An Acad Bras Cienc (2024) 96(Suppl. 1): e20231248 DOI 10.1590/0001-3765202420231248
Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences*
Printed ISSN 0001-3765 I Online ISSN 1678-2690
www.scielo.br/aabc | www.fb.com/aabcjournal

PALEONTOLOGY

Skeletally immature individuals nest together in the phylogenetic tree of early dinosaurs

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Abstract: The phylogenetic affinities of early dinosaurs are a controversial topic. There are disputing scenarios aiming to explain the evolutionary tree of these reptiles. A number of factors play a role on this issue. High levels of intraspecific variation experienced by the earliest forms are pointed by distinct authors as one of the main sources of phylogenetic biases. In the present study, we performed experimental analyses incorporating skeletally immature individuals as distinct operational taxonomic units in order to investigate the effect of ontogeny on the phylogeny and morphospace of early Late Triassic sauropodomorphs. The results support an "artificial" grouping of skeletally immature individuals of early dinosaurs in the phylogenetic trees, which is controlled by ontogenetic development. Such results are interpreted as the effect of ontogenetic control on the states of certain morphological characters, producing false synapomorphies. In addition, the morphological disparity analysis indicated a significant difference between the skeletally immature and mature individuals, corroborating previous assumptions. At this point, we suggest caution during the scoring process of early dinosaurs. Some approaches that avoid ontogenetically sensitive characters revealed a putative solution. Nevertheless, additional specimens and alternative tools are mandatory in order to properly deal with this issue.

Key words: Cladistics, Dinosauria, phylogenetics, ontogeny, Saurischia, Sauropodomorpha.

INTRODUCTION

Dinosaurs arose approximately 230 million years ago (Novas et al. 2021), diversifying into three main lineages (i.e., Theropoda, Sauropodomorpha, and Ornithischia), which are composed of ecomorphologically diverse groups (Brusatte et al. 2010, Langer et al. 2010, Müller et al. 2023). There is no consensus regarding the inner phylogenetic affinities of Dinosauria (Baron 2020, Černý & Simonoff 2023). For instance, it is uncertain if Theropoda is the sister-group to Ornithischia or to Sauropodomorpha (Baron et al. 2017, Langer et al. 2017, Cau 2018). The position of several early forms is disputed by distinct hypotheses (Martinez et al. 2011, Sereno et al. 2013, Agnolin & Rozadilla 2018, Marsola et al. 2018). Additionally, there are no unequivocal records of ornithischians from the Triassic Period (Müller & Garcia 2020a, Norman et al. 2022).

Phylogenetic hypotheses are affected by numerous issues, including taxon sampling (Zwickl & Hillis 2002, Baron 2022), intraspecific variation (Wiens et al. 2005, Tsai & Fordyce 2014, Cau 2021, Sharma et al. 2017, Wang et al. 2017), taphonomic deformation (Murdock et al. 2016, Müller et al. 2018a), tree search mechanism and strategy (Goloboff et al. 2008), among others. Different factors play a role on this instability of phylogenetic trees of dinosaurs, such as the scarce fossil record of earliest forms (Novas et al. 2021, Norman et al. 2022), lack of consensus regarding the construction of phylogenetic data matrices (Baron et al. 2017, Langer et al. 2017, Nesbitt et al. 2017, Baron 2020, Ezcurra et al. 2020, Müller & Garcia 2020a, Černý & Simonoff 2023), effect of taphonomy on the quality of preservation (Martinez et al. 2013, Agnolin & Rozadilla 2018, Müller et al. 2018a), and high levels of intraspecific variation (Raath 1990, Griffin & Nesbitt 2016a, Garcia et al. 2019, Müller et al. 2019, Chapelle et al. 2021, 2022). The latter is particularly important because this may occur through distinct conditions, including suggestions of sexual dimorphism (Raath 1990, Piechowski et al. 2014, Pintore et al. 2022), individual variation (Marsola et al. 2018, Barta et al. 2018, Piechowski et al. 2019), ontogeny (Choiniere et al. 2014, Griffin & Nesbitt 2016b, Müller et al. 2019, Garcia et al. 2019, Poole 2023), among others. Actually, the unusually high intraspecific variation of early dinosaurs was suggested to be one of the contributors to the rise of the group's dominance through the end of the Triassic Period (Griffin & Nesbitt 2016a). Whereas it is difficult to determine the source of intraspecific variation of a limited sample, authors agree that early dinosaurs and related groups experienced high levels of plasticity during its postnatal development (Chapelle et al. 2021, Barta et al. 2022). Thus, it is unambiguous that ontogeny deeply affects the shape of dinosaur bones, changing proportions, as well as affecting the presence and shape of specific structures (Piechowski et al. 2014, Griffin & Nesbitt 2016a, Garcia et al. 2019, Müller et al. 2019). In some cases, the postnatal development is so complex that individuals change their gait and posture during their growth (Otero et al. 2019). On the other hand, the effect of ontogeny on phylogenetic trees is poorly investigated. Some authors pointed to the need for caution during the scoring process for determinate morphological characters (Nesbitt 2011, Müller et al. 2019). For instance, skeletally immature individuals lack several muscle attachment structures that are widely employed in phylogenetic analyses (Griffin & Nesbitt 2016b, Marsola et al. 2018, Müller et al. 2019). Moreover, it was noticed that disparity scores between skeletally immature and mature individuals of the same species are higher than the disparity scores between skeletally mature individuals of distinct close-repeated species of early dinosaurs (Müller et al. 2019, Müller & Garcia 2020b). In the present study, we performed experimental analyses incorporating skeletally immature individuals as distinct operational taxonomic units (OTU) in order to investigate the effect of ontogeny on the phylogeny and morphospace of early Late Triassic sauropodomorphs.

MATERIALS AND METHODS

Materials

Because body size is a poor indicator of maturity (Griffin et al. 2021), assessing ontogenetic stages in extinct taxa is a challenging task. In order to avoid misinterpretations regarding the concept of "maturity", in the present study we employed the concept of "skeletal maturity" (*sensu* Griffin et al. 2021), which differs from "sexual maturity". Therefore, we recognized ontogenetic status according to osteological indicators (e.g., presence and shape of muscle attachment structures; bone texture). We selected four specimens (Table I; Fig. 1) that present osteological indicators of skeletal immaturity as described below.

CAPPA/UFSM (Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia da Universidade Federal de Santa Maria, Rio Grande do Sul, Brazil) 0028 (Fig. 1a, b, i, j, q): this specimen was tentatively referred to *Pampadromaeus barberenai* according to topotype and some shared traits (Müller et al. 2019). It was excavated from the "Várzea do Agudo" site (= Janner site), situated in the municipality of Agudo, southern

Table I. Measurements (in mm) of the studied femora.

Specimen	Length	Maximum proximal width	Maximum distal width
CAPPA/UFSM 0028	113	14	20
ULBRA-PVT056	89	1.5	1.5
MCN-FZB 1864	87	1.6	1.5
LPRP/USP 0651	120	2.5	2.4

Brazil. The outcrop belongs to the Candelária Sequence of the Santa Maria Supersequence (Zerfass et al. 2003, Horn et al. 2014). The fossiliferous content of the “Várzea do Agudo” site is part of the *Hyperodapedon* Assemblage Zone (AZ), which is Carnian in age (Langer et al. 2007, Schultz et al. 2020). The specimen comprises a 113 mm long left femur with strong evidence of sedimentary compression. The compression deformed the specimen in the lateromedial plane. Therefore, its diaphysis and extremities exhibit an unnatural morphology, especially the femoral head. The proximal articular surface also seems affected by erosion. Nevertheless, the bone surface of the specimen is well-preserved. CAPPA/UFSM 0028 comprises a skeletally immature individual because of the presence of patches of longitudinal parallel striations on the bone surface and the absence of a raised anterolateral scar on the proximal portion of the femur (Müller et al. 2019, Müller 2022).

ULBRA-PVT056 [Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia/Universidade Federal de Santa Maria, São João do Polêsine, Rio Grande do Sul, Brazil (previously Museu de Ciências Naturais, Universidade Luterana do Brasil, Canoas, Brazil)] (Fig. 1c, d, k, l, r): this specimen was tentatively referred to *Buriolestes schultzi* (Müller et al. 2018b, Müller 2022) according to topotypy. The specimen was unearthed from the “Buriol” site, which is situated in the municipality of São João do Polêsine, southern Brazil. The reddish mudstones of this site belong to the Candelária Sequence of the Santa Maria Supersequence (Zerfass et al. 2003, Horn et al. 2014). The site is considered Carnian in age according to the fossiliferous content that is compatible with that of the *Hyperodapedon* AZ (Roberto-da-Silva et al. 2014, Cabreira et al. 2016). The specimen preserves some vertebrae, pelvic and hind limb elements. Its femur is 89 mm in length and lack signals of sedimentary compression. The bone surface is well-preserved. It was regarded as a skeletally immature individual according to the absence of a raised anterolateral scar and trochanteric shelf on the proximal portion of the femur (Müller 2022).

MCN-FZB (Museu de Ciências Naturais, Secretaria Estadual do Meio Ambiente e Infraestrutura, Porto Alegre, Rio Grande do Sul, Brazil) 1864 (Fig. 1e, f, m, n, s): this specimen comprises an indeterminate saurischian excavated from the “Faixa Nova” site, municipality of Santa Maria, southern Brazil (Kischlat 2003). The site is part of the Candelária Sequence of the Santa Maria Supersequence (Zerfass et al. 2003, Horn et al. 2014) and is considered Carnian in age according to the presence of the genus *Hyperodapedon* (Langer et al. 2007). MCN-FZB 1864 comprises an isolated right femur with 87 mm in length. The specimen is the smaller femur of the sample. It is relatively well-preserved, lacking part of the fourth trochanter. The bone surface is well-preserved and there

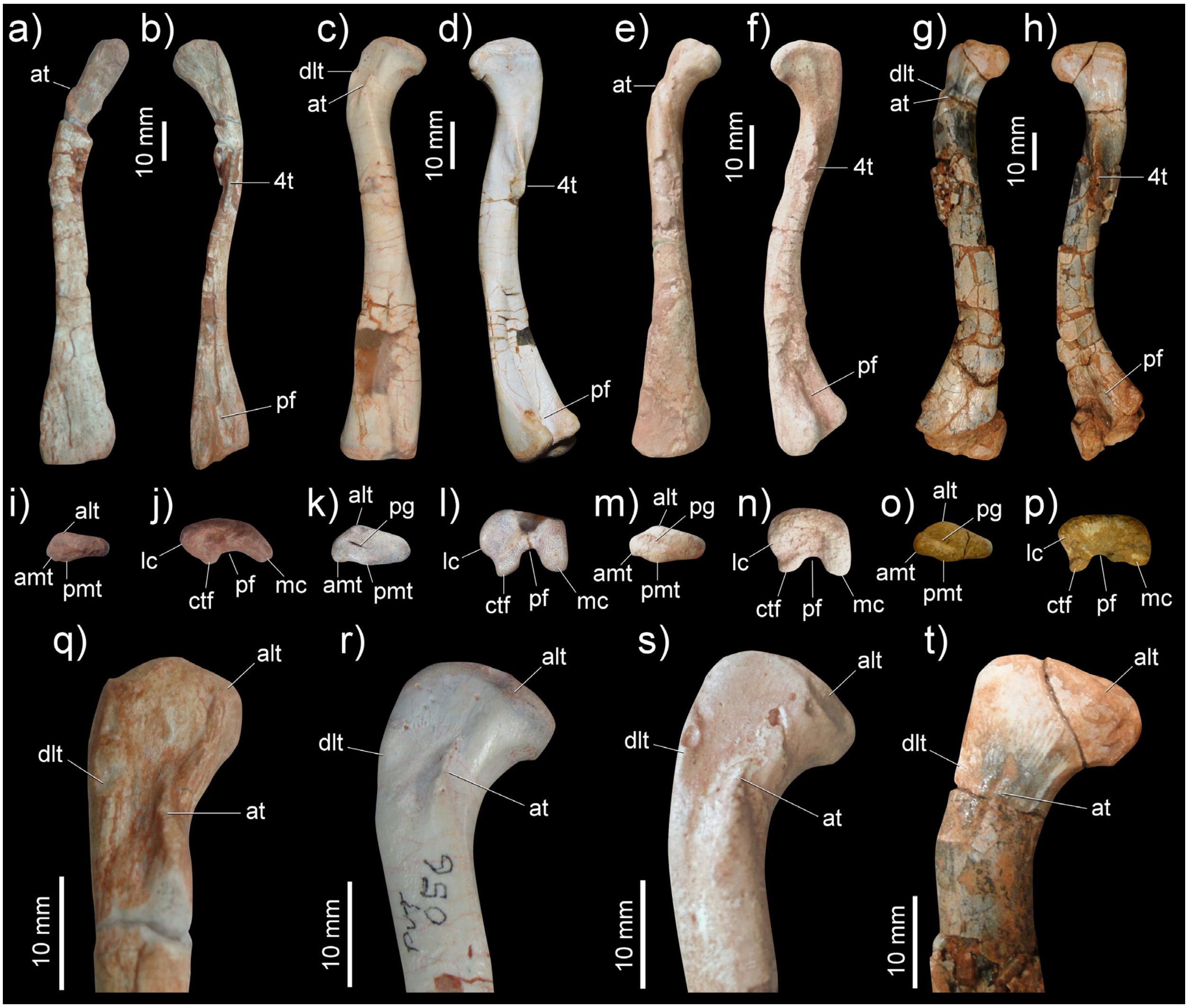

Figure 1. Sampled femora of skeletally immature early dinosaurs from Candelária Sequence (Late Triassic) of Southern Brazil in (a, c, e, g) anterior, (b, d, f, h) posteromedial, (i, k, m, o) proximal, (j, l, n, p) distal, and (q, r, s, t) lateral views. a, b, i, j, q, CAPPA/UFSM 0028 (reversed). c, d, k, l, r, ULBRA-PVT056. e, f, m, n, s, MCN-FZB 1864. g, h, o, p, t, LPRP/USP 0651. Abbreviations: 4t, fourth trochanter; alt, anterolateral tuber; amt, anteromedial tuber; at, anterior trochanter; ctf, crista tibiofibularis; dlt, dorsolateral trochanter; lc, lateral condyle; mc, medial condyle; pf, popliteal fossa; pmt, posteromedial tuber.

is no significant evidence of sedimentary compression. In addition to the small size, the absence of a raised anterolateral scar and a trochanteric shelf, as well as the sharp morphology of the dorsolateral trochanter are indicators of skeletal immaturity (e.g., Nesbitt 2011, Griffin & Nesbitt 2016b, Müller 2022).

LPRP/USP (Laboratório de Paleontologia de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, Brazil) 0651 (Fig. 1g, h, o, p, t): it is the holotype of *Nhandumirim waldsangae* (Marsola et al. 2018). The specimen comes from the "Cerro da Alemoa" site (= Waldsanga), municipality of Santa Maria, southern Brazil. This site belongs to the Candelária Sequence of the Santa Maria Supersequence (Zerfass et al. 2003, Horn et al. 2014) and is Carnian in age according to radioisotopic investigations (Langer et al. 2018). The specimen comprises some vertebrae, pelvic, and hind limb elements. Whereas the bone surface of the elements is well-preserved, some portions are incomplete or compressed. The specimen preserves the right femur, which is 120 mm long (Marsola et al. 2018). This specimen is regarded as a skeletally immature individual according to its osteohistology and non-closure of the neurocentral suture of the vertebrae (Marsola et al. 2018). Furthermore, the specimen preserves some patches of longitudinal parallel striations on the bone surface of the femur and lack a raised anterolateral scar and trochanteric shelf.

Phylogenetic analysis procedure

In order to investigate the effect of ontogeny on the phylogenetic affinities of early dinosaurs, we scored the femur of four skeletally immature specimens (Supplementary Material - Data SI) in the data matrix of Langer et al. (2022; Data SII). According to these authors, this data matrix was constructed to access the alpha taxonomy of the earliest sauropodomorph dinosaurs. We chose the femur to perform this experiment because it is the best sampled bone of early dinosaurs and most of the skeletally immature individuals of our sample are limited to the femur. Furthermore, it is known that the femoral anatomy is quite plastic during the postnatal development of early dinosaurs and related groups (Nesbitt et al. 2009, Piechowski et al. 2014, Griffin & Nesbitt 2016b, Griffin et al. 2019, Müller et al. 2019). We performed the phylogenetic analyses in the software TNT v. 1.5 (Goloboff & Catalano 2016) following the same parameters employed by Langer et al. (2022). Hence, *Lewisuchus admixtus* was used to root the most parsimonious trees (MPTs), which were constructed employing equal weights parsimony. All characters received the same weight and the following multistate characters were treated as additive (i.e., ordered): 1, 13, 14, 23, 27, 43, 49, 56, 63, 71, 72, 73, 89, 91, 94, 97, 109, 120, 135, 137, 163, 165, 173, 174, 176, 177, 190, 195, 197, 214, 219, 221, 224, 237, 269, 271, 274, 275, 276, 282, 284, 299, 300, 302, 314, 341, 343, 344, 345, 352, 358, 370, 379, 382, 383, 384, 385, 393, 394, 398, 407, 415, 429, 439, 446, 454, 455, 461, 462, 463, 472, 477, 478, 486, 501, 504, 509, 518, 520, 524, 552, 557, 562, 564, 587, 588, 593, 596, 601, 606, 609, 612, 613, 616, 618, 623, 640, 643, 659, 660, 668, 676, 681, 690, 692, 693, 695, 701, 718, 719, 731, 744, 762, 766, 767, and 768. Following the analysis by Langer et al. (2022), we applied two constrains using an a priori built tree that forced the monophyly of Sauropodomorpha and a clade composed of post-Carnian sauropodomorphs (i.e., *Macrocollum itaquii*; *Pantydraco caducus*; *Efraasia minor*; and *Plateosaurus engelhardti*) within Sauropodomorpha. The skeletally immature individuals inserted in the data matrix were forced within Sauropodomorpha. Although *Nhandumirim waldsangae* (LPRP/USP 0651) was originally described as a putative theropod (Marsola et al. 2018), subsequent investigations recovered it as an early sauropodomorph (Pacheco et al. 2019, Müller & Garcia 2020a, Norman et al. 2022). The MPTs were reconstructed based on a random addition sequence+tree bisection reconnection, which included 1000 replicates of Wagner trees (with random seed = 0), tree bisection reconnection and branch swapping (holding 10 trees saved per replicate). Consistency and retention indices were calculated employing the script by Spiekman et al. (2021) that does not take into account a priori deactivated terminals.

We performed six analyses. In the first four analyses, the phylogenetic affinities of each one of the skeletally immature individuals were investigated separately. Therefore, for each analysis, only one of the four individuals was activated. Moreover, all the specimens of *Eoraptor lunensis*, *Saturnalia tupiniquim*, and *Buriolestes schultzi* were combined into a single OTU for each species, following the approach by Langer et al. (2022). In the fifth analysis, the distinct specimens of *Eoraptor lunensis* (n=3), *Saturnalia tupiniquim* (n=3), and *Buriolestes schultzi* (n=2), as well as all the four skeletally immature specimens were activated, whereas the combined version of each one of these sauropodomorphs was deactivated. In the sixth analysis, the combined versions of *Eoraptor lunensis*, *Saturnalia tupiniquim*, and *Buriolestes schultzi* were activated and the OTUs composed by isolated individuals of these species were deactivated. All the four skeletally immature specimens were activated.

Morphological disparity analysis procedure

In addition to the phylogenetic analyses, we performed two morphological disparity analyses in order to assess the distribution of the four skeletally immature individuals in the morphospace of early sauropodomorphs. We followed the protocol and dataset of Langer et al. (2022). In the first analysis we employed the complete dataset, whereas in the second analysis we selected only femoral characters. The taxon-character distance matrix was calculated with the R Package Claddis v.0.6.3 (Lloyd 2016, R Core Team). The 'MORD' (Maximum Observable Rescaled Distance) was used for both analyses (Lehmann et al. 2019). *Panphagia protos* was excluded from both analyses because it caused empty cells in the distance matrix. A Principal Coordinate Analysis (PCoA) was conducted on the distance matrix, using the Lingoes correction. Finally, the two main axes from the PCoAs were plotted in a bivariate graph in order to visualize the area occupied by the specimens. In order to test if there is a significant difference between the skeletally immature and mature individuals, we employed a permutational multivariate analysis of variance (PERMANOVA) using PCoA outcomes. We followed the parameters of Langer et al. (2022) and the procedure was performed in the R package Vegan 2.6-4 with 100001 permutations. In the first PERMANOVA, we used the first four coordinates from the PCoA employing the complete dataset after verifying the major break in the plot of explained variance (57.13% of variance). In the second PERMANOVA, we used the first three coordinates from the PCoA with femoral characters (51.91% of variance) after observing the major break in the plot of explained variance.

RESULTS

Phylogenetic analysis

The first analysis was performed with CAPPA/UFSM 0028 activated (Fig 2a). It recovered one MPT of 1458 steps (Consistency Index = 0.47257; Retention Index = 0.38034). CAPPA/UFSM 0028 nests as the sister taxon of *Pampadromaeus barberenai* supported by the femoral head with an incipient posteromedial tuber (616: 1→0) and the medially inset tibiofibular crest of the distal end of the femur (643: 0→1). The topology resembles that recovered by Langer et al. (2022).

The next analysis was performed with ULBRA-PVT056 activated (Fig. 2b). It recovered one MPT of 1456 steps (Consistency Index = 0.47321; Retention Index = 0.38145). Whereas it follows the topology of the first analysis, ULBRA-PVT056 lies as the sister taxon of *Buriolestes schultzi* supported by the articular surface of the femoral head extensive to the medial face (614: 2→1) and the ligament groove of the femoral head bound medially by a posterior lip (624: 0→1).

The analysis with MCN-FZB 1864 activated recovered two MPTs of 1457 steps (Consistency Index = 0.47289; Retention Index = 0.38065). Both trees mirror the general topology of the previous analyses. In the first MPT (Fig. 2c), MCN-FZB 1864 is the sister taxon of *Pampadromaeus barberenai* supported by the medially inset

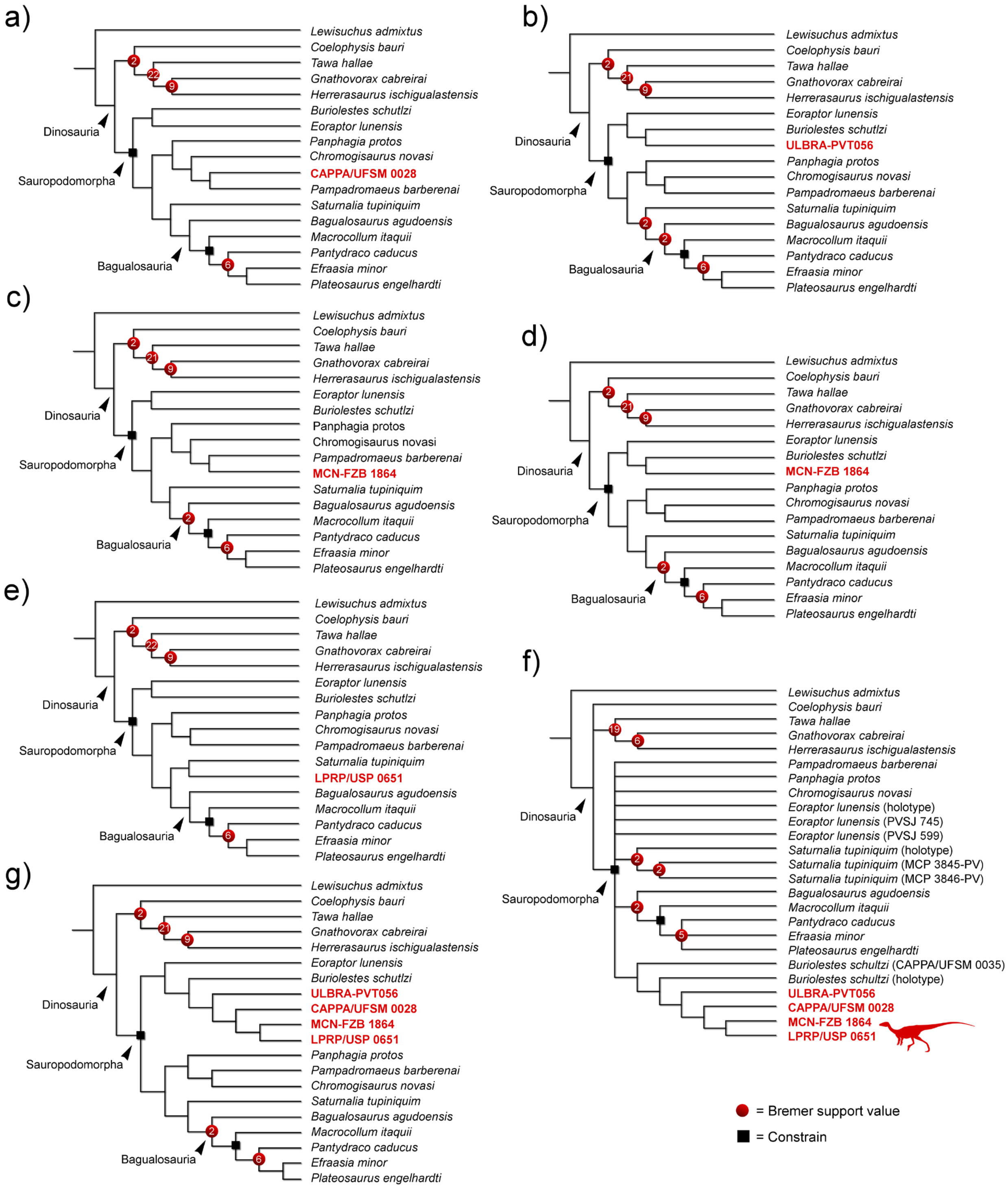

Figure 2. Results of the phylogenetic analysis. a, single MPT from the analysis where CAPPA/UFSM 0028 is activated. b, single MPT from the analysis where ULBRA-PVT056 is activated. c, first MPT from the analysis where MCN-FZB 1864 is activated. d, second MPT from the analysis where MCN-FZB 1864 is activated. e, single MPT from the analysis where LPRP/USP 0651 is activated. f, strict consensus tree from the analysis where the distinct specimens of *Eoraptor lunensis*, *Saturnalia tupiniquim*, and *Buriolestes schultzi* were activated. g, single MPT from the analysis where the four skeletally immature specimens are activated.

tibiofibular crest of the distal end of the femur (643: 0→1) and the area occupied by lateral and medial condyles in the distal end are subequal (648: 0→1). In the second MPT (Fig. 2d), MCN-FZB 1864 nests as the sister taxon to *Buriolestes schultzi*, which is supported by the ligament groove of the femoral head bound medially by a posterior lip (624: 0→1).

In the analysis with LPRP/USP 0651 activated recovered one MPT (Fig. 2e) of 1454 steps (Consistency Index = 0.47387; Retention Index = 0.38107). Following the previous analyses performed here, the general topology is the same recovered by Langer et al. (2022). LPRP/USP 0651 lies as the sister taxon of *Saturnalia tupiniquim*. This arrangement is supported by the ligament groove of the femoral head bound medially by a posterior lip (624: 0→1).

The fifth phylogenetic analysis (Fig. 2f) recovered 10 MPTs of 1552 steps (Consistency Index = 0.44910; Retention Index = 0.40584). The general topology of the strict consensus tree resembles that recovered by Langer et al. (2022), where there is a large polytomy at the base of Sauropodomorpha. The holotypes of *Pampadromaeus barberenai*, *Panphagia protos*, *Chromogisaurus novasi*, and *Eoraptor lunensis*, as well as the two referred specimens of *Eoraptor lunensis* forms the polytomy with three other clades. The holotype and two paratypes of *Saturnalia tupiniquim* are grouped together. Bagualosauria is composed by *Bagualosaurus agudoensis* plus post-Carnian sauropodomorphs. Finally, the third group is composed by a referred specimen of *Buriolestes schultzi* as the sister-group to a node composed by the holotype of *Buriolestes schultzi* plus a group exclusively of the four skeletally immature femora. The latter node is supported by an anterior trochanter of the femur that is proximodistally oriented ridge instead of a small rounded tubercle (627: 0→1) and a lateral condyle of the distal end of the femur that is anteroposteriorly longer than transversely wide (650: 1→0). ULBRA-PVT056 is the basalmost member of the group composed of juveniles. It is the sister-taxon to a node joining CAPPA/UFSM 0028 as the sister-taxon to MCN-FZB 1864 plus LPRP/USP 0651. This node is supported by the a continuous to slightly concave margin between the fibular and lateral condyles of the distal end of the femur (651: 1→0). Finally, the node supporting MCN-FZB 1864 and LPRP/USP 0651 is supported by the articular surface of the femoral head extending to medial and distal faces (614: 1→2).

The sixth phylogenetic analysis recovered one single MPT (Fig. 2g) of 1462 steps (Consistency Index = 0.47674; Retention Index = 0.38653). Again, except for the four new OTUs, this analysis mirrors the results recovered by Langer et al. (2022). The same group composed of the four skeletally immature femora was recovered with the same arrangement and same characters supporting each node. This group is the sister-group to *Buriolestes schultzi*, whereas the node supporting *Buriolestes schultzi* plus the skeletally immature specimens is the sister-group to *Eoraptor lunensis*.

Morphological disparity analysis

In the first analysis (i.e., all characters), the PCo 1 accounts for 18.59% of variance and the PCo 2 accounts for 13.61% of variance. The PERMANOVA showed significant differences between the skeletally immature and mature individuals ($p < 0.01$). The four skeletally immature specimens lie on an exclusive area of the same quadrant when both axes are combined (Fig. 3a). When the PCo 1 is considered, there is some degree of overlapping between the skeletally immature specimens and the two specimens of *Saturnalia tupiniquim* (MCP 3845-PV and MCP 3846-PV). Conversely, in the PCo 2 there is overlap

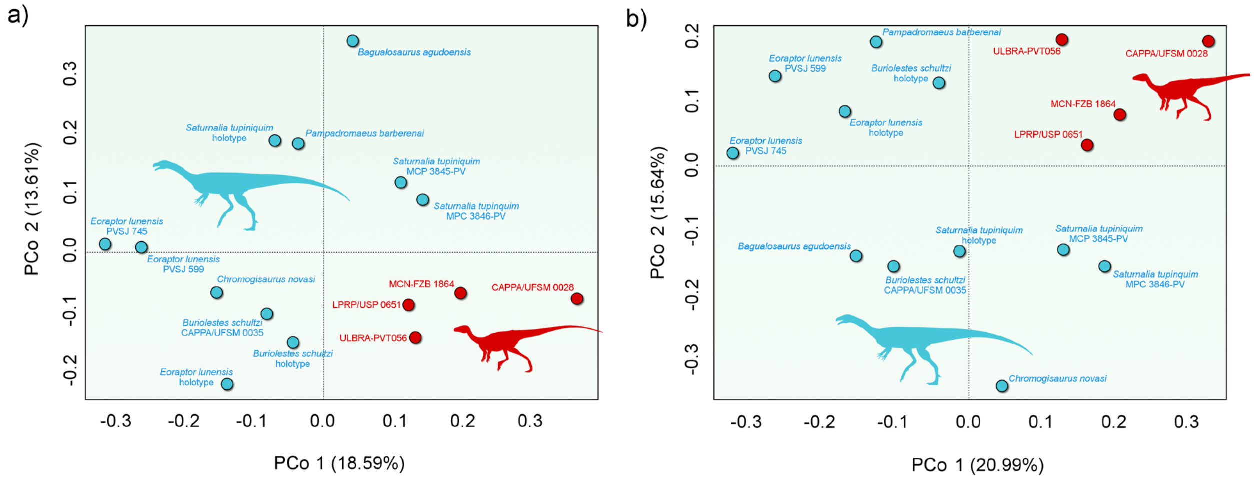

Figure 3. Bivariate plots showing the results of the morphospace occupation analysis. a, using all the characters. b, using only femoral characters. Red dots are the skeletally immature individuals.

between the skeletally immature specimens and *Chromogisaurus novasi* and the two specimens of *Buriolestes schultzi* (ULBRA-PVT280 and CAPPA/UFSM 0035).

In the second analysis (i.e., only femoral characters), the PCo 1 accounts for 20.99% of variance and the PCo 2 accounts for 15.64% of variance. The PERMANOVA showed significant differences between the skeletally immature and mature individuals ($p < 0.01$). Such as in the first analysis, the four skeletally immature specimens lie on an exclusive area of the same quadrant when both axes are combined (Fig. 3b). There is some degree of overlap between the skeletally immature specimens and two specimens of *Saturnalia tupiniquim* (MCP 3845-PV and MCP 3846-PV). In the PCo 2, the skeletally immature specimens are close to the three specimens of *Eoraptor lunensis*, the holotype of *Buriolestes schultzi* and *Pampadromaeus barberenai*.

DISCUSSION

Both exploratory analyses (i.e., phylogenetic and disparity) produced similar results that support an "artificial" grouping of skeletally immature individuals of early dinosaurs, which is controlled by ontogenetic development. Actually, the morphological disparity analysis indicated a significant difference between the skeletally immature and mature individuals. This is particularly interesting because when each skeletally immature individual is inserted into the datasets without the other three specimens, the tree topologies are far distinct from the analyses when all the four skeletally immature specimens are included. This result is interpreted as the effect of ontogenetic control on the states of certain morphological characters, producing mistaken synapomorphies. Wiens et al. (2005) recovered similar results investigating the role of ontogeny on the salamander phylogenetic relationships. The authors demonstrated that grouping of the paedomorphic groups in a single clade reflects the effects of paedomorphosis rather than phylogenetic history. Moreover, major changes in development can lead to incorrect phylogenetic topologies, even at higher taxonomic levels (Wiens et al. 2005). Cau (2021) also recovered a similar scenario investigating theropods. The author recovered a putative polyphyletic grouping of immature individuals, which is not supported when the author performed an analysis attempting to minimize the impact of ontogeny on the topology.

Most authors agree that the use of incompatible semaphoronts or "ontogenetic stages" produces biased topologies (Wiens et al. 2005, Tsai & Fordyce 2014, Sharma et al. 2017, Wang et al. 2017, Müller et al. 2019, Cau 2021). According to our results, it is true for early dinosaurs, which is not a surprise given the high levels of intraspecific variation reported for dinosauromorphs and related groups (Raath 1990, Nesbitt et al. 2009, Piechowski et al. 2014, Griffin & Nesbitt 2016a, Garcia et al. 2019, Müller et al. 2019, Barta et al. 2022). Whereas a single operational taxonomic unit composed of a skeletally immature individual is able to nest in a natural position, the inclusion of multiple operational taxonomic units from skeletally immature individuals could result in unnatural groups (e.g., Wiens et al. 2005, Cau 2021, and here), biasing the topology. We are not advocating against the use of skeletally immature individuals in phylogenetic analysis. In vertebrate paleontology, it is not unusual that some species are known from a single specimen (e.g., Colbert 1970, Martinez & Alcober 2009, Ezcurra 2010, Pacheco et al. 2019), which is, sometimes, a skeletally immature individual (e.g., Marsola et al. 2018, Colbert 1970). Conversely, we suggest caution during the scoring process. While there is not consensus regarding the handling of phylogenetic characters that also change through ontogeny (Poole 2023), one putative solution is to avoid characters controlled by ontogenetic variation (i.e., "ontogenetically sensitive characters" *sensu* Poole 2023). This approach was employed by Choiniere et al. (2014) in order to investigate the phylogenetic affinities of a theropod dinosaur. Poole (2023) followed a similar approach in order to minimize the impact of ontogenetic variance during the investigation of the phylogenetic affinities of an ornithischian dinosaur known from juvenile specimens (Forster et al. 2023). Regarding ontogenetically sensitive characters in early dinosaurs and related groups, an example includes the shape of the dorsolateral trochanter of the femur, which varies from sharp to rounded (Raath 1990, Nesbitt 2011, Piechowski et al. 2014, Griffin & Nesbitt 2016b). Several specimens revealed that it is affected by ontogeny, with the "sharp" condition occurring in skeletally immature individuals and the "rounded" condition occurring in ontogenetic advanced individuals. If a specimen that is clearly recognized as a skeletally immature individual expresses this condition, we recommend keeping it as a "missing" data. This approach is able to avoid the selection of ambiguous synapomorphies. On the other hand, this approach becomes problematic when paedomorphic traits are considered. For instance, the trochanteric shelf occurs in the femora of early sauropodomorphs (Sereno et al. 1993, Langer et al. 1999, Ezcurra 2010, Cabreira et al. 2016). However, it is absent in skeletally immature individuals (Marsola et al. 2018, Müller et al. 2018b, 2019). Curiously, the trochanteric shelf is absent in skeletally mature sauropodomorphs from post-Carnian strata (Otero & Pol 2021). As a consequence, the absence in ontogenetic advanced sauropodomorphs represents a neotenic trait with phylogenetic importance. In sauropodomorphs phylogenetically more advanced than *Bagualosaurus agudoensis*, the trochanteric shelf is absent. Therefore, this issue is more complex than just scoring certain characters as "missing data'' as a solution. Additional efforts in order to construct an ontogenetic series of early dinosaurs are mandatory at this point.

The results of present contribution are restricted to the analysis of femoral characters.

This is because this bone is one of the best sampled element for early dinosaurs (e.g., Colbert 1970, Novas 1993, Langer et al. 1999, Sereno et al. 2013, Cabreira et al. 2016, Marsola et al. 2018, Pacheco et al. 2019). Moreover, the pelvic girdle and hind limb are strongly specialized in dinosaurs (Hutchinson 2001, Langer et al. 2010, Nesbitt 2011), reflecting the postural evolution experienced by these reptiles (Tsai et al. 2018). These regions of the skeleton are far more represented in phylogenetic data matrices than other portions. Therefore, the effect of ontogeny on the phylogenetic trees of early dinosaurs need further investigations employing additional skeletal portions. Future studies should test if similar scenarios are recovered considering distinct parts of the skeleton or more complete skeletons, which is not viable to properly test with the present data.

Acknowledgments

We thank Christopher Griffin, Federico Agnolin, and Matthew Baron for suggestions that improved this manuscript. We also extend our gratitude to the Willi Hennig Society for the gratuity of the TNT software. This work was carried out with aid of Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 404095/2021-6; 303034/2022-0; and 406902/2022-4) to Rodrigo Temp Müller and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES 23081.021978/2022-71) to Lísie Vitória Soares Damke.

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SUPPLEMENTARY MATERIAL

DATA SI, SII.

How to cite

MÜLLER RT, DAMKE LVS & TERRAS R. 2024. Skeletally immature individuals nest together in the phylogenetic tree of early dinosaurs. An Acad Bras Cienc 96: e20231248. DOI 10.1590/0001-3765202420231248.

Manuscript received on November 17, 2023
accepted for publication on March 04, 2024

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