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# Anatomy and functional morphology of the largest marine reptile known, *Mosasaurus hoffmanni* (Mosasauridae, Reptilia) from the Upper Cretaceous, Upper Maastrichtian of The Netherlands

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## SUMMARY

*Mosasaurus hoffmanni*, one of the latest known mosasaurs, comes from the Upper Maastrichtian, Upper Cretaceous Chalk of The Netherlands. Although the first specimen was discovered over 200 years ago, it is here fully described for the first time to provide detailed insights into its anatomy, functional morphology and evolution. Many characters of the skull show that *M. hoffmanni* was among the most advanced mosasaurs. The skull is robustly constructed and is the least kinetic in the Mosasauridae and, with a tightly assembled palatal complex, provided greater cranial stability in this large-headed mosasaur. The cranial musculature is highly modified. The four-bar linkage system of lizards and early mosasaurs is non-functional in *M. hoffmanni*. The elements of the lower jaw are also more tightly united than in other mosasaurs.

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Tooth crowns are divided into several distinct, unique cutting surfaces or prisms. A functional analysis of the marginal teeth shows that they are particularly adapted to powerful bite forces although pterygoidal teeth are small and reduced in importance in ratchet feeding.

Moderately large orbits and poorly developed olfactory organs suggest that *Mosasaurus hoffmanni* was a surface-swimming animal. A relatively lower level of binocular vision than in some other mosasaurs may indicate a somewhat uncomplicated habitat. Geological and palaeontological evidence indicates that *M. hoffmanni* lived in fairly deep nearshore waters of 40–50 m depth, with changing temperatures and rich vertebrate and invertebrate life. Several severely broken and healed mandibles suggest either a violent lifestyle in predation or in fighting.

## 1. INTRODUCTION

Mosasaurs were marine varanoid reptiles known exclusively from the Upper Cretaceous deposits. They spread rapidly throughout the major oceans of the world in a geologically brief period of 25–30 Ma during which time they evolved to great size. Although *Hainosaurus bernardi* (Lingham-Soliar 1992*a*), at approximately 15 m, is usually regarded as the largest mosasaur, an enormous almost complete dentary of *Mosasaurus hoffmanni*, NHMM 009002 (Meijer 1983, figure 3) measuring 900 mm (complete estimate = 1000 mm), suggests an even greater total size. The entire lower jaw is reliably estimated at 1600 mm. Using a 1:10 head to body ratio (see Russell 1967, p. 210 for *M. maximus*) the length of the whole animal is estimated at 17.6 m, making it the largest marine reptile known. Huge size in *M. hoffmanni* is also indicated by isolated specimens of an enormous quadrate NHMM 603092 and humerus TSMHN 11252 (figure 9*i*, *j*).

Remains of mosasaurs are found on all continents including Antarctica (e.g. Chatterjee *et al.* 1985). They make their appearance as fully fledged marine forms during the Early–Middle Turonian (Lingham-Soliar 1994*b*). The only alleged Cenomanian material (Russell 1967) proves, from a microfaunal analysis, to be Mid–Late Turonian in age (J. Young & J. Burnett, personal communication 1991). This abrupt appearance of mosasaurs presents problems regarding their ancestry (e.g. see Carroll & deBraga 1992). Mosasaurs disappeared suddenly 65 Ma ago.

The first jaw bones of *Mosasaurus hoffmanni* were found in 1766 in St. Pieter's Mountain, Maastricht, The Netherlands (Van Regteren Altena 1956). However, in 1780, in the same vicinity, a more sensational discovery followed, that of the better preserved, incomplete skull (~ 1.2 m long) of the 'Grand animal de Maestricht' (figure 1). The early literature, including the first record in the Transactions of the Royal Society (Camper 1786), was primarily concerned with its identity (later named *Mosasaurus* by Conybeare in 1822). The emphasis has since focused on its chequered history, which includes capture by Napoleon Bonaparte's army in 1795, and removal to Paris (e.g. see Russell 1967).

Most investigators of the time believed that the skull was crocodilian (e.g. Faujas de Saint-Fond 1799) although Pieter Camper (1786) was convinced that it belonged to a whale. Nevertheless, he correctly pointed out many characters that were not consistent with those of crocodiles. He was, however, unable to correctly place two (typically mosasaurian) characters: anteriorly concave and posteriorly convex vertebral articulations and the formation of succeeding teeth posteromedially within the bony substance of the mature teeth.

The true identity of the skull was left to Adriaan Gilles Camper (1800), Pieter Camper's son, who demonstrated that the fossil was neither a crocodile nor a whale but a giant lizard closely related to *Varanus niloticus* (A. G. Camper's *Lacerta dracaena*). (The lizard status of mosasaurs was first communicated by A. G. Camper in letters to Cuvier in 1790 and 1791 and followed in several later publications (e.g. 1812)). His identification was based on the following characters: (i) presence of hypapophyses on the cervical vertebrae; (ii) lower jaw composed of many elements; (iii) jaws joined by a ligamentous symphysis anteriorly; (iv) articulation between dentary and posterior jaw; (v) opening for the chorda tympani on the posterior extremity of the lower jaw; (vi) presence of pterygoidal teeth; (vii) external nares on the anterior snout (they lie between the eyes in for instance whales and porpoises); (viii), (ix) and (x), Pieter Camper's two incorrectly placed characters mentioned above.

Although Baron Georges Cuvier is widely regarded as responsible for identifying the 'Grand animal de Maestricht' as a lizard (e.g. Buffetaut 1987), it was clearly axiomatic in view of A. G. Campers earlier findings. However, because Cuvier's (1824, 1834–1836, p. 165) study is better known, his description of twelve hypapophysis-bearing cervicals, in contrast to A. G. Camper's (1800) six (the usual number in mosasaurs), is an error that has caused confusion since (e.g. in Russell 1967, p. 140). It is, however, clear from Cuvier's (1808, 1824, 1834–1836) accounts that he had not seen the vertebral specimen himself and that his cervical vertebral number had been derived from A. G. Camper's figure (1800, plate 20). In my view, the inclination of the vertebral section caused Cuvier to mistake the left transverse processes, outlined against the ventral surfaces of the vertebrae, for hypapophyses. I recently confirmed the presence of just six hypapophysis-bearing cervical vertebrae in A. G. Camper's original material, TSMHN 11209, although in any case the specimen is referable to *Plioplatecarpus* not *M. hoffmanni.*

*Mosasaurus hoffmanni* is one of the most advanced mosasaurs known. Because of its enormous size, certain biomechanical advances are seen for the first time in mosasaurs. This paper has three main objectives: (i) a

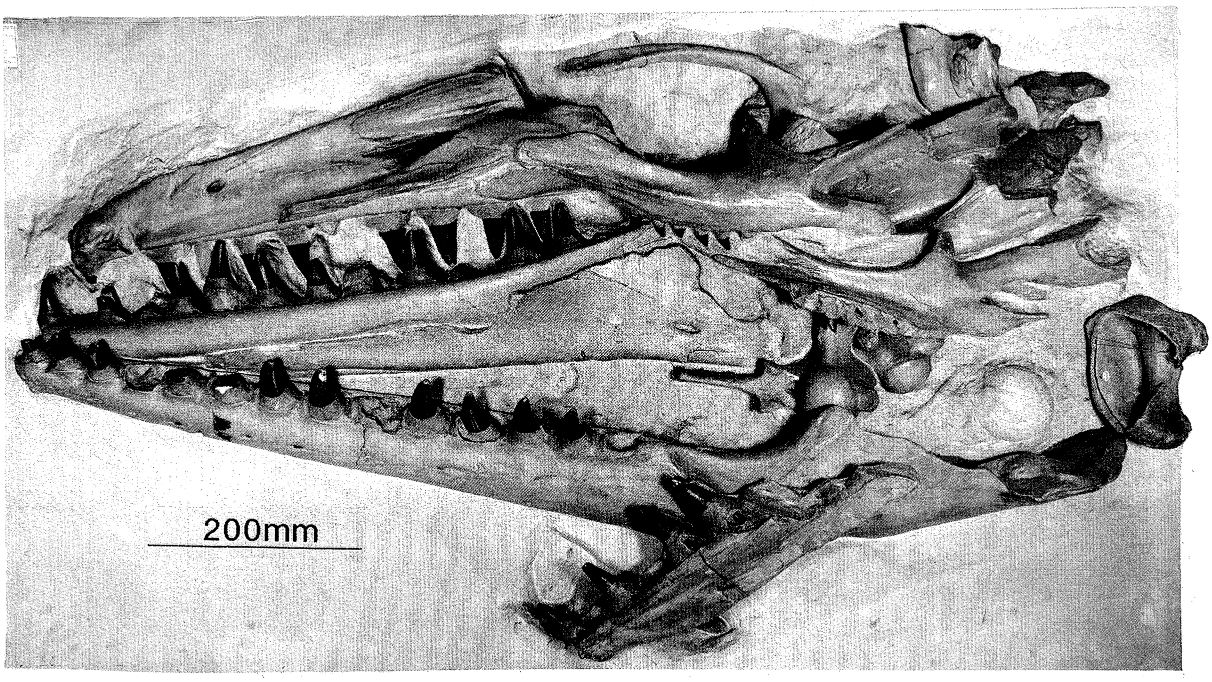


Figure 1. Cast of the holotype of *Mosasaurus hoffmanni* BMNH 11589.

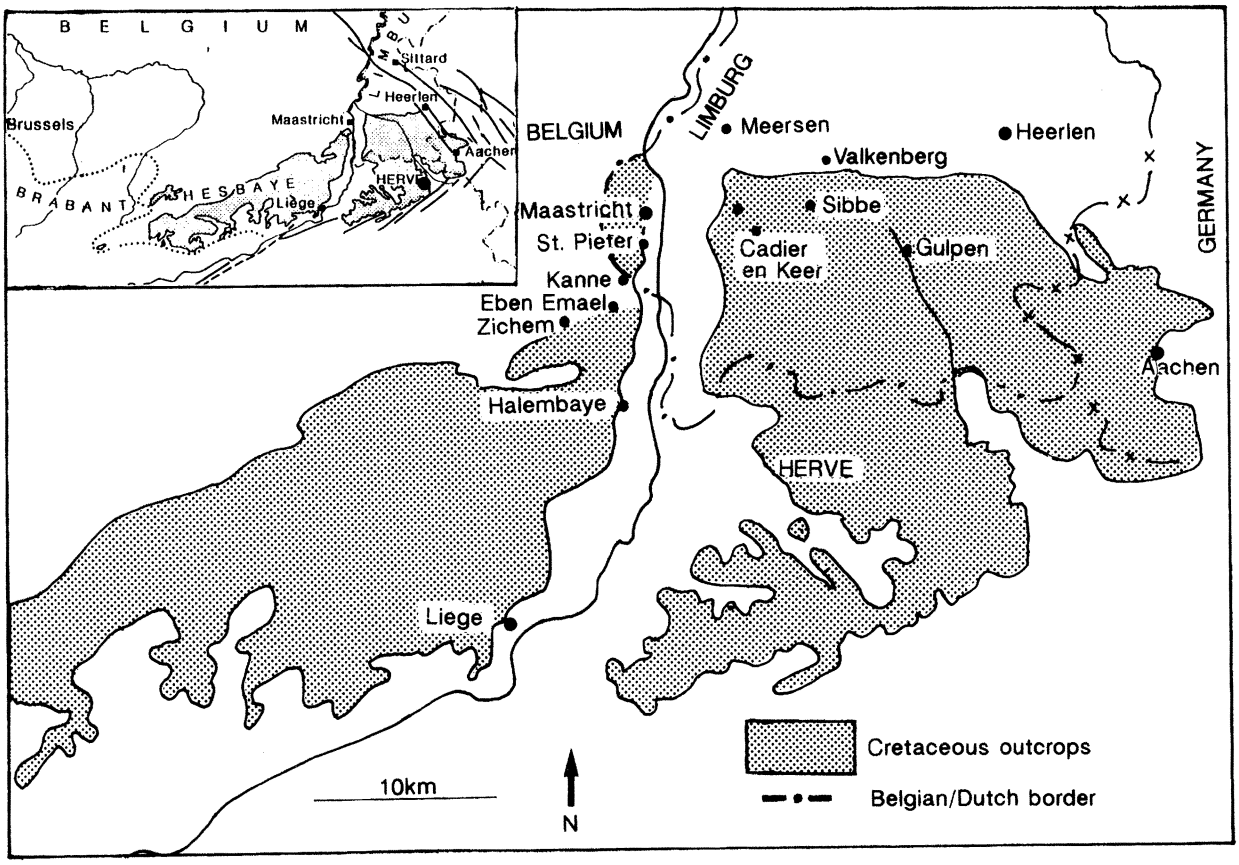


Figure 2. Locality map of Upper Cretaceous Chalk in The Netherlands and Belgium with principal locations of finds of *Mosasaurus hoffmanni* noted.

morphological and anatomical description of *Mosasaurus hoffmanni*; (ii) a discussion of head mobility and mechanics in relation to feeding on large prey; and (iii) an analysis of the evolution and lifestyle of *M. hoffmanni*.

## 2. GEOLOGICAL SETTING

*Mosasaurus hoffmanni* material came primarily from the locality of St. Pieters Mountain and Zichem (figure 2; for early records, see Van Regteren Altena 1956). Most specimens were discovered in the Tuffeau of Maastricht (type Maastrichtian = Maastricht Formation of Felder 1975), in the Nekum Chalk. The only exceptions are that described by Ubaghs (1879) and material belonging to Mr R. Garcet (Case 1978), from the Upper Gulpen Formation, Lanaye Chalk (reviewed, Lingham-Soliar 1994*a*).

## 3. TAPHONOMY

Although a great deal of the mosasaur material in the Upper Maastrichtian of the Maastricht region is disarticulated and broken, surface preservation is excellent and retains considerable detail. The disarticulated and broken nature of the specimens is apparently a result of the high water energy level in the Upper Maastricht Formation. Perhaps because of the size and robustness of *Mosasaurus hoffmanni*, its remains have suffered less in this respect than those of smaller mosasaurs such as *Plioplatecarpus* and *Leiodon* (Lingham-Soliar 1994*a*, 1993 respectively).

## 4. MATERIALS AND METHODS

Besides the holotype of *Mosasaurus hoffmanni* MNHN AC. 9648, other specimens are in the collections of NHMM, TSMHN, IRSNB and BMNH. Descriptions are of prepared museum material mostly of the head. The best preserved and most complete cranial material is from a relatively small specimen, IRSNB R12, which is slightly disarticulated and still partly embedded in matrix (figure 3). Only the dorsal part of the skull is obscured from examination. Braincase data come from BMNH 11262 (Van Breda Collection, Maastricht, the Netherlands), IRSNB R12 and R26. Excellent preparation by Mr R. Croucher (BMNH) of a frontal and partial parietal BMNH 42929 (Van Breda Collection), enabled a description for the first time (figure 6*e*, *f*).

Dorsal and lateral restorations of the skull (figure 4) are based on a composite, primarily IRSNB R26 and BMNH 11589 (cast of the holotype). The palatal and lower jaw restorations are based almost entirely on IRSNB R12. The overall size of the restoration is based on the holotype NMHN AC 9648 and IRSNB R26. Restoration of the atlas–axis complex is based on IRSNB R12 and R26, and the humerus and anterior paddle on IRSNB R12 and NHMM 1993024 respectively. The pelvic girdle is based on NHMM 006690. Descriptions of the head are based primarily on the holotype specimen NMHN AC 9648 (and cast, BMNH 11589), and on the beautifully preserved specimens IRSNB R12 (figure 3) and IRSNB R26 (figure 5). Comparisons are made with the American species *Mosasaurus maximus* as described by Russell (1967, pp. 138–141).

The head and neck region of a fresh specimen of *Varanus bengalensis* was dissected to aid muscle restorations of *Mosasaurus hoffmanni*.

Synonymies are represented in *selected* lists; anatomical abbreviations in the text (in parentheses) are those used in the figures.

*Abbreviations of Repositories*

BMNH: The Natural History Museum, Cromwell Road, London SW7 5BD

GPIT: Geologisches und Paläontologisches Institut Tübingen, Universität Tübingen, Sigwartstrasse 10, Tubingen D-72076 IRSNB: Institut Royal des Sciences Naturelles de Belgique, Rue Vautier 29, B-1040 Bruxelles

NHMM: Natuurhistorisch Museum Maastricht, Dienst Kco, Post 882, NL-6200 AW Maastricht

NMHN: National Muséum d'Histoire Naturelle, Rue du Buffon, Paris

TSMHN: Teylers Strichtina Museum, Spaarne 16, 2011 CH Haarlem.

## 5. TAXONOMY

Class: Reptilia Linnaeus, 1758
Superorder: Squamata Oppel, 1811
Order: Sauria (= Lacertilia Owen, 1842) McCartney, 1802
Infraorder: Platynota Duméril & Bibron, 1836
Family: Mosasauridae Gervais, 1853
Subfamily: Mosasaurinae Williston, 1897
Genus: *Mosasaurus* Conybeare, 1822

Type species: *Mosasaurus hoffmanni* Mantell, 1829 (figures 1, 3–27)

1820 *Lacerta gigantea* Sömmerring, 54.
1829 *Mosasaurus hoffmanni* Mantell, 207.
1829 *Mosasaurus belgicus* Holl, 84.
1832 *Mosasaurus camperi* Meyer, 113–114.
1840–1845 *Mosasaurus hoffmanni* Mantell; Owen, 261.
1869–1870 *Mosasaurus giganteus* (Sömmerring), Cope, 189 (part 2).
1879 *Mosasaurus camperi* Meyer; Ubaghs, 240–245, pls 1, 2.
1889 *Mosasaurus camperi* Meyer; Dollo, 277–279, pl. 9, fig. 1, pl. 10, figs 12, 13.
1924 *Mosasaurus giganteus* (Sömmerring); Dollo, 172.
1942 *Mosasaurus hoffmanni* Mantell; Camp, 45–46.
1959 *Mosasaurus hoffmanni* Mantell; Persson, 461.
1967 *Mosasaurus hoffmanni* Mantell; Russell, 8, 122, 131–132, 140, 210.
1980 *Mosasaurus hoffmanni* Mantell; Hamoir, 1446–1448.
1983 *Mosasaurus hoffmanni* Mantell; Meijer, 269–271, figure 3.
1987 *Mosasaurus hoffmanni* Mantell; Buffetaut
1989 *Mosasaurus hoffmanni* Mantell; Lingham-Soliar & Nolf, 156, 158, 174, figure 52, 175.
1991*b* *Mosasaurus hoffmanni* Mantell; Lingham-Soliar, 665.

*Holotype*: NMHN AC. 9648. A disarticulated partial skull, two cervical vertebrae and a femur.

*Horizon and locality of holotype*: Type Maastrichtian, Maastricht Formation, near St. Pietersberg, Maastricht, The Netherlands.

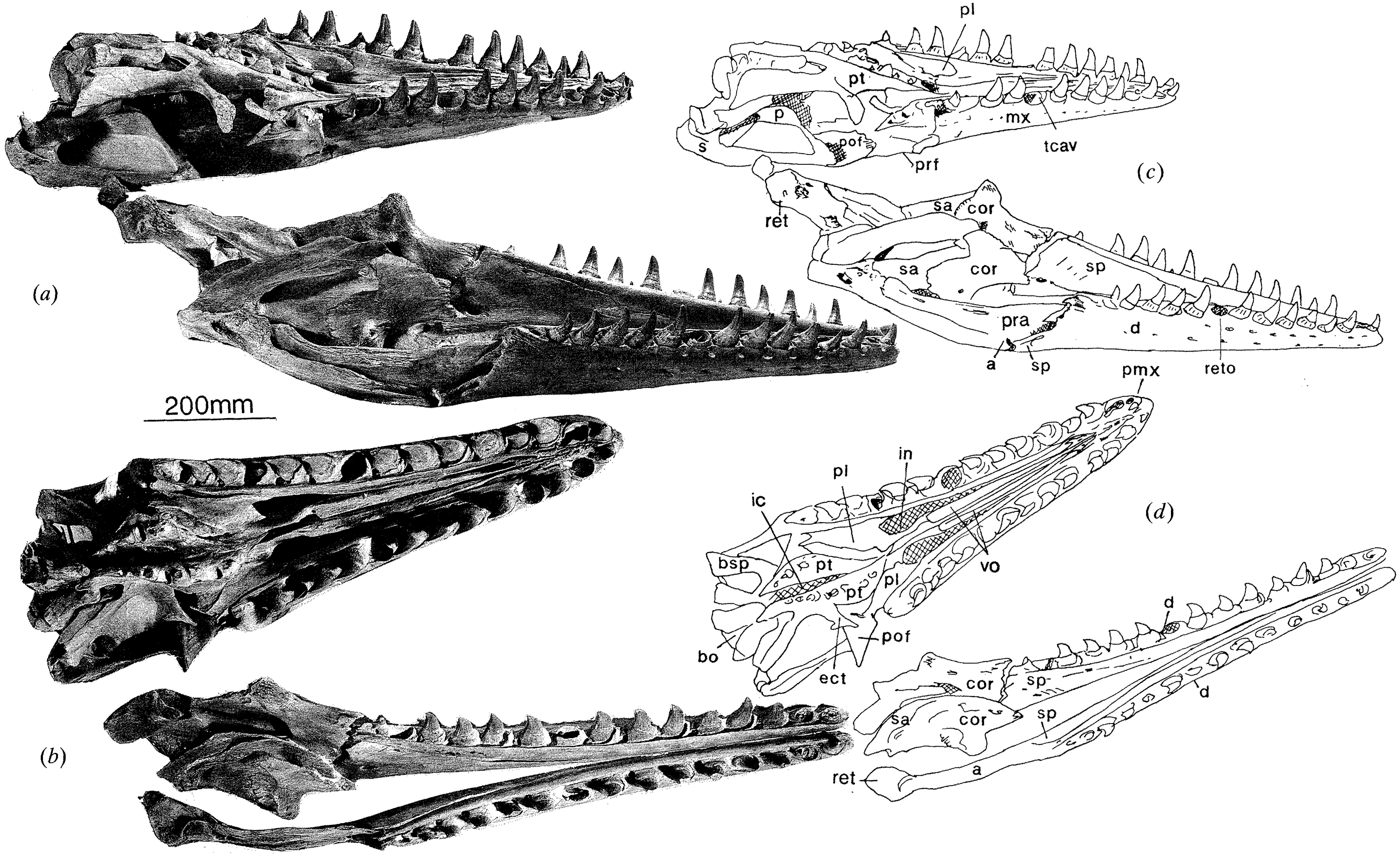
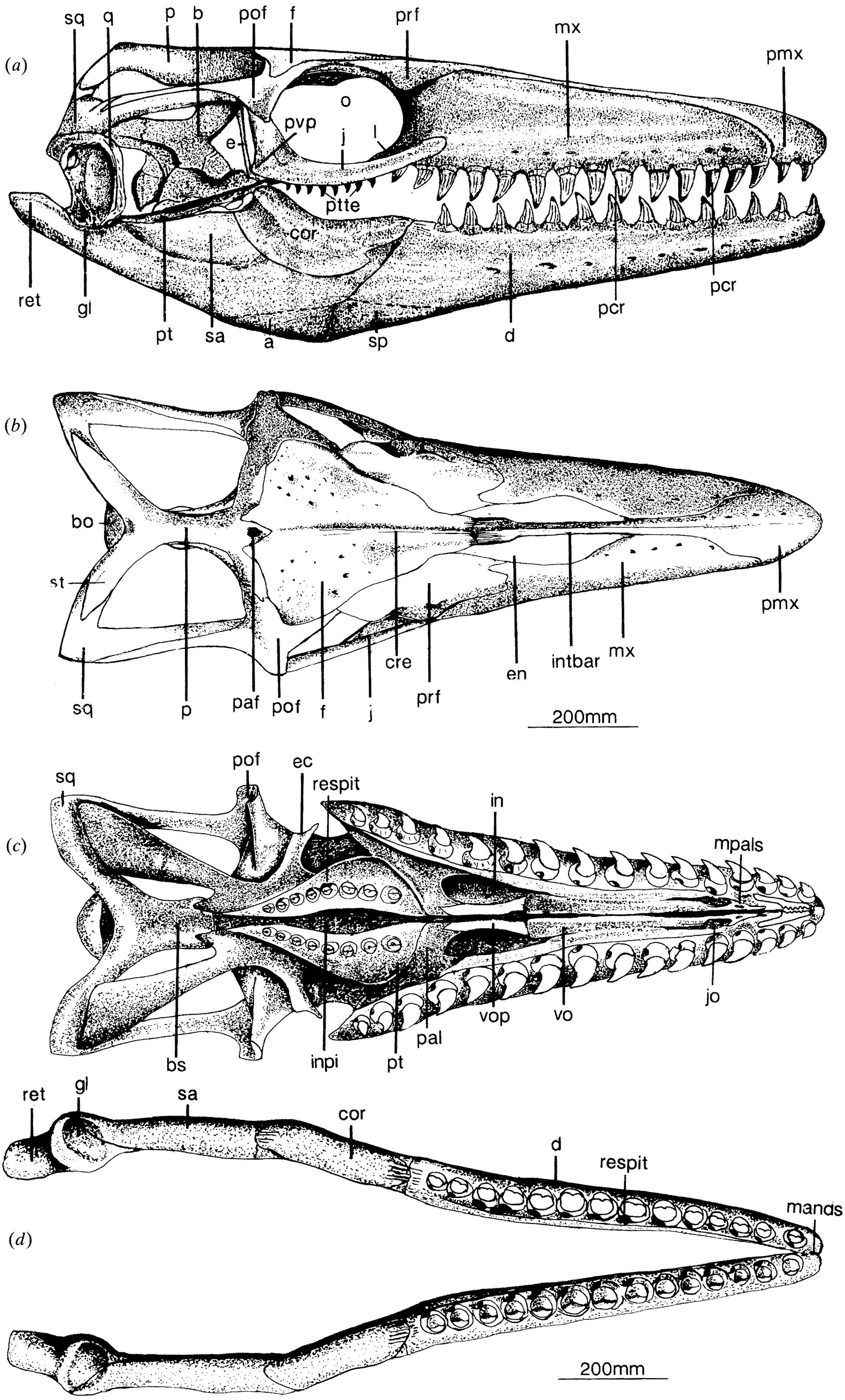


Figure 3. (*a*) Dorsolateral view of the skull (inverted) and mandibles of *Mosasaurus hoffmanni* IRSNB R12 superficially embedded in a matrix block; (*b*) the same view from above and (*c*) and (*d*) respective bone maps.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*Referred specimens* (in parenthesis = IRSNB old specimen nos.): IRSNB: R12, R24 (R1506), R25 (R1503), R26 (R1483), R27 (R1559), R1621, R1626, IG 8444, IG 8427, IG 8697; BMNH: 42928/9, R1223/4/5; NHMM: 009002, 006696, 1989127, 603092; TSMNH: 11201/2, 11243/4, 11208, 11376, 17281.

*Horizon and locality of referred specimens*: IRSNB R12, IG 8427: Upper Maastrichtian, Maastricht Calcarenite, locality of Zichem; IRSNB, R25, R26, IRSNB 1621, IG 8444, BMNH, NHMM and TSMHN specimens: Maastricht Calcarenite, locality of St. Pietersberg, Maastricht; IRSNB R27: Maastricht Calcerenite, locality of Kanne; IRSNB 1626: Maastrichtian, locality of Kunrade, The Netherlands; R24 and Mr Garcet's specimens are from the Maastricht Calcarenite, Upper Gulpen Formation, Lanaye Chalk near Maastricht, The Netherlands; IRSNB IG 8697: Ciply Phosphatic Chalk, locality of St. Symphorien (carrière Hardenport).

*Emended diagnosis*: Very large mosasaurine mosasaur. Narial emargination begins at approximately 4/5th maxillary tooth. Maxilla extends posteriorly to middle of horizontal arm of jugal. Ventrally the parietal overlaps and slots into a recess on the anteroventral surface of the frontal. Palatal elements closely united. Suprastapedial process of quadrate moderately large, infrastapedial process small. Pterygoid sits on a broad platform of the palatine and is overlapped by it. Anteroventral wing of coronoid very well developed on medial surface of lower jaw, posterior wing moderately developed. Enormous lateral excavation on surangular; anterior process of surangular fits into a splenial foramen. Marginal teeth highly prismatic. Barrel-shaped ribs.

## 6. KEY TO ABBREVIATIONS USED IN THE FIGURES

*Cranial morphology*

| | |
|---|---|
| a | angular |
| aa | atlas |
| ala | alar process of basisphenoid, or prefrontal |
| b | braincase |
| basip | basisphenoid process of pterygoid |
| bo | basioccipital |
| bs | basisphenoid |
| bt | basipterygoid process |
| cem | cement between tooth crown and base |
| che | cerebral hemispheres |
| cor | coronoid |
| core | coronoid eminence or apex |
| cre | crest |
| d | dentary |
| dentr | dental ramus |
| e | epipterygoid |
| ec | ectopterygoid or ectopterygoid process |
| en | external naris |
| f | frontal or frontal suture |
| fmag | foramen magnum |
| for | foramen |
| gl | intermandibular articulation |
| iam | internal auditory meatus |
| in | internal naris |
| inpi | incisura piriformis |
| intbar | internarial bar |
| istp | infrastapedial process of quadrate |
| j | jugal |
| jo | aperture for Jacobson's organ |
| l | lachrymal |
| mands | mandibular symphysis or syndesmosis |
| mpals | foramen for median palatine sinus |
| meckca | Meckelian canal |
| meckfo | Meckelian fossa |
| mx | maxilla or maxillary suture |
| o | orbit |
| of | olfactory lobe |
| op | opisthotic |
| ot | otosphenoidal crest of basisphenoid |
| p | parietal or suture for parietal |
| paf | parietal foramen |
| pal | palatine |
| ptpalu | sutural union between pterygoid and palatine |
| pcr | posterior carina on tooth crown |
| pmx | premaxilla |
| pofex | postorbitofrontal excavation |
| pof | postorbitofrontal or suture for postorbital frontal |
| popr | paroccipital process of opisthotic |
| pra | prearticular |
| prf | prefrontal or suture for prefrontal |
| prf ala | prefrontal alar |
| ps | parasphenoid |
| pt | pterygoid |
| ptte | pterygoid teeth |
| pvp | postero-ventral process of jugal |
| q | quadrate |
| quap | quadratic process of pterygoid |
| qcond | quadratic condyle |
| respit | resorption pit on tooth base |
| ret | retroarticular process |
| reto | replacement tooth |
| ro | roughened area (e.g. pitted or striated) |
| ros | rostrum |
| rosforfrn | roughened area for sutural contact between frontal and premaxilla |
| sstp | suprastapedial process of quadrate |
| sa | surangular |
| sep | septomaxilla |
| soc | supraoccipital |
| sm | branch of M. depressor mandibulae |
| sp | splenial |
| spit | stapedial pit |
| spl | splint supporting premaxilla and maxilla |
| sq | squamosal |
| st | supratemporal |
| tcav | tooth cavity |

Figure 4. *Mosasaurus hoffmanni* restored skull. (*a*) Lateral view based on the holotype (cast) and IRSNB R26; (*b*) dorsal view based on IRSNB R26 and BMNH 42929; (*c*) ventral view based on IRSNB R12 and BMNH 42929; (*d*) *l. jaw.*

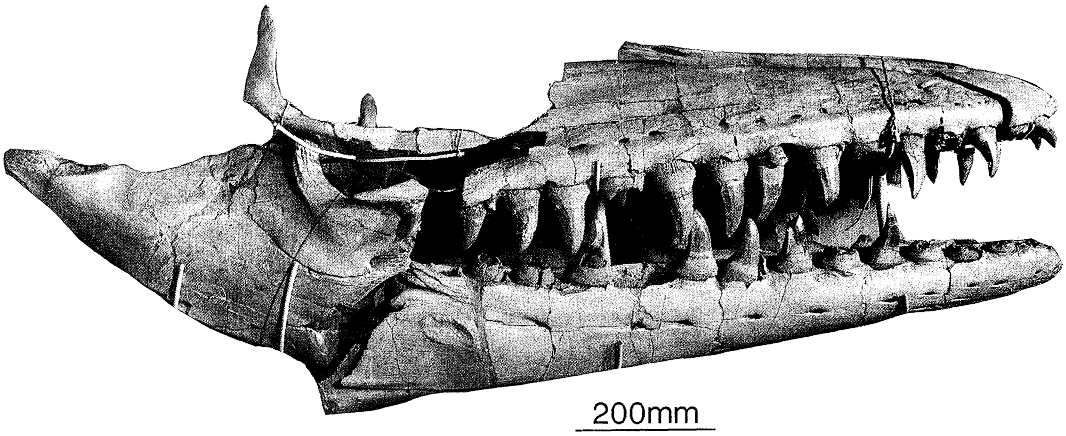

Figure 5. Partial skull of *Mosasaurus hoffmanni* IRSNB R26 (frontal and parietal absent).

| | |
|---|---|
| toba | tooth base |
| tym | tympanum |
| vc | vidian canal |
| vo | vomer |
| vop | vomerine process |

*Postcranial morphology*

| | |
|---|---|
| aa | atlas |
| ac | atlas centrum |
| ai | atlas intercentrum |
| ax | axis |
| atnear | atlas neural arch |
| ect | ectepicondyle crest |
| ent | entepicondyle crest |
| h | humerus |
| hyp | vertebral hypapophysis |
| hyppr | vertebral hypapophyseal process |
| i | intermedium |
| mc 1–5 | metacarpals 1–5 |
| pc | pectoral crest |
| pf | pisiform |
| pgp | postglenoid process |
| r | radius |
| ra | radiale |
| raduart | humerus articulation with radius and ulna |
| ster | sternum |
| u | ulna |
| ula | ulnare 1–4, distal carpals 1–4 |
| vert | vertebra |

*Cranial nerves*

| | |
|---|---|
| V | trigeminal nerve |
| VI | abducens nerve |
| VII | facial nerve |
| VIII | acoustic nerve, a, anterior branch, p, posterior branch |
| IX | glossopharyngeal nerve |
| X | vagus nerve |
| XI | accessory nerve |
| XII | hypoglossal nerve |

## 7. DESCRIPTION OF THE HEAD

The head in *Mosasaurus hoffmanni* is an enormous anteriorly pointed cone (figures 4 and 5). Cranial sutures of the upper skull are fine and the bones either overlap or are more closely associated than in other mosasaurs.

### (*a*) *Skull roof* (figures 4*b*, *c*, 6*a–f*, 7, 8, 9*a–c and 10*)

The *premaxilla* (pmx) (figures 6*a*, *b* and 7) is tapered anteriorly and slightly pointed. A smoothly rounded median dorsal crest is bounded on either side by a row of foramina somewhat as in *Clidastes* (Russell 1967, p. 16). From the alveolar margin the premaxillary/maxillary suture forms a shallow embayment in the premaxilla. The squamose sutural contact between the maxilla and the prefrontal is absent in all specimens examined. Premaxillary teeth are relatively very small and slightly procumbent (figures 4, 5 and 7). Ventrally a pair of medially serrated splints (spl) of bone are adpressed to the anteromedial walls of the premaxilla, overlaps the maxilla, and probably provided support between the two elements. The relatively narrow internarial bar (intbar) constricts in the region between the external nares. Anterodorsally a thin sliver of bone, firmly sutured on either side of the internarial bar, represents the septomaxilla (sep), rarely observed in mosasaurs (cf. *Leiodon mosasauroides*, Lingham-Soliar 1993).

The *maxilla* (mx) is very broad and deep and supports 14 large prismatic teeth with enormous barrel-shaped bases. Terminal branches of the maxillary nerve emerge from a row of large foramina above the gum line and from smaller foramina scattered on the lateral surface of the maxilla. A very large foramen on the anterior part of the maxilla (figure 1) presumably provided the exit for a major branch innervating the anterodorsal snout. The maxilla terminates posteriorly in a narrow extension that forms just over half of the ventral border of the orbit (o) and is overlapped by the jugal (j).

The *lachrymal* (l) (figure 9*a*, *b*) is known solely from BMNH 11589 and is characteristically an arrowhead-shaped bone. Dorsomedially an excavation marks a strong sutural union with the prefrontal.

The *frontal* (f) (figures 6*c–f* and 8) is similar to that of *M. maximus* (Russell 1967, p. 19, figure 3). It is broad posteriorly, narrowing anteriorly to form the posteriormost part of the internarial bar, in sharp contrast to the

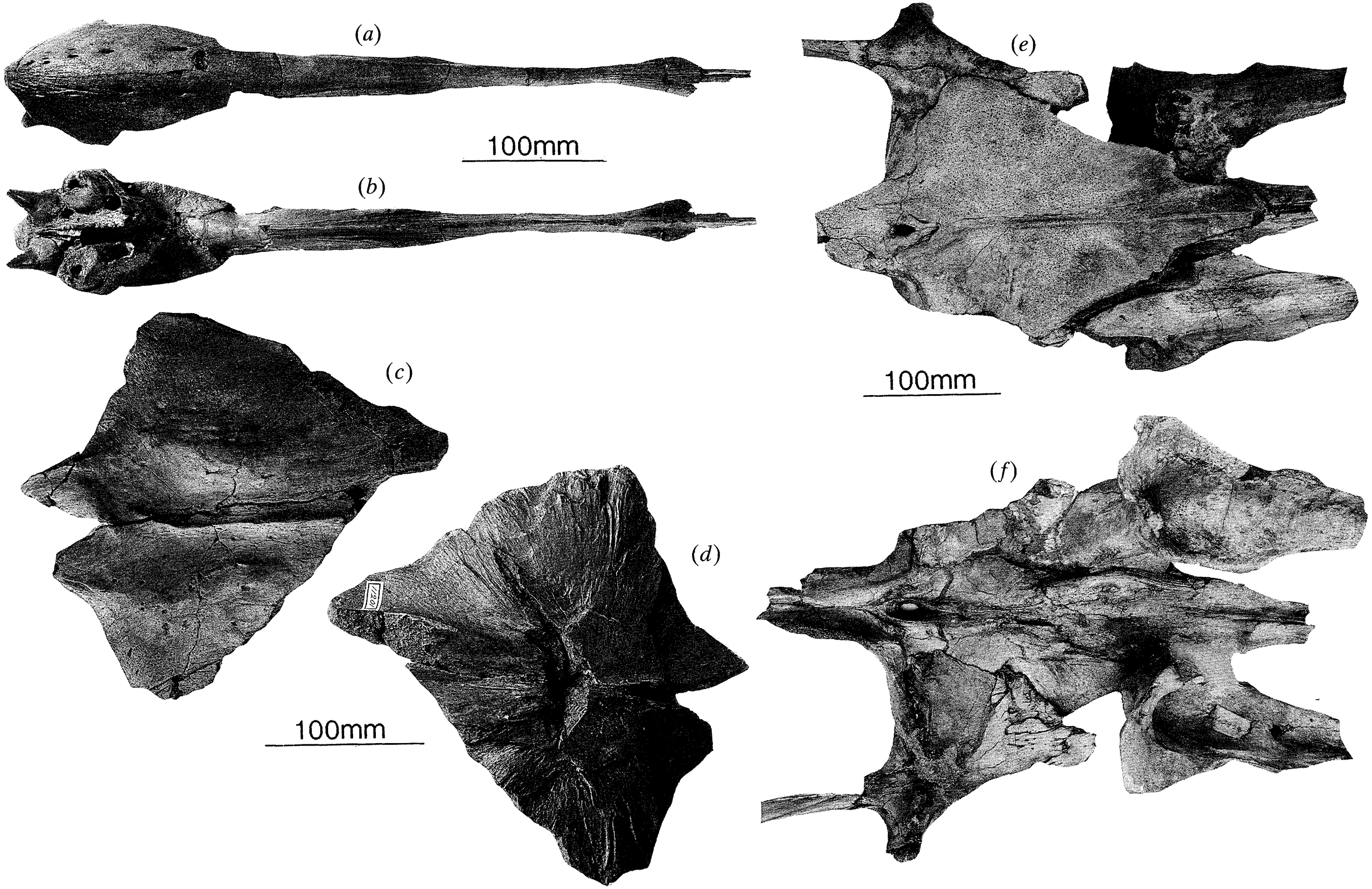

Figure 6. Premaxilla of *Mosasaurus hoffmanni* IRSNB R26. (*a*) and (*b*) Dorsal and ventral views respectively. Frontal TSMHN 11201 (*c*) and (*d*) dorsal and ventral views respectively. Frontal BMNH 42929 associated with prefrontals, postorbitofrontal and partial parietal (*e*) and (*f*) dorsal and ventral views respectively.

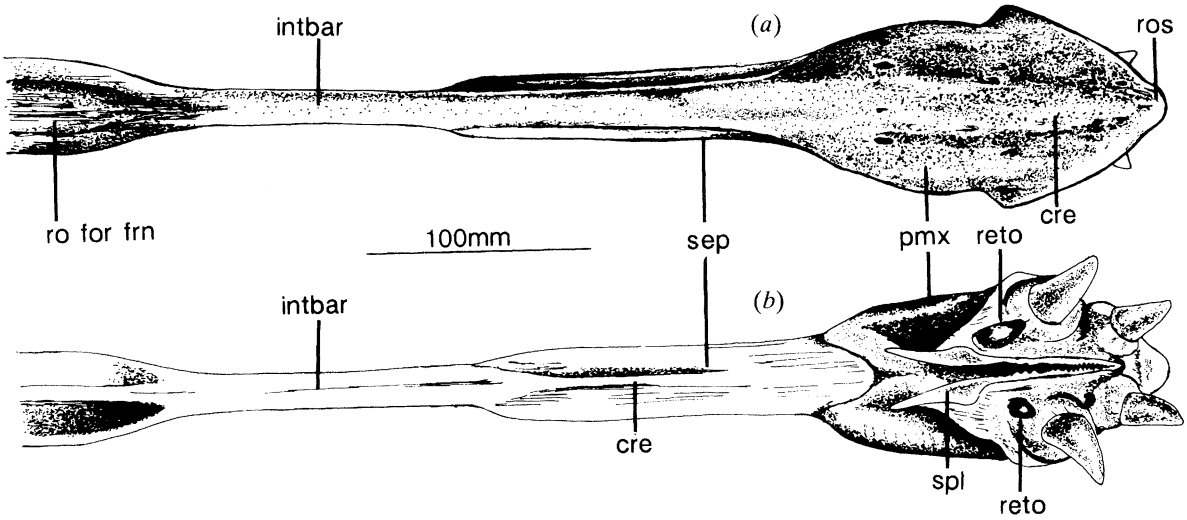

Figure 7. Premaxilla of *Mosasaurus hoffmanni* IRSNB R26. (*a*) Dorsal view; (*b*) ventral view.

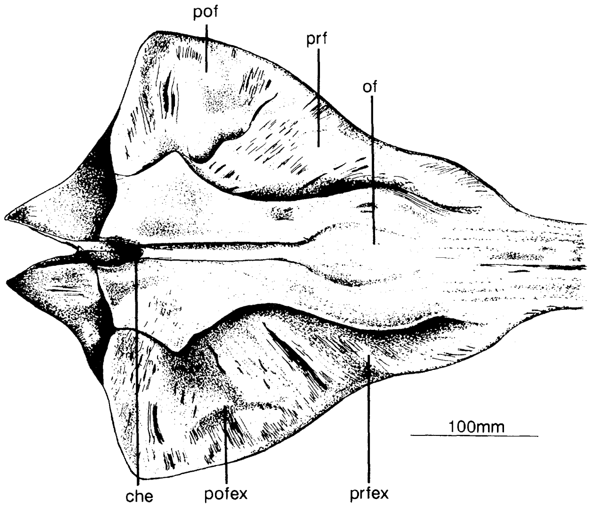

Figure 8. Restoration of the ventral surface of the frontal of *Mosasaurus hoffmanni* based on BMNH 42929 and TSMHN 11201.

condition in tylosaurines (Lingham-Soliar 1992*a*) where the internarial bar is formed entirely by the premaxilla that penetrates deep into the frontal. A dorsal crest (cre) extends its entire length (figures 6*c*, *e*). In BMNH 42929 and TSMHN 11201 (figure 6*c*, *e*), tongue-like extensions or tabs overlap the mesokinetic axis on either side of the parietal foramen (paf) as in *M. lemonnieri* and *M. maximus* although uniquely, ventral tabs from the parietal also overlap the mesokinetic axis. The excavation for the olfactory lobes (of) on the ventral surface is very shallow and lacks the descending processes seen for instance in *M. lemonnieri* (Lingham-Soliar in preparation).

Rugosities and excavations (ro in figure 10) on the *prefrontal* (prf) e.g. TSMHN 17281 and BMNH 42929 (figures 9*c* and 10) show that in life it was firmly united to the maxilla, frontal and lachrymal. The supraorbital alar (prf ala) is large. The posterior wing of the prefrontal and the broad triangular anterior wing of the postorbitofrontal are united along the lateral edge of the frontal in a strong, interdigitated suture and together form the orbital margin. A flattened posteroventral sutural surface marks the contact with the palatine.

The *postorbitofrontal* (pof) wing to the squamosal extends to the posterolateral edge of this bone. The extent is variable in mosasaurs. In *Mosasaurus maximus* (Russell 1967, p. 24) it terminates slightly anterior to the position noted in *M. hoffmanni*. The medial wing forms a sutural union with the long lateral process from the parietal (p). The ventrolateral wing to the jugal is short, bearing a deep posteromedial recess distally that overlaps the tip of the vertical arm of the jugal. Striae on the distal tip of the jugal indicate a relatively firm connection with the postorbitofrontal.

The *jugal* (figure 9*d*–*f*) is robust. The vertical arm lies at about 90 ° to the horizontal arm and flattens distally. The posteroventral process is moderately large. In IRSNB R26, an excavation extends from approximately the midpoint of the medial surface to the tip of the horizontal arm, presumably marking an area of strong ligamentous connection with the maxilla.

The *squamosal* (sq) is comma-shaped (figure 9*g*, *h*). The broad head is dorsally rugose and striated suggesting strong muscle attachments. A deeply striated ventral surface indicates a strong connection with the quadrate. A deep trench on the dorsolateral surface of the anterior wing received the posterior postorbitofrontal process. The elongated processes from the squamosal and postorbitofrontal together formed a relatively robust and straight temporal arcade. A second and considerably smaller wing of the squamosal unites with the suspensorial ramus of the parietal. Ventrolaterally a vertical facet slightly overlaps the dorsolateral surface of the quadrate.

The *orbits*, separated by wide frontals, are moderately large and set well back in the skull.

A beautifully preserved *sclerotic ring* of *Mosasaurus hoffmanni* was described by Plesnier-Ladame & Coupatez (1969). There are twelve individual plates or ossicles all distinctive in their shape and pattern of overlap although there is probably little taxonomic value unless the sclerotic ring is found in the original position (Lingham-Soliar & Nolf 1989, pp. 153, 155).

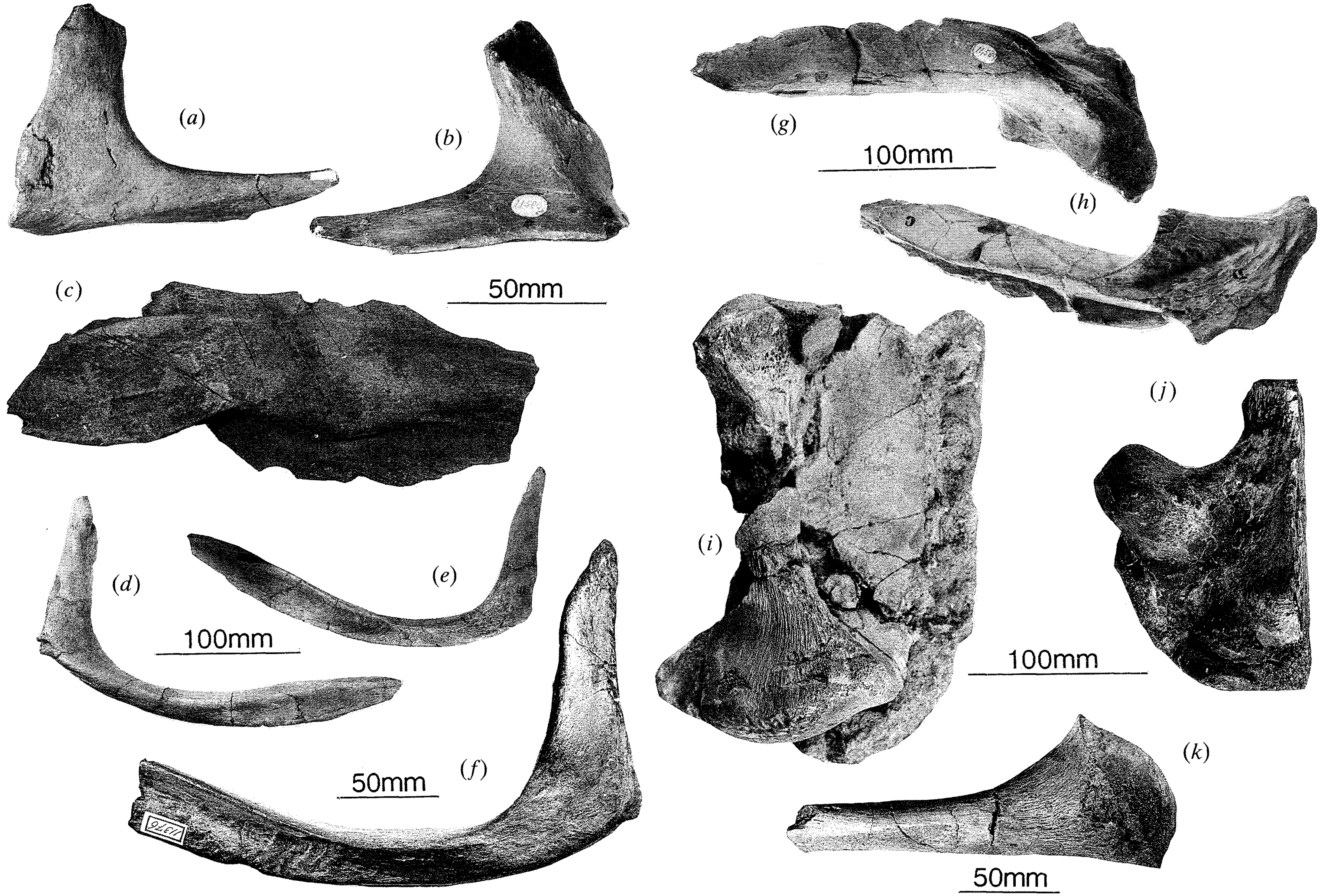

Figure 9. Lachrymal BMNH 11589. (*a*) and (*b*) Lateral and medial views respectively. Prefrontal TSMHN 17281. (*c*) Lateral view. Jugal IRSNB R26. (*d*) and (*e*) Lateral and medial views respectively. TSMHN 11376. (*f*) Medial view. Squamosal BMNH 11589. (*g*), (*h*) Dorsal and ventral views respectively. Quadrate NHMM 603092. (*i*) Lateral view. Humerus TSMHN 11252. (*j*) Flexor view. Ilium TSMHN (unnumbered). (*k*) Medial view.

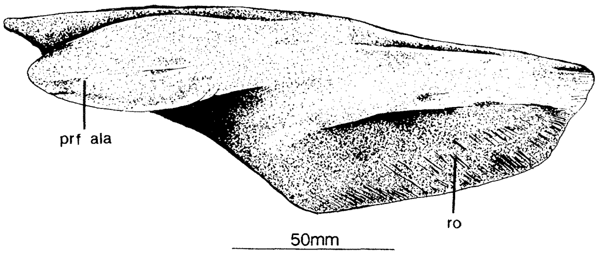

Figure 10. Restoration of the right prefrontal of *Mosasaurus hoffmanni* based on TSMHN 17281.

### (*b*) *The palatal complex* (figures 3, 4*c*, 6*a*, *b* and 11)

The bones of the palate are in tight association and the size of the openings are considerably reduced relative to other mosasaurs.

Each *pterygoid* (pt) is moderately proportioned extending to under a half of the length of the skull (figure 11). The tooth-bearing segment supports eight small teeth, the largest located towards the centre of the segment. The quadratic process (quap) is somewhat narrower than in, for instance, *Tylosaurus* (Russell 1967, p. 42, figure 21) and is striated (ro) on the ventromedial surface. A flattened tongue-like basi-

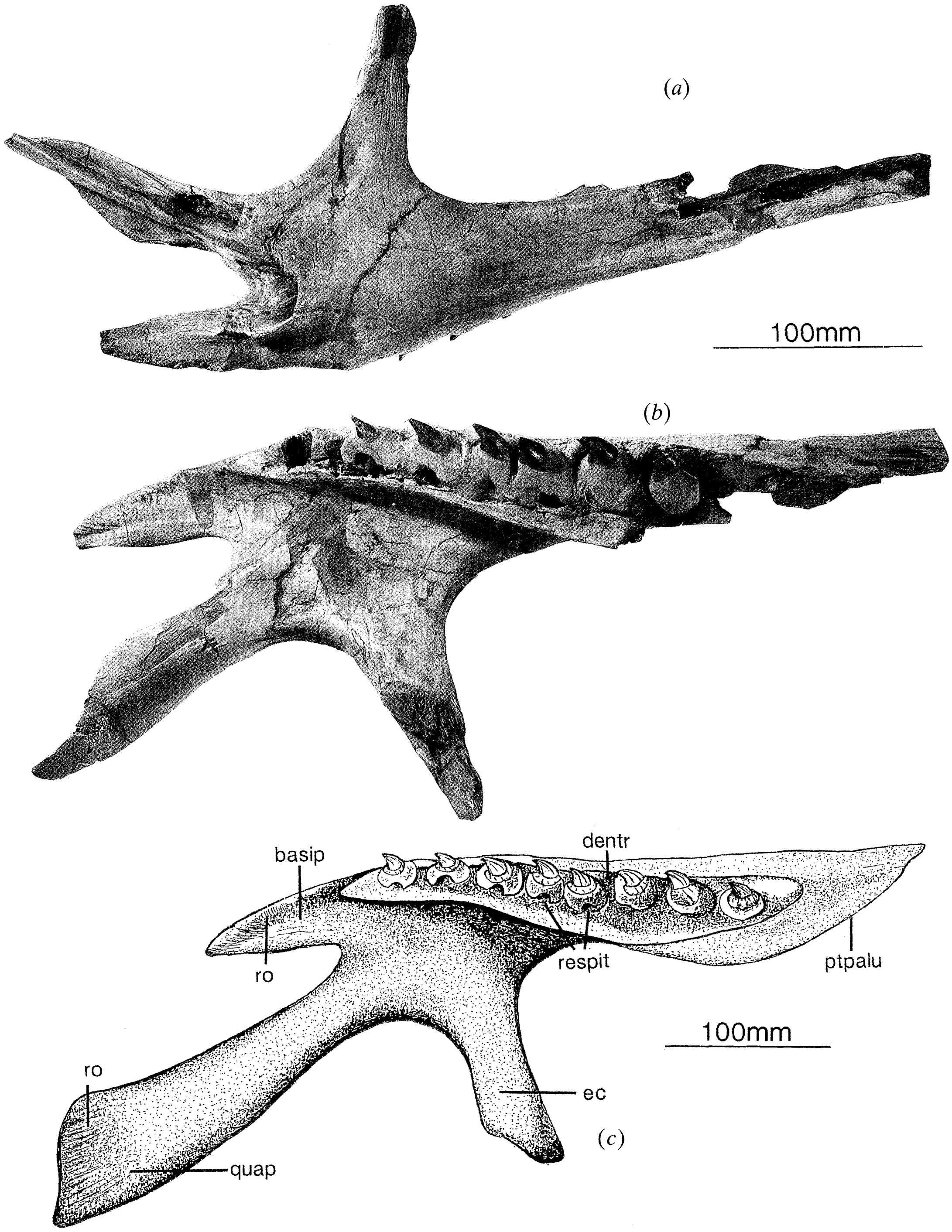

Figure 11. Left pterygoid of *Mosasaurus hoffmanni* IRSNB R26. (*a*) Dorsal view; (*b*) ventral view and (*c*) restoration.

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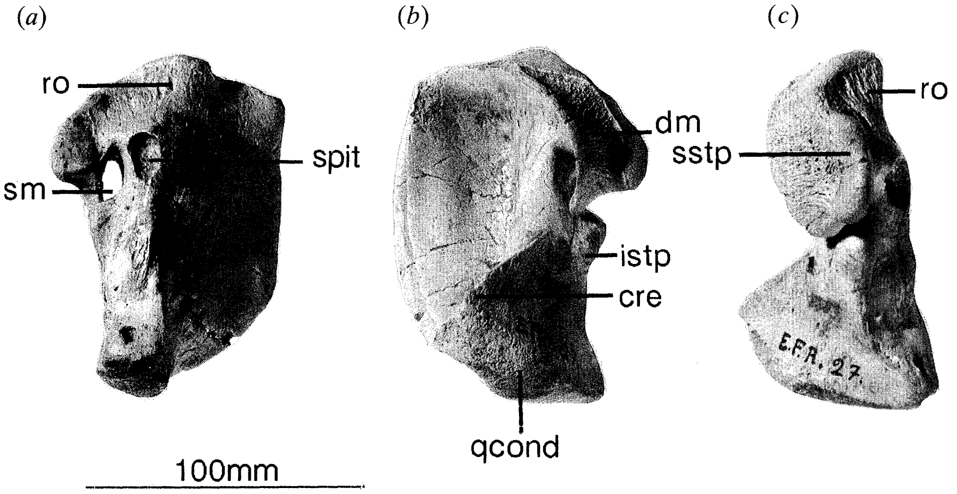

Figure 12. Left quadrate of *Mosasaurus hoffmanni* IRSNB R26. (*a*) Medial view; (*b*) lateral view; (*c*) posterior view.

sphenoid process (basip) extends from the posterior part of the dental segment (dentr). Its finely striated ventral surface (ro) presumably provided attachment for the fibres of the M. pterygoideus superficialis (Russell 1967, p. 44). Ventrally, at the junction of the basisphenoid and quadratic processes, a deeply pitted area indicates a muscle attachment site. The ectopterygoid process (ec) emerges from a broad base at about the midpoint of the bone and at right angles to it. It forms an expanded undulating suture with the ectopterygoid. Anteriorly the pterygoid is firmly buttressed against the palatine (pal) in a squamose suture.

The *palatines* are rarely found intact in mosasaurs. However, they are beautifully preserved *in situ* (figures 3 and 4*c*) in *Mosasaurus hoffmanni*, IRSNB R12. Each element is dorsoventrally flattened and roughly Y-shaped (cf. *P. solvayi*, Lingham-Soliar & Nolf 1989, pp. 147–148). The pterygoid fitted into a fairly broad, relatively shallow ledge along approximately two-thirds of the posteromedial edge of the palatine. A narrow lip on the ledge overlapped the pterygoid, and the remaining margin of the palatine was sutured to the vomerine process. Laterally the palatine is firmly buttressed to the maxilla.

The *vomers* (vo) (figures 3 and 4*c*) are long slender processes, almost touching along the midline. They complete the medial margins of the internal nares and are fused to the vomerine processes posteriorly (see Russell 1967). They are completely free in only one mosasaur, *Prognathodon solvayi* (Lingham-Soliar & Nolf 1989, p. 148). Free, delicate processes anteriorly terminate near the first maxillary tooth. In contrast, in *Platecarpus* they are sutured to the medial wall of the maxilla (Russell 1967, p. 26) and apparently to each other. From each tip a short barbule-like process, adpressed to the medial wall of the maxilla, encloses part of the somewhat pinched aperture for each Jacobson's organ (jo) lying on either side of the maxilla, adjacent to the third maxillary tooth. The tip of each vomer is pierced by a small eye-like slit through which the vein to the median palatine sinus (mpals) passed. It is similar in *Platecarpus* although in *Tylosaurus* the foramen is bounded laterally by the maxilla (Russell 1967, p. 26). In *Varanus* the palatine sinus vein emerges posterior to the Jacobson's organs (Bahl 1937, p. 163) rather than anterior to it as in mosasaurs.

The *vomerine processes* (vop) are straight and short relative to the length of the vomers rather than long as in *Platecarpus* (Russell 1967, pp. 25–26). This presumably is connected with smaller external nares in *M. hoffmanni* than in *Platecarpus* (approximately 21–24% of the skull length in *M. hoffmanni* and 28–34% in *Platecarpus*).

The *septomaxillae* (sep in figure 7) in mosasaurs are slender splints of bone that are presumably of dermal and endodermal origin as in recent lizards. They overlie the Jacobson's organs. Anteriorly there is little expansion of each septomaxilla although ventrally it extends over the internarial bar encapsulating it along its anterior end and forming a ventral crest along the midline (figures 6*a*, *b* and 7). On either side of the crest the ventral surface of the septomaxilla is markedly striated, probably denoting the suture for the cartilaginous internasal septum. (The nasals in mosasaurs, unlike in *Varanus*, are vestigial; Camp 1942, pp. 27–28, figure 14). The septomaxilla in mosasaurs was previously known only in *Tylosaurus* (Merriam 1894, p. 21, plate 1, figure 3), and in the type skull of *Plotosaurus bennisoni* (Camp 1942, pp. 28–29) although Huene's (1910) turbinals in *Tylosaurus* GPIT 256/8/1 (Lingham-Soliar 1995) are septomaxillae.

### (*c*) ***The parietal unit*** (**figures 4*b* and 12**)

The *parietal* in IRSNB R12 is relatively narrow with somewhat concave lateral margins. It branches into straight, laterally diverging suspensorial rami. Uniquely, antero-ventral extensions of the parietal overlap the mesokinetic joint on either side of the parietal foramen, clearly contributing to the suppression of movement along the mesokinetic axis.

The *quadrate* (q) is robustly built with little intraspecific variation in *Mosasaurus hoffmanni* (figure 12). The suprastapedial process (sstp) is relatively large, the distal tip somewhat laterally inflected, touching or almost touching, the infrastapedial process (istp) (a fairly large tuberosity situated close to the

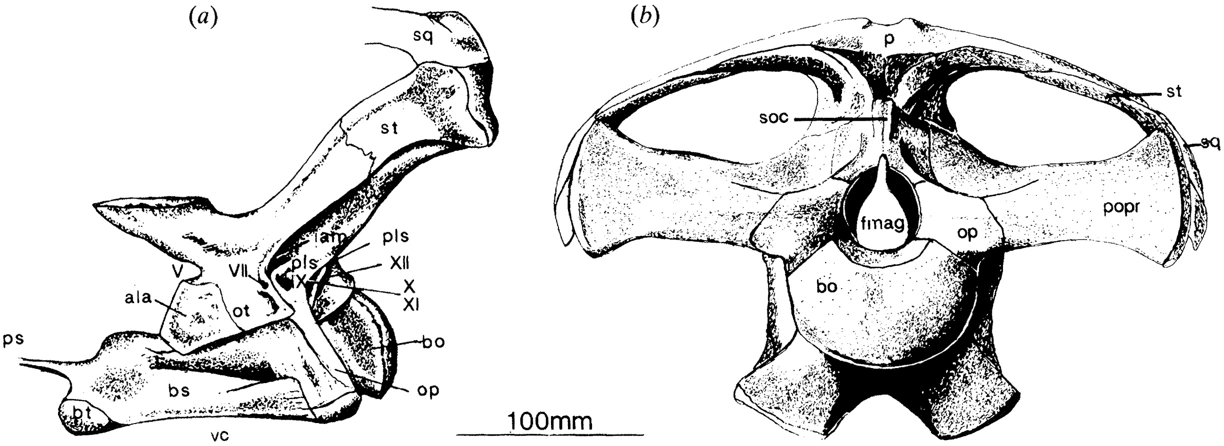

Figure 13. Restoration (major) of the braincase of *Mosasaurus hoffmanni* based on BMNH 11262 and IRSNB R26. (*a*) Left lateral view; (*b*) posterior view.

midpoint of the posterior surface of the bone). A delicate crest (cre in figure 12*b*) rises along the lateral surface of the quadrate from the condyle (qcond) and almost makes contact with the infrastapedial process. A continuation of this crest along the anterolateral surface of the bone supported the quadratic tympanum in life. The base of the quadrate is relatively very broad from side to side. In the largest quadrate of *M. hoffmanni*, NHMM 603092 (figure 9*i*), the condyle is heavily pitted, indicating a strong cartilaginous surface. At the top of the anterior surface a shallow excavation marks the insertion point for the fibres of the M. depressor mandibulae. Below this is the elliptical or egg-shaped stapedial pit (spit) which received the processes internus of the extracolumellar (e.g. see Dollo 1905; Camp 1942, p. 34 and figures 7 and 23).

The quadrates in *Mosasaurus hoffmanni* show no obvious differences to those of Dollo's (1888) *M.* '*giganteus*' IRSNB R27 (= *M. hoffmanni*) although he used them to distinguish two forms. However, there are apparent differences between the quadrates of *M. hoffmanni* and *M. maximus* (Russell 1967). The suprastapedial process in *M. hoffmanni* is large, in striking contrast to that of *M. maximus* (Russell 1967, p. 46, figure 24), and has a broader and deeper insertion area for the fibres of the M. depressor mandibulae. The quadratic condyle, viewed from the posterior, is more convex than in *M. maximus*, (figure 12*c*, cf. Russell 1967, figure 24), perhaps contributing to a stronger articulation with the lower jaw.

### (*d*) ***The braincase*** (**figure 13**)

The braincase (b) (figure 13) is essentially as described for *Clidastes* (Russell 1967) with minor differences noted below. The *basioccipital* (bo) is strikingly similar to that of *Clidastes propython* although the basal tubera are larger.

In the *prootic* of specimen IRSNB R12 the otosphenoidal crest, although large, does not obscure the foramen for cranial nerve VII, situated relatively low on the prootic.

In the *opisthotic–exoccipital* (op) the foramen for cranial nerve IX is enormous and located very close to the prootic, in contrast to the condition in *Clidastes* (Russell 1967, p. 34, figure 12).

From brain casts (see method in Camp 1942) it is clear that despite *Plioplatecarpus marshi* being approximately half the size of *Mosasaurus hoffmanni*, the brain is twice the size. The excavation for the optic lobes and cerebral hemispheres is also enormous in *Plioplatecarpus* whereas in *M. hoffmanni* it is relatively both narrow and quite shallow. It seems reasonable to infer that the optic lobes and cerebral hemispheres were relatively much smaller in *M. hoffmanni*. In addition, the parietal foramen is among the smallest in the Mosasauridae, in striking contrast to the enormous parietal foramen in *Plioplatecarpus*, presumably reflecting differences in the size of the pineal eye. Such differences were presumably associated with different lifestyles.

### (*e*) ***Lower jaw*** (**figures 3, 4*a*, *d*, 5, 14 and 23*c***)

The *dentary* (d) is robust and deeper rather than broad. Just below the gum line a row of fairly large foramina parallels the dorsal margin of the bone. Fourteen prismatic teeth are present with tooth bases pointing posteriorly at an angle of ~ 45° to the horizontal (figure 14*a*). The mandibular foramen, formed between the dentary and splenial, received the anterior blade of the prearticular (pra in figure 23*c*) although uniquely, a second small channel or foramen, seen in IRSNB R12, received a small anterior process from the surangular (sa in figure 23*c*) contributing to the suppression of intramandibular movement.

A broad and relatively thin ala of the *splenial* arises medially and sheaths the Meckelian fossa (meckfo in figure 23*c*) as far as the anterior third of the bone.

The *coronoid* (cor) is typically saddle-shaped (figures 14*b*, *c* and 23*c*; also Ubaghs 1879) and well developed although the lateral wing is less expansive and the posterodorsal eminence (core in figure 23*c*) not as deep as in *Prognathodon* (Lingham-Soliar & Nolf 1989). The anteromedial wing is enormous, extending to the anterodorsal edge of the angular. Deep striae indicate that the two elements were sutured tightly together. The posterior wing of the coronoid is small. Striae on the anterolateral surfaces of the coronoid, and

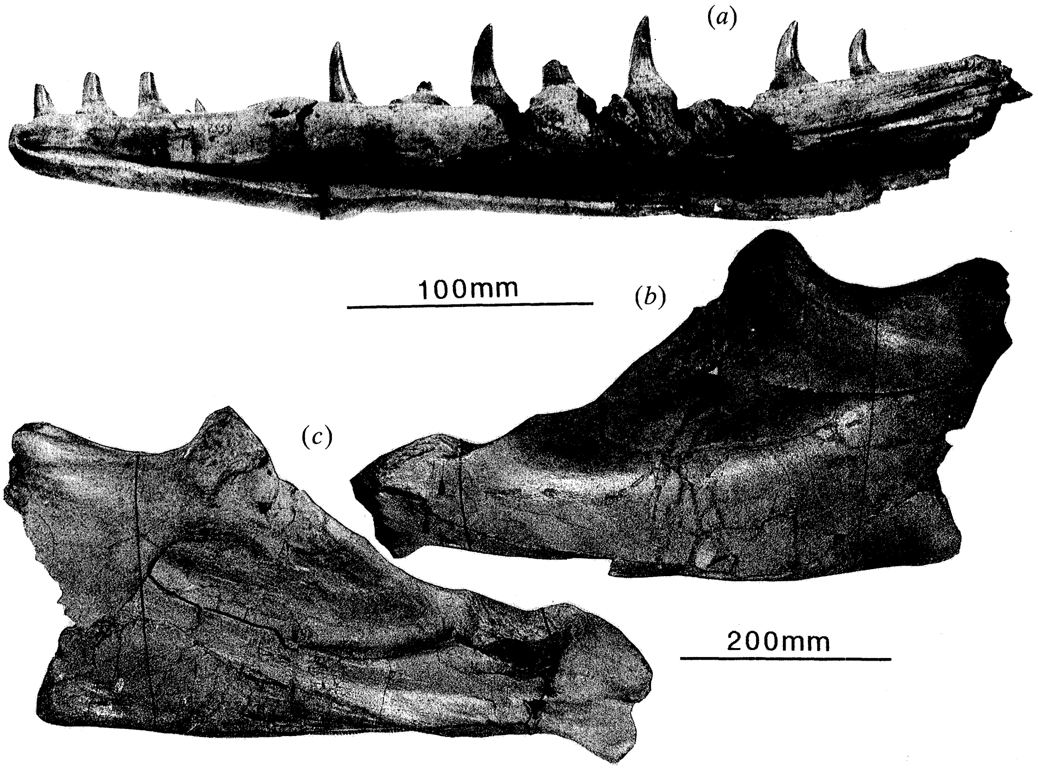

Figure 14. Dental and post mandibular unit (pmu) in *Mosasaurus hoffmanni*. Right dentary IRSNB R27. (*a*) Medial view. Right pmu IRSNB R26. (*b*) and (*c*) Lateral and medial views respectively.

dorsolateral surfaces of the posterior portion of the dentary provide further evidence of a tightening of the elements between the two moieties of the lower jaws.

In IRSNB R26 and R24 the *prearticular* process was apparently large, although it is broken off at a point adjacent to the anterior termination of the coronoid in both specimens.

The *surangular* is massive and vertically deep. Laterally there is an unusually broad excavation that apparently provided major muscle insertions.

### (*f*) ***Dentition*** (figures 15 and 26)

Mosasaur teeth are thecodont. The tooth bases are cemented in deep pits. Successional teeth emerge from the posteromedial region of each tooth, occurring in waves (Edmund 1960). Teeth are uniform in size along the length of the tooth rows with only the first two and last two teeth showing any significant reduction in size. This excludes the premaxilla in which the teeth are very small.

The most characteristic feature of the teeth is the uniquely pronounced development of external tooth facets or prisms (figure 15). In most specimens the tooth crowns possess two prisms anteriorly increasing to five posteriorly. The U-shaped tooth bases are strongest anteriorly, becoming less pronounced posteriorly with the external surface changing from flat to slightly convex (changing earlier in the tooth row of the maxilla). The internal surface is nevertheless always greater than the external. Associated with the changes in shape and number of prisms, the posterior carina (pcr in figure 4) shifts from a somewhat lateral position in the anterior teeth, to a posterior position further along the tooth row (figure 4*a*). In the lingual surfaces of the maxillary teeth the striae are not clearly discernible until the sixth or seventh tooth crowns.

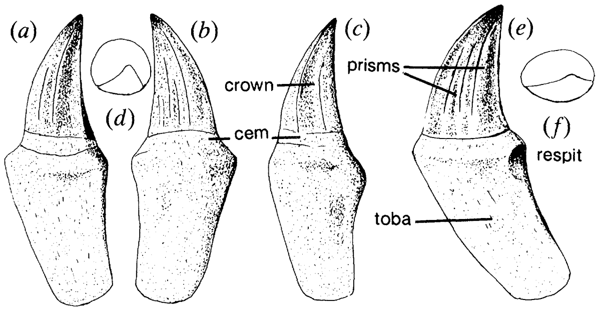

Figure 15. Teeth of *Mosasaurus hoffmanni* IRSNB R26. (*a*)–(*d*) Anterior tooth, buccal, lingual, anterior and occlusal views; (*e*) and (*f*) mid-posterior tooth, buccal and occlusal views.

## 8. DESCRIPTION OF THE POSTCRANIAL SKELETON

### (*a*) ***Axial skeleton*** (figures 16–18)

In most respects the *atlas* (aa) (figures 16*a–c* and 17) is as in other mosasaurs. The articular surface for the basioccipital condyle is somewhat dorsoventrally compressed and slightly emarginated dorsally. Further smooth surfaces (ac) on the intercentrum (ai) anteriorly and on each neural arch (atnear) anteromedially, completed the articulation with the large basioccipital condyle. There are no zygantra.

The *axis* (ax) is well preserved in IRSNB R26 (figure 16*d*, *e*). It is robust with a very broad neural spine that almost equals the length of the centrum. Distally the spine is cut off obliquely, exposing an expansive,

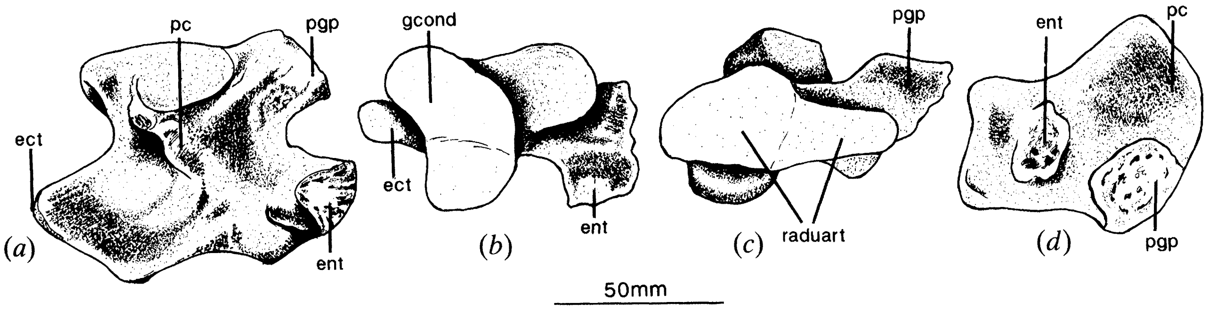

Figure 20. Humerus of *Mosasaurus hoffmanni* IRSNB R12. (*a*) Medial view; (*b*) proximal view; (*c*) distal view; (*d*) posterior view.

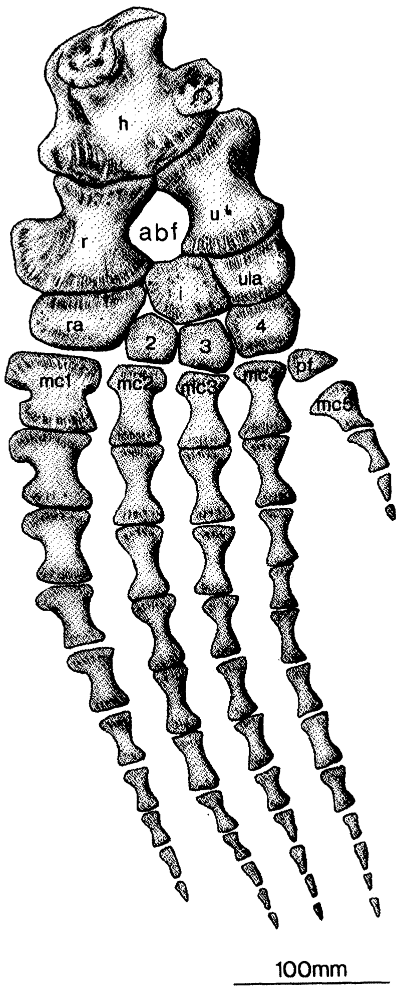

Figure 21. Restoration (minor) of the anterior paddle of *Mosasaurus hoffmanni* based on a cast NHMM 1993024 of material in the private collection of Mr R. Garcet.

pygal vertebrae which in my opinion seems scant evidence for the erection of a genus. Indeed such conditions are seen in the pygal vertebrae of *Mosasaurus nigeriensis* (Swinton 1930). Furthermore, great similarity of the pelvis and astragalus of *M. hoffmanni* to those of *Amphekepubis* supports Camp's (1942, p. 25) view that *Amphekepubis* be synonymized with *Mosasaurus*.

*Plotosaurus* is perhaps the only mosasaur in which the intermedium is excluded from the antebrachial foramen (Russell 1967, p. 96, figure 54). In *Clidastes*, on the other hand, the antebrachial foramen is large bordered by margins of the radiale (ra) and intermedium whilst in *Platecarpus* it is bordered by margins of the ulnare (ula) and the intermedium. Widening of the antebrachial foramen is presumably associated with more divaricate paddles. The similarity in the compressed paddles of *Mosasaurus* and *Plotosaurus* may reflect an adaptation to faster swimming.

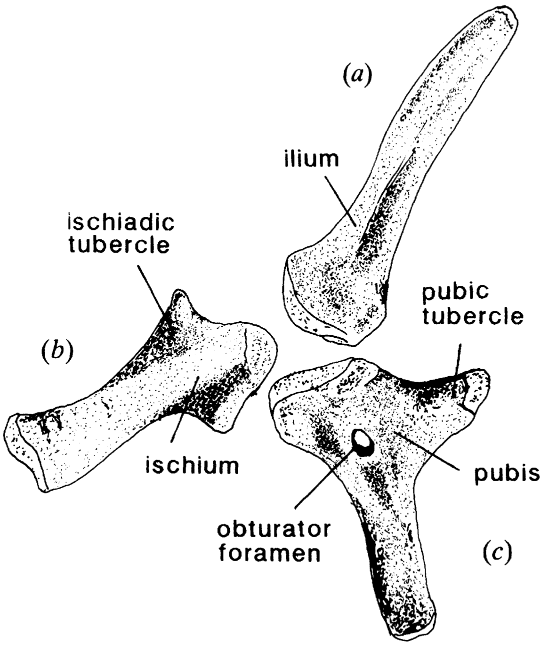

Figure 22. Restoration of the pelvic girdle of *Mosasaurus hoffmanni* NHMM 002006. (*a*) Ilium; (*b*) ischium; (*c*) pubis.

## 9. RESTORATION OF THE HEAD MUSCULATURE

The cranial musculature in mosasaurs was previously described by Russell (e.g. 1967), Callison (1967) and Lingham-Soliar (1991*c*). Although these descriptions are closely based on the head musculature of *Varanus niloticus*, they were applied to relatively small forms of mosasaurs (*Clidastes liodontus* and *Prognathodon solvayi*). The following description is therefore the first attempt to establish the main cranial muscles, their locations and actions in a large mosasaur viz. *Mosasaurus hoffmanni*. It is based upon muscle scars (figure 23) noted on numerous head specimens of *M. hoffmanni*. *Varanus bengalensis* provided the essential groundplan for the muscle restorations although other living reptiles, based on the literature, were used as models.

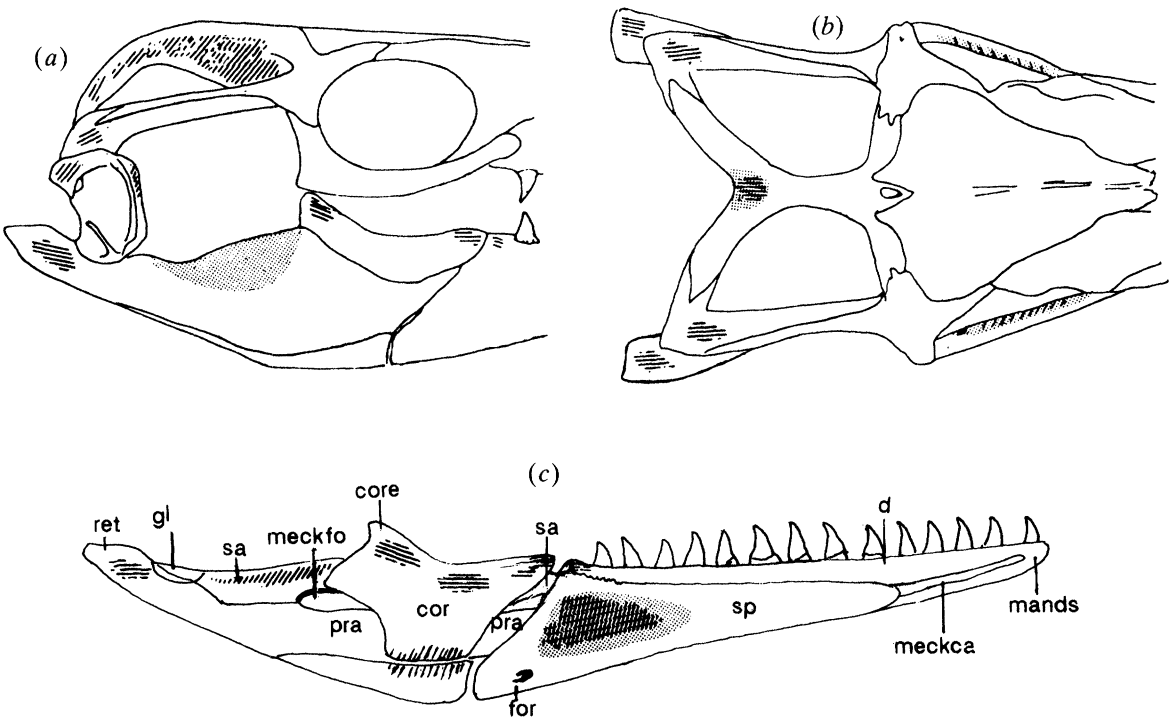

Figure 23. Muscle scars (hatched) and excavations (stippled) in *Mosasaurus hoffmanni*. (*a*) and (*b*) Lateral and dorsal views of the skull respectively; (*c*) medial view of lower jaw. (see figure 4 for abbreviated labels on (*a*) and (*b*)).

Previous descriptions are avoided unless essential to the present understanding.

Fine surface detail of the bone shows up very well the striae, furrows, foramina and rugose areas that are associated with connective tissue and muscle attachment. However, muscle scars and surface texture alone, as for instance, pointed out by Taylor (1992), do not give a complete picture of muscle size nor the nature of the muscle e.g. whether pinnate or non-pinnate, intrinsic or extrinsic. This deficiency should be noted in fossil muscle restorations.

The mandibular adductor musculature (for closing the jaws) consists of the M. adductor externus and M. pseudotemporalis (figure 24*a*–*d*). In *Varanus bengalensis* the M. adductor externus is a complexly pinnate muscular system (see Frazzetta 1983) and is divided into three segments. Based on muscle scars and excavations, the M. adductor externus is reconstructed as originating on the postorbitofrontal, squamosal and lateral surface of the quadrate and inserting on the lateral surface of the coronoid including the coronoid eminence (figure 24*a*, *c*). The insertion on the coronoid eminence, although present in *Varanus*, is omitted by Russell (1964, 1967) and Callison (1967). An enormous lateral excavation on the surangular indicates a further site for a major insertion of the M. adductor externus (figure 24*b*). This is noted in only one other mosasaur, *Prognathodon solvayi* (Lingham-Soliar & Nolf 1989). In *Varanus* the more lateral fibres of the M. adductor externus also insert directly on the mandible although this insertion is omitted in mosasaurs by previous authors.

The M. adductor externus medialis lies immediately deeper than, with its fibres parallel to those of, the M. adductor externus. It presumably inserted on a basal aponeurosis, as in *Varanus*.

The M. adductor mandibulae profundus originates from the anterior surface of the quadrate and inserts on the posterior part of the mandibular (Meckelian) fossa (figure 24*a*). The posttemporal portion arises from the medial surface of the supratemporal (filling the posttemporal fossa) and inserts on the medial surface of the basal aponeurosis.

The M. pseudotemporalis consists of two distinct superimposed muscles, the M. pseudotemporalis superficialis and the M. pseudotemporalis profundus (figure 24*c*, *d*). The M. pseudotemporalis superficialis originates from the lateral surface of the parietal and bulges dorsally into the upper temporal fossa. It inserts on a tendinous sheet, indicated by well developed furrowing and countersunk foramina on the medial surface of the coronoid apex as in *Varanus*. The M. pseudotemporalis profundus originates from the ventral border of the descending process of the parietal and from the wall of the braincase and posteriorly from the ventral edge of the parietal and from the ventral margin of the anterior end of the prootic. It inserts on the medial surfaces of both the surangular and prearticular. Russell (1967) shows a single insertion either directly or via a basal aponeurosis on the medial surface of the surangular whereas Callison's (1967) restoration shows insertions on the lateral surface of the coronoid and surangular.

Bone scarring and a relatively deep excavation on the broad posteromedial surface of the splenial in *M. hoffmanni* suggests an anterior extension of the adductor muscles (figure 24*e*), probably the M. adductor mandibulae externus or the M. pseudotemporalis profundus as in *Xenosaurus grandis* or *Tupinambis teguixin* respectively.

Muscle scarring on the pterygoid, including on the ventral surface of the basisphenoid process, indicates condyle acting as a pulley on the radius and ulna, providing very little lateral movement. Such differences in articulations of the lower jaws are presumably because of highly different feeding styles in the two groups. Crocodiles tear off chunks of flesh and require very stable jaw joints. In mosasaurs, in contrast, the prey is swallowed whole. Hence the ingestion of relatively large food items by permitting the jaw joints to spread laterally by rotating outwards at the quadrato-mandibular and quadrato-squamosal joints, would be a distinct advantage. Dislocation of the joint may have been avoided by medial tendons close to the joint.

Several conditions in mosasaurs facilitated an increase in lateral gape: a relatively open intermandibular joint, a short, ligamentous mandibular symphysis, loose ligamentous connections of the pterygoids to the quadrates and by pivotal movements at the quadrato-squamosal joint. These conditions compensate for the relatively narrow skull of mosasaurs in comparison to that of plesiosaurs for instance. Furthermore, splaying out of the quadratic condyles tends to swing the dorsal portions of the articular units outwards. The pterygoideus muscle supplements this by drawing the ventral part of the articular unit inwards. In addition, the increased height of the articular unit in *M. hoffmanni* (cf. the much lower unit in plesiosaurs and ichthyosaurs) provides an increased lever arm for operating each jaw ramus about its longitudinal axis.

Taylor (1992) proposed that the large plesiosaur *Rhomaleosaurus* probably needed powerful depressor muscles to open the jaws quickly in water when seizing or manipulating prey. In my view an increased musculature was probably less essential in *M. hoffmanni*. Several conditions facilitated jaw opening. For instance, compared with plesiosaurs, the narrow lower jaws (figure 4*d*) produced less drag, each pivotal point was relatively longer, and the lower jaw mass probably greater (note depth of the mandibles in figures 4*a* and 5). Tendons (indicated by concentrated tendinous attachments on the coronoids (figures 3–5 and 14) under tension may have acted as a restraining force on the final stages of jaw opening (consider the weak quadrato-mandibular joint). Furthermore, work done by such tendons when the jaws were opened, would be transformed into stored elastic strain energy and then gravitational potential energy to accelerate the jaws shut. Similar force production and energy conservation are seen in the actions of ligamentum nuchae on the heavy heads of large grazing animals (facilitating their frequent raising and lowering).

### (*e*) ***Functional analysis of the teeth*** (**figure 26**)

The teeth of *Mosasaurus hoffmanni* combine robustness with sharp cutting edges. Penetration of the skin of the prey is rendered by the sharp anterior and posterior carina and unique cutting edges or suction-breaking grooves of the prisms on the buccal surfaces of the teeth. The teeth are moderately recurved posteromedially and the tips are slightly blunt. These conditions (also see *Pliosaurus* in Taylor & Cruickshank 1993) show an adaptation to great loadings. Broad tooth bases reduce forces per unit area. Oblique posteriorly sloping tooth bases may have interesting functional implications. During vertical loading of the tooth crown, because of tooth curvature, tension will build up on one side of the tooth base and compression on the other resulting in tensile stresses that will tend to break the tooth crowns off at the ankylosed surface with the base. However, with the obliquely posterior sloping tooth base, vertical loading forces on the recurved tips would continue to pass through the tooth bases (figure 26) reducing tension along the anterior base and lower stress. Consequently shear stress is less along the surface of ankylosis. Medially the tooth bases are more swollen and presumably acted in the same way to prevent shearing (see Rieppel's (1979) study on *Varanus*). On the other hand it may not even be the slope of the tooth base that is of biomechanical importance but the fact that it determines tooth orientation in the jaw that results in less recurvature and hence reduced tension on the anterior tooth crown surface (Michael Taylor personal communication 1994).

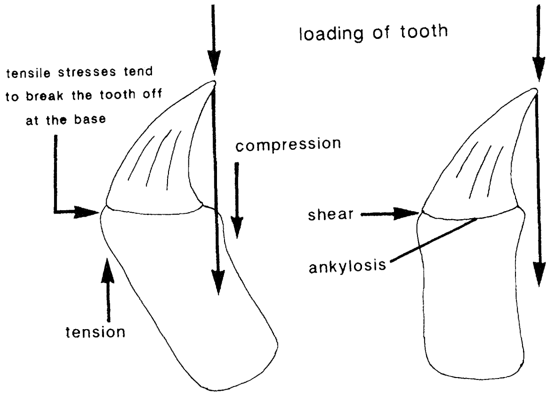

Figure 26. Functional analysis of the teeth in *Mosasaurus hoffmanni* shows (*a*) loading on normally orientated tooth bases and (*b*) loading if tooth bases are vertically orientated.

### (*f*) ***Postcranial mobility***

*Mosasaurus hoffmanni* swam using the tail in an axial subundulatory mode whilst the limbs would have been used for manoeuvring (Lingham-Soliar 1991*a*). Previously Camp (1942, p. 17) suggested that the great increase in the size of the muscle attachments on the distal end of the humerus in *Plotosaurus* facilitated considerable bending at the phalangeal joints although I suggest that it was more likely to be connected with rotation and pronation of the paddles (cf. otariids, English 1976). The glenoid articulation was presumably adequate for dorsoventral movements of the paddle. I cannot see any mechanical advantage in large scale dorsoventral bending at the phalangeal joints. Furthermore, such bending would clearly disrupt the uniformity of movement of the whole paddle blade and hence its efficiency. Two reasons for enhanced muscle attachments on the distal surfaces of the humerus are: (i) an increased length of the paddles such as in *Mosasaurus hoffmanni*, *M. lemonnieri* and *Plotosaurus*, would result in greater loadbearing on the

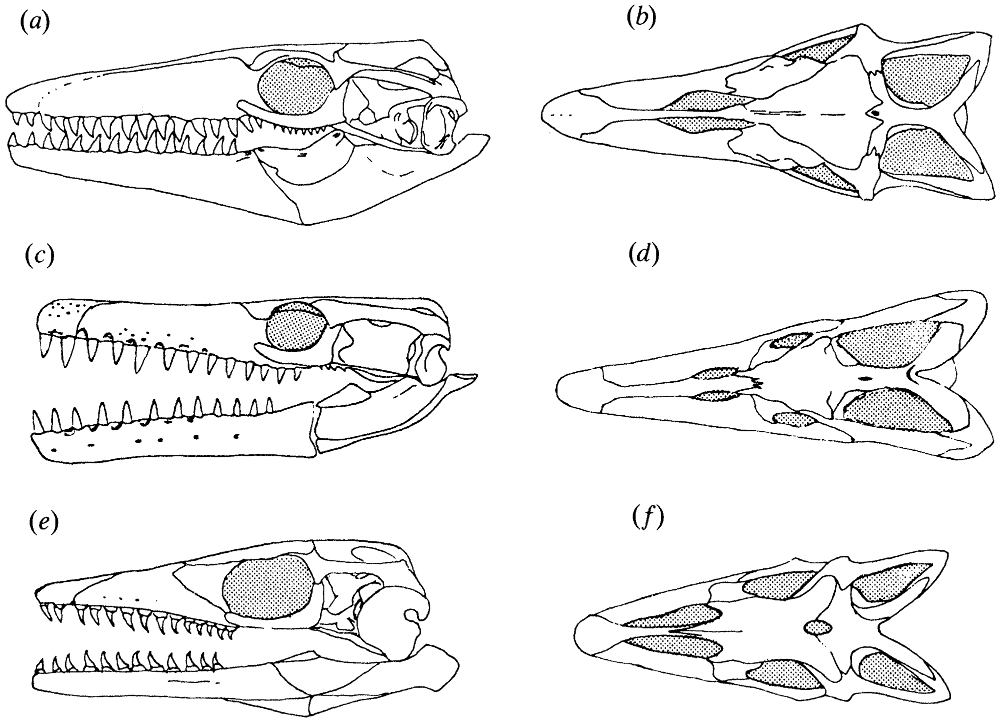

Figure 27. Mosasaur skulls (lateral and dorsal views respectively). (*a*) and (*b*) *Mosasaurus hoffmanni*; (*c*) and (*d*) *Goronyosaurus nigeriensis*; (*e*) and (*f*) *Plioplatecarpus houzeaui*.

humerus. Muscles located on the radius and ulna would distribute this load (English 1976); (ii) pronation at the humero-radio-ulnar joint during steering. The shape of the paddle indicates that it was used as a hydrofoil in turning movements by changes in the angle of attack. An enhanced facility for pronation at the scapulo-humero and humero-radio-ulnar joints would allow tighter control in elevating or depressing the leading edge, and hence greater efficiency in steering (Lingham-Soliar 1992*b*).

The huge forces that would result when such an enormous animal as *Mosasaurus hoffmanni* attempted to change direction by means of the paddles is apparent from a large specimen of the ilium, TSMHN 11208. The cap or head of the bone shows a strong area of separation (osteological damage) with the stem. They may indicate the effects of powerful shear forces at the articulation joint, apparently resulting from powerful rotations of the limbs (Pieter Dullmeijer, personal communication 1991).

## 11. EVOLUTION AND ECOLOGY

### (*a*) *Morphology and anatomy* (figure 27)

The earliest known mosasaurs, *Clidastes* (Russell 1967) and *Platecarpus* (Lingham-Soliar 1994*b*), are Turonian in age. At the other end of the evolutionary scale, *Mosasaurus hoffmanni*, from the Upper Maastrichtian Chalk, represents the peak of mosasaur evolution generally and shows a number of autapomorphies. For instance the largest body size in marine reptiles was achieved (Cope's rule). Telescoping of the cranial elements reached a relatively advanced state in *M. hoffmanni* although less than in cretaceans. Cranial kinesis seen in earlier mosasaurs was virtually lost. Overlapping of the frontal on the parietal dorsally and parietal on the frontal ventrally played a key part in the suppression of cranial kinesis. It was reinforced by e.g. the extension of the maxilla to the midpoint of the jugal including a strong ligamentous union between the two elements. Furthermore, bones of the palatal complex were closely united, resembling a secondary palate. Openings for the internal nares and the incisura piriformis (inpi in figure 4*c*) were reduced in size. Radinsky (1987) posed an interesting question regarding the evolution of the secondary palate. Did it arise primarily as skull support against forces generated during feeding and secondarily for the separation of air and food passages or vice versa? In *Mosasaurus hoffmanni* the indications are that the palate functioned as skull support. In the lower jaw overlapping of the surangular onto the articular and a unique extension of the surangular into the dentigerous unit furthered the trend towards a more tightly constructed unit.

The moderately sized external nares have moved relatively further posteriorly by an anterior extension of the skull, only exceeded in both conditions in *Goronyosaurus* (figure 27*c*, *d*; Lingham-Soliar 1991*b*).

The head musculature in *Mosasaurus hoffmanni* had become more differentiated, more powerful and more mechanically effective. These conditions led to greater control of skull and jaw movements.

*Mosasaurus hoffmanni* shows the most advanced form of tooth facetting in marine reptiles; each crown providing numerous cutting or breaking edges.

### (*b*) *Senses*

Relatively large orbits in *Mosasaurus hoffmanni* suggest that sight was good although binocular vision would have been relatively poor, as in most mosasaurs. An exception is noted in *Plioplatecarpus houzeaui* (figure 27*e*,

Upper Cretaceous of Northwestern Bulgaria. *N. Jb. Geol. Pal. monat.* 1976, 608–613.

Owen, R. 1840–1845 *Odontography* (2 volumes). London.

Parkinson, J. 1822 *Outlines of oryctology: an introduction to the study of fossil organic remains.* London.

Persson, P.O. 1959 Reptiles from the Senonian of Scania. *Ark. Miner. Geol.* **2**(5), 431–480.

Plesnier-Ladame, F. & Coupatez, P. 1969 Etude morphologique de l'anneau sclérotique de *Mosasaurus hoffmanni* Mantell, 1829. *Bull. Soc. belge. Géol. Paléont. Hydrol.* **78**, 253–265.

Radinsky, L.B. 1987 *The evolution of vertebrate design.* University of Chicago Press.

Rieppel, O. 1979 A functional interpretation of the varanid dentition (Reptilia, Lacertilia, Varanidae). *Gegenbaurs morph. Jahrb. Leipzig* **125**(6), 797–817.

Robaszynski, F., Bless, M.J.M., Felder, P.J., Foucher, J.C., Legoux, O., Manuuit, H., Meesen, J.P.M. Th. & Van Der Tuuk, L.A. 1985 La limite Campanien–Maastrichtien dans le limburg belgo–néerlandais. *Géol. Medit.* **10**(3–4), 59–72.

Russell, D.A. 1967 Systematics and morphology of American Mosasaurs. *Bull. Peabody Mus. nat. Hist.* **23**, 1–237.

Smith, K.K. 1980 Mechanical significance of streptostyly in lizards. *Nature, Lond.* **283**, 778–779.

Sömmerring, S.T. Von. 1820 Ueber die *Lacerta gigantea* der Vorwelt Denk. *Denkschr. Acad. Wiss.* **6**, 1816–1817 [1820], 37–58, plate 9.

Sulimski, A. 1968 Remains of Upper Cretaceous (Reptilia) of Central Poland. *Acta Palaeont. pol.* **13**(2), 243–250.

Swinton, W.E. 1930 On Fossil Reptilia from Sokoto Province. *Bull. Geol. Surv. Nigeria* **13**, 1–56.

Taylor, M.A. 1992 Functional anatomy of the head of the large aquatic predator *Rhomaleosaurus zetlandicus* (Plesiosauria, Reptilia) from the Toarcian (Lower Jurassic) of Yorkshire, England. *Phil. Trans. R. Soc. Lond.* B **335**, 247–280.

Taylor, M.A. & Cruickshank, A.R.I. 1993 Cranial anatomy and functional morphology of *Pliosaurus brachyspondylus* (Reptilia: Plesiosauria) from the Upper Jurassic of Westbury, Wiltshire. *Phil. Trans. R. Soc. Lond.* B **341**, 399–418.

Ubaghs, C. 1879 Description de quelques grand vertébrés de la Craie Supérieure de Maastricht. *Description Géologique et Paléontologique du sol du Limbourg.* **1879**, 238–249.

Van Regteren Altena, C.O. 1956 Achttiende-eeuwse Verzamelaars van fossielen te Maastricht en het lot hunner collecties. Natuurhistorisch Genootschap in Limburg. C. v. Drukkerij v.h. Cl. Goffin, Maastricht.

Williston, S.W. 1899 Some additional characters of mosasaurs. *Kans. Univ. Q.* **8**, 39–41.

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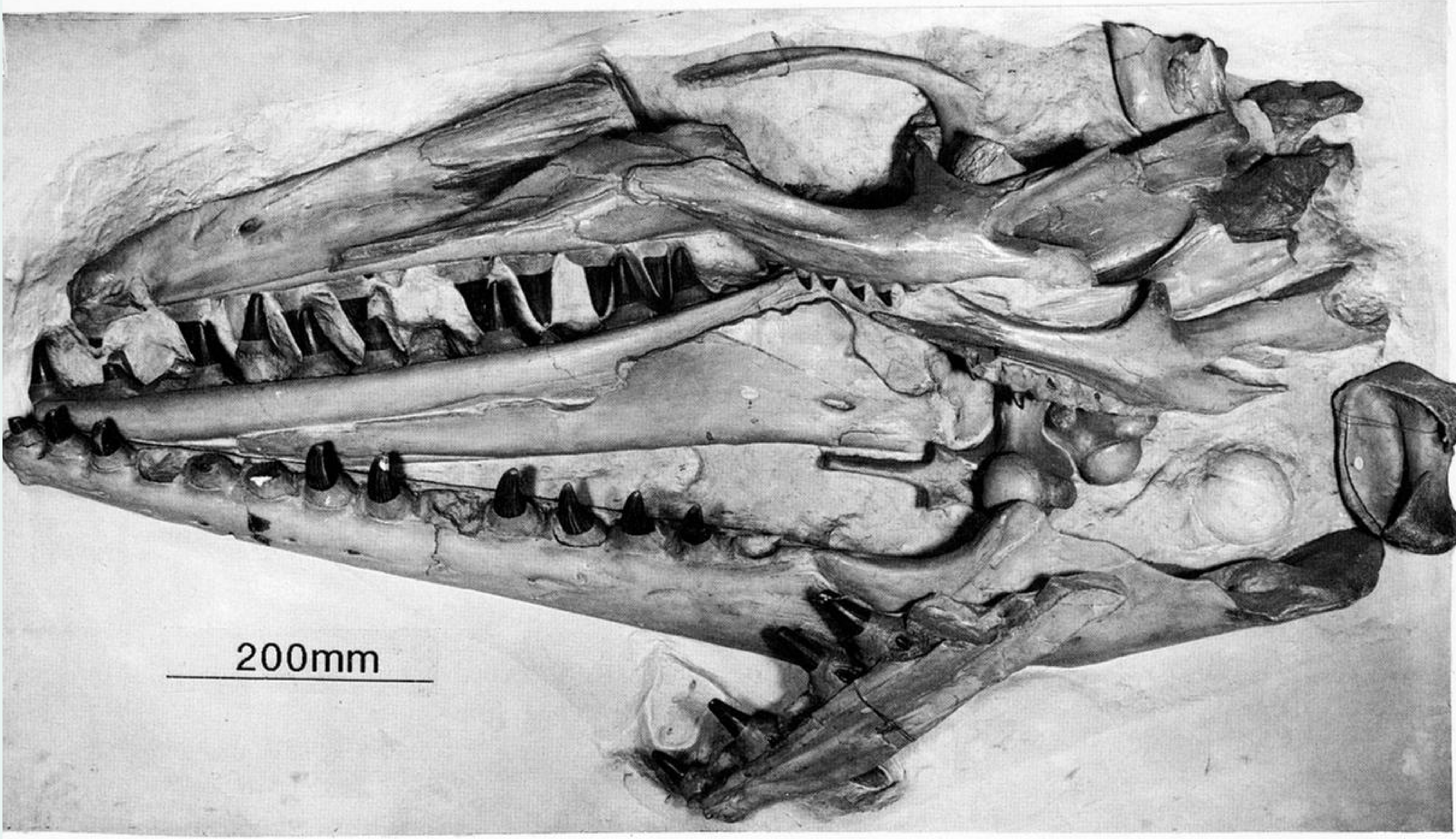


Figure 1. Cast of the holotype of *Mosasaurus hoffmanni* BMNH 11589.

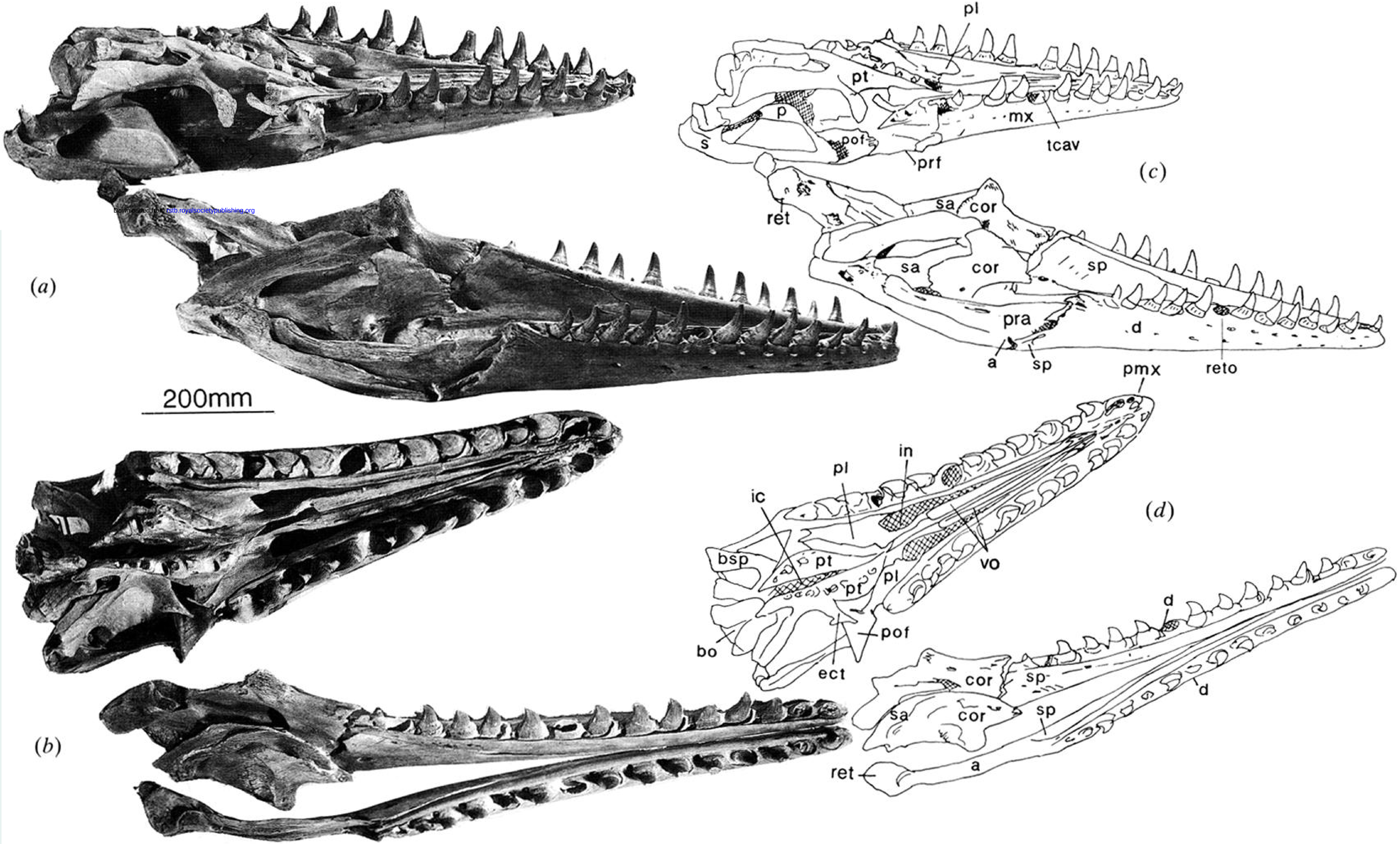
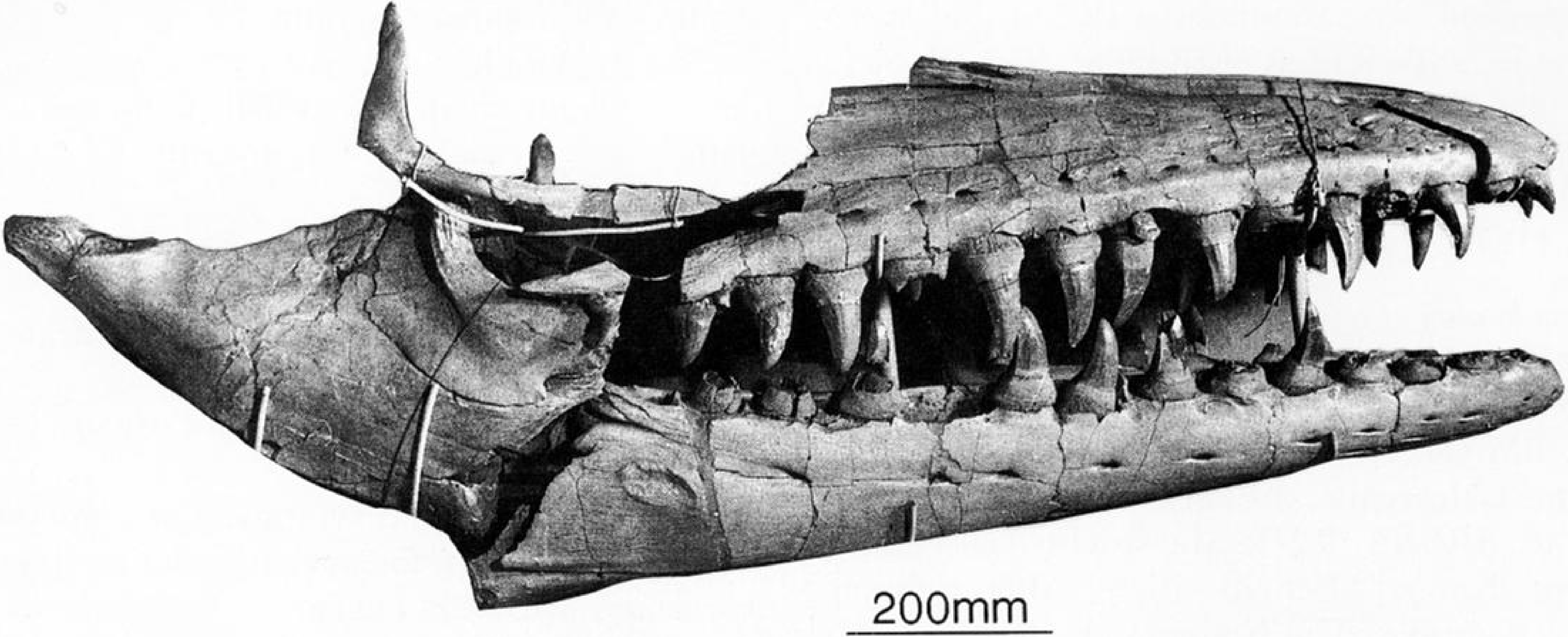
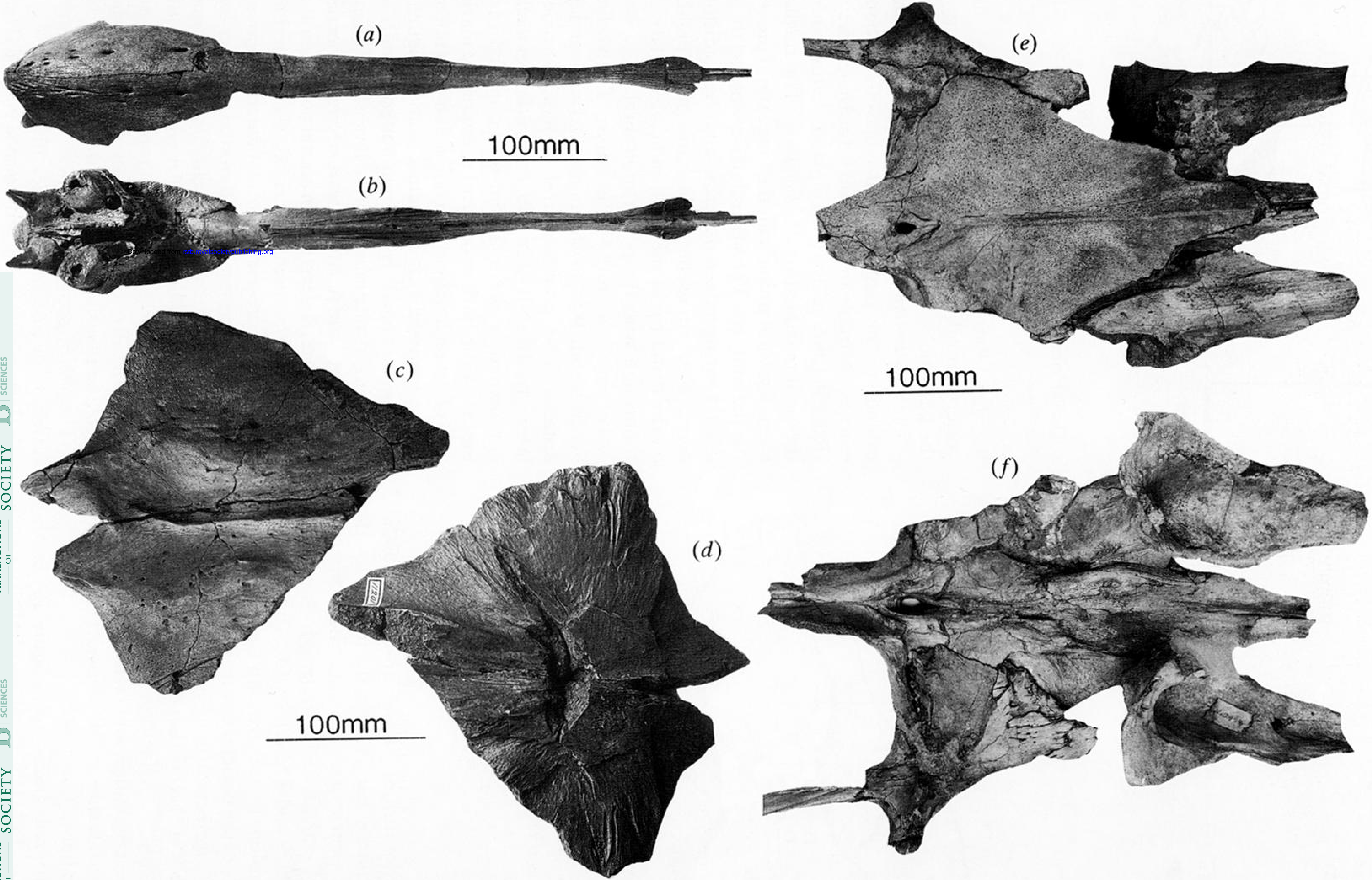


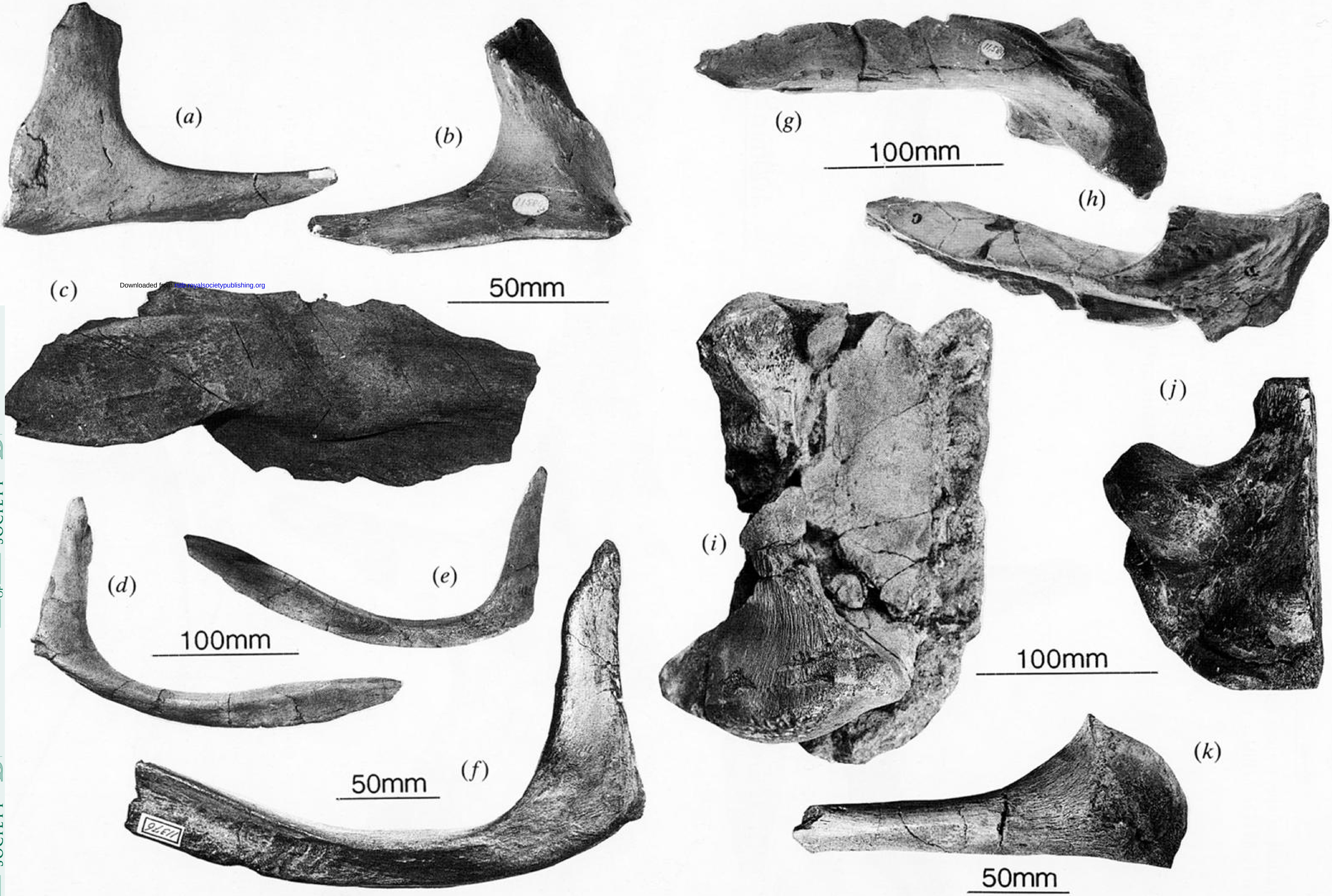
Figure 3. (*a*) Dorsolateral view of the skull (inverted) and mandibles of *Mosasaurus hoffmanni* IRSNB R12 superficially embedded in a matrix block; (*b*) the ame view from above and (*c*) and (*d*) respective bone maps.



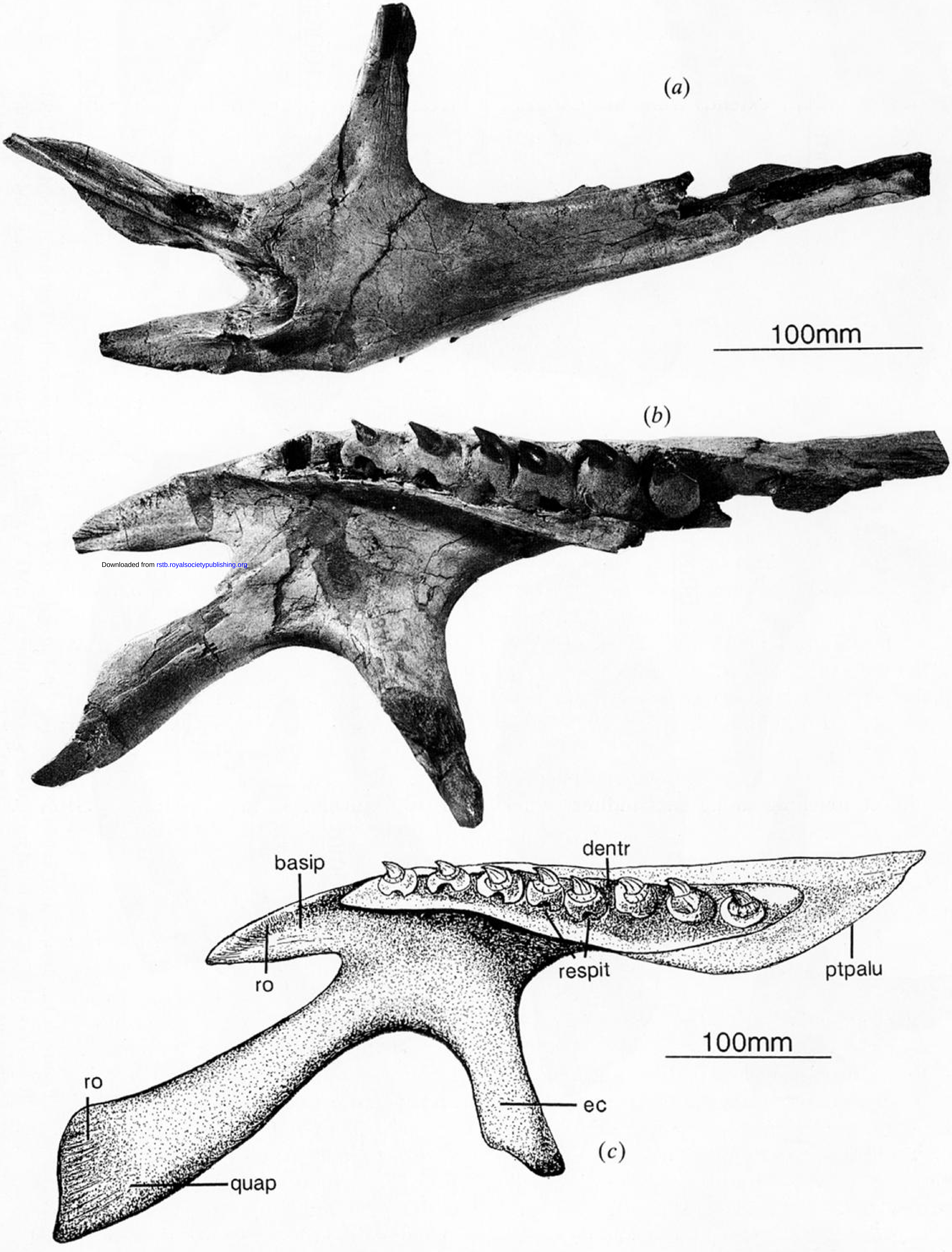
igure 5. Partial skull of *Mosasaurus hoffmanni* IRSNB R26 (frontal and parietal absent).



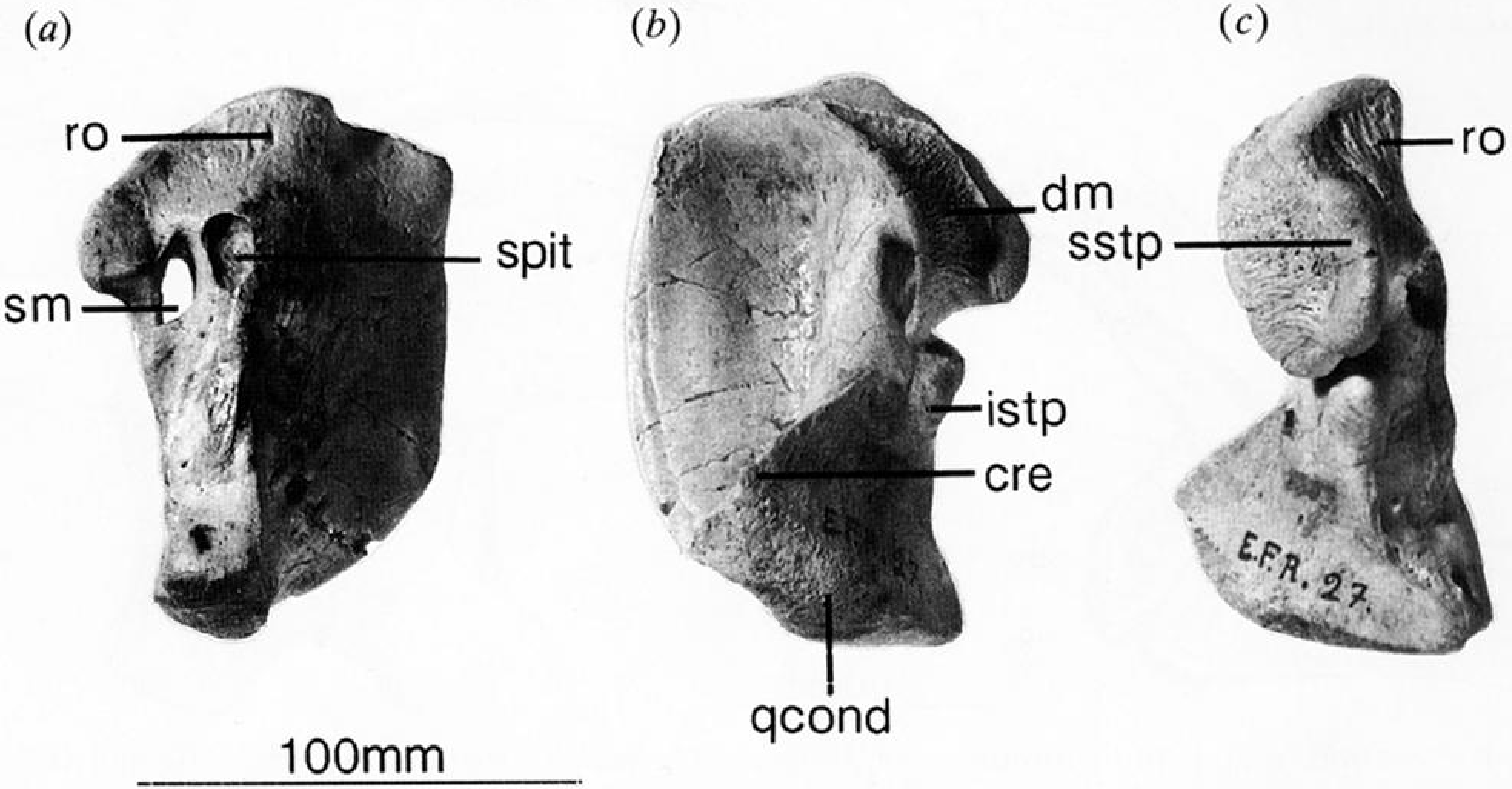
igure 6. Premaxilla of *Mosasaurus hoffmanni* IRSNB R26. (*a*) and (*b*) Dorsal and ventral views respectively. Frontal TSMHN 11201 (*c*) and (*d*) dorsal and entral views respectively. Frontal BMNH 42929 associated with prefrontals, postorbitofrontal and partial parietal (*e*) and (*f*) dorsal and ventral views espectively.



igure 9. Lachrymal BMNH 11589. (*a*) and (*b*) Lateral and medial views respectively. Prefrontal TSMHN 17281. (*c*) Lateral view. Jugal IRSNB R26. (*d*) and (*e*) Lateral and medial views respectively. TSMHN 11376. (*f*) Medial view. Squamosal BMNH 11589. (*g*), (*h*) Dorsal and ventral views espectively. Quadrate NHMM 603092. (*i*) Lateral view. Humerus TSMHN 11252. (*j*) Flexor view. Ilium TSMHN (unnumbered). (*k*) Medial view.



igure 11. Left pterygoid of *Mosasaurus hoffmanni* IRSNB R26. (*a*) Dorsal view; (*b*) ventral view and (*c*) restoration.



igure 12. Left quadrate of *Mosasaurus hoffmanni* IRSNB R26. (*a*) Medial view; (*b*) lateral view; (*c*) posterior view.

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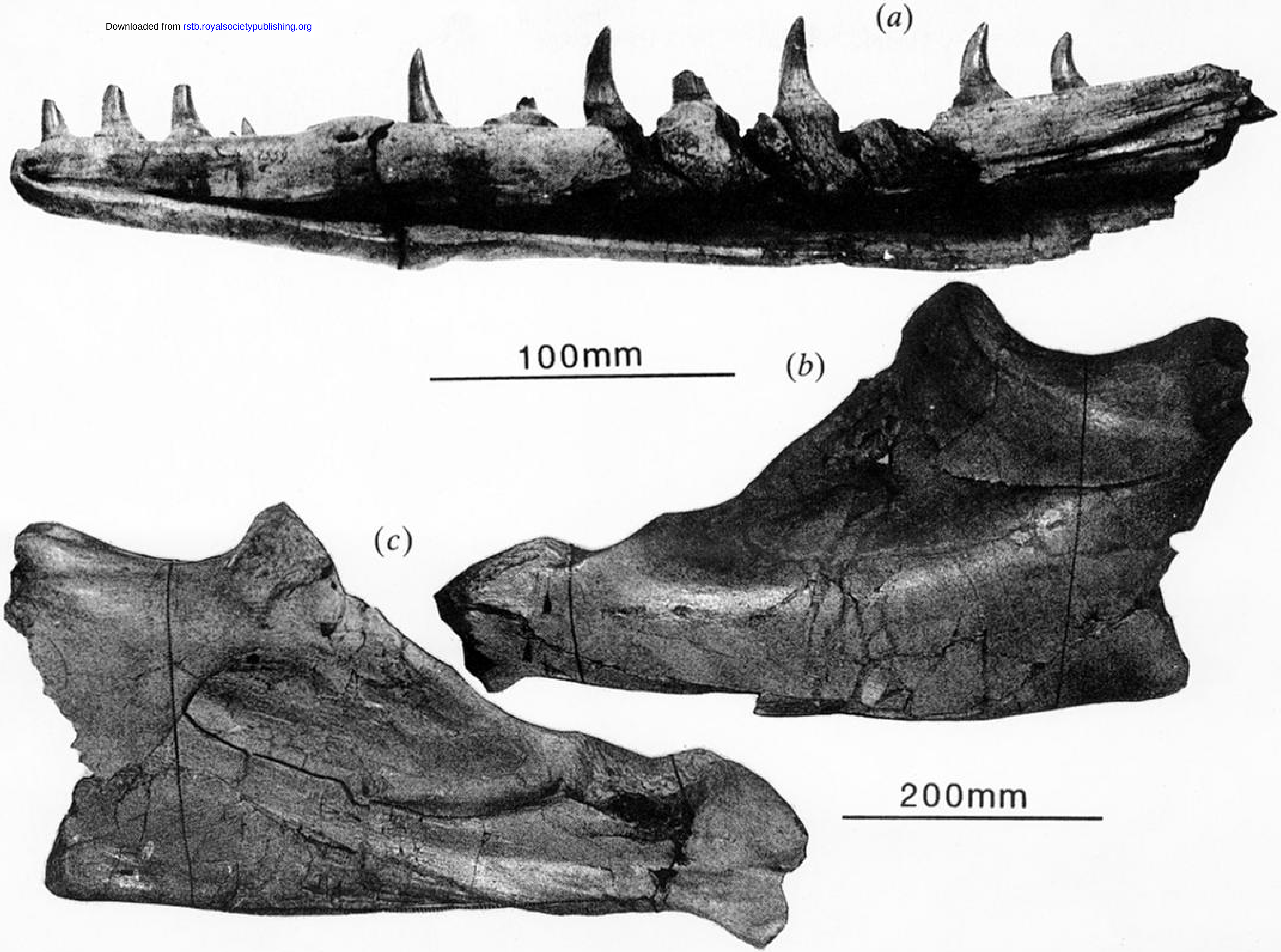

igure 14. Dental and post mandibular unit (pmu) in *Mosasaurus hoffmanni*. Right dentary IRSNB R27. (*a*) Medial ew. Right pmu IRSNB R26. (*b*) and (*c*) Lateral and medial views respectively.