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A mosasaur from the Maastrichtian Fox Hills Formation of the northern Western Interior Seaway of the United States and the synonymy of *Mosasaurus maximus* with *Mosasaurus hoffmanni* (Reptilia: Mosasauridae)

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Abstract

We report here a large mosasaur skull, preserved three-dimensionally in a concretion recovered from Ziebach County, South Dakota, USA. This fossil represents the first articulated mosasaur skull from the Trail City Member of the Fox Hills Formation and the first definitive occurrence of *Mosasaurus hoffmanni* Mantell, 1829 from that area and the northernmost occurrence in the Western Interior Seaway, greatly extending the paleobiogeographic range of this taxon. The age of this specimen is determined to be between 68.3 and 67.6 Ma based on the associated invertebrate fauna. Although previous authors have suggested synonomy of the North American *Mosasaurus maximus* Cope, 1869 and the European *M. hoffmanni,* this is the most comprehensive analysis to date and is based on comparisons with *Mosasaurus* specimens recovered across the Northern Hemisphere, allowing an emended diagnosis of the species *M. hoffmanni*. Minor differences are considered individual variation or to reflect ontogenetic stage, including slender dentaries in some individuals, range of development of the C-shaped notch of the coronoid and differences in the shape of the supratemporal fenestra.

Keywords: biogeography, biostratigraphy, morphology, Late Cretaceous, Plotosaurini, taxonomy

Introduction

We report here on a fairly complete and well preserved skull of a large adult specimen of the genus *Mosasaurus* (Squamata, Mosasauridae) (Figs 1 and 2). We describe the new material and compare it with the holotypes and referred specimens of *Mosasaurus hoffmanni* Mantell, 1829 and *Mosasaurus maximus* Cope, 1869 housed in North American and European collections. We assess the geological age of the specimen and perform a phylogenetic analysis and assess the relationships. We then address the taxonomy, biogeography and chronostratigraphic distribution of two nominal species (*M. hoffmanni* and *M. maximus*). The specimen described herein is considered significant because of the scarcity of mosasaur material from the Fox Hills Formation, its unique mode of preservation and because it represents the first reported occurrence of the species *M. hoffmanni* from the northern Great Plains of the USA. The specimen was discovered in 1993 by Helen Ross of Timber Lake, South Dakota, and Owen Fights Lone (*alias* Owen Long Elk) of Bullhead, South Dakota (both now deceased), as float in the channel of the Moreau River in Zeibach County, South Dakota, on the Woodward Farm (then owned by Lawrence and Virginia Woodward of Dupree, South Dakota). Ms. Ross maintained possession of the fossil until 2002, when it was donated to the Timber Lake and Area Museum (TLAM) in Timber Lake, South Dakota, where it is now housed under the accession number TLAM NH.HR.2009.032.0001. Later in 2002, members of the Ross and Woodward families, the Timber Lake museum, Native American tribal officials and others returned to the collecting site (Nelson, 2002), recovering additional portions of the muzzle. Later (Nelson, 2003) this specimen was brought to the attention of vertebrate paleontologists at the South Dakota School of Mines and Technology (SDSMT) and the New Jersey State Museum.

Fig. 1. Right lateral view of M. hoffmanni skull (TLAM NH.HR.2009.032.0001). Scale bar is 10 cm.

The current work is largely derived from the Masters thesis of the first author (Harrell, 2010) while a student at SDSMT. The thesis consists of specimen-based comparisons of morphological features, primarily focused on the cranial region, for species of *Mosasaurus* from the northern hemisphere.

Location and geological setting

The specimen described herein was collected as float from the channel of the Moreau River approximately 2.0 km west of the bridge crossing State Highway 65 in Ziebach County, South Dakota (Fig. 3). The site was designated as SDSMT locality number V9325 (coordinates and details on file at SDSMT, Rapid City, South Dakota). This site is located on the Woodward farm, which is privately deeded land within the boundaries of the Cheyenne River Indian Reservation.

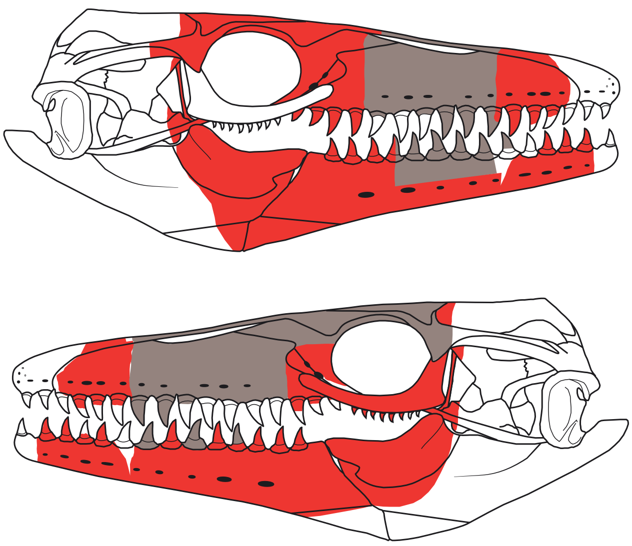

Fig. 2. Diagram indicating preserved portions of right (top) and left (bottom) sides of M. hoffmanni *skull (TLAM NH.HR.2009.032.0001). Red areas indicate preserved bone while gray areas indicate portions preserved as moulds of the internal surface of skull bones. Line drawing modified from Lingham Soliar (1995).*

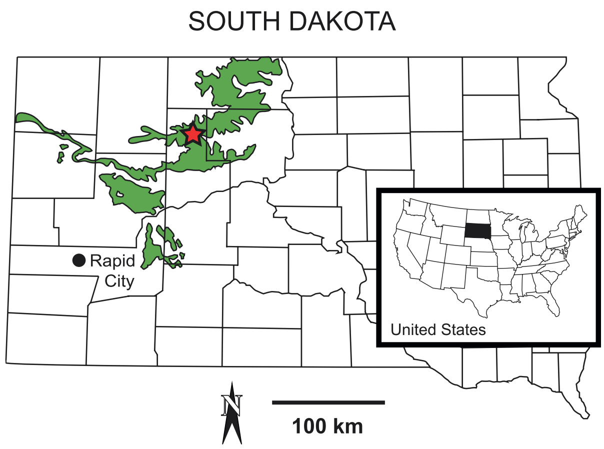

Fig. 3. Distribution of Fox Hills Formation outcrops in South Dakota, USA. TLAM NH.HR.2009.032.0001 locality (SDSM V9325) indicated by star.

The TLAM is currently the exclusive investigator of the site where TLAM NH.HR.2009.032.0001 was discovered, through an agreement with the current land owners. Since the specimen was found out of context, an assessment of the age of the specimen was based on lithological comparisons of matrix removed from the skull with local geological units in the recovery locality and on the ammonite biostratigraphy of the area.

Matrix excavated from the skull of TLAM NH.HR.2009.032.0001 reveals that it was encased in a silty, sandy, carbonate concretion. The concretion is light gray on fresh exposures and weathers to tan or reddish brown. Microscopic analysis shows that the clastic material of the concretion consists primarily of lithic fragments. The presence of medium-grained clasts suggests that the source of the specimen is the Trail City Member of the Fox Hills Formation rather than the underlying shaley, fine-grained Elk Butte Formation (Fig. 4). No microfossils were recovered from the matrix, consistent with the observations of Landman & Waage (1993) of the Fox Hills Formation.

Fossil invertebrates from the site include the ammonites *Hoploscaphites nicolleti*, *Jeletzkytes spendeni*, *Discoscaphytes conradi* and *Discoscaphytes rossi* (J. Nelson, pers. comm., 2007), and the bivalves *Ostrea* sp. and *Nucula* sp. (Waage, 1968). The presence of *J. spendeni* places the site within the *H. nicolletti* Range Zone described by Landman & Waage (1993). The presence of *J. spendeni*, which is restricted to the *H. nicolletti* Range Zone (Landman & Waage, 1993), suggests that TLAM NH.HR.2009.032.0001 is likely also from this biozone. The *H. nicolletti* Range Zone is of Middle Maastrichtian age, equivalent to the *Globotruncana gansseri* Zone of the Atlantic and Gulf Coastal Plains (Landman & Waage, 1993). Cobban et al. (2006) assigned the *H. nicolletti* Range Zone an Upper Maastrichtian age, in agreement with the European-style bipartite division of the Maastrichtian. Kauffman et al. (1993) and Harries (2003) indicated that the numerical age of the *H. nicolletti* biozone falls between 68.3 and 67.6 Ma based on radiometric correlation with ammonite biozones. TLAM NH.HR.2009.032.0001 was deposited during this period of time. This numerical age estimate does

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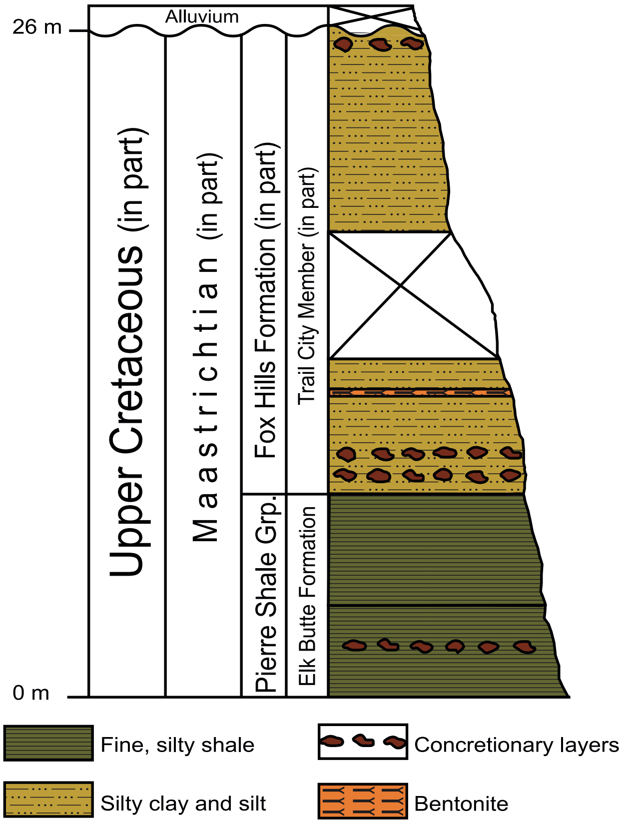

Fig. 4. Generalised weathering profile and stratigraphic column of site SDSM V9325 where TLAM NH.HR.2009.032.0001 was recovered.

not include any adjustment to the K/Pg boundary based on recent astronomical calibration (Husson et al., 2011).

Materials and methods

TLAM NH.HR.2009.032.0001 consists of a partial skull preserved in three-dimensional articulation in a fine-grained, carbonate mud, sandstone concretion. It was found broken into four portions. The two posteriormost blocks of the skull are the largest, and were reunited and mechanically prepared. The interior of the skull was not prepared so that the various elements would remain in articulation for public display. Small areas of the right dentary and right prefrontal were restored, as were several of the marginal teeth on both sides of the skull. The two remaining blocks consist of the anterior region of the muzzle unit and the anterior portions of the dentaries. The specimen was moulded and a cast (SDSM C672) was placed into the SDSMT Museum of Geology collection. The serrations of the marginal dentition were digitally imaged using a Zeiss® Supra40VP variable pressure scanning electron microscope in the Department of Geology at SDSMT under the supervision of Dr Edward Duke.

Comparisons were made with specimens located in museums across the USA and Western Europe. A list of cranial measurements for TLAM NH.HR.2009.032.0001 is given in Table 1.

Institutional abbreviations used in this report are as follows: ALMNH – University of Alabama Museums, Tuscaloosa, Alabama, USA; AMNH – American Museum of Natural History, New York, New York, USA; IRSNB – Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; MNHNP – Museum National d'Histoire Naturelle Paris, France; NHMM – Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands; NHMUK – Natural History Museum, London, UK; NJSM – New Jersey State Museum, Trenton, New Jersey, USA; SDSM – South Dakota School of Mines and Technology, Rapid City, South Dakota, USA; TLAM – Timber Lake and Area Museum, Timber Lake, South Dakota; TM – Teylers Museum, Haarlem, the Netherlands; TMM – Texas Memorial Museum, University of Texas-Austin, USA.

The following osteological abbreviations are used in the figures: La – lachrymal; Laf – lachrymal foramen; Mx – maxilla

Table 1. Cranial measurements of M. hoffmanni TLAM NH.HR.2009.032.0001

Measurement	Size (mm)
Maximum preserved length of skull	840
Maximum preserved width of skull	350 (across posterior maxillae)
Right maxilla length	780*
Right maxilla height	135 (at 11th maxillary tooth)
Right prefrontal length	440*
Right prefrontal height	130 (at orbital margin)
Right lachrymal length	200
Right lachrymal height	40
Frontal length	520
Frontal maximum width	320*
Right postorbitofrontal width	110
Right postorbitofrontal length	225 (preserved)
Parietal width at frontal suture	220*
Left dentary preserved length (dorsal)	680 (to posterior margin of 2nd tooth)
Left dentary preserved length (ventral)	770
Right coronoid length	260*
Right coronoid height	195
Left coronoid length	210 (preserved)
Left coronoid height	200
Left ectopterygoid length	141
Left ectopterygoid width	79
Left epipterygoid observable length	119
Left epipterygoid observable width	11

* Estimate

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(L. left and R. right); Paf – palatine foramen; Pal – palatine; Pmx – premaxilla; Prf – prefrontal; Sptmx – septomaxillae; Vom – vomers.

Systematic paleontology

Order Squamata Oppel, 1811
Superfamily Mosasauroidea Gervais, 1853
Family Mosasauridae Gervais, 1853
Subfamily Mosasaurinae Gervais, 1853
Genus *Mosasaurus* Conybeare, 1822
Mosasaurus hoffmanni Mantell, 1829
Lacerta gigantea (von Sömmerring, 1820)
Mosasaurus belgicus (Holl, 1829–1830)
Mosasaurus camperi (von Meyer, 1832)
Mosasaurus dekayi (Bronn, 1838)
Mosasaurus major (DeKay, 1842)
Mosasaurus mitchilli (Leidy, 1865)
Mosasaurus meirsii (Marsh, 1869)
Mosasaurus princeps (Marsh, 1869)
Mosasaurus maximus (Cope, 1869)
Mosasaurus giganteus (Cope, 1869–1870)
Mosasaurus fulciatus (Cope, 1869–1870)
Mosasaurus oarthus (Cope, 1869–1870)

Holotype

MNHNP AC 9648, partial skull including the maxillae, prefrontal, pterygoids, palatine, jugal, squamosal, quadrate, dentaries, splenials, angular, surangulars, coronoids, prearticulars and articulars. Two cervical vertebrae and a femur are also associated with this specimen. (See Bardet & Jagt (1996), Mulder (2004) and Pieters et al. (2012) for a detailed account of the history of this specimen.)

Type locality and horizon

Subterraneous quarry at St Peter's Mount near St Pietersberg, southwest of Maastricht, the Netherlands. Late Maastrichtian, Maastricht Formation.

Notable referred specimens

NHMUK 11589, 42929, IRSNB R12, R1506, R25, R26, R27, NHMM 006696, TM 11202, 11245, TLAM NH.HR.2009.032.0001, AMNH 1389, NJSM 11052, NJSM 11053, TMM 313-1, ALMNH PV 1988.0018, ALMNH PV 1990.0003

Emended cranial diagnosis

Low, rounded median dorsal crest on premaxilla; narial emargination begins at point between fifth and sixth maxillary teeth; 13–14 teeth in maxilla; anterolateral projection on frontal does not form any part of the border of the external nares; posteriorly projecting processes of frontal bracket the pineal foramen on parietal and extend well beyond the posterior border of the pineal foramen; palatal elements tightly united; eight pterygoid teeth; suprastapedial process of quadrate moderately large and medially deflected distally; infrastapedial process small; 14–15 dentary teeth; dentary deep posteriorly, rapidly narrows anteriorly; medial and lateral anterior flanges of coronoid very well-developed; single C-shaped notch on anterior lateral flange of coronoid in mature individuals; surangular deep and short in relation to dentary; marginal dentition robust and long with well-developed, serrated carinae; two to five buccal facets; anterior teeth D-shaped in cross–section, becoming more elliptical posteriorly; swollen, barrel-shaped tooth roots.

Geographic and temporal distribution

In the eastern hemisphere *M. hoffmanni* has been reported from the Netherlands (Mantell, 1829), Niger (Lingham-Soliar, 1991), Belgium (Lingham-Soliar, 1995), Turkey (Bardet & Tunoğlu, 2002), Poland (Machalski et al., 2003), Denmark (Bonde, 1997; Lindgren & Jagt, 2005) and Bulgaria (Jagt et al., 2006). Recently, in the western hemisphere, the Antarctic Peninsula (Martin & Crame, 2006) and Argentina (Fernández et al., 2008) were tentatively added to the geographic distribution of *M. hoffmanni*.

Stratigraphically, definitive occurrences of *M. hoffmanni* in the eastern hemisphere range from the Lower Maastrichtian Ciply Phosphatic Chalk of Belgium (Bardet & Tunoğlu, 2002) to the Upper Maastrichtian Formation, uppermost Meerssen Member, subunit IVf-6, just below the Cretaceous/Paleogene (K/Pg) boundary (Jagt et al., 2008). This stratigraphically youngest record consists of a partial skull *in situ* and not simply an isolated tooth. Machalski et al. (2003) referred isolated material from the Upper Campanian of Maruszów in Poland to *Mosasaurus* cf. *hoffmanni* but this identification is uncertain.

In the western hemisphere specimens previously assigned to *M. maximus* have been reported from the Navesink and basal Hornerstown formations of New Jersey (Cope, 1869; Gallagher, 1993; Staron et al., 2001), the Navarro Formation in Texas (Langston, 1966), the Coon Creek Formation of Tennessee (Russell, 1967), the Merchantville Formation in Delaware (Russell, 1967; Baird & Galton, 1981), the Severn Formation in Maryland (Baird, 1986), the Ripley Formation of Alabama (Ikejiri et al., 2013) and the Prairie Bluff Chalk of Alabama (Bryan, 1992). Since the two taxa were synonymised by Mulder (1999), *M. hoffmanni* was reported from the Ripley Formation in Alabama (Kiernan, 2002) and a tsunamite deposit at the top of the Owl Creek Formation in Missouri within the K/Pg boundary interval (Campbell & Lee, 2001; Gallagher et al., 2005; Campbell et al., 2008).

Stratigraphically, in the western hemisphere specimens previously referred to the *M. maximus* range from the Upper Campanian Coon Creek Formation of Tennessee (Russell, 1967) and the Merchantville Formation of Delaware (Baird & Galton, 1981)

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to the Upper Maastrichtian of Alabama (Bryan, 1992) and New Jersey (Gallagher et al., 2012).

Comments on previous taxonomy and diagnoses

The most recent diagnosis for *M. hoffmanni* was provided by Lingham-Soliar (1995, p. 161): '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.' Aside from the described narial emargination, these criteria are also characteristic of *M. maximus*. However, some *M. hoffmanni* specimens (IRSNB R27) also have narial emarginations located more posteriorly than those described by Lingham-Soliar.

Russell (1967, p. 139) diagnosed *M. maximus* as having '[a] slight medial dorsal crest on premaxilla. Small triangular ala projects laterally from supraorbital wing of prefrontal. Narial emargination begins dorsal to point between fifth and sixth maxillary tooth. Parietal foramen large, bounded by two long tongues from frontal. Large keel-shaped tuberosity below stapedial pit on lower medial body of quadrate, suprastapedial and infrastapedial process very small in lateral profile. Ventral wings of coronoid well developed on medial and lateral surface of lower jaw. Splenial has strong median dorsal keel on articulating surface. Fourteen teeth in dentary. Dentary deep posteriorly, rapidly narrows coming to nearly pointed tip anteriorly. Marginal teeth long with posteriorly recurved tips, prisms few in number (2–3) on external face, absent or nearly absent on internal face.' These characters are not unique to *M. maximus* and should not have been included in the diagnosis of the species. Opinions of the sizes of the supra- and infrastapedial processes of the quadrate appear to be subjective, as first suggested by Mulder (1999). These characteristics given by Russell for *M. maximus* are also found in *M. hoffmanni*.

Previous phylogentetic analyses of Mosasaurus

Bell (1997) conducted a phylogenetic analysis of all Mosasauroidea before the synonymy of *M. hoffmanni* and *M. maximus* using 142 characters to code 36 taxa. The results of his analysis showed *M. maximus* as being most closely related to an as yet undescribed species of *Mosasaurus* in the Nebraska Museum of Natural History. The defining characteristics of this relationship are a shallow alar concavity of the quadratic conch, large quadrate tympanic rim size, almost as high as the quadrate, and quadrate dorsal median ridge as a low, broadly inflated dome. Bell's analysis was restricted to taxa of North America and the Adriatic, but these three characters are also shared with *M. hoffmanni* in Europe.

Polcyn & Bell (2005) conducted an additional phylogenetic analysis of Mosasauroidea based on Bell's (1997) analysis but with the inclusion of new material to better constrain the basal region of mosasaur phylogeny. Their results for the genus *Mosasaurus* are the same as those in Bell (1997).

Taxonomic assignment of the Ross mosasaur

The taxonomic assignment of TLAM NH.HR.2009.032.0001 to the genus *Mosasaurus* (*sensu* Russell,1967) is supported by 13 teeth in maxilla; prefrontal forms small portion of posterolateral border of external nares; small to large triangular ala projects laterally from supraorbital wing of prefrontal (broken); frontal not emarginated above orbits; median dorsal ridge along midline of frontal; parietal foramen moderately large, closely embraced on either side by tongues from the frontal; ventral process of postorbitofrontal to jugal confluent with well-exposed dorsal surface of postorbitofrontal; ventroposterior process on jugal large; dorsal edge of surangular rather thin lamina of bone, rising anteriorly to middle of posterior surface of coronoid; mandibular teeth prismatic with relatively flat external and rounded internal surfaces. The specimen TLAM NH.HR.2009.032.0001 is further referred to the species *M. hoffmanni* Mantell, 1829 on the basis of two to five buccal facets on the marginal dentition, a single C-shaped notch on the anterolateral flange of the coronoid and the posteriorly projecting tongues of the frontal extend well beyond the pineal foramen of the parietal.

Examination of identified specimens of *M. hoffmanni* from Europe and *M. maximus* from the southern and eastern USA revealed no distinguishing characteristic that could be used to support two separate species. The emended cranial diagnosis for *M. hoffmanni* presented in the systematic paleontology section above was based on data augmented by TLAM NH.HR.2009.032.0001 and other North American specimens.

Description and comparisons

Premaxilla

Only the internarial bar remains of the premaxilla. The dorsal surface of the internarial bar is very rounded, somewhat inflated and projects well above the level of the premaxillary–maxillary suture. The suture is very deep and is not squamous. The premaxillary–maxillary suture extends posteriorly to a point between the fifth and sixth maxillary teeth where the premaxilla and maxilla diverge and the openings for the external nares originate. These openings are preserved as natural casts.

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Posteriorly, the internarial bar becomes extremely narrow, splint-like and articulates between two anteriorly projecting flanges from the frontal. Two small pathological osseous nodules are present on the internarial bar.

The premaxillae in both *M. hoffmanni* and *M. maximus* are well-preserved in numerous specimens. In smaller, more juvenile individuals (IRSNB R12), the rostrum forms a more acute angle in both the vertical and horizontal planes whereas more mature individuals display a more rounded, robust rostrum in both planes (NHMM 00696, NJSM 11053, TMM 313-1). On the medial dorsal surface of the tooth-bearing portion of the premaxilla is an inflated ridge that extends posteriorly along the internarial bar. The premaxillary teeth are much reduced in size in comparison to the maxillary dentition and are somewhat prognathous. In the first premaxillary teeth the anterior carinae are slightly more medial whereas the posterior carinae are more laterally oriented. Comparisons show that both species are identical, with minor degrees of individual and ontogenetic variation (see Mulder, 1999, fig. 3).

Maxilla

The right maxilla is the better preserved of the two, but most of the middle portion between maxillary teeth five and 11 has been lost to weathering. A natural mould of the internal surface of the right maxilla remains, which permits at least a partial description. Fourteen tooth alveoli are present and the 11th to 14th teeth on the right side are nearly complete. A dental count of the missing portion of the maxilla was accomplished by counting the indentations of the tooth roots left on the internal mould of the maxilla.

The external nares begin at a point dorsal to between the fifth and sixth maxillary tooth positions and terminate, bordered by the prefrontals, at a point dorsal to the 11th maxillary tooth, as indicated by the impression remaining on the matrix. A robust, laterally projecting bulge is present just dorsal to the alveolar border along the length of the maxilla. The anterior lateral surfaces of the maxillae are covered with a vermiculate-like texture.

The maxillae of both *M. hoffmanni* and *M. maximus* are robust elements that contain alveoli for 14 teeth per side. Some individuals referred to *M. maximus* possess only 13 maxillary teeth (NJSM 11053) but it is uncertain whether this count is accurate. Many Cretaceous marine fossils from New Jersey are heavily damaged by pyrite disease (personal observation) and may be inaccurately reconstructed. Furthermore, tooth counts are known to vary in numerous extant reptile species (Greer, 1991; Rasmussen, 1996) and tooth counts in other *Mosasaurus* species (*M. conodon*) are reported to be bilaterally asymmetrical (see Ikejiri & Lucas, 2014). Therefore, this criterion is not considered significant enough to justify separation of *M. hoffmanni* and *M. maximus* into different species.

In lateral view, the suture with the premaxilla ascends from the alveolar border, curving anteriorly to posteriorly in a smooth arc. At a point dorsal to the labial foraminal row, the suture becomes nearly straight and ascends posterodorsally to the internarial bar just posterior to the second maxillary tooth. The suture continues posteriorly in a nearly straight line to a point dorsal to between the fifth and sixth maxillary teeth where the maxilla and premaxilla diverge to form the external nares. This condition is matched in both *M. hoffmanni* and *M. maximus* but is not observed in other species of *Mosasaurus*.

On the lateral surface of the maxilla dorsal to the dental alveoli and ventral to the labial foraminal row is a robust, horizontally oriented bulge that extends nearly the entire length of the maxilla. Posteriorly, the maxilla terminates in a point of bone that extends approximately halfway across the width of the orbit along the ventral border of the orbit. This point of bone is overlain by the horizontal ramus of the jugal. This condition of the maxilla is developed to the same extent in *M. hoffmanni* and *M. maximus*.

Prefrontal

The right prefrontal, which is the better preserved of the two, has lost the laterally projecting ala to erosion. The anterior portion of the right prefrontal is also missing but the internal sutures are preserved as a mould on the matrix. The prefrontal is bordered anteroventrally by the maxilla, posteroventrally by the lachrymal, posteromedially by the frontal and posteriorly contacts the postorbitofrontal. Anteriorly, the prefrontal comprises the posterolateral half of the external nares. Posteriorly, the prefrontal terminates at a point approximately midway across the orbit where it contacts the postorbitofrontal, excluding the frontal from the orbital margin. There are no apparent differences in the prefrontals of *M. hoffmanni* and *M. maximus*.

Lachrymal

The right lachrymal is the better preserved of the two and is positioned along the ventroanterior border of the orbit and projects anteriorly between the maxilla and the prefrontal (Fig. 5). The lachrymal appears to be divided into three separate units by two large foramina. The larger, posterior foramen is likely the palatal foramen while the anterior opening is the

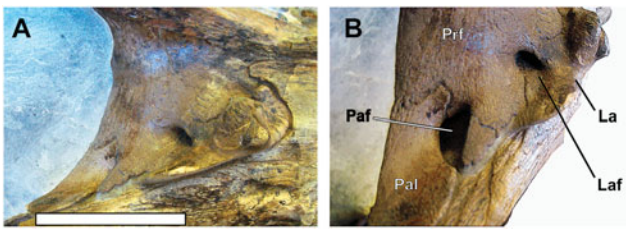

Fig. 5. A, Right lachrymal of M. hoffmanni *(TLAM NH.HR.2009.032.000)1 in lateral view. Anterior to right. Scale bar is 10 cm. B, Posterolateral view of right lachrymal showing palatine (Paf) and lachrymal (Laf) foramina.*

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lachrymal foramen (M. Polcyn, pers. comm., 2014). A large, apparently pathological feature is found anteriorly on the right lachrymal. The anterior half of the lachrymal has a laterally projecting shelf along its ventral margin that may have been attached to the anterodorsal edge of the jugal. The lateral outline of the lachrymal is somewhat quadrilateral in shape.

The only previously described lachrymal in *M. hoffmanni* (NHMUK 11589) was reported by Lingham-Soliar (1995, fig. 9a–b). However, the 'arrow-shaped' element figured appears more like an ectopterygoid than a lachrymal.

Frontal

The right half of the frontal is relatively well preserved whereas most of the left half is missing. The dorsal outline of the frontal is somewhat triangular (Fig. 6C). A pronounced median dorsal keel is especially prominent anteriorly. The anteromedially projecting tongues of the frontal form the posteromedial border of the external nares. These projections could have been overlain by the posterior portion of the internarial bar of the premaxilla. Laterally, the frontal is excluded from the orbit by the prefrontal and postorbitofrontal. The medial, posteriorly projecting tongues of the frontal extend caudally along the dorsal surface of the parietal, bracketing the pineal opening which lies anteriorly on the parietal table. These projections extend 3.0 cm beyond the posteriormost border of the pineal opening. The pineal opening is not shared with the frontal. The ventral portion of the frontal cannot be observed.

The frontal is a large shield-shaped element with a prominent mid-sagittal crest. In both *M. hoffmanni* and *M. maximus* a large

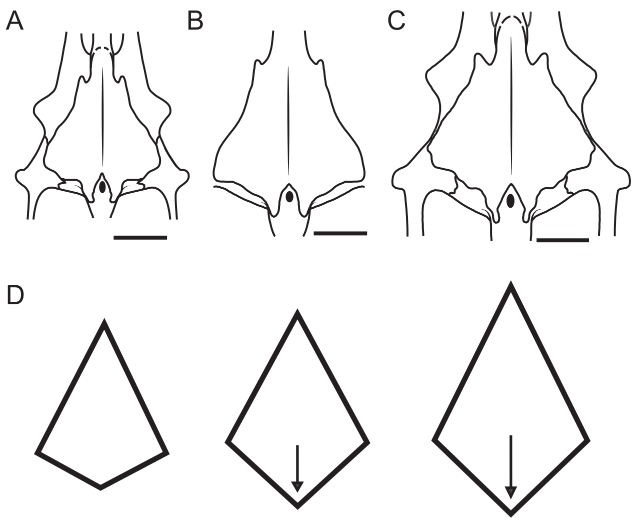

Fig. 6. A, Restored outline of frontals in M. hoffmanni *in dorsal view (NHMUK 42929, adapted from Mulder, 1999). B,* M. maximus *(NJSM 11052, adapted from Russell, 1967). C, Restored frontal of Ross mosasaur (TLAM NH.HR.2009.032.0001). D, Apparent direction (indicated by arrow) of ontogenetic change in shape of frontal in* M. hoffmanni. *Scale bars equal 10 cm.*

anterolateral projection extends anteriorly into the posteromedial border of the prefrontal on the left and right sides. This projection does not form any part of the border of the external nares. This condition is not matched in any other described species of *Mosasaurus*.

On the posteromedial border of the frontal, two tongues of bone project posteriorly and bracket the pineal opening of the parietal. In both *M. hoffmanni* and *M. maximus* the projections from the frontal extend beyond the posterior border of the pineal opening by at least the length of the pineal opening itself. Lingham-Soliar (1995) described the presence of a recess in the [posteroventral] surface (mistakenly called 'anteroventral surface' on p. 161) of the frontal that received an anteroventral process from the parietal that is present in *M. hoffmanni* and absent in *M. maximus*. However, this recess is present in *M. maximus* specimen ALMNH PV 1988.0018 from Alabama.

The morphology of the frontal appears to some extent dependent on the ontogeny of the individual (Fig. 6). Smaller specimens have straighter, less convoluted sutures and the posterior border with the parietal is straighter. In dorsal outline the frontal is primarily triangular. In more mature individuals the frontal is broader and extends more posteriorly, appearing more diamond-shaped in dorsal outline.

Parietal

Only the anteriormost portion of the parietal is preserved but most of the left side has been lost to erosion. The parietal forms the anterior and medial borders of the superior temporal fenestrae, which are subrectangular in outline anteriorly. Most of the dorsal parietal table has been lost to erosion, but it is somewhat rectangular in outline anteriorly and becomes slightly constricted posteriorly near its midpoint. The medial portion of the frontal-parietal suture is W-shaped to accommodate the posteriorly directed tongues of the frontal. The pineal foramen lies anteriorly in the medial wedge of the W-shape. Only the right border of the pineal foramen remains and is 2.5 cm in length. The intricately sutured frontal-parietal contact effectively negated any cranial kinesis in this region of the skull. Laterally the parietal is sutured with the postorbitofrontal.

Postorbitofrontal

Only a portion of the right postorbitofrontal is preserved while the entire left element is missing. The posterior process of the right postorbitofrontal is broken and missing. The dorsal surface of the postorbitofrontal is broadly exposed posterior to the frontal. The majority of the descending portion is broken and eroded away. The dorsal, posteriorly projecting process of the postorbitofrontal rests in a deep V-shaped trough of the ventrally positioned squamosal.

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The postorbitofrontal is large and robust in both *M. hoffmanni* and *M. maximus*. Lingham-Soliar (1995) stated that the posteriorly projecting ramus of the postorbitofrontal terminates more anteriorly on the squamosal in *M. maximus* than in *M. hoffmanni*. An examination of *M. maximus* (TMM 313-1) demonstrates that the postorbitofrontal extends posteriorly to the same degree in both species.

Jugal

The left jugal of TLAM NH.HR.2009.032.0001 is nearly complete (Fig. 7A). The horizontal bar of the jugal is gently concave upward and the anterior portion is eroded. A prominent tuberosity extends posteriorly from the horizontal portion of the jugal. The ascending process of the jugal has a very broad base where it contacts the horizontal portion. Both the horizontal and vertical processes are gently concave laterally.

Squamosal

Only the anteriormost portion of the right squamosal is preserved. The left squamosal is entirely missing. The squamosal tapers anteriorly to a point, ventral to the postorbitofrontal. This bone possesses a deep V-shaped trough in which the dorsally positioned posterior process of the postorbitofrontal rests. This trough is deep enough to nearly divide the squamosal in half.

Quadrate

Neither quadrate from TLAM NH.HR.2009.032.0001 has been recovered to date, but the quadrate in *M. hoffmanni* and *M. maximus* has often been a point of contention in the synonymy of these two taxa. Descriptions have often been lacking in detail and sharply contradictory between researchers (Russell, 1967; Welles & Gregg, 1971; Lingham-Soliar, 1995; Mulder, 1999).

Although many of the *M. maximus* quadrate specimens from New Jersey are damaged by pyrite disease (Ex. AMNH 1389), no substantial differences are obvious compared to the quadrates of *M. hoffmanni* (Fig. 8). The better preserved left quadrate of *M. maximus* (TMM 313-1) from Texas (Fig. 8C) is nearly identical in size and shape to the holotype of *M. hoffmanni* (MNHNP AC 9648, Fig. 8E). The shape of the tympanic ala, the shape and medial angle of deflection of the suprastapedial process, and the convexity of the ventral condyle are very similar in both species. There appears to be a significant amount of intraspecific variation in regards to the infrastapedial process and the median eminence located on the shaft of the quadrate in both species. As asymmetrical quadrates have been reported in individual specimens of *M. hoffmanni* (IRSNB R12 in Mulder, 1999)

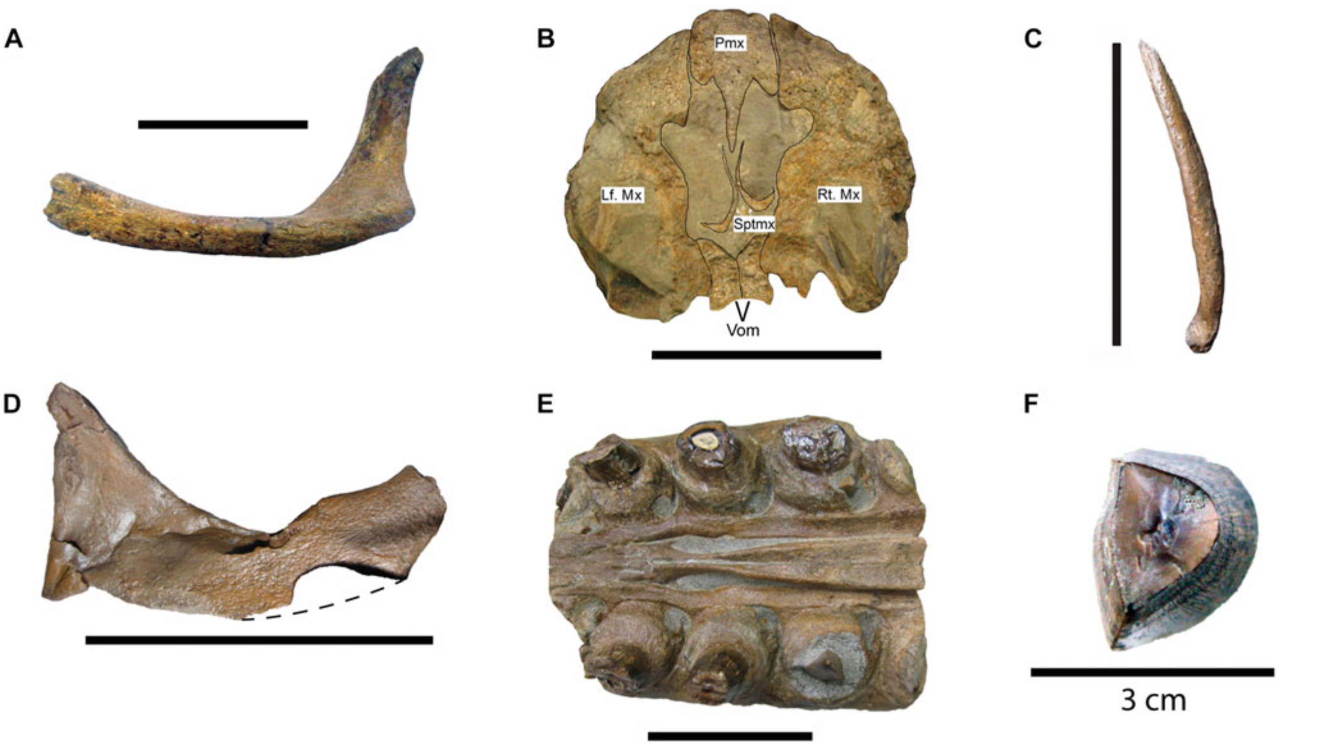

Fig. 7. Various skeletal elements of M. hoffmanni *(TLAM NH.HR.2009.032.0001). A, Left jugal in lateral view, anterior to left. B, Posterior view of cross-section of muzzle unit showing location of septomaxillae. C, Left epipterygoid, anterior to left. D, Left ectopterygoid. E, Ventral view of muzzle unit showing anterior portion of vomers. Anterior to left. F, Anterior marginal tooth showing D-shaped cross-section. Labial surface flat, lingual surface U-shaped. Scale bars 10 cm except where noted.*

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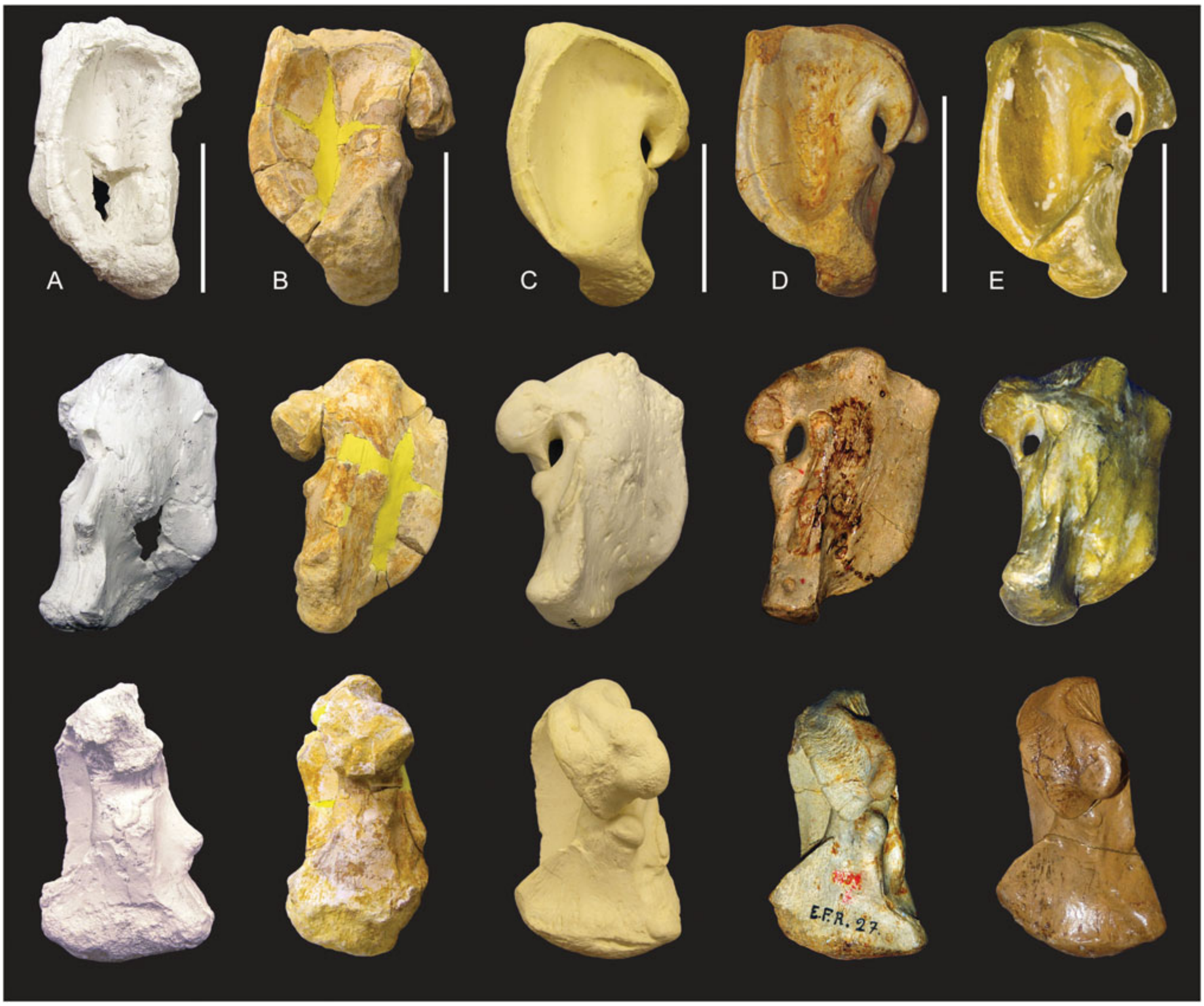

Fig. 8. Comparison of left quadrates in M. maximus *(A, B, C) and* M. hoffmanni *(D, E). in lateral view (top), medial view (middle) and posterior view (bottom). A, Cast of holotype, AMNH 1389. B, ALMNH PV 1988.0018. C, TMM 313-1 (cast). D, IRSNB R27. E, Cast of holotype, MNHNP AC 9648. Scale bars 10 cm.*

and observed by the author in *M. maximus* (TMM 313-1), the amount of variation that exists between *M. hoffmanni* and *M. maximus* is considered insufficient to separate the two at the specific level.

Septomaxilla

The septomaxillae are preserved in life position but are only visible in cross-section between the anterior muzzle and the posterior portion of the skull. These thin slivers of bone are not fused together and are just dorsal to the vomers. In vertical cross-section, each septomaxilla has a distinctive J-shape (Fig. 7B) with the horizontal component directed laterally. This description is only valid at the position of the fifth maxillary tooth.

The septomaxillae in *M. hoffmanni* (IRSNB R27) described by Lingham-Soliar (1995, Figs 6a–b and 7) appear to be fragmentary in comparison with those present in TLAM NH.HR.2009.032.0001, which appear to be similar to the septomaxillae described in *Plotosaurus* (Camp, 1942). Future analysis of TLAM NH.HR.2009.032.0001 using computer-aided tomography may allow these structures to be fully described in detail.

Palate

The palate of TLAM NH.HR.2009.032.0001 is intact but is almost completely obscured by matrix. Only the anteriormost portion of the vomers, which are tightly adpressed together, can be observed (Fig. 7E). Two small foramina that served the vomeronasal organ in life are present medial to the third maxillary teeth.

The palate comprises the vomers, palatines and pterygoids located in the roof of the oral cavity. In both *M. hoffmanni*

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and *M. maximus* the palate is tightly united with most of the fenestrae reduced in size. This condition has only been reported in *M. hoffmanni* (Lingham-Soliar, 1995), *M. maximus* (Mulder, 1999) and *M. beaugei* (Bardet et al., 2004). Bardet et al. (2004) reported that the palatine in *M. beaugei* is perpendicular to the long axis of the skull whereas in *M. hoffmanni–M. maximus* the palatine is oblique to the long axis. No significant differences exist in the palate between *M. hoffmanni* and *M. maximus*.

Epipterygoid

The left epipterygoid (Fig. 7C) is in articulation vertically along the posterior border of the left orbit. Both the dorsal and ventral terminations of the epipterygoid are concealed by the overlying matrix. The epipterygoid consists of a simple, slender rod of bone that is spirally twisted along its length. The spiral twisting results in a slightly concave bow that is directed anteriorly.

Ectopterygoid

The left ectopterygoid (Fig. 7D) can be observed along the ventral margin of the left orbit. This L-shaped bone is partially concealed by matrix and is preserved in disarticulation. The lateral, anteriorly projecting portion of the ectopterygoid tapers anteriorly and is broken just before the terminus. The medially projecting process that articulates with the ectopterygoid process of the pterygoid forms a nearly 90° angle with the anterior process.

Dentary

The right dentary is the more complete of the two but is not preserved in its entirety. The dentary exhibits a gentle upward concavity. The anterior end is narrow and deepens significantly posteriorly. A total of 13 teeth are present in the right dentary, with some being only partially preserved. Posteroventrally and medially the dentary articulates with the very robust splenial.

A small pathology is present on the right dentary, ventral to the fourth dentary tooth position, represented by a raised dome of bone with the top portion of the dome removed to reveal a cavity. A larger pathology, similar in form to the pathology on the right dentary, is present anteriorly on the left dentary, also ventral to the fourth dentary tooth position and ventral to the foraminal row. These pathologies (along with those on the internarial bar of the premaxilla) are similar to those that have been described previously in *M. hoffmanni* (Lingham-Soliar, 2004).

In lateral view, the dentaries of both species are relatively narrow and gently concave upward. From anterior to posterior, the dentaries gradually increase in depth, reaching their maximum adjacent to the posterior terminus. The anteriormost teeth in both species are considerably procumbent but become less so as the tooth row continues posteriorly. Most specimens possess 14 teeth per dentary, but a few individuals of both species (TMM 313-1 (*M. maximus*), IRSNB R12 (*M. hoffmanni*)) display alveoli for 15 dentary teeth. This is not considered to be a significant difference considering that modern snakes and lizards often have different intraspecific tooth counts (Greer, 1991; Rasmussen, 1996). The dentaries of *M. hoffmanni* and *M. maximus* are essentially identical and are inseparable at the specific level.

Splenial

Only the posterolateral sides of the splenials are visible in this specimen. The posterior end of the splenial diverges from the ventral margin of the dentary by an angle of approximately 20°. The posterior articulating surface which meets with the anterior surface of the angular is concave.

Coronoid

Overall the coronoid is a massive, saddle-shaped bone that rests on the anterodorsal surface of the surangular (Fig. 9D). The coronoid has a horizontal anterior portion and rises dorsally at the posterior end to a nearly 90° angle to the horizontal portion. A projection of bone from the dorsal margin of the surangular extends anteriorly along the posterodorsal edge of the coronoid and forms a buttress against the ascending process of the coronoid. A large lateral flange descends ventrally from the coronoid along the lateral side of the surangular. On the anterior margin of the lateral flange is a distinct and deeply emarginated C-shaped notch. The lateral flange extends posteriorly beyond the border of the ascending process. Both coronoids are preserved in TLAM NH.HR.2009.032.0001 but neither is complete. The right coronoid is the better preserved, being nearly complete except for the posteriormost portion of the lateral flange. Neither coronoid can be observed on its medial side.

The coronoid is a massive bone in both *M. hoffmanni* and *M. maximus*. In lateral view the coronoid is situated anteriorly on the dorsal margin of the surangular. Posteriorly, the ascending process of the coronoid curves dorsally to form a near right angle with the horizontal. The dorsal tip of the ascending process has a small deflection on its anterior surface. A small process from the surangular extends up the posterior edge of the ascending process of the coronoid, forming a buttress.

Fig. 9 illustrates the progression in the development of the lateral flange. The left coronoid of *M. hoffmanni* (TM 11202, Fig. 9A, reversed for comparison) represents the least mature individual of the group as shown by the poor development of the anterolateral notch. The right coronoid of *M. hoffmanni* (TM 11245, Fig. 9B) displays increased development of the anterolateral flange and a deepening of the indentation of the anterolateral notch. The right coronoid of *M. hoffmanni* (IRSNB R27, Fig. 9C) shows completion of the C-shaped notch.

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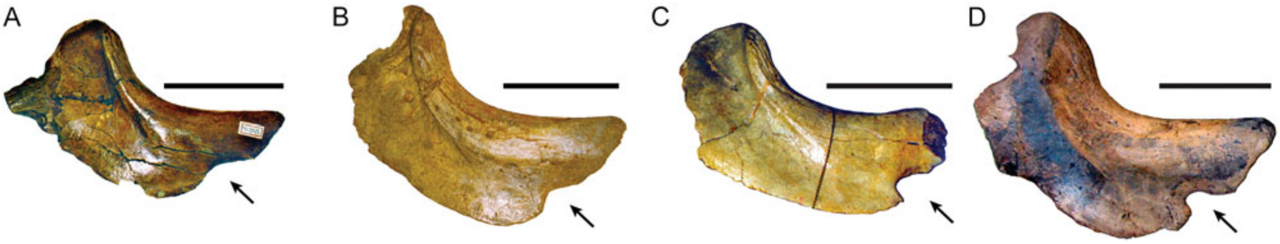

Fig. 9. Presumed ontogenetic series of the coronoid in M. hoffmanni. *A, Left coronoid TM 11202 (reversed). B, TM 11245 Right coronoid. C, IRSNB R27 Right coronoid. D, TLAM NH.HR.2009.032.0001 right coronoid. Right lateral view, anterior to right in all specimens. Note development of C-shaped notch on anterolateral flange. Scale bars equal 10 cm.*

The right coronoid of TLAM NH.HR.2009.032.0001 (Fig. 9D) displays maximum development of the anterolateral flange and C-shaped notch. In medial view the coronoid exhibits an anteromedial flange that is developed to an even greater extent than the anterolateral flange. The ventral-most portion of the medial flange extends to contact the angular along the ventral border of the surangular. The two coronoid flanges, along with the anterior ramus of the prearticular, effectively eliminate movement in the intramandibular joint.

The known coronoids of *M. maximus* fit well within the ontogenetic series of coronoids described above for *M. hoffmanni*.

Marginal dentition

All marginal teeth are posteromedially recurved and strongly bicarinate, with fine serrations that are visible to the unaided eye extending from the crown base to the apex. A finely wrinkled texture covers the enamel surfaces of all the marginal teeth. The labial surfaces of the teeth are distinctly divided into two to five prism-like facets, with the fewest facets on anterior teeth and increasing in number posteriorly in the tooth row. Lingual surfaces exhibit more numerous and less distinct facets compared to those on the labial surface. Dentary tooth facets are less distinct than those on the maxillary teeth. Several horizontally oriented ridges occur near the crown tips on a number of dentary teeth. Anteriorly, the teeth are somewhat D-shaped in horizontal cross-section, with a nearly flat labial surface. The strongly curved lingual surface of these anteriormost teeth is directed posteromedially. Posteriorly, the teeth become more symmetrical in cross-section but the lingual face remains larger in circumference. The anterior marginal teeth are relatively short, reach their greatest height near the midlength of the jaws and taper in size to the posteriormost teeth. Anterior teeth are slightly procumbent, being especially evident in the roots.

The marginal teeth of *M. hoffmanni* and *M. maximus* are among the most robust of any species of *Mosasaurus*, are exceptionally long and are posteromedially recurved. Anterior teeth are D-shaped in horizontal cross-section (Fig. 7F) and are somewhat prognathous, with tooth roots displaying the highest degree of anterior incline. Both species have between two and five labial facets on the marginal dentition. The roots are extremely large, having been described as ‘barrel-shaped’ by Lingham-Soliar (1995) in *M. hoffmanni*. The marginal teeth of *M. hoffmanni* and *M. maximus* are indistinguishable.

An SEM was taken of the carina of one of the anterior marginal tooth crowns of TLAM NH.HR.2009.032.0001 in order to further investigate the serrations (Fig. 10A). Micrographs show that serrations are more accurately to be termed crenulations because of the irregular wavy pattern displayed. Apices of the crenulations are spaced approximately 200 µm apart. A comparison was made to a large, anterior tooth of a *Tylosaurus proriger* (SDSM 39968, Fig. 10B) to determine if serrations/crenulations can be used as a diagnostic tool at the generic level in mosasaurs. Preliminary results show that serrations in *M. hoffmanni*

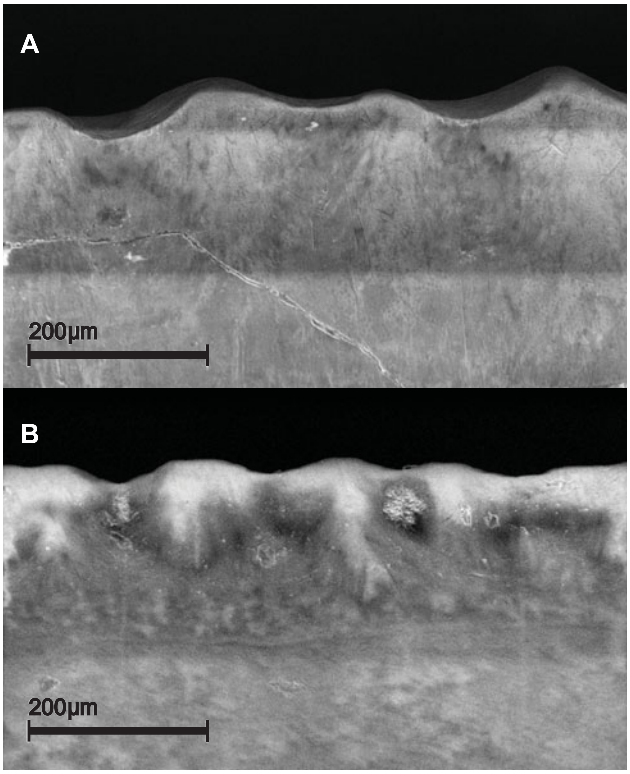

Fig. 10. Comparison of tooth serrations. A, M. hoffmanni *(TLAM NH.HR.2009.032.0001). B,* Tylosaurus proriger *(SDSM 39968). Scale is 200 µm. Note larger, more irregular serrations in* M. hoffmanni.

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are larger and more irregular than those in *Tylosaurus*, but further analyses will be necessary to determine the usefulness of tooth serrations as a diagnostic criterion.

Postcrania

None of the postcranial skeleton of TLAM NH.HR.2009.032.0001 has been recovered to date. Attempts to locate additional material from this specimen are currently underway.

The vertebral columns of *M. hoffmanni* and *M. maximus* are remarkably similar, although no complete column is known in either species. Cervical vertebrae have nearly circular articulations of the centra. Functional pre- and postzygapophyses are present, as are zygosphenes-zygantra. Hypopophyses are large and inclined posteroventrally. Thoracic vertebrae are large and have circular articulations. Pre- and postzygopophyses are present anteriorly in the vertebral column but gradually become smaller posteriorly in the column. In the pygal vertebrae the zygopophyses disappear completely and centra articulations become subtriangular in outline. Caudal vertebrae have fused haemal arches. Although postcranial skeletons are much less diagnostic than cranial material, the comparable postcranial elements are indistinguishable between *M. hoffmanni* and *M. maximus*.

Discussion and conclusions

TLAM NH.HR.2009.032.0001 can be referred to *M. hoffmanni* by possession of 13 maxillary teeth, two to five labial facets on the marginal dentition, external nares beginning dorsal to between fifth and sixth maxillary teeth, robust posteroventral process of jugal, a single C-shaped notch on the anterolateral flange of the coronoid and the posteriorly projecting tongues of the frontal extending well beyond the posterior limit of the parietal foramen. TLAM NH.HR.2009.032.0001 represents the first definitive example of *M. hoffmanni* from the northern portion of the Western Interior Seaway and the Fox Hills Formation and as such is an extension of its known geographic range.

Synonymy of Mosasaurus maximus with Mosasaurus hoffmanni

No distinguishing characteristic can be used to differentiate *M. hoffmanni* and *M. maximus*, supporting the synonomy of these two taxa (e.g. Mulder, 1999). Although the arguments made by Mulder for synonymy were convincing, many of his morphological descriptions of *M. hoffmanni* versus *M. maximus* were lacking in detail. The present examination of the morphology of *M. hoffmanni* and *M. maximus* provided no reasonable evidence to support their separate species designation. Differences observed between individual specimens were minor and could be attributed to individual variation, ontogeny and/or diagenetic deformation. The differences that were noted occurred in specimens on both sides of the Atlantic Ocean and were not endemic to one region. *M. maximus* Cope, 1869 should be synonymized with *M. hoffmanni* Mantell, 1829 with the latter having senior priority. This conclusion supports the suggestion of Mulder (1999).

Biogeographic and biostratigraphic distribution of Mosasaurus hoffmanni

The synonymy of *M. maximus* with *M. hoffmanni* prompts a review of the stratigraphic and biogeographic ranges of *M. hoffmanni*. Stratigraphically, *M. hoffmanni* now ranges from the upper Campanian Coon Creek Formation of Tennessee (Russell, 1967) and Merchantville Formation of Delaware (Baird & Galton, 1981) to the upper Maastrichtian Owl Creek Formation of Missouri (Campbell & Lee, 2001; Gallagher et al., 2005; Campbell et al., 2008), basal Hornerstown Formation of New Jersey (Staron et al., 2001) and the Maastrichtian Formation, uppermost Meerssen Member, subunit IVf-6 of the Netherlands (Jagt et al., 2008). TLAM NH.HR.2009.032.0001 represents the first definitive example of *M. hoffmanni* from the northern portion of the Western Interior Seaway and the Fox Hills Formation and as such is an extension of its known biogeographic range.

Biogeographically, the *M. hoffmanni* range includes Northern Europe, Eastern Europe and Asia Minor. Synonymy with *M. maximus* expands the known range to large areas of North America. Plotting definitive localities for *M. hoffmanni* on a paleogeographic map of the continents during the mid-Maastrichtian age (Fig. 11) reveals that the majority of specimens existed in a region between 30° and 40° north paleolatitude. The only significant exception to the restricted latitudinal gradient for *M. hoffmanni* is TLAM NH.HR.2009.032.0001, which was located at approximately 50°° north latitude during the mid-Maastrichtian. The three reported occurrences from the southern hemisphere (Lingham-Soliar, 1991; Martin & Crame, 2006; Fernández et al., 2008) are based on poorly preserved, isolated remains and merely compare favourably with *M. hoffmanni* rather than being definitively identified to the species.

Lingham-Soliar (1991, p. 665) described the possible specimen from Niger as '…a fragment of a large tooth crown… The tooth probably belongs to *M. hoffmanni*, representing a middle-posterior tooth on the dental ramus, although there is some resemblance to teeth found in larger examples of *M. lemonnieri*, especially in the slight beading present between a few of the facets.'

Fernández et al. (2008, p. 185), in their description of Patagonian mosasaurs, conclude that 'Although mosasaurs from the late Maastrichtian of northern Patagonia do not provide, at this point, definitive empirical support of endemism at a specific level, the presence of *Mosasaurus* sp. aff. *M. hoffmanni*, which may be a new species but is similar to *M. hoffmanni*, suggests

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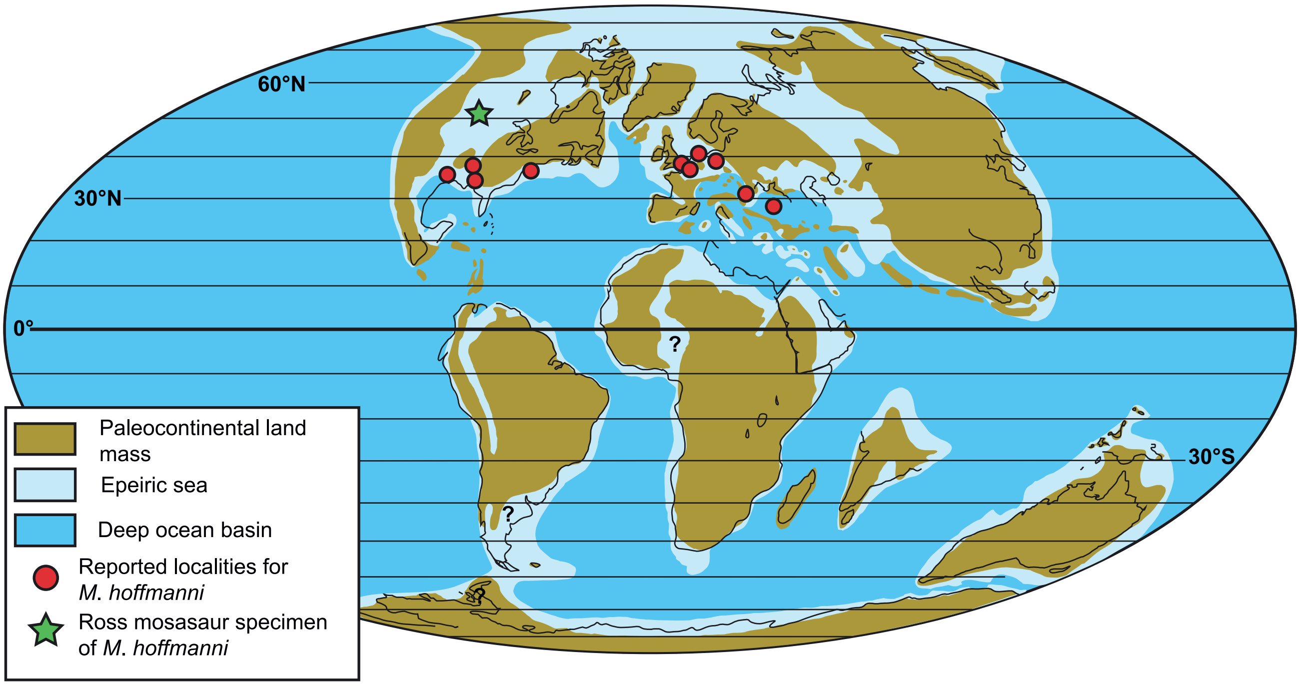

Fig. 11. Paleogeographic map of the continents during the mid-Maastrichtian (~67.0 mybp). Note that the majority of definitive M. hoffmanni *specimens occur between 30° and 40° north paleolatitude. See text for discussion on possible southern hemisphere specimens. Map based on Vrielynck & Bouysse (2003).*

that at least one species of *Mosasaurus* could be endemic of a southern Gondwanan fauna.'

Another possible austral reference to *M. hoffmanni* is reported from Antarctica, in which large bone fragments and faceted teeth compared favourably with those known for *M. hoffmanni* (Martin & Crame, 2006). However, *M. beaugei* has been reported (Bardet et al., 2004) at sizes comparable to *M. hoffmanni* and also possesses strongly faceted, crenulated teeth that are not discernable from those of *M. hoffmanni*. Therefore, large size and strongly faceted teeth alone are not sufficient enough to provide positive identification at the specific level.

In all three of the instances cited above, the described specimens would be best referred to *Mosasaurus* sp. indet. rather than *M. hoffmanni*, *Mosasaurus* sp. aff. *M. hoffmanni* or *Mosasaurus* sp. *cf. M. hoffmanni* until better preserved, more complete material is discovered. The possibilities exist that a new species that is morphologically similar to *M. hoffmanni* is present in the southern hemisphere (Fernández et al., 2008) or that the range of the morphologically similar *M. beaugei* extended south from North Africa and accounts for the described specimens.

Conclusions

TLAM NH.HR.2009.032.0001 from the Fox Hills Formation in South Dakota is referred to *M. hoffmanni* and is paleogeographically the most northerly and westerly definitive occurrence of this taxon and is an extension of its paleobiogeographic range.

Biostratigraphically, *M. hoffmanni* ranges from the upper Campanian to the uppermost Maastrichtian, very near the K/Pg boundary.

Anatomically, the lachrymals and septomaxillae of *M. hoffmanni* are accurately described and figured here for the first time. Measurements of TLAM NH.HR.2009.032.0001 indicate that it is one of the larger examples of this taxon.

The reexamination of the morphology of *M. maximus* and *M. hoffmanni* reveals that the two forms are indistinguishable from one another and should remain synonymised, with *M. hoffmanni* as the senior nomen, as first proposed by Mulder (1999). TLAM NH.HR.2009.032.0001 reinforces this synonymy as it displays characteristics of both *M. hoffmanni* and *M. maximus* in the elements that are preserved.

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