



INSTITUTO DE GEOCIÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM GEOCIÊNCIAS

**CONTRIBUIÇÃO AO CONHECIMENTO DOS GRUPOS
“RAUISUCHIA”, ORNITHOSUCHIDAE E ERPETOSUCHIDAE
(ARCHOSAURIA, PSEUDOSUCHIA) E SUA IMPORTÂNCIA NO
CONTEXTO DA COMPOSIÇÃO PALEOFAUNÍSTICA DO
TRIÁSSICO DO RIO GRANDE DO SUL, BRASIL**



MARCEL BAÊTA LACERDA SANTOS

Orientador: Prof. Dr. Cesar Leandro Schultz

Porto Alegre – 2017

UNIVERSIDADE FEDERAL DO RIO GRANDE DO SUL
INSTITUTO DE GEOCIÊNCIAS
PROGRAMA DE PÓS-GRADUAÇÃO EM GEOCIÊNCIAS

CONTRIBUIÇÃO AO CONHECIMENTO DOS GRUPOS “RAUISUCHIA”,
ORNITHOSUCHIDAE E ERPETOSUCHIDAE (ARCHOSAURIA,
PSEUDOSUCHIA) E SUA IMPORTÂNCIA NO CONTEXTO DA COMPOSIÇÃO
PALEOFAUNÍSTICA DO TRIÁSSICO DO RIO GRANDE DO SUL, BRASIL

MARCEL BAÊTA LACERDA SANTOS

ORIENTADOR: Prof. Dr. Cesar Leandro Schultz

BANCA EXAMINADORA

Prof. Dr. Marco Brandalise de Andrade – Faculdade de Biociências,
Pontifícia Universidade Católica, PUC, Porto Alegre, RS.

Profa. Dra. Marina Bento Soares-Instituto de Geociências, Universidade
Federal do Rio Grande do Sul, UFRGS, Porto Alegre, RS.

Profa. Dra. Julia Brenda Desojo-Divisão de Paleontologia, Universidade
Nacional de La Plata, La Plata, Argentina.

Tese de Doutorado apresentada ao Programa de
Pós-Graduação em Geociências como requisito
parcial para a obtenção do título de Doutor em
Ciências

Porto Alegre - 2017

CIP - Catalogação na Publicação

Santos, Marcel Baêta Lacerda
CONTRIBUIÇÃO AO CONHECIMENTO DOS GRUPOS
"RAUISUCHIA", ORNITHOSUCHIDAE E ERPETOSUCHIDAE
(ARCHOSAURIA, PSEUDOSUCHIA) E SUA IMPORTÂNCIA NO
CONTEXTO DA COMPOSIÇÃO PALEOFAUNÍSTICA DO TRIÁSSICO
DO RIO GRANDE DO SUL, BRASIL / Marcel Baêta Lacerda
Santos. -- 2017.
292 f.
Orientador: Cesar Leandro Schultz.

Tese (Doutorado) -- Universidade Federal do Rio
Grande do Sul, Instituto de Geociências, Programa de
Pós-Graduação em Geociências, Porto Alegre, BR-RS,
2017.

1. Archosauria. 2. Pseudosuchia. 3. Triássico. 4.
Filogenia. 5. Paleontologia do Rio Grande do Sul. I.
Schultz, Cesar Leandro, orient. II. Título.

Aos meus pais Vivian e Mauro



- Calvin & Hobbes, Bill Waterson

AGRADECIMENTOS

Com o doutorado, eu aprendi que mesmo sendo a principal meta a elaboração de uma tese, a vivência, o conhecimento e a experiência adquirida durante esta jornada é tão relevante quanto o resultado do trabalho em si. Ao longo desta época, tive importante apoio da minha família, principalmente de minha mãe, Vivian, que sempre apoiou meu interesse pela paleontologia, a ciência e a leitura, e de meu pai, Mauro, que me ensinou a entender e gostar do ambiente acadêmico. Infelizmente, está além das minhas capacidades expressarem o meu agradecimento pelos inúmeros momentos de apoio, carinho e a importância deles ao longo de minha vida e na construção da pessoa que eu sou hoje. Eu agradeço também aos meus avôs, Ney e Mauro, e minhas avós, Éclair e Ana Maria, por me apoiarem de sua maneira e pelo carinho que eles sempre me demonstraram, independente do caminho profissional que eu escolhi. Também sou muito grato pelo apoio e convívio de meus padrinhos Ana Regina e Alexandre, meus tios Ana Paula e José Renato; Antônio e Rita; e Luis Augusto; meus irmãos Bruno e Amanda; aos meus primos, que apesar da pouca convivência nos últimos anos por morar longe de Curitiba, os tenho no coração. Eu agradeço de todo o coração a Elisabete Dassie pelo seu apoio e o carinho ao longo destes anos. Gostaria de dizer mais, mas minhas limitações poéticas me impedem de expressar de forma adequada o quão importante ela é para mim. Sem todo este apoio e suporte, eu tenho certeza que não teria conseguido realizar esta etapa de meu sonho profissional e me sinto extremamente afortunado em tê-los em minha vida.

Eu agradeço imensamente meu orientador Dr. Cesar Schultz pelo apoio, discussões e encorajamento ao longo do processo de elaboração desta tese. Sou grato também a Dra. Marina Bento Soares pelo apoio e o convívio. Agradeço ao prof. Fernando Sedor e ao Dr. Eliseu Dias, que sempre serão meus professores e, mais importante, meus amigos e referências de profissionais da área da paleontologia e ciências naturais.

Devido à necessidade da vida de estudante vindo de outro estado, tive a grande oportunidade de dividir moradia em Porto Alegre com pessoas incríveis

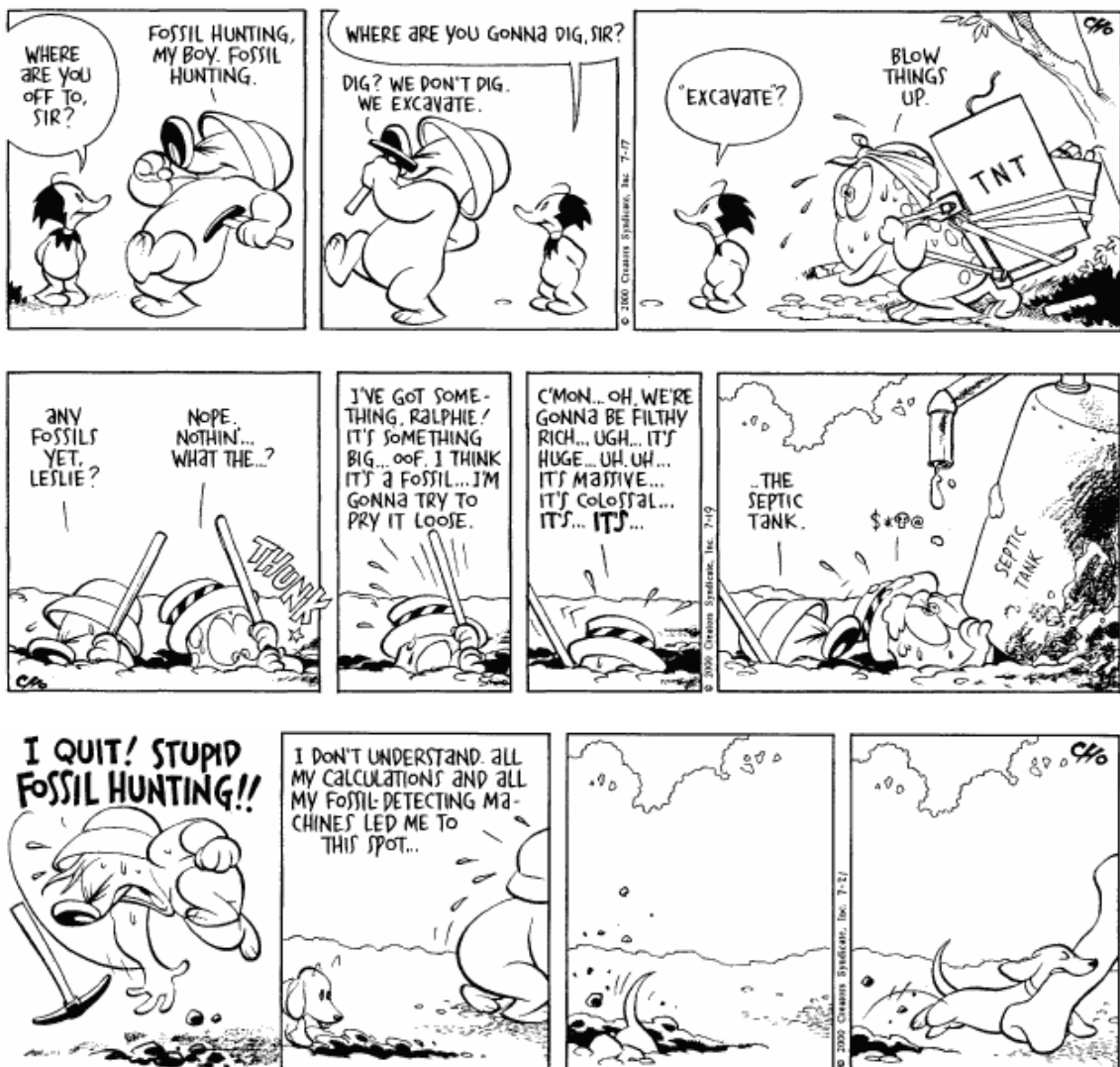
que hoje conto como grandes amigos. Sou muito grato ao Alexandre Liparini e ao Marco Aurélio França, pela ajuda com moradia quando eu me mudei para Porto Alegre e pela amizade derivada desde então. Agradeço aos meus amigos do museu da UFPR e hoje, colegas de profissão, David Dias, Rafael Silva, Thiago Carlisbino e Victor Pauliv, pelo convívio, amizade e pelo apoio tanto na paleontologia quanto na vida. Ao Agustin Martinelli, pela amizade e os incentivos derivados das várias e frutíferas discussões sobre paleontologia tanto no laboratório quanto nas muitas saídas de campo. Ao Heitor Francischini e a Paula Dias pela sua amizade e apoio. Ao Felipe Pinheiro e Leonardo Kerber, colegas e amigos da época do mestrado e que hoje seguem na profissão acadêmica de forma notável. Ao Marcos Sales, pela sua amizade e companheirismo, tanto no velho continente quanto no novo.

Sou muito grato pelas várias amizades que fiz na paleontologia no Rio Grande do Sul, principalmente a Ana Emilia Quevedo, Adriana Strapasson, Alessandra Boos, Ana Burst, Andressa Paim, Bianca Mastrantonio, Brodsky Macedo, Camila Mello, Clara Heinrich, Daniel Fortier, Elver Mayer, Fábio Veiga, Flávio Pretto, Morgan Guignard, Maurício Schmitt, Paulo Romo de Vivar, Pedro Morais, Pedro Xavier, Tiago Raugust, Tomaz Melo e Voltaire Paes. Agradeço ao Luís Flávio Lopes (UFRGS) pelas fotografias de incrível qualidade, ao professor Dr. Vitor Pereira e ao Protássio Paim (UFRGS) pelo apoio, o aprendizado e o acesso ao banco de dados das análises de elementos de terras raras.

Também agradeço meus amigos André Bongestabs, Rodrigo Fiedler, Thomas Killing, Gustavo D'agnoluzzo, Denis Miranda, Guilherme Wahrhafting, William Gnoatto, Vicente Pereira, Rodrigo Costa, Ricardo Santos e Alexandre Guiss pela amizade ao longo de mais de 15 anos de incontáveis histórias e momentos que nunca vou esquecer, muitos dos quais me fazem rir até hoje.

Agradeço pelo acesso às coleções científicas a: Átila Da-Rosa (UFMS), Ana Maria Riberio (FZB), Carlos Nunes Rodrigues (MMACR), Christian Klung (PIZ), Henrik Stöhr (GPIT), Jorge Ferigolo (FZB), Lorna Steel (NHMUK), Lucas Fioreli (CRILAR), Marco Brandalise (MCP), Oliver Rauhut (BSPG), Rainer Schoch (SMNS), Ricardo Martinez (PVSJ), Sandra Chapman (NHMUK), Tomaz

Sulej (ZPAL). Agradeço também ao CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) pela bolsa de doutorado e ao programa DAAD (Deutscher Akademischer Austauschdienst) pela bolsa de curta duração que me permitiu ver coleções na Europa e ao Dr. Rainer Schoch que cordialmente aceitou ser meu orientador durante o período de duração desta bolsa. Agradeço também a aos membros da banca examinadora Dr. Marco Brandalise de Andrade e Dra. Julia Brenda Desojo.



- Liberty Meadows, por Frank Cho

RESUMO

Os arcossauros (Archosauria) são um grupo monofilético de diápsidos que apresentaram uma rica história evolutiva de diversificação de formas, com os únicos representantes vivos apenas as aves e os crocodilianos. A evolução do grupo durante o Período Triássico é uma das áreas dentro da paleontologia de vertebrados que tem apresentado um acréscimo de interesse nos últimos 20 anos. Isto se deve a uma gama de novas descobertas que, combinados com revisões de espécimes historicamente problemáticos e/ou pouco conhecidos na literatura, tem resultado em um melhor entendimento na variação morfológica do grupo e permitido análises filogenéticas mais robustas devido a um maior número amostral de táxons. A presente tese consiste em um detalhado Estado da Arte do conhecimento da origem e evolução dos arcossauros, com ênfase na linhagem Pseudosuchia. A sua contribuição para esta área é na forma de três artigos: 1) A descrição da nova espécie de “rauissuquídeo” (“Rauisuchia”) *Dagasuchus santacruzensis*, da Zona de Associação (ZA) de *Santacruzodon* e sua importância para a distribuição paleofaunística do Triássico do Rio Grande do Sul; 2) A descrição de novos espécimes atribuídos ao “rauissuquídeo” (“Rauisuchia”) *Prestosuchus chiniquensis*, considerados como formas juvenis, que teriam importância na identificação das variações ontogenéticas desta espécie e as consequências disto na escolha de caracteres para matrizes de estudos filogenéticos; 3) A descrição de *Pagosvenator candelariensis*, da ZA de *Dinodontosaurus*, o primeiro erpetossuquídeo (Erpetosuchidae) para o Triássico do Rio Grande do Sul e suas implicações para o conhecimento sobre a distribuição paleobiogeográfica deste grupo e suas afinidades filogenéticas com outro grupo de arcossauros, os ornitossuquídeos (Ornithosuchidae).

Palavras chave: Archosauria, Pseudosuchia, Erpetosuchidae, Ornithosuchidae, “Rauisuchia”, Triássico, Filogenia, Taxonomia.

ABSTRACT

Archosaurs (Archosauria) are a monophyletic group of diapsids that display a rich and diverse evolutionary history, with the only extant forms being the birds and crocodylians. The evolution of this group during the Triassic Period is one of the fields of study within vertebrate paleontology that has displayed an increase in interest in the past 20 years. This is due to a large number of new discoveries that combined with the revision and historically important but not well described specimens have resulted in a better understanding of the morphological and phylogenetic variation presented in early archosaurs. This, in turn, has allowed for better sampled data matrixes and better supported cladistic studies. This thesis presents a State of the Art of the current knowledge of the origins and evolution of Archosauria, with a focus on the Pseudosuchian lineage during the Triassic. Its contribution is in the form of three publications: 1) the description of a new species of “rauisuchian” (“Rauisuchia”) archosaur *Dagasuchus santacruzensis*, from the *Santacruzodon* Assemblage Zone (AZ) and discuss its importance in the paleofaunistic distribution of the Triassic of the Rio Grande do Sul State. 2) the description and study of new specimens attributed to the “rauisuchian” taxon *Prestosuchus chiniquensis*, which are identified as juvenile forms, which has important ramifications in the identification of ontogenetic variation in species and in establishing character states when constructing data matrixes for use in cladistic studies; 3) the description of *Pagosvenator candelariensis*, from the *Dinodontosaurus* AZ, which is the first erpetosuchid (Erpetosuchidae) for the Triassic of the Rio Grande do Sul State and has interesting implications in the paleobiogeographical distribution of this group and its phylogenetic affinities with another group of Triassic archosaurs, the ornithosuchians (Ornithosuchidae).

Keywords: Archosauria, Pseudosuchia, Erpetosuchidae, Ornithosuchidae, “Rauisuchia”, Triassic, Phylogeny; Taxonomy.

LISTA DE FIGURAS

Figura 1. Diagrama simplificado da evolução dos arcossauros segundo a proposta por Gauthier (1986), utilizando a nomenclatura dos grupos presente em Nesbitt (2011).....	12
Figura 2. Localização e extensão da Bacia do Paraná e das supersequências Sanga do Cabral e Santa Maria, baseado em Zerfass <i>et al.</i> (2003). Tabela crono e bioestratigrafia das unidades triássicas sul-brasileiras, modificado de Horn <i>et al.</i> (2014) com a correlação estratigráfica entre as faunas desta idade com Madagascar, Argentina e África	15
Figura 3. Mapas de distribuição dos climas ao longo do Pangea, ao longo do Período Triássico	19
Figura 4. Exemplos de arcossauriformes.....	22
Figura 5. Exemplos de arcossauros	25
Figura 6. Cladograma baseado em Pough (2006) modificado com resultados apresentados nas propostas de Nesbitt (2011) e Ezcurra (2016) representando a distribuição temporal dos grandes grupos de descendentes dos diápsidos.....	26
Figura 7. Cladogramas apresentando o consenso sobre o conhecimento da filogenia dos arcossauromorfos em dois momentos históricos	27
Figura 8. Proposta de Chatterjee (1982) da evolução dos arcossauros baseada na articulação mesotarsal	28
Figura 9. Cladograma detalhando a distribuição temporal dos grupos mais inclusivos dentro de Archosauria (Modificado de BUTLER <i>et al.</i> , 2014)	31
Figura 10. Distribuição global de táxons de “rauissuquídeos” (Modificado de NESBITT <i>et al.</i> , 2013; LESSNER <i>et al.</i> , 2016).....	33
Figura 11. Exemplos de padrão corporal de alguns “rauissuquídeos”.....	35
Figura 12. Esquema apresentando a porção rostral, em norma esquerda, de alguns táxons de arcossauriformes, indicando os diferentes tipos de aberturas acessórias presentes na região de contato do pré-maxilar com o maxilar	38

Figura 13. Esquema comparativo das características da cintura pélvica e posicionamento dos apêndices locomotores posteriores em arcossauriformes.....	39
Figura 14. Ilustração esquemática comparativa entre dois ilium de “rauissuquídeos”	40
Figura 15. Cladograma redesenhado da proposta filogenética de Gauthier (1986) onde arcossauros são divididos em duas linhagens, uma que futuramente daria origem aos crocodilos (Pseudosuchia) e outra as aves (Ornithosuchia).....	48
Figura 16. Cladograma redesenhado da proposta filogenética de Benton & Clark (1988) onde a linhagem pró-crocodiliana, dentro de Archosauria, foi renomeada Crocodylotarsi	49
Figura 17: Cladograma redesenhado da proposta de Sereno & Arcucci (1990) para Archosauria	50
Figura 18. Diagrama filogenético de Sereno (1991) indicando a barra temporal encurtada formada pelo pós-orbital e o esquamosal (em vermelho) e a fenestra infratemporal de aspecto triangular característica dos súquios, na comparação com três <i>outgroups</i> . Modificado de Mastrantonio (2010)	51
Figura 19. Cladograma redesenhado da proposta filogenética de Parrish (1993) onde Prestosuchidae e Rausuchidae estão separados, com apenas este último em Rausuchia	52
Figura 20. Cladograma redesenhado da proposta filogenética de Juul (1994)	53
Figura 21. Cladograma redesenhado da proposta filogenética de Gower (2002)	57
Figura 22. Cladograma redesenhado da proposta de Nesbitt (2003).....	59
Figura 23. Análise filogenética de Gower & Nesbitt (2006) apresentando o consenso dos três cladogramas mais parcimoniosos	61
Figura 24. Árvore de consenso dos dois cladogramas mais parcimoniosos da análise de Weinbaum & Hungerbühler (2007).....	62

Figura 25. Proposta de Nesbitt (2007) com <i>Effigia okeeffeae</i> dentro dos arcossauros basais	63
Figura 26. Análise de Brusatte <i>et al.</i> (2010) de consenso estrito de 70 árvores mais parcimoniosas.....	68
Figura 27. Proposta de Gauthier <i>et al.</i> (2011) baseada em Nesbitt (2009, 2011) para o holótipo de <i>Poposaurus gracilis</i> e o novo espécime do mesmo táxon	72
Figura 28. Proposta filogenética de Nesbitt (2011).....	73
Figura 29. Árvore de consenso estrito de Mastrantonio <i>et al.</i> (2013) apresentando as afinidades de <i>Prestosuchus chiniquensis</i> baseados apenas em caracteres da caixa craniana.....	74
Figura 30. Distribuição dos caracteres-chave na evolução de Poposauroidea nas hipóteses de Nesbitt (2011) e Brusatte <i>et al.</i> (2011) baseados na matrizes modificadas de Butler <i>et al.</i> (2011).....	76
Figura 31. Cladograma de consenso estrito indicando as afinidades filogenéticas de <i>Vivaron haydeni</i> dentro de Rausuchidae (Retirado de Lessner <i>et al.</i> , 2016)	78
Figura 32. Cladograma simplificado de consenso estrito de 81 AMPs, indicando a distribuição dos dois estados do novo carácter proposto no artigo entre os táxons. Modificado de Silva <i>et al.</i> , (2016).....	79
Figura 33. Cladograma de consenso estrito de 180 AMPs de Nesbitt & Desojo (2017) das interrelações filogenéticas de <i>Luperosuchus</i> dentro de Archosauria	80
Figura 34. Alguns elementos dos lectótipo de <i>Prestosuchus chiniquensis</i>	80
Figura 35. Fotografia do grande crânio do espécime UFRGS-PV-0156-T, e desenhos esquemáticos na mesma. Modificado de Barberena (1978) e Azevedo (1993).....	82
Figura 36. Desenho esquemático do espécime UFRGS-PV-0629-T, com os ossos como foram encontrados. Retirado de Mastrantonio (2010).....	83

Figura 37. Desenho esquemático do espécime ULBRA-PVT-281 Retirado de Silva <i>et al.</i> (2016)	84
Figura 38. Desenho esquemático do espécime MCP-146 em vista dorsal (A); Fotografia (B) do mesmo espécime na mesma vista que (A) indicando as diferentes costelas sacrais e seu contato com o íleo, comparando a articulação com o presente em UFRGS-PV-0629-T (C).....	85
Figura 39. Reconstrução do esqueleto de <i>Rauisuchus tiradentes</i> mostrando os elementos preservados Retirado de Lautenschlager & Rauhut (2014).....	87
Figura 40. Detalhes de alguns elementos do lectótipo de <i>Ruisuchus tiradentes</i> . Fotografia (A) e figura esquemática (B) do pré-maxilar direito em vista lateral; Figuras esquemáticas da sexta vértebra cervical em normas (C) anterior, (D) lateral direita e (E) posterior; Fotografia (F) e ilustração esquemática (G) de uma vértebra caudal da série anterior em vista lateral esquerda. Retirado de Lautenschlager & Rauhut (2014).....	88
Figura 41. Fotografias de alguns elementos do lectótipo de <i>Procerosuchus celer</i>	89
Figura 42, o fêmur (BSPG AS XXV 53) e tíbia direitos (BSPG AS XXV 54) atribuídos a <i>Hoplitosuchus raii</i> , mas interpretado por Kishlat & Barberena (1999) e Ezcurra (2012) como pertencendo a um dinossauriforme	90
Figura 43. Fotografia e ilustração esquemática do crânio de <i>Decuriasuchus quartacolonia</i> e reconstrução do esqueleto. Retirado de França <i>et al.</i> (2011)	92
Figura 44. Figura esquemática da assembleia contendo os nove espécimes de <i>Decuriasuchus quartacolonia</i> (MCN PV10105a-i). Retirado de França <i>et al.</i> (2011).....	93
Figura 45. Reconstrução de <i>Ornithosuchus woodwardi</i> (<i>sensu</i> von BACZKO & EZCURRA, 2016) em postura bípede com a concepção antiga da cauda arrastando no solo (Retirado de Walker, 1964).....	95
Figura 46. Proposta redesenhada de Bonaparte (1975) para a evolução dos arcossauros onde Ornithosuchia seria derivado de Euparkeridae	98

Figura 47. Proposta filogenética de Gauthier (1986).....	98
Figura 48. Cladograma redesenhado da proposta filogenética de Sereno (1991).....	99
Figura 49. Cladograma simplificado redesenhado da proposta filogenética de von Baczko <i>et al.</i> (2014).....	101
Figura 50. Distribuição global dos táxons atribuídos a Ornithosuchidae. Modificado de von Baczko & Ezcurra (2013).....	102
Figura 51. Desenhos esquemáticos dos crânios de <i>Ornithosuchus longidens</i> e <i>Riojasuchus tenuisiceps</i> , modificado de Sereno (1991) com alterações em <i>R. tenuisiceps</i> baseado em von Baczko & Desojo, (2016).....	104
Figura 52. Fotografias e desenhos interpretativos do holótipo (PVL 2578) de <i>Venaticosuchus rusconii</i> em vistas lateral direita (A) e esquerda (B). Modificado de von Baczko <i>et al.</i> (2014).....	106
Figura 53. Filogenia de Thecodontia e sua distribuição temporal modificada de Bonaparte (1982)	111
Figura 54. Distribuição global dos táxons atribuídos Erpetosuchidae. Modificado de Nesbitt & Butler (2012).....	113
Figura 55. Ilustrações esquemáticas dos diferentes elementos de <i>Erpetosuchus granti</i> . Modificado de Benton & Walker (2002)	114
Figura 56. Ilustração esquemática do espécime AMNH 29300 em vista lateral direita. Modificado de Olsen <i>et al.</i> (2000).....	116
Figura 57. Fotografias de alguns elementos do holótipo (NHMUK R8646) de <i>Parringtonia gracilis</i> . Modificado de Nesbitt & Butler (2012)	117
Figura 58. Fotografia do holótipo (SMNS 4760) de <i>Dyoplax arenaceus</i>	118
Figura 59. Fotografia (A) e desenho esquemático (B) do crânio de <i>Dyoplax arenaceus</i>	120

LISTA DE ABREVIACOES INSTITUCIONAIS

BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munique, Alemanha.

CAMZM, University Museum of Zoology, Cambridge, Reino Unido.

CPEZ, Coleção de Paleontologia do Museu Walter Ilha, São Pedro do Sul, Rio Grande do Sul, Brasil.

CRILAR, Centro Regional de Investigaciones Científicas y Transferencia Tecnológica de La Rioja, La Rioja, Argentina.

ELGNM, Elgin Museum, Elgin, Reino Unido.

GPIT, Institut für Geowissenschaften, Universität Tübingen, Alemanha

MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul (FZBRS), Porto Alegre, Rio Grande do Sul, Brasil.

MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, EUA.

MMACR PV-T, Museu Municipal Aristides Carlos Rodrigues (PV-T, Coleção de Paleovertebrados do Triássico), Candelária, Rio Grande do Sul, Brasil.

NHMUK (ex BMNH), Natural History Museum, Londres, Reino Unido.

PVL, Instituto Miguel Lillo, Universidad Nacional de Tucumán (Colección Paleontologia de Vertebrados), San Miguel de Tucumán, Argentina.

PVSJ, Museo de Ciencias Naturales, Universidad nacional de San Juan, San Juan, Argentina.

SMNS, Staatliches Museum für Naturkunde, Stuttgart, Alemanha.

TTUP, Texas Tech University Paleontological Collections, Lubbock, Texas, EUA.

ULBRA-PVT, Universidade Luterana do Brasil, (PV, Coleção de paleovertebrados; T, Triássico), Canoas, Rio Grande do Sul, Brasil.

UFRGS-PV-T, Universidade Federal do Rio Grande do Sul (PV, Paleontologia de Vertebrados; T, Triássico), Porto Alegre, Rio Grande do Sul, Brasil.

ZPAL, Institute of Paleobiology, Polish Academy of Science, Warsaw, Polnia.

SUMÁRIO

Parte 1

1. INTRODUÇÃO	11
1.2. Contexto geológico e paleoambiental	13
2. ORIGEM E EVOLUÇÃO DOS ARCOSSAUROS	20
3. O CLADO ARCHOSAURIA	23
4. A LINHAGEM PSEUDOSUCHIA-QUESTÕES NOMENCLATURAIS	27
5. “RAUISUCHIA”	32
5.1. Uma breve caracterização dos “rauissuquídeos”	32
5.2 Estado da arte	41
5.3. “Rauissuquídeos” do Brasil	80
<i>Prestosuchus chiniquensis</i>	80
<i>Rauisuchus tiradentes</i>	87
<i>Procecosuchus celer</i>	89
<i>Hoplitosuchus raii</i>	90
<i>Decuriasuchus quartacolonia</i>	91
6. ORNITHOSUCHIDAE	94
6.1. Uma breve caracterização de Ornithosuchidae	94
6.2. Estado da arte	95
6.3. Lista de Táxons de Ornithosuchidae	102
<i>Ornithosuchus longidens</i>	102
<i>Riojasuchus tenuisiceps</i>	104

<i>Venaticosuchus rusconii</i>	105
7. ERPETOSUCHIDAE	107
7.1. Estado da arte	108
7.2. Lista de Táxons de Erpetosuchidae	113
<i>Erpetosuchus granti</i>	113
<i>Erpetosuchus sp.</i>	115
<i>Parringtonia gracilis</i>	116
<i>Dyoplax arenaceus</i>	118
8. ANÁLISE INTEGRADORA DOS ARTIGOS DA TESE	121
9. REFERÊNCIAS	125

Parte 2

10. Artigos da Tese

Artigo 1. LACERDA, M.B.; Schultz, C.L. & Bertoni-Machado, C. 2015. First ‘Rauisuchian’ archosaur (Pseudosuchia, Loricata) for the Middle Triassic Santacruzodon Assemblage Zone (Santa Maria Supersequence), Rio Grande do Sul State, Brazil.....	127
Artigo 2. LACERDA, M.B.; Mastrantonio, B.M.; Fortier, D.C. & Schultz, C.L. 2016. New insights on Prestosuchus chiniquensis Huene, 1942 (Pseudosuchia, Loricata) based on new specimens from the “Tree Sanga” Outcrop, Chiniquá Region, Rio Grande do Sul, Brazil.....	140
Artigo 3. LACERDA, M.B.; França, M.A.G. & Schultz, C.L. A new erpetosuchid (Pseudosuchia, Archosauria) from the Middle-Late Triassic of Southern Brazil.	188

11. Trabalhos Complementares

11.1 Artigos

Sales, M.A.F.; LACERDA, M.B.; Horn, B.L.D.; Oliveira, I.A.P. & Schultz, C.L.
2016. The “X” of the matter: Testing the relationship between paleoenvironments
and three theropod clades.....249

Pinheiro, F.L.; França, M.A.G.; LACERDA, M.B.; Butler,R.J. & Schultz, C.L.
2016. Na exceptional fóssil skull from South America and the origins of the
archosauriform radiation.....275

11.2. Resumos publicados em congressos283

11.3. Histórico escolar do aluno.290

TEXTO EXPLICATIVO DA ESTRUTURA DA TESE

Esta Tese de Doutorado está estruturada em torno de artigos publicados ou submetidos para a avaliação em periódicos científicos de acordo a Norma 103 do Programa de Pós-Graduação em Geociências-PPGGEO/IG/UFRGS. A Tese está dividida em um único volume, composto por duas partes:

Parte 1. É composta pela introdução, aspectos geológicos e paleobiogeográficos, seguidos de uma apresentação e o estado da arte dos três grupos de arcossauros que foram os mais relevantes para os estudos elaborados ao longo da Tese. Optou-se por não apresentar um tópico específico sobre os Materiais e Métodos devido às variações em cada artigo

Parte 2. É dividida em:

A) . Os três artigos principais da tese;

B) Artigos publicados em revistas científicas que foram elaborados ao longo do período da Tese, mas que não são diretamente referentes ao tema abordado na mesma;

C) Lista de resumos em anais de congresso, publicados ao longo do período da Tese, diretamente referentes ou não aos temas da mesma;

D) Histórico escolar do aluno.

PARTE 1

1. INTRODUÇÃO

Os arcossauros são um grupo que apresenta uma rica história evolutiva desde seu aparecimento no registro fóssil, ocorrido entre o fim do Neopermiano e início do Eotriássico (e.g. BRUSATTE, *et al.*, 2010a; EZCURRA, *et al.*, 2014). Apresentaram uma grande diversidade de formas após a extinção Permo-Triássica, quase que concomitantemente ao surgimento de outras linhagens no Triássico, o Período inicial da Era Mesozóica, como a dos peixes Teleostei (MARJANOVIC & LAURIN, 2008), dos Squamata (EVANS, *et al.*, 2010), dos Testudines (e.g. LYSON, *et al.*, 2010) e dos Mammaliaformes (ROWE, 1988; LUO, 2007; RUTA, *et al.*, 2013). Comparativamente com estes grupos, os arcossauros vão apresentar um destaque nas faunas continentais e alcançar uma participação majoritária nas teias tróficas dos tetrápodes terrestres que foram estabelecidas ao longo do Mesozoico e, em menor escala, mas não menos significativamente, durante o Cenozoico (BRUSATTE *et al.*, 2010a, 2010b; NESBITT, 2011; BUTLER, *et al.*, 2011; EZCURRA, *et al.*, 2014; EZCURRA, 2016).

No Triássico, o histórico evolutivo dos arcossauros (Fig. 1) vai derivar em duas grandes linhagens, uma denominada Avemetatarsalia Benton, 1999 (*sensu* NESBITT, 2011) cujos representantes viventes são as aves, e a outra denominada de Pseudosuchia Zittel 1887-1890 (*sensu* NESBITT, 2011) composta pelos crocódilianos (GAUTHIER, 1984; BENTON & CLARK, 1988; PARRISH, 1993; JUUL, 1994; BRUSATTE *et al.*, 2010b; NESBITT, 2011; EZCURRA, 2016). Destas duas linhagens, a avemetatarsaliana, em grande parte por apresentar os grupos dos dinossauros e dos pterossauros, é o foco de maior interesse por parte dos paleontólogos e do público em geral em detrimento da linhagem pseudossúquia (e.g. HOLTZ & BRETT-SURMANN, 1997; SUES & FRASER, 2009; BRUSATTE, *et al.*, 2010a). Um aumento de interesse pela evolução da linhagem Pseudosuchia nos últimos 20 anos tem modificado nossa visão sobre a origem e evolução dos grupos temporalmente restritos ao Triássico, assim como as suas relações filogenéticas, algumas ainda não completamente esclarecidas (e.g. NESBITT, 2003; NESBITT & NORELL, 2007; EZCURRA, *et al.*, 2014; NESBITT, *et al.*; 2016; STOCKER, *et al.*, 2017).

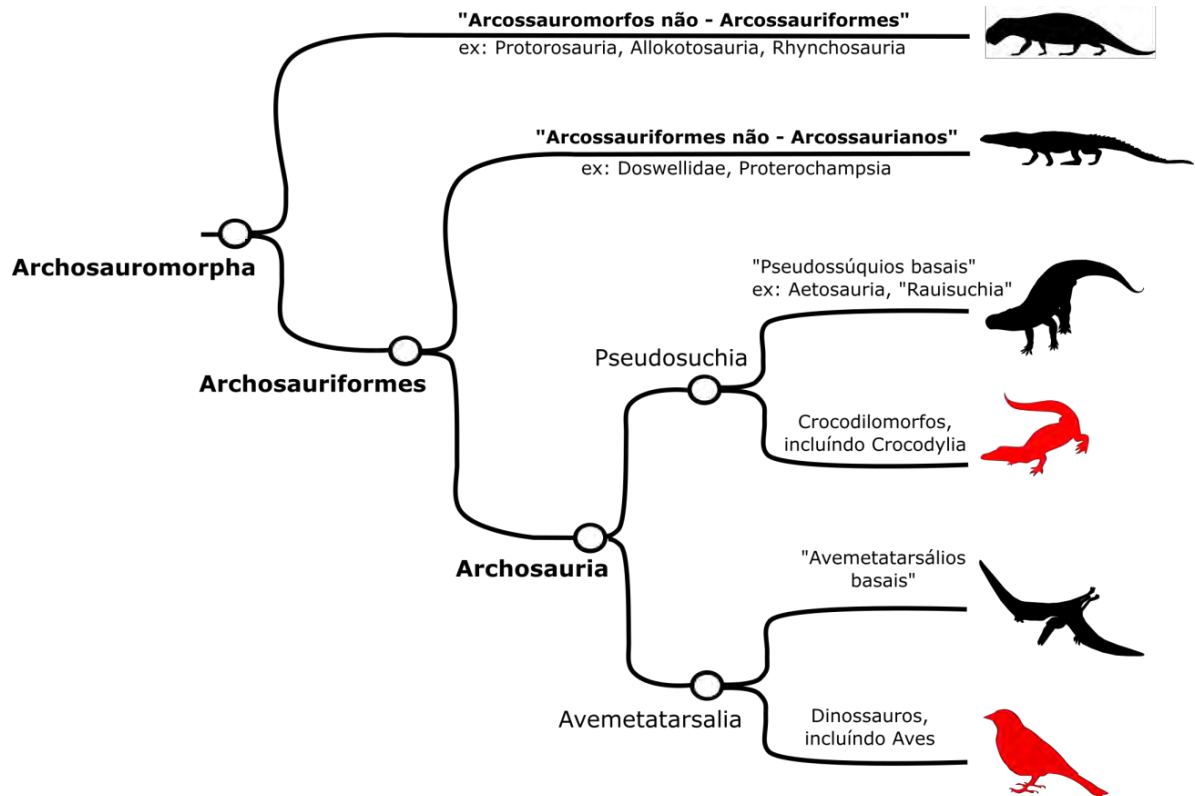


Figura 1. Diagrama simplificado da evolução dos arcossauros segundo a proposta por Gauthier (1986), utilizando a nomenclatura dos grupos presente em Nesbitt (2011). Silhuetas em vermelho indicam táxons com representantes vivos.

A contribuição do Brasil para esta área da paleontologia de vertebrados se dá a partir de trabalhos envolvendo várias descobertas feitas nos afloramentos da Supersequência Santa Maria (Meso-Neotriássico), localizada na região central do Estado do Rio Grande do Sul. Desde os primeiros trabalhos envolvendo descobertas feitas na região, no final dos anos 1920 (von HUENE, 1935-42; 1942; BELTRÃO, 1965), tem sido produzido um registro amplo de muitos grupos de arcossauros e arcosauriformes não-arcosaurianos, incluindo aetossauros (DESOJO *et al.*, 2012; Da-Silva *et al.*, 2014), "rauissuquídeos" (von HUENE, 1935-42; BARBERENA, 1978, FRANÇA *et al.*, 2013, LAUTENSCHLAGER & RAUHUT, 2014; DA-SILVA *et al.*, 2016), fitossauros (KISCHLAT & LUCAS, 2003), proterocâmpsídeos (BERTONI-MACHADO & KISCHLAT, 2003; RAUGUST *et al.*, 2013), afanossaurios (NESBITT *et al.*, 2017), pterossauros (BONAPARTE *et al.*, 2010) e dinossauriformes (e.g. COLBERT, 1970; BONAPARTE *et al.*, 1999; LANGER, *et al.*, 1999; LEAL, *et al.*, 2004; FERIGOLO & LANGER, 2006; CABREIRA *et al.*, 2011, 2016; PINHEIRO, 2016).

Os objetivo do presente projeto de doutoramento é contribuir para este conhecimento na forma de três artigos: o primeiro é a descrição do novo táxon *Dagasuchus santacruzensis*, um “rauissuquídeo” e a relevância deste para conhecimento da distribuição temporal do grupo no Triássico do Rio Grande do Sul; o segundo artigo aborda a descrição de novos espécimes atribuídos a *Prestosuchus chiniquensis* von Huene, 1942, em conjunto com um estudo sobre os aspectos da paleobiologia deste táxon, especificamente em relação a sua ontogenia; o terceiro e ultimo artigo também é de cunho descritivo, com a descrição de um novo táxon¹, que seria a primeira ocorrência de um Erpetosuchidae para o Triássico do Rio Grande do Sul, e seu status filogenético dentro de Pseudosuchia. A elaboração destes três artigos são os objetivos específicos da tese.

A presente tese é dividida em duas partes: A primeira é composta por uma introdução com uma abordagem geral sobre a geologia e paleogeografia do Período Triássico, seguido da origem e evolução dos arcossauros. Os três grupos de maior relevância para a tese são apresentados em sessões específicas.. A segunda parte é composta pelos três principais artigos da tese, mais outros trabalhos produzidos ao longo do período do doutoramento, incluindo artigos e resumos, finalizando com o histórico escolar do aluno.

1.2. Contexto geológico e paleoambiental

Todos os fósseis estudados na presente tese são provenientes de localidades na Bacia do Paraná, que é uma bacia sedimentar intracratônica da plataforma Sul-Americana de aproximadamente 1,5 milhões de km² de área (Fig. 2), distribuída entre os territórios do Brasil meridional, Paraguai oriental, nordeste da Argentina e norte do Uruguai (MILANI *et al.*, 2007). No Rio Grande do Sul, os afloramentos de idade Triássica se concentram na porção central do Estado, em uma faixa de aproximadamente 500 km orientada em sentido Leste-Oeste (SCHULTZ *et al.*, 2000; LANGER *et al.*, 2007; DA-ROSA, 2015). Historicamente, os pacotes desta idade foram divididos nas formações Sanga do Cabral (ANDREIS *et al.*, 1980), Santa Maria (GORDON, 1947) e Caturrita (ANDREIS *et al.*, 1980). Com base na cronoestratigrafia, Faccini (1989) identificou quatro sequências deposicionais, onde

¹ Como o táxon descrito no terceiro artigo apresentado na presente tese ainda não foi publicado formalmente, com o artigo ainda em revisão, foi escolhido não citar o nome.

a Formação Sanga do Cabral formaria a parte superior da Sequência Depositional I enquanto que as formações Santa Maria e a parte inferior da Caturrita formariam a Sequência Depositional II.

Zerfass *et al.* (2003) dividiram o pacote sedimentar do Triássico do Rio Grande do Sul em duas Supersequências: Sanga do Cabral (inferior) e Santa Maria (superior). Esta última foi dividida em três sequências deposicionais de terceira ordem denominadas Santa Maria 1, 2 e 3, onde a sequência 1 seria a mais antiga. Fósseis de tetrápodes são encontrados apenas nas sequências 1 e 2 (BARBERENA *et al.*, 1985; SCHULTZ, 1995; SCHULTZ *et al.*, 2000; LANGER *et al.*, 2007). A Sequência Santa Maria 1 se inicia com um conjunto de conglomerados massivos e areias de origem fluvial, depositados por rios de baixa sinuosidades e alta energia que são sucedidos por depósitos pelíticos de origem lacustre de pouca profundidade (ZERFASS *et al.*, 2003; 2004). Estes depósitos se formaram em um clima com sazonalidade de períodos secos e úmidos (HOLZ & BARBERENA, 1994; ZERFASS *et al.*, 2003). O início da Sequência Santa Maria 2 é caracterizado por um pacote de arenitos e conglomerados depositados em canais fluviais entrelaçados, com baixa sinuosidade e multilaterais (ZERFASS *et al.*, 2003). Em sua porção mediana, ocorre a presença de camadas pelíticas maciças ou laminadas, depositadas em planícies de inundação e canais isolados da “Formação Santa Maria” e da base da “Formação Caturrita”. O restante da “Formação Caturrita” é constituído de arenitos fluviais de canais meandrantos (ZERFASS *et al.*, 2003; 2004).

Horn *et al.* (2014) apresentaram uma nova proposta na qual a Supersequência Santa Maria está dividida, da base para o topo, em: Sequência Pinheiros-Chiniquá, Sequência Santa Cruz e Sequência Candelária (Fig. 2). Esta será a proposta seguida na presente tese. Na Sequência Pinheiros-Chiniquá é reconhecida a Zona de Associação (ZA) de *Dindontosaurus*, na Sequência Santa Cruz a ZA de *Santacruzodon*, enquanto que na Sequência Candelária são reconhecidas as ZA de *Hyperodapedon* e ZA de *Riograndia* (SOARES *et al.*, 2014) (Fig. 2).

Os afloramentos clássicos e as novas localidades fossilíferas têm providenciado numerosos espécimes e uma quantidade considerável de novos táxons que, nas últimas duas décadas, têm permitido um biozoneamento mais refinado da Supersequência e correlações mais robustas com outras bacias na

América do Sul e no mundo (e.g. LANGER, 2005a, b; LANGER *et al.*, 2007; ABDALA & RIBEIRO, 2010; MARTINELLI *et al.*, 2017).

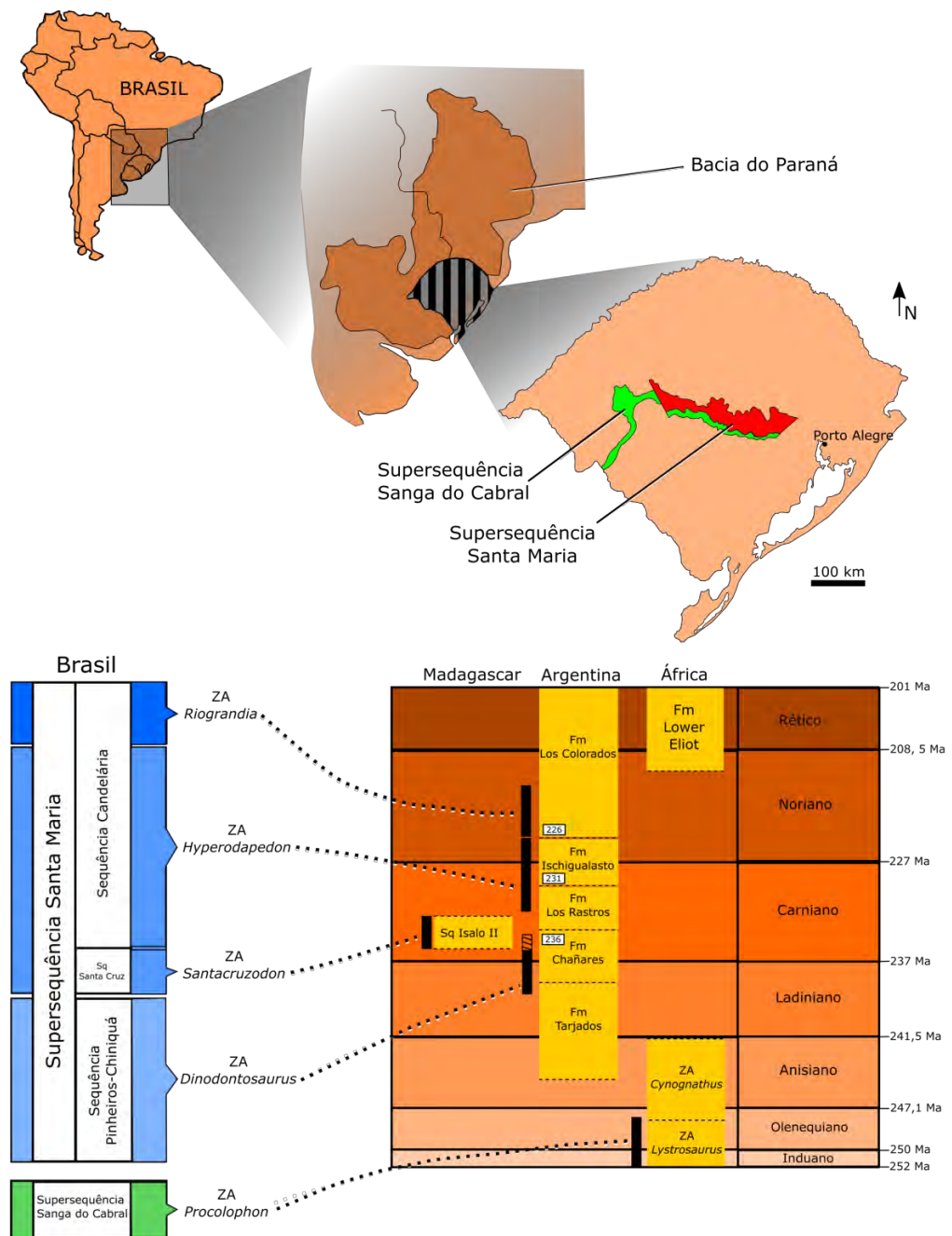


Figura 2. Localização e extensão da Bacia do Paraná e das supersequências Sanga do Cabral e Santa Maria, baseado em Zeffass *et al.* (2003). Tabela crono e bioestratigrafia das unidades triássicas sul-brasileiras, modificado de Horn *et al.* (2014) com a correlação estratigráfica entre as faunas desta idade com Madagascar, Argentina e África. Os números nos retângulos brancos indicam datações baseadas em Martinelli *et al.*, (2017). A continuação vertical rachurada da ZA de *Dinodontosaurus* indica a possível extensão, como discutido por Martinelli *et al.*,

(2017). As datações seguem a Tabela Cronoestratigráfica Internacional (GRADSTEIN *et al.*, 2012). Abreviações: Fm, formação; Ma, milhões de anos; Sq, sequência; ZA, zona de associação.

A principal ferramenta para a correlação dos afloramentos do Triássico do Rio Grande do Sul são os fósseis de tetrápodes (BARBERENA *et al.*, 1985; SCHULTZ, 1995; SCHULTZ *et al.*, 2000; LANGER *et al.*, 2007; SOARES *et al.* 2011; MARTINELLI *et al.*, 2017) (Fig. 2). É estabelecida uma idade Meso-Neotriássica (Neoladiniano–Eocarniano) para a ZA de *Dinodontosaurus* devido à correlação com a Formação Chañares da província de La Rioja da Argentina, com base no registro compartilhado dos cinodontes *Chiniquodon theotonicus* Huene, 1936 (ABDALA; GIANNINI, 2002) e do gênero *Massetognathus* Romer, 1967 (ABDALA; GIANNINI, 2000; LANGER *et al.*, 2007).

A ZA de *Santacruzodon* compartilha com a Formação Chañares a presença do proterocampsídeo *Chanaresuchus bonapartei* Romer, 1971 (RAUGUST *et al.*, 2013), mas a presença do cinodonte *Menadon besairiei* Flynn, 2000 indicaria uma possível correlação com a sequência Isalo II de Madagascar (FLYNN *et al.*, 1999), o que sugere uma idade Neotriássica (início do Carniano) (MELO *et al.*, 2015). A correlação com a Formação Chañares foi reforçada a partir de datações radiométricas feitas por Philipp *et al.* (2013), com base em zircões dentríticos originários de eventos de vulcanismo do Grupo Choyoi, que indicou uma isócrona U-Pb de $236 \pm 1,5$ Ma para o início da Sequência Santa Cruz, o que compartilha com datações feitas na Argentina (MARSICANO *et al.*, 2016) e os limites da ZA de *Santacruzodon* (MARTINELLI & SOARES; 2016; MARTINELLI *et al.*, 2017). Esta correlação também oferece suporte para a hipótese de que esta ZA poderia ser uma continuação da ZA de *Dinodontosaurus* (e.g. LANGER *et al.*, 2007; ABDALA *et al.*, 2009), com base na presença de vários táxons de cinodontes e arcossauros de afinidade filogenética próxima, combinado com a presença de espécimes similares a *Dinodontosaurus turpior* von Huene, 1935. Todavia, novos dados são ainda necessários (ver MARTINELLI *et al.*, 2017).

Na sequência Candelária, a ZA de *Hyperodapedon* apresenta uma grande afinidade de fauna de cinodontes (e.g. ABDALA *et al.*, 2002; OLIVEIRA *et al.*, 2010) e arcossaumorfos (e.g. LANGER, 2005a, b; LANGER *et al.*, 2007; DESOJO & EZCURRA, 2016) com a Formação Ischigualasto, também de La Rioja, do Neotriássico (Neocarniano -Eonoriano) da Argentina. A ZA de *Riograndia* é

correlacionada amplamente com a Formação Los Colorados da Argentina, de idade Neotriássica (Noriano) com base na presença do dicinodonte *Jachaleria* (ARAÚJO & GONZAGA, 1980). Estas duas associações apresentam um grande registro de fauna de archosauriformes, principalmente abordando a origem e evolução de Dinosauria (e.g. LANGER, 2004; EZCURRA, 2012; CABREIRA *et al.*, 2011; 2016). Fósseis de arcossauros da linhagem Pseudosuchia são descritos para as ZA de *Dinodontosaurus*, *Santacruzodon* e *Hyperodapedon* (SCHULTZ *et al.*, 2000; KISCHLAT, 2000; LANGER, *et al.*, 2007; DESOJO *et al.*, 2012; NESBITT *et al.*, 2013; SILVA *et al.*, 2014; LACERDA, *et al.*, 2014; DESOJO & EZCURRA, 2016).

Para o Triássico do Rio Grande do Sul, segundo Holz e Barberena (1994), a paleolatidade média da região onde hoje é o Rio Grande do Sul estaria entre 42-43° Sul, o que corresponderia à localização cerca de 1300 km mais ao sul do que sua posição atual, com um clima que variava de árido a úmido/árido. O supercontinente Pangea já estava completamente formado durante a transição Permo–Triássica, onde os continentes da Laurásia e Gondwana combinaram com as massas de terra que hoje são o Cazaquistão, Sibéria, porções da China e do sudeste da Ásia (ZIEGLER *et al.*, 1983; KLIMETZ, 1983; VEEVERS, 1991; SUES & FRASER, 2009; HOLZ, 2015). Com isso, a superfície total teria aproximadamente 130 milhões de km², se estendendo do 85° Norte até 90° Sul, praticamente de um polo a outro (FRAKES, 1979; ZIEGLER, *et al.*, 1983). Com a exceção do *rifting* da Gondwana, devido a abertura do Oceano Índico, e a separação da Índia e da Austrália no Eotriássico (RAD, *et al.*, 1993), a posição do Pangea se manteve, ao longo do Período, relativamente centrado no equador (ZIEGLER *et al.*, 1983).

O continente era rodeado pelo Oceano Pantalassa, com um golfo oceânico profundo, chamado de Mar de Tétis, que cortava o supercontinente e estava latitudinalmente confinado a um trecho entre 30° Norte e 30° Sul (ZIEGLER, *et al.*, 2003; PRETO, *et al.*, 2010). Em virtude da concentração de uma extensa área de terra, da ausência de polos cobertos de gelo e do aumento global do nível do mar, houve uma grande alteração no perfil climático do planeta (HOLZ *et al.*, 2014).

Diferente do Permiano, em que a taxa maior de umidade atmosférica estimulou a presença de florestas abundantes de glossopteridales, gigantopteridales e licópsidas no final do Fanerozoico, o clima no início do Mesozoico mudou para um sistema predominantemente seco (SUES & FRASER, 2009; HOLZ, 2015). A

maior parte do Pangea deveria apresentar períodos de grandes tempestades sazonais, denominados de mega-monções (PARRISH, 1993). Estes eventos, ao longo dos milhões de anos, acabaram expandindo a extensão das regiões de clima árido, antes mais centralizadas, para mais próximas aos polos, conseqüentemente reduzindo a taxa de umidade e evaporação nas latitudes médias da porção central do continente.

A temperatura média ao longo do Período ainda não é um tópico bem conhecido. A noção que predominava em trabalhos pretéritos era que o Triássico apresentava uma temperatura elevada predominante e quase constante ao longo de toda a sua duração (e.g. PRETO, *et al.*, 2010; WHITESIDE, *et al.*, 2011; HOLZ, 2015). Este paradigma tem sido revisto e do Eo- até o Neotriássico apresentam características de temperatura distintas (Fig. 3): o Eotriássico apresentava um clima rigoroso de temperaturas altas, possivelmente em decorrência dos eventos de vulcanismo ocorridos nos *Deccan Traps*, no que hoje é centro-oeste da Índia, durante a extinção Permo-Triássica, evidenciado pela uniformidade de fauna e flora que indicaria pouca variação de temperatura do Equador até os polos (e.g. DICKINS, 1993; PRETO, *et al.*, 2010); no Mesotriássico, um clima quente e árido na região equatorial é evidenciado a partir da abundância de microfósseis de plantas e palinóforos nesta região, mas porções continentais a Leste do Pangea, margeando o Tétis, apresentavam grandes florestas de pteridófitas, o que indicaria uma sazonalidade maior na variação da temperatura e um aumento na incidência de chuvas (ZIEGLER, *et al.*, 1993; SIMMS, *et al.*, 1995; PRETO, *et al.*, 2010); o Neotriássico seria a época onde as previamente mencionadas mega-monções cíclicas teriam maior atividade devido à condição de circulação atmosférica mais propícias (PRETO, *et al.*, 2010) — a porção central do Pangeia apresentaria uma região árida de temperaturas quentes que não variavam muito ao longo do ano e um clima temperado quente, intercalado com estações de chuva, ocuparia porções norte e mais ao sul, enquanto porções tropicais estariam presentes na região central do Tétis (SUES & FRASER, 2009; PRETO, *et al.*, 2010). O fim do Neotriássico também é marcado por um aumento significativo da umidade entre o início e o fim do Carniano, onde ocorrem grandes alterações ambientais e bióticas, cujas causas e intensidades ainda são debatidas (ver PRETO, *et al.*, 2010).

No contexto da evolução das diferentes linhagens dos arcossauros e dos arcossauriformes não-arcossaurianos ao longo do Período Triássico, o nível

estratigráfico dos táxons é necessário para estabelecer a distribuição paleobioambiental entre os grupos e sua amplitude temporal ao longo do Período. Para um entendimento melhor da paleobiogeografia e dos padrões climáticos do Período se torna de suma importância para um melhor refinamento bioestratigráfico.

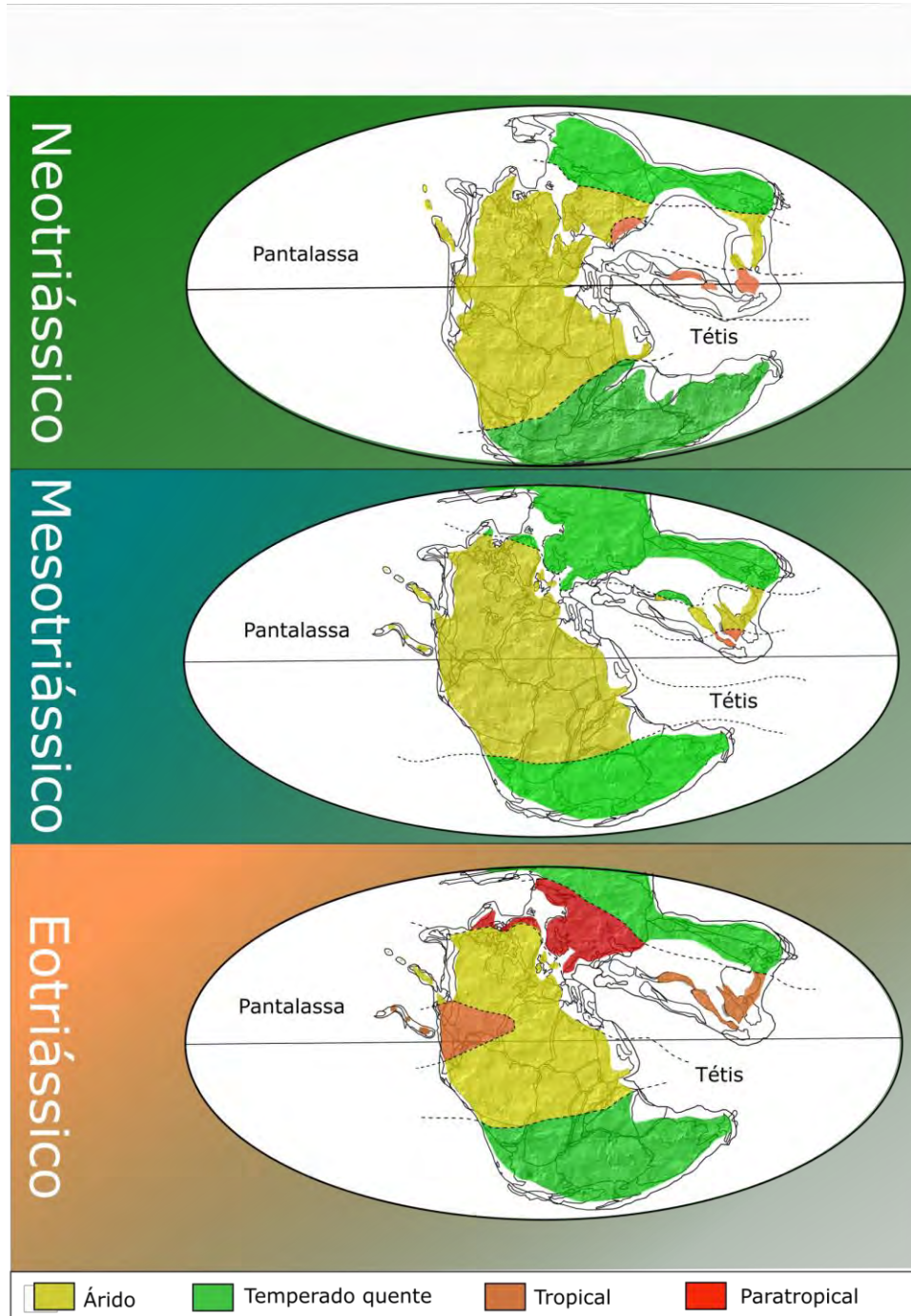


Figura 3. Mapas de distribuição dos climas ao longo do Pangea, ao longo do Período Triássico. As linhas tracejadas indicam os limites das zonas climáticas. (Modificado de SUES& FRASER, 2009).

2. ORIGEM E EVOLUÇÃO DOS ARCOSSAUROS

Archosauria Cope, 1869-70 (*sensu* Gauthier, 1986) é um clado que compreende crocodilianos, aves e todos os descendentes do seu ancestral mais comum, incluindo dinossauros não-avianos, pterossauros e pseudossúquios basais (GAUTHIER & PADIAN, 1985; GAUTHIER, 1986; BENTON & CLARK, 1988; BENTON, 1990; SERENO & ARCCUCI, 1990; SERENO, 1991; PARRISH, 1993; JUUL, 1994; BRUSATTE *et al.*, 2010; NESBITT, 2011, BUTLER, *et al.*, 2011; EZCURRA, *et al.*, 2014; FOTH, *et al.*, 2014; EZCURRA, 2016). Este clado faz parte de um grupo mais amplo, os Archosauromorpha Huene 1946 (*sensu* GAUTHIER *et al.*, 1988), que compreende vários táxons de distribuição temporal do Mesopermiano até o Mesotriássico. Este grupo reúne táxons que apresentam maiores afinidades filogenéticas entre si do que com Lepidosauromorpha Benton, 1983, clado que compreende os Squamata (serpentes e lagartos) e Rhynchocephalia (tuataras) (GAUTHIER, *et al.*, 1988; EZCURRA, *et al.*, 2014; BENTON *et al.*, 2015; EZCURRA, 2016).

Os primeiros registros dos arcosauromorfos datam do Neopermiano, mas seu histórico evolutivo inicial é pouco conhecido, sendo representado principalmente por icnofósseis (BRUSATTE *et al.*, 2010; NESBITT, 2011; BUTLER, *et al.*, 2011; EZCURRA *et al.*, 2013; 2014; 2015; 2016; EZCURRA, 2016). Atualmente as espécies mais antigas são: *Protorosaurus speneri*, Meyer, 1832 (GOTTMANN-QUESADA & SANDER, 2009) da Inglaterra e Alemanha; *Eorasaurus olsoni* Sennikov, 1988 da Rússia (SENNIKOV, 1997; GOWER & SENNIKOV, 2000) e *Aenigmastropheus parringtonia* Ezcurra *et al.*, 2014, da Tanzânia (EZCURRA *et al.*, 2014). Estes táxons apresentam um corpo lacertiforme, similar aos de seus antepassados diápsidos, mas diferem por apresentar, entre outras características, um forame pineal reduzido ou ausente e a borda posterior dos pré-maxilares com um processo que é direcionado posterior ou ventralmente na borda anterior dos maxilares (*e.g.* NESBITT, 2011; EZCURRA *et al.*, 2014; EZCURRA, 2016). Outros espécimes foram descritos na literatura, provenientes da África do Sul (CRUICKSHANK, 1972), Brasil (MARTINELLI *et al.*, 2016), Tanzânia (PARRINGTON, 1956) e Uruguai (DIAS-DA-SILVA, *et al.*, 2006; EZCURRA *et al.*, 2015) mas, por serem muito fragmentários, um diagnóstico em nível genérico é impossível (EZCURRA *et al.*, 2014; 2015; MARTINELLI *et al.*, 2016).

Os arcossaumorfos são um dos grupos que sobreviveram à extinção em massa do Permo-Triássico e apresentam uma rica história evolutiva durante o restante do Mesozóico (e.g. BRUSATTE *et al.*, 2010; NESBITT, 2011; EZCURRA, 2016). O registro durante o Eotriássico é escasso, mas a presença de fósseis de Proterosuchidae Huene, 1908 (*sensu* EZCURRA *et al.*, 2013) e táxons como o rincossauro basal *Noteosuchus colleti* Watson, 1912 (EZCURRA *et al.*, 2015) e *Teyujagua paradoxa* Pinheiro *et al.*, 2016 (ver PARTE 2 desta tese) são evidências de uma rápida recuperação e diversificação após uma extinção em massa (EZCURRA, 2016).

É durante o Mesotriássico que o registro de arcossaumorfos não-archosauriformes vai apresentar uma diversidade maior, com grupos como Tanystropheidae Gervais, 1858 (*sensu* DILKES, 1998), composto por formas lacertóides de possível hábito semi-aquático que apresentam um alongamento notável da coluna cervical proporcionalmente em relação ao resto do corpo, Allokotosauria Nesbitt *et al.*, 2015, que seria composto por formas robustas de dentição adaptada para herbivoria, Rhynchosauria Osborn, 1903 (*sensu* EZCURRA, 2016), previamente apresentado, Prolacertidae Parrington, 1935 (*sensu* EZCURRA, 2016), representado apenas pelo táxon lacertiforme *Prolacerta broomi* Parrington, 1935.

Paralelo a estes grupos, de origem no Neopermiano, existem ainda os Proterosuchidae Huene 1914 (*sensu* EZCURRA, 2016), composto por formas de tamanho mediano e aspecto crocodiliano (Fig. 4: A), que são os possíveis ancestrais do grupo dos Erythrosuchidae Watson, 1917 (*sensu* EZCURRA *et al.*, 2010), formas carnívoras robustas de grande porte (Fig. 4: B), e os Eucrocopoda Ezcurra, 2016, que formariam o clado Archosauriformes Gauthier *et al.*, 1988 (*sensu* NESBITT, 2011). Esta apresenta apomorfias tais como uma fenestra antero-orbital, pós-parietais fusionados ou ausentes, lateroesfenóide ossificado, um quarto trocânter bem desenvolvido no fêmur, o metatarsal III mais largo que o IV e uma fenestra mandibular lateralizada². Destes, o clado Eucrocopoda é composto por Proterochampsia, Archosauria e um agrupamento problemático de táxons restritos ao Mesotriássico como *Euparkeria capensis* Broom, 1913 (Fig. 4: C) e *Dorosuchus neoetus* Sennikov, 1989 conhecidos como “euparkerídeos” (SOOKIAS & BUTLER, 2013; EZCURRA, 2016).

² Mas presente no arcossaumorfo *Teyujagua paradoxa*, ver PINHEIRO *et al.*, 2016

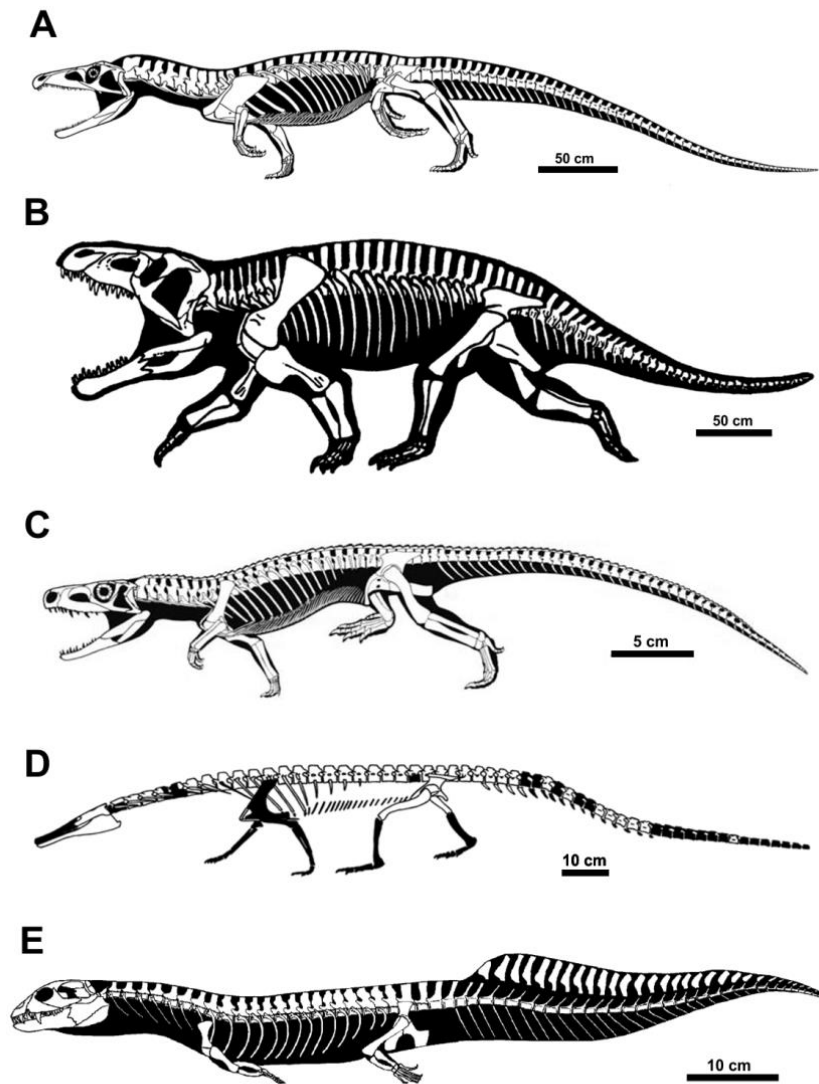


Figura 4. Exemplos de arcossauriformes. (A) *Proterosuchus fergusi* (retirado de EZCURRA *et al.*, 2013); (B) *Erythrosuchus africanus* (retirado de EZCURRA, *et al.*, 2013); (C) *Euparkeria capensis* (retirado de SOOKIAS & BUTLER, 2013); *Doswellia capensis* (modificado de SUES *et al.*, 2013); *Vancleaveae campi* (retirado de NESBITT *et al.*, 2009).

O clado Proterochampsia é constituído por dois grupos: Proterochampsidae Sill, 1967 (*sensu* EZCURRA, 2016), integrado por formas sul-americanas de distribuição temporal do Meso até o Neotriássico e composto de formas de crânios de rostró alongado, dorso-ventralmente achatados com órbitas e narinas externas mais dorsalizadas, o que são considerados como adaptações para um hábito de vida semi-aquático (e.g. SILL, 1967; BONAPARTE, 1971; ROMER, 1971; BARBERENA, 1982, KISCHLAT, 2000; TROTTEYN *et al.*, 2013); e Doswellidae

Weems, 1980 (*sensu* EZCURRA, 2016), composto por formas morfológicamente similares aos proterocâmpsídeos (Fig. 4: D), porém diferindo dos mesmos por apresentarem uma extensa cobertura de osteodermos restrita à região dorsal e de morfologia sub-retangular (como em *Doswellia klatenbachi* Weems, 1980) ou exibindo morfologia de osteodermos diversa e cobrindo outras porções do corpo, como os apêndices locomotores (como é caso de formas mais derivadas tipo *Vancleaveae campi* Long & Murray, 1995 *sensu* NESBITT *et al.*, 2009) (Fig. 4: E).

3. O CLADO ARCHOSAURIA

O clado Archosauria é composto por duas grandes linhagens: Avemetatarsalia e Pseudosuchia³. Com base nas formas derivadas que são encontradas no Eotriássico, a origem dos arcossauros é inferida para o limite do Permo-Triássico, (e.g. KUBO & BENTON; 2009; BRUSATTE *et al.*, 2010a, 2010b; NESBITT, 2011; EZCURRA *et al.*, 2014) com a separação das duas grandes linhagens ocorrendo ao final do Permiano (EZCURRA, 2016). Esta diversificação seria um indicativo da rápida recuperação faunística que ocorreu após a extinção em massa do Permo-Triássico (SIDOR, *et al.*, 2013). Os primeiros fósseis atribuídos a este grupo são inconfósseis do início do Olenequiano (Eotriássico) de localidades nas Holy Cross Mountains da região central da Polônia, Europa (BRUSATTE *et al.*, 2011) enquanto que os primeiros somatofósseis aparecem apenas no fim do Olenequiano, com *Ctenosauriscus koeneni* Huene, 1902, da Alemanha, e *Xilosuchus sapingensis* Wu, 1981, da China, ambos pertencentes ao clado Poposauroidea da linhagem que posteriormente iria dar origem aos crocodilos (BUTLER *et al.*, 2011).

A partir do Mesotriássico, arcossauros se tornam mais comuns no registro fóssil e já apresentavam uma ampla distribuição paleogeográfica (BRUSATTE, *et al.* 2010; NESBITT, 2011; EZCURRA, 2016). Da Formação Manda da Tanzânia são descritos *Asilisaurus kongwe* Nesbitt *et al.*, 2010, *Nyasasaurus parringtoni* Nesbitt *et al.*, 2013 e *Teleocrater rhadinus* Nesbitt *et al.*, 2017 da linhagem avemetatarsaliana e *Nundasuchus songeaensis* Nesbitt *et al.*, 2014 para a pseudossuquiana. Na China, da Formação Buttang, Kelamayi e Guanling são descritos os popossaurídeos

³Ver discussão a partir da página 28.

Quianosuchus mixtus Li *et al.*, 2006, *Turfanosuchus dabanensis* Young, 1973 e *Lotosaurus adentus* Zhang, 1975 (NESBITT, *et al.*, 2013). Na Índia, da Formação Yerrapalli, é descrito *Yarasuchus deccanensis* Sen, 2005 e na Rússia, na Formação Donguz, *Dongusuchus efremovi*, Sennikov, 1988 (ambos pertencentes à Aphanosauria *sensu* NESBITT *et al.*, 2017). Nos Estados Unidos, na Formação Moenkopi, é descrito *Arizonasaurus babbitti* Welles, 1947 (um popossaurídeo do grupo dos Ctenosauriscidae *sensu* NESBITT *et al.*, 2013).

Os primeiros membros da linhagem Pseudosuchia pertencem ao grupo dos Puposauroida, que é proximamente relacionado a um clado composto por formas mais próximas dos crocodilianos, cunhado de Crocodylomorpha Walker, 1968 (*sensu* NESBITT, 2011) e, curiosamente, são formas já bastante derivados anatomicamente, apresentando adaptações para herbivoria e apófises neurais das vértebras muito alongados (e.g. *Lotosaurus adentus*). Isto indicaria que o grupo apresentou uma rápida diversificação de formas após a extinção Permo-Triássica.

A partir do Mesotriássico, os arcossauros vão apresentar uma grande diversidade de grupos, apresentando um histórico evolutivo que seria apenas rivalizado pela irradiação dos crocodilomorfos durante o Cretáceo (NESBITT, 2011; STUBBS, *et al.*, 2013; FIORELLI *et al.*, 2016). Entretanto, esta irradiação no Mesotriássico ainda não é completamente entendida (EZCURRA, 2016). O táxon *Nundasuchus songeaensis*, *p. ex.*, apresenta similaridades com outros grupos de arcossauros (e.g. “rauissuquídeos”), mas apresenta características plesiomórficas: dentes no palato (presente fora de Archosauria, mas ocorrendo em dinossauros basais como *Eoraptor lunensis* Rauhut, 2003, *Eodromaeus murphi* Martinez *et al.*, 2011 e no pseudossuquídeo *Turfanosuchus dabanensis* Wu & Russel, 2001 [*sensu* NESBITT, 2011]) e um arranjo de cinco osteodermos a cada duas vértebras (uma condição presente em Proterochampsidae e nos arcossauros *Gracilisuchus stipanicorum* Romer, 1972 e *Saurosuchus galilei* Reig, 1959) ao invés de dois ou quatro (NESBITT *et al.*, 2014). Devido a isso, o seu posicionamento filogenético é controverso, com hipóteses encontrando *N. songeaensis* seria o grupo irmão de Phytosauria quando este está fora de Archosauria (NESBITT, 2011), mais distante entre os pseudossuquídeos (NESBITT *et al.*, 2014), ou como grupo irmão de um clado composto por Ornithosuchidae von Huene, 1914 (*sensu* Sereno, 1991) mais Suchia Krebs, 1974 (*sensu* NESBITT 2011: o clado menos inclusivo composto por

Aetosaurus ferratus Fraas, 1877; *Rauisuchus tiradentes* von Huene 1942; *Prestosuchus chiniquensis* e *Crocodylus niloticus* Laurenti, 1768) (EZCURRA, 2016).

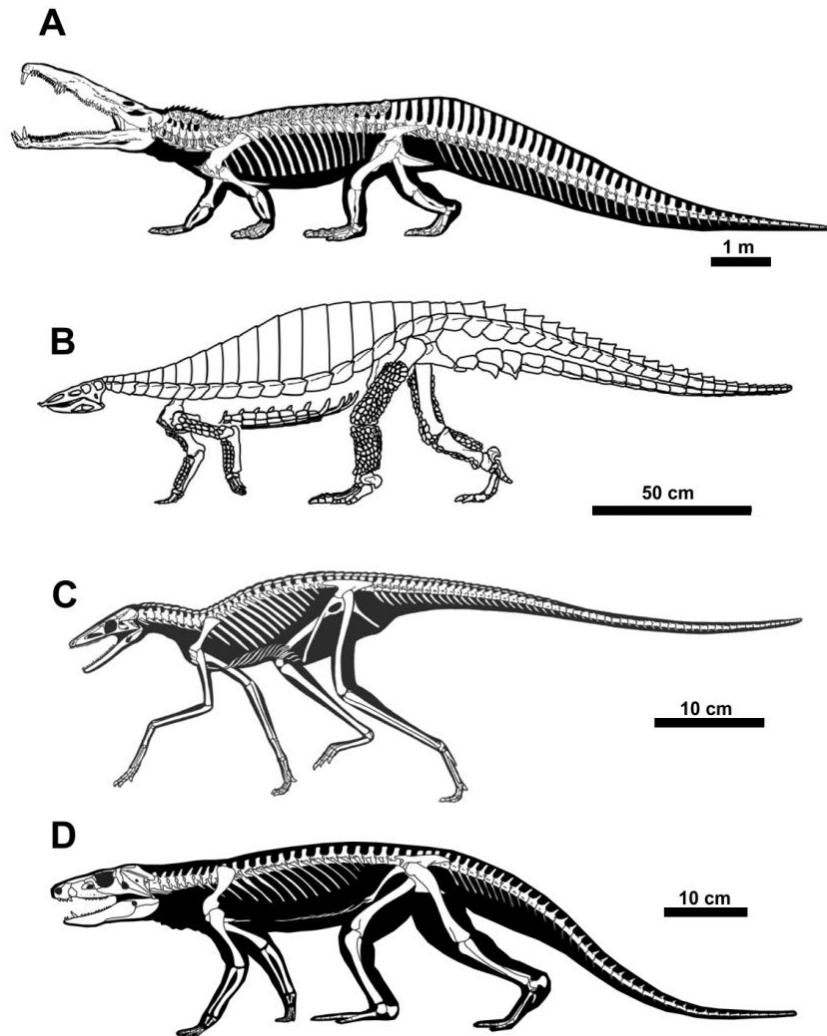


Figura 5. Exemplos de arcossauros: (A) o fitossauro *Smilosuchus gregorii* (*sensu* STOCKER & BUTLER, 2013, modificado de LONG & MURRAY, 1995); (B) o aetossauro *Typothorax coccinarum* (retirado de HECKERT *et al.*, 2010); os crocodylomorfos basais (C) *Terristrisuchus gracilis* e (D) *Protosuchus richardsoni* (modificado de IRMIS *et al.*, 2013).

Outros clados dentro de Pseudosuchia seriam Phytosauria⁴ (STOCKER *et al.*, 2013) que apresenta formas carnívoras com um crânio de rostro alongado portando vários dentes cônicos que possivelmente apresentavam um hábito de vida similar aos crocodylios vivos (Fig. 5: A), mais especificamente os gaviais; e Suchia

⁴ Na presente tese consideramos que Phytosauria faria parte de Archosauria segundo as análises recentes de Ezcurra (2016).

(NESBITT, 2011; DESOJO *et al.*, 2013), que inclui os Aetosauria (DESOJO *et al.*, 2013), composto por formas onívoras que apresentavam uma extensa cobertura dorsal e ventral de osteodermos retangulares (Fig. 5: B), os Gracilisuchidae (BUTLER *et al.*, 2014), pequenos e cursoriais e os Crocodylomorpha (IRMIS *et al.*, 2013) (Fig. 5: C, D). Os grupos restantes são os “rauissuquídeos”, Ornithosuchidae e Erpetosuchidae, que foram o foco dos três trabalhos principais elaborados ao longo da produção da presente tese e serão vistos em detalhes nos próximos capítulos (Fig. 6).

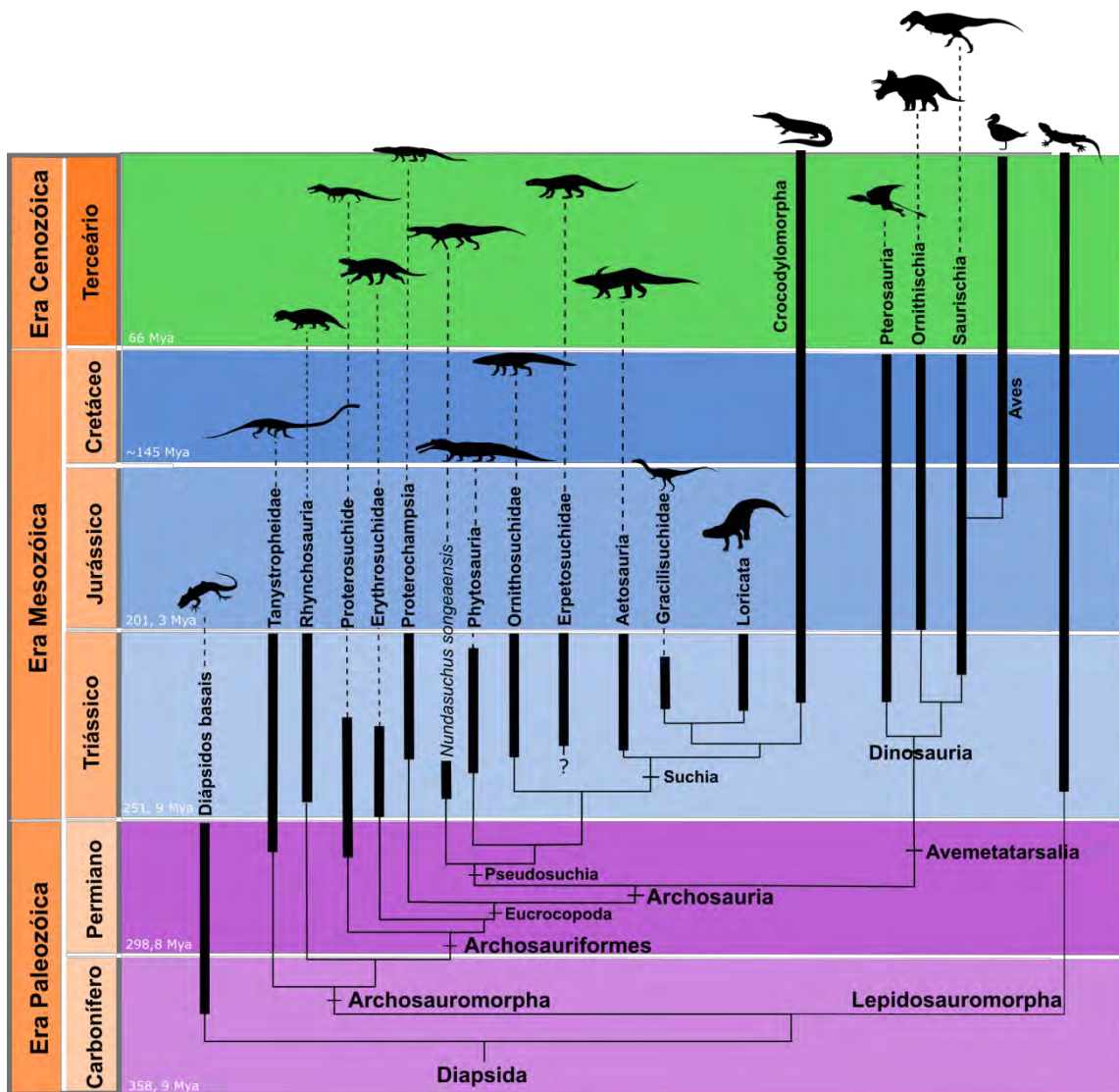


Figura 6. Cladograma baseado em Pough (2006) modificado com resultados apresentados nas propostas de Nesbitt (2011) e Ezcurra (2016) representando a distribuição temporal dos grandes grupos de descendentes dos diápsidos. A posição incerta de Erpetosuchidae no cladograma, próximo a Ornithosuchidae, mas fora de Suchia, é baseado em uma das topologias encontradas em Nesbitt & Butler (2012).

As barras mais espessas indicam o registro fóssil e amplitude temporal dos diferentes táxons. Datação retirada do ICS (COHEN *et al.*, 2016).

4. A LINHAGEM PSEUDOSUCHIA- QUESTÕES NOMENCLATURAIS

Historicamente, os táxons que compõe os arcossauromorfos estavam inseridos no grado “Thecodontia” Owen, 1989, que representaria um “estoque basal” de arcossauriformes não-arcossaurianos onde estariam os ancestrais dos grandes grupos de arcossauros, como Aetosauria, Phytosauria, Dinosauria, Pterosauria e Crocodylia, mas cuja filogenia variava dependendo do pesquisador e do número de táxons usados nas amostras das análises filogenéticas (e.g. CHARIG, 1976, 1993; BONAPARTE, 1982) (Fig. 7). Ademais, o suporte para alguns parentescos era tênue porque algumas propostas focalizavam em uma única característica morfológica em detrimento de outras, como é o caso da proposta classificatória de Chatterjee (1985) baseada na articulação tarsal (Fig. 8), seguindo as ideias de trabalhos pretéritos (KREBS, 1963, 1974; WALKER, 1964; BONAPARTE, 1971, CHARIG, 1972; CRUICKSHANK, 1979;).

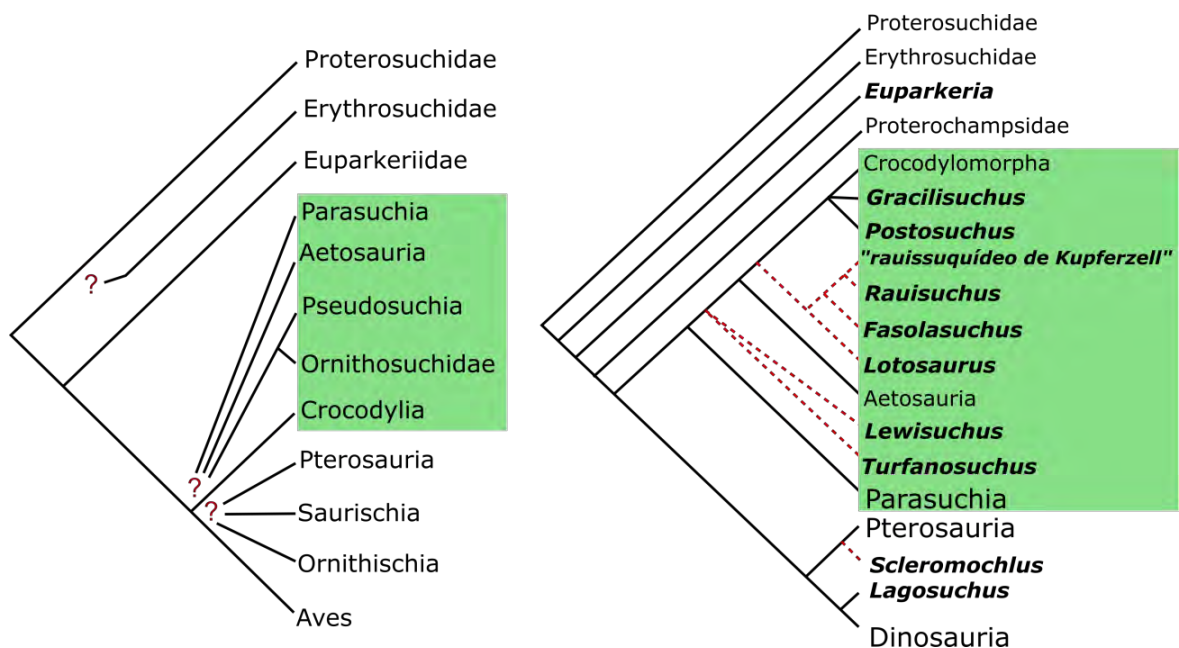


Figura 7. Cladogramas apresentando o consenso sobre o conhecimento da filogenia dos arcossauromorfos em dois momentos históricos. **A)** Análise proposta por Charig (1993) para representar o estado do conhecimento durante os anos 1950; **B)** Análise proposta por Gower & Wilkinson (1996) resultado de uma síntese de quatro matrizes (ARCUCCI & SERENO, 1990; SERENO, 1991; PARRISH, 1993; JUUL, 1994)

publicadas nos anos 1990. Linhas vermelhas tracejadas indicam táxons presentes em apenas uma única matriz das quatro analisadas e quadrado em verde indica os componentes do que hoje consideramos a linhagem Pseudosuchia. Modificado de Gower & Wilkinson (1996).

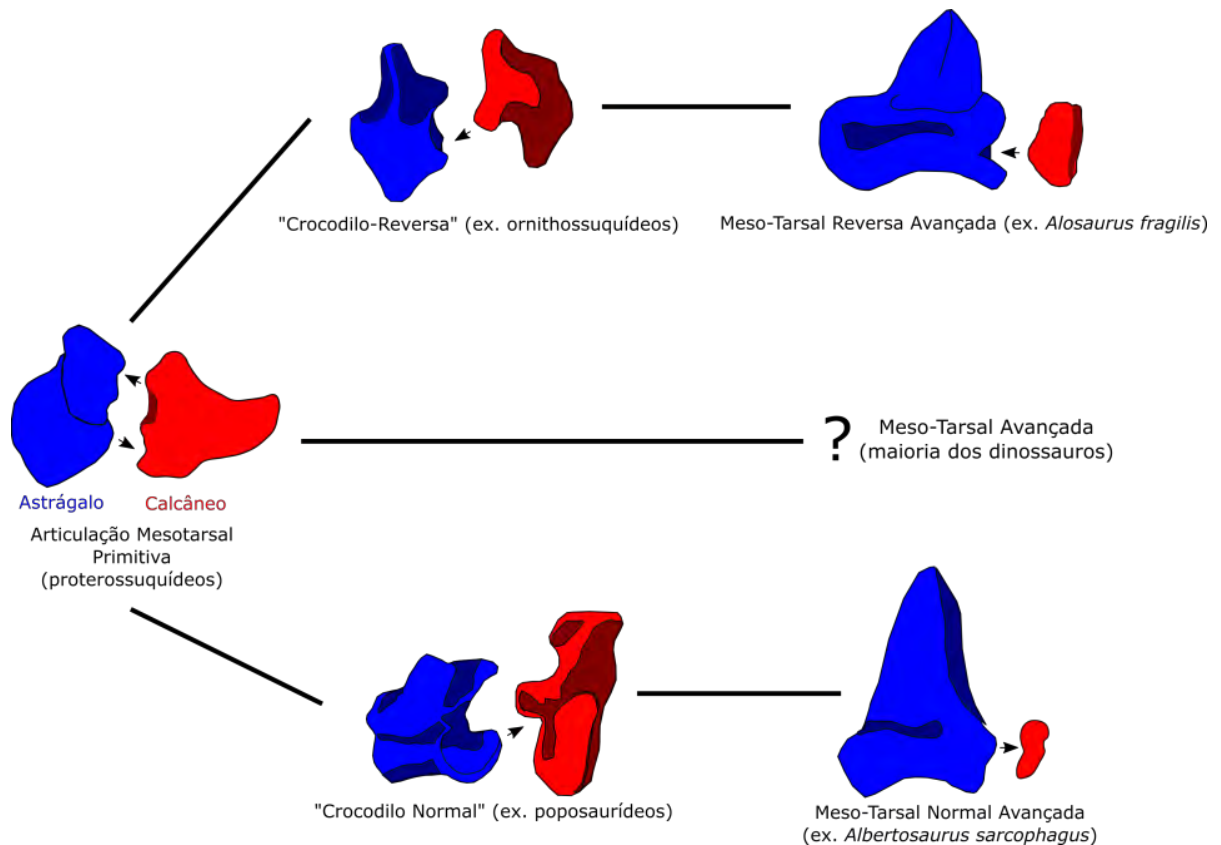


Figura 8. Proposta de Chatterjee (1982) da evolução dos arcossauros baseada na articulação mesotarsal. Todos representam a estrutura tarsal em norma anterior esquerda. As setas indicam a posição do soquete oposto à cavilha correspondente.

Esta visão começou a mudar durante a década de 1980 através do uso de metodologias cladísticas (e.g. GAUTHIER, 1984; 1986; GAUTHIER & PADIAN, 1985; BENTON, 1985; BENTON & CLARK, 1988) que apresentaram três pontos principais de consenso: 1) crocodilos e aves viventes apresentam afinidades filogenéticas mais próximas entre si do que com outros grupos viventes e compartilham um ancestral comum que viveu durante o Triássico; 2) "Thecodontia" seria parafilético, e muitos dos seus táxons estariam fora de Archosauria ou distribuídos ao longo das linhagens que posteriormente iriam originar as aves ou os

crocodilianos; 3) dinossauros formam um grupo monofilético (NESBITT, 2011). Entretanto, estas análises utilizavam poucos táxons e não disponibilizavam suas matrizes numéricas na publicação, dificultando a replicabilidade.

A partir do fim dos anos oitenta e começo dos noventa, novas hipóteses foram propostas (SERENO, 1991; PARRISH, 1993; JUUL, 1994) e publicadas incluindo uma matriz de caracteres e de táxons. Devido às limitações dos métodos cladísticos disponíveis na época e do poder de processamento dos computadores, foram apenas usados táxons supra-genéricos. Apesar disso, permitiu-se a realização de análises mais detalhadas do que na década passada (*i.e.*, identificação de estados de caracteres homoplásticos) que serviriam como modelo para as matrizes utilizadas em estudos futuros (BENNET, 1996; BENTON, 1999; 2004; NESBITT & NORELL, 2006; IRMIS *et al.*, 2007; NESBITT, 2007; BRUSATTE, *et al.*, 2007; 2010).

Gower & Wilkinson (1996) publicaram uma síntese das quatro matrizes filogenéticas (ARCUCCI & SERENO, 1990; SERENO, 1991; PARRISH, 1993; JUUL, 1994; [Fig. 5: B]) e apresentaram quatro pontos de consenso: 1) proterossuquídeos, eritrossuquídeos, *Euparkeria capensis* e proterocâmpsidos são mais proximamente aparentados entre si do que com Archosauria; 2) Archosauria é composto por duas grandes linhagens; 3) aetossauros, fitossauros, “rauisuchia”, ornitossúquideos e crocodilomorfos compõe a linhagem que posteriormente iria dar origem aos crocodilos; 4) pterossauros, dinossauros e alguns táxons basais compõe a linhagem que posteriormente iria dar origem as aves. Em suma, concluíram que um consenso havia sido atingido na relação da composição dos maiores clados de archosauriformes, mas que o parentesco e posição de alguns táxons variavam e isto ainda seria motivo de controvérsia (GOWER & WILKINSON, 1996).

Os estudos cladísticos mais recentes (*e.g.* BRUSATTE *et al.*, 2010; NESBITT, 2011; EZCURRA *et al.*, 2014; NESBITT & EZCURRA, 2015; EZCURRA, 2016) também se basearam nos caracteres anteriormente propostos, mas adicionaram nas listas vários novos, seguidos de descrições detalhadas e abordando um número maior de táxons como grupos terminais. Entretanto, vários pontos ainda apresentam certa contenda, como a posição de Phytosauria dentro ou fora de Archosauria (NESBITT, 2011; STOCKER *et al.*, 2017 *contra* EZCURRA, 2016), a composição e filogenia de “Rauisuchia” (NESBITT, 2011; BUTLER, *et al.*, 2011; NESBITT *et al.*,

2013) e as afinidades de alguns clados (e.g. *Erpetosuchidae* [NESBITT & BUTLER, 2012]).

Todavia, as últimas duas décadas tem testemunhado um aumento significativo no interesse da história evolutiva dos arcossauriformes basais, que sempre foram relegados devido a um interesse muito maior pelas formas mais derivadas dentro da linhagem que daria origem as aves (BRUSATTE, *et al.*, 2010; NESBITT, 2011; EZCURRA, *et al.*, 2016) e novas descobertas têm evidenciado que esta história foi muito mais rica em diversidade do que previamente imaginado (e.g. EZCURRA, *et al.*, 2015; PINHEIRO, *et al.*, 2016; STOCKER, *et al.*, 2016).

Para poder abordar a linhagem que posteriormente iria dar origem aos crocodilos, com o intuito de clareza e para justificar a nomenclatura utilizada na presente tese, torna-se necessário apresentar um breve histórico e contextualização das suas várias propostas nomenclaturais.

Na primeira análise sobre a filogenia da linhagem crocodiliana utilizando metodologia cladística, Gauthier & Padian (1986) designaram esta linhagem de *Pseudosuchia* e a definiram com base estémica, composta por “crocodilos e todos os arcossauros mais próximos de crocodilos do que de aves” (GAUTHIER & PADIAN, 1986: 189). Esta proposta nomenclatural foi criticada (e.g. PARRISH, 1993, BROCHU, 1997) já que *Pseudosuchia* havia recebido várias outras definições desde sua proposição original por Zittel (1887-1890) (e.g. como uma subordem da Ordem *Thecodontia* em Romer, [1976]) e por apresentar uma aparente contradição, já que a linhagem dos “falsos crocodilos” incluiria os *Eusuchia* ou “crocodilos verdadeiros”.

Benton & Clark (1988), em sua análise, propuseram o nome *Crocodylotarsi*, de base nodal, mas não apresentaram uma nova definição, apenas que seria igual a “*Pseudosuchia sensu lato*, Gauthier & Padian, 1985; Gauthier 1986”. Sereno & Arcucci (1990) ergueram o nome *Crurotarsi*, que seria apenas definido em Sereno (1991) de base nodal, como sendo composto por “*Parasuchia* (=fitossauros [CHATTERJEE, 1978]), *Ornithosuchidae*, *Prestosuchus chiniquensis*, *Suchia* e os descendentes de seu ancestral mais comum”. A maior diferença desta proposta para as outras previamente apresentadas seria a remoção de *Ornithosuchidae* da base da linhagem aviana para a crocodiliana, que foi seguido em trabalhos subseqüentes junto com o uso de *Crurotarsi* (PARRISH, 1993; JUUL, 1994; BENTON, 2004; BRUSATTE *et al.*, 2010). Entretanto, esta topologia foi questionada por Nesbitt

(2011) que encontrou o clado Phytosauria (=Parasuchia) como grupo irmão de Archosauria, tornando Crurotarsi uma designação inválida. Devido a isso, o autor utilizou Pseudosuchia, com a mesma definição estémica, para designar a linhagem crocodiliana, já que historicamente era a denominação mais antiga.

A base para o arcabouço filogenético na presente tese (Fig. 9) vai utilizar os trabalhos de Nesbitt (2011), modificado com o a inclusão de Phytosauria dentro de Archosauria segundo a proposta por Ezcurra (2016). Estes dois estudos são as análises mais abrangentes publicadas recentemente sobre o tema e, conseqüentemente, as mais utilizadas em outros trabalhos (e.g. BUTLER *et al.* 2011; NESBITT & BUTLER, 2012; BUTLER *et al.*, 2014; von BACZKO *et al.*, 2014; STOCKER, *et al.*, 2017).

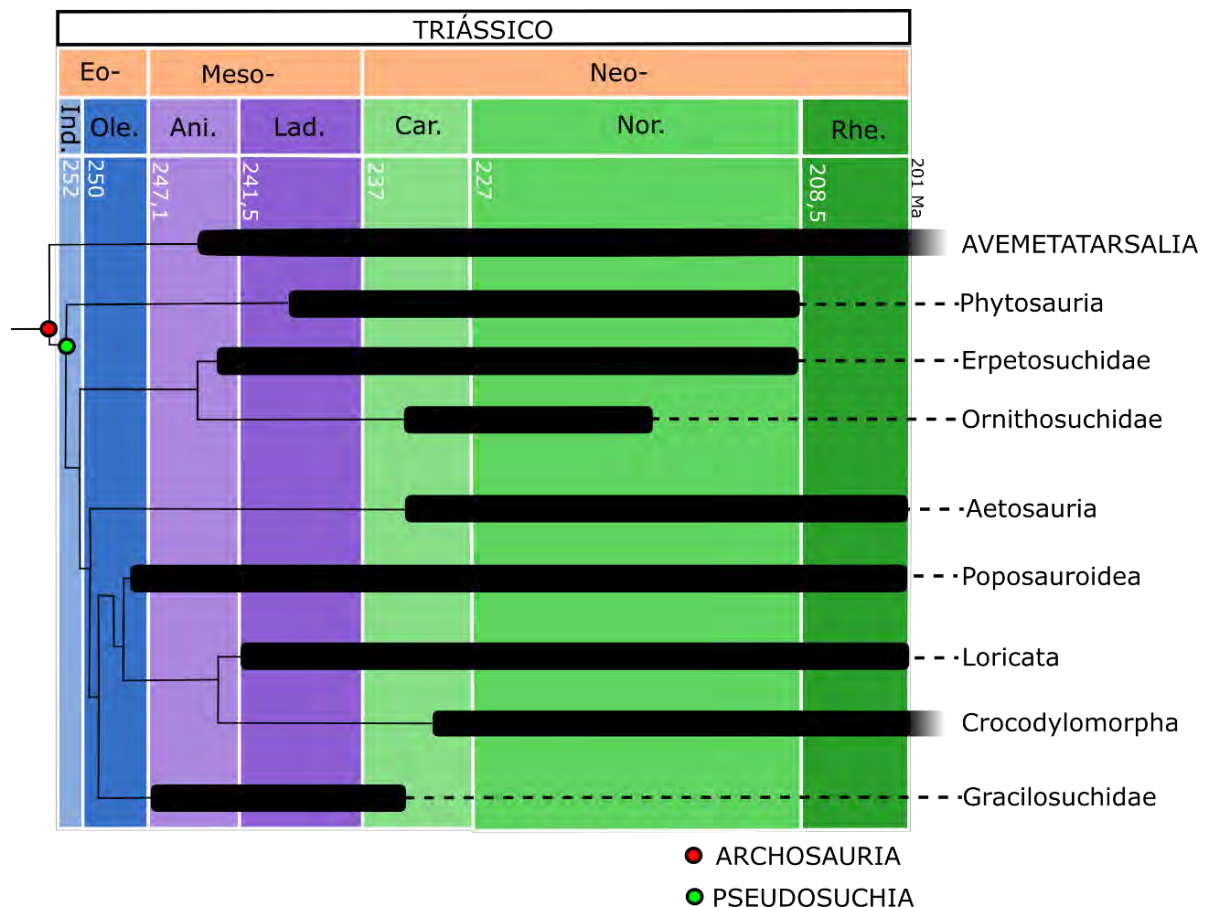


Figura 9. Cladograma detalhando a distribuição temporal dos grupos mais inclusivos dentro de Archosauria (Modificado de BUTLER *et al.*, 2014, Ornithosuchidae como grupo irmão de Erpetosuchidae é baseado em uma das possíveis topologias encontradas por NESBITT & BUTLER, 2012). As idades (em milhões de anos) seguem a Tabela Cronoestratigráfica Internacional (GRADSTEIN *et al.*, 2012).

Abreviações: Eo-. Eotriássico; Meso- Mesotriássico; Neo-. Neotriássico; Ind. Induano; Ole. Olenequiano; Ani. Anisiano; Lad. Ladiniano; Car. Carniano; Nor. Noriano; Rhe. Rético.

A contribuição a ser apresentada nesta tese para o conhecimento dos arcossauros será para três grupos pseudossuquídeos: os Ornithosuchidae, os Erpetosuchidae e “Rauisuchia”, que representaria um agrupamento parafilético composto por Loricata+Puposauroidea (Fig. 8). A origem, o histórico evolutivo e o estado da arte do conhecimento de cada um desses grupos serão abordados em detalhe ao longo de suas respectivas sessões. É necessário destacar que, Erpetosuchidae e Ornithosuchidae são clados bem estabelecidos, mas a nomenclatura de “Rauisuchia” é problemática existindo dúvida se representaria um grupo monofilético (GOWER, 2000; NESBITT, *et al.*, 2013). Logo, a designação Rauisuchia, utilizado sem aspas, será usada para se referir especificamente ao possível grupo monofilético, enquanto que abordagens informais utilizando aspas (como “rauissuquídeos”/ “rauissúquios”) serão utilizadas ao longo do texto para se referir a todos os táxons dos diferentes subgrupos inseridos historicamente no grupo (*i.e.* Rauisuchidae, Prestosuchidae, Puposauridae, Chatterjeeidae, *loc. cit.* GOWER, 2000; BRUSATTE *et al.*, 2010; NESBITT, 2011; NESBITT *et al.*, 2013; NESBITT & DESOJO, 2017;) no contexto de um grado. Os outros grupos de arcossauriformes e a linhagem que posteriormente iria dar origem as aves (Avemetatarsalia *sensu* NESBITT, 2011) estão fora do tema principal da tese e não serão abordados.

5. “RAUISUCHIA”

5.1. Uma breve caracterização dos “rauissuquídeos”

Este grupo é composto por vários táxons de distribuição quase cosmopolita (Fig. 10), com exceção da Oceania e da Antártida (BENTON, 1984; GOWER, 2000), que, em estudos filogenéticos pré-cladísticos, acabaram sendo tentativamente agrupados devido a similaridades cranianas, de cintura pélvica e de articulação tarsal mais próximas entre si do que de outros grupos mais inclusivos de arcossauros do Triássico (GOWER, 2000). Entretanto, como vai ser abordado ao longo desta sessão, não existe um consenso se este representaria um grupo natural, já que hipóteses discordantes apresentando o grupo como mono-, para- ou polifilético já foram publicadas (e.g. GOWER & NESBITT, 2006; BRUSATTE *et al.*, 2010; NESBITT, 2011; FRANÇA, 2011, FRANÇA *et al.*, 2011; NESBITT & DESOJO, 2017).

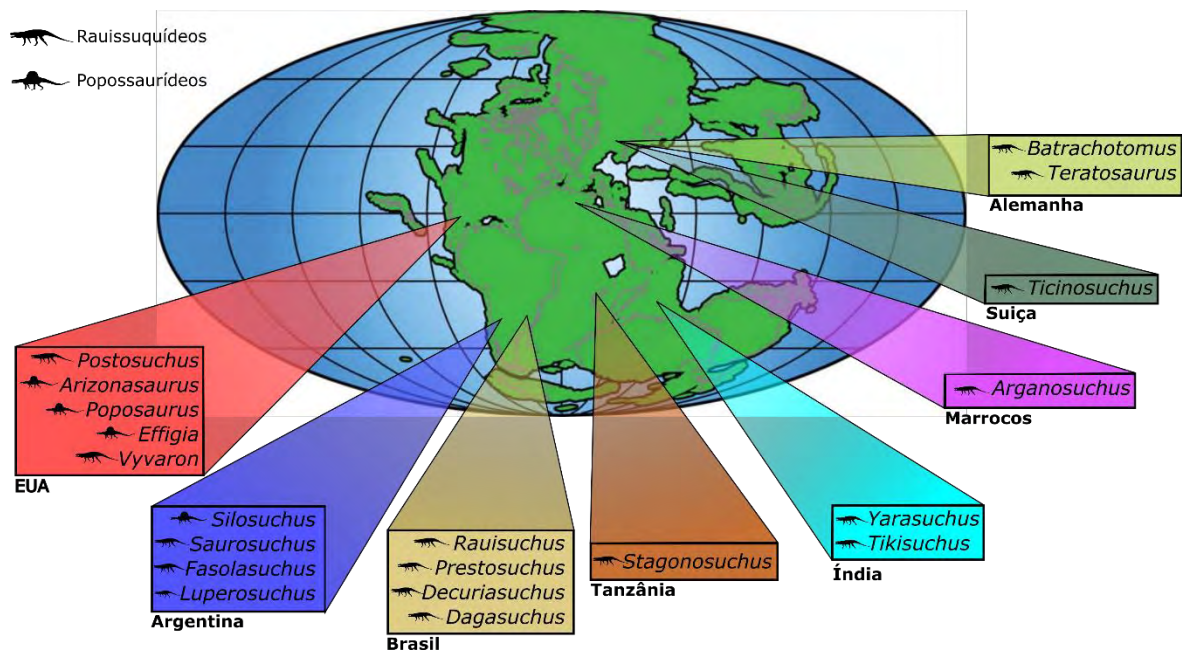


Figura 10. Distribuição global de táxons de “rauissuquídeos” (Modificado de NESBITT *et al.*, 2013; LESSNER *et al.*, 2016).

A visão atual sobre a filogenia destas formas (NESBITT, 2011; BUTLER, *et al.*, 2011) seria que representa um grupo parafilético, composto pelos seguintes clados: Loricata Merrem 1820 (*sensu* Nesbitt, 2011), composto por *Ticinosuchus tenax*; *Batrachotomus kupferzellensis*; *Saurosuchus galilei*; *Prestosuchus chiniquensis*; Puposauroida Brusatte *et al.*, 2010, composto por *Qianosuchus mixtus* Li *et al.*, 2006, *Arizonasaurus babbitti* Welles, 1947, *Xilousuchus sapingensis* Wu, 1981; *Ctenosauriscus koeneni* von Huene, 1902, *Poposaurus gracilis* Mehl,

1915 e *Lotosaurus adentus* Zhang, 1975; o clado Shuvosauridae, composto por *Sillosuchus longicervix* Alcober & Parrish, 1997, *Shuvosaurus inexpectatus* Chatterjee, 1993, *Effigia okeeffeae* Nesbitt & Norell, 2007 e o clado Rausuchidae, composto por *Rausuchus tiradentes* von Huene, 1942, *Polonosuchus silesiacus* Sulej, 2005, *Postosuchus kirkpatricki* Chatterjee, 1985 e *Postosuchus alisonae* Peyer *et al.*, 2008.

Os táxons normalmente referenciados a este grupo apresentam diferentes planos e adaptações corporais, algumas inclusive apresentando convergência com formas da linhagem avemetatarsaliana, variando de animais carnívoros de grande porte, quadrúpedes ou bípedes ocasionais (e.g. *Batrachotomus kupferzellensis*; *Saurosuchus galilei*; *Prestosuchus chiniquensis*), predadores cursoriais de grande-médio porte (*Postosuchus kirkpatricki*), formas mais gráceis e cursoriais (e.g. *Effigia okeeffeae*; *Poposaurus gracilis*), formas edêntulas, possivelmente com a mandíbula revestida com um bico córneo (*E. okeeffeae* e *Lotosaurus adentus*, respectivamente) e com as apófises neurais das vértebras alongadas com um aspecto de vela dorsal (e.g. *Arizonasaurus babbitti* e *Ctenosauriscus koeneni*) (Fig. 11).

As propostas sinapomorfias do grupo derivam da problemática concepção pré-cladística do mesmo, que acabou sendo perpetuada nos estudos modernos (SERENO, 1991; GOWER, 2000; NESBITT *et al.*, 2013). Os exemplos mais clássicos desta problemática seriam em relação à presença de uma abertura acessória no rosto e de características da cintura pélvica.

No crânio, alguns táxons apresentam uma abertura acessória, localizada no contato entre o pré-maxilar/maxilar, que apresenta diferentes designações na literatura, sendo referida como “fenestra subnarinal” por Galton (1985), Chatterjee (1985) e Parrish (1993) ou “fenestra anterorbital acessória” por Sill (1974), Dawley *et al.* (1979), Benton (1986) e Long & Murry (1995). Em algumas propostas cladísticas (e.g. CHATTERJEE, 1985; BENTON, 1986; FRANÇA *et al.*, 2013; SILVA *et al.*, 2016) sua presença é considerada um caractere filogeneticamente significativo de “rauissuquídeos”. Entretanto, esta interpretação apresenta alguns problemas. Primeiramente, alguns autores (BENTON & CLARK, 1988; PARRISH, 1993; JUUL, 1994) a consideram homoplástica. Ademais, uma abertura similar estaria presente em diferentes grupos de arcossauros coronais e não coronais (Fig. 12), como o eritrossuquídeo *Shansisuchus shansisuchus* (GOWER, 2000), sendo

que Welman (1998) e França (2011) também a descrevem em *Proterosuchus fergusi*.

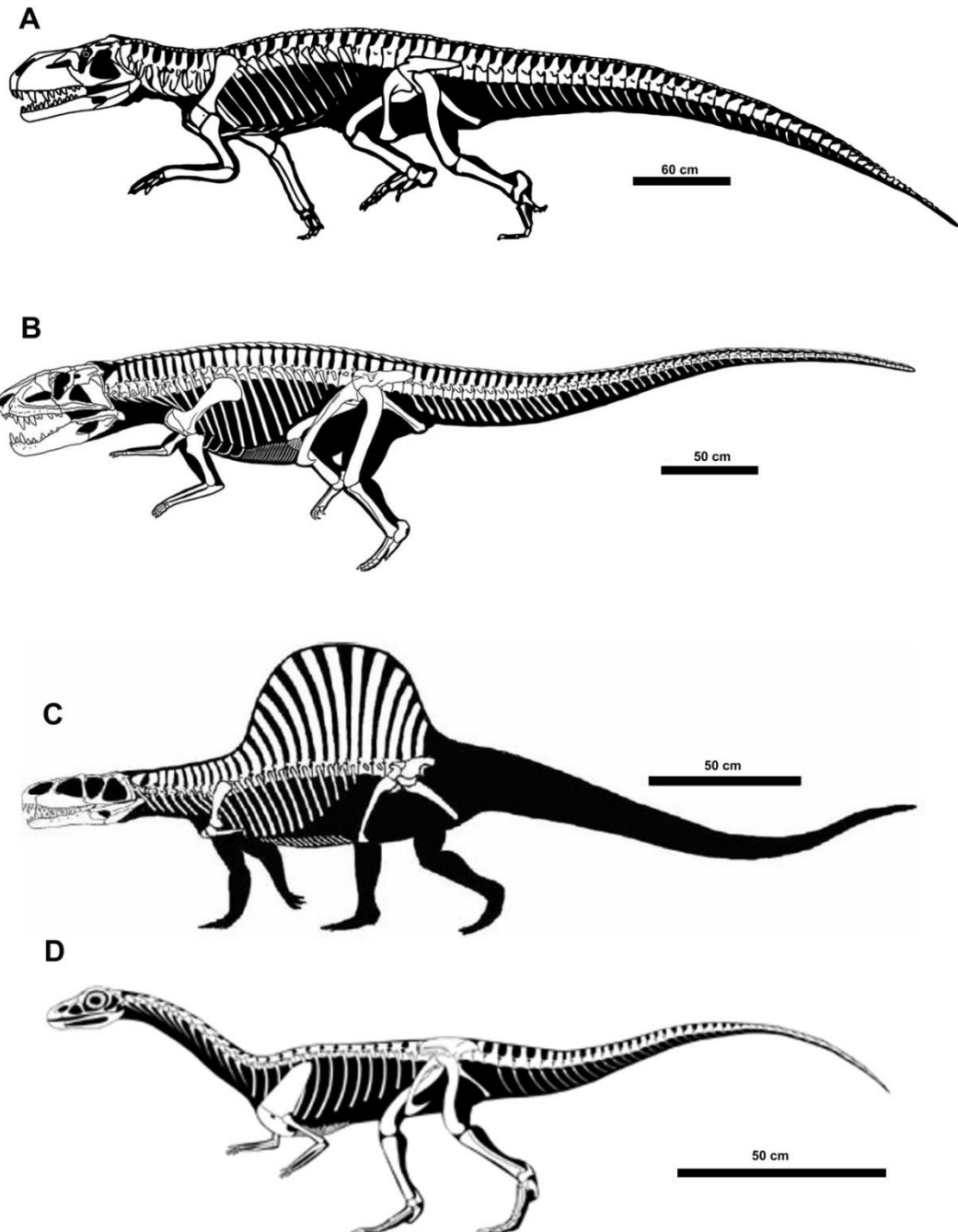


Figura 11. Exemplos de padrão corporal de alguns “rauissuquídeos”. (A) *Prestosuchus chiniquensis* (baseado em Barberena, 1978; Azevedo, 1991), (B) *Postosuchus kirkpatricki* (retirado de Weinbaum, 2013), (C) *Arizonasaurus babbitti* (retirado de Nesbitt, 2005), (D) *Effigia okeeffeae* (retirado de Nesbitt, 2007).

Inferências biomecânicas atribuem um nível de cinetismo na porção anterior do rosto, principalmente no contato entre o pré-maxilar e o maxilar (BENTON, 1986; LONG & MURRAY, 1995; LIPARINI, 2008; MASTRANTONIO, 2010), enquanto que outras funções biológicas como a passagem de vasos sanguíneos ou nervos (GOWER, 2000) ou uma expressão mais lateral de um órgão vomeronasal (CHATTERJEE, 1985) já foram propostas, mas não foram bem aceitos (WITMER, 1995; GOWER, 1999; SULEJ, 2005; WEINBAUM, 2013; NESBITT *et al.*, 2013).

Uma estrutura similar também foi descrita em pterossauros (ÖSI *et al.*, 2010) e dinossauros. (JUUL, 1994). Destes últimos, *Herrerasaurus ischigualastensis* Sereno & Novas, 1993 apresenta um “forame subnarinal” localizado ventralmente à narina e, internamente, ventralmente ao palato pré-maxilar, além de uma “fenestra pré-maxilar-maxilar” localizada posteriormente à narina e, internamente, dorsalmente ao palato pré-maxilar. Para estes autores, a “fenestra pré-maxilar-maxilar” seria uma autapomorfia de *H. ischigualastensis* e o “forame subnarinal” seria uma sinapomorfia de *H. ischigualastensis* + dinossauros saurísquios que teria evoluído convergentemente em outros táxons como os “rauissuquídeos” (e.g. *Saurosuchus galilei*).

Nesbitt (2011) considerou a abertura acessória como sendo um caractere homoplástico, citando os problemas discutidos por Gower (2000) e interpretou ao menos no caso de um espécime de *S. galilei* (PVSJ 32), como sendo na realidade um artefato tafonômico devido à desarticulação dos pré-maxilares com os maxilares. Para este autor, a sua presença ou ausência seria determinada pela condição de preservação dos espécimes e não representaria uma característica osteológica válida, o que justificaria a ausência desta em alguns táxons (e.g. *Lotosaurus adentus*). Esta posição também foi discutida em maiores detalhes em uma publicação recente publicação de novos materiais do táxon *Luperosuchus fractus* (NESBITT & DESOJO, 2017)

Entretanto, existem propostas na literatura que discordam da origem puramente tafonômica desta abertura acessória. França (2011) considerou esta abertura distinta demais e muito recorrente em diferentes táxons para ser apenas devido a fatores preservacionais. Ademais, o tamanho da fenestra aparenta sofrer variações ao longo da ontogenia como no caso de *P. chiniquensis*, onde há

evidência de uma nas formas juvenis, similar a aquelas de *S. galilei* e *Decuriasuchus quartacolonia* (ALCOBER, 2000; FRANÇA *et al.* 2011, 2013), que vai diminuindo de tamanho nas sub-adultas até ficar muito reduzida ou completamente desaparecer nas formas adultas (LACERDA *et al.*, 2016). Estas variações afetavam interpretações filogenéticas, já que a inclusão de *P. chiniquensis* entre os “rauissuquídeos” era considerada problemática porque o grande crânio completo do espécime UFRGS-PV-0156-T, atribuído a este táxon por Barberena (1978) e Azevedo (1991) não apresentava esta característica. Porém, a presença de uma abertura acessória no rostro do espécime UFRGS-PV-0629-T, descrito por Mastrantonio (2010) como um *P. chiniquensis* de idade sub-adulta, mudou este panorama. A autora argumentou que o contato “frouxo” entre o pré-maxilar e o maxilar, considerado por Gower (2000) como uma articulação móvel, mesmo que não implicasse necessariamente em algum tipo de cinetismo, poderia interferir na posição de preservação dos dois ossos (mais afastados, caracterizando uma fenestra, ou mais próximos, dando a impressão de uma ausência da mesma) o que teria ocorrido no espécime UFRGS-PV-0156-T.

Mais recentemente, Silva *et al.* (2016) descreveram um “foramen subnarial” em formato de gota com um entalhe no premaxilar direto do espécime UBLRA-PVT-281, também atribuído a *P. chiniquensis*. Desta forma, este táxon se torna o único que apresenta três tipos de abertura acessória ao longo de quatro espécimes (Fig. 12).

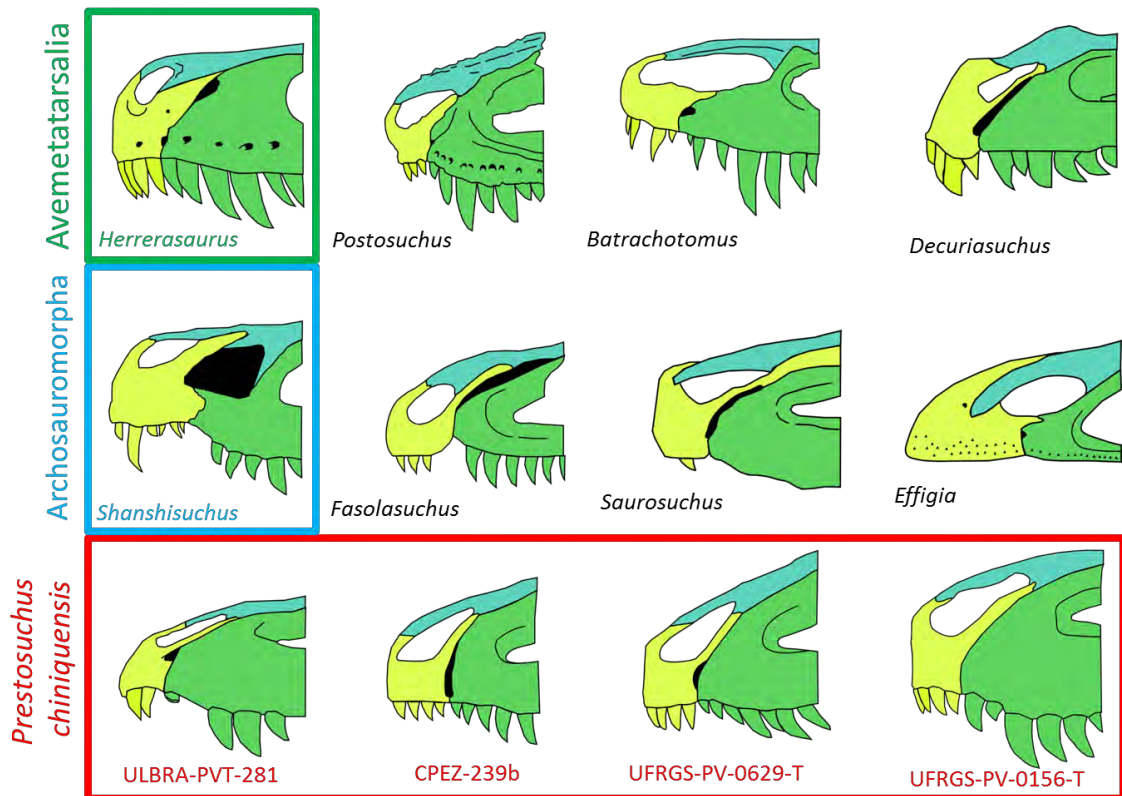


Figura 12. Esquema apresentando a porção rostral, em norma esquerda, de alguns táxons de arcossauriformes, indicando os diferentes tipos de aberturas acessórias presentes na região de contato do pré-maxilar com o maxilar. Figura modificada de Silva *et al.*, (2016) com a inclusão de *Effigia* (Nesbitt, 2007); *Batrachotomus* redesenhado baseado em Gower & Schoch (2009) e o rosto de *Prestosuchus chiniquensis* (CPEZ-239b, UFRGS-PV-0629-T e UFRGS-PV-0156-T) baseado em Lacerda *et al.* (2016).

As características da cintura pélvica foram primeiro discutidos por Bonaparte (1984) que considerou que o posicionamento mais ventralizado dos acetábulos iria colocar o fêmur praticamente na vertical, o que possibilitaria um movimento parasagital dos apêndices locomotores posteriores, de uma maneira convergente com os dinossauros (Fig. 13). Isto se daria pela combinação de dois fatores: devido a um direcionamento mais ventralizado das costelas sacrais que posicionariam os acetábulos mais ventralmente e a articulação com a epífise proximal do fêmur, que teria um condição similar a um pilar em posição totalmente vertical (chamado de “pillar-erect”), onde o corpo da porção proximal do fêmur é praticamente reto, ao contrário do aspecto onde ao epífise proximal do fêmur apresenta um espessamento ou “cabeça” direcionado medialmente para a articulação com o acetábulo (ou

butress-erect), como encontrado em dinossauros. Neste mesmo trabalho, Bonaparte considerou estas características como sendo as principais para definir Rausuchidae (*sensu* BONAPARTE, 1984).

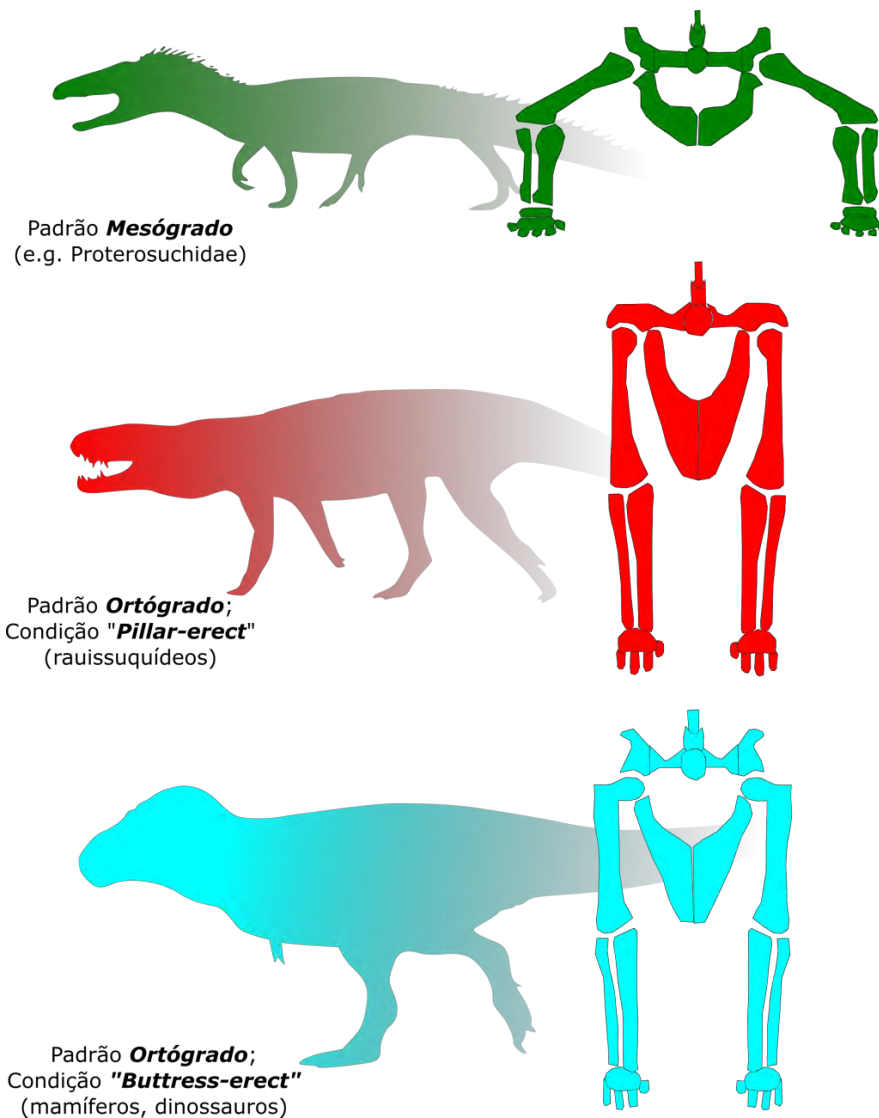


Figura 13. Esquema comparativo das características da cintura pélvica e posicionamento dos apêndices locomotores posteriores em arcosauriformes.

Tal proposta foi seguida por outros pesquisadores, como Benton & Clark (1988), mas estes identificaram esta característica também em popossaurídeos. Entretanto, o padrão da estrutura pélvica iria variar dentro dos “rauissuquídeos”, como no caso *Poposaurus gracilis* onde Long & Murray (1995) argumentaram que as costelas sacrais não apresentam uma ventralização tão acentuada, mas que a crista supra-acetabular poderia suportar a porção proximal do fêmur para permitir um tipo de articulação vertical parasagital.

A presença de um espessamento ou uma crista projetada lateralmente na margem dorsal do acetábulo e um acetábulo totalmente fechado também seriam outras características previamente diagnósticas para os “rauissuquídeos” (Fig. 14). Esta projeção lateral ou crista/processo supra-acetabular, varia entre as espécies, de mais latero-medialmente baixa, como em *Stagonosuchus nyassicus* até uma projetada lateralmente como em *Prestosuchus chiniquensis* e *Batrachotomus kupferzellensis* (GOWER, 2000; MASTRANTONIO, 2010). Entretanto, esta característica é igualmente problemática, já que está presente, em outros táxons não-“rauissuquídeos”, como uma crista baixa no eritrossuquídeo *Erythrosuchus africanus* (GOWER, 2003). A função biomecânica desta projeção lateral seria de suporte para a articulação com a epífise proximal do fêmur e afetaria a posição do apêndice em relação ao eixo sagital do corpo. Com isso, a postura dos apêndices locomotores nos “rauissuquídeos” seria vertical, de postura convergente com dinossauros, mas com variações na articulação dos propódios posteriores com a cintura pélvica.

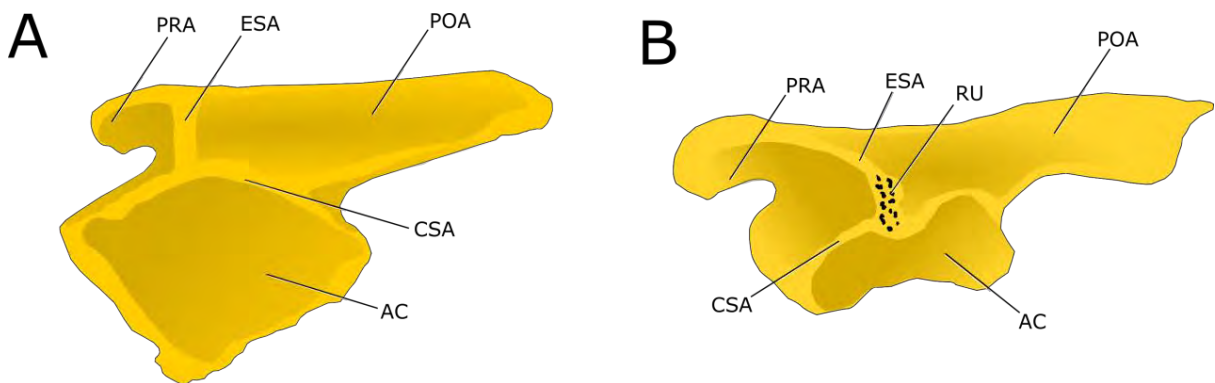


Figura 14. Ilustração esquemática comparativa entre dois ilium de “rauissuquídeos”. (A) Íleo esquerdo de *Saurosuchus galilei* (SILL, 1974); (B) Íleo esquerdo de *Pposaurus gracilis* (WEINBAUM & HUNGERBÜHLER, 2007). Abreviações: AC, acetábulo; CSA, crista supra-acetabular; ESA, espessamento supra-acetabular; POA, processo pós-acetabular; PRA, processo pré-acetabular; RU, rugosidades.

O número de vértebras sacrais varia entre diferentes espécies, com duas vértebras sacrais presentes na grande maioria de formas (e.g. *Decuriasuchus quartacolonis*, *Prestosuchus chiniquensis*; *Saurosuchus galilei*; *Postosuchus kirkpatricki*), mas três vértebras sacrais são descritas em *Teratosaurus suevicus* (GALTON, 1985) e *Batrachotomus kupferzelensis* (GOWER & SCHOCH, 2009)

enquanto que a presença de quatro ou mais é uma sinapomorfia de *Poposauroidae*, como *Sillosuchus longicervix* (ALCOBER & PARRISH, 1997) e *Poposaurus gracilis* (WEINBAUM & HUNGERBÜHLER, 2007).

Como pode ser visto nos dois casos expostos acima, questões acerca da filogenia dos “rauissuquídeos” são complexas e estão longe de algum tipo de resolução, mesmo com o avanço no conhecimento destas formas. Todavia, problemas desta maneira são inerentes do estudo de formas de vertebrados fósseis, onde o número amostral de espécimes geralmente é reduzido. Muito tem se descoberto nos últimos anos, como será apresentado na próxima sessão, mas ainda resta muitos trabalhos de coleta ou revisões em coleções de museus para descobrir espécimes mais informativos.

5.2. Estado da arte

Do ponto de vista histórico, os primeiros táxons descritos do que hoje consideramos “rauissuquídeos” foram *Teratosaurus suevicus*, *Poposaurus gracilis* e pelo menos uma icnoespécie (*Chirotherium barthii* Kaup, 1835, reinterpretado por Soergel em 1925 como marcas de “tecodontes pseudossúquios” [BUFFETAUT, 1987]). Mas, as afinidades de *T. suevicus* e *P. gracilis* foram originalmente consideradas mais próximas aos dinossauros, sendo revisto apenas posteriormente, como será abordado ao longo desta sessão.

A identificação dos “rauissuquídeos” como um grupo fóssil distinto ocorreu a partir dos trabalhos do paleontólogo alemão Frederich von Huene, a partir de espécimes que foram encontrados no interior do Estado do Rio grande do Sul durante sua vinda ao Brasil entre 1928-1929. Nesta viagem ele coletou vários espécimes fósseis que seriam a base de uma série de monografias que seriam publicadas em forma de fascículos começando em 1935 até 1942 (von HUENE, 1935-42). No fascículo publicado em 1938 (von HUENE, 1938), foram apresentados a descrição dos espécimes de arcossauros, incluindo os novos táxons: *Prestosuchus chiniquensis*, *Prestosuchus loricatus*, *Procerosuchus celer*, *Rauisuchus tiradentes*, *Hoplitosuchus raii*, *Rhadinosuchus gracilis* e *Spondylosoma absconditum*.

Alguns anos antes, von Huene (1936) havia proposto a Subfamília Rausuchinae, em referência ao gênero *Rausuchus* (que seria composta apenas por *Rausuchus tiradentes* e *Prestosuchus chiniquensis*) que seria uma subfamília da família Stagonolepididae. Posteriormente, von Huene (1938) incluiu *Prestosuchus chiniquensis*, *Prestosuchus loricatus* e *Procerosuchus celer*, da região de Xiniquá (também presente na literatura com a grafia Chiniquá), próxima ao município de São Pedro do Sul, e *Rausuchus tiradentes* e *Hoplitosaurus (=Hoplitosuchus) rauli*, da região de Santa Maria dentro da Ordem Pseudosuchia, mas foi apenas em 1942 onde propôs a Família Rausuchidae, que seria um membro da Superfamília Stagonolepoidea da mesma Ordem (von HUENE, 1942). O uso da família Rausuchidae seria seguido por autores posteriores (HOFFSTETTER, 1955), mas com variação em sua composição específica. von Huene (1956) posteriormente iria propor a Superfamília Chirotheridae, cujo nome foi baseado no icnogênero *Chirotherium*, onde estariam incluídos as famílias Rausuchidae, Stagonolepididae e Aetosauridae.

Em Romer (1956), *Procerosuchus celer*, *Rausuchus tiradentes* e as duas espécies do gênero *Prestosuchus* estariam incluídos dentro da Família Ornithosuchidae, que para o autor seria uma subordem de Pseudosuchia. Porém, o mesmo não fez menção à proposta de von Huene (1942) da Família Rausuchidae e incluiu um sinal de interrogação [?] antes do nome dos táxons trabalhados, não apresentando argumento justificando estas decisões. Entretanto, este trabalho é o primeiro que tenta desvincular os “rauissuquídeos” dos estagonolepidídeos, ao mesmo tempo inferindo que os táxons pertencentes à Ornithosuchidae teriam se originado a partir arcossauriformes basais como *Euparkeria capensis*.

Charig (1956) apresentou uma descrição de novos espécimes coletados na Formação Manda na Tanzânia, sudeste da África, em sua tese de doutorado. Um destes espécimes representaria um novo “rauissuquídeo”, cunhado “*Mandasuchus*”. Entretanto, esta descrição ficou restrita à sua tese e nunca publicado formalmente (para detalhes sobre esta questão, ver MOODY & NAISH, 2010), o que tornou o táxon um *nomen nudum*. Todavia, quando Charig (1957) propôs a família Prestosuchidae em um resumo, o autor explicitou que a mesma seria formada pelos gêneros “*Mandasuchus*”, *Prestosuchus chiniquensis*, *Stagonosuchus nyassicus* von Huene, 1938 e *Spondylosoma absconditum*. Curiosamente, o gênero “*Mandasuchus*”, por não ser considerado válido como discutido acima, invalidaria

também a diagnose da família, mas esta proposta continuou a ser usada em outras publicações ao longo dos anos (e.g. ROMER, 1966).

Reig (1959) descreveu *Saurosuchus galilei*, da Formação Ischigualasto da Argentina, e o inseriu dentro da Família Ornithosuchidae de Romer (1956). Esta proposta foi revisada pelo mesmo pesquisador alguns anos depois (REIG, 1961), e a Família Ornithosuchidae passou a ser composta por *Rauisuchus tiradentes*, *Prestosuchus chiniquensis*, *Stagonosuchus nyassicus* e *S. galieli*. Neste trabalho o autor separou os “rauissuquídeos” dos estagonolepidídeos, conforme a proposta de Romer (1956), mas diferiu ao utilizar a Família Rauisuchidae, por motivo de prioridade, que seria composta pelos gêneros *R. tiradentes*, *P. chiniquensis*, *S. nyassicus* e *S. galieli*, que em Romer (*op. cit.*) estavam inseridos dentro da Família Ornithosuchidae.

Hughes (1963) propôs que Proterosuchia seria composto por duas famílias Chasmatosauridae e Erythrosuchidae (baseado principalmente em critérios cronológicos). Em sua concepção, Erythrosuchidae incluiria os gêneros *Hoplitosuchus raii*, *Saurosuchus galilei* e *Rauisuchus tiradentes*, estes tradicionalmente considerados como “rauissuquídeos”, junto com *Euparkeria capensis*, *Erythrosuchus africanus* e *Shansisuchus shansisuchus*, baseados principalmente nas características da cintura pélvica.

Krebs (1963) descreveu a estrutura dos tarsos de *Rauisuchus tiradentes* e um novo táxon cunhado de *Ticinosuchus ferox*, do Mesotriássico (Anisiano-Ladiniano) da Suíça, (entretanto esta última seria apenas formalmente descrita em outra publicação [KREBS,1965]) onde incluiu esta espécie dentro da Família Rauisuchidae, junto com os gêneros *R. tiradentes*, *Prestosuchus chiniquensis*, *Procerosuchus celer* e *Stagonosuchus nyassicus*.

Romer (1966) apresentou a primeira proposta de divisão da Ordem Thecodontia (*sensu* Owen, 1859) em quatro Subordens: Proterosuchia, Pseudosuchia, Aetosauria e Phytosauria. Nesta proposta, formalizou a Família Prestosuchidae (dentro da Subordem Pseudosuchia) que havia sido erguida em um resumo por Charig (1957) e composta por *Prestosuchus chiniquensis*, *Procerosuchus celer*, “*Mandasuchus*” e *Stagonosuchus nyassicus*. *Rauisuchus tiradentes* e *Saurosuchus galilei* foram inseridos, com dúvida, fora de Prestosuchidae e dentro de Erythrosuchidae. Entretanto, o autor não apresentou

uma diagnose para as famílias Prestosuchidae e Erythrosuchidae ou uma justificativa para as escolhas dos táxons componentes de cada uma.

Reig (1970), baseando-se em trabalhos anteriores, dissertou sobre a importância dos Proterosuchia para a evolução dos arcossauros, concordou com a proposta de Romer (1956) de que táxons tradicionalmente considerados “rauissuquídeos” teriam evoluído a partir de formas similares a *Euparkeria capensis*.

Bonaparte (1970), utilizando como base a classificação de Romer (1966), apresentou uma proposta onde a Subordem Pseudosuchia teria tido origem a partir de Proterosuchia. Entretanto, usou a designação Família Rausuchidae, composta por *Ticinosuchus ferox*, *Prestosuchus chiniquensis*, *Rausuchus tiradentes*, *Saurosuchus galilei*, *Shansisuchus shansisuchus*, *Stagonosuchus nyassicus*, “*Mandasuchus*” e a espécie chinesa *Fenhosuchus cristatus* Young, 1964, onde considerou que a família fazia parte da Subordem Ornithosuchia.

Romer (1971) descreveu *Luperosuchus fractus* da Formação Chañares (fim do Ladiniano-começo do Carniano, Meso-Neotriássico da Argentina) baseado em um grande crânio incompleto e considerou que seria uma forma mais derivada do que os proterossuquídeos. Esta espécie foi descrita como um pseudossuquídeo da Família Rausuchidae junto com os gêneros *Rausuchus tiradentes*, *Prestosuchus chiniquensis*, *Ticinosuchus ferox*, *Fenhosuchus cristatus*, *Shansisuchus shansisuchus*, *Stagonosuchus nyassicus* e “*Mandasuchus*”, sendo estes últimos quatro gêneros sendo incluídos com dúvidas. Neste mesmo trabalho, Romer também discutiu a hipótese de evolução dos “rauissuquídeos” proposta por Reig (1970) e levantou três hipóteses para a evolução do grupo: teriam evoluído paralelamente a partir dos proterossuquídeos; seriam uma linhagem sem descendentes ou eram aparentados aos ancestrais dos prosaurópodes ou dos saurópodes. O autor não discutiu estas propostas em detalhe e concluiu afirmando que esperava que novas informações fossem apresentadas em um trabalho futuro (ver SILL, 1974).

Romer (1972) mostrou preferência pela designação Prestosuchidae *contra* Rausuchidae, argumentado que esta proposta nomenclatural não tinha muito suporte porque era baseada em um gênero erguido a partir de um espécime muito incompleto. Também voltou a discutir a possibilidade deste grupo ser heterogêneo e abordou novamente a hipótese de que a linhagem Erythrosuchidae –

Prestosuchidae estaria aparentada aos precursores dos saurópodes. Em sua designação dos táxons, *Spondylosoma*, anteriormente considerado um dinossauro (von HUENE, 1938), foi duvidosamente colocado dentro da Família Prestosuchidae, junto com *Prestosuchus chiniquensis*, *Rauisuchus tiradentes*, *Saurosuchus galilei*, *Luperosuchus fractus*, *Ticinosuchus ferox*, *Cuyosuchus hueni* Reig, 1961, *Shansisuchus shansisuchus*, *Hoplitosaurus (=Hoplitosuchus) raii*, *Fenhosuchus cristatus*, *Stagonosuchus nyassicus*, “*Mandasuchus*”, enquanto que *Procerosuchus celer* foi inserido na Família Proterochampsidae.

Sill (1974) descreveu novos materiais de crânio e pós-crânio de *Saurosuchus galilei* e apresentou um estudo filogenético em que o mesmo estaria inserido na Família Rauisuchidae (segundo este autor, a família Rauisuchidae teria prioridade sobre a família Prestosuchidae). No trabalho, o autor também considerou que não havia boas evidências de que os “rauissuquídeos” teriam dado origem aos dinossauros, contrariando a hipótese de Romer (1971; 1972).

Krebs (1974) apresentou uma hipótese corroborando a classificação dos arcossauros baseada em características do tornozelo e da pélvis proposta por Charig (1972) e propôs que os pseudossuquídeos seriam aparentados com os Crocodylia. Neste trabalho ergueu o grupo Suchia (composto por pseudossuquídeos e crocodilianos como grupos irmãos) com base no tipo de articulação do tornozelo. O único “rauissuquídeo” apresentado neste trabalho foi *Ticinosuchus ferox*, sendo considerado como um pseudossuquídeo.

Bonaparte (1975) propôs a evolução dos “rauissuquídeos” a partir dos eritrossuquídeos e inseriu as famílias Rauisuchidae e Erythrosuchidae dentro do grupo denominado Rauisuchia (Subordem Proterosuchia). Quando von Huene (1938) propôs a família Rauisuchidae, ele não atribuiu espécimes-tipo para cada táxon descrito. Com base nisso, Krebs (1976) designou lectótipos e paralectótipos para cada uma das espécies descritas por von Huene, discutindo também que a Família Rauisuchidae seria muito abrangente. Outra questão abordada seria que a espécie chinesa *Fenhosuchus cristatus* não pertenceria a Rauisuchidae e que as espécies *Prestosuchus chiniquensis* e *Prestosuchus loricatus* seriam sinônimos, mas que estes táxons precisavam ser revistos.

Barberena (1978) descreveu preliminarmente um grande sincrânio (UFRGS-PV-0156-T), coletado próximo ao Município de Candelária, no Estado do Rio Grande

do Sul, concluindo que pertenceria à espécie *Prestosuchus chiniquensis*. Também propôs que esta espécie estaria em uma posição intermediária entre *Luperosuchus fractus* e *Saurosuchus galilei*. Este autor concordou com a proposta de Krebs (1976) de designar *P. chiniquensis* como espécie-tipo para o Gênero *Prestosuchus* e que *P. loricatus* seria sinônimo de *P. chiniquensis*.

O táxon *Heptasuchus clarki* foi descrito por Dawley *et al.* (1979) a partir de material do Triássico Superior dos Estados Unidos (Formação Popo Agie do Wyoming). Foi incluído na Família Rausuchidae, junto com *Ticinosuchus ferox*, *Stagonosuchus nyassicus*, “*Mandasuchus*”, *Luperosuchus fractus*, *Rausuchus tiradentes*, *Prestosuchus chiniquensis* e *Saurosuchus galilei*.

Bonaparte (1981) descreveu *Fasolasuchus tenax* (Formação Los Colorados, Neonoriano da Argentina), argumentando, porém, que esta espécie seria problemática devido ao seu estado de preservação e à morfologia dos osteodermos. O novo táxon foi incluído na Família Rausuchidae, segundo classificação proposta anteriormente por esse autor (BONAPARTE, 1975), junto com *Poposaurus gracilis*, *?Heptasuchus clarki*, *Saurosuchus galieli*, *Rausuchus tiradentes*, *?Teratosaurus suevicus*, *Prestosuchus chiniquensis*, *Prestosuchus loricatus*, *Luperosuchus fractus*, *Ticinosuchus ferox*, *Stagonosuchus nyassicus*, o “rauissuquídeo de Kupferzell” (WILD [1980], GALTON [1985], mas apenas descrito como *Batrachotomus kupferzellensis* por GOWER [1999]) e o exemplar de Warwick (descrito como *Bromsgroveia walkeri* por GALTON [1985]). Neste artigo, o autor propôs Rausuchia, composto pelas famílias Rausuchidae e Erythrosuchidae, como uma infraordem dentro de Proterosuchia, mas apresentou uma distinção clara entre a Família Rausuchidae e a Infraordem Rausuchia, utilizando ao longo do trabalho ambos os termos para se referir ao mesmo agrupamento de espécies.

Chatterjee (1982), seguindo outros trabalhos que utilizaram a articulação do tornozelo para classificar os arcossauros (WALKER, 1964; KREBS, 1963, 1974; CHARIG, 1972; CRUICKSHANK, 1979; BONAPARTE, 1971b) apresentou uma classificação dos arcossauros baseada no padrão de articulação do tornozelo. Argumentou que a Infraordem Rausuchia (BONAPARTE, 1981), que seria representada pelas famílias Rausuchidae (formada pelos táxons propostos em Krebs [1965] e Sill [1974]) e Poposauridae, teria uma articulação “crocodilo normal”,

mas não comentou as propostas filogenéticas abordadas em outras publicações (BONAPARTE 1975, 1981).

Gauthier & Padian (1985) apresentaram uma proposta, baseada na tese de doutorado não publicada de Gauthier (1984), onde apresentou uma definição cladística para Archosauria propôs que seria composto por duas grandes linhagens: uma composta pelas aves e seus ancestrais denominado Ornithosuchia, e outro denominado Pseudosuchia, composto pelos crocodilianos e seus ancestrais. Nesta proposta, Rausuchia é monofilético e estaria inserido em Pseudosuchia, com um arranjo similar às definições de Bonaparte (1981) e Krebs (1967). No entanto, os autores não citaram as espécies que comporiam o grupo.

A espécie *Postosuchus kirkpatricki* (Grupo Dockum, Neotriássico dos Estados Unidos) foi descrita por Chatterjee (1985) a partir de material composto por 12 indivíduos (sendo dois de maior porte considerados adultos e os demais interpretados como formas juvenis), como um predador de médio porte incluso em Popsauridae, Neste trabalho, o autor argumentou sobre similaridades desta espécie com os outros membros da Família Popsauridae e propôs que a família Tyrannosauridae teria evoluído a partir dos Popsauridae, baseando-se em semelhanças do crânio, cintura pélvica e estrutura do tornozelo.

Galton (1985) reavaliou o material da espécie *Teratosaurus suevicus* (do Neotriássico [Noriano] da Alemanha) e o reinterpretou como um “rauisúquideo”, redescrivendo o holótipo (maxilar direito com dentes) e apresentando um ílio que havia sido coletado no mesmo nível stratigráfico que o holótipo. Este ílio era bem verticalizado e apresentava um processo supra-acetabular que seria característico da Família Popsauridae. Descreveu também *Bromsgroveia walkeri* (Formação “Bromsgrove Sandstone”, Warwick–Inglaterra) como um novo “rauisúquideo”.

Gauthier (1986) ampliou sua análise cladística de sua tese de doutorado (Gauthier, 1984) e discutiu sobre as propostas de Chatterjee (1985), reconhecendo as similaridades apontadas por aquele autor entre os popossaurídeos e os dinossauros tiranossaurídeos, mas considerou como um caso de convergência. Não foram citadas quais espécies comporiam Rausuchia, mas o autor concluiu que este clado seria agrupado com Crocodylomorpha (Fig. 15).

Benton (1986) fez uma nova análise da espécie *Teratosaurus suevicus* e assegurou que o crânio do holótipo pertenceria a um “rauissuquídeo”, enquanto que os materiais de pós-crânio associados seriam de um dinossauro prossaurópode. Apresentou, ainda, uma argumentação de que os Pseudosuchia não teriam relação com a história evolutiva dos dinossauros.

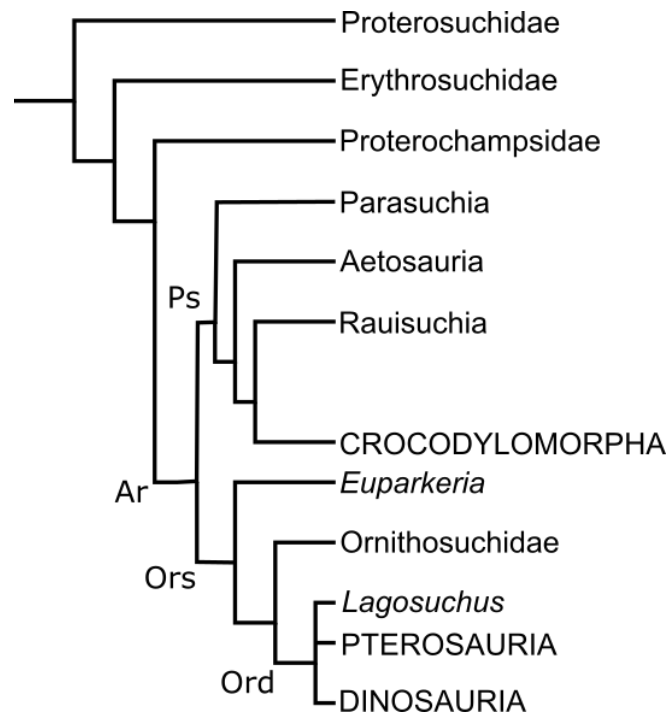


Figura 15. Cladograma redesenhado da proposta filogenética de Gauthier (1986) onde arcossauros são divididos em duas linhagens, uma que futuramente iria dar origem aos crocodianos (Pseudosuchia) e outra as aves (Ornithosuchia). Abreviações: Ar, Archosauria; Ord, Ornithodira; Ors, Ornithosuchia; Ps, Pseudosuchia.

Chatterjee & Majunbar (1987) descreveram *Tikisuchus romeri* (Formação Tiki, Índia), sendo este considerado o primeiro “rauissuquídeo” da Ásia. Neste trabalho, Rausuchia foi composto por duas famílias: Poposauridae (incluindo formas gráceis e bípedes) e Rausuchidae (composta por formas mais robustas e quadrúpedes), sendo que *Tikisuchus* foi inserido nesta última.

Benton & Clark (1988), em uma extensa análise dos arcossauros, propuseram que o clado Pseudosuchia seria composto por apenas duas famílias: os Stagonolepididae (aetossauros) e os Rausuchidae, estes últimos constituindo um

agrupamento parafilético (Fig. 16). Também criaram o termo *Crocodylotarsi* (= *Pseudosuchia lato sensu*, GAUTHIER & PADIAN, 1985; GAUTHIER, 1986) para a linhagem pró-crocodiliana, que incluiria *Phytosauridae* (=Parasuchia), *Crocodylomorpha*, *Stagonolepididae* (aetossauros), *Rauisuchidae* e *Poposauridae*.

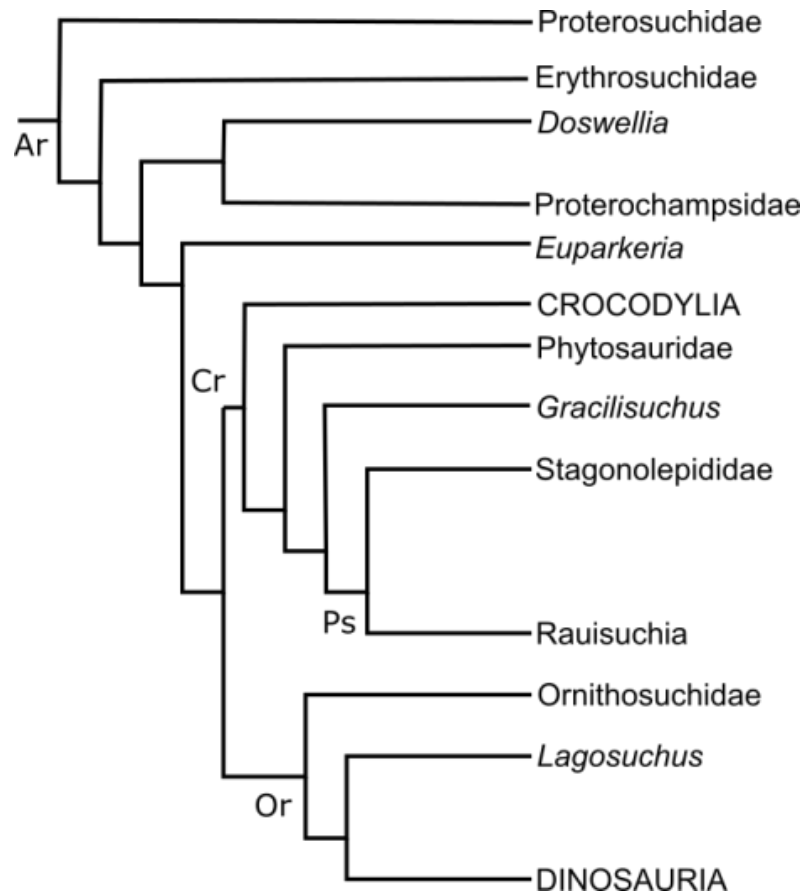


Figura 16. Cladograma redesenhado da proposta filogenética de Benton & Clark (1988) onde a linhagem pró-crocodiliana, dentro de Archosauria, foi renomeada *Crocodylotarsi*. Abreviações: Ar, Archosauria; Cr, *Crocodylomorpha*; Or, *Ornithosuchia*; Os, *Pseudosuchia*.

Sennikov (1988) descreveu diversos táxons atribuídos a *Rauisuchia* provenientes do oeste da Rússia (pouco conhecidos pelos pesquisadores ocidentais da época) apresentando “*Tsylomosuchus*” além de material adicional de *Vytshegdosuchus zheshartensis* e *Dongusuchus efremovi*. O autor apresentou a linhagem dos “rauissuquídeos” dividida em dois grupos: um composto por formas mais robustas, com o acetábulo dirigido ventralmente (e.g. *Prestosuchus chiniquensis*, *Saurosuchus galilei* e *Stagonosuchus nyassicus*) e outro, mais

derivado, constituído por formas mais gráceis, com pescoço mais alongado e com o acetábulo dirigido mais lateralmente (e.g. “*Tsylomosuchus*”, *V. zheshartensis*, *D. efremovi*, *Energosuchus garjainovi* Ochev, 1986 e “*Mandasuchus*”).

Sereno & Arcucci (1990) apresentaram uma revisão dos trabalhos acerca das relações dos arcossauros e propuseram mudanças de nomenclatura para a linhagem pró-crocodiliana, designando-a como Crurotarsi e considerando que a mesma seria composta por formas tanto com a estrutura do tarso tipo crocodilo reversa como as de crocodilo normal, mas que poderiam não constituir um agrupamento monofilético (Fig. 17).

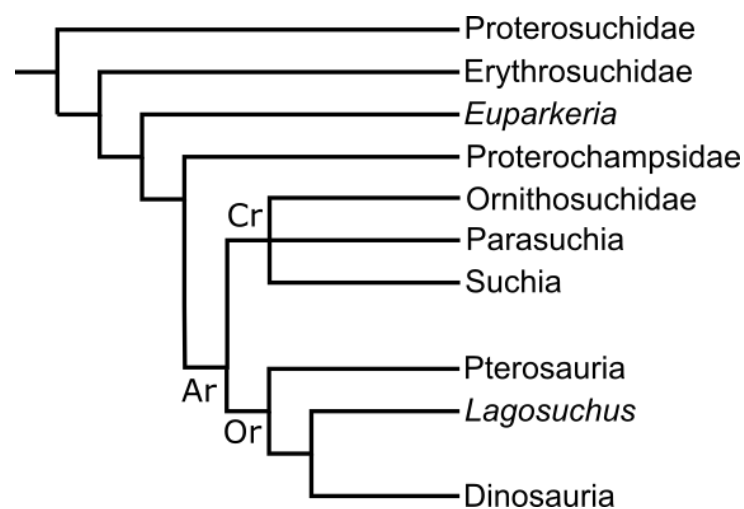


Figura 17: Cladograma redesenhado da proposta de Sereno & Arcucci (1990) para Archosauria. Abreviações: Ar, Archosauria; Cr, Crurotarsi; Or, Ornithodira.

Sereno (1991) identificou que o clado Suchia (formado por *Gracilisuchus stipanicorum*, Aetosauria, Rausuchia, Puposauridae, Crocodylomorpha e todos os descendentes de seu ancestral comum) seria definido apenas por uma sinapomorfia craniana (previamente citada em Benton & Clark, 1988): uma barra temporal formada pelo pós-orbital e o esquamosal (Fig. 18). O crânio descrito por Barberena (1978) foi então retirado de Suchia porque não apresentava esta característica. Esta proposta foi considerada problemática por Mastrantonio (2010) visto que Sereno (1991) se baseou apenas no material de UFRGS-PV-0156-T e não discutiu a região temporal de qualquer outro “rauissuquídeo” para comparação.

Azevedo (1991) apresentou uma descrição mais detalhada do sincrânio do espécime UFRGS–PV-0156-T, originalmente publicado por Barberena (1978), incluindo material associado ao mesmo, composto de 21 vértebras pré-sacrais (incluindo quatro vértebras cervicais mais o atlas e o axis, com a quinta cervical ausente), 11 vértebras caudais e diversos osteodermos. O autor efetuou ainda uma análise paleoecológica acerca do material estudado e uma discussão morfofuncional, que correspondem às únicas partes desta tese até hoje publicada (Azevedo, 1995).

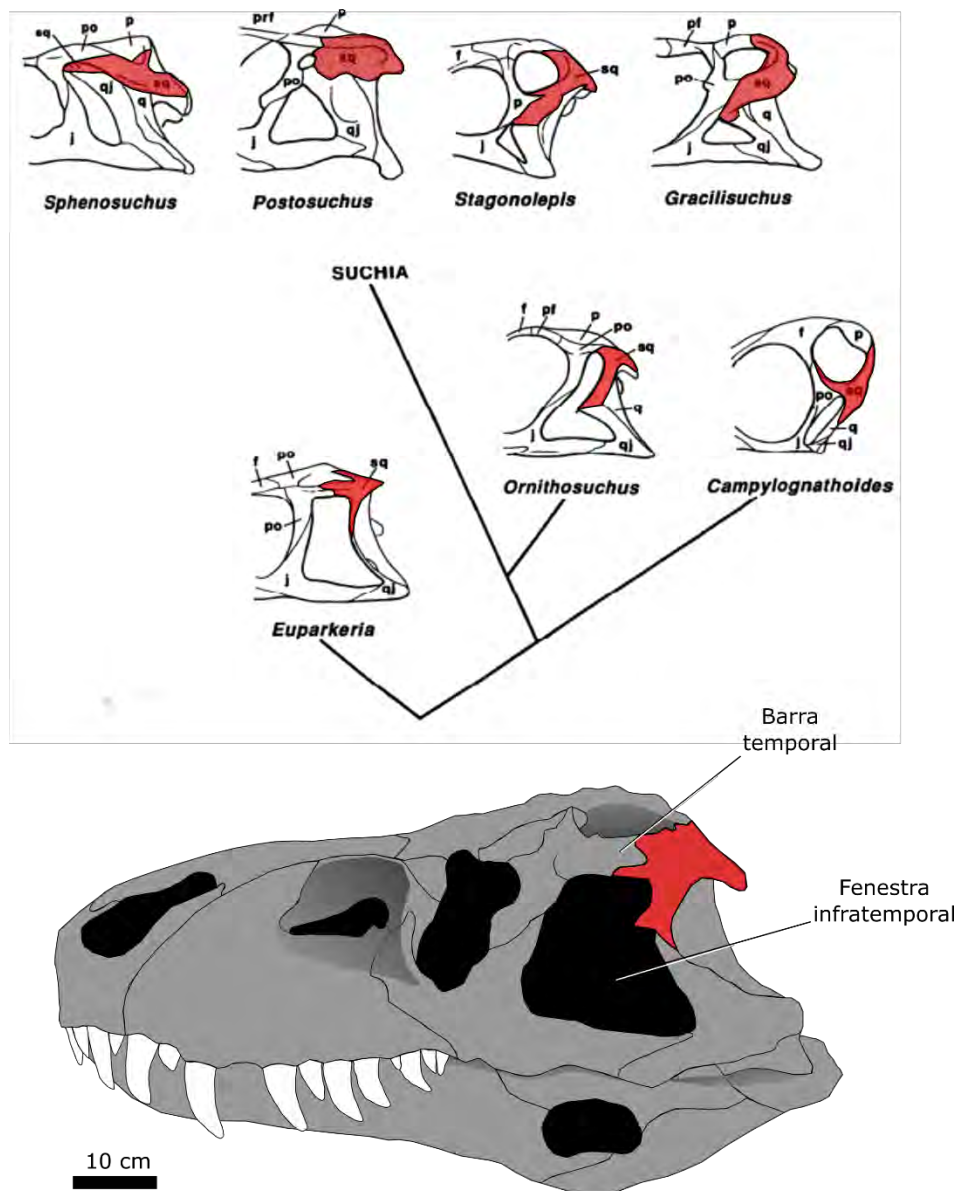


Figura 18. Diagrama filogenético de Sereno (1991) indicando a barra temporal encurtada formada pelo pós-orbital e o esquamosal (em vermelho) e a fenestra infratemporal de aspecto triangular característica dos súquios, na comparação com

três *outgroups*. Desenho do crânio de *Prestosuchus chiniquensis* (Modificado de BARBERENA, 1978) indicando a presença da barra temporal que Sereno (1991) considerou como ausente no táxon (Figura modificado de MASTANTONIO, 2010).

Parrish (1993), em uma análise mais inclusiva, apresentou os “raissuquídeos” como um grupo polifilético, sob a designação “Rauisuchia”, composto pelas famílias Rauisuchidae (*Rauisuchus tiradentes*, *Fasolasuchus tenax*, *Lotosaurus adentus* e o “Material de Kupferzell”= *Batrachotomus*), Pposauridae (*Poposaurus gracilis*, *Postosuchus kirkpatricki*, *Teratosaurus suevicus* e *Bromsgroveia walkeri*) e Prestosuchidae (*Prestosuchus chiniquensis*, *Ticinosuchus ferox* e *Saurosuchus galilei*), além de alguns táxons isolados (Fig. 19). Reuniu, sob o nome *P. chiniquensis*, o crânio descrito por Barberena (1978) e o holótipo de von Huene (1936-42, 1942), mas os codificou separadamente. Também argumentou que *Prestosuchus loricatus* seria sinônimo de *P. chiniquensis*. Porém, esta proposta apresentava problemas na definição e polarização de alguns caracteres, que foram abordados por autores subsequentes (JUUL, 1994; KISCHLAT, 1996; GOWER & WILKINSON, 1996).

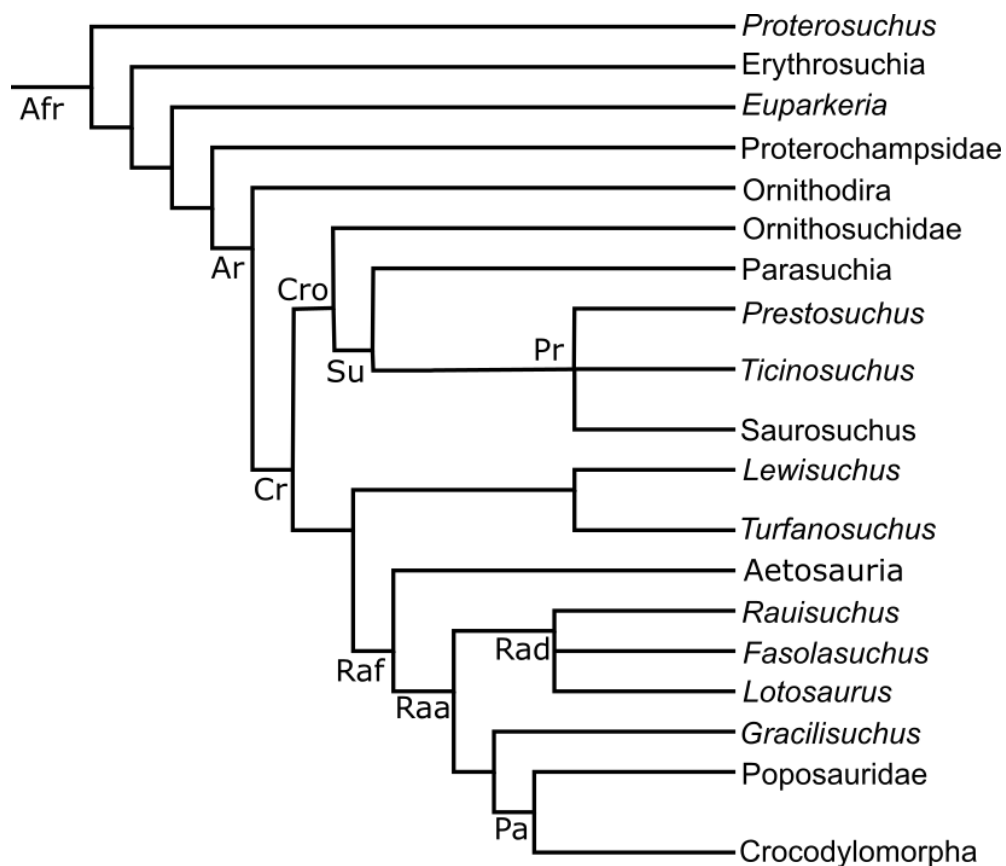


Figura 19. Cladograma redesenhado da proposta filogenética de Parrish (1993) onde Prestosuchidae e Rausuchidae estão separados, com apenas este último em Rausuchia. Abreviações: Ar, Archosauria; Arf, Archosauriformes; Cr, Crurotarsi; Cro, Crocodylotarsi; Pa, Paracrocodylomorpha; Pr, Prestosuchidae; Raa, Rausuchia; Rad, Rausuchidae; Raf, Rausuchiformes.

Juul (1994) apresentou uma análise para Archosauria utilizando 74 caracteres para 17 arcossauros, com três táxons servindo de grupo externo (Fig. 20). Os caracteres usados foram retirados de trabalhos anteriores (GAUTHIER, 1986; GAUTHIER *et al.*, 1988; BENTON & CLARK, 1988; SERENO & ARCUCCI, 1990; SERENO, 1991; NOVAS, 1992; SERENO & NOVAS, 1992; PARRISH, 1993), mas a maioria deles foi modificada para esta análise. Em relação aos “rauissuquídeos”, o autor apresentou Prestosuchidae como um grupo monofilético, mas não especificou qual seria sua composição. Stagonolepididae (=aetossauros) aparece como seu grupo-irmão e a ausência de Rausuchidae na análise não é esclarecida.

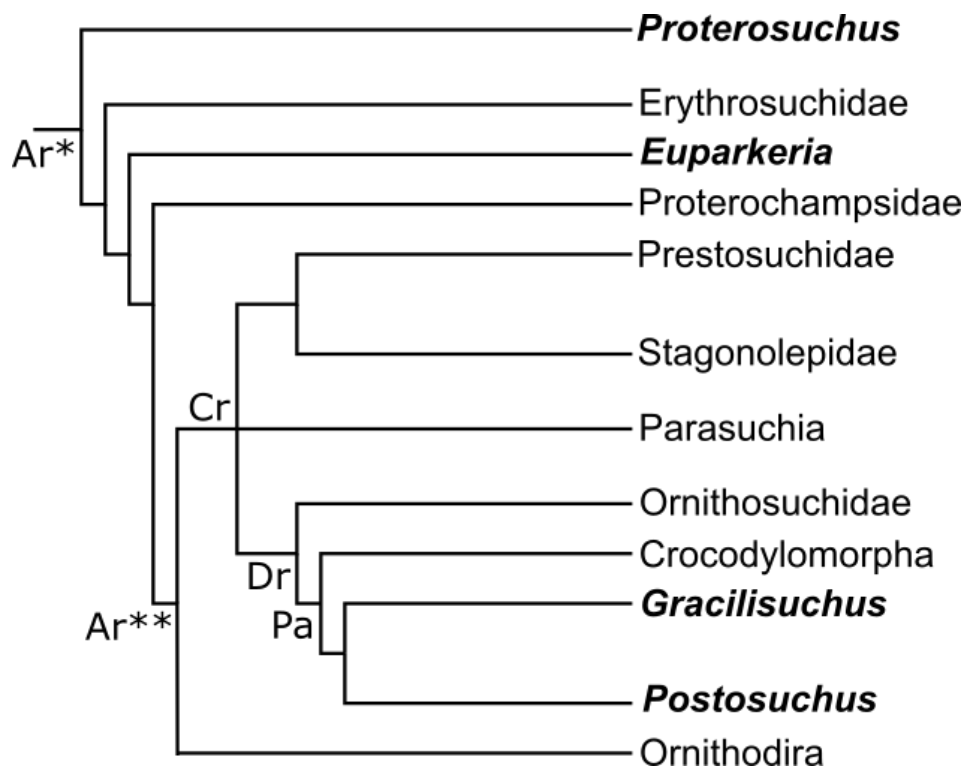


Figura 20. Cladograma redesenhado da proposta filogenética de Juul (1994). Abreviações: Ar*, Archosauria (*sensu lato*); Ar**, Archosauria (*sensu stricto*); Cr, Crurotarsi; Dr, Dromeosuchia; Pa, Paracrocodylomorpha.

Long & Murray (1995) propuseram que a espécie *Postosuchus kirkpatricki*, descrita por Chatterjee (1985) seria composta de outras espécies distintas. Alguns pequenos elementos de pós-crânio que foram atribuídos a *P. kirkpatricki* por Chatterjee (1985) seriam pertencentes a uma nova espécie de “rauissuquídeo”, aqui denominado *Chatterjea elegans* e a nova Família Chatterjeeidae. Os autores também consideraram o crânio de *Shuvosaurus inexpectatus* Chatterjee, 1993, descrito originalmente como um dinossauro, como possivelmente pertencendo ao pós-crânio de *C. elegans*. Um novo popossaurídeo, *Lythrosuchus langston*, baseados em espécimes muito incompletos depositados no Museu Memorial do Texas e que também haviam sido referidos a *P. kirkpatricki* (CHATTERJEE, 1985) também foi erguido. No contexto filogenético, os autores consideraram Rausuchia como sendo monofilético, porém, não descartaram a possibilidade deste ser parafilético. Entretanto, esta proposta não foi testada com metodologia filogenética e foi posteriormente criticada por outros autores (BENTON & GOWER, 1997; GOWER, 1999).

Sennikov (1995) apresentou uma proposta da classificação dos arcossauros basais onde foram incorporadas diversas espécies pouco conhecidas provenientes da Rússia. Para o autor, Rausuchia seria composto pelas famílias Rausuchidae e Puposauridae, mas, como argumentado por Gower (2000), não indicou quais espécies fariam parte de cada família.

Em uma análise comparativa utilizando as matrizes filogenéticas de quatro estudos prévios (SERENO & ARCUCCI, 1990; SERENO, 1991, PARRISH, 1993, JUUL, 1994), Gower & Wilkinson (1996) obtiveram uma árvore de consenso onde *Saurosuchus galielei*, *Ticinosuchus ferox* e *Prestosuchus chiniquensis* apresentava um posicionamento incerto entre os clados Parasuchia e Aetosauria, enquanto que *Rausuchus tiradentes*, *Fasolasuchus tenax* e o espécime “material de Kupferzell”, estariam mais próximos entre si do que a linhagem crocodiliana.

Benton & Gower (1997) revisaram vários espécimes atribuídos historicamente a “tecodontes” das localidades de Bromsgrove e Warwick, do Mesotriássico (Anisiano) da Inglaterra. Ademais, revisaram o holótipo de *Bromsgroveia walkeri* (um ílio direito) e concluíram que esta espécie apresenta afinidades com os popossaurídeos.

Alcober & Parrish (1997) descreveram *Sillosuchus longicervix*, da Formação Ischigualasto (Carniano) da Argentina, a partir de vários fragmentos de esqueleto pós-craniano.

Gower (1999) descreveu o “material de Kupferzell”, que havia aparecido antes em outros trabalhos (e.g. WILD, 1980 e GALTON, 1985), e o denominou de *Batrachotomus kupferzellensis*. Apenas o sincrânio foi descrito neste trabalho (mas sem a caixa craniana) e foram propostas duas potenciais autapomorfias para este táxon: a narina mais larga que a fenestra antero-orbital e a presença de uma depressão ventral na superfície lateral do pós-orbital. Nesta descrição, Gower (*op.cit.*) usou *Rauisuchia* para se referir a todos os táxons que geralmente são classificados pertencendo a este grupo, independente da linhagem ser ou não monofilética.

Kischlat & Barberena (1999) apresentaram uma breve reavaliação do material descrito por Barberena (1978) e Azevedo (1991) juntamente com o paralectótipo de *P. chiniquensis* e “materiais adicionais” (que não foram especificados) como um novo táxon. Este novo táxon recebeu a denominação de “*Crurotarsi indeterminata*” com base em diferenças morfológicas na mandíbula, calcâneo e fêmur dos três espécimes em relação ao lectótipo de *P. chiniquensis*. Esta proposta seria mais elaborada por Kischlat (2000), onde tratou dos arcossauros fósseis do Rio Grande do Sul de forma geral. O autor apresentou três linhagens para *Rauisuchia* sob as denominações informais de “prestossúquios”, “teratossúquios” e “popossáurios”. Os “prestossúquios” (e.g. *Prestosuchus*, *Luperosuchus*, *Saurosuchus* e *Stagonosuchus*) seriam um grupo constituído por formas plantígradas, robustas e de pescoço curto, com um acetábulo ventralmente direcionado e a lâmina do ílio orientada quase horizontalmente. *Procerosuchus celer* foi interpretado como sendo um “prestossúquio” e possivelmente um juvenil de *P. chiniquensis*. Os “teratossáurios” (e.g. *Teratosaurus*, *Batrachotomus*, *Rauisuchus*, *Postosuchus*, *Fasolasuchus*, *Ticinosuchus* e *Tikisuchus*) representariam formas gráceis, de pescoço alongado, um fêmur com uma curvatura sigmoidal distinta e uma pelve mais delgada portando um acetábulo voltado mais lateralmente. Os “popossáurios” (e.g. *Bromsgroveia*, *Heptasuchus*, *Lythrosuchus*, *Chatterjeea* e *Sillosuchus*) seriam compostos por formas mais leves, de pescoço muito alongado e com uma cintura pélvica derivada, com o púbis alongado, o ísquio curto e o acetábulo aberto.

Nesta publicação, Kischlat (2000) citou, pela primeira vez, o nome “*Karamuru vorax*” para se referir a um táxon baseado no material UFRGS-PV-0156-T (descrito anteriormente por BARBERENA [1978] e AZEVEDO [1991]), no paralectótipo de *P. chiniquensis* e em parte do material de *P. loricatus*. Este táxon estaria inserido dentro de “prestossúquios” e diferiria de *P. chiniquensis* por apresentar uma fraca sínfise mandibular (composta pelo dentário e o esplenial), um calcâneo mais estreito com uma tuberosidade mais alongada e um fêmur quase retilíneo, com uma torção similar à das encontradas em crocodilomorfos. Kischlat (2000) relatou ter usado esta denominação em um resumo anterior (KISCHLAT & BARBERENA, 1999), porém este nome não aparece citado. Desse modo, não ficou claro se “*Karamuru*” corresponderia ao que foi mencionado como “*Crurotarsi indeterminata*”.

Alcober (2000) descreveu um novo material craniano de *Saurosuchus galilei* e o interpretou como pertencente a uma forma juvenil. Este crânio apresentava um neurocrânio bem preservado, relevando várias estruturas anatômicas que não haviam sido documentadas antes. O autor considerou que Rausuchidae seria formado por: *Saurosuchus*, *Prestosuchus*, *Ticinosuchus*, *Fasolasuchus*, *Ticinosuchus* e *Rausuchus*, qualificando *Postosuchus* como um poposaurídeo basal. Em sua proposta, considerou preliminarmente que Rausuchidae apresentaria cinco sinapomorfias cranianas: órbita alta, com forma de buraco de fechadura (“keyhole shaped”), apresentando a barra pós-orbital formada pelo pós-orbital e o jugal; fenestra subnarinal localizada entre o pré-maxilar e o maxilar; abertura da fenestra pré-orbitalestreitada rostralmente (BENTON & CLARK, 1988); presença de um processo rostral no ramo ventral do esquamosal e um tubérculo basal mais largo que o côndilo occipital.

Gower (2000) efetuou um trabalho de revisão e crítica sobre a sistemática dos “rauissuquídeos”, apresentando uma das melhores compilações do conhecimento científico disponível sobre este grupo até aquela data. O autor ressaltou que a definição de Rausuchia é pobre e que, devido à falta de um consenso sobre quais táxons iriam compor este grupo, não haveria certeza se seria mono, para ou polifilético. Parte do problema seria devido à falta de informações mais completas sobre alguns táxons, descritos a partir de material muito incompleto, cujo único consenso seria que estariam relacionados à linhagem crocodiliana dos arcossauros.

Benton & Walker (2002), em sua redescritção de *Erpetosuchus granti* Newton, 1894 também apresentaram uma análise filogenética de 14 táxons da linhagem pró-crocodiliana, onde *Ticinosuchus*, *Batrachotomus*, *Prestosuchus*, *Saurosuchus* e *Fasolasuchus* faziam parte dos “rauissuquídeos” e retiraram *Poposaurus* deste grupo. O resultado apresentado foi similar a trabalhos prévios (BENTON & CLARK, 1988; BENTON, 1990; PARRISH, 1993; OLSEN *et al.*, 2000) onde *Postosuchus* seria mais relacionado com Crocodylomorpha do que com Rausuchia, mas os autores argumentaram que tal posicionamento seria mal resolvido devido a muitas sinapomorfias do crânio compartilhadas deste táxon entre os dois grupos.

Gower (2002) completou sua descrição do crânio de *Bratachotomus kupferzellensis* ao descrever o neurocrânio, comparando-o com os neurocrânios dos “rauissuquídeos” *Postosuchus*, *Saurosuchus* e *Tikisuchus* (sem apresentar justificativa para esta seleção) e com outros arcossauros (Fig. 21). A filogenia resultante deste trabalho indicou que os aetossauros seriam mais relacionados com os crocodylomorfos do que com os “rauissuquídeos”, e este último seria um grupo parafilético.

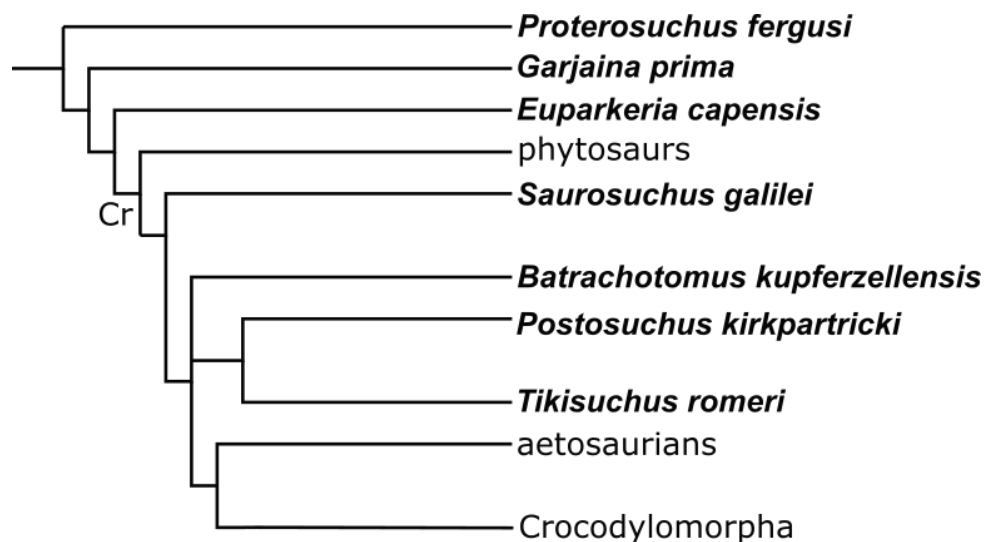


Figura 21. Cladograma redesenhado da proposta filogenética de Gower (2002) onde os táxons tradicionalmente considerados “rauissuquídeos” *Saurosuchus galilei*, *Postosuchus kirkpatricki*, *Tikisuchus romeri* e *Batrachotomus kupferzellensis* seriam um agrupamento parafilético. Abreviações: Cr, Crurotarsi.

Weinbaum (2002), em sua dissertação de mestrado, reexaminou o material de *Postosuchus kirkpatricki*, e utilizando a classificação de Gower (2000) que apresentou 32 gêneros para “rauisuquídeos incluindo poposaurídeos” propôs que este táxon seria mais próximo aos “rauisuquídeos” do que aos poposaurídeos. Ademais, argumentou que os táxons *Chatterjeea elegans* e *Lythrosuchus langston* (LONG & MURRAY, 1995), seriam válidos, mas não apresentou uma justificativa para esta escolha ou uma análise filogenética.

Em sua tese de doutorado não publicada, Kischlat (2003) alterou a composição do material referível a “*Karamuru vorax*” para UFRGS-PV-0156-T [o material previamente descrito como *Prestosuchus chiniquensis* por Barberena (1978) e Azevedo (1995)] e um fêmur esquerdo isolado (UFRGS-PV-0472-T), além do paralectótipo de *P. chiniquensis*. Adicionalmente, propôs o novo gênero “*Abaporu*” para *Prestosuchus loricatus*, baseado em um hábito canibal completamente especulativo. Ambas as propostas apresentam problemas e não podem ser consideradas válidas porque não seguem as normas de proposição de novas espécies postulado pelas regras da Comissão Internacional de Nomenclatura Zoológica (sigla em inglês ICZN). Portanto, não foram publicadas formalmente, apenas em um capítulo de livro e em resumos de simpósio.

Renesto *et al.* (2003) descreveram um dente de carnívoro, coletado em 1978, da Formação Gorno (Lombardi – Itália – Mesocarniano) e atribuíram-no a um “*Rauisuchia indet.*”. Nesbitt (2003) redescreveu *Arizonasaurus babbitti* Welles 1947 baseado em material mais completo (o holótipo deste táxon é composto por uma maxila esquerda incompleta, que já apresentou diversas designações) (Fig. 22). Neste trabalho, os *Rauisuchia* se mostraram monofiléticos, mas incluindo apenas *Postosuchus kirkpatricki*, *Saurosuchus galilei* e *Poposauria* (*A. babbitti*, *Chatterjeea elegans* e *Poposaurus gracilis*).

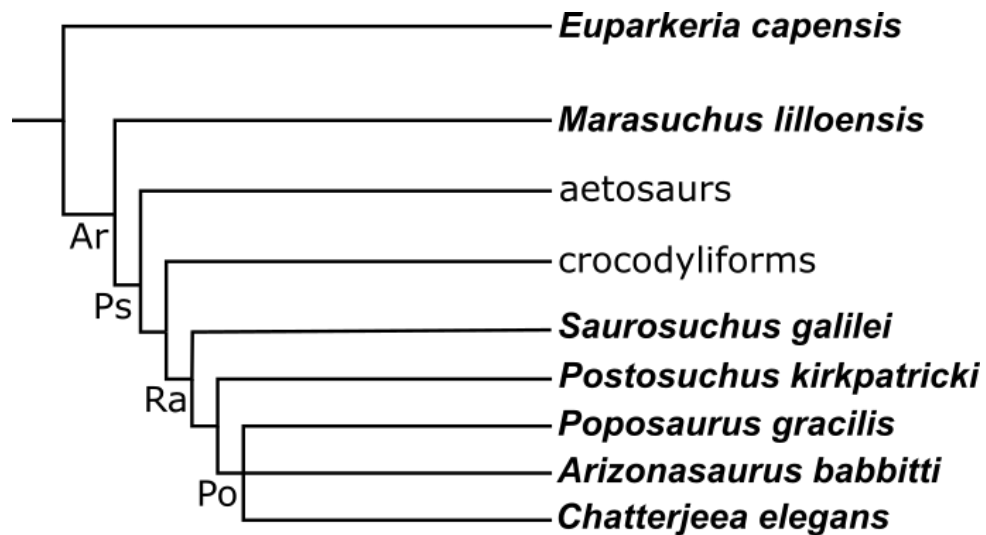


Figura 22. Cladograma redesenhado da proposta de Nesbitt (2003). Abreviações: Ar, Archosauria; Ps, Pseudosuchia; Ra, Rausuchia; Po, Puposauria.

Benton (2004) apresentou uma análise filogenética utilizando 22 táxons de Avesuchia (arcoossauros *stricto sensu*) e seis táxons comumente considerados “rauissuquídeos”, incluindo *Ticinosuchus ferox*, *Prestosuchus chiniquensis*, *Saurosuchus galilei*, *Fasolasuchus tenax*, *Gracilisuchus stipanicorum* e *Postosuchus kirkpatricki*. O resultado foi uma politomia, designada Prestosuchidae (formada por *T. ferox*, *P. chiniquensis* e *S. galilei*), tendo *F. tenax* como grupo externo e excluindo *P. kirkpatricki*.

Gebaur (2004) revisou a espécie *Stagonosuchus nyassicus* da Formação Manda da Tanzânia. Esta autora apresentou uma análise comparativa desta espécie com *Batrachotomus kupferzellensis*, *Ticinosuchus ferox* e *Postosuchus kirkpatricki* e argumentou que a espécie foco de sua revisão apresentava caracteres plesiomórficos e os “rauissuquídeos” possivelmente não seriam um grupo monofilético.

Sen (2005) descreveu *Yarasuchus deccanensis* da Formação Yerrapalli, Mesotriássico (Anisiano) da Índia como sendo um novo Prestosuchidae, similar a “*Mandasuchus*” e *Ticinosuchus ferox*. Sulej (2005) descreveu um novo indivíduo do Gênero *Teratosaurus*, baseado em um sínclânio incompleto e diversas vértebras de um único indivíduo. A nova espécie foi denominada *Teratosaurus silesiacus*, inserida na família Rausuchidae, com base na morfologia de suas vértebras cervicais.

Nesbitt (2005) efetuou um estudo adicional de *Arizonasaurus babbitti*, apresentando duas novas autapomorfias para esta espécie (a presença de uma fossa profunda na parede postero-ventral do processo ascendente do maxilar e uma pequena protuberância no lacrimal) e a comparou com um número maior de táxons de “rauissuquídeos”. O autor discerniu um grupo (denominado de “Grupo X”) com base em 10 caracteres, que incluiria *A. babbitti*, *Bromsgroveia walkeri*, *Poposaurus gracilis*, “*Chatterjeea elegans*” e *Silesuchus longicervix*, mas não apresentou nenhuma análise filogenética testando esta hipótese.

Nesbitt & Norell (2006) descreveram *Effigia okeeffeae* (Formação Chinle – Triássico Superior do Novo México, EUA), classificando este novo táxon como um Suchia, mas com a diferença marcante de não apresentar uma dentição. Esta espécie também apresenta muitas similaridades morfológicas com os dinossauros terópodes, atribuídas a convergências. Devido a isso, os autores interpretaram que o Neotriássico seria marcado por uma grande diversidade de formas que apresentavam planos corporais com características convergentes às das formas da linhagem pró-aviana, enquanto alguns táxons da linhagem pró-crocodiliana ocupariam zonas adaptativas similares àquelas futuramente ocupadas pelos dinossauros. Em sua análise filogenética, estes autores utilizaram uma matriz que apresentava poucos táxons de “rauissuquídeos” não popossaurídeos.

Gower & Nesbitt (2006) descreveram o neurocrânio de *Arizonasaurus babbitti* e efetuaram uma análise filogenética baseada em 27 caracteres do neurocrânio que haviam sido descritos em um trabalho prévio de Gower (2000). Obtiveram como resultado um estado parafilético para os “rauissuquídeos” (diferente do apresentado em NESBITT, 2003 e NESBITT & NORELL, 2006) onde *A. babbitti* teria uma posição mais basal no cladograma em relação à *Batrachotomus kupferzellensis*, *Postosuchus kirkpatricki*, *Saurosuchus galilei* e *Tikisuchus romeri* (Fig. 23).

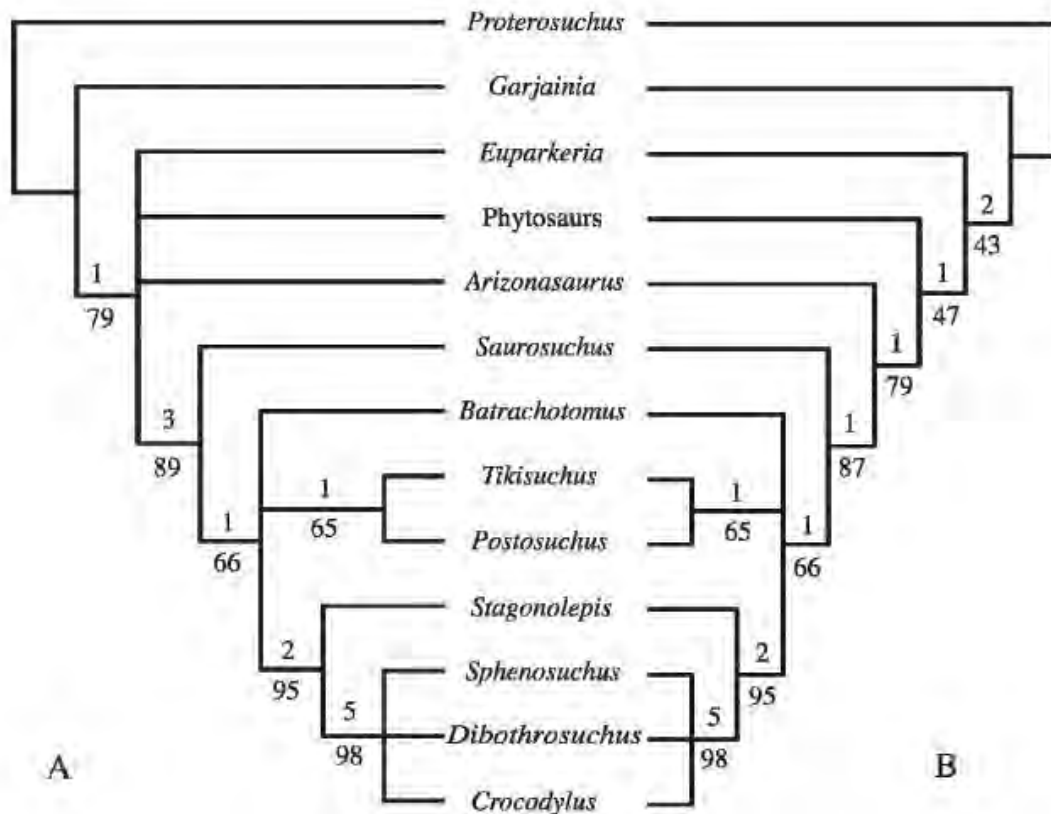


Figura 23. Análise filogenética de Gower & Nesbitt (2006) apresentando o consenso dos três cladogramas mais parcimoniosos. A, Consenso de 15 MPTs (L 40; CI 0.77; RI 0.86) obtidas de uma análise com 2 caracteres ordenados. B, Consenso de 5 MPTs (L 39; CI 0.77; RI 0.86) obtidas de uma análise com todos os caracteres desordenados.

Weinbaum & Hungerbühler (2007) descreveram um novo material do gênero *Poposaurus* e efetuaram uma revisão deste mesmo gênero (Fig. 24). O táxon “*Lythrosuchus langstoni*” foi interpretado como sinônimo júnior de *Poposaurus*, sendo esta proposta contrária à de Long & Murray (1995), que nomearam este material baseado em um ílio incompleto - que havia sido originalmente designado como o parátipo de *Poposaurus* por Chatterjee (1985). Também sinonimizaram o gênero *Lythrosuchus langstoni* como *Poposaurus langstoni*. A análise filogenética apresenta uma matriz de 34 caracteres e apresentou o grupo monofilético Poposauroidae, formado por um ctenossaurídeo (*Arizonasaurus babbitti*) e três popossaurídeos (*Poposaurus gracilis*, *Shuvosaurus inexpectus* e *Sillosuchus longicervix*, com base nas seguintes sinapomorfias: perda de osteodermos; acetábulo com uma incipiente perfuração; presença de três ou mais vértebras

sacrais; a porção anterior do centro vertebral é alongada antero-posteriormente; as apófises neurais das vértebras cervicais são mais alongadas do que altas; costelas sacrais gráceis; a superfície de articulação das costelas sacrais com o ílio projetada lateralmente e a área supra-acetabular apresenta uma crista lateral que é projetada anteriormente. Os “rauissuquídeos” seriam compostos por *Saurosuchus galilei*, *Postosuchus kirkpatricki*, *Batrachotomus kupferzellensis* e *Teratosaurus suevicus*. Estes táxons formariam um agrupamento parafilético, que foi posicionado como grupo-externo a Crocodylomorpha.

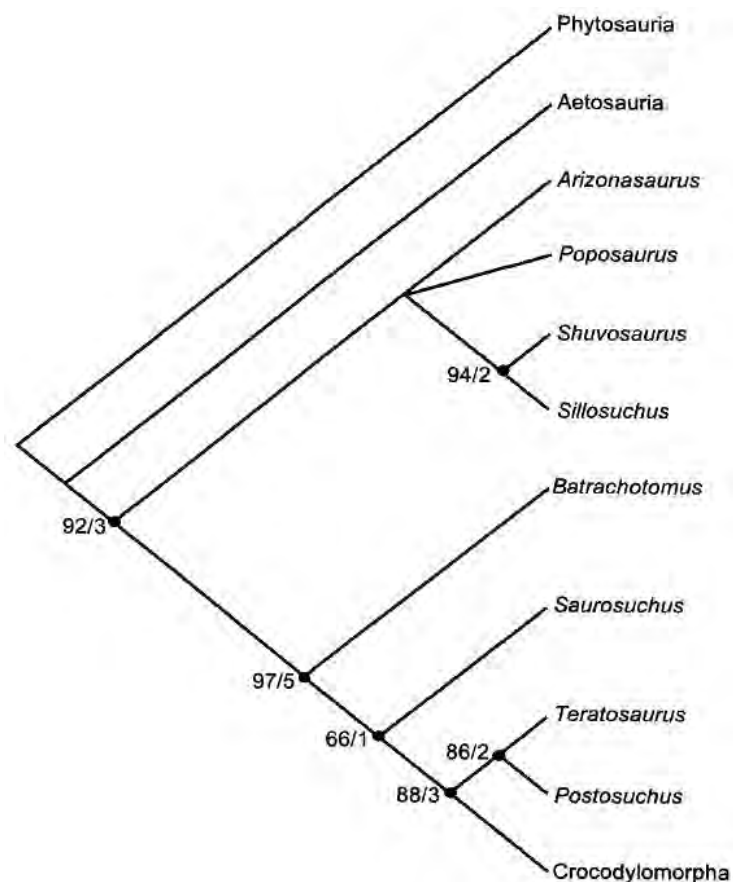


Figura 24. Árvore de consenso dos dois cladogramas mais parcimoniosos da análise de Weinbaum & Hungerbühler (2007) (IC 0,77; IR: 0,86). Os valores indicados são de suporte de Bootstrap/ Suporte de Bremer.

Nesbitt (2007) redescreveu *Effigia okeeffeae* Nesbitt e Norell 2006 e apresentou uma análise filogenética utilizando a mesma matriz de dados publicada em Nesbitt & Norell (2006), com a adição do táxon *Sillosuchus longicervix* e dois caracteres novos, somando 83 caracteres e 21 táxons (Fig. 25). Os resultados obtidos não diferem muito dos apresentados na proposta de Nesbitt e Norell (*op.cit.*) que consideraram “rauissuquídeos” como monofilético. Esta análise também

apresentou um clado formado por *Saurosuchus galilei* e *Postosuchus kirkpatricki* como o grupo-irmão de *Arizonasaurus babbitti* e outros poposaurídeos.

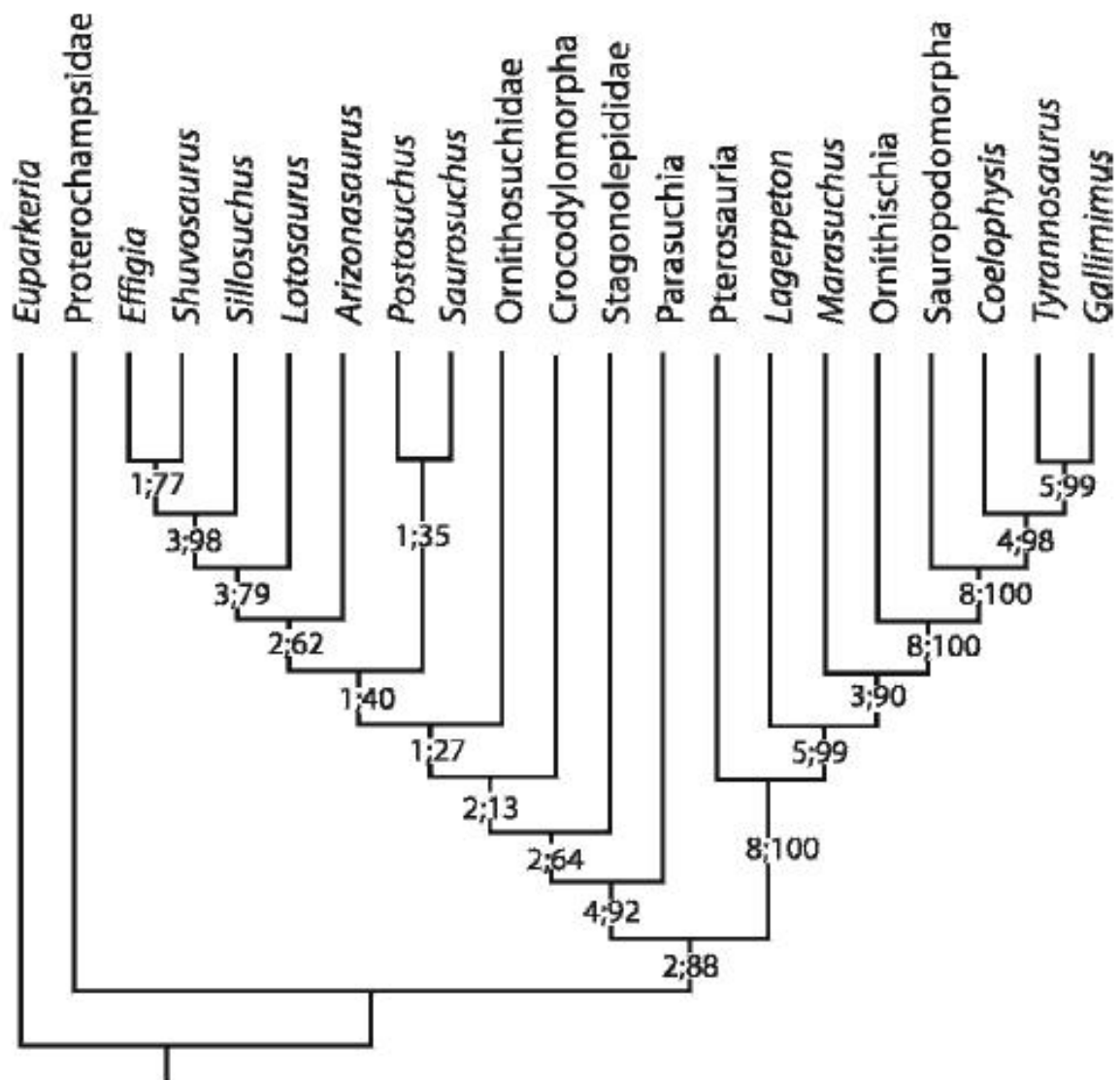


Figura 25. Proposta de Nesbitt (2007) com *Effigia okeeffeae* dentro dos arcossauros basais (IC: 0,59; IR: 0,83). Os valores de decaimento/Bootstrap são indicados abaixo de cada nó.

Jalil & Peyer (2007) descreveram *Arganasuchus dutuiti*, uma espécie de “rauissúquio” descoberta no Marrocos (Bacia de Argana – Triássico Superior) que anteriormente havia sido classificado como um espécime do táxon europeu *Ticinosuchus ferox*.

Peyer *et al.* (2008) descreveram *Postosuchus alisonae* (que seria a segunda espécie do gênero *Postosuchus*), que se diferenciaria dos outros “rauissuquídeos” por apresentar uma falange proximal bem desenvolvida no metacarpal II que se articularia numa abertura no primeiro metacarpal. No estudo comparativo, os autores reconheceram que o Gênero *Postosuchus* apresentaria uma relação mais estreita com *Batrachotomus kupferzellensis*, mas não testaram esta hipótese utilizando uma análise filogenética.

O material-tipo para a espécie *Rauisuchus tiradentes* foi revisado por Lautenschlager (2008) em sua dissertação de mestrado, não publicada. O autor propôs que o material seria composto de dois indivíduos de diferentes tamanhos e excluiu um ílio e um arco neural do material-tipo por não ter sido possível atribuir tais elementos para esta espécie com confiança. Em sua análise filogenética, utilizou a matriz modificada de Nesbitt (2007) com a adição dos táxons *Batrachotomus kupferzellensis*, *Stagonosuchus nyassicus* e *Ticinosuchus ferox*. A análise resultou um grupo monofilético, composto por dois subclados: Poposauridae e Rauisuchidae, onde *R. tiradentes* está incluído neste último.

Desojo & Rauhut (2008) apresentaram, sob a forma de resumo, uma reavaliação dos táxons de “rauissuquídeos” do sul do Brasil, baseados no material originalmente coletado por von Huene (1942). Nesta proposta a espécie *Prestosuchus chiniquensis*, mesmo sendo descrita a partir de material incompleto, seria uma espécie válida. Com base em características como: um entalhe anterior entre a escápula e o coracóide, uma crista longitudinal na face dorsal do ísquio. *Prestosuchus loricatus*, por sua vez, corresponderia a um gênero distinto de “rauissuquídeos” por apresentar muitas características diferentes em comparação com *P. chiniquensis* (apófises neurais das vértebras cervicais apresentam formato triangular em vista lateral, processo acessório nas vértebras caudais, uma concavidade [pit] no terço anterior da porção posterior do ísquio). Por seu turno, o material atribuído a *Procerosuchus celer* e o paralectótipo de *P. loricatus* pertenceriam a *P. chiniquensis*, sendo o primeiro espécime citado pertencente a uma forma juvenil, enquanto que o lectótipo de *P. loricatus* representaria um gênero diferente. Finalmente, *Hoplitosuchus raui* seria *nomen dubium* porque seu holótipo consistiria de ossos sem possibilidade de identificação.

França *et al.* (2008) apresentaram, em forma de resumo, uma possível nova espécie de “rauissuquídeo” para o Triássico do Rio Grande do Sul (ZA de *Dinodontosaurus*, Neotriássico), coletado no Afloramento do Posto, no Município de Dona Francisca. Representado por uma assembleia fóssil monoespecífica contendo oito esqueletos incompletos, inclusive três crânios completos, a nova espécie (não nominada) pode ser identificada com base em uma autapomorfia: a borda posterior da fenestra infra-temporal apresentaria um processo anterior formado pela porção ventral do esquamosal e a porção dorsal do jugal. Um ano depois, os mesmos autores (FRANÇA *et al.*, 2009) aumentaram o número de espécimes de 8 para 10 indivíduos, a partir de novas descobertas durante a preparação. Esta associação foi interpretada pelos autores como sendo evidência de hábito social, mas o táxon continuou sem descrição.

Gower & Schoch (2009) apresentaram uma descrição de material pós-craniano de *Batrachotomus kupferzellensis* e discutiram sobre o problema dos “rauissuquídeos”, mas não apresentaram nenhuma nova proposta. Desojo e Rauhut (2009) apresentaram, em forma de resumo, uma versão ampliada de sua proposta de 2008 (*op.cit.*) repetindo suas conclusões sobre os gêneros brasileiros e abordando a taxonomia e filogenética de *Prestosuchus chiniquensis*. Estes autores apresentaram um clado Rausuchia monofilético, composto por dois clados: Rausuchidae (incluindo *P. chiniquensis*, *Stagonosuchus nyassicus*, *Saurosuchus galilei* e *Postosuchus kirkpatricki* como os mais basais e *B. kupferzellensis*, *Ticinosuchus ferox* e *Rausuchus tiradentes* como os gêneros mais derivados) e Puposauridae (formado por *Arizonasaurus babbitti*, *Lotosaurus adentus*, *Puposaurus gracilis*, *Sillosuchus longicervix*, *Shuvosaurus inexpectus* e *Effigia okeeffeae*).

Lautenschlager (2009) propôs, em forma de resumo, análise similar à sua publicação anterior (Lautenschlager, 2008), mas com uma diferença na interpretação dos caracteres nos gêneros que iriam compor os Rausuchia, sendo Puposauridae caracterizado por: três ou mais vértebras sacrais; presença de uma crista supra-acetabular no ílio e a perda de osteodermos. Rausuchidae, por sua vez, apresentaria: uma fenestra subnarinal; vértebras cervicais com apófises neurais de formato tabular e apresentaria osteodermos.

Brusatte *et al.* (2009) apresentaram uma redescrição do holótipo (um maxilar) de *Teratosaurus suevicus* e o material de *Teratosaurus silesiacus*. Os autores

consideraram apenas duas das quatro diferenças apontadas no trabalho de Sulej (2005) como sendo válidas (uma fossa dentaria conectando as áreas de substituição de dente na face medial do maxilar e a orientação das foraminas de substituição de dentes) e identificaram outras quatro diferenças morfológicas nos ossos maxilares e do palato que distinguem *T. suevicus* de *T. silesiacus*. Estes fatores, combinados com diferenças de tamanho e posicionamento estratigráfico, levaram os autores concluir que não existiria justificativa para que estas duas espécies fossem atribuídas ao mesmo gênero. Assim, removeram *Teratosaurus silesiacus* do Gênero *Teratosaurus* e propuseram a espécie *Polonosuchus silesiacus*.

Butler *et al.* (2009) descreveram *Hypselohraschis mirabilis*, baseados em uma vértebra da coluna toraco-lombar com uma apófise neural muito alongada, proveniente da Formação Manda (Tanzânia-Triássico Médio (?)-Superior da África). Esta espécie seria similar a outros “rauisuquídeos” que apresentam apófises neurais alongadas (*Arizonasaurus babbitti*, *Ctenosauriscus koenei* e *Lotosaurus adentus*), podendo formar com estes um clado denominado Ctenosauridae, que estaria dentro de Rausuchia. Porém, esta proposta não foi testada filogeneticamente e os autores usaram a definição de “Rausuchia” proposta por Gower (2000), com a inclusão das famílias Shuvosauridae e Ctenosauridae.

Desojo & Arcucci (2009) descreveram um novo espécime atribuído a *Luperosuchus fractus*. Este material foi interpretado como sendo pertencente a uma forma juvenil, devido ao seu menor tamanho, redução na ornamentação e padrão das suturas. As autoras consideraram este táxon como sendo um “rauisuquídeo” baseadas em características como: um crânio antero-posteriormente largo e dorso-medialmente estreito, com uma órbita em forma de “buraco de fechadura” (*keyhole-shaped*); uma fenestra subnarinal em forma de fenda (*slit-like*); uma área de articulação entre o pré-maxilar e o maxilar; um “nariz romano” formado pela porção rostro-dorsal do nasal; uma fenestra antero-orbital de formato triangular em vista lateral, que mostra uma estreita angulação rostral e o lacrimal formando a margem dorsal da órbita. Não foi efetuada uma análise filogenética neste trabalho, mas as autoras discutiram não haver evidências para um Rausuchidae monofilético, sendo que *Postosuchus kirkpatricki* e *Teratosaurus suevicus* seriam formas próximas a *L. fractus*.

Brusatte *et al.* (2010) apresentaram uma proposta filogenética mais abrangente do grupo coronal Archosauria [=Avesuchia (Benton, 1999)] usando 187 caracteres (com 47 caracteres novos) e 52 táxons, com proterocâmpsidos, proterossuquídeos e *Euparkeria capensis* formando o grupo externo (Fig. 26). O autor concordou com trabalhos prévios que apresentaram Archosauria como o clado que originou uma linhagem pró-aviana e outra pró-crocodiliana, com os “rauissuquídeos” inseridos nesta última. Os Rausuchia constituíram um grupo monofilético, baseado em dois caracteres (vértebras toraco-lombares que apresentam uma articulação acessória entre hiposfeno e o hipantro e a razão entre o comprimento e a profundidade da lâmina ilíaca, acima do acetábulo, maior que 4.5) e estaria dividido em dois subclados: Rausuchoidea (Prestosuchidae, Rausuchidae e formas próximas a *Ticinosuchus ferox*) e Puposauroida (*Shuvosauridae* e demais popossaurídeos). Os Rausuchoidea seriam definidos com base em duas sinapomorfias: a presença de múltiplos osteodermos dorsais por vértebra, o tubérculo do calcâneo é dorso-ventralmente alinhado com uma depressão em sua porção distal. Este clado seria composto por duas linhagens: Prestosuchidae (composto por *Saurosuchus galilei*, *Batrachotomus kupferzellensis* e *Prestosuchus chiniquensis*) e Rausuchidae (formado por *Tikisuchus romeri*, *Rausuchus tiradentes*, *Postosuchus kirkpatricki* e *Teratosaurus suevicus*). O sub-clado Puposauroida apresentou uma resolução menor que a do seu grupo irmão. Os táxons *Quianosuchus mixtus* e *Yarasuchus deccanensis* seriam formas mais basais em relação a uma politomia formada por *Arizonasaurus babbitti*, *Bromsgroveia walkeri*, *Lotosaurus adentus*, *Poposaurus gracilis*, *Sillosuchus longicervix*, *Effigia okeeffeae* e *Shuvosaurus inexpectus*, com estes dois últimos formando o clado *Shuvosauridae*.

Os autores discutem que os clados estudados não são fortemente suportados, levantando à hipótese de que o grupo não seja monofilético. Segundo eles, as razões disso poderiam ser a ausência de um rigor metodológico no estudo dos “rauissuquídeos”, com matrizes utilizando poucos táxons ou uma tendência a serem considerados um agrupamento monofilético *a priori*.

Mastrantonio (2010) apresentou uma descrição do espécime UFRGS-PV-0629-T que seria um esqueleto parcialmente completo que foi atribuído pela autora ao táxon *Prestosuchus chiniquensis*, sendo este o material mais completo já descrito para o táxon. A análise foi corroborada por dados filogenéticos, utilizando uma

matriz modificada de Brusatte *et al.* (2010), na qual foram alterados os estados de 17 caracteres e retirados dois (26 e 47) totalizando 185 dos 187 caracteres da matriz original. A autora também apresentou uma crítica ao trabalho de Brusatte *et al.* (2010), discutindo que a árvore de consenso apresentada não seria a mais parcimoniosa. Apresentou uma nova árvore de consenso, onde vários nós desapareceram, especialmente dentro de Rausuchia, ressaltando que a resolução das relações internas deste grupo ainda não foi atingida.

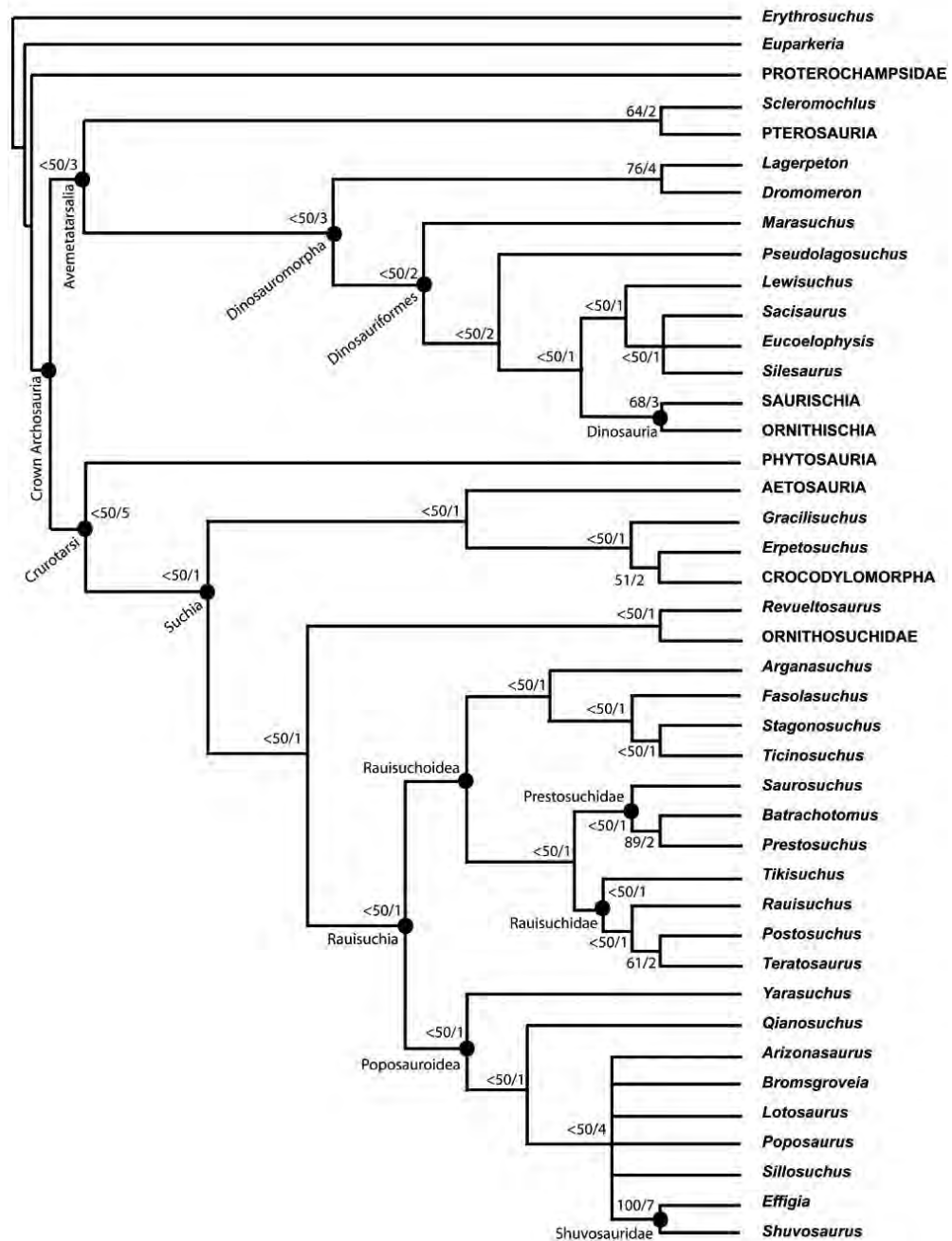


Figura 26. Análise de Brusatte *et al.* (2010) de consenso estrito de 70 árvores mais parcimoniosas (747 passos, CI = 0.31, RI = 0.68). Os números próximos aos cladogramas são as de *Bootstrap*/valor de suporte de Bremer.

Weinbaum (2011) redescreveu o crânio de *Postosuchus kirkpatricki* baseado em uma nova preparação do crânio do holótipo originalmente descrito por Chatterjee (1985). Esta nova preparação revelou novas autapomorfias do crânio como: uma crista rugosa proeminente e arredondada na superfície lateral do maxilar e um forame na superfície ventral da fossa triangular na superfície anteromedial do processo ascendente do maxilar. O tamanho da fenestra subnarinal foi revisado, já que o autor afirma que o diâmetro desta havia sido aumentado devido à articulação do pré-maxilar com o maxilar estar imprecisa. O autor não apresentou uma análise filogenética, argumentando a necessidade de dados anatômicos mais detalhados para este fim. O esqueleto pós-craniano foi descrito dois anos depois (WEINBAUM, 2013). Neste trabalho, o autor considerou que os 'rauissuquídeos' teriam mais afinidades com crocodilomorfos, baseado em características cranianas e pós-cranianas compartilhadas, mas não testou estas afinidades utilizando metodologia cladística.

França *et al.* (2011) descreveram o táxon de médio porte *Decuriasuchus quartacolonia* a partir da assembleia de 10 espécimes incompletos com 3 crânios, descrita de forma preliminar em resumos (França *et al.*, 2008; 2009) encontrada no município de Dona Francisca. Esta espécie se diferencia de outros "rauissuquídeos" por apresentar as seguintes autapomorfias: lacrimal e nasal formam uma expansão lateral que se projeta sobre a maior parte da fenestra anteorbital; a margem dorsal do quadrado-jugal e a margem ventral do esquamosal, em conjunto, formam uma expansão triangular na fenestra temporal. Em sua proposta filogenética, utilizando a matriz de Brusatte *et al.* (2010), *D. quartacolonia* estaria inserido em Prestosuchidae, junto a *Prestosuchus chiniquensis*, *Batrachotomus kupferzellensis* e *Saurosuchus galilei*.

Lautenschlager & Desojo (2011) apresentaram uma revisão das espécies *Ticinosuchus ferox* e *Stagonosuchus nyassicus*. A redescrição de *T. ferox* apresentou novos elementos cranianos que não haviam sido descritos por Krebs (1965) e uma revisão das cinturas escapular e pélvica. Enquanto que a diagnose revisada de *S. nyassicus* apresentou quatro novas características (lâminas

infraprezigapofisiais e infrapozigapofiseais adicionais na oitava vértebra cervical, uma protuberância similar a uma “bossa” [*boss-like*] no processo pós-acetabular da lâmina ilíaca, uma crista dorso-lateral baixa, bem marcada, na porção proximal do ísquio e protuberâncias arredondadas ao longo da margem ventral do ísquio). Os autores também descreveram a presença de processos neurais acessórios em algumas vértebras, a partir da metade da cauda, em alguns “rauissuquídeos” (e.g. *Rauisuchus tiradentes* e *T. ferox*) e articulação do hiposfeno e o hipantro nas vértebras dorsais, argumentando que estas estruturas sugerem uma especialização na coluna vertebral para uma postura mais ereta ou bípede, não dependendo apenas de especializações nos apêndices posteriores e na cintura pélvica.

Trotteyn *et al.* (2011) descreveram novos materiais de pós-crânio de *Saurosuchus galilei* compostos por uma sequência vertebral contendo uma série cervical (formada por um “complexo proatlas-atlas-axis” completo), vértebras truncais e caudais, osteodermos e alguns elementos de cinturas. Os autores apresentam uma descrição detalhada destes elementos e uma comparação com “rauissuquídeos”, discutindo a necessidade de análises morfológicas mais detalhadas no estudo deste grupo para solucionar problemas em estudos morfométricos e filogenéticos.

Gauthier *et al.* (2011) efetuaram o estudo da locomoção de *Poposaurus gracilis* a partir de um espécime quase completo (Fig. 27). Este estudo foi feito utilizando uma abordagem em três etapas: inferir a posição filogenética do táxon estudado; analisar a distribuição dos diferentes modos de locomoção nos diferentes grupos e inferir a sequência de surgimento destes na filogenia, baseado na hipótese de que *P. gracilis* apresentava o mesmo modo de locomoção que seus ancestrais e efetuar uma análise morfofuncional, baseada neste novo espécime, a fim de refinar a hipótese de locomoção. A conclusão dos autores foi a de que *P. gracilis* seria uma forma bípede que apresentava características que seriam convergentes com formas da linhagem pró-aviana (ali denominada pan-aviana), mas que o aparecimento destas características ocorreu de forma diferente nestas duas linhagens. O estudo filogenético utilizado pelos autores baseou-se numa análise de Nesbitt (2011) que, na época, ainda não havia sido publicada. Segundo os autores, os “rauissuquídeos” corresponderiam a uma antiga linhagem que teria um histórico evolutivo próximo aos dos crocodilianos.

Nesbitt (2011) apresentou um amplo estudo filogenético sobre a origem e evolução dos arcossauros, utilizando 412 caracteres, abordando 80 táxons em nível de espécie, distribuídos do Permiano até o início do Jurássico (Fig. 28). Este trabalho apresentou o maior número de táxons (*Ticinosuchus ferox*, *Quianosuchus mixtus*, *Arizonasaurus babbitti*, *Poposaurus gracilis*, *Lotosaurus adentus*, *Sillosuchus longicervix*, *Shuvosaurus inexpectus*, *Effigia okeeffeae*, *Prestosuchus chiniquensis*, *Saurosuchus galilei*, *Batrachotomus kupferzellensis*, *Fasolasuchus tenax*, *Rauisuchus tiradentes*, *Postosuchus kirkpatricki*, *Postosuchus alisonae*, *Polonosuchus silesiacus* e *Xilousuchus sapingensis* Wu, 1981) comumente considerados “rauissuquídeos” até o presente. Esta análise resultou em um clado Poposauridea monofilético (composto por *Q. mixtus*, *A. babbitti*, *X. sapingensis*, dois espécimes de *P. gracilis* ([H]: o holótipo FMNH-357, um espécime incompleto e [Y]: YPM 57100 um espécime quase completo, faltando apenas o crânio), *L. adentus*, *S longicervix*, *S. inexpectus* e *E. okeeffeae*) como o grupo irmão de um “Rauisuchia” parafilético (com um Rauisuchidae composto de *R. tiradentes*, *P. silesiacus*, *P. alisonae* e *P. kirkpatricki*, enquanto *P. chiniquensis*, *S. galilei*, *B. kupferzellensis* e *F. tenax* estariam fora deste agrupamento, sob a designação de Loricata), além de um clado Crocodylomorpha monofilético. Segundo o autor, a única forma de “Rauisuchia” ser monofilético seria se Crocodylomorpha fosse incluído. Devido a esta condição parafilética, propõe o abandono do termo Rauisuchia em análises futuras, já que esta diagnose denotaria uma condição monofilética para um clado contendo Poposauridae, Rauisuchidae e outros “rauissuquídeos”.

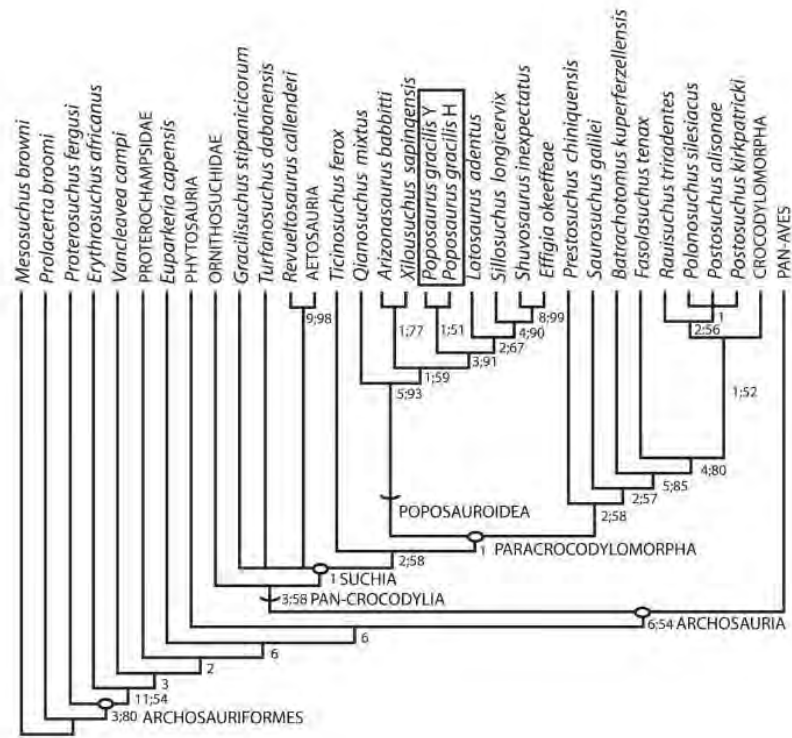


Figura 27. Proposta de Gauthier et al. (2011) baseada em Nesbitt (2009, 2011) para o holótipo de *Potosaurus gracilis* (indicado pelo H maiúsculo) e o novo espécime do mesmo táxon. Os números abaixo dos nós são de suporte de Bremer (na esquerda) e do *Bootstrap* (se maiores que 50%, na direita).

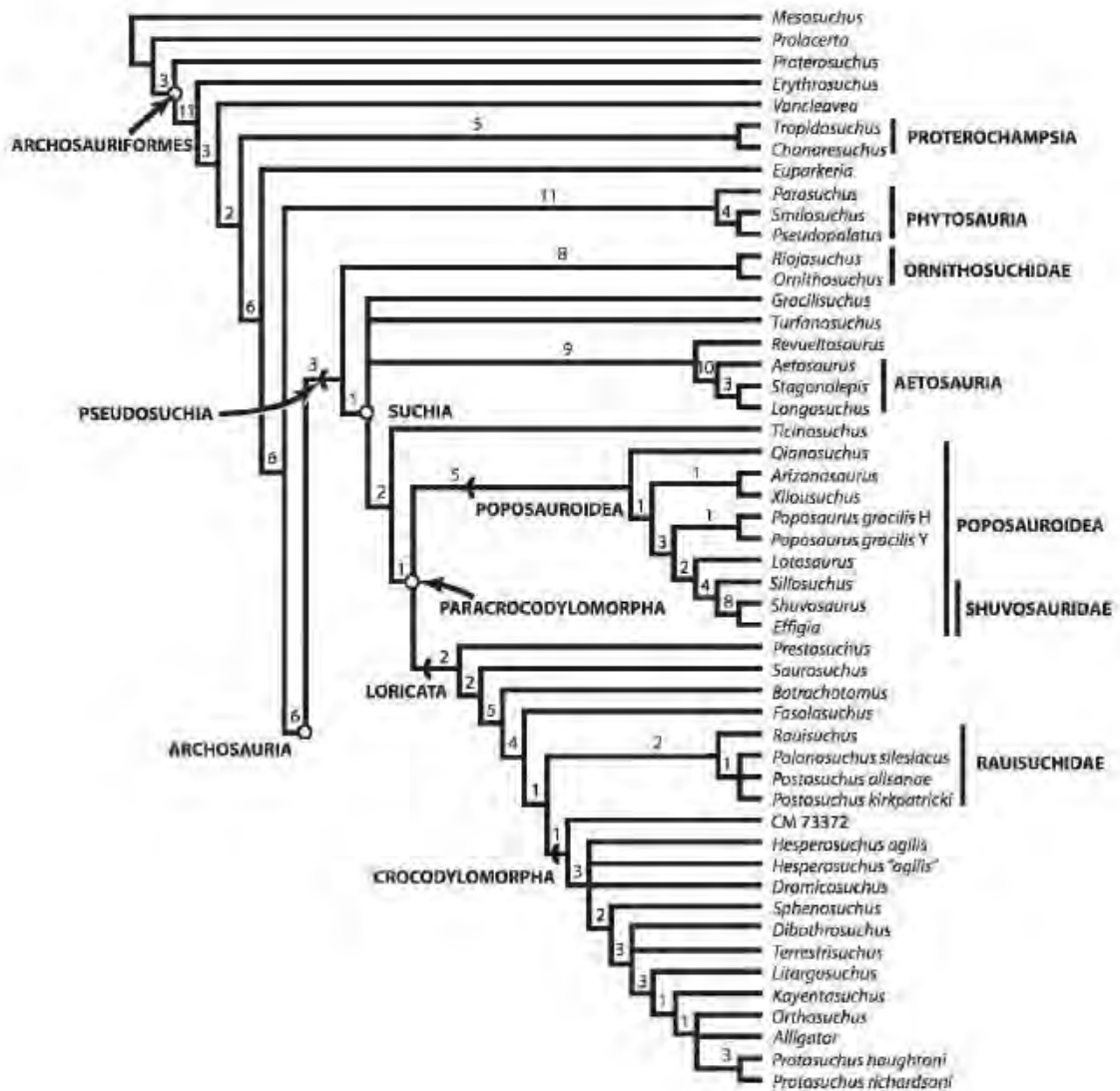


Figura 28. Proposta filogenética de Nesbitt (2011). Os números representam os valores de suporte de Bremer. (Retirado de Nesbitt, 2011).

Butler *et al.* (2011) redescreveram *Ctenosauriscus koeneni* da base da Formação Solling (final do Olenekiano-Eotriássico), da Alemanha. Utilizando as matrizes modificadas de Brusatte *et al.* (2010) e Nesbitt (2011), a análise filogenética resultou em um táxon Ctenosauriscidae monofilético, composto por formas que apresentavam um alongamento dorsal de suas apófises neurais nos gêneros *C. koeneni*, *Hypselorhachis mirabilis*, *Arizonasaurus babbitti*, *Xilosaurus sapingensis* e o “táxon de Waldhaus” dentro de Popsauridea.

França (2011), em sua tese de doutorado, complementou sua descrição dos espécimes de *Decuriasuchus quartacolonis* previamente publicada (França *et al.*,

2011) e os incluiu em uma análise filogenética utilizando uma matriz com 329 caracteres, (sendo 44 inéditos ou pela primeira vez empregados neste tipo de análise), e 53 táxons terminais. A análise resultante encontrou um Rausuchia monofilético composto por três grandes grupos; Rausuchidae, Puposauridae e Prestosuchidae. Destes, apenas o último se encontra pouco resolvido, com *Ticinosuchus ferox* como grupo irmão de um clado composto por uma politomia entre *Prestosuchus chiniquensis* (UFRGS-PV-0156-T; Paralectótipo; Lectótipo), *Procerosuchus celer*, *Prestosuchus loricatus*, *D. quartacolonias*, *Saurosuchus galilei* e *Stagonosuchus nyassicus*. A parte do crânio desta descrição foi publicada posteriormente (FRANÇA *et al.*, 2013).

Nesbitt *et al.* (2013) apresentaram um estado da arte dos estudos envolvendo os “rauissuquídeos”, de uma forma similares ao que foi feito por Gower (2000). Apesar do avanço dos conhecimentos taxonômicos, paleobiológicos e paleoambientais sobre os “rauissuquídeos”, a conclusão dos autores é que os problemas taxonômicos do grupo ainda estão longe de serem resolvidos.

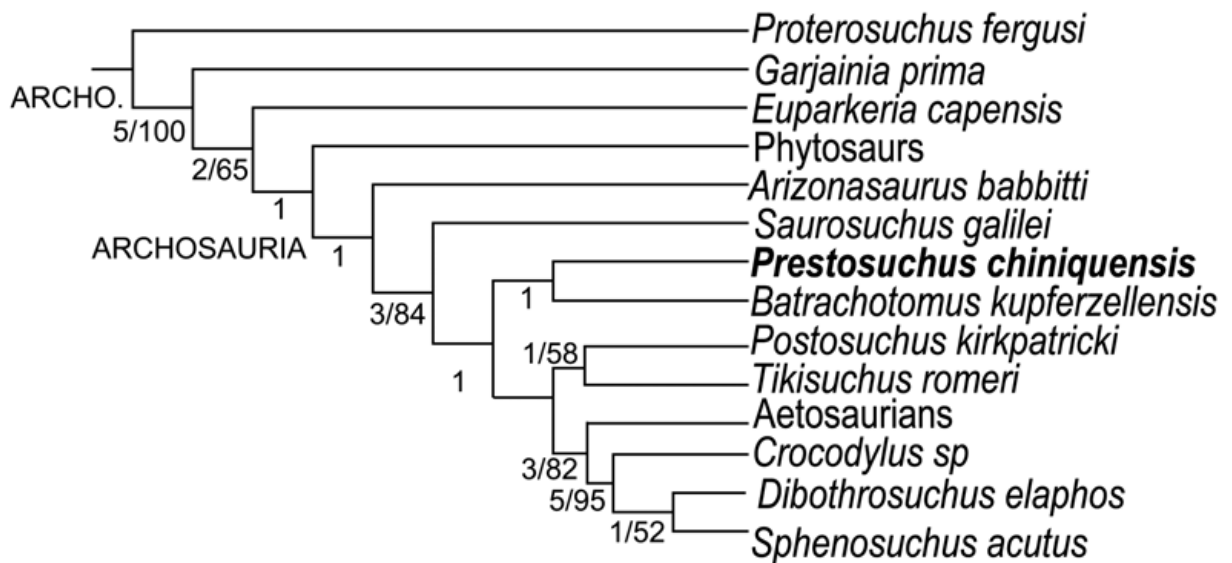


Figura 29. Árvore de consenso estrito de Mastrantonio *et al.* (2013) apresentando as afinidades de *Prestosuchus chiniquensis* baseadas apenas em caracteres da caixa craniana. Valores de decaimento (esquerda) e absolutos (direita) do teste de bootstrap com frequências maior a 50% são apresentados. Abreviatura: ARCHO: arcossauriformes. (Retirado de Mastrantonio *et al.*, 2013)

Mastrantonio *et al.* (2013) apresentou a descrição da caixa craniana de *Prestosuchus chiniquensis*, baseado no espécime UFRGS-PV-0629-T que havia sido descrito, mas não publicado (MASTRANTONIO, 2010), a do grande crânio UFRGS-PV-0156 (BARBERENA, 1978; AZEVEDO, 1991) e uma caixa craniana isolada UFRGS-PV-0473-T, de preservação boa, apresentando similaridades morfológicas muito próximas ao táxon. Uma análise filogenética foi efetuada utilizando a matriz de Gower (2002) composta apenas de caracteres de neurocrânio. A hipótese resultante (Fig. 29) encontrou uma topologia igual à de Gower (2002), onde os crocodilomorfos ficaram mais próximos dos aetossauros do que dos “rauissuquídeos”.

Parker & Nesbitt (2013) apresentaram o espécime PEFO 34865, composto por um maxilar esquerdo, um dentário esquerdo, ambos com dentes, um pré-articular direito, um íleo direito quase completo, um púbis direito a porção proximal de uma tíbia direita, da Formação Chinle. Os autores atribuíram este espécime este ao táxon *Poposaurus gracilis*, devido à sobreposição de características da cintura pélvica com o holótipo (CFMNH UR 357). Duas autapomorfias foram propostas: 1) uma crista espessa posicionada posterior ao acetábulo na lâmina ilíaca e 2) a presença no íleo de um pedúnculo proeminente que serve para a articulação com uma fossa na região prximal do ísquio. Adicionalmente, descreveram dois outros materiais cranianos (TTU-P11610 e TTU-P 11614), um surangular e um articular da Formação Tecovas, igualmente referidos a *P. gracilis*.

Os autores avaliaram vários caracteres-chave na evolução dos “rauissuquídeos” (e.g. evolução do bipedalismo, aparecimento de uma vela dorsal e de perda de dentes foram um bico córneo) e utilizaram as matrizes de Brusatte *et al.* (2010 e de Nesbitt (2011), ambas modificadas por Butler *et al.* (2011) e proposueram as seguintes conclusões (Fig. 30): 1) A presença de bipedalismo em *P. gracilis* demonstra que esta característica apareceu apenas uma vez na base de Poposauroidea; 2) A ausência da vela dorsal em *P. gracilis* suporta um cenário onde a presença desta característica seria plesiomórfica para poposaurídeos e ela é perdida em Shuvosauridae +*P. gracilis*, mas não é possível descartar a possibilidade de que esta característica pode ter sido adquirida em *Lotosaurus adentus* e os Ctenosauriscidae; 3) A hipótese de que a ausência de dentes em Poposauroidea seria plesiomórfica seria menos parcimoniosa do que a possibilidade de que a presença de dentes para este clado seria pleseiomórfica. Todavia, a condição em

alguns táxons ainda não é conhecida, já que alguns espécimes não possuem material craniano (e.g. *Sillosuchus longicervix*, *Ctenosauriscus koeneni*, *Bromsgroveia walkeri* e *Hypselorhachis mirabilis*).

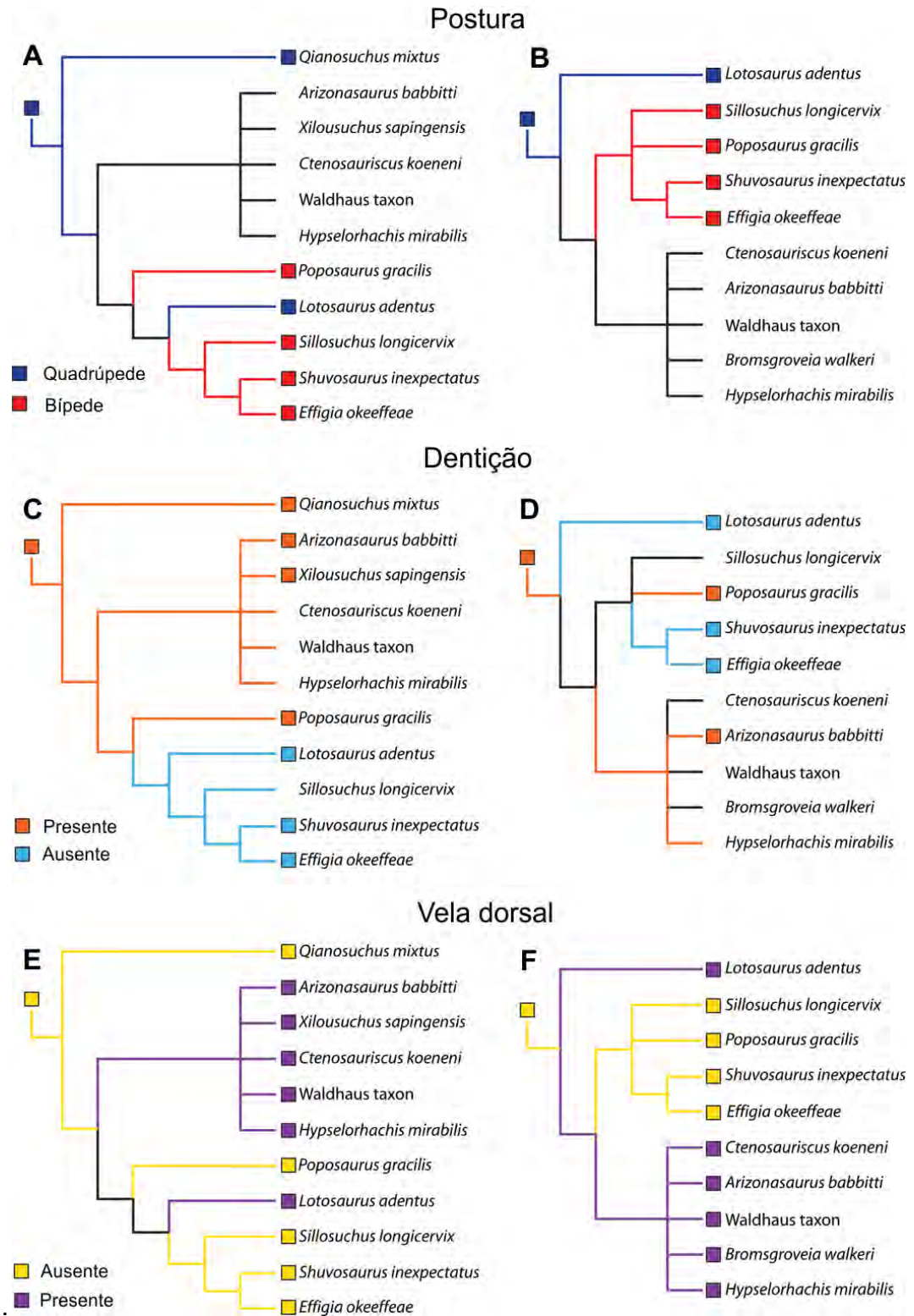


Figura 30. Distribuição dos caracteres-chave na evolução de Poposauroidea nas hipóteses de Nesbitt (A,C,E) e Brusatte et al. (B,D,F) baseados na matrizes modificadas de Butler et al. (2011). Modificado de Parker & Nesbitt (2013).

Raugust (2014) em sua tese de doutorado descreveu o espécime UFRGS-PV-0152-T. Este espécime nunca havia sido devidamente descrito, mas havia sido atribuído a *Prestosuchus chiniquensis* por Nesbitt (2011) e inserido dentro do clado “*Prestosuchus* Combinado” em sua análise. Raugust (2013), entretanto, discordou desta proposta, argumentado que este espécime apresentaria várias características diferentes do restante dos outros espécimes atribuídos ao Gênero *Prestosuchus*, diferenças estas presente nos ossos maxilares, como a presença de uma fenestra pré-orbital longa e de altura proporcionalmente reduzida; uma nítida crista afilada no corpo do maxilar que segue em sua parte posterior; tanto o corpo quanto a processo posterior do maxilar é proporcionalmente mais baixo dorso-ventralmente. Estas diferenças, portanto, diferenciam o espécime estudado de todos os outros atribuídos a *P. chiniquensis*, menos UFRGS-PV-0629-T (MASTRANTONIO, 2010).

Uma análise cladística foi efetuada utilizando uma matriz modificada de Butler et al. (2011) onde as afinidades do espécime estudados foram testadas com relação “*Prestosuchus* Combinado” ou desmantelando esta unidade operacional. A hipótese resultante (Fig. 31) indicou que o espécime UFRGS-PV-0152-T como grupo-irmão do lectótipo de *Prestosuchus chiniquensis* (BSPHG AS 1933L) com a única característica exclusiva do espécime sendo a presença de uma superfície tubercular lateralmente projetada na porção rostro-lateral do maxilar, que tem um aspecto de roldana. Raugust (2014) considerou as diferenças encontradas como sendo de relevância taxonômica e não artefatos tafonômicos, devido à boa condição do material, ou não significativas a ponto de indicarem variação ontogenética, já que as vértebras do espécime não apresentarem suturas abertas, mas escolheu não propor um novo táxon porque considerou os resultados apresentados na tese como sendo inconclusivos, necessitando aprimoramentos em trabalhos futuros.

Lessener et al. (2016) descreveram *Vivaron haydeni* do Membro Petrified Forest (Noriano médio-Neotriássico) da Formação Chinle, sudoeste dos EUA. O registro deste táxon é fragmentário, com o holótipo sendo um osso maxilar direito e vários elementos cranianos e pós-cranianos são referidos como parátipos. A análise

osteológica encontrou similaridades deste com o táxon *Teratosaurus suevicus*. Uma análise cladística utilizando uma matriz modificada de Nesbitt (2011), onde *T. suevicus* e *Tikisuchus romeri* foram adicionados, encontrou *V. haydeni* em uma politomia dentro de Rausuchidae (*sensu* NESBITT, 2011).

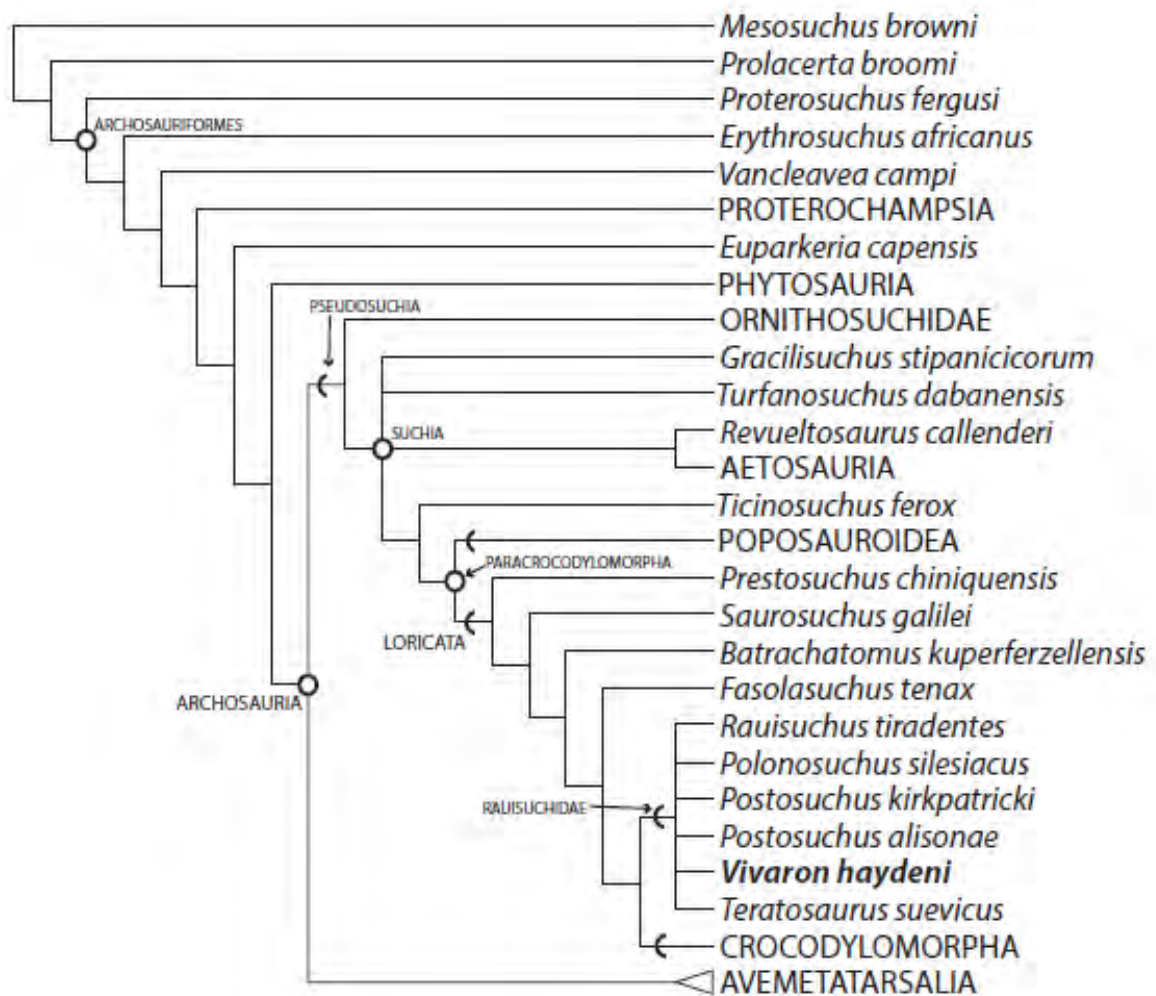


Figura 31. Cladograma de consenso estrito indicando as afinidades filogenéticas de *Vivaron haydeni* dentro de Rausuchidae (Retirado de Lessner *et al.*, 2016).

Silva *et al.* (2016) abordaram a questão de uma abertura subnarial em *Prestosuchus chiniquensis* a partir do novo espécime ULBRA-PVT-281, que apresenta um crânio completo e em posição de articulação da localidade “Posto de Gasolina” da cidade de Dona Francisca, Rio Grande do Sul. A abertura adicional foi considerada pelos autores como sendo morfologicamente significativa e um caracter novo (414) foi adicionado na matriz modificada de Nesbitt (2011) feita por Butler *et al.* (2014) que foi utilizada para fazer uma análise cladística. O cladograma de

consenso estrito (Fig. 32) indicou o caractere novo não alterou a topologia apresentada por Butler *et al.* (2014) onde *P. chiniquensis* está na base de Loricata como grupo irmão de *Saurosuchus galilei*, mas o novo caractere é presente apenas nos dois táxons mais o dinossauro basal *Herrerasaurus ischigualastensis* Reig 1963.

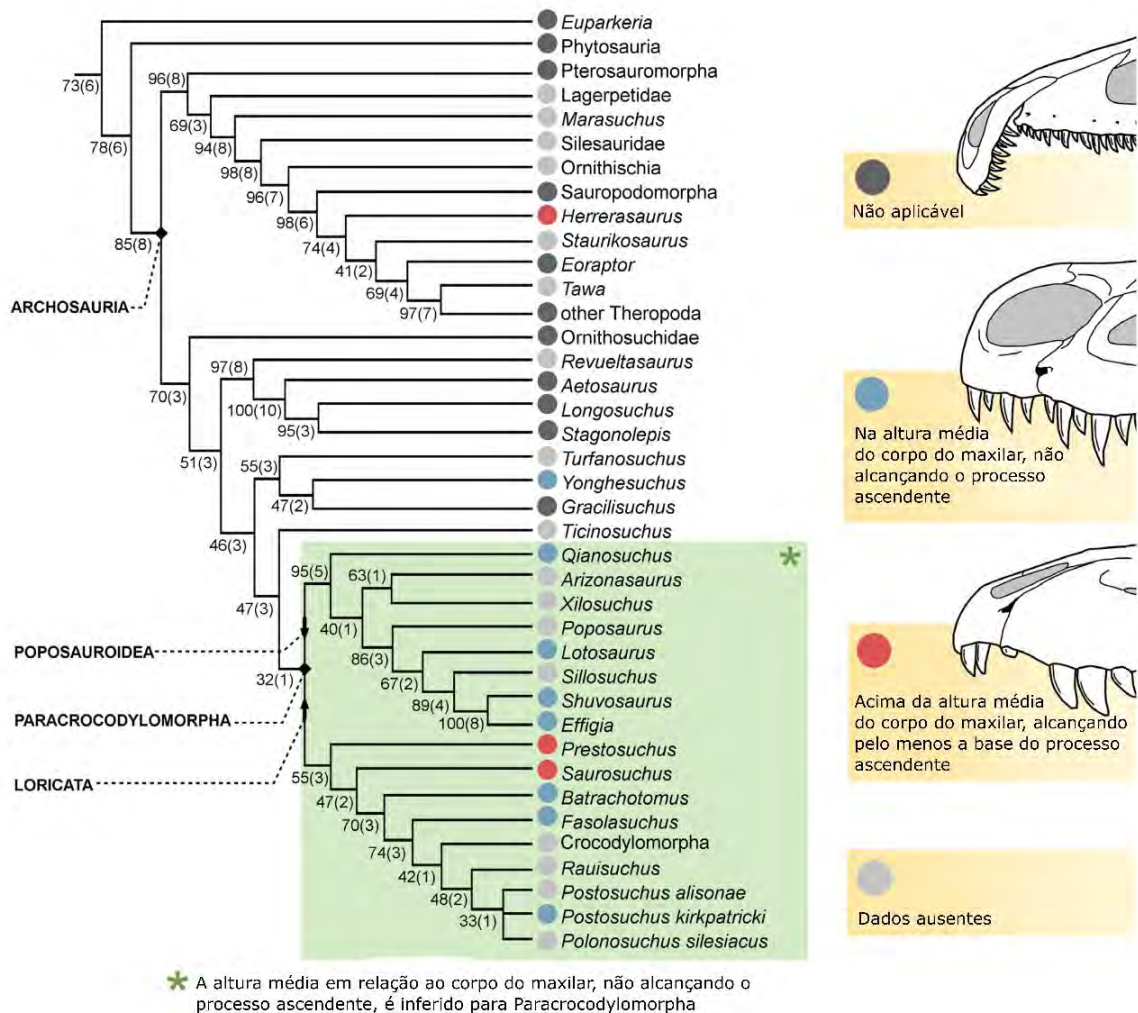


Figura 32. Cladograma simplificado de consenso estrito de 81 AMPs, indicando a distribuição dos dois estados do novo carácter proposto no artigo entre os táxons. Os números associados aos nós representam valores de Bootstrap com os suportes de Bremer entre parênteses. Modificado de Silva *et al.*, (2016).

Nesbitt & Desojo (2017) revisaram *Luperosuchus fractus* da Formação Chañares (Meso-Neotriássico) da Argentina e apresentaram novos fragmentos do holótipo que haviam sido coletados originalmente por Romer nos anos 1970, mas foram esquecidos em uma coleção. Ademais, consideram que o crânio parcial de uma possível forma juvenil atribuído a este táxon por Desojo & Arcucci (2009)

representaria outro táxon, já que as diferenças antes consideradas devido à variação ontogenética seriam muito pronunciadas. A análise filogenética utilizou uma matriz modificada de Nesbitt (2011) onde *L. fractus* formou um clado (Fig. 33) com *Prestosuchus chiniquensis* e *Saurosuchus galilei*.

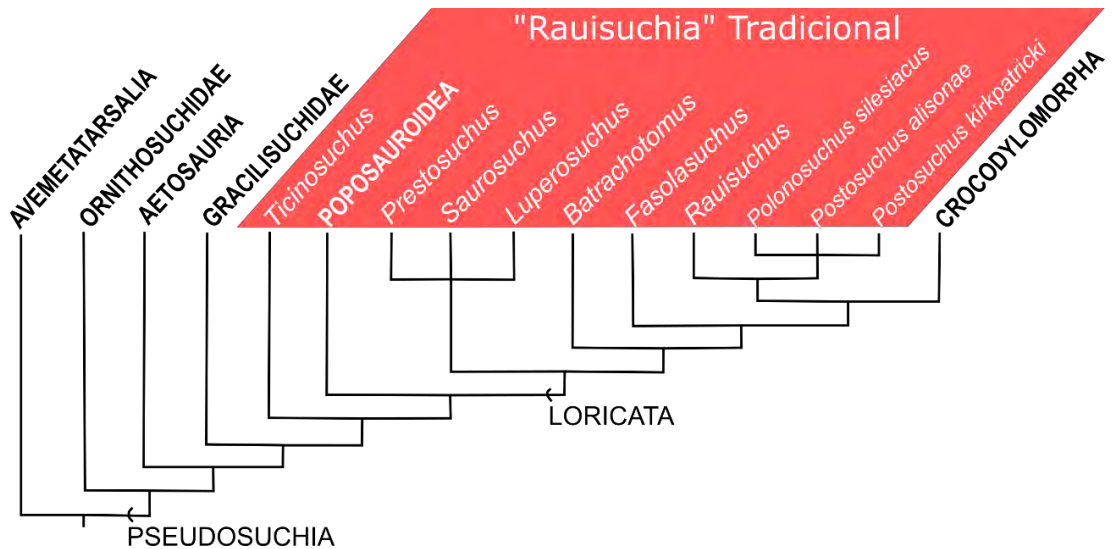


Figura 33. Cladograma de consenso estrito de 180 AMPs de Nesbitt & Desojo (2017) das interrelações filogenéticas de *Luperosuchus* dentro de Archosauria (IC: 0,36; IR: 0,76). Modificado de Nesbitt e Desojo (2017).

5.3. “Rauissuquídeos” do Brasil

Prestosuchus chiniquensis von Huene 1942

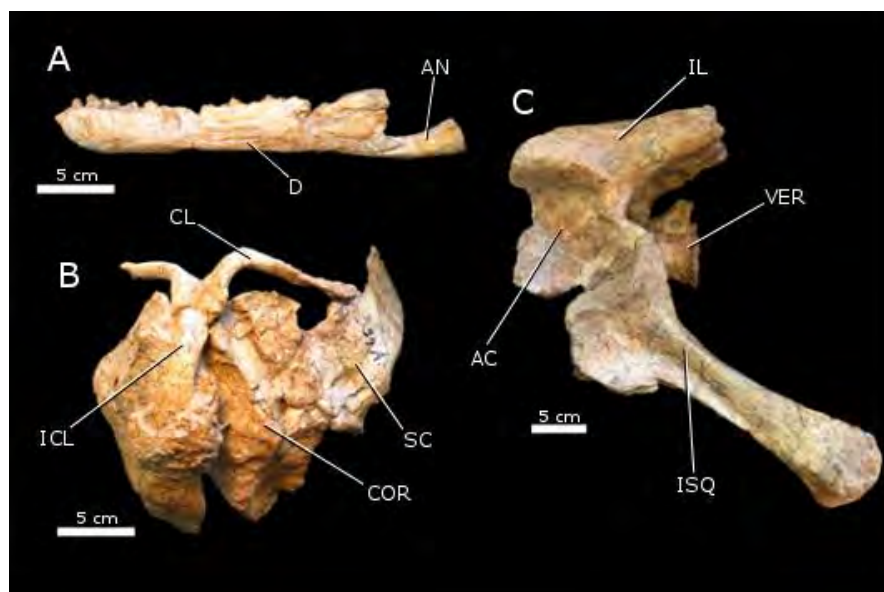


Figura 34. Alguns elementos dos lectótipo de *Prestosuchus chiniquensis*: A) mandíbula (BSPHG 1933L/ 34 a,b) em vista lateral esquerda; B) cintura escapular (BSPHG 1933L/ 12) em vista ventral; C) Porções da cintura pélvica (BSPHG 1933L/ 3a, b) arranjados em posição de articulação. Abreviações: AC, acetábulo; AN, angular; CL, clavícula; COR, coracóide; D, dentário; ICL, interclavícula; IL, íleo; ISQ, ísquio; VER, vértebra.

Lectótipo: BSPHG 1933L/1-3,5-6,8-12,28-35 (escavação 34 cf. von HUENE, 1942: Parte do ramo esquerdo e extremidade distal do ramo direito da mandíbula; alguns fragmentos do crânio, algumas vértebras (incluindo cervicais, dorsais, sacrais e caudais), gastrália, cinturas escapular e pélvica, fragmentos do membro anterior, membro posterior esquerdo completo com um autopódio posterior (Fig. 34).

Paralectótipo: BSPHG 1933L/7 (Escavação 41 cf. von HUENE, 1942): Duas vértebras sacrais em posição de articulação, fragmentos da última vértebra dorsal e da primeira vértebra caudal, metade dorsal do ílio direito com costelas sacrais e uma série de osteodermos associados às apófises neurais das vértebras.

Material referido:

UFRGS-PV-0152-T: Um espécime bem preservado, composto de elementos de sincrânio, esqueleto axial, cinturas e apendiculares incompletos. Foi encontrado próximo da linha férrea da estação Professor Parreira, no Município de Vale Verde, antigo 5º Distrito do Município de general Câmara, que era denominado na época da coleta (1972) como “Vila Melos”, entretanto, não existe maiores informações sobre o local preciso da coleta deste espécime (RAUGUST, 2014). Em sua tese de doutorado, Raugust (2014) apresenta uma descrição detalhada deste espécime e o atribui a uma nova espécie de “rauissuquídeo”. Entretanto, o autor não propôs uma denominação taxonômica, já que uma proposta restrita a uma tese de doutoramento não seria válida segundo os artigos do CIZ, deixando para apresentar esta proposta em uma publicação futura.

UFRGS-PV-0156-T: Um grande crânio completo e em articulação (Fig. 35), associado a um axis mais 30 vértebras da série cervical e pré-sacral; osteodermos em posição de articulação com as respectivas vértebras, desarticulados das

vértebras, mas articulados em baterias ou isolados. Este espécime foi encontrado na Sanga Pascual, na localidade de Pinheiro, município de Candelária.

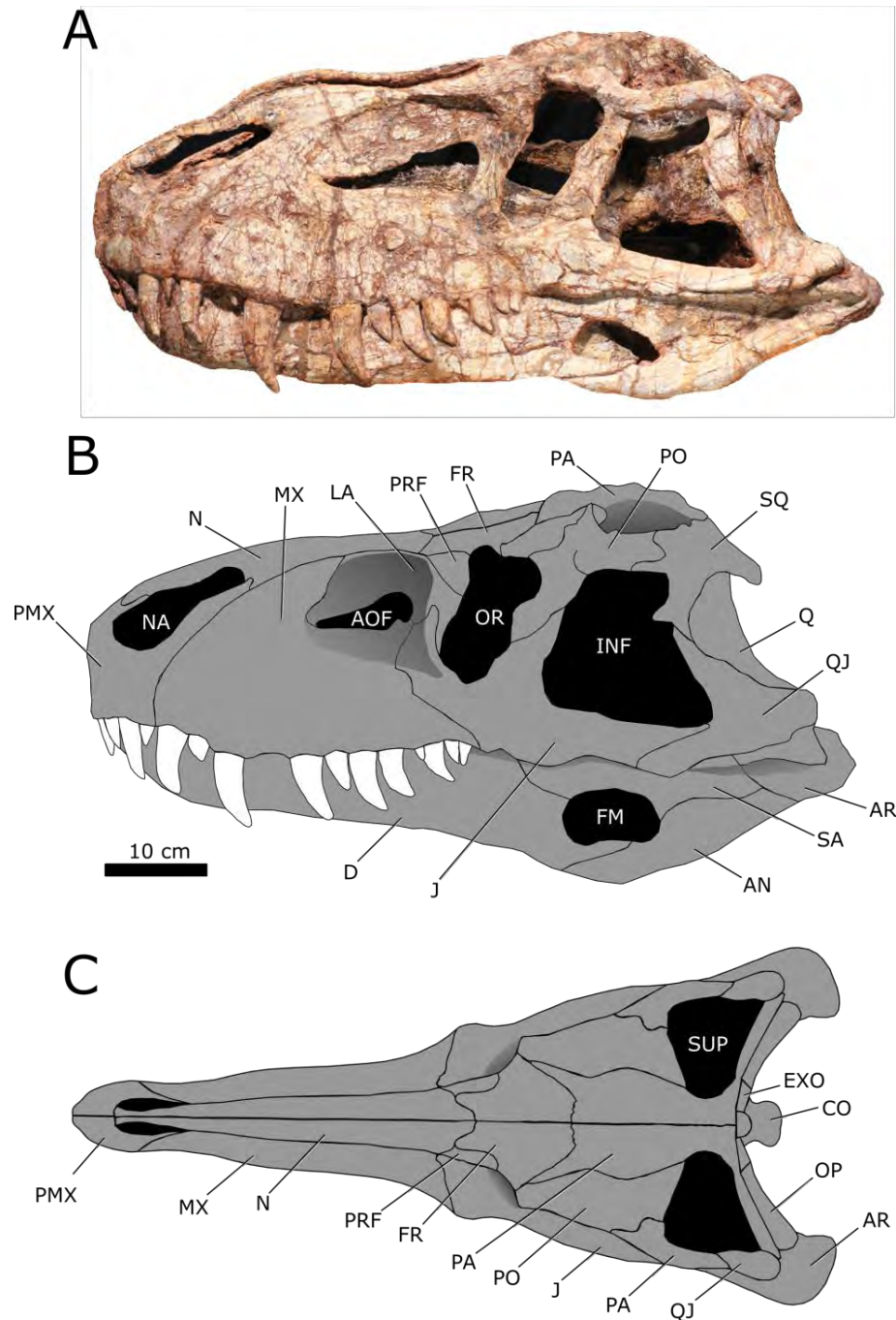


Figura 35. Fotografia (A) do grande crânio do espécime UFRGS-PV-0156-T, em norma lateral esquerda e desenhos esquemáticos na mesma norma (B) e em vista dorsal (C). Abreviações: AN, Angular; AR, Articular; AOF, Fenestra antero-orbital; AOFO, fossa antero-orbital; CO, côndilo occipital; D, Dentário; EXO, Exo-occipital; FM, Fenestra mandibular; FR, Frontal; INF, Fenestra Infra-temporal; J, Jugal; LA, Lacrimal; MX, maxilar; NA, narina externa; N, nasal; OP, opistótico; OR, órbita; PA, parietal; PAP, processo palatal; PMX, pré-maxilar; PO, pós-orbital; PRF, pré-frontal;

Q, quadrado; QJ, quadrado-jugal; SA, supra-angular; SQ, esquamosal; SUP, fenestra supra-temporal;

UFRGS-PV-0629-T: Espécime parcialmente completo (Fig. 36), com um crânio completo e desarticulado; uma sequência vertebral composta por oito cervicais, 13 toraco-lombares, duas sacrais e três caudais; a cintura escapular e pélvica completas; apêndices locomotores praticamente completos, com dois úmeros, porções proximais do rádio e da ulna esquerdo; um metacarpal de um autopódio anterior; os dois fêmures, uma fíbula e tíbia direita; três falanges isoladas de um autopódio posterior e vários fragmentos indeterminados. Este espécime foi descoberto no Afloramento do “Posto de Gasolina”, próximo à entrada do Município de Dona Francisca, à margem da BR 287 (coordenadas: UTM (22) 0270854/6720302). Este espécime foi descrito por Mastrantônio (2010), mas também serviu de base para estudos tafonômicos (OUTA, 2006) e de análises biomecânicas (LIPARINI 2008; 2011; LIPARINI & SCHULTZ, 2013).

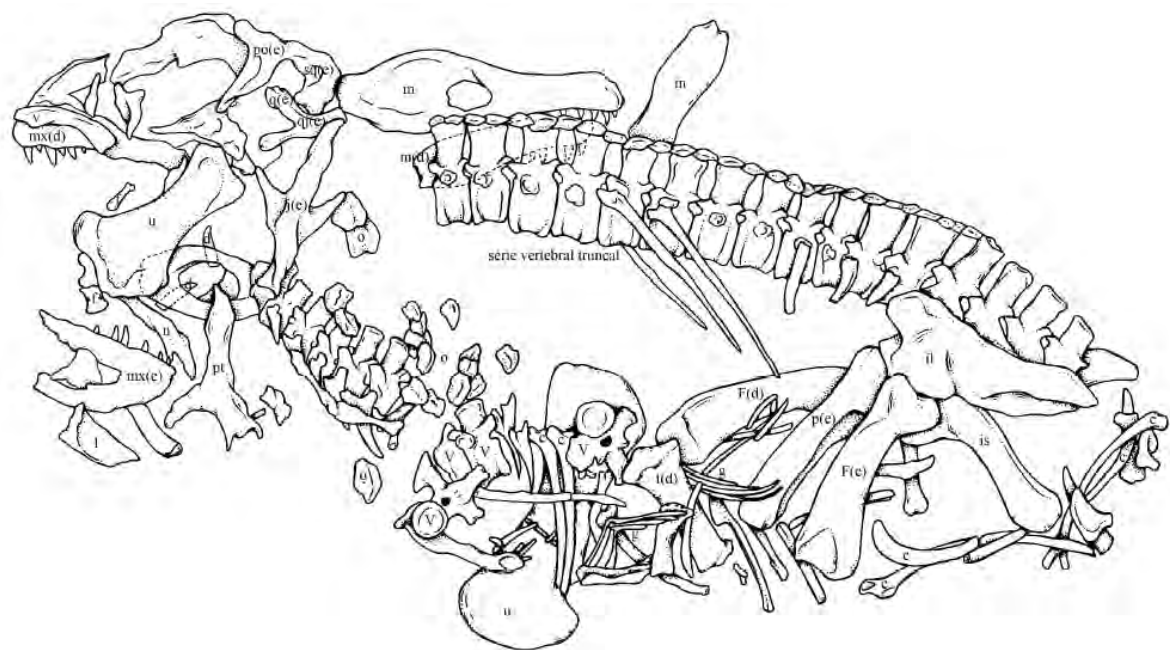
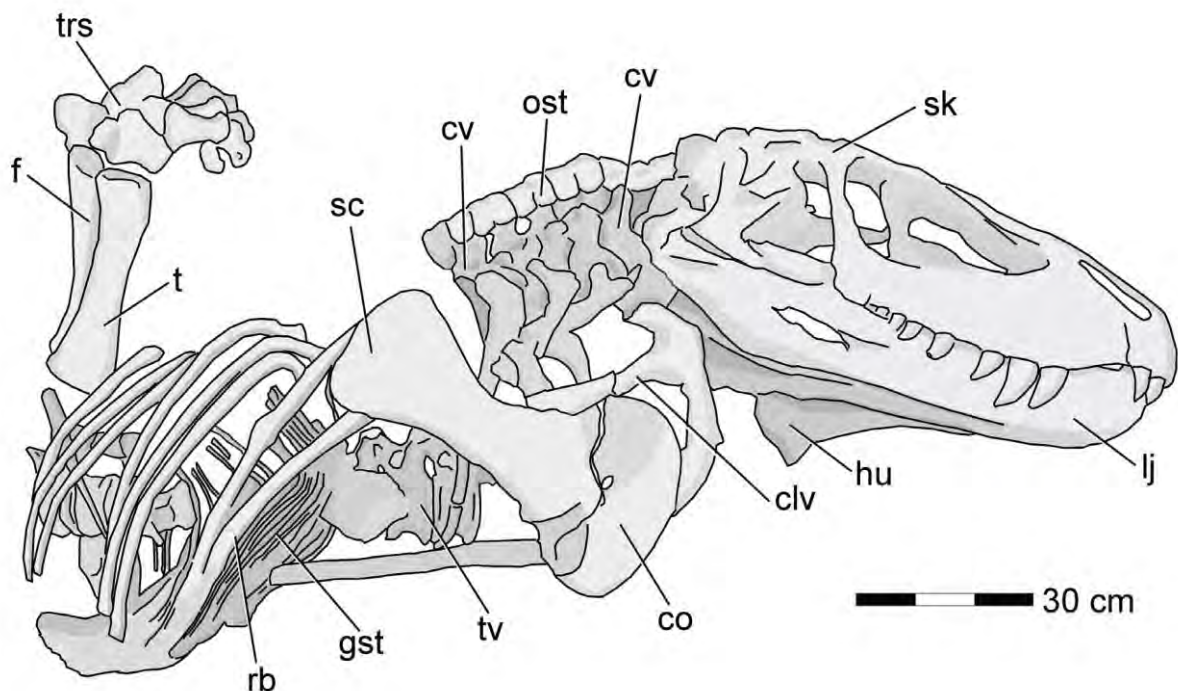


Figura 36. Desenho esquemático do espécime UFRGS-PV-0629-T, com os ossos como foram encontrados. Abreviações: c, costela; d, dente isolado; f, falange; F, fêmur; G, elementos da gastrália; il, Íleo; In, Elemento indeterminado; Is, Ísquio; j, jugal; l, lacrimal; Mn, Mandíbula; Mx, Maxila; N, nasal; o, osteoderme; po, Pós-orbital; Pt, Pterigoide; P, púbis; qj, Quadrado-jugal; q, quadrado; sq, Squamosal; T, tíbia; u, úmero; V, vértebra. (Retirado de MASTRANTONIO, 2010).

CPEZ-239b: Dois crânios incompletos e materiais de pós-crânio de pelo menos dois indivíduos: uma série cervical completa com osteodermas em posição de articulação com as apófises neurais, três vértebras não identificadas incompletas, elementos das cinturas sacral e pélvica incompletos, elementos do pro-, epi- e autopódios incompletos⁵ Foram descobertos na “Sanga da Árvore”, na região de Xiniquá, próximo ao Município de São Pedro do Sul (DESOJO *et al.*, 2011; LACERDA *et al.*, 2016). Entretanto, não está claro se esta corresponderia à mesma localidade descrita por von Huene (1942) devido à perda dos marcos utilizados no mapa feito por este autor, que não puderam ser reconhecidos devido ao crescimento da cobertura vegetal e da erosão (coordenadas: UTM (21) 766622/ 6745570).

ULBRA-PV-281: Um crânio e mandíbula completos, em posição de articulação com uma série cervical e algumas vértebras truncais; uma escápula e coracóide esquerdos, clavícula, um úmero; várias costelas e bateria de gastrálias; uma tibia, fíbula e autopódio em completo e em posição de articulação (Fig. 37). Este espécime também foi coletado também no afloramento “Posto de Gasolina”, próximo à entrada do Município de Dona Francisca, à margem da BR 287 (21°37’38”S 53°22’07”W). Atualmente, apenas uma descrição preliminar da porção anterior do crânio foi publicada (SILVA *et al.*, 2016), com uma descrição detalhada do espécime inteiro a ser publicada em uma data futura.



⁵ Sessão 8, artigo 2.

Figura 37. Desenho esquemático do espécime ULBRA-PVT-281. Abreviações: clv, clavícula; co, coracóide; cv, vértebras cervicais; f, fíbula; gst, gastrália; hu, úmero; lj, mandíbula; ost, osteoderme; rb, costela; sc, escápula; sk, crânio; t, tíbia; trs, tarso; tv, vértebras truncais. Retirado de Silva *et al.* (2016).

Outros espécimes citados na literatura:

UFRGS-PV-0473-T.: Um basicrânio isolado, que foi tentativamente atribuído a *P. chiniquensis* por Mastrantonio *et al.* (2013), por apresentar similaridade geral com a de UFRGS-PV-0156-T.

MCP-146: uma cintura pélvica completa, com a última vértebra toraco-lombar, duas sacrais e a as primeiras três caudais. Na descrição original, Bonaparte (1984) cita e figura o espécime em vista dorsal (Fig. 38: A), notando apenas três vértebras que o autor considera como sendo as sacrais, não sendo mencionado no texto ou nos dados da coleção do MCP se as outras vértebras foram coladas posteriormente. Este espécime difere da codição diagnóstica de duas vértebras sacrais para *P chiniquensis*, mas é possível que a “terceira sacral” descrita por Bonaparte (1984) seja a primeira da série caudal, já que suas costelas não apresentam uma ampla expansão antero-dorsal (Fig. 38: B). Isto pode ser verificado quando é comparada a mesma região com a articulação das sacrais e com a lâmina ílica de UFRGS-PV-0629-T (Fig. 38: C).

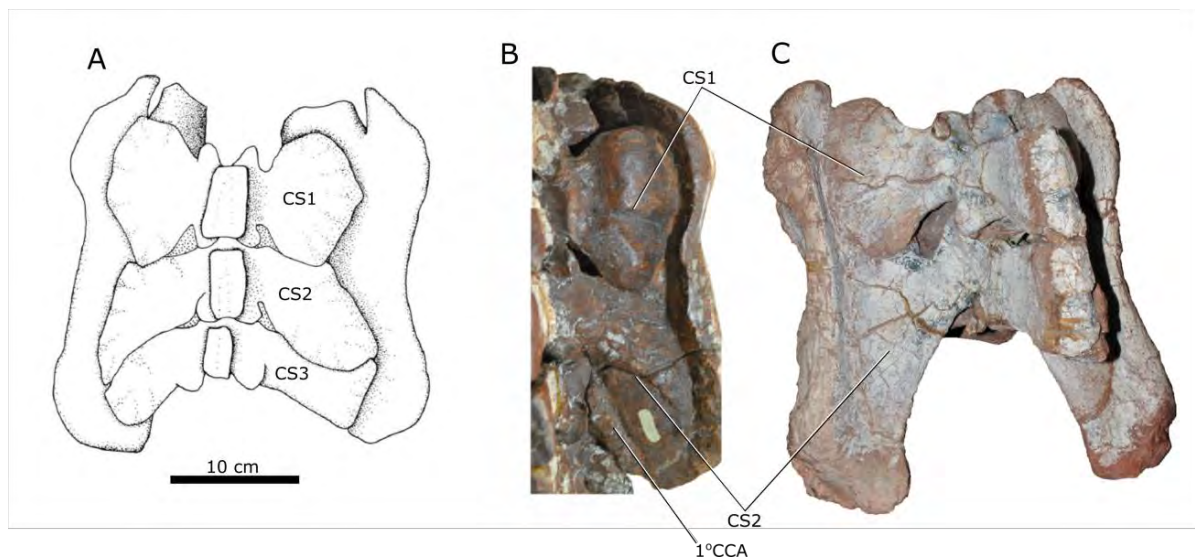


Figura 38. Desenho esquemático do espécime MCP-146 em vista dorsal (A); Fotografia (B) do mesmo espécime na mesma vista que (A) indicando as diferentes costelas sacrais e seu contato com o íleo, comparando a articulação com o presente em UFRGS-PV-0629-T (C). Abreviações: 1°CCA, primeira costela da série caudal;

CS1, primeira costela sacral; CS2, segunda costela sacral; CS3, terceira costela sacral. Abreviações: 1^oCCA, costela da primeira vértebra da série caudal; CS1-3, costelas sacrais e sua posição relativa na série. Imagem A modificada de Bonaparte (1984).

MCZ 4167: Parrish (1993) atribuiu este espécime a *P. chiniquensis*, mas não descreve maiores detalhes, fora que seria mal preservado, mas em posição de articulação. Este espécime apenas é mencionado neste trabalho.

Localidade e Horizonte estratigráfico: O Lectótipo foi encontrado na “Sanga da Árvore” ou *Baum Sanga*, como foi originalmente descrita, na propriedade de Abelo Luiz Silva, a oeste da região de Xiniquá, próximo de São Pedro do Sul (von HUENE, 1942). O paralectótipo foi encontrado na Sanga de Theotônio Béles Xavier, a oeste de Xiniquá. Formação Santa Maria, ZA de *Dinodontosaurus* (ZERFASS *et al.* 2003, HORN *et al.*, 2014).

Idade: Meso-Neotriássico (Neoladiniano–Eocarniano)

Discussão: *Prestosuchus chiniquensis* é o táxon de “rauissuquídeo” com a maior amostragem de espécimes de outras localidades do Triássico do Rio Grande do Sul. Todavia, ele não apresenta problemas em relação a sua resolução taxonômica e possível sinonímia com *Prestosuchus loricatus*, como foi proposta por alguns autores (*e.g.*, KREBS, 1976; BARBERENA, 1978) e que nunca foi adequadamente abordado. Desojo & Rauhut (2008) apresentaram duas autapomorfias para o táxon: um entalhe posicionado anteriormente entre a escápula e o coracóide; uma crista longitudinal na superfície dorsal do íleo. Dos espécimes descritos, apenas quatro apresentam um ou ambos os elementos (MCP-146, ULBRA-PV-281, UFRGS-PV-0629-T e UFRGS-PV-0152-T) e grande parte dos trabalhos utilizam a sobreposição dos caracteres para estabelecer uma definição taxonômica (BRUSATTE, *et al.*, 2010; MASTRANTONIO, 2010; NESBITT, 2011; FRANÇA, 2011; MASTRANTONIO *et al.*, 2013; LACERDA *et al.*, 2016; SILVA *et al.*, 2016). Também, existe uma “tendência” de atribuir qualquer fóssil de arcossauro de grande porte proveniente da ZA de *Dinodontosaurus* ao táxon, o que aumenta a quantidade de espécimes atribuídos. Por motivos de clareza, foram apenas apresentados os espécimes que já foram descritos em publicações.

Rauisuchus tiradentes von Huene 1942

Holótipo: BSPG AS XXV 60-68, 71-100, 105-119, 121 (lectótipo) (Fig.39): Conhecido apenas por quatro exemplares incompletos e mal preservados, contendo restos cranianos, algumas vértebras, ambas as cinturas (pélvica e escapular) incompletas com muitos osteodermos.

Localidade e Horizonte estratigráfico: Segundo von Huene (1942), “O achado provém da escavação 15 da “Sanga dos Dentes”, à margem da estrada que liga Santa Maria a São José, estando incluído em pelitos laminados vermelhos com pouca areia Formação Santa Maria, ZA de *Hyperodapedon* (ZERFASS *et al.* 2003, HORN *et al.*, 2014).

Idade: Neotriássico (Carniano).

Discussão: Um íleo esquerdo isolado (BSPG AS XXV 88) foi originalmente considerado por von Huene (1942) como pertencendo ao mesmo indivíduo que o restante do material, mas Lautenschlager (2008) o considerou como sendo de outro, baseado principalmente na variação de tamanho encontrado entre este osso com o púbis associado. Após o original descrito por von Huene (1938), nenhum outro material foi referido a este táxon. Apesar de ter sido mencionado por outros autores (e.g. ROMER, 1956; KREBS, 1976, KISCHLAT, 2000), Lautenschlager & Rauhut (2014) propuseram as seguintes autapomorfias para este táxon: uma protuberância estufada na base do processo posterior da pré-maxila; vértebras cervicais antero-posteriormente curtas, com uma quilha ventral e sem lâminas pós-zigopodiapofisiais; vértebras caudais antero-posteriormente alongadas com uma apófise neural acessória e uma lâmina pós-apofisiária (Fig. 40).

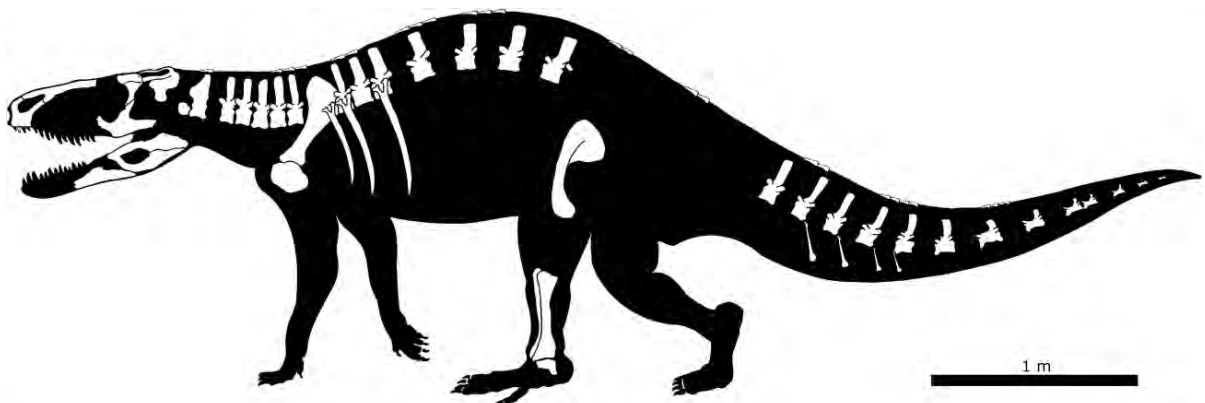


Figura 39. Reconstrução do esqueleto de *Rauisuchus tiradentes* mostrando os elementos preservados Retirado de Lautenschlager & Rauhut (2014).

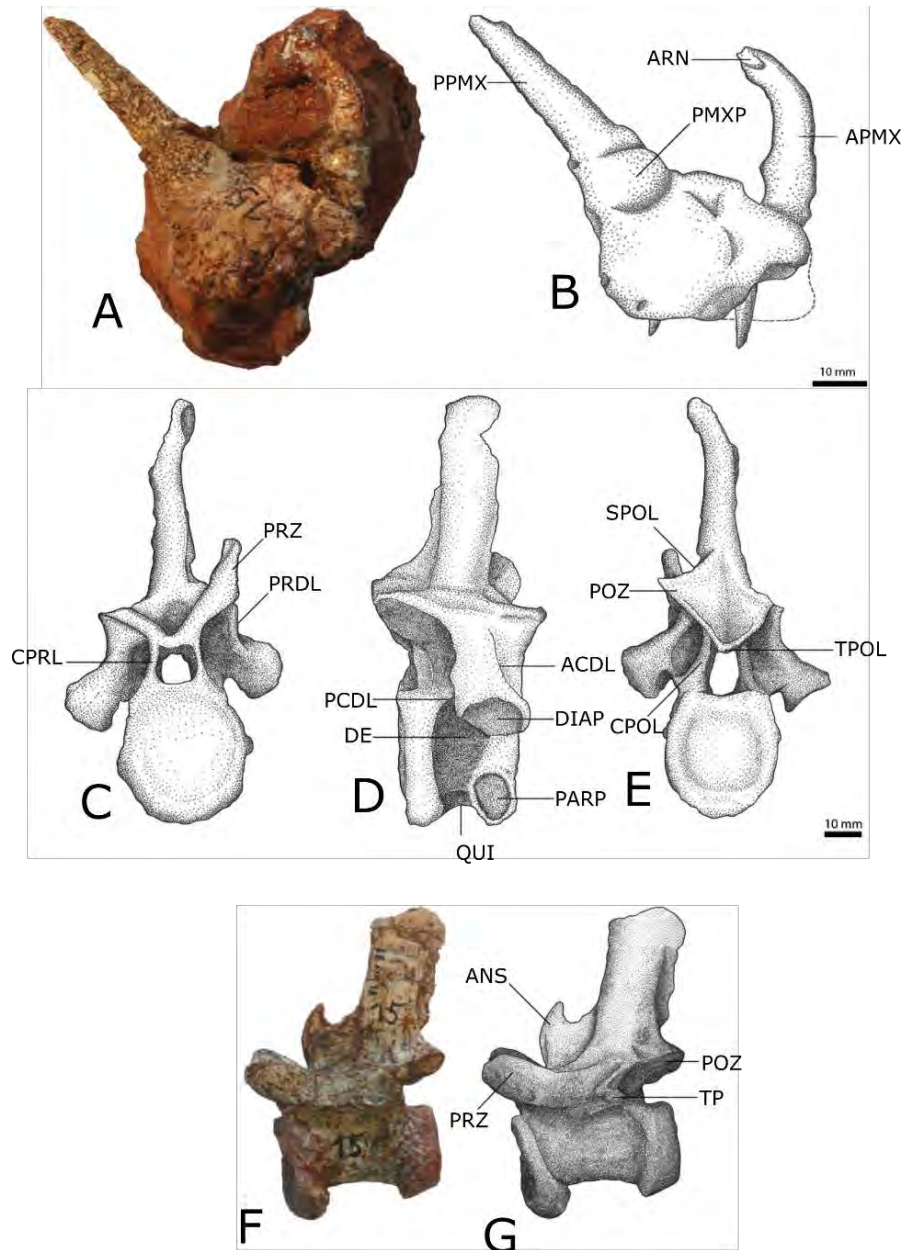


Figura 40. Detalhes de alguns elementos do lectótipo de *Rauisuchus tiradentes*. Fotografia (A) e figura esquemática (B) do pré-maxilar direito em vista lateral; Figuras esquemáticas da sexta vértebra cervical em normas (C) anterior, (D) lateral direita e (E) posterior; Fotografia (F) e ilustração esquemática (G) de uma vértebra caudal da série anterior em vista lateral esquerda. Abreviações: APMX, processo antero-dorsal do pré-maxilar; ARN, área da articulação com o processo anterior do nasal; ACDL, lâmina centrodiafiseal anterior; CPRL, lâmina centroprészigapofiseal; CPOL, lâmina centropószigapofiseal; DE, depressão; DIAP, diafise; PARP, parapófise; PCDL, lâmina centrodiafiseal posterior; PMXP, protuberância do pré-

maxilar; PPMX, processo póstero-dorsal do pré-maxilar; POZ, pós-zigapófises; PRDL, lâmina pré-zigapofiseal; PRZ, pré-zigapófise; TP, processo transverso; TPOL, lâmina intra-pószigapofiseal; . Modificado de Lautenschlager & Rauhut (2014).

Procerosuchus celer von Huene 1942

Lectótipo: BSPG AS XXV131-139, composto por um crânio incompleto, cinturas e membros escapular e pélvico incompletos (Fig. 41).

Localidade e Horizonte estratigráfico: “O achado provém da escavação 37, da parte noroeste da Sanga da Estrada, de Abel Luiz Silva, a oeste de Xiniquá” (von Huene, 1942). Formação Santa Maria, ZA de *Dinodontosaurus*, Meso-Neotriássico (Neoladiniano–Eocarniano).

Idade: Meso-Neotriássico (Neoladiniano–Eocarniano).

Discussão: Existe apenas um exemplar conhecido, que segundo Kischlat (2000) e Desojo & Rauhut (2008), seria uma forma juvenil de *Prestosuchus chiniquensis*.

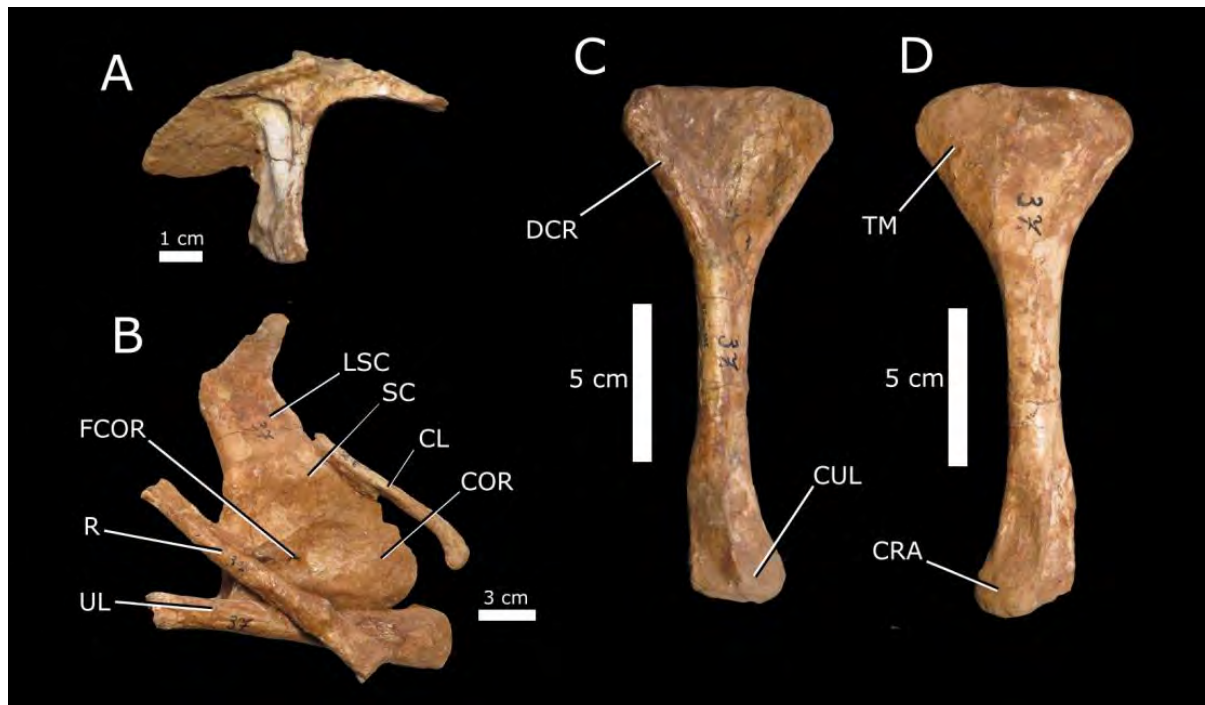


Figura 41. Fotografias de alguns elementos do lectótipo de *Procerosuchus celer*. (A) pterigoide direito (BSPG AS XXV 131) em vista ventral; (B) escapulo-coracóide direitos com elementos do epipódio anterior direito associado (BSPG AS XXV 134);

Úmero direito (BSPG AS XXV 135) em vista medial (C) e lateral (D). Abreviações: CL, clavícula; COR, coracóide; CRA, côndilo radial; CUL, côndilo ulnar; DCR, crista deltopeitoral; FCOR, forame do croacóide; LSC, lâmina escapular; SC, escápula; R, rádio; TM, tuberosidade medial; UL, ulna.

Hoplitosuchus raii von Huene 1942

Lectótipo: BSPG AS XXV/53, 54, 55, 56, 57, 58, 59. Dois osteodermos grandes, com projeções espinhais e alguns elementos pós-cranianos (Fig. 42).

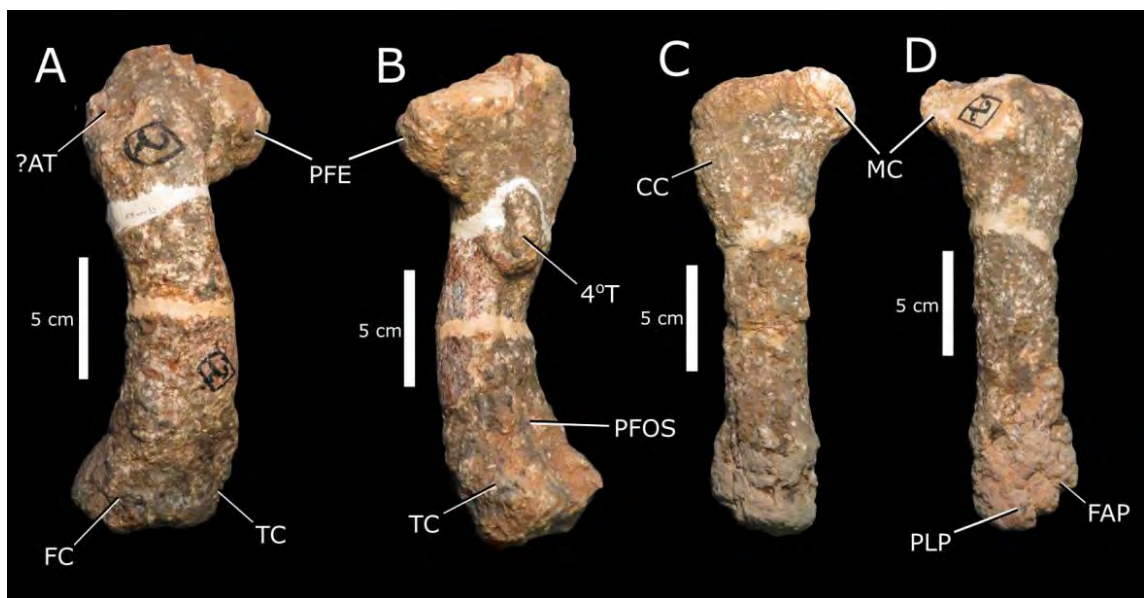


Figura 42, o fêmur (BSPG AS XXV 53) e tíbia direitos (BSPG AS XXV 54) atribuídos a *Hoplitosuchus raii*, mas interpretado por Kishlat & Barberena (1999) e Ezcurra (2012) como pertencendo a um dinossauriforme. O fêmur em vista lateral (A) e medial (B) e a tíbia em vista medial (C) e lateral (D). Abreviações: 4°T, quarto trocânter; ?AT, provável trocânter anterior; CC, crista cnemial; FAP, faceta para o contato do processo ascendente do astrágalo; FC, côndilo fibular; MC, côndilo medial; PFE, porção proximal do fêmur; PFOS, fossa poplietal; PLP, processo póstero-lateral. Modificado de Ezcurra (2012).

Localidade e Horizonte estratigráfico: “O achado provém da Sanga Grande da Alemoa, junto de Santa Maria, no horizonte fossilífero II” (von HUENE, 1942). Formação Santa Maria, ZA de *Hyperodapedon*, Meso-Neotriássico (Neoladiniano–Eocarniano).

Idade: Neotriássico (Carniano).

Discussão: Apenas um exemplar composto por material de pós-crânio descritos por Huene (1942). O fragmento de um fêmur direito (BSPG AS XXV 53) e de uma tíbia direita (BSPG AS XXV 54) foram interpretados como sendo de um dinossauro saurísquio sob a designação “*Teyuwasu barbarena*” por Kischlat e Barberena (1999). Desojo e Rauhut (2008) consideraram *Hoplitosuchus rai* como *nomen dubium* porque o material tipo consiste em ossos impossíveis de serem identificados, enquanto o material referido seria composto por uma mistura de elementos de dinossauro e de “rauissuquídeo”. Ezcurra (2012) considerou “*T. barbarena*” como *nomen dubium* devido à péssima preservação do material combinado com a ausência de autapomorfias, mas considerou que apresentava características que são consistentes com o grupo dos Dinosauromorpha e outros clados mais inclusivos (*i.e.*, a possível presença de um trocânter anterior no fêmur e a porção proximal da tíbia apresentando côndilos posteriores assimétricos) (Fig. 42).

Decuriasuchus quartacolon França, Langer & Ferigolo 2011

Holótipo: MCN PV10105a. Crânio e pós crânio parcialmente completos, faltando apenas a cintura escapular e os apêndices locomotores.

Material referido:

MCN PV10105b: Um esqueleto quase completo, com o crânio e partes dos apêndices locomotores anteriores ausentes.

MCN PV10105c: Um crânio e pós-crânio quase completo.

MCN PV10105d: crânio e sequência de vértebras pré-sacrais

MCN PV10105e: Vértebras da série truncal e caudal.

MCN PV10105f: metade distal de uma cauda.

MCN PV10105g: vértebras caudais, cintura pélvica e dois fêmures.

MCN PV10105h: vértebras caudais, cintura pélvica e os dois apêndices locomotores posteriores completos.

MCN PV10004: Um teto crânio incompleto, que foi encontrado em outro local do afloramento e não em associação com os outros espécimes.

Localidade e Horizonte estratigráfico: Provenientes do “Afloramento do Posto”, próximo ao município de Dona Francisca, 29°37'38"S 53°22'07 W (MCN PV10105) e 29°37'36"S 53°22'02 W (MCN PV10004).

Idade: Meso-Neotriássico (Neoladiniano–Eocarniano).

Discussão: Seria um predador de médio porte, quando comparado a formas maiores como *Prestosuchus* (Fig. 43). Apresenta as seguintes autapomorfias: o lacrimal e o nasal formam a expansão lateral do teto craniano, que cobre a maior parte da fenestra antero-orbital; a margem anterior da porção dorsal do quadrado-jugal e a ventral do esquamosal juntos foram um processo anterior sub-triangular que entra na fenestra infra-temporal. Esta assembléia (Fig. 44) seria a primeira evidência de comportamento gregário entre “rauisuquídeos”. No momento apenas uma descrição preliminar (FRANÇA *et al.*, 2011) e o crânio (FRANÇA *et al.*, 2013) foram publicados.

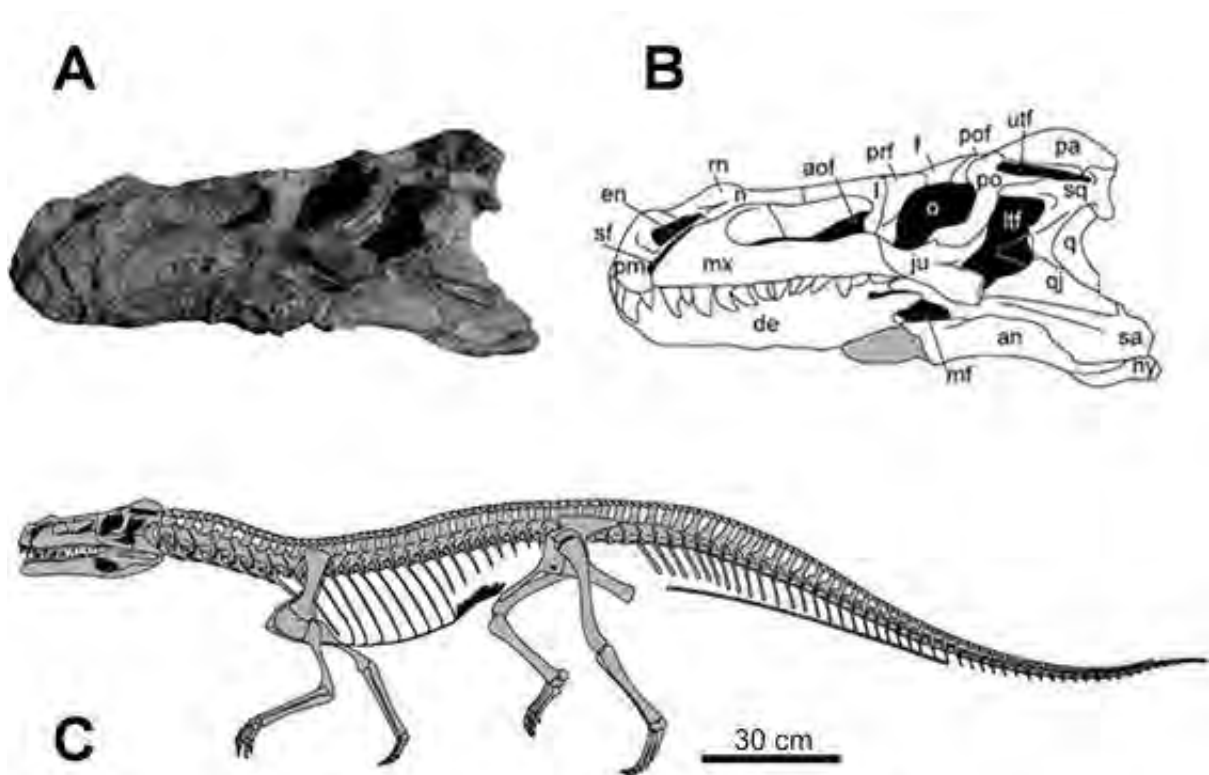


Figura 43. Fotografia (A) e ilustração esquemática (B) do crânio de *Decuriasuchus quartacolonia* e reconstrução do esqueleto (C). Abreviaturas: (an) angular; (aof) fenestra antero-orbital; (de) dentário; (en) narina externa; (f) frontal; (hy) hióide; (ju)

jugal; (l) lacrimal; (ltf) fenestra latero-temporal; (mf) fenestra mandibular; (mx) maxila; (n) nasal; (o) órbita; (pp) processo para-occipital do opistótico; (pa) parietal; (pof) pós-frontal; (po) pós-orbital; (prf) pré-frontal; (pm) pré-maxilar; (q) quadrado; (qj) quadrado-jugal; (rn) “nariz romano”; (sa) supra-angular; (sq) esquamosal; (sf) fenestra sub-narinal; (utf) fenestra supra-temporal. (Retirado de FRANÇA *et al.*, 2011).

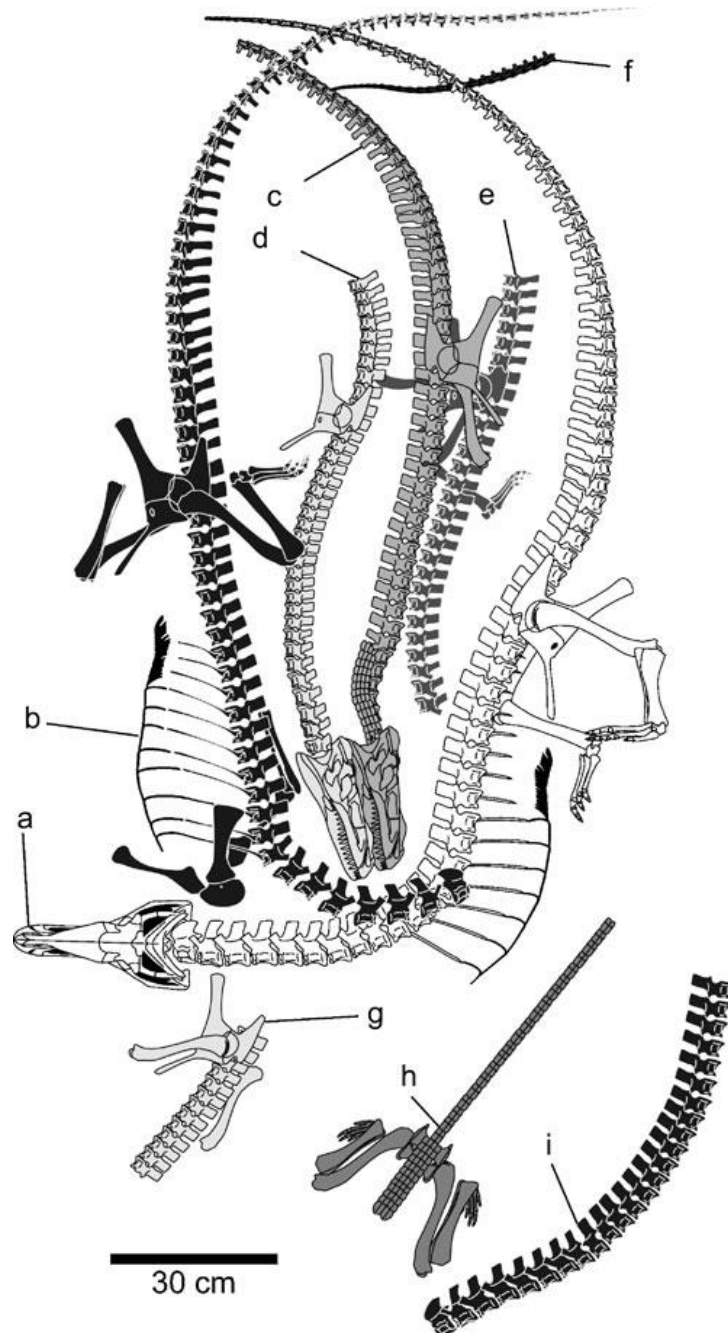


Figura 44. Figura esquemática da assembleia contendo os nove espécimes de *Decuriasuchus quartacolonia* (MCN PV10105a-i). Retirado de França *et al.* (2011).

6. ORNITHOSUCHIDAE

6.1. Uma breve caracterização de Ornithosuchidae

Ornithosuchidae von Huene, 1914 (*sensu* SERENO, 1991) é um grupo de arcossauros pseudossúquios do Triássico, composto por apenas três táxons: *Ornithosuchus woodwardi* Newton, 1894 (*sensu* von BACZKO & EZCURRA, 2016), *Riojasuchus tenuisiceps* Bonaparte, 1969 e *Venaticosuchus rusconii* Bonaparte 1971 (WALKER, 1964; BONAPARTE, 1972; von BACZKO & EZCURRA, 2013). São formas carnívoras que possivelmente atingiam entre dois a quatro metros de comprimento (von BACZKO & EZCURRA 2013; 2016). Apresentavam um crânio grande e dorso-ventralmente alto, com órbitas largas em forma de “gota” com a ponta direcionada ventralmente, uma narina proporcionalmente grande, um jugal que, em norma lateral, apresenta uma forma de ‘Y’ devido a dois processos projetados anterodorso- e posterodorsalmente, que forma a borda ventral da órbita. Entretanto, a característica que mais se destaca do crânio é a porção anterior do rosto, que apresenta uma curvatura antero-ventralmente projetada, de comprimento antero-posterior similar ao da mandíbula, como em *O. woodwardi*, ou mais alongado, como em *R. tenuisiceps* e *V. rusconii*. Ademais, a sequência dentária no rosto é interrompida por um diastema, localizado imediatamente posterior ao último dente do pré-maxilar até o primeiro dente do maxilar.

A sua postura corporal é interpretada como sendo de um bípede facultativo ou totalmente bípede (Fig. 45), devido ao tamanho dos elementos dos autopódios anteriores serem significativamente menores do que dos posteriores (WALKER, 1964). Apresentam também um acetábulo perfurado (EZCURRA, 2016). A articulação metatarsal dos Ornithosuchidae, descrita por Walker (1964) e Bonaparte (1972), apresenta um padrão “crocodilo-reverso” (*sensu* CHATTERJEE, 1978), onde o calcâneo apresentava uma cavilha (*peg*) que iria se articular com um soquete (*socket*) correspondente no astrágalo. Com base neste padrão de articulação, autores subsequentes atribuíam ao grupo afinidades próximas à linhagem que posteriormente iria dar origem as aves (GAUTHIER, 1986; BENTON & CLARK, 1988). Sereno (1991), utilizando caracteres do crânio e se distanciando das “filogenias baseadas nos tarsais”, encontrou uma topologia onde Ornithosuchidae (composto por *Ornithosuchus woodwardi*+*Riojasuchus tenuisiceps*) pertenceriam à linhagem que iria dar origem aos crocodilianos porque considerou as modificações

nos tarsos como sendo homoplasias, ao contrário de pesquisas prévias (e.g. CHATTERJEE, *oput. cit.*). Desde então, as afinidades dos ornitossuquídeos tem se mantido na linhagem crocodiliana em análises posteriores (e.g. BRUSATTE *et al.*, 2010; NESBITT; von BACZKO *et al.*, 2014; BUTLER *et al.*, 2014; EZCURRA, 2016; NESBITT & DESOJO, 2017) como será abordado em detalhe na sessão seguinte.

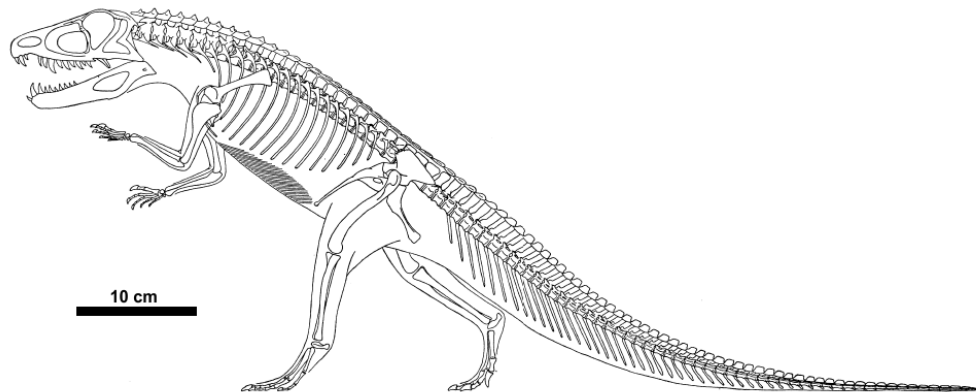


Figura 45. Reconstrução de *Ornithosuchus woodwardi* (*sensu* von BACZKO & EZCURRA, 2016) em postura bípede com a concepção antiga da cauda arrastando no solo (Retirado de Walker, 1964).

6.2. Estado da Arte

Newton (1894) apresentou a descrição do táxon *Ornithosuchus woodwardi* do Neotriássico da Escócia e considerou, de forma provisória, que este teria afinidades próximas aos dinossauros. Esta hipótese seria com base na estrutura geral do crânio e dos dentes, mas também reconheceu similaridades com grupos mais próximos dos crocodilianos (Parasuchia), com base na articulação do astrágalo com o calcâneo. Boulenger (1904) descreveu dois espécimes adicionais (NHMUK PV R2410 e NHMUK PV R3142) de dimensões maiores do que o holótipo, o que o autor considerou como sendo devido à variação ontogenética. Ademais, considerou que *O. woodwardi* teria uma afinidade filogenética mais próxima com Parasuchia, que segundo o autor, seria composta por *Aetosaurus ferratus*, *Herpetosuchus*⁶ (= *Erpetosuchus*) *granti*, *Stagonolepis robertsoni* e fitossauros.

⁶ Sobre esta designação, ver Erpetosuchidae, a partir da página 108.

Huene (1908) ergueu a Ordem Ornithosuchia e a Família Ornithosuchidae, composta por *Ornithosuchus woodwardi*, *Scleromochlus taylori* Woodward, 1907 e *Hallopus victor* Marsh 1881. Broom (1913) considerou que haveria duas espécies dentro do gênero *Ornithosuchus*, baseado principalmente na diferença de tamanho, onde os espécimes maiores, descritos por Boulenger (1904), representariam uma espécie distinta denominada *Ornithosuchus taylori*, que diferiria de *O. woodwardi* apenas no maior tamanho e robustez.

Huene (1921) vai incluir *Saltoposuchus connectens* Huene, 1921 dentro de Ornithosuchidae e subsequentemente (HUENE, 1956) adicionaria *Parringtonia gracilis* Huene, 1939 no mesmo. Neste último trabalho, o autor iria expandir a quantidade de gêneros dentro da família Ornithosuchidae, com *Ornithosuchus*, *Parringtonia*, *Saltoposuchus*, *Erpetosuchus*, *Hesperosuchus*, *Scleromochlus* e 'Mandasuchus'. Haughton e Brink (1954) vão incluir os gêneros *Brownellia*, *Euparkeria* e *Parringtonia* enquanto que Hoffstetter (1956) considerou *Ornithosuchus*, *Erpetosuchus*, *Saltoposuchus*, *Parringtonia* e *Hesperosuchus*. Romer (1956) interpretou que Ornithosuchidae incluiria *Cerritosaurus*, *Hesperosuchus* e, com dúvidas, *Parringtonia* e *Prestosuchus*, apenas argumentando que tais formas foram agrupadas por ele desta maneira porque não eram facilmente incluídas nos grupos mais bem estabelecidos de arcossauros do Triássico.

Walker (1964) apresentou uma revisão detalhada de Ornithosuchidae e considerou que a espécie *Ornithosuchus taylori* seria um sinônimo júnior de *Ornithosuchus woodwardi*, tornando o primeiro nome inválido. Este autor também reconheceu que os espécimes de *Dasygnathus longidens* Huxley 1877 (ELGNM 1, 15 e 29), eram indistinguíveis de *O. woodwardi*, mas como *D. longidens* já era utilizado para um gênero de coleóptero, propôs a renomeação da espécie, com base no princípio da prioridade, para *Ornithosuchus longidens* Huxley, 1877. Walker (*oput. cit.*) também, considerou que Ornithosuchidae estaria na linhagem dinossauriana, sendo uma família da Infraordem Carnosauria.

Para Walker (1964), a Família Ornithosuchidae seria composta por *Ornithosuchus longidens*, *Teratosaurus suevicus* e *Sinosaurus triassicus* Young, 1940. Destas, os dois últimos foram retirados da família por autores posteriores (ROMER, 1966, 1968; CHARIG, 1969; BONAPARTE, 1969, 1972). Reig (1961) foi o primeiro a desconsiderar a relação do grupo com os dinossauros e voltar a propor

uma afinidade mais próxima dos crocodilianos, colocando Ornithosuchidae dentro de Pseudosuchia. Mesmo Romer (1966) e Charig (1967), que inicialmente consideraram os ornitossuquídeos como dinossauros “primitivos”, acabaram concordando com esta hipótese em trabalhos posteriores (ROMER, 1968; CHARIG, 1969).

Bonaparte descreveu *Riojasuchus tenuisiceps*, da Formação Los Colorados, e *Venaticosuchus rusconii* (BONAPARTE, 1969, 1970), da Formação Ischigualasto da Argentina. Estas duas espécies seriam incluídas dentro de Ornithosuchidae junto com *Ornithosuchus longiceps*. O autor considerou que a Infraordem Ornithosuchia pertenceria à linhagem crocodiliana (Pseudosuchia) e seria composta por Ornithosuchidae, Rausuchidae, ‘Pallisteriidae’, ‘Teleocratidae’ e Scleromochlidae, junto com Sphenosuchia e Proterochampsia (BONAPARTE, 1972).

Romer (1972) considerou Pseudosuchia como sendo composta pelas famílias Scleromochlidae e Ornithosuchidae, onde esta última seria composta por *Gracilisuchus stipanicorum* (com dúvida), mais *Parringtonia gracilis* e *Dyoplax arenaceus*.

Bonaparte (1975) apresentou uma revisão da Família Ornithosuchidae, que seria composta por *Ornithosuchus longiceps*, *Riojasuchus tenuisiceps*, *Venaticosuchus rusconii* e *Gracilisuchus stipanicorum*, que junto com a Família Scleromochlidae, formaria Ornithosuchia. Estes, por sua vez, englobariam os ancestrais dos Sphenosuchia, ou seja, dos crocodilianos (Fig. 46).

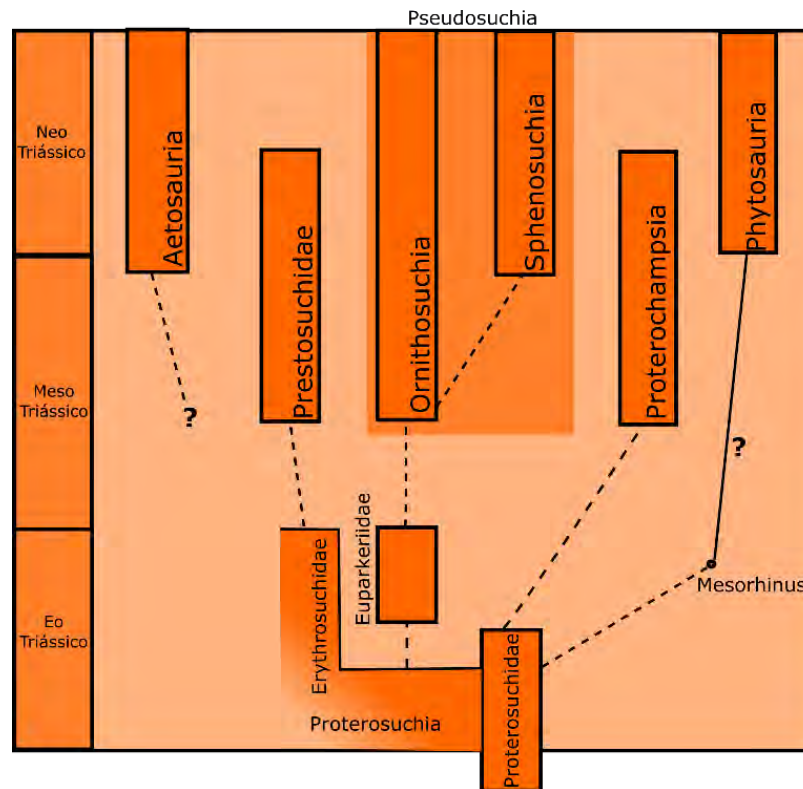


Figura 46. Proposta redesenhada de Bonaparte (1975) para a evolução dos arcossauros onde Ornithosuchia seria derivado de Euparkeridae.

Na primeira proposta filogenética das relações dos diferentes grupos dentro dos arcossauros, Gauthier (1984) encontrou *Ornithosuchus longidens* na base da linhagem aviana, o que serviu de justificativa para Gauthier & Padian (1985) utilizarem o nome Ornithosuchia, re-definido cladisticamente, para se referir a este ramo. Esta topologia se repetiu na análise de Gauthier (1986: Fig 47) e de Benton & Clark (1988).

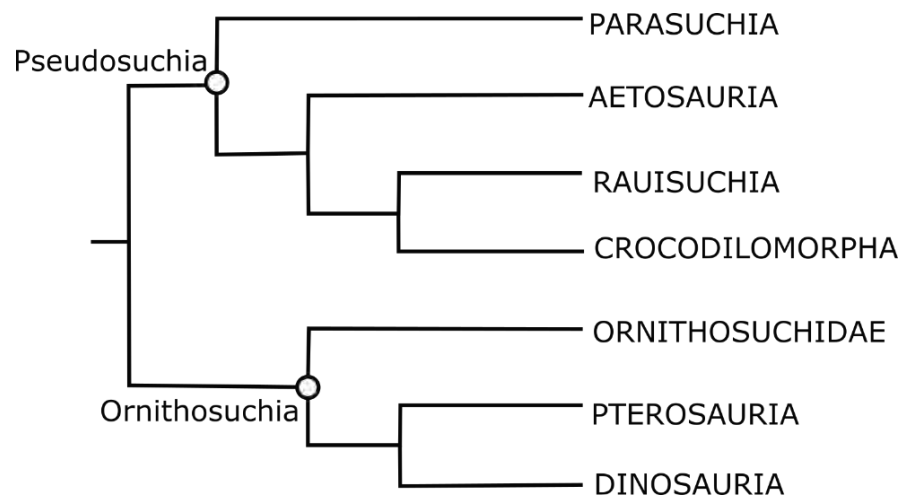


Figura 47. Proposta filogenética de Gauthier (1986).

Entretanto, na proposta de Sereno e Arcucci (1990), Ornithosuchidae foi encontrado como o clado mais próximo da base da linhagem crocodiliana, cunhada pelos autores de Crurotarsi. Sereno (1991) vai apresentar uma definição filogenética para o Ornithosuchidae como o clado mais próximo a Suchia, (que seria o clado menos inclusivo que contém *Gracilisuchus stipanicorum*, Aetosauria, 'Rauisuchia', Puposauridae e Crocodylomorpha) do que à Phytosauria (Fig. 48) em sua hipótese filogenética. Entretanto, na análise de Parrish (1993), os ornitossuquídeos estavam na base de Crurotarsi.

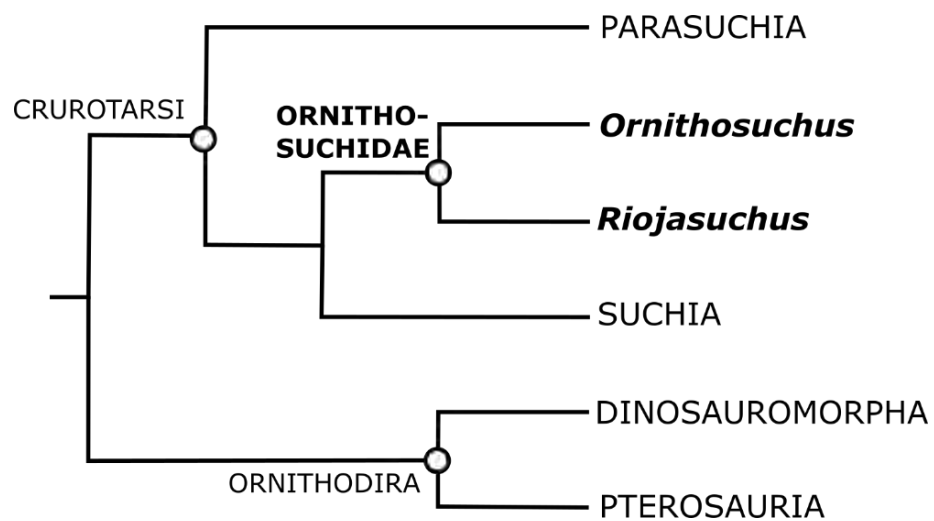


Figura 48. Cladograma redesenhado da proposta filogenética de Sereno (1991).

Juul (1994) encontrou os ornitossuquídeos como o grupo irmão de um clado composto por Crocodylomorpha mais os táxons *Postosuchus kirkpatricki* e *Gracilisuchus stipanicorum*. Long & Murray (1995) descreveram um único fêmur da Formação Colorado City do Grupo Dockum (fim do Carniano até o fim do Retiano) do Texas, sudoeste dos EUA como sendo de um ornitossuquídeo, possivelmente de uma forma similar a *Ornithosuchus longidens*. Entretanto, Nesbitt *et al.* (2010) questionaram esta definição e identificaram uma série de sinapomorfias do grupo dos dinossauriformes silesaurídeos no fêmur (e.g. porção proximal do fêmur com uma superfície articular medial reta; um sulco reto, em sentido transversal na sua superfície proximal; côndilos articulares distais divididos posteriormente entre um quarto a um terço do comprimento da diapófise; tubérculo posteromedial ausente). Devido a isso, Nesbitt e colaboradores (2010) reinterpretaram o espécime como sendo de algum silesaurídeo. Bennett (1996) encontrou uma politomia composta

por Ornithosuchidae, *Euparkeria capensis*, Pseudosuchia (neste caso composto por Suchia+ Phythosauria/Parasuchia) e pela linhagem pró-aviana, denominado por ele de Ornithodira.

Benton (1999) e Benton & Walker (2002) encontraram Ornithosuchidae dentro de Suchia, sendo mais próximo aos 'rauissuquídeos' do que a outros pseudossuquídeos. Entretanto, em uma proposta posterior (Benton, 2004), Ornithosuchidae foi inserido em uma tricotomia composta de um clado formado por Parasuchia + *Gracilisuchus stipanicorum* e um grupo formado por Aetosauria, 'Rauisuchia' e Crocodylomorpha. Esta topologia onde ornitossuquídeos seriam mais próximos dos 'rauissuquídeos' foi repetido em outras propostas subsequentes (e.g. NESBITT & NORELL, 2006; NESBITT, 2007; BRUSATTE *et al.*, 2010).

Ornithosuchidae foi considerado como um grupo monofilético (composto por *Ornithosuchus longidens*+ *Riojasuchus tenuiceps*) por Brusatte *et al.*, 2010 e Nesbitt, 2011), mas com topologia diferente dentro de Pseudosuchia. Nesbitt (2011) apresentou Ornithosuchidae como o clado mais basal desta linhagem, encontrando 13 sinapomorfias para o grupo, enquanto França *et al.* (2011), utilizando uma matriz modificada de Brusatte *et al.* (2010), encontrou Ornithosuchidae dentro de um Rauisuchia monofilético. Entretanto, como foi apresentado previamente, a topologia encontrada na análise de Brusatte *et al.* (2010) deve ser considerado com cautela.

Butler *et al.* (2011), também utilizando uma matriz modificada de Brusatte *et al.* (2010), apresentou os ornitossuquídeos como grupo irmão dos Poposauroidea, concordando, em termos gerais, com a proposta de França *et al.* (2011). Em sua tese de doutorado, França (2011) encontrou uma relação mais estreita entre Ornithosuchidae e Rauisuchia do que o presente em Nesbitt (2011), suportado por sete sinapomorfias (margem distal dos dentes posteriores convexos; crista sagital ao longo da linha média do corpo do parietal ausente; fenestra temporal com uma fossa anterior presente; angulação entre o processo posterior do atlas em relação ao processo lateral igual a 90°; a relação dorso-ventral da apófise espinhal e a altura máxima do centro vertebral são iguais ou menores; a porção distal da apófise neural é antero-ventralmente maior do que da metade de sua altura nas vértebras cervicais anteriores; púbis tem um comprimento igual ou maior que 70% da medida do fêmur). Ademais, este autor incluiu *Luperosuchus fractus*, (descrita como um 'rauissuquídeo' por Romer [1971] e Desojo & Arcucci [2009], com base no espécime PULR 057),

dentro de Ornithosuchidae, onde seria o grupo irmão de um clado composto por *Riojasuchus tenuiceps* e *Ornithosuchus longidens*, baseado na presença de um diastema entre o pré-maxilar e o maxilar.

von Baczko & Ezcurra (2013) vão apresentar um estado da arte do estudo do grupo dos Ornithosuchidae, onde vão interpretar o grupo como sendo composto apenas por *Ornithosuchus longiceps*, *Venaticosuchus rusconii* e *Riojasuchus tenuiceps*. Esta publicação vai ser seguida por alguns trabalhos revisando estes táxons (von BACZKO *et al.*, 2014; von BACZKO & DESOJO, 2016) com uma hipótese filogenética corroborativa onde Ornithosuchidae formado por um clado composto por *R. tenuiceps* mais *V. rusconii* com *O. longiceps* como grupo irmão e mais basal dentro de Pseudosuchia (Fig. 49).

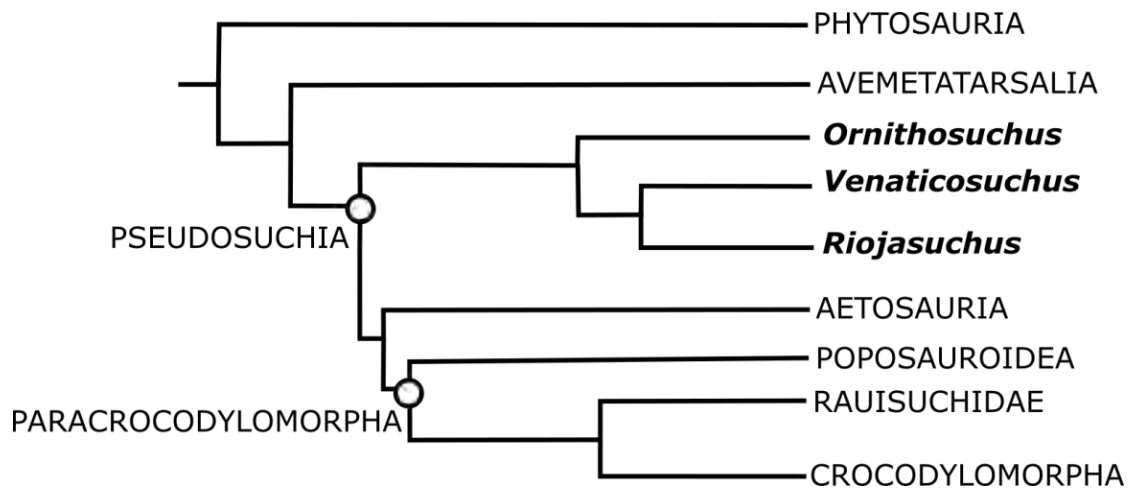


Figura 49. Cladograma simplificado redesenhado da proposta filogenética de von Baczko *et al.* (2014).

von Baczko & Ezcurra (2016) vão apresentar uma revisão taxonômica de *Ornithosuchus longiceps* e *Dasygnathoides longidens*, onde vão concluir que o holótipo de *Dasygnathoides* (= *Dasygnathus*) *longidens* e o parátipo (ELGNM 1 e 15) representam um arcossauriforme distinto que seria o maior predador descrito para o Triássico da Escócia, mas que não teria nenhuma autapomorfia com *Ornithosuchus longiceps*, o que tornaria este nome baseado em uma sinonímia como *nomen dubium*. Devido a isso, os autores consideram a denominação original de *Ornithosuchus woodwardi* como sendo válido.

6.3. Lista de Táxons de Ornithosuchidae (Fig.50).

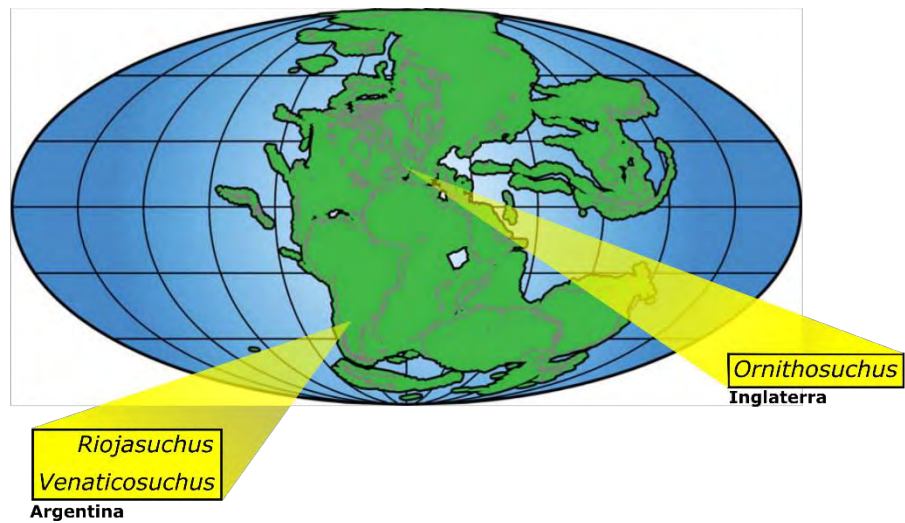


Figura 50. Distribuição global dos táxons atribuídos a Ornithosuchidae. Modificado de von Baczko & Ezcurra (2013).

Ornithosuchus longidens Newton, 1894

Holótipo (NHMUK PV R2409-2410): Um crânio quase completo (Fig. 51: A) associado a elementos de pós-crânio.

Espécimes referidos (WALKER, 1964 *sensu* von BAZCKO & EZCURRA, 2016):

NHMUK PV R3142: A maior parte de um crânio desarticulado, vértebras cervicais com osteodermos; vértebras caudais; vários osteodermos truncais e caudais; uma cintura escapular danificada; úmero direito; porção proximal de um rádio e ulna direitos; porção proximal de um úmero esquerdo; fragmentos de gastrália; vários fragmentos não identificáveis.

NHMUK PV R3143: Um sincrânio incompleto, composto apenas do rosto com a hemi-mandíbula direita completa e o dentário esquerdo em posição de articulação; um quadrado, quadrado-jugal, pterigoide, palatino e jugal direitos; um lacrimal, angular e esplenial esquerdos; vários osteodermos dorsais e fragmentos não identificáveis.

NHMUK PV R3149: Um crânio completo e a maioria do pós-crânio.

NHMUK PV R3561: Uma série de vértebras em posição de articulação, composto da nona dorsal até a parte da extremidade posterior da cauda, todas com osteodermos

em posição de articulação; uma cintura pélvica bem preservada; um fêmur direito; porção proximal de uma tíbia e fíbula direita; fêmur esquerdo.

NHMUK PV R3562: Um crânio incompleto e distorcido; dois osteodermos da série cervical.

NHMUK PV R3916: Uma sequência vertebral da quinta cervical até a primeira sacral, portando uma cobertura de osteodermos; a maior parte de uma cintura escapular; o apêndice locomotor anterior direito completo; úmero esquerdo; cintura pélvica incompleta; porção proximal do fêmur direito; bateria de gastrálias.

NHMUK PV R8170: Uma série de dez pequenas vértebras dorsais com costelas em posição de articulação e cobertura de osteodermos; uma escápula, coracóide e úmero esquerdo.

GSM 91072-78, GSM 91080-81, GSM 91085-86: Uma série de pequenas vértebras em posição de articulação com osteodermos pareados; impressão de elementos de um apêndice locomotor anterior/ dois fêmures com a porção distal ausente.

MANCH 8271: Parte de um crânio, porção posterior da série cervical e/ou truncal; osteodermos; escápula direita e a maior parte de um apêndice locomotor anterior.

Localidade e Horizonte estratigráfico: Pedreiras Findrassie, Lossiemouth West & East e Spynie (principal), Area de Elgin, Moray, noroeste da Escócia (HUXLEY, 1877; NEWTON, 1894; WALKER, 1964). Formação Lossiemouth, Eocarniano-Neonoriano (WALKER, 1964; von BACZKO; EZCURRA, 2013).

Idade: Neocarniano-Eonoriano.

Discussão: Esta espécie é conhecida por uma série de espécimes que apresentam diferentes fases ontogenéticas. Difere dos outros táxons dentro de Orntihosuchidae pela presença de poucas “ornamentações” na superfície dorsal dos frontais, parietais e nos processos anteriores dos pós-orbitais, representadas por endorelevos; extremidade posterior do osso maxilar bifurcada; pós-orbital com uma pronunciada crista central horizontalizada; mandíbula inferior com uma margem ventral côncava e elevada; forâmen supra-angular posicionado próximo da sutura supra-angular com o angular (SERENO, 1991; NESBITT, 2011).

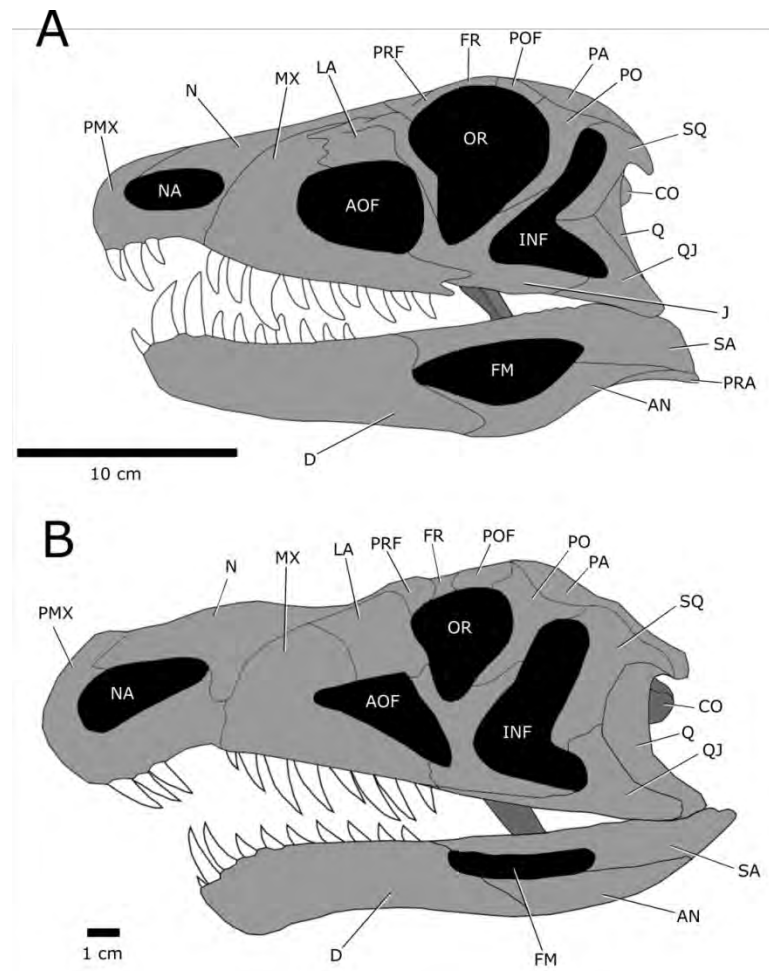


Figura 51. Desenhos esquemáticos dos crânios de *Ornithosuchus longidens* e *Riojasuchus tenuiceps*, modificado de Sereno (1991) com alterações em *R. tenuiceps* baseado em von Bazcko & Desojo, (2016). Abreviações: AN, Angular; AR, Articular; AOF, Fenestra antero-orbital; AOFO, fossa antero-orbital; CO, côndilo occipital; D, Dentário; EXO, Exo-occipital; FM, Fenestra mandibular; FR, Frontal; INF, Fenestra Infra-temporal; J, Jugal; LA, Lacrimal; MX, maxilar; NA, narina externa; N, nasal; OP, opistótico; OR, órbita; PA, parietal; PAP, processo palatal; PMX, pré-maxilar; PO, pós-orbital; PRF, pré-frontal; Q, quadrado; QJ, quadrado-jugal; SA, supra-angular; SQ, esquamosal; SUP, fenestra supra-temporal.

Riojasuchus tenuiceps Bonaparte, 1967

Holótipo (PVL 3827): um crânio completo com a hemi-mandíbula direita em posição de articulação e a esquerda desarticulada (Fig. 51: B); 19 vértebras pré-sacrais, três sacrais e quatro caudais, com osteodermos em posição de articulação em algumas sequências cervicais e truncais; escapula-coracoides incompletos; úmero incompleto; a porção distal de um rádio e ulna esquerdos em posição de articulação

com alguns carpais; um íleo e púbis esquerdo; uma tíbia e fíbula esquerdas que se articulam com um autopódio posterior completo (von BACZKO & DESOJO, 2014).

Espécimes referidos:

PVL 3828: Um crânio incompleto, onde falta os pré-maxilares, os nasais, o jugal e lacrimal esquerdo, ambos os esquamossais; uma mandíbula em posição de articulação onde faltam o surangular esquerdo e o angular e articular esquerdo; 20 vértebras pré-sacrais, 12 caudais; scapulacoracóides, úmeros, rádios e ulnas incompletos; um elemento carpal isolado; um íleo esquerdo; um ísquio esquerdo fragmentário; fêmur esquerdo; fêmur, tíbia e fíbula direitos e incompletos; calcâneo esquerdo e várias falanges desarticuladas.

PVL 3826: 19 vértebras pré-sacrais e nove caudais, parcialmente articuladas, dois escapulo-coracóides fragmentários; um úmero direito; fragmentos de um rádio e de uma ulna; íleo direito incompleto; porção distal de um fêmur esquerdo e uma tíbia incompleta.

PVL 3814: Algumas vértebras isoladas, porção proximal de um úmero; fragmentos de uma tíbia e vários osteodermos isolados

Horizonte Estratigráfico: Formação Los Colorados, Bacia Ischigualasto-Vila Unión,

Localidade: Quebrada de Los Jachaleros, Depto. Lavalle, Província de La Rioja, noroeste da Argentina (BONAPARTE, 1972).

Idade: Noriano.

Discussão: Este táxon difere dos outros ornitossuquídeos pela presença das seguintes características: a porção anterior do rostro projetada anteriormente, ultrapassando o comprimento da mandíbula; fossa antero-orbital profunda que invade o processo horizontal da maxila; base do arco neural do atlas se articulando na porção medial da vértebra (von BACZKO & EZCURRA, 2013), modificado de Sereno, (1991) e Nesbitt, (2011).

Venaticosuchus rusconii Bonaparte 1970

Holótipo (PVL 2578): referente a um rostro com mandíbula (Fig. 52), um apêndice locomotor anterior incompleto e alguns osteodermos originalmente descritos em

Bonaparte (1970, 1975), embora, atualmente, todos os elementos pós-cranianos estejam perdidos (von BACZKO & EZCURRA, 2013; von BACZKO *et al.*, 2014).

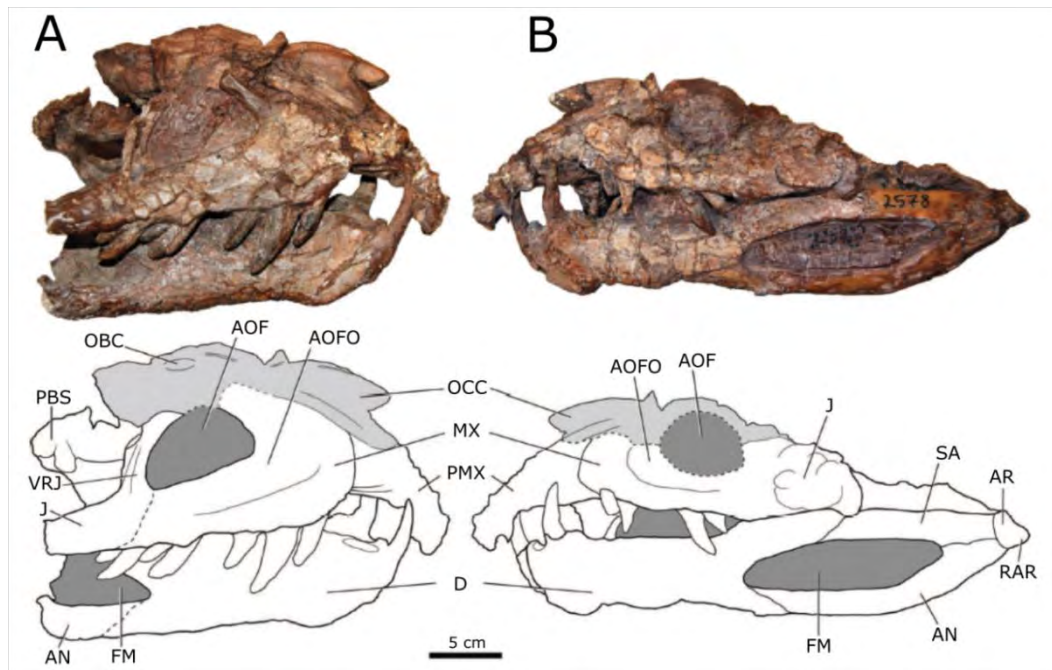


Figura 52. Fotografias e desenhos interpretativos do holótipo (PVL 2578) de *Venaticosuchus rusconii* em vistas lateral direita (A) e esquerda (B). Modificado de von Baczko *et al.* (2014). AN, angular; AR, articular; AOF, fenestra antero-orbital; AOFO, fossa antero-orbital; D, Dentário; EXO, Exo-occipital; FM, Fenestra mandibular; J, Jugal; MX, maxilar; NA, narina externa; N, nasal; OBC, contra-molde da bula olfativa; OCC, contra-molde do canal olfativo; PMX, pré-maxilar; PRF, SA, supra-angular; SQ, esquamosal; RAR, processo retro-articular do articular VRJ, ramo vertical do jugal.

Horizonte Estratigráfico: Porção central da Formação Ischigualasto (von Baczko *et al.*, 2014)

Localidade: Hoyada del Cerro Las Lajas, Província de La Rioja (Bonaparte, 1975; von Baczko *et al.*, 2014).

Idade: Eocarniano-Neonoriano

Discussão: Em sua descrição original, Bonaparte (1970) apresentou três características que diferenciavam *Venaticosuchus rusconii* de *Riojasuchus tenuisiceps* (os dentes do maxilar “mais fortes”; mandíbula proporcionalmente mais

dorso-ventralmente altas e fenestra mandibular comparativamente maior) e duas de *Ornithosuchus longidens* (a constrição do pré-maxilar seria mais atenuada e a porção pré-orbital do crânio seria mais estreita em vista dorsal). Em sua revisão do táxon, von Baczko *et al.*, (2014) consideraram estas variações como não informativas por serem demasiadamente vagas. A única autapomorfia que estes autores propõem que distingue este táxon dos outros ornitossuquídeos seria a ausência de um forame no surangular.

7. ERPETOSUCHIDAE

O clado Erpetosuchidae Watson, 1917 (*sensu* Nesbitt & Butler, 2012) é um grupo pouco conhecido de arcossauros de afinidades filogenéticas controversas. (BENTON & WALKER, 2002; NESBITT & BUTLER, 2012). O grupo é composto por *Erpetosuchus granti* Newton 1894 e *Parringtonia gracilis* (NESBITT & BUTLER, 2012) com *Dyoplax arenaceus* tentativamente atribuído (MAISCH *et al.*, 2013). Estes táxons são formas pequenas que apresentam um crânio baixo, mas alongado antero-posteriormente, em vista lateral, com uma fenestra antero-orbital posicionada mais ventralmente margeada por uma crista bem marcada e dentes sem serrilhas, concentrados apenas na porção anterior da mandíbula. Também apresentam uma cobertura de osteodermos que possuem vários endorelevos e cristas em sua superfície dorsal (NESBITT & BUTLER, 2012).

O grupo foi originalmente denominado por Watson (1917) para incluir *Erpetosuchus granti* Newton 1894, da Formação Lossiemouth, da Escócia, Grã-Bretanha, do Neotriássico (final do Carniano/ início do Noriano). Esta espécie é representada por vários espécimes, a maioria é representada apenas como um contramolde em blocos de rocha, com poucos fragmentos de material osteológico preservado (BENTON & WALKER, 2012). Em sua descrição original, Newton (1894) utilizou moldes feitos com borracha de látex e modelos esculpidos em gesso do crânio e da mandíbula do holótipo (NHMUK R3139) para fins de estudo, replicagem e exposição. Alick Walker, durante os anos 1950-60, re-estudou a espécie, utilizando técnicas e materiais mais modernos na fabricação dos moldes, como policloreto de vinil (PVC), o que produziu réplicas com uma maior clareza de detalhes. Também avançou na preparação mecânica dos espécimes, mas muitos detalhes foram

perdidos ao longo do tempo devido ao desgaste decorrente do processo de fabricação dos moldes (BENTON; WALKER, 2002).

A segunda espécie é *Parringtonia gracilis*, do Mesotriássico (final do Anisiano) do Membro Lifua da formação Manda da Tanzânia, descrita por Huene (1939). Esta é representada apenas por um único espécime incompleto (NHUMK R8646), composto por uma maxila direita e elementos pós-cranianos incompletos e desarticulados. Historicamente, este representa um dos únicos arcossauro descrito para a Formação Manda (ver “Mandasuchus”, nas páginas 43-44).

Um terceiro táxon tentativamente referido ao grupo (e.g. WALKER, 1961; MAISCH *et al.*, 2013) seria *Dyoplax arenaceus*, do Neotriássico (Neocarniano) da parte superior do Schilfsandstein da Formação Stuttgart, na Alemanha (MAISCH, *et al.*, 2013). O único espécime conhecido é o holótipo (SMNS 4760) que é representado por um esqueleto quase completo, faltando as porções distais dos apêndices locomotores e a ponta da cauda, preservado como um contramolde natural em arenito. Entretanto, como será apresentado ao longo desta sessão, esta designação é complicada.

7.1. Estado da Arte

Em sua descrição de *Erpetosuchus granti*, Newton (1894) considerou que este seria um arcossauro de um crânio com rostro alongado, um teto craniano baixo e as aberturas em padrão similar aos de *Teleosaurus cadomensis* Geoffrey, 1825, um mesossuquídeo descrito para o Mesojurássico. O autor considerou que *E. granti* teria afinidade maior com fitossauros (que, naquela época, ainda era considerado como um membro de Crocodilia) porque apresentava um palato menos desenvolvido e uma cintura escapular mais próximos aos do aetossauro *Stagonolepis robertsoni* Agassiz, 1884 e os do gênero *Phytosaurus*, enquanto que as vértebras e os apêndices locomotores eram similares aos crocodilianos.

Boulenger (1904) descreveu alguns espécimes preservados como impressão em fragmentos de rochas que foram atribuídos à *Ornithosuchus woodwardi*, mas uma peça apresentava uma clavícula, atribuível ao táxon previamente mencionado, mas com a impressão de uma interclavícula em formato de “ponta de flecha”, que foi

atribuído a “*Herpetosuchus granti*” (= *Erpetosuchus granti*)⁷, considerado por Krebs [1976] como *lapsus kalami*.

Broom (1906) descreveu alguns elementos pós-cranianos atribuídos ao táxon *Erythrosuchus africanus* e considerou que este fazia parte do grupo dos fitossauros. Entre os materiais descritos, o autor concluiu que a escápula e o coracóide direto apresentavam similaridades com os de *Herpetosuchus* (= *Erpetosuchus*) *granti*, onde o coracóide seria proporcionalmente menor do que o restante da escápula. Alguns anos depois, Broom (1913) apresentou maiores detalhes sobre as afinidades de *E. granti*, mas concordou com a proposta de Newton (*aput. cit.*) que o táxon apresentava afinidades mais próximas com os fitossauros e os aetossauros.

Watson (1917) propôs a família Erpetosuchidae para incluir *Erpetosuchus granti*, dentro da Ordem Thecodontia e considerou como próximo aos Crocodilia. Huene (1936) reconheceu *E. granti* como fazendo parte de Pseudosuchia, mas não utilizou a família Erpetosuchidae, não apresentando justificativa pela escolha.

Huene (1920) em seu trabalho sobre a osteologia do aetossauro *Aetosaurus ferratus* Fraas, 1887 vai discutir também o táxon problemático *Dyoplax arenaceus* Fraas, 1867. Este táxon da Formação Schilfsandstein, Neotriássico (Carniano) da Alemanha, segundo o autor, apresenta similaridades de crânio, de escápula e porta duas fileiras de osteodermos similar aos de *Erpetosuchus granti*, o que indicaria uma afinidade filogenética próxima.

Huene (1939) descreveu *Parringtonia gracilis*, que o autor atribuiu grupo dos Pseudosuchia. Para ele, este táxon apresentaria similaridades com o ornitossuquídeo *Ornithosuchus woodwardi* (*sensu* von BACKZCO *et al.*, 2016) e o crocodilomorfo não-crocodiliforme *Saltoposuchus connectens* Huene, 1921. Todavia, considerou que o único espécime, representado pelo holótipo, não apresentava material suficiente para determinar com precisão suas afinidades filogenéticas.

Romer (1956) tentativamente colocou *Erpetosuchus granti* e *Parringtonia gracilis* na Família Ornithosuchidae, junto com outras formas do Triássico que não apresentavam fácil classificação (*e.g.* *Prestosuchus chiniquensis*) e que não

⁷ *Herpetosuchus* aparece primeiro em Boulenger (1904) e depois é repetido por Broom (1906), todavia, não existe justificativa para esta troca. Devido a isso, Walker (1970) e Krebs (1976) consideraram que seria um caso de *lapsus kalami* (um erro acidental de escrita).

apresentavam uma cobertura extensa de osteodermos suficiente para serem considerados próximos aos aetossauros. Dez anos depois, Romer (1966) vai apresentar uma nova proposta onde vai utilizar a Família Erpetosuchidae como sendo uma parte da Ordem Pseudosuchia composta por *E. granti*, *P. gracilis*, *Dibothrosuchus elaphros* Simmons, 1965; *Hesperosuchus agilis* Colbert, 1952, *Saltoposuchus connectens*, *Stegomosuchus longipes* Emerson & Loomis, 1904, *Strigosuchus licinus* Simmons, 1965, *Cerritosaurus binsfeldi* Price 1946, *Rhadinosuchus gracilis* Huene, 1942 e *Dyoplax arenaceus*, sendo estes dois últimos atribuídos tentativamente.

Walker (1961) igualmente considerou que *Dyoplax arenaceus* e *Erpetosuchus granti* apresentam uma correlação filogenética próxima e junto com *Stegomosuchus longipes* os considerou na Família Erpetosuchidae. Posteriormente, Walker (1968) alterou sua proposta e interpretou *E. granti* como apresentando afinidades mais próximas a linhagem que posteriormente iria dar origem aos crocodilianos, com base na presença de um coracóide com um processo posterior estendido e um espaço entre o epipódio e o autopódio anterior que teria sido ocupado por carpais alongados. O autor vai preliminarmente propor a Ordem Crocodylomorpha, que seria composta pelas subordens Paracrocodylia, Pedeticosauria e Erpetosuchia, este último composto por *E. granti* e *D. arenaceus*. Todavia, o mesmo vai voltar atrás (WALKER, 1970) e retirar *E. granti* da linha evolutiva dos crocodilianos e re-interpretar com sendo um pseudussuquídeo basal, justificando que esta troca foi devido a uma re-interpretação das características que suportavam a hipótese prévia (i.e. altura do quadrado, forma do entalho ótico um a constrição na porção central do corpo do coracóide) como sendo casos de convergência e dificuldade de interpretação devido a preparação insuficiente de espécimes (WALKER, 1970).

Krebs (1965) em sua descrição do “rauissuquídeo” *Ticinosuchus ferox* apontou similaridades entre a escápula de *Erpetosuchus granti* e *Parringtonia gracilis*. O mesmo autor apresentou depois (KREBS, 1976) uma diagnose formal para a Família Erpetosuchidae, que seria composta apenas por *E. granti* e *P. gracilis*, fazendo parte de Pseudosuchia e com afinidades filogenéticas com outras formas de filogenia não bem entendida, como *Euparkeria capensis* e *Ornithosuchus woodwardi*.

Bonaparte (1982) vai apresentar uma proposta análoga a de Walker (1968) para a evolução dos Thecodontia, onde a Família Erpetosuchidae teria uma maior afinidade com crocodilomorfos, fazendo parte da Subordem Sphenosuchia, junto com as famílias Trialestidae e Sphenosuchidae. Esta subordem seria composta por formas ancestrais da linhagem dos crocodilianos e, curiosamente, das aves (Fig. 53).

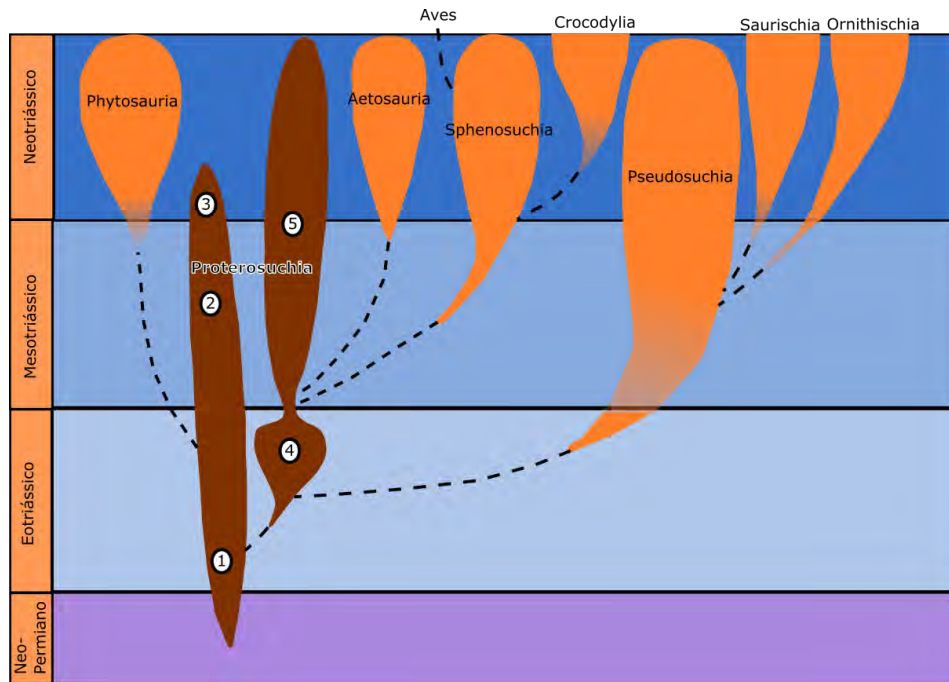


Figura 53. Filogenia de Thecodontia e sua distribuição temporal modificada de Bonaparte (1982). Os números dentro de Proterosuchia representam: 1) Proterosuchidae; 2) Cerritosauridae; 3) Proterochampsidae; 4) Erythrosuchidae e 5) Rausuchidae.

Olsen *et al.* (2000) descreveram um crânio e mandíbula incompletos do Neotriássico (Noriano) da Formação New Haven, Bacia de Hartford, nordeste dos Estados Unidos. Este espécime (AMNH 29300) apresentou várias similaridades com *Erpetosuchus granti* (e.g. dentes restritos apenas na porção anterior da maxila, ampla fossa antero-orbital com um perímetro formado por cristas ósseas altas), mas devido a incompletude do material, optaram por manter a atribuição apenas a *Erpetosuchus* sp. Neste trabalho, os autores testam através de metodologias cladísticas as relações filogenéticas de *E. granti*, utilizando uma matriz de 33 caracteres e encontraram como sendo grupo irmão de Crocodylomorpha.

Benton & Walker (2002) apresentaram uma revisão detalhada do táxon *Erpetosuchus granti*, e realizaram uma análise cladística com base em uma matriz modificada de Olsen *et al.* (2000) onde *E. granti* apareceu como grupo irmão de Crocodylomorpha. Os autores não consideraram *Parringtonia gracilis* como um membro de Erpetosuchidae, argumentando que as similaridades com *E. granti* seriam plesiomórficas para Archosauria. Em sua análise sobre a filogenia dos grupos de arcossauros, Brusatte *et al.* (2010) incluíram *E. granti*. Esta análise encontrou o táxon como grupo irmão de Crocodylomorpha, compondo um clado, junto com *Gracilisuchus stipanicorum*, que seria o grupo irmão de Aetosauria. Nestas três análises, a condição de *E. granti* como grupo irmão de Crocodylomorpha é suportada por três caracteres: a ausência de um elemento pós-frontal; um parietal completamente fusionado e o quadrajugal/quadrado apresentando uma inclinação anterodorsal.

Nesbitt e Butler (2012) revisaram *Parringtonia gracilis* e apresentaram uma definição filogenética para Erpetosuchidae, que seria composto por *P. gracilis* + *Erpetosuchus granti* e o espécime descrito por Olsen *et al.* (2000) como *Erpetosuchus sp.*. Os autores não incluíram *Dyoplax areneus* porque, apesar de apresentar similaridades, como os osteodermos, muita da informação está perdida devido à péssima condição do único espécime e os caracteres comuns que são identificáveis são muito difundidos nos pseudossuquídeos. Entretanto, os autores não descartaram a possibilidade de este táxon pertencer a Erpetosuchidae caso novos espécimes sejam descobertos.

A afinidade do clado com Crocodylomorpha foi questionada por Nesbitt e Butler (2012), já que os caracteres que suportavam a afinidade eram problemáticos (e.g. o parietal único não pode ser verificado com clareza porque o único crânio que apresenta este elemento está preservado como um contramolde, o que não poderia preservar a sutura entre os dois elementos caso esta não fosse muito pronunciada). Para testar as afinidades filogenéticas, Erpetosuchidae foi incluído em uma matriz modificada de Nesbitt (2011) e análise resultou com o clado aparecendo como grupo irmão de diferentes clados de Archosauria. Devido a isso, os autores consideraram que mais informações a partir de novos espécimes seriam necessários para esclarecer as afinidades filogenéticas de Erpetosuchidae.

Maisch e colaboradores (2013) apresentaram uma revisão de *Dyoplax arenaceus* e concluíram que o táxon seria muito similar a Erpetosuchidae, com base na morfologia dos osteodermos e na presença de uma fenestra antero-orbital, presente em uma fossa antero-orbital profunda e circundada por uma crista, que é posicionada mais póstero-ventralmente no rosto. De forma independente a de Nesbitt e Butler, (2012) e sem utilizar uma análise cladística, argumentaram que *Erpetosuchus granti* seria o táxon mais morfologicamente próximo a *D. arenaceus*, mas com diferenças em alguns fatores (e.g. dimensões da fenestra antero-orbital, participação do jugal na fenestra antero-orbital e padrão de fusão do parietal) mas muita informação osteológica estaria faltando para uma atribuição taxonômica mais precisa. Por fim, os autores consideraram que *D. arenaceus* poderia ser atribuído, com ressalvas, a Erpetosuchidae.

8.2. Lista de Táxons de Erpetosuchidae (Fig. 54)

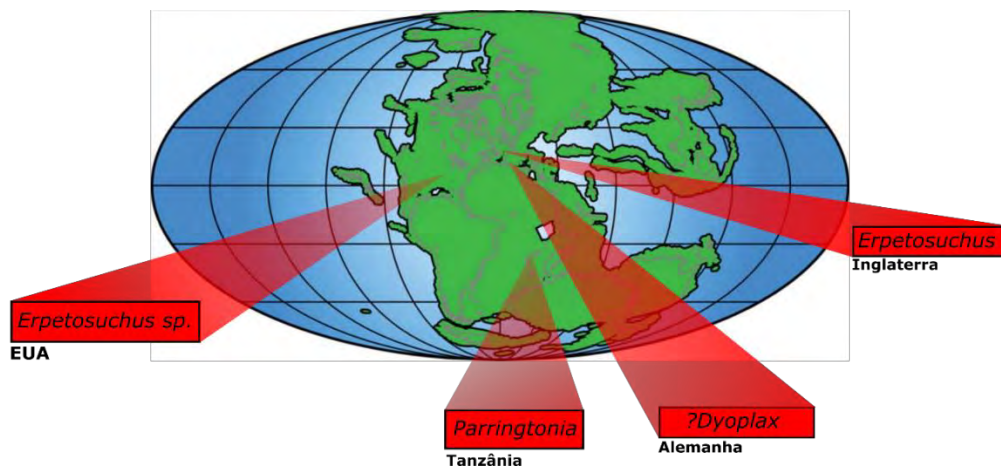


Figura 54. Distribuição global dos táxons atribuídos Erpetosuchidae. Modificado de Nesbitt & Butler (2012).

Erpetosuchus granti Newton, 1894

Holótipo (NHMUK R3139): Um crânio e mandíbula praticamente completo, vertebrae cervicais e da porção anterior da sequência truncal, cintura escapular e os apêndices locomotores anteriores (Fig.55). Estes são representados como impressão nas rochas.

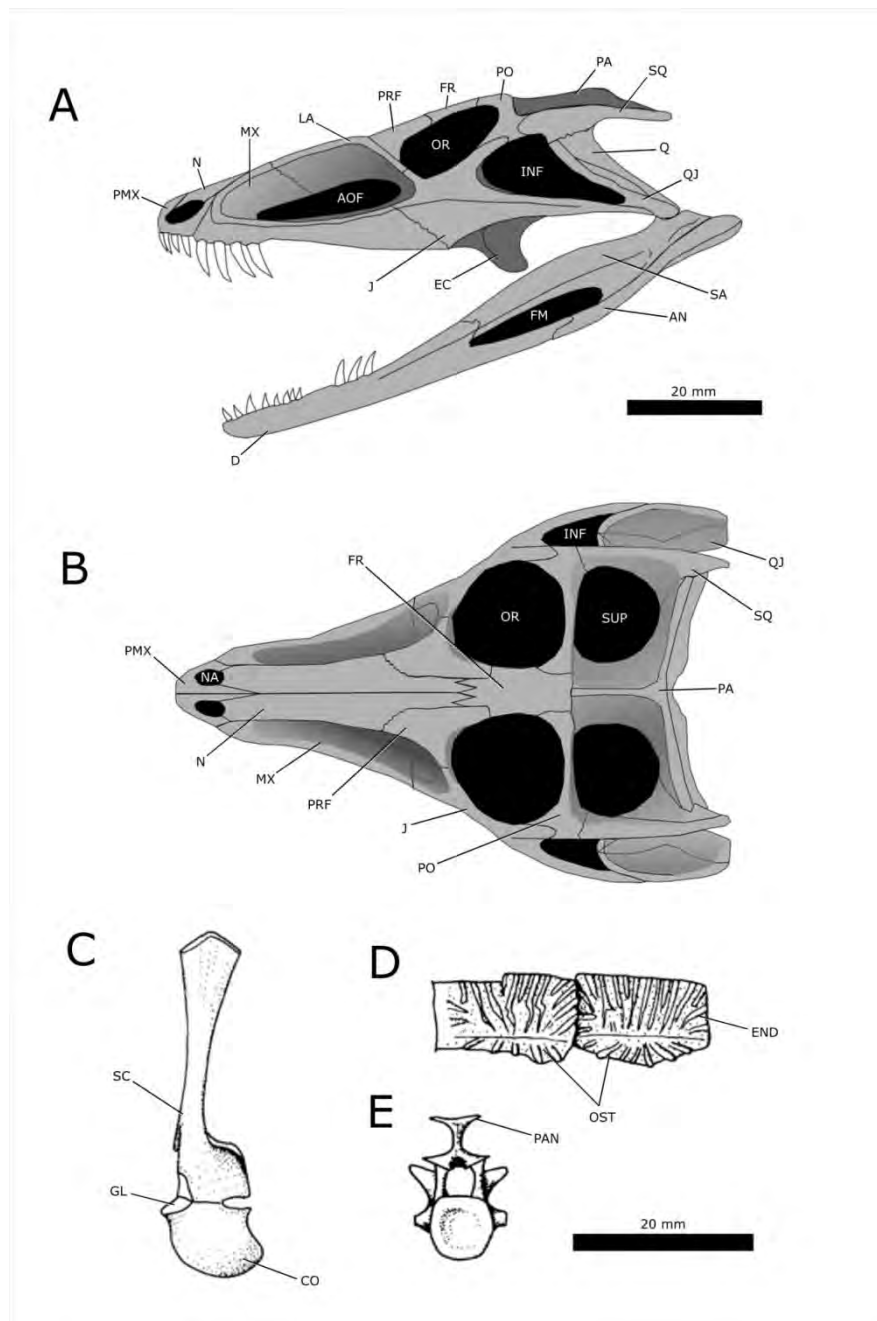


Figura 55. Ilustrações esquemáticas dos diferentes elementos de *Erpetosuchus granti*. Reconstituição do crânio em vista lateral esquerda (A) e dorsal (B); Porção direita da cintura escapular em vista lateral (C); Osteodermas dorsais em vista lateral (D); Vértebra trunca em vista anterior (E). Figuras modificadas de Benton & Walker (2012). Abreviaturas: AN, angular; AOF, fenestra antero-orbital; CO, coracóide; D, Dentário; EC, Ecto-pterigóide; END, endo-relevos; EXO, Exo-occipital; FM, fenestra mandibular; FR, frontal; GL, cavidade glenóide; INF, fenestra infra-temporal; J, Jugal; LA, lacrimal; MX, maxilar; N, nasal; NA, narina externa; OR, órbita; OST, osteodermos; PA, parietal; PAN, plataforma dorsal da apófise neural; PMX, pré-maxilar; PRF pré-frontal; Q, quadrado; QJ, quadrado-jugal; SA, supra-angular; SC, escápula; SQ, esquamosal; SUP, fenestra supra-temporal.

Espécimes referidos:

NMS 1966.43.4A e B: Parte e contraparte de uma pequena área da região dorsal do corpo, com osteodermos e costelas associadas;

NMS 1992.37.1: fragmento de uma sequência cervical com osteodermos associados;

NHMUK R4807: Uma laje com a impressão de vértebras em posição de articulação.

Localidade e Horizonte estratigráfico: *Lossiemouth East & West Quarries*, Eglin, Escócia. Formação Lossiemouth, Neotriássico (von BAZCKO & EZCURRA, 2013).

Idade: Problemático. É estabelecida uma idade Neotriássico (Eocarniano-Neonoriano) para a Formação Lossiemouth, mas é impossível estabelecer algo mais preciso porque não existe um controle bioestratigráfico para as ocorrências dos fósseis de *Erpetosuchus granti*.

Discussão: Este táxon difere dos outros arcossauros por apresentar os seguintes caracteres: dentes localizados apenas na porção anterior do maxilar; uma grande fenestra antero-orbital localizada dentro de uma fossa profunda cujas margens são bem delimitadas por cristas; jugal forma um par de superfícies abaixo da órbita, separados por uma crista longitudinal distinta, a primeira é direcionada dorso-lateralmente e a outra ventralmente, com uma leve torção lateral; um entalhe ótico profundo abaixo da curvatura do esquamosal, formado pelo quadrado-jugal e o jugal, seguindo até a parede lateral do neurocrânio; angular e surangular marcados por uma crista bem distinta; seis dentes ovais, em corte transversal, não apresentando serrilhas (BENTON & WALKER, 2002).

Erpetosuchus sp. Olsen, *et al.* 2000

AMNH 29300: A maior parte da porção direita de um sincrânio (Fig. 56). Toda a porção dorsal e o neurocrânio não foram preservados.

Localidade e Horizonte estratigráfico: Cheshire, Connecticut, Nordeste dos Estados Unidos, Formação New Haven (Grupo Chatham) (OLSEN, *et al.* 2000; NESBITT & BUTLER, 2012).

Idade: Neotriássico (Noriano)

Discussão: Olsen *et al.* (2000) atribuíram uma afinidade filogenética deste espécime com *Erpetosuchus granti* com base nas seguintes sinapomorfias: presença de nove alvéolos no maxilar; dentes maxilares restritos apenas na porção anterior do osso; o jugal forma uma plataforma lateral ampla com uma superfície mais estreita direcionada dorso-lateralmente e outra direcionada ventralmente e lateralmente; o perímetro da fossa antero-orbital delimitado por cristas e a presença de uma crista lateral no ramo mandibular, após a fenestra mandibular.

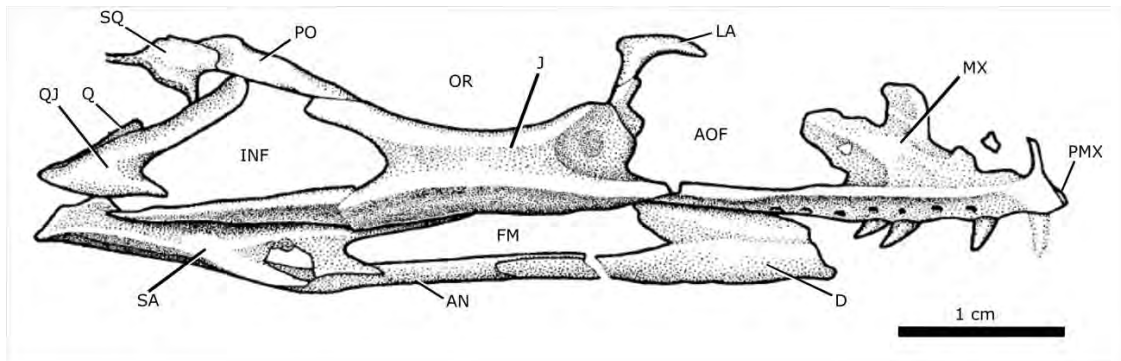


Figura 56. Ilustração esquemática do espécime AMNH 29300 em vista lateral direita. Modificado de Olsen *et al.* (2000). Abreviaturas: AN, angular; AOF, fenestra antero-orbital; D, dentário; FM, fenestra mandibular; INF, fenestra infra-temporal; J, Jugal; LA, lacrimal; MX, maxilar; N, nasal; NA, narina externa; OR, órbita; PO, pós-orbital; PMX, pré-maxilar; PRF pré-frontal; Q, quadrado; QJ, quadrado-jugal; SA, supra-angular; SQ, esquamosal; SUP, fenestra supra-temporal.

Parringtonia gracilis Huene, 1939

Holótipo (NHMUK R8646): Uma maxila direita incompleta, dois centros vertebrais da sequência truncal, dois arcos neurais incompletos da mesma sequência, três vértebras caudais, cinco osteodermos, uma escápula esquerda com a porção distal faltando e um fragmento tentativamente identificado como uma porção proximal de um ísquio (Fig. 57).

Localidade e Horizonte estratigráfico: Localidade B15/1, Mkonoleko/ Njalila, noroeste de Songea, Vale do Ruhuhu, região de Ruvuma, sudoeste da Tanzânia. O exato nível estratigráfico é desconhecido, mas foi coletado no Membro Lifua da Formação Manda, que é correlacionável a Subzona C da Zona de Associação de *Cynognathus* da Bacia do Karoo, na África do Sul (e.g. HANCOX, 2000; ABDALA *et al.*, 2005).

Idade: Mesotriássico (Neoanisiano).

Discussão: *Parringtonia gracilis* compartilha com *Erpetosuchus granti* a presença das seguintes sinapomorfias: dentição restrita apenas na porção anterior do maxilar; uma expansão mediolateral da porção posterior da maxila e uma depressão profunda, orientada anteroposteriormente, na superfície dorsal das apófises neurais. Krebs (1976) considerou que a única diferença entre os dois táxons era o tamanho, mas Nesbitt & Butler (2012) indicaram que *P. gracilis* apresentava as seguintes diferenças: cinco dentes maxilares; presença de um pequeno tubérculo na superfície lateral da escápula, posicionado distalmente à fossa glenóide e osteodermos com formato mais quadrado do que sub-retangular. Ademais, *P. gracilis* difere do espécime AMNH 29300 por apresentar cinco ao invés de seis dentes na maxila.

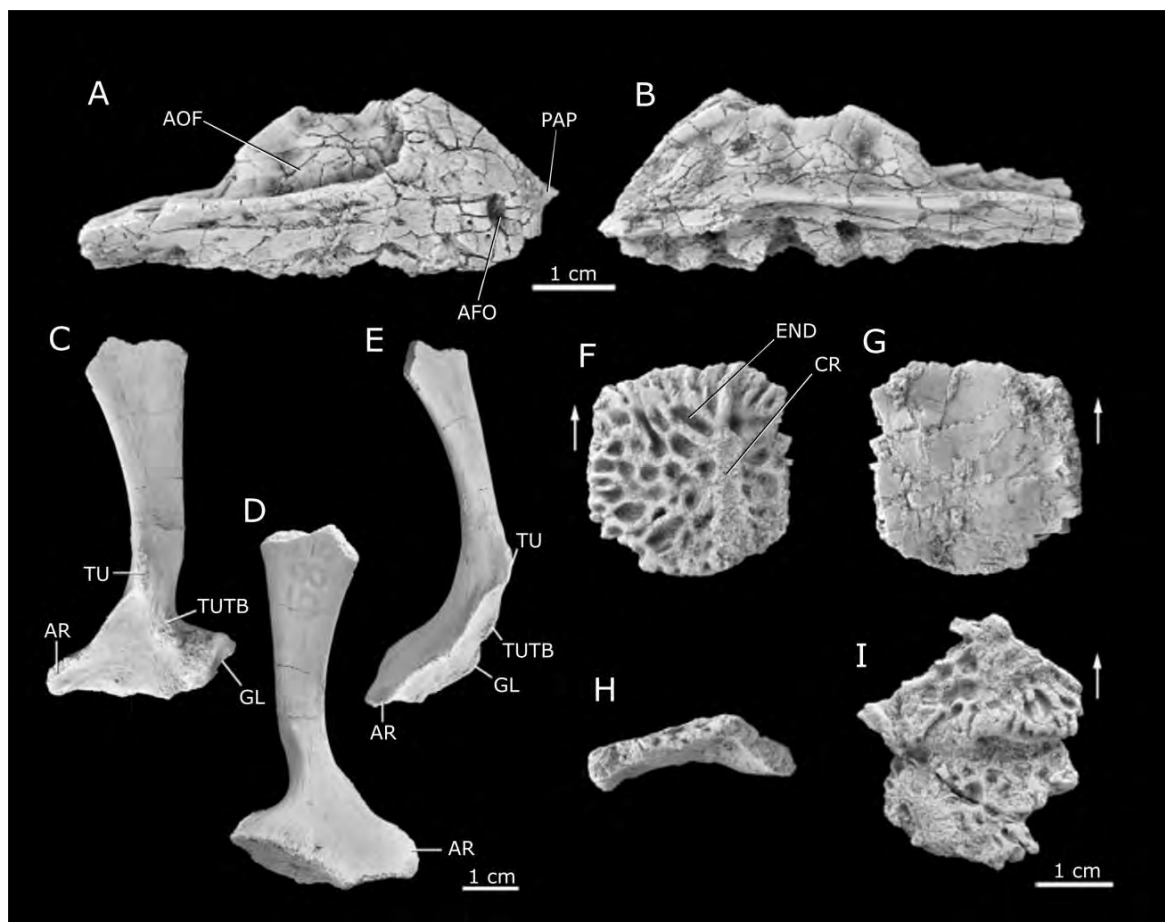


Figura 57. Fotografias de alguns elementos do holótipo (NHMUK R8646) de *Parringtonia gracilis*. Maxila direita em vista lateral (A) e medial (B); Escápula esquerda em vista lateral (C), medial (D) e anterior (E); osteodermo paramedial e dorsal em vista dorsal (F), ventral (G) e anterior (H); dois osteodermos em posição de articulação (I). As setas indicam o sentido do crânio. Modificado de Nesbitt & Butler (2012). Abreviaturas: AFO, forame anterior; AOF, fenestra antero-orbital; AR,

processo acrômio; CR, cristas do osteodermo; END, endo-relevo; GL, fossa glenóide; TU, tuberosidade; TUTB, tubérculo para a inserção do músculo *m. tríceps brachii*; PAP, processo palatal.

Discussão: *Parringtonia gracilis* compartilha com *Erpetosuchus granti* a presença das seguintes sinapomorfias: dentição restrita apenas na porção anterior do maxilar; uma expansão mediolateral da porção posterior da maxila e uma depressão profunda, orientada anteroposteriormente, na superfície dorsal das apófises neurais. Krebs (1976) considerou que a única diferença entre os dois táxons era o tamanho.

Dyoplax arenaceus Fraas, 1867

Holótipo (SMNS 4760): Um contramolde natural de arenito representando um esqueleto quase completo e em posição de articulação, com as porções distais dos apêndices locomotores e da ponta da cauda ausentes (Fig 58).

Localidade e Horizonte estratigráfico: *Leins'scher* Steinburch na “*Sonnenberg*”, Stuttgart, Baden-Württemberg, sudoeste da Alemanha (MAISCH, et al., 2013). Porção superior da *Schilfsandstein*, Formação Stuttgart.

Idade: Neotriássico (Neocarniano).



Figura 58. Fotografia do holótipo (SMNS 4760) de *Dyoplax arenaceus*.

Discussão: Apesar de representar um indivíduo praticamente completo e em posição de articulação, a preservação não permite a identificação de detalhes como suturas e outras estruturas osteológicas mais delicadas. Também, existe uma diferença na preservação do crânio, onde não está claro se o este está preservado apenas como um molde interno ou se é a superfície externa do molde externo que ficou exposto devido à remoção/erosão da cobertura da matriz (NESBITT &

BUTLER, 2013). As ilustrações presentes na descrição de Fraas (1867) parecem indicar que originalmente algumas estruturas eram mais evidentes, o que torna possível que devido ao manejo e a fabricação de réplicas ao longo de mais de 150 anos desde sua descoberta pode ter havido desgaste de estruturas que já eram mal preservadas. Segundo Maisch *et al.*, (2013), a diagnose do táxon seria: um crânio baixo e triangular; pré-maxila com um longo processo postero-dorsal que separa o nasal por um comprimento considerável; nasais, frontais e parietais pareados; uma fenestra antero-orbital de formato oval, baixa, antero-posteriormente alongada, inserida em uma fossa profunda que é circundada por uma crista bem marcada; a fenestra antero-orbital não faz contato com o nasal e o jugal; um jugal profundo e robusto, com uma crista distinta que separa as superfícies ventro-lateral da dorso-lateral; corpo coberto por duas fileiras de osteodermos paramediais; osteodermos laterais presentes na região cervical. As possíveis sinapomorfias entre *Erpetosuchus granti* e *Dyoplax arenaceus* seriam a morfologia da fenestra antero-orbital e os osteodermas, que segundo Nesbitt e Butler, apresentam cristas e endorelevos compatíveis com os de *E. granti* e *P. gracilis*. Entretanto, a preservação do espécime torna a demarcação das suturas e outras atribuições problemáticas (*i.e.*, uma dentição possivelmente limitada só na porção anterior da mandíbula conforme sugerido por MAISCH *et al.*, [2013]) (FIG. 59.) e, o consenso é que são necessários novos espécimes com uma preservação melhor para permitir uma atribuição taxonômica mais segura. (*e.g.*, BENTON; WALKER, 2002; NESBITT; BUTLER, 2012; MAISCH *et al.*, 2013)

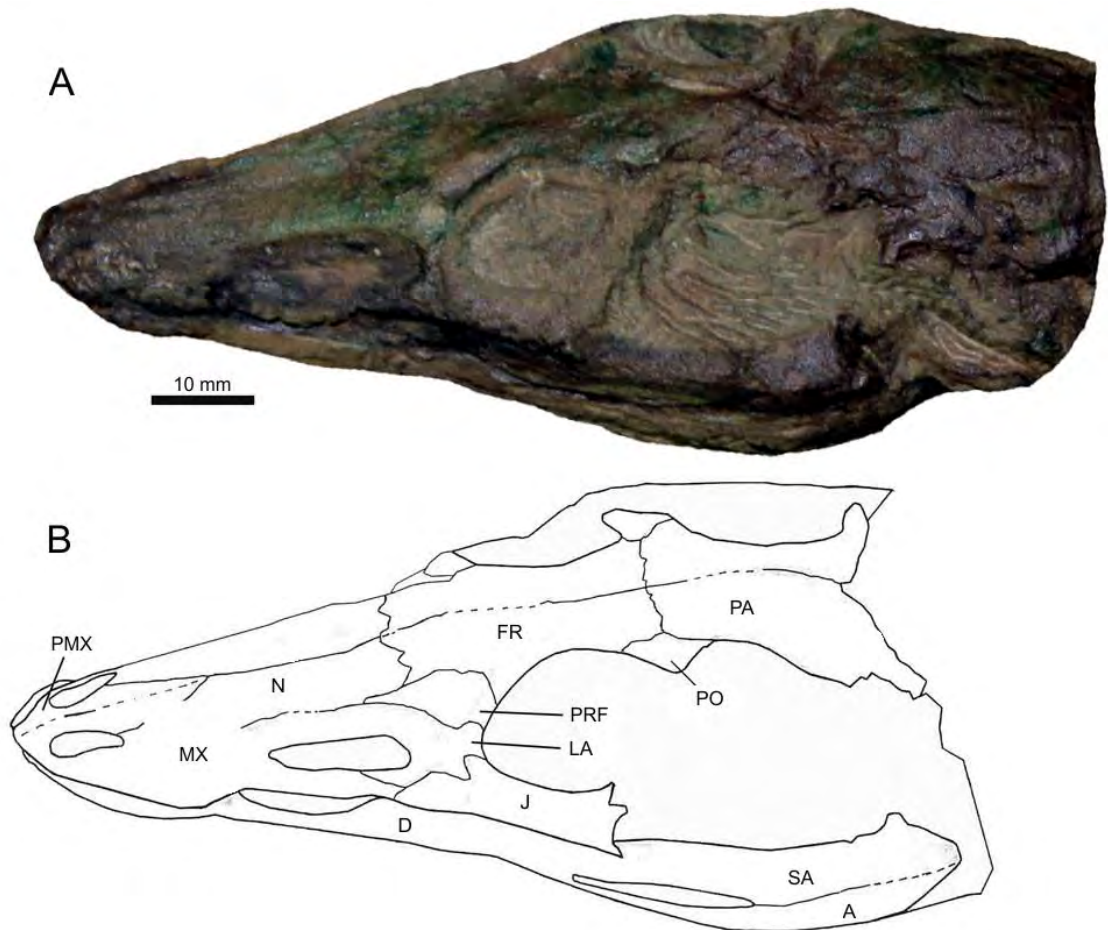


Figura 59. Fotografia (A) e desenho esquemático (B) do crânio de *Dyoplax arenaceus*. A fotografia do crânio foi escurecida usando Corel Photopaint X5 para destacar as estruturas e o desenho esquemático foi modificado de Maisch *et al.*, (2013). Abreviaturas: A, angular; D, dentário; J, Jugal; LA, lacrimal; MX, maxilar; N, nasal; PA, parietal; PO, pós-orbital; PMX, pré-maxilar; PRF pré-frontal; SA, supra-angular; SQ, esquamosal.

8. ANÁLISE INTEGRADORA DOS ARTIGOS DA TESE

Nesta sessão são apresentados, de forma breve, os conteúdos dos artigos desenvolvidos na Tese desde o início de 2013 até o fim de 2017, ressaltando as principais problemáticas e conclusões apresentadas. Os três artigos são apresentados em ordem cronológica, sendo que os dois primeiros já foram publicados e o terceiro e último foi submetido em começo de Junho de 2017.

ARTIGO 1. LACERDA, M.B.; Schultz, C.L. & Bertoni-Machado, C. 2015. *First ‘Rauisuchian’ archosaur (Pseudosuchia, Loricata) for the Middle Triassic Santacruzodon Assemblage Zone (Santa Maria Supersequence), Rio Grande do Sul State, Brazil.* **PLoS One**, v. 10, p. e0118563; DOI: 10.1371/journal.pone.0118563.

Neste artigo é descrito o novo táxon *Dagasuchus santacruzensis* da ZA de Santacruzodon (Sequência Santa Cruz) coletado no afloramento Schoenstatt localizado nas cercanias do município de Santa Cruz do Sul, a 150 km de Porto Alegre. Este táxon é representado apenas pelo holótipo, que constitui elementos de uma cintura pélvica incompleta, composto por um íleo esquerdo (UFRGS-PV-1244-T) e um ísquio direito e esquerdo (UFRGS-PV-1245-T) de um mesmo indivíduo. A presença de um acetábulo fechado, uma crista supra-acetabular e um processo pré-acetabular do íleo mais curto que o pós-acetabular é característico de parte do clado Loricata, parte do agrupamento parafilético “Rauisuchia”, mas difere de todos os táxons por apresentar uma margem dorsal e ventral da lâmina ilíaca lisa e um ísquio comprimido latero-medialmente com uma área antero-dorsal lisa e uma margem antero-ventral contínua, sem a presença de um entalhe. Este também é o primeiro “rauissuquídeo” descrito para a ZA de *Santacruzodon*, que preenche uma lacuna na distribuição temporal do grupo já que táxons são descritos nas ZAs de *Dinodontosaurus* e *Hyperodapedon*. A combinação destes fatores justificou a proposição de um novo táxon e ressalta a importância da participação dos “rauissuquídeos” durante o Triássico do Rio Grande do Sul.

ARTIGO 2. LACERDA, M.B.; Mastrantonio, B.M.; Fortier, D.C. & Schultz, C.L. 2016. *New insights on Prestosuchus chiniquensis Huene, 1942 (Pseudosuchia, Loricata) based on new specimens from the “Tree Sanga” Outcrop, Chiniquá Region, Rio Grande do Sul, Brazil.* **PeerJ**, v. 4, p. e1622; DOI: 10.7717/peerj.1622

Novos espécimes (CPEZ-239b) atribuídos ao táxon *Prestosuchus chiniquensis*, da ZA de *Dinodontosaurus* (Sequência Pinheiros-Chiniquá), com base em uma análise osteológica comparativa e corroborada por uma cladística são descritos neste artigo. Este material foi encontrado na localidade “Sanga da Árvore”, próximo ao Município de São Pedro do Sul, e constitui de pelo menos dois indivíduos (baseado na presença de dois sincrânios incompletos) de dimensões similares. Este artigo também discute que a presença/ausência da abertura acessória localizada entre o pré-maxilar e o maxilar pode ser um fator controlado pela ontogenia, já que há evidências de sua presença apenas no estágio juvenil e sub-adulto, havendo uma redução progressiva até seu fechamento nas formas adultas maiores. Entretanto, uma quantidade amostral muito maior ainda é necessário para reforçar esta hipótese.

ARTIGO 3. LACERDA, M.B.; França, M.A.G. & Schultz, C.L. *A new erpetosuchid (Pseudosuchia, Archosauria) from the Middle-Late Triassic of Southern Brazil.* **Zoological Journal of the Linnean Society**, Submetido.

Aqui é descrito o taxon *Pagosvenator candelariensis*, da ZA de *Dinodontosaurus* (Sequência Pinheiros-Chiniquá). O novo taxon é representado apenas pelo holótipo, que consiste em um sincrânio majoritariamente completo, porém mal preservado, com elementos pós-cranianos associados. Este táxon é a primeira ocorrência de um membro dos Erpetosuchidae no Triássico do Rio Grande do Sul, com base em características como a posição mais posterior da fenestra antero-orbital e a série dentária restrita a porção anterior da maxila. Ademais, ele apresenta características que são compartilhadas com outro grupo de arcossauros, os Ornithosuchidae, tais como a presença de um jugal com um processo dorsal bifurcado em “Y”, formando a borda ventral da órbita. Estas afinidades foram corroboradas pela análise filogenética, mas, a quantidade de dados ausentes pela falta da maior parte do pós-crânio dificultou uma estabelecimento preciso. Uma

análise de táxons instáveis (POL & ESCAPA, 2009) resultou em duas hipóteses entre as árvores mais parcimoniosas: que Erpetosuchidae (com *P. candelariensis*) seria o grupo irmão de Ornithosuchidae e um ramo basal de Pseudosuchia ou seria o grupo irmão de um clado composto por uma politomia formada por Gracilisuchidae, *Ticinosuchus ferox* e Paracrocodylomorpha. Todavia, esta última se torna complicada já que a posição de *T. ferox* fora de Paracrocodylomorpha é controversa. O local preciso de sua descoberta não é conhecido, já que quem doou o holótipo (MMACR PV 036-T) para o Museu Municipal Aristides Carlos Rodrigues não divulgou estas informações. O estabelecimento deste espécime como pertencendo a ZA de *Dinodontosaurus* é baseado nas características de sua preservação e o resultado de uma análise comparativa de elementos de terras raras (ETR) que foi feito correlacionando com um banco de dados de amostras de vários afloramentos do Rio Grande do Sul de riqueza fossilífera já descrita na literatura. Todavia, o espécime não foi originário de alguma destas localidades, e sim, de uma não amostrada no banco de dados.

9. REFERÊNCIAS

- ABDALA, F.; RIBEIRO, A.M. & SCHULTZ, C.L. 2001. A rich cynodont fauna of Santa Cruz do Sul (Santa Maria Formation), Middle-Late Triassic, Southern Brazil. **Neues Jahrbuch für Geologie und Paläontologie**, v. 11, p. 669-687.
- _____; MARTINELLI, A.G.; SOARES, M.B.; de la FUENTE, M. & RIBEIRO, A.M. 2009. South American Middle Triassic continental faunas with amniotes: biostratigraphy and correlation. **Paleontologia Africana**, v. 44, p. 83-87.
- ALCOBER, O. 2000. Redescription of the skull of *Saurosuchus galilei* (Archosauria: Rausuchidae). **Journal of Vertebrate Paleontology** v. 20, n. 2, p. 302-316.
- _____. & PARRISH, J.M. 1997. A new poposaurid from the Upper Triassic of Argentina. **Journal of Vertebrate Paleontology**, v. 7, n. 3, p. 548-556.
- ANDREIS, R.R.; BOSSI, G.E. & MONTARDO, D.K. 1980. O Grupo Rosário do Sul (Triássico) no Rio Grande do Sul. Congresso Brasileiro de Geologia 31, Balneário Camburiú, **Anais**, v. 2, p. 659-673.
- ARAÚJO, D.C. & GONZAGA, T.D. 1980. Uma nova espécie de *Jachaleria* (Therapsidae, Dicynodontia) do Triássico do Brasil. In: Congreso Argentino de Paleontología y Bioestratigrafía 2, e Congreso Latinoamericano de Paleontología 1, Buenos Aires, v. 1, p. 159-174.
- AZEVEDO, S.A.K. 1991. ***Prestosuchus chiniquensis* Huene 1942 (Reptilia, Archosauria, Thecodontia, Proterosuchia, Rausuchidae), da Formação Santa Maria, Triássico do Estado do Rio Grande do Sul, Brasil**. Tese de doutorado, Universidade Federal do Rio Grande do Sul, Porto Alegre, 157 p.
- _____. 1995a. Estudo morfofuncional do aparelho maxilomandibular de *Prestosuchus chiniquensis* Huene 1942. **Ibidem**, v. 67, n. 1, p. 62-65.

- _____.1995b. Paleoeecologia de *Prestosuchus chiniquensis* Huene 1942. Inter-relações paleoecológicas entre as faunas reptilianas do Triássico sul-brasileiro. **Anais da Academia Brasileira de Ciências**, v. 67, n. 1, p. 55-59.
- BACZKO, M.B. von & EZCURRA, M.D. 2013. Ornithosuchidae: a group of Triassic archosaurs with a unique ankle joint. **Geological Society of London, Special Publications**, v. 379, n. 1, p. 187-202.
- _____; DESOJO, J.B. & POL, D. 2014. Anatomy and phylogenetic position of *Venaticosuchus rusconii* Bonaparte, 1970 (Archosauria, Pseudosuchia), from the Ischigualasto Formation (Late Triassic), La Rioja, Argentina, **Journal of Vertebrate Paleontology**, v. 34, n. 6, p. 1342-1356.
- _____ & DESOJO, J.B. 2016. Cranial anatomy and palaeoneurology of the archosaur *Riojasuchus tenuisiceps* from the Los Colorados Formation, La Rioja, Argentina. **PLoSOne**, v. 11, n. 2, e0148575.
- _____ & EZCURRA, M.D. 2016. Taxonomy of the archosaur Ornithosuchus: reassessing Ornithosuchus woodwardi Newton, 1894 and Dasygnathoides longidens (Huxley 1877). **Earth and Environmental Science Transactions of the Royal Society of Edinburgh**, v. 106, p. 199-205.
- BARBERENA, M.C. 1978. A huge thecodont skull from the Triassic of Brazil. **Pesquisas**, v. 7, p. 111-129.
- _____; ARAÚJO, D.C.; LAVINA, E.L. & AZEVEDO, S.A.K. 1985a. O estado atual do conhecimento dos tetrápodes permianos e triássicos do Brasil meridional. In: Coletânea de trabalhos paleontológicos. Trabalhos apresentados no VII Congresso Brasileiro de Paleontologia – 1983. Brasília, p. 21-28.
- _____; ARAÚJO, D.C. & LAVINA, E.L. 1985b. Late Permian and Triassic tetrapods of Southern Brazil. **National Geographic Research**, v.1, p. 5-20.
- BENNET, S.C. 1996. The phylogenetic position of the Pterosauria within Archosauromorpha. **Zoological Journal of the Linnean Society**, v. 118, p. 261-308.

- BENTON, M.J. 1984. Rausuchians and the success of dinosaurs. **Nature**, v. 310, n. 5973, p. 101.
- _____. 1985. Classification and phylogeny of the diapsid reptiles. **Zoological Journal of the Linnean Society of London**, v. 84, p. 97-164.
- _____. 1986. The Late Triassic reptile *Teratosaurus*-a rausuchian, not a dinosaur. **Palaeontology**, v. 29, n. 2, p. 293-301.
- _____. 2004. **Vertebrate Palaeontology**, Blackwell Science Ltd, 472 p.
- _____ & CLARK, J.M. 1988. Archosaur phylogeny and the relationships of the Crocodylia. *In*: M.J. BENTON (ed.), **The Phylogeny and Classification of the Tetrapods**, p. 295-338.
- _____ & GOWER, D.J. 1997. Richard Owen's giant Triassic frogs: archosaurs from the Middle Triassic of England. **Journal of Vertebrate Paleontology**, v. 17, n. 1, p. 74-88.
- _____ & WALKER, A.D. 2002. *Erpetosuchus*, a crocodile-like basal archosaur from the Late Triassic of Elgin, Scotland. **Zoological Journal of the Linnean Society**, v. 136, p. 25-47.
- BONAPARTE, J.F. 1967. Dos nuevas 'faunas' de reptiles Triasicos de Argentina. *In*: **Gondwana Stratigraphy**, UNESCO, I.U.G.S. Symposium, p. 283-306.
- _____. 1970. Annotated list of the South American Triassic Tetrapods. Proceedings of the Godwana Symposium, South Africa, p. 665-682.
- _____. 1971. Los tetrápodos del sector superior del a Formación Los Colorados, La Rioja, Argentina (Triásico Superior). **Opera Lilloana**, v. 22, p. 13-56.

- _____. 1975. Nuevos materiales de *Lagosuchus talampayensis* Romer (Thecodontia, Pseudosuchia) y su significado en el origen de los Saurischia, Chañarenses inferiores, Triásico medio de Argentina. **Acta Geologica Lilloana**, v. 13, p. 5–90.
- _____. 1981. Descripción de "*Fasolasuchus tenax*" y su significado en la sistemática y evolución de los thecodontia. **Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia"**, v. 3, n. 2, p. 55-101.
- _____. 1982. Faunal replacement in the Triassic of South America. **Journal of Vertebrate Paleontology**, v. 2, n. 3, p. 362-371.
- _____. 1984. Locomotion in Raurisuchid thecodonts. **Journal of Vertebrate Paleontology**, v. 3, n. 4, p. 210-218.
- BOULENGER, G.A. 1903. On reptilian remains from the Trias of Elgin. **Philosophical Transactions of the Royal Society B**, v. 196, p. 175-189.
- BRINKMAN, D.B. 1981. The origin of the crocodyloid tarsi and the interrelationships of thecodontian archosaurs. **Brevoria**, v. 464, p. 1-23.
- BROCHU, C.A. 1997. Synonymy, redundancy, and the name of the crocodile stem-group. **Journal of Vertebrate Paleontology**, v. 17, n. 2, p. 448-449.
- BROOM, R. 1906. Contributions to South African paleontology, 1. On the remains of *Erythrosuchus africanus*. **Annals of the South African Museum**, v. 5, p. 187-196.
- _____. 1913. On the South-African pseudosuchian Euparkeria and allied genera. **Proceedings of the Zoological Society of London**, v. 1906, p. 591-600.
- _____. 1932. On Some South African Pseudosuchians. **Annals of the Natal Museum**, v. 7, p. 55-59.

BRUSATTE, S.L.; BENTON, M.J.; RUTA, M.; LLOYD, G.T. 2008. Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. **Science**, v. 321, p. 1485-1488.

_____; BUTLER, R.J.; SULEJ, T.; NIEDZWIEDZKI, G. 2009. The Taxonomy and Anatomy of Raurisuchian Archosaurs from the Late Triassic of Germany and Poland. **Acta Palaeontologica Polonica**, v. 54, n. 2, p. 221-230.

_____; NESBITT, S.J.; IRMIS, R.J.; BUTLER, R.J.; BENTON, M.J.; NORELL, M.A. 2010a. The origin and early radiation of dinosaurs. **Earth-Science Reviews**, v. 101, p. 68-100.

_____; BENTON, M.J.; DESOJO, J.B.; LANGER, M.C. 2010b. The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). **Journal of Systematic Palaeontology**, v. 8, n. 1, p. 3-47.

_____; NIEDZWIEDZKI, G. & BUTLER, R.J. 2011. Footprints pull origin and diversification of dinosaur stem lineage deep into Early Triassic. **Proceedings of the Royal Society B**, v. 278, p. 1107-1113.

BUFFETAUT, E. 1987. **A Short History of Vertebrate Palaeontology**, Croom Helm Publishers, Kent, 223p.

BUTLER, R.J.; BARRETT, P.M.; ABEL, R.L.; GOWER, D.J. 2009. A possible ctenosauriscid archosaur from the Middle Triassic Manda beds of Tanzania. **Journal of Vertebrate Paleontology**, v. 29, p. 1022-1031.

_____; BRUSATTE, S.L.; REICH, M.; NESBITT, S.J.; SCHOCH, R.R.; HORNING, J.J. 2011. The Sail-Backed Reptile from the Latest Early Triassic of Germany and the Timing and Biogeography of the Early Archosaur Radiation. **PLoS One**, v. 6, n. 10, p. e25693.

_____; SULLIVAN, C.; EZCURRA, M.D.; LIU, J.; LECOUNA, A. & SOOKIAS, R.B. 2014. New clade of enigmatic early archosaurs yields insights into early

pseudosuchian phylogeny and the biogeography of the archosaur radiation. **BMC Evolutionary Biology**, v. 14, p. 128.

CARROLL, R.L. 1988. **Vertebrate Paleontology and Evolution**. W. H. Freeman, New York, 698p.

CERDA, I.A.; DESOJO, J.B.; SCHEYER, T.M. & SCHULTZ, C.L. 2013. Osteoderm microstructure of “rauisuchian” archosaurs from South America. **Geobios**, v. 46, p. 273-283.

CHARIG, A.J. 1956. **New Triassic archosaurs from Tanganyika including Mandasuchus and Teleocrater**. Tese de doutorado. University of Cambridge, Cambridge, 503p.

_____. 1957. **New Triassic archosaurs from Tanganyika, including Mandasuchus and Teleocrater**. **Dissertation Abstracts**, Cambridge University, p. 28-29.

_____. 1972. The evolution of the archosaur pelvis and hindlimb: an explanation in functional terms. *In*: K.A. Joysey, and T.S. Kemp (eds.), **Studies in Vertebrate Evolution**, Oliver & Boyd, Edinburgh, p. 121–155.

_____ & REIG, O.A. 1970. Classification of the Proterosuchia. **Biological Journal of the Linnean Society**, v. 2, p. 125-171.

CHATTERJEE, S. 1982. Phylogeny and classification of thecodontian reptile. **Nature**, v. 295, p. 317-320.

_____ 1985. *Postosuchus*, a new thecodontian reptile from the Triassic of Texas and the origin of tyrannosaurs. **Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences**, v. 309, n. 1139, p. 395-460.

_____ & MAJUMDAR, P.K. 1987. *Tikisuchus romeri*, a new rauisuchid reptile from the Late Triassic of India. **Journal of Paleontology**, v. 61, n. 4, p. 787-793.

- CRUICKSHANK, A.R.I. 1972. The Proterosuchian Thecodonts. *In*: K.A. JOYSEY, and T.S. KEMP (eds.), **Studies in Vertebrate Evolution**, Oliver and Boyd, Edinburgh, p. 89–119.
- DAWLEY, R.M.; ZAWISKIE, J.M.; COSGRIFF, J.W. 1979. A raiisuchid thecodont from the Upper Triassic Popo Agie Formation of Wyoming. **Journal of Paleontology**, v. 53, p. 1428–1431.
- DESOJO, J.B. & ARCUCCI, A.B. 2009. New material from *Luperosuchus fractus* (Archosauria: Crurotarsi) from the Middle Triassic of Argentina: the earliest known South American 'Raiisuchian'. **Journal of Vertebrate Paleontology**, v. 29, n. 4, p. 1311-1315.
- _____ & RAUHUT, O. 2009. The taxonomic status and phylogenetic position of the Late Triassic brazilian raiisuchian *Prestosuchus*. **Journal of Vertebrate Paleontology (suppl. 3)**, v. 29, n. 3, p. 87A-88A.
- _____; HECKERT, A.B.; MARTZ, J.W.; PARKER, W.G.; SCHOCH, R.R.; SMALL, B.J.; SULEJ, T. 2013. Aetosauria: a clade of armoured pseudosuchians from the Upper Triassic continental beds. **Earth and Environmental Science Transactions of the Royal Society of Edinburgh**, v. 106, p. 203-239.
- _____ & DESOJO, J.B. 2016. Triassic pseudosuchia archosaurs of South America. **Contribuciones del MACN**, v. 6, p. 57-66.
- EVANS, S. 2003. At the feet of the dinosaurs: the early history and radiation of lizards. **Biological Reviews**, v. 78, p. 513-551.
- EZCURRA, M.D. 2012. Comments on the taxonomic diversity and paleobiogeography of the earliest known dinosaur assemblages (late Carnian – earliest Norian). **Revista de Historia Natural, Nueva Serie**, v.2, p.49-71.

- _____. 2016. The phylogenetic relationships of basal archosauromorphs, with emphasis on the systematics of proterosuchian archosauriforms. **PeerJ**, v. 4, p. e1778.
- _____; LECUONA, A.; MARTINELLI, A. 2010. A new basal archosauriform diapsid from the Loew Triassic of Argentina. **Journal of Vertebrate Paleontology**, v. 30, p. 1433-1450.
- _____; BUTLER, R.J.; GOWER, D.J. 2013. 'Proterosuchia': the origin and early evolution of Archosauriforms. **Geological Society, London, Special Publications**, v. 379, p. 9-33.
- _____; SHEYER, T.M.; BUTLER, R.J. 2014. The origin and early evolution of Sauria: Reassessing the Permian saurian fossil record and the timing of the crocodile-lizard divergence. **PLoS ONE**, v. 9, n. 2, p.e89165.
- _____ & BUTLER, R.J. 2015. Post-hatchling cranial ontogeny in the Early Triassic diapsid reptile *Proterosuchus fergusi*. **Journal of Anatomy**, v. 226, n. 5, p. 387-402.
- _____ & BUTLER, R.J. 2015. Taxonomy of the proterosuchid archosauriforms (Diapsida: Archosauromorpha) from the earliest Triassic of South Africa, and implications for the early Archosauriform radiation. **Palaeontology**, v. 58, n. 1, p. 141-170.
- _____; VELOZO, P.; MENEGHEL, M.; PIÑEIRO, G. 2015. Early archosauromorph remains from the Permo-Triassic Buena Vista Formation of north-eastern Uruguay. **PeerJ**, v. 3, p. e776.
- _____ & DESOJO, J.B. 2016. Non-archosaurian archosauromorphs from Argentina. **Contribuciones del MACN**, v. 6, p. 49-56.
- FRAKES, L.A. **Climates throughout Geological Time**. Elsevier Scientific, Amsterdam, New York, p. 304.

- FRANÇA, M.A.G.; LANGER, M.C.; FERIGOLO, J. 2008. Cranial morphology of new specimens of raiisuchian archosaurs from the Santa Maria Formation (Middle Triassic) of Rio Grande do Sul (Southern Brazil). III Congresso Latinoamericano de Paleontologia de Vertebrados. Neuquén, Patagonia, Argentina, p. 103.
- _____; LANGER, M.C.; FERIGOLO, J. 2009. Novas informações sobre uma nova espécie de *Rauisuchia* (*Pseudosuchia* Zittel 1887-1890) do Triássico Médio Brasileiro (Formação Santa Maria). **Reunião anual da sociedade brasileira de paleontologia-Núcleo Rio Grande do Sul (PaleoRS)**. Porto Alegre, Rio Grande do Sul, Brazil, p. 14-15.
- _____; 2011. **Descrição osteológica de *Decuriasuchus quartacolonia* (Archosauria, Pseudosuchia) e a evolução dos Rauissúquios**. PhD. Thesis, Universidade de São Paulo, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, 434 p.
- _____; FERIGOLO, J.; LANGER, M.C. 2011. Associated skeletons of a new middle Triassic "Rauisuchia" from Brazil. **Naturwissenschaften**, v. 98, n. 5, p. 389-95.
- _____; LANGER, M.C.; FERIGOLO, J. 2013. The skull anatomy of *Decuriasuchus quartacolonia* (*Pseudosuchia*: *Suchia*: *Loricata*) from the middle Triassic of Brazil. **Geological Society of London, Special Publications**, p. 469-501.
- GALTON, P.M. 1985. The poposaurid thecodontian *Teratosaurus suevicus* v. Meyer plus referred specimens mostly based on prosauropod dinosaurs from the Middle Stubensandstein Upper Triassic of Nordwuerttemberg West Germany. **Stuttgarter Beitrage zur Naturkunde Serie B (Geologie und Palaeontologie)**, v. 116, p. 1-29.
- GAUTHIER, J. 1984. **A cladistic analysis of the higher systematic categories of the Diapsida**, PhD. Thesis, University of California, Berkeley. 564 pp.

- _____ & PADIAN, K. 1985. **Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight.** *In*: M.K. HECHT, J.H. OSTROM, G. VIOHL; P. WELLNHOFER (eds.), **The Beginning of Birds**, p. 185–197.
- _____; 1986. Saurischian monophyly and the origin of birds. **Memoirs of the California Academy of Science**, v. 8, p. 1-55.
- _____; KLUGE, A.; ROWE, T.B. 1988. The early evolution of the Amniota, Volume 1: Amphibians, Reptiles, Birds. *In*: M.J. Benton (ed.), **The Phylogeny and Classification of the Tetrapods**, Clarendon Press, p. 103-155.
- _____; NESBITT, S.J., SCHACHNER, E., BEVER, G.S.; JOYCE, W.G. 2011. The bipedal stem crocodylian *Poosaurus gracilis*: inferring function in fossils and innovation in archosaur locomotion. **Bulletin of the Peabody Museum of Natural History**, v. 52, p. 107-126.
- GOWER, D.J. 1999. The cranial and mandibular osteology of a new raurischian archosaur from the Middle Triassic of southern Germany. **Stuttgarter Beiträge zur Naturkunde. Serie B (Geologie und Paläontologie)**, v. 280, p. 1-49.
- _____; 2000. Raurischian archosaurs (Reptilia, Diapsida): An overview. **Neues Jahrbuch für Geologie und Paläontologie Abhandlungen**, v. 218, p. 447-488.
- _____; 2002. Braincase evolution in suchian archosaurs (Reptilia: Diapsida): evidence from the raurischian *Batrachotomus kupferzellensis*. **Zoological Journal of the Linnean Society**, v. 136, p. 49-76.
- _____ & NESBITT, S.J. 2006. The braincase of *Arizonasaurus babbitti*-Further evidence for the non-monophyly of 'raurischian' archosaurs. **Journal of Vertebrate Paleontology**, v. 26, n. 1, p. 79-87.

- _____ & SCHOCH, R.R. 2009. Postcranial Anatomy of the Raurisuchian Archosaur *Batrachotomus kupferzellensis*. **Journal of Vertebrate Paleontology**, v. 29, n. 1, p. 103-122.
- _____ & WILKINSON, M. 1996. Is There Any Consensus on Basal Archosaur Phylogeny? **Proceedings of the Royal Society B**, v. 263, p. 1399-1406.
- HECKERT, A.B.; LUCAS, S.G.; RINEHART, L.F.; CELESKEY, M.D.; SPIELMANN, J.A. & HUNT, A.P. 2010. Articulated skeletons of the aetosaur *Typothorax coccinarum* Cope (Archosauria: Stagonolepididae) from the Upper Triassic Bull Canyon Formation (Revueltian: early-mid Norian), eastern New Mexico, USA. **Journal of Vertebrate Paleontology**, v. 30, p. 619–642.
- HOFFSTETTER, R. 1955. **Thecodontia**. In: Piveteau, J. (ed). *Traité de Paléontologie*, V. 5: Amphibiens, Reptiles, Oiseaux. Masson et Cie, Paris, 665-694.
- HOLZ, M.J. 2015. Mesozoic paleogeography and paleoclimates—discussion of the diverse greenhouse and hothouse conditions of an alien world. **Journal of South American Earth Sciences**, v. 61, p. 91-107.
- _____ & BARBERENA, M.C. 1994. Taphonomy of the South Brazilian Triassic herpetofauna: pattern of death, transport and burial. **Paleogeography, Paleoclimatology, Paleoecology**, v. 107, n. 1994, p. 179-194.
- _____ & SCHERER, C. 1998. Caracterização paleoclimática do Triássico no sul do Brasil. **Ciência e Ambiente**, v. 1, p. 95-103.
- _____ & SCHERER, C. 2000. Sedimentological and paleontological evidence of paleoclimatic change during the Southbrazilian Triassic: the register of a global trend towards a humid paleoclimate. **Zentralblatt für Geologie und Paläontologie, Teil 2, Paläontologie**, v. 1, n. 7-8, p. 1589-1609.
- HUENE, F. von. 1903. Die Dinosaurier der europäischen Triasformation mit Berücksichtigung der aussereuropäischen Vorkommnisse. **Geologische und Paläontologische Abhandlungen 1 (Suppl.)**, p.1-419.

- _____. 1911. Über *Erythrosuchus*, Vertreter der neuen Reptil-Ordnung Pelycosimia. **Geologische und Paläontologische Abhandlungen, Neue Folge**, v. 10, p. 67-122.
- _____. 1936. The constitution of Thecodontia. **American Journal of Sciences**, v. 32, p. 207-217.
- _____. 1938. Die fossilen Reptilien des südamerikanischen Gondwanalandes. **Neues Jahrbuch für Mineralogie, Geologie und Paläontologie**, v. 1938, p. 142-151.
- _____. 1940. Eine Reptilfauna aus der ältesten Trias Nordrusslands. **Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B**, v. 841, p. 1-23.
- _____. 1942. *Die fossilen Reptilien des Südamerikanischen Gondwanalandes. Ergebnisse der Sauriergrabungen in Südbrasilien, 1928/1929*. C. H. Beck'sche, Munchen.
- HUGHES, B. 1963. The earliest archosaurian reptiles. **South African Journal of Science**, v. 59, n. 5, p. 221-241.
- HUXLEY, T.H. 1877. The crocodilian remains found in the Elgin sandstones, with remarks on ichnites of Cummingstone. **Memoirs of the Geological Survey of the United Kingdom Monograph III**, v. 3, p. 1-51.
- JALIL, N.-E. & PEYER, K. 2007. A new Raurisuchian (Archosauria, Suchia) from the Upper Triassic of the Argana Basin, Morocco. **Palaeontology**, v. 50, n. 2, p. 417-430.
- JUUL, L. 1994. The phylogeny of basal archosaurs. *Palaeontologia Africana* v. 31, p. 1-38.

KISCHLAT, E.-E. 2000. Tecodôncios: A Aurora dos Arcossáurios no Triássico. *In*: M. HOLZ; L.F. DE ROS (eds.), **Paleontologia do Rio Grande do Sul**. Editora da UFRGS, Porto Alegre, p. 246-272.

_____. 2003. **Padrão muscular da coxa de arcossauromorfos fósseis: aplicação do cladismo reverso e teste de hipóteses**. Tese de doutorado, Universidade Federal do Rio Grande do Sul, Porto Alegre, 487p.

_____ & BARBERENA, M.C. 1999. *Prestosuchus chiniquensis* (Crurotarsi, Archosauria) does not need a neotype!, **Paleontologia em Destaque**, v. 14, n. 26, p. 53.

KLIMETZ, M.P. 1983. Speculations on the Mesozoic plate tectonic evolution of eastern China. **Tectonics**, v. 2, n. 2, p. 139-166.

KREBS, B. 1965. Die triasfauna der Tessiner Kalkalpen. XIX. *Ticinosuchus ferox*, *nov. gen. nov. sp.* Ein neuer Pseudosuchier aus der Trias des Monte San Giorgio. Schweizerische Palaontologische, **Abhandlungen** v. 81, p.1–140.

_____. 1974. Die Archosaurier. **Naturwissenschaften**, v. 61, n. 1, p. 17-24.

_____. 1976. Pseudosuchia. *In*: Kuhn O, ed. **Handbuch der Paläoherpetologie, Thecodonti** Stuttgart: Gustav Fischer-Verlag, v. 13, p. 40–98.

LAUTENSCHLAGER, S. 2008. **Revision of *Rauisuchus tiradentes* (Archosauria: Rauisuchia) from the Late Triassic (Carnian) Santa Maria Formation of Brazil and its implications for rausuchian phylogeny**. Dissertação de mestado, Ludwig Maximilians Universität, Munique, 77 p.

_____ & DESOJO, J.B. 2011. Reassessment of the Middle Triassic rausuchian archosaurs *Ticinosuchus ferox* and *Stagonosuchus nyassicus*. **Paläontologische Zeitschrift**, v. 85, p. 357-381.

_____ & RAUHUT, O. 2014. Osteology of *Rauisuchus tiradentes* from the Late Triassic (Carnian) Santa Maria Formation of Brazil, and its implications for

rauisuchid anatomy and phylogeny. **Zoological Journal of the Linnean Society**, v. 173, n. 1, p. 55–91.

LI, C., WU, X.-C., CHENG, Y.-N., SATO, T.; WANG, L. 2006. An unusual archosaurian from the marine Triassic of China. **Naturwissenschaften**, v. 93, p. 200–206.

LIPARINI, A. 2008. **Estudo da biomecânica craniana de um rauissuquídeo a partir de tomografias computadorizadas e técnicas de imagens digitais em 3 dimensões**. Dissertação de mestrado. Universidade Federal do Rio Grande do Sul, Porto Alegre, 122p.

_____. 2011. **Aspectos biomecânicos e morfofuncionais do esqueleto apendicular de Prestosuchus chiniquensis (Archosauria: Pseudosuchia) e suas implicações para a locomoção** Tese de doutorado. Universidade Federal do Rio Grande do Sul, Porto Alegre, 209p.

_____ & SCHULTZ, C.L. 2013. A reconstruction of the thigh musculature of the extinct pseudosuchian *Prestosuchus chiniquensis* from the Dinodontosaurus Assemblage Zone (Middle Triassic Epoch), Santa Maria 1 Sequence, Southern Brazil. **Geological Society, London, Special Publications**, n. 379, p. 411-468.

LONG, R.A. & MURRY, P.A. 1995. Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. **New Mexico Museum of Natural History and Science Bulletin**, v. 4, p. 1-254.

LUO, Z.-X. 2007. Transformation and diversification in the early mammalian evolution. **Nature**, v. 450, p. 1011-1019.

LYSON, T.R.; BEVER, G.S.; BHULLAR, B.-A.; JOYCE, W.G. & GAUTHIER, J.A. 2010. Transitional fossils and the origin of turtles. **Biology Letters**, v. 6, p. 830-833.

- MARJANOVIC, D. & LAURIN, M. 2008. Assessing confidence intervals for stratigraphical ranges of higher taxa: the case of Lissanphibia. **Acta Paleontologica Polonica**, v. 53, p. 413-432.
- MASTRANTONIO, B.M. 2010. **Descrição Osteológica de Materiais Cranianos e Pós-cranianos de *Prestosuchus chiniquensis* (Archosauria, Rauisuchia) do Mesotriássico do RS (Biozona de *Dinodontosaurus*, Formação Santa Maria) e Considerações Filogenéticas sobre Rauissúquios**. Tese de doutorado. Universidade Federal do Rio Grande do Sul, Porto Alegre, 247 pp.
- _____; SCHULTZ, C.L.; DESOJO, J.B. & Garcia, J.B. 2013. The braincase of *Prestosuchus chiniquensis* (Archosauria; Suchia). **Geological Society of London, Special Publications**, v. 379, p. 425-440.
- MEHL, M.G. 1915. *Poposaurus gracilis* a New Reptile from the Triassic of Wyoming. **The Journal of Geology**, v. 23, n. 6, p. 516-522.
- MEYER, H.V. 1861. Reptilien aus dem Stubensandstein des oberen Keupers. **Palaeontographica**, v. 7, p. 253-346.
- MOODY, R.T. & NAISH, D. 2010. Alan Jack Charig (1927-1997): an overview of his academic accomplishments and role in the world of fossil reptile research. **Geological Society of London, Special Publications**, v.343, p. 89-109.
- MODESTO, S.P. & SUES, H.-D. 2004. The Skull of the Early Triassic Archosauromorph Reptile *Prolacerta broomi* and its Phylogenetic Significance. **Zoological Journal of the Linnean Society**, v. 140, p. 335-351.
- MORI, A.L.O. 2005. **Tafonomia em sistemas fluviais: um estudo de caso na Formação Santa Maria, Triássico do RS**. M. Sc. Dissertation. Universidade Federal do Rio Grande do Sul, Porto Alegre, 127 p.
- NESBITT, S.J. 2003. *Arizonasaurus* and its implications for archosaur divergence. **Proceedings of the Royal Society of London**, v. 270 (Suppl 2), p. S234-S37.

- _____. 2005. Osteology of the Middle Triassic pseudosuchian archosaur *Arizonasaurus babbitti*. **Historical Biology**, v. 17, p. 19-47.
- _____. 2007. The anatomy of *Effigia okeeffea* (Archosauria, Suchia), theropod-like convergence and the distribution of related taxa. **Bulletin of the American Museum of Natural History**, v. 302, 1-84.
- _____. 2011. The early evolution of archosaurs: relationships and the origin of major clades. **Bulletin of the American Museum of Natrual History**, v. 352, p. 1-292.
- _____; BRUSATTE, S.L.; DESOJO, J.B.; LIPARINI, A.; FRANÇA, M.A.G.; WEINBAUM, J.C. & GOWER, D.J. 2013. 'Rauisuchia'. **Geological Society, London, Special Publications**, v. 379, p. 241-274.
- _____ & NORELL, M.A. 2006. Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda). **Proceedings of the Biological Society of London**, v. 273, n. 1590, p. 1045-8.
- _____; STOCKER, M.R.; SMALL, B.J & DOWNS, A. 2009. The Osteology and Relationships of *Vancleavea campi* (Reptilia: Archosauriformes). **Zoological Journal of the Linnean Society**, v. 157, n. 4, p. 814–864.
- _____ & BUTLER, R.J. 2012. Redescription of the archosaur *Parringtonia gracilis* from the Middle Triassic Manda beds of Tanzania, and the antiquity of Erpetosuchidae. **Geological Magazine**, v. 150, n. 2, p. 225-238.
- NEWTON, E.T. 1894. Reptiles from the Elgin sandstone – description of two new genera. **Philosophical Transactions of the Royal Society of London Series B, Biological Sciences**, v. 185, p. 573–607.
- NOVAS, F.E. 1992. Phylogenetic relationships of the basal dinosaurs, the Herrerasauridae. **Paleontology**, v. 35, n. 1, p. 51-62.
- ÖSI, A.; PRONDVAI, E.; FREY, E.; Pohl, B. 2010. New interpretation of the palate of Pterosaurs. **Anatomical Record**, v. 293, n. 2, p. 243-58.

- PARKER, W.G. 2007. Reassessment of the aetosaur "*Desmatosuchus*" *chamaensis* with a reanalysis of the phylogeny of the Aetosauria (Archosauria: Pseudosuchia). **Journal of Systematic Palaeontology**, v. 5, p. 1-28.
- _____ & BARTON, B. 2008. New Information on the Upper Triassic Archosauriform *Vancleavea campi* Based on New Material from the Chinle Formation of Arizona. **Palaeontologia Electronica**, v. 11, n. 3, p. 1-20.
- PARRISH, J.M. 1993. Phylogeny of the Crocodylotarsi, with Reference to Archosaurian and Crurotarsan Monphyly. **Journal of Vertebrate Paleontology**, v. 13, n. 3, p. 287-308.
- PARRISH, J.T. 1993. Climate of the supercontinent Pangea. **Journal of Geology**, v. 101, p. 215-233.
- PEYER, K.; CARTER, J.G.; SUES, H.-D.; NOVAK, S.E. & OLSEN, P.E. 2008. A new suchian archosaur from the Upper Triassic of North Carolina. **Journal of Vertebrate Paleontology**, v. 28, n. 2, p. 363-381.
- POUGH, F.H.; JANIS, C.M. & HEISER, J.B. 1999. **A vida dos Vertebrados**. 2ed. Atheneu Editora, São Paulo. 798p.
- PRETO, N.; KUSTATSCHER, E. & WIGNALL, P.E. 2010 Triassic climates -State of the Art and perspectives. **Palaeogeography, Palaeoclimatology, Palaeoecology**, v. 290, p. 1-10.
- RAD. U.; DÜRR, S. & OGG, J.G. 1994. The Triassic of Thakkhola (Nepal). I: stratigraphy and paleoenvironment of a northeast Gondwanan rift margin. **Geologische Rundschau**, v. 83, n. 1, p. 76-106.
- REIG, O.A. 1970. The Proterosuchia and the Early Evolution of the Archosaurs; An Essay About the Origin of a Major Taxon. **Bulletin of The Museum of Comparative Zoology**, v. 139, p. 229-292.

- RENESTO, S.; CONFORTINI, F.; GOZZI, E.; MALZANNI, M. & PAGANONI, A. 2003. A possible raiisuchid (Reptilia, Archosauria) tooth from the Carnian (Late Triassic) of Lombardy (Italy). **Rivista del Museo Civico di Scienze Naturali "Enrico Caffi"**, v. 22, p. 109-114.
- ROMER, A.S. 1956. **Osteology of the Reptiles**. University of Chicago Press, Chicago. 772 p.
- _____. 1966. **Vertebrate Paleontology**. University of Chicago Press, Chicago, 468p.
- _____. 1971. The Chañares (Argentina) Triassic reptile fauna. VIII. A fragmentary skull of a large thecodont, *Luperosuchus fractus*. **Brevoria**, v. 373, p. 1-8.
- _____. 1972. The Chañares (Argentina) Triassic reptile fauna. XIII. An early ornithosuchid pseudosuchian, *Gracilisuchus stipanichorum*, *gen. et sp. nov.* **Brevoria** v. 389, p. 1-24.
- ROWE, T. 1988. Definition, diagnosis, and origin of Mammalia. **Journal of vertebrate Paleontology**, v. 8, p. 241-264.
- SCHEYER, T.M. & DESOJO, J.B. 2011. Palaeohistology and external microanatomy of raiisuchian osteoderms (Archosauria: Pseudosuchia). **Palaeontology**, v. 54, p. 1289–1302.
- _____; DESOJO, J.B. & CERDA, I.A. 2011. Comparative palaeohistology of Triassic raiisuchian and aetosaurian osteoderms (Archosauria: Pseudosuchia). **Journal of Vertebrate Paleontology**, v. 31 (suppl. 3), p. 188A.
- SCHOCH, R.R. & SUES, H.-D. 2014. A new archosauriform reptile from the Middle Triassic (Ladinian) of Germany. **Journal of Systematic Palaeontology**, v.12, p. 113-131.
- SEN, K. 2005. A new raiisuchian archosaur from the Middle Triassic of India. **Palaeontology**, v. 48, n. 1, p. 185-196.

- SENNIKOV, A.G. 1990. New data on the raiisuchids of Eastern Europe. **Paleontological Journal**, v. 3, p. 1-12.
- _____. 1996. Evolution of the Permian and Triassic tetrapod Communities of Eastern Europe. **Palaeogeography, Palaeoclimatology, Palaeocology**, v. 120, p. 331-351.
- SERENO, P.C. 1991. Basal archosaurs: phylogenetic relationships and functional implications. **Journal of Vertebrate Paleontology**, v. 10 (Suplement 3), p. 1-53.
- _____ & ARCUCCI, A.B. 1990. The monophyly of crurotarsal archosaurs and the origin of bird and crocodile ankle joints. **Neus Jahrbuch für Geologie und Paläontologie Abhandlugen**, v. 180, p. 21-52.
- _____ & NOVAS, F.E. 1992. The complete skull and skeleton of an early dinosaur. **Science**, v. 258, p. 1137-1140.
- SILL, W.D. 1974. The anatomy of *Saurosuchus galilei* and the relationships of the raiisuchid thecodonts. **Bulletin of The Museum of Comparative Zoology**, v. 146, p. 317–362.
- SIMMS, M.J. & RUFFELL, A. 1991. Climatic and biotic change and the Late Triassic. **Journal of the Geological Society, London**, v. 147, p. 321-328.
- SUES, H.-D. & FRASER, N.C. 2010. **Triassic life on land: The great transition (The critical moments and perspectives in Earth history and paleobiology)**. Columbia Univeristy Press, New York, 224p.
- SULEJ, T. 2005. A new raiisuchian reptile (Diapsida Archosauria) from the Late Triassic of Poland. **Journal of Vertebrate Paleontology**, v. 25, n. 1, p. 78-86.
- TROTTEYN, M.J.; DESOJO, J.B. & ALCOBER, O.A. 2011. Nuevo material postcraniano de *Saurosuchus galilei* Reig (Archosauria: Crurotarsi) del

Triássico Superior del centro-oeste da Argentina. **Ameghiniana**, v. 48, n. 1, v. 605-620.

VEEVERS, J.J. 1991. **Mid-Triassic lacuna of the Gondwanaland platform in context of Pangean fusion and incipient fission**. *In*: Gondwana Symposium 7, São Paulo, p. 603-609.

WALKER, A.D. 1961. Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. **Philosophical Transactions of the Royal Society of London, Series B**, v. 248, p. 53-134.

_____ 1964. Triassic reptiles from the Elgin area, *Ornithosuchus* and the origin of Carnosaurs. **Philosophical Transactions of the Royal Society of London B**, v. 744, p. 53-134.

_____. 1968. *Protosuchus*, *Proterochampsia*, and the origin of phytosaurs and crocodiles. **Geological Magazine**, v. 105, p. 1-14.

_____ 1970. A revision of the Jurassic crocodile *Hallopus*, with remarks on the classification of crocodiles. **Philosophical Transactions of the Royal Society of London B**, v. 257, p. 323-372.

_____ 1990. A revision of *Sphenosuchus acutus* Haughton, a crocodylomorph reptile from the Elliot Formation (late Triassic or early Jurassic) of South Africa. **Philosophical Transactions of the Royal Society of London B**, v. 330, p. 1-120.

WATSON, D.M.S. 1917. A sketch-classification of the pre-Jurassic tetrapod vertebrates. **Proceedings of the Zoological Society, London**, v. 1917, p. 167-186.

WEINBAUM, J.C. 2002. **Osteology and relationships of *Postosuchus kirkpatricki* (Archosauria: Crurotarsi)**, PhD Thesis. Texas Tech University, Lubbock, Texas, 78 p.

- _____. 2010. The skull of *Postosuchus kirkpatricki* (Archosauria: Paracrocodyliformes) from the Upper Triassic of the United States. **PaleoBios**, v. 30, n. 1, p. 18-44.
- _____. 2013. Postcranial skeleton of *Postosuchus kirkpatricki* (Archosauria; Paracrocodylomorpha) from the Upper Triassic of the United States. **Geological Society, London, Special Publications**, v. 379, p. 525-553.
- _____ & HUNGERBÜHLER, A. 2007. A revision of *Poposaurus gracilis* (Archosauria: Suchia) based on two new specimens from the Late Triassic of the southwestern U.S.A. **Paläontologische Zeitschrift**, v. 81, n. 2, p. 131-145.
- ZERFASS, H.; LAVINA, E.L.; SCHULTZ, C.L.; GARCIA, A.J.V.; FACCINI, U.F. & CHEMALE JR, F. 2003. Sequence stratigraphy of continental Triassic strata of Southernmost Brazil: a contribution to Southwestern Gondwana palaeogeography and paleoclimate. **Sedimentary Geology**, v. 161, n. 2003, p. 85-105.
- _____; CHEMALE JR, F.; SCHULTZ, C.L. & LAVINA, H. 2004. Tectonics and sedimentation in Southern South America during the Triassic. **Sedimentary Geology**, v. 166, n. 2004, p. 265-292.
- ZIEGLER, A.M.; SCOTese, C.R. & BARRET, S.F. 1983. **Mesozoic and Cenozoic paleogeographic maps, in Tidal friction and Earths Rotation II**, P. Broche/ J. Sundermann, Eds. Springer-Verlag, Berlin.
- ZHANG, F.-K. 1975. A new thecodont *Lotosaurus*, from the Middle Triassic of Hunan. **Vertebrata PalAsiatica**, v. 13, n. 3, p.144-148.

PARTE 2
ARTIGOS DA TESE

ARTIGO 1. LACERDA, M.B.; Schultz, C.L. & Bertoni-Machado, C. 2015. *First 'Rauisuchian' archosaur (Pseudosuchia, Loricata) for the Middle Triassic Santacruzodon Assemblage Zone (Santa Maria Supersequence), Rio Grande do Sul State, Brazil.* **PLoS One**, v. 10, p. e0118563; DOI: 10.1371/journal.pone.0118563.

RESEARCH ARTICLE

First 'Rauisuchian' archosaur (Pseudosuchia, Loricata) for the Middle Triassic *Santacruzodon* Assemblage Zone (Santa Maria Supersequence), Rio Grande do Sul State, Brazil

Marcel B. Lacerda^{1*}, Cesar L. Schultz¹, Cristina Bertoni-Machado²

1 Instituto de Geociências, Laboratório de Paleovertebrados, Universidade Federal do Rio Grande do Sul, Porto Alegre, RS, Brazil, **2** Centro Superior de Tecnologia TECBrasil, Faculdade de Engenharias, Porto Alegre, RS, Brazil

* marcel.lacerda@yahoo.com.br



OPEN ACCESS

Citation: Lacerda MB, Schultz CL, Bertoni-Machado C (2015) First 'Rauisuchian' archosaur (Pseudosuchia, Loricata) for the Middle Triassic *Santacruzodon* Assemblage Zone (Santa Maria Supersequence), Rio Grande do Sul State, Brazil. PLoS ONE 10(2): e0118563. doi:10.1371/journal.pone.0118563

Academic Editor: Lorenzo Rook, University of Florence, ITALY

Received: October 13, 2014

Accepted: January 15, 2015

Published: February 25, 2015

Copyright: © 2015 Lacerda et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper.

Funding: The funding was made possible by the Conselho Nacional de Desenvolvimento Científico e Tecnológico of the Brazilian government in the form of scholarships for two of the authors (MBL and CLS, specifically). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Abstract

The 'Rauisuchia' are a group of Triassic pseudosuchian archosaurs that displayed a near worldwide distribution. In Brazil, their fossils are found only in the Santa Maria Formation (Paraná Basin) of the Rio Grande do Sul State, specifically in the Middle Triassic *Dinodontosaurus* assemblage zone (AZ) and the Late Triassic *Hyperodapedon* AZ (*Rauisuchus tiradentes*). Between these two cenozones is the *Santacruzodon* AZ (Middle Triassic), whose record was, until now, restricted to non-mammalian cynodonts and the proterochampsian *Chanaresuchus bonapartei*. Here we present the first occurrence of a rauisuchian archosaur for this cenozoone, from the Schoenstatt outcrop, located near the city of Santa Cruz do Sul and propose a new species, based on biostratigraphical evidence and a comparative osteological analysis.

Introduction

The 'rauisuchians' comprise a problematic group of Middle to Late Triassic pseudosuchian archosaurs that are traditionally bundled together due to shared similarities in cranial, pelvic and ankle morphologies, but may not represent a natural group [1–5]. As such, some workers proposed [3,6] that the name be used between commas to refer to them, independently if they are a monophyletic or not, while *Rauisuchia* is used to designate a monophyletic group [3–6]. This is the terminology applied in the present article. The last 20 years have seen an increase in the number of discoveries and redescrptions e.g. [7–19] along with recent cladistic analyses [4, 6, 19] which have contributed to a better understanding of the diversity and relations among 'rauisuchians' within Archosauria. Although the use of more taxa in recent phylogenies has contributed to a better understanding of the diversity found in these forms, their phylogenetic and taxonomic definitions still remain unclear and new studies and more complete specimens are needed to attempt to resolve many problematic topics [3, 4, 5, 6, 11].

Competing Interests: The authors have declared that no competing interests exist.

'Rauisuchians' displayed a near worldwide distribution, with the exception of Oceania and Antarctica [3, 5, 20]. In Brazil, their fossils are found only in the Santa Maria Supersequence [21, 22], Paraná Basin, Rio Grande do Sul State, in the southern part of the country. This Supersequence encompasses two biostratigraphic units bearing 'rauisuchians'; the Middle Triassic *Dinodontosaurus* Assemblage Zone (AZ) with the species *Prestosuchus chiniquensis*, '*Prestosuchus loricatus*' and *Decuriasuchus quartacolonina*, and the Late Triassic *Hyperodapedon* AZ, with the record of *Rauisuchus tiradentes* [5, 14, 23, 24]. Placed between these two biozones, occurs the *Santacruzodon* AZ, for which no 'rauisuchians' had been found until now. The faunal association of this biozone includes mainly traversodontid (*Santacruzodon hopsoni* [25]; *Menadon* sp. [26] and probainognathid (cf. *Probainognathus* [23]) cynodonts, the proterochampsian *Chanaresuchus bonapartei* Romer 1971 [27] and cranial fragments of dicynodonts [26, 27]. The presence of *Menadon* and the close taxonomic relationships between *Santacruzodon hopsoni* and *Dadadon isaloi* [28] indicates a temporal correlation between the *Santacruzodon* AZ and the Ladinian "Isalo II" fauna of Madagascar [28, 29] (Fig. 1).

In the present contribution, we describe the first occurrence of a 'rauisuchian' archosaur for the *Santacruzodon* AZ, based on an incomplete pelvic girdle, and discuss its taxonomic status, proposing it as a new species.

Geological setting

The material here described came from the Schoenstatt site that is located on the outskirts of Santa Cruz do Sul city, (UTM SAD 69-22J-359794°E, 6709033°N) approximately 150km from the capital of Rio Grande do Sul State, Porto Alegre. It is a landfill that is exposed at the west margin of the RS-287 highway in the subdivision of Faxinal Velho, close to the Schoenstatt sanctuary [30]. The geological profile of the site shows an association of channel facies and floodplains (Fig. 2). The fossils occur in a level of massive red mudstones approximately 5 m thick that displays accumulations of disarticulated skeletal elements, with a predominance of skull and jaw elements, interpreted as a biogenic concentration formed by the accumulation of discarded remains by selective predators and carrion eaters [31].

Materials and Methods

No special permits were required for the present study, which complied with all relevant legal regulations. The studied materials were collected and deposited in the paleovertebrate collection of the Laboratório de Paleontologia de Vertebrados of the Instituto de Geociências of the Universidade Federal do Rio Grande do Sul, which is a federal university and as such, specimen collection and housing complies fully with the laws that regulate fossil and mineralogical materials of Brazil. All the other relevant information, such as details of the site where the fossils were collected and their catalogue number are presented and discussed in the "Geological Setting" part of "Introduction" heading and in the present topic, respectively.

The specimen is represented only by an incomplete and disarticulated pelvic girdle, specifically a left ilium (UFRGS-PV-1244-T) along with a right and a left ischium (UFRGS-PV-1245-T). They were found disarticulated but closely associated. The similar dimensions of both ischia (the left one is 18.3cm long and the right one is 19.1cm) and the overall size and aspect of the acetabular area when the left ilium and ischium are placed in articulation suggest that all elements belong to the same individual. It was prepared using mechanical chisels, explorers and brushes.

Systematic Paleontology

ARCHOSAURIA Cope, 1869 *sensu* Gauthier & Padian 1985

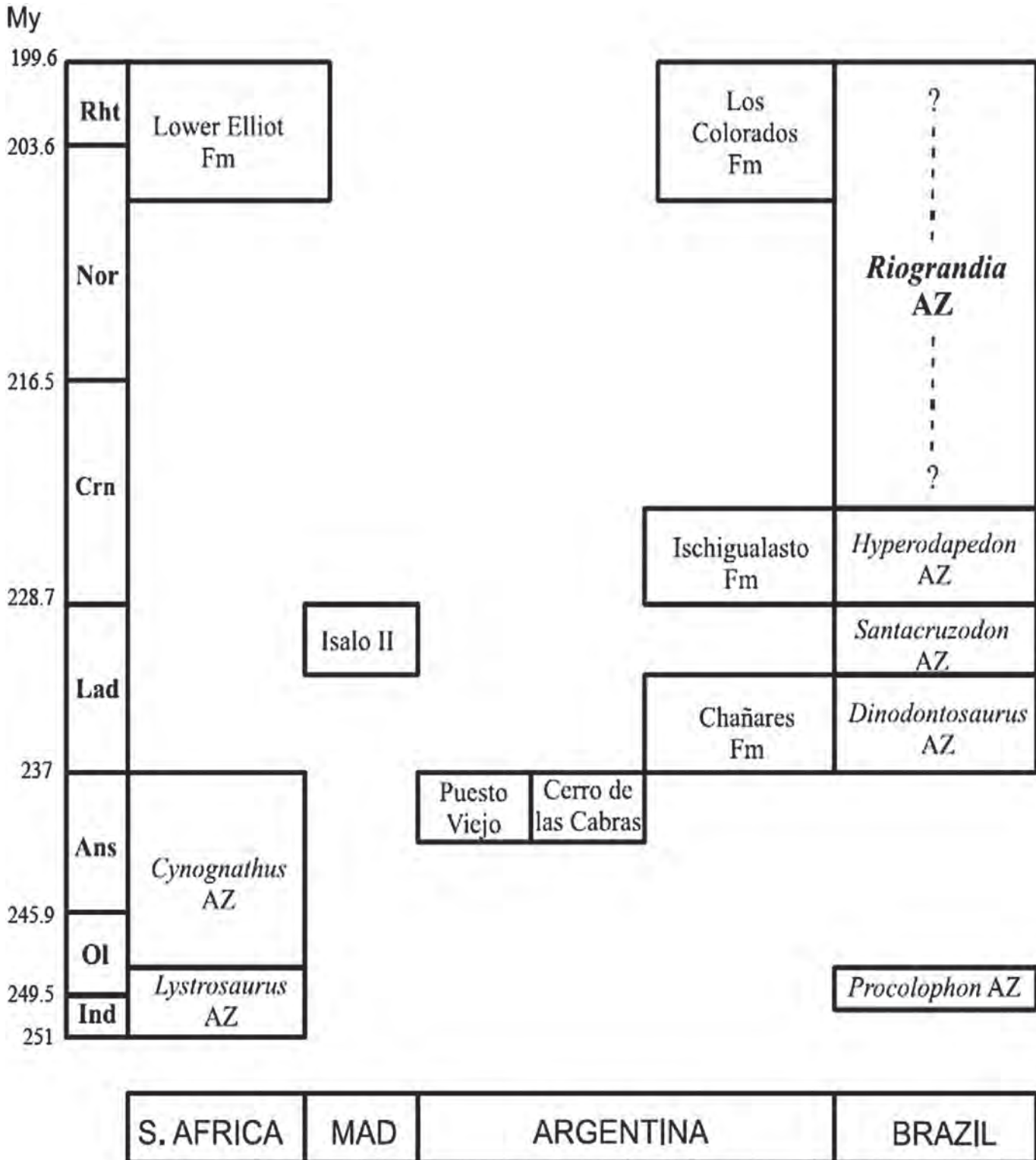


Fig 1. Comparative chart with the biostratigraphical framework of the Santa Maria Supersequence along with the ones from South Africa, Madagascar and Argentina. From [23].

doi:10.1371/journal.pone.0118563.g001

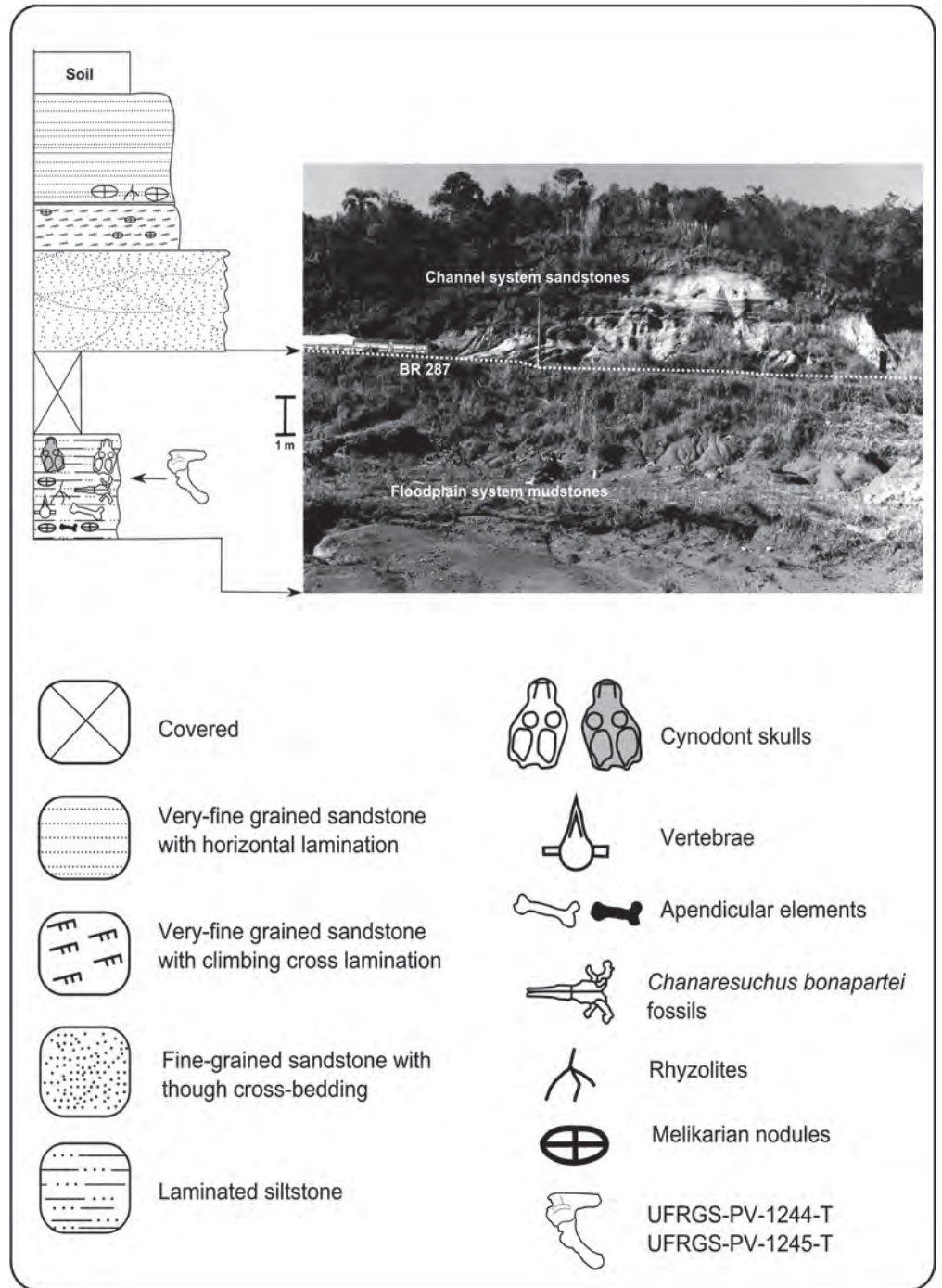


Fig 2. Stratigraphical profile of the upper portion of the Schoenstatt Outcrop (Modified from [31]).

doi:10.1371/journal.pone.0118563.g002

PSEUDOSUCHIA Zittel, 1887–1890 *sensu* Gauthier & Padian 1985

SUCHIA Krebs 1974 (*sensu* Benton & Clark 1988)

LORICATA Merrem 1820 (*sensu* Nesbitt 2011)

Dagasuchus santacruzensis sp. nov., gen. nov., urn:lsid:zoobank.org:act:A3B06825-1F56-4C95-8F75-4393AA32B752

Etymology: From the words *daga*, which is a large knife or dagger in the regional gaúcho jargon, in reference to the pronounced iliac blade and *suchus* from the Greek word for crocodile; *santacruzensis* refers to the city of Santa Cruz do Sul, where the Schoenstatt outcrop is located.

Holotype: UFRGS-PV-1244-T, left ilium; UFRGS-PV-1245-T, right and left ischium, deposited in the paleontological collection of the Laboratório de Paleovertebrados of the Instituto de Geociências of the Universidade Federal do Rio Grande do Sul.

Horizon and Locality: Santa Maria Supersequence, *Santacruzodon* Assemblage Zone, Late Ladinian/Early Carnian, Schoenstatt outcrop, near Santa Cruz do Sul, Rio Grande do Sul State, Brazil.

Diagnosis: medium sized archosaur with imperforate acetabulum and preacetabular process of the ilium shorter than the postacetabular process, similar to that of *Loricata* (*sensu* Nesbitt, 2011), but differs from all known taxa within that grouping (*Saurosuchus galilei*, *Prestosuchus chiniquensis*, *Batrachotomus kupferzellensis*) and *Decuriasuchus quartacolonía* by the presence of the following combination of features: Ilium displays smooth dorsal and ventral margins of the iliac blade, articulation sites for two sacral vertebrae, a 'plate-like' ischium, with smooth anterodorsal area and a continuous anteroventral margin with no apparent notch.

Nomenclatural Acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "<http://zoobank.org/>". The LSID for this publication is: urn:lsid:zoobank.org:pub:59314E74-4A8F-4077-A8F3-BAB5B3B99EB9. The electronic edition of this work was published in a journal with an ISSN, and has been archived and is available from the following digital repositories: PubMed Central and LOCKSS.

Description

The ilium is well preserved, with roughly 19 cm in length and 10 cm tall (Fig. 3). The contact of the blade with the acetabular area is continuous, not displaying a waisted region between both areas. The former is overall complete, with what appears to be only minor damage on both extremities. The dorsal margin of the iliac blade, in lateral view, is smooth and straight, with no sign of any rugose surface as those described for *Batrachotomus* and *Prestosuchus*. Perpendicular to its longitudinal axis there is a low (but distinct) antero-posteriorly wide ridge that projects antero-dorsally on its lateral area from the dorsal border of a robust supra-acetabular crest, dividing the iliac blade into a short preacetabular and longer postacetabular process. The former has the same length as the anterior margin of the acetabular region, with the area near the anterior margin of the crest being preserved, while the postacetabular process projects antero-posteriorly into a dorso-ventrally tall and compressed blade of bone that slightly tapers posteriorly. The ventroposterior portion of this blade is gently expanded laterally, which occupies the rest of the posterior tip.

In dorsal view, the blade is sinuous, with a laterally concave anterior area where the supra-acetabular ridge is located.

The ventral portion of the acetabulum, in lateral view, especially close to the area of articulation with the ischium and the pubis, was lightly eroded by weathering and when the ilium and the ischium are placed in articulation the contact is extremely narrow, indicating that the

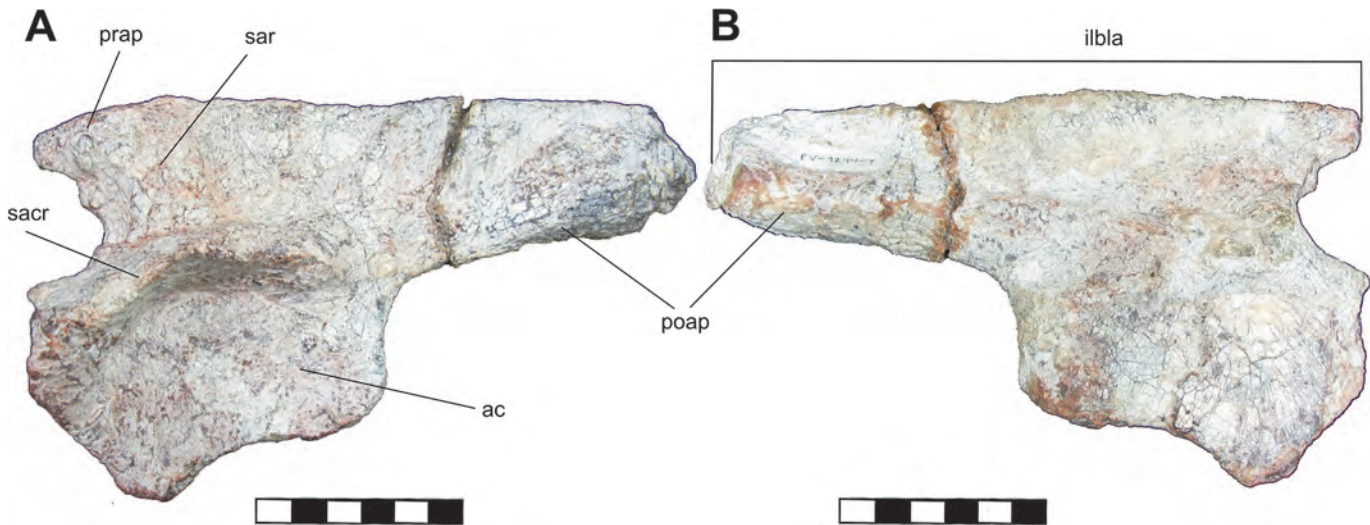


Fig 3. Left ilium (UFRGS-PV-1244-T) in lateral (A) and medial (B) views. Abbreviations: **ac**, acetabule; **ilba**, iliac blade; **prap**, pre-acetabular process; **poap**, post-acetabular process; **sar**, supra-acetabular crest; **sacr**, supra-acetabular ridge. Scale: 5cm.

doi:10.1371/journal.pone.0118563.g003

acetabulum is most likely imperforate. The acetabulum is overall slightly oval and deep, gradually rising laterally up to the anterior portion of the supra-acetabular rim.

In medial view, the anterior portion of the base of the iliac blade displays a medially expanded surface with a dorsal depression that would be the site for the articulation of the rib of the first sacral vertebrae. Posteriorly to this area, along the blade, there is a shallow depression along its length, up onto a medially projecting area of the base of the blade, at about 45° to the sagittal plane, which posteriorly forms a platform for the articulation of the rib of the second sacral vertebrae. The ventroposterior portion of the blade, between the medial crest and the lateroventral margin of post-acetabular process does not display any fossa or depression. On the acetabular area, there is a slightly oval sub-horizontal depression located where the above-mentioned platform begins, which would correspond to another rib articulation site.

The right ischium is better preserved than the left one (Fig 4). Both are dorso-ventrally elongated plate-like elements, with a more robust and smooth dorsal body and expanded proximal and distal ends. In the right ischium, the proximal area, in lateral view, displays a sinuous dorsal portion, and is bordered ventrally by a laterally expanded semi-circular ventroposterior border of the acetabulum. Posteroventrally to this area, a sheet of bone projects ventrally and expands to form an irregular lateromedially compressed surface that is more distinct on the first third of the ischium, that decreases in size posteriorly and continues along the body of the bone up to distal end. The distal ends of the ischia, in lateral view, display an expanded and posteriorly directed “ischium boot”.

The ventral margins of both elements are partially eroded by weathering. If both elements are positioned in relative articulation, the lateromedially compressed area is the main surface for the articulation of both ischia anteriorly. Distally, a gap appears between them in anterior view, but it is unclear if this gap is natural or a result of diagenetic alteration to the bones. The case for the latter is reinforced by the presence of some distortion in the left ischium, which is more transversally curved than the right one.

Additionally, there is a small, roughly triangular-shaped fragment of bone that was preserved on the medial area of the ilium. However, this piece does not display any diagnostic feature and thereby is not figured here.

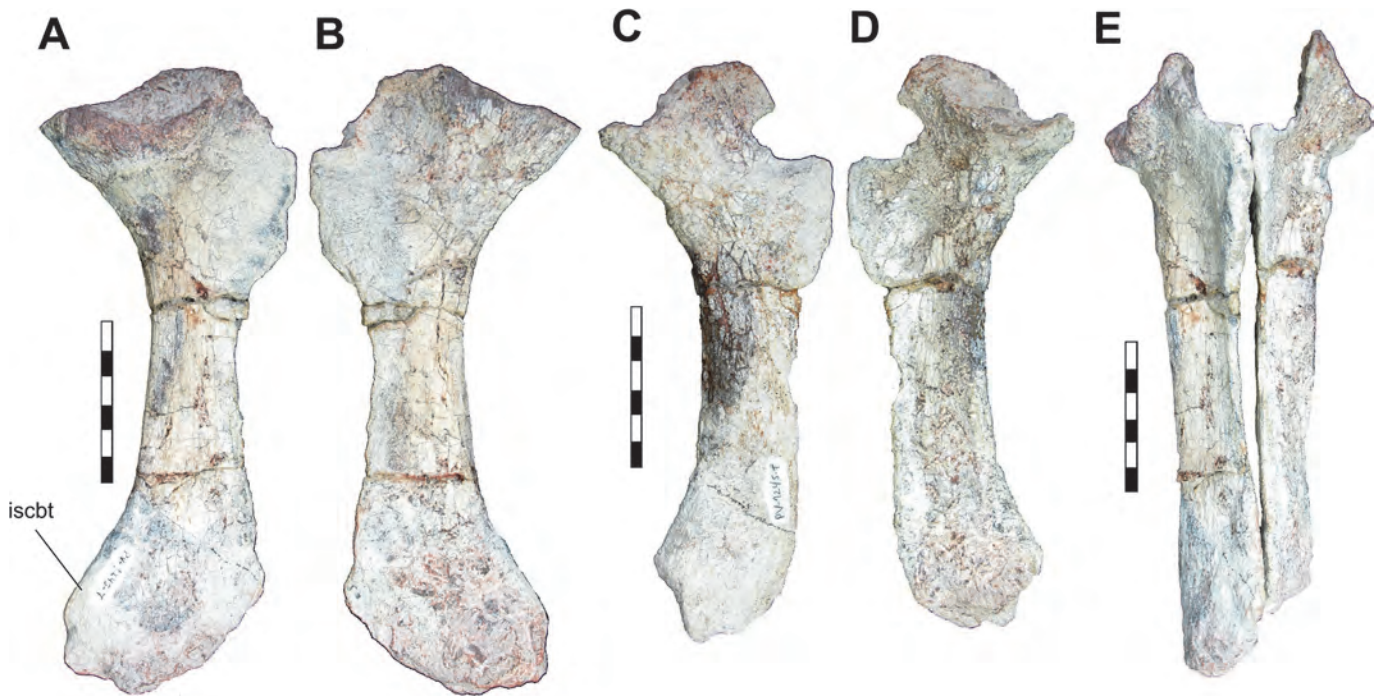


Fig 4. Right ischium in lateral (A) and medial (B) views; Left ischium in medial (C) and lateral (D) views; Both ischia in articulation in anterior view (E). Abbreviations: **iscbt**, Ischium boot. Scale: 5cm.

doi:10.1371/journal.pone.0118563.g004

Discussion

The studied pelvic girdle presents an imperforate acetabulum, a laterally expanded, semicircular supra-acetabular crest and an antero-dorsally orientated supra-acetabular ridge. These features, as well as the overall aspect and the antero-posterior length of the iliac blade match those described for 'rauisuchian' taxa within *Loricata sensu* Nesbitt (2011), differing from those of other more derived forms within *Poposauridea*. The comparative osteological analysis indicates that it is morphologically similar to *Saurosuchus galilei* [32] of the Ischigualasto Formation (Carnian), *Batrachotomus kupferzellensis* [13] of the Lettenkeuper of Germany (Late Ladinian), as well as *Prestosuchus chiniquensis* [24] and *Decuriasuchus quartacolonía* [14] of the *Dinodontosaurus* AZ (Ladinian) of Brazil. The overall aspect of the ilium is different from one originally described for *Rauisuchus tiradentes* by Huene [33] (BSPG AS XXV 88), although now considered as not belonging to the same individual as the lectotype based on size differences [34], the acetabulum is restricted to the ilium, while in the presently described specimen it is likely composed by all three pelvic elements. Although it is similar to *Stagonosuchus nyassicus* from the Manda Formation (Anisian) it differs in having a significantly more pronounced supra-acetabular crest, a supra-acetabular ridge and absence of a medial protuberance on the lateral surface of the iliac blade [35, 36].

Additional diagnostic features would be the articulation sites for only two sacral vertebrae (Fig. 5), a condition that is described for *Prestosuchus chiniquensis* [24, 37], *Saurosuchus galilei* [34] and *Decuriasuchus quartacolonía* [14] but not for *Batrachotomus kupferzellensis*, which has 3 [13].

The pelvic girdle here described differs from that of *Decuriasuchus quartacolonía* [14] by an overall larger acetabulum, shorter iliac blade and a more sinuous and plate-like ischia. Additionally, in the specimen MCN PV10105c figured in França *et al.* [14], the ilia are comparatively

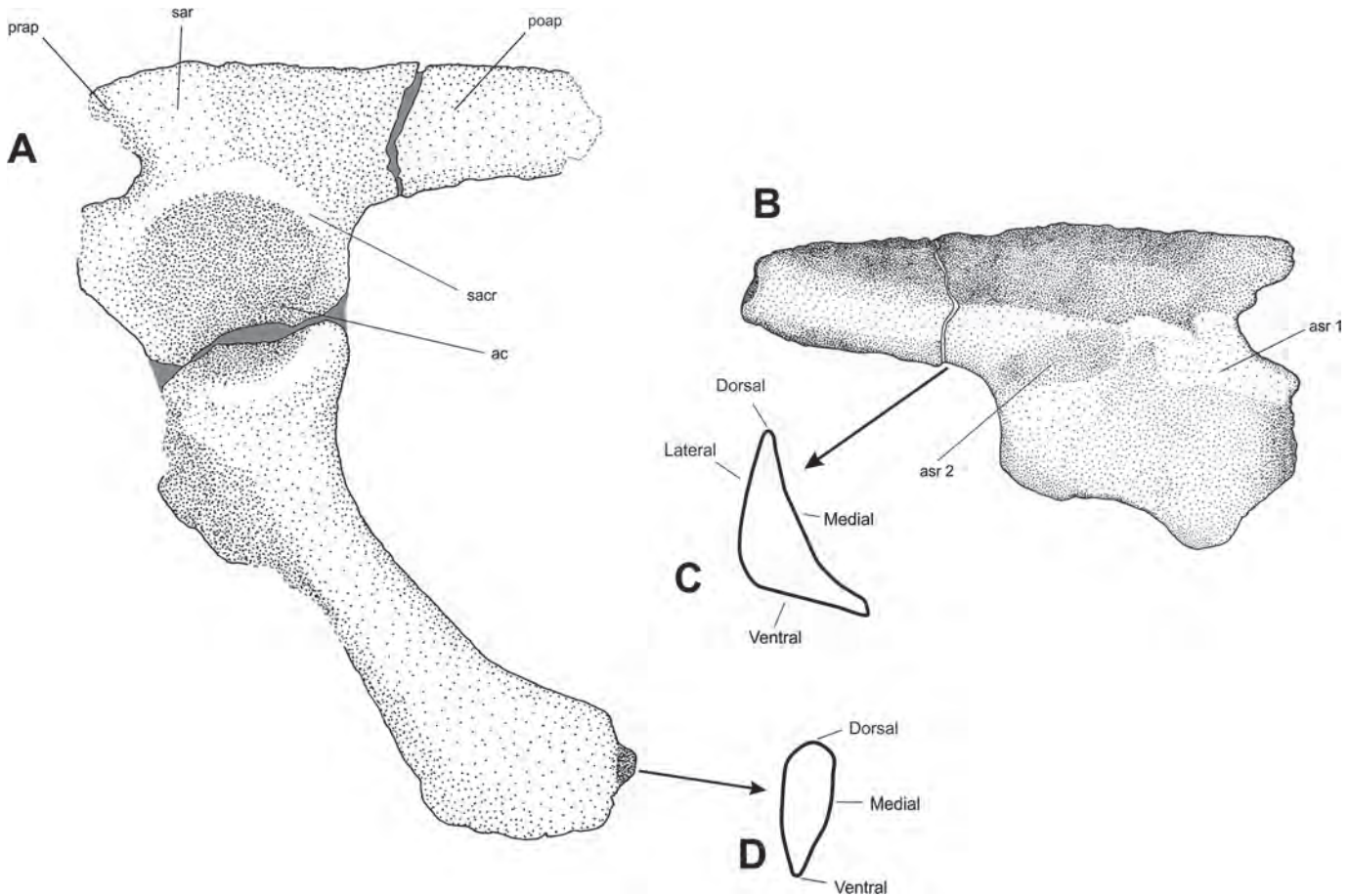


Fig 5. (A) Composite illustration of the left ilium with the better preserved right ischium in articulation; (B) illustration of the ilium in medial view; (C) cross-section of the ilium in posterior view; (D) cross-section of the ischium in distal view. Abbreviations: as Fig. 2 plus: **asr 1**, articulation site for the sacral rib of the first sacral vertebra; **asr 2**, articulation site for the sacral rib of the second sacral vertebra. Damaged areas in grey.

doi:10.1371/journal.pone.0118563.g005

smaller and more gracile than the one here described (MBL pers. obs.). These features might be considered problematic in differentiating species, since it is also possible to attribute such variations to intraspecific factors, however, as França *et al.* [14] considered all specimens of *Decuriasuchus quartacolonina* as adult forms due to the presence of closed sutures between the skull elements as well as ossified vertebrae, the overall larger size of the present specimen can be used to differentiate it from that taxon.

Another pelvic girdle attributed to *Prestosuchus chiniquensis* by Nesbitt [4]-specimen UFRGS-PV-0152-T—displays similar dimensions and overall aspect of the one here described, but differs in the presence of an iliac blade which is much shorter dorsoventrally and that displays rugosities along its anterodorsal surface along with an ischium with a marked “notch” on the anteroventral margin. As this specimen is currently being studied as the subject of a PhD thesis, it is not figured here aside from the former comments.

The ischium differs from *Prestosuchus chiniquensis* [24, 33, 37] and *Saurosuchus galilei* [32] due to a more plate-like than rod-like morphology ([4]: character 9) and the absence of ridges on the dorsal surface of the iliac blade. It is possible to consider this feature as not morphologically significant, since the comparatively smaller size of the specimen in regards the above-mentioned species could be considered as ontogenetic and such ridges should be more developed as the animal grew, but this appears to be not the case, since the material is well preserved

and no ridges are apparent. Additionally, the ischia further differs from *Prestosuchus chiniquensis* due to the absence of a notch on the ventral margin ([4]: character 296) and displaying a smooth anterodorsal surface, distally to the expanded proximal area, which lacks a low dorsal crest that is considered a sinapomorphy for this species, being present in the lectotype of *Prestosuchus chiniquensis* described by Huene [33, 37] and assigned by Krebs [38], with a more pronounced one in the more complete specimen (UFRGS-PV-0629-T) attributed to this taxon (see discussion in [24]). This comparative morphological analysis shows that none of the previously described species share the combination of features that is found in the presently described specimen. As such, it is clearly distinct from other 'rauisuchians', but the absence of clear autapomorphies combined with the incompleteness of the individual makes the proposition of a new taxon questionable.

Additional evidence to support a new taxon would be the biostratigraphical position of this specimen in the Santa Maria Supersequence. As presented earlier, all other 'rauisuchian' taxa have been limited to the *Dinodontosaurus* and *Hyperodapedon* assemblage zones. The *Santacruzodon* AZ is a unique third order sequence within the Santa Maria Supersequence, with paleofaunal correlation with the "Isalo II" fauna from Madagascar [22, 23, 25, 26], where no 'rauisuchian' has been described. However, the presence of *Chanaresuchus* [27, 30] in both the *Dinodontosaurus* and *Santacruzodon* assemblage zones, as well as in the Chañares and Ischigualasto faunas would indicate that at least one taxon continued across the Ladinian/Carnian transition. As such, the possibility of a previously described Ladinian 'rauisuchian' taxon that existed up to the Late Ladinian/ Early Carnian cannot be completely excluded. However, we consider that all the other evidences presented here (Fig. 6) along with the biostratigraphical data justifies the distinction of this specimen as unique among other 'rauisuchian' taxa, and as such, would be more than only a "rauisuchian indet." or a similar provisional designation.

Conclusion

Although incomplete, the combination of features of the described specimen permits a taxonomic designation to a new 'rauisuchian' species *Dagasuchus santacruzensis*. This new species adds to the knowledge of the diversity of the group in the Triassic and fills in a gap in the temporal distribution of these forms in South America. Major steps in the study of these forms have been made in recent years, however, new finds are still required to clarify the problematic topics presented in this paper, in 'rauisuchian' studies and Triassic continental biostratigraphical data in general.

Acknowledgments

We would like to thank Dr. Marco Aurélio G. de França for his invaluable assistance and encouragement in the elaboration of this work. Additionally, we thank Dr. Felipe L. Pinheiro, Dr. Tiago Raugust and Dr. Bianca Mastrantonio for the many helpful discussions, the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and the anonymous reviewers for their time and attention.

Author Contributions

Wrote the paper: MBL CLS CBM. Graphics and illustrations: MBL.

References

1. Benton MJ, Clark JM (1988) Archosaur phylogeny and the relationships of the Crocodylia. In: Benton MJ, editor. *The Phylogeny and Classification of the Tetrapods*. Oxford, Clarendon Press. pp. 295–338.

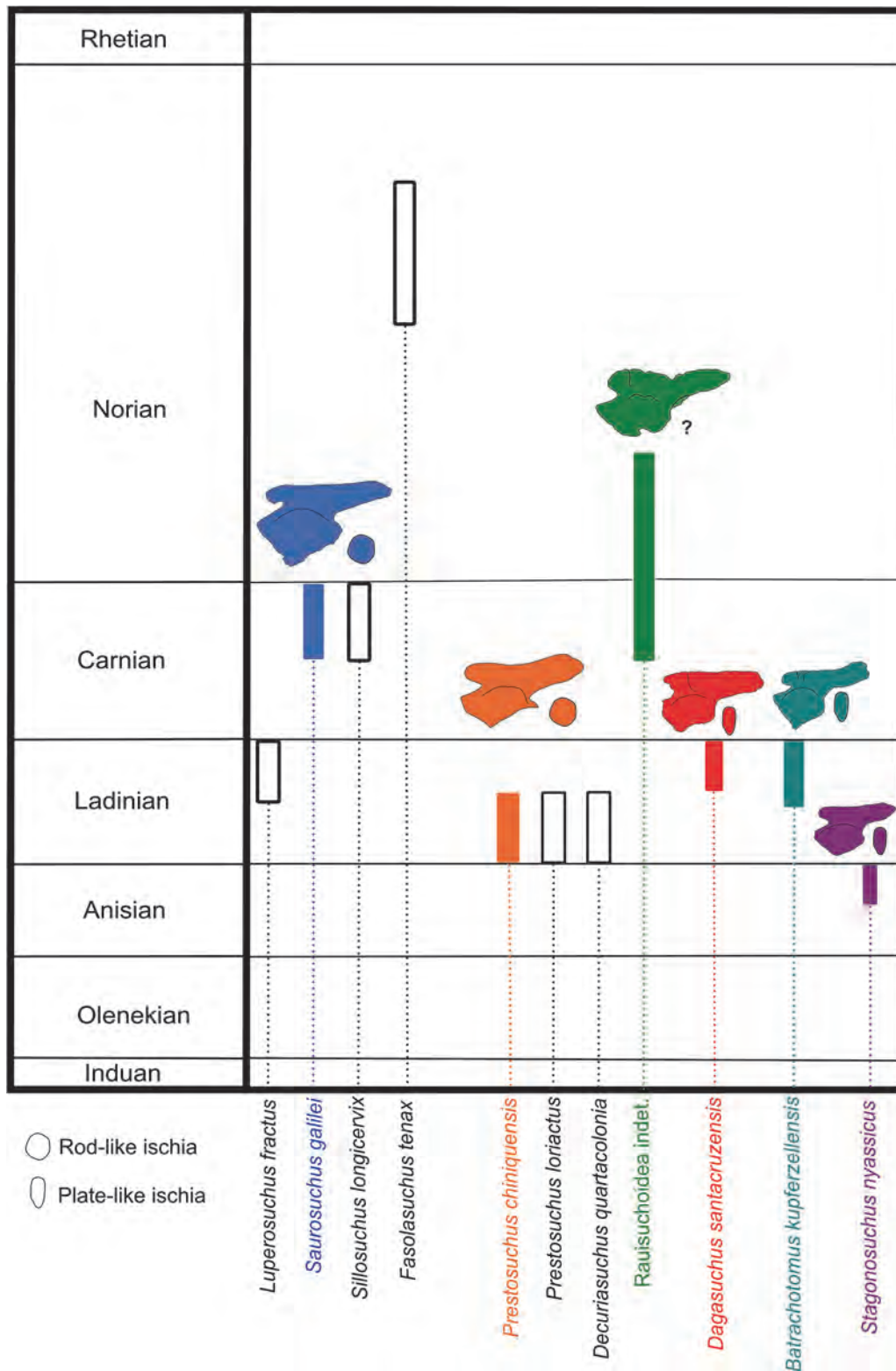


Fig 6. Temporal distribution of 'rauisuchian' taxa of South America and those with morphology of ilia and ischia similar to *Dagasuchus santacruzensis*, emphasizing the shape of the supra-acetabular crest and supra-acetabular ridge on the ilium and the outline of the section of the ischium: *Stagonosuchus nyassicus* (A) and *Batrachotomus kuperzellensis* (B) based on [3]; *Prestosuchus chiniquensis* (C) based on [24] (2010); *Rauisuchoidea* indet. (D) based on [34]; *Saurosuchus gallei* based on [32]. On the right, comparative temporal distribution of these species, along with other South American ones (Modified from [5]). Comparative bones are not to scale.

doi:10.1371/journal.pone.0118563.g006

2. Sereno PC (1991) Basal archosaurs: phylogenetic relationships and functional implications. *J Vert Paleontol* 10 Suppl 3: 1–53.
3. Gower DJ (2000) Rauisuchian archosaurs (Reptilia, Diapsida): An overview. *Neus Jahr Geol P-A* 218: 447–488.
4. Nesbitt SJ (2011) The early evolution of archosaurs: relationships and the origin of major clades. *Bull Am Mus Nat Hist* 352: 1–292.
5. Nesbitt SJ, Brusatte SL, Desojo JB, Liparini A, França MG, Weinbaum JC, et al. (2013) Rauisuchia. In: Nesbitt SJ, Desojo JB, Irmis RB, editors. *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and the Kin*. London: The Geological Society, Special Publications. pp.241–274.
6. Brusatte SL, Benton MJ, Desojo JB, Langer MC (2010) The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). *J Syst Palaeontol* 8: 3–47.
7. Gower DJ (1999) The cranial and mandibular osteology of a new rauisuchian archosaur from the Middle Triassic of southern Germany. *Stuttg Beitr Nat kd B Geol Paläontol* 280: 1–49.
8. Nesbitt SJ (2003) *Arizonasaurus* and its implications for archosaur divergence. *Proc Biol Sci* 270 Suppl 2: S234–237. PMID: [14667392](#)
9. Nesbitt SJ (2005) Osteology of the Middle Triassic pseudosuchian archosaur *Arizonasaurus babbitti*. *Hist Biol* 17: 19–47.
10. Sulej T (2005) A new rauisuchian reptile (Diapsida Archosauria) from the Late Triassic of Poland. *J Vert Paleontol* 25: 78–86.
11. Nesbitt SJ, Norell MA (2006) Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda). *Proc Biol Sci* 273: 1045–1048. PMID: [16600879](#)
12. Jalil N-E, Peyer K (2007) A new Rauisuchian (Archosauria, Suchia) from the Upper Triassic of the Argana Basin, Morocco. *Palaeontology* 50: 417–430.
13. Gower DJ, Schoch RR (2009) Postcranial Anatomy of the Rauisuchian Archosaur *Batrachotomus kupferzellensis*. *J Vert Paleontol* 29: 103–122.
14. França MAG, Ferigolo J, Langer MC (2011) Associated skeletons of a new middle Triassic "Rauisuchia" from Brazil. *Naturwissenschaften* 98: 389–395. doi: [10.1007/s00114-011-0782-3](#) PMID: [21445632](#)
15. Gauthier JA, Nesbitt SJ, Schachner E, Bever GS, Joyce WG (2011) The bipedal stem crocodylian *Poposaurus gracilis*: inferring function in fossils and innovation in archosaur locomotion. *Bull Peabody Mus Nat Hist* 52: 107–126.
16. Trotteyn MJ, Desojo JB, Alcobar OA (2011) Nuevo material postcraneano de *Saurosuchus galilei* Reig (Archosauria: Crurotarsi) del Triásico Superior del centro-oeste de Argentina. *Ameghiniana* 48: 605–620.
17. Weinbaum JC (2010) The skull of *Postosuchus kirkpatricki* (Archosauria: Paracrocodyliformes) from the Upper Triassic of the United States. *PaleoBios* 30: 18–44.
18. Weinbaum JC (2013) Postcranial skeleton of *Postosuchus kirkpatricki* (Archosauria; Paracrocodylomorpha) from the Upper Triassic of the United States. In: Nesbitt S, Desojo JB, Irmis RB, editors. *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and the Kin*. London: Geological Society of London, Special Publications. pp. 525–553.
19. Butler RJ, Brusatte SL, Reich M, Nesbitt SJ, Schoch RR, Hornung JJ (2011) The Sail-Backed Reptile from the Latest Early Triassic of Germany and the Timing and Biogeography of the Early Archosaur Radiation. *PLoS One* 6: e25693. doi: [10.1371/journal.pone.0025693](#) PMID: [22022431](#)
20. Benton MJ (1986) The Late Triassic reptile *Teratosaurus*—a rauisuchian, not a dinosaur. *Palaeontology* 29: 293–301.
21. Zeffass H, Lavina EL, Schultz CL, Garcia AGV, Faccini UF, Chemale F (2003) Sequence stratigraphy of continental Triassic strata of southernmost Brazil: a contribution to southwestern Gondwana palaeogeography and palaeoclimate. *Sediment Geol* 161: 85–105.
22. Horn BLD, Melo TM, Schultz CL, Philipp RP, Kloss HP, Goldberg K (2014) A new third order sequence stratigraphic framework applied to the Triassic of the Paraná Basin, Rio Grande do Sul, Brazil, based on structural, stratigraphical and paleontological data. *J S Am Earth Sci* 55: 123–132.
23. Soares MB, Schultz CL, Horn BLD (2011) New information on *Riograndia guibensis* Bonaparte, Ferigolo & Ribeiro, 2001 (Eucynodontia, Trithelodontidae) from the Late Triassic of southern Brazil: anatomical and biostratigraphical implications. *An Acad Bras Ciênc* 83: 329–354.
24. Mastrantonio BM (2010) Descrição Osteológica de Materiais Cranianos e Pós-cranianos de *Prestosuchus chiniquensis* (Archosauria, Rauisuchia) do Mesotriássico do RS (Biozona de *Dinodontosaurus*, Formação Santa Maria) e Considerações Filogenéticas sobre Rauissúquios. Programa de Pós-Graduação em Geociências: Universidade Federal do Rio Grande do Sul. 247 p.

25. Abdala F, Ribeiro AM (2003) A new traversodontid cynodont from the Santa Maria Formation (Ladinian-Carnian) of Southern Brazil, with a phylogenetic analysis of the Gondwanan traversodontids. *Zool J Linn Soc-Lond* 139: 529–545.
26. Melo TM, Soares MB, Oliveira TV (2009) Primeiro registro do traversodontídeo *Menadon* sp. (Flynn et al. 2000) na Biozona de Traversodontídeos da Formação Santa Maria, Triássico Médio do Rio Grande do Sul, Brasil. *Paleo 2009—Reunião Anual da Sociedade Brasileira de Paleontologia*. Rio Grande do Sul. pp. 16.
27. Raugust T, Lacerda M, Schultz CL (2013) The first occurrence of *Chanaresuchus bonapartei* (Archosauriformes, Proterochampsia) of the Middle Triassic of Brazil from the Santacruzodon Assemblage Zone, Santa Maria Formation (Paraná Basin). In: Nesbitt SJ, Desojo JB, Irmis RB, editors. *Anatomy, Phylogeny and Paleobiology of Early Archosaurs and their Kin*. London: The Geological Society of London. pp. 303–318.
28. Flynn JJ, Parrish JM, Rakotosamimanana B, Ranivoharimana L, Simpson WF, Wyss AR (2000) New traversodontids (Synapsida: Eucynodontia) from the Triassic of Madagascar. *J Vert Paleontol* 20: 422–427.
29. Flynn JJ, Nesbitt SJ, Parrish JM, Ranivoharimanana L, Wyss AR (2010) A new species of *Azendohsaurus* (Diapsida: Archosauromorpha) from the Triassic Isalo Group of southwestern Madagascar: cranium and mandible. *Palaeontology* 53: 669–688.
30. Bertoni-Machado C, Kishlat E-E (2003) Novo registro de Rhadinosaurs (Archosauriformes: Proterochampsia) para o Mesotriássico do Brasil. *Paleo 2003—Paleontologia em Destaque Porto Alegre: Sociedade Brasileira de Paleontologia*. pp. 47. doi: [10.1097/PHM.000000000000020](https://doi.org/10.1097/PHM.000000000000020) PMID: [24247756](https://pubmed.ncbi.nlm.nih.gov/24247756/)
31. Bertoni-Machado C, Holz M (2006) Biogenic fossils concentration in fluvial settings: an example of a cynodont taphocoenosis from the Middle Triassic of Southern Brazil. *Rev Bras Paleontol* 9: 273–282.
32. Sill WD (1974) The anatomy of *Saurosuchus galilei* and the relationships of the rausuchid thecodonts. *Bull Mus Comp Zool* 146: 317–362.
33. Huene FV (1938) Die fossilen Reptilien des südamerikanischen Gondwanalandes. *Neus Jahrb Geol* 1938: 142–151.
34. Lautenschlager S (2008) Revision of *Rauisuchus tiradentes* (Archosauria: Rauisuchia) from the Late Triassic (Carnian) Santa Maria Formation of Brazil and its implications for rausuchian phylogeny: Ludwig Maximilians Universität, 77 p.
35. Gebauer EVI (2004) Neubeschreibung von *Stagonosuchus nyassicus* v. Huene, 1938 (Thecodontia, Rauisuchia) from the Manda Formation (Middle Triassic) of southwest Tanzania. *Neues Jahr Geol P-A* 231: 1–35.
36. Lautenschlager S, Desojo JB (2011) Reassessment of the Middle Triassic rausuchian archosaurs *Ticinosuchus ferox* and *Stagonosuchus nyassicus*. *Paläontolo Z* 85: 357–381.
37. Huene FV (1942) Die fossilen Reptilien des Sudamerikanischen Gondwanalandes. *Ergebnisse der Sauriergrabungen in Sudbrasilien, 1928/1929*. Munchen: C. H. Beck'she. 332 p.
38. Krebs B (1976) Pseudosuchia. In Kuhn O, editor. *Handbuch der Palaeoherpetologie*: Gustav Fischer-Verlag. pp.40–98.

PARTE 2

ARTIGOS DA TESE

ARTIGO 2. LACERDA, M.B.; Mastrantonio, B.M.; Fortier, D.C. & Schultz, C.L. 2016. *New insights on Prestosuchus chiniquensis Huene, 1942 (Pseudosuchia, Loricata) based on new specimens from the “Tree Sanga” Outcrop, Chiniquá Region, Rio Grande do Sul, Brazil.* **PeerJ**, v. 4, p. e1622; DOI: 10.7717/peerj.1622.

New insights on *Prestosuchus chiniquensis* Huene, 1942 (Pseudosuchia, Loricata) based on new specimens from the “Tree Sanga” Outcrop, Chiniquá Region, Rio Grande do Sul, Brazil

Marcel B. Lacerda¹, Bianca M. Mastrantonio¹, Daniel C. Fortier² and Cesar L. Schultz¹

¹Instituto de Geociências, Laboratório de Paleovertebrados, Universidade Federal do Rio Grande do Sul–UFRGS, Porto Alegre, Rio Grande do Sul, Brazil

²CHNUFPI, Campus Amílcar Ferreira Sobral, Universidade Federal do Piauí, Floriano, Piauí, Brazil

ABSTRACT

The ‘rauisuchians’ are a group of Triassic pseudosuchian archosaurs that displayed a near global distribution. Their problematic taxonomic resolution comes from the fact that most taxa are represented only by a few and/or mostly incomplete specimens. In the last few decades, renewed interest in early archosaur evolution has helped to clarify some of these problems, but further studies on the taxonomic and paleobiological aspects are still needed. In the present work, we describe new material attributed to the ‘rauisuchian’ taxon *Prestosuchus chiniquensis*, of the *Dinodontosaurus* Assemblage Zone, Middle Triassic (Ladinian) of the Santa Maria Supersequence of southern Brazil, based on a comparative osteologic analysis. Additionally, we present well supported evidence that these represent juvenile forms, due to differences in osteological features (*i.e.*, a subnarial fenestra) that when compared to previously described specimens can be attributed to ontogeny and indicate variation within a single taxon of a problematic but important osteological structure in the study of ‘rauisuchians.’

Submitted 23 August 2015
Accepted 4 January 2016
Published 1 February 2016

Corresponding author
Marcel B. Lacerda,
marcel.lacerda@yahoo.com.br

Academic editor
Jérémy Anquetin

Additional Information and
Declarations can be found on
page 40

DOI 10.7717/peerj.1622

© Copyright
2016 Lacerda et al.

Distributed under
Creative Commons CC-BY 4.0

OPEN ACCESS

Subjects Paleontology

Keywords Pseudosuchia, Middle triassic, Prestosuchus, Santa Maria Supersequence, Ontogeny

INTRODUCTION

The evolution of archosaurs along the pseudosuchian lineage during the Triassic led to the appearance of many diverse groups that occupied a variety of stages along global trophic webs (*Gauthier, 1984; Gauthier & Padian, 1985; Benton & Clark, 1988; Sereno, 1991; Juul, 1994; Brusatte et al., 2010; Nesbitt, 2011*). Although some taxa can be assigned to clearly monophyletic groups, such as aetosaurs (*e.g. Nesbitt, 2011; Desojo et al., 2013*), a number of forms that historically did not fit within the less inclusive clades were assigned to the ‘Rauisuchia.’ This group is traditionally composed of taxa that possess a variety of body plans, from large-bodied quadruped predators (*e.g. Prestosuchus chiniquensis Huene, 1942, Saurosuchus galilei Reig, 1959, Fasolasuchus tenax*

Bonaparte, 1981) to small cursorial, bipedal, endentulous forms (e.g. *Shuvosaurus inexpectatus* (*Chatterjee, 1993*), *Effigia okeeffeae* (*Nesbitt & Norell, 2006*)) but due to shared cranial traits (additional openings in the dermatocranium) and similarities in hindlimb, pelvic and ankle morphologies (*Gower, 2000; Nesbitt et al., 2013*) were “bunched” together. There is no current consensus on the taxonomic definition of “Rauisuchia” and the content of the different proposed subgroups (Rauisuchidae, Prestosuchidae, Poposauridae, Chatterjeeidae) has varied (*Gower, 2000; Nesbitt, 2011; Nesbitt et al., 2013*). Most phylogenetic studies lack a consensus on the stability of the group, since there are no clear ‘rauisuchian’ apomorphies (*Gower, 2000; Nesbitt et al., 2013*). Among the proposed hypotheses, some have considered them as monophyletic (*Brusatte et al., 2010; França, Ferigolo & Langer, 2011*) or paraphyletic (*Benton & Clark, 1988; Parrish, 1993; Juul, 1994; Weinbaum & Hungerbühler, 2007; Gauthier et al., 2011; Nesbitt, 2011; Butler et al., 2011*), with recent works discussing the abandonment of the name altogether (see detailed discussion in *Nesbitt et al. (2013)*). The problematic alpha taxonomy of this group is due, in part, to the incomplete condition of many of the described specimens (*Gower, 2000; Nesbitt, 2011; Nesbitt et al., 2013*). However problematic, “Rauisuchia” is still used in recent works (e.g. *Nesbitt et al., 2013*), but placed between commas, to reflect the unclear affinities. Since the topic of the present article is beyond this problem, we will follow this trend in referring to this group to simplify the presentation of our work.

‘Rauisuchians’ displayed a temporal range from the Early to Late Triassic (*Butler et al., 2011*), with their fossils being found in all continents except Antarctica (*Benton, 1984; Benton, 1986; Bonaparte, 1984; Gower, 2000; Nesbitt et al., 2013*). In South America, they are found in Brazil and Argentina. In the latter, the oldest taxon is *Luperosuchus fractus* (*Romer, 1971*) from the Chañares Formation (Middle-Late Triassic) (*Romer, 1971; Desojo & Arcucci, 2009*). Among Late Triassic taxa, *Sillosuchus longicervix* (*Alcober & Parrish, 1997*) and *Saurosuchus galilei* occur in the Ischigualasto Formation (*Sill, 1974; Alcober & Parrish, 1997; Alcober, 2000; Nesbitt, 2011; Trotteyn, Desojo & Alcober, 2011; Nesbitt et al., 2013*), whereas *Fasolasuchus tenax* (*Bonaparte, 1981*) occurs in the Los Colorados Formation (Late Triassic).

In Brazil, all ‘rauisuchian’ taxa are found only in the Pinheiros-Chiniquá and Santa Cruz sequences of Santa Maria Supersequence of the Rio Grande do Sul State (*Zerfass et al., 2003; Horn et al., 2014*). In this region, during the 1920’s, the German paleontologist Friedrich von Huene and his collaborators discovered the first fossil remains of what he would later designate as ‘rauisuchians.’ The species described were *Rauisuchus tiradentes*, *Prestosuchus loricatus*, *Prestosuchus chiniquensis* and *Procerosuchus celer* (*Huene, 1935–42; Huene, 1942*). Of these, *Prestosuchus chiniquensis* and *Prestosuchus loricatus*, occur in the Pinheiros-Chiniquá Sequence, (Middle Triassic, *Dinodontosaurus* Assemblage Zone; (*Zerfass et al., 2003; Langer et al., 2007; Mastrantonio, 2010; Soares, Schultz & Horn, 2011; Horn et al., 2014*). *Prestosuchus chiniquensis* and *Prestosuchus loricatus* have been considered as synonyms by *Krebs (1976)* and *Barberena (1978)*, but *Desojo & Rauhut (2009)* argued that only the paralectotype of *P. loricatus* can be attributed to *P. chiniquensis*, while the lectotype would be of a different species. This issue was also discussed by *Kischlat (2000)*, who attributed it to the new genus “*Abaporu loricatus*,”

but this proposal is problematic because this designation only appears in the above-mentioned publication as a new generic proposal for *P. loricatus*, but this is not clearly stated in the text. As such, this proposal was not formally presented, which would be invalid according to the ICZN. Due to these problems, we consider only *Prestosuchus chiniquensis* as a valid species since it presents more referred specimens (see below).

A large skull and postcranial elements (UFRGS-PV-0156-T) were assigned to *Prestosuchus chiniquensis* by [Barberena \(1978\)](#); [Azevedo \(1991\)](#); [Azevedo \(1995a\)](#); [Azevedo \(1995b\)](#) and other authors ([Sereno, 1991](#); [Parrish, 1993](#); [Schultz & Langer, 2007](#); [Mastrantonio, 2010](#)). [Kischlat & Barberena \(1999\)](#) proposed that it represents a new taxon, along with the paralectotype of *Prestosuchus chiniquensis* (BSPG 1933L/7). Afterwards ([Kischlat, 2000](#)) considered the more complete specimen UFRGS-PV-0152-T as belonging to this taxon, but some of the characters used in this hypothesis are problematic and have been discussed by other authors (e.g. [Mastrantonio, 2010](#)). Also, as in the case of “*Abaporu loricatus*,” there are nomenclatural complications.

In an abstract, [Kischlat & Barberena \(1999\)](#) referred to this new taxon as *Crurotarsi indeterminata*, pending an official taxonomic proposal, but in a book chapter published a year later, [Kischlat \(2000\)](#) already cites “*Karamuru vorax*” as a valid taxon, considered as being proposed in the above-mentioned abstract. In his doctoral thesis ([Kischlat, 2003 v.1: 261](#)) presents a “preliminary exercise in description . . .” of this taxon, pending a formal publication, thus the name “*Karamuru vorax*” also does not follow the ICZN parameters and must also be considered *nomen nudum*. A much more detailed discussion on this topic will be presented in a future work by other researchers (Julia Desojo, personal communication).

A mostly complete specimen (~75%) attributed to *Prestosuchus chiniquensis* was described by [Mastrantonio \(2010\)](#) with a more detailed description of the braincase being published later ([Mastrantonio et al., 2013](#)). This is the most complete specimen described for this species thus far and has also added to the knowledge of possible ontogenetic variation in ‘rauisuchians’ ([Mastrantonio, 2010](#); [Mastrantonio et al., 2013](#); [Nesbitt et al., 2013](#)), possible paleobiological implications ([Liparini, 2008](#); [Liparini & Schultz, 2013](#)) and phylogenetic analysis ([Mastrantonio, 2010](#); [Mastrantonio et al., 2013](#)). Another well preserved and mostly complete specimen attributed to *P. chiniquensis* was discovered in the same locality as UFRGS-PV-0629-T, but it remains in preparation and study ([Cabreira et al., 2010](#)). The specimen UFRGS-PV-0152-T was also referred to *Prestosuchus* by [Nesbitt \(2011\)](#), but was never fully studied. A detailed description of this specimen will be published in a future work (Tiago Raugust, personal communication).

Hoplitosuchus rauli was described by [Huene \(1935–42\)](#) and [Huene \(1942\)](#) as being a “rauisuchian,” but in a brief revision of this material by [Desojo & Rauhut \(2008\)](#) it was found to be composed by a mix of dinosaur and pseudosuchian remains and thus would be a *nomen dubium*. Previously, a right femur (BSPG AS XXV 53) and tibia (BSPG AS XXV 54) assigned to this taxon were used by [Kischlat & Barberena \(1999\)](#) to propose a new basal dinosaur taxon; “*Teyuwasu barbarenai*.” However, [Ezcurra \(2012\)](#), in a recent revision, considered *T. barbarenai* as a *nomen dubium*, due to the lack of any autapomorphies or unique combination of characters combined with the poor state of

preservation of the specimen, even though it has features that are consistent with Dinosauromorpha and more inclusive clades (*i.e.* the possible presence of an anterior trochanter on the femur and the tibia with asymmetric posterior condyles on the proximal end). *Huene (1935–42)* & *Huene (1942)* also described *Procerosuchus celer*, which is considered a juvenile form of *Prestosuchus chiniquensis* (*Kischlat, 2000; Desojo & Rauhut, 2009*). The only recently described ‘rauisuchian’ for the *Dinodontosaurus* Assemblage Zone is *Decuriasuchus quartacolonía* (*França, Ferigolo & Langer, 2011*), based on 10 mostly incomplete but well preserved specimens.

In the other assemblage zones there are other ‘rauisuchian’ taxa; *Dagasuchus santacruzensis* (*Lacerda, Schultz & Bertoni-Machado, 2015*) was described for the *Santacruzodon* AZ (Middle Triassic; *Bertoni-Machado & Holz, 2006; Soares, Schultz & Horn, 2011*) and *Rauisuchus tiradentes* from the *Hyperodapedon* AZ (Late Triassic) (*Huene, 1935–42; Huene, 1942; Lautenschlager & Rauhut, 2014*).

In the present article, we contribute to the knowledge of ‘rauisuchians’ from the Brazilian Triassic with the description, taxonomy and phylogenetic analysis of at least two new individuals and attribute them to *Prestosuchus chiniquensis*. These fossils are from part of an assemblage that was collected in the Xiniquá (also spelled Chiniquá) region of the central Rio Grande do Sul State (*Desojo, Ezcurra & Schultz, 2011*). Based on comparative osteological and corroborative histological analysis (*Cerda et al., 2013*), these specimens contribute to the understanding of ontogenetic variation within this taxon and this variation would impact important characters that are used in cladistics studies of these forms.

Institutional abbreviations

BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany; **CPEZ**, Paleontology Collection of the Museu Paleontológico e Arqueológico Walter Ilha, São Pedro do Sul, Brazil; **MCN**, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre; **MCP**, Paleontology Collection of the Museu de Ciências e Tecnologia of the Pontifícia Universidade do Rio Grande do Sul, Porto Alegre, Brazil; **MCZ**, Museum of Comparative Zoology, Harvard, Cambridge, United States of America; **MSM**, Arizona Museum of Natural History, Mesa, United States of America; **NHMUK**, Natural History Museum, London, United Kingdom; **PULR**, Museu de Ciencias Naturales, Universidad Nacional de La Rioja, La Rioja, Argentina; **PVL**, Instituto Miguel Lillo, Tucuman, Argentina; **PVSJ**, Division of Vertebrate Paleontology of the Museo de Ciencias Naturales de la Universidad Nacional de San Juan, San Juan, Argentina; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **UFRGS-PV**, Paleovertebrate Collection of the Laboratório de Paleovertebrados of the Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; **ZPAL**, Institute of Paleobiology, Polish Academy of Science, Warsaw, Poland.

Geological setting

The assemblage was discovered in an outcrop which belongs to the Pinheiros-Chiniquá Sequence of the Santa Maria Supersequence (*Horn et al., 2014*). The outcrop, like

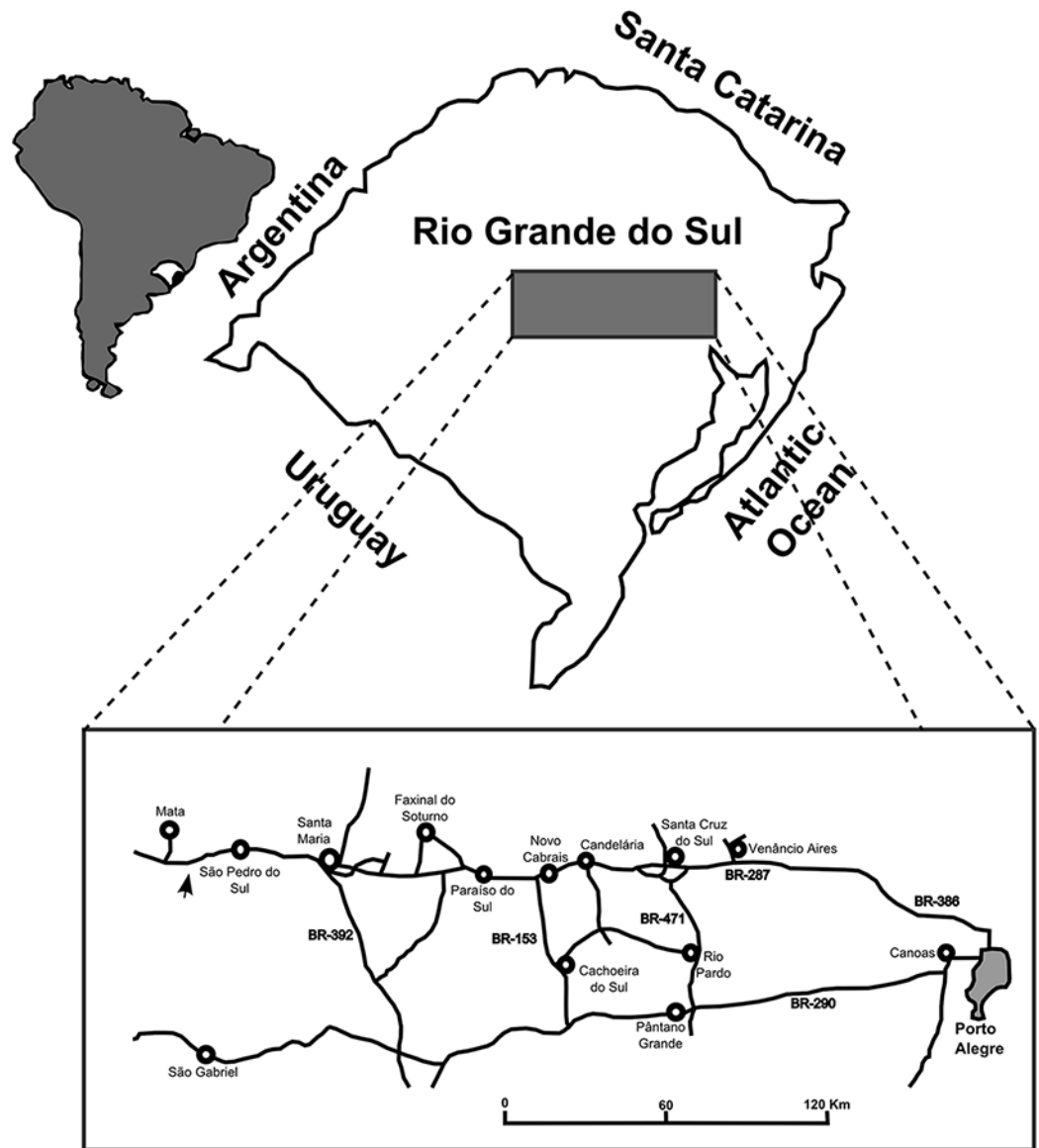


Figure 1 Map of the location of the “Tree Sanga” outcrop. Location of the “Tree Sanga” outcrop, indicated by the arrow (Modified from [Reichel et al. \(2005\)](#)).

others in the general area, is composed of massive red mudstones. Biostratigraphically, it is within the *Dinodontosaurus* Assemblage Zone, which can be correlated with the Chañares fauna of the Chanãres Formation of Argentina ([Rubert & Schultz, 2004](#); [Langer et al., 2007](#)). Chronologically, it is considered of Ladinian or Ladinian-earliest Carnian age ([Desojo, Ezcurra & Schultz, 2011](#); [Fiorelli et al., 2013](#); [Mancuso et al., 2014](#)).

The site is located between the cities of São Pedro do Sul, Mata and São Vicente do Sul (approximate coordinates: 29°39'21"S, 54°25'38"W (UTM: 21J 749033 6716582)), 71 km from Santa Maria ([Fig. 1](#)). This region is where Huene collected fossils in his visit to the Rio Grande do Sul State in 1928–29 and also where *Stahleckeria potens* ([Huene, 1942](#)), *Prestosuchus chiniquensis* ([Huene, 1942](#)) and *Hoplitosuchus raii* ([Huene, 1942](#)) were

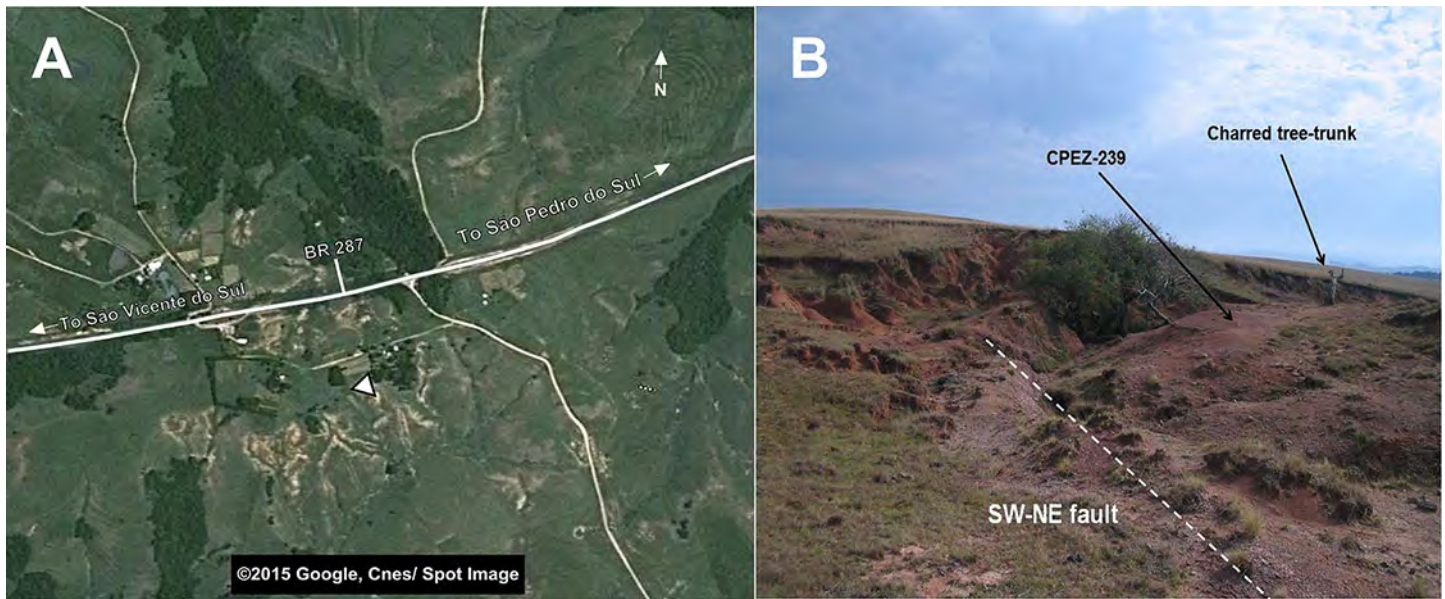


Figure 2 Images of the general area near the “Tree Sanga” outcrop. (A) Satellite image of the general area of the outcrop; (B) Picture of the outcrop indicating details and the area where the CPEZ-239 fossil assemblage was discovered. Map data ©2015 Google Cnes/Spot Image.

discovered. Unfortunately, the exact location of the discoveries is now lost (*Desojo, Ezcurra & Schultz, 2011*). This is mostly due to the loss of the reference points that Huene used in his field notes, possibly due to almost 90 years of erosion combined with growth of vegetation cover and human activities (see full discussion below).

Another feature of this outcrop is the existence of a subvertical fault plane that is oriented southwest-northeast. Although it is not possible to ascertain the presence of a significant horizontal displacement between the layers on both sides of the fault, its presence would indicate that the fossils on either side of the fault might have been preserved in strata of different ages. Furthermore, the existence of nearby outcrops that display layers of approximately 5 m of vertical displacement would corroborate this condition (*Fig. 2*).

MATERIALS AND METHODS

Huene (1935–42) coined one of the outcrops of this region “Baum Sanga” (=Tree Sanga) due to the presence of a large “Timbaúva” tree (*Enterolobium contortisiliquum*). *Beltrão (1965)* reported that this tree was later struck by lightning and burned, but some of its original remains were still present at the outcrop up until the 1960’s. During the discovery of the assemblage in the early 1990’s, there were pieces of a charred tree trunk and roots close by, but with the lack of the reference points used by Huene to identify the original site, there is no certainty if this would be the its true location. A query with the owner of the private property where the original sanga and the outcrop are located, whose family lives on the land since before the time of Huene’s expedition, was unproductive (Max Langer, personal communication). As such, it is unclear if the original “Tree Sanga” and the outcrop where CPEZ-239 was discovered are the same place or are two different

sites. As it is impossible to clarify this problem at the present time, we choose to follow to the designation of the site as proposed previously by [Desojo, Ezcurra & Schultz \(2011\)](#).

The assemblage was collected at an elevation slightly above the area near the charred tree remains. Initially, it received the designation CPEZ-239 when it was deposited in the paleontological collection of the Museu Paleontológico e Arqueológico Walter Ilha in the city of São Pedro do Sul. [Desojo, Ezcurra & Schultz \(2011\)](#) described the archosauriform *Archeopelta arborensis* based on part of the material and designated it as CPEZ-239a, while the rest was designated CPEZ-239b. It was never fully prepared nor described and only the complete femur was used in a comparative morphometric study ([Pretto et al., 2008](#)) and was referred as “cranial and postcranial remains of a medium-sized ‘rauisuchian’ by [Desojo, Ezcurra & Schultz \(2011:841\)](#). Portions of an osteoderm from a cervical vertebra were used in a histological study by [Cerdeira et al. \(2013\)](#).

The material CPEZ-239b is comprised of cranial and post-cranial elements of at least two individuals of roughly the same size, based on the presence of 2 sets of mandible bones of similar dimensions (e.g. articulated right maxilla with a length of 186 mm while the disarticulated right maxilla has 173 mm; complete measurements presented in the supplementary material). Of cranial elements, there is an articulated rostrum and posterior portion of a skull with associated mandibular elements and two separate jaws of a second skull. Of post-cranial material, there is a vertebral sequence including the axis, the first 8 cervical vertebrae and 3 neural arches of indeterminate position in the axial sequence. All these vertebrae display osteoderms. A right scapula and coracoid and a dorsal portion of a scapula are the only elements preserved of a shoulder girdle, while the pelvic girdle is represented by a fragment of an anterior process of an iliac blade and a ventral portion of a right ischium.

The appendicular elements are represented by a complete right humerus and an incomplete left ulna, while of the posterior elements there is a complete left femur, the distal portion of a right femur and an incomplete left tibia. The autopodials are represented only by a right fifth metatarsal and some incomplete phalanges.

The preparation of these fossils occurred in two stages: the first one was made following the fossils discovery. Along with mechanical preparation, dilute hydrochloric acid was used, but the concentration is unknown. Unfortunately, further damage to the bones occurred due to complications in the chemical preparation, hindering the clarity of some anatomical details. The fossil was originally covered by a thick layer of shellac resin, which was used as an adhesive, and the acidic reaction melted the resin which resulted in a yellowish overall hue and covering foramina, sutures and other small details in certain areas.

The second stage of preparation of this material started in 2009 by one of us (M.B.L.) as the focus of his M.Sc. dissertation, at the Laboratory of Paleovertebrados of the Universidade Federal do Rio Grande do Sul (UFRGS). At this stage, only mechanical preparation was used, where the fossils were prepared using pneumatic hammers and engravers, dental instruments, needles, hammers and chisels. Because several pieces were already fragile, some were not fully prepared so as not to risk further damage or loss. To depict these features in the schematic drawings, the grey areas indicate matrix/adhesive cover and the dark grey areas indicate damaged ones.

To facilitate the description of the more representative material (a skull with mandible), the articulated portion of the rostrum was designated “Series A,” while a posterior portion, which also features vertebrae associated with the posterior portion of a mandible was designated “Series B.” The disarticulated skull elements were not given a specific designation and have been described separately as with the rest of the material based on which body or appendage section they belong.

In the description of the cervical vertebrae, only the right side was described, because the left side was too damaged to allow visualization of structures clearly.

A comparative morphological study was made based on the observation of material at the Paleovertebrate Collection of the Laboratório de Paleovertebrados of the Universidade Federal do Rio Grande do Sul (UFRGS-PV-0156-T and UFRGS-PV-0629-T, both assigned to *Prestosuchus chiniquensis* (Azevedo, 1991; Mastrantonio, 2010)) and specimens described in the literature. The result was then tested by cladistic methodology, using TNT version 1.1 (Goloboff, Farris & Nixon, 2008). The details of this process will be discussed in the appropriate sections.

As was presented previously, CPEZ-239b consists of at least two individuals of the same species based on two pairs of morphologically similar jaw material of approximately the same size. The pattern of disarticulation of the posterior portion of a skull matches the state of the articulated rostrum (left side more disarticulated than the right one). However, it is impossible to rule out that more than two individuals are present in the assemblage, since that besides the cervical sequence that articulates with the Series B, is impossible to assign the remaining post-cranial bones at the individual level.

Systematic paleontology

Archosauria Cope, 1869 (*sensu* Gauthier & Padian, 1985)

Pseudosuchia Zittel, 1887–1890 (*sensu* Gauthier & Padian, 1985)

Suchia Krebs, 1974 (*sensu* Benton & Clark, 1988)

Loricata Merrem, 1820 (*sensu* Nesbitt, 2011)

Prestosuchus Huene, 1942

Prestosuchus chiniquensis Huene, 1942.

Lectotype (Krebs, 1976): BSPG 1933L 1-3/5-11/28-41/41 (Excavation 34; Huene, 1942): Splenial, anterior portion of the surangular, anterior portion of the angular, prearticular, right partial maxilla, fragmentary dentary, three incomplete cervical vertebrae, fragmentary ribs, one sacral vertebrae, two sacral ribs, five anterior caudal vertebrae with chevron bones, 14 middle and posterior caudal vertebrae, right and left scapulacoracoid, interclavicle and clavicle, distal left humerus, right proximal and distal humerus, distal radius, fragmentary ulna, one manual phalanx, incomplete ilium, fragmentary ischia, pubes and a complete left hind limb.

Paralectotype: BSPG 1933L/7 (Excavation 41; Huene, 1942): a articulated vertebral sequence, composed of two sacral vertebrae with sacral ribs, incomplete last dorsal and first caudal vertebrae, dorsal portion of the right ilium, a series of osteoderms articulated with the neural spines.

Type Locality and Stratigraphic horizon: “Weg Sanga,” Pinheiros-Chiniquá Sequence of the Santa Maria Supersequence, (Ladinian), *Dinodontosaurus* Assemblage Zone.

Diagnosis: Two autapomorphies are described for this taxon ([Desojo & Rauhut, 2008](#)): an anterior notch between the scapula and the coracoid; a longitudinal ridge on the dorsal surface of the ilium. Although *P. chiniquensis* is one of the better represented ‘rauisuchian’ taxa from Brazil, only two specimens are relatively complete (see below), so the taxonomic designation of all the additional specimens was made due to overlapping characters and tested in recent phylogenetic analyses ([Brusatte et al., 2010](#); [Mastrantonio, 2010](#); [Nesbitt, 2011](#); [França, 2011](#); [Mastrantonio et al., 2013](#)). However a detailed revision of all the described specimens is needed to achieve a clear diagnosis.

Additional specimens

UFRGS-PV-0156-T ([Barberena, 1978](#); [Azevedo, 1991](#)): A large and complete skull, 31 vertebrae, including the axis, many with articulated osteoderms, along with unidentified fragmentary material;

UFRGS-PV-0629-T ([Mastrantonio, 2010](#); [Mastrantonio et al., 2013](#)): A mostly complete specimen, composed of a complete but disarticulated skull, complete presacral vertebrae sequence (eight cervical, 13 dorsal), two sacral and three caudal vertebrae; complete scapular and pelvic girdle, mostly complete appendicular elements, composed of both humerus; proximal portions of the left ulna and radius; one left metacarpal of an anterior *manus*; femora, a right tibia and fibula, three isolated phalanges of a *pes*;

UFRGS-PV-0473-T ([Mastrantonio et al., 2013](#)): an isolated braincase that was attributed, with uncertainty, to *Prestosuchus chiniquensis*, based on similarities between it and those of UFRGS-PV-0156-T and UFRGS-PV-0629-T;

UFRGS-PV-0152-T ([Nesbitt, 2011](#)): A mostly complete specimen. It is composed of an incomplete skull, with maxillae, nasals, quadrates, partial quadratojugal, braincase, parietal, ectopterygoid, partial pterygoid, jugal, squamosal, anterior portion of the dentary, prearticular, articular, vertebral sequence composed of cervical, dorsal, sacral and caudal elements, complete scapular and pelvic girdles, humerus, proximal portion of a ulna, femora, tibia and fibulas, complete calcaneum and *pes*, chevrons and osteoderm cover. [Nesbitt \(2011:33\)](#) considered this specimen to be indistinguishable from UFRGS-PV-0156-T and BSPG XXV 1-3/5-11/28-41/41, due to overlapping features, but as it is now still being fully studied (as mentioned above), we will consider [Nesbitt’s \(2011\)](#) interpretation of this specimen.

MCP-146 ([Bonaparte, 1984](#)): A complete pelvic girdle with the last dorsal, two sacral and three caudal vertebrae preserved in articulation. This specimen is roughly the same size as the one in UFRGS-PV-0629-T and was figured in [Bonaparte \(1984\)](#), but this author considered the first caudal vertebra as belong to the sacral sequence. A new inspection by one of us (M.B.L.) indicates that this might not be the case, but a detailed review will be presented in a future work.

MCZ 4167 ([Parrish, 1993:297](#)): composed of a poorly preserved but articulated specimen from the Santa Maria Formation, referable to *Prestosuchus*, but no other information is available on this specimen.

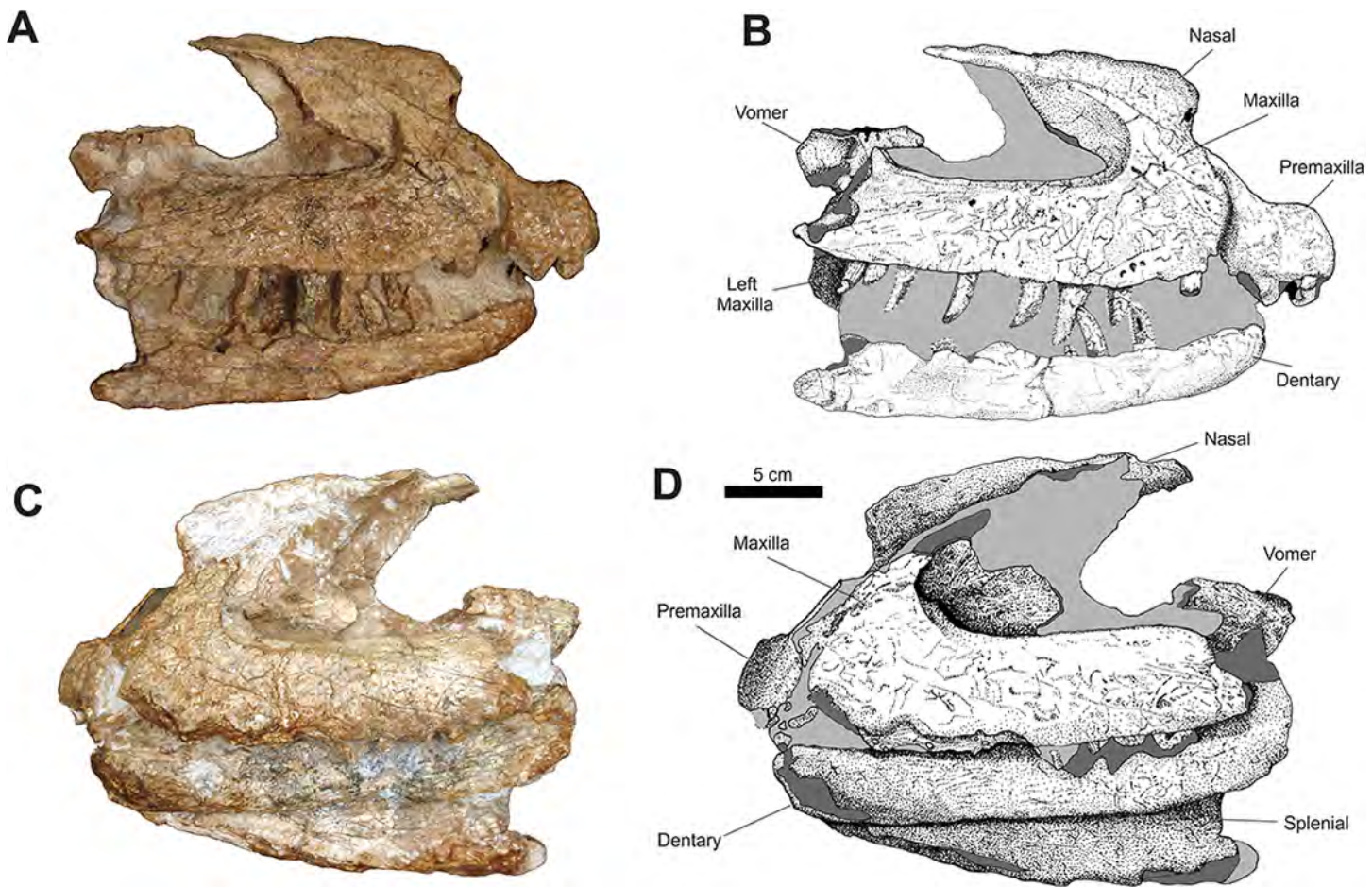


Figure 3 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, Series A, composed of an incomplete rostrum and anterior portion of a mandible. (A–B) right and (C–D) left lateral views.

Description

Series A (articulated rostrum and anterior mandibular rami)

In the anterior portion of the rostrum, both premaxillae are articulated, but are separated from the rest of the rostrum and laterally dislocated, causing a distortion on the anterior part of the rostrum (Fig. 3).

In lateral view, the main portion of the premaxillae is sub-rectangular, with its anterior margins slightly convex. A small depression in the anterodorsal area that, in dorsal view, displays a circular fracture that would correspond to the site of the anterior process. The anterior processes are lost, while the posterior processes are preserved, but incomplete, lacking the posterior tips. These processes are slender, similar to those in *Prestosuchus chiniquensis* (UFRGS-PV-0156-T and UFRGS-PV-0629-T; [Azevedo, 1991](#); [Mastrantonio, 2010](#)), but not as dorso-ventrally wide as that of *Fasolasuchus tenax* ([Bonaparte, 1981](#)) and *Saurosuchus galilei* ([Alcober, 2000](#)). However, they are not as slender as those of *Decuriasuchus quartacolonina* ([França, Ferigolo & Langer, 2011](#)).

One incomplete premaxillary tooth is preserved, near a cluster of fragments of rock, bone and other teeth, which is located ventroposteriorly to the ventral margin of the left

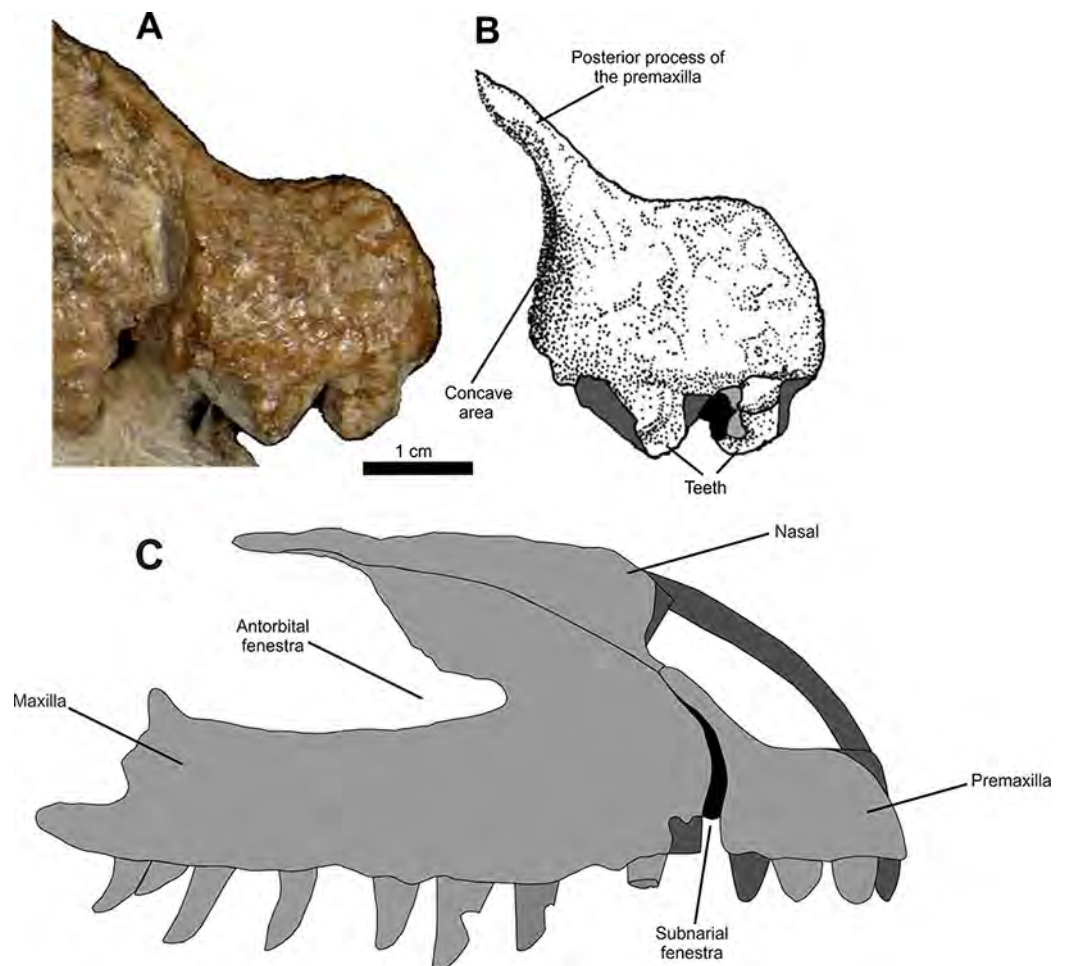


Figure 4 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, detail of the right premaxilla of Series A and its possible articulation. (A–B) indicating its posterior margin and the concave surface; (C) reconstruction of right premaxilla and maxilla, in lateral view, indicating the possible size and appearance of the subnarial fenestra.

premaxilla. On its ventral margin, the right premaxilla displays three incomplete teeth and one alveolus, which is exposed due to a fracture on the lateral surface, indicating the total count of four premaxillary teeth. This condition is described for *Saurosuchus galilei* (Reig, 1959; Sill, 1974; Alcober, 2000), *Fasolasuchus tenax* (Bonaparte, 1981), *Batrachotomus kupferzellensis* (Gower, 1999), *Postosuchus kirkpatricki* (Long & Murry, 1995; Weinbaum, 2011), *Polonosuchus* (Sulej, 2005), *Rauisuchus tiradentes* (Huene, 1935–42; Huene, 1942; Lautenschlager & Rauhut, 2014), *Prestosuchus chiniquensis* (Mastrantonio, 2010) and *Decuriasuchus quartacolonina* (França, Ferigolo & Langer, 2011).

The posteroventral border of the right premaxilla is slightly curved anteriorly, forming a low, concave area on the posterior surface, followed by a thickened area that expands posteriorly on its posteroventral margin (Fig. 4). This concave surface is morphologically similar to the anterior margin of the subnarial fenestra described for *Saurosuchus galilei* (Alcober, 2000), *Decuriasuchus quartacolonina* (França, Ferigolo & Langer, 2011) and, in lesser form, *Postosuchus kirkpatricki* (Weinbaum, 2011). Also, it is larger than the one

described for *Prestosuchus chiniquensis* (UFRGS-PV-0629-T; [Mastrantonio, 2010](#)) and while the posteroventral border of the premaxilla is similar to that of other taxa (e.g. *Rauisuchus tiradentes*; [Lautenschlager & Rauhut, 2014](#)), in other specimens of *Prestosuchus chiniquensis* (UFRGS-PV-0156-T), this area is almost vertical and doesn't display any rough area.

In CPEZ-239b, the right maxilla of the articulated rostrum is the one that is best preserved. In lateral view, its main portion is sub-rectangular and anteroposteriorly elongated. The ascending process is dorsoposteriorly orientated and is articulated with the ventral part of the right nasal. The dorsoposterior portion of this process is incomplete, with only an irregular dorsoventrally expanded plate of bone that forms the dorsal and anterodorsal margins of the antorbital fenestra. This area of the ascending process is located more medially than the rest of this region, boarded anteriorly by a well-marked fossa that margins the anterior to the antorbital fenestra.

The ventral border of the antorbital fenestra projects posteriorly, displaying a small ridge that precedes a small, dorsoposteriorly arranged, triangular process located on its posterior end. After this process, the border of the maxilla continues ventroposteriorly up to a fracture located above the ventral margin. The lateral surface of the posterior half of this maxilla, next to region of this fracture, is slightly lateromedially flattened. On the ventral margin, posterior to the ventral border of the premaxilla, there is a fracture that displays an empty alveolus. After this fracture, the border is damaged but displays the proximal portion of a tooth, and continues along a slight curvature, above which are three small foramina. After this curvature, the ventral margin straightens and is almost parallel to the ventral margin of the antorbital fenestra.

In lateral view, the left maxilla has its anterior margin damaged, with the area that would contact the premaxilla medially curved and with a smooth surface. There is a sinuous fracture that exposes small tooth fragments. After this fracture, this margin continues straight until its posterior portion displaying three incomplete teeth.

On its dorsal margin, the ascending process is incomplete, with only its ventral portion preserved. The sheet of bone that would correspond to the medial portion of the antorbital fossa is dorsoventrally expanded and only the area closest to the anterior tip of the antorbital fenestra is preserved. The left antorbital fossa is deeper than its right counterpart, but this condition is possibly due to diagenetic factors, since the left maxilla is more laterally expanded than the right one.

The shape of the anterodorsal border of the maxilla and its proximity to the antorbital fenestra is very similar to that found in *Prestosuchus chiniquensis* (UFRGS-PV-0156-T, UFRGS-PV-0629-T), *Teratosaurus suevicus* (NHM 38646), *Polonosuchus silesiacus* (ZPAL AbIII/563) and *Batrachotomus kupferzellensis* (SMNS 80260), which are comparatively anteroposteriorly shortened, whereas this same region in *Fasolasuchus tenax* (PVL 3851) and in a lesser condition in *Saurosuchus galilei* (PVL 2062; PVSJ 32) tends to be more elongated posteriorly. The overall aspect of the ascending process and the fossa of the antorbital fenestra is very similar to that present in *Prestosuchus chiniquensis* (UFRGS-PV-0156-T and UFRGS-PV-0629-T). In specimen UFRGS-PV-0156-T both suffered diagenetic alteration.

The two nasals are preserved in the articulated rostrum of the Series A. Both bones are incomplete, with only the medial portion closest to the contact of both nasals being preserved. In lateral view, the right nasal is articulated with the ascending process of the right maxilla and with the left nasal. Its descending process is medial to the ascending process of the premaxilla due to the dislocation of the latter.

The anterior portion of the right nasal is laterally compressed. This area is almost flat and is projected anterodorsally, exposing a part of the inner channel of the nasal and its posterior portion is convex. Above this area, the margin of the nasal is orientated dorsally until it is parallel to the sagittal axis, where it follows posteriorly, with a slight concave area on half its body. A small laterally projected ridge is present and follows until the end of the preserved bone. A portion of the posterior length of the nasal is visible posteriorly to the lateromedially compressed area.

The nasals are similar to those of *Saurosuchus galilei* (Alcober, 2000) and of *Prestosuchus chiniquensis* (UFRGS-PV-0156-T and UFRGS-PV-0629-T). A rugose area present along the dorsoventral margin of this bone is described for *Batrachotomus* and *Postosuchus*, while a more reduced one is described for *Prestosuchus* and *Rauisuchus*. Furthermore, in the former taxon, a depression on the dorsal area of the skull is similar to the one present on the nasals of CPEZ-239b.

In lateral view, the convex aspect of the nasals appears to form a roman nose aspect that is described in some taxa. However, this is not the case in CPEZ-239b, since both bones were laterally compressed, which clearly caused a dorsoventral expansion of the nasals that gave them the aforementioned aspect.

Associated to the dorsoposterior portion of the maxilla and located medially in this series are two incomplete vomers. In lateral view, their form is of an irregular lateromedially compressed bones that are dorsally dislocated. Their anterior portion is absent and the posterior portion displays a small depression, limited anteroventrally by two small, damaged and incomplete ridges. On the ventral portion of the left vomer there is an incomplete process that is oval in shape, and is slightly lateromedially flattened, which is located ventrally to its anterior portion. This appears to be a border of a fenestra, but due to the incomplete nature of this bone, it is impossible to correctly determine.

Of the incomplete jaw, the right mandibular ramus displays an anteroposteriorly elongated dentary, which is slightly curved anteriorly, with a short dorsoventral convex expansion on its anterior tip in lateral view. On its ventral margin, there are five incomplete teeth while the rest of the alveoli are not visible. In lateral view, the left mandibular ramus is more dorsally placed than its right counterpart, located almost between the right and left maxillae. In this view, only the dentary is present. This bone is fractured on its anterior edge and displays a posterior margin that is more complete than the right one, but due to damage by chemical preparation, it is impossible to identify sutures or if there are any other parts of articulated jaw bones. In left lateral view, the right splenial is visible and articulated on the medial side of the right mandibular ramus. The dorsal portion of this bone is hidden due to the obstruction of the left mandibular ramus, but it appears that its overall aspect is of a sub-triangular bone, with its tip orientated

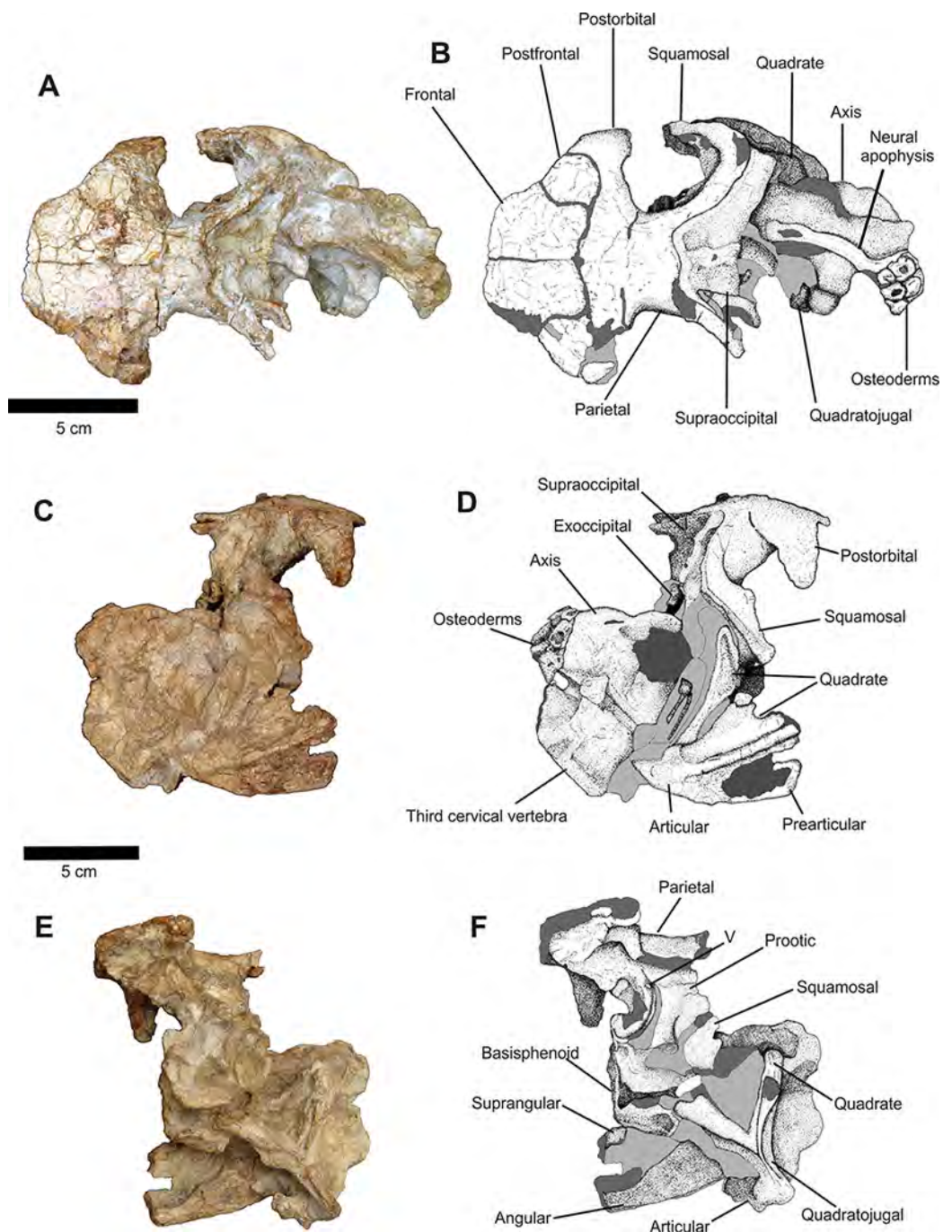


Figure 5 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, Series B composed of dermal roof, neurocranium and mandibular elements. (A–B) dorsal, (C–D) right lateral and (E–F) left lateroventral views.

anteriorly and its ventral margin following obliquely the ventral border of the dentary, until near the posterior border of the latter, where it projects dorsally by a sinuous suture along a fractured area.

Series B (posterior portion of a skull and mandibles)

The majority of the sutures of the dermal bones in this series have been eroded and the contact between the bones has been widened (Fig. 5). However, these sutures appear to not have been completely fused initially. The anterior end of the skull roof is formed by the posterior portions of two incomplete frontals, with the right one being better preserved, while the left one displays a large fracture on its lateral portion. They are sub-rectangular, dorsoventrally compressed bones that meet lateroposteriorly with the dorsomedial border of the postfrontal. Posteriorly, a large suture (that clearly has been widened due to preservation) delimitates the articulation with the postfrontals and with the anterior margin of the parietals.

The postfrontals are small, circular in dorsolateral view, dorsoventrally flattened bones that form, along with the lateral border of the frontals and the anterior margin of the postorbitals and the dorsoposterior border of the orbit. This detail is better preserved on the right side of the skull.

The right postorbital is better preserved than its left counterpart. In dorsal view, it is articulated ventrolaterally with the postfrontal, which projects laterally to form, a ventrally projected process that would form the ventroposterior margin of the orbit which is more clearly visible in lateral view. Of the left postorbital, only the portion close to the articulation with the other bones of the skull roof is preserved.

It is unclear if the parietals are fused since the corresponding area is badly damaged. Although there are fractures running parallel to the sagittal axis of this element(s), we describe the parietal as a single bone. It is located on the third half of this part of the skull. In dorsal view, the parietal is sub-rectangular, laterally convex, with its anterior portion expanded anterolaterally, articulating with the posterior margin of the frontal and the postorbital along the widened suture. From its middle half, two posterior processes project posterolaterally, with the right one being better preserved than its left counterpart, and delimitating the posterior margin of the skull with the occipital region and forming the dorsal and dorsoposterior border of the supratemporal fenestra. There is no evidence of a sagittal ridge, condition similar to what is found in *Prestosuchus chiniquensis* (Mastrantonio, 2010) and *Saurosuchus galilei* (Alcober, 2000).

The overall aspect of the right supratemporal fenestra is less damaged than the left one. Both the interior portions of the fenestra are smooth, with no indication of a ridge or any other structure. On the lateral margin of the parietal, located medially to the supratemporal fenestra, there is a small ridge that limits both fenestra, but this structure is clearly due to a fracture on both the lateral sides of the parietal.

In right lateral view, the dorsoposterior border of the orbit curves lateroventrally, forming a slender, ventrally projected process that is composed of part of the postfrontal and of the postorbital, that is dorsoventrally elongated and has a damaged rounded tip.

The posterior portion of the parietal displays a slight ventral curvature. In lateral view, it is possible to see that the body of this element forms all the dorsolateral wall of the dorsal region of the neurocranium. It is not possible, in this view, to establish the presence of a suture between the parietal and the dorsal elements of the skull due to preservation.

The right squamosal is a lateromedially compressed bar that is positioned ventrally, starting from its suture with the parietal and ending in a rounded area, which marks the dorsoposterior margin of the infratemporal fenestra, while also being projected slightly anteriorly. There is no evidence of an anterior process (the “stepped” middle portion *sensu* (Brusatte *et al.*, 2010), that would be an anterior projection of the squamosal in the infratemporal fenestra) on the anterior margin of the squamosal.

Located posteriorly to the squamosal there is an incomplete ramus of the right quadratojugal. It is dislocated posterolaterally and is more medially displaced than the squamosal, close to the lateral area of the occipital region. A ventral portion of the quadratojugal is near to the dorsal margin of the portion of the right mandibular ramus that is associated in this series.

In right lateral view, the prootic is present, but its exact form cannot be determined and its contact with other elements is not clear. Anteroventrally, its anterior margin meets the laterosphenoid and forms the posterior border of the trigeminal foramen. The area circumventing this foramen on the right side is expanded and damaged. Ventroposteriorly to the prootic, a large circular, indeterminate fragment is located, with a concave surface on its dorsolateral area. This fragment covers the right lateral side of the neurocranium, along with a concretion composed of fragments of sediment and bones. Due to the damaged condition already discussed, this area was not further prepared.

Two incomplete quadrate parts are preserved. The first one is the dorsal portion that is associated to the lateral portion of the quadratojugal. The other part is the ventral third of this element that is still articulated with the posterior portion of the right mandible. This portion of the mandible is dislocated posterodorsally and is positioned dorsally on the posterior portion of the skull.

The majorities of the dermal bones on the left side of the posterior part of the skull area are disarticulated or absent, thus exposing the neurocranium in lateral view. The absence of sutures appears to indicate that an incomplete left prootic occupies all the dorsal portion of the neurocranium, ventrally to the parietal and separated by a fracture. Its anterior margin is sinuous and follows posteroventrally to a lateral fossa, where the trigeminal foramen is located, close to a large fracture. This area continues deeply from its anterior border and curves anteriorly, forming a similar structure to a channel that would be the area of the eustachian tube. Furthermore, this area was distorted to the left at an approximately 45° angle.

On its lateral body, the left prootic is bordered ventrally by an area of concretion. Dorsal to this, there is an incomplete portion of the prootic ridge, highlighted from the rest of the prootic because it is laterally expanded and with an oval cavity located ventrally. The overall shape of this area and the position of the foramen are almost identical to the one on the right side of the skull and, aside from the trigeminal foramen, there is no evidence of foramina on this bone.

The basisphenoid is split in two halves that are dislocated along the sagittal plane, with the left half being oriented more dorsally while the right one is located more ventrally. Both halves are dislocated laterally, following the deformation of the anterior portion of the neurocranium. The ventral portion of the right one is visible and is sub-rectangular

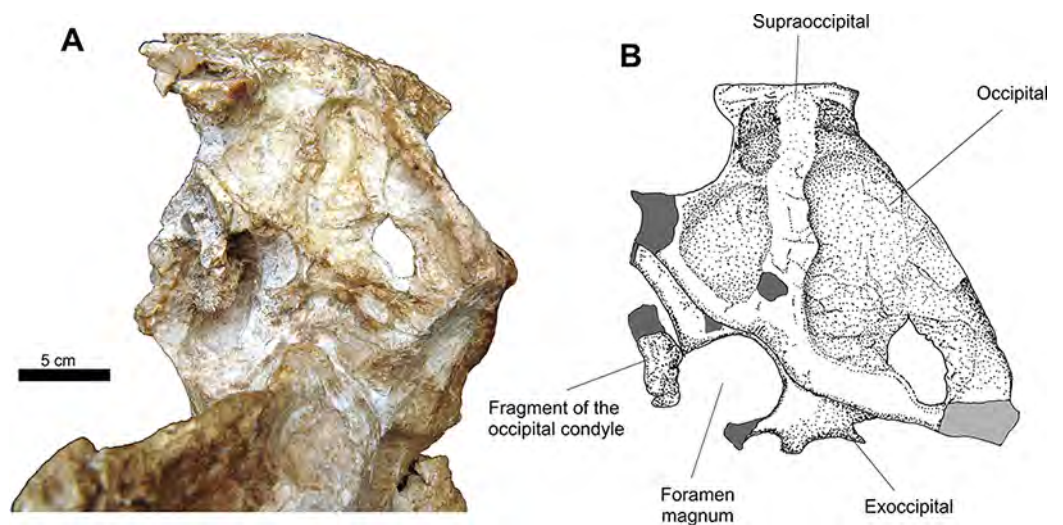


Figure 6 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, detail of Series B in occipital view. (A) close up picture of the cranial elements of Series B in occipital view; (B) close up illustration of the area around the foramen magnum.

in form, with a shallow fossa on its posterior half. A fragment of the dorsal portion of the left squamosal is preserved but is dislocated ventrally near an opening formed by an extension composed of part of a concretion and the posterior portion of the basisphenoid, leaving only the lateroposterior portion of the left squamosal visible.

The quadratojugal is divided into two parts. Its dorsal portion is adhered to a concretion and is laterally dislocated, positioned ventrolaterally to the foramen magnum. The other portion is located near the posterior of Series B, lateral to the associated cervical vertebrae. The form of the quadratojugal is of a tri-radiated bone that has an anterior process projected medially, with its anterior tip located close to the medial region of the left portion of the basisphenoid. Another process is oriented dorsally and located laterally to the left quadrate. It follows posteriorly the main body of the quadratojugal along a posterior process of the left quadrate that extends a little short of ventral area of articulation of this bone. A fragment of the medial face of the quadratojugal, arranged more medially, is articulated with the articular surface of the quadrate. Their overall aspect is similar to the ones found in *Batrachotomus* (SMNS 52970 and 80260), *Saurosuchus* (PVSJ 32) and *Prestosuchus* (UFRGS-PV-0156-T and UFRGS-PV-0629-T) with the position of the quadratojugal and the jugal being similar to the one in *Prestosuchus*, where the quadratojugal in lateral view is more exposed than the jugal.

The quadrate, in lateral view, is articulated with the quadratojugal, but is positioned more medially among the dorsal and posterior processes of this bone and is located close to the lateral area of the cervical vertebrae. Its aspect is of anteroposteriorly elongated bone, with a slightly convex body that ends in a concave, lateromedially expanded, articular condyle.

A small fragment, anteriorly orientated, and articulated with the medial border of the quadrate and lateroventrally to the third cervical vertebra, is possibly a piece of the medial portion of the articular of the left mandible.

The occipital region is incomplete (Fig. 6). There are two fragments of the exoccipital that border the foramen magnum and two other elements that are the dorsoposterior portion of the basioccipital. Due to diagenetic alteration, this region was pushed anteriorly, which resulted in the posterior portion of the neurocranium being anteroventrally inserted in the skull cavity while another dislocation further altered this area in the horizontal plane. This is inferred based on the odd arrangement of the occipitals relative to the rest of the skull and the absence of the lateral portions of the exoccipitals, the paraoccipital process of the opisthotics and the uneven level of the suture of the supraoccipital with the exoccipitals.

The supraoccipital is sub-triangular, meeting dorsally with the posterior margin of the parietal and directed ventrally with lateral expansions, until it is articulated with the occipitals, similar to the ones found in *Batrachotomus* (SMNS 80260), *Prestosuchus* (UFRGS-PV-0156-T), *Saurosuchus* (PVSJ 32) and *Arizonasaurus* (MSM P4590). The left lateral and ventral border of this bone are distorted due to compression, which resulted in the left side of this element being comparatively smaller than its right counterpart. A crooked, low dorsal ridge is present. On both sides of this ridge there are shallow fossae.

The exoccipitals form the lateroposterior border of the foramen magnum and are articulated with the occipital dorsally along the ventral margin of this bone. The posterior process of the left exoccipital is more complete than its right counterpart, with a fragment of the occipital condyle of the basioccipital preserved.

Associated with this series is an incomplete posterior portion of a right mandibular ramus. In right lateral view, it is impossible to identify the sutures of the bones that would compose this structure. This portion of the mandibular ramus is anteroposteriorly elongated, with its ventral border curving anteroposteriorly up to the posterior margin of the articular. Ventrally to this contact there is a well-defined ridge that is parallel to the dorsal margin and continuously reduces in height up to the lateroposterior face of the articular.

In left lateral view, only the posterior portion of the prearticular and the medial portion of the surangular are preserved. The prearticular is expanded anteroposteriorly, with its dorsal border parallel to its ventral margin, until a dorsoposterior border. The surangular is a mostly flat bone, which displays a depression on its medial surface.

Disarticulated skull elements

The left and right isolated maxillae do not display any great morphological differences in comparison to the maxillae present in the Series A. The most notable variation between these two isolated elements is that, in lateral view, the right maxilla is more anteroposteriorly elongated while the left one is comparatively shorter and its anterior portion is more dorsoventrally expanded. The preserved incomplete teeth are similar to those found in the articulated rostrum, but their condition is poor and it is impossible to determine the number of alveoli on each maxilla. In medial view, both maxillae display articulated, slightly sub-rectangular dental plates. On their medial side, these plates are perforated by small foramina (Figs. 7 and 8).

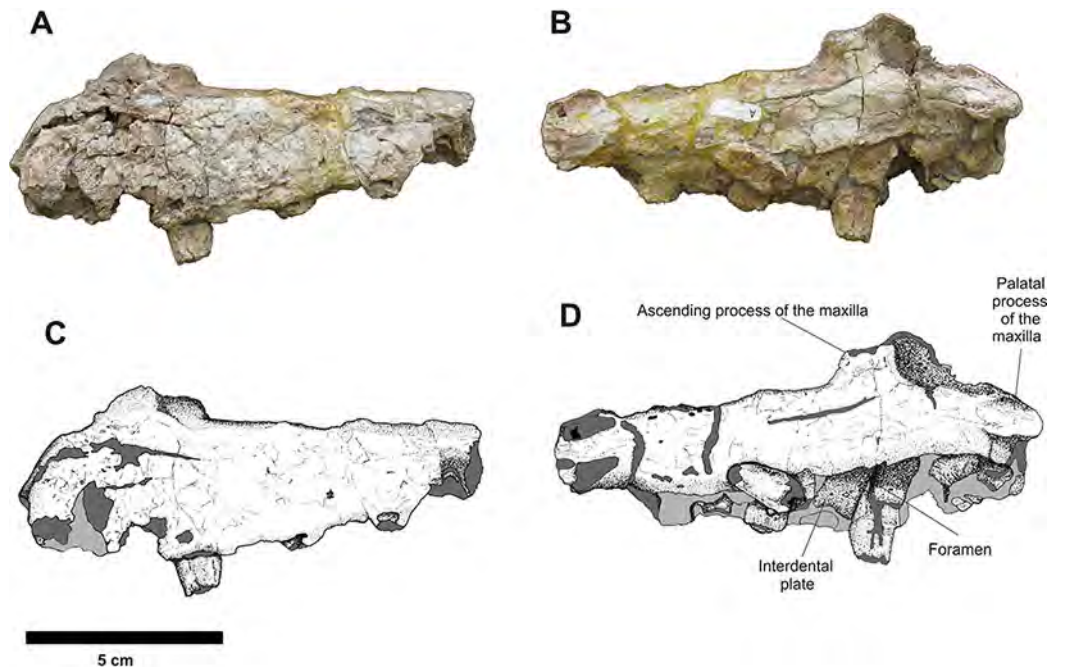


Figure 7 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, left desarticulated maxilla. (A–C) lateral and (B–D) medial views.

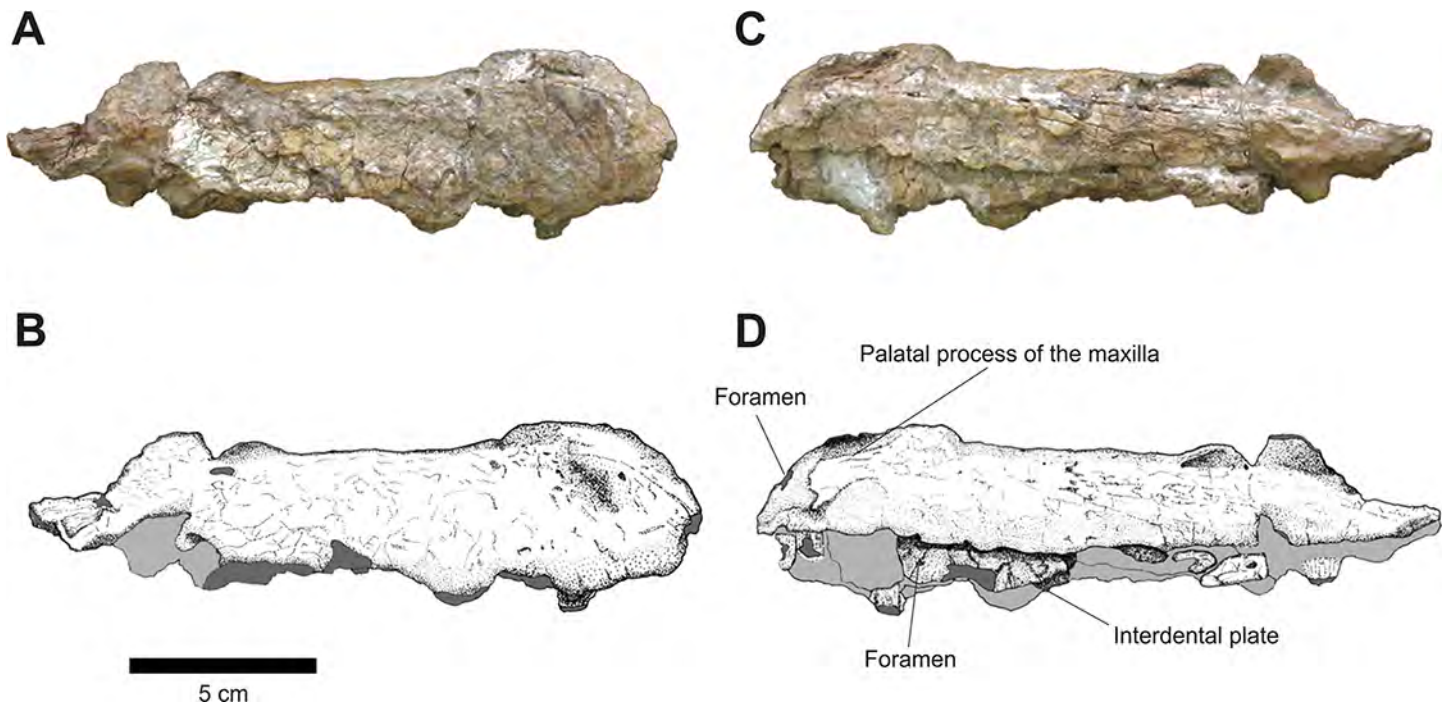


Figure 8 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, desarticulated right maxilla. (A–B) lateral and (C–D) medial views.

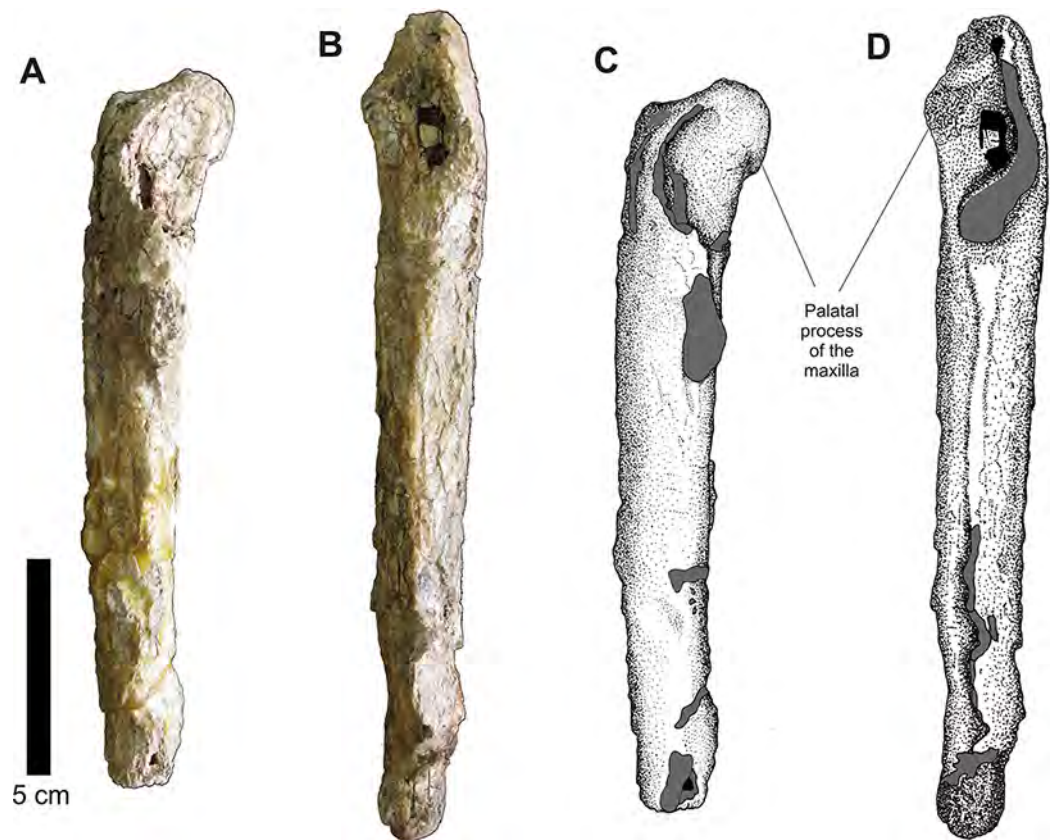


Figure 9 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, desarticulated maxillae. (A–C) left and (B–D) right desarticulated maxillae in dorsal views.

In dorsal view, the right desarticulated maxilla is elongated and lateromedially compressed. Its anterior portion displays a medial orientated curvature that forms the palatal process (= anteromedial process; Galton, 1985). This process extends beyond the anterior border of the maxilla. On its anterior face, there exists a small opening that would be for the passage of a rostralateral/anterior opening foramen. This structure is better preserved on the left maxilla, because the same area on the right one has a fracture that begins on the most anterior margin and continues posterolaterally along the lateral surface of this bone (Fig. 9).

The presence of only one lateral anterior foramen is described in suchian taxa for *Teratosaurus suevicus* (Galton, 1985), *Batrachotomus kuperferzellensis* (Gower, 1999), *Polonosuchus silesiacus* (Sulej, 2005) and *Prestosuchus chiniquensis* (Mastrantonio, 2010). In CPEZ-239b, both desarticulated maxilla display a small opening in the general region where this foramen occurs in other taxa, but their position varies slightly in both elements due to diagenetic alteration of the dimensions of the bones.

Both isolated nasals are in articulation (Fig. 10). The left nasal has its anterior portion orientated horizontally while its posterior portion is projected anteroposteriorly. Anteriorly, on the left nasal, there is a preserved portion of the anterodorsal process and the posterior margin of the external naris. A fracture along the rugose area on the

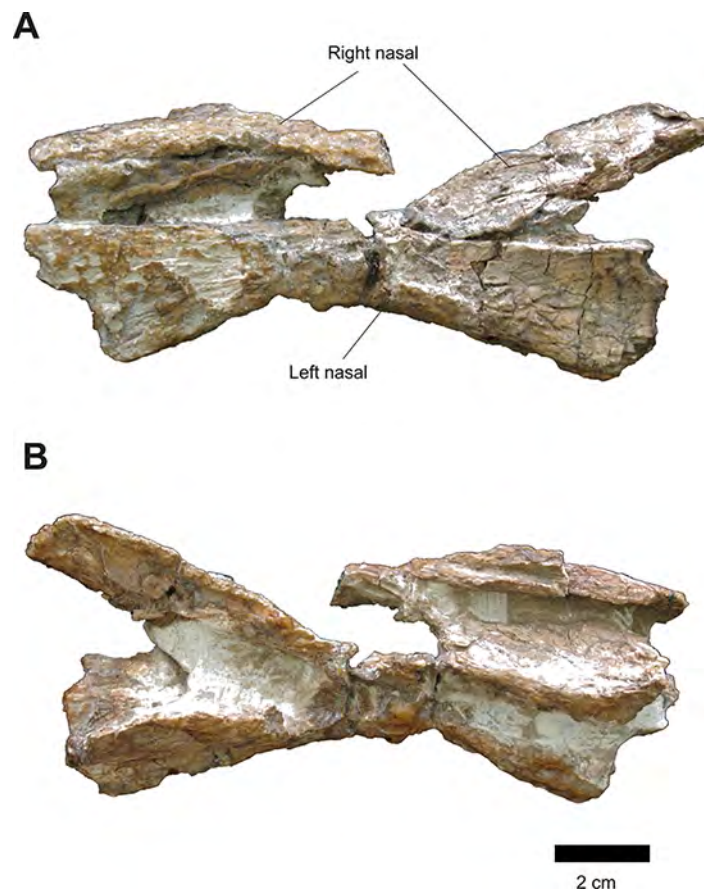


Figure 10 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, left and right disarticulated nasals. (A) dorsal and (B) ventral views.

laterodorsal face of this nasal caused its posterior portion to be split in two. Apparently, the right nasal suffered a compression, leaving it with a concave form and its lateral border directed medially.

In medial view, there is a sheet of bone that is similar to the one that separates the nasal septum, but in this case, it is likely to be medial portion of a nasal that is distorted and turned ventrally. The left nasal is compressed laterally, being represented only by the portion that would contact the right nasal, in lateral view, the compression of the left nasal is more apparent. The form of the nasal is overall similar to those of the Series A. Furthermore, the left nasal displays a shallow depression on its posterior portion that would be similar to that present on the right nasal of the Series A.

There is only one articulated left lacrimal and prefrontal in this assemblage of bones. They are associated to the ventral portion of a cervical vertebrate sequence (Fig. 11). In lateral view, the lacrimal is rectangular, with its posterior portion slightly expanded dorsoventrally and the anterior portion is incomplete. Dorsoposteriorly, there occurs a thickening, forming a ridge that extends up to the end of the dorsal margin and continues ventrally along the posterior border. On the end of this ridge, located ventroposteriorly, there exists a small structure that would be the dorsal margin of the lacrimal canal.

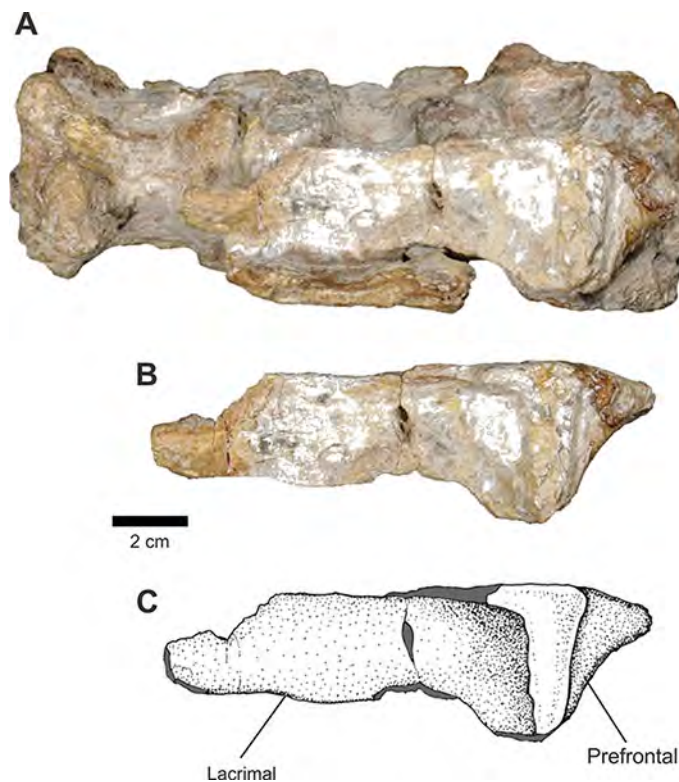


Figure 11 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, left lacrimal and prefrontal. (A) ventral portion of the cervical vertebrae; (B) close-up and (C) schematic illustration of the left lacrimal and prefrontal in lateral views.

The anterior portion of the prefrontal is triangular shaped, with its vertices posteriorly directed. This point is a small process that projects posteriorly and whose tip is absent. Its surface of articulation with the lacrimal is a wide area that occupies all the anterior margin of the body of the prefrontal.

Of the isolated mandibular elements, there are two damaged, incomplete left and right rami. The right one is better preserved than its left counterpart. Also, the left one is more lateromedially expanded, that probably caused its break and distortion, as well as the alteration in the orientation of its dorsal margin. This alteration makes both fragments seem to be of the same side, but the distortion of the dorsal margin is clear and there are pieces of the left splenial on its medial side.

The right mandible, in dorsal view, is elongated and compressed lateromedially. It also displays a medial pointing distortion that is more pronounced on its anterior and posterior sides. Due to its preservation, it's possible that this distortion was heightened by diagenetic action, especially on its posterior region. There are five incomplete teeth and some alveolus are present in this ramus, but its dorsal border displays large concretions that makes it impossible to establish the exact number of teeth.

In medial view (Fig. 12), the area of articulation of the mandibular symphysis of the right incomplete mandible is broken. On its dorsal margin, there are a series of incomplete teeth and the dorsal margin of fractured dental plates. The splenial is an

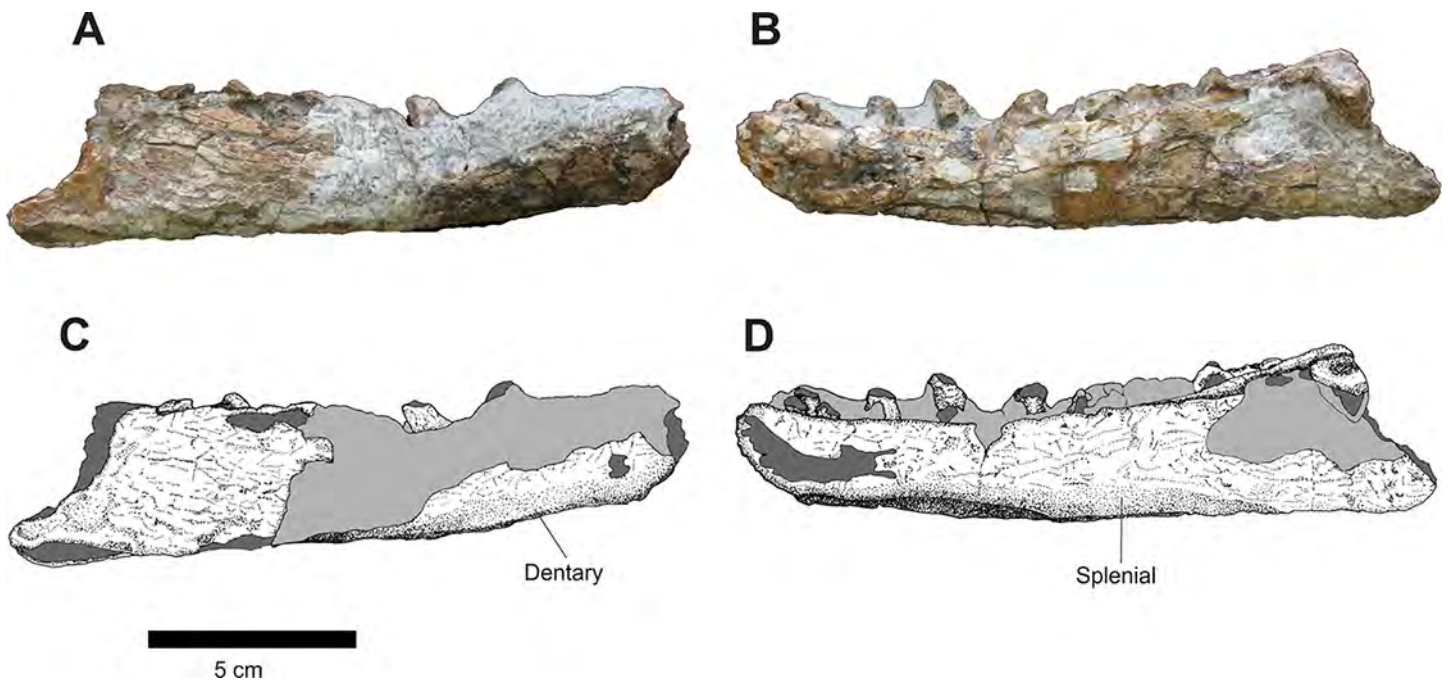


Figure 12 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, desarticulated right mandibular ramus. (A–C) lateral and (B–D) medial views.

elongated bone. Its anterior portion contacts the posterior margin of the approximated area of the contact with the mandibular symphysis by a long, anterior process, which follows dorsally up to the border of the dentary. The ventral margin follows the length of the ventromedial surface of this bone, while its dorsal margin is too damaged to establish its limits.

The left mandible is the most damaged (Fig. 13). A large fracture on its posterior half shows a mesial located area that would be the space for the meckelian channel. In medial view, it is similar to its right counterpart, but possibly due to the fracture, the dentary is more laterally displaced while the splénial is comparatively located more medially.

Of the disarticulated mandibular rami, the right one displays eight incomplete teeth and an undetermined number of alveoli due to concretions. Furthermore, there is no evidence of dental plates. On the left one, there are six incomplete teeth. The more ventrally located tooth is exposed, laterally, due to the damaged state of this ramus, and is still located inside its alveolus.

An incomplete posterior portion of the left mandible is preserved (Fig. 14). In lateral view, the anterior portion of this fragment is formed by the posterior margin of an incomplete surangular located anterodorsally with the anterolateral portion of the prearticular located ventrally. The articular is preserved and occupies the area of this fragment. Its shape is sub-triangular, with a rounded area of articulation corresponding to its apex directed posteriorly. At the dorsal edge of the articular, after a fracture located on the edge of its posterior margin, there is a slightly perpendicular, laterally

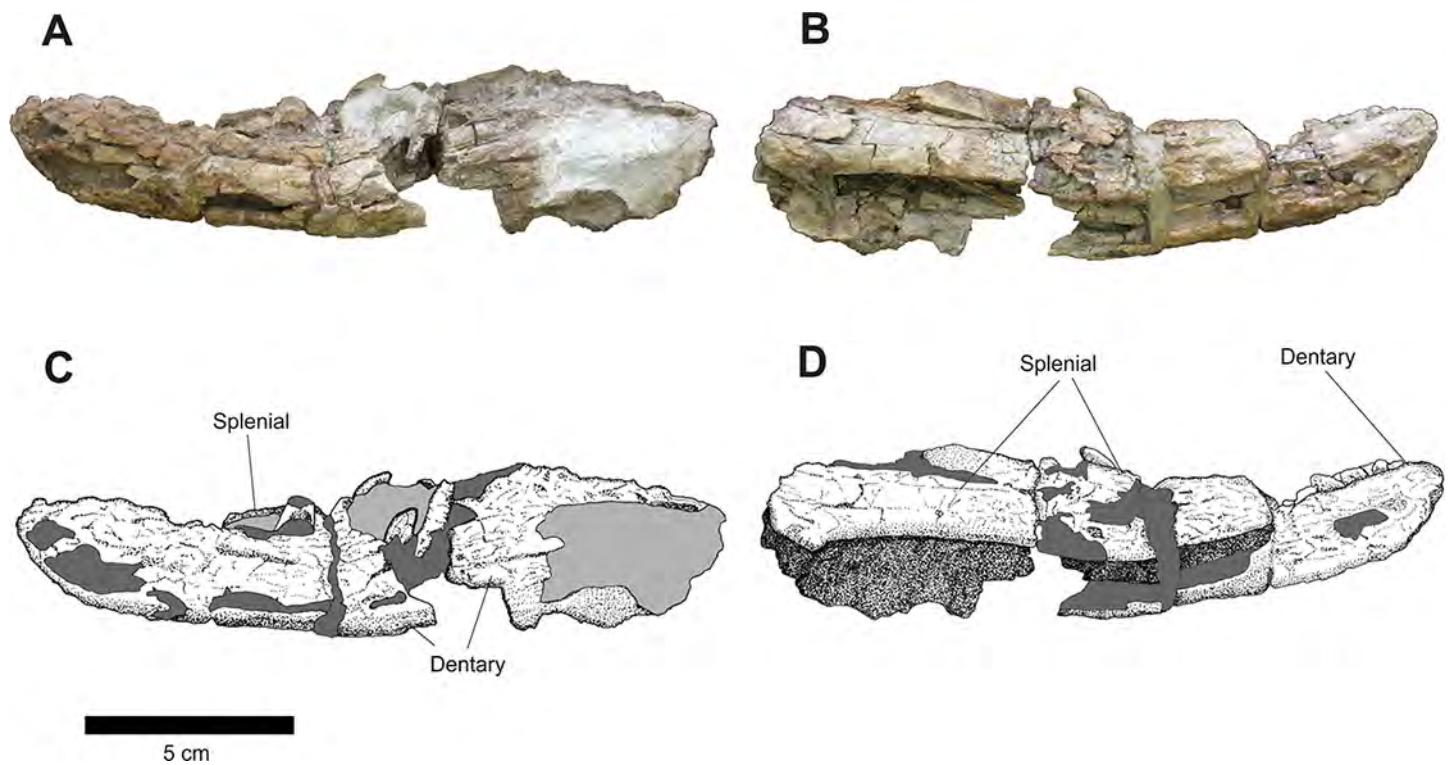


Figure 13 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, desarticulated left mandibular ramus. (A–C) lateral and (B–D) medial views.

projected crest, whose height continuously decreases up to near the posterior portion of the articular.

In medial view, a large concretion occupies the entire medial portion of this fragment. The medial aspect of the supraoccipital occupies the anterodorsal portion of this ramus, while incomplete fragments of the prearticular occupy the ventral region of the posterior fragment of the left mandible. In the posterior portion, located after a damaged area and a concretion is the process of the medial region of the retro-articular joint. This process forms a basis for a dorsoventral fossa, located posteriorly on the medial side of the joint.

Postcranial elements

Of the axial skeleton, there are seven cervical vertebrae, separated into three sets (Fig. 15) and three incomplete vertebrae represented only by parts of the neural arches, not being possible to infer their place in the vertebral series (Fig. 17).

The cervical vertebrae, with the exception of the axis and the third cervical vertebra, have only the right side preserved enough to identify their structures, while the left is severely damaged by acid corrosion. Additionally there are four incomplete cervical ribs, preserved in articulation with on vertebrae Cv5, Cv7 and Cv8 and only the dorsal portion of the rib preserved in Cv6.

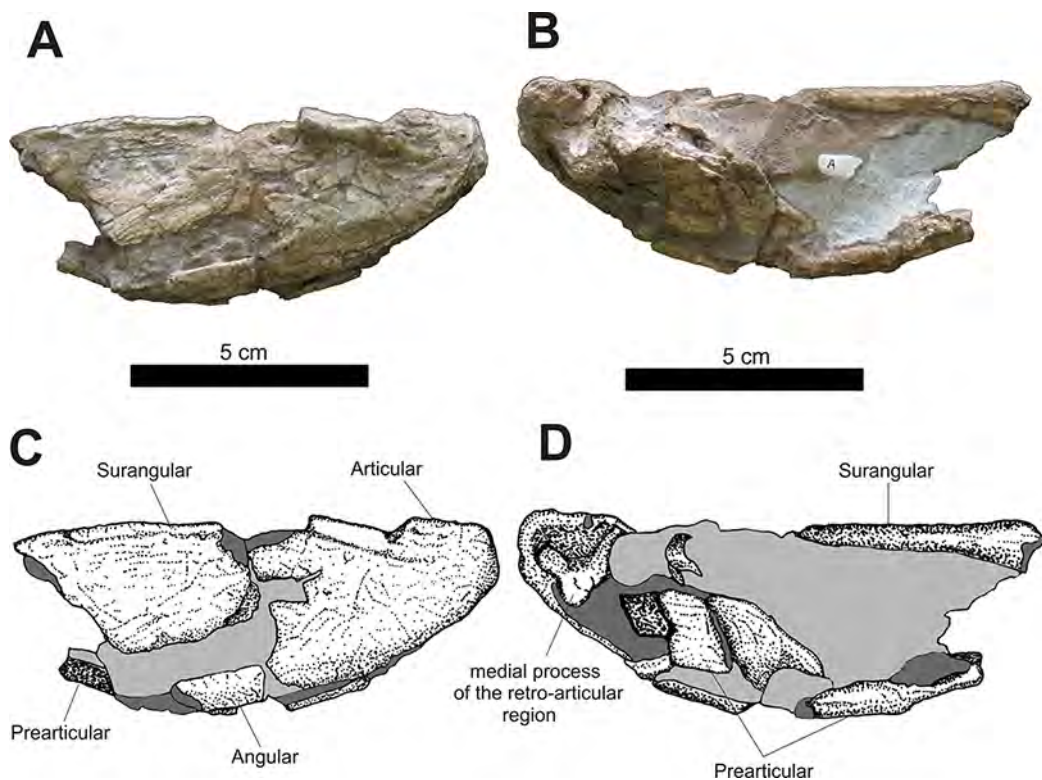


Figure 14 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, posterior portion of a left mandibular ramus. (A–C) lateral and (B–D) medial views.

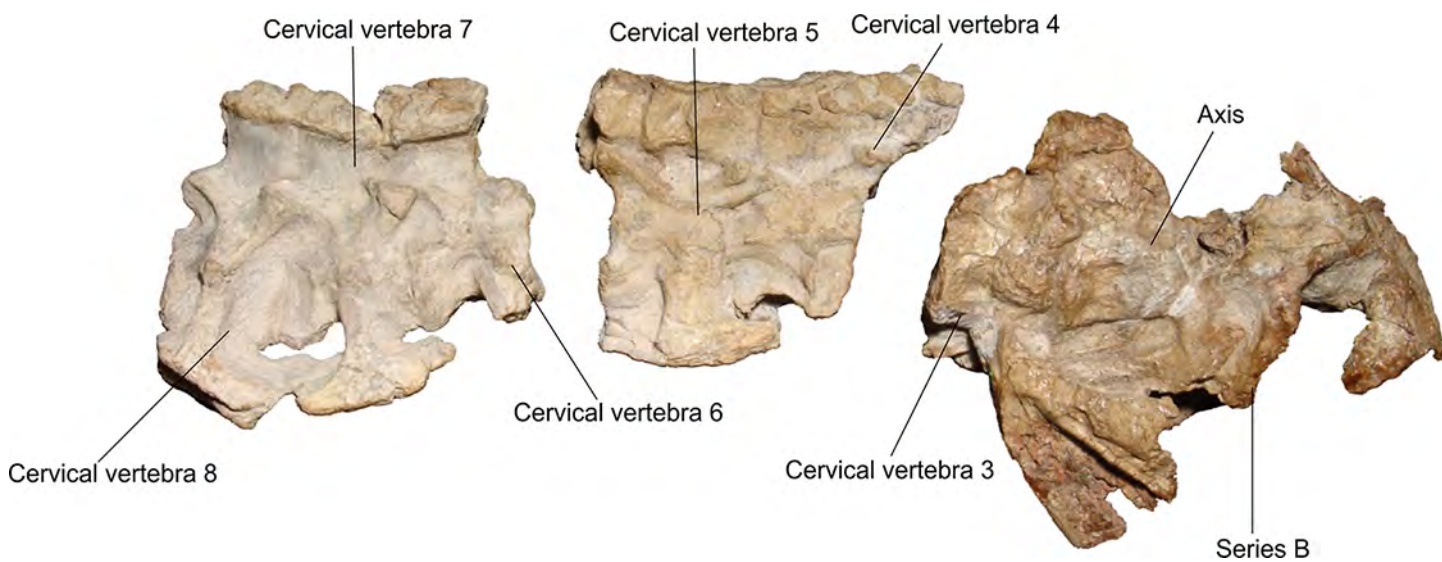


Figure 15 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, cervical sequence. Arranged cervical sequence of CPEZ-239b in left lateral view.

The three series of cervical vertebrae consist of: a set formed by the axis and the third cervical vertebra (Cv3) that are associated with the posterior portion of the cranium described as Series B. Another set is represented only of the dorsal neural apophysis and the third vertebra osteoderms, in articulation with the fourth and fifth vertebrae (Cv4 and Cv5) and the final set composed of the sixth, seventh and eighth cervical vertebrae (Cv6, Cv7 and Cv8). There is no evidence of the atlas because all elements ventral to the foramen magnum were lost.

In the anterior end of the first cervical sequence, the right side displays a large carbonate concretion that covers the entire anterior portion of the axis, leaving only its spinal apophysis and the posterior half of its centrum exposed. On the axis there is a small pit, located laterally next to a fracture that is in the anterior portion of the vertebra. Its right postzygapophysis was fractured along with the prezygapophysis of vertebra Cv3 due to a distortion that displaced the latter vertebrae more dorsally. On the axis there is also a thickening on the posterior margin of the vertebral center. The neural spine of the axis, in lateral view, is a sub-triangular, lateromedially compressed blade that is posterodorsally projected, with a slightly convex dorsal margin and an irregular border, culminating dorsally with a few small fragments of osteoderms on its dorsal tip.

The Cv3 is the only vertebra in which the posterior region is exposed and relatively undamaged. The opening of the neural channel is tear-shaped with the tip tapering dorsally. This is due to a fracture that exposed the posterior part of the neural arch. The channel is filled with sediment and the opening is covered by a thick layer of coating, which prevented further preparation by the fear of further damage this structure.

The second set of vertebrae, formed by the vertebrae Cv4 and Cv5, presents, in lateral view a projection on its anterior edge which corresponds to the rounded portion of the neural spine of the vertebra Cv3, which is present in the assembly described above (Fig. 16). The row of osteoderms of this series is arranged more laterally than the second set, particularly in its most anterior third. The neural spine of Cv4 is covered by a layer of concretions, while only the rear portion of the Cv5 is visible. The dorsal margin of the Cv5 vertebra is prominent, especially its area near the postzygapophyses. One area covered in concretions occupies the entire ventral region of this vertebra. A rib is articulated with the Cv5 vertebra, but the aforementioned concretion prevents a clear view of its articulation with the vertebrae. Only the proximal part is preserved. Its anterior portion is anteroposteriorly elongated; with the posterior sub-triangular process of rib is thinning posteriorly.

The third set of cervical vertebrae is better preserved than the previous ones (Fig. 16). The centrum is equilateral. The Cv6 vertebra has a fossa on its ventrolateral portion. In ventral view, there exists a small depression that is parallel to the sagittal axis. This depression appears to be bordered by two small ridges that run parallel the inside edge of a joint surface from the center to the other. The other two vertebrae have few areas exposed. The neural spine of these vertebrae is also visible. In side view, they are short and are anteroposteriorly wide.

The prezygapophysis-postzygapophysis laminae are more apparent in the Cv8 while the blade that connects the center of the vertebra with the zygapophyses is better preserved than in Cv5 in Cv8, since this last it was eroded this blade.

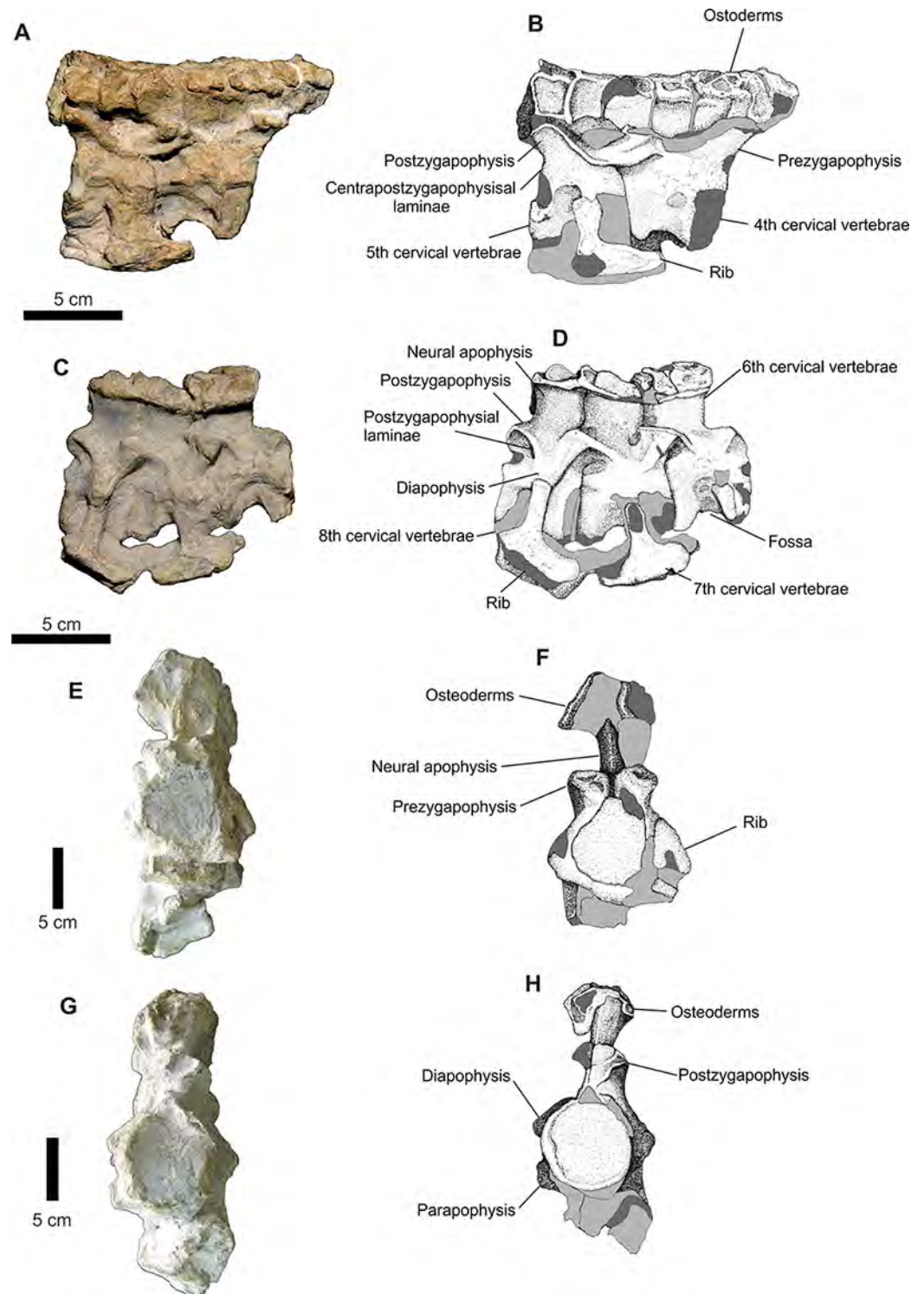


Figure 16 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, cervical vertebrae. (A–D) first and second sets of cervical vertebrae in right lateral views; (E) second set of cervical vertebrae and (F) schematic drawing of only the 6th cervical vertebrae in anterior view; (G) second set of cervical vertebrae and (H) the 8th cervical vertebrae in posterior view.

The parapophysis is best preserved in the Cv8 and is positioned anteroventrally in the vertebral body, with the diapophysis as a short transverse process. The transverse process and its articulation with the tubercle of a proximal fragment of a rib are best preserved in Cv7 vertebrae. The overall aspect of the ribs is more apparent in the one articulated with vertebrae Cv5, although its anterior edge is more rounded.

The cervical vertebrae are similar to the ones in other 'rauisuchian' taxa, with a shortened, slightly amphicoelic vertebral centra, with two surfaces for articulation and an anteroposteriorly widerneuropophysis, when compared with the centra. This pattern matches the one found in *Prestosuchus* and *Stagonosuchus*, but differs from the one in *Batrachotomus*, *Fasolasuchus* and *Rauisuchus*.

Three other incomplete neural arches are preserved. These display two parallel rows of osteoderms articulated with the neural apophysis of two vertebrae. The shape of these osteoderms is similar to those found in cervical sequence described above, but these are much more damaged and no structure is apparent on its dorsal surface. It is impossible to determine which portion of the vertebrae they belong to, due to their damaged state, although their size is similar to those of the cervical vertebrae.

All osteoderms present in CPEZ-239b are in articulation with their corresponding vertebrae. They increase gradually in size along the axial skeleton, with the first ones as small irregular discs with a central fossa and the posterior ones being larger, slightly oval shaped, with a sinuous posterior border and a dorsal ridge, such as the better preserved ones articulated on the last vertebrae (Cv8). None of the anterior portions of the osteoderms are preserved, being lost or covered by the ones in front. The dorsal ridge extends almost to all the dorsal area of the osteoderm, being slightly high anteriorly and decreasing posteriorly up until the posterior border. They share overall similarities to the ones in *Prestosuchus* (Azevedo, 1991; Mastrantonio, 2010), *Ticinosuchus* (Krebs, 1965; Lautenschlager & Desojo, 2011), *Rauisuchus* (Lautenschlager & Rauhut, 2014), *Teratosaurus* (Brusatte et al., 2009) and *Yarasuchus* (Sen, 2005).

Two incomplete cervical ribs are present in this assembly (Fig. 17). In lateral view, their shape is elongated, slender with a slight posterior curvature. The proximal portion of the second rib displays an expansion that forms the capitulum and tuberculum where a small blade extends posteriorly and follows the ventroposterior border of the rib, tapering gradually until it ends near the middle portion of the rib.

Appendicular skeleton

Girdles

Of the shoulder girdle, an articulated portion of the right scapula and coracoid is preserved, which corresponds to the area around the glenoid fossa. Additionally, there is a fragment of the scapular blade, but it is not possible to discern from which side (Fig. 18).

In lateral view, the fragment of the scapula+coracoid has a sub-rectangular shaped anterior portion with a dorsal margin that continuous dorsally to a semi-circular fracture that is on the central third of its body. After this fracture, the dorsal margin follows posteriorly at a more ventral level than its parallel margin. The ventral edge of the coracoid

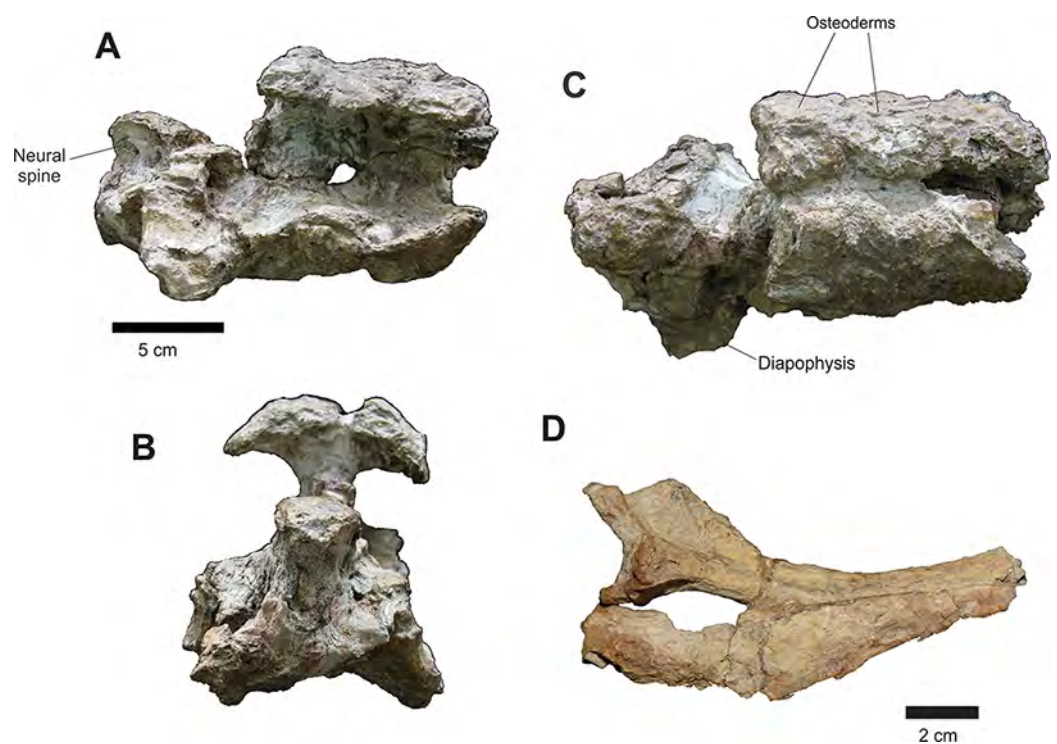


Figure 17 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, disarticulated vertebrae and ribs. (A) lateral, (B) anterior and (C) dorsal views; (D) incomplete cervical ribs in lateral view.

continues straight anteroposteriorly until the thick edge of the glenoid fossa. This, in turn, is concave, semi-lunar shaped and occupies much of the ventral portion of the bone. The preserved portion of the posterior border of the coracoid is relatively dorsoventrally straight.

In medial view, the coracoid presents no remarkable feature, with only one lateral thickening in its latter portion. The ventral edge of the glenoid fossa is ventrolaterally orientated and directed posteriorly, with its entire anterior margin next to a thickening located above the glenoid fossa. Posterior to the glenoid cavity is a fracture with rounded edge which corresponds to the opening of the coracoid foramen. The portion where the anterior notch would be is not preserved (*Desojo & Rauhut, 2009*).

A piece of a left scapula, in lateral view (*Fig. 18B*), is expanded anteromedially with all its edges damaged. The anterior border is sinuous and continues dorsally to a posterodorsally convex area that forms a slightly rounded area, occupying much of its dorsal portion. After this, the margin follows ventrally to an area with a fracture slightly rounded that is located on its ventral portion. In anterior view, the scapula fragment is a lateromedially compressed blade, which has a medially orientated curvature.

The only elements present in the pelvic girdle of CPEZ-239b are an incomplete ventral portion of a left ischium and a fragment of the anterior process of a right ilium (*Figs. 17C, 17D and 17E*). In dorsal and ventral views, the fragment of the ischium is roughly sub-rectangular shaped and slightly elongated. Its lateral edge is rounded where it expands medially.

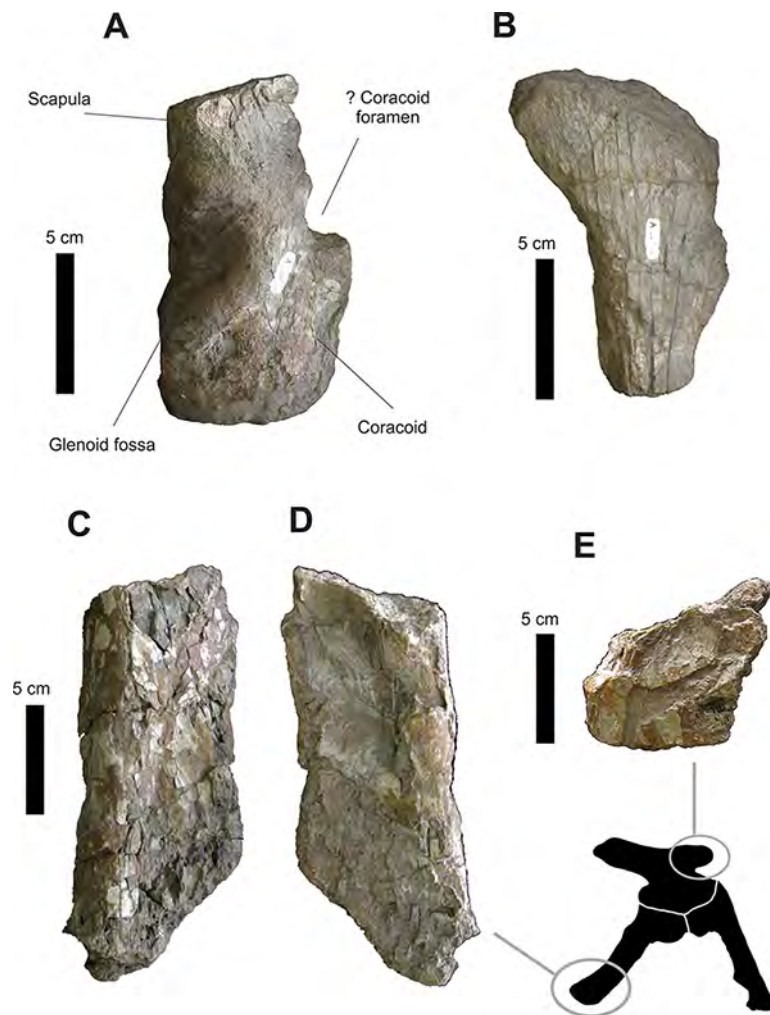


Figure 18 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, preserved fragments of the shoulder and pelvic girdles. (A–B) fragments of the shoulder and (C–E) of the pelvic girdle.

The fragment of the anterior process of the ilium, in lateral view, shows a sub-rectangular shape, longer than tall, with its dorsal edge irregular and slightly rounded. In anterior and posterior views, the ventral portion of this fragment expands medially to form a flat surface that occupies the entire area of the dorsal bone.

Propodial elements

Only a complete right humerus is preserved in the assemblage (Fig. 19). In anterior view, the anterior border of the proximal humerus is irregular, with a prominent deltopectoral crest. The proximal margin is convex and irregular, with a large and thick posteromedially located area and a prominent medial tuberosity. Between these two structures there is a depression across its anterior face. Distally, the humerus tapers lateromedially in a very fragmented diaphysis and expands again in its distal portion, forming a slightly convex distal margin where there is radial and ulnar condyle.

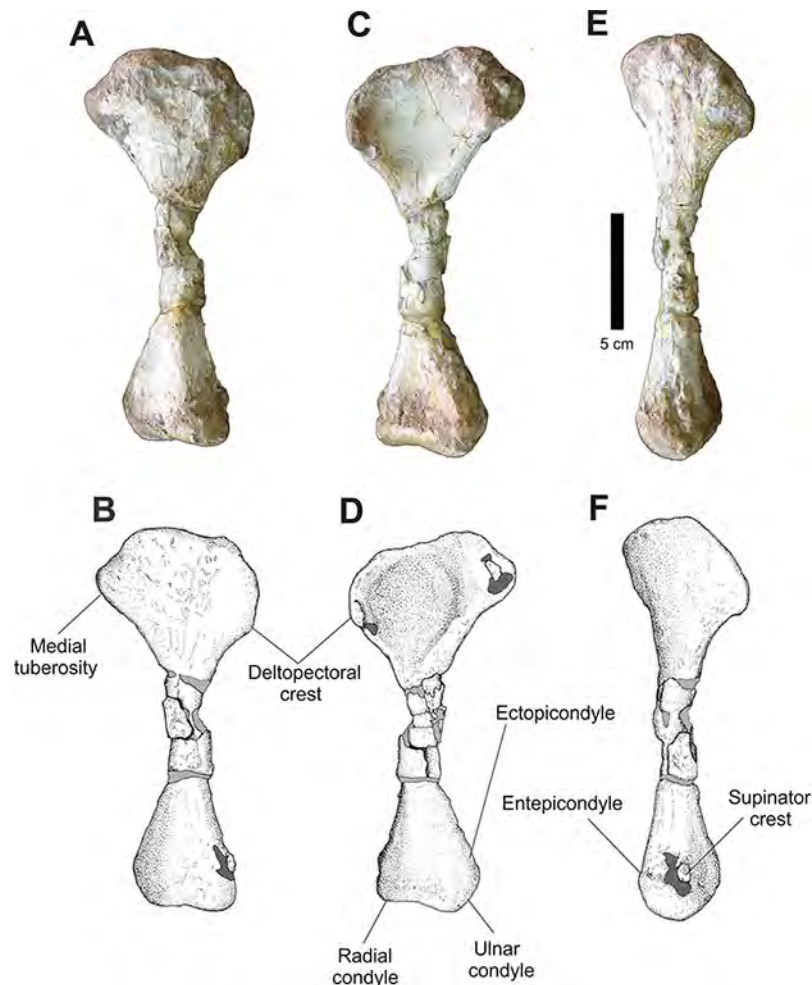


Figure 19 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, right humerus. (A–B) lateral, (C–D) medial and (E–F) and anterior views.

In posterior view, the torsion between the proximal and distal epiphysis is clearer. All the proximal border of the proximal epiphysis is irregular and slightly compressed transversally. The proximal epiphysis, in lateral view, possesses a lateral margin with an attenuated anterior curvature and a distinct deltopectoral crest. In its distal end, there is a small supinator crest, located near to the radial condyle.

Damage on the surface of the humerus by chemical preparation makes it impossible to clearly ascertain if the condition of the epiphysis would be un-ossified, a feature that has been used to establish ontogenetic variation within *Prestosuchus chiniquensis* (Mastrantonio, 2010).

The humerus of *Prestosuchus chiniquensis* (Mastrantonio, 2010) and *Ticinosuchus ferox* (Krebs, 1965) are the closest matching the one of CPEZ-239b. However, we must consider that most of the humeri described are morphologically similar and diagenetic alterations are rarely discussed in most works, which complicates precise identification.

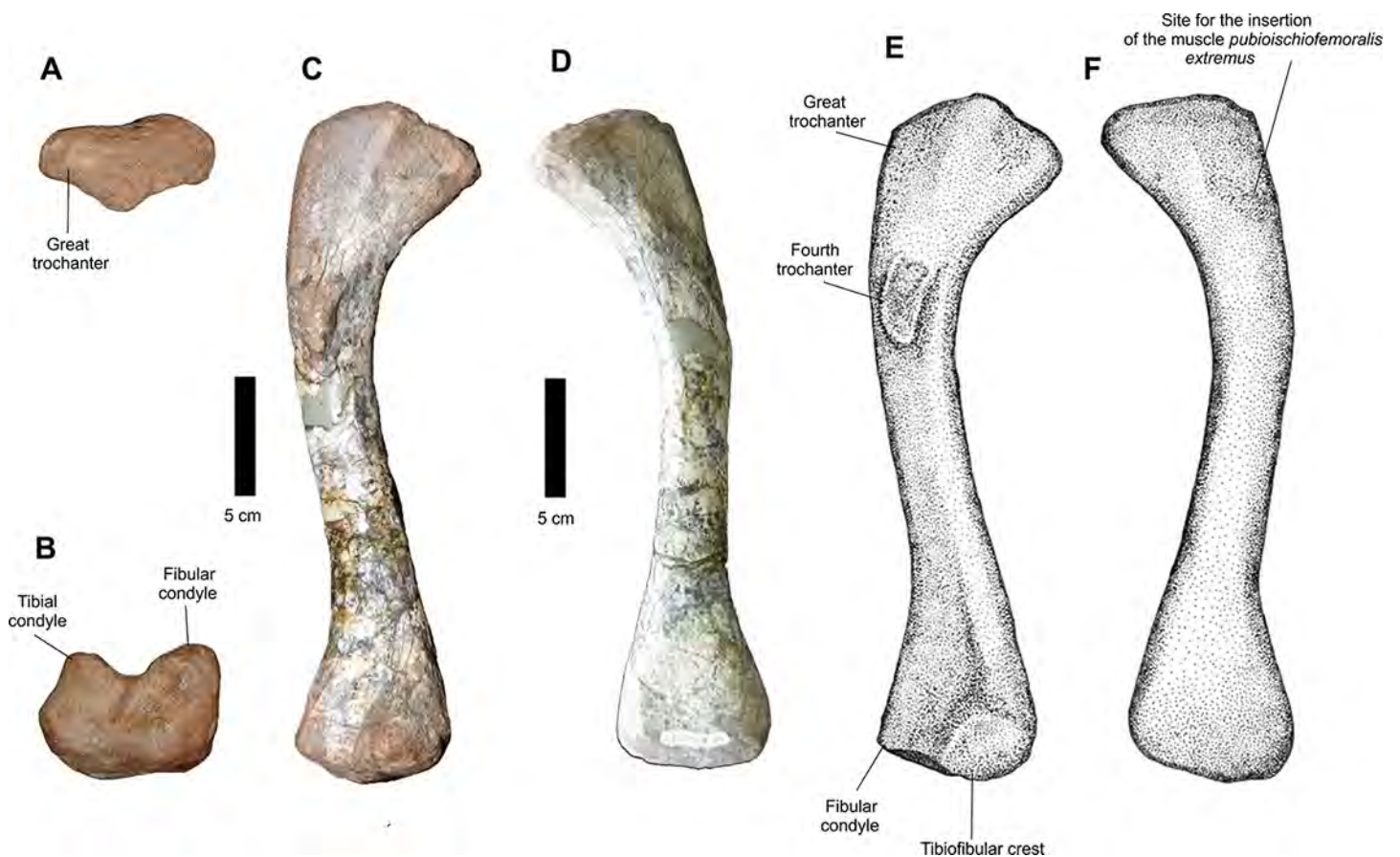


Figure 20 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, left femur. (A) proximal, (B) distal, (C–E) medial and (D–F) and lateral views.

Of the posterior propodium, a well preserved left femur (Fig. 20) and a distal portion of a right one are present in CPEZ-239b. The more complete one is an elongated bone, with a robust proximal epiphysis and a distal anteroposteriorly compressed one. The trochanter is not well marked, such as the ones present in other specimens of *Prestosuchus chiniquensis* (Huene, 1935–42; Mastrantonio, 2010). The torsion of the proximal area turns medially. This area displays a well-defined medial incline, while the greater trochanter has a smooth margin. In dorsal view, the articular surface is anteroposterior narrow and completely smooth. In posterior view, the proximal region displays a short projection that would correspond to the central ridge (*sensu* Gower & Schoch, 2009). This ridge possesses a rough surface, which extends dorsally to the articular area and has, in dorsal view, a triangular aspect with a rounded apex. Located ventrally to this elevation there is the fourth trochanter, which is projected laterally from the body of the femur, is a dorsoventrally elongated structure and is positioned obliquely to the axis of the femur. Its structure, in medial view, presents a broad proximal margin, which tapers slightly distally.

A rough surface on the anterolateral area of the proximal end, close to the anterior margin of the greater trochanter, continues across a quarter of the total length of

the femur. This area corresponds to the insertion site for the *pubioischiofemoralis externus* muscle. The distal articular region is divided into a fibular condyle, in lateral position, and a medial tibial condyle, both separated by a shallow longitudinal intercondylar groove.

The preserved fragment of a right femur is a distal epiphysis, anteroposteriorly compressed and damaged. Although it does not display any features, its overall form makes it possible to identify it as a right femur, based on the based on its dorsoventral expansion when compared to the most complete femur of the assemblage.

Comparatively, the best preserved femur of CPEZ-239b is similar to the ones of *Prestosuchus chiniquensis*, especially the rugose area on its anterolateral surface. However, it is more slender than the ones described on the aforementioned work and the sigmoidal torsion is not as pronounced, but this can vary even in the same specimen due to diagenetic factors ([Mastrantonio, 2010](#)).

Epipodial elements

Among the elements of the forelimb, only a fragment of a proximal right ulna is preserved ([Fig. 21](#)). In medial view, the distal portion is elongated, with the two margins running parallel up to the proximal area, where the anterior margin expands anteroposteriorly to form the olecranon process. In lateral view, the olecranon is concave and low, located proximally to the dorsal surface (*sensu* [Gower, 2000](#)), similar to the one in *Ticinosuchus ferox* ([Krebs, 1965](#)), but differing from taller ones, such as those of *Postosuchus kirkpatricki* ([Weinbaum, 2013](#)), *Postosuchus alisonae* ([Peyer et al., 2008](#)), *Fasolasuchus tenax* ([Bonaparte, 1981](#)) and *Prestosuchus chiniquensis* ([Mastrantonio, 2010](#)).

A left tibia is also present in this material ([Fig. 22](#)). In lateral view, its proximal end is expanded lateromedially, tapering near the diaphysis and maintaining the diameter similar to its distal end. Its most distal portion is incomplete. In cross section, the shape of the diaphysis is oval, whereas in lateral view, there is a lateromedially pronounced curvature.

At the distal end of the proximal area, shortly after its expanded proximal portion, there is an anteromedial groove, which would correspond to the insertion site of the *puboischiotibialis externus* muscle.

Autopodial elements

Some incomplete phalanges are preserved attached to the side of the right disarticulated mandibular ramus ([Fig. 23](#)) but were separated during preparation. These are small, slightly cuboid bones that range from 5 to 3 cm in length and it is unclear from which autopodium these phalanges belong. A single right fifth metatarsal is preserved, displaying the characteristic hooked shape.

Phylogenetic analysis

The phylogenetic analysis was made using the data matrix of [Nesbitt \(2011\)](#) altered to include CPEZ-239b as an Operational Taxonomic Unit (OTU) and following the same parameters (a heuristic search of 1000 replicates of Wagner trees with TBR branch swapping, holding 10 trees per replicates). The OTUs *Prestosuchus chiniquensis*,



Figure 21 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, right ulna. Proximal portion in lateral view.

UFRGS-PV-0152-T and UFRGS-PV-0156-T were removed from the analysis and only

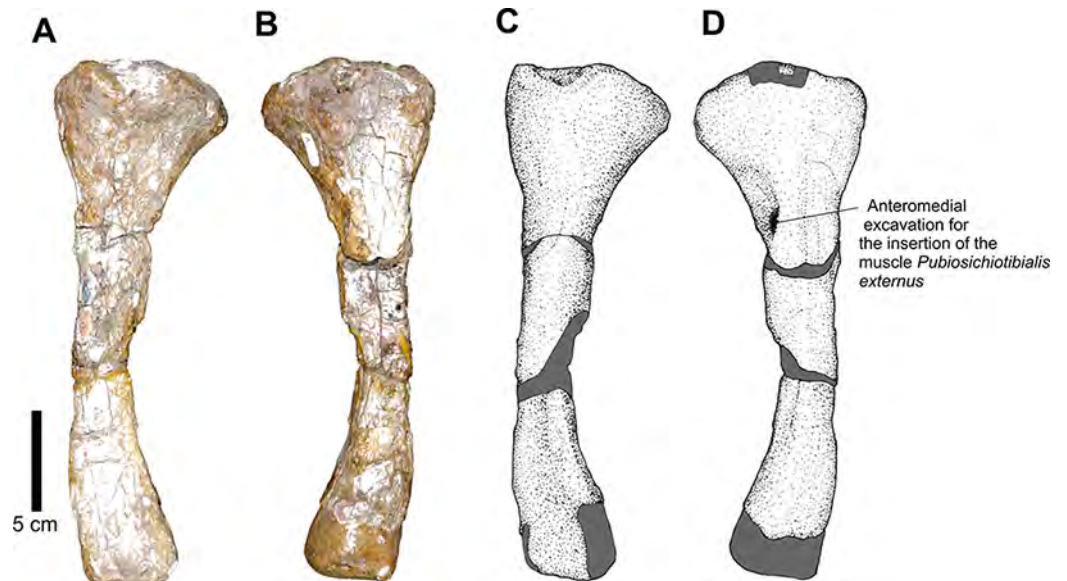


Figure 22 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, left tibia. (A–C) anterior and (B–D) posterior views.

“Combined *Prestosuchus*” was used since all 4 OTUs formed a polytomy both in *Nesbitt’s (2011)* and in our own initial tests. Nodal support was tested in TNT by using Bremer support and bootstrap resampling parameters.

The analysis resulted in 360 equally Most Parsimonious Trees (MPT) of 1280 length steps (retention index [RI]: 0,778 and consistency index [CI]: 0,376). CPEZ-239b was recovered in all MPTs as the sister taxon to “Combined *Prestosuchus*” by only a single step and with good nodal support this result (*Fig. 24*).

Our initial tests found only one autapomorphy for CPEZ-239b character 31; Maxilla, anterolateral surface, large anteriorly opening foramen: (0) present; (1) absent

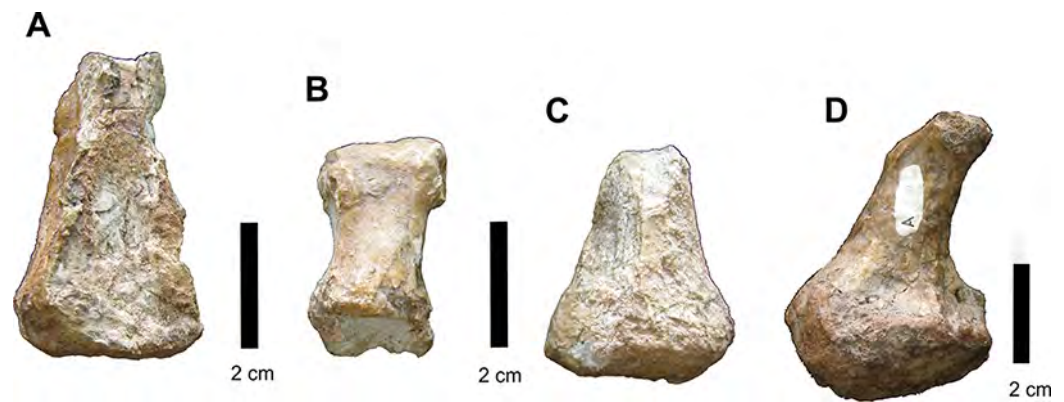


Figure 23 Osteology of *Prestosuchus chiniquensis* specimen CPEZ-239b, autopodial elements. (A–D) different phalangeal elements of CPEZ-239b, including (D) the “hooked” 5th metatarsal.

(Nesbitt, 2011:66) with “Combined *Prestosuchus*” being (0) and CPEZ-239b (1). However, this result was problematic. No such structure is present in the three specimens that form “Combined *Prestosuchus*.” The lectotype and paralectotype do not have preserved maxilla, UFRGS-PV-0156-T and UFRGS-PV-0152-T both do, but do not possess any feature similar to the one described for this character state. As such, we altered this state in “Combined *Prestosuchus*” from 0 to 1, thus turning character 31 to a synapomorphy of Combined *Prestosuchus*+CPEZ-239b and not finding any autapomorphies for the latter, thus indicating that both OTUs would belong to the same taxon.

RESULTS

Both the comparative morphological and the quantitative phylogenetic analyses indicate that CPEZ-239b can be attributed to *Prestosuchus chiniquensis*. Although it presents features that differ from other specimens described for this taxon, the resulting strong support for the taxonomic attribution would indicate that these are likely due to some form of intraspecific variation. The first and most obvious factor would be the smaller size of CPEZ-239b in comparison to all the specimens that compose the “Combined *Prestosuchus*” of Nesbitt (2011) and UFRGS-PV-0629-T, which would be too great to be considered as sexual dimorphism. The most likely possibility would be ontogenetic variation, but the problem in establishing this in *P. chiniquensis*, or in any other ‘rauisuchian’ and Triassic pseudosuchian taxa, must be addressed.

DISCUSSION

As presented by Irmis (2007), size alone is problematic when used to determine ontogenetic variation within archosaurs. Very few taxa are represented by a large number of mostly complete specimens to clearly test for intraspecific variation (e.g. Brochu, 1992; Irmis, 2007; Schoch, 2007; Nesbitt et al., 2013). This is not restricted to Triassic forms, being intrinsic to the study of fossil organisms, but the chance to clearly view this within a fossil vertebrate group is very rare (e.g. Brinkman, 1988; Dodson, 1976; Colbert, 1992; Raath, 1992; Carr, 1999) and must be considered with uttermost caution.

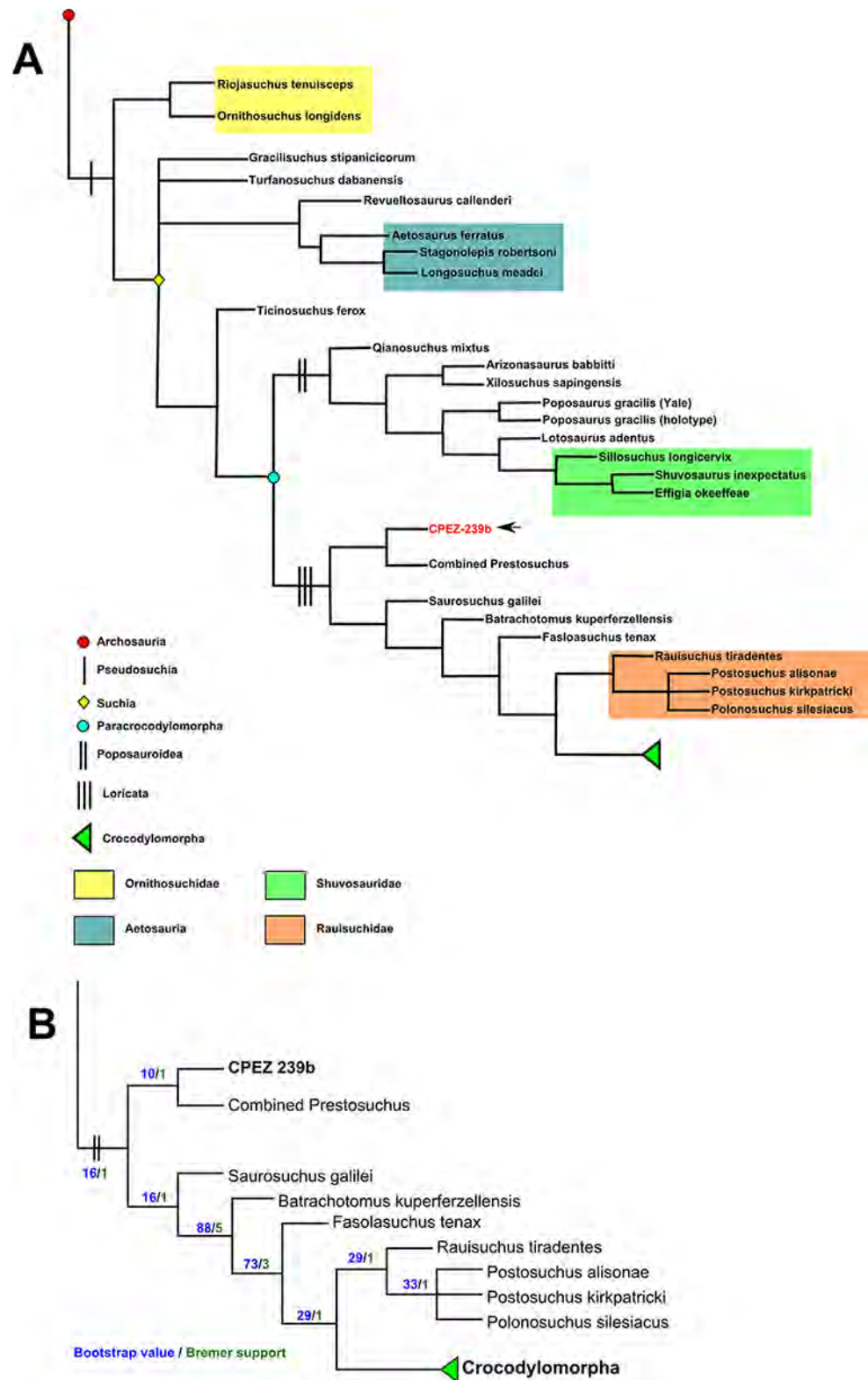


Figure 24 Phylogenetic analysis results. (A) Portion of the consensus trees of the analysis indicating the CPEZ-239b (indicated by the arrow) as the sister taxon of “Combined *Prestosuchus*”; (B) Bootstrap and Bremer support values tree.

In studies of ontogeny in the pseudosuchian lineage, living crocodylians are logically considered as proxies to the extinct forms ([Brochu, 1992](#); [Brochu, 1996](#); [Rieppel, 1993](#); [Irmis, 2007](#); [Ricqlès, Padian & Horner, 2003](#); [Ricqlès et al., 2008](#)), although this also is not without its problems (see [Irmis, 2007](#), for a more detailed discussion on this topic). In the case of ‘rauisuchians,’ there are descriptions of juvenile forms in the literature based mainly on morphological features. [Desojo & Arcucci \(2009\)](#) described a partial skull roof and palate (PULR 057) that they attributed to a juvenile form of *Luperosuchus fractus*, based on its size (one third of the type specimen PULR 04), the loose condition of its sutures, comparatively reduced ornamentation on the surface of the bones and a more pronounced excavation between the premaxillae and maxillae. [Chatterjee & Majumdar \(1987\)](#) in their description of *Tikisuchus romeri*, found that its skull would be proportionally longer than the pre-sacral length of its axial skeleton and this, along with clearly defined sutures among some elements of the skull and the disjointed neural arches, would indicate poor ossification, which the authors concluded would be evidence of an immature individual. [Gower & Schoch \(2009\)](#) described the postcranial skeleton of *Batrachotomus kupferzellensis* based on four small and one large individuals. These authors did not discuss the presence of sexual dimorphism and individual variation among described specimens, but indicated that the smaller forms displayed minor differences in the pelvic girdle and locomotor appendages, in comparison to the larger specimen (specifically longer and more robust pubic boots in the larger specimen, ilia with less developed rugosities on the iliac blade and slender limb bones with less developed trochanters in the smaller ones).

In the description of *Arizonasaurus babbitti* ([Nesbitt, 2005](#)), other incomplete specimens were attributed to the species, but the author did not discuss any case of variation, possibly due to the incomplete state of the material. [França, Ferigolo & Langer \(2011\)](#) and [França, Langer & Ferigolo \(2013\)](#) described *Decuriasuchus quartacolonina* based on 10 incomplete individuals, which shared approximate dimensions and were identified by the authors as adult forms due to the closed neurocranial and neurocentral sutures ([França, Ferigolo & Langer, 2011:390–391](#)). Outside of ‘rauisuchians,’ specific work on ontogeny was made for phytosaurs, aetosaurs and proterosuchid archosauriforms ([Martz, 2002](#); [Irmis, 2007](#); [Lucas, Heckert & Rinehart, 2007](#); [Parker, Stocker & Irmis, 2008](#); [Ezcurra & Butler, 2015](#)). Alternatively to macroscopic features, histological studies have been done, being used to establish age estimations in crocodylomorphs ([Erickson & Brochu, 1999](#); [Hill & Lucas, 2006](#); [Ikejiri, 2012](#)), aetosaurs ([Parker, Stocker & Irmis, 2008](#); [Cerdeira & Desojo, 2011](#); [Taborda, Cerdeira & Desojo, 2013](#)) and ‘rauisuchians’ ([Ricqlès et al., 2008](#); [Taborda, Cerdeira & Desojo, 2013](#)).

In the case of *Prestosuchus chiniquensis*, ontogeny is mainly inferred by comparative means. [Azevedo \(1991\)](#) considered the specimen UFRGS-PV-0156-T to be of an adult form due to its size (skull length about 1 m long), while [Mastrantonio \(2010\)](#) proposed that specimen UFRGS-PV-0629-T would be of a sub-adult, based on its comparatively smaller size relative to the one described by [Barberena \(1978\)](#) and [Azevedo \(1991\)](#). Additionally, these authors also consider that the condition of the articulation of the

skull elements as ontogenetic: UFRGS-PV-0156-T has tightly fused elements while the disarticulated condition of the ones of UFRGS-PV-0629-T would indicate that its sutures were not completely closed, thus indicative of an immature individual. In CPEZ-239b, the disarticulated condition of the cranial elements are similar to those of UFRGS-PV-0629-T ([Mastrantonio, 2010](#)), and the ones of the dermal roof display clear sutures, such as the one of the frontal-parietal, that would indicate a weak ossification. This is further supported by the distorted condition of the neurocranium and the disarticulated mandibular elements.

The absence of a subnarial fenestra in *P. chiniquensis* has long been inferred based on its lack on the complete skull of UFRGS-PV-0156-T, but the possibility of one being present but closing as the animal aged was considered by some workers (e.g. [Alcober, 2000](#)). However, clear evidence of its existence was only detected in UFRGS-PV-0629-T ([Mastrantonio, 2010](#)). As we present here, a similar structure does exist in CPEZ-239b, even with the anterior portion of the rostrum distorted. However, its exact dimensions must be considered with caution, since this site would represent some degree of kinetic articulation and thus be more susceptible to suffering distortion during fossilization ([Gower, 2000](#); [Liparini, 2008](#); [Mastrantonio, 2010](#)), but when comparing the size of the anterior border in CPEZ-239b relative to the overall dimensions of the premaxillae and maxillae in UFRGS-PV-0156-T and UFRGS-PV-0629-T, it would appear to be comparatively larger than the one in the latter. Additionally, it appears that what would regulate the dimensions of the opening would primarily be the growth of the maxilla. This is observed when comparing the area of the antorbital fossa of the three aforementioned specimens relative to their dimensions in the maxilla ([Fig. 25](#)). CPEZ-239-b and UFRGS-PV-0629-T are relatively similar, but the one in UFRGS-PV-0156-T is greatly expanded and the area of the fossa is comparatively reduced. This is of course a tentative inference based only on three specimens and remains to be quantitatively tested, but require a larger sample size of specimens which is impossible at this time.

The cervical vertebrae of CPEZ-239b do not display any sutures, so are fully fused. Alternately, the three incomplete vertebrae that lack the centra possess sutures that are well clearly marked. The absence of centra would indicate that the suture between them and the neural arches was not a strong one, therefore these 3 other vertebrae would belong to another portion of the axial skeleton other than the cervical sequence, although the exact position is impossible to establish.

The epiphysis of the appendicular bones of the propodium of the smaller specimen are not ossified ([Mastrantonio, 2010](#)), which would be additional evidence of a younger ontogenetic state. Furthermore, these authors also state that the specimens described by [Huene \(1935–42\)](#) displayed appendicular elements in similar condition, which would indicate that both would belong to the same ontogenetic stage. Since the size of all the bones present in CPEZ-239b would be smaller than the ones of the above-mentioned specimens ([Huene, 1935–42](#); [Huene, 1942](#); [Azevedo, 1991](#); [Mastrantonio, 2010](#)), this would further corroborate our size/ontogenetic stage correlation hypothesis.

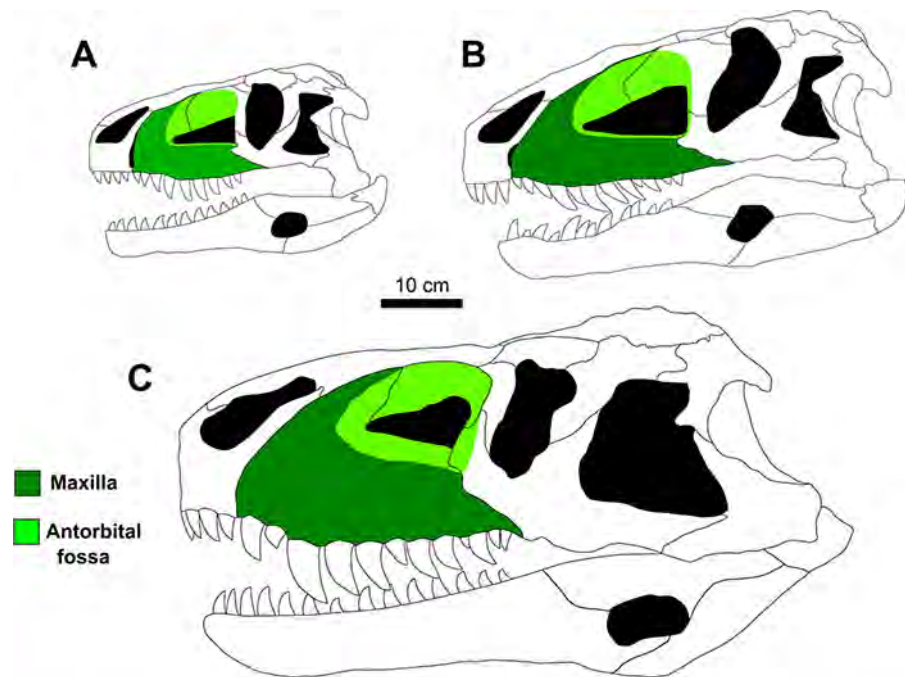


Figure 25 Skull comparison diagram of the inferred ontogenetic sequence in *Prestosuchus chiniquensis*. (A) reconstruction of the skull of CPEZ-239b; (B) the skull of UFRGS-PV-0629-T (redrawn based on [Liparini \(2008\)](#)) and (C) UFRGS-PV-0156-T (redrawn based on [Barberena \(1978\)](#)) but modified to correct diagenetic distortion and with an open jaw, reconstructed based on the mandible of UFRGS-PV-0629-T). The dimensions of the maxillae and of the antorbital fossa are highlighted to indicate the apparent changes that occurred in these elements as the animal aged and the impact this would have on the size of the sub-narial fenestra.

Further evidence of a young ontogenetic stage for CPEZ-239b comes from [Cerdeira et al. \(2013\)](#) histological study, where an osteoderm of this assemblage was used along with other South American ‘rauischians.’ The estimated age for CPEZ-239b, assuming that the preserved growth marks were annually deposited would be 6 years, while UFRGS-PV-0629-T would be 8 years old and the *Saurosuchus* specimen PVSJ 32 would have 16 years. The authors were unable to estimate the age of UFRGS-PV-0156-T due to extensive secondary remodeling of the sampled osteoderm core ([Cerdeira et al., 2013](#)).

CONCLUSIONS

Even with the incomplete condition of CPEZ-239b, both the comparative morphological study and the phylogenetic analysis indicate that it can be assigned to *Prestosuchus chiniquensis*. The differences between this material and other specimens described for this taxon are minor and did not cause any significant changes in the resulting taxonomic determination. Therefore, this would indicate that these variations would be intraspecific in nature. Based on the corroborative evidence presented and discussed here, we conclude that CPEZ-239b would be composed of juvenile aged individuals and this along with the presence of a subnarial opening in this material corroborates the hypothesis that

such a structure is present in *P. chiniquensis* but it would close or greatly reduce as the animal aged. However, this conclusion is not ideal, since a quantitative analysis to ascertain the different steps that occurred during ontogeny to better determine it is needed to clearly verify our conclusions, but unfortunately this is beyond reach at the present time due to the very low number of described specimens and the previously discussed need for the taxonomic revision of this taxon.

ACKNOWLEDGEMENTS

This article is one of the results presented in M.B.L. masters dissertation, under co-advisement by B.M.M. and C.L.S. D.C.F. worked in conjunction with M.B.L. in the phylogentic analysis. We would like to thank Julia Desojo, Marco Aurélio Gallo de França, Felipe Pinheiro, Agustin Martinelli and Tiago Raugust for the many helpful discussions and opinions during the elaboration of the present article and Marco Brandalise for access to the collections at the Museu de Ciências Naturais da PUC. The photographs were skillfully taken by Luiz Flávio Lopes (UFRGS).

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

Funding was provided in the form of a master's scholarship offered by CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior) to M.B.L. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Marcel B. Lacerda conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables.
- Bianca M. Mastrantonio conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, reviewed drafts of the paper.
- Daniel C. Fortier performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, reviewed drafts of the paper.
- Cesar L. Schultz conceived and designed the experiments, performed the experiments, analyzed the data, wrote the paper, reviewed drafts of the paper.

Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.1622#supplemental-information>.

REFERENCES

- Alcober O. 2000.** Redescription of the skull of *Saurosuchus galilei* (Archosauria: Rausisuchidae). *Journal of Vertebrate Paleontology* **20**(2):302–316
DOI [10.1671/0272-4634\(2000\)020\[0302:ROTSOS\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2000)020[0302:ROTSOS]2.0.CO;2).
- Alcober O, Parrish JM. 1997.** A new poposaurid from the Upper Triassic of Argentina. *Journal of Vertebrate Paleontology* **17**(3):548–556 DOI [10.1080/02724634.1997.10011001](https://doi.org/10.1080/02724634.1997.10011001).
- Azevedo SAK. 1991.** *Prestosuchus chiniquensis* (Huene 1942) (Reptilia, Archosauria, Thecodontia, Proterosuchia, Rausisuchidae), da Formação Santa Maria, Triássico do Estado do Rio Grande do Sul, Brasil. Ph.D. Thesis Porto Alegre: Universidade Federal do Rio Grande do Sul.
- Azevedo SAK. 1995a.** Estudo morfofuncional do aparelho maxilomandibular de *Prestosuchus chiniquensis* Huene 1942. *Anais da Academia Brasileira de Ciências* **67**:61–65.
- Azevedo SAK. 1995b.** Paleoecologia de *Prestosuchus chiniquensis* Huene 1942. Inter-relações paleoecológicas entre as faunas reptilianas do Triássico sul-brasileiro. *Anais da Academia Brasileira de Ciências* **67**:55–59.
- Barberena MC. 1978.** A huge thecodont skull from the Triassic of Brazil. *Pesquisas* **7**:111–129.
- Beltrão R. 1965.** Paleontologia de Santa Maria e São Pedro do Sul, Rio Grande do Sul, Brasil. *Boletim do Instituto de Geociências UFSM* **2**:5–114.
- Benton MJ. 1984.** Rausisuchians and the success of dinosaurs. *Nature* **310**:101
DOI [10.1038/310101a0](https://doi.org/10.1038/310101a0).
- Benton MJ. 1986.** The Late Triassic reptile *Teratosaurus*—a rausisuchian, not a dinosaur. *Palaeontology* **29**:293–301.
- Benton MJ, Clark JM. 1988.** Archosaur phylogeny and the relationships of the Crocodylia. In: Benton MJ, ed. *The Phylogeny and Classification of the Tetrapods*. Oxford: Clarendon Press, 295–338.
- Bertoni-Machado C, Holz M. 2006.** Biogenic fossils concentration in fluvial settings: an example of a cynodont taphocoenosis from the Middle Triassic of Southern Brazil. *Revista Brasileira de Paleontologia* **9**(3):273–282 DOI [10.4072/rbp.2006.3.02](https://doi.org/10.4072/rbp.2006.3.02).
- Bonaparte JF. 1981.** Descripción de “*Fasolasuchus tenax*” y su significado en la sistemática y evolución de los thecodontia. *Revista del Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”* **3**(2):55–101.
- Bonaparte JF. 1984.** Locomotion in Rausisuchid thecodonts. *Journal of Vertebrate Paleontology* **3**(4):210–218 DOI [10.1080/02724634.1984.10011976](https://doi.org/10.1080/02724634.1984.10011976).
- Brinkman D. 1988.** Size-independent criteria for estimating relative age in *Ophiacodon* and *Dimetrodon* (Reptilia, Pelycosauria) from the Admiral and lower Belle Plains formations of west-central Texas. *Journal of Vertebrate Paleontology* **8**(2):172–180
DOI [10.1080/02724634.1988.10011695](https://doi.org/10.1080/02724634.1988.10011695).
- Brochu CA. 1992.** *Ontogeny of the postcranium in crocodylomorph archosaurs*. M.A. Dissertation Austin: The University of Texas at Austin, Texas.
- Brochu CA. 1996.** Closure of neurocentral sutures during crocodylian ontogeny: implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology* **16**(1):49–62
DOI [10.1080/02724634.1996.10011283](https://doi.org/10.1080/02724634.1996.10011283).
- Brusatte SL, Butler RJ, Sulej T, Niedzwiedzki G. 2009.** The taxonomy and anatomy of rausisuchian archosaurs from the late triassic of germany and poland. *Acta Palaeontologica Polonica* **54**(2):221–230 DOI [10.4202/app.2008.0065](https://doi.org/10.4202/app.2008.0065).

- Brusatte SL, Nesbitt SJ, Irmis RB, Butler RJ, Benton MJ, Norell MA. 2010. The origin and early radiation of dinosaurs. *Earth-Science Reviews* 101(1–2):68–100 DOI 10.1016/j.earscirev.2010.04.001.
- Butler RJ, Brusatte SL, Reich M, Nesbitt SJ, Schoch RR, Hornung JJ. 2011. The sail-backed reptile from the latest early triassic of germany and the timing and biogeography of the early archosaur radiation. *PLoS ONE* 6(10):e25693 DOI 10.1371/journal.pone.0025693.
- Cabreira SF, Silva LR, Soares MB, Schultz CL, Raugust T, Lacerda M, Liparini A, Mastrantonio BM. 2010. Nova ocorrência de Rausuchia para a Formação Santa Maria (Bacia do Paraná). *Reunião Anual da Sociedade Brasileira de Paleontologia–Paleo 2010, seção RS*. Porto Alegre: Livro Digital de Resumos Paleo RS 2010 p. 18.
- Carr TD. 1999. Craniofacial ontogeny in Tyrannosauridae (Dinosauria, Coelurosauria). *Journal of Vertebrate Paleontology* 19(3):497–520 DOI 10.1080/02724634.1999.10011161.
- Cerda IA, Desojo JB. 2011. Dermal armour histology of aetosaurs (Archosauria: Pseudosuchia), from the Upper Triassic of Argentina and Brazil. *Lethaia* 44(4):417–428 DOI 10.1111/j.1502-3931.2010.00252.x.
- Cerda IA, Desojo JB, Scheyer TM, Schultz CL. 2013. Osteoderm microstructure of “rauisuchian” archosaurs from South America. *Geobios* 46(4):273–283 DOI 10.1016/j.geobios.2013.01.004.
- Chatterjee S. 1993. *Shuvosaurus*, a new theropod. *National Geographic Research and Exploration* 9(3):274–285.
- Chatterjee S, Majumdar PK. 1987. *Tikisuchus romeri*, a new rausuchid reptile from the Late Triassic of India. *Journal of Paleontology* 61(4):787–793 DOI 10.1017/S0022336000029139.
- Colbert EH. 1992. Variation in *Coelophysis bauri*. In: Carpenter K, Currie PJ, eds. *Dinosaur Systematics: Approaches and Perspectives*. Cambridge: Cambridge University Press, 81–90.
- Cope ED. 1869. Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Transactions of the America Philosophical Society* 14(1):1–252 DOI 10.2307/1005355.
- Desojo JB, Rauhut O. 2008. New insights on ‘rauisuchian’ taxa (Archosauria: Crurotarsi) from Brazil. In: Dyke G, Naish D, Parkes M, eds. *SVPCA 12, PALAEOLOGY*. Dublin: National Museum of Ireland, 31.
- Desojo JB, Arcucci AB. 2009. New material from *Luperosuchus fractus* (Archosauria: Crurotarsi) from the Middle Triassic of Argentina: the earliest known South American ‘Rauisuchian.’ *Journal of Vertebrate Paleontology* 29(4):1311–1315 DOI 10.1671/039.029.0422.
- Desojo JB, Ezcurra MD, Schultz CL. 2011. An unusual new archosauriform from the Middle–Late Triassic of southern Brazil and the monophyly of Doswelliidae. *Zoological Journal of the Linnean Society* 161(4):839–871 DOI 10.1111/j.1096-3642.2010.00655.x.
- Desojo JB, Heckert AB, Martz JW, Parker WG, Schoch RR, Small BJ, Sulej T. 2013. Aetosauria: a clade of armoured pseudosuchians from the Upper Triassic continental beds. In: Nesbitt SJ, Desojo JB, Irmis RB, eds. *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and the Kin*. London: The Geological Society, Special Publications, 203–239 DOI 10.1144/sp379.17.
- Desojo JB, Rauhut O. 2009. The taxonomic status and phylogenetic position of the Late Triassic brazilian rausuchian *Prestosuchus*. *Journal of Vertebrate Paleontology* 29(suppl 3):87A–88A.
- Dodson P. 1976. Quantative aspects of relative growth and sexual dimorphism in *Protoceratops*. *Journal of Paleontology* 50(5):929–940.
- Erickson GM, Brochu CA. 1999. How the “terror crocodile” grew so big. *Nature* 398:205–206 DOI 10.1038/18343.
- Ezcurra MD. 2012. Comments on the taxonomic diversity and paleobiogeography of the earliest known dinosaur assemblages (late Carnian–earliest Norian). *Historia Natural, tercera serie* 2(1):49–71.

- Ezcurra MD, Butler RJ. 2015.** Post-hatchling cranial ontogeny in the Early Triassic diapsid reptile *Proterosuchus fergusi*. *Journal of Anatomy* **226**(5):387–402 DOI [10.1111/joa.12300](https://doi.org/10.1111/joa.12300).
- Fiorelli LE, Ezcurra MD, Hechenleitner EM, Argañaraz E, Taborda JRA, Trotteyn MJ, von Baczko MB, Desojo JB. 2013.** The oldest known communal latrines provide evidence of gregarism in Triassic megaherbivores. *Scientific Reports* **3**:3348 DOI [10.1038/srep03348](https://doi.org/10.1038/srep03348).
- França MAG. 2011.** Decrição osteológica de *Decuriasuchus quartacolonina* (Archosauria, Pseudosuchia) e a evolução dos Rauissúquios. PhD dissertation. Universidade de São Paulo.
- França MAG, Ferigolo J, Langer MC. 2011.** Associated skeletons of a new middle Triassic “Rauisuchia” from Brazil. *Naturwissenschaften* **98**(5):389–395 DOI [10.1007/s00114-011-0782-3](https://doi.org/10.1007/s00114-011-0782-3).
- França MAG, Langer MC, Ferigolo J. 2013.** The skull anatomy of *Decuriasuchus quartacolonina* (Pseudosuchia: Suchia: Loricata) from the middle Triassic of Brazil. In: Nesbitt S, Desojo JB, Irmis RB, eds. *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin*. London: The Geological Society of London, 469–501.
- Galton PM. 1985.** The poposaurid thecodontian *Teratosaurus suevicus* von Meyer plus referred specimens mostly based on prosauropod dinosaurs from the Middle Stubensandstein Upper Triassic of Nordwürttemberg West Germany. *Stuttgarter Beitrage zur Naturkunde Serie B (Geologie und Palaeontologie)* **116**:1–29.
- Gauthier J. 1984.** *A cladistic analysis of the higher systematic categories of the Diapsida* PhD. Berkeley: University of California.
- Gauthier J, Padian K. 1985.** Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight. In: Hecht MK, Ostrom JH, Viohl G, Wellnhofer P, eds. *The Beginning of Birds*. Eichstatt: Freunde des Jura Museums, 185–197.
- Gauthier JA, Nesbitt SJ, Schachner E, Bever GS, Joyce WG. 2011.** The bipedal stem crocodylian *Poposaurus gracilis*: inferring function in fossils and innovation in archosaur locomotion. *Bulletin of the Peabody Museum of Natural History* **52**(1):107–126 DOI [10.3374/014.052.0102](https://doi.org/10.3374/014.052.0102).
- Goloboff PA, Farris JS, Nixon KC. 2008.** TNT, a free program for phylogenetic analysis. *Cladistics* **24**(5):774–786 DOI [10.1111/j.1096-0031.2008.00217.x](https://doi.org/10.1111/j.1096-0031.2008.00217.x).
- Gower DJ. 1999.** The cranial and mandibular osteology of a new rauisuchian archosaur from the Middle Triassic of southern Germany. *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)* **280**:1–49.
- Gower DJ. 2000.** Rauisuchian archosaurs (Reptilia, Diapsida): an overview. *Neus Jahrbuch für Geologie und Paläontologie Abhandlugen* **218**:447–488.
- Gower DJ, Schoch RR. 2009.** Postcranial anatomy of the rauisuchian archosaur *Batrachotomus kupferzellensis*. *Journal of Vertebrate Paleontology* **29**(1):103–122 DOI [10.1080/02724634.2009.10010365](https://doi.org/10.1080/02724634.2009.10010365).
- Hill RV, Lucas SG. 2006.** New data on the anatomy and relationships of the Paleocene crocodylian *Akanthosuchus langstoni*. *Acta Palaeontologica Polonica* **51**:455–464.
- Horn BLD, Melo TM, Schultz CL, Philipp RP, Kloss HP, Goldberg K. 2014.** A new third order sequence stratigraphic framework applied to the Triassic of the Paraná Basin, Rio Grande do Sul, Brazil, based on structural, stratigraphical and paleontological data. *Journal of South American Earth Sciences* **55**:123–132 DOI [10.1016/j.jsames.2014.07.007](https://doi.org/10.1016/j.jsames.2014.07.007).
- Huene FV. 1935–42.** *Die fossilen Reptilien des südamerikanischen Gondwanalandes, Ergebnisse der Sauriergrabungen in Südbrasilien 1928/29*. München: C.H. Beck'sche Verlagsbuchhandlung.
- Huene FV. 1942.** *Die fossilen Reptilien des Sudamerikanischen Gondwanalandes. Ergebnisse der Sauriergrabungen in Sudbrasilien, 1928/1929*. Munchen: C. H. Beck'she.

- Ikejiri T. 2012.** Histology-based morphology of the neurocentral synchondrosis in *Alligator mississippiensis* (Archosauria, Crocodylia). *The Anatomical Record* **295**(1):18–31 DOI [10.1002/ar.21495](https://doi.org/10.1002/ar.21495).
- Irmis RB. 2007.** Axial skeleton ontogeny in the parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *Journal of Vertebrate Paleontology* **27**(2):350–361 DOI [10.1671/0272-4634\(2007\)27\[350:ASOITP\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2007)27[350:ASOITP]2.0.CO;2).
- Juul L. 1994.** The phylogeny of basal archosaurs. *Palaeontologia Africana* **31**:1–38.
- Kischlat E-E. 2000.** Tecodôncios: a Aurora dos Arcossáurios no Triássico. In: Holz M, De Ros LF, eds. *Paleontologia do Rio Grande do Sul*. Porto Alegre: Editora da UFRGS, 246–272.
- Kischlat E-E. 2003.** Padrão muscular da coxa de arcossauromorfos fósseis: aplicação do cladismo reverso e teste de hipóteses. PhD dissertation. Universidade Federal do Rio Grande do Sul.
- Kischlat E-E, Barberena MC. 1999.** *Prestosuchus chiniquensis* (Crurotarsi, Archosauria) does not need a neotype!. *Paleontologia em Destaque* **14**:53.
- Krebs B. 1965.** Die triasfauna der Tessiner Kalkalpen. XIX. *Ticinosuchus ferox*, nov. gen. nov. sp. Ein neuer Pseudosuchier aus der Trias des Monte San Georgio. *Schweizerische Palaontologische, Abhandlungen* **81**:1–140.
- Krebs B. 1974.** Die Archosaurier. *Naturwissenschaften* **61**(1):17–24 DOI [10.1007/BF00602887](https://doi.org/10.1007/BF00602887).
- Krebs B. 1976.** Pseudosuchia. In: Kuhn O, ed. *Handbuch der Paläoherpologie Thecodonti* Stuttgart: Gustav Fischer-Verlag, **13**:40–98.
- Lacerda MB, Schultz CL, Bertoni-Machado C. 2015.** First ‘Rauisuchian’ archosaur (Pseudosuchia, Loricata) for the Middle Triassic *Santacruzodon* Assemblage Zone (Santa Maria Supersequence), Rio Grande do Sul State, Brazil. *PLoS ONE* **10**(2):e0118563 DOI [10.1371/journal.pone.0118563](https://doi.org/10.1371/journal.pone.0118563).
- Langer MC, Ribeiro AM, Schultz CL, Ferigolo J. 2007.** The continental tetrapod-bearing Triassic of South Brazil. In: Lucas SG, Spielmann JA, eds. *The Global Triassic*. Albuquerque: New Mexico Museum of Natural History and Science Bulletin, 201–218.
- Lautenschlager S, Desojo JB. 2011.** Reassessment of the Middle Triassic rauisuchian archosaurs *Ticinosuchus ferox* and *Stagonosuchus nyassicus*. *Paläontologische Zeitschrift* **85**(4):357–381 DOI [10.1007/s12542-011-0105-1](https://doi.org/10.1007/s12542-011-0105-1).
- Lautenschlager S, Rauhut O. 2014.** Osteology of *Rauisuchus tiradentes* from the Late Triassic (Carnian) Santa Maria Formation of Brazil, and its implications for rauisuchid anatomy and phylogeny. *Zoological Journal of the Linnean Society* **173**(1):55–91 DOI [10.1111/zoj.12196](https://doi.org/10.1111/zoj.12196).
- Liparini A. 2008.** Estudo da Biomecânica Craniana de um Rauissuquídeo a partir de Tomografias Computadorizadas e Técnicas de Imagens Digitais em 3 Dimensões M.Sc. Universidade Federal do Rio Grande do Sul.
- Liparini A, Schultz CL. 2013.** A reconstruction of the thigh musculature of the extinct pseudosuchian *Prestosuchus chiniquensis* from the *Dinodontosaurus* Assemblage Zone (Middle Triassic Epoch), Santa Maria 1 sequence, southern Brazil. In: Nesbitt S, Desojo JB, Irmis RB, eds. *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin*. London: The Geological Society of London, **379**:441–468.
- Long RA, Murry PA. 1995.** Late Triassic (Carnian and Norian) tetrapods from the southwestern United States. *New Mexico Museum of Natural History and Science Bulletin* **4**:1–254.
- Lucas SG, Heckert AB, Rinehart LF. 2007.** A giant skull, ontogenetic variation and taxonomic validity of the Late Triassic phytosaur *Parasuchus*. In: Lucas SG, Spielmann JA, eds. *The Global Triassic*. Albuquerque: New Mexico Museum of Natural History & Science, 222–228.

- Mancuso AC, Gaetano LC, Leardi JM, Abdala F, Arcucci AB. 2014.** The Chañares Formation: a window to a Middle Triassic tetrapod community. *Lethaia* 47(2):244–265 DOI 10.1111/let.12055.
- Martz JW. 2002.** *The Morphology and Ontogeny of Typothorax coccinarum (Archosauria, Stagonolepididae) from the Upper Triassic of the American Southwest*. M.Sc. Thesis Lubbock: Texas Tech University.
- Mastrantonio BM. 2010.** *Descrição Osteológica de Materiais Cranianos e Pós-cranianos de Prestosuchus chiniquensis (Archosauria, Rauisuchia) do Mesotriássico do RS (Biozona de Dinodontosaurus, Formação Santa Maria) e Considerações Filogenéticas sobre Rauissúquios*. Ph.D. Thesis Porto Alegre: Universidade Federal do Rio Grande do Sul.
- Mastrantonio BM, Schultz CL, Desojo JB, Garcia JB. 2013.** The braincase of *Prestosuchus chiniquensis* (Archosauria: Suchia). In: Nesbitt S, Desojo JB, Irmis RB, eds. *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin*. London: The Geological Society of London, 379:425–440.
- Merrem B. 1820.** *Versuch eines Systems der Amphibien*. Johann Marburg: Christian Krieger.
- Nesbitt SJ. 2005.** Osteology of the Middle Triassic pseudosuchian archosaur *Arizonasaurus babbitti*. *Historical Biology* 17(1–4):19–47 DOI 10.1080/08912960500476499.
- Nesbitt SJ. 2011.** The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History* 352:1–292 DOI 10.1206/352.1.
- Nesbitt SJ, Norell MA. 2006.** Extreme convergence in the body plans of an early suchian (Archosauria) and ornithomimid dinosaurs (Theropoda). *Proceedings of the Royal Society B: Biological Sciences* 273(1590):1045–1048 DOI 10.1098/rspb.2005.3426.
- Nesbitt SJ, Brusatte SL, Desojo JB, Liparini A, França MG, Weinbaum JC, Gower DJ. 2013.** Rauisuchia. In: Nesbitt SJ, Desojo JB, Irmis RB, eds. *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and the Kin*. London: The Geological Society, Special Publications, 379:241–274.
- Parker WG, Stocker MR, Irmis RB. 2008.** A new desmatosuchine aetosaur (archosauria: Suchia) from the Upper Triassic Tecovas Formation (Dockum Group) of Texas. *Journal of Vertebrate Paleontology* 28(3):692–701 DOI 10.1671/0272-4634(2008)28[692:ANDAAS]2.0.CO;2.
- Parrish JM. 1993.** Phylogeny of the Crocodylotarsi, with Reference to Archosaurian and Crurotarsan Monophyly. *Journal of Vertebrate Paleontology* 13(3):287–308 DOI 10.1080/02724634.1993.10011511.
- Peyer K, Carter JG, Sues H, Novak SE, Olsen PE. 2008.** A new suchian archosaur from the Upper Triassic of North Carolina. *Journal of Vertebrate Paleontology* 28(2):363–381 DOI 10.1671/0272-4634(2008)28[363:ANSAFT]2.0.CO;2.
- Pretto FA, Fortier DC, Liparini A, Schultz CL. 2008.** *Medindo Gigantes—estimativas do comprimento e da massa de rauissúquios do Triássico do RS através de morfometria comparada com crocodilianos atuais*. XXVII Congresso Brasileiro de Zoologia. Curitiba: XXVII Congresso Brasileiro de Zoologia—CD de Resumos.
- Raath MA. 1992.** Morphological variation in small theropods and its meaning in systematics: evidence from *Syntarsus rhodesiensis*. In: Carpenter K, Currie PJ, eds. *Dinosaur Systematics: Approaches and Perspectives*. Cambridge: Cambridge University Press, 91–106.
- Reichel M, Schultz CL, Pereira VP. 2005.** Diagenetic pattern of vertebrate fossils from the traversodontidae biozone, Santa Maria Formation (Triassic), Southern Brazil. *Revista Brasileira de Paleontologia* 8(3):173–180 DOI 10.4072/rbp.2005.3.01.
- Reig OA. 1959.** Primeros datos descriptivos sobre nuevos reptiles arcosaurios Del Triásico de Ischigualasto. *Revista de la Asociación Geológica Argentina* 13:257–270.

- Ricqlès Ad, Padian K, Horner JR. 2003.** On the bone histology of some Triassic pseudosuchian archosaurs and related taxa. *Annales de Paléontologie* **89(2)**:67–101 DOI [10.1016/S0753-3969\(03\)00005-3](https://doi.org/10.1016/S0753-3969(03)00005-3).
- Ricqlès AD, Padian K, Knoll F, Horner JR. 2008.** On the origin of high growth rates in archosaurs and their ancient relatives: complementary histological studies on Triassic archosauriforms and the problem of a ‘phylogenetic signal’ in bone histology. *Annales Paléontologie* **94(2)**:57–76 DOI [10.1016/j.annpal.2008.03.002](https://doi.org/10.1016/j.annpal.2008.03.002).
- Rieppel O. 1993.** Studies on skeleton formation in reptiles. V. Patterns of ossification in the skeleton of *Alligator mississippiensis* Daudin (Reptilia, Crocodylia). *Zoological Journal of the Linnean Society* **109(3)**:301–325 DOI [10.1111/j.1096-3642.1993.tb02537.x](https://doi.org/10.1111/j.1096-3642.1993.tb02537.x).
- Romer AS. 1971.** The Chañares (Argentina) Triassic reptile fauna. VIII. A fragmentary skull of a large thecodont, *Luperosuchus fractus*. *Brevoria* 1–8.
- Rubert RR, Schultz CL. 2004.** Um novo horizonte de correlação para o Triássico Superior do Rio Grande do Sul. *Pesquisas em Geociências* **31**:71–88.
- Schoch RR. 2007.** Osteology of the small archosaur *Aetosaurus* from the Upper Triassic of Germany. *Neuen Jahrbuch für Geologie und Paläontologie–Abhandlungen* **246(1)**:1–35 DOI [10.1127/0077-7749/2007/0246-0001](https://doi.org/10.1127/0077-7749/2007/0246-0001).
- Schultz CL, Langer MC. 2007.** Tetrápodes triássicos do Rio Grande do Sul, Brasil. *Paleontologia: Cenários de Vida*. 1 ed. Rio de Janeiro: Interciência, 277–299.
- Sen K. 2005.** A new rauisuchian archosaur from the Middle Triassic of India. *Palaeontology* **48(1)**:185–196 DOI [10.1111/j.1475-4983.2004.00438.x](https://doi.org/10.1111/j.1475-4983.2004.00438.x).
- Sereno PC. 1991.** Basal archosaurs: phylogenetic relationships and functional implications. *Journal of Vertebrate Paleontology* **10(Supplement 3)**:1–53.
- Sill WD. 1974.** The anatomy of *Saurosuchus galilei* and the relationships of the rauisuchid thecodonts. *Bulletin of The Museum of Comparative Zoology* **146**:317–362.
- Soares MB, Schultz CL, Horn BLD. 2011.** New information on *Riograndia guaibensis* Bonaparte, Ferigolo & Ribeiro, 2001 (Eucynodontia, Trithelodontidae) from the Late Triassic of southern Brazil: anatomical and biostratigraphical implications. *Anais da Academia Brasileira de Ciências* **83(1)**:329–354 DOI [10.1590/S0001-37652011000100021](https://doi.org/10.1590/S0001-37652011000100021).
- Sulej T. 2005.** A new rauisuchian reptile (Diapsida Archosauria) from the Late Triassic of Poland. *Journal of Vertebrate Paleontology* **25(1)**:78–86 DOI [10.1671/0272-4634\(2005\)025\[0078:ANRRDA\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2005)025[0078:ANRRDA]2.0.CO;2).
- Taborda JRA, Cerda IA, Desojo JB. 2013.** Growth curve of *Aetosauroides scagliai* Casamiquela 1960 (Pseudosuchia: Aetosauria) inferred from osteoderm histology. In: Nesbitt SJ, Desojo JB, Irmis RB, eds. *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and the Kin*. London: The Geological Society, Special Publications, **379**:413–423.
- Trotteyn MJ, Desojo JB, Alcober OA. 2011.** Nuevo material postcraniano de *Saurosuchus galilei* reig (Archosauria: Crurotarsi) del Triássico Superior del centro-oeste da Argentina. *Ameghiniana* **48(1)**:605–620 DOI [10.5710/AMGH.v48i1\(265\)](https://doi.org/10.5710/AMGH.v48i1(265)).
- Weinbaum JC. 2011.** The skull of *Postosuchus kirkpatricki* (Archosauria: Paracrocodyliformes) from the Upper Triassic of the United States. *PaleoBios* **30**:18–44.
- Weinbaum JC. 2013.** Postcranial skeleton of *Postosuchus kirkpatricki* (Archosauria: Paracrocodylomorpha) from the Upper Triassic of the United States. In: Nesbitt S, Desojo JB, Irmis RB, eds. *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and the Kin*. London: Geological Society of London, Special Publications, **379**:525–553 DOI [10.1144/sp379.7](https://doi.org/10.1144/sp379.7).

- Weinbaum JC, Hungerbühler A. 2007.** A revision of *Poposaurus gracilis* (Archosauria: Suchia) based on two new specimens from the Late Triassic of the southwestern U.S.A. *Paläontologische Zeitschrift* **81**(2):131–145 DOI [10.1007/BF02988388](https://doi.org/10.1007/BF02988388).
- Zerfass H, Lavina EL, Schultz CL, Garcia AGV, Faccini UF, Chemale F Jr. 2003.** Sequence stratigraphy of continental Triassic strata of southernmost Brazil: a contribution to southwestern Gondwana palaeogeography and palaeoclimate. *Sedimentary Geology* **161**(1–2):85–105 DOI [10.1016/S0037-0738\(02\)00397-4](https://doi.org/10.1016/S0037-0738(02)00397-4).
- Zittel KA. 1887–90.** Handbuch der Palaeontologie. *Abteilung Palaeozoologie*. Munich and Leipzig: R. Oldenbourg.

PARTE 2
ARTIGOS DA TESE

ARTIGO 3. LACERDA, M.B.; França, M.A.G. & Schultz, C.L. *A new erpetosuchid (Pseudosuchia, Archosauria) from the Middle-Late Triassic of Southern Brazil. Zoological Journal of the Linnean Society, Submetido.*

Zoological Journal of the Linnean Society

Decision Letter (ZOJ-06-2017-3012)**From:** louise.allcock@nuigalway.ie**To:** marcel.lacerda@yahoo.com.br**CC:****Subject:** Zoological Journal of the Linnean Society - Decision on Manuscript ID ZOI-06-2017-3012**Body:** 14-Oct-2017

Dear Mr. Lacerda:

Manuscript ID ZOI-06-2017-3012 entitled "A new erpetosuchid (Pseudosuchia, Archosauria) from the Middle-Late Triassic of southern Brazil" which you submitted to the Zoological Journal of the Linnean Society, has been reviewed. The comments of the referees(s) are included at the bottom of this letter.

The referees(s) have recommended some minor revisions to your manuscript. Therefore, I invite you to respond to the referees(s)' comments and revise your manuscript.

To submit your revision, click here: *** PLEASE NOTE: This is a two-step process. After clicking on the link, you will be directed to a webpage to confirm. ***

https://mc.manuscriptcentral.com/zoi?URL_MASK=8df7573a9ef74c6098d09d505249fe33

Check everything is still correct. Remove old versions of your files from the site and upload your new files. Check the pdf is correct and submit.

When submitting your revised manuscript, you will be able to respond to the comments made by the referees(s) in the space provided. You can use this space to document any changes you make to the original manuscript. In order to expedite the processing of the revised manuscript, please be as specific as possible in your response to the referees(s).

Because we are trying to facilitate timely publication of manuscripts submitted to the Zoological Journal of the Linnean Society, your revised manuscript should be uploaded by 13-Nov-2017. If it is not possible for you to submit your revision in a reasonable amount of time, please contact us.

Once again, thank you for submitting your manuscript to the Zoological Journal of the Linnean Society and I look forward to receiving your revision.

Sincerely,

Dr. Louise Allcock

Editor, Zoological Journal of the Linnean Society

louise.allcock@nuigalway.ie

A new erpetosuchid (*Pseudosuchia*, Archosauria) from the Middle-Late Triassic of Southern Brazil

MARCEL B. LACERDA^{1*}, MARCO A. G. DE FRANÇA² and CESAR L. SCHULTZ^{1,3}

¹ Programa de Pós-Graduação em Geociências, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Bento Gonçalves Avenue 9500, Porto Alegre, RS, Brazil;

² Universidade Federal do Vale do São Francisco, Campus de Ciências Agrárias/ Colegiado de Ciências Biológicas, Highway BR 407, Km 12, Lote 543, Projeto de Irrigação Senador Nilo Coelho, s/nº - C1, CEP 56.300-990, Petrolina, PE, Brazil;

³ Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Bento Gonçalves Avenue 9500, Porto Alegre, RS, Brazil.

**marcel.lacerda@yahoo.com.br*,

ADDITIONAL KEYWORDS: Pagosvenator – Archosauria – Santa Maria Supersequence – Brazil – Erpetosuchidae – South America – Triassic.

SHORT RUNNING TITLE: A new erpetosuchid from the Santa Maria Supersequence, Late Triassic of Southern Brazil

ACKNOWLEDGMENTS: We like to thank C. Rodrigues and B. Stefanello (MMACR) for access to the specimen for study. V.P. Pereira and P.A.V. Paim (UFRGS) for access to the sample database and invaluable help in the REE analysis part of this study. A. Martinelli, J. Desojo, B. Mastrantonio, E. Dassisti, V. Neto and M. Langer for the many helpful discussions, comments and suggestions that greatly improved this manuscript. We especially thank F. Pinheiro for the helpful suggestions in regards to the naming of the specimen. L.F. Lopes (UFRGS) for the skillful photographs. We also thank the people that allowed us access to the collections under their care: A. Ribeiro and J. Ferigolo (MCN), J. Powell (PVL), L. Steel and S. Chapman (NHMUK), O. Rauhut (BSPG), R. Martinez (PVSJ), R. Schoch (SMNS), S. Kaal (SAM), and S. Martin (PULR). This research was funded by the doctorate scholarship given to M. Lacerda by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) grant 141378/2013-1 and a short term grant by the Deutscher Akademischer Austauschdienst (DAAD) nº 57130097. Access to the free version of TNT 1.1 was granted by the Willi Henning Society.

ABSTRACT

The evolution and diversification of Triassic pseudosuchian lineages has been the subject of much interest and revision in the last couple of decades, fueled by new and important discoveries, which consequently allowed for better sampled phylogenetic analysis. In the present contribution we add to this by describing a new taxon, *Pagosvenator candelariensis*, for the Middle-Late Triassic *Dinodontosaurus* Assemblage Zone of the Santa Maria Supersequence of southernmost Brazil. A comparative osteological analysis combined with a phylogenetic one supports its inclusion within the clade Erpetosuchidae and provides an insight into the phylogenetic relationship and evolutionary history of this clade, with two possibilities for the Erpetosuchidae relationship: as an early branch of pseudosuchians, being sister group of Ornithosuchidae; or a closer relationship with the clade composed by Gracilisuchidae and Paracrodylomorpha. Additionally, the results presented and discussed in the article are of biostratigraphical importance, since the described taxon is from Ladinian/Carnian age would fill a temporal gap that exists within Erpetosuchidae, in between *Parringtonia gracilis* from Anisian to *Erpetosuchus* from late Carnian to Norian, and would be the first occurrence of a member of this clade in South America.

Introduction

Archosauria is a diverse clade composed by the crocodylians, birds and many extinct lineages (Gauthier, 1984; Gauthier & Padian, 1985; Benton & Clark, 1988; Sereno, 1991; Juul, 1994; Brusatte *et al.*, 2010; Nesbitt, 2011; Butler *et al.*, 2011; Ezcurra, 2016). Historically, aside from dinosaurs, there has been reduced enthusiasm over this clade and other non-archosaurian archosauriforms that also evolved in the Triassic Period, but recent rekindled interest, sparked by new discoveries (*e.g.* Nesbitt *et al.*, 2014; Ezcurra & Butler, 2015; Pinheiro *et al.*, 2016; Stocker *et al.*, 2016) along with revisions of previously described taxa indicate a much richer diversity that was previously imagined (Brusatte *et al.*, 2011). These discoveries have allowed for better sampled matrixes that and more robust cladistics analysis (Brusatte *et al.*, 2010; Nesbitt, 2011; Butler *et al.*, 2011; Bazcko *et al.*, 2014, Nesbitt *et al.* 2015; Ezcurra, 2016).

Although consensus has been reached in some topologies, with historically clear monophyletic groups, such as Aetosaurs (Brusatte *et al.*, 2010; Nesbitt, 2011; Desojo *et al.*, 2013; Parker, 2016), others, such as the relationship of Phytosauria among archosauriforms (see discussion in Nesbitt, 2011 and Ezcurra, 2016) and problematic taxa which are represented by mostly incomplete specimens display low support due to data matrixes with ambiguous characters or a history of conflicting topologies (*e.g.* Gower, 2000; Brusatte *et al.*, 2010; Nesbitt, 2011; Nesbitt & Butler, 2012; Nesbitt *et al.*, 2013; Ezcurra, 2016). Unfortunately, even with these new insights, there are still many taxa only represented by few or mostly incomplete specimens and a large number of ghost lineages still haunt our view of the Triassic biotas. This is, of course, inherit of the fossil record, so the need for new discoveries is key to advance our understanding and to achieve better supported phylogenetic analyses (Fig.1: A, B).

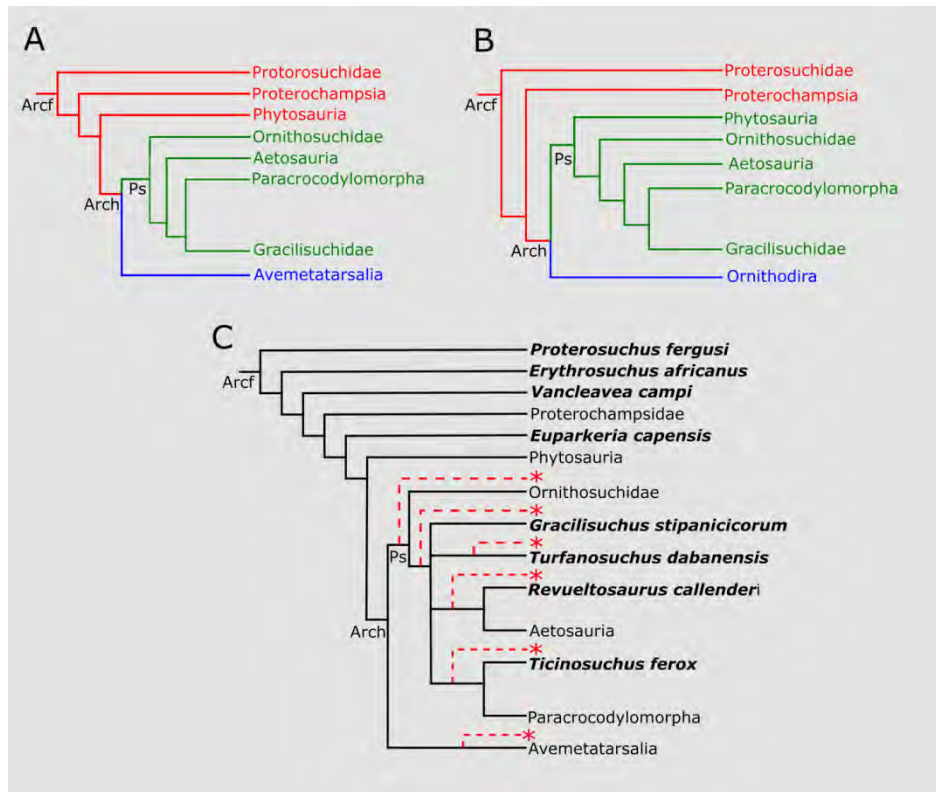


Figure 1. Distinct proposals of phylogenetic relationships within Archosauriforms and Archosaurs. (A) Butler et al., (2014) based on a modified matrix of Nesbitt (2011); (B) Ezcurra (2016). (C) Modified cladogram of Butler and Nesbitt (2012), with the red lines and asterisks indicating the possible phylogenetic positions of Erpetosuchidae. Abbreviations: **Arcf.** Archosauriforms; **Arch.** Archosauria; **Ps.** Pseudosuchia.

The Triassic outcrops of the Santa Maria Supersequence (Middle-Late Triassic) located in the central region of the Rio Grande do Sul State of southern Brazil have historically been the site of many important finds since they were first scientifically prospected in the late 1920's (Huene, 1935-42; 1942; Beltrão, 1965). Efforts have continued during the subsequent decades to explore these and new localities (Barberena, 1977; Barberena *et al.*, 1985; Schultz *et al.*, 2000; Da-Rosa, 2014; Horn *et al.*, 2014; Müller *et al.*, 2014) which have produced an ample record for many groups of archosaurs and non-archosaurian archosauriforms, such as aetosaurs (Desojo *et al.* 2012; Da-Silva *et al.* 2014), doswellids (Desojo *et al.*, 2011), early branch loricatans (Barberena, 1978; França *et al.*, 2011; Lacerda *et al.*, 2015; Da-Silva *et al.*, 2016); raiisuchids (Huene, 1935-42; Lautenschlager & Rauhut, 2014), poposaurids (França *et al.*, 2014), phytosaurs (Lucas & Kischlat, 2003), proterochampsids (Bertoni-Machado & Kischlat, 2003; Raugust *et al.*, 2013), aphanosaurians (Nesbitt *et al.*, 2017), pterosaurs (Bonaparte *et al.*, 2010) and dinosauriforms (*e.g.* Colbert, 1970; Bonaparte *et al.*, 1999;

Langer *et al.* 1999; Leal *et al.*, 2004; Ferigolo & Langer, 2006; Cabreira *et al.*, 2011; 2016; Pinheiro, 2016).

In the present article, we add to this record by describing a new taxon. This increases the diversity of archosaur lineages for the Triassic of this region by presenting the first occurrence of a member of the Erpetosuchidae in South America, which, in turn, proposes interesting questions on the paleobiogeographical distribution and evolution of this clade. Erpetosuchidae was proposed by Watson (1917) to include *Erpetosuchus granti*, which was described by Newton (1894) based on specimens from the Lossiemouth Sandstone Formation (late Carnian–Norian / Late Triassic), Scotland, which recognized its relationship within Archosauria, possibly closer to phytosaurs and aetosaurs, but also displaying some similarities with crocodylians (Benton & Walker, 2002). Huene (1939) described *Parringtonia gracilis* from the Lifua Member of the Manda Beds of Tanzania (latest Anisian / Middle Triassic) and referred it to Pseudosuchia, acknowledging some of its similarities to *Ornithosuchus woodwardi* (Newton, 1894; *sensu* Baczko & Ezcurra, 2016) and *Saltopus elginensis* (Huene, 1910), but considered the preserved material insufficient to determine if the taxon was closely related to these taxa or if instead it would represent a new pseudosuchian lineage. Similarities on the scapulae of *Parringtonia* and *Erpetosuchus* were noted by Krebs (1965), but the inclusion of both taxa in a single group was proposed in several articles by Walker (1961; 1968; 1970), with a formal diagnosis of Erpetosuchidae only provided later by Krebs (1976), which retained both taxa. The removal of *Parringtonia* from this group was proposed by Benton & Walker (2002), suggesting that the similarities were possible plesiomorphies. An incomplete specimen (AMNH 29300) is referred to *Erpetosuchus* sp. by Olsen, Sues & Norell (2002) from the Late Triassic (Norian) New Haven Formation of Connecticut, USA. Lastly, Nesbitt & Butler (2012) phylogenetically defined Erpetosuchidae as a branch based clade that includes *Parringtonia* and *Erpetosuchus*, but displayed a poor resolution within Archosauria (Fig. 1: C) In addition, *Dyoplax arenaceus* (Fraas, 1867; Maisch *et al.*, 2013) from the Schilfsandstein Formation (early Carnian / Late Triassic) of Germany, was proposed by Walker (1961; 1968; 1970) as member of the Erpetosuchidae. The phylogenetic position of this taxon has been largely debated, having been considered closer to Aetosauria (Huene, 1903), Erpetosuchidae (Walker, 1961, 1968, 1970; Maisch *et al.*, 2013), or Crocodylomorpha (Lucas *et al.*, 1998; Benton & Walker, 2002). In the

analysis by Nesbitt and Butler (2012), *Dyoplax* was not included because these authors concluded that the taxon cannot display features that clearly indicate that it belongs to Erpetosuchidae, but did not, however, completely exclude such possibility, considering its overall morphology, but this would require a better understanding of its osteology, only possible by the discovery and study of new materials.

Materials and Methods

The specimen is composed by a single mostly complete but badly preserved skull with mandibles, associated with some post-cranial elements (holotype MMACR PV 036-T). The majority of the description and comparative osteological study is based on the structures present on the right side of the skull, which is better preserved.

Preparation of the specimen was made using mechanical chisels and microtools at the start of its study by one of the authors (MBL). However, due to its hardened preservation, especially of the underlying rock matrix, mechanical preparation was very limited, and most of the ventral portion of the fossil remained concealed by the matrix. Computer tomography was used to view inaccessible areas such as the palatal region and to discover the number of alveoli on the jaws. The specimen was scanned at the Serpal Clínica de Diagnósticos, Porto Alegre, Brazil, under a medical GE Light Speed Machine with the following settings: slice thickness of 1 mm, slice increment (interslice spacing) of 0.6 mm, field of view of 250 mm, 120 kV and 150 mA. The data was outputted from the scanner in DICOM format.

The type locality is unknown. The specimen was donated to the Museu Municipal Aristides Carlos Rodrigues in the Municipality of Candelária by a local citizen that requested, emphatically, to remain anonymous and did not reveal the place of the discovery. The only information that was provided to the museum curator was that the fossil was discovered 20 years ago at the margin of one of the many artificial ponds (“açudes”) that exist in that region. The donor collected the specimen not considering it as a fossil, but as an “odd, skull shaped rock” and subsequently used it as a curiosity piece in his living room for the following two decades. Then, on Christmas Day, 2013, he donated it to the local museum. This was likely motivated by an increase in the knowledge of fossils and prehistoric life of the citizens of the town and region due to efforts of the local museum curator and staff.

The preservation pattern would be a clue of its origin, at least at the biostratigraphical level, since it matches the fossil preservation of specimens from the *Dinodontosaurus* Assemblage Zone (Holz & Schultz, 1998) but further support was needed. A rare earth element (REE) analysis was chosen to test this inference, as such methodology has been successfully used for establishing specimen origins (*e.g.* Lukens *et al.*, 2009; Suarez *et al.*, 2009). Samples were collected from the studied specimen and from an unprepared and undescribed dicynodont, deposited in the collection of the Laboratório de Paleovertebrados of the Universidade Federal do Rio Grande do Sul, which was discovered in the “Sanga Pascual” outcrop near the Municipality of Candelária and which has been biostratigraphically established as belonging to the *Dinodontosaurus* AZ (Barberena, 1977; Schultz *et al.*, 2000). The samples were prepared following the standard methodology and sent to Activation Laboratories Ltd, Ontario, Canada, where they were subjected to a UT-7 Sodium Peroxide Fusion (ICPMS) analytical package.

The results were included in a database of REE samples from fossil bearing outcrops of major sedimentary basins in Brazil that is currently in the final stages of construction at UFRGS by P.A.V. Paim and V.P. Pereira (See supplementary material 1). The results indicated a close match with samples of the Santa Maria Supersequence and specially of the *Dinodontosaurus* AZ, but displayed a signature that did not match that of any outcrop that was included in the database, thus indicating that the fossil was not discovered in any of the more well-known sites. The full description of the methods used and the results are presented in the complementary material.

Nomenclatural Acts

The electronic edition of this article conforms to the requirements of the amended International Code of Zoological Nomenclature, and hence the new names contained herein are available under that Code from the electronic edition of this article. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix <http://zoobank.org/>. The LSID for this publication is: urn:lsid:zoobank.org:pub23F5E491-32A2-41EC-A821-

CE8ADAF65E86. The electronic edition of this work was published in a journal with an ISSN, and has been archived and are available on PubMed ad LOCKSS.

Institutional Abbreviations

BSPG, Bayerische Staatssammlung für Paläontologie und Geologie and Department of Earth and Environmental Sciences, Munich, Germany; **CPEZ**, Coleção de Paleontologia do Museu Paleontológico e Arqueológico Walter Ilha, São Pedro do Sul, Brazil. **MCN**, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; **MMACR**, Museu Municipal Aristides Carlos Rodrigues, Candelária, Brazil; **NHMUK**, The Natural History Museum, London, UK; **PULR**, Museo de Ciencias Naturales, Univerisdade Nacional de La Rioja, La Rioja, Argentina; **PVL**, Paleontología de Vertebrados, Instituto ‘Miguel Lillo’, San Miguel de Tucumán, Argentina; **PVSJ**, División de Paleontología de Vertebrados del Museo de Ciencias Naturales y Universidad Nacional de San Juan, San Juan, Argentina; **SAM**, Iziko South African Museum, Cape Town, South Africa; **SMNS**, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; **UFRGS-PV**, Laboratório de Paleovertebrados da Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

Systematic Paleontology

Archosauria Cope 1869 *sensu* Gauthier and Padian 1985

Pseudosuchia Zittel 1887-1890 *sensu* Gauthier and Padian 1985

Erpetosuchidae Watson, 1917 *sensu* Nesbitt and Butler 2012

Pagosvenator candelariensis gen. et sp. nov.

Etymology: “*pagos*” is a regional gaucho jargon term (sometimes used in the singular *pago*, but its plural use is more common) that is derived from the latin “*pagus*” that means “countryside” or “rural community”; “*venator*” is Latin for “hunter” due to it being a relatively large carnivore; and “*candelariensis*” is in regard to the city of Candelária, where is located the museum in which the specimen is deposited. The name means “the hunter from the surroundings of Candelária”.

Holotype: MMACR PV 036-T; mostly complete and articulated skull and lower jaws, associated with two incomplete vertebrae and 5 heavily ornamented osteoderms.

Diagnosis: Pseudosuchian (Erpetosuchidae) archosaur, with the following unique combination of characters: four premaxillary teeth; maxilla with an edentulous posterior margin, large and posteriorly deep antorbital fossa and a posteriorly positioned antorbital fenestra; ascending process of the jugal bifurcates dorsally into a V shaped structure that composes the ventral margin of the orbit; palpebral bones; sub-rectangular osteoderms with heavily ornamented dorsal surfaces, displaying small pits and short ridges.

Type Locality and Age: The locality is unknown (see discussion in the previous topic and in the Supplementary material 1). The type of the preservation of the specimen with a supporting Rare Earth Element analysis indicates it belongs to a site from the *Dinodontosaurus* Assemblage Zone, Middle-Late Triassic (late Ladinian-earliest Carnian age) whose outcrops are placed southwards of the city of Candelária.

Description

Skull overview

The skull of *Pagosvenator candelariensis* suffered taphonomic alterations, with the majority of the elements that form the infratemporal fenestra being altered, in the case of the left side, or lost, such as in the case of the right one (Fig. 2). The anterior part of the rostrum was damaged and rotated 15° clockwise. The right side of the skull displays major distortions, with many elements, specifically the ones that form the ventral margin of the maxilla, the ventroposterior border of the orbit and the infratemporal fenestra being displaced or lost. Some suture patterns were also distorted, which resulted that some paired elements do not display mirrored features.

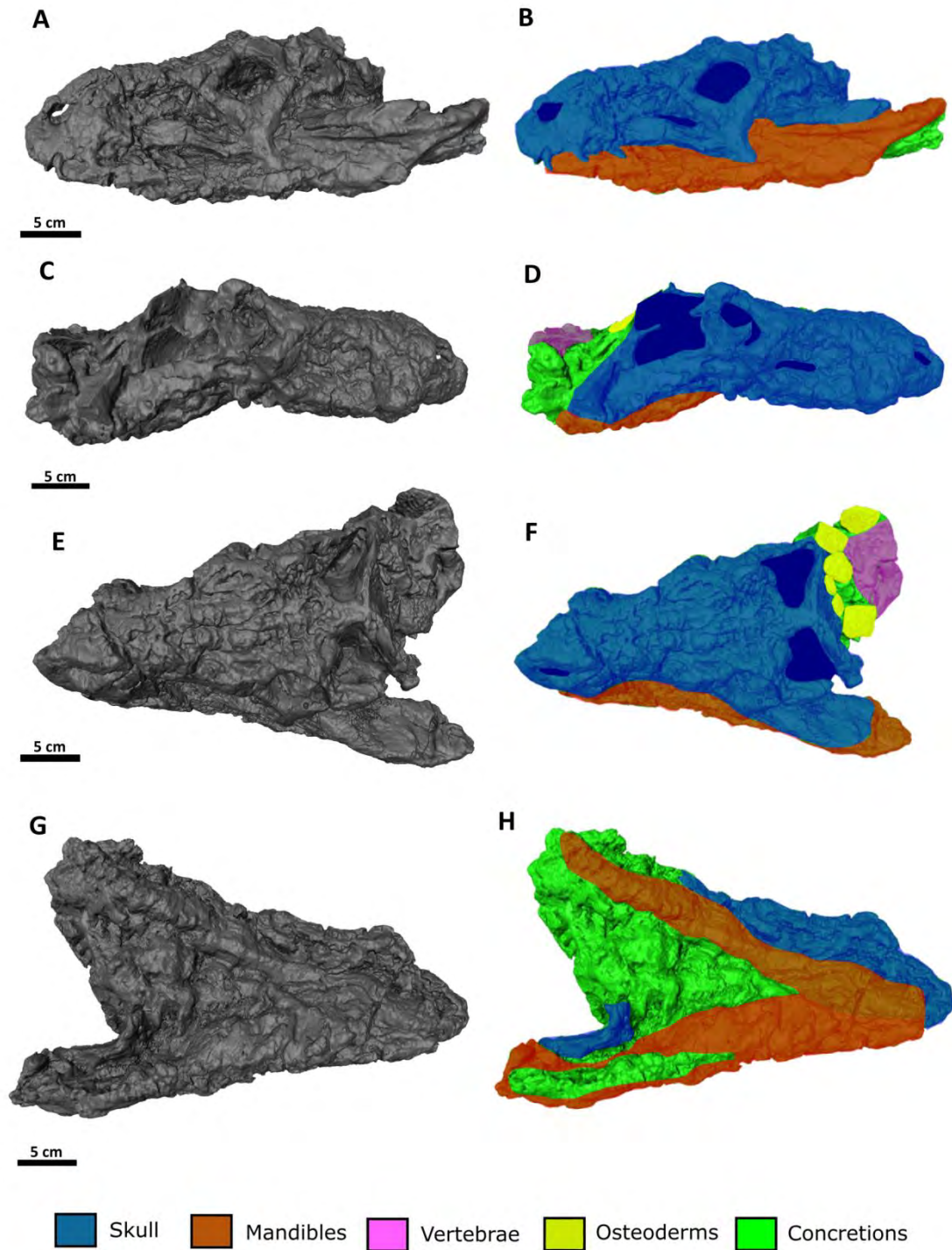


Figure 2. Computer tomography models of MMACR PV 036-T, presenting the different portions of the specimen and some of the preservational alterations that the specimen suffered: (A-B) dorsal, (C-D) ventral, (E-F) left and (G-H) right lateral views. Not to scale.

The **premaxilla** is formed by a subquadrangular main body, a gracile anterodorsal process and a narrow posterodorsal one. Although both premaxillae are

morphologically similar, the right one is distorted and dorsoventrally shorter due to a heightened ventral curvature. In lateral view, the anterior margin of the main body is sub-vertical with an anteroventral margin that is recurved up to the remains of the first premaxillary tooth (Fig. 3). This margin displays a small dorsoposterior curvature that ends at the base of the anterodorsal process, which initially was interpreted as similar to condition found in Ornithosuchidae (Lacerda *et al.* 2016). This ventroposterior curvature was heightened due to the compression of the anterior portion of the rostrum which created an effect similar to the “downturned” condition present in that clade. The dorsal third of the body of the premaxillae is more medially compressed, forming a marked fossa that forms the anteroventral border of the external naris.

The anterodorsal process is narrow and articulates dorsoposteriorly between two anteroventral projections of the nasals in a V shaped contact (Fig. 3), similar to the one described in *Riojasuchus tenuisiceps* (PVL 3827; Bonaparte, 1967; Baczko *et al.*, 2016). This area suffered a dorsoventral compression which altered its dimensions and the majority of the dorsal border of the naris, which slightly reduced its height but not its overall form. The posterodorsal process of the premaxilla displays a wide base that tapers posteriorly with its most posterior end articulating between two ventral processes of the nasal and located posterior to the nasal opening. This process is greater than the anteroposterior length of the main body of premaxilla, similar to Gracilisuchidae and early branch loricatans, but diverges on the comparatively smaller process of *Erpetosuchus* (NHMUK R3139, Ornithosuchidae (NHMUK PV R3143; PVL 3827) and Aetosauria (*e.g.* SMNS 5770) (Nesbitt, 2011; Nesbitt & Butler, 2012). The posterodorsal process is better observed in dorsal norm, as in lateral view, due to the abovementioned alteration on this region of the skull, it appears as a smaller, acute process. Its distal end fits on a slot in the nasal, similar to *Revueltosaurus callenderi* (Hunt, 1989; Parker *et al.*, 2005) and Gracilisuchidae (Butler *et al.*, 2014).

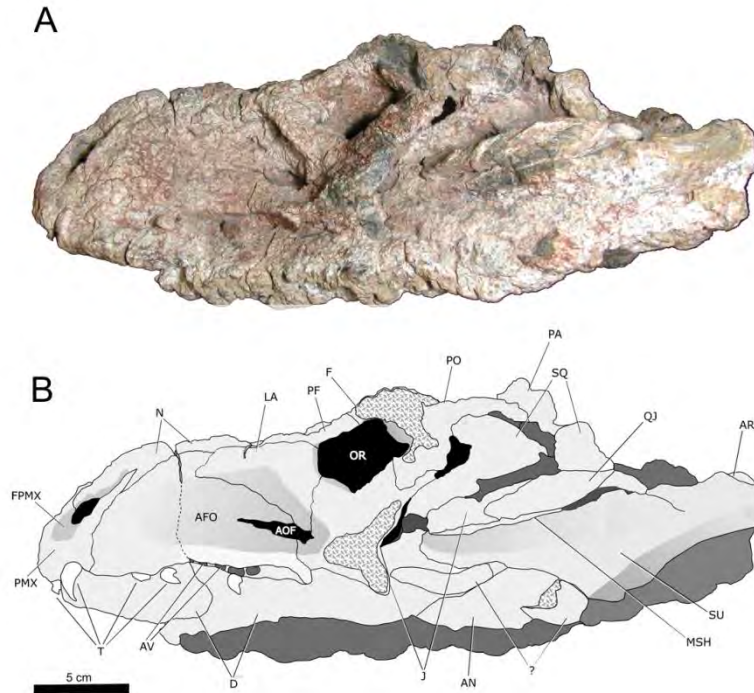


Figure 3. Photograph (A) and interpretive illustration (B) of specimen MMACR PV 036-T in left lateral view. **Abbreviations:** AFO, antorbital fossa; AN, angular; AOF, antorbital fenestra; AR, articular; AV, alveoli; F, frontal; FPMX, premaxillary fossa; J, jugal; LA, lacrimal; MSH, mandibular shelf; N, nasal; OR, orbit; PA, parietal; PF, prefrontal; PMX, premaxilla; PO, postorbital; QJ, quadratojugal; SQ, squamosal; SU, surangular; T, teeth; ? Unidentified bone fragments. Concretions are in dark grey, cranial openings in black, broken areas in crosshatching.

Tooth remains are preserved on the anterolateral and ventral portions of the rostrum, but only the two on the left premaxilla are inserted in their sockets, with the most posterior one being the better preserved. The abovementioned altered ventral curvature damaged most of the area and its remains were preserved in a large concretion mixed with bone and tooth fragments that obscures most of this area. The number of alveoli was only determined by CT-scans, which revealed four on each premaxilla (Fig. 4). The number of premaxillary teeth is a plastic feature in Pseudosuchians. Four teeth are considered to *Erpetosuchus* (NHMUK R3139), *Aetosaurus ferratus* (SMNS 5770; Schoch, 2011), *Gracilisuchus stipanicorum* (Romer, 1972, Butler et al., 2014) and early branch taxa of Loricata, whereas some taxa like *Stagonolepis robertsoni* (Walker, 1961), *Revueltosaurus*, *Turfanosuchus dabanensis* (Wu et al., 2001a) e *Yonghesuchus sangbiensis* (Wu et al., 2001b) bear five teeth, and *Ornithosuchus woodwardi* and

Riojasuchus tenuisiceps show three teeth on premaxilla (Nesbitt, 2011; Nesbitt & Butler, 2012).

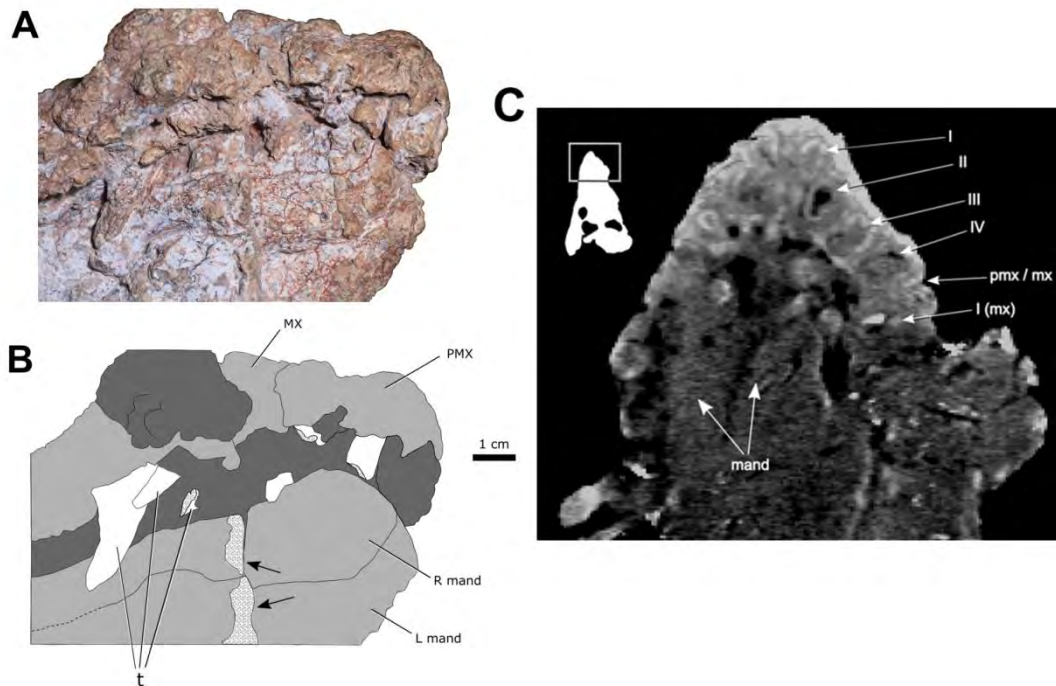


Figure 4. Detail photograph (A) and interpretative drawing (B) of the rostral region of MMACR PV 036-T in ventral view. Arrows indicate the fracture points of the anterior tips of the mandibles. (C) CT capture of the same region, in ventral view, indicating the number of alveoli on the premaxilla and the first maxillary tooth immediately after the premaxilla-maxilla contact. Abbreviations: **MX**. Maxilla; **PMX**. Premaxilla; **R mand**. Right mandible; **L mand**. Left mandible; **t**. teeth; **I-IV**. Premaxillary teeth; **I(mx)**. First maxillary tooth; **pmx/ mx**. Contact between the premaxilla and maxilla. Concretions in dark grey, broken areas in crosshatching.

The **maxilla** is divided in a subrectangular main body and a dorsoventrally tall and anteroposteriorly wide ascending process. The anterior portion, which articulates with the premaxilla, in dorsal view, has a marked transverse expansion which is mirrored in both maxillae, a condition which is uncommon in archosaurs but is described in *Parringtonia gracilis* (NHMUK R8646; Nesbitt & Butler, 2012). In lateral view, the main body is dorsoventrally expanded and both anterior and posterior areas display similar dorsoventral depths. The premaxilla-maxilla suture is tightly closed, not displaying any foramina or accessory openings, as well as not displaying a diastema between the elements, unlike Ornithosuchidae (NHMUK PV R3143; PVL 3827). The

anterior margin is rounded; slopping dorsoposteriorly into the anteroposteriorly elongated ascending process which articulates posteriorly between the nasal and posteroventrally with the anterodorsal and anterior margins of the lacrimal. The posterior portion forms the majority of the anterior margin of the antorbital fenestra. The anterior portion of the ventral margin is straight up to the area where the rostrum is damaged. From there, it is slightly concave and the ventral area with the alveoli is more laterally projected. This projection was likely caused by taphonomic compression. On the posterior end of this margin there is a small ventroposterior process that extends eight millimeters beyond the articulation with the jugal. The posterior process of the maxilla has almost same dorsoventral height on the posterior region, not tapering as in Ornithosuchidae (NHMUK PV R3143; PVL 3827) or expanding as in *Erpetosuchus* (NHMUK R3139) and *Parringtonia* (NHMUK PV R8646) (Nesbitt & Butler, 2012). However, the lateromedial length is greater than dorsoventral height on level of the lacrimal, a characteristic shared with *Erpetosuchus* and *Parringtonia* (Nesbitt & Butler, 2012).

The antorbital fossa occupies the majority of the lateral surface of the maxilla. This fossa gradually deepens posteriorly, reaching its deepest point close to the ventral area of the lacrimal and the anterior margin of the jugal. The antorbital fenestra is half the anteroposterior length of the fossa and is posteriorly located on the rostrum. It is subtriangular but very dorsoventrally compressed, almost to a point of a slit, with a rounded anterior tip, and displays a 25° dorsoventral inclination in regards to the central axis of the maxilla. The nearly pointed anterior margin of the antorbital fenestra is shared with *Erpetosuchus* and some ornithosuchid taxa (*Venaticosuchus rusconi* and *Riojasuchus tenuisiceps*), but a gently rounded anterior margin is observed on *Ornithosuchus woodwardi* (Nesbitt & Butler, 2012; Baczko *et al.*, 2014; Baczko & Desojo, 2016; Baczko & Ezcurra, 2016).

Due to the lateral distortion of the ventral margin of the left maxilla, the posterior third of this element is turned laterally; exposing the ventral margin with five concretion filled alveoli and an edentulous posterior region after the last alveolus. Computer imaging identified teeth starting immediately posterior to the articulation with the premaxilla, so at least six maxillary teeth would be present. With the exception of archosaurs that display a more specialized maxilla for herbivory (*e.g.* poposaurids), an edentulous posterior region of the maxilla is described only in Erpetosuchidae

(Nesbitt, 2011; Butler *et al.*, 2012; Nesbitt & Butler, 2012). However, this would differ from *Parringtonia gracilis*, which only has five and *Erpetosuchus granti* with four, but is similar to the possible nine maxillary teeth inferred for a specimen attributed to *Erpetosuchus* sp. (Olsen, Sues & Norell, 2002: AMNH 29300;).

All teeth are badly preserved, being incomplete or covered in a thick layer of concretion. The two largest ones are on the ventral border of the right maxilla and three disarticulated teeth are preserved along the underlining lateral face of the left mandible. The teeth are anteroposteriorly recurved and lateromedially compressed and there is no indication of any serrations (Fig. 3).

The **nasals** are anteroposteriorly elongated elements that form the majority of the anterodorsal and dorsolateral surface of the rostrum, with both elements articulating medially. The dorsal surface is smooth, and continues the length of the skull roof, with no indication of a convexity or “roman nose” like feature as in *Decuriasuchus quartacolonias* (MCN PV10.105a; França *et al.*, 2011; 2013). The anterior portion, in lateral view, is anteroventrally curved and divided into two processes. The anteroventral one forms the majority of the dorsal and dorsoposterior border of the external naris and contacts the dorsal tip of the anterodorsal process of the premaxilla and it extends laterally and anteroventrally up to half its length. The posteroventral process is comparatively short and narrow. It articulates with the posterodorsal process of the premaxilla, forming a depressed area for this contact, with a piece of a process occupying an area between the premaxilla and maxilla. The main body of the nasal forms the anterior portion of the skull roof, with a broad lateromedial length, whereas the posterior process is located on its medial half and posteriorly tapering along the articulation with the frontal. The nasal has a broad contact with the prefrontal, on posterior margin of main body and the lateroanterior region of posterior process, unlike Ornithosuchidae in that the contact of these bones are absent (Walker, 1964; Baczko & Ezcurra, 2013; Baczko *et al.*, 2016). In addition, *Pagosvenator* does not share with the Gracilisuchidae and some loricatans (*e.g.* Rausisuchidae) the nasal contributing with the antorbital fossa (Nesbitt, 2011; França *et al.*, 2013; Butler *et al.*, 2014).

The **lacrimal** is divided in two processes; an anterior L-shaped one that is anteroposteriorly inclined, and a posteroventral process that forms $\frac{3}{4}$ of the anterior margin of the orbit (Fig. 3). This bone is completely covered dorsally, lacking any

contribution to the skull roof. The anterior process delimits the posterior half of the dorsal and all the posterodorsal margins of the antorbital fossa, along with the dorsoposterior margin of the antorbital fenestra. It forms, with the prefrontal and the jugal a thick anterolateral expansion or ridge along the extent of the antorbital bar. This ridge forms a deep pocket on the posterodorsal end of the fossa, similar to the one in *Riojasuchus tenuisiceps*, Theropods and basal saurischians (Nesbitt, 2011; Bazcko *et al.*, 2016), but it displays a more lateral expression, but this may have been heightened due to the distortion already described.

The **prefrontal** is a wide element of the skull roof, with a discrete presence on the lateral norm (Fig. 2, 3). It articulates anteromedially with the nasals, posteromedially with the frontal and ventromedially with the jugal, forming the majority of the anterior border of the orbit. Its anterior portion is not in articulation with the rostrum, anteriorly, due to the distortion that this part of the skull suffered, indicated by a transverse fracture on the the anterior portion of both prefrontals, but would indicate the overall aspect of the anterior margins. In dorsal view it is subrectangular, with a straight anterior margin, a convex posterior one and a small lateral process that covers ventrolaterally the lacrimal. The dorsal surface displays a deep fossa that is mirrored on both elements. This fossa is lateral to the anterior processes of the frontal and is near and area that displays a large number of fossae and ridges that appear not be formed by taphonomic alterations, which would indicate a heavy ornamented region of the skull roof. The lateroventral process, along with the dorsoposterior region of the lacrimal forms a bar that delimits dorsoposteriorly the deepest part of the antorbital fossa.

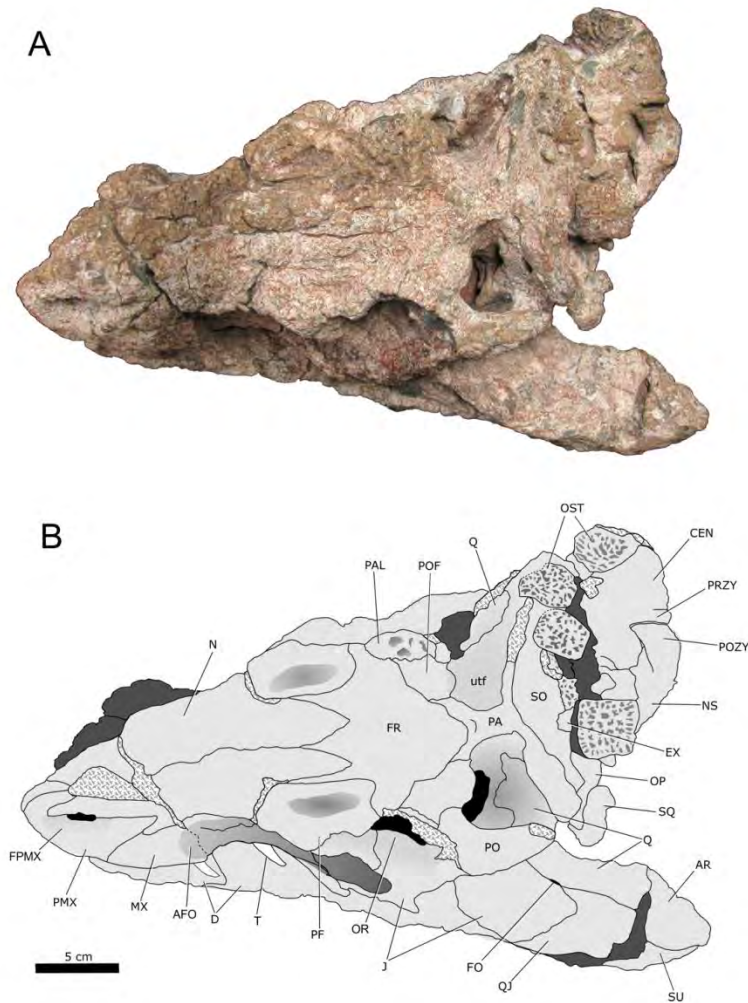


Figure 5. Photograph (A) and interpretive drawing (B) of MMACR PV 036-T in dorsal view. Abbreviations: **AR**, articular; **AFO**, antorbital fossa; **CEN**, centrum; **EX**, exoccipital; **FO**, quadratojugal-quadrato foramen; **FPMX**, premaxillary fossa; **FR**, frontal; **J**, jugal; **MX**, maxilla; **N**, nasal; **NS**, neural spine; **OP**, opisthotic; **OR**, orbit; **OST**, osteoderm; **PA**, parietal; **PAL**, palpebral; **PF**, prefrontal; **PMX**, premaxilla; **PO**, postorbital; **POF**, postfrontal; **POZY**, postzygapophysis; **PRZY**, prezygapophysis; **QJ**, quadratojugal; **Q**, quadrate; **SO**, supraoccipital; **SQ**, squamosal; **UTF**, upper temporal fenestra. Concretions in dark grey, cranial openings in black, broken areas in crosshatching.

The **frontal** is a wide, dorsoventrally compressed element that articulates anteriorly with the nasals by two narrow anterior processes, anterolaterally with the prefrontal along a sinuous contact, posterolaterally with the postorbital and posteriorly with the parietal along a lateromedially wide U shaped process (Fig. 3). In anterior view the lateral portion near the orbits display a marked dorsal curvature and its surface is marked by deep pits and ridges that are mirrored on both sides of the element and continue up to the palpebrals. It composes the dorsal border of the orbit and articulates lateroposteriorly with a palpebral element, which is better observed on its right side.

The presence of a single frontal and the rare pattern of the nasal-frontal suture in archosaurs, matches the condition described for *Erpetosuchus* (Benton & Walker, 2002), but in *Pagosvenator* this region of the skull roof is more lateromedially wide, whereas in the former it is more constrained. No longitudinal ridge along the midline or the anterior portion anteriorly tapering is observed in *Pagosvenator*, differing from Gracilisuchidae and some early branch loricatans in that these features are present (Nesbitt, 2011; Nesbitt & Butler, 2012).

The right **palpebral** is mostly preserved, with the left one represented only by its medial portion that is still in articulation with the other elements on the dorsal margin of the orbit along a large fracture. The majority of this damaged area corresponds to that which is occupied of the left side by the other palpebral and the dorsal portion of the postorbital. Additionally, the palpebral articulates posteromedially with the postfrontal and posteriorly with the postorbital. In dorsal view (Fig. 3), its shape is subrectangular with a thick and rugose lateral margin, while the dorsal surface displays a series of pits and the lateral continuation of some ridges that arise on the frontal. The presence of a palpebral element is described in Aetosaurs, Loricatans, Poposaurids, Crocodylomorphs and Ornithischians (Nesbitt *et al.*, 2013) and the overall morphology of the ones described for the studied specimen is similar to those in the abovementioned groups, but the overall form and the presence of excavated pits are significantly more distinct.

The **postfrontal**, in dorsal view, is an irregular bone that articulates anterolaterally with the palpebral, anteriorly and anteromedially with the frontal, posteromedially with the parietal and posterolaterally with the postorbital. As such, it does not participate in the margin of the orbits, but its convex posterior margin forms the majority of the anterior border of the supratemporal fenestra. It differs from the ones described in basal suchians, but its posterior region is similar to the ones in *Riojasuchus* (PVL 3827; Baczko *et al.*, 2016).

The left **postorbital** is mostly preserved and divided into an incomplete dorsal and a ventral portion, while the right one is represented only by a fragment of the anterior portion. In dorsal view, it is anteroposteriorly elongated, with its anterior region being lateromedially thick with a reduced anteromedial process. This articulates with the lateral margin of the postfrontal and the posterior processes, which forms the lateral margin of the supratemporal fenestra along a narrow posterior process that is turned

lateromedially up to its broken tip. The anterior contact of the ventral portion articulates along the damaged area of the palpebral while its main body projects anteroventrally and forms the posterodorsal and posterior border of the orbit. The posterior process contacts the squamosal on a restrict dorsal area, unlike aetosaurs, *Gracilisuchus* and *Yonghesuchus*, where it is ventrally broad. The ventral process of the postorbital in *Pagosvenator* is similar in length to the jugal on the composition of postorbital bar.

Only the left **squamosal** is preserved and divided into two segments (Fig. 2, 3). The first is anteriorly displaced and is ventral to the dorsal portion of the postorbital. It displays an anteroposteriorly wide dorsal section that has on its anterodorsal surface a shallow fossa for the articulation of the posterior portion of the postorbital and an anteroposteriorly curved ventral process that contacts the postorbital ramus of the ascending process of the jugal, near the articulation of this element with the ventral process of the postorbital. Due to the damaged suffered by the posterior region of the skull, it is twisted 30° counterclockwise and displaced more anteriorly, between the anterior and posterior ramus of the posterior process of the jugal. Due to this distortion, it occupies the area equivalent to the infratemporal and exposes only to two small lateral openings. The second is a small fragment of the posteromedial region that is positioned more posteriorly and is in articulation with the paraoccipital process. The dorsal surface of the squamosal on the supratemporal fenestrae is smooth, without any ridges or marked edges. The ventral process lacks the lateral ridge or the anteroventral projection found in some loricatans, such as *Saurosuchus galilei* (PVSJ 32; Alcober, 2000) and *Prestosuchus chiniquensis* (UFRGS-PV-0156-T; Barberena, 1978; Azevedo, 1991).

The **parietal** is a single element, with no indication of a parasagittal suture, similar to the condition of the frontal. In dorsal view, its main body is subrectangular and dorsoventrally flat, with an anterior portion formed by two anterolateral processes that form, anteriorly, a sub-circular contact with the frontal and articulate anterolaterally with the postfrontals. Two elongated, anterolaterally compressed, posterolateral processes are present projecting from the posterior half of the main body and form occipital flanges, similar to *Ornithosuchus woodwardi* (NHUMK R2409; Walker, 1964). However, this process is nearly vertical, whereas in Ornithosuchidae and aetosaurs this process is more than 45° inclined anteriorly. The left one is preserved but the right has been damaged; only preserving the fragments closer to the contact with the occipital. The presence of a single parietal is uncommon in archosauriforms, being

described in *Erpetosuchus* and in some Crocodylomorphs. However, as observed in the modern taxa of the latter group, the parietal can arise as two separate elements and fuse during late ontogeny (Rieppel, 1993; but this is impossible to infer if this was the case in the current specimen.

The **jugal** is a triradiated element, divided in a main body, anterior, dorsal and posterior processes. The posterior process is broken in two segments due to the collapse of the area of the infratemporal fenestra and disarray of the quadratojugal-jugal series. The anterior process is anteroposteriorly short and articulates with the main body of the maxilla, forming the posterior rim of the antorbital fossa and the posterior margin of the antorbital fenestra, a condition that is also described in *Proterosuchus fergusi*, some proterochampsids, phytosaurs, ornithosuchids, sauropodomorphs and ornithischians (Nesbitt, 2011; Baczko *et al.*, 2016; Ezcurra, 2016). However, the closest match is the one described in *Erpetosuchus* (Benton & Walker, 2002), which displays a jugal with five process, but has its two anterior ones form a posterior limit of a deep antorbital fossa, which is morphologically the closest to the one in *Pagosvenator*.

The dorsal process is divided into preorbital and postorbital rami, which forms the ventral margin of the orbit and has a distinct V-shaped aspect, as the one described in *Erpetosuchus* (Benton & Walker, 2002) and in ornithosuchids, but is ventrally more rounded like the one in the *Riojasuchus*, opposed the more acute one in *Ornithosuchus*. (Baczko & Desojo, 2016). The preorbital ramus articulates with the lacrimal along a broad vertical suture, whereas the postorbital ramus contacts the postorbital bone.

A large, damaged area is present on the lateral portion of the main body and on most of the posterior process. A longitudinal ridge is present on the lateral surface of main body of the jugal in *Pagosvenator*, although it does not display a bulbous appearance such as those in rauisuchids (*e.g.* Gower, 1999; Lautenschlager & Rauhut, 2014). The posterior process is broken into two segments, its anterior part is wedge shaped and positioned more ventroposteriorly whereas the posterior portion is preserved in articulation with the quadratojugal on the dorsal margin of the mandible. This articulation is similar to the one in *Riojasuchus* and *Ornithosuchus* (Walker, 1964; Baczko *et al.*, 2016), but taphonomic alterations twisted this area dorsolaterally, displaying the ventral area where the quadratojugal articulates with the jugal along a wide, rounded contact. The posterior process is dorsal to the quadratojugal on this

contact, with posterior limits anterior to the posterior margin of lower temporal fenestra, unlike *Erpetosuchus*, *Gracilisuchus* and *Yonghesuchus* in that the process is located posterior to the fenestra.

The elements of the lateroposterior regions of the skull have suffered major displacement, whereas most of the ones of the right side have been lost. The **quadratojugal** is represented only by the posterior portion of the left element, with only its posterior half visible due to the swivel of the ventral bar of the infratemporal fenestra. In dorsal view, it is a subrectangular, with a sinuous lateral margin and a lateromedially broad posterior region, which has a small fracture on its lateral margin. In lateral view, it articulates with the posterior process of the jugal along a V shaped suture and medially with the posterior region of the quadrate. Despite the taphonomic bias, the quadratojugal is not dorsally expanded, occupying less than 80% of posterior border of lower temporal fenestra, unlike *Erpetosuchus*, Gracilisuchidae and aetosaurs.

The **quadrate** is anteroposteriorly elongated bone which, due to the disarticulation of the posterior elements of the skull, is more anteriorly located where its anterior portion is positioned lateral to the braincase and twisted dorsally (Fig. 3). It articulates laterally with the quadratojugal with a small foramen in its central portion. Its posterior tip is lateromedially expanded along a straight margin of the articular condyle.

The right lateral and ventral portion of the occipital region is covered by concretions and osteoderm fragments, also obscuring most elements of this side of the skull and completely covering the foramen magnum (Fig. 6). The **supraoccipital**, in posterior view, is a dorsoventrally short but lateromedially wide subtriangular element. It articulates dorsally with the parietal along its posterolateral processes, lateroventrally with the opisthotic and ventrolaterally with the exoccipitals. The dorsal surface of its main body is smooth, with no indication of a ridge or process. Its dorsolateral process forms the medial and medioventral margins of a posttemporal opening. Only the proximal portion of the **opisthotic** is preserved, with a reduced posterolaterally projecting paraoccipital process that ends on a fragment of a medial portion of the squamosal. Due to an accumulation of osteoderms on the right side of the ventral portion of supraoccipital, only the left **exoccipital** is visible. It is a small, quadrangular

element that is tightly fused anteriorly with the supraoccipital and anterolateral with the opisthotic.

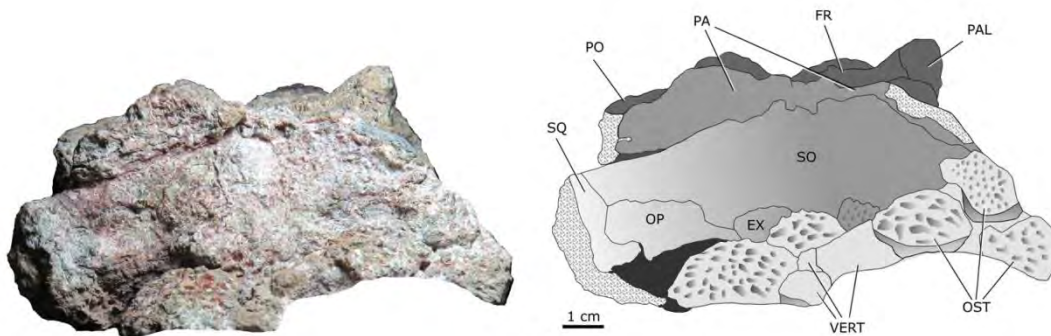


Figure 6. Photograph (A) and interpretive drawing (B) of the occipital region in posterior view. Vertebral elements were removed to more clearly detail this region. Abbreviations: **EX**, exoccipital; **FR**, frontal; **OP**, opisthotic; **OST**, osteoderms; **PA**, parietal; **PAL**, palpebral; **PO**, postorbital; **SQ**, squamosal; **VERT**, vertebra (portions). Concretions in dark grey, broken areas in crosshatching.

Mandibles

Both mandibles are present but are not in articulation with the skull, being positioned under and roughly inside the mouth cavity. This placement made it impossible to visualize the tooth bearing dorsal margin of the mandibles and CT-scans proved unreliable to provide useful information. The anterior tip of the mandibles were fractured along with the rest of the rostrum and are also dislocated, with the right piece being displaced more medially and the left one more laterally, covering the region posterior to where the fracture occurred (Fig. 4). The left mandible is twisted, with its lateral face placed laterodorsally, while only the ventral portion of the right mandible is visible outside mouth cavity. Due to these alterations, all of the medial regions of the mandibles, with the exception of the posteriormost region of the left one, are impossible to observe.

Although mostly covered by the skull and distorted, the presence of a mandibular fenestra is inferred due to the overall aspect of the bones ventral to the jugal, but its exact appearance and dimensions are impossible to establish.

The dorsoventral height of the **dentary** is unknown due to the obstruction of the dorsal margin, the surface ventral to the posterior area of the maxilla indicates a

dorsoventrally expanded and anteroposteriorly elongated element, that which is dorsoventrally reduced anteriorly and forms a smooth rounded ventral margin of the tip of the mandible. Its dorsoposterior margin has a short dorsal process that meets a concretion that is also at the ventral base of the squamosal, posterolaterally with the surangular and posteroventrally with the angular. The mandibular fenestra is not clear, but this is due to the posterior portion of the left mandible being covered by the jugal and associated unidentified bone fragments, although the shape of mandible bones (posterior end of dentary; anterior end of surangular and angular) indicate its presence.

The **surangular** is a lateromedially compressed element that displays a dorsoventrally short anterior portion that expands posteriorly up to $2/3$ its length. It extends posteriorly forming the majority of the posterior portion of the mandible, as almost completely excludes the articular in lateral view. This condition is similar to the one described in *Erpetosuchus*, but in this taxon, the surangular completely obscures the articular laterally (Walker & Benton, 2002). It displays a sharp lateral ridge that forms along the anteroposterior length of its dorsal surface, which would correspond to the lateral shelf of Sampson and Witmer (2007), with an underlying fossa that runs ventral to the shelf.

The **articular** in dorsal view, it is a triangular element that articulates laterally with the surangular, which excludes it almost entirely from the lateral portion of the mandible. Its anterior portion presents an anteroposteriorly wide, concave glenoid fossa, which is covered in a thick concretion, but lacks any transverse ridge, aside from a small dorsal projection on the end of its medial portion. The medial process is present and robust, but does not present any foramen as in the *Batrachotomus* and *Decuriasuchus* (Gower, 1999; França *et al.*, 2013). The retroarticular region displays an angled posterior process with a longitudinal ridge that extends dorsoventrally the posterior margin of this element. Due to the preservation of the medial portion of the mandible, it is impossible to interpret the form and sutures of the prearticular and coronoid bones.

A number of unidentified fragments are observed on the left side of skull. The most anterior one is elongated, narrow and is positioned on the posterior region of the dentary. The second one covers the lateral side of angular, with a semicircular posterior

region and a broken anterior facet. Considering the anatomical position, both bones could be skull fragments, but their poor preservation prevents a clear identification.

Post cranial elements

The remains of two articulated vertebrae lying on their right sides were preserved behind the occipital region of the skull (Fig. 5). One vertebra is represented only by its neural spine and left postzygapophysis while the second has a complete, sub-rectangular, vertebral body and ventral portion of the neural arch, with the left prezygapophysis in articulation with the corresponding postzygapophysis of the adjacent preserved vertebra.

Six osteoderms are associated with the specimen (Fig. 5, 6). Two are complete and four are incomplete, with the largest and better preserved one, being sub-rectangular (32mm anteroposterior length, and 33 mm lateromedial width). The borders are smooth, lacking a similar anterior process like the ones in aetosaurs (Nesbitt & Butler, 2012; Desojo *et al.*, 2013) and the doswellidae *Archeopelta arborensis* (CPEZ-239a; Desojo *et al.*, 2011) (Fig. 7). All osteoderms are heavily ornamented, with a dorsal surface covered with small pits and short ridges, but lacking a central anteroposteriorly extended ridge, like the one in *Erpetosuchus* and *Parringtonia* (Nesbitt & Butler, 2012). Due to the disarticulated condition of the post cranial elements, it is unclear how the osteoderms were arranged when in articulation and which part of the cervical sequence would be their origin, even though they were preserved near the skull. However, the length of osteoderms are consistent with two anteroposterior segments per vertebra, with probably paired sagittal axis.

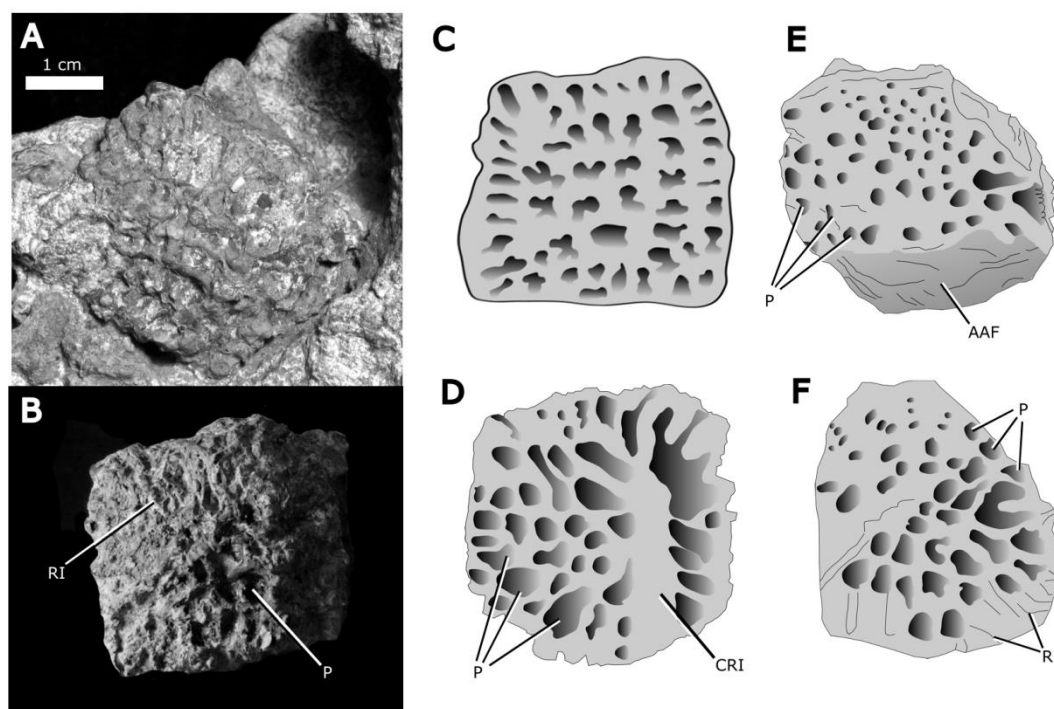


Figure 7. Photographs of the best preserved osteoderm in MMACR PV 036-T (**A**) in detail, (**B**) isolated and with heightened shadows to better display the ornamentation cover. Interpretative illustrations of various ornamented osteoderms of archosauriforms for comparison: (**C**) osteoderm of *Pagosvenator candelariensis* (MMACR PV 036-T); (**D**) osteoderm of *Parringtonia gracilis* in dorsal view (NHMUK R3139, redrawn based on Nesbitt & Butler, 2012); (**E**) osteoderm of *Archeopelta arborensis* (CPEZ-239a, redrawn based on Desojo *et al.*, 2012); (**F**) osteoderm of *Tarjadia ruthae* (PULR 063, redrawn based on Arcucci & Marsicano, 1998). Abbreviations: **AAF**, anterior articular facet; **CRI**, central ridge; **P**, pit; **RI**, ridge. Osteoderms are not to scale.

Phylogenetic Analysis

Methods

The new taxon, *Pagosvenator candelariensis*, was included in a matrix with 418 characters and 85 terminal taxa. The matrix is based on the original analysis of Nesbitt (2011), with compilations of its modified versions by Butler *et al.* (2011), Nesbitt & Butler (2012), Butler *et al.* (2014), and Baczcko *et al.* (2016). Additionally, one new character is proposed and some characters states were altered, using information based on personal study of specimens and on recently articles (full details in the Supporting Information). The matrix was analyzed in TNT (Goloboff *et al.*, 2008), using a heuristic search with 10,000 replicates of Wagner trees, tree bisection and reconnection (TBR)

branch swapping (holding 10 trees per replicate), with collapsed branch with zero length. Some multistate characters were ordered, according to parameters stated in the original analysis and abovementioned works: 32, 52, 121, 137, 139, 156, 168, 188, 223, 247, 258, 269, 271, 291, 297, 328, 356, 377, 399, 198, 416. Bootstrap and Bremer Support were calculated with scripts on TNT. Additional analysis in searching for unstable taxa were conducted on TNT, using the IterPCR script proposed by Pol & Escapa (2009).

Results

The cladistics analysis resulted in 360 most parsimonious trees, with 1358 steps. *Pagosvenator candelariensis* was found as sister group of *Erpetosuchus granti* plus *Parringtonia gracilis*, composing the earliest branch of the Erpetosuchidae clade (Fig. 8).

In previous analyses, this group had been considered as an unstable taxa (Nesbitt & Butler, 2012), with six alternative position: (i) earliest branch from Pseudosuchia; (ii) earliest branch from Suchia (including *Gracilisuchus stipanicorum*, *Turfanosuchus dabanensis*, Aetosauria, Paracrocodylomorpha and other their relatives taxa); (iii) sister group of *T. dabanensis* (not found as sister group of *G. stipanicorum* in this analysis); (iv) earliest branch of the Aetosauria lineage, being sister group of the clade composed by *Revueltosaurus* plus Aetosauria; (v) earliest branch of the Paracrocodylomorpha lineage, being sister group of clade composed by *Ticinosuchus ferox* (Krebs, 1965) plus Paracrocodylomorpha; and (vi) earliest branch of Avemetatarsalia (Fig. 1C). Butler *et al.* (2014) considered Erpetosuchidae as a wildtaxa, also revealing this unstable position in the evolution of Archosauria, with the consensus tree from this analysis being poorly resolved and displaying a major polytomy at the base of Archosauria.

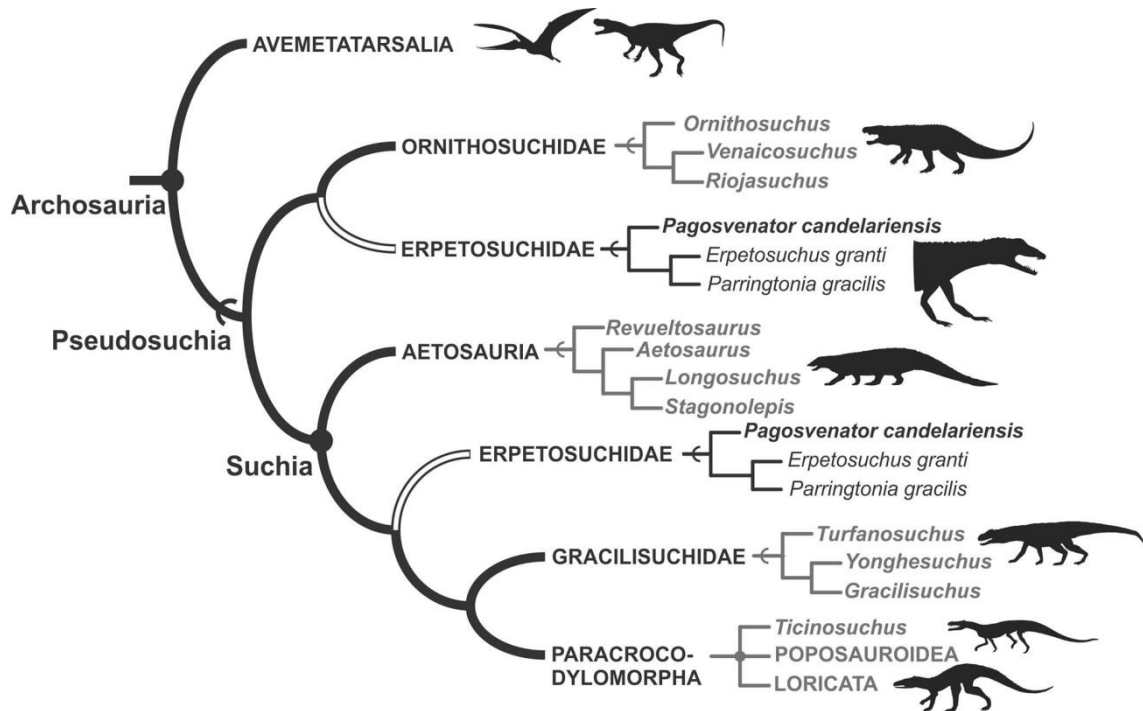


Figure 8. Alternative positions of Erpetosuchidae among the evolution of Pseudosuchia, indicating a simplified version of the Strict Consensus trees, obtained on 360 Most Parsimonious Tree with 1358 steps, using a phylogenetic matrix composed by 84 terminal taxa and 417 characters.

In the present analysis, the strict consensus (see Supplementary information) reveals a similar topology. However, there is a polytomy at the base of the pseudosuchian lineage, formed by Erpetosuchidae, Ornithosuchidae, the clade composed by *Revueltosaurus* plus Aetosauria, and the clade composed by Gracilisuchidae plus *Ticinosuchus ferox* and Paracrocodylomorpha. Accordingly, the alternative positions of Erpetosuchidae as sister group of *Turfanosuchus dabanensis*, or early branch of Paracrocodylomorpha, or early branch of Avemetatarsalia were refuted on this analysis. In addition, the result of unstable taxa analysis (Pol & Escapa, 2009) was performed, excluding the alternative position of Erpetosuchidae as an early branch of Pseudosuchia, or early branch of the Aetosauria lineage (sister group of *Revueltosaurus* plus Aetosauria). The results of the analysis reveals, before one iteration, only two possible positions of Erpetosuchidae among the most parsimonious trees: as sister group of Ornithosuchidae, composing an early branch lineage of Pseudosuchia, or sister group of the clade composed by polytomy among Gracilisuchidae, *Ticinosuchus ferox* and Paracrocodylomorpha. A brief consideration about this latter clade is needed. In Nesbitt (2011), *Ticinosuchus* is considered sister

group of Paracrocodylomorpha, a clade composed by Poposauroidea (including *Qianosuchus mixtus*, ; *Poposaurus gracilis*, *Shuvosaurus inexpectus* and their relative taxa) plus Loricata (including *Prestosuchus chiniquensis*; *Saurosuchus galilei*; Raurisuchidae, Crocodylomorpha, and their relative taxa). Paracrocodylomorpha is phylogenetically defined as node based clade composed by the least inclusive clade containing *Poposaurus* and *Crocodylus niloticus* Laurenti, 1768 (Nesbitt, 2011). In this sense, Paracrocodylomorpha is revealed in the present analysis, although it would not be accurate if *T. ferox* belongs to the group. Likewise, it is important to consider that other phylogenetic analyses support Phytosauria as an early branch on Pseudosuchia (e.g. Brusatte *et al.* 2010; Ezcurra, 2016), contrasting with the analysis of Nesbitt (2011) and probably influencing the relative topology on Pseudosuchia with polarization/optimization of character states among transformational series.

The forced constrains among Erpetosuchidae and Ornithosuchidae resulted in 180 most parsimonious trees, with zero Bremer support. The only controversial synapomorphy for this clade is the presence of anteroposteriorly longer than wide dorsal presacral osteoderms, shared by *Pagosvenator candelariensis*, *Erpetosuchus granti* (NHMUK R3139R) and *Ornithosuchus woodwardia* (HHMUK R2410), whereas the osteoderms of *Parringtonia* (NHMUK R8646) are squared, those in *Riojasuchus tenuisiceps* (PVL 3827) are wider than long, and none in *Venaticosuchus rusconii* (Bonaparte, 1972; Baczko *et al.*, 2014) are preserved (character 407). A previous preliminary analysis of *P. candelariensis* (Lacerda *et al.* 2016), proposed it as an early branch of Ornithosuchidae. However, this analysis did not incorporate *E. granti* and *P. gracilis*, and some character states were modified with a more accurate anatomy revision, as well as CT-Scan analysis (e.g. the relative inclination between pre-maxilla and maxilla is not sustainable; number of premaxillary teeth and number and position of the maxillary ones was revealed only by means of X-ray images).

The alternative position of Erpetosuchidae, as sister group of a clade composed by Gracilisuchidae and Paracrocodylomorpha (including *Ticinosuchus ferox*), also has zero Bremer support. However, the clade composed by Erpetosuchidae plus Paracrocodylomorpha is supported by two synapomorphies: presence of ventromedial process on the articular (character 157), being reversed to absence on *Gracilisuchus stipanicorum* (Romer, 1972; Butler *et al.*, 2014) and some Poposauroidea (Nesbitt, 2011) (*Shuvosaurus inexpectus*, *Effigia okeeffeae* and *Lotosaurus adentus*); and the

scapula bearing a tear drop shaped tuber on the posterior edge for attachment of *m. triceps* (character 219), being reversed on *Postosuchus kirkpatricki* (Chatterjee, 1985; Weinbaum, 2013), Crocodylomorpha, and Loricata (Nesbitt, 2011), whereas in *Pagosvenator candelariensis* this character is placed as missing data since this bone was not preserved.

The Erpetosuchidae clade displays a low support, with a Bremer value of 1 and Bootstrap at 64. Two synapomorphies support this clade: maxillary teeth only present on the anterior region of bone (character 17), being only converging with *Ornithosuchus woodwardia* (NHMUK R2409, R3143); and maxillary region ventral to the lacrimal has a mediolateral height greater than its dorsoventral length (character 21), only converging with *Lotosaurus adentus* and *Effigia okeeffeae*. Both characters are scored in *Pagosvenator candelariensis*, *Erpetosuchus granti* and *Parringtonia gracilis*. In addition, two synapomorphies support a closer relationship among *E. granti* and *P. gracilis*: absence of tooth serration (character 168); and a longitudinal bend on the dorsal presacral osteoderms (character 404), being converging with *Euparkeria capensis* (SAM PK5867, 6047, 6049), Gracilisuchidae (Butler *et al.*, 2014), *Batrachotomus kupferzellensis* (SMNS MHI 1895); *Fasolasuchus tenax* (PVL 3850); Rausisuchidae (BSPG AS XXV 92, 97; Chatterjee, 1985; Weinbaum, 2013) and several crocodylomorphs (Nesbitt, 2011).

Discussion

Erpetosuchidae is formally represented only by two taxa: *Parringtonia gracilis*, from the Middle Triassic (Anisian) Lifua Member of the Manda Beds of Tanzania, and *Erpetosuchus granti*, from the Late Triassic (Carnian) Lossiemouth Sandstone Formation of Scotland (Fig.9). An incomplete fragmentary skull is referred to *Erpetosuchus* sp. by Olsen, Sues & Norell (2002) from the Late Triassic (Norian), New Haven Formation of Connecticut, USA. The osteology of Erpetosuchidae are poorly understood, since there is no complete specimen described until the present, with species based only in fragmentary materials of skull and postcranial elements, influencing on the phylogenetic affinities hypothesis (Nesbitt & Butler, 2012). Although *Pagosvenator candelariensis* is mostly represented by cranial material, it is sufficient to propose a new taxon for the Middle-Late Triassic (Late Ladinian- earliest Carnian) of

Southern Brazil and the comparative osteological and phylogenetic analysis indicates a strong case for assigning it to this clade as the earlier branch taxon.

In addition to this, *Pagosvenator candelariensis* displays clear features that are synapomorphic with Ornithosuchidae, such as the Y shaped ascending process of the jugal and the distinct articulation of the anterodorsal process of the maxilla with the nasals, whereas differing from this group by having only four premaxillary teeth, no downturned rostrum and no diastema on the premaxilla-maxilla contact.

Comparatively to Erpetosuchidae, Ornithosuchidae is better known, being represented by three taxa: *Ornithosuchus woodwardi* (Newton 1894, Walker 1964; Bazcko & Ezcurra, 2013), from the Lossiemouth Sandstones Formation of Scotland (Late Carnian – earliest Norian), *Venaticosuchus rusconii* (Bonaparte 1970; Bazcko *et al.*, 2014) from the Ischigualasto Formation (Late Carnian – earliest Norian) and *Riojausuchus tenuisiceps* (Bonaparte, 1967; Bazcko & Desojo, 2016) from the Los Colorados Formation (Middle Norian), both from Argentina (Fig. 9). This clade has historically been considered an odd, but important group in the early evolutionary history of pseudosuchians (Brinkman, 1981; Chatterjee, 1982; Cruickshank & Benton, 1985; Novas, 1989; Sereno, 1991; Parrish, 1993; Bazcko & Ezcurra, 2013), which diverges from the rest of Archosauria by the presence of an apomorphic ‘crocodile-reversed’ ankle joint (Chatterjee, 1982). Similarities between Erpetosuchidae and Ornithosuchidae were described by Huene (1939) and Nesbitt and Butler (2012), but these were mostly superficial due to the incomplete or badly samples nature of the taxa and have not been explored further in the literature.

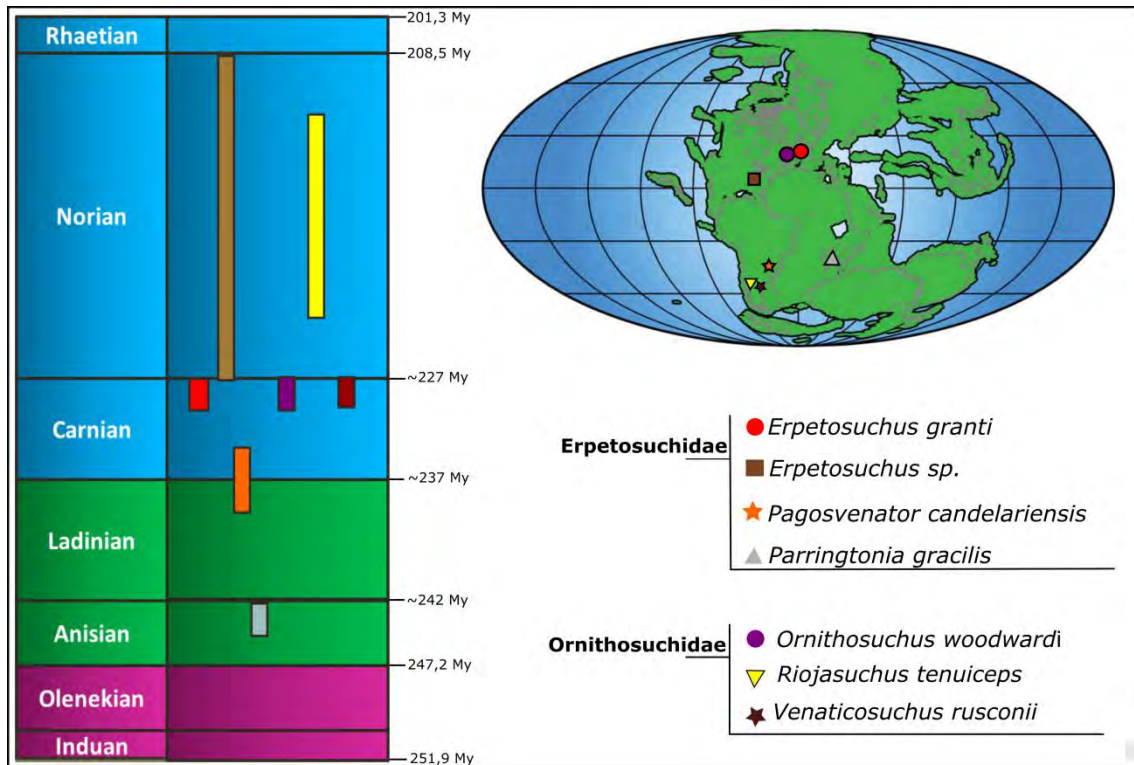


Figure 9. Temporal and paleogeographical distribution of the taxa of the clades Erpetosuchidae and Ornithosuchidae, based on Olsen, Sues & Norell (2000), Benton & Walker (2002), Nesbitt & Butler (2012) and Backzo & Ezcurra (2013). Temporal constrains based on ICS 2016 chart; global map modified from Nesbitt *et al.* (2013).

Erpetosuchidae as sister taxon to Ornithosuchidae would indicate that the evolutionary history of this lineage would be more complex than previously thought and considered. This mirrors what recent studies have proposed (*e.g.* Nesbitt *et al.*, 2014; Nesbitt *et al.*, 2015; Ezcurra & Butler, 2016; Pinheiro *et al.*, 2016; Ezcurra, 2016; Stocker *et al.*, 2016) where Triassic archosauriforms display a richer evolutionary history.

Alternatively, the phylogenetic analysis reveals that Erpetosuchidae also has affinities with the clade Gracilisuchidae plus Paracrocodylomorpha. This closer relationship is based on the presence of ventromedial process on the articular, and the scapula bearing a tear drop shaped tuber on the posterior edge for the attachment of the *m. triceps*. However, among Erpetosuchidae taxa, both characteristics are only preserved and codified in *Pagosvenator candelariensis*. In this sense, these morphologies, present on *P. candelariensis*, cannot be representative of the

Erpetosuchidae clade, indicating a case of morphological convergence with paracrocodylomorphs or is an autapomorphic condition for this taxon. To clarify this, more information on *Erpetosuchus granti* and *Parringtonia gracilis* is needed, which will require new specimens.

Additionally, *Pagosvenator candelariensis* is the first member of the Erpetosuchidae described for the southwestern Pangea. The chronologically older and more derived *Parringtonia gracilis* would indicate a complex diversification history of these forms that would present many interesting questions for future works in Triassic archosauriform evolution. Furthermore, there are other factors that must be analyzed, such as the role that the major biotas would play in the evolution of these lineages, since *P. candelariensis* would belong to a highly competitive trophic web (the *Dinodontosaurus* Assemblage Zone), which would be co-habitated with some similar forms that shared likely similar habits, such as medium sized carnivores like *Decuriasuchus quartacolonias* and the much larger *Prestosuchus chiniquensis*.

Conclusion

The present work describes the new taxon *Pagosvenator candelariensis*, from Middle/Late Triassic (Ladinian/Carnian) of Brazil, representing the earliest branch of Erpetosuchidae. The cladistic analysis reveals a new interpretation on pseudosuchian evolution, with two possibilities for Erpetosuchidae relationship: early branch of pseudosuchians, being sister group of Ornithosuchidae; or a closer relationship with the clade composed by Gracilisuchidae and Paracrocodylomorpha. Unfortunately, the specimen here described is destitute from meaning post cranial remains, preventing a more accurate comparison among pseudosuchians. *P. candelariensis* co-habitated the southern of Brazil with other ecological similar taxa of predators, being a medium to large size carnivore. On the time distribution, the new taxa from Ladinian/Carnian age fills the temporal gap on Erpetosuchidae clade, between *Parringtonia gracilis* from Anisian to *Erpetosuchus granti* from late Carnian to Norian.

Acknowledgments

We like to thank C. Rodrigues and B. Stefanello (MMACR) for access to the specimen for study. V.P. Pereira and P.A.V. Paim (UFRGS) for access to the sample database and invaluable help in the REE analysis part of this study. A. Martinelli, J. Desojo, B. Mastrantonio, E. Dassisti, V. Neto and M. Langer for the many helpful discussions, comments and suggestions that greatly improved this manuscript. We especially thank F. Pinheiro for the helpful suggestions in regards to the naming of the specimen. L.F. Lopes (UFRGS) for the skillful photographs. We also thank the people that allowed us access to the collections under their care: A. Ribeiro and J. Ferigolo (MCN), J. Powell (PVL), L. Steel and S. Chapman (NHMUK), O. Rauhut (BSPG), R. Martinez (PVSJ), R. Schoch (SMNS), S. Kaal (SAM), and S. Martin (PULR). This research was funded by the doctorate scholarship given to M. Lacerda by the Conselho Nacional de Pesquisa (CNPq) grant 141378/2013-1 and a short term grant by the Deutscher Akademischer Austauschdienst (DAAD) n° 57130097. Access to the free version of TNT 1.1 was granted by the Willi Henning Society.

References

- Alcober O. 2000.** Redescription of the skull of *Saurosuchus galilei* (Archosauria: Raurisuchidae). *Journal of Vertebrate Paleontology* **20**: 302-316.
- Arcucci AB, Marsicano CA. 1998.** A distinctive new archosaur from the Middle Triassic (Los Chañares Formation) of Argentina. *Journal of Vertebrate Paleontology* **18**: 228-232.
- Azevedo SAK. 1991.** *Prestosuchus chiniquensis* Huene 1942 (Reptilia, Archosauria, Thecodontia, Proterosuchia, Raurisuchidae), da Formação Santa Maria, Triássico do Estado do Rio Grande do Sul, Brasil. Unpublished PhD, Universidade Federal do Rio Grande do Sul.
- Barberena MC. 1977.** Bioestratigrafia preliminar da Formação Santa Maria. *Pesquisas* **7**: 111-129.
- Barberena MC. 1978.** A huge thecodont skull from the Triassic of Brazil. *Pesquisas* **7**: 111-129.
- Barberena MC, Araújo DC, Lavina EL, Azevedo SAK. 1985.** O estado do conhecimento sobre os tetrápodos permianos e triássicos do Brasil meridional

- Trabalhos apresentados no VII Congresso Brasileiro de Paleontologia -1983.* Brasília: Ministério de Minas e Energia, Departamento Nacional de Produção Mineral. 21-28.
- Baczko MBv, Desojo JB. 2016.** Cranial Anatomy and Palaeoneurology of the Archosaur *Riojasuchus tenuisiceps* from the Los Colorados Formation, La Rioja, Argentina. *PLoS One* **11**: e0148575.
- Baczko MBv, Desojo JB, Pol D. 2014.** Anatomy and phylogenetic position of *Venaticosuchus rusconii* Bonaparte, 1970 (Archosauria, Pseudosuchia), from the Ischigualasto Formation (Late Triassic), La Rioja, Argentina. *Journal of Vertebrate Paleontology* **34**: 1342-1356.
- Baczko MBv, Ezcurra MD. 2013.** Ornithosuchidae: a group of Triassic archosaurs with a unique ankle joint. In: Nesbitt S, Desojo JB and Irmis RB, eds. *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin*. London, Special Publications: The Geological Society. 187-202.
- Baczko MBv, Ezcurra MD. 2016.** Taxonomy of the archosaur Ornithosuchus: reassessing *Ornithosuchus woodwardi* Newton, 1894 and *Dasygnathoides longidens* (Huxley 1877). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **106**: 199-205.
- Beltrão R. 1965.** Paleontologia de Santa Maria e São Pedro do Sul, Rio Grande do Sul, Brasil. *Boletim do Instituto de Geociências UFSM* **2**: 5-114.
- Benton MJ, Clark JM. 1988.** Archosaur phylogeny and the relationships of the Crocodylia. In: Benton MJ, ed. *The Phylogeny and Classification of the Tetrapods*. Oxford,: Clarendon Press. 295-338.
- Benton MJ, Walker AD. 2002.** *Erpetosuchus*, a crocodile-like basal archosaur from the Late Triassic of Elgin, Scotland. *Zoological Journal of the Linnean Society* **136**: 25–47.
- Bertoni-Machado C, Kishlat E-E. 2003.** Novo registro de Rhadinosuchidae (Archosauriformes: Proterochampsia) para o Mesotriássico do Brasil *Paleo 2003 - Paleontologia em Destaque* Porto Alegre: Sociedade Brasileira de Paleontologia. 47.
- Bonaparte JF. 1967.** Dos nuevas ‘faunas’ de reptiles Triasicos de Argentina *Gondwana Stratigraphy*. I.U.G.S. Symposium: Prís, UNESCO. 283–306.
- Bonaparte JF. 1972.** Los tetrápodos del sector superior del a Formación Los Colorados, La Rioja, Argentina (Triásico Superior) I Parte. *Opera Lilloana* **22**.

- Bonaparte JF, Ferigolo J, Ribeiro AM. 1999.** A new early Late Triassic saurischian dinosaur from Rio Grande do Sol state, Brazil. *National Science Museum Monographs* **15**: 89-109.
- Bonaparte JF, Schultz CL, Soares MB. 2010.** Pterosauria from the Late Triassic of southern Brazil. In: Bandyopadhyay B, ed. *New Aspects of Mesozoic Biodiversity, Lecture Notes in Earth Sciences*. 63-71.
- Brinkman DB. 1981.** The origin of the crocodyloid tarsi and the interrelationships of thecodontian archosaurs. *Brevoria* **464**: 1-23.
- Brusatte SL, Benton MJ, Desojo JB, Langer MC. 2010.** The higher-level phylogeny of Archosauria (Tetrapoda: Diapsida). *Journal of Systematic Palaeontology* **8**: 3-47.
- Brusatte SL, Benton MJ, Lloyd GT, Ruta M, Wang SC. 2011.** Macroevolutionary patterns in the evolutionary radiation of archosaurs (Tetrapoda: Diapsida). *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **101**: 367–382.
- Butler RJ, Brusatte SL, Reich M, Nesbitt SJ, Schoch RR, Hornung JJ. 2011.** The Sail-Backed Reptile from the Latest Early Triassic of Germany and the Timing and Biogeography of the Early Archosaur Radiation. *PLoS One* **6**: e25693.
- Butler RJ, Sullivan C, Ezcurra MD, Liu J, Lecuona A, Sookias RB. 2014.** New clade of enigmatic early archosaurs yields insights into early pseudosuchian phylogeny and biogeography of the archosaur radiation *BMC Evolutionary Biology* **14**: 1-16.
- Cabreira SF, Kellner AWA, Dias-Da-Silva S, da Silva LR, Bronzati M, Marsola JCA, Müller RT, Bittencourt JS, Batista BJ, Raugust T, Carrilho R, Brodt A, Langer MC. 2016.** A Unique Late Triassic Dinosauromorph Assemblage Reveals Dinosaur Ancestral Anatomy and Diet. *Current Biology* **26**: 3090-3095.
- Cabreira SF, Schultz CL, Bittencourt JS, Soares MB, Fortier DC, Silva LR, Langer MC. 2011.** New stem-sauropodomorph (Dinosauria, Saurischia) from the Triassic of Brazil. *Naturwissenschaften* **98**: 1035-1040.
- Chatterjee S. 1982.** Phylogeny and classification of thecodontian reptile. *Nature* **295**: 317-320.
- Colbert EH. 1970.** A saurischian dinosaur from the Triassic of Brazil. *American Museum Novitates* **2405**: 1-39.

- Cope ED. 1869.** Synopsis of the extinct Batrachia, Reptilia and Aves of North America. *Transactions of the America Philosophical Society* **14**: 1–252.
- Cruickshank ARI, Benton MJ. 1985.** Archosaur ankles and the relationships of the thecodontian and dinosaurian reptiles. *Nature* **317**: 715-717.
- DaRosa AAS. 2014.** Geological context of the Dinosauriform-Bearing outcrops from The Triassic of Southern Brazil. *Journal of South American Earth Sciences* **61**.
- da Silva LR, Desojo JB, Cabreira SF, Schiller Aires AS, Müller RT, Pacheco CP, Dias-Da-Silva S. 2014.** A new aetosaur from the Upper Triassic of the Santa Maria Formation, southern Brazil. *Zootaxa* **3764**: 240-278.
- da Silva LR, França MAG, Cabreira SF, Müller RT, Dias-da-Silva S. 2016.** On the presence of the subnarial foramen in *Prestosuchus chiniquensis* (Pseudosuchia: Loricata) with remarks on its phylogenetic distribution. *Anais da Academia Brasileira de Ciências* **88**: 1309-1323.
- Desojo JB, Ezcurra MD, Kischlat EE. 2012.** A new aetosaur genus (Archosauria: Pseudosuchia) from the early Late Triassic of southern Brazil. *Zootaxa* **3166**: 1-33.
- Desojo JB, Ezcurra MD, Schultz CL. 2011.** An unusual new archosauriform from the Middle–Late Triassic of southern Brazil and the monophyly of Doswelliidae. *Zoological Journal of the Linnean Society* **161**: 839–871.
- Desojo JB, Heckert AB, Martz JW, Parker WG, Schoch RR, Small BJ, Sulej T. 2013.** Aetosauria: a clade of armoured pseudosuchians from the Upper Triassic continental beds. In: Nesbitt SJ, Desojo JB and Irmis RB, eds. *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and the Kin*. London: The Geological Society, Special Publications. 203-239.
- Ezcurra MD. 2016.** The phylogenetic relationships of basal archosauromorphs, with an emphasis on the systematics of proterosuchian archosauriforms. *PeerJ* **4**. e.1778.
- Ezcurra MD, Butler RJ. 2015.** Taxonomy of the proterosuchid archosauriforms (Diapsida: Archosauromorpha) from the earliest Triassic of South Africa, and implications for the early archosauriform radiation. *Palaeontology* **58**: 141-170.
- Ferigolo J, Langer MC. 2006.** A Late Triassic dinosauriform from south Brazil and the origin of the ornithischian predentary. *Historical Biology* **19**: 1-11.
- França MAG, Ferigolo J, Langer MC. 2011.** Associated skeletons of a new middle Triassic "Rauisuchia" from Brazil. *Naturwissenschaften* **98**: 389-395.

- França MAG, Lacerda MB, Pretto FA, Schultz CL, Langer MC. 2014.** Primeiro registro brasileiro de Poposauroida (Sequência Santa Maria II, Zona-Associação de *Rio-grandia*, Neotriássico). In: Simões TR, Figueiredo RG, Delcourt R and Rodrigues T, eds. *IX Simpósio Brasileiro de Paleontologia de Vertebrados*. Vitória: Boletim de Resumos/ Paleontologia em Destaque: Boletim Informativo da Sociedade Brasileira de Paleontologia. 64.
- França MAG, Langer MC, Ferigolo J. 2013.** The skull anatomy of *Decuriasuchus quartacolonia* (Pseudosuchia: Suchia: Loricata) from the middle Triassic of Brazil. In: Nesbitt S, Desojo JB and Irmis RB, eds. *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin*. London: The Geological Society of London. 469-501.
- Gauthier J. 1984.** A cladistic analysis of the higher systematic categories of the Diapsida. Unpublished PhD, University of California, Berkeley.
- Gauthier J, Padian K. 1985.** Phylogenetic, functional, and aerodynamic analyses of the origin of birds and their flight. In: Hecht MK, Ostrom JH, Viohl G and Wellnhofer P, eds. *The Beginning of Birds*. Eichstatt: Freunde des Jura Museums. 185–197.
- Goloboff PA, Farris JS, Nixon KC. 2008.** TNT, a free program for phylogenetic analysis. *Cladistics* **24**: 774–786.
- Gower DJ. 1999.** The cranial and mandibular osteology of a new rauisuchian archosaur from the Middle Triassic of southern Germany. *Stuttgarter Beiträge zur Naturkunde. Serie B (Geologie und Paläontologie)* **280**: 1-49.
- Gower DJ. 2000.** Rauisuchian archosaurs (Reptilia, Diapsida): An overview. *Neus Jahrbuch für Geologie und Paläontologie Abhandlungen* **218**: 447-488.
- Holz M, Schultz CL. 1998.** Taphonomy of the south Brazilian Triassic herpetofauna: fossilization mode and implications for morphological studies. *Lethaia* **31**: 335-345.
- Horn BLD, Melo TM, Schultz CL, Philipp RP, Kloss HP, Goldberg K. 2014.** A new third order sequence stratigraphic framework applied to the Triassic of the Paraná Basin, Rio Grande do Sul, Brazil, based on structural, stratigraphical and paleontological data. *Journal of South American Earth Sciences* **55**: 123-132.
- Huene Fv. 1935-42.** *Die fossilen Reptilien des südamerikanischen Gondwanalandes, Ergebnisse der Sauriergrabungen in Südbrasilien 1928/29*. C.H. Beck'sche Verlagsbuchhandlung: München.

- Huene Fv. 1939.** Ein kleiner Pseudosuchier und ein Saurischier aus den ostafrikanischen Mandaschichten. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen Beilage-Bände Abteilung B* **81**: 61-69.
- Huene Fv. 1942.** *Die fossilen Reptilien des Sudamerikanischen Gondwanalandes. Ergebnisse der Sauriergrabungen in Sudbrasilien, 1928/1929.* C. H. Beck'she: Munchen.
- Hunt AP. 1989.** A new ?ornithischian dinosaur from the Bull Canyon Formation (Upper Triassic) of east-central New Mexico. In: Lucas SG and Hunt AP, eds. *Dawn of the Age of Dinosaurs in the American Southwest.* Albuquerque: New Mexico Museum of Natural History. 355-358.
- Juul L. 1994.** The phylogeny of basal archosaurs. *Palaeontologia Africana* **31**: 1-38.
- Kischlat EE, Lucas SG. 2003.** A phytosaur from the Upper Triassic of Brazil. *Journal of Vertebrate Paleontology* **23**: 464-467.
- Krebs B. 1965.** Die Triasfauna der Tessiner Kalkalpen. XIX. *Ticinosuchus ferox*, nov. gen. nov. sp. Ein neuer Pseudosuchier aus der Trias des Monte San Giorgio. *Schweizerische Palaontologische, Abhandlungen* **81**: 1-140.
- Lacerda MB, França MAG, Schultz CL. 2016.** A New Triassic Pseudosuchian Archosaur from Brazil and the Evolution of the Ornithosuchidae *30 Jornadas Argentinas de Paleontologia de Vertebrados.* Buenos Aires: Libro de Resúmens. 31.
- Lacerda MB, Schultz CL, Bertoni-Machado C. 2015.** First 'Rauisuchian' archosaur (Pseudosuchia, Loricata) for the Middle Triassic *Santacruzodon* Assemblage Zone (Santa Maria Supersequence), Rio Grande do Sul State, Brazil. *PLoS One* **10**: e0118563.
- Langer MC, Abdala F, Richter M, Benton MJ. 1999.** A sauropodomorph dinosaur from the Upper Triassic (Carman) of southern Brazil. *Comptes Rendus de l'Académie des Sciences - Series IIA - Earth and Planetary Science* **329**: 511-517.
- Lautenschlager S, Rauhut O. 2014.** Osteology of *Rauisuchus tiradentes* from the Late Triassic (Carnian) Santa Maria Formation of Brazil, and its implications for rauisuchid anatomy and phylogeny. *Zoological Journal of the Linnean Society* **173**: 55-91.

- Leal LA, Azevedo SAK, Kellner AWA, Da Rosa AAS. 2004.** A new early dinosaur (Sauropodomorpha) from the Caturrita Formation (Late Triassic), Paraná Basin, Brazil. *Zootaxa* **690**: 1-24.
- Li C, Wu X-C, Cheng Y-N, Sato T, Wang L. 2006.** An unusual archosaurian from the marine Triassic of China. *Naturwissenschaften*, **93**: 200–206.
- Lukens WE, Grandstaff DE, Terry Jr. DO. 2009.** Rare earth element signatures in fossil bones: a tool for mitigating fossil poaching on federal lands. In: Foss, S, Cavin J, Brown T, Kirkland J and Stantucci V, eds. *Proceedings of the Eighth Conference on Fossil Resources* May 19-21, St. George, UT. 10-13.
- Müller RT, Da Rosa AAS, da Silva LR, Schiller Aires AS, Pacheco CP, Branco Pavanatto AE, Dias-Da-Silva S. 2014.** Wachholz, A new exquisite dinosaur-bearing fossiliferous site from the Upper Triassic of southern Brazil. *Journal of South American Earth Sciences* **61**: 120-128.
- Nesbitt SJ. 2011.** The early evolution of archosaurs: relationships and the origin of major clades. *Bulletin of the American Museum of Natural History* **352**: 1-292.
- Nesbitt SJ, Brusatte SL, Desojo JB, Liparini A, França MG, Weinbaum JC, Gower DJ. 2013.** Rauisuchia. In: Nesbitt SJ, Desojo JB and Irmis RB, eds. *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and the Kin*. London: The Geological Society, Special Publications. 241-274.
- Nesbitt SJ, Butler RJ. 2012.** Redescription of the archosaur *Parringtonia gracilis* from the Middle Triassic Manda beds of Tanzania, and the antiquity of Erpetosuchidae. *Geological Magazine* **150**: 225-238.
- Nesbitt SJ, Butler RJ, Ezcurra MD, Barrett PM, Stocker MR, Angielczyk KD, Smith RMH, Sidor CA, Niedzwiedzki G, Sennikov AG, Charig A. 2017.** The earliest bird-line archosaurs and the assembly of the dinosaur body plan. *Nature*.
- Nesbitt SJ, Flynn JJ, Pritchard JM, Parrish JM, Ranivoharimanana L, Wyss AR. 2015.** Postcranial osteology of *Azendohsaurus madagaskarensis* (?Middle to Upper Triassic, Isalo Group, Madagascar) and its systematic position among stem archosaur reptiles. *Bulletin of the American Museum of Natural History* **398**: 1-126.
- Nesbitt SJ, Sidor CA, Angielczyk KD, Smith RMH, Tsuji LA. 2014.** A new archosaur from the Manda beds (Anisian, Middle Triassic) of southern Tanzania

- and its implications for character state optimizations at Archosauria and Pseudosuchia. *Journal of Vertebrate Paleontology* **34**: 1357-1382.
- Nesbitt SJ, Turner AH, Weinbaum JC. 2013.** A survey of skeletal elements in the orbit of Pseudosuchia and the origin of the crocodylian palpebral. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **103**: 365-381.
- Newton ET. 1894.** Reptiles from the Elgin sandstone – description of two new genera. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **185**: 573–607.
- Novas FE. 1989.** The tibia and tarsus in Herrerasauridae (Dinosauria, incertae sedis) and the origin and evolution of the dinosaurian tarsus. *Journal of Paleontology* **63**: 677-690.
- Olsen PE, Sues H-D, Norell MA. 2000.** First record of *Erpetosuchus* (Reptilia: Archosauria) from the Late Triassic of North America. *Journal of Vertebrate Paleontology* **20**: 633-636.
- Parker WG. 2016.** Revised phylogenetic analysis of the Aetosauria (Archosauria: Pseudosuchia); assessing the effects of incongruent morphological character sets. *PeerJ* **4**: e1583.
- Parker WG, Irmis RB, Nesbitt SJ, Martz JW, Browne LS. 2005.** The Late Triassic pseudosuchian *Revueltosaurus callenderi* and its implications for the diversity of early ornithischian dinosaurs. *Proc Biol Sci* **272**: 963-969.
- Parrish JM. 1993.** Phylogeny of the Crocodylotarsi, with Reference to Archosaurian and Crurotarsan Monphyly. *Journal of Vertebrate Paleontology* **13**: 287-308.
- Pinheiro FL. 2016.** A fragmentary dinosaur femur and the presence of Neotheropoda in the upper Triassic of Brazil. *Revista Brasileira de Paleontologia* **19**: 211-216.
- Pinheiro FL, França AB, Lacerda MB, Butler RJ, Schultz CL. 2016.** An exceptional fossil skull from South America and the origins of the archosauriform radiation. *Scientific Reports* **6**: 22817.
- Pol D, Escapa IH. 2009.** Unstable taxa in cladistic analysis: Identification and the assessment of relevant characters. *Cladistics* **25**: 515–527.
- Raugust T, Lacerda M, Schultz CL. 2013.** The first occurrence of *Chanaresuchus bonapartei* (Archosauriformes, Proterochampsia) of the Middle Triassic of Brazil from the Santacruzodon Assemblage Zone, Santa Maria Formation (Paraná Basin). In: Nesbitt SJ, Desojo JB and Irmis RB, eds. *Anatomy,*

- Phylogeny and Paleobiology of Early Archosaurs and their Kin*. London: The Geological Society of London. 303-318.
- Rieppel O. 1993.** Studies on skeleton formation in reptiles. V. Patterns of ossification in the skeleton of *Alligator mississippiensis* Daudin (Reptilia, Crocodylia). *Zoological Journal of the Linnean Society* **13**: 31-47.
- Romer AS. 1972.** The Chañares (Argentina) Triassic reptile fauna. XIII. An early ornithosuchid pseudosuchian, *Gracilisuchus stipanicorum*, gen. et sp. nov. *Brevoria* **389**: 1-24.
- Sampson SD, Witmer LM. 2007.** Craniofacial anatomy of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. In: Sampson SD and Krause DW, eds. *Majungasaurus crenatissimus (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar*: Society of Vertebrate Paleontology Memoir 8. *Journal of Vertebrate Paleontology*. 27(2, suppl.). 32-102.
- Schoch RR. 2007.** Osteology of the small archosaur *Aetosaurus* from the Upper Triassic of Germany. *Neuen Jahrbuch für Geologie und Paläontologie - Abhandlungen* **246**: 1-35.
- Schultz CL, Scherer CMS, Barberena MC. 2000.** Biostratigraphy of southern Brazilian Middle-Upper Triassic. *Revista Brasileira de Geociências* **30**: 491-494.
- Sereno PC. 1991.** Basal archosaurs: phylogenetic relationships and functional implications. *Journal of Vertebrate Paleontology* **10 (Supplement 3)**: 1-53.
- Stocker MR, Nesbitt SJ, Criswell KE, Parker WG, Witmer LM, Rowe TB, Ridgely RC, Brown MA. 2016.** A dome-headed stem archosaur exemplifies convergence among Dinosaurs and their distant relatives. *Current Biology* **26**: 2674-2680.
- Stocker MR, Zhao L-J, Nesbitt SJ, Wu X-C, Li C. 2017.** A Short-Snouted, Middle Triassic Phytosaur and its Implications for the Morphological Evolution and Biogeography of Phytosauria. *Scientific Reports* **7**: 46028.
- Suarez CA, Macpherson, GL Grandstaff DE. 2009.** Rare earth element geochemistry of fossil bone: using geochemical patterns to trace illegally excavated fossils. In: Foss, S, Cavin J, Brown T, Kirkland J and Stantucci V, eds. *Proceedings of the Eighth Conference on Fossil Resources* May 19-21, St. George, UT. 4-6.

- Walker AD. 1961.** Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. *Philosophical Transactions of the Royal Society of London B* **244**: 104-202.
- Walker AD. 1964.** Triassic reptiles of the Elgin Area: *Ornithosuchus* and the origins of Carnosaurs. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences* **248**: 53-164.
- Watson DMS. 1917.** A sketch-classification of the pre-Jurassic tetrapod vertebrates. *Proceedings of the Zoological Society, London* **1917**: 167-186.
- Wu X-C, Liu J, Li J-L. 2001a.** The anatomy of the first archosauriform (Diapsida) from the terrestrial Upper Triassic of China. *Vertebrata Palasiatica* **39**: 251-265.
- Wu X-C, Russell A. 2001b.** Redescription of *Turfanosuchus dabanensis* (Archosauriformes) and new information on its phylogenetic relationships. *Journal of Vertebrate Paleontology* **21**: 40-50.
- Zittel KA. 1887-1890.** *Handbuch der Palaeontologie. I. Abtheilung Palaeozoologie. III Band. Vertebrata (Pisces, Amphibia, Reptilia, Aves)*. Munchen and Leipzig: Munchen.

APPENDICES

Measurements of the skull (left side) and post-cranial elements
in MMACR-PV-036-T (in cm)

Skull length (PMX-EX)	34,2
Skull maximum height	11,5
Premaxilla body length	5,2
Premaxilla body height	3,5
Maxilla maximum length	13,6
Maxilla maximum height	5,3
Antorbital fenestra length	4,5
Antorbital fenestra height	1,3
Nasal length	14,3
Lacrimal length	6,4
Lacrimal height (exposed in lateral view)	4,2

Frontal width	5,7
Prefrontal length	6,7
Prefrontal width	3,3
Orbita length	4,4
Orbit height	4,8
Frontal length	7,8
Supratemporal fenestra length	4,7
Supratemporal fenestra width	4,9
Quadratojugal length	10,2
Parietal maximum width	12,6
Parietal minimum width	1,2
Supraoccipital height	4,2
Supraoccipital width	11,7
Left mandible length	38
Vertebral centrum length	4,7
Vertebral centrum width	3,8

RARE EARTH ELEMENT ANALYSIS

The current article on the description and study of specimen MMACR PV 036-T demonstrates its importance for our understanding of Triassic pseudosuchian evolution. However, due to the lack of any information on its type locality, it is not possible to establish its biostratigraphical position in the framework of the Brazilian Triassic. Although its preservation matches those of some specimens from the *Dinodontosaurus* Assemblage Zone (AZ) (Holz & Schultz, 1998), without any other information of its collection, a search was made of a means by which to test this inference.

Rare Earth Elements (REE), also called the lanthanide, comprise 15 metallic chemical elements that display atomic numbers between 57 and 71 (La, Ce, Pr, Nd, Pm, Sm, Eu, Gd, Tb, Dy, Ho, Er, Tm, Yb, Lu) along with the chemically similar scandium and yttrium. REE analyses has been used in paleontology for determining the origin of fossil specimens and their taphonomy (Metzger et al., 2004; Patrick et al., 2004; Martin et al., 2005; Anderson et al., 2007), with an additional application in the identification of illegally removed specimens from government land (Lukens et al., 2009; Terry et al., 2009; Suarez et al., 2009). Due to its success in the various applications described above and the access to an ongoing REE research program focused on its use in paleontology of the major sedimentary basins in southernmost Brazil being done at our university, this method was chosen to test our inferences on the biostratigraphical origin of specimen MMACR PV 036-T.

An osteoderm of specimen MMACR PV 036-T, that was originally removed to be used for histological studies, was used as the fossil bone sample, which also contained portions of the underlying rock matrix. To test the inference that it came from an outcrop of the *Dinodontosaurus* AZ, a rock matrix sample of the was collected from a specimen deposited at the Coleção de Paleovertebrados of the Instituto de Geociências at the Universidade Federal do Rio Grande do Sul. This specimen is unprepared and undescribed, still partially encased within a plaster jacket and comprises the disarticulated elements of a dicynodont, was collected at the Sanga Pascoal outcrop in the early 1990's. This outcrop was located in the region of the Municipality of Candelária and was established, based geological evidence and on other dicynodont remains, to belong to the *Dinodontosaurus* AZ. Unfortunately, geographic coordinates

for this outcrop were not taken during the time of the discoveries and today, the location of this outcrop is lost due to almost 20 years of vegetation overgrowth in the region.

The samples were prepared following the standard methodology with great care to avoid contamination, and sent to Activation Laboratories Ltd, Ontario, Canada, where they were subjected to a UT-7 Sodium Peroxide Fusion (ICP-MS) analytical package (Longerich *et al.*, 1990). The results were viewed and analyzed using Microsoft Excel (Microsoft Office package, version 2013) and the normalization values are based on McDonough & Sun (1995). The results of REE analyses of the studied samples are presented in Table 1.

Table 1: Results of the REE analysis, indicating base and normalized values; values of normalization parameters (marked in yellow) from McDonough & Sun (1995)

	La	Ce	Pr	Nd	Sm	Eu	Gd	Tb	Dy	Ho	Er	Tm	Yb	Lu
Sanga Pascoal Sample	23	44,8	5,5	22	3,8	0,8	3,9	0,8	3,6	0,8	2,5	0,3	2,3	X
Candelária Sample	69,9	47,6	10,2	39,3	6,2	1,5	9	1,8	9,1	2,2	6,9	0,9	5,3	X
McD+S (1995)	0,237	0,613	0,0928	0,457	0,148	0,0563	0,199	0,0361	0,246	0,0546	0,16	0,0247	0,161	0,0246
	La	Ce	Pr	Nd	Sm	Eu	Gd	Tb	Dy	Ho	Er	Tm	Yb	
Sanga Pascoal Sample	97,04641	73,0832	59,26724	48,14004	25,67568	14,20959	19,59799	22,16066	14,63415	14,65201	15,625	12,14575	14,28571	
Candelária Sample	294,9367	77,6509	109,9138	85,99562	41,89189	26,64298	45,22613	49,8615	36,99187	40,29304	43,125	36,43725	32,91925	

The resulting analyses (tables 2-3) indicate that the Candelária sample displays close affinity to the one from the Sanga Pascoal (Table 4). With the exception of cerium (Ce), the rest of the REE values of the Candelária sample are richer than those of the Sanga Pascoal sample. However, the comparative pattern of these elements indicates a very close affinity between both materials. As such, our original inference that the specimen MMACR PV 036-T would be from the *Dinodontosaurus* AZ based only on the characteristics of its preservation gains additional support. The observed discrepancy on the comparative levels of REE would indicate that both samples came from a different site, but would overall belong to the same geological unit.

Table 2: Base (left) and normalized (right) REE values of the Sanga Pascoal sample.

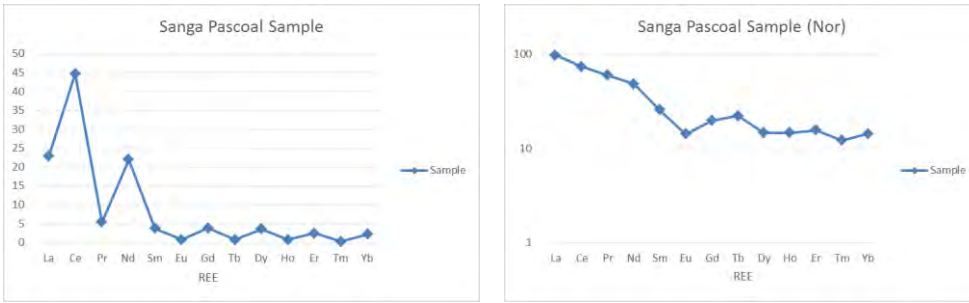


Table 3: Base (left) and normalized (right) REE values of the Candelária sample.

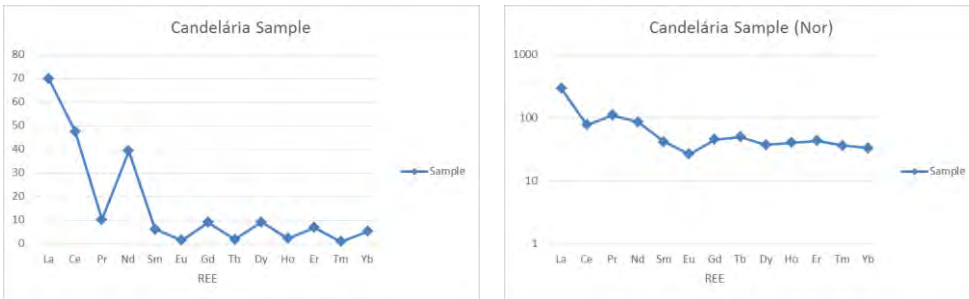
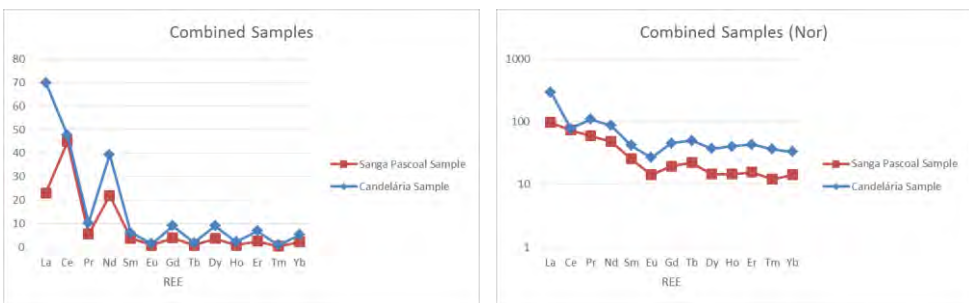


Table 4: Base (left) and normalized (right) comparative analysis of the levels of REE of both samples.



To further test which geological unit would be the origin of specimen MMACR PV 036-T, the resulting REE data was included in a larger database composed of fossil specimens and rock matrix samples from their type locality of different geological formations of southern Brazil. This database, which is in the final stages of construction and study, is part of the M.Sc. dissertation by Protásio Antônio Vervloet Paim. As such, due to the unpublished nature of this data and as to rightly ascribed priority to this researcher for his efforts, in the present study we only present and display the information that is directly significant to our study, as a much more extensive and detailed presentation of this data will be presented in an upcoming publication.

The normalized REE results of the Candelária sample was added to the database abovementioned database and was testes along samples of the Santa Maria Supersequence (Table 5), the Irati Formation (Table 6), the Rio do Rasto Formation (Table 7) and the Caturrita Formation (Table 8). Results indicated that the Candelária sample displays closer affinities to the ones of the Santa Maria Supersequence (Table 5) more than to any other geological unit in southern Brazil.

The results of the REE analyses combined with the characteristics of the preservation of the specimen strongly support our initial hypothesis that specimen MMACR PV 036-T came from the *Dinodontosaurus* AZ. As such, there is strong support to ascribe it to this biostratigraphical unit in the Santa Maria Supersequence of the Rio Grande do Sul States.

Table 5: Comparative REE analyses (Normalized) of the Candelária Sample with the ones from the Santa Maria Supersequence.

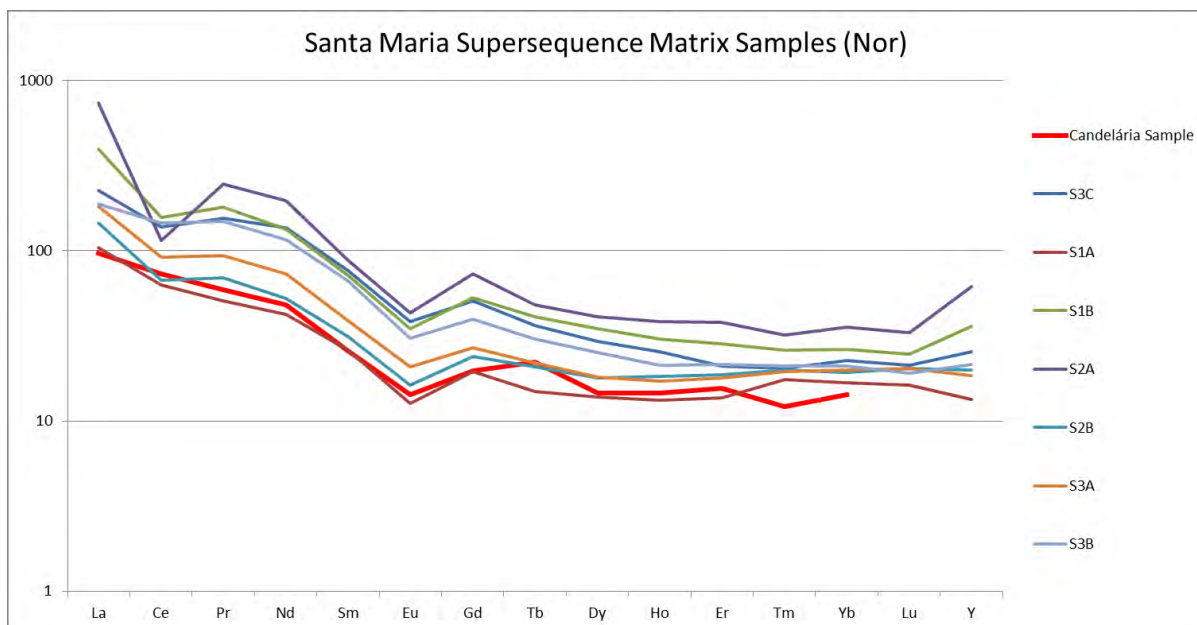


Table 6: Comparative REE analyses (Normalized) of the Candelária Sample with the ones from the Caturrita Formation.

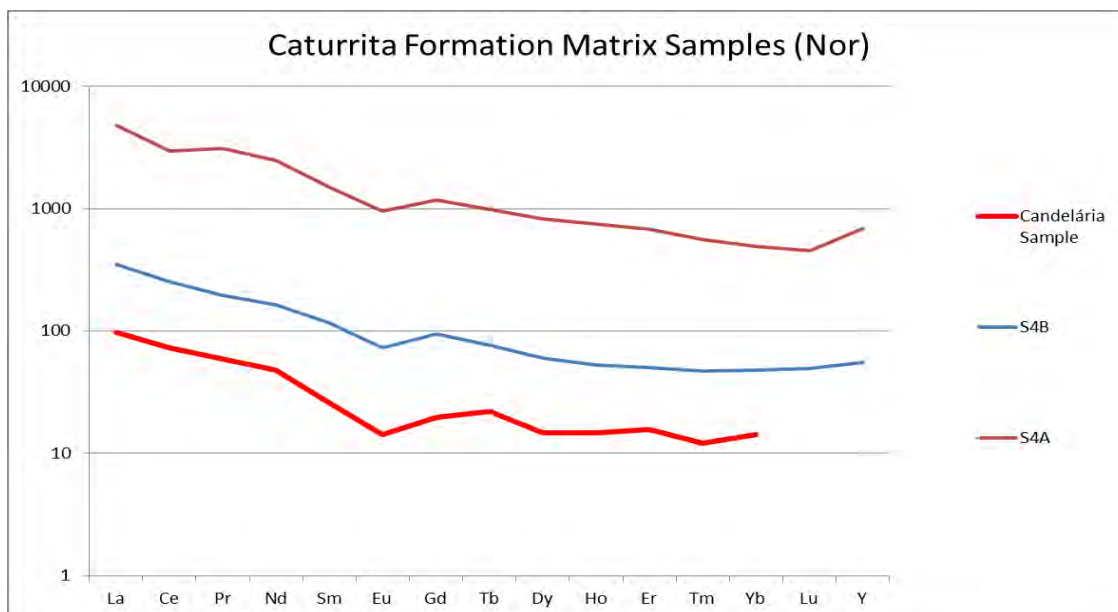


Table 7: Comparative REE analyses (Normalized) of the Candelária Sample with the ones from the Rio do Rasto Formation.

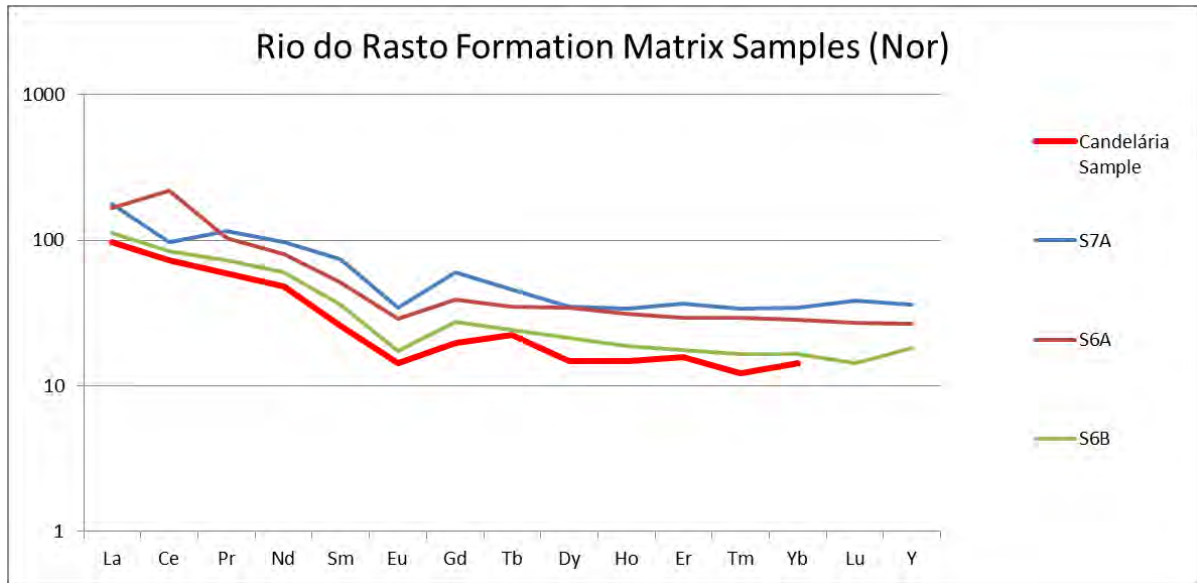
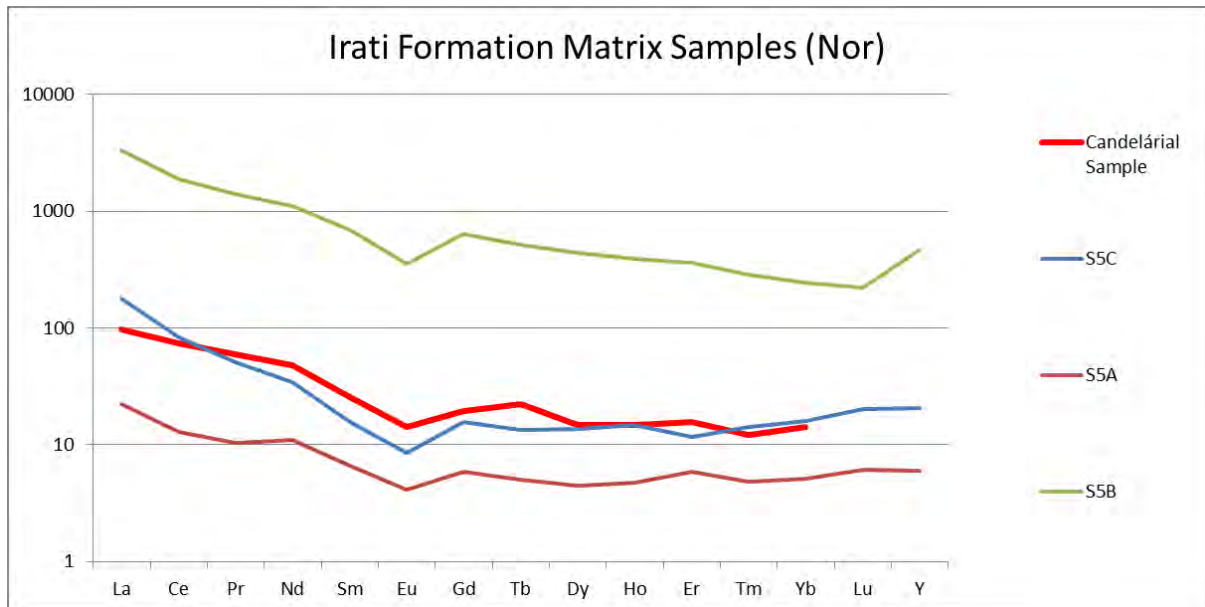


Table 8: Comparative REE analyses (Normalized) of the Candelária Sample with the ones from the Irati Formation.



Phylogenetic Analysis

Supporting Information

Nesbitt (2011) performed an original analysis from archosaurs evolution, with 412 characters and 77 terminal taxa. The original matrix published included the original 77 taxa from analysis and 6 excluded taxa: (1) *Archosaurus*; (2) *Prestosuchus chiniquensis*, (3) UFRGS 156=T, and (4) UFRGS 0152=T were compiled on only terminal taxa used on matrix, namely Combined *Prestosuchus*; (5) *Lewisuchus* and (6) *Pseudolagosuchus* were compiled on only terminal taxa used on matrix, namely *Lewisuchus/Pseudolagosuchus*).

A modified version on this original matrix was used in Butler *et al.* (2011), focusing the poposaurids evolution. These authors included 3 taxa (*Ctenosauriscus*, *Hypseolorhachis*, “Waldhaus taxa”) and 3 characters (413, 414 and 415), using a matrix with 80 taxa and 415 characters. Additionally, some characters and scores were modified: add new state on character 198, considered ordered. The present analysis considered this data set as start point of version used on this article.

Posteriorly, Nesbitt & Butler (2012) included *Parringtonia* and *Erpetosuchus* on original matrix (Nesbitt, 2011). Here, the scores for these two taxa were included on matrix of Butler *et al.* (2011), with scoring of three last characters, following personal analysis of species:

Character	<i>Parringtonia</i>	<i>Erpetosuchus</i>
413	?	0
414	?	?
415	0	0

Here, the data matrix of present analysis consist of 415 characters and 82 terminal taxa.

The redescription of *Yonghesuchus* reveals the Gracilisuchidae group on analysis showed in Butler *et al.* (2014). These authors rescoring some taxa (*Gracilisuchus*, *Turfanosuchus*), including *Yonghesuchus* on matrix and add new character (413) on original analysis (Nesbitt, 2011). The data set from this 3 taxa is included on present analysis, consisting now of 83 terminal taxa and 416 characters (the character 413 from Nesbitt & Butler, 2012, is here the number 416). Additionally, the authors performed a revision of some character states from some taxa, followed here:

Character	Modifications
4	Gracilisuchus (0 --> 3)
6	Gracilisuchus (0 --> 1)
12	Turfanosuchus (0 --> ?)

- 15 Turfanosuchus (0 --> ?); Gracilisuchus (0 --> 0&1)
- 22 Turfanosuchus (0 --> ?)
- 27 Turfanosuchus (? --> 0); Erythosuchus (0 --> 2); Chanaresuchus (0 --> 0&1); Euparkeria (1 --> 2); Prolacerta (0 --> ?); Tropidosuchus (? --> 0&1); Stagonolepis (2 --> 0); Longosuchus (2 --> 0); Aetosaurus (2 --> 0);
- Character statement and character states modified
- 32 Gracilisuchus (? --> 1)
- 42* Turfanosuchus (0 --> 1)
- 43 Gracilisuchus (0 --> 1); Turfanosuchus (0 --> 1)
- 45 Gracilisuchus (0 --> 1); Turfanosuchus (0 --> ?)
- 49 Gracilisuchus (0 --> 1)
- 55 Gracilisuchus (0 --> 1)
- 56 Gracilisuchus (0 --> ?)
- 58 Gracilisuchus (0 --> 1)
- 61* Turfanosuchus (0 --> ?)
- 67 Turfanosuchus (0 --> 1)
- 69 Gracilisuchus (0 --> 1)
- 75 Character states modified; ORDERED
- 84* Gracilisuchus (0 --> ?); Turfanosuchus (0 --> 1)*
- 85 Turfanosuchus (? --> 0)
- 87 Turfanosuchus (0 --> ?)
- 94 Turfanosuchus (1 --> 0)
- 95 Gracilisuchus (? --> 1&2)
- 101 Gracilisuchus (0 --> ?)
- 108 Gracilisuchus (0 --> 0&1)
- 111 Gracilisuchus (? --> 0)
- 115 Gracilisuchus (? --> 0&1); Turfanosuchus (0 --> ?)
- 126 Gracilisuchus (? --> 1)
- 132 Gracilisuchus (? --> 0)
- 146 Gracilisuchus (1 --> 0&1); Turfanosuchus (1 --> ?)
- 152 Gracilisuchus (? --> 0)
- 153 Gracilisuchus (? --> 1)
- 163 Gracilisuchus (0 --> ?)
- 177 Turfanosuchus (1 --> ?)
- 178 Gracilisuchus (0 --> ?)
- 179 Turfanosuchus (? --> 0)

181	Gracilisuchus (0 --> 1)
182	Gracilisuchus (? --> 0); Turfanosuchus (? --> 0)
190	Gracilisuchus (? --> 0); Turfanosuchus (0 --> ?)
192*	Gracilisuchus (0 --> ?)
195*	Gracilisuchus (0 --> ?)*; Turfanosuchus (0 --> ?)
197	Gracilisuchus (? --> 1)
198	Turfanosuchus (? --> 0)
211	Gracilisuchus (? --> 0); Turfanosuchus (? --> 0)
212	Gracilisuchus (0 --> ?); Turfanosuchus (? --> 0)
234	Turfanosuchus (0 --> ?)
278	Gracilisuchus (1 --> 0)
286	Gracilisuchus (0 --> ?); Turfanosuchus (0 --> ?)
287	Gracilisuchus (0 --> 2)
297	Gracilisuchus (0 --> ?)
300*	Gracilisuchus (? --> 0); Turfanosuchus (? --> 1)*
301	Turfanosuchus (? --> 1)
305	Gracilisuchus (? --> 1)
313	Gracilisuchus (0 --> ?)
320	Gracilisuchus (0 --> 1)
328	Gracilisuchus (0 --> ?)
330	Turfanosuchus (1 --> 0)
337	Turfanosuchus (? --> 1)
339	Turfanosuchus (1 --> ?)
340	Turfanosuchus (0 --> ?)
341	Turfanosuchus (0 --> 1)
347	Gracilisuchus (0 --> ?)
352	Gracilisuchus (? --> 1)
353	Gracilisuchus (? --> 1)
354	Turfanosuchus (? --> 0)
355	Turfanosuchus (? --> 0)
356	Turfanosuchus (? --> 0)
357	Turfanosuchus (? --> 0)
361	Turfanosuchus (? --> 0)
362	Turfanosuchus (? --> 0)
363	Turfanosuchus (? --> 1)
364	Turfanosuchus (? --> 0)

365	Turfanosuchus (? --> 1)
366	Turfanosuchus (? --> 0)
367	Gracilisuchus (0 --> 1)
371	Gracilisuchus (1 --> 2); Turfanosuchus (1 --> 1&2)
372	Gracilisuchus (1 --> 0); Turfanosuchus (1 --> 0)
375	Gracilisuchus (0 --> 1); Turfanosuchus (? --> 1)
389	Turfanosuchus (? --> 0)
397	Turfanosuchus (? --> 0)
398	Gracilisuchus (1 --> 0); Turfanosuchus (? --> 0); Ornithosuchus (1 --> ?); Riojasuchus (1 --> 0)
404	Gracilisuchus (0 --> 1); Turfanosuchus (0 --> 1)
407	Euparkeria (0 --> 1)
408	Gracilisuchus (0 --> ?)
410*	Gracilisuchus (1 --> 0)
413	Add new character (here considered as 416); ORDERED

*characters with differences scores among text of support information and data matrix in Butler *et al.* (2014)

Seven states in Butler *et al.* (2014) show difference among support information file that indicate, verbatim, the modifications on matrix and the data set matrix. In this case, we used the literature for solve this mistakes, following:

Character	taxon	Nesbitt (2011) score	Text modification	Matrix score	Score here used
42	<i>Gracilisuchus</i>	0	0 --> 1	0	1 (based on figures of Butler <i>et al.</i> , 2014)
61	<i>Turfanosuchus</i>	?	0 --> ?	0	0 (based on figures of Butler <i>et al.</i> , 2014)
84	<i>Turfanosuchus</i>	0	0 --> 1	?	? (based on matrix of Ezcurra, 2016)

192	<i>Gracilisuchus</i>	0	0 --> ?	0	0	(based on matrix of Ezcurra, 2016)
195	<i>Gracilisuchus</i>	?	0 --> ?	0	0	(based on matrix of Ezcurra, 2016)
300	<i>Turfanosuchus</i>	1	? --> 1	?	1	(based on matrix of Ezcurra, 2016)
410	<i>Gracilisuchus</i>	1	1 --> 0	1	1	(based on matrix of Ezcurra, 2016)

Baczko *et al.* (2016) provide a redescription and incorporation on Nesbitt (2011) matrix for *Venaticosuchus*. The authors also included a new character on matrix (413, but here considered as character 417 on present analysis). In parallel, suggest the modification of character 75 for *Ornithosuchus* to 1 from 0 (0 --> 1). The inclusion of new character from Baczko *et al.* (2016) analysis on present matrix requires the scores of this character for *Parringtonia* (score ?, jugal not preserved on specimens), *Erpetosuchus* (score 0, based on personal analysis of specimens), and *Yonghesuchus* (0, based on Butler *et al.*, 2014). In this moment, the matrix of present analysis is composed by 84 terminal taxa and 417 characters.

Finally, a new character is proposed here (considered as character 418). In some archosaurians, the dorsal surface of osteoderm is almost smooth, like *Euparkeria*, *Ticinosuchus*, *Saurosuchus* and *Riojasuchus*. However, a deep pit and grooves are observed on phytosaurs, aetosaurs, *Ornithosuchus*, *Erpetosuchus* and crocodylomorphs. Thus, the following character is proposed: 418- Deep pits and grooves that covers the dorsal surface of dorsal median osteoderms: (0) absent or present as weakly ornamentation; (1) present as strongly ornamentation. The new taxa here described is included in matrix.

Considering these modification, the matrix of present analysis is composed by 85 terminal taxa and 418 characters: 1-413 original from Nesbitt (2011); 414-415 included by

Butler *et al.* (2011); 416 included by Butler *et al.* (2014); 417 included by Baczko *et al.* (2016); and character 418 here proposed.

Furthermore, some states from species were rescores based on personal analysis from specimens or in a few cases on base on literature. The modification are:

Character	Modifications	Based
2	<i>Ornithosuchus</i> (? --> 1); <i>Turfanosuchus</i> (0 --> 1); <i>Yonghesuchus</i> (? --> 1)	Personal analysis; Wu & Russel (2000) and Butler <i>et al.</i> (2014); Butler <i>et al.</i> (2014)
12	<i>Saurosuchus</i> (0 --> 1); <i>Prestosuchus</i> (0 --> 1); <i>Turfanosuchus</i> (? --> 0)	Personal analysis; Personal analysis; Butler <i>et al.</i> (2014) and Ezcurra (2016)
29	<i>Ornithosuchus</i> (? --> 1); <i>Erpetosuchus</i> (? --> 1)	Personal analysis
30	<i>Parringtonia</i> (0--> ?)	Personal analysis
33	<i>Revueltosaurus</i> (0--> 1); <i>Postosuchus</i> (0--> 1)	Parker <i>et al.</i> (2005); Weinbaum (2011)
42	<i>Prestosuchus</i> (0 --> 1)	Personal analysis
45	<i>Turfanosuchus</i> (? --> 1)	Wu & Russel (2000) and Butler <i>et al.</i> (2014)
69	<i>Prestosuchus</i> (?--> 1)	Personal analysis
75	<i>Prestosuchus</i> (?--> 1)	Personal analysis
85	<i>Prestosuchus</i> (?--> 0)	Personal analysis
160	<i>Saurosuchus</i> (?--> 0)	Personal analysis
191	<i>Prestosuchus</i> (?--> 2)	Personal analysis
195	<i>Parringtonia</i> (?--> 0)	Nesbitt & Butler (2012) and Personal analysis

219	<i>Saurosuchus</i> (?--> 1)	Personal analysis
265	<i>Prestosuchus</i> (0--> 1)	Personal analysis
287	<i>Ticinosuchus</i> (0--> 1)	Personal analysis
308	<i>Ticinosuchus</i> (?--> 0)	Personal analysis
320	<i>Gracilisuchus</i> (1--> 0)	Nesbitt (2011), p. 152
330	<i>Ticinosuchus</i> (?--> 1)	Personal analysis
339	<i>Revueltosaurus</i> (0--> 1); <i>Ticinosuchus</i> (0--> 1)	Nesbitt (2011), p. 157; Personal analysis
395	<i>Prestosuchus</i> (1--> 0)	Personal analysis
410	<i>Parringtonia</i> (?--> 0)	Nesbitt & Butler (2012) and Personal analysis
411	<i>Erpetosuchus</i> (?--> 1); <i>Parasuchus</i> (?--> 1)	Personal analysis; Chatterjee (1978)

For additive character, followed the Nesbitt (2011) protocol, with 18 character ordered (32, 52, 121, 137, 139, 156, 168, 188, 223, 247, 258, 269, 271, 291, 297, 328, 356, 399). The character 198 is also ordered by Butler *et al.* (2011). Nesbitt & Butler (2012) and Baczko *et al.* (2016) followed the original analysis, without modification. Butler *et al.* (2014) ordered the characters 75 and 413 (here character 416). In addition, the present analysis also considered ordered the character 377. Summarizing, the present analysis considered as ordered 22 characters: 32, 52, 75, 121, 137, 139, 156, 168, 188, 198, 223, 247, 258, 269, 271, 291, 297, 328, 356, 377, 399, 416.

For outgroup taxon, Nesbitt (2011) uses *Mesosuchus browni* from Middle Triassic of South Africa. Others phylogenetic analysis also reveals this early branch position on Archosauromorpha evolution (e.g. Ezcurra, 2016). Thus, this taxon also is here considered as outgroup.

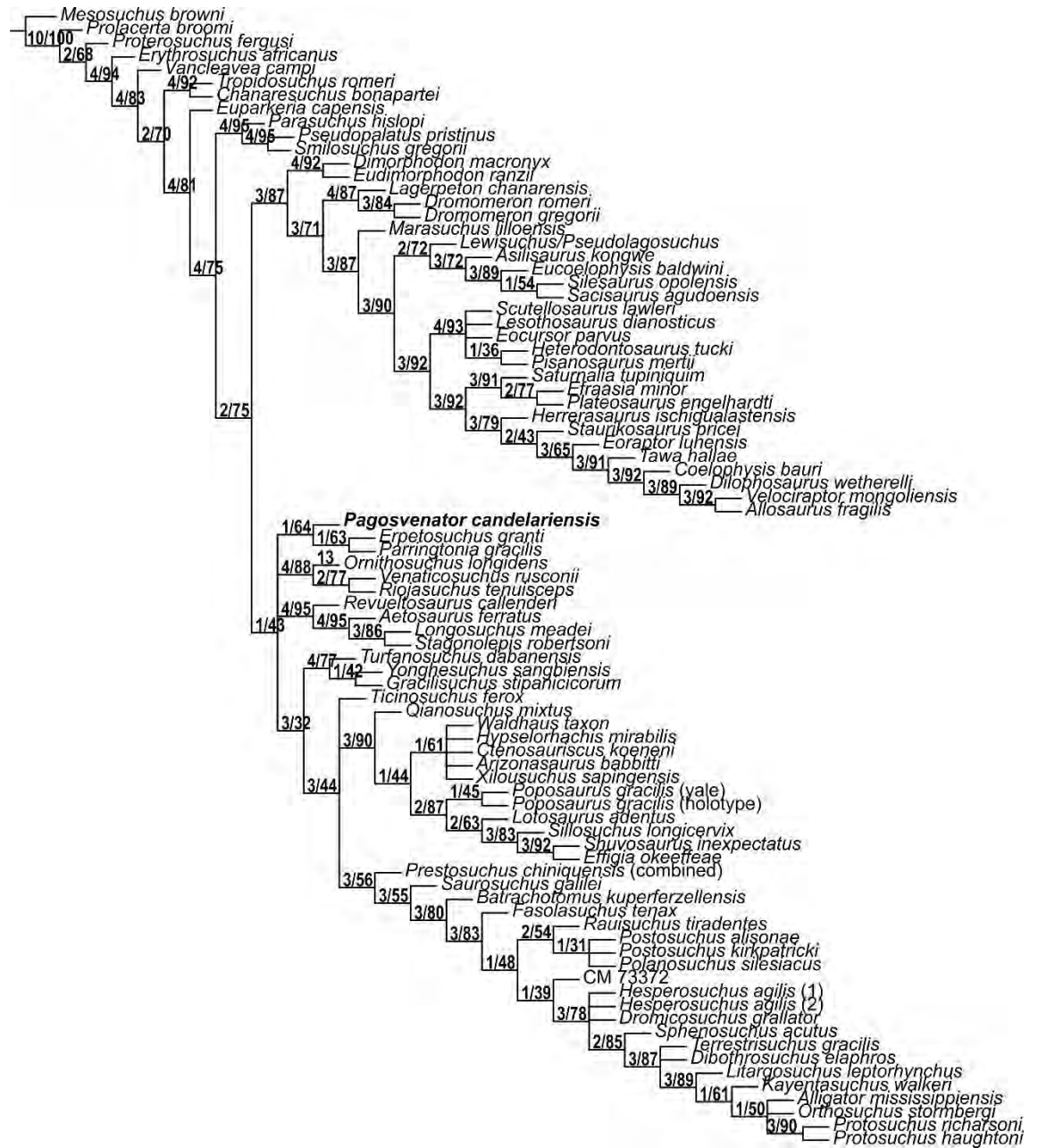


Figure 1. Strict consensus of 360 Most Parsimonious Trees with 1358 steps, obtained from cladistic analysis of matrix composed by 84 terminal taxa and 417 characters. Numbers are referred the Bremer Support and Bootstrap, respectively.

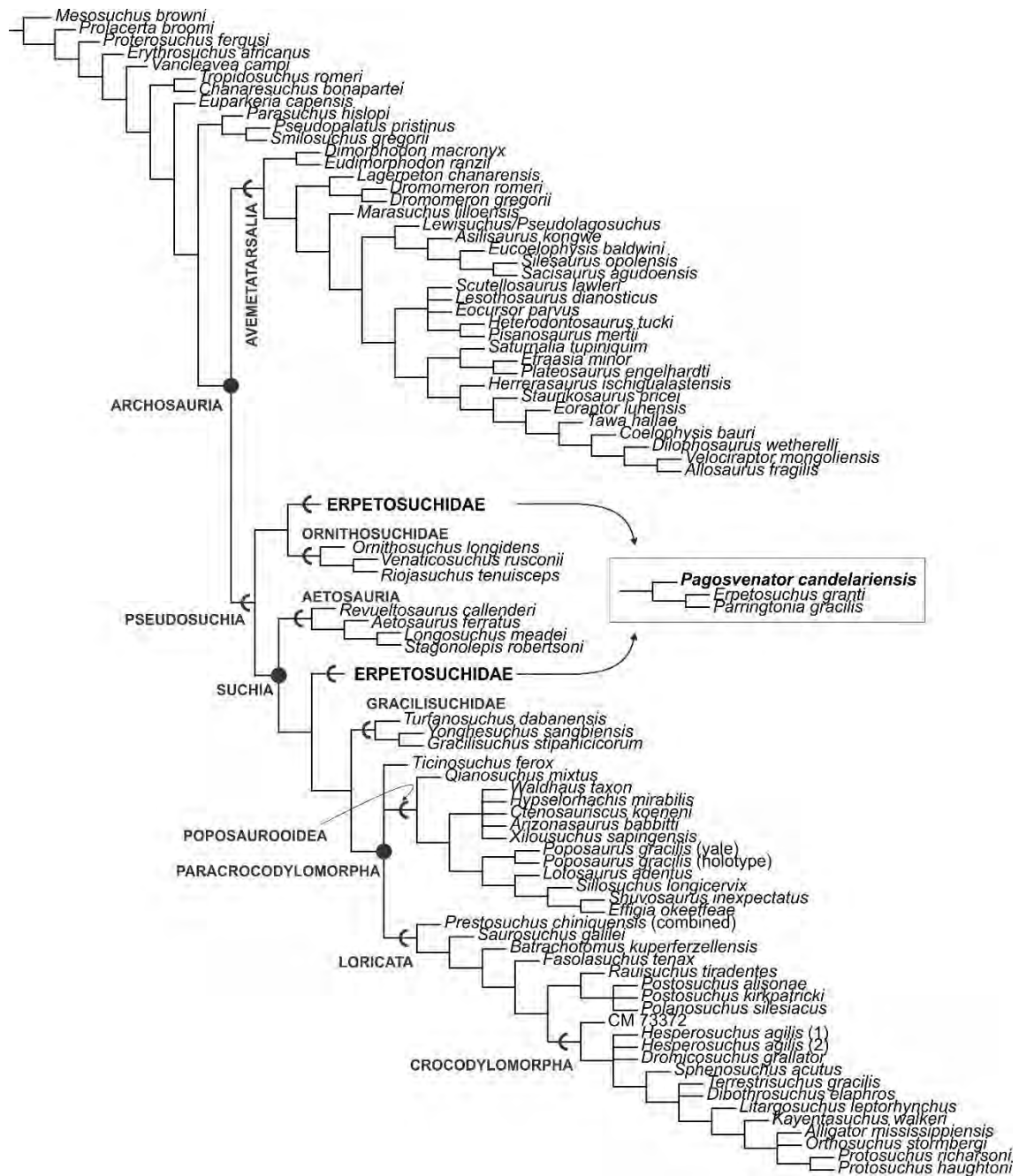


Figure 2. Strict Consensus with IterPCR script to identified unstable taxa (Pol & Escapa, 2009), before 1 iteration, showing the two alternative positions for Erpetosuchidae.

PARTE 2

11. Trabalhos Complementares

11.1 Artigos

Sales, M.A.F.; LACERDA, M.B.; Horn, B.L.D.; Oliveira, I.A.P. & Schultz, C.L.
2016. The “X” of the matter: Testing the relationship between paleoenvironments
and three theropod clades. **PLoS One**, v. 11, n. 2, p. e0147031

RESEARCH ARTICLE

The “ χ ” of the Matter: Testing the Relationship between Paleoenvironments and Three Theropod Clades

Marcos A. F. Sales^{1*}, Marcel B. Lacerda¹, Bruno L. D. Horn^{1,2}, Isabel A. P. de Oliveira³, Cesar L. Schultz¹

1 Departamento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, Rio Grande do Sul, Brazil, **2** Serviço Geológico do Brasil (CPRM), Superintendência Regional de Recife, Pernambuco, Brazil, **3** Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil

✉ Current address: Grupo Ampla, Fortaleza, Ceará, Brazil

* marcos.paleo@yahoo.com.br



Abstract

The view of spinosaurs as dinosaurs of semi-aquatic habits and strongly associated with marginal and coastal habitats are deeply rooted in both scientific and popular knowledge, but it was never statistically tested. Inspired by a previous analysis of other dinosaur clades and major paleoenvironmental categories, here we present our own statistical evaluation of the association between coastal and terrestrial paleoenvironments and spinosaurids, along with other two theropod taxa: abelisaurids and carcharodontosaurids. We also included a taphonomic perspective and classified the occurrences in categories related to potential biases in order to better address our interpretations. Our main results can be summarized as follows: 1) the taxon with the largest amount of statistical evidence showing it positively associated to coastal paleoenvironments is Spinosauridae; 2) abelisaurids and carcharodontosaurids had more statistical evidence showing them positively associated with terrestrial paleoenvironments; 3) it is likely that spinosaurids also occupied spatially inland areas in a way somehow comparable at least to carcharodontosaurids; 4) abelisaurids may have been more common than the other two taxa in inland habitats.

OPEN ACCESS

Citation: Sales MAF, Lacerda MB, Horn BLD, de Oliveira IAP, Schultz CL (2016) The “ χ ” of the Matter: Testing the Relationship between Paleoenvironments and Three Theropod Clades. PLoS ONE 11(2): e0147031. doi:10.1371/journal.pone.0147031

Editor: Faysal Bibi, Museum für Naturkunde, GERMANY

Received: June 16, 2015

Accepted: December 28, 2015

Published: February 1, 2016

Copyright: © 2016 Sales et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are within the paper and its Supporting Information files.

Funding: This work was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico, Ph.D. scholarship, grant number 141268/2013-1 MAFS.

Competing Interests: The authors have declared that no competing interests exist.

Introduction

Paleontology, as a science which deals with ancient life, was never solely a descriptive activity; therefore, some attempts to “resurrect” extinct organisms can be found since its earliest days. This task must rely on empirical evidence, comparisons with modern analogues, and bio-mechanical modeling [1], along with methodological frameworks, like the Extant Phylogenetic Bracket [2], and new technologies, like computed tomography and isotopic analyses [3–8]. In this regard, dinosaurs are common targets of these approaches and they are undeniably good examples of the turnovers of ideas and (mis)conceptions about the way the ancient ecosystems have been seen [9].

Solving the puzzle of dinosaur paleoecology also requires investigations on their spatial niche, which are relatively few in number when compared with, for example, works focusing on diet and feeding habits, even though some studies focusing on the latter may also encompass the former [5, 10, 11]. In general, this kind of inference is scattered among anatomical and morphological statements and arises from more restricted or qualitative assessments of the patterns of the fossil record [9, 11–15]. Butler and Barrett [15] designed a simple but logical way of testing the relationships between paleoenvironments and Cretaceous herbivorous dinosaur taxa. They first collected occurrence data of all these taxa and classified them by their respective paleoenvironments, i.e., terrestrial, coastal, and marine. Then, the Chi-square tests were used to identify associations between clades and paleoenvironments. Thus, they were able to corroborate previous hypotheses of overrepresentation of nodosaurid ankylosaurs and hadrosaurid ornithomimids in marine sediments [12, 13], whilst they also found that marginocephalians, ankylosaurid ankylosaurs, sauropods, and supposedly herbivorous theropods were positively associated with terrestrial paleoenvironments.

Spinosaurid theropods are another dinosaur taxon for which there are hypotheses linking them to particular habitats. Their crocodile-like skulls along with evidence from gut contents, histological thin sections and isotopic data seem to corroborate an inferred semi-aquatic lifestyle (e.g., [7, 16–21]) and, for some, it may also indicate or be related to a possible preference for marginal and coastal habitats [19, 21]. This sort of conception is not present only in scientific literature, but also in the popular view regarding these animals, fed by documentary shows, some of which also proposing a linkage between the extinction of these animals and the loss of their habitats due to the rise of sea levels during the beginning of the Late Cretaceous [22].

If there is a positive association between spinosaurs and any sort of paleoenvironment in comparison with other theropod taxa, the approach mentioned above is supposed to be able to identify it. Thus, here we present the results of such a test. In addition to spinosaurid theropods, we included in this analysis two other taxa, Abelisauridae and Carcharodontosauridae. We chose them because: 1) they are theropod taxa generally regarded as inhabiting terrestrial settings; 2) they are the less inclusive medium to large-bodied theropod clades with some specimens found in the same formations of spinosaurs, which *may* indicate some level of sympatry among them (e.g., [20, 23–26]); and 3) they are related to the episode of faunal turnover in Gondwana during the Late Cretaceous, mirrored by the one in North America: spinosaurids and carcharodontosaurids went extinct, whilst abelisaurids became the top predators [27–30]. Dealing with a smaller number of occurrences than Butler and Barrett [15] also enabled us to take into account the effects of other variables as explained below.

Material and Methods

Compilation and classification of occurrences

The worldwide occurrences of Abelisauridae, Carcharodontosauridae, and Spinosauridae were compiled consulting the Paleobiology Database (PaleoDB) through the Fossilworks webpage (see [S1 Appendix](#) for further details) as the primary source of such data. The occurrences listed therein were later compared to the literature in order to evaluate their validity (e.g., [31]). Hence, we were able to both remove and add occurrences to the PaleoDB list for this analysis. The removal of an occurrence was performed when the references listed by the PaleoDB in fact did not indicate the presence of a particular taxon, neither did any additional reference. We also removed from our analysis those occurrences based on footprints, as they are not diagnostic for any large-bodied theropod clade of our interest. On the other hand, we added occurrences when we found references that were not present in the PaleoDB. This was especially the

case of recent papers, so we took into account references published until December 31, 2014. As some occurrences of the PaleoDB were based also on conference abstracts and other scientific meeting papers, we also included this kind of reference when they were not listed by the PaleoDB. However, all occurrences based on this type of publications were considered as dubious (see below).

We compiled a total of 198 localities ([Fig 1](#); [S1 Dataset](#)), some of which representing the occurrence of only one of the taxa mentioned above, while others were shared by two or all three families. Spinosauridae had the greatest number of occurrences (82), followed by Abelisauridae (72), and then Carcharodontosauridae (66). These occurrences were then classified according to the following broad paleoenvironmental categories proposed by Butler and Barrett [15]: terrestrial (166), coastal (25), and marine (7). In order to do this, the localities were checked for stratigraphic, sedimentologic, and paleoenvironmental studies. Although the PaleoDB represented the main basis of our dataset, our classification regarding the paleoenvironments differed partially (see details ahead) from that of the PaleoDB and also from that of Butler and Barrett [15] for those localities listed by them and shared with our study.

Although Butler and Barrett [15] mentioned that some of their results were not easily explained by taphonomy or by selective transportation, they did not use any taphonomic parameter other than the body plan of the analyzed taxa and this was performed only as a qualitative assessment. However, as already historically observed by Sternberg [12], preferences for particular habitats should have had implications over the fossil record, with those taxa which inhabited closer to the depositional environment having a more complete and better preserved fossil record than that of taxa which inhabited further [33–35]. So, in order to take this issue into account as far as it was possible regarding our dataset, we also divided the occurrences in two broad taphonomic categories: category 1, formed by those occurrences based on records *including* cranial and/or postcranial remains found (semi)articulated or associated; and category 2, corresponding *solely* to those occurrences with records of isolated and fragmentary materials (see [S1 Dataset](#)). It is the assumption of the present analysis that these broad categories are more related to transportation than to other factors like anatomical peculiarities, especially where two or more taxa were found together and present different fossil records with respect to completeness, because abelisaurids, carcharodontosaurids, and spinosaurids have generally similar body plans and overlap in size. However, some references just pointed the occurrence of a taxon in a given locality without detailing its fossil record. Those cases were considered as dubious (see below) and also excluded specifically from analyses of broad taphonomic categories.

Problematic occurrences

Now, it may be appropriate to specify the concept of “occurrence”. Butler and Barrett [15] defined it as “the presence of a particular taxon at a particular locality”. In this work, an occurrence is the presence of a particular taxon at a particular locality and *time*. Although, in most cases, Butler and Barrett’s [15] concept of occurrence is, in practice, also specific regarding time, there are occasions in which it is not true. For instance, this is the case of the occurrence of Spinosauridae in the Late Jurassic of Tanzania. For the PaleoDB the presence of two isolated teeth attributable to spinosaurids is counted as a single occurrence. However, as Buffetaut [36] indicated that they come from different stratigraphic levels with distinct ages, we consider each tooth as a single occurrence, so in our dataset there are two occurrences of spinosaurids in Tanzania ([S1 Dataset](#)). We adopted the same procedure whenever possible.

This leads to other questions. For instance, what about two localities that belonged to the same paleoenvironment? If they are counted individually we may be overestimating the

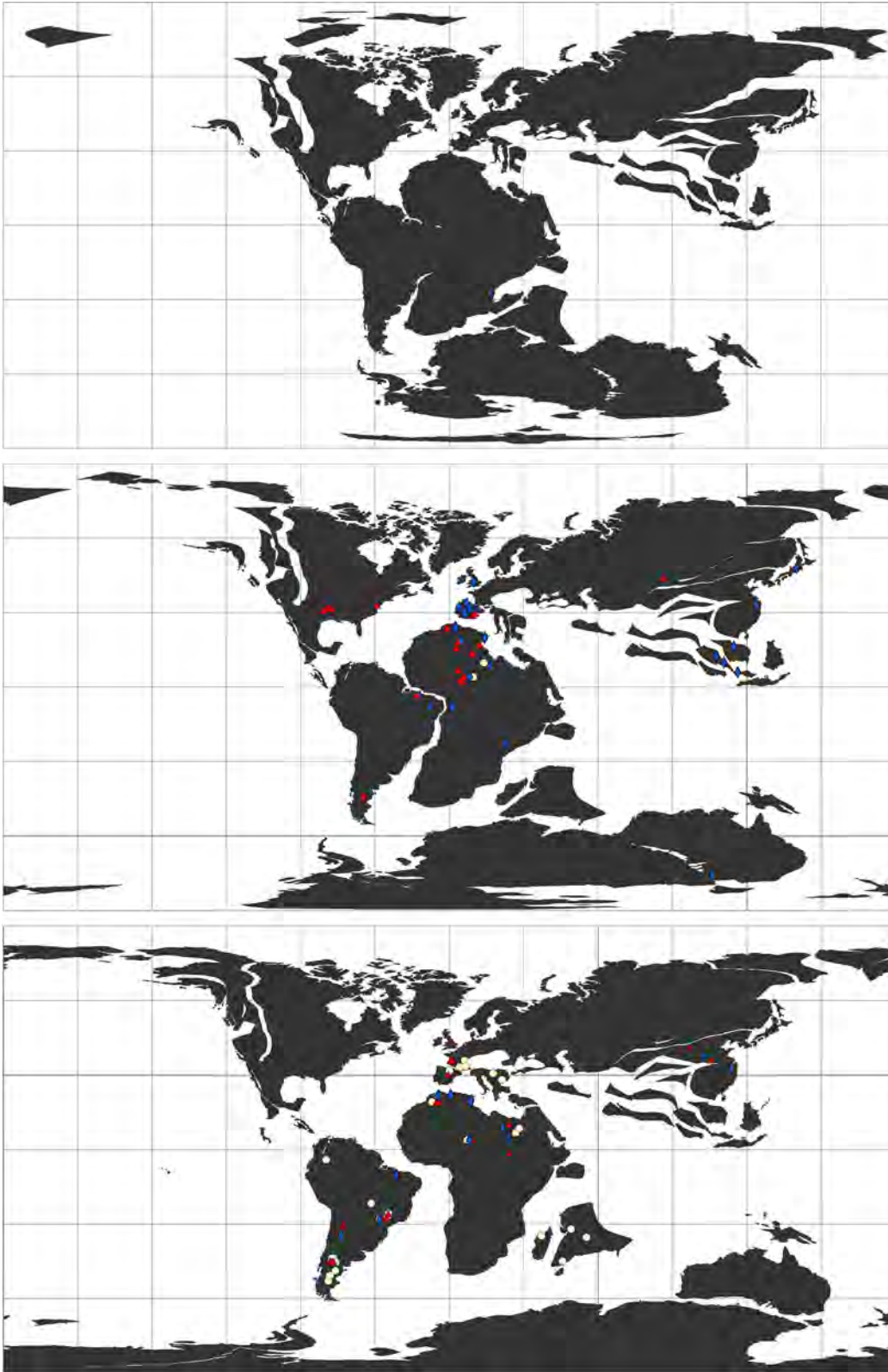


Fig 1. Global occurrences of Abelisauridae (white circles), Carcharodontosauridae (red lozenges), and Spinosauridae (blue triangles). From top to bottom: Late Jurassic, Early Cretaceous, and Late Cretaceous paleomaps. For the paleogeographic reconstructions and plotting the occurrences it was used the software Point Tracker [32].

doi:10.1371/journal.pone.0147031.g001

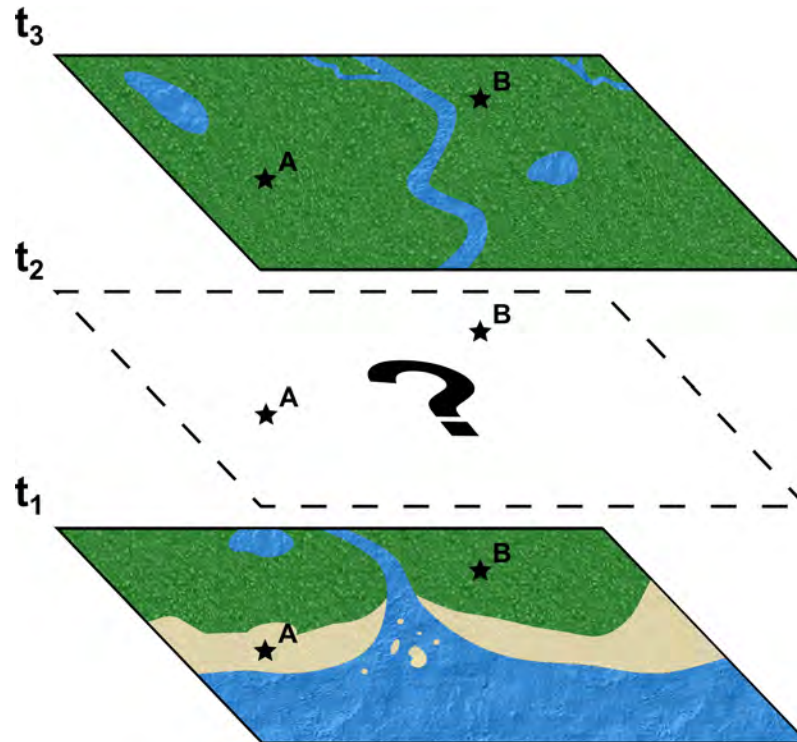


Fig 2. Schematic illustration of the concept of possibly paralogous occurrences. Consider two distinct localities A and B indicated by dark stars. In a given time t_1 , A and B are placed in distinct paleoenvironments, coastal and terrestrial, respectively. However, in t_3 , A and B are part of the same broad ecosystem, so counting these localities as distinct occurrences leads to the overrepresentation of a particular fossil taxon, present in both localities, in this paleoenvironment within the dataset. Thus, distinct localities and occurrences pertaining to the same stratigraphic units and ages and classified as the same broad paleoenvironment are considered as possibly paralogous occurrences. Also, locality B is part of terrestrial paleoecosystems in both t_1 and t_3 . However, as usual, the sedimentary and, consequently, the fossil records may be fragmentary and doubtful (t_2), so it is not possible to track the entire paleoenvironmental history of locality B and, hence, be sure if it represents the same paleoenvironment in t_1 and t_3 .

doi:10.1371/journal.pone.0147031.g002

presence of a particular taxon in a particular environment (Fig 2). We called these occurrences as “possibly paralogous occurrences”. Although possibly paralogous occurrences encompass mainly localities which pertain to the same geological formation and are close to each other, clearly it will not be the case for close localities classified as different paleoenvironments, i.e., terrestrial and coastal, terrestrial and marine, or coastal and marine (Fig 2). For practical purposes, we considered all occurrences pertaining to the same stratigraphic unit and age that are attributable to the same broad paleoenvironmental category as possibly paralogous occurrences (S1 Dataset). Distinct fossils coming from close localities, but lacking detailed stratigraphic data were also considered as possibly paralogous occurrences.

Questions may arise regarding the possibility of occurrences also being paralogous in relation to time. This possibility is real because one paleoenvironment might have existed for a time long enough to be represented in different stratigraphic levels. However, keeping in mind that the sedimentation is rather episodic and that there are many gaps in the stratigraphic sequence, it may be argued that it is not possible to rule out the hypothesis of these same paleoenvironments being temporally unrelated and distinct from each other (Fig 2). Due to the virtual impossibility of evaluating all of these parameters and that many sedimentary deposits

lack a detailed stratigraphic analysis, we limited the concept of paralogy to the criteria mentioned in the previous paragraph.

Another issue that pervades this kind of analysis is the taxonomic one: different authors, different taxonomic attributions. We followed recent taxonomic reviews and phylogenies for our taxonomic assignments (e.g., [37–39]). However, different assignments are sometimes symptomatic of the fragmentary nature of the fossil record. Furthermore, some occurrences listed in the PaleoDB are based on references that did not figure the material attributed to a particular taxon. This was the case of some complete papers and abstracts published in some annals (e.g., [40–44]). These occurrences were considered as dubious. Again, for practical purposes, those occurrences based on a single tooth, which correspond to a relevant portion of our dataset, were also kept as dubious (e.g., [45–48]). One special case is that of the post-Cenomanian Brazilian occurrences of carcharodontosaurids. Due to their questioned identities because of temporal unconformity with other global occurrences, they were also considered as dubious. All dubious occurrences are indicated in [S1 Dataset](#).

There are practical implications when considering some occurrences as possibly paralogous and/or dubious. As detailed below, we performed statistical tests including and excluding those kinds of problematic occurrences. So, when two or more occurrences were considered as possibly paralogous, they were counted only once for the tests excluding paralogy, a procedure we called as “synonymization of occurrences”. When the paralogy was between valid and dubious occurrences, the occurrence resulted from the synonymization procedure was no longer considered as dubious. Also, when the paralogy was between those pertaining to different taphonomic categories, the combined occurrences were included in category 1 after being synonymized. In short, the number of occurrences analyzed by the tests excluding both paralogous and dubious ones was not simply their total number minus the number of both possible paralogies and dubious records, especially when considering the taphonomic categories (see below).

The statistical tests

Butler and Barrett [15] used the Chi-square tests to identify significant associations between herbivorous dinosaur clades and each type of paleoenvironment. As stated by them, a positive or negative association obtained for a given taxon does not have to do with it being only or never found in that environment, respectively. Actually, it means that this taxon has a greater or fewer number of occurrences in a certain environment than expected if all taxa are assumed to be distributed evenly across all environments. On the other hand, the absence of a significant association between a taxon and a paleoenvironment suggests that the number of its occurrences is within the range predicted by probability models.

The statistical treatment of each paleoenvironment separately deserves some consideration. This sort of test is based on a table of several lines (according to the number of taxa) and one column (a particular paleoenvironment). Thus, in practice, this means that the way the expected value for the occurrences of each taxon in this particular environment is calculated is a simple division of all occurrences in that paleoenvironment by the number of taxa. So, this approach does not exactly take into account the fact of some taxa being more widespread distributed than others. The same reasoning is applicable for the tests we performed here regarding the taphonomic categories, as there is no logical basis for inferring the same expected value of occurrences for each category within each paleoenvironment—clearly, the number of occurrences based on isolated materials is greater than that of more complete records as it is expected.

As our study was partially based on Butler and Barrett’s [15] approach, we performed the same tests with Abelisauridae, Carcharodontosauridae, and Spinosauridae, including analysis

Table 1. Different datasets of occurrences.

Taxon or Period	Taphonomic Category or Epoch	Dataset I		Dataset II		Dataset III		Dataset IV	
		C	T	C	T	C	T	C	T
Abeli. (72)	1	1	26	1	12	1	24	1	11
	2	2	37	2	13	1	29	1	8
	Not specified	0	0	0	0	0	0	0	0
Carch. (66)	1	0	15	0	11	0	15	0	10
	2	9	41	6	20	5	27	5	13
	Not specified	1	0	1	0	0	0	0	0
Spino. (82)	1	6	12	3	10	5	10	3	8
	2	8	52	7	20	4	32	4	13
	Not specified	2	1	1	1	0	0	0	0
Cretaceous (194)	Early	14	77	9	34	10	54	8	27
	Late	8	88	4	36	3	74	3	28

C and T refer to the coastal and terrestrial paleoenvironmental categories, respectively, while taxa are indicated by Abeli. (Abelisauridae), Carch. (Carcharodontosauridae), and Spino. (Spinosauridae). On the other hand, taphonomic categories are indicated by their respective numbers except for those occurrences lacking data about the nature of their fossil record, whose taphonomic categories were considered as not specified. Within brackets is the total number of occurrences of each taxon or period.

doi:10.1371/journal.pone.0147031.t001

of the taphonomic categories, using the software R version 3.1.1 [49]. After the compilation of all occurrences, we excluded those in marine environments due to their very low number (Tables 1, 2 and 4). However, in order to reduce the problems cited in the last paragraph regarding the expected values of different taxa and our broad taphonomic categories, we used two additional approaches. The first of them was performing tests with more than one environment at the same time (Tables 3 and 5), because adding a new column, i.e., a new paleoenvironment, changed the way the expected value was calculated. In contingency tables with more than one line and more than one column, the expected value for each cell is calculated in terms of probability—the expected value of each cell is the chance of a sample pertaining to the same line of the cell multiplied by the chance of a sample pertaining to the same column of the cell and the total number of samples or observations [50]. The second approach was testing the relationship between taphonomic categories and paleoenvironments for each taxon separately

Table 2. Results of Chi-square Test 1 as presented by software R.

Test 1	Dataset I		Dataset II		Dataset III		Dataset IV	
	C	T	C	T	C	T	C	T
Abeli.	-	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Carch.	+	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Spino.	+	n/a	n/a	n/a	n/a	n/a	n/a	n/a
χ^2	8.7586	0.7283	4.5714	0.8276	4.625	1.7664	2.7143	0.381
p-value	0.01253*	0.6948	0.1017	0.6611	0.09901	0.4135	0.2894 [‡]	0.8266

C and T refer to the coastal and terrestrial paleoenvironmental categories, respectively, while taxa are indicated by Abeli. (Abelisauridae), Carch. (Carcharodontosauridae), and Spino. (Spinosauridae). Positive, negative or lack of any association are signaled by +, -, and n/a, respectively. For the residual analysis values that indicate the type of association see [S1 File](#).

* Significant p-value.

[‡] p-value obtained in Chi-square test using the Monte Carlo analysis.

doi:10.1371/journal.pone.0147031.t002

Table 3. Results of Chi-square Test 2 as presented by software R.

Test 2	Dataset I		Dataset II		Dataset III		Dataset IV	
	C	T	C	T	C	T	C	T
Abeli.	-	+	n/a	n/a	n/a	n/a	n/a	n/a
Carch.	+	-	n/a	n/a	n/a	n/a	n/a	n/a
Spino.	+	-	n/a	n/a	n/a	n/a	n/a	n/a
χ^2	7.3431	2.6081	5.5498	1.9352				
p-value	0.02544*	0.2714	0.07246 [‡]	0.4308 [‡]				

C and T refer to the coastal and terrestrial paleoenvironmental categories, respectively, while taxa are indicated by Abeli. (Abelisauridae), Carch. (Carcharodontosauridae), and Spino. (Spinosauridae). Positive, negative or lack of any association are signaled by +, -, and n/a, respectively. For the residual analysis values that indicate the type of association see [S1 File](#).

* Significant p-value.

[‡] p-value obtained in Chi-square test using the Monte Carlo analysis.

doi:10.1371/journal.pone.0147031.t003

(Tables 6–8). In this case in particular, our contingency tables were 2x2 (two taphonomic x two paleoenvironmental categories), so we used Fisher’s exact test in addition to the Chi-square tests as a supplementary source of corroboration (or refutation) of the results obtained. As most taxa of this study are Cretaceous in age, we also verified the relation between paleoenvironmental categories and epochs, i.e., Early Cretaceous and Late Cretaceous (Table 9). We excluded the Jurassic occurrences only from this analysis in particular for the same reasons for the exclusion of marine occurrences—the very low number.

Each test was performed four times with different datasets regarding the problematic occurrences: 1) “dataset I”, composed by all occurrences; 2) “dataset II”, with possibly paralogous occurrences synonymized; 3) “dataset III”, which lacked the dubious occurrences; 4) “dataset IV”, which excluded the dubious occurrences and contained all possibly paralogous occurrences synonymized (Table 1). These dataset are very different in relation to the number of occurrences. With the exception of the analysis with the Fisher’s exact test, in those cases where the software R presented a warning message for the results, we repeated the Chi-square

Table 4. Results of Chi-square Test 3 as presented by software R.

Test 3	Dataset I		Dataset II		Dataset III		Dataset IV	
	C	T	C	T	C	T	C	T
Abeli. 1	-	-	-	n/a	n/a	+	n/a	n/a
Abeli. 2	-	+	-	n/a	n/a	+	n/a	n/a
Carch. 1	-	-	-	n/a	n/a	-	n/a	n/a
Carch. 2	+	+	+	n/a	n/a	+	n/a	n/a
Spino. 1	+	-	-	n/a	n/a	-	n/a	n/a
Spino. 2	+	+	+	n/a	n/a	+	n/a	n/a
χ^2	16.9231	39.918	12.2632	7.0698	9.5	16.0657	8.2857	2.4286
p-value	0.0065* [‡]	1.55E-07*	0.03698* [‡]	0.2155	0.09845 [‡]	0.006659*	0.1554 [‡]	0.7872

C and T refer to the coastal and terrestrial paleoenvironmental categories, respectively, while taxa are indicated by Abeli. (Abelisauridae), Carch. (Carcharodontosauridae), and Spino. (Spinosauridae). Numbers after the taxa represent the taphonomic categories. Positive, negative or lack of any association are signaled by +, -, and n/a, respectively. For the residual analysis values that indicate the type of association see [S1 File](#).

* Significant p-value.

[‡] p-value obtained in Chi-square test using the Monte Carlo analysis.

doi:10.1371/journal.pone.0147031.t004

Table 5. Results of Chi-square Test 4 as presented by software R.

Test 4	Dataset I		Dataset II		Dataset III		Dataset IV	
	C	T	C	T	C	T	C	T
Abeli. 1	-	+	n/a	n/a	-	+	n/a	n/a
Abeli. 2	-	+	n/a	n/a	-	+	n/a	n/a
Carch. 1	-	+	n/a	n/a	-	+	n/a	n/a
Carch. 2	+	-	n/a	n/a	+	-	n/a	n/a
Spino. 1	+	-	n/a	n/a	+	-	n/a	n/a
Spino. 2	+	-	n/a	n/a	+	-	n/a	n/a
χ^2	14.6137	5.3791	13.8029	5.3592				
p-value	0.01249* [‡]	0.3923 [‡]	0.01549* [‡]	0.3758 [‡]				

C and T refer to the coastal and terrestrial paleoenvironmental categories, respectively, while taxa are indicated by Abeli. (Abelisauridae), Carch. (Carcharodontosauridae), and Spino. (Spinosauridae). Numbers after the taxa represent the taphonomic categories. Positive, negative or lack of any association are signalized by +, -, and n/a, respectively. For the residual analysis values that indicate the type of association see [S1 File](#).

* Significant p-value.

[‡] p-value obtained in Chi-square test using the Monte Carlo analysis.

doi:10.1371/journal.pone.0147031.t005

test choosing the option for the Monte Carlo analysis. The latter is a general term that refers to tests that employ random numbers usually in the form of a computer model (or simulation). The Monte Carlo significance test procedures consist in the comparison between the observed data and random samples generated in accordance with the hypothesis being tested [51]. In other words, we used this method to produce a reference distribution, based on randomly generated samples, which had the same size as the originally tested sample, in order to compute p-values when the Chi-square test requirements were not satisfied. For that, we adopted the R software default parameters [52], which follow Patefield [53]. Finally, the indication of positive or negative associations was obtained by the residual analysis in the Chi-square tests.

As the new approaches applied here represented tests differing in some assumptions, they also tested different hypotheses. So, they are summarized in [S1 Table](#) according to the hypothesis they tested, the statistics applied (Chi-square or Fisher's), and the type of table of contingency. For a more practical reference to each test performed with a particular dataset, we will refer to them throughout the text as "test N^F-X", where N is the number of the test, the superscript F indicates those analyses with Fisher's exact test whenever appropriate, and X is the Roman numeral indicative of the used dataset.

Table 6. Results of Chi-square Test 5 as presented by software R.

Test 5	Dataset I		Dataset II		Dataset III		Dataset IV	
	C	T	C	T	C	T	C	T
Abeli. 1	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Abeli. 2	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
χ^2	0.0746	0.2317	0.0173	0.0461				
p-value	1 [‡]	1 [‡]	1 [‡]	1 [‡]				
Fischer's	0.71509	0.55326	1.20416	0.73856				
p-value	0.8003	0.8611	0.7071	0.8286				

C and T refer to the coastal and terrestrial paleoenvironmental categories, respectively. Numbers after Abeli. (Abelisauridae) represent the taphonomic categories. Positive, negative or lack of any association are signalized by +, -, and n/a, respectively. For the residual analysis values that indicate the type of association see [S1 File](#).

[‡] p-value obtained in Chi-square test using the Monte Carlo analysis.

doi:10.1371/journal.pone.0147031.t006

Table 7. Results of Chi-square Test 6 as presented by software R.

Test 6	Dataset I		Dataset II		Dataset III		Dataset IV	
	C	T	C	T	C	T	C	T
Carch. 1	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Carch. 2	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
χ^2	3.1339	3.0298	2.6228	3.3816				
p-value	0.1054 [‡]	0.1669 [‡]	0.1599 [‡]	0.1329 [‡]				
Fischer's	0	0	0	0				
p-value	0.1033	0.1505	0.1617	0.1282				

C and T refer to the coastal and terrestrial paleoenvironmental categories, respectively. Numbers after Carch. (Carcharodontosauridae) represent the taphonomic categories. Positive, negative or lack of any association are signaled by +, -, and n/a, respectively. For the residual analysis values that indicate the type of association see [S1 File](#).

[‡] p-value obtained in Chi-square test using the Monte Carlo analysis.

doi:10.1371/journal.pone.0147031.t007

Results

The results are presented below for each test in particular and are summarized in the following tables and [S1 File](#).

Test 1: Taxa and each paleoenvironment separately

Test 1 was performed for each paleoenvironment in particular ([Table 2](#)). Regarding the coastal paleoenvironments, only the Chi-square test based on all occurrences, i.e., dataset I (test 1-I), was significant, with a p-value less than 0.05, so rejecting H_0 and accepting H_1 –taxa and paleoenvironments are not independent variables. The Chi-square test also showed a positive association between this paleoenvironment and both carcharodontosaurids and spinosaurids, while there was a negative association with abelisaurids. All the other tests, however, obtained p-values greater than 0.05, so they do not reject H_0 –taxa and paleoenvironments were independent variables and the distribution did not differ significantly from that expected by chance.

On the other hand, all tests for the terrestrial paleoenvironments obtained p-values greater than 0.05, so all of them failed to reject H_0 –the faunal composition in terrestrial paleoenvironments did not differ significantly from that predicted by simple probability models.

Table 8. Results of Chi-square Test 7 as presented by software R.

Test 7	Dataset I		Dataset II		Dataset III		Dataset IV	
	C	T	C	T	C	T	C	T
Spino. 1	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Spino. 2	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
χ^2	3.7607	0.038	3.5979	0.0499				
p-value	0.08196 [‡]	0.8455 [‡]	0.09645 [‡]	1 [‡]				
Fischer's	3.19102	0.86042	3.8733	1.21006				
p-value	0.07777	0.5857	0.1022	0.7505				

C and T refer to the coastal and terrestrial paleoenvironmental categories, respectively. Numbers after Spino. (Spinosauridae) represent the taphonomic categories. Positive, negative or lack of any association are signaled by +, -, and n/a, respectively. For the residual analysis values that indicate the type of association see [S1 File](#).

[‡] p-value obtained in Chi-square test using the Monte Carlo analysis.

doi:10.1371/journal.pone.0147031.t008

Table 9. Results of Chi-square Test 8 as presented by software R.

Test 8	Dataset I		Dataset II		Dataset III		Dataset IV	
	C	T	C	T	C	T	C	T
Early Cretaceous	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
Late Cretaceous	n/a	n/a	n/a	n/a	n/a	n/a	n/a	n/a
χ^2	2.2376	5.7445	1.8742	2.056				
p-value	0.1347	0.01654*	0.171	0.1516				
Fischer's	1.99268	4.52091	2.35822	2.72479				
p-value	0.1739	0.02031*	0.231	0.1955				

C and T refer to the coastal and terrestrial paleoenvironmental categories, respectively. Positive, negative or lack of any association are signaled by +, -, and n/a, respectively. For the residual analysis values that indicate the type of association see [S1 File](#).

* Significant p-value.

doi:10.1371/journal.pone.0147031.t009

Test 2: Taxa and both paleoenvironments simultaneously

This test took into account both paleoenvironments simultaneously and only test 2-I obtained a p-value less than 0.05, i.e., H_0 was rejected ([Table 3](#)). In this case the Chi-square test found a positive association between coastal paleoenvironments and both Carcharodontosauridae and Spinosauridae, but a negative one between it and Abelisauridae. However, regarding the terrestrial paleoenvironments, the result was the contrary of the coastal settings: there was a positive association between terrestrial environments and Abelisauridae and a negative one between this environment and both Carcharodontosauridae and Spinosauridae.

Test 3: Taphonomic categories and each paleoenvironment separately

Here, all tests dealing with coastal occurrences were implemented with Monte Carlo analysis ([Table 4](#)). Only tests 3-I and 3-II were significant (p-value less than 0.05), so rejecting H_0 , and they both showed a negative association between this paleoenvironment and taphonomic categories 1 and 2 of Abelisauridae and category 1 of Carcharodontosauridae, whilst it found a

Table 10. Concordance among tests with significant p-values.

Tests	1-I (C)	2-I	3-I (C)	3-I (T)	3-II (C)	3-III (T)	4-I	4-III
1-I (C)	x	3/3	x	x	x	x	x	x
2-I	3/3	x	x	x	x	x	x	x
3-I (C)	x	x	x	x	5/6	x	6/6	6/6
3-I (T)	x	x	x	x	x	5/6	2/6	2/6
3-II (C)	x	x	5/6	x	x	x	5/6	5/6
3-III (T)	x	x	x	5/6	x	x	3/6	3/6
4-I	x	x	6/6	2/6	5/6	3/6	x	12/12
4-III	x	x	6/6	2/6	5/6	3/6	12/12	x

C and T refer to paleoenvironments tested alone by tests 1 and 3. The degree of concordance or discordance are indicated by the number of similar associations found by two significant tests in relation to the total number of possible associations tested in common by them. Only tests with similar hypothesis (see [S1 Table](#)) were compared and when the comparison was not suitable it was indicated by the letter x. Tests with insignificant results were not included due to their promptly recognized agreement among them and disagreement with tests with significant results. As mentioned in the text, all Fisher's exact tests are also concordant with Chi-square tests for the same datasets, as all of them obtained insignificant p-values, so they were not also included here.

doi:10.1371/journal.pone.0147031.t010

positive association with taphonomic category 2 of Carcharodontosauridae and category 2 of Spinosauridae. Regarding category 1 of Spinosauridae, tests obtained different results: 3-I found a positive relationship with coastal paleoenvironments and 3-II, a negative one.

With respect to the terrestrial paleoenvironments, none of the tests needed the Monte Carlo implementation and only tests 3-II and 3-IV obtained p-values greater than 0.05, so failing to reject H_0 . Those significant tests, i.e., rejecting H_0 and accepting H_1 , obtained different associations between taphonomic categories and terrestrial paleoenvironments. Test 3-I showed a negative association between taphonomic category 1 of all taxa and the paleoenvironment and a positive association for taphonomic category 2 of all taxa. However, with the exclusion solely of dubious occurrences (test 3-III), negative associations were found only between taphonomic category 1 of both Carcharodontosauridae and Spinosauridae and terrestrial paleoenvironments, whereas all other associations were positive.

Test 4: Taphonomic categories and both paleoenvironments simultaneously

Test 4 was analogous to test 2, but evaluating taphonomic categories (Table 5). Here, only tests 4-I and 4-III obtained significant results, hence rejecting H_0 and pointing to a non-random relationship (association) between paleoenvironmental and taphonomic categories. Both significant tests had similar results: coastal paleoenvironments were only positively associated with taphonomic category 2 of Carcharodontosauridae and both categories of Spinosauridae, while the other categories were negatively associated with it; and, terrestrial paleoenvironments were only negatively associated with taphonomic category 2 of Carcharodontosauridae and both categories of Spinosauridae, whilst the other categories were positively associated with it.

Tests 5 and 5^F: Abelisaurid taphonomic categories and both paleoenvironments simultaneously

The Chi-square tests implemented with the Monte Carlo analysis found no significant result for all datasets, which did not reject H_0 , i.e., the taphonomic categories of Abelisauridae were randomly distributed within both coastal and terrestrial paleoenvironments (Table 6).

Regarding Fisher's exact tests (tests 5^F), all tests obtained p-values greater than 0.05, thus not rejecting H_0 , being similar to the results of test 5.

Tests 6 and 6^F: Carcharodontosaurid taphonomic categories and both paleoenvironments simultaneously

Tests 6 for all datasets did not have significant results (Table 7). Thus, H_0 is still held as valid, which means that taphonomic categories of Carcharodontosauridae and coastal and terrestrial paleoenvironments are independent variables.

With respect to tests 6^F, all p-values obtained were also greater than 0.05, being not significant and, hence, similar to the results mentioned above.

Tests 7 and 7^F: Spinosaurid taphonomic categories and both paleoenvironments simultaneously

Again, all Chi-square tests required the Monte Carlo analysis, but none of them was able to find a significant result, thus not rejecting H_0 and suggesting a random association between taphonomic categories of Spinosauridae and both paleoenvironments (Table 8). These results were corroborated by the Fisher's exact tests, which also found only insignificant p-values.

Tests 8 and 8^F: Cretaceous epochs and both paleoenvironments simultaneously

Tests 8, in general, obtained p-values greater than 0.05, so not being significant and failing to reject H_0 (Table 9). This suggests that paleoenvironmental categories are randomly distributed throughout the Cretaceous epochs. Only test 8-II recovered p-values less than 0.05 and showed positive associations between coastal paleoenvironments and the Early Cretaceous epoch and between terrestrial paleoenvironments and the Late Cretaceous epoch. It also found a negative association between coastal paleoenvironments and the Late Cretaceous epoch and between terrestrial paleoenvironments and the Early Cretaceous epoch.

Tests 8^F are similar to tests 8 when comparing the results. In general, they also obtained non-significant results, so failing to reject H_0 . Moreover, only test 8^F-II presented a p-value less than 0.05, and, hence, suggests a non-random relationship between Cretaceous epochs and the compiled number of paleoenvironmental categories.

Discussion

Keeping in mind the different hypotheses and types of contingency tables, we performed eight different sets of tests, each one possessing its own assumptions (S1 Table). So, it is not surprising to find somehow different (and sometimes contrasting) results (Table 10 and Fig 3). Moreover, these tests were supposed to show only if there was or not any non-random relationship between the variables under consideration. In other words, the nature and causes of the presence or absence of non-random relationships are essentially interpretative and require caution to be inferred, especially when the results were divergent. Thus, in order to better compare and discuss our results, this section is divided according to the different aspects we cover both directly and indirectly. When different tests are more similar in their results, we can be more confident about the inferences, while the contrary implies a lower degree of confidence.

The implementation of Chi-square tests with the Monte Carlo analysis

We performed Chi-square tests with the Monte Carlo analysis whenever necessary, i.e., in the cases of warning messages given by the software R. To evaluate the reliability of the results obtained with this implementation it is necessary to compare them with the results of other independent approaches, which is the case for tests 5, 5^F, 6, 6^F, 7, 7^F, 8 and 8^F. In those tests, all contingency tables contained two lines and two columns, and for this type of table Fisher's exact tests are generally supposed to be the most appropriate statistical analysis [50]. In all of them, Chi-square and Fisher's approaches obtained similar results for the same datasets regarding their statistical significance (or not) (Tables 6, 7, 8, and 9, and S1 File). We consider this as evidence that the Monte Carlo implementation worked well in the sense of not providing unreal significant or non-significant results.

Effects of problematic occurrences over the different results

Problematic occurrences encompass both possibly paralogous and dubious occurrences. The exclusion of one of these types of occurrences or both was responsible for obtaining different results. This was particularly true for the exclusion of possibly paralogous occurrences (i.e., the synonymization of possibly paralogous occurrences), which was performed in order to diminish possibly untrue overrepresentation of a given taxon in a given environment. Abelisauridae and Spinosauridae were the taxa most affected by this procedure in the sense of obtaining different results when varying the dataset for the tests, the implications of which will be discussed below. The synonymization of possibly paralogous occurrences seemed to affect Abelisauridae

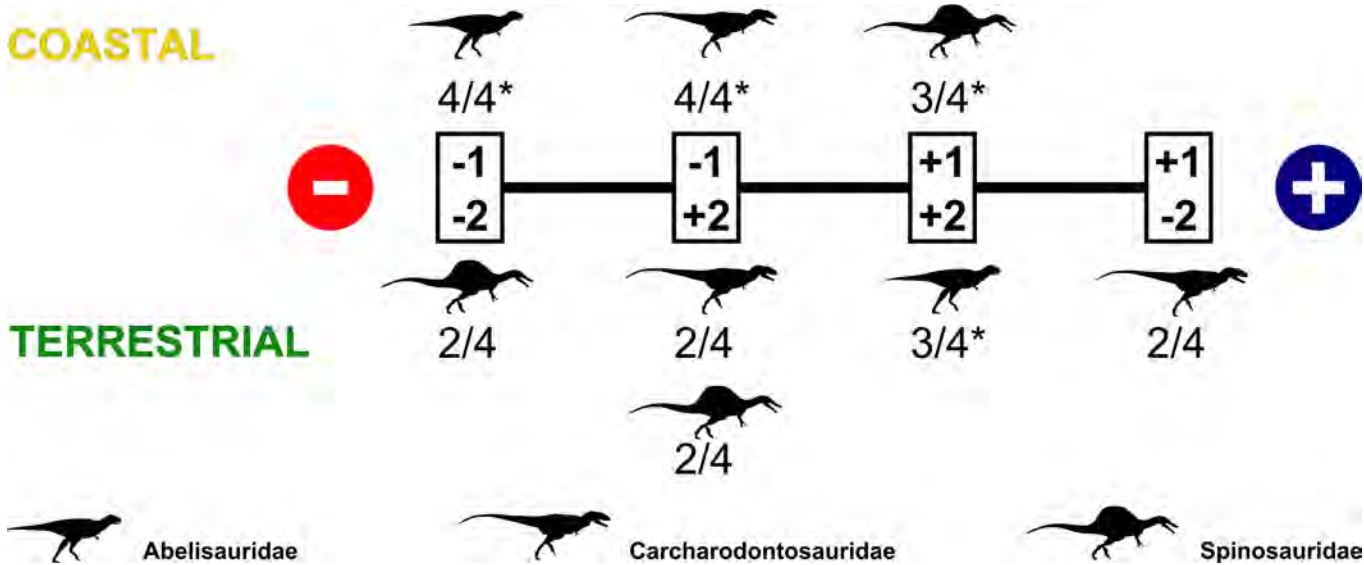


Fig 3. Most frequent associations found between taphonomic categories of each taxon and paleoenvironments in significant tests (3-I, 3-II only for coastal paleoenvironments, 3-III only for terrestrial paleoenvironments, 4-I, and 4-III). The minus and plus signs inside the circles indicate decreasing and increasing trends regarding associations with a particular paleoenvironment, respectively. The rectangles encompass all possible combinations among taphonomic categories and types of association (if negative or positive), which are represented by the numbers and associated signs, respectively. The condition represented by a positively associated category 1 and a negatively associated category 2 (the rightmost rectangle) are closer to an ideal scenario than a real one with respect to the fossil record, as occurrences based on fragmentary records are in general more numerous than those based on more complete specimens. The fractions below the body icons represent the number of times that a given taxon obtained a particular association with a given paleoenvironment (numerator) in relation to the total number of analyses testing this same relationship (denominator). Only associations with a ratio equal or greater than 0.5 are shown, with an asterisk indicating the latter ones.

doi:10.1371/journal.pone.0147031.g003

especially in tests 3 for terrestrial environments. For instance, we gathered 24 abelisaurid occurrences in Madagascar, but all of them pertain to the Maevarano Formation and are close enough to be considered as only one occurrence after the synonymization procedure (see [S1 Dataset](#)). On the other hand, the synonymization procedure seemed to affect Spinosauridae especially in tests 3 for coastal settings. Indeed, with respect to paleoenvironments, the coastal ones are those that suffered the greatest relative loss of occurrences by removing the problematic ones and this is clearly exemplified by the results of tests 1, 2, 3, and 4, which in general required the Monte Carlo analysis ([Table 2–5](#) and [S1 File](#)).

Ideally, the dataset IV was supposed to be the most reliable one for statistical purposes. However, due to the removal of a considerable amount of occurrences, all tests based on it are non-significant and so their results must be seen from a relatively skeptical and comparative point of view instead of considering it alone as providing the most reliable results. We believe that further records along with new findings in the localities listed in this work will reduce the effects of the removal of problematic occurrences over the significance of the results.

The distribution of paleoenvironments throughout the Cretaceous epochs

Considering the Early and the Late Cretaceous as distinct epochs, we found (except for tests 8-II and 8^F-II) a random distribution of both coastal and terrestrial paleoenvironments throughout the period. For instance, this implies that the results for Abelisauridae, which had more occurrences in the Late Cretaceous terrestrial paleoenvironments, were more due to the paleoecology of this taxon instead of an uneven distribution of compiled occurrences classified as terrestrial across Cretaceous epochs, which was not the case.

The significant results obtained by tests 8-II and 8^F-II may be due to the synonymization of paralogous occurrences especially concerning the coastal occurrences. This increased the weight of Early Cretaceous coastal occurrences within the overall period occurrences in relation to the other datasets, which is in accordance with its positive association found by the residual analysis ([S1 File](#)). Moreover, as none of the Chi-square test 8 required the Monte Carlo analysis, we interpret this as evidence of the reliability of the dataset IV for this test even with a smaller number of occurrences, which, as already mentioned, should be the most reliable dataset. So, tests 8-IV and 8^F-IV must be the ones that hold the most persuasive results, indicating the lack of association between Cretaceous epochs and paleoenvironmental categories and being contrary to tests 8-II and 8^F-II.

Taxa and coastal paleoenvironments

As explained by Butler and Barrett [15], the concept of a taxon being positively and negatively associated with any paleoenvironment is relative to the other taxa sampled. In light of this, tests 1-I and 2-I found a negative association between Abelisauridae and coastal paleoenvironments, but also a positive one between this paleoenvironment and both Carcharodontosauridae and Spinosauridae. Tests with other datasets did not obtain significant results, probably due to the reduced number of occurrences in relation to dataset I. The significant result mentioned above could suggest that both carcharodontosaurids and spinosaurids were more distributed in coastal paleoenvironments than abelisaurids in a way that differed significantly from that predicted by simple probability models.

Nevertheless, test 3-I and 3-II showed that all taphonomic categories of Abelisauridae and category I of Carcharodontosauridae were negatively associated with coastal paleoenvironments, while category 2 of Carcharodontosauridae and Spinosauridae were positively associated. In addition, Test 3-I found a positive association also between category 1 of Spinosauridae and coastal areas. Tests 4-I and 4-III also obtained significant results, being similar to those of test 3-I ([Table 10](#)). These results suggest that, despite the number of occurrences of Carcharodontosauridae in coastal sediments being statistically more comparable to that of Spinosauridae than to Abelisauridae, the fossil record of carcharodontosaurids in this paleoenvironment is basically composed by fragmentary and isolated specimens, which points to a higher degree of transportation, whereas spinosaurids in coastal sediments are represented by more complete specimens, implying that they suffered significantly lower degrees of transportation ([Fig 3](#)). As the presence of fragmented and disarticulated fossil remains is more expected for distal sedimentary systems like deltas and coastal settings, which was the case for carcharodontosaurids and abelisaurids, the presence of articulated remains in these settings implies that spinosaurids were “truly” occupying coastal environments or at least habitats close by, while the other theropods in general had more inland habitats ([Fig 4](#)). It is likely that there were also some differences between abelisaurids and carcharodontosaurids, with the former inhabiting (or being more common in) even more inland areas than the latter, which could explain the negative association of category 2 of the abelisaurids and the positive one of category 2 of carcharodontosaurids with coastal paleoenvironments. If it was the case for species with overlapping geographic ranges, so abelisaurids and carcharodontosaurids might have been sympatric, but not exactly syntopic [11].

Taxa and terrestrial paleoenvironments

Discussing the type of association between those taxa and terrestrial paleoenvironments is a more complicated issue given the different results for some of them. Test 1 obtained no significant result for all datasets, suggesting that no taxon was significantly more distributed in inland

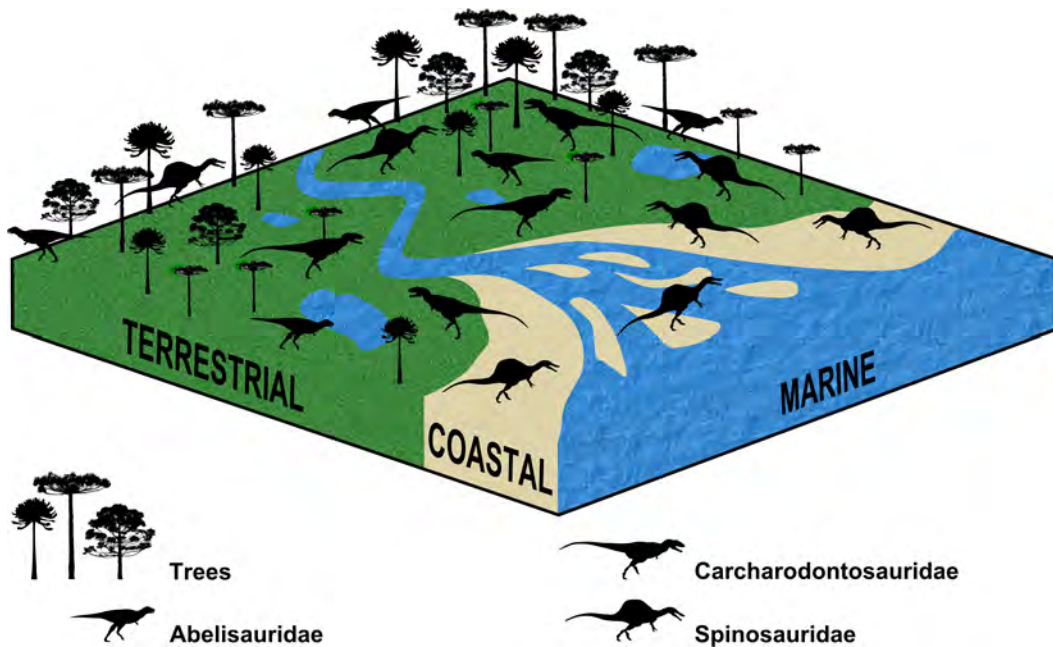


Fig 4. Schematic illustration of the spatial distribution of Abelisauridae, Carcharodontosauridae, and Spinosauridae throughout coastal and terrestrial paleoenvironments. Spinosaurids seem to have been natural inhabitants of coastal settings, while terrestrial and more inland habitats were shared by them and both abelisaurids and carcharodontosaurids. Note that the number of body icons (not to scale) does not reflect perfectly the relative abundance of these taxa within each paleoenvironment.

doi:10.1371/journal.pone.0147031.g004

areas than the others. Here may be one of the few cases where results based on datasets II, III, and IV are more reliable, because the number of occurrences in this paleoenvironment were still high despite the exclusion of paralogous and dubious occurrences. Actually, considering the large number of possibly paralogous occurrences of Malagasy abelisaurids, it would be more cautious to base inferences on these datasets instead of only on dataset I as in the other tests mentioned above.

However, test 2 differed somehow from test 1. Test 2-I found a positive association between Abelisauridae and terrestrial paleoenvironments, whilst both Carcharodontosauridae and Spinosauridae were negatively associated with them. Test 2 with other datasets found no significant result. As test 2 took into account both coastal and terrestrial paleoenvironments, the non-significance of some results may be due to two different factors. The first one is the removal of problematic coastal occurrences, which may be responsible for not finding any positive or negative relationship of any taxa with coastal environments, as explained before. The second factor is that the synonymization of possibly paralogous occurrences made the number of occurrences in terrestrial environments of each taxon more similar in relation to the others, and, if this was the case, so observations made above for test 1 might be also valid for test 2. On the other hand, the significance of test 2-I may be more due to the coastal occurrences than exactly the number of terrestrial occurrences attributable for each clade.

Given the statements above, the comparisons between the results of tests 1 and 2 seem to point in general for the absence of any taxon significantly associated with terrestrial paleoenvironments, be it a positive or negative association. This makes sense when considering that abelisaurids and carcharodontosaurids were in general considered essentially terrestrial, and the positive association of the first and the negative association of the latter were possibly the result of the inflated number of Malagasy abelisaurid possibly paralogous occurrences in terrestrial sediments and the higher number of carcharodontosaurid occurrences in coastal areas, instead

of a more widespread distribution of abelisaurids in inland areas. An alternative is that abelisaurids, independently of being or not more widespread, could have been more numerous in inland habitats than carcharodontosaurids and this could have enhanced the potential for preserving more remains of the former in relation to the latter (and also spinosaurids; see below).

However, the fact that the occurrences of Spinosauridae in terrestrial paleoenvironments are not significantly different from those of Abelisauridae and Carcharodontosauridae may be somehow surprising, and understanding the real meaning of this result in particular requires a taphonomic approach. Test 3 found three different results. As already mentioned, the type of association between taphonomic categories of Abelisauridae and terrestrial paleoenvironments varies according to the dataset used (see the residual analysis in [S1 File](#)). On the other hand, where the results were significant (using datasets I and III), the association between taphonomic categories and this paleoenvironment were similar for both Carcharodontosauridae and Spinosauridae: category 1 being negatively associated and category 2 positively associated ([Table 4](#) and [Fig 3](#)). As these taphonomic categories are supposed to be related to transportation, these similarities between carcharodontosaurids and spinosaurids might suggest they occupied spatially inland habitats in a way more similar than usually depicted. This is also supported by tests 3-II and 3-IV, which found no significant association between terrestrial paleoenvironments and the taphonomic categories of any clade.

On the other hand, test 4 found positive associations between all categories of Abelisauridae and terrestrial sediments when the p-values were significant (using datasets I and III). It also obtained positive associations between the latter and category 1 of Carcharodontosauridae, while categories 2 of carcharodontosaurid and both taphonomic categories of Spinosauridae were negatively associated. These results contrast with those of test 3, suggesting distinct ways of occupation of inland habitats for carcharodontosaurids and spinosaurids ([Fig 3](#)). However, the observations made for test 2 also apply to test 4 with respect to the effects of few occurrences in coastal sediments especially for Abelisauridae and Carcharodontosauridae, as test 4 also analyzed both paleoenvironments simultaneously. For instance, all tests that included coastal occurrences of dataset I and analyzed all taxa simultaneously obtained significant p-values.

It may be now appropriate to take into consideration the results of tests 5, 5^F, 6, 6^F, 7, and 7^F. As they analyzed each taxon in particular, they might reflect the statistical behavior of the taphonomic categories in relation to each paleoenvironment without the interference of the number of occurrences of other taxa. All tests had non-significant results. This could be a consequence of the low number of occurrences in coastal environments along with the removal of problematic occurrences in the cases of datasets other than dataset I, but these results may be somehow logical. For instance, spinosaurids are supposed to have had semi-aquatic lifestyles and a probable preference for marginal habitats [[7](#), [16](#), [19](#), [20](#)], which were not restricted to coastal areas: they may also have inhabited river and lake margins located more inland. If this was the case, it could be speculated that the taphonomic categories should behave statistically in a similar way for both coastal and terrestrial paleoenvironments, instead of the results shown by tests 4-I and 4-III, which took into account the relative amount of occurrences of the other taxa. It could be also a consequence of the way we defined the taphonomic categories and the types of problematic occurrences, which were a direct consequence of the amount of available data, being, in turn, related to collection efforts. New findings may increase the number of occurrences for each category, reduce the number of problematic ones (especially those dubious), and even enable a more refined definition of the taphonomic and paleoenvironmental categories. This reasoning is applicable to all taxa.

At this time, considering all the available information, it is not possible to rule out the hypothesis of spinosaurids occupying spatially inland habitats in a way somehow similar to

that of other terrestrial taxa, like carcharodontosaurids (Figs 3 and 4). This implies that spinosaurids could have been more generalist or at least less specialized than usually suggested regarding types of habitats, being well represented in from coastal to inland areas ([7] contra [21]). Also, the differences observed between the taphonomic categories of Abelisauridae and Carcharodontosauridae may be more due to the greater number of problematic (especially possibly paralogous) occurrences of Abelisauridae than to real and disparate differences regarding the spatial niche of these two taxa. However, the possibility of abelisaurids having been more numerous within continental settings than carcharodontosaurids may also have played a role in this regard, which could explain the association found for the category 1 of each taxa (the most abundant taxon would have more potential to have a fossil record composed by more complete specimens).

Other paleoecological implications

Differences regarding the number of occurrences among the three taxa could be first seen by some as an indirect measurement of their relative abundance. In fact, Hone et al. [48] suggested that spinosaurids could have been rare animals when compared to other theropod taxa with larger fossil record, like tyrannosaurids and allosaurids, a view somehow opposed by that of Benyoucef et al. [21]. However, as our work dealt primarily with locations and as each location may be the source of more than one fossil specimen, our compilation of occurrences had more to do with large-scale geographic distribution than with relative abundance. However, as taphonomic category 1 is based on more complete and better preserved specimens and some localities yielded only one specimen, it can be used as indirect information on the minimum number of at least this type of record for each clade. Category 2, on the other hand, may be less informative because it is based on isolated and fragmentary remains, encompassing mainly isolated teeth. The number of occurrences classified into category 1 is 27, 15, and 18 for Abelisauridae, Carcharodontosauridae, and Spinosauridae, respectively. Despite the number of other skeletal materials eventually classified into category 2 and one special case of category 1 of Thai spinosaurids (see below), our dataset shows that the number of spinosaurid skeletal materials is not considerably fewer than that of the other taxa—actually, category 1 of spinosaurids is more numerous than category 1 of carcharodontosaurids.

Given the number of skeletal materials for tyrannosaurids and allosaurids mentioned by Hone et al. [48], if one assumes spinosaurids as rare faunal components, the same inference must be applied to carcharodontosaurids and possibly to abelisaurids, depending on the adopted concept of rareness. However, it is unlikely that all these taxa were rare components in comparison to other medium to large-bodied theropod clades, although they would be minor components of local paleofaunas in comparison to sympatric small-bodied theropods, as proposed for tyrannosaurids [54, 55]. Indeed, as suggested above, some differences may have existed between the abundance of abelisaurids and carcharodontosaurids, with the former being more numerous, as expected due to their difference in body size [11]—carcharodontosaurids were bigger, although some taxa overlap in size with abelisaurids—and roughly indicated by the number of category 1 occurrences of each taxa and their behavior in tests 3-I, 3-III, 4-1, and 4-III regarding terrestrial paleoenvironments.

Most occurrences of Abelisauridae, Carcharodontosauridae, and Spinosauridae are Gondwanan, and collection efforts in Africa and South America in general are considerably smaller than in Asia and North America, from which came most of the fossil record of tyrannosaurids and allosaurids. Moreover, many specimens of tyrannosaurids and allosaurids came from bonebeds, some of them being monodominant assemblages in some outcrops, which may be related to social behavior and mass death events [11, 54, 56]. Bonebeds containing Jurassic and Cretaceous

large theropods are quite rare in Gondwana. Actually, Laje do Coringa in the Northeastern Brazil is one of such sites, but its fossils are very fragmentary as they seem to have been reworked. Not surprisingly, the most common theropod remains there are teeth, and the only theropod cranial material from this site reported so far are the holotypic premaxillae (and a partial maxilla) of the spinosaurine spinosaurid *Oxalaia quilombensis*. As the Laje do Coringa bonebed is supposed to have been formed within a coastal setting, it is more probable that *O. quilombensis* was a species that “truly” inhabited this paleoenvironment, while the abundant teeth of carcharodontosaurids might have come from further inland areas [25, 57, 58].

Hone et al. [48] also commented that a taphonomic bias in favor of spinosaurid remains in the fossil record in comparison to other theropod taxa should be expected, as the former might have inhabited preferentially aquatic habitats. However, the rareness of spinosaurid specimens would suggest the contrary, and this could correlate with the rareness of these theropods in the fossil record, although the most abundant dinosaur remains in the Romualdo Formation are those identified as spinosaurids [59–64]. Besides, they also suggest that spinosaurids should have been present also in North America (see also [65]) and their absence in the North American fossil record should be considered as evidence further corroborating the hypothesis of their scarcity in paleoecosystems. Actually, the evidence for the presence of spinosaurids in North America during the Late Jurassic is dubious (S1 Dataset) and the hypothesis of rareness requires much more evidence. Interestingly, some of our results suggest that the fossil records in terrestrial sediments of spinosaurids and carcharodontosaurids are equivalent, which points to some similarity regarding the spatial distribution across inland habitats, as mentioned earlier.

Some might consider this hypothesis as unlikely, especially after the work of Ibrahim et al. [20] on new materials attributed to the spinosaurine spinosaurid *Spinosaurus aegyptiacus* from the Kem Kem beds of Morocco. Benyoucef et al. [21] also discussed the vertebrate fossil record of the Mid-Cretaceous Saharan deposits, pointing the overabundance of spinosaurids in some Algerian localities and suggesting that this taxon preferentially inhabited environments with few plant-eating dinosaurs and close to the seashore. However, an association with a particular habitat may have more to do with avoidance of other competitors or predators than with a real preference for it, and this is especially difficult to be tested regarding the fossil record (see examples in Farlow and Pianka [11]). Furthermore, our test 4 could not rule out the inference of spinosaurids being able to inhabit also inland or non-marginal paleoenvironments. Additionally, our dataset also comprises species other than *S. aegyptiacus*, which clearly had body plans different from the one proposed by Ibrahim et al. [20]. In fact, despite of all spinosaurid taxa possessing anatomical features indicative of semi-aquatic lifestyles or a mostly piscivorous diet, there is also evidence suggesting that these theropods could have behaved more plastically than usually inferred. The fossil record of predation by spinosaurids indicates that they also included other animals in their diet. Spinosaurids seem to have fed also on iguanodontids, pterosaurs, and sauropods [16, 62, 66, 67], and the latter were found to be positively associated with terrestrial paleoenvironments (and negatively associated with the coastal ones) by Butler and Barrett [15]. In fact, the Thai record of predation of sauropods by spinosaurids comes from a paleoecological setting interpreted as terrestrial (Fig 5; S1 Dataset) [66, 67] and this could also explain the rareness of herbivorous dinosaurs in coastal localities with spinosaur remains, as the most common herbivores of the Mid-Cretaceous of Gondwana were sauropods [27, 28]. Moreover, Therrien et al. [68] found a mandibular force profile for the baryonychine spinosaurid *Suchomimus tenerensis* that would have made it able to feed on small to medium-size terrestrial prey, whereas the robust forelimbs could have been used for hunting large ones [69]. Also, the same study that found isotopic values indicative of semi-aquatic lifestyles for spinosaurids also reported some values comparable to those of terrestrial taxa, including



Fig 5. Reconstruction of the terrestrial paleoenvironmental setting of the Sao Khua Formation. In the center, a generalized spinosaurid feeds on a sauropod. This trophic relationship is hypothesized based on isolated tooth crowns found in association with a sauropod skeleton [67]. In the background, a small pack of the ornithomimosaur theropod *Kinnareemimus*. Both sauropods and ornithomimosaurs (as part of the “herbivorous” theropods) were found to be positively associated with terrestrial paleoenvironments by Butler and Barrett [15].

doi:10.1371/journal.pone.0147031.g005

specimens from Morocco [7]. So, in short, the taphonomic evidence showed that spinosaurids also inhabited distal sedimentary environments, although clearly not exclusively or even mostly.

Occupying more inland areas may have compensated for the supposed bias favoring the preservation of spinosaurid remains (where it is not observed) and this hypothesis has also other paleoecological implications. Although the proposition of extinction by the destruction of coastal habitats due to the increase of sea levels is specific for *Spinosaurus* and *Carcharodontosaurus* [22], one might extend this for their respective families as a whole. However, as shown above, carcharodontosaurids were more associated with terrestrial habitats, whilst spinosaurids were also present in more inland areas. So, the rise of sea level may not explain the extinction of these taxa during the early Late Cretaceous in Gondwana. Besides, the rise of sea level affects more strongly the inland fauna, as coastal environments migrate backwards into the continent, diminishing the habitable areas. Actually, the possible occurrences of these taxa in more young deposits located both inside and outside Gondwana (S1 Dataset) (e.g., [38, 48, 70]) further complicate this scenario, and different causes acting in different settings and moments may have been responsible for the extinction of these clades in each region in particular [29]. Once extinct, carcharodontosaurids and, possibly, spinosaurids were replaced by abelisaurids—whose fossil record is trackable until the Late Jurassic [71]—as the top predators of inland areas especially in Gondwana [28, 29]. Although megaraptoran and unenlagiid theropods are also thought to have played an important role as medium to large-size predators, we were not able to include them in our analysis due to the small number of occurrences.

However, we hope this will change in the near future due to the new findings that have been reported continuously [29, 72].

Final Remarks

Our study aimed to evaluate statistically the relationship between Abelisauridae, Carcharodontosauridae, and Spinosauridae and coastal and terrestrial paleoenvironments. In short, our results are: 1) spinosaurids were the taxon with the largest amount of statistical evidence showing it positively associated with coastal paleoenvironments; 2) abelisaurids and carcharodontosaurids were more associated with terrestrial paleoenvironments; 3) some of our results support the idea of spinosaurids also inhabiting inland areas, being comparable at least to carcharodontosaurids regarding the spatial distribution throughout this paleoenvironment; 4) abelisaurids could have been more numerous than carcharodontosaurids and, possibly, spinosaurids in inland habitats.

They also point to some practical details pervading this sort of analysis. Some fossil sites may represent the same paleoenvironment, and, in this case, they play a significant role in the statistical significance of some results. So, it is useful to address this sort of bias in order to have a more complete appreciation of the robustness of the positive or negative (if any) associations recovered. Chi-square tests implemented with the Monte Carlo analysis also seemed to have worked well, due to the coherence between the results found using it and those of Fisher's exact test, so they can be used in further analysis. Also, classifying occurrence in taphonomic categories enabled further refinements of the nature of the associations eventually found by our tests. Although these new approaches make some of our tests not exactly similar to the ones performed by Butler and Barrett [15], we consider our methodology as complementary to the latter.

We are aware that our results are valid within the assumptions stated here—from our conceptual framework to our geological and taxonomic assignments—and until new occurrences are included in our datasets, and, so, all inferences made by us can be seen as hypothesis for further tests. This will be necessary when new records change the absolute number of occurrences of the taphonomic categories or each paleoenvironment and we hope this happens as science is replicable in essence. Actually, this is already the case, as our deadline for gathering published references was December 31, 2014 and new discoveries have been reported since then (e.g., [21, 73, 74]). However, it is not one, two, or three new findings that will change the validity of our results, especially when they come from localities already recorded in our datasets for each clade and/or do not change the taphonomic categories in which a given occurrence was classified. Furthermore, our results can be reappraised also by changing some of our concepts, like those regarding problematic occurrences or taphonomic categories. One can also change the classification of the occurrences into the broad paleoenvironmental categories in case of disagreement with our propositions. In fact, new discoveries may be also responsible for this re-evaluation. Finally, a hypothesis is more robust when different approaches support it, thus the propositions here presented may be strengthened by new analyses with other methodological bases and data.

Supporting Information

S1 Appendix. Data collection through Fossilworks webpage.

(RTF)

S1 Dataset. List of occurrences.

(XLSX)

S1 File. Results of Chi-square and Fisher's exact tests, including residual analysis. The residual analysis is presented for each taxon and paleoenvironment as the numbers within the cells. (XLSX)

S1 Letter. Terms of image use. (PDF)

S1 Table. Summarization of the main features of each statistical test performed. (RTF)

Acknowledgments

We are indebted to Felipe Pinheiro and Alessandra Boos, who provided valuable comments on the early drafts of this manuscript. We also thank Ralf Kosma and an anonymous reviewer for the critical revisions and suggestions. Renata Cunha drew the artistic reconstruction of the Sao Khua Formation paleoenvironment and Christopher Scotese kindly provided access to the software Point Tracker. This research was partially funded by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq).

Author Contributions

Conceived and designed the experiments: MAFS MBL BLDH IAPO CLS. Performed the experiments: MAFS MBL BLDH IAPO. Analyzed the data: MAFS MBL BLDH IAPO. Contributed reagents/materials/analysis tools: BLDH IAPO. Wrote the paper: MAFS MBL BLDH IAPO CLS.

References

1. Benton MJ. Studying function and behavior in the fossil record. *PLoS Biol.* 2010; 8(3):e1000321. doi: [10.1371/journal.pbio.1000321](https://doi.org/10.1371/journal.pbio.1000321) PMID: [20209139](https://pubmed.ncbi.nlm.nih.gov/20209139/)
2. Witmer LM. The Extant Phylogenetic Bracket and the importance of reconstructing soft tissues in fossils. In: Thomason J, editor. *Functional Morphology in Vertebrate Paleontology*. New York: Cambridge University Press; 1995. p. 19–33.
3. Witmer LM, Chatterjee S, Franzosa J, Rowe TB. Neuroanatomy of flying reptiles and implications for flight, posture and behaviour. *Nature.* 2003; 425: 950–3. PMID: [14586467](https://pubmed.ncbi.nlm.nih.gov/14586467/)
4. Amiot R, Lécuyer C, Buffetaut E, Escarguel G, Fluteau F, Martineau F. Oxygen isotopes from biogenic apatites suggest widespread endothermy in Cretaceous dinosaurs. *Earth Planet Sci Lett.* 2006; 246: 41–54. doi: [10.1016/j.epsl.2006.04.018](https://doi.org/10.1016/j.epsl.2006.04.018)
5. Fricke HC, Pearson DA. Stable isotope evidence for changes in dietary niche partitioning among hadrosaurian and ceratopsian dinosaurs of the Hell Creek Formation, North Dakota. *Paleobiology.* 2008; 34: 534–52.
6. Witmer LM, Ridgely RC, Dufeu DL, Semones MC. Using CT to peer into the past: 3D visualization of the brain and ear regions of birds, crocodiles, and nonavian dinosaurs. In: Endo H, Frey R, editors. *Anatomical Imaging: Towards a New Morphology*. Springer; 2008. p. 67–87.
7. Amiot R, Buffetaut E, Lécuyer C, Wang X, Boudad L, Ding Z, et al. Oxygen isotope evidence for semi-aquatic habits among spinosaurid theropods. *Geology.* 2010; 38: 139–42. doi: [10.1130/G30402](https://doi.org/10.1130/G30402)
8. Grady JM, Enquist BJ, Dettweiler-Robinson E, Wright NA, Smith FA. Evidence for mesothermy in dinosaurs. *Science.* 2014; 344: 1268–72. doi: [10.1126/science.1253143](https://doi.org/10.1126/science.1253143) PMID: [24926017](https://pubmed.ncbi.nlm.nih.gov/24926017/)
9. Bakker RT. *The Dinosaur Heresies*. Citadel Press; 1986.
10. Coombs WP. Sauropod habits and habitats. *Palaeogeogr Palaeoclimatol Palaeoecol.* 1975; 17: 1–33.
11. Farlow JO, Pianka ER. Body size overlap, habitat partitioning and living space requirements of terrestrial vertebrate predators: implications for the paleoecology of large theropod dinosaurs. *Hist Biol.* 2003; 16: 21–40.
12. Sternberg CM. Relationships and habitat of *Troödon* and the Nodosaurus. *J Nat Hist.* 1933; 11: 231–5.

13. Horner JR. Upper Cretaceous dinosaurs from the Bearpaw Shale (marine) of south-central Montana, with a checklist of Upper Cretaceous remains from marine sediments in North America. *J Paleontol.* 1979; 53.
14. Lehman TM. Late Maastrichtian paleoenvironments and dinosaur biogeography in the western interior of North America. *Palaeogeogr Palaeoclimatol Palaeoecol.* 1987; 60: 189–217.
15. Butler RJ, Barrett PM. Palaeoenvironmental controls on the distribution of Cretaceous herbivorous dinosaurs. *Naturwissenschaften.* 2008; 95: 1027–32. doi: [10.1007/s00114-008-0417-5](https://doi.org/10.1007/s00114-008-0417-5) PMID: [18581087](https://pubmed.ncbi.nlm.nih.gov/18581087/)
16. Charig AJ, Milner AC. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bull Nat Hist Mus Lond Geol.* 1997; 53: 11–70.
17. Sereno PC, Beck AL, Dutheil DB, Gado B, Larsson HCE, Lyon GH, et al. A long-snouted predatory dinosaur from Africa and the evolution of spinosaurids. *Science.* 1998; 282: 1298–302. PMID: [9812890](https://pubmed.ncbi.nlm.nih.gov/9812890/)
18. Dal Sasso C, Maganuco S, Buffetaut E, Mendez MA. New information on the skull of the enigmatic theropod *Spinosaurus*, with remarks on its size and affinities. *J Vertebr Paleontol.* 2005; 25: 888–96.
19. Rayfield EJ, Milner A, Xuan VB, Young PG. Functional morphology of spinosaur ‘crocodile-mimic’ dinosaurs. *J Vertebr Paleontol.* 2007; 27: 892–901.
20. Ibrahim N, Sereno PC, Dal Sasso C, Maganuco S, Fabbri M, Martill D, et al. Semiaquatic adaptations in a giant predatory dinosaur. *Science.* 2014; 345: 1613–6. doi: [10.1126/science.1258750](https://doi.org/10.1126/science.1258750) PMID: [25213375](https://pubmed.ncbi.nlm.nih.gov/25213375/)
21. Benyoucef M, Lång E, Cavin L, Mebarki K, Adaci M, Bensalah M. Overabundance of piscivorous dinosaurs (Theropoda: Spinosauridae) in the mid-Cretaceous of North Africa: The Algerian dilemma. *Cretaceous Res.* 2015; 55: 44–55.
22. Paterson N, director. Planet Dinosaur [TV series]; 2011. Jellyfish Pictures.
23. Canudo JI, Ruiz-Omeñaca JI. Los restos directos de dinosaurios terópodos (excluyendo Aves) en España. In: Lorente FP, Molina MMR, Carrera PV, coordinators. *Dinosaurios y otros reptiles mesozoicos en España.* Universidad de La Rioja; 2003. p. 347–73.
24. Sereno PC, Wilson JA, Conrad JL. New dinosaurs link southern landmasses in the Mid-Cretaceous. *Proc R Soc Lond B Biol Sci.* 2004; 271: 1325–30. doi: [10.1098/rspb.2004.2692](https://doi.org/10.1098/rspb.2004.2692)
25. Medeiros MA, Lindoso RM, Mendes ID, Carvalho IS. The Cretaceous (Cenomanian) continental record of the Laje do Coringa flagstone (Alcântara Formation), northeastern South America. *J South Am Earth Sci.* 2014; 53: 50–8.
26. Mo J, Huang C, Xie S, Buffetaut E. A megatheropod tooth from the Early Cretaceous of Fusui, Guangxi, Southern China. *Acta Geol Sin.* 2014; 88: 6–12. doi: [10.1111/1755-6724.12177](https://doi.org/10.1111/1755-6724.12177)
27. Novas FE, Valais S, Vickers-Rich P, Rich T. A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. *Naturwissenschaften.* 2005; 92: 226–30. doi: [10.1007/s00114-005-0623-3](https://doi.org/10.1007/s00114-005-0623-3) PMID: [15834691](https://pubmed.ncbi.nlm.nih.gov/15834691/)
28. Novas FE. Evolution of South American Dinosaurs. In: Carvalho IS, Cassab RCT, Schwanke C, Carvalho MA, Fernandes ACS, Rodrigues MAC, et al., editors. *Paleontologia: Cenários da Vida.* Vol. 1. Rio de Janeiro: Interciência; 2007. p. 333–53.
29. Novas FE, Agnolín FL, Ezcurra MD, Porfiri J, Canale JI. Evolution of the carnivorous dinosaurs during the Cretaceous: The evidence from Patagonia. *Cretaceous Res.* 2013; 45: 174–215.
30. Zanno LE, Makovicky PJ. Neovenatorid theropods are apex predators in the Late Cretaceous of North America. *Nat Commun.* 2013; 4: 1–9. doi: [10.1038/ncomms3827](https://doi.org/10.1038/ncomms3827)
31. Weishampel DB, Dodson P, Osmolska H. *The Dinosauria.* 2nd Ed. ed. Berkley: University of California; 2004.
32. Scotese CR. *The PALEOMAP Project paleoatlas for ArcGIS.* Arlington, Texas.: PALEOMAP Project; 2008.
33. Behrensmeyer AK. Transport/hydrodynamics of bones. In: Briggs DEG and Crowther PR, editors. *Palaeobiology: A Synthesis.* Oxford: Blackwell Scientific Publications, 1990. pp. 232–235.
34. Behrensmeyer AK. Terrestrial vertebrate accumulations. In: Allison P and Briggs DEG, editors. *Taphonomy: Releasing the Data Locked in the Fossil Record.* New York: Plenum, 1991. pp. 291–335.
35. Behrensmeyer AK. Bones through time: The importance of biotic versus abiotic taphonomic processes in the vertebrate fossil record. In: De Renzi M, Alonso MPV, Belinchon M, Penalver E, Montoya P, editors. *Current Topics on Taphonomy and Fossilization.* Valencia: Ayuntamiento de Valencia, 2002. pp. 297–304.
36. Buffetaut E. An early spinosaurid dinosaur from the Late Jurassic of Tendaguru (Tanzania) and the evolution of the spinosaurid dentition. *ORYCTOS.* 2011; 10: 1–8.

37. Carrano MT, Sampson SD. The Phylogeny of Ceratosauria (Dinosauria: Theropoda). *J Syst Palaeontol*. 2008; 6: 183–236. doi: [10.1017/S1477201907002246](https://doi.org/10.1017/S1477201907002246)
38. Carrano MT, Benson RBJ, Sampson SD. The phylogeny of Tetanurae (Dinosauria: Theropoda). *J Syst Palaeontol*. 2012; 10: 211–300. doi: [10.1080/14772019.2011.630927](https://doi.org/10.1080/14772019.2011.630927)
39. Tortosa T, Buffetaut E, Vialle N, Y D, Turini E, Cheylan G. A new abelisaurid dinosaur from the Late Cretaceous of southern France: Palaeobiogeographical implications. *Ann Paleontol*. 2014; 100: 63–86.
40. Astibia H, Buffetaut E, Buscalioni AD, Cappetta H, Corral C, Estes R, et al. The fossil vertebrates from the Lano (Basque Country, Spain); new evidence on the composition and affinities of the Late Cretaceous continental faunas of Europe. *Terra Nova*. 1990; 2: 460–6.
41. Churcher CS, Russell DA. Terrestrial vertebrates from Campanians strata in Wadi el-Gedid (Kharga and Dakleh Oases), western desert of Egypt. *J Vertebr Paleontol*. 1992; 12(3, suppl): 23A.
42. Churcher CS, De Iuliis G. A new species of *Protopterus* and a revision of *Ceratodus humei* (Dipnoi: Ceratodontiformes) from the Late Cretaceous Mut Formation of Eastern Dakhleh Oasis, western desert of Egypt. *Palaeontology*. 2001; 44: 305–23.
43. Buffetaut E. Late Cretaceous vertebrates from the Saint-Chinian area (Southern France): a review of previous research and an update on recent finds. *Acta Pal Rom*. 2005; 5: 39–48.
44. Buffetaut E, Suteethorn V, Le Loeuff J, Khansubha S, Tong H, Wongko K. The Dinosaur Fauna from the Khok Kruat Formation (Early Cretaceous) of Thailand. *International Conference on Geology, Geo-technology and Mineral Resources of Indochina (GEOINDO 2005)*; Khon Kaen, Thailand. 2005. p. 575–81.
45. Dalla-Vecchia FM. Second record of a site with dinosaur skeletal remains in Libya (Northern Africa). *Natura Nascosta*. 1995; 11: 16–9.
46. Buffetaut E, Escuillié F, Pohl B. First theropod dinosaur from the Maastrichtian phosphates of Morocco. *Current Research in Vertebrate Palaeontology, 3rd Annual Meeting of the European Association of Vertebrate Palaeontologists (EAVP)*; Darmstadt, Germany. 2005. p. 3–8.
47. Smith JB, Lamanna MC. An abelisaurid from the Late Cretaceous of Egypt: implications for theropod biogeography. *Naturwissenschaften*. 2006; 93: 242–5. doi: [10.1007/s00114-006-0092-3](https://doi.org/10.1007/s00114-006-0092-3) PMID: [16541232](https://pubmed.ncbi.nlm.nih.gov/16541232/)
48. Hone DW, Xu X, Wang D-Y. A probable Baryonychine (Theropoda: Spinosauridae) tooth from the Upper Cretaceous of Henan Province, China. *Vertebrat Palasiatic*. 2010; 48: 19–26.
49. R Development Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2008. ISBN 3-900051-07-0, Available: <http://www.R-project.org>.
50. Gotelli NJ, Ellison AM. *Princípios de Estatística em Ecologia*. Porto Alegre: Artmed Editora; 2010.
51. Hope ACA. A simplified Monte Carlo significance test procedure. *Journal of the Royal Statistical Society. Series B (Methodological)*. *J R Stat Soc Series B Stat Methodol*. 1968; 30: 582–598.
52. Robert PC, Casella G. *Introducing Monte Carlo Methods with R*. Springer Science & Business Media; 2010.
53. Patefield WM. Algorithm AS159. An efficient method of generating $r \times c$ tables with given row and column totals. *Appl. Stat*. 1981; 30: 91–97.
54. Currie PJ, Eberth DA. On gregarious behavior in *Albertasaurus*. *Can J Earth Sci*. 2010; 47: 1277–89.
55. Carbone C, Turvey ST, Bielby J. Intra-guild competition and its implications for one of the biggest terrestrial predators, *Tyrannosaurus rex*. *Proc R Soc Lond B Biol Sci*. 2011; 278: 2682–90. doi: [10.1098/rspb.2010.2497](https://doi.org/10.1098/rspb.2010.2497)
56. Gates TA. The Late Jurassic Cleveland-Lloyd Dinosaur Quarry as a drought-induced assemblage. *PALAIOS*. 2005; 20: 363–75. doi: [10.2110/palo.2003.p03-22](https://doi.org/10.2110/palo.2003.p03-22)
57. Medeiros MA, Freire PC, Pereira AA, Santos RAB, Lindoso RM, Coêlho AFA, et al. Another African dinosaur recorded in the Eocenomanian of Brazil and a revision of the Laje do Coringa site. In: Carvalho IS, Cassab RCT, Schwanke C, Carvalho MA, Fernandes ACS, Rodrigues MAC, et al., editors. *Paleontologia: Cenários de Vida*. Vol. 1. Rio de Janeiro: Editora Interciência; 2007. p. 413–23.
58. Kellner AWA, Azevedo SAK, Machado EB, Carvalho LB, Henriques DDR. A new dinosaur (Theropoda, Spinosauridae) from the Cretaceous (Cenomanian) Alcântara Formation, Cajual Island, Brazil. *An Acad Bras Cienc*. 2011; 83: 99–108. PMID: [21437377](https://pubmed.ncbi.nlm.nih.gov/21437377/)
59. Kellner AWA, Campos DA. First Early Cretaceous theropod dinosaur from Brazil with comments on Spinosauridae. *N Jahrb Geol Paläontol A*. 1996; 199: 151–66.
60. Sues HD-, Frey E, Martill D, Scott DM. *Irritator challengerii*, a spinosaurid (Dinosauria: Theropoda) from the Lower Cretaceous of Brazil. *J Vertebr Paleontol*. 2002; 22: 535–47.

61. Bittencourt JS, Kellner AWA. On a sequence of sacrocaudal theropod dinosaur vertebrae from the Lower Cretaceous Santana Formation, northeastern Brazil. *Arq Mus Nac.* 2004; 62: 309–20.
62. Buffetaut E, Martill D, Escuillié F. Pterosaurs as part of a spinosaur diet. *Nature.* 2004; 430: 33. PMID: [15229562](#)
63. Machado EB, Kellner AWA. On a supposed ornithischian dinosaur from the Santa Formation, Araripe Basin, Brazil. In: Carvalho IS, Cassab RCT, Schwanke C, Carvalho MA, Fernandes ACS, Rodrigues MAC, et al., editors. *Paleontologia: Cenários de Vida.* Vol. 1. Rio de Janeiro: Editora Interciência; 2007. p. 291–9.
64. Machado EB, Kellner AWA. An overview of the Spinosauridae (Dinosauria, Theropoda) with comments on the Brazilian material. *J Vertebr Paleontol.* 2008; 28(3, suppl): 109A.
65. Allain R, Xaisanavong T, Richir P, Khentavong B. The first definitive Asian spinosaurid (Dinosauria: Theropoda) from the early cretaceous of Laos. *Naturwissenschaften.* 2012; 99: 369–77. doi: [10.1007/s00114-012-0911-7](#) PMID: [22528021](#)
66. Buffetaut E, Suteethorn V. A sauropod skeleton associated with theropod teeth in the Upper Jurassic of Thailand: remarks on the taphonomic and palaeoecological significance of such associations. *Palaeogeogr Palaeoclimatol Palaeoecol.* 1989; 73: 77–83.
67. Buffetaut E, Suteethorn V. The dinosaur fauna of the Sao Khua Formation of Thailand and the beginning of the Cretaceous radiation of dinosaurs in Asia. *Palaeogeogr Palaeoclimatol Palaeoecol.* 1999; 150: 13–23.
68. Therrien F, Henderson DM, Ruff CB. Bite me: Biomechanical models of theropod mandibles and implications for feeding behavior. In: Carpenter K, editor. *The Carnivorous Dinosaurs.* Bloomington: Indiana University Press; 2005. p. 179–237.
69. Farlow JO, Holtz TR. The fossil record of predation in dinosaurs. In: Kowalwski M, Kelley PH, editors. *The Fossil Record of Predation.* The Paleontological Society; 2002. p. 251–66.
70. Canudo JI, Filippi L, Salgado L, Garrido A, Cerda IA, García R, et al. Dientes de terópodos asociados con una carcasa de saurópodo en el Cretácico Superior (Formación Plottier) de Rincón de los Sauces (Patagonia, Argentina). In: Hurtado PH, Baldor FTF, editors. *IV Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno; Salas de los Infantes, Burgos, Spain; 2009.* p. 321–30.
71. Hendrickx C, Mateus O. Abelisauridae (Dinosauria: Theropoda) from the Late Jurassic of Portugal and dentition-based phylogeny as a contribution for the identification of isolated theropod teeth. *Zootaxa.* 2014; 3759: 1–74. doi: [10.11646/zootaxa.3759.1.1](#) PMID: [24869965](#)
72. Porfiri J, Novas FE, Calvo JO, Agnolín FL, Ezcurra MD, Cerda IA. Juvenile specimen of Megaraptor (Dinosauria, Theropoda) sheds light about tyrannosauroid radiation. *Cretaceous Res.* 2014; 51: 35–55.
73. Gianechini FA, Apesteguía S, Landini W, Finotti F, Valieri RJ, Zandonai F. New abelisaurid remains from the Anacleto Formation (Upper Cretaceous), Patagonia, Argentina. *Cretaceous Res.* 2015; 54: 1–16.
74. Serrano-Martínez A., et al., New theropod remains from the Tiourarén Formation (?Middle Jurassic, Niger) and their bearing on the dental evolution in basal tetanurans. *Proc Geol Assoc.* 2015; 126: 107–118.


PARTE 2

11. Trabalhos Complementares

11.1 Artigos

Pinheiro, F.L.; França, M.A.G.; LACERDA, M.B.; Butler, R.J. & Schultz, C.L. 2016. Na exceptional fóssil skull from South America and the origins of the archosauriform radiation. **Scientific Reports**, v. 6, p. 22817.

SCIENTIFIC REPORTS



OPEN

An exceptional fossil skull from South America and the origins of the archosauriform radiation

Felipe L. Pinheiro¹, Marco A. G. França², Marcel B. Lacerda³, Richard J. Butler⁴ & Cesar L. Schultz³

Received: 18 December 2015

Accepted: 22 February 2016

Published: 11 March 2016

Birds, dinosaurs, crocodylians, pterosaurs and their close relatives form the highly diverse clade Archosauriformes. Archosauriforms have a deep evolutionary history, originating in the late Permian, prior to the end-Permian mass extinction, and radiating in the Triassic to dominate Mesozoic ecosystems. However, the origins of this clade and its extraordinarily successful body plan remain obscure. Here, we describe an exceptionally preserved fossil skull from the Lower Triassic of Brazil, representing a new species, *Teyujagua paradoxa*, transitional in morphology between archosauriforms and more primitive reptiles. This skull reveals for the first time the mosaic assembly of key features of the archosauriform skull, including the antorbital and mandibular fenestrae, serrated teeth, and closed lower temporal bar. Phylogenetic analysis recovers *Teyujagua* as the sister taxon to Archosauriformes, and is congruent with a two-phase model of early archosauriform evolution, in response to two mass extinctions occurring at the end of the Guadalupian and the Permian.

Birds, dinosaurs, crocodylians, and pterosaurs all belong to the clade Archosauriformes¹, an extraordinarily diverse group that dominated terrestrial tetrapod faunas worldwide for nearly the entire Mesozoic Era^{2–4}, around 175 million years, and plays a major role in the modern biota, with birds comprising around a third of extant tetrapod biodiversity^{5,6}. The Permian origin of the clade and its major diversification during the Triassic following the end-Permian mass extinction event were events of exceptional significance that fundamentally reshaped ecosystems on land^{2,7–11}. Several classic anatomical features relating to carnivorous adaptations and cranial pneumaticity characterize the archosauriform skull^{1,8,11}. However, the acquisition of this highly successful cranial morphology from more primitive reptiles is poorly understood due to the patchy and fragmentary nature of the early archosauriform fossil record, and the absence of key transitional taxa showing intermediate morphologies^{10,11}.

The oldest known archosauriforms consist of rare and highly fragmentary remains from the Permian of Russia¹¹. Following the end-Permian mass extinction, c. 252 million years ago, fossils of archosauriforms and their nearest relatives become more common and globally distributed, but articulated specimens remain almost unknown outside a small number of well-sampled areas in South Africa and China^{8,10–12}. Here, we report a new, exceptionally preserved skull from the Triassic of Brazil, which is the most complete tetrapod fossil yet discovered from the Lower Triassic of South America. This skull represents a previously unknown species that is the sister taxon to Archosauriformes and which fills a major morphological gap in understanding of early archosauriform evolution.

Results

Systematic palaeontology. Diapsida Osborn, 1903 *sensu* Laurin, 1991

Sauria McCartney, 1802 *sensu* Gauthier *et al.* 1988

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

Teyujagua paradoxa gen. et sp. nov.

Etymology. Genus named after Teyú Yaguá, one of the seven legendary beasts in the mythology of the Guarani ethnic group, who occupied a large territory of central east South America, including the type locality

¹Laboratório de Paleobiologia, Universidade Federal do Pampa, São Gabriel, Brazil. ²Laboratório de Paleontologia e Evolução de Petrolina, Universidade Federal do Vale do São Francisco, Petrolina, Brazil. ³Laboratório de Paleontologia de Vertebrados, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil. ⁴School of Geography, Earth & Environmental Sciences, University of Birmingham, Birmingham, UK. Correspondence and requests for materials should be addressed to F.L.P. (email: felipepinheiro@unipampa.edu.br)

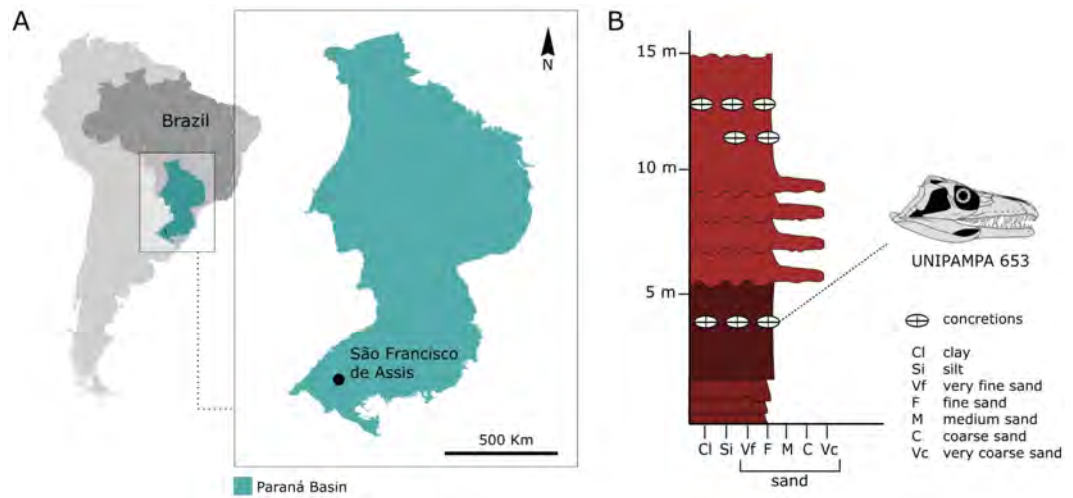


Figure 1. Type locality of *Teyujagua paradoxa*. (A), geographic map with the location of the Paraná Basin within Brazil and *Teyujagua* type location; (B), simplified stratigraphic profile of the outcrop, showing the level where *Teyujagua* was found. Area map was modified from Strapasson *et al.*³⁰; stratigraphic profile modified from Da Rosa, *et al.*¹³.

of the new species. Teyú Yaguá, literally meaning ‘fierce lizard’, is commonly represented as a dog-headed lizard. Species name derived from *paradoxa*, Greek meaning ‘paradoxical’, ‘unexpected’, owing to its unusual combination of plesiomorphic and derived characters.

Holotype. UNIPAMPA 653, an almost complete, well-preserved skull with associated cervical vertebrae.

Type locality and age. Exposure of the Sanga do Cabral Formation¹³, Paraná Basin, São Francisco de Assis municipality, Rio Grande do Sul State, Southern Brazil (29°36′56″S, 55°03′10″W) (Fig. 1). An Induan to early Olenekian age (Lower Triassic) is inferred for the Sanga do Cabral Formation based on the presence of the parareptile *Procolophon trigoniceps*, and comparisons with the coeval *Lystrosaurus* Assemblage Zone of the South African Karoo^{13–15}. *Teyujagua* was found in close association with archosauromorph vertebrae, cranial and postcranial remains of *P. trigoniceps*, temnospondyl amphibians and as-yet-identified tetrapod bones.

Diagnosis. Archosauromorph with the following unique character combination: confluent, dorsally positioned external nares; maxilla participating in orbital margin; antorbital fenestra absent; trapezoidal infratemporal fenestra with incomplete lower temporal bar; teeth serrated on distal margins; surangular bearing a lateral shelf; external mandibular fenestrae present and positioned beneath the orbits when the lower jaw is in occlusion (autapomorphic for *Teyujagua*).

Description. The 115 mm long skull is well preserved and almost complete, and is associated with four cervical vertebrae (Figs 2 and 3; Supplementary Fig. 1). The occipital and palatal regions and parts of the left side of the skull are still covered by the enclosing matrix, but were partially examined using computed tomography (CT) (Supplementary Fig. 2).

The snout is relatively broad and flattened, with dorsally positioned, confluent external nares. Dorsal confluent nares are an unusual condition that is often linked to aquatic or semi-aquatic habits, being present in many crocodyliforms, although they also occur in the terrestrial rhynchosaurs¹⁶, which are near relatives of early archosauriforms. The nasals contribute substantially to the skull table, followed by short and broad frontals, and parietals that bear a small pineal foramen. Although the loss of the pineal foramen has been identified as a synapomorphy of archosauriforms⁸, this structure is variably absent or present in the early archosauriform *Proterosuchus fergusi*¹² and the close archosauriform relative *Prolacerta broomi*¹⁷. The prefrontals and sculptured postfrontals almost exclude the frontals from the dorsal orbital margin, whereas the maxilla participates in the anteroventral orbital margin. The orbits face anterolaterally, and were probably capable of at least limited binocular vision. The slender supratemporals are visible in dorsal view.

The premaxillae have well-developed, slender posterodorsal processes but lack anterodorsal processes, as a result of the confluent nares. An antorbital fossa/fenestra is absent from the maxillae (Fig. 3C). The jugals are triradiate, with main bodies ornamented with longitudinal ridges. The posterior jugal process tapers distally and does not reach the quadratojugal (Fig. 3B). The trapezoidal infratemporal openings were ventrally bordered by incomplete lower temporal bars, similar to the condition in non-archosauriform archosauromorphs such as *Prolacerta*, *Proterosuchus* and *Mesosuchus*^{16,17}. By contrast, the lower temporal bar is complete in nearly all archosauriforms, although this character is variable in *Proterosuchus fergusi*¹².

On the lower jaw, the surangulars bear lateral shelves that match closely with the ventral margins of the posterior processes of the jugals. The external mandibular fenestra is present, unusually anteriorly positioned, and ventrally bordered by a slender ascending process of the angular. The posterior contacts of the dentaries with

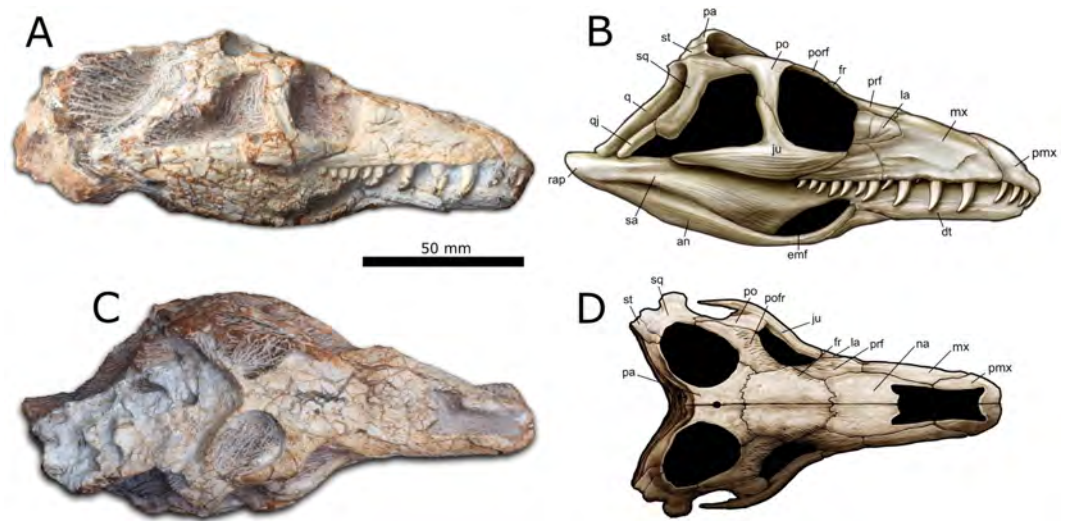


Figure 2. *Teyujagua paradoxa* holotype (UNIPAMPA 653). Photographs and interpretative drawings in right lateral (A,B) and dorsal (C,D) views. Abbreviations: an, angular; dt, dentary; emf, external mandibular fenestra; fr, frontal; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; pa, parietal; pmx, premaxilla; po, postorbital; pofr, postfrontal; prf, prefrontal; q, quadrate; qj, quadratojugal; rap, retroarticular process; sa, surangular; sq, squamosal; st, supratemporal. Artwork by J. Anderson.

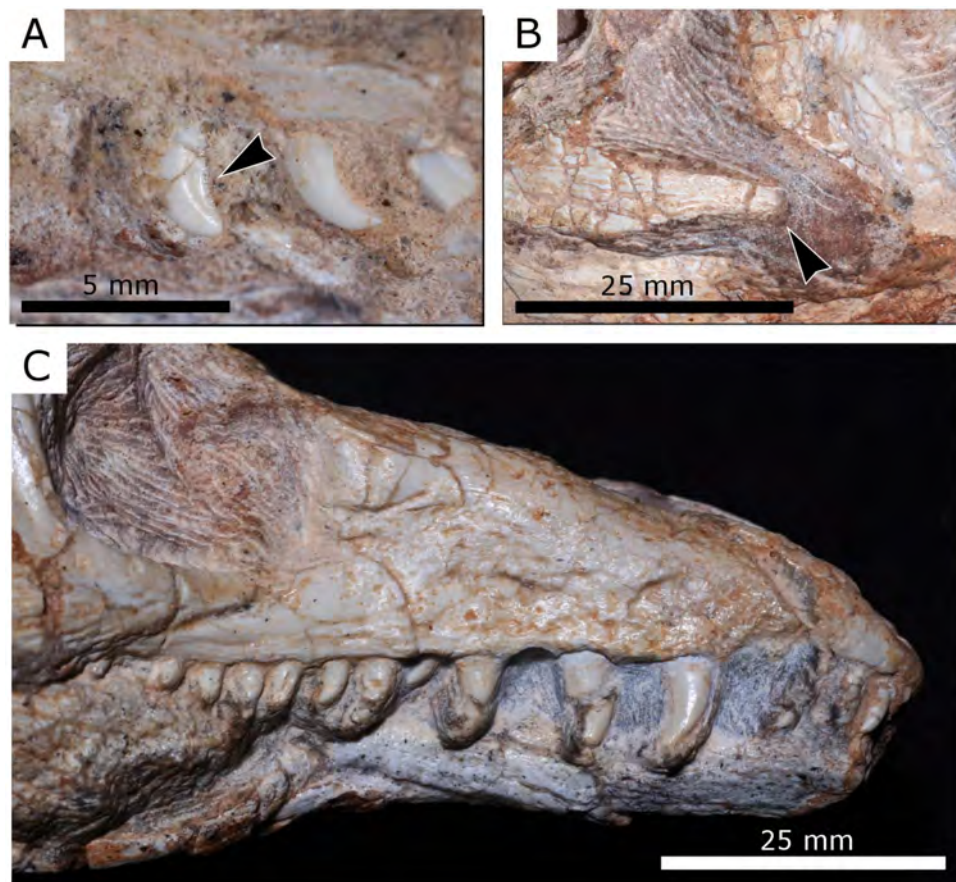


Figure 3. Close ups of the skull of *Teyujagua paradoxa* (UNIPAMPA 653). (A), posterior left maxillary teeth, showing serrations; (B), posterior process of the left jugal; (C), rostrum.

the post-dentary bones cannot be identified. However, CT scans reveal that the dentary tooth row ends slightly anterior to the maxillary one (Supplementary Fig. 2).

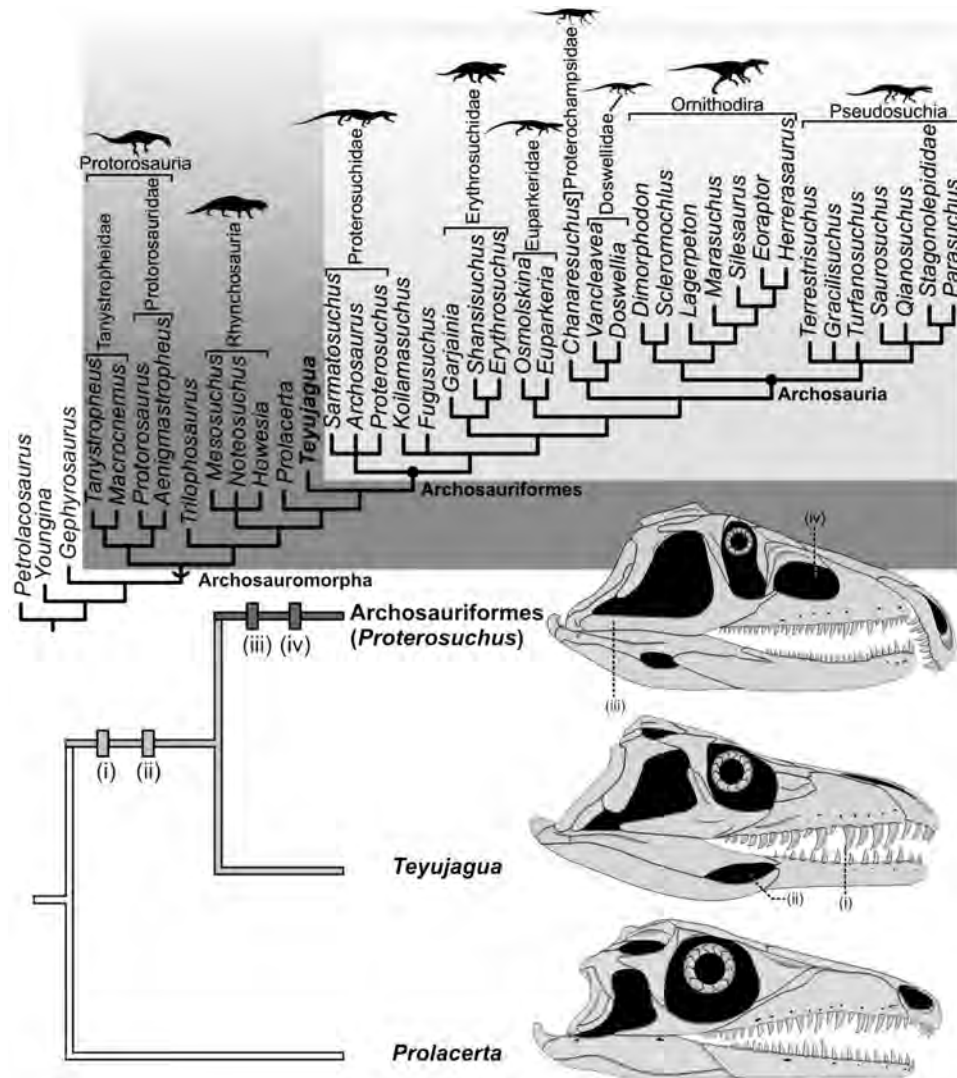


Figure 4. Archosauromorph phylogeny showing the recovered position of *Teyujagua*. Top: strict consensus tree summarising phylogenetic results. Bottom: sequence of acquisition of archosauriform features among the archosauromorphs *Prolacerta*, *Teyujagua* and the basal archosauriform *Proterosuchus*. (i) serrated teeth; (ii) external mandibular fenestra; (iii) closed lower temporal bar; (iv) antorbital fenestra. *Prolacerta* and *Proterosuchus* skulls redrawn from an artwork by M. Ezcurra. Not to scale.

Each premaxilla possesses four teeth and the maxilla had a maximum of 15. The teeth bear serrations on their distal margins only, as in proterosuchid archosauriforms, but differing from the condition in more derived archosauriforms in which serrations are usually present on both mesial and distal margins¹⁸ (Fig. 3A). Pronounced heterodonty is evident, with small premaxillary teeth followed by considerably larger anterior maxillary teeth. The teeth are labiolingually compressed, held in well-defined sockets, and not firmly associated with surrounding alveolar bone. Implementation therefore appears to be thecodont, rather than ankylothecondont as in many of the earliest archosauriforms¹⁹.

Phylogeny. Our novel cladistic analysis recovered two most parsimonious trees with 872 steps (Supplementary Fig. 3). The strict consensus of these topologies (Fig. 4) positions *Teyujagua* as the sister taxon of Archosauriformes, a position previously occupied by the Lower Triassic *Prolacerta*^{8,11,17}. The clade *Teyujagua* plus Archosauriformes is supported by five synapomorphies: (i) Serrations on tooth crowns; (ii) trapezoidal shape of the infratemporal fenestrae; (iii) frontal-parietal suture at right angle to parasagittal plane; (iv) mandible bearing an external fenestra; (v) lateral shelf on surangular.

Archosauriformes includes the traditional basal groups, such as Proterosuchidae and Erythrosuchidae, together with the crown group Archosauria. Proterosuchidae consists of *Proterosuchus*, *Archosaurus* and *Sarmatosuchus*, although the relationships within this clade are unresolved. *Fugusuchus*, *Koilamasuchus* and the clade *Erythrosuchus* + Archosauria also have unresolved positions relative to one another. The clade *Chanaresuchus* + (*Doswellia* + *Vancleavea*) is recovered as the sister group of Archosauria, and Euparkeriidae is the sister group of this

less inclusive clade. As such, four recognised groups compose non-archosaurian Archosauriformes: Proterosuchidae, Erythrosuchidae, Euparkeriidae and the clade including *Chanaresuchus* + (*Doswellia* + *Vancleavea*).

Another analysis was performed including the poorly known *Eorasaurus*, which may be the oldest known archosauriform. The analysis recovered 14 most parsimonious trees with 873 steps. Most of the recovered topologies are similar to those recovered in the first phylogenetic analysis. The consensus tree differs in positioning *Eorasaurus* in an unresolved polytomy together with *Koilamasuchus*, *Fugusuchus*, erythrosuchid taxa, and a clade composed of Euparkeriidae + Proterochampsia + Archosauria (Supplementary Fig. 5). This provides additional support for the archosauriform affinities of *Eorasaurus*, and the existence of archosauriform ghost lineages extending into at least the middle Wuchiapingian¹¹.

Discussion

Teyujagua presents an unexpected combination of basal archosauromorph and typical archosauriform features. For example, *Teyujagua* resembles basal archosauromorphs in lacking an antorbital fenestra and retaining open lower temporal bars^{1,8,11,20}. However, *Teyujagua* possesses external mandibular fenestrae and serrated teeth, features previously considered unique to Archosauriformes^{8,11}. Comparisons between *Prolacerta*, *Teyujagua* and early archosauriforms demonstrate for the first time that these key anatomical features of Archosauriformes were acquired in a mosaic fashion (Fig. 4). Serrated teeth and external mandibular fenestrae, important features underpinning the evolution of large, powerful hypercarnivores, were acquired before a closed lower temporal bar and the antorbital opening. Thus, key dietary adaptations emerged in the early history of the Archosauriformes before the onset of the major skull pneumatization that played an important role in the group's later evolutionary history²¹.

The oldest known unambiguous archosauriform is *Archosaurus rossicus*, from the uppermost Permian of Russia^{11,19}. However, the late Guadalupian to early Lopingian age of the possible archosauriform *Eorasaurus*¹¹ suggests that the clade had a substantial evolutionary history before the end-Permian mass extinction. Although hampered by the scarcity of Permian archosauromorph remains, the results of our phylogenetic analysis are congruent with two major pulses of opportunistic radiation experienced by early archosauriforms and close relatives such as *Teyujagua*. The first of these would be a phylogenetic diversification during the Lopingian, coincident with the recovery from the end-Guadalupian mass extinction^{22,23} (Fig. 5), perhaps as disaster taxa filling empty niches of small piscivores and predators. The rarity of archosauriform body fossils in Permian strata suggests that the clade formed a minor component in latest Palaeozoic faunas, when terrestrial trophic chains had therapsids as the main higher-level predators^{7,22,24}. The end-Permian extinction disrupted these food chains, and during the faunal recovery the Archosauriformes underwent a major increase in abundance, size and species richness^{7,19,22,24}, becoming the main terrestrial predators^{7,22,24}, and later expanding to also dominate large herbivorous niches^{8,9}. The ichnological record provides additional support for this two-phase radiation²⁵. The discovery of *Teyujagua* thus helps to clarify early archosauriform evolution, allowing a better understanding of how this clade rose to dominate Mesozoic faunas and shape the modern biota.

Methods

Type horizon and locality. The type locality of *Teyujagua paradoxa* is a known fossil site that has been thoroughly described by Da Rosa *et al.*¹³. The locality is informally known as Bica São Tomé and is situated about 10 km east of São Francisco de Assis municipality, Rio Grande do Sul State, Southern Brazil. *Teyujagua* was found in one of the five outcrops that compose the Bica São Tomé (outcrop 5 of Da Rosa *et al.*¹³). The outcrop consists of a 15 m thick section with a predominance of fine reddish sandstones, intercalated with coarse sandstones and intraformational conglomerates, this being a typical lithology of the Sanga do Cabral Formation¹³. The *Teyujagua* holotype was found in a layer rich in calcareous concretions, about 5 m from the baseline of the outcrop. The fossil assemblage so far reported for the Bica São Tomé site is dominated by procolophonoid cranial and postcranial material, some of which is referable to *Procolophon trigoniceps*. Less commonly, the site has produced temnospondyl cranial and postcranial fragments, incomplete long bones attributable to Cynodontia and incomplete archosauromorph vertebrae. Sanga do Cabral Formation fossils are typically found in association with the intraformational conglomerates and, as a result, show signs of intense reworking and fragmentation. The holotype of *Teyujagua paradoxa* is the most complete vertebrate specimen collected in this sedimentary unit to date. An Induan to early Olenekian (Lower Triassic) age is inferred for the Sanga do Cabral Formation based on the presence of *Procolophon trigoniceps*, which is restricted to the upper Katberg Formation (*Lystrosaurus* Assemblage Zone) in the Karoo Basin of South Africa^{13–15}. *Procolophon trigoniceps* is the only taxon from the Sanga do Cabral Formation to provide biostratigraphic correlations with other Lower Triassic sedimentary units. Notably, in the South African Karoo Basin the oldest remains of *Procolophon trigoniceps* are found 116 m above the Permian–Triassic boundary²⁴.

Phylogenetic analysis. In order to test the phylogenetic position of *Teyujagua*, a novel data matrix was assembled including taxa and morphological characters from two previous studies that aimed to address the phylogeny of Archosauromorpha and that of basal archosauriforms outside Archosauria^{11,26}. In total, the dataset included 44 operational taxonomic units (OTUs) and 252 morphological characters (see the supplementary material for full details).

The analysis was performed using TNT version 1.1²⁷. *Petrolacosaurus* was considered the outgroup taxon and all characters were treated with equal weight. Of the 252 characters, 205 are binary and 47 are multistate. The following 35 multistate characters were *a priori* considered as ordered: 18, 19, 20, 21, 26, 33, 39, 42, 43, 55, 62, 64, 65, 69, 74, 81, 103, 113, 118, 127, 144, 148, 149, 155, 159, 165, 167, 170, 173, 177, 193, 206, 218, 231, 238.

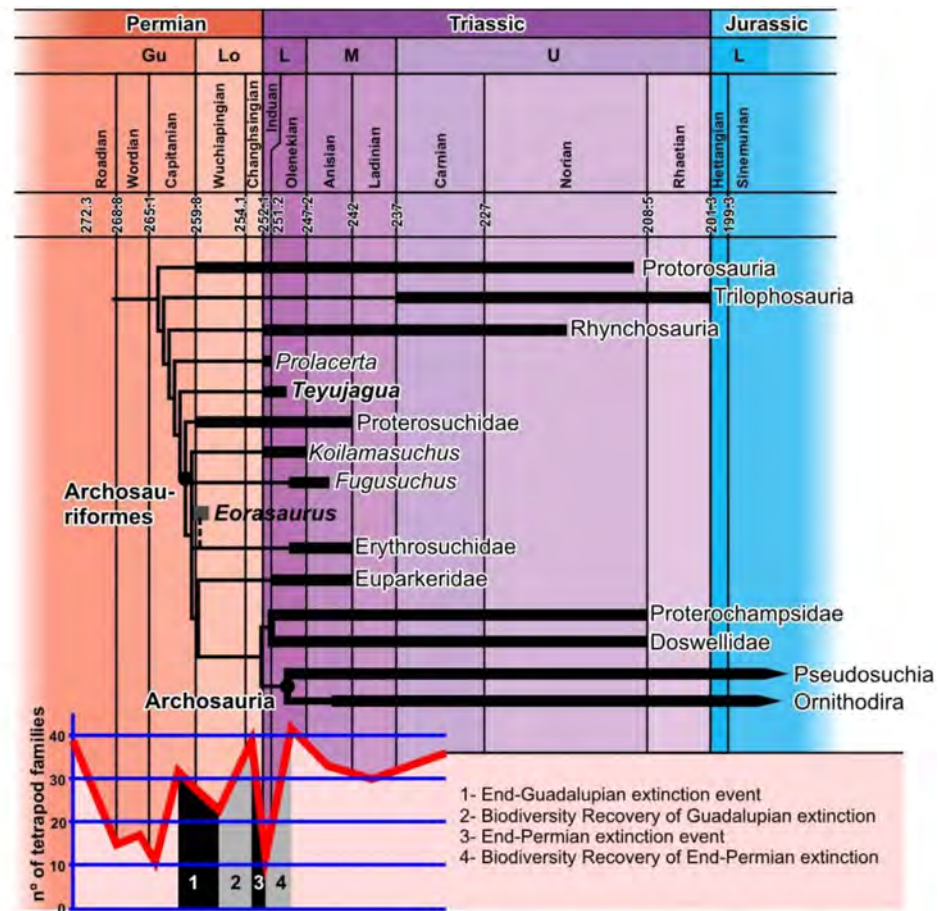


Figure 5. Simplified temporally calibrated phylogeny of Archosauriformes and close relatives (Archosauromorpha).

A substantial diversification of archosauriforms and close relatives occurred in the late Permian (Lopingian), following the end-Guadalupian mass extinction, with a second radiation immediately following the end-Permian crisis. Diversity curve from Sahney and Benton²².

The analysis consisted of a heuristic search of 1000 replicates using random addition sequences followed by tree-bisection-reconnection (TBR) branch swapping, retaining ten trees per replicate, with branches not supported by at least one synapomorphy collapsed following the search. If some replications overflowed during the first round of analysis, a traditional search was again employed, this time using trees from RAM. Bremer and Bootstrap supports were obtained following the analysis^{28,29} (Supplementary Fig. 4).

References

- Gauthier, J. A. Saurischian monophyly and the origin of birds. *Mem. Calif. Acad. Sci.* **8**, 1–55 (1986).
- Brusatte, S. L., Benton, M. J., Ruta, M. & Lloyd, G. T. Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. *Science* **321**, 1485–1488 (2008).
- Claessens, L. P. A. M., O'Connor, P. M. & Unwin, D. M. Respiratory evolution facilitated the origin of pterosaur flight and aerial gigantism. *PLoS ONE* **4**, e4497 (2009).
- Benson, R. B. J. & Choiniere, J. N. Rates of dinosaur limb evolution provide evidence for exceptional radiation in Mesozoic birds. *Proc. Roy. Soc. B* **280**, 20131780 (2013).
- Alfaro, M. E. *et al.* Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proc. Natl Acad. Sci. USA* **106**, 13410–13414 (2009).
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in space and time. *Nature* **491**, 444–448 (2012).
- Benton, M. J., Tverdokhlebov, V. P. & Surkov, M. V. Ecosystem remodeling among vertebrates at the Permian–Triassic boundary in Russia. *Nature* **432**, 97–100 (2004).
- Nesbitt, S. J. The early evolution of archosaurs: relationships and the origin of major clades. *Bull. Am. Mus. Nat. Hist.* **352**, 1–292 (2011).
- Sookias, R. B., Butler, R. J. & Benson, R. B. J. Rise of dinosaurs reveals major body size transitions are driven by passive processes of trait evolution. *Proc. Roy. Soc. B* **279**, 2180–2187 (2012).
- Nesbitt, S. J., Desojo, J. B. & Irmis, R. B. *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin* (eds Nesbitt, S., Desojo, J. B. & Irmis, R. B.) Ch. 1, 1–8 (The Geological Society, London, 2013).
- Ezcurra, M. D., Scheyer, T. M. & Butler, R. J. The origin and early evolution of Sauria: reassessing the Permian saurian fossil record and the timing of the crocodile-lizard divergence. *PLoS ONE* **9**, e97828 (2014).
- Ezcurra, M. D. & Butler, R. J. Taxonomy of the proterosuchid archosauriforms (Diapsida: Archosauromorpha) from the earliest Triassic of South Africa, and implications for the early archosauriform radiation. *Palaeontol.* **58**, 141–170 (2015).

13. Da Rosa, A. A. S. *et al.* Bica São Tomé, a new fossiliferous site for the early Triassic of southern Brazil. *Rev. Bras. Paleontol.* **12**, 67–76 (2009).
14. Cisneros J. & Schultz, C. L. *Procolophon brasiliensis* n. sp., a new procolophonid reptile from the Lower Triassic of southern Brazil. *Neues Jb. Geol. P. M.* **2002**, 641–648 (2002).
15. Dias-da-Silva, S., Modesto, S. P. & Schultz, C. L. New material of *Procolophon* (Parareptilia: Procolophonoidea) from the Lower Triassic of Brazil, with remarks on the ages of the Sanga do Cabral and Buena Vista formations of South America. *Can. J. Earth Sci.* **43**, 1685–1693 (2006).
16. Dilkes, D. W. The Early Triassic rhynchosaur *Mesosuchus browni* and the interrelationships of basal archosauromorph reptiles. *Phil. Trans. R. Soc. B* **353**, 501–541 (1998).
17. Modesto, S. P. & Sues, H.-D. The skull of the Early Triassic archosauromorph reptile *Prolacerta broomi* and its phylogenetic significance. *Zoo. J. Linn. Soc.* **140**, 335–351 (2004).
18. Modesto, S. P. & Botha-Brink, J. Evidence of a second, large archosauriform reptile in the Lower Triassic Katberg Formation of South Africa. *J. Vert. Paleontol.* **28**, 914–917 (2008).
19. Ezcurra, M. D., Butler, R. J. & Gower, D. J. in *Anatomy, Phylogeny and Palaeobiology of Early Archosaurs and their Kin* (eds Nesbitt, S., Desojo, J. B. & Irmis, R. B.) Ch. 2, 9–32 (The Geological Society, London, 2013).
20. Müller, J. Early loss and multiple return of the lower temporal arcade in diapsid reptiles. *Naturwissenschaften* **90**, 473–476 (2003).
21. Witmer, L. M. The evolution of the antorbital cavity of archosaurs: a study in soft-tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. *Mem. Soc. Vert. Paleontol.* **3**, 1–73 (1997).
22. Sahney, S. & Benton, M. J. Recovery from the most profound mass extinction of all time. *Proc. Roy. Soc. B* **275**, 759–765 (2008).
23. Day, M. O. *et al.* When and how did the terrestrial mid-Permian mass extinction occur? Evidence from the tetrapod record of the Karoo Basin, South Africa. *Proc. R. Soc. B* **282**, 20150834 (2015).
24. Botha, J. & Smith, R. M. H. Rapid vertebrate recuperation in the Karoo Basin of South Africa following the end-Permian extinction. *J. Afr. Earth Sci.* **45**, 502–514 (2006).
25. Bernardi, M., Klein, H., Petti, F. M. & Ezcurra, M. D. The origin and early radiation of archosauriforms: integrating the skeletal and footprint record. *PLoS ONE* **10**, e0128449 (2015).
26. Ezcurra, M. D., Lecuona, A. & Martinelli, A. A new basal archosauriform diapsid from the Early Triassic of Argentina. *J. Vert. Paleontol.* **30**, 1433–1450 (2010).
27. Goloboff, P., Farris, S. & Nixon, K. TNT, a free program for phylogenetic analysis. *Cladistics* **24**, 1–8 (2008).
28. Bremer, K. Bremer branch support and tree stability. *Cladistics* **10**, 295–304 (1994).
29. Felsenstein, J. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* **39**, 783–791 (1985).
30. Strappasson, A., Pinheiro, F. L. & Soares, M. B. On a new stereospondylomorph temnospondyl from the Middle-Late Permian of Southern Brazil. *Acta Palaeontol. Pol.* **60**, 843–855.

Acknowledgements

We thank M. Benton, A. Martinelli and J. Cisneros for discussion, J. Anderson for drawings, C. Ernandes, C. Da Rosa, D. Oliveira, G. Ugalde and M. Marks for field assistance, G. Furtado for etymological assistance, J. Bruno for advice on images, and S. Brusatte and two anonymous reviewers for helping improve an early version of the manuscript. This work was partially funded by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). R.J.B. was supported by a Marie Curie Career Integration Grant (PCIG14-GA-2013-630123).

Author Contributions

F.L.P. designed the project; F.L.P., M.A.G.F. and M.B.L. conducted the experiments; F.L.P., M.A.G.F., M.L.B., C.L.S. and R.J.B. analysed and interpreted the results; F.L.P., M.A.G.F., M.B.L. and R.J.B. wrote the manuscript.

Additional Information

Supplementary information accompanies this paper at <http://www.nature.com/srep>

Competing financial interests: The authors declare no competing financial interests.

How to cite this article: Pinheiro, F. L. *et al.* An exceptional fossil skull from South America and the origins of the archosauriform radiation. *Sci. Rep.* **6**, 22817; doi: 10.1038/srep22817 (2016).



This work is licensed under a Creative Commons Attribution 4.0 International License. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in the credit line; if the material is not included under the Creative Commons license, users will need to obtain permission from the license holder to reproduce the material. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>

PARTE 2

11.2 Resumos publicados em congressos

ON THE EVOLUTION OF THE ANTORBITAL FENESTRA IN ARCHOSAURIFORMES

M.A. GALLO DE FRANÇA¹, F. LIMA PINHEIRO², M. LACERDA³

Archosauriformes is composed of several fossil groups and birds and crocodylians. A characteristic of this clade is the presence of an antorbital fenestra, located between the orbit and the nasal aperture. This fenestra involves the morphologic modification of the maxilla, jugal and lacrimal bones. The recently described taxon *Teyujagua paradoxa* displays archosauriform features, such as serrated teeth and a mandibular fenestra, but shares plesiomorphies with basal Archosauromorpha, like the absence of antorbital fenestra and an opened lower temporal one. In basal Archosauriformes, like *Proterosuchus*, the oval antorbital fenestra is encircled by the ascending process of maxilla (ventral and anterodorsally), lacrimal (posterodorsally and posteriorly) and the jugal. In these taxa, the lacrimal is larger than the prefrontal, both forming a bone pillar between the orbit and antorbital fenestra. In basal archosauromorphs, like *Macrocnemus*, *Mesosuchus* and *Prolacerta*, the reverse occurs, with the prefrontal larger than the lacrimal, which is slender and posteroventrally inclined. In *T. paradoxa*, the lacrimal bone is semicircular, with a vertical margin on the posterior region that composes the orbital rim and the prefrontal is dorsally restricted. The modification present in Archosauriformes is an excavated lacrimal on its anteroventral region, forming the antorbital fenestra and its L-shaped aspect. CT-scans of the skull of *T. paradoxa* reveal a hollow anteroventral region of lacrimal, bounded on the posterodorsal region by a buttress. As such, the evolution of antorbital fenestra would be a consequence of the verticalization and size increase of the lacrimal, with a development of a notched anteroventral region.

¹Laboratório de Paleontologia e Evolução de Petrolina, Universidade Federal do Vale do São Francisco, Petrolina, Brazil.

²Laboratório de Paleobiologia, Universidade Federal do Pampa, São Gabriel, Brazil

³Laboratório de Paleontologia de Vertebrados, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil

REAPPRAISAL OF THE EARLY CRETACEOUS SAUROPOD DINOSAUR *AMARGATITANIS MACNI* (APESTEGUÍA, 2007), FROM NORTHWESTERN PATAGONIA, ARGENTINA

P.A. GALLINA¹

Amargatitanis macni Apesteguía, 2007 was described as a purported titanosaur sauropod. However, this referral and even the systematic validity of the taxon were questioned. Here, all the available remains of the taxon are evaluated including a description of unpublished elements. The identity of the type material is discussed based on a first-hand examination of the specimens and evaluation of the original field notes as reliable evidence for bone association. The original holotype of *Amargatitanis* is a chimaera, as pointed out by previous authors. Herein a new, modified holotype for *Amargatitanis* is proposed. This analysis presents a revised diagnosis for *Amargatitanis macni* as a valid taxon. Several features observed on the modified type material revealed closer affinities to diplodocoids than macronarians. The presence of a fibular facet of the astragalus facing posterolaterally, and the absence of a lateral bulge in the femur, link *Amargatitanis* with Diplodocoidea. Additionally, the presence of a posterolateral projection on the distal condyle of the first metatarsal, and anterior caudal centra with procoelous/distoplatyan articular surfaces, are shared with other flagellicaudatans. The position of the highest point of the femoral head laterally shifted, above the main portion of shaft, and the anterior caudal transverse processes directed dorsally, also support affinities with dicraeosaurids. The inclusion of *Amargatitanis macni* in an updated phylogenetic analysis revealed the presence of a second species of the family Dicraeosauridae in the La Amarga Formation, suggesting that, at present, there is no record of titanosaur body fossils in Patagonia prior to Cenomanian times.

¹CONICET, Área de Paleontología, Fundación de Historia Natural Félix de Azara, CEBBAD, Universidad Maimónides. Hidalgo 775, 1405 Ciudad Autónoma de Buenos Aires, Argentina. pablogallina@gmail.com

ON THE TOOTH VARIATION OF *PRESTOSUCHUS CHINIQUENSIS* (PSEUDOSUCHIA: LORICATA): THE LARGEST PREDATOR OF THE MIDDLE TRIASSIC OF BRAZIL

C.B. DE MELLO, V.D. PAES NETO, A.G. MARTINELLI, M.B. LACERDA and C.L. SCHULTZ

“Raiusuchia” is a cosmopolitan group of Triassic pseudosuchians that includes a variety of forms, such as large hypercarnivorous taxa with recurved serrated teeth. In the *Dinodontosaurus* Assemblage Zone of the Santa Maria Supersequence of Brazil, one of the best represented “raiusuchians” is *Prestosuchus chiniquensis*. We investigated the tooth variability of three previously referred specimens (UFRGS-PV-0156-T, 0629-T, CEPZ 239B) of *P. chiniquensis* to better assess their ontogenetic and functional signal. We identify an evident heterodonty on the skull UFRGS-PV-0156-T. All teeth are ziphodont and mesiodistally enlarged (as in all available specimens), but in the premaxillary set they are conical and less labiolingually compressed when compared with maxillary teeth. In the anterior part of the maxilla, teeth have high crowns and are mostly fang-shaped, with smooth convex mesial margins, whereas in the middle portion some teeth with high crowns present an abrupt change on the mesial curvature, showing a “hook-shaped” morphology. This inflection is observed in the posterior set of the maxilla, where teeth have short and proportionally more mesiodistally wide crowns. This “hook-shaped” morphology is not observed on the middle maxillary teeth of UFRGS-PV-0629-T, a middle-sized adult, but is present in the posterior shorter teeth. Maxillary teeth of the juvenile CEPZ 239B seems to be more fang-shaped, including those posteriorly placed. The individual variation on teeth morphology of these specimens may suggest that *P. chiniquensis* heterodonty increased during ontogeny, implying a functional change in the maxillary teeth, particularly on the maxillary posterior set.

Universidade Federal do Rio Grande do Sul, Instituto de Geociências, Departamento de Paleontologia e Estratigrafia, Avenida Bento Gonçalves, 9500, Agronomia, CEP 91501-970 - Porto Alegre, RS, Brazil.

FÓSILES DEL CLADO [*CERATOPHRYS AURITA-C. JOAZEIRENSIS*] EN EL HOLOCENO DE LAGOA SANTA (MINA GERAIS, BRASIL): ANÁLISIS DE LA OSTEOLOGÍA Y POSIBLES SINAPOMORFÍAS DE LOS ESCUERZOS DEL ESTE DE BRASIL

L. NICOLI¹

En 1859 Günther describió y asignó a la especie viviente *Ceratophrys cornuta* una serie de cráneos fósiles provenientes de Lagoa Santa, Mina Gerais, Brasil. Esta evidencia resultaba sumamente interesante considerando que *C. cornuta* tiene actualmente una amplia distribución a través de la selva amazónica, alrededor de 1500 km al noroeste de Lagoa Santa. Este material, sin embargo, se encontraba extraviado. Recientemente, los restos fueron localizados en el Natural History Museum de Londres. Se trata de dos cráneos fuertemente osificados y ornamentados que incluyen todas las posibles sinapomorfias de *Ceratophrys*. Asimismo, poseen una serie de caracteres que permiten diferenciarlos claramente de *C. cornuta* (e.g. cráneo dos veces más ancho que alto, con crestas mediales y laterales, escamoso con placa ótica subcuadrangular extendida hasta el nivel de los cóndilos occipital y dientes vomerinos vs. cráneo más de dos veces más ancho que alto, sin crestas, con placa ótica elongada sobrepasando posteriormente el nivel de los cóndilos y vómeres sin dientes en *C. cornuta*). Estos caracteres constituyen, sin embargo, una combinación exclusiva de los escuerzos del este de Brasil, *Ceratophrys aurita* y *C. joazeirensis*, que constituyen un clado fuertemente soportado en base a información molecular. El análisis de la anatomía esquelética de estos y otros *Ceratophrys*, en el contexto de sus relaciones filogenéticas, permite proponer la elevada altura del cráneo y la presencia de una serie de crestas craneales dorsales como sinapomorfias exclusivas para [*C. aurita-C. joazeirensis*]. Su presencia en los fósiles de Lagoa Santa permite asignarlos con confianza a dicho clado.

¹Division Herpetologia. Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”- CONICET. Buenos Aires, Argentina.

A NEW TRIASSIC PSEUDOSUCHIAN ARCHOSAUR FROM BRAZIL AND THE EVOLUTION OF THE ORNITHOSUCHIDAE

M. B. LACERDA¹, M. A. G. DE FRANÇA² and C. L. SCHULTZ¹

The evolution and diversity of pseudosuchian archosaurs during the Triassic is still controversial, but new fossils and the revision of previously described specimens have provided new insights and led to better supported phylogenetic analysis. However, there are a lot of ghost lineages and taxa with unresolved phylogenetic affinities. Here we present a new fossil from the Santa Maria Supersequence (Middle-Late Triassic) of the Rio Grande do Sul State, southern Brazil, which possibly represents a new taxon. The specimen MMACR-PV-036-T is deposited in the collection of the Museu Municipal Aristides Carlos Rodrigues in the city of Candelária and is composed of a complete skull and mandible with associated cervical vertebrae and osteoderms. The diagenetic pattern fits well with that of fossils from the *Dinodontosaurus* AZ (Ladinian) that occur in the region south of the city of Candelária but the collection site is unknown. The presence of features such as a rounded orbit with a distinct ventral point which is surrounded by a “V” shaped dorsal process of the jugal would indicate close affinities with the Ornithosuchidae. This group is composed by only 3 taxa; *Ornithosuchus longidens* from the Lossiemouth Sandstone Formation of Scotland, *Riojasuchus tenuiceps* from the Los Colorados Formation and *Venaticosuchus rusconii* from the Ischigualasto Formation, both in Argentina. MMACR-PV-036-T differs from these by having features such as a not so pronounced ventral projection of the rostrum, palpebral bones and markedly ornamented dermal roof and osteoderms. Preliminary cladistic tests indicate that MMACR-PV-036-T would be the sister group of Ornithosuchidae.

¹Laboratório de Paleontologia de Vertebrados, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

²Laboratório de Paleontologia e Evolução de Petrolina, Universidade Federal do Vale do São Francisco, Petrolina, Brazil.

MACELOGNATHUS VAGANS (ARCHOSAURIA; CROCODYLOMORPHA): NEW INFORMATION ON THE BRAINCASE USING CT-DATA

J.M. LEARDI¹, D. POL² and J. CLARK³

Macelognathus vagans was originally described as a dinosaur by Marsh from the Late Jurassic Morrison Formation of Wyoming and in 1971 Ostrom suggested crocodylian affinities. In 2005, Göhlich and collaborators identified new material from Colorado as a basal crocodylomorph. However, a partial skull found in association with mandibular and postcranial remains was not described. The skull preserves most of the posterior part, including the braincase, and probably belongs to a juvenile given its dorsal curvature. Due to the small size and delicate structures within the braincase, micro CT studies were performed on this specimen. This new material reinforces the non-crocodyliform crocodylomorph affinities of *Macelognathus* as it bears a large otic aperture, unfused frontals and lacks ornamentation on the dorsal cranial bones. The internal structures also support these affinities as this specimen has traits (i.e., heavily pneumatized and expanded basisphenoid; the presence of additional pneumatic features on the braincase; and the otoccipital-quadrante contact) not present in most basal crocodylomorphs. Furthermore, the presence of a wide supraoccipital and a cranioquadrante passage are traits shared with *Almadasuchus* from the early Late Jurassic of Argentina. The new anatomical information was incorporated in a phylogenetic dataset, expanding both character and taxon sampling. *Macelognathus* was recovered as one of the most derived non-crocodyliform crocodylomorphs, forming a clade with two other Late Jurassic taxa (*Almadasuchus* and the Morrison *Hallopus*). This derived clade is characterized by having a higher degree of suturing of the braincase, posteriorly closed otic aperture (paralleled in mesoeucrocodylians) and cursorial adaptations.

¹ CONICET, Instituto de Estudios Andinos Don Pablo Groeber, Departamento de Ciencias Geológicas, Facultades de Ciencias Exactas y Naturales, Pabellón II, Universidad de Buenos Aires, Intendente Güiraldes 2160, 1428, Buenos Aires, Argentina, jmleardi@gl.fcen.uba.ar

² CONICET, Museo Paleontológico Egidio Feruglio, Avenida Fontana 140, Trelew 9100, Chubut, Argentina, dpol@mef.org.ar

³ Department of Biological Sciences, George Washington University, Washington, DC, 20052, U.S.A., jclark@gwu.edu



PALEO RS 2015
4 a 6 de dezembro - São Gabriel, RS



A ZONA DE ASSEMBLEIA DE *RIOGRANDIA*: A “PEDRA DE ROSETA” NA EVOLUÇÃO DOS MICROVERTEBRADOS DO NEOTRIÁSSICO

A. MARTINELLI¹; M. LANGER²; M. LACERDA¹; M. CASTRO²; E. DASSIE²; M. GUIGNARD¹; V. PAES NETO¹; H. FRANCISCHINI¹; F. PRETTO¹; F. VEIGA¹; M. SOARES¹; C. SCHULTZ¹
¹Laboratório de Paleovertebrados, Instituto de Geociências, UFRGS, Av. Bento Gonçalves 9500, Agronomia, Porto Alegre, RS, Brasil. ²Laboratório de Paleontologia, Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Av. Bandeirantes 3900, Ribeirão Preto, SP, Brasil.

agustin_martinelli@yahoo.com.ar, mclanger@ffclrp.usp.br, marcel.lacerda@yahoo.com.br, marielacastro@yahoo.com.br, elisabetedassie@hotmail.com, guignard.morgan@gmail.com, voltairearts@gmail.com, heitorfrancischini@hotmail.com, flavio_pretto@yahoo.com.br, fhveiga@gmail.com, marina.soares@ufrgs.br, cesar.schultz@ufrgs.br

O reconhecimento das sucessivas associações faunísticas do Triássico continental no sul do Brasil tem sido importante para o estudo da diversidade e evolução das comunidades fossilíferas logo após a grande extinção do limite Permo/Triássico. Particularmente, a mais recente associação Triássica com vertebrados corresponde à Zona de Assembleia (ZA) de *Riograndia*, Sequência Candelária (Supersequência Santa Maria). Os principais afloramentos fossilíferos desta ZA encontram-se em Candelária, Faxinal do Soturno, Agudo e São Martinho da Serra, sendo que, nos dois primeiros municípios, o conteúdo de microvertebrados é notável. A intensificação da prospeção e coleta de fósseis em rochas desta idade teve seu início na década dos 90, quando o Padre Daniel Cargnin, então na cidade de Mata (RS), mencionou a pesquisadores da FZB do RS (J. Ferigolo), UFRGS (M. Barberena) e MACN (J. Bonaparte) a presença de restos de pequenos vertebrados em Faxinal do Soturno e Candelária. Prospeções sistemáticas revelaram uma grande diversidade de vertebrados de pequeno porte, previamente desconhecida para o Triássico mundial, além de formas arcossaurianas de maior porte (*Phytosauria* indet., *Guaibasaurus*). Entre as formas de pequeno porte destacam-se o procolofônio *Saturnia*, o lepidossauromorfo *Cargninia*, o esfenodonte *Clevosaurus*, o arcossauro *Faxinalipterus* e os cinodontes *Riograndia*, *Irajatherium*, *Botucaraitherium*, *Brasilodon*, *Brasilitherium* e *Minicynodon*. As coletas feitas ao longo destes anos tem fornecido material para diversos estudos, incluindo TCCs, mestrados e doutorados. Um dos últimos trabalhos de campo, realizado em Maio de 2015, em parceria entre a UFRGS e a USP/Ribeirão Preto, nos sítios Linha São Luís, Sesmaria do Pinhal 1, Poste e Cerro Botucaraí, resultou no achado de numerosos novos espécimes. Destacam-se restos de diferentes estágios ontogenéticos de esfenodontídeos e cinodontes probainognatios (*Riograndia* e *Brasilitherium*), um segundo exemplar de *Botucaraitherium* e diversos materiais ainda em fase de preparação, mas que brindarão novos dados sobre esta ZA que constitui a “Pedra de Roseta” para a compreensão da diversidade faunística do Planeta ao final do Triássico. [FAPESP, CNPq, CAPES]

O “X” da questão: testando a relação entre Spinosauridae e paleoambientes terrestres

Marcos A. F. SALES¹; Marcel B. LACERDA¹; Bruno L. D. HORN^{1,2}; Isabel A. P. de OLIVEIRA³; Cesar L. SCHULTZ¹

O táxon Spinosauridae compreende dinossauros terópodes com possíveis hábitos de vida semiaquáticos, para os quais há proposições de uma estreita associação com habitats costeiros. Tendo em vista a negligência quanto à relação desses terópodes com o ambiente terrestre e a fim de analisá-la estatística e comparativamente a outros táxons de terópodes (Abelisauridae e Carcharodontosauridae), foram realizados o teste do quiquadrado (X^2) e o teste exato de Fischer conforme detalhado abaixo. Foi compilado um total de 206 ocorrências dos táxons citados, caracterizando-as quanto aos respectivos ambientes deposicionais e subdividindo-as nas seguintes categorias tafonômicas: (1) ocorrências com espécimes (semi)articulados; (2) ocorrências somente com materiais isolados e/ou fragmentados. Algumas ocorrências foram ainda classificadas como duvidosas ou parálogas, estas últimas com o sentido de ocorrências que possivelmente representavam mais de uma vez um mesmo ambiente. Os dois primeiros testes (usando X^2) foram aplicados no sentido de verificar se a distribuição das ocorrências dessas famílias no ambiente terrestre, com e sem a distinção das categorias tafonômicas, poderia ser devida somente ao acaso. O terceiro teste (Fischer) avaliou, por sua vez, se a distribuição das categorias tafonômicas referentes somente a Spinosauridae, entre os ambientes costeiro e terrestre, era aleatória ou não. Todos os testes foram replicados quatro vezes de forma a avaliar as diferenças entre os resultados quando da inclusão e da exclusão de ocorrências duvidosas e parálogas. Em geral, os resultados dos dois testes do quiquadrado indicam que nenhum táxon analisado apresentou uma associação positiva com o ambiente terrestre, isto é, nenhum táxon é significativamente mais amostrado em relação aos demais. A associação entre as categorias tafonômicas de Spinosauridae e o ambiente terrestre foi semelhante à verificada para

Carcharodontosauridae, sugerindo que ambos poderiam ocupar tais ambientes de forma similar. Por outro lado, a exclusão simultânea das ocorrências parálogas e duvidosas gerou diferentes associações entre as categorias tafonômicas de Abelisauridae e o ambiente terrestre. Esse fato é indicativo da influência que esses vieses podem ter em uma análise que não os mensure adequadamente, além de levantar a possibilidade de que a ocupação do ambiente terrestre por esses terópodes não se deu exatamente da mesma forma que por Spinosauridae e Carcharodontosauridae. Por fim, o terceiro teste não corroborou enfaticamente a ideia de Spinosauridae estando estreitamente relacionado com paleoambientes costeiros em detrimento dos terrestres, sugerindo, juntamente com os outros resultados, que esses animais teriam sido mais generalistas quanto ao seu nicho espacial, mesmo possuindo prováveis hábitos semiaquáticos.

¹Laboratório de Paleovertebrados, Departamento de Paleontologia e Estratigrafia, Universidade Federal do Rio Grande do Sul. CNPq, marcos.paleo@yahoo.com.br; marcel.lacerda@yahoo.com.br; cesar.schultz@ufrgs.br

²Superintendência de Recife, Serviço Geológico do Brasil. brunoldhorn@gmail.com

³Laboratório de Ecologia e Conservação de Vertebrados, Universidade Federal do Amapá. beloliveira.bio@gmail.com

A Toca da Boa Vista, localizada no município de Campo Formoso, região norte do semiárido baiano, é a mais extensa caverna do hemisfério sul, cuja formação carbonática constitui-se de calcários e dolomitos do Grupo Una, que se estendem da região central da Bahia (Chapada Diamantina) até o norte do Estado. Seu potencial paleontológico é conhecido por meio dos depósitos químicos secundários, cujas datações em incrustações calcíticas em ossos de megamamíferos quaternários proporcionaram calibrações cronológicas que tem servido de importante registro das mudanças climáticas durante o quaternário da região. Estudos relativos à mastofauna de pequeno porte, organismos com peso inferior a 5 kg, associada a esta cavidade ainda são incipientes, não obstante os extensos depósitos fósseis ósseos e de guano encontrados ao longo de seus condutos e salões. Datações C14 realizadas em ossos de morcegos e guano indicam uma idade estimada em 24 mil anos, carecendo calibrações para roedores e didelfimorfos. As ordens mais representativas registradas para a Toca da Boa Vista são Chiroptera, Rodentia e Didelphimorphia, sendo este último, o foco do presente estudo. Na análise preliminar da composição taxonômica das amostras crânio-mandibulares dos marsupiais tombados na Coleção de Paleontologia do Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais foram identificados até o momento 235 espécimes ósseos (187 peças mandibulares; 48 crânios), categorizados em onze padrões morfotípicos afins aos seguintes taxa: i) *Monodelphis* sp. (07;00); ii) *Monodelphis domestica* (Wagner, 1842) (61;33); iii) *Monodelphis americana* (Müller, 1776) (10;09); iv) *Marmosops incanus* (Lund, 1842) (73;05); v) *Didelphis* sp. (Linnaeus, 1758) (11;00); vi) *Gracilinanus* sp. (Gardner & Creighton, 1989) (07;00); vii) *Gracilinanus agilis* (Burmeister, 1854) (08;00); viii) *Gracilinanus microtarsus* (Wagner, 1842) (05;00); ix) *Micoureus demerarae* (Thomas, 1905) (01;00); x) *Metachirus nudicaudatus* (Geoffroy, 1803) (02;00); xi) *incertae sedis* (03;00); indefinido (04;01). A composição das espécies levantadas sugerem fisionomias diversificadas para espécies com variada amplitude fitofisionômica. Os taxa *M. domestica*, *M. incanus*, *G. agilis*, *M. demerarae*, *M. nudicaudatus* e *Didelphis* sp. indicam fisionomias abertas (campos e cerrados) e fechadas (florestas de galeria e de encosta), enquanto *G. microtarsus* sugere a ocorrência de Floresta perenifólia úmida para e Floresta estacional caducifólia espinhosa, como observada na paisagem atual a região da Toca da Boa Vista, o que não é condizente para *M. americana*. A conclusão da análise é a de que nessa região de clima semiárido, ocorreram composições fitofisionômicas pretéritas que podem ter sido alteradas por mudanças climáticas favorecendo espécies de clima seco e quente.

PRIMEIRA OCORRÊNCIA DE ORNITHOSUCHIDAE PARA O TRIÁSSICO DO ESTADO DO RIO GRANDE DO SUL, BRASIL

MARCEL B. LACERDA, CESAR L. SCHULTZ

Laboratório do Setor de Paleontologia de Vertebrados do Departamento de Paleontologia e Estratigrafia, Instituto de Geociências da Universidade Federal do Rio Grande do Sul.

marcel.lacerda@yahoo.com.br, cesar.schultz@ufrgs.br

A família Ornithosuchidae compreende formas de pseudossúquios do Triássico, sendo que apenas três táxons são conhecidos no mundo todo: *Ornithosuchus longidens* da Formação Lossiemouth Sandstone da Escócia; *Riojasuchus tenuiceps* da Formação Los Colorados e *Venaticosuchus rusconii*, da Formação Ischigualasto, ambos da Argentina. No final do ano de 2012, um espécime fóssil curioso foi doado para o Museu Municipal Aristides Carlos Rodrigues, composto de um sínclínio completo que apresenta ainda vértebras cervicais em posição de articulação, além de alguns osteodermas cervicais associados. Este espécime apresenta a órbita direita com forma de gota invertida, com a ponta direcionada ventralmente e o jugal direito, que é o melhor preservado, possui aspecto de “Y”, com dois processos ascendentes formando a borda ventral da órbita. Estas

duas características são típicas de Ornithosuchidae, de modo que este espécime constitui-se na primeira ocorrência deste táxon para o Brasil. Além disso, o espécime brasileiro difere das espécies acima citadas pela presença de outras características, como um pré-maxilar não tão anteriormente projetado, uma cobertura de endorelevos no teto dérmico e a presença de ossos palpebrais ou um espessamento lateral dos frontais e pós-frontais. Entretanto, um estudo e uma descrição mais detalhada são necessários para um estabelecimento taxonômico preciso. Ademais, é de importância chave para o estudo deste material descobrir a sua exata procedência, uma vez que o local de coleta permanece desconhecido. Somente de posse desta informação será possível estabelecer o posicionamento bioestratigráfico do material brasileiro em relação aos demais táxons do grupo e entender sua evolução ao longo do Triássico.

O QUE FAZER QUANDO NÃO HÁ DIFERENÇAS NAS ESTRUTURAS OCLUSAIS DOS MOLARIFORMES? UM EXEMPLO COM *XENORHINOTHERIUM BAHIENSE* CARTELLE & LESSA, 1988

LEONARDO S. LOBO, GISELE LESSA, PEDRO S. R. ROMANO
 Universidade Federal de Viçosa
leoloboo@gmail.com

A resistência estrutural dos dentes dos mamíferos faz com que eles sejam amplamente representados no registro fóssil. Além disso, os dentes apresentam grande variedade morfológica que está relacionada intimamente com a dieta e a posição de inserção. A arcada dentária é composta por morfotipos básicos (incisivo, canino, pré-molar e molar) que são distinguíveis através da sua complexidade oclusal. Porém, nos Ungulados os pré-molares e molares apresentam grande similaridade estrutural. Concomitantemente com o aparecimento da dentição permanente, o desgaste dentário decorrente da alimentação abrasiva ocasiona o desaparecimento de muitas estruturas oclusais diagnósticas. Assim, o objetivo deste trabalho foi testar se há diferença na forma dos molariformes de *Xenorhinotherium bahiense*, um Litopterna extinto no final do Pleistoceno, mesmo com a atuação do desgaste. Todos os espécimes analisados são oriundos da Toca dos Ossos, município de Ouroândia, região Centro-Norte da Bahia. O material está depositado na coleção de Paleontologia do Museu de Ciências Naturais da PUC-MG. Sendo composto no total por 47 dentes, 18 P4, 17 M1 e 12 M2. Para a análise foram utilizados nove marcos anatômicos, digitalizados no programa tpsDig 2.7 e para as demais análises utilizou-se o programa MorphoJ 1.05. Uma Análise de Variáveis Canônicas (AVC) sobre a matriz de resíduos de Procruste foi efetuada para observar as variáveis que diferenciam os três molariformes. A variância foi acumulada em dois eixos canônicos que evidenciaram dois padrões, o VC1 (64,08%) possibilitou delimitar as diferenças entre P4 e M1 e o VC2 (35,92%) possibilitou distinguir o M2 dos outros molares. As diferenças observadas no P4 são stilos menos proeminentes, expansão da região mesio-labial e fossetas linguais com pouco desnivelamento. No M1 as diferenças entre a média são stilos mais proeminentes em direção labial, retração da região mesio-labial e fossetas linguais mais desniveladas do que observada no P4. A forma do M2 difere da média em stilos mais proeminentes em direção labial e Parastilo mais proeminente em direção mesial, deslocamento distal do Metacone, deslocamento do Mesostilo em direção mesial e fossetas linguais com o maior grau de desnivelamento. Assim, há diferenças na forma dos molares que estão ligadas com a posição ocupada na arcada dentária. Esse resultado poderá auxiliar na maior resolução da identificação dos molariformes isolados de *Xenorhinotherium bahiense* e na construção de futuros perfis populacionais.

Primeiro registro brasileiro de Poposauroida (Sequência Santa Maria II, Zona-Associação de *Riograndia*, Neotriássico)

Marco Aurélio Gallo de FRANÇA¹; Marcel Baêta LACERDA²; Flavio Augusto PRETO²; Cesar Leandro SCHULTZ²; Max Cardoso LANGER³

Poposauroida é um grupo de arcossauros pseudossáurios com posicionamento filogenético ainda incerto entre os sáurios, mas de monofiletismo amplamente corroborado. Distribuem-se desde o Eotriássico (Olenekiano) até o final do Período (Rético), compondo um dos grupos mais diversos/discrepantes de arcossauros basais em termos de morfologia/inferências funcionais: alguns táxons possuem espinhos neurais alongados, compondo estrutura dorsal em forma de vela; locomoção varia de quadrúpede a bípede com elevada cursorialidade; hábito alimentar varia de carnívoria à herbívoría/onívoria, com alguns possuindo dentes serrilhados e encurvados para trás, sendo outros desprovidos de dentes e com bico córneo. Apesar da distribuição quase cosmopolita no Triássico (China, Índia, Reino Unido, Alemanha, Tanzânia, Estados Unidos), incluindo a América do Sul (Argentina), nenhum Poposauroida foi reportado para o Brasil. O presente resumo trata da descrição e possíveis relações taxonômicas de dois espécimes relacionados ao grupo, composto por dois segmentos parciais de vértebras sacrais provenientes da localidade Cerro Botucaraí (Sequência Santa Maria II, Triássico Superior, Carniano/Noriano). O espécime MCP-0204-PV inclui duas vértebras sacrais parciais, com centros vertebrais e zigapófises coossificadas, além de um fragmento da zigapófise de uma terceira vértebra sacral. O centro é mais elevado que comprido, sendo os espinhos neurais relativamente baixos (20% da altura total da vértebra), com a dimensão de cada vértebra aproximada de 3,5 cm de comprimento e 8cm de altura. O segundo espécime está depositado no Museu Aristides Carlos Rodrigues, em Candelária-RS, ainda não numerado, e inclui quatro vértebras sacrais parcialmente preservadas, também possuindo centros e zigapófises coossificados entre si, com dimensões aproximadas

de 5cm de comprimento e 14cm de altura em cada vértebra. Apesar do centro vertebral ser mais elevado que comprido, os espinhos neurais também são relativamente elevados, ocupando cerca de 35% da altura total da vértebra. A presença de três ou mais vértebras sacrais, com centros e zigapófises coossificados, é característica distintiva de Poposauroida derivados, como *Arizonasaurus*, *Poposaurus*, *Lotosaurus*, *Sillosuchus*, *Effigia* e *Shuvosaurus*. Entre estes, a morfologia do segundo espécime assemelha-se mais com a de *Poposaurus*, pois o espinho neural é relativamente elevado (35% da altura da vértebra). MCP-0204-PV possui uma maior semelhança com *Sillosuchus*, *Effigia* e *Shuvosaurus*, sugerido pelo menor grau de individualização dos centros vertebrais e espinhos neurais relativamente baixos, apesar do centro vertebral ser mais elevado que comprido (que o diferencia de tais táxons). Sendo assim, os novos registros indicam a presença de dois Poposauroida distintos no Brasil, fornecendo informações adicionais sobre a biodiversidade triássica do país e estendendo a distribuição paleobiogeográfica do grupo.

¹Laboratório de Paleontologia de Petrolina, Universidade Federal do Vale do São Francisco. marco.franca@univasf.edu.br

²Laboratório de Paleontologia de Vertebrados, Universidade Federal do Rio Grande do Sul

³Laboratório de Paleontologia de Ribeirão Preto, Universidade de São Paulo

PARTE 2

11.3. Histórico escolar do aluno

Aluno



Marcel Baeta Lacerda Santos

184327

Lista das atividades de ensino do aluno avaliadas pelo curso.

**HISTÓRICO CURSO
GEOCIÊNCIAS - Doutorado - 01/03/2013**

Período Letivo	Código	Disciplina	Créditos	Conceito	Situação
2016/02	GEB00119	EVOLUÇÃO DOS MAMÍFEROS SUL-AMERICANOS	3	-	Matriculado
2014/01	GEP00067	Evolução; Epistemologia e História	3	A	Aprovado
2014/01	BAN00003	Fundamentos de Taxonomia Zoológica	2	A	Aprovado
2014/01	GEB41-39	T. E. em Paleontologia: Evolución y Paleobiología de Archosauriformes Tr	2	B	Aprovado
2014/01	GEB41-36	T.E. em Paleontologia: Fidelidade quantitativa - A interface entre a bio	2	A	Aprovado
2013/01	GEB41-31	T. E. em Paleontologia: sistemática cladística aplicada à paleontologia	2	B	Aprovado
15/05/2015		Exame de Qualificação	-	-	Aprovado
		Aproveitamento de Crédito neste Ingresso	24	-	Aprov, neste ingresso
		Aproveitamento de Inglês	-	-	-
		Espanhol em 04/06/2016	-	-	-

Totais

Créditos Matriculados neste Ingresso:	3
Créditos Cursados com Aprovação neste Curso:	11
Aproveitamento de Créditos neste Ingresso:	24
Total:	38

ANEXO I

Título da Dissertação/Tese:

"CONTRIBUIÇÃO AO CONHECIMENTO DOS GRUPOS "RAUISUCHIA",
ORNITHOSUCHIDAE E ERPETOSUCHIDAE (ARCHOSAURIA, PSEUDOSUCHIA) E
SUA IMPORTÂNCIA NO CONTEXTO DA COMPOSIÇÃO PALEOFAUNÍSTICA DO
TRIÁSSICO DO RIO GRANDE DO SUL, BRASIL"

Área de Concentração: Paleontologia

Autor: **Marcel Baêta Lacerda Santos**

Orientador: Prof. Dr. Cesar Leandro Schultz

Examinadora: Profa. Dra. Julia Brenda Desojo

Data: 30/11/2017

Conceito: C, Regular

PARECER:

El trabajo de tesis está organizado bien en un estado del arte introductorio seguido por una sección con 3 papers publicados, y una 3 parte de artículos complementarios.
El estado del arte hace una descripción de los Archosauria, especialmente los Pseudosuchia con ceteros y todo como parte que estudio los Pseudosuchia, Euplesiosuchia y Ornithosuchia. Sin embargo, no es clara la organización interna de esta primera parte. Los otros claros los artículos de la tesis: por ejemplo por qué estudiar los Ornithosuchia. Tanto de esta sección debe aclararse la bibliografía con trabajos más recientes, completa los cita bibliografía correcta: no de May que no existe, veris una de autor -> USN tiene 1938 (no 1942) lo profico es muy bueno, claro, con buena metodología (mapas, cladogramas).
La sección de los papers publicados es correcta, son 3 trabajos en revistas internacionales y escritos como fue en arte, con un alto nivel de rigor.

El trabajo es muy concreto, con material fragmentado pero una excelente descripción e interpretación bioestadística.
El 2º trabajo es resultado de su Master, el 3º publicación de sus resultados. El 3º publicación está en revisión. Este último no incluye los resultados reales que indica una ventajosa comparación de *Popovitchia* con *Archaeofella*, presencia o no de la ZA *Dendrofontosaurus*, lo cual cambió el primer resultado a conclusiones. Mas halla de los nuevos resultados y publicación que se deben incluir en la presente tesis, lo mismo fue el caso de algunos resultados científicos y de calidad, por lo cual el comentario se refiere a la incapacidad de las modificaciones requeridas. La tesis incluye una parte no publicada que debe aparecer o que lo sea pero no incluir el nombre y la información.

Assinatura:



Data:

30/11/2017

Ciente do Orientador:

Ciente do Aluno:

ANEXO I

Título da Dissertação/Tese:

**"CONTRIBUIÇÃO AO CONHECIMENTO DOS GRUPOS "RAUISUCHIA",
ORNITHOSUCHIDAE E ERPETOSUCHIDAE (ARCHOSAURIA, PSEUDOSUCHIA) E
SUA IMPORTÂNCIA NO CONTEXTO DA COMPOSIÇÃO PALEOFAUNÍSTICA DO
TRIÁSSICO DO RIO GRANDE DO SUL, BRASIL"**

Área de Concentração: Paleontologia

Autor: **Marcel Baêta Lacerda Santos**

Orientador: Prof. Dr. Cesar Leandro Schultz

Examinadora: Profa. Dra. Marina Bento Soares

Data: 30/11/2017

Conceito: C

PARECER:

A tese aparentemente é composta de três artigos científicos que atendem às normas do PPGEO-UFRS. Entretanto, uma série de problemas foram verificadas ao longo do texto "Estado-da-Arte" incluindo vários erros de digitação e ortografia, equívocos conceituais, falta de especificação de objetivos de tese, falta de procedimentos críticos sobre a problemática (esta, por sinal, não delimitada adequadamente) e ausência de análise interpretativa.

Sobre os dados referentes aos elementos Teras, Neras, constantes do material suplementar do Artigo 3, os dados não deveriam ter sido apresentados por constituirem dados inéditos desenvolvidos por este aluno de Mestrado sob minha orientação, mas deveriam ter referências do artigo. Manter compromissos do aluno e do orientador sobre a retinção dos dados.

Em face aos aspectos levantados, meu conceito é C.

Lined area for text or drawing, crossed out with a diagonal line.

Assinatura: *Loni Quaw*

Data: 30/11/2017

Ciente do Orientador:

Ciente do Aluno:

ANEXO I

Título da Dissertação/Tese:

**"CONTRIBUIÇÃO AO CONHECIMENTO DOS GRUPOS "RAUISUCHIA",
ORNITHOSUCHIDAE E ERPETOSUCHIDAE (ARCHOSAURIA, PSEUDOSUCHIA) E
SUA IMPORTÂNCIA NO CONTEXTO DA COMPOSIÇÃO PALEOFAUNÍSTICA DO
TRIÁSSICO DO RIO GRANDE DO SUL, BRASIL"**

Área de Concentração: Paleontologia

Autor: **Marcel Baêta Lacerda Santos**

Orientador: Prof. Dr. Cesar Leandro Schultz

Examinador: Prof. Dr. Marco Brandalise de Andrade

Data: 30/11/2017

Conceito: C, APROVADO

PARECER:

O trabalho representa um esforço genuíno e autoral de produção científica, atingindo o mérito de produzir informação nova com influência no contexto de Archosauria. No entanto, ressalvo a ocorrência frequente de erros de grafia, problemas de organização e redundância. Somado a estes conjunto problemas na construção da figura da página 82, onde existe dispersão morfológica e nomenclatural dos elementos 'A', 'B' e 'C'.

Finalmente, recomendo fortemente a retificação ou veto à impressão dos dados referentes a terras raras, desnecessários ao artigo e à tese, por serem potencialmente danosos ao candidato e às pessoas que forneceram estes dados não publicados.

