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## Ingroup relationships of Lagerpetidae (Avemetatarsalia: Dinosauromorpha): a further phylogenetic investigation on the understanding of dinosaur relatives

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### Abstract

Despite representing a key-taxon in dinosauromorph phylogeny, Lagerpetidae is one of the most obscure and enigmatic branches from the stem that leads to the dinosaurs. Recent new findings have greatly increased our knowledge about lagerpetids, but no phylogenetic analysis has so far included all known members of this group. Here, we present the most inclusive phylogenetic study so far conducted for Lagerpetidae. Phylogenetic analyses were performed based on three independent data matrixes. In two of them, *Lagerpeton chanarensis* Romer, 1971 is the sister taxon to all other known Lagerpetidae, whereas *Ixalerpeton polesinensis* Cabreira *et al.*, 2016 is in a sister group relationship with a clade that includes PVSJ 883 and *Dromomerion*. Conversely, the other analysis supports an alternative topology, where *I. polesinensis* is the sister taxon to either *L. chanarensis* or all other Lagerpetidae. Although coeval and geographically close, *I. polesinensis* and PVSJ 883 do not form a clade exclusive of other lagerpetids. As previously suggested *D. gigas* Martínez, Apaldetti, Correa & Abelín, 2016 is the sister taxon of *D. romeri* Irmis *et al.*, 2007. The phylogenetic analyses also indicate that the earliest lagerpetids are restricted to southwestern Pangea, whereas later forms spread across the entire western portion of the supercontinent. Finally, quantification of the codified characters of our analysis reveals that Lagerpetidae is one of the poorest known among the Triassic dinosauromorph groups in terms of their anatomy, so that new discoveries of more complete specimens are awaited to establish a more robust phylogeny.

**Key words:** cladistics, basal dinosauromorphs, late triassic, paleobiogeography, phylogeny

### Introduction

The discovery of some peculiar small archosaur skeletons from the early Carnian Chañares Formation, in Argentina, shed light on the bauplan of dinosaur precursors (Romer 1971; Bonaparte 1975; Arcucci 1987). Among these, the enigmatic *Lagerpeton chanarensis* Romer, 1971 was the only known Lagerpetidae for some decades, nesting alone in the sister lineage of Dinosauriformes (e.g., Sereno & Arcucci 1994; Novas 1996; Ezcurra 2006). A new lagerpetid, *Dromomerion romeri* Irmis *et al.*, 2007, was only described in 2007, from the Norian beds of the Chinle Formation in New Mexico. The discovery of *D. romeri* revealed that non-dinosaurian dinosauromorphs and dinosaurs shared the same environments nearly until the end of the Triassic (Irmis *et al.* 2007). Two years later, *D. gregorii* Nesbitt *et al.*, 2009, a second species of the genus, was described from the Dockum Group of Texas. In the same year, Small (2009) reported new lagerpetid specimens from the Chinle Formation of Colorado comprising femoral elements. More recently, Martínez *et al.* (2012) described a highly fragmentary specimen (PVSJ 883) from the Ischigualasto Formation, late Carnian of Argentina. Despite its fragmentary condition, PVSJ 883 bears several traits that support an assignment within Lagerpetidae as the sister group to *Dromomerion* (Martínez *et al.* 2012). The specimen filled a temporal gap, as lagerpetids were previously recorded in the early Carnian and Norian, but not in the late Carnian. More recently, two further South American species were described: *Dromomerion gigas* Martínez, Apaldetti, Correa & Abelín, 2016, from the late Norian–Rhaetian strata of the Quebrada del Barro in

Argentina (Martínez *et al.* 2016), and *Ixalerpeton polesinensis* Cabreira *et al.*, 2016, from the late Carnian *Hyperodapedon* biozone of the Santa Maria Formation, in southern Brazil (Cabreira *et al.* 2016). Finally, Sarigül (2016) presented additional specimens of *Dromomeron*, including the lowest occurrences of *D. gregorii* and *D. romeri*, challenging a possible faunal succession between the two taxa. These additional specimens were recovered from various localities of the Dockum Group of Texas, ranging from early Norian to mid-late Norian in age (Sarigül 2017).

The latest South American discoveries have greatly increased our knowledge about lagerpetids by revealing unexpected information, such as the retention of extremely plesiomorphic structures (e.g. postfrontal) and large body size (Martínez *et al.* 2016; Cabreira *et al.* 2016). However, no phylogenetic analysis has so far included all known Lagerpetidae and a more comprehensive phylogenetic work is required to evaluate whether the inclusion of further operational taxonomic units influence the topology, especially regarding South American taxa. For instance, is *D. gigas* closer to the North American species of the genus than to other South American forms? In this study, we aim to investigate this question, based on the most inclusive phylogenetic study of the Lagerpetidae so far conducted.

**Institutional abbreviations:** **AMNH**, American Museum of Natural History, New York, USA; **GR**, Ruth Hall Museum of Paleontology at Ghost Ranch, New Mexico, USA; **MCZ**, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; **NMMNH**, New Mexico Museum of Natural History and Science, New Mexico, USA; **PVL**, Istituto Miguel Lillo, Tucuman, Argentina; **PVSJ**, Instituto y Museo de Ciencias Naturales, San Juan, Argentina; **TMM**, Texas Memorial Museum, Austin, Texas, USA; **TTU**, Museum of Texas Tech University, Texas, USA; **UCMP**, University of California Museum of Paleontology, California, USA; **ULBRA-PVT**, Universidade Luterana do Brasil, Coleção de Paleovertebrados, Rio Grande do Sul, Brazil; **UNLR**, Museo de Paleontología, Universidad Nacional de La Rioja, La Rioja, Argentina; **WTAMU**, West Texas A&M University, Texas, USA.

## Material and methods

**Taxonomic sample.** Specimens of *Lagerpeton chanarensis* and *Ixalerpeton polesinensis* were studied first-hand, whereas the remaining taxa are scored based on the literature and photographic material. The lagerpetids used in this phylogenetic analysis are listed below:

### *Lagerpeton chanarensis* Romer, 1971 (Fig. 1A)

**Age.** early–mid Carnian, Late Triassic (Marsicano *et al.* 2015).

**Occurrence.** Chañares Formation, Argentina.

**Holotype.** UNLR 06, articulated right hind limb.

**Referred material.** PVL 4619, articulated sacrum, pelvis, and partial right and left hind limbs; PVL 4625, articulated vertebral column including truncal, sacral, and anterior caudal vertebrae, left pelvis, and left femur; MCZ 4121, partial right and left femora.

### *Ixalerpeton polesinensis* Cabreira *et al.*, 2016 (Fig. 1B)

**Age.** late Carnian, Late Triassic (Cabreira *et al.* 2016).

**Occurrence.** Candelária Sequence of the Santa Maria Supersequence, Brazil.

**Holotype.** ULBRA-PVT059, partially articulated skeleton, including skull roof, braincase, 23 pre-sacral, two sacral, and nine tail vertebrae, right scapula, left humerus, paired pelvic girdle, femur, tibia, and fibula.

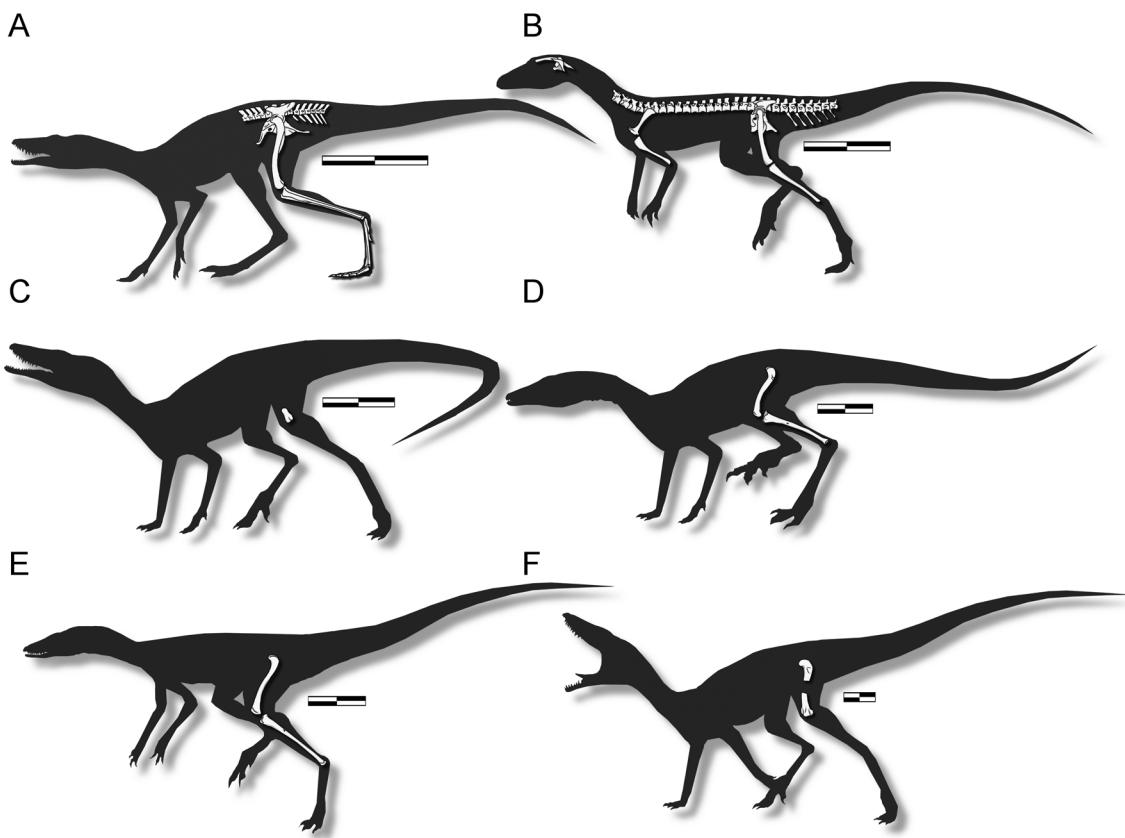
**Paratype.** ULBRA-PVT058, pair of femora.

### PVSJ 883 (Fig. 1C)

**Age.** late Carnian, Late Triassic (Martínez *et al.* 2011).

**Occurrence.** Ischigualasto Formation, Argentina.

**Material.** distal end of the left femur (see Martínez *et al.* 2012).



**FIGURE 1.** Skeletal reconstructions depicting the preserved parts of the lagerpetids used in this phylogenetic analysis: A, *Lagerpeton chanarensis* [modified from Sereno & Arcucci (1994)]; B, *Ixalerpeton polesinensis* [modified from Cabreira *et al.* (2016)]; C; PVSJ 883; D, *Dromomeron gregorii*; E, *Dromomeron romeri*; F, *Dromomeron gigas*. Scale bars = 10 mm.

***Dromomeron gregorii* Nesbitt *et al.*, 2009** (Fig. 1D)

**Age.** early–mid Norian, Late Triassic.

**Occurrence.** Dockum Group, Texas, USA and Chinle Formation, Arizona, USA

**Holotype.** TMM 31100-1306, right femur.

**Paratypes.** TMM 31100-464, right femur; TMM 31100-1308, right femur; TMM 31100-1234, right femur; TMM 31100-764, right femur; TMM 31100-278, right tibia; TMM 31100-1314, left tibia.

**Referred material.** UCMP 25815, distal portion of a left femur; TTU-P11282, left femur; TTU-P18331, proximal end of left femur; TTU-P20046, distal end of left femur; WTAMU-V-8302, proximal end of right femur; WTAMU-V-8303, proximal end of right tibia.

***Dromomeron romeri* Irmis *et al.*, 2007** (Fig. 1E)

**Age.** Norian, Late Triassic (Irmis *et al.* 2007).

**Occurrence.** Dockum Group, Texas, USA and Chinle Formation, New Mexico, USA.

**Holotype.** GR 218, left femur.

**Paratypes.** GR 219, right femur; GR 220, left tibia; GR 221, partial left femur; GR 234, right femur; GR 222, left tibia; GR 223, astragalocalcaneum.

**Referred material.** GR 235, partial articulated skeleton; GR 236, partial right tibia; NMMNH P-35379, astragalocalcaneum; AMNH FR 2721, distal portion of a femur; AMNH FR 30648, distal portion of a right tibia; AMNH FR 30649, distal portion of a right tibia; TTU-P12537X, proximal end of right tibia; WTAMU-V-8301, distal end of right femur.

***Dromomeron gigas* Martínez *et al.*, 2016** (Fig. 1F)

**Age.** late Norian – Rhaetian, Late Triassic (Martínez *et al.* 2015).

**Occurrence.** Quebrada Del Barro Formation, Argentina.

**Holotype.** PVSJ 898, a partial left femur represented by its proximal and distal portions.

**Dataset and procedure.** The phylogenetic relationships within Lagerpetidae were investigated under the cladistic paradigm with the aid of computational tools. We added the scores for *Dromomeron gigas* (PVSJ 898) and the unnamed lagerpetid from the Ischigualasto Formation (PVSJ 883) to the data matrix of Cabreira *et al.* (2016), which already included the lagerpetids *Lagerpeton chanarensis*, *Ixalerpeton polesinensis*, *D. gregorii*, and *D. romeri*. For several characters, the codification of the added Operational Taxonomic Units (OTUs) followed that of Martínez *et al.* (2012). In addition, we also included three femoral characters proposed by Martínez *et al.* (2016) and one by Nesbitt (2011), because these characters vary among lagerpetids: characters 291, 292, and 293 of Martínez *et al.* (2016) were renumbered here as 257, 258, and 259, respectively, and character 322 of Nesbitt (2011) was renumbered 260. After these modifications, the data matrix summed up 260 characters and 45 OTUs (see the supplementary files for full coding).

The phylogenetic analysis was conducted in the software TNT v1.1 (Goloboff *et al.* 2008). As in Cabreira *et al.* (2016), all characters received the same weight and 31 (3, 4, 6, 11, 36, 60, 62, 64, 83, 115, 123, 139, 147, 148, 157, 160, 171, 173, 175, 178, 179, 182, 195, 200, 201, 202, 205, 216, 222, 240, and 248) were treated as ordered. *Euparkeria capensis* Broom, 1913 was used to root the most parsimonious cladograms (MPCs), which were recovered with a ‘Traditional search’ (random addition sequence + tree bisection reconnection) with 1000 replicates of Wagner trees (with random seed = 0), tree bisection reconnection and branch swapping (holding 20 trees save per replicate). Decay indices (Bremer support values), as well as bootstrap values (1000 replicates), were also obtained with TNT v1.1. In addition, two constrained analyses were carried out, both using the same parameters of the first analysis. The first of them was conducted to access the required number of extra steps to recover *Ixalerpeton polesinensis* and PVSJ 883 as sister groups, considering that both are coeval and geographically close. The second constrained analysis assessed how many additional steps it would take to recover monophyletic South American and North American groups.

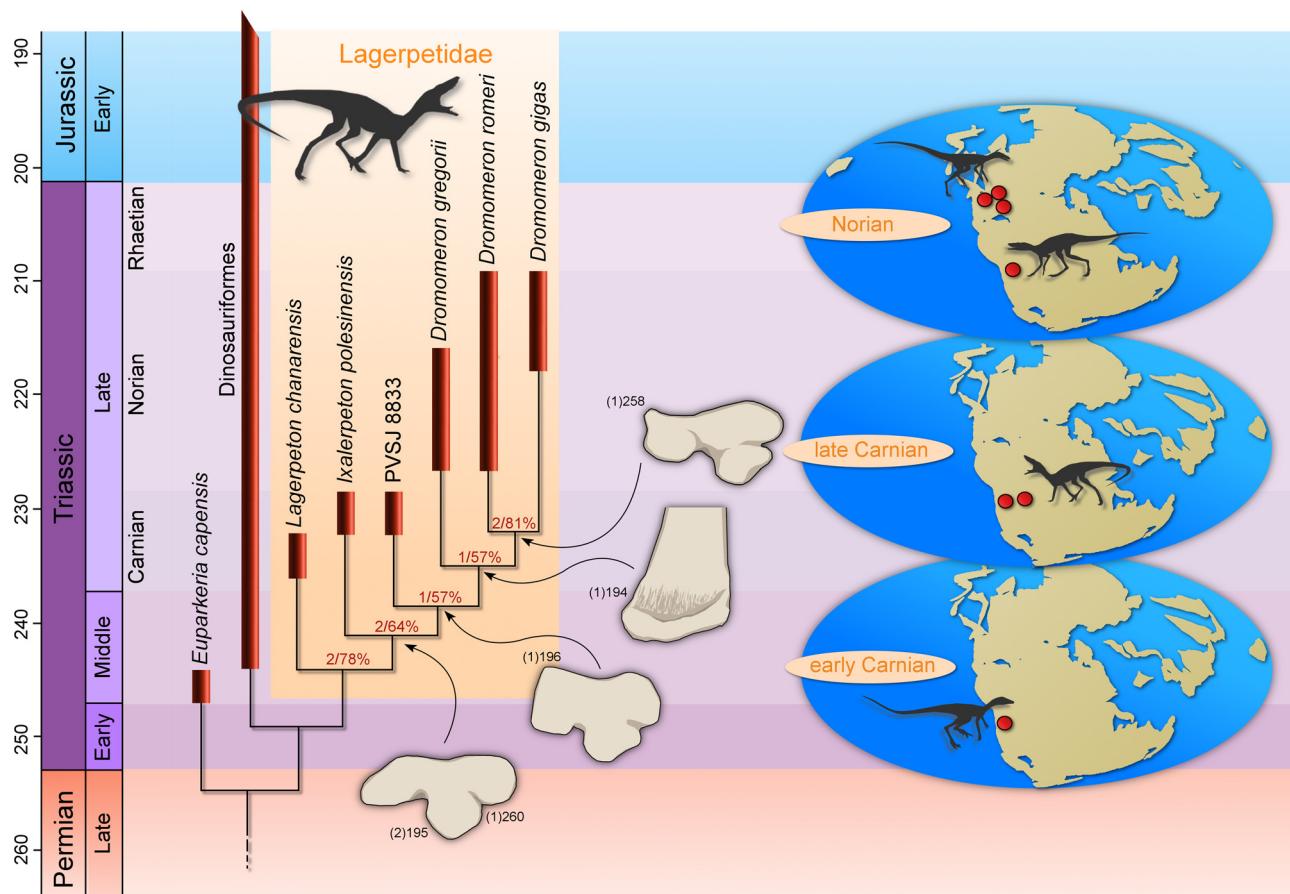
We also performed an additional analysis employing the data matrix by Nesbitt *et al.* (2017) as it increases the taxon sampling of basal dinosauromorphs. This data matrix originally includes *Lagerpeton chanarensis*, *Dromomeron gregorii*, and *D. romeri*. Therefore, we added *D. gigas*, the unnamed lagerpetid from the Ischigualasto Formation (PVSJ 883), and *Ixalerpeton polesinensis* as new OTUs. Three femoral characters proposed by Martínez *et al.* (2016) were also included in the data matrix. Accordingly, these characters were renumbered here as 420, 421, and 422, respectively. With these modifications, the data matrix comprises 422 characters and 88 OTUs (see the supplementary files). As in Nesbitt *et al.* (2017), all characters received the same weight and 19 (32, 52, 121, 137, 139, 156, 168, 188, 223, 247, 258, 269, 271, 291, 297, 328, 356, 399, and 413) were treated as ordered. This second analysis was also run with TNT v1.1 (Goloboff *et al.* 2008). *Mesosuchus browni* Watson, 1912 was used to root the MPCs, which were recovered following the parameters of the first analysis.

Finally, we also performed an analysis derived from the data matrix of Langer *et al.* (2017), which is a modified version of that of Baron *et al.* (2017a). The only OTU included was the unnamed lagerpetid from the Ischigualasto Formation (PVSJ 883), as the other lagerpetid species were already scored. Five additional characters that vary among lagerpetids were also included: characters 291, 292, and 293 of Martínez *et al.* (2016) were respectively renumbered here as 458, 459, and 460, whereas characters 322 and 327 of Nesbitt (2011) were renumbered as 461 and 462. Thus, the data matrix summed up 462 characters and 84 OTUs. As in Baron *et al.* (2017a), all characters received the same weight and 40 (24, 35, 39, 60, 68, 71, 117, 145, 167, 169, 174, 180, 197, 199, 206, 214, 215, 222, 251, 269, 272, 286, 289, 303, 305, 307, 313, 322, 333, 334, 338, 353, 360, 376, 378, 387, 393, 442 and 446) were treated as ordered. *Euparkeria capensis* was used to root the MPCs, which were recovered following the parameters of the previous analyses.

## Results

The unconstrained phylogenetic analysis with the data matrix by Cabreira *et al.* (2016) recovers 54 MPCs of 851 steps each (CI = 0.350; RI = 0.643; RC = 0.225). The topology of the strict consensus cladogram (Fig. 2) is

identical to that of Cabreira *et al.* (2016), except for the ingroup relations of lagerpetids. Lagerpetidae is supported by 14 synapomorphies, all related to the pelvic girdle and hindlimb elements. However, pelvic elements are preserved solely in *Lagerpeton chanarensis* and *Ixalerpeton polesinensis*. The synapomorphies related to pelvic girdle include: thicker (lateralomedially) portion of the supraacetabular crest of the ilium positioned at the center of the acetabulum (state “0” of character 145); supraacetabular crest extends along the pubic peduncle length (state “1” of character 146); and pubic peduncle of the ilium ventrally oriented (state “0” of character 157). As in previous analyses (Martínez *et al.* 2016; Cabreira *et al.* 2016), *Lagerpeton chanarensis* is the sister taxon to a clade including *Ixalerpeton polesinensis*, PVSJ 883, and all species of *Dromomeron*. This clade is supported by two synapomorphies, one related to a large and globular crista tibiofibular of the femur (state “2” of character 196), and another to a deep groove between the lateral condyle and the crista tibiofibularis on the distal surface of the femur (state “1” of character 260). Further, the phylogenetic affinity between PVSJ 883 and *Dromomeron* is supported by an acute craniomedial corner of the distal end of the femur (state “1” of character 196). The *Dromomeron* clade is supported by a mediolaterally orientated scar on the cranial surface of the distal portion of the femur (state “1” of character 194). In agreement with Martínez *et al.* (2016), *D. gigas* and *D. romeri* are sister taxa, as supported by two synapomorphies: a sharp ridge on the craniomedial edge of the distal end of the femur (state “1” of character 257) and a lateral tuberosity on the craniolateral edge of the distal end of the femur (state “1” of character 258).

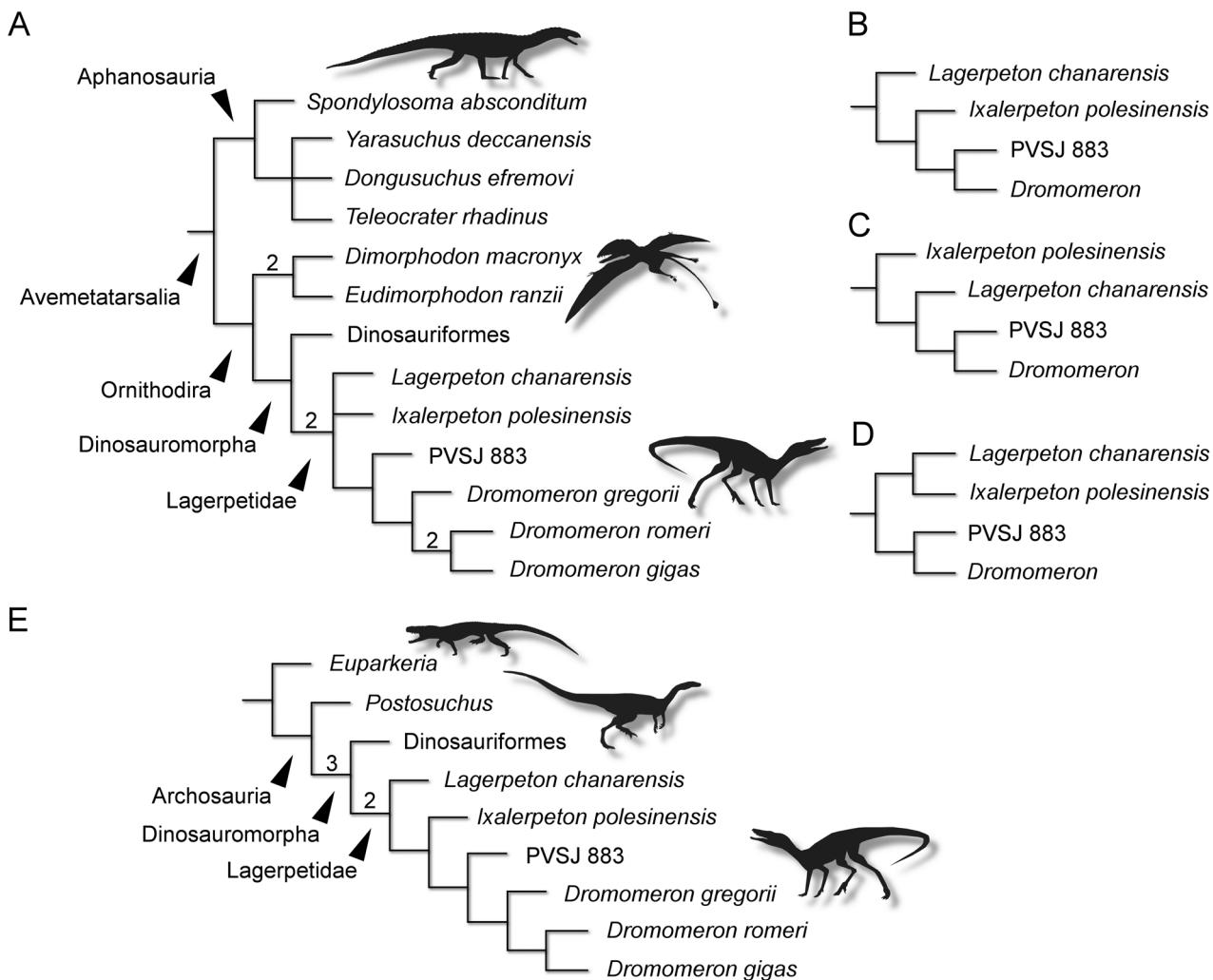


**FIGURE 2.** Reduced strict consensus cladogram of the analysis with the data matrix by Cabreira *et al.* (2016) depicting some synapomorphies of the less inclusive groups within Lagerpetidae and geographic distribution of the group along the time. Numbers on nodes represent Bremer support and Bootstrap values, respectively.

The constrained analysis forcing a *Ixalerpeton polesinensis* plus PVSJ 883 clade produced 54 MPCs of 852 steps each (CI = 0.350; RI = 0.642; RC = 0.224), whereas that forcing the monophyly of the South American and North American forms recovered 54 MPCs of 858 steps each (CI = 0.347; RI = 0.638; RC = 0.221). These are respectively one and seven steps longer than the MPCs of the unconstrained analysis.

The phylogenetic analysis with the data matrix by Nesbitt *et al.* (2017) recovered 720 MPCs of 1405 steps each (CI = 0.350; RI = 0.761; RC = 0.266). Lagerpetidae is supported by six synapomorphies, all related to the hindlimb

elements. The inner affinities of the clade in the strict consensus cladogram resemble those from the first analysis (Fig. 3A). However, *Lagerpeton chanarensis* and *Ixalerpeton polesinensis* are in a trichotomy with the clade of PVSJ 883 plus *Dromomeron*. Actually, three distinct placements are found for both species. The first arrangement replicates the result from the first analysis, with *L. chanarensis* as the sister taxon to all other Lagerpetidae (Fig. 3B). An alternative topology suggests *I. polesinensis* in that position (Fig. 3C), a hypothesis already supported by Baron *et al.* (2017b). Finally, the last hypothesis suggests sister taxon relation between *L. chanarensis* and *I. polesinensis* (Fig. 3D). The internal affinities of *Dromomeron* agree with the first analysis.



**FIGURE 3.** Results of phylogenetic analyses: A, simplified phylogenetic relationships of lagerpetids based on the data matrix by Nesbitt *et al.* (2017); B, hypothesis were *Lagerpeton chanarensis* lies as the basalmost member of Lagerpetidae with the data matrix by Nesbitt *et al.* (2017); C, hypothesis were *Ixalerpeton polesinensis* lies as the basalmost member of Lagerpetidae with the data matrix by Nesbitt *et al.* (2017); D, sister taxon affinity between *L. chanarensis* and *I. polesinensis* with the data matrix by Nesbitt *et al.* (2017); E, simplified phylogenetic relationships of lagerpetids based on the data matrix by Langer *et al.* (2017). Numbers on nodes represent Bremer support values higher than 1.

The phylogenetic analysis with the data matrix of Langer *et al.* (2017) recovers 297648 MPCs of 1936 steps each (CI = 0.275; RI = 0.620; RC = 0.170). The inner topology of Lagerpetidae in the strict consensus cladogram is the same recovered in the first analysis (Fig. 3E), where *Lagerpeton chanarensis* is the sister taxon to a clade including *Ixalerpeton polesinensis*, PVSJ 883, and all species of *Dromomeron*. Lagerpetidae nests as the sister group to Dinosauriformes, supported by nine synapomorphies. Except by the pubis with less than or equal to 0.5 of the total length of the femur (state “0” of character 340), the other synapomorphies are all related to hindlimb: hook shaped femoral head in lateral/medial view; ventral emargination at the anterolateral side of the femoral head; and crista tibiofibular larger than the medial condyle of the femur. Additional features supporting the inner relationships of Lagerpetidae resemble those from the first analysis. An exception is the absence of the fourth

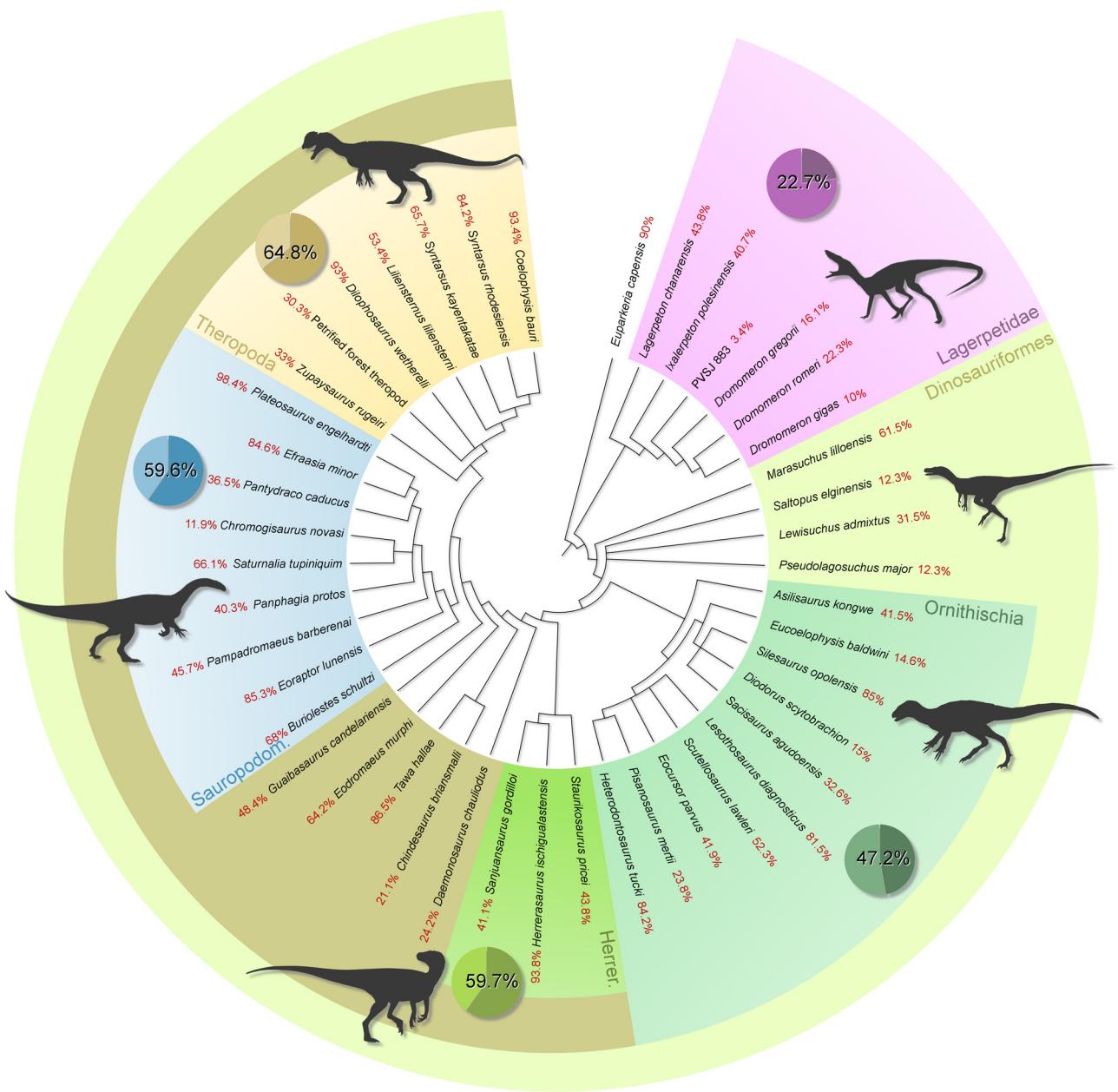
trochanter (state “0” of character 377), which here provide additional support for the sister taxon relationship between *D. romeri* and *D. gigas*.

## Discussion

The diversity of lagerpetids has increased recently due to new discoveries from South America (Martínez *et al.* 2012; 2016; Cabreira *et al.* 2016). Yet, the basic anatomy of a lagerpetid is still poorly known, given the limited skeletal portions collected so far. As a result, the lagerpetid ingroup relationship generally holds upon femoral characters. Indeed, all synapomorphies supporting their inner relationships are related that single bone. Despite the low support indexes (Bremer support) of the internal lagerpetid clades [1-2 (increasing to 2-4 with the exclusion of PVSJ 883)], the prevalence of missing entries do not result in unresolved nodes, revealing a stepwise structure from early diverging to later forms, in the first analysis. On the other hand, the phylogenetic position of *Lagerpeton chanarensis* and *Ixalerpeton polesinensis* is unsolved in the analysis derived from the data matrix of Nesbitt *et al.* (2017). In any case, the results from all analyses agree that, so far, the basalmost members of the clade are from South America. Indeed, the oldest lagerpetids date back to early (Marsicano *et al.* 2016) to late Carnian (Martínez *et al.* 2011) of that continent (Fig. 2), whereas younger forms have been discovered in the late Norian–Rhaetian strata of both South (Martínez *et al.* 2016) and North America (Irmis *et al.* 2007). This situation corroborates the biogeographic scenario proposed by Martínez *et al.* (2016), where early lagerpetids are restricted to southwestern Pangea and later forms spread across the entire western portion of the supercontinent. In fact, the sister group relationship between *Dromomeron gigas* and *D. romeri* reinforces a peculiar pattern of distribution that is not exclusive of lagerpetids, as other South American dinosauromorphs are also closely related to geographically distant taxa. As an example, the Brazilian sauropodomorph *Unaysaurus tolentinoi* Leal, Azevedo, Kellber & Da-Rosa, 2004 is frequently considered the sister taxon of the northern genus *Plateosaurus* (Apaldetti *et al.* 2013; Otero & Pol 2013; McPhee *et al.* 2015). Actually, forcing the monophyly of two geographically distinct groups of lagerpetids (South and North American forms) results in a much less parsimonious hypothesis of relationships, which is a compelling argument against this biogeographic scenario. Although the three analyses deriving from independent data sources support a Gondwanan origin for lagerpetids, the records of *D. gregorii* and *D. romeri* from lower Norian strata of Texas (Sarigül 2016; 2017) suggest a Laurasian origin for the genus *Dromomeron*, which later dispersed to Gondwana, where the genus is represented by *D. gigas* (Martínez *et al.* 2016).

The topology of the *Dromomeron* clade agrees in the three analyses, with *D. gigas* more closely related to *D. romeri* than to *D. gregorii*. These affinities were previously suggested by Martínez *et al.* (2016), but not supported in further studies (Baron *et al.* 2017a; 2017b; Langer *et al.* 2017). In contrast, these studies supported a sister taxon relationship between *D. gigas* and *D. gregorii*. However, these studies did not incorporate the two character states (i.e. a sharp ridge on the craniomedial edge of the distal end of the femur and a lateral tuberosity on the craniolateral edge of the distal end of the femur) that support the sister group affinity between *D. gigas* and *D. romeri* in the study by Martínez *et al.* (2016). In addition to these two features, this affinity receives additional support from the absence of the fourth trochanter in our third analysis, derived from the dataset by Langer *et al.* (2017).

The clade Lagerpetidae, that just a few years ago was thought to be quite low in diversity, have had a considerable increase in the number of specimens, comprising at this point six putative species (considering PVSJ 883), almost reaching the diversity of other Triassic dinosauromorphs, such as silesaurids, and even surpassing others, like herrerasaurids. However, quantification of the codified characters in the modified data matrix by Cabreira *et al.* (2016) reveals that Lagerpetidae is one of the less anatomically sampled dinosauromorph groups (Fig. 4), with only 22.75% of the characters scored; 26.61% if the fragmentary PVSJ 883 is not considered. The average for all dinosauriforms is about 45%, with other major dinosauriform groups having far higher indexes: 47.24% for Ornithischia, 59.69% for Sauropodomorpha, 59.71% for Herrerasauridae, and 64.86% for Theropoda. Sampling of Silesauridae, represented in the employed phylogenetic study by *Eocoelophysoides baldwini* Sullivan & Lucas, 1999, *Silesaurus opolensis* Dzik, 2003, *Sacisaurus agudoensis* Ferigolo & Langer, 2007, and *Diodorus scytobrachion* Kammerer, Nesbitt & Shubin, 2012, is slightly poorer (36.82%) than that of the other groups, but still better than that of Lagerpetidae.



**FIGURE 4.** Strict consensus cladogram depicting the percentage of codified characters for each OTU and for some more inclusive groups in the data matrix by Cabreira *et al.* (2016). Abbreviations: Herrer., Herrerasauridae; Sauropodom., Sauropodomorpha.

## Conclusion

The different analyses performed here do not express a consensus regarding the basalmost member of Lagerpetidae, but agree that the basalmost known putative member of the clade comes from South America. The position of PVSJ 883 in a sister group relationship to *Dromomerion* also is consensual, as well as the sister taxon affinities between *Dromomerion gigas* and *D. romeri*. Despite its geographical proximity, neither analysis supported sister taxon affinities between *Ixalerpeton polesinensis* and PVSJ 883. In conclusion, Lagerpetidae is one of the poorly sampled Triassic dinosauromorphs in terms of anatomy, rendering mandatory the necessity of increasing efforts in order to collect more complete specimens of the group.

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