

First Record of a Tylosaurine Mosasaur from the Latest Cretaceous Phosphates of Morocco

Trevor H. Rempert^{1*}, Brennan P. Martens^{2,3}, Alexander P. M. Vinkeles Melchers³

¹Department of Physiology and Biophysics, Case Western Reserve University, Cleveland, USA ²Department of Biological Sciences, University of Alberta, Edmonton, Canada ³The Vancouver Paleontological Society, Richmond, Canada Email: *thr14@case.edu

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Abstract

The latest Cretaceous Phosphates of Morocco preserve the highest biodiversity of mosasaurid squamates anywhere in the world. Intensive sampling over the past century has uncovered at least ten genera and thirteen species from the mosasaur subgroups Halisauromorpha, Plioplatecarpinae, and Mosasaurinae. Notably missing from the assemblage are members of the macropredatory Tylosaurinae. The Tylosaurinae were globally rare in the Maastrichtian and their apparent absence has been previously explained by either collecting bias, ecological preference for deeper waters, or habitat restriction to higher paleolatitudes. Here, we describe a new tylosaurine mosasaurid, Hainosaurus boubker sp. nov., based on several partial skulls and isolated teeth originating from the Couche III layer of the Sidi Chennane Phosphate guarry near Oued Zem, Morocco. It is unique amongst tylosaurine mosasaurids in possessing blade-like teeth that are laterally compressed, encircled by enamel facets, and differentiated along the dental margin. The discovery of this new taxon in the Maastrichtian of Morocco is remarkable as it represents both the youngest species of Tylosaurinae and the first occurrence in North Africa.

Keywords

Cretaceous, Mosasaur, Morocco, Africa, Tylosaurinae

1. Introduction

Mosasaurs (Squamata, Mosasauridae) are extinct marine reptiles that achieved widespread distribution in the oceans and epicontinental seas of the Late Cretaceous. The Tylosaurinae, one of the longest-lived mosasaur lineages, first appeared in the Turonian as medium-sized generalists, though quickly evolved into giant macropredators by Coniacian-Santonian times [1] [2] [3] [4]. Considered the top predators of Late Cretaceous marine environments, tylosaurine mosasaurs experienced a marked reduction in diversity and prevalence during the mid-Campanian that persisted until their extinction at the end of the Cretaceous [5] [6] [7].

The increased rarity of tylosaurine mosasaurs in the Maastrichtian is likely related to the diversification of several derived mosasaur lineages in the mid-Campanian [6] [7]. The evolution of specialized longirostrine plioplatecarpines, brevirostrine halisaurines, and durophagous mosasaurine taxa allowed for increased morphofunctional disparity at the expense of macropredatory generalists [8]-[13]. Maastrichtian outcrops in Angola, Belgium/The Netherlands, Morocco, and New Jersey, repeatedly show mosasaur assemblages dominated by highly adapted mosasaurines, with few halisaurines and plioplatecarpines, and little or no record of tylosaurine presence [14]. This is especially apparent in the phosphate basins of central Morocco, where intensive sampling has uncovered 13 unique species, with 10 hailing from Mosasaurinae, 2 from Halisaurinae, 1 from Plioplatecarpinae, and none from Tylosaurinae (**Table 1**). Indeed, the fossil record of Tylosaurinae is sparse in the latest Cretaceous and near exclusively at paleolatitudes greater than 30° [15] [16].

Here, we report the first discovery of a tylosaurine mosasaur from the upper Maastrichtian Phosphates of Morocco, North Africa. *Hainosaurus boubker* sp. nov. is described based on material from several individuals originating in the Couche III layer of the Sidi Chennane Phosphate quarry near Oued Zem, Morocco (paleolatitude 25°N). The new fossil material records the geologically

 Table 1. List of mosasaur taxa present in the Moroccan Phosphates. Arranged in order of first description.

Taxon	Subfamily	Authority
Mosasaurus hoffmannii	Mosasaurinae	Mantell, 1829 [17]
Carinodens belgicus	Mosasaurinae	(Woodward, 1891) [18]
Mosasaurus beaugei	Mosasaurinae	Arambourg, 1952 [19]
Gavialimimus ptychodon	Plioplatecarpinae	(Arambourg, 1952) [19]
Prognathodon currii	Mosasaurinae	Christiansen & Bonde, 2002 [20]
Globidens phosphaticus	Mosasaurinae	Bardet <i>et al.</i> , 2005 [8]
Halisaurus arambourgi	Halisaurinae	Bardet <i>et al.</i> , 2005 [9]
Carinodens minalmamar	Mosasaurinae	Schulp, Bardet & Bouya, 2009 [21]
Eremiasaurus heterodontus	Mosasaurinae	LeBlanc, Caldwell & Bardet, 2012 [22]
Globidens simplex	Mosasaurinae	LeBlanc, Mohr & Caldwell, 2019 [23]
Xenodens calminechari	Mosasaurinae	Longrich <i>et al.</i> , 2021 [12]
Pluridens serpentis	Halisaurinae	Longrich <i>et al.</i> , 2021 [11]
Thalassotitan atrox	Mosasaurinae	Longrich <i>et al.</i> , 2022 [13]
Hainosaurus boubker sp. nov.	Tylosaurinae	Present note

youngest occurrence of Tylosaurinae and an unusually southern record of this mosasaur subfamily. The taxonomic history of *Hainosaurus* is reviewed and the paleoecology of Maastrichtian tylosaurines is given in summary. This paper adds to our knowledge on the biodiversity, paleobiogeography, and paleoecology of mosasaurid reptiles immediately prior to the end Cretaceous extinction event.

2. Location, Materials and Methods

2.1. Geological Setting

The Moroccan Phosphates are a component of the Mediterranean Tethyan phosphogenic province, a complex of warm and shallow marine platforms linked to low latitude upwelling currents and intense phosphatic sedimentation along the southern margin of the Mediterranean Tethys during the Late Cretaceous and early Paleogene. Phosphate deposits extend from South America (Pernambuco Province of Brazil) through North and West Africa (Algeria, Egypt, Mauritania, Morocco, Togo, Tunisia, Senegal) and into the Middle East (Iraq, Israel, Jordan, Syria) [24].

The phosphatic successions of Morocco have been known since 1905 and exploited since 1921 as an economically valuable source of phosphorite [25]. Stratigraphically, they range in age from Late Cretaceous (Maastrichtian) to early Eocene (Lutetian), spanning approximately 24 Ma with apparent continuity [24]. The Moroccan Phosphates outcrop in five major basins, from northeast to southwest, they are the Oulad Abdoun, Ganntour, Meskala, Sous, and Oued Eddahab basins [9] [26] (**Figure 1**).

The Oulad Abdoun phosphatic series is divided into informal mining layers [25]. No formations or members are named due to drastic local lateral facies



Figure 1. Map and stratigraphic column. (A) Map of the major phosphate basins in Morocco. (B) Stratigraphic section of the Oulad Abdoun basin. Abbreviations: Ph, phosphates; Ma, marls; Li, limestones.

changes and a paucity of invertebrate and floral biostratigraphic markers. Three primary mining layers (termed "Couches") are present throughout the Oulad Abdoun basin: Couche I (Ypresian), Couche II (Thanetian), and Couche III (Maastrichtian) [26]. The Maastrichtian component of the phosphatic series is condensed, being only 2 - 5 m thick. It is divided into a basal unit of grey limestone, a lower layer of yellow phosphates (Lower Couche III), and an upper layer of highly fossiliferous grey phosphates (Upper Couche III) [9] (Figure 1). Selachian biostratigraphy dates these horizons to late Maastrichtian, and carbon and oxygen isotope chemostratigraphy further constrains the age to latest Maastrichtian (less than 1 Ma prior to the K-Pg boundary) [27] [28] [29].

Fossils described here originate from the Upper Couche III layer of Oulad Abdoun Basin. The Upper Couche III layer is rich in remains of sharks [19] [27], fish [19] [30], pachyvaranid squamates [31], plesiosaurs [32] [33], chelonoid turtles [34], crocodilians [35], pterosaurs [36], and even rare dinosaurs [37]. As far as mosasaurs are concerned, they represent the most numerically abundant and taxonomically diverse marine amniote remains in the phosphates [8] [9] [11] [12] [13] [19] [21] [22] [23] [38] [39].

2.2. Terminology

The osteological terminology follows Russell (1967) [1]. Dental crown characters are described following Hornung and Reich (2015) [40].

2.3. Institutional Abbreviations

IRSNB, Institut Royal des Sciences Naturelles de Belgique (Brussels, Belgium); **MNHM**, Muséum National d'Historie Naturelle (Paris, France); **VANPS**, Paleontological Museum of The Vancouver Paleontological Society (Richmond, British Columbia, Canada); **YPM**, Peabody Museum of Natural History (New Haven, Connecticut, USA).

3. Results

3.1. Systematic Paleontology

SQUAMATA Oppel, 1811 [41] MOSASAURIDAE Gervais, 1853 [42] TYLOSAURINAE Williston, 1897 [43] *Hainosaurus* Dollo, 1885 [44] Type Species – *Hainosaurus bernardi* Dollo 1885 [45] *Hainosaurus boubker* sp. nov.

Nomenclatural acts. This publication is registered under ZooBank LSID urn:lsid:zoobank.org:pub:3CA71F4D-1860-444F-8008-30DE7684BCE8. The specific name *H. boubker* is registered under LSID

urn: lsid: zoobank. org: act: 31A503B9-6631-423D-9B3C-9F90CE028FC8.

Syntypes. VANPS 13.0120 premaxilla and anterior internarial bar (**Figure 2**) (**Figure 3**); VANPS 13.0121 premaxilla, maxillae, right dentary, and marginal

dentition (Figure 2) (Figure 4) (Figure 6).

Referred. VANPS 13.0122 premaxilla and right maxilla preserved together on matrix (**Figure 5**); VANPS 13.0124 rooted tooth (**Figure 7**); VANPS 13.0125 - 13.0165 isolated marginal tooth crowns (**Figure 7**) (**Figure 8**).

Locality. Syntypes and referred specimens originate from the Sidi Chennane quarry, South of Oued Zem, Khouribga Province, Morocco (**Figure 1**).

Horizon. Upper Couche III layer of the Oulad Abdoun Basin; Late Maastrichtian (**Figure 1**).

Etymology. In recognition of Boubker Chaibi for his discovery and donation of the type material.



Figure 2. *Hainosaurus boubker* sp. nov., premaxilla. Upper Couche III, Oulad Abdoun Basin, Sidi Chennane, Morocco. (A) VANPS 13.0120 dorsal view. (B) VANPS 13.0120 ventral view. (C) VANPS 13.0121 dorsal view. (D) VANPS 13.0121 ventral view. Abbreviations: alv, alveolus; for, foramina; nub, nubbin; resp, resorption pit; ros, rostrum; vom, vomer. Scale bars = 10 cm.



Figure 3. *Hainosaurus boubker* sp. nov., premaxillary rostrum. Upper Couche III, Oulad Abdoun Basin, Sidi Chennane, Morocco. (A) VANPS 13.0120 lateral view. (B) VANPS 13.0120 lateral view interpretive drawing. Abbreviations: for, foramina; knob, dorsal knob; nub, nubbin. Scale bar = 5 cm.



Figure 4. *Hainosaurus boubker* sp. nov., VANPS 13.0121 left and right maxilla. (A) left maxilla lateral view. (B) left maxilla medial view. (C) right maxilla medial view. (D) right maxilla lateral view. Abbreviations: dbs, double-buttressed suture; pm-m, premaxillary-maxillary suture. Scale bars = 10 cm.

Diagnosis. Large tylosaurine mosasaurid (adult total length 8 - 12 m). Premaxillary rostrum rectangular in lateral profile, circular in coronal cross-section; double-buttressed premaxillary-maxillary suture; approximately twelve to thirteen maxillary teeth; premaxillary-maxillary suture ending above the 4th maxillary tooth position; external nares U-shaped anteriorly, marked by deep emargination into the maxillae; predental process of the dentary elongated and lacking dorsal ridge; Meckelian canal of the dentary initiating below the first tooth position; marginal teeth laterally compressed (Crown Base Width: Crown Base Length = 0.71) and markedly heterodont; Anterior marginal teeth hook-like, unicarinate anteriorly, and lanceolate in cross-section; mid-marginal teeth tall, anterolaterally bicarinate, and oval in cross-section; posterior marginal teeth robust, anterolaterally bicarinate, and basally inflated; tooth enamel surfaces decorated by large facets and well-developed basal, third-order striations; tooth crowns bear 5 - 6 facets labially, 5 - 7 facets lingually; carinae pronounced and serrate; posterior carina curves laterally, dividing the tooth into asymmetrical labial and lingual surfaces.

Hainosaurus boubker differs from Hainosaurus bernardi Dollo 1885 [44] in the maxilla being deeply emarginated for the opening of the external nares, the marginal tooth crowns bearing more developed facets, and the carinae of tooth crowns dividing the tooth into subequal labial and lingual faces. Differs from Tylosaurus spp. Marsh 1872 in marginal dentition highly differentiated, marginal tooth crowns laterally (buccolingually) compressed and posteriorly curved (basally inflated and posteromedially curved in Tylosaurus), tooth surfaces bearing facets, tooth carinae being more developed, and the Meckelian canal of the dentary being retracted to below the first dentary tooth position [45]. Differs from Tylosaurus nepaeolicus Cope 1874 and Tylosaurus kansasensis Everhart 2005 in having a longer premaxillary rostrum that is rectangular in lateral view and external nares that originate above 4th maxillary tooth position [46] [47]. Further differs from T. nepaeolicus in having the vomerine process of the premaxilla originate between the first premaxillary teeth (originates after the first premaxillary tooth position in *T. nepaeolicus*). Differs from *Taniwhasaurus* spp. Hector 1874 by the absence of a median dorsal ridge on the premaxillary internarial bar and the presence of serrations on the tooth carinae [48].

3.2. Description

Premaxilla. An elongated rostrum is present anterior to the premaxillary dentigerous body (**Figure 2**). The outline of the rostrum is rectangular in lateral aspect, V-shaped in dorsal and ventral aspect, and circular in cross-section. The edentulous rostrum's morphology resembles that of *H. bernardi* and *T. proriger*, but it is larger and less rounded than those seen in *T. nepaeolicus*, *T. kansasensis*, and *Taniwhasaurus* spp. Oval-shaped foramina perforate the lateral surfaces of the rostrum marking the exits of the ophthalmic ramus the fifth cranial nerve (CN V) [1]. In lateral view, the premaxillary-maxillary suture traces the outline of a double-pointed buttress with the maxilla, then rises to a dorsal termination above the 4th maxillary tooth position.

In ventral view, a nubbin located on the midline of the edentulous rostrum marks the anterior limit of the gum line [1] (Figure 3). Behind it, four alveoli for the first and second premaxillary tooth positions are visible. Premaxillary teeth

project ventrally without procumbence or prognathism. The vomerine process of the premaxilla initiates between the anterior-most premaxillary teeth and bifurcates into two narrow projections. The paired vomers extend posteriorly along the ventral midline with no gap between the two ridges.

In VANPS 13.0120, the internarial bar emerges from the dentigerous body of the premaxilla and projects posteriorly (**Figure 2**). It is widest at its first contact with the maxillae and constricts between the 4th maxillary tooth positions, where it forms the medial border of the external nares. The dorsal cortical surface is smooth and gently convex. The ventral surface is deeply sulcate. Unlike in *Taniwhasaurus*, the premaxillary internarial bar lacks a median dorsal ridge [49]. In cross-section, the internarial bar is inverted trapezoidal in shape with a ventrally projecting keel.

Maxilla. The partial left maxilla in VANPS 13.0121 preserves only the first three tooth positions with the second maxillary tooth crown intact (**Figure 4**). The right maxillae in VANPS 13.0121 and VANPS 13.0122 are more complete, preserving the first seven and ten tooth positions, respectively (**Figure 4**) (**Figure 5**). Despite missing the posterior maxilla, the shape and height of the present material allows for a rough approximation of twelve to thirteen maxillary teeth. Tooth alveoli are more widely spaced apart than in *T. proriger* resulting in ample space between anterior and mid-marginal teeth but cramped interdigitation between the basally inflated mid-marginal to posterior teeth. Resorption pits are positioned posteromedially to tooth alveoli. The medial parapet is shorter than the labial one.

In lateral view, the maxilla has a double-buttressed suture with the premaxilla. The dorsal margin rises posterodorsally until the termination of the premaxillary-maxillary suture above the 4th maxillary tooth position. Following this, the upper rim of the maxilla is deeply emarginated for the openings of the external nares. Emargination of the maxilla and constriction of the internarial bar gives the external nares a U-shaped anterior opening. Exits for the fifth cranial nerve are aligned in a row above the dental margin and randomly distributed near the anterior edge of the bone [1]. The cortical surface of the maxillae is smooth.



Figure 5. *Hainosaurus boubker* sp. nov., VANPS 13.0122 premaxilla and right maxilla. Abbreviations: m, maxilla; pm, premaxilla. Scale bar = 10 cm.

Dentary. The right dentary in VANPS 13.0121 is in two parts, an anterior section preserving the five anteriormost tooth positions and a posterior section preserving five posterior tooth positions (**Figure 6**). The second and fourth dentary teeth are preserved occupying their natural locations. Protruding in front of the first tooth alveolus is a long predental process that lacks a dorsal ridge. The longitudinal axis of the dentary is gently concave upwards, as are its dorsal and ventral margins. The medial parapet is higher than the lateral one. The lateral surface is convex and bears a row of foramina for the mandibular terminal branch of the fifth cranial nerve [1]; foramina occur at half the height of the bone in a row parallel to the dental margins. The medial surface of the dentary is marked by the deep excavation of the Meckelian canal. The origin of the Meckelian canal is retracted, initiating below the first dentary tooth rather than near the interdentary symphysis.

Dentition. The marginal dentition of *H. boubker* is markedly heterodont. Three crown morphologies are observed depending on position in the dental ramus: anterior marginal (tooth positions 1 - 4), mid-marginal (tooth positions 5 - 10), and posterior marginal (tooth positions 10+). These unique crown morphologies are mirrored in both the upper and lower jaws.

Anterior marginal teeth (VANPS 13.125-13.132) (**Figure 7**) are hook-like owing to a high degree of posterior curvature. These teeth bear only a single serrated anterior carina that runs from the apex to the base of the crown. The enamel surface is striate and encircled by apico-basally striking facets. In cross-section, the crown is lanceolate in outline.



Figure 6. *Hainosaurus boubker* sp. nov., VANPS 13.0121 right dentary. (A) right dentary anterior section in lateral view. (B) right dentary anterior section in medial view. (C) right dentary posterior section in lateral view. Abbreviations: for, foramina; epr, edentulous protrusion of the dentary; meckca, Meckelian canal. Scale bar = 10 cm.



Figure 7. *Hainosaurus boubker* sp. nov., anterior marginal tooth crowns. (A) VANPS 13.0125 labial, posterior, and lingual view. (B) VANPS 13.0127 lingual and posterior view. (C1) VANPS 13.0124 lingual view. (C2) VANPS 13.0124 labial view. (D) VANPS 13.0126 lateral and posterior view. (E) VANPS 13.0130 labial and lingual view. Scale bar = 3 cm.

Mid-marginal teeth (VANPS 13.0133 - 13.0147) (**Figure 8**) are tall and bladelike. They are bicarinate, possessing both anterior and posterior carinae. The posterior carina divides the tooth surface into subequal labial and lingual faces by forming a 210-degree intercarinal angle with the anterior carina. The labial surface bears 5 - 6 facets, while the lingual surface bears 5 - 7 facets. In crosssection, the teeth are elliptical in outline.

Posterior marginal teeth (VANPS 13.0148 - 13.0157) (**Figure 8**) resemble mid-marginal teeth, though are shorter and more robust. These teeth have a stocky appearance and are often marred by self-inflicted gashes produced by occlusion with teeth from the opposing jaw. Posterior marginal teeth are similarly bicarinate to mid-marginal teeth, although serrations on the carinae are often abraded from wear.

Irrespective of position in the jaw, all marginal teeth are strongly laterally compressed. In *H. boubker*, the Crown Base Width (CBW) to Crown Base Length (CBL) ratio is measured to be approximately 0.71 throughout all tooth positions. Teeth with these dimensions are more slender than those of *T. proriger* (CBW:CBL \geq 0.81) but similar to teeth reported in *H. bernardi* [50].



Figure 8. *Hainosaurus boubker* sp. nov., mid-marginal and posterior marginal tooth crowns. (F) VANPS 13.0135 mid-marginal tooth crown in labial and lingual view. (G) VANPS 13.0138 mid-marginal tooth crown in labial and lingual view. (H) VANPS 13.0136 mid-marginal tooth crown in lingual and labial view. (I) VANPS 13.0139 mid-marginal tooth crown in labial and lingual view. (J) VANPS 13.0147 mid-marginal tooth crown in labial, posterior, and lingual view. (K) VANPS 13.0157 posterior marginal tooth in lingual view. (M) VANPS 13.0148 posterior marginal tooth in labial and lingual view. (M) VANPS 13.0148 posterior marginal tooth in lingual and labial view. (N) VANPS 13.0144 mid-marginal tooth crown in lingual, posterior, and labial view. (S) VANPS 13.0150 posterior, and labial view. (N) VANPS 13.0148 posterior marginal tooth in lingual and labial view. (N) VANPS 13.0144 mid-marginal tooth crown in lingual, posterior, and labial view. Scale bar = 3 cm.

Teeth of *H. boubker* are differentiated from *H. bernardi* based on the position of the posterior carinae. In *H. bernardi*, marginal tooth crowns are nearly symmetrically bi-carinate. In *H. boubker*, the mid-marginal and posterior marginal teeth are divided into subequal labial and lingual faces by a labially twisting posterior carina. This results in the lingual face being larger than the labial face in *H. boubker*, while they are approximately the same size in *H. bernardi*. Additionally, enamel facets are more prominent in *H. boubker* than in *H. bernardi*. The apicobasal ridges making up facet borders are so well-defined that they bear a superficial resemblance to the pronounced enamel prism faces observed in the

teeth of *Mosasaurus beaugei* Arambourg, 1952 [19] [38]. Within facet planes, tightly spaced tertiary striae give the enamel a lineated texture.

All tooth morphologies have strong posterior curvature, but unlike most tylosaurines, the teeth of *H. boubker* have little to no medial curvature.

4. Discussion

4.1. Taxonomic History of Hainosaurus

The laterally compressed heterodont dentition of the new Moroccan material is a character exclusive to the tylosaurine genus *Hainosaurus* and therefore allows for referral to that taxon [40] [50]-[55]. The taxonomic status of *Hainosaurus* has been questioned based on the relatively few cranial, dental, and vertebral characters differentiating it from Marsh's *Tylosaurus* [56]. As such, it is necessary to review its taxonomic history in detail.

4.1.1. Dollo's Initial Descriptions

First described in a series of papers by Dollo [44] [57] [58] [59] [60], *Hainosaurus bernardi* was erected based on a nearly complete, although heavily abraded, skeleton collected from the Lower Maastrichtian Ciply Chalk near Mesvin, Belgium. Dollo identified three types of marginal teeth in the holotype (IRSNB R23): 1) teeth almost circular in cross-section, conical, slender, and bearing a single anterior carina, 2) tall-crowned teeth, strongly buccolingually compressed and adorned with two carinae, 3) teeth similar to the second category, but with shorter crowns. He further noted that *Hainosaurus* differed from other tylosaurs by its larger number of precaudal vertebrae, greater length of the femur relative to the humerus, and reduced suprastapedial and infrastapedial processes on the quadrate. Dollo described a second species, *Hainosaurus lonzeensis* (no specimen number; Dollo 1904), based on a poorly preserved premaxillary fragment from the Coniacian/Santonian of Lonzée, Belgium, but this taxon has been universally considered *nomen dubium* [3] [40] [50] [61].

4.1.2. 20th Century Discoveries

In his review of North American mosasaurs, Russell (1967) commented on the poor preservation of the type material and suggested the suprastapedial process on the quadrate may have originally been "as large as in *Tylosaurus*" [1]. In his opinion, the only distinguishing character between *Hainosaurus* and *Tylosaurus* was a greater number of vertebrae between the cranium and the chevron-bearing caudals in the former genus.

Nicholls (1988) paired the description of a new species, *Hainosaurus pembinensis*, with the first major reexamination of *Hainosaurus* [61]. In her generic diagnosis, Nicholls identified the following characters: 1) prominent rectangular rostrum anterior to the first tooth on premaxilla and to a lesser degree on dentary; 2) 12 teeth in maxilla, 12 - 13 teeth in dentary; 3) external nares relatively longer than in *Tylosaurus*, constituting 28% - 31% of skull length; 4) frontal excluded from dorsal border of the orbit by contact of the prefrontal with the postorbitofrontal; 5) suprastapedial process of the quadrate short, infrastapedial process of the quadrate reduced to small swelling half-way up the quadrate shaft; 6) scapula much smaller in area than coracoid, coracoid not notched; 7) femur longer than humerus; 8) 63 - 64 vertebrae anterior to chevron-bearing caudals; 9) adult body size very large, estimated 12 - 15 m. Unfortunately, reviewing Ni-cholls' diagnosis against the modern record of tylosaurine fossils reveals some problems. Characters 2, 4, 6, and 9 are not exclusive to *Hainosaurus* but are generally characteristic of both *Hainosaurus* and *Tylosaurus*. Further, character 3 is unique only to *H. pembinensis* and not seen in the type.

Bardet (1990) recognized tylosaurine affinities in *Mosasaurus gaudryi* Thévenin 1896 and reassigned it to *Hainosaurus* on the basis of its large size, exclusion of the frontal from the upper margin of the orbit by a prefrontal-postorbitofrontal contact, and greater length of the external nares [62] [63]. The type and only skull of *M. gaudryi* (MNHN 1896-15) was further referred to *H. bernardi* based on its heterodont dentition. This reassessment was made despite the type material of *M. gaudryi* being from the Upper Santonian of France while the type material of *H. bernardi* was from the Early Maastrichtian of Belgium.

Lingham-Soliar (1992) conducted a second major reexamination of *Haino-saurus* [3]. In his assessment of the *H. bernardi* type skeleton (IRSNB R23) and a new referred skull (IRSNB 3672), he identified new *Hainosaurus* characters: a premaxillary-maxillary suture that forms a two-pointed "double-buttress"; and a prefrontal that contributes to the posterior margin of the external nares. Ling-ham-Soliar also assessed the other species of *Hainosaurus*. He reaffirmed Bardet's reclassification of *M. gaudryi* to *Hainosaurus* but suggested it represents its own species based on the straight frontoparietal suture and the location of the parietal foramen some distance from the frontoparietal suture. He noted that *H. pembinensis* lacked the two new *Hainosaurus* characters that he identified but suggested that the larger number of precaudal vertebrae was sufficient to maintain it in the genus *Hainosaurus*.

4.1.3. 21st Century Revisions

Lindgren and Siverson (2002) redescribed *Mosasaurus ivoensis* Persson 1963 and referred it to *Tylosaurus* on the basis of its dental and vertebral morphology [50] [64]. Included in this study was a thorough examination of the type and topotypic material of *H. bernardi, H. gaudryi, H. pembinensis*, and *T. proriger*. They provided the following characters for differentiating *Hainosaurus* from *Tylosaurus*: 1) the marginal tooth crowns are more compressed buccolingually in *Hainosaurus* than they are in *Tylosaurus*; 2) the carinae are more developed on marginal tooth crowns of *Hainosaurus* than *Tylosaurus*; 3) the carinae on the pterygoid teeth have minute serrae in *Hainosaurus*, whereas the carinae lack serrations in *Tylosaurus*; 4) the suprastapedial process on the quadrate is small in *Hainosaurus*, while it is relatively large in *Tylosaurus*; 5) the infrastapedial process on the quadrate is virtually absent in *Hainosaurus*, whereas it is well developed in *Tylosaurus*; 6) in lateral view, the quadrate has the shape of a vertical rectangle in Hainosaurus, whereas it is more circular in outline in Tylosaurus; 7) the femur is longer than the humerus in Hainosaurus, while the two elements are more or less equal in length in Tylosaurus; 8) there is a larger number of vertebrae between the cranium and the chevron-bearing caudals in Hainosaurus than there is in Tylosaurus (49+ in Hainosaurus vs. 35 - 37 in Tylosaurus); 9) anteriorly situated intermediate caudal vertebral centra are wider and shorter in Hainosaurus than they are in Tylosaurus. Following this, they noted that the double-buttressed premaxillary-maxillary suture regarded by Lingham-Soliar as diagnostic of Hainosaurus was also present in Tylosaurus (e.g., T. nepaeolicus YPM 3974) and could not be used to distinguish the genera. They additionally noted that the difference in the length of the external nares between H. bernardi and T. proriger is insignificant, with elongated nares only being a trait of H. pembinensis. Lindgren and Siverson took special care to discuss the underutilized taxonomic power of isolated mosasaur tooth crowns. They claimed that isolated mosasaur teeth could be used to resolve genera and even species given a sufficiently large sample size, high-quality descriptions, and narrow stratigraphic intervals. Subsequent publications [51] [52] built on the revisions to Hainosaurus to move H. pembinensis and H. gaudryi to Tylosaurus.

Martin (2007) erected a new species of North American *Hainosaurus* based on a partial skull, paddle bones, and vertebrae from the Late Campanian DeGrey Formation of the Pierre Shale Group [53]. *Hainosaurus neumilleri* was diagnosed based on: 1) premaxillary-maxillary suture sinusoidal in shape; 2) parietal foramen in frontoparietal suture; 3) relatively wide snout; 4) quadrate with large, deep, bowl-shaped excavation incorporating stapedial pit and covering much of the medial quadrate; 5) suprastapedial with relatively long internal process; 6) suprastapedial deflected later-ally compared with axis perpendicular to distal condyle; 7) teeth relatively well faceted and symmetrically flattened. Martin noted that the long suprastapedial process and prominent infrastapedial process on the quadrate of *H. neumilleri* were reminiscent of *T. proriger* and *T. pembinensis*. He suggested that early Campanian tylosaurines such as *T. pembinensis* and *T. ivoensis* represented the initial divergence of *Hainosaurus* from *Tylosaurus* and that the late Campanian H. *neumilleri* was the first species after the divergence completed.

A critical review of *Hainosaurus* was conducted by Bullard and Caldwell (2010) [65]. Contained in this study was a formal redescription of *Hainosaurus pembinensis* as *Tylosaurus pembinensis* and an assessment of the generic diagnosability of *Hainosaurus*. Bullard and Caldwell reviewed the characters outlined in Nicholls (1988), Lingham-Soliar (1992), and Lindgren and Siverson (2002) that supposedly diagnosed *Hainosaurus*. They found that most characters in Nicholls' diagnosis described a typical tylosaurine condition with the exception of the femur being longer than the humerus. They reiterated Lindgren and Siverson's comments that elongated external nares are only unique to *T. pembinensis* and that a double-buttressed premaxillary-maxillary suture is not exclusive to *Hainosaurus*. Further, they noted that the contribution of the prefrontal

to the posterior margin of the external nares, observed by Lingham-Soliar in the *H. bernardi* type, is a character of questionable validity due to the poor preservation of the prefrontal and the posterior maxilla. Reviewing Lindgren and Siverson's informal diagnosis of *Hainosaurus*, they remarked that it was "the best to date," although advised caution regarding the diagnosability of the longer femur to humerus length and the wider and shorter anterior intermediate caudal centra.

Building on Bullard, Jiménez-Huidobro and Caldwell (2016) recommended fully synonymizing Hainosaurus with Tylosaurus [56]. In their opinion, the differences in the shape of the dentition, quadrate, jugal, femur to humerus length, and vertebral column were insufficient to warrant recognizing Hainosaurus as its own genus. Specifically addressing the characters outlined by Lindgren and Siverson (2002), they noted the following: 1) the teeth of Tylosaurus also possess buccolingual compression; 2) more developed carinae are difficult to discern and could represent a species level trait; 3) they could not observe serrated pterygoid teeth on the type and referred material of *H. bernardi*, 4) the preservation of the quadrate makes ascertaining the length of the suprastapedial and infrastapedial process difficult; 5) the femur are humerus length are "virtually equal" and a longer femur is also observed in T. pembinensis; 6) vertebrae counts can be misleading since the vertebral series in *H. bernardi* is incomplete; 7) anterior intermediate caudal centra shape is qualitative and hard to assess. Jiménez-Huidobro and Caldwell concluded that Hainosaurus should be regarded as a junior synonym of Tylosaurus with 'Tylosaurus' bernardi sister to T. proriger. The taxonomic status of H. neumilleri was left uncertain.

Most recently, a series of papers reporting isolated tylosaurine dental material from the Campanian of Germany contend that the crown morphologies of *Hainosaurus* and *Tylosaurus* teeth can be differentiated based on curvature, carination, and enamel ornamentation [40] [54] [55]. These papers describe *Hainosaurus* sp. teeth as labio-lingually compressed, recurved, and nearly symmetrical.

4.1.4. Generic Diagnosability of Hainosaurus

In summary, *Hainosaurus* is a taxon with a long history. Unreconciled differences between *Hainosaurus* from *Tylosaurus* include:

Marginal dentition heterodont with three distinct crown morphologies [44]
 [57] [61];

2) Marginal tooth crowns laterally (buccolingually) compressed [40] [50]-[55];

3) Carinae on marginal tooth crowns more developed [50];

4) Enamel surfaces ornamented by both facets and striae [3] [40] [52] [53] [54] [55];

5) Posteriorly (rather than posteromedially) curving marginal dentition [40] [54];

6) Small suprastapedial and infrastapedial process on the quadrate [44] [50] [57] [59] [61];

7) Anteriorly situated intermediate caudal vertebrae wider and shorter than in

Tylosaurus [50] [52];

8) Larger number of precaudal vertebrae [1] [3] [50] [52] [58] [59] [61] [65].

Characters 1 - 5 describe the unique dental morphology observed in *Haino-saurus*. Characters 6 and 7, while qualitative, do identify discernable differences between the genera and should not be disregarded. Character 8, an increased number of precaudal vertebrae, can be surmised based on the preserved elements of the *Hainosaurus* type despite the vertebral series being incomplete. Given these differences, the authors here elect to maintain *Hainosaurus* and *Ty-losaurus* as distinct genera.

4.2. Derived Dental Morphology

Mosasaur teeth are highly specialized to exploit a wide range of ecological niches. This is especially apparent in Campanian-Maastrichtian taxa, where even isolated teeth are highly diagnostic [8] [12] [14] [40] [50] [51].

Teeth of *Hainosaurus* possess a suite of characters that differentiate them from all other tylosaurines and suggest a unique feeding strategy. Unlike *Taniwhasaurus*, which has conical, minimally curving teeth, and *Tylosaurus*, which has stout, posteromedially curving teeth, the teeth of *Hainosaurus* are laterally compressed and posteriorly curved [1] [3] [49]. Combined with trenchant, serrated carinae, the teeth of *Hainosaurus* exhibit a morphology well-adapted for cutting apart large prey.

During the mid-Campanian, a transition occurred from the robust teeth of *Tylosaurus* to the blade-like teeth of *Hainosaurus*. This change in morphology likely reflects a difference in prey processing. As mosasaurine lineages rapidly diversified to take advantage of several niches during the Campanian, the plesiomorphic condition of robust, multipurpose mosasaurid teeth gave way to a variety of tooth morphologies linked to different feeding habits [40]. In tylosaurines, this manifests as a shift towards a cutting dentition specialized in carving large prey items into swallowable chunks. Increased niche-partitioning via variation in tooth morphology allowed for sympatricity of many large-bodied mosasaurs and explains the multitude of macropredatory mosasaur species in the Moroccan Phosphates [14] [40].

4.3. Body Size Estimation

The length of the premaxillary rostrum in tylosaurines can be used as a proxy for total body length (rostrum = 0.7% of total body length) [1] [66] [67]. In VANPS 13.0120, 13.0121, and 13.0122, the length of the premaxillary rostrum is 58 mm, 58 mm, and 70 mm, respectively. Assuming *H. boubker* is similarly proportioned to *T. proriger*, the premaxillary rostra predict an adult body length of 8 - 10 m.

These results are supported by an alternative body size calculation outlined in Giltaij *et al.* (2021), which notes the linear relationship between tooth crown height and total body length [68]. Comparing dental records of *Tylosaurus* spp.

[1] [15] and *Hainosaurus bernardi* [3] to those of *H. boubker* (avg. CH = 40 - 60 mm) again estimates total body length at 8 - 10 m, with large teeth ($CH \ge 75$ mm) projecting a body length in excess of 10 meters.

4.4. Paleoecology and Paleobiogeography of Hainosaurus

The Moroccan Phosphates were formed during the Maastrichtian at approximately 24°N under the descending limb of the northern Hadley Cell [69]. As a high productivity upwelling center, the phosphates were able to support the highest biodiversity of mosasaur fauna known anywhere in the world [14]. The faunal composition is mostly consistent with Maastrichtian outcrops of the Southern Tethys Margin paleoprovince (North Africa, Middle East, Brazil; paleolatitude 20°S - 20°N), with abundant remains from *Globidens, Gavialiminus, Halisaurus*, and *Prognathodon* [8] [9] [10] [14].

Within the rich mosasaur fauna of the Moroccan Phosphates (Table 1), the discovery of *Hainosaurus boubker*, at 8 - 12 m in length, adds a fifth species of macropredatory mosasaur to the ecosystem (Figure 9). The multitude of large-bodied mosasaurs described from the phosphates is indicative of a tremendous level of niche specialization at the highest trophic level. Tooth morphology among large-bodied taxa is widely disparate, varying between cutting blades (*Hainosaurus boubker*, *Mosasaurus beaugei*), robust meat-hooks (*Mosasaurus hoffmannii*), and crushing domes (*Prognathodon currii, Thalassotitan atrox*), and supports distinct prey preference and feeding strategies [8] [13] [20] [38] [39].

Despite mosasaur diversity being at its peak during the Maastrichtian, members of Tylosaurinae were globally rare, known only by *Hainosaurus bernardi*



Figure 9. Hainosaurus boubker sp. nov., life reconstruction. Art by Carlos Espinosa.

from the early Maastrichtian of Belgium. *Hainosaurus boubker* is the first tylosaurine mosasaur described from the late Maastrichtian. Thus, it fills the temporal gap at the end of the Cretaceous and shows that tylosaurs survived until the K-Pg extinction.

Until now, *Hainosaurus* has been found exclusively in the Campanian to early Maastrichtian of northern Europe and North America. Occurrences include Belgium [3] [44], Germany [54] [55] [70], Poland [51], Sweden [52], and South Dakota, USA [53]. Tylosaurs in general occur near exclusively at high latitudes between 40° - 70° [15]. The only previous reports of tylosaurine material in Africa include *Tylosaurus iembeensis* Antunes 1964 from the Turonian of Angola and "*Tylosaurus" capensis* from the Santonian of South Africa [71] [72]. Thus, the discovery of *H. boubker* in the late Maastrichtian of Morocco (paleolatitude 24°N) expands the paleobiogeographic range of tylosaurines into subtropical latitudes.

5. Conclusion

Hainosaurus boubker sp. nov. is the latest surviving species of Tylosaurinae and the first record of the subfamily in North Africa. *Hainosaurus* brings the total number of mosasaurid genera from the Moroccan Phosphates up to a minimum of eleven, contributing to our knowledge of the most taxonomically rich assemblage of mosasaurids known. The new *Hainosaurus* fossil material is well-preserved and supports the conclusion that *Hainosaurus* represents an advanced group of tylosaurines with a blade-like dental structure. The discovery of *H. boubker* in the Moroccan Phosphates records an unusually equatorial occurrence of Tylosaurinae, a mosasaur subfamily typically found exclusively at higher latitudes.

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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