



Article

# A Prognathodontin Mosasaur from the Maastrichtian of the Dakhla Oasis, Western Desert, Egypt

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**Abstract:** Mosasaurs were diverse in the Upper Cretaceous in Africa, but relatively little is known about the mosasaur fauna of Egypt. Here, associated teeth and postcranial skeletal elements are reported for a mosasaur from the Maastrichtian Dakhla Shale of the Dakhla Oasis. The specimen includes tooth crowns, cervical, dorsal, and caudal vertebrae, and ribs. Teeth and bones exhibit features allowing referral to Prognathodontini. The teeth are relatively straight and blunt, suggesting affinities with *Prognathodon overtoni* or *P. currii*. Prognathodontins were important predators in the Maastrichtian of Africa, previously being recorded in Morocco, Congo, and Angola.

**Keywords:** Mosasauridae; *Prognathodon*; Upper Cretaceous; Maastrichtian; Dakhla Oasis; Western Desert; Egypt



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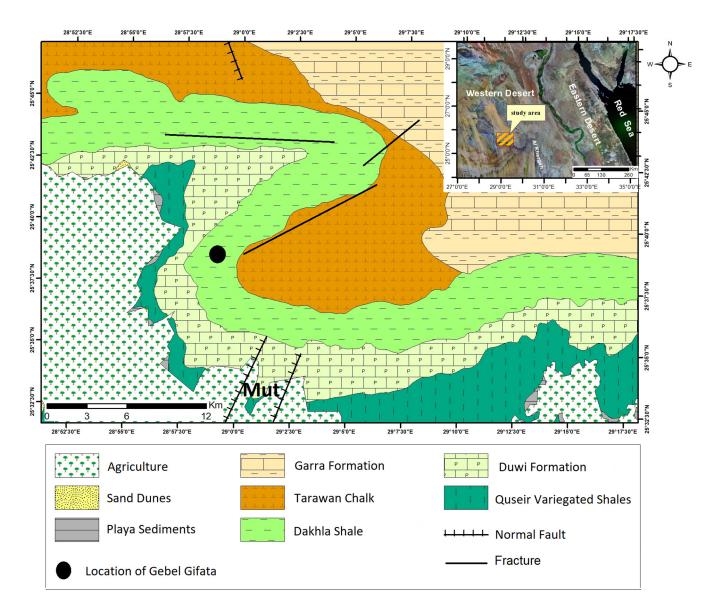


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# 1. Introduction

The mosasaurs (Mosasauridae) are an extinct group of marine reptiles that became abundant and diverse in the Upper Cretaceous [1]. Early work on mosasaurs focused heavily on Europe and North America [2–7], where paleontology first began as a science. Later on, they were also documented in South America and Antarctica [8–18]. However, mosasaurs appear to have been particularly diverse in the tropics and subtropics [2], which have until recently been relatively poorly known. Far and away the most diverse mosasaurid faunas are those of Africa [19,20], with representatives of all major groups of mosasaur having been found in Africa. These include Mosasaurinae [21–28], Halisaurinae [29–32], Tylosaurinae [33], and Plioplatecarpinae [34–37], along with Pachyvaranidae [38], which may represent a primitive, basally diverging branch of Mosasauroidea. In Egypt, mosasaurids have previously been recorded from the Upper Cretaceous deposits of the Eastern Desert [39–45], the Nile Valley [46], and the Western Desert [47–50] (see Appendix A).

This study reports a mosasaurid collected from the Maastrichtian of the Dakhla Shale, at Dakhla Oasis (Figure 1). The teeth show features suggesting affinities with *Prognathodon* or an allied species of Prognathodontini. The Prognathodontini are a subgroup of Mosasaurinae that include *Prognathodon* and its relatives, sometimes recovered as a distinct clade [24], and sometimes as close relatives of *Globidens* in Globidensini. More than a dozen species of *Prognathodon* have been identified around the world from Africa, Asia, Europe, and North America [27,51–53].



**Figure 1.** Geological map of Dakhla area, showing the location of Gebel Gifata, 12 km NW of Mut, Dakhla Oasis (modified after [54]).

Anatomical abbreviations: CL, centrum length; H, height; Hyp, hypapophysis; L, length; Prz, prezygapophysis; Poz, Postzygaphophysis; W, width; W(con), condyle width; W(cot), cotyle width; H(con), condyle height; H(cot), cotyle height; S, synapophysis.

#### 2. Materials and Methods

The studied specimens come from the Maastrichtian of the Dakhla Shale (Figure 2), and include two nearly complete marginal tooth crowns, and three cervical, nine dorsal, and three caudal vertebrae. The fossils were found in association (Figure 3), with the material being exposed and weathered prior to collection.

The specimens described here were accessioned and housed in the New Valley Vertebrate Center (NVP), New Valley University, Kharga, under N° NVP025. Fossils were consolidated using polyvinyl acetate and prepared using brushes and air scribes. Photographs were taken using a digital camera Nikon D780 (the equipment was manufactured in Tokyo, Japan and sourced from Cairo, Egypt) and lens (Af-S Nikkor 70–200 mm 1:28E F/28L ED VR), cropped with Adobe Photoshop Version 22.4.2.

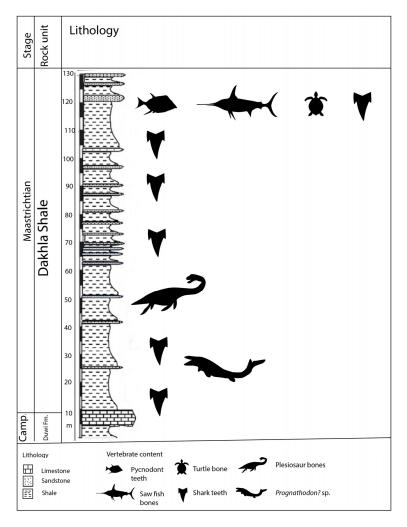


Figure 2. Stratigraphic section of Gebel Gifata (modified after [54]).



 $\textbf{Figure 3.} \ \ Photo \ of the \ associated \ vertebrae \ of \ \textit{Prognathodon} \ sp. \ (blue \ arrows).$ 

# 3. Stratigraphy and Age

Five formations are exposed in the Dakhla Oasis, ranging in age from Upper Cretaceous to Upper Paleocene. From the base to the top, these are the Taref Sandstone, the

Quseir Variegated Shales, the Duwi Formation, the Dakhla Shale, and the Tarawan Chalk. The Taref Sandstone is predominantly formed of cross-bedded, medium- to coarse-grained sandstones. It is largely unfossiliferous. The age of the Taref Sandstone is unclear. At times it has been assigned ages ranging from Turonian [55] to Maastrichtian [56], but the ages of overlying formations constrain its age to no later than Campanian. The Quseir Variegated Shales Formation lies exposed in low buttes scattered in the plain, adjacent to the northern cliff. It is well exposed in the area of Gebel Gifata and is about 30 m thick. It is subdivided into two units, designated Units I (lower) and II (upper) by Hermina et al., (1961) [57], and Mut Member (lower) and Hindaw Member (upper) by [58]. The lower unit, made of clays, is characterized by its brick-red coloration. The upper unit consists of brown and gray gypsiferous sandy clays with a distinctive glauconitic green bed in the middle, and laminated fine sandstones at the very top. Locally, the Quseir Variegated Shales is rich in plant remains, but it is generally unfossiliferous. Recently, a titanosaurian sauropod, Mansourasaurus shahinae, was recovered from the upper member of the formation north of the road between Mut and Balat [59], along with sauropod and non-avian theropod remains [60]. The Quseir Variegated Shales has few useful index fossils and so its age is uncertain, but it is typically assigned to the Campanian [49,55,59,61-63]. The Duwi Formation, 10-25 m thick, comprises several phosphatic layers separated by dark beds of shale. It is the most important phosphate formation of the Upper Cretaceous of Egypt. It is largely made of polished, rounded phosphatic grains of various sizes and is particularly rich in fish teeth, including both bony fishes and elasmobranchs. The Duwi Formation is dated to the upper Campanian by macroinvertebrates, mainly ammonites [64,65] and planktic foraminifera [66]. Its contact with the overlying Dakhla Shale coincides with the Campanian-Maastrichtian boundary [66]. The Dakhla Shale consists predominantly of dark gray shales and mudstones, intercalated by thin- to thick-bedded light gray and brown sandstones. The Dakhla Shale constitutes almost the entirety of the scarp face to the north of the Dakhla Oasis, attaining nearly 200 m in thickness at Gebel Gifata. It is Maastrichtian to upper Paleocene based on planktic foraminifera and calcareous nannofossils [66,67]. The Tarawan Chalk forms the top of the plateau that bounds the Dakhla oasis to the north. It is around 20 m thick. The Tarawan Chalk is upper Paleocene, based on planktic foraminifera [67].

The fossils described here were collected from the lower part of the Dakhla Shale at Gebel Gifata, some 15 m above the base of the formation. Their low stratigraphic position suggests that they are likely lower Maastrichtian in age. Tantawy et al. [66] identified, in the lower 3 m of the Dakhla Shale, a planktic foraminiferal assemblage indicative of Zone CF8b; hence the basal Maastrichtian. An interval of about 70 m above this zone is reportedly barren of both planktic foraminifera and calcareous nannofossils [66]. Above this barren interval, Tantawy et al. (2001) [66] recorded rich microfossil assemblages indicating the calcareous nannofossil Zone CC25a and the upper part of the planktic foraminiferal Zone CF7 (upper Maastrichtian).

#### 4. Results

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4.1. Systematic Paleontology
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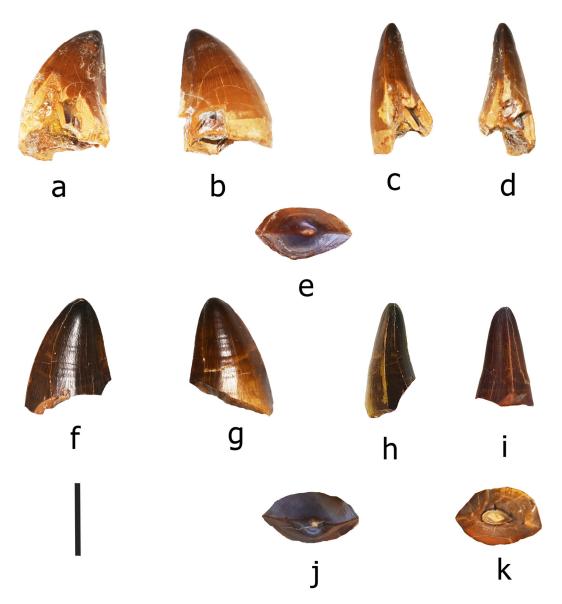
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Squamata Oppel, 1811 [68];
Mosasauroidea Gervais, 1853 [69];
Mosasauridae Gervais, 1853 [69];
Mosasaurinae Gervais, 1853 [69];
Prognathodontini Russell, 1967 [2];
Prognathodon sp. Dollo, 1889 [70];
Locality. Gebel Gifata, 12 km NW of Mut, Dakhla Oasis;
Horizon. Lower part of the Dakhla Shale, lower Maastrichtian;
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*Material*. NVP025, two marginal teeth, three cervical, nine dorsal, three caudal vertebrae, and ribs, found in association (Figure 3).

#### 4.2. Comparative Description

#### 4.2.1. Dentition

The dentition of NVP 025 includes two nearly complete marginal tooth crowns. The height of the more complete crown is 35 mm (Figure 4a,b); it has an aspect ratio (height/basal width) in lateral view equal to 1.4. The teeth are large, robust, and triangular in shape in the lateral view. Overall, the teeth resemble those of other Prognathodontini in having a robust, conical crown and weak curvature. In morphology, they are intermediate between the relatively sharp teeth of *P. solvayi* [71], *P. saturator* [52], and *Thalassotitan atrox* [24], and the blunt teeth of *P. overtoni* [72] and *P. currii* [51].



**Figure 4.** *Prognathodon* sp., NVP025, Gebel Gifata, Dakhla Oasis, Western Desert (Egypt), lower Maastrichtian. Teeth in lingual  $(\mathbf{a},\mathbf{f})$ , buccal  $(\mathbf{b},\mathbf{g})$ , anterior  $(\mathbf{c},\mathbf{h})$ , posterior  $(\mathbf{d},\mathbf{i})$ , and apical  $(\mathbf{e},\mathbf{j})$  views, basal cross section  $(\mathbf{k})$ . Figure shows tooth carina and wrinkles of the crown and shape of basal cross section. Bar scale = 2 cm.

The crowns are bucco-lingually compressed, with elliptical to oval cross sections, and are slightly lingually curved. They are inflated at the base and narrow gradually to the tip. The apex is blunt, similar to *P. overtoni* and *P. currii*. The enamel is generally smooth, although there are faint anastomosing ridges and shallow wrinkles as in *P. solvayi*,

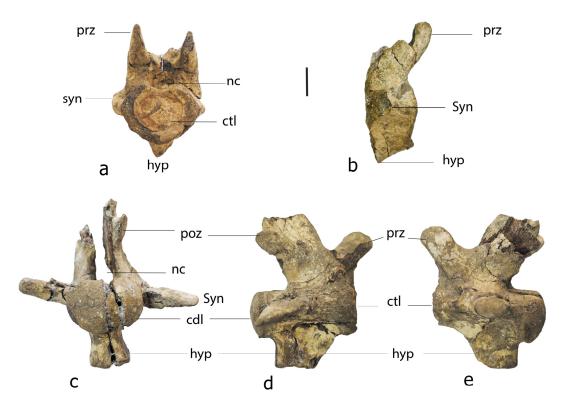
*P. giganteus* [71], *P. currii* [51], *P. lutugini* [73], *T. atrox* [24], *Globidens* spp. [23,74], and *Carinodens belgicus* [21]. There are very faint facets extending up to two-thirds of the height of the crown.

Carinae are prominent on the anterior and posterior margins of the tooth, as is typical of Mosasaurinae. The anterior carina has a pronounced anterior curvature, and the posterior one is almost straight. Serrations are absent except for very faint serrations on the posterior carina. The carinae divide the teeth into two asymmetrical surfaces. The two surfaces are convex, with the buccal surface being wider and more convex than the lingual surfaces.

## 4.2.2. Postcranial Skeleton

The postcranial elements of NVP025 are represented by three cervical vertebrae, some ribs, nine dorsal vertebrae and three caudal vertebrae, found in association.

Cervical vertebrae. The smallest cervical vertebra (Figure 5) is missing its posterior end. Its centrum in the anterior view is oval-shaped, with a shallow cotyle. The prezygapophyses are large. The length of the centrum cannot be measured because it is broken; the synapophyses are also broken. Part of a v-shaped hypapophyseal peduncle is present. The neural arch has a sub-triangular shape. The neural canal, seen from the front, is oval in outline, and wider than high.



**Figure 5.** *Prognathodon* sp., NVP025, Gebel Gifata, Dakhla Oasis, Western Desert (Egypt), lower Maastrichtian. Cervical vertebrae in anterior (a), posterior (c), lateral (b,d,e) views. Abbreviations: cdl, condyle; ctl, cotyle; hyp, hypapophysis; nc, neural canal; poz, postzygapophysis; prz, prezygapophysis; syn, synapapophysis. Bar scale = 2 cm.

The other cervical vertebrae can be generally described as follows. The centrum is longer than it is high or wide. It is waisted, with a constriction between condyle and cotyle. The condyle and cotyle surfaces are oval in cross section, with a dorsal flat surface; they are wider than they are tall (Table 1). The condyle has a hemispherical apex, while the cotyle has shallow to moderately deep depression. The neural arch is located on the midline of the centrum and very close to the condyle face. It is dorsoventrally tall and antero-posteriorly short.

Vertebra No.	W(con)	W(cot)	H(con)	H(cot)	CL	6	НҮР			D.,	
						S	Н	W	W L	Prz	Poz
1		50.38		36.43							
2	48.74	49.2	33.32	37.08	74.75	40.48	23.94	33.05	26.43	40.80	20.91
3		51.5		39.02		43.75	31.45	29350	25.54		

**Table 1.** Measurements of cervical vertebrae, in millimeters (mm).

Prezygapophyses are large and oval in shape, mediolaterally compressed, and dorsoventrally steeply inclined. The prezygapophyses are approximately as tall as the anterior articular face of the vertebra. They are separated from the neural arch by a slightly long pedicle and more projected past the cotyle epiphysis. The postzygapophyses are smaller than the pre-zygapophyses and steeply inclined mediolaterally, forming elliptical shapes.

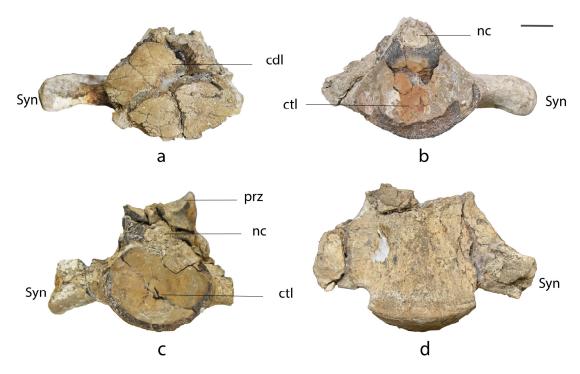
Anterior and posterior zygapophyses are well-developed. Zygosphenes and zygantra are absent as in *P. overtoni* [71], but unlike in *P. solvayi* [71], *P. giganteus* [71], *P. saturator* [52], *P. lutugini* [73], and *Thalassotitan atrox* [24], where cervical vertebrae have functional zygosphenes and zygantra.

Each cervical vertebra bears a robust, posteriorly directed hypaphophysis on the posterior half of the centrum's ventral surface. It is long with an oval and concave facet on the ventral side (Figure 5). The synapophysis is well developed, dorsoventrally compressed, and extends posterolaterally from the centra, with the long axis forming an angle approximately 90° from the sagittal plane. The synapophysis is anteroposteriorly positioned nearly above the midline of the centra. It is oval in cross section. It is thick and wide at the base and tapers toward their lateral ends.

Dorsal vertebrae. Dorsal vertebrae (Figure 6) are distinguished from cervical vertebrae by the lack of the hypapophyseal peduncle. The centra are longer than they are tall or wide; generally, they possess sub—triangular to oval or kidney-shaped condylar articulations, which are dorsoventerally compressed (condyles are not higher than wide; see Table 2). One dorsal vertebra preserves the prezygapophyses. They are large, but smaller than those of the cervical vertebrae. The synapophyses are robust, and wider than in the cervical vertebrae. They are dorsoventrally compressed, horizontally oriented, projecting anteroposteriorly from the midline portion of the centra, and taper at their ends. The centra of the dorsal vertebrae vary in shape from oval to subtriangular, and the cotyles vary in depth from shallower to deeper, indicating that they come from different places in the body. The neural canal is smaller than in cervical vertebrae, forming a sub-triangular opening that is taller than it is wide. The dorsal spines are poorly preserved.

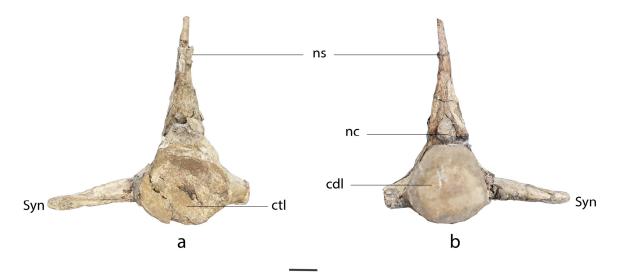
Tab	le 2	2. N	Лeas	urem	ents (	ot c	dorsal	vert	ebrae	, in	mil	lime	ters	(mm)	).
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Vertebra No.	W(con)	W(cot)	H(con)	H(cot)	CL	S
1		72.57		51.30	79.95	43.52
2	64.55	65.18	45.97	46.82	76.13	44.6
3		64.79		47.12		57.38
4		59.49		41.63		50.79
5	67.50		51.41			47.21
6		71.92				
7		71.11		47.81		
8	70.34		53.01		78.21	52.59
9		58.30		38.36	70.71	



**Figure 6.** *Prognathodon* sp., NVP025, Gebel Gifata, Dakhla Oasis, Western Desert (Egypt), lower Maastrichtian. Dorsal vertebrae in posterior (a), anterior (b,c), and dorsal (d) views. Abbreviations: cdl, condyle; ctl, cotyle; nc, neural canal; prz, prezygapophysis; syn, synapapophysis. Bar scale = 2 cm.

Caudal vertebrae. Three caudal vertebrae were found. One vertebra is well-preserved (Figure 7). They generally have long neural spines, long and broad transverse processes and lack haemal arches (have straight ventral surfaces), which may refer to the caudal vertebrae. The centra are long, unlike *P. solvayi* [71]. The neural arch is triangular. The condylar articulation is shallower than in dorsal vertebrae and its shape becomes more subtriangular or subcircular. The condyles and cotyles are not dorsoventrally compressed. The ratio between the height and width of the vertebral centra is 1:1. The neural arch is longer than in cervical vertebrae.



**Figure 7.** *Prognathodon* sp., NVP025, Gebel Gifata, Dakhla Oasis, Western Desert (Egypt), lower Maastrichtian. Caudal vertebrae in anterior (**a**) and posterior (**b**) views. Abbreviations: cdl, condyle; ctl, cotyle; nc, neural canal; ns, neural spine; syn, synapapophysis. Bar scale = 2 cm.

#### 5. Discussion

#### 5.1. Comparison

NVP025 shows features of Prognathodontini, such as the large, robust tooth crowns and the presence of smooth enamel, supporting the attribution of NVP025 to *Prognathodon* [75–77]. The teeth of NVP025 are also constricted at the base and show slight inflation just above the base that is characteristic of *Prognathodon* [3,75,78].

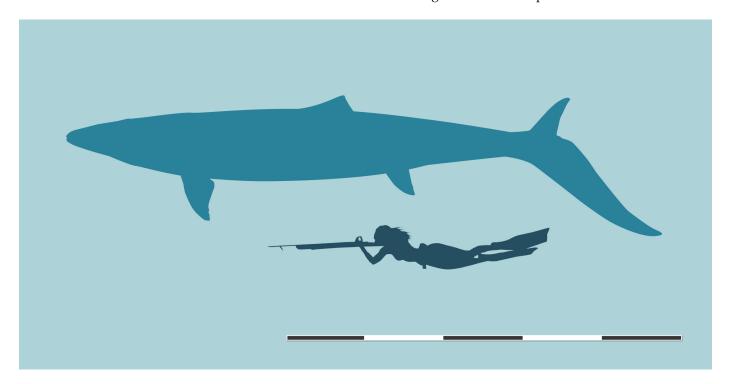
NVP025 can be distinguished from the type species of P. solvayi [70,71] in that P. solvayi teeth have vertical striae, well-defined facets [77], and more sharply pointed apices. Although the teeth of NVP025 resemble the teeth of P. overtoni [53], they differ from P. overtoni in that P. overtoni teeth have completely smooth enamel [72]. Some specimens referred to as P. overtoni have relatively sharp tooth apices [79] (Figure 4), but others have blunter teeth, more like those of NVP025 [79] (Figure 4); the significance of this variation (i.e., whether it is individual variation, ontogenetic, or interspecific) remains unclear. NVP025 differs from *P. currii* [20,51] (Lower Maastrichtian of Ganntour Basin, Morocco, Maastrichtian of Negev-Israel), in that P. currii teeth have blunter apices and straighter crowns, and have blunt massive carinae, unlike the sharp carinae of NVP025. P. currii also has highly rugose enamel at the tooth apex, and is a much larger animal. NVP025 differs from P. saturator [52], in that P. saturator teeth are rounded in cross-section and more inflated, and have no medial curvature; they are also generally smooth, and have blunter apices. NVP025 differs from P. giganteus [80], in that P. giganteus (Maastrichtian of Belgium) teeth are more inflated with a subcircular cross section [71]. It differs from Prognathodon lutugini [73,81] in that P. lutugini teeth have slender shaped crowns and strongly serrated carinae. It also differs from Prognathodon kianda [27], in that P. kianda teeth have completely smooth enamel and more pointed crowns. It also differs from Prognathodon waiparaensis [82] (Maastrichtian of New Zealand), in that P. waiparaensis teeth have a curved, well-serrated posterior carina and have defined facets. It differs from Prognathodon hudae [83] in that the apex of NVP025 is relatively more pointed, the teeth are more laterally compressed, and the anterior and posterior carinae are strong and pronounced in contrast with P. hudae, which has faint anterior carinae. It differs from Prognathodon compressidens [84] (Campanian of France) in that P. compressidens teeth are much smaller and more slender [27]. It differs from *Prognathodon sectorius* [85] in that *P. sectorius* teeth have straight anterior and posterior carinae with more flat lateral surface and equal labial and lingual surfaces [86,87]. It differs in shape from *T. atrox* [24] in that the teeth of *T. atrox* have a conical shape and sharp apices; meanwhile, NVP025 has more compressed teeth and blunter apices. It also differs from all Mosasaurus spp., which have well-defined faceted crowns and pointed apices. It differs from Eremiasaurus heterodontus [25], in that E. heterodontus teeth have pointed apices and well-defined facets.

NVP025 can also be distinguished by vertebral morphology when compared with other *Prognathodon* species, particularly for the cervicals. The cervical vertebrae show several distinctive characters, including the unusually large and steeply inclined prezygapophyses, the very large hypapohyses, and the dorso-ventrally compressed synapophyses. In the synapophyses, NVP025 differs from *P. solvayi*, *P. gigantus*, and *P. lutugini* [71,73], which have cervical vertebrae with synapophyses originating from the anterior-most part of the centra, while NVP025 has synapophyses that extend from the central part of the vertebra. It also differs from *P. solvayi*, which has a broad and very long transverse process and a relatively small neural spine of the caudal vertebrae [71].

Nearly all the vertebral processes in *Mosasaurus* spp. cervicals are heavily "buttressed" [88], or have wide, sloping bases, but the synapophyses in NVP025 are more "discrete" in that they arise more abruptly from the sides of the centrum. NVP025 differs from *Mosasaurus hoffmannii* [89] in that the space between the prezygapophyses is wider in *M. hoffmannii* than in NVP025 (as in the space across the midline between the prezygapophyses of a single vertebra) [88]. The prezygapophyses and hypophyses are relatively taller in NVP025 than in *M. hoffmannii*. Also, the transverse processes are more dorso-ventrally compressed in NVP025 than is typical of *Mosasaurus* spp. NVP025 cervical

vertebrae differ from the cervical vertebrae of *T. atrox* in that the hypapophyseal peduncle is much larger in NVP025.

Overall, the morphology of the teeth and vertebrae, and the size of the animal (Figure 8), seem most similar to *P. overtoni*. However, because of the lack of diagnostic cranial elements, it is provisionally placed in Prognathodontini as *Prognathodon* sp. Future finds will hopefully provide diagnostic material for this species, either allowing a confident referral to *P. overtoni* or the recognition of a new species.



**Figure 8.** Silhouette showing the approximate size of *Prognathodon* sp. Scale = 5 m.

## 5.2. Implications for Prognathodon Biodiversity and Biogeography

Discoveries over the past half century have shown the widespread presence of *Prognathodon* in the subtropics of Africa and the Middle East, with *Prognathodon* now known in Egypt, Morocco, Israel, Congo, and Angola [6,24,29,90]. The discovery of the present *Prognathodon* specimens from Egypt increases our knowledge of the diversity and distribution of the Maastrichtian mosasaurs in Egypt and North Africa, and emphasizes the endemism of mosasaur faunas (Figure 9).

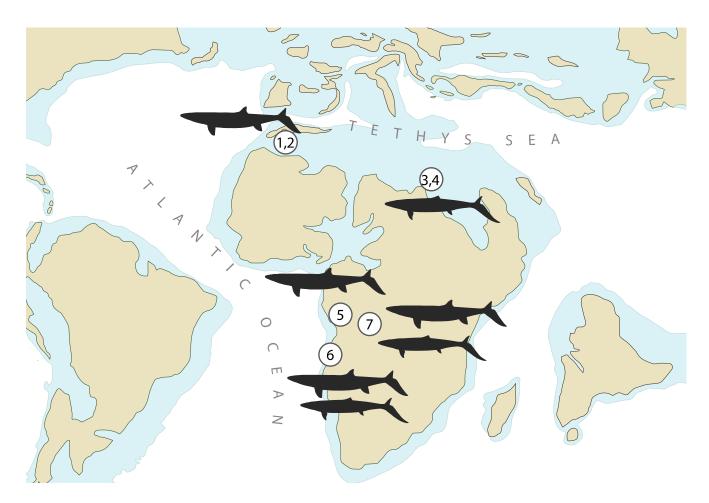


Figure 9. Map showing distribution of prognathodontins in Africa during the Upper Cretaceous. 1, Ouled Abdoun Basin, Morocco, *Thalassotitan atrox*; 2, Ganntour Basin, Morocco, *Thalassotitan atrox*, *Prognathodon currii*, *Prognathodon giganteus* [20,91]; 3, Gebel Duwi, Egypt, cf. *Thalassotitan* [43]; 4, Gebel Gifata, Egypt, *Prognathodon* sp. (this paper); 5, Congo, *Prognathodon* cf. *giganteus* [92]; 6, Namibe basin, Angola, *Prognathodon kianda*, *Prognathodon* cf. *saturator* [27,93]; 7, Cabinda basin, Angola, *Prognathodon* sp., *Prognathodon* cf. *currii* [6]. Map redrawn after map by Ron Blakey.

**Author Contributions:** Conceptualization, G.A.A.E.-K., A.A.S., H.P.S., N.R.L. and A.S.; investigation, G.A.A.E.-K., A.A.S., N.R.L. and A.S.; writing—original draft preparation, G.A.A.E.-K., A.A.S., H.P.S. and A.S.; writing—review and editing, A.A. and M.A. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: All the data used in the study are included in the paper.

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**Conflicts of Interest:** The authors declare no conflict of interest.

# Appendix A

**Table A1.** Table showing previously reported Mosasauridae specimens from the Upper Cretaceous of Egypt.

Taxon Synonymy		Loc	ation	Stage	References
Mosasauridae indet.			Wadi Qena	Turonian?	[40,42]
Mosasauridae indet.			Wadi Gedami	Santonian	[39,40]
Halisaurus arambourgi			Wadi Um Hemaiet	Campanian	[6,41]
cf. Thalassotitan atrox	Prognathodon sp. nov		Gebel Duwi	Campanian	[6,24,43]
Igdamanosaurus aegyptiacus	Globidens aegyptiacus	Eastern Desert	Um el Huetat phosphate mines near Safaga	Maastrichtian	[44,94]
Prognathodon giganteus			Um el Huetat phosphate mines near Safaga	Maastrichtian	[44,94]
Globidens phosphaticus			phosphates of Quseir	Maastrichtian	[6,45]
Mosasauridae indet.		Nile Valley	phosphate deposits of Sibaiya	Campanian- Maastrichtian	[6]
Mosasauridae indet.			Qasr ElDakhla	Maastrichtian	[47]
cf. Platecarpus			Nubian Sandstone of Mahamid	Campanian	[48]
Globidens sp.		Western Desert	Duwi Formation near the village of Teneida, Dakhla Oasis	Campanian	[49]
Globidens			Dakhla Shale, Dakhla Oasis	Maastrichtian	[50]
Prognathodon? sp.			Dakhla Shale, Dakhla Oasis, near AL-Rashda village	Maastrichtian	This paper

# Appendix B

**Table A2.** Comparing the characteristics of the teeth of Prognathodontini species.

Species	er Carinae	Apex	Cross Section	Ornamentation	Faces	Shape
Prognathodon solvayi	Bicarinate	Pointed?	Rounded	Deeply striated	Faceted or prismatic	Slender
Prognathodon overtoni	Weakly bicarinate	Blunt	Rounded	Smooth	Unfaceted	Slender, inflated
Prognathodon currii	Bicarinate, and some bear rough serrations	Blunt	Ellipsoid	Smooth enamel, fine anastomosing lines towards the apices	Unfaceted	Subconical, robust, straight

Table A2. Cont.

Species Character	Carinae	Apex	Cross Section	Ornamentation	Faces	Shape
Prognathodon saturator	Bicarinate?	Blunt	Rounded	Smooth	Unfaceted	Massive, rounded
Prognathodon giganteus	Bicarinate	Blunt	Rounded	Smooth	Unfaceted	Conical
Prognathodon lutugini	Strongly bicarinate with a weak serration on both carinae	Blunt?	Rounded	Minor wrinkles at the tip of the crowns	Unfaceted	Barrel-shaped
Prognathodon kianda	Bicarinate, unserrated	Pointed	Rounded?	Smooth, except very fine anastomosing ridges	Unfaceted	Slender
Prognathodon waiparaensis	Bicarinate with serration on both carinae	Blunt	Rounded	Smooth	Unfaceted	Conical shape
Prognathodon hudae	Weakly bicarinate and unserrated	Blunt	Suboval	Smooth with very faint anastomosing ridges	Unfaceted	Slender
Prognathodon sectorius	Bicarinate	Blunt	Ellipsoid	Smooth and silky	Unfaceted?	Slender
Thalassotitan atrox	Bicarinate	Pointed		Ornamented with coarse bumps and anastomosing ridges	Unfaceted	Conical in shape
Eremiasaurus heterodontus	Bicarinate, serrated	Pointed		Smooth	Faint traces of facets	High and slender, blade-like
Prognathodon? sp.	Bicarinate, unserrated	Blunt	Ellipsoid	Smooth with faint anastomosing ridges	Faint traces of facets	Triangular, laterally compressed

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