Occurrence of *Mosasaurus hoffmannii* Mantell, 1829 (Squamata, Mosasauridae) in the Maastrichtian Phosphates of Morocco

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Abstract: Marginal tooth crowns from the hypercarnivorous marine reptile *Mosasaurus hoffmannii* Mantell, 1829 are reported for the first time from the Late Cretaceous (Maastrichtian) phosphates of Morocco. Fossilized remains of this species are previously known from Campanian and Maastrichtian outcrops in Europe, North America, and western Asia at a paleolatitudinal belt of 30-45°N. New fossil material originates from the Upper Couche III layer of the Oulad Abdoun Basin, south of Oued Zem, Morocco. The discovery of *M. hoffmannii* in Morocco extends its paleobiogeographic range south to 25°N and into the southern margin of the Mediterranean Tethys.

1. INTRODUCTION

Mosasaurids (Squamata: Mosasauridae) were a group of specialized marine reptiles that lived in oceans and epicontinental seas during the last 25 million years of the Late Cretaceous (Everhart, 2005). Their fossilized remains are abundant and have been reported from Upper Cretaceous marine deposits on all continents and major landmasses (Bardet, 2012; Bardet et al., 2014; Palci et al., 2014; Russell, 1967). During their geologically brief existence, mosasaurids evolved from small, shore-dwelling lizards into a variety of fully marine carnivores. Peak mosasaurid diversity occurs during the latest Cretaceous (Campanian-

Maastrichtian), when they showed maximum disparity in body size, locomotion style, tooth morphology, and diet (Bardet et al., 2015; Everhart, 2005; Longrich et al., 2021a; Massare, 1987; Russell, 1967).

The Maastrichtian component of the Moroccan phosphates preserves the highest diversity of mosasaurid squamates from a single horizon (Arambourg, 1952; Bardet et al., 2015). The Moroccan assemblage consists of 10 genera represented by at least 14 species (Table 1). These mosasaurids occupied a wide range of marine predatory niches, including piscivores (Halisaurus), durophages (Carinodens, Globidens, Prognathodon), and apex predators (Mosasaurus) (Bardet et al., 2004; Bardet et al., 2005a, Bardet et al., 2005b, Bardet et al., 2015, Longrich et al., 2021a). Here, we add to the already high species diversity by reporting *Mosasaurus hoffmannii* Mantell, 1829 for the first time from the Moroccan phosphates.

Mosasauridae	
Mosasaurinae	
Mosasaurus hoffmannii	Mantell, 1829
Prognathodon sp. (=*Leiodon anceps*)	Owen, 1840-1845
Carinodens belgicus	Woodward, 1891
Prognathodon giganteus	Dollo, 1904
Mosasaurus beaugei	Arambourg, 1952
Prognathodon currii	Christiansen and Bonde, 2002
Globidens phosphaticus	Bardet et al., 2005a
Carinodens minalmamar	Schulp, Bardet, and Bouya, 2009
Eremiasaurus heterodontus	LeBlanc et al., 2012
Globidens simplex	LeBlanc, Mohr, and Caldwell, 2019
Xenodens calminechari	Longrich et al., 2021b
Plioplatecarpinae	
Gavialimimus alamghribensis	Strong et al., 2020
Tylosaurinae	
Tylosaurinae indet.	T.R. unpublished specimen
Halisaurinae	
Halisaurus arambourgi	Bardet et al., 2005b
Pluridens serpentis	Longrich et al., 2021a

Table 1. List of mosasaurid taxa from the Maastrichtian phosphates of Morocco (Oulad Abdoun and Ganntour Basins). Modified from Bardet et al., 2015.

The mosasaurine *Mosasaurus hoffmannii* is among the largest and latest known mosasaurids. Achieving a total body length of 14 m and exhibiting robust jaws lined with sharp, weakly prismatic teeth, *M. hoffmannii* would have fed at the apex trophic level of the Late Cretaceous marine ecosystem (Lingham-Soliar, 1995; Street and Caldwell, 2017). First discovered over 200 years ago in the upper Maastrichtian chalk quarries of St Pieter's Mountain, south of Maastricht, the Netherlands, the species is reported from Campanian and Maastrichtian marine deposits within a geographic belt ranging from the paleolatitudes 30-45°N (Mantell, 1829; Lingham-Soliar, 1995; Bardet and Tunoğlu, 2002; Jagt et al., 2008).

Newly discovered mosasaurid teeth are identified as *Mosasaurus hoffmannii* based on unique crown morphology and enamel ornamentation. The new material represents an unusually far south occurrence for this species and provides evidence that the paleobiogeographic range of *M. hoffmannii* may have been larger than previously thought.

2. GEOLOGICAL CONTEXT

The Moroccan phosphates have been known since 1908 and commercially exploited since the 1920s (Office Chérifien des Phosphates, 1989). They are a component of the Mediterranean Tethyan phosphogenic province, an extensive belt of sedimentary rock that extends around the Mediterranean Sea, from North Africa to the Middle East (Lucas and Prévót-Lucas, 1996). The phosphate successions in Morocco were deposited continuously in a warm and shallow marine environment from the Late Cretaceous (Maastrichtian) to early Eocene (Lutetian) (Lucas and Prévót-Lucas, 1996; Bardet et al., 2004; Bardet et al., 2010). These deposits outcrop in five major basins in central Morocco: Oulad Abdoun, Ganntour, Meskala, Souss, and Oued Eddahab (Bardet et al., 2010, LeBlanc et al., 2012) (Fig. 1). The new mosasaurid material described here comes from the Maastrichtian component of the Oulad Abdoun Basin in the area surrounding the Sidi Daoui and Sidi Chennane quarry zones (Fig. 2).

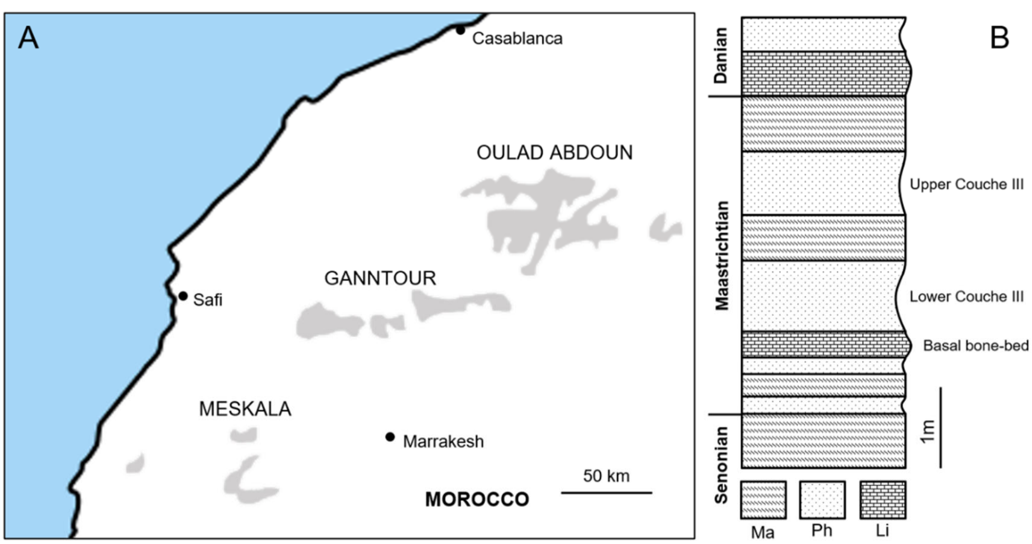

Figure 1. Map and stratigraphic column of the Oulad Abdoun Basin, Morocco. (A), map of Morocco and the main phosphatic basins (B), stratigraphy of the Oulad Abdoun Basin. Abbreviations: Ma, marl; Ph, phosphates; Li, limestones.

Figure 2. Excavation zone in the Sidi Chennane phosphate quarry.

Accurate dating of the Moroccan phosphates has proven difficult due to local lateral facies changes and a lack of invertebrate and floral biostratigraphic markers. In place of formation assignment, the phosphatic deposits in the Oulad Abdoun Basin have been divided into a series of informal beds (termed "Couches") on the basis of vertebrate remains (Arambourg, 1952, Bardet et al., 2010). Three layers, Couche I (Ypresian), Couche II (Thanetian) and Couche III (late Maastrichtian), are present throughout the Oulad Abdoun Basin (Bardet et al., 2010; Cappetta et al., 2014) (Fig. 3). A fourth layer of grey phosphate, Couche IV (middle Maastrichtian), is present only in the area surrounding Sidi Chennane.

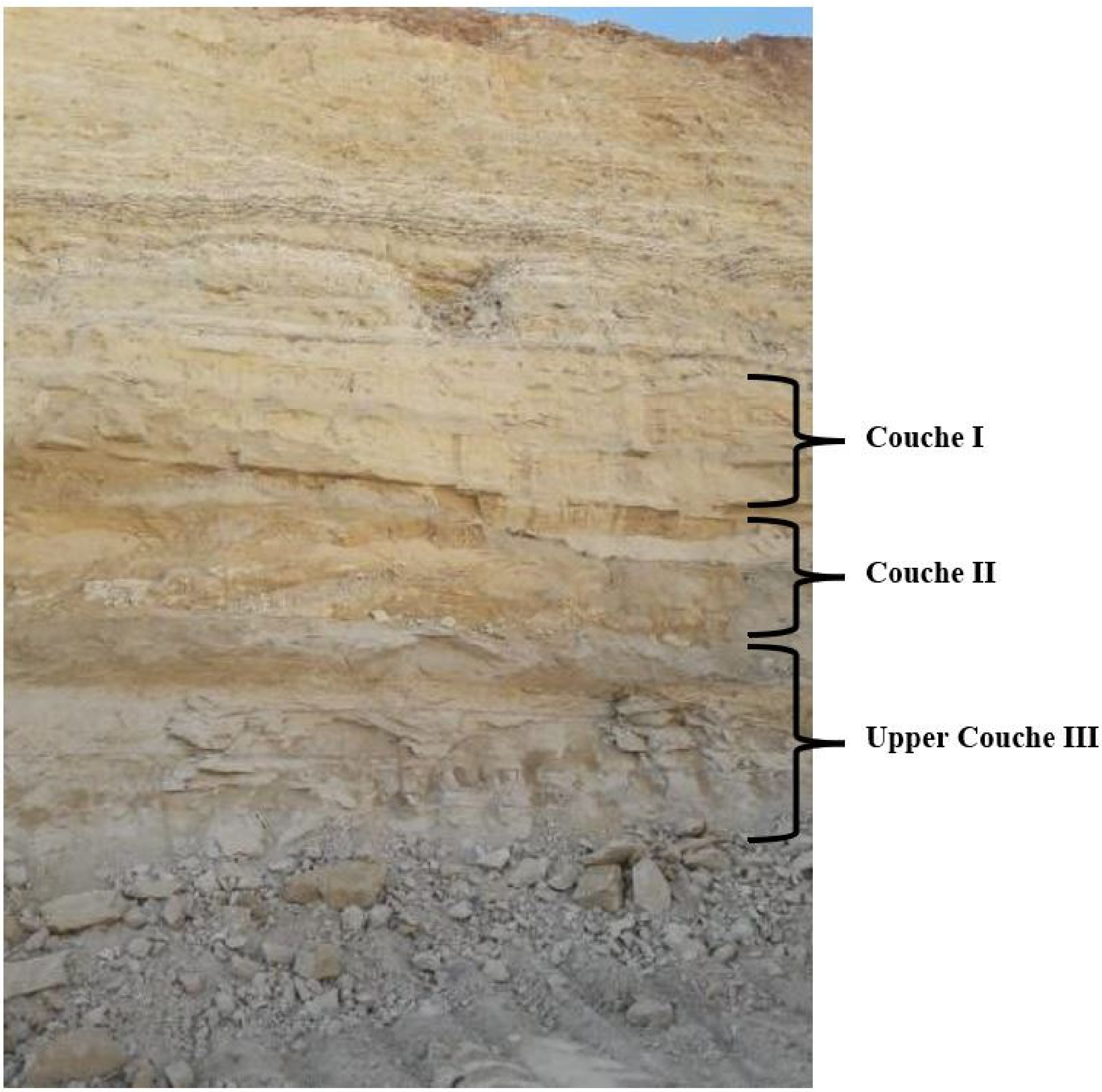

Figure 3. Lithostratigraphical units of the Sidi Chennane Phosphate Quarry; mosasaurid remains originate from the Upper Couche III layer.

Couche III is rich in marine vertebrate remains, especially selachians, bony fish, and aquatic reptiles (Arambourg, 1952; Bardet et al., 2005b). Vertebrate biostratigraphy using selachian teeth dates Couche III as late Maastrichtian, and carbon and oxygen isotope chemostratigraphy constrains it to within 1 Ma of the K-T boundary (Cappetta, 1987; Cappetta et al., 2014). Couche III is divided into three subunits: a basal bonebed, an intermediate layer of soft, yellow phosphates (Lower Couche III), and an upper layer of grey phosphates (Upper Couche III; UCIII) (Arambourg, 1952; Bardet et al., 2004; Bardet et al., 2005b; Strong et al., 2020).

The fossils described here were collected by miners working in the local fossil industry. While the exact provenance is unknown for some specimens, the matrix and state of preservation conforms with material found in the Upper Couche III layer of the Oulad Abdoun Basin. Selachian teeth from the index taxa Serratolamna maroccana Arambourg, 1935, Squalicorax bassanii Gemmellaro, 1920, and Squalicorax pristodontus Agassiz, 1835, found in close association with the mosasaurid remains correlate to the late Maastrichtian (Cappetta et al., 2014). Gray phosphatic matrix encrusting several specimens is consistent with the description of the Upper Couche III layer, further supporting a likely origin from the Oulad Abdoun Basin, in central Morocco (Bardet et al., 2005b; Longrich et al., 2021b).

Institutional Abbreviations: AVM, Alexander Vinkeles Melchers Private Collection, France; CORN, George Corneille Private Collection, Ireland; REMPC, Rempert Research Collection, Chicago, Illinois, USA; TM, Teylers Museum, Haarlem, the Netherlands.

3. SYSTEMATIC PALEONTOLOGY

Order SQUAMATA OPPEL, 1811

Superfamily MOSASAUROIDEA GERVAIS, 1853 (nom. transl. CAMP, 1923)

Family MOSASAURIDAE GERVAIS, 1853

Subfamily MOSASAURINAE GERVAIS, 1853 (nom. transl. WILLISTON, 1897)

Genus Mosasaurus CONYBEARE, 1822

Mosasaurus hoffmannii MANTELL, 1829

Material: REMPC M0001, a marginal tooth crown from the median of the jaw (UCIII, Sidi Daoui) (Fig. 4, A); REMPC M0002, M0003, two isolated marginal tooth crowns (UCIII, Sidi Chennane) (Figs. 4, B and C); AVM 01, a premaxillary tooth crown (UCIII, exact provenance unknown) (Fig. 5, D); AVM 02, a marginal maxillary tooth crown (UCIII, exact provenance unknown) (Fig. 5, E); CORN 01, a marginal tooth crown (UCIII, exact provenance unknown) (Fig. 6).

Horizon and Locality: Phosphatic deposits, Upper Couche III layer, upper Maastrichtian; Sidi Daoui and Sidi Chennane quarry zones, Oulad Abdoun Basin, Morocco.

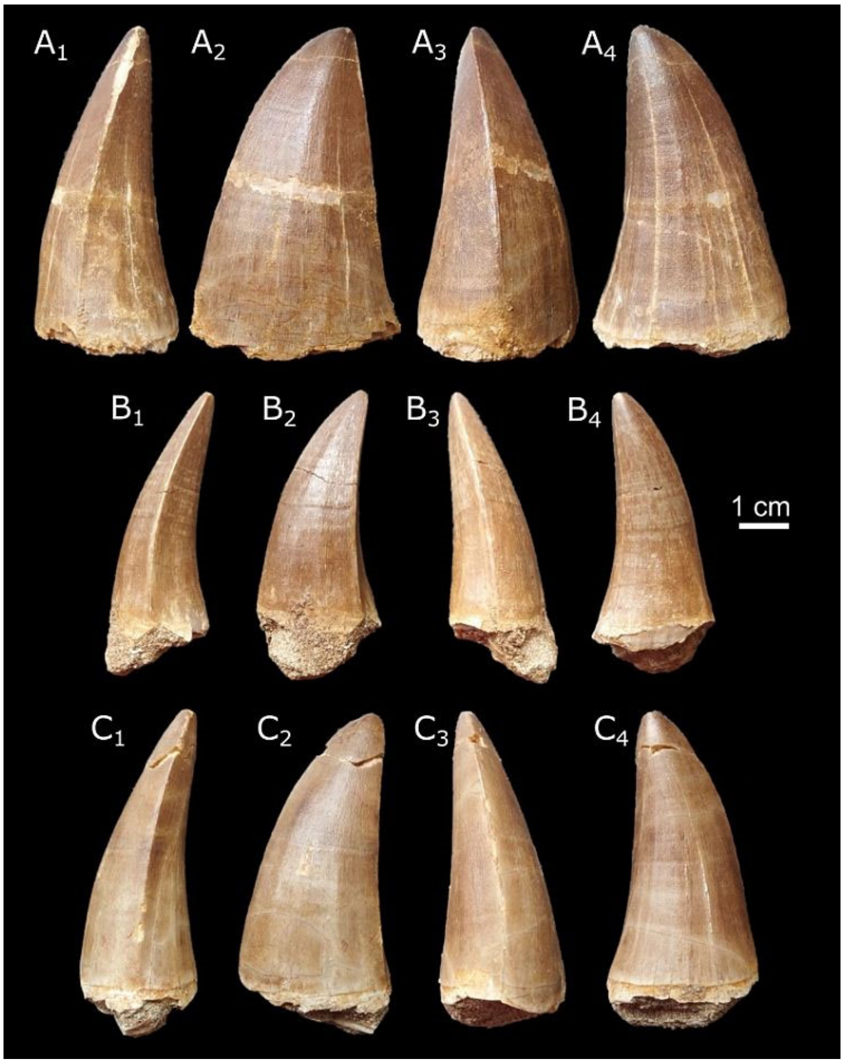

Figure 4. *Mosasaurus hoffmannii* Mantell, 1829, from the Moroccan phosphates. A. REMPC M0001, UCIII (Maastrichtian) layer, Oulad Abdoun Basin, Sidi Daoui, in posterior (A1), labial (A2), anterior (A3), and lingual (A4) view. B. REMPC M0002, UCIII (Maastrichtian) layer, Oulad Abdoun Basin, Sidi Chennane, in posterior (B1), labial (B2), anterior (B3), and lingual (B4) view. C. REMPC M0003, UCIII (Maastrichtian) layer, Oulad Abdoun Basin, Sidi Chennane, in posterior (C1), labial (C2), anterior (C3), and lingual (C4) view.

Description: REMPC M0001 (Fig. 4, A) is a large marginal tooth with a crown height of 62.3 mm. The tooth exhibits a robust base that tapers to a labiolingually curving apex (crossing the midline of the tooth). Trenchant anterior and posterior carinae point antero-posteriorly, indicating origin from the median of the jaws (Konishi et al., 2012). The carinae are minutely serrated and divide the crown into asymmetrical labial and lingual surfaces (lingual inflated). The labial surface is approximately flat, giving the crown a U-shaped cross-section. Faint prismatic cutting planes (termed "prism faces") partition the enamel on the labial surface into three longitudinal sections. The lingual surface is convex and smooth.

REMPC M0002 (Fig. 4, B) is a comparatively small anterior crown measuring 48.8 mm high. The tooth is bicarinate, labiolingually curved, and U-shaped in cross-section. The posterior carina points laterally forming strongly unequal labial and lingual surfaces. The high degree of labiolingual asymmetry indicates origin from the front of the jaw (Grigoriev, 2014). The labial surface is divided into three barely visible prism faces; the lingual surface bears indiscernible facets. REMPC M0002 is slender in lateral profile, a morphology consistent with subadult teeth from *M. hoffmannii* (Machalski et al., 2003).

REMPC M0003 (Fig. 4, C) is an isolated tooth with a crown height measuring 57.3 mm. The tooth is gently labiolingually curved and is U-shaped in cross-section. The apex of the tooth is cracked, having been broken and reattached. A small wear facet extends from the apex of the tooth down the first 3 mm of the anterior carina. Carinae point anteroposteriorly and bear minute serrations. The labial surface is divided into three weak prism faces and the lingual surface has indiscernible facets.

AVM 01 (Fig. 5, D) is a small tooth crown measuring 43.6 mm in height. It is bicarinate with a strongly asymmetrical U-shaped cross-section. The labial surface is mildly convex and shows three weak prism faces. Lingually, only one facet can be made out, with others being indiscernible. The distally pointed carinae are minutely, but distinctly crenulated, while a faint anastomosing texture covers the enamel of the entire tooth. The number of prism faces and angle at which the carinae are offset from each other indicate that this is a premaxillary tooth (Street and Caldwell, 2017).

AVM 02 (Fig. 5, E) is a small marginal tooth crown 39.7 mm tall. It has a U-shaped cross-section and crenulated carinae both mesially and distally. Three weak prism faces divide the nearly flat labial surface, with at least five facets being visible on the lingual surface (the rest being indiscernible). The enamel is smooth, but damage from the preparation process scars the anterior portion of the lingual surface. Labiolingual asymmetry suggests a more anterior position in the jaw, while the number of prism faces places it in the maxilla (Grigoriev, 2014; Street and Caldwell, 2017). Apical curvature is mediodistally oriented.

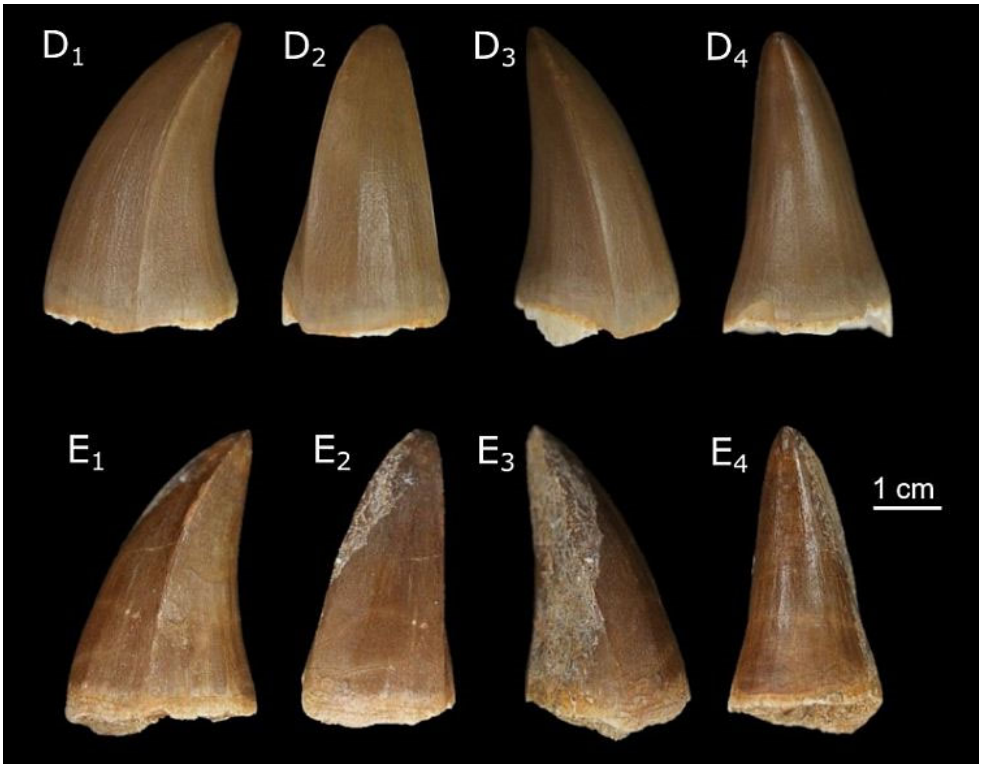

Figure 5. Mosasaurus hoffmannii Mantell, 1829, from the Moroccan phosphates. D. AVM 01, UCIII (Maastrichtian) layer, Oulad Abdoun Basin, in posterior (D1), labial (D2), anterior (D3), and lingual (D4) view. Upper Couche III (Maastrichtian) layer, Oulad Abdoun Basin, Morocco. E. AVM 02, UCIII (Maastrichtian) layer, Oulad Abdoun Basin, in posterior (E1), labial (E2), anterior (E3), and lingual (E4) view.

CORN 01 (Fig. 6, F) is a massive marginal tooth crown with a total length (apex to base of partial root) measuring over 9 cm. The tooth is labiolingually curved and bears prominent carinae. Both anterior and posterior carina bear light serrations, though they have been abraded away along the upper portion of the anterior carina. Ornamentation on both the labial and lingual surfaces is imperceptible, a feature consistent with some exceptionally large tooth crowns from *M. hoffmannii* (Kuypers et al., 1998).

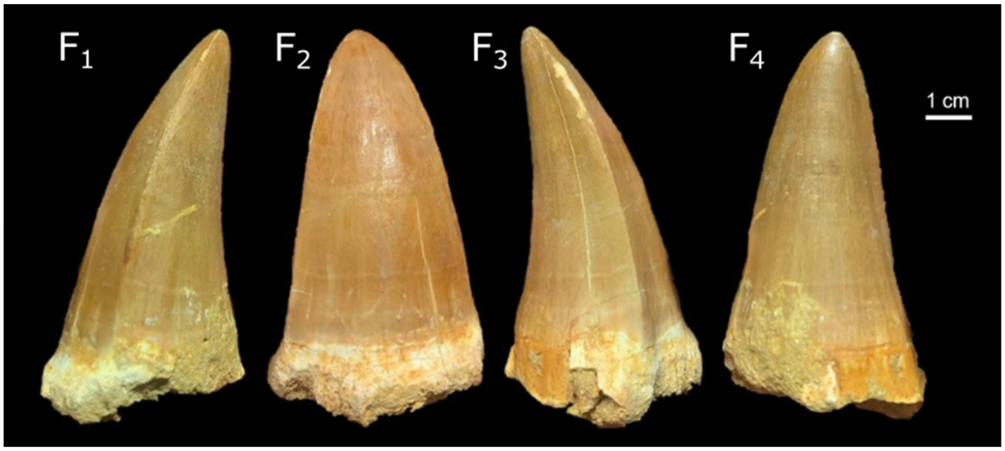

Figure 6. *Mosasaurus hoffmannii* Mantell, 1829, F. CORN 01 in anterior (F1), labial (F2), posterior (F3), and lingual (F4) view. Upper Couche III (Maastrichtian) layer, Oulad Abdoun Basin, Morocco (Image courtesy of George Corneille).

Comparisons and Systematic Attribution: The morphologies of mosasaurid teeth are taxonomically informative and often diagnostic to the generic and even specific level (Bardet et al., 2015). The great size and robustness of the Moroccan specimens rules out all but the largest mosasaurid taxa as potential identities. Lack of closely spaced vertical striations on the enamel surface precludes affiliation with Russellosaurinae (Bell, 1997). Moreover, the U-shaped cross-section of the crowns is characteristic of the genus Mosasaurus (Russell, 1967; Bardet and Tunoğlu, 2002; Bardet et al., 2013). Further synapomorphies of Mosasaurus featured in the Moroccan specimens include: (1) asymmetrical labial and lingual surfaces (lingual inflated); (2) flattened labial surface; (3) convex lingual surface; (4) two prominent carinae; (5) light serrations along anterior and posterior carina; (6) labiolingual tooth curvature (Russell, 1967; Lingham-Soliar, 1995; Bardet et al., 2004).

The most characteristic feature of Mosasaurus teeth is the prism faces present on marginal tooth crowns, the number and size which are used to diagnose different species. Street and Caldwell (2017) note that, "[i]n *M. hoffmannii* the anterior marginal teeth tend to have two or three lateral facets [prism faces], two being more common on the anterior dentary teeth and three being more common on the anterior maxillary teeth of the holotype. The medial facets are more numerous and less distinct, but there are usually at least five." The diminished nature of the lingual facets has led to their count being reported as greater than five (Lingham-Soliar, 1995; Street and Caldwell, 2017 or indistinguishable (Bardet et al., 2004) (Figure 7).

Figure 7. Teeth from the first discovered Mosasaurus hoffmannii specimen, TM 7424, Teylers Museum, Haarlem, the Netherlands, A. in lingual view; B. in labial view showing prism faces; C. in lingual view showing indiscernible lingual facets, light serrations on the carinae, and medial tooth curvature.

The tall and robust shape of the Moroccan teeth, as well as the tooth surfaces bearing three prism faces labially and indiscernible facets lingually identifies these specimens as *Mosasaurus hoffmannii* (Lingham-Soliar, 1995; Bardet and Tunoğlu, 2002; Machalski et al., 2003; Street and Caldwell, 2017). When compared with the tooth crowns of the other Moroccan Mosasaurus species, *M. beaugei*, the *M. hoffmannii* teeth possess wider bases, weaker curvature, and fewer and less-developed prism faces (Bardet et al., 2004; Lindgren and Jagt, 2005; Street and Caldwell, 2017).

4. PALEOBIOGEOGRAPHIC DISTRIBUTION AND IMPLICATIONS

Paleobiogeographic Implications: Maastrichtian mosasaurid assemblages in the northern and southern margins of the Mediterranean Tethys are faunally distinct. The Northern Margin (paleolatitudes 30-40°N) is characterized by *Mosasaurus hoffmannii*, *Tylosaurus (Hainosaurus) bernardi*, and *Plioplatecarpus marshi*, while the Southern Margin (20°S-20°N) is known for abundant remains from Prognathodon sp. (*Leiodon anceps*), *Eremiasaurus heterodontus*, *Gavialimimus alamghribensis*, and *Globidens phosphaticus* (Bardet and Tunoğlu, 2002; Bardet, 2012).

The Oulad Abdoun Basin is a component of the Southern Tethys Margin and displays close paleobiogeographical affinity with Brazil and the Arabo-African Platform consisting of Angola, Egypt, Israel, Jordan, and Syria (Bardet, 2012). When comparing the Moroccan assemblage with mosasaurids from the Maastricht Formation (the Netherlands; Northern Tethys Margin), Bardet et al. (2015) notes that comparable ecological niches were filled by regionally unique, though morphologically convergent species. This is evidenced by the Northern taxa *Mosasaurus hoffmannii*, *Plioplatecarpus marshi*, and *Halisaurus ortliebi* having Southern parallels in *M. beaugei*, *G. alamghribensis*, and *H. arambourgi*. A pattern of regionally unique mosasaurid fauna is also present in northern and southern regions of the Western Interior Seaway and has been explained by a paleolatitudinal species gradient resulting from ecological preferences and/or paleocurrents (Nicholls and Russell, 1990; Bardet, 2012; Bardet et al., 2015).

Despite the apparent segregation of taxa in the Northern and Southern Tethys Margin, there are some mosasaurids known from both realms. Remains from *Carinodens belgicus*, *Prognathodon giganteus*, and now *Mosasaurus hoffmannii* have been found in sediments from both regions (Bardet et al., 2015). The discovery of *M. hoffmannii* in the Moroccan phosphates represents the most southern definite occurrence of this species. A review of the geographic range of M. hoffmannii is provided below (Table 2).

Stratigraphy, Locality, Age, Paleolatitude (Lower-Upper Bound)	Taxon recorded	Reference
López de Bertodano Fm., Seymour Island, Antarctica Maastrichtian; -64.3° (-66.8°, -61.8°)	**Mosasaurus* sp. aff. *M. hoffmannii*	Martin and Crame, 2006
Jagüel Fm., Rio Negro, Argentina Maastrichtian; -43.7° (-46.2°, -41.2°)	**Mosasaurus* sp. aff. *M. hoffmannii*	Fernández et al., 2008
Bentiaba, Namibe, Angola Maastrichtian; -29.7° (-32.3, -27.2)	**Mosasaurus* sp. aff. *M. hoffmannii*	Jacobs et al., 2006; Mateus et al., 2011
Craie de Ciply, Belgium Maastrichtian; 39.7° (37.3°, 42.3°)	*Mosasaurus hoffmannii*	Lingham-Soliar, 1995
Kajlâka Fm., Pleven, Bulgaria Maastrichtian; 33.8° (31.4°, 36.4°)	*Mosasaurus* cf. *hoffmannii*	Jagt et al., 2006

Manzadi, Democratic Republic of the Congo Maastrichtian; -21.5° (-24.1°, -19.1°)	*cf. *Mosasaurus hoffmannii*	Lingham-Soliar, 1994
Danish White Chalk Fm., Holtug, Stevns Klint, Denmark Maastrichtian; 44.9° (42.4°, 47.4°)	*Mosasaurus hoffmannii*	Lindgren and Jagt, 2005
Rügen, Germany Maastrichtian; 44.0°, (41.5°, 46.5°)	*Mosasaurus* cf. *hoffmannii*	Reich et al., 2005
Argille di Viano Fm., San Valentino, Italy Paleocene-middle Eocene (reworked); unconstrained plate	*Mosasaurus* cf. *hoffmannii*	Palci et al., 2014
Muwaqqar Chalk Marl Fm., Jordan Maastrichtian; 12.1°, (9.7°, 14.7°)	**Mosasaurus* cf. *hoffmannii*	Mustafa and Zalmout, 2001
Oulad Abdoun Basin, Oued Zem, Morocco Maastrichtian; 24.2° (19.9°, 29.1°)	*Mosasaurus hoffmannii*	present note
Nekum Chalk, The Netherlands Maastrichtian; 40.2° (37.8°, 42.8°)	*Mosasaurus hoffmannii*	Mantell, 1829; Lingham-Soliar, 1995
Dukamaje Formation, Mt. Igdaman, Niger Maastrichtian; 0.7° (-1.8°, 3.2°)	*cf. *Mosasaurus hoffmannii*	Lingham-Soliar, 1991
Greensand Fm., Poland Paleocene, Danian (reworked); 42.5° (40.0°, 45.0°)	*Mosasaurus* cf. *hoffmannii*	Sulimski, 1968; Machalski et al., 2003
Penza, Russian Federation Maastrichtian; 45.5° (43.1°, 48.1°)	*Mosasaurus hoffmannii*	Grigoriev, 2014
Condado de Treviño, Spain Maastrichtian; 34.6° (30.3°, 39.5°)	*Mosasaurus hoffmannii*	Bardet et al., 2013
Davutlar Fm., Devrekani, Turkey Maastrichtian; 30.0°, unconstrained plate	*Mosasaurus hoffmannii*	Bardet and Tunoğlu, 2002
Ripley Fm., Alabama, United States Maastrichtian; 33.5° (31.0°, 36.0°)	*Mosasaurus hoffmannii*	Russell, 1967; Kiernan, 2002
Merchantville Fm., Delaware, United States Campanian; 37.9° (35.4°, 40.4°)	*Mosasaurus hoffmannii*	Russell, 1967; Baird and Galton, 1981
Severn Fm., Maryland, United States Maastrichtian; 36.8° (34.4°, 39.4°)	*Mosasaurus hoffmannii*	Baird, 1986
Owl Creek Fm., Missouri, United States Maastrichtian; 38.4° (35.9°, 40.9°)	*Mosasaurus hoffmannii*	Gallagher et al., 2005
Navesink Fm., New Jersey, United States Maastrichtian; 37.4° (35.0°, 40.0°)	*Mosasaurus hoffmannii*	Cope, 1869; Mulder, 1999; Gallagher, 2005
Fox Hills Fm., South Dakota, United States Maastrichtian; 49.4°, (46.9°, 51.9°)	*Mosasaurus hoffmannii*	Harrell and Martin, 2015
Ripley Fm., Tennessee, United States	*Mosasaurus hoffmannii*	Russell, 1967

Late Campanian; 36.6° (34.2°, 39.2°)		
Navarro Fm., Texas, United States Maastrichtian; 34.7° (32.2°, 37.2°)	*Mosasaurus hoffmannii*	Russell, 1967

Table 2. Distribution of reported Mosasaurus hoffmannii occurrences. Locations demarcated by (*) represent dubious occurrences where fossil material is insufficient for specific identification (better identified as Mosasaurus indet.). Paleolatitudinal coordinates from van Hinsbergen et al., 2015.

Northern occurrences of *M. hoffmannii*: Fossil remains of Mosasaurus hoffmannii have previously been documented in upper Campanian and Maastrichtian sediments within a paleolatitudinal belt between 30°N and 45°N (Bardet and Tunoğlu, 2002; Jagt et al., 2008; Bardet et al., 2013). Definitive occurrences include Belgium (Lingham-Soliar, 1995), Bulgaria (Jagt et al., 2006), Denmark (Lindgren and Jagt, 2005), the Netherlands (Mantell, 1829; Lingham-Soliar, 1995), the Russian Federation (Grigoriev, 2014), Spain (Bardet et al., 2013), and Turkey (Bardet and Tunoğlu, 2002). Fragmentary remains attributed to Mosasaurus cf. hoffmannii may represent additional occurrences in Germany (Reich et al., 2005), Italy (Palci et al., 2014), and Poland (Sulimski, 1968; Machalski et al., 2003). Synonymy of Mosasaurus maximus Cope, 1869 with M. hoffmannii extends its range west into North America where it is reported in the United States from Alabama (Kiernan, 2002; Russell, 1967), Delaware (Baird and Galton, 1981), Maryland (Baird, 1986), Missouri (Gallagher et al., 2005), New Jersey (Cope, 1869; Mulder, 1999; Gallagher, 2005), South Dakota (Harrell and Martin, 2015), Tennessee (Russell, 1967), and Texas (Russell, 1967).

Austral occurrences of *M. hoffmannii*: Reported occurrences of Mosasaurus below the paleolatitude 30°N are numerous, though based on isolated, poorly preserved specimens. Remains have been reported from Antarctica (Martin and Crame, 2006), Argentina (Fernández et al., 2008), Angola (Jacobs et al., 2006; Mateus et al., 2011), Democratic Republic of the Congo (Lingham-Soliar, 1994), Jordan (Mustafa and Zalmout, 2001), and Niger (Lingham-Soliar, 1991). Despite the multitude of finds, the described fossil material is insufficiently diagnostic for species attribution. As such, the presence of M. hoffmannii in the southern hemisphere is uncertain. Possible occurrences are reviewed below.

Lingham-Soliar (1991) reported a fragment of a tooth from Niger as cf. Mosasaurus hoffmannii. The tooth is heavily worn and missing the distal tip and anteroventral surface. The labial face bears five "facets," a feature dissimilar with M. hoffmannii (2-3 labial prism faces) and more consistent with *Mosasaurus beaugei* and *Mosasaurus lemmonnieri*. Lingham-Soliar (1994) further reported two worn, partial tooth crowns from the Congo as cf. Mosasaurus hoffmannii. In both teeth, poor preservation has worn away the enamel surface and precluded specific level identification.

Mustafa and Zalmout (2001) report a single tooth from the At-Tayyba area of northwest Jordan as Mosasaurus cf. hoffmannii. It is described as, "curved orally, rounded at both anterior and posterior sides. The anterior face of the crown is slightly convex with a thin carina, that is absent on the posterior side. Thin lines and fine striae (4-5 striae / mm) convergent toward the tip." Absence of a posterior carina precludes identification as Mosasaurus. Striated enamel, rather than faceted, is a trait more associated with Russellosaurine mosasaurids (Bell, 1997).

Martin and Crame (2006) attributed large bone fragments and partial teeth from Seymour Island, Antarctica to Mosasaurus sp. aff. M. hoffmannii. Species determination was made based on large tooth size and strong facets visible on the enamel surface. However, large tooth size and faceted enamel is typical of the genus Mosasaurus as a whole (Lingham-Soliar, 1995; Harrell and Martin, 2015). The Antarctic material lacks diagnostic features necessary for species level identification.

Fernández et al. (2008) identified fragmentary skull sections as Mosasaurus sp. aff. M. hoffmannii from the upper part of the Jagüel Formation, Malargüe Group in Patagonia, Argentina. They noted that "MML-PV1 [the skull] may represent a new species, because certain characteristics, such as the weak postglenoid process of the humerus, are not shared with other Mosasaurus… In this context, MML-PV1 is referred to Mosasaurus aff. M. hoffmanni, following the recommendations in open nomenclature of Bengtson (1988)."

Mateus et al. (2011) report isolated shed teeth and partial humeri from Bentiaba, Angola as Mosasaurus sp. aff. M. hoffmannii. This contrasts with two previous studies which referred Mosasaurus fossils from this region to *Mosasaurus beaugei* (Carvalho, 1961; Antunes, 1964). No species level distinguishing features are noted and analysis of dental ornamentation was not performed. As the species of Mosasaurus differ based on enamel ornamentation, specific level assignment without proper examination of prism counts is premature.

5. CONCLUSION

Newly discovered remains of the marine reptile *Mosasaurus hoffmannii* from the Late Cretaceous (Maastrichtian) phosphates of Morocco represent the furthest south occurrence of this species and the first definite occurrence on the African continent. The addition of another apex predator to the Moroccan mosasaurid assemblage provides further evidence of the tremendous diversity of Mesozoic marine reptiles in the southern margin of the Mediterranean Tethys.

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