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1 Endocranial anatomy of plesiosaurians (Reptilia, Plesiosauria) from the Late Cretaceous
2 (Turonian) of Goulmima (Southern Morocco)

3 RÉMI ALLEMAND, ^{*1,2} ALEXANDRA HOUSSAYE, ² NATHALIE BARDET, ¹ and
4 PEGGY VINCENT¹

5 ¹Centre de Recherches sur la Paléobiodiversité et les Paléoenvironnements, CR2P - UMR
6 7207 – CNRS – UPMC – Muséum National d’Histoire Naturelle, Sorbonne Université, 57 rue
7 Cuvier, CP38, F-75005, Paris, France, remi.allemand@edu.mnhn.fr,
8 nathalie.bardet@mnhn.fr, peggy.vincent@mnhn.fr;

9 ²Mécanismes Adaptatifs et Evolution, MECADEV – UMR 7179 – CNRS – Muséum
10 National d’Histoire Naturelle, Sorbonne Université, 55 rue Cuvier, CP55, F-75005, Paris,
11 France, alexandra.houssaye@mnhn.fr

12 RH: ALLEMAND ET AL. —ENDOCRANIAL ANATOMY OF PLESIOSAURIANS

26 ABSTRACT—Despite recent advances in non-invasive imaging, Plesiosauria remains one of
27 the least explored clade of reptiles with respect to palaeoneuroanatomy. Only partial
28 endocasts, obtained from either latex casts or imprints left on the braincase, have been
29 described so far. In this contribution, the digital endocasts of three plesiosaurian specimens
30 were analysed: two referred to the Elasmosauridae *Libonectes morgani* and one undetermined
31 Polycotylidae, all from the Late Cretaceous (Turonian) of Goulmima (Morocco). They were
32 CT-scan generated in order to provide new anatomical information on the plesiosaurian
33 endocast, endosseous labyrinth and cranial nerves. Results show that the three endocasts are
34 very similar to each other. They appear anteroposteriorly elongated and horizontally oriented
35 in lateral view, with long olfactory tracts, relatively small and incomplete olfactory bulbs, a
36 reduced pineal organ, distinguishable optic lobes, and a possible large cerebellum constituting
37 the main component in size of the endocast. The endocranial features reconstructed here are
38 compared to those of other plesiosaurians, as well as other marine reptiles, notably to discuss
39 their intraspecific and interspecific variability. This study provides pioneer data in order to
40 estimate the impact of both phylogenetical and ecological constraints on the endocranial
41 morphology of plesiosaurians and proposes a few preliminary paleobiological suggestions.

42

43

INTRODUCTION

44

45 Plesiosaurians are extinct large predatory animals that represent one of the longest-
46 ranging groups of Mesozoic marine reptiles, extending stratigraphically from the Late Triassic
47 to the latest Cretaceous (e.g., Vincent et al., 2011; Benson et al., 2012; Bardet et al., 2014). By
48 the earliest Jurassic, they were an important component of the marine ecosystem (e.g.,
49 Sennikov and Arkhangelsky, 2010). Plesiosaurians possess an unusual body plan with a short
50 and stiff trunk, a short tail and four enlarged hydrofoil-shaped propulsive flippers for

51 swimming (e.g., Bardet et al., 2014). The proportions between head size and neck length
52 result in a gradation in body form between “plesiosauromorph” (long neck, small head) and
53 “pliosauromorph” (short neck, large head) morphotypes, which occurred independently in
54 multiple phylogenetic lineages (e.g., Benson et al., 2012). Their degree of adaptation to the
55 aquatic realm have been extensively studied based on skeletal (e.g., Caldwell, 1997; O’Keefe,
56 2002; Araújo et al., 2014), micro-anatomical and histological (e.g., Wintrich et al., 2017), as
57 well as physiological (i.e., diet, reproduction, thermoregulation; Massare, 1987, 1988;
58 Bernard et al., 2010; O’Keefe and Chiappe, 2011) features. Different lifestyles, as well as
59 different ecological niches and feeding guilds have been inferred from their diverse
60 morphologies and locomotor abilities (e.g., O’Keefe, 2002; Bardet et al., 2014). Most
61 plesiosaurians are presumably piscivorous (e.g., Tarlo, 1959; Massare, 1987; Storrs, 1995;
62 Sato and Tanabe, 1998). However, tooth marks on isolated bones indicated that some large
63 pliosauromorphs preyed upon other reptiles (Clark and Etches, 1992) and that some
64 plesiosauromorphs were specialized predators of invertebrates dwelling on marine sediments
65 (e.g., McHenry et al., 2005; O’Keefe et al., 2017; Vincent et al., 2017). In addition, several
66 studies suggested that all plesiosaurians were viviparous taxa with a K-selected reproduction
67 strategy suggesting social behaviour and maternal care (O’Keefe and Chiappe, 2011; Wintrich
68 et al., 2017), able to regulate their body temperature independently from the surrounding
69 water temperature (Bernard et al., 2010), capable of performing deep, prolonged, and/or
70 repetitive dives (Rothschild and Storrs, 2003), and to migrate, at least occasionally, over long
71 distances (Vincent et al., 2017).

72 Although recent advances in non-invasive imaging have increased the number of taxa
73 for which the endocranial morphology is accessible (e.g., Paulina-Carabajal et al., 2013;
74 Cuthbertson et al., 2015; Kishida et al., 2015; Marek et al., 2015; Voeten et al., 2018), only
75 the plesiosaurian endosseous labyrinth has been so far analysed (e.g., Neenan et al., 2017),

76 and the current understanding of their neuroanatomy remains poor. Partial endocasts are
77 known for *Brancaosaurus brancai* (Edinger, 1928 see Hopson, 1979), *Libonectes morgani*
78 (Carpenter, 1997) and *Terminonatator ponteixensis* (Sato, 2003). The endocast of
79 *Brancaosaurus* is a wax cast modelled based on isolated cranial elements (Hopson, 1979;
80 Sachs et al., 2016). Edinger (1928) illustrated the cast but did not provide an associated
81 description that shows little useful detail (Hopson, 1979), only the posterior part of the
82 endocast, the inner cavity, and the pituitary fossa being indicated (Sachs et al., 2016). The
83 endocast of *Libonectes* was taken from a latex cast of the braincase (Carpenter, 1997). The
84 partial endocast is more detailed than that of *Brancaosaurus* and Carpenter (1997) gave a brief
85 description of the structure. Finally, Sato (2003) provided a short description of the dorsal
86 endocranial surface in *T. ponteixensis* based on prints left on the ventral surface of the
87 braincase roof.

88 Here, the use of microtomography on three plesiosaurian specimens from the
89 Goulmima area, Southern Morocco, offers access to endocranial structures that are described
90 in detail. These new data are a first step to better interpret the endocranial morphology of
91 plesiosaurians in general.

92 **Institutional Abbreviations**—**D**, Musée de Paléopolis, Gannat, France; **MNHN**,
93 Muséum National d'Histoire Naturelle, Paris, France; **SMNS**, Staatliches Museum für
94 Naturkunde, Stuttgart, Germany; **SMU SMP**, Shuler Museum of Paleontology, Southern
95 Methodist University, Dallas, U.S.A.

96

97 MATERIAL AND METHODS

98

99 The three specimens analysed come from the Goulmima area, Er-Rachidia Province in
100 Southern Morocco. Stratigraphically, they come from the Unit T2a of the Akrabou Formation

101 defined by Ettachfini and Andreu (2004) and lower Turonian in age (Kennedy et al., 2008; see
102 Fig. 1 in Allemand et al., 2017a for the paleogeographical location and the stratigraphical
103 range). As often in the Goulmima area, very well preserved zones alternate with others in
104 which the bones are dissolved so that only their imprints are preserved. The fossils are
105 embedded in nodules so that they present the advantage to be preserved in three dimensions
106 and to be relatively undistorted (Fig. 1).

107 The three specimens were scanned at the AST-RX platform of the MNHN (Paris,
108 France) using a GEphoenix|Xray|v|tome|x L240. The virtual three-dimensional reconstruction
109 of the skulls was performed for the specimen descriptions and taxonomic assignment
110 (Allemand et al., 2017a, 2018). The specimens SMNS 81783 and D1-8213 are referred to the
111 elasmosaurid *Libonectes morgani* (Allemand et al., 2017a, 2018) and MNHN F-GOU14 to an
112 undetermined polycotyloid (Allemand et al., 2018). For this study, virtual three-dimensional
113 reconstructions of the brain endocasts, cranial nerves and endosseous labyrinths were
114 performed at the Palaeontology Imaging Unit of the UMR 7207 CR2P CNRS/MNHN/UPMC
115 using the MIMICS (Materialise Interactive Medical Image Control System) Innovation Suite
116 software (Materialise®, release 19).

117 The endocranial cavity of each specimen being filled with matrix, reconstructions
118 were performed manually with the multiple 2D cross-sectional slices edit tool of MIMICS and
119 interpolation between selections on non-contiguous slices. The isolation of the endocranial
120 cavity was performed based on contrast differences between the bones, with darker grayscale
121 values, and the matrix (Fig. 2 and Appendix 1). The posterior part of the brain endocast was
122 delimited from the surrounding supraoccipital (dorsally; Fig. 2G, H), by the prootics and the
123 exoccipital-opisthotic (laterally; Fig. 2G-I), by the basioccipital and the parabasisphenoid
124 (ventrally; Fig. 2G-I) based on these contrast-differences. However, since the ventral and
125 lateral walls of the anterior portion of the braincase are not ossified in plesiosaurians

126 (O’Keefe 2001), accurate reconstruction of the anterior part of the endocast was not possible
127 through segmentation (Fig. 2C-E).

128

129 DESCRIPTION OF THE ENDOCRANIAL ANATOMY

130

131 The cranial endocast of D1-8213 was almost completely reconstructed, together with
132 the cranial nerves and the endosseous labyrinth (Fig. 3A). Only the olfactory bulbs were not
133 reconstructed due to state of preservation. The dorsal surface of the brain cast in SMNS
134 81783 was reconstructed from the olfactory bulbs to the cerebellum, as well as few cranial
135 nerves; however, the poor contrast-differences prevented the reconstruction of the endosseous
136 labyrinth (Fig. 3B). The brain cast of MNHN F-GOU14 is the less complete and the more
137 crushed one (Fig. 3C). Only its dorsal surface could be partially reconstructed; and both the
138 anteriormost and posteriormost parts, as well as endosseous labyrinth and cranial nerves, are
139 missing due to state of preservation.

140

141 **Brain Endocast**

142 Although the endocast is rarely a representation of the brain itself (Hurlburt et al.,
143 2013), we use the brain anatomical nomenclature to describe the different structures of the
144 plesiosaurian endocasts.

145 The endocranial morphology of the three plesiosaurian specimens is globally similar.
146 Brain casts are elongated and mediolaterally narrow. The three specimens exhibit a slight
147 ventral flexure at the level of the contact between the olfactory tracts and the cerebrum (Fig.
148 3A-C). The most anterior part of the brain cast corresponds to the olfactory bulbs. They have
149 been reconstructed only in SMNS 81783 (Fig. 3B), in which the ventral surface of the
150 dorsomedian ridge of the premaxilla and the anterior part of the frontal show their

151 impressions. Despite a partial reconstruction that does not allow to observe their ventral
152 surface, the olfactory bulbs appear wider than the olfactory tracts (Fig. 3B). The later are
153 projected through the ventral wall of the frontal and appear elongated. The olfactory tracts
154 become more mediolaterally compressed at their mid-length, and widen at the contact with
155 the cerebrum (Fig. 3B). The anteroposterior length of the olfactory tracts is approximately 76
156 mm in SMNS 81783, which corresponds to about half of the length of the brain cast. No
157 separation is visible between the olfactory tracts (Fig. 3A-C). The cast of the tracts continues
158 posteriorly until they meet the cast of the cerebrum, visible on the ventral surface of the
159 parietal. The cerebrum extends anteroposteriorly; however, due to the open condition of the
160 braincase, its lateral and ventral extensions are not preserved. The dorsal surface of the
161 cerebrum appears dorsoventrally concave just posterior to the contact with the olfactory tracts.
162 The concavity is more strongly marked in both *Libonectes morgani* specimens (Fig. 3A-B)
163 than in the undetermined polycotyloid (Fig. 3C), and appears more extended antero-posteriorly
164 in D1-8213 than in SMNS 81783. Posteriorly to the concavity observed on the dorsal surface
165 of the cerebrum, a small bulge may correspond to the pineal organ (Fig. 3A-C). Its position in
166 the mid-section of the parietals coincides with the foramen within the parietals in the
167 undetermined polycotyloid MNHN F-GOU14 (Allemand et al., 2018) but not with the pineal
168 foramen located more anteriorly at the level of the postorbital bar in the *L. morgani* specimen
169 SMNS 81783 (Allemand et al., 2017a). Posteriorly to the possible pineal organ, a more
170 pronounced bulge on the dorsal surface of the brain cast indicates the position of the optic
171 lobes (Fig. 3A-C), which are enclosed dorsally by the parietal. Ventrally to the optic lobes, the
172 pituitary bulb is projected more ventrally than the ventral surface of the posterior part of the
173 brain cast (Fig. 3A-B). Its ventral surface is horizontal and a pair of internal carotid foramen
174 is visible at the posterior end of the pituitary bulb. The posterior part of the brain cast, the
175 rhombencephalon, consists of the cerebellum and the medulla oblongata (Fig. 3A-B). The

176 cerebellum is incomplete in SMNS 81783 and MNHN F-GOU14 but, in the three specimens
177 it forms an anteroposteriorly developed bulge on the dorsal surface of the endocast (Fig. 3A-
178 B). Its dorsal surface slopes posterodorsally and constitutes the main structure of the
179 plesiosaurian brain cast. The medulla oblongata, more complete in D1-8213 is thin and
180 laterally constricted (Fig. 3A), enclosed by the prootics and the exoccipitals. Ventrally, the
181 surface can be reconstructed with reasonable accuracy, as it is framed by the dorsal surfaces
182 of the basisphenoid and basioccipital.

183

184 **Cranial Nerves**

185 Following the descriptions made on plesiosaurian braincases (e.g., Sato et al., 2011;
186 Sachs et al., 2015), it is possible to identify the trigeminal nerve (V) as it corresponds to the
187 prootic fenestra (Carpenter, 1997) but not its extension (Fig. 3A). The abducens nerve (VI) is
188 anteriorly projected through the dorsolateral foramen of the pituitary fossa (Fig. 3A-B and
189 Fig. 4A). The canal for the facial nerve (VII) exits from the foramen on the prootic,
190 posteriorly to the abducens nerve and just anterior to the endosseous labyrinth (Fig. 3A and
191 4A). The width of the facial nerve is similar to that of the abducens nerve. The
192 vestibulocochlear nerve (VIII) is not visible on the endocast reconstructions. Just posterior to
193 the endosseous labyrinth, two foramina pierce the medial surface of the exoccipital adjacent
194 to its ventral surface. The most anterior one is for the exit of the glossopharyngeal nerve (IX),
195 which represents the largest cranial nerve (Fig. 3A-B and 4A), and the dorso-posteriorly
196 foramen is for the vagus-accessory nerves (X + XI). Branches of the hypoglossal nerve (XII)
197 pass through the three foramina in each of the exoccipitals, ventrally to the vagus-accessory
198 nerves. The branches of the hypoglossal nerve are thin and arranged in a triangular pattern on
199 each side of the medulla oblongata.

200

201 **Endosseous Labyrinth**

202 Left and right endosseous labyrinths of D1-8213 are preserved, except the most
203 ventral part of the lagena (Fig. 4B). The endosseous labyrinth is positioned ventrally to the
204 cerebellum and its general aspect is similar to the plesiosaurian endosseous labyrinths already
205 described by Evans (1999) and Neenan et al. (2017). The vestibule is rounded and the
206 semicircular canals are square-shaped in lateral view, robust and low (Fig. 4B). Even if the
207 true ventral extent of the lagena is unknown, it seems to be relatively short, robust and
208 uncoiled. The endosseous labyrinth is approximately 24 mm tall and has a maximum width of
209 20 mm at the level of the semi-circular canals. The anterior semicircular canal (asc) is longer
210 than the two other ones, which seem to be similar in length. Diameter comparisons indicates
211 that the posterior semicircular canal (psc) is the thickest one ($psc > asc > lsc$). The dorsal
212 margins of both anterior and posterior semicircular canals are at the same level (Fig. 4B). The
213 angles formed between the anterior and posterior semicircular canals is approximately 113° ;
214 96° between the anterior and lateral semicircular canals and 84° between the posterior and
215 lateral semicircular canals. The anterior and posterior canals meet at the common crus (Fig.
216 4B), which is approximately of similar diameter as the canals themselves. In lateral view (Fig.
217 4B), a larger gap is observed between the anterior canal and the common crus than between
218 the posterior canal and the crus (Fig. 4B).

219

220

DISCUSSION

221

222 **Comparisons with Extinct and Extant Marine Reptiles**

223 Endocranial reconstructions of either extinct or extant reptilian taxa living in marine
224 ecosystems are scarce. Data are limited to a few endocranial studies dealing exclusively or

225 partially with extant aquatic snakes, marine turtles, ichthyosaurians, mosasauroids,
226 thalattosuchians and sauropterygians (see Table 1 for a review of the literature).

227 Endocranial comparisons with the existing data show that plesiosaurians exhibit a
228 unique combination of endocranial characteristics not found in any other extant or extinct
229 marine reptile. Plesiosaurian olfactory tracts, elongated anteroposteriorly and not separated
230 along their length (Fig. 3), are similar to those reported in mosasauroids and nothosaurians
231 (Camp, 1942; Voeten et al., 2018) but differ from the short olfactory tracts observed in turtles
232 (Paulina-Carabajal et al., 2013) and the more or less separated olfactory tracts found in snakes
233 (Allemand et al., 2017c), thalattosuchians (e.g., Pierce et al., 2017) and ichthyosaurs (e.g.,
234 Marek et al., 2015). Plesiosaurian endocasts are nearly linear (Fig. 3), both the anterior and
235 posterior parts being at the same dorsoventral level, similarly as reported in snakes (Allemand
236 et al., 2017c), thalattosuchians (e.g., Pierce et al., 2017), nothosaurians (Voeten et al., 2018)
237 and turtles (Paulina-Carabajal et al., 2013), a condition differing from that of *Placodus gigas*
238 (Neenan and Scheyer, 2012), in which the structure appears anteroposteriorly inclined and
239 sigmoidal. The horizontal projection of the plesiosaurian pituitary differs from the tilted one
240 observed in snakes (Allemand et al., 2017c) and thalattosuchians (e.g., Pierce et al., 2017). In
241 plesiosaurians, the cerebellum seems strongly developed and easily discernible (Fig. 3). This
242 differs from other marine reptiles, in which the cerebellum is not always distinguishable
243 (snakes, turtles and Triassic sauropterygians; Neenan and Scheyer, 2012; Paulina-Carabajal et
244 al., 2013; Allemand et al., 2017c; Voeten et al., 2018) or, when visible (thalattosuchians and
245 ichthyosaurs; Marek et al., 2015; Pierce et al., 2017), is not as developed as in plesiosaurians.

246

247 **Intraspecific Variability**

248 The endocast of the holotype of *Libonectes morgani*, SMUMP 69120 (Carpenter,
249 1997) is similar to those of the two specimens of *L. morgani* studied here. Although the

250 endocranial proportions are similar, there is, however, one noticeable difference in the ventral
251 flexure of the endocast. The reconstruction of Carpenter (1997) shows that the cerebellum in
252 SMUMP 69120 is located more ventrally than the plane defined by the olfactory tracts in
253 lateral view, whereas in D1-8213 and SMNS 81783, both olfactory tracts and the cerebellum
254 are in the same plane, resulting in a nearly horizontal endocast. Thus, among the three
255 specimens of *Libonectes morgani*, SMUMP 69120 shows the more pronounced flexure of its
256 endocast, whereas the skull of SMNS 81783 and D1-8213 show a more horizontal
257 development of their brain cavities.

258 According to Giffin (1989), the main causes of the endocranial flexure are the absolute
259 size of the skull and the relative size of the eyes. Smaller taxa tend to show an endocast with a
260 more pronounced flexure than larger ones, the same pattern being observed in young
261 individuals as compared to older ones of the same species (Giffin, 1989). The loss of the
262 flexure would thus be a consequence of the increase in skull size. The skull growing at a
263 higher speed than the brain, the latter has relatively more space in the larger individuals and
264 “unfolds” (Hopson, 1979). Conversely, when the cranial cavity is relatively smaller, the brain
265 presents a more or less pronounced “S” shape, with an anterior part located higher than the
266 posterior one (Hopson, 1979). In addition, large eyes, which could be related to a juvenile
267 state within a species or to an ecologic adaptation to a particular lifestyle (e.g., nocturnality,
268 see Konishi et al., 2016), may compress the occipital region as well as the brain and could
269 increase the flexure (Starck, 1979). Surprisingly, the specimen of *Libonectes* that presents the
270 longest skull (SMUMP 69120: about 500 mm in length, see Carpenter, 1997) shows the more
271 pronounced flexure. The two other specimens (are smaller (SMNS 81783 is 295 and D1-8213
272 350 mm long) but show no flexure of the endocast. Size being usually correlated with the age
273 of the individuals, this observation thus questions Giffin’s (1989) assumption. Thus, the

274 plesiosaurian endocranial flexure does not necessarily correspond to an ontogenetical
275 variation, but it could possibly reflect an individual variability.

276

277 **Plesiosaurian Pineal Organ**

278 Both the parapineal organ (also named parietal eye or pineal eye) housed in the
279 parietal foramen and the associated pineal organ form the pineal complex (Smith et al., 2018).
280 In reptiles, the parapineal organ contains highly developed photoreceptor cells capable of
281 transducing photic information and assuming the/a predominant photosensory role (Concha
282 and Wilson, 2001; Smith et al., 2018). In addition, the pineal organ of reptiles, which contains
283 rudimentary photoreceptor cells, is retained as a neuroendocrine gland governing melatonin
284 secretion and distribution (Falcón, 1999). The pineal complex in these taxa influences
285 behaviour, body temperature regulation, seasonal cycles, spatial orientation and regulation of
286 the circadian rhythm (Quay, 1979; Tosini, 1997).

287 It is not possible to distinguish the parapineal organ from the pineal one based on
288 endocranial reconstructions, in both extinct and extant non-avian reptiles. A pineal complex
289 has been reported for various clades of extinct marine reptiles such as mosasauroids (Camp,
290 1942; Allemand et al., unpub. data 2017b), ichthyosaurians (Marek et al., 2015) and Triassic
291 sauropterygians (Neenan and Scheyer, 2012; Voeten et al., 2018). On the contrary, although a
292 pineal complex occurs in extant turtles and snakes (Wyneken, 2003, 2007), the structure is
293 covered by the dorsal longitudinal vein (Aurboonyawat et al., 2008) and not visible from the
294 endocast (Paulina-Carabajal et al., 2013; Allemand et al., 2017c). In this study, we
295 hypothesize that the bulge visible on the dorsal surface of the endocast of the three
296 plesiosaurian specimens (Fig. 3) could correspond to a small pineal complex. Its position, at
297 the junction between the parietals, coincides with the parietal foramen located within the
298 parietals in the undetermined polycotyloid MNHN F-GOU14 (Allemand et al., 2018). On the

299 contrary, the parietal foramen in the elasmosaurid *L. morgani* specimen SMNS 81783 is
300 located more anteriorly than the identified pineal organ, at the level of the postorbital bar and
301 above the olfactory canals (Allemand et al., 2017a). Such anteriorly located parietal foramen,
302 reported in the elasmosaurid *Callawayasaurus colombiensis* (Welles, 1952) but possibly also
303 in another elasmosaurid, *Terminonatator ponteixensis* (Sato, 2003), is found in different
304 reptilian clades (e.g., squamates Lacertidae, Iguanidae) and depends principally upon
305 increasing elevation of the forebrain that reflect an increase in the size of the orbit (Quay,
306 1979). Thus, such variability in the position of the plesiosaurian parietal foramen could be
307 related to morphological modifications associated to the short skull length and the relatively
308 high position of the orbit in Elasmosauridae compared to Polycotylidae (e.g., Carpenter,
309 1997).

310 The pineal complex among extinct marine reptiles displays a great variability in size.
311 According to Holloway et al. (2013), it seems that the relative size of the pineal organ in non-
312 avian reptiles is reduced, following reduction of the parietal foramen. Indeed, the small
313 parietal foramen and the reduced pineal organ observed in the elasmosaurid *Libonectes* differ
314 from the medium-sized pineal organ that is associated to a relatively larger parietal foramen in
315 the undetermined polycotylid (Allemand et al., 2018), but also in mosasauroids,
316 ichthyosaurians and Triassic sauropterygians (Neenan and Scheyer, 2012; Marek et al., 2015;
317 Connolly, 2016; Voeten et al., 2018). However, the exact ecological functions of such
318 variability in size are still unclear. In extant lizards, it is suggested that the size of the pineal
319 complex strongly correlates with latitude, species restricted to high latitudes having a larger
320 pineal complex, probably for detecting light, than low latitude ones (Gundy et al., 1975;
321 Ralph, 1975). However, recent quantitative studies from both extinct (mosasauroids:
322 Connolly, 2016) and extant (*Liolaemus* lizards: Labra et al., 2010) squamates question this
323 hypothesis by showing no correlation between the size of the pineal complex and latitude.

324 Instead, Labra et al. (2010) found a weak relation between the size of the pineal complex and
325 thermal regulation and corroborate the particular role of the pineal complex in the “fine-
326 tuning” thermoregulation already suggested for extant lizards (Hutchison and Kosh, 1974;
327 Ralph et al., 1979). In addition, in mammals, it was hypothesized that the reduction and loss
328 of the pineal complex reflects the transition from ectothermy to endothermy (Benoit et al.,
329 2016). Although the small elasmosaurid pineal complex could be related to the ability to
330 regulate its body temperature independently from the surrounding water temperature (Bernard
331 et al., 2010), the large pineal complex found in non-elasmosaurid plesiosaurians and
332 ichthyosaurians, which have also an elevated metabolic rate (Bernard et al., 2010), questions
333 this assumption.

334 The reduction of the pineal complex in elasmosaurids, which occurred independently
335 in pseudosuchians, theropods and sauropods (Holloway et al., 2013), remains difficult to
336 explain. Although it could be related to differences in both photoreceptive and neuroendocrine
337 functions, additional studies illustrating variability in the reptilian pineal complex and
338 associated physiological roles are needed to better interpret this structure.

339

340 **Plesiosaurian Endocast: Functional Hypotheses**

341 Several studies in extant mammals and reptiles (including birds) have shown that the
342 endocast morphology bears both phylogenetical and ecological signals, and could provide,
343 similar to the brain, some information about species sensory abilities (e.g., Macrini et al.,
344 2006, 2007; Corfield et al., 2015; Allemand et al., 2017c). An endocast does not represent the
345 morphology of the brain and brainstem only, but also the contours of associated brain tissues
346 in contact with the internal surface of the braincase, such as the meninges, the blood vessels,
347 the cerebrospinal fluid and the venous system (Witmer and Ridgely, 2009). Depending on
348 clades, these tissues may account for a significant proportion of the endocranial space

349 (Witmer et al., 2008) and strongly affect the degree to which the endocast reflects the brain. In
350 non-avian reptiles, although snakes and amphisbaenians are known to have a brain that fills
351 most of the endocranial space (Nieuwenhuys et al., 1998), a wide range of brain vs.
352 endocranial space proportions occur depending on clades (Kim and Evans, 2014) or
353 ontogenetic stage (Jirak and Janacek, 2017). Here, the absence of extant representatives for
354 plesiosaurians and their ambiguous phylogenetic bracketing prevent making strong biological
355 inferences based on their endocasts, but comparisons with other marine reptiles can allow to
356 highlight some traits and attempt preliminary paleobiological suggestions.

357 Little is known about plesiosaurian sensorial abilities, and how they differ depending
358 on their mode of adaptation to an aquatic life and niche partitioning. A few studies have
359 suspected: 1) underwater olfaction based on the postero-dorsal position of external nostrils
360 related to the internal nares (Cruickshank et al., 1991, but see Buchy et al., 2006); 2) a
361 possible well-developed and binocular vision based on the large size and forward-looking
362 position of the orbits and the presence of sclerotic plates (Andrews, 1913; Shuler, 1950;
363 Forrest, 2000); 3) a system involved in prey detection similar to crocodile pressure receptors
364 or shark electroreceptors based on extensive bifurcating neurovascular channels (Foffa et al.,
365 2014).

366 From the endocasts described herein, discussing olfaction abilities appears difficult
367 since the olfactory bulbs seem very incomplete. However, endocranial reconstructions show
368 that both the optic lobes and the cerebellum seem to constitute important components of the
369 plesiosaurian endocast. Indeed, although these structures may be covered dorsally by the
370 venous system (Aurboonyawat et al., 2008) affecting strongly their sizes, both the optic lobes
371 and the cerebellum form distinct bulges from the rest of the endocast, whereas in other marine
372 reptiles such distinction is more difficult (e.g, Voeten et al., 2018).

373 In vertebrates, it is generally admitted that, as the superficial layers of the optic lobes
374 receive visual inputs from the retina through the optic (II) nerves (Butler and Hodos, 2005),
375 their size is correlated to the importance of vision (e.g., Jerison, 1973; Butler and Hodos,
376 2005). Conversely, the more internal layers of the optic lobes are involved in auditory and
377 somatosensory inputs (e.g., Buttler and Hodos, 2005). From endocasts, it is not possible to
378 determine which layer of the optic lobe is more developed than the other as only the external
379 morphology of the structure is visible. However, the relatively large size of the plesiosaurian
380 optic lobes could suggest well-developed abilities to localize preys or predators, from vision
381 and/or auditory inputs.

382 The cerebellum is multisensory and plays an important role in cognitive functions,
383 such as touch, proprioception, vision, hearing, and has a role in maintaining postural
384 equilibrium (Wyneken, 2007), and influences locomotor behaviour (Thach and Bastian, 2004;
385 Buttler and Hodos, 2005). Among vertebrates, the cerebellum shows a great variability in
386 size, shape and organization (Butler and Hodos, 2005) that is difficult to interpret. In non-
387 avian reptiles, this structure generally has a modest size and forms a flat plate just posterior to
388 the optic lobes (Butler and Hodos, 2005). Since, the plesiosaurian cerebellum differs from that
389 of all non-avian reptiles, including turtles that share a similar mode of sub-aquatic flight
390 locomotion (Paulina-Carabajal et al., 2013), or other highly aquatic extinct taxa such as
391 ichthyosaurs (Marek et al., 2015), such enlargement could be related to the relative length of
392 the neck and its role in maintaining postural equilibrium. The investigation of the endocast
393 morphology of short-necked taxa should allow to verify this hypothesis.

394

395 **Plesiosaurian Endosseous Labyrinth**

396 The endosseous labyrinth reconstructed for the elasmosaurid *Libonectes morgani*
397 specimen D1-8213 exhibits the elasmosaurid morphology reported in *Callawayasaurus*

398 *colombiensis* and *Libonectes morgani* specimen SMUMP 69120 by Neenan et al. (2017). It
399 corresponds to a square appearance in lateral view, a compact, bulbous labyrinth, with a wide
400 crus communis, as well as short and wide semicircular canals (Fig. 4B; Neenan et al., 2017:
401 Fig.1). However, *Callawayasaurus* exhibits a taller endosseous labyrinth than both *Libonectes*
402 specimens (Neenan et al., 2017) resulting in a dorsal extension of both the posterior and
403 anterior semicircular canals and a longer crus communis. Such variability could rely on a
404 phylogenetic signal (e.g., Palci et al., 2017) but also be linked to ecological factors (e.g., Palci
405 et al., 2018). According to Neenan et al. (2017), the labyrinth in sauropterygians is closely
406 linked with both locomotor style and body proportions. However, both *Callawayasaurus* and
407 *Libonectes* seem to have the same swimming mode, with a four-flippered underwater flight.
408 In addition, both are characterized by an extreme elongation of the neck (respectively 56 and
409 48 cervical vertebrae in *Callawayasaurus* and *Libonectes*, Welles, 1952; Sachs and Kear,
410 2015) and display similar body proportions. Thus, the ecologic arguments here do not seem
411 sufficient to explain such difference, and the phylogenetic signal reflected by the labyrinth
412 must be confirmed by adding elasmosaurid endosseous labyrinth.

413

414

CONCLUSIONS

415

416 The resort to computed tomography enables the first detailed descriptions of
417 plesiosaurian endocasts and provides additional information about other delicate structures
418 such as the endosseous labyrinth and cranial nerves. Endocranial comparisons with other
419 plesiosaurians allow to discuss their intraspecific and interspecific variability. The endocranial
420 flexure is thought as an individual variability rather than an ontogenetic one, and the
421 differences observed on the elasmosaurid endosseous labyrinth could reflect more a
422 phylogenetic signal than an ecological one. In addition, we suggest that the possible pineal

423 organ observed on the two endocasts of *Libonectes* and its position related to the more
424 anteriorly located parietal foramen is part of morphological modifications associated to the
425 elasmosaurid skull length and the high position of their orbit. Finally, comparisons with other
426 marine reptiles allow a few preliminary paleobiological suggestions concerning the well-
427 developed plesiosaurian abilities in vision and audition, and question the role of the
428 cerebellum in long-necked plesiosaurians. This study is part of pioneer works relative to
429 plesiosaurian neuroanatomy. Biological inferences based on endocast features should
430 naturally be made with caution as several other non-functional and non-phylogenetical factors
431 may affect the endocast morphology and as data available are extremely scarce. Further
432 investigations on plesiosaurian endocast should enable to better evaluate which structures are
433 preserved along their evolutionary history and which ones are modified for a specific
434 ecological and/or functional adaptation.

435

436

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448

449

LITERATURE CITED

450

451 Abele, A. 2017. Digital reconstruction of skull and endocranium of the Cretaceous ichthyosaur

452 *Platypterygius longmani* from Australia, regarding sensory perception and internal structures;

453 pp. 41 in O. Hampe, D. Schwarz and M. Voss (eds), 8th International meeting Secondary

454 adaptation of Tetrapods to life in water. Berlin, Germany, 3–8 April 2017.

455 Agassiz, L. 1833. *Recherches sur les Poissons Fossiles*, Vol. I. Neuchâtel, Imprimerie de

456 Petitpierre, France, 17 pp.

457 Allemand, R., N. Bardet, A. Houssaye, and P. Vincent. 2017a. Virtual re-examination of a

458 plesiosaurian specimen (Reptilia, Plesiosauria) from the Late Cretaceous (Turonian) of

459 Goulmima (Southern Morocco) thanks to computed tomography. *Journal of Vertebrate*

460 *Paleontology* 37:e1325894

461 Allemand, R., P. Vincent, A. Houssaye, and N. Bardet. 2017b. Endocranial microtomographic

462 study of marine reptiles (Plesiosauria and Mosasauroida) from the Turonian (Late

463 Cretaceous) of Morocco: palaeobiological and behavioral implications. Ph.D. dissertation,

464 Muséum National d'Histoire Naturelle, Paris, France, 285 pp.

465 Allemand, R., P. Vincent, A. Houssaye, and N. Bardet. 2018. New plesiosaurian specimens

466 (Reptilia, Plesiosauria) from the Late Cretaceous (Turonian) of Goulmima (Southern

467 Morocco). *Cretaceous Research* 82:83–98.

468 Allemand, R., R. Boistel, Z. Blanchet, R., Cornette, N., Bardet, P., Vincent, and A. Houssaye, A.

469 2017c. Comparative morphology of snake (Squamata) endocasts: evidence of phylogenetical

470 and ecological signals. *Journal of Anatomy* 231:849–868.

471 Andrews, C. W. 1913. A descriptive catalogue of the Marine Reptiles of the Oxford Clay. Based on
472 the Leeds Collection in British Museum (Natural History), Part II. British Museum (Natural
473 History), London, 206 pp.

474 Araújo, R., M. J. Polcyn, A. S. Schulp, O. Mateus, L. L. Jacobs, A. O. Goncalves, and M. L.
475 Morais. 2014. A new elasmosaurid from the early Maastrichtian of Angola and the
476 implications of girdle morphology on swimming style in plesiosaurs. *Netherlands Journal of*
477 *Geosciences* 94:109–120.

478 Burboonyawat, T., V. Pereira, T. Kring, F. Toulgoat, A. Churojana, and P. Lasjaunias. 2008.
479 Patterns of the Cranial Venous System from the Comparative Anatomy in Vertebrates: Part II.
480 The Lateral-Ventral Venous System. *Interventional Neuroradiology* 14:21–31.

481 Bardet, N., X. Pereda Suberbiola, and N. E. Jalil. 2003. A new mosasauroid (Squamata) from the
482 Late Cretaceous (Turonian) of Morocco. *Comptes Rendus Palevol* 2:607–616.

483 Bardet, N., J. Falconnet, V. Fischer, A. Houssaye, S. Jouve, X. Pereda Suberbiola, A. Perez-Garcia,
484 J-C. Rage, and P. Vincent. 2014. Mesozoic marine reptile palaeobiogeography in response to
485 drifting plates. *Gondwana Research* 26:869–887.

486 Benoit, J., F. Abdala, P. R. Manger, and B. S. Rubidge. 2016. The sixth sense in mammalian
487 forerunners: Variability of the parietal foramen and the evolution of the pineal eye in South
488 African Permo-Triassic eutheriodont therapsids. *Acta Palaeontologica Polonica* 61:777–789.

489 Benson, R. B. J., M. Evans, and P. S. Druckenmiller. 2012. High diversity, low disparity and small
490 body size in Plesiosaurs (Reptilia, Sauropterygia) from the Triassic–Jurassic boundary. *PLoS*
491 *ONE* 7(3): e31838. doi:10.1371/journal.pone.0031838.

492 Bernard, A., C. Lécuyer, P. Vincent, R. Amiot, N. Bardet, E. Buffetaut, G. Cuny, F. Fourrel, F.
493 Martineau, J-M. Mazin, and A. Prieur. 2010. Regulation of body temperature by some
494 Mesozoic marine reptiles. *Science* 328:1379–1382.

495 Blainville, H. D. de. 1853. Lettre de Monsieur de Blainville; pp. 103–13 in E. Deslongchamps (ed),
496 Lettres sur les Crocodiles vivants et fossiles. Mémoires Société Linnéenne de Normandie,
497 Caen, France.

498 Bronn, H. G. 1841. Über die fossilen Gaviale der Lias Formation und der Oolithe. Archiv für
499 Naturgeschichte, Berlin 8:77–82.

500 Brusatte, S. L., A. Muir, M. T. Young, S. Walsh, L. Steel, and L. M. Witmer. 2016. The braincase
501 and neurosensory anatomy of an Early Jurassic marine crocodylomorph: Implications for
502 crocodylian sinus evolution and sensory transitions. *The Anatomical Record* 299:1511–1530.

503 Buchy, M. C., E. Frey, and S. W. Salisbury. 2006. The internal cranial anatomy of the Plesiosauria
504 (Reptilia, Sauropterygia): evidence for a functional secondary palate. *Lethaia* 39:289–303.

505 Butler, A. B., and W. Hodos. 2005. *Comparative Vertebrate Neuroanatomy: Evolution and*
506 *Adaptation*. John Wiley and Sons, Inc., Hoboken, NJ, U.S.A., 744 pp.

507 Caldwell, M. W. 1997. Modified perichondral ossification and the evolution of paddle-like limbs in
508 ichthyosaurs and plesiosaurs. *Journal of Vertebrate Paleontology* 17:534–547.

509 Camp, C. L. 1942. *California mosasaurs*. Berkeley, California, University of California Press,
510 U.S.A., 67 pp.

511 Carpenter, K. 1997. Comparative cranial anatomy of two North American Cretaceous plesiosaurs;
512 pp. 191–216 in J. M. Callaway and E. L. Nicholls (eds.), *Ancient Marine Reptiles*. San Diego
513 Academic Press, California.

514 Clarke, J., and S. Etches. 1992. Predation among Jurassic reptiles. *Proceedings of the Dorset*
515 *Natural History and Archaeological Society* 113:202–205.

516 Concha, M. L., and S. W. Wilson. 2001. Asymmetry in the epithalamus of vertebrates. *The Journal*
517 *of Anatomy* 199:63–84.

518onnolly, A. 2016. Exploring the Relationship between Paleobiogeography, Deep-Diving
519 Behavior, and Size Variation of the Parietal Eye in Mosasaurs. Master dissertation, University
520 of Kansas, U.S.A., 43 pp.

521orfield, J. R., K. Price, A. N. Iwaniuk, C. Gutierrez-Ibanez, T. Birkhead, and D. R. Wylie. 2015.
522 Diversity in olfactory bulb size in birds reflects allometry, ecology and phylogeny. *Frontiers*
523 in *Neuroanatomy* 9:doi:10.3389/fnana.2015.00102.

524ruickshank, A. R., P. G. Small, and M. A. Taylor. 1991. Dorsal nostrils and hydrodynamically
525 driven underwater olfaction in plesiosaurs. *Nature* 352:62–64.

526uthbertson, R. S., H. C. Maddin, R. B. Holmes, and J. S. Anderson. 2015. The braincase and
527 endosseous labyrinth of *Plioplatecarpus peckensis* (Mosasauridae, Plioplatecarpinae), with
528 functional implications for locomotor behavior. *The Anatomical Record* 298:1597–1611.

529dinger, T. 1921 Über Nothosaurus. II. Zur Gaumenfrage. *Senckenbergiana* 3:193–205.

530dinger, T. 1928. Über einige fossile Gehirne. *Paläontologische Zeitschrift* 9:379–402.

531ttachfni, E. M., and B. Andreu. 2004. Le Cénomaniens et le Turonien de la plate-forme
532 Préafricaine du Maroc. *Cretaceous Research* 25:277–302.

533vans, M. 1999. A new reconstruction of the skull of the Callovian elasmosaurid plesiosaur
534 *Muraenosaurus leedsii* Seeley. *Mercian Geologist* 14:191–198.

535alcon, J. 1999. Cellular circadian clocks in the pineal. *Progress in neurobiology* 58:121–162.

536offa, D., J. Sasson, A. R. Cuff, M. N. Mavrogordato, and M. J. Benton. 2014. Complex rostral
537 neurovascular system in a giant pliosaur. *Naturwissenschaften* 101:453–456.

538orrest, R. 2000. A large rhomaleosaurid pliosaur from the Upper Lias of Rutland. *Mercian*
539 *Geologist* 15:37–40.

540arman, S. 1880. On certain species of Chelonioidae. *Bulletin of the Museum of Comparative*
541 *Zoology, Harvard* 6:123–126.

542 Gasparini, Z. L., and D. Dellapé. 1976. Un nuevo cocodrilo marino (Thalattosuchia,
543 Metriorhynchidae) de la Formacion Vaca Muerta (Jurásico, Titoniano) de la provincia de
544 Neuquén. Actas I Congreso Geológico Chileno 1:1–21.

545 Giffin, E. B. 1989. Pacycephalosaur Paleoneurology (Archosauria: Ornithischia). Journal of
546 Vertebrate Paleontology 9:67–77.

547 Gundy, G. C., C. L. Ralph, and G. Z. Wurst. 1975. Parietal eyes in lizards: zoogeographical
548 correlates. Science 190:671–673.

549 Herrera, Y. 2015. Metriorhynchidae (Crocodylomorpha: Thalattosuchia) from Upper Jurassic–
550 Lower Cretaceous of Neuquén Basin (Argentina), with comments on the natural casts of the
551 brain. Publicación Electrónica de la Asociación Paleontológica Argentina 15 :159–171.

552 Herrera, Y., M. S. Fernández, and Z. Gasparini. 2013. The snout of *Cricosaurus araucanensis*: a
553 case study in novel anatomy of the nasal region of metriorhynchids. Lethaia 46:331–340.

554 Herrera Y, J. M. Leardi, and M. S. Fernández. 2018. Braincase and endocranial anatomy of two
555 thalattosuchian crocodylomorphs and their relevance in understanding their adaptations to the
556 marine environment. PeerJ 6:e5686 <https://doi.org/10.7717/peerj.5686>

557 Halloway, W. L., K. M. Claesson, and F. R. O’Keefe. 2013. A virtual phytosaur endocast and its
558 implications for sensory system evolution in archosaurs. Journal of Vertebrate Paleontology
559 33:848–857.

560 Hopson, J. A. 1979. Paleoneurology; pp. 39–146 in C. Gans, R. G. Northcutt, and P. Ulinsky (eds),
561 Biology of the Reptilia. Vol. 9A. London: Academic Press.

562 Hurlburt, G. R., Ridgely, R. C., Witmer, L. M. 2013. Relative size of brain and cerebrum in
563 tyrannosaurid dinosaurs: an analysis using brainendocast quantitative relationships in extant
564 alligators; pp. 134–155 in J. M. Parrish, R. E. Molnar, P. J. Currie, and E. B. Koppelhus (eds),
565 Tyrannosaurid paleobiology. Indiana University Press, Bloomington.

566 Hutchison, V. H., and R. J. Kosh. 1974. Thermoregulatory function of the parietal eye in the lizard
567 *Anolis carolinensis*. *Oecologia* 16:173–177.

568 Grison, H. J. 1973. *Evolution of the brain and intelligence*. New York Academic, 482 pp.

569 Rak, D., and J. Janacek. 2017. Volume of the crocodylian brain and endocast during ontogeny.
570 PLoS ONE 12:doi.org/10.1371/journal.pone.0178491

571 Kennedy, W. J., A. S. Gale, D. J. Ward, and C. J. Underwood. 2008. Early Turonian ammonites
572 from Goulmima, southern Morocco. *Bulletin de l'Institut Royal des Sciences Naturelles de*
573 *Belgique* 78:149–177.

574 Kim, R., and D. Evans D. 2014. Relationships among brain, endocranial cavity, and body sizes in
575 reptiles; pp. 159 in E. Maxwell and J. Miller-Camp (eds), *Society of Vertebrate Paleontology*
576 *74th Annual Meeting*. Berlin, Germany, November 5-8, 2014.

577 Kishida, T., J. G. M. Thewissen, T. Hayakawa, H. Imai, and K. Agata. 2015. Aquatic adaptation
578 and the evolution of smell and taste in whales. *Zoological Letters* 1:1–9.

579 Oken, E. 1893. Beitrage zur Kenntnis der Gattung Nothosaurus. *Zeitschrift der deutschen*
580 *geologischen Gesellschaft* 45:337–377.

581 Konishi, T., M. W. Caldwell, T. Nishimura, K. Sakurai, and K. Tanoue. 2016. A new halisaurine
582 mosasaur (Squamata: Halisaurinae) from Japan: the first record in the western Pacific realm
583 and the first documented insights into binocular vision in mosasaurs. *Journal of Systematic*
584 *Palaeontology* 14:809–839.

585 Abra, A., K. L. Voje, H. Seligmann, and T. F. Hansen. 2010. Evolution of the third eye: a
586 phylogenetic comparative study of parietal-eye size as an ecophysiological adaptation in
587 *Liolaemus* lizards. *Biological journal of the Linnean Society* 101:870–883.

588 Reidy, J. 1865. *Cretaceous reptiles of the United States*. Washington, Smithsonian Institution,
589 U.S.A., 135 pp.

590 Linnaeus, C. 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera,*
591 *species, cum characteribus, differentiis, synonymis, locis. Tomus II. Editio duodecima,*
592 *reformata, Laurentius Salvius, Stockholm, Holmiae, 824 pp.*

593 Linnaeus, C. 1766. *Systema naturæ per regna tria naturæ, secundum classes, ordines, genera,*
594 *species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio duodecima,*
595 *reformata, Laurentii Salvii, Stockholm, Holmiae, 532 pp.*

596 Macrini, T. E., T. Rowe, and M. Archer. 2006. Description of a cranial endocast from a fossil
597 platypus, *Obdurodon dicksoni* (Monotremata, Ornithorhynchidae), and the relevance of
598 endocranial characters to monotreme monophyly. *Journal of Morphology* 267:1000–1015.

599 Macrini, T. E., T. Rowe, and J. L. VandeBerg. 2007. Cranial endocasts from a growth series of
600 *Monodelphis domestica* (Didelphidae, Marsupialia): A study of individual and ontogenetic
601 variation. *Journal of Morphology* 268:844–865.

602 Marek, R. D., B. C. Moon, M. Williams, and J. Benton. 2015. The skull and endocranium of a
603 Lower Jurassic ichthyosaur based on digital reconstructions. *Palaeontology* 58:723–742.

604 Massare, J. A. 1987. Tooth morphology and prey preference of Mesozoic marine reptiles. *Journal*
605 *of Vertebrate Paleontology* 7:121–137.

606 Massare, J. A. 1988. Swimming capabilities of Mesozoic marine reptiles: implications for method
607 of predation. *Paleobiology* 14:187–205.

608 McGowan, C. 1973. The cranial morphology of the Lower Liassic latipinnate ichthyosaurs of
609 England. *Bulletin of the British Museum (Natural History), Geology* 24:1–109.

610 McHenry, C. R., A. G. Cook, and S. Wroe. 2005. Bottom-feeding plesiosaurs. *Science* 310: 75.

611 Münster, G. 1834. Vorliufige Nachricht fiber einige neue Reptilien im Muschelkalke von Baiern.
612 *Neues Jahrbuch ffir die Mineralogie, Geognosie, Geologie und Petrefactenkunde* 1834:521–
613 527.

614 Neenan, J. M., and T. M. Scheyer. 2012. The braincase and inner ear of *Placodus gigas*
615 (Sauropterygia, Placodontia), a new reconstruction based on micro-computed tomographic
616 data. *Journal of Vertebrate Paleontology* 32:1350–1357.

617 Neenan, J. M., T. Reich, S. W. Evers, P. S. Druckenmiller, D. F. A. E. Voeten, J. N. Choiniere, P.
618 M. Barrett, S. E. Pierce, and R. B. J. Benson. 2017. Evolution of the Sauropterygian Labyrinth
619 with Increasingly Pelagic Lifestyles. *Current Biology* 27:3852–3858.

620 Nieuwenhuys, R., H. J. ten Donkelaar, and C. Nicholson. 1998. *The Central Nervous System of*
621 *Vertebrates*. Berlin: Springer, 2214 pp.

622 'Keefe, R. F. 2001. A cladistic analysis and taxonomic revision of the Plesiosauria (Reptilia:
623 Sauropterygia). *Acta Zoologica Fennica* 213:1–63.

624 'Keefe, R. F. 2002. The evolution of plesiosaur and pliosaur morphotypes in the Plesiosauria
625 (Reptilia: Sauropterygia). *Paleobiology* 28:101–112.

626 'Keefe, R. F., and L. M. Chiappe. 2011. Viviparity and K-selected life history in a Mesozoic
627 marine plesiosaur (Reptilia, Sauropterygia). *Science* 333:870–873.

628 'Keefe, R. F., R. A. Otero, S. Soto-Acuña, J. P. O'Gorman, S. J. Godfrey, and S. Chatterjee. 2017.
629 Cranial anatomy of *Morturneria seymourensis* from Antarctica, and the evolution of filter
630 feeding in plesiosaurs of the Austral Late Cretaceous. *Journal of Vertebrate Paleontology*
631 37:doi:10.1080/02724634.2017.1347570

632 Palci, A., M. N. Hutchinson, M. W. Caldwell, and M. S. Lee. 2017. The morphology of the inner
633 ear of squamate reptiles and its bearing on the origin of snakes. *Royal Society open science*
634 4:doi: 10.1098/rsos.170685

635 Palci, A., M. N. Hutchinson, M. W. Caldwell, and J. Scanlon. 2018. Palaeoecological inferences for
636 the fossil Australian snakes *Yurlunggur* and *Wonambi* (Serpentes, Madtsoiidae). *Royal*
637 *Society Open Science* 5:doi:10.1098/rsos.172012

638 Paulina-Carabajal, A. P., J. Sterli, J. Muller, and A. Hilger. 2013. Neuroanatomy of the marine
639 Jurassic turtle *Plesiochelys etalloni* (Testudinata, Plesiochelyidae). PLoS ONE
640 8:doi:10.1371/journal.pone.0069264

641 Pictet, F. J., and A. Humbert. 1857. Description d'une émyde nouvelle (*Emys Etalloni*) du terrain
642 jurassique supérieur des environs de St-Claude; pp. 256–273 in F. J. Pictet (ed), Matériaux
643 pour la paléontologie suisse. Première série, Genève, Suisse.

644 Pierce, S. E., M. Williams, M., and R. B. J. Benson. 2017. Virtual reconstruction of the endocranial
645 anatomy of the early Jurassic marine crocodylomorph *Pelagosaurus typus* (Thalattosuchia).
646 PeerJ 5:e3225.

647 Quay, W. B. 1979. The parietal eye-pineal complex; pp. 245–406 in C. Gans, R. G. Northcutt, and
648 P. Ulinski (eds), Biology of the Reptilia. Volume 9 Neurology A. London, Academic Press.

649 Ralph, C. L. 1975. The pineal gland and geographical distribution of animals. International Journal
650 of Biometeorology 19:289–303.

651 Ralph, C. L., B. T. Firth, and J. S. Turner. 1979. The role of the pineal body in ectotherm
652 thermoregulation. American Zoologist 19:273–293.

653 Rothschild, B. M., and G. W. Storrs. 2003. Decompression syndrome in plesiosaurs (Sauropterygia:
654 Reptilia). Journal of Vertebrate Paleontology 23:324–328.

655 Sachs, S., and B. P. Kear. 2015. Postcranium of the paradigm elasmosaurid plesiosaurian
656 *Libonectes morgani* (Welles, 1949). Geological Magazine 152:694–710.

657 Sachs, S., J. Lindgren, and M. Siversson. 2015. A partial plesiosaurian braincase from the Upper
658 Cretaceous of Sweden. Geological Society, London, Special Publications 434: 293–301.

659 Sachs, S., J. J. Hornung, and B. P. Kear. 2016. Reappraisal of Europe's most complete Early
660 Cretaceous plesiosaurian: *Brancaosaurus brancai* Wegner, 1914 from the "Wealden facies" of
661 Germany. PeerJ 4:doi:10.7717/peerj.2813

662 ato, T. 2003. *Terminonatator ponteixensis*, a new elasmosaur (Reptilia; Sauropterygia) from the
663 Upper Cretaceous of Saskatchewan. *Journal of Vertebrate Paleontology* 23:89–103.

664 ato, T., and K. Tanabe. 1998. Cretaceous plesiosaurs ate ammonites. *Nature* 394:629–630.

665 ato, T., X.C. Wu, A. Tirabasso, A., and P. Bloskie. 2011. Braincase of a polycotyloid plesiosaur
666 (Reptilia: Sauropterygia) from the Upper Cretaceous of Manitoba, Canada. *Journal of*
667 *Vertebrate Paleontology* 31:313–329.

668 eely, H. G. 1880. Note on the cranial characters of a large teleosaur from the Whitby Lias
669 preserved in the Woodwardian museum of the University of Cambridge, indicating a new
670 species, *Teleosaurus eucephalus*. *Quarterly Journal of the Geological Society* 36: 627–634.

671 ennikov, A. G., and M. S. Arkhangel'sky. 2010. On a typical Jurassic sauropterygian from the
672 Upper Triassic of Wilczek Land (Franz Josef Land, Arctic Russia). *Paleontological Journal*
673 44:567–572.

674 huler, E. W. 1950. A new elasmosaur from the Eagle Ford Shale of Texas. *Fondren Science Series*
675 1:1–33.

676 mith, K. T., B-A. S. Bhullar, G. Köhler, and J. Habersetzer. 2018. The only known jawed
677 vertebrate with four eyes and the Bauplan of the pineal complex. *Current Biology* 28: 1101–
678 1107.

679 arck, D. 1979. Cranio-cerebral relations in Recent reptiles; pp. 1–38 in C. Gans, R. G. Northcutt,
680 and P. Ulinski (eds.), *Biology of the Reptilia*. Vol. 9 (Neurology A). Academic Press,
681 London.

682 orrs, G. W. 1995. A juvenile specimen of *?Plesiosaurus* sp. from the Lias (Lower Jurassic,
683 Pliensbachian) near Charmouth, Dorset, England. *Proceedings of the Dorset Natural History*
684 *and Archaeological Society* 116:71–76.

685 arlo, L. B. 1959. *Pliosaurus brachyspondylus* (Owen) from the Kimeridge Clay. *Palaeontology*
686 1:283–291.

687hach, W. T., and A. J. Bastian. 2004. Role of the cerebellum in the control and adaptation of gait
688 in health and disease. *Progress in brain research* 143:353–366.

689osini, G. 1997. The pineal complex of reptiles: physiological and behavioral roles. *Ethology*
690 *Ecology & Evolution* 9:313–333.

691andelli, D. 1761. *Epistola de holothurio, et testudine coriacea ad celeberrimum Carolum*
692 *Linnaeum equitem naturae curiosum Dioscoridem II. Conzatti, Padua, 12 pp.*

693ignaud, P. 1998. Une Nouvelle espèce de *Steneosaurus* (Thalattosuchia, Teleosauridae) dans le
694 Callovien du Poitou (France) et la systématique des *Steneosaurus* longirostres du Jurassique
695 moyen d'Europe occidentale. *Palaeovertebrata* 27:19–44.

696ignaud, P., and Z. B. Gasparini. 1996. New *Dakosaurus* (Crocodylomorpha, Thalattosuchia) from
697 the Upper Jurassic of Argentina. *Comptes Rendus de l'Académie des Sciences Paris* 322:245–
698 250.

699incient, P., R. Allemand, P. D. Taylor, G. Suan, E. E. Maxwell. 2017. New insights on the
700 systematics, palaeoecology and palaeobiology of a plesiosaurian with soft tissue preservation
701 from the Toarcian of Holzmaden, Germany. *The Science of Nature* 104:51.

702incient, P., N. Bardet, X. Pereda Suberbiola, B. Bouya, M. Amaghazaz, and S. Meslouh. 2011.
703 *Zarafasaura oceanis*, a new elasmosaurid (Reptilia: Sauropterygia) from the Maastrichtian
704 Phosphates of Morocco and the palaeobiogeography of latest Cretaceous plesiosaurs.
705 *Gondwana Research* 19:1062–1073.

706oeten, D. F. A. E., T. Reich, R. Araujo, and T. M. Scheyer. 2018. Synchrotron microtomography
707 of a *Nothosaurus marchicus* skull informs on nothosaurian physiology and neurosensory
708 adaptations in early Sauropterygia. *PLoS ONE* 13: doi.org/10.1371/journal.pone.0188509

709ade, M. 1990. A review of the Australian Cretaceous longipinnate ichthyosaur *Platypterygius*
710 (Ichthyosauria: Ichthyopterygia). *Memoirs of the Queensland Museum* 28:115–137.

711 Welles, S. P. 1952. A review of the North American Cretaceous elasmosaurs. University of
712 California, Publications in Geological Sciences 29:47–144.

713 Wenz, S. 1968. Contribution à l'étude du genre *Metriorhynchus*. Crâne et moulage endocrânien de
714 *Metriorhynchus superciliosus*. Annales de Paléontologie (Vertébrés) 54: 149–183.

715 Westphal, F. 1961. Zur Systematik der deutschen und englischen Lias Krokodilier. Neues Jahrbuch,
716 für Geologie und Paläontologie. Abhandlungen 113:207-218.

717 Wharton, D. S. 2000. An enlarged endocranial venous system in *Steneosaurus pictaviensis*
718 (Crocodylia: Thalattosuchia) from the Upper Jurassic of Les Lourdines, France. Comptes
719 Rendus de l'Académie des Sciences, Series IIA, Earth and Planetary Science 331 :221–226.

720 Wintrich, T., S. Hayashi, A. Houssaye, Y. Nakajima, and P. M. Sander. 2017. A Triassic
721 plesiosaurian skeleton and bone histology inform on evolution of a unique body plan. Science
722 advances 3:doi:10.1126/sciadv.1701144

723 Witmer, L. M., and R. C. Ridgely. 2009. New insights into the brain, braincase, and ear region of
724 tyrannosaurs (Dinosauria, Theropoda), with implications for sensory organization and
725 behavior. The Anatomical Record 292:1266–1296.

726 Witmer, L. M., R. C. Ridgely, D. L. Dufeau, and M. C. Semones. 2008. Using CT to peer into the
727 past: 3D visualization of the brain and ear regions of birds, crocodiles, and nonavian
728 dinosaurs; pp. 67–88 in H. Endo, and R. Frey (eds), *Anatomical imaging: towards a new*
729 *morphology*. Tokyo, Japan, Springer.

730 Wyneken, J. 2003. The external morphology, musculoskeletal system, and neuro-anatomy of sea
731 turtles; pp. 39–77 in P. L. Lutz, J. A. Musick, and J. Wyneken (eds), *The biology of sea*
732 *turtles*. Vol. 2, CRC Press, London.

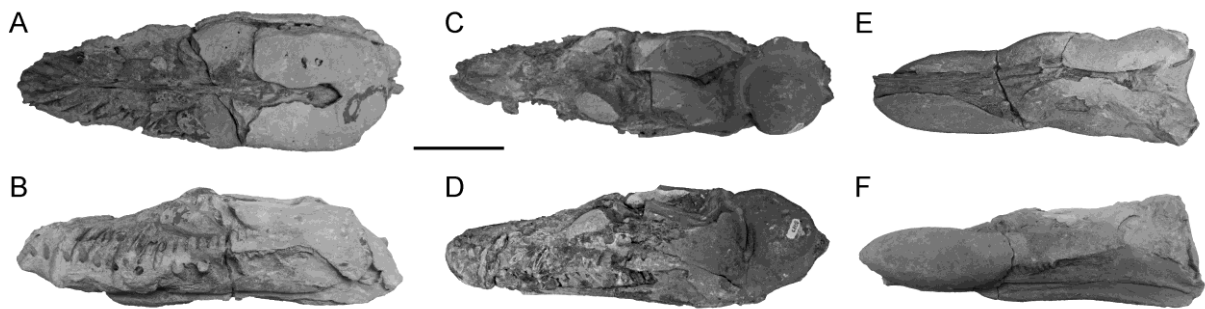
733 Wyneken, J. 2007. Reptilian neurology: anatomy and function. *Veterinary Clinics of North*
734 *America: Exotic Animal Practice* 10:837–853.

735 Submitted May 17, 2018; accepted Month DD, YYYY

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FIGURES

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739 FIGURE 1. Photographs of the *Libonectes morgani* specimens D1-8213 (**A**, **B**) and SMNS
740 81783 (**C**, **D**); and of the undetermined polycotyloid MNHN F-GOU14 (**E**, **F**), all from the
741 lower Turonian of Goulmima (Morocco) in dorsal (up) and left lateral (down) views. Scale
742 bar equals 10mm. [planned for page width]

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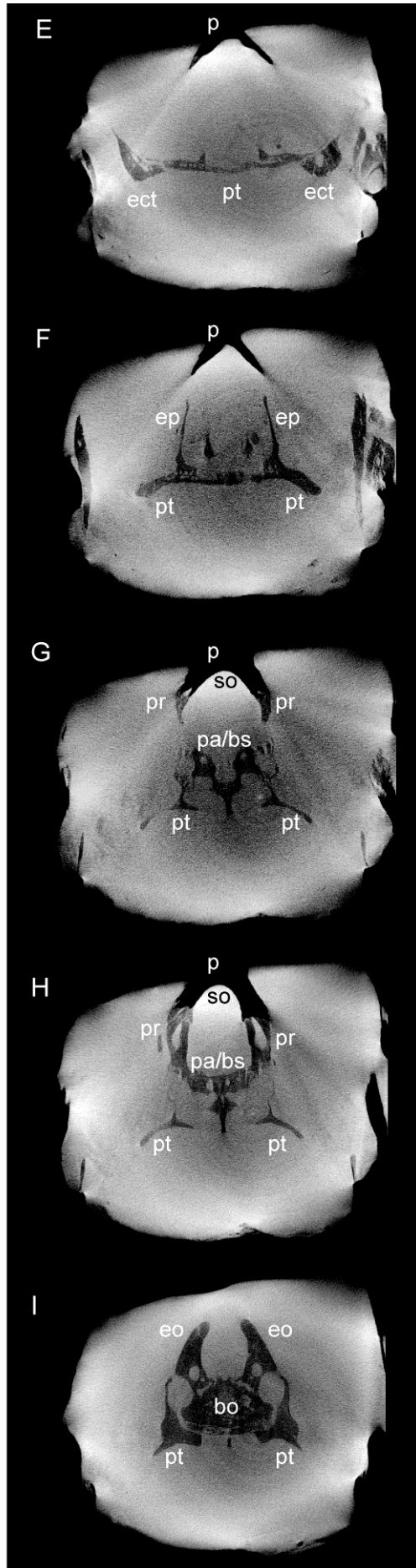
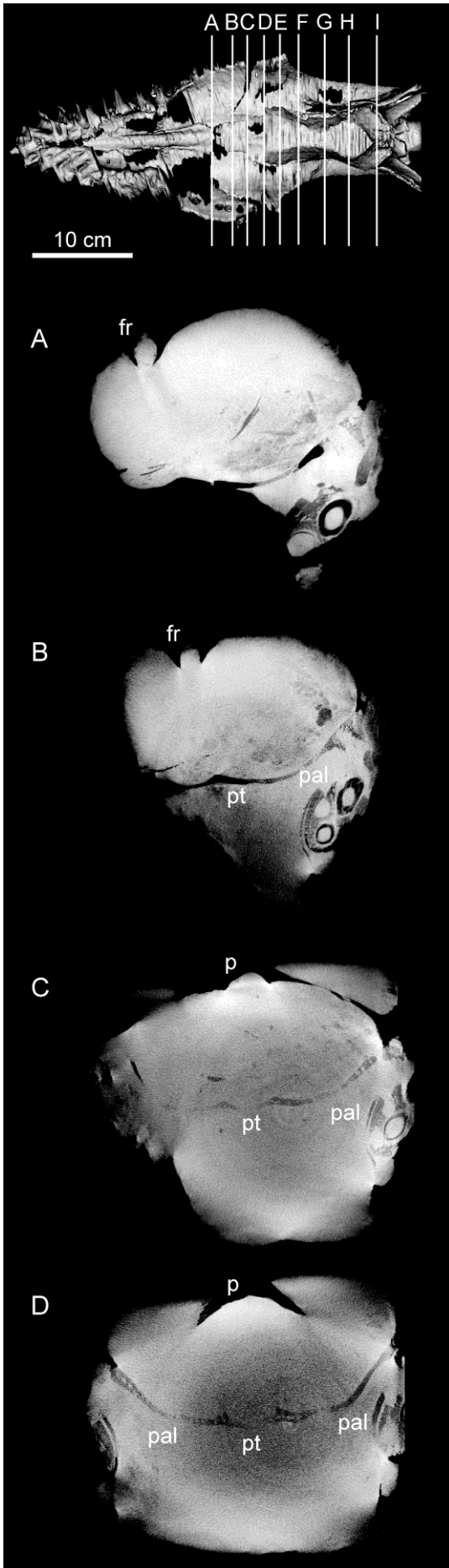
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748 FIGURE 2. Individual slice data (**A-I**) through the cranium of *Libonectes morgani* (D1-8213).
749 Positions of the transverse sections are shown in dorsal cranial surface model. Images in **A-I**
750 not to scale. **Abbreviations:** **bo**, basioccipital; **ect**, ectopterygoid; **ep**, epipterygoid; **eo**,
751 exoccipital-opisthotic; **fr**, frontal; **p**, parietal; **pa/bs**, parabasisphenoid; **pal**, palatin; **pr**,
752 prootic; **pt**, pterygoid; **so**, supraoccipital. See Appendix 1 for cross sections from the two
753 other specimens. [planned for page width]

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758 FIGURE 3. Virtual plesiosaurian endocasts of the *Libonectes morgani* specimens D1-8213
759 (A) and SMNS 81783 (B); and the undetermined Polycotyliidae MNHN F-GOU14 (C) in
760 dorsal (top) and left lateral (bottom) views. **Abbreviations:** **cb**, cerebellum; **cer**, cerebral
761 hemispheres; **ic**, internal carotid; **mo**, *medulla oblongata*; **ob**, olfactory bulbs; **ol**, optic lobes;
762 **ot**, olfactory tracts; **po?**, pineal organ; **pit**, pituitary bulb; **V**, trigeminal nerve; **VI**, abducens
763 nerve; **VII**, facial nerve; **IX**, glossopharyngeal nerve; **X-XI**, vagus and accessory nerves; **XII**,
764 hypoglossal nerves. Scale bars equal 20 mm. The dotted-lines indicate the missing parts, the
765 specimen A is used as a reference for other two specimens. [planned for 2/3 of a whole page
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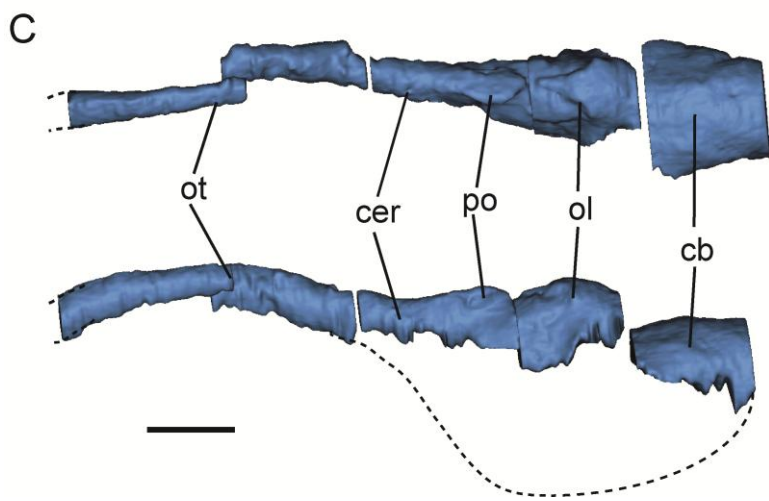
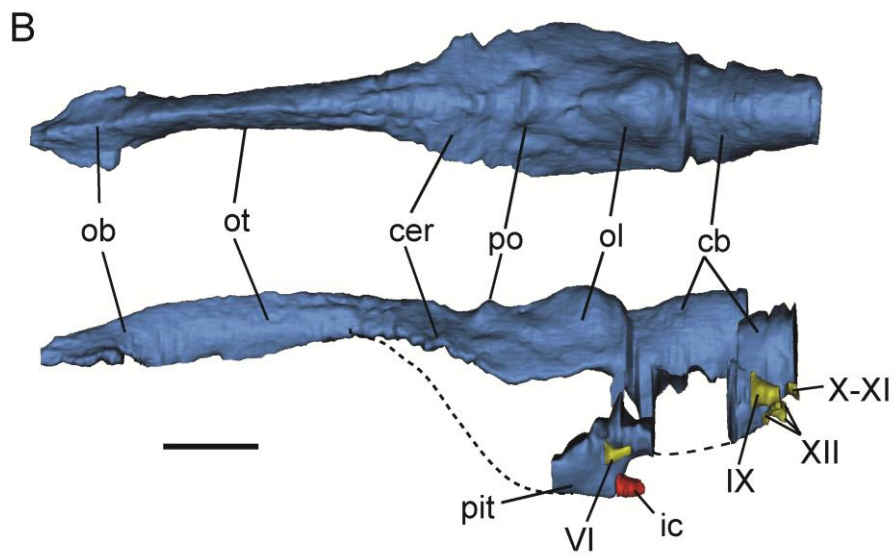
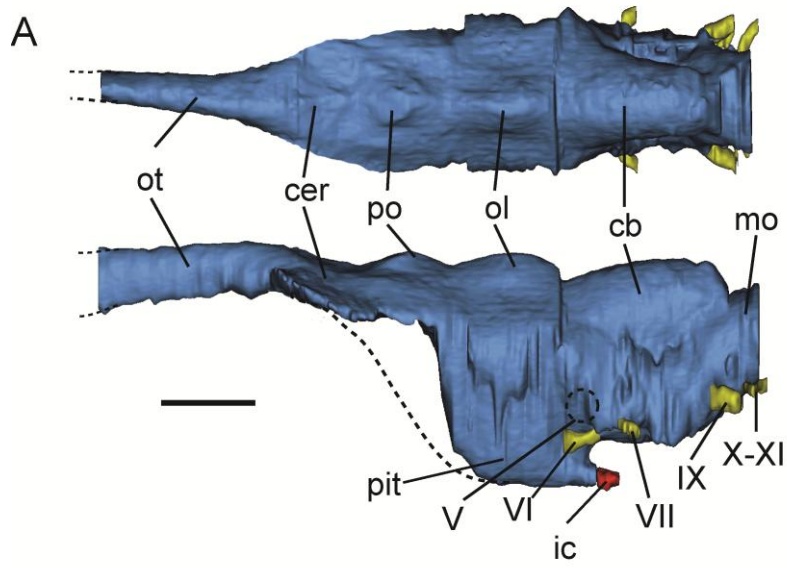
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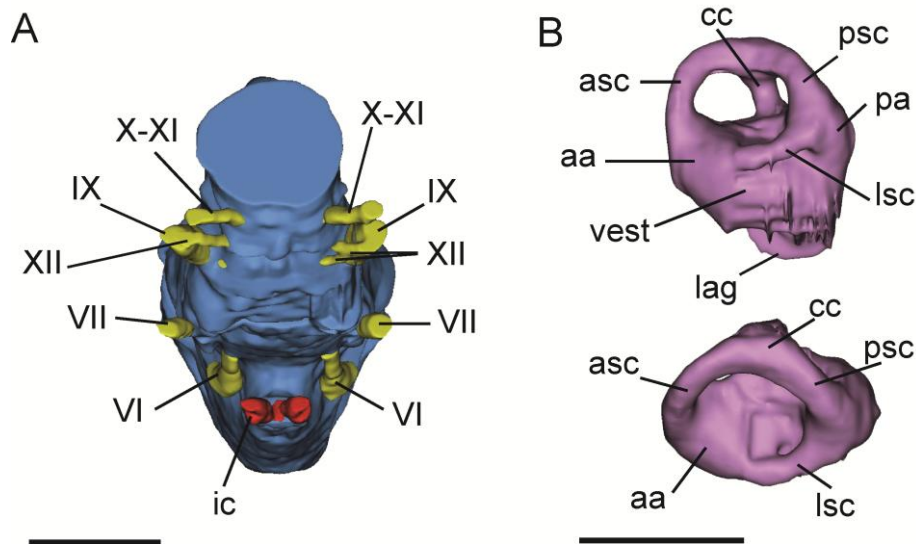
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780 FIGURE 4. (A) Endocast of the more complete *Libonectes morgani* specimen D1-8213 in
 781 ventroposterior view showing the position of each cranial nerves. (B), Left endosseous
 782 labyrinth of D1-8213 in lateral (top) and dorsal (bottom) views. **Abbreviations:** **aa**, anterior
 783 ampulla; **asc**, anterior semicircular canal; **cc**, common crus; **ic**, internal carotid; **lag**, lagena;
 784 **lsc**, lateral semicircular canal; **pa**, posterior ampulla; **psc**, posterior semicircular canal; **vest**,
 785 vestibule; **VI**, abducens nerve; **VII**, facial nerve; **IX**, glossopharyngeal nerve; **X-XI**, vagus
 786 and accessory nerves; **XII**, hypoglossal nerves. Scale bars equal 20 mm. [planned for 2/3 of a
 787 whole page width]

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