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Tiane Macedo de Oliveira

NOVOS ESPÉCIMES DE ARCOSSAUROMORFOS (SAURIA: ARCHOSAUROMORPHA) DO TRIÁSSICO INFERIOR DA AMÉRICA DO SUL E SUAS IMPLICAÇÕES FILOGENÉTICAS

Santa Maria, RS

2019

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Dissertação apresentada ao Curso de Mestrado do Programa de Pós-Graduação em Biodiversidade Animal, Área de Concentração em Sistemática e Biologia Evolutiva, da Universidade Federal de Santa Maria (UFSM, RS), como requisito parcial para obtenção do título de **Mestre em Biodiversidade Animal.**

Orientador: Prof. Dr. Leonardo Kerber

Coorientador: Prof. Dr. Felipe Pinheiro

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Santa Maria, RS

2019

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Á minha família, em especial minha mãe Neusa e meu pai Fernando, por todo apoio e suporte necessários.

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A todos o mais sincero Obrigada.

“Women are the real architects of society”.

Harriet Beecher Stowe

RESUMO

NOVOS ESPÉCIMES DE ARCOSSAUROMORFOS (SAURIA: ARCHOSAUROMORPHA) DO TRIÁSSICO INFERIOR DA AMÉRICA DO SUL E SUAS IMPLICAÇÕES FILOGENÉTICAS

AUTORA: TIANE MACEDO DE OLIVEIRA
ORIENTADOR: LEONARDO KERBER
COORIENTADOR: FELIPE PINHEIRO

Archosauromorpha é definido como o clado que compreende todos os diápsidos mais intimamente relacionados com a linhagem de aves (Ornithodira) e crocodilianos (Pseudosuchia) do que com lepidossauros. A presente dissertação tem como objetivo principal descrever novos espécimes de arcossauromorfos basais descobertos em rochas do início do período Triássico do Rio Grande do Sul, Brasil. Esses materiais foram recuperados em diferentes localidades pertencentes à Formação Sanga do Cabral. Os espécimes são representados por vértebras cervicais isoladas (UFRGS-PV-492-T, UFRGS-PV-647-T e UNIPAMPA 733) pertencentes da Universidade Federal do Rio Grande do Sul (UFRGS) e Universidade Federal do Pampa (UNIPAMPA) e por um membro posterior com vértebras e elementos da cintura (UFSM 11471), atribuído a uma nova espécie cedido pela Universidade Federal de Santa Maria (UFSM). A análise filogenética, reforçada por comparações anatômicas, permitiu a atribuição dos novos espécimes a formas relacionadas ao clado Tanystropheidae, arcossauromorfos basais com distribuição entre o Triássico Inferior e Superior da Ásia, Europa e América do Norte. Juntamente com outros tetrápodes já relatados para a Formação Sanga do Cabral, este registro aumenta o conhecimento da diversificação biótica durante o início do Triássico e concorda com prévias interpretações em que os tanistrofeídeos tiveram sua origem em uma área central da Pangeia, possivelmente na porção sudoeste do Gondwana e que seus ancestrais apresentavam hábito possivelmente terrestre. Estes novos materiais contribuem para com o conhecimento sobre a diversificação de Archosauromorpha após a extinção do Permo-Triássica.

Palavras-chave: Diapsida, Tanystropheidae, Formação Sanga do Cabral, Extinção Permo/Triássica, diversificação.

ABSTRACT

NEW ARCHOSAUROMORPH SPECIMENS (SAURIA: ARCHOSAUROMORPHA) FROM THE LOWER TRIASSIC OF SOUTH AMERICA AND THEIR PHYLOGENETIC IMPLICATIONS

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CO-ADVISOR: FELIPE PINHEIRO

Archosauromorpha is defined as the clade that comprises all diapsids more closely related to the lineage of birds (Ornithodira) and crocodilians (Pseudosuchia) than with lepidosaurs. The main objective of this dissertation is to describe new specimens of basal archosauromorphs discovered in Triassic rocks from the Rio Grande do Sul state, Brazil. These materials were recovered in different localities belonging to the Sanga do Cabral Formation. The specimens are represented by isolated cervical vertebrae (UFRGS-PV-492-T, UFRGS-PV-647-T and UNIPAMPA 733) belonging to Universidade Federal do Rio Grande do Sul (UFRGS) and Universidade Federal do Pampa (UNIPAMPA) and a posterior limb with vertebrae and pelvic elements (UFSM 11471), the latter attributed to a new species given by the Universidade Federal de Santa Maria (UFSM). The phylogenetic analysis, reinforced by anatomical comparisons, allowed the attribution of the new specimens to forms related to the clade Tanystropheidae, basal archosauromorphs with distribution between the Early and Late Triassic of Asia, Europe, and North America. Together with other tetrapods already reported for the Sanga do Cabral Formation, this record increases the knowledge of the biotic diversification during the beginning of the Triassic and agrees with previous interpretations in which the tanystropheids originated in a central area of Pangea, possibly in the southwest portion of the Gondwana, and that their ancestors possibly had a terrestrial lifestyle. These new specimens contribute to the knowledge about the diversification of Archosauromorpha after the Permo-Triassic extinction.

Keywords: Diapsida, Tanystropheidae, Sanga do Cabral Formation, Permo/Triassic Extintion, diversification.

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LISTA DE ABREVIATURAS E SIGLAS

AMNH	American Museum of Natural History, Nova York
BP	Evolutionary Studies Institute, University of the Witwatersrand, África do Sul
CAPPA	Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia, São João do Polêsine, RS
FMNH	Field Museum of Natural History, Chicago, Ilinois
GR	Ruth Hall Museum of Paleontology, Ghost Ranch, México
LASEPE	Laboratório de Sedimentologia e Petrologia
MCSN	Museo Civico di Storia Naturali Milano, Itália
MCSNB	Museo Civico di Scienze Naturali Enrico Caffi, Bergamo, Itália
MCZ	Museum of Comparative Zoology, Cambridge, E.U.A.
MSNM	Museo di Storia Naturale, Milano, Itália
NHMUK	Natural History Museum of the United Kingdom, Londres
NMQR	National Museum Bloemfontein, Bloemfontein, África do Sul
PIMUZ	Paleontological Institut und Museum, Zürich, Suíça
PIN	Paleontological Institute of the Russian Academy of Sciences, Russia
PUCRS	Pontíficia Universidade Católica do Rio Grande do Sul, Rio Grande do Sul, Brasil
SAM PK	Iziko Museum, Cape Town, África do Sul
SMNS	Staaliches Museum für Naturkunde Stuttgart, Stuttgart, Alemanha
TMM	Texas Memorial Museum, Austin, Texas, E.U.A.
UFRGS	Universidade Federal do Rio Grande do Sul, Porto Alegre, Brasil
UFSM	Universidade Federal de Santa Maria, Santa Maria, Rio Grande do Sul, Brasil
UNIPAMPA	Universidade Federal do Pampa, São Gabriel, Brasil
UWBM	Burke Museum of Natural History and Culture, E.U.A.
UMCZ	Universidad de Murcia, Espanha
YPM R	Herpetology collections of Yale Peabody Museum of Natural History, New Haven, E.U.A.
YPM VP	Vertebrate Paleontology collections of Yale Peabody Museum of Natural History New Haven, E.U.A.
ZAR	Muséum national d'Histoire naturelle (Zarzaitine collection), Paris, França

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APRESENTAÇÃO DA ESTRUTURA DA DISSERTAÇÃO

A presente dissertação de mestrado objetiva descrever novos espécimes de arcossauromorfos do Triássico Inferior do Rio Grande do Sul e discutir suas implicações filogenéticas e paleobiogeográficas. A dissertação foi elaborada em forma de artigos científicos e sua estrutura está organizada de acordo com as normas do Manual de Dissertações e Teses da UFSM (MDT), e integra os requisitos necessários para a obtenção do título de Mestre em Ciências Biológicas – área Biodiversidade Animal, pelo Programa de Pós-Graduação em Biodiversidade Animal da Universidade Federal de Santa Maria.

O **Capítulo 1** é composto por uma contextualização sobre Archosauromorpha com ênfase nos representantes iniciais, seguida de uma breve introdução aos principais clados de arcossauromorfos não-arcossauriformes, bem como aos aspectos relacionados a diversificação inicial dos arcossauromorfos após a extinção Permo-Triássica.

No **Capítulo 2** se apresentam os manuscritos produzidos durante o desenvolvimento do mestrado. O primeiro artigo (**Capítulo 2.1**) intitulado "Tanystropheid archosauromorphs in the Lower Triassic of Gondwana" objetiva a descrição de vértebras isoladas atribuídas a ?Tanystropheidae (Archosauromorpha) pertencentes a Formação Sanga do Cabral (Triássico Inferior). Este estudo apresenta de forma breve a distribuição paleobiogeográfica do grupo e, em conjunto ao manuscrito principal desta dissertação, demonstra a presença de tanistrofeídeos (ou formas proximamente relacionadas) no Triássico Inferior do Gondwana. Este trabalho é apresentado de acordo com as normas de formatação exigidas pelo periódico científico *Acta Palaeontologica Polonica* (Qualis Capes B1), no qual foi publicado no ano de 2018. O segundo manuscrito (**Capítulo 2.2**) tem como foco realizar descrição osteológica de um novo táxon e testar seu posicionamento filogenético, bem como analisar suas implicações paleobiogeográficas e paleobiológicas. Este manuscrito encontra-se em fase final de preparação, e será submetido a um periódico a ser definido após a defesa da presente dissertação.

Por questões de brevidade, os materiais e métodos empregados, bem como a geologia das localidades de estudo, estão descritos diretamente nos artigos científicos.

No **Capítulo 3**, são apresentadas as principais conclusões referentes a unificação dos resultados e interpretações obtidos a partir dos objetivos propostos inicialmente.

CAPÍTULO 1 *– CONTEXTUALIZAÇÃO*

1 INTRODUÇÃO

1.1 ARCHOSAUROMORPHA VON HUENE, 1946

Cerca de 30 milhões de anos (Ma) após o maior evento de extinção em massa já registrado (final do Período Permiano, ~251 Ma), a diversidade da comunidade de tetrápodes terrestres já havia recuperado níveis semelhantes aos observados no intervalo que antecedeu a extinção (BENTON, 2003; SAHNEY e BENTON, 2008). As linhagens de tetrápodes que sobreviveram incluem anfíbios Temnospondyli, os pararrépteis Procolophonoidea, Dicynodontia, Therocephalia, Cynodontia (estes três últimos pertencentes a Synapsida) e Archosauromorpha, diápsidos cuja recuperação ecológica no Triássico Inferior foi, como tradicionalmente considerado, relativamente lenta (BENTON et al., 2004). A evolução inicial dos arcossauromorfos durante o Triássico é um excelente exemplo de radiação adaptativa no registro fóssil, contribuindo para remodelar os ecossistemas terrestres mesozoicos e atuais (BRUSATTE et al., 2008; NESBITT, 2011; EZCURRA, 2016; FOTH et al., 2016; EZCURRA e BUTLER, 2018).

Os registros mais antigos de Archosauromorpha são representados por quatro espécies restritas a rochas do Permiano Superior da Europa e África (*Protorosaurus speneri* Meyer, 1832; *Archosaurus rossicus* Tatarinov, 1960; *Eorasaurus olsoni* Sennikov, 1997; *Aenigmastropheus parringtoni* Ezcurra, Scheyer e Butler 2014) (EZCURRA, 2016). Seguindo a extinção em massa Permo-Triássica, o registro fóssil de arcossauromorfos é consideravelmente mais abundante e morfologicamente diverso em outras regiões do mundo (*e.g.* África, Índia), incluindo membros de Rhynchosauria, Tanystropheidae, Prolacertidae, Proterosuchidae, Erythrosuchidae, Euparkeriidae e Archosauria (NESBITT, 2011; EZCURRA et al., 2013; SOOKIAS e BUTLER, 2013). Durante o Período Triássico, os arcossauromorfos diversificaram-se ocupando quase todos os tipos de habitats e nichos ecológicos. A ampla irradiação adaptativa deste grupo propiciou a diversificação para diferentes tipos de ambientes e o desenvolvimento de padrões corporais distintos. De forma geral, estes grupos incluem formas cursoriais, semiaquáticas, marinhas e de locomoção aérea (NESBITT, 2011; EZCURRA et al., 2014; FOTH et al., 2016; EZCURRA e BUTLER, 2018).

A partir do Triássico Inferior, o registro fóssil de arcossauromorfos tornou-se consideravelmente abundante e morfologicamente diverso. Dentre os arcossauromorfos não pertencentes ao grupo coronal Archosauria, destacam-se membros herbívoros terrestres de tamanho relativamente grande (Allokotosauria), herbívoros com dentição altamente

especializada (Rhynchosauria) e formas aquáticas, muitas vezes de pescoço excepcionalmente longo (Tanystropheidae) (DILKES, 1998; GOWER e SENNIKOV, 2000; BUTLER et al., 2011; NESBITT, 2011). Estes grupos, juntamente com Prolacertidae, são os principais clados irmãos sucessivos de Archosauriformes. Este, por sua vez, inclui Archosauria, representado atualmente por aves e crocodilianos, mas com complexa história evolutiva no registro fóssil e uma grande diversidade de formas extintas (Figura 1).

Archosauriformes consiste em um clado diverso que inclui raras espécies do Permiano (e.g., *Archosaurus rossicus*) e uma amostra diversa de formas do Triássico ao recente (EZCURRA, 2016). Os arcossauriformes não-arcossauros representam táxons com morfologias distintas que atingiram a máxima diversidade e alcançaram uma distribuição global cosmopolita durante o Triássico Médio e Superior (GOWER e SENNIKOV, 2000; NESBITT et al., 2009; DESOJO et al., 2011; EZCURRA, 2016; FOTH et al., 2016; EZCURRA e BUTLER, 2018).

A diversidade paleoecológica entre os arcossauromorfos não-arcossauriformes parece ter excedido àquela de arcossauriformes não-arcossauros, que são representados principalmente por formas semelhantes aos crocodilos (i.e proterossuquídeos, proterocâmpsios, doswelídeos) e clados de grandes predadores (i.e eritrossuquídeos) (EZCURRA, 2016). Hipóteses filogenéticas atuais de Archosauriformes indicam que a origem e a diversificação inicial de Archosauria ocorreu durante o Triássico Inferior, após a extinção Permo-Triássica (NESBITT, 2011).

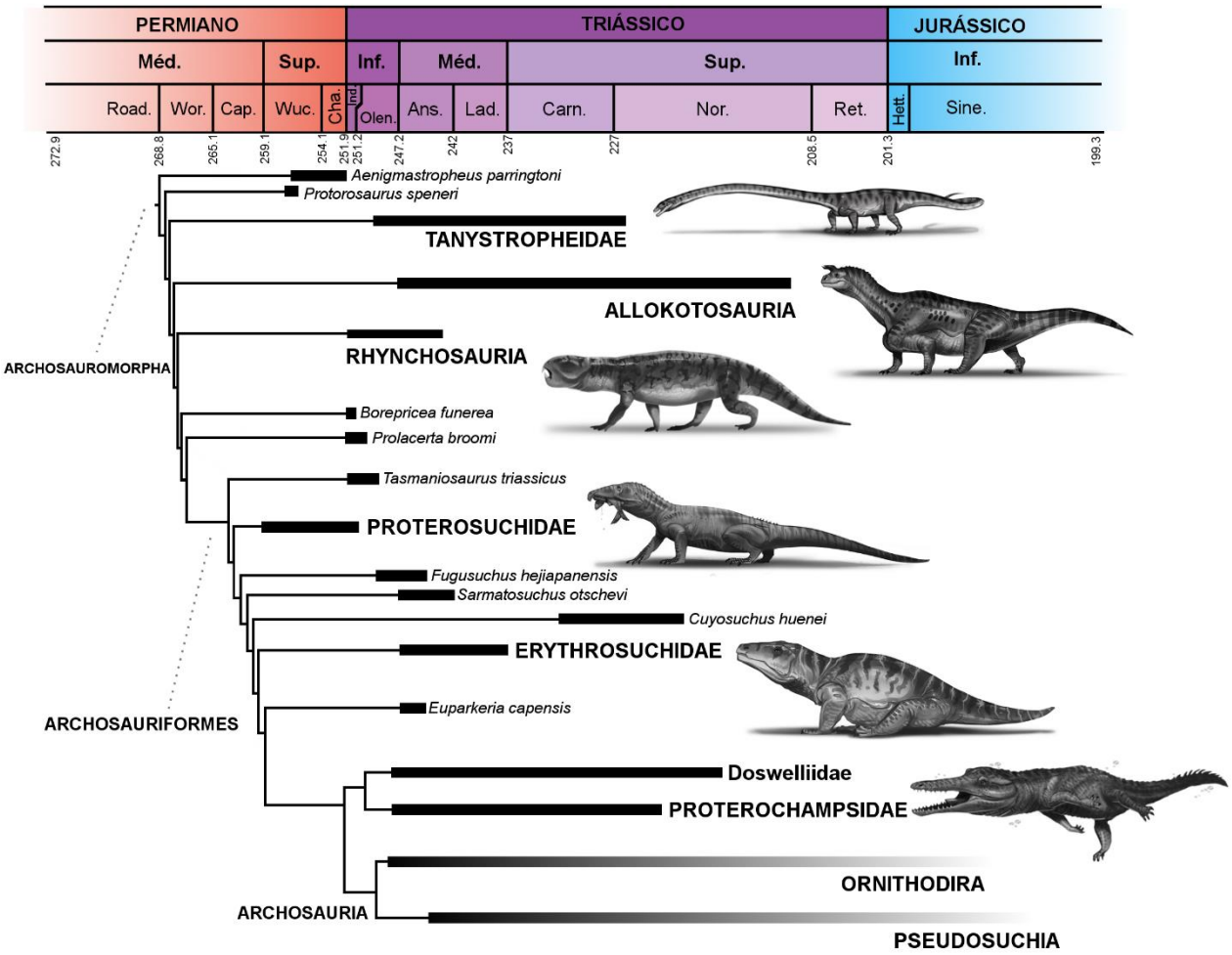
A aquisição de uma postura de membros verticais e uma marcha parassagital foi uma inovação chave na evolução e diversificação dos arcossauriformes (KUBO e BENTON, 2009; PADIAN et al., 2010). A posição dos membros abaixo do corpo permitiu um incremento na rapidez dos movimentos com menor gasto calórico em comparação com a marcha dos animais planígrados (BERNARDI et al., 2015).

Como já ressaltado, os arcossauriformes foram altamente abundantes em ecossistemas terrestres durante o Mesozoico, diversificando-se em numerosas espécies e ecomorfótipos. Os grupos mais antigos de Archosauriformes são representados principalmente por membros de Proterosuchidae e Erythrosuchidae, conhecidos mundialmente a partir do Permiano Superior e do Triássico Inferior e Médio. Estes dois grupos foram historicamente incluídos em 'Proterosuchia', com aproximadamente 30 espécies (EZCURRA, 2016).

O clado Archosauria (Pseudosuchia – rauissuquídeos, crocodilianos, entre outros, e Ornithodira – pterossauros, dinossauros), foi um dos principais grupos terrestres de tetrápodes durante o Mesozoico (GAUTHIER, 1986), e constitui um dos clados taxonomicamente mais

diversos de amniotas existentes (BERNARDI et al., 2015), que inclui milhares de espécies de dinossauros (incluindo Aves), Pterosauria, Crocodylia e Rauisuchia (BENTON e CLARK, 1988).

Figura 1 - Relações entre os principais grupos Archosauromorpha, Archosauriformes e Archosauria.



Fonte: Imagem adaptada de EZCURRA (2016). Barras representam a dispersão juntamente com possíveis linhagens fantasmas dos principais grupos de Archosauromorpha.Tabela do tempo baseada em Gradstein et al. (2012). Reconstrução artística dos táxons: Márcio Castro.

Durante o período Triássico, os arcossauros irradiaram uma variedade diversa de tamanhos de corpo, ecologias e morfologias. A classificação tradicional de Archosauria diz respeito principalmente à subdivisão de acordo com classificações adaptativas ou locomotoras.

As articulações do tornozelo aviário e crocodiliano diferem consideravelmente na estrutura e na função. A articulação do tornozelo aviano é uma dobradiça côncavo-convexa simples desenvolvida no tarso principalmente entre os tarsais proximal e distais, enquanto a articulação do tornozelo de crocodilos é intensificada, com a superfície articular passando entre o tarsal proximal, o astrágalo e o calcâneo (SERENO e ARCUCCI, 1990; SERENO, 1991).

A evolução da locomoção em Archosauria é um tema muito estudado na paleontologia de vertebrados devido às variadas adaptações desenvolvidos durante o Mesozoico pelas diferentes linhagens deste clado (CHARIG, 1972; BONAPARTE, 1984). A evolução de diferentes morfologias nos ossos dos membros permitiu a adaptação do grupo a hábitos locomotores específicos. Cada nova característica poderia, ou não, comportar novas funcionalidades, levando as espécies a ocupar novos nichos ou tornando-as mais ou menos aptas a competir pelo espaço já ocupado (LIPARINI, 2011). Contudo, tais inovações evolutivas sempre estiveram fortemente relacionadas às barreiras físicas ambientais e à história filogenética de cada grupo.

1.2 PRINCIPAIS GRUPOS DE ARCOSSAUROMORFOS NÃO-ARCOSSAURIFORMES

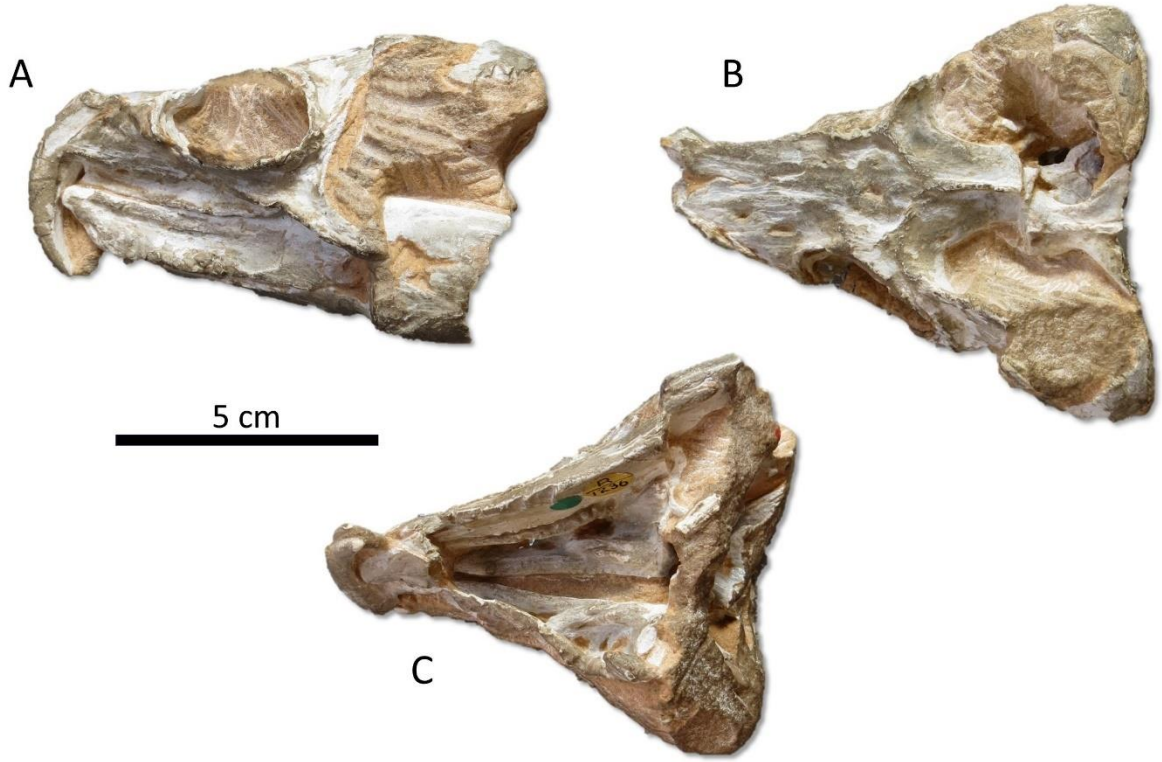
As linhagens independentes de arcossauromorfos não-arcossauriformes foram morfologicamente e ecologicamente diferentes durante o Triássico, incluindo grandes herbívoros terrestres (Allokotosauria), herbívoros altamente especializados (Rhynchosauria), além dos bizarros Tanystropheidae. Vários táxons de arcossauromorfos não-arcossauriformes foram classicamente agrupados em um táxon não-monofilético anteriormente conhecido como “Prolacertiformes” (EZCURRA, 2016).

1.2.1 Rhynchosauria Osborn, 1903

Os representantes de Rhynchosauria são encontrados na América do Sul e do Norte, África, Madagascar, Índia e Europa (vide Ezcurra, 2016 para a definição filogenética). Rincossauros são os tetrápodes mais comumente encontrados no Triássico (principalmente os pertencentes ao gênero *Hyperodapedon*), o que significa que são os arcossauromorfos herbívoros mais abundantes deste período. Como resultado, os rincossauros tem sido amplamente utilizados em correlações bioestratigráficas (LANGER, 2005; LUCAS, 2010; MARTÍNEZ et al., 2012; MUKHERJEE e RAY, 2014). Os representantes desse grupo

apresentavam um crânio transversalmente largo e uma dentição altamente especializada (CHATTERJEE, 1980; BENTON, 1985; LANGER e SCHULTZ, 2000). A característica mais marcante deste grupo são as pré-maxilas direcionadas ventralmente formando um "bico" que dá o nome ao grupo (*rhynchos* = bico + *saurus* = réptil) (Figura 2), embora formas mais antigas (e.g. *Mesosuchus*) ainda não apresentassem essa estrutura (MONTEFELTRO et al., 2010; EZCURRA et al., 2016). Essa especialização ("bico" e dentes) parece ter sido uma adaptação para a alimentação à base de frutos com sementes duras (EZCURRA et al., 2016).

Figura 2 – O rincossauro *Rhynchosaurus articeps* (espécime NHMUK PV R 1236, Anisiano da Inglaterra), demonstrando a morfologia característica do grupo. Crânio em A, vista lateral esquerda; B, vista dorsal e C, vista ventral.



Fonte: Fotografias de Felipe Pinheiro.

Os registros mais antigos de rincossauros remontam ao Triássico Inferior. No entanto, a origem permiana do clado é sugerida por topologias filogenéticas, com uma linhagem fantasma se estendendo através do limite Permo-Triássico, no Permiano Lopingiano

(EZCURRA et al., 2016). No Triássico Inferior (Induano), *Noteosuchus colletti* Watson,1912 é o mais antigo representante conhecido, constituído por um único e parcialmente articulado pós-crânio, coletado na base da Zona de Assembleia de *Lystrosaurus*, na Bacia do Karoo da África do Sul (WATSON, 1912; BROOM, 1925; DILKES, 1998; EZCURRA, 2016; EZCURRA et al., 2016).

Registros de rincossauros são mais frequentes (ainda que escassos) no início do Triássico Médio. Em rochas desta idade da Bacia do Karoo, na África, três espécies são designadas para Rhynchosauria: *Mesosuchus browni* Dilkes, 1998, *Howesia browni* Broom, 1905, e *Eohyosaurus wolvaardti* Butler et al. 2015, todas pertencentes à Zona de Assembleia de *Cynognathus* (BUTLER et al., 2015; EZCURRA et al., 2016). *Mesosuchus browni* é a espécie de rincossauro basal mais bem conhecida, e tem sido amplamente utilizada como um representante da morfologia do grupo em análises filogenéticas de arcossauromorfos (EZCURRA, 2016).

Os rincossauros sul-americanos são encontrados em rochas da Supersequência Santa Maria, (Bacia do Paraná, Rio Grande do Sul), representando 80% dos fósseis encontrados na Zona de Associação de *Hyperodapedon*, e na Bacia de Ischigualasto (Argentina) (LANGER e SCHULTZ, 2000; EZCURRA et al., 2016). Espécimes redescritos atualmente indicam uma razoável diversidade da fauna de rincossauros para estas localidades. O rincossauro anteriormente referido como o "rincossauro de mariante" foi formalmente descrito como um novo gênero e espécie (*Brasinorhynchus mariantensis* Schultz et al. 2016) baseado em dois espécimes: um crânio (sem a mandíbula) articulado com as três primeiras vértebras cervicais e um conjunto de maxila e dentário direito (LANGER e SCHULTZ, 2000; LANGER et al., 2007; SCHULTZ et al., 2016). Ambos os espécimes são pertencentes aos depósitos da Supersequência Santa Maria, considerada de idade Ladiniana (Triássico Médio). *Teyumbaita sulcognathus*, pertencente a Sequência Santa Maria II (Triássico Superior), foi originalmente descrito por Azevedo e Schultz (1987) como *Scaphonyx sulcognathus* e, mais tarde, transferido para um novo gênero por Montefeltro et al. (2010), baseado em um conjunto de características cranianas, o material atribuído a este táxon consiste de dois crânios quase completos e um parcialmente preservado (MONTEFELTRO et al., 2010; MONTEFELTRO et al., 2013).

1.2.2 “Prolacertiformes” Camp, 1945

Vários arcossauromorfos do Permiano-Triássico foram atribuídos historicamente aos "Prolacertiformes". A análise filogenética inicialmente proposta por Jalil (1997) encontrou 14 gêneros dentro de "Prolacertiformes": *Protorosaurus* Meyer, 1830, *Prolacerta* Parrington, 1935, *Prolacertoides* Yang, 1973, *Malutinisuchus* Otschev, 1986, *Kadimakara* Bartholomai, 1979, *Boreopricea* Tatarinov 1978, *Malerisaurus* Chatterjee 1980, *Jesairosaurus* Jalil, 1997 e seis gêneros provavelmente aquáticos que são agrupados dentro de Tanystropheidae (*Trachelosaurus* Broili e Fischer 1917, *Macrocnemus* Nopcsa, 1930, *Langobardisaurus* Renesto 1994, *Cosesaurus* Ellenberger e Villalta 1974, *Tanystropheus* Wild, 1973, *Tanytrachelos* Olsen, 1979) (CAMP, 1945; EVANS, 1988; JALIL, 1997; RIEPPEL et al., 2003; EZCURRA, 2016). No entanto, em análises filogenéticas recentes, "Prolacertiformes" não é recuperado como monofilético, sendo que espécies supostamente “Prolacertiformes” estão distribuídas entre diferentes linhagens de arcossauromorfos não-arcossauriformes (PRITCHARD et al., 2015; EZCURRA, 2016; PRITCHARD e NESBITT, 2017).

1.2.3 Tanystropheidae Gervais, 1858

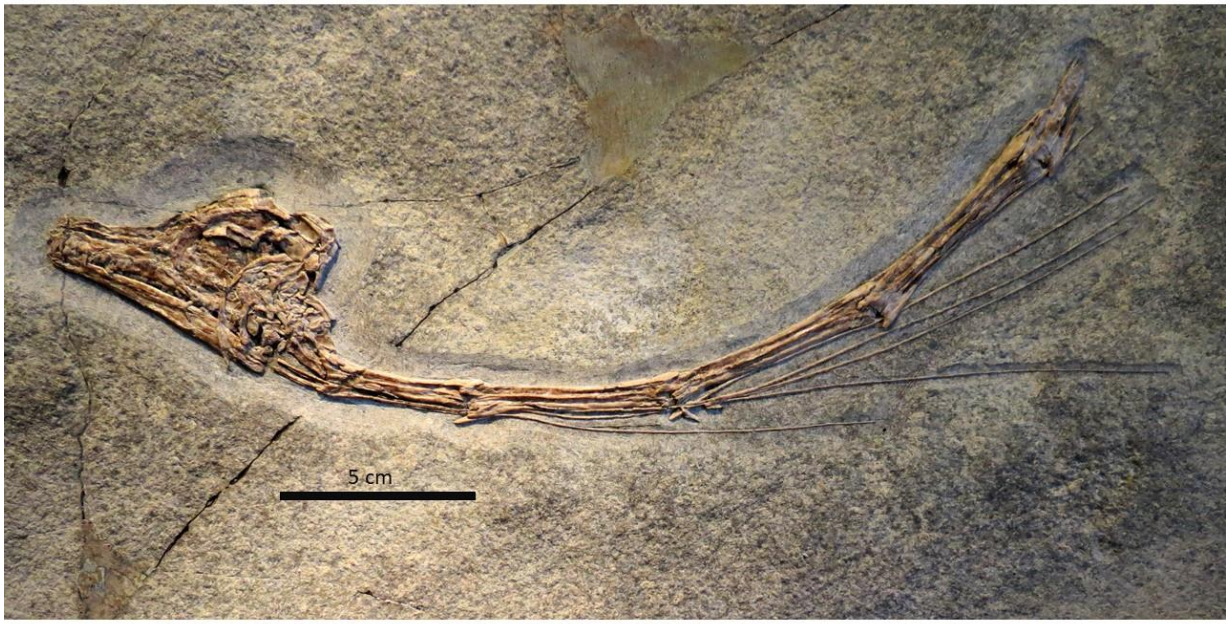
Os únicos representantes outrora agrupados como “prolacertiformes” clássicos recuperados nas primeiras análises filogenéticas de Archosauromorpha como um clado são agrupados em Tanystropheidae, representados, por exemplo, pelos táxons *Tanystropheus longobardicus* Bassani, 1886 (Figura 3) e *Macrocnemus bassanii* Nopcsa, 1930 (Figura 4).

Tanystropheidae é definido como o ancestral comum mais recente de *Macrocnemus*, *Tanystropheus*, *Langobardisaurus* e todos os seus descendentes (DILKES, 1998) e é um dos grupos representantes dos arcossauromorfos basais com registros no Triássico Inferior/Superior da Ásia, Europa e América do Norte (RIEPPEL, 1989; PRITCHARD et al., 2015).

De acordo com recentes contribuições (NESBITT et al., 2015; PRITCHARD et al., 2015; EZCURRA, 2016), Tanystropheidae inclui *Macrocnemus bassanii* e *Tanystropheus longobardicus* do Triássico Médio da Suíça e Itália, *Macrocnemus fuyuanensis* Li, Zhao e Wang, 2007 do Triássico Médio da China (LI et al., 2007; JIANG et al., 2011), *Langobardisaurus pandolfii* do final do Triássico da Itália e Áustria (RENESTO e DALLA VECCHIA, 2007; SALLER et al., 2013), *Tanytrachelos ahynis* Olsen, 1979 do Triássico Superior dos EUA, *Amotosaurus rotfeldensis* Fraser e Rieppel, 2006 do Triássico Inferior da Alemanha e até então registro mais antigo do grupo, *Augustaburiania* Sennikov, 2011, pertencente ao Triássico Inferior da Rússia (SENNIKOV, 2011). Os primeiros fósseis de

Tanystropheidae conhecidos (por exemplo, *Amotosaurus*), foram recuperados da margem noroeste da província de Tethys (Rússia; Alemanha), enquanto *Jesairosaurus lehmani*, o táxon-irmão do Tanystropheidae (EZCURRA, 2016), vem da Argélia, com distribuição do Olenekiano ao Anisiano (JALIL, 1997) (Figura 5).

Figura 3 – O tanistrofeídeo *Tanystropheus* (espécime PIMUZ T3901), crânio e vértebras cervicais anteriores em vista lateral esquerda.



Fonte: Fotografia de Felipe Pinheiro.

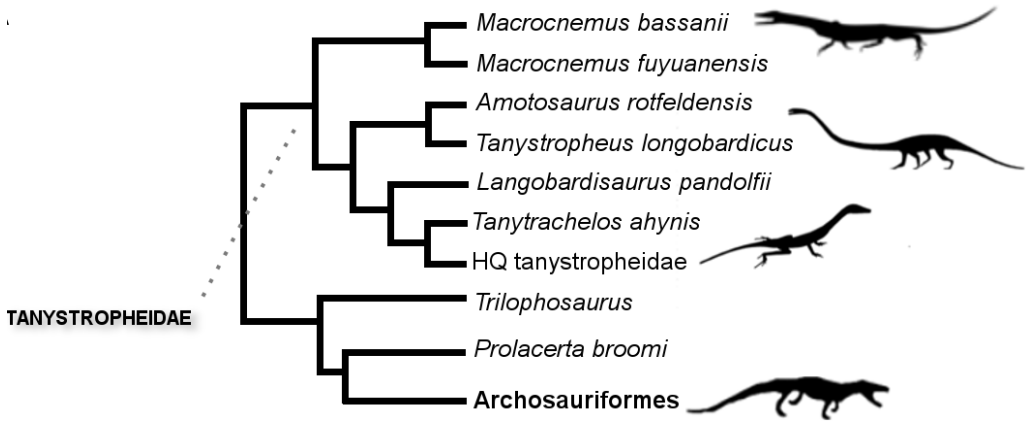
Tanystropheus e *Macrocnemus* possuem vértebras cervicais alongadas, uma característica particularmente pronunciada neste grupo (JAQUIER e SCHEIER, 2017). A morfologia corporal de *Macrocnemus* está de acordo com um hábito terrestre (RIEPPEL, 1989; RENESTO, 2005). Em contraste, o estilo de vida de *Tanystropheus* não é claramente identificável. Análises osteológicas recentes não suportam um hábito totalmente aquático para esse táxon (JAQUIER e SCHEIER, 2017).

Figura 4 – O tanistrofeídeo *Macrocnemus* (espécime PIMUZ T4355), esqueleto parcialmente completo.

Fonte: Fotografia de Felipe Pinheiro.

Registros de Tanystropheidae eram, até a presente contribuição, pouco conhecidos na América do Sul e restritos a materiais isolados atribuídos a "Protorosauria", como a vértebra descrita por Dias-da-Silva (1998) para a Formação Sanga do Cabral. Mais recentemente, um registro de arcossauromorfo indeterminado representado por um fragmento de úmero com características similares a de tanistrofeídeos (Permiano, Formação Rio do Rasto) foi descrito por Martinelli et al. (2016).

Figura 5 – Relacionamento filogenético de Tanystropheidae.



Fonte: Filogenia apresentada por Pritchard et al. (2015).

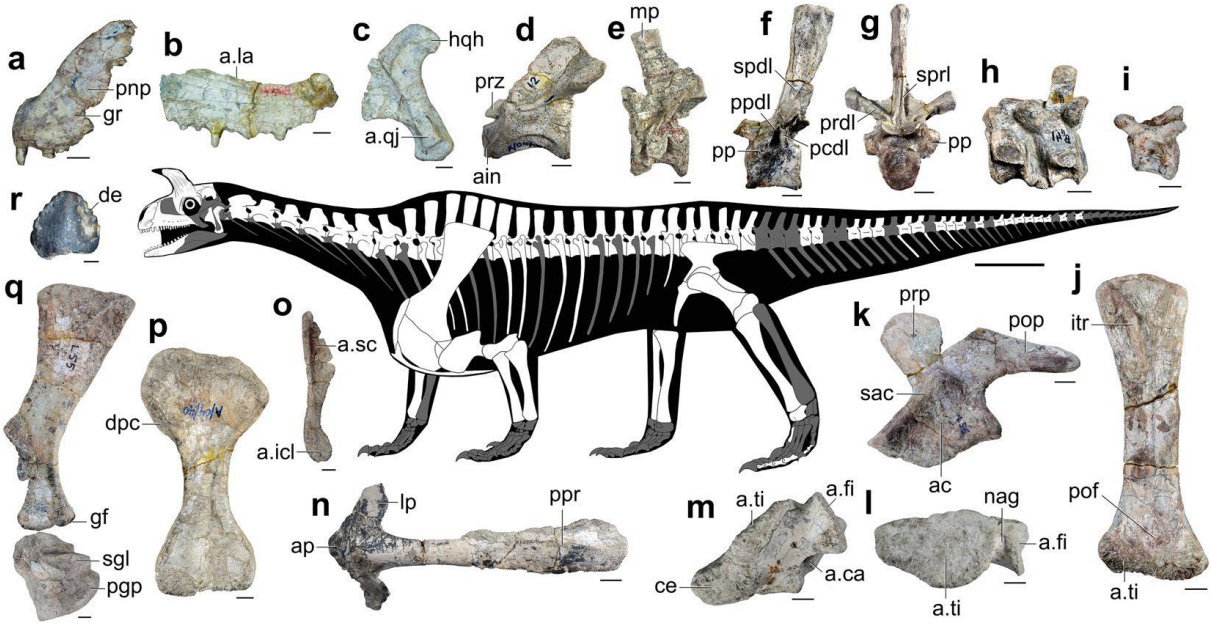
1.2.4 Allokotosauria Nesbitt et al. 2015

Allokotosauria é um clado que agrupa Azendohsauridae, Trilophosauridae e seus parentes mais próximos (*Pamelaria dolichotrachela* Sen, 2003, *Teraterpeton hrynewichorum* Sues, 2003, *Spinosuchus caseanus* Huene, 1932 e *Trilophosaurus* Case, 1928), excluindo outros arcossauromorfos (NESBITT et al., 2015; EZCURRA, 2016). Embora *Azendohsaurus* Flynn et al. 2010, tenha sido inicialmente considerado um dinossauro basal (com base em várias características dentárias semelhantes às que caracterizam certos subgrupos de dinossauros), novos registros relativamente completos mostram que esta atribuição estava equivocada (FLYNN et al., 2010). O nome deste novo grupo de arcossauromorfos significa "répteis estranhos" em grego e é formado por um conjunto de táxons de idade Triássica com uma alta disparidade de características crânio-dentárias tipicamente associadas à herbivoria (NESBITT et al., 2015). Com distribuição na Ásia, África, Índia, América do Norte e Europa, estes herbívoros terrestres destacam-se pelo tamanho relativamente grande, chegando a 3-4 m de comprimento total, e também por um pescoço moderadamente longo (SPIELMANN et al., 2007; NESBITT et al., 2015; EZCURRA, 2016; SENGUPTA et al., 2017).

Dentre os registros mais recentes, *Shringasaurus indicus* Sengupta et al. 2017, pertencente a Azendohsauridae, apresenta crânio proporcionalmente pequeno, com um focinho

curto e um par de grandes chifres supraorbitais que se assemelham aos de alguns dinossauros ceratopsídeos (Figura 6).

Figura 6 – O Allokotosauria *Shringasaurus*. Reconstituição esqueletal e elementos ósseos selecionados. A, pré-maxila; B, maxila; C, quadrado; D-I, vértebras; J, fêmur; K, ílio; L e M, tarsais proximais; N, interclavícula; O, clavícula; P, úmero; Q, escápula; R, dente isolado. Ossos preservados em cor branca. Para abreviações anatômicas, consultar fonte original.



Fonte: Sengupta et al. (2017).

A presença de chifres nesta espécie é considerada dimórfica, e essas estruturas provavelmente foram selecionadas sexualmente e usadas como armas em combates intraespecíficos (SENGUPTA et al., 2017). Este caso representa o primeiro registro de dimorfismo sexual em chifres em arcossauromorfos basais. *Pamelaria dolichotrachela*, do Triássico Médio, foi orginalmente descrito por Sen (2003), representado por um crânio e esqueleto parcial (holótipo), como um arcossauromorfo “prolacertiforme”. Mais recentemente, Nesbitt et al. (2015) recuperou esta espécie como o membro mais basal de Allokotosauria. As análises filogenéticas recentes deste grupo suportam o monofiletismo de Allokotosauria, mas, por outro lado, há evidências de que *Pamelaria dolichotrachela* possa pertencer a Azendohsauridae (NESBITT et al., 2015; EZCURRA, 2016).

1.2.5 Prolacertidae Parrington, 1935

As análises atuais para as relações filogenéticas de arcossauromorfos basais (NESBITT et al., 2015; EZCURRA, 2016), propõem tanistrofeídeos, rincossauros e alokotossauros como sucessivos grupos-irmãos de *Prolacerta* e Archosauriformes, sendo assim, mais consistentes com análises anteriores que repetidamente recuperavam Tanystropheidae como mais basal do que Rhynchosauria (e.g., GAUTHIER, 1994; DILKES, 1998; MÜLLER, 2004; GOTTMANN-QUESADA e SANDER, 2009; EZCURRA, EZCURRA et al., 2014). Prolacertidae é definido como todos os táxons mais intimamente relacionados a *Prolacerta broomi* do que a *Protorosaurus speneri*, Meyer, 1832, *Tanystropheus longobardicus* Bassani, 1886, *Proterosuchus fergusi* Broom, 1903 ou *Euparkeria capensis* Broom, 1913, e inclui atualmente *Prolacerta* e *Kadimakara australiensis* Bartholomai, 1979 (EZCURRA, 2016). *Prolacerta* é conhecido geralmente de depósitos do Triássico Inferior da África e alguns espécimes relativamente pequenos da Antártica (GOW, 1975; COLBERT, 1987) (Figura 7). A descoberta de novos materiais associados a esse arcossauromorfo levou a novas descobertas sobre o estilo de vida e sua morfologia. Seu conteúdo estomacal confirma que *Prolacerta* predava pequenos vertebrados e seu tamanho poderia adotar um tamanho considerável (crânio de espécimes adultos em torno de 8cm), quando comparado com outros animais da época (SPIEKMAN, 2018). *Kadimakara* apresenta registos do Triássico Inferior (Induano) da Austrália. O holótipo deste material é baseado na região pós-orbital de um crânio (QMF 6710) e apresenta morfologia consistente com a de um animal semelhante ao arcossauromorfo não-arcossauriforme *Prolacerta broomi* (EZCURRA, 2016). O registro fóssil destes grupos de transição entre arcossauromorfos basais e arcossauriformes é importante para elucidar as relações filogenéticas entre estes dois grandes grupos. O arcossauromorfo *Teyujagua paradoxa*, descrito por Pinheiro et al. (2016) pertencente ao Triássico Inferior do Rio Grande do Sul, é representado por um crânio bem preservado, e sua análise filogenética o recuperou em uma posição antes ocupada por *Prolacerta*, como grupo-irmão de Archosauriformes.

Figura 7 – *Prolacerta broomi* (espécime AMNH 9520), crânio de indivíduo juvenil em vista lateral esquerda.

Fonte: Fotografia de Felipe Pinheiro.

1.3 EXTINÇÃO PERMO-TRIÁSSICA, SUA INFLUÊNCIA NA RADIAÇÃO ADAPTATIVA DOS ARCOSSAUROMORFOS E A IMPORTÂNCIA DOS FÓSSEIS DA FORMAÇÃO SANGA DO CABRAL

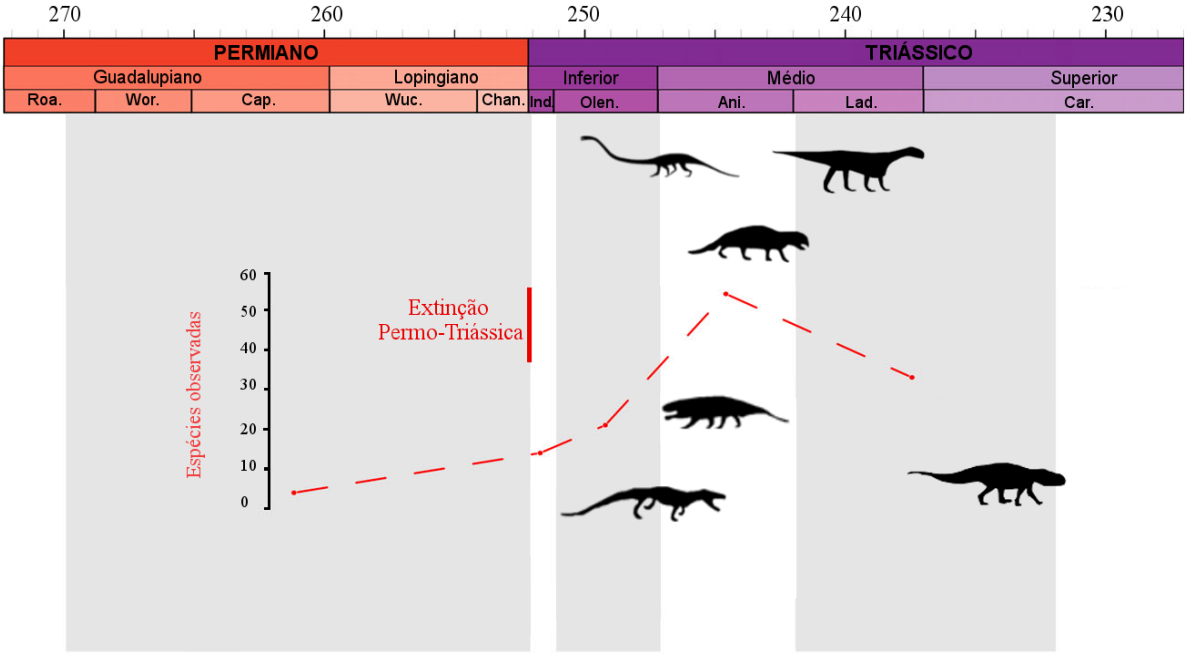
O Triássico representa um momento crítico na evolução dos vertebrados terrestres. Nesse intervalo de tempo, uma série de eventos resultou em uma importante transição faunística das comunidades paleozoicas, dominadas por sinápsidos e pararrépteis, para faunas incluindo clados como crocodilomorfos, dinossauros, lepidossauros e tartarugas, além dos grupos anteriormente mencionados (BUTTON, 2017). Perturbações ambientais, como por exemplo, vulcanismo e os efeitos dos gases liberados durante erupções vulcânicas, teriam causado crises de efeito estufa de curto prazo sucessivas e mudanças ambientais rápidas (IRMIS e WHITESIDE, 2011; BARNOSKI, 2011; BURGESS e BOWRING, 2015; EZCURRA e BUTLER, 2018). Este intervalo de instabilidade ainda coincide com temperaturas globais geralmente elevadas, o que teria limitado a diversidade faunística nas regiões equatoriais (SIDOR et al., 2013; BENTON e NEWELL, 2014; EZCURRA e BUTLER, 2018).

Análises recentes apontam para um modelo de diversificação entre os arcossauromorfos em resposta aos eventos da extinção em massa do Permo-Triássico. Este grupo teve sua origem provavelmente no Permiano com sua dispersão através do Pangeia (EZCURRA et al. 2014;

BERNARDI et al., 2015; EZCURRA e BUTLER, 2018). No entanto, a disparidade permaneceu reduzida e a baixa abundância de fósseis sugere que os arcossauromorfos continuaram sendo componentes muito menores dos ecossistemas terrestres do Permiano, ou que essa diversificação ocorreu em regiões geográficas ou ambientes que continuam sendo pouco amostrados (Figura 8) (EZCURRA e BUTLER, 2018).

No Olenekiano (~1 a 5 milhões de anos após o evento P/T), os arcossauromorfos aparecem no registro fóssil já anatomicamente bem diversificados, (e.g. *Noteosuchus colletti*) com a origem ou irradiação inicial de importantes clados, apresentando formas semiaquáticas ou inteiramente aquáticas como os tanistrofeídeos e herbívoros altamente especializados como rincossauros (EZCURRA, 2016).

Figura 8 - Abundância de arcossauromorfos do final do período Permiano e início do Carniano. Contagem de espécies observadas (linha vermelha tracejada), baseada na revisão de Archosauromorpha de Ezcurra (2016).



Fonte: Modificado de Ezcurra e Butler (2018).

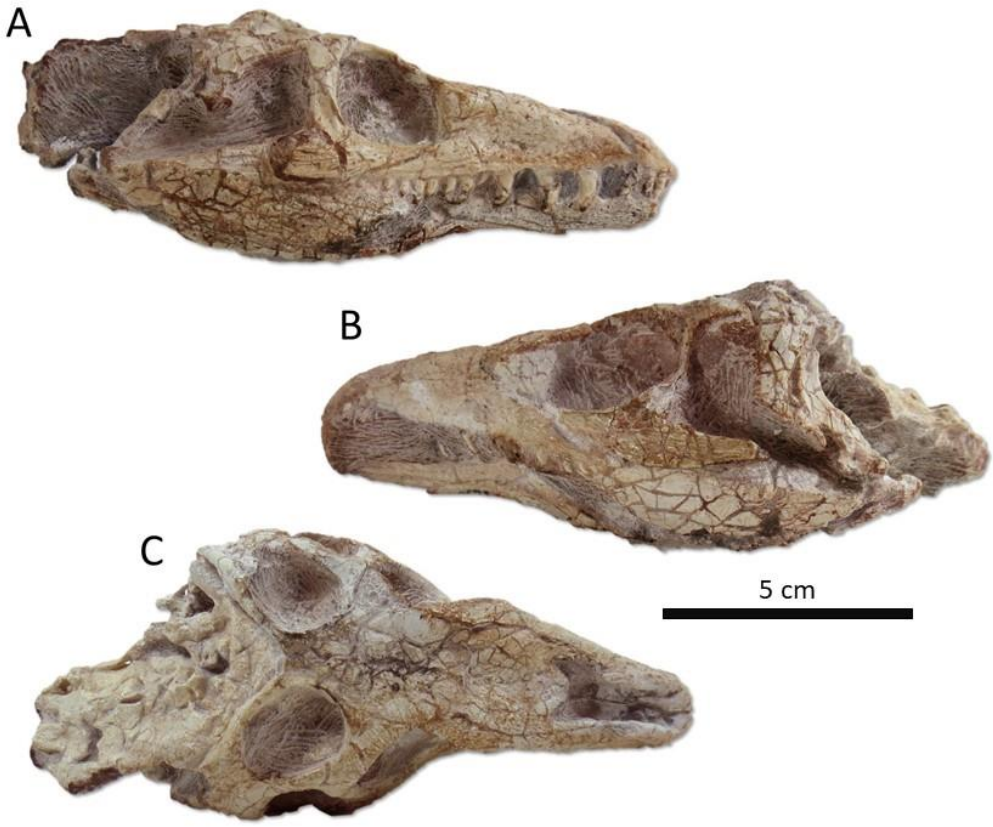
Uma generalização comum é que as extinções em massa são seguidas por períodos de aumento do cosmopolitismo faunístico durante o Triássico. As comunidades bióticas do Triássico Inferior são consideradas como "faunas de desastre", sendo globalmente homogêneas,

dominadas por um pequeno número de táxons amplamente distribuídos e abundantes (EZCURRA, 2016; BUTTON et al., 2017). O grande evento Permo-Triássico levou a uma redução profunda de biodiversidade, porém, os principais grupos sobreviventes diversificaram-se devido ao desaparecimento de espécies ou linhagens inteiras, abrindo novas vagas no espaço ecológico (SCHLUTER, 2000; YODER et al., 2010). Assim, esse padrão geral sugere que a diversificação dos arcossauromorfos foi uma resposta ao espaço ecológico vago após a extinção do final do Permiano (EZCURRA, 2016; EZCURRA e BUTLER, 2018).

O arcossauromorfo mais antigo da América do Sul, até o momento, é representado por uma porção distal de um úmero esquerdo (UFRGS-PV-0546-P) da Formação Rio do Rasto, Guadalupiano (Permiano) (Bacia do Paraná) (MARTINELLI et al., 2016). Embora o fóssil não possua nenhuma característica particular a algum grupo, o padrão geral deste espécime se assemelha mais aos tanistrofeídeos do que a outros arcossauromorfos (MARTINELLI et al., 2016). Apesar da morfologia do úmero descrita por Martinelli et al. (2016) se assemelhar a Tanystropheidae, a natureza fragmentária desse espécime impede uma atribuição categórica.

No Triássico Inferior da América do Sul, os registros de arcossauromorfos são notoriamente escassos, normalmente restritos a ossos isolados da Formação Sanga do Cabral, Triássico Inferior do Rio Grande do Sul (LANGER e SCHULTZ, 1997; DIAS-DA-SILVA, 1998; LANGER e LAVINA, 2000; DA-ROSA et al., 2009; DIAS-DA-SILVA e DA-ROSA, 2011) e Formação Buena Vista, do nordeste do Uruguai (EZCURRA et al., 2015). Poucos são os materiais encontrados articulados bem preservados, como é o caso do arcossauromorfo *Teyujagua paradoxa*, recuperado em rochas da Formação Sanga do Cabral (Figura 9). Esse último apresenta ótimo estado de preservação e foi descrito como um arcossauromorfo não-arcossauriforme. O material consiste de um crânio praticamente completo, com alguns elementos pós-cranianos associados (PINHEIRO et al., 2016).

Figura 9 – *Teyujagua paradoxa* (espécime UNIPAMPA 653), crânio em A, vista lateral direita; B, vista lateral esquerda e C, vista dorsal.



Fonte: Fotografia de Felipe Pinheiro.

Nesse sentindo, por ser uma das poucas unidades geológicas do início do Triássico da América do Sul, a Formação Sanga do Cabral é uma peça chave na compreensão da recuperação faunística ao longo do Triássico. Os novos espécimes aqui descritos, juntamente com os materiais já registrados para a Formação Sanga do Cabral, demonstram o alto potencial fossilífero dessa localidade, que ainda é pouco amostrada em relação a outros sítios de idade Triássica do Rio Grande do Sul. Assim, os fósseis descritos na presente dissertação contribuem para a compreensão sobre a biodiversidade e recuperação dos ecossistemas do Gondwana ocidental após a maior extinção já registrada.

2 OBJETIVOS

2.1 OBJETIVO GERAL

Estudar a anatomia de novos espécimes de arcossauromorfos não-arcossauriformes provenientes do Triássico Inferior da Supersequência Sanga do Cabral, Rio Grande do Sul e analisar suas relações filogenéticas.

2.2 OBJETIVOS ESPÉCIFICOS

I - Descrever a anatomia dos espécimes UNIPAMPA 733, UFRGS-PV-492-T; UFRGSPV-647-T e UFSM 11471;

II - Testar a posição filogenética dos novos espécimes no contexto dos Archosauromorpha;

III - Contextualizar os novos espécimes no panorama da diversificação de Archosauromorpha após a extinção Permo-Triássica.

CAPÍTULO 2*– MANUSCRITOS CIENTÍFICOS*

2.1 ARTIGO 1

TANYSTROPHEID ARCHOSAUROMORPHS IN THE LOWER TRIASSIC OF GONDWANA

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Tanystropheidae is a clade of early archosauromorphs with a reported distribution ranging from the Early to the Late Triassic of Asia, Europe, and North America. Although some specimens with possible tanystropheid affinities from the Lower Triassic beds of Brazil have been previously attributed to “Protorosauria”, little is known about the tanystropheid record in Gondwana. Here, two new and one previously reported specimen from the Sanga do Cabral Formation (Induan–Olenekian) of Brazil are described and interpreted as ?Tanystropheidae. These records, together with other tetrapods previously reported for the Sanga do Cabral Formation, increase the knowledge of the biotic diversification during the beginning of the Triassic. This contribution reinforces that the archosauromorph diversification occurred shortly after the Permo-Triassic extinction, making the Sanga do Cabral Formation an important unit for the study of early Mesozoic faunas.

Key words: Diapsida, Archosauromorpha, Tanystropheidae, Triassic, Sanga do Cabral Formation, Brazil.

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Introduction

Archosauromorphs were one of the first diapsid groups to diversify in body size and morphological disparity in Triassic terrestrial and marine ecosystems from Pangea. The wide radiation of Archosauromorpha resulted in adaptations to different environments and the development of distinct body plans. In sum, these groups include cursorial, semiaquatic, marine and flying forms (e.g., Nesbitt 2011; Ezcurra et al. 2014; Ezcurra 2016; Foth et al. 2016; Pinheiro et al. 2016). Bizarre body plans acquired by archosauromorphs include long-necked presumably aquatic forms (Tanystropheidae), relatively large terrestrial herbivores, sometimes with skull ornaments (Allokotosauria), and highly specialized herbivores (Rhynchosauria) (Nesbitt 2011; Jaquier and Scheier 2017; Sengupta et al. 2017).

Several Permian–Triassic long-necked archosauromorphs of varied sizes have historically been attributed to the "Prolacertiformes" (e.g., *Protorosaurus* Meyer, 1830, *Macrocnemus* Nopcsa, 1930, *Tanystropheus* Wild, 1973, *Prolacerta* Parrington, 1935) in several taxonomic proposals (e.g., Camp 1945; Evans 1988). However, recent phylogenetic analyses recovered most of the representatives of this group in a widely polyphyletic arrangement, distributed among different lineages of archosauromorphs and early Diapsida (Dilkes 1998; Sues 2003; Modesto and Sues 2004; Senter 2004; Ezcurra et al. 2014; Pritchard et al. 2015; Ezcurra 2016; Pinheiro et al. 2016; Pritchard and Nesbitt 2017). The only classical "prolacertiform" representatives recovered in these analyses as a clade are placed within Tanystropheidae, represented for ex- ample by the well-known taxa *Tanystropheus longobardicus* Bassani, 1886 and *Macrocnemus bassanii* Nopcsa, 1930, usually used as terminal taxa in phylogenetic analyses.

Tanystropheidae is regarded as a node-based clade, defined as the most recent common ancestor of *Macrocnemus, Tanystropheus, Langobardisaurus* Renesto, 1994, and all of its descendants (Dilkes 1998), with records in the Early– Late Triassic of Asia, Europe, and North America (Rieppel 1989; Renesto 2005; Dalla Vecchia 2006; Li et al. 2007; Jiang et al. 2011; Pritchard et al. 2015). Fossils with tanystropheid affinities are poorly known in South America and restricted to a few isolated bones attributed to "Protorosauria" (Langer and Schultz 1997; and Dias-da-Silva 1998).

The Middle Triassic taxa *Tanystropheus* and *Macrocnemus* have elongated cervical vertebrae, a notably pronounced feature of this group (Ezcurra 2016; Jaquier and Scheier 2017). The body morphology of *Macrocnemus* is in accordance with a terrestrial habit (Rieppel 1989; Renesto 2005). In contrast, the lifestyle of *Tanystropheus* is still debatable. However, recent

osteological analyses do not support a fully aquatic habit for this animal (Jaquier and Scheier 2017).

The Lower Triassic archosauromorph record is notably scarce, what hinders a satisfactory understanding of one of the most important radiation events of this clade. In this con- text, the South American Sanga do Cabral, and Buena Vista Formations from Brazil and Uruguay recently contributed with important specimens (Ezcurra et al. 2015; Pinheiro et al. 2016). In this work, we describe isolated archosauromorph vertebrae from the Sanga do Cabral Formation and analyze their phylogenetic relationships. One of the specimens (UFRGS-PV-492-T) was briefly presented by Dias-da-Silva (1998), and attributed to "Protorosauria". Based on comparative anatomy and phylogenetic protocol, we attribute the vertebrae here presented to ?Tanystropheidae. As most tanystropheids come from North America, Europe, and Asia, the Sanga do Cabral Formation specimens provide valuable information on the geographic distribution of this group.

Institutional abbreviations.—LASEPE, Laboratório de Sedimentologia e Petrologia; PUCRS, Pontifícia Universi- dade Católica do Rio Grande do Sul, Brazil; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; UNIPAMPA, Universidade Federal do Pampa, São Gabriel, Brazil; ZAR, Muséum national d'Histoire naturelle (Zarzaitine collection), Paris, France.

Material and methods

The specimens described here belong to the paleontological collections of the Universidade Federal do Rio Grande do Sul (UFRGS-PV-492-T and UFRGS-PV-647-T) and Universidade Federal do Pampa (UNIPAMPA 733). To test the phylogenetic affinities of the new specimens, these were scored in the archosauromorph morphological character matrix proposed by Sengupta et al. (2017) which, by its turn, is a modification of Ezcurra (2016) database. After the addition of the new operational taxonomic units using the software Mesquite 3.2 (Maddison and Maddison 2015), the analyses were conducted using the software TNT 1.5 (Goloboff and Catalano 2016). Analyses were made using both reduced and complete matrixes of Sengupta et al. (2017). The reduced matrix of Sengupta et al. (2017), excludes problematic taxa (e.g., taxa with uncertain positioning due to a large amount of missing data), in accordance to Ezcurra

(2016) (see also SOM 1, Supplementary Online Material available at http://app.pan.pl/SOM/app63-Oliveira_etal_SOM.pdf).

A first analysis was conducted using the New Technology Algorithms until the best result was hit 100 times and, subsequently, running heuristic searches of 1000 replicates using random addition sequences followed by the TBR (Tree Bisection Reconnection) branch rearrangement algorithm, retaining ten trees per replicate. If some replications overflowed (some of the MPT's may not have been found) during the first round of analysis, a traditional search was again employed, this time using trees from RAM. The following experiments were performed: (i) analysis of the three cervical vertebrae individually (UNIPAMPA 733, UFRGS-PV- 492-T, and UFRGS-PV-647-T); (ii) analysis of the specimens (UNIPAMPA 733 and UFRGS-PV-492-T) together. Additionally, we used micro-CT scan to analyze the specimens UNIPAMPA 733, UFRGS-PV-492-T, and UFRGS- PV-647-T, and generate tridimensional models. The images were obtained at the Laboratório de Sedimentologia e Petrologia (LASEPE), Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), Brazil, through a micro-CT scanner Skyscan 1173, using a voltage of 75 kV and amperage of 106 μa. A total of 1723 (1551 slices with information) slices were generated. The image pixel size is 15.166192 μm. 3D Slicer 4.8 (Fedorov et al. 2012) was employed to generate 3D models of this specimens.

Geological setting

The cervical vertebrae UNIPAMPA 733 and UFRGS-PV- 492-T come from the Ramal Abandonado locality (municipality of Dilermando de Aguiar). The fossiliferous levels of this outcrop are composed of an intercalation of fine sandstone and intraformational conglomerate, in which argillaceous intraclasts and carbonate nodules are frequent (Zerfass et al. 2003; Da-Rosa et al. 2009; Dias-Da-Silva et al. 2017). Specimen UFRGS-PV-647-T has an indeterminate provenance, but, according to collection records, was collected from a Sanga do Cabral Formation outcrop. The Sanga do Cabral Formation (Induan–early Olenekian), was deposited in a vast alluvial plain in southwestern Gondwana (Zerfass et al. 2003). The Brazilian Sanga do Cabral Formation, together with the Buena Vista Formation (Uruguay), constitutes the Sanga do Cabral Supersequence. This unit also includes occasional well-selected fine to medium sandstones with massive cross-bedding stratifications, interpreted as aeolian in origin and indicating constant reworking of the alluvial plain (Faccini 1989; Dias-Da-Silva et al. 2017).

The fossil assemblage of the Sanga do Cabral Formation so far includes procolophonids, temnospondyls, and archosauromorphs (Dias-Da-Silva et al. 2005, 2006; Pinheiro et al. 2016). Vertebrate fossils are often found isolated and disarticulated. This preservation mode suggests extensive exposure and post-mortem transport of bones during the biostratinomic phase, and subsequent reworking after diagenesis. Archosauromorph records are scarce in the Sanga do Cabral Formation, with only a few specimens reported so far (e.g., Langer and Schultz 1997; Dias-Da-Silva 1998; Da-Rosa et al. 2009; Pinheiro et al. 2016; Dias-Da-Silva et al. 2017). In addition to the scarcity of fossils, the lack of anatomical studies focusing on small isolated specimens contributes to the limited knowledge about the diversity of archosauromorphs in this sedimentary unit. Articulated specimens remain almost unknown, except for a few records (e.g., Pinheiro et al. 2016).

An Induan–Olenekian age (251–247Ma) (Cohen et al. 2013) is inferred for this formation based on the presence of the parareptile *Procolophon trigoniceps* Owen, 1876, and comparisons with the *Lystrosaurus* Assemblage Zone of the South African Karoo (Dias-Da-Silva et al. 2006; Botha and Smith 2006; Da-Rosa et al. 2009). Currently, no fossil taxa indicate a Permian age for the Sanga do Cabral Supersequence (see Dias-Da-Silva et al. 2017 for a comprehensive revision), and all the biostratigraphically informative fossils so far collected from the Sanga do Cabral and Buena Vista formations reinforce the attribution of a Lower Triassic age for the Sanga do Cabral Supersequence (Dias-Da-Silva et al. 2017). The age of the Sanga do Cabral and Buena Vista formations, lithostratigraphically equivalent, has been the focus of numerous discussions, being alternatively considered as Permian or a broader Permo-Triassic age (Piñeiro et al. 2004, 2007; Ezcurra et al. 2015). According to Piñeiro et al. (2015), at least part of the Sanga do Cabral Formation is Permian in age, but a comprehensive revision provided by Dias-da-Silva et al. (2017) supported an Early Triassic age for the unit.

Systematic palaeontology

Diapsida Osborn, 1903 (*sensu* Laurin 1991)

Archosauromorpha Huene, 1946 (*sensu* Gauthier et al. 1988)

Tanystropheidae Gervais, 1859

?Tanystropheidae indet.

Material.—UNIPAMPA 733, UFRGS-PV-492-T, UFRGS- PV-647-T: isolated cervical vertebrae from Sanga do Cabral Formation (Induan–early Olenekian).

Description.—UNIPAMPA 733 (Fig. 1) presents an elongated and amphicoelous centrum. The parapophyses and diapophyses are poorly developed and situated in different processes and near each other in the centrum. In lateral view, the anterior articular surface of UNIPAMPA 733 is raised dorsally relative to the posterior surface. The neural spine is dorsoventrally low and laminar, lacking a transverse expansion (spine-table) and presenting a post-spinal fossa. The neural spine is abraded in its anterior and posterior extremities, preventing the recognition of a possible "overhang" (*sensu* Ezcurra 2016). A faint longitudinal keel runs the length of the centrum. In ventral view, UNIPAMPA 733 shows a thin anteroposterior keel extending through the whole centrum. The specimen has a total length of 18.45 mm.

Among the vertebrae, UFRGS-PV-492-T (Fig. 2) is better preserved. However, this specimen has a broken neural spine, making it impossible to analyze the shape of this structure. The preserved portion of the neural spine, however, is reminiscent of a thin and low longitudinal lamina, possibly extending for almost the entire anteroposterior length of the centrum. With a total length of 20.26 mm, UFRGS-PV-492-T shows an elongated amphicoelous centrum and a higher anterior articular surface with relation to the posterior one. The diapophyses and parapophyses are close to each other on the anterior surface of the centrum. Notably, this specimen displays a clear longitudinal keel that extends laterally on the centrum. The ventral surface of the centrum shows a keel that extends along its entire length. Although a ventral keel is also present in specimens UNIPAMPA 733 and UFRGS-PV-647-T, they are not as well preserved as in UFRGS-PV-492-T. The ventral surface of the centrum (excluding the keel) is slightly rounded. In lateral view, the postzygapophysis of UFRGS-PV-492-T is slightly elevated dorsally above the level of the prezygapophysis, with short and spaced articular surfaces. Due to the preservation, it is not possible to evaluate the presence of epipophyses or the transpostzygapophyseal lamina.

The preserved portion of the neural spine of UFRGS- PV-647-T (Fig. 3) indicates a dorsoventrally deep lamina. The vertebral body is elongated, and the centrum is amphicoelous. Due to poor preservation, the parapophyses and diapophyses are not readily distinguishable. However, these structures seem to be poorly developed. It is also not possible to determine if the postzygapophyses are separated or connected to each other. In lateral view, UFRGS-PV-

647-T shows the anterior articular surface of the centrum raised dorsally relative to the posterior one. The centrum also possesses a lateral transverse keel. This specimen shows a ventral keel that does not reach the anterior articular margin. Specimen UFRGS-PV-647-T has a total length of 15.40 mm.

In all the vertebrae, it is not possible to determine whether the neural spine ends anteriorly or posteriorly to the postzygapophyses.

Phylogenetic analyses

First of all, the cervical vertebrae were evaluated individually using the reduced matrix of Sengupta et al. (2017). The analysis including UNIPAMPA 733 resulted in this specimen as the sister taxon to Tanystropheidae (*Macrocnemus bassanii* and (*Tanystropheus longobardicus + Amotosaurus rotfeldensis* Fraser and Rieppel, 2006)) (SOM 3: fig. 1). The clade formed by UNIPAMPA 733 and Tanystropheidae has *Jesairosaurus lehmani* Jalil, 1997 as sister taxon.

In the analysis including UFRGS-PV-492-T, this specimen occupies the same position as UNIPAMPA 733 in the previous analysis (SOM 3: fig. 2). These two analyses generated one tree with 2783 steps, consistency index 0.291 and retention index 0.633. Phylogenetic analysis including UFRGS-PV-647-T resulted in a strict consensus with low resolution and a large number of polytomies. This analysis generated six trees, with 2783 steps, retention index 0.633 and consistency index 0.291. The low resolution presented in the strict consensus can be justified by the lack of informative morphological characters, reflecting poor preservation of relevant structures. In the analysis including both UFRGS-PV-492-T and UNIPAMPA 733, these specimens were recovered into a polytomy together with *Jesairosaurus lehmani, Macrocnemus bassanii* and (*Tanystropheus longobardicus + Amotosaurus rotfeldensis*) (Fig. 4). This analysis generated three trees with 2783 steps, consistency index 0.291 and retention index 0.633. This last analysis did not include specimen UFRGS-PV-647-T due to the lack of informative character-states.

Discussion

Anatomical and taxonomic remarks.—Most of the Tanystropheidae fossil record is concentrated in Europe, Asia, and North America. Isolated bones assigned to “Protorosauria” were briefly presented for Lower Triassic deposits of Brazil (Langer and Schultz 1997; Dias-

Da-Silva 1998) and were so far the only records of the group in South America. The specimen UFRGS-PV-492-T was originally described as a "protorosaurid" cervical vertebra (Dias-Da-Silva 1998), a taxonomical attribution mostly based on its elongated amphicoelous centrum and a laminar neural spine.

The three vertebrae here described, UFRGS-PV-492-T, UFRGS-PV-647-T, and UNIPAMPA 733 are morphologically compatible with the Tanystropheidae. These materials resemble this group in displaying a dorsoventrally short and laminar neural spine (Ezcurra 2016). Also, it is possible to distinguish a laterodorsal keel directed to the pre and postzygapophysis throughout the length of the centra of all specimens, which, according to Wild (1973) and Nosotti (2007), is diagnostic for Tanystropheidae.

The cervical vertebrae have the anterior articular surface of the centrum elevated dorsally relative to the posterior one. In contrast, the anterior and posterior surfaces of non-archosauromorph diapsids and some archosauriforms (*Proterochampsa barrionuevoi* Dilkes and Arcucci, 2012; *Riojasuchus tenuisceps* Bonaparte, 1967) are located at the same dorsoventral level in lateral view. As a result, the neck is mainly straight in these latter taxa, instead of sigmoidal as in most archosauromorphs (Ezcurra 2016).

According to Jalil (1997) and Ezcurra (2016) anteroposteriorly long and dorsoventrally low cervical neural spines are present in putative "prolacertiforms" (e.g., *Protorosaurus speneri, Amotosaurus rotfeldensis, Macrocnemus bassanii, Tanystropheus longobardicus, Prolacerta broomi, Boreopricea funerea*), being also a present in other archosauromorphs, such as *Trilophosaurus* (Gregory, 1945) and *Azendohsaurus* (Flynn, Nesbitt, Parrish, Ranivoharimanana, and Wyss, 2010), whereas most non-archosaurian archosauriforms possess dorsoventrally taller cervical neural spines (e.g., *Proterosuchus fergusi* Broom, 1903, *Proterosuchus alexanderi* Hoffman, 1965), *Garjainia prima* Ochev, 1958, *Euparkeria capensis* Broom, 1913). Following recent phylogenetic proposals (Ezcurra 2016), the sister-taxon to Tanystropheidae is *Jesairosaurus lehmani*, described based on cranial and postcranial remains from the Zarzaitine Series (Olenekian–Anisian) of Algeria. As described above, our phylogenetic analysis with the inclusion of both UFRGS-PV-492-T and UNIPAMPA 733 in the data matrix of Sengupta et al. (2017) resulted in a polytomy including the new specimens, *J. lehmani*, and tanystropheid taxa. Although the cervical vertebrae of the holotype of *J. lehmani* (ZAR 06) are well preserved, they are still partially covered by matrix. However, is possible to see that they differ from the material described herein in several characters. In ZAR 06 all preserved cervical neural spines are anterodorsally oriented, being the posteriormost cervical

neural arches low, narrow, and slightly concave laterally (Jalil 1997; Ezcurra 2016). The vertebrae described herein are significantly more elongated than those of ZAR 06. In ZAR 06, the presence of lateral keels in the cervical centra cannot be determined. In addition, our material shows dorsoventrally lower neural spines than those of *J. lehmani*.

Comparisons with *Macrocnemus* and *Tanystropheus* demonstrate that the pronounced elongation of the vertebral body, as well as the presence of lateral and ventral keels and a low neural spine present in the referred Sanga do Cabral Formation specimens, are, together, typical features of tanystropheid cervicals. This same combination of features is present not only in the well-known Macrocnemus bassanii and Tanystropheus longobardicus but in all known Tanystropheidae (e.g., Nosotti 2007; Jaquier and Scheier 2017).

Phylogenetic remarks.—In recent studies, Tanystropheidae and *Jesairosaurus lehmani* (previously identified as belonging to "Protorosauria"/"Prolacertiformes") were recovered as more related to each other than to other archosauromorphs and as the sister-taxa to Crocopoda (Ezcurra 2016). The unnamed clade formed by *Jesairosaurus* + Tanystropheidae has a distribution from the Early Triassic (e.g., *Augustaburiania vatagini* Sennikov, 2011) to the Norian (Late Triassic) (e.g., *Tanytrachelos ahynis* Fraser, Grimaldi, and Olsen, 1996) (Ezcurra 2016).

Based on the current dataset, the results of our analyses including both UNIPAMPA 733 and UFRGS-PV-492-T provide phylogenetic support for the attribution of the new material to Archosauromorpha more closely related to Tanystropheidae than to other archosauromorphs. The individual analysis of UNIPAMPA 733 and UFRGS-PV-492-T recovered these specimens as a sister taxon of Tanystropheidae (*Macrocnemus* and [*Tanystropheus* + *Amotosaurus*]). However, the specimens share some characters with tanystropheids that are not present in Jesairosaurus (see above). Both UNIPAMPA 733 and UFRGS-PV-492-T have morphologies similar to what is recognized as the standard tanystropheid pattern. For instance, these specimens exhibit elongated centra, neural spine consisting of a thin lamina and the presence of a lateral keel, while *Jesairosaurus lehmani* presents the posteriormost cervical neural arches low, narrow, slightly concave laterally and the neural spine substantially higher than what is displayed by the material we describe. Hence, although the specimens are not placed within the node-based clade Tanystropheidae, they are more similar to tanystropheids than to *J. lehmani*, and the placement of UNIPAMPA 733 and UFRGS-PV-492-T outside Tanystropheidae may reflect the low number of phylogenetic characters present in a single bone element.

Paleobiogeographic relevance.—As a consequence of the mass extinction that marks the Permian/Triassic boundary, the continental communities at the beginning of the Triassic were remarkably depleted, and the diversity was represented only by few, mainly unspecialized tetrapod taxa (Benton 2003, 2016; Sennikov 2011; Irmis and Whiteside 2011). In archosauriforms, for example, the morphological disparity remained low and did not expand much until the late Olenekian (late Early Triassic) to early Anisian (early Middle Triassic), when erythrosuchids, Euparkeria and poposauroid pseudosuchians are recorded for the first time (Gower and Sennikov 2000; Butler et al. 2011; Ezcurra and Butler 2015). During the Early Triassic, the diversity of the terrestrial biota was gradually restored. The tetrapod fauna already documented in the Sanga do Cabral Formation is composed of procolophonoids, temnospondyls, and archosauromorphs (including the tanystropheids described herein). Like most tetrapods in the Early Triassic, ?Tanystropheidae representatives were smaller in size than their younger representatives. The Sanga do Cabral fauna provide evidence for a relatively complex community that lived in western Gondwana during the Early Triassic.

The oldest archosauromorph from South America is represented by a distal portion of a left humerus (UFRGS-PV- 0546-P) from the Guadalupian (mid-Permian) Rio do Rasto Formation (Paraná Basin) (Martinelli et al. 2016). Although the humerus does not possess any particular apomorphy of any archosauromorph group, the overall pattern of this specimen more closely resembles tanystropheids than other archosauromorphs (Martinelli et al. 2016). Although the morphology of the humerus described by Martinelli et al. (2016) indeed resembles Tanystropheidae, the fragmentary nature of this specimen precludes a categorical attribution.

Before the end of the Early Triassic, the archosauromorphs were already anatomically diversified, including semi-aquatic or entirely aquatic forms such as the Tanystropheidae (Renesto 2005; Benton 2016; Ezcurra 2016). The oldest representatives of the group traditionally called “Protorosauria” were probably terrestrials and include the enigmatic Aenigmastropheus parringtoni Ezcurra, Scheyer, and Butler, 2014 from Permian of Tanzania and the well- known Protorosaurus speneri Meyer, 1832 from middle–late Permian of Germany and England (Ezcurra 2016). According to recent contributions (Nesbitt et al. 2015; Pritchard et al. 2015; Ezcurra 2016), Tanystropheidae include *Macrocnemus bassanii* and *Tanystropheus longobardicus* from the Middle Triassic of Switzerland and Italy, *Macrocnemus fuyuanensis* Li, Zhao, and Wang, 2007 from the Middle Triassic of China (Li et al. 2007; Jiang et al. 2011*)*, *Langobardisaurus pandolfii* from the Late Triassic of Italy and Austria (Renesto and Dalla

Vecchia 2007; Saller et al. 2013), *Tanytrachelos ahynis* Olsen, 1979 from the Late Triassic of the USA, *Amotosaurus rotfeldensis* Fraser and Rieppel, 2006 from the Middle Triassic of Germany and *Augustaburiania* from the Early Triassic of Russia (Sennikov 2011) (Fig. 5). The earliest fossils of known Tanystropheidae (e.g., *Amotosaurus* Fraser and Rieppel, 2006) have been recovered from the northwest margin of Tethys Province, *while Jesairosaurus lehmani*, the sister-taxon to the Tanystropheidae (Ezcurra, 2016), comes from Algeria with distribution from the Olenekian to the Anisian (Jalil 1997).

According to previous paleobiogeographic scenarios (e.g., Pritchard et al. 2015; Jaquier and Scheier 2017), it is proposed that tanystropheids diversified from their Permian and Early Triassic ancestors during the Early Triassic, with an initial dispersion along the western margin of the Tethys ocean, while the dispersion to what is now North America began only sometime later, during the Middle Triassic. The record of ?Tanystropheidae indet. in South America indicates an initial dispersion in a central region of Pangaea, following to the west of Gondwana during the Early Triassic and, later, to the region that is currently North America, becoming abundant during the Middle Triassic.

The first and sparse records of Tanystropheidae dates back to the Early Triassic, and the most significant diversity peak of this clade occurs only during the Middle/Late Triassic. The presence of fossils related to this clade in Lower Triassic strata suggests that it had a substantial evolutionary history right after the mass extinction at the end of the Permian, with an initial diversification that could date to even earlier than the Triassic.

The fossils here studied significantly expands the geographical range of these organisms to the West Gondwana but is in accordance with the Early Triassic paleogeography. The arrangement of continents during that time allowed the dispersion of terrestrial animals (e.g., Ezcurra 2010), making possible a cosmopolitan distribution of several groups (Button et al. 2017).

The Sanga do Cabral Formation was deposited in a system of ephemeral, high-energy river channels in broad and extensive alluvial plains, containing a rich assemblage of terrestrial and aquatic tetrapods (Holz and Souto-Ribeiro 2000; Da-Rosa et al. 2009). The presence of amphibians indicates shorter and more humid phases and the associated growth of lakes and perennial ponds in the floodplains (Zerfass et al. 2003). Most tanystropheids were probably specialized to live in coastal environments and margins of aquatic ponds, although the considerable continental record of the clade indicate that some taxa were terrestrial. This is probably the reason why they reached a diversity peak in the Middle Triassic epicontinental

marine basin of Central Europe, with shallow banks, indented coastline, many islands, gulfs, and lagoons, as well as abundant marine biota (Sennikov 2011). It should, however, be also taken into account that the best-preserved fossils come from marine deposits of Central Europe and Eastern China, and the fragmentary record from other localities may be hiding a considerable diversity in terrestrial environments.

Conclusions

The morphology of the specimens here studied resembles more Tanystropheidae than Jesairosaurus and other archosauromorphs (see Discussion). On the other hand, phylogenetic analyses of these specimens were not able to unambiguously recover them inside Tanystropheidae (SOM 3: figs. 1, 2), what is possibly related to the scarcity of phylogenetic characters present in isolated bones. Hence, although the specimens display a combination of features typical of Tanystropheidae, we considered then as ?Tanystropheidae indet., depending on further findings to solve this question.

This study contributes to the understanding of the diversity of archosauromorphs after the Permo-Triassic extinction in western Gondwana. Considering that most representatives of Tanystropheidae are known from Middle and Upper Triassic strata, the material here described represents some of the oldest fossils that can be related to Tanystropheidae, suggesting a wide distribution of such forms during the Early Triassic. The fossil record found in the Sanga do Cabral Formation is mostly represented by isolated and fragmented bones. The lack of anatomical and phylogenetic analysis of these fossils contributes to limited knowledge on the archosauromorph diversity of this sedimentary unit and consequently about the diversification of these animals after the greatest extinction ever recorded.

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APPENDIX I

Figures

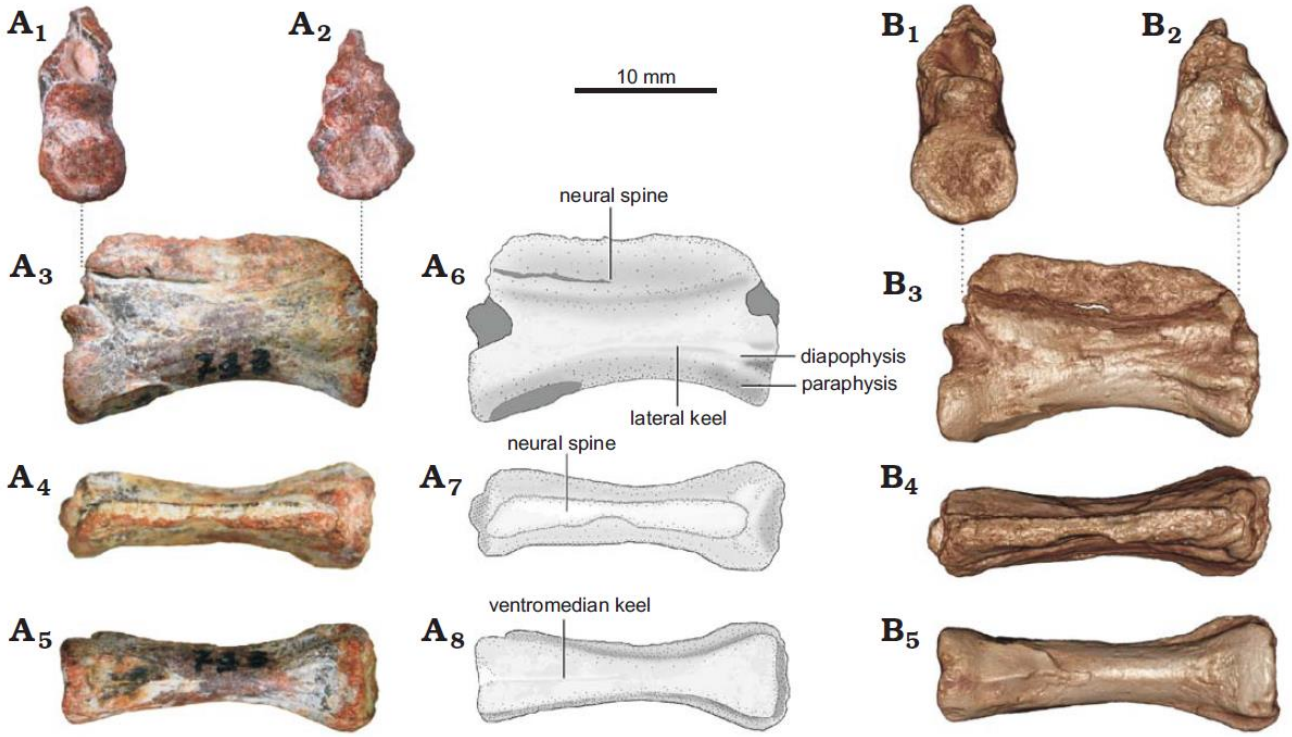


Fig. 1. Cervical vertebra (UNIPAMPA 733) of ?Tanystropheidae indet. from Sanga do Cabral Formation (Induan–early Olenekian). A. Photographs (A1–A5) and explanatory drawings (A6–A8). B. Virtual 3D reconstructions (see SOM 2). In posterior (A1, B1), anterior (A2, B2), right lateral (A3, A6, B3), dorsal (A4, A7, B4), and ventral (A5, A8, B5) views.

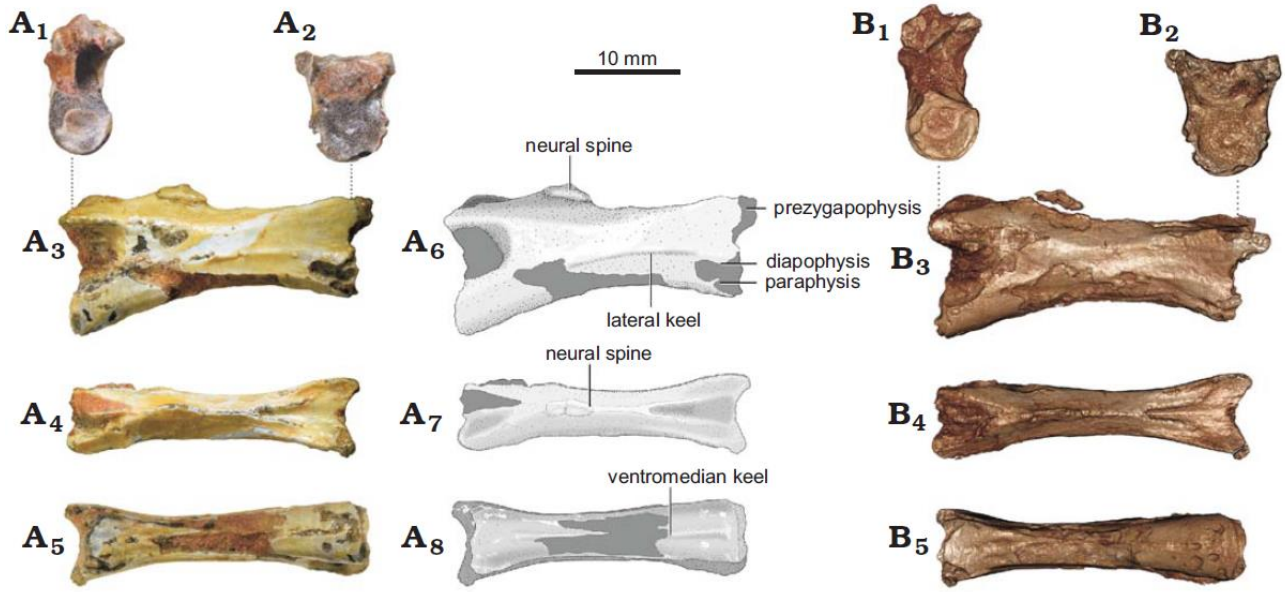


Fig. 2. Cervical vertebra (UFRGS-PV-492-T) of ?Tanystropheidae indet. from Sanga do Cabral Formation (Induan–early Olenekian). A. Photographs (A1–A5) and explanatory drawings (A6–A8). B. Virtual 3D reconstructions (see SOM 2). In posterior (A1, B1), anterior (A2, B2), right lateral (A3, A6, B3), dorsal (A4, A7, B4), and ventral (A5, A8, B5) views.

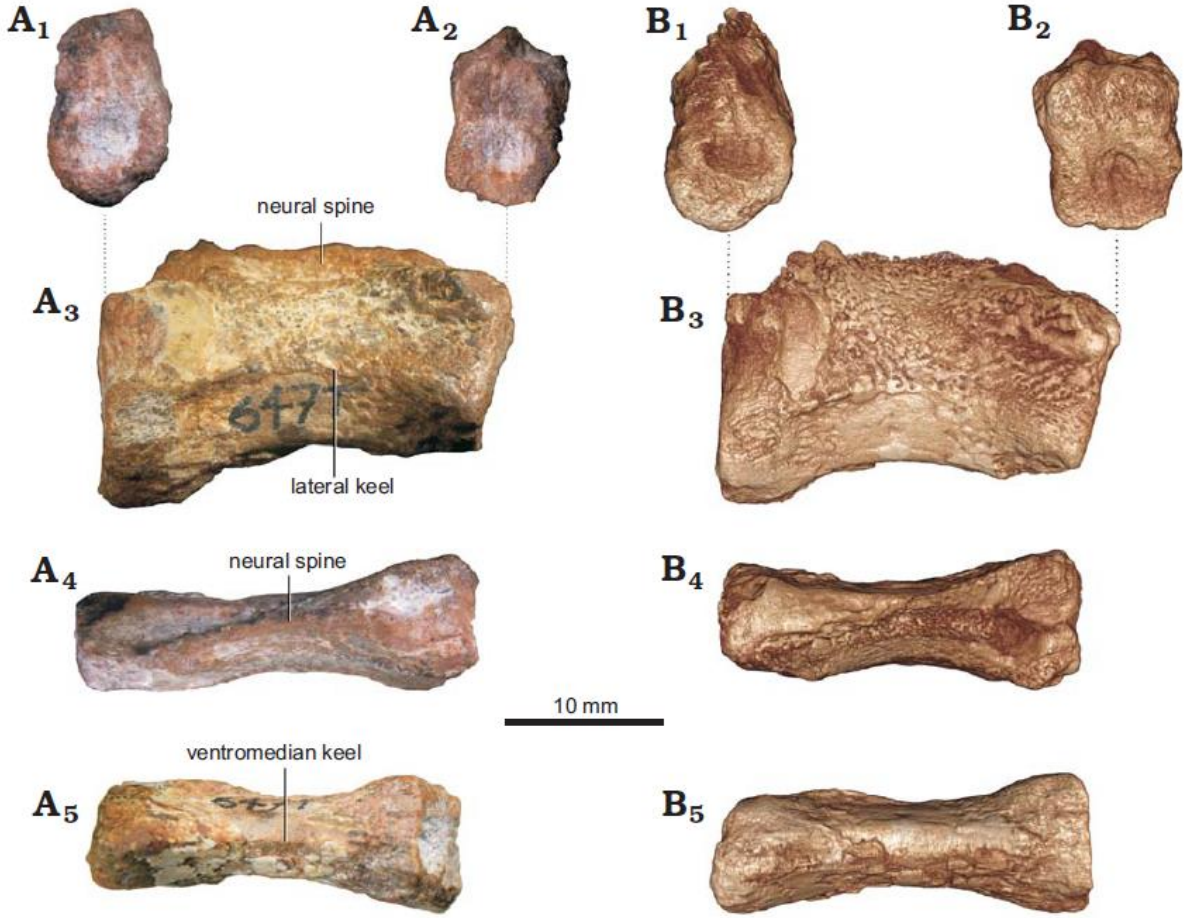


Fig. 3. Cervical vertebra (UFRGS-PV-647-T) of ?Tanystropheidae indet. from Sanga do Cabral Formation (Induan–early Olenekian). A. Photographs. B. Virtual 3D reconstructions (see SOM 2). In posterior (A1, B1), anterior (A2, B2), right lateral (A3, B3), dorsal (A4, B4), and ventral (A5, B5) views.

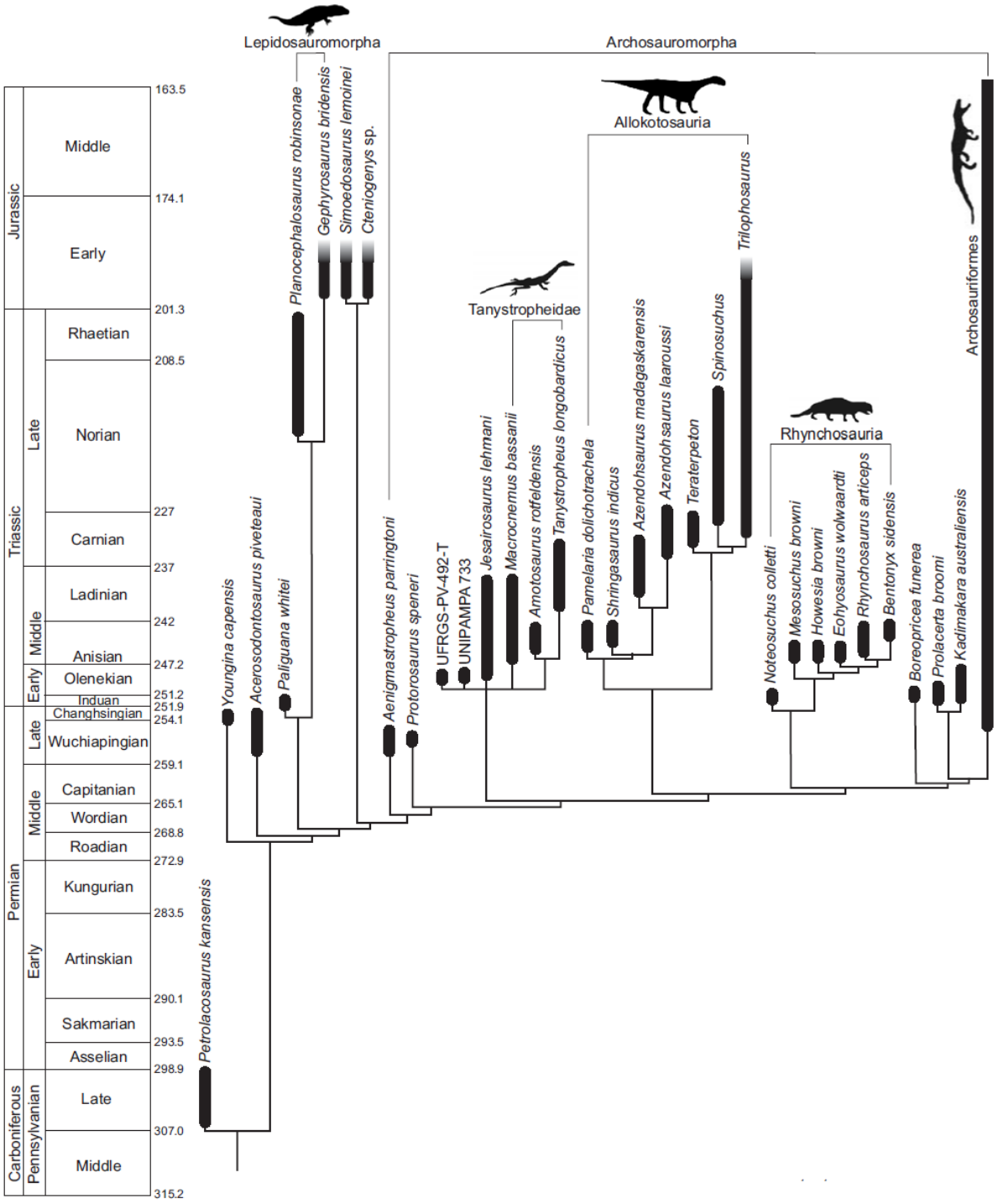


Fig. 4. Strict consensus of the analysis including UNIPAMPA 733 and UFRGS-PV- 492-T (analysis ii) based on the reduced matrix of Sengupta et al. (2017).

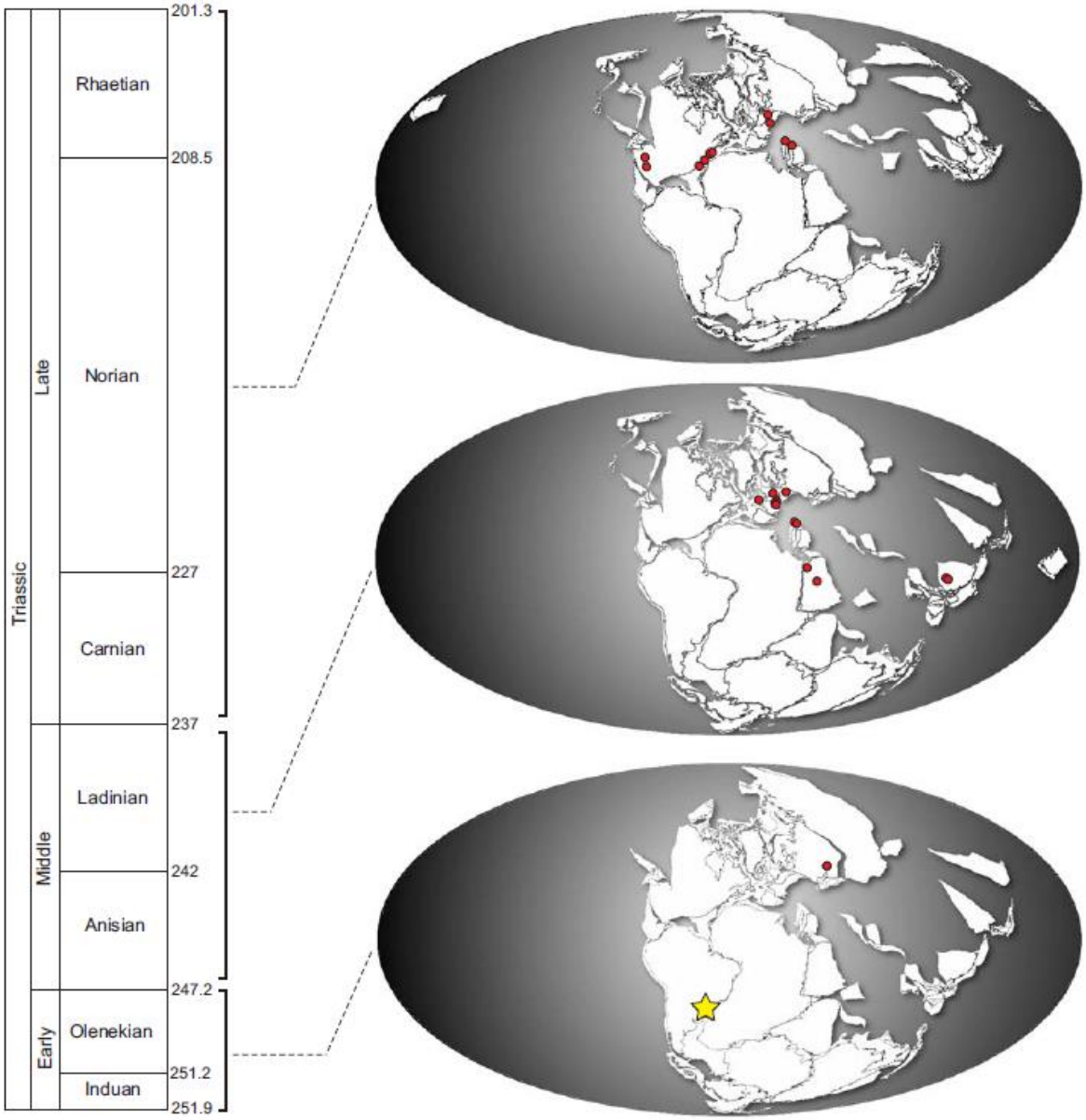


Fig. 5. Geographic distribution maps for Tanystropheidae through time (circles) and the brazilian fossil record (star) (data from the Paleobiology Database, https://paleobiodb.org/#/) and timescale from Gradstein et al. (2012).

Supplementary material

Tanystropheid archosauromorphs in the Lower Triassic of Gondwana

Supplementary Online Material

SOM 1. Taxa excluded a priori from the analysis

SOM 2. 3D reconstruction available at:

http://app.pan.pl/SOM/app63-Oliveira_etal_SOM/SOM_2.pdf

SOM 3. Results of the phylogenetic analysis

Fig. 1. Result of the phylogenetic analysis including specimen UNIPAMPA 733.

Fig. 2. Result of the phylogenetic analysis including specimen UFRGS-PV-492-T.

SOM 4. List of synapomorphies

SOM 1. Taxa excluded a priori from the analysis

The analyses conducted here are based in the reduced matrix proposed by Sengupta et al. (2017), which is a modification of Ezcurra (2016) database. We exluded 23 terminals a priori from the analyses. Excluded terminals are OUT's considered as problematic both by Ezcurra (2016) and Sengupta et al. (2017): *Eorasaurus olsoni*, *Prolacertoides jimusarensis*, *Kadimakara australiensis* holotype, *Archosaurus rossicus, "Proterosuchus fergusi*" holotype, "*Chasmatosaurus ultimus", Ankistrodon indicus, Exilisuchus tubercularis, Blomosuchus georgii*, *Vonhuenia friedrichi*, *Chasmatosuchus rossicus* combined, *Chasmatosuchus magnus*, *Gamosaurus lozovskii*, *Chasmatosuchus magnus* combined, *Chasmatosuchus vjushkovi*, SAM P41754 Long Reef, *Kalisuchus rewanensis*, *Garjania madiba* holotype, *Shansisuchus kuyeheensis, "Dongusia colorata", Uralosaurus magnus* holotype, and *Uralosaurus magnus* combined.

SOM. 3

Fig. 1. Result of the phylogenetic analysis including specimen UNIPAMPA 733.

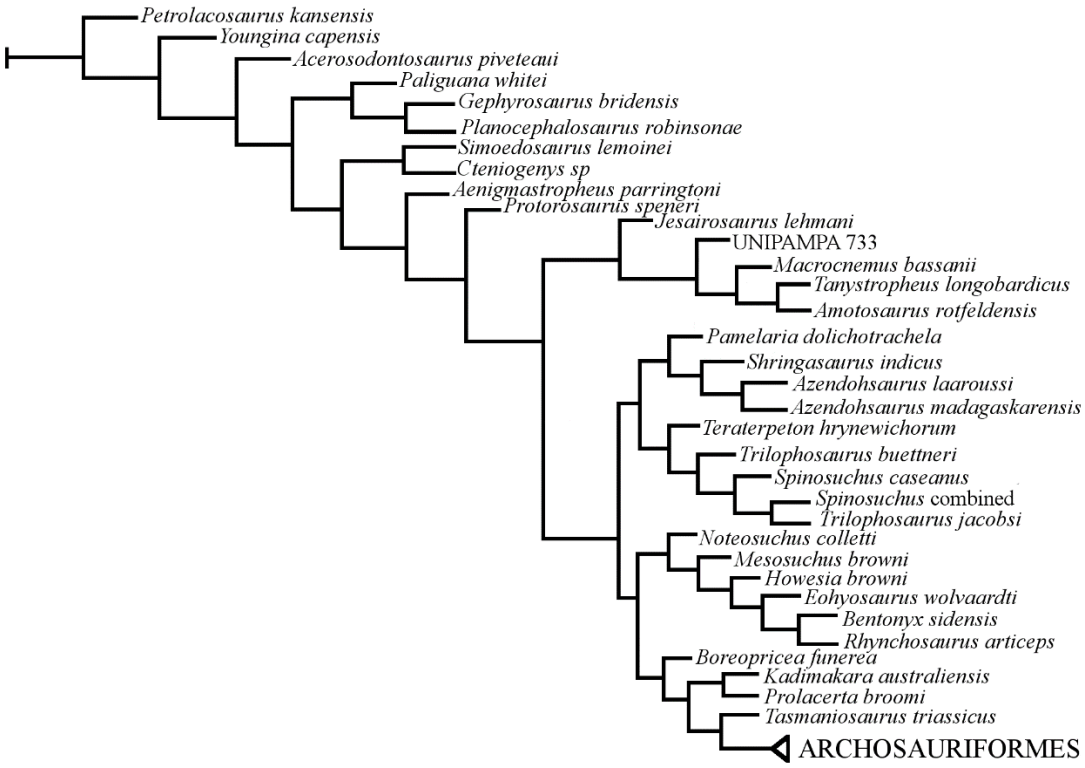
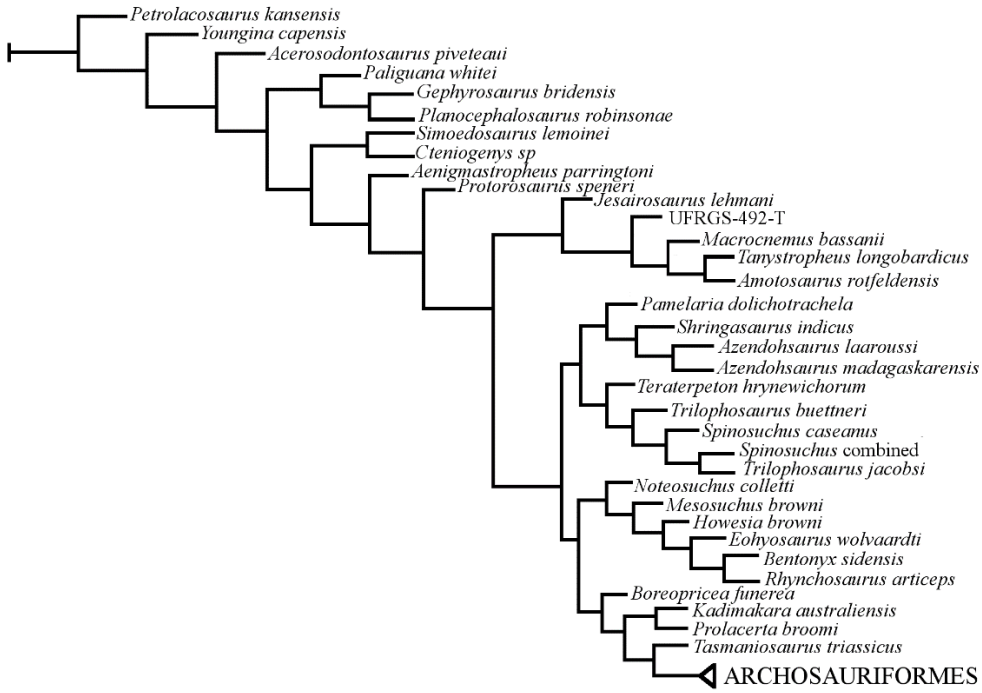


Fig. 2. Result of the phylogenetic analysis including specimen UFRGS-PV-492-T.



SOM 4. List of synapomorphies of the clade composed by the specimens UNIPAMPA 733, UFRGS-492-T, *Jesairosaurus lehmani* and Tanystropheidae recovered in the analysis with specimens UFRGS-PV-492-T and UNIPAMPA 733:

42 : 2->1
121 : 0->1
131 : 0->1
160 : 0->1
197 : 0->1
202 :1->2
340 : 0->1
407 : 0->1
425 : 1->0
446 : 2->1
558 : 0->1
564 : 0->1
565 : 0->1

2.2 ARTIGO 2

A NEW ARCHOSAUROMORPH FROM THE LOWER TRIASSIC OF SOUTH AMERICA PROVIDES INSIGHTS ON THE EARLY DIVERSIFICATION OF TANYSTROPHEIDS

Abstract

After the Permo-Triassic mass extinction, the fossil record of archosauromorphs is considerably abundant and morphologically diverse, including semi-aquatic or entirely aquatic forms (e.g., tanystropheids, doswelliids, proterochampsids), highly specialized herbivores (e.g., allokotosaurians, rhynchosaurs), and massive predators (e.g., erythrosuchids). Among those, tanystropheids gather attention for sometimes reaching extreme skeletal adaptations in response to very specialized lifestyles. Here, a new Early Triassic archosauromorph is described and phylogenetically recovered as the sister-taxon to the Tanystropheidae. The material is composed of a complete posterior limb articulated with pelvic elements and bones of the foot. The specimen was collected from the locality Bica São Tomé (Sanga do Cabral Formation, Brazil), which have already yielded a typical Early Triassic vertebrate assemblage of temnospondyls, procolophonoids and scarce archosauromorph remains. The new taxon provides refreshed insights on the early diversification of tanystropheids, as well as furnish further evidence for wide paleobiogeographic distribution, reaching the western Gondwana, already during the early evolution of this clade. Furthermore, the morphology of the new specimen is consistent of a terrestrial lifestyle, indicating this condition as plesiomorphic for Tanystropheidae.

Key words: Archosauromorpha, Tanystropheidae, Triassic, Sanga do Cabral Formation, Western Gondwana.

1 Introduction

The Archosauromorpha comprises an exceptionally diverse clade of diapsids originated during the Permian period and progressively increasing in diversity during the Mesozoic and Cenozoic eras. The most critical adaptive radiation of the Archosauromorpha took place during the aftermath of the Permo-Triassic mass extinction when the clade diversified to occupy a wide spectrum of habitats and ecological niches (NESBITT, 2011; EZCURRA, 2016). After the

Permo-Triassic crisis, the fossil record of archosauromorphs is considerably abundant and morphologically diverse, including highly specialized herbivores (rhynchosaurs), large apex predators (erythrosuchids), aquatic predators (phytosaurs), armored crocodile-like forms (aetosaurs), and gracile dinosaur precursors (NESBITT, 2011; EZCURRA, 2016; EZCURRA and BUTLER, 2018).

One of the early archosauromorph groups that better illustrates the morphological disparity of the clade is the Tanystropheidae, which comprises *Macrocnemus* Nopcsa 1930, *Tanystropheus* Wild, 1973, *Amotosaurus* Fraser and Rieppel, 2006, *Langobardisaurus* Renesto, 1994, *Tanytrachelos* Olsen, 1979 (NESBITT et al., 2015; PRITCHARD et al., 2015; EZCURRA, 2016; PRITCHARD et al. 2018). Tanystropheidae is remarkable for being one of the archosauromorph clades with most bizarre representatives (PRITCHARD et al., 2015). Members of this clade are recognizable by their long necks, composed by eight (*Macrocnemus*) to thirteen (*Tanystropheus*) moderately to excessively elongated cervical vertebrae with very long and low reduced neural spines (SENNIKOV, 2011; RENESTO and SALLER, 2018).

Tanystropheid *bauplan* is traditionally regarded as possibly of semiaquatic or even completely aquatic lifestyles (WILD, 1973; TSCHANZ, 1985; RENESTO, 2005; NOSOTTI, 2007). However, recent studies failed to support a fully aquatic habit for some tanystropheids, demonstrating that *Macrocnemus* was presumably terrestrial, whereas the lifestyle of the enigmatic *Tanystropheus*, the largest and most bizarre of all tanystropheids, remains elusive (JAQUIER et al., 2017; RENESTO and SALLER, 2018). Most tanystropheid records and related forms come from the Middle/Late Triassic of Asia, Europe and North America (RIEPPEL, 1989; PRITCHARD et al., 2015), and the clade is thus far exceptionally rare in Lower Triassic rocks (see JALIL, 1997; FRASER and RIEPPEL, 2006; SENNIKOV, 2011; PRITCHARD et al., 2015; EZCURRA, 2016). Although the fossil record of Tanystropheidae was, until recently, restricted to the Northern Hemisphere, De-Oliveira et al. (2018) described isolated cervical vertebrae that share synapomorphies with this clade from the Induan/Olenekian Sanga do Cabral Formation, Brazil. Besides, a humeral fragment compatible with Tanystropheidae was reported from the Upper Permian strata of Rio do Rasto Formation, Brazil (MARTINELLI et al., 2016).

Based upon its tetrapod content, the Sanga do Cabral Formation is regarded as Lower Triassic, being correlated to the Katberg Formation of South African Karoo (*Lystrosaurus* Assemblage Zone) (CISNEROS, 2008; DIAS-DA-SILVA et al., 2017). Although recent collection efforts substantially increased the number of archosauromorph specimens recovered

from the Sanga do Cabral Formation (e.g. DA-ROSA et al., 2009; PINHEIRO et al., 2016; DE-OLIVEIRA et al., 2018), the diversity of this clade in South American Lower Triassic is still poor when compared to coeval deposits from South Africa, which have yielded the rhynchosaur *Noteosuchus* Broom, 1925, besides the well-known *Prolacerta* Parrington, 1935 and the archosauriform *Proterosuchus* Broom, 1903 (BOTHA and SMITH, 2006). Nevertheless, Sanga do Cabral Formation is the oldest Triassic sedimentary unit yielding fossil vertebrates from South America and provides a unique opportunity to study the biotic recovery after the P/T boundary.

Here, we describe a new archosauromorph species that is phylogenetically positioned as the sister-taxon to Tanystropheidae. The specimen was found in the Sanga do Cabral Formation, Early Triassic of Brazil and provides insights on the hidden diversity of archosauromorphs from the western Gondwana after the Permo-Triassic global crisis. Until recently, only few remains assigned to Archosauromorpha indet. were known from Sanga do Cabral Formation. Now, at least two independent lineages were reported for this sedimentary unit (DA-ROSA et al., 2009; PINHEIRO et al., 2016; DE-OLIVEIRA et al., 2018 and this work). Although rare, these fossils demonstrate that archosauromorphs were already diversified in the Early Triassic of western Gondwana, while the new taxon provides insights on the early distribution and lifestyle of tanystropheid-like archosauromorphs.

2 Methodology

2.1 Material

The UFSM11471 study material consists of a complete posterior limb with articulated femur, tibia, and fibula, and whole. In this material are also preserved portions of the pelvic girdle, sacral vertebra and caudal vertebrae.

2.2 Phylogenetic analysis

The phylogenetic analyses conducted here aim to access the affinities of UFSM 11471 with relation to other early archosauromorphs. Experiments were performed by the inclusion of UFSM 11471 as an operational taxonomic unit (OTU) in the data matrix of Pritchard et al. (2018). This data matrix was chosen for including greater representativeness of tanystropheid

as terminal taxa than other datasets. The analysis protocol consisted of heuristic searches of 1000 replications using random addition sequences followed by the Tree Bisection Reconnection (TBR) algorithm, retaining ten trees by replication. The database of Pritchard et al. (2018) does not include *Jesairosaurus lehmani* Jalil, 1997 as an OTU. The phylogenetic position of this species, formerly regarded as a member of "Prolacertiformes" has not been tested by recent quantitative analyses until the work of Ezcurra (2016). This latter recovered *J. lehmani* as the sister-taxon to the Tanystropheidae, even though it differs from tanystropheids in several decisive features. As first-hand assessment of *J. lehmani* was not possible, we chose not to include this taxon as an OTU in the analysis conducted here. After estimation of Bremer supports (also using TNT), a search for suboptimal trees with one extra step was conducted. This second search aimed to verify the percentage of recovery, in suboptimal trees, of specific nodes with low Bremer supports.

3 Systematic Paleontology

Diapsida Osborn, 1903 (*sensu* Laurin 1991)

Archosauromorpha Huene, 1946 (*sensu* Gauthier et al. 1988)

Gen. et sp. nov.

3.1 Holotype

UFSM 11471 – Partially articulated hind limb associated with axial elements, composed by femur articulated to the tibia, fibula, pelvic girdle bones, sacral and caudal vertebrae, as well as an almost complete pes. The specimen is permanently housed at the paleontological collection the Laboratório de Paleobiologia e Estratigrafia of the UFSM, Santa Maria, Rio Grande do Sul, Brazil.

3.2 Diagnosis

UFSM 11471 differs from all known archosauromorphs based on a unique combination of characters: Second sacral vertebra rib elongated, with a robust articular surface and bifurcated distally; transverse processes of the caudal vertebrae inclined posterodorsally; strongly sigmoidal femur; tibia and fibula longer than femur; metatarsals increase in size from the first

to the fourth toe; fifth metatarsal short, with a proximal hook-shaped end; presence of a calcaneal tuber.

3.3 Locality and horizon

UFSM 11471 was collected at the locality known as Bica São Tomé, Sanga do Cabral Formation, Paraná Basin, São Francisco de Assis municipality, Rio Grande do Sul State, Southern Brazil (29°36′ 56″ S, 55°03′ 10″ W) (DA-ROSA et al., 2009). UFSM 11471 was found in one of the five outcrops that compose the Bica São Tomé (outcrop 5 of DA-ROSA et al., 2009). The Induan-Olenekian age (251-247 Ma) (COHEN et al., 2013) is inferred for this formation based on the presence of the parareptile *Procolophon trigoniceps* Owen, 1876, and comparisons with the *Lystrosaurus* Assemblage Zone, South Africa (DIAS-DA-SILVA et al., 2006; BOTHA and SMITH, 2006; DA-ROSA et al., 2009; DIAS-DA-SILVA et al., 2017). UFSM 11471 represents the most complete postcranial skeleton so far recovered from Sanga do Cabral Formation, as fossils from this unit are often found as fragmentary cranial and postcranial remains, with rare occurrences of associated elements (Figure 1).

4 Comparative Description

Specimen UFSM 11471 is composed of an almost complete hindlimb associated with pelvic girdle bones and partially articulated sacral and caudal vertebrae. Although some elements show signs of compression (e.g. femur, tibia), all bones are close to natural position. The exception is a slight displacement of some tarsal elements and the lack of distal phalanges in most digits. As discussed below, the specimen is morphologically compatible with basal archosauromorphs, especially with Tanystropheidae.

4.1 Vertebrae

The specimen UFSM 11471 preserves a complete second sacral vertebra associated to caudal vertebrae I-III (Figure 2). The first sacral is present as scattered fragments articulated to sacral II. This latter is well preserved and articulated to the ilium. The pleurapophysis of the second sacral vertebra is bifurcated distally, with a posterior process ending in a pointed tip.

The distal end of the pleurapophysis is expanded and presents a wide triangular surface (as observed in dorsal view) that contacts the ilium.

The elongated and distally bifurcated pleurapophysis of the second sacral vertebra resembles the condition observed in tanystropheids such as *Macrocnemus* (GREGORY, 1945; NOSOTTI, 2007). This condition, however, is also present in *Trilophosaurus buettneri* Case, 1928 and *Prolacerta*, as well as in some extant lizards (HOFFSTETTER and GASC, 1969; RIEPPEL, 1989; NOSOTTI, 2007; PRITCHARD et al., 2015). *Augustaburiania vatagini* shows an alternative condition, where the sacral vertebrae present small sacral ribs that deviate laterally in the middle of the centrum (SENNIKOV, 2011). *Tanystropheus longobardicus*, the best-known tanystropheid, has no distally bifurcated sacral ribs, while *Amotosaurus rotfeldensis* presents the bifurcation of the second sacral rib more anteroposteriorly expanded than the new specimen. UFSM 11471 presents the posterior process of the second sacral rib distally sharp, ending in a pointed tip, while in *Prolacerta* this process is terminally blunt (PRITCHARD et al., 2018).

The anterior most caudal vertebra has the same anteroposterior length as the second sacral and shows prominent transverse processes, projecting distinctly laterally to the pleurapophysis of the sacral vertebrae and to the dorsal part of the ilium. In dorsal view, the transverse processes are posterolaterally directed. Although the transverse processes of the second caudal vertebra are broken, they reveal to be slightly longer than those borne by the first caudal vertebra.

Distinct transverse processes are also observed on the anterior caudal vertebrae of *Tanystropheus* and *Langobardisaurus* (WILD, 1973; SALLER et al., 2013). *Tanytrachelos* does not present a bifurcate second sacral rib and, together with *Jesairosaurus lehmani*, presents the transverse processes of the caudal vertebrae slightly inclined posterolaterally.

4.2 Pelvic Girdle

The pelvic girdle is fragmented, with its bones only partially preserved and exposed, being relatively small in size when compared to the large hindlimbs. The ilium is discernible in dorsolateral view, and it is not clear whether the pubis and ischium are preserved. The ilium is expanded into a dorsal lamina that articulates with the large pleurapophysis of the sacral

vertebra. Anteriorly to this, the ilium presents a strongly projected process. The dorsal margin of the iliac lamina is predominantly straight, with horizontal orientation. The supra-acetabular surface is thickened, and the lateral surface of the acetabulum is roughly circular. The posterior process of the ilium is strongly developed, extending posteriorly to the acetabulum.

The pelvic girdles of *Prolacerta* and tanystropheids are similar to that of UFSM 11471 in the presence of a posterodorsally directed triangular blade on the ilium. Although the iliac lamina of UFSM 11471 is partially broken, it is possible to discern a short pre-acetabular process similar to that observed in *Macrocnemus bassanii* (specimen T 2472). This is a robust process in this specimen, being also present (albeit less pronounced) in *Tanystropheus longobardicus* (specimen MSNM BES SC 1018). The opposite is observed in *Prolacerta*, in which the anterior margin of the ilium is convex, the same occurring in *Jesairosaurus lehmani* (GOW, 1975; RIEPPEL, 1989; JALIL, 1997; NOSOTTI, 2007; SPIEKMAN, 2018).

4.3 Femur

With a total size of 64.85 mm, the femur is slightly shorter than the tibia and fibula. The proximal part of the femur is poorly preserved and strongly compressed (Figure 3). The width of the distal part of the femur measures 16,55 mm and the proximal part 15.44 mm. It is a gracile bone, being the ratio between the transversal width of the distal end and the total length of the bone 3,91. Despite compression due to preservation, UFSM 11471 femur is strongly sigmoid. It differs from the specimen GR-304 described by Pritchard et al. (2015) because the latter presents a nearly straight format, tuning distally from the proximal head.

Tanystropheus longobardicus (MSNM BES SC 265) and *Tanytrachelos* (YPM 7622) present a more subtle femur curvature when compared to UFSM 11471 (OLSEN, 1979; NOSOTTI, 2007; PRITCHARD et al., 2015; NESBITT et al., 2000; EZCURRA, 2016). In this respect, UFSM 11471 resembles *Macrocnemus bassanii* (T 4355) and *Augustaburiania*, both of which present gracile and strongly sigmoidal femora (RIEPPEL, 1989; SENNIKOV, 2011).

Probably as a consequence of poor preservation, the proximal surface of the femur has a quadrangular outline. The femoral head is not distinctly displaced from the remaining of the bone, being confluent with the shaft. The dorsolateral margin of the proximal portion of the femur is smooth and featureless, as is the transition between the femoral head and diaphysis. The femoral head is weakly expanded in tanystropheids (e.g., *Tanytrachelos ahynis*, AMNH FARB 7206, GR 301). In other basal archosauromorphs such as *Azendohsaurus*

madagaskarensis Flynn et al. 2010 (UA 7-20-99-653), the proximal end is modestly expanded relative to the midshaft, as it is in some rhynchosaurs and early archosauriforms (e.g., *Proterosuchus alexanderi* Hoffman, 1965, NMQR 1484; *Erythrosuchus africanus* Gower, 1996 NHMUK 3592) (NESBITT et al., 2015). The internal trochanter is present as a ridge-shaped process that defines a relatively wide intertrochanteric fossa, converging to the proximal end. The internal trochanter is continuous with the proximal articular surface. The transition from the plesiomorphic condition of a proximal trochanter including an inner trochanter and a posterior trochanter (e.g. *Erythrosuchus africanus*; *Trilophosaurus buettneri*) to a large fourth trochanter and a larger trochanter (e.g. *Alligator*, Hutchinson, 2001; dinosaurs), occurs within archosauriforms (NESBITT et al., 2009; NESBITT, 2011; PRITCHARD et al., 2015). As so, the presence of an internal trochanter allied to the absence of a fourth trochanter strongly supports that UFSM 11471 belongs to a clade outside Archosauriformes. A well-developed internal trochanter projecting from the proximal end of the femur is present in early archosauromorphs, including tanystropheids (e.g. *Macrocnemus bassanii* and *Tanystropheus longobardicus*). An internal trochanter that does not reach the proximal surface of the femur is evident in rhynchosaurs and some archosauriforms, such as *Proterosuchus fergusi* Broom, 1903 and *Erythrosuchus africanus* (CRUICKSHANK, 1972; GOWER, 2003; PRITCHARD et al., 2015; EZCURRA, 2016).

Despite the strong compression of UFSM 11471 femur, the diameter of its diaphysis appears to be constant and slightly widened distally. Distally expanded femora (although in a lesser degree) occur in *Prolacerta broomi* (BP/1/2676) and tanystropheids (e.g. *Tanystropheus*, WILD, 1973; GR 301, PRITCHARD et al., 2015).

The distal end of the femur is marked by two delineated, unequal distal condyles, in which the lateral condyle is larger than the medial one. These condyles are distinctly expanded beyond the circumference of the femoral shaft. In distal view, the shape of the fibular condyle presents a slightly triangular lateral surface.

4.4 Tibia and Fibula

The poor preservation the tibia hiders a proper evaluation of bone morphology. Tibia and fibula present a length about 12% greater than the femur. The length of the femur relative to the tibia/fibula has been considered as an important feature in the phylogeny of basal archosaurs (see EZCURRA, 2016). Among those, the tibia is longer than the femur in basal pterosaurs (e.g.

Preondactylus Wild, 1984, *Lagerpeton* Romer, 1971, *Dromomeron* Irmis et al. 2007, *Marasuchus* Sereno and Arcucci, 1994, *Pseudolagosuchus* Arcucci, 1987, basal ornithischians, *Eoraptor* Sereno et al. 1993 and small basal theropods (NESBITT, 2011). Within non-archosauriforms, this characteristic is prominent among some tanystropheids (e.g. *Macrocnemus*). Compared to the forelimbs, the hindlimbs of *Macrocnemus* are strongly elongated (RIEPPEL, 1989), what is mainly acquired by an elongation of the tibia/fibula.

Besides, a short femur relative to the tibia and fibula is also displayed by *Prolacerta* (AMNH 9502, BP / 1/2676) (GOW, 1975; COLBERT, 1987). Although also having a proportionally short femur, *Prolacerta* specimen described by Spiekman (2018) (UWBM 95529) shows a smaller ratio when compared to some tanystropheids (e.g. *Macrocnemus*) and UFSM 11471. Specimen UWBM 95529 has a femur measuring 72.4 mm, while the tibia has 69.3 mm in length.

Tibial and fibular length at least 20% larger than the femur is one of the synapomorphies that compose the diagnosis of *Macrocnemus* (PRITCHARD et al., 2015). Some differences in this respect are reported by Li et al. (2007) and Fraser and Furrer (2013) between *Macrocnemus bassanii*, *Macrocnemus fuyuanensis* and *Macrocnemus obristi*. Some authors even suggest that these differences in proportions may be related to sexual dimorphism (JAQUIER et al., 2017).

Much thicker than the fibula, the tibia is still embedded in the rock matrix, with its distal end articulated with mesopodial elements. The distal end of the tibia is scattered, what may be a result of pre-burial fracturing. Although the tibia is severely damaged, it is possible to observe a small groove in the lateral surface of its distal end, a feature only observed in some dinosaurs and proterochampsids (e.g. *Chanaresuchus* Reig, 1971, *Tropidosuchus* Arcucci, 1990) (NESBITT, 2011). In the context of non-archosauriforms, thus, this may potentially be an autapomorphy of the new taxon described herein. However, as this character is possibly an artifact of poor preservation, it should be regarded with caution. The proximal end of the fibula is fragmented, and this bone is slightly longer than the femur (73 mm). Its proximal end is compressed in proximal view, being rounded and symmetrical in lateral view. The area of insertion of the *M. iliofibularis* is evident by the presence of a distinct but low tubercle located near the proximal portion of the bone. The distal portion in lateral view is slightly asymmetrical.

4.5 Pes

The metatarsals and phalanges are articulated and arranged more or less in natural position, with only a slight displacement of some elements. UFSM 11471 preserves the metatarsals I-V, though the fifth digit lacks its phalanges. The metatarsals increase in length from the first to the fourth digit, where the metatarsal IV is distinctly larger than the III (Figure 4).

The fourth digit of non-archosauriform archosauromorphs pes (e.g., rhynchosaurs, *Trilophosaurus*, *Prolacerta*) is the longest, whereas digit 3 is the longest in *Euparkeria* Broom, 1913 (UMCZ T692) and all the archosaurs in which this character can be accessed (GAUTHIER, 1984; NESBITT, 2011; EZCURRA, 2016). The metatarsals increase in size from the first to the fourth toe in *Macrocnemus bassanii* [T 2477; A III/208; T 2472], *Amotosaurus* [SMNS 54810], *Prolacerta* and *Langobardisaurus* (COLBERT, 1987; RIEPPEL, 1989; FRASER and RIEPPEL, 2006; SALLER et al., 2013). The metatarsus of *Tanystropheus* is asymmetrical, although not in the same manner as *Macrocnemus* and *Langobardisaurus* because, in *Tanystropheus*, the longest metatarsal is the third one. *Tanytrachelos* [YPM 7540] apparently has a similar metatarsal configuration (OLSEN, 1979; NOSOTTI, 2007).

The fifth metatarsal is short and has a proximal hook-shaped end: its proximal process is abruptly flexed and, as a result, the metatarsal acquires an L-shape in ventral view. This morphology is observed in *Macrocnemus bassanii*, allokotosaurs (e.g. *Pamelaria dolichotrachela* Sen, 2003, *Azendohsaurus madagaskarensis*), a few basal rhynchosaurs (e.g. *Noteosuchus colletti* Watson, 1912), *Boreopricea funerea* Tatarinov, 1978, *Prolacerta broomi* and some archosauriforms (e.g. *Proterosuchus fergusi* Broom, 1903) (NESBITT, 2011; EZCURRA, 2016). Among tanystropheids, metatarsal V morphology of UFSM 11471 resembles the condition displayed by *Macrocnemus* [PIMUZ T AIII / 208] (RIEPPEL, 1989) and differs from *Langobardisaurus* and *Tanystropheus* [MSNM V 3730] (NOSOTTI, 2007), these presenting a less pronounced hook-shaped element. The metatarsals diverge from the tarsus distally but overlap proximally. In digits I and II the distal phalanges are not preserved and the digits III and IV present two middle and one distal phalanges. The lack of some distal phalanges prevents an exact account of the phalangeal formula.

Six tarsals are preserved in UFSM 11471, including the proximal tarsals (astragalus and calcaneum), and four ossifications identified here as the distal tarsal elements I, III, IV, and the centrale (Figure 5). Except by the centrale, these elements are displaced laterally towards the calcaneum, distal to the tibia and proximal to the metatarsals I and II. A fifth distal tarsal is lacking. Of the distal elements, the fourth and the centrale are the largest. Distal tarsal IV is

located between the astragalus and calcaneus, proximal to the metatarsals III and IV, whereas the distal tarsals III and I are positioned medial to the centrale.

Four distal tarsals occur in most early archosauromorphs (e.g., *Mesosuchus browni* Watson, 1912, SAM 7416; *Protorosaurus speneri* Meyer, 1832; *Trilophosaurus buettneri*, TMM 31025- 140) (NESBITT et al., 2015). *Macrocnemus bassanii* presents four distal tarsals, one being the centrale. However, only three distal tarsals occur in *Macrocnemus fuyuanensis* and *Amotosaurus*, and only two in *Tanystropheus longobardicus* (MCSN BES SC 1018; MCSN V 3730) (RIEPPEL, 1989; GOTTMANN-QUESADA and SANDER, 2009; JIANG et al., 2011; NESBITT et al., 2015). *Prolacerta broomi* [BP/1 2676] (GOW, 1975) was described as having a centrale in close contact with the mesial surface of the astragalus, besides four distal elements, of which the first three are small and featureless. Colbert (1987) argued that the centrale is absent in AMNH 9502 in contrast to Gow's description for *Prolacerta* (1975). However, according to Colbert (1987), this bone had likely been lost during fossilization. *Prolacerta* specimen UWBM 95529 (SPIEKMAN, 2018) preserves central bone, in agreement with that initially presented by Gow (1975) being, therefore, similar to what is observed in UFSM 11471. No centrale bones appear to be present in *Tanystropheus longobardicus* (MCSN V 3730), although the distal tibial articular surface is wide. In *Tanystropheus*, the astragalar body and centrale thus are possibly indistinguishably fused (NESBITT et al., 2015). The presence of a cartilaginous centrale in *Tanystropheus* also remains highly conjectural (NOSOTTI, 2007). *Langobardisaurus* and *Macrocnemus* have the area distal and/or medial to the astragalus occupied by an ossified centrale (NOSOTTI, 2007). According to Rieppel (1989), in *Macrocnemus*, the tibia articulates with the astragalus, bearing a distinct articular facet on its medial side. This facet forms the proximal part of an embayment completed by the centrale and distal tarsal I, within which the tibia is accommodated during the stride phase when maximal propulsive force is applied.

In UFSM 11471, the astragalus and calcaneum are not fused and lack a perforating foramen. Contrary to the condition of *Prolacerta* (SPIEKMAN, 2018), it is possible to observe the presence of a perforating foramen between the astragalus and calcaneum in UWBM 95529. No perforating foramen is present in *Langobardisaurus* (MCSNB 2883, MCSNB 4870, MFSN 1921, MFSN 26829) or *Tanytrachelos* (VMNH 120015, YPM 8600), although this absence may be a consequence of small size, or even an artifact of preservation (RENESTO and DALLA VECHIA, 2007; PRITCHARD et al., 2015). Rieppel et al. (2010) consider the foramen absent in *Tanystropheus cf. Ta. longobardicus*. A larger perforating foramen is noted in *M. bassanii*

and *Amotosaurus* (RIEPPEL, 1989; FRASER and RIEPPEL, 2006; PRITCHARD et al., 2015). The tibial articulation surface of the calcaneum is slightly rounded, and the articular surface to distal tarsal IV is concave. The articular surface for the astragalus appears to be continuous with the articulation of the distal tarsals.

The calcaneum is quadrangular in lateral view, being wider in its anteroposterior axis than it is proximo-distally, becoming L-shaped distal to the fibula. The proximal surface of the calcaneum is marked by the presence of a rough tuberosity, the calcaneal tuber. In proximal view, the calcaneal tuber is square-shaped, longer proximodistally than dorsoventrally, and the distal part presents a curvature. The tuber longer (proximodistally) than tall (dorsoventrally), are similar proportions seen in most early archosauromorphs (e.g., *Tanytrachelos ahynis*, GR 306; *Trilophosaurus buettneri*, TMM 31025-140; *Azendohsaurus*, FMNH PR 2776) (NESBITT et al., 2015), resembling to what is presented in UFSM 11471. There is a notch between the main body of the calcaneus and the tuber. Among tanystropheids, the presence of a calcaneal tuber is only observed in *Tanytrachelos ahynis* Olsen, 1979, although it is a typical characteristic of several clades within Archosauriformes. According to Nesbitt et al. (2015) the fibular facet continuous with the lateral tuber is present in some *Trilophosaurus* (AMNH FARB 30836), *Proterosuchus alexanderi* Hoffman, 1965 (MCZ 4301), and *Erythrosuchus africanus* (NHMUK R3592). Pritchard et al. (2015) assigned specimen GR 306 to *Tanytrachelos* based on features of the calcaneus, such as the strongly laterally expanded distal end and the distal curvature of the calcaneal tuber. The calcaneal tuber of GR 306 is still larger than that observed in other taxa. This structure is well evident in UFSM 11471 and compatible with that observed in GR 306, as the proximal surface of the calcaneum is marked by the development of its lateral margin, characterizing a rough tuberosity. Nesbitt et al. (2015) noted a similar condition to *Tanytrachelos ahynis* (GR 306) in *Azendohsaurus* (FMNH PR 2776).

5 Phylogenetic analysis

The analysis recovered only one MPT with 1120 steps, consistency index 0.321 and retention index 0.642. This tree recovers UFSM 11471 as sister taxa of Tanystropheidae (Figure 6). According to recent phylogenetic studies, Tanystropheidae is a node-based clade defined as the most recent common ancestor of *Macrocnemus, Tanystropheus,* and *Langobardisaurus* and all its descendants (DILKES, 1998). UFSM 11471 exhibits some characters in similar

conditions to what is expected for Tanystropheidae, as the pleurapophysis of the second sacral vertebra distally bifurcated (character-state 131:0→1), tibia and fibula with a total length slightly larger than the femur (character-state 516:0→2, EZCURRA, 2016) the fifth metatarsal in hook shape (character-state 197:0→1). The sister taxon relationship between UFSM 11471 and Tanystropheidae is supported by the presence of the posterior process of the second sacral rib sharp distally, and the transverse process of the anterior caudal vertebrae angled posterolaterally. In addition, the new specimen presents some features only found in more specialized members within Tanystropheidae, such as the presence of a well-developed calcaneal tuber with a rough lateral margin.

Albeit Bremer support for the clade (UFSM 11471 + Tanystropheidae) is low (=1), this particular node was present in 66% of the 36 sub-optimal trees with one extra step recovered by the second analysis.

6 Discussion

6.1 Taxonomic remarks

The specimen described herein is morphologically compatible with non-archosauriform archosauromorphs (e.g. morphology of the vertebrae, femur and digits), being a close relationship with Tanystropheidae supported by several characters (see above).

Recent phylogenetic analyzes recovered Tanystropheids and *Jesairosaurus lehmani* more closely related to each other than to other archosauromorphs (EZCURRA, 2016). The matrix of Pritchard et al. (2018), used in this work, does not include *Jesairosaurus lehmani* (see above). Despite that UFSM 11471 differs from *J. lehmani* in several characters. According to Ezcurra (2016), it is not possible to observe the presence of an internal trochanter or fourth trochanter in *J. lehmani*. Besides, the calcaneum, although poorly preserved, lacks a calcaneal tuber (present in UFSM 11471), and the distal end of the femur does not taper distally in dorsal view.

Among the basal archosauromorphs, tibia/fibula longer than the femur is observed in Tanystropheidae and *Prolacerta*. Although *Prolacerta* is one of the best represented early archosauromorphs, its postcranial morphology remains poorly known, and most studies have focused on cranial anatomy. Its postcranial anatomy, however, was discussed by Gow (1975), Colbert (1987) and, more recently, Spiekman (2018). Despite the overall similarity between

UFSM 11471, Tanystropheidae (e.g. *Macrocnemus*), and *Prolacerta*, the specimen described here is more consistent with Tanystropheidae than to *Prolacerta*. A foramen perforating the astragalus/calcaneum was present in *Prolacerta* (SPIEKMAN, 2018), while UFSM 11471 does not exhibit this feature. Good preservation of proximal tarsals in UFSM 1141 suggests that the absence of this foramen is not a preservation bias. Moreover, the posterior process of the bifurcated second sacral rib of UFSM 11471 is distally sharp, while in *Prolacerta* this process is described as blunt (PRITCHARD et al., 2018).

Teyujagua paradoxa Pinheiro et al. 2016 lacks comparable elements with UFSM 11471, this species was recovered as the sister taxon to the Archosauriforms, and is thus more closely related to proterosuchids than is *Prolacerta* and, consequently, UFSM 11471 (PINHEIRO et al., 2016; SPIEKMAN, 2018).

6.2 Biogeographical implications

As a result of the Permian–Triassic crisis, earliest Triassic continental communities were extremely impoverished, including few small and unspecialized tetrapod taxa (SAHNEY and BENTON, 2008; BOTHA and SMITH, 2006; SENNIKOV, 2011). Adaptive radiation of early archosauromorphs and, then, tanystropheids, occurred during the Early Triassic. Although the most abundant and the better-known records of this group belong to the Middle Triassic, (Ladinian) of Switzerland and Italy, this group also have rare records in Lower Triassic strata. *Amotosaurus rotfeldensis* and *Augustaburiania vatagini* are thus far the earliest nominal taxa of Tanystropheidae, being known from non-marine rocks of Germany and Russia (FRASER and RIEPPEL, 2006; SENNIKOV, 2011; PRITCHARD et al., 2015).

Of all the genera mentioned above, only *Macrocnemus* and *Tanystropheus* are known to occur from both the western and eastern Tethyan province, with the specimens of *M. fuyuanensis* and *T. longobardicus* from Europe being slightly older (Late Anisian to early Ladinian) than the Chinese specimens (Ladinian) (JAQUIER et al., 2017).

Jaquier et al. (2017) and Pritchard et al. (2015) proposed that during the Late Early Triassic, tanystropheids reptiles first evolved from their Late Permian and Early Triassic ancestors in central Pangea and dispersed afterward along the western and eastern margins of the Tethys Ocean during the Middle Triassic.

The specimen described here, in addition to the specimens reported by De-Oliveira et

al. (2018), are the only materials related to the clade thus far recorded in South America. The recovery of UFSM 11471 as the sister-taxa to Tanystropheidae implies the diversification of tanystropheid-related forms in South America during the Early Triassic. Furthermore, it corroborates an early diversification of the group in central Pangea, possibly with a Gondwanan origin, reaching cosmopolitan distribution already during the early Mesozoic.

The transition of tanystropheids to semiaquatic and, then, aquatic and even marine mode of life along the Triassic was probably connected with the diversification of the terrestrial biota, niche packing, increasing competitive pressure within continental communities, and diversification of predators, such as early archosaurs (SENNIKOV, 2011). UFSM 11471 may represent one of the oldest Tanystropheidae-related archosauromorphs to date. The fact that the new specimen was collected in a depositional environment of ephemeral fluvial systems in an arid landscape, quite distinct from the marine deposits where tanystropheids are usually found, attests the ecological plasticity of the clade.

6.3 Tanystropheidae ecology and the lifestyle of UFSM 11471

Tanystropheidae is a clade mainly characterized by a long neck formed by elongate cervical vertebrae with low neural spines (LI et al., 2007; NOSOTTI, 2007; SENNIKOV, 2011; PRITCHARD et al., 2015). Some tanystropheids possibly had terrestrial or semi-aquatic habits, while more specialized forms may have been fully aquatic. Tanystropheid lifestyle, however, is still a matter of controversy. *Macrocnemus* and *Langobardisaurus* were supposedly terrestrial (RIEPPEL, 1989; RENESTO et al., 2002; RENESTO and SALLER, 2018). The association of *Tanytrachelos ahynis* with numerous fossil fishes, a lacustrine insect assemblage, abundant branchiopods, and phyllocarids, suggests it was aquatic, living in freshwater environments (OLSEN, 1979). Some researchers indicate a digitigrade stance in the pes of *Tanytrachelos* (PETERS, 2000), *Macrocnemus* (AVANZINI and RENESTO, 2002) and *Langobardisaurus* (RENESTO et al., 2002), and to a possibly bipedal posture, during rapid locomotion – as previously stated by Rieppel (1989) for *Macrocnemus* – or even while standing and walking (NOSOTTI, 2007). The foot of *Macrocnemus* appears to suit terrestrial locomotion, a conclusion which is further supported by the structure of its pelvic girdle (RIEPPEL, 1989). The lifestyle of *Tanystropheus*, the largest and most bizarre of all tanystropheids, is still debatable. Recent osteological analyses do not support a fully aquatic habit for this animal (JAQUIER and SCHEIER, 2017), even though many skeletal features indicative of terrestrial habits in *Macrocnemus* are absent in *Tanystropheus*: this latter does not

present bifurcating pleurapophyses on the second sacral vertebra; the ilium bears no preacetabular process; the tarsal ossifications show a greater degree of reduction; the hooked fifth metatarsal is less distinctly differentiated; finally, the metatarsus is far less asymmetrical (RIEPPEL, 1989). One of the most striking features would be the much longer neck present in *Tanystropheus*. Renesto (2005) emphasized that the neck of *Tanystropheus* was rather mobile and held horizontally or considerably raised. Tschanz (1985) drawing a comparison with extant reptiles (*Iguana* and *Varanus*) concluded that *Tanystropheus* neck would be almost inflexible, indicative of a fully aquatic habit. Moreover, the reduced size of the forelimb suggests that it was not a major contribution to any kind of locomotion (RENESTO, 2005; NOSOTTI, 2007). Reassessing this genus, Nosotti (2007) regarded *Tanystropheus* as an aquatic animal with close terrestrial ancestors, living in shallow waters and probably returning to land for reproduction. Recently, some authors have proposed that the locomotion of *Tanystropheus* is consistent both with feeding on aquatic prey and with a semi-aquatic life-style in the near-shore environments (RENESTO and SALLER, 2018). The skeletal anatomy of *Tanystropheus* is unique, and there is no analogs in present-day or extinct animals. This peculiar structure, along with the impressive overall size of *Tanystropheus* (the largest individuals of *T. longobardicus* reached up to five meters in length) render the animal a weird appearance, which is still a palaeoecological and functional enigma (RENESTO and SALLER, 2018).

A specimen of *Tanytrachelos* (AMNH FARB 7206) was described by Pritchard et al., (2015) as having a calcaneal tuber similar to what is displayed by UFSM 11471. Some authors have argued for the absence of calcaneal tuber in tanystropheids (e.g., RIEPPEL, 1989; NOSOTTI, 2007). The absence of this tuber in more specialized forms might be attributable to an aquatic lifestyle (RIEPPEL, 1989; PRITCHARD et al., 2015).

Based on the presence of a calcaneal tuber, the hooked fifth metatarsal and the distally bifurcating pleurapophyses on the second sacral vertebra, we propose a terrestrial habit for UFSM 11471, similar to what is argued for *Macrocnemus* and *Tanytrachelos*, and distinct from what is most of the times proposed for *Tanystropheus*. This interpretation agrees with some authors (NOSOTTI, 2007; SENNIKOV, 2011; PRITCHARD et al., 2015) in which tanystropheids or close relatives were able to inhabit a wide range of climatic conditions and that, although possessing most of its representatives with affinities to an aquatic lifestyle, this group possibly presents close ancestors with terrestrial habit.

The interpretation based on the foot morphology is also supported by the depositional model of the locality where UFSM 11471 was collected. The Sanga do Cabral formation is

characterized as a system of ephemeral, high energy river channels with wide and extensive alluvial plains, containing a rich assemblage of terrestrial and aquatic tetrapods composed of temnospondyls, procolophonoids, and archosauromorphs (HOLZ and SOUTO-RIBEIRO, 2000; DA-ROSA et al., 2009; DIAS-DA-SILVA et al., 2017). Considering the environment described for the locality of Bica São Tomé, this animal would be terrestrial and probably inhabited shallow water and possibly low-sinuosity river environments.

7 Conclusions

A new basal archosauromorph recovered as the sister-taxon to the Tanystropheid is described for the Lower Triassic of Brazil. UFSM 11471 was collected from rocks reminiscent of continental environments dominated by ephemerous water bodies. Most representatives of Tanystropheidae (e.g. *Tanystropheus*) belong to marine environments. In this work, the hypothesis is raised that the terrestrial habit was plesiomorphic for Tanystropheidae, and maintained by some of its representatives (e.g. *Macrocnemus*). The record of Tanystropheidae-related materials in Permian and Lower Triassic layers of South America indicates a wide distribution of this clade, with a possible Gondwanan origin.

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APPENDIX II

A New Archosauromorph from South America provides insights on the early diversification of Tanystropheids

Figures

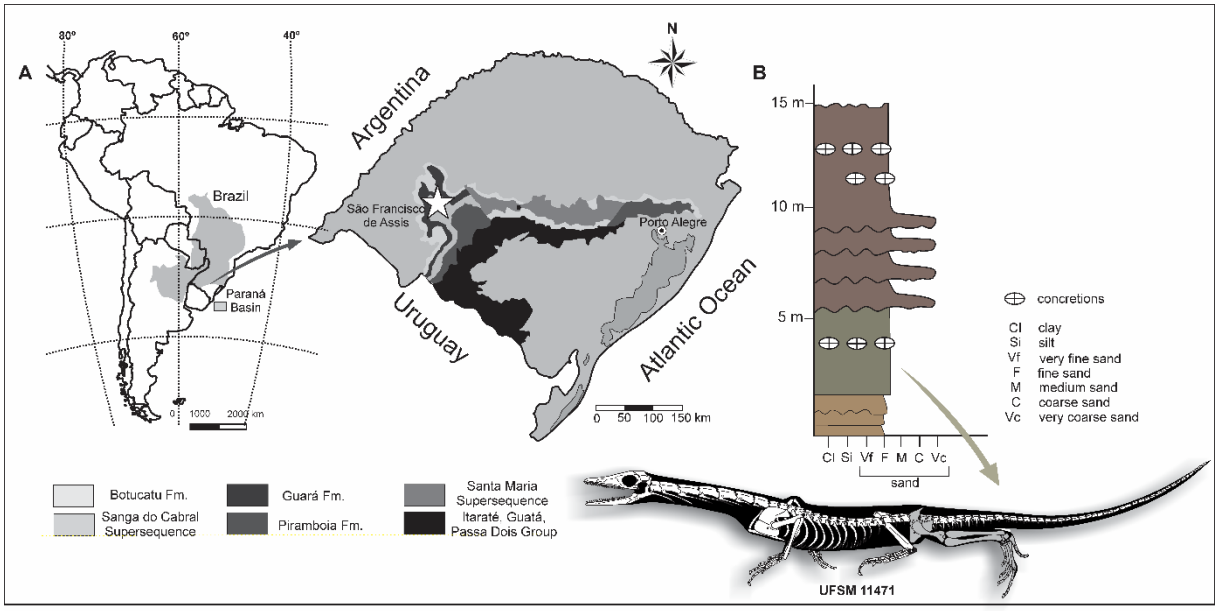

Figure 1. Type locality of UFSM 11471. **A.** Geographic map with the location of UFSM 11471, (São Francisco de Assis, Brazil); **B.** Simplified stratigraphic profile of the outcrop, showing the level where UFSM 11471 was found. Map was modified from Zerfass et al. (2003) and stratigraphic profile modified from Da-Rosa et al. (2009) and Pinheiro et al. (2016); silhouette adapted from Rieppel (1989), showing bones preserved of UFSM 11471 in dark gray color.

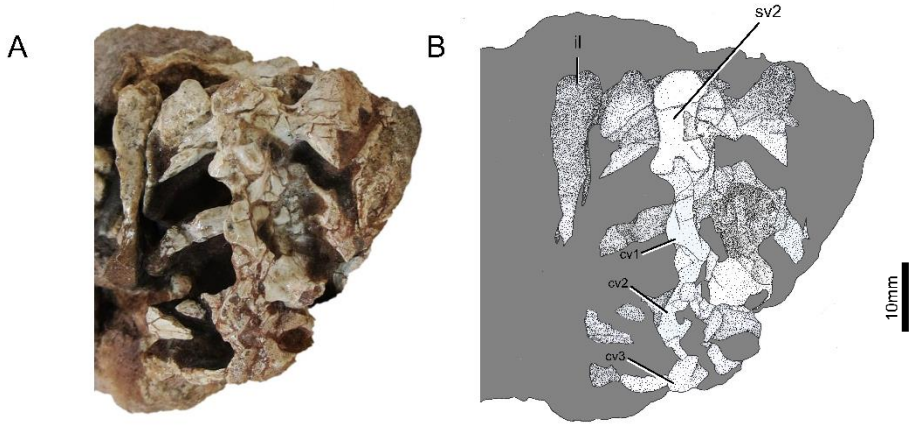

Figure 2. Dorsal view of UFSM 11471 from Sanga do Cabral Formation (Lower Triassic), Brazil. Photograph (**A**), explanatory drawing (**B**). Abbreviations: **il**, ilium; **sv2**, second sacral vertebra; **cv**, caudal vertebrae 1-3.

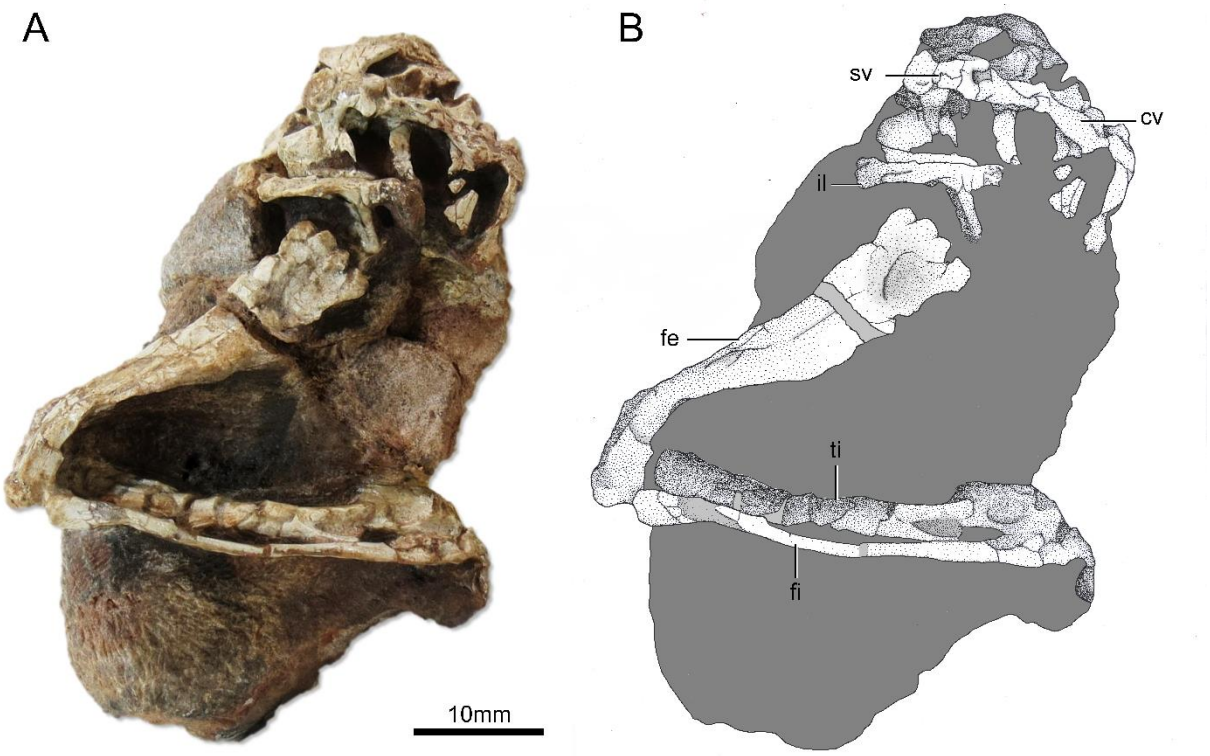

Figure 3. Dorsal view of UFSM 11471 from Sanga do Cabral Formation (Lower Triassic), Brazil. Photograph (**A**) and explanatory drawing (**B**). Abbreviations: **fe**, femur; **ti**, tibia; **fi**, fibula; **il**, ilium; **sv**, sacral vertebra; **cv**, caudal vertebrae.

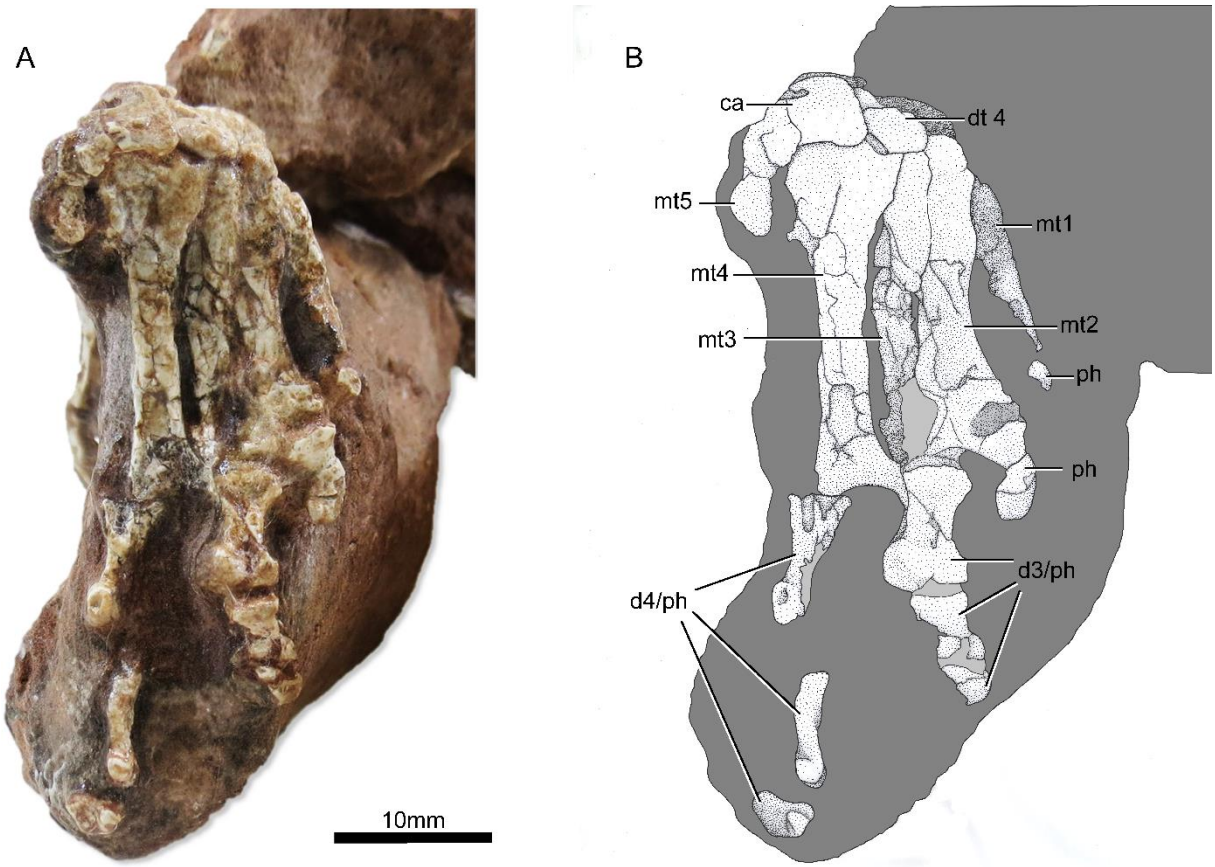

Figure 4. Plantar view of UFSM 11471 from Sanga do Cabral Formation (Lower Triassic), Brazil. Photograph (**A**) and explanatory drawing (**B**). Abbreviations: **ca**, calcaneum; **dt 4**, distal tarsal 4; **mt**. metatarsal 1-5; **d3** - **d4**, digits; **ph**, phalange.

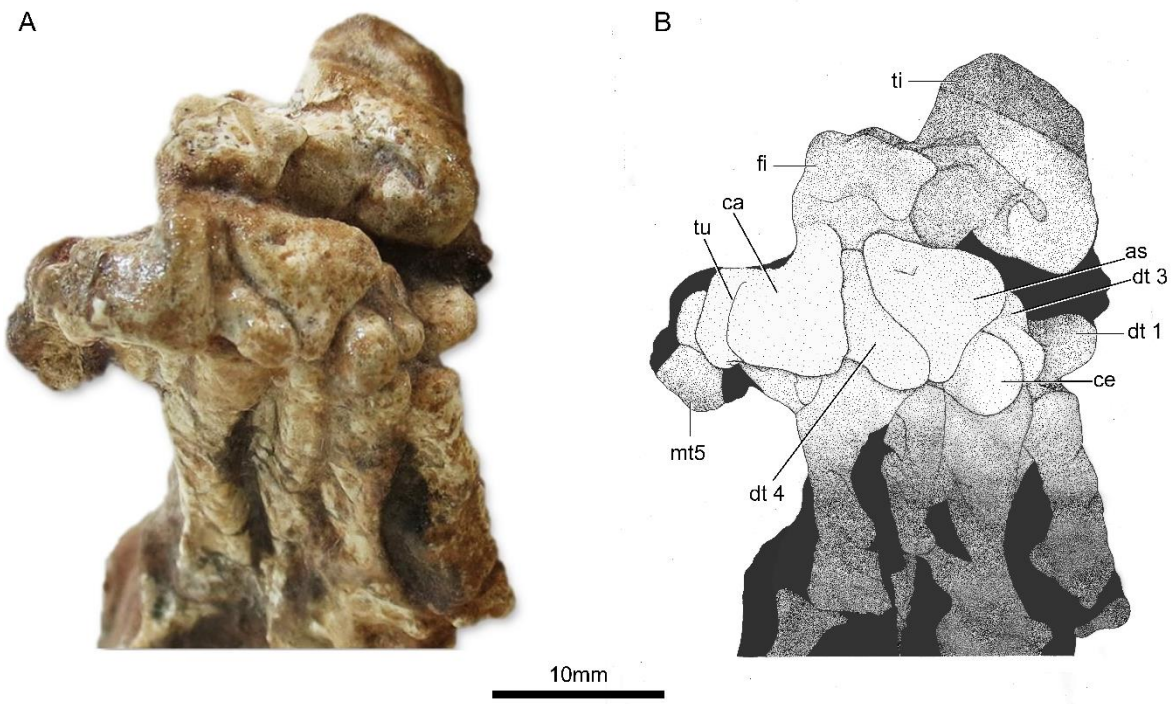

Figure 5. Plantar view of UFSM 11471 from Sanga do Cabral Formation (Lower Triassic), Brazil. Photograph (**A**) and explanatory drawing (**B**). Abbreviations: **ti**, tibia; **fi**, fíbula; **ca**, calcaneum; **as**. astragalus; **tu**, calcaneal tuber; **mt**, metatarsal 5; **dt 1**, distal tarsal 1; **ce**, centrale; **dt 3**, distal tarsal 3; **dt 4**, distal tarsal 4. Drawings (2-5): Lívia Roese Miron.

Figure 6. Archosauromorph phylogeny showing the recovered position of UFSM 11471, from the matrix of Pritchard et al. (2018).

CAPÍTULO 3 *– CONSIDERAÇÕES FINAIS*

3 CONSIDERAÇÕES FINAIS

Os novos materiais aqui descritos são morfologicamente compatíveis com os arcossauromorfos basais relacionados aos Tanystropheidae, sendo estes os primeiros materiais com essa posição filogenética provenientes do Triássico Inferior da América do Sul (oeste do Gondwana). As vértebras apresentam morfologia condizente com esse grupo, apresentando corpo vertebral alongado com espinho neural dorsoventralmente curto e laminar. Por outro lado, a análise filogenética das vertebras cervicais UNIPAMPA 733 e UFRGS-PV-492-T na matriz de dados de Sengupta et al. (2017) resultou em uma politomia incluindo os novos espécimes, *Jesairosaurus* e Tanystropheidae. Este resultado pode ser justificado pela impossibilidade de visualização de caracteres informativos devido à preservação dos materiais. Devido à baixa quantidade de caracteres diagnósticos, as vértebras cervicais foram considerados como ?Tanystropheidae indeterminados.

UFSM 11471 é representado por um membro posterior, com cintura pélvica e vértebras sacrais e caudais. Também apresenta morfologia semelhante ao que é descrito para os táxons incluídos em Tanystropheidae, principalmente em relação à segunda vértebra sacral, fêmur e a configuração dos dígitos e elementos do tarso. Por apresentar mais informações anatômicas do que as vértebras acima mencionadas, e possuir uma combinação única de características não presentes em outros arcossauromorfos, o espécime é considerado um novo táxon. A topologia recuperada resultou na hipótese em que UFSM 11471 se agrupa como grupo-irmão de Tanystropheidae. Portanto, tanto as vértebras cervicais quanto UFSM 11471 são classificados como arcossauromorfos basais, mais próximos filogeneticamente aos Tanystropheidae do que a outros arcossauromorfos.

A relação entre a morfologia do membro posterior de tanistrofeídeos e uma possível locomoção terrestre ou totalmente aquática é amplamente discutida na literatura. De forma geral, hábitos aquáticos são inferidos para a maior parte dos tanistrofeídeos. Por outro lado, *Tanytrachelos* apresenta uma tuberosidade calcaneal, não presente nas formas aquáticas, indicativa de um hábito terrestre. Tal estrutura também está presente em UFSM 11471, o que permite relacionar esse novo material aos representantes terrestres do grupo. De acordo com a hipótese filogenética aqui levantada, onde UFSM 11471 é posicionado como grupo-irmão de Tanystropheidae, as formas basais seriam predominantemente terrestres, embora possivelmente habitando águas rasas.

As vertebras cervicais, juntamente a UFSM 11471, apresentam tamanho reduzido em relação a alguns grandes representantes do grupo (e.g. *Tanystropheus*). Assim, não se desconsidera que tanto as vértebras quanto UFSM 11471 poderiam pertencer ao mesmo táxon.

As extinções em massa impactaram profundamente a evolução da vida, não só reduzindo a diversidade taxonômica, mas também reformulando ecossistemas e padrões biogeográficos. A reestruturação biogeográfica global das comunidades biológicas associadas a esses eventos de extinção em massa fornece evidências para a liberação de restrições bióticas, o que teria facilitado a radiação de grupos novos ou anteriormente marginais, como os arcossauromorfos, após a extinção em massa Permo-Triássica (SIDOR et al., 2013). Outro possível fator que poderia ter influenciado a origem de novos táxons no Triássico Inferior é a seleção ambiental para a tolerância à aridez. Muitos desses novos táxons são arcossauromorfos e pararrépteis, que podem ter sido pré-adaptados a um ambiente árido (BOTHA e SMITH, 2006). O registro de tanistrofeídeos em toda a América do Norte, juntamente com os novos materiais relacionados ao grupo na América do Sul, sugere que estes animais foram capazes de ocupar uma série de condições climáticas durante sua evolução inicial. A presença destes vertebrados na América do Sul também indicaria uma possível distribuição cosmopolita já no Triássico Inferior, e concorda com alguns autores (NOSOTTI, 2007; JAQUIER et al., 2017), que os tanistrofeídeos tiveram sua origem em uma área central do Pangeia, possivelmente na porção sudoeste do Gondwana.

Por fim, a futura codificação dos espécimes aqui estudados, principalmente UFSM 11471, em uma nova matriz de dados morfológicos focada principalmente em tanistrofeídeos e formas relacionadas, pode vir a elucidar as relações filogenéticas das formas sul-americanas com os demais táxons, bem como tratar da própria definição filogenética do clado em questão.

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