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Mosasaurids Bare the Teeth: An Extraordinary Ecological Disparity in the Phosphates of Morocco Just Prior to the K/Pg Crisis †

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† In memory of Henri Cappetta (1946–2024), whose selachians swam with mosasaurids in the same Phosphate seas.

Abstract: Mosasaurid teeth are abundant in the fossil record and often diagnostic to low taxonomic levels, allowing to document the taxonomic diversity and ecological disparity through time and with fewer biases than in other marine reptiles. The upper Maastrichtian Phosphates of Morocco, with at least fifteen coeval species representing a wide range of sizes and morphologies, undoubtedly represent the richest outcrop in the world for this clade of iconic Mesozoic squamates and one of the richest known marine tetrapod assemblages. Until now, the methods used to link tooth morphology to diets in marine amniotes were mainly qualitative in nature. Here, using the dental morphology of mosasaurids from Morocco, we combine two complementary approaches—a thorough comparative anatomical description and 2D/3D geometric morphometry—to quantitatively categorize the main functions of these teeth during feeding processes and infer diet preferences and niche-partitioning of these apex predators. Our results from combining these two approaches show the following: (1) Mosasaurids from the upper Maastrichtian Phosphates of Morocco occupy the majority of dental guilds ever colonized by Mesozoic marine reptiles. (2) As seen elsewhere in the Maastrichtian, mosasaurines dominate the regional mosasaurid assemblage, exhibiting the greatest taxonomic diversity (two-thirds of the species) and the largest range of morphologies, body sizes (2 m to more than 10 m) and ecological disparities (participating in nearly all predatory ecological guilds); strikingly, mosasaurines did not developed flesh piercers and, conversely, are the only ones to include durophagous species. (3) Halisaurines, though known by species of very different sizes (small versus large) and cranial morphologies (gracile versus robust), maintain a single tooth shape (piercer). (4) Plioplatecarpines were medium-size cutters and piercers, known by very morphologically diverging species. (5) Tylosaurines currently remain scarce, represented by a very large generalist species; they were largely replaced by mosasaurines as apex predators over the course of the Maastrichtian, as observed elsewhere. Also, when comparing tooth shapes with body sizes, the largest taxa (>8 m long) occupied a restricted area of tooth shapes (generalist, durophagous), whereas small and medium-sized

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species (<8 m long) range across all of them (generalists, durophagous, cutters, piercers). In other words, and probably related to the specificities and advantages of biomechanical resistance, apex predators are never dedicated piercers, micro-predators are conversely never generalists, and meso-predators show the widest range of dental adaptations. These diversities and disparities strongly suggest that Tethyan mosasaurids evolved strong niche-partitioning in the shallow marine environment of the upper Maastrichtian Phosphates of Morocco. Such a high diversity sensu lato just prior to the K/Pg biological crisis suggests that their extinction was rather sudden, though the exact causes of their extinction remain unknown. Finally, *Gavialimimus* Strong et al., 2020 is systematically reassigned to *Gavialimimus ptychodon* (Arambourg, 1952), and an emended diagnosis (for teeth and dentition) is proposed for this species.

Keywords: mosasaurid squamates; Morocco; phosphates; Late Cretaceous; comparative anatomy; morphometrical analyses; diet preferences; niche-partitioning

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1. Introduction

Mosasaurids were a specialized clade of large marine squamates that underwent a spectacular radiation during the Late Cretaceous, before becoming extinct during the K/Pg biological crisis (e.g., [1,2]). They exhibit a high species diversity, as well as a wide range of morphotypes and body sizes (about 1–17 m), suggesting a high ecological disparity. They were also widely distributed from the Santonian up to the end of the Maastrichtian. Among the most diverse and abundant mosasaurid faunas are those from the Santonian-Campanian of the Western Interior Sea of North America, the Campanian–Maastrichtian of New Zealand and the Maastrichtian of the Netherlands (where they were first unearthed at the end of the 18th century), Belgium, Angola and Morocco (e.g., [2,3]). Among them, with sixteen species described up to now, the Maastrichtian Phosphates of Morocco undoubtedly represent the richest outcrop for mosasaurids worldwide.

The exceptional richness of fossil vertebrates in the Maastrichtian–Ypresian Phosphates of Morocco has been known since the pioneering works of the French paleontologist Camille Arambourg [4]. At present, almost 400 species of vertebrates are known from these deposits, of which more than 95% are marine. These include a plethora of selachians, actinopterygians and marine reptiles, as well as scarce continental taxa, including Maastrichtian non-avian dinosaurs and pterosaurs, Paleogene mammals and birds originating from the nearby African Craton (e.g., [5–8]).

After selachians (e.g., [9,10]), marine reptiles are the most common and diverse group in the Phosphates, both in the Maastrichtian and Paleogene [5,11]. Mosasaurid squamates dominate the Maastrichtian ecosystems and, as a mirror, the dyrosaurid crocodyliforms the Paleogene ones [12]. In addition to mosasaurids, the Maastrichtian marine reptile assemblage include elasmosaurid plesiosaurians [13,14], chelonioid turtles [15,16], gavialoid crocodilians [12] and pachyvaranid squamates [17].

Mosasaurids are by far the most abundant marine reptiles in the Maastrichtian Phosphates of Morocco, being known by at least fifteen coeval species (Tables 1 and A1). They are represented by a plethora of specimens of all sizes, morphologies and ecologies. Many of these species were previously unknown [3–5,18–33], and some are typical of the Tethyan Southern Margin [34].

At the interface between predators and their environment, teeth are a major component of food acquisition and processing, and their shape is closely linked to eaten items, making it possible to infer possible diets [35,36]. Despite a widespread belief that reptilian teeth are poorly informative from a systematical and ecological point of view, and except for some overlaps in gross morphology [36], it has been shown that mosasaurids possess series of diagnostic traits in their teeth. These turn out to be useful for systematic identification (at the generic and even specific levels) when only isolated teeth are found (e.g., [3,37]).

In addition, mosasaurid teeth are characterized by a diverse range of external macrostructures (shape, ornamentation, wear) (e.g., [3,38–43]), internal microstructures (enamel/dentin texture and composition) (e.g., [44–47]) and attachment and replacement modes (e.g., [48–50]). These played an important role in feeding process and as such reveal a large spectrum of diets and niche occupation in the water column. The rich fossil record of mosasaurid teeth is therefore capable of documenting both the taxonomical and ecological diversity of mosasaurid faunas and their evolution, with fewer biases than in other marine reptile groups.

Here, focusing on the dental morphology of the mosasaurid assemblages from the upper Maastrichtian Phosphates of Morocco, we combine two complementary approaches, namely, a thorough qualitative comparative anatomy and two quantitative geometric morphometry analyses (2D and 3D), to identify their tooth shape and infer the diet preferences, predation modes and possible niche-partitioning of these predators in the regional marine ecosystem, just prior to the K/Pg biological crisis.

Institutional abbreviations. HUJ, Hebrew University of Jerusalem; IRScNB, Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium; MGUAN, Museo Geológico da Universidade Agostino Neto, Luanda, Angola; MHNM, Muséum d'Histoire Naturelle de Marrakech, Université Cadi Ayyad (UCAM), Marrakech, Morocco; MNHN, Muséum National d'Histoire Naturelle, Paris, France; OCP, Office Chérifien des Phosphates, Khouribga, Morocco; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada; ULg, Université de Liège, Belgique; VANPS, Paleontological Museum of the Vancouver Paleontological Society, Richmond, British Columbia, Canada.

2. Geographical and Geological Settings

The Phosphates of Morocco are part of an extensive belt of sedimentary deposits named the 'Mediterranean (Tethyan) Phosphogenic Province' that developed during the Late Cretaceous and early Paleogene epochs. These formed primarily in subtropical paleolatitudes 12–22° in shallow marine paleoenvironments (e.g., [51,52]). Currently, these phosphatic deposits widely crop out in the Middle East and northwest Africa, up to the Pernambuco Province of Brazil, where they are exploited as a valuable economical resource [51,52].

Historically, the Phosphates have been known in Morocco since the beginning of the 20th century [53,54] and have been exploited on a large scale since 1921 by the Office Chérifien des Phosphates [55]. Morocco has the world's largest phosphatic deposits and reserves (more than 70%) and is the leading exporter and second-largest producer of phosphates in the world, after China [56].

The Phosphates currently crop out in four main basins distributed through central Morocco, these being the Oulad Abdoun, Ganntour, Meskala and Souss basins (Figure 1A). Only the Oulad Abdoun and Ganntour basins are economically exploited, especially in the Sidi Daoui, Sidi Chennane (Oulad Abdoun) and Ben Guerir (Ganntour) areas (Figure 1B,C), favoring the local discoveries of vertebrate fossil remains.

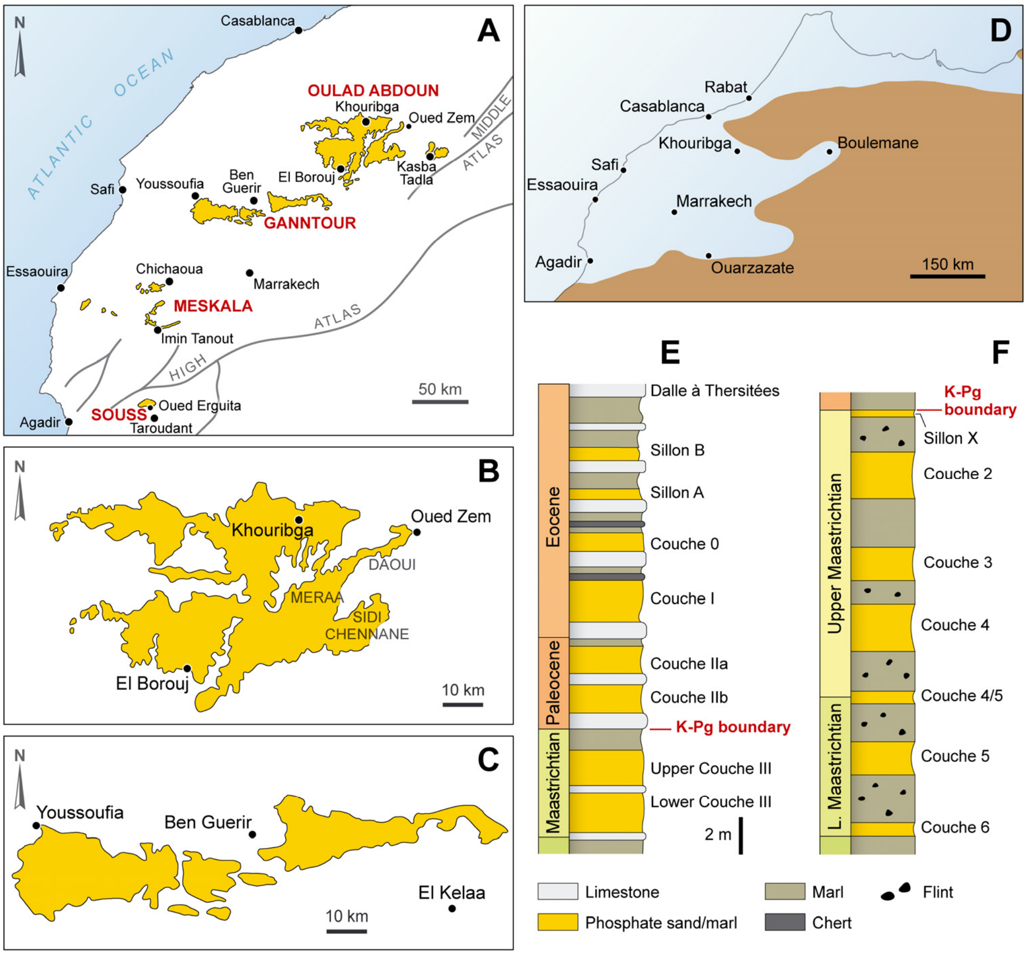


Figure 1. The Phosphates of central Morocco. (**A**) Geographical map showing the main phosphatic basins, from NE to SW: Oulad Abdoun and Ganntour (economically exploited), Meskala and Souss (not exploited). (**B**,**C**) Details of the Oulad Abdoun and Ganntour basins' geography. (**D**) Paleogeographical reconstruction of Morocco during the Late Cretaceous, after [57]. (**E**,**F**) Synthetic stratigraphical column of the phosphatic series in the Oulad Abdoun (Maastrichtian–Paleogene) and Ganntour (Maastrichtian only) basins. All figures modified from [3,5]. Drawings and design © Alexandre Lethiers (CR2P/ISteP, Paris).

Paleogeographically, the phosphatic sediments were deposited in a large shallow marine gulf located on the northwest margin of the African craton (Figure 1D). This large area was characterized by a high productivity upwelling system that developed from the Late Cretaceous up to present times along the western coast of Africa, driven by the trade winds pushing surface waters offshore (e.g., [2,51,52,56]). The upwelling system probably permitted the development of the exceptional local biomass [58], whereas the phosphatogenesis favored a high and selective conservation of vertebrate remains, as opposed to microfossils and invertebrates, which are frequently dissolved and/or recrystallized (e.g., [59]). The two phenomena—upwelling and phosphatogenesis—are probably responsible for the exceptional richness in marine vertebrate remains, both in terms of abundance, preservation and taxonomical diversity, which characterizes the Maastrichtian–Ypresian Phosphates of Morocco.

Stratigraphically, the Phosphates of Morocco range from the base of the Maastrichtian to the top of the Ypresian, spanning about 24 My without major unconformities [60,61]. As such, they represent the most time-expanded phosphatic deposits of the above-mentioned 'Phosphogenic Mediterranean Province' [51,52]. In all basins, the phosphate series include an alternation of soft and hard phosphatic beds (only the soft ones are exploited), marls and limestones, with frequent flint accumulations and chert levels. The series is usually topped by the '*Dalle à Thersitées*', a calcareous reference level (Figure 1E). Note that the different beds are named '*Sillon*' and '*Couche*' ('layer' in French, 'sillon' being a specific mining name for layer) and are numbered in Roman numbers in the Oulad Abdoun Basin and in Arabic ones in the Ganntour Basin, mainly for age differentiation. As an example, *Couche* 2 of the Ganntour Basin is late Maastrichtian in age, whereas *Couche* II of the Oulad Abdoun Basin is Paleocene. Due to subsidence, the thickness of the Maastrichtian series of central Morocco increases from NE to SW, being less than 10 m thick in the NE of the Oulad Abdoun Basin (Figure 1E), about 25 m in the Ganntour Basin (Figure 1F) and reaching 300 m in the Atlasic basins of Meskala and Souss [22,55].

Mosasaurid remains are very frequent in all levels of the Maastrichtian series, as isolated remains (mainly teeth and vertebrae) in levels *Couche* 6 to *Couche* 2 of the Ganntour Basin and as articulated, sometimes complete, specimens in lower and Upper *Couche* III of the Oulad Abdoun Basin.

3. Materials and Methods

The present work is based on the teeth of most of the mosasaurid species known in the Maastrichtian Phosphates of Morocco (Tables 1 and A1).

Each species is briefly introduced, with indication of its global spatiotemporal occurrences and a short discussion of its systematical validity and reassignment, if necessary. The main clades to which they belong are also briefly introduced, using main recent references (see in respective parts).

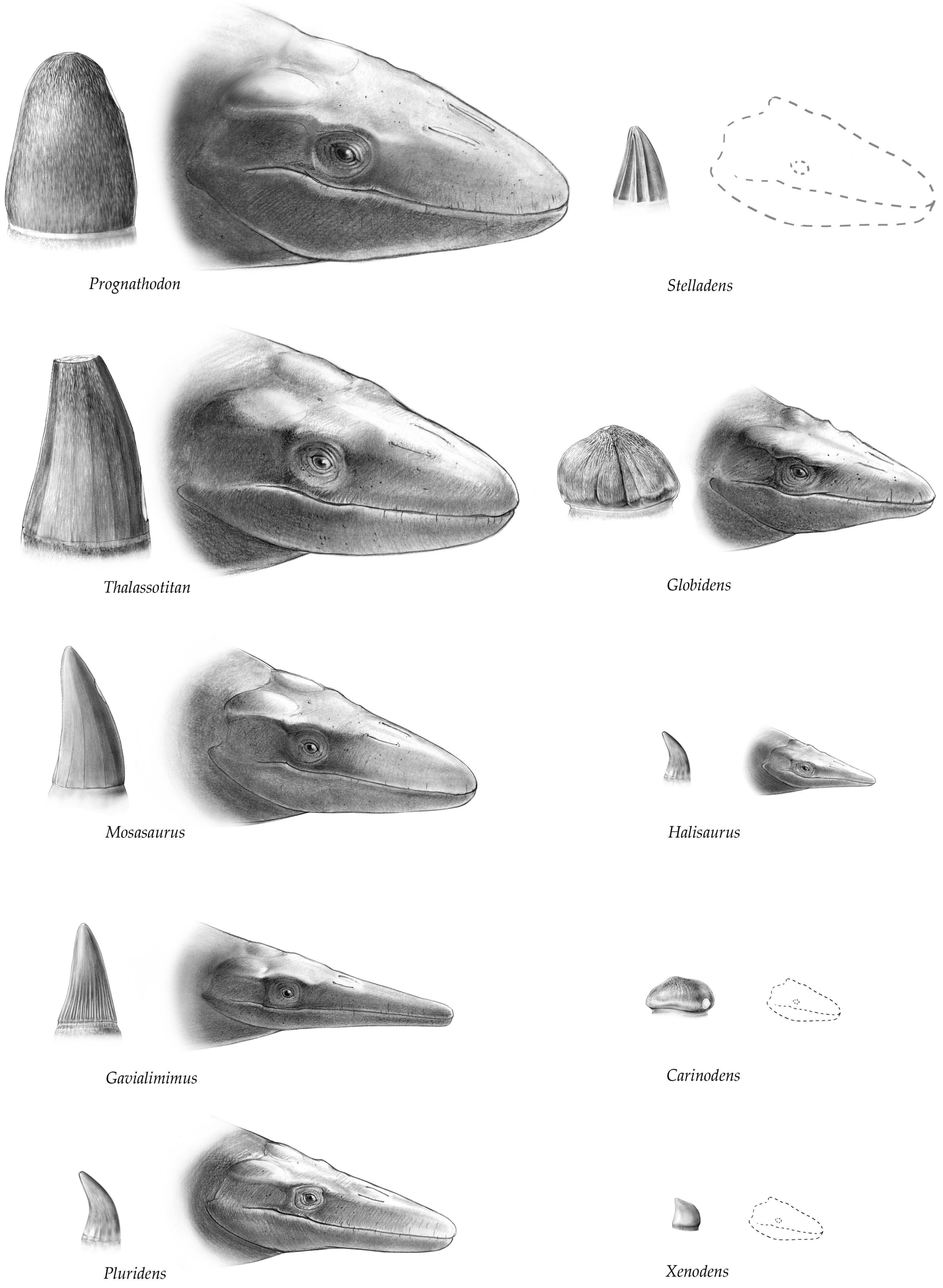
3.1. Material Acquisition and Selection

The tooth sample has been gathered thanks to several field campaigns of level-by-level systematic collection by some of the authors (NB, XPS) in the *Couche* 6 to *Couche* 2 (lower to uppermost Maastrichtian) of the Ganntour Basin [22] and to more than two decades of fieldwork by the authors in the *Couche* III (upper Maastrichtian) of the Oulad Abdoun Basin. This work was carried out into the framework of the long-term *PhosphaPal* French–Moroccan program of scientific collaboration and of the recent agreement between the University of Bath and the Cadi Ayyad University (see details in Acknowledgments). The specimens personally sampled, studied and analyzed by the authors are kept in the collections of the Office Chérifien des Phosphates (OCP), the Muséum d'Histoire Naturelle de Marrakech (MHNM, UCAM), the Muséum National d'Histoire Naturelle of Paris (MNHN) and the Université de Liège (ULg); some teeth are issued from private collections (controlled by the authors).

From more than a thousand isolated mosasaurid teeth collected, representing hundreds for the most common species, we selected for each taxon a representative 'Sample' of about ten well-preserved median marginal teeth, because they are both the reference ones for systematical identifications (e.g., [62]) and also those mainly used in food procurement (see rationale in [36]). This sample is used for the thorough anatomical descriptions. From this sample, in turn, one tooth is chosen as representing the 'Standard' (Figure 2) of each species and used for the morphometric analyses.

When available, the most complete and best-preserved skulls of each species are also measured to assess their general morphology and proportions, as well as to estimate the overall size of the taxon.

In order to make sensible faunal comparisons, only coeval taxa from the late Maastrichtian were included in the study (Table 1); as such, *Prognathodon giganteus*, from the lower Maastrichtian of the Ganntour Basin [22], was excluded. The few species not sampled nor described personally were included in the anatomical descriptions (using the original bibliography as a support) but excluded from the morphometric analyses see below Section 3.3.



Prognathodon *Stelladens*

Thalassotitan *Globidens*

Mosasaurus *Halisaurus*

Gavialimimus *Carinodens*

Pluridens *Xenodens*

Figure 2. Mosasauridae from the Maastrichtian Phosphates of Morocco: head reconstructions and 'Standard' tooth drawings. The head reconstructions are on scale (with *Mosasaurus* = 1 m) and based on a selection of main representative species and most-complete specimens (see Tables A1 and A2). Living monitors, especially *Varanus niloticus*, a highly aquatic species, were chosen as a model. Skulls are deliberately reconstructed 'snout wide shut' in order to better appreciate the proportions of the main regions (jaw, orbit, temporal zones) and, above all, to highlight two constant features of extant squamates (assumed to be identical in mosasaurids, too often reconstructed archosaur-like): a high fleshy area above the gums, giving a thicker aspect to the jaws, and no teeth protruding from them. Tooth drawings on scale (with *Halisaurus* = 1 cm). Paleoartistic reconstructions, drawings and design © Charlène Letenneur (CR2P, MNHN, Paris).

Table 1. Mosasaurids from the Maastrichtian Phosphates of Morocco. Species known from the Upper *Couche* III (upper Maastrichtian) of the Oulad Abdoun Basin. See details in Table A1.

Mosasaurinae
Mosasaurus beaugei Arambourg, 1952 [4]
Carinodens belgicus (Woodward, 1891) [63]
Carinodens minalmamar Schulp et al., 2009 [33]
Xenodens calminechari Longrich et al., 2021a [25]
Eremiasaurus heterodontus LeBlanc et al., 2012 [23]
Thalassotitan atrox Longrich et al., 2022 [27]
Prognathodon currii Christiansen and Bonde, 2002 [64]
Globidens phosphaticus Bardet and Pereda-Suberbiola, 2005b [20]
Globidens simplex LeBlanc et al., 2019 [24]
Stelladens mysteriosus Longrich et al., 2023 [28]
Halisaurinae
Halisaurus arambourgi Bardet and Pereda-Suberbiola, 2005a [19]
Pluridens serpentis Longrich et al., 2021b [26]
Plioplatecarpinae
Gavialimimus ptychodon (Arambourg, 1952) [4,32]—**new combination**
Khinjaria acuta Longrich et al., 2024b [29]
Tylosaurinae
Hainosaurus boubker Rempert et al., 2022 [31]

3.2. Comparative Anatomy and Morphofunctional Interpretation

Teeth of the above-defined 'Sample' are thoroughly described for each species, using a suite of comparable and reproductible characters such as general size, shape of the crown, basal cross-section, curvature, ornamentation of the enamel, carinae occurrence and crenulations, wear facets, etc. This aims, firstly, to define the often unique tooth morphology of each species and, secondly, to qualitatively approach to which general dental guilds sensu Massare [38] it belongs.

Two ratios using the height (H) and width (W) compared to the length (L) of the crown are used (see Table A2): H/L ratio estimates whether the crown is high (H/L > 1), as high as long (H/L = 1) or low (H/L < 1); W/L ratio estimates whether the crown is strongly labiolingually compressed (W/L < 0.5), moderately compressed (W/L > 0.5) or not compressed (round section, W/L =1). Measurements were taken on the 'Sample' teeth, and the ratios correspond to the average value (or to a range of values if notable differences are observed).

Global characteristics of the entire dental series (including pterygoid teeth)—when preserved—are given, in order to estimate both the degree of homodonty/heterodonty and the respective size between marginal and pterygoid teeth. They have importance in seizing and manipulating prey.

The general morphology of the skull (or skull portions) is briefly described and is focused on characteristics allowing the inference of size, robustness and proportions of some key regions. These also have importance in predation and feeding processes. As for teeth, if several skulls are measured, the ratios correspond to the average value (or to a range of value if notable differences are observed). A paleoartistic fleshy reconstruction of the heads of main species based on close comparisons with extant varanids is proposed (Figure 2).

The following ratios were calculated, using skull length (measured from the premaxilla tip to a perpendicular line passing by the skull posterolateral corners (formed by squamosal–supratemporal)), as the reference measurement (see Table A2):

- W/L ratio (skull width/skull length): approximates robustness. Skull width is measured between postorbitofrontal/frontal lateral margins and/or the posterolateral corners of the skull. The higher the ratio value, the more robust the skull (and vice versa). It should be noted, however, that the width of a mosasaurid skull is difficult to access and often biased because of dorso-ventral crushing during taphonomical processes of burial and fossilization that artificially increases the real width. This ratio should thus be taken with caution. The external margins of the frontal are however considered as a relatively good proxy, as, this bone being flat, its natural morphology is de facto poorly affected by dorso-ventral crushing.
- PreO/L ratio (preorbital length/skull length): approximates snout elongation compared to skull length. Preorbital length is measured from the premaxilla tip to the anterior orbital margin. The higher the ratio value, the more elongated the snout in relation to skull length (and vice versa).
- PostO/L ratio (postorbital length/skull length): approximates adductor muscle volume. Postorbital length is measured from the posterior orbital margin (or, if not preserved, from a line passing by the frontal–parietal–postorbitofrontal suture (dorsally) or the postorbitofrontal–jugal suture (laterally)) to the perpendicular line passing by the skull posterolateral corners. The higher the ratio value, the more elongated the posterior part of the skull in relation to skull length (and vice versa).
- Orb/L ratio (orbit length/skull length): approximates the capability for vision in low-light or turbid environments. Measured in the median part of the orbit, from the posterior margin of the prefrontal to the anterior margin of the postorbitofrontal–jugal bar. The higher the ratio value, the larger the orbit (and vice versa).

The overall size (or size range) of each species is estimated, using as proxy the length of the skull or of isolated bones permitting the estimation of it (e.g., maxilla, dentary, posterior mandibular unit) (see Table A2).

A morphofunctional interpretation of the feeding process and inferred prey preferences, using Massare's dental guilds [38], is given for each species (Figure 3), to be complemented by quantitative analyses (see below).

3.3. Morphometric Analyses

We quantitatively analyzed the disparity of crown shapes in mosasaurids from the Phosphates of Morocco using two methods. The first one is two-dimensional and uses a modification of the Fourier transform to analyze shapes [65]. The second one is three-dimensional and uses surface semi-landmarks, in a geometric morphometrics framework.

Some mosasaurids species were excluded from the morphometric analyses because we did not have access to their teeth, either described by other authors (*H. boubker*, *G. simplex*) or very scarce and/or poorly preserved (*C. minalmamar*). In total, the teeth of eleven species on fifteen were analyzed (see Table A3). We also assembled a dataset of skull lengths (see Table A2).

3.3.1. 2D Shape Analyses Using Fourier Transform

We gathered photographs (or snapshots of 3D models in orthographic view) of teeth from the median part of the jaw. We used these images to draw the basal and the labiolingual outlines of the teeth, creating full, closed black masks over a white background. Each of these images was then imported and transformed as an outline in the R statistical environment v4.3.1 using the package Momocs v1.4.1 [65]. Each closed outline was centered and scaled. The teeth of *Globidens* and *Xenodens* are labiolingually longer than apicobasally high, resulting in erroneous alignments (and thus incorporation of a rotation factor in PC1) if we normalized Fourier coefficients. Therefore, all images were aligned prior to importation in R, and 'norm' was set to FALSE in the efourier function.

Then, a principal component analysis was run on the Fourier coefficients, yielding one morphospace of labiolingual shape and another of basal crown section shape. Because both analyses of shapes concentrated most of the variance (≈80%) in their respective first axes, we extracted these coordinates to produce a composite morphospace, where the x-axis is the PC1 of the labiolingual PCA, and the y-axis is the PC1 of the basal PCA. We also extracted theoretical shapes along each of these axes for visualization purposes.

Finally, we computed the density of morphospace occupation using a Kernel density estimator. We provide the 2D masks as .jpg files and the R script as Supplementary Files to fully replicate the procedure.

3.3.2. 3D Geometric Morphometric Analyses

For each tooth, we used the semi-automated high-density 3D geometric morphometric protocol established by Fischer and collaborators [36]. Essentially, this method pseudo-landmarks a 3D 'dome' shape (2000 surface semi-landmarks) and uses it as an atlas to patch these surface semi-landmarks onto each crown 3D model, using five fixed landmarks as anchor points.

First, we obtained 3D models from a previous study [36], which sampled particularly well-preserved crowns from the median part of the jaws. We then complemented this sample by digitizing the crowns of additional species, still focusing our efforts on the median part of the jaws, using a handheld laser scanner (Creaform Handyscan 300, 0.2 mm scan resolution, Creaform, Lewis, Canada). Then, we placed five fixed landmarks (one at the apex of the tooth and four at the base of the crown: labially, lingually, distally and mesially) on the dome and on each crown model, using Stratovan Checkpoint v20.10.13.0859.

The rest of the procedure was fully automatized by an R script, using the packages geomorph v4.0.6, Morpho v2.12 and MASS v7.3-60.0.1 for data treatment and the packages ggplot2 v3.4.4, plotly v4.10.3, ggrepel v0.9.4 for visualisations, all in R v4.3.1. Basically, the meshes and their coordinates were imported, and the atlas was created and patched onto each crown model. The resulting 3D coordinates of the crowns were subjected to a generalized Procrustes superimposition, then in turn subjected to a principal component analysis. We computed the density of morphospace occupation using a Kernel density estimator (see [36]). We provide the atlas, the 3D models, the fixed landmark coordinates and R script as Supplementary Files to fully replicate the procedure.

4. Results

4.1. *Comparative Anatomy and Morphofunctional Interpretation (Figures 2 and 3, Tables A1 and A2)*

4.1.1. Mosasaurinae

With around 11 genera and 35–40 species known worldwide, mosasaurines are the most diverse clade of mosasaurids. They range from the Turonian up to the end of the Maastrichtian and reach a worldwide distribution by Campanian–Maastrichtian time (e.g., [2,3,27,66,67]). Mosasaurinae include two clades: Mosasaurini as a sister group of an unamed clade (previously referred to as Globidensini (sensu [68,69]), including the tribes Prognathodontini and Globidensini [27]. As did previous analyses (e.g., [66,67]), this last work recognized *Mosasaurus* and *Prognathodon* as paraphyletic taxa. With a wide range of sizes (about 2–17 m), morphologies and tooth shapes, mosasaurines exhibit a much higher ecological plasticity than other mosasaurid subfamilies [3].

Eight genera and 10 species of Mosasaurinae are so far recognized in the upper Maastrichtian Phosphates of Morocco.

- Mosasaurini

Mosasaurus beaugei Arambourg, 1952 is based on an isolated large antero-median tooth crown (MNHN PMC 7) from the Maastrichtian of the Oulad Abdoun Basin ([4], p. 282, pl. 39, fig. 13). In Arambourg's time, only isolated teeth were known, coming from all the Maastrichtian phosphatic basins of Morocco [3,4,18,70]. In the last two decades, however, more complete specimens, including skulls and mandibles, have been unearthed in the Upper *Couche* III (upper Maastrichtian) of the Daoui area (Oulad Abdoun Basin) and described [18]. Additional teeth have also been collected in the *Couches* 3 and 2 (upper Maastrichtian) of the Ben Guerir area (Ganntour Basin) [22]. These new specimens permit to significantly improve our knowledge of this species, both anatomically (diagnosis emended) and stratigraphically (range precised); it is considered a valid taxon among Mosasaurini [18,71]. Compared to other taxa and despite its large size, *M. beaugei* remains relatively scarce in the Phosphates of Morocco, a point already mentioned by Arambourg [4]. This species has been found only in the upper Maastrichtian Phosphates of Morocco and contemporaneous formations of the Southern Margin of the Mediterranean Tethys/Southern Atlantic (Brazil, ?Egypt) [34].

Description—Median teeth are large (crowns can reach 4 cm in height), robust and faceted, with a sharp, pointed apex. They are almost twice as high as long (H/L ratio 1.8–1.9), slightly laterally compressed (W/L ratio 0.6–0.7) and weakly posteriorly recurved. The anterior surface is slightly convex and the posterior one slightly concave. Both bear over their entire height a sharp carina bearing minute serrations. The labial surface is almost flat and smaller than the strongly convex lingual one, resulting in a U-shape cross-section, which is characteristic of the genus *Mosasaurus,* sensu [62]. The labial surface bears 3–5 large facets (average number, 4) separated by sharp edges; the lingual surface bears 6–9 less-distinct ones (average number, 8). In both surfaces, most facets do not reach the apex; they are less numerous and discernable on the largest and posteriormost teeth. The enamel is thick but smooth, with a shiny appearance. Wear facets are rare and, when present, mostly occur along the carinae as very narrow elongated zones and at the apex as a small, rounded area.

The dentition is subhomodont along the jaws, exhibiting only the minor variations usual in mosasaurids: the median teeth are the largest; anterior ones are slender; posterior ones are lower and wider; maxillary teeth are slightly larger than dentary ones [18]. Pterygoid teeth are hook-like and much smaller than the marginal teeth (about one-third the height of median teeth); they are strongly posteriorly recurved, with a rounded cross-section and a finely ridged enamel [18].

The skull is 80 cm to 110 cm long. It is robustly built but long and relatively narrow, with its width almost one-fourth of the length, giving it a rather gracile appearance. The jaws are noteworthy in being long, more than one-half the skull length, straight and narrow. The postorbital part of the skull remains short, being only about one-fourth of the skull length; the orbit is relatively small. The body size of *M. beaugei* is estimated to be about 8–10 m long [3].

Paleoecology—The sharp general aspect of the teeth of *M. beaugei*, with a pointed apex, several marked cutting structures (carinae, large prisms separated by cutting edges) and a smooth enamel, coupled to subhomodont dentition and small pterygoid teeth, indicate that *M. beaugei* mainly performed 'cutting' sensu Massare [38]. However, from the near-lack of wear facets and breakages, as well as the elongate, narrow morphology of the skull and the short postorbital region, leverage was probably reduced, indicating low biting force. Food manipulation and processing were probably limited to a preliminary phase of seizing, followed by simple cutting and ingestion of small prey or large flesh pieces. Its diet probably consisted of relatively soft fleshy items, possibly cephalopods, large fish like *Enchodus* Agassiz, 1833–1845 [72] and small marine reptiles. Given its large size, estimated at 8–10 m, this species was one of the local apex predators but probably occupied a more distinct niche than *Thalassotitan atrox*, *Prognathodon currii* or *Hainosaurus boubker*.

Carinodens belgicus (Woodward, 1891) is a very rare mosasaurid, based on an incomplete toothed dentary (IRScNB R 43) from the upper Maastrichtian of the Maastricht area, Limburg, The Netherlands [73]. Since that time, scarce additional remains, mostly consisting of isolated teeth and a couple of dentaries, have been found in the upper Maastrichtian of Europe (including Russia), South America, the Middle East and Africa [21,33,69,74]. Despite its scarcity, *C. belgicus*'s paleobiogeographical distribution is extensive, including both Northern/Southern margins of the Mediterranean Tethys and Southern Atlantic; however, its stratigraphic range is limited to the upper Maastrichtian [34]. In the upper Maastrichtian Phosphates of Morocco, this species has been unearthed in the Upper *Couche* III of the Oulad Abdoun Basin as isolated teeth (Daoui) and dentaries (Sidi Chennane) and in the *Couche* 3 of the Ganntour Basin as isolated teeth (Ben Guerir) [21,22,33]. *Carinodens* Thurmond, 1969 [75] has been classically considered a member of Globidensini [33,69], but recent work suggests closer affinities with Mosasaurini [27].

Description—The crowns are subrectangular, half as high as long (H/L ratio about 0.5) and strongly laterally compressed (W/L ratio about 0.55). The base is swollen, with a strong constriction between the crown and the slender root, giving the teeth a mushroom aspect. Both labial and lingual surfaces are convex and subequal in size, so that the cross section is oval. The anterior surface of the crown is much larger than the posterior one, rising up almost vertically, then curving at an almost right angle to form a long horizontal 'plateau' up to the apex, that is, de facto posteriorly displaced from the middle of the crown. The posterior surface is slightly concave posterior to the apex, then strongly convex. There are two faint, curved, unserrated carinae developed only on the upper half of the crown. The enamel is thick and ornamented by coarse, anastomosed ridges that become larger and thicker on the upper third of the crown, especially near the apex. The apex usually bears a large and rounded wear facet. Worn areas are also frequent on the anteroventral corner of the labial surface and on the posteroventral corner of the lingual one.

The dental series of *C. belgicus* is strongly heterodont, both in morphology and size, with small, pointed, recurved anterior teeth; large, blunt median teeth; smaller and lower posterior teeth. Also noteworthy, with 17–18 versus 13 teeth (on holotype IRScNB R 43), the dentaries from Morocco show that this bone was longer than previously thought, which has implications for its possible bite force and inferred diet [33]. Pterygoid teeth remain unknown on *C. belgicus*, but *Carinodens palistinicus* Kaddumi, 2009 from Jordan exhibits pterygoid teeth [76], which are hook-like and smaller than the marginal teeth, as in most mosasaurids (e.g., [62]).

The dentaries are long, straight and slender; the skull was probably long and gracile, like that of *C. palistinicus* [76]. Based on the dentary size, *C. belgicus* skull length was probably less than 40 cm long [3], suggesting a total body length of about 2.5–3 m.

Paleoecology—Both the small size of *C. belgicus* and its highly heterodont and specialized dentition suggest that food processing was basically suitable for 'crushing' sensu Massare [38] but probably also included a preliminary gripping phase and a final one of finer crushing [33]. If pterygoid teeth are present in *C. belgicus*, like in *C. palistinicus*, where they are small hooks, they could have been used in helping the engulfment process. The inferred diet probably consisted of small mollusks and arthropods [77]; however, the re-estimation of the greater length of the dentary suggests that the biting force was probably less than expected, suggesting also that prey were probably softer (with thinner shells?) than previously thought [33].

Carinodens minalmamar Schulp et al., 2009 is based on two dentaries from the same individual (OCP DEK/GE 453)—one with two in situ teeth—coming from the upper Maastrichtian *Couche* III of probably Sidi Chennane, Oulad Abdoun Basin [33]. It should be noted that this species was first described in the Phosphates of Morocco by Arambourg ([4], pl. 40, fig. 3) on the basis of an isolated tooth, for a long time considered lost but recently found (MNHN PMC 29), from Oued Meskoura, north of El Borouj (Oulad Abdoun Basin). The tooth was first referred by [4] to *Globidens aegyptiacus* Zdansky, 1935 [78] (a species originally described in Egypt; see [20] for details), later reassigned to *C. belgicus* [3,20,21] and then to *C. minalmamar* [33]. Up to now, *C. minalmamar* is known only from the upper Maastrichtian of Morocco and Russia [33,74].

Description—The crowns are generally comparable to those of *C. belgicus* in being rectangular in lateral view, twice as long as high, basally swollen and with a finely anastomosed enamel and faint carinae. However, they differ in being lower (H/L ratio about 0.4) and much more compressed (W/L ratio less than 0.4, reaching 0.3 on MNHN PMC 29), and in bearing two pronounced vertical sulci on the median part of the labial surface, reminiscent of those found in *G. phosphaticus* Bardet and Pereda-Suberbiola, 2005b [20,33], as well as faint, straight carinae. On MNHN PMC 29, because of these sulci, the labial surface is slightly concave, whereas the lingual surface is gently convex. As in *C. belgicus*, rounded wear facets are located on the apex, as well as on the anteroventral corner of the labial surface and on the anterior extremity of the horizontal 'plateau' of the anterior surface.

As for *C. belgicus*, the teeth preserved on the holotype OCP DEK/GE 453 show that the dentition was also probably strongly heterodont.

The dentary is long, straight and narrow but smaller and slender than that of *C. belgicus*, indicating a more gracile taxon; also, the alveoli indicate that teeth were more imbricated along the dentary than in *C. belgicus* [33]. The skull length was possibly around 35 cm and the estimated total length around 2.5 m.

Paleoecology—Compared to *C. belgicus*, the smaller and slender dentary of *C. minalmamar*, as well as its more packed and laterally compressed teeth, indicate that its diet was slightly different from that of *C. belgicus*, possibly including smaller and/or softer prey [33].

Xenodens calminechari Longrich et al., 2021a is a very rare and small-sized mosasaurid, so far known only by a complete maxilla with four teeth (MHNM.KHB.331) [25]. The holotype was unearthed in the Upper *Couche* III (upper Maastrichtian) of Sidi Chennane, Oulad Abdoun Basin [25]. *Xenodens* is thus far known only known from the upper Maastrichtian Phosphates of Morocco. The unique tooth structure and implantation suggest affinities with *Carinodens* among Mosasaurini [25].

Description—The crowns are very distinct from those of any other mosasaurid. They are quadrangular and low, about as high as long (H/L ratio about 1), with a sharp hooked apex, and are very laterally compressed (W/L ratio about 0.4). The anterior surface is strongly convex and twice the size of the slightly-concave-to-straight posterior one. Both surfaces are almost flat, bearing only two subtle ridges and sharp unserrated carinae. The enamel is totally smooth and shiny; wear facets are absent. The teeth preserved are closely packed and laid obliquely to the jaw margin, whereas their roots are anteroposteriorly expanded and fused, forming a continuous ridge of bone. As a whole, the teeth and their root arrangement are remarkable in forming a single sawblade-shaped cutting edge, not only unique among mosasaurids but also among tetrapods [25].

The maxilla size and morphology suggest that *Xenodens* was a small, gracile species, with a skull length not exceeding 30 cm and a total size estimated around 2 m [25]. *Xenodens* is so far the smallest known mosasaurid from the Maastrichtian Phosphates of Morocco but also worldwide, being even smaller than some basal mosasaurids like *Tethysaurus* Bardet et al., 2003 [79].

Paleoecology—The flattened, bladelike and closely packed teeth of *Xenodens* have never been observed in any other mosasaurid nor any known reptile, but comparable dental apparati are known in dogfish sharks and in several bony fishes [25]. This highly specialized 'cutting' dentition—but of very small size and lacking wear facet, contrary to Massare's [38] characteristics of cutting dentition—indicates previously unknown feeding strategies, diet preferences and niche occupation. *Xenodens* probably used its sawblade battery to remove pieces of flesh from large prey during scavenging or predation, but its diet could also have included smaller prey like fish, crustaceans and cephalopods [25].

- Prognathodontini

Eremiasaurus heterodontus LeBlanc et al., 2012 is based on the syntypes OCP DEK/GE 112, a partial skeleton with precisely known spatiotemporal occurrences (Upper *Couche* III of Sidi Daoui, upper Maastrichtian, Oulad Abdoun Basin) and UALVP 51744, a subcomplete skeleton whose occurrence remains uncertain (probably *Couche* III of the Oulad Abdoun Basin) [23]. Among the isolated teeth that Arambourg [4] described indistinctly as *Mosasaurus* (*Leiodon*) cf. *anceps* (Owen, 1841) [80]—a taxon now considered a nomen dubium by [81]—the smaller and slenderer ones (MNHN PMC41, 42, 45, 48, 50, respectively pl. 38, figs. 1, 25, 8, 10 of [4]) match remarkably well with those of *Eremiasaurus* [23], while the others match with *Thalassotitan* [27] (see below). *Eremiasaurus* has been recovered in the whole Maastrichtian series (*Couche* 6 to *Couche* 2) of Ben Guerir, in the Ganntour Basin [22]. This species is rather common in the Maastrichtian Phosphates of Morocco, known by countless isolated teeth and some more complete remains. It is a typical taxon from the Southern Margin of the Mediterranean Tethys, having also been found in the Negev Desert and in Brazil [34]. *Eremiasaurus* has initially been considered a sister group of *Mosasaurus* Conybeare, 1822 [82] and *Plotosaurus* Camp, 1942 [83] among Mosasaurini [23], but it has also been recovered as a sister group of *Prognathodon kianda* Schulp et al., 2008 [81] within Prognathodontini [27].

Description—The crowns are high and robust pointed cones (H/L ratio about 1.9), only slightly laterally compressed (W/L around 0.8) and posteriorly recurved. The anterior surface is gently convex and the posterior one gently concave, both having aligned sharp carinae running along their height and bearing minute serrations. The apex is sharp and pointed. The labial and lingual surfaces are subequal and convex, resulting in an oval cross-section. The enamel is totally smooth, thin and shiny; faint traces of facets expanded along two-thirds of the crown height are sometimes present. Wear facets are rare and, when present, are reduced to a small rounded apical area and slender zones at the base of the anterior carina, mostly as in *M. beaugei*. As a whole, median teeth are blade-like.

The dentition exhibits pronounced heterodonty (hence its specific name) with straight and conical anterior teeth, large, blade-like; more compressed median teeth; strongly posteriorly recurved posterior teeth [23]. Also, the upper and lower teeth strongly interdigitate anteriorly, fitting into interdental pits on the jaws, but astonishingly become superimposed medially and posteriorly, the maxillary teeth masking the dentary ones [23]. Pterygoid teeth, though smaller than the median marginal ones, are large, approaching the size of the posterior marginal teeth; they are typically hook-like, rounded in cross-section and smooth [23].

The skull as a whole is robust but relatively narrow (width about one-fourth of the length), with almost straight and slender jaws giving it a relatively gracile appearance, reminiscent of *M. beaugei* and *P. kianda* [23]. The jaws are surprisingly gracile compared to the large teeth they housed: in UALVP 51744, the anterior teeth are nearly as high as the dentary, but this becomes less marked posteriorly as dentaries become deeper [23]. The preorbital portion is long, being half the total skull length, the postorbital region is rather short [3] and the orbits rather small. The syntype skulls are around 65–70 cm long, and the total body length of *Eremiasaurus* is estimated to be around 4.5–5 m [3,23].

Paleoecology—The bladelike and closely packed teeth of *Eremiasaurus* indicate that their main function was probably 'cutting' sensu Massare [38], which is coherent with its long and narrow, but robust skull. However, teeth are almost devoid of wear facets and breakages, indicating probably relatively soft prey. The estimated body length (around 5 m) of *Eremiasaurus* suggests it was a meso-predator in the trophic network of the Maastrichtian Phosphates of Morocco. It occupied a distinct niche from ecologically distinct predators of the same size (*Globidens*, *Pluridens*) and was rather comparable in shape to the apex predator *M. beaugei*. However, its smaller size suggests that it probably preyed on different items, such as smaller fish, cephalopods or small marine reptiles. Noteworthy, the increase in the number of pygal vertebrae suggest that this was probably a high-speed pursuit predator, comparable to *Plotosaurus* [23,84].

Thalassotitan atrox Longrich et al., 2022 is based on the complementary syntypes OCP DEK/GE 417, a partial skeleton (crushed skull and mandible, cervical and dorsal vertebrae, girdle and limb elements) and MHNM.KHB.231, a well-preserved complete and articulated mandible (plus some dorsal vertebrae), both unearthed in the upper Maastrichtian Upper *Couche* III of Sidi Daoui, Oulad Abdoun Basin [27]. It should be noted that: (1) this taxon has for a long time been called *Prognathodon* nov. sp. (e.g., [3,5,34]); (2) as previously mentioned for *Eremiasaurus*, among the isolated teeth that Arambourg ([4], pl. 38) described indistinctly as *Mosasaurus* (*Leiodon*) cf. *anceps*, the largest and stoutest ones, namely MNHN PMC 43, 44, 46, 47, 49, 51 (respectively figs. 3, 4, 6, 7, 9 and 11 of [4]) most probably belong to *Thalassotitan* [27]. *Thalassotitan* is a very common taxon in the Phosphates of Morocco, known both by countless isolated teeth and several more complete specimens [27]. Articulated skeletons come from the Upper *Couche* III of most areas of the Oulad Abdoun Basin (Sidi Daoui, Meraa Lharach, Sidi Chennane) [27], whereas isolated teeth come from the same areas as well as from the *Couches* 3 and 2 of the Ben Guerir area, in the Ganntour Basin [22]; its stratigraphical range appears thus limited to the upper Maastrichtian. *Thalassotitan* is a characteristic taxon from the Southern Margin of the Mediterranean Tethys, having been found in Jordan, Negev, Egypt, Angola and Brazil, but possibly also in Poland, underlining a broader paleobiogeographical distribution [34]. Among Prognathodontini mosasaurines, *Thalassotitan* is considered a close relative of *Prognathodon currii* Christiansen and Bonde, 2002 [64] and *Prognathodon saturator* Dortangs et al., 2002 [27,85].

Description—Teeth are very large and robust (crowns can reach 5–6 cm high and 3–4 cm long). Median crowns are conical and massive, of medium height (H/L ratio 1.5 to 1.8). The basal cross-section is ovoid, almost rounded (W/L about 0.8–0.9) and slightly swollen, as in *P. currii*. The apex is moderately pointed and very often broken. The crowns are weakly posteriorly recurved, with a slightly convex anterior surface becoming more convex in its upper half, and a nearly straight posterior surface. Both bear a marked carina with fine denticulations, which are notably 'pinched' from the shaft of the crown, creating a strong cutting edge. This 'pinching' is more pronounced in the upper half of the carinae, making them protrude more than their lower part, giving the crown this particular upper inflated shape in lateral view. The labial and lingual surfaces are equal in size and regularly convex. They are smooth, lacking facets or prisms, except from some few indistinct vertical ridges present variably on the lingual surface in largest specimens. The enamel is thick and smooth, with a silky aspect, except apically, where it is coarsely anastomosed. In complete teeth, the wrinkles are reduced to the upper third of the crown but are not as pronounced as in *P. currii*. One of the main characteristics of both the marginal and pterygoid teeth of *Thalassotitan* is the presence of heavy spalling, breakage and wear facets, to a degree (both in frequency and extent) not found in any other mosasaurid [27]. Apical breakage is large and irregular, often removing up to one-fifth of the crown height and seem to result from violent impacts due to strong bite forces; sometimes, the broken apex is also worn by use, indicating that despite being damaged, the tooth was still functional. Large wear facets also occur along the carinae and on the lingual surface as large zones exposing dentine.

The dentition as a whole exhibits a developed heterodonty, with anterior teeth narrow, high and basally circular; median teeth conical, being the largest and most robust; posterior teeth smaller, as broad as tall, laterally compressed and posteriorly recurved. The dentary teeth are slightly more laterally compressed than the maxillary teeth. The pterygoid teeth are astonishingly very large and robust, about the same size and shape as the marginal ones, like in other prognathodontins and *Plesiotylosaurus* Camp, 1942 [27,83].

The skull is overall massively built and wide (W/L ratio about 0.38, the largest with that of *P. currii*), remarkably akinetic, with short and very robust jaws, a short postorbital region but a relatively large orbit. The dentary is short, deep and bowed, with a reduced tooth count compared to other mosasaurids [27]. The mandible mirrors the skull in being short, high and very massively built but with a still-functional intramandibular joint [27]. The skull of this species is one of the largest of the Morocco phosphatic fauna, being 1.20–1.30 m long, for a total body length estimated at 9–10 m [27].

Paleoecology—The large, short, conical teeth of *Thalassotitan*, ornamented with thick enamel and exhibiting numerous and large breakage/wear zones, indicate they were specialized to resist large forces when handling, biting and shredding large bony prey [27]. They range into the ‘crush–cut’ guild of [3]. The akinetic, short, massive and robust skull combined with the short, massive but still kinetic mandible increased biting force and the general withstanding of the skull, permitting the ingestion of large prey items. The reduction in tooth number observed in *Thalassotitan* also occurs in carnivorous apex predators like extant orcas, the extinct whale *Livyatan* Lambert et al., 2010 [86] and the theropod dinosaur *Tyrannosaurus* Osborn, 1905 [27,87]. The ecology of *Thalassotitan* was probably comparable to that of the extant white shark and killer whale [27]. All these characteristics suggest that *Thalassotitan* was probably the largest apex predator of the Maastrichtian Phosphates of Morocco, highly adapted for carnivory and probably preying on any of the abundant regional marine vertebrate faunas, including large sharks, large bony fish like *Enchodus* and other marine reptiles [27].

Prognathodon currii Christiansen and Bonde, 2002 is based on a complete skull and some vertebrae (HUJ.OR 100) found in the Main Phosphorite bed of the Mishash Formation, Oron phosphatic mine, Negev Desert [64]. Long dated as late Campanian-early Maastrichtian, the age of the Main Phosphorite bed has been reevaluated to early Maastrichtian on the basis of selachian faunas [88]. In Morocco, *P. currii* is very rare and known up to now only by a dozen isolated teeth found in the *Couche* 6 to *Couche* 2—i.e., along the Maastrichtian stage—of Ben Guerir, Ganntour Basin [20,22]. This species is however typical of the Southern Mediterranean Tethys Margin, and, in addition to Morocco and Negev, it possibly also occurs in the Maastrichtian of Angola [34]. Among Prognathodontini, *P. currii* is considered a sister group of *P. saturator* and *Thalassotitan* [27].

Description—The teeth are unique among mosasaurids in being straight and robust cones. They are large (crowns about 4–5 cm high), relatively high (H/L ratio about 1.3) and weakly laterally compressed (W/L ratio 0.77) with a generally blunt apex. The anterior and posterior surfaces are equal in size, straight and parallel along their height except when they converge to the apical nubbin. Anterior and posterior strong serrated carinae extend over the whole height of the crown and are more pronounced in its apical half because they are 'pinched' from the shaft of the crown, as occurs in *Thalassotitan*. The labial and lingual surfaces are also equal, being regularly convex, giving the crown an ovoid to almost rounded cross section. The enamel is very thick and anastomosed, this texture being more marked on the upper half of the crown. The apex is rounded. Wear facets are frequent, located mainly at the apex and along the carinae as large rounded or elongated ovoid zones, exposing the underlying dentine.

On the holotype, the preserved marginal teeth are homogenous in size and shape, indicating that the dentition was probably subhomodont, with only the small variations expected for the mosasaurid marginal series. The dentition is reduced (12 dentary teeth). Pterygoid teeth are very large, heavy and markedly recurved teeth, subequal in size to the marginal teeth [64].

The holotype skull of *P. currii* is probably the largest mosasaurid skull ever found (L = 1.40 m; W/L about 0.4). It is very robustly built and looks mostly akinetic. The jaws are massive, and the dentary is deep and bowed, relatively short but not as much as in *Thalassotitan*. The postorbital region is also relatively short, and the orbit very small. The size of the animal is estimated to be 10 m or more.

Paleoecology—The unique teeth of *P. currii* range into the 'crunch' guild of Massare [38]. These high, robust, anastomosed and straight cones are reminiscent of those of the large teleosauroid thalattosuchian *Machimosaurus* Meyer, 1837 [89,90]. The very robustly constructed skull and jaws of *P. currii*, coupled with these resistant, massive, conical, blunt teeth, indicate a powerful, crushing bite. Its large size makes it one of the apex predators of the Maastrichtian Phosphates of Morocco. It was probably adapted for predominately hunting large, bony prey, including large sharks, fish and marine reptiles, occupying as such an ecological niche close to that of *Thalassotitan*, but, like *Machimosaurus*, probably with a component of armored prey in the diet, such as large ammonites and turtles [91].

- Globidensini

Globidens phosphaticus Bardet and Pereda-Suberbiola, 2005b is based on thirteen isolated teeth representing a hypothetical dental series, including holotype (OCP DEK/GE 361, OCP DEK-GE 338-343) and referred specimens (OCP DEK/GE 344-348, MNHN PMC 17) [20]. Most of the teeth come from the *Couche* 3 (and some from the *Couches* 6, 4 and 2) of Ben Guerir (Ganntour Basin), ranging thus from the lower to upper Maastrichtian [20,22]. This species was firstly described in the Phosphates of Morocco as *Globidens aegyptiacus* by Arambourg, on the basis of isolated teeth (MNHN PMC 17, 18, 19) from the *Couche* III (upper Maastrichtian) of several localities of the Oulad Abdoun Basin ([4], pl. 40, figs. 1, 2). More recently, cranial and axial elements from the Maastrichtian of Angola have significantly improved our knowledge of this species and confirm its validity [92]. *G. phosphaticus* was a typical tropical to subtropical (10° N–25° S paleolatitudes) species from the Southern Margin of the Mediterranean Tethys (North Africa, Middle East) and South Atlantic (Brazil, Angola) [20,34,92].

Description—Median teeth are large, inflated and low compared to other mosasaurids except *Carinodens*, giving them a bulbous appearance. They are roughly as high as long (H/L ratio 1 to 0.7) and labiolingually expanded in an irregular fashion (W/L ratio 0.8 anteriorly to 0.65 posteriorly). The apex is large, rounded and usually worn. It lies near the middle of the crown or is slightly posteriorly displaced, and is slightly posteriorly and—very unusually—labially (and not lingually, as usual in mosasaurids) oriented. In apical view, the crown has a very irregularly oval cross section, being divided into a large inflated anterior surface and a smaller posterior one [20]. In lateral view, the anterior surface is regularly convex, the posterior one being slightly concave just posterior to the apex (reminiscent of what is observed in *Carinodens*), then strongly convex. Both surfaces are totally devoid of carinae (very discrete ones are still present on anteriormost teeth). The crown is typically swollen at the base, as in other Globidensini, giving it a mushroom-like shape. Both labial and lingual surfaces bear unique deep vertical sulci (average number 2–3) in their median part, similar to those observed in *C. minalmamar*. These sulci deeply notch the labial surface, resulting in its irregular shape in apical view (inflated—concave—inflated). The lingual sulci are less marked, so that this surface is roughly convex. The enamel is thick and ornamented by crude anastomosed ridges that become larger (and the enamel thicker) from the upper half of the crown up to the apex. Wear facets are frequent and usually round to oval large zones, located mainly at the apex but also irregularly on labial and lingual surfaces.

The dentition of *G. phosphaticus* is strongly heterodont, with subconical anterior teeth being higher than long (H/L ratio about 1.5), posteriorly recurved and prognathous; median teeth large, bulbous and lower (1.5 < H/L ratio < 1); posterior teeth large, bulbous and very low (H/L ratio around 0.5). The largest teeth are probably those occupying the 6th to 8th position of the dentary [20,92]. There is so far no evidence of pterygoid teeth in *Globidens* Gilmore, 1912 [93], a unique characteristic in mosasaurids [62]. Interestingly, as noted by [92], most of the teeth of the specimen from Angola were found complete (crowns and attached roots) but displaced in, or out of their respective sockets.

The cranial elements of *G. phosphaticus* (from Angola) show that the skull was short, robust and probably wide (according to frontal width), with robust bowed dentary about one-half the total length, being unique among mosasaurids in being shorter than the posterior mandibular unit [24]. The orbit was probably relatively small (estimated from coronoid dorsal curvature) and the postorbital portion was of medium size. The skull length is estimated to be about 75–80 cm, and the total body size to be 5–6 m.

Paleoecology—The highly specialized dentition of *G. phosphaticus*, composed of low and bulbous teeth with thick anastomosed and often worn enamel, indicates that its main function was 'crushing' sensu Massare [38]. The conical anterior teeth were probably used in grasping prey. The lack of pterygoid teeth suggests that the prey were ground into small pieces directly by the powerful crushing battery, as such not requiring prey to be held before being engulfed. Most of the teeth (seen on the Angola specimen) have been found complete and preserved out of the jaws, which suggests that the periodontal ligaments did not mineralize in life [94]. This is interpreted as a possible adaptation to increased loading due to durophagous habits [92] (see also below for *G. simplex*). The robustness and shortness of the skull (known from the Angola specimen) imply that bite force was probably high.

All these characteristics suggest a diet based on rather small but hard prey such as small-shelled cephalopods, echinoderms, large bivalves, etc., a view confirmed by stomach contents preserved in other *Globidens* species [24]. However, compared to them, especially the coeval *G. simplex*, the highly heterodont dentition and irregular shape of the median teeth of *G. phosphaticus* indicate a specific, slightly different durophagous diet.

Globidens simplex LeBlanc et al., 2019 is based on a partial disarticulated but three-dimensionally preserved skull and associated cervical vertebrae (formerly UALVP 51746, now MHNM.KHB.221) [24]. Though its exact provenance remains unknown, the rock matrix suggests it was probably unearthed from the Upper *Couche* III of the Oulad Abdoun Basin [24].

Description—Median teeth are typically low and bulbous (H/L ratio 0.65 to 0.77) and slightly labiolingually compressed (W/L ratio 0.73 to 0.82), giving them an ovoid cross-section. This compression is more marked in the posterior teeth. The crown is broadly triangular in lateral view, with symmetrical, slightly convex to almost straight anterior and posterior surfaces converging to the apex. The apex is rounded, not recurved and often worn. The base is strongly swollen, giving the teeth a mushroom aspect. The enamel is thick and strongly anastomosed. There are no carinae or sulci [24].

The dental series of *G. simplex* is strongly heterodont, with anterior teeth conical, rounded, higher than long and posteriorly recurved; median teeth about as high than long, bulbous and slightly compressed labiolingually; and posterior teeth bulbous, low (height about half the length) and more compressed. The general shape of the teeth is more regular than in *G. phosphaticus*, being globally ovoid and without carinae or sulci. As in *G. phosphaticus*, most of the teeth of *G. simplex* are preserved complete (crowns and roots) and separated from the jaws [24].

The skull is overall short and robust, completely akinetic and probably wide. Unlike *G. phosphaticus* (and other *Globidens* species), the dentary is very straight and relatively slender, but, as in *G. phosphaticus*, it is shorter than the posterior mandibular unit [24]. As in *G. phosphaticus*, the orbit is relatively small and the postorbital portion of medium size. The skull length is estimated to be about 75–80 cm, for a total body size of about 5–6 m.

Paleoecology—The dentition and skull morphology of *G. simplex* clearly indicate a durophagous species ranging into the ‘crush’ guild of Massare [38], which probably fed on shelled invertebrates (mollusks, echinoderms). Unlike most mosasaurids (including the Campanian species of *Globidens*) and squamates in general, whose teeth are firmly ankylosed by their roots to the jaws, most of the teeth of *G. simplex*, as in *G. phosphaticus*, are preserved complete and out of the jaws, indicating a dental gomphosis (ligamentous tooth attachment, as in archosaurs and mammals) [24]. This unique dental attachment shared only by the two Maastrichtian species of *Globidens* is interpreted as an adaptative response for resisting and absorbing shocks when biting [24,92,94]. A dentary shorter than the posterior mandibular unit is also interpreted as an adaptation to increase the mechanical advantage for shell-crushing [24]. The akinetic skull as well as the straight and slender dentary of *G. simplex* are however unusual for a durophagous species, as all extant shell-crushing squamates possess kinetic skulls and a bowed dentary [24]. *G. simplex* exhibits the same size range as *G. phosphaticus* but differs in having a different dentition and a slenderer/straighter dentary; this suggests that both species had a slightly different diet and niche.

- Mosasaurinae incertae sedis

Stelladens mysteriosus Longrich et al., 2023 is a very scarce taxon based on a dentary fragment and two associated teeth (MHNM.KHB.1436) found in the *Couche* III (upper Maastrichtian) of Sidi Chennane, Oulad Abdoun Basin [28]. So far, *Stelladens* is only known from the Maastrichtian Phosphates of Morocco. The global morphology of the teeth and dentary suggest mosasaurine affinities [28].

Description—The crowns are triangular and rather low (L/H ratio about 1.3–1.4), weakly laterally compressed (W/L ratio about 0.7–0.8) and posteriorly recurved, with a convex anterior surface and a slightly concave posterior one. The apex is pointed. There are two prominent sharp and serrated carinae, the posterior one being stronger and more ‘pinched’ than the anterior one. The enamel is ornamented with minute anastomosing ridges, giving it a silky aspect. Wear facets are present at the apex of the teeth and on the posterior carina as large but narrow zones. The labial surface of the teeth is almost flat, and the lingual surface is strongly convex, giving the crown a U-shaped section typical of many mosasaurines. Whereas the labial surface bears five to eight poorly differentiated ridges, the lingual surface bears two to four large protruding cutting ridges, separated by deep, V-shaped grooves. These large ridges are unique among mosasaurids (and not pathological, as they are present on all teeth), giving the lingual surface a zig-zag aspect, and the crown in dorsal view the shape of the tip of a Phillips screwdriver. Another remarkable and unique among mosasaurids fact is that these ridges are serrated, like the carinae. The serrations extend full length on the anterior ridges, but only apically on the posterior ones.

The relative size and robustness of the dentary and associated teeth suggest *S. mysteriosus* was a medium-sized species, with a skull length estimated at about 80 cm and a total body length at about 5 m [28].

Paleoecology—The presence of prominent sharp serrated ridges is not only entirely unique among mosasaurids but also has no extant or extinct analogues, indicating a highly specialized and previously unknown diet [28]. This battery of large, sharp and serrated carinae (main carinae and accessory ridges acting as carinae) coupled with relatively low crowns bearing a subtle anastomosed enamel and large wear facets suggests that the teeth were probably used for both cutting and crushing, but also holding the prey, being as such globally generalists. *Stelladens*' diet probably included semi-hard prey, either bony (medium size fish) or with a thin carapax/shell (crustaceans, cephalopods) [28].

4.1.2. Halisaurinae

Halisaurines are basal mosasaurids known by only four genera and about ten species, with a stratigraphic range from the Coniacian to the end of the Maastrichtian and a worldwide distribution (e.g., [2,3,19,26,66,67,95,96]). During the Maastrichtian, the clade exhibits its greatest diversity and distribution, being common in subtropical assemblages of Africa and Middle East but remaining scarcer in higher latitudes (North America, Europe, Japan) [26,95,96]. Halisaurines include two tribes with very different morphology and sizes and therefore different habits and niches: the gracile and small Halisaurini (around 3 m in body length) and the large and robust Pluridensini (up to 8 m) [26].

Both Halisaurini and Pluridensini are present in the Phosphates of Morocco and are represented by one species each. As previously pointed out [11], despite the great abundance of halisaurine teeth in all Maastrichtian phosphatic deposits of Morocco, Arambourg [4], who collected in these outcrops hundreds of mosasaurid teeth (including very small ones), surprisingly did not mention or even collect a single tooth belonging to this taxon, nor mistake them with fish ones (NB. pers. obs. on the Arambourg collection; MNHN, Paris); the reason for this collecting bias remains unknown.

- Halisaurini

Halisaurus arambourgi Bardet and Pereda-Suberbiola, 2005a is based on a partial skeleton (MNHN PMC 14), including a skull, mandible and part of a vertebral column, found in the Upper *Couche* III (upper Maastrichtian) of Sidi Daoui, Oulad Abdoun Basin [19]. It is among the most common species in the Phosphates of Morocco, being known by countless isolated teeth in all phosphatic basins and by articulated skeletons in the Oulad Abdoun Basin [19]. The species ranges from *Couche* 6 to *Couche* 2 of the Ben Guerir area (Ganntour Basin), thus spanning the Maastrichtian stage [22]. It is a typical species of the Southern Margin of the Mediterranean Tethys, being known in the Maastrichtian of Syria, Jordan, Negev and Angola [34]. Among Halisaurini, *H. arambourgi* is recovered as a sister taxon of *Halisaurus platypsondylus* Marsh, 1869 [97] from the Maastrichtian of North America [26,96].

Description—The crowns are small (height 0.5 to 1 cm maximum), delicate, hook-like, and have a sharply pointed apex. They are high (H/L ratio 2, the highest in proportion of all the Phosphate mosasaurids) and weakly labiolingually compressed, being ovoid to rounded in cross section (W/L around 0.8). The anterior surface is strongly convex and the posterior one strongly concave; at about mid-height, both surfaces are abruptly recurved posteriorly, giving the crown its typical hooked shape. Both anterior and posterior surfaces bear a small unserrated carina, present only on the upper two-thirds of the crown and more marked above the median-height abrupt curvature. The anterior carina is more marked than the posterior one, which is slightly displaced labially. Both labial and lingual surfaces are regularly convex, but the labial one is slightly flatter. The enamel is ornamented by minute striae, giving it a silky aspect. These striae are present on two-thirds of the crown and are more marked and slightly anastomosed around mid-height. The upper third of the enamel crown is smooth and shiny. In the lower third of the crown, some underlying 'folds' or flutings, variable in number, position and extension, are present on some teeth. Wear facets are lacking and, when present, reduced to a tiny apical rounded area.

The dentition of *H. arambourgi* is homodont, comprised of numerous teeth (16 Mx, 19 De, 12 Pt) and poorly differentiated both in shape and size along the jaws [19]. Anteriormost and posteriormost teeth are slightly smaller than median teeth, but their shape is similar; the position of isolated teeth on the jaws is thus difficult to assess. The pterygoid teeth differ from the marginals only in being about half as high and even more hooked.

The skull of *H. arambourgi* is long and slender, gracile, with long, straight jaws occupying one-half of the total skull length, a short postorbital region and large orbits (about one-fifth of the total length). It is also highly kinetic, skulls being often found completely disarticulated. Its average size is around 35–40 cm long for a total observed body length (on OCP specimens, NB, pers. obs.) of 3–4 m [19].

Paleoecology—*H. arambourgi*, with numerous small, hook-like teeth devoid of wear facets, is clearly placed into the 'piercing I' guild of Massare [38]. The teeth resemble those of *Plioplatecarpus* (Dollo, 1882) [98], although they are much slender, and also those of some plesiosauroids (e.g., [99]). This suggest a diet based on soft and small prey (cephalopods, fish), probably harpooned and captured in the trap made by these numerous, needle-sharp teeth, before being swallowed whole. Like other Halisaurini, the large orbits (and supposed eyes) of *H. arambourgi* and a degree of binocularity suggest a visual hability for detecting prey in low-light conditions, either at night or at depth [26,95]. However, *Halisaurus* rarely exhibits the avascular necrosis of bone tissue common to deep divers [100], suggesting open sea nocturnal habits such as looking for phosphorescent cephalopods, as in *Phosphorosaurus* Dollo, 1889b [95], rather than deep diving habits [101].

- Pluridensini

Pluridens serpentis Longrich et al., 2021b is based on the complementary syntypes OCP DEK/GE 548 (complete skull) and MHNM.KHB.262 (complete skull with articulated mandible and some cervical vertebrae), both from the upper Maastrichtian Upper *Couche* III of Sidi Daoui, Oulad Abdoun Basin [26]. Compared to other mosasaurids, this species remains uncommon, and articulated material has primarily been found so far in the Daoui area (Oulad Abdoun Basin), though isolated teeth are known in all basins. The teeth of *P. serpentis* being indistinguishable from those of *H. arambourgi* except being twice their size (NB, pers. obs.), large teeth interpretated previously as belonging to *H. arambourgi* [19,22] may therefore belong to *Pluridens*. As such, both its stratigraphical range (lower to uppermost Maastrichtian) and paleobiogeographical distribution (Southern Margin of the Mediterranean Tethys) could be the same that of *H. arambourgi* [34]. Among Pluridensini, *P. serpentis* is considered a sister group of the two *Pluridens* Lingham-Soliar, 1998 [102] species from the Maastrichtian Iullemmeden Basin of Niger and Nigeria [26,102].

Description—The teeth of *P. serpentis* are identical to those of *H. arambourgi*; see above for detailed description. The only notable difference is that, because they are twice the size (1.5 cm to 2 cm high), features such as carinae, striations, basal flutings, etc. appear more marked/visible than on *H. arambourgi*.

As in *H. arambourgi*, the dentition of *P. serpentis* is characterized by a high tooth count (18 Mx, 26–28 De) and is remarkably homodont. However, it differs in that tooth roots are obliquely (and not vertically) oriented with respect to the long jaw axis, and in that replacement pits are positioned medianly (and not posteriorly) on the roots; both are autapomorphies of *Pluridens* [26].

Despite similar tooth shape, increase of tooth count and homodont dentition, the *P. serpentis* skull Bauplan differs drastically from the small, delicate one of *H. arambourgi*. It is overall elongated but massively built, especially in its anterior two thirds. The jaws are almost half the skull length, very robust and deep, contrasting with the small and delicate teeth they bear, and have numerous neurovascular foramina. The orbits are small (Orb/L ratio 0.12, the smallest of all Phosphate mosasaurids), with a large dorsal prefrontal–postorbitofrontal contact, forming a kind of reinforced protective flange. The postorbital part of the skull is, on the contrary, rather long and slender, about one-third of the skull length. The skull is large, 70 to 90 cm long, and the estimated body size is 5–6 m [26].

Paleoecology—*Pluridens* is unusual among mosasaurids in combining a large and robust skull—rivalling other coeval meso-predators like *Eremiasaurus* or *Gavialimimus*—with a dentition indicating as a whole ‘piercing I’ habits sensu Massare [38] and a diet probably composed of small prey like fish and cephalopods [26]. However, these teeth being twice the size of those of *H. arambourgi*, the prey were probably larger (though still soft).

Pluridens is also characterizsed by small orbits, reinforced dorsally by a rim of bone, and by numerous neurovascular foramina on the jaws. These characteristics suggest both a possible adaptation to diving and a feeding strategy probably relying on chemo- and mechanoreception rather than on visual cues [26]. If *Halisaurus* (large orbits) and *Pluridens* (small orbits) were probably adapted to prey on dark waters and to feed in small soft items, their hunting strategies were probably quite different, revealing very different niche occupations: *Halisaurus* was probably a visual hunter, preying at night in open sea (see above), whereas *Pluridens* was probably a chemo-tactile predator, looking for hidden prey at depth, in burrows and crevices [26,96].

4.1.3. Plioplatecarpinae

With about 14 genera known from the Turonian to the end of the Maastrichtian, plioplatecarpines were diversified and widespread mosasaurids (e.g., [2,3,29,66,67,103]). They reach a maximum diversity during the Campanian and achieved a worldwide distribution during the Maastrichtian, where they are known in Europe, Africa, the Middle East, North and South America and Antarctica [29,104]. Plioplatecarpinae include several basal taxa and two main tribes: the small to medium-sized (3–6 m) Plioplatecarpini of ‘piercing’ type, distributed worldwide in medium-high paleolatitudes; and the larger (around 8 m), more robust Selmasaurini of ‘cutting’ type, found in low paleolatitudes of both the Western Interior Seaway (North America) and the Arabo-African platform (northwestern Africa and the Middle East) [29].

In the Phosphates of Morocco, plioplatecarpines are so far represented only by Selmasaurini, which are known by two genera.

- Selmasaurini

Gavialimimus ptychodon (Arambourg, 1952) **new combination** (see below) was originally described as *Platecarpus* (?) *ptychodon* by [4]. The species was based on an isolated median tooth (MNHN PMC 30) from the Maastrichtian *Couche* III of Sidi Daoui, Oulad Abdoun Basin ([4], pl. 39, fig. 2). Several isolated teeth and some caudal vertebrae were also attributed to this species ([4], pl. 39, figs. 1, 3–7, 12). Both the teeth bearing ridges and striae and the vertebrae with unfused chevrons are russellosaurine synapomorphies [68,105]. The discovery in the last decade of more complete specimens in both Morocco and Angola confirmed it was a new plioplatecarpine genus [106], as glimpsed by Arambourg [4]. Then, the new genus and species *Gavialimimus almaghribensis* Strong et al., 2020 was described, on the basis of a complete skull and mandible with teeth (MHNM.KHG.1231) from the Maastrichtian Phosphates of Morocco [32]. If the creation of the genus *Gavialimimus* is not in doubt, the proposal of the new species name *almaghribensis* to replace Arambourg's original one *ptychodon* is here challenged (see below). Teeth of this species are very abundant in the Maastrichtian Phosphates of Morocco, having been unearthed both in the *Couche* III of the Oulad Abdoun Basin and in the whole Maastrichtian series (*Couche* 6 to *Couche* 2) of the Ganntour Basin [22]. *G. ptychodon* is a characteristic taxon of the Southern Margin of the Mediterranean Tethys and of the Southern Atlantic, having been found in the Maastrichtian of the Middle East (Syria, Jordan, Negev) and northwestern Africa (Morocco, Angola) [34,106]. It represents one of the few plioplatecarpines known from the Arabo-African platforms. Among plioplatecarpines, *Gavialimimus* has been recovered as a Selmasaurini, a sister taxon of either *Selmasaurus* Wright and Shannon, 1988 [32,107] or *Goronyosaurus* Azzaroli et al., 1972 [108] and *Khinjaria* [29].

Description and emended diagnosis (for teeth and dentition)—Median teeth are of medium size (1 to 2.5 cm high), triangular in shape, with a relatively long base and medium height (H/L ratio around 1.5), and bear a sharp and pointed apex. They are distinctly labiolingually compressed (W/L ratio around 0.7), with a convex labial surface and a flatter lingual one, resulting in an irregular ovoid basal cross section. They are slightly posteriorly recurved, with slightly recurved anterior and posterior surfaces, both bearing a sharp unserrated carina. Lingual and labial surfaces are ornamented by both strong protruding ridges (about 12–15 labially and twice lingually) extending about one-half to two-thirds of the crown height (slightly lower lingually), and shorter and thinner striae, variably inserted between the strong ridges and less extended upwards. As none reach the apex, the upper third to half of the crown height is smooth and shiny. All these ridges and striae are separated by shallow grooves, giving them a fluted aspect that may continue on the upper part of the root. The enamel is thin, and wear facets are very rare, limited when present to a small apical point.

The dentition is almost homodont (both in shape and size) along the jaws, so that isolated teeth are difficult to position in the jaws. Teeth are few (13 Mx, 16 De), despite the very elongated gavial-like jaws, and are spaced well apart from each other. The pterygoid teeth are typically hook-like, half the size of the marginal ones, similarly ornamented but slightly labiolingually compressed.

The skull as a whole is large (about 90 cm) and narrow (W/L = 0.25), with remarkably long, straight and slender jaws about two-thirds of the skull length. The jaws bear widely spaced, interfingering teeth, with accommodation pits on the opposite jaw. The appearance of the skull and jaws is gharial-like (hence the generic name) [32]. The orbital region is short, with a very small isosceles-triangle-shaped frontal bone. The postorbital region is long and slender. *Gavialimimus* is also unique among mosasaurids for its extremely retracted nares [32,106]. The body size is estimated at 6 m.

Paleoecology—The high, sharp, ridged teeth without wear facets range into the 'piercing II' guild of Massare [38], indicating a diet composed of possibly small fish and soft cephalopods. However, they also approach the 'cutting' guild by the presence of sharp carinae, lateral compression and the characteristic protruding vertical ridges present on two-thirds of both lingual and labial surfaces, which may have helped to both cut and penetrate the flesh [3]. Alternatively, these features were interpreted by [32] as rather indicative of 'pierce II' close to 'pierce I' functions, and the tooth flutings an adaptation to piscivory (this last interpretation being not contradictory with [3] arguments). *Gavialimimus* also shows a suite of characters indicating advanced adaptations to aquatic life, the most spectacular being the very retracted nares and the shortening of the skull posterior to the snout, reminiscent of the 'telescopation' observed in cetacean evolution (e.g., [109]). *Gavialimimus* was probably an open-sea meso-predator that fed on small fish and soft cephalopods [3,32], both representing a particularly abundant biomass in this area of intense upwelling [58]. The elongate jaws suggest the prey was seized using rapid strikes of the jaws, similar to gharials and river dolphins, rather than high-speed pursuit as in porpoises and dolphins.

Systematic reassignment—The main arguments of Strong and collaborators [32] to justify the creation of the new species *almaghribensis* to the detriment of the already-existing *ptychodon* were these: (1) the teeth of *P.* (?) *ptychodon* are not diagnostic, looking similar by convergence to many other mosasaurids; (2) Arambourg's original diagnosis was unprecise and applied to many taxa, such as the mosasaurines *Mosasaurus lemonnieri* Dollo, 1889b [101] and *Prognathodon solvayi* Dollo, 1889a [110], the plioplatecarpine *Platecarpus somenensis* Thévenin, 1896 [111], as well as the tylosaurines *Tylosasaurus ivoensis* (Persson, 1963) [112] and *Taniwhasaurus* Hector, 1874 [113]. As a result, [32] considered the species *P.* (?) *ptychodon* as a nomen dubium, because diagnosis and holotype were insufficient to characterize it.

Here, we challenge this view by thoroughly examining and comparing the *Gavialimimus* teeth to those of not only *P.* (?) *ptychodon* and the species considered by [32] as 'similar' by convergence but also to those of mosasaurid subfamilies as a whole.

First of all, the teeth of the holotype skull (MHNM.KHG.1231) of *G. almaghribensis* are indistinguishable from the holotype (MNHN PMC-30) and referred teeth (MNHN PMC-31-34) of *P.* (?) *ptychodon*, not because they exhibit vague convergent traits but, on the contrary, a suite of diagnostical ones, as described above.

Second, all the characteristics mentioned by Arambourg [4] in his original diagnosis of *P.* (?) *ptychodon*—that are: '*teeth relatively low and wide at the base of the crown, slightly compressed, with obtuse anterior and posterior carinae without crenulations; lingual and labial surfaces ornamented by numerous irregular vertical ridges extending from the base of the crown only two-thirds of the way up*' (translated from French)—are found in our description. It thus appears more parsimonious to emend this original diagnosis rather than to consider this species (cited many times since Arambourg) as a nomen dubium.

Third, [32] did not provide any precise descriptions of the teeth of the species they consider as 'similar' to *P.* (?) *ptychodon*. The morphological overlap they mention results only from very superficial observations.

As mentioned above, the presence of both ridges and striae on labial and lingual surfaces of the crowns of *Gavialimimus* is a russellosaurine (Plioplatecarpinae + Tylosaurinae) synapomorphy (e.g., [68,105]), de facto never present in Mosasaurinae (including *Mosasaurus lemonnieri* and *Prognathodon solvayi* used by [32]). Conversely, all *Mosasaurus* species exhibit a characteristic U-shape cross section [62], and both *M. lemonnieri* and *P. solvayi* have large smooth facets and serrated carinae; none of these characteristics are observed in *Gavialimimus* or any other plioplatecarpine, even on replacement and worn teeth.

The teeth of basal mosasaurids like *Tethysaurus* [79], *Dallasaurus* Bell and Polcyn, 2005 [114] and *Russellosaurus* Polcyn and Bell, 2005 [105] and of Halisaurinae [19,26] are small and slender posteriorly recurved sharp cones, finely striated or smooth, diverging greatly from *Gavialimimus*.

Tylosaurinae teeth differ from *Gavialimimus* in being large, robust, high cones, either asymmetrical (*Tylosaurus* Marsh, 1872 [115]) or flattened and symmetrical (*Hainosaurus* Dollo, 1885 [116]) [37,117]. Though their teeth bear ridges and striae, they are present only basally and lingually, often reach the apex, but not continues basally as flutings. *Taniwhasaurus* teeth are smaller and slender, bearing marked striations that disappear near the apex, resembling as such *Gavialimimus*; however, *Taniwhasaurus* differs in lacking posterior carinae on anterior teeth [118] and, as is noteworthy, in having higher and more-slender crowns bearing large wear facets (NB, pers. obs.).

Among plioplatecarpines, Plioplatecarpini [29] bear small teeth with rounded to oval cross sections that are strongly posteriorly recurved at the mid-height of the crown [68,105], differing greatly from *Gavialimimus*. As mentioned by [32], *Platecarpus somenensis* teeth are similar at first glance to *Gavialimimus* in being high and slender, of comparable size (1–2.5 cm high), poorly posteriorly recurved, laterally compressed and exhibiting two unserrated carinae, as well as labial and lingual surfaces ornamented by ridges and striae that do not reach the apex. However, in the details, *P. somenensis* holotype (MNHN 1895-7) shows obvious differences: the median crowns are straighter and more compressed than in *Gavialimimus* (W/L = 0.5 versus 0.6–0.8) and, as is noteworthy, the labial and lingual surfaces bears few ‘facets’ (seven labially, about seven lingually) reminiscent of those of mosasasaurines, rather than numerous ridges (12–15 labially, twice lingually) as in *Gavialimimus*. Between these ‘facets’, minute striae extending over one-fourth to one-third of the crown height are interspersed, forming a basal striated ‘ring’. These minute striae are also present on pterygoid teeth. Finally, wear facets are frequent and relatively large. Among Selmasaurini, *Gavialimimus* teeth strongly differs from those of *Goronyosaurus* and *Khinjaria* that are large, straight, smooth and dagger-like [29]. Although the teeth of *Selmasaurus* show some resemblances with those of *Gavialimimus* (poorly posteriorly recurved, subequal labial and lingual surfaces, two unserrated carinae, very rare wear facets and basal flutings), they however differ in being higher, slender (H/L ratio about 2) and ornamented by strong but few ridges (five to six labially, six to seven lingually) [119] contrary also to the numerous ones of *Gavialimimus*.

To sum up, the median standard teeth of *Gavialimimus almaghribensis* are similar to those of *P.* (?) *ptychodon* but differ from those of any other mosasaurids. They bear a suite of diagnostical characteristics (described above)—some of them already mentioned by Arambourg in his original diagnosis of *P.* (?) *ptychodon* [4]—that make them unique and recognizable at first sight among hundreds of mosasaurid teeth. As a result, we propose to accomplish the following:

(1) Rehabilitate the name *ptychodon* as a valid species, *almagribensis* being considered its junior synonym;
(2) Emend Arambourg’s original diagnosis (for teeth and dentition only), using the description detailed above;
(3) Consider for nomenclatural stability MNHN PMC 30 (holotype of *P.* (?) *ptychodon*, with well-known geographical and stratigraphical occurrences) and MHNM.KHG.1231 (holotype of *G. almaghribensis*, with geographical origin uncertain and stratigraphical occurrence obtained second hand) as complementary syntypes of the new combination *G. ptychodon* (Arambourg, 1952).

Khinjaria acuta Longrich et al., 2024b is known by a unique incomplete skull (MHNM.KHG.521) found in the Lower *Couche* III of Sidi Chennane, Oulad Abdoun Basin [29]. Lower *Couche* III being considered as middle-late Maastrichtian in age [61], *Khinjaria* is probably slightly older than the other mosasaurids from the Upper *Couche* III assemblage; as such, it has not been included in the morphometric analyses of this work. *Khinjaria* is up to now only known in the Phosphates of Morocco. Among Selmasauri, it shows close affininities with *Goronyosaurus* from the Maastrichtian Iullemmeden Basin of Niger and Nigeria [120–122], with which it forms a clade, sister group of *Gavialimimus*, all knownfrom Northwest Africa and the Middle East. These genera represent a distinct clade of specialized mosasaurids, so far unknown outside of the Arabo-African platform [29].

Description—The crowns are very high, slender (H/L ratio estimated to 1.8) and dagger-like in shape. Though they cannot be measured (because the holotype is still partly imbedded in matrix), they are clearly labiolingually compressed, with a lenticular cross section. Strikingly, they are not posteriorly recurved, with the anterior and posterior surfaces being almost straight along most of their height, except apically, where they converge to the rounded tip. This character is particularly marked in the large anterior and median teeth. The smaller posterior teeth are slightly posteriorly recurved. The anterior and posterior surfaces of the crowns bear a prominent, unserrated carina, 'pinched' from its shaft, which reinforces its sharp aspect, particularly in the anterior and median teeth. The enamel is completely smooth and shiny, without any ornamentation except some variably subtle ridges labially and lingually. There is no trace of wear facets on any of the functional teeth.

The dentition is strongly heterodont in size rather than in shape (most teeth are dagger-like), with anterior teeth forming large fangs (a characteristic shared with *Goronyosaurus*), about twice the length of the median ones. This condition is unique in mosasaurids, where median teeth are always the largest [29,62]. The posteriormost teeth are small, being one-quarter the height of the anterior teeth, another unusual character. The tooth count is low (10–11 Mx, 12 De), and the teeth are well-spaced from each other. They are strongly interlocking, and large interdental pits for the housing of the opposite teeth during occlusion are present on both the maxilla and dentary, as in *Gavialimimus*. Pterygoid teeth remain unknown.

The skull of *Khinjaria* is highly akinetic and is characterized by a short and robust rostrum, a long postorbital region with large temporal fenestrae and probably reduced orbits [29]. A noteworthy feature is that the dentary deepens in its symphyseal region (probably mirrored on the premaxilla) to accommodate the large anterior teeth. This is also unique among mosasaurids, where the jaws always gently taper anteriorly [29,62]. These reinforcement of the anterior part of the rostrum, coupled with the large anterior fangs they hold (share with *Goronyosaurus*), are reminiscent of the 'spatulated' symphysis of pliosaurs, which also housed the largest teeth of the dental series [29]. *Khinjaria* was a medium to large taxon, with a skull estimated to be 90 cm long and a total body size of 8 m [29].

Paleoecology—The large dagger-like teeth and strong interlocking dentition of *Khinjaria* indicate a clear adaptation for 'cutting', though they lack wear facets. Its short and robust jaws were suitable to resist high bite forces, favored by large mandibular adductor muscles housed in expanded temporal fenestrae [29]. As a whole, the large size of *Khinjaria* and its noteworthy short robust skull armed with large sharp teeth indicate it was an apex predator, with a diet probably composed of large prey, but that adapted a different strategy to avoid competition with the larger coeval *Thalassotitan*, *P. currii*, *Mosasaurus* and *Hainosaurus*. Indeed, the lack of wear facets on the teeth indicates that prey must not have been very hard - like the fish *Enchodus* or other marine vertebrates of comparable size and consistency - and that their manipulation was probably simple and restricted to a rough cut into large pieces swallowed whole. Also, the apparently small eyes and lack of neurovascular foramina on jaws (characteristics shared with *Goronyosaurus*) suggest non-visual hunting, probably based on olfaction [29], as previously suggested for *Goronyosaurus* [123].

Non-visual hunting is probably linked to ambush predators with feeding strategies carried out by night, at great depth or in shallow waters with low visibility (reefs, crevices) [29].

4.1.4. Tylosaurinae

Tylosaurinae are a clade of poorly diversified (two to three genera, according to the authors) mosasaurids, known from the Turonian to the early Maastrichtian [123,124]. They were mainly widespread during Santonian–Campanian times, but during the Maastrichtian were largely replaced as apex predators by mosasaurines [2,125]. Except for the Turonian taxa found in subtropical paleolatitudes, younger tylosaurines all occurred in higher paleolatitudes (35–70°) of both hemispheres, mainly in North America and Europe, but also in Japan, New Zealand and Antarctica [123–127]. However, these spatiotemporal distributions have been challenged recently by the discovery of tylosaurine remains in the late Maastrichtian Phosphates of Morocco [31], representing not only the unique post-Turonian subtropical occurrence of the clade but also its youngest record. Tylosaurines include some of the largest mosasaurid taxa (10 to 12 m), rivaling in size the largest mosasaurines.

Tylosaurines remain extremely scarce in the Maastrichtian Phosphates of Morocco, being up to now known from one species only.

Hainosaurus boubker Rempert et al., 2022 is based on upper and lower jaw fragments and isolated teeth (syntypes VANPS 13.0120-13.0121) originating from the upper Maastrichtian Upper *Couche* III of Sidi Chennane, southern part of the Oulad Abdoun Basin [31]. It should be noted that the specific name *boubker*, dedicated to Mr. Boubker Chaibi (discoverer and donator of the specimens) should preferably have been *boubkeri* (*Hainosaurus* 'from Boubker', Latin genitive) following the recommendations of the ICZN. Though the referral of some isolated teeth to tylosaurines is questionable (NB, pers. obs.), most specimens bear two of the main tylosaurine synapomorphies, that are premaxilla and dentary bearing a large edentulous rostrum, and large, robust teeth ornamented by both facets and striations. Pending the discovery of more complete specimens, this species is considered here as valid.

Description—The crowns are large (average height 5 cm), robust high cones (H/L about 1.6), moderately posteriorly recurved and strongly laterally compressed (W/L ratio about 0.7, see [31]). The apex is sharp. The anterior surface is regularly convex and the posterior one concave, both bearing a marked cutting carina with tiny serrations, more marked on the anterior carina. The labial and lingual surfaces are subequal, convex and strongly compressed, resulting in an elliptical cross-section. The labial surface bears five to six large but poorly marked facets. The lingual surface bears also five to seven large facets, even more difficult to distinguish. In addition to these facets, fine striae are superimposed around the basal part (about one-fourth of the total height) of the crown, a typical tylosaurine character [37,117]. As in *M. beaugei*, wear facets occur both at the apex of the crown and on the carinae, especially on the anterior one (tooth cutting leading edge).

Contrary to [31], we consider the heterodonty to be only moderate, falling within the range of variation along the jaws shown in most mosasaurids, with slender recurved anterior teeth, large blade-like median teeth, and lower and more robust posterior teeth.

On the basis of the jaw fragments, the prenarial part of the premaxilla indicates a skull possibly about 1,20 m and a total body length estimated at 8–12 m [31].

Paleoecology—With *T. atrox*, *P. currii* and *M. beaugei*, *H. boubker* is part of the apex predators of the Maastrichtian Phosphates of Morocco. However, unlike these three taxa, whose remains are commonly and jointly found, *H. boubker* remains very scarce, a fact that cannot be explained by collection bias. *H. boubker* possibly occupied a quite different ecological niche than the previously mentioned taxa, both in term of adaptation and of habitat (more offshore species?). The teeth of *H. boubker* indicate that their function was 'cutting' sensu Massare [38]. They are roughly comparable to those of *M. beaugei* in their sharp appearance but are larger and more robust. The diet of *H. boubker* could therefore have included comparable but larger items than that of *M. beaugei*, such as large fish and small marine reptiles.

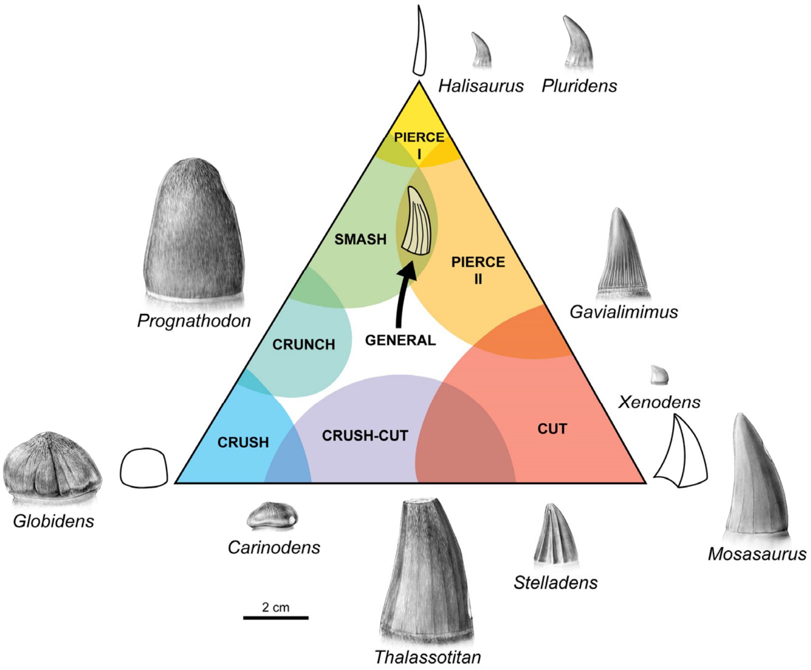


Figure 3. Mosasauridae from the Maastrichtian Phosphates of Morocco: niche partitioning using Massare's dental guilds [38]. Based on the same taxon selection as in Figure 2. Teeth on scale to appreciate size and proportion differences (see measurements and ratios in Table A2). Modified from [3]. Teeth drawings © Charlène Letenneur (CR2P, MNHN, Paris); canvas and design © Alexandre Lethiers (CR2P, ISTeP, Paris).

4.2. Morphometric Analyses (Figures 4 and 5)

4.2.1. High-Density 3D Geometric Morphometrics

Our semi-automated high-density 3D geometric morphometric (HD3DGM) procedure recovers a signal similar to that carried by a global set of marine amniote tooth crowns [36]. Most of the shape signal is indeed dominated by the aspect ratio of the crown and its distal concavity (Figure 4A). In this mosasaurid-only dataset, the presence of cutting edges is also captured by PC1 (which accounts for 86.2% of the total variance): crowns in positive values are pointed, recurved and possess two cutting edges; crowns in negative values are bulbous, at least in labial or lingual view. PC2 (accounting for 9% of the total variance) captures the labiolingual flattening of the crown, as well as the direction of curvature: distally in negative values and distolingually in positive values. Most teeth of the sample are conical and slightly recurved; indeed, this region concentrates most clades and a range of crown volumes/sizes (Figure 4A), with large prognathodontins (*T. atrox*, *E. heterodontus*), one mosasaurin (*M. beaugei*), the halisaurines (*H. arambourgi*, *P. serpentis*) and the only plioplatecarpine of our sample (*G. ptychodon*), the last two subfamilies having fairly small crowns. Three species are isolated from the dense region of phenotypes, disseminated in the negative quadrant of PC1 and dictate most of the signal captured by PC2: the giant 'crush–cut' prognathodontin *P. currii*, as well as the durophagous mosasaurin *C. belgicus* and the globidensin *G. phosphaticus*.

4.2.2. Fourier Transforms

Principal component analyses of Fourier transform coefficients yielded a dominant first axis for both the labiolingual and the basal outline analyses (PC1 = 84.8% of the total variance in the labiolingual outline analysis and PC1 = 79% of the total variance of the basal outline analysis; Figures 4B, A1 and A2). The labiolingual signal is dominated by the aspect ratio, as evidenced by the shape variation along PC1 (Figures 4B, A1 and A2). The first principal component also carries a signal of distal concavity, giving bulbous outlines in negative values and pointed, recurved cones in positive values. The signal of basal outline analysis is dominated by labiolingual compression, giving flattened outlines with straight, parallel labial and lingual surfaces in negative values and rounded outlines in positive values.

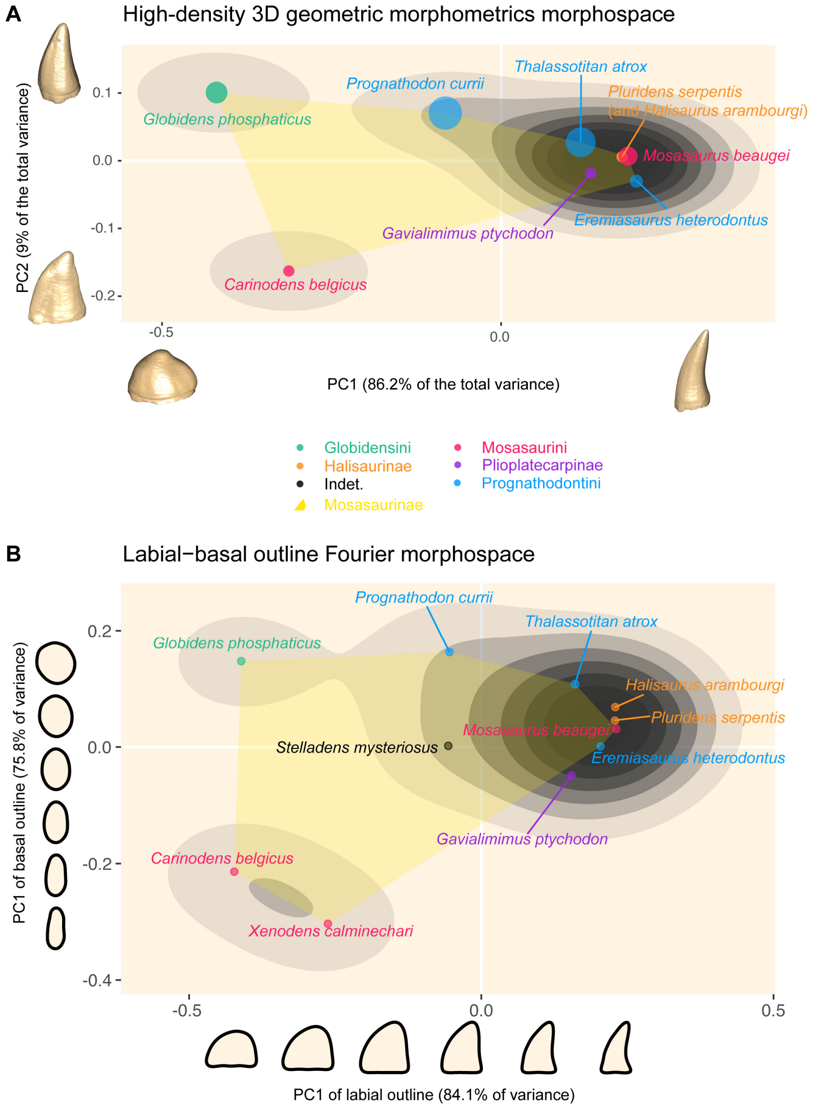


Figure 4. Mosasauridae from the Maastrichtian Phosphates of Morocco: crown shape morphospaces. (**A**) Morphospace (PC1 and PC2) resulting from the principal component analysis of high-density 3D geometric morphometrics, using Fischer and collaborators method [36]. The diameter of each dot is directly proportional to centroid size. We grouped *P. serpentis* and *H. arambourgi* because their teeth are morphologically uncannily similar. To visualize the morphological variation captured by each axis, we generated 3D meshes at the extremes of each axis (20% further than the sampled extremes) using thin-plate splines. (**B**) Composite morphospace using the PC1 of the Fourier analyses of the labiolingual and basal outlines. Kernel density of occupation in both morphospaces is visualized by shades of grey (darker = higher density). Teeth data in Tables A2 and A3.

Combining the PC1s of both outline analyses yields two axes representing most of the signal, which can therefore be used as axes of a two-dimensional composite morphospace. Kernel density estimation indicates a main region of recurring phenotypes, centred on slightly recurved conical crowns with an oval basal cross section. This region concentrates most clades, with representatives of mosasaurin (*M. beaugei*) and prognathodontin (*T. atrox*, *E. heterodontus*) among mosasaurines, halisaurines (*H. arambourgi*, *P. serpentis*) and a plioplatecarpine (*G. ptychodon*). Two highly peculiar crown shapes are located on the border of this region, the gigantic prognathodontin *P. currii* and the mosasaurine *S. mysteriosus*. Three taxa are located clearly outside of the 'common' shape region; all have semioval to square labial outlines, with varying degrees of labiolingual compression: *G. phosphaticus* (rounded labial outline and basal cross section), *C. belgicus* (labiolingually flattened cross section) and *X. calminechari* (squared labial outline, extreme labiolingual compression).

4.2.3. Comparison of Geometric Morphometric Methods and Caveats

Though the very high ecological disparity morphologically exhibited by the mosasaurid assemblages from the upper Maastrichtian Phosphates of Morocco, our HD3DGM and Fourier transform protocols, despite using markedly different techniques and slightly dissimilar datasets (the two highly peculiar species *Stelladens* and *Xenodens* are absent from the HD3DGM analysis), recovered uncannily similar signals, morphospaces and phenotype densities (Figure 4). This means that the main signals present in the dataset are clear and easy to capture. Indeed, most of the shape signal can be summarized as a combination of crown aspect ratio, crown distal curvature and basal cross section. Because most marine amniote crowns seem to vary along the same traits [36], the similarity between the results of both techniques suggests that our protocol using Fourier transform offers a fast, cheap and easy-to-implement alternative to high-density 3D geometric morphometrics of simple conical objects such as marine tetrapod tooth crowns.

Namely, a dense region of 'common' phenotypes (teeth conical, pointed, recurved and bearing two carinae) concentrates most of the species in positive values, independently of their volume and size, varying from gigantic mosasaurines (*Thalassotitan*, *Mosasaurus*) to medium and small-size mosasaurines (*Eremiasaurus*), plioplatecarpines (*Gavialimimus*) and halisaurines (*Halisaurus*, *Pluridens*). Noteworthy are *Halisaurus* and *Pluridens*, which occupy the same position despite their drastically different skull morphologies. Their teeth are morphologically indistinguishable except for a difference in size (1:2 ratio), indicating a fully isometric tooth-growth difference between both species. Three taxa corresponding to bulbous or squared and variably labiolingually compressed teeth (*Globidens*, *Carinodens*, *Xenodens*) are always found isolated from the 'common' shape region and disseminated in negative values. The gigantic *Prognathodon curri*, combining features of both 'crushing' and 'cutting' teeth sensu [3], occupies a median position, as does the mysterious *Stelladens*.

Yet, this also means that both techniques, because they rely on principal component analyses and, for Fourier transform, simple outlines, cannot discern the fine details of crown shape and texture in the first (main) axes of variation. Indeed, when the sample includes teeth as different as the crushing teeth of *Globidens* and the elongate, slightly recurved teeth of *Eremiasaurus*, most of the variation in X, Y, Z coordinates or outline shapes will evidently be the aspect ratio and the labiolingual flattening. Therefore, features like the precise position of cutting edges (which are still captured in PC1 in the HD3DGM method), the rugose enamel texture in *Globidens* or the apicobasal ridges in *Stelladens* will result in only slight variations of X, Y, Z coordinates in HD3DGM and, depending on how they are oriented in the crown, no change in outline shape in the Fourier transform method. Therefore, the shape signal carried by these traits will either be very small compared to other features (and thus captured by PC axes accounting for a very small amount of the total variance in HD3DGM) or not captured at all (Fourier transform). Despite being minor modifications of the global shape, these features can be of importance when trying to assess diet and the finer functional capabilities of teeth [36,38,128]. Therefore, even though it goes without saying, quantitative analyses in isolation are not sufficient to fully discuss and interpret the complexity of functional anatomy.

4.2.4. Skull Size/Crown Shape Relationships

As observed in a broader dataset of aquatic amniotes [36], there is no obvious skull size–tooth shape correlation, in the sense that both small and medium-sized mosasaurids (i.e., with skull lengths less than 1 m) have a wide range of tooth shapes (bulbous, conical, recurved) (Figure 5A,B,D,E), whereas larger taxa seem to occupy a restricted area of tooth shapes, being close to origin of main axis of variance (here, *Thalassotitan* and *Prognathodon currii*). These taxa indeed have 'intermediate' morphologies, with robust crowns still possessing protruding carinae; this prompted [3] to create the crush–cut guild for animals like *Thalassotitan*. Similarly, *P. currii* possesses large, blunt teeth with blunt carinae forming two opposite apicobasal ridges.

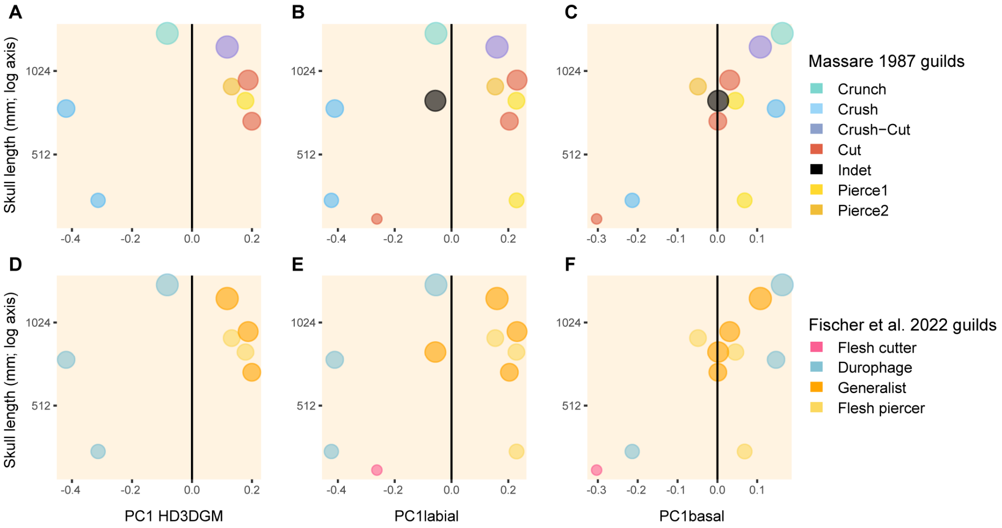


Figure 5. Mosasauridae from the Maastrichtian Phosphates of Morocco: skull size–crown shape relationships. (**A**,**D**) Skull size versus PC1 of the high-density 3D geometric morphometrics. (**B**,**E**) skull size versus PC1 of the Fourier analysis of the labiolingual outline. (**C**,**F**) Skull size versus PC1 of the Fourier analysis of the basal outline, with a mapping of the guilds of Massare [38] (**A**–**C**) and the guilds of Fischer and collaborators [36] (**D**–**F**). Data about skull size in Table A2.

This zone of the morphospace, close to the center of the axis, is weakly populated in smaller forms. The only medium-sized taxon with such a 'median' tooth shape is the highly peculiar *Stelladens* (Figure 5B,E), which actually possesses a series of highly unusual ornamentations that are not captured in the main axis of variation of dental shape. Another zone appears unpopulated: labiolingually compressed teeth in medium and large taxa (Figure 5C,F). Indeed, highly compressed teeth are restricted to the smallest taxa (*Carinodens*, *Xenodens*) (Figure 5C,F); the drivers and effects of these size–shape relationships are discussed below.

5. Discussion

5.1. Paleobiodiversity (Figure 6)

Despite the description over the last decade of many new mosasaurid taxa in the upper Maastrichtian Phosphates of Morocco, the respective diversity of each sub-family expressed as a percentage of the total species number remains surprisingly constant compared to previous work (compare ([3], fig. 6) to this work Figure 6). This stability, despite the increased sampling, suggests it is a genuine paleobiodiversity pattern, rather than collection or description biases.

Notably, Mosasaurinae (eight genera, ten species) accounts for about 60% of the genera and almost 70% of the species described so far in these Moroccan Phosphates. Such a proportion also corresponds to patterns observed in other coeval localities worldwide [2,3,129]. Also, the Moroccan genera represent about half to three-quarters (depending on the taxa considered valid) of the mosasaurines known worldwide, whereas most of the species are solely known in the Southern margin of the Mediterranean Tethys [34].

Halisaurinae and Plioplatecarpinae are less diverse (two genera and two species each), representing about 13% of the species and 15% of the genera currently known in the upper Maastrichtian Phosphates of Morocco. However, this represents about half of the total halisaurine genera versus one-seventh of the plioplatecarpine genera known worldwide, emphasizing the greater global diversity of this last clade during Maastrichtian times and a poor representation in Morocco.

Finally, Tylosaurinae remain extremely scarce (one genus, one species), representing about 6% of the species and 7% of the genera of the Phosphates of Morocco mosasaurid faunas and one-third of the worldwide tylosaurine genera.

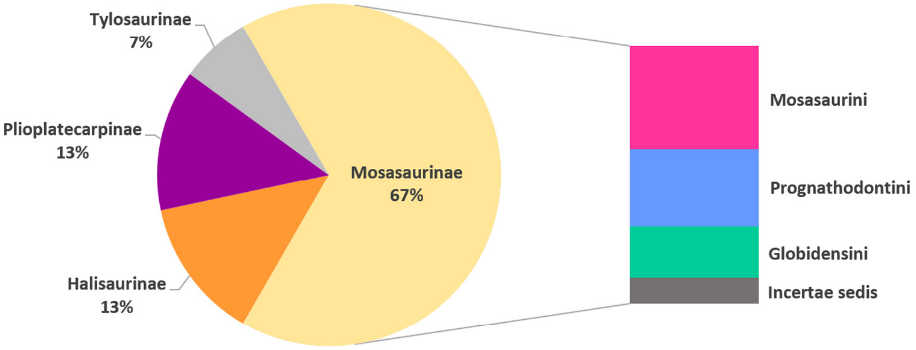


Figure 6. Mosasauridae from the Maastrichtian Phosphates of Morocco: taxonomic paleobiodiversity, expressed for each subfamily as a percentage of the total species number (15). The same for mosasaurine tribes (on the right). Colors are the same as in Figure 4 for ease of comparison.

5.2. Paleoecology and Niche-Partitioning (Figure 7)

In addition to their high taxonomic diversity, the mosasaurid faunas from the upper Maastrichtian Phosphates of Morocco exhibit a wide range of phenotypes (body sizes, skull morphologies, dental shapes) (Figures 2 and 3) (e.g., [this work, [3,130]]), strongly suggesting diverse diet preferences and predation modes, as well as niche-partitioning in the regional environment. In the present work, when using the framework of Massare [38] and subsequent modifications and additions by Chatterjee and Small [130] (trap guild) and Bardet and collaborators [3] (crush–cut guild), Moroccan mosasaurids (10/15 taxa used) occupied a wide range of dental guilds: crunch (*Prognathodon*), crush (*Globidens*, *Carinodens*), crush–cut (*Thalassotitan*), cut (*Mosasaurus*, *Eremiasaurus*, *Xenodens*, ?*Khinjaria*, ?*Hainosaurus*), pierce I (*Halisaurus*, *Pluridens*) and pierce II (*Gavialimimus*) (Figures 3, 5A–C and 7B). The peculiar *Stelladens* occupied a unique, so-far unknown guild, possibly located between ‘cut’ and ‘crush’ in that canvas. Without taking *Stelladens* into account, mosasaurids of this ecosystem therefore occupied 75% (6/8) of Massare’s guilds ever colonized by marine reptiles.

Only two guilds—‘smash’ and ‘trap’—were not occupied by mosasaurids; this is true not only for the upper Maastrichtian Phosphates of Morocco but also worldwide. The ‘trap’ guild was defined by [130] to characterize the long, slim and labially directed teeth of long-necked plesiosauroids, notably aristonectine elasmosaurids during the Maastrichtian [131]. None of the marine reptiles known in the upper Maastrichtian Phosphates of Morocco appears to precisely occupy it. Though the anteriorly protruding and usually unworn teeth of the local elasmosaurid plesiosaurian *Zarafasaura* [13] could probably act as a trap, their robust shape and large size proportionally to the skull rather match with the 'pierce' guild of Massare [38]. The 'smash' guild, occupied during the Mesozoic by several ichthyosaurians, is characterized by teeth resembling small, straight cones, with acute but round apexes and without carinae [38]. In the upper Maastrichtian Phosphates of Morocco, such a dental shape is found in crocodylomorphs, more especially in the small gavialoid *Ocepesuchus* [12]. It should be pointed out that sea-going crocodylomorphs remain very scarce and small in the regional Maastrichtian, becoming abundant and larger only after the extinction of the mosasaurids during the K/Pg biological crisis [12]. Their rarity suggests that they may have inhabited freshwater or marine ecosystems, rather than being fully marine.

When using the guilds of Fischer and collaborators [36], Maastrichtian Moroccan mosasaurids occupied 100% (4/4) of the main raptorial feeding guilds (generalist, durophage, cutter, piercer), covering a wide range of crown sizes and shapes: three durophages (*Carinodens*, *Globidens*, *Prognathodon*), one flesh cutter (*Xenodens*), three flesh piercers (*Halisaurus*, *Pluridens*, *Gavialimimus*) and four generalists (*Thalassotitan*, *Mosasaurus*, *Eremiasaurus* and *Stelladens*), two of them being very large (*Prognathodon*, *Thalassotitan*) (Figures 5D–F and 7B). The main difference with Massare's canvas is the presence of more generalist species (resulting from the inclusion in that guild of most of the large 'cutting' species), whereas species specializing in crushing and piercing remain roughly the same (Figure 7B). Specifically, we interpret *Thalassotitan atrox* as a generalist and *Prognathodon currii* as a durophagous predator of large, shelled animals like turtles, even though its size and robustness, comparable to *Thalassotitan*, probably allowed it to kill and consume a wide range of prey items (see [36] for a discussion of diet–size relationships). These ecological differences are also reflected by a different positioning ('crunch' versus 'crush–cut') in Massare's qualitative canvas (Figure 3). *Hainosaurus* and *Khinjaria* were not quantitatively analyzed here, but they are expected to occupy, respectively, the generalist and the flesh cutter guilds.

To sum up, by combining both canvases as well as our Fourier-transform analyses, we observe for each mosasaurid subfamily grosso modo the same trends in ecological disparity as those observed for taxonomic diversity (compare Figures 3, 4 and 7):

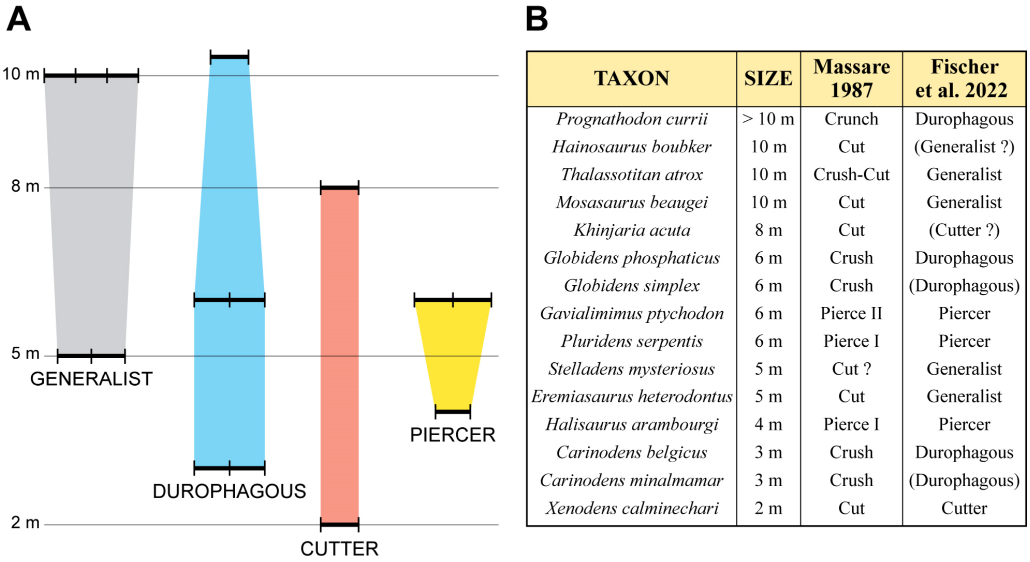
(1) Mosasaurinae exhibit the largest disparity of tooth guilds (generalists, durophagous, flesh cutters), combined with a widest range of body sizes (2 m in *Xenodens* to more than 10 m in *P. currii*). However, the clade did not evolve flesh piercers, either here or worldwide. Mosasaurins (*Mosasaurus*, *Eremiasaurus*, *Carinodens*) usually have longer and more gracile skulls armed with labio-lingually compressed teeth either to cut or to crush, whereas prognathodontins (*Thalassotitan*, *Prognathodon*) and globidensins (*Globidens*) are characterized by shorter and more-robust brevirostrine skulls and teeth, indicating stronger bite force and more durophagous habits [130] (Figure 2). Also noteworthy is that Mosasaurinae are the only mosasaurid clade to have developed durophagous species distributed over its three tribes, which exhibit a wide range of both body sizes and crushing tooth shapes (compressed in the 3 m long mosasaurin *Carinodens*, bulbous in the 6 m long globidensin *Globidens*, conical in the up-to-10 m long prognathodontin *P. currii*) and this repeatedly (at least two coeval species of *Carinodens* and two of *Globidens* in the Phosphates of Morocco), once again indicating a larger plasticity of this clade.

(2) Halisaurinae retain the mosasaurid primitive tooth shape and, despite their very different skull morphologies and sizes (3 m gracile *Halisaurus* versus up to 8 m robust *Pluridens*) (Figure 2), have similar teeth, indicating they were flesh piercers in the 'grasping' group of [129].

(3) Plioplatecarpinae are represented in Morocco only by two medium-sized selmasaurins (Figure 2), exhibiting astonishing and drastically opposed skull and tooth morphologies: the longirostrine flesh-piercer *Gavialimimus* and the brevirostrine flesh-cutter *Khinjaria*.

(4) Finally, Tylosaurinae, though poorly known so far in Morocco, are represented by a generalist taxon, whose skull and tooth morphologies are reminiscent of those of Mosasaurini like *Mosasaurus* and *Eremiasaurus*, although much larger.

Also, when comparing tooth shapes with global sizes (Figure 7A), the same trends as those observed with skull sizes (Figure 5) are found, with the largest taxa (more than 8 m long) occupying a restricted area of tooth shapes (generalist, durophagous), as previously shown by [36], whereas small- and medium-sized species (less than 8 m long) occupy all tooth morphologies (generalists, durophagous, cutters, piercers). In the details, flesh piercers appear to have a restricted size-range between 4 and 6 m, whereas generalists are usually larger than 5 m long, and durophages range along all sizes (Figure 7A). In other words, and probably related to the specificities and advantages of biomechanical resistance, apex predators are never dedicated piercers, micro-predators are conversely never generalists, and meso-predators occupy the widest range of dental adaptations (compare Figures 5 and 7A). This signal in the upper Maastrichtian Phosphates of Morocco, where some of the size-shape possibilities are unexplored, also possibly results from the reduction of generalist predators among Northern Hemisphere mosasaurids during the Maastrichtian [130]. Finally, strictly cutting species remain rare among these mosasaurid faunas; these ecological niches were probably occupied by other predators, most likely selachians [22].



TAXON	SIZE	Massare 1987	Fischer et al. 2022
Prognathodon currii	> 10 m	Crunch	Durophagous
Hainosaurus boubker	10 m	Cut	(Generalist ?)
Thalassotitan atrox	10 m	Crush-Cut	Generalist
Mosasaurus beaugei	10 m	Cut	Generalist
Khinjaria acuta	8 m	Cut	(Cutter ?)
Globidens phosphaticus	6 m	Crush	Durophagous
Globidens simplex	6 m	Crush	(Durophagous)
Gavialimimus ptychodon	6 m	Pierce II	Piercer
Pluridens serpentis	6 m	Pierce I	Piercer
Stelladens mysteriosus	5 m	Cut ?	Generalist
Eremiasaurus heterodontus	5 m	Cut	Generalist
Halisaurus arambourgi	4 m	Pierce I	Piercer
Carinodens belgicus	3 m	Crush	Durophagous
Carinodens minalmamar	3 m	Crush	(Durophagous)
Xenodens calminechari	2 m	Cut	Cutter

Figure 7. Mosasauridae from the Maastrichtian Phosphates of Morocco: niche-partitioning. Expressed for each species by combining body sizes and dental guilds (**A**) of Massare [38] and Fischer and collaborators [36]. List of taxa and inferred guilds (**B**), with diets suggested by anatomy, but not quantitatively analyzed, indicated in parentheses. Colors are the same as in Figure 3 for ease of comparison.

Despite these constraints, mosasaurids from the upper Maastrichtian Phosphates of Morocco likely were widespread in a wide range of niches in this shallow marine ecosystem, both vertically (water column) and horizontally (coast to open sea). Apex predators (*P. currii*, *T. atrox*, *M. beaugei*) probably fed on any other large bony marine vertebrates, with a harder component in *Thalassotitan* and even harder in *P. currii*, which possibly was a turtle consumer. Meso-predators were the most ecologically diverse and probably the most widely distributed in the water column, avoiding as such some niche overlaps. They include piscivores (*G. ptychodon*, *P. serpentis*), generalists (*E. heterodontus*, *S. mysteriosus*), flesh cutters (*K. acuta*) and consumers of hard invertebrates (*G. phosphaticus*, *G. simplex*). Some taxa like *Pluridens* were probably ambush hunters in dark waters, either at night or in the depths of crevices. *Globidens* is represented by two species with different dentition, indicating the hard-shelled invertebrates they fed on were probably different. Finally, the smallest mosasaurids of the assemblage were either piscivorous (or consumers of soft invertebrates) (*H. arambourgi*), scavengers (*X. calminechari*) or durophagous (*C. minalmamar*, *C. belgicus*). Here also, the niche-partitioning was pronounced, with *Halisaurus* being possibly a rapid night hunter of soft phosphorescent cephalopods, whereas *Carinodens* (just like *Globidens*) developed two species with different dentition, indicating slightly different semi-hard invertebrate diets.

Compared to the other marine vertebrate predators with which they interacted and shared trophic resources, mosasaurids were much more systematically and ecologically diverse than were coeval plesiosaurians and chelonioid turtles (see list in [5]) but much less so than selachians (e.g., [10]). The coexistence of this totally astonishing plethora of marine vertebrate predators in the same rather restricted environment of the Phosphate Sea (Figure 1D) implies that niche partitioning was particularly high, not only among mosasaurids but also among marine vertebrates as a whole, probably as an evolutionary answer to resist competition pressure.

The intense upwelling system that developed along the western coast of Africa from the Cretaceous [2] is probably responsible for this extraordinary paleobiodiversity and, more specifically, for that abundance of large predators coexisting locally [58]; this mirrors what is observed nowadays in upwelling zones that attract, by their high productivity, a huge range of marine predators (selachians, fishes, marine mammals) [27,58]. The use of Calcium isotopes as a diet marker has however revealed that, despite their huge ecological disparity, most of the marine vertebrate predators of the upper Maastrichtian Phosphates of Morocco (selachians, marine reptiles including mosasaurids) were feeding on a single decipherable calcium source [58]. This therefore suggests that, as also observed in extant upwelling zones, even if all these predators were able to hunt on a wide range of prey, as illustrated by very different morphologies and tooth shapes, the upwelling system facilitated their feeding by providing an important single biomass, likely schools of small teleost fish (like those of today, sardines and anchovies), whose remains are innumerable throughout the series of the Phosphates of Morocco.

6. Conclusions

The anatomical descriptions and quantitative methods used in this work have highlighted their complementarity to tackle the vast array of tooth morphologies in upper Maastrichtian mosasaurids from Morocco and infer the diets of their bearers. They also show their limits when used alone: while comparative anatomy fails to precisely locate teeth into a dental guild, morphometric analyses fail to capture the complex details of tooth ornamentations, which in reptiles probably play a role as important in feeding process as the multiple cusps of mammals. The two methods combined permit to approach the complexity of tooth shape, structure and ornamentation in its entirety.

With at least 15 species known so far, exhibiting a wide range of sizes, morphologies and tooth shapes covering the majority of dental guilds defined for marine amniotes, the mosasaurid faunas from the upper Maastrichtian Phosphates of Morocco reveal an extraordinarily high taxonomical diversity and ecological disparity, unknown elsewhere. Small spike hook-like teeth (*Halisaurus arambourgi*, *Pluridens serpentis*, *Gavialimimus ptychodon*) to spear soft fish and invertebrates, large robust pointed teeth to catch large marine vertebrates (*Thalassotitan atrox*, *Mosasaurus beaugei*, *Hainosaurus boubker*, *Eremiasaurus heterodontus*), blade-like teeth to cut large vertebrates (*Khinjaria acuta*), robust cones to smash large bony prey like turtles (*Prognathodon currii*), low and blunt teeth to crush variable hard-shelled prey such as mollusks, crustaceans and echinoids (*Carinodens belgicus* and *Carinodens minalmamar*, *Globidens phosphaticus* and *Globidens simplex*) and, finally, totally unique morphologies (*Xenodens calminechari*, *Stelladens mysteriosus*) whose ecological function remain mysterious: this plethora of tooth shapes exhibited by the faunas of the upper Maastrichtian Phosphates of Morocco highlight the great plasticity of mosasaurid teeth in general.

This extreme diversity and disparity indicate that mosasaurids were still markedly diversified in the late Maastrichtian of Morocco, just prior to the K/Pg biological crisis. The intense upwelling system that developed in this Phosphate Sea at this time is probably responsible for this high biodiversity and, more specifically, for the unusual abundance of large coeval predators in the region. However, upwelling ecosystems (at least the current ones) are structured on the wasp-waist food web model, making them particularly fragile to environmental changes. It is thus possible that this upwelling system became a double-edged sword when disruptive abiotic events (whatever they are) occurred at the end of the Cretaceous, leading to the mass extinction of the K/Pg boundary.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d17020114/s1, SuppInfo 2DFourier File: tooth crown outlines of the 11 mosasaurid species studied, in basal and lingual views for Fourier analyses; SuppInfo HD3DGM File: 3D models of tooth crowns of the 8 mosasaurid species studied, the fixed landmark coordinates for each specimen, the 3D template for the automated patching procedure, R scripts, specimen metadata.

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Data Availability Statement: All data are available in the main body of the paper and on the appendices and Supplementary Files.

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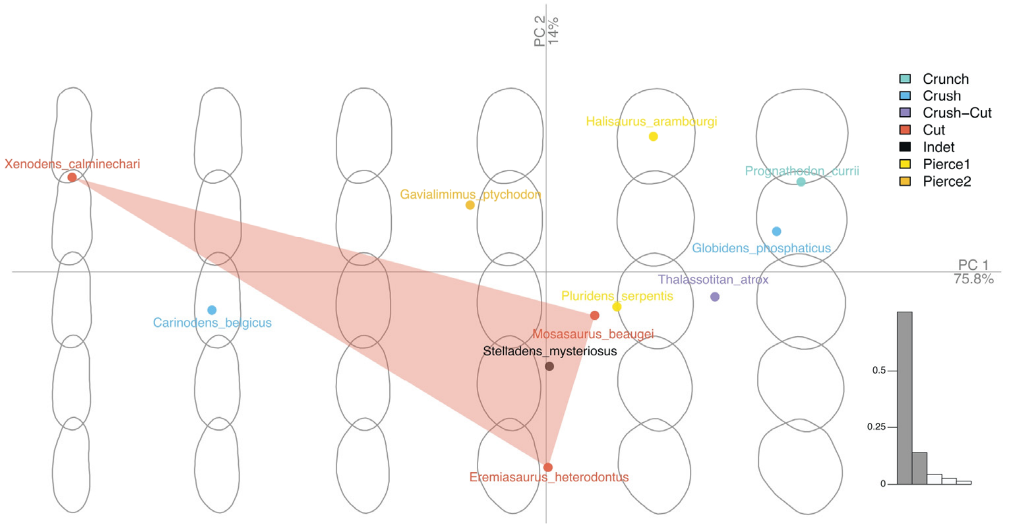
Conflicts of Interest: The authors declare no conflicts of interest.

Appendix A

A **Basal Fourier morphospace, Massare guilds**



B **Basal Fourier morphospace, Fischer et al. guilds**

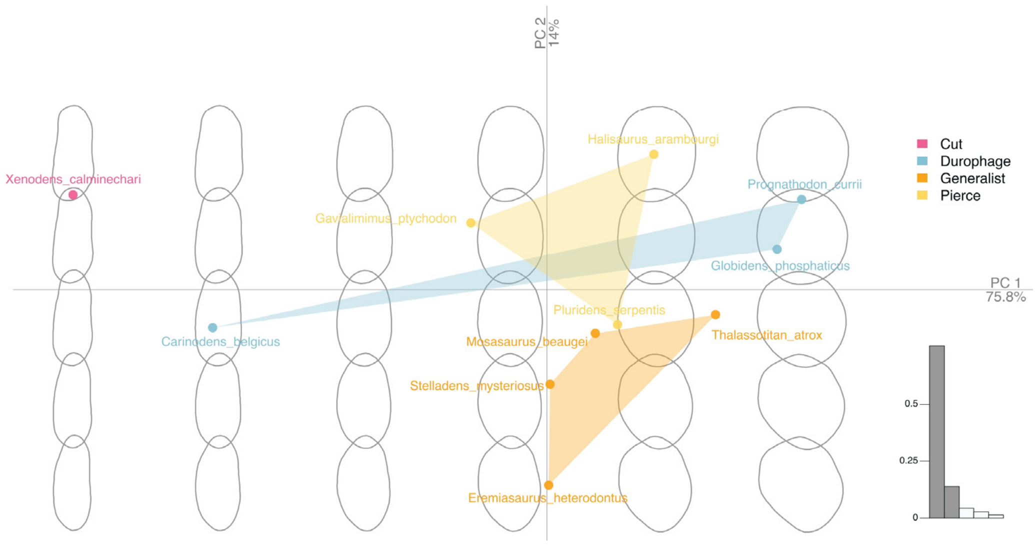
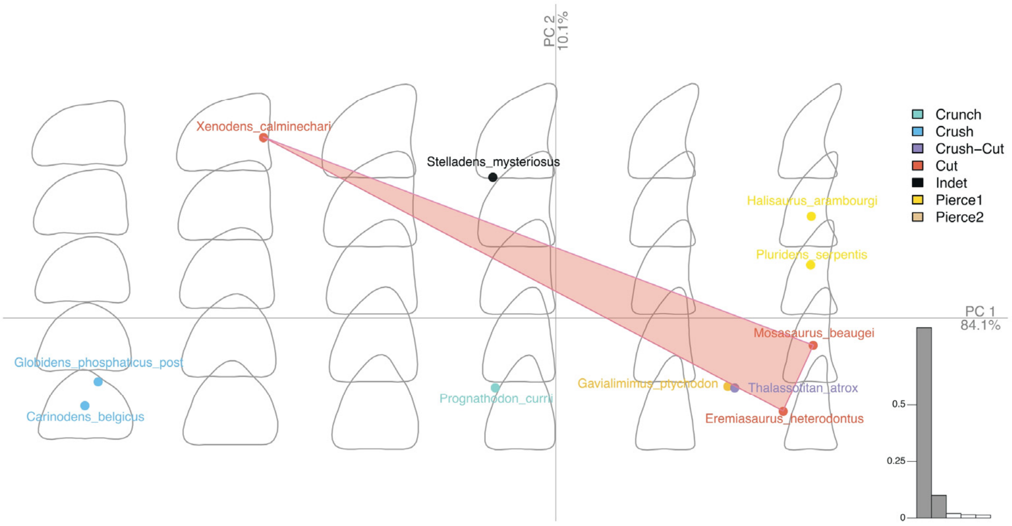


Figure A1. Mosasauridae from the upper Maastrichtian Phosphates of Morocco: PCA basal. Using Massare guilds [38] and Fischer and collaborators guilds [36] for comparisons.

A **Labiolingual Fourier morphospace, Massare guilds**



B **Labiolingual Fourier morphospace, Fischer et al. guilds**

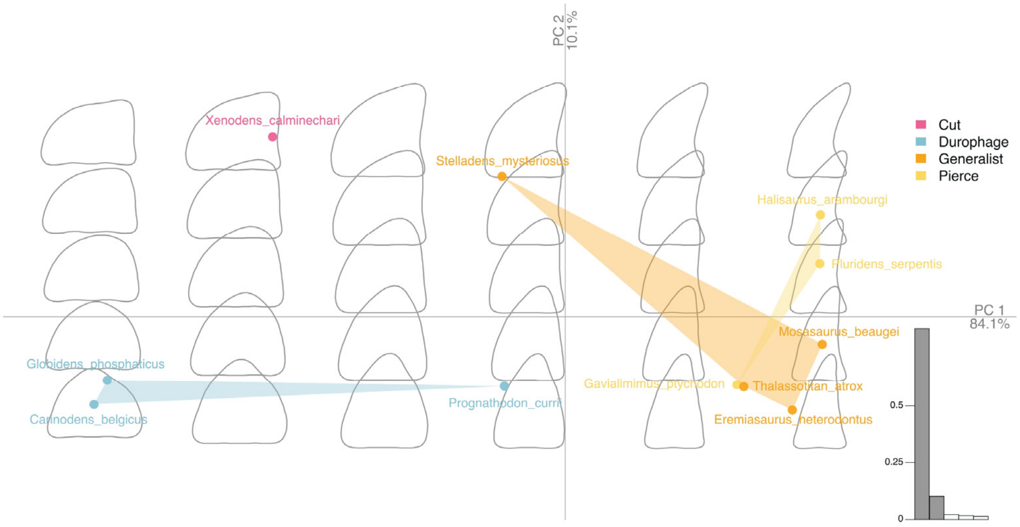


Figure A2. Mosasauridae from the upper Maastrichtian Phosphates of Morocco: PCA labial. Using Massare guilds [38] and Fischer and collaborators guilds [36] for comparisons.

Table A1. Mosasauridae from the upper Maastrichtian Phosphates of Morocco: list of species and main information concerned. Systematic abbreviations: Mosa, Mosasaurinae; Hali, Halisaurinae; Plio, Plioplatecarpinae; Tylo, Tylosaurinae. Stratigraphical abbreviations: C, *Couche* (layer in French). Collection number abbreviations: (h), holotype; (p), paratype; (r), referred specimen, (s), syntype. Institutional abbreviations: MHNM, Muséum d'Histoire Naturelle de Marrakech, Université Cadi Ayyad, Marrakech, Morocco; MNHN, Muséum National d'Histoire Naturelle, Paris, France; OCP, Office Chérifien des Phosphates, Khouribga, Morocco; UALVP, University of Alberta Laboratory for Vertebrate Paleontology, Edmonton, Alberta, Canada; ULg, Université de Liège, Belgium; VANPS, Paleontological Museum of the Vancouver Paleontological Society, Richmond, British Columbia, Canada.

CLADE		TAXON	GEOGRAPHY	STRATIGRAPHY	SPECIMENS	REFERENCES
MOSA	**Mosasaurini**	*Mosasaurus beaugei* Arambourg, 1952	Sidi Daoui, Oulad Abdoun; Ben Guerir, Ganntour	Upper CIII, C2, upper Maastrichtian	MNHN PMC 7 (h), 8–13, 55, 60 (r); OCP DEK/GE 83, 303, 551, 660 (r)	Arambourg, 1952 [4]; Bardet et al., 2004 [18]; Cappetta et al., 2014 [22]
		Carinodens belgicus (Woodward, 1891)	Sidi Daoui, Sidi Chennane, Oulad Abdoun; Ben Guerir, Ganntour	CIII, C3, upper Maastrichtian	OCP DEK/GE 445–447, 454–455 (r); MNHN casts 6314, 6338, 6340–6342	Bardet et al., 2008 [21]; Schulp et al., 2009 [33]; Cappetta et al., 2014 [22]
		Carinodens minalmamar Schulp, Bardet & Bouya, 2009	?Sidi Chennane, Oued Meskoura, Oulad Aboun	CIII, upper Maastrichtian	OCP DEK/GE 453 (h); MNHN PMC 29 (r)	Arambourg, 1952 [4]; Schulp et al., 2009 [33]
		Xenodens calminechari Longrich et al., 2021a	Sidi Chennane, Oulad Abdoun	Upper CIII, upper Maastrichtian	MHNM.KH.333 (h)	Longrich et al., 2021a [25]
	Prognathodontini	*Eremiasaurus heterodontus* LeBlanc, Caldwell & Bardet, 2012	Sidi Daoui, Oulad Abdoun; Ben Guerir, Ganntour	Upper CIII, C6-C2, lower to upper Maastrichtian	UALVP 51744 + OCP DEK/GE 112 (s); OCP DEK/GE 663, inedites (r); MNHN PMC41, 42, 45, 48, 50 (r)	Arambourg, 1952 [4]; LeBlanc et al., 2012 [23]; Cappetta et al., 2014 [22]
		Thalassotitan atrox Longrich et al., 2022	Sidi Daoui, Meraa Lahrach, Sidi Chennane, Oulad Abdoun; Ben Guerir, Ganntour; Meskala	Upper CIII, C4-C2, upper Maastrichtian	MNHM.KHG.231 + OCP DEK/GE 417 (s); OCP DEK/GE 10, 90, 98, 109, 497, 665 (r); MHNM.KHB.324-326, 330, 396, 1047, 1051, 1253 (r); MNHN PMC 43, 44, 46, 47, 49, 51 (r)	Arambourg, 1952 [4]; Cappetta et al., 2014 [22]; Longrich et al., 2022 [27]
		Prognathodon currii Christiansen & Bonde, 2002	Ben Guerir, Ganntour	C6-C2, lower to upper Maastrichtian	OCP.DEK/GE 349, 350, 5 inedite teeth (r)	Bardet et al., 2005b [20]; Cappetta et al., 2014 [22]
	Globidensini	*Globidens phosphaticus* Bardet & Pereda-Suberbiola, 2005b	Ben Guerir, Ganntour	C3 (h, p), C6-C2, lower to upper Maastrichtian	OCP.DEK/GE 361 (h), 338–343 (p), 346–348 (r), inedites; MNHN PMC 17–19 (r)	Arambourg, 1952 [4]; Bardet et al., 2005b [20]; Cappetta et al., 2014 [22]
		Globidens simplex LeBlanc, Mohn & Caldwell, 2019	Unknown locality, ?Oulad Abdoun	? Upper CIII, upper Maastrichtian	MHNM.KHG.221 (ex UALVPPPP 51746) (h)	LeBlanc et al., 2019 [24]
	Incertae sedis	*Stelladens mysteriosus* Longrich et al., 2023	Sidi Chennane, Oulad Abdoun	Lower CIII, upper Maastrichtian	MHNM.KHG.1436 (h)	Longrich et al., 2023 [28]

Table A1. *Cont.*

CLADE		TAXON	GEOGRAPHY	STRATIGRAPHY	SPECIMENS	REFERENCES
HALI	**Halisaurini**	*Halisaurus arambourgi* Bardet & Pereda-Suberbiola, 2005a	Sidi Daoui, Oulad Abdoun; Ben Guerir, Ganntour	Upper CIII, C6-C2, lower to upper Maastrichtian	MNHN PMC 14 (h), PMC 15–16, OCP DEK/GE 100–103, etc. (r)	Bardet et al., 2005a [19]; Cappetta et al., 2014 [22]
	Pluridensini	*Pluridens serpentis* Longrich et al., 2021b	Sidi Daoui, Oulad Abdoun; Ben Guerir, Ganntour	Upper CIII, C6-C2, lower to upper Maastrichtian	OCP DEK/GE 548 + MHNM.KH.262 (s); OCP DEK/GE 662, MHNM.KH.386-395 (r)	Bardet et al. 2005a [19]; Cappetta et al., 2014 [22]; Longrich et al., 2021b [26]
PLIO	**Selmasaurini**	*Gavialimimus ptychodon* (Arambourg, 1952)	Sidi Daoui, Oulad Abdoun; Ben Guerir, Youssoufia, Ganntour	Upper CIII, C6-C2, lower to upper Maastrichtian	MNHN PMC 30 (h) + MHNM.KHG.1231 (h?) + MNHN PMC 31–34, 53 (r); OCP DEK/GE 304, 356, 476, 560, 661, inedites (r)	Arambourg, 1952 [4]; Cappetta et al., 2014 [22]; Bardet et al., 2015, 2017 [3,5]; Strong et al., 2020 [32]
		Khinjaria acuta Longrich et al., 2024	Sidi Chennane, Oulad Abdoun	Lower CIII, upper Maastrichtian	MHNM.KHG.521 (h)	Longrich et al., 2024 [29]
TYLO		*Hainosaurus boubker* Rempert, Martens & Melchers, 2022	Sidi Chennane, Oulad Abdoun	Upper CIII, upper Maastrichtian	VANPS 13.0120 + 13.0121 (s), 13.0122-165 (r)	Rempert et al., 2022 [31]

Table A2. Mosasauridae from the Maastrichtian Phosphates of Morocco: comparative anatomy data. Measurement and ratio definitions provided in text. Abbreviations: L, skull length; Orb, orbit length; PreO, preorbital length; PostO, postorbital length; W, skull width.

CLADE		TAXON	TEETH			SKULL							SIZE
			H/L	W/L	SPECIMENS	L	W	W/L	PreO/L	PostO/L	Orb/L	SPECIMENS	
MOSA	**Mosasaurini**	*Mosasaurus beaugei*	1.8–1.9	0.6–0.7	MNHN PMC 8, 55, 60	80–110 cm	25–28 cm	0.28	0.55	0.25	0.17	OCP DEK/GE 83, 551	8–10 m
		Carinodens belgicus	0.5	0.55	OCP DEK/GE 447, 454	<40 cm	?	?	?	?	?	OCP DEK/GE 454	2.5–3 m
		Carinodens minalmamar	0.4	0.4	MNHN PMC 29	?	35 cm	?	?	?	?	OCP DEK/GE 453	2.5 m
		Xenodens calminechari	1	0.4	MHNM.KHG.333	30 cm	?	?	?	?	?	MHNM.KHG.333	2 m
	Prognathodontini	*Eremiasaurus heterodontus*	1.8–1.93	0.8–0.85	OCP DEK/GE 663, inedites	65–70 cm	17 cm	0.24	0.49	0.3	0.19	OCP DEK/GE 112; UALVP 51744	4.5–6 m
		Thalassotitan atrox	1.5–1.83	0.82–0.9	OCP DEK/G 665, inedites	120–130 cm	45–55 cm	0.38	0.5	0.32	0.18	MHNM.KHB.231; OCP DEK/GE 497, 109, 417, 10 (pt)	9–10 m
		Prognathodon currii	1.3	0.77	OCP DEK/GE 349	140 cm	49 cm (est)	0.4	0.48	0.32	0.14	HUJ.OR 100 (Negev)	>=10 m

Table A2. *Cont.*

CLADE		TAXON	TEETH			SKULL							SIZE
			H/L	W/L	SPECIMENS	L	W	W/L	PreO/L	PostO/L	Orb/L	SPECIMENS	
	Globidensini	*Globidens phosphaticus*	1 (ante)-0.69 (post)	0.83 (ante)-0.65 (middle)	OCP DEK/GE 361, 343, 346, 492, inedites	75–80 cm	?	0.55 (est)	0.31 (est)	0.17 (est)	?	OCP DEK/GE 492, inedite; PA 24 (Angola)	5–6 m
		Globidens simplex	0.65–0.77	0.73–0.82	MHNM.KHB.221 (figs. E-F and G-H)	75–80 cm	?	0.46 (est)	0.36 (est)	0.16 (est)	?	MHNM.KHB.221	5–6 m
	Incertae sedis	*Stelladens mysteriosus*	1.33–1.44	0.73–0.8	MHNM.KHB.1436	?	80 cm	?	?	?	?	MHNM.KHB.1436	5 m
HALI	**Halisaurini**	*Halisaurus arambourgi*	2	0.77–0.85	MNHN PMC 14, 15	35 cm	10 cm	0.29	0.53	0.28	0.18	MNHN PMC 14, 15	3–4 m
	Pluridensini	*Pluridens serpentis*	1.87–2.1	0.7–0.9	OCP DEK/GE 662; MHNM.KHB.389, 394	70–90 cm	20–25 cm	0.3	0.48	0.35	0.12	OCP DEK/GE 548, MHNM.KHB.262	5–6 m
PLIO	**Selmasaurini**	*Gavialimimus ptychodon*	1.44–1.8	0.62–0.85	MNHN PMC 30, 31, OCP DEK/GE 661	90 cm	22 cm	0.25	0.62	0.27	0.13	MHNM.KHG.1231, OCP DEK/GE 560	6 m
		Khinjaria acuta	?	1.8	MHNM.KHG.521	90 cm	?	0.39 (est)	0.5 (est)	?	?	MHNM.KHG.521	8 m
TYLO		*Hainosaurus boubker*	1.62	0.71–0.72	VANPS 13.0133-13.0147, OCP DEK/GE inedite	?	120 cm	?	?	?	?	VANPS 13.0120-13.022	8–12 m

Table A3. Mosasauridae from the Maastrichtian Phosphates of Morocco: morphometric analysis data. Species and specimens used and their digitalization procedures. Abbreviations: NA, non-available.

CLADE		TAXON	FILE_ID	SPECIMENS	SOURCE	REGION
MOSA	**Mosasaurini**	*Mosasaurus beaugei*	Mosasaurus_beaugei	MNHN - Collection Bardet	This paper, laser, 0.2 mm precision	NA
		Carinodens belgicus	Carinodens_belgicus	MNHN - Cast 6341	Fischer et al., 2022 [36]	NA, Mirrored
		Xenodens calminechari	Xenodens_calminechari	MHNM.KHB.333	Longrich et al., 2021a, Fig. 5 [25]	Maxilla
	Prognathodontini	*Eremiasaurus heterodontus*	Eremiasaurus_heterodontus	Sparla collection, #2	Photogrammetry	NA
		Thalassotitan atrox	Thalassotitan_atrox	OCP DEK-GE 665	This paper, laser, 0.2 mm precision	NA, Mirrored
		Prognathodon currii	Prognathodon_currii	ULg PA20220209-1	Fischer et al., 2022 [36]	NA, sediment removed
	Globidensini	*Globidens phosphaticus*	Globidens_phosphaticus_post	MNHN - Collection Bardet	This paper, laser, 0.2 mm precision	NA, posterior tooth
	Incertae sedis	*Stelladens mysteriosus*	Stelladens_mysteriosus	MHNM.KHG.1436	Longrich et al., 2023, Fig. 4 [28]	NA
HALI	**Halisaurini**	*Halisaurusarambourgi*	Halisaurus_arambourgi	OCP DEK/GE inedite	This paper, caliper measurement	NA
	Pluridensini	*Pluridens serpentisi*	Pluridens_serpentis	OCP DEK-GE 662	This paper, laser, 0.2 mm precision	NA
PLIO	**Selmasaurini**	*Gavialimimus ptychodon*	Gavialimimus_ptychodon	OCP DEK-GE 661	This paper, laser, 0.2 mm precision	NA, Mirrored

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