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1 **A bizarre new plioplatecarpine mosasaurid from the Maastrichtian of**

2 **Morocco**

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11 ABSTRACT

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

27

28 Keywords: Squamata, Mosasauridae, Plioplatecarpinae, Morocco, Maastrichtian, Phosphates

29 **1. Introduction**

30

31 Following the extinction of ichthyosaurs and the last of the giant pliosaurids in the mid-
32 Cretaceous (Fischer et al., 2016; Zverkov and Pervushov, 2020), the Late Cretaceous marine
33 ecosystem saw a major radiation of mosasaurids (Polcyn et al., 2014). Mosasaurids were giant
34 marine squamates, with specialized flipper-like limbs and tails (DeBraga and Carroll, 1993)
35 allowing them to exploit the open ocean and the deep sea (Rothschild and Martin, 1987; Schulp
36 et al., 2013). Near the end of the Cretaceous, mosasaurids became increasingly diverse and
37 specialized (Bardet et al., 2014; Longrich et al., 2021a; Longrich et al., 2021b; Longrich et al.,
38 2022; Schulp et al., 2009; Strong et al., 2020), culminating in the highly diverse mosasaurid
39 fauna of the late Maastrichtian (Bardet et al., 2015).

40 Mosasaurid diversity appears to peak just before the end-Cretaceous mass extinction,
41 in the Maastrichtian (Bardet et al., 2015; Longrich et al., 2022; Polcyn et al., 2014).
42 Mosasaurids are especially diverse in Africa, with the most diverse known fauna coming from
43 Morocco. Here, more than a dozen species are currently known. Four major groups are known,
44 the Mosasaurinae (Bardet et al., 2005a; Bardet et al., 2004; LeBlanc et al., 2012; Longrich et
45 al., 2021b; Longrich et al., 2022; Schulp et al., 2009), Halisaurinae (Bardet et al., 2005b;
46 Longrich et al., 2021a), Tylosaurinae (Rempert et al., 2022), and Plioplatecarpinae
47 (Arambourg, 1952; Bardet et al., 2015; Strong et al., 2020); Pachyvaranidae (Houssaye et al.,
48 2011) also occur.

49 Plioplatecarpines have previously been reported from the Phosphates of Morocco based
50 on isolated teeth and vertebrae, originally named *Platecarpus ptychodon* by Arambourg
51 (Bardet et al., 2015) and recently renamed *Gavialimimus almaghribensis* (Strong et al., 2020).
52 *Gavialimimus* represents a highly specialized, longirostrine species. Here, we report a distinct
53 but closely related plioplatecarpine, characterized by a bizarre skull morphology. The new

54 species has short, robust jaws, dagger-like teeth, and an elongated posterior region of the skull.
55 It is closely related to *Goronyosaurus nigeriensis* from Niger and Nigeria (Lingham-Soliar,
56 1988), and more distantly related to *Gavialimimus almaghribensis* (Strong et al., 2020) and
57 *Selmasaurus* spp. from North America (Polcyn and Everhart, 2008; Wright and Shannon,
58 1988). These species, along with *Plioplatecarpus* from the Maastrichtian of Europe (Lingham-
59 Soliar, 1994), show that Plioplatecarpinae staged a radiation in the latest Cretaceous alongside
60 the radiation of Mosasaurinae (Bardet et al., 2015; Polcyn et al., 2014) and Halisaurinae
61 (Longrich et al., 2021a).

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

67

68 **Institutional Abbreviations**

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

70

71 **2. Geological setting**

72

73 MHNM.KHG.521, the holotype and only known specimen of *Khinjaria acuta*, comes from the
74 Phosphates of Sidi Chennane, in the Oulad Abdoun Basin Khouribga Province, Morocco (Fig.
75 1). The Phosphates consist of phosphatic sands, marls, and limestones laid down in an
76 embayment on the eastern edge of the Atlantic near the end of the Late Cretaceous and the
77 early Paleogene (Yans et al., 2014). They are divided into a series of beds which are, from
78 bottom to top, Couche III, Couche II, Couche I, Couche 0, and Sillons A and B (i.e. Kocsis et

79 al., 2014; Yans et al., 2014). Couche III is Maastrichtian in age, with the transition between
80 Couche III and Couche II marking the Cretaceous-Paleogene transition. MHNM.KHG.521
81 comes from the lower part of Couche III.

82 Couche III consists of about 5 m of sediments (Fig. 2). Sediments are condensed, and
83 so may span a significant range of time. Upper Couche III spans the final million years or so
84 before the K-Pg boundary (Yans et al., 2014), and so is latest Maastrichtian in age. The age of
85 the lower part of Couche III is less well-constrained. Selachian teeth from lower Couche III
86 suggest a late Maastrichtian age (Cappetta, 1987) but preliminary study of the fauna suggests
87 turnover of mosasaurids between lower Couche III and upper Couche III; many if not all
88 mosasaurid species in lower Couche III are distinct from those in upper Couche III. However,
89 if mosasaurids evolved rapidly, as in marine invertebrates such as ammonites (Witts et al.,
90 2015) and terrestrial vertebrates such as dinosaurs (Mallon et al., 2012), as little as one or two
91 million years could account for the faunal differences. Accordingly, lower Couche III might
92 tentatively be considered late, but not latest Maastrichtian, in agreement with the selachians
93 fossils.

94 The phosphates contain an extraordinary diversity of Cretaceous and Paleogene
95 vertebrates. The Cretaceous fauna is dominated by selachian teeth (Arambourg, 1952;
96 Cappetta, 1987; Cappetta et al., 2014; Noubhani and Cappetta, 1997) and osteichthyan remains
97 (Arambourg, 1952; Vullo et al., 2017), but marine reptiles are abundant and diverse (Bardet et
98 al., 2017). Elasmosaurid plesiosaurs (Vincent et al., 2013; Vincent et al., 2011) and chelonioid
99 turtles (Bardet et al., 2013; Lapparent de Broin et al., 2013) are common, as well as small
100 pachyvaranid squamates (Houssaye et al., 2011), and rare crocodylians (Jouve et al., 2008).
101 However, far and away the most common and diverse reptiles are mosasaurids, known by more
102 than a dozen species (Bardet et al., 2015; Bardet et al., 2005a; Bardet et al., 2005b; Bardet et
103 al., 2004; LeBlanc et al., 2012; Longrich et al., 2021a; Longrich et al., 2021b; Longrich et al.,

104 2022; Longrich et al., 2023; Rempert et al., 2022; Schulp et al., 2009; Strong et al., 2020).
105 Pterosaurs also occur (Longrich et al., 2018; Pereda-Suberbiola et al., 2003), as well as rare
106 dinosaurs (Longrich et al., 2017; Longrich et al., 2021c; Pereda-Suberbiola et al., 2004).

107 In upper Couche III, mosasaurids are represented by isolated teeth (Arambourg, 1952),
108 isolated bones, disarticulated skulls and skeletons, and frequent articulated remains. These are
109 preserved in coarse-grained phosphatic sands and as part of dense bonebeds that extend tens of
110 kilometers in all directions. Fossils occur in finer-grained sediments, and as a result, show more
111 compaction.

112

113 **3. Systematic Paleontology**

114 Squamata Opperl, 1811

115 Mosasauridae Gervais, 1852

116 Plioplatecarpinae Williston, 1897

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

120

121 ***Khinjaria acuta*** gen. et sp. nov.

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

123

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

126

127 *Holotype*. MHNM.KHG.521, partial skull including part of the premaxilla, maxillae,
128 prefrontals, frontal, parietal, right postorbitofrontal, partial right squamosal, right dentary,
129 associated trunk(?) vertebra.

130

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

133

134 *Diagnosis*. Plioplatecarpine mosasaurid characterized by the following character combination:
135 skull with a short rostrum, elongate temporal region, reduced orbits; deep, subrectangular
136 maxilla with deep and short narial emargination and upturned jugal process; dentary robust and
137 deep anteriorly, with a prominent, ventrally projecting symphysis; maxilla and dentary bearing
138 long grooves for opposing teeth; frontal triangular, very short and broad, with a staircase-
139 shaped suture for prefrontals; strongly interlocking W-shaped contact of the frontal and parietal
140 with two long and thin processes on either side of the parietal; parietal extremely elongated,
141 without table and with a slit-like foramen; large and elongate supratemporal fenestrae, with
142 supratemporal fossae expanding anteriorly onto the frontals; heterodont dentition with very
143 large anterior teeth and small posterior ones; anterior teeth extremely elongate and knife-like,
144 with labiolingually compressed crowns, smooth enamel, and prominent, convex anterior and
145 posterior carinae lacking serrations.

146

147 *Description*.

148 *General preservation* (Figs. 3-7). The holotype includes an incomplete skull, dentary, and an
149 associated vertebra. Bones are well-preserved overall but with cracks and distortion caused by
150 compaction of the matrix. The skull is partially disarticulated, with the right maxilla and
151 dentary displaced to the left side of the skull and the left maxilla displaced away from the skull.

152 The reconstruction (Fig. 8) suggests a skull with a proportionally short and powerfully
153 constructed rostrum, and a long postorbital region.

154

155 *Maxilla* (Figs. 3, 4). The maxilla bears 10 or 11 teeth. The maxilla is short and deep, as in
156 *Selmasaurus johnsoni* (Polcyn and Everhart, 2008), and unlike the more elongate maxilla of
157 *Goronyosaurus nigeriensis* (Azzaroli et al., 1972; Azzaroli et al., 1975; Lingham-Soliar, 1988,
158 1991), *Plioplatecarpus* spp. (Lingham-Soliar, 1994) and *Platecarpus* (Konishi et al., 2012), or
159 the low, hyper-elongate maxilla of *Gavialimimus* (Strong et al., 2020). In lateral view, the
160 anterior maxilla forms a tall, rectangular blade with a convex dorsal margin where it contacts
161 the premaxilla.

162 Dorsally, the narial emargination is deep and short, similar to *Goronyosaurus*
163 (Lingham-Soliar, 1988). The narial emargination is shallower in *Gavialimimus* (Strong et al.,
164 2020) and *Selmasaurus johnsoni* (Polcyn and Everhart, 2008), but is deep in some other
165 plioplatecarpines including *Platecarpus tympaniticus* (Konishi et al., 2012). The prefrontal
166 process is tall and triangular; it would have broadly contacted the prefrontal dorsally and
167 hooked over it posteriorly.

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

172 The maxilla's lateral surface bears a series of long, deep grooves, perpendicular to the
173 tooth row, to accommodate the teeth of the lower jaw when the jaws closed. Similar occlusal
174 pits occur on *Goronyosaurus* (Lingham-Soliar, 1988) but are not as tall. *Gavialimimus* (Strong
175 et al., 2020) has occlusal pits on the maxillae but not grooves. Pits are absent in *Selmasaurus*
176 *johnsoni* (Polcyn and Everhart, 2008) and other plioplatecarpines, but occlusal pits occur

177 convergently in certain mosasaurines, e.g. *Eremiasaurus heterodontus* (LeBlanc et al., 2012).
178 The maxilla's medial surface is slightly concave. It has a straight ventral margin, with lateral
179 and medial parapets equal in height.

180

181 *Prefrontal* (Figs. 3, 5). The prefrontal has a narrow, triangular contribution to the skull roof.
182 The prefrontal contacted the frontal's lateral margin and overlaps it anteriorly, while
183 underlapping it posteriorly. The prefrontal may have contacted the premaxillary process and
184 premaxilla as well, largely excluding the frontal from the naris. A similar condition is present
185 in *Goronyosaurus* (Azzaroli et al., 1972; Azzaroli et al., 1975; Lingham-Soliar, 1988, 1991).
186 The prefrontal's stepped medial margin would have interlocked with the stepped edge of the
187 frontal, limiting mobility, a condition unique among mosasaurids. Posteriorly the prefrontal
188 contacts the postorbitofrontal, excluding the frontal from the orbit.

189

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

202 margins bear a series of flanges and notches forming a stepped edge corresponding to the
203 stepped edge of the prefrontal.

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

210 The posterodorsal surface of the frontal bears deep fossae on either side, marking the
211 anterior extent of the supratemporal musculature, as in *Goronyosaurus nigeriensis* (Lingham-
212 Soliar, 1988). This condition is approached in *Selmasaurus russelli* (MJP pers. obs.) where the
213 fossae invade the posterior margin of the frontal by 5 or 6 millimeters. Extension of the
214 supratemporal musculature onto the frontals is unusual among mosasaurids, but occurs in
215 carnivorous dinosaurs such as tyrannosaurids (Currie, 2003) and dromaeosaurids (Currie,
216 1995).

217 Medially, the frontal-parietal suture is W-shaped. A strong midline notch receives the
218 parietal and lateral to this, triangular, spur-like paramedian processes wrap around the pineal
219 foramen. A similar condition occurs in *Gavialimimus* (Strong et al., 2020), but the spur-like
220 processes are shorter. Notches in the parietal of *Goronyosaurus* (Lingham-Soliar, 1988)
221 suggest it also had interlocking spurs here (Lingham-Soliar, 1991). An interlocking frontal-
222 parietal suture, reducing skull kinesis, also occurs in mosasaurines such as *Plotosaurus*,
223 *Mosasaurus* (LeBlanc et al., 2013) "*Liodon asiaticum*" (Bardet et al., 2021), *Thalassotitan*
224 (Longrich et al., 2022), *Prognathodon saturator* (Schulp, 2006), and *Globidens phosphaticus*
225 (Polcyn et al., 2010).

226

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

235 Anterolaterally, the postorbitofrontal bears a large shelf that projects to form a short,
236 very wide postorbital process. A similar condition occurs in *Goronyosaurus*. Although the
237 condition in *Goronyosaurus* is debated (Lingham-Soliar, 1988), it has been reconstructed as
238 having extremely broad postorbital process contacting a dorsally broad jugal (Lingham-Soliar,
239 1991). If so, *Khinjaria* may have shared this condition. Medially, the postorbitofrontal
240 underlaps the frontal and abuts the anterolateral wing of the parietal, making a small
241 contribution to the supratemporal fenestra.

242

243 *Parietal* (Figs. 3, 5). The parietal is very long and narrow, measuring over twice the midline
244 length of the frontal. No other mosasaurid is known to have such an extreme shape; however,
245 the parietal is broken posteriorly in *Goronyosaurus* (Azzaroli et al., 1972; Lingham-Soliar,
246 1988, 1991). This elongate parietal increased the area for insertion of jaw adductor muscles
247 and resembles, for example, the very large supratemporal fenestrae of some thalattosuchian
248 crocodyliforms (NB, pers. obs.).

249 The narrow parietal table is pierced by a slit-like pineal foramen. The parietal foramen
250 is recessed into an ovoid depression, and approaches but does not participate in the
251 frontoparietal suture. *Goronyosaurus* is the only other mosasaurid with a similar parietal

252 morphology. The anterolateral alae originate from the body of the parietal posterior to the
253 pineal depression. The alae project anterolaterally, forming the anteromedial wall of the
254 supratemporal fenestrae. Behind the pineal depression, the parietal forms a tall, long, and
255 narrow bar of bone. The dorsal surface of the parietal forms a low, narrow ridge where the
256 supratemporal fossae meet along the midline. Posteriorly the ridge splits, and bounds a
257 triangular fossa. Again, reduction of the parietal table and the medial extension of the
258 supratemporal fossae increased the area of origin for the jaw adductor muscles. The
259 posterolateral processes of the parietals are broken distally.

260

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

265

266 *Dentary (Figs. 3, 6)*. The dentary resembles that of *Goronyosaurus* (Azzaroli et al., 1975;
267 Lingham-Soliar, 1988), but is overall deeper, especially posteriorly. The dentary has 12 tooth
268 positions, as in many other derived plioplatecarpines. The symphyseal region is deep as in
269 *Goronyosaurus*, but the symphysis extends back as far as the third tooth position; in
270 *Goronyosaurus* it only extends to the second tooth. The dentary becomes shallower in the
271 middle of the jaw, then deeper again posteriorly. This condition is unique in mosasaurids, where
272 the dentary tapers from back to front, but resembles some pliosaurids, where the symphysis is
273 enlarged to accommodate the largest teeth (NB, pers. obs.).

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

276 posterodorsal margin of the dentary may have accommodated the tip of the coronoid when the
277 jaw was closed. There is no edentulous posterodorsal process.

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

284

285 *Dentition* (Figs. 3, 4, 6, 7). There are 10 or 11 maxillary teeth; *Goronyosaurus* appears to have
286 11 (Lingham-Soliar, 1991). *Gavialimimus* has 12 (Strong et al., 2020); *Selmasaurus johnsoni*
287 probably had 11 or 12 (Polcyn and Everhart, 2008); *Plioplatecarpus peckensis* has 11
288 (Cuthbertson and Holmes, 2015), and *Platecarpus tympaniticus* has 12 (Konishi et al., 2012).

289 The dentary bears 12 teeth, as in *Goronyosaurus* (Lingham-Soliar, 1991);
290 *Gavialimimus* has 10 (Strong et al., 2020); *Selmasaurus johnsoni* has 11 (Polcyn and Everhart,
291 2008), *Platecarpus tympaniticus* has 12 (Konishi et al., 2012). Proportionately, teeth are very
292 large, similar to *Selmasaurus johnsoni*, versus the smaller teeth of *Gavialimimus* and most other
293 plioplatecarpines.

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

299 Teeth are large in diameter and have very long crowns anteriorly, and become smaller
300 and shorter towards the back of the jaw, a condition approached by other plioplatecarpines

301 including *Selmasaurus johnsoni* (Wright and Shannon, 1988), *Gavialimimus almaghrebensis*
302 (Strong et al., 2020), *Plioplatecarpus houzeaui* (Lingham-Soliar, 1994) and *Platecarpus*
303 *tympaniticus* (Konishi et al., 2012).

304 Tooth crowns are straight, they are weakly curved in *Gavialimimus* and *Selmasaurus*
305 *johnsoni*; and more hooked in *Plioplatecarpus*, e.g. *P. houzeaui* and *Platecarpus tympaniticus*.
306 In contrast to the teeth of most plioplatecarpines, which have conical crowns with sharp apices
307 (Konishi et al., 2012; Lingham-Soliar, 1994; Wright and Shannon, 1988), the crowns are
308 dagger-like in *Khinjaria*. Crowns are labiolingually compressed with a lenticular cross section;
309 the tips, rather than tapering to a needle point, have convex anterior and posterior carinae. The
310 two prominent carinae form sharp cutting edges, lack serrations. The condition in
311 *Goronyosaurus* is difficult to assess owing to poor preservation but the teeth appear to be
312 slightly compressed, and have convex anterior and posterior carinae on at least some dentary
313 teeth; they may have approached the condition seen in *Khinjaria*.

314 Tooth surfaces are smooth, with a silky appearance. Most lack facets, ridges, fluting, or
315 sculpturing of the enamel. However, the second maxillary tooth shows subtle ridging labially
316 and strong ridging and fluting lingually, with perhaps 8-10 ridges. This relatively smooth crown
317 stands in contrast to plioplatecarpines in general, which exhibit either well-developed ridges
318 and fluting as in *Gavialimimus* (Strong et al., 2020), *Selmasaurus johnsoni* (Wright and
319 Shannon, 1988), and *Platecarpus tympaniticus* (NL pers. obs.), or very fine striations as in
320 *Plioplatecarpus* (Lingham-Soliar, 1994). It is unclear whether teeth in *Goronyosaurus* bore
321 ridges, fluting, or other ornament. The smooth enamel and sharp cutting carinae in *Khinjaria*
322 are reminiscent of that of some mosasaurines, for example *Eremiasaurus* (LeBlanc et al.,
323 2012), *Prognathodon kianda* (Schulp et al., 2008) and ‘*Prognathodon*’ *mosasauroides* Gaudry,
324 1892 (NB, pers. obs.).

325

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

332

333 **4. Phylogenetic analysis**

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

343 The sister-group to Selmasaurini is Plioplatecarpini, comprising *Plioplatecarpus* spp.,
344 *Latoplatecarpus*, *Platecarpus tympaniticus*, and *Plesioplatecarpus planifrons*. Plioplatecarpini
345 is defined as all species closer to *Plioplatecarpus marshi* than *Selmasaurus russelli*. The
346 Selmasaurini and Plioplatecarpini form a clade, with *Ecteneosaurus* representing a lineage
347 basal to these two major clades. *Yaguarasaurus* and *Russellosaurus* fall out at the base of the
348 tree, consistent with the hypothesis that they represent basal plioplatecarpines (Polcyn et al.,
349 2023).

350 *Khinjaria acuta* is most closely related to and most closely resembles *Goronyosaurus*
351 *nigeriensis* from the Maastrichtian of Nigeria and Niger (Azzaroli et al., 1972; Azzaroli et al.,
352 1975; Lingham-Soliar, 1988, 1991). The two are united by large, canine-like anterior teeth,
353 strong interlocking of the teeth, occlusal pits developed as deep grooves on jaws, deep
354 symphyseal region of the mandible, and highly specialized parietal. *Khinjaria* is more
355 specialized in terms of the deep rostrum and mandible, and the highly modified frontal shape.

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

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

372

373 **5. Functional Morphology and Ecology**

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

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

395 The large, fanglike teeth likewise suggest adaptation to take large prey (Fischer et al.,
396 2022). Large teeth are correlated with the consumption of large prey; while the bladelike tooth
397 shape recalls that of mako sharks, *Isurus* spp. (Garrick, 1967), which feed on small and large
398 fish, squid, occasionally other sharks (Maia et al., 2006), and dolphins approaching their own

399 size (Porsmoguer et al., 2015). By analogy, *Khinjaria* may have fed on large fish such as
400 *Enchodus* which are common in the Phosphates (Arambourg, 1952), and occasionally sharks
401 and other mosasaurids. Blade-shaped teeth also occur in *Hainosaurus* (Hornung and Reich,
402 2015; Jagt et al., 2005) and in the lateral teeth of some mosasaurines, such as *Eremiasaurus*
403 *heterodontus* (LeBlanc et al., 2012), *Prognathodon kianda* (Schulp et al., 2008) and
404 ‘*Prognathodon*’ *mosasauroides* (NB, pers. obs.). As with cranial kinesis, it appears that
405 multiple mosasaurid clades independently evolved specialized dentition to seize and cut large
406 prey.

407 Finally, *Khinjaria* is a relatively large animal, with its length estimated at ~8 meters,
408 larger than a great white shark (Tricas and McCosker) (Fig. 10). Large size represents another
409 adaptation for taking large prey. There is a strong correlation between predator size and prey
410 size in marine ecosystems. Although large predators can take small prey, both maximum and
411 average prey size increase in fish and marine reptiles as they become larger (Fischer et al.,
412 2022; Scharf et al., 2000). Similarly, in toothed whales, larger animals take larger prey
413 (McCurry et al., 2017). Dolphins and porpoises take small fish and squid, sperm whales take
414 giant squid, sharks, skates and large fish. Although *Khinjaria* does not approach the giant
415 mosasaurines and tylosaurines in size, it was larger than earlier plioplacatines such as
416 *Platycarpus tympaniticus*.

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

423 Yet the distinct morphology of *Khinjaria* suggests it hunted in a different way than other
424 mosasaurids, to avoid competition with other top predators. *Khinjaria* apparently had small
425 eyes, as in *Goronyosaurus* (Azzaroli et al., 1975; Lingham-Soliar, 1991), suggesting it foraged
426 using non-visual cues, perhaps olfaction, to hunt, as suggested for *Goronyosaurus* by Lingham-
427 Soliar. In contrast to *Pluridens*, where reduced eyes are associated with elaboration of the
428 neurovascular foramina of the snout, likely for tactile nerves (Longrich et al., 2021a), no
429 elaboration of the neurovascular foramina is seen in *Goronyosaurus* or *Khinjaria*. This seems
430 consistent with Lingham-Soliar's idea that olfaction played an important role in hunting. Such
431 a hunting strategy might be useful either at night or in waters with low visibility, and for low-
432 speed ambush predation and hunting in shallow waters, for example, beaches, bays, and reefs,
433 or benthic feeding in deep water. Hunting with non-visual cues would seem less suitable to
434 hunting at high speeds or in open sea environments, where sight would be needed.

435 The dagger-like teeth are likewise distinct from those of other large Maastrichtian
436 mosasaurids. *Thalassotitan* had conical teeth similar to orcas, which would have functioned to
437 tear large prey apart (Longrich et al., 2022). *Prognathodon currii* has blunt teeth designed for
438 crushing (Bardet et al., 2005a). *Mosasaurus*' sharp conical teeth (Bardet et al., 2004; Lingham-
439 Soliar, 1995) were specialized for cutting. The teeth of *Hainosaurus* (Jagt et al., 2005) are
440 laterally compressed for cutting but not as elongate or straight as those of *Kinjaria*. The
441 remarkable variety of tooth morphologies suggest that these apex predators had different ways
442 of hunting and distinct diets.

443

444 **6. Mosasaur Paleobiogeography**

445 Two major clades of plioplatecarpines occur in the latest Cretaceous, the broad-snouted
446 Plioplatecarpini and the narrow-snouted Selmasaurini (Fig. 9), and appear to have different
447 distributions (Fig. 11). In the northern hemisphere, Plioplatecarpini are common in the Western

448 Interior Seaway of North America (Cuthbertson and Holmes, 2015; Holmes, 1996; Konishi
449 and Caldwell, 2011), and Europe (i.e. Lingham-Soliar, 1994). From the southern hemisphere,
450 plioplatecarpines have been reported from high latitudes in Patagonia (Fernández et al., 2008)
451 and Antarctica (Martin, 2006). However, Plioplatecarpini have not been reported from lower
452 latitude faunas, such as those of Morocco, Egypt, Niger, Nigeria, and Angola. Meanwhile,
453 selmasaurines are rare in the Western Interior Seaway (Wright and Shannon, 1988) but appear
454 to be common and diverse in Africa (Lingham-Soliar, 1991; Strong et al., 2020).
455 Plioplatecarpines remain unknown from the Pacific. These patterns support previous
456 hypotheses of mosasaurid endemism (Longrich et al., 2021a). Given that mosasaurids could
457 swim long distances, factors other than dispersal ability must drive endemism. These might
458 include climatic tolerances, habitat specialization, dietary specializations, or competition
459 between species.

460 These patterns show the difficulty of trying to infer global biodiversity patterns from
461 local faunas. Europe's late Maastrichtian faunas differ in faunal composition and diversity from
462 those of North Africa and Middle East (Bardet, 2012); European mosasaurid faunas might be
463 seen as showing relatively low diversity prior to the end-Cretaceous mass extinction, while
464 Moroccan ones show extremely high diversity. This could be linked to palaeolatitudinal
465 differences (Bardet, 2012). African mosasaurids also include lineages that are so far unknown
466 from elsewhere, such as the long-snouted *Gavialimimus*, the short-snouted *Khinjaria* and
467 *Goronyosaurus*, as well as the strange *Xenodens* (Longrich et al., 2021b) and *Stelladens*
468 (Longrich et al., 2023). Furthermore, areas such as the upwelling zone along the eastern margin
469 of the Atlantic (Martin et al., 2017; Polcyn et al., 2013) may also have been able to support
470 much higher diversity than elsewhere, emphasizing that global diversity results from the
471 diversity of distinct local faunas.

472

473

474 **7. Conclusions**

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

485

486

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724

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731 NRL, NB, MP, NEJ, XPS wrote the paper. NRL prepared figures and led the project.

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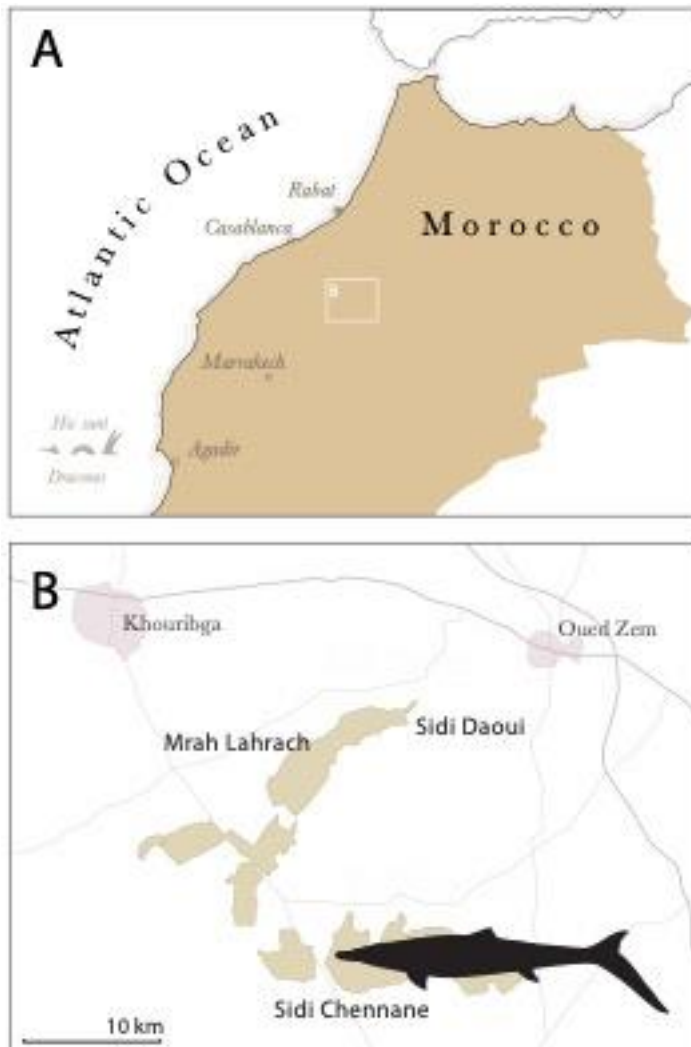
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741

FIGURES

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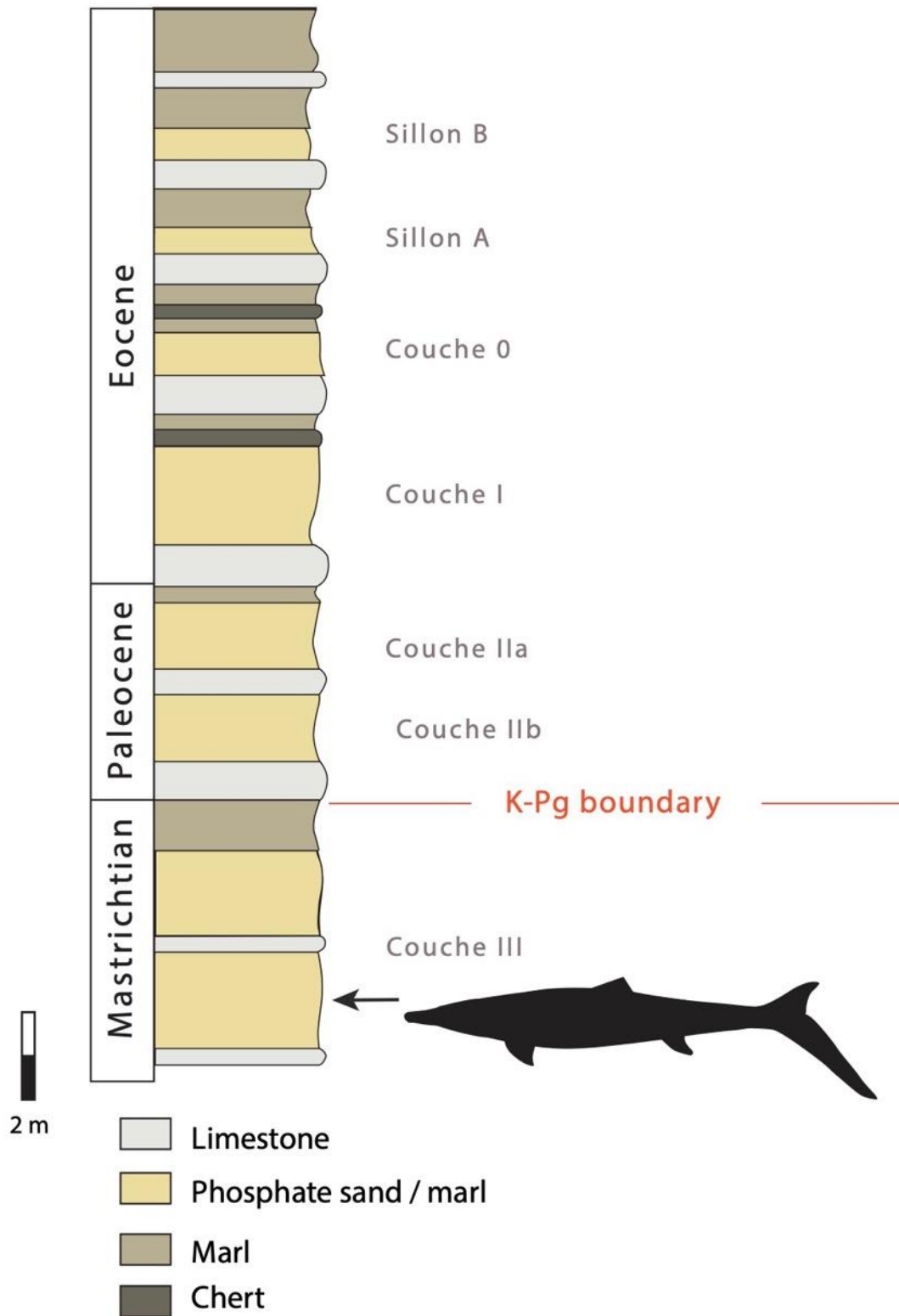
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744 **Figure 1.** Map of Morocco showing A, location of the phosphate mines of the Oulad Abdoun

745 Basin, B, the Sidi Chennane phosphate mines, southern Oulad Abdoun Basin, that produced

746 *Khinjaria acuta*.

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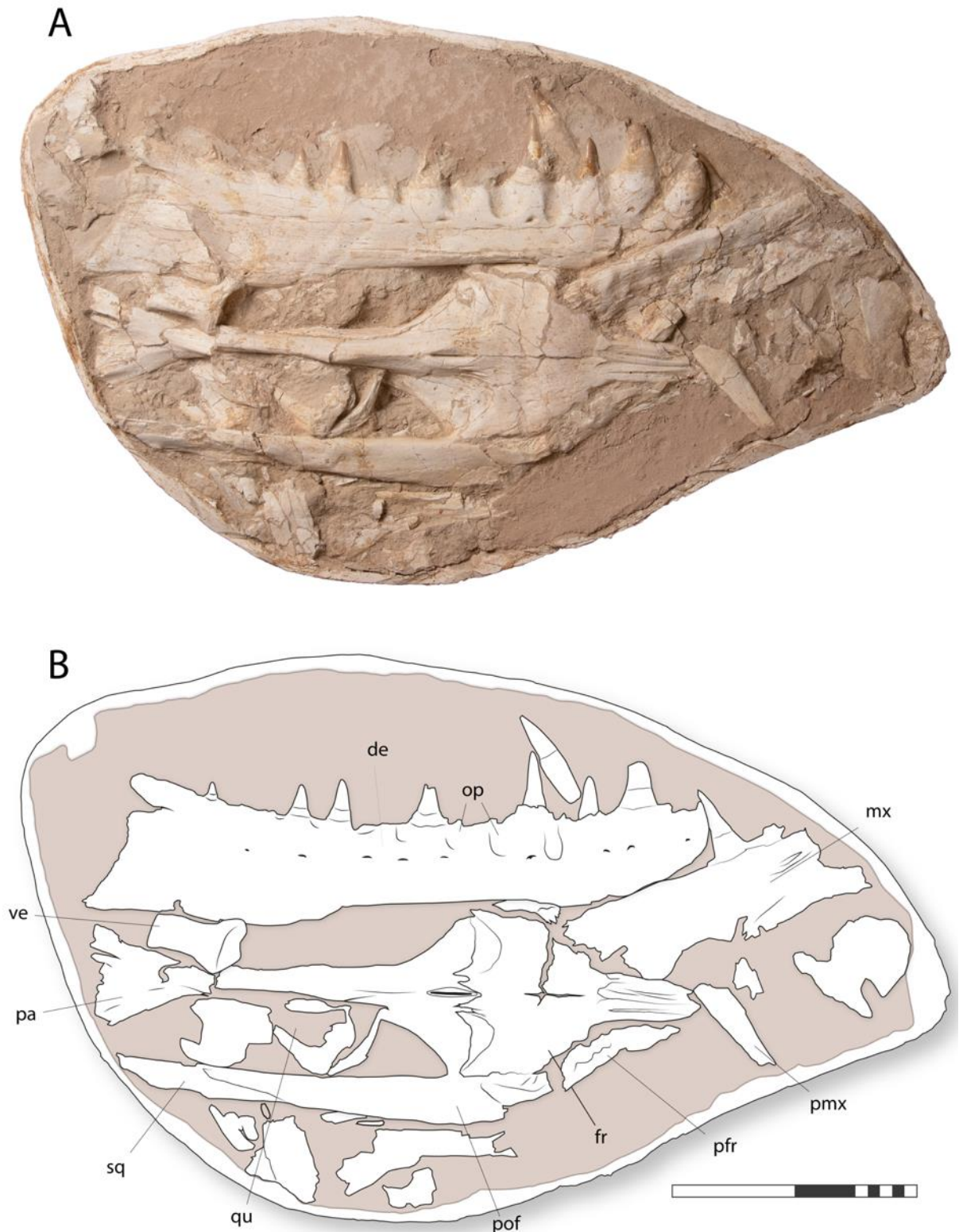


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749 **Figure 2.** Synthetical stratigraphical column of the Upper Cretaceous – Palaeogene

750 Phosphate series of the Oulad Abdoun Basin of Morocco, showing the stratigraphical

751 occurrence of *Khinjaria acuta* in lower Couche III. After Kocsis et al. (Kocsis et al., 2014).



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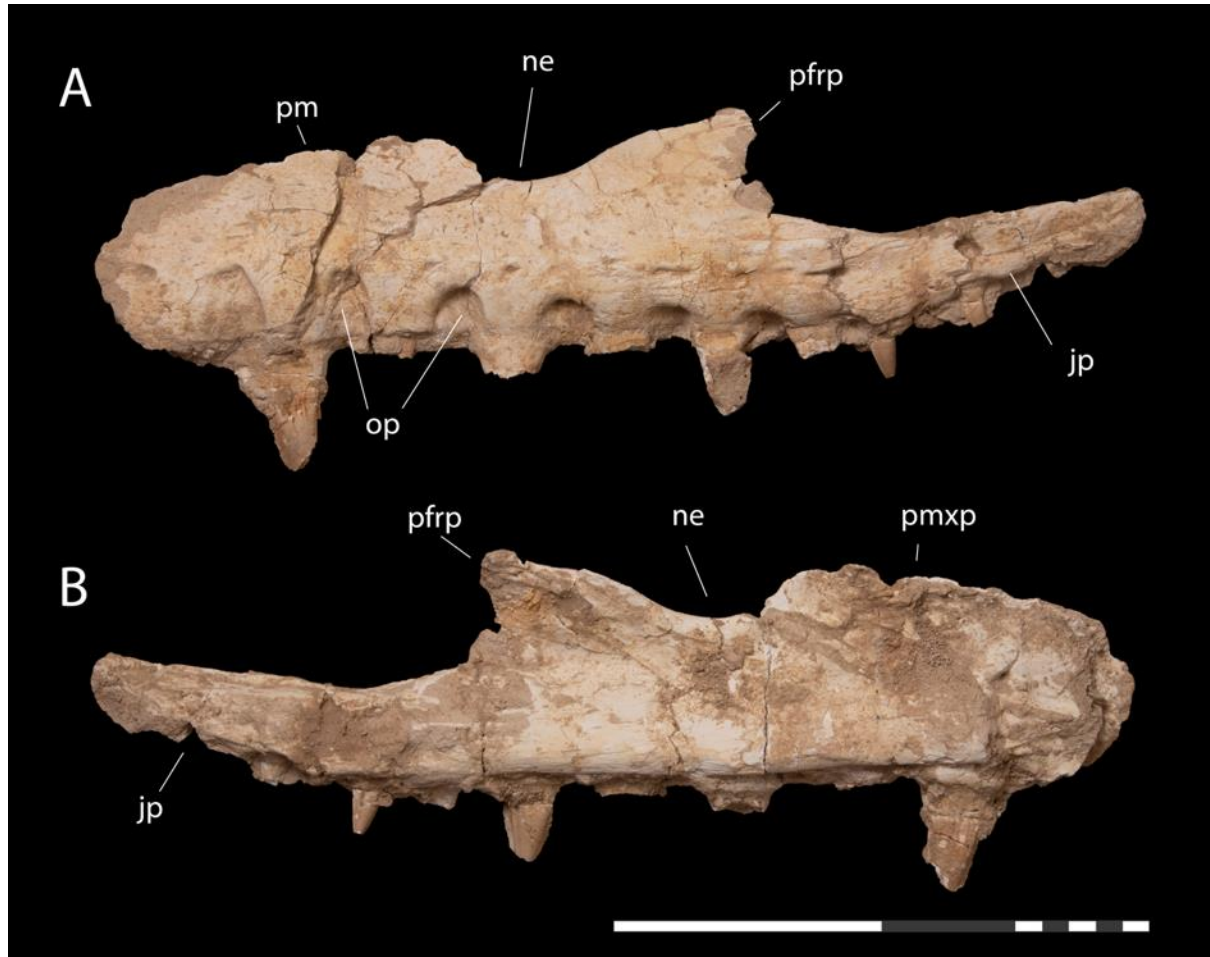
753 **Figure 3.** *Khinjaria acuta*, MHNM.KHG.521, holotype partial skull Sidi Chennane, Oulad

754 Abdoun Basin, Morocco, lower Couche III, upper Maastrichtian. A, skull in jacket; B, line

755 drawing. Abbreviations: de, dentary; fr, frontal; mx, maxilla; op, oclusal pits; pa, parietal;

756 pmx, premaxilla; pof, postorbitofrontal; pfr, prefrontal; qu, Quadrate; sq, squamosal; ve,
757 vertebra. Scale = 20 cm.

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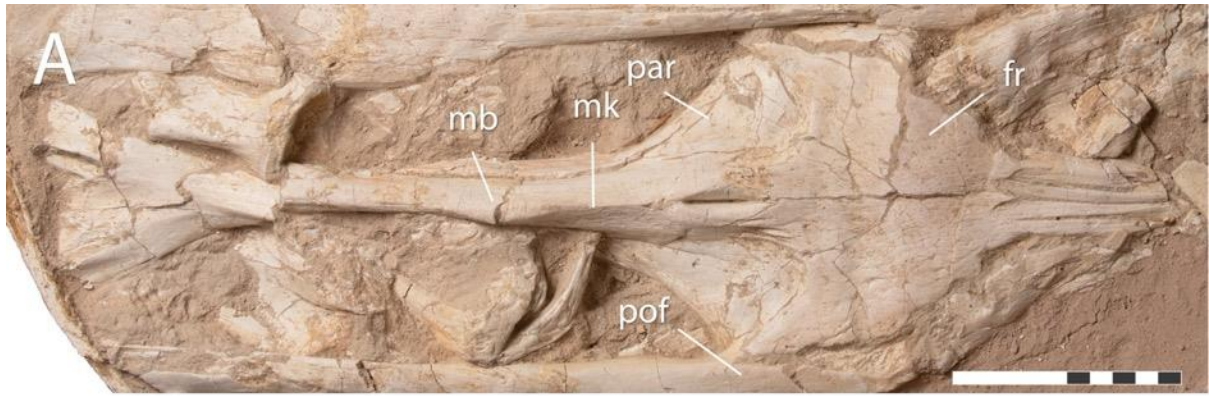


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760 **Figure 4.** *Khinjaria acuta*, MHNM.KHG.521, holotype left maxilla, Sidi Chennane, Oulad
761 Abdoun Basin, Morocco, lower Couche III, upper Maastrichtian in A, lateral and B, medial
762 views. Abbreviations: jp, jugal process; ne, narial emargination; op, occlusal pits; pfrp,
763 prefrontal process; pmxp, premaxillary process. Scale = 20 cm.

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767 **Figure 5.** *Khinjaria acuta*, MHNM.KHG.521, holotype, Sidi Chennane, Oulad Abdoun Basin,

768 Morocco, lower Couche III, upper Maastrichtian. A, frontoparietal complex closeup; B, frontal

769 closeup. Abbreviations: fac, prefrontal articular facet for frontal; fla, interlocking flanges of

770 frontal clasp; par, parietal; pfr, prefrontal; pmp, frontal premaxillary process; pmx, sutural contact

771 and grooves for premaxilla; pof, postorbitofrontal; pp, postorbital process; st, stepped margin

772 of frontal. Scale = 10 cm (A), 5 cm (B).

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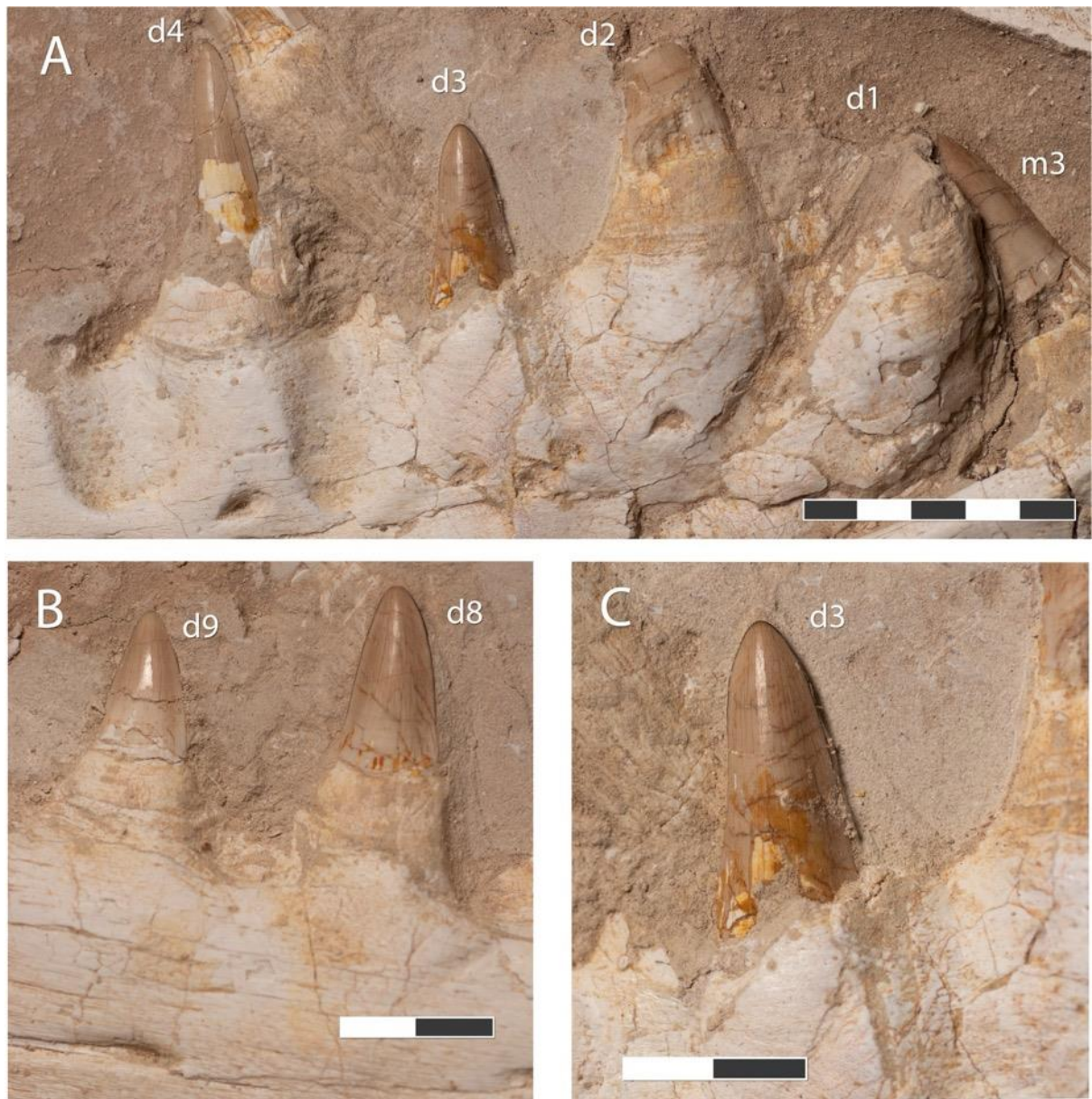
777 **Figure 6.** *Khinjaria acuta*, MHNM.KHG.521, holotype left dentary (in lateral view), closeup,

778 Sidi Chennane, Oulad Abdoun Basin, Morocco, lower Couche III, upper Maastrichtian.

779 Abbreviations: cor, notch for coronoid; imj, intramandibular joint; op, occlusal pit; sym,

780 symphysis. Scale = 10 cm.

781



782

783 **Figure 7.** *Khinjaria acuta*, MHNM.KHG.521, holotype, dentary teeth closeup, Sidi Chennane,

784 Oulad Abdoun Basin, Morocco, lower Couche III, upper Maastrichtian. A, anterior teeth; B,

785 posterior teeth, C, anterior tooth. d1-4,8,9 = dentary teeth 1-4, 8-9, m5, maxillary tooth 5.

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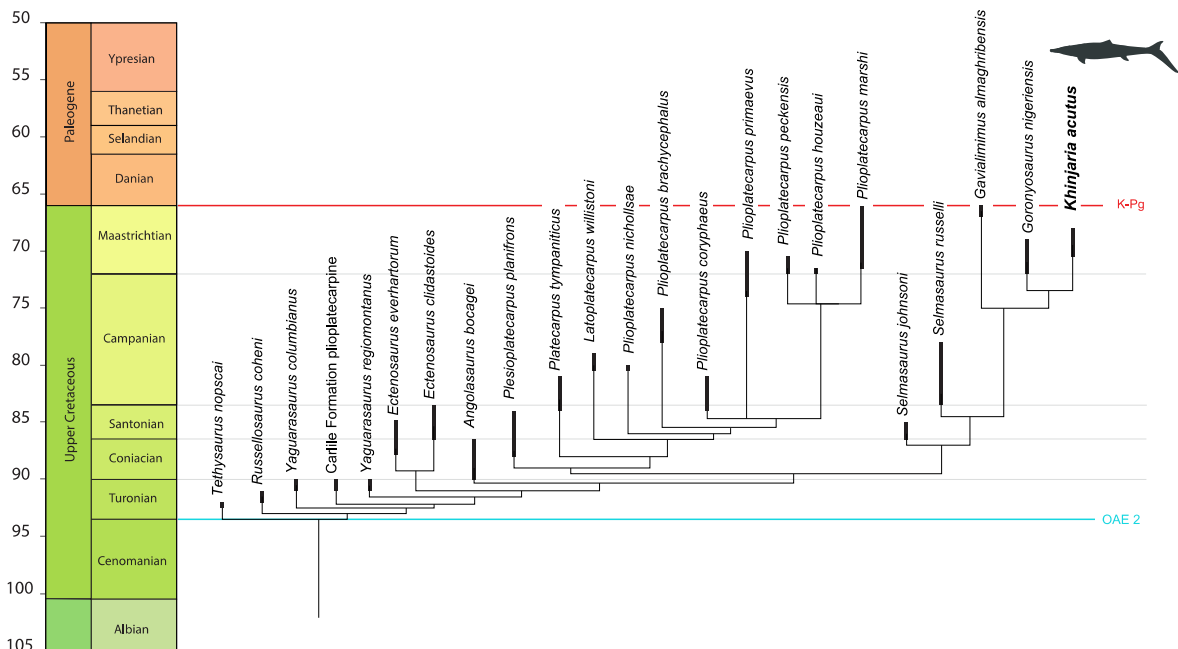
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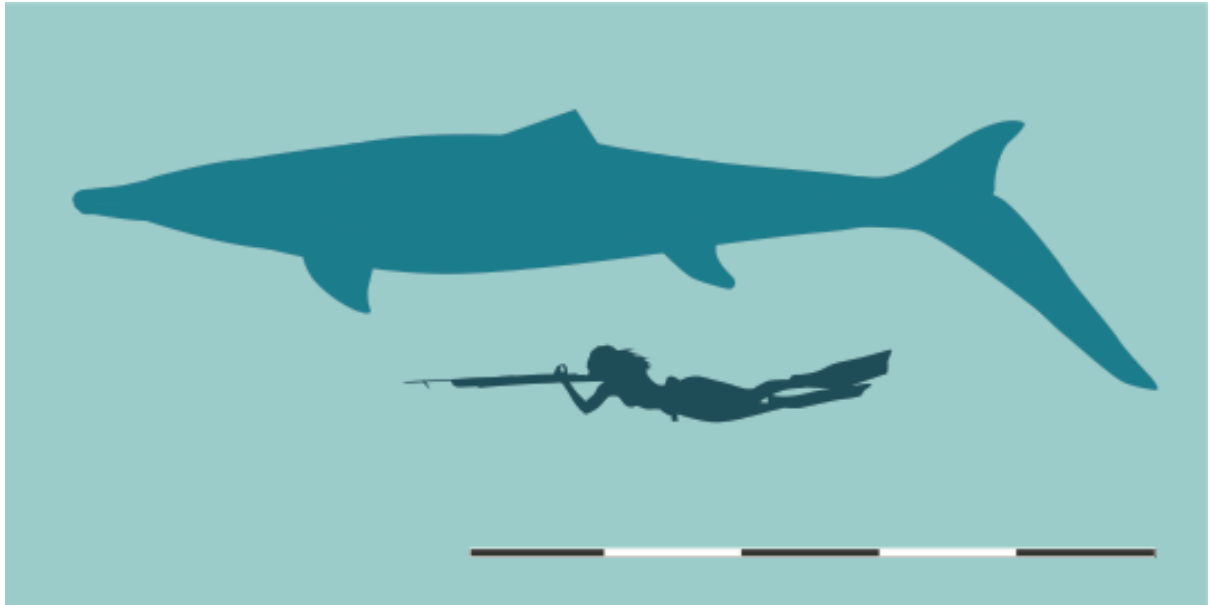
789 **Figure 8.** Skull of *Khinjaria acuta*, reconstructed after MHNM.KHG.521 and *Goronyosaurus*
 790 *nigeriensis*. Scale = 20 cm.

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

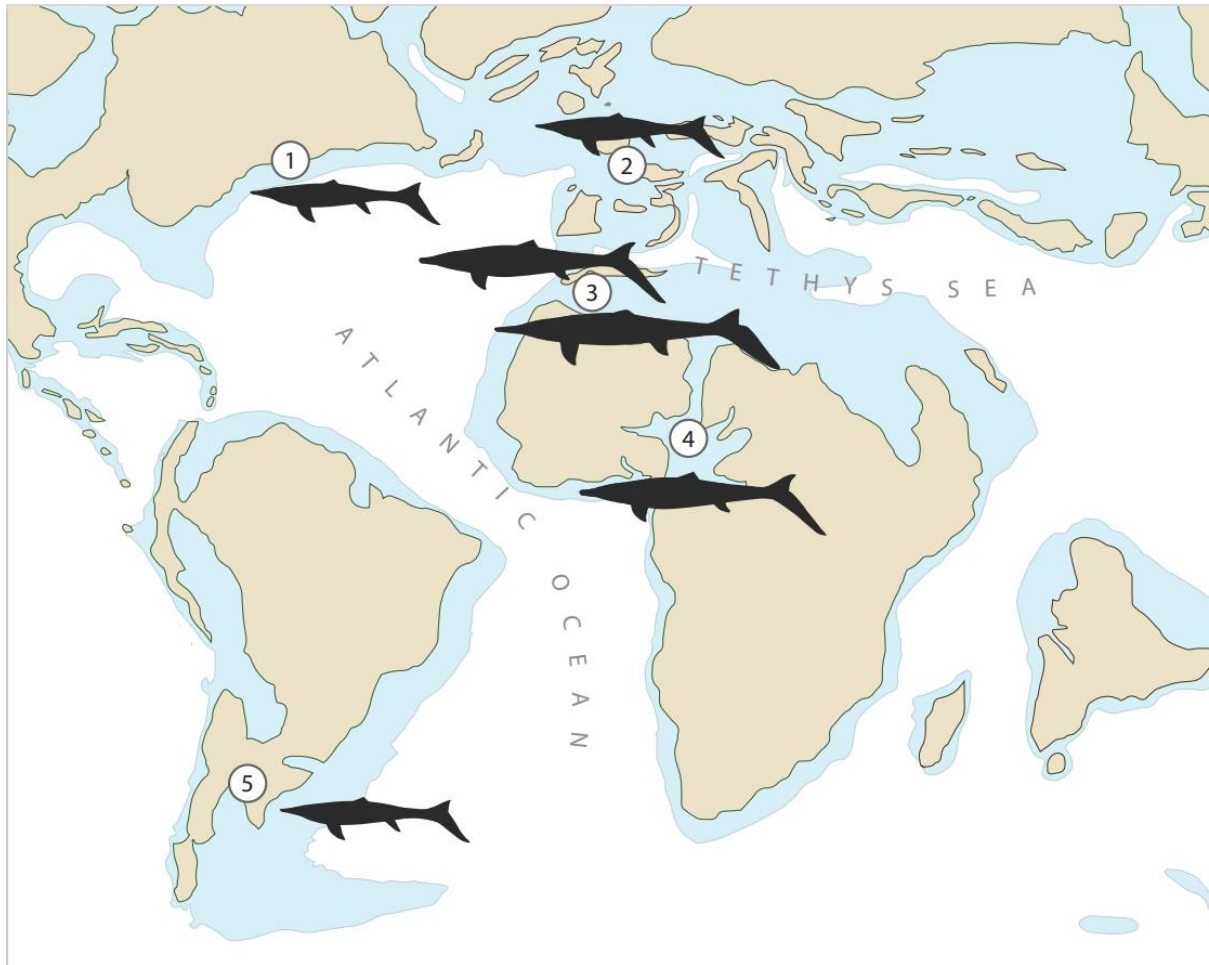


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796 **Figure 10.** *Khinjaria acuta* shown to scale with *Homo sapiens*. Scale = 5 meter.

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

803



804

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