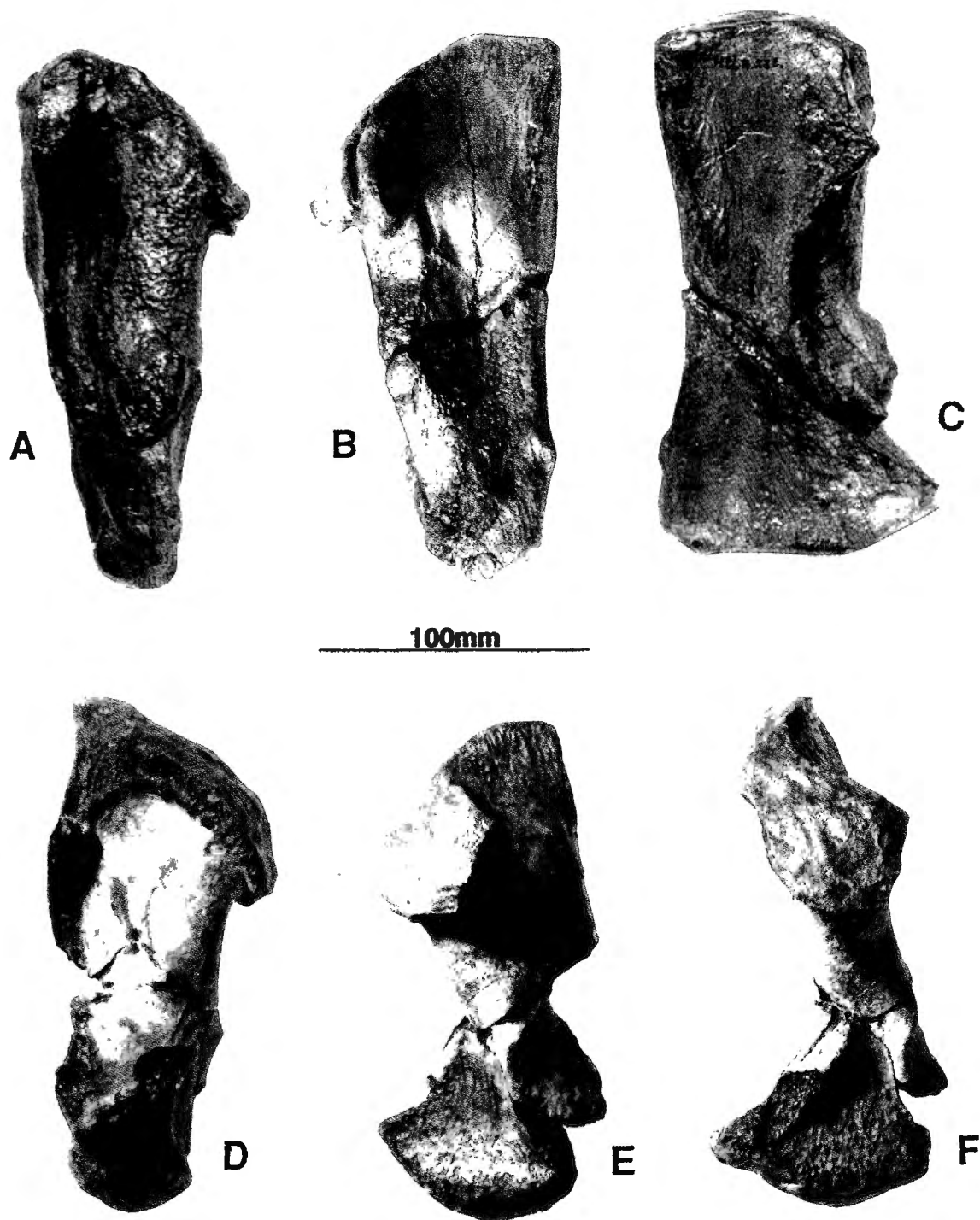


Fig. 9 — *Hainosaurus quadrates*. (IRSNB R23). A, lateral view; B, medial view; C, anterior view. IRSNB 3672. D, lateral view, E, medial view, F, posterior view.

3672. In the holotype the dorsal margin is apparently more concave (campylorhynchus of WILLISTON, 1898) a condition that may be accounted for by the larger size of this specimen. Poor preservation makes a description of the ventral border inconclusive. The mandibular foramina are large in IRSNB 3672 and extend along the length of the dentary at about the vertical midpoint of the bone.

In IRSNB 3672 the right and left dentaries held 13 teeth in each ramus although the left dentary gives the impression of 14 because of a large replacement tooth. There are just three moderately preserved teeth altogether, the fifth in both dentaries and the 13th in the right dentary. Each of the two anterior teeth have a single, sharp anterior carina. The posterior tooth possesses both anterior and posterior carinae. All the teeth show faint

facets. The best preserved teeth however, are in the French *Hainosaurus*, specimen MNHN 1896-15 (Pl. 3/51) in which the striae are clearly developed in both the buccal and lingual surfaces (described later).

DISCUSSION

It is clear that there are no significant differences in the dentaries of *Hainosaurus* and *Tylosaurus*. The somewhat stouter appearance of the dentary of *H. peminensis*, (NICHOLLS, pers. comm.) may be the result of gypsum swelling.

SPLENIAL

Fragments of the splenial are preserved in the holotype and IRSNB 3672 (Pl.3D). The articulation contacts are moderately deep excavations on the splenial and slightly tuberos on the angular.

SURANGULAR

The surangular is a rather expansive bone, characteristically cone shaped with the point posteriorly directed. It does not extend past the quadratic cotyle. Immediately in front of the glenoid articulation, a large foramen is present in IRSNB 3672. In the holotype, in contrast, this foramen is absent. The surangular fits into a recess in the articular, the latter bone is missing in IRSNB 3672. Deep striae on the anterior wall of the surangular and posterolateral wall of the dentary suggests the presence of a powerful ligamentous sheet attaching the two moieties of the jaw.

CORONOID

The coronoid is poorly preserved in the holotype. The right coronoid in IRSNB 3672 on the other hand is moderately well preserved. Compared with *Tylosaurus nepaeolicus*, for example, the coronoid eminence rises more sharply and the lateral wing is more substantially developed.

The coronoid is, however, relatively smaller than in most other mosasaurs with the exception of *Plioplatecarpus* (DOLLO, 1889).

ARTICULAR

The articular is a very robust, laterally compressed bone in the holotype of *Hainosaurus bernardi* and forms part of the excavation for the quadratic condyle.

VERTEBRAE AND RIBS

Descriptions are essentially as for *Tylosaurus* (RUSSELL, 1967, p.171 and herein Pls. 5 & 6)

SCAPULA AND CORACOID

The scapula and coracoid are as in *Tylosaurus* (RUSSELL, 1967) and are relatively the smallest in the Mosasauridae (Pl. 6; also see Fig. 13).

PADDLES

The paddles in *Hainosaurus* are characteristically tylosaurine showing the most reduced condition in the Mosasauridae (Fig.10).

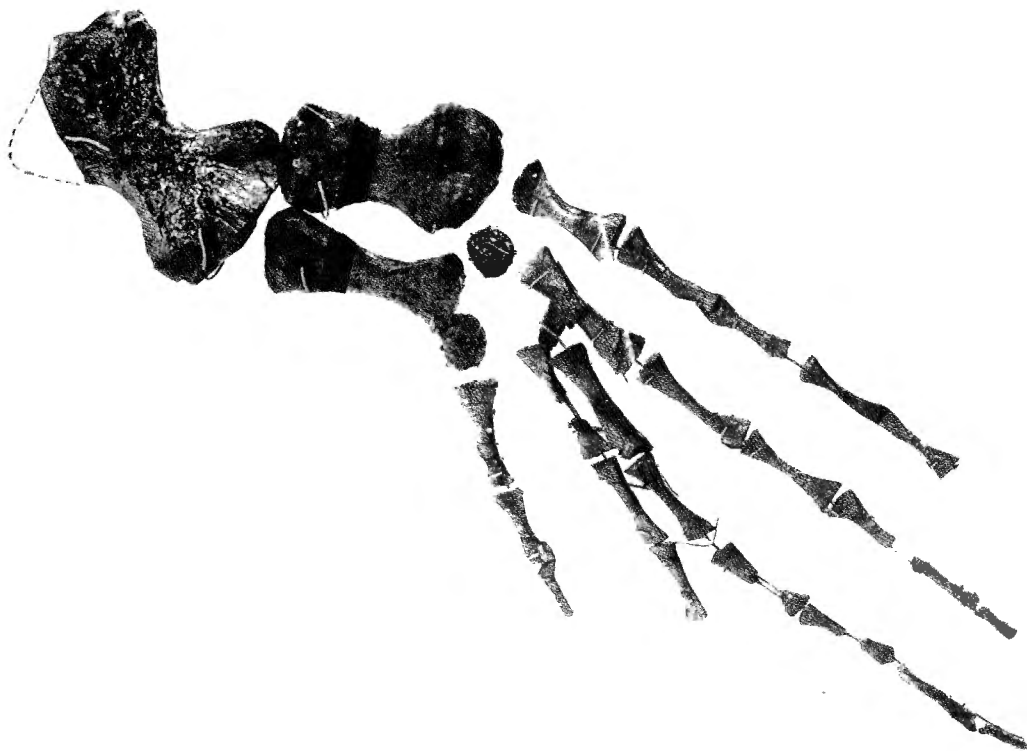


Fig. 10 — Attenuated paddle of *Hainosaurus bernardi*, (IRSNB R23)

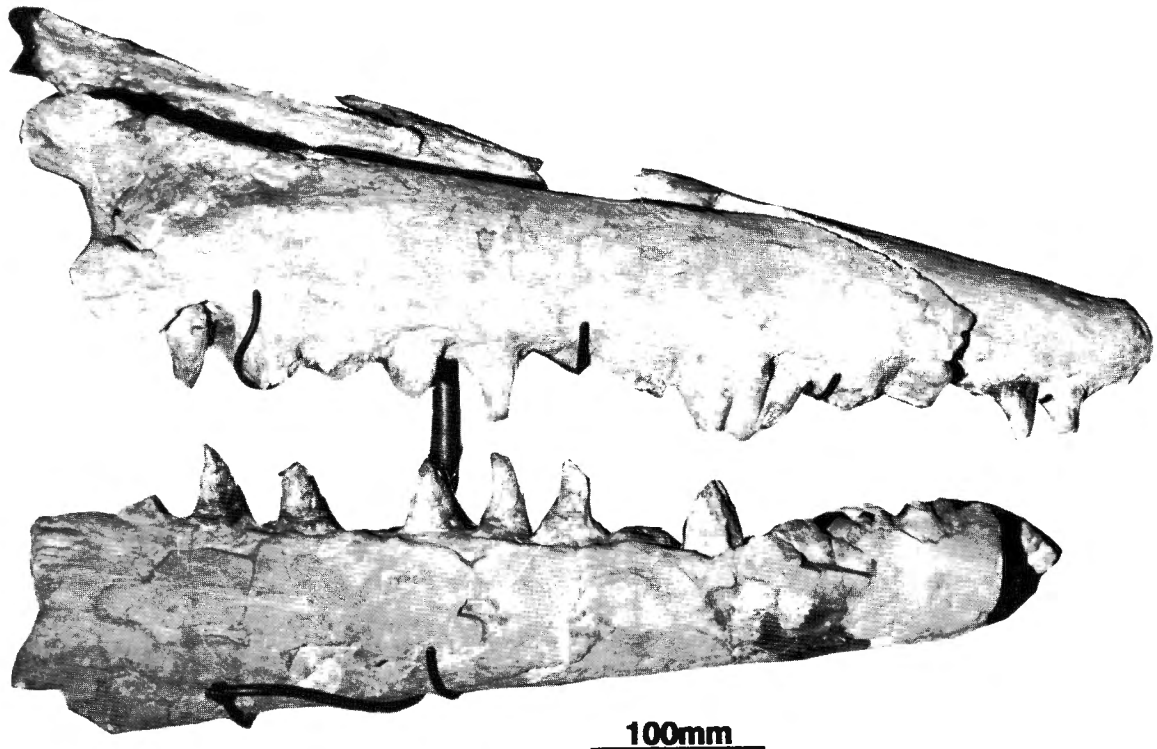


Fig. 11 — Anterior portion of the skull of *Hainosaurus gaudryi* (1896-15).

Hainosaurus gaudryi (THÉVENIN, 1896)
(Fig. 11, Pl. 7)

Mosasaurus gaudryi THEVENIN, 1896: 900.

Mosasaurus gaudryi SUZUKI, 1985: 51.

Hainosaurus bernardi BARDET, 1990: 752.

Generic type

Hainosaurus bernardi, DOLLO

HOLOTYPE

MNHN 1896-15. Partial skull, premaxilla, dentaries, maxillaries, frontal and partial parietal.

HORIZON AND LOCALITY

Phosphatic Chalk, Upper Santonian. Eclusier-Vaux near Péronne (Somme), France.

DIAGNOSIS

Relatively short premaxillary rostrum for the subfamily. Straight fronto-parietal suture. Parietal foramen situated some distance from the fronto-parietal suture.

DISCUSSION

In June, 1990, I reassigned *Mosasaurus gaudryi* MNHN 1896-15 to *Hainosaurus ?bernardi* on the basis of a character I had previously established for the genus, based on IRSNB R23 and 3672, the unique double buttressing of the premaxillary suture (evident in MNHN 1896-15 despite considerable abrasion; Fig.11). THÉVENIN

(1896, p. 903) had mistakenly considered that the slightly smaller (in tylosaurine terms) premaxillary rostrum was intermediate between the megarhynchus and mesorhynchus types of rostrum of DOLLO (1890, p.163) and consequently assigned the specimen to a new species of *Mosasaurus*. At the University of Paris VI, I also assigned to *Hainosaurus?* sp. vertebral material (USTL BUG, 2-28, SL, 1-10, JOU 5-12) on loan to Miss N. BARDET, which she presented to me for comment. This material from Sougraigne, in the department of Aude in France, had previously been assigned to *Platecarpus ictericus* (CORROY, 1927, SÉNESSE, 1936). Both determinations have subsequently appeared in print (BARDET, 1991). However, regarding specimen MNHN 1896-15, two important diagnostic characters indicate that it warrants recognition on the specific level - the fairly straight fronto-parietal suture and the location of the parietal foramen some distance from the fronto-parietal suture. In striking contrast in *H. bernardi* the postorbitofrontal wings on either side of the parietal foramen form rather deep invasions of the frontal forming an irregular fronto-parietal suture. Secondly the parietal foramen is situated on the fronto-parietal suture. The plesiomorphic states of a straight fronto-parietal suture and location of the parietal foramen well within the parietal were discussed previously by LINGHAM-SOLIAR & NOLF (1989). They also coincide with the early geological age of *H. gaudryi* MNHN 1896-15 when compared with *H. bernardi* IRSNB R23 and 3672.

In the American forms of *Tylosaurus* the location of the parietal foramen shows a similar distinction in the two species. In the earlier occurring *Tylosaurus nepaeolicus* the parietal foramen is situated some distance from the fronto-parietal suture while in the later form, *T. proriger* it is situated on the fronto-parietal suture (RUSSELL, 1967, p.174). This character seems to be highly consistent in earlier forms of mosasaurs (e.g. in the earliest member of the genus *Platecarpus bocagei*, LINGHAM-SOLIAR, in press b) and in itself is sufficiently diagnostic for specific recognition.

DENTITION

For the first time, specimen MNHN 1896-15 makes available relatively well preserved teeth for the genus *Hainosaurus*. The teeth are clearly robust as in *Tylosaurus*, cutting edges are not particularly pronounced, there is no ribbing of the carina, cross-sections are almost circular and the tooth crowns are deeply striated (Pl. 7A).

DISCUSSION

MERRIAM (1894, p.14) demonstrated that the teeth of *Leiodon* are smooth, resembling those of *Clidastes*, in contrast to striated labial crowns in *Tylosaurus*. Despite this, as I have already mentioned, DEPERET & RUSSO (1925) and PERSSON (1959) have both suggested such close similarities in the teeth of these two forms as to make them congeneric. Clearly the above description of the teeth in *Hainosaurus gaudryi* indicates that there is no resemblance between the teeth of *Hainosaurus* and *Leiodon anceps* whatsoever. Indeed a well preserved tooth in *H. peminensis* (NICHOLLS, 1988 pers. comm.) also demonstrates that it is quite unlike anything seen in *Leiodon* and more consistent with those of the *Tylosaurinae*.

Because of the fragmentary nature of the tylosaurine material described below, it is difficult to distinguish between *Tylosaurus* and *Hainosaurus* and the specimens are therefore tentatively referred to as *Tylosaurus*.

Tylosaurus MARSH, 1872

Leiodon in part, COPE, 1869-1870: 200

Rhinosaurus MARSH, 1872a: 461 (preoccupied, FISHER von WALDHEIM, 1847).

Rhamphosaurus COPE, 1872: 141 (preoccupied, FITZINGER, 1843)

Tylosaurus MARSH, 1872b: 147.

Generic type

Tylosaurus proriger (COPE, 1869).

DIAGNOSIS

(see RUSSELL, 1967, pp.171-173)

Tylosaurus capensis BROOM, 1912

Tylosaurus capensis BROOM, 1912: 332-333, pl.22.

HOLOTYPE

South African Museum SAMK5625. Consists of an almost complete frontal, anterior portion of parietals and portions of postorbitofrontals. Found in the Upper Cretaceous chalk of the Transkei (= Pondoland).

DIAGNOSIS

Large frontal lacking dorso-median crest, posterior margins relatively convex, small parietal foramen, some distance from fronto-parietal suture.

DISCUSSION

The distance of the parietal foramen from the fronto-parietal suture suggests that the specimen is probably closer related to *Tylosaurus nepaeolicus* than to *T. proriger*.

Tylosaurus iembeensis (TELLES-ANTUNES, 1964)

Mosasaurus iembeensis TELLES-ANTUNES, 1964, p.165, pls.23-25.

HOLOTYPE

S.G.M.A. specimen (no number, Universidade nova de Lisboa, Lisbon, Portugal). Poorly preserved, incomplete skull material consisting of portions of dentaries, posterior jaws, premaxilla, maxilla, pterygoid, quadrate and basioccipital.

HORIZON AND LOCALITY

Upper Cretaceous, Upper Turonian Chalk, "Camadas do Tadi" near the town of Iembe in Angola.

DIAGNOSIS

Distinct premaxillary rostrum although relatively smaller than in other members of the *Tylosaurinae*. Suprastapedial process of quadrate very short, infrastapedial process reduced, tympanum shallow, pinched stapedial pit. Robust dentary, rostrum present. Marginal teeth large, striated (not prismatic), subcircular cross-sections; twelve maxillary teeth, 13 dentary. Pterygoid teeth moderately large. Zygosphenes absent on cervical vertebrae.

DISCUSSION

The large size of the specimen combined with the characters in the above diagnosis indicate that the material is referable to *Tylosaurus*. These characters are inconsistent with those of *Mosasaurus hoffmanni* the only other known mosasaur of equal proportions. Its Upper Turonian age makes it the oldest member of the subfamily. The previously oldest *Tylosaurus* specimen came from the ?Coniacian of the U.S.A. It is quite probable that the relatively smaller rostrum may reflect an earlier evolutionary stage of this structure. Indeed the Santonian *Hainosaurus gaudryi* shows a relative size increase of the rostrum intermediate between *T. iembeensis* and *H. bernardi*.

Biomechanical implications of the skull structure and the lifestyle of hainosaurs and tylosaurs.

RUSSELL previously suggested that the massive rostrum in members of the Tylosaurinae was probably used as a ram in defence, or to stun prey (1967, p.69), comparable to the ramming behaviour in certain dolphins (WATSON, 1988; MARTIN & ROTHSCHILD 1989). However, such a prospect has not been examined further. While superficially the comparison with dolphins may be a good one, the problem involves two highly different types of skulls: a more or less solidly fused mammalian skull, and a reptile skull composed of numerous delicate and lightly sutured bones. Of prime consideration must be the fact that the impact on the skull during ramming would clearly have been enormous. The key structure I therefore looked at in tylosaurs and hainosaurs was the bone leading from the rostrum and premaxilla, the internarial bar, which is generally very slender and delicate in mosasaurs and sutured to a narrow anterior extension of the frontals between the external nares. In striking contrast, in the Tylosaurinae, it is unique in two ways: it is exceedingly robust and broad and arises from a wide rectangular base. Of further significance is the deeply interdigitated nature of the suture well within the frontal, that provides a large interfacial shear area, thus allowing the transfer of increased stress (Fig.12B). Hence there is greater resistance to forces such as bending, shearing and breaking. The significance of the highly modified internarial bar in tylosaurs and hainosaurs is of fundamental importance for absorption of

the initial shock waves to the head during ramming. A delicate bar sutured between the external nares, as in virtually all other mosasaurs, would simply have fractured or dislocated. Furthermore, location of the mosasaur brain in a robust bony case that formed a sliding joint with the skull roof at the posteriormost part of the exceedingly long skull was probably sufficient to cushion the brain from any severe shock. Further support for this hypothesis lies in the unique condition of a double locking suture between the premaxilla and maxilla in *Hainosaurus* (Fig. 12A) that presumably provided stability of the rostrum by a lock and key arrangement with the maxilla. This was enhanced by the large ventral projections from the premaxilla that acted as a strut between the maxilla and premaxilla.

The number of biomechanical changes in tylosaurine skulls tends to indicate rather convincingly the functional feasibility of the use of the rostrum in ramming. However, the possibility that it was used purely in sexual behaviour i.e. male-male combat as distinct from predation also needs consideration. THURMOND's (1969) study indicates that there was little variation in the size of the rostrum in *Tylosaurus* specimens which would imply that they were of generally similar size in males and females. It would thus be curious if a rostrum capable of use in combat between large male sexual rivals was not used, by clearly a voracious predator (see MARTIN & BJORK, 1987), in securing food (the situation is very different in e.g. deer rutting, primarily because they are herbivores).

Tylosaurs and hainosaurs were probably not the fastest of swimmers (sustained) in the Mosasauridae (for swimming in mosasaurs see LINGHAM SOLIAR, 1991a and in press a). This is indicated by, for instance, their rather poorly developed tail fins. However, there appears to have been a massive reduction in body weight in these forms. For instance pectoral and pelvic girdles, including the paddles, are highly reduced, relatively the smallest in the mosasaurs (Fig. 13). A further striking condition associated with weight reduction is indicated by WILLISTON's (1897) observation that the bones of *Tylosaurus* are highly cancellous and were probably impregnated in life, with fat, a condition that presumably increased buoyancy. This cannot just be accounted for by the large size of tylosaurines and need for enhanced buoyancy because an equally large or even larger mosasaur, *Mosasaurus hoffmanni* (paper in prep.), lacks highly cancellous bones. Such an apparently enormous weight loss suggests that tylosaurs and hainosaurs were evidently much more conservative in their energy requirements. Presumably this was useful for patrolling by stealth rather than by speed, over perhaps a fairly wide ranging area, moving from one ambush site to another. Sharks probably provide the best modern day analogue (WEBB, 1984). Furthermore the lower density probably assisted in rapid acceleration when prey was sighted, a condition WEBB & SKADSEN (1979) described in pike and tiger musky. Again, the long powerful tail of the tylosaurines was an ideal adaptation for burst

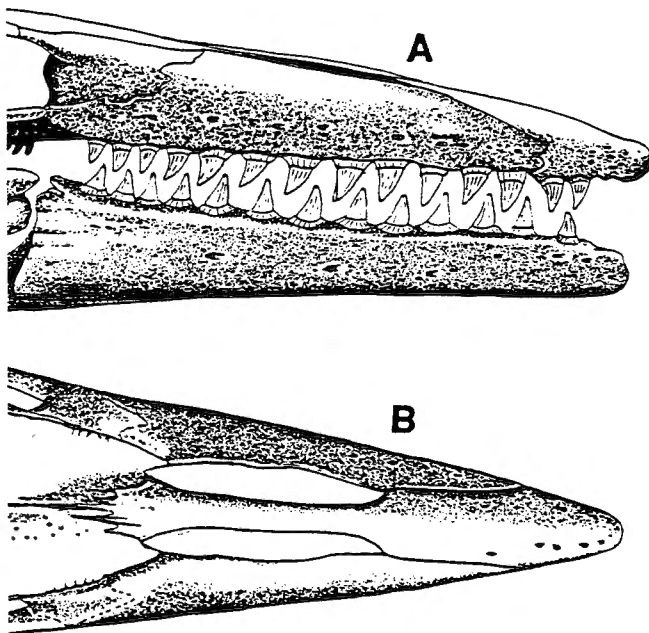


Fig. 12 Anterior portion of the skull of *Hainosaurus bernardi* (IRSNB 3672). A, lateral view; B, dorsal view.

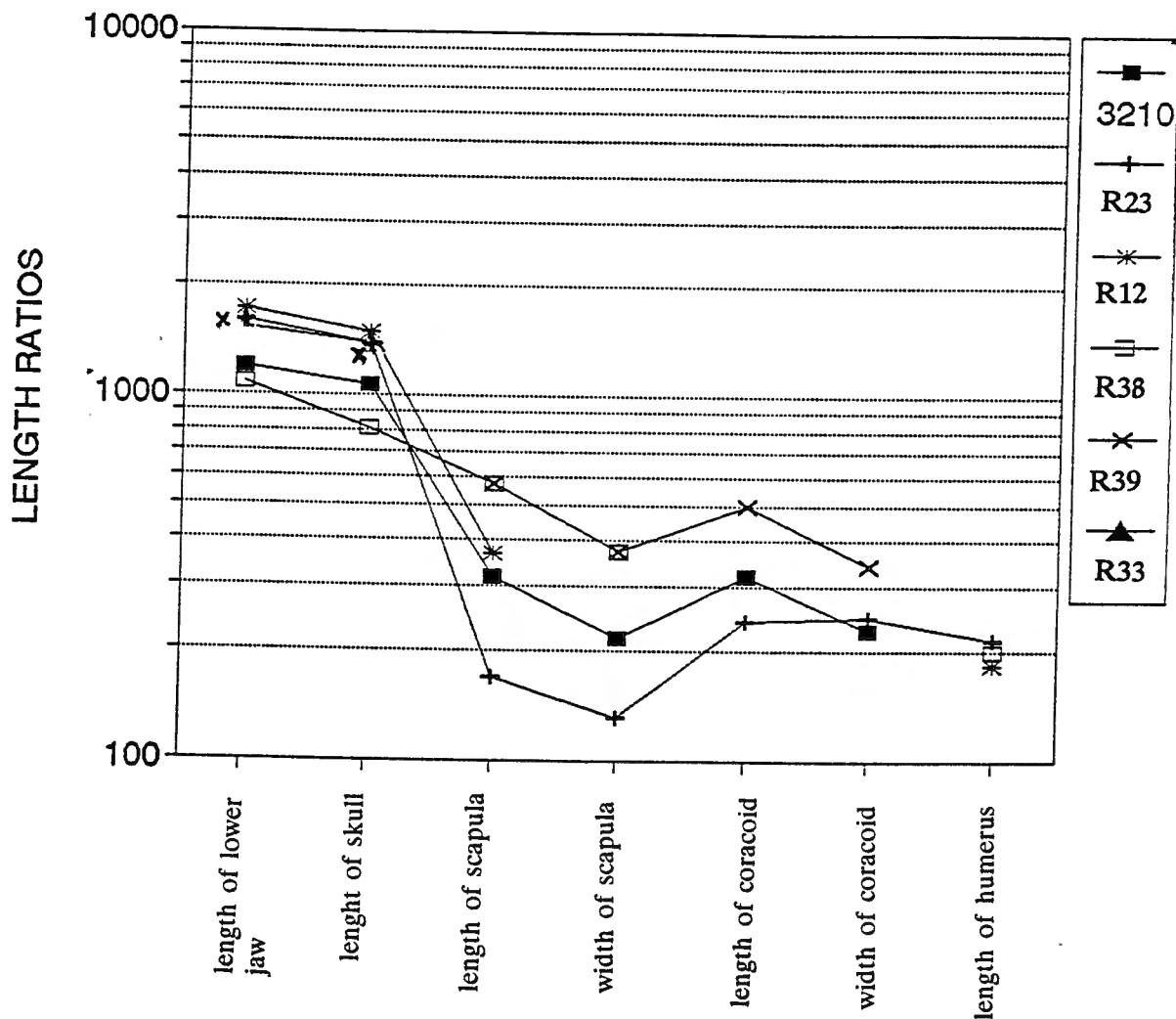


Fig. 13 — Log graph of cranial and postcranial ratios in four mosasaur taxa, *Mosasaurus lemonnieri* (IRSNB 3120), *Hainosaurus bernardi* (IRSNB R23), *Mosasaurus hoffmanni* (IRSNB R12), *Plioplatecarpus marshi* (IRSNB R39 & R38).

speeds, as seen in crocodiles (MASSARE, 1988; LINGHAM-SOLIAR, 1991a). This in combination with a large solid rostrum provided the potential for a powerful blow that may have killed or stunned the prey.

I am not convinced that hainosaurs and tylosaurs were deep divers as postulated by MARTIN & ROTH-SCHILD (1989), certainly not in the way that many whales are. There is no evidence in mosasaurs for the enormous morphological and physiological changes connected with deep diving that are seen for instance in sperm whales. On the other hand dives of up to approximately 50 m seems more conceivable. Such depths are at any rate sufficient to produce problems such as the bends and would not invalidate MARTIN & ROTH-

SCHILD's (1989) theory that certain necrotic vertebrae in for example *Tylosaurus* were caused by this phenomena. While as they suggest, squid was probably part of the diet of the tylosaurs and hainosaurs it seems probable that they were more pelagic forms. Large size of tylosaurs and an ambush form of predation would clearly favour a much more mixed diet (LINGHAM-SOLIAR, 1991c). This is in fact supported by MARTIN & BJORK's (1987) record of the gastric contents of a *Tylosaurus* specimen in the South Dakota School of Mines that shows a rather awesome and varied diet consisting of part of a small mosasaur (confirmation of cannibalism first intimated by RUSSELL, 1967), the marine teleost *Bananogmius*, a shark, and part of the Cretaceous

diving bird *Hesperornis*. There is also record of turtle bones in the gut cavity of *Hainosaurus bernardi* (DOLLO, 1891).

Concluding remarks

The main distinction between *Hainosaurus peminensis* and *Tylosaurus* and similarity with *H. bernardi* appears to be in the larger number of precaudal vertebrae in the genus *Hainosaurus*. I must point out though that *H. peminensis* lacks some of the diagnostic characters of the European *Hainosaurus*, for instance the double but tressed premaxillary/maxillary suture (NICHOLLS, pers. comm.) and prefrontal that forms part of the external

border. I feel it necessary to add that a variation in presacral vertebral numbers particularly in the pygal region is not uncommon to the same species. I have noted this in specimens of *Mosasaurus lemonnieri* (in which there are a number of postcranial skeletons) where the pygal number may be anything between 12 and 22. Because of such differences it is important that the large quantities of tylosaurine material in particularly in the U.S.A., are examined closely.

Acknowledgements

I would like to express my thanks to M. Benton (Bristol) and D. Russell (Ottawa) for reviewing this manuscript.

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Typescript submitted: Sept. 15, 1991
 Corrected typescript accepted: Dec. 20, 1991

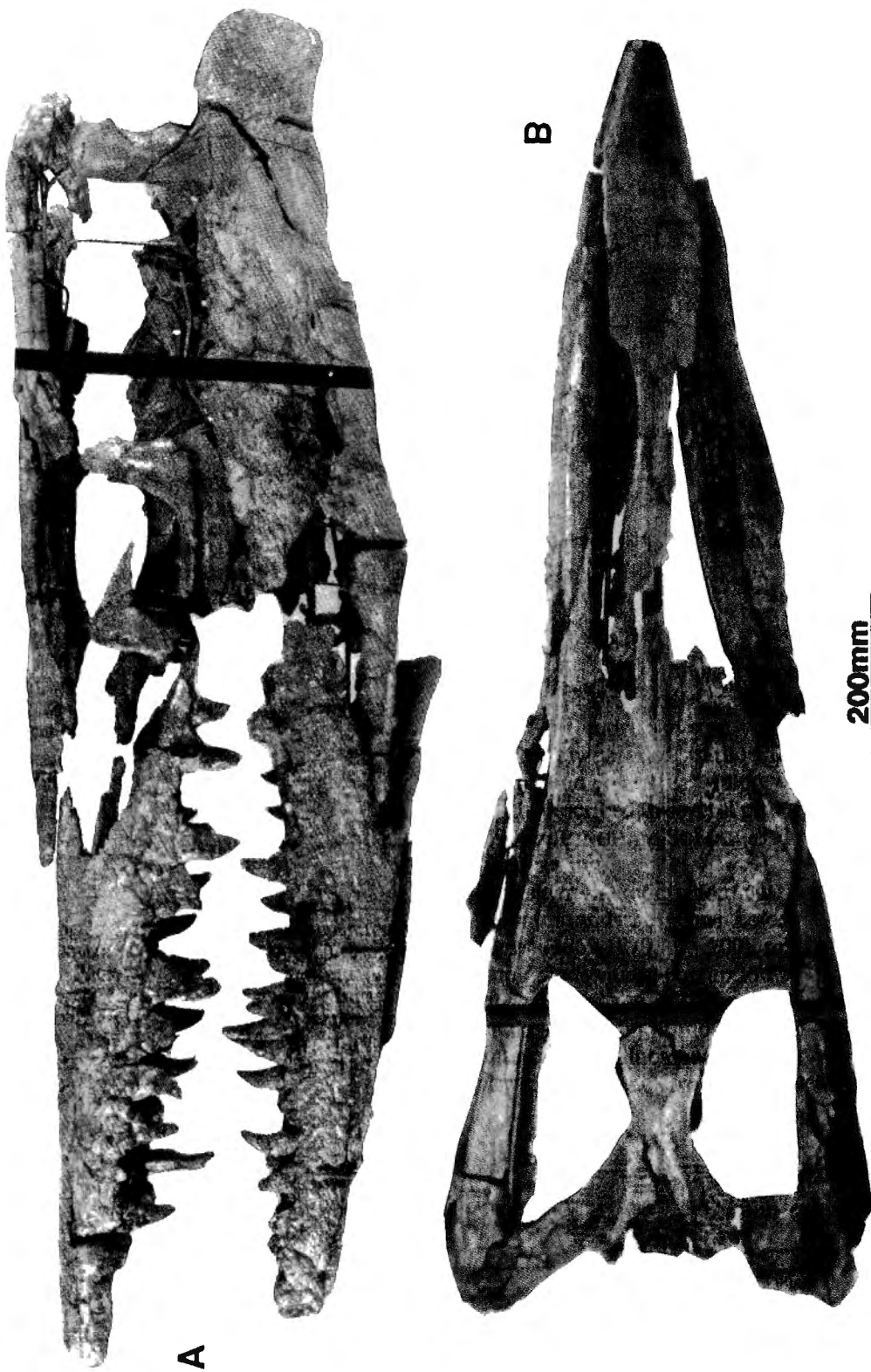


PLATE 1

Hainosaurus bernardi (IRSNB 1564). A, left lateral view; B, dorsal view.

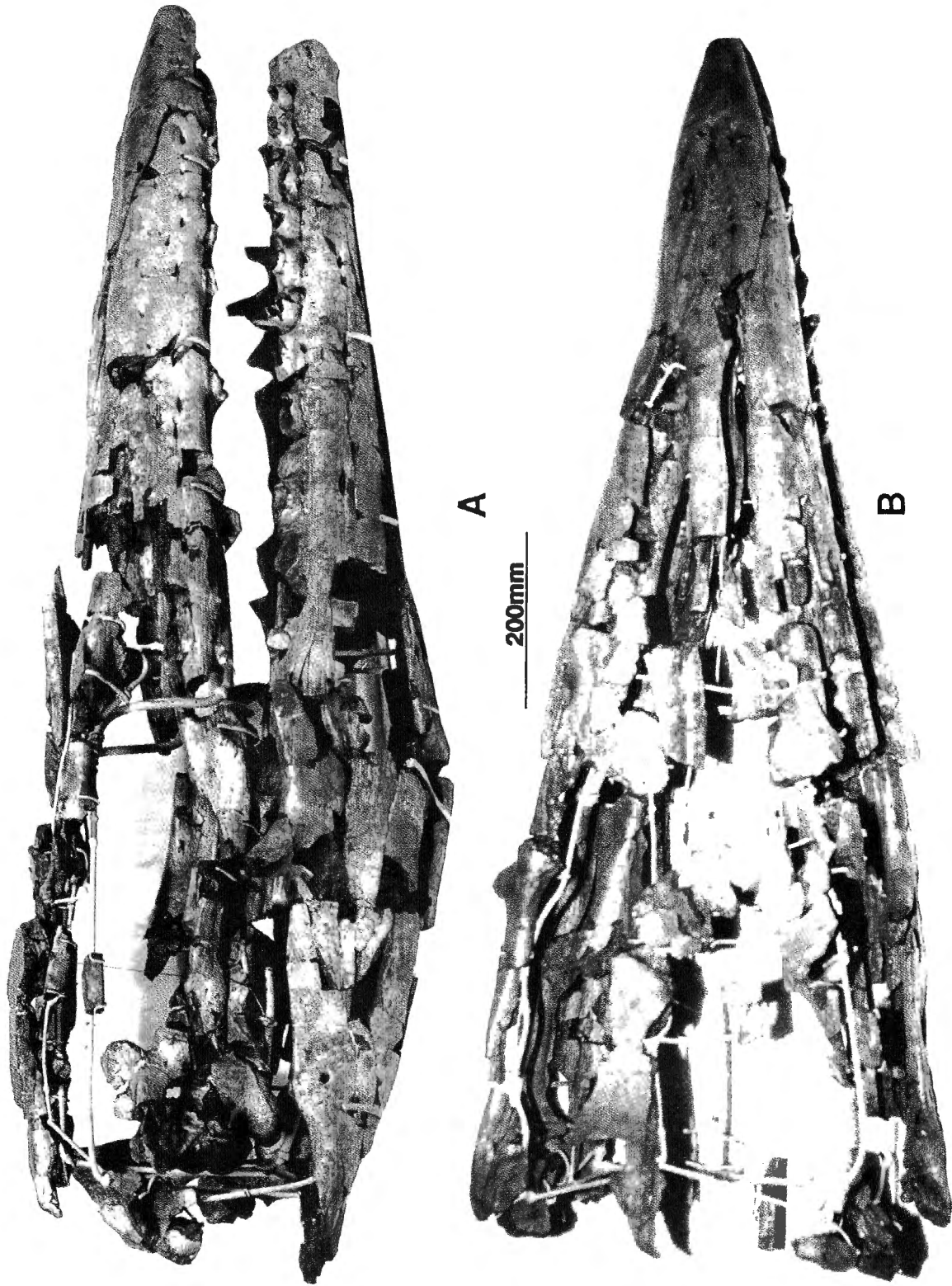
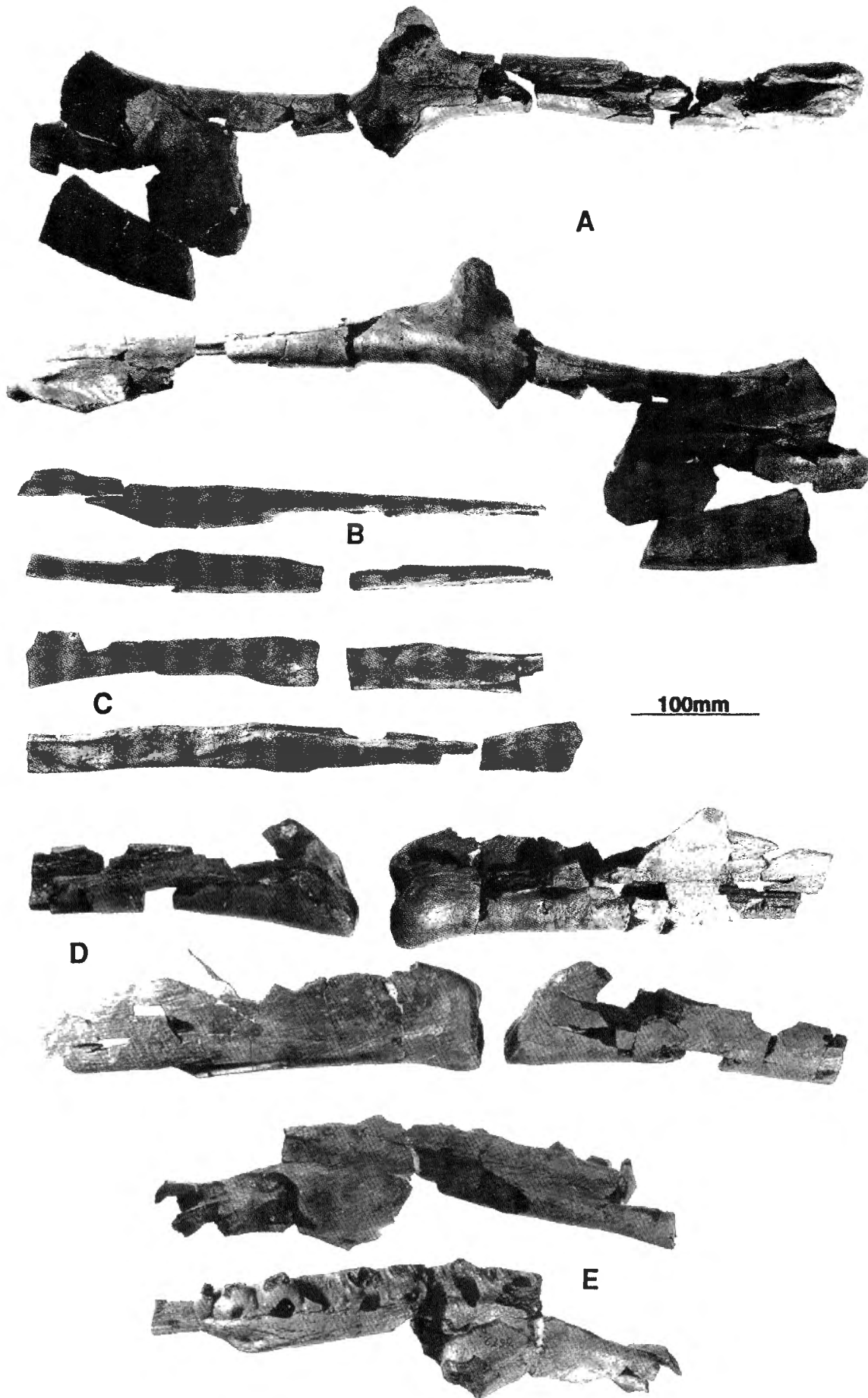


PLATE 2

Hainosaurus bernardi (IRSNB 3672). A, right lateral view of skull; B, dorsal view.

PLATE 3

Hainosaurus bernardi (IRSNB 3672). A: ventral and dorsal views of POF and portion of squamosal; B, dorsal view of vomers; C, ventral view of vomers; D, medial and lateral views of splenio angular articulation; E, dorsal and ventral views of pterygoid. →



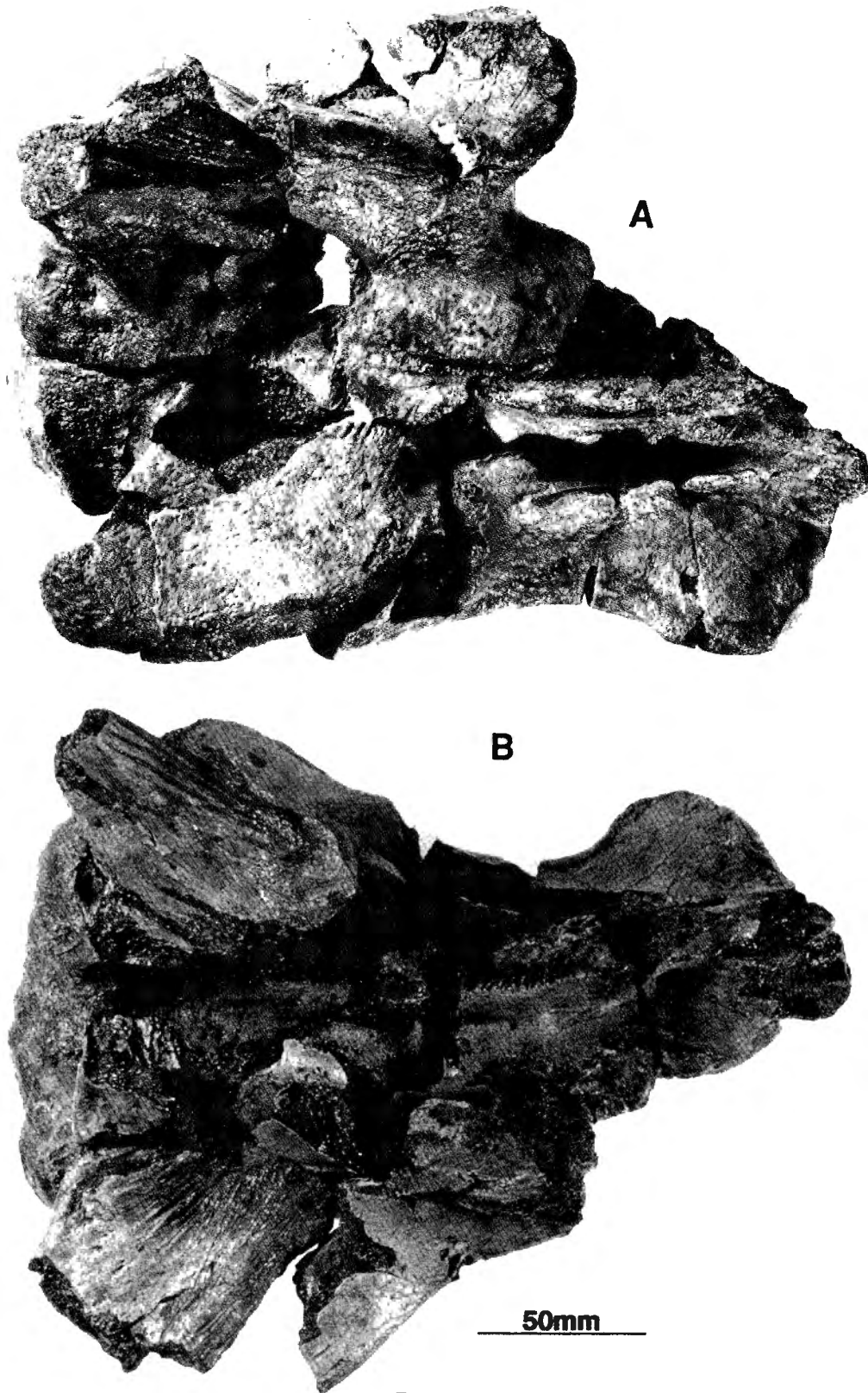
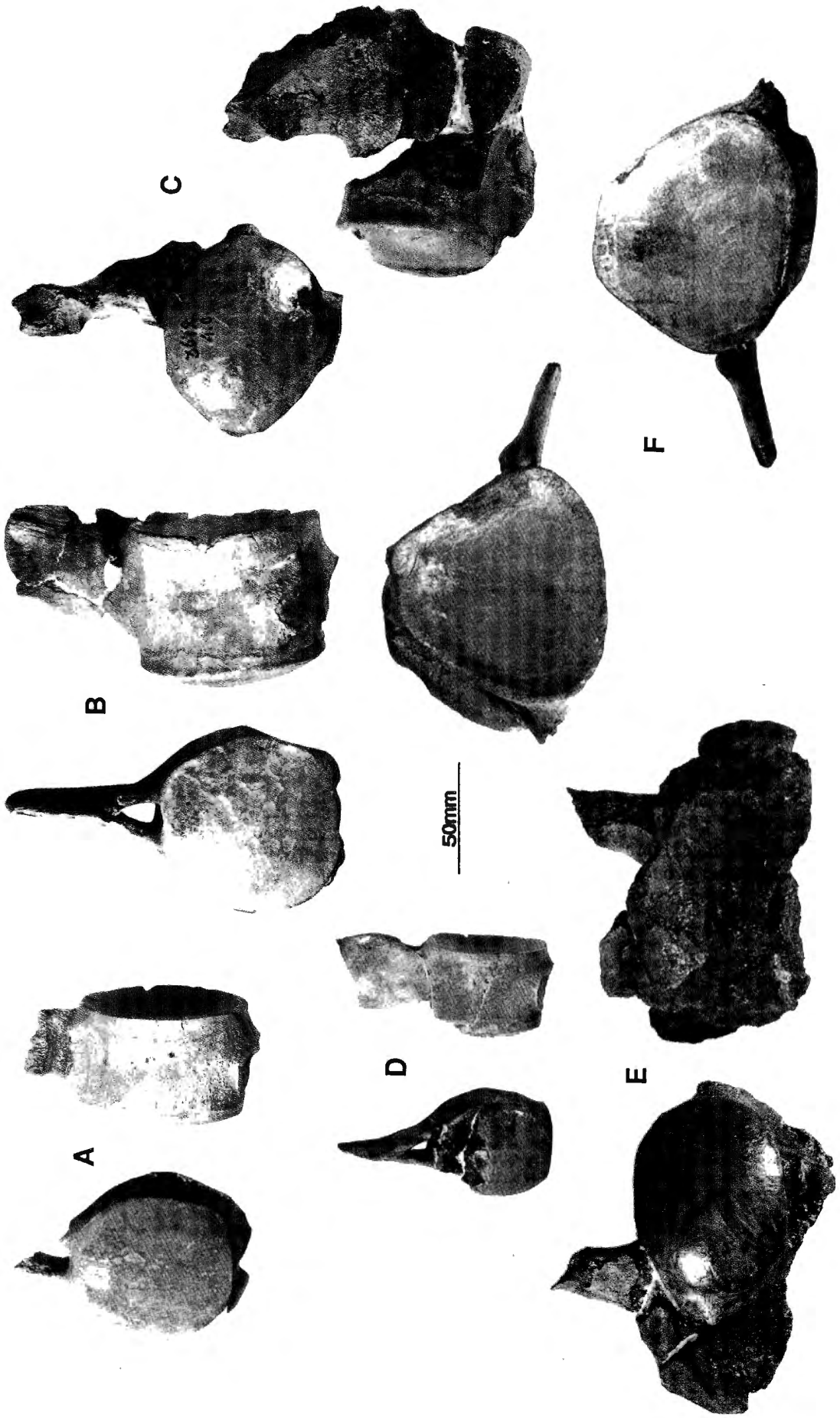


PLATE 4

Hainosaurus bernardi (IRSNB 3672). Basioccipital. A, right lateral view; B, dorsal view.

PLATE 5

Hainosaurus bernardi (IRSNB 3672). Vertebrae. Caudals. A, B, posterior and lateral views. Cervicals. C, posterior and lateral views. Posterior caudal. D, posterior and lateral views. Axis. E, posterior and lateral views. Pygal. F, posterior and anterior views. →



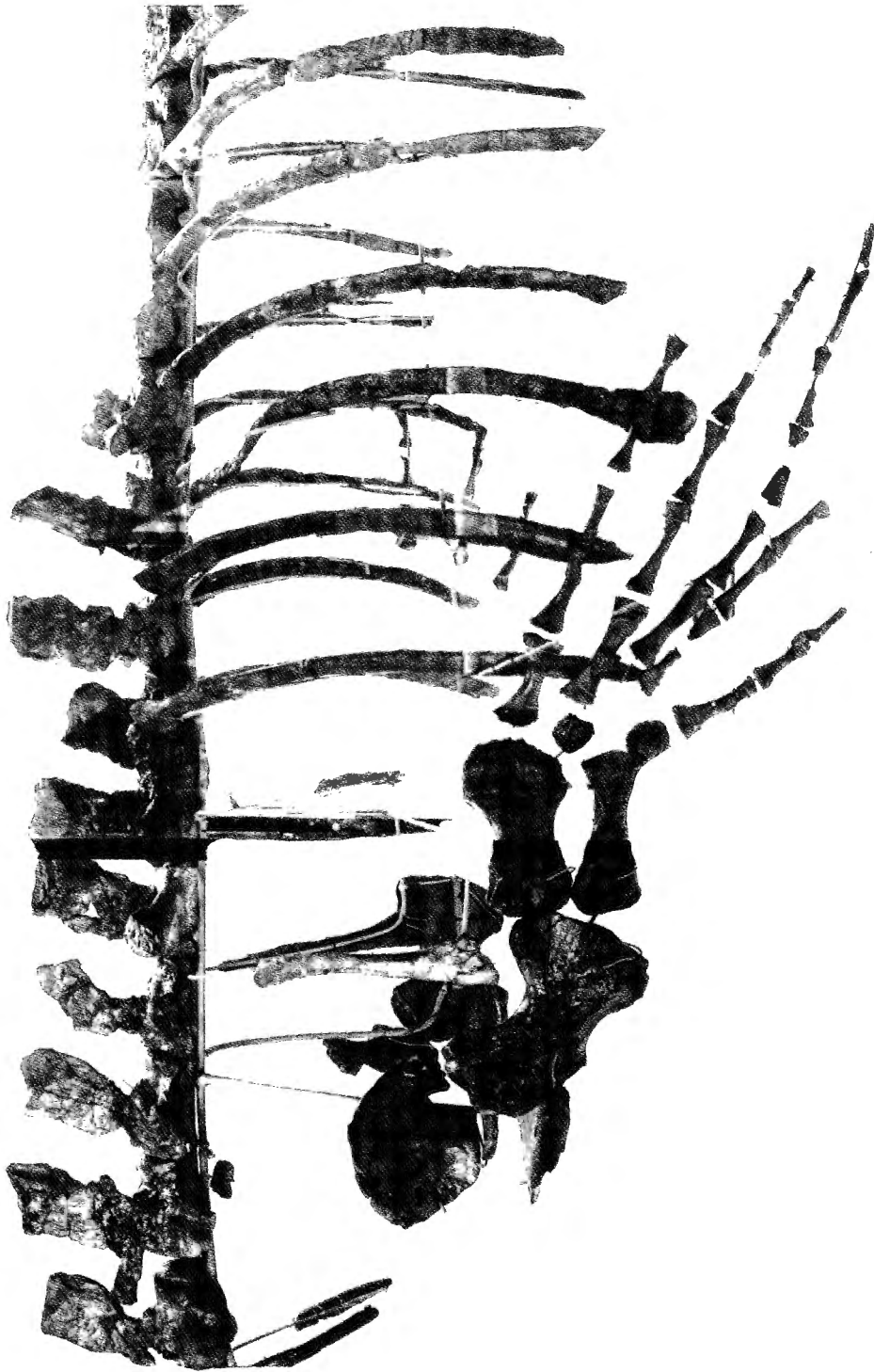


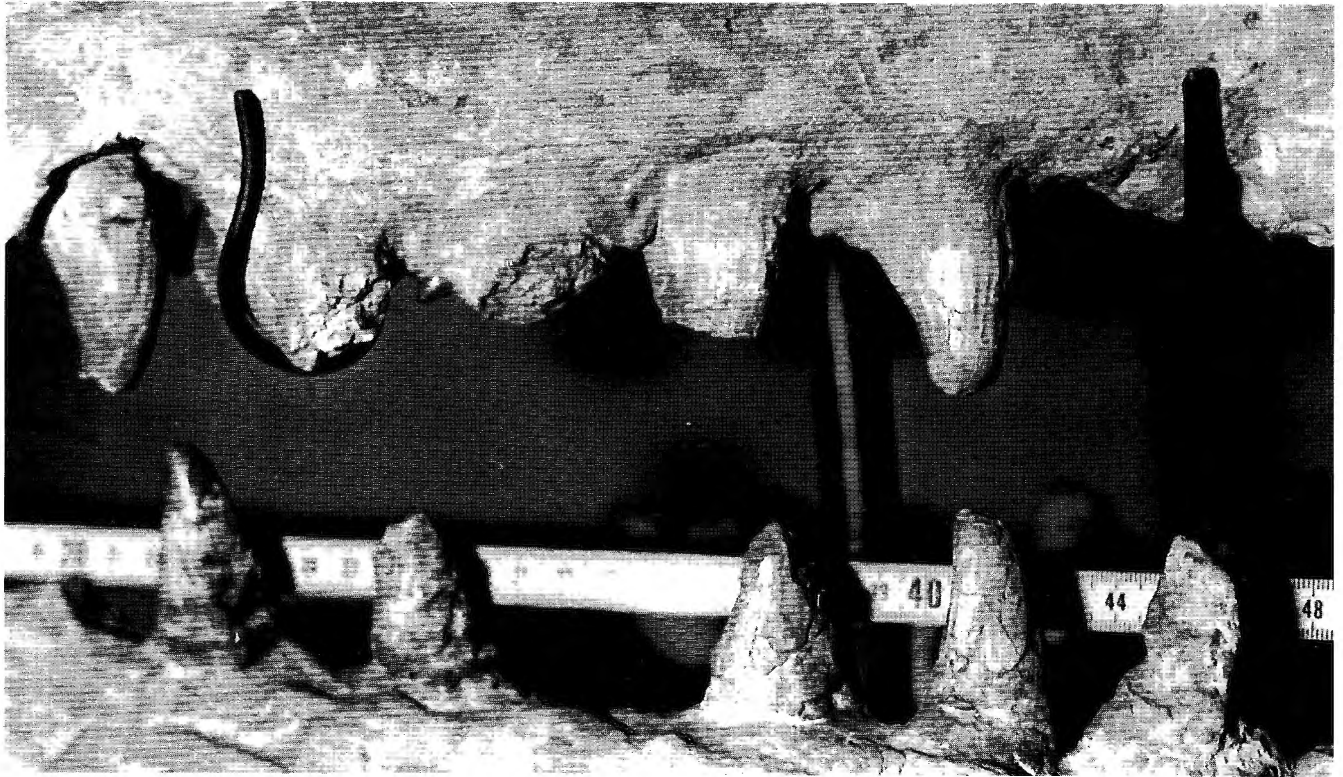
PLATE 6

Cervical and thoracic region of *Hainosaurus bernardi* (IRSNB R23) showing vertebrae, ribs, scapula, coracoid and paddle.

PLATE 7

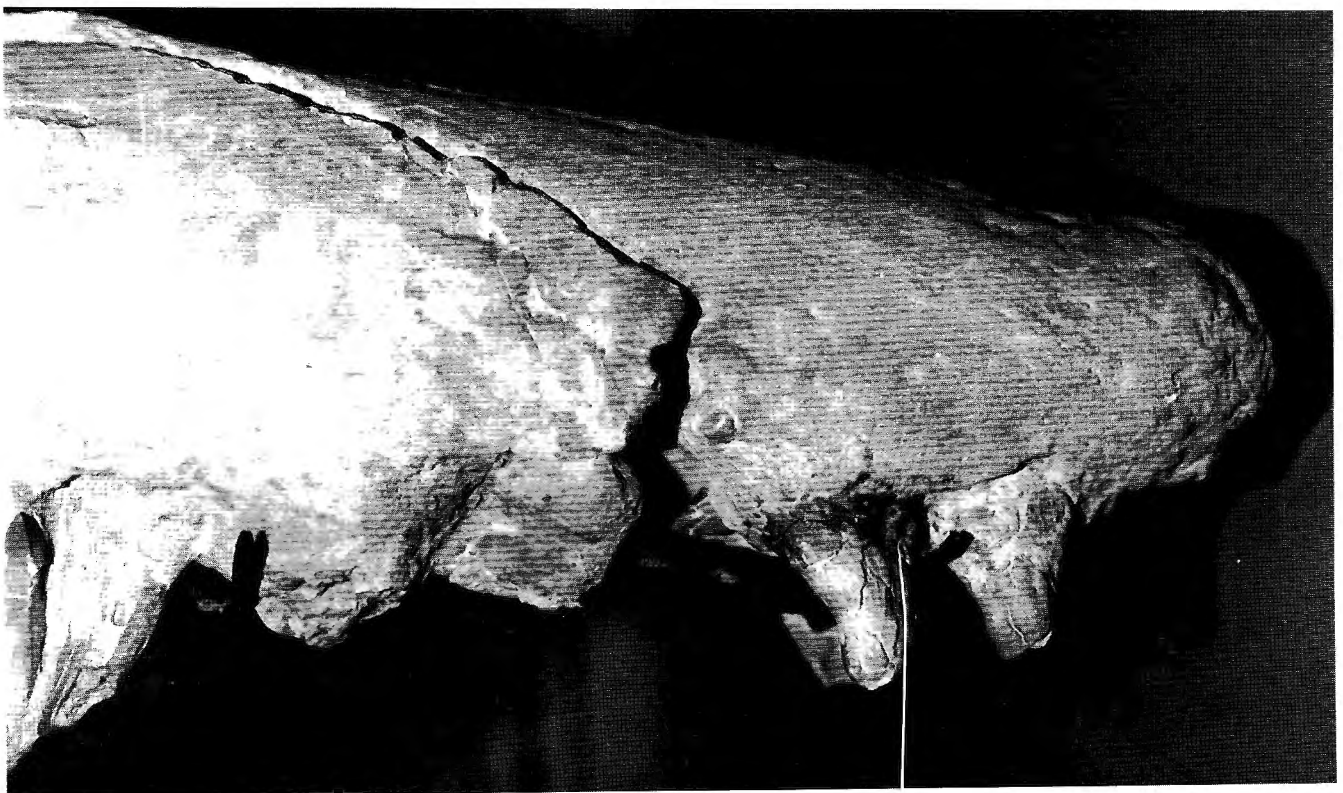
Hainosaurus bernardi (MNHN 1896-15) (= *Mosasaurus gaudryi*, Thevenin, 1896). A, detail of maxilla and dentary showing striae on teeth; B, double buttressing of the premaxillary/maxillary suture evident despite erosion. ➡

A



B

50mm



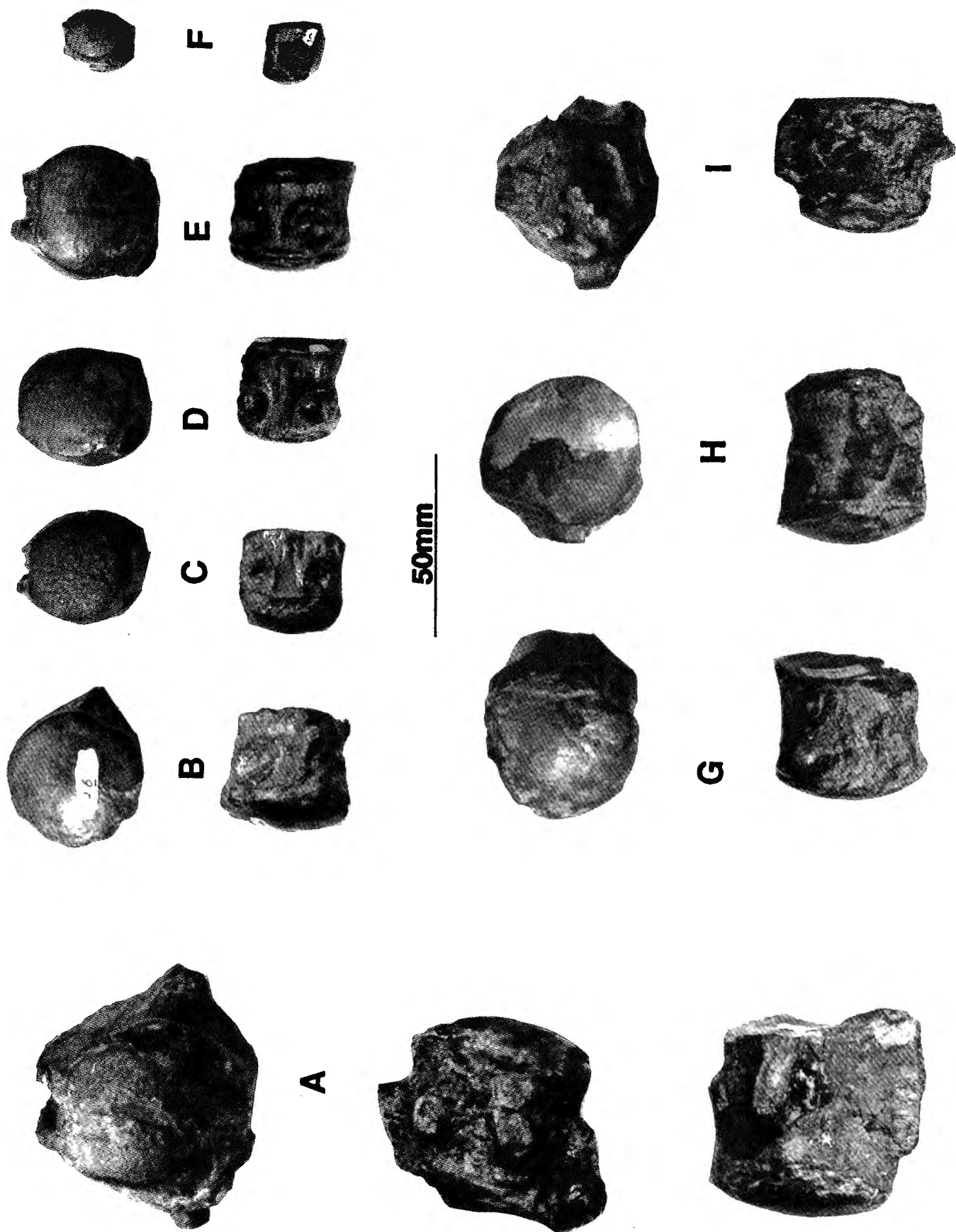


PLATE 8

Hainosaurus sp. (USTL BUG 2-28, SL 1-10, Jou 5-12). Vertebrae. Caudals.