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1 **A reassessment of the taxonomic position of mesosaurs, and a surprising phylogeny of**  
2 **early amniotes**

3

4 By

5

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7

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18

19 **Abstract**

20 We reassess the phylogenetic position of mesosaurs by using a data matrix that is updated and  
21 slightly expanded from a matrix that the first author published in 1995 with his former thesis  
22 advisor. The revised matrix, which incorporates anatomical information published in the last  
23 twenty years and observations on several mesosaur specimens (mostly from Uruguay)  
24 includes seventeen terminal taxa and 129 characters (four more taxa and five more characters  
25 than the original matrix from 1995). The new matrix also differs by incorporating more  
26 ordered characters (all morphoclines were ordered). Parsimony analyses in PAUP 4 using the  
27 branch and bound algorithm show that the new matrix supports a position of mesosaurs at the  
28 very base of Sauropsida, as suggested by the first author in 1995. The exclusion of mesosaurs  
29 from a less inclusive clade of sauropsids is supported by a Bremer (Decay) index of 4 and a  
30 bootstrap frequency of 66%, both of which suggest that this result is moderately robust. The  
31 most parsimonious trees include some unexpected results, such as placing the anapsid reptile  
32 *Paleothyris* near the base of diapsids, and all of parareptiles as the sister-group of  
33 younginiforms (the most crownward diapsids included in the analyses). Turtles are placed  
34 among parareptiles, as the sister-group of pareiasaurs (and in diapsids, given that parareptiles  
35 are nested within diapsids). This unexpected result offers a potential solution to the long-  
36 lasting controversy about the position of turtles because previous studies viewed a position  
37 among diapsids and among parareptiles as mutually exclusive alternatives.

38

39 **Key words:** Mesosauridae, Sauropsida, Reptilia, Amniota, Permian

40

## 41 **Introduction**

42

43 Mesosaurs, a small clade (the three nominal genera and species usually recognized are  
44 currently in revision) of Early Permian amniotes known from South America (Brazil and  
45 Uruguay) and southern Africa (Namibia and South Africa) are notable in several respects  
46 (Piñeiro, 2008). They are the only Early Permian amniotes known from high-latitudes. They  
47 have long been considered marine, but a recent study of their paleoenvironment suggests that  
48 they inhabited a moderately hypersaline sea (Piñeiro et al., 2012c). Likewise, the occasional  
49 suggestions that they were piscivorous (e.g. Bakker, 1975) seem unlikely because the few  
50 acanthodians and actinopterygians that occur in the same formations as mesosaurs appear to  
51 be present in different strata, and the stomacal content of mesosaurs is known to contain only  
52 pygocephalomorph crustaceans and possibly, younger mesosaurs, which may also represent  
53 embryos still in utero (Piñeiro et al., 2012c) or carrion (Silva et al., 2017). Mesosaurs  
54 apparently captured their prey with their long snout and sieve-like long, slender teeth. They  
55 typically measured less than 2 m in total length, and apparently did not swim very fast, with  
56 an optimal swimming speed estimated at 0.15 to 0.55 m/s (Villamil et al., 2016).

57

58 Mesosaurs were the first amniotes to return to an aquatic lifestyle (Canoville and Laurin,  
59 2010). Even though uncertainty remains about just how terrestrial the first amniotes were, the  
60 latest bone microanatomical study suggests that they had become fairly terrestrial (Laurin and  
61 Buffrénil, 2016). Romer (1957, 1958) had initially suggested that the first amniotes were still  
62 largely aquatic to amphibious and came onto land mostly to lay eggs. This idea was based  
63 largely on the assumed primitively aquatic to amphibious lifestyle of limnoscelids (which  
64 remain to be assessed using bone microanatomy) and of the early synapsid *Ophiacodon*.  
65 However, it now appears that *Ophiacodon* was more terrestrial than initially thought, and the

66 geologically older ophiacodontid *Clepsydrops* has a typically terrestrial bone microanatomy  
67 (Felice and Angielczyk, 2014; Laurin and Buffrénil, 2016). This leaves the mesosaurs as the  
68 first amniotes to have reverted to a clearly aquatic lifestyle.

69  
70 Mesosaurs also document the first case of extended embryo retention, probably in the form of  
71 viviparity (Piñeiro et al., 2012a), given that most of the clues that have been used to suggest  
72 viviparity in several Mesozoic marine amniotes also occur in mesosaurs, except for embryos  
73 engaged in the birth canals, documented so far only in ichthyosaurs (Motani et al., 2014).  
74 These include very small individuals present in the abdominal cavity of much larger ones,  
75 though some may represent cannibalism rather than viviparity, as well as parental care of  
76 juveniles (Piñeiro et al., 2012a).

77  
78 Last but not least, mesosaurs have been hypothesized to have been either the sister-group of a  
79 large clade that includes parareptiles and eureptiles (Laurin and Reisz, 1995), or the basalmost  
80 parareptiles (Modesto, 1999). All this, coupled with the presence of temporal fenestration in  
81 mesosaurs (Piñeiro et al., 2012b), makes reassessing the taxonomic affinities of mesosaurs  
82 timely.

83  
84 This study makes no serious attempt at reassessing the origin of turtles, a fascinating but  
85 challenging topic that would require a paper of its own. Until the 1990s, turtles were  
86 considered to be closely related to captorhinid eureptiles (Clark and Carroll, 1973; Gauthier et  
87 al., 1988), which, like all extant turtles, have an anapsid temporal configuration. In the 1990s,  
88 the consensus shifted towards an origin of turtles among parareptiles, either as sister-group of  
89 procolophonoids (Reisz and Laurin, 1991; Laurin and Reisz, 1995) or of pareiasaurs (Lee,  
90 1993, 1996; Lyson et al. 2010), before shifting swiftly (though not unanimously) thereafter

91 for an origin among diapsids, based on morphological (Rieppel and deBraga 1996; deBraga  
92 and Rieppel, 1997) and molecular data (Hugall et al., 2007; Chiari et al. 2012). A possible  
93 stem-turtle, which appears to have a temporal fenestra (Schoch and Sues, 2015, 2017), further  
94 supports this hypothesis. To complicate things further, some recent studies suggest that the  
95 position of turtles is difficult to resolve with confidence because various genes suggest  
96 conflicting histories, and that this reflects the “true state of nature” (Lu et al., 2013). Thus,  
97 reassessing this question seriously would require adding many additional taxa, and ideally,  
98 incorporating molecular as well as morphological data. Clearly, this is an endeavor distinct  
99 from assessing the affinities of mesosaurs, which is the goal we pursue in this study.  
100 Nevertheless, the taxonomic sample selected here might allow a very limited test of where,  
101 among parareptiles, turtles fit, if they fit there at all. Diapsid diversity is great and given that  
102 very little of it is sampled here, our study is not designed to try to assess the relative merits of  
103 these two competing hypotheses (turtles inside vs. outside diapsids). Given the controversy  
104 surrounding the affinities of turtles, in this paper, this vernacular word will refer to crown-  
105 turtles, as well as all undoubted stem-turtles with at least a partial carapace, namely, among  
106 the taxa discussed below, *Proganochelys* and *Odontochelys*.

107

## 108 **Methods**

109

### 110 *Taxon selection*

111

112 We started from the matrix of Laurin and Reisz (1995), given that this was the matrix that we  
113 knew best, that we had confidence in the accuracy of the anatomical scoring, and that we were  
114 confident that we could apply the revised scores in a manner coherent with the original  
115 scoring. This last point is particularly important because even if a matrix was scored by a

116 systematist in a perfectly coherent and justified way, another systematist may score additional  
117 taxa, or revise the scoring based on new information, in a way that is internally coherent, but  
118 incoherent with the original scoring. Using reliably a matrix produced by other authors  
119 requires assessing how states were conceived and delimited, and applying the same  
120 delimitations in the revised or new scores.

121

122 As explained above, our taxon selection is inadequate to test the position of turtles (within vs.  
123 outside diapsids). Therefore, some sensitivity analyses were performed to assess the  
124 robustness of our conclusions to the inclusion or exclusion of turtles; this allows assessing if  
125 the position of turtles (close to mesosaurs, among parareptiles, or much farther, deep inside  
126 diapsids) impacts on the assessment of the affinities of mesosaurs, or on the robustness of our  
127 conclusions. The only additional taxa, compared to the matrix of Laurin and Reisz (1995) are  
128 thus the early parareptile *Acleistorhinus*, which is now much better known because of the  
129 anatomical description given by deBraga and Reisz (1996), the procolophonoid *Owenetta*  
130 *kitchingorum*, which was thoroughly described by Reisz and Scott (2002), and the stem-turtle  
131 *Odontochelys* (Li et al., 2008). We also split the OTU Testudines, which incorporated  
132 *Proganochelys* in the scoring of Laurin and Reisz (1995), into separate *Proganochelys* and  
133 *Chelonii*, which we scored based on all turtles crownward of *Proganochelys*. The source of  
134 the scores is documented in the Mesquite Nexus file (SOM 1, on the HAL web site) as notes  
135 in individual cells and in the taxon name cell, but in the case of *Chelonii*, scoring is based on  
136 several stem-turtles, such as *Australochelys* (Gaffney and Kitching, 1995), *Condorchelys*  
137 (Sterli, 2008), *Palaeochersis* (Sterli et al., 2007), *Kayentachelys* (Sterli and Joyce, 2007), and  
138 *Indochelys* (Datta et al., 2000), in addition to extant and extinct crown-turtles (Gaffney, 1979;  
139 Gaffney et al., 2006). The revised matrix thus has seventeen terminal taxa, up from thirteen  
140 taxa in Laurin and Reisz (1995). We deliberately changed the name of the OTU including

141 extant turtles and part of its stem from Testudines to Chelonii to draw attention to the fact that  
142 this OTU has changed somewhat. The choice of the name is further justified simply by the  
143 fact that Brongniart (1800) was the first to erect a higher taxon (from the class-series [which  
144 encompasses orders], rather than family-series) that encompassed all or most turtles that were  
145 then known, and he named it “Chéloniens”, soon thereafter latinized as “Chelonii” by  
146 Latreille (1800; see also Dubois and Bour, 2010). The zoological code does not include rules  
147 of priority for class-series nomina, but by analogy to such rules for family and genus-series  
148 nomina, Dubois and Bour (2010) suggest using this name, and their suggestion is followed  
149 here, given that Testudines were clearly intended as genus- and family-series nomina. Finally,  
150 note that the composition of Chelonii as delimited here does not match Testudines as defined  
151 by Joyce et al. (2004), which applies the turtle crown.

152

### 153 *Character coding*

154

155 We did not add new characters to the matrix, but we ordered some characters because they  
156 appear to form morphoclines. In this respect, our approach differs from that followed by  
157 Laurin and Reisz (1995), which we quote in full because it is highly relevant to what follows.  
158 They stated: “A few characters were ordered in this study (Appendix 1). The controversy over  
159 whether multi-state characters should be ordered or left unordered is not settled. Some have  
160 argued against the use of ordered characters (Hauser & Presch, 1991; Mabee, 1989), while  
161 others have argued that characters should be ordered when possible (Mickevich & Lipscomb,  
162 1991; Slowinski, 1993). We have used a mixed approach. All multi-state characters exhibiting  
163 what seemed to be a morphocline were mapped on the shortest tree (found with unordered  
164 characters only) using MacClade 3.0 (Maddison & Maddison, 1992). When the optimization  
165 of the character supported the existence of a morphocline, the character was ordered. Support



166 for the morphocline required that all state transformations for the relevant character be  
167 compatible with the morphocline. If a single transformation was ambiguous, the character was  
168 not ordered. This procedure allowed us to order six characters (Appendix 1).”

169  
170 In the more than 20 years that passed between after publication of that paper, one of us (ML)  
171 has become involved in research on this topic (Grand et al., 2013; Rineau et al., 2015), and  
172 this simulation-based work has shown unambiguously that characters that form morphoclines  
173 should be ordered because this maximizes resolution power (the ability to recover correct  
174 clades) and minimizes false resolutions (artifactual clades). The additional criterion invoked  
175 by Laurin and Reisz (1995) consisting in requiring that optimization of each initially  
176 unordered character be fully compatible with the ordering scheme now appears invalid, for  
177 two main reasons.

178  
179 First, this assumes that the initially-obtained tree is the correct one, which is never certain in  
180 an empirical study, and even less so if ordering scheme of multi-state characters is  
181 suboptimal. In this respect, note that in the extreme case of each taxon having a different  
182 state, an unordered character has no phylogenetic information content, whereas an ordered  
183 character will convey maximal phylogenetic information content if all taxa have a different  
184 state.

185  
186 Second, requiring state optimization to match the presumed morphocline on the tree assumes  
187 that all relevant taxa have been included. This is generally not the case, for several reasons:  
188 most empirical studies do not include all known extant species of a clade; in some taxa, only a  
189 small fraction of the extant biodiversity has been described (Mora et al., 2011); not all extinct  
190 taxa (if any) known from the fossil record are typically included, and in any case, the fossil

191 record of most taxa is fragmentary at best (Foote and Sepkoski, 1999; Didier et al., 2015).

192 Thus, this second reason alone would be more than sufficient grounds not to require a priori  
193 ordering schemes to be validated through optimization of unordered states onto a tree.

194

195 Many more characters (21) were thus ordered. These are (in our numbering; this does not  
196 match the numbers in Laurin and Reisz, 1995): 6, 15, 17, 19, 25, 35, 37, 40, 49, 51, 57, 74,  
197 85, 93, 99, 101, 110, 112, 121, 123 (which was binary in Laurin and Reisz, 1995), 128, and  
198 129. In some cases, the states had to be reordered because the initial scheme of Laurin and  
199 Reisz (1995) had state 0 as the primitive state; this is not necessarily the case here because the  
200 primitive condition may be in the middle of a morphocline. Thus, the states were not  
201 necessarily listed by Laurin and Reisz (1995) in an order coherent with a morphocline. This  
202 was not problematic for Laurin and Reisz (1995) given that they treated these characters as  
203 unordered, but treating them as morphoclines, as done here, requires reordering the states.  
204 The only difficult cases are those in which the morphocline seems likely but not absolutely  
205 certain. For instance, we ordered character 48 (ectopterygoid: large [0]; small [1]; absent [2])  
206 because we hypothesize that the ectopterygoid was lost through reduction in size rather than  
207 fusion to a neighboring element, a hypothesis supported by the fact that some Permian  
208 amniotes, such as *Owenetta kitchingorum* (Reisz & Scott, 2002) have a diminutive  
209 ectopterygoid, but that there is no firm evidence that this bone fused to neighboring bones in  
210 amniotes or in lissamphibians (Müller et al., 2005). In a broader taxonomic context, this is  
211 also consistent with the finding that in temnospondyls, the closest relatives of *Doleserpeton*,  
212 which lacks an ectopterygoid, have a small ectopterygoid, though lepospondyls apparently  
213 provide a counter-example (Kimmel et al., 2009).

214 However, if that hypothesis turned out to be false, this ordering would be unwarranted. More  
215 information about the characters that were ordered and the exact ordering schemes can be  
216 seen in SOM 1 (the matrix in a Mesquite Nexus format).

217

218 In the same spirit, we also split some characters that appeared to encompass two or more  
219 distinct characters, or merged characters that seem to reflect a single cline. Thus, character 27  
220 (“occipital flange of squamosal”), from Laurin & Reisz (1995), was split into two characters  
221 (here, numbers 27 and 28) because we think that the original character can be better  
222 considered to consist of two logically independent characters. The initial formulation thus  
223 included six states: “Occipital flange of squamosal: in otic notch and overlaps pterygoid (0);  
224 gently convex all along the posterior edge of the skull (1); convex above quadrate  
225 emargination and concave medial to tympanic ridge (2); absent (3); medial to tympanic ridge,  
226 facing posteromedially (4); medial to tympanic ridge, concave, facing posterolaterally or  
227 ventrolaterally (5).” These six states were unordered and indeed, it is difficult to see how they  
228 could have been ordered, but this rendered this character of little usefulness, given that there  
229 were 13 OTUs. We think that it is better to separate the presence or absence of a squamosal  
230 contribution to the otic notch or quadrate emargination (in the emargination) and the position  
231 of the squamosal, either mostly on the cheek (primitive condition) or largely on the skull table  
232 (derived condition). These two binary characters may capture most of the information content  
233 of this character. Under both the initial formulation and the new one, accurate scoring requires  
234 reasonably undistorted skulls because on severely flattened ones, exact orientation of the  
235 squamosal would be difficult to determine.

236

237 Conversely, characters 24 and 25 (maxillary region and maxillary tooth) were merged into a  
238 single ordered character because these can be conceptualized as increasing differentiation of

239 the tooth row, from a homogeneous tooth row, to the presence of a caniniform region, and  
240 finally, the presence of a genuine caniniform tooth (a tooth much larger than the neighboring  
241 ones; two positions may be concerned, but normally, only one is occupied by a tooth, because  
242 of the continuous replacement pattern).

243

#### 244 *Character scoring*

245

246 The scores that have been changed relative to Laurin and Reisz (1995) are highlighted in  
247 yellow in SOM 1. These need not all be commented here, but a few highlights can be given.  
248 For mesosaurs, some scores that were unknown (?) in the matrix of Laurin and Reisz (1995)  
249 have been entered based on personal observations of the authors on several specimens made  
250 in the last five years, mostly of the collections of the Faculty of Sciences of the University of  
251 the Republic (Montevideo). These collections include dozens of *Mesosaurus* specimens from  
252 the Early Permian Mangrullo Formation (Uruguay). To a lesser extent, we also exploited  
253 collections in Brazil, Germany and the more limited collection of mesosaurs in Paris. The list  
254 of studied *Mesosaurus* specimens is provided in SOM 2, a table detailing specimen number,  
255 geographic provenance and brief description. In addition, we also checked the literature to  
256 revise the entire matrix, occasionally revising the scoring, whenever warranted.

257

258 A few of the revisions can be commented here. The foramen orbitonasale (character 10) was  
259 not documented in Laurin and Reisz (1995), but our observations suggest that it is absent in  
260 mesosaurs. Similarly, a postorbital/supratemporal contact (character 12), scored as being  
261 present in mesosaurs by Laurin and Reisz (1995) is now considered to have been absent  
262 (Piñeiro et al. 2012b). The postorbital is now also considered to be located far from the

263 occiput (character 13), whereas Laurin and Reisz (1995) had scored it as being close to it  
264 (Figs. 1-2).

265

266 There was a problem with character 22 (maxilla/quadratojugal contact), for which the list of  
267 states had been inverted in appendix 1 (list of characters and states) of Laurin and Reisz  
268 (1995), though they were stated correctly in the main text and in appendix 2 (the data matrix).

269 The correct coding is that state 0 (the primitive condition) consists in the two bones to be  
270 separated in lateral view, and this condition prevails in mesosaurs (Figs. 1-2).

271

272 The lower temporal fenestra (character 32), considered to have been absent in Laurin and  
273 Reisz (1995) is now considered present (Piñeiro et al. 2012b), as had been correctly assessed  
274 by our great predecessor von Huene (1941). The tabular bone is now considered to have been  
275 mid-sized (character 17), a state that was absent from the initial coding.

276

277 The jugal was changed from not reaching the anterior orbital rim (as coded in Laurin and  
278 Reisz, 1995) to reaching that level. This condition is shown in Uruguayan specimens (Piñeiro  
279 et al., 2012b: fig. 1; Fig. 1 herein).

280

281 Mesosaurs seem to have a low maxillary eminence (Piñeiro et al., 2012b: fig. 1) that even  
282 appears to contact the nasal in a short suture between the external naris and the foramen  
283 nariale obturatum. However, given that this low eminence reaches its maximal extent anterior  
284 and just posterior to the external naris, we consider it not to be homologous with the anterior  
285 process found in several other amniotes, such as *Acleistorhinus* (deBraga and Reisz, 1996).

286 To clarify this, we have added, in the character formulation, that this process is located  
287 posterior to the naris.

288

289 Surprisingly, mesosaurs seem to have a slender stapes in all ontogenetic stages in which it is  
290 documented (Fig. 3). There is no evidence that it was associated with a tympanum (character  
291 69), which would make no sense in an aquatic animal like mesosaurs.

292

293 The number of coronoid bones is unclear. Some of our specimens might possibly show two,  
294 but this interpretation is highly tentative. We don't see strong evidence that there was a single  
295 coronoid either. Thus, we have changed the scoring from a single coronoid (in Laurin and  
296 Reisz, 1995) to unknown.

297

298 We updated the number of scapulocoracoid ossifications from three to only two (Piñeiro,  
299 2004; Modesto, 2010: 1387).

300

301 Laurin and Reisz (1995) had a character (102) entitled "Ectepicondylar foramen and groove".  
302 Given that the groove may occur without the foramen, and that a foramen may occur without  
303 a groove (whenever the foramen leads into a canal that is sharply angled relative to the bone  
304 surface), we have decided to split these into two characters. Mesosaurs were scored by Laurin  
305 and Reisz (1995) as having either only the groove, or the groove and foramen. Our  
306 observations suggest that the foramen is always present, though it is not always easy to  
307 observe (Fig. 4). Therefore, we have scored both as present.

308

309 All these changes in scoring, and others not commented here for lack of space, are  
310 documented in SOM 1, a Mesquite Nexus file incorporating the data matrix and several trees,  
311 which can be accessed in the HAL open archive (<https://hal.archives-ouvertes.fr/>) through this  
312 link: (will be entered once paper is accepted; HAL does not accept datasets before

313 **acceptance**). Note that the Nexus format can also be read by MacClade 3.0 (Maddison and  
314 Maddison, 1992) and PAUP 4.0 (Swofford, 2003), but the yellow highlighting to mark the  
315 changes are visible only in Mesquite.

316

### 317 *Phylogenetic analysis*

318

319 The data matrix was analyzed using parsimony (with some states ordered, as mentioned  
320 above) using the branch and bound algorithm of PAUP 4.0a155 (Swofford, 2003), which  
321 guarantees to find all the most parsimonious trees (Hendy and Penny 1982). Robustness of  
322 the results was assessed both by non-parametric bootstrap analysis (Felsenstein, 1985) with  
323 200 replicates and decay (Bremer) index (Bremer, 1988), both using the branch and bound  
324 algorithm. Bootstrap frequencies reported below are rounded off to the nearest percent. To  
325 establish the number of extra steps required to move mesosaurs to alternative locations in the  
326 tree, skeletal topological constraints were enforced. To assess the robustness of our results to  
327 taxonomic sampling, we repeated the analyses with some taxa deleted (Mesosauridae,  
328 Chelonii, *Proganochelys*, and *Odontochelys*).

329

## 330 **Results**

331

### 332 *Exhaustive taxonomic sample*

333

334 The search yielded two most parsimonious tree requiring 383 steps, with a CI of 0.5666 and  
335 with a retention index of 0.6605 (Fig.5). All lengths reported here were computed in Mesquite  
336 3.1, by distinguishing between partial uncertainty and polymorphism; under the default  
337 settings PAUP 4 considers all these as uncertainty, though settings can be changed to interpret

338 these data as in Mesquite. This introduces only a difference in tree lengths between both  
339 programs, though the shortest trees in one program remain the shortest ones in the other. In  
340 these trees, mesosaurs appear as the sister-group of all other sauropsids, as they were in  
341 Laurin and Reisz (1995). However, sauropsid phylogeny differs strongly from the topology  
342 recovered by Laurin and Reisz (1995) and most recent analyses because parareptiles appear to  
343 be nested within diapsids, as the sister-group of younginiforms (more crownward diapsids are  
344 not included in our taxonomic sample). Not surprisingly, this result is not very robust; the  
345 smallest clade that includes younginiforms and parareptiles has a Bremer index of 3 and a  
346 bootstrap frequency of only 39%. This low bootstrap frequency suggests considerable  
347 character conflict. Pareiasaurs appear to be the sister-group of turtles, as previously suggested  
348 by Lee (1993, 1996), but procolophonoids appear to be paraphyletic, given that *Procolophon*  
349 is closer to that clade, in the most parsimonious trees, than to *Owenetta kitchingorum*. In  
350 addition, the romeriid *Paleothyris* appears nested within diapsids, another counter-intuitive  
351 result, though this one is the least robust clade (Bremer index of 1; bootstrap frequency of  
352 20%).

353

354 The clade that includes all sauropsids except for mesosaurs has a bootstrap frequency of 66%,  
355 which is relatively low, but moving mesosaurs within the clade that includes other reptiles,  
356 such as the position at the base of parareptiles, previously suggested by Gauthier et al. (1988:  
357 fig. 4.4) and Modesto (1999: fig. 4A) requires four extra steps. Moving mesosaurs to other  
358 phylogenetic positions requires three additional (386) steps. Among the 48 trees of that  
359 length, mesosaurs occur in various positions, but always outside the smallest clade that  
360 includes all other sauropsids. In four of these trees, mesosaurs are the sister-group of a clade  
361 that includes amniotes and diadectomorphs (in which diadectomorphs appear at the base of  
362 Synapsida); in three of these trees, mesosaurs are the sister-group of amniotes. In the 41 other



363 trees of that length, mesosaurs appear in their most parsimonious position, as the sister-group  
364 of all other sauropsids. The most frequent clade that includes mesosaurs and a subset of the  
365 other sauropsids (in this case, all others except for *Acleistorhinus*) has a low bootstrap  
366 frequency (12%).

367

368 The characters discussed below were presented in detail by Laurin and Reisz (1995), with  
369 very few exceptions. Thus, except for characters not taken from that paper, the discussion of  
370 the nature of these characters is kept short, and the emphasis is on their revised taxonomic  
371 distribution.

372

373 The sauropsid status of mesosaurs is supported by the following four unambiguous  
374 synapomorphies, given our data and the shortest trees (the numbers in parentheses following a  
375 character number designate the character state):

376

377 Character 35(1). Quadrate anterior process short. This process is long in *Seymouria*,  
378 limnoscelids and Synapsida (ancestrally). In these taxa, this process overlaps at least half of  
379 the length of the quadrate ramus of the pterygoid. The derived condition (short process  
380 overlapping less than half of quadrate ramus of pterygoid) occurs in mesosaurs (Modesto,  
381 2006), captorhinids, *Paleothyris*, araeoscelidians and younginiforms, but parareptiles revert to  
382 having a long anterior process.

383

384 Character 62(1). Posttemporal fenestra large. In *Seymouria*, diadectids and synapsids  
385 ancestrally, the posttemporal fenestra is small; it looks almost like a large foramen. Mesosaurs  
386 (Modesto, 2006: 347) and most other sauropsids, except *Acleistorhinus*, have a larger  
387 posttemporal fenestra. The fenestra was apparently convergently enlarged in limnoscelids.

388

389 Character 105(1). Supinator process parallel to shaft. The supinator process was ancestrally  
390 sharply angled to the shaft, as seen in *Seymouria*, diadectomorphs and early synapsids. All  
391 early sauropsids in which this character is documented have a supinator process which is  
392 oriented at a much lower angle to the shaft.

393

394 Character 123(1). Presence of a single pedal centrale in the adult. Ancestrally in cotylosaurs,  
395 two pedal centralia were present, as seen in diadectomorphs and most Permo-Carboniferous  
396 synapsids. In synapsids, the situation is somewhat uncertain. Most eupelycosaurs have two  
397 centralia, but in Caseasauria, there is no evidence of two centralia; *Casea* is usually shown  
398 with two, but only one is actually preserved (Romer and Price, 1940: fig. 41H), and in  
399 *Cotylorhynchus* only one is preserved, though Stovall et al. (1966: 24) indicate that the  
400 presence of a second centrale is uncertain. Polymorphism could have been scored for this  
401 taxon, but given how poorly known this character is in Caseasauria, we have provisionally  
402 kept a scoring that represents the prevailing condition in Eupelycosauria, where it is much  
403 better documented (Romer and Price, 1940: fig. 41). Sauropsids have a single pedal centrale  
404 in the adult and there is no strong evidence of a second centrale in juveniles, though the  
405 ontogeny of most Paleozoic sauropsids (except mesosaurs) is too poorly known to be sure that  
406 a second centrale was absent in early ontogeny (state 2). The well-documented ontogeny of  
407 mesosaurs shows that in this taxon, fusion occurred fairly late in the ontogeny (state 1; Piñeiro  
408 et al., 2016). In this respect, mesosaurs may display an intermediate condition. This character  
409 is ordered because it appears to form a cline.

410

411 The position of mesosaurs outside the clade that includes all other sauropsids is supported by:

412

413 Character 39(2). Intertemporal vacuity long, at least 15% of the skull length. This character is  
414 reversed in *Procolophon*, pareiasaurs, and *Odontochelys*, which have a shorter interpterygoid  
415 vacuity.

416

417 Character 49(1). Suborbital foramen present. This is transformed into a fenestra (2) in  
418 araeoscelidians, *Youngina*, *Proganochelys* and some crown-turtles. *Acleistorhinus* lost the  
419 foramen (0).

420

421 Character 51(1). Absence of parasphenoid wings.

422

423 Character 54(1). Presence of supraoccipital anterior crista.

424

425 Character 55(2). Supraoccipital plate narrow. The supraoccipital becomes even narrower (3)  
426 in *Procolophon*, pareiasaurs and turtles, whereas it becomes broader (1) in *Acleistorhinus*.

427

428 The surprising inclusion of parareptiles in the smallest clade that comprises also  
429 Araeoscelidians, *Youngina* and *Paleothyris* is supported by:

430

431 Character 16(2). A reduction in size of the tabular, which is further reduced in the clade that  
432 includes *Owenetta*, *Procolophon*, pareiasaurs and turtles. This character is reversed in  
433 pareiasaurs, which re-acquire a larger tabular (state 1).

434

435 Character 57(1). Paroccipital process contacts tabular distally. This character may  
436 characterize a more inclusive clade because it is inapplicable in captorhinids, which lack a

437 tabular, and mesosaurs, in which the situation is uncertain given contradictory information  
438 provided by various specimens.

439

440 Character 119(1). Carpus and tarsus long and slender (longer globally than wide). This is a  
441 weak synapomorphy because among parareptiles, it is documented only in millerettids. This  
442 character is reversed in the smallest clade that includes *Procolophon*, pareiasaurs and turtles,  
443 and it not documented in *Acleistorhinus* and *Owenetta*.

444

445 Character 126(1). Metapodials overlapping. This is another moderately convincing  
446 synapomorphy because among parareptiles, it is documented in *Procolophon* and in some  
447 millerettids (Thommasen and Carroll, 1981). It is also present in turtles, but it is absent in  
448 pareiasaurs, and undocumented in *Acleistorhinus* and *Owenetta*.

449

450 The position of *Paleothyris* as sister-group of the smallest clade that includes *Youngina*,  
451 parareptiles and turtles is supported by:

452

453 Character 89(1). Posterior trunk (lumbar) neural arches narrow. This is reversed (to swollen;  
454 2) in *Owenetta*, *Procolophon*, and pareiasaurs.

455

456 Character 90(1). Posterior trunk (lumbar) zygapophyseal buttresses narrow. This refers to the  
457 antero-posterior width of the buttresses, not the width of the neural arches, which is typically  
458 assessed in anterior or posterior view. This character does not have the same distribution as  
459 the previous one as there is no evidence of reversal in the clade.

460

461 The equally surprising position of parareptiles as the sister-group of *Youngina* is weakly  
462 supported with a bootstrap frequency of 47% and a Bremer (decay) index of 3. While we  
463 view this result with some suspicion and consider it provisory, we provide a list of  
464 synapomorphies supporting it. To mention only the characters that unambiguously support  
465 this topology, this includes:

466

467 Character 9(1). The lacrimal is excluded from the naris and septomaxilla; this is reversed in  
468 millerettids and pareiasaurs.

469

470 Character 18(1). A high anterodorsal process of the maxilla that reaches the nasal. This is  
471 reversed in millerettids (state 0, anterodorsal process absent) and pareiasaurs (state 1, low,  
472 anterodorsal process does not reach nasal). Note that there is a strong logical link between  
473 both characters (9 and 18), which were both in the matrix of Laurin and Reisz (1995;  
474 characters 9 and 18); to solve this problem, we have downweighted both characters to 0.5.

475

476 Character 24(1). Caniniform tooth (2) replaced by caniniform region (1). The trend towards  
477 less differentiation in tooth size (0) continues within parareptiles, as some millerettids (0&1)  
478 and all procolophonids and pareiasaurs lack a caniniform region or tooth (0). Mesosaurs are  
479 convergent in having a homodont dentition (0), under this topology.

480

481 Character 48(1). Absence of ectopterygoid teeth.

482

483 Character 70(1). Stapedial dorsal process unossified or absent.

484

485 Character 94(1). Transverse processes present on at least 12 caudal vertebrae. This character  
486 is undocumented in several parareptiles (*Acleistorhinus*, millerettids and *Owenetta*) and in  
487 *Odontochelys*, so this synapomorphy is only moderately well-established.

488

489 Character 101(1). Supraglenoid foramen absent.

490

491 Character 110(1). Olecranon process small, with small articular facet facing proximally. This  
492 synapomorphy is only moderately satisfactory because it could not be scored for

493 *Acleistorhinus*, millerettids and *Owenetta*, so the condition at the base of parareptiles is poorly  
494 documented.

495

496 Character 113(1). Iliac blade dorsally expanded and distally flared.

497

498 Character 114(1). Large acetabular buttress, overhanging strongly. This synapomorphy is  
499 poorly documented because it could not be scored for *Acleistorhinus*, millerettids and

500 *Owenetta*, and *Odontochelys*.

501

502 *Taxonomic subsampling*

503

504 When Mesosauridae is deleted from the matrix, we recover a more conventional phylogeny,  
505 in which parareptiles form the sister-group of eureptiles, and in which *Paleothyris* is excluded  
506 from diapsids. The only unorthodox result with this taxonomic sampling is that  
507 procolophonoids remain paraphyletic with respect to pareiasaurs and turtles.

508

509 Deleting Chelonii from the matrix does not alter the topology of the shortest tree, except that  
510 there is no longer a basal trichotomy of turtles. The robustness of the position of mesosaurs  
511 outside the smallest clade that includes all other sauropsids is strong, with a Bremer (decay)  
512 index of 4, and a bootstrap frequency of 56%. In the bootstrap tree (though not in the most  
513 parsimonious tree), *Paleothyris* is outside Diapsida. However, with that taxonomic sample,  
514 the most robust clade (with a Bremer index of 7 and a bootstrap frequency of 97%) includes  
515 Pareiasauria, *Owenetta*, *Procolophon*, and stem-turtles. This remains one of the most robust  
516 clade, with a Bremer index of 6 and a bootstrap frequency of 97%, when *Proganochelys* is  
517 removed (in addition to Chelonii), whereas the position of mesosaurs outside the clade that  
518 includes the other sauropsids remains fairly robust, with a Bremer index of 5 and a bootstrap  
519 frequency of 68%. Further removing *Odontochelys*, results in two trees (length of 291 steps in  
520 PAUP). Their strict consensus is compatible with the results from the complete taxonomic  
521 sample, but much less resolved. The four eureptile taxa and Parareptilia form a large  
522 polytomy (Parareptilia remains monophyletic), and two trichotomies are present within  
523 Parareptilia (one with *Acleistorhinus*, Millerettidae, and a clade including pareiasaurs plus  
524 both procolophonoids, and a second polytomy including *Owenetta*, *Procolophon*, and  
525 pareiasaurs).

526

## 527 **Discussion**

528

529 The position of mesosaurs outside the clade that includes all other sauropsids as suggested by  
530 Laurin and Reisz (1995) appears to be a reasonably robust result, though various parareptile  
531 clades are more robust. The relatively low bootstrap frequency (58% for Sauropsida; 66% for  
532 the largest sauropsid clade that excludes mesosaurs) is not overly convincing, but three  
533 additional steps are required to place mesosaurs elsewhere in the tree, and in these alternative

534 trees, mesosaurs fall outside Sauropsida; the position of sister-group of other parareptiles,  
535 previously suggested by Gauthier et al. (1988) and Modesto (1999), or other positions within  
536 parareptiles imply at least four extra steps and these alternative positions have bootstrap  
537 frequencies of 12% or less. Given the mix of primitive and derived features of the mesosaur  
538 skeleton, the obtained results are not unexpected. Thus, several characters present in  
539 mesosaurs are shared with those present in basalmost amniotes or close relatives of amniotes  
540 (see above). This placement of mesosaurs in amniote phylogeny is slightly more robust than  
541 in Laurin and Reisz (1995), in which the clade that included all sauropsids except mesosaurs  
542 had a Bremer index of only one, but a similar bootstrap frequency of 67%. This moderate  
543 robustness improvement (at least as assessed by the Bremer index) benefits from several new  
544 anatomical studies on mesosaurs. However, the previous suggestions that mesosaurs are basal  
545 parareptiles (Gauthier et al., 1988; Modesto, 1999) are not surprising because mesosaurs share  
546 some features with procolophonoids, such as the presence of swollen neural arches and the  
547 postorbital not reaching the supratemporal. The relatively low bootstrap frequency (66%)  
548 presumably reflects a fair amount of character conflict.

549

550 The position of parareptiles in our tree, though unorthodox, offers a possible resolution  
551 between two hypotheses about the position of turtles that were previously considered  
552 mutually incompatible, namely among parareptiles, as suggested by some paleontological  
553 studies (Reisz and Laurin, 1991; Lee, 1993, 1996; Laurin and Reisz, 1995), or among diapsids  
554 as suggested by most recent molecular (Hugall et al., 2007; Chiari et al., 2012) and some  
555 paleontological phylogenies (Rieppel and deBraga, 1996; deBraga and Rieppel, 1997;  
556 Piñeiro, 2004). The possibility that parareptiles are actually diapsids that lost one or both of  
557 the fenestrae (the upper fenestra having never been found in the group), which is raised by our  
558 results, offers a way out of this controversy, given that turtles can be both parareptiles and



559 diapsids. Under that hypothesis, the upper temporal fenestra closure described by Bever et al.  
560 (2015) in the ontogeny of *Eunotosaurus* might actually characterize parareptiles as a whole.  
561 In *Eunotosaurus*, this closure is achieved by anterior expansion of the supratemporal. The  
562 supratemporal is fairly large in most parareptiles (deBraga and Reisz, 1996; Lee, 1997; Reisz  
563 and Scott, 2002; Tsuji et al., 2012), so it is possible that they share this mechanism of upper  
564 temporal fenestra closure with *Eunotosaurus*. This possibility could be checked through CT-  
565 scanning or mechanical preparation of the internal surface of the skull roof. However, the  
566 morphology of the basalmost parareptiles (assuming recent phylogenies are correct) is not  
567 consistent with this scenario. Thus, millerettids and the even older and more basal *Microleter*  
568 and *Australothyris* are among the parareptiles with the smallest supratemporal (Gow, 1972;  
569 Tsuji et al., 2010). Clearly, this intriguing by-product of our study on mesosaur affinities will  
570 need to be evaluated both with an expanded taxon and character sample and with new  
571 anatomical studies of the temporal area of most parareptiles. This is not done here because the  
572 purpose of our study was to assess the position of mesosaurs in amniote phylogeny. Assessing  
573 the position of parareptiles as a whole, and the controversial issue of turtle origins are much  
574 more ambitious goals that our study was not designed to assess.

575

576 The position of parareptiles within diapsids obtained here should be tested further because our  
577 taxonomic sample of diapsids is sparse, with only two stem-diapsid taxa (araeoscelidians and  
578 younginiforms) represented. The fact that this topology is not recovered (with parareptiles  
579 forming the sister-group of eureptiles) when Mesosauridae is deleted from the matrix further  
580 reinforces this note of caution. When mesosaurs are excluded from the analysis, eureptiles are  
581 united by six synapomorphies (character number in parentheses): postorbital/supratemporal  
582 contact absent (12); posterolateral corner of skull table formed by parietal and small  
583 supratemporal (15); supratemporal small (17); squamosal and posttemporal fenestra in contact

584 (25); quadrate anterior process short (35); and arcuate flange of pterygoid absent (42). The  
585 fact that mesosaurs share half of these characters (12, 35, and 42) weakens support for  
586 Eureptilia. This topology is new to our knowledge, although Lee (2013) had found, in some of  
587 his 12 analyses (eight of a diapsid-focused dataset, and four of a parareptile-focused dataset),  
588 that the parareptile *Eunotosaurus*, which has been claimed to be a close relative of turtles  
589 (Lyson et al, 2010; Bever et al., 2015), also fit within diapsids. However, our results differ  
590 (with the complete taxonomic sample) in placing all parareptiles within diapsids. Still, this  
591 new hypothesis is supported by some frequently-discussed characters, such as a temporal  
592 emargination, which is present in most parareptiles (Müller and Tsuji, 2007) as well as in  
593 crown-diapsids (Laurin, 1991) and turtles. This part of the results is the most surprising  
594 though it is possible that morphological support for the taxon Eureptilia (excluding  
595 parareptiles) is weaker than commonly realized. For instance, in the analysis of Tsuji et al.  
596 (2010), bootstrap frequency for that clade is only 58% (one of the lowest of the tree), and  
597 Bayesian posterior probability is 86% (higher, but among the most weakly-supported half of  
598 the clades of their tree). Similarly, in the analysis of Laurin and Reisz (1995), Eureptilia had a  
599 bootstrap frequency of only 69%, which placed it among the most weakly-supported clades.  
600 Strangely, Procolophonoidea is found here to be paraphyletic with respect to pareiasaurs and  
601 turtles, despite the fact that we included one of its most obvious synapomorphies, namely the  
602 posterior extension of the orbit (character 37), which *Owenetta* and *Procolophon* are the only  
603 ones to display in our matrix. This result is moderately robust (bootstrap frequency of 64%  
604 and Bremer index of 5) and it persists with the deletion of Mesosauridae from the analysis.  
605 However, we have added *Owenetta* without adding synapomorphies of Procolophonoidea, so  
606 this result may be artefactual.  
607

608 The position of *Paleothyris* within diapsids is equally surprising, but this result is not robust,  
609 and it disappears when mesosaurs are removed from the analysis. The bootstrap frequency of  
610 this clade (in the analysis with all taxa) is barely 20%, and its Bremer (decay) index is only 1,  
611 which means that only one more character supports this position for *Paleothyris* than the next  
612 most supported position. This topology reflects partly the fact that the position of mesosaurs  
613 at the base of Sauropsida makes the presence of the lower temporal fenestra an amniote  
614 synapomorphy (reversed in Captorhinidae, *Paleothyris*, and most parareptiles and turtles);  
615 removing mesosaurs changes the history of this character at the base of amniotes, which in  
616 turn supports diapsid monophyly. Furthermore, various studies have de-emphasized the  
617 importance of fenestration as a systematic character (Fucik, 1991; Hamley and Thulborn,  
618 1993; Müller, 2003; Cisneros et al., 2004; Tsuji et al., 2010; Bever et al., 2015), and temporal  
619 morphology may be influenced by several factors (Werneburg, 2012), which complicates  
620 interpretation of observed morphology. Thus, the question of diapsid monophyly (aside from  
621 the inclusion of turtles) might be worth investigating further.

622

623 To sum up, our study suggests that mesosaurs are the basalmost sauropsids; this result appears  
624 to be fairly well-supported, at least with our dataset. Moreover, our results raise several  
625 problems about the phylogeny of early amniotes, some of which might be worth being  
626 reinvestigated with an increased sample of taxa and characters, and a fresh look at various  
627 specimens. In addition to suggesting yet another hypothesis about the origin of turtles, our  
628 results highlight the importance of including mesosaurs in phylogenetic analyses of amniotes,  
629 because they can potentially change the topology near the base of Amniota and weaken  
630 support for Eureptilia and Diapsida. Including mesosaurs in such analyses is not the  
631 established practice (e.g., Reisz et al., 2011; Lyson et al., 2013).

632

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640

641

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- 833

834 Figure legends

835

836 Figure 1. Skull of *Mesosaurus tenuidens* (GP-2E- 669a) in right lateral view showing the  
837 lower temporal fenestra; picture (A) and interpretive labeled line drawing (B). This specimen  
838 is an almost complete skull and part of the postcranial skeleton (not shown) housed in the  
839 Fossil Vertebrate Collection of Instituto de Geociencias, São Paulo University. Scale bar: 10  
840 mm. Abbreviations: a, angular; ax, axis; cev, cervical vertebra; d, dentary; f, frontal; j, jugal;  
841 l, lacrimal; ltf, lower temporal fenestra; mx, maxila; n, nasal; p, parietal; pf, postfrontal; po,  
842 postorbital; pp, postparietal; prf, prefrontal; q, quadrate; qj, quadratojugal; sa, surangular; sm,  
843 septomaxilla; sp, splenial; sq, squamosal; st, supratemporal.

844

845 Figure 2. Mesosaur skull reconstruction based on recent new evidence. A: dorsal view; B,  
846 lateral view. Modified from Piñeiro et al. (2012).

847

848 Figure 3. Two specimens of *Mesosaurus tenuidens* with the stapes. Almost complete, foetus  
849 at an advanced stage of development (FC-DPV 2504) in (A) general view, with a picture (B)  
850 and labeled line drawing (C) of the braincase, including the stapes, occipital elements and  
851 stapes, which have been displaced from the rest of the specimen. Picture (D) and labeled line  
852 drawing (E) of a second, almost complete but slightly disarticulated adult specimen (FC-DPV  
853 3067) showing the braincase with the right stapes approximately in its anatomical position  
854 (though its distal tip has moved anteriorly). In the interpretive drawings (C and E), the stapes  
855 is highlighted in yellow. Both specimens are from the Early Permian Mangrullo Formation  
856 of Uruguay. Scale for D and E: 10 mm. Anatomical abbreviations: ask, anterior skull; bo,  
857 basioccipital; bpt, basipterygoid; cev, cervical vertebrae; eo, exoccipital; ga, gastralia; op,

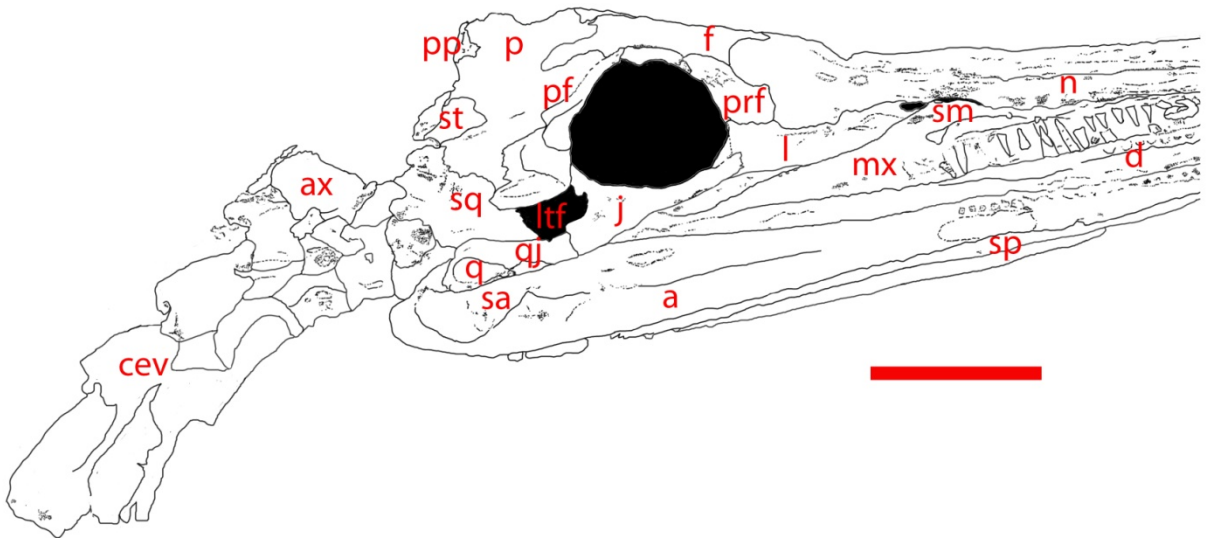
858 opisthotic; pbs, parabasisphenoid; pro, prootic; psk, posterior skull; qj, quadratojugal; so,  
859 supraoccipital; sta, stapes.

860

861 Figure 4. Specimens of *Mesosaurus tenuidens* showing how various part and counter-part can  
862 lead to divergent interpretations about the presence of the ectepicondylar foramen. A-C. FC-  
863 DPV 2042, 2488 and 2103 respectively, photographs of several humerus of adult individuals  
864 from the Mangrullo Formation of Uruguay, showing the presence of both ectepicondylar  
865 foramen (red arrow) and groove. Scale bars: 3 mm. D-E. FC-DPV 2385 photographs of a  
866 partially articulated mesosaur trunk region preserved as part (A) and counterpart (B). The  
867 humerus in (A) suggests that the ectepicondylar foramen is not present, but it can be perfectly  
868 seen in (B). Scale bar: 2 mm.

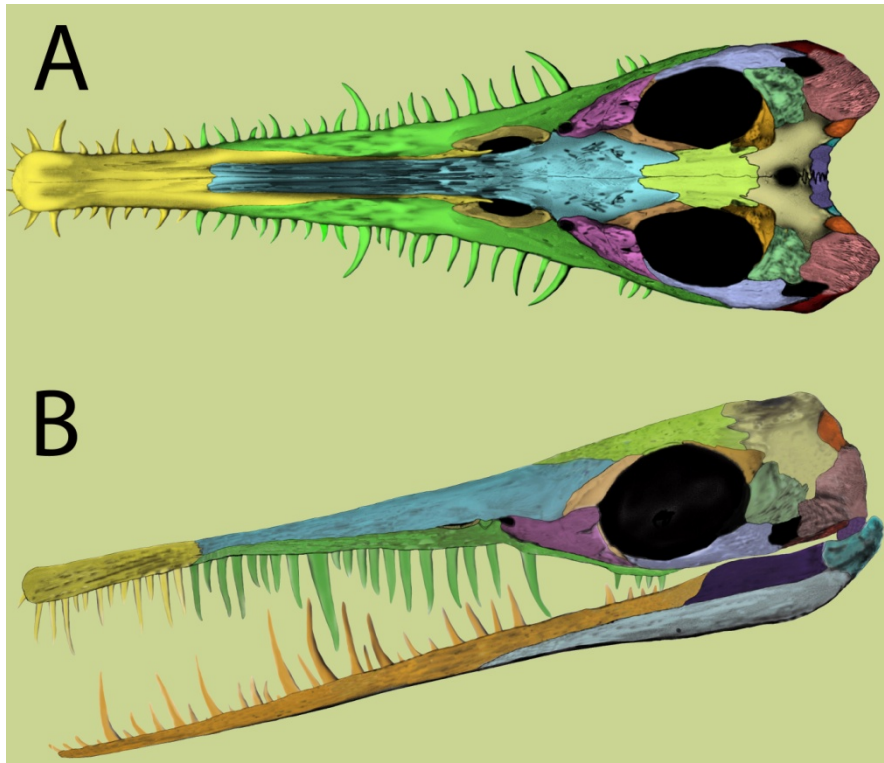
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870 Figure 5. Phylogenetic position of mesosaurs among early amniotes and selected related taxa.  
871 This cladogram results from a parsimony analysis of a matrix updated from that of Laurin and  
872 Reisz (1995) with our observations of mesosaur specimens (mostly from material collected in  
873 Uruguay, but also, to a lesser extent, material observed in Brazil and France) and with recent  
874 literature. Characters that form a cline were ordered; the branch and bound algorithm of  
875 PAUP 4 was used. This is a strict consensus of 2 trees that require 383 steps (in Mesquite).  
876 They have a CI (Consistency Index) of 0.56527 and a RI (Retention Index) of 0.65741 (see  
877 text for details). Robustness of the results is shown through the bootstrap (based on 200  
878 branch and bound replicates) and Bremer Index (before and after slash, respectively). Note  
879 that diapsids do not form a clade under this topology, but to make this more obvious, the  
880 smallest clade that includes both diapsid taxa is labeled as “Diapsids”.



881

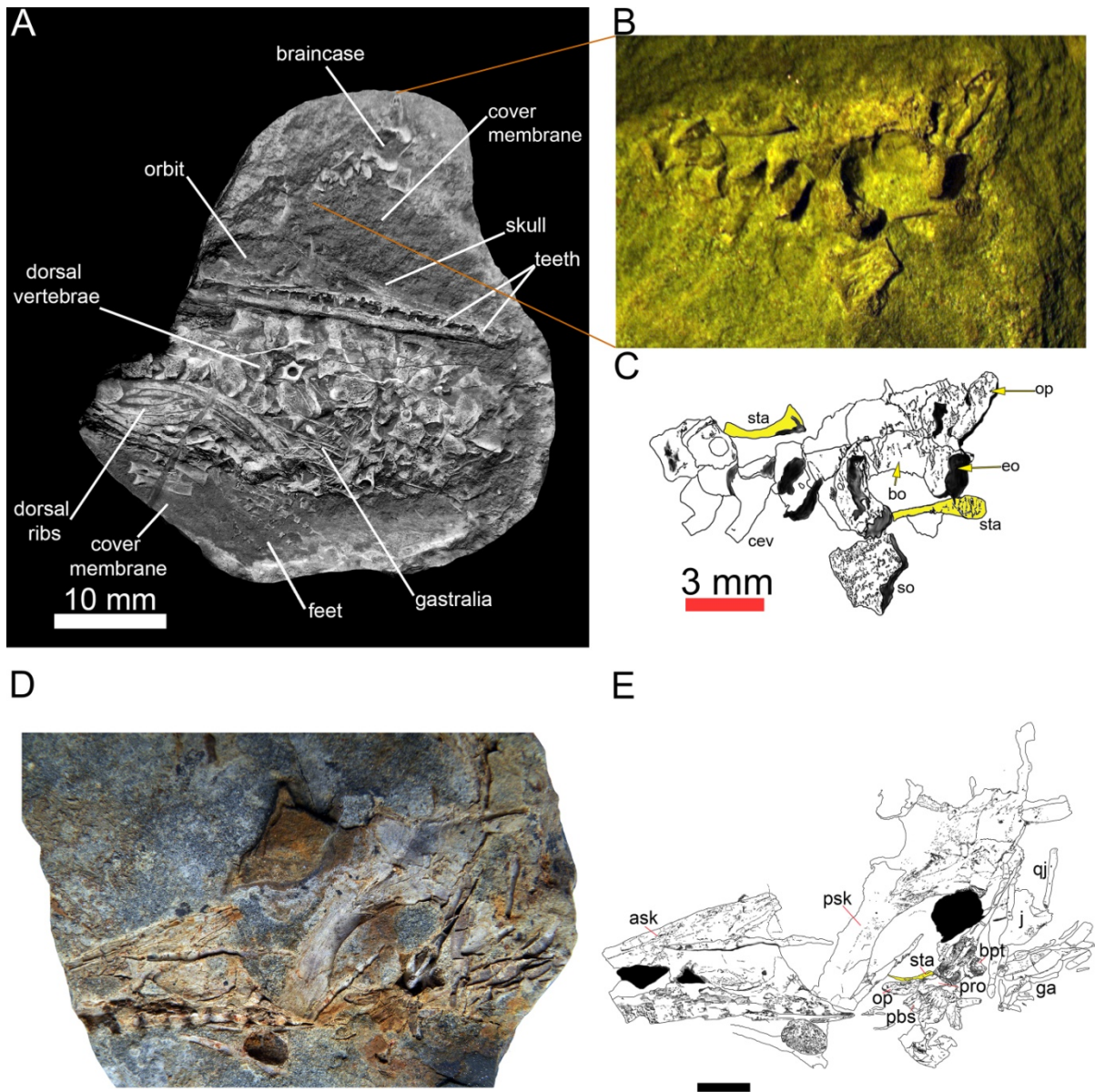
882 Figure 1



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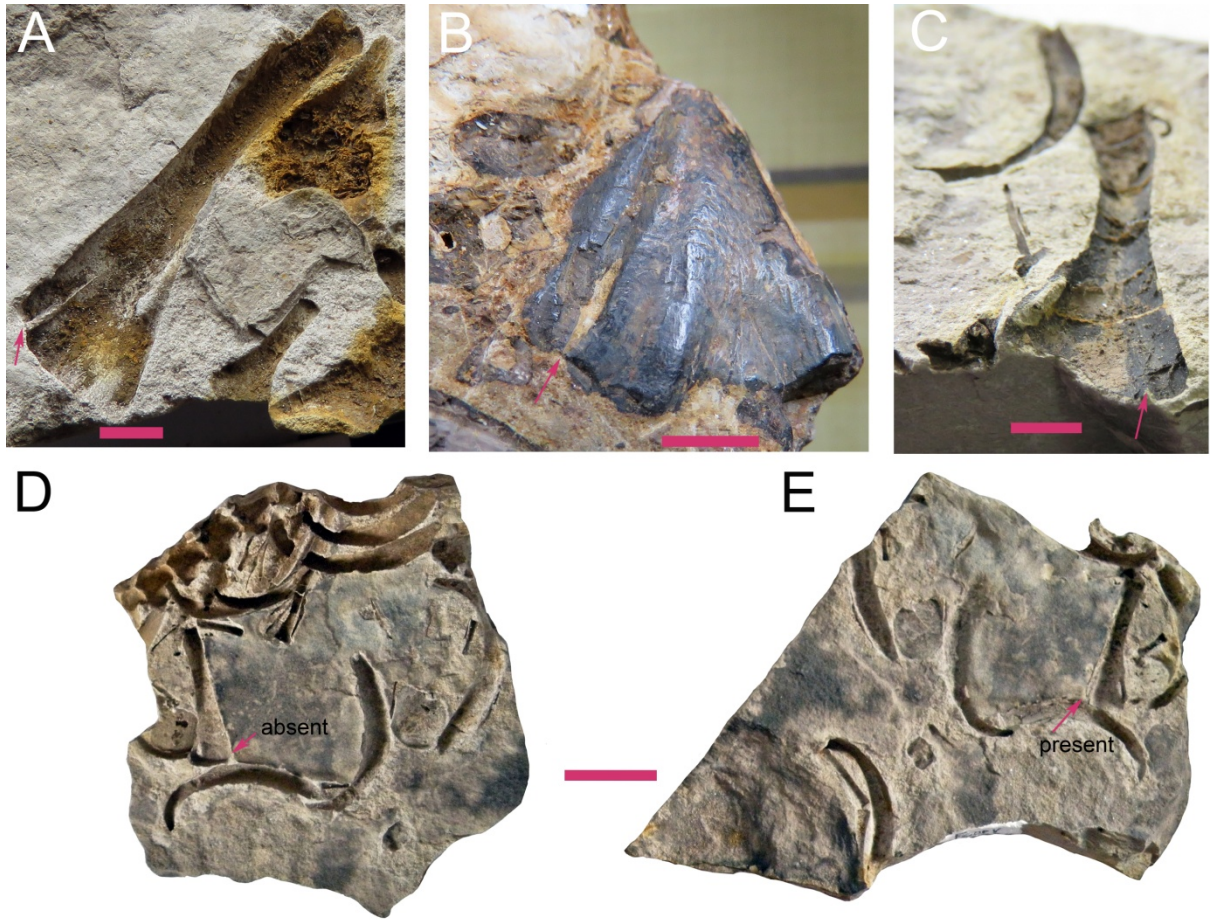
884 Figure 2





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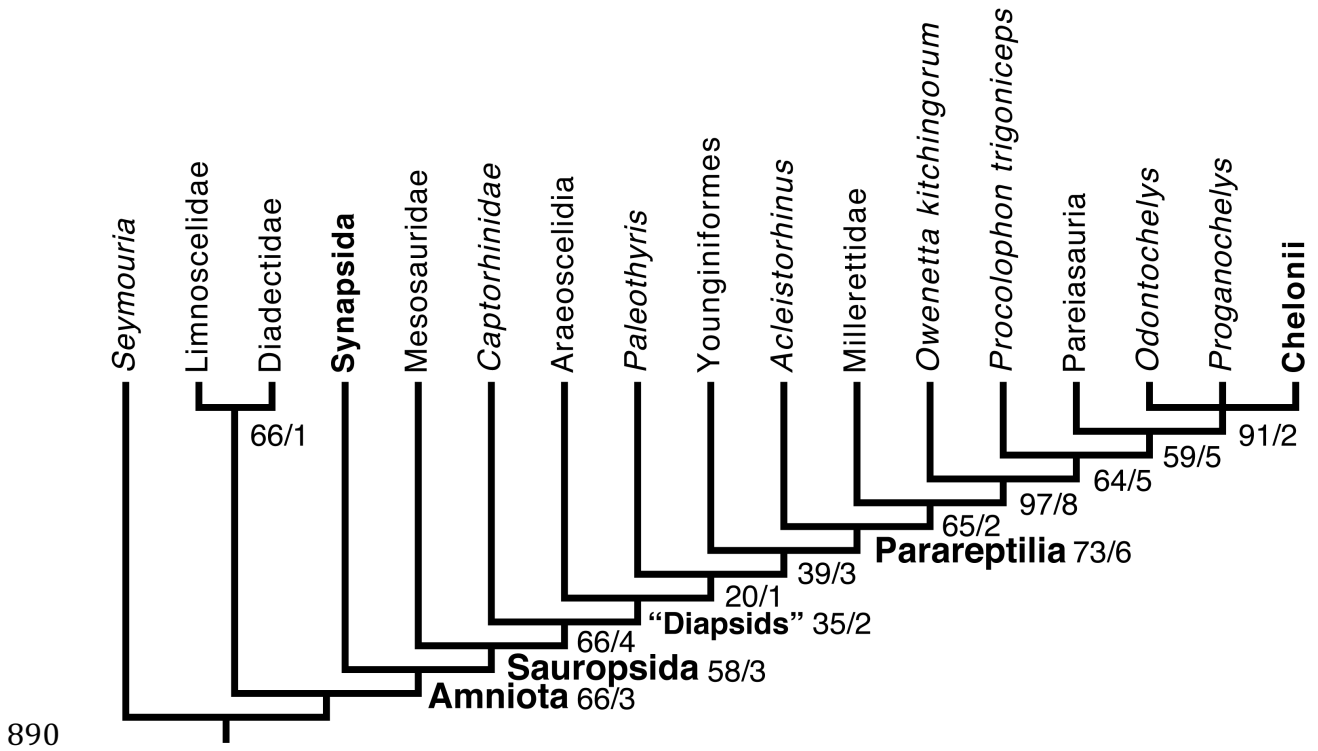
886 Figure 3



887

888 Figure 4

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890

891 Figure 5