

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 microsaurs like *Tuditanus* 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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2 amniotic astragalus

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26 **INTRODUCTION**

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28 The origin of the astragalus and the calcaneum in the ankle of basal amniotes has been
29 considered as an adaptation to terrestrial locomotion and a key innovation in the origin of
30 Amniota (Romer, 1956). Taking into account the elements present in the tarsus of basal
31 tetrapods, it is clear that there was a strong reduction in the number of bones that form the
32 primitive amniotic tarsus. This reduction can be explained by the fusion or loss of some tarsal
33 bones in the ancestral amniotes despite the homology of these elements not always being well
34 established. According to previous contributions, it is widely acknowledged that the calcaneum
35 is derived from the fibulare, ie. from only one of the precursor bones present in the tarsus of non-
36 amniote tetrapods. However, the origin of the astragalus, as well as the identification of the
37 ancestral bones that give origin to it, are contentious (Peabody, 1951; Rieppel, 1993; Kissel,
38 Dilkes & Reisz, 2002; Berman & Henrici, 2003; O'Keefe et al., 2006; Meyer & Anderson,
39 2013). Some authors supported the classic hypothesis of a unitary origin for the astragalus, from
40 the intermedium (e.g. Romer or perhaps from the fusion of this bone to the tibiale (e.g.
41 Holmgren, 1933; Gegenbaur, 1864 in Schaeffer, 1941). However, Peabody, 1951, following
42 Holmgren (1933), suggested that the origin of the astragalus is produced by the fusion of three

43 bones; mainly the intermedium, one of the proximal centralia (c4) and perhaps, the tibiale
44 (Peabody, 1951, figure 2). A modification of this proposal, although supporting the composite
45 origin for the astragalus, was suggested by O'Keefe et al. (2006) by including also the third
46 centrale as a component of the fused element (four-center hypothesis). Indeed, there is evidence
47 of a fusion between the tibiale and the proximal centrale (c4) in *Gephyrostegus* (Schaeffer, 1941;
48 Holmes, 1984) which possesses an amniote-like tarsus (Carroll, 1970), thus, this fusion may
49 have occurred early in the evolution of the amniotic tarsus. Peabody's (1951) hypothesis was
50 subsequently refuted by Rieppel (1993) who stated, based on embryological evidence from
51 extant reptiles, that the reptilian astragalus is a neomorph. But Rieppel's (1993) suggestion was
52 not widely accepted and the hypothesis on the multipartite structure of the reptilian astragalus
53 remains plausible. Recent reports of well-preserved tarsi from apparently young individuals of
54 several captorhinid species (Kissel, Dilkes & Reisz, 2002; Berman & Henrici, 2003; O'Keefe et
55 al., 2005, 2006), which will be discussed later, demonstrate that the matter is still open.

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

62 Another characteristic of the primitive amniotic tarsus is the articulation of the proximal
63 tarsal elements (astragalus and calcaneum) with centralia 1 and 2, which are placed distally and
64 often fuse to each other (Peabody, 1951). The fused element (c1+c2), commonly named the
65 centrale or lateral centrale, has been suggested to form the navicular bone, characteristically

66 present in therapsid-grade synapsids and mammals (Broom, 1915; 1924, Jenkins, 1971).

67 Moreover, five distal tarsals are present, the first and the fourth commonly being the largest.

68 Here we investigate the origin and evolution of the amniotic astragalus by a thorough
69 study of several almost complete and some incomplete mesosaur skeletons and natural external
70 molds and casts, including well-preserved feet. Moreover, well preserved, isolated astragali and
71 calcanea of individuals in different ontogenetic stages, including the tarsus of one non-hatched
72 *Mesosaurus tenuidens* and hatchling individuals, were also analyzed for completing an
73 ontogenetic sequence previously unknown for any other Early Permian amniote. This amazing
74 record provides useful data for characterizing the tarsal structure in early and late juvenile stages,
75 and helps us to understand the transition towards the acquisition of the adult tarsal morphology.

76 We present a synoptic view of the evidence we found for homologizing the primitive amniotic
77 astragalus to the intermedium plus possibly the tibiale and proximal centralia, and propose that
78 the suturing of these elements occurred during the embryonic stage, producing a very specialized
79 single bone in the hatchlings. We also report the invariable presence of a navicular-like bone
80 (fusion of c1+c2?) in *Mesosaurus tenuidens* (*contra* Modesto, 1996a-b; 1999) and discuss the
81 possibility if this character is polymorphic for mesosaurs as observed in basal synapsids (Romer
82 & Price, 1940).

83

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

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89 **MATERIALS AND METHODS**

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

100

101 **Methods**

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

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108 *Distinction of juvenile from adult mesosaurs*

109 The recognition of young, immature individuals from adult, mature ones was not easy to
110 determine in mesosaurs. Modesto (1996a, 1999, 2006, 2010) made a detailed study of the
111 characters that can be used to recognize the three monospecific genera that compose the Family

112 Mesosauridae. He concluded that the main characters (e.g. tooth morphology, head-to-neck
113 ratios, presacral vertebral counts, presence/absence of pachyostotic ribs and hemal arches) used
114 for taxonomic purposes are valid to separate three monospecific mesosaurid taxa. Nevertheless,
115 Piñeiro (2002, 2004, 2008) revised some of the characters that have been previously used as
116 taxonomically diagnostic and found that they could instead be ontogenetic conditions
117 distinguishing alternatively immature and mature specimens or could even represent sexual
118 dimorphism. Reliable characters that can be useful to differentiate juvenile (immature) from
119 adult (mature) mesosaurid individuals can be derived from changes in the morphology and
120 structure of the coracoid and the scapula in the shoulder girdle and the pubis in the pelvic girdle
121 (Piñeiro, 2004). These bones are simple rounded plate-like structures in very young individuals,
122 only acquiring the suchlike shape in adults; the coracoid develops into a roughly rectangular
123 bone with anterior and medial convex margins (Modesto, 1996; Piñeiro, 2004). The coracoid
124 notch pierces the bone medially but is very poorly developed in young individuals. It becomes a
125 true coracoid foramen in adults, when both bones suture and eventually fuse to form the scapulo-
126 coracoid. These bones can fuse leaving no trace of any suture between them, even in apparently
127 young adults, or the suture may remain visible even in large, adult individuals (Piñeiro, 2002),
128 evidencing perhaps intraspecific or sexual variability (Piñeiro, 2004). Similar morphological
129 changes are seen in the pubis, from being a small, plate-like rounded bone to a more kidney-
130 shaped element that develops a pubic notch or a true obturator foramen totally enclosed by bone.
131 Other aspects of the skeleton morphology will be part of a forthcoming paper, and will not,
132 therefore, be discussed here. Even though the characters reviewed above are useful as
133 complementary data to help identify the development stage in mesosaurs, the presence of well
134 ossified carpal and tarsal bones was the most useful feature for considering maturity in

135 mesosaurs. We consider here that an individual is mature when in the tarsus, the astragalus and
136 the calcaneum approach each other and the foramen for the perforating artery appears between
137 them.

138 *Centralia and Navicular Nomenclature*

139 The c1 is often named as the lateral centrale and the c2 as the medial centrale. But, when
140 only one distal tarsal is seen (it could result from the fusion of c1+ c2 or it could be just the c2),
141 it is often identified as the centrale (e.g. Schaeffer, 1941, Currie, 1981, Lewis, 1964, Reisz &
142 Fröbisch, 2014), or as the distal centrale (e.g. Carroll, 1970) or as the lateral centrale (e.g.
143 Peabody, 1952, Modesto, 1999, Reiz & Dilkes, 2003), even though these bones are always
144 placed medially in the tarsus, or even as the navicular (Schaeffer, 1941). Similarly, the c4 is
145 called the proximal centrale (e.g. Kissel, Dilkes & Reisz, 2002; Berman & Henrici, 2003) or
146 posterior centrale (Olson 1964). On the other hand, there is no stable designation for the c3 and it
147 can be mistaken for the c4 when it is called the proximal centrale (Carroll, 1970; Holmgren,
148 1933) or even considered a distal centrale (Fröbisch, 2008; Hall, 2007). This lack of consensus in
149 the literature on how to refer to specific centralia increases the confusion about the establishment
150 of evolutionary patterns for the early amniotic tarsus. Therefore, we decided to establish a
151 naming criterion: we refer to the bone (or fused bones) placed distally to the astragalus in the
152 mesosaur tarsus as the ‘navicular’, and we use the name "proximal centrale" only when it cannot
153 be determined if it is the c4 or c3.

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155 **SYSTEMATIC PALAEONTOLOGY**

156 Amniota Haeckel, 1866

157 Proganosauria Baur, 1889

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Mesosauridae Baur, 1889

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Mesosaurus tenuidens Gervais, 1864—1865

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Figures 1—9

161

The mesosaurid tarsus (Figs. 1-9) displays a primitive construction regarding the

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structures observed in other basal amniotes as *Hylonomus lyelli*, *Paleothyris acadiana* and

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Petrolacosaurus kansensis (Carroll, 1964, 1969; Peabody, 1952; Reisz, 1981). It is essentially

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equivalent to the tarsus of basal synapsids (Romer & Price, 1940; Romer, 1956) and it even

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mirrors the structure described for some microsaurs, particularly *Tuditanus*, and *Pantylus*, the

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embolomere *Proterogyrinus*, *Westlothiana* and *Gephyrostegus* (Carroll, 1968; 1970; Carroll &

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Baird, 1968; Holmes, 1984; Smithson, 1989, although see also Smithson et al., 1994) (Fig. 10).

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Description. All specimens from Uruguay were collected either in bituminous or non-

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bituminous shale of the Early Permian (Artinskian) Mangrullo Formation (Piñeiro, 2004; Piñeiro

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et al., 2012a, b); all the material coming from Brazil was collected in the correlative Iratí

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Formation (Santos et al., 2006). Each of the constituent tarsal elements will be described for the

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specimens representing the transition regarding their ontogenetic stage and the morphological

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changes detected:

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1) FC-DPV 2504 (Figs. 1-2A, 9). An almost complete and well preserved non-hatched

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Mesosaurus tenuidens from Uruguay, which is curled as if within an egg (Piñeiro et al., 2012b).

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It consists of an external mould of a small, still poorly ossified skeleton that suffered strong

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dorsoventral compression during diagenesis. This is evidenced by the displacement of the ribs

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and feet which are overlapping each other, as well as by the reduced three-dimensionality

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(suggesting strong compression) of the delicate skeleton, which represents the smallest mesosaur

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

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

205 The distal tarsals are no visible in the specimen. They could be still unossified judging
206 from the fact that distal tarsals ossify later than metatarsals in amniotes and at least metatarsals
207 II, III, IV and V were partially, or possibly completely ossified in FC-DPV 2504, but no
208 metatarsal I, which is apparently absent (see Sheil & Portik, 2008 and references therein).
209 Otherwise (but very improbably) due to their very small size, they would not be visible if they
210 were displaced between the overlapping metatarsals.

211 2) GP-2E 272 (Figs. 1-3B). This specimen is a well preserved very young individual from Brazil.
212 The ribs are not as pachyostotic as can be observed in other immature specimens, but apart from
213 that condition, the specimen does not show relevant anatomical differences to *M. tenuidens*. The
214 silhouette of part of the body can be reconstructed due to the preservation of the skin. The
215 interdigital membrane that unites the toes to the claws can be delimited as well as the robustness
216 of the leg musculature, even in such a young individual. What could have been the plantar
217 aponeurosis covers most of the tarsal bones (Fig. 3B). However, two elements (maybe
218 mineralized cartilages) placed very close to the fibula are interpreted here as a possible astragalus
219 (the largest bone) and an incipient, smaller calcaneum, which was distally displaced. It is
220 difficult to believe that, covered by the, highly resistant plantar membrane, this tarsal bone can
221 appear as displaced from its original anatomical position. But considering that in very early
222 stages of development the astragalus and the calcaneum are the only bones ossified, we
223 hypothesize that the small size of the bone and gravity combined to move it distally after the
224 decay of flesh tissues started, particularly damaging the skin and muscle insertions. Otherwise,
225 the calcaneum is covered by the aponeurosis and it is not visible or it is a very small fragmentary

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

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

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

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

253 5) MN 4741 and SMF-R 4934 (Figs. 1-3E-F respectively) and SMF-R 4513 (Figs. 1-3G) from
254 Brazil are a little larger than the specimens previously described. Even though their similar still
255 small size, SMF-R 4513 is probably ontogenetically older judging for the tarsal features. We can
256 see for the first time the morphological differences between both the proximal tarsal bones in the
257 ontogenetic series, the astragalus being transformed into a more stylized and more easily
258 recognizable element (see for instance Fig. 3G). Astragalus and calcaneum are preserved close
259 to each other, and the foramen for the perforating artery is incipient but visible at approximately
260 the midpoint length between these bones (see SMF-R 4513, Figs. 1-3G). SMF-R 4513 (Figs. 1-
261 3G) is probably an adult or a subadult individual. There are three bones present; two proximal
262 tarsal elements are visible, the larger one being the astragalus which features a morphology
263 which is similar to those observed in more mature individuals (Fig.3). It is a stout bone tending
264 to reach the L-shaped outline characteristic of the basalmost amniotes and some other tetrapods
265 (see the distribution and schematic morphology of the tarsal bones in Fig. 10). The foramen for
266 the perforating artery is placed at the midlength of the lateral margin, and an intimate area of
267 contact is being generated between astragalus and calcaneum at this point (Fig 3G). A small
268 bone can be seen distal to the astragalus-calcaneum contact in SMF-R 4513, which is located
269 proximal to the distal tarsal elements, including probably the dt4. It could be the ‘navicular’
270 starting to ossify, which will be well developed later, in mature *Mesosaurus* specimens.

271 6) At later stages, these bones develop a short contact through the lateral margin of the astragalus
272 and the medial margin of the calcaneum (Figs. 4-6H to P), so, the remaining analysed specimens
273 (FC-DPV 2497, GP-2E 114, GP-2E 5610, SMF-R 4710, SMF-R 44 70, GP-2E 5816, GP-2E
274 6576, GP-2E 5740 and FC-DPV 2058 (see figures 4-6H-P) represent adult individuals. Most of
275 them possess the complete series of tarsal elements: astragalus, calcaneum and ‘navicular’, as
276 well as five distal tarsals, where the first and the fourth are often the largest, although this can be
277 very variable (Fig. 6).

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

283

284 RESULTS

285

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

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

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

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

327

328 **Limb ossification patterns**

329

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

340 the evidence provided by the non-hatched specimen, the mesosaurid tarsal ossification proceeds
341 in the following sequence: intermedium, tibiale+centrale 4 (and c3?, see Fig. 9 and O'Keefe et
342 al. 2006), calcaneum, distal tarsal four, the 'navicular' and the remaining bones (distal tarsals
343 3—1 and 5). The sequence of ossification of the distal tarsal bones is not clear, however.

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

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

361
362

363 **DISCUSSION**

364

365 **The astragalus during ontogeny**

366

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

369 The shape of the astragalus changes dramatically during ontogeny; mature individuals
370 show a stout, roughly squared bone with broad articulating facets for the crus (Fig. 8 A and C).

371 This bone also possesses a wide, shelf-like latero-distal facet for receiving the centrale or
372 ‘navicular’ (Figs. 6-7), which can be totally separated from the astragalus, or partially fused so
373 that the free, unfused part of the bone can only be seen on the ventral surface (Fig. 8).

374 However, the astragalus of immature mesosaurids is a delicate, roughly rounded or
375 maybe subquadrangular bone bearing an evident thick dorso-medial border which developed into
376 very well defined articulating areas during growth, producing a slightly excavated central area in
377 the dorsal margin for the fibula and a broad, medially placed almost sub-triangular surface for
378 the tibia. These thickened margins can be seen even in very small newborn individuals (see Fig.
379 1-3 C-G).

380 In his 1993 study, Rieppel stated that the mesosaurid astragalus does not show any
381 evidence of being a fusion of the plesiomorphically separated tarsal elements; to him all the
382 suture-like structures (e.g. delicate grooves or thickenings) seen on the ventral surface
383 correspond to attachments of muscles and tendons, and the medial groove delimits the passage
384 of the perforating artery. Even though the mesosaur astragalus of post-hatching stages does not
385 show the tripartite structure described in *Captorhinus* (Peabody, 1951; Fox & Bowman, 1966;
386 Kissel, Dilkes & Reisz, 2002 and references therein), it seems to have been derived from the

387 junction of at least three bones, as we can deduce from the tarsus of the non-hatched mesosaurid
388 (Fig. 9) where we interpret although with doubts, that the incipient astragalus is the only bone in
389 the tarsus, showing suturing for the intermedium, the tibiale and maybe both the proximal
390 centralia (c4+c3). Actually, some of the original joints remained in some specimens, but they
391 show a slightly different pattern from that described by Peabody (1951) because the mediolateral
392 Y-shaped suture for intermedium, c4 and c3 is not as evident in the studied specimens (see
393 figures 3, 6, 8).

394

395 **The mesosaur ‘navicular’**

396

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

406 The presence of the ‘navicular’ in *Mesosaurus* is a novel characteristic, as all but one
407 (Modesto, 1996a, b; 1999) of the previous workers did not mention its presence in descriptions
408 of the mesosaurid tarsus. Indeed, Modesto (1996a,b) described the presence of a lateral centrale
409 only in *Stereosternum* and stated that this bone is never present in *Mesosaurus*. We have enough

410 evidence to confirm that a transversely elongated bone is invariably present distal to the
411 astragalus in all the analysed mature specimens—most frequently representing two sutured
412 bones—identified as the centralia c1 and c2 present in “pelycosaurs” and other basal amniotes.
413 As these bones suture to the astragalus in very mature individuals, as also seems to occur in
414 *Captorhinus aguti* (Peabody, 1951), it becomes difficult to identify its presence in the tarsus, as
415 probably occurred with the specimens studied by Modesto (1996,1999) assigned to *Mesosaurus*
416 *tenuidens*. We first become aware of the presence of a ‘navicular’ in *Mesosaurus* from an
417 isolated, relatively large astragalus where the fusion of c1 and c2 has not yet been completed (see
418 Fig. 8 for more detail of this condition). It firstly appears as two sutured (but not fused) bones
419 (Figs. 4 and 6 H-I), and there seems to be a reduction in the size of c1, which becomes a pointed
420 medial tip that is not preserved in most individuals because of the fragility of its suture to c2 (see
421 Figs. 3G; 8B-C). As a result, in *Mesosaurus*, the ‘navicular’ strongly abuts the platform-like
422 facet on the distal margin of the astragalus (Figs. 6P, 8).

423 This variable condition concerning the fusion of centralia 1 and 2 recalls that observed in
424 ‘pelycosaurs’, in which some species show the centralia 1 and 2 as separate bones (e.g.
425 *Ophiacodon*), while others show them fused (e.g. *Haptodus*) (Romer & Price, 1940) (Fig. 10). It
426 is likely that this is an ontogenetic, perhaps heterochronic condition in mesosaurs (L. Gaetano
427 and D. Marjanović, personal communication), but this needs to be tested by analysis of more
428 than one individual of the same species at different stages of development. For instance, the
429 morphology of the c1 in mesosaurids is very similar to that of the putative medial centrale of
430 *Sphenacodon ferox* (according to Henrici et al., 2005), and if it is repositioned medially to the
431 lateral central we can obtain a navicular-like bone in *Sphenacodon*. Thus, the small size of the
432 tarsal bones of early amniotes and the possibility that they can be displaced from their original

433 positions, plus to the fact that the recognition of homologous bones seems to be a difficult
434 endeavor, make it likely that the real nature of the tarsus structure in several taxa could remain
435 obscure. Mesosaurs may provide a good opportunity to revisit and gain a better understanding of
436 the processes that are involved in the origin and early evolution of the amniotic tarsus.

437

438 **Morphological changes supporting an evolutionary transition in the origin of the amniote**
439 **tarsus**

440

441 Although most previous workers (e.g. Carroll, 1964; Berman & Henrici, 2003; O'Keefe
442 et al., 2006; Meyer & Anderson, 2013, and references therein) accepted the composite origin of
443 the astragalus following the contribution of Peabody in 1951, the reappraisal of that condition
444 and its significance performed by Rieppel in 1993 introduced controversy. This last author
445 rejected the multipartite origin of the astragalus, arguing that there was a lack of unequivocal
446 ontogenetic evidence that would show that the bones which would form the composite astragalus
447 are present in at least some stage of development. He rejected the proposed composite origin of
448 the astragalus by Peabody (1951) mainly based on the fact that this bone derives from a single
449 ossification center in extant reptiles and that, according to Sewertzoff (1908), lizards have just a
450 single block of cartilage close to the distal end of the fibula and tibia where the astragalus and the
451 calcaneum later ossifies. In *Sphenodon punctatus*, the astragalus originates by the condensation
452 of more than one chondrogenic element, but they fuse during the embryonic stage (Rieppel,
453 1993). Moreover, the presence of more than one cartilage condensation, apparently homologous
454 with the ancestral tetrapod tarsals, has been recently described to be present during early
455 embryonic stages in the development of six different orders of modern birds (Ossa Fuentes,

456 Mpodozis & Vargas, 2015) and also in chameleons (Diaz & Trainor, 2015). Even though we
457 consider that a comparison with animals that possess an extreme adaptation to flying and
458 perching and that are temporally and phylogenetically so distant from the taxa included in this
459 study, is not appropriate, we will discuss on this subject later.

460 Indeed, there are several known examples of tetrapods, possibly stem amniotes, that
461 allow us to deduce the steps of fusion of the tarsal bones leading to the attainment of the amniote
462 condition. Thus, it is possible that, as the embryology of extant lizards suggests, the fusion of
463 these elements in the development of the amniote ankle is produced in the embryonic stage and
464 so, it is not possible to address their original ossification centers any more (Gauthier et al., 1988).
465 Rieppel (1993) observed that associations of tarsal bones are common in amphibians and that,
466 while centralia 1 and 2 can be fused or separated, c3 and c4 may be fused, or rather, one of them
467 can be lost. Thus, according to Rieppel (1993) the association between the tibiale and c4 may be
468 casual and may not represent a condition of phylogenetic relevance. However, we can see a real
469 transition from closely related, supposedly non amniote taxa (e.g. *Gephyrostegus*, *Westlothiana*,
470 *Tuditanus*, *Pantylus* (see Ruta, Coates & Quicke, 2003 and Marjanović & Laurin, 2015, for the
471 phylogenetic position of these taxa), to the acquisition of the primitive amniotic tarsal
472 configuration (see figure 10). Thus, if we consider the association of the tibiale and c4 observed
473 in some *Proterogyrinus* specimens (Holmes, 1984) and possibly present in the tarsus of the non-
474 hatched mesosaurid (see Fig. 9) as the first step towards the development of the amniotic tarsus
475 (Holmes, 1984), we can reconstruct the succession including *Gephyrostegus* (see Carroll, 1970
476 as a reference of the tarsal structure in this last taxon) where the tibiale+c4 (and c3?, see O'Keefe
477 et al., 2006) complex is associated with the intermedium to form the composite amniotic
478 astragalus, a configuration that is also present in some microsaurs (e.g. *Tuditanus punctulatus*,

479 Carroll & Baird, 1972; Carroll & Gaskill, 1978 and *Pantylus cordatus*, Carroll, 1968) and
480 possibly in *Westlothiana* (Smithson, 1989 but see Smithson et al. 1994). Within that
481 transformation, the fibulare becomes the calcaneum and c1 and c2 remain as the only centralia
482 present, either as separated bones or fused to form a single element, the ‘navicular’.

483

484 *Phylogenetic context supporting the evolutionary transition*

485

486 On a phylogenetic point of view, even considering that there is not complete consensus
487 about the relationships of the taxa involved in the transition, their relationships seem to be
488 supported by the most recent cladistics analyses of basal tetrapods: Ruta, Coates & Quicke,
489 2003; Vallin & Laurin, 2004; Klembara, 2005; Ruta & Coates, 2007; Marjanović & Laurin,
490 2009, 2015 (see Fig. 11). These phylogenies show *Proterogyrinus* as an embolomere
491 anthracosaur, although the relationships of this taxon are contentious and were not completely
492 resolved (see Ruta, Coates & Quicke, 2003). *Gephyrostegus* is very close to Seymouriamorpha
493 and to microsaurs, a hypothesis supported by the Laurin & Reisz (1997) tree, which also argues
494 that lepospondyls are a monophyletic group closely related to amniotes (see also Marjanović &
495 Laurin, 2015). Otherwise, if microsaurs are paraphyletic to other lepospondyls and to the
496 amniote stem, as other workers suggest (Olori, 2015), they could have been the last phylogenetic
497 intermediaries in our evolutionary transformation series.

498 It is noteworthy that some taxa which are not classified as amniotes have an amniote-like
499 tarsus or at least developed the large proximal tarsal bones that characterize the amniotic tarsus,
500 the astragalus and the calcaneum (Fig. 10). Notable examples of this feature are the diadectids
501 earlier analysed (Romer & Byrne, 1931; Romer, 1944), although adults show a somewhat

502 autapomorphic condition of a fusion between both the proximal bones to produce an
503 astragalocalcaneum bone. Within lepospondyls, the microsaurs *Pantylus* (Carroll, 1968) and
504 *Tuditanus punctulatus* have intriguingly, an amniote-like tarsus (Carroll & Baird, 1972).
505 Moreover, the proterogyrinid *Proterogyrinus scheelei*, *Gephyrostegus boemicus* and probably
506 *Westlothiana lizziae* also have an amniote-like tarsus (see Carroll, 1970; Holmes, 1984;
507 Smithson, 1989). Because mesosaurids are very basal amniotes (Laurin & Reisz, 1995; Piñeiro et
508 al., 2012b) or basal parareptiles (Modesto, 1996 a-b; Modesto, 1999; Piñeiro, 2004) we explored
509 these taxa in order to find homologies between putative plesiomorphic, non-amniotic tarsi and
510 their corresponding structure in mesosaurids according to the different ontogenetic stages
511 described for the group.

512

513 *The status of Westlothiana and microsaurs and its role in the transition*

514

515 Regarding the condition in *Westlothiana*, Smithson (1989), reconstructed the tarsus as
516 very amniote-like, including within it nine bones (see Smithson, 1989, figure 2d). There were
517 certainly nine bones in the preserved material although they were not preserved in their original
518 anatomical position. But, later, (Smithson et al., 1994) pointed out that, the tarsus of
519 *Westlothiana* is indeed very plesiomorphic (or amphibian-like) because it included ten, rather
520 than nine bones (see figure 20A in Smithson et al., 1994). We do not find enough evidence to
521 refute the former reconstruction or for validate the latter, thus, a proposal about the tarsus
522 structure in *Westlothiana* would be very speculative at this stage. Moreover, the renaming of the
523 two large, proximally placed bones originally described as the astragalus and the calcaneum as
524 an intermedium and a fibulare, thereby introducing the presence of a putative fibulare bone, is

525 also speculative because this last bone is difficult to identify from the preserved specimen, where
526 the foot bones are mostly disarticulated and obscured by the caudal vertebrae (Smithson et al.,
527 1994). Besides, according to these authors, the putative intermedium is L-shaped, a characteristic
528 very frequently found in the astragalus of early amniotes. Despite *Westlothiana* possessing other
529 advanced conditions that may suggest its relation to the amniote clade, it also retains some
530 plesiomorphic features in the skeleton such as a prefrontal-postfrontal contact, excluding the
531 frontal from the orbital margin (Smithson, 1989). Thus, the reconstruction of the real structure of
532 the tarsus in *Westlothiana* may be crucial to an understanding of the evolutionary transition to
533 the origin of the amniotic astragalus as we have figured it out in this contribution. We hope that
534 our paper will encourage new studies on this taxon.

535 Concerning microsaurs, these ecologically diverse, small-bodied tetrapods are credible
536 candidates for being part of the stem leading to the emergence of the earliest amniotes. They
537 develop a tarsus with a very amniote-like morphology, and as was recently demonstrated they
538 even show a similar ossification pattern, with the intermedium (?astragalus) and the fibulare
539 (?calcaneum) being the first tarsal bones to ossify (see Olori, 2015). They are also the only
540 proximal elements in the tarsus as in all amniotes, and naming them as intermedium and fibulare
541 is just arbitrary at this stage, if we have no embryological information to prove their identity. We
542 have to take into account that in mesosaurids the astragalus and the calcaneum are the only
543 proximal tarsal bones in born individuals, despite the former deriving from the fusion of three or
544 four bones.

545

546 *Diadectids*

547

548 Diadectids were recently considered to be amniotes (Berman, 2000), and as such, they
549 would have had an amniote tarsus. Recent discoveries of possible juvenile diadectid tarsi
550 including a putative composite astragalus formed by the intermedium, the tibiale and the
551 proximal centrale (c4, as it was identified) introduced interesting new data to the origin of the
552 amniotic astragalus (Berman & Henrici, 2003). Later, this material was assigned to the species
553 *Orobates pabsti*, a diadectid (Berman et al., 2004). Nevertheless, the holotype specimen of
554 *Orobates* described by Berman & Henrici (2003) and Berman et al. (2004: 29) as having a
555 tripartite astragalus (MNG 10181) was recently subjected to an in-deep study using micro-focus
556 computed tomography scans (Nyakatura et al., 2015), which allowed for a thoughtful anatomical
557 understanding of the specimen. The scanned image and digital reconstruction show that there are
558 seven separated bones in the tarsus of *Orobates*, which morphology suggests could be
559 homologized with immature astragalus and calcaneum plus two centralia (c1+c2) and three small
560 distal tarsals. Indeed, despite the very good preservation of the individual, it was apparently
561 subjected to severe diagenetic distortion; the bones were embedded in a crystalline calcite matrix
562 and there was a significant chemical substitution around their margins (cf. Nyakatura et al.,
563 2015). That taphonomic feature could have produced a configuration that, under direct
564 examination, led to the interpretation of Berman & Henrici (2003) about the presence of a
565 composite astragalus in *Orobates*.

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

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

582 Some groups like diadectids and seymouriamorphs for instance, show a high plasticity in
583 producing different patterns often correlated to a different expression of otherwise highly
584 conserved regulatory genes (Shubin, 2002). Therefore, the expression of these genes and the
585 consecutive structure of the tarsus may be regulated by the different ecological pressures to what
586 some have to adapt along the different stages of their development. Juvenile or young adult
587 *Diadectes* show a conservative tarsus, and distinct astragalus and calcaneum were described as
588 being present (Romer & Byrne, 1931; Romer, 1944; Berman & Henrici, 2003). However,
589 astragalocalcaneum fusion is shown to occur in very large and mature individuals, where it
590 would seem that the movement between these bones becomes very limited or null (Romer,
591 1944).

592

593 *Hylonomus lyelli*

594

595 Revising the evidence from other basal amniotes such as *Hylonomus lyelli* (Carroll, 1964;
596 Meyer & Anderson, 2013) we found some inconsistencies related to the identification of the
597 bones figured, perhaps as an attempt to follow the Peabody's (1951) suggestion of a tripartite
598 origin of the astragalus. Thus, Meyer & Anderson (2013), following Carroll (1964, fig. 1),
599 identified the astragalus and calcaneum from a partially disarticulated specimen where the feet
600 are completely disassociated and considered the calcaneum of *Hylonomus* as two times larger
601 than the astragalus. According to the information found in Carroll (1964, p. 72, fig. 8) and based
602 on the ontogenetic succession that we described here for mesosaurs, the calcaneum can
603 sometimes be equal in size to the astragalus or even a little larger, but never that much larger.
604 Thus, we could deduce both that it is an incomplete astragalus missing the intermedium, as
605 Meyer & Anderson proposed in the text and in figure 3 (but this would suggest that the type
606 specimen of *Hylonomus lyelli* belonged to a very young individual and it does not appear to be
607 the case, see figure 1 of Carroll, 1964), or that the bone identified as the calcaneum is the
608 astragalus or that the bone is neither the astragalus nor the calcaneum. We are inclined to accept
609 the last hypothesis because the overall small size of the individual suggests that these bones are
610 much too large to be tarsal bones; they seem to be elements of the pelvic girdle, possibly the
611 pubis (see figure 1 of Carroll, 1964). The well identified astragalus of *Hylonomus lyelli* (see
612 figure 8 of Carroll, 1964) does not show any trace of sutures.

613

614 *Captorhinids*

615

616 Taking into account the previous evolutionary transition in favor of a composite origin of
617 the amniotic astragalus, which of course may also include other taxa, the interpretation of
618 Peabody (1951) and later workers of the presence of more than one ossification center in the
619 astragalus of *Captorhinus* and other basal amniotes seems sensible. However, other extensive
620 descriptions of *Captorhinus* (e.g. Fox & Bowman, 1966) do not provide more conclusive
621 evidence about the structure of the tarsus and, as Rieppel (1993) claimed, it is necessary to have
622 ontogenetic evidence (e.g. articulated skeletons of very young individuals of *Captorhinus* and/or
623 of related taxa) to demonstrate the homology of the bones composing the tripartite astragalus and
624 their presence in the earliest stages of development. Isolated astragali from the Lower Permian of
625 Oklahoma were described by Kissel, Dilkes & Reisz (2002) as belonging to *Captorhinus*
626 *magnus*, showing the putative tripartite structure visible only from the dorsal surface of the
627 bones. However, this feature was discussed by Rieppel (1993) who argued that the putative
628 unclosed sutures should be interpreted as areas of muscular attachment, or grooves for blood
629 vessel irrigation, or fractures.

630 Concerning *Captorhinus*, most of the isolated astragali figured by Peabody (1951) clearly
631 belong to mature animals, according to their size and structure (see Fox and Bowman, 1966, for
632 comparison); the smallest one already shows the same morphology seen in the larger ones. If the
633 astragali shown by Peabody (1951) partially represent an ontogenetic transformation series, they
634 cannot confidently demonstrate that the apparent tripartite structure is derived from the fusion of
635 three or four of the plesiomorphic tarsal bones. A feature that could not support the hypothesis of
636 the tripartite structure is that the sutural lines and groove patterns present in *Captorhinus* as
637 described by Peabody (1951) are only visible on the ventral surface of the bone; alternatively, it
638 suggests that the fusion started on the dorsal surface and was not completed in adult individuals.

639 The same condition can be observed in the large captorhinid *Captorhinus magnus* (Kissel, Dilkes
640 & Reisz, 2002).

641 Fragmentary pedes referred to juvenile and adult individuals of the giant, largest known
642 captorhinid *Moradisaurus grandis* from the Upper Permian of Niger, were figured and described
643 by O'Keefe et al. (2005, 2006). Even though the bones were found in association and it was
644 possible to recognize the identity of some of them, they represent isolated and disarticulated
645 pedes whose referral to *Moradisaurus* can be possible but not accurate, at least no more, than to
646 any other basal tetrapod of the same size. Nevertheless, based on the pes assigned to a juvenile
647 captorhinid, O'Keefe et al. (2006) suggested that the c3 is also a component of the multipartite
648 amniote astragalus, occupying its latero-distal corner. However, the individualization of the
649 constituent bones of the juvenile tarsus and all the possible arrangements show that there is a
650 bone, dorsal to the intermedium that does not belong to the tarsus, unless it is part of the
651 intermedium yet not totally ossified because the juvenile condition of the specimen. But, that
652 bone is the only that is totally isolated from the rest of the tarsus, which excepting the four distal
653 tarsals, appears as a co-ossified structure.

654 Even though our reconstruction of the non-hatched *Mesosaurus* tarsus is consistent with
655 the O'Keefe et al. (2006) reconstruction of the *Moradisaurus* tarsus in the fact that the c3 may be
656 part of the astragalus, the arrangement of the bones seems to have been very different in both
657 taxa. Moreover, the putative calcaneum has a very developed notch for the perforating artery,
658 which does not match with the condition in the astragalus, including the evident individualization
659 of the constituent bones. It is also difficult to include the O'Keefe et al. (2006) specimen because
660 their reconstruction does not show an evident fusion between the tibiale and the c4, and because
661 it is a unique, isolated, putatively juvenile pes of *Moradisaurus*, where the identity of the bones

662 is highly subjective. The other fragmentary pes, interpreted to pertain to an adult specimen
663 displays the typical amniotic tarsal structure and the astragalus shows no sign of the composite
664 origin.

665

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

668

669 In 1941, Friedrich von Huene proposed for the first time a phylogenetic relationship
670 between *Mesosaurus* and some basal ‘pelycosaurs’. That suggestion was not generally
671 acknowledged by later authors who developed the currently accepted hypothesis that
672 mesosaurids are the basalmost sauropsids (Laurin & Reisz, 1995) or the basalmost parareptiles
673 (Modesto, 1999). More recently, Piñeiro (2004) found some evidence that she understood gave
674 support to von Huene’s hypothesis (1941) but acknowledged that it should be tested in a
675 phylogenetic context. Moreover, the nature of the mesosaurid skull, long discussed during more
676 than a hundred years, has been recently reassessed to show the presence of a synapsid-like lower
677 temporal fenestra in *Mesosaurus tenuidens* (Piñeiro et al., 2012c). This contribution gave credit
678 to the observations made by von Huene (1941) about the morphology of the mesosaur skull.
679 Similarly, the tarsus of mesosaurs has been studied by several authors, and here we have
680 demonstrated that its structure is almost identical to that described for basal synapsids, but also it
681 is equivalent to that of basal sauropsids, including one of the basalmost diapsid *Petrolacosaurus*
682 *kansensis* (Reisz, 1981).

683 Basal synapsids show a greater development of the calcaneum (Romer & Price, 1940),
684 which in some taxa roughly acquires the size of the astragalus. In contrast to this, the calcaneum

685 of *Mesosaurus* is smaller than the astragalus (although the size differences are less significant in
686 adult individuals), and develops a lateral expansion in the area of the heel, possibly for insertion
687 of extensor tendons including the Achilles tendon (Fig. 7).

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

694

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

696

697 The morphological ontogenetic transformation presented here for *Mesosaurus tenuidens*
698 is the most complete known for a basal amniote (cf. Laurin & Reisz, 1995) and as such, it
699 constitutes a relevant database for studies of a different nature. The information provided for this
700 data base on the origin of the amniotic tarsus suggests that, as Peabody (1951) and previous
701 authors (e.g. Holmgren, 1933) have stated, the earliest astragalus originated from at least four
702 ossification centers (taking into account that the tibiale and c4 fuse together early in the
703 ontogeny), near the tibial and fibular distal margins. More than one ossification center appears to
704 be present at the early embryonic stages of some extant groups (cf. Ossa-Fuentes, Mpodozis &
705 Vargas, 2015; Diaz & Trainor, 2015) but their homology to the earliest amniote condition is
706 difficult to establish, as the pattern is observed in very specialized groups such as birds and
707 chameleons. Indeed, in the above mentioned papers, (Ossa-Fuentes, Mpodozis & Vargas, 2015;

708 Diaz & Trainor, 2015) it is suggested that the intermedium and the tibiale (although the latter is
709 not pretty much apparent from the figures provided by Diaz & Trainor, 2015) appear as
710 independent ossifications at very early stages of the development. On the other hand, Ossa-
711 Fuentes, Mpodozis & Vargas (2015) observed that in the six groups that they studied, in contrast
712 to the most common condition in birds (i+fe), the intermedium forms a separate ossification
713 center that later fuses to the ‘astragalus’ (sic) forming the ascending process characteristic of
714 dinosauromorphs. Thus, the ‘astragalus’ should be the tibiale? Moreover, the pattern of
715 ossification that Ossa-Fuentes, Mpodozis & Vargas (2015) suggest, where the fibulare is the first
716 to ossify, followed by the putative intermedium and later by the tibiale, is very different to that
717 currently accepted to occur in basal amniotes.

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

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

731 According to our observations of the non-hatched *Mesosaurus tenuidens* which possesses
732 an astragalus formed by at least four bones, we can say that the mesosaurid astragalus is not a
733 neomorphic as Rieppel (1993) has suggested, unless we consider that once united in the earliest
734 stages of the development, these bones form a new element. Even the evidence taken from taxa
735 such as the embolomere *Proterogyrinus scheelei* Romer, 1970 can provide support for the
736 multipartite hypothesis and the identification of the bones provided in the present work (Holmes,
737 1984).

738 We made several interesting observations that support the already established homologies
739 and possible evolutionary paths towards the origin of the primitive amniotic astragalus.
740 Particularly in *Proterogyrinus* the intermedium has a very similar structure to that of the
741 astragalus of young mature mesosaurs, and the tibiale is clearly sutured against the medial corner
742 formed by c4 and the intermedium. The fibulare is also very similar to the calcaneum of the same
743 stage (see Figs. 1-6), so it is logical to presume that these bones are homologous, as already
744 stated. The main question is what happens to the remaining bones to obtain the mesosaurid (=
745 basal amniote) tarsus consisting of two large proximal elements plus one or two centralia and
746 five distal tarsals. We find evidence for the presence of c3 early in the ontogeny (Fig. 9); it is
747 possible that it fuses to c4 in the described mesosaur ontogenetic transformation after the c4
748 fuses to the tibiale. Indeed, based on the structure shown by *Proterogyrinus* (Holmes, 1984),
749 where apparently the tibiale fuses to c4, and taking into account that shown by the tarsus in the
750 captorhinomorph *Labidosaurus* (Williston, 1917) where the intermedium and the tibiale also fuse
751 to c4, we hypothesized three possibilities or combinations: A, the astragalus is just formed by the
752 intermedium+tibiale only, and c4 and c3 undergo a reduction in size until they finally disappear
753 (not plausible, given the probable presence of c4 and c3 in the tarsus of the non-hatched

754 mesosaurid); B, the astragalus is formed by intermedium+tibiale+c4, and c3 is reduced to be lost
755 (not probable given its putative presence in the tarsus of the non-hatched mesosaurid and taking
756 into account the proposal by O'Keefe et al., 2006); C, the astragalus results from the fusion of all
757 bones, i+te+c4+c3 (Figs. 9 and 12A). The last possibility (C) seems to be supported by the
758 materials that we described here, and is consistent with that suggested by O'Keefe et al., 2006,
759 who provided evidence for the inclusion of c3). It does not imply the loss of bones but a re-
760 patterning to produce the amniotic tarsus. Moreover, there are also two possibilities for the
761 formation of the 'navicular': 1, it results from fusion of c1 and c2; 2, it is formed by the c2 after
762 the reduction and loss of c1 (see Fig. 12B). We found probable evidence of some of these fusions
763 (the tibiale+?c4+ intermedium, c1+c2) in early stages of *Mesosaurus tenuidens*'s development,
764 but not in all individuals.

765 If the hypotheses of the astragalus and the 'navicular' formation are combined, we can
766 have the following six possibilities: A-1; A-2; B-1; B-2; C-1; C-2, but the evidence from
767 mesosaurs might support just C-1.

768

769 CONCLUSIONS

770

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

777 The mesosaur tarsus includes 8 or 9 bones: astragalus and calcaneum plus centralia 1 and
778 2 (fused to form the mesosaur ‘navicular’) and five distal tarsals. The ‘navicular’ is proved to be
779 present in all subadult and adult mesosaurs, even in *Mesosaurus* where it fuses to the astragalus
780 in mature individuals. The early amniote astragalus is a composite bone as can be evidenced by
781 the presence of at most three sutured bones in the tarsus of a non-hatched mesosaurid in an
782 advanced stage of development. These bones seem to be the intermedium and the tibiale, and the
783 later fused to c4; and the c3. Thus, our study rejects the hypothesis that the amniotic astragalus is
784 neomorphic.

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

790 Current morphological and comparative studies on the mesosaurid skeleton suggest other
791 interesting similarities between mesosaurids and basal synapsids that will be properly described
792 in a forthcoming paper. However, these features are also shared with other basal sauropsids and
793 taxa that are not even amniotes. For instance, mesosaurs share characters with taxa previously
794 known to be closer to Amniota (Panchen & Smithson, 1988; but see also Smithson et al., 1994)
795 but these hypotheses were not phylogenetically evaluated. These taxa are now considered as
796 stem or crown-tetrapods (Olori, 2015; Marjanović & Laurin, 2015) or their affinities are not yet
797 well defined (e.g. *Westlothiana*), but they still remain close to the earliest amniotes. This
798 commonly shared morphology among apparently unrelated but very basal taxa reflects the
799 primitive nature of mesosaurids, as already noted by Huene (1941) and other paleontologists.

800 The example of the similar tarsal structure observed in mesosaurids, some microsaurs, basal
801 synapsids and non-amniote tetrapods suggests that the evolution of the astragalus and calcaneum
802 as the most typical bones in the amniotic tarsus could be an acquisition obtained much earlier
803 than when the first recognized amniote appeared and walked on the planet.

804

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822

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1048 **Figure captions**

1049

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1102 perforating artery. Notable is the variation in size and shape of the distal tarsals observed
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1114 morphology with respect to the dorsal one. Note that there are no traces of the ‘navicular’

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1116 GP-2E 5203, photograph and interpretive drawing of astragalus, calcaneum and incipient
1117 ‘navicular’ of a young individual in dorsal view. Recall on that the ‘navicular’ is already
1118 united to the astragalus by c2, being formed by c1 and c2 and the suture between them is
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1120 astragalus from an adult individual in dorsal, ventral and medial view. Observe that the
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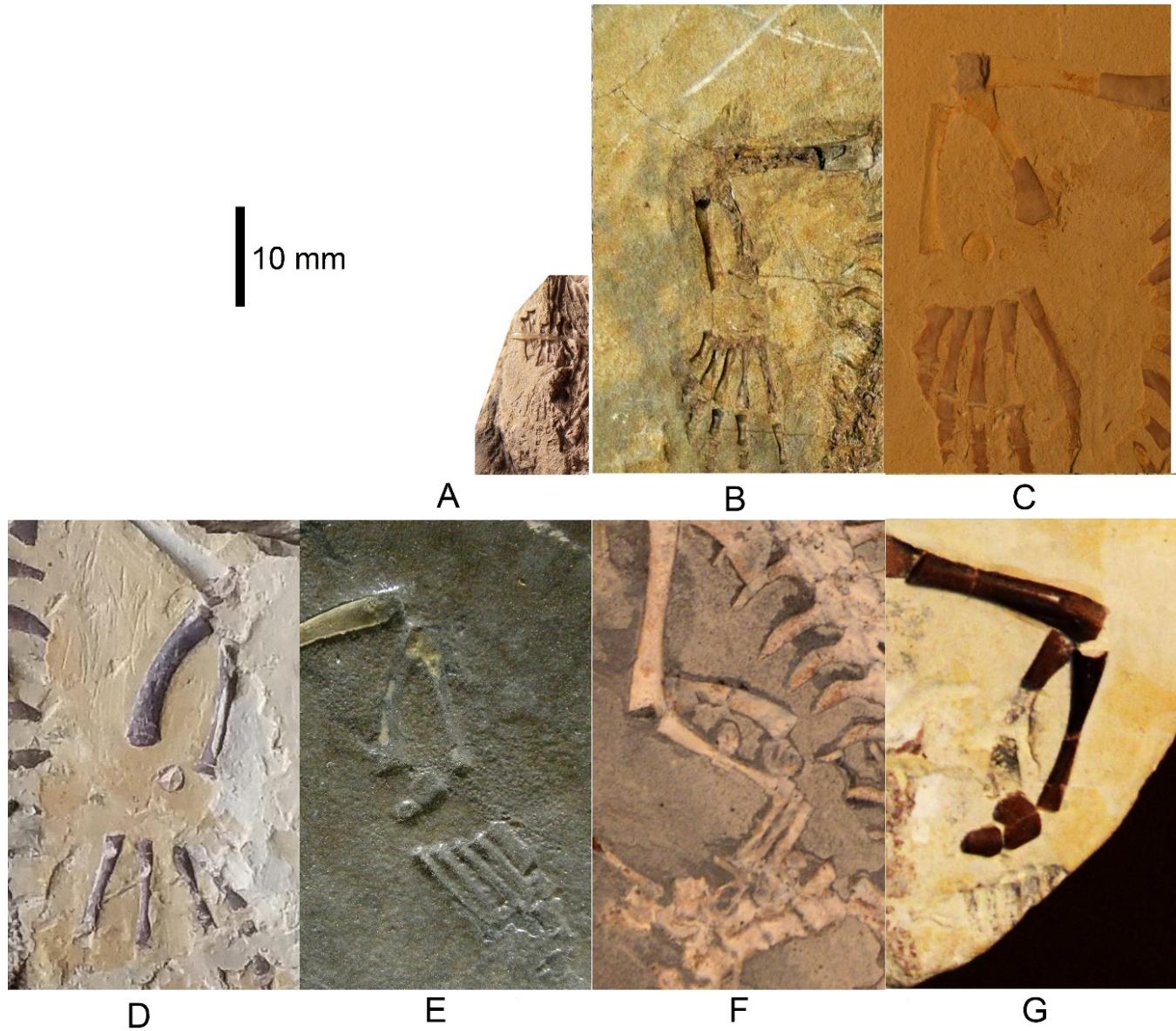
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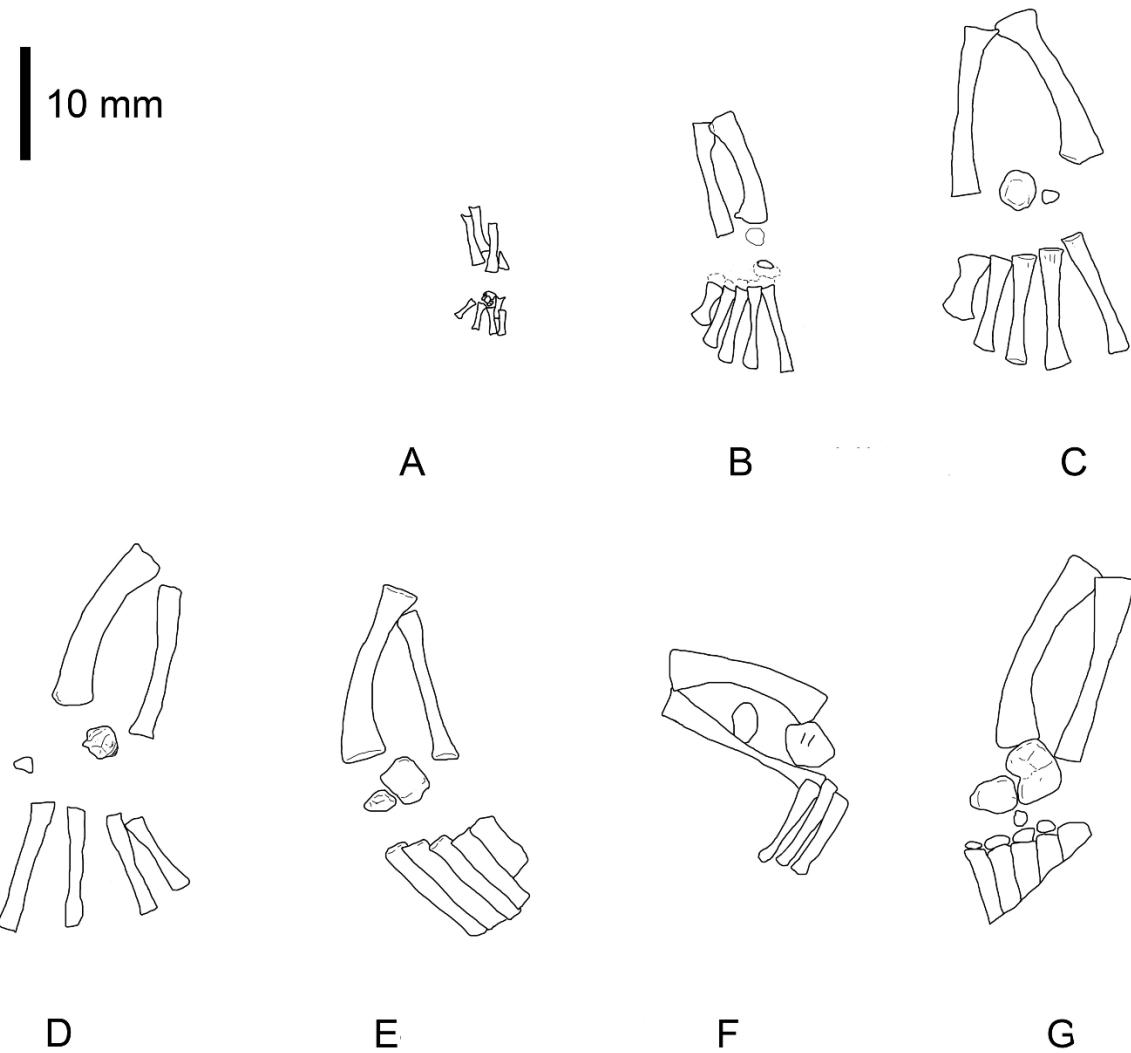
1157 Figure 12. Hypotheses about the astragalus and the navicular formation. The schematic diagram
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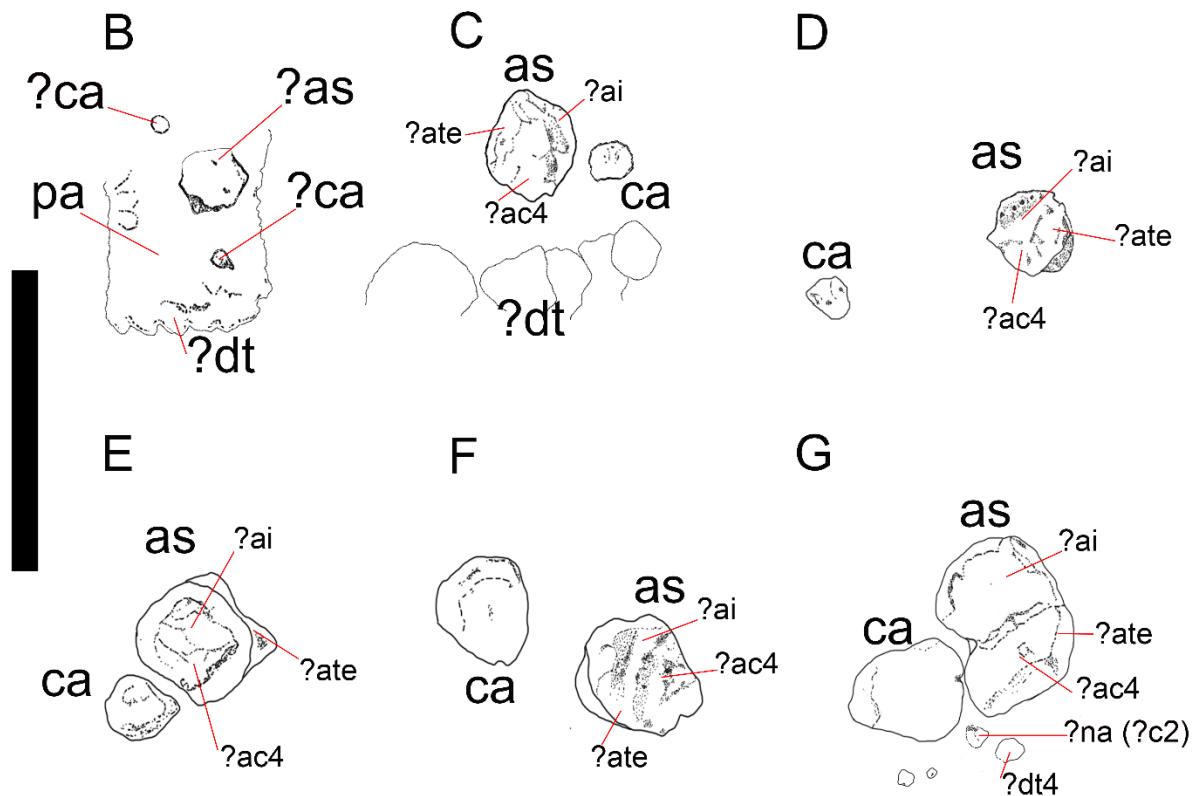
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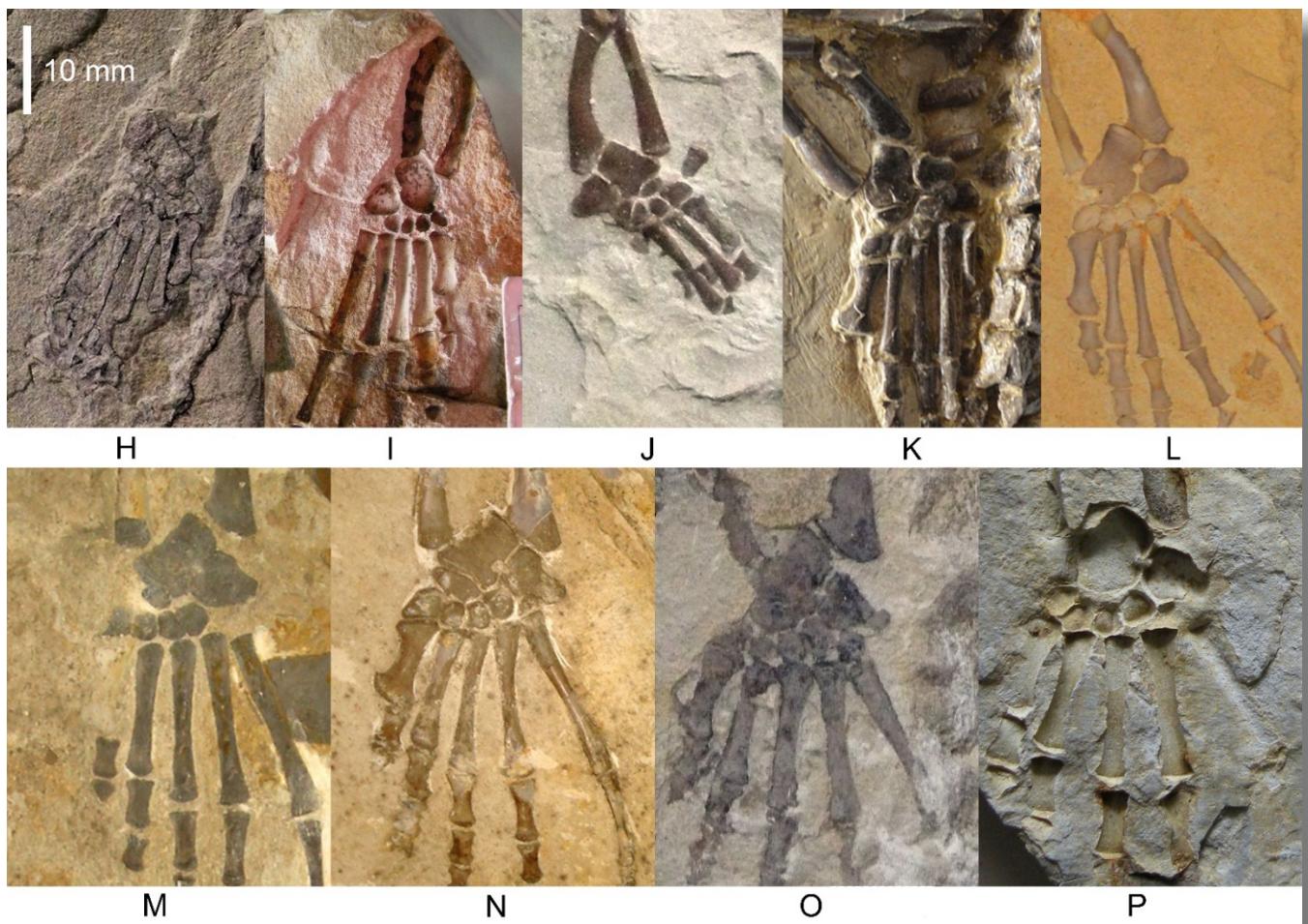
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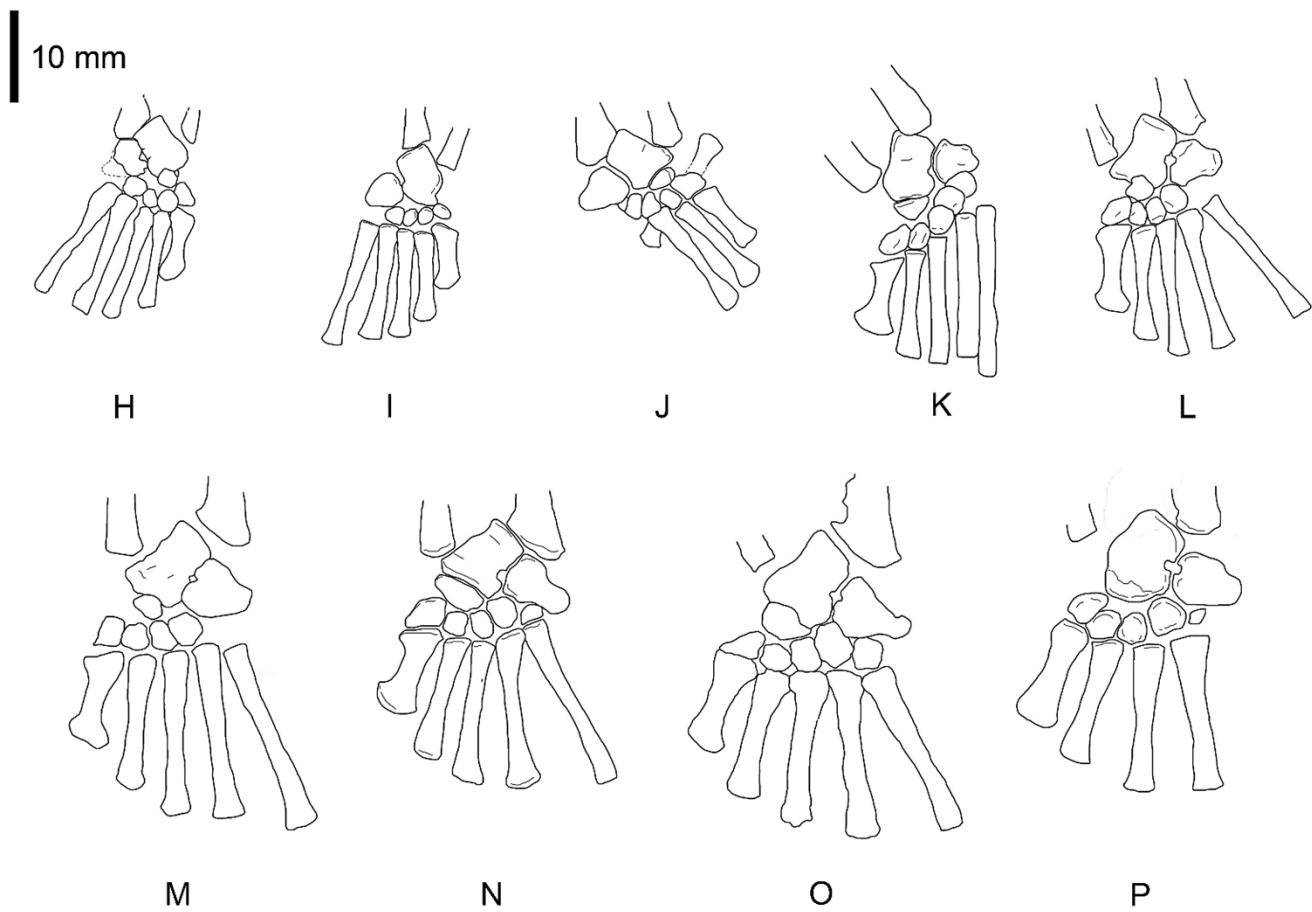
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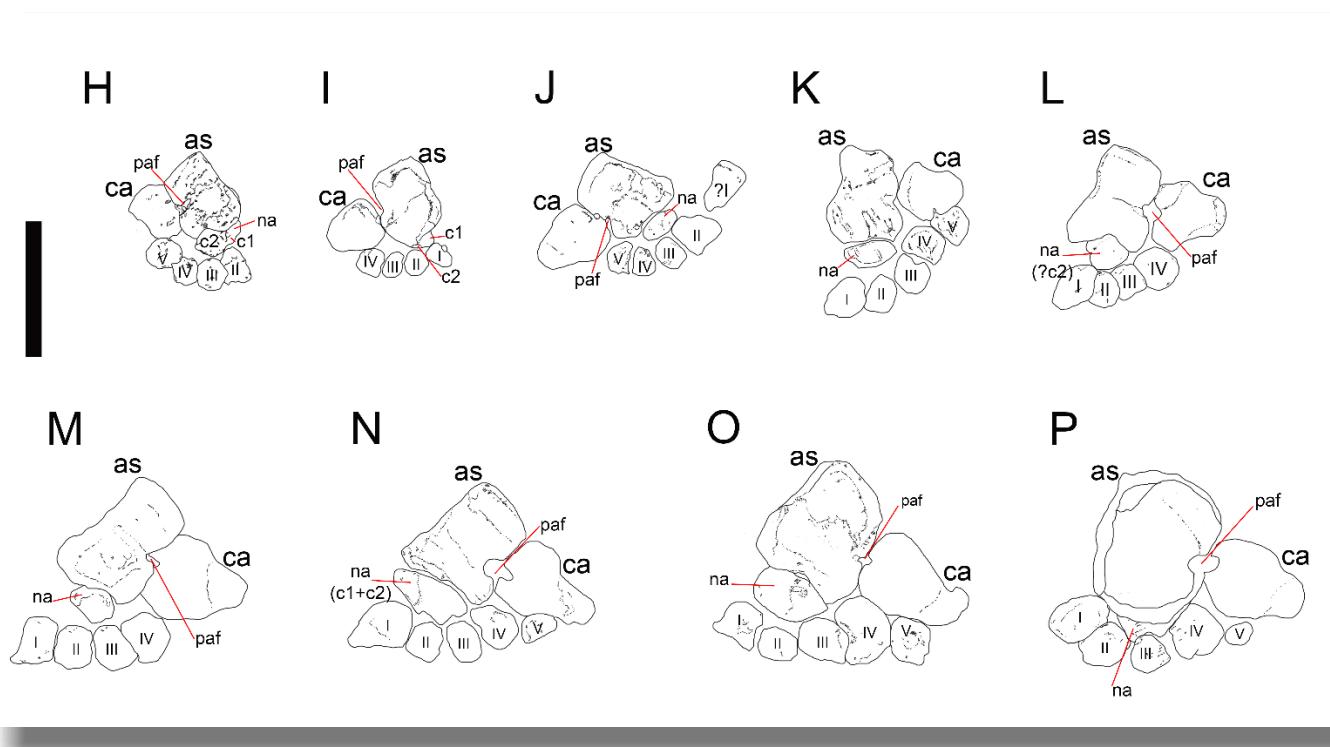
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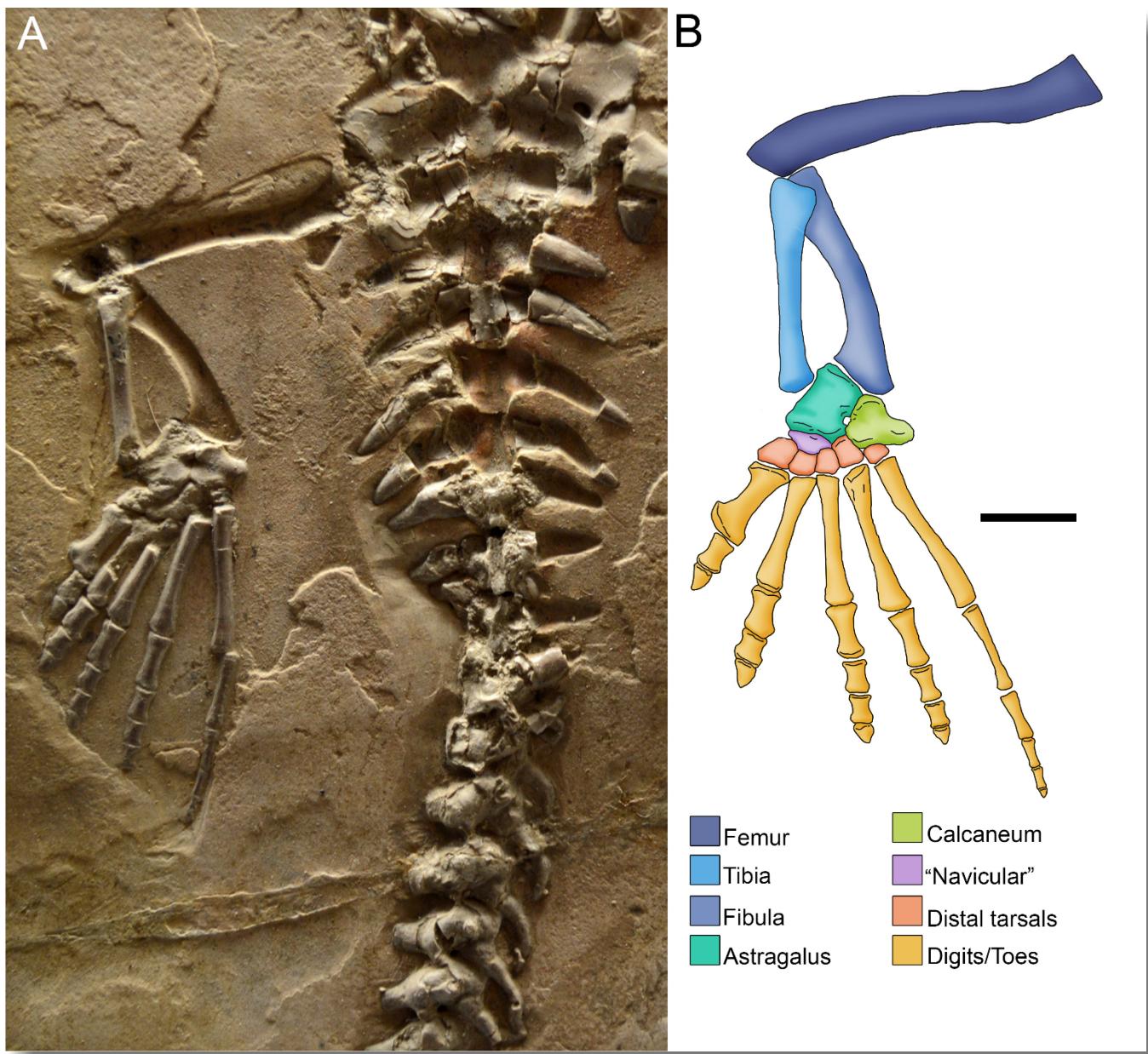
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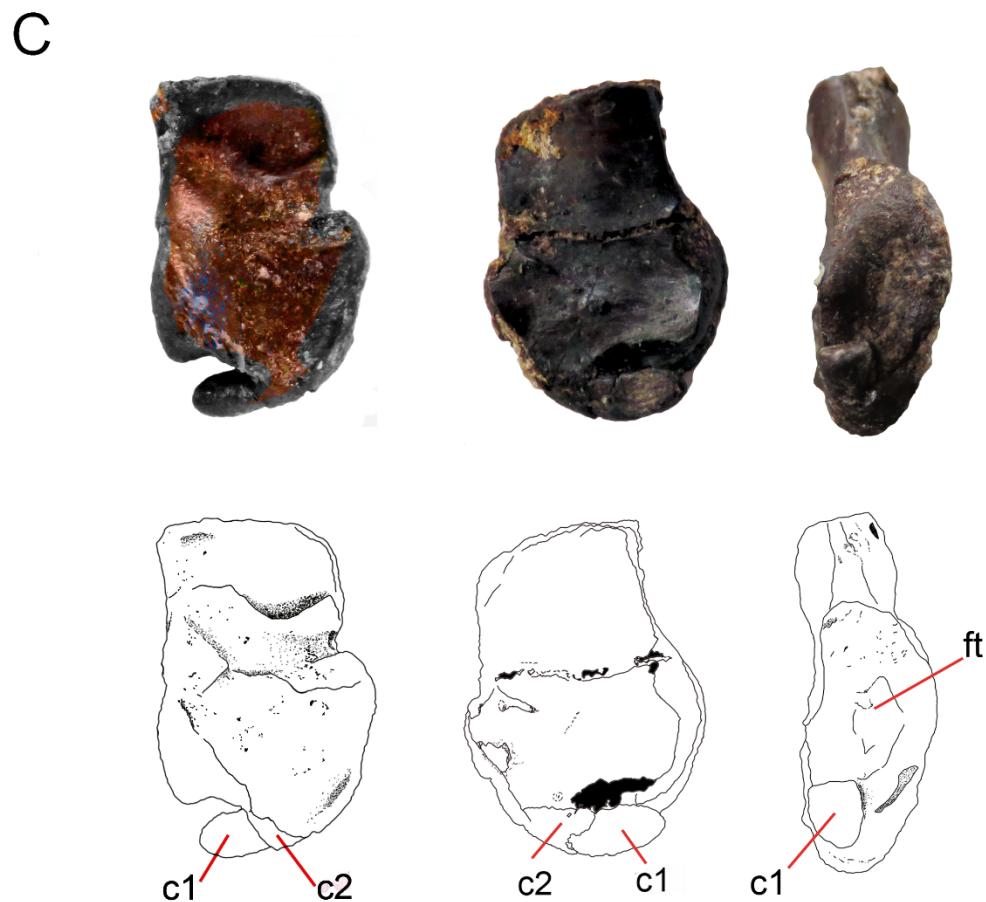
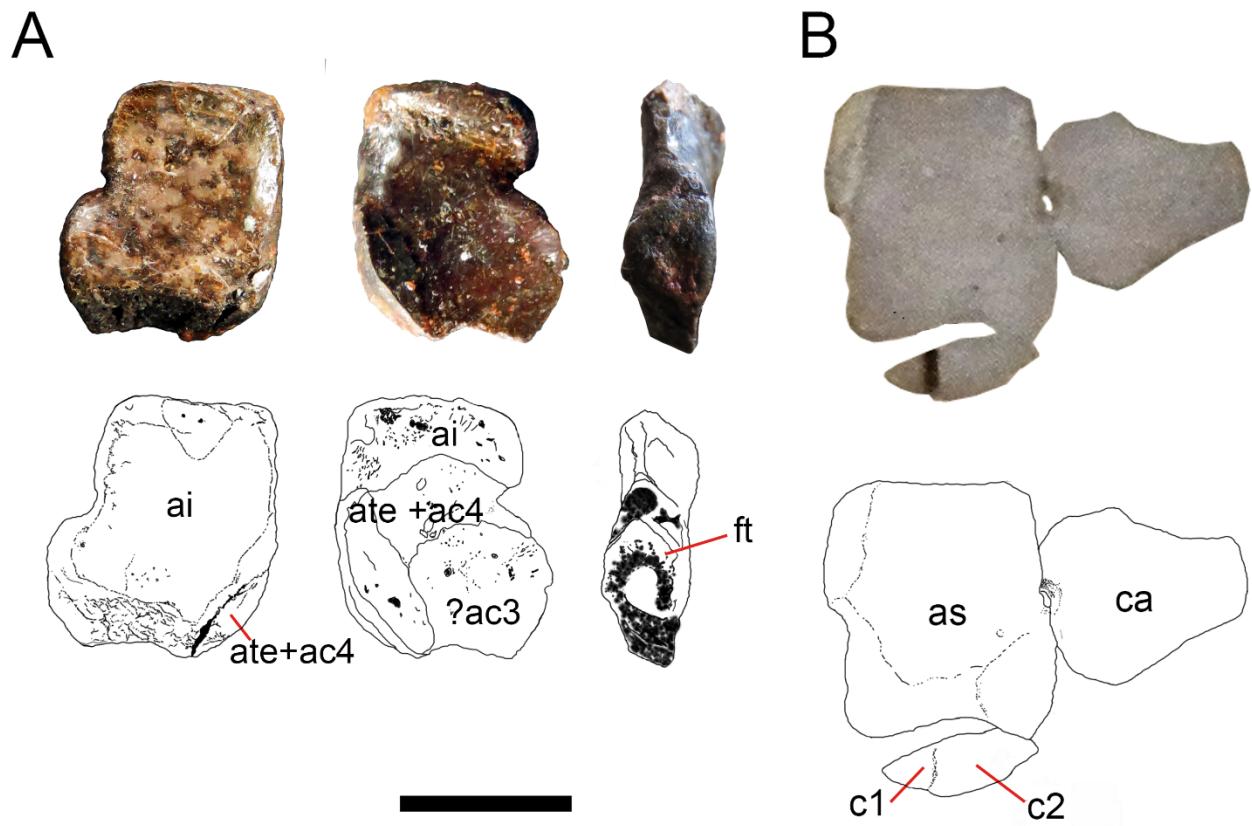
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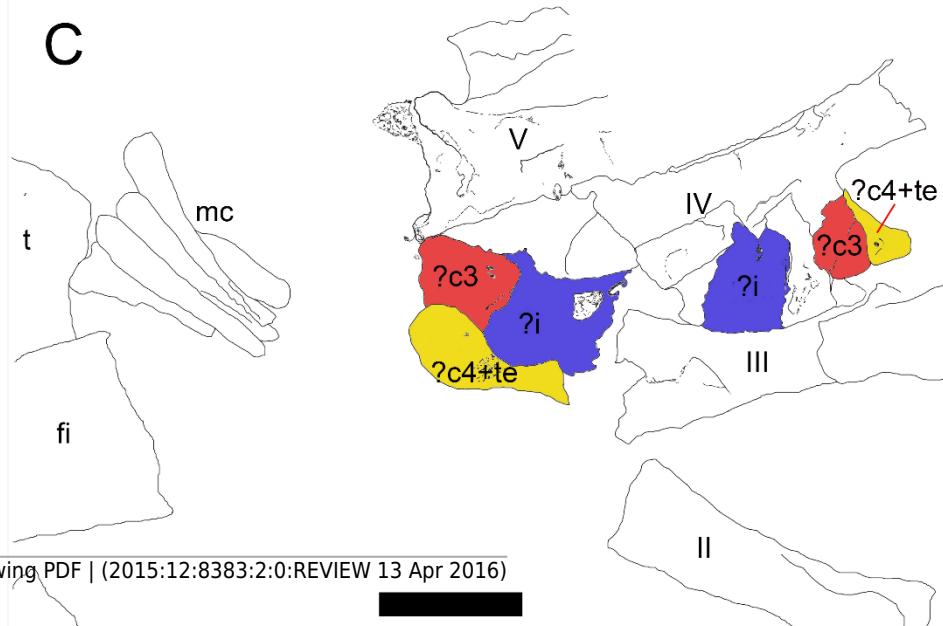
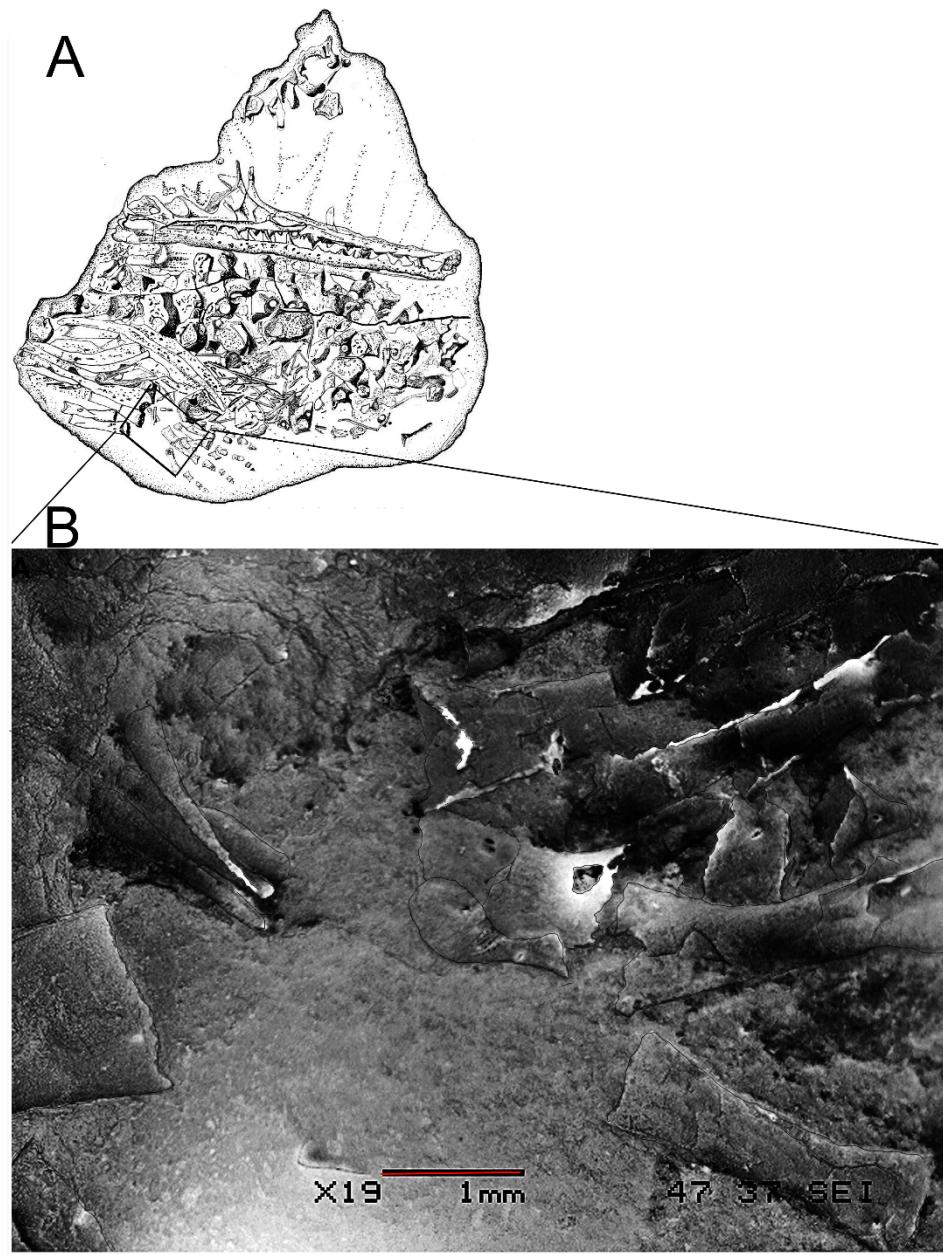
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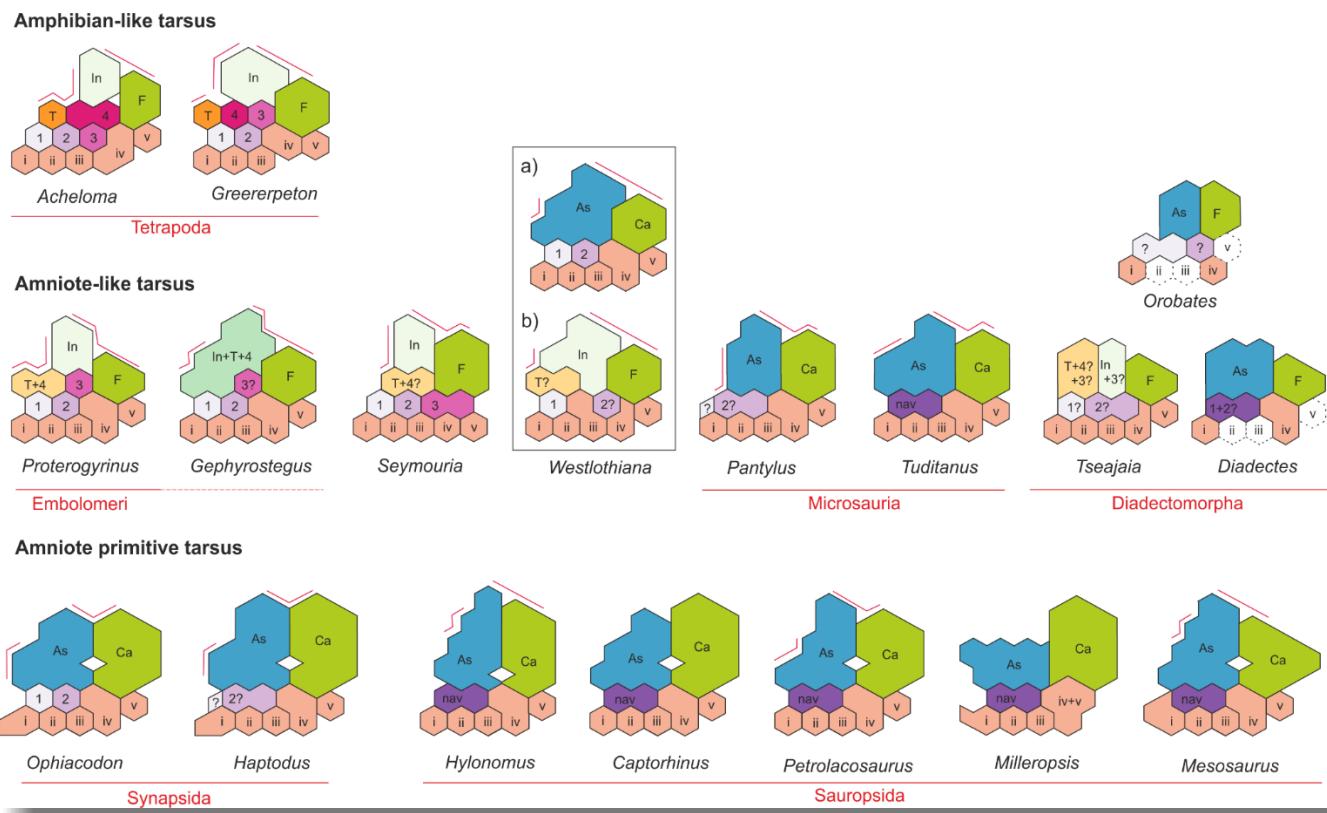


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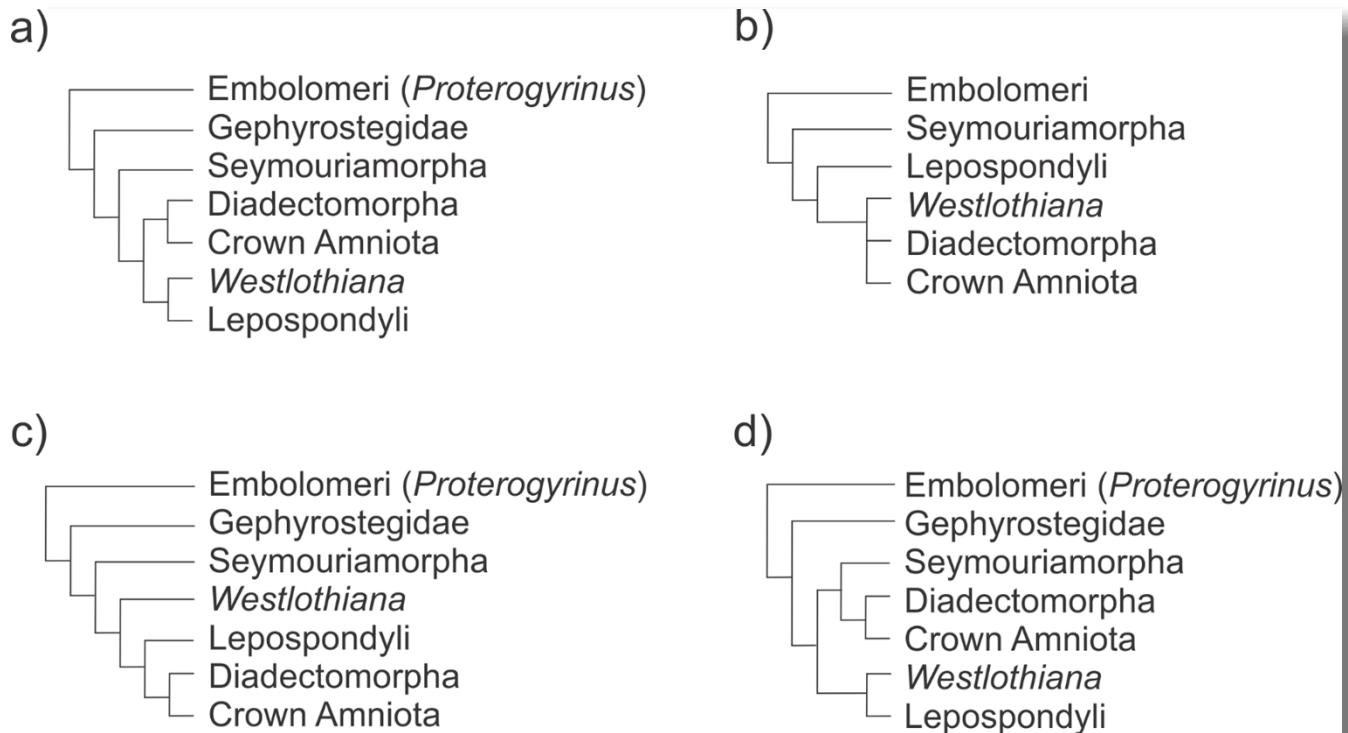


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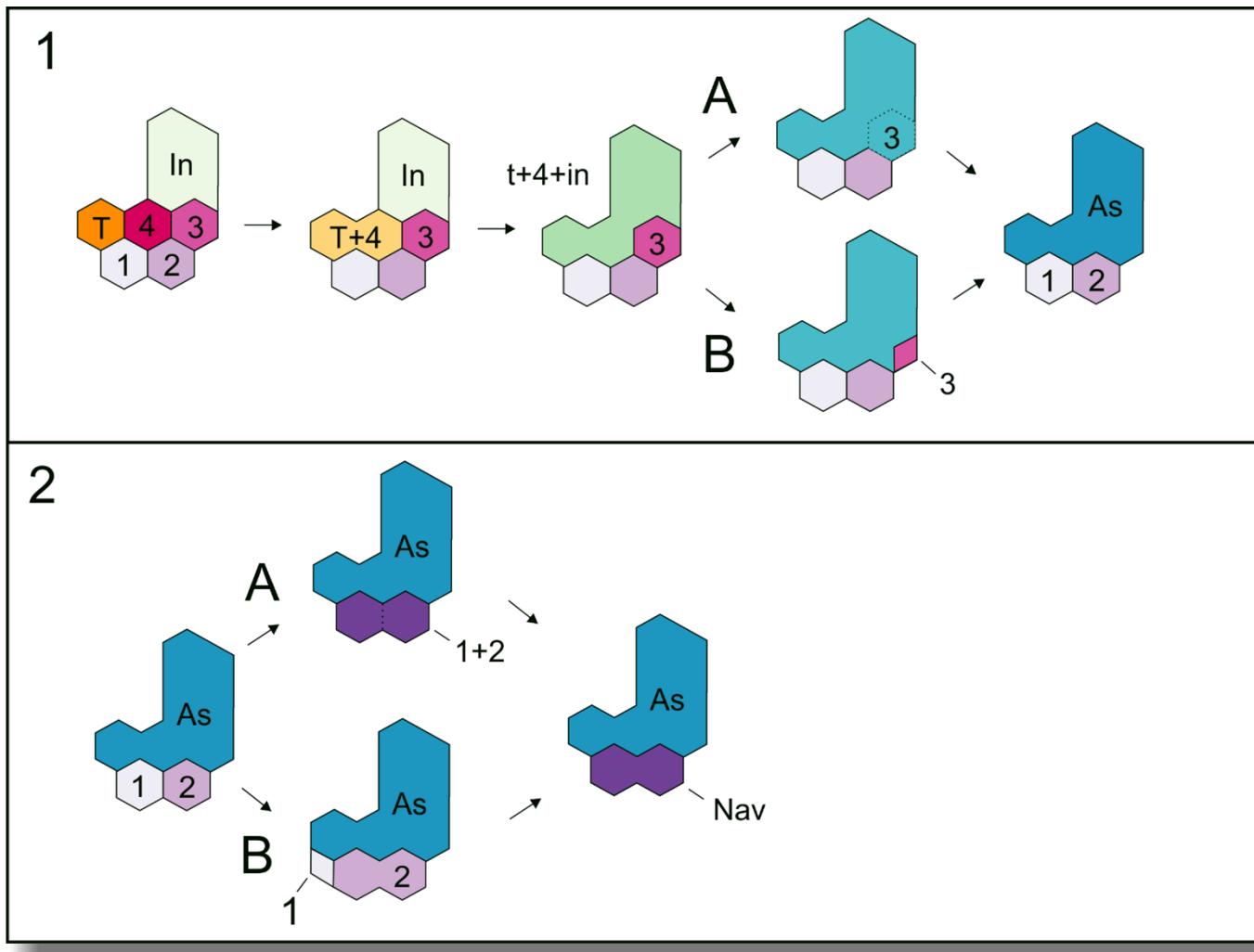
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1282

1283 Figure 12. Hypotheses about the astragalus and the navicular formation. The schematic diagram
1284 shows the steps that lead to the formation of the amniotic tarsus, regarding the series of
1285 possible transformations that could have produced the primitive astragalus (A) as well as
1286 those that prevailed into the evolution of the 'navicular' bone (B).

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