

# A new proterochampsid archosauriform from the Middle–Upper Triassic of Southern Brazil

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Proterochampsidae is a clade of carnivorous archosauriforms that lived during the Triassic and is characterized by an elongated rostrum with dorsally oriented external nares, and a unique pes configuration. Although the majority of proterochampsids are found in South America, recent phylogenetic studies suggest a broader geographical distribution for this clade. Most proterochampsids are known from cranial remains; if postcranial elements are known they are frequently poorly preserved. This study describes a new proterochampsid, *Retymaijychampsia beckerorum* gen. et sp. nov., from the Middle–Late Triassic, based on an almost complete and articulated hindlimb. The holotype was excavated at the Linha Várzea 2 (Becker) Site, located in the municipality of Paraíso do Sul, Rio Grande do Sul, Brazil. The fossils from this locality places it within the *Dinodontosaurus* Assemblage Zone, which is Ladinian to early Carnian in age according to biostratigraphic investigations. The new taxon is the second proterochampsid described from the Pinheiros-Chiniquá Sequence and represents one of the oldest known members of the clade worldwide. An interesting aspect of *R. beckerorum* gen. et sp. nov. is its phylogenetic position because it is more closely related to *Proterochampsia* than to rhadinosuchine proterochampsids. Therefore, the discovery of the new proterochampsid partially fills a long ghost lineage extending from the Middle Triassic to the early Late Triassic. Furthermore, the presence of two proterochampsid species within the Pinheiros-Chiniquá Sequence deposits supports the hypothesis of significant ecomorphological diversity among proterochampsians in Triassic environments.

**Key words:** Archosauromorpha, Proterochampsia, Proterochampsidae, phylogeny, Carnian, Ladinian, South America, Brazil.

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## Introduction

The Triassic Period witnessed the emergence and extinction of numerous groups of reptiles (Benton 2016), including the Proterochampsidae (Trotteyn et al. 2013). Although this clade was previously considered endemic to South America (Ezcurra 2010; Trotteyn et al. 2013), recent phylogenetic investigations indicate a broader geographical distribution (Ezcurra and Sues 2021; Paes-Neto et al. 2024). The oldest known proterochampsids have been found in the Ladinian/lower Carnian deposits of Argentina and Brazil (Romer 1971; Arcucci 1990; Hsiou et al. 2002; Trotteyn and Ezcurra 2020; Paes-Neto et al. 2024), whereas the most recent records come from the upper Carnian/lower Norian in the same region (Reig 1959; Barberena 1982). Phylogenetic analyses place Proterochampsidae within Proterochampsia, a clade of archosauriforms that is the sister-group to Archosauria

(Ezcurra 2016; Ezcurra and Sues 2021; Müller et al. 2022; Paes-Neto et al. 2024). Because of its affinities, the clade is particularly important for understanding the early evolution of archosaurs. In addition, proterochampsids evolved a relatively diverse array of body plans, with some forms exhibiting putative semi-aquatic adaptations, whereas other were adapted to a terrestrial life style (Reig 1959; Sill 1967; Arcucci et al. 2019; Ezcurra et al. 2021; García Marsa et al. 2023). The diversity within the group includes gracile forms, such as *Tropidosuchus romeri* Arcucci, 1990, as well as species with flat skulls adorned with protuberances (Reig 1959; Barberena 1982). Proterochampsids are characterized by an elongated skull, particularly a long rostrum, dorsally oriented external nares, and a unique configuration of the pes, which is notably asymmetrical (Trotteyn et al. 2013).

Most proterochampsids are known exclusively from cranial remains (Price 1946; Reig 1959; Barberena 1982;

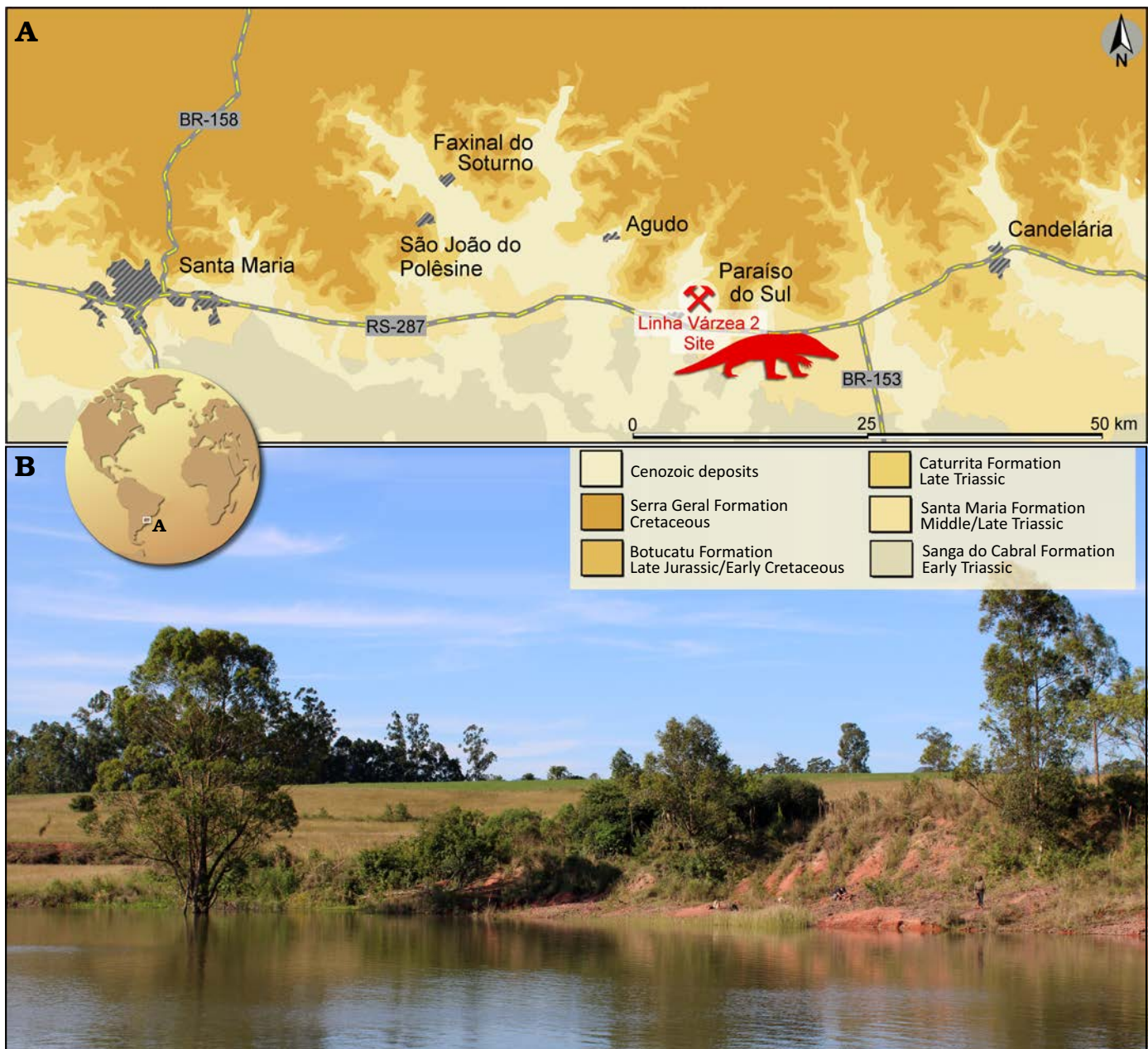


Fig. 1. Provenance of the proterochampsid archosauriform *Retymaijychampsia beckerorum* gen. et sp. nov. **A.** Location and geological context of the Linha Várzea 2 (Becker) Site, Paraíso do Sul, Rio Grande do Sul, Brazil; silhouette based on the artwork of Matheus Fernandes Gadelha (Limoeiro do Norte, Brazil). **B.** General view of the site (taken in August 2024).

Paes-Neto et al. 2024). In addition, details of certain postcranial structures are often poorly preserved in specimens that include postcranial elements (Trotteyn 2011; Trotteyn and Ezcurra 2014). Therefore, new specimens that preserve such remains are essential for clarifying aspects of the anatomy, biology, and evolution of proterochampsids. Since the pelvic girdle and hindlimb play a crucial role in the phylogenetic context of Archosauria and related groups (Sereno 1991; Nesbitt 2011; Ezcurra 2016), these structures are especially important for investigating the evolution of these groups. The extensive diversity in the structure of the pelvic girdle and hindlimb among early archosaurs and

related groups reflects a broad range of postures and ecological adaptations (Hutchinson and Gatesay 2000; Li et al. 2016; Müller et al. 2023; Agnolín et al. 2024). In the present study, a new proterochampsid from the Middle–Upper Triassic of Southern Brazil (Fig. 1) is described. The specimen consists of an almost complete and articulated hindlimb, making it one of the few specimens with these bones preserved from Brazil.

*Institutional abbreviations.*—CAPP/UFMS, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia/Universidade Federal de Santa Maria, São João do Polêsine, Rio Grande do Sul, Brazil; MCP, Museu de Ciências e Tecnologia,

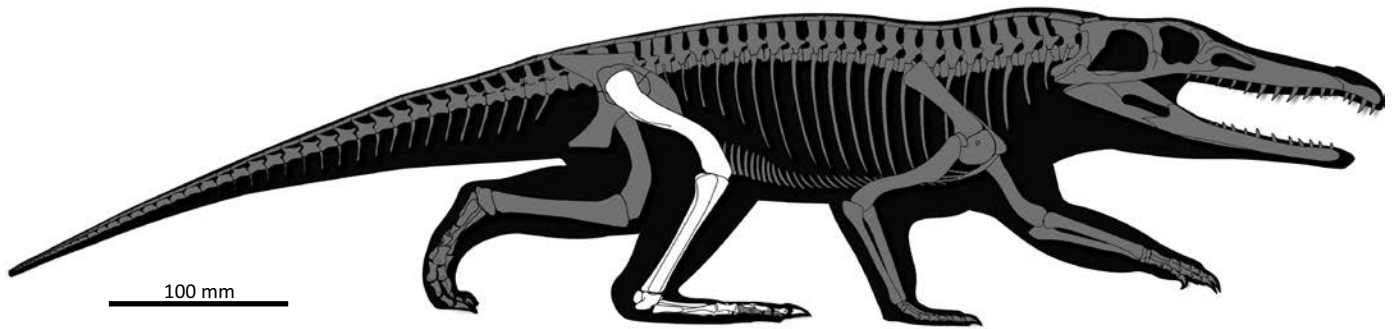


Fig. 2. Reconstruction of the skeleton of *Retymaijychampsia beckerorum* gen. et sp. nov. depicting the preserved elements; based on the artwork of Mauricio Silva Garcia (São João do Polêsine, Brazil).

Pontificia Universidade Católica, Porto Alegre, Brazil; PVL, Paleontología de Vertebrados, Instituto Miguel Lillo, Tucumán, Argentina; PVSJ, División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina; UFRGS-PV-T, Triassic Vertebrate Collection of the Museo de Paleontología da UFRGS “Irajá Damiani Pinto,” Universidade Federal de Rio Grande do Sul, Porto Alegre, Brazil.

*Nomenclatural acts.*—This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the International Code of Zoological Nomenclature. The LSID for this publication is: urn:lsid:zoobank.org:pub:FA6231E7-5E62-4221-AB07-E1B1C42BC107.

## Material and methods

The phylogenetic affinities of the new proterochampsid were examined using a new data matrix modified from that published by Sengupta et al. (2024). The former data matrix was constructed to investigate a broader context of archosauromorphs (Ezcurra 2016). Therefore, to investigate the affinities of the new taxon within Proterochampsia, a reduced set of operational taxonomic units (OTUs) was selected, which includes all proterochampsians from the previous study. Additionally, *Euparkeria capensis*, *Gnathovorax cabreirai*, *Buriolestes schultzi*, *Gracilisuchus stipanicorum*, *Prestosuchus chiniquensis*, and *Diandongosuchus fuyuanensis* were selected to compose the outgroup. Following a similar approach to that employed by Langer et al. (2022), only informative characters that vary within the present sample were selected from the original data matrix. A new character based on the ratio between the width of the proximal end of the tibia and the total length of the bone was included (character number 339). The final data matrix is composed of 401 morphological characters and 26 OTUs (see SOM, Supplementary Online Material available at [http://app.pan.pl/SOM/app70-Muller\\_SOM.pdf](http://app.pan.pl/SOM/app70-Muller_SOM.pdf)).

The most parsimonious trees (MPTs) were reconstructed using equally weighted parsimony analysis with the software TNT v. 1.5 (Goloboff and Catalano 2016). Characters 1, 2,

7, 12, 13, 19–23, 30, 31, 34, 36, 41, 44, 46, 52, 57, 58, 62, 76, 90, 111, 116, 118, 126–130, 146, 151, 165, 167, 169, 181, 207, 216, 219, 222, 224, 227, 235, 240, 241, 243, 247, 249, 255, 260, 262, 268, 269, 278, 283, 288, 290, 291, 293, 294, 296, 300, 301, 306, 310, 312, 313, 315, 316, 325, 330, 338, 339, 343, 352, 359, 360, 364, 370, 373, 374, 385, 388, and 389 were set as ordered following previous iterations of the original data matrix (Ezcurra 2016; Ezcurra et al. 2017, 2020; Müller et al. 2023; Sengupta et al. 2024). *Euparkeria capensis* was used to root the MPTs, which were recovered using the random addition sequence + tree bisection reconnection (TBR), which included 1000 replicates of Wagner trees (with random seed = 0), TBR and branch-swapping (holding 10 trees saved per replicate). Nodes without synapomorphies were collapsed after the search. Decay indices (Bremer support values) and bootstrap values (1000 replicates) were obtained with TNT v. 1.5.

## Systematic palaeontology

Archosauromorpha Huene, 1946 (sensu Dilkes 1998)

Archosauriformes Gauthier et al., 1988

Proterochampsidae Sill, 1967 (sensu Trotteyn 2011)

Clade Proterochampsinae nov.

*Type genus:* *Proterochampsia* Reig, 1959.

*Definition.*—Most inclusive clade including *Proterochampsia barrionuevoi* Reig, 1959, but not *Cerritosaurus binsfeldi* Price, 1946, nor *Rhadinosuchus gracilis* Huene, 1938.

*Diagnosis.*—Ratio between the maximum width of the skull and length of the presacral vertebral column 0.336–0.440; distinct coarse ornamentation on lateral surface of the surangular and angular; in medial view, the area ventral to the internal mandibular fenestra showing a larger contribution from the angular bone compared to the prearticular, or both bones contribute equally; prearticular with ventral margin posterior to its contact with the splenial straight or ventrally curved on the anterior half of the bone in medial or lateral view; and presence of ventral keel on ninth presacral vertebral centrum.

## Genus *Retymaijychamps* nov.

ZooBank LSID: urn:lsid:zoobank.org:act:99025E25-552E-47C4-BEC4-C2FCCCEADEEE

Type species: *Retymaijychamps beckerorum* gen et sp. nov., monotypic, see below.

*Etymology*: The combination of Guarani *retyma*, leg and *ijy*, strong with Greek *champs*, crocodile; referring to the robust constitution of the animal's hindlimb.

*Diagnosis*.—Same as for the only known species.

### *Retymaijychamps beckerorum* sp. nov.

Fig. 3.

ZooBank LSID: urn:lsid:zoobank.org:act:80A4B7E7-6C18-4A81-B668-B623A9D416A4

*Etymology*: In honor of the family Becker, the owners of the property where the Linha Várzea 2 site is located.

*Holotype*: CAPP/UFMS 0430, a complete and articulate right hindlimb.

*Type locality*: Linha Várzea 2 (= Becker) site (29°44'03" S, 53°09'07" W), Paraíso do Sul, Rio Grande do Sul, Brazil (Fig. 1).

*Type horizon*: Santa Maria Formation (Schultz et al. 2020); Pinheiros-Chiniquá Sequence (Horn et al. 2014) of the Santa Maria Supersequence (Zerfass et al. 2003), Paraná Basin. This third-order sequence is associated with the *Dinodontosaurus* Assemblage Zone, which is Ladinian to early Carnian in age (Ezcurra et al. 2017; Schultz et al. 2020; Novas et al. 2021; Müller and Garcia 2022).

*Material*.—Holotype only.

*Diagnosis*.—*Retymaijychamps beckerorum* gen. et sp. nov. differs from all other known proterochampsids with comparable skeletal material based on the following local autapomorphies: absence of an extensor fossa on the anterior surface of the distal portion of the femur, resulting in a straight anterior margin in distal view; fibular condyle of the femur projects more ventrally than tibial condyle, forming an uneven distal surface in anterior view; and markedly robust tibia, with a ratio of 0.37 between the maximum width of the proximal end and the total length of the bone.

*Description*.—Although the femur lacks the proximal portion, it clearly had a sigmoid shape (Fig. 3A<sub>1</sub>). The preserved segment of the shaft includes the distal half of the fourth trochanter, which forms an elongated ridge (Fig. 3A<sub>6</sub>). The distal portion of the trochanter merges smoothly with the shaft. Whereas the femur is not completely preserved, it is evident that the fourth trochanter is distally elongated, similar to the condition seen in most proterochampsids (Trotteyn et al. 2013). Conversely, the fourth trochanter of *Stenoscelida aurantiacus* Müller et al., 2022 (CAPP/UFMS 0293; Müller et al. 2022) and *Tropidosuchus romeri* Arcucci, 1990 (PVL 4601; Arcucci 1990) is short. The distal portion of the femur expands relative to the shaft and is arched posteriorly. The popliteal fossa is not elongated. Unlike other proterochampsids (Trotteyn 2011; Trotteyn and Ezcurra 2020; Müller et al. 2022; Paes-Neto et al. 2024), this specimen lacks an extensor fossa on the anterior surface of the distal portion of the femur, resulting in a straight anterior margin in distal view (Fig. 3A<sub>4</sub>, A<sub>8</sub>). In addition, compared to other pro-

Table 1. Measurements (in mm) of the right hindlimb of *Retymaijychamps beckerorum* gen. et sp. nov. (CAPP/UFMS 0430). \* incomplete; ? not preserved or inaccessible.

Element	Length	Maximum proximal width	Maximum distal width
femur	66.7*	?	16.6
tibia	70.5	26.3	16.5
fibula	64.7	11.5	9.7
metatarsal I	18.4	8.2	4.9
metatarsal II	28.7	14.4	10.7
metatarsal III	34.8	12.8	7.8
metatarsal IV	43.7	?	3.4
metatarsal V	14.5	?	2.9

terochampsids, the fibular condyle projects more ventrally than the tibial condyle, forming an uneven distal surface in anterior view. The tibiofibular crest is not strongly expanded and there are no distinguishing features between the lateral surface of the tibiofibular crest and the lateral condyle.

The complete tibia (Table 1) is notably robust, with a ratio of 0.37 between the maximum width of the proximal end and the total length of the bone. For comparison, the ratio for the holotype of *Stenoscelida aurantiacus* (CAPP/UFMS 0293) is 0.25 and for the holotype of *Kuruxuchampsia dornellesi* Paes-Neto et al., 2024 (UFRGS-PV-0877-T) is 0.26. In lateral/medial view, the proximal portion of the tibia is expanded both anteriorly and posteriorly relative to the shaft (Fig. 3A<sub>5</sub>). The anterior projection comprises the cnemial crest, which tapers to a point and is straight (Fig. 3A<sub>6</sub>). The posterior projection is the medial condyle, which is positioned further posteriorly relative to the lateral condyle. The proximal articular surface is flat. The shaft of the tibia is straight and expands distally, with the expansion predominantly oriented anteroposteriorly. This condition differs the specimen from *Tropidosuchus romeri* (PVL 4601; Arcucci 1990), in which the distal end of the tibia is not expanded. The posterior margin of the distal end of the tibia of CAPP/UFMS 0430 is gently concave (Fig. 3A<sub>7</sub>).

The fibula is slender, with a shaft that has approximately half the transverse width of the tibial shaft (Fig. 3A<sub>6</sub>). The fibula is slightly shorter than the tibia (Table 1). The proximal end is expanded posteriorly relative to the shaft and is compressed transversely (Fig. 3A<sub>6</sub>). The shaft is straight along its length, differing from the arched shaft of the fibula in most pseudosuchians (Nesbitt 2011; Ezcurra 2016). The width of the shaft remains consistent along the entire length of the fibula, whereas in *Stenoscelida aurantiacus* (CAPP/UFMS 0293; Müller et al. 2022) the proximal half of the shaft is wider. There is no tubercle or ridge for the attachment of the iliofibularis muscle, such as in *Proterochampsia barrionuevoi* Reig, 1959 (PVSJ 606; Trotteyn et al. 2013). The distal end expands relative to the shaft, and the distal articular surface is flat.

The astragalus is transversely expanded (Fig. 3A<sub>7</sub>). The dorsal margin of its medial surface is concave, while its ventral surface of the bone is convex anteroposteriorly. There is

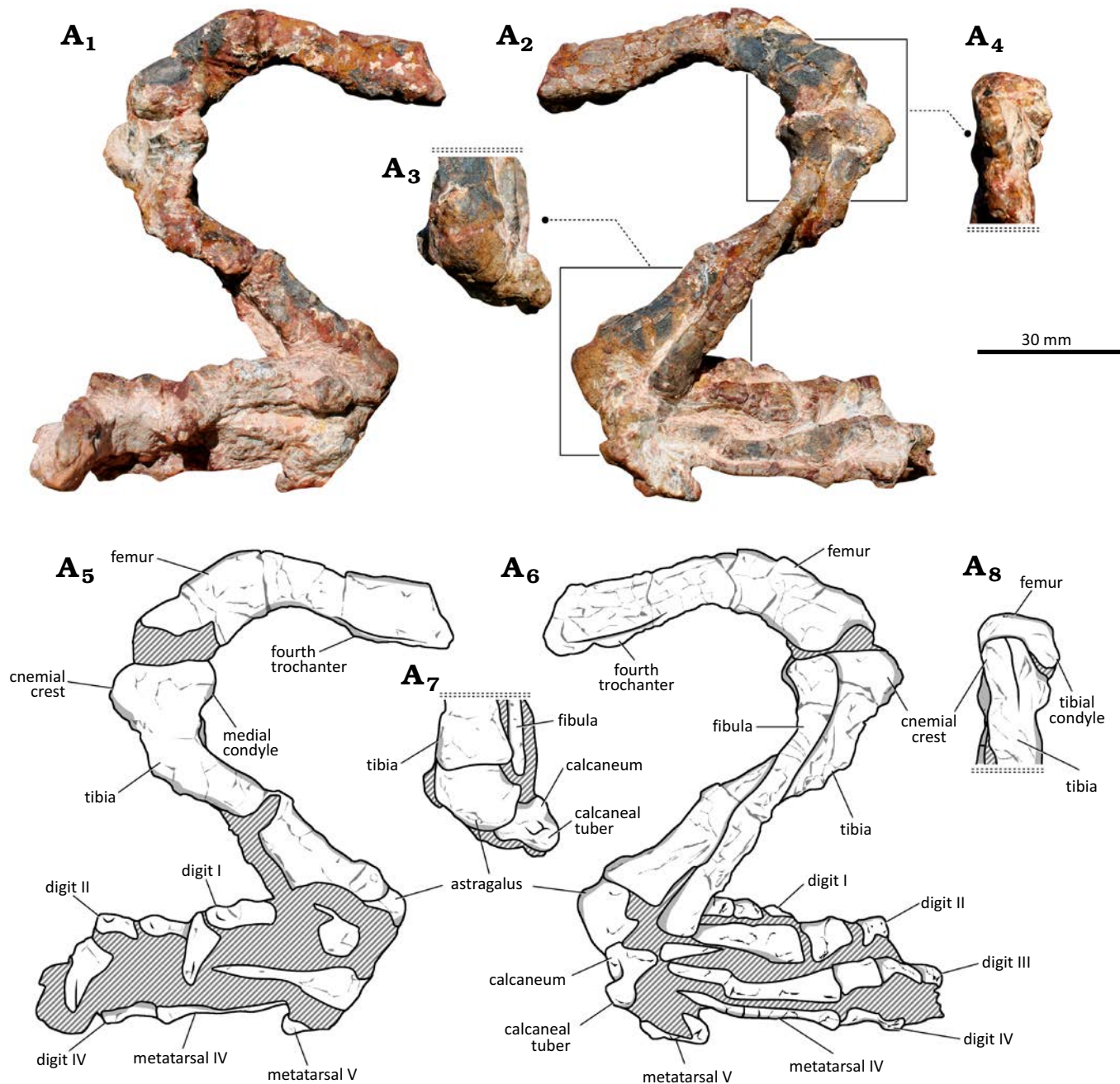


Fig. 3. Holotype of the archosauriform proterochampsid *Retymaijychampsia beckerorum* gen. et sp. nov. (CAPPA/UFMS 0430) from the Linha Várzea 2 (Becker) Site, Paraíso do Sul, Rio Grande do Sul, Brazil; Ladinian to lower Carnian, Middle to lower Upper Triassic. Right hindlimb in medial (A<sub>1</sub>, A<sub>5</sub>), lateral (A<sub>2</sub>, A<sub>6</sub>), posterior (A<sub>3</sub>, A<sub>7</sub>), and anterior (A<sub>4</sub>, A<sub>8</sub>) views. Photographs (A<sub>1</sub>–A<sub>4</sub>) and explanatory drawings (A<sub>5</sub>–A<sub>8</sub>). The stippled lines associated with A<sub>3</sub>, A<sub>4</sub>, A<sub>7</sub>, and A<sub>8</sub> indicate that there is continuity of the bones, but they are not represented in the images.

no anterior expansion at the anteromedial corner. The posterior margin lacks a dorsal process. The calcaneum is lateromedially shorter than the astragalus (Fig. 3A<sub>6</sub>, A<sub>7</sub>). The facet for the fibula is oriented dorsomedially. The calcaneal tuber is well-developed and perpendicular to the main body of the calcaneum (Fig. 3A<sub>6</sub>). There is a depression between the main body of the bone and the posterior surface of the calcaneal tuber (Fig. 3A<sub>6</sub>, A<sub>7</sub>).

The configuration of the metatarsals is consistent with that in other proterochampsids (Table 1): metatarsal I is

short; metatarsal II is slightly longer than metatarsal I and the stoutest of the elements; metatarsal III is longer than metatarsal II and more slender; metatarsal IV is quite slender and as long as metatarsal III; and metatarsal V is reduced and tapers distally. Pedal digit I includes two phalanges (Fig. 3A<sub>5</sub>). The specimen differs from *Tropidosuchus romeri* (PVL 4601; Arcucci 1990) and *Stenoscelida aurantiacus* (CAPPA/UFMS 0293; Müller et al. 2022) in that both of the latter taxa have a shorter digit I. Whereas pedal digit II is longer than digit I, it is shorter than digit III (Fig. 3A<sub>6</sub>). Digit IV

preserves one phalanx, which is quite slender (Fig. 2A<sub>5</sub>, A<sub>6</sub>). As this phalanx is not an ungual bone, the total number of phalanges in this digit remains uncertain. There are no phalanges in the digit V. This condition is shared with other proterochampsids, whereas a putative vestigial phalanx has been reported for *Stenoscelida aurantiacus* (CAPPA/UFSM 0293; Müller et al. 2022).

*Stratigraphic and geographic range.*—Type locality and horizon only.

## Phylogenetic analysis

The phylogenetic analysis recovered a single most parsimonious tree (Fig. 4) of 914 steps each, with a consistency index of 0.521 and a retention index of 0.557. *Retymaijychampsia beckerorum* gen. et sp. nov. is found in a trichotomy with both species of *Proterochampsia*, based on the elongated fourth trochanter of the femur (ch. 329: 0→1) and the ratio between

the maximum width of the proximal end and the total length of the tibia (ch. 339: 2→3). *Sphodrosaurus pennsylvanicus* is the sister taxon to the node comprising *R. beckerorum* gen. et sp. nov. plus both species of *Proterochampsia*. The clade comprising these four OTUs is named here Proterochampsinae and is supported by five synapomorphies: ratio between the maximum width of the skull and length of the presacral vertebral column ranging from 0.336 to 0.440 (ch. 12: 1→3); distinct coarse ornamentation on lateral surface of the surangular and angular (ch. 187: 0→1); in medial view, the area ventral to the internal mandibular fenestra shows a larger contribution from the angular bone compared to the prearticular, or both bones contribute equally (ch. 188: 0→1); prearticular with ventral margin posterior to its contact with the splenial straight or ventrally curved on the anterior half of the bone in medial or lateral view (ch. 189: 1→0); and presence of ventral keel on the centrum of the ninth presacral vertebra (ch. 231: 0→1). *Stenoscelida aurantiacus* is recovered as the sister taxon to Proterochampsidae. The inner composition of

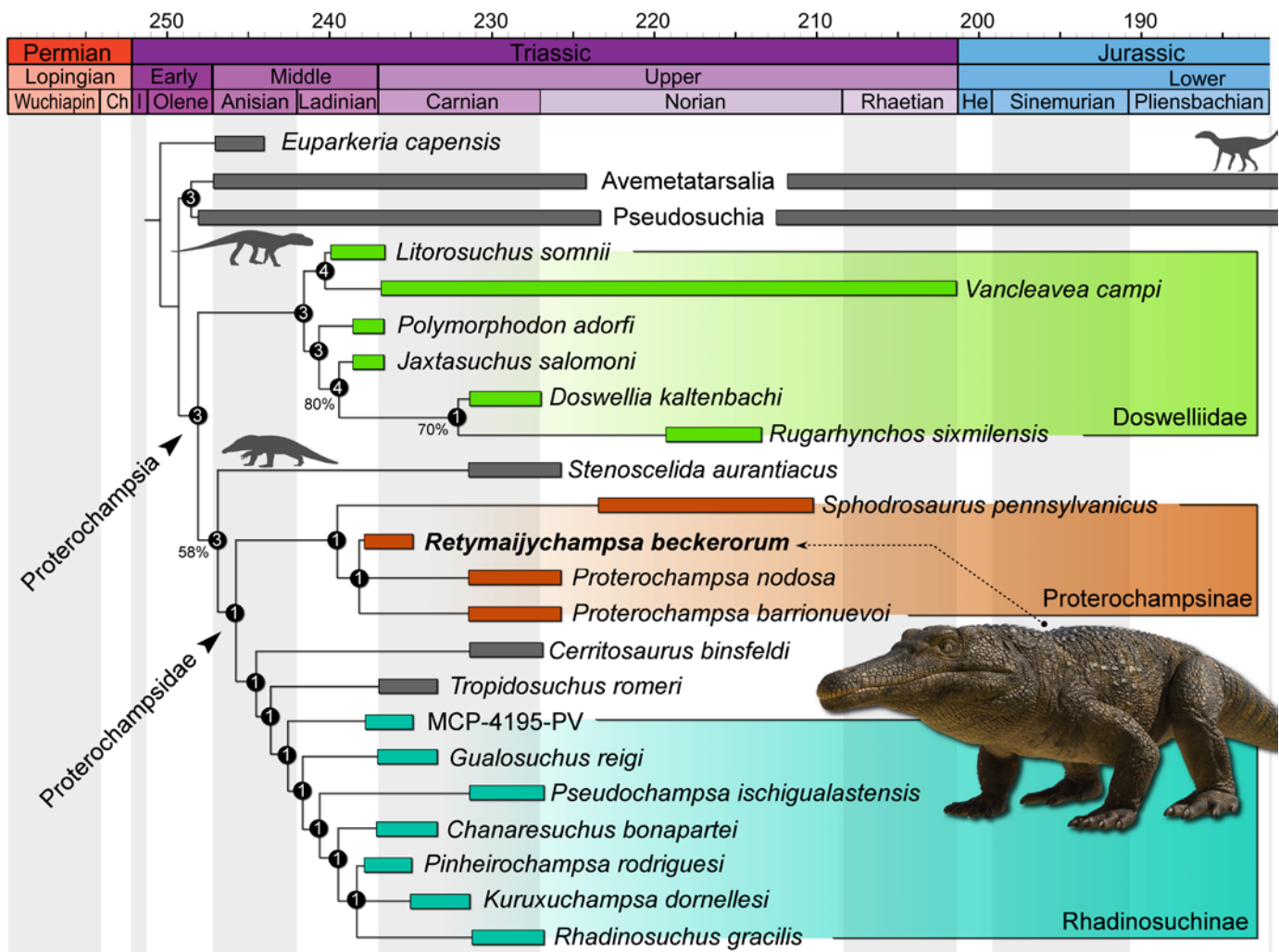


Fig. 4. Time-calibrated most parsimonious tree depicting the phylogenetic position of *Retymaijychampsia beckerorum* gen. et sp. nov. Number on nodes represent Bremer support values and Bootstrap values higher than 50%. The temporal bars for each OTU represent the maximum and minimum ages of each geological unit. Life reconstruction of *Retymaijychampsia beckerorum* gen. et sp. nov. by Caio Fantini (Guarulhos, Brazil). Silhouettes based on the artwork of Matheus Fernandes Gadelha (Limoeiro do Norte, Brazil). Abbreviations: Ch, Changhsingian; He, Hettangian; I, Induan.

Proterochampsidae and Doswelliidae follows previous analyses of the original data matrix (Paes-Neto et al. 2024).

An interesting aspect to note is that, prior to the advent of computational phylogenetic analyses, Bonaparte (1971) divided proterochampsians into two main families: “Proterochampsidae” and “Cerritosauridae”. Although far fewer proterochampsian species were known at the time, this subdivision closely aligns with the results obtained in the present analysis

## Discussion

Although most typical traits of proterochampsids concern cranial bones (Ezcurra 2016), *Retymaijychampsia beckerorum* gen. et sp. nov. is confidently assigned to Proterochampsidae based on the configuration of the pes, which

has a stout metatarsal II combined with a rather slender metatarsal IV (e.g., Trotteyn et al. 2013). On the other hand, the new proterochampsid had a unique set of traits that are associated with the robustness of the hindlimb and the shape of the distal end of the femur. The significance of these features is uncertain. Perhaps *R. beckerorum* gen. et sp. nov. had a posture or mode of locomotion distinct from other proterochampsids. In addition, the holotype (CAPPA/UFSM 0430) represents a small individual. In proterochampsids, the tibia length ranges from approximately 75% (*Proterochampsia barrionuevoi*; Trotteyn 2011) to 100% (*Tropidosuchus romeri*; Arcucci 1990) of the total femur length. Based on the tibia length of 70.5 mm and the cited tibia-to-femur ratios in proterochampsids, the estimated femoral length of CAPPA/UFSM 0430 should range between 70.5 mm and approximately 94 mm. According to these values, the length of the skull of CAPPA/UFSM 0430 is es-

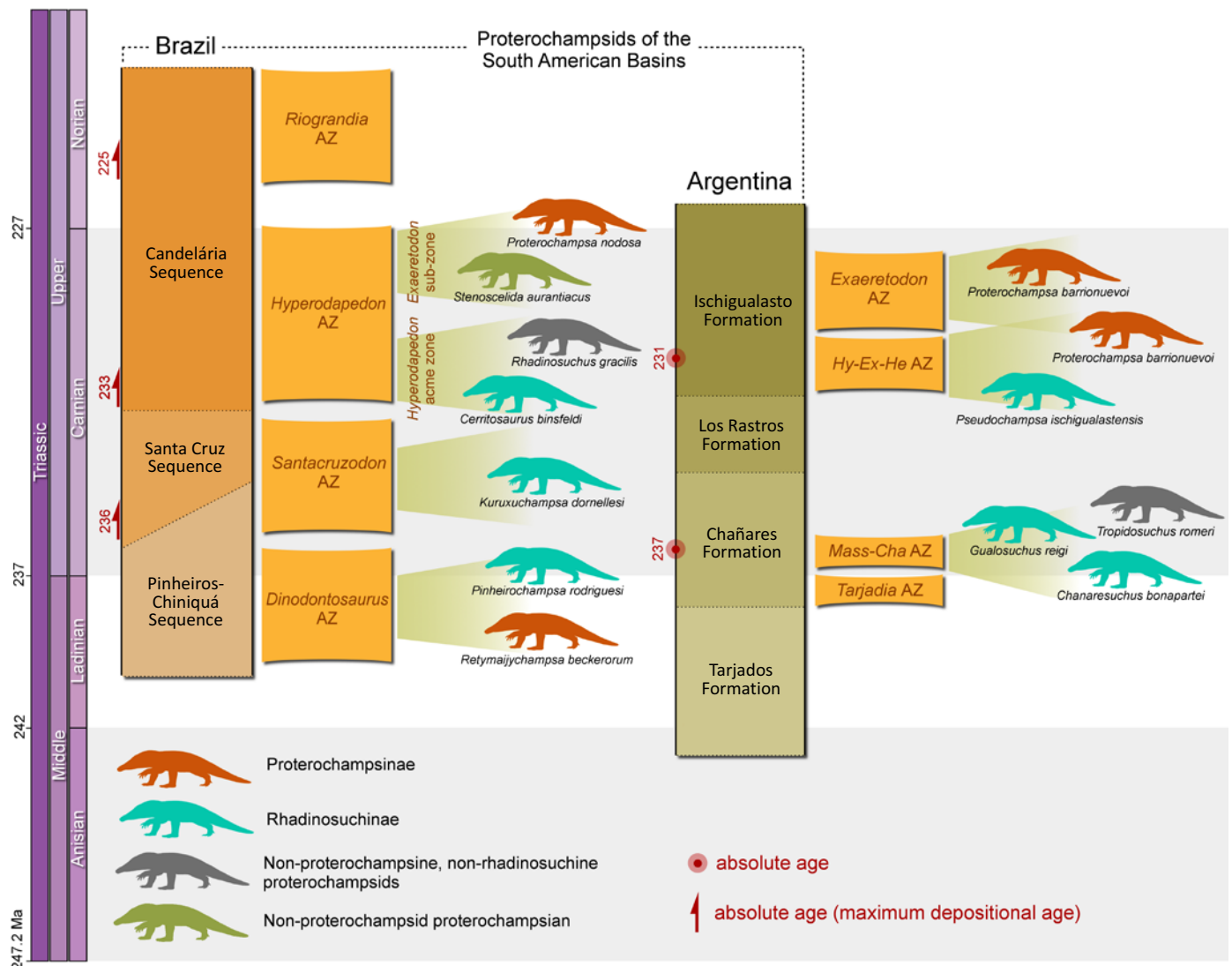


Fig. 5. Stratigraphic distribution of proterochampsids in South American deposits. Radioisotopic data according to Martínez et al. (2011), Marsicano et al. (2016), Ezcurra et al. (2017), Langer et al. (2018), and Philipp et al. (2018). Silhouettes based on the artwork of Matheus Fernandes Gadelha (Limoeiro do Norte, Brazil). Abbreviations: AZ, Assemblage Zone; Hy-Ex-He, Hyperodapedon–Exaeretodon–Herrerasaurus; Mass-Cha, Massetognathus–Chanaresuchus.



Fig. 6. Artistic representation of a Middle–Late Triassic landscape of southern Brazil depicting two individuals of the proterochampsid archosauriform *Retymaijychampsia beckerorum* gen. et sp. nov. Artwork by Caio Fantini (Guarulhos, Brazil).

timated between 79.8 to 126.4 mm based on the regression calculated by Müller et al. (2022). Therefore, the holotype of *R. beckerorum* gen. et sp. nov. was a small-sized proterochampsid when compared to most members of the clade. For comparison, the skull of the holotype of *Pinheirochampsia rodriguesi* is 276.5 mm in length (Paes-Neto et al. 2024), that of the holotype of *Gualosuchus reigi* is 330 mm (Romer 1971), and the skulls of some specimens of *Proterochampsia barrionuevoi* reached approximately 500 mm (Dilkes and Arcucci 2012). Nevertheless, there are some small proterochampsids, such as *Tropidosuchus romeri*, whose skull was approximately 76 mm in length (Arcucci 1990). Despite the reduced size, a histological investigation suggested that a specimen of *Tropidosuchus romeri* (PVL 4606) reached sexual and skeletal maturity, though somatic maturity could not be inferred (García Marsa et al. 2023). Therefore, whereas small proterochampsids are present in the fossil record, further investigations and/or specimens are necessary to determine whether CAPP/UFMS 0430 represents a skeletally immature individual.

*Retymaijychampsia beckerorum* gen. et sp. nov. represents the second proterochampsid from the Pinheiros-Chiniquá Sequence. The other species, *Pinheirochampsia rodriguesi*, is known solely from cranial remains (Paes-Neto et al. 2024). Therefore, a direct comparison between CAPP/UFMS 0430 and specimens of *Pinheirochampsia rodriguesi* is not feasible. Even the size difference between CAPP/UFMS 0430 and specimens of *Pinheirochampsia rodriguesi* are an ambiguous difference because the de-

velopment degree of CAPP/UFMS 0430 is uncertain. On the other hand, both species belong to different clades according to the phylogenetic analysis performed here. *Retymaijychampsia beckerorum* gen. et sp. nov. nests within Proterochampsinae, whereas *Pinheirochampsia rodriguesi* is a derived member of Rhadinosaurs. Therefore, although more complete specimens are needed to further investigate this taxonomic issue, the cladistic data supports the presence of two phylogenetically distinct proterochampsids in the Pinheiros-Chiniquá Sequence. Actually, the co-occurrence of different proterochampsian species is common in South American deposits (Fig. 5). For instance, in the *Massetognathus–Chanaresuchus* Assemblage Zone of the Argentinean Chañares Formation there are three coeval species (Ezcurra et al. 2021). In the *Hyperodapedon* Assemblage Zone of the Brazilian Candelária Sequence, there are four species distributed across two sub-zones (Müller et al. 2022). The co-occurrence of *R. beckerorum* gen. et sp. nov. and *Pinheirochampsia rodriguesi* reinforces an ecological model in which proterochampsians were relatively diverse in Middle to early Late Triassic environments (Fig. 6). Moreover, if the size differences between the two species are not due to ontogenetic variation, it is plausible that these species occupied distinct niches, especially if the unique hindlimb morphology of *R. beckerorum* gen. et sp. nov. is associated with a distinct locomotor strategy compared to other proterochampsians. In fact, archosauriforms evolved a broad range of postures and locomotor strategies during the Triassic (Agnolín et al. 2024).



Another interesting aspect of the discovery of *R. beckerorum* gen. et sp. nov. concerns its phylogenetic position. So far, there have been no records of Ladinian to early Carnian proterochampsids more closely related to *Proterochampsia* (i.e., Proterochampsinae) than to rhadinosuchines, resulting in a ghost lineage extending from the Middle to early Late Triassic (Ezcurra and Sues 2021; Paes-Neto et al. 2024). *Retymaijychampsia beckerorum* gen. et sp. nov. partially fills this gap and represents the oldest known proterochampsine proterochampsid worldwide. It highlights the phylogenetic importance of postcranial remains in order to further explore the evolutionary history of these archosauriforms. In addition, the composition of Proterochampsinae including three South American taxa along with the North American *Sphodrosaurus pennsylvanicus* (Paes-Neto et al. 2024; here), suggests a wide geographical distribution of this clade. These affinities add to the growing number of Triassic tetrapod taxa shared between deposits in South America and North America (Irmis et al. 2007; Martínez et al. 2016; Novas et al. 2021; Ezcurra and Sues 2022; Fitch et al. 2023; Müller et al. 2023).

## Conclusions

*Retymaijychampsia beckerorum* gen. et sp. nov. represents the second proterochampsid from the Pinheiros-Chiniquá Sequence (Ladinian to upper Carnian) of Brazil and comprises one of the oldest proterochampsids worldwide. It has a diagnostic set of hindlimb traits and is phylogenetically close to *Proterochampsia*, partially filling a ghost lineage of proterochampsids more closely related to *Proterochampsia* than to Rhadinosuchinae. Finally, the co-occurrence of *R. beckerorum* gen. et sp. nov. and *Pinheirochampsia rodriguesi* provides further support for the idea of high ecomorphological diversity among proterochampsians in Middle to early Late Triassic environments.

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