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

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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  $113^\circ$ ;  
214  $96^\circ$  between the anterior and lateral semicircular canals and  $84^\circ$  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

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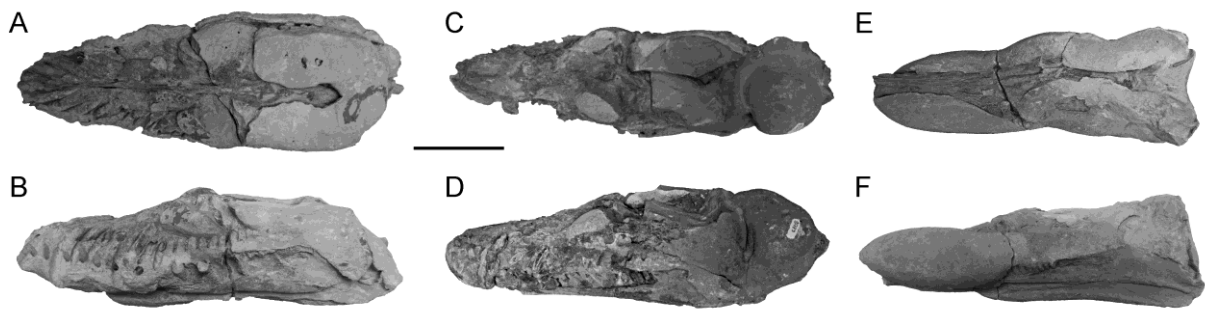
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FIGURES

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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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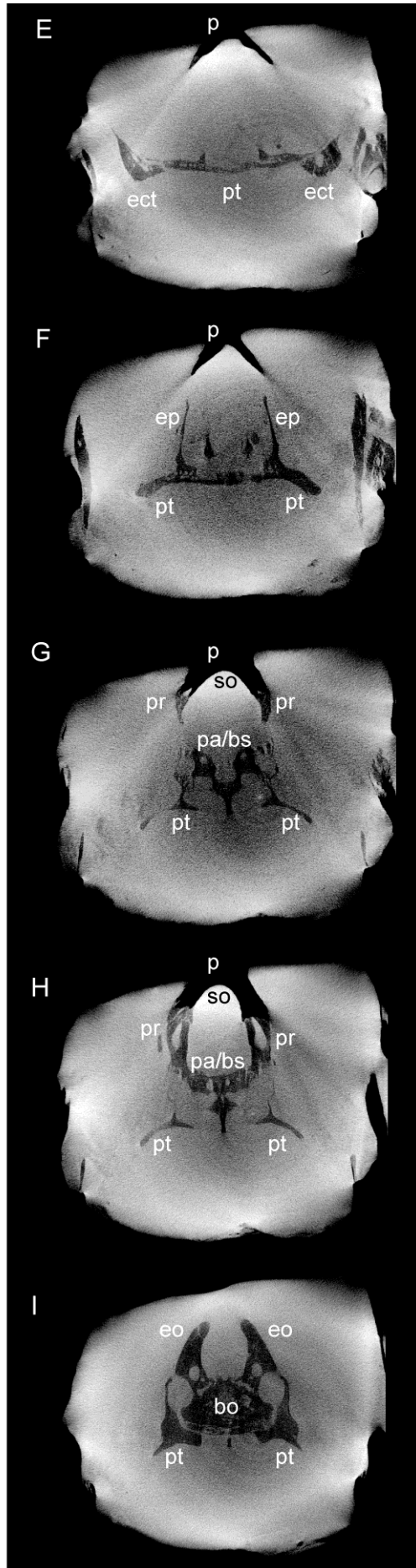
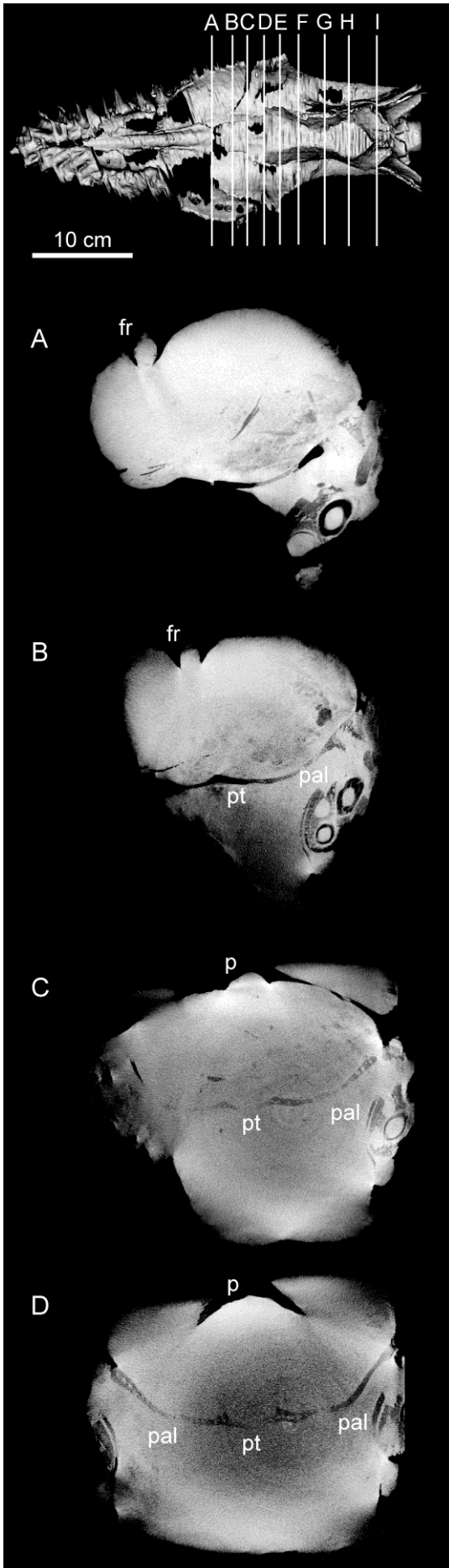
748 FIGURE 2. Individual slice data (**A-I**) through the cranium of *Libonectes morgani* (D1-8213).  
749 Positions of the transverse sections are shown in dorsal cranial surface model. Images in **A-I**  
750 not to scale. **Abbreviations:** **bo**, basioccipital; **ect**, ectopterygoid; **ep**, epipterygoid; **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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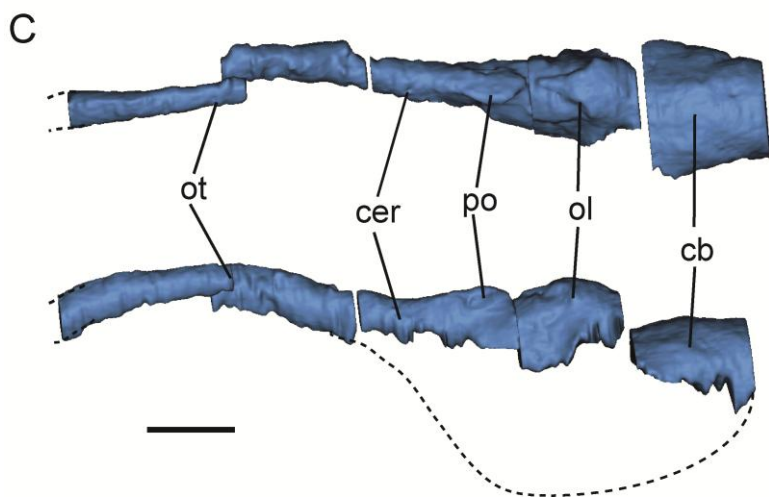
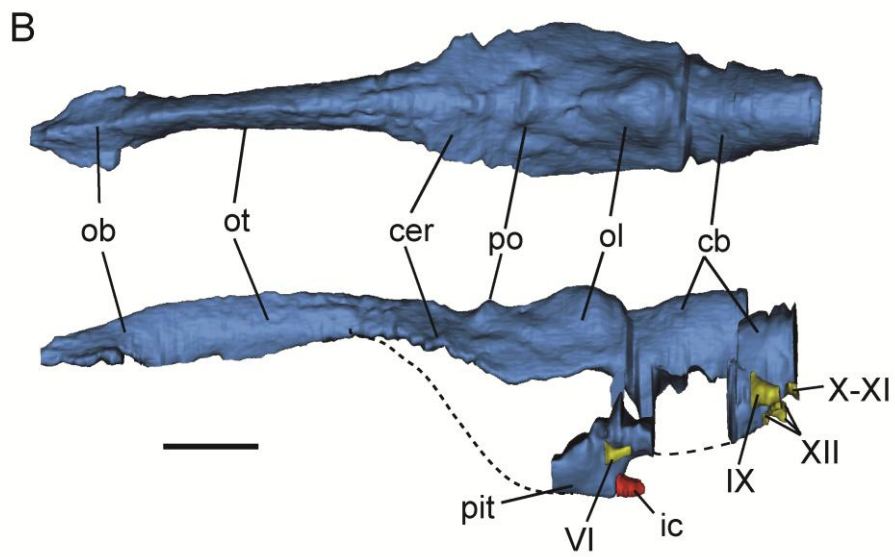
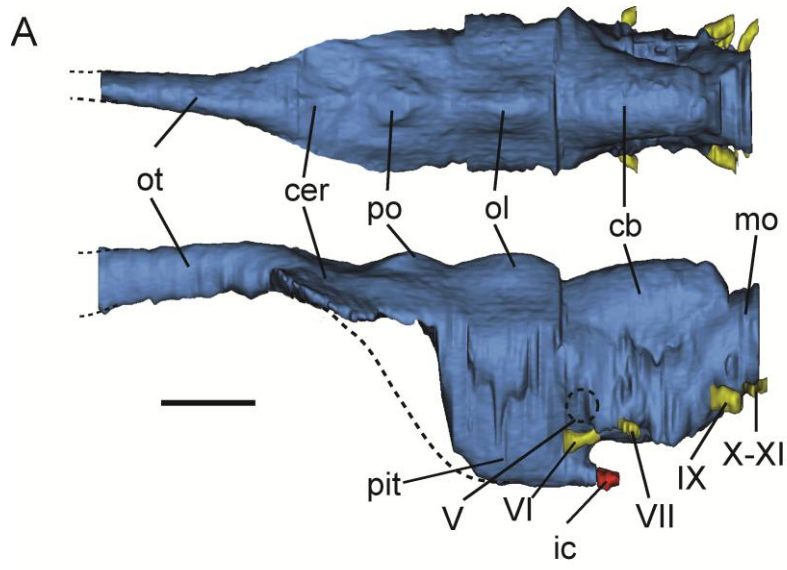
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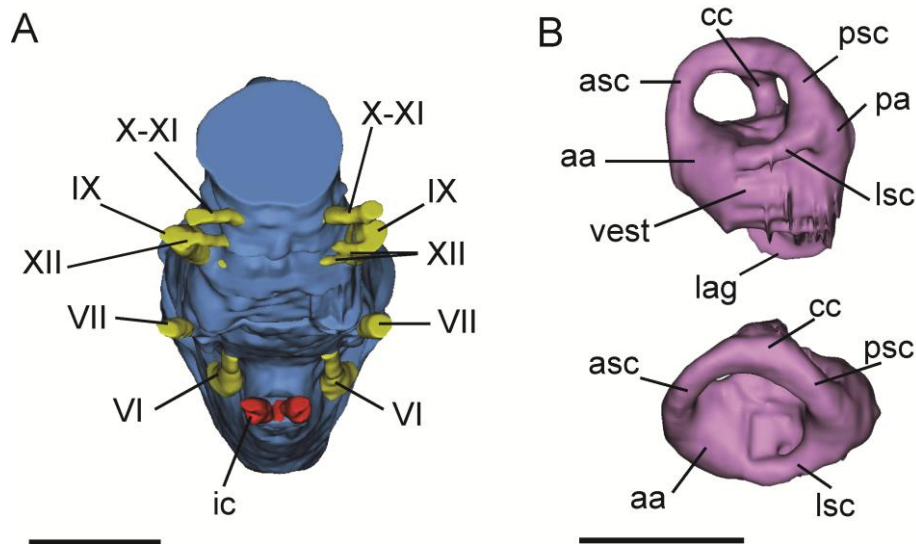
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780 FIGURE 4. (A) Endocast of the more complete *Libonectes morgani* specimen D1-8213 in  
 781 ventroposterior view showing the position of each cranial nerves. (B), Left endosseous  
 782 labyrinth of D1-8213 in lateral (top) and dorsal (bottom) 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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