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Sensory evolution and ecology of early turtles revealed by digital endocranial reconstructions

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The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

Author contribution statement

S.L. and I.W. conceived and designed the study, S.L. performed the three-dimensional reconstruction, I.W. provided digital datasets, S.L., G.S.F. and I.W. collected, analyzed and interpreted the data. S.L. and G.S.F. created figures and supplementary data. S.L., G.S.F. and I.W. contributed equally to the discussion, preparation and writing of the paper.

Keywords

Neuroanatomy, sensory adaptation, 3D visualization, Digital endocast, stem-turtle, turtle origin

Abstract

Word count: 184

In the past few years, new fossil finds and novel methodological approaches have prompted intensive discussions about the phylogenetic affinities of turtles and rekindled the debate on their ecological origin, with very distinct scenarios, such as fossoriality and aquatic habitat occupation, proposed for the earliest stem-turtles. While research has focused largely on the origin of the anapsid skull and unique postcranial anatomy, little is known about the endocranial anatomy of turtles. Here, we provide 3D digital reconstructions and comparative descriptions of the brain, nasal cavity, neurovascular structures and endosseous labyrinth of *Proganochelys quenstedti*, one of the earliest stem-turtles, as well as other turtle taxa. Our results demonstrate that *P. quenstedti* had retained a simple tube-like brain morphology with poorly differentiated regions and mediocre hearing and vision, but a well-developed olfactory sense. Endocast shape analysis indicates that an increase in size and regionalization of the brain took place in the course of turtle evolution, achieving an endocast diversity comparable to other amniote groups. Based on the new evidence, we further conclude that *P. quenstedti* was a highly terrestrial, but most likely not a fossorial taxon

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Ethics statements

(Authors are required to state the ethical considerations of their study in the manuscript, including for cases where the study was exempt from ethical approval procedures)

Does the study presented in the manuscript involve human or animal subjects: No

1 **Sensory evolution and ecology of early turtles revealed by digital**
2 **endocranial reconstructions**

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19

20 **Abstract**

21 In the past few years, new fossil finds and novel methodological approaches have prompted
22 intensive discussions about the phylogenetic affinities of turtles and rekindled the debate on their
23 ecological origin, with very distinct scenarios, such as fossoriality and aquatic habitat occupation,
24 proposed for the earliest stem-turtles. While research has focused largely on the origin of the
25 anapsid skull and unique postcranial anatomy, little is known about the endocranial anatomy of
26 turtles. Here, we provide 3D digital reconstructions [and comparative descriptions](#) of the brain, nasal
27 cavity, neurovascular structures and endosseous labyrinth of *Proganochelys quenstedti*, one of the
28 earliest stem-turtles, as well as other turtle taxa. Our results demonstrate that *P. quenstedti* had
29 retained a simple tube-like brain morphology with poorly differentiated regions and mediocre
30 hearing and vision, but a well-developed olfactory sense. Endocast shape analysis indicates that an
31 increase in size and regionalization of the brain took place in the course of turtle evolution,
32 achieving an endocast diversity comparable to other amniote groups. Based on the new evidence
33 [presented herein](#), we further conclude that *P. quenstedti* was a highly terrestrial, but most likely not
34 a fossorial, taxon.

35
36 **Keywords:** neuroanatomy; sensory adaptation; 3D visualization; digital endocast; stem-turtles;
37 turtle origin
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39 Introduction

40 Turtles (Testudinata sensu Joyce et al., 2004) are a diverse group of reptiles with an unusual ~~body~~
41 ~~plan~~: 'bauplan' fundamentally different from that of other amniotes. Unique morphological
42 characters, including the anapsid cranial configuration, which lacks temporal fenestrations, and the
43 presence of a bony shell formed by a dorsal carapace and a ventral plastron have long obfuscated
44 the phylogenetic affinities of turtles (Rieppel, 2007; Lyson et al., 2010). While most molecular
45 studies have recovered turtles nested within diapsid reptiles and often as a sister-group to
46 Archosauria (birds and crocodiles) (Hedges and Poling, 1999; Wang et al., 2013; Field et al., 2014),
47 most studies based on comparative anatomy have placed turtles outside of Diapsida (Gauthier et al.,
48 1988; Lee, 1997; Werneburg and Sánchez-Villagra, 2009; Neenan et al., 2013; Scheyer et al., 2017)
49 or alternatively inside Lepidosauromorpha (deBraga and Rieppel, 1997; Rieppel and Reisz, 1999;
50 Li et al., 2008; Liu et al., 2011). The scant fossil record of stem-turtles (i.e., non-Testudines
51 Testudinata) has further obscured the evolutionary origin of this group. Recent discoveries of new
52 species and ~~the~~ reanalysis of existing specimens with novel methodological approaches (e.g.
53 computed tomography and digital visualization) have provided new data to the debate of turtle
54 ancestry (Li et al., 2008; Bever et al., 2015; Schoch and Sues, 2015). These studies found support
55 for the diapsid origin of turtles and produced potential evidence for ~~a~~-closure of the temporal
56 fenestrae early in their evolutionary history (Schoch and Sues, 2015; Lyson et al., 2016;
57 Werneburg, 2015).

58 Regarding the environmental origin of the group, although all Triassic turtles were clearly
59 terrestrial (Joyce, 2015), data provided by recently described taxa have painted an ambiguous
60 picture regarding the paleoecological setting in which the Testudinata ancestors evolved. While the
61 ~~potentially~~-earliest ~~known potential~~ proto-turtle (i.e., non-Testudinata Pantestudines) *Eumotosaurus*
62 *africanus* (ca. 260 Ma) has been found in terrestrial environments (Lyson et al., 2016), the
63 somewhat younger *Pappochelys rosinae* (ca. 240 Ma) and *Odontochelys semitestacea* (ca. 220 Ma)
64 were retrieved from lacustrine and deltaic deposits and were considered to have been semi-aquatic
65 (Li et al., 2008; Rieppel, 2013; Schoch and Sues, 2015). In the ~~latter last~~ two taxa, the
66 dorsoventrally flattened, expanded ribs and thickened gastralia have been interpreted as
67 ~~mechanisms to control~~ adaptations for buoyancy ~~control~~ in an aquatic environment (Schoch and
68 Sues, 2015). In contrast, the morphology of the ribs, ~~the as well as the~~ more rigid body wall,
69 powerful forelimbs and ~~a~~-triangular skull, have been considered to represent adaptations to
70 fossoriality in *E. africanus* (Lyson et al., 2016). On the other hand, the type localities of both *P.*
71 *rosinae* and *O. semitestacea* have also yielded terrestrial taxa (Joyce, 2015; Schoch and Sues, 2017)
72 and, in fact, terrestrial diapsid remains are dominant ~~in~~ at the type locality of the former (Schoch

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73 and Sues, 2015). Additionally, Joyce (2015) argued in favor of *Odontochelys semitestacea* as a
74 terrestrial proto-turtle, based on its phalangeal formula. Hence, terrestrial, fossorial ~~or~~ and semi-
75 aquatic habits ~~were all previously~~ have all been suggested ~~as the ecological settings during~~ for the
76 early stages of turtle evolution, before the origin of ~~a~~ the protective shell characteristic of the
77 definitely terrestrial stem-turtles (Joyce and Gauthier, 2004; Scheyer and Sander, 2007; Joyce,
78 2015).

79 While research on early turtles has focused largely on the acquisition of the anapsid
80 condition and the evolution of the postcranial anatomy employing comparative morphology,
81 histology and genetics, little is known about the endocranial anatomy of stem-turtles (~~as well as~~ or
82 indeed turtles in general). Using micro-computed tomography (μ CT) scanning and digital
83 visualization, we here provide a reconstruction of the endocranial anatomy of *Proganochelys*
84 *quenstedti*, one of the earliest testudines from the Late Triassic of Germany. We further compare
85 the reconstructed brain anatomy with different stem- and crown-turtles (Testudines) and other
86 vertebrate taxa using endocast outline analysis to elucidate related anatomical and ecological
87 aspects of turtle origins.

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90 **Materials and Methods**

91 For ~~the~~ digital reconstruction of endocranial anatomy (brain, inner ear, neurovascular structures,
92 nasal cavity) two specimens of *Proganochelys quenstedti* from the Late Triassic of Germany were
93 studied: MB 1910.45.2 (Museum für Naturkunde Berlin) from the Baerecke and Limpricht Quarry,
94 Halberstadt (Jaekel, 1918), and SMNS 16980 (Staatliches Museum für Naturkunde Stuttgart) from
95 the *Plateosaurus*-quarry in Trossingen. ~~(~~ Gaffney, 1990). Both specimens consist of nearly
96 complete and articulated cranial skeletons. MB 1910.45.2 shows substantial taphonomic ~~artei~~ facts
97 in the form of anteroposterior shearing and some moderate mediolateral crushing and deformation.
98 However, these ~~artei~~ facts only marginally affect the braincase and the digital reconstruction of the
99 ~~respective~~ various endocranial structures (see Results for more details).

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100 MB 1910.45.2 was CT scanned at ~~the~~ Leibniz-Institut für Zoo- und Wildtierforschung
101 Berlin / Germany (IZW) using a Toshiba Aquilon ONE medical CT scanner. Scanning parameters
102 ~~properties~~ were set at 225 kV and 300 μ A resulting in an image stack of 512 x 512 x 213 pixels and
103 a voxel size of 2.0 mm per slice. The dataset was subsequently 'upsampled' (1024 x 1024 x 426
104 pixels, 0.5 mm effective voxel size) by averaging the existing slice data. This process does not
105 increase the actual resolution of the data, but provides more slices available for segmentation
106 permitting clearer identification of features and resulting in smoother surface models.

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107 SMNS 16980 was scanned at [the Riedberg Campus of Goethe-Universität Frankfurt /](#)
108 Germany using a Phoenix Nanotom m scanner. Due to [the-its](#) relatively large size, the specimen
109 was scanned in three stages. The resulting image stacks were combined into a single stack with
110 3583 x 4011 x 5658 pixels and a voxel size of 0.025 mm per slice. The dataset was subsequently
111 downsampled (870 x 954 x 1161 pixels, 0.1 mm voxel size) to permit further processing and
112 segmentation.

113 Datasets [of-for](#) both specimens were imported into Avizo 8 (Visualisation Science Group)
114 for the segmentation of endocranial structures. Due to [the-poor greyscale-grayscale](#) attenuation (in
115 particular for SMNS 16980), [the-segmentation process](#) was performed manually using the
116 paintbrush and interpolation tools in the Avizo segmentation editor ([both reconstructions performed](#)
117 [by the first author for consistency following Balanoff et al. 2016](#)). 3D surface models and volumes
118 were created to visualize the endocranial components. In addition, surface models of the individual
119 structures were downsampled to a degree that allowed for small file sizes but preserved all details,
120 and were exported as separate OBJ-files for the creation of the interactive 3D-figures provided in
121 the supplementary material as outlined in Lautenschlager (2014b) using Adobe 3D reviewer (Adobe
122 Systems Inc.).

123 To provide a basis for comparisons, the endocranial anatomy of nine extant turtles and of
124 one additional stem-turtle, *Naomichelys speciosa* (FMNH PR273), was reconstructed in the [same](#)
125 manner [as-](#)described above. FMNH PR273 was scanned at [the Institut für Naturwissenschaftliche](#)
126 Archäologie at [the Universität Tübingen](#) at a resolution of 0.1 mm resulting in an image stack [with](#)
127 [of 1068 x 1382 x 622 pixels](#). The [following](#) extant species were scanned at the Steinmann-Institut
128 für Geologie, Mineralogie & Paläontologie / Rheinische Friedrich-Wilhelms-Universität Bonn /
129 Germany and at [the Museum für Naturkunde Berlin / Germany: *Podocnemis unifilis* \(SMF 55470\),](#)
130 *Chelodina reimanni* (ZMB Herpetologie 49659), *Emydura subglobosa* (PIMUZ lab# 2009.37),
131 *Pelodiscus sinensis* (IW576-2), *Chelonia mydas* (ZMB 37416 MS), *Macrochelys temminckii*
132 (TCGT, Teaching collection Geowissenschaften Towisse), *Emys orbicularis* (WGJ 1987a),
133 *Platysternon megacephalum* (SMF 69684), *Malacochersus tornieri* (SMF 58702) (see
134 Supplemental [Information-Material](#) for [collection-Collection](#) abbreviations). Data derived from the
135 reconstructions was further used for a shape analysis of [the-brain](#) morphology.

136 Due to the absence of unambiguous and [clearly-consistently](#) identifiable landmarks on the
137 endocast across different amniote taxa, outline shape analysis was performed to quantify
138 morphological differences. Although this approach uses only two-dimensional outlines (in contrast
139 to three-dimensional landmarks), it allows [for-the](#) quantification of shape data [of-for](#) geometries
140 lacking homologous landmarks (Haines & Crampton, 2000). For shape analysis, [a](#) sagittal cross-

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141 sections through the surface models of ~~each the~~ brain (i.e., digital cast of the endocranial cavity)
142 ~~were was~~ produced in Avizo for ~~all each~~ reconstructions. Contours of the two-dimensional cross-
143 sections were imported into tpsDig2.16 (Rohlf, 2010), ~~digitised digitized~~ and saved as 1000 x/y-
144 coordinate pairs. All outline data were subsequently analyzed in PAST 23, 17 (Hammer et al.,
145 2001) ~~to performing~~ Fast Fourier transformation (FFT) and principal components analysis (PCA)
146 ~~using with the handle module~~ as outlined in Crampton & Haines (1996) and Lautenschlager (2014a).
147 Outlines were smoothed ten times to eliminate pixel noise, and ~~24-23~~ Fourier harmonics were found
148 to describe the outlines of all sampled taxa sufficiently (average Fourier power > 99%) (see also
149 Supplementary Material). In addition to the reconstructed endocasts, further outlines of 52 taxa
150 were collected from the literature (Hopson, 1979; Franzosa, 2004; Neenan and Scheyer, 2012; Bona
151 and Paulina-Carabajal, 2013; Carabajal et al., 2013; George and Holliday, 2013; Herrera et al.,
152 2013; Holloway et al., 2013; Laab et al., 2017; Paulina-Carabajal et al., 2017; von Baczko and
153 Desojo, 2016; Lautenschlager and Butler, 2016; Jirak and Janacek, 2017; Pierce et al., 2017; and
154 Digimorph) for different turtle, archosauromorph, lepidosauromorph and other amniote taxa (for list
155 of taxa see Table S2). These outlines were redrawn in Adobe Illustrator to ensure sufficient
156 resolution for the digitization process. For PCA, ~~all taxa were each taxon was~~ assigned to a
157 phylogenetic and an ecological (marine, freshwater, terrestrial, fossorial) group. To test for
158 significant differences between those groups, we also conducted a non-parametric MANOVA test
159 (Anderson, 2001) using PC scores representing 95% of total variance transformed into an Euclidean
160 distance matrix, and replicated with 10000 permutations and compared using Bonferroni correction
161 for the post-hoc analyses for test significance of pairwise distances.

163 Results

165 Endocranial anatomy

166 The reconstruction of MB 1910.45.2 (Figures 1A–1D) provided most details of the endocranial
167 anatomy, but exhibited some moderate medio-lateral deformation. In comparison, the
168 reconstruction of SMNS 16980 (Figures 1E–1H) showed no obvious artifacts, but the poor
169 ~~greyscale grayscale~~ contrast permitted only a few structures (i.e., brain, pituitary fossa and some
170 cranial nerves) to be visualized. In combination, both specimens allowed for a detailed
171 reconstruction of most endocranial components.

172 The brain endocast is anteroposteriorly elongate and straight in both specimens, with only
173 moderate cephalic and pontine flexures (Figures 1B, 1F). The endocasts are tubular and
174 mediolaterally narrow without prominent expansion or constriction of the fore-, mid- or hindbrain

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175 regions. The close similarity of these features in both specimens confirms that this morphology is
176 natural and unlikely to be a result of taphonomic deformation. The olfactory nerve (CN I)
177 contributes approximately a third to half of the full endocast's length, but a clear distinction
178 between the base of the olfactory nerve and the cerebral hemispheres is not visible. The olfactory
179 bulbs are only weakly reproduced by the ventral surfaces of the nasals. Cerebral hemispheres or
180 distinct optic lobes are not visible in ~~both-either~~ specimens, suggesting that ~~either-both~~ structures
181 ~~was-were~~ very small and/or that the venous sinus and the dura mater obscured the underlying
182 morphology.

183 The midbrain region is confluent with the forebrain and only weakly demarcated. The only
184 distinguishing feature is a dorsal expansion extending above the level of the olfactory nerve. This
185 dural peak or cartilaginous rider (Zangerl, 1960; Gaffney and Zangerl, 1968; Paulina-Carabajal et
186 al., 2017) is more prominently developed in MB 1910.45.2 (Figure 1B). In SMNS 16980, the dorsal
187 expansion is shallower and somewhat separated from the main body of the midbrain by a bony
188 margin, suggesting that this structure corresponds to the cartilaginous portion of the supraoccipital,
189 which ends abruptly anteriorly in *Proganochelys quenstedti* (Gaffney, 1990). The pituitary fossa is
190 visible in SMNS 16980 and forms a pendant pocket, projecting ventrally from the main body of the
191 midbrain endocast.

192 The hindbrain region is anteroposteriorly short and not constricted mediolaterally between
193 the endosseous labyrinths. Floccular lobes are not visible. Posteriorly, the hindbrain exits the
194 braincase through the foramen magnum, which is oval and wider than high in SMNS 16980 and
195 slightly higher than wide in MB 1910.45.2. The latter may be the result of the mediolateral
196 compression of this specimen.

197 The nasal cavity is very enlarged when compared to the other sampled taxa (Figures 2, 3;
198 Table 1). The strong lateral compression of ~~MB 1910.45.2 the latter specimen~~ may be responsible
199 for the seemingly increased volume, and, hence, we consider the reconstruction of the nasal cavity
200 in SMNS 16980 more reliable. Usually, three portions of the nasal cavity can be identified in turtles
201 and other reptilians (Parsons, 1959, 1970; Halpern, 1992; Paulina-Carabajal et al., 2017): the
202 vestibulum nasi, which connects the nasal chamber to the external nares; the ductus
203 nasopharyngeus, connecting the nasal chamber to the choanae; and the cavum nasi proprium, the
204 chamber itself, bounded anteriorly by the vestibulum, posteroventrally by the ductus, and
205 posterodorsally by the olfactory nerve (CN I). The ductus nasopharyngeus can be distinguished
206 from the rest of the nasal cavity in *P. quenstedti* as two ventrolateral projections (Figure 1). A
207 proper duct ~~was not expected~~ (at least not bounded by bone) ~~was not expected~~, since the choanae in
208 *P. quenstedti* are very extensive, and occupy almost the whole ventral surface of the nasal cavity.

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209 The vestibulum, on the other hand is short, as in most other turtles (Paulina-Carabajal et al., 2017),
210 connected to the large cavum nasi proprium, which constitutes most of the nasal cavity. The cavity
211 as a whole is considerably broad and also high in comparison (Figures 2, 3) to several other taxa
212 (Carabajal et al., 2013; Paulina-Carabajal et al., 2017).

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213 The endosseous labyrinth is reconstructed only for MB 1910.45.2 ~~only~~, as the ~~grey~~-scale
214 attenuation did not allow ~~a~~-differentiation of the ~~respective~~-bony housing in SMNS 16980. It is
215 dorsoventrally compressed and compact. The anterior and posterior semicircular canals are small,
216 ~~and~~ anteroposteriorly longer than high and have low internal radii. The crus communis is also very
217 low in comparison to other taxa (Carabajal et al., 2013; Mautner et al., 2017; Paulina-Carabajal et
218 al., 2017; Ferreira et al., in press) ~~and which~~ results in an almost horizontal orientation of the
219 anterior and posterior semicircular canals (Figure 4). The lateral semicircular canal barely extends
220 ~~medi~~laterally from the vestibulum. The cochlear duct is expanded ventrally, but short. The canal of
221 the fenestra ovalis is clearly visible projecting anterolaterally from the vestibulum.

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222 The proximal portion of the majority of cranial nerves could be reconstructed for MB
223 1910.45.2 (Figure 1), whereas only some of the larger nerve canals are visible in SMNS 16980. The
224 optic nerves (CN II) exit the braincase through two large (3 mm in diameter each) foramina
225 anteriorly and ventrally from the cerebral region of the endocast in MB 1910.45.2. Posterior and
226 lateral to CN II, the oculomotor (CN III) and possibly the trochlear nerve (CN IV) (Gaffney, 1990)
227 originate ventrolaterally. In SMNS 16980, CN II-IV could not be reconstructed. The foramina
228 through which those three cranial nerves (II-IV) exit the braincase are formed by the laterosphenoid
229 (=“pleurosphenoid”) (Gaffney, 1990; Bhullar & Bever, 2009). This is the second *P. quenstedti*
230 specimen with a preserved laterosphenoid, however ~~the fact that this ossification is its~~ severely
231 ~~erushing-crushed refrain leads us to refrain~~ from ~~further~~-commenting ~~further~~ on ~~the-its~~ morphology
232 ~~of this ossification~~. The trigeminal nerve (CN V) is large (ca. 6 mm in diameter) and exits the
233 braincase laterally in both specimens through the prootic foramen. Based on both specimens (as
234 well as other specimens described by Gaffney, 1990) we confirm that this foramen is surrounded
235 exclusively by the prootic bone, contrary to Bhullar & Bever’s (2009) interpretation that the
236 laterosphenoid would form its anterior margin. A separation of the ophthalmic branch (CN V₁) is
237 apparent on the right side in MB 1910.45.2, but this could be ~~the-a~~ result of the high degree of
238 distortion of this specimen.

239 The abducens nerve (CN VI), clearly visible in both specimens, originates from the ventral
240 surface of the endocast. It pierces the basisphenoid through the foramen nervi abducens and enters
241 ~~laterally~~ the pituitary fossa ~~laterally~~, which is bottomed by the sella turcica (Gaffney, 1990).
242 Posterior to CN V, the facial nerve (CN VII) exits the braincase laterally through the prootic. In MB

1910.45.2, a distal branching of CN VII outside the braincase wall is visible, also on the prootic bone. The vestibulocochlear nerves (CN VIII) could not be reconstructed in either specimen. The foramina for the CN VIII branches are usually very small and may lie on cartilaginous structures (Gaffney, 1979), so they are not expected to leave unambiguous traces on fossilized skulls. The glossopharyngeal (CN IX), vagus (CN X) and accessory nerves (CN XI) originate immediately posterior to the endosseous labyrinth and exit the braincase through the anterior jugular foramen in MB 1910.45.2. Although the sutures are not very clear, this foramen is thought to be formed by the exoccipital, basioccipital and opisthotic in *P. quenstedti* (Gaffney, 1990). In SMNS 16980, a large nerve canal originates ~~from in~~ a more dorsolateral position (Figure 1). Due to the low resolution, it is unclear whether this canal represents the anterior jugular foramen or ~~more likely~~ parts of the longitudinal sinus, ~~though the latter is more likely~~. The hypoglossal nerve (CN XII) is transmitted through a single foramen on each side of the basioccipital (posterior to the jugular foramen) in both specimens.

Endocast outline analysis

The morphology of the endocast of *P-Proganochelys quenstedti* was compared to different turtles and other amniote taxa using shape analysis. The PCA results show that the first three PCs account for 71.7% (Table 2) of the brain endocast outline shape variation (Figures 5, 6). In ~~all no~~ PC plots ~~is~~ there ~~is no~~ clear separation between either the phylogenetic or the ecological groups considered. However, the PERMANOVA tests support ~~s significant differences of that~~ Lepidosauromorpha ~~differs significantly~~ from Archosauromorpha ($p = 0.0006$) and from Testudinata ($p = 0.003$) ~~and~~ ~~although these tests find no~~ significant differences between the ecological groups (Table 3). The outgroup *Diadectes* is recovered consistently in a position inside the morphospace occupied by ~~the~~ other groups, whereas *P. quenstedti* is ~~displaced from the occupied area in all plots; however, on the~~ PC1 axis, *Kawingasaurus* is even more displaced ~~on in~~ the positive direction (Figures 5, 6). *P. quenstedti* is distant from other turtles and the minimum spanning-tree (see Supplementary Material) ~~shows a places it~~ closer ~~position~~ to the lepidosauromorphs *Placodus* and *Chalarodon*, and to the archosauromorph *Pseudopalatus*, on the PC1/PC2, PC1/PC3 and PC2/PC3 plots, respectively. ~~Considering~~ ~~With regard to~~ the ecological morphospaces, *P. quenstedti* is similarly found in a position outside ~~of~~ all the groups, except on ~~the~~ PC1/PC3 plot, ~~in on~~ which it is inside the fossorial ~~morphospace~~ and ~~much very~~ close to the terrestrial ~~occupied morphospaces one~~ (Figure 5D).

Discussion

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278 **Ancestral condition for Testudinata**

279 Even though more taxa have been assigned to the turtle stem-lineage recently (Li et al., 2008;
280 Lyson et al., 2010; Schoch and Sues, 2015), *Proganochelys quenstedti* remains one of the most
281 important stem-turtles, given its phylogenetic position as the earliest shelled turtle with a
282 completely preserved skull (Parsons, 1959, 1970; Halpern, 1992; Joyce et al., 2016). Its endocast is
283 a relatively simple structure when compared to that of crown-turtles (Carabajal et al., 2013;
284 Mautner et al., 2017; Paulina-Carabajal et al., 2017; Ferreira et al., in press). It has a tube-like
285 shape, with only small pontine and cephalic flexures and poorly differentiated brain regions. As in
286 other amniotes, the portion between the fore- and midbrain is the most voluminous, but this is
287 achieved exclusively by an increase in height, since ~~the endocast its width~~ is nearly constant in
288 width as long as the over its entire endocast length (Figure 1). Another striking feature is the pendant
289 pituitary fossa, which is very common in archosaurs (Witmer et al., 2008; Lautenschlager and
290 Butler, 2016; Araújo et al., 2017; Pierce et al., 2017), but does not occur in extant turtles, in which
291 the dorsum sellae and the sella turcica are aligned, positioning the pituitary fossa approximately at
292 the same level as the posterior portions of the endocast (Figures 2, 3). Although the pituitary fossa
293 of turtles can also house other smaller structures (e.g., internal carotid and abducens nerve) the size
294 of the pituitary gland should be at least partially responsible for ~~a the~~ larger size of the fossa in *P.*
295 *quenstedti*. A similar condition was found for sauropod and theropod dinosaurs (Witmer et al.,
296 2008), in which enlarged pituitary glands have been linked to larger body sizes (Edinger, 1942).
297 While *P. quenstedti* reached a carapace length size of at least 67 cm ~~of carapace length~~ (based on
298 MB 1910.45.2) (Gaffney, 1990), it was not one of the largest turtles, being much smaller than some
299 extant turtles (e.g., up to 150-200 cm in *Chelonia mydas* and *Pelochelys cantorii*) (Angielczyk et
300 al., 2015) and meiolanids (Gaffney, 1996). Turtles included in our sample ~~with that are~~ comparable
301 in size to *P. quenstedti*, such as *Podocnemis unifilis* and *Macrochelys temminckii* (up to 68 and 66
302 cm of carapace length) (Angielczyk et al., 2015), and also *Chelonia mydas*, do not show a pendant
303 pituitary fossa (Figures 2, 3). An alternative explanation is that it is not the pituitary fossa that is
304 larger in *P. quenstedti*, but rather the brain that was comparatively smaller. Indeed, in our sample,
305 this taxon has the lowest value for the ratio endocast volume/basicranial length (Table 1),
306 supporting the hypothesis that the brain increased in size during turtle evolution.

307 The brain endocast in turtles does not seem to be consistent with general skull anatomy.
308 Taxa with higher/lower and wider/thinner endocasts do not possess similar skull proportions,
309 which, ~~on the contrary,~~ seems more related to the size and shape of the adductor chamber and the
310 associated supraoccipital and squamosal crests (Figure 7). Proportional changes observed in the

311 adductor chamber throughout the turtle lineage rather reflect the distinct volume and size of the
312 external jaw adductor musculature in different taxa (Claude et al., 2004; Foth and Joyce, 2016; Foth
313 et al., 2017; Ferreira and Werneburg, in press). Also, the position of the exits of the cranial nerves
314 ~~change~~ only slightly ~~change~~, even with profound changes in the arrangement of related structures
315 such as ~~the eyes position~~ and ~~muscles anatomy~~. For example, in *P. quenstedti* the external jaw
316 adductor musculature innervated by the trigeminal nerve (CN V₃) is vertically oriented and entirely
317 positioned anteriorly to the quadrate (Ferreira and Werneburg, in press), while in crown-turtles it
318 extends far posteriorly, following the enlargement of the supraoccipital and squamosal crests
319 (Poglayen-Neuwall, 1953; Werneburg, 2011, 2013). However, the relative position of the exit of
320 CN V remains roughly the same through turtle evolution when compared to the remainder of the
321 endocast and the surrounding bones (Figure 7). Hence, the actual change that occurs when the
322 muscles expand posteriorly involves only ~~a~~ growth and reorientation of distal V₃-branches and not
323 a repositioning of the trigeminal nerve foramen (Poglayen-Neuwall, 1953; Schumacher, 1973).

324

325 **Sensory capabilities of *Proganochelys***

326 The endosseous labyrinth of *Proganochelys quenstedti* is slightly distinct from that of crown-turtles
327 in being more compact and robust, with short and thick semicircular canals and a low crus
328 communis resulting in almost horizontally oriented canals (Figure 4). The anterior and posterior
329 semicircular canals (ASC and PSC, respectively) are nearly at the same level as the lateral
330 semicircular canal (LSC), whereas in other turtles the ~~former-first~~ two run dorsally in relation to the
331 ~~latter-last~~ (Carabajal et al., 2013; Mautner et al., 2017; Paulina-Carabajal et al., 2017; Ferreira et al.,
332 in press). The angle between ~~the~~ ASC and LSC is also very wide (Table 1), with similar values to
333 meiolaniids and tortoises (Paulina-Carabajal et al., 2017). This combination of features suggests
334 that the semicircular canals of *P. quenstedti* were not very sensitive during movements ~~along-within~~
335 the sagittal (head moving up and down) and coronal planes (head tilt) (Brichta et al., 1988; Spoor et
336 al., 2007; David et al., 2010). Instead, the LSC was likely more effective in stabilizing gaze during
337 yaw movements (head moving left and right). Thus, the labyrinth anatomy of *P. quenstedti*
338 indicates ~~it-as~~ ~~this species was~~ slow and non-agile (Spoor et al., 2007; David et al., 2010),
339 compatible with a highly terrestrial and possibly fossorial lifestyle. This is also tentatively indicated
340 by ~~the-its position in~~ morphospace ~~occupation~~ outside of, but close to, a terrestrial and fossorial
341 ~~habitat-groupings~~ in the shape analysis (Figure 6).

342 Although *P. quenstedti* cervical vertebrae were capable of ~~a~~ certain level of mobility
343 (Werneburg et al., 2015a), its short neck coupled with ~~the~~ relatively low carapace, strong
344 osteoderms on the dorsal neck surface and cervical ribs (Gaffney, 1990) imply restricted mobility

345 along the same planes (sagittal and coronal) (Werneburg et al., 2015a, 2015b) as indicated by its
346 labyrinth morphology. Crown-turtles, however, evolved longer necks and several taxa are capable
347 of complex and, sometimes, very fast neck and head movements (Poglayen-Neuwall, 1953; Herrel
348 et al., 2008; Werneburg et al., 2015a, 2015b). This could be related to the apparent increase in size
349 of the semicircular canals in crown-turtles (Spoor, 2003; Spoor et al., 2007) when compared to
350 those of *P. quenstedti* (although when compared to more agile reptiles, all turtles possess short
351 canals; Witmer et al., 2008).

352 Hearing was likely not well-developed in *P. quenstedti*, given the small overall size of the
353 endosseous cochlear duct (Walsh et al., 2009) in comparison to other turtles. Even though its
354 quadrate does not form the characteristic lateral round structure that encloses the cavum tympani in
355 crown-turtles (Figures 4F–H), it possibly had a tympanic ear, similar to those of extant squamates
356 and cheloniids, in which ~~it~~ the tympanum is supported by both bone and connective tissue (Henson,
357 1974; Gaffney, 1990). However, the stapes of *P. quenstedti* was much stouter than that of crown-
358 turtles (Figures 4D, E), and possibly articulated with the quadrate (Gaffney, 1990), suggesting that
359 it was not as effective as the thin vibratory element characteristic of extant amniotes with tympanic
360 hearing, including modern turtles (Baird, 1970; Clack, 1997). As proposed by Clack (1997) for
361 diapsids, ~~the~~ elongation of the paraoccipital process of the opisthotic and its tight ~~suture-suturing~~ to
362 the squamosal, ~~that~~ which occurred in the group including all testudinales but *Proganochelys*
363 *quenstedti* (Sterli et al., 2010), may have completely released the stapes from its ancestral structural
364 function (connecting the quadrate to other elements of the braincase) during turtle evolution.

365 The nasal cavity of *P. quenstedti* represents at least 42.2% of the total endocast volume
366 (Table 1), fitting in the volume spectrum of terrestrial turtle taxa, which ranges from 29–43% in
367 tortoises and 58.5–64% in meiolaniids (Carabajal et al., 2013). Larger nasal cavities have been
368 related to occupation of arid environments, thermoregulation, sound-production or higher olfactory
369 capabilities (Parsons, 1959, 1970; Paulina-Carabajal et al., 2017). In *P. quenstedti*, the cavum nasi
370 proprium represents most of the volume of the nasal cavity and extends far dorsally and posteriorly.
371 ~~Within the nasal cavity, Sensory-sensory~~ epithelium ~~on the nasal cavity~~ occurs only on the cavum
372 walls (Parsons, 1970), and, as such, ~~its~~ the cavum's relative size could be used as a proxy for
373 inferences ~~on~~ about olfactory capability in extinct reptiles. This connection, however, should be
374 ~~taken-interpreted~~ cautiously, due to ~~its~~ the possible relation ~~between cavum size and~~ other
375 functions, such as thermoregulation or vocalization (Bourke et al., 2014; Paulina-Carabajal et al.,
376 2017).

377 The size and volume of the olfactory bulbs have been shown to be related to a greater
378 reliance on the olfactory sense in mammals and birds (Bang, 1971; Bang & Wenzel, 1985; Healy

379 and Guilford, 1990; Gittleman, 1991). In a series of studies the olfactory ratio (ratio between
380 olfactory bulb and cerebral hemisphere maximum diameters; OR values) were used as a proxy to
381 study ~~the~~ olfactory acuity and capacity in theropod dinosaurs (including birds) and crocodylians
382 (Zelenitsky et al., 2009, 2011). More recently this has also been applied ~~for~~ to turtles (Paulina-
383 Carabajal et al., 2017), showing that tortoises and meiolaniids (both terrestrial taxa) ~~show~~ have the
384 highest OR values (36-62% and 20-45%, respectively). Even though OR may not be an exact
385 measure of olfactory acuity it is currently the best available proxy and its use for a variety of
386 reptilian taxa (Zelenitsky et al., 2009, 2011; Paulina-Carabajal et al., 2017) makes it a useful
387 ~~comparable-comparative~~ metric. Here, we show that the OR is even higher in *P. quenstedti*,
388 between 57-62% (Table 1), but in this case, these values may be also related to the less-developed
389 cerebral hemispheres rather than to larger olfactory bulbs. Nevertheless, ~~its~~ the large nasal cavity in
390 association with the high OR values supports our hypothesis that ~~the~~ olfaction was possibly the
391 most developed sense in *P. quenstedti*.

392

393 **Evolution of the turtle brain endocast**

394 ~~As demonstrated by the results of~~ In the shape analysis, *Proganochelys quenstedti* is not contained
395 in the morphospace occupied by any of the considered phylogenetic groups (Figure 5). There is
396 extensive overlap in the PCA plots, but, at the same time, the PERMANOVA test shows a
397 separation between Lepidosauromorpha, Testudinata and Archosauromorpha (Table 3). These
398 results suggest that all amniotes (excluding dinosaurs and mammals) share a similar plesiomorphic
399 brain endocast morphology, but that those lineages evolved in different directions in the
400 morphospace.

401 Comparing general ecological groups (freshwater, marine, terrestrial and fossorial) provided
402 similar results, with extensive overlap among the occupied morphospaces (Figure 6). *P. quenstedti*
403 is contained in the morphospace occupied by the fossorial group ~~considering-on~~ the PC1/PC3 plot,
404 but it falls outside every group on the other plots. Additionally, the statistical tests do not support
405 significant differences between any of the considered groups (Table 3). On the other hand, the
406 minimum spanning trees (see Supplementary Material) show that even when inside the fossorial
407 morphospace *P. quenstedti* is ~~closer~~ closest to *Placodus*, a marine lepidosauromorph, and
408 *Pseudopalatus*, an aquatic archosauromorph. A phylogenetic proximity to Sauropterygia (the
409 lepidosauromorph lineage that includes *Placodus*) has been proposed previously (deBraga and
410 Rieppel, 1997) and is associated ~~to~~ with the hypothesis that turtles originated in marine
411 environments (Joyce and Gauthier, 2004; Joyce, 2015). The proximity of *P. quenstedti* and
412 *Placodus* in our PC1/PC2 plot (Figure 6) may recall this hypothesis, but the poor sampling of

413 sauropterygians together with the extensive overlap between all groups (phylogenetic and
414 ecological) ~~cause us to refrain us~~ from considering this a robust interpretation.

415 The shape analysis presented here is the first attempt to explore the evolution of
416 neuroanatomy in amniotes with a quantitative approach. Even though our results do not support
417 inferences about lifestyles from neuroanatomical data, the significant separation ~~of-between~~ some of
418 the considered phylogenetic groups (Figure 5, Table 3) seems promising. We can identify some
419 caveats in our sample (e.g., few marine reptiles, synapsids and early amniotes) that can be easily
420 overcome with the increasing use of computer tomography in paleontological and anatomical
421 studies. Our approach using sagittal cross-section outlines could have also influenced the results,
422 since there is a loss of information when the 3D endocast is simplified to a 2D outline.

423 More recently, Lyson et al. (2016) thoroughly analyzed the morphology of *Eumotosaurus*
424 *africanus*, identifying some osteological correlates that led them to conclude that it was likely well-
425 adapted for fossoriality. The authors also identified some of those correlates (e.g., large claws) in
426 other proto- (e.g., *Odontochelys semitestacea*) and stem-turtles (*Proganochelys quenstedti* and
427 *Palaeochersis talampayensis*), concluding that “fossoriality played an important role in the early
428 evolution of turtles” (Lyson et al., 2016). Although in the PC1/PC3 plot (Figure 6) *P. quenstedti* is
429 contained in the fossorial morphospace, the minimum spanning tree (see Supplementary Material)
430 shows it ~~to be closest~~ to the terrestrial non-fossorial taxon *Chalarodon* and the statistical analyses
431 do not support any significant differences between the considered groups (Table 3). While the shape
432 analyses do not shed light on this problem conclusively, other sources of data are more convincing.
433 *Proganochelys quenstedti* fossils were found in ~~terrestrial-continental~~ deposits (Gaffney, 1990) and
434 analyses of forelimb proportions (Joyce and Gauthier, 2004) and paleohistology (Scheyer and
435 Sander, 2007) support it as a terrestrial turtle. The morphology of its endosseous labyrinth with
436 short semicircular canals oriented ~~with-at~~ high angles to each other and the large cavum nasi
437 proprium (Parsons, 1970; David et al., 2010; Paulina-Carabajal et al., 2017) agrees with these
438 previous studies, strongly supporting ~~the interpretation~~ that *P. quenstedti* was a well-adapted
439 terrestrial turtle. However, since its vestibule is not particularly large, in contrast to the condition of
440 truly fossorial taxa (Yi and Norell, 2015) or of the semi-fossorial tortoise *Gopherus* (Paulina-
441 Carabajal et al., 2017), ~~we conclude the present data suggest it that it~~ was likely not a fossorial
442 taxon. In *P. quenstedti*, ~~the seemingly the relatively enlarged~~ vestibule ~~in comparison to the other~~
443 ~~turtles in this study~~ results from the relatively small semicircular canals. Thus, even if fossoriality
444 had an important role during the early evolution of shell components (Lyson et al., 2016), our data
445 suggests the complete turtle shell first appeared ~~eds~~ in a terrestrial ~~taxon, with no evident link to~~
446 ~~fossoriality but most likely not fossorial turtle (i.e.,~~ at the Testudinata node).

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447 If we assume that the relatively simple morphology of *P. quenstedti* ~~more~~ closely resembles
448 that of the testudinate ancestors, some trends can be inferred for the evolution of endocranial
449 structures in turtles. An increase in overall encephalization, for example, with longer and more
450 voluminous endocasts in relation to skull length is found already in the stem-turtle *Naomichelys*
451 *speciosa* and ~~is extended~~ continues in crown-turtles (Figures 2, 3). Some regions became more
452 pronounced as well. In *N. speciosa*, meiolaniids (Paulina-Carabajal et al., 2017), ~~as well as~~
453 *Plesiochelys etalloni* (Carabajal et al., 2013) and all other crown-turtles (Mautner et al., 2017;
454 Ferreira et al., in press) the cerebral hemispheres are clearly distinguishable from the remainder of
455 the endocast and ~~they~~ are wider in relation to skull and endocast length ~~when compared to~~ than in *P.*
456 *quenstedti* (Figures 2, 3). The olfactory bulb can also be seen in the endocasts of some taxa, e.g.,
457 *Testudo graeca* and *Plesiochelys etalloni* (Carabajal et al., 2013; Paulina-Carabajal et al., 2017).
458 However, this does not seem to be a general trend but rather one of the features that show
459 noteworthy variations among crown-turtles, as are the degree of development of the cephalic and
460 pontine inflexions and the sizes of the nasal cavity and the orbits. Considering that the brain of *P.*
461 *quenstedti* was a simple tube-like structure with poorly differentiated regions, an increase in size
462 and in regionalization of the brain took place later during the course of turtle evolution, similarly
463 (although in a much lesser degree) to the trend observed during bird evolution (Balanoff et al.,
464 2013), and achieved an endocast diversity comparable to other groups of amniotes, such as
465 lepidosaurs and archosaurs (excluding dinosaurs; Figures 5, 6). Indeed, extant turtles possess high
466 brain weights in relation to body weight, comparable to that of crocodiles (Gürtürkün et al. 2016),
467 but that was not the ancestral condition of the group based on our analyses. ~~Given the recurrent~~
468 results of phylogenetic analyses suggesting that turtles have parareptilian affinity ~~of turtles~~ (e.g.,
469 Laurin and Piñeiro, 2017), it is important to sample the endocast diversity in that clade and explore
470 the similarities between turtles and all other reptilian lineages. The simpler brain structure together
471 with the large nasal cavity and nearly horizontal and short semicircular canals of the inner ear
472 supports a picture of *P. quenstedti* as a terrestrial but most likely not fossorial turtle, with likely
473 mediocre hearing and vision, but a well-developed olfactory sense.

474
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482 [manuscript.](#)

483
484 **Author contribution statement.** Author contributions. S.L. and I.W. conceived and designed the
485 study, S.L. performed the three-dimensional reconstruction, I.W. provided digital datasets, S.L.,
486 G.S.F. and I.W. collected, analyzed and interpreted the data. S.L. and G.S.F. created figures and
487 supplementary data. S.L., G.S.F. and I.W. contributed equally to the discussion, preparation and
488 writing of the paper.

489
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738 **Tables**

739 **Table 1. Measurements and ratios for sampled taxa.** ASC-PSC, angle between anterior and
 740 posterior semicircular canals; BL, basicranial length; CE/BL, cubic root of endocast
 741 volume/basicranial length; CE/SL, cubic root of endocast volume/skull length; EV, endocast
 742 volume; NV, nasal cavity volume; N/E, nasal cavity/endocast volume ratio; OR, olfactory ratio; SL,
 743 skull length.

Taxon	Specimen ID	SL [mm]	BL [mm]	EV [mm³]	NV [mm³]	N/E	CE/SL	CE/BL	OR [%]	ASC-PSC
<i>Proganochelys</i>	MB1910.45.2	175	148.75	8170.84	12209.34	1.49	11.51	13.54	62.5	107°
<i>Proganochelys</i>	SMNS 16980	97	85.36	3790.56	3709.39	0.98	16.07	18.27	57.14	-
<i>Naomichelys</i>	FMNH PR273	117	103.50	9805.97	4077.77	0.42	18.29	20.68	15-19	79°
<i>Podocnemis</i>	SMF 55470	67	51.32	1732.45	531.57	0.31	17.93	23.40	13.39	81°
<i>Chelodina</i>	ZMB H 49659	36	36.00	760.10	140.84	0.18	25.35	25.35	11.34	98°
<i>Chelonia</i>	ZMB 37416 MS	112	80.64	7077.93	2667.23	0.38	17.14	23.81	31.65	94°
<i>Macrochelys</i>	GPIT/RE/10801	120	105.88	9583.53	3568.33	0.37	17.70	20.06	38.18	88°
<i>Platysternon</i>	SMF 69684	60	46.43	898.13	314.33	0.35	16.08	20.78	28.23	82°
<i>Malacochersus</i>	SMF 58702	35	40.92	1364.13	669.45	0.49	31.69	27.11	16.06	86°
<i>Emys</i>	WGJ 1987a	31	30.42	668.07	118.54	0.18	28.20	28.74	17.31	102°
<i>Emydura</i>	PIMUZ 2009.37	35	35.00	1556.29	160.65	0.10	33.11	33.11	9.80	90°
<i>Pelodiscus</i>	IWS76-2	59	39.48	707.23	444.09	0.63	15.10	22.57	20.25	79°

744

745

746 **Table 2.** Summary of the results of the principal component analyses of the brain outlines of
747 different turtles specimens of turtles and other groups. Summary of the results of the Principal
748 Component Analyses.

PC	Eigenvalue	% variance	% cumulative variance
1	0.01042	41.4	41.4
2	0.00464	18.5	59.9
3	0.00298	11.8	71.7
4	0.00174	6.9	78.7
5	0.00137	5.5	84.1
6	0.00093	3.7	87.8
7	0.00067	2.6	90.5
8	0.00042	1.7	92.1
9	0.00032	1.3	93.4
10	0.00028	1.1	94.5
11	0.00021	0.8	95.4

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In review

751 **Table 3.** Results of one-way PERMANOVA test (10000 permutations) with 95% of variance (PC1-
 752 PC11), excluding *Proganochelys* and *Diadectes* (for phylogenetic groups only).

Phylogenetic groups			
Permutation N	10000		
Total sum of squares (SQ)	1,901		
Within-group SQ	1,599		
F	3,653		
p	1.00E-01		
	Testudinata	Archosauromorpha	Lepidosauromorpha
Testudinata			
Archosauromorpha	0.8423		
Lepidosauromorpha	0.003	0.0005999	
Synapsida	0.327	0.1056	0.4488
Ecological groups			
Permutation N	10000		
Total SQ	77		
Within-group SQ	72		
F	1		
p	0.1656		
	Terrestrial	Aquatic	Marine
Terrestrial			
Aquatic	1		
Marine	0.252	1	
Fossorial	0.6485	1	0.8387

753

754

755 **Figures**

756 **Figure 1. Endocranial anatomy of *Proganochelys quenstedti* specimens (A-D) MB 1910.45.2**
 757 **and (E-H) SMNS 16980.** Endocast and nasal cavity (A, B) *in situ* in left lateral oblique view with
 758 bone rendered semi-transparent and isolated endocast in (B, F) left lateral, (C, G) dorsal and (D, H)
 759 ventral views. Abbreviations: car, carotid artery; [duc. ductus nasopharyngeus](#); dur, dural peak;
 760 endo, brain endocast; lab, endosseous labyrinth; nas, endocast of nasal cavity; pit, pituitary fossa; I,
 761 olfactory nerve; II, optic nerve canal; oculomotor nerve canal; IV, trochlear nerve canal; V,
 762 trigeminal nerve canal; VI, abducens nerve canal; VII, facial nerve canal; IX-XI shared canal for the
 763 glossopharyngeal, vagus and spinal accessory nerve; XII, hypoglossal nerve canal.

764

765 **Figure 2. Comparative endocranial anatomy of different stem-Testudines and pleurodiran**
766 **taxa.** Original reconstructions and redrawn endocasts (*Plesiobaena antiqua* from Gaffney, 1982;
767 *Meiolania platyceps* from Paulina-Carabajal et al., 2017; *Yuraramirim montealtensis* from Ferreira
768 et al., in press) in left lateral view. Topology based on Joyce et al. (2016), Guillon et al. (2012) and
769 Ferreira et al. (in press). Heat mapping on branches based on the ratio (CE/BL) between cubic root
770 of endocast volume and basicranial length (Table 1).

771

772 **Figure 3. Comparative endocranial anatomy of different pan-cryptodiran taxa.** Original
773 reconstructions and redrawn endocasts (*Plesiochelys etalloni* from Carabajal et al., 2013; *Gopherus*
774 *berlandieri* from Paulina-Carabajal et al., 2017) in left lateral view. Topology based on Joyce et al.
775 (2016), and Guillon et al. (2012). Heat mapping on branches based on the ratio (CE/BL) between
776 cubic root of endocast volume and basicranial length (Table 1).

777

778 **Figure 4. Inner ear and otic region anatomy of *Proganochelys quenstedti*.** Digital reconstruction
779 of the right endosseus labyrinth of *P. quenstedti* in (A) right lateral, (B) dorsal, and (C) anterior
780 views. Skulls of (D) *P. quenstedti* and (E) *Eubaena cephalica* in posterior view, redrawn from
781 Gaffney (1990) with opisthotic and stapes colored in green and blue, respectively. Skulls of (F)
782 *Sphenodon punctatus*, (G) *Emydura macquarii*, and (H) *P. quenstedti* in lateral view, redrawn from
783 Ferreira & Werneburg (in press), with quadrate colored in red. Note the larger proportions of the
784 stapes and its contact with the quadrate bone in *P. quenstedti*, and its slender and tall quadrate,
785 similar to that of *S. punctatus*, and distinct from the round one of other turtles, ~~that~~ which
786 completely encloses the tympanic membrane. Abbreviations: asc, anterior semicircular canal; cc,
787 crus communis; ex, exoccipital; fo, fenestra ovalis; lsc, lateral semicircular canal; pa, parietal; psc,
788 posterior semicircular canal; qu, quadrate; sq, squamosal; ves, vestibulum.

789

790 **Figure 5. Two dimensional morphospace plots of brain endocast outlines based on the first**
791 **three PC axes** using a priori defined phylogenetic groups. *Diadectes* is shown as a black cross,
792 *Proganochelys quenstedti* (SMNS 16980) in bold. The symbols are used to identify the clade to
793 which a point was assigned. Different vertebrate groups are indicated by convex hulls.

794

795 **Figure 6. Two dimensional morphospace plots of brain endocast outlines based on the first**
796 **three PC axes** using a priori defined ecological groups. *Diadectes* is shown as a black cross,
797 *Proganochelys quenstedti* (SMNS 16980) in bold. The symbols are used to identify the clade to
798 which a point was assigned. Different vertebrate groups are indicated by convex hulls.

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800 **Figure 7.** Overall skull shape and ~~proportional~~ relation to cranial structures in different turtle taxa.
801 Brain endocast and adductor chamber plotted in left lateral (first and third rows) and dorsal (second
802 and fourth rows) views. Note the similar position of the trigeminal nerve exit regardless of ~~the~~
803 changes in surrounding structures.

In review

Figure 1.JPEG

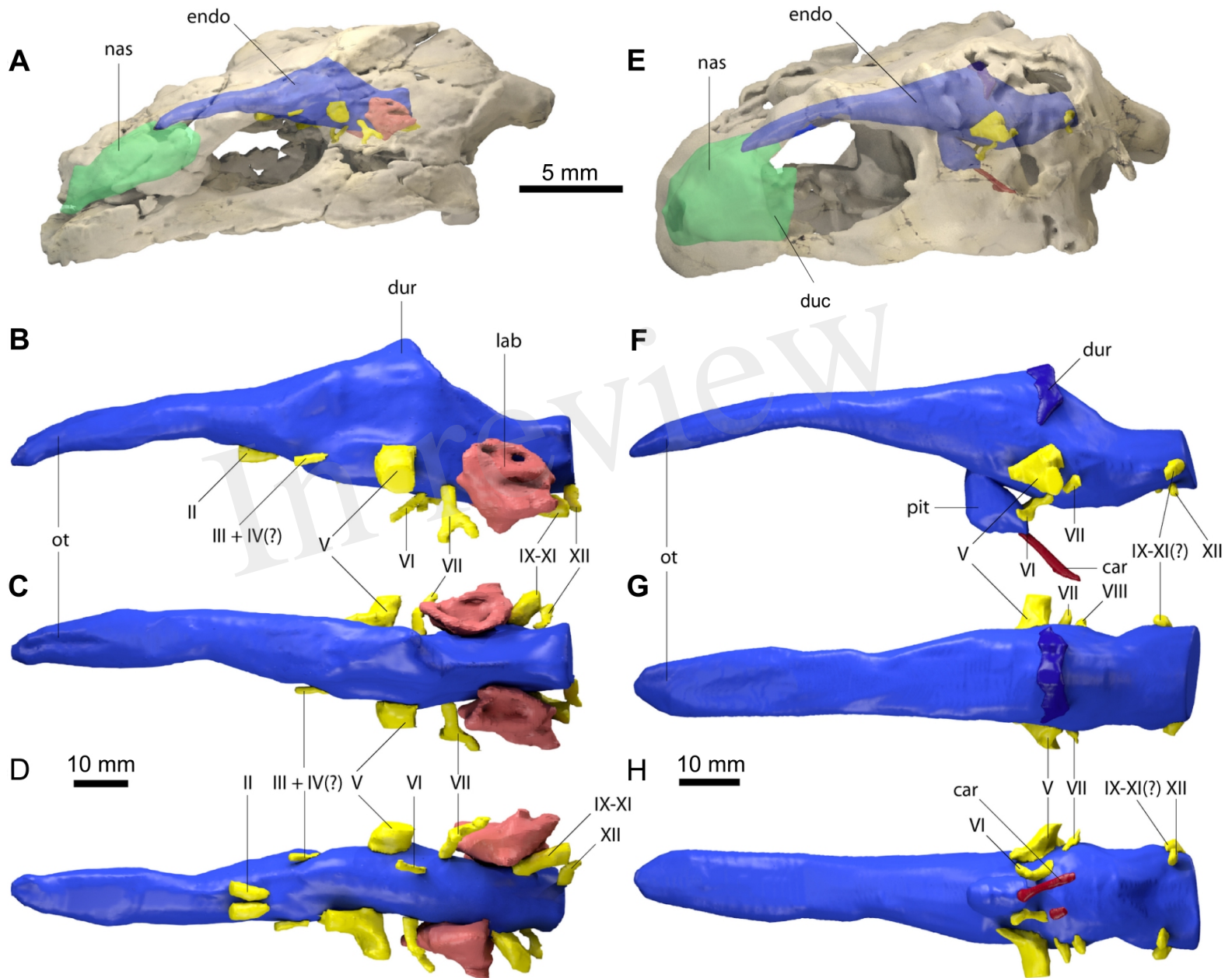
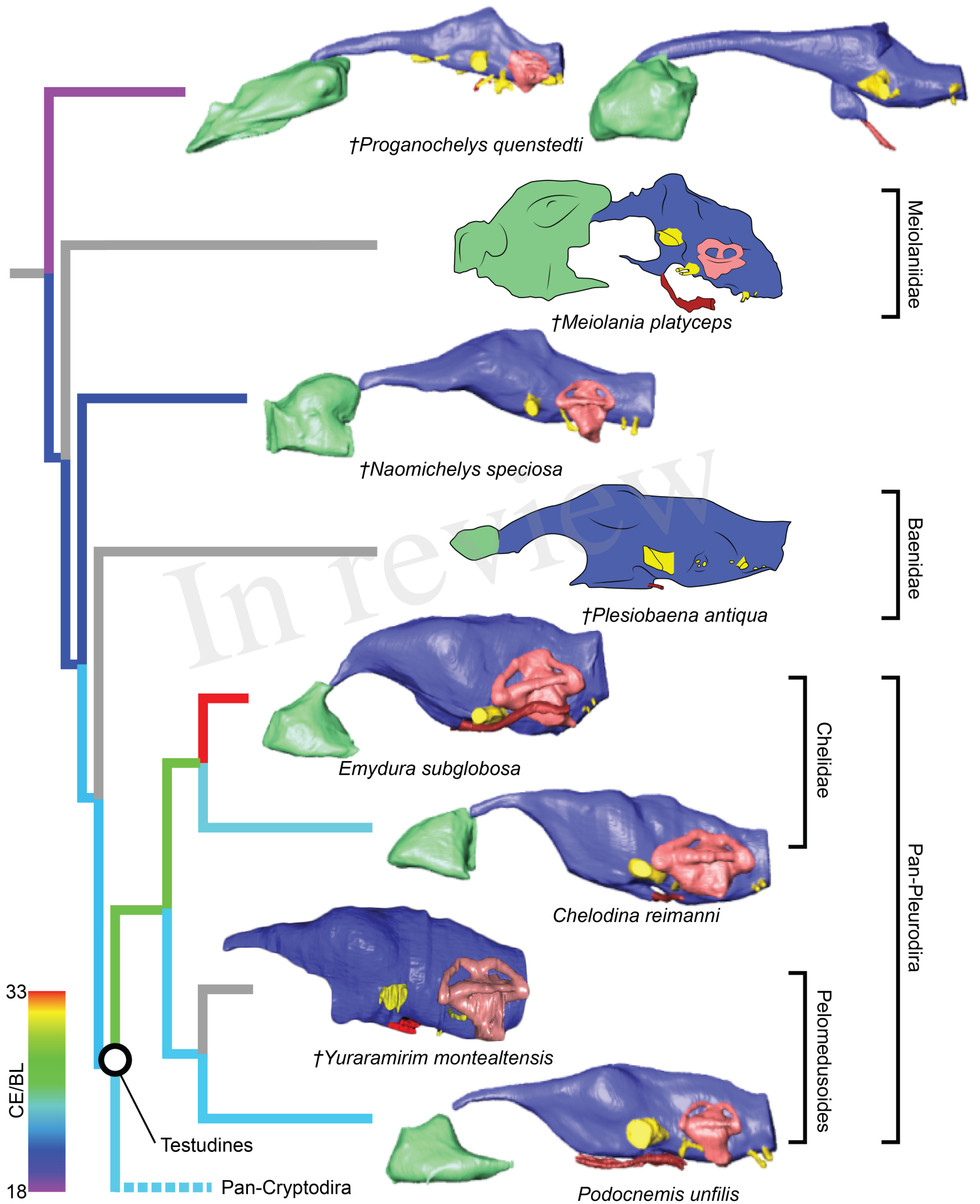
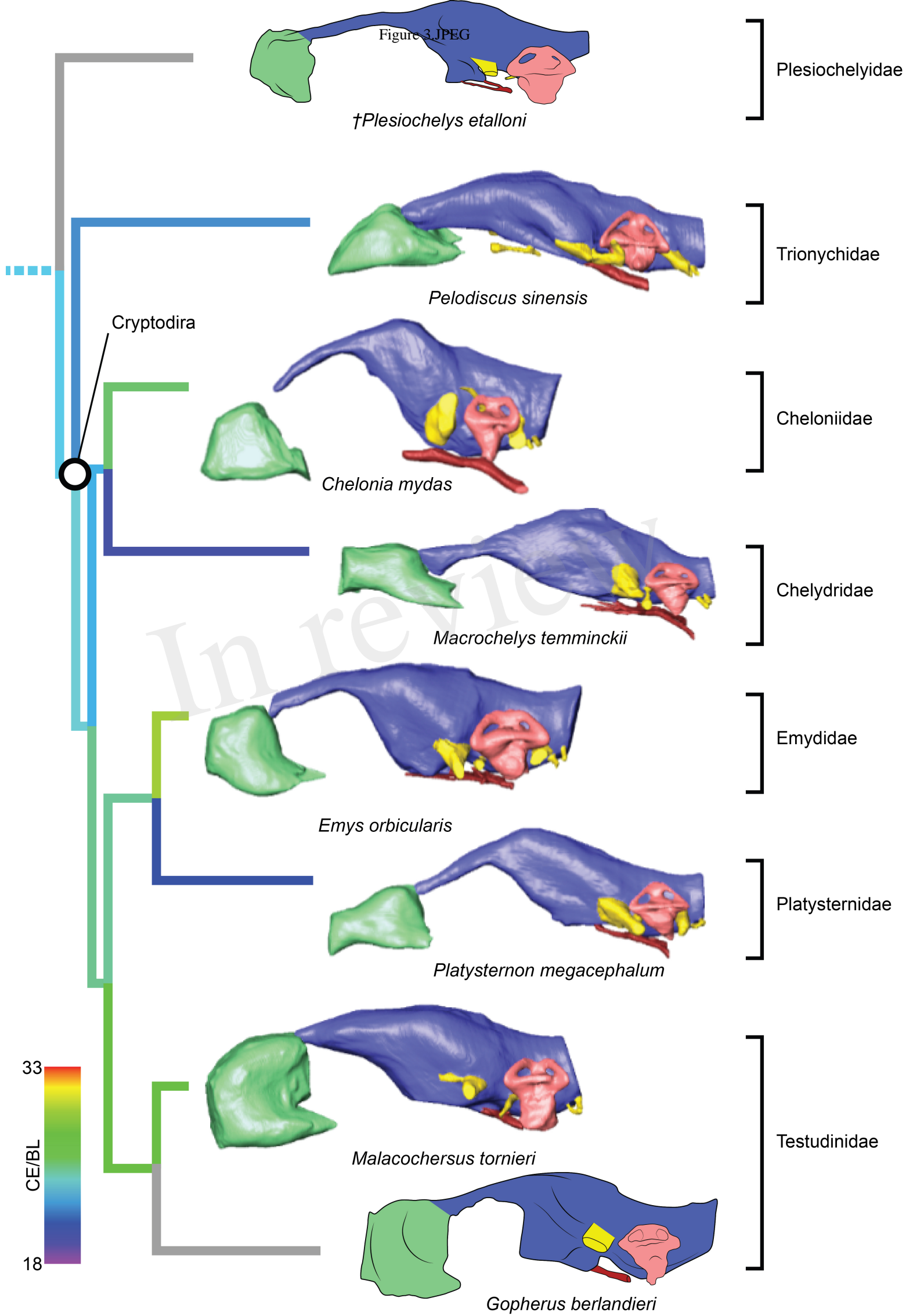
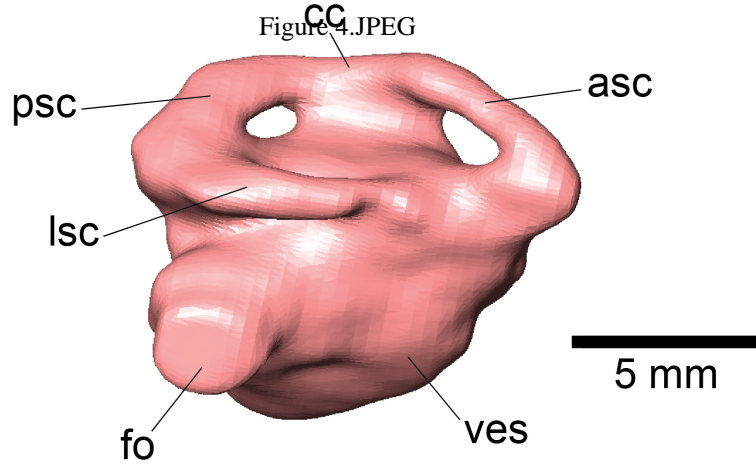
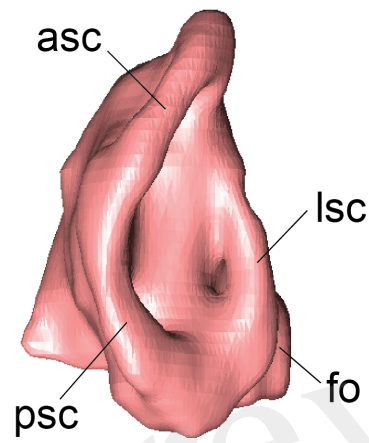
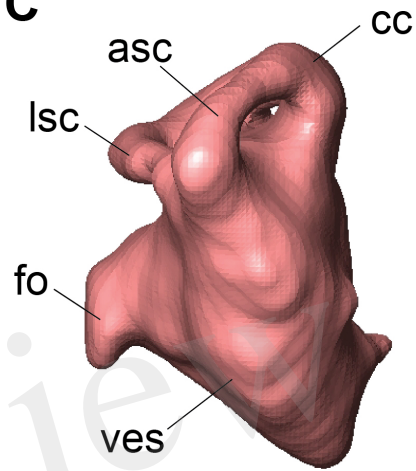
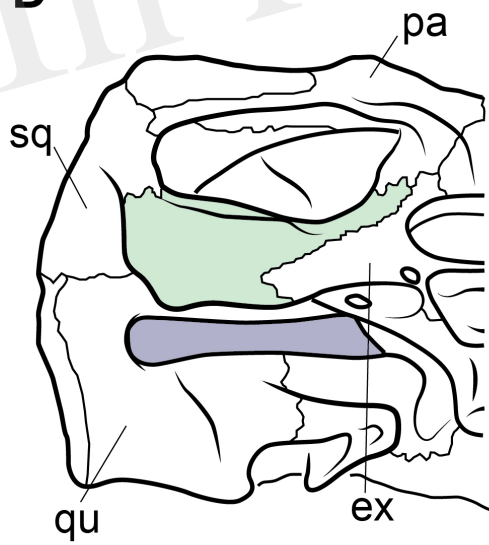
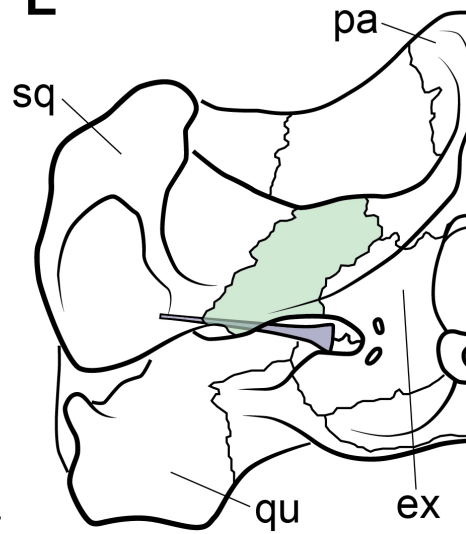
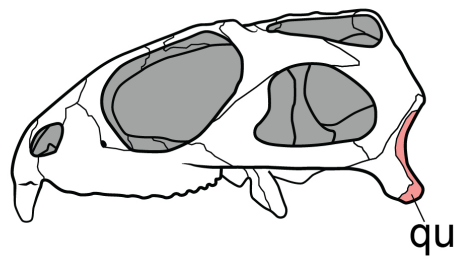
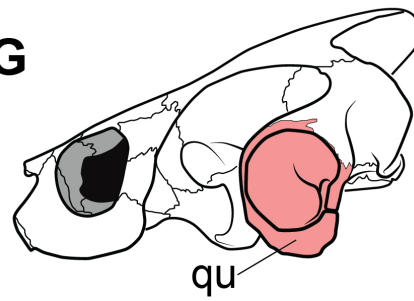
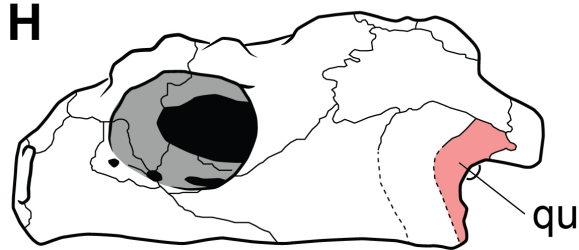
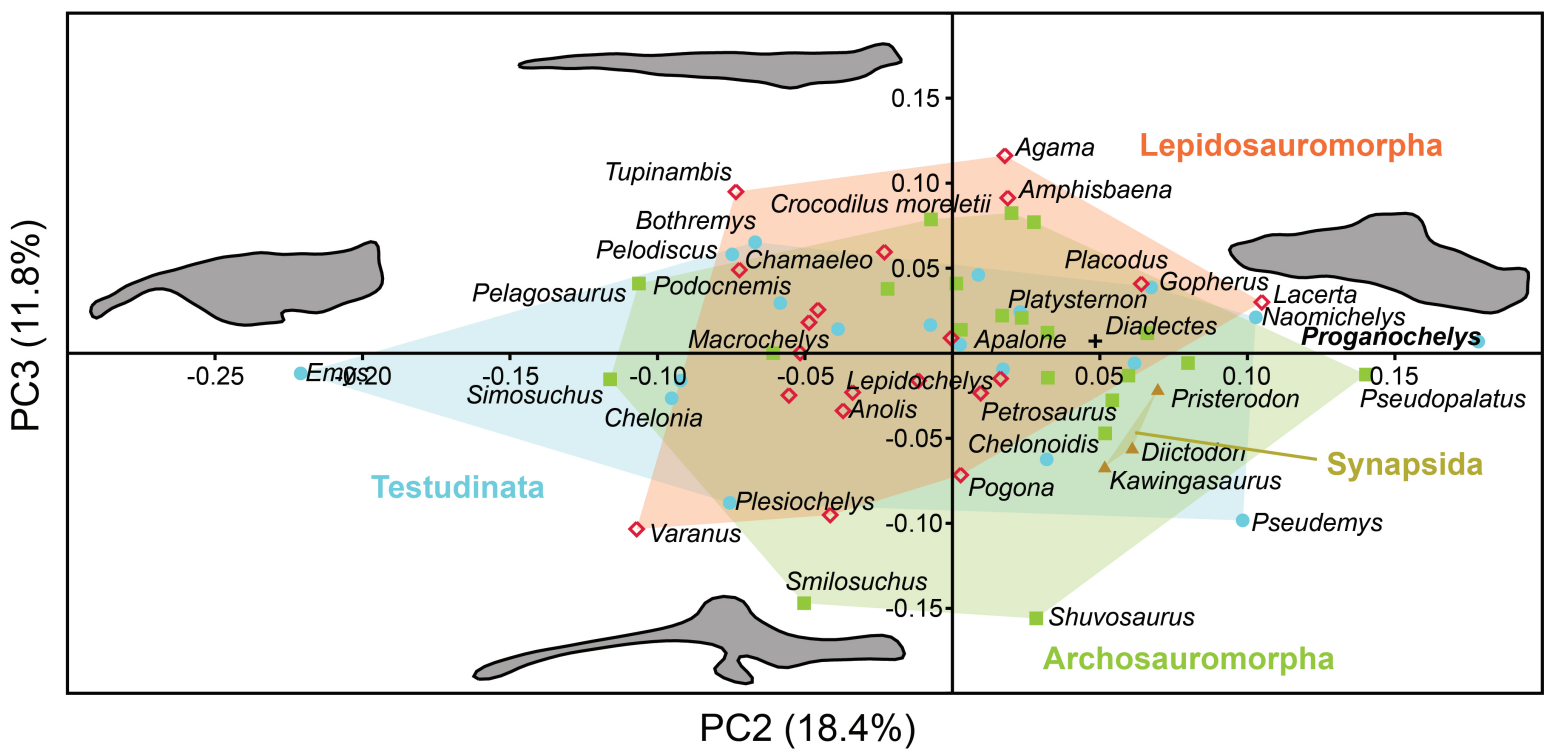
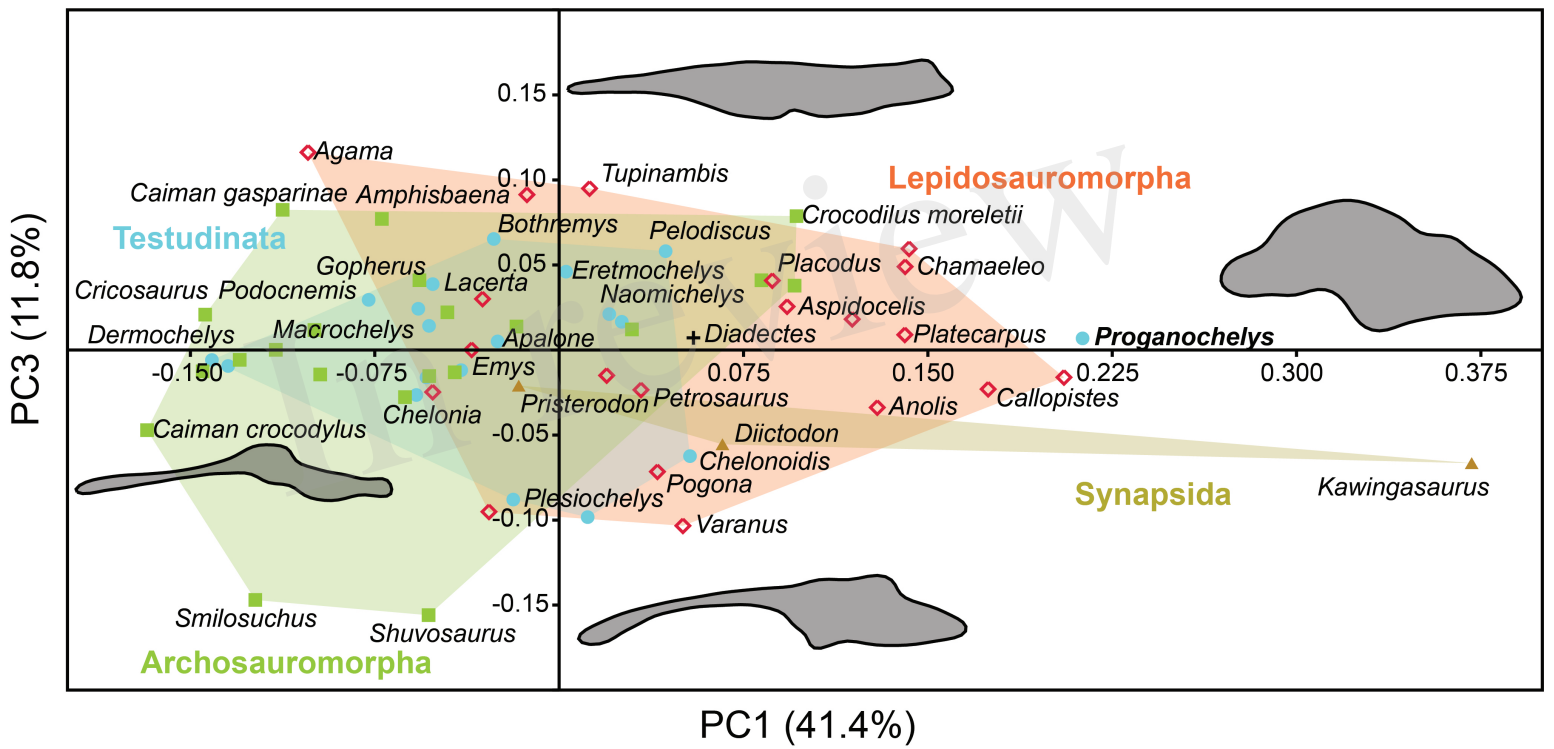
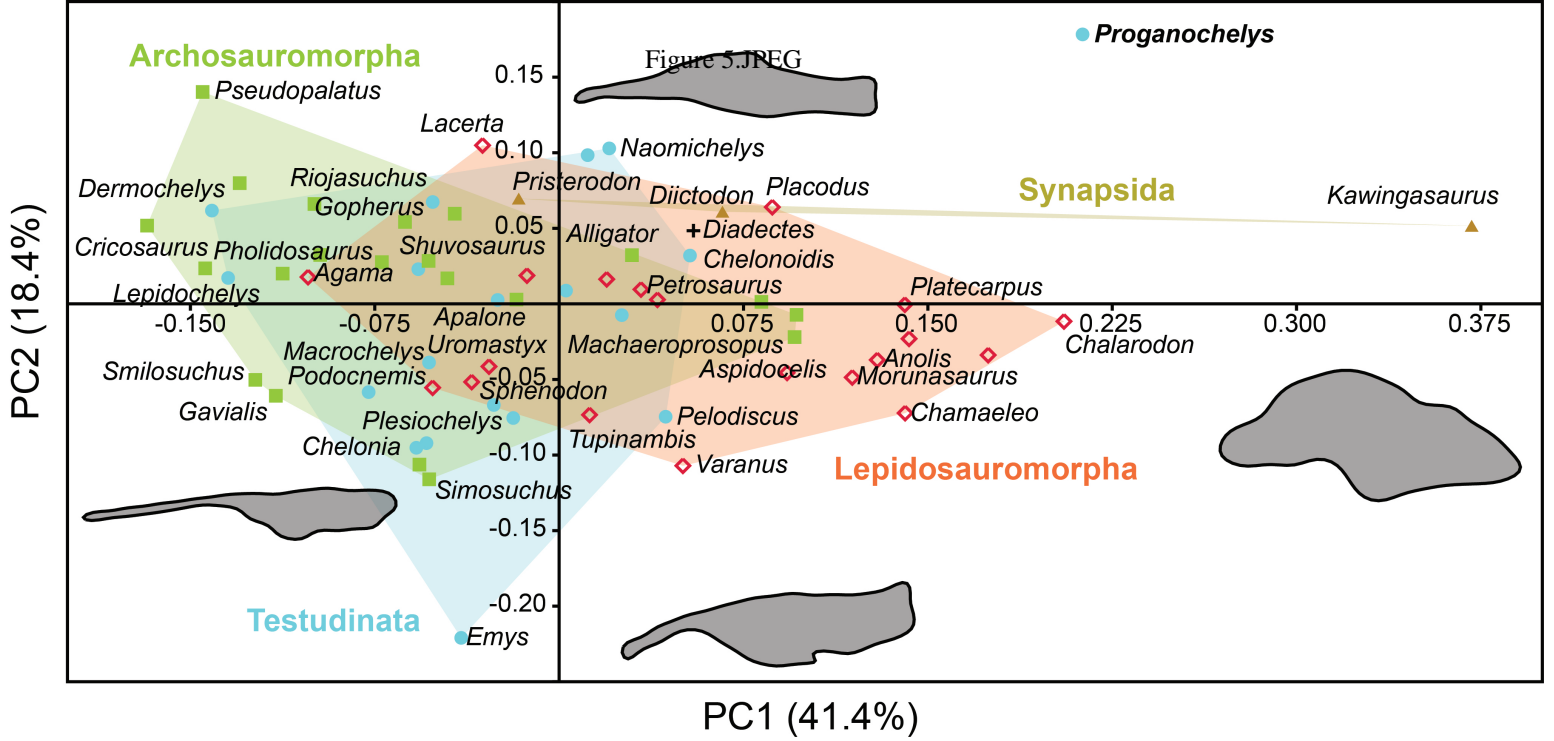


Figure 2.JPEG





A**B****C****D****E****F****G****H**



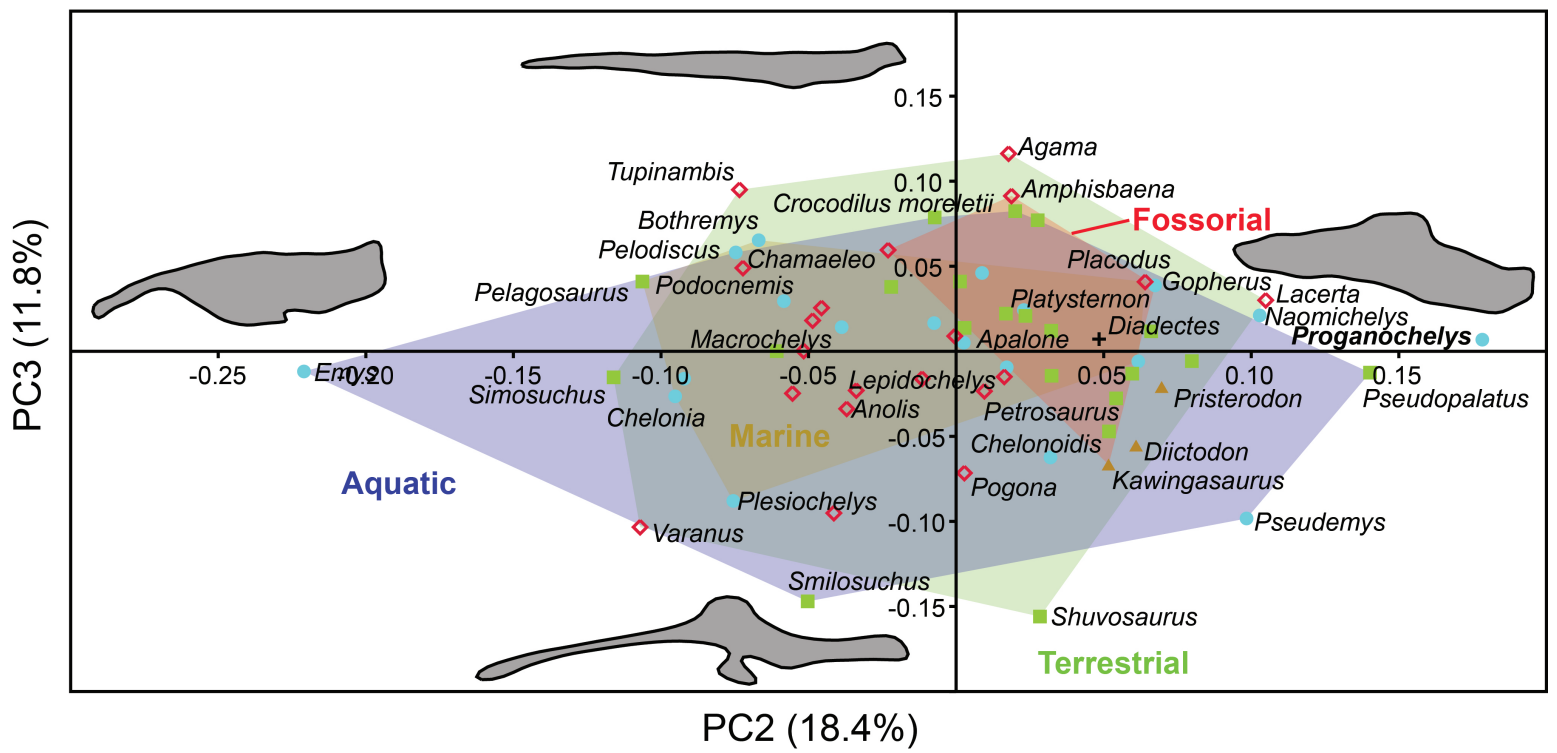
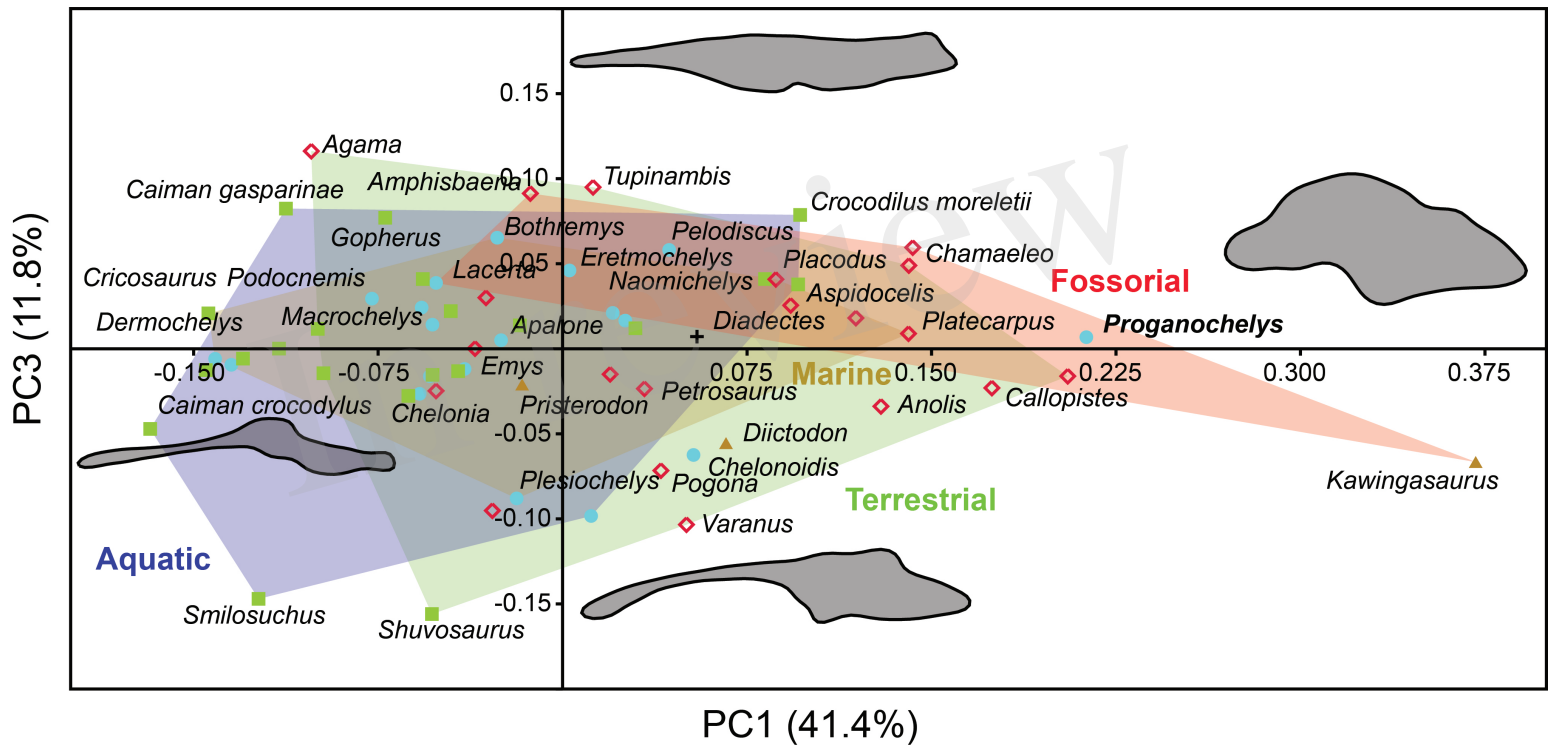
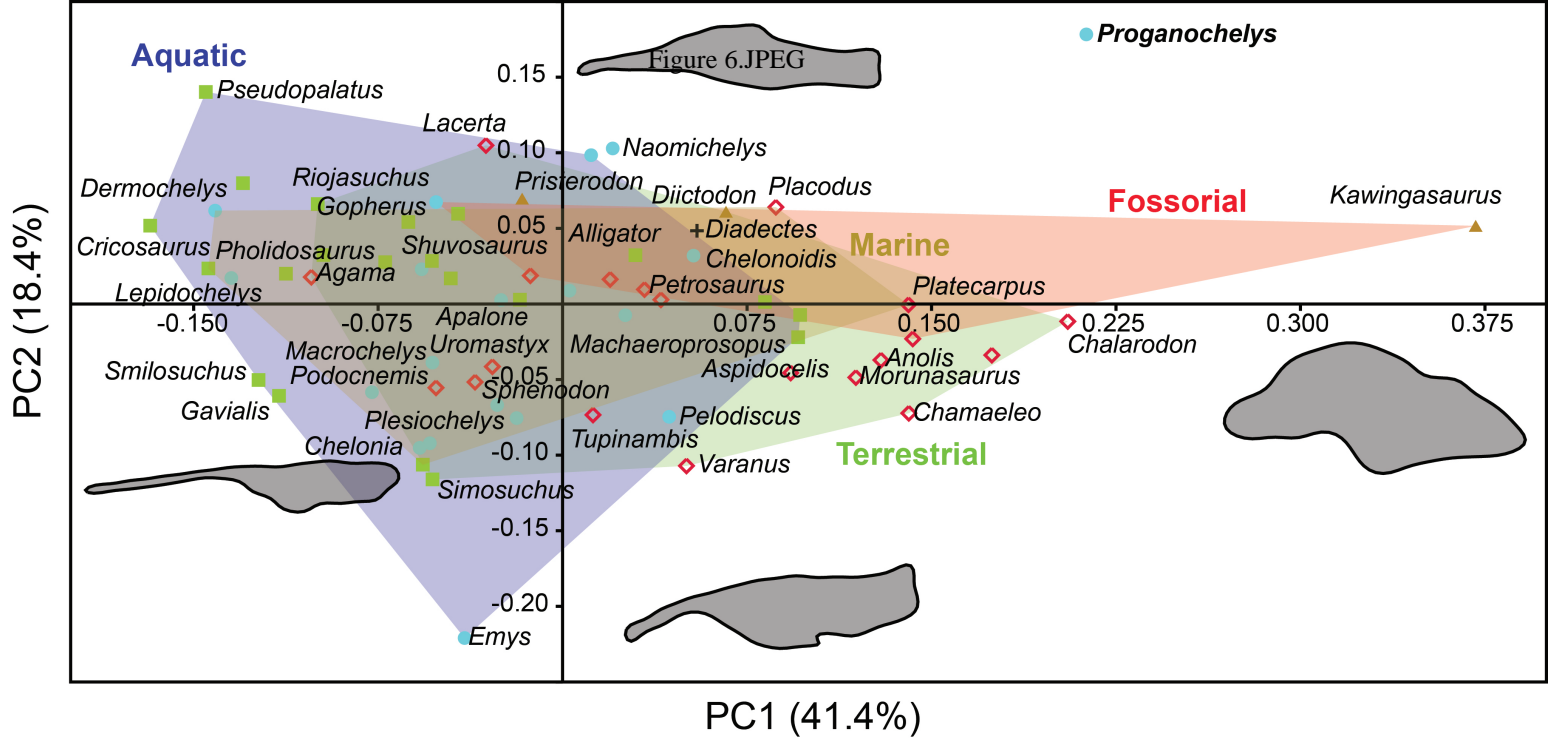


Figure 7.JPEG

