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**A reassessment of the enigmatic diapsid *Paliguana whitei*
and the early history of Lepidosauromorpha**

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Does your article include research that required ethical approval or permits?:

This article does not present research with ethical considerations

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Data

It is a condition of publication that data, code and materials supporting your paper are made publicly available. Does your paper present new data?:

Yes

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1. The PPC-SR μ CT data for this study, including all mesh files in .ply format generated from the data together with the tiff stacks for AM3585 are available to the editor/reviewers on the following link:

https://www.dropbox.com/sh/ldz0tdgfo6o47c3/AAAqaEYP0QMct_Y-CB7V00ima?dl=0

These data will be made available on MorphoSource (URL

www.morphosource.org/projects/000362825)

2. supplementary data has been uploaded in the submission files. In addition, the NEXUS file, character/taxon matrix and Bayesian script for the phylogenetic analysis have been uploaded on to Dryad. These data can be accessed temporarily using the following link:

<https://datadryad.org/stash/share/LqiQxH3jy20ud2HCt65tOPaY8vuaiOcuEHTXyKMjLjC>

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1 A reassessment of the enigmatic diapsid *Paliguana whitei* and the early history of
2 Lepidosauromorpha.

3

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17

18 ABSTRACT

19

20 Lepidosaurs include lizards, snakes, amphisbaenians and the tuatara, comprising

21 a highly speciose evolutionary radiation with widely varying anatomical traits.

22 Their stem-lineage originated by the late middle Permian 259 million years ago,

23 but its early fossil record is poorly documented, obscuring the origins of key

24 anatomical and functional traits of the group. *Paliguana whitei*, from the Early

25 Triassic of South Africa, is an enigmatic fossil species with potential to provide

26 information on this. However, its anatomy and phylogenetic affinities remain
27 highly uncertain, and have been debated since its discovery more than 100 years
28 ago. We present microtomographic 3D imaging of the cranial anatomy of
29 *Paliguana whitei* that clarifies these uncertainties, providing strong evidence for
30 lepidosauromorph affinities based on the structure of the temporal region and
31 the implantation of marginal dentition. Phylogenetic analysis including these
32 new data recovers *Paliguana* as the earliest known stem-lepidosaur, within a
33 long-lived group of early-diverging lepidosauromorphs that persisted to at least
34 the Middle Jurassic. Our results provide insights into cranial evolution on the
35 lepidosaur stem-lineage, confirming that characteristics of pleurodont dental
36 implantation evolved early on the lepidosaur stem-lineage. In contrast, key
37 functional traits related to hearing (quadrate conch) and feeding (streptostyly)
38 evolved later in the lepidosaur crown-group.

39

40 INTRODUCTION

41

42 Lepidosaurs include squamates (snakes, lizards and amphisbaenians) and the
43 tuatara, with ca. 11,000 extant species (Uetz *et al.* 2020). Their phylogenetic
44 stem-lineage diverged from all other living reptiles, i.e., turtles + archosaurs, no
45 later than the Capitanian (middle Permian), around 259 million years ago (Ma),
46 based on the timing of early fossil archosaurs (Ezcurra *et al.* 2014) and
47 molecular clock divergence analysis (Jones *et al.* 2013). Little is known of early
48 fossil stem-lepidosaurs (i.e., non-lepidosaurian lepidosauromorphs; Evans 2003)
49 which are key to understanding the pattern of evolutionary changes that gave
50 rise to their extant groups. Only a few Early/Middle Triassic lepidosauromorphs

51 have been described in detail, e.g., *Megachirella wachtleri* (Renesto and Posenato
52 2003), *Sophineta cracoviensis* (Evans and Borsuk-Białynicka 2009), *Fraxinisaura*
53 *rozynekae* (Schoch and Sues 2018), and *Vellbergia bartholomaei* (Sobral *et al.*
54 2020). The anatomy of these species is incompletely characterised, and their
55 evolutionary relationships remain subject to debate (e.g., Simões *et al.* 2018,
56 Griffiths *et al.* in press). This obscures a wider understanding of the evolutionary
57 divergences that gave rise to extant reptile diversity.

58

59 *Paliguana whitei* Broom 1903, from the Lower Triassic of the Eastern Cape
60 province of South Africa, has long been recognised as possessing
61 lepidosauromorph apomorphies. However, due to relatively poor preservation,
62 the anatomy of the skull of *Paliguana* is difficult to interpret and poorly
63 understood, and its affinities have been debated for over 100 years.
64 Hypothesised affinities of *Paliguana* have varied depending on interpretations of
65 the anatomy of the temporal region and quadrate morphology, both of which are
66 poorly preserved (Evans 2003, Ezcurra 2016). Broom (1903) originally
67 considered the holotype of *Paliguana*, a partially complete skull 3cm in length
68 (Fig.1A, C), as a squamate, based on possessing a quadrate with a lateral conch
69 and a ventrally incomplete lateral temporal opening. This interpretation was
70 supported by Camp (1923), and in part by Carroll (1975a, 1975b, 1977), who
71 agreed with Broom's (1903) original interpretation of the temporal region and
72 with squamate affinities. However, other early studies did not support squamate
73 affinities and some dismissed the specimen as being indeterminate or
74 problematic (Watson 1914, Boulenger 1918). Broom (1925) later assigned
75 *Paliguana* to Eosuchia, a now paraphyletic assemblage of diapsid stem-reptiles,

76 based on a revised interpretation of the temporal region as including a
77 quadratojugal that formed the ventral border of an enclosed lateral temporal
78 opening. Carroll (1975a, 1975b, 1977) proposed a close relationship between
79 *Paliguana* and two other South African taxa, *Saurosternon baini* (a headless
80 skeleton) and *Palaeagama vielhaueri* (a poorly preserved partial skeleton) and
81 assigned these taxa to the revised Paliguanidae Broom 1926. Subsequently,
82 *Kudnu mackinlayi*, from the Early Triassic of Australia, was also added to this
83 new family of early squamates (Bartholomai 1979). However, later studies found
84 no synapomorphies to support this grouping (Evans 1984, Benton 1985), further
85 emphasising the uncertain affinities of *Paliguana*.

86

87 Early cladistic analysis rejected the hypothesis of *Paliguana* as a squamate or
88 stem-squamate. Instead *Paliguana* was recovered as a stem-lepidosaur, more
89 closely related to the crown-group (rhynchocephalians + squamates) than to
90 other diapsid reptiles (Gauthier *et al.* 1988), based primarily on the presence of a
91 prominent lateral conch of the quadrate (and as originally described by Broom
92 1903). Later studies urged caution due to the lack of clear morphological data
93 (Evans 2003, Jones *et al.* 2013), but *Paliguana* has nevertheless recently been
94 regarded as a stem-lepidosaur mostly based on the presence of this feature
95 (Evans and Borsuk-Białynicka 2009, Ezcurra 2014, Schoch and Sues 2018). The
96 lack of consensus on this topic is clear. For example, a recent large-scale analysis
97 of deep reptilian divergences, which considered the quadrate conch to be absent,
98 recovered unresolved affinities for *Paliguana* in a polytomy with
99 Archosauromorpha and Lepidosauromorpha at the base of the reptilian crown-
100 group (Simões *et al.* 2018). This highlights ongoing uncertainties regarding the

101 anatomy of *Paliguana* and its potential significance for understanding early
102 reptile evolution.
103
104 We present the results of a new analysis of the holotype of *Paliguana whitei*
105 using synchrotron radiation micro-computed tomography at the European
106 Synchrotron Radiation Facility (ESRF). We clarify the temporal morphology of
107 *Paliguana* and identify the key diagnostic elements of this taxon. Applying these
108 new data to a modified version of a recent phylogenetic analysis (Griffiths *et al.*
109 in press), we find that *Paliguana whitei* is a stem-lepidosaur, and the
110 stratigraphically earliest member of a clade that co-existed with crown-group
111 lepidosaurs from the Middle Triassic to at least the Middle Jurassic. *Paliguana*
112 also provides insights into the anatomical transitions involved in the basal
113 divergence of living reptiles.

114

115 SYSTEMATIC PALAEOLOGY

116

117 DIAPSIDA Osborn, 1903

118 LEPIDOSAURMORPHA Gauthier, Estes and de Queiroz 1988

119 PALIGUANA WHITEI Broom 1903

120

121 Holotype – AM 3585, partial skull, with the following bones preserved:
122 incomplete frontal and parietal, right jugal and postfrontal, right postorbital
123 missing posterior process, right squamosal missing anterior process, right
124 quadratojugal, right quadrate with ventral condylar region separated, right
125 supratemporal fragment, right ectopterygoid, left postfrontal, partial left jugal,

126 postorbital and quadrate, right exoccipital, left prootic, partial right dentary and
127 splenial, partial left dentary and splenial, posterior right hemimandible, partial
128 right vomer, pterygoid and palatine fragments. Partial maxillae, lacrimals and
129 prefrontals. Premaxillae and nasals not preserved.

130

131 Horizon and age – *Lystrosaurus declivis* Assemblage Zone (LAZ), Upper Katberg
132 Formation, Tarkastad Subgroup, Beaufort Group, Karoo Supergroup. Induan,
133 Early Triassic (Botha and Smith 2020). The specimen was recovered from a
134 matrix of red sandy clay (Carroll 1975a), a deposit currently regarded as upper
135 LAZ (P. Viglietti pers. comm. 2019).

136

137 Locality - Donnybrook Farm 349 (32.2 S, 26.56 E) approx. 35.5km southeast of
138 Tarkastad, Chris Hani District, Eastern Cape, South Africa.

139

140 Diagnosis – *Paliguana whitei* is characterised by the following autapomorphies:

141 (1) Large quadratojugal foramen for the passage of the mandibular veins

142 (quadrate foramen *sensu* Romer 1956) formed by the quadrate posteriorly, the

143 quadratojugal and quadrate ventrally and the squamosal anteriorly. (2)

144 Suborbital process of jugal extends anteriorly close to the level of the anterior

145 margin of the orbit, posterior process short and spur-like. (3) Subcircular raised

146 boss on the anterodorsal surface of the parietal, extending onto the

147 posterodorsal surface of the frontal. A detailed description of the anatomy of the

148 skull of *Paliguana whitei* is provided in Supplementary Data 1.

149

150 MATERIAL AND METHODS

151

152 *Paliguana whitei* is represented by a single specimen, AM 3585 (holotype), held
153 at the Albany Museum, Grahamstown, Eastern Cape, South Africa. The specimen
154 was characterised at the ID19 beamline of the European Synchrotron Radiation
155 Facility (ESRF, Grenoble, France) using propagation phase contrast synchrotron
156 radiation micro-computed tomography (PPC-SR μ CT). The experimental setup
157 consisted of filtered white beam (wiggler W150 gap 58 mm, filters: Cu 5 mm)
158 with a total integrated detected energy of 80 keV, a sample-detector propagation
159 distance of 2.5 m and an indirect detector (200 μ m LuAG scintillator; 1.5x
160 magnification from two photographic Hasselblad lenses, sCMOS PCO edge 4.2
161 Gold) producing data with an isotropic voxel size of 4.35 μ m. Refer to
162 Supplementary Data 3 for details on the acquisition of the reconstructed volume.

163

164 The specimen was digitally segmented using Mimics materialise v.19.0
165 (<http://www.biomedical.materiale.com/mimics>). The 3D models made in
166 Mimics were exported as .ply files and imported into Blender v.2.81a
167 (<https://www.blender.org>) and rendered as 2D images for the figures in this
168 study. The PPC-SR μ CT data for this study, including all mesh files in .ply format
169 generated from the data together with the tiff stacks for AM3585 are available in
170 MorphoSource (<https://www.morphosource.org/projects/000362825>).

171

172 ANATOMICAL OBSERVATIONS

173 Our synchrotron tomographic visualisation provides new data and clarifies
174 earlier observations on key aspects of the anatomy of *Paliguana whitei*, resolving

175 long-standing uncertainties regarding the cranial morphology of this enigmatic
176 taxon (Figs. 1, 2 and Supplementary Data 1). *Paliguana* shares several features
177 with stem-lepidosaurs, e.g., *Fraxinisaura* (Schoch and Sues 2018) and
178 *Marmoretta* (Griffiths *et al.* in press). For example, we confirm the lateral
179 temporal opening is not enclosed ventrally (*contra* Broom 1925), and that the
180 posteroventral process of the jugal formed a small, spur-like projection (Fig.2);
181 the lacrimal is greatly reduced and confined to the orbital margin (see
182 Supplementary Data 1, Fig.2A); the postfrontals and postorbital are separate
183 elements (see Supplementary Data 1, Fig. 3) and the frontals are fused (see
184 Supplementary Data 1, Fig.4), features also present in *Marmoretta* (Griffiths *et al.*
185 in press).

186

187 Importantly, our data provide clear evidence that the lateral conch of the
188 quadrate is absent in *Paliguana*, confirming the score of that character in the
189 phylogenetic matrix of Simões *et al.* (2018). The conch is also absent in the
190 Jurassic stem-lepidosaur *Marmoretta* (Griffiths *et al.* in press), but is present in
191 most crown-group lepidosaurs, including Triassic taxa such as *Megachirella*
192 (Simões *et al.* 2018) and *Sophineta* (Evans and Borsuk-Białynicka 2009). The
193 quadrate conch is formed by the posterolateral curvature of the anterior lamina
194 of the quadrate and is associated with the anterior point of contact of the
195 tympanic membrane and the evolution of impedance matching hearing in
196 lepidosaurs (Evans 2008). Debate regarding its presence in *Paliguana* has been
197 central to hypotheses of its phylogenetic affinities (Carroll 1975a, Evans and
198 Borsuk-Białynicka 2009, Ezcurra 2014, Schoch and Sues 2018; Simoes *et al.*
199 2018), underlining the importance of this observation.

200

201 *Paliguana* possesses a large quadratojugal foramen, enclosed ventrally by a small
202 horizontally oriented quadratojugal (Fig. 2). This opening was considered to be
203 an artefact of preservation in some previous studies (Carroll 1975a) and is
204 absent in most other lepidosauromorphs, in which the quadratojugal, if present,
205 is reduced to a small vertically oriented bone in close contact with or
206 incorporated into the anteroventral surface of quadrate (Evans 2003). An
207 exception to this can be seen in fossil and extant rhynchocephalians, where the
208 quadratojugal forms an enlarged quadratojugal foramen with the quadrate, e.g.,
209 *Sphenodon*, *Zapatadon* and *Sphenotitan* (Evans 2008, Reynoso and Clark 1998,
210 Martinez *et al.* 2013).

211

212 *Paliguana* exhibits ‘subpleurodont’ (Presch 1974, Zaher and Rieppel 1999)
213 implantation of the marginal dentition. Its teeth are set in a shallow groove, the
214 labial wall being twice the height of the lingual wall (Fig. 3). The tooth bases are
215 partially enclosed mesially and distally by a short interdental lamina projecting
216 from the lingual wall (see Supplementary Data 1, Fig.12). The root is encased in
217 alveolar bone. However, material of attachment, which is separate from the
218 alveolar bone and possibly represents a mineralised ligament, is present along
219 the lingual surface of the tooth root (Fig. 3). This is somewhat similar to the
220 ankylosing bone present at the base of marginal dentition in *Sophineta* (Evans
221 and Borsuk-Białynicka 2008) and extant teiid squamates (Bertin *et al.* 2018).
222 The relative height of the lingual wall and the presence of short interdental
223 laminae contrasts with the situation in many extant squamates, which often have
224 a lower or absent lingual wall, and the absence of interdental laminae. These

225 observations suggest that tooth implantation in *Paliguana* may represent an
226 intermediate morphology between the subthecodonty of diapsid stem-reptiles,
227 e.g., *Orovenator* (Ford and Benson 2019), and the pleurodonty of derived
228 lepidosaurs such as *Huehuecuetzpalli* (Reynoso 1998) and *Eichstaettisaurus*
229 (Simões *et al.* 2017).

230

231 We also find that *Paliguana* retains plesiomorphic diapsid features that have
232 been lost in early lepidosaurs. For example, the postfrontal is excluded from the
233 upper temporal fenestra (UTF) by contact between the postorbital and parietal
234 (Fig. 2), as in diapsid stem-reptiles, e.g., *Petrolacosaurus* (Reisz 1981), *Araeoscelis*
235 (Reisz *et al.* 1984) and *Youngina* (Reisz *et al.* 2000). This contrasts with other
236 lepidosauromorphs in which the postfrontal, where recognised as a separate
237 element from the postorbital, contributes to the UTF, e.g., *Marmoretta* (Griffiths
238 *et al.* in press), *Sophineta* (Evans and Borsuk-Białynicka 2009), *Gephyrosaurus*
239 (Evans 1980), *Huehuecuetzpalli* (Reynoso 1997) and *Eichstaettisaurus* (Simões *et*
240 *al.* 2017). *Paliguana* also shows absence of an alar process on the prootic and of
241 the crista prootica (see Supplementary Data 1, Fig.10), as generally considered to
242 be primitive for reptiles, although also absent in the extant tuatara and
243 chamaeleonids (Evans 2008).

244

245 PHYLOGENETIC ANALYSIS

246

247 We included new data on the anatomy of *Paliguana* to the phylogenetic data
248 matrix of Griffiths *et al.* (in press), which was extensively modified from Simões
249 *et al.* (2018). In addition to re-scoring the anatomy of *Paliguana*, we also revised

250 the characters concerning the implantation of marginal dentition. Multistate
251 characters 212 and 213 of the original character-taxon matrix were removed and
252 replaced by six new binary characters (c.376-381), which recognise independent
253 variation in the morphology of tooth implantation among reptiles. We also added
254 a recently reported species to the dataset (*Vellbergia bartholomaei*). The
255 modified character-taxon matrix was analysed using a non-time calibrated
256 Bayesian Mkv model in MrBayes v.3.2.5 (Ronquist *et al.* 2012). Our results were
257 expressed in a 50% majority rule tree and a maximum clade credibility (MCC)
258 tree. Refer to Supplementary Data 2 for extended details.

259

260 Our initial analysis recovered a highly unstable phylogenetic position for one
261 taxon, the possible lepidosauromorph *Palaeagama vielhaueri*, which was
262 therefore excluded from our main analyses. This taxon is known from very
263 incomplete data from which it is difficult to make confident anatomical
264 interpretations. *Palaeagama*, from the late Permian/Early Triassic of South
265 Africa, was originally described as a stem-reptile (Broom 1926), and later
266 hypothesised to form a group with *Paliguana* (Carroll 1975a, 1975b, 1977).
267 Recent analysis has recovered *Palaeagama* as a neodiapsid stem-reptile (Ezcurra
268 *et al.* 2014), an archosauromorph (Simões *et al.* 2018), and an early stem-
269 lepidosaur (Sobral *et al.* 2020). The inclusion of *Palaeagama* in our dataset
270 recovers this taxon in a broad polytomy with crown-group reptile clades in the
271 50% majority rule tree, or as a crown-group squamate in the MCC tree (see
272 Supplementary Data). We consider the phylogenetic position of *Palaeagama* as
273 currently problematic (and also see Sobral *et al.* 2020), pending further
274 investigation of the holotype and only specimen held at the McGregor Museum,

275 Kimberley (refer to Supplementary Data 5 for details on these changes, together
276 with a revised character list).

277

278 *Paliguana whitei* is recovered as a stem-lepidosaur in both tree topologies,
279 within a clade that includes *Marmoretta* and *Fraxinisaura* (posterior probability
280 = 0.73 - see Fig. 3 and Supplementary Data). We find strong support for the
281 inclusion of this group within Lepidosauromorpha (posterior probability = 1).
282 *Paliguana* is therefore the stratigraphically earliest member of a long-lived group
283 of non-lepidosaurian lepidosauromorphs that co-existed with the crown-group,
284 differing substantially from other recent studies which did not recover *Paliguana*
285 as a lepidosauromorph (Simões *et al.* 2018; Griffiths *et al.* in press).

286

287 We find both *Sophineta* and *Vellbergia* as crown-group lepidosaurs, more closely
288 related to rhynchocephalians than squamates in the MCC tree, although support
289 for *Sophineta* in this respect is relatively low (posterior probability = 0.27).

290 *Megachirella* is recovered as a stem-squamate in the MCC tree, in accordance
291 with recent studies (Simões *et al.* 2018, Sobral *et al.* 2020, Griffiths *et al.* in
292 press). Support for this taxon within Squamata, however, is poor (posterior
293 probability = 0.38). We recover *Megachirella* as a crown-group lepidosaur in a
294 polytomy with rhynchocephalians, squamates and *Sophineta* in the 50% majority
295 rule tree (see Supplementary Data 2).

296

297 Kuehneosaurs, an enigmatic group of early gliding reptiles, are recovered as
298 early diverging lepidosauromorphs in the MCC tree, with low support (posterior
299 probability = 0.33), and as an unresolved group in the 50% majority rule tree

300 (see Supplementary Data 2). The phylogenetic affinities of kuehneosaurs
301 therefore remain largely unresolved, with recent analyses suggesting a position
302 within Archosauromorpha (Pritchard and Nesbitt 2017, Pritchard and Sues
303 2019, Sobral *et al.* 2020).

304

305 DISCUSSION

306

307 The new data on *Paliguana* and its phylogenetic position as an early diverging
308 lepidosauromorph provides evidence on the ancestral condition and
309 evolutionary assembly of key functional traits along the lepidosaur stem-lineage
310 (Fig. 4). We find that several typically lepidosaurian traits were present in the
311 common ancestor of the reptilian crown-group, based on their presence both in
312 early lepidosauromorphs and early archosauromorphs. These include absence of
313 the lower temporal bar and a bowed posterior surface of the quadrate (see
314 Evans 2003, Müller 2003, Evans and Jones 2010). All lepidosauromorphs possess
315 a reduced lacrimal and, with some exceptions (see below), subpleurodont or
316 pleurodont marginal dentition as synapomorphies of the group. Therefore, this
317 characteristic mode of dental implantation seen in many extant squamates
318 appeared early on the lepidosaur stem-lineage. *Paliguana* exhibits
319 subpleurodont implantation (Fig. 3 and Supplementary Data 1). This suggests
320 that subpleurodonty is the primitive condition for Lepidosauromorpha, and is
321 intermediate between subthecodonty of many early amniotes, and pleurodonty
322 that is widespread in squamates. Acrodont tooth implantation subsequently
323 appeared independently in some crown-lepidosaurs, e.g., partial acrodonty in
324 *Vellbergia* (Sobral *et al.* 2020) and rhynchocephalians (other than

325 *Gephyrosaurus*), acrodont iguanians (agamids and chameleons, Evans 2008) and
326 trogonophid amphisbaenians (Macey *et al.* 2004). Stem-lepidosaurs,
327 rhynchocephalians and the early stem-squamate *Megachirella* also share an
328 orbital exposure of the maxilla, which was lost in many squamates. The lateral
329 conch of the quadrate is a synapomorphy of crown-group lepidosaurs that is
330 absent in all known stem-lepidosaurs but was acquired convergently in
331 kuehneosaurs.

332

333 *Paliguana* possesses an anteroventral process of the squamosal that contacts
334 both the quadrate and quadratojugal (Fig. 2), negating the possibility of a
335 streptostylic skull. Streptostyly is an important functional characteristic of the
336 skull of extant squamates, in which the quadrate hinges anteroposteriorly during
337 biting, thereby increasing bite force (Rieppel 1978, Iordansky 2011), and some
338 studies considered it to be present in *Paliguana* (e.g., Smith 1980). However, in
339 *Paliguana* the anteroventral process of the squamosal makes extensive contact
340 with the quadrate and quadratojugal preventing significant motion of the
341 quadrate within the skull (Evans 2008). Lack of streptostyly in *Paliguana* is also
342 supported by a broad pterygoid wing of the quadrate (see Supplementary Data 1,
343 Fig.5), suggesting extensive contact with the quadrate ramus of the pterygoid. A
344 similar condition is present in *Megachirella*, in which the pterygoid wing of the
345 quadrate is very well developed (Simões *et al.* 2018), implying the absence of
346 streptostyly even among possible early members of the squamate stem-lineage.
347 Nevertheless, the loss the anteroventral process of the squamosal and the partial
348 fusion of the quadratojugal to the quadrate in *Megachirella* (Simões *et al.* 2018)
349 could indicate a stepwise evolutionary origin of the prerequisites of streptostyly

350 in squamates. Crown-group squamates exhibit reduction of the
351 pterygoid/quadrates overlap and dorsal condyle of the quadrate, and the
352 presence of a synovial joint between the epipterygoid and pterygoid. These traits
353 together allow a greater degree of cranial kinesis, culminating in the
354 hyperstreptostylic quadrate of many extant lizards, e.g., some iguanians,
355 agamids, chameleons and lacertids (Evans 2008).

356

357 Kuehneosaurs possess a reduced dorsal condyle of the quadrate, and together
358 with the loss of the anteroventral process of the squamosal, this may have
359 permitted some movement of the quadrates in relation to the skull, although
360 with an extensive pterygoid/quadrates overlap this is not considered homologous
361 with squamate streptostyly (Evans 2009), as it would involve a bilateral
362 movement of both pterygoid and quadrate together, widening the posterior part
363 of the interpterygoid vacuity.

364

365 Our anatomical data and phylogenetic results provide strong support for the
366 lepidosauromorph affinities of *Paliguana*. Furthermore, based on its earliest
367 Triassic age, *Paliguana* is currently the oldest unambiguous lepidosauromorph.
368 This contrasts with the age of the earliest known unequivocal archosauromorph,
369 *Protorosaurus speneri* from the middle Wuchiapingian of Germany and England
370 (Ezcurra *et al.* 2014), which implies that lepidosaur stem-lineage had originated
371 by the middle Permian (259.1 Ma) (Evans and Jones 2010, Jones *et al.* 2013,
372 Ezcurra *et al.* 2014). Lepidosauromorpha is therefore characterised by a ghost
373 lineage, indicating at least 7 million years of missing information in their early
374 evolutionary history. Our results also provide insights into the co-existence of

375 the lepidosaur crown-group with their stem-lineage. On current evidence,
376 *Paliguana*, *Fraxinisaura* and *Marmoretta* belong to a monophyletic group of
377 early-diverging stem-lepidosaurs. Inclusion of *Paliguana*, the earliest known
378 lepidosauromorph, suggests that this group originated very early in the history
379 of Lepidosauromorpha, and then persisted alongside rhynchocephalians and
380 squamates well into the Jurassic (based on the Middle Jurassic occurrence of
381 *Marmoretta*). The mixed nature of Triassic–Middle Jurassic lepidosauromorph
382 assemblages contrasts with the exclusive occurrence of squamates in almost all
383 geographic regions in the present day.

384

385 *Paliguana whitei* is the earliest known member of a relatively small number of
386 Early/Middle Triassic lepidosauromorphs, a group that includes *Fraxinisaura*
387 *rozynekae*, *Vellbergia bartholomaei*, *Sophineta cracoviensis* and *Megachirella*
388 *wachtleri*. New discoveries and continued study of these important fossil
389 specimens has considerable potential to further enhance understanding of the
390 ancestral traits of lepidosauromorphs and the origins of modern squamates.

391

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400

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405

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665 **Figure captions**

666

667 **Figure 1.** AM 3585, holotype of *Paliguana whitei*. A-B, right dorsolateral view; B,
668 bones segmented from the μ CT scan of specimen. C-D, right lateral view; C, bones
669 segmented from the μ CT scan of specimen.

670

671 **Figure 2.** Segmented bones of the temporal region of *Paliguana whitei* in right
672 lateral view. A, reconstruction of the right temporal region; B, diagram of the
673 hypothetical complete temporal region of *Paliguana whitei*.

674

675 **Figure 3.** Transverse section of right dentary of *Paliguana whitei*, showing
676 attachment of marginal tooth to the jawbone. A, Synchrotron scan in mesial view;
677 B, diagrammatical representation of the scan slice.

678

679 **Figure 4.** Time calibrated tree topology based on results of Bayesian Mkv model
680 (halfcompat – 50% majority rule) recovered from the revised dataset of Griffiths
681 *et al.* (in press) and condensed to highlight early lepidosauromorph phylogeny.
682 Red bars indicate appearance ranges based on the fossil record. Red arrows
683 indicate extended appearance ranges beyond the parameters of the figure. Black
684 arrows indicate first appearance datum beyond the parameters of the figure.
685 Abbreviations: U, D, A = Unambiguous, Deltran and Acctran optimisation in
686 halfcompat tree.

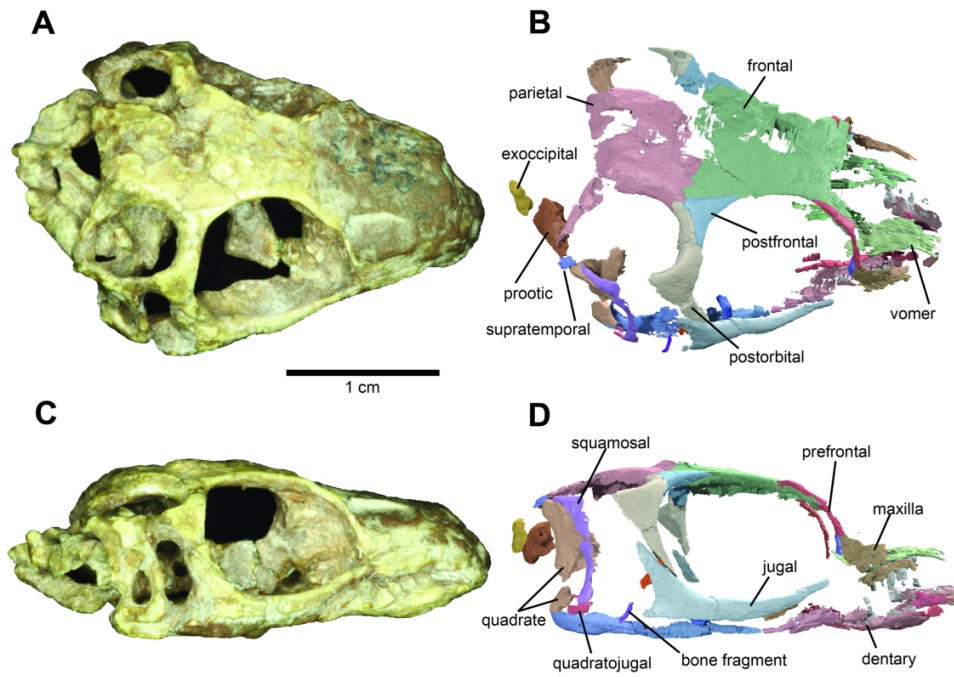


Figure 1. AM 3585, holotype of *Paliguana whitei*. A-B, right dorsolateral view; B, bones segmented from the μ CT scan of specimen. C-D, right lateral view; C, bones segmented from the μ CT scan of specimen.

168x120mm (300 x 300 DPI)

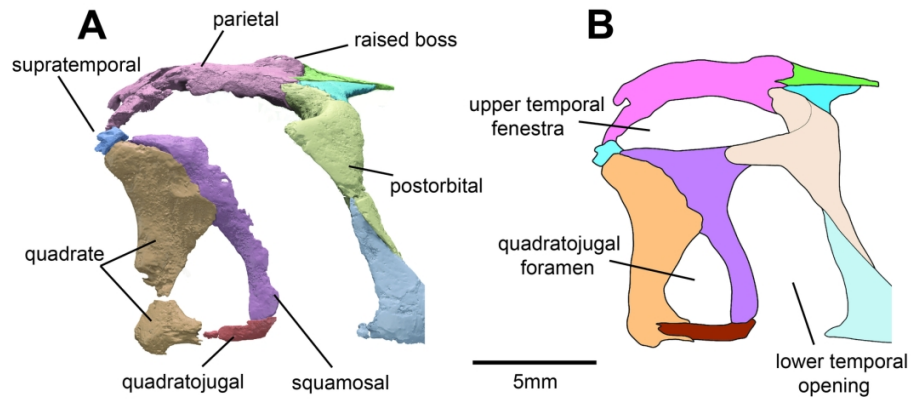


Figure 2. Segmented bones of the temporal region of *Paliguana whitei* in right lateral view. A, reconstruction of the right temporal region; B, diagram of the hypothetical complete temporal region of *Paliguana whitei*.

170x73mm (300 x 300 DPI)

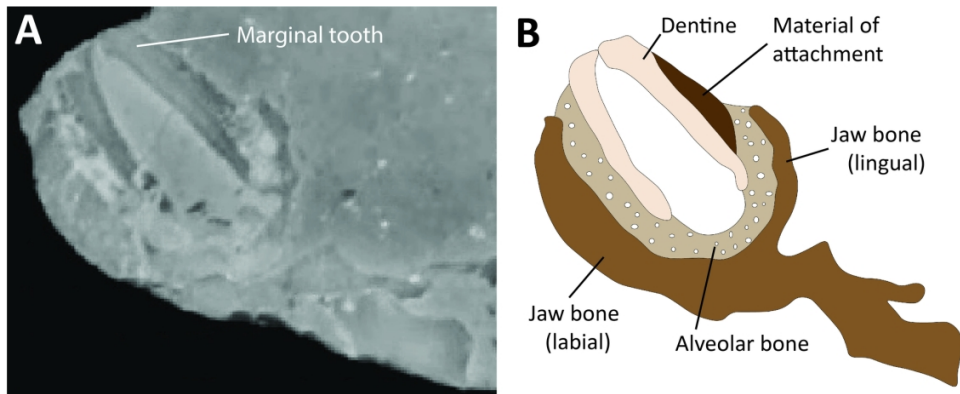


Figure 3. Transverse section of right dentary of *Paliguana whitei*, showing attachment of marginal tooth to the jawbone. A, Synchrotron scan in mesial view; B, diagrammatical representation of the scan slice.

173x69mm (300 x 300 DPI)

A REASSESSMENT OF THE ENIGMATIC DIAPSID PALIGUANA WHITEI AND THE EARLY HISTORY OF LEPIDOSAUROMORPHA

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SUPPLEMENTARY DATA 1

Description

The holotype (AM 3585) is a partial skull, 30mm in anteroposterior length and 20mm in maximum transverse width (Fig.1). The antorbital region of the skull is anteroposteriorly short compared to the orbit and postorbital region. However, some degree of anteroposterior crushing is evident in the medial bowing of the anterior right hemimandible and the displacement of the right maxilla. The preservation of the bones on the left of the skull is poor, and most of the elements described are from the right side of the skull. Fragments of the anterior palate are preserved, along with palatal dentition. Some bones of the braincase are present, but only the right exoccipital and right prootic can be identified with any confidence.

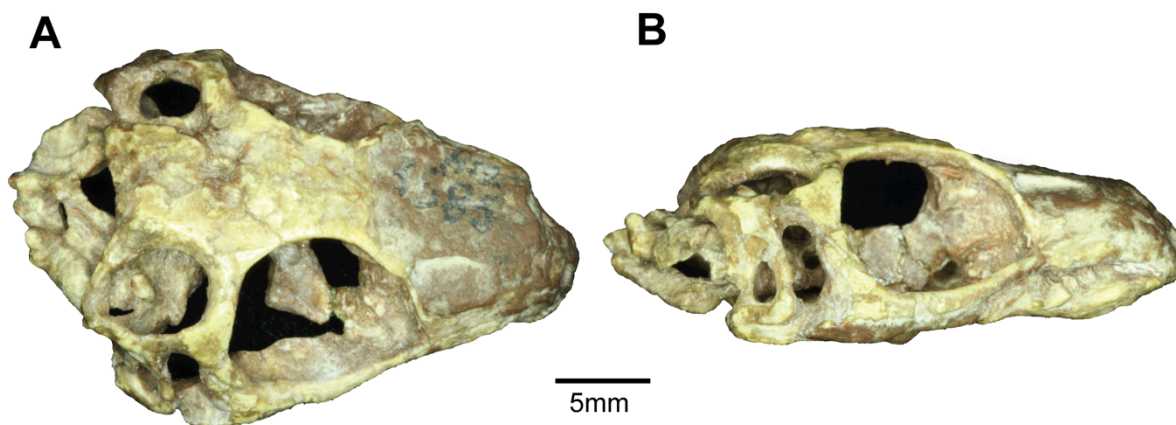


Figure 1. AM 3585, holotype of *Paliguana whitei*. A, right dorsolateral view; B, right lateral view.

Rostrum

Many of the bones of the rostrum are absent, e.g. premaxilla, nasals, anterior maxilla and anterior prefrontals, or very poorly preserved (Broom 1903; Carroll 1975a). However, the right lacrimal and parts of the maxilla and prefrontal are present, providing important diagnostic detail.

Maxilla. Both maxillae are partially preserved. The right maxilla has been displaced dorsally relative to the jugal (Fig.2A). The facial process of the right maxilla extends dorsally to the midpoint of the orbit where it contacts the prefrontal and the anterior surface of the lacrimal, restricting the lacrimal to the orbital margin (Fig.2A). The dorsoventral height of the facial process diminishes only slightly anteriorly, at least until the preserved bone terminates before reaching the midpoint of the snout. The left maxilla, although poorly preserved, also exhibits a tall facial process immediately anterior to the orbit (Fig.2B). A small tooth-bearing portion of right maxilla is preserved ventral to the facial process and bears three partial teeth in situ (Fig.2A).

A small fragment of the posterior (suborbital) process of the right maxilla is present ventral to and in contact with the anterior process of the jugal (Fig.2A). This extends posteriorly just short of the midpoint of the orbit. It is probable that the maxilla contributed to the anteroventral margin of the orbit. This is best illustrated by the left maxilla, in which the suborbital process of

the maxilla narrows to a dorsoventrally thin ramus that follows the curve of the orbit margin posteriorly (Fig.2B). A contribution of the maxilla to the orbit margin is also present in early lepidosauromorphs and rhynchocephalians (Evans and Borsuk-Białynicka 2009, Schoch and Sues 2018, Griffiths *et al.* in review) and kuehneosaurs (Robinson 1962, Colbert 1970). It differs from early diapsids (Currie 1980, Reisz 1981, Reisz *et al.* 2000) and some early archosauromorphs (Sen 2003, Modesto and Sues 2004, Gottman-Quesada and Sander 2009), in which the maxilla is excluded from the orbit margin by contact between the jugal and lacrimal. Exclusion of maxilla from the orbit occurs in many squamates, including *Ardeosaurus*, *Eichstaettisaurus* and *Huehucuetzpalli* (Mateer 1982, Reynoso 1998, Simões *et al.* 2017)

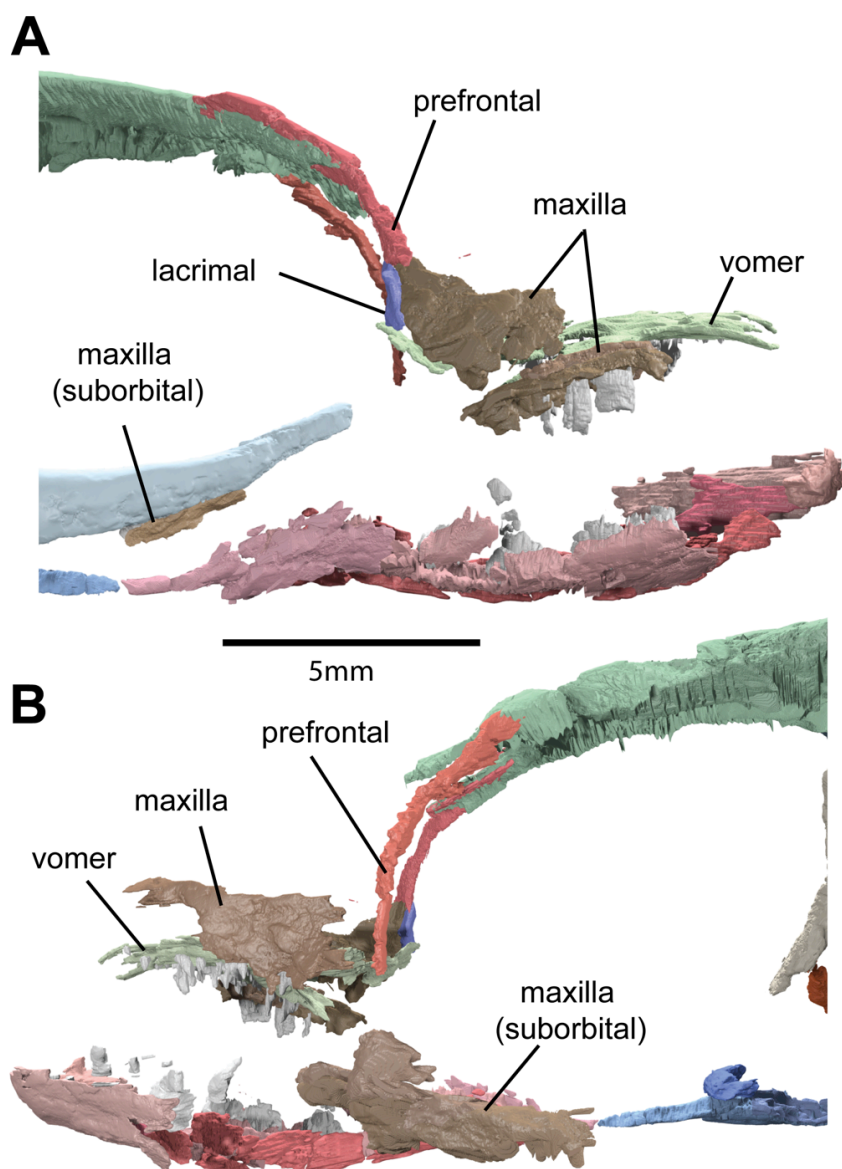


Figure 2. Segmented bones of *Paliguana whitei*. A, right lateral view of anterior region of skull; B, left lateral view.

Lacrimal. The right lacrimal is a small bone confined to the posterior rim of the orbital margin, contacting the prefrontal dorsally and the maxilla anteriorly (Fig.2A). This is contrary to the interpretation described and illustrated by Carroll (1975a), where the lacrimal has an anterior extension, extending half way along the snout. The absence or reduction of the lacrimal to a dorsoventrally orientated bone confined to the orbital margin is a lepidosaur synapomorphy (Gauthier *et al.* 1988), a condition also found in stem-lepidosaurs, e.g. *Fraxinisaura* (Schoch and Sues 2018) and probably *Marmoretta* (Evans 1991, Griffiths *et al.* in review). It is also reduced

or absent in rhynchocephalians (Evans 1980, Whiteside 1986). In early archosauromorphs, e.g. *Protorosaurus* (Gottman-Quesada and Sander 2009), *Macrocnemus fuyuanensis* (Jiang *et al.* 2011), *Pamelaria* (Sen 2003) and *Prolacerta* (Modesto and Sues 2004), in kuehneosaurs (Robinson 1962, Colbert 1970, Evans 2009) and in neodiapsids (Gow 1975, Modesto and Reisz 2002) the lacrimal bears a distinct anterior process, which extends onto the lateral margin of the snout.

Prefrontal. The left prefrontal is badly crushed and poorly preserved. Only the posterior surface of the right prefrontal is preserved, where it forms the anterodorsal and anterior margin of the orbit (Fig.3). The dorsal process is a narrow wedge-shaped region, tapering posteriorly. The suture with the frontal, where present, is anteroposteriorly orientated, and probably continued anteriorly along the snout, judging from the broken anterior surface of the dorsal process. The prefrontal extends ventrally to contact the lacrimal and maxilla.

Skull Roof

The general condition of the skull roof is poor (Fig.3). Many areas of bone are missing, giving the appearance of a pitted and irregular surface. This makes it difficult for a visual examination to determine the presence of sutures and other features, such as the parietal foramen. Our scan data resolve some uncertainties, for example providing high-resolution data on cross-sections of the frontal. However, other morphologies cannot be determined, such as the presence or absence of a parietal foramen and the fusion of the parietal.

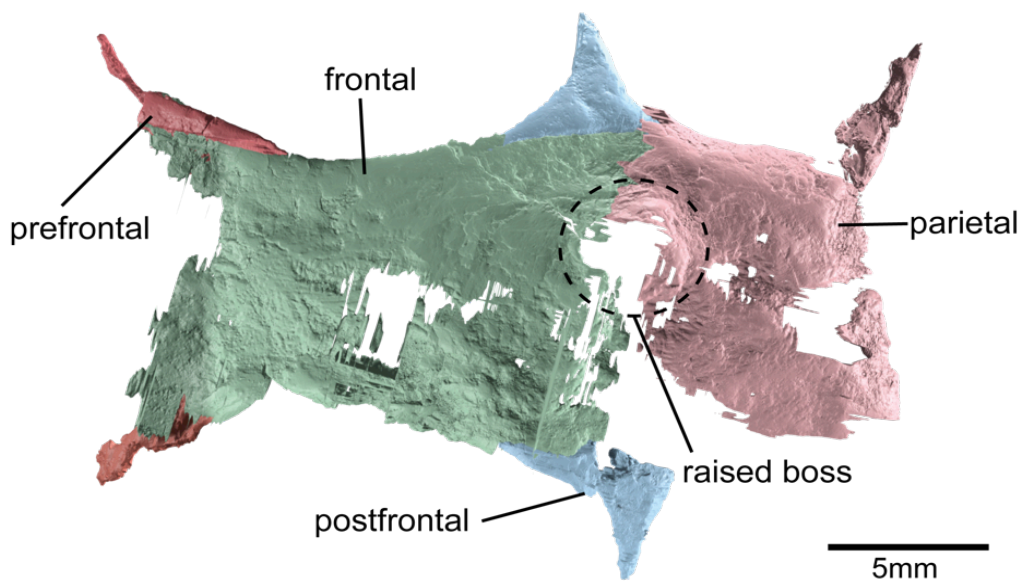


Figure 3. Segmented bones of the skull roof of *Paliguana whitei* in dorsal view.

Frontal. The midline suture of the frontals is not present in our scan data, suggesting that the frontals were fused (Fig.4). This differs from the interpretations of both Broom (1903) and Carroll (1975a), who described the frontals as paired bones. The lateral surface of the frontal contributes broadly to the orbital margin, separating the prefrontal from the postfrontal. Much of the anterior part of the frontal is missing, and, as preserved, it does not extend beyond the anterior orbital margin (Fig.3). The suture with the postfrontal is oriented anteroposteriorly and is best preserved on the right side of the skull roof. The frontoparietal contact is an irregular transverse suture with only a very slight posterolateral extension, which terminates at the posterodorsal margin of the postfrontal (Fig.3). Part of the posterior region of the frontal bears an elevated area of bone associated with a raised subcircular boss on the anterodorsal surface of the parietal (Figs.3 and 5). The ventral surface of the frontal bears low, rounded crista cranii, which are best preserved adjacent to the right orbit (Fig.4). The subolfactory process of the crista cranii is absent.



Figure 4. Scan data from *Paliguana whitei* - transverse cross-section of anterior region of frontal in anterior view.

Parietal. The condition of the parietal region is too poorly preserved to determine the presence or absence of a midline suture. The right side of the post-orbital skull roof is the best preserved, including its anterolateral region. This shows contact of the parietal with the frontal, postfrontal and postorbital (Figs.3 and 5). The ventrally directed lateral edge of the parietal forms the medial margin of a large upper temporal fenestra (UTF) (Fig. 2 main text and Fig.3). The posterolateral process of the parietal forms the posterior margin of the UTF (Fig. 2 main text and Fig.4). This process is inclined slightly ventrally and posterolaterally, at around 70 degrees from the midline of the skull, and tapers distally. It is a relatively long process, preserved with a transverse break around the midpoint. There is a shallow concave recess on the distal anterior surface, which may have received the small supratermporal (Carroll 1975a).

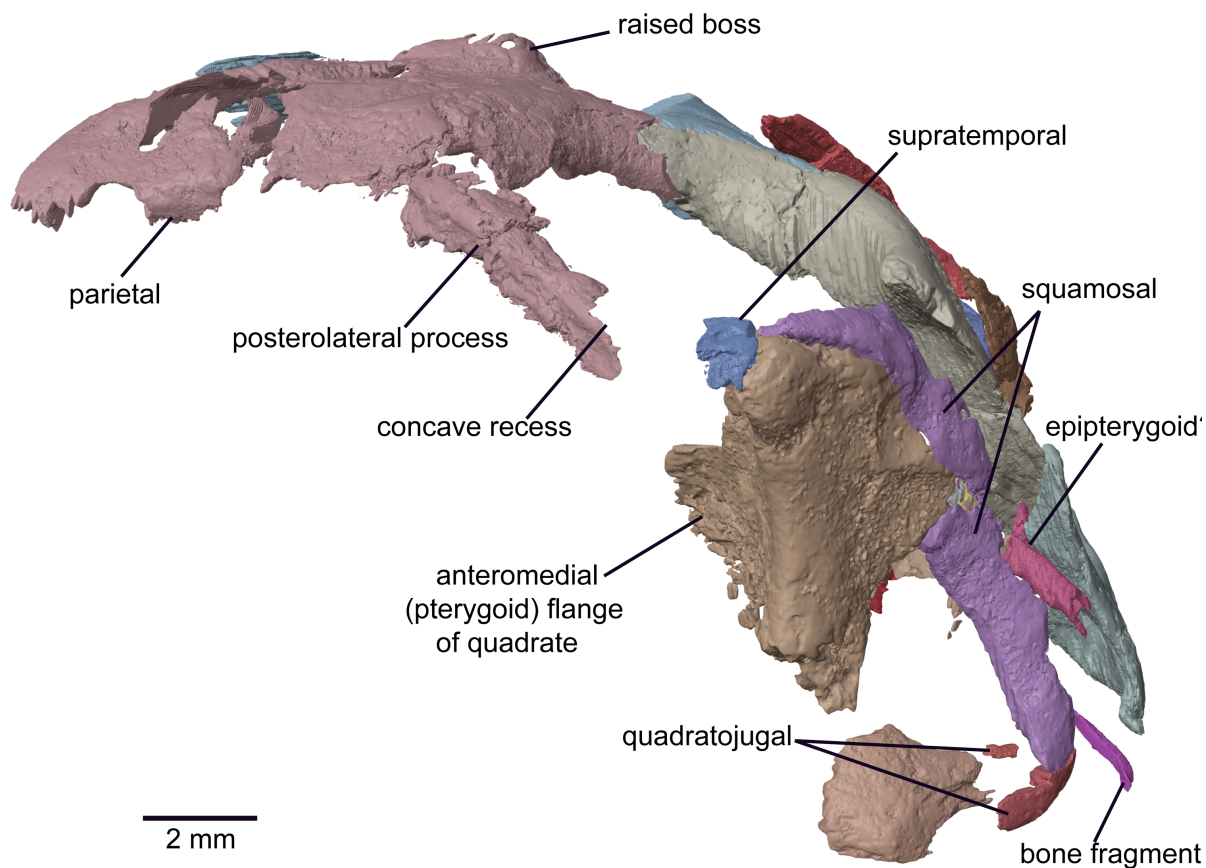


Figure 5. Segmented bones of the right temporal region of *Paliguana whitei* in posterior view.

The posterior region of the parietals is inclined posteroventrally. This is particularly visible on the left side, where the posterolateral process is broken and missing (Figs.3 and 5). This morphology indicates a slight occipital exposure of the parietal and we found no evidence of sutures that would indicate the presence of independent occipital elements forming this region. Our interpretation therefore differs from that of Broom (1925), who considered the posteroventral surface of the parietal as a possible 'interparietal' (=fused postparietals), and Carroll (1975a, 1975b), who suggests the presence of paired postparietal and tabular bones. Subsequent phylogenetic analyses, agreed with this interpretation, (e.g. Gauthier *et al.* 1988 c.5 and c.6, Evans 1991 c.7 and c.8). However, more recent studies have considered the tabular as absent, and the postparietal as either absent or indeterminate (Ezcurra 2016 c.171 and c.173, Simões *et al.* 2018 c.64 and c.65).

The dorsal surface of the parietal bears a prominent, raised subcircular boss anteriorly to the right of the midline (Figs.3 and 5). Most of this has been eroded away, and only the posterior, right lateral and anterior surfaces have been preserved. The anterior surface of the boss extends onto the frontal and is traversed by the frontoparietal suture. Broom (1925) suggested that two raised areas of the parietal may have been present either side of the midline, each supporting a small horn or bony scales, but this cannot be determined for the left-side of the midline.

There is no indication of a parietal foramen. However, its absence cannot be unequivocally determined due to the somewhat fragmentary condition of the parietal along the midline. Carroll (1975a) suggested that a large parietal foramen was located centrally on the midline, and Broom (1925) suggested it was located anteriorly between raised bosses. Neither observation can be confirmed. The presence of a parietal foramen is a plesiomorphic trait that is present in all non-saurian reptiles (Fox and Bowman 1966, Gow 1975, Reisz 1981, Modesto 2006, Ford and Benson 2019). It is also present in *Sophineta* (Evans and Borsuk-Białynicka 2009) and rhynchocephalians, e.g. *Gephyrosaurus* (Evans 1980) and *Diphydontosaurus* (Whiteside 1986). However, it is absent in other lepidosauromorphs, e.g. *Marmoretta* (Griffiths *et al.* in review), and there is no evidence of the foramen in *Fraxinisaura* (Schoch and Sues 2018). The foramen is also absent in kuehneosaurs (Evans and Borsuk-Białynicka 2009), and early archosauromorphs, e.g. *Protorosaurus* (Gottman-Quesada and Sander 2009) and *Macrocnemus* (Jiang *et al.* 2011).

Temporal region

The temporal region of *Paliguana* is the best-preserved part of the skull, but has nevertheless been widely debated from both an anatomical and diagnostic viewpoint. Much of the debate has focused on the presence or absence of traits typically attributed to lepidosauromorphs, i.e. a 'conch' on the anterolateral surface of the posteriorly bowed quadrate, a small dorsally positioned squamosal, the diminution or absence of the quadratojugal and the incomplete ventral margin of the lateral temporal fenestra (LTF). These features can now be substantially determined.

Postfrontal. The postfrontal is a sub-triangular bone that forms the posterodorsal rim of the orbit (Fig. 2 main text and Fig.3) and articulates with the anterodorsal surface of the postorbital in a (unfused) sutural contact. The postfrontal tapers ventrally and terminates at the midpoint of the dorsal process of the postorbital. Dorsally, the anterior process contacts the frontal along its medial edge in an anteroposteriorly-straight suture. The postfrontal bears no distinct posterodorsal process, and only makes a very narrow contact with the parietal at its posterodorsal corner (Fig.2 main text and Fig.3). Carroll (1977) described the postfrontal as contributing to the UTF. However, the postfrontal is excluded from the UTF by contact between the dorsal process of the postorbital and the anterolateral corner of the parietal (Fig.2 main text).

The exclusion of the postfrontal from the UTF is a plesiomorphic feature of diapsid reptiles, and the participation of the postfrontal in the UTF, resulting from the loss of contact between the postorbital and parietal, an apomorphy of lepidosauromorphs (deBraga and Rieppel 1997) or rhynchocephalians (Gauthier *et al.* 1988). The postfrontal participates in the UTF in the non-lepidosaurian lepidosauromorph *Marmoretta* (Griffiths *et al.* in press) and in the lepidosaur *Sophineta* (Evans and Borsuk-Białynicka 2009), in rhynchocephalians (Evans 1980, Whiteside 1986, Fraser 1988), and in squamates where the bone is present as a separate element, with the exception of some iguanians where the postfrontal is absent or greatly reduced (Evans 2008).

Postorbital. The postorbital is a large triradiate bone, forming the posterior margin of the orbit and the anterior margin of the UTF (Fig.2 main text). The right postorbital is the best preserved, although its posterior process is broken. The robust dorsal process extends dorsomedially to contact the parietal. The anterior surface of the dorsal process makes a broad contact with the postfrontal. The ventral process of the postorbital is elongate and tapering, and contacts the anterodorsal surface of the jugal. Only the anterior part of the posterior process is preserved. It is broken around its midlength, and its presumed contact with the squamosal is not preserved. It is likely that this process tapered posteriorly, and overlay the anterior process of the squamosal, as is common in many diapsids, forming the lateral margin of the upper temporal fenestra and the dorsal margin of the lateral temporal opening or emargination (Fig.2 main text).

Jugal. The right jugal is complete and largely undamaged (Fig.2 main text). The dorsal process is robust and tapers dorsally, contacting the posterior surface of the ventral process of the postorbital. The suborbital process is long, tapering anteriorly and terminating close to the anterior margin of the orbit. The ventral margin of the jugal is 'V'-shaped in cross-section, whereas the dorsal margin is rounded. There is no maxillary facet on the jugal. It is likely that the maxilla separated the jugal from the lacrimal, based on the preserved suborbital region of the left maxilla (Fig.2B).

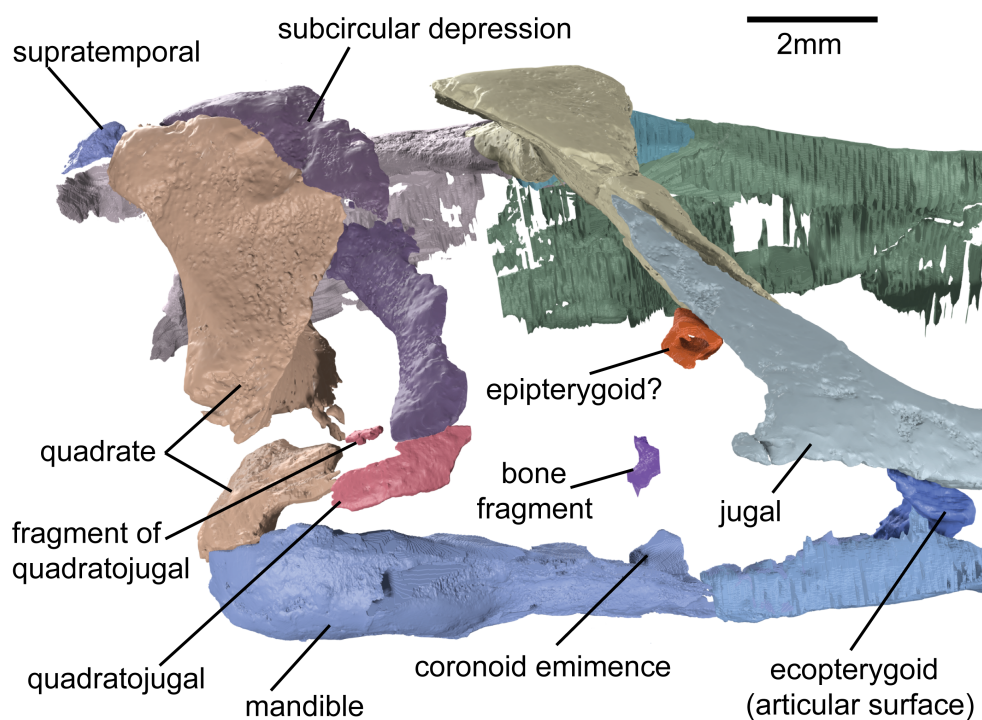


Figure 6. Segmented bones of the posterior region of the skull of *Paliguana whitei* in ventrolateral view.

The jugal bears a small, spur-like posteroventral process (Fig.6). The posterior surface of the jugal is therefore distinctly concave. This process does not contact the quadratojugal, and the lower temporal bar (LTB) of the lateral opening is absent. A LTB, formed by contact between the

posterior process of the jugal and the anterior process of the quadratojugal, was probably absent in the common ancestor of archosauromorphs and lepidosauromorphs (Müller 2003, Evans and Jones 2010), as well as in derived non-saurian neodiapsids of the late Permian, e.g. *Claudiosaurus* (Carroll 1981), *Coelurosauravus* (Evans 1982), and *Acerosodontosaurus* (Bickelmann *et al.* 2009). The LTB is absent in all fossil and extant lepidosauromorphs, with some exceptions where a complete bar was formed, e.g. some sphenodontian rhynchocephalians (Reynoso and Clark 1998, Evans 2008, Martinez *et al.* 2013) and some Cretaceous squamates (Lu *et al.* 2008, Mo *et al.* 2010, Simões *et al.* 2016). It is also absent in early archosauromorphs, e.g. *Protorosaurus* (Gottman-Quesada and Sander 2009), *Pamelaria* (Sen 2003), *Mesosuchus* (Dilkes 1998), and *Jesairosaurus* (Jalil 1997).

A small fragment of bone posterior to the posteroventral process of the jugal (Figs.5 and 6) was first identified by Broom (1903) as a fragment of the lower jaw, then by Carroll (1975a) as a possible rudiment of the quadratojugal. Although the mandible is badly damaged and crushed along its entire length, this narrow fragment of bone lies dorsolateral to the lower jaw-line, and seems unlikely to have been detached from the mandible. Equally, it does not form part of the jugal or the quadratojugal, and remains unidentified. Another, somewhat larger bone lies across the medial surface of the dorsal process of the jugal (Figs.5 and 6). This is a short length of tubular bone that may have formed part of the columnar process of the epipterygoid or could also be a hyoid element.

Squamosal. Most of the right squamosal is present, although the anterodorsal process that contacts the postorbital is missing. As preserved, it is a dorsoventrally elongate bone, extending from the lateral margin of the upper temporal fenestra to the quadratojugal ventrally (Fig.2 main text and Fig.6). The posterodorsal part of the squamosal contacts the anterodorsal surface of the quadrate and extends posterodorsally, terminating close to the cephalic head of the quadrate. The squamosal does not enclose the quadrate head dorsally, but rather tapers to a point where it terminates just anterior to this. The quadrate head instead is enclosed by the supratemporal, a small part of which is preserved (Fig.2 main text and Fig.5). Contact of the squamosal with the posterolateral process of the parietal would therefore have been limited to a small area on the posterodorsal surface of the squamosal. This condition is similar to extant iguanids (Evans 2008) and is unlike many crown-group reptiles, in which a posteroventral process of the squamosal caps the dorsal head of quadrate, e.g. *Sophineta* (Evans and Borsuk-Białynicka 2009), *Gephyrosaurus* (Evans 1980), *Protorosaurus* (Gottman-Quesada and Sander 2009), *Macrocnemus* (Jiang *et al.* 2011) and *Pamelaria* (Sen 2003).

The anteroventral process of the squamosal is anteroposteriorly narrow, and is detached from the rest of the squamosal by a diagonal fracture, visible in medial view (Fig.6). This fracture is partially concealed in lateral view by the anterolateral flange of the quadrate (Fig.6). The anteroventral process terminates in a convex region that contacts the quadratojugal (Figs.6 and 7). The anterior surface of the anteroventral process is damaged. The posterior surface is smooth, unbroken, and forms the slightly concave anterior margin of a large opening, the quadratojugal foramen ('quadrate' foramen *sensu* Romer 1956). This is a large fenestrate opening, similar to the large foramen enclosed by the quadrate and quadratojugal in *Sphenodon* (Evans 2008), but unlike the smaller aperture seen in early lepidosauromorphs including early rhynchocephalians, e.g. *Diphydontosaurus* (Whiteside 1986). This opening was first described as a quadrate foramen by Broom (1925), an interpretation that was questioned by Carroll (1975a, 1977) who suggested it was an artefact of preparation or a weathered area of an otherwise complete quadrate, with the squamosal limited to the dorsal surface of the quadrate. More recently, however, the opening has been recognised as a large foramen, along with the presence of a ventral process of the squamosal (Simões *et al.* 2018).

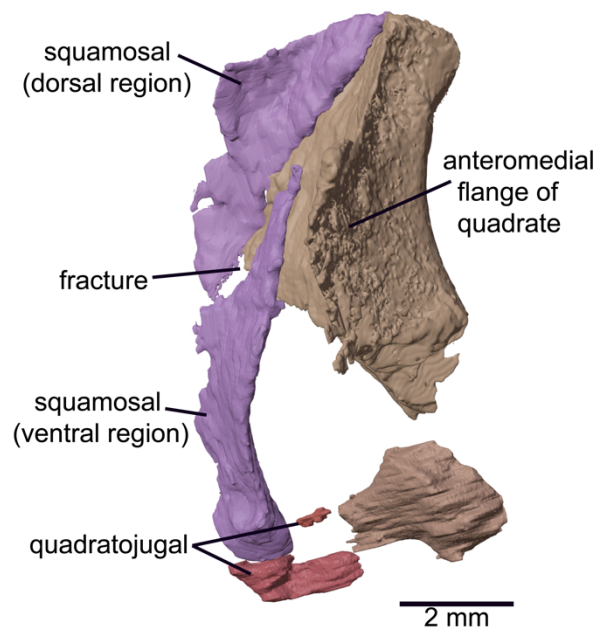


Figure 7. Segmented bones of the quadrate, squamosal and quadratojugal of *Paliguana whitei* in medial view.

An anteroventral process of the squamosal that extends along the anterior surface of the quadrate is considered a plesiomorphic condition in diapsids (Evans and Borsuk-Białynicka 2009). It is retained in rhynchocephalians (Evans 1980, Fraser 1988) and *Sophineta* (Evans and Borsuk-Białynicka 2009). The reduction or loss of this process occurs in squamates (Mateer 1982, Reynoso 1998, Evans and Barbadillo 1999, Simões *et al.* 2017), and was noted as a squamate synapomorphy by Gauthier *et al.* (1988). It is absent, for example, in *Megachirella* (Simões *et al.* 2018), but also convergently in kuehneosaurs.

Quadratojugal. This is a rectangular, horizontally oriented bone that contacts the squamosal anterodorsally and the quadrate posteriorly. An isolated splinter of bone between the squamosal and the quadrate may be a detached portion of the quadratojugal (Figs.5 and 7). Anteriorly, the quadratojugal extends dorsally as a low ramus, with a concave dorsal surface that articulates with the ventral process of the squamosal. The ventral surface of the quadratojugal forms a sharp longitudinal ridge. Posteriorly, the quadratojugal has separated from the quadrate, probably as a result of the diagonal fracture in the squamosal noted above. However, it is evident from the roughly textured recess on the anteroventral process of the quadrate that the quadratojugal contacted the lateral surface of this process in life, thus forming the ventral margin of the quadratojugal foramen (Fig.2 main text)

In early lepidosauromorphs the quadratojugal, although present, is reduced to a small vertically orientated bone that is either firmly sutured or fused to the anteroventral surface of the quadrate, e.g. *Marmoretta* (Griffiths *et al.* in review), *Sophineta* (Evans and Borsuk-Białynicka 2009), *Gephyrosaurus* (Evans 1980) and *Megachirella* (Simões *et al.* 2018). In early archosauromorphs the quadratojugal is either similarly present, e.g. *Pamelaria* (Sen 2003) and *Prolacerta* (Modesto and Sues 2004), or entirely absent, e.g. *Jesairosaurus* (Jalil 1997), *Macrocnemus* (Jiang *et al.* 2011) and *Tanystropheus* (Nosotti 2007). Although the quadratojugal in *Paliguana* is somewhat reduced in size, its horizontal orientation is unique among early crown-group reptiles. In Permian neodiapsids, only *Youngina* possesses a horizontally orientated quadratojugal that contacts the squamosal posteriorly (the nature of the contact with the quadrate is unknown) (Gow 1975). However, exceptionally for neodiapsids, the LTB is complete in *Youngina*, although this was possibly independently acquired, as in some polyglyphanodonts squamates as noted above, and in the extant *Sphenodon* (Evans and Jones 2010).

Quadrate. The left quadrate shaft is too poorly preserved to describe in any detail. Much of the right quadrate is preserved, however, including the cephalic condyle, most of the posterior shaft and the anterior flanges (Fig.8). Ventral to this region of bone, the shaft of the quadrate is broken, and the remaining part of the quadrate, including the lateral condyle and a short anteroventral process, is detached from the rest of the quadrate shaft.

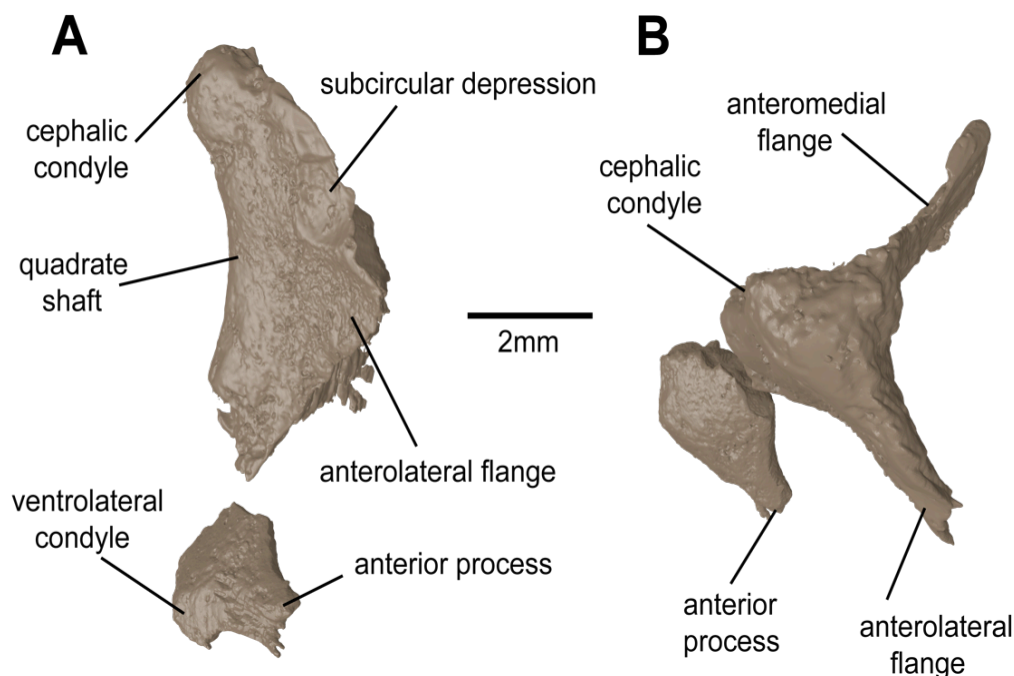


Figure 8. Segmented right quadrate of *Paliguana whitei*. A, in lateral view; B, in dorsal view.

The quadrate shaft is a robust pillar of bone that is sub-triangular in cross-section and forms the posterior surface of the quadrate (Fig.8A). The shaft is bowed anteriorly in lateral view, as in many early crown-group reptiles, e.g., *Pamelaria* (Sen 2003), *Sophineta* (Evans and Borsuk-Białynicka 2009), *Macrocnemus* (Jiang *et al.* 2011) and *Megachirella* (Simões *et al.* 2018). The smooth articular surface of the cephalic head is therefore oriented slightly posterodorsally. Ventrally, the shaft is broken close to the condyles. The detached region includes the lateral condyle, with a rounded ventral surface, which contacts the posterodorsal surface of the mandible (Fig.6). A short but prominent process extends anteriorly from the ventral region of the quadrate adjacent to the lateral condyle and bears a facet for articulation with the quadratojugal.

The anteromedial (pterygoid) flange extends anteromedially at an angle of 45° from the quadrate shaft (Fig.8B). Its dorsal margin slopes anteroventrally from the dorsal head of the quadrate. Its ventral region forms a dorsoventrally broad sheet of bone that extends anteriorly, but is broken and incomplete anteriorly. The anterolateral flange of the quadrate extends anterolaterally at an angle of 45° from the shaft (Fig.8B). It is a dorsoventrally deep flange, with a triangular outline in lateral view, attenuating anteriorly and articulating with the posterior surface of the squamosal, reaching its anteriormost point midway along the squamosal and bounding the quadratojugal foramen dorsally and posterodorsally (Fig.2 main text). A smooth, subcircular depression is present on the dorsolateral surface of the flange (Fig.8A), extending anterodorsally on to the squamosal (Fig.6). Nevertheless, the quadrate ‘conch’ is clearly absent, contrary to the interpretation of several studies (Carroll 1975a, Evans and Borsuk-Białynicka 2009, Ezcurra 2014).

The lateral ‘conch’ of the quadrate is formed by the posterolateral curvature of the anterior lamina of the anterolateral flange of the quadrate, forming a recess or concavity in the lateral surface. The tympanic crest is formed by the association of the ‘conch’ with a thickened ridge of

bone extending dorsoventrally along its anterior surface. This morphology was considered a synapomorphy of lepidosauromorphs (Gauthier *et al.* 1988), although the present study finds the ‘conch’ as present only in lepidosaurs. In extant squamates it provides an anterior point of contact for the tympanic membrane (Evans 2008). The ‘conch’ and tympanic crest are absent in non-saurian neodiapsids, e.g. *Youngina* (Gow 1975), *Claudiosaurus* (Carroll 1981) and *Acerosodontosaurus* (Bickelmann *et al.* 2009), although convergently present in kuehneosaurs (Evans 2009).

Supratemporal. The supratemporal is represented by a fragment of bone lying dorsal to the cephalic condyle of the quadrate (Fig. 2 main text and Fig.5). Although irregularly shaped and incomplete, it is anteroposteriorly elongate and probably capped the cephalic head of the quadrate and articulated with the distal tip of the posterolateral process of the parietal. It is not possible to determine the nature of contact between the supratemporal and squamosal. Broom (1925) noted the presence of a ‘splint-like’ tabular (= supratemporal) in *Paliguana*. The supratemporal is also present in early lepidosauromorphs, e.g. *Sophineta* (Evans and Borsuk-Białynicka 2009), early rhynchocephalians, e.g. *Clevosaurus* (Chambri-Trowell *et al.* 2019) and most squamates, including Jurassic taxa like *Eichstaettisaurus* (Simões *et al.* 2017) and *Ardeosaurus* (Mateer 1982), where it combines with the squamosal to provide the typical squamate quadrate suspension (Robinson 1967).

Palate

Several fragments of the palate are preserved, although only the right vomer and palatal process of the pterygoid can be identified with certainty. The complete right ectopterygoid is preserved *in situ* associated with the right jugal.

Vomer. The right vomer can be identified from its concave lateral surface, which forms the medial margin of the right internal naris (Fig.9A). The ventral surface of the vomer bears two irregular rows of sharply pointed teeth that meet anteriorly. One row commences at the posterolateral corner of the vomer, extending anteromedially, and the second is oriented anteroposteriorly along the ventromedial surface. The lateral surface of the vomer, which forms the medial margin of the internal naris, is thickened and raised somewhat dorsally from the rest of the vomer. Our scan data show that this lateral surface is subcircular in transverse section, with an internal cavity or canal that extends along the length of the margin of the internal naris. A similar condition is found in the early rhynchocephalian *Gephyrosaurus* (Evans 1980).

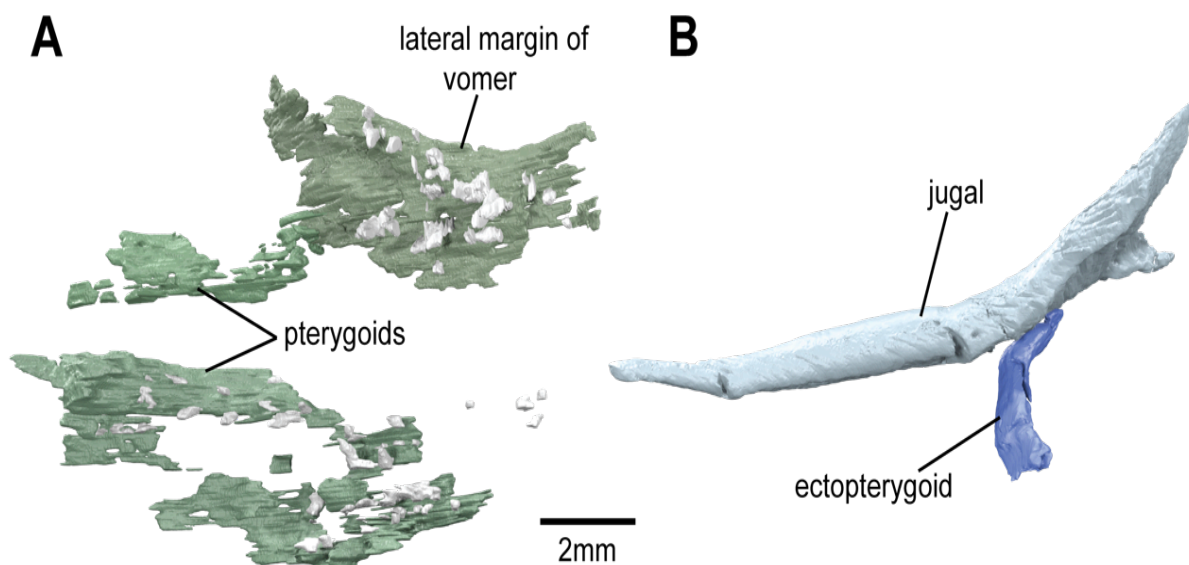


Figure 9. Segmented right jugal and palatal bones of *Paliguana whitei*. A, partial vomers and pterygoids in ventral view; B, right ectopterygoid and right jugal in dorsomedial view.

Teeth on the ventral surface of the vomer are absent in all squamates, with the exception of some anguids and glyptosaurines (Gauthier *et al.* 1988). A vomerine dentition is present in neodiapsids, e.g. *Youngina* (Gow 1975), and rhychocephalians, e.g. *Gephyrosaurus* (Evans 1980), *Diphydontosaurus* (Whiteside 1986). The presence of vomerine teeth in *Paliguana* confirms this feature is likely to have been the ancestral condition for lepidosauromorphs, as hypothesised by Gauthier *et al.* (1988).

Pterygoid. The anterior palatal rami of the pterygoids are represented by two fragments of anteroposteriorly elongate bone lying close to the midline of the palate (Fig.9A). Their medial surfaces are quite straight. The left fragment bears several pointed teeth. As preserved, they demonstrate that the pterygoid and vomer were in contact medially, excluding the palatines from the interpterygoid vacuity.

Ectopterygoid. The right ectopterygoid is complete, apart from a diagonal fracture separating the lateral head from the medial ramus (Fig.9B). The lateral head is expanded posteriorly as a spur-like process, with a slightly concave lateral articulating surface that contacts the jugal. There is no anterior process on the lateral head. The medial ramus is ribbon-like and has a concave posterior surface and convex anterior surface, giving a somewhat semi-lunate shape to the bone (Fig.9B). There is a shallow recess on the dorsomedial surface, which probably received the transverse process of the pterygoid. The medial head is not bifurcated, as in *Sophineta* and early rhychocephalians (Evans 1980, Whiteside 1986, Fraser 1988, Evans and Borsuk-Białynicka 2009), but terminates as a single, slightly anteroposteriorly-expanded facet, similar to the medial ramus in *Fraxinisaura* (Schoch and Sues 2018).

Braincase

Several occipital elements are preserved. They are, however, badly crushed and the bone is fragmented and highly cancellous in nature. Furthermore, preparation of the specimen has resulted in the loss of some bone surface, further complicating interpretation of the braincase anatomy. Only the right exoccipital and left prootic can be identified and described.

Exoccipital. The disarticulated right exoccipital is preserved, and was previously noted by Carroll (1975a). It is a dorsoventrally tall bone with a mediolaterally narrow dorsal portion that widens ventrally into a broad base for contact with the basioccipital (Fig.10B). A slight concavity of the medial surface provided the lateral margin of the foramen magnum. Based on its morphology, it is unlikely that the right exoccipital contacted its partner, either dorsally or ventrally. Consequently, the basioccipital and the supraoccipital participated in the foramen magnum. This is likely also the case in *Gephyrosaurus* (Evans 1980) and *Marmoretta* (Evans 1991), in which the exoccipital is similar to that of *Paliguana*. The exoccipital is not fused with either the basioccipital or the opisthotic. Hypoglossal foramina were not visible from the scan data.

The fusion of the exoccipital to the opisthotic to form the oto-occipital occurs prenatally or neonatally in squamates (Maisano 2001), creating the subdivision of the metotic fissure by apposition of the exoccipital to the ampullary swelling of the posterior semi-circular canal, a synapomorphy of squamates (Gauthier *et al.* 1988, Evans 2008). In *Paliguana* the exoccipital is preserved as unfused to either the opisthotic or the basioccipital, a condition considered plesiomorphic for diapsids (Gauthier *et al.* 1988). The exoccipital is not fused to the opisthotic in rhychocephalians, e.g. *Gephyrosaurus* (Evans 1980), *Planocephalosaurus* (Fraser 1982), and in *Marmoretta* (Evans 1991). The condition is unknown in other stem-lepidosaurs, although it is likely that the exoccipital was unfused to the opisthotic in the basal squamate *Huehuecuetzpalli* (Reynoso 1998).

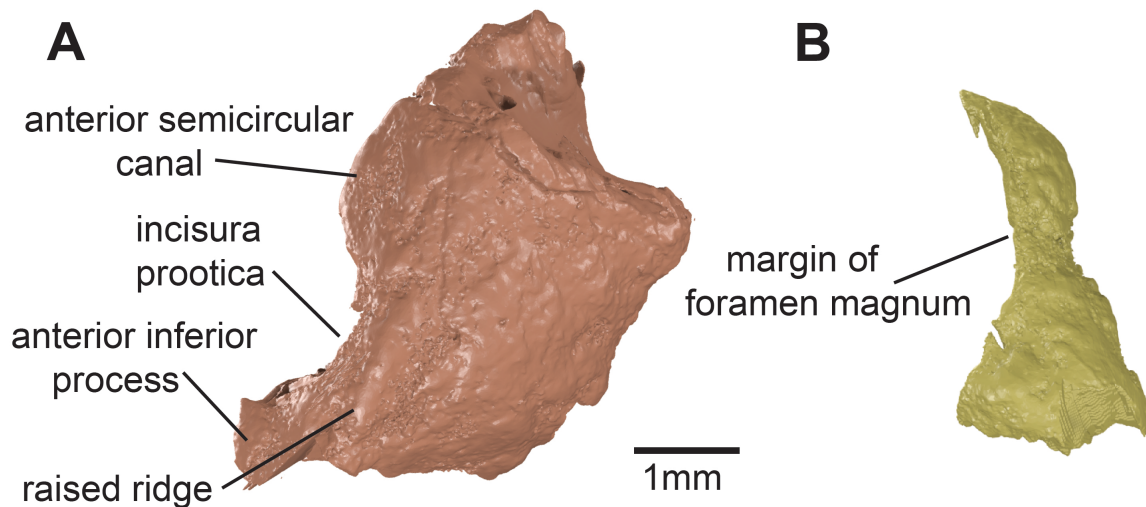


Figure 10. Segmented bones of the braincase of *Paliguana whitei*. A, left prootic in lateral view; B, right exoccipital in posterior (occipital) view.

Prootic. The left prootic is disarticulated and has moved to a position posterior to the right exoccipital and anteromedial to the right quadrate, where it is re-oriented such that its dorsal surface faces ventrally. The lateral surface of the prootic is smoothly convex. There is a slight raised ridge posterior to the incisura prootica. This is not interpreted as the crista prootica, and this feature is considered as absent (Fig.10A). The alar process is also absent, and the incisura prootica is a shallow concavity. There is a prominent anterior inferior process, which contacted the clinoid process of the basisphenoid. Unfortunately, the condition of the bone is not sufficiently well preserved to allow a description of the endosseous canals.

The absence of the crista prootica and alar process of the prootic, and the shallow incisura prootica are plesiomorphic for diapsids (Evans 1986, 1987). The morphology of the prootic in *Paliguana* is remarkably similar to that of the late Permian non-saurian diapsid *Youngina* (Gardner *et al.* 2010).

Mandible

The right hemimandible has been crushed dorsoventrally, and its anterior region is also foreshortened anteroposteriorly (Fig.11A). Overall it is badly distorted, and most individual mandibular elements cannot be identified with certainty. However, parts of the dentary, splenial and surangular can be identified. The left hemimandible is very fragmented or missing apart from the anterior region of the dentary and splenial (Fig.11A).

Dentary. The anterior region of the left dentary, posteriorly up to the sixth alveolus, is partially preserved (Fig.11B). The labial parapet is raised dorsally above the lingual. The dentary terminates anteriorly in a pointed tip, with a short edentulous region about half the anteroposterior length of a single alveolus between the first tooth position and the tip of the dentary. Nutrient foramina are not visible on the lateral surface of the dentary, as found in *Sophineta* (Evans and Borsuk-Białynicka 2009) and there is no indication of a well-defined symphyseal articulation. Medially, a distinct gap between the dorsal and ventral regions of the dentary provides the lateral opening to the Meckelian canal, which extends anteriorly to the tip of the dentary. The canal is enclosed medially by the splenial (Fig.11B). Part of the anterior right dentary is preserved, and this has a similarly raised labial surface. This region also provides evidence of the anteroposterior crushing of the snout, with the dentary and splenial showing a 'bowing' of the medial surface (Fig.11A). The posterior region of the dentary is too poorly

preserved to determine the extent of the posterior dentition or the length of the post-dentulous (coronoid) process.

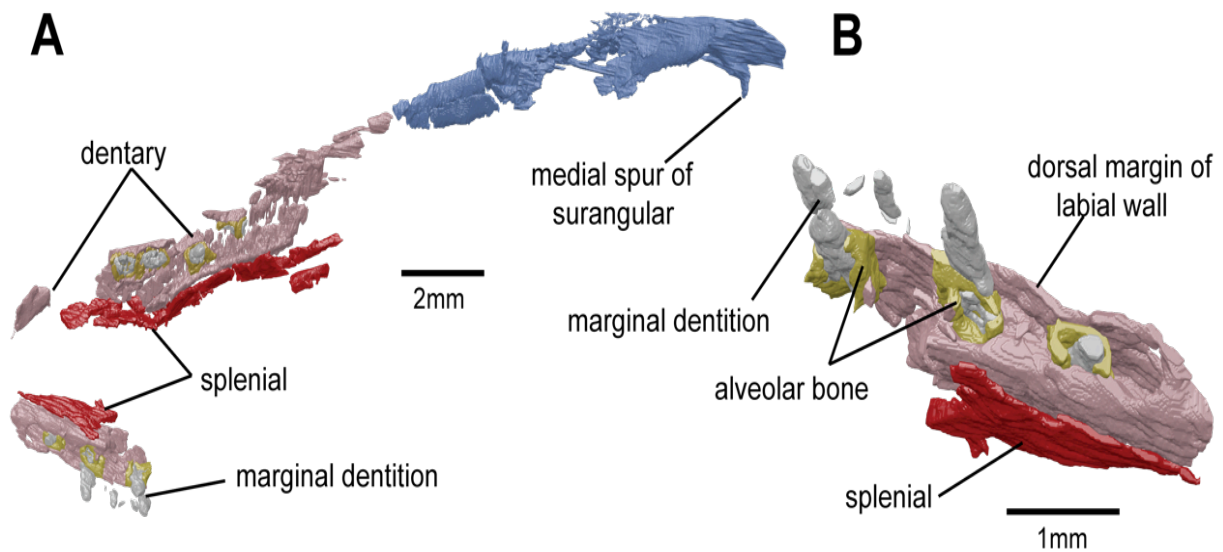


Figure 11. Segmented bones of the mandible of *Paliguana whitei*. A, partial right and anterior left hemimandible in dorsal view. B, left anterior hemimandible in dorsomedial view.

Splenial. Parts of both splenials are present. The anterior region of the left splenial attenuates anteriorly and terminates at the tip of the dentary, enclosing the Meckelian canal (Fig.11B). It is possible that the splenial contributed to the symphysis, but this cannot be unequivocally determined.

Surangular. The middle section of the right hemimandible is a thin and dorsoventrally crushed area of bone. The posterior region, however, maintains some degree of the original morphology. The surangular can be identified by the medial spur-like flange, which would have braced the posterior margin of the articular (Fig.11A). The lateral surface is dorsoventrally deep, and curves posteromedially. The lateral condyle of the quadrate is preserved in close association with the posterodorsal surface of the surangular (Fig.6). The articular is not preserved, and the absence or presence of a retroarticular process cannot be determined, although it is unlikely that the surangular contributed the process, if present.

Coronoid eminence. The subtemporal region of the right hemimandible is poorly preserved. However, a distinctive sub-triangular flange of bone extends dorsally from the lateral surface of this region, which is here interpreted as the coronoid eminence (Fig.6), although the contribution of individual bones to this eminence cannot be determined. The flange is mediolaterally thin, and is positioned ventral to the small posterior process of the jugal. A prominent dorsal process of the coronoid is present in many early lepidosauromorphs and squamates, e.g. *Marmoretta* (Griffiths *et al.* in review), *Megachirella* (Simões *et al.* 2018), *Huehucuetzpalli* (Reynoso 1997) and *Meyasaurus* (Evans and Barbadillo 1997).

Marginal dentition

The maxilla and mandible of *Paliguana* are poorly preserved and few marginal teeth are present. The right maxilla retains three partial teeth, as does the right dentary. The anterior region of the left dentary has three teeth *in situ*.

Tooth morphology. All of the preserved teeth are mediolaterally compressed with oval cross-sections at the base of the crown. The apicobasal root-to-crown length of the right dentary teeth

is 0.75mm. The mesiodistal length at the root is 0.3mm, and transverse width is 0.16mm for both the dentary and maxillary teeth in the same region. There is no evidence of carina on those parts of the crown that are preserved.

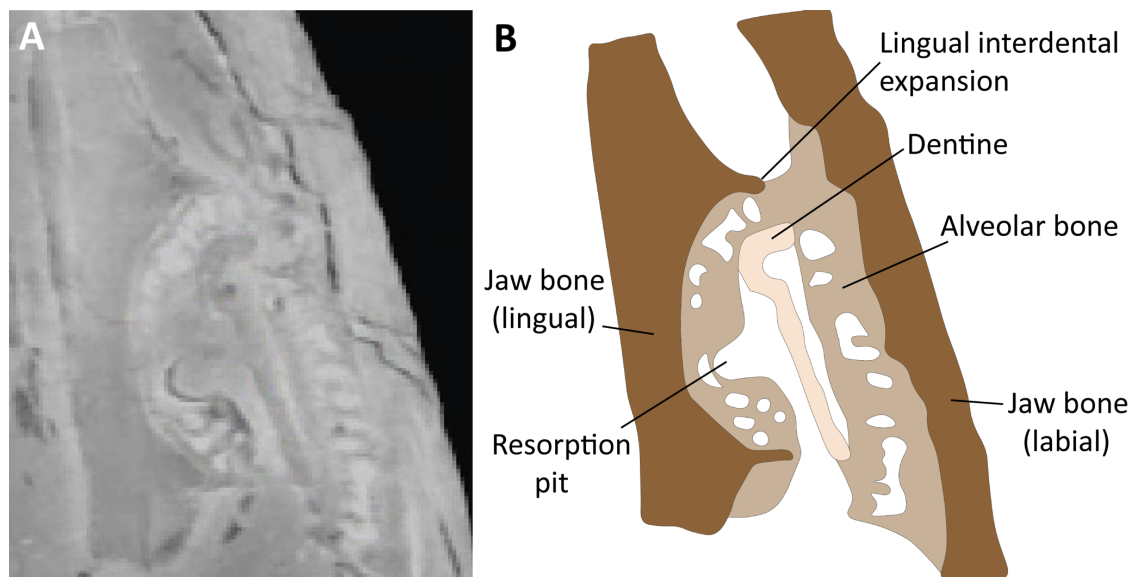


Figure 12. Section of left dentary of *Paliguana whitei*, showing root of mature marginal tooth and resorption pit. A, Synchrotron scan slice in dorsal view; B, diagrammatical representation of the scan slice.

Tooth implantation. The dentary teeth in *Paliguana* are set in shallow grooves, with each tooth partly delineated by an interdental expansion of the lingual wall of the dentary, which does not make contact with the labial wall (Fig.12). The root of the tooth is encased in a layer of vascularized alveolar bone that is ankylosed to the surrounding dentary bone. There is no discernable layer of periodontal ligaments or cementum separating the root from the alveolar bone, although these structures may only be revealed by histological analysis (Snyder *et al.* 2020). The labial wall is around twice the dorsoventral height of the lingual wall (Fig.3 main text and Fig.11B). The labial surface of the tooth root is ankylosed to the alveolar bone attached to the labial wall of the dentary. The dentine of the root extends deep into the groove and is not restricted to the dorsal region of the labial wall, unlike in typical pleurodont implantation (Bertin *et al.* 2018). Lingually, the base of the root is ankylosed to alveolar bone attached to the dorsal region of the lingual wall of the dentary (Fig.3 main text). Material of attachment extends from the alveolar bone along the lingual surface of the tooth root (Fig.3 main text). Tooth implantation in *Paliguana* is similar to that of other lepidosauromorphs, which is commonly described as pleurodont, e.g., *Fraxinisaura* (Schoch and Sues 2018) and *Megachirella* (Simões *et al.* 2018) or subpleurodont, e.g., *Marmoretta* (Griffiths *et al.* in press). We describe this as subpleurodont here, for reasons outlined below.

The implantation geometry of marginal dentition in reptiles has often been used to infer systematic and phylogenetic relationships (Camp 1923, Jones *et al.* 2013). *Paliguana* is therefore of great interest in this respect, since it may shed light on the stepwise changes that occurred in dental implementation around the basal divergence of crown-group reptiles.

In diapsids primitively, the marginal dentition is implanted in shallow discrete sockets (alveoli) on the dorsal surface of the subdental ridge (Vaughn 1955, Reisz 1981). The labial and lingual laminae are of similar dorsoventral height and interdental plates form the mesial and distal margins of each socket. The thecodont tooth implantation in mammals, archosaurs and bolosaurid parareptiles (Zaher and Rieppel 1999, Snyder *et al.* 2020) retained the symmetrical alveolus, but with a deeper socket. In contrast, lepidosaurs possess two forms of implantation; acrodonty, where the base of the tooth is ankylosed to the crest of the jaw bone, no root is present and there is no tooth replacement, e.g. in some rhynchocephalians and some squamates

(Jenkins *et al.* 2017), and pleurodony, where the tooth root is ankylosed to the dorsomedial surface of the labial wall, either directly or via bone of attachment, and teeth are regularly replaced. Pleurodont dentition is associated with the asymmetry of the labial and lingual walls (Presch 1974). However, it should be noted that pleurodony is not unique to lepidosauromorphs, and may have been present in other groups, such as shastasaurid ichthyosaurs (Callaway and Massare 1989) and weigeltisaurids (Pritchard *et al.* 2021).

In *Paliguana*, the extensive attachment of the tooth root and alveolar bone to the labial wall and the slightly raised lingual wall of the dentary suggest that the dental implantation is not pleurodont *sensu stricto* (i.e. see Presch 1974, Zaher and Rieppel 1999, Bertin *et al.* 2018). However, the asymmetry of the labial and lingual walls, the encasement of the root in alveolar bone and the dorsal extension of material of attachment along the lingual margin of the tooth root are strikingly similar to the tooth implantation in extant teiids (Bertin *et al.* 2018) – a condition described as both subpleurodont (Presch 1974) and subthecodont (Bertin *et al.* 2018). Subpleurodony has been specifically associated with the invasion of the lingual surface of the tooth root by bone of attachment (Zaher and Rieppel 1999), and this structure is present in *Paliguana* and the early lepidosauromorph *Sophineta* (Evans and Borsuk-Białynicka 2009). However, we also find that the slightly raised lingual wall in *Paliguana* retains a socket-like function and interdental plates are present, though incomplete. The implantation of marginal dentition in *Paliguana* therefore displays both primitive and derived traits that support a basal position among lepidosauromorphs.

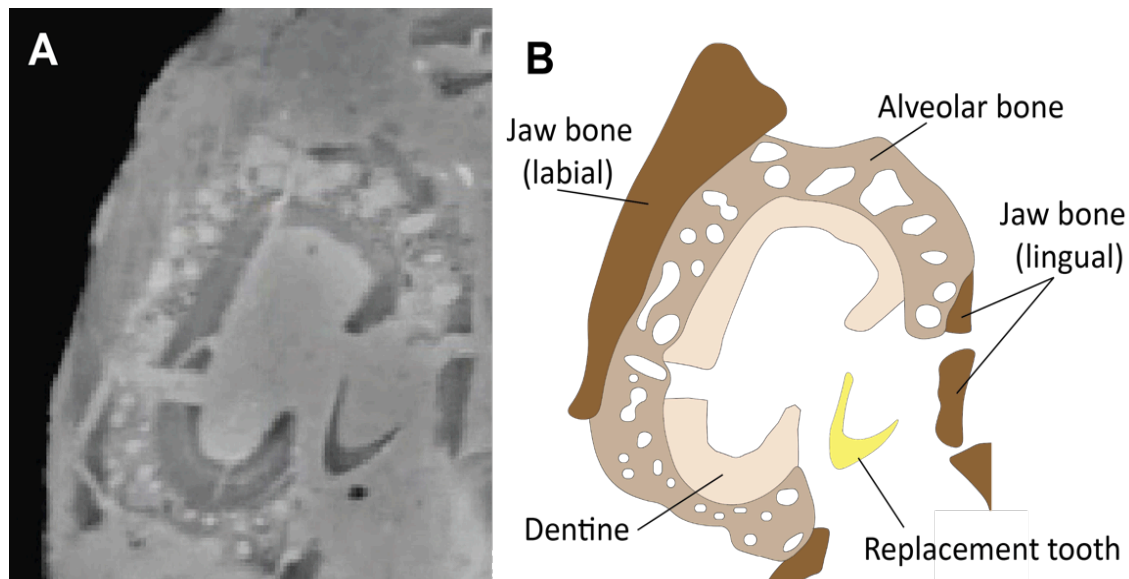


Figure 13. Section of right dentary of *Paliguana whitei*, showing replacement tooth. A, Synchrotron scan in dorsal view; B, diagrammatical representation of the scan.

Tooth replacement. In several of the preserved teeth resorption pits are present (Figs.12 and 13). They appear as circular vacuities in the alveolar bone attached to the lingual wall of the dentary, eventually resorbing the dentine of the root and reaching the pulp cavity. The replacement tooth develops inside the resorption pit (Fig.13). This replacement pathway is consistent with labio-vertical replacement in squamates, which always is associated with the presence of resorption pits (Bertin *et al.* 2018).

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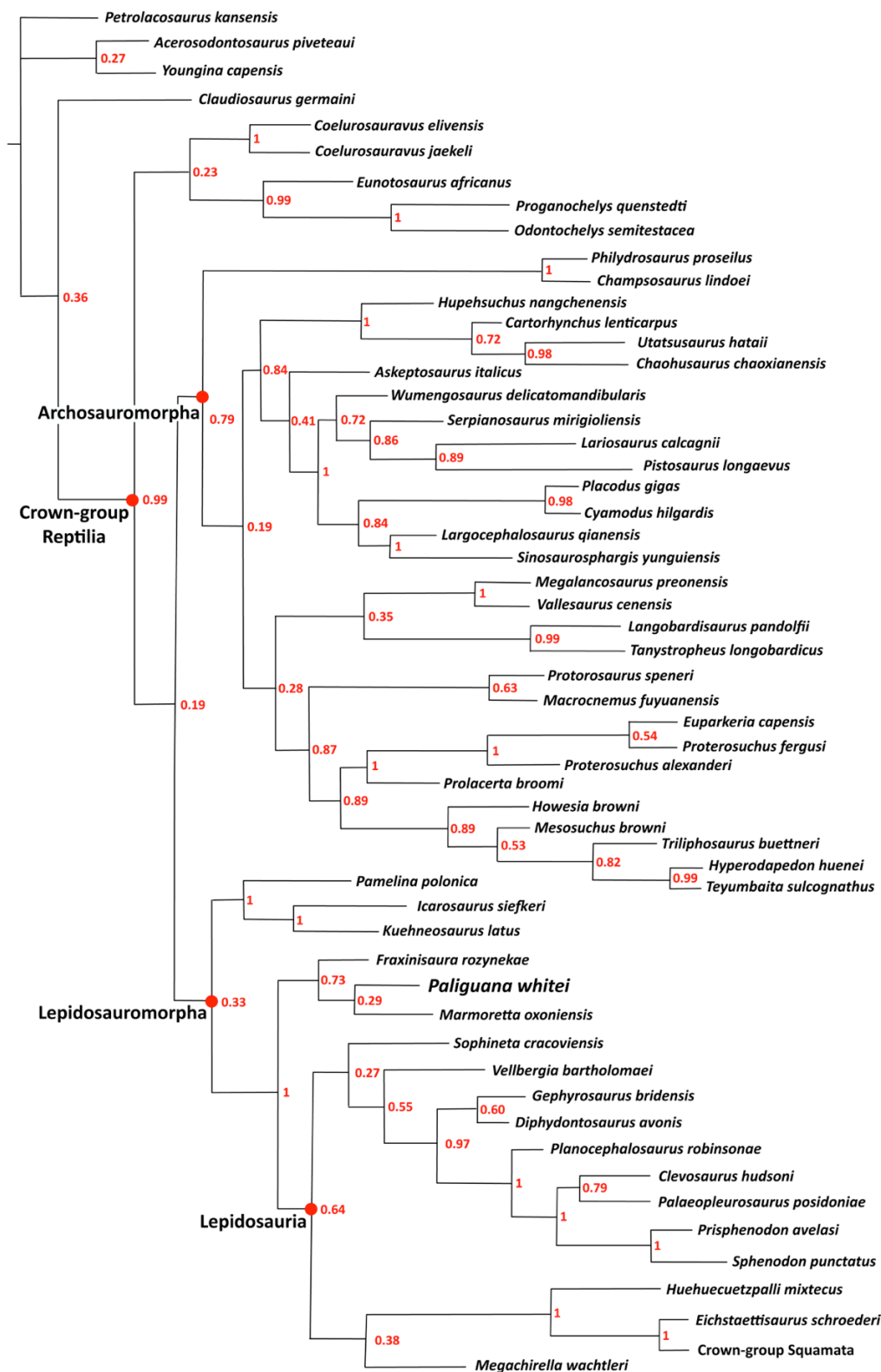
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A REASSESSMENT OF THE ENIGMATIC DIAPSID PALIGUANA WHITEI AND THE EARLY HISTORY OF LEPIDOSAUROMORPHA

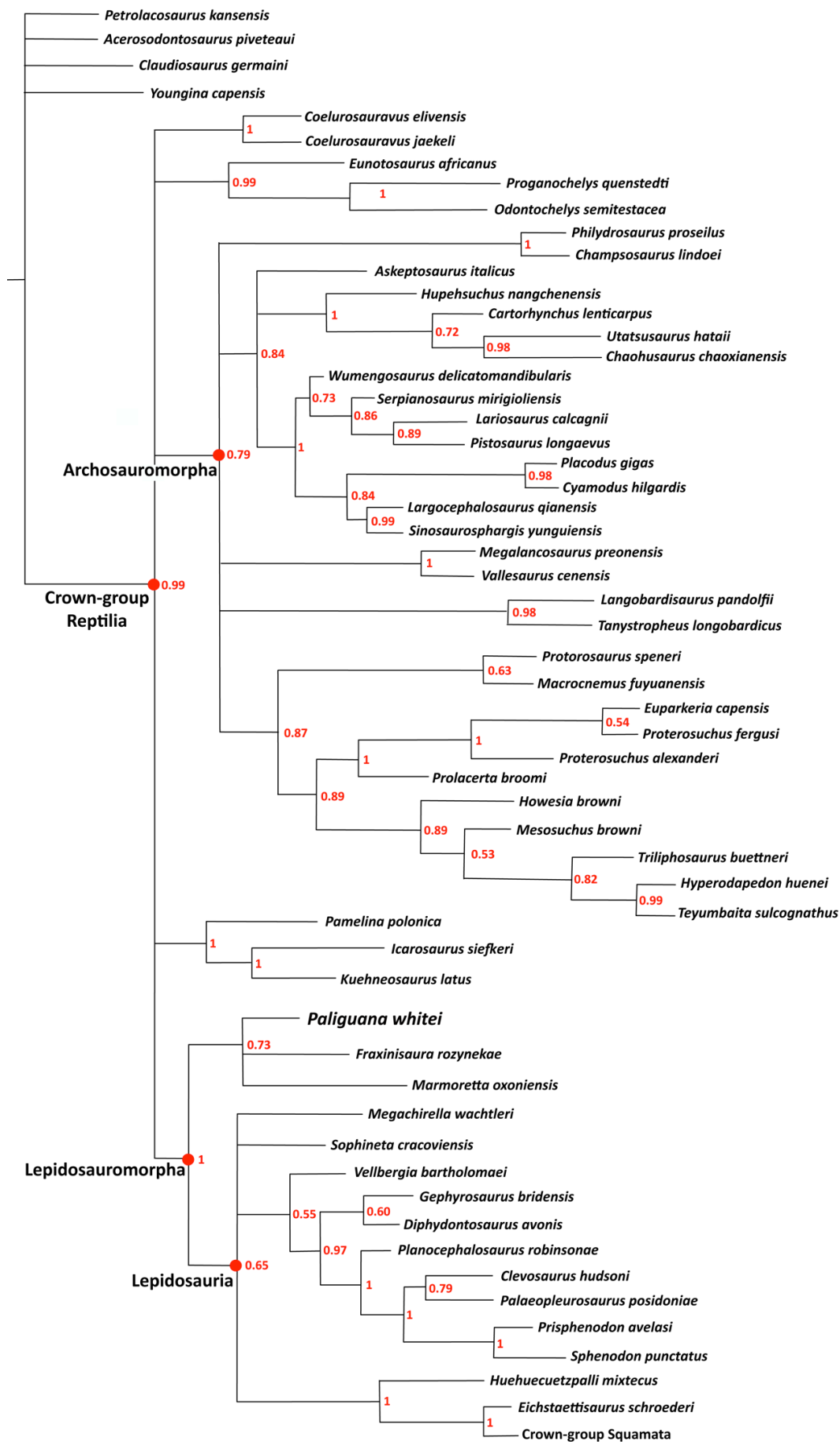
Authors: David P. Ford, Susan E. Evans, Jonah N. Choiniere, Vincent Fernandez and Roger B.J. Benson

SUPPLEMENTARY DATA 2

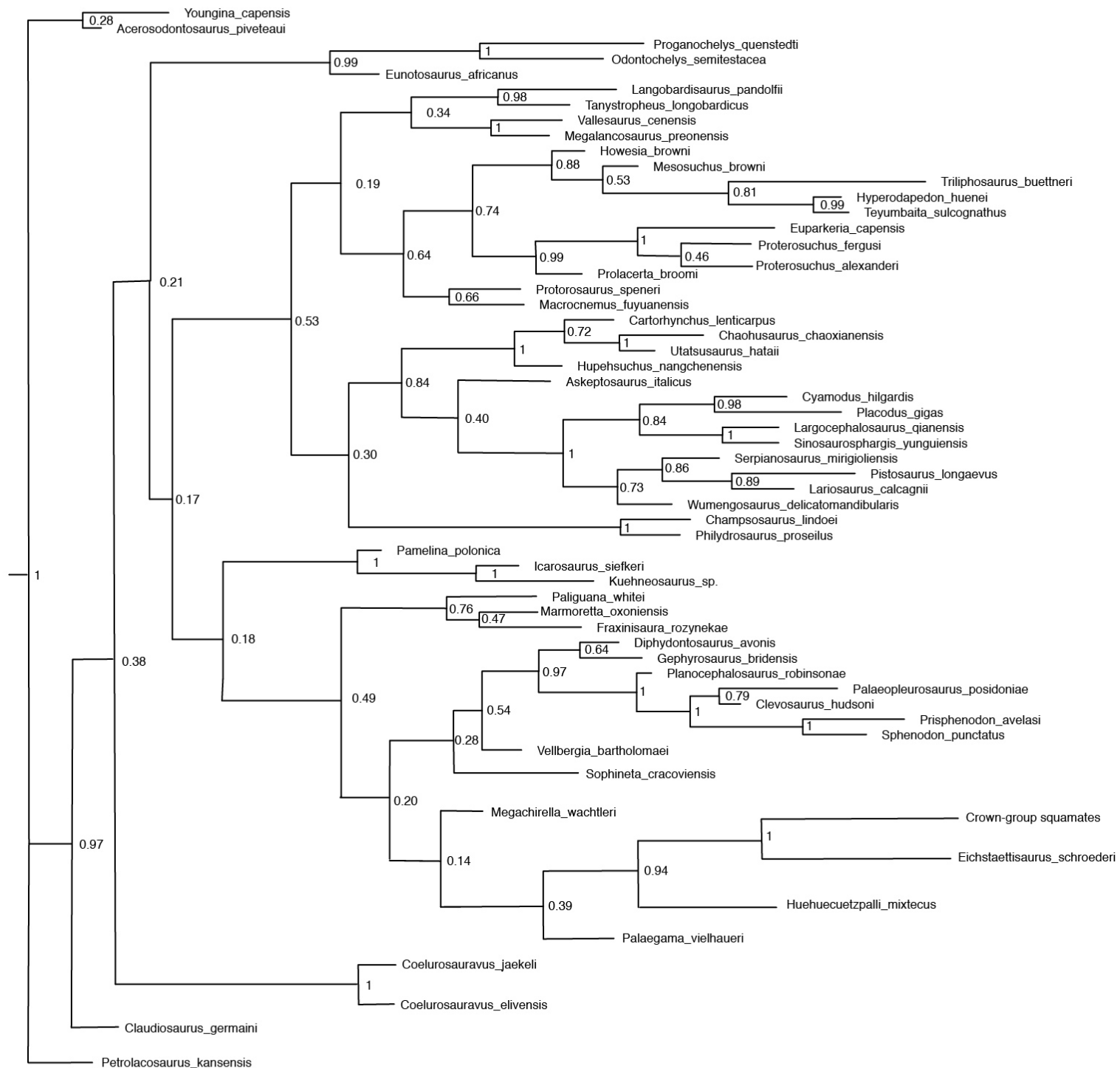
Results of phylogenetic analyses



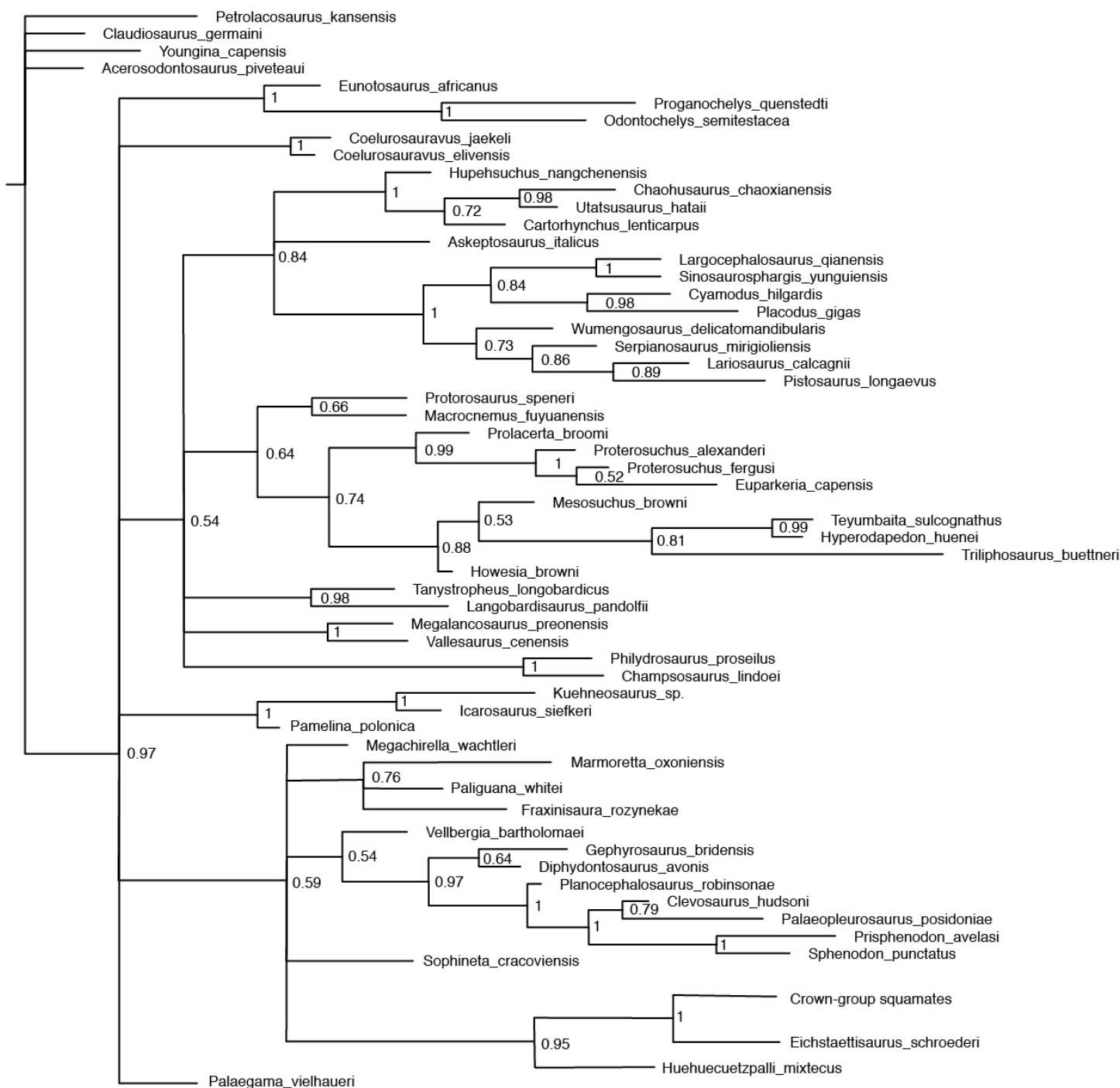
Supplementary Data 2 – Figure 1. Maximum Clade Credibility tree from Bayesian Mkv analysis, with posterior probabilities of each node in red.



Supplementary Data 2 – Figure 2. 50% majority rule tree (halfcompat command) from Bayesian analysis, with posterior probabilities of each node in red



Supplementary Data 2 – Figure 3. Maximum Clade Credibility tree from Bayesian analysis with *Palaeagama vielhaueri* added to operational taxonomic units. Posterior probabilities of each node in black.



Supplementary Data 2 – Figure 4. 50% Majority Rule tree (halfcompat command) from Bayesian analysis with *Palaeagama vielhaueri* added to operational taxonomic units. Posterior probabilities of each node in black.

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SUPPLEMENTARY DATA 3

Extended Methods

PPC-SR μ CT acquisition and reconstruction protocol

The reconstructed volume obtained with the methods outlined in the main article represents a cylinder of 8.91 mm in length and 8.91 mm in diameter. Because the specimen could not fit in such a volume, measuring approximately 30 mm in length and have a maximum width of 22 mm, multiple acquisitions were necessary to image the whole skull. The sample was mounted in order to place its longest dimension vertically; covering the vertical extend of the specimen was done by performing several acquisitions along the vertical axis. To extend the horizontal field of view, the first approach was to shift the centre of rotation by about 80 %, increasing the reconstructed diameter to 15.87 mm. While the dorso-ventral width of the skull fitted in this extended volume, it was not the case of the latero-lateral width (reaching 22 mm). As these two solutions would allow to reconstruct a cylindrical volume of 30 mm in length and 15.87 mm in diameter, it was decided to perform this process twice, focusing each time on one side of the skull and merge the two obtained cylindrical volumes. Doing so it was possible to cover the full extent of the specimen.

For each cylindrical reconstruction, 7 acquisitions were performed on the vertical axis, keeping a 50% overlap between consecutive scans. Using a translation motor aligned with the maximum width of the skull, the specimen was moved by 6.75 mm, allowing to reach a maximum reconstructed field of view of 22.60 in the long axis (i.e., the width). Each acquisition consisted of 6000 projections of a total integration time of 0.2 seconds over a rotation of 360°. Before reconstruction, radiographs from the 7 vertical scans were merged together (Benoit *et al.* 2020). Tomographic reconstruction was done using PyHST2 (Mirone *et al.* 2014) and the single distance phase retrieval approach (Paganin *et al.* 2002). Post reconstruction processing included modification of the bit depth from 32-bit to 16-bit as a stack of tiff and ring correction (Lyckegaard *et al.* 2011).

Phylogenetic analysis

The modified character-taxon matrix was analysed using a non-time calibrated Bayesian Mkv model in MrBayes v.3.2.5 (Ronquist *et al.* 2012). The 'standard' datatype was used for morphological data, and the coding was set at 'variable' (that is, only variable characters being sampled) with rates set to a gamma distribution. The Mkv model analysis was performed with two runs of four chains each for 50 million generations, with tree sampling every 500th generation and a 25% burn-in. The average effective sample size for the two parameters (tree length and shape of gamma distribution) were in excess of 50,000, and the average potential scale reduction factor was 1.000, with both chains demonstrating good convergence (average standard deviation of split frequencies 0.0028). Our results were expressed in a 50% majority rule tree (halfcompat command in MrBayes) and in a maximum clade credibility tree (MCC). The MCC tree is a single tree in the posterior sample with the maximum sum of posterior clade probabilities across all the constituent bifurcations (Heled and Bouckarert 2013). We used TreeAnnotator (v1.10.4 Rambaut and Drummond 2002-2018) to recover the MCC from a combination of the posterior tree files of the two runs from MrBayes output (.t files), less the 25% burn-off, producing a total of 150,000 trees. The script for the Bayesian analysis is provided in Part 6 of Supplementary Data. Optimisation of the 50% majority rule tree and the MCC tree were performed for both ACCTRAN and DELTRAN in PAUP v.4.0a, build 169 (Swofford, D.L. 2002).

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EARLY HISTORY OF LEPIDOSAUROMORPHA**

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Roger B.J. Benson

SUPPLEMENTARY DATA 4

Optimisation of characters states at key nodes

MCC tree

Crown-group Reptilia:

Unambiguous:

175 0→1

237 1→0

303 1→0

Acctran:

39 0→1

190 0→1

199 1→0

235 1→0

244 1→0

307 1→0

320 1→0

332 1→0

337 0→1

348 0→1

355 0→1

357 1→2

368 0→1

Deltran:

64 0→1

65 0→1

140 0→1

220 0→1

229 1→0

274 1→0

348 0→1

Lepidosauromorpha:

Unambiguous -

167 0→1

350 0→1

Acctran -

20 0→1
121 0→1
125 0→1
201 1→0
217 0→1
235 0→1
263 0→1
269 0→1
271 0→1
284 0→1
320 0→1
333 1→0
334 0→1
342 0→1
354 1→0
376 0→1
377 0→1
379 0→1
380 0→1

Deltran -

120 0→1
301 0→1
349 0→1
377 0→1

Paliguana + Fraxinisaura + Marmoretta:

Unambiguous:

101 0→1

Acctran:

8 0→1
81 1→0
82 0→1
121 1→0
140 1→0
144 0→1
181 2→0
189 1→0
190 1→0
200 1→0
219 0→1
290 0→2
294 1→0
305 3→0
369 1→0

Deltran:

20 0→1

73 0→1

291 0→1

Lepidosauria:

Unambiguous:

69 0→1

229 0→1

296 0→1

Acctran:

20 1→0

61 0→1

73 1→0

188 0→1

Deltran:

39 0→1

98 0→1

109 1→0

121 0→1

190 0→1

195 1→0

217 0→1

237 0→1

238 0→1

269 0→1

284 0→1

312 0→1

332 1→0

333 1→0

334 0→1

336 1→0

338 0→1

Rhynchocephalia + *Sophineta* + *Vellbergia*:

Unambiguous:

45 1→0

227 1→0

Acctran:

25 0→1

55 0→1

62 1→0

78 0→1

92 0→1
 118 1→0
 125 1→0
 182 0→1
 188 1→2
 263 1→0
 291 1→0
 295 0→1
 360 0→1
 361 0→1

Deltran:

50 0→1
 68 0→1

Rhynchocephalia + *Vellbergia*:

Unambiguous:

211 0→1

Acctran:

59 2→1
 61 1→0
 111 0→1
 173 0→1
 210 0→1
 347 0→1
 351 1→0
 362 0→1

Deltran:

23 0→1

Rhynchocephalia:

Unambiguous:

176 1→0

Acctran:

67 0→1
 352 1→0

Deltran:

55 0→1
 59 2→1
 111 0→1
 114 0→1
 173 0→1
 182 0→1

188 0→2
308 0→1
331 1→0
347 0→1
360 0→1
361 0→1

Squamata (including *Megachirella*):

Unambiguous:

198 0→1
322 0→1

Acctran:

7 0→1
21 0→1
27 0→1
50 1→0
67 0→1
68 1→0
71 0→1
89 1→0
95 0→1
114 1→0
116 0→1
124 1→0
151 0→1
162 0→1
170 0→1
224 0→1
270 0→1
286 0→1
289 0→2
308 1→0
346 1→0
347 0→2
357 2→0

Squamata (excluding *Megachirella*):

Unambiguous:

36 1→0
38 0→1
123 0→1
225 0→1
282 0→1
340 1→0
354 0→1
355 0→1

365 0→1

Acctran:

85 1→0

97 1→0

105 1→0

135 0→1

138 0→2

142 0→1

171 0→1

314 0→1

350 1→0

362 0→1

367 1→2

369 1→0

Deltran:

27 0→1

188 0→1

234 0→1

263 0→1

271 0→1

346 1→0

359 0→1

50% Majority Rule tree

Crown-group Reptilia:

Unambiguous:

39 0→1

64 0→1

65 0→1

156 0→1

175 0→1

199 0→1

229 1→0

235 1→0

237 1→0

244 1→0

274 1→0

293 0→1

303 1→0

320 1→0

337 0→1

347 0→1

Acctran:

86 1→0

109 1→0
120 0→1
140 0→1
181 0→2
185 0→1
227 0→1
301 0→1
307 1→0
350 0→1
357 0→2
368 0→1

Deltran:

140 0→1
220 0→1
273 1→0
278 1→0
305 2→3
348 0→1

Lepidosauromorpha:

Unambiguous:

42 0→1
68 0→1
167 0→1
201 1→0
309 1→0
349 0→1
352 0→1
358 0→1
376 0→1
379 0→1

Acctran:

23 0→1
50 0→1
67 0→1
98 0→1
195 1→0
217 0→1
234 0→1
235 0→1
237 0→1
238 0→1
269 0→1
271 0→1
284 0→1
291 0→1

302 0→1
307 0→1
312 0→1
320 0→1
322 0→1
329 0→1
331 1→0
332 1→0
333 1→0
334 0→1
336 1→0
338 0→1
339 0→1
342 0→1
347 1→0
359 0→1
380 0→1

Deltran:

33 1→0
185 0→1
301 0→1
350 0→1
368 0→1

Paliguana + Fraxinisaura + Marmoretta:

Unambiguous:

20 0→1
73 0→1
81 1→0
101 0→1

Acctran:

8 0→1
82 0→1
140 1→0
144 0→1
181 2→0
190 1→0
200 1→0
219 0→1
290 0→2
294 1→0
305 3→0
308 0→1

Deltran:

50 0→1

227 0→1

Lepidosauria:

Unambiguous:

69 0→1

121 0→1

229 0→1

296 0→1

Acctran:

45 1→0

61 0→1

188 0→1

227 1→0

369 0→1

Deltran:

30 1→0

98 0→1

109 1→0

120 0→1

195 1→0

217 0→1

235 0→1

237 0→1

238 0→1

269 0→1

284 0→1

312 0→1

320 0→1

332 1→0

333 1→0

334 0→1

336 1→0

338 0→1

Rhynchocephalia + *Vellbergia*:

Unambiguous:

211 0→1

Acctran:

25 0→1

55 0→1

59 2→1
 61 1→0
 62 1→0
 92 0→1
 111 0→1
 114 0→1
 173 0→1
 182 0→1
 188 1→2
 210 0→1
 289 2→0
 291 1→0
 308 0→1
 322 1→0
 347 0→1
 351 1→0
 360 0→1
 361 0→1
 362 0→1

Deltran:
 23 0→1

Rhynchocephalia:

Unambiguous:
 176 1→0

Acctran:
 118 1→0
 352 1→0

Deltran:
 50 0→1
 55 0→1
 59 2→1
 111 0→1
 114 0→1
 173 0→1
 182 0→1
 188 0→2
 291 1→0
 308 0→1
 331 1→0
 360 0→1
 361 0→1

Squamata (excluding *Megachirella*):

Unambiguous:

27 0→1
36 1→0
38 0→1
123 0→1
225 0→1
263 0→1
282 0→1
340 1→0
346 1→0
354 0→1
355 0→1
365 0→1

Acctran:

7 0→1
45 0→1
50 1→0
68 1→0
71 0→1
85 1→0
89 1→0
95 0→1
97 1→0
105 1→0
116 0→1
124 1→0
125 0→1
135 0→1
138 0→1
142 0→1
151 0→1
162 0→1
170 0→1
171 0→1
198 0→1
224 0→1
270 0→1
286 0→1
314 0→1
347 0→2
350 1→0
362 0→1
367 1→2
369 1→0

Deltran:

188 0→1
234 0→1

271 0→1
359 0→1

A REASSESSMENT OF THE ENIGMATIC DIAPSID PALIGUANA WHITEI AND THE EARLY HISTORY OF LEPIDOSAUROMORPHA

Authors: David P. Ford, Susan E. Evans, Jonah N. Choiniere, Vincent Fernandez and Roger B.J. Benson

SUPPLEMENTARY DATA 5

Taxon choice and character List

Taxon choice

All operational taxonomic units (OTU) included in the analysis are in accordance with the dataset of Griffiths *et al.* (in review). Four putative Permo-Triassic lepidosauromorphs were omitted from the list of OTU:

- i) *Saurosternon bainii* (Huxley 1868, Carroll 1975a) – a skeleton lacking the cranium from the late Permian of South Africa. Recognised by Carroll (1975a) as an early lizard (squamate), and included in the suborder ‘Paliguanidae’, an affiliation later disputed (Evans 1984, Benton 1985). This taxon was recovered as stem-reptile in recent analyses (Simões *et al.* 2018, Sobral *et al.* 2020). Considered a ‘problematic’ taxon by Evans (2003).
- ii) *Kudnu australiensis* (Bartholomai 1979) – based on a single partial skull lacking the postorbital region, from the early Triassic of Australia. Referred to ‘Paliguanidae’, the specimen has been attributed with an anteroposteriorly elongate lacrimal, extending almost to the external naris, with teeth set in a shallow groove. This taxon is excluded pending tomographic analysis.
- iii) *Feralisaurus corami* (Cavicchini *et al.* 2020) – Middle Triassic of Devon, UK. A poorly preserved and dorsoventrally compressed partial skull, with some post-cranial material. The specimen has been scanned using microtomography to a resolution of 48.45 microns, but the resulting anatomical detail is limited due to poor preservation. Phylogenetic analysis was inconclusive, with the taxon recovered as a stem-reptile or in broad polytomy within the crown-group. The short posterior process of the jugal and well-developed coronoid process of the mandible suggest crown-group reptile affinities.
- iv) *Vinitasaura lizae* (Sues and Kligman 2021) – this specimen from the late Triassic of Virginia, USA, consists of a single dentary with 27 teeth *in situ*. Phylogenetic analysis was not performed due to the limited data available, and likewise we omit this taxon from our dataset. Comparison of the specimen to the dentaries of Permo-Triassic diapsids suggest this taxon may be affiliated to non-lepidosaurian lepidosauromorphs or early-diverging lepidosaurs (Sues and Kligman 2021).

Additional References

Cavicchini, I., Zaher, M. and Benton, M.J., 2020. An Enigmatic Neodiapsid Reptile from the Middle Triassic of England. *Journal of Vertebrate Paleontology*, 40(3), <https://doi.org/10.1080/02724634.2020.1781143> .

Huxley, T.H., 1868. I.—On *Saurosternon Bainii*, and *Pristerodon McKayi*, Two New Fossil Lacertilian Reptiles from South Africa. *Geological Magazine*, 5(47), pp.201-205. <https://doi.org/10.1017/s0016756800207784>

Sues, H.D. and Kligman, B.T., 2021. A new lizard-like reptile from the Upper Triassic (Carnian) of Virginia and the Triassic record of Lepidosauromorpha (Diapsida, Sauria). *Journal of Vertebrate Paleontology*, . <https://doi.org/10.1080/02724634.2021.1879102>

Character list

The 381 discreet morphological characters used in our phylogenetic analyses are taken from the 377 characters used in the phylogenetic analysis of Griffiths *et al.* (in press), which was a revised version of the 347 morphological characters of Simões *et al.* (2018). We refer to these publications for explanatory notes on the individual characters.

We have made 8 changes to the character list of Griffiths *et al.* (in review), all of which concern characters describing the implantation of marginal dentition. They can be summarised as follows:

(i) Omission of character 212 - posterior dentary teeth, delimitation by tooth bearing bone) by a labial wall only (0)/ by a three-sided socket (1)/ by a four-sided socket (2)/ by a lingual and labial wall only (3).

(ii) Omission of character 213 - posterior maxillary teeth, delimitation by tooth bearing bone: by a labial wall only (0)/ by a three-sided socket (1)/ by a four-sided socket (2)/ by a lingual and labial wall only (3).

(iii) Additional character 376 - dentary teeth, interdental plates: contact both labial and lingual walls of alveolar groove, fully separating adjacent teeth (0)/ do not contact both labial and lingual walls of alveolar groove or are absent (1)

(iv) Additional character 377 - dentary teeth, asymmetry of dorsoventral height of labial and lingual walls of alveolar groove: lingual wall subequal in height to labial wall (0)/ lingual wall absent or low, less than half the height of the labial wall (1)

(v) Additional character 378 - dentary teeth, dorsoventral height of lingual wall of alveolar groove: low, less than half the height of the labial wall (0) absent (1) - when labial and lingual walls are subequal in height this character is scored as inapplicable.

(vi) Additional character 379 - maxillary teeth, interdental plates: contact both labial and lingual walls of alveolar groove, fully separating adjacent teeth (0)/ do not contact both labial and lingual walls of alveolar groove or are absent (1)

(vii) Additional character 380 - maxillary teeth, asymmetry of dorsoventral height of labial and lingual walls of alveolar groove: lingual wall subequal in height to labial wall (0)/ lingual wall absent or low, less than half the height of the labial wall (1)

(viii) Additional character 381 - maxillary teeth, dorsoventral height of lingual wall of alveolar groove: low, less than half the height of the labial wall (0) absent (1) - when labial and lingual walls are subequal in height this character is scored as inapplicable.

The omitted characters (212 and 213) were new characters in the morphological dataset of Simões *et al.* (2018), designed to describe the delimitation of tooth implantation. However, this approach fails to recognise independent variation in the comparative height of the labial and lingual wall of the alveolar groove – a key characteristic in defining tooth implantation types (Zaher and Rieppel 1999, Bertin *et al.* 2018). The addition of characters 376-381 concerns the comparative height of these features and independently recognises the enclosure of the mesial and distal surfaces of the tooth root.

In the present study, there are 343 binary characters and 38 multistate characters. All multistate characters are unordered.

1. **Premaxillae, fusion:** unfused (0)/ fused (1)
2. **Premaxillae, nasal process:** present, external nares are separated by the premaxillae (0)/ absent, the external nares are a single aperture (1)
3. **Premaxillae, posterodorsal process:** absent (0)/ present (1)
4. **Premaxillae, dentition:** present (0)/ absent medially only (1)/ entirely absent (2)
5. **Premaxillae, dentigerous beak:** absent (0) / present (1)
6. **Premaxillae, ventral bony beak:** absent (0)/ present (1)
7. **Premaxillae, incisive process:** absent (0)/ present (1)
8. **Premaxillae, ventral surface, premaxillary foramina:** absent (0)/ present (1)
9. **Premaxillae, vomerine medial flange:** absent (0)/ present (1)
10. **Septomaxillae:** present (0)/ absent (1)

11. **Septomaxillae, position:** on narial margin (0)/ within nasal capsule (1)
12. **Septomaxillae, shape, anteriorly:** flat (0)/ convex dorsally (1)/ convex ventrally (2)/ laterally compressed (3)
13. **Septomaxillae, midline crest, dorsal projection:** absent (0)/ present (1)
14. **Maxillae, contact, with premaxilla:** syndesmotoc (0)/ sutural (1)
15. **Maxilla-premaxilla fenestra, ventrally:** absent (0)/ present (1)
16. **Maxillae, anterior superior alveolar foramen:** absent (0)/ present (1)
17. **Maxillae, nasal (facial) process:** absent (0)/ present (1)
18. **Maxillae, posterior emargination, between nasal and orbital processes:** absent (0)/ present (1)
19. **Maxillae, antorbital fossa:** absent (0)/ present (1)
20. **Maxillae, premaxillary process:** present (0)/ absent (1)
21. **Maxillae, premaxillary process, groove for the passage of the internal ramus of the subnarial artery on dorsal surface:** absent (0)/ present (1)
22. **Nasals, fusion:** paired (0)/ fused (1)
23. **Nasals, anterolateral process:** absent (0)/ present (1)
24. **Nasals, anterolateral process, position, relative to maxillary nasal process:** posteriorly (0)/ anteriorly (1)/ dorsally (2)
25. **Nasals, foramina:** absent (0)/ present (1)
26. **Nasals, ventromedial crest:** absent (0)/ present (1)
27. **Lacrimals:** present (0)/ absent (1)
28. **Lacrimals, position, relative to prefrontal lateral margin:** ventral (0)/ anterior (1)
29. **Lacrimal duct, foramen, division:** single (0)/ double (1)
30. **Lacrimal duct, posterior opening on skull surface, position:** posteriorly (0)/ laterally
31. **Lacrimals, shape, curved anteriorly:** absent (0)/ present (1)
32. **Prefrontals, ornamentation on external surface:** absent (0)/ rugosities (1)/ tubercles (2)/ pits (3)

33. **Prefrontal crest:** absent (0)/ present (1)
34. **Supraorbital bones:** absent (0)/ present (1)
35. **Jugals:** present (0)/ absent (1)
36. **Jugals, posteroventral process:** absent (0)/ present (1)
37. **Jugals, posteroventral process, shape:** separate from dorsal process (0)/ connected to dorsal process by bony flange (1)
38. **Quadratojugals:** present (0)/ absent (1)
39. **Quadratojugals, anterior extension:** present (0)/ absent (1)
40. **Quadratojugals, ventral margin, medially inflected flange:** absent (0)/ present (1)
41. **Quadratojugals, ornamentation, on external surface:** absent (0)/ present (1)
42. **Quadratojugal foramen:** absent (0)/ present (1)
43. **Postorbitals:** present (0)/ absent (1)
44. **Postorbitals, fusion to postfrontal:** unfused (0)/ fused (1)
45. **Postorbitals, dorsal margin, position relative to postfrontal:** laterally (0)/ posteriorly (1)/ anteriorly (2)
46. **Postorbitals, dorsal process:** absent (0)/ present (1)
47. **Postorbitals, ventral process:** absent (0)/ present (1)
48. **Postorbitals, dorsal concavity:** absent (0)/ present (1)
49. **Squamosals:** present (0)/ absent (1)
50. **Squamosals, anteroventral process:** absent (0)/ present (1)
51. **Squamosals, dorsal process:** absent (0)/ present (1)
52. **Squamosal, dorsal process, contact with supratemporal or supratemporal process of parietal:** sutured (0)/ not sutured, forms a buttress for posterolateral corner of the skull roof (1)
53. **Squamosals, occipital flange:** present (0)/ absent (1)

54. **Squamosals, ventral margin, medial inflection:** absent (0)/ present (1)
55. **Squamosal, anterior process, dorsoventral length:** narrow, < one-quarter of the dorsoventral length of the postorbital region (0)/ deep, > one-third of the dorsoventral length of the postorbital region (1)
56. **Postfrontals:** present (0)/ absent (1)
57. **Postfrontals, distal process:** present (0)/ absent (1)
58. **Postfrontals, distal process, division:** single (0)/ double (1)
59. **Postfrontals, medial margin, position, relative to parietal:** ventral (0)/ dorsal (1)/ lateral (2)/ anterior (3)
60. **Postfrontals, parietal process:** absent (0)/ present (1)
61. **Postfrontals, concavity between the frontal and parietal processes (dorsomedial margin of postfrontal):** absent (0)/ present (1)
62. **Supratemporals:** absent (0)/ present (1)
63. **Supratemporals, temporal process:** absent (0)/ present (1)
64. **Tabulars:** present (0)/ absent (1)
65. **Postparietals:** present (0)/ absent (1)
66. **Postparietals, number:** single (0)/ paired (1)
67. **Frontals, fusion to each other:** unfused (0)/ fused (1)
68. **Frontals, parietal tabs:** absent (0)/ present (1)
69. **Frontals, subolfactory processes:** absent (0)/ present (1)
70. **Frontals, subolfactory processes, fusion to each other:** absent (0)/ present (1)
71. **Frontals, orbitonasal projection:** absent (0)/ present (1)
72. **Parietals, fusion:** unfused (0)/ fused (1)
73. **Parietal foramen:** present (0)/ absent (1)
74. **Parietals, supratemporal process:** absent (0)/ present (1)
75. **Parietals, supratemporal process, distal end, division:** single (0)/ bifid (1)

76. **Parietals, ornamentation:** absent (0)/ rugosities (1)/ tubercles (2)/ pits (3)
77. **Parietals, lateral frill:** absent (0)/ present (1)
78. **Parietals, frontal tabs of parietal:** absent (0)/ present (1)
79. **Parietals, nuchal fossa:** absent (0)/ present (1)
80. **Parietals, nuchal fossa, roofing by parietal posterior flange:** unroofed (0)/ roofed (1)
81. **Parietals, ventral side, parietal fossa:** present (0)/ absent (1)
82. **Parietals, ventral side, parietal fossa, posterior margin:** open (crests extend posterolaterally) (0)/ closed (crests meet at midline) (1)
83. **Parietals, posteromedial (= postparietal) process:** absent (0)/ present (1)
84. **Parietals, posteromedial (= postparietal) process, division:** single (0)/ bifid (1)
85. **Parietals, parietal table, shape:** margins ventrally directed, sagittal crest present (0)/ margins ventrally directed, without sagittal crest (1)/ margins laterally directed (2)
86. **Parietals, dorsal surface, parasagittal crests:** absent (0)/ present (1)
87. **Parietals, crista cranii parietalis, epipterygoid process:** absent (0)/ present (1)
88. **Vomers, fusion:** unfused (0)/ fused (1)
89. **Vomers, teeth:** absent (0)/ present (1)
90. **Vomers, anterior premaxillary process:** absent (0)/ present (1)
91. **Vomers, lateral expansion:** absent (0)/ present (1)
92. **Vomers, ventral surface, midline crest (=longitudinal ridge):** absent (0)/ present (1)
93. **Vomers, ventral surface, lateral crest (=longitudinal ridge):** absent (0)/ present (1)
94. **Vomers, ventral foramina, in each vomerine element:** present (0)/ absent (1)
95. **Vomers, shape in cross-section:** flat (0)/ convex ventrally (1)

96. **Vomers, posteroventral process (=descending tubercle):** absent (0)/ present (1)
97. **Palatines, teeth:** absent (0)/ present (1)
98. **Palatines, ascending process:** absent (0)/ present (1)
99. **Palatines, dorsomedially directed process:** absent (0)/ present (1)
100. **Palatines, ventral surface, sulcus choanalis:** absent (0)/ present (1)
101. **Palatines, infraorbital foramen:** present (0)/ absent (1)
102. **Palatine foramen:** absent (0)/ present (1)
103. **Palatines, maxillary process, ventral aspect:** absent (0)/ present (1)
104. **Palatines, subchoanal shelf:** absent (0)/ present (1)
105. **Pterygoids, teeth:** absent (0)/ present (1)
106. **Pterygoids, anteromedial processes, anterior end division:** single (0)/ bifurcate (1)
107. **Pterygoids, transverse processes:** absent (0)/ present (1)
108. **Pterygoids, transverse process:** posteroventrally orientated (0)/ flat, on same plane as the posterior region of the palatal ramus of the pterygoid (1)
109. **Pterygoids, transverse process, teeth:** absent (0)/ present (1)
110. **Pterygoids, main body, concave in ventral aspect:** absent (0)/ present (1)
111. **Pterygoids, arcuate flange:** absent (0)/ present (1)
112. **Pterygoids, quadrate rami, posterolateral excavation:** absent (0)/ present (1)
113. **Ectopterygoids:** absent (0)/ present (1)
114. **Ectopterygoids, lateral process:** absent (0)/ present (1)
115. **Epipterygoid:** present (0)/ absent (1)
116. **Epipterygoid, base shape:** base flared out (0)/ base columnar, inserting into a pit on the surface of the pterygoid (1)

117. **Quadrates, articulating surface:** flat (0)/ with condyles (1)
118. **Quadrate foramen:** present (0)/ absent (1)
119. **Quadrates, pterygoid process:** present as broad, overlapping quadrate/pterygoid suture (0)/ absent or reduced to a small lappet on the ventromedial surface of the quadrate (1)
120. **Quadrates, posterior emargination:** absent (0)/ present (1)
121. **Quadrates, quadrate conch:** absent (0)/ present (1)
122. **Quadrates, posterodorsal suprastapedial recess with ventrally directed 'hook-like' process:** absent (0)/ present (1)
123. **Quadrates, cephalic condyle, notch for the squamosal:** absent (0)/ present (1)
124. **Carotid foramina, entrance in braincase, position:** lateral wall of braincase (0)/ ventral surface of braincase (1)
125. **Supraoccipital, lateral ascending processes:** absent (0)/ present (1)
126. **Supraoccipital, medial ascending process:** absent (0)/ present (1)
127. **Supraoccipital, fusion to exoccipitals:** unfused (0)/ fused (1)
128. **Supraoccipital, sagittal crest:** absent (0)/ present (1)
129. **Supraoccipital, lateral nuchal crest:** absent (0)/ present (1)
130. **Basioccipital/basisphenoid, sphenoid tubercles:** absent (0)/ present (1)
131. **Sphenooccipital epiphyses:** absent (0)/ present (1)
132. **Basioccipital, fusion, to exoccipital:** unfused (0)/ fused (1)
133. **Basioccipital, fusion to basisphenoid:** unfused (0)/ fused (1)
134. **Basioccipital, ventral aspect, shape, concavity:** single (0)/ divided (1)/ absent (2)
135. **Basisphenoid, Vidian canal:** open (0)/ fully enclosed (1)
136. **Basisphenoid, basiptyergoid processes:** present (0)/ absent (1)
137. **Basisphenoid, dorsum sellae:** absent (0)/ present (1)
138. **Basisphenoid (or fused parabasisphenoid), ventral aspect, shape, concavity:** single (0)/ divided (1)/ absent (2)

139. **Basisphenoid, lateral depression:** absent (0)/ present (1)
140. **Prootics, prootic crest:** absent (0)/ present (1)
141. **Prootics, prootic crest, shape:** crest (0)/ curved flange (1)
142. **Prootics, alar crest:** absent (0)/ present (1)
143. **Prootics, supratrigeminal process:** absent (0)/ present (1)
144. **Prootics, anterior inferior process:** present (0)/ absent (1)
145. **Prootics, lateral wall, facial foramen:** absent (0)/ present (1)
146. **Prootics, lateral wall, facial foramen, division:** single (0)/ double (1)
147. **Parasphenoid, teeth:** absent (0)/ present (1)
148. **Parasphenoid, orbitosphenoid processes:** absent (0)/ present (1)
149. **Opisthotics, crista interfenestralis:** present (0)/ absent (1)
150. **Exoccipitals, lateral flange:** absent (0)/ present (1)
151. **Exoccipitals, fusion:** unfused (0)/ to opisthotics only (1)/ to opisthotics and prootics (2)
152. **Exoccipitals, occipital condyle process:** absent (0)/ present (1)
153. **Exoccipitals, crista tuberalis:** absent (0)/ present (1)
154. **Exoccipitals (or exoccipital portion of the otoccipitals), contact to each other, medially:** absent (0)/ present (1)
155. **Stapes, dorsal process:** present (0)/ absent (1)
156. **Stapes, stapedia foramen:** present (0)/ absent (1)
157. **Laterosphenoids:** absent (0)/ present (1)
158. **Orbitosphenoids:** absent (0)/ present (1)
159. **Orbitosphenoids, fusion to each other:** unfused (0)/ fused medially (1)
160. **Ossified sphenethmoid:** present (0)/ absent (1)
161. **Ossified sphenethmoid, shape:** without orbital septum (0)/ with orbital septum also ossified (1) / only orbital septum (2)

162. **Anterior mylohyoidal foramen:** absent (0)/ present (1)
163. **Posterior mylohyoidal foramen:** absent (0)/ present (1)
164. **Anterior inferior alveolar foramen:** absent (0)/ present (1)
165. **Dentaries, symphyses, fusion to each other:** unfused (0)/ fused (1)
166. **Dentaries, symphyseal area, shape:** flat (0)/ convex (1)
167. **Dentaries, anterior end, split by Meckelian canal:** absent (0)/ present (1)
168. **Dentaries, anterior end, symphyseal articular facet, position:** on dorsal margin only (0)/ on dorsal and ventral margins (1)/ on ventral margin only (2)
169. **Dentaries, subdental shelf:** present (0)/ absent (1)
170. **Dentaries, dorsal margin, contact, with ventral margin in medial view:** absent (0)/ present (1)
171. **Dentaries, dorsal margin, fusion, with ventral margin in medial view:** absent (0)/ present (1)
172. **Dentaries, coronoid process:** absent (0)/ present (1)
173. **Dentaries, coronoid process, dorsal expansion:** absent (0)/ present (1)
174. **Dentaries, coronoid process, division:** single (0)/ double (1)
175. **Dentaries, posteroventral process:** absent (0)/ present (1)
176. **Splenials:** absent (0)/ present (1)
177. **Splenials, fusion to dentary:** unfused (0)/ fused (1)
178. **Splenials, symphyseal process:** absent (0) / present (1)
179. **Splenials, anterior border, shape:** rounded (0)/ notched (1)/ flat (2)/ tapering (3)
180. **Angulars:** present (0)/ absent (1)
181. **Angulars, anterior end, medial view, position relative to splenial:** lateral (0)/ dorsal (1)/ ventral (2)/ posterior (3)
182. **Surangulars, coronoid process:** absent (0)/ present (1)

183. **Surangulars, lateral adductor crest:** absent (0)/ present (1)
184. **Surangulars, anterior surangular foramen:** absent (0)/ present (1)
185. **Surangulars, posterior surangular foramen:** absent (0)/ present (1)
186. **Surangulars, mandibular fenestra:** absent (0)/ present (1)
187. **Articulars, lateral shelf:** absent (0)/ present (1)
188. **Articulars, fusion:** unfused (0)/ to prearticular only (1)/ to prearticular + surangular only (2)/ to prearticular + surangular + angular only (3)/ to prearticular + surangular + angular + splenial (4)
189. **Articulars, foramen chorda tympani:** absent (0)/ present (1)
190. **Articulars, retroarticular process:** absent (0)/ present (1)
191. **Articulars, retroarticular process, dorsal fossa:** absent (0)/ present (1)
192. **Articulars, retroarticular process, lateral notch:** absent (0)/ present (1)
193. **Articulars and prearticulars, medial process:** absent (0)/ present (1)
194. **Articulars and prearticulars, medial process, prearticular crest:** absent (0)/ present (1)
195. **Preatriculars, retroarticular process:** absent (0)/ present (1)
196. **Preatriculars, mandibular fossa:** present (0)/ absent (1)
197. **Coronoids, dorsal process:** absent (0)/ present (1)
198. **Coronoids, anterolateral (=labial) process:** absent (0)/ present (1)
199. **Coronoids, anteromedial process:** present (0)/ absent (1)
200. **Coronoids, posterodorsomedial process:** present (0)/ absent (1)
201. **Coronoid, posteroventromedial process:** present (0)/ absent (1)
202. **Dentition, crown apical striations, labial side:** absent (0)/ present (1)
203. **Dentition, mesiodistal serration:** absent (0)/ present (1)
204. **Posterior dentition, accessory cusps, mesiodistally oriented:** absent (0)/ present (1)

205. **Posterior dentition, accessory cusps, labiolingually oriented:** absent (0)/ present (1)
206. **Posterior dentition, replacement teeth:** absent (0)/ present (1)
207. **Posterior dentition, resorption pits:** present (0)/ absent (1)
208. **Posterior dentition, replacement teeth, position in relation to functional teeth:** lingual (0)/posterolingual (1)
209. **Posterior dentition, tooth shape, concave anteriorly:** absent (0)/ present (1)
210. **Posterior dentary teeth, position, relative to dentary crista dorsalis (apex of labial wall) of dentary:** lingual (0)/ apical (1)/ apicolingual (2)
211. **Posterior dentary teeth, ankylosis to crista dorsalis (apex of labial wall) of dentary:** absent (0)/ present (1)
212. **Posterior dentary dentition, lingual and labial carinae:** absent (0)/ present (1)
213. **Anterior dentary teeth:** present (0)/ absent (1)
214. **Anterior dentary teeth, position relative to the jaw apical margin (dentary dorsal crest or maxillary ventral crest):** lingual (0)/ apical (1)/ apicolingual (2)
215. **Posterior maxillary teeth, posteromedial ridge:** absent (0)/ present (1)
216. **Anterior maxillary teeth, alternating teeth series:** absent (0)/ present (1)
217. **Atlas, pleurocentrum, fusion to axis:** unfused (0)/ fused (1)
218. **Atlas, neural arches:** separate (0)/ sutured to each other (1)/ sutured to axis neural spine (2)
219. **Atlas, neural arches, postzygapophyses:** absent (0)/ present (1)
220. **Atlas, ribs:** present (0)/ absent (1)
221. **Axis, pleurocentrum, fusion to neural arch:** unfused (0)/ fused (1)
222. **Axis, intercentrum:** present (0)/ absent (1)
223. **Axis, connectivity to intercentra:** to intercentra 2 only (0)/ to intercentra 2 and 3 (1)

224. **Axis, intercentrum, fusion to axial pleurocentrum:** unfused (0)/ fused (1)
225. **Axis, ribs:** present (0)/ absent (1)
226. **Presacral pleurocentra, orientation of centrum:** amphicoelous (0)/ procoelous (1)/ opisthocoelous (2)/ platycoelous (3)/ amphiplatyan (4)
227. **Presacral pleurocentra, notochord, persistent in adults:** present (0)/ absent (1)
228. **Presacral parapophyses:** present (0)/ absent (1)
229. **Presacral pleurocentra, midventral crest, cervical vertebrae:** absent (0)/ present (1)
230. **Presacral pleurocentra, midventral crest, posterior dorsal vertebrae:** absent (0)/ present (1)
231. **Posterior presacral pleurocentra, precondylar constriction:** absent (0)/ present (1)
232. **Posterior presacral pleurocentra, dorsal vertebrae, margo ventralis (= ventrolateral crest):** absent (0)/ present (1)
233. **Sacral vertebrae, number:** zero (0)/ one (1)/ two (2)/ three (3)/ four (4)
234. **Caudal vertebrae, autotomic septum:** absent (0)/ present (1)
235. **Intercentra, on cervical vertebrae:** absent (0)/ present (1)
236. **Intercentra, on cervical vertebrae, position:** intervertebral (0)/ on preceding centrum body (1)/ on following centrum body (2)
237. **Intercentra, on dorsal vertebrae:** absent (0)/ present (1)
238. **Intercentra, on anteriormost caudal:** absent (0)/ present (1)
239. **Intercentra, on anteriormost caudal, shape:** wedge-like elements (0)/ modified into chevron elements (1)
240. **Intercentra, on posterior caudals (chevron bones = haemal arches):** present (0)/ absent (1)
241. **Chevron bones, articulation:** between pleurocentra (0)/ with pleurocentrum, on articular facets (1)/ with pleurocentrum, on haemapophyses (=pedicles) (2)

242. **Chevron bones, fusion to pleurocentrum:** unfused (0)/ fused (1)
243. **Chevron bones, distal fusion:** separate elements (0)/ “V” shaped (1) / “Y” shaped (2)/elliptically shaped (3)
244. **Neural arches, dorsal vertebrae, ventral bridge, posterior borders of neural arches:** absent (0)/ present (1)
245. **Neural arches, prezygapophyses, presacral vertebrae, processes ventrolaterally on prezygapophyses:** absent (0)/ present (1)
247. **Neural arches, presacral vertebrae, zygosphenes orientation:** facing dorsolaterally (0)/ facing ventrolaterally (1)
248. **Neural arches and pleurocentrum, diapophysis, anterior dorsal vertebrae, fusion to parapophysis:** absent (0)/ present (1)
249. **Neural arches, margo lateralis, posterior presacral vertebrae:** absent (0)/ present (1)
250. **Neural spine, cervical vertebrae, posterior notch:** absent (0)/ present (1)
251. **Neural spine, cervical vertebrae, apically, lateral expansion:** absent (0)/ present (1)
252. **Dermal neural spine, dorsal vertebrae:** absent (0)/ present (1)
253. **Neural spine, dorsal vertebrae:** present (0)/ absent (1)
254. **Neural spine, dorsal vertebrae, anterior midline process:** absent (0)/ present (1)
255. **Neural spine, dorsal vertebrae, mammillary process:** absent (0)/ present (1)
256. **Neural spine, dorsal vertebrae, apically, lateral expansion:** absent (0)/ present (1)
257. **Presacral ribs, anteroposterior crests:** absent (0)/ present (1)
258. **Presacral ribs, cervical ribs:** present (0)/ absent (1)
259. **Presacral ribs, cervical ribs, anterior process:** absent (0)/ present (1)
260. **Presacral ribs, uncinat processes, anterior dorsals:** absent (0)/ present (1)

261. **Presacral ribs, anteroventral process at rib head (= pseudotuberculum):** absent (0)/ present (1)
262. **Presacral ribs, posterodorsal process at rib head (= pseudotuberculum):** absent (0)/ present (1)
263. **Posteriormost presacral vertebra, ribs:** present (0)/ absent (1)
264. **Posteriormost presacral vertebra, ribs articulation:** ribs unfused (0)/ ribs fused (1)
265. **Sacral ribs, distal forking:** absent (0)/ on first sacral rib only (1)/ on first and second sacral ribs (2)/ on second sacral rib only (3)
266. **Sacral/Cloacal ribs, fusion to pleurocentra:** unfused (0)/ fused (1)
267. **Anterior caudal ribs:** absent (0)/ present (1)
268. **Anterior caudal ribs, fusion to pleurocentra:** unfused (0)/ fused (1)
269. **Presternum, mineralized:** absent (0)/ present (1)
270. **Xiphisternum:** absent (0)/ present (1)
271. **Mineralized poststernal inscriptional ribs:** absent (0)/ present (1)
272. **Distal ribs:** absent (0)/ present (1)
273. **Scapula, supraglenoid foramen:** absent (0)/ present (1)
274. **Scapula, supraglenoid buttress:** absent (0)/ present (1)
275. **Scapula, scapula ray:** absent (0)/ present (1)
276. **Scapula, dorsal acromion process:** absent (0)/ present (1)
277. **Scapula, supracoracoidal acromion process:** absent (0)/ present (1).
278. **Scapula, posterior emargination:** absent (0)/ present (1)
279. **Scapula, anterior emargination:** absent (0)/ present (1)
280. **Procoracoid, supracoracoid foramen:** absent (0)/ notch (1)/ complete foramen (2)
281. **Procoracoid, angulation medially:** absent (0)/ present (1)
282. **Procoracoid, coracoid emargination:** absent (0)/ anterior emargination (1)/ anterior and posterior emarginations (2)

283. **Posterior coracoid:** absent (0)/ present (1)
284. **Epicoracoids:** absent (0)/ present (1)
285. **Clavicles, secondary curvature anteroposteriorly:** absent (0)/ present (1)
286. **Clavicles, proximoventral fenestration:** absent (0)/ present (1)
287. **Clavicles, posterior process:** absent (0)/ present (1)
288. **Clavicles, dorsolateral flange:** absent (0)/ present (1)
289. **Clavicles, position (at point of contact), in relation to anterior margin of scapula:** laterally (0)/ medially (1)/ anteriorly (2)
290. **Clavicles, position (at point of contact), in relation to anterior margin of the interclavicle:** ventrally (0)/ dorsally (1)/ anteriorly (2)
291. **Interclavicle, anterior process:** absent (0)/ present (1)
292. **Interclavicle, posterior process:** present (0)/ absent (1)
293. **Cleithra:** present (0)/ absent (1)
294. **Ilia, posterodorsal notch, on acetabular margin:** absent (0)/ present (1)
295. **Ilia, supraacetabular buttress:** absent (0)/ present (1)
296. **Ilia, anterior pubic process:** absent (0)/ present (1)
297. **Ilia, anterior (=preacetabular) process:** absent (0)/ present (1)
298. **Pubes, obturator foramen:** absent (0)/ complete foramen (1)/ notch (2)
299. **Pubes, pubic tubercle:** absent (0)/ present (1)
300. **Ischia, fusion to pubes:** absent (0)/ present (1)
301. **Ischia, anterior border, emargination:** absent (0)/ present (1)
302. **Ischia, ischiadic tuberosity:** absent (0)/ present (1)
303. **Ischia, ischiadic neck:** absent (0)/ present (1)
304. **Ischia, facet, for hypischium:** absent (0)/ present (1)

305. **Humeri, ectepicondyle foramen:** absent (0)/ groove (1)/ notch (2)/ complete foramen (3)
306. **Humeri, epicondyles:** present (0)/ absent (1)
307. **Humeri, entepicondyle foramen:** absent (0)/ present (1)
308. **Humeri, expanded radial condyle (= capitellum):** present (0)/ absent (1)
309. **Humeri, pectoral process:** present (0)/ absent (1)
310. **Humeri, pectoral process, connection to humeral head:** separate (0)/ connected (1)
311. **Humeri, shaft angulation:** straight (0)/ angulate posteriorly (1)
312. **Humeri, secondary ossification of epiphyses:** absent (0)/ present (1)
313. **Humeri, anterior flange:** absent (0)/ present (1)
314. **Radia, distal epiphysis, styloid process:** absent (0)/ present (1)
315. **Radia, anteroproximal process:** absent (0)/ present (1)
316. **Ulnae, ossified olecranon process:** present (0)/ absent (1)
317. **Ulnae, distal epiphysis, expansion:** absent (0)/ present (1)
318. **Perforating foramen, manus:** absent (0)/ between ulnare and intermedium (1)/ between radiale and intermedium (2)
319. **Intermedium:** present (0)/ absent (1)
320. **Pisiform:** absent (0)/ present (1)
321. **Palmar sesamoid:** absent (0)/ present (1)
322. **Distal carpal 1:** present (0)/ absent (1)
323. **Distal carpal 5:** present (0)/ absent (1)
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324. **Femora:** present (0)/ absent (1)
325. **Femora, internal trochanter:** present (0)/ absent (1)
326. **Femora, fourth trochanter:** absent (0)/ present (1)
327. **Femora, intertrochanteric fossa:** present (0)/ absent (1)

328. **Tibiae, distal epiphysis, notch:** absent (0)/ present (1)
329. **Astragalus and calcaneum:** as totally separate elements (0)/ fused (1)
330. **Astragalus, shape, concave laterally:** absent (0)/ present (1)
331. **Calcaneum, lateral tuber (or process) of the calcaneum:** present (0)/ absent (1)
332. **Calcaneum, foramen for perforating artery, position:** absent (0)/ between astragalus and calcaneum (1)/ between proximal ends of tibia and fibula (2)
333. **Pedal lateral centrale:** absent (0)/ present (1)
334. **Distal tarsal 1:** present (0)/ absent (1)
335. **Distal tarsal 2:** present (0)/ absent (1)
336. **Distal tarsal 4, proximal peg:** present (0)/ absent (1)
337. **Distal tarsal 5:** present (0)/ absent (1)
338. **Metatarsal 5, hooked:** absent (0)/ present (1)
339. **Metatarsal 5, plantar tubercle:** absent (0)/ present (1)
340. **Gastralia:** absent (0)/ present (1)
341. **Dorsal trunk osteoderms:** absent (0)/ present (1)
342. **Dorsal trunk osteoderms, imbrication:** not imbricated (0)/ imbricated (1)
343. **Plastron plate:** absent (0)/ present (1)
344. **Neural plates:** absent (0)/ present (1)
345. **Costal plates:** absent (0)/ present (1)
346. **Skull proportions:** preorbital skull length equal to postorbital length (0)/ preorbital length exceeds postorbital skull length (1)/ postorbital length exceeds preorbital skull length (2).
347. **Prefrontal/palatine antorbital contact:** absent (0)/ narrow forming less than 1/3 the transverse distance between the orbits (1)/ contact broad, forming at least 1/2 the distance between the orbits (2)

348. **Postfrontal contribution to upper temporal fenestra:** postfrontal excluded (0)/ postfrontal included (1).
349. **Angular lateral exposure:** exposed along 1/3 of the lateral face of the mandible (0)/ exposed only as a small sliver along the lateral face (1)
350. **Maxilla orbital exposure:** absent (0)/ present (1).
351. **Maxilla length:** extends at least to the posterior orbital margin (0)/ does not reach posterior margin of orbit (1)
352. **Frontal morphology:** parallelogram shaped (0)/ hourglass shaped (1)
353. **Dorsal vertebrae, transverse processes:** short no more than the total transverse width of the neural arch (0)/ long exceeding the transverse width of the neural arch (1)
354. **Orientation of transverse flange of pterygoid:** directed predominantly laterally or posterolaterally (0)/ oriented in an anterolateral direction (1)
355. **Humeral torsion:** proximal and distal end are offset at an angle of at least 45°(0)/ off set is reduced to no more than 20° (1)
356. **Adductor chamber:** small, quadrate does not extend well below level of occipital condyle (0)/ enlarged adductor chamber, and quadrate extends well below occipital condyle (1)
357. **Metacarpals, length of third and fourth:** fourth metacarpal longer than third (0)/ third and fourth metacarpals subequal in length (1)/ fourth metacarpal shorter than third (2).
358. **Lacrima size:** large, with an anterior or posterior (suborbital) process which is longer anteroposteriorly than the dorsoventral length of the lacrima in lateral view (0)/ small, dorsoventral length greater than anteroposterior length confined to the orbital rim (1)
359. **Fibula, articulation with femur:** fibula/femur articulation end to end (0)/ fibula sits in a recess on lateral margin of distal end of femur (1)
360. **Lateral row of enlarged palatine teeth:** absent (0)/ lateral tooth row present on palatine, converging posteriorly (1)
361. **Dentaries, posterior extent:** extends posteriorly no further than the level of coronoid eminence or slightly beyond (0)/ extends posteriorly more than halfway between coronoid eminence and articular condyle (1)
362. **Ectopterygoid, contact with maxilla:** absent (0)/ present (1)

363. **Cervical and dorsal vertebrae, anterior centrodiapophyseal or paradiapophyseal lamina in cervicals or dorsals:** absent (0)/ present (1)
364. **Cervical and dorsal vertebrae, prezygodiapophyseal lamina in posterior cervicals and/or anterior dorsals:** absent (0)/ present (1)
365. **Jugal, anterior suborbital extension:** broadly separated from prefrontal or posterior to the midpoint of the orbit (0)/ reaches level of prefrontal or anterior margin of orbit (1)
366. **Basioccipital, articular surface of the occipital condyle:** concave (0)/ hemispherical (1)
367. **Jugal lateral exposure below orbit:** absent (0)/ partly exposed above orbital margin of maxilla (1)/ entirely exposed above orbital margin of maxilla (2).
368. **Penultimate phalanges in hand:** shorter than or equal to antepenultimate (0)/ longer than antepenultimate (1)
369. **Jugals, posteroventral process:** short or spur-like, anteroventrally less than 20% of the total ventral length (0)/ long, greater than 25% of the total ventral length (1)
370. **Jugal-quadratojugal, contact:** absent (0)/ present(1)
371. **Vomers, contact with anterior region of maxilla:** absent (0)/ present (1)
372. **Prefrontal, contact with counterpart at midline:** absent (0)/ present (1)
373. **Interclavicle, notch on anterior margin:** absent (0)/ present (1)
374. **Tibia, contact with centrale:** absent (0)/ present (1)
375. **Premaxilla, contact with prefrontal:** absent (0)/ present (1)
376. **Dentary teeth, interdental plates:** contact both labial and lingual walls of alveolar groove, fully separating adjacent teeth (0)/ do not contact both labial and lingual walls of alveolar groove or are absent (1)
377. **Dentary teeth, asymmetry of dorsoventral height of labial and lingual walls of alveolar groove:** lingual wall subequal in height to labial wall (0)/ lingual wall absent or low, less than half the height of the labial wall (1)
378. **Dentary teeth, dorsoventral height of lingual wall of alveolar groove:** low, less than half the height of the labial wall (0)/ absent (1) - when labial and lingual walls are subequal in height this character is scored as inapplicable.

379. **Maxillary teeth, interdental plates:** contact both labial and lingual walls of alveolar groove, fully separating adjacent teeth (0)/ do not contact both labial and lingual walls of alveolar groove or are absent (1)

380. **Maxillary teeth, asymmetry of dorsoventral height of labial and lingual walls of alveolar groove:** lingual wall subequal in height to labial wall (0)/ lingual wall absent or low, less than half the height of the labial wall (1)

381. **Maxillary teeth, dorsoventral height of lingual wall of alveolar groove:** low, less than half the height of the labial wall (0)/ absent (1) - when labial and lingual walls are subequal in height this character is scored as inapplicable.