



PALEONTOLOGY

Triassic pterosaur precursors of Brazil: catalog, evolutionary context, and a new hypothesis for phylogenetic relationships of Pterosauromorpha

MAURÍCIO S. GARCIA & RODRIGO T. MÜLLER

Abstract: Pterosaurs, remarkable for their extensive evolutionary history and role as the first vertebrates to achieve active flight, have long intrigued paleontologists and the public alike. Spanning over 150 million years and vanishing at the end of the Mesozoic Era, pterosaurs represent a major evolutionary radiation within terrestrial ecosystems. Despite their prominence, the origins of pterosaurs have remained a complex puzzle in paleontology for over 200 years. We present a comprehensive catalog of pterosaur precursors specimens from the Upper Triassic of the Candelária Sequence within the Santa Maria Supersequence in southern Brazil and discuss their significance for understanding pterosauriform radiation and the origins of Pterosauria. Additionally, we carried out a phylogenetic analysis to investigate the hypothesis that lagerpetids are closely related to pterosaurs, incorporating new data into the most comprehensive dataset of Triassic dinosauriforms. Our results support the hypothesis that lagerpetids are pterosauriforms, offering new insights into the evolutionary relationships between non-pterosaur pterosauriforms and their better known volant relatives. This study highlights the importance of detailed anatomical and phylogenetic analyses in resolving the complex origins of pterosaurs and underscores the value of the Triassic fossil record in understanding the early evolution of pterosauriforms.

Key words: Pterosauromorpha, Pterosauria, Lagerpetidae, Cladistics, Candelária Sequence.

INTRODUCTION

Pterosaurs, with their dramatic presence in popular culture, frequently appear in books and films and include some of the largest flying animals ever discovered (Padian 1984, Andres 2012). Their evolutionary history spans over 150 million years, concluding at the end of the Mesozoic Era. As the first vertebrates to evolve active flight (Padian 1984), pterosaurs were a major evolutionary radiation in the terrestrial ecosystems of the Mesozoic. Despite their prominence, the origins of pterosaurs have remained a complex and unresolved puzzle in paleontology since the 19th century (Baron 2021).

The Middle Triassic to Late Triassic marked a decisive phase in the evolution of terrestrial vertebrates, witnessing the emergence of diverse lineages that would become significant in Mesozoic ecosystems (Irmis et al. 2011, Martínez et al. 2012, Ezcurra 2016, Schultz et al. 2020). The oldest pterosaurs, dating from the Upper Triassic, were found in Argentina, Europe and North America (Dalla Vecchia 2013, Martínez et al. 2022). These early pterosaurs quickly diversified into a range of ecomorphologically distinct groups by the Middle to Late Jurassic (Prentice et al. 2011, Andres 2012). Despite extensive study, the evolutionary relationships of pterosaurs remain uncertain, with hypotheses

suggesting affinities to various reptilian clades, including dinosaur relatives (Ezcurra et al. 2020, Baron 2021, Silva et al. 2022).

The oldest recognized pterosaurs exhibited a highly specialized body plan adapted for flight, a feature that was maintained across the group (Prentice et al. 2011). This specialized anatomy creates a considerable morphological gap between pterosaurs and other Mesozoic reptiles. Early pterosaur specimens, however, are often small and represented by poorly preserved, nearly two-dimensional skeletons (Dalla Vecchia 2013). These preservation issues, combined with a lack of “transitional” fossils, have made the origin of pterosaurs one of the most challenging questions in vertebrate evolution for over two centuries.

Modern cladistic analyses have largely supported the view that pterosaurs are part of the clade Pan-Aves (bird-line archosaurs), which includes both pterosaurs, dinosaurs, and their closest relatives (Benton 1999, Nesbitt 2011, Ezcurra et al. 2020, Baron 2021, Müller et al. 2023). The body fossils of the early branches of Pan-Aves, unambiguously dating from the Middle to Late Triassic, have been identified across various continents, with notable abundance in South Pangea (Langer et al. 2010, 2013, Nesbitt et al. 2017, 2023, Müller et al. 2018b, Garcia et al. 2019, Ezcurra et al. 2020, Foffa et al. 2022; but see Ezcurra et al. 2023 for a possible Early Triassic record). Fossil deposits from late Ladinian-Carnian periods in southern Brazil have revealed a wealth of early pan-avians, including aphanosaurs (Nesbitt et al. 2017), lagerpetids (Cabreira et al. 2016, Garcia et al. 2019, 2024b, Müller et al. 2023), and dinosauiromorphs (Langer et al. 1999, Cabreira et al. 2011, Langer & Ferigolo 2013, Pacheco et al. 2019, Müller & Garcia 2022).

Lagerpetids, once considered enigmatic precursors to dinosaurs (Sereno & Arcucci 1994, Irmis et al. 2007, Nesbitt et al. 2009, Müller et

al. 2018b), have recently been reevaluated and are now thought to be closely related to pterosaurs (Kammerer et al. 2020, Ezcurra et al. 2020, Baron 2021, Müller et al. 2023). Recent research suggests lagerpetids are the sister group to Pterosauria, positioning them within the broader clade Pterosauiromorpha. This new understanding highlights the importance of lagerpetids in unraveling the early evolution of pterosaurs. The first studies primarily focused on hindlimb anatomy (Sereno & Arcucci 1994, Irmis et al. 2007, Nesbitt et al. 2009), but based on new discoveries, recent research has expanded to include cranial and forelimb anatomy, offering deeper insights into lagerpetid anatomy and their role in pterosaur evolution (Kammerer et al. 2020, Ezcurra et al. 2020, McCabe & Nesbitt 2021, Foffa et al. 2022, Müller et al. 2023, Bronzati et al. 2024).

The ongoing research into lagerpetid anatomy and phylogeny is fundamental for enhancing our understanding of early pterosaur evolution. The advancements in this field underscore the significance of continued exploration and analysis in revealing the complexities of pterosaur origins and their evolutionary relationships.

In this contribution, we present a catalog of pterosaur precursor specimens, including putative assignments, from the Triassic of southern Brazil. We discuss their significance and implications for the study of lagerpetid radiation and the origins of Pterosauria. Additionally, we evaluate the affinities between lagerpetids and pterosaurs through an independent phylogenetic analysis, distinct from previous studies.

MATERIALS AND METHODS

Institutional abbreviations

CAPPA/UFMS, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia da

Universidade Federal de Santa Maria, São João do Polêsine, Brazil; ULBRA, Centro de Apoio à Pesquisa Paleontológica da Quarta Colônia, Universidade Federal de Santa Maria, São João do Polêsine, Rio Grande do Sul, Brazil (previously Museu de Ciências Naturais, Universidade Luterana do Brasil, Canoas, Brazil); UFRGS, Universidade Federal de Rio Grande do Sul, Porto Alegre, Brazil; UFSM, Coleção de Paleontologia do Laboratório de Estratigrafia e Paleobiologia, Universidade Federal de Santa Maria, Santa Maria, Brazil.

Phylogenetic analysis

To investigate the phylogenetic relationships of Lagerpetidae within Pan-Aves, we scored six new taxa into the dataset of Garcia et al. (2024b). This is a modified version of the dataset of Müller & Garcia (2020a) after several iterations (Norman et al. 2022, Müller & Garcia 2023, Garcia et al. 2024a). This is the most comprehensive dataset focused on Triassic pan-avians, especially dinosauromorphs, however, it did not include any pterosaurs, until now. Therefore, the present analysis aims to test the hypothesis that lagerpetids and pterosaurs are closely related groups, as recovered in other independent datasets (Ezcurra et al. 2020, Kammerer et al. 2020, Baron 2021, Müller et al. 2023).

We added six new operational taxonomic units (OTUs), including an early-diverging pan-avian, as well as five early-diverging pterosaurs (see Appendix I): *Mambachiton fiandohana* Nesbitt et al. (2023); *Arcticodactylus cromptonellus* Jenkins et al. (2001); *Austriadactylus cristatus* Dalla Vecchia et al. (2002); *Austriadraco dallavecchiai* Kellner (2015); *Carniadactylus rosenfeldi* Dalla Vecchia (1995); including data from *Bergamodactylus wildi* Kellner (2015), which is considered a junior synonym of the former (Dalla Vecchia 2018); *Seazzadactylus venieri* Dalla Vecchia (2019).

Although *Maehary bonapartei* Kellner et al. (2022) was formerly described as a pterosauiromorph, subsequent studies have recovered it as a gracilisuchid pseudosuchian (Müller et al. 2023, Müller 2024a). Consequently, due to the absence of pseudosuchians in our current sample, this taxon was not included in the present analysis. We excluded the *Soumyasaurus aenigmaticus* OTU due to its fragmentary nature (a partial dentary) and potential taxonomic issues. The only known specimen lacks a unique combination of silesaurid apomorphies, also sharing several character states with other archosauromorphs.

Scores for several OTUs have been revised and changed (see Appendix II) based in recent literature and new observations. 13 characters were added (see Appendix III), most of which are from the dataset of Müller et al. (2023). These were included because most of them are either diagnostic for pterosauiromorphs or vary within them, therefore they are potentially informative regarding pterosauiromorph affinities.

The dataset for this analysis totalized 83 OTUs and 305 characters. The analysis was conducted using TNT v1.5 software (Goloboff & Catalano 2016). Methodology applied herein is the same used in previous iterations of this dataset (Müller & Garcia 2020a, 2023, Garcia et al. 2021, 2024a, b, Norman et al. 2022), which is also detailed below. This phylogenetic analysis was based on equally weighted parsimony and is hereafter referred to as the main analysis. Characters 4, 13, 18, 25, 63, 82, 83, 84, 87, 89, 109, 142, 166, 174, 175, 184, 186, 190, 201, 203, 205, 209, 212, 225, 235, 236, 239, 250, 256, 291, and 306 were treated as additive (ordered). *Euparkeria capensis* served as the outgroup to root the most parsimonious trees (MPTs). The MPTs were acquired through 'Traditional search': random addition sequence + tree bisection reconnection (TBR), which included 1000 replicates of Wagner trees (with random seed = 0), TBR and

branch-swapping (holding 20 trees saved per replicate). Topologies retained as replicates were branch-swapped for MPTs using TBR. The strict consensus tree was produced using all trees recovered in the analysis and all OTUs.

Constrained and implied weighting analyses were performed using the same search parameters as the main analysis to test alternative hypotheses of pterosauiromorph interrelationships, to assess the number of extra steps required to recover them, and to test the effect of homoplasies. In addition, implied weighting analyses were run with concavity constants (k) of 3, 6, and 10, following the results of Ezcurra (2024).

Geological setting

The Triassic beds of the Santa Maria Supersequence of the Paraná Basin outcrop in the central region of the Rio Grande do Sul state, southern Brazil (Zerfass et al. 2003, Horn et al. 2014). This second order sequence is subdivided into third order sequences, from oldest to youngest: Pinheiros-Chiniquá Sequence (Ladinian-early Carnian), Santa Cruz Sequence (early Carnian), Candelária Sequence (late Carnian-early Norian), and Mata Sequence (Rhaetian) (Horn et al. 2014). The first three include a plethora of tetrapod body fossils (Schultz et al. 2020). Faunal assemblage zones (AZs) within the Santa Maria Supersequence document the faunal successions that took place in the transition from the Middle Triassic to the Late Triassic (Ezcurra et al. 2017, Langer et al. 2018, Garcia et al. 2019, Schultz et al. 2020). Below, we will focus on the Geological Setting relevant for the pterosaur precursor record in the Triassic of southern Brazil.

The record of pterosaur precursors in the Triassic of southern Brazil occurs solely in the Candelária Sequence (Fig. 1a). It is encompassed by the older *Hyperodapedon* AZ and the younger

Riograndia AZ (Langer et al. 2007, 2018, Soares et al. 2011, Schultz et al. 2020). The *Hyperodapedon* AZ is subdivided into an older *Hyperodapedon* Acme Zone and a younger *Exaeretodon* sub-Zone (Langer et al. 2007, Cabreira et al. 2011, Müller & Garcia 2020b, Schultz et al. 2020). The division in the *Hyperodapedon* AZ is based on the relative abundance of the index taxa in the corresponding strata, that is corroborated by biostratigraphic data from Argentina (Martínez et al. 2012, Desojo et al. 2020). Sites from the mentioned assemblages that yield pterosaur precursors are: Buriol (*Hyperodapedon* Acme) (Fig. 1c), Cerro da Alemoa (*Hyperodapedon* Acme) (Fig. 1b), and Linha São Luíz (*Riograndia* AZ) (Fig. 1d).

The age of the *Hyperodapedon* Acme fauna is established based on biostratigraphical correlations, especially with the Ischigualasto Formation of Argentina (Martínez et al. 2011, 2012), and on radioisotopical dating (U-Pb decay of detrital zircon) of the upper mudstone layers of the Cerro da Alemoa site (Da-Rosa 2015), of the Cerro da Alemoa complex (Garcia et al. 2019), yielding a maximum depositional age of 233.23 ± 0.73 Ma, late Carnian (Langer et al. 2018). Other sites of the *Hyperodapedon* Acme Zone of the Candelária Sequence, such as the Buriol (Müller et al. 2017), are biostratigraphically correlated to the Cerro da Alemoa due to shared presence of the hyperodapedontine rhynchosaur *Hyperodapedon*, and therefore are also considered late Carnian in age. Similarly, the *Riograndia* AZ layers in the Linha São Luíz site also have their age established via biostratigraphical correlation and radioisotopical dating, yielding a maximum age of 225.42 ± 0.25 Ma, early Norian (Martínez et al. 2012, Kent et al. 2014, Langer et al. 2018).

The faunal content of the *Hyperodapedon* Acme zone includes temnospondyls (Dias da Silva et al. 2012), cynodonts (Martinelli

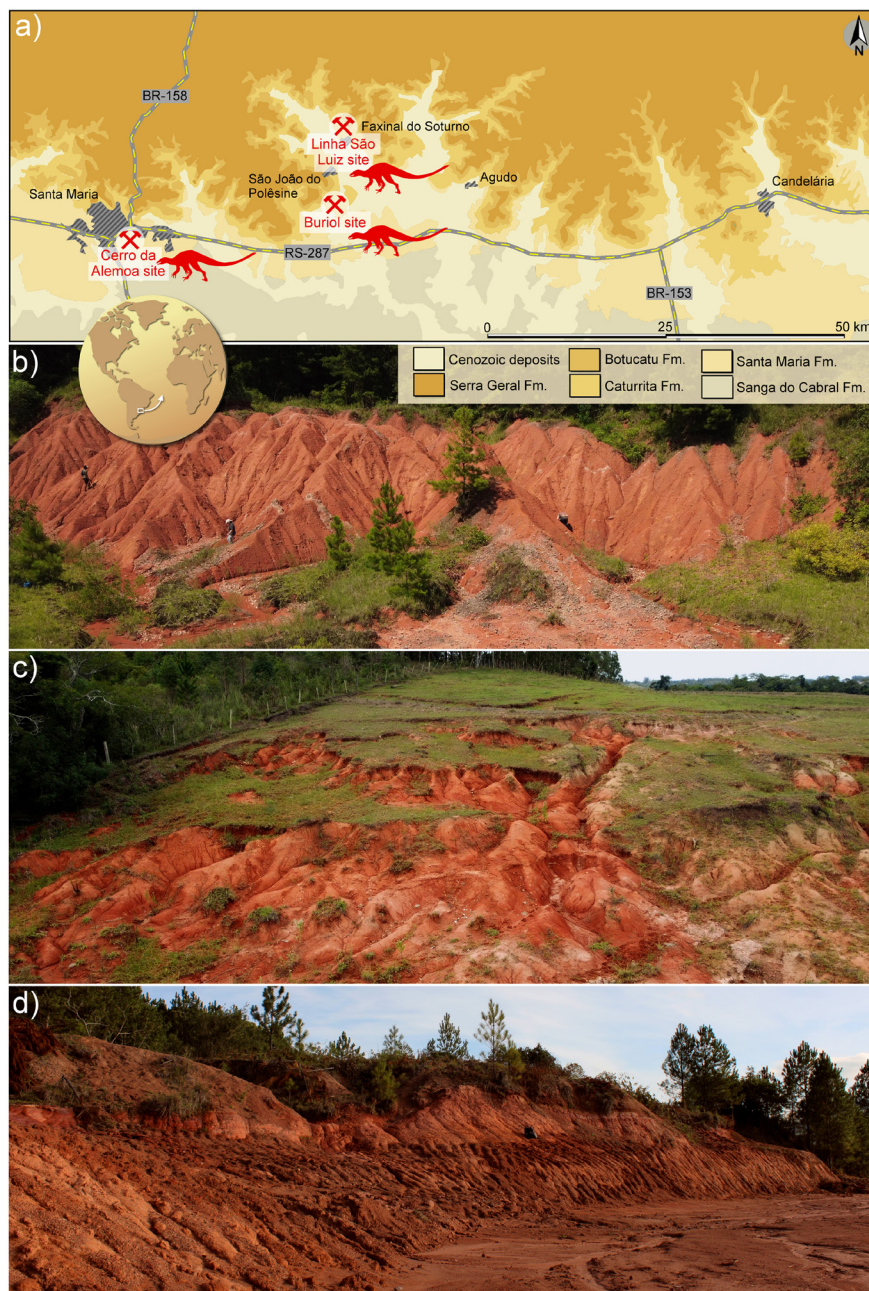


Figure 1. Provenance of Triassic pterosaur precursors from southern Brazil. a) geological context of the central region of Rio Grande do Sul depicting the three sites with records of pterosauiromorphs. b) general view of the Cerro da Alemoa site, Santa Maria. c) general view of the Buriol site, São João do Polêsine. d) general view of the Linha São Luiz site, Faxinal do Soturno. Silhouettes based on artwork by Matheus Fernandes Gadelha.

et al. 2017, Pacheco et al. 2018), and many archosauromorphs, including but not limited to rhynchosaurs (Schiefelbein et al. 2024), proterochampsids (Ezcurra et al. 2015), pseudosuchians (Lautenschlager & Rauhut 2015, Paes-Neto et al. 2021, Damke et al. 2022), and pan-avians (Langer et al. 1999, Cabreira et al. 2016, Pacheco et al. 2019, Müller & Garcia 2023).

As for the *Riograndia* AZ its faunal content includes dicynodonts (Martinelli et al. 2021), cynodonts (Bonaparte et al. 2005, Soares et al. 2011, Oliveira et al. 2011, Abdala et al. 2023), rhynchocephalians (Bonaparte & Sues 2006), pseudosuchians (Kellner et al. 2022), and pan-avians (Bonaparte et al. 1999, Kellner et al. 2022, Bem & Müller 2023).

Systematic palaeontology

Archosauria Cope 1869 sensu Gauthier & Padian 2020

Pan-Aves Gauthier & De Queiroz 2001 sensu Ezcurra et al. 2020

Faxinalipterus minimus Bonaparte et al. 2010

Holotype. UFRGS-PV-0927-T (Fig. 2a) consists of a right humerus, two fragments of a left humerus, a possible proximal portion of a left femur, tibiae and fibulae, and two fragmentary metatarsals. All bones were associated within a single sandstone block.

Provenance and horizon. Orange medium sandstone in the lower level of the Linha São Luiz site (29°33' 8" S, 53°26'54" W), municipality of Faxinal do Soturno, Rio Grande do Sul State, southern Brazil (Soares et al. 2011). This outcrop belongs to the *Riograndia* AZ (Soares et al. 2011) of the Candelária Sequence (Horn et al. 2014), early Norian, Late Triassic (Langer et al. 2018).

Remarks. *Faxinalipterus minimus* is one of the smallest pan-avians known worldwide (preserved portion of the femur measures ca 14.2 mm) and was initially regarded as an early pterosaur (Bonaparte et al. 2010). If so, it would represent one of the, if not the earliest, record of Pterosauria worldwide. A study by Kellner et al. (2022) reinterpreted the taxon as a putative lagerpetid instead. As a lagerpetid, *Faxinalipterus minimus* would be the youngest occurrence of the clade in southern Brazil, and the solely occurrence in post-Carnian rocks of the Candelária Sequence. *Faxinalipterus minimus* lacks some of the classical lagerpetid apomorphies (see Discussion), resulting in some studies recovering it as an early-diverging pan-avian instead (Garcia et al. 2024a, b, this study). More material is needed to better understand

the anatomy and affinities of *Faxinalipterus minimus*.

Ornithodira Gauthier 1986 sensu Ezcurra et al. 2020

Pterosauiomorpha Padian 1997 sensu Andres & Padian 2020

Lagerpetidae Arcucci 1986 sensu Ezcurra et al. 2020

Ixalerpeton polesinensis Cabreira et al. 2016

Holotype. ULBRA-PVT059 (Fig. 2b) consists of a partially articulated skeleton including partial right maxilla, right prefrontal, both frontals, postfrontals and parietals, left laterosphenoid, braincase, both dentaries, 23 presacral, two sacral, and nine caudal vertebrae, right scapula, left humerus, pelvic girdle, femora, tibia, and fibula.

Provenance and horizon. Orange mudstone in the upper level of the Buriol site (29°39'31" S, 53°26'10" W), below the pinkish uppermost layers, municipality of São João do Polêsine, Rio Grande do Sul State, southern Brazil (Müller et al. 2017, 2023). This outcrop belongs to the *Hyperodapedon* Assemblage Zone (Langer et al. 2007), *Hyperodapedon* Acme Zone (Langer et al. 2007, Müller & Garcia 2020b, Schultz et al. 2020), of the Candelária Sequence (Horn et al. 2014), late Carnian, Late Triassic (Langer et al. 2018).

Remarks. *Ixalerpeton polesinensis* was the first unequivocal lagerpetid to be published with associated cranial elements. At first, only the skull roof elements and the braincase were associated with the holotype (Cabreira et al. 2016), but afterwards, some tooth-bearing bones were also included (Ezcurra et al. 2020). The holotype was excavated in association with the holotype of the early-diverging sauropodomorph dinosaur *Buriolestes schultzi* (Cabreira et al. 2016) and with a putative juvenile specimen of

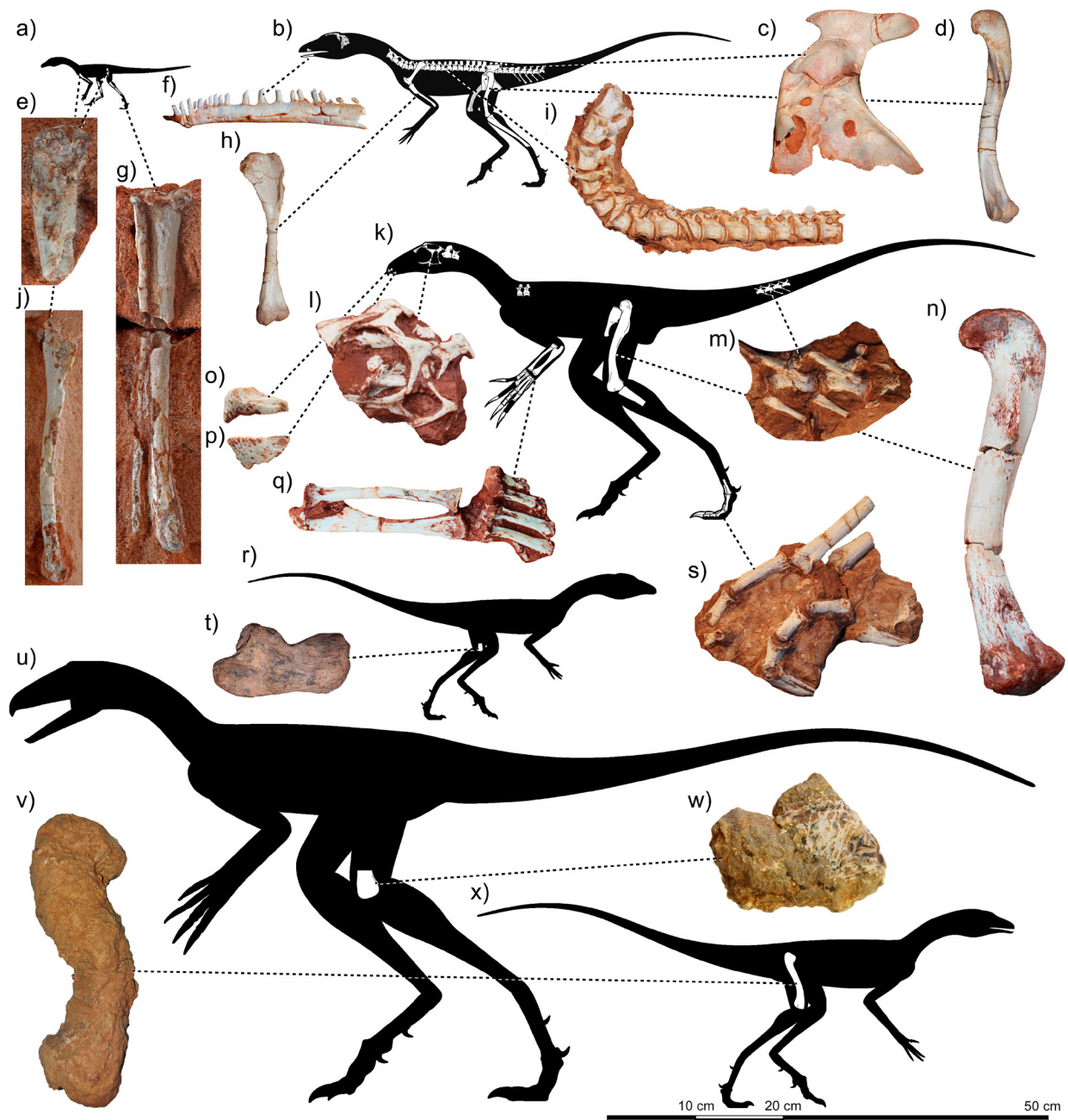


Figure 2. Triassic pterosaur precursors from southern Brazil. Rigorous skeletal reconstructions to scale and photographs of selected elements not to scale. *Faxinalipterus minimus* UFRGS-PV-0927-T (a, e, g, j), *Ixalerpeton polesinensis* ULBRA-PVT059 (b, c, d, f, h, i), *Venetroaptor gassenae* CAPPA/UFSM 0356 (k, l, m, n, o, p, q, s), Lagerpetidae indeterminate UFSM 11611 based on the lower size estimative (r, t), Lagerpetidae indeterminate CAPPA/UFSM 0355 based on the lower size estimative (u, w), Lagerpetidae indeterminate UFSM 11625 (v, x). c, pelvic girdle (reversed, digitally articulated) in lateral view (pubis in medial view). d, femur in posterior view. e, proximal half of the femur in posterior view. f, dentary in lateral view (reversed). g, tibia and fibula in posterior view. h, humerus in anterior view. i, articulated presacral vertebral series in lateral view. j, humerus in lateral view. l, posterior half of the skull in lateral view. m, articulated caudal vertebrae and chevrons in lateral view. n, femur in posterior view. o, premaxilla in lateral view. p, anterior end of the dentary in lateral view (reversed). q, articulated forearm and metacarpus in lateral view. s, articulated partial pes in lateral view. t, femur in distal view. v, femur in anterior view. w, femur in distal view. References in the main text.

the same taxon (Müller et al. 2018a, Müller & Garcia 2020b). *Ixalerpeton polesinensis* is the most complete lagerpetid known, and several of its remains (e.g., ulna, pes) are still undescribed. In addition, other more incomplete specimens (mostly comprised by femora) are known from the same site, but these also remain undescribed.

***Venetraptor gassenae* Müller et al. 2023**

Holotype. CAPPA/UFSM 0356 (Fig. 2k) consists of a partially articulated skeleton including partial left premaxilla, partial right dentary, left frontal, prefrontal, postfrontal, postorbital, jugal, quadratojugal, quadrate, squamosal, partial braincase, cervical vertebrae including axis, dorsal and caudal vertebrae, right radius, ulna, and metacarpus, phalanx I of digit V, several phalanges from the other digits, including unguals, right pubis, femur, fibula and partial pes.

Provenance and horizon. Orange mudstone in the upper level of the Buriol site (29°39'31" S, 53°26'10" W), below the pinkish uppermost layers, municipality of São João do Polêsine, Rio Grande do Sul State, southern Brazil (Müller et al. 2017, 2023). This outcrop belongs to the *Hyperodapedon* Assemblage Zone (Langer et al. 2007), *Hyperodapedon* Acme Zone (Langer et al. 2007, Müller & Garcia 2020b, Schultz et al. 2020), of the Candelária Sequence (Horn et al. 2014), late Carnian, Late Triassic (Langer et al. 2018).

Remarks. *Venetraptor gassenae* was the first lagerpetid to preserve a premaxilla, showing that, at least in this taxon, this element was edentulous and formed a ventrally recurved beak, with correlates for a keratin sheath or rhamphotheca (Müller et al. 2023). It also preserves some of the best cranial elements for any lagerpetid, with most of the back half of the skull exquisitely preserved and mostly articulated (Müller et al. 2023). The manus of *Venetraptor gassenae* is equally well preserved

and differs from the manus of *Dromomeron romeri*, in that the metacarpal IV is the longest, as in pterosaurs (Müller et al. 2023). Compared to *Ixalerpeton polesinensis*, which comes from the same site, *Venetraptor gassenae* has a femur which is twice as long and much more robust. This was the first unequivocal evidence of sympatry among lagerpetids, and their dissimilar morphology and size suggest that *Venetraptor gassenae* and *Ixalerpeton polesinensis* occupied different niches (Müller et al. 2023).

Lagerpetidae indeterminate

Material. UFSM 11611 (Fig. 2r), a distal portion of a left femur.

Provenance and horizon. Orange mudstone in the upper level of the Cerro da Alemoa (= Waldsanga) site (29°41'51" S, 53°46'26" W), below the yellowish uppermost sandstone layers, Alemoa complex (Garcia et al. 2019), urban area of the municipality of Santa Maria, Rio Grande do Sul State, southern Brazil (Da-Rosa 2015, Garcia et al. 2019). This outcrop belongs to the *Hyperodapedon* Assemblage Zone (Langer et al. 2007), *Hyperodapedon* Acme Zone (Langer et al. 2007, Müller & Garcia 2020b, Schultz et al. 2020), of the Candelária Sequence (Horn et al. 2014), late Carnian, Late Triassic (Langer et al. 2018).

Remarks. This specimen is small, having a similar size as *Ixalerpeton polesinensis*, but, UFSM 11611 shows signs that it was likely a skeletally immature individual (Garcia et al. 2019). This specimen also comes from a site that yielded several types of pan-avians, including lagerpetids (Garcia et al. 2019, 2024b), silesaurids (Mestriner et al. 2023), herrerasaurids (Garcia et al. 2021), and sauropodomorphs (Langer et al. 1999, Marsola et al. 2018). This specimen presented a unique combination of features among lagerpetids, but its ontogenetic status and its fragmentary nature precluded its

assignment to a genus and/or species (Garcia et al. 2019).

Material. CAPP/UFMS 0355 (Fig. 2u), a distal portion of a right femur.

Provenance and horizon. Orange mudstone in the intermediate level of the Cerro da Alemoa site (29°41'51" S, 53°46'26" W), below the yellowish uppermost sandstone layers, Alemoa complex (Garcia et al. 2019), urban area of the municipality of Santa Maria, Rio Grande do Sul State, southern Brazil (Da-Rosa 2015, Garcia et al. 2019). This outcrop belongs to the *Hyperodapedon* Assemblage Zone (Langer et al. 2007), *Hyperodapedon* Acme Zone (Langer et al. 2007, Müller & Garcia 2020b, Schultz et al. 2020), of the Candelária Sequence (Horn et al. 2014), late Carnian, Late Triassic (Langer et al. 2018).

Remarks. This specimen comes from the same site as UFSM 11611; however, it is much larger than the latter. Although badly preserved, this specimen is potentially one of the, if not the, largest lagerpetid specimens known so far (but see Beyl et al. 2020), with an estimate femoral length ranging from 223.15 mm to 278.47 mm based on measurements of other lagerpetids (Garcia et al. 2024b). This specimen can also be distinguished from other lagerpetids and does not seem to represent an ontogenetic advanced individual of the same taxon as UFSM 11611 or other lagerpetids from the Candelária Sequence (Garcia et al. 2024b).

Material. UFSM 11625 (Fig. 2x), a complete right femur.

Provenance and horizon. Orange mudstone in the lower level of the Cerro da Alemoa site (29°41'51" S, 53°46'26" W), below the yellowish uppermost sandstone layers, Alemoa complex (Garcia et al. 2019), urban area of the municipality of Santa Maria, Rio Grande do Sul State, southern Brazil (Da-Rosa 2015, Garcia et al. 2019). This outcrop belongs to the *Hyperodapedon* Assemblage Zone (Langer et al.

2007), *Hyperodapedon* Acme Zone (Langer et al. 2007, Müller & Garcia 2020b, Schultz et al. 2020), of the Candelária Sequence (Horn et al. 2014), late Carnian, Late Triassic (Langer et al. 2018).

Remarks. It comes from the same site as UFSM 11611 and CAPP/UFMS 0355. The presence of several lagerpetid specimens in the same site but which cannot be assigned to the same taxon demonstrates that lagerpetids are likely more diverse and that sympatry was also more common in lagerpetids than previously thought (Müller et al. 2023, Garcia et al. 2024b).

RESULTS

Phylogenetic analysis

The analysis generated 294,336 MPTs of 1225 steps each (CI = 0.284; RI = 0.697). Most of the topology of the strict consensus tree is similar to that of Garcia et al. (2024a, b) (Fig. 3a).

In the strict consensus tree *Mambachiton fiandohana* nested as an early-diverging pan-avian in a polytomy with a collapsed Aphanosauria and a clade formed by *Faxinalipterus minimus* + Ornithodira. In some of the MPTs, *Mambachiton fiandohana* is recovered as the earliest-diverging pan-avian, but in others it is recovered as an aphanosaur sister to the clade *Teleocrater rhadinus* + *Spondylosoma absconditum* (117: 0→1, presence of hyposphene-hypantrum accessory articulations). *Faxinalipterus minimus* nests outside Ornithodira, as in previous iterations of this dataset (Garcia et al. 2024a, b).

Pterosauiomorpha is sister to Dinosauromorpha and includes taxa commonly recovered as lagerpetids and Pterosauria (see Appendix IV for a list of synapomorphies of Pterosauiomorpha and clades within; Fig. 4). The inner affinities of Pterosauiomorpha are noteworthy. Instead of a monophyletic Lagerpetidae composed of taxa such as *Dromomeron romeri*, *Ixalerpeton polesinensis*,

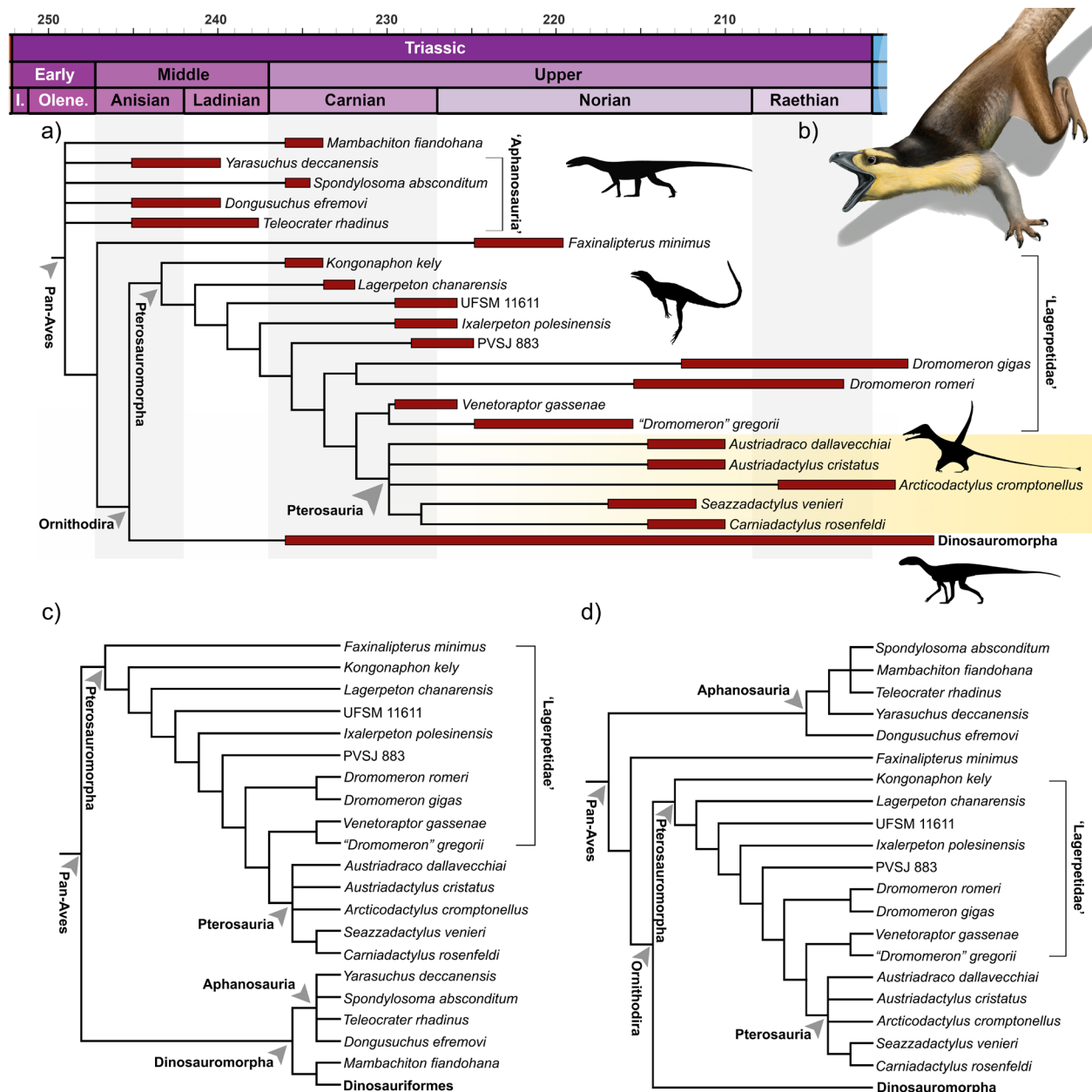


Figure 3. Abbreviated strict consensus trees of the phylogenetic analyses focusing on early-diverging pan-avians and Pterosauroomorpha. a) time-calibrated strict consensus tree of the equal weighting analysis. Red bars indicate temporal occurrence. Lagerpetid silhouette based on artwork by Caetano Soares. b) paleoart depicting a life reconstruction of a lagerpetid by Caetano Soares. c) implied weighting analyses (k = 3 and 6). d) implied weighting analysis (k = 10).

and *Venetraptor gassenae*, our analysis recovered lagerpetids as a paraphyletic array towards Pterosauria, and therefore Lagerpetidae (sensu Ezcurra et al. 2020) contains only *Lagerpeton chanarensis*.

In this topology, the earliest-diverging pterosauroomorph is *Kongonaphon kely*, followed by a stepwise arrangement including *Lagerpeton chanarensis*, the unnamed Cerro da Alemoa form (UFSM 11611), *Ixalerpeton*

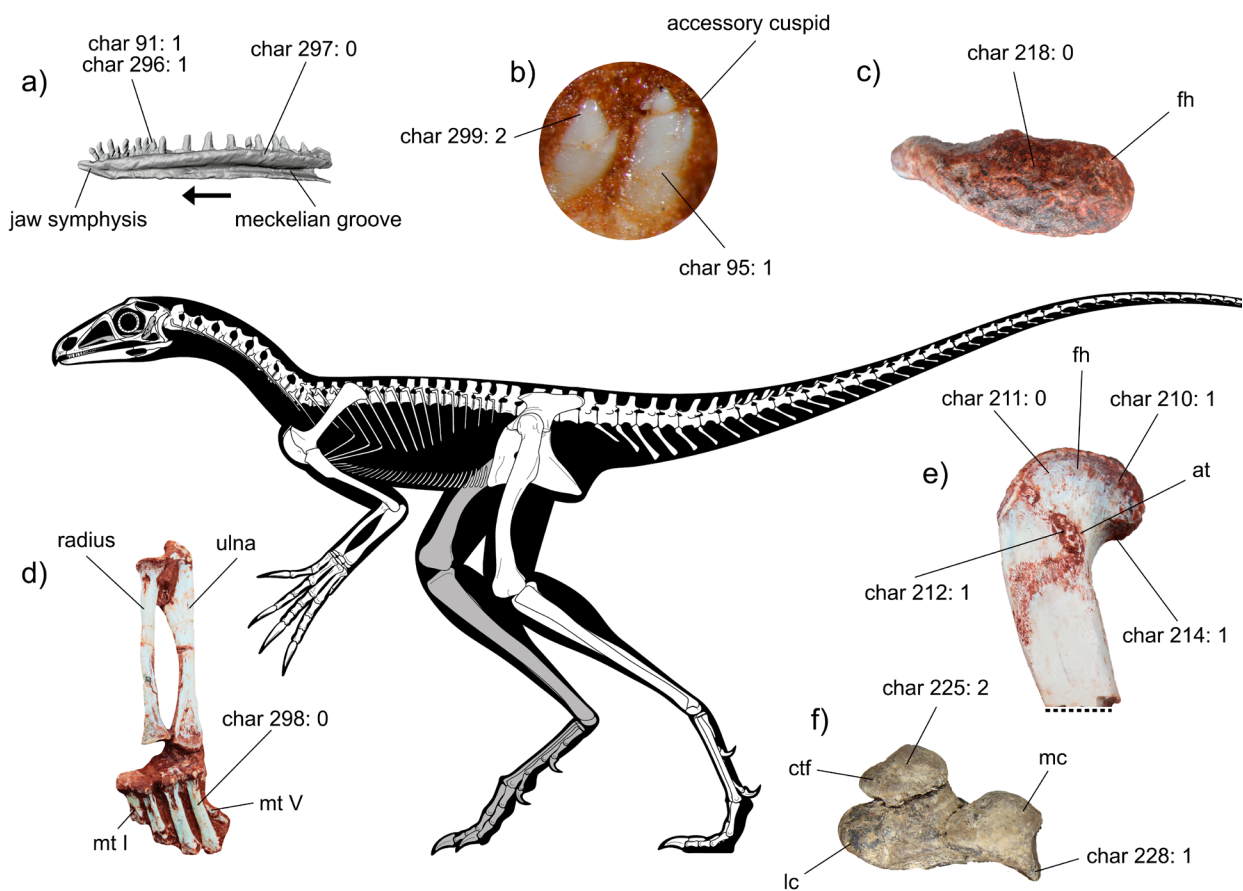


Figure 4. Synapomorphies in early-diverging pterosauiromorphs. Skeletal reconstruction of *Venetoraptor gassenae* represents the body plan of non-pterosaur pterosauiromorphs. a) *Ixalerpeton polesinensis* (ULBRA-PVT059) dentary (reversed) in medial view (modified from Ezcurra et al. 2020). b) *Ixalerpeton polesinensis* (ULBRA-PVT059) dentary teeth in lateral view. c) *Venetoraptor gassenae* (CAPPA/UFSM 0356) femoral head in proximal view. d) *Venetoraptor gassenae* (CAPPA/UFSM 0356) forelimb in lateral view (reversed). e) *Venetoraptor gassenae* (CAPPA/UFSM 0356) proximal half of the femur in anterior view. f) *Dromomeron romeri* (GR 218) distal end of the femur in distal view. Elements not to scale. Black arrow point to the anterior direction. Abbreviations: at: anterior trochanter; char: character; ctf: crista tibiofibularis; fh: femoral head; lc: lateral condyle; mc: medial condyle; mt: metacarpal.

polesinensis, and the unnamed Ischigualasto Formation form (PVSJ 883) successively. A clade formed by *Dromomeron romeri* + *Dromomeron gigas* diverges next, nesting as sister taxon of a clade containing *Venetoraptor gassenae* + “*Dromomeron*” *gregorii* and Pterosauria.

The newly added pterosaurs form a monophyletic Pterosauria composed of a clade of *Carniadactylus rosenfeldi* + *Seazzadactylus venieri*. *Arcticodactylus cromptonellus*, *Austriadactylus cristatus*, and *Austriadraco*

dallavecchiai nested in a polytomy with the former clade.

Two constrained analyses were carried out. The first forced a monophyletic Lagerpetidae, including all forms traditionally assigned to the clade (*Faxinalipterus minimus* was set as floating taxa), and the second forced a monophyletic Lagerpetidae sister to Pterosauria. Both resulted in MPTs 25 steps longer than those of the unconstrained analysis. Therefore, a more

inclusive Lagerpetidae is less parsimonious in the current dataset.

Three implied weighting analyses were run with concavity constants (k) of 3, 6, and 10, respectively. The first one resulted in 54 MPTs with a Fit of 133.48301 (Fig. 3c). A strict consensus tree reveals a Pan-Aves clade formed solely by Pterosauiomorpha plus Dinosauromorpha. Position of lagerpetids and pterosaurs within Pterosauiomorpha is the same as in the main (equal weighting) analysis, except for the inclusion of *Faxinalipterus minimus* as the earliest-diverging pterosauiomorph. On the other hand, Aphanosauria is recovered as a clade at the base of Dinosauromorpha. In this topology, *Mambachiton fiandohana* is the sister taxon to Dinosauriformes. The second one resulted in 324 MPTs with a Fit of 90.36078, maintaining most of the topology of the first analysis (Fig. 3c). The third analysis resulted in 63 MPTs with a Fit of 63.556356 (Fig. 3d). The topology is more like that of the main analysis, except that Aphanosauria is monophyletic and includes *Mambachiton fiandohana* in a trichotomy with *Spondylosoma absconditum* and *Teleocrater rhadinus*.

DISCUSSION

Herein we discuss the results of the performed phylogenetic analyses. The discussion will be based on the main (equal weighting) analysis, unless otherwise stated.

The position of *Mambachiton fiandohana* is similar to that of Nesbitt et al. (2023), thereafter recovered as the earliest-diverging pan-avian. Alternative placements for *Mambachiton fiandohana* as an aphanosaur or as a dinosauromorph sister taxon to Dinosauriformes are found in the implied weighting analyses. The latter placement as also recovered by Cau (2024). The plesiomorphic nature of the earliest pan-avians is underscored by this result. We

understand that the addition of characters that vary among aphanosaurs or that characterize the clade (such as the extra articular surface between the parapophysis and diapophysis for three-headed ribs in posterior cervicals; Nesbitt et al. 2017) is necessary so that the relationships of these early pan-avians can be properly investigated.

Faxinalipterus minimus was recovered outside Ornithodira, as in previous iterations of this dataset (Garcia et al. 2024a, b), differing from its position in the analysis of Kellner et al. (2022), where it nests as a lagerpetid pterosauiomorph. This is likely due to the lack of well-known lagerpetid apomorphies in the specimen, especially in the femur, as also pointed out by Foffa et al. (2024). Several of these apomorphies occur in the proximal and distal ends of the femur, such as the hook-shaped head and the enlarged and globular crista tibiofibularis in the distal end (Nesbitt et al. 2009, Nesbitt 2011, Ezcurra 2016, Müller et al. 2018b, 2023, Ezcurra et al. 2020, Garcia et al. 2024b). Nevertheless, our results align with those of Kellner et al. (2022), suggesting that contrary to the original description by Bonaparte et al. (2010), *Faxinalipterus minimus* does not represent a member of Pterosauria. In two of the implied weighting analyses ($k = 3$ and 6), however, *Faxinalipterus minimus* was recovered as the earliest-diverging lagerpetid.

The nesting of lagerpetids as sisters to Pterosauria was also recovered in iterations of other two independent datasets. Kammerer et al. (2020), which worked upon a modified version of the dataset of Nesbitt (2011) recovered Lagerpetidae as sister taxon of the clade *Scleromochlus taylori* + Pterosauria. When *Scleromochlus taylori* was not included in the analysis, the authors recovered Lagerpetidae within Dinosauromorpha, a traditional position at the time. Afterwards, Baron (2021) included

several new pterosaur OTUs in the dataset and recovered similar results. Convergently, the analysis by Ezcurra et al. (2020), which is a highly modified version of the dataset of Ezcurra (2016), also recovered Pterosauriomorpha comprised by the clade Lagerpetidae + Pterosauria. Müller et al. (2023) subsequently modified this dataset, including the newly discovered *Venetraptor gassenae* and recovered similar results. Therefore, our analysis here reinforces relationships between lagerpetids and pterosaurs, being the third independent dataset to recover such affinities within Pterosauriomorpha.

Although the results are similar, the topology in all the analyses performed here has a key difference in relation to those previously mentioned. Herein, Pterosauriomorpha is comprised of Pterosauria at the end of a succession of low diversity branches of taxa traditionally regarded as part of Lagerpetidae. This is particularly interesting, especially because 25 extra steps are necessary to form a traditional monophyletic Lagerpetidae as seen in all previous phylogenies (Nesbitt et al. 2009, Müller et al. 2018b, Ezcurra et al. 2020, Foffa et al. 2022). This is the first time such result is recovered, though it is not completely unforeseen. Comparable but not identical results are those of Kammerer et al. (2020) and Baron (2021), where Lagerpetidae is sister taxon of *Scleromochlus taylori* + Pterosauria. In recent contributions, Foffa et al. (2022, 2024) explored the anatomy and phylogenetic affinities of *Scleromochlus taylori*, reinforcing its placement within Pterosauriomorpha.

As of recent discoveries, it became known that several of the so called lagerpetids share apomorphies with pterosaurs which, until recently, were considered exclusive of the latter among ornithodirans (Ezcurra et al. 2020, Foffa et al. 2022, Müller et al. 2023, this study). Some of these include multicuspid teeth,

reduced to absent splenial, and a pubo-ischiatic plate (Ezcurra et al. 2020) (Fig. 4a, b), though the latter is a pan-avian sympleisiomorphy in our analyses, therefore not exclusive to Pterosauriomorpha. This is similar to the case of the silesaurids, previously considered a clade of dinosauriforms with several convergent features with ornithischian dinosaurs (Dzik 2003, Ferigolo & Langer 2007, Nesbitt et al. 2010, Langer et al. 2010, Langer & Ferigolo 2013), being included within the clade Ornithischia with increasing support in recent years (Cabreira et al. 2016, Müller & Garcia 2020a, 2023, Norman et al. 2022, Cau 2024, Fonseca et al. 2024, Müller 2024b). In our analyses, the clade including *Venetraptor gassenae* + "*Dromomeron gregorii*" and Pterosauria is supported by a metacarpal IV that is longer than the metacarpal III, a peculiar trait seen only in *Venetraptor gassenae* and pterosaurs among Triassic archosaurs (Fig. 4d). In the topology recovered by Müller et al. (2023), this is a convergent trait between lagerpetids and pterosaurs, which could potentially be shared among both groups. However, since the only other unequivocal lagerpetid with a preserved manus (i.e., *Dromomeron romeri*) presents a different character state, the distribution and evolution of that trait among non-pterosaur dinosauriforms remains elusive (but see Foffa et al. 2022, 2024). Moreover, as in previous analyses (Müller et al. 2023, Garcia et al. 2024b), "*Dromomeron*" *gregorii* is recovered away from *Dromomeron romeri* and *Dromomeron gigas*, rendering the genus paraphyletic and urging for a revision of "*Dromomeron*" *gregorii* considering new lagerpetid data. Regarding the affinities between the added pterosaur taxa, some deserve further thoughts. The sister taxon of *Seazzadactylus venieri* in our analysis is *Carniadactylus rosenfeldi*, which differs from the analysis of Baron (2021), where the sister taxon of the former is *Caviramus schesaplanensis*,

and also differs from Müller et al. (2023), where it is *Austriadraco dallavecchiai*. These differences are likely due to taxon sampling and character choice. All the above also differ slightly from an analysis using a pterosaur-focused dataset (Martínez et al. 2022), where *Seazzadactylus venieri* is recovered as the sister taxon of a clade including *Carniadactylus rosenfeldi* (*Eudimorphodon rosenfeldi* therein), *Arcticodactylus cromptonellus* (*Eudimorphodon cromptonellus* therein), and *Eudimorphodon ranzii*. Although our dataset currently does not include *Eudimorphodon ranzii* as an OTU, it does include *Arcticodactylus cromptonellus* and *Carniadactylus rosenfeldi*. Therefore, the sister taxon relationship between *Seazzadactylus venieri* and *Carniadactylus rosenfeldi* in our analysis is somewhat similar to that of Martínez et al. (2022).

Finally, we emphasize the exploratory nature of our analyses, and that the resultant topologies should be considered preliminary and will be tested further soon, with the inclusion of more characters and more OTUs, especially early-diverging pterosaurs.

CONCLUSIONS

This study provides a catalog of the pterosaur precursor taxa from the Late Triassic of southern Brazil. The discovery of these pterosaur precursors has provided significant new insights into the diversity and evolutionary context of the rise of Pterosauria from small ornithodiran forms found in the global South (Fig. 5). Our phylogenetic analyses, incorporating newly scored taxa such as the early-diverging pan-avian *Mambachiton fiandohana* and several pterosaurs, alongside revised character data, have lend support to the hypothesis that small ornithodirans traditionally grouped in the clade Lagerpetidae are the closest relatives of Pterosauria. Moreover, a novel, though preliminary, hypothesis of relationships among pterosauiromorphs has been recovered, with lagerpetids forming a grade of successive forms towards pterosaurs. Further testing is still needed to provide the necessary foundation for this topology, but if true, it closes the ghost-lineage between the earliest pterosaur precursors and true pterosaurs. The morphological disparity



Figure 5. Paleoart depicting a life reconstruction of the pterosaur precursor *Venetoraptor gassenae* by Matheus Fernandes Gadelha.

between the volant pterosaurs and other pterosauiromorphs has been gradually reduced but is still considerable and only with new finds will this gap be filled. Some of these finds have already occurred in the Triassic rocks of southern Brazil, ensuring a global impact for the pterosaur precursors found in this region. These results underscore the importance of the Brazilian Triassic beds in contributing to the global understanding of pterosaur origins and their early evolutionary history. The new data highlight the potential for future discoveries in the region to further elucidate the origins and early diversification of pterosaurs.

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Appendix I. Scores for the new operational taxonomic units.

Mambachiton fiandohana ??????????????????
 ?????????????0????????????????????????????
 ?????????????????????????????00?1?00000?0110?11?
 00????100?1????010????????????????????????100
 1000?1001?11010????????????010100?0?100?0?11
 0?0??
 ?????1????0????0????????????????

Arcticodactylus cromptonellus ?010??1111?????
 ?????020?1????0????0?00?0???0?100?????????
 ?????0?00????????01?000101????0?0???11?00?
 ?????????????????0101??1???0????????????????
 ??0??1????????????????????????????????0?100??
 0????0????????0????????????????????????????
 ??0??????0????????10?0?1??10?0????1?

Austriadactylus cristatus ?010001111????0??10?0
 ?1020??100??0??1?10000?0??0011??0?????????
 ???01?00??????101?000[01]01100?0?0??1??0?00
 ?????????????????0101???01100100???1??????
 ???0??101??00??000??00??000??0?0??0000???
 ?0?100??0????0????????0????????????????
 ?????????????????00????0????10?0?1010002111?1?

Austriadraco dallavecchiai ?0??????1?????????
 ?????????????0????011????????????????
 0??00?00?21??????00??????0??????0?00??????
 ???????????0101???011?01????????????????
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 ?????????????????????????????????????
 ?0????????10?0?1??10?[02]?11?1?

Carniadactylus rosenfeldi ?010001111??1200??1
 000?1020??100??0??1?10011?1??0011??01?????
 ?????0000?00?00?221?101?000101001?0????1?1
 0?00??????1??1????????0101??101100100??1?
 1100??0??0??101??00??000??00??000??0?0??
 0000????0?100??0????0????????1????????
 ?????1????11??????0????010000??0?01??10?0?
 1111000111112

Seazzadactylus venieri ?01000111??0200??1000?
 1020??1????????11????011????????????01
 00?00?00?221?101?000101001?0????1??1?00????
 ???????1??????01???011?0100??1?1100??0??0?

?101??00??000??00??0000??0?0??0000?????0??00
 ??0????0???????????1?????????????????????????
 ?????????????0?????01???10?0?111100011?11?

Appendix II. Changes to the scores of operational taxonomic units.

Asilisaurus kongwe

Character 92: changed from (?) to (0).
 Character 98: changed from (?) to (0).
 Character 181: changed from (1) to (0).
 Character 220: changed from (1) to (0).

Diodorus scytobrachion

Character 212: changed from (1) to (?).

Gamatavus antiquus

Character 206: changed from (1) to (0).
 Character 220: changed from (1) to (0).

Ixalerpeton polesinensis

Character 74: changed from (?) to (1).
 Character 90: changed from (?) to (0).
 Character 91: changed from (?) to (0).
 Character 92: changed from (?) to (0).
 Character 93: changed from (?) to (1).
 Character 94: changed from (?) to (0).
 Character 95: changed from (?) to (1).
 Character 96: changed from (?) to (1).
 Character 97: changed from (?) to (0).
 Character 98: changed from (?) to (1).
 Character 100: changed from (?) to (0).

Kongonaphon kely

Character 23: changed from (0) to (?).
 Character 25: changed from (1) to (2).

Kwanasaurus williamparkeri

Character 203: changed from (0) to (1).
 Character 212: changed from (1) to (2).

Lagerpeton chanarensis

Character 74: changed from (?) to (1).
 Character 90: changed from (?) to (0).
 Character 91: changed from (?) to (0).
 Character 92: changed from (?) to (0).
 Character 93: changed from (?) to (1).
 Character 94: changed from (?) to (0).
 Character 95: changed from (?) to (1).

Character 96: changed from (?) to (1).
 Character 97: changed from (?) to (0).
 Character 98: changed from (?) to (1).
 Character 100: changed from (?) to (0).

Lewisuchus admixtus

Character 203: changed from (0) to (1).
 Character 204: changed from (0) to (1).
 Character 206: changed from (0) to (1).

Lutungutali sitwensis

Character 200: changed from (1) to (?).
 Character 201: changed from (0) to (1).
 Character 203: changed from (0) to (1).
 Character 220: changed from (1) to (0).

Venetoraptor gassenae

Character 291: changed from (0) to (?).

Appendix III. Added characters.

293 (new). Proximal tarsals unfused to tibia (0); fused to tibia, forming a tibiotarsus (1).

294 (278 of Müller et al. 2023). Dentary, tooth row teeth present along entire length of the dentary (0); teeth absent in the anterior end (1); dentary edentulous (2).

295 (753 of Müller et al. 2023). Splenial, development anteriorly developed covering more than three-quarters of the length of the dentary (0); reduced to the level of the posterior half of the dentary or bone absent (1).

296 (680 of Müller et al. 2023 modified). Teeth, generalized morphology of maxillary and dentary tooth crowns single, pointed crown (0); flattened platform with pointed cusps (1); mesiodistally arranged cusps

297 (1 of Müller et al. 2023). Skull and lower jaws, interdental plates absent (0); present, small and well-spaced from each other (1); present, large and close to or contacting with each other (2).

298 (450 of Müller et al. 2023). Metacarpus, metacarpal IV longer than metacarpal III (0); equal or shorter than metacarpal III (1).

299 (304 of Müller et al. 2023). Teeth, serrations on the maxillary/dentary crowns absent or

present in just a two or a few centrally placed maxillary crowns (0); distinctly present on the distal margin and usually apically restricted, low or absent on the mesial margin of most crowns (1); present and distinct on both margins of most crowns (2).

300 (776 of Müller et al. 2023). Pteroid bone absent (0); present (1).

301 (300 of Müller et al. 2023). Teeth, maxillary and/or dentary tooth crowns generally homodont (0); markedly heterodont (gross change in morphology) (1).

302 (771 of Müller et al. 2023). Haemal arches, haemal spines developed as filiform processes below and parallel to adjacent centra posterior to the first three to seven caudal vertebrae absent (0); present (1).

303 (799 of Müller et al. 2023). Prepubis, as a separate ossification absent (0); present (1).

304 (773 of Müller et al. 2023). Coracoid, relative dorsoventral length less than 2/3 length of scapula (0); 2/3 or more length of scapula (1).

305 (398 of Müller et al. 2023). Coracoid, posterior border in lateral view unexpanded posteriorly (0); moderately expanded posteriorly (1); strongly expanded posteriorly - the entire border, not only the posteroventral region as is the case in the postglenoid process - and, as a result, the shoulder girdle acquires an L-shape in lateral view (2).

Appendix IV. Synapomorphies of Pterosauromorpha and clades within from the main analysis.

Pterosauromorpha: Char. 25: 0 & 1 → 2 (rostradorsal margin of the maxilla with a strong inflection at the base of the ascending ramus); Char. 95: 0 → 1 (middle maxillary/dentary teeth with a straight long axis); Char. 210: 0 → 1 (hook-shaped femoral head in medial and lateral views); Char. 211: 1 → 0 (absent dorsolateral trochanter of the femur); Char. 297: 2 → 0 (interdental plates absent); Char.

299: 2 → 0 (serrations on the maxillary/dentary crowns absent or present in just a two or a few centrally placed maxillary crowns).

Lagerpeton chanarensis plus other pterosaururomorphs: Char. 93: 0 → 1 (maxillary/dentary teeth with an apicobasally short and subtriangular crown shape); Char. 214: 0 → 1 (craniolateral surface of the femoral head with a ventral emargination); Char. 218: 1 → 0 (absent transverse groove on proximal surface of the femoral head); Char. 296: 0 → 1 (generalized morphology of maxillary and dentary tooth crowns flattened platform with pointed cusps).

Ixalerpeton polesinensis plus other pterosaururomorphs: Char. 225: 1 → 2 (crista tibiofibularis on the distal end of the femur larger (or equal) than the lateral condyle and globular).

PVSJ 883 plus other pterosaururomorphs: Char. 226: 0 → 1 (squared off near 90° or acute craniomedial corner of the distal end of the femur).

Dromomeron romeri plus Dromomeron gigas: Char. 228: 0 → 1 (femoral distal end with sharp ridge on the anteromedial edge); Char. 229: 0 → 1 (femoral distal end with lateral tuberosity on the anterolateral edge).

Dromomeron romeri and Dromomeron gigas plus other pterosaururomorphs: Char. 224: 0 → 1 (cranial surface of the distal portion of the femur with a distinct scar mediolaterally orientated).

Venetoraptor gassenae plus 'Dromomeron gregorii': Char. 212: 0 → 1 (femoral anterior/lesser trochanter present and forms a steep margin with the shaft but is completely connected to it).

Venetoraptor gassenae and 'Dromomeron gregorii' plus Pterosauria: Char. 298: 1 → 0 (metacarpal IV longer than metacarpal III).

Pterosauria: Char. 9: 0 → 1 (rostral edge of the laterotemporal fenestra rostral to the caudal edge of the orbit); Char. 37: 0 → 1 (absent postfrontal); Char. 50: 0 → 1 (jugal acute

angle between ascending process and caudal process); Char. 169: 0 → 1 (absent manual digit V); Char. 293: 0 → 1 (proximal tarsals fused to tibia, forming a tibiotarsus); Char. 300: 0 → 1 (pteroid bone present); Char. 302: 0 → 1 (haemal spines developed as filiform processes below and parallel to adjacent centra posterior to the first three to seven caudal vertebrae).

***Seazzadactylus venieri* plus *Carniadactylus rosenfeldi*:** Char. 42: 0 → 1 (jugal long axis oblique to the alveolar margin of the maxilla); Char. 43: 0 → 1 (jugal rostral and caudal rami ventral margin forming an angle of less than 180°; Char. 74: 1 → 0 (dorsal surface of the rostral tip of the dentary at nearly the same plane as the rest of the alveolar margin of the bone); Char. 83: 1 → 2 (absent mandibular fenestra); Char. 96: 1 → 0 (maximum of 25 dentary teeth).

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