

The ontogenetic transformation of the mesosaurid tarsus: a contribution to the origin of the primitive amniotic astragalus

Graciela Piñeiro, Pablo Núñez Demarco, Melitta D Meneghel

The hypotheses about the origin of the primitive amniotic tarsus are very speculative. Early studies argued that the origin of the astragalus, one of the largest proximal bones in the tarsus of basal amniotes, was produced by either the fusion of two, three, or even four of the original tarsal bones, the intermedium, the tibiale and the proximal centralia (c4 and c3), or that the intermedium alone transforms into the primitive astragalus. More recent studies have shown that the structure of the tarsus in *Captorhinus* supports the former hypothesis about a fusion of the intermedium, the tibiale, the proximal centrale (c4) and eventually c3, producing a purportedly multipartite structure of the amniotic astragalus, but the issue remained contentious. Very well preserved tarsi of the Early Permian aquatic amniote *Mesosaurus tenuidens* Gervais, 1864-1865, which represent the most complete ontogenetic succession known for a basal amniote (the other exceptional one is provided by the Late Permian diapsid *Hovasaurus boulei* Piveteau, 1926), suggest that there is more than one ossification center for the astragalus and that these fuse during late embryonic stages or maybe early after birth. A non-hatched *Mesosaurus* in an advanced stage of development shows that the tarsus is represented by a single bone, most probably the astragalus, which seems to be formed by the suturing of three bones, which we interpret as being the intermedium, the tibiale, which could have already integrated the c4 in an earlier stage of the development, and the c3. An amniote-like tarsal structure is observed in very basal Carboniferous and Permian tetrapods such as *Proterogyrinus*, *Gephyrostegus*, the diadectids *Diadectes* and *Orobates*, some microsaurids like *Tuditonus* and *Pantylus*, and possibly *Westlothiana*, taxa that were all considered as true amniotes in their original descriptions. Therefore, the structure of the amniotic tarsus, including the configuration of the proximal series formed by the astragalus and the calcaneum, typically a pair of enlarged bones, could have been established well before the first recognized amniote walked on Earth. Accordingly, the tarsus of these taxa does not constitute specialized convergences that appeared in unrelated groups, they might be instead, part of a transformation series that involves taxa closely related to the early amniotes as some hypotheses have suggested.

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The hypotheses about the origin of the primitive amniotic tarsus are very speculative. Early studies argued that the origin of the astragalus, one of the largest proximal bones in the tarsus of basal amniotes, was produced by either the fusion of two, three, or even four of the original tarsal bones, the intermedium, the tibiale and the proximal centralia (c4 and c3), or that the intermedium alone transforms into the primitive astragalus. More recent studies have shown that the structure of the tarsus in *Captorhinus* supports the former hypothesis about a fusion of the intermedium, the tibiale, the proximal centrale (c4) and eventually c3, producing a purportedly multipartite structure of the amniotic astragalus, but the issue remained contentious. Very well preserved tarsi of the Early Permian aquatic amniote *Mesosaurus tenuidens* Gervais, 1864-1865, which represent the most complete ontogenetic succession known for a basal amniote (the other exceptional one is provided by the Late Permian diapsid *Hovasaurus boulei* Piveteau, 1926), suggest that there is more than one ossification center for the astragalus and that these fuse during late embryonic stages or maybe early after birth. A non-hatched *Mesosaurus* in an advanced stage of development shows that the tarsus is represented by a single bone, most probably the astragalus, which seems to be formed by the suturing of three bones, which we interpret as being the intermedium, the tibiale, which could have already integrated the c4 in an earlier stage of the development, and the c3. An amniote-like tarsal structure is observed in very basal Carboniferous and Permian tetrapods such as *Proterogyrinus*, *Gephyrostegus*, the diadectids *Diadectes* and *Orobates*, some microsaurids like *Tuditanus* and *Pantylus*, and possibly

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Therefore, the structure of the amniotic tarsus, including the configuration of the proximal series formed by the astragalus and the calcaneum, typically a pair of enlarged bones, could have been established well before the first recognized amniote walked on Earth. Accordingly, the tarsus of these taxa does not constitute specialized convergences that appeared in unrelated groups, they might be instead, part of a transformation series that involves taxa closely related to the early amniotes as some hypotheses have suggested.

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69 **INTRODUCTION**

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71 The origin of the astragalus and the calcaneum in the ankle of basal amniotes has been
72 considered as an adaptation to terrestrial locomotion and a key innovation in the origin of
73 Amniota (Romer, 1956). Taking into account the elements present in the tarsus of basal
74 tetrapods, it is clear that there was a strong reduction in the number of bones that form the
75 primitive amniotic tarsus. This reduction can be explained by the fusion or loss of some tarsal
76 bones in the ancestral amniotes despite the homology of these elements not always is well
77 established. According to previous contributions, it is widely acknowledged that the calcaneum
78 is derived from the fibulare, ie. from only one of the precursor bones present in the tarsus of non-
79 amniote tetrapods. However, the origin of the astragalus, as well as the identification of the
80 ancestral bones that give origin to it, are contentious (Peabody, 1951; Rieppel, 1993; Kissel,
81 Dilkes & Reisz, 2002; Berman & Henrici, 2003; O’Keefe et al., 2006; Meyer & Anderson,
82 2013). Some authors supported the classic hypothesis of a unitary origin for the astragalus, from
83 the intermedium (see Romer, 1956) or perhaps from the fusion of this bone to the tibiale (e.g.
84 Holmgren, 1933; Gegenbaur, 1864 in Schaeffer, 1941). However, Peabody, 1951, following
85 Holmgren (1933), suggested that the origin of the astragalus is produced by the fusion of three
86 bones; mainly the intermedium, one of the proximal centralia (c4) and perhaps, the tibiale
87 (Peabody, 1951, figure 2). A modification of this proposal, although supporting the composite

88 origin for the astragalus, was suggested by O’Keefe et al. (2006) by including also the third
89 centrale as a component of the fused element (four-center hypothesis). Indeed, there is evidence
90 of a fusion between the tibiale and the proximal centrale (c4) in *Gephyrostegus* (Schaeffer, 1941;
91 Holmes, 1984) which possesses an amniote-like tarsus (Carroll, 1970), thus, this fusion may
92 have occurred early in the evolution of the amniotic tarsus. Peabody’s (1951) hypothesis was
93 subsequently refuted by Rieppel (1993) who stated, based on embryological evidence from
94 extant reptiles, that the reptilian astragalus is a neomorph. But Rieppel’s (1993) suggestion was
95 not widely accepted and the hypothesis on the multipartite structure of the reptilian astragalus
96 remains plausible. Recent reports of well-preserved tarsi from apparently young individuals of
97 several captorhinid species (Kissel, Dilkes & Reisz, 2002; Berman & Henrici, 2003; O’Keefe et
98 al., 2005, 2006), which will be discussed later, demonstrate that the matter is still open.

99 Embryological studies show only two cartilaginous condensations close to the distal end
100 of the fibula in most extant reptiles, one for the astragalus and the other for the calcaneum
101 (Schaeffer, 1941; Rieppel, 1993), but the presence of additional anlagen for the tibiale, remains
102 contentious. Mainly due to this evidence, the widespread view about the origin of the astragalus
103 before Peabody’s (1951) contribution was in favor of a slightly transformed intermedium as the
104 astragalus precursor.

105 Another characteristic of the primitive amniotic tarsus is the articulation of the proximal
106 tarsal elements (astragalus and calcaneum) with centralia 1 and 2, which are placed distally and
107 often fuse to each other (Peabody, 1951). The fused element (c1+c2), commonly named the
108 centrale or lateral centrale, has been suggested to form the navicular bone, characteristically
109 present in therapsid-grade synapsids and mammals (Broom, 1915; 1924, Jenkins, 1971).
110 Moreover, five distal tarsals are present, the first and the fourth commonly being the largest.

111 Here we investigate the origin and evolution of the amniotic astragalus by a thorough
112 study of several almost complete and some incomplete mesosaur skeletons and natural external
113 molds and casts, including well-preserved feet. Moreover, well preserved, isolated astragali and
114 calcanea of individuals in different ontogenetic stages, including the tarsus of one non-hatched
115 *Mesosaurus tenuidens* and hatchling individuals, were also analyzed for completing an
116 ontogenetic sequence previously unknown for any other Early Permian amniote. This amazing
117 record provides useful data for characterizing the tarsal structure in early and late juvenile stages,
118 and helps us to understand the transition towards the acquisition of the adult tarsal morphology.
119 We present a synoptic view of the evidence we found for homologizing the primitive amniotic
120 astragalus to the intermedium plus possibly the tibiale and proximal centralia, and propose that
121 the suturing of these elements occurred during the embryonic stage, producing a very specialized
122 single bone in the hatchlings. We also report the invariable presence of a navicular-like bone
123 (fusion of c1+c2?) in *Mesosaurus tenuidens* (*contra* Modesto, 1996a-b; 1999) and discuss the
124 possibility if this character is polymorphic for mesosaurs as observed in basal synapsids (Romer
125 & Price, 1940).

126

127 **Institutional Abbreviations:** FC-DP: Fossil Vertebrates of Facultad de Ciencias, Montevideo,
128 Uruguay; GP/2E: Instituto de Geociências (section Palaeontology), São Paulo University, São
129 Paulo, Brazil; SMF-R: Senckenberg-Institut, Frankfurt, Germany, MN: Museu Nacional de Rio
130 de Janeiro, Brazil; AMNH: American Museum of Natural History, New York, USA.

131

132 MATERIALS AND METHODS

133

134 The specimens used in this study are part of several palaeontological collections and consist of
135 almost complete and well preserved *Mesosaurus tenuidens* individuals and partially preserved
136 skeletons that include the hind limbs, which are the subject of our study. They allow us to
137 address the structure of the mesosaur tarsus and its component bones at different stages of
138 development. All these materials plus isolated complete astragali and calcanea from juvenile and
139 mature individuals were analyzed by using a binocular microscope and different techniques of
140 photography, as well as by digital drawings. Specimens from FC-DPV, GP/2E, MN and SMF-R
141 were personally analyzed by the senior author (GP), while the specimens from the AMNH were
142 studied from photographs kindly provided by personnel of that institution.

143

144 **Methods**

145 In order to evaluate the structure and ontogenetic variation of the mesosaurid tarsus, particularly
146 that of the astragalus, we carried out an anatomical study of 50 mesosaurid specimens assigned
147 to the species *Mesosaurus tenuidens*. We selected 18 individuals with well-preserved tarsi,
148 including a non-hatched individual in a late stage of development, to represent an idealized
149 ontogenetic transition (Figs. 1-6).

150

151 *Distinction of juvenile from adult mesosaurs*

152 The recognition of young, immature individuals from adult, mature ones was not easy to
153 determine in mesosaurs. Modesto (1996a, 1999, 2006, 2010) made a detailed study of the
154 characters that can be used to recognize the three monospecific genera that compose the Family
155 Mesosauridae. He concluded that the main characters (e.g. tooth morphology, head-to-neck
156 ratios, presacral vertebral counts, presence/absence of pachyostotic ribs and hemal arches) used

157 for taxonomic purposes are valid to separate three monospecific mesosaurid taxa. Nevertheless,
158 Piñeiro (2002, 2004, 2008) revised some of the characters that have been previously used as
159 taxonomically diagnostic and found that they could instead be ontogenetic conditions
160 distinguishing alternatively immature and mature specimens or could even represent sexual
161 dimorphism. Reliable characters that can be useful to differentiate juvenile (immature) from
162 adult (mature) mesosaurid individuals can be derived from changes in the morphology and
163 structure of the coracoid and the scapula in the shoulder girdle and the pubis in the pelvic girdle
164 (Piñeiro, 2004). These bones are simple rounded plate-like structures in very young individuals,
165 only acquiring the suchlike shape in adults; the coracoid develops into a roughly rectangular
166 bone with anterior and medial convex margins (Modesto, 1996; Piñeiro, 2004). The coracoid
167 notch pierces the bone medially but is very poorly developed in young individuals. It becomes a
168 true coracoid foramen in adults, when both bones suture and eventually fuse to form the scapulo-
169 coracoid. These bones can fuse leaving no trace of any suture between them, even in apparently
170 young adults, or the suture may remain visible even in large, adult individuals (Piñeiro, 2002),
171 evidencing perhaps intraspecific or sexual variability (Piñeiro, 2004). Similar morphological
172 changes are seen in the pubis, from being a small, plate-like rounded bone to a more kidney-
173 shaped element that develops a pubic notch or a true obturator foramen totally enclosed by bone.
174 Other aspects of the skeleton morphology will be part of a forthcoming paper, and will not,
175 therefore, be discussed here. Even though the characters reviewed above are useful as
176 complementary data to help identify the development stage in mesosaurs, the presence of well
177 ossified carpal and tarsal bones was the most useful feature for considering maturity in
178 mesosaurs. We consider here that an individual is mature when in the tarsus, the astragalus and

179 the calcaneum approach each other and the foramen for the perforating artery appears between
180 them.

181 *Centralia and Navicular Nomenclature*

182 The c1 is often named as the lateral centrale and the c2 as the medial centrale. But, when
183 only one distal tarsal is seen (it could result from the fusion of c1+ c2 or it could be just the c2),
184 it is often identified as the centrale (e.g. Schaeffer, 1941, Currie, 1981, Lewis, 1964, Reisz &
185 Fröbisch, 2014), or as the distal centrale (e.g. Carroll, 1970) or as the lateral centrale (e.g.
186 Peabody, 1952, Modesto, 1999, Reiz & Dilkes, 2003), even though these bones are always
187 placed medially in the tarsus, or even as the navicular (Schaeffer, 1941). Similarly, the c4 is
188 called the proximal centrale (e.g. Kissel, Dilkes & Reisz, 2002; Berman & Henrici, 2003) or
189 posterior centrale (Olson 1964). On the other hand, there is no stable designation for the c3 and it
190 can be mistaken for the c4 when it is called the proximal centrale (Carroll, 1970; Holmgren,
191 1933) or even considered a distal centrale (Fröbisch, 2008; Hall, 2007). This lack of consensus in
192 the literature on how to refer to specific centralia increases the confusion about the establishment
193 of evolutionary patterns for the early amniotic tarsus. Therefore, we decided to use the following
194 naming criterion: we refer to the bone (or fused bones) placed distally to the astragalus in the
195 mesosaur tarsus as the ‘navicular’, and we use the name "proximal centrale" only when it cannot
196 be determined if it is the c4 or c3.

197

198

SYSTEMATIC PALAEONTOLOGY

199

Amniota Haeckel, 1866

200

Proganosauria Baur, 1889

201

Mesosauridae Baur, 1889

202 *Mesosaurus tenuidens* Gervais, 1864—1865

203 Figures 1—9

204 The mesosaurid tarsus (Figs. 1-9) displays a plesiomorphic construction regarding the
205 structures observed in other basal amniotes as *Hylonomus lyelli*, *Paleothyris acadiana* and
206 *Petrolacosaurus kansensis* (Carroll, 1964, 1969; Peabody, 1952; Reisz, 1981). It is also
207 essentially equivalent to the tarsus of basal synapsids (Romer & Price, 1940; Romer, 1956) and it
208 even mirrors the structure described for some microsaurids, particularly *Tuditonus*, and *Pantylus*,
209 the embolomere *Proterogyrinus*, *Westlothiana* and *Gephyrostegus* (Carroll, 1968; 1970; Carroll
210 & Baird, 1968; Holmes, 1984; Smithson, 1989, although see also Smithson et al., 1994) (Fig.
211 10).

212

213 **Description.** All specimens from Uruguay were collected either in bituminous or non-
214 bituminous shale of the Early Permian (Artinskian) Mangrullo Formation (Piñeiro, 2004; Piñeiro
215 et al., 2012a, b); all the material coming from Brazil was collected in the correlative Iratí
216 Formation (Santos et al., 2006). Each of the constituent tarsal elements will be described for the
217 specimens representing the transition regarding their ontogenetic stage and the morphological
218 changes detected:

219 1) FC-DPV 2504 (Figs. 1-2A, 9). An almost complete and well preserved non-hatched
220 *Mesosaurus tenuidens* from Uruguay, which is curled as if within an egg (Piñeiro et al., 2012b).
221 It consists of an external mould of a small, still poorly ossified skeleton that suffered strong
222 dorsoventral compression during diagenesis. This is evidenced by the displacement of the ribs
223 and feet which are overlapping each other, as well as by the reduced three-dimensionality
224 (suggesting strong compression) of the delicate skeleton, which represents the smallest mesosaur

225 yet found (see Figs. 1-2 to better appreciate the small size of the specimen). While some of the
226 constituent bones of the feet may not be completely ossified (considering the small size and the
227 poor preservation of the manus), the extraordinary preservation of the specimen allowed us to
228 reconstruct the structure of the tarsus and to describe the bones that seem to be present (Fig. 9).
229 Both astragali are preserved, but only one of them shows the precursor bones articulated (see
230 Fig. 9); the other was probably affected by the lateral compression that the specimen suffered
231 during the early stages of fossilization, producing the separation of the bones. Neither one is
232 preserved in its original anatomical position, but they were not too much displaced. Most
233 probably, considering the curled disposition of the skeleton, the astragali dropped from their
234 original position close to the zeugopodium to near the metatarsals when the soft tissues were
235 decomposed. A similar displacement is observed in very young specimens of *Hovasaurus boulei*
236 as figured by Caldwell (1994). The composite astragalus is shown as if it has turned itself over
237 before reaching its final position. This was obviously favored by the presence of the enclosing
238 egg membrane that prevented long transportation and loss of such tiny bones. Considering this
239 taphonomic explanation, and following the anatomical disposition of the bones we interpreted
240 the sutured bones, to be the intermedium, the tibiale (which possibly has fused to c4) and
241 possibly the c3, confirming Peabody's (1951) and O'Keefe et al. (2006) theory about the
242 presence of a composite astragalus in the tarsus of early amniotes. The c4 (and maybe also c3)
243 ossifies early in aquatic and terrestrial reptiles (Shubin & Alberch 1986; Rieppel, 1992a,b, 1993;
244 Caldwell, 1994, among others), and the former fuses to the tibiale in *Proterogyrinus scheelei*
245 (Holmes, 1984). On the other hand, c1 and c2 (=‘navicular’) may ossify very late in mesosaurs,
246 (Figs. 4-6, 8). Thus, taking into account the tarsal structure shown by early amniotes, and

247 considering that mesosaurids are a very basal group, our suggested tarsal arrangement for the
248 non-hatched mesosaurid tarsus is plausible.

249 The distal tarsals are no visible in the specimen. They could be still unossified judging
250 from the fact that distal tarsals ossify later than metatarsals in amniotes and at least metatarsals
251 II, III, IV and V were partially, or possibly completely ossified in FC-DPV 2504, but no
252 metatarsal I, which is apparently absent (see Sheil & Portik, 2008 and references therein).

253 Otherwise (but very improbably) due to their very small size, they would not be visible if they
254 were displaced between the overlapping metatarsals.

255 2) GP-2E 272 (Figs. 1-3B). This specimen is a well preserved very young individual from Brazil.

256 The ribs are not as pachyostotic as can be observed in other immature specimens, but apart from
257 that condition, the specimen does not show relevant anatomical differences to *M. tenuidens*. The
258 silhouette of part of the body can be reconstructed due to the preservation of the skin. The
259 interdigital membrane that unites the toes to the claws can be delimited as well as the robustness
260 of the leg musculature, even in such a young individual. What could have been the plantar
261 aponeurosis covers most of the tarsal bones (Fig. 3B). However, two elements (maybe
262 mineralized cartilages) placed very close to the fibula are interpreted here as a possible astragalus
263 (the largest bone) and an incipient, smaller calcaneum, which was distally displaced. It is
264 difficult to believe that, covered by the, highly resistant plantar membrane, this tarsal bone can
265 appear as displaced from its original anatomical position. But considering that in very early
266 stages of development the astragalus and the calcaneum are the only bones ossified, we
267 hypothesize that the small size of the bone and gravity combined to move it distally after the
268 decay of flesh tissues started, particularly damaging the skin and muscle insertions. Otherwise,
269 the calcaneum is covered by the aponeurosis and it is not visible or it is a very small fragmentary

270 bone that is observed medially to the fibula (see Fig. 3B). It is also possible to see shadow-like
271 structures that can be interpreted as some of the distal tarsals (e.g. dt4), which begin to ossify at
272 very early ontogenetic stages in extant reptiles (Caldwell, 1994; Sheil & Portik, 2008). What
273 appear to be scratch marks (according to Sedor & Costa Da-Silva, 2004) are observed close to
274 the left foot, possibly produced by the individual before its sudden death. But these structures
275 more likely are part of the muscle and skin that form the base of the tail, exquisitely preserved.
276 These taphonomic features support the hypothesis that the tarsal elements, even if still
277 cartilaginous, could have been perfectly preserved, but covered by the plantar aponeurosis,
278 which is not frequently observed in fossil tetrapods.

279 3) SMF-R 4496 (Figs. 1-3C). This specimen constitutes an external mould of a partially
280 preserved posterior trunk and tail, with associated pelvic girdle and limbs from the Iratí
281 Formation. This is the specimen that best shows the structure of the tarsus in immature, juvenile
282 mesosaurids; the preserved bones might be partially ossified. The specimen is comparatively
283 larger than the two described above; its tarsus is formed by two small roughly rounded bones,
284 which can be homologized with the astragalus (the larger one) and the calcaneum (the smaller
285 one), which do not meet, but lie one in front of the other and are positioned as in adult
286 individuals. Despite its apparent general subcircular outline, the astragalus indeed shows a
287 structure similar to that preserved in adults or sub-adult individuals, bearing thickened
288 articulating areas and some suture lines. Although it is difficult to establish with confidence
289 which of the original bones are involved, it is possible to suggest a putative arrangement based
290 on the astragalus of the non-hatched mesosaurid (see Fig. 3C).

291 4) AMNH 23795 (Figs. 1-3D) is an articulated, very complete skeleton of a young mesosaur,
292 which bears a tarsus showing the same structure seen in SMF-R 4496 (probably because they are

293 individuals of equivalent age). Both the astragalus and the calcaneum can be seen close to each
294 other. Again, the astragalus shows the same structure as in the small, previously analysed
295 specimens, and what appear to be sutures between component bones can be seen on the dorsal
296 surface (see Fig. 3D).

297 5) MN 4741 and SMF-R 4934 (Figs. 1-3E-F respectively) and SMF-R 4513 (Figs. 1-3G) from
298 Brazil are a little larger than the specimens previously described. Even though their similar still
299 small size, SMF-R 4513 is probably ontogenetically older judging for the tarsal features. We can
300 see for the first time the morphological differences between both the proximal tarsal bones in the
301 ontogenetic series, the astragalus being transformed into a more stylized and more easily
302 recognizable element (see for instance Fig. 3G). Astragalus and calcaneum are preserved close
303 to each other, and the foramen for the perforating artery is incipient but visible at approximately
304 the midpoint length between these bones (see SMF-R 4513, Figs. 1-3G). SMF-R 4513 (Figs. 1-
305 3G) is probably an adult or a subadult individual. There are three bones present; two proximal
306 tarsal elements are visible, the larger one being the astragalus which features a morphology
307 which is similar to those observed in more mature individuals (Fig.3). It is a stout bone tending
308 to reach the L-shaped outline characteristic of the basalmost amniotes and some other tetrapods
309 (see the distribution and schematic morphology of the tarsal bones in Fig. 10). The foramen for
310 the perforating artery is placed at the midlength of the lateral margin, and an intimate area of
311 contact is being generated between astragalus and calcaneum at this point (Fig 3G). A small
312 bone can be seen distal to the astragalus-calcaneum contact in SMF-R 4513, which is located
313 proximal to the distal tarsal elements, including probably the dt4. It could be the ‘navicular’
314 starting to ossify, which will be well developed later, in mature *Mesosaurus* specimens.

315 6) At later stages, these bones develop a short contact through the lateral margin of the astragalus
316 and the medial margin of the calcaneum (Figs. 4-6H to P), so, the remaining analysed specimens
317 (FC-DPV 2497, GP-2E 114, GP-2E 5610, SMF-R 4710, SMF-R 44 70, GP-2E 5816, GP-2E
318 6576, GP-2E 5740 and FC-DPV 2058 (see figures 4-6H-P) represent adult individuals. Most of
319 them possess the complete series of tarsal elements: astragalus, calcaneum and ‘navicular’, as
320 well as five distal tarsals, where the first and the fourth are often the largest, although this can be
321 very variable (Fig. 6).

322 In summary, the mesosaur tarsus consists of two proximal bones identified as the
323 astragalus and the calcaneum plus a single navicular-like element and five elements in the distal
324 tarsal series (Fig. 7), resulting in 8 or 9 tarsal bones. The bones that form the ‘navicular’ may be
325 the centralia 1 and 2 considering that c4 and c3 ossify very early in the ontogeny of other fossil
326 and extant sauropsids, while the former are the last to become visible (Caldwell, 1994).

327

328 **RESULTS AND DISCUSSION**

329

330 Following the evidence provided by the studied specimens, which notably includes the
331 partially preserved tarsus of a non-hatched mesosaurid in an advanced stage of development, we
332 can see the significant morphological transformation that the mesosaur astragalus experienced
333 during ontogeny. The non-hatched *Mesosaurus tenuidens* found in the Early Permian of Uruguay
334 (see Piñeiro et al., 2012a, b) is so exquisitely preserved that it allows us to describe the
335 morphology of what we interpret to be a composite astragalus that is one millimeter in length! It
336 possibly shows the precursors of the typical amniotic astragalus united by weak sutures (Fig. 9).
337 The following postnatal, early stages of mesosaur ontogeny are characterized by the presence of

338 sub-circular to roughly square small bones, mainly representing the astragalus as a single bone
339 (and the more frequently preserved), although some young specimens still show the tripartite
340 structure (Figs. 1-3 C-E) which is not easy to observe directly from photographs because of the
341 very small size of the specimens. The sutures between the precursor bones in the astragalus of
342 larger, adult individuals can often be deduced from not always well preserved features (e.g.
343 sutures, rugose surfaces and thickened margins) (Figs. 6 and 8C).

344 In the early stages of development, astragalus and calcaneum seem to have been
345 separated, as there is no evidence of contact between them. The foramen for the perforating
346 artery is not visible; we consider both these features as useful in identifying juvenile, immature
347 mesosaurids. At the following stage, the astragalus becomes more quadrangular in shape,
348 approaches the calcaneum, and an incipient foramen for the perforating artery develops. At this
349 stage, mesosaurids appear to be young adults and possibly, mature individuals, judging by the
350 further ossification of the overall skeleton. The remaining transformations are crucial for the
351 growth of the individuals for improving their capabilities for capturing prey and for their
352 reproductive traits (see Ramos, 2015; Villamil et al., 2015; Piñeiro et al., 2012a). The proximal
353 border of the astragalus in adult individuals is deep and bears an extended rectangular facet for
354 the fibula, making an almost immobile articulation between these bones, as in basal synapsids
355 (Romer & Price, 1940). The foramen for the perforating artery is well developed in large
356 (mature) individuals where the notches in both bones approach each other to form a conspicuous
357 true foramen (see Figs. 4-6 H to P). The groove for the passage of the perforating artery crosses
358 the bone medially and proximally, where a rugose area is visible (Figs. 4 and 6). Probably it
359 marks the line of suture of both of the larger bones seen in the astragalus of the non-hatched
360 mesosaurid, implicating the intermedium and the c4+tibiale complex. Considering this

361 hypothesis as the most probable, another line of suture located at the medial corner of the
362 astragalus of adult individuals may correspond to the delimitation of the tibiale and includes the
363 articular facet for the tibia at the medial margin (Figs. 6, and 8). This suture line is also seen to
364 be continue at the medial margin, where it runs just above the articular facet for the tibia. This
365 facet is wide and teardrop-shaped, which allows for a broad (comparatively motile) articulation
366 with the tibia (Fig. 8 A and C), considering the oblique angle and the short surface at which the
367 contact is produced. It is interesting to note that the same type of articulations (and very similarly
368 shaped facets) for the fibula and the tibia were described for the ‘pelycosaur’ tarsus, as well as
369 the presence of a medio-ventral extension interpreted as a cartilaginous remnant of the tibiale
370 (Romer & Price, 1940).

371

372 **Limb ossification patterns**

373

374 In *Mesosaurus* a significant delay in mesopodial ossification is noted, following the pattern
375 observed in most aquatic tetrapods (Rieppel, 1992 a-b; Caldwell, 1994) such as *Hovasaurus*
376 *boulei* Currie, 1981, from which we also know an almost complete ontogenetic succession in the
377 development of the tarsus (Caldwell, 1994). Thus, long bones (propodials, epipodials and
378 metapodials) become ossified while the mesopodials are still formed of cartilage. However,
379 unlike in *Hovasaurus*, where the astragalus and the calcaneum of very young specimens are of
380 nearly the same size, in *Mesosaurus* the first is clearly larger than the latter, thus supporting the
381 hypothesis that the astragalus is the first bone to ossify in the mesosaur tarsus, arising from the
382 suturing and later fusion of at least three bones that are present in the non-hatched mesosaurid.
383 Taking into account this information, along with the evidence from Carboniferous tetrapods and

384 the evidence provided by the non-hatched specimen, the mesosaurid tarsal ossification proceeds
385 in the following sequence: intermedium, tibiale+centrale 4 (and c3?, see Fig. 9 and O’Keefe et
386 al. 2006), calcaneum, distal tarsal four, the ‘navicular’ and the remaining bones (distal tarsals
387 3—1 and 5). The sequence of ossification of the distal tarsal bones is not clear, however.

388 Contrary to what seen in extant sauropsids, where the calcaneum is the first tarsal element
389 that ossifies (Fröbisch, 2008), the fibulare (the calcaneum homologous) ossifies much later in
390 mesosaurs and aquatic fossil diapsids; in *Hovasaurus boulei* it is suggested that it appears after
391 the c4 does (after Caldwell, 1994). Thus, it may be possible that it is already present in the tarsus
392 of the non-hatched mesosaurid (Fig. 9), but if so, it should have been very small. Considering the
393 presence of only two bones in juvenile individuals, identified as the astragalus and the calcaneum
394 (Figs. 1-3), it is possible that the intermedium and the tibiale (which possibly is a composite bone
395 if it already fused to c4) fuse early in ontogeny, as some previous workers have suggested (e.g.
396 Gegenbaur & Williston, in Schaeffer, 1941). Indeed, the tibiale fuses to c4 in *Proterogyrinus*,
397 suggesting that these bones also ossify early, and this event was proposed as the first step
398 towards the formation of the amniotic astragalus, as both these bones also fuse to the
399 intermedium later (Holmes, 1984).

400 This pattern of ossification is mostly in agreement with recent discoveries in those fields
401 of paleontology and developmental genetics looking for patterns and processes of vertebrate limb
402 evolution (Caldwell, 2002 and references therein). Moreover, it highlights, at least in basal
403 tetrapods, the potential conservatism of the underlying genetic controls of limb development
404 patterns, exceptions are related to different ecological and functional adaptations (see below).

405

406

407 **The astragalus during ontogeny**

408

409 The astragalus is the largest bone in the mesosaurid tarsus, featuring an L-shaped outline
410 in dorsal view in mature specimens (see Figs. 4, 7).

411 The shape of the astragalus changes dramatically during ontogeny; mature individuals
412 show a stout, roughly squared bone with broad articulating facets for the crus (Fig. 8 A and C).
413 This bone also possesses a wide, shelf-like latero-distal facet for receiving the centrale or
414 ‘navicular’ (Figs. 6-7), which can be totally separated from the astragalus, or partially fused so
415 that the free, unfused part of the bone can only be seen on the ventral surface (Fig. 8).

416 However, the astragalus of immature mesosaurids is a delicate, roughly rounded or
417 maybe subquadrangular bone bearing an evident thick dorso-medial border which developed into
418 very well defined articulating areas during growth, producing a slightly excavated central area in
419 the dorsal margin for the fibula and a broad, medially placed almost sub-triangular surface for
420 the tibia. These thickened margins can be seen even in very small newborn individuals (see Fig.
421 1-3 C-G).

422 In his 1993 study, Rieppel stated that the mesosaurid astragalus does not show any
423 evidence of being a fusion of the plesiomorphically separated tarsal elements; to him all the
424 suture-like structures (e.g. delicate grooves or thickenings) seen on the ventral surface
425 correspond to attachments of muscles and tendons, and the medial groove delimitates the passage
426 of the perforating artery. Even though the mesosaur astragalus of post-hatching stages does not
427 show the tripartite structure described in *Captorhinus* (Peabody, 1951; Fox & Bowman, 1966;
428 Kissel, Dilkes & Reisz, 2002 and references therein), it seems to have been derived from the
429 junction of at least three bones, as we can deduce from the tarsus of the non-hatched mesosaurid
430 (Fig. 9) where we interpret although with doubts, that the incipient astragalus is the only bone in

431 the tarsus, showing suturing for the intermedium, the tibiale and maybe both the proximal
432 centralia (c4+c3). Actually, some of the original joints remained in some specimens, but they
433 show a slightly different pattern from that described by Peabody (1951) because the mediiodistal
434 Y-shaped suture for intermedium, c4 and c3 is not as evident in the studied specimens (see
435 figures 3, 6, 8).

436

437 **The mesosaur ‘navicular’**

438

439 The ‘navicular’ is a bone present in both synapsid and sauropsid amniotes. In the latter, it
440 is observed at least in their basalmost representatives: a ‘navicular’ is found in captorhinids,
441 basal diapsids, some Parareptilia and Mesosauridae and in all pelycosaur (Figs. 8, and 10).
442 Later, it becomes a bone that is only characteristic of derived synapsids and living mammals and
443 it is lost in crown diapsids. In mesosaurs it ossifies at a late stage (at the same time that the
444 foramen for the perforating artery forms) and is separated from the astragalus in most individuals
445 or abuts against the distal margin of this bone, even fusing partially with it in mature individuals
446 (Figs. 6 and 8). That means that the presence of the ‘navicular’ in mesosaurs is indicative of
447 maturity.

448 The presence of the ‘navicular’ in *Mesosaurus* is a novel characteristic, as all but one
449 (Modesto, 1996a, b; 1999) of the previous workers did not mention its presence in descriptions
450 of the mesosaurid tarsus. Indeed, Modesto (1996a,b) described the presence of a lateral centrale
451 only in *Stereosternum* and stated that this bone is never present in *Mesosaurus*. We have enough
452 evidence to confirm that a transversely elongated bone is invariably present distal to the
453 astragalus in all the analysed mature specimens—most frequently representing two sutured

454 bones— identified as the centralia c1 and c2 present in “pelycosaurs” and other basal amniotes.
455 As these bones suture to the astragalus in very mature individuals, as also seems to occur in
456 *Captorhinus aguti* (Peabody, 1951), it becomes difficult to identify its presence in the tarsus, as
457 probably occurred with the specimens studied by Modesto (1996,1999) assigned to *Mesosaurus*
458 *tenuidens*. We first become aware of the presence of a ‘navicular’ in *Mesosaurus* from an
459 isolated, relatively large astragalus where the fusion of c1 and c2 has not yet been completed (see
460 Fig. 8 for more detail of this condition). It firstly appears as two sutured (but not fused) bones
461 (Figs. 4 and 6 H-I), and there seems to be a reduction in the size of c1, which becomes a pointed
462 medial tip that is not preserved in most individuals because of the fragility of its suture to c2 (see
463 Figs. 3G; 8B-C). As a result, in *Mesosaurus*, the ‘navicular’ strongly abuts the platform-like
464 facet on the distal margin of the astragalus (Figs. 6P, 8).

465 This variable condition concerning the fusion of centralia 1 and 2 recalls that observed in
466 ‘pelycosaurs’, in which some species show the centralia 1 and 2 as separate bones (e.g.
467 *Ophiacodon*), while others show them fused (e.g. *Haptodus*) (Romer & Price, 1940) (Fig. 10). It
468 is likely that this is an ontogenetic, perhaps heterochronic condition in mesosaurs (L. Gaetano
469 and D. Marjanović, personal communication), but this needs to be tested by analysis of more
470 than one individual of the same species at different stages of development. For instance, the
471 morphology of the c1 in mesosaurids is very similar to that of the putative medial centrale of
472 *Sphenacodon ferox* (according to Henrici et al., 2005), and if it is repositioned medially to the
473 lateral central we can obtain a navicular-like bone in *Sphenacodon*. Thus, the small size of the
474 tarsal bones of early amniotes and the possibility that they can be displaced from their original
475 positions, plus to the fact that the recognition of homologous bones seems to be a difficult
476 endeavor, make it likely that the real nature of the tarsus structure in several taxa could remain

477 obscure. Mesosaurs may provide a good opportunity to revisit and gain a better understanding of
478 the processes that are involved in the origin and early evolution of the amniotic tarsus.

479

480 **Morphological changes supporting an evolutionary transition in the origin of the amniote**
481 **tarsus**

482

483 Although most previous workers (e.g. Carroll, 1964; Berman & Henrici, 2003; O’Keefe
484 et al., 2006; Meyer & Anderson, 2013, and references therein) accepted the composite origin of
485 the astragalus following the contribution of Peabody (1951), the reappraisal of that condition and
486 its significance performed by Rieppel (1993) introduced controversy. This last author rejected
487 the multipartite origin of the astragalus, arguing that there was a lack of unequivocal ontogenetic
488 evidence that would show that the bones which would form the composite astragalus are present
489 in at least some stage of development. He rejected the proposed composite origin of the
490 astragalus by Peabody (1951) mainly based on the fact that this bone derives from a single
491 ossification center in extant reptiles and that, according to Sewertzoff (1908), lizards have just a
492 single block of cartilage close to the distal end of the fibula and tibia where the calcaneum and
493 the astragalus later ossifies. In *Sphenodon punctatus*, the astragalus originates by the
494 condensation of more than one chondrogenic element, but they fuse during the embryonic stage
495 (Rieppel, 1993), and interestingly, there are also two chondrogenic condensations distal to the
496 fibula in pleurodiran turtles (Fabrezi et al. 2009). In *Podocnemis* species for instance, one is the
497 intermedium and the other is an elongated element, postaxially placed, which is interpreted to be
498 the tibiale+c4 (Fabrezi et al. 2009). There is also a connective connection between c4 and the
499 intermedium in *Phrynops hylarii*, showing a tarsal pattern that seems to be consistent with the

500 basic early amniote tarsal construction as suggested by mesosaurs and other basal, non-amniote
501 taxa.

502 In lizards, the tarsal formation is not as clear as in turtles. Rieppel (1992a), considered
503 that the proximal cartilage anterior to the fibulare is the astragalus, however, there are not
504 conclusive embryological studies that show the homology of the anterior tarsal cartilages in
505 lizards (Fabrezi, Abdala & Martínez Oliver, 2007). The morphogenetic approach of Shubin and
506 Alberch (1986) seems to be useful to reconstruct the skeletal morphology in lizard limbs, and
507 then, to identify the developmental constrains that can produce deviations in some groups from
508 the otherwise apparently conservative pattern (see Fabrezi, Abdala & Martínez Oliver, 2007).

509 On the other hand, the presence of more than one cartilage condensation, apparently
510 homologous with the ancestral tetrapod tarsals, has been recently described to be present during
511 early embryonic stages in the development of six different orders of modern birds (Ossa Fuentes,
512 Mpodozis & Vargas, 2015) and also in chameleons (Diaz & Trainor, 2015). However, their
513 homology to the earliest amniote condition is difficult to establish, when the pattern is observed
514 in such very specialized groups. Indeed, in the above mentioned papers, (Ossa-Fuentes,
515 Mpodozis & Vargas, 2015; Diaz & Trainor, 2015) it is suggested that the intermedium and the
516 tibiale (although the latter is not pretty much apparent from the figures provided by Diaz &
517 Trainor, 2015) appear as independent ossifications at very early stages of the development. On
518 the other hand, Ossa-Fuentes, Mpodozis & Vargas (2015) observed that in the six groups that
519 they studied, in contrast to the most common condition in birds (i+fe), the intermedium forms a
520 separate ossification center that later fuses to the ‘astragalus’ (sic) forming the ascending process
521 characteristic of dinosauiromorphs. Thus, the ‘astragalus’ should be the tibiale? Moreover, the
522 pattern of ossification that Ossa-Fuentes, Mpodozis & Vargas (2015) suggest, where the fibulare

523 is the first to ossify, followed by the putative intermedium and later by the tibiale, is very
524 different to that currently accepted to occur in basal amniotes.

525 The centralia, which are considered basic components of the astragalus structure, are
526 recognized in stem-lepidosaurs. However, these bones are not detected in dinosauiromorphs and
527 in many extant diapsids (e.g., chameleons and birds). Therefore, they must have fused to a
528 different bone than the astragalus or disappeared during the evolution of modern sauropsids as
529 they are not recognizable during the ontogeny of the most advanced taxa".

530 Selective pressures to reduce the number of tarsal bones in the sense that they are an
531 extension of the epipodials, favour stability by strengthening the feet to drive the body forward.
532 Thus, the acquisition of unitary, stout structures instead of several separate, delicate bones was
533 an improvement for sustained locomotion capabilities. Therefore, we have to be cautious
534 regarding these findings, considering the high variability shown by the chameleons' tarsal
535 structure, and the lack of embryological evidence in the fossil taxa for use in comparison.
536 Therefore, as we previously mentioned, the possibility that neomorphic elements are present in
537 such derived groups cannot be ruled out with the available data.

538 Indeed, there are several known examples of tetrapods, possibly stem amniotes, that
539 allow us to deduce the steps of fusion of the tarsal bones leading to the attainment of the amniote
540 condition. Thus, as the embryology of extant lizards suggests, the fusion of these elements in the
541 development of the amniote ankle is produced in the embryonic stage (Fabrezi, Abdala &
542 Martínez Oliver, 2007) and so, it is not possible to address their original ossification centers any
543 more (Gauthier et al., 1988). Rieppel (1993) observed that associations of tarsal bones are
544 common in amphibians and that, while centralia 1 and 2 can be fused or separated, c3 and c4
545 may be fused, or rather, one of them can be lost. Thus, according to Rieppel (1993) the

546 association between the tibiale and c4 may be casual and may not represent a condition of
547 phylogenetic relevance. However, we can see a real transition from closely related, supposedly
548 non amniote taxa (e.g. *Gephyrostegus*, *Westlothiana*, *Tuditanus*, *Pantylus* (see Ruta, Coates &
549 Quicke, 2003 and Marjanović & Laurin (2015), for the phylogenetic position of these taxa), to
550 the acquisition of the primitive amniotic tarsal configuration (see figure 10). Thus, if we consider
551 the association of the tibiale and c4 observed in some *Proterogyrinus* specimens (Holmes, 1984)
552 and possibly present in the tarsus of the non-hatched mesosaurid (see Fig. 9) as the first step
553 towards the development of the amniotic tarsus (Holmes, 1984), we can reconstruct the
554 succession including *Gephyrostegus* (see Carroll, 1970 as a reference of the tarsal structure in
555 this last taxon) where the tibiale+c4 (and c3?, see O’Keefe et al., 2006) complex is associated
556 with the intermedium to form the composite amniotic astragalus, a configuration that is also
557 present in some microsaurids (e.g. *Tuditanus punctulatus*, Carroll & Baird, 1972; Carroll &
558 Gaskill, 1978 and *Pantylus cordatus*, Carroll, 1968) and possibly in *Westlothiana* (Smithson,
559 1989 but see Smithson et al. 1994). Within that transformation, the fibulare becomes the
560 calcaneum and c1 and c2 remain as the only centralia present, either as separated bones or fused
561 to form a single element, the ‘navicular’.

562

563 *Phylogenetic context supporting the evolutionary transition*

564

565 On a phylogenetic point of view, even considering that there is not complete consensus
566 about the relationships of the taxa involved in the transition, their relationships seem to be
567 supported by the most recent cladistics analyses of basal tetrapods: Ruta, Coates & Quicke,
568 2003; Vallin & Laurin, 2004; Klembara, 2005; Ruta & Coates, 2007; Marjanović & Laurin,

569 2009, 2015 (see Fig. 11). These phylogenies show *Proterogyrinus* as an embolomere
570 anthracosaur, although the relationships of this taxon are contentious and were not completely
571 resolved (see Ruta, Coates & Quicke, 2003). *Gephyrostegus* is very close to Seymouriamorpha
572 and to microsaur, a hypothesis supported by the Laurin & Reisz (1997) tree, which also argues
573 that lepospondyls are a monophyletic group closely related to amniotes (see also Marjanović &
574 Laurin, 2015). Otherwise, if microsaur is paraphyletic to other lepospondyls and to the
575 amniote stem, as other workers suggest (Olori, 2015), they could have been the last phylogenetic
576 intermediaries in our evolutionary transformation series.

577 It is noteworthy that some taxa which are not classified as amniotes have an amniote-like
578 tarsus or at least developed the large proximal tarsal bones that characterize the amniotic tarsus,
579 the astragalus and the calcaneum (Fig. 10). Notable examples of this feature are the diadectids
580 earlier analysed (Romer & Byrne, 1931; Romer, 1944), although adults show the autapomorphic
581 condition of a fusion between both the proximal bones to produce an astragalocalcaneum bone.
582 Within lepospondyls, the microsaur *Pantylus* (Carroll, 1968) and *Tuditanus punctulatus* have
583 intriguingly, an amniote-like tarsus (Carroll & Baird, 1972). Moreover, the proterogyrinid
584 *Proterogyrinus scheelei*, *Gephyrostegus bohemicus* and probably *Westlothiana lizziae* also have
585 an amniote-like tarsus (see Holmes, 1984; Smithson, 1989). Because mesosaurids are very basal
586 amniotes (Laurin & Reisz, 1995; Piñeiro et al., 2012b) or basal parareptiles (Modesto, 1996 a-b;
587 Modesto, 1999; Piñeiro, 2004) we explored these taxa in order to find homologies between
588 putative plesiomorphic, non-amniotic tarsi and their corresponding structure in mesosaurids
589 according to the different ontogenetic stages described for the group.

590

591 *The status of Westlothiana and microsaur and its role in the transition*

592

593 Regarding the condition in *Westlothiana*, Smithson (1989), reconstructed the tarsus as
594 very amniote-like, including within it nine bones (see Smithson, 1989, figure 2d). There were
595 certainly nine bones in the preserved material although they were not preserved in their original
596 anatomical position. But, later, (Smithson et al., 1994) pointed out that the tarsus of *Westlothiana*
597 is indeed very plesiomorphic (or amphibian-like) because it included ten, rather than nine bones
598 (see figure 20A in Smithson et al., 1994). We do not find enough evidence to refute the former
599 reconstruction or for validate the latter, thus, a proposal about the tarsus structure in
600 *Westlothiana* would be very speculative at this stage. Moreover, the renaming of the two large,
601 proximally placed bones originally described as the astragalus and the calcaneum as an
602 intermedium and a fibulare, is also speculative because this last bone is difficult to identify from
603 the preserved specimen, where the foot bones are mostly disarticulated and obscured by the
604 caudal vertebrae (Smithson et al., 1994). Besides, according to these authors, the putative
605 intermedium is L-shaped, a characteristic very frequently found in the astragalus of early
606 amniotes. Despite *Westlothiana* possessing other advanced conditions that may suggest its
607 relation to the amniote clade, it also retains some plesiomorphic features in the skeleton such as a
608 prefrontal-postfrontal contact, excluding the frontal from the orbital margin (Smithson, 1989).
609 Thus, the reconstruction of the real structure of the tarsus in *Westlothiana* may be crucial to an
610 understanding of the evolutionary transition to the origin of the amniotic astragalus as we have
611 figured it out in this contribution. We hope that our paper will encourage new studies on this
612 taxon.

613 Concerning microsaur, these ecologically diverse, small-bodied tetrapods are credible
614 candidates for being part of the stem leading to the emergence of the earliest amniotes. They

615 develop a tarsus with a very amniote-like morphology, and as was recently demonstrated they
616 even show a similar ossification pattern, with the intermedium (?astragalus) and the fibulare
617 (?calcaneum) being the first tarsal bones to ossify (see Olori, 2015). They are also the only
618 proximal elements in the tarsus as in all amniotes, and naming them as intermedium and fibulare
619 is just arbitrary at this stage, if we have no embryological information to prove their identity. We
620 have to take into account that in mesosaurids the astragalus and the calcaneum are the only
621 proximal tarsal bones in born individuals, despite the former deriving from the fusion of three or
622 four bones.

623

624 *Diadectids*

625

626 Diadectids were recently considered to be amniotes (Berman, 2000), and as such, they
627 would have had an amniote tarsus. Recent discoveries of possible juvenile diadectid tarsi
628 including a putative composite astragalus formed by the intermedium, the tibiale and the
629 proximal centrale (c4, as it was identified) introduced interesting new data to the origin of the
630 amniotic astragalus (Berman & Henrici, 2003). Later, this material was assigned to the species
631 *Orobates pabsti*, a diadectid (Berman et al., 2004). Nevertheless, the holotype specimen of
632 *Orobates* described by Berman & Henrici (2003) and Berman et al. (2004: 29) as having a
633 tripartite astragalus (MNG 10181) was recently subjected to an in-deep study using micro-focus
634 computed tomography scans (Nyakatura et al., 2015), which allowed for a thoughtful anatomical
635 understanding of the specimen. The scanned image and digital reconstruction show that there are
636 seven separated bones in the tarsus of *Orobates*, whose morphology suggests that could be
637 homologized with immature astragalus and calcaneum plus two centralia (c1+c2) and three small

638 distal tarsals. Indeed, despite the very good preservation of the individual, it was apparently
639 subjected to severe diagenetic distortion; the bones were embedded in a crystalline calcite matrix
640 and there was a significant chemical substitution around their margins (cf. Nyakatura et al.,
641 2015). That taphonomic feature could have produced a configuration that, under direct
642 examination, led to the interpretation of Berman & Henrici (2003) about the presence of a
643 composite astragalus in *Orobates*.

644 Berman & Henrici (2003) also described two associated (maybe sutured) tarsal bones
645 which they recognized as the intermedium and the fibulare of a juvenile *Diadectes*. However, the
646 shape of the bones, mostly subcircular, and their relative size and proportions, remind us of the
647 astragalus and calcaneum of a very young individual, taking into account the ontogenetic stages
648 described here for the very basal amniote *Mesosaurus tenuidens*.

649 This new configuration matches the pattern of the tarsus already known for diadectids:
650 distinct astragalus and calcaneum in young individuals, which fuse later to produce an
651 astragalocalcaneum in very mature adults. Thus, diadectids have a very amniote-like tarsus. The
652 non-diadectid diadectomorphs (*Tseajaia campi*) do not have a well-defined tarsus, but this can be
653 masked by the not sufficiently good preservation of the specimen feet. Even though, in *Tseajaia*
654 *campi*, three distinct bones seem to form the proximal line (Moss, 1972), some fusions tending to
655 achieve the amniote-like pattern can be hypothesized to be present: the tibiale fuses to c4 as the
656 evolutionary transition reviewed above suggests, and the intermedium, shown by Moss (1972) as
657 fusing to c4, indeed fuses to c3 (see Figs. 10, 12), supporting the putative incorporation of both
658 centralia into the amniotic astragalus as O'Keefe et al. 2006 have suggested and as it is shown by
659 the tarsus in the non-hatched mesosaurid (Fig.9).

660 Some groups like diadectids and seymouriamorphs for instance, show a high plasticity in
661 producing different patterns often correlated to a different expression of otherwise highly
662 conserved regulatory genes (Shubin, 2002). Therefore, the expression of these genes and the
663 consecutive structure of the tarsus may be regulated by the different ecological pressures to what
664 some have to adapt along the different stages of their development. Juvenile or young adult
665 *Diadectes* show a conservative tarsus, and distinct astragalus and calcaneum were described as
666 being present (Romer & Byrne, 1931; Romer, 1944; Berman & Henrici, 2003). However,
667 astragalocalcaneum fusion is shown to occur in very large and mature individuals, where it
668 would seem that the movement between these bones becomes very limited or null (Romer,
669 1944).

670

671 *Hylonomus lyelli*

672

673 Revising the evidence from other basal amniotes such as *Hylonomus lyelli* (Carroll, 1964;
674 Meyer & Anderson, 2013) we found some inconsistencies related to the identification of the
675 bones figured, perhaps as an attempt to follow the Peabody's (1951) suggestion of a tripartite
676 origin of the astragalus. Thus, Meyer & Anderson (2013), following Carroll (1964, fig. 1),
677 identified the astragalus and calcaneum from a partially disarticulated specimen where the feet
678 are completely disassociated and considered the calcaneum of *Hylonomus* as two times larger
679 than the astragalus. According to the information found in Carroll (1964, p. 72, fig. 8) and based
680 on the ontogenetic succession that we described here for mesosaurs, the calcaneum can
681 sometimes be equal in size to the astragalus or even a little larger, but never that much larger.
682 Thus, we could deduce both that it is an incomplete astragalus missing the intermedium, as

683 Meyer & Anderson proposed in the text and in figure 3 (but this would suggest that the type
684 specimen of *Hylonomus lyelli* belonged to a very young individual and it does not appear to be
685 the case, see figure 1 of Carroll, 1964), or that the bone identified as the calcaneum is the
686 astragalus or that the bone is neither the astragalus nor the calcaneum. We are inclined to accept
687 the last hypothesis because the overall small size of the individual suggests that these bones are
688 much too large to be tarsal bones; they seem to be elements of the pelvic girdle, possibly the
689 pubis (see figure 1 of Carroll, 1964). The well identified astragalus of *Hylonomus lyelli* (see
690 figure 8 of Carroll, 1964) does not show any trace of sutures.

691

692 *Captorhinids*

693

694 Taking into account the previous evolutionary transition in favor of a composite origin of
695 the amniotic astragalus, which of course may also include other taxa, the interpretation of
696 Peabody (1951) and later workers of the presence of more than one ossification center in the
697 astragalus of *Captorhinus* and other basal amniotes seems sensible. However, other extensive
698 descriptions of *Captorhinus* (e.g. Fox & Bowman, 1966) do not provide more conclusive
699 evidence about the structure of the tarsus and, as Rieppel (1993) claimed, it is necessary to have
700 ontogenetic evidence (e.g. articulated skeletons of very young individuals of *Captorhinus* and/or
701 of related taxa) to demonstrate the homology of the bones composing the tripartite astragalus and
702 their presence in the earliest stages of development. Isolated astragali from the Lower Permian of
703 Oklahoma were described by Kissel, Dilkes & Reisz (2002) as belonging to *Captorhinus*
704 *magnus*, showing the putative tripartite structure visible only from the dorsal surface of the
705 bones. However, this feature was discussed by Rieppel (1993) who argued that the putative

706 unclosed sutures should be interpreted as areas of muscular attachment, or grooves for blood
707 vessel irrigation, or fractures.

708 Concerning *Captorhinus*, most of the isolated astragali figured by Peabody (1951) clearly
709 belong to mature animals, according to their size and structure (see Fox and Bowman, 1966, for
710 comparison); the smallest one already shows the same morphology seen in the larger ones. If the
711 astragali shown by Peabody (1951) partially represent an ontogenetic transformation series, they
712 cannot confidently demonstrate that the apparent tripartite structure is derived from the fusion of
713 three or four of the plesiomorphic tarsal bones. A feature that could not support the hypothesis of
714 the tripartite structure is that the sutural lines and groove patterns present in *Captorhinus* as
715 described by Peabody (1951) are only visible on the ventral surface of the bone; alternatively, it
716 suggests that the fusion started on the dorsal surface and was not completed in adult individuals.
717 The same condition can be observed in the large captorhinid *Captorhinus magnus* (Kissel, Dilkes
718 & Reisz, 2002).

719 Fragmentary pedes referred to juvenile and adult individuals of the giant, largest known
720 captorhinid *Moradisaurus grandis* from the Upper Permian of Niger, were figured and described
721 by O'Keefe et al. (2005, 2006). Even though the bones were found in association and it was
722 possible to recognize the identity of some of them, they represent isolated and disarticulated
723 pedes whose referral to *Moradisaurus* can be possible but not accurate, at least no more, than to
724 any other basal tetrapod of the same size. Nevertheless, based on the pes assigned to a juvenile
725 captorhinid, O'Keefe et al. (2006) suggested that the c3 is also a component of the multipartite
726 amniote astragalus, occupying its latero-distal corner. However, the individualization of the
727 constituent bones of the juvenile tarsus and all the possible arrangements show that there is a
728 bone, dorsal to the intermedium that does not belong to the tarsus, unless it is part of the

729 intermedium yet not totally ossified because the juvenile condition of the specimen. But, that
730 bone is the only that is totally isolated from the rest of the tarsus, which excepting the four distal
731 tarsals, appears as a co-ossified structure.

732 Even though our reconstruction of the non-hatched *Mesosaurus* tarsus is consistent with
733 the O’Keefe et al. (2006) reconstruction of the *Moradisaurus* tarsus in the fact that the c3 may be
734 part of the astragalus, the arrangement of the bones seems to have been very different in both
735 taxa. Moreover, the putative calcaneum has a very developed notch for the perforating artery,
736 which does not match with the condition in the astragalus, including the evident individualization
737 of the constituent bones. It is also difficult to include the O’Keefe et al. (2006) specimen because
738 their reconstruction does not show an evident fusion between the tibiale and the c4, and because
739 it is a unique, isolated, putatively juvenile pes of *Moradisaurus*, where the identity of the bones
740 is highly subjective. The other fragmentary pes, interpreted to pertain to an adult specimen
741 displays the typical amniotic tarsal structure and the astragalus shows no sign of the composite
742 origin.

743

744 *The presumable “implicit” relationship between mesosaurids and basal synapsids regarding the*
745 *structure of their skull and tarsus*

746

747 Friedrich von Huene (1941) proposed for the first time a phylogenetic relationship
748 between *Mesosaurus* and some basal ‘pelycosaurs’. That suggestion was not generally
749 acknowledged by later authors who developed the currently accepted hypothesis that
750 mesosaurids are the basalmost sauropsids (Laurin & Reisz, 1995) or the basalmost parareptiles
751 (Modesto, 1999). More recently, Piñeiro (2004) found some evidence that she understood gave

752 support to von Huene's hypothesis (1941) but acknowledged that it should be tested in a
753 phylogenetic context. Moreover, the nature of the mesosaurid skull, discussed during more than a
754 hundred years, has been recently reassessed to show the presence of a synapsid-like lower
755 temporal fenestra in *Mesosaurus tenuidens* (Piñeiro et al., 2012c). This contribution gave credit
756 to the observations made by von Huene (1941) about the morphology of the mesosaur skull.
757 Similarly, the tarsus of mesosaurs has been studied by several authors, and here we have
758 demonstrated that its structure is almost identical to that described for basal synapsids, but also it
759 is equivalent to that of basal sauropsids, including one of the basalmost diapsid *Petrolacosaurus*
760 *kansensis* (Reisz, 1981).

761 Basal synapsids show a greater development of the calcaneum (Romer & Price, 1940),
762 which in some taxa roughly acquires the size of the astragalus. In contrast to this, the calcaneum
763 of *Mesosaurus* is smaller than the astragalus (although the size differences are less significant in
764 adult individuals), and develops a lateral expansion in the area of the heel, possibly for insertion
765 of extensor tendons including the Achilles tendon (Fig. 7).

766 Indeed, the tarsus in early amniotes is both structural and morphologically equivalent in
767 the two groups, except that in 'pelycosaurs' there is no evidence for the multipartite formation of
768 the astragalus, thus generating doubts about the homology of these bones in synapsid and
769 sauropsid amniotes (Rieppel, 1993). However, the multipartite original structure can be seen just
770 in very young mesosaurs and it disappears before the achievement of the adult stage; but it seems
771 to be evident in captorhinids, being possibly an heterochronic pattern.

772

773 *Evolutionary paths for the development of amniote tarsus: the mesosaur contribution*

774

775 The morphological ontogenetic transformation presented here for *Mesosaurus tenuidens*
776 is the most complete known for a basal amniote (cf. Laurin & Reisz, 1995) and as such, it
777 constitutes a relevant database for studies of a different nature. The information provided for this
778 data base on the origin of the amniotic tarsus suggests that, as Peabody (1951) and previous
779 authors (e.g. Holmgren, 1933) have stated, the earliest astragalus originated from at least four
780 ossification centers (taking into account that the tibiale and c4 fuse together early in the
781 ontogeny), near the tibial and fibular distal margins.

782 According to our observations of the non-hatched *Mesosaurus tenuidens* which possesses
783 an astragalus formed by at least four bones, we can say that the mesosaurid astragalus is not a
784 neomorphic as Rieppel (1993) has suggested, unless we consider that once united in the earliest
785 stages of the development, these bones form a new element. Even the evidence taken from taxa
786 such as the embolomere *Proterogyrinus scheelei* Romer, 1970 can provide support for the
787 multipartite hypothesis and the identification of the bones provided in the present work (Holmes,
788 1984).

789 We made several interesting observations that support the already established homologies
790 and possible evolutionary paths towards the origin of the primitive amniotic astragalus.
791 Particularly in *Proterogyrinus* the intermedium has a very similar structure to that of the
792 astragalus of young mature mesosaurs, and the tibiale is clearly sutured against the medial corner
793 formed by c4 and the intermedium. The fibulare is also very similar to the calcaneum of the same
794 stage (see Figs. 1-6), so it is logical to presume that these bones are homologous, as already
795 stated. The main question is what happens to the remaining bones to obtain the mesosaurid (=
796 basal amniote) tarsus consisting of two large proximal elements plus one or two centralia and
797 five distal tarsals. We find evidence for the presence of c3 early in the ontogeny (Fig. 9); it is

798 possible that it fuses to c4 in the described mesosaur ontogenetic transformation after the c4
799 fuses to the tibiale. Indeed, based on the structure shown by *Proterogyrinus* (Holmes, 1984),
800 where apparently the tibiale fuses to c4, and taking into account that shown by the tarsus in the
801 captorhinomorph *Labidosaurus* (Williston, 1917) where the intermedium and the tibiale also fuse
802 to c4, we hypothesized three possibilities or combinations: A, the astragalus is just formed by the
803 intermedium+tibiale only, and c4 and c3 undergo a reduction in size until they finally disappear
804 (not plausible, given the probable presence of c4 and c3 in the tarsus of the non-hatched
805 mesosaurid); B, the astragalus is formed by intermedium+tibiale+c4, and c3 is reduced to be lost
806 (not probable given its putative presence in the tarsus of the non-hatched mesosaurid and taking
807 into account the proposal by O’Keefe et al., 2006); C, the astragalus results from the fusion of all
808 bones, i+te+c4+c3 (Figs. 9 and 12A). The last possibility (C) seems to be supported by the
809 materials that we described here, and is consistent with that suggested by O’Keefe et al. (2006),
810 who provided evidence for the inclusion of c3). It does not imply the loss of bones but a re-
811 patterning to produce the amniotic tarsus. Moreover, there are also two possibilities for the
812 formation of the ‘navicular’: 1, it results from fusion of c1 and c2; 2, it is formed by the c2 after
813 the reduction and loss of c1 (see Fig. 12B). We found probable evidence of some of these fusions
814 (the tibiale+ ?c4+ intermedium, c1+c2) in early stages of *Mesosaurus tenuidens*’s development,
815 but not in all individuals.

816 If the hypotheses of the astragalus and the ‘navicular’ formation are combined, we can
817 have the following six possibilities: A-1; A-2; B-1; B-2; C-1; C-2, but the evidence from
818 mesosaurs might support just C-1.

819

820 **CONCLUSIONS**

821

822 The changes produced in the mesosaur tarsus structure during ontogeny were established
823 based on the study of several specimens preserved in different stages of development. This
824 transformation series is the most complete known for a basal amniote as it includes even
825 embryological information. Our results allow for a better recognition of intraspecific
826 (ontogenetic) from interspecific variation in mesosaurs and provides more informative characters
827 that can be used in comparative studies of amniote relationships.

828 The mesosaur tarsus includes 8 or 9 bones: astragalus and calcaneum plus centralia 1 and
829 2 (fused to form the mesosaur ‘navicular’) and five distal tarsals. The ‘navicular’ is proved to be
830 present in all subadult and adult mesosaurs, even in *Mesosaurus* where it fuses to the astragalus
831 in mature individuals. The early amniote astragalus is a composite bone as can be evidenced by
832 the presence of at most three sutured bones in the tarsus of a non-hatched mesosaurid in an
833 advanced stage of development. These bones seem to be the intermedium and the tibiale, and the
834 later fused to c4; and the c3. Thus, our study rejects the hypothesis that the amniotic astragalus is
835 neomorphic.

836 Regarding the analyzed ontogenetic series, we could determine that the attainment of
837 maturity in mesosaurs can be related to a determinate tarsus structure, which can be a good age
838 indicator to extrapolate to other groups of basal amniotes. Moreover, the morphological changes
839 observed in the mesosaur ontogeny could have strong implications in the recognition of until
840 now undocumented, ancestral developmental features of early amniotes.

841 Current morphological and comparative studies on the mesosaurid skeleton suggest other
842 interesting similarities between mesosaurids and basal synapsids that will be properly described
843 in a forthcoming paper. However, these features are also shared with other basal sauropsids and

844 taxa that are not even amniotes. For instance, mesosaurs share characters with taxa previously
845 known to be closer to Amniota (Panchen & Smithson, 1988; but see also Smithson et al., 1994)
846 but these hypotheses were not phylogenetically evaluated. These taxa are now considered as
847 stem or crown-tetrapods (Olori, 2015; Marjanović & Laurin, 2015) or their affinities are not yet
848 well defined (e.g. *Westlothiana*), but they still remain close to the earliest amniotes. This
849 commonly shared morphology among apparently unrelated but very basal taxa reflects the
850 primitive nature of mesosaurids, as already noted by Huene (1941) and other paleontologists.
851 The example of the similar tarsal structure observed in mesosaurids, some microsaurids, basal
852 synapsids and non-amniote tetrapods suggests that the evolution of the astragalus and calcaneum
853 as the most typical bones in the amniotic tarsus could be an acquisition obtained much earlier
854 than when the first recognized amniote appeared and walked on the planet.

855

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873

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1104

1105 **Figure captions**

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1107 Figure 1. *Mesosaurus tenuidens*, ontogenetic transformation in the tarsus formation. Photographs
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1116 and just shadows of astragalus and distal tarsals can be seen. See interpretive drawings in
1117 figure 2B for details, C. SMF-R 4496, well preserved tarsus of a young individual, both

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1119 in Fig. 2C for a more detailed anatomical description of the specimen. D. AMNH 23795,
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1137 morphology and relationships of the tarsal bones preserved in FC-DPV 2504, the non-
1138 hatched mesosaurid (see Fig. 9 and text for further descriptions of each the included
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1147 4470, GP-2E 5816, GP-2E 6576, GP-2E 5740, FC-DPV 2058. All the specimens are
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1149 morphology fit into the typical pattern for basal amniotes: 2 large proximal bones
1150 (astragalus and calcaneum), a ‘navicular’ (often preserving the suture between c1 and c2)
1151 and 5 distal tarsals. See Figs. 5 and 6 for interpretive drawings of the preserved bones and
1152 their main characteristic features.

1153 Figure 5. *Mesosaurus tenuidens*, ontogenetic transformation in the tarsus formation. Interpretive
1154 drawings of the specimens in Fig.2 (H-P) showing the adult stages in the ontogenetic
1155 sequence. See text for further descriptions of each the included specimens.

1156 Figure 6. *Mesosaurus tenuidens*, ontogenetic transformation in the tarsus formation. Detailed
1157 interpretive drawings of the specimens in Fig. 2 showing the morphology of the tarsus in
1158 adult individuals. The formation of the ‘navicular’ by the fusion of c1 and c2 is shown
1159 through the series, as well as the formation and development of the foramen for the
1160 perforating artery. Notable is the variation in size and shape of the distal tarsals observed
1161 in the analysed specimens. Anatomical abbreviations: as, astragalus; c1: centrale 1; c2,
1162 centrale 2; ca, calcaneum; na: ‘navicular’; paf, foramen for the perforating artery;
1163 I,II,III,IV,V, distal tarsals.

1164 Figure 7. Photograph (A) and anatomical reconstruction (B) of the crus in an adult *Mesosaurus*
1165 *tenuidens*. Colours indicate the identity of the different elements that form the tarsus and
1166 the crus. Scale bar: 10 mm.

1167 Figure 8. Ontogenetic transition of the ‘navicular’ in *Mesosaurus tenuidens*. A, FC-DPV 1502,
1168 from left to right, photographs and interpretive drawings of isolated astragalus from a
1169 young individual, in dorsal, ventral and medial views respectively. The bone shows the
1170 typical square outline of immature individuals and the remains of sutures between the
1171 original anlagen more visible on its ventral surface, which appears to display a different
1172 morphology with respect to the dorsal one. Note that there are no traces of the ‘navicular’
1173 preserved along the distal surface of the astragalus, which bears a concave margin. B,
1174 GP-2E 5203, photograph and interpretive drawing of astragalus, calcaneum and incipient
1175 ‘navicular’ of a young individual in dorsal view. Recall on that the ‘navicular’ is already
1176 united to the astragalus by c2, being formed by c1 and c2 and the suture between them is
1177 still well visible. C, FC-DPV 1479, photographs and interpretive drawings of an isolated
1178 astragalus from an adult individual in dorsal, ventral and medial view. Observe that the
1179 ‘navicular’ is now a single bone almost completely fused to the astragalus to produce the
1180 finally resultant adult outline. C1 has transformed into a tip-like bone and remains
1181 separated from the astragalus, but it can just be seen from the ventral view, which still
1182 features different from the dorsal one. The wide and triangular facet for articulation with
1183 the tibia can be seen from the medial view. Anatomical abbreviations: a, astragalus; ca,
1184 calcaneum; c1, centrale one; c2, centrale two; ac3, ancestral centrale three; ft, facet for
1185 the articulation of the tibia; ai, ancestral intermedium; ate+ac4, ancestral tibiale plus
1186 ancestral central four. Scale bar: 5 mm.

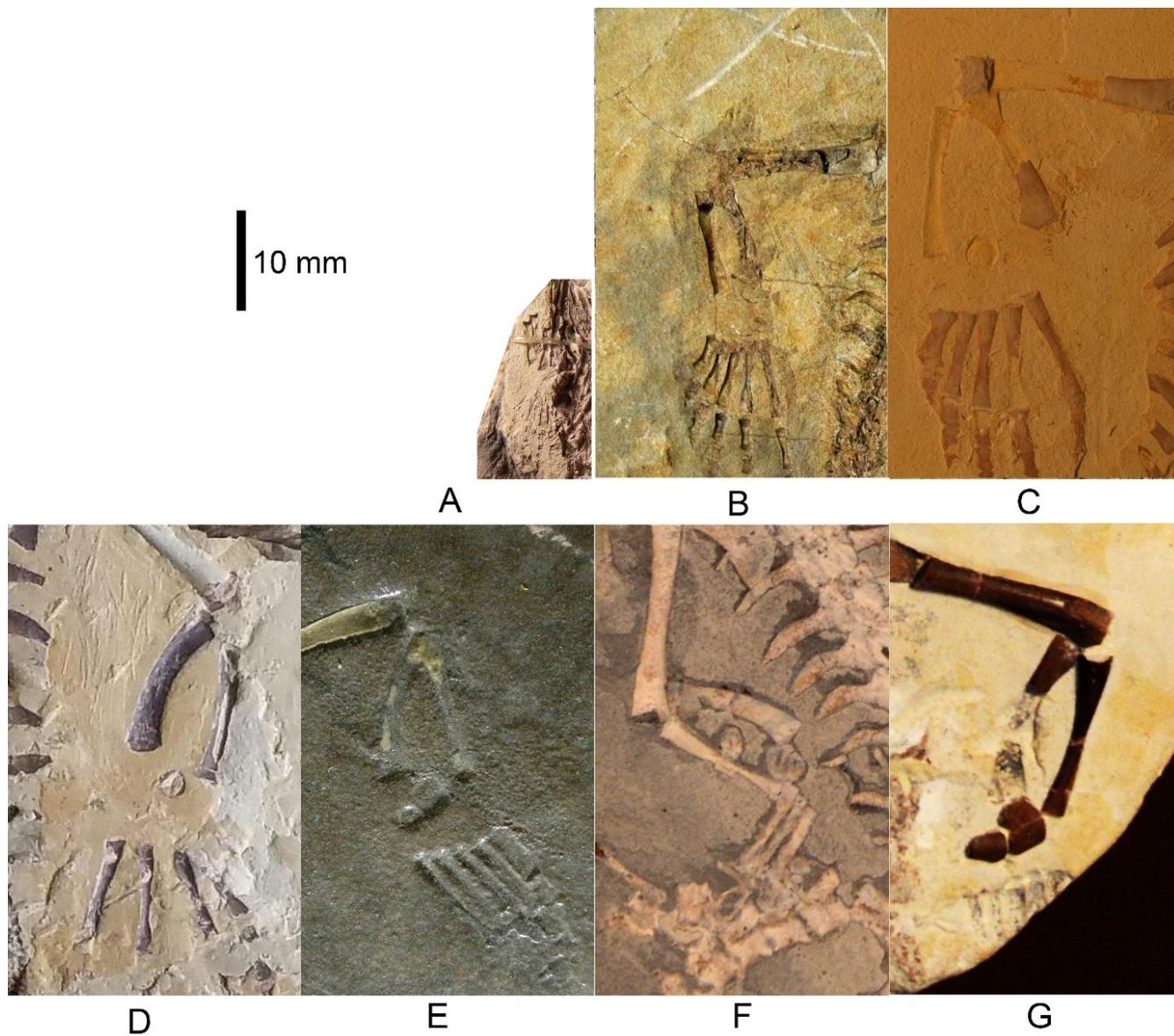
1187 Figure 9. Preserved tarsus in a *Mesosaurus tenuidens* non-hatched individual. A, FC.DPV 2504,
1188 a non-hatched mesosaurid in the egg, showing the two feet overlapping each other by
1189 compression. B, SEM image of the foot of FC-DPV 2504 focusing on the tarsal area. The
1190 astragali can be seen in the center of the figure, mixed between the metatarsals. The
1191 astragalus seems to be not preserved. C, Interpretive drawing of the tarsus including a
1192 possible identification of the preserved bones by regarding previous hypotheses about the
1193 origin of the amniotic astragalus. The composing elements of the astragalus were colored
1194 to favour identification of the isolated bones of the left foot. Anatomical abbreviations:
1195 ?i, possible intermedium; ?c4, possible central four; fi, fibula; mc, metacarpals; ?te,
1196 possible tibiale; t, tibia. Scale bar: 1mm.

1197 Figure 10. Tarsus structure in basal tetrapods, including amniote and non-amniote taxa.
1198 Schematic diagram for comparing the tarsus structure in the basal tetrapods *Acheloma*
1199 and *Greererpeton* (amphibian-like tarsus) with regard to that of embolomeres and
1200 microsaur (amniote-like tarsus) and early amniotes. Note the similar structure and
1201 construction of the microsaur tarsus with respect to the early amniote *Hylonomus*. See
1202 text for more details of the evolutive significance of the selected taxa. Abbreviations: as,
1203 astragalus; i, intermedium; te, tibiale; 1,2,3,4, centralia; i,ii,iii,iv,v, distal tarsals. Taxa
1204 were redrawn from the following sources: *Acheloma* (Dilkes, 2015); *Greererpeton*
1205 (Godfrey, 1989); *Proterogyrinus* (Holmes, 1984); *Gephyrostegus* (Carroll, 1970);
1206 *Seymouria* (Berman et al., 2000); *Westlothiana* (Smithson 1989, Smithson et al.,1994);
1207 *Pantylus* (Carroll, 1968); *Tuditanus* (Carroll, 1968); Diadectomorphs (Moss, 1972;
1208 Berman & Henrici 2003;); *Ophiacodon* and *Haptodus* (Romer & Price, 1940);

1209 *Hylonomus* (Carroll, 1964); *Captorhinus* (Fox & Bowman, 1966); *Petrolacosaurus*
1210 (Peabody, 1952; Reisz, 1981).

1211 Figure 11. Schematic representation of recent phylogenetic hypotheses of early tetrapod
1212 relationships showing the position of the taxa involved in the evolutionary transition to
1213 the formation of the early amniotic astragalus (see text for the figure context). A. Ruta &
1214 Coates, 2007; B. Carroll, 1995; C. Laurin & Reisz, 1999; D. Marjanović & Laurin, 2015.

1215 Figure 12. Hypotheses about the astragalus and the navicular formation. The schematic diagram
1216 shows the steps that lead to the formation of the amniotic tarsus, regarding the series of
1217 possible transformations that could have produced the primitive astragalus (A) as well as
1218 those that prevailed into the evolution of the ‘navicular’ bone (B).

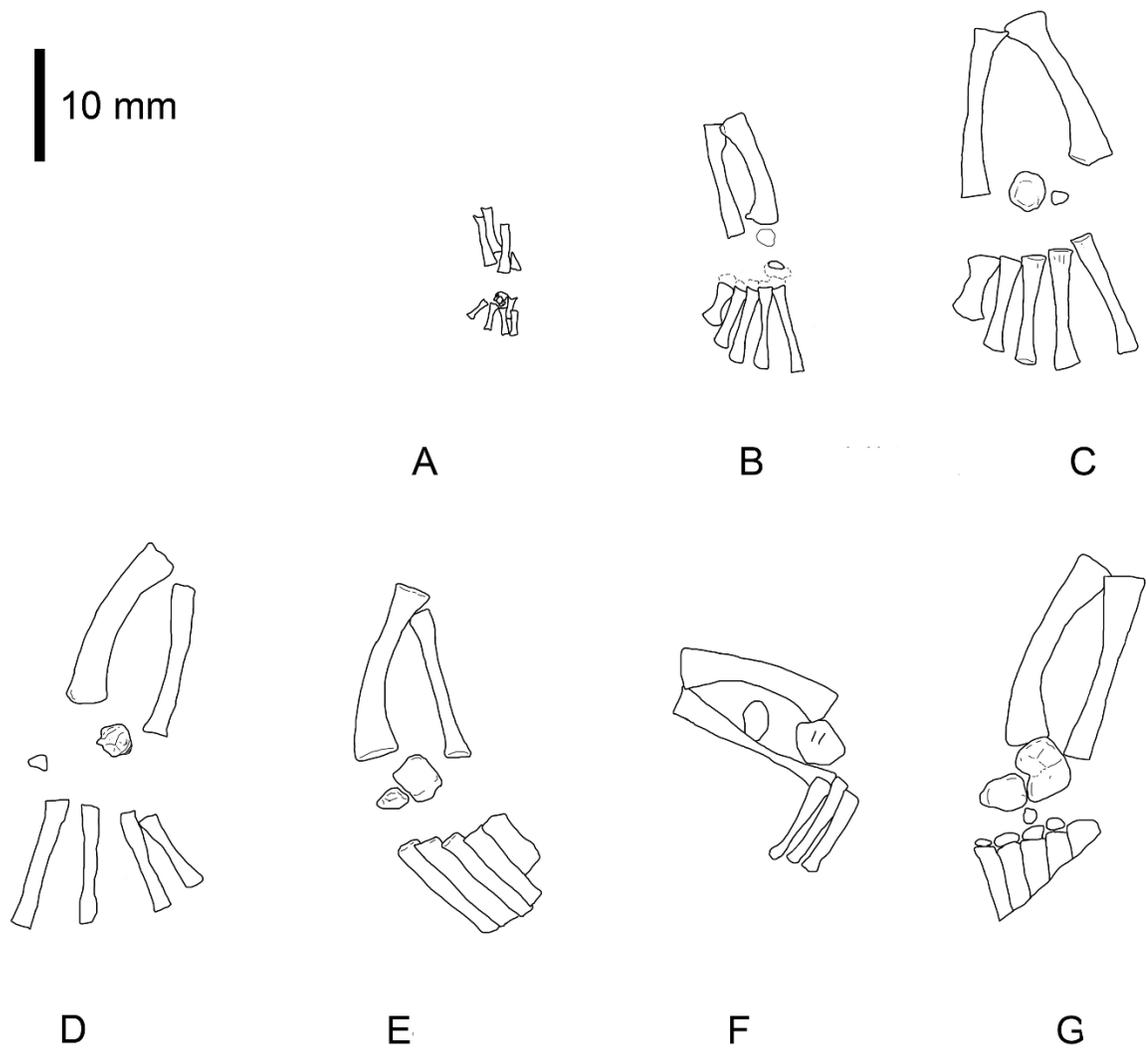


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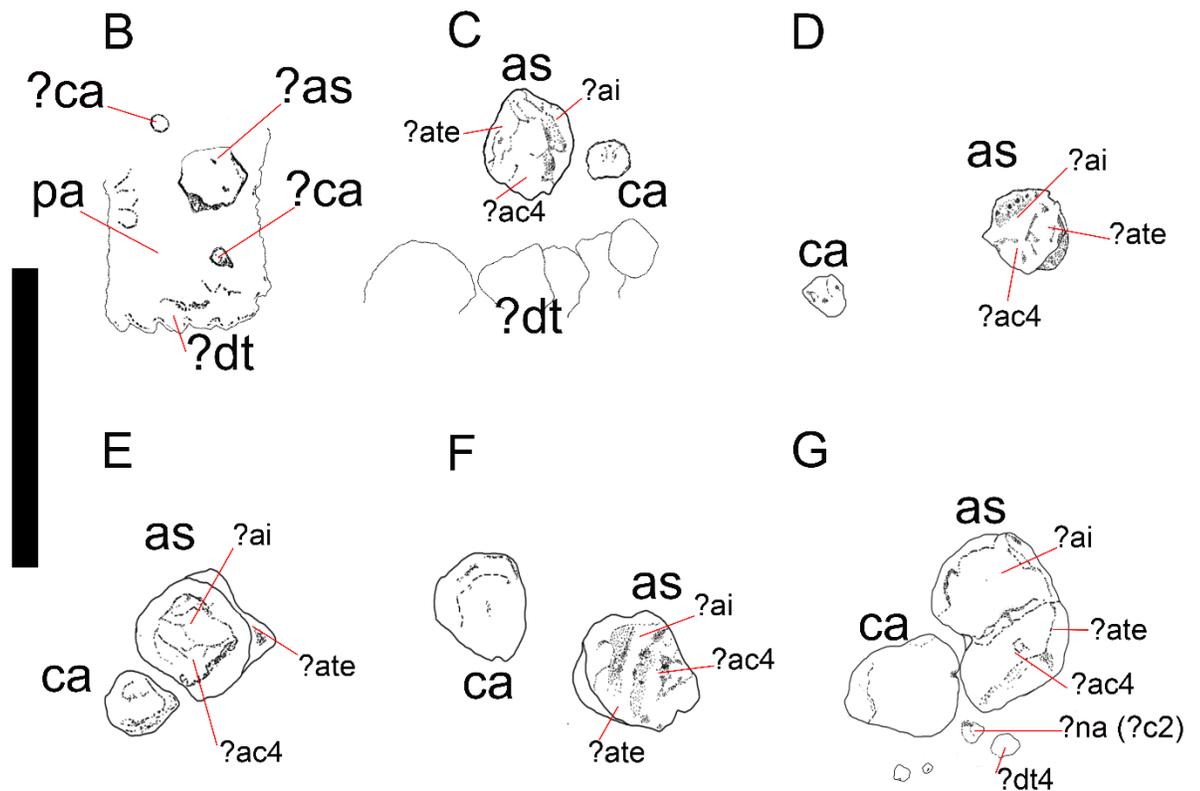


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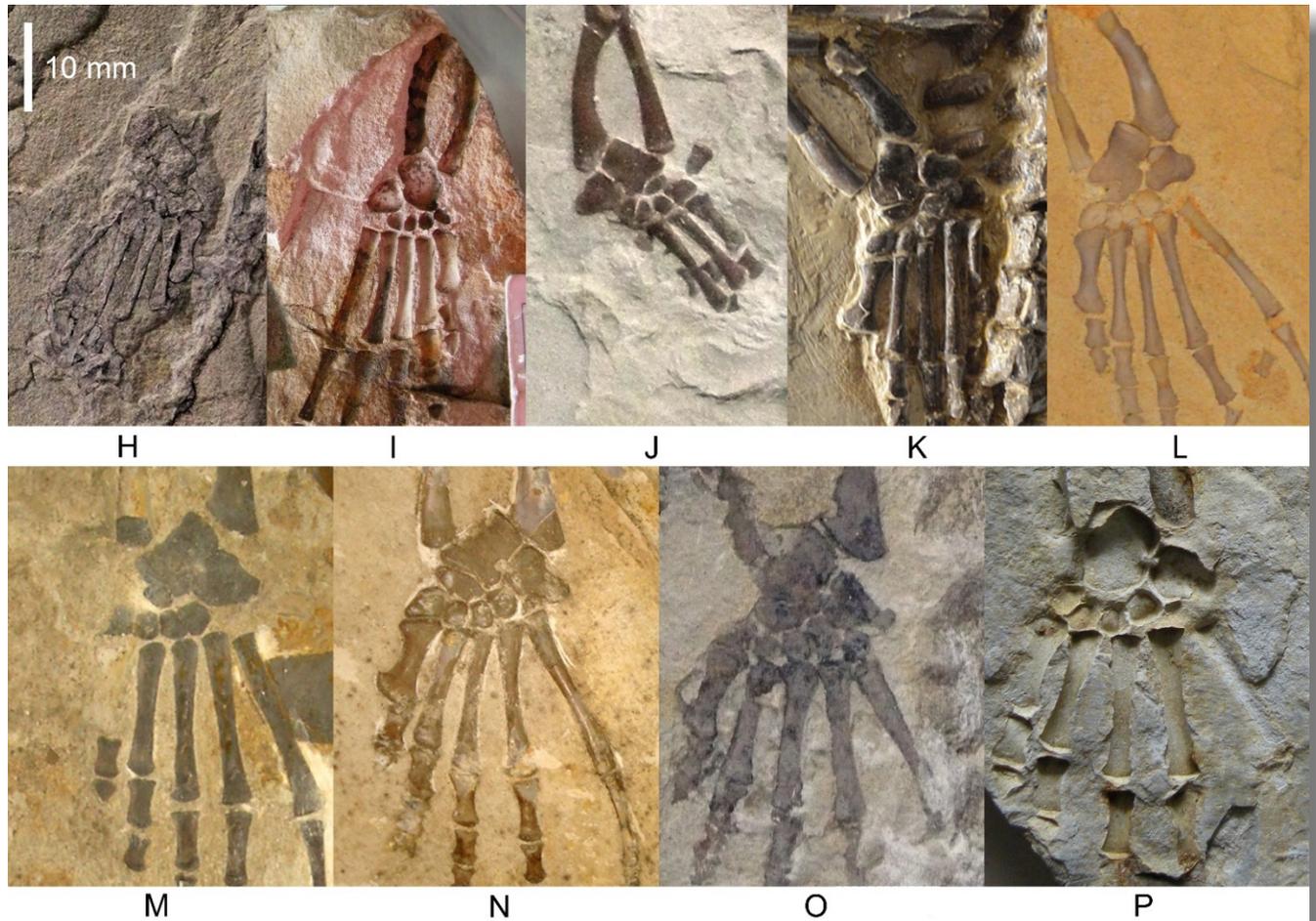
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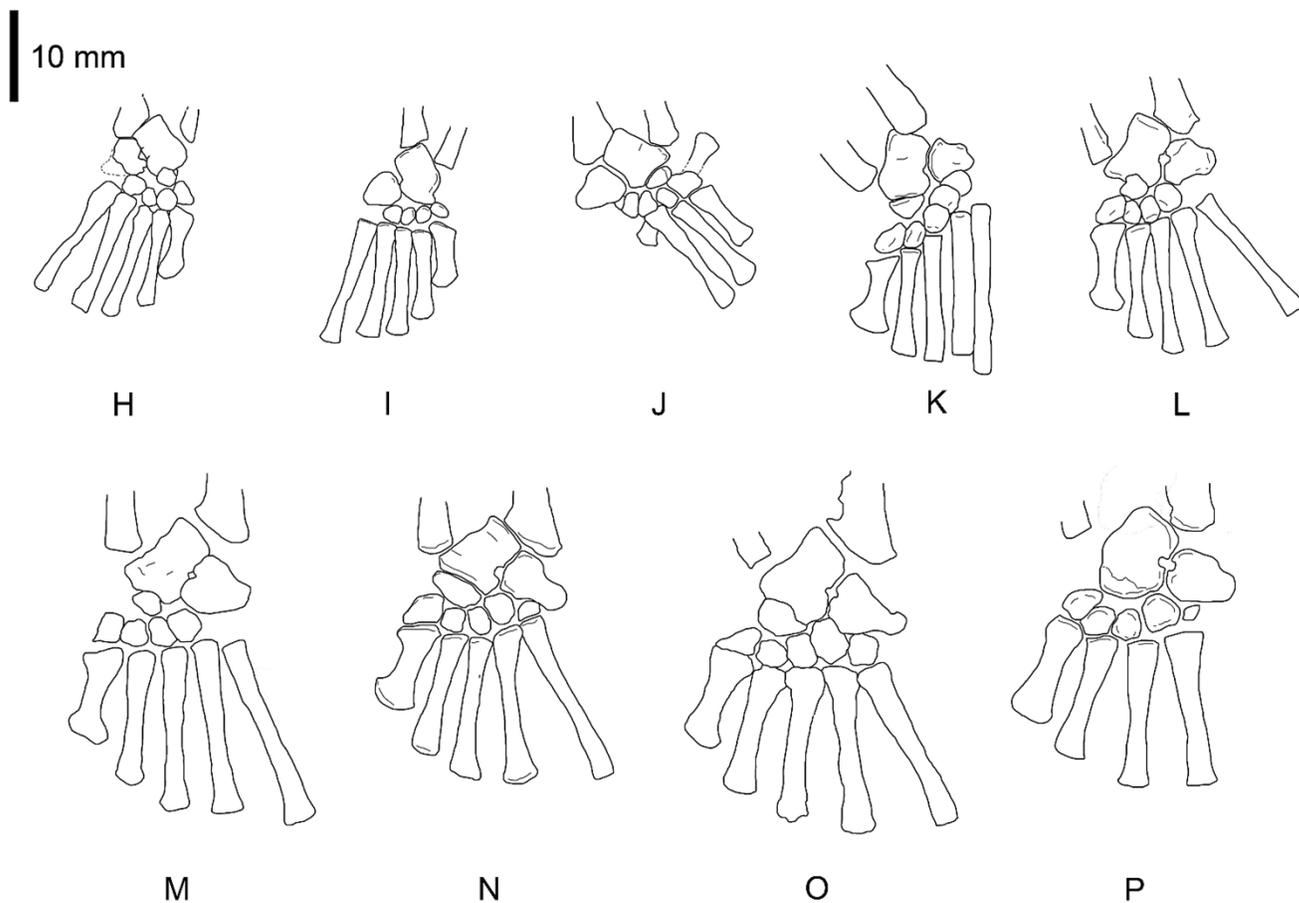
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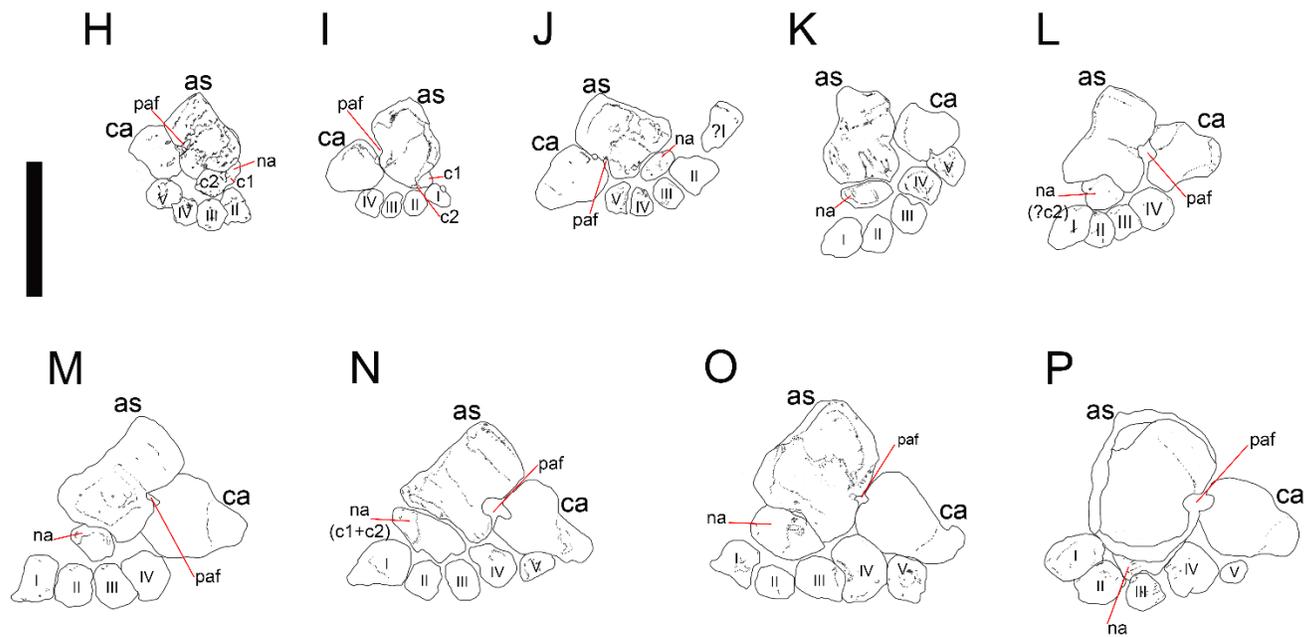
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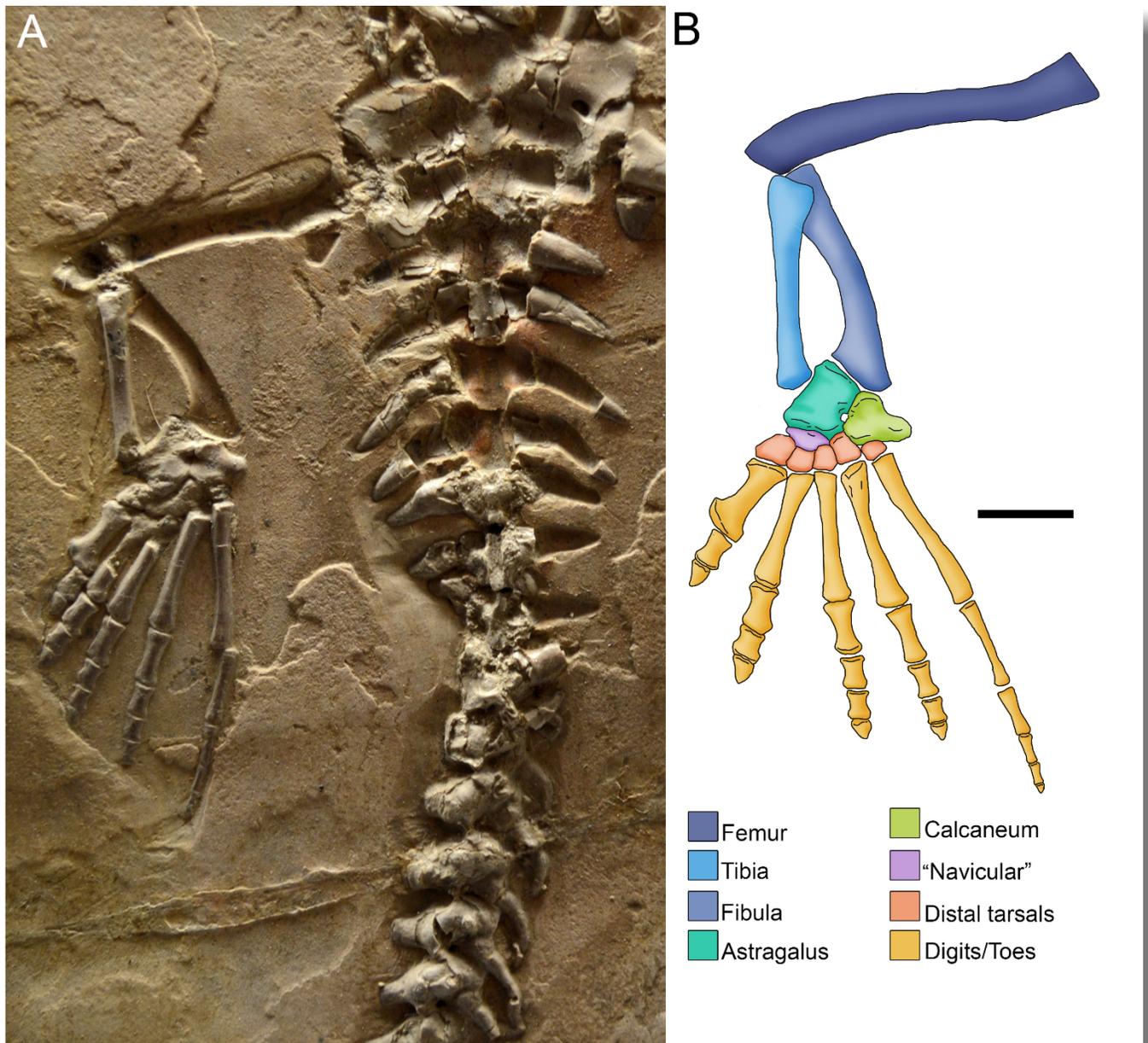
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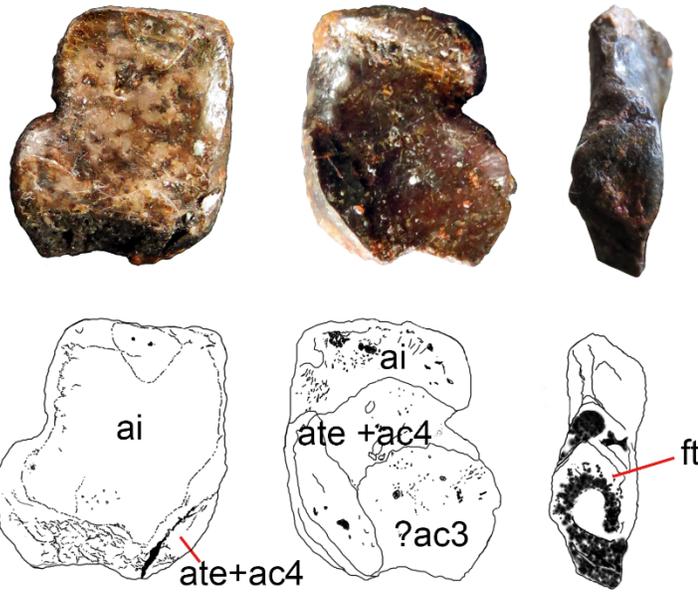
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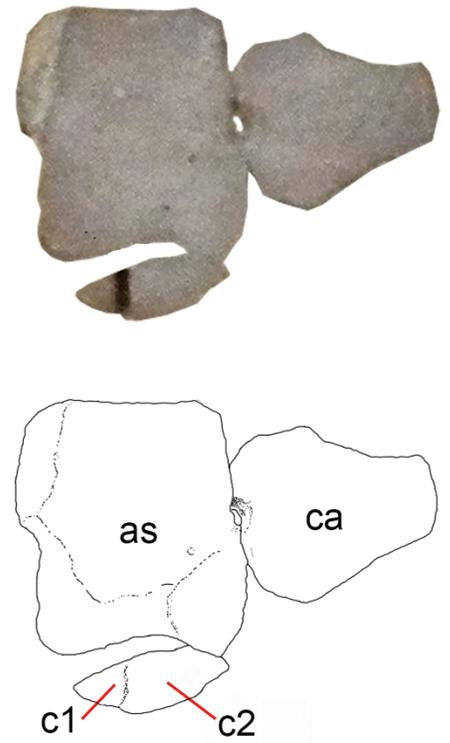
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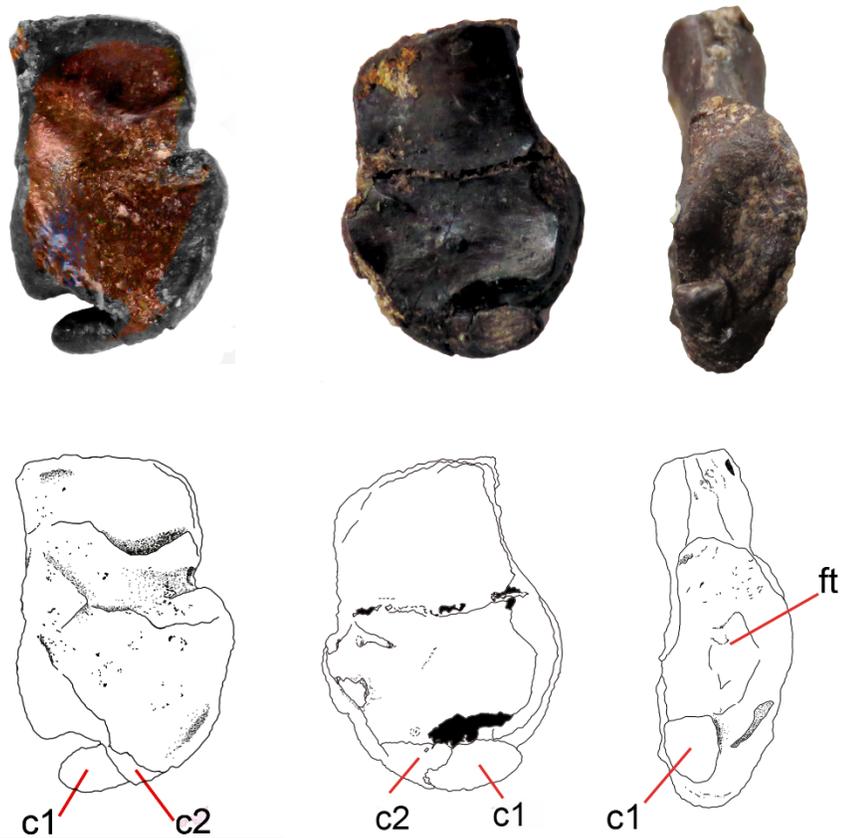
A



B

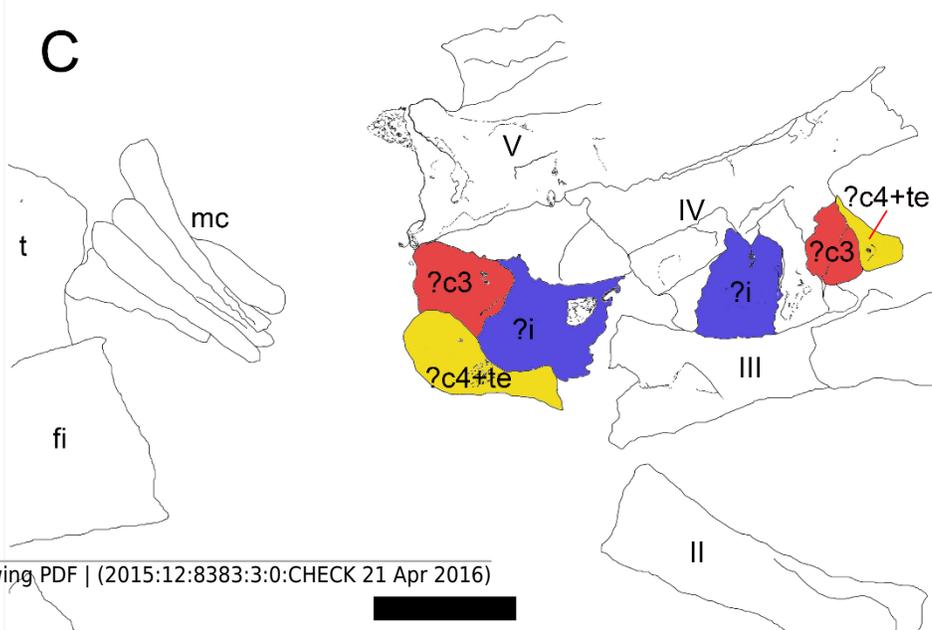
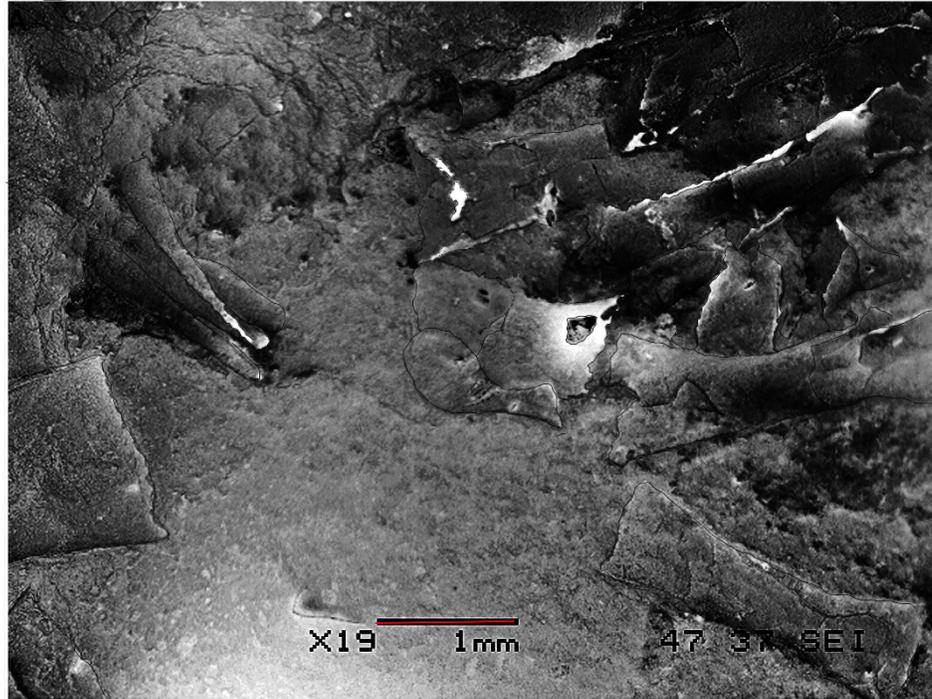
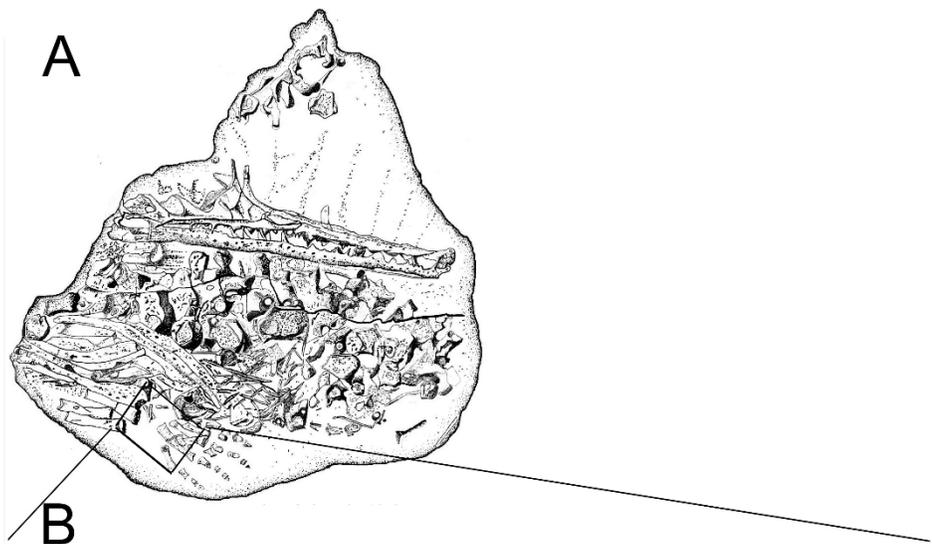


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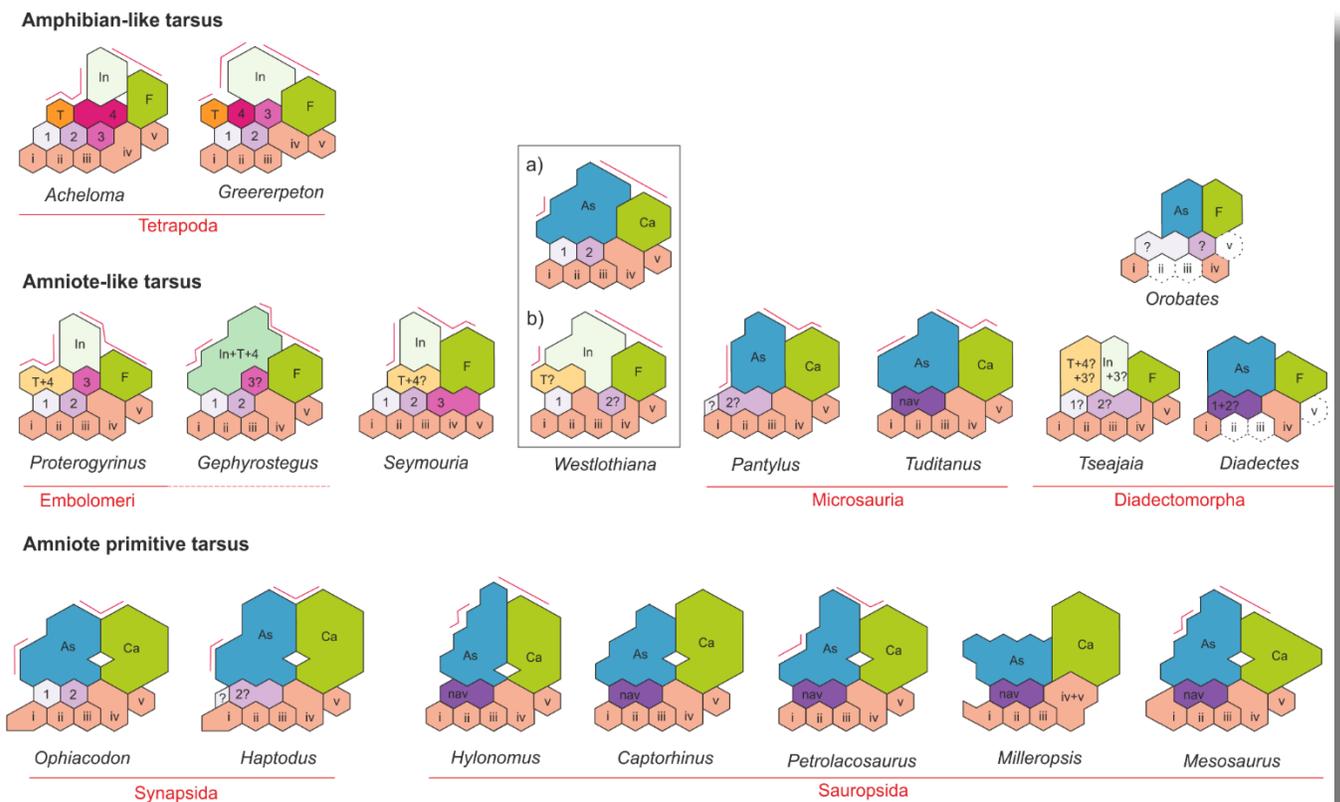


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1291 young individual, in dorsal, ventral and medial views respectively. The bone shows the
1292 typical square outline of immature individuals and the remains of sutures between the
1293 original anlagen more visible on its ventral surface, which appears to display a different
1294 morphology with respect to the dorsal one. Note that there are no traces of the ‘navicular’
1295 preserved along the distal surface of the astragalus, which bears a concave margin. B,
1296 GP-2E 5203, photograph and interpretive drawing of astragalus, calcaneum and incipient
1297 ‘navicular’ of a young individual in dorsal view. Recall on that the ‘navicular’ is already
1298 united to the astragalus by c2, being formed by c1 and c2 and the suture between them is
1299 still well visible. C, FC-DPV 1479, photographs and interpretive drawings of an isolated
1300 astragalus from an adult individual in dorsal, ventral and medial view. Observe that the
1301 ‘navicular’ is now a single bone almost completely fused to the astragalus to produce the
1302 finally resultant adult outline. C1 has transformed into a tip-like bone and remains
1303 separated from the astragalus, but it can just be seen from the ventral view, which still
1304 features different from the dorsal one. The wide and triangular facet for articulation with
1305 the tibia can be seen from the medial view. Anatomical abbreviations: a, astragalus; ca,
1306 calcaneum; c1, centrale one; c2, centrale two; ac3, ancestral centrale three; ft, facet for
1307 the articulation of the tibia; ai, ancestral intermedium; ate+ac4, ancestral tibiale plus
1308 ancestral central four. Scale bar: 5 mm.

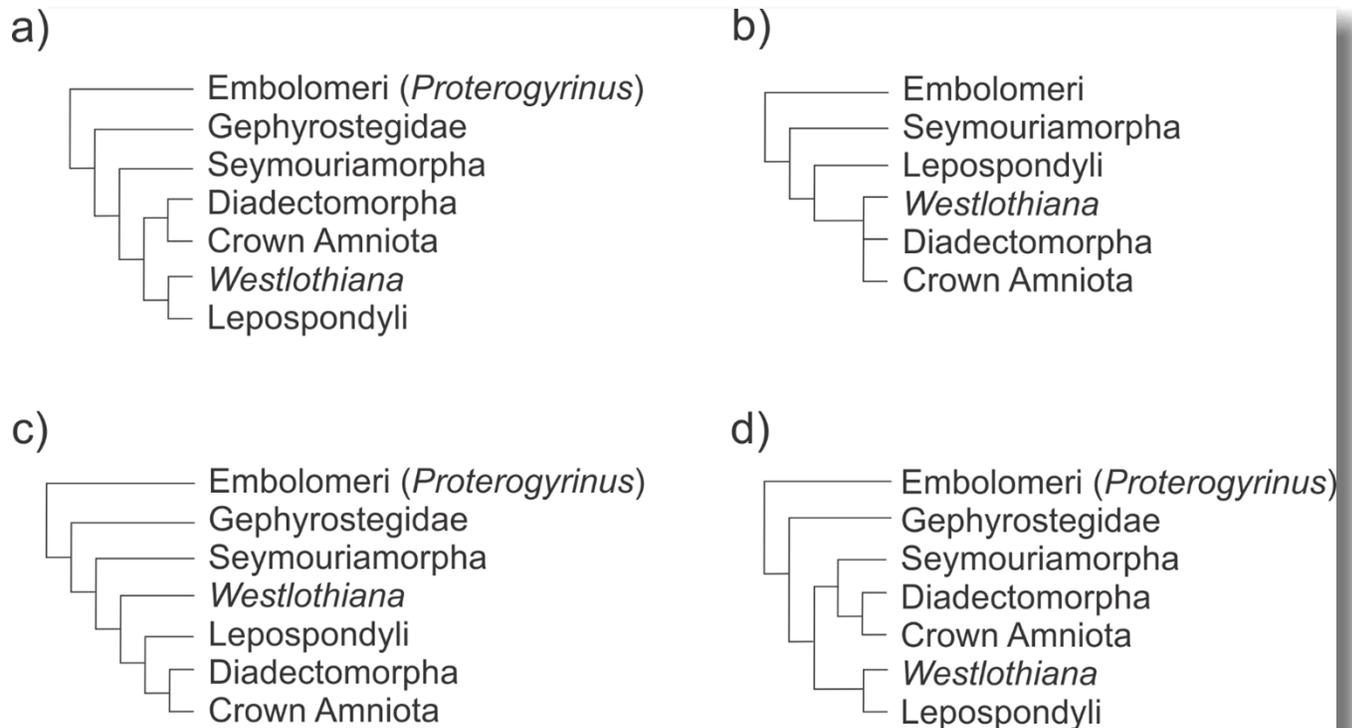


1310 Figure 9. Preserved tarsus in a *Mesosaurus tenuidens* non-hatched individual. A, FC.DPV 2504,
 1311 a non-hatched mesosaurid in the egg, showing the two feet overlapping each other by
 1312 compression. B, SEM image of the foot of FC-DPV 2504 focusing on the tarsal area. The
 1313 astragali can be seen in the center of the figure, mixed between the metatarsals. The
 1314 astragalus seems to be not preserved. C, Interpretive drawing of the tarsus including a
 1315 possible identification of the preserved bones by regarding previous hypotheses about the
 1316 origin of the amniotic astragalus. The composing elements of the astragalus were colored
 1317 to favour identification of the isolated bones of the left foot. Anatomical abbreviations: ?i,
 1318 possible intermedium; ?c3, possible central three; fi, fibula; mc, metacarpals; ?te+c4,
 1319 possible tibiale plus possible central four; t, tibia. Scale bar: 1mm.



1320

1321 Figure 10. Tarsus structure in basal tetrapods, including amniote and non-amniote taxa.
1322 Schematic diagram for comparing the tarsus structure in the basal tetrapods *Acheloma*
1323 and *Greererpeton* (amphibian-like tarsus) with regard to that of embolomeres and
1324 microsaur (amniote-like tarsus) and early amniotes. Note the similar structure and
1325 construction of the microsaur tarsus with respect to the early amniote *Hylonomus*. See
1326 text for more details of the evolutive significance of the selected taxa. Abbreviations: as,
1327 astragalus; i, intermedium; te, tibiale; 1,2,3,4, centralia; i,ii,iii,iv,v, distal tarsals. Taxa
1328 were redrawn from the following sources: *Acheloma* (Dilkes, 2015); *Greererpeton*
1329 (Godfrey, 1989); *Proterogyrinus* (Holmes, 1984); *Gephyrostegus* (Carroll, 1970);
1330 *Seymouria* (Berman et al., 2000); *Westlothiana* (Smithson 1989, Smithson et al.,1994);
1331 *Pantylus* (Carroll, 1968); *Tuditanus* (Carroll, 1968); Diadectomorphs (Moss, 1972;
1332 Berman & Henrici 2003;); *Ophiacodon* and *Haptodus* (Romer & Price, 1940);
1333 *Hylonomus* (Carroll, 1964); *Captorhinus* (Fox & Bowman, 1966); *Petrolacosaurus*
1334 (Peabody, 1952; Reisz, 1981).
1335



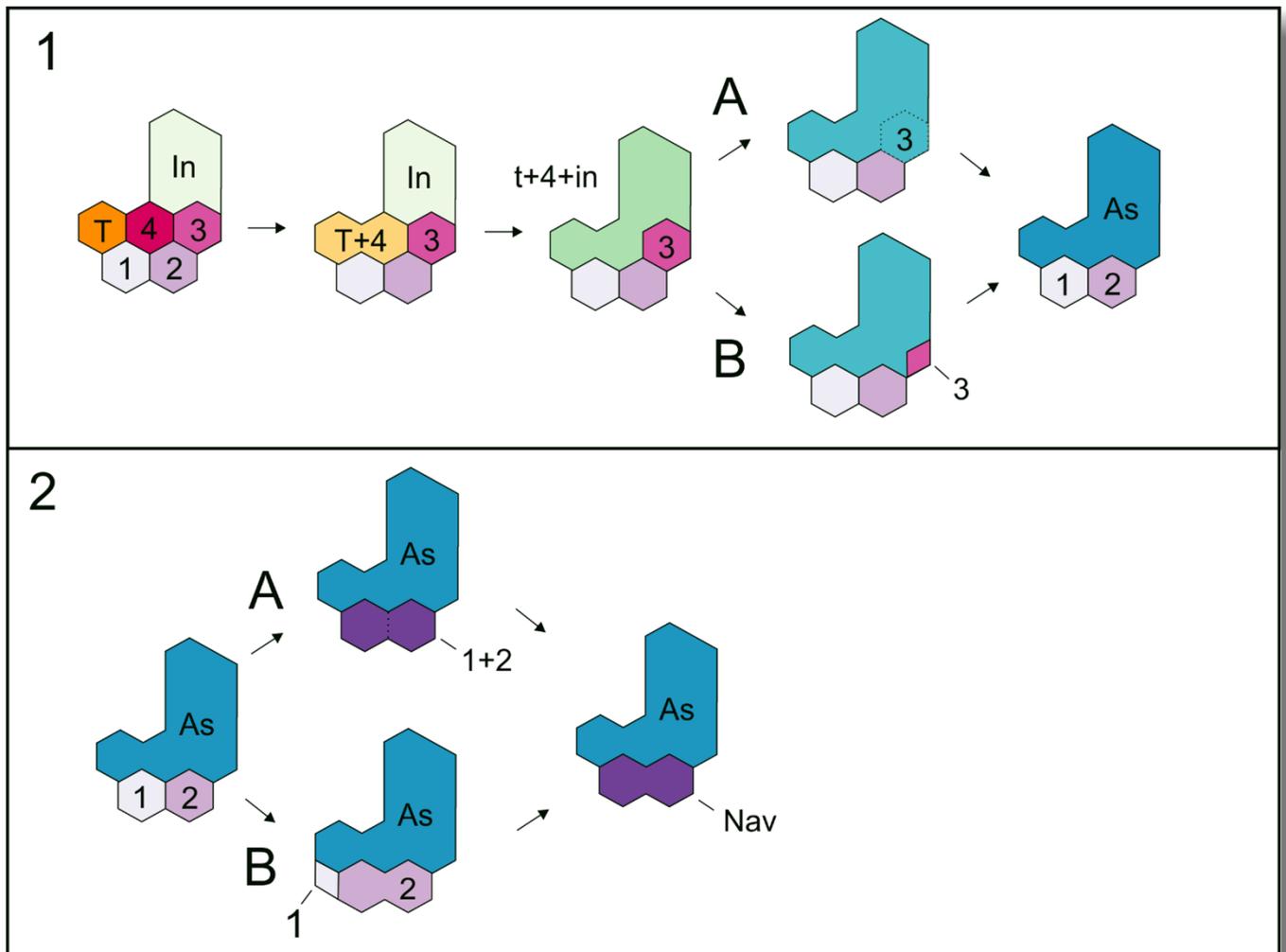
1336

1337 Figure 11. Schematic representation of recent phylogenetic hypotheses of early tetrapod

1338 relationships showing the position of the taxa involved in the evolutionary transition to

1339 the formation of the early amniotic astragalus (see text for the figure context). A. Ruta &

1340 Coates, 2007; B. Carroll, 1995; C. Laurin & Reisz, 1999; D. Marjanović & Laurin, 2015.



1341

1342 Figure 12. Hypotheses about the astragalus and the navicular formation. The schematic diagram
 1343 shows the steps that lead to the formation of the amniotic tarsus, regarding the series of
 1344 possible transformations that could have produced the primitive astragalus (A) as well as
 1345 those that prevailed into the evolution of the 'navicular' bone (B).

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1347