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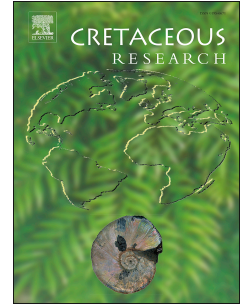
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Author statement

NRL: Conceptualization, Investigation, Writing, Visualization, Supervision

NB: Investigation, Writing Original Draft & Editing

AS: Investigation, Writing Original Draft & Editing

NEJ: Investigation, Writing Original Draft & Editing

Journal Pre-proof

1 ***Xenodens calminechari* gen. et sp. nov., a bizarre mosasaurid**
2 **(Mosasauridae, Squamata) with shark-like cutting teeth from the**
3 **upper Maastrichtian of Morocco, North Africa**

4

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16 A B S T R A C T

17

18 The mosasaurids (Mosasauridae) were a group of lizards that became highly specialized for
19 marine life in the mid-Cretaceous. By the end of the Cretaceous, they had undergone an
20 adaptive radiation, and showed a wide range of body sizes, locomotor styles, and diets. Their
21 ranks included piscivores, apex predators, and durophages. Here, we report a new taxon,
22 *Xenodens calminechari* gen. et sp. nov., from the upper Maastrichtian phosphates of
23 Morocco, with dental specializations unlike those of any known reptile. Teeth form a unique
24 dental battery in which short, laterally compressed and hooked teeth formed a saw-like blade.
25 Unique features of tooth structure and implantation suggest affinities with the durophagous
26 *Carinodens*. The tooth arrangement seen in *Xenodens* not only expands known disparity of
27 mosasaurids, but is unique among Squamata, or even Tetrapoda. The specialized dentition
28 implies a previously unknown feeding strategy, likely involving a cutting motion used to
29 carve pieces out of large prey, or in scavenging. This novel dental specialization adds to the
30 already considerable disparity and functional diversity of the late Maastrichtian mosasaurids
31 and marine reptiles. This provides further evidence for a diverse marine fauna just prior to the
32 K-Pg extinction.

33

34 Keywords: Mosasauridae, Squamata, Cretaceous, Maastrichtian, Africa

35

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37 1. Introduction

38

39 Mosasaurids were a highly specialized group of marine reptiles that first appeared in the early
40 Late Cretaceous, then radiated and dispersed during the latest Cretaceous to occupy a wide
41 range of ecological niches (Russell, 1967; Polcyn et al., 2013; Bardet et al., 2014).
42 Mosasaurids ranged in size from a few meters in length to over 15 meters long (Polcyn et al.,
43 2013); in mass they would have spanned over two orders of magnitude. They were
44 characterized by flipper-like limbs and a shark-like tail (Lindgren et al., 2011; Lindgren et al.,
45 2013) that let them exploit open ocean habitats. Mosasaurids were also specialized divers.
46 Some species show avascular necrosis (“the bends”) suggesting they were capable of deep
47 diving (Rothschild and Martin, 1987), perhaps to kilometers below the surface, as in modern
48 deep-diving elephant seals and sperm whales (Watwood et al., 2006).

49 In their diets and feeding strategies, mosasaurids were similarly diverse. They evolved
50 a range of dental morphotypes (Massare, 1987; Schulp et al., 2013; Bardet et al., 2015): many
51 had numerous small, conical teeth suitable for spearing and holding small prey items such as
52 fish and cephalopods; others had robust, crushing teeth to crack open shelled prey such as
53 mollusks and turtles; still others had bladelike teeth, suitable for cutting apart large prey
54 items, or massive, conical teeth suitable for tearing apart large vertebrates. Stable isotopes
55 confirm that these diverse tooth structures reflect diverse diets (Polcyn et al., 2013; Schulp et
56 al., 2013). Tooth wear similarly implies diverse feeding strategies (Holwerda et al., 2013).

57 The best known mosasaurid faunas are from the Santonian-Campanian Niobrara
58 Chalks, in Kansas (Everhart, 2001). These have been extensively studied for over 100 years.
59 However, peak mosasaurid diversity was seen in the Maastrichtian, when mosasaurids
60 showed maximum disparity in terms of size (Polcyn et al., 2013) and tooth morphology
61 (Schulp et al., 2013; Bardet et al., 2015).

62 During the Maastrichtian, the most diverse mosasaurid fauna known is from Morocco
63 (Bardet et al., 2004; Bardet et al., 2005a; Bardet et al., 2005b; Schulp et al., 2009; Bardet et
64 al., 2010; LeBlanc et al., 2012; Cappetta et al., 2014; Bardet et al., 2017; LeBlanc et al.,
65 2019; Strong et al., 2020). Here, a diverse assemblage has been described based on teeth and
66 skeletal remains from phosphatic deposits. These are located in the Oulad Abdoun Basin,
67 near Khouribga, and the Ganntour Basin, near Ben Guerir (Cappetta et al., 2014; Bardet et
68 al., 2017). This assemblage has produced taxa and tooth morphologies showing diverse
69 feeding strategies (Bardet et al., 2015). Despite extensive study, new species continue to
70 emerge from these deposits, meaning that diversity is still undersampled.

71 Recently, a strange new mosasaurid fossil was recovered from the Sidi Chennane
72 phosphate mine, in the Oulad Abdoun Basin (Fig 1), from beds of late Maastrichtian age
73 (Fig.2). The new mosasaurid exhibits a dental battery with numerous small, short, bladelike
74 teeth packed together to form a saw-like cutting edge. Features of the jaws and teeth suggest
75 affinities with the mosasaurid *Carinodens*, a taxon with crushing teeth (Bardet et al., 2008;
76 Schulp et al., 2009; Holwerda et al., 2013; Mulder et al., 2013; Milàn et al., 2018).

77

78

79

80 **2. Geological Setting**

81

82 The new mosasaurid remains come from the Sidi Chennane phosphate mine in the
83 Oulad Abdoun Basin of Khouribga Province, Morocco (Fig. 1). Strata exposed here by
84 mining span the Cretaceous-Paleocene boundary, extending in time from the mid?-late
85 Maastrichtian (Kocsis et al., 2014) into the early and middle Eocene (Fig. 2). The phosphatic
86 deposits are divided into a series of beds or ‘couches’ for the purposes of mining.

87 From the top down, these are Couche 0, Couche I, Couche II, and Couche III. The
88 boundary between Couche I and II corresponds to the Paleocene-Eocene boundary and
89 Paleocene-Eocene Thermal Maximum. The boundary between Couche II and III corresponds
90 to the Cretaceous-Paleogene transition, but the K-Pg boundary itself and the Lower
91 Paleocene are not preserved (Bardet et al., 2017). Couche III lacks either calcareous fossils,
92 such as ammonites, bivalves, and foraminifera, or organic microfossils, to constrain its age.
93 However, shark teeth correlate Couche III to the late Maastrichtian (Arambourg, 1935;
94 Cappetta, 1987). Oxygen and carbon isotope stratigraphy corroborate this assignment (Kocsis
95 et al., 2014).

96 The fossil described here was collected by locals working in the mines, rather than by
97 paleontologists, complicating attempts to constrain stratigraphy and provenance. However,
98 the pale white bone, and coarse grey matrix are typical of fossils from upper Couche III at
99 Sidi Chennane.

100 Couche III contains an exceptional assemblage of fossil marine vertebrates. Marine
101 reptiles, including diverse mosasaurid squamates (Bardet et al., 2004; Bardet et al., 2005a;
102 Bardet et al., 2005b; Bardet et al., 2008; Schulp et al., 2009; LeBlanc et al., 2012; Bardet et
103 al., 2015), elasmosaurid (Vincent et al., 2011; Vincent et al., 2013), and chelonioid turtles
104 (Bardet et al., 2013; Lapparent de Broin et al., 2013) dominate the community. Bony fishes
105 and selachians (Arambourg, 1952) were diverse and abundant (see Bardet et al., 2017 for
106 faunal list and references). Above, diverse pterosaurs exploited the seas (Pereda-Suberbiola et
107 al., 2003; Longrich et al., 2018). Rare dinosaurs suggest a nearby terrestrial community
108 (Pereda-Suberbiola et al., 2004; Longrich et al., 2017; Longrich et al., 2020).

109 The epicontinental sea where fossils deposited, at the edge of the West African
110 Craton, was characterized by upwelling (Martin et al., 2017). Upwelling could explain the
111 high abundance, diversity and disparity of marine predators here (Martin et al., 2017). The

112 Couche III assemblage may sample not just a diverse time in mosasaurid history, but a
113 uniquely diverse habitat — a biodiversity hot spot.

114

115

116 Abbreviations. MHNM Muséum d'Histoire naturelle de Marrakech, Université Cadi Ayyad,
117 Morocco; OCP, Office Chérifien des Phosphates, Morocco.

118

119

120 **3. Results**

121

122 *3.1 Systematic paleontology*

123

124 SQUAMATA Opper (1811)

125 MOSASAURIDAE Gervais (1852)

126 MOSASAURINAE Gervais (1852)

127

128 *Xenodens calminechari* gen. et sp. nov.

129

130 *Etymology.* The genus name is derived from the Greek *xenos*, 'strange', and Latin *dens*,
131 'tooth'. The species name derives from the Arabic *calminechari* (كالمنشار), 'like a saw'.

132

133 *Holotype.* MHNM.KH.333 (Figs. 3-5)

134

135 *Horizon and locality.* Upper Maastrichtian of Sidi Chennane phosphate mines, Khouribga
136 Province, Morocco. Matrix and preservation are typical of Sidi Chennane, with a bleached

137 white bone and pale, grey matrix characteristic of Couche III at Sidi Chennane (Fig. 3). The
138 matrix is coarse, with a small fraction of fine particles, and contains teleost fragments. This
139 coarse matrix is typical of fossils from upper Couche III at Sidi Chennane.

140

141 *Diagnosis.* Small mosasaurid (Figs. 6, 7). Anterior end of maxilla long and tapered in lateral
142 view, with premaxilla-maxilla suture forming an angle of 15° with the dentigerous margin.
143 Premaxillary-maxillary suture extends posteriorly 6, perhaps 7, tooth positions. At least
144 thirteen maxillary teeth. Marginal tooth crowns low, strongly laterally compressed, up to
145 twice as long anteroposteriorly as broad labiolingually. Crowns with strongly convex anterior
146 surface bearing a cutting carina. Low apicobasal ridge along the anterior half of the crown
147 defining a shallow groove or gutter on lingual and labial surfaces. Tooth apex strongly
148 hooked posteriorly, behind the base of the crown, and posteriorly concave edge with an
149 unserrated carina. Completely smooth enamel. Bases of crowns oriented obliquely relative to
150 dentigerous margin of jaw in lateral view. Teeth closely packed to form a saw-like cutting
151 edge. Roots of adjacent teeth expanded, fusing into a continuous ridge of dental bone.
152 Anteroposteriorly elongated replacement pits.

153

154 3.2 Description

155

156 **Maxilla (Figs. 3, 4).** The maxilla is small, measuring 100 mm in length. It is broken
157 posteriorly; the jugal process may have extended another centimeter or two. At its apex it
158 measures 26 mm and posteriorly it measures 20 mm tall.

159 The anterior end of the maxilla forms a concave groove for the premaxilla, such that
160 flanges of the maxilla clasped the premaxilla laterally and medially. The medial flange is
161 larger than the lateral flange.

162 In lateral view, the maxilla's tip has an obtuse 'v' shape where it contacted the
163 premaxilla, so that the premaxilla underlapped the maxilla ventrally and overlapped it
164 dorsally. Anterodorsally the premaxillary contact is broadly convex, a feature shared with
165 *Clidastes* and Mosasaurinae (Schulp et al., 2008). The suture continues posteriorly to form a
166 long, straight contact with the premaxilla. This dorsal margin has a thin, sharp edge that
167 would have contacted the premaxilla in a loose suture. The suture extends posteriorly to the
168 sixth or perhaps seventh alveolus. A posteriorly extended suture is derived within
169 mosasaurids. The suture extends as far as the third tooth position in *Prognathodon* spp.
170 (Schulp et al., 2008) and *Globidens* cf. *phosphaticus* (Polcyn et al., 2010), as far as the fourth
171 tooth in *Globidens alabamensis* (Gilmore, 1912) and *Mosasaurus hoffmanni* (Lingham-
172 Soliar, 1995), to the fifth or sixth tooth in *Clidastes* (Russell, 1967), and the sixth or seventh
173 tooth in *Halisaurus arambourgi* (Bardet et al., 2005b). The suture lies at a low angle, about
174 15 degrees, relative to the maxilla's ventral margin. Posteriorly there is a large, concave
175 embayment for the retracted external naris.

176 Ventral and posterior to the naris, the sutural contact for the prefrontal is preserved
177 with its typical zigzag shape. Given the shape of this suture and its wide dorsal extension, the
178 prefrontal probably participates in the naris.

179 The lateral surface of the maxilla, just dorsal to the gum line, is covered by
180 neurovascular foramina corresponding to the terminal branches of the maxillary nerve, as is
181 typical of mosasaurids (Fig. 4A) (Russell, 1967). These foramina are very small and
182 numerous anteriorly, then become larger posteriorly and form a distinct line. The line is
183 distinctly elevated above the maxilla's ventral margin, an unusual condition shared with
184 *Globidens alabamaensis* (Gilmore, 1912) but not other *Globidens* (Polcyn et al., 2010), or
185 other Mosasaurini. The elaboration of these foramina may be associated with the
186 development of nerves for mechanoreceptors (Martill et al., 2021), which similar to modern sea

187 snakes (Crowe-Riddell et al., 2016; Crowe-Riddell et al., 2019), may have been used to sense
188 water pressure.

189 In medial view, the dental parapet is deep posteriorly then strongly tapers anteriorly,
190 being reduced to a low ridge at the anterior end (Fig. 4). It is sharp and distinctly separated
191 from the body of the maxilla by a groove. Anteriorly, a low, thin, mediodorsally directed
192 flange of bone lies just above the dental parapet. Just above this flange a large, oval foramen.
193 The medial dental parapet appears slightly less developed ventrally than the lateral one. This
194 character is seen in primitive mosasaurids such as *Russellosaurus coheni* (Polcyn and Bell,
195 2005) and *Halisaurus arambourgi* but also in *Globidens* spp. (Gilmore, 1912; Polcyn et al.,
196 2010).

197 Positions for 13 teeth are preserved. Two or three more were probably present
198 posteriorly where the maxilla is broken away.

199
200 **Dentition.** Tooth crowns (Fig. 5) are bladelike and labiolingually flattened to a degree not
201 seen in other Mosasauridae, although this condition is approached in *Carinodens* (Schulp et
202 al., 2009). Here the teeth are more like those of varanids or theropods than other mosasaurids,
203 where teeth have a more conical shape. Crowns are low and trapezoidal in lateral view. There
204 is a strongly convex, crescentic anterior margin with a sharp carina, a hooked apex, and a
205 weakly concave posterior margin with an unserrated carina. Again, teeth are like those of
206 *Carinodens* (Schulp et al., 2009) in being low and broad, with convex anterior edges. Enamel
207 is totally smooth, and lacks the ornamentation seen in *Carinodens* (Schulp et al., 2009),
208 *Globidens* (Bardet et al., 2005a; Polcyn et al., 2010), and some *Prognathodon* species
209 (Konishi et al., 2011), where a rugose texture of coarse bumps and wrinkles extends down
210 from the tooth apex.

211 The enameled crowns are borne on a pedicel formed of bone of attachment (Rieppel
212 and Kearney, 2005) as in other Mosasauridae (Russell, 1967; Caldwell, 2007). In most
213 Mosasauridae, e.g. *Mosasaurus* (Rieppel and Kearney, 2005) this pedicel is tall, but in
214 *Xenodens* it is short, as in *Carinodens* and *Globidens*. Crowns do not sit perpendicular to the
215 pedicel, as typical of Mosasauridae, and instead are slightly inclined backwards. The line
216 formed by the base of the enamel therefore lies at an oblique angle to the jaw. This is another
217 unusual feature shared with *Carinodens* (Schulp et al., 2009).

218 Tooth roots insert into thecae, formed laterally by the lingual margin of the maxilla,
219 medially by a ventrally extended, bony parapet of the maxilla, and anteriorly and posteriorly
220 by septa formed of interdental bone (Rieppel and Kearney, 2005; Caldwell, 2007). Tooth
221 roots are mediolaterally compressed and expanded anteroposteriorly so that adjacent roots
222 contact each other and fuse to create a wall of bone supporting the teeth. This configuration is
223 unique among squamates, with the exception of *Carinodens*, which shares these fused tooth
224 bases (Schulp et al., 2009).

225 Tooth roots bear large replacement pits, as in most mosasaurids (Bell Jr, 1997;
226 Rieppel and Kearney, 2005). These pits extend deep into the pedicel forming interdental
227 crypts. The openings for these crypts are developed as anteroposteriorly elongate and narrow
228 slots. A similar morphology is seen in *Carinodens* (LeBlanc et al., 2012), and to a much
229 lesser degree, in *Eremiasaurus* (LeBlanc et al., 2012). These openings are displaced
230 posteriorly relative to the crown, which seems to result from anterior displacement of the
231 crown relative to the tooth root.

232 Teeth are closely packed, with a slight gap between the anterior carina of one tooth
233 and the posterior carina of the other. A similar arrangement is seen in *C. minalmamar*
234 (Schulp et al., 2009). The effect is to create a single, serrated cutting edge, like a sawblade.

235

236

237 **4. Discussion**

238

239 *4.1 Affinities of Xenodens*

240

241 Despite the unusual morphology of the teeth of *Xenodens*, multiple characters allow
242 confident referral to the Mosasauridae. These include a long, low, triangular maxilla,
243 elongate premaxilla-maxilla contact, such that the naris would be posteriorly retracted; tooth
244 crowns being borne on bony pedicels, tooth bases implanting into distinct thecae, and deep
245 replacement pits developing as crypts.

246 The unique dental morphology and arrangement in *Xenodens* warrants recognition of
247 a distinct genus and species. Several features suggest affinities with *Carinodens*, a
248 specialized, durophagous mosasaurid. Three species of *Carinodens* have been described:
249 *Carinodens belgicus*, from the upper Maastrichtian of Belgium and the Netherlands, *C.*
250 *minalmamar*, from the upper Maastrichtian of Morocco, and *C. palisticus* from Jordan
251 (Kaddumi, 2009). Isolated teeth of *Carinodens* have been described from elsewhere (Schulp
252 et al., 2009; Mulder et al., 2013; Milàn et al., 2018).

253 Teeth of *Xenodens* resemble *Carinodens* in many respects. These include (i) low,
254 anteroposteriorly broad crowns, (ii) the strongly convex anterior carina, (iii) labiolingual
255 compression of the crown. The teeth however differ from those of *Carinodens* in being
256 posteriorly hooked, with sharp apices, and in being much more laterally compressed. The
257 enamel is also completely smooth, unlike the sculpturing and sulci seen in both *Carinodens*
258 species and particularly in *C. belgicus*, which in this feature is like that of *Globidens*.

259 Teeth of *Xenodens* also resemble *Carinodens* in terms of implantation and
260 arrangement. Unlike other mosasaurids, (v) tooth crowns are obliquely oriented relative to

261 the dental parapet in lateral view, (vi) tooth pedicels are anteroposteriorly expanded and
262 contacting, forming a continuous ridge of bone, and (vii) alveolar crypts are anteroposteriorly
263 expanded in both genera.

264 Finally, (viii) the small reconstructed size of *Xenodens* and *Carinodens* and (xi) the
265 relatively long, straight and low maxilla and high tooth count (mirroring the dentary of
266 *Carinodens*) suggest affinities between the two.

267 Given that *Carinodens* is known from lower jaws and *Xenodens* from the upper, this
268 poses the question of whether the two could come from one, heterodont animal. However, the
269 shape, arrangement and ornamentation of the teeth in *Xenodens* being so distinct from
270 *Carinodens*, it is unlikely they are the same species. Moreover, in mosasaurids as a whole,
271 upper and lower teeth are so similar that it is difficult to determine whether teeth come from
272 the upper or lower jaw (e.g. Russell, 1967, p 56-57). From a functional standpoint, pairing
273 *Xenodens*-like upper teeth and *Carinodens*-like lower teeth is implausible since it would
274 imply that upper and lower teeth functioned in radically different ways- one cutting soft-
275 bodied prey, the other crushing armor. Different tooth functions are seen along the tooth row
276 in squamates, and some species combine cutting and crushing teeth (e.g. *Varanus niloticus*).
277 However, such variation is between anterior and posterior teeth, never (to our knowledge)
278 uppers and lowers.

279
280 Apomorphies therefore identify *Xenodens* and *Carinodens* as a clade, exclusive of other
281 mosasaurids. Beyond this, their relationships are unclear.

282 *Carinodens* has been allied with *Globidens*, in Globidensini (Schulp et al., 2004;
283 Mulder et al., 2013; Milàn et al., 2018). The two genera share several adaptations, including a
284 blunt tooth apex. *C. belgicus* also shares with *Globidens* rugose, ornate enamel (possibly
285 absent in *C. minalmamar*) and both *Carinodens* species share the characteristic sulci present

286 in some *Globidens* (Schulp et al., 2009). Blunt crowns and rugose, anastomosing enamel
287 texture are also seen in some species of *Prognathodon* including *P. currii* where it is
288 pronounced (Schulp, 2006). *Carinodens* and *Globidens* also share extreme heterodonty, with
289 anterior teeth reduced, and middle teeth greatly enlarged. Blunt, inflated tooth crowns and
290 rugose enamel are adaptations for durophagy (Schulp et al., 2004).

291 However, such characters are highly homoplastic. Blunt teeth and heterodonty
292 evolved repeatedly in durophagous squamates. Molariform teeth are found in the caiman
293 lizard *Dracaena* (Teiidae) (Dalrymple, 1979), the Nile monitor, *Varanus niloticus*
294 (Varanidae) (D'Amore, 2015), the scincid *Tiliqua scincoides* (Scincidae) (Estes and
295 Williams, 1984), the anguid *Diploglossus cruscus* (Anguidae) (Estes and Williams, 1984).
296 It also evolved independently in the amphisbaenians *Trogonophis* (Trogonophidae)
297 (Westphal et al., 2019) and *Amphisbaena ridleyi* (Amphisbaenidae) (Pregill, 1984).
298 Molariform teeth are also found in extinct lizards such as *Odaxosaurus piger* (Anguidae)
299 (Pregill, 1984) and *Chromatogenys tiliqoides* (Scincidae) (Makádi and Nydam, 2015).

300 Ridged enamel is also seen in taxa with molariform teeth, including *Tiliqua*,
301 *Diploglossus*, and *Odaxosaurus*. These features –molariform teeth, heterodonty, and enamel
302 ridges– form a suite of functionally correlated characters that evolved repeatedly in
303 durophagous lizards. Even within Mosasauroida, durophagy likely evolved multiple times –
304 once in the lineage leading to *Globidens*, again within *Prognathodon*, and in the basal
305 mosasauroid *Coniasaurus* (Caldwell and Cooper, 1999).

306 This does not prove that these features are convergent but suggests caution in using
307 homoplastic characters. The absence of durophagous adaptations in *Xenodens* shows these
308 characters are homoplastic even in *Carinodens*-like mosasaurids. If *Xenodens* and
309 *Carinodens* are related, then durophagous adaptations were either lost in *Xenodens* (and
310 absence of durophagy is a reversal) or independently gained in *Carinodens* from a non-

311 durophagous common ancestor (and durophagy in *Carinodens* and *Globidens* are
312 convergent).

313 Last, there are differences between the jaws of *Carinodens*-like mosasaurids and
314 *Globidensini*. *Carinodens* has a longer, more slender, straighter mandible than *Globidens* and
315 *Prognathodon*, where it is short, deep, and bowed (Lingham-Soliar and Nolf, 1989; Polcyn et
316 al., 2010; Konishi et al., 2011). The low, triangular maxilla of *Xenodens* and *Carinodens* also
317 differs from *Globidens* and *Prognathodon* (ibid). Instead, the long, low profile of the maxilla
318 and elongate premaxilla-maxilla suture are like Mosasaurini. Strikingly, postcrania described
319 for *Carinodens* (Kaddumi, 2009) show the short, broad first metacarpal and phalanges of
320 digit I with anterior processes on their proximal and distal ends, giving them a ‘butterfly’
321 appearance. Such processes are well-developed on the first manus and pes digits in
322 *Mosasaurus* and *Plotosaurus* (Russell, 1967; Lingham-Soliar, 1995; Lindgren et al., 2008)
323 but not in other Mosasauridae, suggesting that *Carinodens* (and by extension, *Xenodens*) are
324 part of Mosasaurini.

325 Only the swollen tooth crown seems to connect *Xenodens* to the *Globidensini*, though
326 this character is weakly developed compared to *Globidens*, *Carinodens* and *Prognathodon*
327 (Schulp et al., 2004).

328 The elevated medial parapet of the dentary and the well-developed tooth crypts are
329 both derived features, shared with Mosasaurinae and Tylosaurinae and absent in Halisaurinae
330 (Schulp et al., 2004). Beyond this, few features are available to resolve the higher-level
331 affinities of the *Carinodens-Xenodens* group.

332

333

334 *4.2 Function and Ecology*

335

336 The unusual dental battery of *Xenodens* indicates a specialized feeding mode. Mosasaurid
337 teeth as a whole present a common Bauplan, generally being conical in cross-section,
338 homodont to weakly heterodont, and widely spaced (Russell, 1967). The “standard” or
339 default plesiomorphic mosasaurid teeth are small, acutely conical hooks, like those of
340 *Tethysaurus*, (Bardet et al., 2003), *Russellosaurus* (Polcyn and Bell, 2005), and *Halisaurus*
341 (Bardet et al., 2005b). Such teeth are suitable for piercing small prey, indicating a diet of
342 small prey like fish and soft-bodied invertebrates such as cephalopods.

343 However, over the course of the Late Cretaceous, mosasaurid teeth evolved a wide
344 range of morphologies, suitable for piercing and holding (*Halisaurus*, *Plioplatecarpus*,
345 *Clidastes*, etc.), piercing and cutting (*Mosasaurus*, *Tylosaurus*, etc.) or crushing (*Globidens*,
346 *Prognathodon currii*, *Carinodens*, etc.), following the morphoguilds defined by Massare
347 (Massare, 1987).

348 In some species, such as *Eremiasaurus heterodontus* (LeBlanc et al., 2012) and
349 *Mosasaurus hoffmanni* (Lingham-Soliar, 1995) (Lingham-Soliar and Nolf, 1989), marginal
350 teeth are large, laterally compressed, and serrated. This morphology is likely effective for
351 seizing and tearing apart large prey. A similar morphology is seen in some varanids, such as
352 *Varanus acanthurus*.

353 In others, like *Globidens* (Gilmore, 1912), *Carinodens* (Schulp et al., 2009), and to a
354 lesser degree, *Prognathodon currii* (Christiansen and Bonde, 2002) lateral teeth are large,
355 straight, with blunt apices, and low, bulbous crowns. These adaptations facilitate crushing of
356 hard prey, either shelled invertebrates or bony vertebrates. Ornament in the form of bumps
357 and ridges is well-developed on the enamel.

358 Tooth form and arrangement in *Xenodens* are different from any previously described
359 morphology. Teeth are laterally compressed and bladelike to a degree unlike any other
360 mosasaurid or squamate. Crowns are low and rectangular, the apex is hooked, and carinae are

361 sharp but unserrated. Crowns are closely packed, leaving narrow slots between adjacent
362 crowns. The tooth arrangement creates a slotted saw blade, similar to a circular saw. There is
363 no similar arrangement in any other mosasaurid or lizard, or to our knowledge, any other
364 tetrapod.

365 Surprisingly, a similar arrangement is seen in sharks, specifically dogfish
366 (Squaliformes) (Fig. 8). Here, low, hooked, bladelike teeth are packed in a row to form a
367 cutting blade (Underwood et al., 2016). This arrangement is seen in upper and lower jaws of
368 most dogfish (Squalidae) and in the lower jaws of gulper sharks (Centrophoridae), sleeper
369 sharks (Somniosidae) and lantern sharks (Etmophoridae) (Underwood et al., 2016). A
370 sawblade is also seen in piranhas, the pycnodont *Serrasalmimus* (Vullo et al., 2017), and the
371 squalimorph *Isistius* (cookiecutter shark) (Underwood et al., 2016) but these fishes differ in
372 that they have fewer and larger teeth, and the crowns are taller and more triangular.

373 In dogfish sharks, the jaws apparently function as cutting blades. Long-axis roll of the
374 jaws, a 'head shake' (Wilga and Motta, 1998) is used to saw prey in half. The bladelike lower
375 teeth of Pacific sleeper sharks (*Somniosus pacificus*) allow them to gouge huge,
376 hemispherical bolts of flesh from prey, as seen in large halibut caught on long line gear (NRL
377 pers. obs.). The specialized cutting blades seen in Squaliformes therefore seem to be an
378 adaptation allowing for relatively small predators to feed on proportionately large prey.

379 Despite these specializations, Squaliformes have broad diets, and take a range of food.
380 *Squalus acanthias* feeds on fish, crustaceans, mollusks, nematodes and sea anemones (Jones
381 and Geen, 1977; Avsar, 2001). Dogfish also scavenge on marine mammals (Bigelow, 1994).
382 Rather than limiting the diet, specialized jaws and teeth seem to expand the range of prey,
383 and may allow small sharks to feed on larger prey items than would otherwise be possible.
384 Similarly, the piranha's bladelike teeth are effective for eating meat but piranhas also take
385 fruit and nuts (Prudente et al., 2016).

386 By analogy, the bladelike teeth in *Xenodens* may have allowed it to take a range of
387 prey. Given the animal's small estimated size, prey likely included small invertebrates such
388 as crustaceans and cephalopods, fish, and potentially, larger prey items, including large fish
389 and cephalopods, or scavenging of large mosasaurids and plesiosaurs (Fig. 9).

390 So far, *Xenodens* appears to be rare in the fauna, but given the abundance of isolated
391 mosasaur teeth in the phosphates, it is likely that teeth are present in the assemblage but
392 misidentified as shark teeth. *Xenodens* teeth can be distinguished from other mosasaurids by
393 their distinctive shape. Shed *Xenodens* teeth could readily be distinguished from shark's teeth
394 by the absence of a root, and a basal resorption pit, which are characteristic of shed
395 mosasaurid teeth.

396

397 **5. Conclusions.**

398 A new mosasaurid, *Xenodens calminechari* gen. et sp. nov., is represented by a small upper
399 jaw from the upper Maastrichtian phosphates of Morocco. The new mosasaurid exhibits a
400 dentition that is not just unique among mosasaurids, but among tetrapods, with bladelike
401 teeth closely packed to form a serrated cutting surface. Some sharks convergently evolved
402 similar dentition (Underwood et al., 2016), suggesting that the jaws of *Xenodens* were used to
403 carve apart large prey items. Regardless of the jaw's precise function, the unusual dental
404 morphology of *Xenodens* suggests a feeding strategy that was unique among mosasaurids or
405 other marine tetrapods. Along with other specialized morphologies in mosasaurids – the
406 button-shaped, crushing teeth of *Carinodens* and *Globidens*, the peg-like teeth of
407 *Prognathodon currii*, bladelike teeth in *Eremiasaurus*, or the conical, orca-like teeth in large
408 *Prognathodon* sp. – the teeth of *Xenodens* expand the remarkable functional and ecological
409 diversity of late Maastrichtian mosasaurids, especially in the African Tethys (Bardet et al.,
410 2015; Bardet et al., 2017). Insofar as predator diversity is driven by abundance and diversity

411 of prey, high mosasaurid diversity prior to the K-Pg extinction suggests a diverse, stable
412 marine ecosystem, cut down in its prime by the Chicxulub impact.

413

414

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416

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640

641 **Table 1**

642 List of Mosasauridae from the Phosphates of the Oulad Abdoun Basin, Morocco, upper

643 Couche III, latest Maastrichtian. Modified from Bardet et al. (2017)

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645

646 Mosasaurinae

647 *Mosasaurus beaugei* Arambourg, 1952648 *Eremiasaurus heterodontus* LeBlanc et al., 2012649 *Prognathodon* aff. *currii* Christiansen & Bonde, 2002650 *Prognathodon* aff. *saturator*651 *Globidens* cf. *phosphaticus* Bardet & Pereda Suberbiola, 2005652 *Carinodens minalmamar* Schulp et al., 2009653 *Carinodens belgicus* (Woodward, 1891)654 *Xenodens calminechari* new genus and species

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657 Plioplatecarpinae

658 *Gavialimimus almaghribensis*, Strong et al. 2020

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661 Halisaurinae

662 *Halisaurus arambourgi* Bardet & Pereda Suberbiola, 2005a

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FIGURE CAPTIONS

Fig. 1. Map of Northern Morocco showing the location of the Sidi Chennane phosphate mines in the Khouribga region.

Fig. 2. Stratigraphic column of Sidi Chennane, Khouribga Province, showing the stratigraphic occurrence of *Xenodens*. Stratigraphic column after Kocsis et al. (2014).

Fig. 3. MHNM.KH.331, *Xenodens calminechari* new genus and species, holotype left maxilla in matrix. Maastrichtian, Sidi Chennane, Oulad Abdoun Basin, Khouribga province, Morocco.

Fig. 4. MHNM.KH.331, *Xenodens calminechari* new genus and species. Maastrichtian, Sidi Chennane, Oulad Abdoun Basin, Khouribga Province, Morocco. Holotype left maxilla, in lateral (A), ventral (B), medial (C), and dorsal (D) views.

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694 **Fig. 5.** MHNM.KH.331, dentition of *Xenodens calminechari* new genus and species.
695 Maastrichtian, Sidi Chennane, Oulad Abdoun Basin, Khouribga Province, Morocco. In
696 medial (A), lateral (B) and occlusal (C) views.

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698 **Fig. 6.** Reconstruction of the skull of *Xenodens calminechari*, after *Mosasaurus hoffmanni*
699 (Lingham-Soliar, 1995).

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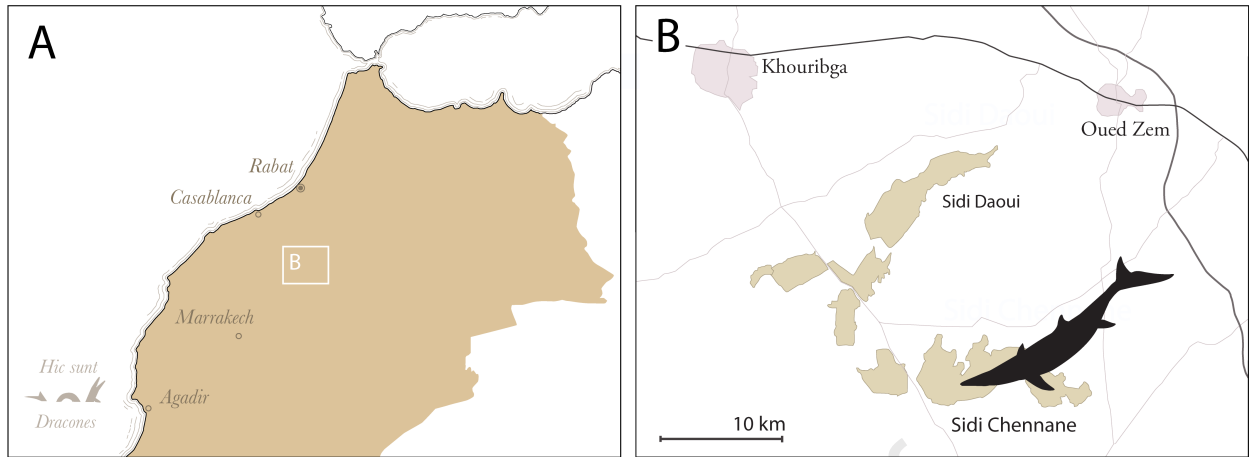
701 **Fig. 7.** Silhouette showing approximate size of *Xenodens calminechari*, with *Homo sapiens*
702 for scale. Scale bar = 1 meter.

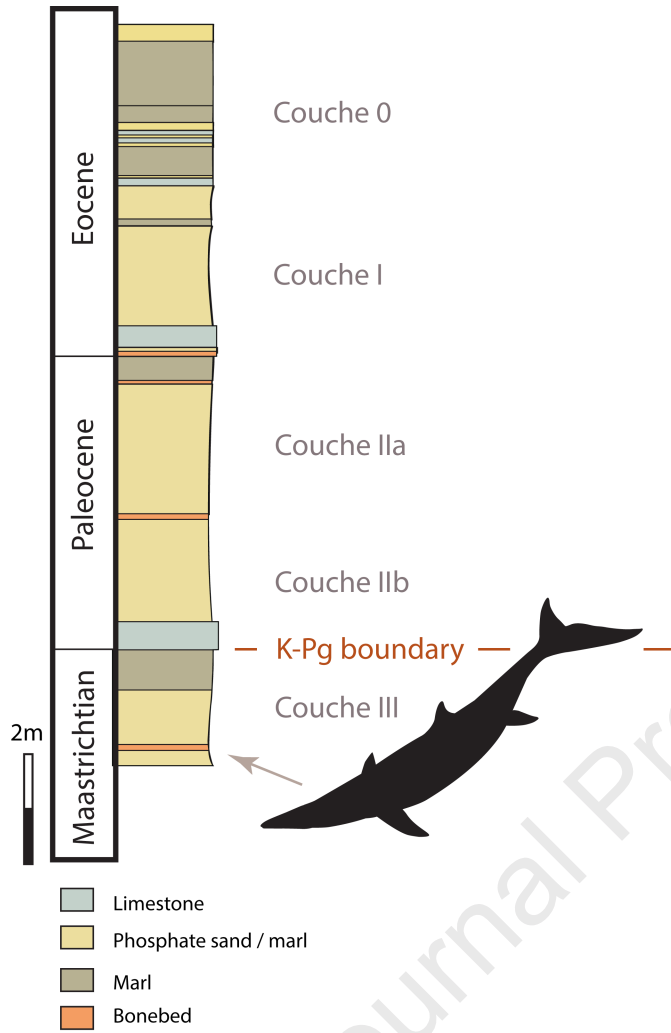
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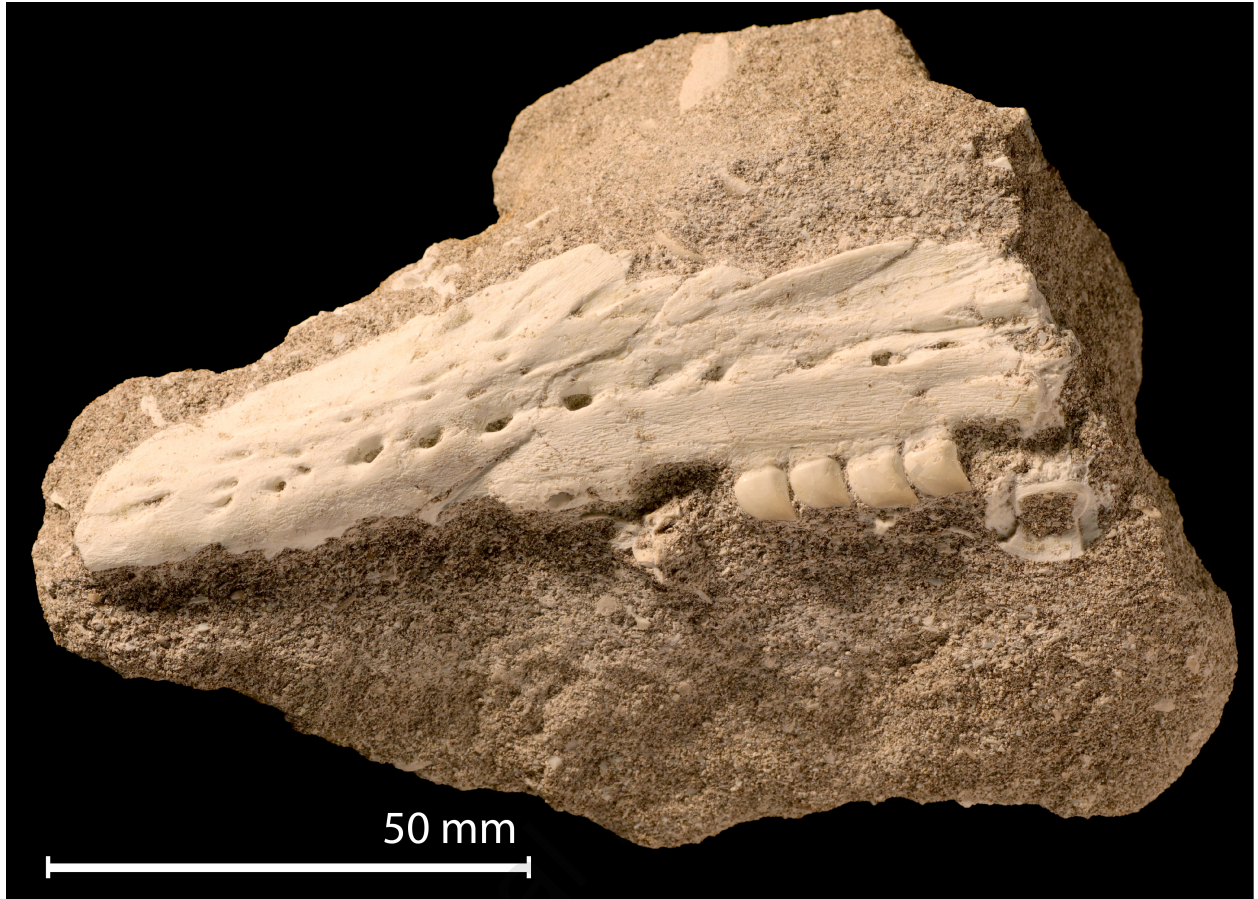
704 **Fig. 8.** Dogfish shark, *Squalus acanthias*, upper and lower teeth. Note teeth arranged in
705 serrated cutting blades. Courtesy Ross Robertson, Smithsonian Tropical Research Institute.

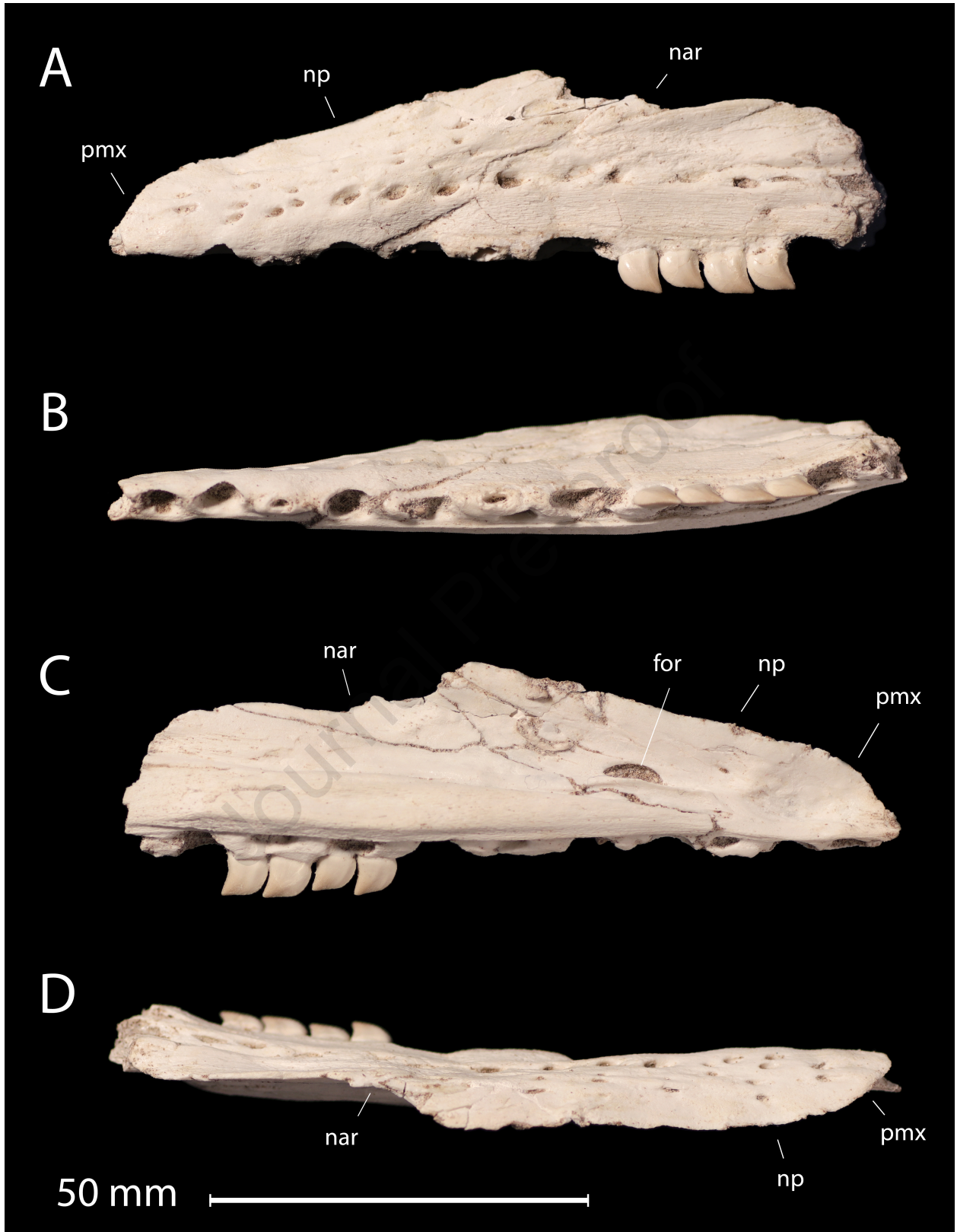
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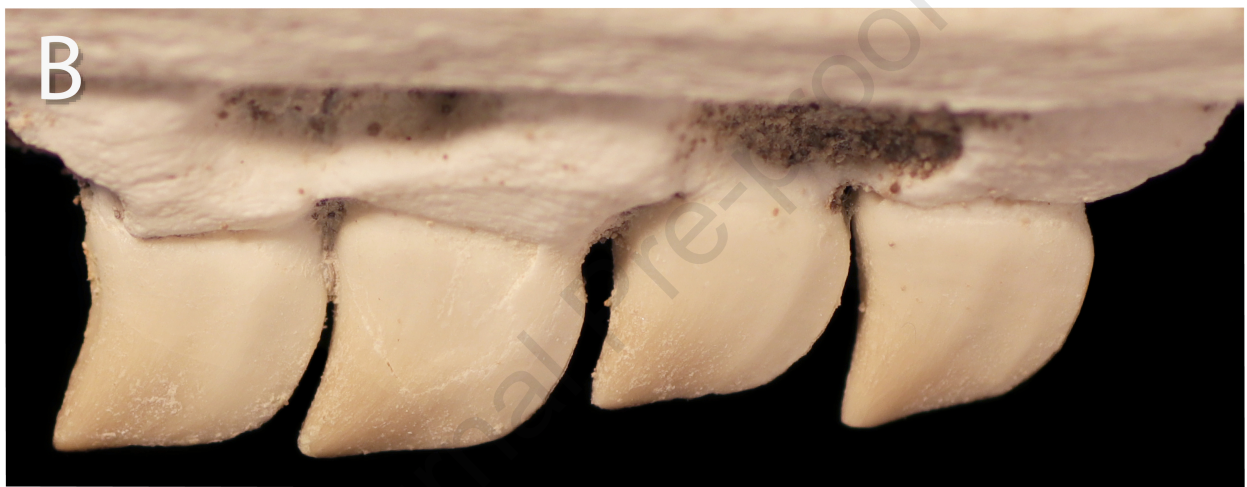
707 **Figure 9.** Reconstruction of *Xenodens calminechari* scavenging a carcass of the elasmosaurid
708 *Zarafasaura oceanis*. Artwork by Andrey Atuchin, 2020.

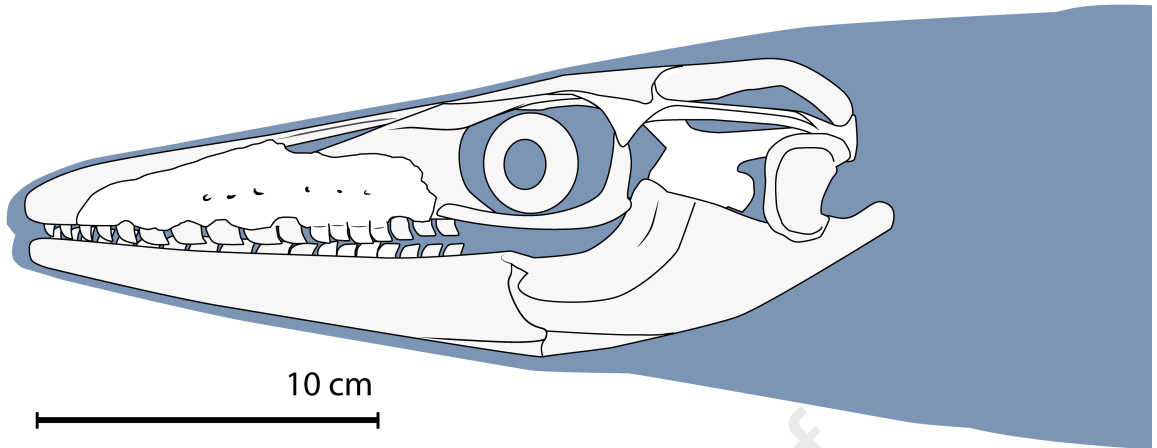




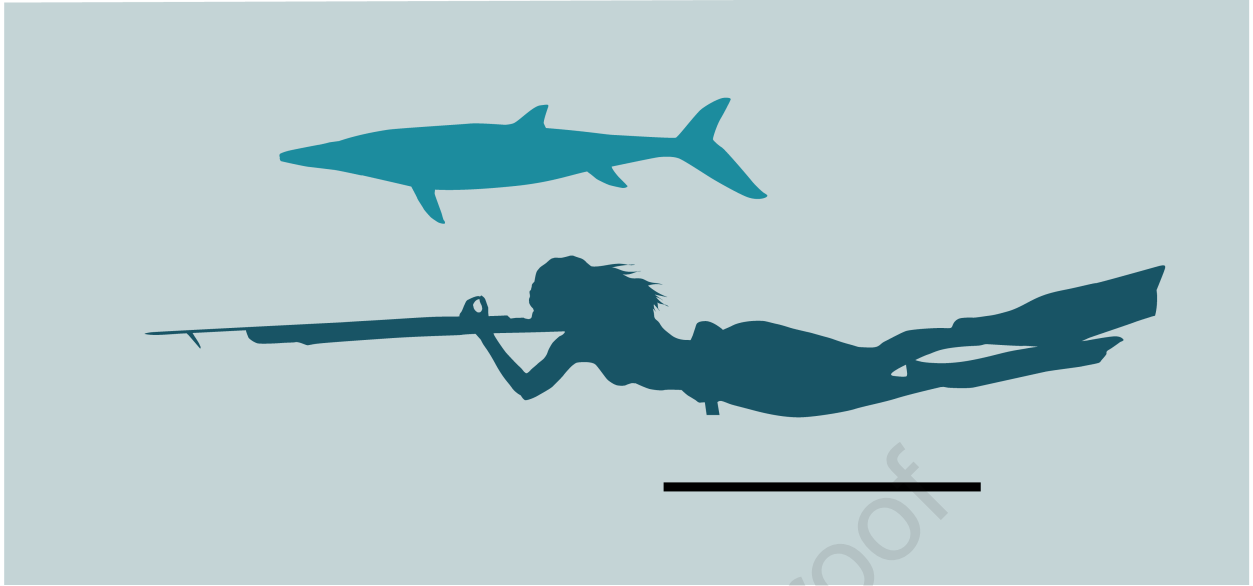








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Declaration of interests

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.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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