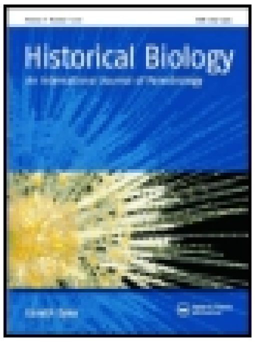

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The role of ontogeny on character polarization in early dinosaurs: a new specimen from the Late Triassic of southern Brazil and its implications

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ABSTRACT
Only recently, new ontogenetic series of early dinosaurs and related groups have been described. Here, we present an isolated immature dinosauriform femur from the Late Triassic of southern Brazil and investigate its influence on character polarization. Because the specimen shares a number of synapomorphies with *Pampadromaeus barberenai*, herein we postulate that it corresponds to a juvenile individual of that taxon. Accordingly, we investigate the morphological variation between juvenile and mature individuals of *P. barberenai*. Scoring these character states into a published phylogenetic data-set of Dinosauromorpha reveals that morphological variation is higher than that observed among closely-related taxa. Ontogenetic variation thus exerts influence on character polarization. In addition, modification of the scores affected by ontogeny produces different topologies, as noted by the reduction in both the number of most parsimonious trees and number of steps, and increased inclusivity of some clades and reduction of polytomies as well. Our study, together with other recent contributions, sheds light on the morphologic pathways seen during dinosauromorph ontogenetic development, which is crucial to more reliably assess phylogenetic reconstructions and macroevolutionary patterns of this widespread and successful group.

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Introduction

Different causes may explain distinct morphologies in duplicated bones of purportedly the same fossil species: taphonomy (Holz and Schultz 1998), pathologies (Trotteyn and Martínez 2013), sexual dimorphism (Raath 1990), ontogeny (Hone et al. 2016), and independent individual variation. When fossil remains are scarce, deciding on these alternatives is difficult, which might lead to misinterpretations and misconceptions (e.g. Vega-Dias et al. 2005; Brusatte et al. 2016). As external morphology is usually the only available tool to infer phylogenetic relations of extinct taxa, the understanding of controlling factors that shape a given structure is crucial. As stated by Raath (1990) 'only once the limits of intraspecific variation have been established can the real taxonomic significance of morphological character suites be assessed'. Among these factors, ontogeny represents a powerful shape controller, requiring much effort in order to be properly recognized, as ontogenetic series of extinct taxa are rare. In spite of this, accessing ontogenetic information is quite important, as the identification of development pathways allows a better understanding of biological aspects, e.g. postural changes adopted throughout the life (Zhao et al. 2013). By disregarding distinct ontogenetic stages during phylogenetic studies, a given data-set can produce contradicting results, as character states are susceptible to change through the life of an individual (e.g. Steyer 2000). Although character states can also on occasion be stable, but this needs to be determined through an adequately sampled fossil record (Kear and Zammit 2014).

Brown and Schlaikjer (1940) were the first authors to drew attention to the ontogeny of dinosaurs. However, the ontogeny of early dinosaurs and related groups is still poorly understood. Pioneer contributions by Raath (1990) and Colbert (1990) started such investigations, and more recently, new ontogenetic series have been recognized and described (e.g. Nesbitt et al. 2009; Piechowski et al. 2014; Griffin and Nesbitt 2016a; Wang et al. 2017). These works have challenged the understanding of several anatomical structures extensively applied in phylogenetic analyses of dinosauromorphs (e.g. Nesbitt 2011), bringing to attention the need to discuss ontogenetic data. In addition, southern Brazil has recently yielded a considerable amount of new early dinosaur remains (e.g. Cabreira et al. 2011, 2016; Pretto et al. 2015; Müller et al. 2016), most of them still under preparation and study. Among these, an isolated femur is investigated here. Its small size suggests that it belonged to an immature individual, raising the opportunity to assess developmental patterns on an early dinosaur femur and to investigate their phylogenetic implications.

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Material and methods

The new specimen comes from the Janner site (*Hyperodapedon* Assemblage Zone), at the municipality of Agudo, Rio Grande do Sul, Brazil (Figure 1). It is housed at the Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia (CAPPA/UFSM), São João do Polêsine, Brazil, under the code CAPPA/UFSM 0028. The Janner site is included in the Candelária Sequence (*sensu* Horn et al. 2014) of the Santa Maria Supersequence (Zerfass et al. 2003). Its dinosaurian content is among the oldest known worldwide, given that the *Hyperodapedon* Assemblage Zone) is dated as Carnian in coeval strata from Argentina (Martínez et al. 2011).

CAPPA/UFSM 0028 is a 113 mm long left femur (Figure 2) exhumed from the basal-most fossiliferous horizon of the Janner site sequence. It was associated with a partially articulated juvenile specimen of the traversodontid cynodont *Exaeretodon*, and occurred on the same bedding layer as the holotype of *Pampadromaeus barberenai* (ULBRA-PVT016), as well as an isolated left femur also referred to *P. barberenai* (CAPPA/UFSM 0027, see Müller et al. 2016). As typical of the site, sedimentary compression strongly affected the shape of CAPPA/UFSM 0028. The deformation was mainly mediolaterally oriented, resulting in a very thin femoral shaft in cranial and caudal views (Figure 2(A)). Despite the deformation, the bone has a well-preserved surface, allowing for recognition of even the most delicate structures. This was also supplemented by a 3D virtual model obtained by 3D scan using a ZScanner 700® with surface resolution of 0.2 mm (Figure 2).

As the first step in our attempt to identify the affinities of CAPPA/UFSM 0028, we assessed its degree of ossification by following two macroscopic, size independent criteria: (1) epiphysis development analysis according to the patterns observed by Bennett (1993) – note that we apply the term 'epiphysis' to the end of a long bone, not to independent ossification centers – (Watanabe and Matsuoka 2013); and (2) the bone surface texture analysis termed 'textural ageing' by Tumarkin-Deratzian et al. (2006). Those authors tested and applied this approach in various vertebrate groups (e.g. Johnson 1977; Tumarkin-Deratzian et al. 2006; Watanabe and Matsuoka 2013), including dinosaurs (e.g. Tumarkin-Deratzian 2009; Rauhut et al. 2012; Sekiya et al. 2014). In both methods, the bone surface of CAPPA/UFSM 0028 was examined under a stereomicroscope (with 10 × magnification).

The second step of our study includes a taxonomic evaluation of CAPPA/UFSM 0028 based upon its external morphology and attempting to identify synapomorphies usually considered diagnostic for dinosaurs and related groups (e.g. Nesbitt 2011). Direct comparisons with CAPPA/UFSM 0027 and ULBRA-PVT016, both ascribed to *P. barberenai* (Cabreira et al. 2011; Müller et al. 2016) were also undertaken. ULBRA-PVT016 is housed at the Museu de Ciências Naturais of Universidade Luterana do Brasil, Canoas, Brazil. Morphological differences among the specimens were evaluated from an ontogenetic perspective based on observations from previous studies of dinosauromorph femoral development (Raath 1990; Nesbitt et al. 2009a; Piechowski et al. 2014; Griffin and Nesbitt 2016a).

To assess the effects of ontogenetic variation on the polarization of femoral characters, we scored CAPPA/UFSM 0028 (Table 1) in the data-set of Bittencourt et al. (2015), computing the percentage of coding differences in relation to *P. barberenai* [considering the hypothesis that CAPPA/UFSM 0028 belongs to this taxon (see below)]. The femur of *P. barberenai* was rescored (Table 1) based on new data provided by Müller et al. (2016). We also computed the percentage of codification differences of femoral characters between *P. barberenai* (disregarding CAPPA/

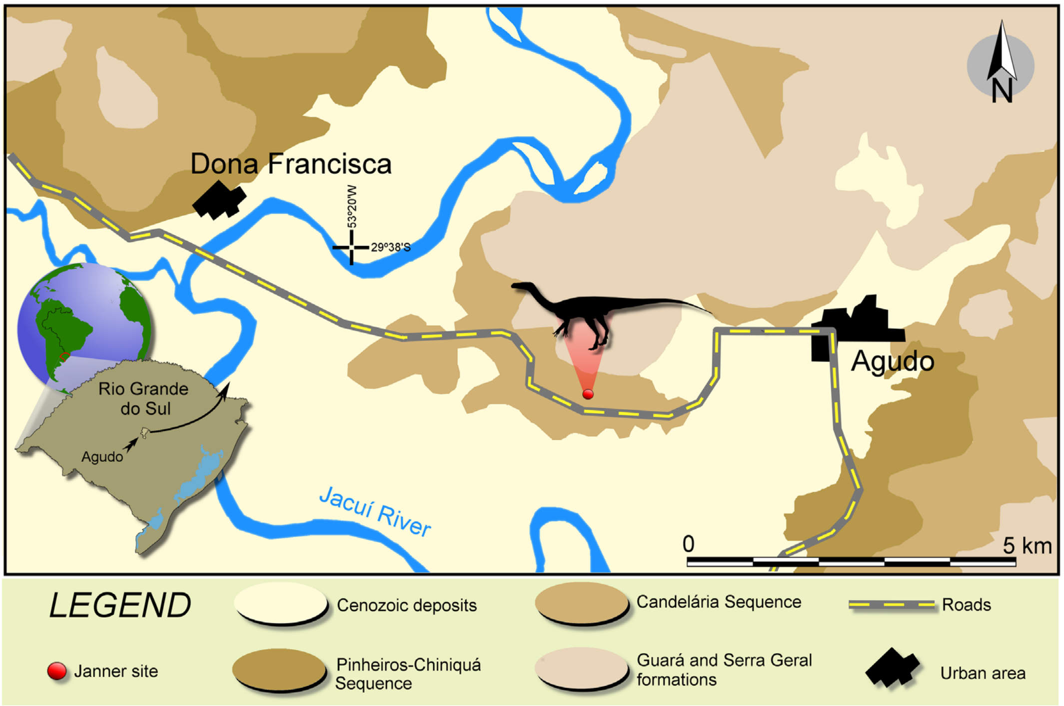

Figure 1. Map of the Agudo area, Rio Grande do Sul, Brazil, showing the location of the Janner site. Surface distribution of geological units according to Zerfass et al. (2007), names of the geological units updated according to Horn et al. (2014).

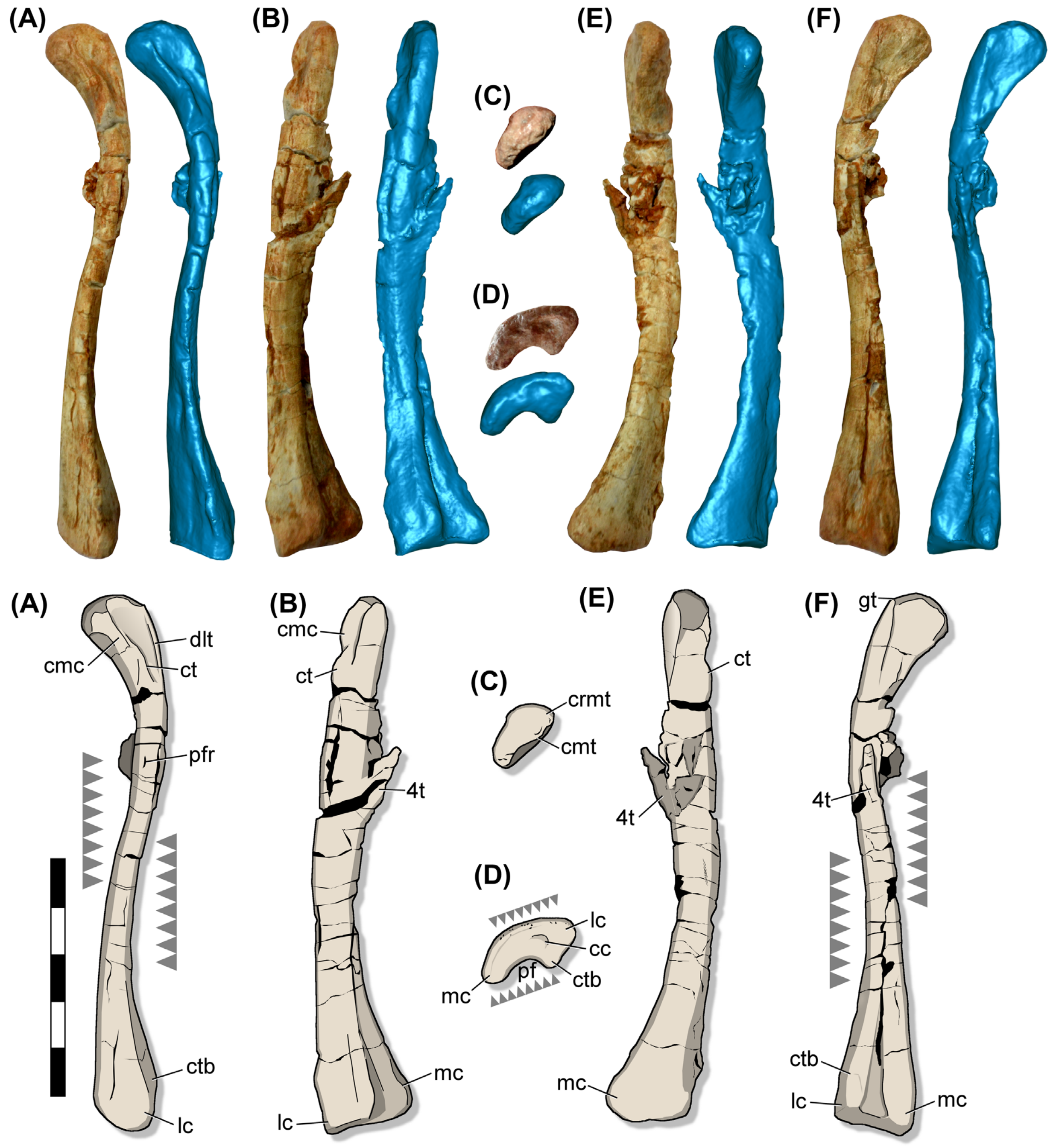

Figure 2. CAPPA/UFSM 0028, a left femur in: (A), cranial; (B), lateral; (C), proximal; (D), distal; (E), medial; and (F), caudal views. Note: the arrows in the drawings indicate the orientation of the sedimentary compaction.
Abbreviations: 4t, fourth trochanter, cc, concavity; cmc, craniomedial crst; cmt, caudomedial tuber; crmt, craniomedial tuber; ct, cranial trochanter; ctb, crista tibiofibularis; dlt, dorsolateral trochanter; gt, greater trochanter; lc, lateral condyle, mc, medial condyle; pf, popliteal fossa; pfr, perforating foramina. Scale bar = 50 mm.

UFSM 0028) and some coeval dinosaurs in order to compare divergent results (e.g. ontogeny versus taxonomy). Femoral character scores followed Bittencourt et al. (2015) for the following taxa: *Saturnalia tupiniquim* (Langer et al. 1999), *Eoraptor lunensis* (Sereno et al. 1993), *Eodromaeus murphi* (Martínez et al. 2011), *Herrerasaurus ischigualastensis* (Reig 1963), and *Staurikosaurus pricei* (Colbert 1970).

A quantitative morphospace analysis including only femoral characters from the data-set by Bittencourt et al. (2015) was also conducted. This analysis aimed to compare morphospace occupation by CAPPA/UFSM 0028, CAPPA/UFSM 0027, and ULBRA-PVT016. For such analysis, the operational taxonomic units (OTUs) that lack preserved femora were excluded (e.g. *Panphagia protos*, *Lewisuchus admixtus*). All polymorphic scores were modified to uncertain (?). First, a Euclidian distance matrix (EDMA) was calculated using the software MATRIX (Wills 1998). A Principal Coordinate Analysis (PCO) was then performed for the EDMA with the multivariate package GINKGO (Bouxin 2005). The parameters selected in GINKGO include the centroid of all OTUs as the origin of the multivariate axes and the Calliez method of negative eigenvalue correction. The PCO axes 1 and 2 were plotted in a bivariate graph with

Table 1. Codification of CAPPA/UFSM 0027 *plus* ULBRA-PVT 016 and CAPPA/UFSM 0028 to the 27 femoral characters of Bittencourt et al. (2015). ? = missing data.

Character number and abbreviated description	CAPPA/UFSM 0027 and ULBRA-PVT016	CAPPA/UFSM 0028
216: craniomedial tuber	(1) small and rounded	(1) small and rounded
217: caudomedial tuber	(0) present and small	(0) present and small
218: craniolateral tuber	(0) absent	(0) absent
219: medial articular surface of the head in dorsal view	(0) rounded	(0) rounded
220: ventral to the proximal head	(2) concave emargination	(?)
221: femoral head orientation angle with respect to the transverse axis through the femoral condyles	(1) craniomedial, 20–60 degrees	(1) craniomedial, 20–60 degrees
222: femoral head in medial and lateral views	(0) rounded	(0) rounded
223: dorsolateral margin of the proximal portion	(1) sharp ridge	(1) sharp ridge
224: cranial trochanter M. iliofemoralis cranialis insertion	(1) present and forms a steep margin with the shaft but is completely connected to the shaft	(1) present and forms a steep margin with the shaft but is completely connected to the shaft
225: medial articular facet of the proximal portion	(0) rounded	(0) rounded
226: craniolateral side of the femoral head	(0) smooth, featureless	(0) smooth, featureless
227: cranial trochanter shelf proximal to the fourth trochanter	(1) present	(?)
228: facies articularis antitrochanterica of the head	(1) level with 'greater trochanter'	(0) ventrally descended
229: 'greater trochanter' shape	(1) angled	(1) angled
230: extension of proximal articular surface of head	(0) extended distally	(0) extended distally
231: proximal surface	(1) transverse groove that is straight	(0) rounded and smooth
232: mediolateral positon of the cranial trochanter	(0) closer to the medial edge	(0) closer to the medial edge
233: dorsoventral position of the fourth trochanter	(0) distal end of fourth trochanter within proximal 30–40% of the femur length	(0) distal end of fourth trochanter within proximal 30–40% of the femur length
234: fourth trochanter shape	(1) a sharp flange	(1) a sharp flange
235: fourth trochanter symmetry	(1) asymmetrical with distal margin forming a steeper angle to the shaft	(?)
236: surface between the lateral condyle and crista tibiofibularis on the distal surface	(1) deep groove	(0) smooth
237: surface between the lateral condyle and crista tibiofibularis on the distal surface	(?)	(?)
238: distal condyles of the femur divided caudally	(0) less than 1/4 the length of the shaft	(?)
239: cranial surface of the distal portion	(0) smooth	(0) smooth
240: crista tibiofibularis	(0) smaller or equal in size to the medial condyle	(0) smaller or equal in size to the medial condyle
241: craniomedial corner of the distal end	(0) rounded	(0) rounded
242: tibiofibularis crest distal shape	(0) distally semicircular	(0) distally semicircular

the software *PAST* (Hammer et al. 2001). Convex hulls were drawn according the phylogenetic relationships recovered by Bittencourt et al. (2015).

Finally, in order to verify the putative influence of ontogeny on the phylogenetic relationships of early dinosaurs we conducted an exploratory analysis of the data matrix of Bittencourt et al. (2015) following the same parameters (except for 1000 rather than 10,000 random additional sequences), with modifications on femoral characters that we do not consider influenced by ontogenetic control. States '1' and '2' of character 223, related to the form of the dorsolateral trochanter (Nesbitt 2011), were collapsed into a single state ('presence' = 1), following the conclusions of Raath (1990) and Piechowski et al. (2014), which associated this variation to ontogeny and sexual dimorphism. In this case, immature individuals of both sexes may share the same morphology, but during development, sexual dimorphism becomes more evident. Another modification includes the rescore of character 227 (presence/absence of trochanteric shelf) for some OTUs. The presence of such structure has been exhaustively recognized as the effect of both ontogeny and sexual dimorphism (Raath 1990; Nesbitt 2011; Piechowski et al. 2014; Griffin and Nesbitt 2016a) making its phylogenetic signal doubtful. Accordingly, we rescored as 'missing data' ('?') all OTUs previously coded as 'absent' (0) in which there is no ontogenetic control, as these could be sampled only on immature specimens. This includes *Sacisaurus agudoensis* (Feirolgo and Langer 2007) and *Guaibasaurus candelariensis* (Bonaparte et al. 1999). The lagerpetid *Dromomeron gregorii* was coded as '0' in the data matrix of Bittencourt et al. (2015), but Nesbitt (2011) shows that the trochanteric shelf is present in the large individuals, thus it was rescored as '1'. The taxon was not scored as polymorphic because juvenile individuals of many OTUs are unknown and we avoid the combination of distinct ontogenetic stages in an OTU, preferring to score the mature condition. As such, the polymorphic condition of *Silesaurus opolensis* was rescored as 'present' (1), rather than 'absent' and 'present' (0/1). The analysis was carried out in TNT v1.1 (Goloboff et al. 2008).

Results

Degree of ossification

Regarding epiphyseal ossification, both articular surfaces of CAPPA/UFSM 0028 are rough and irregular (Figure 3(A, E–F)), suggesting that the epiphyseal cartilage was not yet completely ossified, a pattern observable in immature animals (Bennett 1993) but differing from the fully ossified smooth bone surfaces of mature animals (Bennett 1993; Holliday et al. 2010). In addition, an abrupt unevenness divides the proximal rough surface from the remaining bone (Figure 3(A)). According to Holliday et al. (2010), the long bones of non-avian adult dinosaurs have calcified cartilage laminae on their ends. When this develops, it should form a continuous, rather than uneven bone surface (Holliday et al. 2010). Therefore, the presence of that unevenness suggests that a fully calcified lamina on the specimen had not started growing.

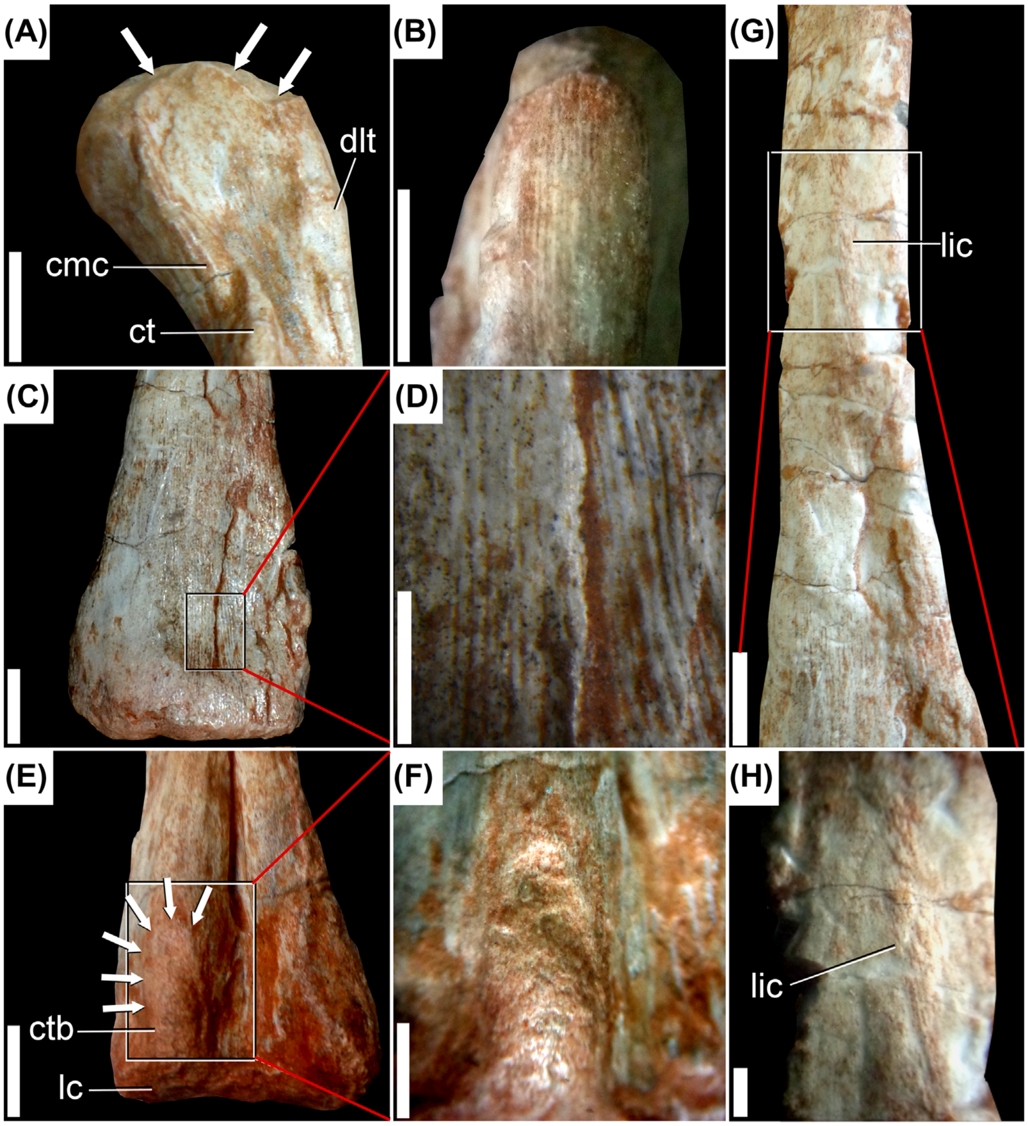

Figure 3. Ossification degree of the femur of CAPPA/UFSM 0028: (A), cranial view of the proximal portion, the arrows indicate unevenness; (B), lateral view of the proximal portion, note the longitudinal striation on the dorsolateral trochanter; (C), cranial view of the distal portion; (D), magnification of the cranial surface of the distal portion, note the longitudinal striations; (E), caudal view of the distal portion, the arrows point to rough surface; (F), magnification of the cristatibiofigularis in caudal view; (G), craniomedial view of the femoral shaft; (H), magnification of the the linea intermuscularis cranialis in craniomedial view.

Abbreviations: cmc, craniomedial crest; ct, cranial trochanter; ctb, crista tibiofibularis; dlt, dorsolateral trochanter; lc, lateral condyle; lic, linea intermuscularis cranialis. Scale bars = 5 mm in A, B, C, E, G, 2 mm in D, F, H.

The external surface of the entire bone reveals several patches of longitudinal parallel striations clustered on both proximal and distal portions (Figure 3(B–D)). These striations differ from typical rugosities or tuberosities of muscle scars (Bennett 2015), but resemble those observed in a wide range of immature vertebrates (Tumarkin-Deratzian et al. 2006; Rauhut et al. 2012; Watanabe and Matsuoka 2013). Striations are absent in the middle of the femoral shaft, where bone surface is smooth, except for a series of faint striations on its craniad surface that probably correspond to an early development stage of the *linea intermuscularis cranialis* (Figure 3(G–H)). Apart from this, there are no other areas with scars that could be related to soft tissue attachment. According to Raath (1969), the amount of muscle scarring is indicative of advanced age in dinosaurs, and their lack is an additional indicator of immaturity, a statement recently corroborated by Griffin and Nesbitt (2016a).

Taxonomic assignation

The presence and shape of several muscle attachment areas in CAPPA/ UFSM 0028 support its inclusion within Dinosauriformes: a small caudomedial tuber (Figure 2(C)); protruding cranial trochanter (Figure 2(A) and 3(A)); dorsolateral trochanter (Figure 2(A) and 3(A)); craniomedial crest (*sensu* Bittencourt and Kellner 2009) (Figures 2(A) and 3(A)); and sharply-flanged fourth trochanter (Figure 2(F)). CAPPA/ UFSM 0028 further differs from femora of non-dinosauriform dinosauromorphs because lacks a hook shaped head (Figure 3(A)), but possesses a craniolateral tuber (Figure 4(A)), reduced crista tibiofibularis (Figure 2(D)), and rounded craniomedial corner of the distal end (Figure 2(D)).

Among dinosauromorphs, transition from the femoral shaft to the ventral portion of the head may manifest a smooth transition, be notched, or have a concave emargination (Nesbitt 2011).

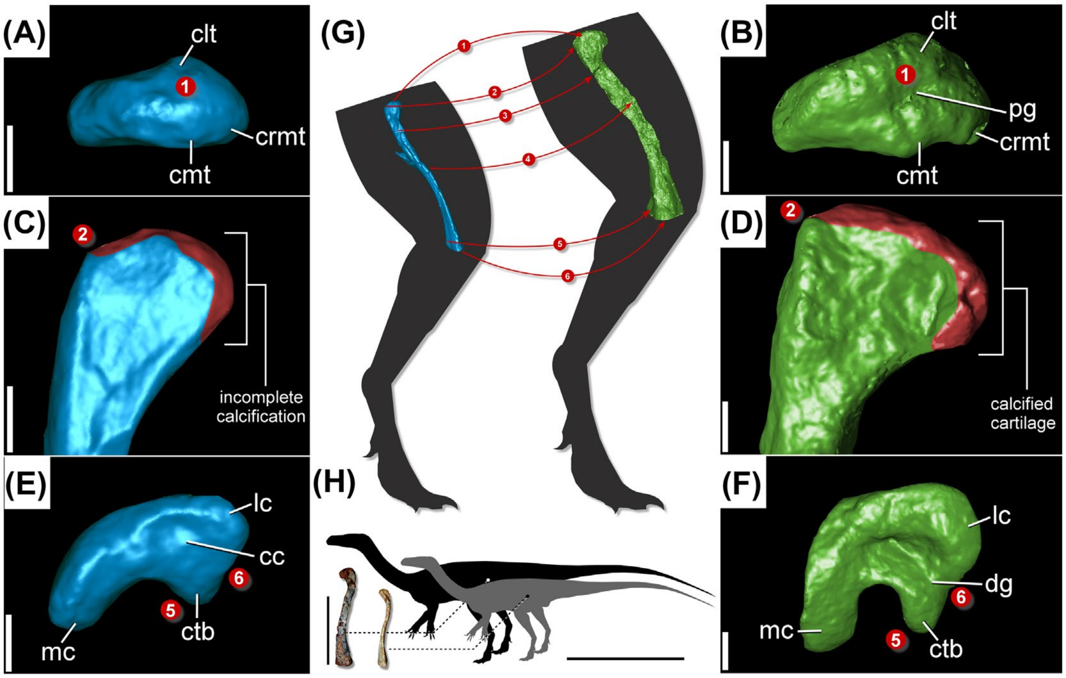

Figure 4. Comparison between 3D scan femora of CAPPA/UFSM 0028 and CAPPA/UFSM 0027: (A), proximal view of CAPPA/UFSM 0028; (B), proximal view of CAPPA/UFSM 0027; (C), caudal view of the proximal portion of CAPPA/UFMS 0028; (D), caudal view of the proximal portion of CAPPA/UFMS 0027; (E), distal view of CAPPA/UFSM 0028; (F), distal view of CAPPA/UFSM 0027; (G), illustrated summary of main modifications related to ontogeny between the specimens; (H), size comparison between CAPPA/UFSM 0028 (grey) and UFSM 0027 (black) based in femoral proportions.

Abbreviations: cc, concavity; clt, craniolateral truber; cmt, caudomedial tuber; crmt, craniomedial tuber; ctb, crista tibiofibularis; lc, lateral condyle; mc, medial condyle; dg, distal groove. Note: the number 1 indicates the change related to the proximal surface (proximal groove); 2 indicates the form of the greater trochanter; 3 indicates the caudolateral extension of the trochanteric shelf; 4 indicates the development degree of the linea intermuscularis cranialis; 5 indicates the development degree of the crista tibiofibularis; 6 indicates the formation of the distal groove. Scale bars = 5 mm in A, B, C, D, E, F, 100 mm in femora and 500 mm in silhouettes of H.

According to Langer and Ferigolo (2013), the difference between a notch and emargination reflects only greater expansion of the head. A smooth transition occurs in lagerpetids and *Marasuchus lilloensis*, whereas the notch is found in silesaurids, and a concave emargination in dinosaurs (Nesbitt 2011). CAPPA/UFSM 0028 bears a smooth transition, but more detailed observation indicates the presence of an arcuate line setting the shaft/head boundary (Figures 2(A) and 3(A)); this closely resembles the concave emargination diagnostic for dinosaurs but could also reflects ontogenetic immaturity. Indeed, the craniomedial portion of the femoral head is characterized by a rough and irregular surface, indicating that the epiphyseal cartilage was not yet ossified. This, together with the extreme mediolateral compression, affected the shape of the femoral head.

Although CAPPA/UFSM 0028 lacks obvious dinosaur synapomorphies, a combination of traits suggests affinities with *Pampadromaeus barberenai*. CAPPA/UFSM 0028 was derived from the same site that yielded both holotype and a referred femur of *P. barberenai* (Müller et al. 2016), thus it is plausible that all these elements represent the same taxon. Among coeval Brazilian dinosauriforms, CAPPA/UFSM 0028 shares some exclusive features with *P. barberenai*. (1) The 'sulcus for the *ligamentum capitis femoris*' is narrow due the position of the caudomedial tuber (Figure 4(A)), whereas all coeval saurischians bear a wider sulcus (Müller et al. 2016). (2) The proximal portion of the cranial trochanter is fully connected to the femoral shaft (Figure 2(B)), whereas a cleft is evident between the trochanter and the femoral shaft in *Saturnalia tupiniquim* (Langer 2003). (3) A well-developed craniomedial crest extends between the craniomedial tuber and the cranial trochanter (Figures 2(A) and 3(A)), whereas the homologous surface is less prominent in other coeval dinosauriforms, such as *Saturnalia tupiniquim*, *Staurikosaurus pricei*, and *Buriolestes schultzi* (Langer 2003; Bittencourt and Kellner 2009; Cabreira et al. 2016). (4) The crista tibiofibularis is reduced (Figure 4(E)), which represents a demonstrable autapomorphy of *P. barberenai* (Müller et al. 2016).

Ontogenetic patterns of Pampadromaeus barberenai

We interpret CAPPA/UFSM 0028 as an immature individual of *Pampadromaeus barberenai*. The holotype femora of this taxon (ULBRA-PVT016) are fractured but show similar proportions. The referred femur CAPPA/UFSM 0027 is about 142 mm long (comparable to ULBRA-PVT016). In contrast, CAPPA/UFSM 0028 is only 113 mm long and thus belongs to a substantially smaller individual. However, Griffin and Nesbitt (2016a) demonstrated that individuals of *Asilisaurus kongwe* reached maturity at different body sizes. ULBRA-PVT016 and CAPPA/UFSM 0027) are, nevertheless, still considered more mature than CAPPA/UFSM 0028 because both have fully ossified articular surfaces and well-developed muscle attachment structures (see comparison below). In addition, ULBRA-PVT016 also has well-formed bone surface texturing, which is not visible in CAPPA/UFSM 0027 because of poor preservation.

In contrast to the minor variation found in femoral head morphologies of *Dromomeron gregorii* (Nesbitt et al. 2009a), the craniomedial tuber of CAPPA/UFSM 0028 is reduced (Figure 4(A)) and lacks a medially descending bone wall (Figure 4(C)) otherwise present in CAPPA/UFSM 0027 (Figure 4(D)). In CAPPA/UFSM 0027, a shelf connects the craniomedial and caudomedial tuberosities (Figure 4(D)), but is absent in the proximal articular surface of CAPPA/UFSM 0028 (Figure 4(C)). The craniolateral tuber is also taller and more prominent in the osteologically more mature specimens. In contrast, the entire periphery of the proximal articular surface is poorly developed in CAPPA/UFSM 0028. This condition could explain weaker tuberosity development and the absence of a groove on the proximal end of the femur of CAPPA/UFSM 0028 (Figure 4(A)); this structure is likewise poorly developed in a small individuals (AbIII/457L) of *Silesaurus opolensis* (Dzik 2003), but well-incised in larger specimens [see the figure 9 of Piechowski et al. (2014)]. Finally, CAPPA/UFSM 0028 lacks a ventrally descended *facies articularis antitrochanterica* on the proximal portion of the femur (Figure 4(C)).

The greater trochanter of CAPPA/UFSM 0028 possesses a rounded shape (Figure 4(C)), unlike the more angular trochanters of the larger specimens (Figure 4(D)). All three share a 'sharply-ridged' dorsolateral trochanter. In contrast, Nesbitt (2011) and Piechowski et al. (2014) showed that only the smaller femora of *S. opolensis* conformed to this morphology, whereas larger femora of the same taxon have a rounded ridge. In addition, Griffin and Nesbitt (2016a) demonstrated that this ridge is absent in smaller femora attributed to *A. kongwe*, but becomes more developed, and also changes in shape and position with increasing body size.

The larger specimens of *P. barberenai* have a well-developed trochanteric shelf, but this structure is not visible on the smaller individual because the distal portion of the craniad trochanter is badly fractured (Figure 2(A)). Irrespectively, we suggest that the trochanteric shelf was probably poorly developed because it does not reach the preserved caudolateral corner of the femoral shaft. Indeed, Raath (1990) ascribed the presence of a trochanteric shelf to sexual dimorphism in *Syntarsus rhodensis*, while Nesbitt et al. (2009a) stated that it is present in larger, but not in smaller individuals of *D. gregorii*. Piechowski et al. (2014) argued that the trochanteric shelf appears only in larger specimens of *S. opolensis*, and followed Raath (1990) in concluding that this feature might be related to ontogeny and/or sexual dimorphism. Recently, Griffin and Nesbitt (2016a) recognized the absence of the trochanteric shelf in smaller specimens of *A. kongwe*.

Nesbitt et al. (2009a) identified the *linea intermuscularis cranialis* only in the largest specimen (TMM 31100-1306) of *D. gregorii*. A series of faint striations on the craniad surface of the mid-shaft in CAPPA/UFSM 0028 might correspond to an early developmental stage of this intermuscular line. Indeed, it is not as long as in the larger individuals, and does not form a raised process as in ULBRA-PVT016. Other intermuscular lines are absent in CAPPA/UFSM 0028. Like ULBRA-PVT016, CAPPA/UFSM 0028 bears a foramen on the craniad surface of the proximal half of the bone (Figure 2(A)).

The distal end of the crista tibiofibularis is slightly more caudally projected in the larger individuals (Figure 4(F)). This conforms with the observations of Nesbitt et al. (2009a), who suggested that an increase in the size of the distal condyles occurred with ontogeny in *D. gregorii*. The surface between the lateral condyle and the crista tibiofibularis also forms only a shallow concavity and does not extend to the caudolateral corner of the bone in CAPPA/UFSM 0028 (Figure 4(E)). In contrast, CAPPA/UFSM 0027 has a deep and well marked groove that extends to the caudolateral corner of the bone and separates the crista tibiofibularis from the lateral condyle (Figure 4(F)). Rough muscle scars are observable all over the outer surfaces of both femora of ULBRA-PVT016, and include the cranial trochanter, trochanteric shelf, dorsolateral trochanter, and the lateral surface on the distal end of the femur. On the other hand, CAPPA/UFSM 0028 does not show any muscle scars in these areas.

Ontogenetic implications on character polarization

The Bittencourt et al. (2015) data-set includes 291 morphological characters, of which 27 (about 9% of the total character number) are related to the femur. Of these, characters 228, 231, and 236 score differently for CAPPA/UFSM 0028 vs. CAPPA/UFSM 0027 and ULBRA-PVT016. For example, the ventrally descended 'facies articularis antitrochanterica' on the femoral head (character 228) is absent in CAPPA/UFSM 0028 (Figure 4(C)), but present in the other specimens referred to *Pampadromaeus barberenai* (Figure 4(D)). The transverse groove on the proximal surface of the femoral head (character 231) is likewise absent in CAPPA/UFSM 0028 (Figure 4(A); compare with Figure 4(B)). The groove between the lateral condyle and crista tibiofibularis on the distal surface of the femur (character 236) is shallow and does not divide the lateral condyle and crista tiobiofibularis in CAPPA/UFSM 0028 (Figure 4(E)); it is alternatively deep in *P. barberenai* (Figure 4(F)). Finally, a trochanteric shelf (character 227) is present in *P. barberenai* but may be absent in CAPPA/UFSM 0028 (see above). These differences correspond to 13.63% of the comparable femoral scores (17.39% if the trochanteric shelf character is considered). All these features are located in bone portions usually affected by the maturation degree of the individual (e.g. Holliday et al. 2010; Griffin and Nesbitt 2016b). Therefore is possible that they are related to ontogeny.

Amongst the 26 femoral characters coded for *P. barberenai* (CAPPA/UFSM 0027 and ULBRA-PVT016) and *Saturnalia tupiniquim*, only two (= 7.69%) have substantially different scores. The same percentage is recovered in comparison to *Eoraptor lunensis*, with 1 differently and 12 identical character scores. To *Eodromaeus murphi* 18 characters are equally coded, and 1 (= 5.26%) differently scored. The difference with *Herrerasaurus lunensis* is 11.53%, with 3 distinct entries out of 26 scored characters. This contrasts with the 4% of difference recovered in the comparison with *Staurikosaurus pricei*, where 1 coding out of 25 is distinct from those of *P. barberenai*. Accordingly, the highest difference in scoring occurs between the two ontogenetic stages of *P. barberenai* (13.63%) (Figure 5). On the other hand, the 11 comparable characters between *E. lunensis* and CAPPA/UFSM 0028 are equally scored. From the 16 comparable characters between *E. murphi* and CAPPA/UFSM 0028, only 1 (6%) is scored differently. *Staurikosaurus pricei* differs in 2 (10%) of the 20 comparable characters, while *H. ischigualastensis* has 18% difference (4 of the 22 comparable characters) scored for this specimen. Finally, the difference with *S. tupiniquim* is 22% (5 of the 22 comparable characters).

The results of the disparity analysis place CAPPA/UFSM 0028 within the morphospace of saurischian dinosaurs (Figure 6). However, CAPPA/UFSM 0028 lies outside of sauropodomorph morphospace, and is distant from *P. barberenai* as opposed to *Eoraptor lunensis* and *Eodromaeus murphi*.

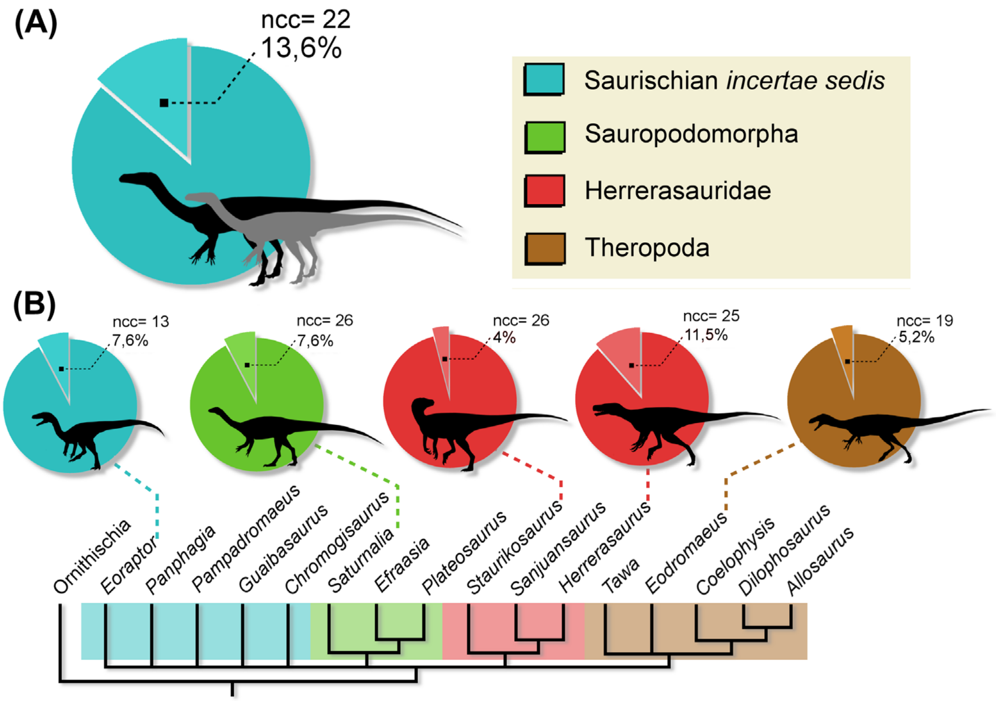

Figure 5 Ontogenetic influence on the polarization of femoral characters: (A), percentage of difference between *Pampadromaeus barberenai* and the immature individual (CAPPA/UFSM 0028); (B), percentage of difference between *Pampadromaeus barberenai* and related basal saurischians plotted in a simplified strict consensus tree from Bittencourt et al. (2015).
Abbreviation: ncc, number of comparable characters.

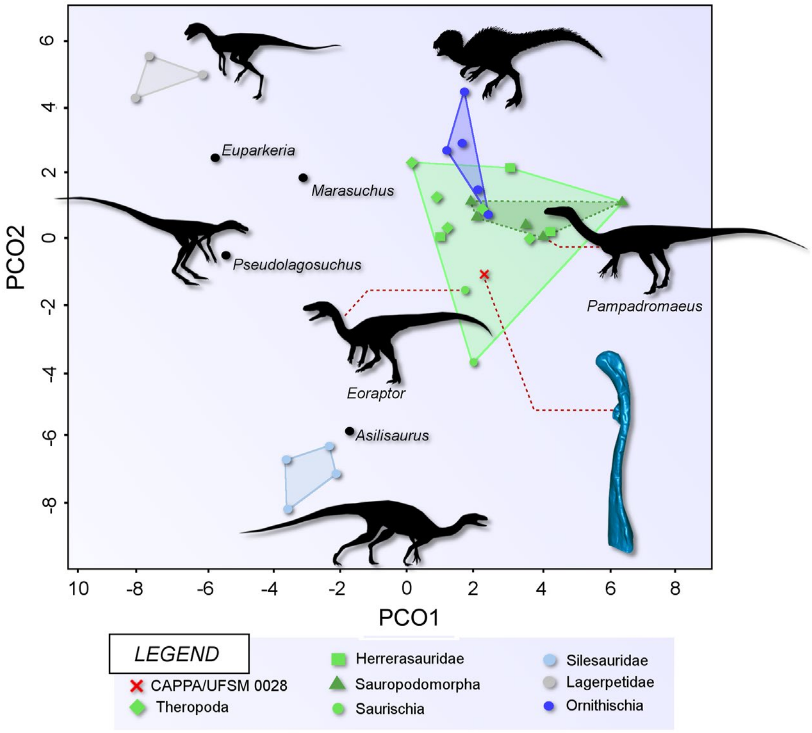

Figure 6. Bivariate plot showing the results of the morphospace occupation analysis.
Note: light green polygon, saurischians; dark green, sauropodomorphs; light blue, silesaurids; dark blue, ornithischians; grey, lagerpetids.

Ontogenetic influence on the phylogenetic relationships

A heuristic search on the modified data matrix resulted in six most parsimonious trees (MPTs) of 778 steps (Consistency Index = 0.43; Retention Index = 0.60), while the original analysis resulted in 27 MPTs of 781 steps (Bittencourt et al. 2015). In contrast to Bittencourt et al. (2015), the saurischian branch does not include an initial polytomy (Figure 7). *Pampadromaeus barberenai* is placed as the sister taxon of all other sauropodomorphs (Figure 7(B)), as proposed by Cabreira et al. (2011). *Guaibasaurus candelariensis*, *Panphagia protos* (Martinez & Alcober, 2009), and *Chromogisaurus novasi* (Ezcurra 2010) are also recovered within Sauropodomorpha (Figure 7(B)). Herrerasauridae and *Eoraptor lunensis* are nested within Theropoda (Figure 7(B)). Another difference is the position of *Asilisaurus kongwe* (Nesbitt et al. 2010), which was found here as the sister-group of all other Silesauridae (Figure 7(B)). In the original analysis the dorsolateral trochanter formed by a sharp ridge (state '1' of character 223) corresponds to one of the synapomorphies that support a dinosauriform clade more derived than *Marasuchus liloensis*. This does not correspond to a synapomorphy for the same group in the new analysis. Another synapomorphy from the original study that was not recovered here includes the dorsolateral trochanter formed by a rounded ridge (state '2' of character 223). This provides support to Sauropodomorpha, which includes *Saturnalia tupiniquim*, *Efraasia minor*, and *Plateosaurus* sp. in the analysis of Bittencourt et al. (2016), while our analysis recovered a more inclusive Sauropodomorpha (Figure 7(B)). The absence of a trochanteric shelf (state '0' of character 227) is not a synapomorphy to the node supporting *Plateosaurus* sp. and *Efraasia minor* in the former analysis, contrasting with the present results. In addition, the presence of a trochanteric shelf on the femur (state '1' of character 227) supports Dinosauriformes in this new analysis but not in the first one.

Discussion

Morphological features of CAPPA/UFSM 0028, including the shape of the proximal and distal ends of the femur, match those of immature individuals, such as *Struthio camelus*, *Megapnosaurus rhodesiensis*, and *Pteranodon* sp. (Bennett 1993; Holliday et al. 2010; Griffin and Nesbitt 2016b). As such, the ossification degree might explain conflicting osteological features, although sexual dimorphism and intraspecific variation could also influence shape (see Raath 1990; Piechowski et al. 2014). Indeed, features such as the absence of grooves on the proximal and distal ends of the femur and the lack of a ventrally descended 'facies articularis antitrochanterica' can be assigned to the incomplete calcification of cartilage around the articulations. In any case, our analyses suggest that femoral traits in an osteologically immature individual contrast with ontogenetically mature conspecifics more than with other phylogenetically distinct taxa. Actually, Müller (2017) obtained percentages similar to those recovered here, gathered from small and large specimens of two species of dinosauromorphs (16% to *Dromomeron gregorii* and 13% to *Silesaurus opolensis*). Curiously, in our study, femoral scores were identical to *Eoraptor lunensis* and only manifest 6% difference relative to *E. murphi*. However, both species share few common characters with CAPPA/UFSM 0028. Based on the data presented here and previous contributions (Nesbitt et al. 2009a; Nesbitt 2011; Piechowski et al. 2014) it is possible to conclude that at

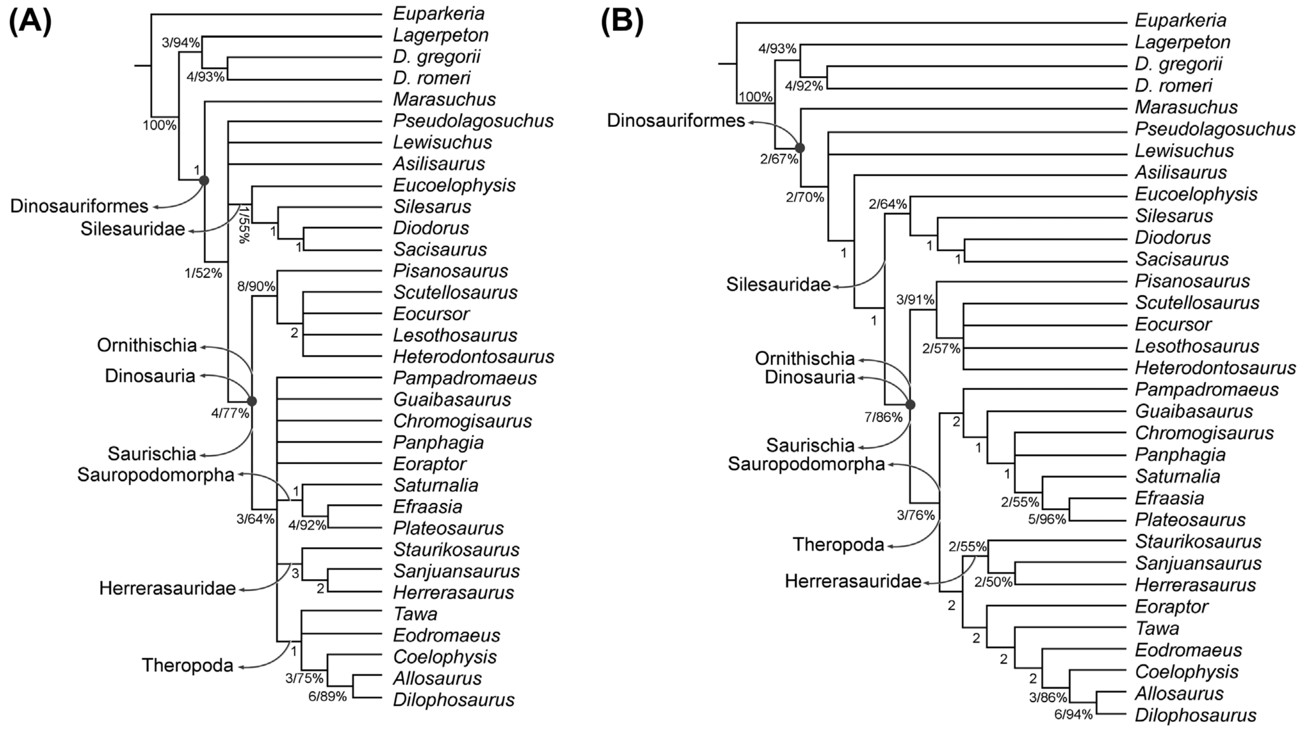

Figure 7. Comparison between the strict consensus tree of 27 most parsimonious trees of Bittencourt et al. (2015) (A) and the strict consensus tree of the 6 most parsimonious trees recovered here (B).

Note: values associated with nodes correspond to Bremer support and bootstrap proportions (above 50%).

least 27% of the femoral characters codified in the data matrix of Bittencourt et al. (2015) are susceptible to misinterpretation as a result of ontogenetic variation.

Although most phylogenetic studies on early dinosaurs and related groups comprise rigorous cladistics methodologies (Benton et al. 2014), their relationships are still controversial (Langer 2014). We consider that the lack of ontogenetic control might partially explain this situation, as ontogenetic series are still extremely scarce for most taxa (Nesbitt et al. 2009a). Indeed, there is evidence that some valid early dinosaur taxa comprise immature individuals. This is the case for *Guaibasaurus candelariensis* (Bonaparte et al. 1999), in which both the holotype (MCN PV2355) and the referred specimen (UFRGS PV0725T) possess unfused neurocentral sutures on the dorsal and caudal vertebrae; see Brochu (1996) and Irmis (2007) for discussions on the significance of these traits. Similarly, the epiphyses of the holotype and the metatarsal ends of the paratype (MCN PV2356) are either incompletely ossified or damaged by preparation (Langer et al. 2011). *Staurikosaurus pricei* (Colbert 1970; Bittencourt and Kellner 2009; Ezcurra 2010; Nesbitt 2011) also displays features suggesting that the only known specimen (MCZ 1669) is less ontogenetically developed than other herrerasaurids including *Herrerasurus ischigualastensis* (Reig 1963) and *Sanjuansaurus gordilloi* (Alcober and Martínez 2010). These two taxa exhibit a well-developed trochanteric shelf on the femur, which is absent or considerably reduced in the holotype of *S. pricei* (Bittencourt and Kellner 2009). Also, the lack of a deep groove dividing the lateral condyle from the crista tibiofibularis on the distal end of the femur may be related to incomplete ossification. This accords with the small size of the specimen relative to other herrerasaurids: the femoral length of MCZ 1669 is 220 mm (Carrano 2006), compared to 482 mm in *H. ischigualastensis* (Carrano 2006) and 395 mm in *S. gordilloi* (Alcober and Martínez 2010).

Recently, Barrett et al. (2015) described a large sized silesaurid femur estimated at 345.8 ± 50 mm in length. Until then, the largest femur recorded in the group belonged to *Silesaurus opolensis*, reaching about 210 mm (Piechowski et al. 2014). All known femora of *Sacisaurus agudoensis* from southern Brazil (Feirolgo and Langer 2007) are approximately half the length of those recovered for *S. opolensis* (Langer and Ferigolo 2013). This could imply that the holotype of *S. agudoensis* is osteologically immature. Actually, Piechowski et al. (2014) suggested that a distinct tuberosity and lack of a trochanteric shelf on the femora of *S. agudoensis* were indicative juvenile or male individuals. In addition, Langer and Ferigolo (2013) recognized the presence of a striated area on the distal portion of some femora of *S. agudoensis*. This resembles the condition found in the osteologically immature remains described here.

The aforementioned cases are examples of the scarcity of ontogenetic control on early dinosaurs and related groups, generally occurring in response to limited sampling. However, ontogenetic markers as body size, opening of neurocentral sutures, and robustness of the trochanteric shelf are not unambiguous. Therefore, new specimens, as well as future studies based on bone histology will probably help this matter. Fortunately, recent contributions (e.g. Nesbitt et al. 2009a; Piechowski et al. 2014; Griffin and Nesbitt 2016a, 2016b) are shedding light on the morphologic pathways of dinosauromorphs along their development, which is crucial to access reliable phylogenetic affinities and macroevolutionary patterns (e.g. Brusatte et al. 2008a, 2008b). Among these studies, that of Griffin and Nesbitt (2016b) particular demonstrates that an extremely high amount of intraspecific variation was evident in early dinosaurs and their relatives. In addition, Wang et al. (2017) noted that inclusion of osteologically immature specimens compromises topological resolution, and corroborates Sharma et al. (2016) who found that the inclusion of distinct developmental stages as terminal taxa does not provide reliable phylogenetic information. On the other hand, Sharma et al. (2016) also argued that phylogenetic trees with fossil taxa are valid if ontogenetic stages are easy to detect. Ontogenetic variation can otherwise be accommodated by scoring polymorphisms for 'juvenile' versus 'adult' states; however, we advocate caution and suggest that ontogenetic variation should be continuously revaluated as new fossils come to light.

Conclusions

CAPPA/UFM 0028 derived from an osteologically immature dinosauriform consistent with *Pampadromaeus barberenai*. Comparisons with other specimens reveals reduced tuberi, the absence of a transverse groove on the proximal end of the femur, and a ventrally descended 'facies articularis antitrochanterica'; features that are alternatively present in more osteologically mature individuals. The trochanteric shelf is absent or badly developed in CAPPA/UFM 0028, but alternatively prominent in 'adults', in which the linea intermuscularis cranialis forms a raised process. Furthermore, the deep groove separating the lateral condyle from the crista tiobiofibularis on the distal end of the femur is only observed in 'adult' examples. The dorsolateral, cranial, and fourth trochanters are present in all evaluated specimens.

Analyses of morphological variation using a published phylogenetic detatset of Bittencourt et al. (2015) found considerable disparity between the putative 'juvenile' and 'adult' specimens of *P. barberenai*, and more so relative to indirectly related taxa. Modifications to the scoring of femoral characters influenced by ontogeny returned conflicting topologies. We therefore conclude that ontogenetic assessment of additional skeletal elements might improve the current understanding of early dinosaur relationships.

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