



HAL
open science

Pluridens serpentis, a new mosasaurid (Mosasauridae: Halisaurinae) from the Maastrichtian of Morocco and implications for mosasaur diversity

Nicholas R Longrich, Nathalie Bardet, Fatima Khaldoune, Oussama Khadiri Yazami, Nour-Eddine Jalil

► **To cite this version:**

Nicholas R Longrich, Nathalie Bardet, Fatima Khaldoune, Oussama Khadiri Yazami, Nour-Eddine Jalil. *Pluridens serpentis, a new mosasaurid (Mosasauridae: Halisaurinae) from the Maastrichtian of Morocco and implications for mosasaur diversity.* *Cretaceous Research*, In press, 10.1016/j.cretres.2021.104882 . hal-03370833

HAL Id: hal-03370833

<https://hal.science/hal-03370833v1>

Submitted on 8 Oct 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 ***Pluridens serpentis*, a new mosasaurid (Mosasauridae: Halisaurinae) from the**
2 **Maastrichtian of Morocco and implications for mosasaur diversity**

3

4 Nicholas R. Longrich^{a,*}, Nathalie Bardet^b, Fatima Khaldoune^c, Oussama Khadiri Yazami^c, and Nour-Eddine Jalil^{b,d}

5

6 ^a*Department of Biology and Biochemistry, University of Bath, Claverton Down, Bath, BA2 7AY United Kingdom*

7

8 ^b*CR2P - Centre de Recherche en Paléontologie - Paris, UMR 7207 CNRS-MNHN-Sorbonne Université, Muséum National d'Histoire Naturelle, CP 38, 57 rue Cuvier, 75005*
9 *Paris, France*

10

11 ^c*Office Chérifien des Phosphates (OCP Group S.A.), Khouribga, Morocco*

12

13 ^d*Muséum d'Histoire naturelle de Marrakech, Dept. of Geology (FSSM), University Cadi Ayyad, Marrakech, Morocco*

14

15

16

17

18 *Correspondence and requests for materials should be addressed to NRL (longrich@gmail.com)*

19 A B S T R A C T

20

21

22 Mosasaurids (Mosasauridae) were specialized marine lizards that evolved and radiated in the Late Cretaceous. Their diversity peaked in the
23 Maastrichtian, with the most diverse faunas known from Morocco. Here we describe a new species of mosasaurid from this fauna. *Pluridens*
24 *serpentis* sp. nov. is described based on two complete skulls and referred jaws. It is referred to *Pluridens* based on the elongate and robust jaws,
25 small teeth, and specialized tooth implantation. *Pluridens* is referred to Halisaurinae based on the posteriorly expanded premaxilla, long premaxilla-
26 maxilla suture, broad premaxillary facet on the maxilla, closed otic notch, and small, striated, hooked teeth. The orbits are reduced relative to other
27 halisaurines while the snout is robust and flat with a broad, rounded tip. The jaws bear numerous small, hooked, snake-like teeth. Skulls imply
28 lengths of 5-6 meters; referred material suggests lengths of ≥ 10 meters. *Pluridens*' specialized morphology – especially the contrasting large size
29 and small teeth - suggests a distinct feeding strategy. Small orbits imply that *P. serpentis* relied on nonvisual cues including touch and
30 chemoreception during foraging, as in modern marine snakes. Numerous neurovascular foramina on the premaxillae are consistent with this idea.
31 The small teeth suggest proportionately small prey. The dentary becomes massive and robust in the largest individuals, suggesting sexual selection
32 and perhaps sexual dimorphism, with the mandibles possibly functioning for combat as in modern beaked whales and lizards. The new mosasaur
33 emphasizes how Maastrichtian mosasaurids were characterized by high species richness, functional diversity of niches occupied, and a certain
34 degree of endemism, i.e. geographic specialization. and continued diversifying until the end of the Cretaceous, just prior to the K-Pg extinction.

35

36

37

38 Keywords:

39 Squamata

40 Mosasauridae

41 Halisaurinae

42 Marine reptiles

43 Maastrichtian

44 Paleobiogeography

45

46 **1. Introduction**

47

48 Mosasaurids (Mosasauridae) were a specialized group of squamates that became adapted for marine life in the mid-Cretaceous, before emerging
49 as the dominant predators in marine ecosystems at the end of the Cretaceous (Polcyn et al., 2014). Peak mosasaurid diversity occurred in the
50 Maastrichtian, when mosasaurs achieved high disparity in body size (Polcyn et al., 20134), tooth shape, and jaw morphology (Bardet et al., 2015).
51 These patterns suggest that they occupied a wide range of marine niches broadly analogous to modern marine mammals, although mosasaurid
52 biology would have differed from that of marine mammals, as did the available prey.

53 The most diverse known mosasaurid fauna comes from the upper Maastrichtian phosphates of the Oulad Abdoun Basin (Fig. 1) in the
54 Khouribga Province of Morocco (Table 1) (Bardet et al., 2004; Bardet et al., 2005a; Bardet et al., 2005b; Schulp et al., 2009; LeBlanc et al., 2012)
55 (Bardet et al., 2008; Bardet et al., 2015; Strong et al., 2020; Longrich et al., 2021). Moroccan mosasaurids ranged in size from the small *Halisaurus*
56 to the giant *Mosasaurus* and *Prognathodon*, and their morphology shows a similar diversity. Teeth range from simple cones designed to pierce
57 and hold, to bulbous teeth designed to crush, to cutting blades; jaw morphology is also diverse (Bardet et al., 2015). Yet despite the high known
58 diversity, new species continue to emerge from the assemblage with forms displaying dental specialisation unlike those of any other known reptiles
59 (Longrich et al., 2021), suggesting true diversity was substantially higher. We here report a new species of halisaurine, referred to *Pluridens*,
60 adding to the fauna's diversity.

61 Halisaurines (Bardet et al., 2005b) are a deep-diverging lineage of mosasaurids. As in other mosasaurids, they had aquatic specializations,
62 including retracted nares, flipper-like limbs, and a hypocercal tail (Bardet and Pereda-Suberbiola, 2001; Páramo-Fonseca, 2013), though the limbs
63 are less specialized for aquatic locomotion than in other mosasaurids (Lindgren et al., 2008; Konishi et al., 2012). Unlike the giant Tylosaurinae
64 and Mosasaurinae, which reached lengths of 15 meters or more, most Halisaurinae were small bodied, many were just 2-3 meters long (Polcyn et
65 al., 20134). The exception is *Pluridens*, which grew larger (Lingham-Soliar, 1998).

66 The new material is referable to *Pluridens*, a poorly known genus previously reported from Niger and Nigeria (Lingham-Soliar, 1998; Longrich,
67 2016). The new material supports placement of *Pluridens* in Halisaurinae (Lindgren and Siverson, 2005; Longrich, 2016) and emphasizes the
68 genus' highly distinct morphology and ecology. Finally, it provides further evidence that late Maastrichtian mosasaurids were characterized by
69 remarkably high diversity.

70

71

72 **2. Geological Setting**

73

74 The phosphatic sedimentary series of Morocco were deposited in warm, shallow epicontinental seas along the western margin of the African
75 craton (Bardet et al., 2010; Kocsis et al., 2014; Bardet et al., 2017). The environment represents a gulf or embayment open to the Atlantic Ocean
76 in the west. The area was characterized by upwelling (Kocsis et al., 2014; Polcyn et al., 20134) in a low-latitude environment, resulting in high
77 primary productivity and a large biomass of small forage animals like fish and squid (Martin et al., 2017).

78 The phosphatic series (Fig. 2) extends almost continuously from the latest Cretaceous (Maastrichtian) to the base of the middle Eocene
79 (Lutetian), about 25 MYR (Bardet et al., 2010; Kocsis et al., 2014) Phosphates comprise phosphatic and more or less indurated sands, marls, and
80 limestones; vertebrates occur mostly in the sands (Kocsis et al., 2014). No formation or members are formally named, but the phosphates are
81 divided into beds or layers termed 'couches' (Kocsis et al., 2014). Couche III is middle(?) - upper Maastrichtian (Fig. 2), Couche II is middle to
82 upper Palaeocene, and Couches I and 0 are lower to middle Eocene. Upper Couche III is correlated to the upper Maastrichtian based on shark

83 teeth (Cappetta, 1987). Oxygen and carbon isotope stratigraphy further constrain the age to latest Maastrichtian, ≥ 1 Ma before the K-Pg boundary
84 (Kocsis et al., 2014). Lower Couche III is probably middle to upper Maastrichtian based on biostratigraphy (Kocsis et al., 2014). Most described
85 mosasaurs come from Upper Couche III.

86 Fossils described here come from Upper Couche III at Sidi Daoui (Fig. 1). The matrix and preservation of these beds are distinctive. The
87 matrix contains a high proportion of fine sediments with coarser sand-sized grains, sand grains mostly being fragments of bone. Matrix is yellow-
88 orange- and blue-grey in color, and marbled suggestive of extensive bioturbation. Fish bones, teeth of sharks, mosasaurids, plesiosaurs and
89 coprolites are abundant in the matrix. Skeletons tend to be disarticulated and scattered but bones often retain association and sometimes in
90 articulation. Bones are three-dimensionally preserved, but often cracked and broken due to uneven settling of the matrix.

91 Upper Couche III has an exceptionally rich vertebrate fauna. It comprises sharks (Arambourg, 1952; Cappetta et al., 2014), fish
92 (Arambourg, 1952; Vullo et al., 2017), mosasaurid (Bardet et al., 2005a; Bardet et al., 2005b; Bardet et al., 2008; Bardet et al., 2010; Bardet et al.,
93 2017)(Bardet et al., 2004; Bardet et al., 2005b; Schulp et al., 2009; LeBlanc et al., 2012) (Bardet et al., 2004; Longrich et al., 2021)(LeBlanc et
94 al., 2019; Strong et al., 2020) and pachyvaranid (Houssaye et al., 2011) squamates, elasmosaurid plesiosaurs (Vincent et al., 2011; Vincent et al.,
95 2013), marine turtles (Bardet et al., 2013; Lapparent de Broin et al., 2013), and rarely crocodylians (Jouve et al., 2008). Pterosaurs are diverse and
96 abundant (Pereda-Suberbiola et al., 2003; Longrich et al., 2018), and rare dinosaurs are also present (Pereda-Suberbiola et al., 2004; Longrich et
97 al., 2017; Longrich et al., 2020).

98

99 2.1 Institutional Abbreviations

100

101 MHNM— Muséum d'Histoire naturelle de Marrakech, Université Cadi Ayyad, Marrakech, Morocco.

102 OCP, Office Chérifien des Phosphates, Khouribga, Morocco.

103

104

105 3. Systematic Paleontology

106

107 Squamata (Oppel, 1811)

108 Mosasauridae (Gervais, 1852)

109 Halosaurinae Bardet and Pereda Suberbiola, 2005 in (Bardet et al., 2005b)

110 Pluridensini new taxon

111 *Pluridens* (Lingham-Soliar, 1998)

112 *Pluridens serpentis* sp. nov.

113

114 **Syntypes:** OCP DEK-GE 548 (Figs. 3, 4), skull; MHNM.KH.262 (Figs. 5-7), articulated skull, lower jaw, cervical vertebrae 1-4.

115 **Referred:** (Figs. 8-11) MHNM.KH.386, fragmentary skull including dentaries, maxillae, and dentition; MHNM.KH.387, left and right

116 maxillae; MHNM.KH.388, right maxilla (Fig. 8); MHNM.KH.393, partial right dentary (Fig. 9); MHNM.KH.394, right dentary (Fig. 10),

117 MHNM.KH.389, left and right dentaries (Fig. 11B); MHNM.KH.390, left dentary (Fig. 11C); MHNM.KH.391, left dentary (Fig. 11A);

118 MHNM.KH.392, right dentary; MHNH.KH395a-b, left and right dentaries of the same individual.

119 **Locality:** Syntypes and referred specimens come from phosphate mines in Sidi Daoui area, Oulad Abdoun Basin, Khouribga Province,

120 Morocco (Fig. 1).

121
122
123
124
125
126
127
128
129
130
131
132
133
134
135
136
137
138
139
140
141
142
143
144
145
146
147
148
149
150
151
152
153
154
155
156
157
158

Horizon: Upper Couche III of the phosphatic series, latest Maastrichtian (Fig. 2).

Diagnosis: Large halisaurine, skull length to ~120 cm, total length to ~10 meters. Snout short, rostrum ~50% of skull length. Snout low, broad, and bluntly rounded anteriorly, with dense neurovascular foramina. Premaxilla very broad, with premaxilla-maxilla suture extending posteriorly as far as the ninth maxillary tooth. Maxilla strap-like, with anterior end of maxilla blunt, parallel dorsal and ventral margins. Nasals large and with large, triangular tongue-like overlaps onto frontals. Prefrontals with long anterior process largely excluding the maxilla from the external naris. Prefrontal-postorbitofrontal lateral contact, excluding frontals from orbit. Parietal foramen anteroposteriorly elongate. Jugal small and L-shaped with prominent posteroventral process, orbits small relative to skull length. Dentary relatively long and tapered, becoming massive with a strongly cylindrical cross section in the largest individuals. Large contribution of surangular to coronoid process. Up to 28 dentary and ?18 maxillary teeth. Teeth small, strongly hooked cones, carinae weak and unserrated, with 4-5 rounded apicobasal ridges separated by shallow grooves. Enamel covered with microscopic anastomosing ridges. Tooth roots obliquely inclined relative to crown and separated by tall interdental septa (shared with *Pluridens walkeri* and *P. calabaria*). Weak mediolateral expansion of tooth sockets.

Pluridens serpentis can be differentiated from the closely related *Pluridens walkeri* and *P. calabaria* in that the dentary is evenly tapered along its length, similar to the condition in *Halisaurus*. By contrast, in both *P. walkeri* and *P. calabaria* the dentary is narrow anteriorly and then strongly expanded posteriorly. Teeth are larger than in *P. walkeri*, more similar to the condition in *P. calabaria*. The tooth sockets are moderately expanded mediolaterally, versus more strongly expanded in *P. calabaria* and especially *P. walkeri*.

4. Description

4.1 Skull

Premaxillae. The anterior part of the premaxilla (Figs. 3, 4A) is proportionately short and broad to a degree not seen in other mosasaurids except *Tethysaurus* (Bardet et al., 2003), being about twice as broad as long. It has a blunt, rounded tip. This contrasts with *Halisaurus arambourgi* (Bardet et al., 2005b), *Halisaurus platyspondylus* (Polecyn and Lamb, 2012), *Eonatator coellensis* (Páramo-Fonseca, 2013) and all other Mosasauridae, where the premaxilla is narrower and often acutely pointed anteriorly (Russell, 1967; Bell Jr., 1997). The main body of the premaxilla broadly contacts the tips of the maxillae. Its dorsal surface is covered with large neurovascular foramina (Fig. 4A) which represent the exits for the ramus nasalis medialis of the trigeminal nerve (Álvarez-Herrera et al., 2020). Similar foramina are found in all mosasaurs. The foramina in *Pluridens* are more numerous than in *H. platyspondylus* or taxa such as *Platecarpus* and *Clidastes*, but neurovascular foramina are numerous in other taxa, especially tylosaurines such as *Tylosaurus* (Russell, 1967) and *Taniwhasaurus* (Álvarez-Herrera et al., 2020).

As in other mosasaurids, an elongate narial process contacts the dorso-medial margins of the maxillae anteriorly and would contact the frontals posteriorly (see nasal description below). The narial process resembles other Halisaurinae in being narrow anteriorly, then broader posteriorly, just ahead of the nares, such that where the maxillae contact the premaxilla it is distinctly pinched or constricted between them in dorsal view. This posteriorly expanded narial process is shared with *Halisaurus arambourgi* (Bardet et al., 2005b), a halisaurine from the early Campanian of Alabama (Lindgren and Siverson, 2005) and *Eonatator coellensis* (Paramo-Fonseca, 2013) and is considered here a derived feature of Halisaurinae. In other mosasaurids, the narial process is straight-sided (Tylosaurinae) or tapers in dorsal view (Plioplatecarpinae, Mosasaurinae) (Russell, 1967; Bell Jr., 1997).

159 The narial process forms an elongate lateral contact with the maxillae, with the premaxilla-maxilla suture extending posteriorly to at least
160 the ninth tooth position, and about 40% the length of the maxilla. A long premaxilla-maxilla suture characterizes Halisaurinae, extending to the
161 fifth tooth in *H. platyspondylus* (Polcyn and Lamb, 2012) and the sixth or seventh tooth in *H. arambourgi* (Bardet et al., 2005b). Primitively, and
162 in most other mosasaurids the suture extends just to three teeth (e.g. *Platecarpus* (Konishi et al., 2012), *Prognathodon overtoni* (Konishi et al.,
163 2011)), but an elongate suture evolves independently (e.g. *Mosasaurus hoffmanni* (Lingham-Soliar, 1995); *Clidastes* spp. (Lively, 2018)). The
164 shape of the contact with the maxilla is vertical anteriorly, oblique behind this, then horizontal posteriorly, a derived condition shared with
165 *Halisaurus* (Bardet et al., 2005b).

166
167 *Maxilla*. The maxilla (Figs. 3, 4, 5, 6, 8) resembles other Halisaurinae in being long and low, but uniquely among Mosasauridae is subrectangular
168 and strap-like in shape in lateral view. The maxilla's anterior tip has a blunt, squared-off shape. Its anterior margin is perpendicular to the dorsal
169 contact with the premaxillae, so that the premaxilla makes a T-shaped contact with the maxilla in dorsal view. The contacts with the premaxilla
170 are angled or curved in other mosasaurids in general (Russell, 1967) such as, e.g., *Halisaurus platyspondylus* (Polcyn and Lamb, 2012), *Platecarpus*
171 *tympaniticus* (Konishi et al., 2012), *Mosasaurus hoffmanni* (Lingham-Soliar, 1995; Street and Caldwell, 2017) and *Tylosaurus proriger* (Russell,
172 1967) so that the premaxilla wedges between the maxillae in dorsal view.

173 The tip of the maxilla is unusual in having subparallel dorsal and ventral margins, not tapering in lateral view as in other halisaurines
174 (Bardet et al., 2005b; Polcyn and Lamb, 2012) and other mosasaurids (Russell, 1967). It is also unusual in that the anterior end of the maxilla is as
175 deep as the posterior end.

176 The concave narial emargination seen in other halisaurines and other mosasaurids in general is absent; the narial margin is straight to
177 slightly concave. Posteriorly, the ascending process of the maxilla is low, as in other Halisaurinae (Polcyn and Lamb, 2012), but to a greater degree
178 in *P. serpentis*. The jugal process of the maxilla is short and deep compared to other Halisaurinae (Bardet et al., 2005b; Polcyn and Lamb, 2012;
179 Konishi et al., 2016).

180
181 *Nasals*. Surprisingly, large individualized nasal bones appear to be preserved on both OCP DEK-GE 548 and MHNM.KH.262 (Figs. 3, 4, 5, 6, 7).
182 Though crushing and breakage obscure the nasal's shape and their contacts, they contact the premaxillae anteriorly and the frontals posteriorly.
183 They are narrow anteriorly and contribute to the narial bar, and expand posteriorly where they contact the frontals. Here the nasals form a pair of
184 triangular tongue-shaped processes that overlap the frontals and appear separated from each other by a median sharp tongue of the frontal. In OCP
185 DEK-GE 548 the posterior triangular portions are preserved though in MHNM.KH.262 only the sutural surface on the frontal is kept. This condition
186 is seen in *Eonatator coellensis* though the shape and size of these nasal bones differ. However, crushing and breakage obscures the nasal's shape
187 and their contacts. The presence and shape of the nasals is not known in other halisaurines. Nasals are highly reduced or absent in other mosasaurids
188 (Russell, 1967).

189
190 *Prefrontals*. The prefrontals (Figs. 3, 4, 5, 6, 7) contact the maxillae anteriorly, the frontals medially, and the postorbitofrontals posteriorly. They
191 resemble other mosasaurids (Russell, 1967) being platelike dorsally with a triangular descending ala. The prefrontal's anteroventral margin
192 contacts the maxilla obliquely in a straight suture. The anteromedial margin forms the posterolateral margin of the external nares as in most
193 mosasaurids (Russell, 1967). The medial margin of the prefrontal is regularly convex where it articulates with the frontal's concave lateral margin.

194 The prefrontal's dorsolateral margin bears an incipient supraorbital process, resembling the small, ridgelike one seen in other Halisaurinae
195 (Russell, 1967; Bell Jr., 1997; Polcyn and Lamb, 2012). The large, winglike supraorbital process, as seen in Mosasaurinae (Lively, 2018)(Lingham-
196 Soliar, 1995) is absent.

197 The posterior portion of the prefrontal is distinctly elongate and tapers to form a V-shaped joint with the anterior branch of the
198 postorbitofrontal, excluding the frontals from the orbital rim. Exclusion of the frontals from the orbital rim by a prefrontal-postorbitofrontal contact
199 is absent in other Halisaurinae (Bardet et al., 2005b; Polcyn and Lamb, 2012; Konishi et al., 2016), but resembles the condition in Mosasaurinae
200 (Lingham-Soliar, 1995; Bell Jr., 1997).

201

202 *Frontals.* The frontals (Figs. 3, 4, 5, 6, 7) are fused, triangular elements as typical of Mosasauridae (Russell, 1967). They contact the premaxillae
203 anteriorly, prefrontals anterolaterally, postorbitofrontals posterolaterally, and parietals posteriorly. They do not participate in the orbits.

204 The frontals are relatively short for halisaurines, the main body (excluding the narial process) being ~140% as long as wide. This contrasts
205 with the very long and slender frontals seen in *Eonatator sternbergii* (Bardet and Pereda-Suberbiola, 2001) and *Phosphorosaurus ortliebi*
206 (Lingham-Soliar, 1996), and more closely resembles “*Phosphorosaurus*” *ponpetelegans* (Konishi et al., 2016), *Halisaurus platyspondylus* (Polcyn
207 and Lamb, 2012), and *H. arambourgi* (Bardet et al., 2005b).

208 The frontals’ anterior margin has two V-shaped embayments where the frontals participated in the nares. The participation in the nares is
209 broad, about 40% the width across the postorbital processes, as in *H. arambourgi*, *H. platyspondylus*, *P. ortliebi*, and *P. ponpetelegans* (ibid.).
210 Frontal participation in the nares is narrower in *E. sternbergii* (ibid.).

211 The frontal’s anterolateral margins are concave where they contact the prefrontals. In contrast to *H. arambourgi*, *H. platyspondylus*, *P.*
212 *ortliebi*, and *P. ponpetelegans*, where the frontals are expanded between the ends of the prefrontals, with a broad, convex supraorbital flange, the
213 frontals are narrow here in *P. serpentis*, about 40% the width across the postorbital processes, more similar to the condition in *E. sternbergii*.

214 The frontals’ posterolateral alae are roughly triangular. The suture for the parietal has a complex, interlocking contact. A pair of tongue-like
215 processes of the parietal project forward, between them is a triangular median process of the frontal, and to either side are a pair of short, broad
216 triangular lappets of the frontal that project posteriorly. A similar median projection of the frontal is seen in *Eonatator sternbergii*, and a very
217 small median eminence is found on the frontal in *P. ponpetelegans*. That of *Halisaurus arambourgi* forms a broadly convex V-shaped contact with
218 the parietal; the contact is shallowly concave in *H. platyspondylus*, and the parietal foramen participates in the frontal in *Phosphorosaurus ortliebi*
219 (Lingham-Soliar, 1996).

220 The dorsal surface of the frontal is smooth and lacks foramina, as in other Halisaurinae. This is a primitive character, and contrasts with
221 the presence of large foramina in tylosaurines (Everhart, 2005), plioplatecarpines (Konishi and Caldwell, 2011), and mosasaurines (Lingham-
222 Soliar, 1995). Just behind the nares, the dorsal surface of the frontals bears the midline ridge characteristic of mosasaurids (Russell, 1967). It is
223 weakly developed in *P. serpentis* relative to the condition observed in other halisaurines, where the median ridge forms a thick, tall dorsal keel
224 (Lingham-Soliar, 1996; Bardet et al., 2005b; Polcyn and Lamb, 2012; Konishi et al., 2016). Just behind the nares are a pair of depressions. In other
225 mosasaurids, there are often a pair of shallow channels or fossae here, perhaps the posterior extension of the narial fossae. The deep triangular
226 depressions seen in *P. serpentis* may instead be articular surfaces, receiving the posterior ends of the large nasals. This feature is not seen in other
227 halisaurines or other mosasaurids. Posteriorly, the frontal’s dorsal surface is flat where it contacts the parietals. This contrasts with other
228 Halisaurinae, where a triangular median boss lies ahead of the frontal-parietal suture (Lingham-Soliar, 1996; Polcyn and Lamb, 2012; Konishi et
229 al., 2016). This median boss is a derived feature of Halisaurinae. The dorsal surface of the frontal of *P. serpentis* also differs significantly from
230 that of *H. arambourgi* by lacking the two anterior oblique ridges converging posteriorly around mid-part of the bone (Bardet et al., 2005b).

231

232 *Postorbitofrontals.* The postorbitofrontals (Figs. 3, 4, 5, 6, 7) contact the prefrontals anteriorly, the frontals and parietals dorsomedially, the jugal
233 ventrolaterally, and the squamosals posteriorly. The anterior end of the postorbitofrontal is elongate and broad, reaching the prefrontal in an
234 interdigitating suture. By contrast, in *P. ponpetelegans*, the postorbitofrontal has a short and narrow anterior projection that makes a limited

235 contribution to the dorsal margin of the orbit, such that the frontals broadly participate in the orbits. The sutures of the frontals suggest a similar
236 morphology in other Halisaurinae (Lingham-Soliar, 1996; Polcyn and Lamb, 2012)(Polcyn et al., 2012) (Bardet et al., 2005b). Medially, the
237 postorbitofrontal has a process that wraps around the back of the frontal's posterolateral ala. A similar process is present in most mosasaurids, e.g.
238 *Platecarpus* (Konishi et al., 2012) and *Mosasaurus* (Lingham-Soliar, 1995) but it is reduced in *P. ponpetelegans*; in this respect *P. serpentis* is
239 primitive. The posterior process is straight, and more robust than in *P. ponpetelegans*, resembling that of *H. arambourgi* (Bardet et al., 2005b). It
240 extends about 75% the length of the supratemporal fenestra. It broadly overlaps the squamosal in a long scarf joint, as in other mosasaurids. The
241 descending process of the postorbitofrontal contacts the jugal, and together they form the posterior margin of the orbit. The descending process is
242 relatively short and robust compared to that of *P. ponpetelegans*.

243

244 *Parietals*. The fused parietals (Figs. 3, 5, 7) are typically Y-shaped. As in other mosasaurids, the bone contacts the frontals and postorbitofrontals
245 anteriorly and the squamosals posterolaterally, forming the medial and posterior margins of the large, ovoid supratemporal fenestrae.

246 Anteriorly, the parietal table is long but narrow, with a reduced exposure between the enlarged supratemporal fossae, with a narrow
247 exposure between the enlarged supratemporal fossae, compared to *Halisaurus sternbergii* (Holmes and Sues, 2000), *H. arambourgi* (Bardet et al.,
248 2005b; Polcyn et al., 2012), *P. ponpetelegans* (Konishi et al., 2016), and most other mosasaurids. The lateral margins of the parietal table are
249 straight. They are distinctly convex in *Halisaurus platyspondylus*, *H. arambourgi* and *P. ponpetelegans*, a condition widely but variably distributed
250 in Mosasauridae.

251 The parietal foramen is fully enclosed in the parietal. It is enlarged, anteroposteriorly elongate, and surrounded by a lip of bone, such that
252 it is distinctly elevated above the parietal table. A similar striated rim around the parietal table is seen in *Halisaurus arambourgi* where it is
253 particularly marked (Bardet et al., 2005b; Polcyn et al., 2012). Posteriorly the lateral rami of the parietal are elongate, strap shaped, and bowed
254 posteriorly, as typical of Mosasauridae. The lateral rami are distinctly elongate relative to *H. arambourgi* (Bardet et al., 2005b; Polcyn et al., 2012),
255 *Eonatator sternbergii* (Holmes and Sues, 2000), *P. ponpetelegans* (Konishi et al., 2016), and their tips are strongly turned outward, forming a
256 broad obtuse angle, whereas they form a narrower angle in the other taxa.

257

258 *Squamosals*. As in other mosasaurids, the squamosals (Figs. 3, 5, 7) contact the postorbitofrontals anterolaterally, the parietals posteromedially,
259 and the quadrate ventrally. They contribute medially to the supratemporal bar by a very long anteromedial tongue of bone that imbricates with the
260 posterolateral one of the postorbitofrontal in a long oblique suture, defining the lateral margin of the long supratemporal fenestra.

261

262 *Supratemporal*. As in other mosasaurids (Russell, 1967) a long, flat supratemporal articulates with the underside of the squamosal lateral rami.
263 The tip of the squamosal is exposed in dorsal view. Its end articulated with the top of the quadrate.

264

265 *Jugal*. The jugal (Figs. 3, 5) is a relatively small, L-shaped bone contacting the postorbitofrontal dorsally and the maxilla anteriorly. It has a short,
266 very broad dorsal process whose posterior edge hooks backwards. Below, there is a broad, robust jugal posterior tuberosity that projects posteriorly.
267 The ventral ramus of the jugal forms the ventral border of the orbit. It is longer and more slender than the dorsal process but far more robust than
268 the ventral ramus in other halisaurs (Konishi et al., 2016)

269 The jugal's morphology differs greatly from both *Halisaurus arambourgi* (Bardet et al., 2005b) and "*Phosphorosaurus*" *ponpetelegans*
270 (Konishi et al., 2016). In those taxa, the jugal is a large, comma-shaped element, with a tall dorsal ramus, no posterior tuberosity, and a long,
271 slender, broadly arched ventral ramus. The enlarged, comma-shaped jugal is a derived characteristic associated with enlargement of the eyes in
272 these taxa.

273 The small jugal in *P. serpentis* is associated with smaller orbits, which represents either the primitive condition, or perhaps even a reduction
274 of the orbits relative to the primitive condition in other Mosasauridae.

275

276 *Quadrate*. The quadrate (Figs. 5, 7) is typical of Mosasauridae in bearing a broad lateral conch. There is a well-developed suprastapedial process
277 that curls back and down around the stapedial notch. This suprastapedial process is fused to the infrastapedial process a derived feature shared
278 with all other Halisaurinae (Bardet et al., 2005b; Fernández and Talevi, 2015; Konishi et al., 2016). There is no visible sutural contact between
279 the two processes. The quadrate is proportionately short and broad. The lateral conch is about as wide as tall, with a broadly rounded dorsal margin,
280 and a slightly triangular ventral rim. This shape is similar to *Eonatator sternbergii* (Bardet and Pereda-Suberbiola, 2001) and a halisaurine from
281 the late Maastrichtian Jagüel Formation of Argentina (Fernández and Talevi, 2015). It differs from these taxa in having a very broad bony rim
282 around the margin of the conch, ornamented by wrinkled ridges.

283

284 **4.2. Mandible**

285

286 *Dentary*. The dentary (Figs. 5-7, 10, 11, 12) articulates with the splenial and the articular, which is fused with the pre-articular in mosasaurids
287 (Russell, 1967; DeBraga and Carroll, 1993) medially, and posteriorly with the surangular, and perhaps the coronoid. It resembles other
288 Halisaurinae and *Pluridens* spp. (Fig. 12) in relatively being long and slender, but its shape varies with size, with the largest individuals having a
289 more robust dentary with a strongly cylindrical section (Fig. 11).

290 The tip of the dentary forms a bluntly rounded, protruding prow that mirrors the premaxillary one. It is not preserved in either *P. walkeri*
291 or *P. calabaria*, making comparisons impossible. However, this blunt prow is absent in *Halisaurus arambourgi* (Bardet et al., 2005b) and the
292 Mooreville Chalk halisaurine (Lindgren and Siverson, 2005).

293 Anteriorly, the dentary's lateral surface is convex and rounded. The syntype MHNM.KH.262 lacks the highly convex lateral surface and
294 distinctive circular cross-section seen in the middle Maastrichtian *P. walkeri* (Lingham-Soliar, 1998), or the strong lateral shelf of the dentary seen
295 in that taxon; in this respect the jaw is actually more primitive and similar to the older, late Campanian *P. calabaria* (Longrich, 2016). However,
296 a large referred specimen (MHNM.KH.386) shows this strongly convex lateral surface (Fig. 11C), suggesting that this feature is correlated to size
297 and/or maturity.

298 The lateral surface of the dentary bears large foramina for exit of the terminal branches of the 5th mandibular nerve (Russell, 1967), and
299 the anterior end of the bone bears randomly distributed round to oval foramina, as in other mosasaurids. A dorsal row of foramina parallels the
300 dorsal margin of the dentary. These foramina are roughly circular at the tip of the dentary, and enlarge regularly to become elongated, narrow slots
301 posteriorly. The posteriormost foramina are the largest, they reach up to 2.5 cm long x 2 mm wide.

302 The dentary's dorsal margin is gently concave and the ventral one gently convex. The anteroventral margin is very gently bowed; in
303 *Halisaurus arambourgi*, the ventral margin of the dentary is slightly downturned at the tip (Bardet et al., 2005b), a derived feature absent here.
304 The posteroventral margin is more strongly convex. The posteroventral margin of the dentary in *Pluridens walkeri* appears to be bowed (Longrich,
305 2016), as is that of *E. sternbergii* (Bardet and Pereda-Suberbiola, 2001). The posteroventral margin of the dentary is straight in *Halisaurus*
306 *arambourgi* (Bardet et al., 2005b) and *Halisaurus* sp. from Chile (Jiménez-Huidobro et al., 2019). The bowed posteroventral margin is probably
307 primitive, being seen in outgroups such as *Tylosaurus* (Everhart, 2005) and particularly pronounced in *Prognathodon* (e.g. (Lingham-Soliar and
308 Nolf, 1989).

309 Posteriorly the dentary is relatively shallow in lateral view, similar to the condition in *Halisaurus* (Jiménez-Huidobro et al., 2019). By
310 contrast, the posterior end of the dentary is strongly expanded in *P. walkeri* and *P. calabaria* (Longrich, 2016), a derived character uniting the two.

311 The posterior margin of the dentary bears a well-developed crescentic emargination, forming a mobile intramandibular joint with the
312 surangular, a primitive condition for mosasaurids. The articulation with the coronoid appears to be a simple overlapping contact, a primitive
313 condition shared with *Halisaurus arambourgi* (Bardet et al., 2005b; Jiménez-Huidobro et al., 2019); in Mosasaurinae a distinct notch in the dentary
314 receives the coronoid (Lingham-Soliar, 1995).

315 In medial view, the Meckelian groove is broadly open posteriorly, and strongly tapers anteriorly, ending very anteriorly at the level of the
316 3rd-4th dentary tooth. The Meckelian groove is bounded below by a prominent ventral lip. A well-developed ventral lip of the dentary characterizes
317 Halosaurinae (Longrich, 2016), but it is especially well-developed in *P. serpentis*, extending posteriorly about half the length of the dentary, a
318 derived condition shared with *P. walkeri* and *P. calabaria* (Longrich, 2016).

319 Dorsally, there is a long edentulous process posterior to the last tooth, like in *Halisaurus* (Bardet et al., 2005b) and other *Pluridens* species.
320 The medial dental parapet is slightly lower than the lateral one, a plesiomorphic character (Bell Jr., 1997) so that it does not extend the full height
321 of the dentary as in derived mosasaurids such as *Mosasaurus hoffmanni* (Lingham-Soliar, 1995). Instead, the medial surface of the tooth roots is
322 broadly exposed, as well as the tooth replacement pit. Interdental septa arise from the dentary and separate the tooth roots into almost individual
323 dental alveolae. They are very well-developed, and project well above the medial parapet. These prominent septa are shared with *P. walkeri* and
324 *P. calabaria* (Longrich, 2016) and also *Globidens simplex* (LeBlanc et al., 2019), but absent from *Halisaurus arambourgi* (Bardet et al., 2005b)
325 and *Halisaurus* sp. from Chile (Jiménez-Huidobro et al., 2019). The septa extend posterodorsally rather than dorsally, in association with the
326 oblique orientation of the tooth roots relative to the jaw (see below).

327

328 *Splénial*. The splénial (Fig. 5, 7) is largely obscured by the dentary in lateral view. Only its posteroventral margin being visible: it is a low triangular
329 tongue of bone tapering anteriorly and disappearing at about the two thirds of the dentary length. On the contrary, its medial wing is widely
330 expanded and largely covers the Meckelian groove of the dentary on its entire length. Posteroventrally it bears a large oval foramen that transmits
331 the inferior alveolar nerve into the Meckelian canal (Russell, 1967). Caudally the splénial contacts the angular to form a mobile intramandibular
332 joint as in other mosasaurids (Russell, 1967).

333 In lateral view, the splénial hangs well below the mandible, a derived feature of Mosasauridae that is absent in the dolichosaurid
334 *Coniasaurus* (Caldwell and Cooper, 1999) and other squamates. It forms a mobile contact with the angular, as in dolichosaurids (Caldwell and
335 Cooper, 1999) and Mosasauridae (Russell, 1967).

336 The articular surface for the angular is strongly extended forward onto the lateral surface of the splénial to receive a large lateral lappet of
337 the angular, such that the splénial-angular contact is C-shaped in lateral view. The shape of the joint remains unknown as both bones are articulated
338 in MHNM.KH.262. A similar C-shaped contact is seen in other halosaurines (Holmes and Sues, 2000)(Bardet et al., 2005b), but appears to be more
339 well-developed in *P. serpentis*.

340

341 *Coronoid*. The coronoid (Figs. 3, 5, 7) is a crescentic element forming the apex and anterior margin of the coronoid process, as in other
342 Mosasauridae (Russell, 1967). It overlapped the dorsal and lateral surfaces of the surangular, and contacted an ascending process of the surangular
343 posteriorly to form the coronoid process of the jaw. It may have overlapped the dentary anteriorly when the jaws were closed. It exhibits the
344 plesiomorphic condition of a simple low saddle-shaped bone without developed lateral (nor most probably medial) wings (Bell Jr., 1997).

345 The anterior end of the coronoid is a flat, tongue-shaped process and may have overlapped onto the dentary when the jaw closed, but was
346 not tightly connected to it; there may have been a ligamentous connection between the two bones contributing the intramandibular joint. Behind
347 this, the coronoid curves up vertically to form the apex of the coronoid process. The coronoid is strongly curved in lateral view to a degree not
348 seen in other halosaurines, e.g. "*Phosphorosaurus*" *ponpetelegans* (Konishi et al., 2016), a feature associated with the elevated coronoid process.

349 There is a limited lateral overlap of the surangular ventrally, and a broad, convex contact with the dorsal wing of the surangular. A thick lateral
350 ridge marks the anterior margin of the adductor fossa of the coronoid process, as in other mosasaurids (Russell, 1967).

351

352 *Angular*. The angular (Figs. 3, 5, 7) resembles that of other mosasaurids (Russell, 1967). It contacts the splenial anteriorly, the surangular dorsally,
353 and the articular posteriorly. The anterior contact with the splenial is unusual in that a long lappet of the angular extends anteriorly to overlap the
354 lateral surface of the splenial. The joint may have been developed more as a saddle joint than the typical concavo-convex joint seen in other
355 mosasaurids. The ventral margin of the angular is straight. The lateral wing is low, exposed below the surangular, and tapers to overlap the articular
356 in a posteroventral tongue ending roughly ventral to the glenoid articulation.

357

358 *Surangular*. The surangular (Figs. 5, 7) is a large, triangular plate occupying most of the lateral surface of the posterior portion of the mandible. It
359 articulates with the dentary anteriorly in a mobile oblique joint, dorsally with the coronoid, ventrally with the angular, and posteriorly with the
360 articular, where it forms part of the glenoid.

361 The anterior end is gently convex where it underlapped the dentary to form an oblique mobile intramandibular joint, as in other mosasaurids
362 (Russell, 1967). The ventral margin is straight where it overlaps the angular. Posteriorly the surangular tapers to form a blunt, rounded end where
363 it overlaps the articular.

364 The dorsal margin of the surangular is unusual in being elaborated into a tall and very robust coronoid buttress. In other Halisaurinae, the
365 surangular has a concave dorsal margin and is elevated anteriorly to make a limited contribution to the coronoid process, e.g. *Halisaurus*
366 *platyspondylus* (Holmes and Sues, 2000) and *Halisaurus arambourgi* (Bardet et al., 2005b). The surangular makes a very limited contribution to
367 the coronoid process in Tylosaurinae and Plioplatecarpinae (Russell, 1967). The surangular does however make an extensive contribution to the
368 coronoid process in *Clidastes* (Russell, 1967) and Mosasaurinae in general (Lingham-Soliar, 1995; Bell Jr., 1997). A large coronoid buttress
369 appears to evolve convergently in *Pluridens* and in Mosasaurinae.

370

371 *Articular*. As in other mosasaurids, the articular and prearticular (Figs. 5, 7) are fused (DeBraga and Carroll, 1993). The articular contacts the
372 angular ventrally and the surangular anteriorly. It is broad and triangular in shape, expanding posteriorly to form a large retroarticular process. The
373 angular has a long, slender posterior spur that overlapped onto the articular; whereas the surangular has a broader, tongue-like flange that
374 overlapped onto the articular. The posterior end of the articular is broadly expanded to form a fan-shaped retroarticular process nearly vertical as
375 in *Halisaurus arambourgi* (Bardet et al., 2005b) but much more robust. The wide retroarticular process is derived relative to *Halisaurus*
376 *platyspondylus* (Holmes and Sues, 2000) and *Phosphorosaurus ponpetelegans* (Konishi et al., 2016). The relative contribution of the surangular
377 and articular to the glenoid cavity is not visible.

378

379 **4.3. Dentition**

380

381 The premaxilla is damaged in MHNM.KH.262 (Fig. 5, 6) and the teeth are not visible in OCP DEK-GE 548 (Figs. 3, 4), but it presumably bore
382 four teeth as in other mosasaurids. There are roughly 18 maxillary teeth and around 26 to 28 dentary teeth, depending on the specimens (Figs. 5,
383 6, 8). The maxillary tooth count is unknown for *Pluridens*, but the estimated count of *P. serpentis* (18) is higher than that of *H. arambourgi* (16)
384 (Bardet et al., 2005b). The dentary tooth count (Figs. 5, 10, 11, 12) is similar to that estimated for *P. calabaria* (~25, Longrich, 2016) and the
385 Mooreville Chalk halisaurine (Lindgren and Siverson, 2005). Teeth of *Pluridens walkeri* are more numerous (~30, Longrich, 2016) and

386 correspondingly much smaller. *Halisaurus arambourgi* has 19 dentary teeth (Bardet et al., 2005b). Exact tooth counts are unknown for other
387 halisaurines.

388 Tooth crowns resemble those of other Halosaurinae and basal mosasauroids such as *Tethysaurus nopscai* (Bardet et al., 2003) in being
389 sharp, slender, recurved cones (Figs. 5, 6, 8-11). They are around 1.5 cm height but can reach 2 cm in largest specimens. Low but discrete carinae,
390 lacking serrations, are present anteriorly and posteriorly.

391 The basal cross-section is circular, and both lingual and labial surfaces are convex. In lateral view, crowns are strongly posteriorly recurved
392 as in *Tethysaurus* (Bardet et al., 2003), other halisaurines and *Plioplatecarpus* (Lingham-Soliar, 1994). Basally, the tooth crowns bear ridges,
393 grooves, and striations that extend halfway to two-thirds the way up the crown. The lingual surface of the tooth bears up to five, six, or even seven
394 broad, rounded ridges extending up to one-third of the crown height, which may be separated by deep, concave grooves or fluting. The ridges and
395 grooves are better developed on the labial surface of the crowns than on the lingual face. Development of ridges and grooves varies along the tooth
396 row and specimens but shows no clear pattern. It is weakly developed in MHNM.KH.262, but better developed in referred specimens. Similar
397 variation in the development of ridges is seen in other mosasaurs.

398 Just dorsal to the base, around midpoint, the crowns abruptly curve posteriorly. The upper part of the crown does not bear grooves and
399 fluting, only minute ridges, giving the enamel a silky, smoother texture. Tooth apices are sharply hooked with slender tips, their shape being
400 reminiscent of snake teeth. The teeth of the Alabama halisaurine (Lindgren and Siverson, 2005) and *Phosphorosaurus ponpetelegans* (Konishi et
401 al., 2016) are more slender. Those of *H. platyspondylus* (Polcyn and Lamb, 2012), *H. arambourgi* (Bardet et al., 2005b) and *Halisaurus* sp. from
402 Chile (Frey et al., 2016) are more weakly curved.

403 As usual in mosasaurids (Russell, 1967) teeth are short anteriorly, taller near the middle of the tooth row, then become small again
404 posteriorly. But they are noteworthy in being only weakly heterodont in *P. serpentis*, showing very limited variation in size and shape along the
405 toothrow. Teeth are too poorly preserved in *H. walkeri* and *H. calabaria* (Lingham-Soliar, 1998; Longrich, 2016) hindering comparisons, but a
406 similar pattern is seen in the teeth of the Mooreville chalk halisaur (Lindgren and Siverson, 2005) as well as in *H. arambourgi* (Bardet et al., 2003)
407 and *Phosphorosaurus ponpetelegans* (Konishi et al., 2016).

408 As in other Mosasauridae, the teeth are borne on a massive root that projects above the dentary, which is fused to the jaw by a mineralized
409 periodontal ligament (Caldwell, 2007; Luan et al., 2009; Liu et al., 2016)(Russell, 1967; Rieppel and Kearney, 2005; LeBlanc et al., 2017).
410 Implantation is thecodont, with the root deeply inserting and fusing into a socket or theca (Fig. 9). The theca is formed by the lateral parapet of the
411 dentary, a medial parapet formed by the subdental ridge, and by interdental ridges separating adjacent alveoli (ibid.).

412 The roots and thecae are unusual in *P. serpentis*, however, in being obliquely oriented with respect to the long axis of the dentary (Fig. 9).
413 Tooth roots therefore emerge posterodorsally rather than vertically. This feature is shared by *Pluridens walkeri* and *P. calabaria*, but not by other
414 halisaurines (Frey et al., 2016; Jiménez-Huidobro et al., 2019) (Konishi et al., 2016) or other mosasaurids (Russell, 1967), and represents a unique
415 derived character of these taxa.

416 Roots are deeply excavated by replacement pits (Fig. 9), as in other mosasaurids (Russell, 1967; Rieppel and Kearney, 2005; Caldwell,
417 2007). The replacement pits are noteworthy in being very large and located medially. Medially placed replacement pits shared with *Pluridens*
418 *walkeri*, *P. calabaria*, (Longrich, 2016) and the Mooreville Chalk halisaurine (Lindgren and Siverson, 2005). In *Halisaurus arambourgi* (Bardet
419 et al., 2005b), *Halisaurus* sp. from Chile, and other mosasaurids (Russell, 1967; Rieppel and Kearney, 2005; Caldwell, 2007), replacement pits
420 are located more posteromedially than medially. Medial placement of replacement pits is thus probably a unique, derived feature of *Pluridens*.

421

422 **4.4 Postcranium**

423 MHNM.KH.262 preserves the axis, atlas, and C3 in articulation, C4 is disarticulated (Fig. 5) . The cervicals are typical of Halisaurinae (Holmes
424 and Sues, 2000). The centra are moderately elongate relative to the condition in Plioplatecarpinae (Russell, 1967) and Mosasaurinae (LeBlanc et
425 al. 2012), and in this respect resemble *Halisaurus* and primitive mosasauroids such as *Tethysaurus nopscai* (Bardet et al., 2003) and
426 *Dallasaurus* (Bell and Polcyn, 2005) . The atlas neural spine is triangular, moderately elongate, and raked backwards. The neural spines of C3
427 and C4 are moderately elongate, rectangular, and raked backwards. Synapophyses are well-developed. The hypapophysis is well-developed.
428 Prezygapophyses are elongate and well-developed.

429

430 **5. Phylogenetic analysis, Systematics and evolution of *Pluridens* and Halisaurinae.**

431

432 Phylogenetic analysis was undertaken to understand the placement of *P. serpentis* within Halisaurinae. The analysis includes 10 ingroup
433 taxa, 3 outgroups, and 26 characters (see SI). Several characters are taken from Konishi et al. (2016); most are new. Phylogenetic analysis was run
434 using PAUP 4.0 B10 with implied weighting and $K = 2$.

435 The analysis recovers 6 most parsimonious trees (treelength = 45, CI = .6512, RI = .4881). The tree recovers two groupings within
436 Halisaurinae, Halisaurini and Pluridensini (Fig. 13), defined below.

437 Numerous features of *Pluridens serpentis* support its placement in Halisaurinae. These include the premaxilla's posteriorly expanded narial
438 process, a long premaxilla-maxilla contact, broad articulation of the maxilla and premaxillary narial process, the low dorsal wing of the maxilla, a
439 closed otic notch of the quadrate, contribution of the surangular to the coronoid process, high tooth count, weakly heterodont dentition, tooth
440 crowns strongly posteriorly recurved with basal ridges and grooves, weakly developed, unserrated carinae, and finely striated enamel (Bardet et
441 al., 2005b; Longrich, 2016).

442 Other features are unusual among Halisaurinae. These include exclusion of the frontals from the orbits by a prefrontal-postorbitofrontal
443 contact (shared with Mosasaurinae) and the large dorsal coronoid buttress of the surangular contributing to the coronoid process (shared with
444 Mosasaurinae and *Clidastes*). Given other features supporting halisaurine affinities, these are likely convergent.

445 Within Halisaurinae, *P. serpentis* appears to be closely related to *P. walkeri* and *P. calabria*. Features supporting this assignment include
446 the animal's large size, a dentary that is laterally convex at its end, the high tooth count, obliquely oriented tooth bases, and large, medially
447 positioned tooth replacement pits. Together, *P. serpentis*, *P. calabria*, and *P. walkeri*, as well as the halisaurine from the Mooreville Chalk of
448 Alabama, form a distinct, specialized lineage of Halisaurinae, here named Pluridensini.

449

450 **Pluridensini** is defined as all species closer to *Pluridens walkeri* than to *Halisaurus platyspondylus*.

451 Pluridensini are characterized by dental specializations including increased tooth count and obliquely oriented tooth roots; teeth are smaller
452 anteriorly than in the middle of the toothrow, but it is unclear if this is a primitive or derived characteristic. An isolated dentary from the Early
453 Campanian Mooreville Chalk of Alabama shows similarities to *Pluridens* including a high tooth count and obliquely inclined tooth bases. Referred
454 to *Halisaurus* (= *Eonatator*) *sternbergii* (Lindgren and Siverson, 2005), it is here recovered with Pluridensini.

455 Diagnosing various *Pluridens* species is necessarily restricted to differences in jaws and teeth. *P. serpentis* differs from *P. walkeri* and *P.*
456 *calabria* in lacking strong posterior expansion of the dentary. It has more teeth than in *P. calabria*, but dentary tooth count (~26-28) is similar
457 to that inferred for *P. walkeri* (~30). The shape of the mandible also differs, being more evenly tapered in *P. serpentis*, versus straight and rodlike
458 in *P. walkeri*. The cylindrical shape of the anterior dentary in *P. walkeri* was initially assumed to be diagnostic, but this feature appears ontogenetic
459 or even due to sexual dimorphism. The extensive variation seen here suggests some caution in diagnosing species on the basis of jaws, but we note
460 that none of the large series of dentaries known from Morocco conform closely to either *P. walkeri* or *P. calabria* in morphology, arguing that

461 *P. serpentis* is distinct from either. Tooth count and tooth shape appear to vary little with size, supporting the distinction between *P. calabaria* and
462 *P. walkeri*. Pluridensini are characterized by an increased tooth count, which suggests specialization on relatively small prey.

463

464 A new taxon, Halisaurini, is also created here and defined as all species closer to *Halisaurus platyspondylus* than *Pluridens serpentis*. It
465 includes *Halisaurus platyspondylus*, *H. arambourgi*, *Phosphorosaurus ortliebi*, *Phosphorosaurus ponpetelegans*, *Eonatator coellensis*, and
466 *Eonatator sternbergii* as sister group of all the former.

467 Halisaurini are united by a prominent frontal keel, a median frontal boss along the frontoparietal suture and in at least some taxa, very
468 large, slender and comma-shaped jugals. Within Halisaurini, *Halisaurus platyspondylus* and *H. arambourgi* are united by broad frontals in which
469 the preorbital part of the frontals is short and broad. *Halisaurus*, “*Phosphorosaurus*” *ponpetelegans* and “*Eonatator*” *coellensis* all share extremely
470 large, comma-shaped jugal associated with enlarged orbits. *Phosphorosaurus ortliebi* appears to have a different jugal morphology. In contrast to
471 *P. serpentis*, Halisaurini are characterized by enlarged orbits and a degree of binocularity, both of which increase the ability to gather light from
472 an object to form an image. These features suggest visual detection of prey in low-light conditions, either at night or at depth.

473

474 Both the specialized morphology of Pluridensini and Halisaurini and their diversity - at least six halisaurines occur in the Maastrichtian,
475 and at least four in the late Maastrichtian- reject previous interpretations of declining halisaurine diversity in the latest Cretaceous (Polcyn et al.,
476 20134). Instead, Halisaurinae appear to diversify and peak in their diversity (Fig. 13), niche occupation, and large geographic range (Fig. 14) over
477 the course of the Late Cretaceous, paralleling the adaptive radiation seen in Mosasaurinae, while presumably occupying distinct niches.

478

479

480 **6. Discussion**

481

482 **6.1 Ecology of Pluridens**

483

484 *Pluridens* is unlike other mosasaurs in terms of morphology and presumably ecology. In comparison with the other mosasaurids taxa of the
485 Maastrichtian Phosphates of Morocco, *Pluridens serpentis* was far larger than the contemporary *Halisaurus arambourgi* and probably rivalled
486 mosasaurines such as *Eremiasaurus* in size (Fig. 15) as well as plioplatecarpines like *Gavialomimus almaghribensis* (Strong et al., 2020). Despite
487 the animals large size, the teeth are small, numerous and weakly heterodont, suggesting it fed on small prey such as fish and cephalopods, which
488 stable isotopes suggest were abundant (Martin et al., 2017) .

489 The proportions of the orbits also suggest a very different hunting strategy than in Halisaurini. Halisaurini had proportionally large orbits
490 and presumably correspondingly large eyes, and a degree of binocular vision, suggesting visual foraging (Konishi et al., 2016). These adaptations
491 may have been useful for using visual cues in low-light conditions- dusk, dawn, night, and deep water, or simply for tracking small and/or fast-
492 moving prey items.

493 *Pluridens* meanwhile had relatively small orbits, reinforced by a large prefrontal-postorbitofrontal contact above orbit forming a robust rim
494 of bone. The small eyes suggest a distinct hunting strategy. Large eyes may have been less important during the day or at shallow depths, where
495 light levels were high. Another possibility is that *Pluridens* hunted using non-visual cues.

496 Some species of sea snakes (Hydrophiinae) (Dunson and Minton, 1978; Udyawer et al., 2015), sea kraits (*Laticauda*) (Dunson and Minton,
497 1978) and filesnakes (*Acrochordus*) (Shine and Lambeck, 1985) forage nocturnally. Non-visual senses appear to play a key role in foraging in
498 these species, and many of them, including *Acrochordus* and many species of sea snake, have small eyes. In particular tongue-flicking is used by

499 sea snakes (Kutsuma et al., 2018), sea kraits (Radcliffe and Chiszar, 1980) and filesnakes (Vincent et al., 2005) to detect chemical cues, specifically
500 water-soluble molecules in the water, which are transported by the tongue to the vomeronasal organ (VNO). Tongue-flicking is also used by
501 semiaquatic lizards, e.g. *Varanus* (Mayes et al., 2005). It has previously been suggested that mosasaurids may have had a forked tongue (Schulp
502 et al., 2005). Given that mosasaurs appear closely related to snakes and anguimorphs (Martill et al., 2015; Reeder et al., 2015), it is likely they had
503 a forked tongue used for chemoreception, as in these taxa. It may have played an important role where visual cues were lacking.

504 Sense of touch likely contributed to foraging as well. Mosasaurs in general have a large number of neurovascular foramina in the premaxilla,
505 maxilla, and dentary, especially at the tip (Russell, 1967) suggesting extensive innervation of the face to receive tactile cues (Álvarez-Herrera et
506 al., 2020). *Pluridens* is unusual in having more neurovascular foramina than in *Halisaurus*, suggesting elaboration of mechanoreceptors relative
507 to other halisaurines and mosasaurids in general. A number of modern and extinct taxa have sophisticated mechanoreception allowing them to
508 forage using tactile cues. Numerous mechanoreceptors in the scales of sea (Crowe-Riddell et al., 2016; Crowe-Riddell et al., 2019) and filesnakes
509 (Van Der Kooij and Povel, 1996) for example, increase touch sensitivity and perhaps also sense variations in water pressure caused by prey.
510 Similar tactile sensors also occur in crocodylians (Leitch and Catania, 2012; Di-Poï and Milinkovitch, 2013) where they are associated with
511 elaboration of facial nerves similar to that seen in mosasaurs. Increased numbers of neurovascular foramina are also seen in tactile foraging birds
512 such as sandpipers and kiwis (Martill et al., 2021). Among extinct taxa, the densely innervated premaxillae of pliosaurs (Foffa et al., 2014) and
513 certain pterosaurs (Martill et al., 2021) have been proposed to be adaptations for foraging using mechanoreception.

514 The different foraging strategies, visual versus nonvisual, have advantages and disadvantages. Visual foraging can detect prey at long
515 ranges, which is effective for foraging in open habitats, or hunting fast-moving prey. Chemoreception is presumably less useful in open habitats
516 where chemical cues quickly disperse, and the slow process of following chemical trails is of little use for tracking fast-moving prey. However,
517 olfaction can be effective where visual cues are not. For example olfaction can be effective at night when too little light is available to hunt using
518 vision. It is also useful for finding hidden prey, such as fish in crevices and burrows in reefs, or species concealed by camouflage. Many marine
519 snakes therefore use chemoreception and mechanoreception to hunt at night when visual cues are less useful, and/or specialize on hidden prey
520 such as eels in burrows and crevices (Brischoux et al., 2007, 2009) that are difficult for a visually hunting predators to find.

521

522 **6.2 Variation in jaw morphology**

523

524 *Pluridens* shows a remarkable change in jaw morphology from the smallest to the largest individuals, with the largest individual having an
525 extremely robust, massive jaw relative to the smaller individuals (Figs. 3 to 12). It was initially assumed that two different species of *Pluridens*
526 might exist in the assemblage. However, the jaws seem to show continuous variation and share features such as curvature, tooth size, tooth count,
527 and arrangement of the neurovascular foramina, suggesting an ontogenetic series. Preliminary studies of other mosasaurids in the fauna (*Halisaurus*
528 *arambourgi*, cf. *Prognathodon*) suggest that the jaws of mosasaurs became more robust as they grew larger, but the extremely massive jaw seen
529 in the largest individual is striking.

530 It is possible that the robust jaws were in some way related to feeding and the need to generate high bite forces. This raises the question
531 however of why large individuals would need much more robust jaws than younger ones. Also, the dentary is unusual in that it is not simply deep
532 (which improves the jaws resistance in dorsoventral bending experienced during biting down) but expanded mediolaterally which would increase
533 strength in mediolateral bending and torsion. Furthermore, the small, conical teeth of *Pluridens* imply that they were used to pierce and hold
534 relatively small prey items, which raises the issue of why the jaws would be so massive.

535 Another possibility is that the mandibles were used for fighting. Combat is common in modern whales such as sperm whales (Carrier et
536 al., 2002) and beaked whales (Heyning, 1984; MacLeod, 2002). Male sperm whales appear to use their enlarged melon as a battering ram in

537 combat, and are capable of sinking ships with it, as in the infamous case of the whaleship Essex. In the beaked whale *Mesoplodon*, males bear
538 large bladelike teeth. Scars on their flanks suggest that the teeth are used in combat (Heyning, 1984), and in some species, the bone of the rostrum
539 is extremely dense, which is thought to be an adaptation for combat (MacLeod, 2002).

540 By analogy, the robust jaws of the largest individuals of *Pluridens serpentis* might be an adaptation for combat. A pathological lesion on
541 one specimen (Fig. 10) is consistent with the idea that the jaws of *Pluridens serpentis* were used in combat, and sometimes suffered injury.
542 Although preservation is poor, rugosity on the lateral surface of the mandible in the holotype of *Pluridens walkeri* may also indicate pathology.
543 Evidence of traumatic injury is also seen in other mosasaurids, including *Mosasaurus hoffmanni* (Lingham-Soliar, 2004) and *Tylosaurus kansensis*
544 (Everhart, 2008), suggesting it may have been common in mosasaurids. Similar injuries are seen in the jaws of the lepidosaur *Gephyrosaurus*
545 (Evans, 1983), extant lizards, and the jaws of theropod dinosaurs (Tanke and Currie, 1998).

546 Combat could potentially be over territory or mates. Although mosasaurids would have been able to range widely in search of food, feed
547 is likely to have been highly localized, good ‘fishing spots’ would have been in demand and mosasaurs may have aggressively defended foraging
548 territories. In whales, combat in both sperm whales (Carrier et al., 2002) and beaked whales (Heyning, 1984) is between males, over mates. By
549 analogy, larger and more robust *Pluridens* jaws may represent males engaging in combat. Among lizards, males sometimes have larger skulls than
550 females (Carothers, 1984) as an adaptation for combat. If so, the differences in size in the *Pluridens* in our sample may at least in part reflect
551 differences in head size, rather than overall body size.

552

553 **6.3 Paleobiodiversity and palaeobiogeography of Halisaurinae prior to the K-Pg extinction**

554

555 The late Maastrichtian Phosphates of the Oulad Abdoun Basin of Morocco have the most diverse known mosasaur fauna known from this period,
556 or any other (Bardet et al., 2015). With the addition of *Pluridens*, at least ten species of mosasaur are known (Table 1). Here, as elsewhere,
557 Mosasaurinae dominate in terms of number of species, with other groups such as Plioplatecarpinae and Halisaurinae playing a subordinate role
558 (Bardet et al., 2015). Some species- *Prognathodon* aff. *saturator*, *Mosasaurus beaugei*, *Halisaurus arambourgi*, *Eremiasaurus heterodon*, and
559 *Gavialimimus almaghribensis* dominate in terms of specimens, the others being uncommon to rare. As a result, following discovery of the relatively
560 few common species of the assemblage, uncommon and rare species such as *Pluridens* continue to be discovered. The implication is that the
561 diversity of the fauna remains poorly known and that additional sampling will continue to produce new species. The Moroccan assemblage may
562 therefore be far more diverse than we have appreciated. Future finds will test this hypothesis.

563 In addition to adding to the species richness of the fauna, *Pluridens* appears to occupy a niche distinct from previously known species in
564 the assemblage. Moroccan mosasaurids were extremely diverse in terms of their ecology (Cappetta et al., 2014; Bardet et al., 2015). In size, the
565 marine squamates ranged from the diminutive *Pachyvaranus* and small *Halisaurus* to the giant *Mosasaurus* and *Prognathodon*. Tooth morphology
566 shows remarkable variation as well, teeth included simple cones, cutting blades, and blunt crushing morphologies (Bardet et al., 2015); likewise
567 jaw and skull structures vary, suggesting distinct feeding styles.

568 *Pluridens* is distinct from other Moroccan mosasaurids in terms of combining large size (estimated 6-10 m long), relatively small piercing
569 and poorly heterodont dentition, and small eyes. It apparently hunted in a different way than *Halisaurus* or other mosasaurids in the assemblage.
570 *Pluridens* therefore expands not just the species richness but the ecological disparity and functional diversity of the fauna.

571 In addition to contributing to our understanding of diversity and disparity, mosasaurid faunas from the Maastrichtian of Morocco document
572 the existence of a distinct fauna found in the southern Tethys Margin Province, including the Arabo-African Platform and Brazil. The fauna of this
573 province differs from those known elsewhere at the time such as the northwest Pacific of California, the southwest Pacific of New Zealand, and
574 especially the Northern Tethys Margin Province of New Jersey and Europe (Bardet, 2012; Cappetta et al., 2014; Bardet et al., 2015). The faunas

575 can be segregated into these two provinces (as defined by Bardet, 2012), respectively developed around palaeolatitudes 20°N-20°S into
576 intertropical environments *versus* palaeolatitudes 30-40°N into warm-temperate environments. The precise reasons for these differences remain
577 unknown, but these patterns probably reveal palaeoecological preferences linked to differences in palaeolatitudinal gradients and/or to
578 palaeocurrents (Bardet, 2012).

579 Within the palaeobiogeographical framework of the Southern Tethys Margin Province, and specifically the Arabo-African Platform, the
580 mosasaurids (and Maastrichtian marine reptiles in general) from Morocco show high affinities with those of Angola and the Middle-East. Those
581 from the Iullemeden intracratonic basin - one of the major Meso-Cenozoic basins of Central West Africa, cropping out mainly in Niger and
582 Nigeria - were considered as endemic (see Bardet, 2012 for details). The most emblematic mosasaurids of the Iullemeden Basin are
583 *Goronyosaurus nigeriensis*, *Igdamanosaurus aegyptiacus* and *Pluridens walkeri* (see Bardet, 2012 for details). With the recent description of new
584 species of *Pluridens* in Niger (Longrich, 2016) and now Morocco (this work), this palaeobiogeographical framework is changing: *Pluridens* no
585 longer represents an endemic taxon from the Iullemeden Basin but rather emphasizes a broader African distribution. It seems probable that the
586 Trans-Saharan Seaway (and the Iullemeden Basin, being a diverticulum of it) that connected the Tethys to the southern Atlantic ocean during
587 the Maastrichtian transgression (Moody and Sutcliffe, 1991; Rat et al., 1991) played an important role in dispersion of these faunas and of *Pluridens*
588 in particular (Fig. 14). *Pluridens*, being unknown in coeval Maastrichtian assemblages from the Northern Tethys Margin Province (Europe and
589 New Jersey; Bardet, 2012), or the Moreno Formation of California (Lindgren and Schulp, 2010), underscores this pattern.

590 Given their high degree of aquatic specialization, mosasaurids should have dispersed readily across oceans. Some genera, such as
591 *Mosasaurus*, *Prognathodon*, *Halisaurus*, and even *Carinodens* did so (Bardet et al., 2014). Other lineages with more restricted distributions, such
592 as *Pluridens* and *Plotosaurus*, apparently did not. The biogeographical distribution of some current nectonic cetaceans - able to cross oceans due
593 to their high degree of marine specialisation like mosasaurids, shows the complexity of these patterns: whereas *Orca* and *Physeter* have worldwide
594 distributions, the delphinid *Lagenorhynchus* exhibits narrow latitudinal distributions, with for example *L. cruciger* being tropical and *L. albirostris*
595 being circum-Antarctic (Bardet, 2012). It is commonly thought that large taxa are more able than smaller ones to disperse across large marine
596 expanses. The mosasaurid examples cited above – especially *Plotosaurus* versus *Carinodens* - suggest that size does not necessarily play a primary
597 role in driving dispersal and geographic range.

598 The endemism seen in mosasaurs was thus likely driven not by dispersal ability, but by constraints imposed by climate, food availability,
599 competitors, and predators. Endemism can be seen as another kind of niche specialization- geographic and habitat specialization- and in this light,
600 agrees with the idea that many Maastrichtian mosasaurids, including *Pluridens*, were highly specialized.

601 Taken together, the mosasaurid fauna from the Maastrichtian Phosphates of Morocco suggests high species richness, a high diversity of
602 niches occupied, and of endemism, i.e. geographic specialization. This last pattern also predicts that global mosasaur diversity, both in terms of
603 niche occupation and species richness, will increase as geographic sampling improves.

604

605

606 7. Conclusions

607

608 Mosasaurid fossils from the late Maastrichtian Phosphates of Morocco document a new species of halisaurine, *Pluridens serpentis*,
609 emphasizing the high diversity of the fauna. *Pluridens* is unusual among mosasaurs in combining large size and specializations for capturing small
610 prey. Small eyes and numerous neurovascular foramina in the rostrum imply a reliance on nonvisual foraging, perhaps at great depths, or at night.
611 Absence of *Pluridens* from Europe and North America suggests that despite being able to disperse long distances, this taxon was rather endemic
612 to the epicontinental seas of western Africa (Oulad Abdoun Basin of Morocco and Iullemeden Basin of Niger-Nigeria). *Pluridens. serpentis*

613 provides additional evidence for the existence of a highly diverse, specialized, and mosasaurid fauna with specialized distribution in the late
614 Maastrichtian, mirroring patterns observed for other marine reptiles (Vincent et al., 2011), immediately prior to the end-Cretaceous mass extinction.
615 These patterns support a catastrophic extinction of marine reptiles at the K-Pg boundary.

616

617 **Acknowledgements.** Thanks to Mustapha Meharich for translation and additional assistance to N.R.L. in Oued Zem. Thanks to Mike Polcyn
618 (Southern Methodist University, Dallas, USA) for discussions. Thanks to Alexandre Lethiers (ISTeP - Institut des Sciences de la Terre de Paris,
619 France) who produced the interpretative drawings of the specimens. Thanks to Gérard Barbe who kindly donated personal specimens of his private
620 collection for study. Finally thanks to Aaron LeBlanc (King's College London, UK) and an anonymous reviewer for constructive comments that
621 have improved this paper.

622 **References**

623

- 624 Álvarez-Herrera, G., Agnolin, F., Novas, F., 2020. A rostral neurovascular system in the mosasaur *Taniwhasaurus antarcticus*. *The Science of*
625 *Nature* 107, 1-5.
- 626 Arambourg, C., 1952. Les vertébrés fossiles des gisements de phosphates (Maroc-Algérie-Tunisie). *Notes et Mémoires du Service Géologique*
627 *du Maroc*. 92, 1-372.
- 628 Bardet, N., 2012. Maastrichtian marine reptiles of the Mediterranean Tethys: a palaeobiogeographical approach. *Bulletin de la Société*
629 *Géologique de France* 183, 573-596.
- 630 Bardet, N., Falconnet, J., Fischer, V., Houssaye, A., Jouve, S., Pereda-Suberbiola, X., Perez-García, A., Rage, J.-C., Vincent, P., 2014. Mesozoic
631 marine reptile palaeobiogeography in response to drifting plates. *Gondwana Research* 26, 869-887.
- 632 Bardet, N., Gheerbrant, E., Noubhani, A., Cappetta, H., Jouve, S., Bourdon, E., Pereda-Suberbiola, X., Jalil, N.-E., Vincent, P., Houssaye, A., Solé,
633 F., El Houssaini Darif, K., Adnet, S., Rage, J.-C., Lapparent de Broin de, F., Sudre, J., Bouya, B., Amaghaz, M., Meslouh, S., 2017. Les Vertébrés
634 des phosphates crétacés-paléogènes (72, 1-47, 8 Ma) du Maroc, *Mémoires de la Société Géologique de France N.S.* 180, pp. 351-452.
- 635 Bardet, N., Houssaye, A., Vincent, P., Pereda-Suberbiola, X., Amaghaz, M., Jourani, E., Meslouh, S., 2015. Mosasaurids (Squamata) from the
636 Maastrichtian phosphates of Morocco: biodiversity, palaeobiogeography and palaeoecology based on tooth morphoguilds. *Gondwana*
637 *Research* 27, 1068-1078.
- 638 Bardet, N., Jalil, N.-E., de Lapparent de Broin, F., Germain, D., Lambert, O., Amaghaz, M., 2013. A Giant Chelonioid Turtle from the Late
639 Cretaceous of Morocco with a Suction Feeding Apparatus Unique among Tetrapods. *PLoS ONE* 8, e63586.
- 640 Bardet, N., Pereda-Suberbiola, X., 2001. The basal mosasaurid *Halisaurus sternbergii* from the Late Cretaceous of Kansas (North America): a
641 review of the Uppsala type specimen. *Comptes Rendus de l'Académie des Sciences-Series IIA-Earth and Planetary Science* 332, 395-402.
- 642 Bardet, N., Pereda-Suberbiola, X., Iarochène, M., Amalik, M., Bouya, B., 2005a. Durophagous Mosasauridae (Squamata) from the Upper
643 Cretaceous phosphates of Morocco, with description of a new species of *Globidens*. *Netherlands Journal of Geosciences* 84, 167-175.
- 644 Bardet, N., Pereda-Suberbiola, X., Iarochène, M., Bouya, B., Amaghaz, M., 2005b. A new species of *Halisaurus* from the Late Cretaceous
645 phosphates of Morocco, and the phylogenetical relationships of the Halosaurinae (Squamata: Mosasauridae). *Zoological Journal of the Linnean*
646 *Society* 143, 447-472.
- 647 Bardet, N., Pereda-Suberbiola, X., Iarochène, M., Bouyahyaoui, F., Bouya, B., Amaghaz, M., 2004. *Mosasaurus beaugei* Arambourg, 1952
648 (Squamata, Mosasauridae) from the Late Cretaceous phosphates of Morocco. *Geobios* 37, 315-324.
- 649 Bardet, N., Pereda-Suberbiola, X., Jalil, N.-E., 2003. A new mosasauroid (Squamata) from the Late Cretaceous (Turonian) of Morocco. *Comptes*
650 *Rendus Palevol* 2, 607-616.
- 651 Bardet, N., Pereda-Suberbiola, X., Jouve, S., Bourdon, E., Vincent, P., Houssaye, A., Rage, J.-C., Jalil, N.-E., Bouya, B., Amaghaz, M., 2010.
652 Reptilian assemblages from the latest Cretaceous–Palaeogene phosphates of Morocco: from Arambourg to present time. *Historical Biology* 22,
653 186-199.
- 654 Bardet, N., Pereda-Suberbiola, X., Schulp, A.S., Bouya, B., 2008. New material of *Carinodens* (Squamata, Mosasauridae) from the Maastrichtian
655 (Late Cretaceous) phosphates of Morocco, *Proceedings of the Second Mosasaur Meeting. Fort Hays Studies, Special*, pp. 29-36.
- 656 Bell, G., Polcyn, M., 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the Middle Turonian of Texas and comments on the
657 phylogeny of Mosasauridae (Squamata). *Netherlands Journal of Geosciences* 84, 177.
- 658 Bell Jr., G.L., 1997. A phylogenetic revision of North American and Adriatic Mosasauroida, *Ancient marine reptiles*. Elsevier, pp. 293-332.
- 659 Brischoux, F., Bonnet, X., Shine, R., 2007. Foraging ecology of sea kraits *Laticauda* spp. in the Neo-Caledonian Lagoon. *Marine Ecology Progress*
660 *Series* 350, 145-151.
- 661 Brischoux, F., Bonnet, X., Shine, R., 2009. Determinants of dietary specialization: a comparison of two sympatric species of sea snakes. *Oikos*
662 118, 145-151.
- 663 Caldwell, M.W., 2007. Ontogeny, anatomy and attachment of the dentition in mosasaurs (Mosasauridae: Squamata). *Zoological Journal of the*
664 *Linnean Society* 149, 687-700.
- 665 Caldwell, M.W., Cooper, J.A., 1999. Redescription, palaeobiogeography and palaeoecology of *Coniasaurus crassidens* OWEN, 1850 (Squamata)
666 from the Lower Chalk (Cretaceous; Cenomanian) of SE England. *Zoological Journal of the Linnean Society* 127, 423-452.
- 667 Cappetta, H., 1987. Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. *Handbook of paleoichthyology* 3, 1-193.
- 668 Cappetta, H., Bardet, N., Pereda-Suberbiola, X., Adnet, S., Akkrim, D., Amalik, M., Benabdallah, A., 2014. Marine vertebrate faunas from the
669 Maastrichtian phosphates of Benguerir (Ganntour Basin, Morocco): Biostratigraphy, palaeobiogeography and palaeoecology.
670 *Palaeogeography, Palaeoclimatology, Palaeoecology* 409, 217-238.
- 671 Carothers, J.H., 1984. Sexual selection and sexual dimorphism in some herbivorous lizards. *The American Naturalist* 124, 244-254.

- 672 Carrier, D.R., Deban, S.M., Otterstrom, J., 2002. The face that sank the Essex: potential function of the spermaceti organ in aggression. *Journal of Experimental Biology* 205, 1755-1763.
673
- 674 Crowe-Riddell, J.M., Snelling, E.P., Watson, A.P., Suh, A.K., Partridge, J.C., Sanders, K.L., 2016. The evolution of scale sensilla in the transition
675 from land to sea in elapid snakes. *Open biology* 6, 160054.
- 676 Crowe-Riddell, J.M., Williams, R., Chapuis, L., Sanders, K.L., 2019. Ultrastructural evidence of a mechanosensory function of scale organs
677 (sensilla) in sea snakes (Hydrophiinae). *Royal Society open science* 6, 182022.
- 678 DeBraga, M., Carroll, R.L., 1993. The origin of mosasaurs as a model of macroevolutionary patterns and processes, *Evolutionary biology*.
679 Springer, pp. 245-322.
- 680 Di-Poï, N., Milinkovitch, M.C., 2013. Crocodylians evolved scattered multi-sensory micro-organs. *EvoDevo* 4, 1-16.
- 681 Dunson, W.A., Minton, S.A., 1978. Diversity, distribution, and ecology of Philippine marine snakes (Reptilia, Serpentes). *Journal of Herpetology*,
682 281-286.
- 683 Evans, S.E., 1983. Mandibular fracture and inferred behavior in a fossil reptile. *Copeia* 1983, 845-847.
- 684 Everhart, M., 2005. *Tylosaurus kansasensis*, a new species of tylosaurine (Squamata, Mosasauridae) from the Niobrara Chalk of western
685 Kansas, USA. *Netherlands Journal of Geosciences-Geologie en Mijnbouw* 84, 231-240.
- 686 Everhart, M.J., 2008. A bitten skull of *Tylosaurus kansasensis* (Squamata: Mosasauridae) and a review of mosasaur-on-mosasaur pathology in
687 the fossil record. *Transactions of the Kansas Academy of Science* 111, 251-262.
- 688 Fernández, M.S., Talevi, M., 2015. An halisaurine (Squamata: Mosasauridae) from the Late Cretaceous of Patagonia, with a preserved tympanic
689 disc: insights into the mosasaur middle ear. *Comptes Rendus Palevol* 14, 483-493.
- 690 Foffa, D., Sassoon, J., Cuff, A.R., Mavrogordato, M.N., Benton, M.J., 2014. Complex rostral neurovascular system in a giant pliosaur.
691 *Naturwissenschaften* 101, 453-456.
- 692 Frey, E., Mulder, E.W., Stinnesbeck, W., Salazar, C., Quinzio-Sinn, L.A.H., 2016. A mosasaur, cf. *Plotosaurus*, from the upper Maastrichtian
693 Quiriquina Formation in Central Chile. *Cretaceous Research* 61, 17-25.
- 694 Gervais, P., 1852. *Zoologie et paléontologie françaises (animaux vertébrés): nouvelles recherches sur les animaux vivants de la France*. Arthus
695 Bertrand.
- 696 Heyning, J.E., 1984. Functional morphology involved in intraspecific fighting of the beaked whale, *Mesoplodon carlhubbsi*. *Canadian Journal of*
697 *Zoology* 62, 1645-1654.
- 698 Holmes, R.B., Sues, H.-D., 2000. A partial skeleton of the basal mosasaur *Halisaurus platyspondylus* from the Severn Formation (Upper
699 Cretaceous: Maastrichtian) of Maryland. *Journal of Vertebrate Paleontology* 74, 309-316.
- 700 Houssaye, A., Bardet, N., Rage, J.-C., Pereda-Suberbiola, X., Bouya, B., Amaghazaz, M., Amalik, M., 2011. A review of *Pachyvaranus*
701 *crassispondylus* Arambourg, 1952, a pachyostotic marine squamate from the latest Cretaceous phosphates of Morocco and Syria. *Geological*
702 *Magazine* 148, 237-249.
- 703 Jiménez-Huidobro, P., Otero, R.A., Soto-Acuña, S., Caldwell, M.W., 2019. Reassessment of cf. *Plotosaurus* from the upper Maastrichtian of
704 Chile, with comments on the South American distribution of halisaurine mosasaurs. *Cretaceous Research* 103, 104162.
- 705 Jouve, S., Bardet, N., Jalil, N.-E., Pereda-Suberbiola, X., Bouya, B., Amaghazaz, M., 2008. The oldest African crocodylian: phylogeny,
706 paleobiogeography, and differential survivorship of marine reptiles through the Cretaceous-Tertiary boundary. *Journal of Vertebrate*
707 *Paleontology* 28, 409-421.
- 708 Kocsis, L., Gheerbrant, E., Mouflih, M., Cappetta, H., Yans, J., Amaghazaz, M., 2014. Comprehensive stable isotope investigation of marine
709 biogenic apatite from the Late Cretaceous–Early Eocene phosphate series of Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology*
710 394, 74-88.
- 711 Konishi, T., Brinkman, D., Massare, J.A., Caldwell, M.W., 2011. New exceptional specimens of *Prognathodon overtoni* (Squamata,
712 Mosasauridae) from the upper Campanian of Alberta, Canada, and the systematics and ecology of the genus. *Journal of Vertebrate*
713 *Paleontology* 31, 1026-1046.
- 714 Konishi, T., Caldwell, M.W., 2011. Two new plioplacatid (Squamata, Mosasauridae) genera from the Upper Cretaceous of North America,
715 and a global phylogenetic analysis of plioplacatids. *Journal of Vertebrate Paleontology* 31, 754-783.
- 716 Konishi, T., Caldwell, M.W., Nishimura, T., Sakurai, K., Tanoue, K., 2016. A new halisaurine mosasaur (Squamata: Halisaurinae) from Japan: the
717 first record in the western Pacific realm and the first documented insights into binocular vision in mosasaurs. *Journal of Systematic*
718 *Palaeontology* 14, 809-839.
- 719 Konishi, T., Lindgren, J., Caldwell, M.W., Chiappe, L., 2012. *Platycarpus tympaniticus* (Squamata, Mosasauridae): osteology of an exceptionally
720 preserved specimen and its insights into the acquisition of a streamlined body shape in mosasaurs. *Journal of Vertebrate Paleontology* 32,
721 1313-1327.
- 722 Kutsuma, R., Sasai, T., Kishida, T., 2018. How snakes find prey underwater: sea snakes use visual and chemical cues for foraging. *Zoological*
723 *science* 35, 483-486.

- 724 Lapparent de Broin, F.d., Bardet, N., Amaghaz, M., Meslouh, S., 2013. A strange new chelonoid turtle from the Latest Cretaceous phosphates
725 of Morocco. *Comptes Rendus Palevol* 13, 87-95.
- 726 LeBlanc, A.R., Lamoureux, D.O., Caldwell, M.W., 2017. Mosasaurs and snakes have a periodontal ligament: timing and extent of calcification,
727 not tissue complexity, determines tooth attachment mode in reptiles. *Journal of Anatomy* 231, 869-885.
- 728 LeBlanc, A.R., Mohr, S.R., Caldwell, M.W., 2019. Insights into the anatomy and functional morphology of durophagous mosasaurines
729 (Squamata: Mosasauridae) from a new species of *Globidens* from Morocco. *Zoological Journal of the Linnean Society* 186, 1026-1052.
- 730 LeBlanc, A.R.H., Caldwell, M.W., Bardet, N., 2012. A new mosasaurine from the Maastrichtian (Upper Cretaceous) phosphates of Morocco and
731 its implications for mosasaurine systematics. *Journal of Vertebrate Paleontology* 32, 82-104.
- 732 Leitch, D.B., Catania, K.C., 2012. Structure, innervation and response properties of integumentary sensory organs in crocodylians. *Journal of*
733 *Experimental Biology* 215, 4217-4230.
- 734 Lindgren, J., Caldwell, M.W., Jagt, J.W., 2008. New data on the postcranial anatomy of the California mosasaur *Plotosaurus bennisoni* (Camp,
735 1942)(Upper Cretaceous: Maastrichtian), and the taxonomic status of *P. tuckeri* (Camp, 1942). *Journal of Vertebrate Paleontology* 28, 1043-
736 1054.
- 737 Lindgren, J., Schulp, A.S., 2010. New material of *Prognathodon* (Squamata: Mosasauridae), and the mosasaur assemblage of the Maastrichtian
738 of California, USA. *Journal of Vertebrate Paleontology* 30, 1632-1636.
- 739 Lindgren, J., Siverson, M., 2005. *Halisaurus sternbergi*, a small mosasaur with an intercontinental distribution. *Journal of Paleontology* 79, 763-
740 773.
- 741 Lingham-Soliar, T., 1994. The mosasaur *Plioplatecarpus* (Reptilia, Mosasauridae) from the Upper Cretaceous of Europe. *Bulletin-Institut royal*
742 *des sciences naturelles de Belgique. Sciences de la terre* 64, 177-211.
- 743 Lingham-Soliar, T., 1995. Anatomy and functional morphology of the largest marine reptile known, *Mosasaurus hoffmanni* (Mosasauridae,
744 Reptilia) from the Upper Cretaceous, Upper Maastrichtian of the Netherlands. *Philosophical Transactions of the Royal Society of London. Series*
745 *B: Biological Sciences* 347, 155-180.
- 746 Lingham-Soliar, T., 1996. The first description of *Halisaurus* (Reptilia Mosasauridae) from Europe, from the Upper Cretaceous of Belgium.
747 *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* 66, 129-136.
- 748 Lingham-Soliar, T., 1998. A new mosasaur *Pluridens walkeri* from the Upper Cretaceous, Maastrichtian of the Iullemeden Basin, southwest
749 Niger. *Journal of Vertebrate Paleontology* 18, 709-717.
- 750 Lingham-Soliar, T., Nolf, D., 1989. The mosasaur *Prognathodon* (Reptilia, Mosasauridae) from the Upper Cretaceous of Belgium. *Bulletin de*
751 *l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 59, 137-190.
- 752 Lingham-Soliar, T., 2004. Palaeopathology and injury in the extinct mosasaurs (Lepidosauromorpha, Squamata) and implications for modern
753 reptiles. *Lethaia* 37, 255-262.
- 754 Liu, M., Reed, D.A., Cecchini, G.M., Lu, X., Ganjawalla, K., Gonzales, C.S., Monahan, R., Luan, X., Diekwisch, T.G., 2016. Varanoid tooth eruption
755 and implantation modes in a late Cretaceous mosasaur. *Frontiers in Physiology* 7, 145.
- 756 Lively, J.R., 2018. Taxonomy and historical inertia: *Clidastes* (Squamata: Mosasauridae) as a case study of problematic paleobiological
757 taxonomy. *Alcheringa: An Australasian Journal of Palaeontology* 42, 516-527.
- 758 Longrich, N.R., 2016. A new species of *Pluridens* (Mosasauridae: Halisaurinae) from the upper Campanian of Southern Nigeria. *Cretaceous*
759 *Research* 64, 36-44.
- 760 Longrich, N.R., Bardet, N., Schulp, A.S., Jalil, N.-E., 2021. *Xenodens calminechari* gen. et sp. nov., a bizarre mosasaurid (Mosasauridae,
761 Squamata) with shark-like cutting teeth from the upper Maastrichtian of Morocco, North Africa. *Cretaceous Research*, 104764.
- 762 Longrich, N.R., Martill, D.M., Andres, B., 2018. Late Maastrichtian pterosaurs from North Africa and mass extinction of Pterosauria at the
763 Cretaceous-Paleogene boundary. *PLoS Biology* 16, e2001663.
- 764 Longrich, N.R., Pereda-Suberbiola, X., Jalil, N.-E., Khaldoune, F., Jourani, E., 2017. An abelisaurid from the latest Cretaceous (late Maastrichtian)
765 of Morocco, North Africa. *Cretaceous Research* 76, 40-52.
- 766 Longrich, N.R., Pereda-Suberbiola, X., Pyron, R.A., Jalil, N.-E., 2020. The first duckbill dinosaur (Hadrosauridae: Lambeosaurinae) from Africa
767 and the role of oceanic dispersal in dinosaur biogeography. *Cretaceous Research*, 104678.
- 768 Luan, X., Walker, C., Dangaria, S., Ito, Y., Druzinsky, R., Jarosius, K., Lesot, H., Rieppel, O., 2009. The mosasaur tooth attachment apparatus as
769 paradigm for the evolution of the gnathostome periodontium. *Evolution & development* 11, 247-259.
- 770 MacLeod, C.D., 2002. Possible functions of the ultradense bone in the rostrum of Blainville's beaked whale (*Mesoplodon densirostris*).
771 *Canadian Journal of Zoology* 80, 178-184.
- 772 Martill, D.M., Smith, R.E., Longrich, N., Brown, J., 2021. Evidence for tactile foraging in pterosaurs: a sensitive tip to the beak of *Lonchodraco*
773 *giganteus* (Pterosauria, Lonchodectidae) from the Upper Cretaceous of southern England. *Cretaceous Research* 117, 104637.
- 774 Martill, D.M., Tischlinger, H., Longrich, N.R., 2015. A four-legged snake from the Early Cretaceous of Gondwana. *Science* 349, 416-419.

- 775 Martin, J.E., Vincent, P., Tacail, T., Khaldoune, F., Jourani, E., Bardet, N., Balter, V., 2017. Calcium isotopic evidence for vulnerable marine
776 ecosystem structure prior to the K/Pg extinction. *Current Biology* 27, 1641-1644. e1642.
- 777 Mayes, P., Thompson, G., Withers, P., 2005. Diet and foraging behaviour of the semi-aquatic *Varanus mertensi* (Reptilia: Varanidae). *Wildlife*
778 *Research* 32, 67-74.
- 779 Moody, R., Sutcliffe, P., 1991. The Cretaceous deposits of the Iullemeden basin of Niger, central West Africa. *Cretaceous Research* 12, 137-
780 157.
- 781 Opperl, M., 1811. Die Ordnungen, Familien und Gattungen der Reptilien als Prodrum einer Naturgeschichte derselben. Lindauer, München.
- 782 Páramo-Fonseca, M.E., 2013. *Eonatator coellensis* nov. sp. (Squamata: Mosasauridae), a new species from the Upper Cretaceous of Colombia.
783 *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* 37, 499-518.
- 784 Pereda-Suberbiola, X., Bardet, N., Iarochène, M., Bouya, B., Amaghaz, M., 2004. The first record of a sauropod dinosaur from the Late
785 Cretaceous phosphates of Morocco. *Journal of African Earth Sciences* 40, 81-88.
- 786 Pereda-Suberbiola, X., Bardet, N., Jouve, S., Iarochène, M., Bouya, B., Amaghaz, M., 2003. A new azhdarchid pterosaur from the Late
787 Cretaceous phosphates of Morocco. *Geological Society, London, Special Publications* 217, 79-90.
- 788 Polcyn, M.J., Jacobs, L.L., Araújo, R., Schulp, A.S., Mateus, O., 2013. Physical drivers of mosasaur evolution. *Palaeogeography,*
789 *Palaeoclimatology, Palaeoecology* 400, 17-27.
- 790 Polcyn, M.J., Lamb, J., 2012. The snout of *Halisaurus platyspondylus* Marsh 1869: phylogenetic and functional implications. *Bulletin de la*
791 *Societe Geologique de France* 183, 137-143.
- 792 Polcyn, M.J., Lindgren, J., Bardet, N., Cornelissen, D., Verding, L., Schulp, A.S., 2012. Description of new specimens of *Halisaurus arambourgi*
793 Bardet & Pereda Suberbiola, 2005 and the relationships of Halosaurinae. *Bulletin de la Société Géologique de France* 183, 123-136.
- 794 Radcliffe, C.W., Chiszar, D.A., 1980. A descriptive analysis of predatory behavior in the yellow lipped sea krait (*Laticauda colubrina*). *Journal of*
795 *Herpetology* 14, 422-424.
- 796 Rat, P., Lang, J., Alzouma, K., Dikouma, M., Johnson, A., Laurin, B., Mathey, B., Pascal, A., 1991. Coastal marine basins as records of continental
797 palaeoenvironments (Gulf of Guinea and Iullemeden Cretaceous and Tertiary basins). *Journal of African Earth Sciences (and the Middle East)*
798 12, 23-30.
- 799 Reeder, T.W., Townsend, T.M., Mulcahy, D.G., Noonan, B.P., Wood Jr, P.L., Sites Jr, J.W., Wiens, J.J., 2015. Integrated Analyses Resolve
800 Conflicts over Squamate Reptile Phylogeny and Reveal Unexpected Placements for Fossil Taxa. *PloS one* 10, e0118199.
- 801 Rieppel, O., Kearney, M., 2005. Tooth replacement in the Late Cretaceous mosasaur *Clidastes*. *Journal of Herpetology* 39, 688-692.
- 802 Russell, D.A., 1967. Systematics and morphology of American mosasaurs. *Bulletin of the Peabody Museum of Natural History* 23, 1-240.
- 803 Schulp, A.S., Bardet, N., Bouya, B., 2009. A new species of the durophagous mosasaur *Carinodens* (Squamata, Mosasauridae) and additional
804 material of *Carinodens belgicus* from the Maastrichtian phosphates of Morocco. *Netherlands Journal of Geosciences* 88, 161-167.
- 805 Schulp, A.S., Mulder, E., Schwenk, K., 2005. Did mosasaurs have forked tongues? *Netherlands Journal of Geosciences* 84, 359-371.
- 806 Shine, R., Lambeck, R., 1985. A radiotelemetric study of movements, thermoregulation and habitat utilization of Arafura filesnakes (Serpentes:
807 *Acrochordidae*). *Herpetologica*, 351-361.
- 808 Street, H.P., Caldwell, M.W., 2017. Rediagnosis and redescription of *Mosasaurus hoffmannii* (Squamata: Mosasauridae) and an assessment of
809 species assigned to the genus *Mosasaurus*. *Geological Magazine* 154, 521-557.
- 810 Strong, C.R., Caldwell, M.W., Konishi, T., Palci, A., 2020. A new species of longirostrine plioplatecarpine mosasaur (Squamata: Mosasauridae)
811 from the Late Cretaceous of Morocco, with a re-evaluation of the problematic taxon '*Platecarpus*' *ptychodon*. *Journal of Systematic*
812 *Palaeontology*, 1-36.
- 813 Tanke, D.H., Currie, P.J., 1998. Head-biting behavior in the theropod dinosaurs: paleopathological evidence. *Gaia* 15, 167-184.
- 814 Udyawer, V., Simpfendorfer, C.A., Heupel, M.R., 2015. Diel patterns in three-dimensional use of space by sea snakes. *Animal Biotelemetry* 3,
815 29.
- 816 Van Der Kooij, J., Povel, D., 1996. Scale sensillae of the file snake (Serpentes: *Acrochordidae*) and some other aquatic and burrowing snakes.
817 *Netherlands Journal of Zoology* 47, 443-456.
- 818 Vincent, P., Bardet, N., Houssaye, A., Amaghaz, M., Meslouh, S., 2013. New plesiosaur specimens from the Maastrichtian Phosphates of
819 Morocco and their implications for the ecology of the latest Cretaceous marine apex predators. *Gondwana Research* 24, 796-805.
- 820 Vincent, P., Bardet, N., Pereda Suberbiola, X., Bouya, B., Amaghaz, M., Meslouh, S., 2011. *Zarafasaura oceanis*, a new elasmosaurid (Reptilia:
821 *Sauropterygia*) from the Maastrichtian Phosphates of Morocco and the palaeobiogeography of latest Cretaceous plesiosaurs. *Gondwana*
822 *Research* 19, 1062-1073.
- 823 Vincent, S.E., Shine, R., Brown, G.P., 2005. Does foraging mode influence sensory modalities for prey detection in male and female filesnakes,
824 *Acrochordus arafurae*? *Animal Behaviour* 70, 715-721.

825 Vullo, R., Cavin, L., Khalloufi, B., Amaghaz, M., Bardet, N., Jalil, N.-E., Jourani, E., Khaldoune, F., Gheerbrant, E., 2017. A unique Cretaceous–
826 Paleogene lineage of piranha-jawed pycnodont fishes. *Scientific reports* 7, 1-9.
827
828

Figure Captions

829

830

831

832 **Fig. 1.** Map of northern Morocco (A) showing the location of the OCP Group phosphate mines of Sidi Daoui and Sidi Chennane (B).

833

834 **Fig. 2.** Schematic stratigraphic column showing the position of *Pluridens serpentis* sp. nov. in the upper Maastrichtian strata of Couche III, Sidi
835 Daoui, Khouribga Province, Morocco. Stratigraphic column after Kocsis et al. (2014).

836

837 **Fig. 3.** *Pluridens serpentis* sp. nov., OCP DEK-GE 548, syntype skull ., Couche III, Oulad Abdoun Basin, Sidi Daoui, Morocco. A, skull in dorsal
838 view; B, interpretive drawing. Abbreviations: Ang, angular; Co, coronoid; en, external naris; Fr, frontal; ib, internarial bar; Ju, jugal; Mx, maxilla;
839 or, orbit; Pa, parietal, Pfr, prefrontal, Pmx, premaxilla; Pofr, postorbitofrontal; Sp, splenial; Sq, squamosal; Su, supraoccipital; Sur, surangular; tf,
840 temporal fenestra.

841

842 **Fig. 4.** *Pluridens serpentis* sp. nov.. OCP DEK-GE 548, syntype skull. Couche III, Oulad Abdoun Basin, Sidi Daoui , Morocco. A, closeup of
843 rostrum; B, closeup of skull roof. Abbreviations: en, external naris; Fr, Frontal; ib, internarial bar; Ju, jugal; Mx, Maxilla; Na?, Nasal; or, orbit;
844 Pa, Parietal; Pfr, Prefrontal; Pofr, postorbitofrontal. Scale bars = 10 cm.

845

846 **Fig 5.** *Pluridens serpentis* sp. nov.. MHNM.KH.262, syntype skull and jaws. Couche III, Oulad AbBdoun Basin, Sidi Daoui , Morocco.
847 Abbreviations: Ang, angular; Art, articular; Ax, Axis; Axi, axial intercentrum; CV, cervical vertebra; Co, coronoid; De, dentary; en, external naris;
848 Fr, frontal; hy, hypapophysis; ib, internarial bar; Ju, jugal; Mx, maxilla; or, orbit; Op-Ex, Opisthothic-Exoccipital; Pa, parietal; Part, prearticular;
849 pf, parietal foramen; Pfr, prefrontal, Pmx, premaxilla; Pofr, postorbitofrontal; Q, quadrate; Sp, splenial; Sq, squamosal; St, Supratemporal; Su,
850 supraoccipital; Sur, surangular; tf, temporal fenestra; V, vertebra.

851

852 **Fig. 6.** *Pluridens serpentis* sp. nov., MHNM.KH.262, syntype skull and jaws. Couche III, Oulad Abdoun Basin, Sidi Daoui , Morocco. **A**, rostrum;
853 **B**, anterior dentition. Abbreviations: De, dentary; Fr, frontal; Mx, maxilla, Pfr, prefrontal; Pmx, premaxilla; Pofr, postorbitofrontal.

854

855 **Fig. 7.** *Pluridens serpentis* sp. nov., MHNM.KH.262, syntype skull and jaws. Couche III, Oulad Abdoun Basin, Sidi Daoui , Morocco. **A**, Closeup
856 of cranial roof, **B**, closeup of posterior mandible and quadrate. Abbreviations: Ang, angular; Art, articular; Co, coronoid; Fr, frontal; Ju, jugal; lc,
857 lateral conch; Pa, parietal; pf, pineal foramen; Pofr, postfrontal; Pfr, prefrontal; Q, quadrate; ret, retroarticular process; Sp, splenial; Sq, squamosal;
858 Sur, surangular.

859

860 **Fig. 8.** *Pluridens serpentis* sp. nov., MHNM.KH.390, referred maxilla in medial view. Couche III, Oulad Abdoun Basin, Sidi Daoui , Morocco.
861 Abbreviations: alv, alveolus; en, external naris; idp, interdental plate; pmx, premaxilla contact; prf, prefrontal contact.

862

863 **Fig. 9.** *Pluridens serpentis* sp. nov., MHNM.KH.389. Couche III, Oulad Abdoun Basin, Sidi Daoui , Morocco. A, referred dentary in medial view;
864 B, closeup showing teeth. Abbreviations: br, broken apex; cr, crown; fl, fluting; idp, interdental plate; mec, meckelian canal; mp, medial parapet;
865 ro, root; rp, replacement pit; sym, symphysis; vl, ventral lip.

866

867 **Fig. 10.** *Pluridens serpentis* sp. nov., referred dentary. Couche III, Oulad Abdoun Basin, Sidi Daoui , Morocco. MHNM.KH.394, right dentary in
868 A, medial, B, dorsal, C lateral views; D, closeup showing pathology.

869

870 **Fig. 11.** *Pluridens serpentis* sp. nov., referred mandibles. Couche III, Oulad Abdoun Basin, Sidi Daoui , Morocco. A, MHNM.KH.387, left dentary
871 in lateral view; B, MHNM.KH.388, left and right dentaries (reversed) in medial and lateral views respectively, C, MHNM.KH.386, left dentary in
872 lateral view.

873

874 **Fig. 12.** Dentaries compared for *Pluridens walkeri*, *P. calabaria*, *P. serpentis* sp. nov.

875

876 **Fig 13.** Phylogeny of Halisaurinae, Strict consensus of 6 most parsimonious trees (treelength = 45, CI = .6512, RI = .4881), showing placement of
877 *P. serpentis* sp. nov. and split of Halisaurinae into the new tribes Pluridensini and Halisaurini.

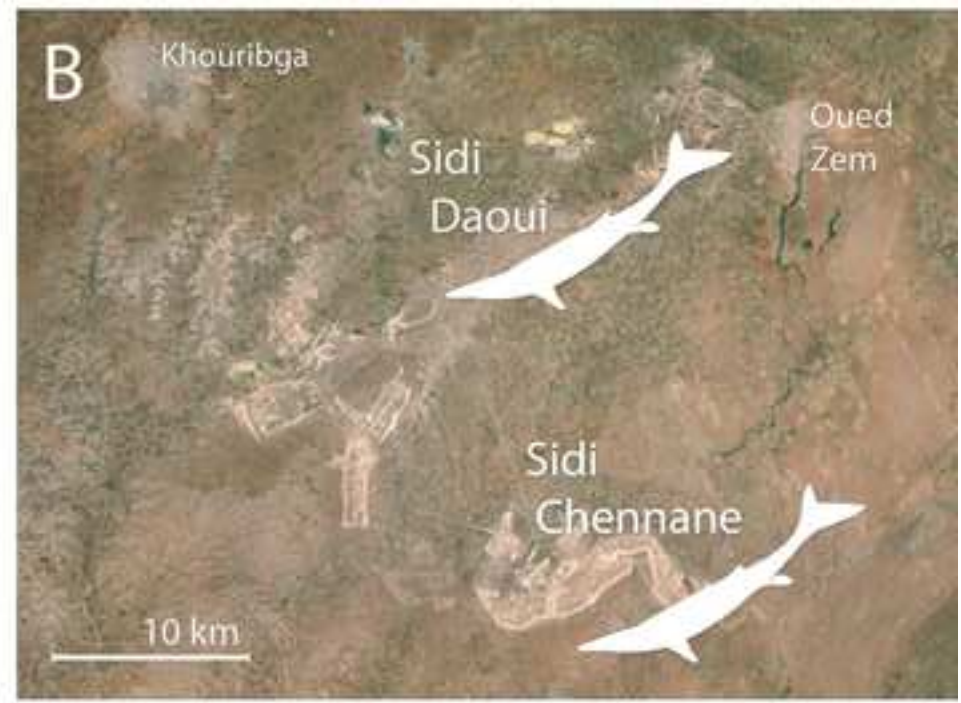
878

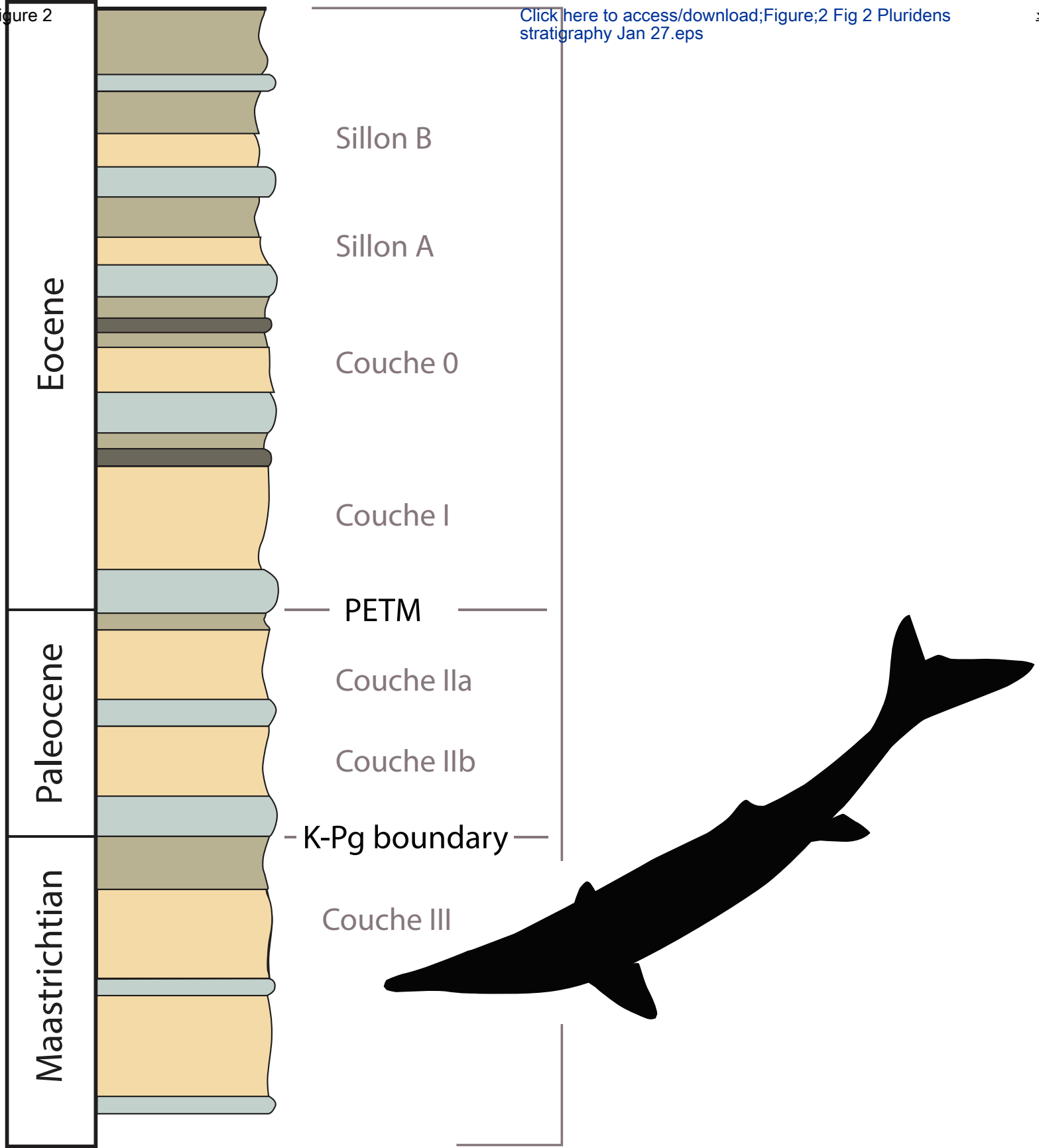
879 **Fig. 14.** Relative size of *Pluridens serpentis* sp. nov., syntypes and largest referred specimens, *Halisaurus arambourgi*. *Homo sapiens* for scale.
880 Body shape after *Eonatator sternbergii* (*P. serpentis*) and “*Eonatator*” *coellensis* (*H. arambourgi*). Scale = 1 meter.





881

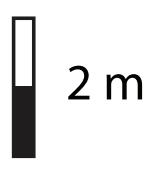
882 **Fig. 15.** Occurrences of Pluridensini. 1, *Pluridens walkeri*, early Maastrichtian, Niger; 2, *Pluridens calabaria*, late Campanian, Nigeria; 3,
883 *Pluridens serpentis* sp. nov., late Maastrichtian, Morocco; 4, aff. *Pluridens.*, early Campanian, Alabama, USA; ?Pluridensini, late Maastrichtian,
884 Argentina.. Map by R. Blakey.

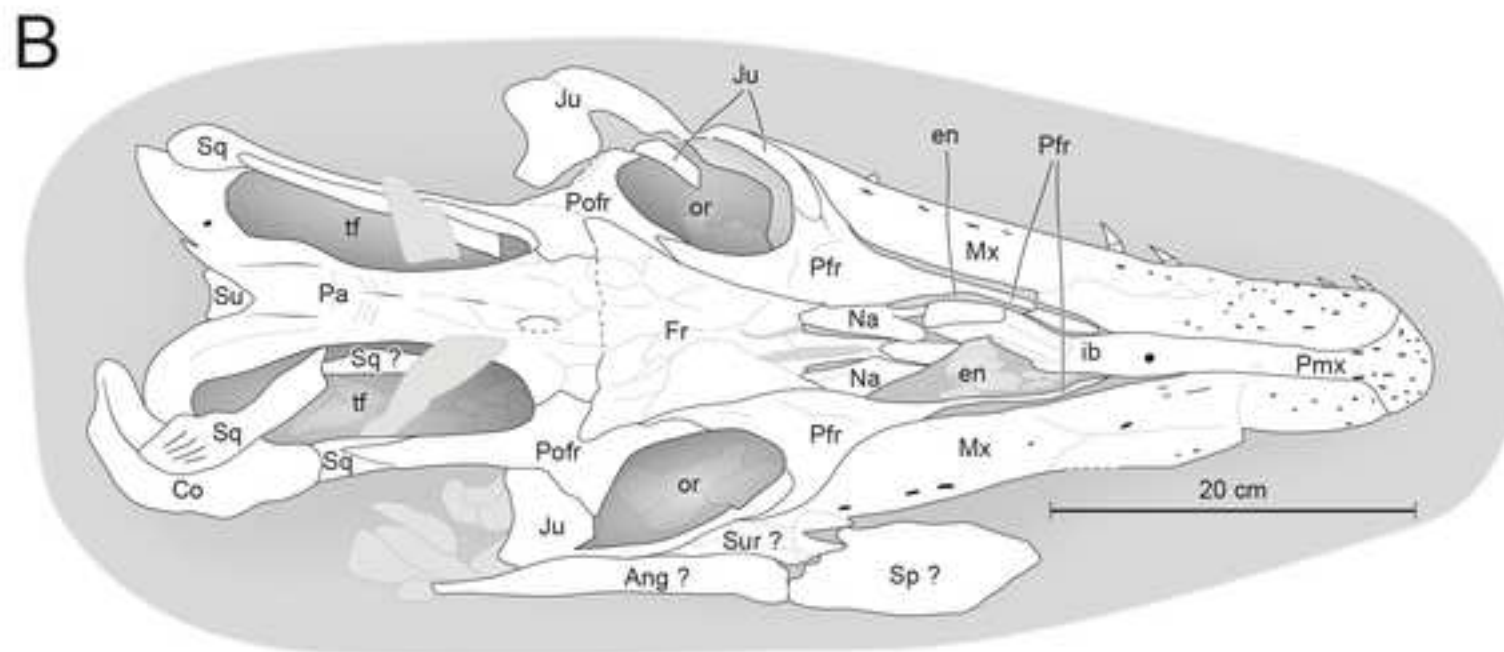
885

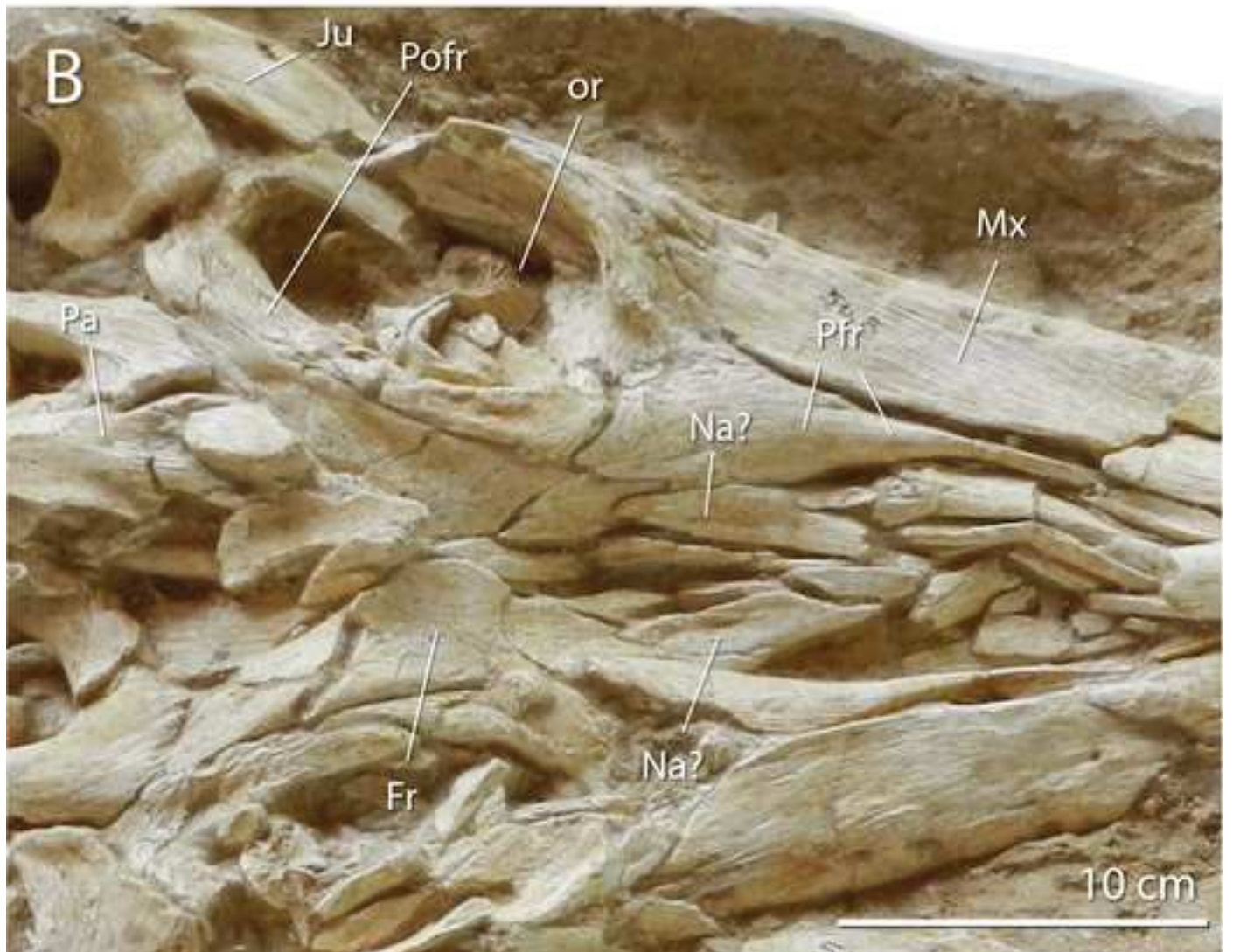
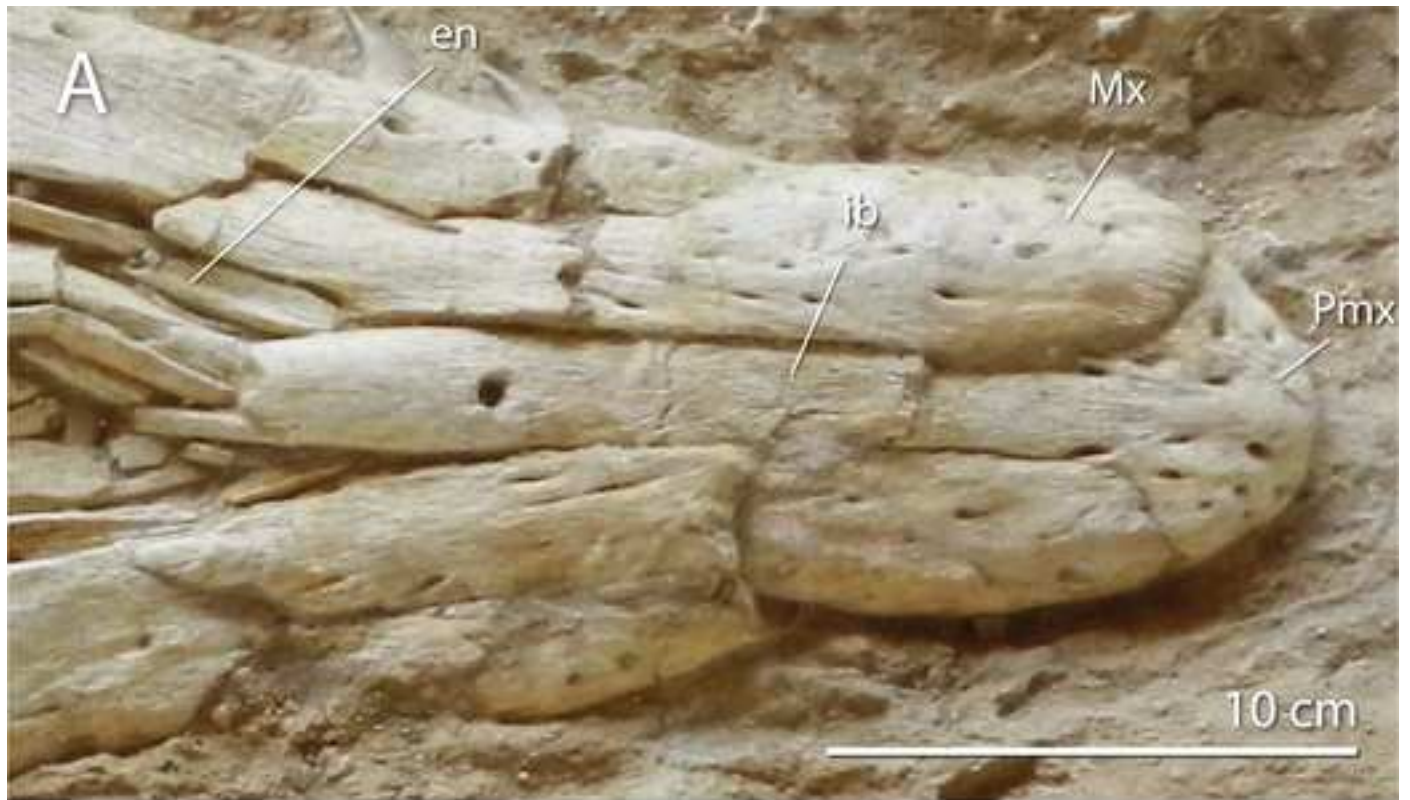


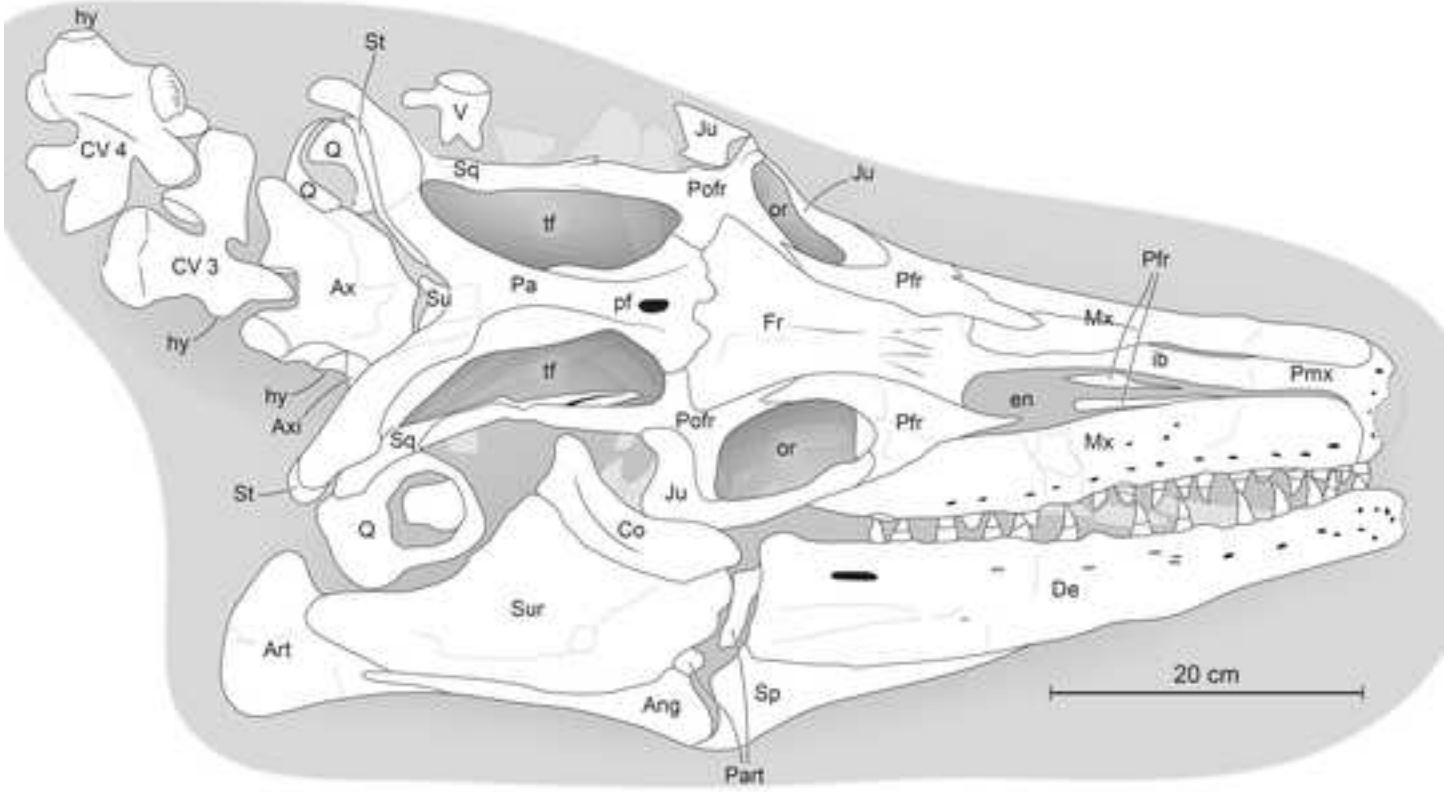


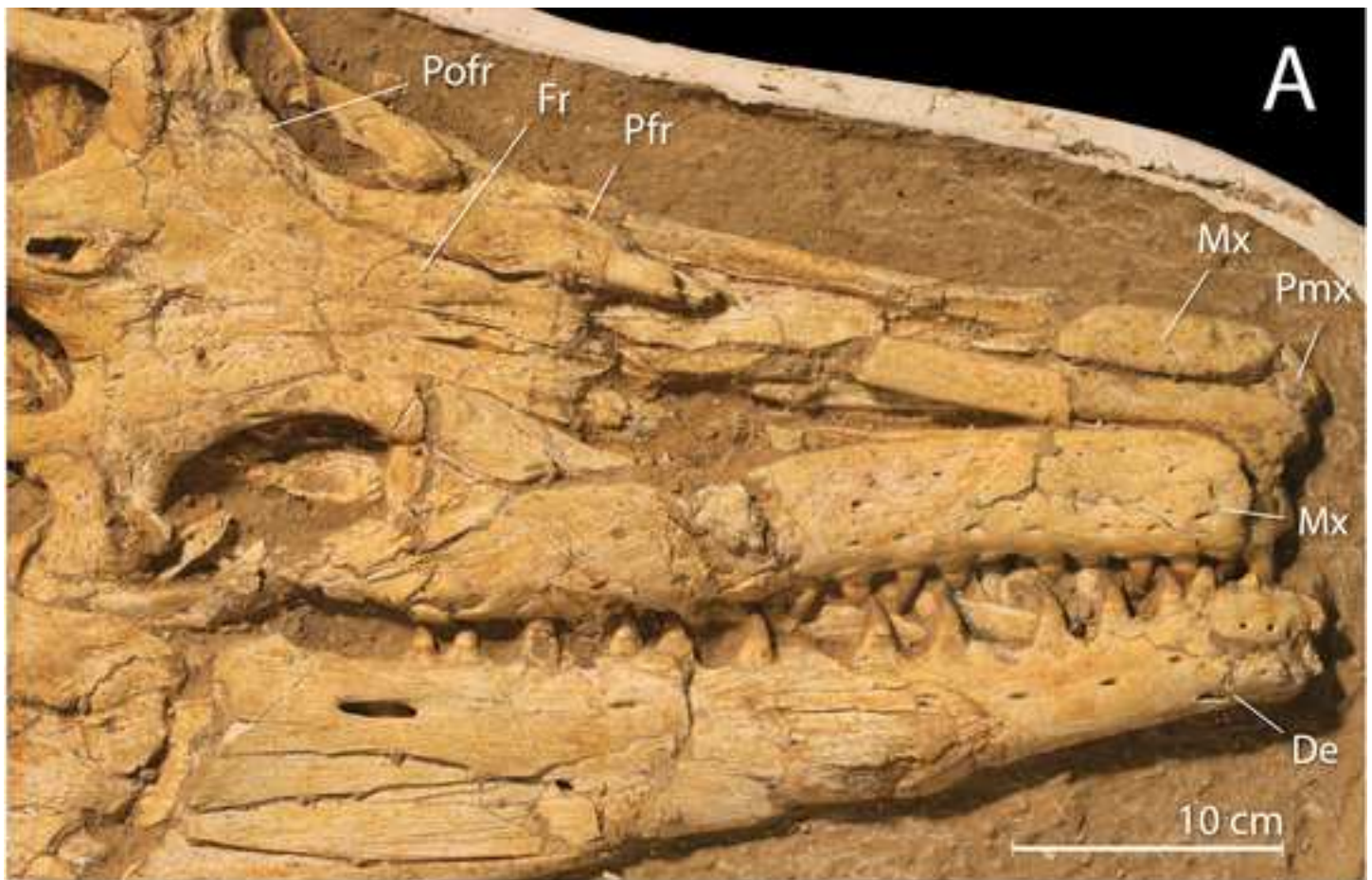
-  Limestone
-  Phosphate sand / marl
-  Marl
-  Chert

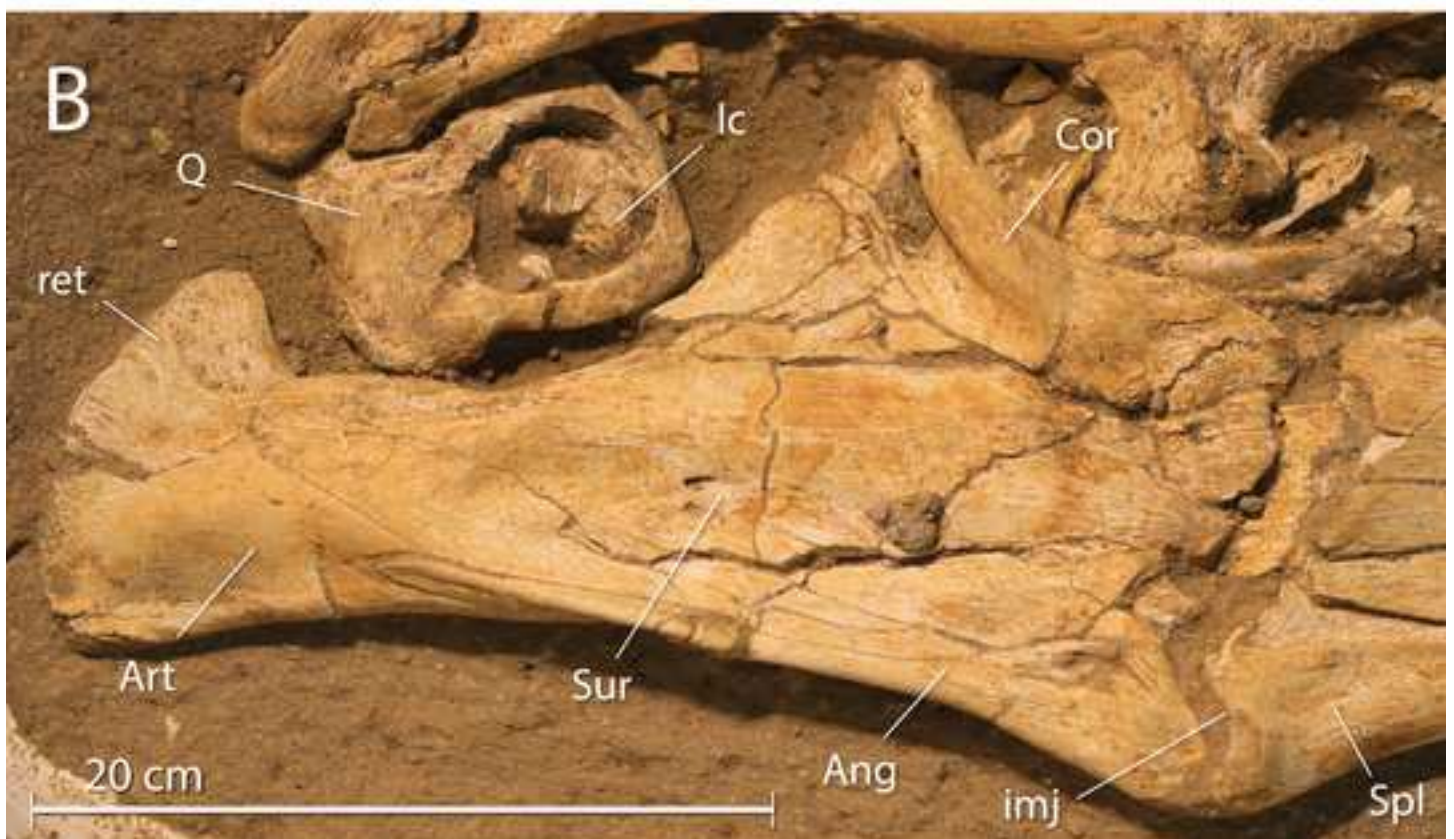
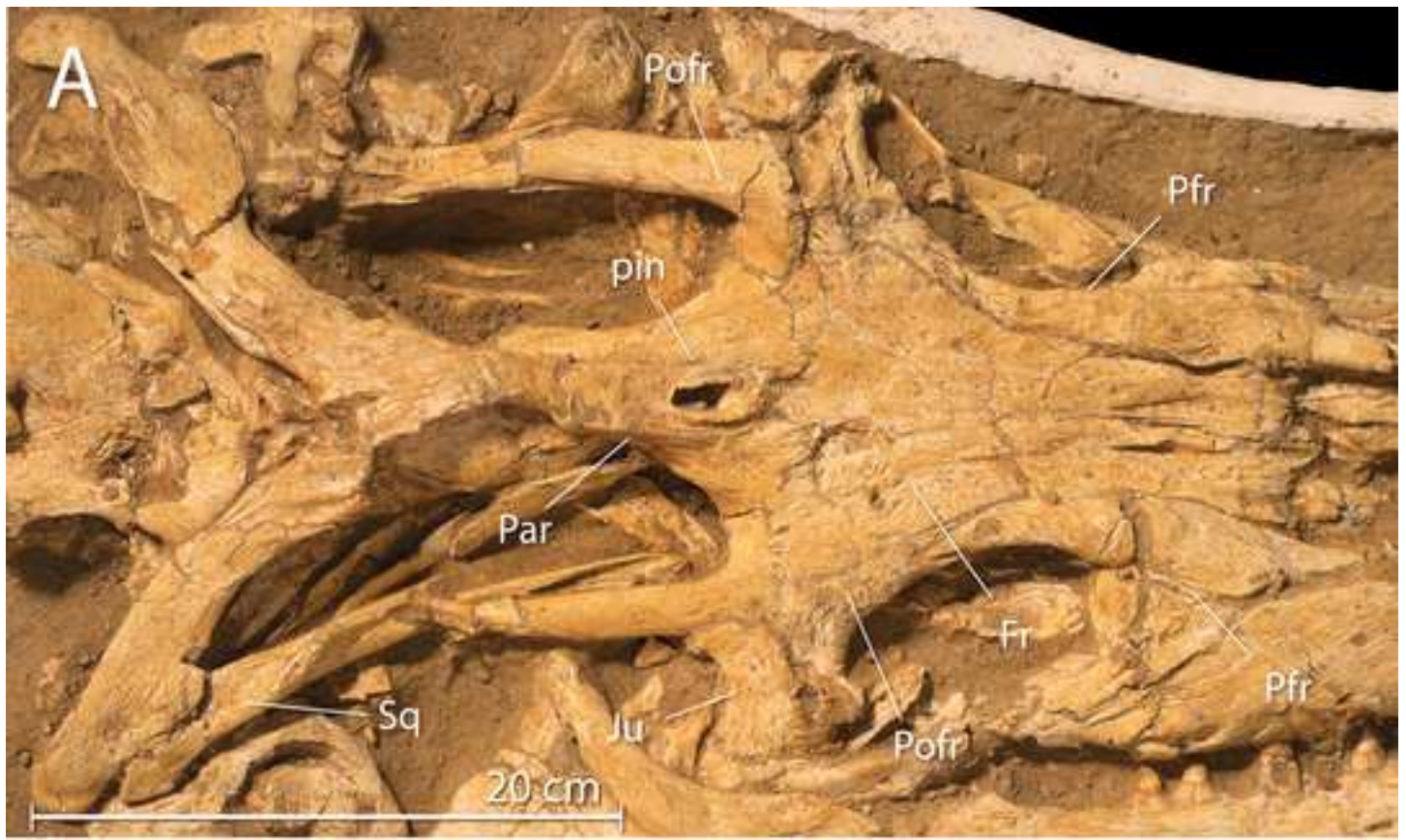


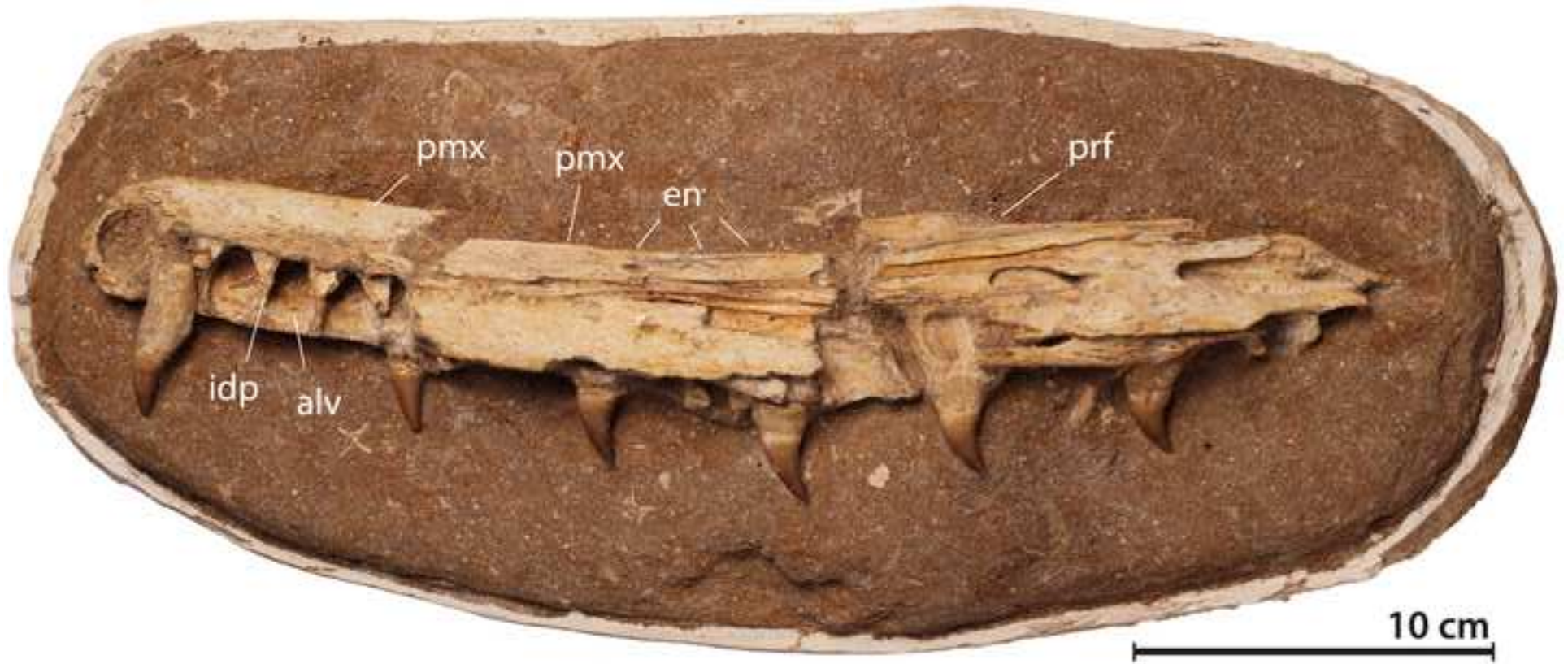


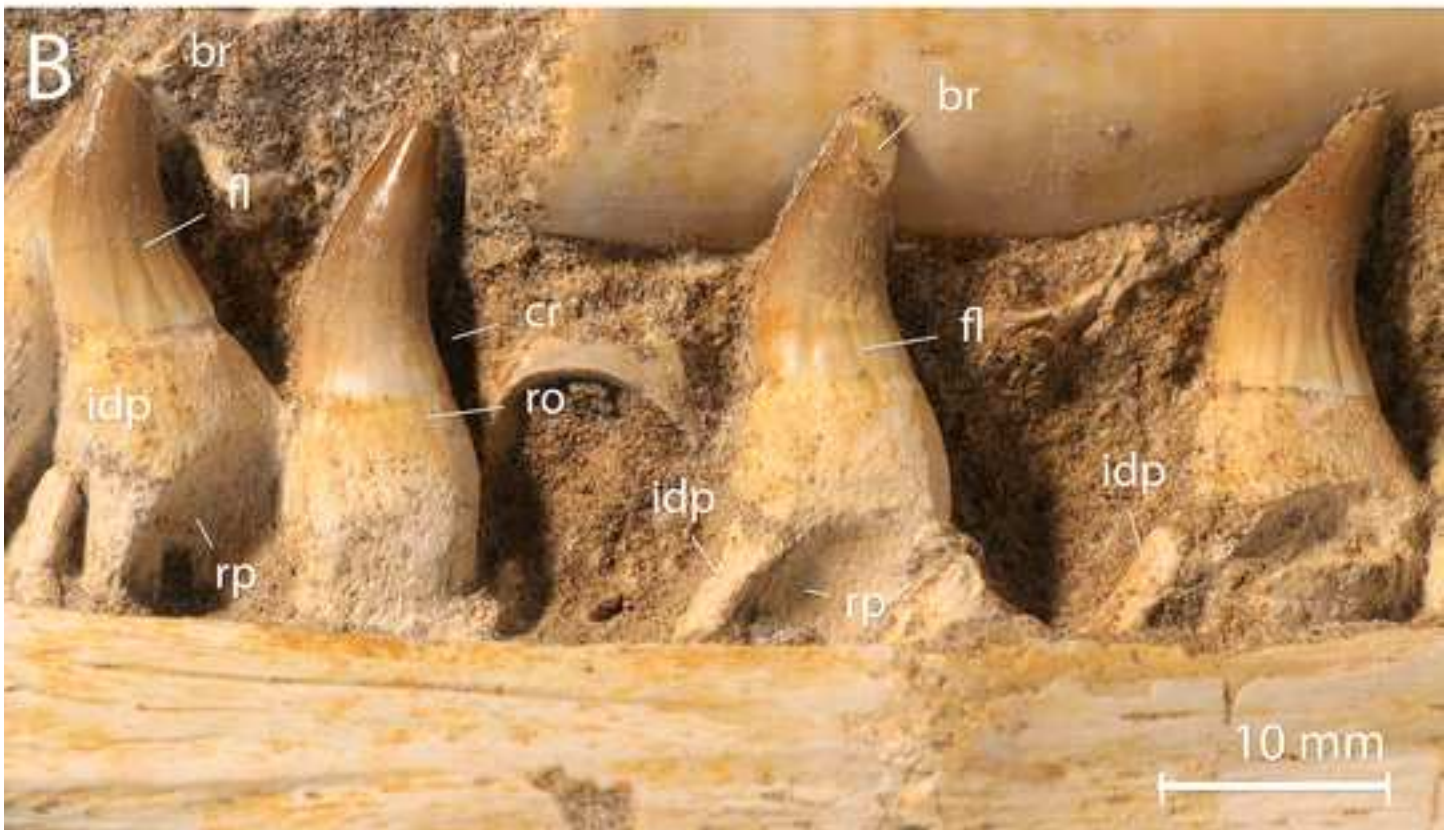
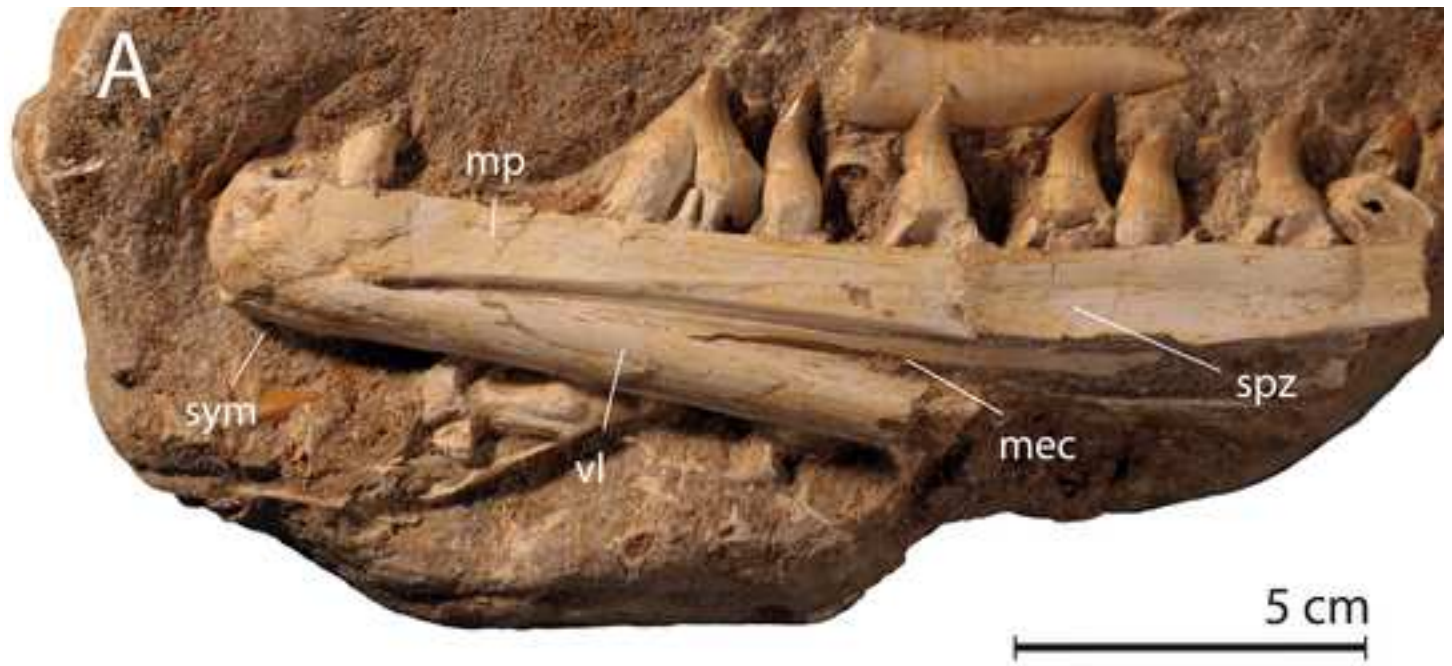


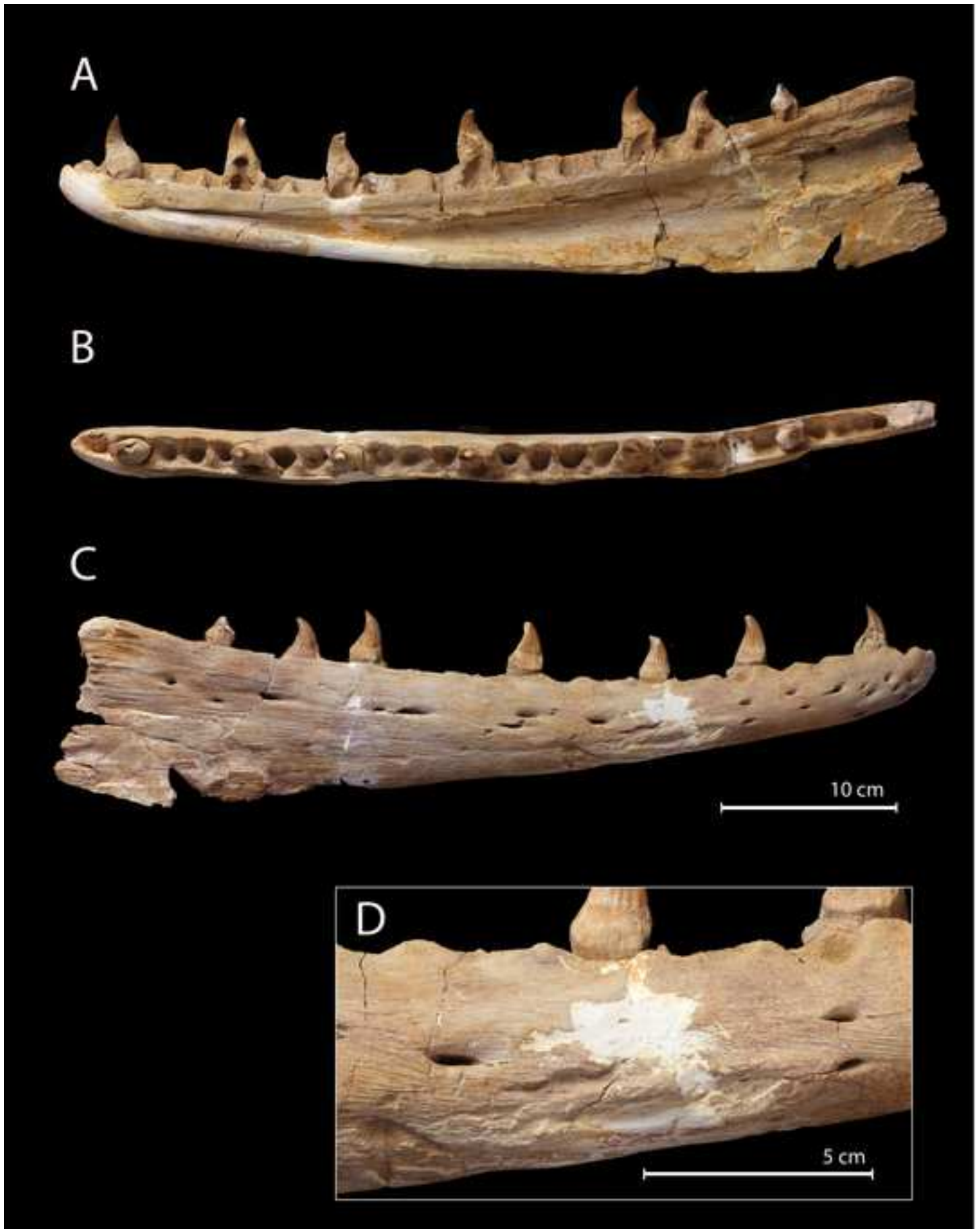












A



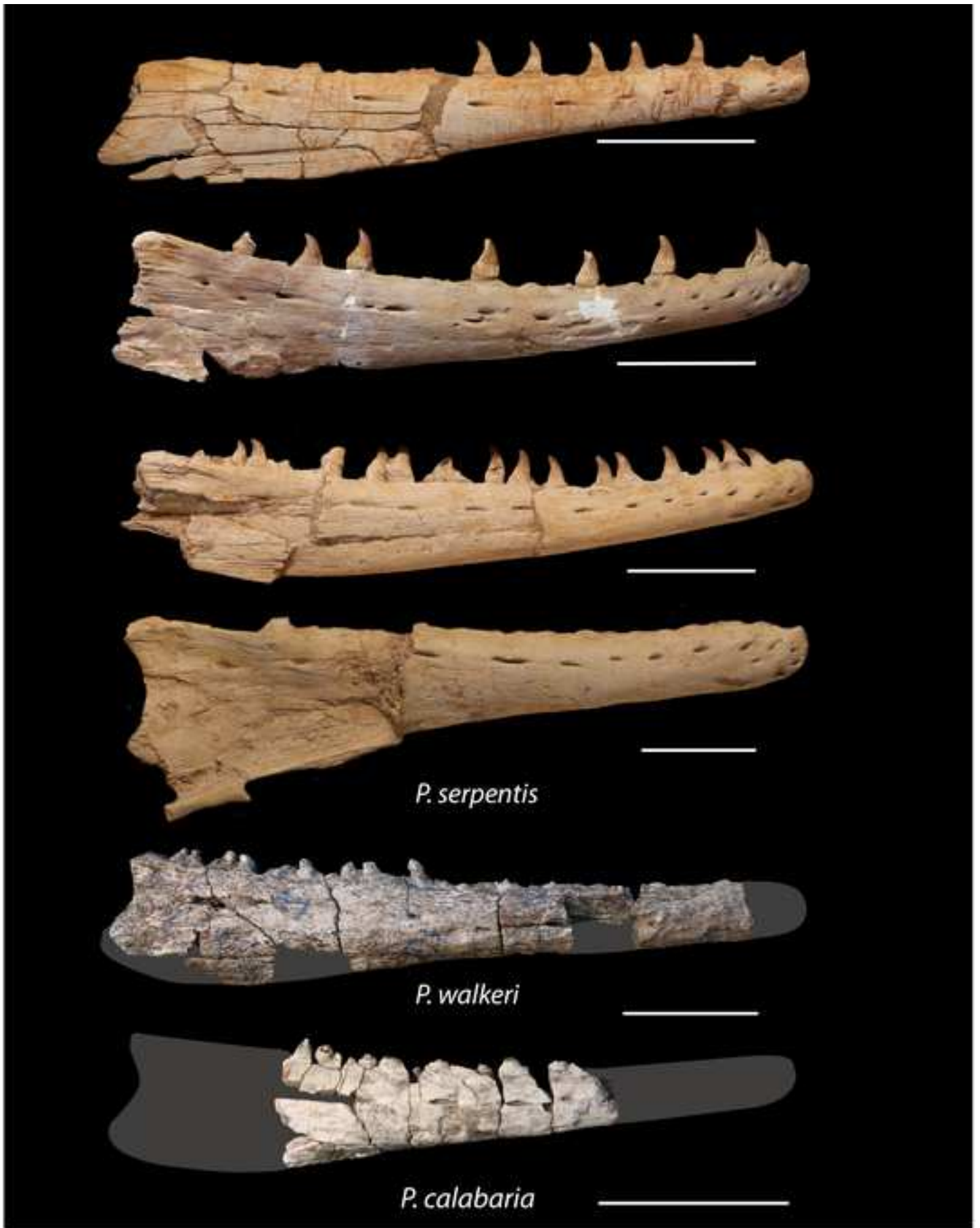
B

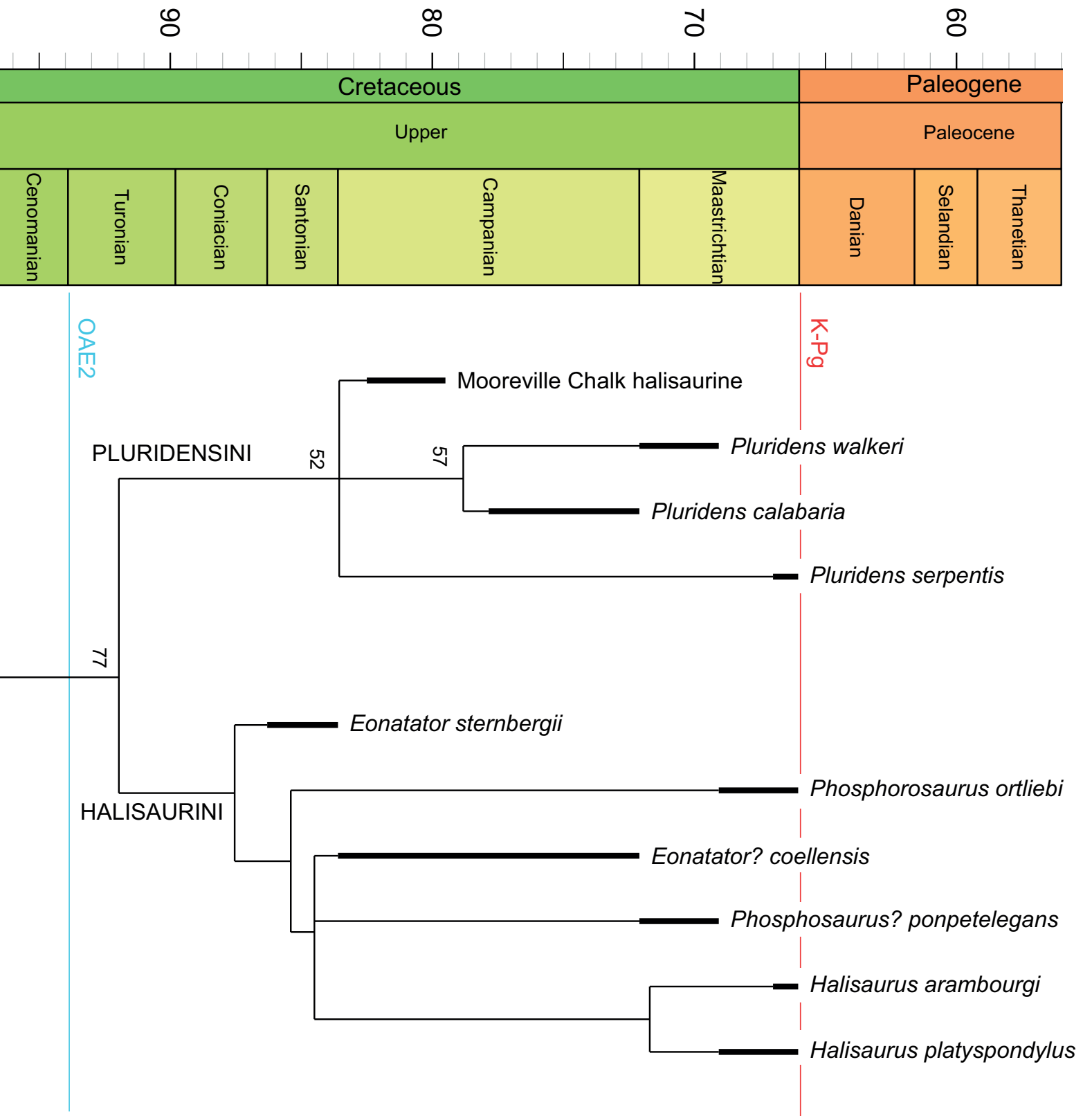


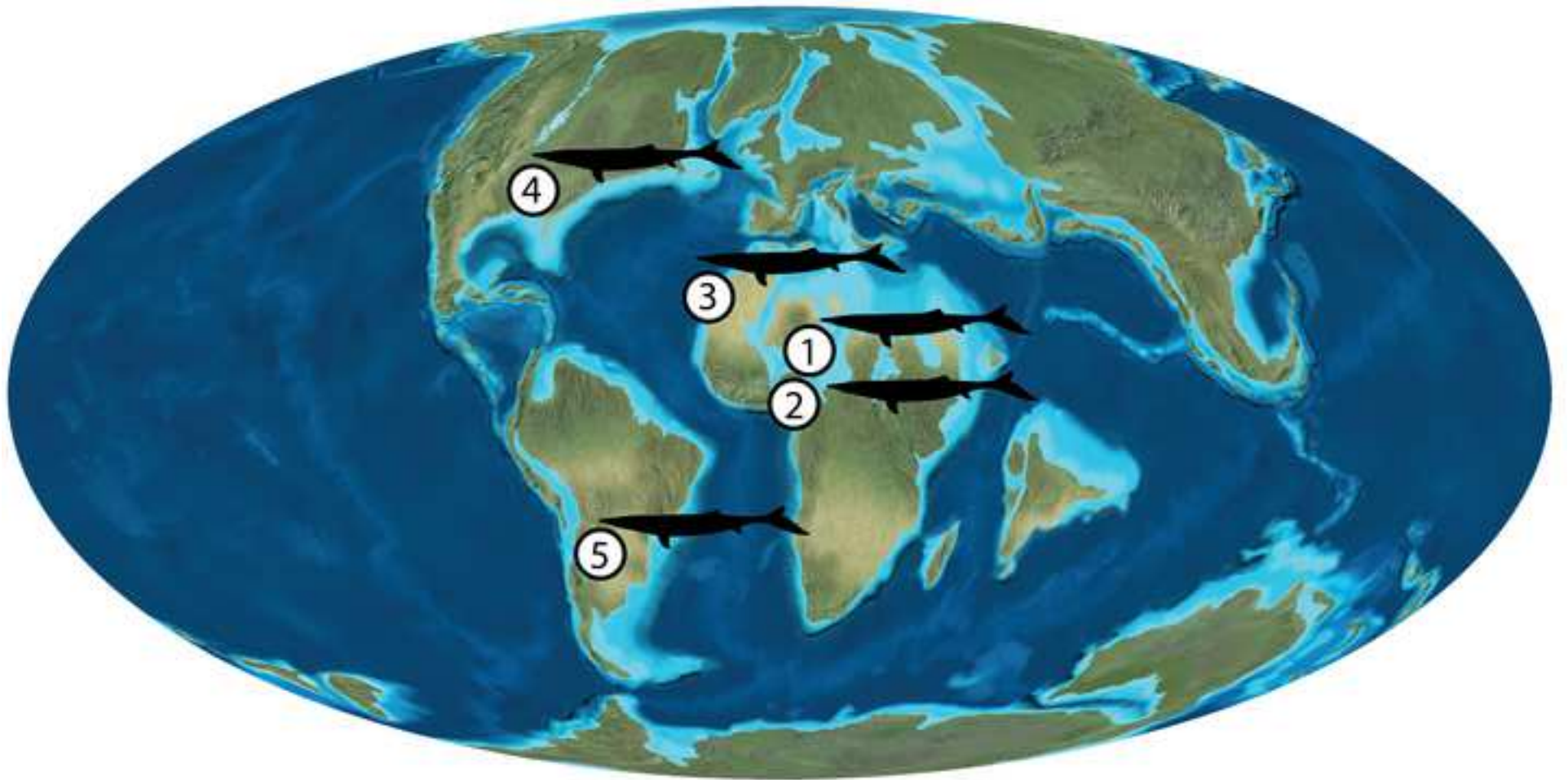
C



20 cm









Pluridens serpentina MHNM.KH.262

Pluridens serpentina MHNM.KH.386



Halisaurus arambourgi



Mososauridae

Mososaurinae

Mosasaurus beaugei Arambourg 1952

Prognathodon aff. *Saturator* Dortangs et al. 2002

Prognathodon aff. *currii* Christiansen & Bonde 2002

Globidens aff. *phosphaticus* Bardet et Pereda-Suberbiola 2005a

Eremiasaurus heterodontus LeBlanc et al. 20012

Carinodens minalmamar Schulp et al. 2009

Xenodens calminechari Longrich et al. 2021

Halisaurinae

Halisaurus arambourgi Bardet & Pereda-Suberbiola 2005b

Pluridens serpentis sp. nov.

Plioplatecarpinae

Gavialimimus almaghrebensis Strong et al. 2020

Pachyvaranidae

Pachyvaranus crassispondylus Arambourg, 1952

Table 2. Geographic and stratigraphic occurrence of Halisaurinae.

Taxon	Stratigraphy	Location	Age	References
<i>Eonatator sternbergi</i>	Smoky Hill Member, Niobrara Chalk Fm.	Kansas, United States	Santonian	(Bardet and Pereda-Suberbiola, 2001)
Pluridensini indet.	Mooreville Chalk Formation	Alabama, United States	Early Campanian	(Lindgren and Siverson, 2005)
Halisaurinae indet.		Sweden	Early Campanian	(Lindgren and Siverson, 2005)
“ <i>Eonatator</i> ” <i>coellensis</i>	Nivel de Lutitas y Arenas	Tolima, Colombia	Campanian	(Páramo-Fonseca, 2013)
<i>Pluridens calabaria</i>	Nkporo Shale	Nigeria	Late Campanian	(Longrich, 2016)
<i>Pluridens walkeri</i>	Farin-Doutchi Formation	Niger	Early? Maastrichtian	(Lingham-Soliar, 1998)
<i>Halisaurus</i> aff. <i>platyspondylus</i>	Tierra Loma Shale, Moreno Formation	California, USA	Mid-Maastrichtian	(Lindgren, 2007)
<i>Phosphorosaurus</i> (?) <i>ponpetelegans</i>	Hakobuchi Formation	Hokkaido, Japan	Earliest Maastrichtian	(Konishi et al., 2016)
<i>Phosphorosaurus</i> <i>ortliebi</i>	Ciply Phosphatic Chalk	Belgium	Late Maastrichtian	Lingham-Soliar, 1996
Pluridensini?	Jagüel Formation	Argentina	late Maastrichtian	(Fernández and Talevi, 2015)
cf. <i>Halisaurus</i>	Quiriquina Formation	Chile	Late Maastrichtian	(Jiménez-Huidobro et al., 2019) (Frey et al., 2016)
<i>Halisaurus</i> cf. <i>platyspondylus</i>	Severn Formation	Maryland, United States	mid Maastrichtian	(Holmes and Sues, 2000)
<i>Halisaurus</i> <i>platyspondylus</i>	New Egypt Formation	New Jersey, United States	Late Maastrichtian	(Polcyn and Lamb, 2012)
<i>Halisaurus</i> <i>arambourgi</i>	Upper Couche III	Khouribga Province, Morocco	Late Maastrichtian	(Bardet et al., 2005a)