

A bizarre new plioplatecarpine mosasaurid from the Maastrichtian of Morocco

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ABSTRACT

The Upper Maastrichtian of Morocco has produced a remarkably diverse fauna of mosasaurids, the most diverse known for any time or place. As apex predators, Mosasauridae provide a picture of the marine ecosystem just before the end-Cretaceous mass extinction. Here we describe a bizarre new plioplatecarpine mosasaurid, *Khinjaria acuta*, characterized by enlarged, dagger-like anterior teeth, short, robust jaws, and posterior elongation of the skull. *Khinjaria* is related to *Goronyosaurus nigeriensis* from Nigeria and Niger, and *Gavialimimus almaghribensis* from Morocco. These species form a distinct clade of specialized mosasaurids so far unknown outside of Africa. Mosasaurids show high endemism in the Maastrichtian, with different lineages occurring in different regions, implying that mosasaurid diversity is underestimated because of limited geographic sampling. The large size, robust jaws, akinetic skull, and bladelike teeth of *Khinjaria* suggest it was an apex predator, but the unusual skull and jaw differ from those of contemporary predators like *Hainosaurus*, *Thalassotitan*, and *Mosasaurus*, suggesting a distinct feeding strategy. Mosasaurids became increasingly specialized in the latest Cretaceous, repeatedly evolving to occupy the apex predator niche, suggesting a diverse marine ecosystem persisted up to the K/Pg boundary. Late Cretaceous marine ecosystems differ from modern marine ecosystems in the high diversity of large predators.

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1. Introduction

Following the extinction of ichthyosaurs and the last of the giant pliosauroids in the mid-Cretaceous (Fischer et al., 2016; Zverkov and Pervushov, 2020), the Late Cretaceous marine ecosystem saw a major radiation of mosasaurids (Polcyn et al., 2014). Mosasaurids were giant marine squamates, with specialized flipper-like limbs and tails (DeBraga and Carroll, 1993) allowing them to exploit the open ocean and the deep sea (Rothschild and Martin, 1987; Schulp et al., 2013). Near the end of the Cretaceous, mosasaurids became increasingly diverse and specialized (Schulp et al., 2009; Bardet et al., 2014; Strong et al., 2020; Longrich et al., 2021a; Longrich et al., 2021b; Longrich et al., 2022), culminating in the highly

diverse mosasaurid fauna of the late Maastrichtian (Bardet et al., 2015).

Mosasaurid diversity appears to peak just before the end-Cretaceous mass extinction, in the Maastrichtian (Polcyn et al., 2014; Bardet et al., 2015; Longrich et al., 2022). Mosasaurids are especially diverse in Africa, with the most diverse known fauna coming from Morocco. Here, more than a dozen species are currently known. Four major groups are known, the Mosasaurinae (Bardet et al., 2004; Bardet et al., 2005a; Schulp et al., 2009; LeBlanc et al., 2012; Longrich et al., 2021b; Longrich et al., 2022), Halisaurinae (Bardet et al., 2005b; Longrich et al., 2021a), Tylosaurinae (Rempert et al., 2022), and Plioplatecarpinae (Arambourg, 1952; Bardet et al., 2015; Strong et al., 2020); Pachyvaranidae (Houssaye et al., 2011) also occur.

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Plioplatecarpines have previously been reported from the Phosphates of Morocco based on isolated teeth and vertebrae, originally named *Platecarpus ptychodon* by Arambourg (Bardet et al., 2015) and recently renamed *Gavialimimus almaghribensis* (Strong et al., 2020). *Gavialimimus* represents a highly specialized, longirostrine species. Here, we report a distinct but closely related plioplatecarpine, characterized by a bizarre skull morphology. The new species has short, robust jaws, dagger-like teeth, and an elongated posterior region of the skull. It is closely related to *Goronyosaurus nigeriensis* from Niger and Nigeria (Lingham-Soliar, 1988), and more distantly related to *Gavialimimus almaghribensis* (Strong et al., 2020) and *Selmasaurus* spp. from North America (Wright and Shannon, 1988; Polcyn and Everhart, 2008). These species, along with *Plioplatecarpus* from the Maastrichtian of Europe (Lingham-Soliar, 1994), show that Plioplatecarpinae staged a radiation in the latest Cretaceous alongside the radiation of Mosasaurinae (Polcyn et al., 2014; Bardet et al., 2015) and Halisaurinae (Longrich et al., 2021a).

The new species also emphasizes the distinct nature of low-latitude mosasaurid assemblages and the mosasaurids of Africa, suggesting that increased diversity was accompanied by increased endemism. Finally, it shows the remarkable diversity of the mosasaurids at the end of the Cretaceous. In particular, they repeatedly evolved to occupy the top predator niche, although different lineages did so in very different ways.

Institutional abbreviations

MHNM, Muséum d'Histoire Naturelle de Marrakech, Marrakech, Morocco.

2. Geological setting

MHNM.KHG.521, the holotype and only known specimen of *Khinjaria acuta*, comes from the Phosphates of Sidi Chennane, in the Oulad Abdoun Basin Khouribga Province, Morocco (Fig. 1). The Phosphates consist of phosphatic sands, marls, and limestones, which were laid down in an embayment on the eastern edge of the Atlantic near the end of the Late Cretaceous and the early Paleogene (Yans et al., 2014). They are divided into a series of beds which are, from bottom to top, Couche III, Couche II, Couche I, Couche 0, and Sillons A and B (Arambourg, 1952; Kocsis et al., 2014; Yans et al., 2014). Couche III is Maastrichtian in age, with the transition between Couche III and Couche II marking the Cretaceous-Paleogene transition. MHNM.KHG.521 comes from the lower part of Couche III.

Couche III consists of about 5 m of sediments (Fig. 2). Sediments are condensed, and so may span a significant range of time. Upper Couche III spans the final million years or so before the K-Pg boundary (Yans et al., 2014), and so is latest Maastrichtian in age. The age of the lower part of Couche III is less well-constrained. Selachian teeth from lower Couche III suggest a late Maastrichtian age (Cappetta, 1987) but preliminary study of the fauna suggests turnover of mosasaurids between lower Couche III and upper Couche III; many if not all mosasaurid species in lower Couche III are distinct from those in upper Couche III. However, if mosasaurids evolved rapidly, as in marine invertebrates such as ammonites (Witts et al., 2015) and terrestrial vertebrates such as dinosaurs (Mallon et al., 2012), as little as one or two million years could account for the faunal differences. Accordingly, lower Couche III might tentatively be considered late, but not latest Maastrichtian, in agreement with the selachian fossils.

The phosphates contain an extraordinary diversity of Cretaceous and Paleogene vertebrates. The Cretaceous fauna is dominated by selachian teeth (Arambourg, 1952; Cappetta, 1987;

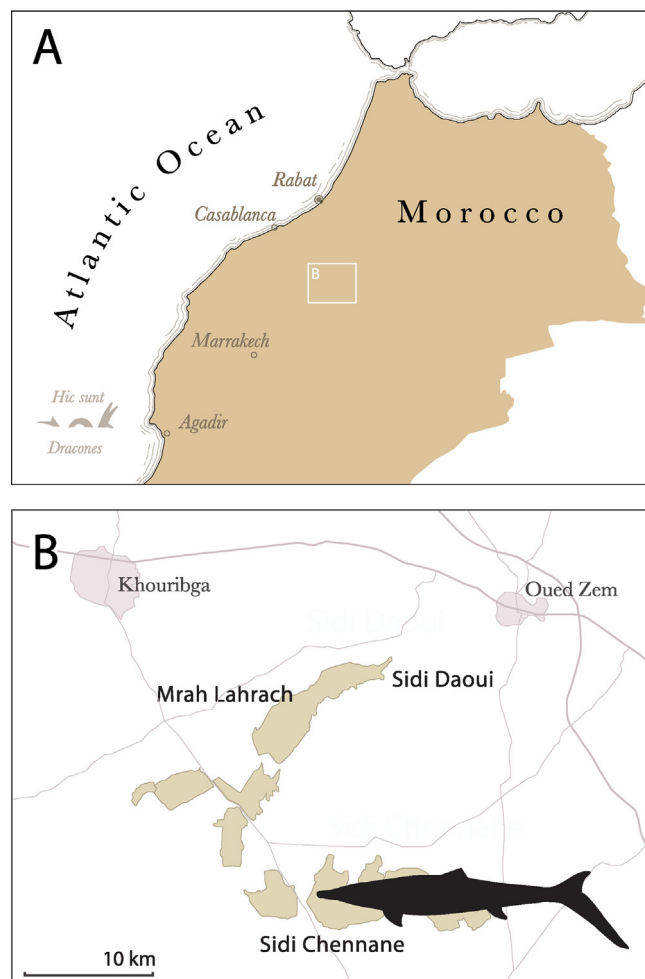


Fig. 1. Map of the central part of Morocco showing A, location of the phosphate mines of the Oulad Abdoun Basin, B, the Sidi Chennane phosphate mines, southern Oulad Abdoun Basin, that produced *Khinjaria acuta*.

Noubhani and Cappetta, 1997; Cappetta et al., 2014) and osteichthyan remains (Arambourg, 1952; Vullo et al., 2017), but marine reptiles are abundant and diverse (Bardet et al., 2017). Elasmosaurid plesiosaurs (Vincent et al., 2011; Vincent et al., 2013) and chelonoid turtles (Bardet et al., 2013; Lapparent de Broin et al., 2013) are common, as well as small pachyvaranid squamates (Houssaye et al., 2011), and rare crocodylians (Jouve et al., 2008). However, far and away the most common and diverse reptiles are mosasaurids, known by more than a dozen species (Bardet et al., 2004; Bardet et al., 2005a; Bardet et al., 2005b; Schulp et al., 2009; LeBlanc et al., 2012; Bardet et al., 2015; Strong et al., 2020; Longrich et al., 2021a; Longrich et al., 2021b; Longrich et al., 2022; Rempert et al., 2022; Longrich et al., 2023). Pterosaurs also occur (Pereda-Suberbiola et al., 2003; Longrich et al., 2018), as well as rare dinosaurs (Pereda-Suberbiola et al., 2004; Longrich et al., 2017; Longrich et al., 2021c).

In upper Couche III, mosasaurids are represented by isolated teeth (Arambourg, 1952), isolated bones, disarticulated skulls and skeletons, and often articulated remains. These are preserved in coarse-grained phosphatic sands and as part of dense bonebeds that extend tens of kilometers in all directions. In lower Couche III, isolated remains are rare, but associated and articulated specimens are common. Fossils occur in finer-grained sediments, and as a result, show more compaction.

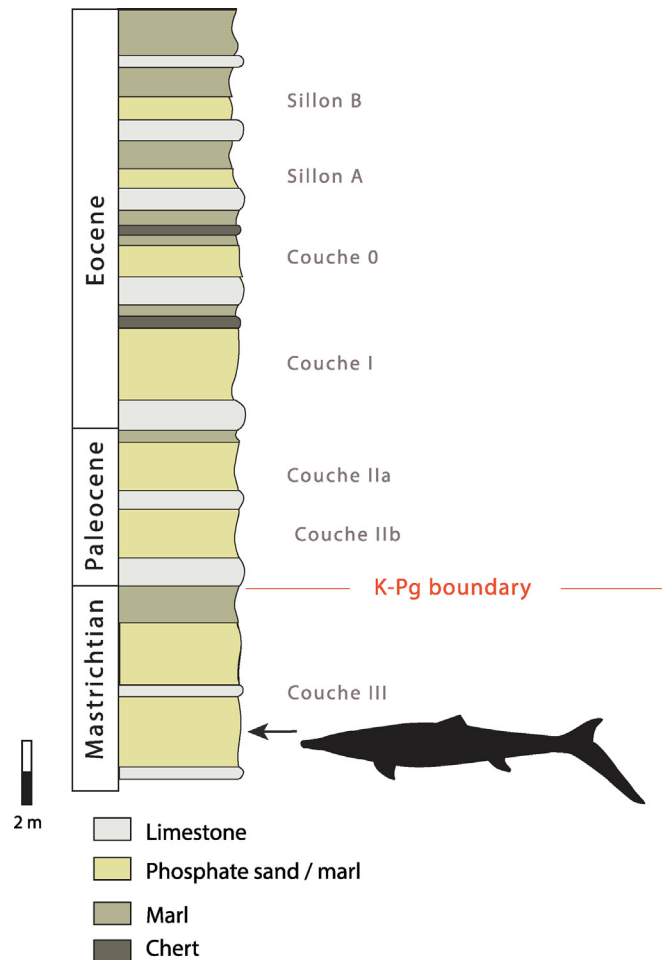


Fig. 2. Synthetical stratigraphical column of the Upper Cretaceous – Palaeogene Phosphate series of the Oulad Abdoun Basin of Morocco, showing the stratigraphic position of *Khinjaria acuta* in lower Couche III. After Kocsis et al. (Kocsis et al., 2014).

3. Systematic paleontology

Squamata Oppel, 1811

Mososauridae Gervais, 1852

Plioplatecarpinae Williston, 1897

Selmasaurini, new taxon. Selmasaurini is defined as the clade comprising *Selmasaurus russelli* and all taxa closer to it than *Plioplatecarpus marshi* or *Platecarpus tympaniticus*.

Khinjaria acuta gen. et sp. nov.

LSID urn:lsid:zoobank.org:pub:0DE2932B-2C65-4416-8DAC-403DAAC431A5

Etymology. From the Arabic *Khinjar* = dagger, and Latin *acuta* = sharp, in reference to tooth morphology.

Holotype. MHN.M.KHG.521, partial skull including part of the premaxilla, maxillae, prefrontals, frontal, parietal, right post-orbitofrontal, partial right squamosal, quadrate, right dentary, associated trunk(?) vertebra.

Locality and stratigraphy. Lower Couche III, upper Maastrichtian, Sidi Chennane, Oulad Abdoun Basin of Khouribga Province, Morocco (Figs. 1–2).

Diagnosis. Plioplatecarpine mososaurid characterized by the following character combination: skull with a short rostrum, elongate temporal region, reduced orbits; deep, subrectangular maxilla with deep and short narial emargination and upturned

jugal process; dentary robust and deep anteriorly, with a prominent, ventrally projecting symphysis; maxilla and dentary bearing long grooves for opposing teeth; frontal triangular, very short and broad, with a staircase-shaped suture for prefrontals; strongly interlocking W-shaped contact of the frontal and parietal with two long and thin processes on either side of the parietal; parietal extremely elongated, without parietal table and with a slit-like parietal foramen; large and elongate supratemporal fenestrae, with supratemporal fossae expanding anteriorly onto the frontals; heterodont dentition with very large anterior teeth and small posterior ones; anterior teeth extremely elongate and knife-like, with labiolingually compressed crowns, smooth enamel, and prominent, convex anterior and posterior carinae lacking serrations.

Description

General preservation (Figs. 3–7). The holotype includes an incomplete skull, dentary, and an associated vertebra. Bones are well-preserved overall but with cracks and distortion caused by compaction of the matrix. The skull is partially disarticulated, with the right maxilla and dentary displaced to the left side of the skull and the left maxilla displaced away from the skull. The reconstruction (Fig. 8) suggests a skull with a proportionally short and powerfully constructed rostrum, and a long postorbital region.

Maxilla (Figs. 3, 4). The maxilla bears 10 or 11 teeth. The maxilla is short and deep, as in *Selmasaurus johnsoni* (Polcyn and Everhart, 2008), and unlike the more elongate maxilla of *Goronyosaurus nigeriensis* (Azzaroli et al., 1972; Azzaroli et al., 1975; Lingham-Soliar, 1988, 1991), *Plioplatecarpus* spp. (Lingham-Soliar, 1994) and *Platecarpus* (Konishi et al., 2012), or the low, hyper-elongate maxilla of *Gavialimimus* (Strong et al., 2020). In lateral view, the anterior maxilla forms a tall, rectangular blade with a convex dorsal margin where it contacts the premaxilla.

Dorsally, the narial emargination is deep and short, similar to *Goronyosaurus* (Lingham-Soliar, 1988). The narial emargination is shallower in *Gavialimimus* (Strong et al., 2020) and *Selmasaurus johnsoni* (Polcyn and Everhart, 2008), but is deep in some other plioplatecarpines including *Platecarpus tympaniticus* (Konishi et al., 2012). The prefrontal process is tall and triangular; it would have broadly contacted the prefrontal dorsally and hooked over it posteriorly.

There is an elongate, strongly curved jugal ramus which would have extended back beneath the orbit, similar to *Goronyosaurus* (Lingham-Soliar, 1988). The jugal process is short in *Gavialimimus* (Strong et al., 2020), *Selmasaurus*, and *Platecarpus*. This suborbital process hooks upwards posteriorly; that of *Goronyosaurus* is straighter.

The maxilla's lateral surface bears a series of long, deep grooves, perpendicular to the tooth row, to accommodate the teeth of the lower jaw when the jaws closed. Similar occlusal pits occur on *Goronyosaurus* (Lingham-Soliar, 1988) but are not as tall. *Gavialimimus* (Strong et al., 2020) has occlusal pits on the maxillae but not grooves. Pits are absent in *Selmasaurus johnsoni* (Polcyn and Everhart, 2008) and other plioplatecarpines, but occlusal pits occur convergently in certain mososaurines, e.g. *Eremiasaurus heterodontus* (LeBlanc et al., 2012). The maxilla's medial surface is slightly concave. It has a straight ventral margin, with lateral and medial parapets equal in height.

Prefrontal (Figs. 3, 5). The prefrontal has a narrow, triangular contribution to the skull roof. The prefrontal contacted the frontal's lateral margin and overlaps it anteriorly, while underlapping it posteriorly. The prefrontal may have contacted the premaxillary process and premaxilla as well, largely excluding the frontal from the naris. A similar condition is present in *Goronyosaurus* (Azzaroli et al., 1972; Azzaroli et al., 1975; Lingham-Soliar, 1988, 1991). The

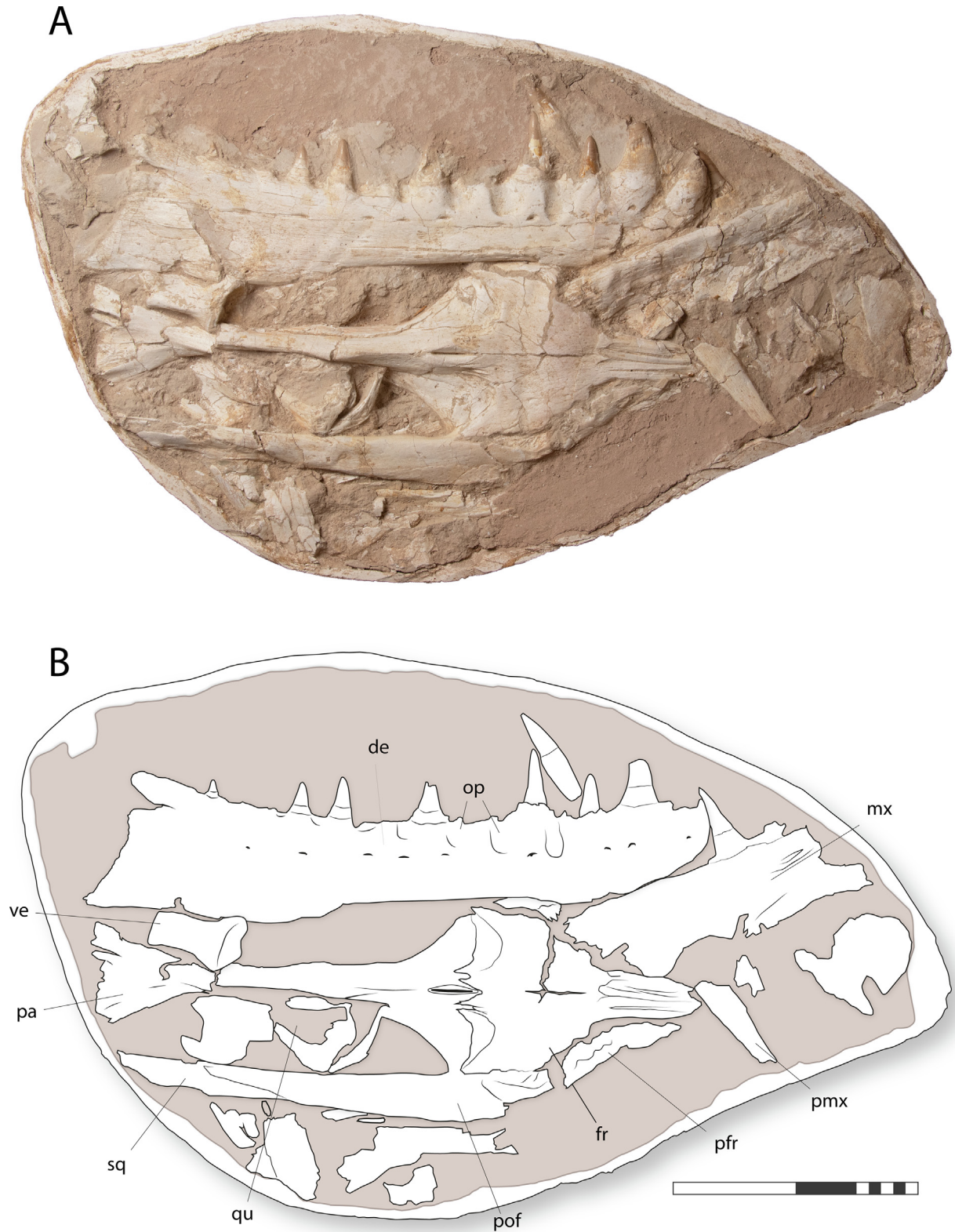


Fig. 3. *Khinjaria acuta*, MHNM.KHG.521, holotype partial skull Sidi Chennane, Oulad Abdoun Basin, Morocco, lower Couche III, upper Maastrichtian. A, skull in jacket; B, line drawing. Abbreviations: de, dentary; fr, frontal; mx, maxilla; op, occlusal pits; pa, parietal; pmx, premaxilla; pof, postorbitofrontal; pfr, prefrontal; qu, quadrate; sq, squamosal; ve, vertebra. Scale = 20 cm.

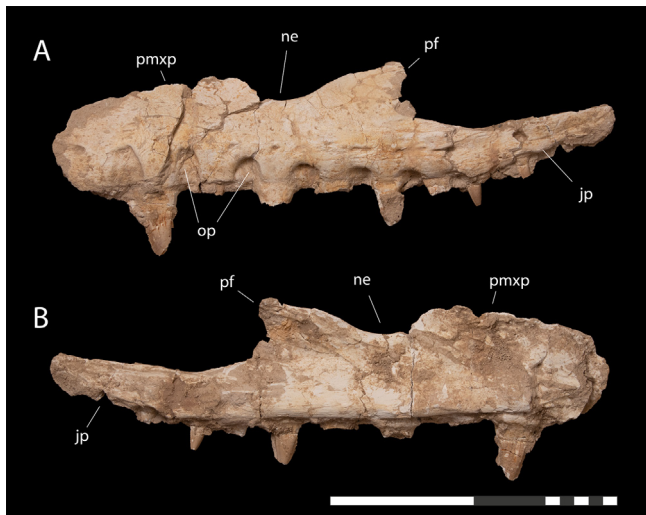


Fig. 4. *Khinjaria acuta*, MHN.M.KHG.521, holotype left maxilla, Sidi Chennane, Oulad Abdoun Basin, Morocco, lower Couche III, upper Maastrichtian in A, lateral and B, medial views. Abbreviations: jp, jugal process; ne, narial emargination; op, opclusal pits; pfp, prefrontal process; pmxp, premaxillary process. Scale = 20 cm.

prefrontal's stepped medial margin would have interlocked with the stepped edge of the frontal, limiting mobility, a condition unique among mosasaurids. Posteriorly the prefrontal contacts the postorbitofrontal, excluding the frontal from the orbit.

Frontal (Figs. 3, 5). The frontal is short, broad and triangular. The width across the postorbitofrontal processes exceeds the length of the main body of the frontals (i.e. midline length excluding the narial process), a more extreme condition than even that of *Goronyosaurus* (Azzaroli et al., 1972; Azzaroli et al., 1975; Lingham-Soliar, 1988) and *Gavialimimus* (Strong et al., 2020), where the main body is about as long as wide (Lingham-Soliar, 1988). The premaxillary process is extremely broad, about 25% the width of the frontal, suggesting a broad frontal-premaxilla suture. The edges of the premaxillary process are straight and subparallel. The dorsal surface of the premaxillary process has three deep, narrow grooves suggesting an interlocking contact with the premaxilla. A similar condition is seen in *Goronyosaurus* and perhaps *Selmasaurus russelli* (Wright and Shannon, 1988) but not *Gavialimimus* (Strong et al., 2020). There is an M-shaped suture where the premaxilla terminated posteriorly; a similar suture occurs in *Goronyosaurus*. The frontal's anterolateral margins bear a series of flanges and notches forming a stepped edge corresponding to the stepped edge of the prefrontal.

The frontal's posterolateral margins are straight and subparallel, as in *Selmasaurus johnsoni* (Polcyn and Everhart, 2008). In *Goronyosaurus* (Lingham-Soliar, 1988), *Gavialimimus* (Strong et al., 2020) and *S. russelli* (Wright and Shannon, 1988), the frontal's posterolateral margins converge anteriorly, giving the bone a triangular shape. The frontal is excluded from the orbit by the prefrontal-postorbitofrontal contact, as in *Goronyosaurus*, *Gavialimimus* and *Selmasaurus*.

The posterodorsal surface of the frontal bears deep fossae on either side, marking the anterior extent of the supratemporal musculature, as in *Goronyosaurus nigeriensis* (Lingham-Soliar, 1988). This condition is approached in *Selmasaurus russelli* (MJP, pers. obs.) where the fossae invade the posterior margin of the frontal by 5 or 6 mm. Extension of the supratemporal musculature onto the frontals is unusual among mosasaurids, but occurs in carnivorous dinosaurs such as tyrannosaurids (Currie, 2003) and dromaeosaurids (Currie, 1995).

Medially, the frontal-parietal suture is W-shaped. A strong midline notch receives the parietal and lateral to this, triangular, spur-like paramedian processes wrap around the pineal foramen. A similar

condition occurs in *Gavialimimus* (Strong et al., 2020), but the spur-like processes are shorter. Notches in the parietal of *Goronyosaurus* (Lingham-Soliar, 1988) suggest it also had interlocking spurs here (Lingham-Soliar, 1991). An interlocking frontal-parietal suture, reducing skull kinesis, also occurs in mosasaurines such as *Plotosaurus*, *Mosasaurus* (LeBlanc et al., 2013) "*Liodon asiaticum*" (Bardet et al., 2021), *Thalassotitan* (Longrich et al., 2022), *Prognathodon saturator* (Schulp, 2006), and *Globidens phosphaticus* (Polcyn et al., 2010).

Postorbitofrontal (Figs. 3, 5). The postorbitofrontal contacts the prefrontal anteriorly, the frontal and parietal medially, and the squamosal posteriorly. It is a long, deep bar of bone that projects posteriorly to form the anterior lateral margin of the supratemporal fenestra. This deep lateral bar is shared with *Goronyosaurus* (Lingham-Soliar, 1988, 1991) and *Gavialimimus* (Strong et al., 2020). Posteriorly the bone tapers and twists so that the surface of the bar slopes ventrolaterally. The postorbitofrontal has a long, oblique contact with the squamosal, with a long, triangular spur of the postorbitofrontal overlapping and inserting in a slot in the squamosal.

Anterolaterally, the postorbitofrontal bears a large shelf that projects to form a short, very wide postorbital process. A similar condition occurs in *Goronyosaurus*. Although the condition in *Goronyosaurus* is debated (Lingham-Soliar, 1988), it has been reconstructed as having extremely broad postorbital process contacting a dorsally broad jugal (Lingham-Soliar, 1991). If so, *Khinjaria* may have shared this condition. Medially, the postorbitofrontal underlaps the frontal and abuts the anterolateral wing of the parietal, making a small contribution to the supra-temporal fenestra.

Parietal (Figs. 3, 5). The parietal is very long and narrow, measuring over twice the midline length of the frontal. No other mosasaurid is known to have such an extreme shape; however, the parietal is broken posteriorly in *Goronyosaurus* (Azzaroli et al., 1972; Lingham-Soliar, 1988, 1991). This elongate parietal increased the area for insertion of jaw adductor muscles and resembles, for example, the very large supratemporal fenestrae of some thalattosuchian crocodyliforms (NB, pers. obs.).

The narrow parietal table is pierced by a slit-like pineal foramen. The parietal foramen is recessed into an ovoid depression, and approaches but does not participate in the frontoparietal suture. *Goronyosaurus* is the only other mosasaurid with a similar parietal morphology. The anterolateral alae originate from the body of the parietal posterior to the pineal depression. The alae project anterolaterally, forming the anteromedial wall of the supra-temporal fenestrae. Behind the pineal depression, the parietal forms a tall, long, and narrow bar of bone. The dorsal surface of the parietal forms a low, narrow ridge where the supratemporal fossae meet along the midline. Posteriorly the ridge splits, and bounds a triangular fossa. Again, reduction of the parietal table and the medial extension of the supratemporal fossae increased the area of origin for the jaw adductor muscles. The posterolateral processes of the parietals are broken distally.

Squamosal (Fig. 3). Only the anterior part of the squamosal is preserved. It is a deep bar of bone that receives the postorbitofrontal dorsally, forming a long, oblique joint in lateral view. The postorbitofrontal lies within the dorsal sulcus of the squamosal and overlaps it almost to its preserved end.

Dentary (Figs. 3, 6). The dentary resembles that of *Goronyosaurus* (Azzaroli et al., 1975; Lingham-Soliar, 1988), but is overall deeper, especially posteriorly. The dentary has 12 tooth positions, as in many other derived plioplatecarpines. The symphyseal region is deep as in *Goronyosaurus*, but the symphysis extends back as far as the third tooth position; in *Goronyosaurus* it only extends to the second tooth. The dentary becomes shallower in the middle of the

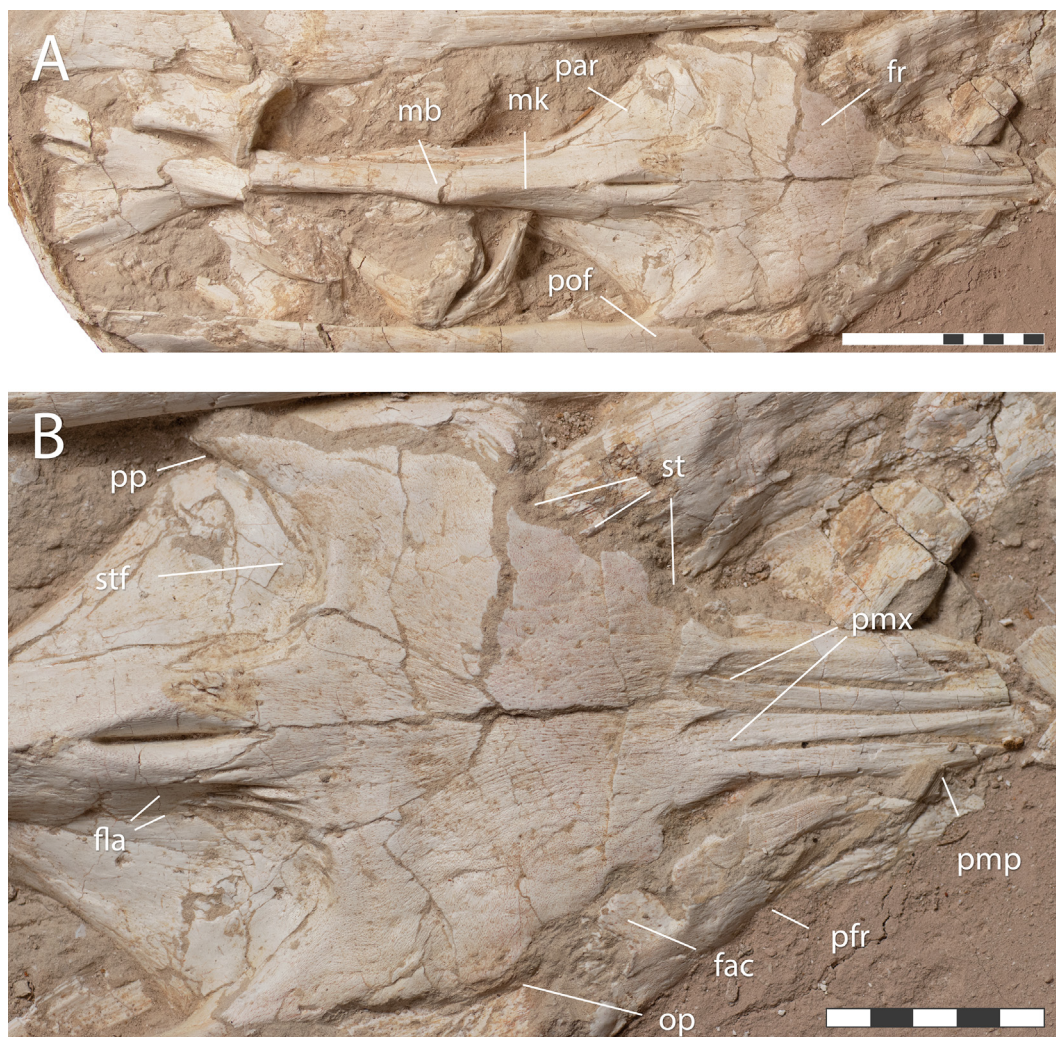


Fig. 5. *Khinjaria acuta*, MHNM.KHG.521, holotype, Sidi Chennane, Oulad Abdoun Basin, Morocco, lower Couche III, upper Maastrichtian. A, frontoparietal complex closeup; B, frontal closeup. Abbreviations: fac, prefrontal articular facet for frontal; fla, interlocking flanges of frontal claspings parietal; fr, frontal; mb, median boss; mk, median keel; op, supraorbital process of frontal; par, parietal; pfr, prefrontal; pmp, frontal premaxillary process; pmx, sutural contact and grooves for premaxilla; pof, postorbitofrontal; pp, postorbital process; st, stepped margin of frontal; stf, supratemporal fossa. Scale = 10 cm (A), 5 cm (B).

jaw, then deeper again posteriorly. This condition is unique in mosasaurids, where the dentary tapers from back to front, but resembles some pliosaurids, where the symphysis is enlarged to accommodate the largest teeth (NB, pers. obs.).

The dentary's posterior edge is broadly concave where it overlapped the surangular, as part of a mobile intramandibular joint, as in other mosasaurids (Russell, 1967). A notch at the posterodorsal margin of the dentary may have accommodated the tip of the



Fig. 6. *Khinjaria acuta*, MHNM.KHG.521, holotype right dentary (in lateral view), closeup, Sidi Chennane, Oulad Abdoun Basin, Morocco, lower Couche III, upper Maastrichtian. Abbreviations: cor, notch for coronoid; imj, intramandibular joint; op, occlusal pit; sym, symphysis. Scale = 10 cm.

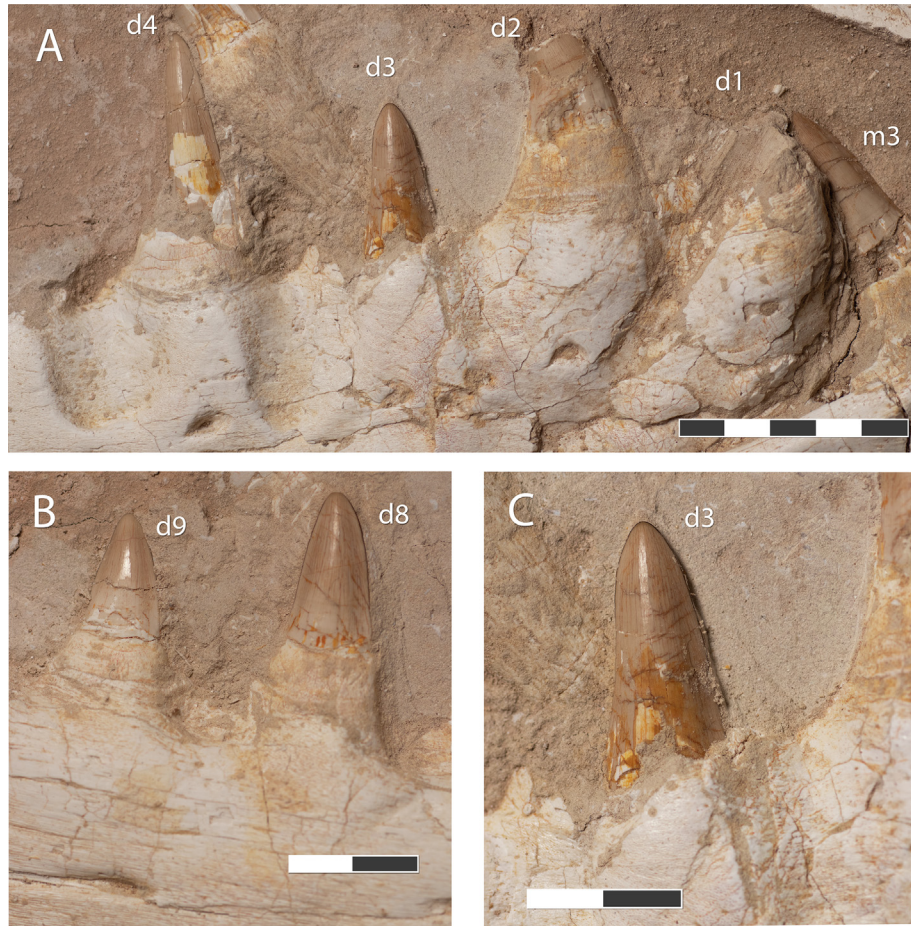


Fig. 7. *Khinjaria acuta*, MHNM.KHG.521, holotype, dentary teeth closeup, Sidi Chennane, Oulad Abdoun Basin, Morocco, lower Couche III, upper Maastrichtian. A, anterior teeth; B, posterior teeth, C, anterior tooth. d1-4,8-9 = dentary teeth 1-4, 8-9, m3, maxillary tooth 3.



Fig. 8. Skull of *Khinjaria acuta*, reconstructed after MHNM.KHG.521 and *Goronyosaurus nigeriensis*. Scale = 20 cm.

coronoid when the jaw was closed. There is no edentulous post-erodorsal process.

The jaw's lateral surface bears a series of broad, deep grooves to accommodate the tips of the premaxillary and maxillary teeth when the jaws closed. Similar grooves occur in *Goronyosaurus*. *Gavialimimus* has pits to accommodate the upper teeth (Strong et al., 2020), but not grooves; *Selmasaurus* (Wright and Shannon, 1988) and other plioplatecarpines lack occlusal pits. As for the maxilla, similar pits occur in the dentary of crocodylians (NB, pers. obs.).

Dentition (Figs. 3, 4, 6, 7). There are 10 or 11 maxillary teeth; *Goronyosaurus* appears to have 11 (Lingham-Soliar, 1991). *Gavialimimus*

has 12 (Strong et al., 2020); *Selmasaurus johnsoni* probably had 11 or 12 (Polcyn and Everhart, 2008); *Plioplatecarpus peckensis* has 11 (Cuthbertson and Holmes, 2015), and *Platecarpus tympaniticus* has 12 (Konishi et al., 2012).

The dentary bears 12 teeth, as in *Goronyosaurus* (Lingham-Soliar, 1991); *Gavialimimus* has 10 (Strong et al., 2020); *Selmasaurus johnsoni* has 11 (Polcyn and Everhart, 2008), *Platecarpus tympaniticus* has 12 (Konishi et al., 2012). Proportionately, teeth are very large, similar to *Selmasaurus johnsoni*, versus the smaller teeth of *Gavialimimus* and most other plioplatecarpines.

An unusual character observed in *Khinjaria* and shared with *Goronyosaurus* (Lingham-Soliar, 2002) is that the anterior teeth are greatly enlarged in the premaxilla, maxilla, and dentary and are about twice the length of the lateral teeth; usually, the largest teeth in mosasaurids lie in the middle of the toothrow (Russell, 1967). Lingham-Soliar (2002) described these teeth as 'caniniform' but they are more bladelike than mammalian canines.

Teeth are large in diameter and have very long crowns anteriorly, and become smaller and shorter towards the back of the jaw, a condition approached by other plioplatecarpines including *Selmasaurus johnsoni* (Wright and Shannon, 1988), *Gavialimimus almaghribensis* (Strong et al., 2020), *Plioplatecarpus houzeaui* (Lingham-Soliar, 1994) and *Platecarpus tympaniticus* (Konishi et al., 2012).

Tooth crowns are straight; they are weakly curved in *Gavialimimus* and *Selmasaurus johnsoni*; and more hooked in *Plioplatecarpus*, e.g. *P. houzeaui* and *Platecarpus tympaniticus*. In contrast to the teeth of most plioplatecarpines, which have conical crowns with sharp

apices (Wright and Shannon, 1988; Lingham-Soliar, 1994; Konishi et al., 2012), the crowns are dagger-like in *Khinjaria*. Crowns are labiolingually compressed with a lenticular cross section; the tips, rather than tapering to a needle point, have convex anterior and posterior carinae. The two prominent carinae form sharp cutting edges, lack serrations. The condition in *Goronyosaurus* is difficult to assess owing to poor preservation but the teeth appear to be slightly compressed, and have convex anterior and posterior carinae on at least some dentary teeth; they may have approached the condition seen in *Khinjaria*.

Tooth surfaces are smooth, with a silky appearance. Most lack facets, ridges, fluting, or sculpturing of the enamel. However, the second maxillary tooth shows subtle ridging labially and strong ridging and fluting lingually, with perhaps 8–10 ridges. This relatively smooth crown stands in contrast to plioplatecarpines in general, which exhibit either well-developed ridges and fluting as in *Gavialimimus* (Strong et al., 2020), *Selmasaurus johnsoni* (Wright and Shannon, 1988), and *Platecarpus tympaniticus* (NL, pers. obs.), or very fine striations as in *Plioplatecarpus* (Lingham-Soliar, 1994). It is unclear whether teeth in *Goronyosaurus* bore ridges, fluting, or other ornament. The smooth enamel and sharp cutting carinae in *Khinjaria* are reminiscent of that of some mosasaurines, for example *Eremiasaurus* (LeBlanc et al., 2012), *Prognathodon kianda* (Schulp et al., 2008) and '*Prognathodon*' *mosasauroides* Gaudry, 1892 (NB, pers. obs.).

Vertebrae (Fig. 3). A single vertebra is preserved between the parietal and dentary. The centrum is long and mediolaterally compressed, but this compression may be due to postmortem compaction of the sediment. Its ventral surface forms a rounded keel, with a low, narrow ridge running along the keel. The cotyle is strongly concave and has low, ovoid shape, but the highly elliptical shape of the cotyle may be exaggerated by distortion. The shape of the centrum suggests it is a trunk vertebra.

4. Phylogenetic analysis

A phylogenetic analysis of Plioplatecarpinae was undertaken, using 23 plioplatecarpine taxa, with *Tethysaurus nopcsai* Bardet et al., 2003 and *Clidastes* spp. as outgroups (Fig. 9), based on a recent analysis of Plioplatecarpinae (Rivera-Sylva et al., 2023). Maximum parsimony analysis was conducted in PAUP* 4.0 b10 (Swofford, 2002), with a branch-and-bound search recovering 3 most parsimonious trees (Fig. 9) of treelength = 152; consistency index = 0.5263; retention index = 0.7551. Two major clades emerge. The first clade, Selmasaurini, contains *Khinjaria*, *Goronyosaurus* and *Gavialimimus*, with *Selmasaurus russelli* and *Selmasaurus johnsoni* as more basally diverging members. These species are characterized by interlocking teeth, retracted nares, a narrow rostrum, and a broad premaxilla contact with the frontal.

The sister-group to Selmasaurini is Plioplatecarpini, comprising *Plioplatecarpus* spp., *Latoplatecarpus*, *Platecarpus tympaniticus*, and *Plesioplatecarpus planifrons*. Plioplatecarpini is defined as all species closer to *Plioplatecarpus marshi* than *Selmasaurus russelli*. The Selmasaurini and Plioplatecarpini form a clade, with *Ecteneosaurus* representing a lineage basal to these two major clades. *Yaguarasaurus* and *Russellosaurus* fall out at the base of the tree, consistent with the hypothesis that they represent basal plioplatecarpines (Polcyn et al., 2023).

Khinjaria acuta is most closely related to and most closely resembles *Goronyosaurus nigeriensis* from the Maastrichtian of Nigeria and Niger (Azzaroli et al., 1972; Azzaroli et al., 1975; Lingham-Soliar, 1988, 1991). The two are united by large, canine-like anterior teeth, strong interlocking of the teeth, occlusal pits developed as deep grooves on the jaws, a deep symphyseal region

of the mandible, and a highly specialized parietal. *Khinjaria* is more specialized in terms of the deep rostrum and mandible, and the highly modified frontal shape.

The two species represent an unusual morphology among mosasaurids, which is characterized by a relatively short snout and a long postorbital region of the skull. Surprisingly, the short-snouted *Khinjaria* and *Goronyosaurus* appear to be closely related to the longirostrine *Gavialimimus almaghribensis* (Strong et al., 2020). Despite having an overall very different skull and tooth shape, they share pits on the mandible for the occlusion of the upper teeth, a long maxilla-premaxilla suture, and an elongate parietal foramen. Together, these highly specialized mosasaurids are most closely related to *Selmasaurus russelli* and *S. johnsoni*.

Selmasaurus russelli shares with *Khinjaria*, *Goronyosaurus*, and *Gavialimimus* a broad, grooved facet on the frontals for the premaxilla, small and posteriorly positioned orbital processes of the frontal, strongly hooked postorbitofrontal processes, and a narrow parietal table between the supratemporal fenestrae (Wright and Shannon, 1988). The jaws and teeth are unfortunately unknown. The older *Selmasaurus johnsoni* appears to be a more primitive taxon, but still shows long, spikelike anterior teeth, a broad frontal-premaxilla contact, and parietal with a narrow table and long, narrow median bar (Polcyn and Everhart, 2008). The short, deep maxilla of *S. johnsoni* suggests that a brevirostrine skull morphology is primitive for Selmasaurini.

5. Functional morphology and ecology

Khinjaria has a highly derived and unusual skull morphology among mosasaurids. The rostrum is relatively short and robust; the postorbital region of the skull is elongate. These features increase the jaws' mechanical advantage. The jaws form a third-class lever system; elongating the postorbital region of the skull places the jaw joint, forming the fulcrum, further from the coronoid process, which acts as the in-lever; reducing the relative length of the mandible reduces the out-lever. Together these adaptations meant the jaws close slowly, but with high force. The skull also shows adaptations to increase the attachment area for jaw adductors, including expansion of the supratemporal fenestrae anteriorly onto the frontal and medially to the midline of the parietal, and overall elongation of the parietal. This resulted in a large cross-sectional area of the adductor muscles, further increasing bite force. Meanwhile, the short but deep dentary increases bending strength (Gordon, 1978), allowing the jaws to resist high bite forces exerted by the muscles and exerted on prey.

The skull is also highly akinetic. Kinesis is reduced by a long premaxilla-maxilla suture, strong overlap of the premaxilla and frontal, an interlocking prefrontal-frontal suture, prefrontal-postorbitofrontal contact, interlocking of the frontal and parietal, an elongate jugal-postorbitofrontal joint, and an elongate suborbital process of the maxilla underlapping the jugal. This loss of kinesis is approached by *Goronyosaurus* (Azzaroli et al., 1975) and *Gavialimimus* (Strong et al., 2020) to a degree, and evolved convergently in Tylosaurinae and Mosasaurinae (LeBlanc et al., 2013; Longrich et al., 2022). Again, these adaptations likely served to increase the forces the jaws could exert and withstand, allowing *Khinjaria* to attack and kill large prey.

The large, fanglike teeth likewise suggest adaptation to take large prey (Fischer et al., 2022). Large teeth are correlated with the consumption of large prey; while the bladeliike tooth shape recalls that of mako sharks, *Isurus* spp. (Garrick, 1967), which feed on small and large fish, squid, occasionally other sharks (Maia et al., 2006), and dolphins approaching their own size (Porsmoguer et al., 2015).

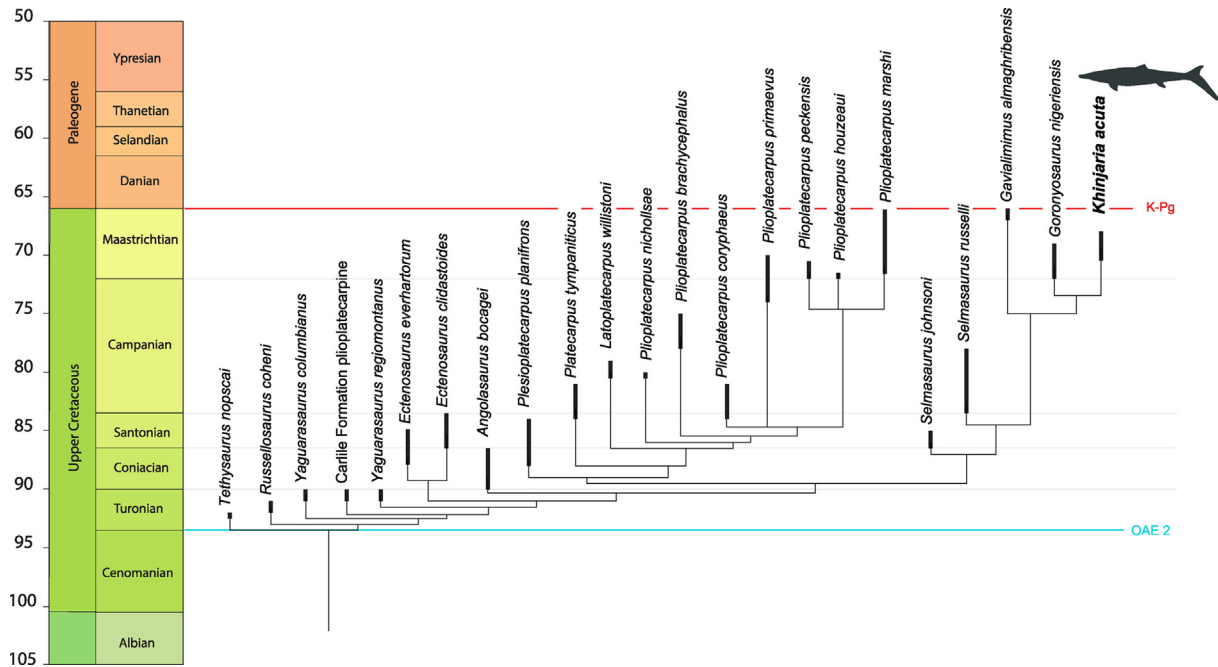


Fig. 9. Evolutionary tree of Plioplatecarpinae showing placement of *Khinjaria acuta* in Selmasaurini. Timescale after Cohen et al. (Cohen et al., 2013).

By analogy, *Khinjaria* may have fed on large fish such as *Enchodus* which are common in the Phosphates (Arambourg, 1952), and occasionally sharks and other mosasauroids. Blade-shaped crowns also occur in *Hainosaurus* (Jagt et al., 2005; Hornung and Reich, 2015) and in the lateral teeth of some mosasauroines, such as *Eremiasaurus heterodontus* (LeBlanc et al., 2012), *Prognathodon kianda* (Schulp et al., 2008) and ‘*Prognathodon*’ *mosasauroides* (NB, pers. obs.). As with cranial kinesis, it appears that multiple mosasaurid clades independently evolved specialized dentition to seize and cut large prey.

Finally, *Khinjaria* is a relatively large animal, with its length estimated at ~8 m, larger than a great white shark (*Tricas* and *McCosker*) (Fig. 10). Large size represents another adaptation for taking large prey. There is a strong correlation between predator size and prey size in marine ecosystems. Although large predators can take small prey, both maximum and average prey size increase in fish and marine reptiles as they become larger (Scharf et al.,

2000; Fischer et al., 2022). Similarly, in toothed whales, larger animals take larger prey (McCurry et al., 2017). Dolphins and porpoises take small fish and squid, sperm whales take giant squid, sharks, skates and large fish. Although *Khinjaria* does not approach the giant mosasauroines and tylosaurines in size, it was larger than earlier plioplatecarpines such as *Platecarpus tympaniticus*.

All these adaptations — robust jaws, an akinetic skull, bladelike teeth, large size — show that the lineage represented by *Khinjaria* evolved to move up the food chain and take larger prey. This pattern is paralleled in other lineages of Mosasaurinae (see Bardet et al., 2015), such as Mosasaurini (Lingham-Soliar, 1995), Prognathodontini (Longrich et al., 2022), and Tylosaurinae (Hornung and Reich, 2015), with large animals specialized to take large prey appearing in the late Campanian and Maastrichtian.

Yet the distinct morphology of *Khinjaria* suggests it hunted in a different way than other mosasauroids, to avoid competition with other top predators. *Khinjaria* apparently had small eyes, as

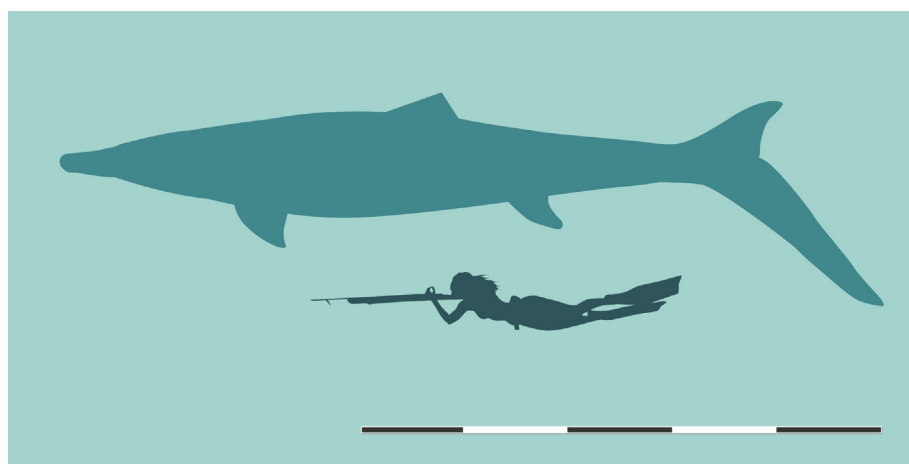


Fig. 10. *Khinjaria acuta* shown to scale with *Homo sapiens*. Scale = 5 m.

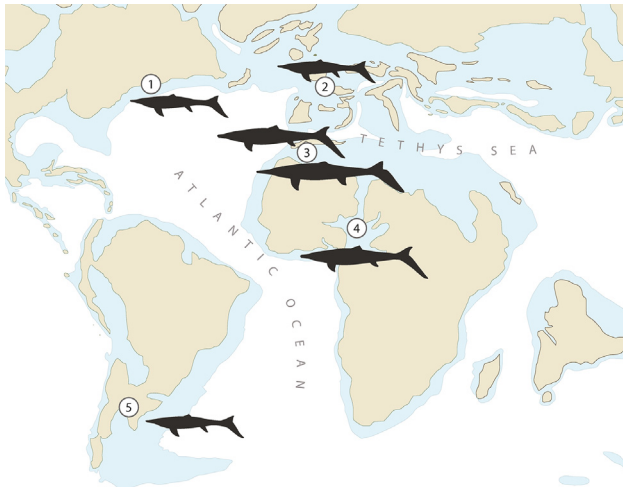


Fig. 11. Map showing distribution of Plioplatecarpinae in the Maastrichtian. 1, *Plioplatecarpus depressus*, 2, *Plioplatecarpus marshi*, 3, *Khinjaria acuta* and *Gavialimimus almaghribensis*, 4, *Goronyosaurus nigeriensis*, 5, *Plioplatecarpus* sp.



Fig. 12. Reconstruction of *Khinjaria acuta* by Andrey Atuchin. The head is reconstructed after the type specimen and *Goronyosaurus nigeriensis*; the body after *Platecarpus ictericus*; prey are *Enchodus libycus*, which are found in abundance in the Phosphates of Morocco.

in *Goronyosaurus* (Azzaroli et al., 1975; Lingham-Soliar, 1991), suggesting it foraged using non-visual cues, perhaps olfaction, to hunt, as suggested for *Goronyosaurus* by Lingham-Soliar (1991). In contrast to *Pluridens*, where reduced eyes are associated with elaboration of the neurovascular foramina of the snout, likely for tactile nerves (Longrich et al., 2021a), no elaboration of the neurovascular foramina is seen in *Goronyosaurus* or *Khinjaria*. This seems consistent with Lingham-Soliar's idea that olfaction played an important role in hunting. Such a hunting strategy might be useful either at night or in waters with low visibility, and for low-speed ambush predation and hunting in shallow waters, for example, beaches, bays, and reefs, or benthic feeding in deep water. Hunting with non-visual cues would seem less suitable to hunting at high speeds or in open sea environments, where sight would be needed.

The dagger-like teeth are likewise distinct from those of other large Maastrichtian mosasaurids. *Thalassotitan* had conical teeth similar to orcas, which would have functioned to tear large prey apart (Longrich et al., 2022). *Prognathodon currii* has blunt teeth designed for crushing (Bardet et al., 2005a). *Mosasaurus*' sharp

conical teeth (Lingham-Soliar, 1995; Bardet et al., 2004) were specialized for cutting. The teeth of *Hainosaurus* (Jagt et al., 2005) are laterally compressed for cutting but not as elongate or straight as those of *Kinjaria*. The remarkable variety of tooth morphologies suggest that these apex predators had different ways of hunting and distinct diets.

6. Mosasaurid paleobiogeography

Two major clades of plioplatecarpines occur in the latest Cretaceous, the broad-snouted Plioplatecarpini and the narrow-snouted Selmasaurini (Fig. 9), and appear to have different distributions (Fig. 11). In the northern hemisphere, Plioplatecarpini are common in the Western Interior Seaway of North America (Holmes, 1996; Konishi and Caldwell, 2011; Cuthbertson and Holmes, 2015), and Europe (Lingham-Soliar, 1994). In the southern hemisphere, Plioplatecarpini have been reported from high latitudes in Patagonia (Fernández et al., 2008) and Antarctica (Martin, 2006). However, Plioplatecarpini have not been reported from lower latitude faunas, such as those of Morocco, Egypt, Niger, Nigeria, and Angola. Meanwhile, selmasaurines are common and diverse in Africa (Lingham-Soliar, 1991; Strong et al., 2020) but rare in Kansas (Polcyn and Everhart, 2008) and Alabama (Wright and Shannon, 1988) and seem to be absent from high-latitude assemblages. Plioplatecarpines remain unknown from the Pacific. These patterns support previous hypotheses of mosasaurid endemism (Longrich et al., 2021a). Given that mosasaurids could swim long distances, factors other than dispersal ability must drive endemism. These might include climatic tolerances, habitat specialization, dietary specializations, or competition between species.

These patterns show the difficulty of trying to infer global biodiversity patterns from local faunas. Europe's late Maastrichtian faunas differ in faunal composition and diversity from those of North Africa and Middle East (Bardet, 2012); European mosasaurid faunas might be seen as showing relatively low diversity prior to the end-Cretaceous mass extinction, while Moroccan ones show extremely high diversity. This could be linked to palaeolatitudinal differences (Bardet, 2012). African mosasaurids also include lineages that are so far unknown from elsewhere, such as the long-snouted *Gavialimimus*, the short-snouted *Khinjaria* and *Goronyosaurus*, as well as the strange *Xenodens* (Longrich et al., 2021b) and *Stelladens* (Longrich et al., 2023). Furthermore, areas such as the upwelling zone along the eastern margin of the Atlantic (Polcyn et al., 2014; Martin et al., 2017) may also have been able to support much higher diversity than elsewhere, emphasizing that global diversity results from the diversity of distinct local faunas.

7. Conclusions

Khinjaria acuta represents a new, highly specialized mosasaurid from the upper Maastrichtian Phosphates of Morocco. It was characterized by a short rostrum, robust jaws, dagger-like, interlocking teeth, and an elongate postorbital skull (Fig. 12). Together with *Goronyosaurus* and *Gavialimimus* it was part of a clade of mosasaurids currently known only from Africa. The short, robust jaws, long postorbital regions of the skull and large teeth suggest adaptations for taking large prey, showing that plioplatecarpines paralleled tylosaurines and mosasaurines in evolving to become apex predators. Nevertheless, the unusual jaw proportions and small orbits suggest a specialized hunting strategy. The evolution of apex predators in Plioplatecarpinae parallels the appearance of apex

predators in Tylosaurinae, Mosasaurini and Prognathodontini, suggesting mosasaurids continued to diversify up to the K-Pg boundary.

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CRedit authorship contribution statement

Nicholas R. Longrich: Writing – review & editing, Writing – original draft, Visualization, Project administration, Methodology, Investigation, Conceptualization. **Michael J. Polcyn:** Writing – review & editing, Investigation. **Nour-Eddine Jalil:** Writing – review & editing, Project administration, Investigation. **Xabier Pereda-Suberbiola:** Writing – review & editing, Investigation. **Nathalie Bardet:** Writing – review & editing, Writing – original draft, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2024.105870>.