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## Mosasaurs (Squamata: Mosasauridae) from the Late Cretaceous (Late Maastrichtian) of North Carolina, USA

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### ABSTRACT

During April 2022, offshore dredging for a storm damage beach renourishment project placed large quantities of Upper Cretaceous (upper Maastrichtian) Peedee Formation sediment onto the shores of Holden Beach in Brunswick County, North Carolina, USA. The Cretaceous sediment is highly fossiliferous and has yielded a rich and diversified assemblage of fossils from mosasaurid reptiles. New fossil material, namely isolated teeth, consists of several dental morphologies from the mosasaur subfamilies Halisaurinae and Mosasaurinae. Five species are recognized: *Halisaurus* sp., *Mosasaurus* cf. *beaugei* Arambourg, 1952, *Mosasaurus* cf. *hoffmannii* Mantell, 1829, *Prognathodon* cf. *solwayi* Dollo, 1889 and *Prognathodontini* indet. In this assemblage, prognathodontins predominate, being the most abundant marine reptile find, with all other species being comparatively rare. The mosasaur assemblage of North Carolina shows close affinity with the phosphates of Morocco, containing species typical of both the northern and southern margins of the Mediterranean Tethys. These new discoveries improve our knowledge of the biodiversity of mosasaur fauna from the late Maastrichtian of North Carolina and add to the known paleobiogeographical distribution of these taxa. The material described within was collected courtesy of the efforts of amateur fossil hunters and seasonal tourists combing Holden Beach for fossilized remains.

**Key words:** Cretaceous, *Halisaurus*, Maastrichtian, Mosasauridae, *Mosasaurus*, North Carolina, *Prognathodon*

## Мозазавры (Squamata: Mosasauridae) из позднего мела (поздний маастрихт) Северной Каролины, США

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## РЕЗЮМЕ

В апреле 2022 г. в ходе дноуглубительных работ по восстановлению пострадавшего от урагана пляжа Холден-Бич в округе Брансуик, Северная Каролина, США, на берег был высыпан большой объем верхнемеловых (верхнемаастрихтских) отложений формации Пиди. Эти отложения содержали многочисленные ископаемые остатки, что позволило собрать богатый и разнообразный комплекс мозазаврид. По различиям в морфологии зубов были определены представители подсемейств *Halisaurinae* и *Mosasaurinae*. Было идентифицировано пять таксонов: *Halisaurus* sp., *Mosasaurus* cf. *beaugei* Arambourg, 1952, *Mosasaurus* cf. *hoffmannii* Mantell, 1829, *Prognathodon* cf. *solwayi* Dollo, 1889 и *Prognathodontini* indet. В этом комплексе преобладают *Prognathodontini*, которые являются наиболее многочисленной группой остатков морских рептилий, тогда как все остальные виды сравнительно редки. Комплекс мозазавров Северной Каролины показывает близкое родство с аналогичным комплексом из фосфатов Марокко и содержит виды, типичные как для северных, так и для южных окраин средиземноморского Тетиса. Новые находки расширяют наши знания о биоразнообразии фауны мозазавров позднего маастрихта Северной Каролины и дополняют представления о палеобиогеографическом распределении этих таксонов. Описанный здесь материал был собран благодаря усилиям палеонтологов-любителей и сезонных туристов, прочесывавших Холден-Бич в поисках окаменелых остатков.

**Ключевые слова:** мел, *Halisaurus*, маастрихт, *Mosasauridae*, *Mosasaurus*, Северная Каролина, *Prognathodon*

## INTRODUCTION

Mosasaur remains from North America were first described in 1818 when Georges Cuvier noted a report on the discovery of a “saurian [...] resembling (the) famous reptile of Maestricht” from the Atlantic Highlands sea cliffs along Raritan Bay, New Jersey (Mitchill 1818). Since then, numerous remains have been reported from Campanian and Maastrihtian strata from the Atlantic Coastal Plain running from New Jersey to South Carolina (Russell 1967).

Along the eastern coast of the United States, Cretaceous deposits outcrop in New Jersey, Delaware, and Maryland, are overlain by Cenozoic deposits in Virginia and northern North Carolina, and remerge in southeastern North Carolina, South Carolina, Georgia, and through the Gulf states into eastern Texas (Stephenson 1923; Richards 1950). In the Carolinas, Cretaceous outcrops are rare, largely confined to river valleys between the Roanoke River in North Carolina and the Pee Dee River in South Carolina (Sohl and Owens 1991). Cretaceous deposits also expose offshore, where they weather out and wash up on the beaches in Horry County, South Carolina, and Brunswick County, North Carolina (Self-Trail 2002).

Previous reports on mosasaurs in the Carolinas focused on exposures of the Campanian Black Creek Group along the Cape Fear River, especially at Phoebus Landing near Elizabethtown, Bladen County, North Carolina (Emmons 1858; Stephenson 1923; Richards 1950; Wheeler 1966). The presence of the mosasaurs *Mosasaurus* sp. (Emmons 1858; Miller

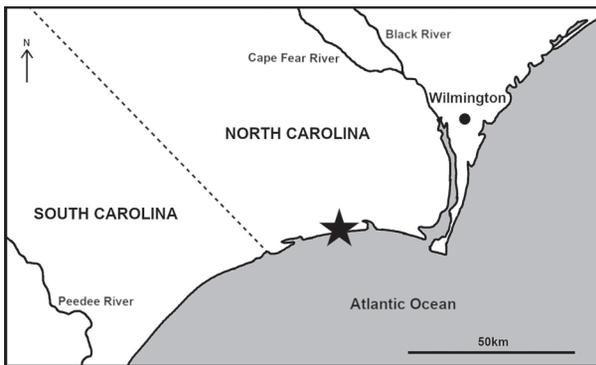
1967; Russell 1967), *Prognathodon* sp. (Emmons 1858; Marsh 1870; Miller 1967; Russell 1967), and *Tylosaurus* sp. (Wheeler 1966) were documented. Many of these localities are now lost, having been completely covered with silt and debris (Richards 1950).

Offshore dredging during April 2022 displaced large quantities of Cretaceous-aged sediment onto the shores of Holden Beach in Brunswick County, North Carolina. The fossiliferous sediment is faunally typical of the Pee Dee Formation, consisting of abundant remains of the index echinoid *Hardouinia mortonis* Michelin, 1850. The present contribution describes isolated mosasaur tooth crowns found by amateur beachcombers and provides the first description of the mosasaur assemblage in the late Maastrihtian of North Carolina.

**Institutional abbreviations.** SCSM – South Carolina State Museum (Columbia, South Carolina USA); USNM – The United States National Museum (Washington, D.C., USA); VANPS – Museum of the Vancouver Paleontological Society (Richmond, British Columbia, Canada). Material retained in amateur collections: CW – Cooper Williams collection; JA – Jayme Alweis collection; LM – Liz Minnich collection; PM – Peter Maguire collection; SS – Steve Smith collection.

## MATERIAL AND METHODS

The new mosasaur material was collected in loose association with the Pee Dee Formation by amateur beachcombers along the shores of Holden Beach in



**Fig. 1.** Map showing the North Carolina and South Carolina coast. The specimens come from Holden Beach, west of Wilmington, North Carolina.

Brunswick County, North Carolina, USA (Fig. 1). The Peedee Formation is a marine sequence that was deposited in moderately deep offshore water during the late Maastrichtian (Late Cretaceous) (Stephenson 1923). It rests unconformably upon the Donoho Creek Formation and is disconformably overlain by deposits that range in age from Paleocene to Holocene (Richards 1950; Sohl and Owens 1991). The Peedee Formation falls within the *Exogyra costata* zone of the Atlantic and Gulf Coastal Plain (Stephenson 1923). It is analogous to and nearly synchronous with the Monmouth Group of Maryland and New Jersey, the Ripley Formation of the eastern Gulf region, and the Navarro Group of Texas (Richards 1950; Harris and Self-Trail 2006).

In April 2022, the town of Holden Beach undertook a beach renourishment project to address storm damage to Holden Beach's Central Reach shoreline sustained during Hurricane Dorian in 2019. Two trailing suction hopper dredgers operated by Weeks Marine, Inc. pumped approximately 1,000,000 m<sup>3</sup> of sediment across 7,600 meters to widen the beam of Holden Beach. Dredged sediment contained abundant remains of Peedee Formation fauna, including mosasaurs, sharks, rays, and fish. Collecting dredged fossilized remains has since become a popular attraction that has drawn tourists and collectors to the beach. The fossil specimens described here were collected by amateur fossil hunters and graciously measured and photographed for study.

Photographs were prepared using GIMPshop 2.10.20. The osteological terminology is based on Russell (1967). Dental characters are described following Hornung and Reich (2015).

## SYSTEMATICS

### Order Squamata Oppel, 1811

### Family Mosasauridae Gervais, 1853

### Subfamily Halisaurinae Bardet et Pereda Suberbiola, 2005

### *Halisaurus* Marsh, 1869

### *Halisaurus* sp.

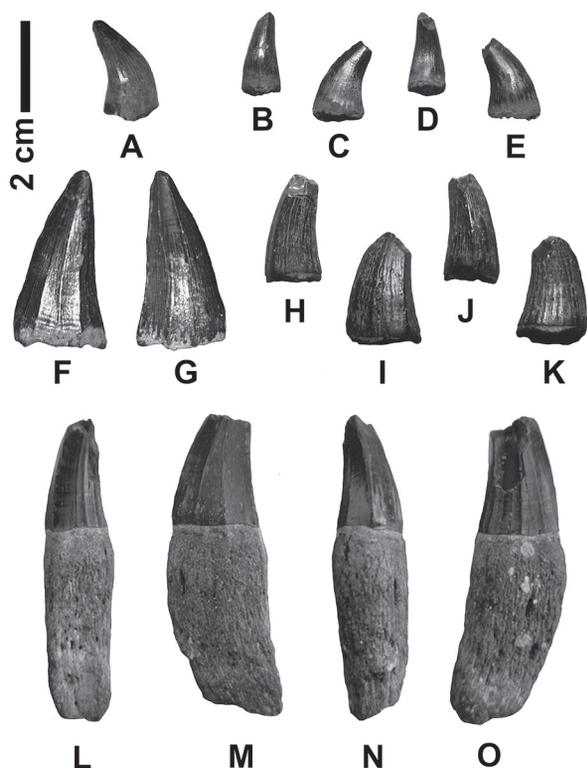
(Fig. 2A–E)

**Material.** JA.001, a marginal tooth crown (Fig. 2A); VANPS 13.0184, a marginal tooth crown (Fig. 2B–E).

**Locality and horizon.** Holden Beach, Brunswick County, North Carolina, USA. Peedee Formation (upper Maastrichtian) (Stephenson 1923).

**Description.** The teeth are small, hook-shaped crowns between 1 and 2 cm in height. They are sharp, slender, and bicarinate, with circular basal cross-sections and subequal labial and lingual surfaces. Abrupt posterior curvature around the midpoint of the crown gives the teeth a hook-like shape. The carinae are weakly developed and unserrated. The enamel surface is minutely striated. Basal enamel ridges are not distinguishable, although these may have been lost due to wear.

**Remarks.** Sharp, slender, recurved teeth are typical in Halisaurinae, some Plioplatecarpinae, and basal mosasauroids such as *Tethysaurus* (Bardet et al. 2003; Longrich et al. 2021). However, abrupt posterior curvature at approximately half the crown height is diagnostic of marginal teeth of halisaurine mosasaurs (Bardet et al. 2005). Plioplatecarpines such as *Platecarpus tympaniticus* and *Latoplatecarpus willistoni* possess proportionally taller crowns with posteromedially curving apices and defined enamel striations (Russell 1967; Konishi and Caldwell 2011). The posterior curvature in plioplatecarpine teeth generally occurs over a more gradual angle than in the teeth of halisaurines; medial curvature is found throughout the marginal dentitions of some plioplatecarpine species but has never been documented in halisaurine teeth (T.H.R. pers. obs.). Halisaurine carinae, such as those seen in *H. arambourgi* and *Pluridens serpentis*, are typically less pronounced than those present in plioplatecarpines (Bardet et al. 2005; Longrich et al. 2021). The plesiomorphic condition seen in mosasauroids such as *Tethysaurus nopscai* and *Romeosaurus*



**Fig. 2.** *Halisaurus* sp. (JA.001) marginal tooth crown, A – labial view; *Halisaurus* sp. (VANPS 13.0184) marginal tooth crown, B – anterior view, C – lingual view, D – posterior view, E – labial view; *M. cf. beaugei* (SS.001) marginal tooth crown, F – lingual view, G – labial view; *M. cf. beaugei* (VANPS 13.0185) marginal tooth crown, H – posterior view, I – labial view, J – anterior view, K – lingual view; *M. cf. beaugei* (CW.001) rooted marginal tooth, L – anterior view, M – labial view, N – posterior view, O – lingual view.

*fumanensis* consists of marginal tooth crowns that are comparably sized but more gradually posteriorly curved than halisaurine teeth (Palci et al. 2013).

Despite being known from a wide geographic range in the eastern United States, halisaurine mosasaurs are generally rare in the fossil record (Baird 1986). Various isolated remains referred to *Halisaurus* Marsh, 1869 have been reported from the North Atlantic Coastal Plain: from the New Egypt Formation (upper Maastrichtian) of New Jersey (Marsh 1869), the Navesink Formation (lower Maastrichtian) of New Jersey (Bukowski 1983), the Severn Formation (middle Maastrichtian) of Maryland (Baird 1986), the Mount Laurel Formation (lower Maastrichtian) of Delaware (Baird 1986), and the Merchantville Formation (lower Campanian) of Delaware (Baird 1986).

### Subfamily Mosasaurinae Gervais, 1853

#### Genus *Mosasaurus* Conybeare, 1822

#### *Mosasaurus* cf. *beaugei* Arambourg, 1952

(Fig. 2F–O)

**Material.** CW.001, a rooted marginal tooth (Fig. 2L–O); SS.001, a marginal tooth crown (Fig. 2F–G); VANPS 13.0185, a marginal tooth crown (Fig. 2H–K).

**Locality and horizon.** Holden Beach, Brunswick County, North Carolina, USA. Peedee Formation (upper Maastrichtian) (Stephenson 1923).

**Description.** The crowns of these teeth are typical of *Mosasaurus* bearing well-developed anterior and posterior carinae, strong curvature in both posterior and medial directions, D-shaped basal cross-sections, and subequal labial and lingual faces. The labial surface is flattened and bears 3–5 prism faces, while the lingual surface is convex and bears 8–9 enamel facets. Minute serrations are present along the entire length of the carinae. In profile, teeth are more compressed than those of *M. hoffmannii* (Rempert et al. 2022).

**Remarks.** *Mosasaurus beaugei* is identified at the species level based on the unique number of enamel planes adorning the crown's surface (Bardet et al. 2004). While facet count varies depending on placement in the dental margin (increasing posteriorly), the enamel ornamentation on *Mosasaurus* teeth is generally conserved with regard to different species and ontogenetic stages. The count of labial prism faces to lingual facets for the various *Mosasaurus* species is as follows: *M. hoffmannii* 2–3, 4–5; *M. beaugei* 3–5, 8–9; *M. conodon* indistinct, indistinct; *M. lemonnieri* 4–7, 7–10\*; *M. missouriensis* 4–6, 8 (Bardet et al. 2004). With respect to general morphology, the teeth of *M. beaugei* are generally more labiolingually compressed than those of *M. hoffmannii* and possess stronger medial curvature than those of *M. lemonnieri* (T.H.R. pers. obs.).

This typically southern species is recognized for the first time in North America, although teeth with enamel ornamentation comparable with *M. beaugei* were first reported from the Carolinas as early as the mid-19th century (Emmons 1858; Bardet 2012). Emmons (1858) referred a tooth (USNM 7445) from the Black Creek Group/Peedee Formation of North Carolina to *Mosasaurus* (sic) *maximiliani* (nomen vanum) on the basis of multiple angularities on the tooth's surface.

***Mosasaurus* cf. *hoffmannii* Mantell, 1829**

(Fig. 3A–D)

**Material.** VANPS 13.0180, a large marginal tooth crown (Fig. 3A–D).

**Locality and horizon.** Holden Beach, Brunswick County, North Carolina, USA. Peedee Formation (upper Maastrichtian) (Stephenson 1923).

**Description.** VANPS 13.0180 is a large tooth crown that exhibits strong medial curvature. Well-developed serrated carinae point anteroposteriorly, dividing the enamel into nearly symmetrical labial and lingual faces. The labial surface is approximately flat and bears three prism faces. The lingual surface is convex and is divided into five weak facets. The tooth is D-shaped in basal cross-section.

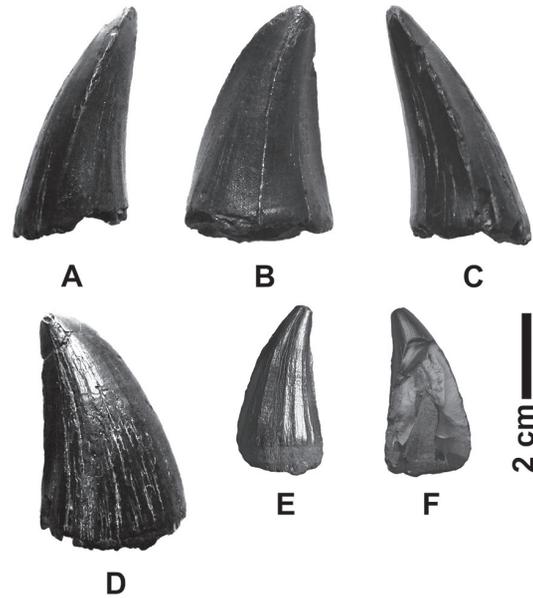
**Remarks.** Teeth of *M. hoffmannii* consist of recurved pyramidal crowns bearing 2–3 labial prism faces and approximately 4–5 weakly defined lingual facets. The degree of enamel ornamentation on the teeth of *M. hoffmannii* is more muted when compared to those of *M. beaugei*, *M. missouriensis*, and *M. lemonnieri*. When comparing teeth originating from the same part of the jaws, *M. hoffmannii* generally has proportionally wider labiolingual crown base widths than other *Mosasaurus* species (Rempert et al. 2022). In VANPS 13.0180, the positioning of the carinae, the size of the labial and lingual surfaces, and the increased number of prisms on the lingual face indicate that this tooth originated from the posterior part of the jaws (Bardet et al. 2013).

*Mosasaurus hoffmannii* is known from a wide geographical distribution of Maastrichtian fossil sites in and around the Western Interior Seaway of North America, the North American Atlantic Coastal Plain, and the Northern Margin of the Mediterranean Tethys (Russell 1967). Its remains have been found in Belgium, Bulgaria, Denmark, Germany, Italy, Morocco, Spain, the Netherlands, Poland, Turkey, Russia, and the United States (Bardet 2012; Street and Caldwell 2017; Rempert et al. 2024).

**Tribe Prognathodontini Russell, 1967*****Prognathodon* Dollo, 1889*****Prognathodon* cf. *solwayi* Dollo, 1889**

(Fig. 3E–F)

**Material.** VANPS 13.0181, a fragmentary marginal tooth crown (Fig. 3E–F).



**Fig. 3.** *M. cf. hoffmannii* (VANPS 13.0180) marginal tooth crown, A – anterior view, B – lingual view, C – posterior view, D – labial view; *P. cf. solwayi* (VANPS 13.0181) marginal tooth crown, E – lingual view, F – labial view.

**Locality and horizon.** Holden Beach, Brunswick County, North Carolina, USA. Peedee Formation (upper Maastrichtian) (Stephenson 1923).

**Description.** A partial bicarinate tooth crown ornamented by fluted enamel on its lingual surface bears strong resemblance to *P. solwayi* Dollo, 1889 from the early Maastrichtian of Belgium (Lingham-Soliar and Nolf 1989). The tooth is broken sagittally and missing its lingual half. The apex is spalled, likely due to wear during life. The carinae are positioned antero-posteriorly and well-developed. Heavy abrasion prevents observation of potential serrations. Inferring from the symmetrical placement of the carinae, the tooth likely had labial and lingual crown faces equal in size and a circular basal cross-section. In anterior view, the tooth has minimal medial curvature. The posterior margin of the crown is straight and vertical. Apicobasal striking enamel ridges divide the lingual surface into 8 concave flutes.

**Remarks.** While ridged enamel ornamentation is characteristic of certain mosasaur genera (i.e., faceting in *Mosasaurus*), such structures occur infrequently amongst members of Prognathodontini. The heavy anastomosing enamel and approximately conical morphology of the crown allow for generic identification of the tooth to *Prognathodon* (Bardet et

al. 2015). Deep enamel flutes are thus far exclusively known in the type species of the genus, *P. solwayi*. Despite this, the fragmentary nature of the present material makes it insufficient to identify with certainty, and open nomenclature is used. *Prognathodon solwayi* is known from the late Campanian of the Netherlands (Mulder et al. 1998), the early Maastrichtian of Belgium (Dollo 1889; Lingham-Soliar and Nolf 1989), and the late Maastrichtian of Spain (Bardet et al. 2013).

### Prognathodontini indet.

(Fig. 4A–T)

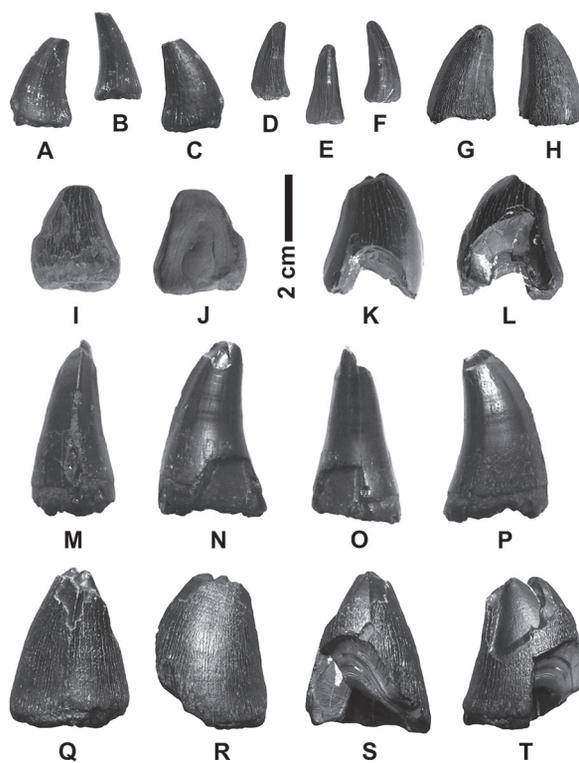
**Material.** CW.002 (Fig. 4G–H), LM.001 (Fig. 4I–J), LM.002 (Fig. 4K–L), PM.003 (Fig. 4D–F), VANPS 13.0182 (Fig. 4M–P), VANPS 13.0183 (Fig. 4A–C), VANPS 13.0185 (Fig. 4Q–T).

**Locality and horizon.** Holden Beach, Brunswick County, North Carolina, USA. Peedee Formation (upper Maastrichtian) (Stephenson 1923).

**Description.** The teeth consist of large crowns with subcircular basal cross-sections, near equal convex labial and lingual faces, two carinae, and heavy anastomosing enamel, especially near the blunt apical region. Enamel surfaces are smooth, without conspicuous prisms or fluting. The apical regions often bear fractures or wear facets indicative of heavy wear during life. When preserved, crown apices curve slightly posteromedially, especially in the more conical anterior teeth. Carinae pinch off the crown body and bear minute serrations. Tooth shape is generally short and conical, although teeth originating from the anterior portion of the jaws (PM.003; VANPS 13.0182) are less robust and proportionally taller.

**Remarks.** Unfluted prognathodontin teeth are the most abundant mosasaurid fossils recovered from Holden Beach. The teeth are robust, with stouter dimensions than *Prognathodon saturator* and *Prognathodon overtoni*, but comparable to *Thalassotitan atrox* from the Moroccan Phosphates (Longrich et al. 2022). Large prognathodontin teeth from Holden Beach bear a strong resemblance to teeth that amateur collectors informally attribute to “*Prognathodon rapax/Ancylocentrum hungerfordi*” from the Maastrichtian of New Jersey; however, a lack of diagnostic dental remains in the type material of these taxa prevents comparison.

Large prognathodontin mosasaur teeth were previously described from the Campanian of North Carolina

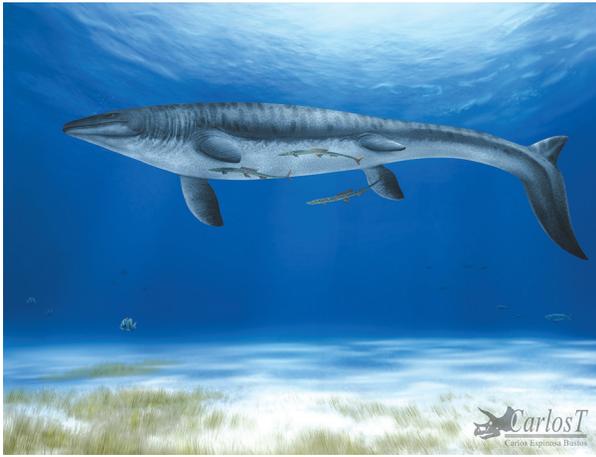


**Fig. 4.** Prognathodontini indet. (VANPS 13.0183) marginal tooth crown, A – lingual view, B – posterior view, C – labial view; Prognathodontini indet. (PM.003) marginal tooth crown, D – lingual view, E – posterior view, F – labial view; Prognathodontini indet. (CW.002) marginal tooth crown, G – lingual view, H – labial view; Prognathodontini indet. (LM.001) posterior marginal tooth crown, I – lingual view, J – labial view; Prognathodontini indet. (LM.002) posterior marginal tooth crown, K – labial view, L – lingual view; Prognathodontini indet. (VANPS 13.0182), anterior marginal tooth crown, M – anterior view, N – lingual view, O – posterior view, P – labial view; Prognathodontini indet. (VANPS 13.0185), posterior marginal tooth crown, Q – posterior view, R – labial view, S – anterior view, T – lingual view.

rolina as *Mosasaurus crassidens* Marsh, 1870 (nomen dubium) and *Elliptonodon compressus* Emmons, 1858 (nomen dubium) (Russell 1967). Schwimmer et al. (2015) reported a single posterior marginal tooth crown (SCSM 84.176.1) of probable Peedee Formation origin from the vicinity of Myrtle Beach in Horry County, South Carolina.

### CONCLUSION

Isolated tooth crowns indicate a high biodiversity of mosasaurid squamates during the late Maastrichtian of North Carolina (Fig. 5). Unique dental



**Fig. 5.** Reconstruction of *M. beaugei* from the upper Maastrichtian of North Carolina. Illustration by Carlos Espinosa.

morphologies allow for the recognition of at least five species. Species typically associated with the Northern Margin (*P. solvayi*) and Southern Margin (*M. beaugei*) of the Mediterranean Tethys are found together, extending their respective geographic ranges. The new fossil material provides increased resolution to the Late Cretaceous marine reptile assemblage from the Atlantic coast of North Carolina.

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