

1 The locomotor and predatory habits of unenlagiines (Theropoda, Paraves):  
2 inferences based on morphometric studies and comparisons with Laurasian  
3 dromaeosaurids

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## 27 **Abstract**

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29 Unenlagiinae is mostly recognized as a subclade of dromaeosaurids. They have the modified  
30 pedal digit II that characterize all dromaeosaurids, which is typically related to predation.

31 However, derived Laurasian dromaeosaurids (eudromaeosaurs) differ from unenlagiines in  
32 having a shorter metatarsus and pedal phalanx II-1, and more ginglymoid articular surfaces in  
33 metatarsals and pedal phalanges. Further, unenlagiines have a subarctometatarsal condition,  
34 which could have increased the mechanical efficiency during locomotion. All these

35 discrepancies possibly reflect different locomotor and predatory habits. To evaluate this we  
36 conducted morphometric analyses and comparisons of qualitative morphological aspects. The

37 former consisted in two phylogenetic principal component analyses, one of them based on  
38 lengths of femur, tibia and metatarsus, and width of metatarsus, and the other based on

39 lengths of pedal phalanges. The data sampling covered several coelurosaurian and non-  
40 coelurosaurian taxa. The first analysis showed the unenlagiines close to taxa with long tibiae

41 and long and slender metatarsi, which are features considered to provide high cursorial

42 capacities. Instead, eudromaeosaurs are close to taxa with shorter tibiae and shorter and wider

43 metatarsi, which can be considered with low cursorial capacities. The second analysis showed

44 that eudromaeosaurs and unenlagiines have similar phalangeal proportions. Moreover, they

45 share the elongation of distal phalanges, which is a feature related to the capacity of grasping.

46 The shorter and wider metatarsus, more ginglymoid articular surfaces and a shorter pedal

47 phalanx II-2 of eudromaeosaurs possibly allowed them to exert a greater gripping strength.

48 Thus, they had the potential of hunting large prey. Instead, the longer and slender

49 subarctometatarsus, lesser ginglymoid articular surfaces and a longer pedal phalanx II-2 of

50 unenlagiines possibly gave to them greater cursorial capacities and the ability to hunt smaller

51 and elusive prey on the ground. Thus, the different morphological evolutionary paths of  
52 dromaeosaurids lineages seem to indicate different locomotor and predatory specializations.

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## 54 **Introduction**

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56 Unenlagiinae is a clade of Gondwanan paravians first recognized by Bonaparte [1] and which  
57 have been generally considered as a subfamily of dromaeosaurids from the phylogenetic  
58 analysis made by Makovicky et al. [2]. However, more recently other studies have challenged  
59 the dromaeosaurian affinities of unenlagiines and instead have proposed an alternative  
60 phylogenetic hypothesis in which these theropods are located within the stem of Avialae [3–  
61 4]. Despite this and beyond the discussion about the relationships of unenlagiines, there are  
62 many shared morphologic features between unenlagiines and dromaeosaurids. One of these  
63 shared traits is the presence of a modified pedal digit II, with a hyperextensible phalanx II-2  
64 and a hypertrophied sickle-shaped claw. The peculiar form of this digit has led many  
65 researchers to make multiple interpretations about its possible function (e.g., [5–9]), although  
66 they all agree that it was involved in food obtaining, mainly through the submission and/or  
67 causing the death of the prey. Nevertheless, these functional interpretations are based mainly  
68 on the anatomy of derived Laurasian taxa (i.e., Dromaeosaurinae + Velociraptorinae or  
69 Eudromaeosauria following some authors, e.g., [10–11]), such as *Deinonychus*, *Velociraptor*,  
70 *Saurornitholestes*, *Achillobator* and *Dromaeosaurus*, in which the phalanges are markedly  
71 modified with respect to the plesiomorphic theropod morphology. Regarding the digit II of  
72 unenlagiines, it is similarly modified, although there are some anatomic differences with the  
73 digit II of eudromaeosaurs.

74 Moreover, the anatomical differences between unenlagiines and eudromaeosaurs are  
75 not limited to those in this pedal digit, but also in other parts of the hindlimb. Mainly, the

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76metatarsus differs between the two groups, since in unenlagiines is generally observed a  
77subarctometatarsal condition, as in microraptorine dromaeosaurids and some basal  
78troodontids, whereas in eudromaeosaurs the metatarsus is more robust and it has a structure  
79more similar to the plesiomorphic condition in theropods. In the subarctometatarsal condition  
80the metapodium has a similar morphology to the arctometatarsus, a type of metatarsal  
81morphology observed in some theropod groups, such as tyrannosaurids, ornithomimids, and  
82alvarezsaurids. White [12] pointed out the way in which both morphologies differ, indicating  
83that in the subarctometatarsus the proximal end of the metatarsal III, although constrained, is  
84equally visible in anterior and plantar views (completely constrained proximally in the  
85arctometatarsus and not visible); and in plantar view the third metatarsal is visible through the  
86entire length of the metatarsus excluding metatarsals II and IV from buttressing. Several  
87functional hypotheses have been raised regarding the arctometatarsus, most of them linked  
88with an increasing of the mechanical efficiency during locomotion [12–17]. The  
89subarctometatarsal condition could have related also to enhance the locomotor efficiency, and  
90some authors consider it as transitional between the plesiomorphic morphology and the  
91arctometatarsal condition [12].

92 In unenlagiines and eudromaeosaurs the hindlimb, especially the autopodium, is  
93implied both in locomotor and feeding functions, so beyond the phylogenetic relationships  
94between both groups, the morphological differences possibly reflect different locomotor and  
95predatory habits. Based on the previous ideas about the functional implications of the  
96subarctometatarsal and the arctometatarsal condition, likely unenlagiines had locomotor  
97capacities not present in eudromaeosaurs. These hypotheses have already been mentioned by  
98previous authors (e.g., [9]), although not evaluated in a quantitative form, at least not for  
99unenlagiines. The goal of the present contribution is to perform an analysis including taxa of  
100unenlagiines and eudromaeosaurs and to assess, in a quantitative mode, the morphological

101 differences between both groups. Additionally, exhaustive morphological comparisons are  
102 performed in order to arrive to a conclusion about the possibly dissimilar functions.

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## 104 **Materials and methods**

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106 In order to evaluate quantitatively how the unenlagiines and eudromaeosaurs differ  
107 morphologically was performed a morphometric analysis, employing a set of lineal  
108 measurements of the hindlimb bones of several theropod taxa. A diverse sample of theropod  
109 clades was considered, including extant birds, with the aim of covering a wide spectrum of  
110 morphologies, proportions and sizes of the elements of the hindlimb. So, the sample includes  
111 measurements of *Herrerasaurus*, non Tetanurae neotheropods, basal tetanurans, and  
112 representatives of most coelurosaur clades including Mesozoic avialans. It was considered  
113 also data from more recent although extinct groups of birds, i.e., Dinornithiformes, and from  
114 extant taxa, of which the locomotor habit, mode of feeding and capacities of the foot like  
115 ‘grasping’ are known. Extant taxa of birds considered include mainly those ground-dwellers  
116 with cursorial locomotor habits, raptorial birds with different hunting modes and ‘grasping’  
117 capacities, and perching birds with more arboreal habits, such as passeriforms, also with  
118 ‘grasping’ capacities (S1 Appendix). The measurements considered included proximodistal  
119 lengths of the femur (FL), tibiotarsus (TL), metatarsus (MtL), and non-ungual pedal  
120 phalanges, and the lateromedial width of the metatarsus at midshaft (ML). Regarding to MtL,  
121 the measures were taken for the longest element, typically the metatarsal III. For modern birds  
122 was considered the length of the tarsometatarsus, due to the complete fusion of the distal  
123 tarsals and metatarsals. The dimension ML refers to the lateromedial diameter of the  
124 articulated MT II, III and IV at midshaft of these bones.

125 Most of values of these measurements were obtained from previously published  
126 datasets, especially from [15] and also from other authors (see supplementary information),  
127 whereas others were obtained directly from materials deposited in different collections. For  
128 many taxa with published measurements the dimension ML was not considered by the  
129 authors, so in these cases ML was calculated from the published photographs of the  
130 specimens. For each taxon is specified the specimen from which the measurements were  
131 taken, except some not indicated by the author who published the data. In the case of taxa for  
132 which there are published measurements of several specimens, it has been decided to consider  
133 the data of only one of them, specifically the larger one, in order to avoid data of juvenile  
134 forms. Jointly, those specimens that were as complete as possible were taken into account,  
135 i.e., those with all the bones of the hindlimb preserved completely, in order to obtain the data  
136 of all the measurements. In some cases, estimated measurements have been taken of bones  
137 that have a small part not preserved, so even if it is estimated it is quite approximate to the  
138 real one. Additionally, measurements were obtained directly from materials housed in  
139 repositories of Argentina, including one specimen of the alvarezsauroid *Alnashetri*  
140 *cerropoliciensis* (MPCA), 17 specimens of many taxa of extant birds (MACN), and one  
141 specimen of *Struthio camelus* (CFA-OR). These are specified in the S1 Appendix.

142 Regarding lengths of pedal phalanges they were not taking into account the lengths of  
143 unguals, because there is no a consensus on how to measure this length, since some authors  
144 measure it in a straight line from the proximal end to the distal end of the phalanx, while  
145 others measure only the external curvature. So, published lengths of pedal unguals of  
146 theropods are not taken with the same criteria. Neither was considered the lengths of the  
147 phalanges of digit I, because in taxa of some clades included in the analysis, i.e.,  
148 ornithomimids, this digit is reduced and completely absent.

149 From this measurements phylogenetic principal component analyses (Phylogenetic  
150PCA; see [18–19]) instead traditional PCA were performed. The phylogenetic principal  
151component analyses allow the reduction of original variables to principal components  
152correcting the non-independence among the former due the phylogenetic relationships  
153between species. In this way, in a phylogenetic PCA the samples are not considered as  
154independent datapoints, an assumption of the traditional PCA and frequently violated due the  
155phylogenetic relationships between samples [18].

156 Given that the purpose of these analyses was the study of shape changes between  
157species that cover a wide diversity of sizes, the phylogenetic PCA were constructed from,  
158size-standardized, Mosimann variables [20], instead original ones. Each Mosimann variables  
159were obtained as the ratio between the original variable and the geometric mean of all  
160variables considered for the corresponding phylogenetic PCA.

161 From the complete dataset two phylogenetic principal component analyses were  
162performed. One of them includes the long bones of the hindlimb measurements, i.e., FL, TL,  
163MtL and ML, and the other one includes the lengths of the non-ungual pedal phalanges. In  
164relation to the available data (S1 Appendix), the first PCA included 74 taxa, whereas the  
165second one 32 taxa. This analysis design implying different taxonomic representatives in  
166each principal component analysis (in relation to the available data and inability to perform  
167these analyses with missing data), but allowed the maximization of the number of  
168morphologies and taxa considered in each analysis.

169 After computed to Phylogenetic PCA, the phylogenetic relationships between species  
170were projected into bivariate plots of morphospaces, constructing phylomorphospaces [19].  
171To evaluate the phylogenetic signal on each phylogenetic principal component, the K statistic  
172proposed by Blomberg et al. [21] where calculated for each axis. The K statistic provides a  
173measure of the strength of phylogenetic signal data. The values smaller than one indicate a

174lack of phylogenetic signal or strong adaptative processes, values near 1 are expected if the  
175character evolved following the phylogenetic relationships, under a Brownian motion model,  
176and values greater than one show that phylogenetically closer taxa are more similar than  
177expected, and eventually stasis processes [21–22].

178        Additionally, the size-effect on each axis of the morphospaces were calculated using  
179phylogenetic generalized least squares (PGLS) regressions [23], considered the geometric  
180mean as the independent variables. A PGLS regression allows the incorporation of the  
181phylogenetic structure of samples as the error term of the regression equations, and then  
182considering the biases caused by phylogeny in the calculation of the relationship between the  
183analyzed variables.

184        All these analyses were carried out using the software R 3.5.0 [24] and using the  
185PHYTOOLS [19], APE [25], and PICANTE [26] libraries.

186        For the Phylogenetic PCA and the PGLS, both for the analysis based on long bones  
187measurements and that based on lengths of the phalanges, were used composited phylogenies  
188which synthetized the relationships between taxa included in the study. These were based on  
189previously published phylogenies of different theropod clades [27–42].

190        The morphological differences between unenlagiines and other dromaeosaurids also  
191were evaluated through qualitative comparisons of the hindlimb bones, especially of the  
192matatarsals and pedal phalanges. The morphology of dromaeosaurid taxa was observed  
193directly from the holotypes of *Deinonychus* (YPM 5205), *Bambiraptor* (AMNH FR 30556),  
194and *Dromaeosaurus* (AMNH FR 5356), and from the literature (e.g., [5–6, 10, 35, 40, 43–  
19552]). The observations of the unenlagiines were made on the holotypes and referred materials  
196of *Buitreraptor* (MPCA 245, MPCA 238, MPCA 478, and MPCN-PV-598), *Neuquenraptor*  
197(MCF PVPH 77), *Austroraptor* (MML 195 and MML 220), and a cast of the holotype of



198*Rahonavis* (FMNH PR 2830). Additional comparisons with other theropod taxa were made  
199using the literature and in the case of extant birds also using the materials above mentioned.

200 Curvature angles of unguals of unenlagiines and Laurasian dromaeosaurids were  
201measured using the methodology applied by Fowler et al. [53], which in turn is based on that  
202of Pike and Maitland [54]. Both the external and inner curvature angles of the unguals are  
203measured with this methodology, i.e., from the dorsal and ventral borders respectively,  
204obtaining the angle between the base and the tip of the claw. However, as this methodology  
205was used to measure ungual curvatures of extant taxa of birds with soft tissue on digits some  
206modifications were made. For extant birds the base of the claw is considered the point where  
207the keratinous sheath emerges from the skin of the digit, although in fossil unguals lacking the  
208sheath and soft tissue cannot be considered the same base of the claw to the measurement of  
209the curvature angles. So, we take the proximodorsal tip of the ungual bone as the dorsal base  
210to measure the external curvature angle, and the tip of the flexor tubercle as the ventral base  
211(S2 Fig). However, the flexor tubercle shows two ventral tips in unguals of the analyzed  
212theropods, both separated by an extension of the side groove of the claw, so the anterior end  
213was taken as the base to measure the angle of the inner curvature. The angles were taken from  
214photographs of the ungual phalanges using the measure tool in Adobe Photoshop. For  
215incomplete materials which have not preserved the distal or the proximoventral ends these  
216were reconstructed, although in these cases was indicated that the angle values are estimated.

### 217Institutional abbreviations

218AMNH FR, American Museum of Natural History, New York, NY, USA. CFA-OR,  
219Fundación de Historia Natural “Félix de Azara”, Ciudad Autónoma de Buenos Aires,  
220Argentina. FMNH PR, Field Museum of Natural History, Chicago, IL, USA. MACN, Museo  
221Argentino de Ciencias Naturales “Bernardino Rivadavia”, Ciudad Autónoma de Buenos  
222Aires, Argentina. MCF PVPH, Museo “Carmen Funes”, Plaza Huincul, Neuquén, Argentina.

223MML, Museo Municipal de Lamarque, Lamarque, Río Negro, Argentina. MPCA, Museo

224Provincial “Carlos Ameghino”, Cipolletti, Río Negro, Argentina. MPCN-PV, Museo

225Patagónico de Ciencias Naturales, General Roca, Río Negro, Argentina. MUCPv, Museo de

226Geología y Paleontología de la Universidad Nacional del Comahue, Neuquén, Argentina.

227YPM, Yale Peabody Museum, New Haven, CT, USA.

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## 229**Results**

230

### 231**Description of the PPCA based on hindlimb long bones**

#### 232**measurements**

233

234In the PPC analysis based on hindlimb long bones (femur, tibia, and metatarsals)

235measurements, including Mesozoic theropods (MzTer), extant birds, and Dinornithiformes the

236contributions of the osteological variables to the first principal component (PPC1) represent

23757.2% and to the second principal component (PPC2) represent 30.1% of the total variation

238(Fig 1). The PPC1 summarizes a major contribution of tibia and metatarsus lengths

239(negatively correlated with the PPC1) and the mediolateral width of metatarsus at midshaft

240(ML; positively correlated). High negative PPC1 scores depicted taxa with elongated and

241slender metatarsi and elongated tibiae, whereas less negative and positive PPC1 scores

242depicted taxa with shorter and wider metatarsi and shorter tibiae. The PPC2 summarizes a

243major contribution of femur length (positively correlated) and minor contributions of

244metatarsus length and ML (both variables negatively correlated). High positive PPC2 scores

245depicted taxa mainly with elongated femora and slightly short and slightly slender metatarsi,

246whereas negative scores depicted taxa mainly with shorter femora and slightly longer and  
247slightly wider metatarsi.

248

249**Fig 1. Morphospace obtained from the phylogenetic PCA based on the measurements of**  
250**the hindlimb long bones.**

251

252 Extant birds and Dinornithiformes are partially segregated from the MzTer, toward  
253negative scores of PPC1 and PPC2 (Fig 1). This is mainly because these groups of birds have  
254comparatively longer and more slender metatarsi, longer tibiae, and shorter femora in  
255comparison with the MzTer. More specifically, those taxa showing the longest and more  
256slender metatarsi include terrestrial flightless or sparingly flying birds, i.e., the Cariamiformes  
257(*Cariama* and *Chunga*) and the Struthioniformes, as well as some Passeriformes such as  
258*Furnarius*. In fact, the Cariamiformes stand out by having extremely elongated metatarsi and  
259tibiae, with a metatarsus longer than 1.5 times the femur length or even more than twice  
260longer than the femur (as in *Cariama*) and a tibia longer than twice the femur length. The  
261remaining terrestrial birds, i.e., the Tinamiformes and Dinornithiformes, show comparatively  
262shorter metatarsi and tibiae. The Tinamiformes are located on negative PPC1 and positive  
263PPC2 scores, closely to the arcto and subarctometatarsalian MzTer with elongated metatarsi  
264and tibiae. With respect to the Dinornithiformes, they have comparatively wider metatarsi  
265than the Tinamiformes.

266 Some extant raptor birds, such as the accipitrids (*Elanus* and *Geranoaetus*), some  
267Strigiformes (*Asio* and *Bubo*), and some Dinornithiformes (*Megalapteryx*) are on low  
268negative and positive PPC2 scores, closer to the MzTer with the longest and more slender  
269metatarsi and the longest tibiae. These taxa show short and wide metatarsi, when are  
270compared with the remaining extant birds (except the Tinamiformes).

271        Regarding to the MzTer, on high negative PPC1 scores are located the  
272alvarezsauroids, derived ornithomimids, some oviraptorosaurs, basal avialans, troodontids,  
273microraptorines, and unenlagiines, all of them with markedly elongated hindlimbs (more  
274elongated and slender metatarsi and longer tibiae in comparison with the remaining MzTer).  
275Moreover, many of these taxa are characterized by an arctometatarsal or subarctometatarsal  
276condition.

277        The MzTer with the longest and the more slender metatarsi and longest tibiae are  
278located on the highest negative PPC1 scores and among the lowest positive and some negative  
279PPC2 scores. These taxa include the derived alvarezsaurids *Parvicursor* and *Linhenykus*, both  
280with a very slender and markedly elongated arctometatarsalian metatarsus, which significantly  
281surpass the femur length. Also is included in this part of the morphospace the basal avialan  
282*Hongshanornis*, which although does not have an arctometatarsalian condition present a  
283notably elongated and slender metatarsus which equals the femur length, locating on negative  
284PPC2 scores (differing from other basal avialans).

285        Regarding unenlagiines, *Buitreraptor* is closer to *Mahakala*, *Zhongjianornis*,  
286*Zhenyuanlong*, *Struthiomimus*, *Mei*, *Alnashetri*, and *Sinovenator* (Fig 1). These taxa show a  
287long metatarsus, although slightly shorter and wider than in the MzTer above mentioned, so  
288they are located on less negative PPC1 scores and more positive PPC2 scores. *Rahonavis* is  
289closer to the oviraptorosaur *Wulatelong* than to *Buitreraptor* and presents less negative PPC1  
290scores and slightly lower positive PPC2 scores than *Buitreraptor*. This separation is because  
291*Rahonavis* has a slightly shorter and wider metatarsus than *Buitreraptor* and the other taxa  
292closer to it.

293        *Deinonychus* and *Velociraptor* segregate and locate on less negative PPC1 scores than  
294other dromaeosaurids, including *Buitreraptor*, since they have markedly shorter and wider  
295metatarsi and shorter tibiae. In fact, *Deinonychus* is closer to tyrannosaurids than to other

296dromaeosaurids. *Velociraptor* is located on much more positive PPC2 scores, because it has  
297an even shorter metatarsus and tibia comparatively with the femur. *Khaan* is an oviraptorid  
298with hindlimb bones proportions similar to *Deinonychus*.

299       The large-sized tyrannosaurids have short and wide metatarsi and short tibiae,  
300although an arctometatarsalian condition. Many non-arctometatarsalian taxa characterized by  
301relatively elongated although moderately wide metatarsi and moderately elongated tibiae, are  
302located on low negative PPC1 scores and on low positive and negative PPC2 scores. Among  
303these taxa are included basal ornithomimosaur, the oviraptorosaur *Chirostenotes*, the  
304ceratosaur *Elaphrosaurus*, and the dromaeosaurid *Bambiraptor*. It is noteworthy that  
305*Bambiraptor* is separated from the other derived Laurasian dromaeosaurids, mainly due it  
306shows a comparatively longer metatarsus.

307       The basal tetanurans, ceratosaur, coelophysoids, and *Herrerasaurus* are located on  
308the lowest negative and positive PPC1 scores. These taxa have a foot with plesiomorphic  
309morphology showing the shortest and widest metatarsi and shortest tibiae among the  
310theropods included in the analysis. The tyrannosauroid *Dilong* has a longer metatarsus with a  
311more derived morphology, although it remains closer and is grouped with the mentioned taxa  
312due its relatively wide metatarsus.

313

### 314 **Influence of phylogeny in the distribution of taxa along the morphospace**

315

316The K of Blomberg values indicate that the taxa distribution along the PPC1 is strongly  
317influenced by the phylogenetic relationships of major clades (K=2.714) whereas PPC2 is less  
318influenced by deep phylogenetic relationship, and related to the influence of the phylogenetic  
319structure of terminals and more inclusive clade (K= 0.262) (S3 Table). Thus, the segregation  
320and relatively scarcely overlapped distribution of these major clades along the PPC1 can be

321related to the high K value of this axis, while the low K value of PPC2 indicates that there  
322exist many convergences to extreme values in different terminal and less inclusive clades.  
323Observing the phylogenetic relationships plotted on the morphospace (i.e.,  
324phyломorphospace; Fig 2) there exist a main separation trend of birds (including extant taxa  
325and Dinornithiformes) toward negative values of the PPC1 and MzTer in less negative and  
326positive values of PPC1. This separation is because birds have generally a longer and slender  
327metatarsus and a longer tibia than MzTer. In addition, more derived taxa of some MzTer  
328clades generally trend to locate on more negative values of PPC1 (as can be observed in  
329tyrannosauroids, ornithomimosaur, and alvarezsaur), while most primitive taxa considered  
330locate on the extreme positive values of PPC1, in relation with their plesiomorphic metatarsal  
331morphology (Fig 2).

332

**333Fig 2. Phylomorphospace obtained from the phylogenetic PCA based on the  
334measurements of the hindlimb long bones.**

335

336 As was stated above, PPC2 summarizes morphological similarities between minor  
337clades or terminals. Although PPC2 is less influenced by the structure of phylogenetic  
338relationships of major clades, the positive correlation of this component with the femoral  
339length can partially explain the division between MzTer and extant birds and  
340Dinornithiformes, because in the latter there is a general trend to a significant shortening of  
341the femur in comparison with MzTer, reason why they are mostly on negative values of the  
342PPC2. The exception is the Tinamiformes, which are on positive values of PPC2, significantly  
343separated from the remaining modern birds.

344 Regarding the distribution of MzTer along the PPC2 some trends are observed. Thus,  
345in tyrannosauroids and ornithomimosaur there is a marked separation between basal and

346 derived taxa, because basal taxa are located on negative values (with short femora) and  
347 derived taxa tend to more positive values (with longer femora). Derived ornithomimosaur  
348 and alvarezsauroids are characterized by an elongated tibia and metatarsus, although in the  
349 former the trend was a comparatively more marked elongation of the femur whereas in  
350 alvarezsauroids the trend was to shorten the femur in derived forms. In oviraptorosaurs the  
351 direction of the morphological changes was not as clear as in the coelurosaur groups  
352 mentioned, possibly because the small taxon sample is not adequate to show a clearer trend.  
353 Troodontids show a distribution of taxa along PPC2 similar to tyrannosauroids and  
354 ornithomimosaurids, since basal taxa are on low positive values of the axis whereas more  
355 derived taxa are on more positive values and hence they present a longer femur.

356       About the distribution of dromaeosaurids along the phylomorphospace (Fig 2) is  
357 observed an opposite tendency in comparison with other groups mentioned, since more basal  
358 taxa, such as *Mahakala* and the unenlagiines *Buitreraptor* and *Rahonavis*, are located on more  
359 negative values of PPC1, whereas more derived taxa, i.e., *Deinonychus*, *Velociraptor*, and  
360 *Bambiraptor*, are on less negative values of PPC1. In this way, the basal taxa present a longer  
361 metatarsus and tibia than derived forms. Regarding the location of taxa along PPC2,  
362 dromaeosaurids do not show a clear trend, in contrast to the clades already explained. Basal taxa  
363 are located on similar values of PPC2, whereas microraptorines (at least those considered in  
364 this analysis) are more widely distributed. Thus, some microraptorines (i.e. *Microraptor* and  
365 *Zhongjianosaurus*) are on high positive values of PPC2, whereas others (i.e. *Zhenyuanlong*)  
366 are on similar PPC2 values than basal dromaeosaurids, with a shorter femur. Moreover,  
367 *Microraptor* and *Zhongjianosaurus* converge in the morphospace with derived ornithomimids  
368 with long femora. The derived dromaeosaurids are also widely distributed, being *Velociraptor*  
369 on high positive values of PPC2, close to some basal avialans, *Bambiraptor* on negative  
370 values, close to taxa with a shorter femur and longer metatarsus, and *Deinonychus* on an

371intermediate location near derived tyrannosaurids. The location of *Velociraptor* can be  
372explained possibly by its comparatively longer femur with respect to the other derived  
373dromaeosaurids here analyzed.

374

### 375**Influence of size in the distribution of taxa along the morphospace**

376

377The PGLS regressions indicates that the PPC1 in the analysis based on long bones dimensions  
378is significantly influenced by size ( $F = 7.318$ ;  $p\text{-value} = 0.009$ ). The MzTer taxa with the  
379largest body sizes are located to the right side of the morphospace, on less negative and some  
380positive values of the PPC1. Furthermore, Dinornithiformes, the larger modern birds  
381considered in the analysis, are located to the right of the morphospace occupied by birds.  
382These large-sized taxa are characterized by a comparatively short and wide metatarsus, as was  
383explained above. By other side, smaller taxa with slender and longer hindlimbs are situated at  
384the left of the morphospace, whether in the case of MzTer or modern birds. Conversely, PPC2  
385( $F = 2.162$ ;  $p\text{-value} = 0.146$ ) and PPC3 ( $F = 3.260$ ;  $p\text{-value} = 0.075$ ) in not significantly  
386influenced by size, and it result agrees with the distribution of taxa along the axis.

387

### 388**Description of the PPCA based on phalanges lengths**

389

390In the PPC analysis made from phalanges lengths, the contributions of the variables to the  
391first principal component (PPC1) represent 39.0% and to the second principal component  
392(PPC2) represent 29.1% of the total variation (Fig 3). Because these two axes explain a small  
393percentage of the variation, we also analyzed the third component (10.8% of the total  
394variation).

395

31

32



396**Fig 3. Morphospace obtained from the phylogenetic PCA based on the lengths of the**  
397**pedal phalanges (PPC1 vs PPC2).**

398

399 In the graphic of PPC1 vs PPC2 (Fig 3), the PPC1 summarizes a major contribution of  
400the lengths of the proximal phalanges, i.e., Ph. II-1, III-1, IV-1, and III-2 (positively  
401correlated with this component), and the lengths of the distal pre-ungual phalanges, i.e., II-2,  
402III-3, and IV-4 (negatively correlated with this component). In this way high positive PPC1  
403scores depict taxa with elongated proximal phalanges and high negative PPC1 scores depict  
404taxa with elongated distal phalanges. The PPC2 summarizes major contributions of the  
405lengths of the proximal and middle phalanges of digit IV, i.e., IV-2 and IV-3 (positively  
406correlated with this component), and the lengths of the proximal and distal pre-ungual  
407phalanges of digits II and III (negatively correlated). Thus, high positive PPC2 scores depict  
408taxa with long phalanges IV-2 and IV-3 whereas high negative PPC2 scores depict taxa with  
409long proximal or distal pre-ungual phalanges. Considering both principal components and  
410summarizing the distribution along the morphospace, taxa on high positive PPC1 and high  
411negative PPC2 scores are between those showing more elongated proximal phalanges,  
412whereas those taxa located on negative PPC1 scores have relatively more elongated distal  
413phalanges.

414 For the graphic of PPC2 vs PPC3 (Fig 4), in addition to those already commented for  
415PPC2, the PPC3 (10.8% of the total variation) summarizes major contributions of the lengths  
416of all the phalanges of digit II (positively correlated with this component), and to a lesser  
417extent it summarizes contributions of the lengths of phalanges of digit III, mainly Ph. III-2  
418and III-3 (negatively correlated). Thus, high positive PPC3 scores depict taxa with a long digit  
419II whereas high negative PPC2 scores depict taxa with long phalanges III-2 and III-3.

420**Fig 4. Morphospace obtained from the phylogenetic PCA based on the lengths of the**  
421**pedal phalanges (PPC2 vs PPC3).**

422

423 In the morphospace, dromaeosaurids occupy central values of PPC1, high positive of  
424 values of PPC2, and high negative PPC3 scores (Figs 3 and 4). All representatives are mainly  
425 on negative PPC1 scores, except *Bambiraptor* which is on low positive PPC1 values.  
426 *Deinonychus*, *Buitreraptor*, and *Bambiraptor* are located on higher positive PPC2 scores and  
427 *Microraptor* and *Sinornithosaurus* on less positive scores of this component. The high  
428 positive values of PPC2 of dromaeosaurids are linked to a remarkably elongated digit IV, a  
429 feature mainly product of elongation of phalanges IV-2 and IV-3, while the high negative  
430 values on PPC3 are also mainly related to the length of phalanges of digit IV, but also  
431 influenced by the length of Ph. III-2 and III-3. *Deinonychus* and *Buitreraptor* show a  
432 relatively long digit IV in comparison with other dromaeosaurids, although *Deinonychus* is  
433 slightly located on more negative PPC1 scores so the position of this taxon is also specifically  
434 influenced by the length of phalanx IV-4. *Sinornithosaurus* is the taxon with higher PPC3  
435 values, a position influenced by the elongated phalanges III-3 and II-2. The location of  
436 *Microraptor* is due a relatively shorter digit IV in comparison with *Deinonychus*,  
437 *Buitreraptor*, and *Bambiraptor*, whereas the length of phalanx IV-4 influenced in its position  
438 on more negative PPC1 scores.

439 Troodontids show a distribution on the morphospace mainly similar to that of  
440 dromaeosaurids (Figs 3 and 4), except by *Troodon* which is located on negative PPC2 scores,  
441 with relatively shorter digit IV than the others troodontids in the analysis. *Anchiornis* is much  
442 close to *Deinonychus* and *Buitreraptor*, a position mainly influenced by a long digit IV. The  
443 location of *Sinornithoides* and *Talos*, in less negative values of PPC2, is related to their less

444 elongated digit IV in comparison with *Anchiornis*. In turn, *Talos* is close to *Microraptor* and  
445 thus its position is also influenced by the length of phalanx IV-4.

446 Non-coelurosaurian theropods are dispersed in the morphospace (Figs 3 and 4).  
447 *Dilophosaurus* locates on very low negative PPC1, PPC2, and PPC3 scores, showing subtle  
448 elongated distal phalanges and a slightly longer digit III. The two basal tetanurans included in  
449 the analysis, i.e. *Allosaurus* and *Gualicho*, have similar PPC1 and PPC3 values, although they  
450 segregate along PPC2, thus indicating that the difference in length between digit IV and digits  
451 II and III is the main factor influencing the separation of these tetanurans. The position of  
452 *Gorgosaurus*, which is the only tyrannosaurid included in the analysis, is mainly influenced  
453 by relatively long proximal phalanges and especially by those of digit IV.

454 Oviraptorosaurs show a wide distribution on the morphospace (Figs 3 and 4), since  
455 *Corythoraptor* and *Khaan* have a more elongated digit IV whereas *Avimimus* has more  
456 elongated proximal phalanges of digits II and III and a comparatively longer digit III.

457 Ornithomimosaurs are on positive PPC1 and PPC3 scores and on negative PPC2  
458 scores, a location mainly influenced by longer proximal phalanges and a relatively longer  
459 digit II. The position of *Struthiomimus* is related to a longer digit II and Ph. III-1 than those of  
460 *Gallimimus* and *Aepyornithomimus*.

461 Mesozoic avialans are on negative PPC1 and PPC3 scores and on positive and  
462 negative PPC2 scores (Figs 3 and 4). Basal taxa, i.e., *Archaeopteryx* and *Zhongjianornis*, are  
463 on positive PPC2 values, although *Zhongjianornis* highlights due it is located on high  
464 negative PPC3 values. The position of *Archaeopteryx* indicates that it has a long digit IV,  
465 mainly due elongation of Ph. IV-3 and IV-4. The location of *Zhongjianornis*, *Confuciusornis*,  
466 *Yanornis*, and *Yixianornis* is mainly influenced by a greater elongation of distal phalanges of  
467 digits II, III, and IV and by a digit III comparatively longer. Specifically, the position of  
468 *Zhongjianornis* is biased by the length of digits III-2 and III-3, and secondarily influenced by

469a long digit IV, whereas the location of *Yanornis* and *Yixianornis* is more influenced by a  
470longer Ph. III-1 and the position of *Confuciusornis* is secondarily influenced by a longer digit  
471IV.

472 Extant birds are mainly distributed along negative PPC2 and PPC3 scores, although  
473there is observed a dichotomy along the PPC1, because some taxa are on positive scores and  
474others on negative ones (Figs 3 and 4). The position of taxa on positive PPC1, such as *Rhea*,  
475*Nothoprocta*, *Cariama*, and *Chunga* is mainly influenced by long proximal phalanges of  
476digits II, III, and IV. The most notorious bias is observed on *Rhea*, whilst the position of  
477*Cariama* and *Chunga* is also influenced by the length of Ph. III-3. Those taxa on negative  
478PPC1 scores, i.e., *Turdus* and *Bubo* are markedly influenced by the length of distal phalanges  
479of digits II, III, and IV, being the position of *Bubo* the more affected by this trait.

480Additionally, the position of these two taxa is biased by a comparatively longer digit III.

481Moreover, this digit is longer in *Bubo* and *Turdus* in comparison with digit III of the other  
482extant birds analyzed.

483

#### 484**Influence of phylogeny in the distribution of taxa along the morphospace**

485

486The K of Blomberg values indicate that the taxa distribution along the PPC1, PPC2, and  
487PPC3 is strongly influenced by relationships between terminals and less inclusive clades in  
488the case of PPC1 (K=0.303) and PPC2 (K=0.376), and linked to the many morphological  
489convergences between distant taxa described above (S4 Table). The PPC3 also show a K  
490value lesser than 1 but more closer to 1 (K=0.811), fitting more closely with a stochastic  
491model (i.e., the distribution of taxa follows the phylogenetic relationships but is not  
492particularly strong influenced by deep nodes neither terminal relationships).

493 For instance, basal taxa included in the analysis, such as basal tetanurans and the basal  
494coelurosaur *Gorgosaurus* are almost indifferently located on similar values of PPC1, although  
495they are separated along PPC2 and PPC3 (Figs 5 and 6). The ornithomimids also are  
496significantly separated mainly along PPC2, although the scarce sample of this group of  
497theropods and recent phylogenetic analyses [55], which show them in a polytomy on the  
498cladogram, difficult to shed light to how phylogeny and the distribution along the  
499mosphospace are related.

500

501**Fig 5. Phylomorphospace obtained from the phylogenetic PCA based on the lengths of**  
502**the pedal phalanges (PPC1 vs PPC2).**

503

504**Fig 6. Phylomorphospace obtained from the phylogenetic PCA based on the lengths of**  
505**the pedal phalanges (PPC2 vs PPC3).**

506

507 Among oviraptorosaurs it can be observed a wide distribution of taxa along PPC3 (Fig  
5086), whereas in the remaining clades the distribution of taxa is more limited along this  
509component according phylogenetic relationships. Thus, the basal taxon *Avimimus* is  
510remarkably separated from the more derived *Corythoraptor* and *Khaan* mostly throughout the  
511PPC3 and also the PPC2. So, the basal and derived taxa are mainly divided by length  
512differences between the digit IV (larger in derived taxa) and the digits II and III (larger in  
513basal taxa), as can be observed in the PPC2 vs PPC3 axes.

514 Regarding dromaeosaurids, they show a convergence between basal and derived taxa,  
515since *Buitreraptor* is located near the derived eudromaeosaurids *Deinonychus* and  
516*Bambiraptor* (Figs 5 and 6). These three taxa have a comparatively elongated digit IV than

517 *Microraptor* and *Sinornithosaurus*, which are more derived than *Buitreraptor* although more  
518 basal with respect to the eudromaeosaurids.

519       Among troodontids there is observed an evolutionary trend to shorten the digit IV and  
520 to increase the length of digit III and to a slight elongation of proximal phalanges, as shows  
521 the PPC1 vs PPC2 graphic (Fig 5). Thus the basal taxon *Anchiornis* is convergently located  
522 near to *Deinonychus* and *Buitreraptor*, with a proportionally more elongated digit IV, whereas  
523 *Troodon* has the shortest digit IV and a comparatively longer digit III as can be observed in  
524 the PPC2 vs PPC3 graphic (Fig 6).

525       Mesozoic avialans show a similar evolutionary trend than troodontids, since the basal  
526 taxon *Archaeopteryx* has an elongated digit IV whereas in more derived taxa this digit  
527 decreases in length whereas the other digits lengthen, specifically the digit III (Figs 5 and 6).  
528 In turn there is a trend to an elongation of the distal non-ungual phalanges of digits II, III, and  
529 IV in more derived forms, as can be observed in the PPC1 vs PPC2 axes.

530       The sample of extant birds included in this analysis is small, although a certain  
531 evolutionary trend can be observed. In general lines, there is an increase in length of the distal  
532 non-ungual phalanges and of the digit III as a whole. Thus, the more basal *Rhea* has long  
533 proximal phalanges and a digit III comparatively shorter, whereas the more derived *Turdus*  
534 and *Bubo* have markedly longer distal non-ungual phalanges and a particularly elongated digit  
535 III.

536

### 537 **Influence of size in the distribution of taxa along the morphospace**

538

539 Following the result of the PGLS regressions, the axes that compose the morphospace  
540 analyzed for the phalange measures (i.e., PPC1, PPC2, and PPC3) are not significantly  
541 influenced by size (PPC1:  $F = 1.253$ ,  $p\text{-value} = 0.2722$ ; PPC2:  $F = 2.513$ ,  $p\text{-value} = 0.1238$ ;

542PPC3:  $F = 0.6881$ ,  $p\text{-value} = 0.6881$ ). Accordingly, the distribution of taxa along the axes  
543does not follow a pattern controlled by size.

544

## 545**Discussion**

546

547Previous authors enumerated the morphological features of animals traditionally considered  
548as ‘cursorials’: relatively long limbs; hinge-like joints; distal limb segments proportionally  
549elongated; the reduction, compression or loss of the ulna and fibula and of the lateral  
550metapodials and phalanges; reduction or loss of distal muscular groups or proximal location  
551of their scars; a limb motion restricted to the sagittal plane; acquisition of digitigrade or  
552unguligrade stance; and metapodials interlocked, fused or reduced to a single element [13,  
55356–61]. From the perspective of the locomotor performance, animals known as cursorials  
554have the capacity to move at greater velocities or for extensive distances with a low energetic  
555cost [60–63]. However, Carrano [61] considered that a discrete categorization of the  
556locomotor habits could not be appropriate and instead these habits would be evaluated along a  
557multivariate continuum between two locomotor extremes, i.e., strictly graviportal and  
558cursorial. Theropods can be generally considered as cursorial animals (or ‘subcursorial’,  
559according to Coombs [13]), due they were bipeds, digitigrades and with long and  
560parasagittally oriented hindlimbs [64], although different taxa would be dispersed along a  
561continuum that includes different grades of cursoriality. The distribution in the morphospace  
562obtained in the multivariate analyses performed, could reflect such ecomorphological  
563diversity. Thus, those taxa with more elongated distal segments of the hindlimbs (i.e., tibia  
564and metatarsus), a more slender and compressed metapodium, and reduced lateral pedal digits  
565likely had a greater cursorial capacity [59, 61]. These taxa would locate closer to the

566 'cursorial extreme' of the multivariate continuum than taxa with shorter segments of the  
567 hindlimb, with a more robust metapodium, and lateral digits less reduced.

568         The elongation of the distal elements of the hindlimb (i.e., tibia and metatarsus) allows  
569 increasing of the stride length and speed of movements, which are related to a greater  
570 cursorial capacity [9, 61]. Garland and Janis [60] explained that the ratio between the lengths  
571 of metatarsus and femur (MT/F) was repeatedly considered by some authors as a predictor of  
572 locomotor performance in fossil forms. However, Garland and Janis [60] and other authors  
573 [65–67] warned that ratios between hindlimb bones are not good predictors of the type of  
574 locomotion, so limb proportions must be considered with caution. Thus, it is important take to  
575 account also qualitative aspects, such as the morphology of the metapodium, to make  
576 inferences about locomotor capacities.

577         The arctometatarsal and subarctometatarsal conditions could confer significant  
578 cursorial capabilities. Some authors [12, 15] have verified that theropod taxa with these  
579 conditions have distal elements of the hindlimb significantly more elongated than taxa with a  
580 plesiomorphic metapodium. Moreover, many authors have postulated biomechanic  
581 hypotheses about the performance of the arctometatarsal and subarctometatarsal foot, and  
582 how the interaction motions between metatarsals and transfer of forces along the metatarsus  
583 provide advantages during locomotion, which could represent benefits for the cursorial habit  
584 [12–17, 68].

585         Regarding morphology of pedal phalanges, in extant terrestrial birds with a cursorial  
586 locomotor mode and walking capacity (e.g., ratites such as ostriches, emus, *Pterocnemia*, and  
587 *Rhea*) the pre-ungual phalanges tend to shorten distally [9, 69–71]. Further, in these birds the  
588 foot is symmetrical since digit III is the more developed and the main weight bearer, with  
589 non-ginglymoid interphalangeal articular surfaces, whereas digits II and IV have a similar  
590 length to each other, are shorter than digit III and have more ginglymoid interphalangeal



591 articular facets, indicating that they were under higher torsional efforts [9, 72–73]. Similar  
592 features are observed especially in Mesozoic theropod taxa considered with greater cursorial  
593 capabilities, much of them possessing long tibiae and metatarsi and an arctometatarsalian  
594 condition, such as ornithomimids, alvarezsaurids, caenagnathids, and *Avimimus* (e.g., [9, 13,  
595 33, 38, 55, 74–83]).

596 By contrast, extant birds with a foot with grasping capacities are characterized by an  
597 elongation of the distal pre-ungual phalanges of the digits, especially the penultimate phalanx  
598 [69–71, 84–85]. This can be observed either in perching and raptorial extant birds. Even, the  
599 elongation of distal phalanges is convergently observed in arboreal mammals which have  
600 grasping autopodia, such as the sloths ([85], and references herein).

601

## 602 **Interpretation of the PPCA analyses related with the locomotor** 603 **habits of theropods**

604

605 Taking into account the diverse factors and how they affect differentially the hindlimb  
606 elements, it is important to consider both analyses together (i.e., long bones and phalanges  
607 proportions) to make adequate inferences about the locomotor habits of theropods. For  
608 instance, *Avimimus* and *Sinornithoides* are very close to each other in the PPCA morphospace  
609 constructed from the long bones measures, and there no evident differences (Fig 1), while the  
610 PPCA based on phalanges lengths reveals clear dissimilarities between these taxa (Figs 3 and  
611 14). The later analysis indicates that the cursorial capacities of *Avimimus* are greater than those  
612 of *Sinornithoides*, whose phalanges proportions are possibly more related to a grasping  
613 function.

614 Based on the results of the PPCA made from phalanges length, taxa such as *Avimimus*,  
615 *Cariama*, and *Rhea* are considered with greater cursorial capacities [86–88], which are

49

25

50

616 associated with more elongated proximal phalanges and a long digit III (Figs 3, 4 and 7).  
617 Other taxa, such as ornithomimids (especially *Struthiomimus*) also have traits related to more  
618 cursorial capabilities, i.e., more elongated proximal phalanges, although their digit III is not as  
619 long as in the taxa above mentioned. Instead, *Bubo*, *Turdus*, and some Mesozoic avialans  
620 close to them had a foot with elongated distal phalanges which possibly had more grasping  
621 capacities. Concerning taxa such as *Gualicho*, *Allosaurus*, *Gorgosaurus*, *Corythoraptor*, and  
622 *Khaan* they have slightly more elongated proximal phalanges, so could have had certain  
623 cursorial capacities, also taking into account they have a digit IV almost as long as digit III.  
624

625 **Fig 7. Comparison of the autopodium between several theropod taxa, including**

626 **unenlagiines and some extant birds, in anterior view.** (A) *Buitreraptor gonzalezorum*  
627 (based on MPCN-PV-598). (B) *Neuquenraptor argentinus* (based on the holotype, MCF-  
628 PVPH-77; phalanges III-4 and IV-4 lack in the original material). (C) *Rahonavis ostromi*  
629 (based on a cast of the holotype, FMNH PR 2830; phalanges III-4, IV-4 and IV-5 lack in the  
630 original material). (D) *Deinonychus antirrhopus*. (E) *Talos sampsoni*. (F) *Allosaurus gracilis*.  
631 (G) *Gallimimus bullatus*. (H) *Avimimus portentosus*. (I) *Bubo virginianus* (based on MACN  
632 2056a). (J) *Cariama cristata* (based on MACN 23873). (A) is inverted from the original  
633 material to compare better to remain taxa. In (I) and (J) the first digit is showed disarticulated  
634 from its natural position (totally turned backwards) for better visualization. (D), (F) and (G)  
635 modified from Fowler et al. [9]; (E) based on Zanno et al. [151]; (H) based on Vickers Rich et  
636 al. [80].

637

638 The position of dromaeosaurids in the morphospace, including *Buitreraptor*, and other  
639 taxa, such as *Anchiornis*, is related to their long digit IV and elongated distal phalanges (Figs  
640 3, 4 and 7). This feature could be related with their particular morphology where the digit II is

641 markedly short and thus digits III and IV are the main structures of the foot support [6, 8, 89–  
64294].

643 In the analysis based on long bones measurements (Fig 1) the PPC2 is less influenced  
644 by phylogeny and the distribution of taxa along this axis could show a clearer separation  
645 related with habits. The MzTer on more positive values of PPC2 (*Allosaurus*, *Ceratosaurus*,  
646 *Beishanlong*, *Garudimimus*), which show short and robust metatarsi, can be considered with a  
647 minor cursorial capacity than those taxa tending to locate at less positive and negative values  
648 of PPC2 (*Dilong*, *Archaeornithomimus*, *Elaphrosaurus*, and *Herrerasaurus*), which show  
649 longer and slender metatarsi. In the case of modern birds also is observed the same general  
650 trend. Coincidentally, the taxa on negative values generally have comparatively smaller body  
651 sizes, except for *Megalosaurus*.

652 Along the PPC1 those taxa tending to positive or low negative scores can be  
653 considered with less cursorial capacities than those located at more negative scores. Thus,  
654 taxa such as *Linhenykus* and *Parvicursor* are interpreted with high cursorial abilities, in  
655 addition to having a markedly elongated and slender highly derived arctometatarsus [33, 78,  
65695] (Fig 8). Unfortunately, these two taxa have not preserved all the pedal phalanges and so  
657 they cannot be included in the analysis based on phalanges lengths. However, other  
658 alvarezsaurid considered in the analysis, i.e., *Kolghuva* [96], shows pedal phalanges  
659 proportions that indicate cursorial capacities.

660

661 **Fig 8. Comparison of hindlimb bones of different theropod taxa, including unenlagiines**  
662 **and extant birds, showing the proportional lengths of the femur, tibia and metatarsus.**

663 (A) *Buitreraptor gonzalezorum* (based on MPCN-PV-598). (B) *Rahonavis ostromi* (based on  
664 a cast of the holotype: FMNH PR 2830). (C) *Deinonychus antirrhopus*. (D) *Sinornithoides*  
665 *youngi*. (E) *Tyrannosaurus rex*. (F) *Allosaurus fragilis*. (G) *Struthiomimus altus*. (H)

666 *Parvicursor remotus*. (I) *Archaeopteryx lithographica*. (J) *Struthio camelus* (based on CFA-  
667 OR-1560). (K) *Cariama cristata* (based on MACN 23873). (L) *Geranoaetus melanoleucus*  
668 (based on MACN 2129). (M) *Bubo virginianus* (based on MACN 2056a). (N) *Furnarius*  
669 *rufus* (based on MACN 68647). Hindlimbs are not to scale. (C), (E) and (G) modified from  
670 Ostrom [43]; (D) based on Russell and Dong [152]; (F) modified from Gatesy and Middleton  
671 [65]; (H) based on Karhu and Rautian [78]; (I) based on Mayr et al. [153].

672

673 Our quantitative analyses, in addition to other features already described  
674 (subarctometatarsal configuration; [42, 97]) indicate that *Buitreraptor* can be considered with  
675 probable high cursorial capabilities. Other MzTer with probable similar locomotor capacities  
676 are the dromaeosaurids *Zhenyuanlong* and the troodontids *Sinovenator* and *Mei*, which were  
677 already described as possessing an arctometatarsal or subarctometatarsal condition [2, 42, 52,  
678 97–100]. Further, these taxa present hindlimb and pes proportions similar to non-  
679 dromaeosaurid theropods such as *Struthiomimus*, an ornithomimid probably markedly  
680 cursorial, as also indicate the PPCA based on phalanges lengths. Notwithstanding,  
681 *Buitreraptor* has phalanges proportions indicating grasping adaptations and related with a  
682 lesser cursorial performance. Unfortunately, phalanges lengths of *Sinovenator*, *Mei*, and  
683 *Zhenyuanlong* were difficult to obtain, because fragmentary preservation and incomplete  
684 information of the descriptions of the taxa, although in *Sinovenator* phalanges of digit III  
685 appear to shorten distally and the phalanx IV-4 is slightly longer than IV-3 [48].

686

687 **Functional implications of the dromaeosaurid hindlimb**  
688 **morphology and differences between unenlagiines and**  
689 **eudromaeosaurs**

690

## 691 **Long bones proportions, morphology of the metatarsus and motion range**

### 692 **of digits**

693

694 The main differences between the hindlimbs of unenlagiines and eudromaeosaurs are related  
695 with the relative length and form of the metatarsus, and the morphology of the phalanges of  
696 the digit II [4, 42, 101–102]. In unenlagiines the metatarsus is significantly elongated when is  
697 compared with the femur and tibia (except in *Rahonavis*), and it is slender because its  
698 lateromedial width (ML) is significantly lower than its total length (MtL) (except in  
699 *Rahonavis*) (Figs 7 and 8), whereas in eudromaeosaurs the metatarsus is remarkably shorter  
700 and the ratio ML/MtL is larger. Moreover, unenlagiines show a subarctometatarsal condition,  
701 whereas eudromaeosaurs have a metatarsus more similar to the plesiomorphic condition [6,  
702 35, 44, 103–104]. These characters indicate that the metatarsus of eudromaeosaurs is overall  
703 more robust than that of unenlagiines.

704 The metatarsi of *Neuquenraptor* (MCF PVPH 77) and *Austroraptor* (MML 195) are  
705 incomplete, although their approximate length can be estimated, indicating they were very  
706 elongated with respect to the tibia and femur. Thus, these taxa possibly had length proportions  
707 of the hindlimb bones much similar to those of *Buitreraptor*. Moreover, *Neuquenraptor* and  
708 possibly *Austroraptor* (based on the specimen MML 220), also have a subarctometatarsal  
709 condition.

710 The long bone proportions of *Buitreraptor* are remarkably different with respect to  
711 those of eudromaeosaurs here analyzed, i.e., *Velociraptor*, *Deinonychus*, and *Bambiraptor*  
712 (Fig 8). Instead, *Buitreraptor* is more similar to other taxa with a relatively elongated  
713 metatarsus, either with an arctometatarsal, a subarctometatarsal, or non-subarctometatarsal  
714 condition, such as *Mahakala*, *Alnashetri*, *Zhongjianornis*, *Zhenyuanlong*, *Sinovenator*, and

57

29

58

715 *Mei*. These taxa are similar in size or smaller than *Buitreraptor* [50, 52, 98–100, 105–108].

716 According to previous authors a similar size and hindlimb proportions would presumably  
717 indicate a similar locomotor mode [12, 15, 65]. Moreover, this resemblance in the locomotor  
718 mode can be also supported by the similar metatarsus morphology between some of these  
719 taxa.

720 *Rahonavis* departs from the general morphology of other unenlagiines, by its shorter  
721 tibia and a shorter and wider non-subarctometatarsal metatarsus (Figs 7 and 8) [109]. On the  
722 other hand, *Rahonavis* has hindlimb proportions more similar to those of unenlagiines than  
723 those of eudromaeosaurs, especially because it has a comparatively short femur and long tibia.  
724 Thus, *Rahonavis* can be considered as the less cursorial unenlagiine analyzed, although  
725 clearly more cursorial than eudromaeosaurs.

726 Additionally, differences in the distal articular surfaces of metatarsals between  
727 unenlagiines and eudromaeosaurs were also denoted by previous authors (e.g., [3, 9, 42]). In  
728 eudromaeosaurs the MT I, II and III have a well-developed ginglymoid distal articular surface  
729 [5, 6, 9, 44–45]. This could indicate that the first phalanges flexed and extended  
730 predominantly in a single plane [9]. Instead, in unenlagiines the ginglymoid distal facet of the  
731 MT II and III is less developed, so Ph. II-1 and III-1 moved in a predominant vertical plane  
732 although probably with some degree of sideways movement. The distal surface of MT I of  
733 unenlagiines is ball-shaped, as in *Buitreraptor* (MPCA 238, [42, 97]) and *Rahonavis* (FMNH  
734 PR 2830) or it is slightly ginglymoid, as in *Neuquenraptor* [110–111]. Thus, in  
735 *Neuquenraptor* the range of movement was probably more similar to that of digit I of  
736 eudromaeosaurs, whereas in *Buitreraptor* and *Rahonavis* digit I could have had a greater  
737 motion range. The more restricted motion of digits in eudromaeosaurs (which is emphasized  
738 by the more ginglymoid interphalangeal articulations in comparison with unenlagiines) could  
739 be more resistant to torsional stress and thus preventing disarticulation of the joints during

740manipulation of the prey with a greater grasping force [9]. In the case of the distal facet of MT  
741IV it is generally more rounded in dromaeosaurids, which matches with the concave proximal  
742articular facet of Ph.IV-1. This trait possibly indicates more freedom of movement for digit  
743IV [9]. Thus, unenlagiines had the capacity to oppose pedal digits between them in a similar  
744way to *Deinonychus* [9]. Digits I and IV probably had a wide range of motion, which would  
745have allowed these digits converge during flexion, thus achieving a grip position.

746

### 747**Morphology of pedal phalanges**

748

749The only unenlagiine with all the pedal phalanges preserved to date is *Buitreraptor*. Our  
750results indicated that it is similar in phalanges proportions with respect to eudromaeosaurs  
751analyzed, i.e., *Deinonychus* and *Bambiraptor*. The three taxa highlight by their markedly  
752elongated digit IV, with a total length greater than that of digit III (Fig 7). In *Neuquenraptor*  
753and *Rahonavis* it can be estimated that digit IV is shorter than digit III, as in *Sinornithosaurus*  
754and *Microraptor*, because the sum of lengths of the other pre-ungual phalanges of digit IV is  
755significantly lower than the total length of digit III and although Ph. IV-4 has been equal in  
756length or slightly longer than Ph. IV-3 the complete digit IV would have been slightly shorter  
757than digit III. By contrast in other MzTer included in the analysis such as derived troodontids,  
758non-paravian coelurosaurs and basal tetanurans the digit III is the longest and the digit IV is  
759significantly shorter, which are proportions related with probable more cursorial capacities [9,  
76072–73]. So, the length proportions of dromaeosaurids digits, including unenlagiines and  
761especially *Buitreraptor*, seem to indicate a restriction to their cursorial habit.

762       Also, dromaeosaurids show a significant elongation of the distal pre-ungual phalanges,  
763a feature related with grasping capacities (see cited literature above). Generally, in  
764unenlagiines the length proportions of the distal phalanges of digit III are similar to those of

765 eudromaeosaurs, although in the digit II the second phalanx is shorter than the first one (S1  
766 Appendix), indicating slightly lower grasping capacities in unenlagiines. In others  
767 dromaeosaurids, such as *Microraptor*, Ph. III-3 is significantly shorter than III-2, a feature  
768 that also could indicate a decreasing of grasping capacities. Unfortunately, the lack of  
769 preserved elements prevents a more accurate analysis of the phalangeal proportions of  
770 *Neuquenraptor* and *Rahonavis*, although the available data and the apparently long distal  
771 phalanges of digit IV in *Neuquenraptor* indicate for this taxon more accentuated grasping  
772 capacities than other unenlagiines and resembling those of eudromaeosaurs (S1 Appendix).

773        In other groups of MzTer distal phalanges of digit IV generally maintain a similar  
774 length (S1 Appendix and S5 Text). By contrast, the length proportion of distal phalanges of  
775 digits II and III is more variable, due in some taxa these phalanges are shorter than the  
776 proximal ones (taxa considered as more cursorials) whereas in others taxa the distal phalanges  
777 are longer although they not surpass the length of the proximal ones (taxa with possible  
778 grasping abilities of the feet). In extant birds with a grasping foot, such as *Turdus* and *Bubo*,  
779 the distal phalanges are significantly long (S1 Appendix and Fig 7).

780        Many current birds with grasping capacities of the feet are ‘perchers’ and have  
781 arboreal habits, i.e., they are predominantly arboreal foragers [112]. An arboreal habit for  
782 some unenlagiines is difficult to envisage or impossible in taxa such as *Neuquenraptor*,  
783 *Unenlagia*, and *Austroraptor* because of their large sizes. Further, this habit is correlated in  
784 paravians with aerial locomotor capacities, although previous authors considered that  
785 aerodynamical features in large-sized dromaeosaurids were lost, as suggested by the scarce  
786 development or lack of papillae for feather attachment on the ulna [105]. In smaller taxa such  
787 as *Buitreraptor* and *Rahonavis* this lifestyle would have been more probable not only because  
788 of their smaller size but also because they have evidence of feathered forelimbs by preserved  
789 quill knobs (in *Rahonavis* [109]) and many osteological traits which suggest the capacity of



790flapping flight [4]. Also, it is possible that *Buitreraptor* and *Rahonavis* have been able to  
791climb trees, especially considering the claw of pedal digit II as a potential tool for this  
792purpose [7]. However, it is important to take into account the paleoenvironment in which they  
793lived, since for example *Buitreraptor* was found in sedimentites that indicate a mainly aeolian  
794environment and the existence of a large desert [113–116], where the trees were probably  
795very scarce or nonexistent. So, the hindlimb morphology of *Buitreraptor*, mainly that of the  
796metatarsus, is probably more related to a terrestrial habit than to an arboreal one.

797       Concerning qualitative aspects of the digit II of unenlagiines, it is modified as in  
798eudromaeosaurs, although important differences are observed. First, in unenlagiines such as  
799*Buitreraptor*, *Neuquenraptor*, and *Unenlagia paynemili* (MUCPv 1066), the distal articular  
800surface of phalanx II-2 is less proximally extended. This feature restricts the extension of the  
801ungual phalanx, as can be observed in an isolated articulated digit II of *Buitreraptor* (MPCA  
802478 [42]), in which the ungual seems to be totally extended (Fig 9). In *Deinonychus* and  
803*Bambiraptor* this articular surface is more proximally extended (FAG personal observation of  
804YPM 5205 and AMNH FR 30556), and thus the claw had the possibility of a greater  
805extension (see [8]). Additionally, the phalanges of digit II of eudromaeosaurs are  
806comparatively more robust than those of unenlagiines. This digit is the main implied in the  
807predatory function, so a robust digit II in eudromaeosaurs could be advantageous to capture  
808and subdue large prey. Moreover, eudromaeosaurs have a short Ph. II-1. Taking into account  
809that the Ph. II-1 represent part of the out-lever of the flexor muscle of the digit (possibly the  
810*M. flexor perforatus digiti II*, which probably was inserted onto the proximoventral zone of  
811the phalanx as in extant birds [117–118]), the shortness of this phalanx could maximize  
812mechanical advantage of the flexor and the grasping strength of digit II. Another difference is  
813the more proximally extended proximoventral heel of phalanx II-2 of eudromaeosaurs, which  
814possibly was an insertion point of flexor muscles [6].

815

816**Fig 9. Comparison between pedal phalanges II-2 of unenlagiines and eudromaeosaurs,**

817**in dorsal view.** The red dotted line indicates the posterior limit of the collateral ligament pit

818and the yellow dotted line indicates the posterior limit of the distal articular facet. (A)

819*Buitreraptor gonzalezorum* (MPCA 238). (B) *Neuquenraptor argentinus* (MCF PVPH 77).

820(C) *Unenlagia paynemili* (MUCPv 1066). (D) Articulated phalanges II-1, II-2 and II-3 of

821*Buitreraptor gonzalezorum* (the ungual phalanx is totally extended, so it is clear the proximal

822extent of the articular surface). (E) *Bambiraptor feinbergorum* (AMNH FR 30556). (F)

823*Deinonychus antirrhopus* (YPM 5205). Scale bars=1cm. (F) is courtesy of the Division of

824Vertebrate Paleontology; YPM VP.005205, Peabody Museum of Natural History, Yale

825University, New Haven, Connecticut, USA; [peabody.yale.edu](http://peabody.yale.edu); photography by Federico A.

826Gianechini.

827

828 So, although in general traits the unenlagiines and eudromaeosaurs have phalanges of

829digit II with similar morphological characteristics, it is observed that these characters are

830more accentuated in the eudromaeosaurs, including a shorter phalanx II-1, a phalanx II-2 with

831a more proximally extended proximoventral heel, a shorter and more dorsoventrally

832constrained shaft, and a distal articular surface more extended proximally. This seems to

833indicate the presence of a digit II with the capacity of exert stronger predatory efforts in

834eudromaeosaurs, which could be an advantageous feature for subdue large preys. Conversely,

835the mentioned differences in the phalangeal morphology of unenlagiines could indicate weak

836predatory efforts, but the longer Ph. II-1 also suggests faster movements of digit II, what

837could be eventually useful for hunting small preys.

838 Regarding the degree of development and curvature of the claw of digit II it is difficult

839to evaluate differences between eudromaeosaurs and unenlagiines, mainly because most

840unenlagiines have not preserved a complete unguis. With the available data (S6 Table) we do  
841not observe clear evidences indicating that eudromaeosaurs have a more developed and more  
842curved unguis than unenlagiines.

843 Another possible difference between unenlagiines and eudromaeosaurs is respect to  
844the location of digit I, which might have some implications in the grasping function. For  
845instance, in *Deinonychus* the digit I is articulated to the middle zone of the diaphysis of the  
846MT II [6, 9], suggesting it would have closed over the posterior face of the metatarsus during  
847flexion. Moreover, previous authors proposed that in this taxon the metatarsus would have  
848been positioned semi-horizontally while the animal was subject to its prey and thus helping to  
849restrain it [9]. Among unenlagiines only one specimen of *Buitreraptor* (MPCN-PV-598)  
850preserved a complete and articulated foot, in which the digit I seems to be located in the  
851original position, articulated to the medial and distal surface of MT II [97]. This location  
852could indicate that the metatarsus have been in a more vertical position during the submission  
853of the prey, which would have been more effective for the digit I to participate in the gripping  
854function.

855

## 856**Morphological and functional correlates in extant raptorial birds and** 857**possible resemblances with dromaeosaurids**

858

859 An interesting convergence is observed between extant raptorial birds and some  
860eudromaeosaurs, in the morphospace of the long bone measurements. Both groups tend to  
861positive PPC2 values (Fig 1), due they have longer femora and consequently shorter  
862metatarsi. Moreover, raptorial birds converge specifically with *Deinonychus* and *Velociraptor*  
863in the presence of wider metatarsi, as is reflected by their less negative values for PPC1 in  
864both groups. Generally, in current raptorial birds a shorter and robust metatarsus is related

865with the ability of the foot to exert a greater grip force, whereas a longer metatarsus is related  
866with a minor grip force although it has the capacity for rapid movement [9, 53, 66–67, 119–  
867120]. In a general way, owls (Strigiformes) have the shortest and more robust metatarsus  
868whereas falconids and especially accipitrids have a longer and slender metatarsus [53, 119–  
869120]. Thus, owls have a greater grip capacity and strength, although these features also are  
870related to other characters of the foot such as the presence of sesamoids, a specialized tendon  
871locking mechanism and a facultative zygodactyl condition [53, 119–120]. Between the  
872raptorial birds included in our analyses, *Milvago* and *Polyborus* (falconids of the subfamily  
873Polyborinae) are characterized by relatively longer and slender tarsometatarsus when are  
874compared with accipitrids (i.e., *Geranoaetus* and *Elanus*). This could indicate greater  
875cursorial capacities, in agreement to what was expressed by previous authors [121].

876         Analogously, the short and robust metatarsus of eudromaeosaurs, such as *Velociraptor*  
877and *Deinonychus*, could have allowed a great generation of grip force [6, 9]. By contrast, the  
878elongated subarctometatarsus of unenlagiines could have had a greater capacity of rapid  
879movement, like falconids and accipitrids, although it could have reduced grip strength [9].

880         Despite morphological and even functional features can be compared between these  
881theropods and extant raptorial birds, it must be considered that these birds are predominantly  
882aerial with a generally limited terrestrial locomotion (but see [121]). Many common features  
883in the autopodium of raptorial birds can be interpreted as the result of a predominant influence  
884of hunting and grasping specializations (e.g., elongation of distal non-ungual phalanges  
885independently of the specific type of prey and the hunting method employed by them; [69–71,  
88685, 122], instead terrestrial locomotion. Conversely, dromaeosaurids, like most Cretaceous  
887theropods, had a terrestrial locomotion, and it is expectable that both factor of selective  
888pressures, i.e., predation and terrestrial locomotion, have a great influence in the hindlimb and  
889autopodium. This is a main reason to explain the segregation in the morphospace between

890 extant birds and dromaeosaurids, and also it might explain the presence of elongated distal  
891 phalanges in dromaeosaurids although not as strikingly long as those of extant raptorial birds  
892 (see also the study about the modular fashion of evolution of pedal phalanges proportions  
893 [85]). Thus, differences in hindlimb between eudromaeosaurs and unenlagiines can be  
894 considered mainly focusing in these, partially antagonist, specializations. The morphological  
895 design of the eudromaeosaurs autopodia indicates a more marked specialization to the  
896 predatory habit, whereas in unenlagiines a more marked cursorial specialization would have  
897 been occurred.

898

## 899 **Locomotor and predatory habits of *Buitreraptor* and other**

### 900 **unenlagiines**

901

902 Unenlagiines possibly had a better cursorial locomotor performance and the capacity to reach  
903 greater running velocities than eudromaeosaurs with shorter and more robust metatarsi. Of  
904 course, this does not mean that eudromaeosaurs did not have an effective locomotion and the  
905 ability to run fast, but that the morphological characters of the hindlimb of the unenlagiines  
906 would have given these animals greater and more efficient cursorial capacities. Possibly,  
907 eudromaeosaurs may have made sudden runs at high speeds, but for shorter periods of time or  
908 for short distances, while unenlagiines could maintain an accelerated pace for more time and/  
909 or distance. Regarding the metatarsus of eudromaeosaurs it has a structure with functional  
910 capacities possibly more useful to predation than to cursorial locomotion. About the  
911 morphology of pedal phalanges the discrepancies observed between both groups, especially  
912 those of digit II, could be more directly related with different predatory habits.

913         Despite the mentioned dissimilarities between unenlagiines and eudromaeosaurs, it is  
914 remarkable that is the general structure of the metatarsus which shows a more drastic

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37

74

915difference. The metapodium had a greater morphological plasticity along evolution of  
916dromaeosaurids, since its structure differs significantly in unenlagiines and eudromaeosaurs  
917(and in microraptorines, which also have a subarctometatarsal condition), in relation to the  
918relative and different importance of the mechanical benefits associated both with predatory  
919and locomotor functions in both clades. On the other hand, as was explained above, the length  
920proportions of phalanges are not meaningfully dissimilar between these groups. This factor  
921could be related to the phalanges are the main elements implied in predator functions, which  
922exerted a greater selective pressure on their morphology, independently of the feeding  
923strategy and locomotor habit. Nevertheless, some specific differences, such as the longer and  
924slender phalanx II-1 and the greater freedom of movement of the remaining digits of  
925unenlagiines, could allow them a fast and secure grip of small and agile/elusive prey that do  
926not demand great efforts to be subdued.

927        Unenlagiines have similar modifications of the metapodium than microraptorines and  
928probably they had a similar mode of moving on the ground, beyond the capacity of gliding  
929postulated for some microraptorines [123–125]. It can be that these two groups of  
930dromaeosaurids used digit II for predation, although the predatory habits, i.e., the hunting way  
931and the type of prey, were not necessarily the same, also taking into account that  
932microraptorines (at least *Microraptor* and *Sinornithosaurus*) have a phalanx II-1 shorter than  
933II-2 (S1 Appendix), as in eudromaeosaurs. Moreover, some specimens of *Microraptor gui*  
934indicate it fed mammals, enantiornithine birds, and fishes, which is evidence of diverse  
935feeding habits and possibility of exploit different substrates such as ground, trees, and water,  
936in that taxon [126–128].

937        Likely, unenlagiines preyed on rapid and elusive animals, although it is difficult to  
938know more specifically the type of prey that they hunted, even without having direct  
939evidences such as the gut content of *Microraptor* specimens. Nevertheless, it is possible to

940 achieve an approximation of the feeding habits of unenlagiines, especially for the better  
941 represented taxa such as *Buitreraptor*. Regarding other unenlagiines the information is  
942 scarcer, so it is more difficult to infer if among them there were noticeable differences in the  
943 feeding modes and on the types of animals that preyed.

944       Considering the small size, slender proportions (especially those of metapodium), and  
945 the inferred cursorial capacities, *Buitreraptor* probably foraged on the ground searching small  
946 preys, such as invertebrates, reptiles or mammals, throughout large distances and probably  
947 employing high-speed pursuits in some cases. The fauna recorded from the fossiliferous area  
948 of La Buitrera, where *Buitreraptor* was discovered, also includes remains of small tetrapods  
949 such as snakes, sphenodonts, crocodyliforms, and mammals [129–133], which could have  
950 been potential dams. *Buitreraptor* would have employed its pes to subjugate and keep the  
951 prey immobile once it was reached. The fast movements and curved enlarged claw of digit II  
952 would have helped this function, and eventually causing serious injuries or even death of the  
953 prey.

954       Another reliable indicator of the type of diet and feeding strategy is the dental  
955 morphology. The teeth of *Buitreraptor* are numerous, tiny, lateromedially compressed, and  
956 devoid of denticles [134]. Instead, eudromaeosaurs are generally characterized by larger  
957 serrated teeth, such as *Dromaeosaurus*, *Deinonychus*, *Velociraptor*, *Saurornitholestes*, and  
958 *Tsaagan* [5–6, 35, 135–137], although many taxa have denticles only on the distal carina.  
959 These features would have allowed ingesting larger preys or tearing and cutting the flesh from  
960 them into smaller pieces. Feeding models were proposed for some taxa, such as *Deinonychus*  
961 [9], although they are difficult to apply to *Buitreraptor* because the size of their teeth and the  
962 lack of denticles. Due the latter feature and the absence of other flesh-tearing structures (e.g.,  
963 the tomial tooth of extant raptorial birds) it is very likely that *Buitreraptor* has consumed  
964 whole small animals and that the teeth were mainly employed as a tool to hold the dams. Also

965 is possible these teeth have been used to fragment small preys, to consume them in more than  
966 one swallow. In previous works it has been postulated that the dentition of *Buitreraptor*  
967 would indicate a piscivorous feeding mode [134]. Certainly, *Microraptor* also has small non-  
968 serrated teeth and there is evidence that it fed on fishes. However, this unique feature is not a  
969 reliable indicator of piscivory, since other morphological evidences must be taken into  
970 account. Moreover, *Microraptor* included in its diet other animals in addition to fish, as  
971 mentioned above. *Buitreraptor* also is characterized by having long forelimbs and hands [4,  
972 97], so it could also have used them to handle the prey once it was captured and subjugated  
973 with its feet.

974       Among extant long-legged predominantly terrestrial birds that forage on the ground  
975 and hunt small preys are included the seriemas (Cariamiformes) and the secretary bird  
976 (Falconiformes). The secretary bird kicks and stamp on the prey until it is wounded or  
977 incapacitated and then takes it with its beak [138–140]. On the other hand, the red-legged  
978 seriema (*Cariama cristata*) takes the prey with the beak and hits it on the ground with sudden  
979 movements of the head until it is injured [141]. An interesting trait of this seriema is it has a  
980 markedly curved unguis phalanx in the second digit ([142–143]; FAG personal observation of  
981 MACN 23873). Some authors proposed this bird use this claw to hold the prey against the  
982 ground, although others do not agree ([86], and references therein). The extinct phorusrhacids  
983 were terrestrial generally flightless carnivorous birds which also are characterized by having a  
984 markedly developed and curved unguis of the second digit [143–145]. Some authors have  
985 proposed that this claw could be used as a means of apprehension of the prey on the substrate,  
986 then using the beak to tear it apart [143]. *Buitreraptor* could be used its pedal claw in a  
987 similar way than that proposed for seriemas and phorusrhacids, although there are no direct  
988 evidences.



989        Regarding other unenlagiines such as *Austroraptor* it could be proposed a similar  
990strategy of hunting and subjection of the dam than that of *Buitreraptor*. Although  
991*Austroraptor* is significantly larger (estimated total length: 5 m) it has numerous and small  
992teeth in comparison with the size of the skull, and also they lack denticles [134, 146–148].  
993However, the teeth of *Austroraptor* are conical, so they probably were more resistant and  
994could have employed to retain and dismember large prey. Due to *Austroraptor* probably had  
995similar length proportions of the hindlimb bones than *Buitreraptor* and a subarctometatarsal  
996condition it could have had good cursorial capacities. By other side, *Austroraptor* has  
997strikingly shorter arms than other unenlagiines, so it would not have used them to manipulate  
998the prey, or at least not in the same way that *Buitreraptor*.

999        *Rahonavis* probably had less cursorial capacities due its hindlimb morphology,  
1000although it has a relatively long tibia, so fast chases of preys cannot be ruled out as a hunting  
1001strategy used by this taxon. Moreover, *Rahonavis* has a digit II similar to that of other  
1002unenlagiines, so it probably had similar functional capacities. However, the distal phalanges  
1003are shorter than in other unenlagiines, so it probably had slightly lesser gripping abilities.  
1004Unfortunately cranial remains and teeth of *Rahonavis* are unknown, so it is more difficult to  
1005speculate about the type and size of animals that it could have been preyed upon. Surely it fed  
1006on small preys, although is not possible to know if it was able to tear flesh from larger preys.  
1007Cranial remains neither were preserved in *Neuquenraptor*, although the features of its  
1008hindlimb indicate that velocity probably was important to obtain its preys. Regarding others  
1009unenlagiines, such as *Unenlagia comahuensis* and *Unenlagia paynemili*, they have not  
1010preserved cranial bones although have preserved scarce hindlimb remains, especially  
1011phalanges of digit II, which are much similar to those of the other unenlagiines [101–102,  
1012149–150]. So, mainly due to the lack of skull and metatarsus remains and most of pedal  
1013phalanges it is more difficult to infer locomotor and predatory habits of these two species.

1014

## 1015 **Conclusions**

1016

1017 Morphological differences in the hindlimb between unenlagiines and eudromaeosaurs reflect  
1018 differences both in locomotor and predatory habits. In unenlagiines the presence of a long  
1019 tibia and a long, slender and subarctometatarsal metatarsus suggest greater cursorial capacities  
1020 with respect to eudromaeosaurs, which have a shorter, wider and non-subarctometatarsal  
1021 metatarsus. Regarding pedal digits the two groups of dromaeosaurids have similar length  
1022 proportions and based on the elongation of the distal phalanges they probably have the  
1023 capacity of grasping. However, morphological features of eudromaeosaurs, i.e., a more robust  
1024 metatarsus; distal articular surfaces of metatarsal I, II, and III, and interphalangeal articular  
1025 surfaces markedly ginglymoid; and a shorter phalanx II-1, indicate that these dromaeosaurids  
1026 possibly exerted more grip strength than unenlagiines. By contrast, proportions and  
1027 slenderness of unenlagiines would not have allowed them to perform high grasping forces but  
1028 instead they may have been able to make faster movements with both the metatarsal and the  
1029 digit II. Moreover, this morphofunctional difference is analogously observed in extant  
1030 raptorial birds, since in the latter those taxa with the shortest metatarsus, such as owls, have  
1031 the ability to produce the greatest grip force, whereas those taxa with longer metatarsi, such as  
1032 polyborine falconiforms, generate a lesser grip force although can effect faster movements  
1033 with the pes.

1034         Despite the presence of morphological differences of pedal phalanges between  
1035 unenlagiines and eudromaeosaurs, these discrepancies are not as drastic as those observed  
1036 between the metatarsus of both dromaeosaurids groups. This, together with the similar length  
1037 proportions of pedal phalanges seem to indicate that the morphology of these pedal elements

1038 varied scarcely along dromaeosaurid evolution, a factor probably related with a greater  
1039 selective pressure exerted by the predatory function.

1040       Among unenlagiines, *Buitreraptor gonzalezorum*, with its small size, high cursorial  
1041 capacities, a long metatarsus and phalanx II-1, more mobile phalanges, and tiny teeth,  
1042 probably was a terrestrial predator that preyed on small elusive animals, such as arthropods,  
1043 lizards, mammals, etc., through rapid movements of its pes. *Rahonavis ostromi* also was a  
1044 small-sized unenlagiine, although its morphology seems to indicate it had lesser cursorial  
1045 abilities. Probably, its small body size and potential capacity of climbing could capacitate it to  
1046 an arboreal habit. Other unenlagiines, such as the large-sized *Austroraptor cabazai* and the  
1047 medium-sized *Neuquenraptor argentinus* probably preyed on larger animals, also making use  
1048 of its high cursorial faculties. Regarding other taxa, such as *Unenlagia comahuensis* and  
1049 *Unenlagia paynemili*, are more fragmentary and so is much difficult to infer a locomotor and  
1050 predatory habit.

1051       Along dromaeosaurid evolution the different lineages seem to have diverged in varied  
1052 lifestyles, as is documented by unenlagiines, microraptorines, eudromaeosaurs, and recently  
1053 by halszkaraptorines [11]. Future studies, such as reconstructions of the muscular system, will  
1054 be necessary to analyze the hindlimb as an osteo-muscular integrated complex and how it  
1055 would have been involved both in locomotion and depredation in dromaeosaurids. These  
1056 paleobiological aspects will help us to have a better comprehension of the dromaeosaurid  
1057 evolutionary story and about the role of these theropods within the ecosystems in which they  
1058 lived.

1059

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1073

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## 1473 **Supporting information**

### 1474 **S1 Appendix. Database including measurements of taxa used for the phylogenetic**

1475 **principal component analyses.** Measurements include those of long bones of the  
1476 hindlimb and pedal phalanges lengths.

119

120

1477**S2 Fig. Example figure showing the methodology for measuring curvature angles of**

1478 **ungual pedal phalanges.**

1479**S3 Table. Results of the phylogenetic principal component analysis based on long bones**

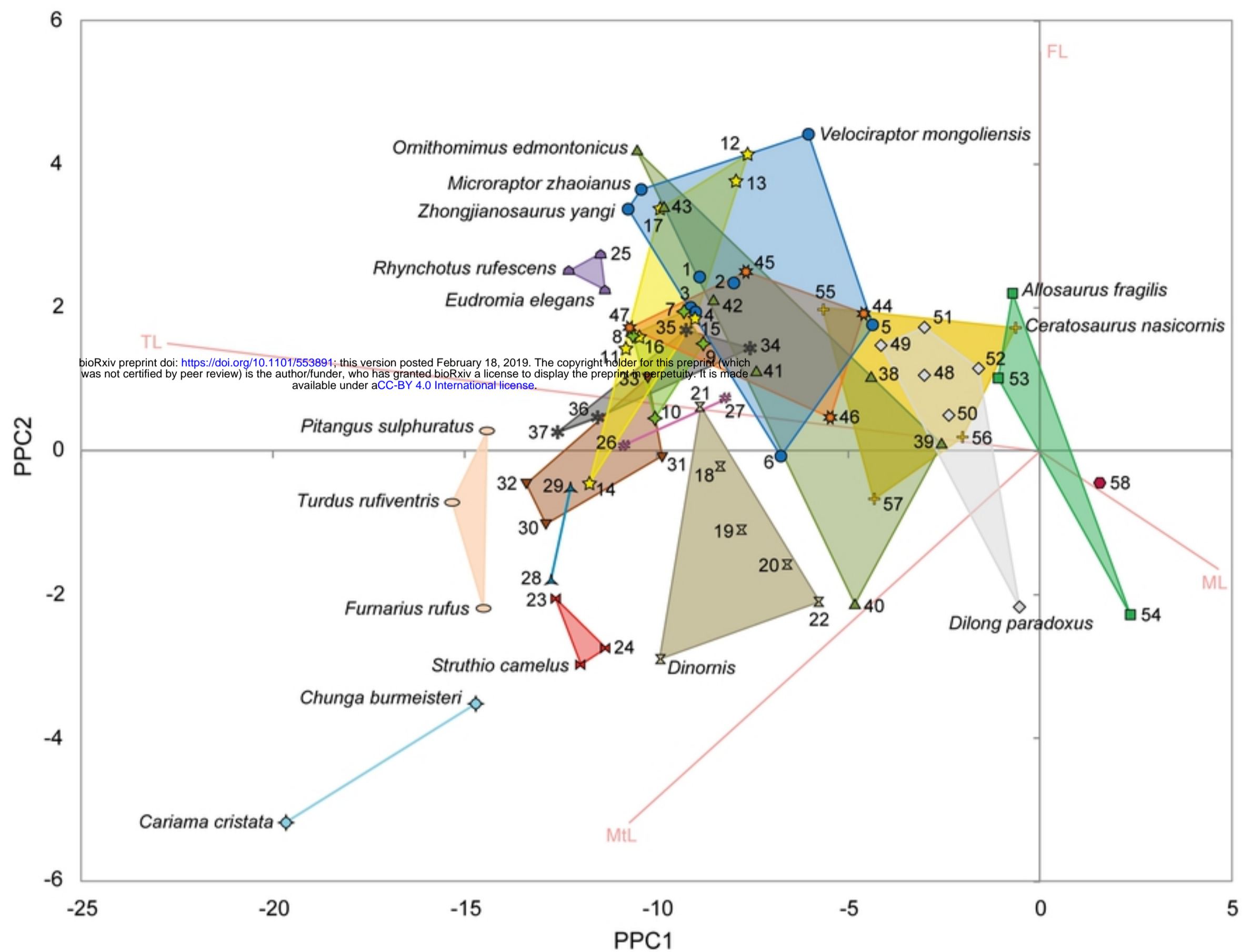
1480 **measurements.**

1481**S4 Table. Results of the phylogenetic principal component analysis based on phalanges**

1482 **lengths.**

1483**S5 Text. Supplementary discussion.**

1484**S6 Table. Curvature angles of pedal ungual phalanges of dromaeosaurids.**



- |                                      |   |  |                              |
|--------------------------------------|---|--|------------------------------|
| 1- <i>Buitreraptor gonzalezorum</i>  | 22- <i>Pachyornis</i>                   | 43- <i>Rativates evadens</i>               | ● Herrerasauridae            |
| 2- <i>Rahonavis ostromi</i>          | 23- <i>Pterocnemia pennata</i>          | 44- <i>Khaan mckennai</i>                  | + non Tetanurae Neotheropoda |
| 3- <i>Mahakala omnogovae</i>         | 24- <i>Rhea americana</i>               | 45- <i>Wulatelong gobiensis</i>            | ■ basal Tetanurae            |
| 4- <i>Zhenyuanlong suni</i>          | 25- <i>Nothoprocta cinerascens</i>      | 46- <i>Chiostenotes pergracilis</i>        | ◇ Tyrannosauroidae           |
| 5- <i>Deinonychus antirrhopus</i>    | 26- <i>Geranoaetus melanoleucus</i>     | 47- <i>Avimimus portentosus</i>            | ▲ Ornithomimosauria          |
| 6- <i>Bambiraptor feinbergi</i>      | 27- <i>Elanus leucurus</i>              | 48- <i>Gorgosaurus libratus</i>            | ★ Oviraptorosauria           |
| 7- <i>Mei long</i>                   | 28- <i>Polyborus plancus</i>            | 49- <i>Albertosaurus sarcophagus</i>       | * Alvarezsauroidea           |
| 8- <i>Sinornithoides youngi</i>      | 29- <i>Milvago chimango</i>             | 50- <i>Daspletosaurus torosus</i>          | ● Dromaeosauridae            |
| 9- <i>Sinovenator changae</i>        | 30- <i>Tyto alba</i>                    | 51- <i>Tarbosaurus bataar</i>              | ◆ Troodontidae               |
| 10- <i>Anchiornis huxleyi</i>        | 31- <i>Bubo virginianus</i>             | 52- <i>Tyrannosaurus rex</i>               | ★ Mesozoic Avialae           |
| 11- <i>Archaeopteryx</i>             | 32- <i>Athene cunicularia</i>           | 53- <i>Eustreptospondylus oxoniensis</i>   | ⊗ Dinornithiformes           |
| 12- <i>Sapeornis chaoyangensis</i>   | 33- <i>Asio flammeus</i>                | 54- <i>Megalosaurus bucklandii</i>         | ⊠ Struthioniformes           |
| 13- <i>Confuciusornis sanctus</i>    | 34- <i>Haplocheirus sollers</i>         | 55- <i>Coelophysis bauri</i>               | ▲ Tinamiformes               |
| 14- <i>Hongshanornis longicresta</i> | 35- <i>Alnashetri cerropoliciensis</i>  | 56- <i>Dilophosaurus wetherilli</i>        | ⊞ Accipitridae               |
| 15- <i>Zhongjianornis yangi</i>      | 36- <i>Linhenykus monodactylus</i>      | 57- <i>Elaphrosaurus bambergi</i>          | ▲ Falconiformes              |
| 16- <i>Yanomys martini</i>           | 37- <i>Parvicursor remotus</i>          | 58- <i>Herrerasaurus ischigualastensis</i> | ▼ Strigiformes               |
| 17- <i>Yixianornis grabaui</i>       | 38- <i>Garudimimus brevipes</i>         |  | ○ Passeriformes              |
| 18- <i>Anomalopteryx didiformis</i>  | 39- <i>Beishanlong grandis</i>          |  | ◆ Cariamiformes              |
| 19- <i>Emeus</i>                     | 40- <i>Archaeornithomimus asiaticus</i> |  |                              |
| 20- <i>Euryapteryx</i>               | 41- <i>Gallimimus bullatus</i>          |  |                              |
| 21- <i>Megalapteryx didinus</i>      | 42- <i>Struthiomimus altus</i>          |  |                              |

Figure 1

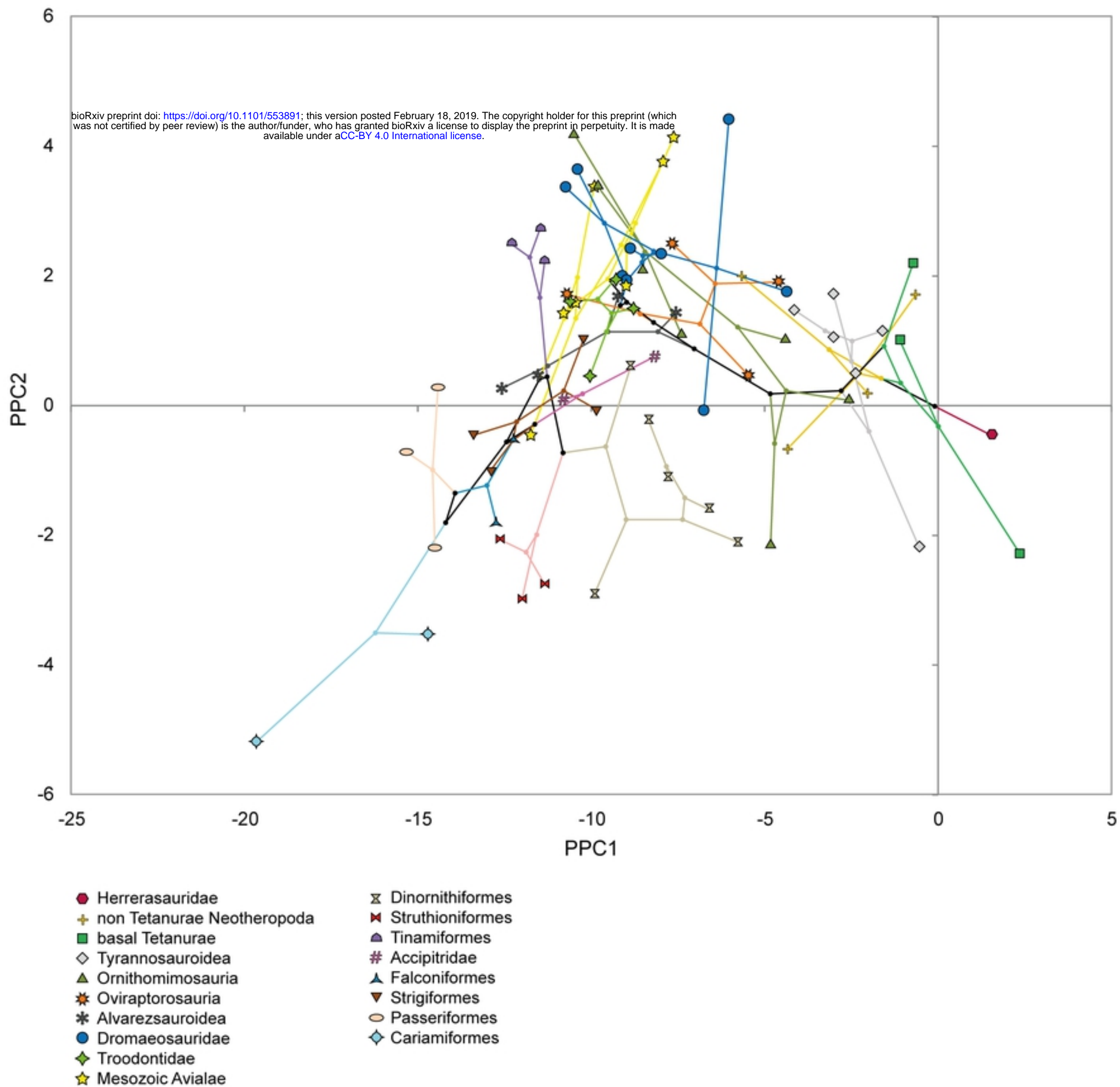


Figure 2

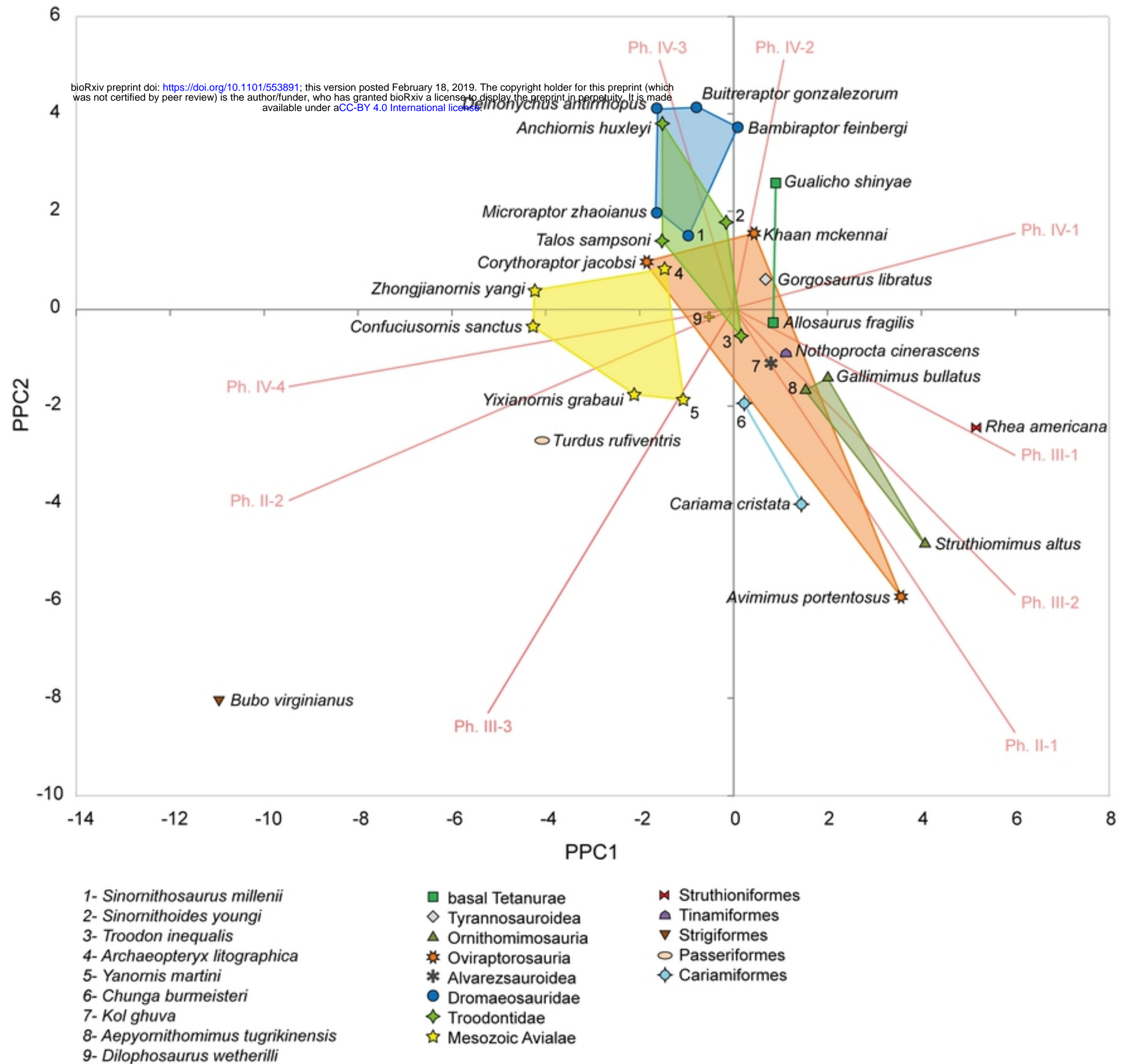
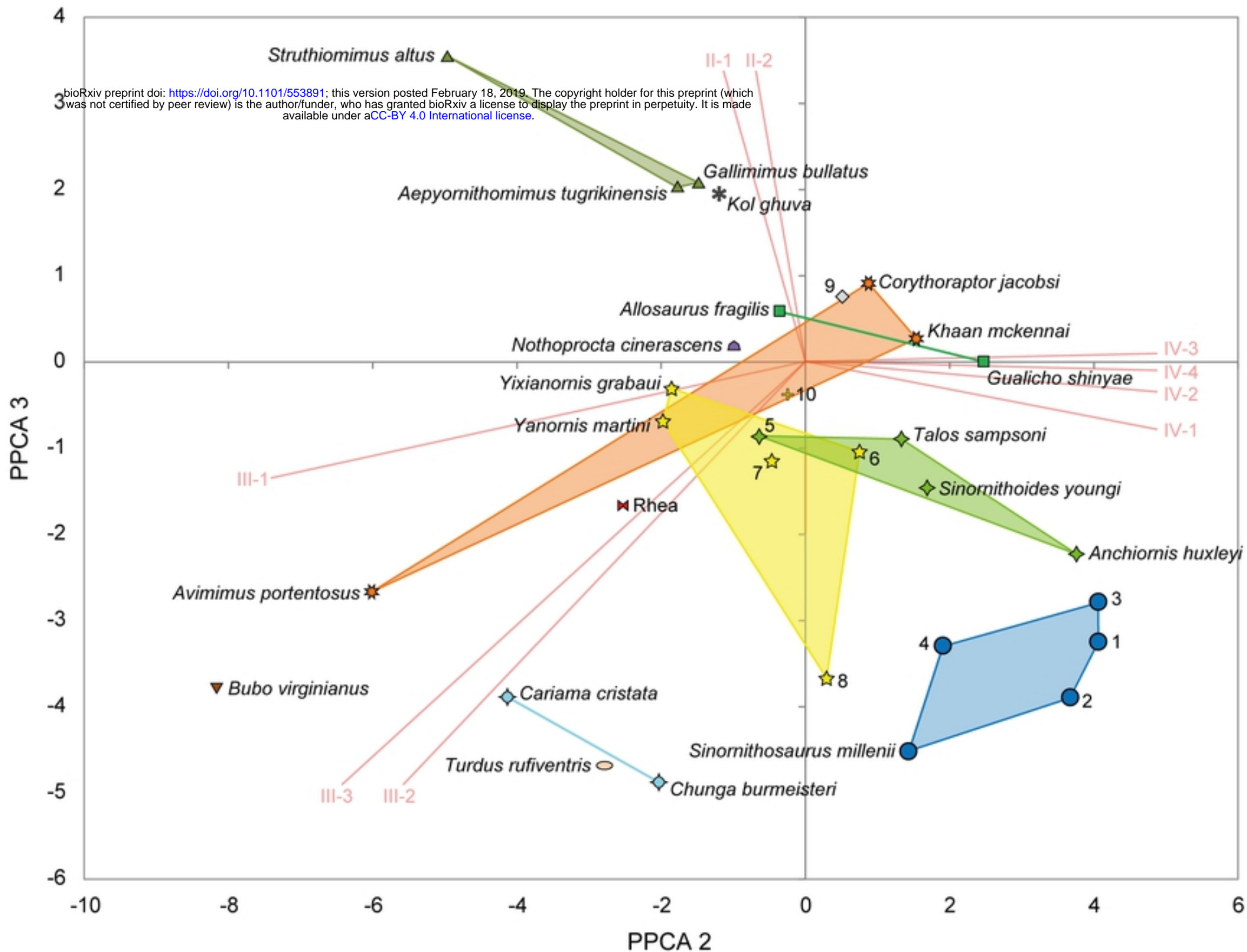


Figure 3





- 1- *Buitreraptor gonzalezorum*
- 2- *Bambiraptor feinbergi*
- 3- *Deinonychus antirrhopus*
- 4- *Microraptor zhaoianus*
- 5- *Troodon inequalis*
- 6- *Archaeopteryx lithographica*
- 7- *Confuciusornis sanctus*
- 8- *Zhongjianornis yangi*
- 9- *Gorgosaurus libratus*
- 10- *Dilophosaurus wetherilli*

- + non Tetanurae Neotheropoda
- basal Tetanurae
- ◇ Tyrannosauroidae
- ▲ Ornithomimosauria
- ★ Oviraptorosauria
- \* Alvarezsauridae
- Dromaeosauridae
- ◆ Troodontidae
- ★ Mesozoic Avialae
- ▣ Struthioniformes
- ▲ Tinamiformes
- ▼ Strigiformes
- Passeriformes
- ◆ Cariamiformes

Figure 4

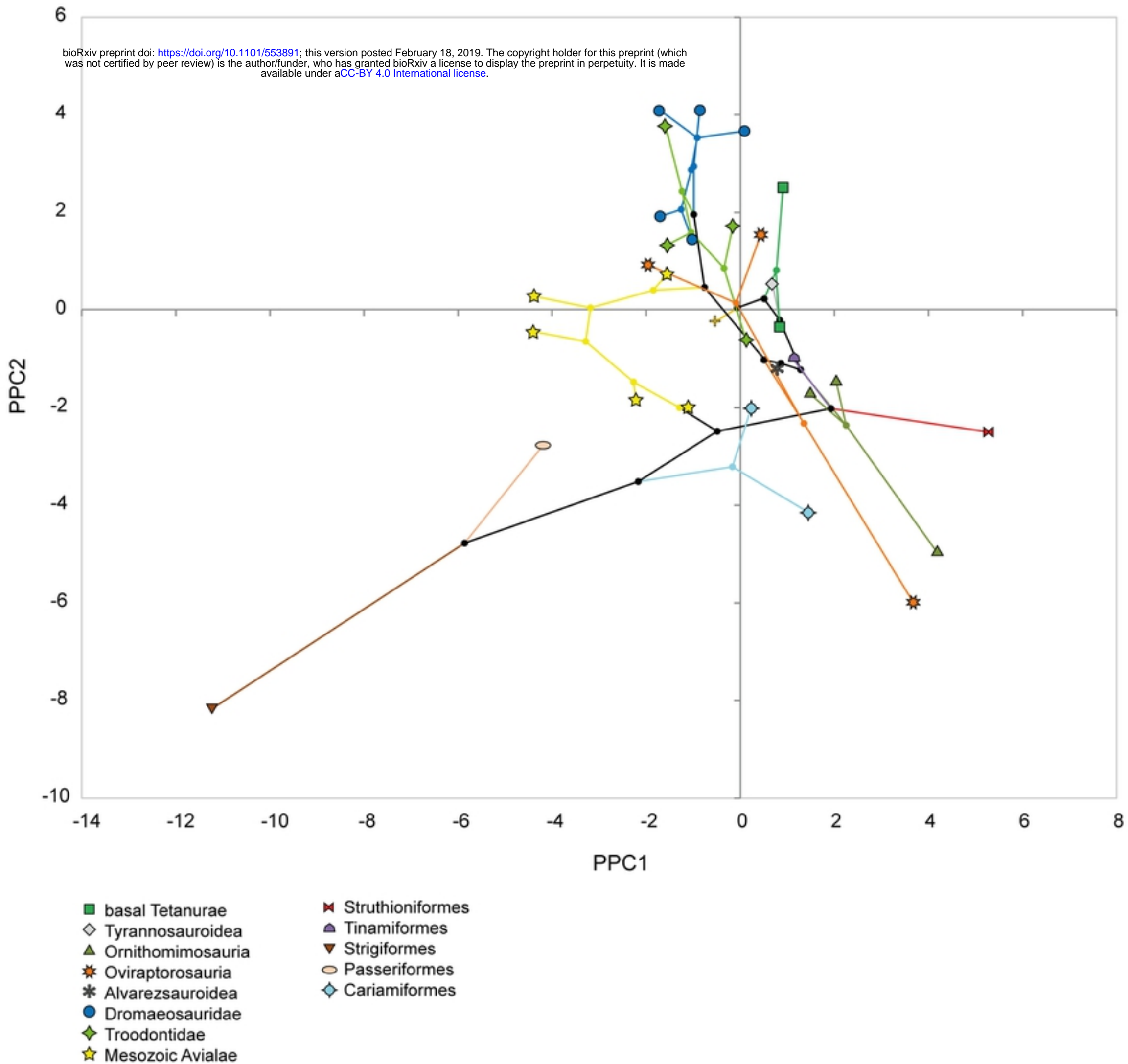


Figure 5

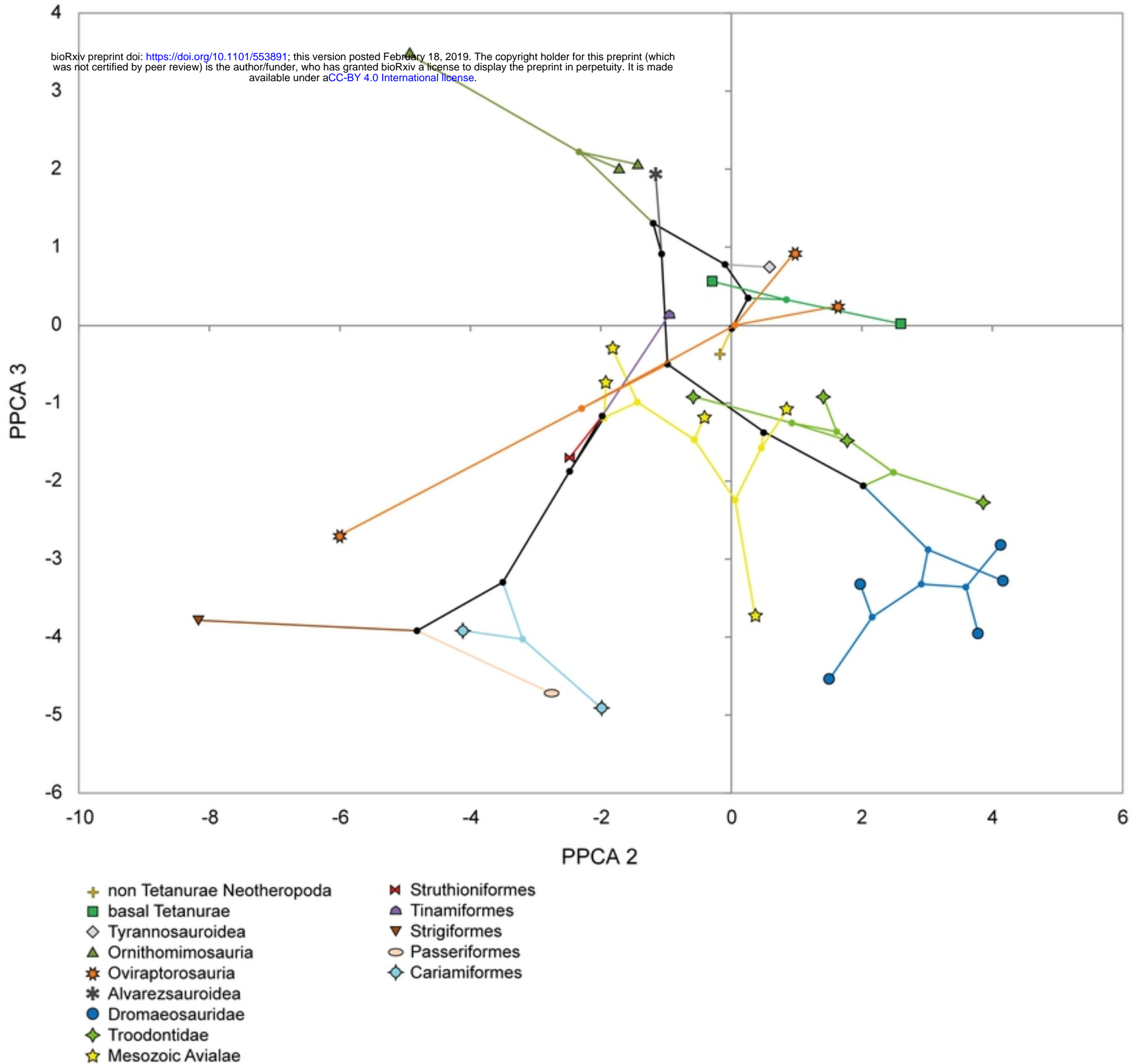


Figure 6

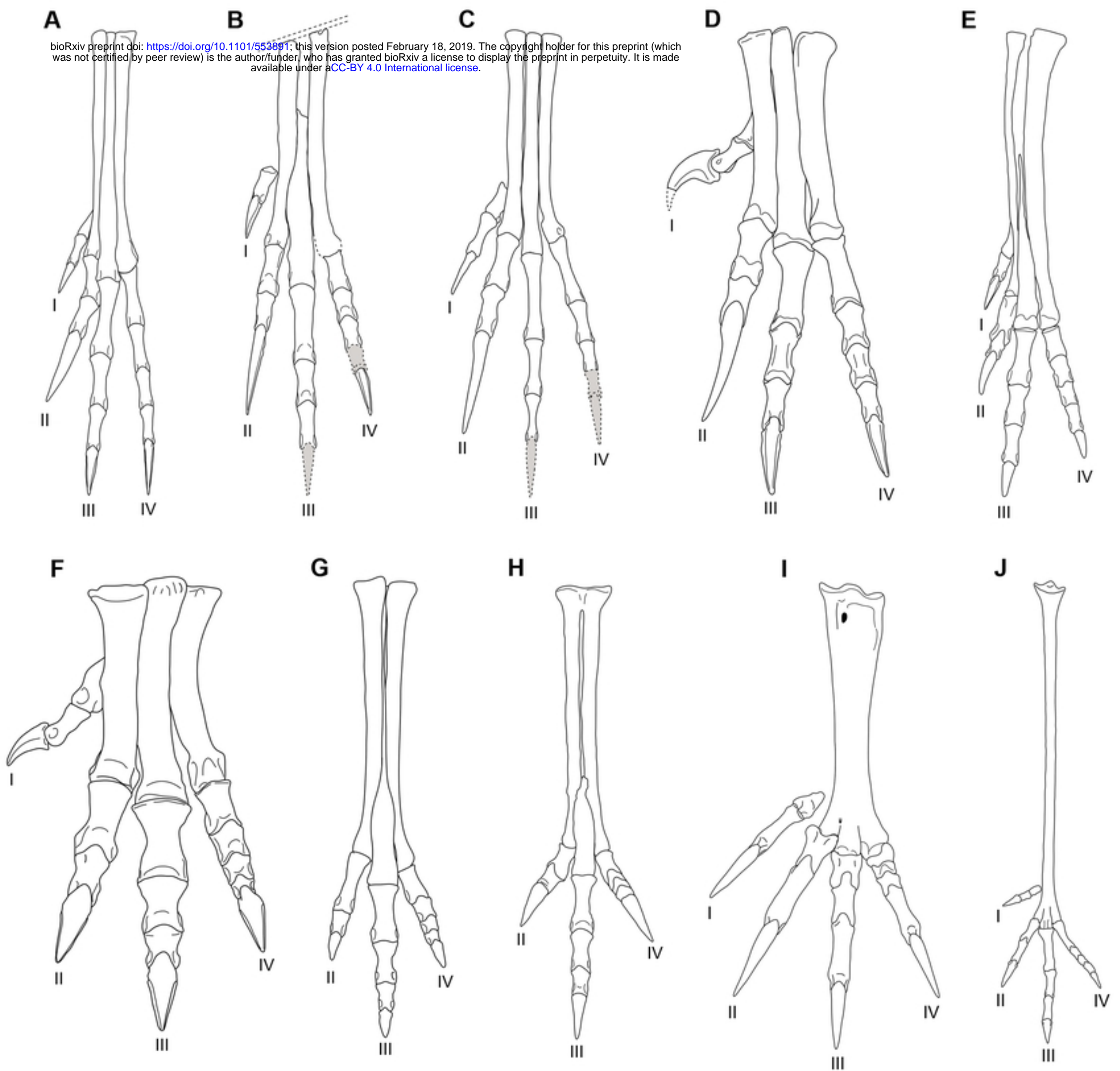


Figure 7

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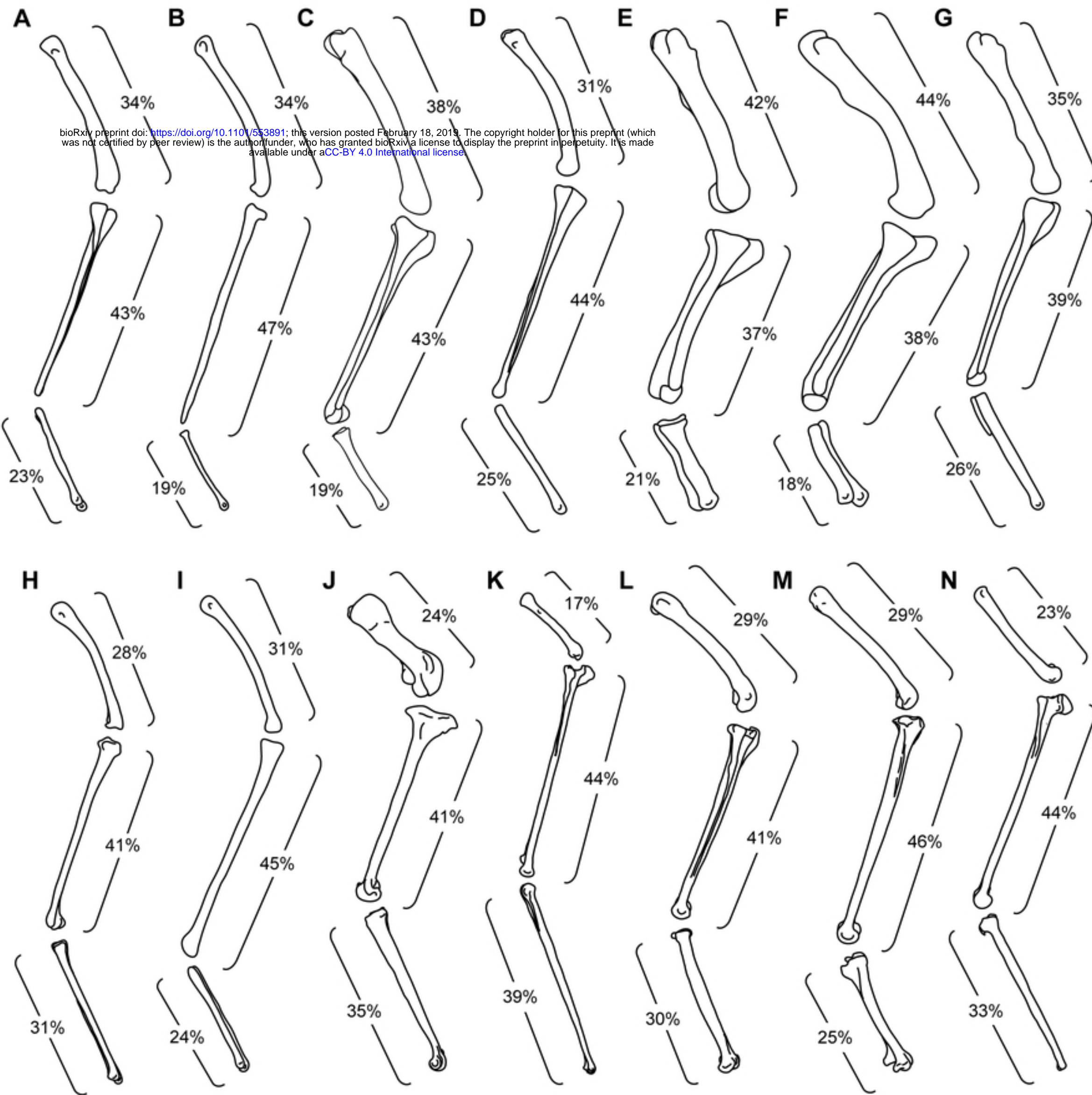


Figure 8

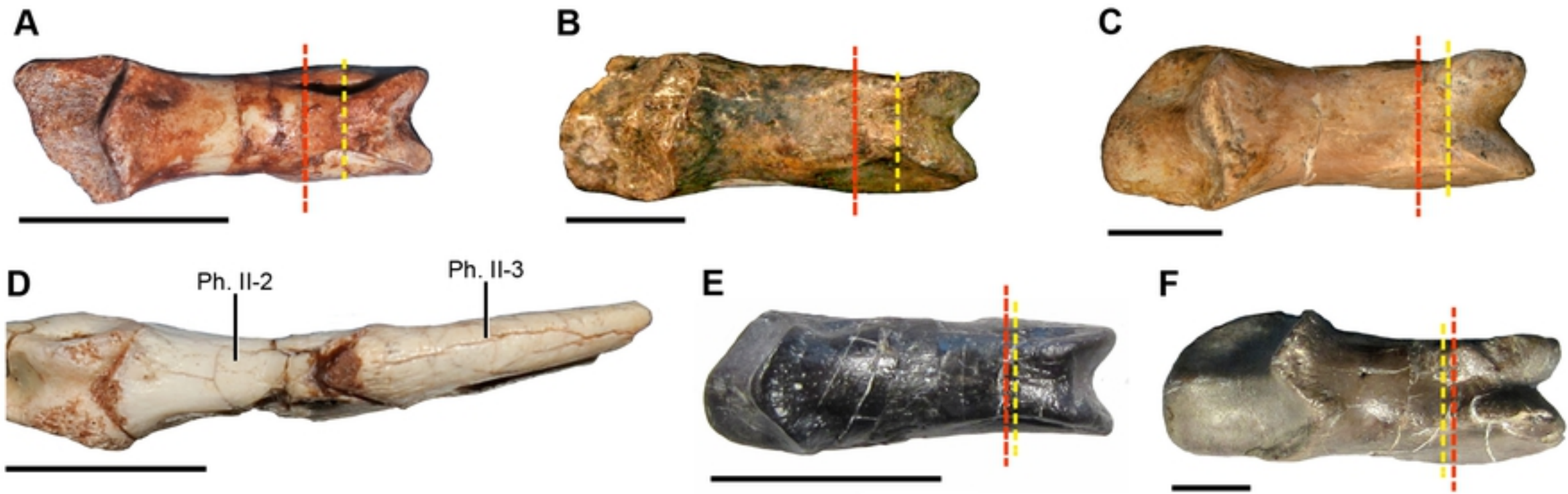


Figure 9