UNIVERSIDADE DE SÃO PAULO
FFCLRP – DEPARTAMENTO DE BIOLOGIA
PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA COMPARADA

**Dinossauromorfos triássicos do Sul do Brasil e padrões biogeográficos da
irradiação dos dinossauros**

Júlio Cesar de Almeida Marsola

Tese apresentada à Faculdade de Filosofia, Ciências
e Letras de Ribeirão Preto da USP, Como Parte das
exigências para a obtenção do título de Doutor em
Ciências, Área: Biologia Comparada

RIBEIRÃO PRETO – SP

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Orientação: Max Cardoso Langer

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RESUMO

Marsola, J. C. A. **Dinossauromorfos triássicos do Sul do Brasil e padrões biogeográficos da irradiação dos dinossauros.** 2018. 199p. Tese (Doutorado) – Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, 2018.

Os depósitos triássicos continentais do sul do Brasil abrigam uma grande diversidade de tetrápodes terrestres, incluindo terápsidos, rincossauros, rincocefálios e arcossauros, como pseudosúquios e dinossauromorfos. Inserida neste contexto, a Formação Santa Maria, de porção superior datada do Carniano superior, tem papel fundamental no entendimento da origem e irradiação inicial dos dinossauromorfos, pois abriga alguns dos mais antigos registros do grupo em todo mundo, incluindo vários fósseis de dinossauros. Atualmente, a fauna de dinossauromorfos desta unidade é representada por *Ixalerpeton polesinensis*, *Teyuwasu barberenai*, *Staurikosaurus pricei*, *Saturnalia tupiniquim*, *Pampadromaeus barberenai*, *Buriolestes schultzi* e *Bagualosaurus agudoensis*, enquanto para o Noriano da Formação Caturrita são conhecidos *Guaibasaurus candelariensis*, *Unaysaurus tolentinoi* e *Sacisaurus agudoensis*. Visando o melhor entendimento da diversidade de dinossauromorfos oriundos destes depósitos, foram descritos, no contexto dessa tese, diversos novos fósseis do grupo: ULBRA-PVT 059, 280, LPRP/USP 0651, MCN PV 10007-8, 10026, 10027 e 10049. Adicionalmente, foi considerado o recente histórico de pesquisas sobre a origens dos dinossauros para examinar o impacto de novas descobertas e das diferentes hipóteses filogenéticas no entendimento dos padrões biogeográficos da irradiação dos dinossauros.

- ULBRA-PVT059 e 280 representam os holótipos de duas espécies de dinossauiromorfos: *Ixalerpeton polesinensis* e *Buriolestes schultzi*. *I. polesinensis* é o primeiro lagerpetídeo descrito para o Brasil e o único no mundo que preserva elementos do crânio e do membro escapular. O material revela que algumas características antes inferidas como sinapomórficas para Dinosauria já estavam presentes em outros dinossauiromorfos. *B. schultzi* é um sauropodomorfo, provável grupo-irmão dos demais representantes do grupo. Além disso, sua anatomia dentária e relações filogenéticas sugerem que os primeiros dinossauros, incluindo os sauropodomorfos, eram adaptados a faunivoria.

- LPRP/USP 0651 é o holótipo de uma nova espécie de dinossauro, *Nhandumirim waldsangae*, da Formação Santa Maria. Apesar de incompleto, as partes preservadas mostram que este se tratava de um indivíduo juvenil, mas que difere em vários aspectos dos demais dinossauros do Carniano, em especial daqueles provenientes dos mesmos níveis estratigráficos. As relações filogenéticas de *N. waldsangae* indicam que o novo táxon se trata de um dinossauro saurísquio não-sauropodomorfo, possivelmente afim aos terópodos.

- MCN PV 10007-8, 10026, 10027 e 10049 se tratam de materiais de dinossauros provenientes da localidade tipo de *Sacisaurus agudoensis*. Estes representam um sauropodomorfo morfologicamente mais semelhante a membros mais recentes do grupo do que aqueles do Carniano. Assim, correlações bioestratigráficas sugeridas pela presença destes sauropodomorfos indicam uma idade mais nova para a localidade tipo de *S. agudoensis* do que a das biozonas carnianas.

- As análises biogeográficas consistentemente otimizaram a porção sul do Gondwana como a área ancestral de Dinosauria, o mesmo se dando para clados mais inclusivos. Estes resultados mostram que a hipótese em questão é robusta mesmo com maior amostragem taxonômica e geográfica, e independentemente das hipóteses filogenéticas. Desta forma, é demonstrado que não há suporte para a hipótese da Laurásia representar a área ancestral dos dinossauros.

ABSTRACT

Marsola, J. C. A. **Triassic dinosauromorphs from southern Brazil and biogeographic patterns for the origin of dinosaurs.** 2018. 199p. Thesis (Doctorate) – Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, 2018.

The Triassic deposits of southern Brazil harbor a great diversity of terrestrial tetrapods, including therapsids, rhynchocephalians, rhynchosaurs, and archosaurs like pseudosuchians and dinosauromorphs. In this context, the Carnian Santa Maria Formation is important for the understanding of the origins and early diversifications of Dinosauromorpha, as it bears one of the oldest records for the group worldwide, including some of the oldest dinosaurs. Its dinosauromorph fauna is currently represented by *Ixalerpeton polesinensis*, *Staurikosaurus pricei*, *Saturnalia tupiniquim*, *Pampadromaeus barberenai*, *Buriolestes schultzi*, *Bagualosaurus agudoensis*, and *Teyuwasu barberenai*. In comparison, the Norian Caturrita Formation have yielded *Guaibasaurus candelariensis*, *Unaysaurus tolentinoi*, and *Sacisaurus agudoensis*. In order to better understand the dinosauromorph diversity from these deposits, several new fossil remains were described as parts of this thesis: ULBRA-PVT 059, 280, LPRP/USP 0651, MCN PV 10007-8, 10026, 10027, and 10049. In addition, the last 20 years of research efforts on the origins of dinosaurs were compiled to investigate the impact of new discoveries and conflicting phylogenetic hypotheses on the biogeographic history of early dinosauromorphs.

- ULBRA-PVT 059 and 280 represent the holotypes of a lagerpetid dinosauromorph, *Ixalerpeton polesinensis*, and a sauropodomorph dinosaur, *Buriolestes schultzi*. *I. polesinensis* is the first lagerpetid described from Brazil and only worldwide that preserves skull and scapular limb remains, showing that some previously inferred dinosaur synapomorphies were already present in other early diverging dinosauromorphs. *B. schultzi* is found as the sister-group to all other sauropodomorphs. In addition, its tooth anatomy and phylogenetic position suggest that early dinosaurs, including sauropodomorphs, were adapted to faunivory.

- LPRP/USP 0651 is the holotype of a new dinosaur, *Nhandumirim waldsangae*, from the Santa Maria Formation. Although incomplete, the preserved parts show that it was a juvenile individual, but differing in several respects from other Carnian dinosaurs, especially those from the same stratigraphic levels. The phylogenetic relations of *N. waldsangae* suggest that the new taxon is a non-sauropodomorph saurischian dinosaur, possibly related to theropods.

- Dinosaur materials from the type-locality of *Sacisaurus agudoensis* (MCN PV 10007-8, 10026, 10027, and 10049) represent a sauropodomorph, more similar morphologically to later members of the group than to those of Carnian age. Hence, biostratigraphic correlations suggested by these sauropodomorphs indicate an age for the type-site of *S. agudoensis* younger than that of the Carnian biozones.

- Biogeographic analyzes consistently optimize southern Gondwana as the ancestral area for Dinosauria, and this is also the case for more inclusive clades. The results show that the South Gondwanan hypothesis for the origin of dinosaurs is robust even with increased taxonomic and geographic sampling, and independent of phylogenetic uncertainties. It is, therefore, demonstrated that there is no support for Laurasia as the ancestral area of dinosaurs.

SUMÁRIO

1. CONTEXTUALIZAÇÃO GERAL DO TEMA	1
1.1. DINOSSAUROS: ASPECTO HISTÓRICO E CONCEPÇÃO DO GRUPO	1
1.2. ORIGEM DOS DINOSSAUROS E OUTROS DINOSSAUROMORFOS	4
1.3. PRINCIPAIS DIVERGÊNCIAS E RELAÇÕES FILOGENÉTICAS DE DINOSAUROMORPHA	8
1.4. IDADES, MODELOS EVOLUTIVOS E INFERÊNCIAS BIOGEOGRÁFICAS PARA A ORIGEM DOS DINOSSAUROS	11
2. ESTRUTURA GERAL DA TESE	13
3. OBJETIVOS	13
4. CONCLUSÕES	14
REFERÊNCIAS BIBLIOGRÁFICAS	16
ANEXO 1	27
ANEXO 2	35
A NEW DINOSAUR WITH THEROPOD AFFINITIES FROM THE LATE TRIASSIC SANTA MARIA FORMATION, SOUTH BRAZIL	37
INTRODUCTION	39
GEOLOGICAL SETTING	41
SYSTEMATIC PALEONTOLOGY	42
HOLOTYPE	42
ETYMOLOGY	43
TYPE LOCALITY AND HORIZON	43
DIAGNOSIS	43
DESCRIPTION	44
AXIAL	44
TRUNK VERTEBRAE	44
SACRAL VERTEBRAE	45
CAUDAL VERTEBRAE AND CHEVRON	47
ILIUM	49
FEMUR	52
TIBIA	55
FIBULA	56
PES	57
OSTEOHISTOLOGY	60
TIBIA	60
FIBULA	63

DISCUSSION	64
COMMENTS ON THE DIAGNOSIS OF <i>NHANDUMIRIM WALDSANGAE</i>	64
ONTOGENY AND TAXONOMIC VALIDITY OF <i>NHANDUMIRIM WALDSANGAE</i>	70
PHYLOGENETIC ANALYSES AND IMPLICATIONS	73
CONCLUSIONS	77
LITERATURE CITED	78
FIGURES	93

ANEXO 3 **112**

SAUROPODOMORPH REMAINS AND CORRELATION OF THE <i>SACISAURUS</i> SITE, LATE TRIASSIC (CATURRITA FORMATION) OF SOUTHERN BRAZIL	
	113
INTRODUCTION	114
GEOLOGICAL SETTINGS	115
MATERIAL	117
COMPARATIVE DESCRIPTION	117
ECTOPTERYGOID	117
NECK VERTEBRA	118
ILIUM	122
FEMORA	127
METATARSAL	129
DISCUSSION	131
CORRELATIONS OF THE <i>SACISAURUS</i> SITE	131
CYNODONT TEETH	131
<i>SACISAURUS</i> SITE CORRELATION	136
CONCLUSIONS	137
REFERENCES	140
FIGURE CAPTIONS	150

ANEXO 4 **159**

INCREASES IN SAMPLING SUPPORT THE SOUTHERN GONDWANAN HYPOTHESIS FOR THE ORIGIN OF DINOSAURS	
	161
ABSTRACT	162
INTRODUCTION	163
2. MATERIAL AND METHODS	164
(A) SOURCE TREES AND TIME SCALING	164
(B) BIOGEOGRAPHICAL ANALYSES	165
3. RESULTS AND DISCUSSION	166
(A) THE INFERRED ANCESTRAL AREA FOR DINOSAURS	166
(B) HISTORICAL PATTERNS	168
(C) SAMPLING BIASES	170
4. CONCLUSIONS	171
REFERENCES	173
FIGURES AND LEGENDS	181

1. CONTEXTUALIZAÇÃO GERAL DO TEMA

1.1. Dinossauros: aspecto histórico e concepção do grupo

De tão singulares, fósseis de dinossauros parecem ter chamado atenção de curiosos desde tempos mais remotos, possivelmente protagonizando o surgimento de mitos populares dos mais diversos. Estes incluem figuras mitológicas como dragões e grifos no leste Asiático, e até serpentes marinhas no Reino Unido (Delair & Sarjeant, 2002). Na literatura científica, fósseis de dinossauros são documentados pela primeira vez apenas na segunda metade do século XVII, todos provenientes do Reino Unido, tendo Plot (1677) descrito o que hoje é tido como a porção distal de um fêmur de *Megalosaurus*. Este registro é seguido pelo de Lhuyd (1699), que descreve vários dentes fossilizados como parecidos com os de peixes. Dentre os inúmeros espécimes listados, havia um dente de cetiossauro (Delair & Sarjeant, 2002).

Na prática, a consequência destes e dos subseqüentes registros esparsos ao longo do século XVIII, principalmente na Europa e nos Estados Unidos, foi o inevitável aumento do interesse dos naturalistas pelos fósseis. Segundo Delair & Sarjeant (2002), os chamados “fossilistas” britânicos estavam certos da ocorrência de restos de um animal muito grande nos depósitos do sul da Inglaterra. Tanto que no começo do século XIX são descritos os primeiros dinossauros: *Megalosaurus bucklandii* (Buckland, 1824; Mantell, 1827), *Iguanodon anglicus* (Mantell, 1825; Holl, 1829) e *Hylaeosaurus armatus* (Mantell, 1833). Alguns anos depois, estes novos táxons levam Sir Richard Owen (1842) a cunhar o nome Dinosauria para o novo grupo que os congregaria. O nome deriva do grego antigo δεινός (deinos), algo como extremamente grande, e σαῦρος (sauros), réptil, em alusão ao grande tamanho dos membros deste novo grupo, por ele definido a partir dos gêneros supracitados.

Anos mais tarde, foi proposto que teria havido duas linhagens distintas de dinossauros: Saurischia e Ornithischia (Seeley, 1887) (Figura 1). Como os próprios nomes dizem, as principais características que levaram a dissociação de Dinosauria em dois grandes grupos estavam na cintura pélvica. O grupo dos que tinham “quadril de lagarto” congregava os dinossauros bípedes e carnívoros, ou terópodos como *Megalosaurus*, e os grandes saurópodes que eram quadrúpedes, herbívoros e de pescoço comprido. Já o grupo dos que tinham “quadril de ave” era o dos ornitíscios, que reunia uma enorme diversidade de grandes herbívoros quadrúpedes e bípedes, com grandes chifres e “armaduras” dorsais, como *Hylaeosaurus*. Por muito tempo os sauríscios e ornitíscios foram considerados grupos muito distintos, e não aparentados (e.g. Colbert, 1964; Charig et al. 1965; Romer, 1966; Brusatte et al. 2010), o que implicaria na parafilia de Dinosauria. Porém, desde que Bakker e Galton (1974) propuseram sua monofilia, diversas novas características foram propostas (e.g. Benton, 1984; Gauthier, 1986; Novas, 1996), sustentando essa classificação até hoje.

Atualmente, o grupo é mundialmente reconhecido por uma diversidade singular que se irradiou no Triássico Superior e que sofreu uma grande perda de diversidade ao fim do Cretáceo. Não extinta, a linhagem persiste até os dias de hoje representada pelas aves. A distribuição temporal do grupo resulta numa história de sucesso evolutivo de aproximadamente 240 milhões de anos (Serenó, 1999; Ezcurra, 2012). Alguns levantamentos (Wang & Dodson, 2006) mostram mais de 500 gêneros de dinossauros não-avianos descritos, estimando que potencialmente haja mais de 1.800 gêneros, a grande maioria dos quais ainda por serem descobertos (Figura 1).

No Brasil, a pesquisa com dinossauros começou já no século XIX a partir dos primeiros registros documentados por Allport (1860) e Marsh (1869) de depósitos do Cretáceo. Todavia, estas e subseqüentes descobertas de dinossauros ao longo da

primeira metade do século XX no Brasil são de afinidades taxonômicas incertas (Kellner e Campos, 2000; Bittencourt e Langer, 2011). Assim, a primeira espécie de dinossauro descrita para o Brasil se trata do herrerasaurídeo *Staurikosaurus pricei* (Colbert, 1970), coletado em sedimentos da Formação Santa Maria (Triássico Superior), na cidade homônima, interior do Rio Grande do Sul, no ano de 1936 (Beltrão, 1965).

Figura 1: Super-árvore de Dinosauria que mostra a diversidade do grupo e as relações entre as principais linhagens, tais como Sauropodomorpha (azul), Theropoda (verde) e Ornithischia (vermelho). Retirado de Lloyd et al. (2008).

1.2. Origem dos dinossauros e outros dinossauromorfos

Dinossauromorpha é o clado mais diverso, e o único com representantes viventes, de Ornithodira, que além dos dinossauromorfos e dinossauros, congrega os pterossauros (Langer et al. 2013). Como parte do grupo, há os lagerpetídeos, silesaurídeos e outros dinossauriformes, além de, claro, os dinossauros.

Os Lagerpetidae são caracterizados pelo seu pequeno porte, provável bipedalismo, com membros pélvicos longos e delgados (Figura 2). Porém, essa caracterização geral se dá pelo fato de que, por muito tempo, a anatomia do grupo foi conhecida apenas a partir dos relativamente incompletos espécimes de *Lagerpeton chanarensis*. Os fósseis mais antigos do grupo são provenientes da Formação Chañares, no noroeste argentino, datados do início do Carniano (Marsicano et al. 2016). *Lagerpeton chanarensis* foi o primeiro a ser descrito (Romer, 1971, 1972; Arcucci, 1986; Sereno & Arcucci, 1994a), enquanto outros lagerpetídeos foram descobertos somente mais recentemente, incluindo as três espécies do gênero *Dromomeron*, *D. romeri* (Irmis et al. 2007), *D. gregorii* (Nesbitt et al. 2009) e *D. gigas* (Martínez et al. 2016), todos do Noriano. Embora já houvesse um primeiro registro de lagerpetídeo para o Carniano tardio da Formação Ischigualasto (Martínez et al. 2012), o registro mais completo para essa idade se trata de *Ixalerpeton polesinensis*, da Formação Santa Maria, (Cabreira et al. 2016), que preserva os primeiros elementos cranianos e do membro escapular conhecidos para o grupo (Figura 2).

Figura 2: Reconstrução esquelética de diversos dinossauros, ilustrando o formato geral do corpo e os elementos preservados. (A) *Ixalerpeton polesinensis*. (B) *Marasuchus lilloensis*. (C) *Silesaurus opolensis*. (D) *Buriolestes schultzi*. A, D, retirado de Cabreira et al. (2016). B-C, retirado de Langer et al. (2013). Escala de 10 cm.

Os lagerpetídeos são grupo irmão dos demais dinossauros, os Dinosauriformes. O registro de dinosauriformes não-dinossauros, é mais amplo que o de lagerpetídeos, tendo sido identificados táxons nas Américas do Norte (Sullivan & Lucas, 1999; Ezcurra, 2006) e do Sul (e.g. Romer, 1971; 1972; Bonaparte, 1975; Sereno & Arcucci, 1994b; Ferigolo & Langer, 2007; Langer & Ferigolo, 2013), Europa (Huene, 1910; Benton & Walker, 2011; Fraser et al. 2002; Dzik, 2003) e África (Nesbitt et al. 2010; Kammerer et al. 2012; Peacock et al. 2013). A forma mais antiga do grupo se trata de *Asilisaurus kongwe* (Nesbitt et al. 2010), do Anisiano da Tanzânia.

Dentre os dinossauriformes não-dinossauros, os silesaurídeos desempenham um papel de maior destaque para o entendimento da evolução dos dinossauros. Aliado ao seu posicionamento como grupo irmão de Dinosauria (Langer et al. 2013; ver também Langer & Ferigolo, 2013; Cabreira et al. 2016), a anatomia do grupo dissociou diversas características tradicionalmente entendidas como sinapomórficas para Dinosauria. Dentre elas, destacam-se a presença de epipófises nas vértebras cervicais, três ou mais vértebras sacrais, e o acetábulo ilíaco pelo menos semi-perfurado, como em *Silesaurus opolensis* (Dzik, 2003; Langer et al. 2013) (Figura 2). Ainda, algumas características mais incomuns como a presença de elemento homólogo ao osso pré-dentário, sugerem que os Silesauridae seriam afins aos dinossauros ornitísquios (Ferigolo & Langer, 2007; Niedzwiedzki et al. 2009; Langer & Ferigolo, 2013; Cabreira et al. 2016).

Já os fósseis mais antigos de dinossauros são representados quase que exclusivamente por saurísquios, como *Saturnalia tupiniquim* e *Staurikosaurus pricei*. Estes registros estão inseridos no contexto dos depósitos cronocorrelatos das formações Ischigualasto (noroeste da Argentina) e Santa Maria (Rio Grande do Sul, Brasil), Carniano tardio (Triássico Superior), do sudeste do Pangeia (Martínez et al. 2011; Langer et al. 2018). Dentre os primeiros dinossauros, Sauropodomorpha é o grupo mais especioso, com sete espécies descritas. Estas ocorrem tanto na Formação Ischigualasto, representados por *Eoraptor lunensis* (Serenó et al. 1993), *Panphagia protos* (Martínez & Alcober, 2009) e *Chromogisaurus novasi* (Ezcurra, 2010), quanto na Formação Santa Maria, representados por *Saturnalia tupiniquim* (Langer et al. 1999), *Pampadromaeus barberenai* (Cabreira et al. 2011), *Buriolestes schultzi* (Cabreira et al. 2016) (Figura 2), e *Bagualosaurus agudoensis* (Pretto et al. 2018). Ao contrário de outros membros mais recentes da linhagem que eram herbívoros, de grandes dimensões, e pesando várias toneladas, estes primeiros sauropodomorfos eram pequenos animais com cerca de 1

metro de comprimento e adaptados para a faunivoria (Cabreira et al. 2016; Bronzati et al. 2017; Müller et al. 2018).

No caso dos terópodos, os registros são mais escassos. Originalmente, interpretou-se que *Eoraptor lunensis* (Serenó et al. 1993) seria um representante do grupo de idade Carniana. Entretanto, essa visão não é mais consensual entre os pesquisadores (e.g. Langer & Benton, 2006; Sereno et al. 2012; Cabreira et al. 2016). Assim, o registro de terópodos carnianos ficaria restrito a *Eodromaeus murphi* (Martínez et al. 2011; Nesbitt & Ezcurra, 2015), cujas relações filogenéticas também são divergentes em alguns trabalhos (Cabreira et al. 2016). Todavia, vários estudos têm recuperado os herrerasaurídeos como um clado de terópodos exclusivo do Carniano (e.g. Nesbitt & Ezcurra, 2015), apesar dessa hipótese também não ser consensual (e.g. Langer & Benton, 2006; Cabreira et al. 2016). Este grupo é composto por predadores de médio a grande porte, atualmente representados por *Herrerasaurus ischigualastensis* (Reig, 1963), *Sanjuansaurus gordilloi* (Alcober & Martínez, 2010) e *Staurikosaurus pricei* (Colbert, 1970).

Na contramão dos prolíferos registros de saurísquios, os de ornitísquios são mais escassos não apenas para o Carniano tardio, como também para o todo o Triássico. O táxon argentino *Pisanosaurus mertii* (Casamiquela, 1967) surge como o representante mais antigo do grupo. Porém, a partir de uma nova proposta que o reclassifica como um sillesaurídeo (Agnolín & Rozadilla, 2017), surge nova perspectiva de que ornitísquios podem ter surgido apenas no Jurássico (Baron, 2017). Isso implicaria em que apenas dinossauros tradicionalmente agrupados sem Saurischia – *sensu* Seeley, 1887; Gauthier, 1986 – estariam presentes no Triássico.

Outros possíveis registros de dinossauros também provêm da parte sul do Pangeia, incluindo os dinossauros mais antigos fora do contexto sul-americano

(Ezcurra, 2012). Foi identificado na Formação Pebbly Arkose, Zimbábue, um fragmento de fêmur, originalmente descrito como afim aos “prosaurópodes” por Raath (1996), reinterpretado por Langer et al. (1999) como semelhante ao de *Saturnalia tupiniquim* e classificado por Ezcurra (2012) como um saurísquio indeterminado.

Dos níveis inferiores da Formação Maleri, Índia, os registros são um pouco mais completos, todavia não muito diagnósticos (Ezcurra, 2012). Chatterjee (1987) atribuiu elementos apendiculares à espécie *Alwalkeria maleriensis*, atualmente considerado um saurísquio de afinidades incertas (Remes & Rauhut, 2005; Novas et al. 2011). Outros fragmentos descritos por Huene (1940) compreendem a porção distal de um fêmur e a porção proximal de uma tíbia, ambos atribuídos a um terópode “coelurosauro” indeterminado, além de três vértebras truncais incompletas relacionadas aos “prossaurópodes”. Mais recentemente, Ezcurra (2012) propõem novas relações para estes fósseis, onde o fragmento femoral e as vértebras teriam afinidades indeterminadas com arcossauromorfos, ao passo que a porção proximal da tíbia poderia ser classificada como um dinossauro saurísquio indeterminado.

1.3. Principais divergências e relações filogenéticas de Dinosauromorpha

Dinosauria compõem, juntamente com Silesauridae e Lagerpetidae, o clado Dinosauromorpha (*sensu* Langer et al. 2010a). O posicionamento de Lagerpetidae como um grupo externo aos outros Dinosauromorpha, como *Marasuchus lilloensis* e Silesauridae, é recorrente na maior parte das análises (e.g. Sereno & Arcucci, 1994; Novas, 1996; Nesbitt, 2011; Bittencourt et al. 2015; Cabreira et al. 2016; Baron et al. 2017) (Figura 3). Por outro lado, diversas incertezas circundam as relações de Dinosauriformes (Langer, 2014). Embora as relações internas de Silesauridae também não sejam muito claras, com o possível posicionamento de *Asilisaurus kongwe* e

Lewisuchus admixtus fora do grupo (Bittencourt et al. 2015; Langer et al. 2017), a maior divergência é quanto ao possível posicionamento de Silesauridae em Dinosauria, na linhagem dos Ornithischia (Langer & Ferigolo, 2013; Cabreira et al. 2016) (Figura 3). Em contrapartida, a visão mais consensual sobre o posicionamento de Silesauridae entre os dinossauriformes é de que o clado seria o grupo-irmão de Dinosauria (Nesbitt, 2011; Bittencourt et al. 2015; Baron et al. 2017; Nesbitt et al. 2017) (Figura 3). O dinossauriforme *Marasuchus lilloensis*, por sua vez, possui relações bem estabelecidas em todas análises cladísticas, onde é sempre recuperado como grupo-irmão de clado congregando todos os demais membros do grupo. Por outro lado, *Saltopus elginensis* continua tendo seu posicionamento dentro de Dinosauriformes disputado em diversas hipóteses, flutuando como grupo-irmão de Silesauridae, Dinosauria, ou mesmo de ambos (e.g. Baron et al. 2017; Langer et al. 2017).

Não obstante o recente avanço nas pesquisas sobre a origem e irradiação inicial de Dinosauria, ainda existem várias divergências quanto ao posicionamento filogenético de algumas espécies ou grupos, a exemplo de Silesauridae, como comentado anteriormente. Herrerasauridae é tanto tido tanto como afim aos terópodos (e. g. Nesbitt & Ezcurra, 2015), como é também interpretado como um grupo de saurísquios não-eusaurísquios (Cabreira et al. 2016). *Eoraptor lunensis*, *Eodromaeus murphi* e *Guaibasaurus candelariensis* são outros exemplos de táxon com relações divergentes, tendo sido inferidos tanto como terópodos, sauropodomorfo, ou saurísquios não-eusaurísquios em diversas análises (Serenó et al. 1993; Ezcurra, 2010; Langer et al. 2010b; Martínez et al. 2011; Nesbitt & Ezcurra, 2015; Cabreira et al. 2016; Baron et al. 2017; Langer et al. 2017).

Figura 3: Filogenia calibrada no tempo mostrando as relações entre os primeiros dinossauromorfos. Barras pretas representam a distribuição temporal dos táxons. Números se referem a Dinosauriomorpha (1), Dinosauriformes (2), Ornithischia (3), Silesauridae (4), Herrerasauridae (5), Eusaurischia (6). Retirado de Cabreira et al. (2016).

Dentre as várias propostas recentes, a mais divergente diz respeito ao rearranjo das relações entre as três principais linhagens de Dinosauria: Ornithischia, Theropoda e

Sauropodomorpha. A nova hipótese levantada por Baron et al. (2017; mas veja Langer et al. 2017) questiona o esquema de classificação clássico (Seeley, 1887; Gauthier 1986), e sugere que Ornithischia e Theropoda seriam mais proximamente relacionados, formando o clado Ornithoscelida, ao passo que Saurischia seria composto apenas por Sauropodomorpha e Herrerasauridae.

1.4. Idades, modelos evolutivos e inferências biogeográficas para a origem dos dinossauros

Os recentes esforços para o melhor entendimento da origem dos dinossauros também incluíram a datação radioisotópica dos depósitos que abrigam estes e outros dinossauiromorfos. A datação Formação Chañares (Marsicano et al. 2016), de onde provém *Lagerpeton chanarensis*, *Marasuchus lilloensis*, *Lewisuchus admixtus* e *Pseudolagosuchus major*, revelou que o depósito tem uma idade máxima de 236 Ma (milhões de anos), o que corresponde ao Carniano inferior, sendo 5-10 Ma mais nova do que previamente inferido. Já os níveis inferiores da Formação Ischigualasto, nos quais são encontrados a maior parte dos dinossauros da unidade, forneceram uma idade máxima de 231,4 Ma (Martínez et al. 2011), enquanto a Formação Santa Maria foi mais recentemente datada em aproximadamente 233,2 Ma (Langer et al. 2018). Porém, considerando a idade Anisiana inferida para os Manda Beds, estrato-tipo de *Asilisaurus kongwe* (Nesbitt et al. 2010, 2017), a origem dos dinossauros e sua divergência de outros grupos de dinossauiromorfos teria ocorrido muito antes, durante o Triássico Médio, sendo as espécies do Triássico Superior representantes de linhagens que persistiram por alguns milhões após seu surgimento (Langer et al. 2013).

Por mais diversos que parecessem ser, os primeiros dinossauros não eram os principais componentes faunísticos de sua época. Uma grande diversidade de

pseudosúquios, rincossauros e terápsidos não só compartilhava os mesmos habitats que os dinossauros e outros dinossauromorfos durante o Triássico Superior, como eram mais abundantes (Langer, 2005a,b; Brusatte et al. 2008 a,b; 2010; Langer et al. 2010a; Martínez et al. 2012, 2016; Sookias et al. 2012; Benton et al. 2014). Assim, credita-se que este cenário teria restringido uma possível maior diversificação dos dinossauros. Todavia, após a extinção destes grupos, após a passagem Triássico-Jurássico, os dinossauros teriam oportunisticamente se irradiado em uma grande diversidade de espécies, se estabelecendo como as formas dominantes nos ecossistemas terrestres de todo o mundo (Brusatte et al. 2008 a,b; Benton et al. 2014). Possivelmente, esse processo teve como fator facilitador as altas taxas de crescimento corpóreo do grupo (Sookias et al. 2012).

Devido ao fato dos mais abundantes e antigos registros de dinossauromorfos serem de depósitos da América do Sul e África, convencionou-se inferir a porção sudoeste do Pangeia, ou oeste do Gondwana, como área ancestral dos dinossauros e outros dinossauromorfos (Nesbitt et al. 2010, 2013; Marsicano et al. 2016; Baron et al. 2017). Com inferido, inclusive, com base em análises biogeográficas quantitativas (Nesbitt et al. 2009). Entretanto, esta hipótese foi recentemente questionada por Baron et al. (2017), sugerindo que, dependendo das relações filogenéticas de *Saltopus elginensis* e Silesauridae, os dinossauros pudessem ter se originado ao norte do Pangeia, em sua porção Laurasiana. Essa nova proposição foi alvo de críticas, principalmente por não ser subsidiada por nenhuma sorte de análise quantitativa (Langer et al. 2017). De fato, estes demonstraram que independentemente do rearranjo filogenético proposto por Baron et al. (2017), a região sul do Pangeia detém as maiores probabilidades de corresponder à área ancestral para Dinosauria.

2. ESTRUTURA GERAL DA TESE

Esse documento é composto do presente texto integrador e de um conjunto de quatro anexos, os quais correspondem ao desenvolvimento dos objetivos da tese, apresentados a seguir. Os anexos estão apresentados em inglês e no formato de artigos conforme publicados e/ou submetidos. Os mesmos são precedidos por uma folha de rosto contendo título, citação e síntese em português. Antecedendo a sessão dos anexos estão as conclusões gerais da tese, ao passo que pontos mais específicos, como discussão e metodologia empregada, se encontram no corpo dos mesmos.

3. OBJETIVOS

Dois objetivos centrais justificam este estudo: (1) descrição anatômica e estabelecimento das relações filogenéticas de um conjunto de dinossauromorfos do Triássico Superior do Rio Grande do Sul e (2) análise dos padrões biogeográficos da irradiação dos dinossauros. Ambos melhor delineados na sequência:

- Descrição anatômica, avaliação das relações filogenéticas e paleoecológicas dos espécimes de dinossauromorfos ULBRA-PVT 059 e 280.
- Descrição anatômica (incluindo osteohistologia), avaliação ontogenética e das relações filogenéticas do espécime de dinossauro LPRP/USP 0651, e suas implicações macro evolutivas para a origem dos dinossauros.
- Descrição anatômica de materiais isolados de dinossauros (MCN PV 10007, 10008, 10026, 10027, 10040 e 10049) e seu significado para as correlações bioestratigráficas da localidade-tipo do sillessaurídeo *Sacisaurus agudoensis*.

- Investigação dos possíveis efeitos das recentes descobertas de novos táxons de dinossauromorfos Triássicos (i.e., aumento da diversidade) e de novas e conflitantes hipóteses filogenéticas no estabelecimento de modelos biogeográficos da irradiação inicial dos dinossauros.

4. CONCLUSÕES

A partir dos trabalhos anexados, as principais conclusões desta tese são:

- ULBRA-PVT 059 e 280 representam duas novas espécies de dinossauromorfos do Carniano tardio do Sul do Brasil: *Ixalerpeton polesinensis* e *Buriolestes schultzi*. *I. polesinensis* é o primeiro lagerpetídeo brasileiro a ser descrito e o que primeiro no mundo que preserva elementos do crânio e do membro escapular. *B. schultzi* é um sauropodomorfo, recuperado filogeneticamente como o grupo-irmão dos demais Sauropodomorpha. Além disso, sua anatomia dentária, juntamente com seu posicionamento filogenético, sugere que os primeiros dinossauros teriam sido adaptados à faunivoria, e que a herbivoría aparece mais tardiamente em Sauropodomorpha.
- LPRP/USP 0651 se trata de uma nova espécie de dinossauro do Carniano tardio do sul do Brasil: *Nhandumirim waldsangae*. Apesar de fragmentário, as partes preservadas de seu esqueleto mostram que era um indivíduo jovem, mas que difere em vários aspectos dos demais dinossauros do Carniano, em especial daqueles provenientes da mesma localidade e níveis estratigráficos, i.e. *Saturnalia tupiniquim* e *Staurikosaurus pricei*. As relações filogenéticas de *N. waldsangae*, recuperadas a partir de duas análises com bancos de dados distintos, concordam

que o novo táxon é um dinossauro. Apesar de consistentemente aparecer fora da linhagem dos sauropodomorfos, suas relações mais específicas são ainda controversas, apesar de ser sugerido alguma afinidade com a linhagem dos terópodos.

- Os materiais de dinossauros provenientes da localidade-tipo de *Sacisaurus agudoensis* representam um sauropodomorfo morfologicamente mais semelhante com sauropodomorfos mais recentes do que com aqueles do Carniano. Aliada com a avaliação dos materiais de cinodontes "brasilodontídeos" do mesmo sítio, as correlações bioestratigráficas impostas pela presença destes sauropodomorfos sugerem uma idade mais nova para a localidade tipo de *S. agudoensis* do que aquela das biozonas carnianas onde predominam *Hyperodapedon* e *Exaeretodon*.
- Apesar dos recentes avanços nas pesquisas sobre a origem dos dinossauros nos últimos 20 anos, as análises biogeográficas consistentemente otimizam a porção sul do Gondwana como a área ancestral de Dinosauria. O mesmo ocorre com clados mais inclusivos, como Dinosauromorpha, e mostram que essa hipótese é robusta mesmo com o aumento da amostragem taxonômica e geográfica, bem como com base em hipóteses filogenéticas conflitantes. De acordo com os resultados, não há suporte para que a Laurásia seja considerada a área ancestral dos dinossauros, como recentemente proposto. Os resultados mostram que a origem de Dinosauria ao sul do Gondwana se sustenta como hipótese mais plausível, dado o atual conhecimento da diversidade dos primeiros dinossauros e dinosauromorfos não-dinossauros.

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ANEXO 1

Dinossauromorfos do Triássico Superior do Brasil revelam a anatomia e dieta ancestral dos dinossauros

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Material suplementar: se encontra disponível no CD-ROM anexado ao final da Tese, ou *online* pelo link abaixo.

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Síntese do anexo 1

Conhecidos desde o Triássico Médio, o clado Dinosauromorpha inclui não somente os dinossauros, mas também uma série de espécies filogeneticamente próximas ao grupo. Dentre estes, os Lagerpetidae foram o grupo-irmão dos Dinosauriformes e ocorrências conjuntas destes táxons com dinossauros são raras. Este trabalho descreve um novo lagerpetídeo encontrado ao lado de um dinossauro saurísquio, no contexto da Formação Santa Maria, sul do Brasil. Ambos os fósseis estão bem preservados e completos, o que mostra que esses animais eram contemporâneos desde os primeiros estágios da evolução dos dinossauros. O novo lagerpetídeo, *Ixalerpeton polesinensis*, preserva o primeiro crânio conhecido para o grupo, além de grande parte do esqueleto apendicular,

revelando como os dinossauros adquiriram várias de suas características típicas, como uma longa crista deltopeitoral do úmero. Além disso, uma nova análise filogenética sugere o dinossauro *Buriolestes schultzi*, também descrito nesse trabalho, seja o sauropodomorfo irmão de todos os demais representantes do grupo. Seus dentes plesiomórficos, estritamente adaptados para faunivoria, fornecem dados importantes para inferir o hábito alimentar dos primeiros dinossauros. Neste contexto, sugere-se que os primeiros dinossauros foram faunívoros, incluindo os membros mais antigos de Sauropodomorpha, um grupo caracterizado por animais gigantescos e herbívoros.

A Unique Late Triassic Dinosauriform Assemblage Reveals Dinosaur Ancestral Anatomy and Diet

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SUMMARY

Dinosauriforma includes dinosaurs and other much less diverse dinosaur precursors of Triassic age, such as lagerpetids [1]. Joint occurrences of these taxa with dinosaurs are rare but more common during the latest part of that period (Norian-Rhaetian, 228–201 million years ago [mya]) [2, 3]. In contrast, the new lagerpetid and saurischian dinosaur described here were unearthed from one of the oldest rock units with dinosaur fossils worldwide, the Carnian (237–228 mya) Santa Maria Formation of south Brazil [4], a record only matched in age by much more fragmentary remains from Argentina [5]. This is the first time nearly complete dinosaur and non-dinosaur dinosauriform remains are found together in the same excavation, clearly showing that these animals were contemporaries since the first stages of dinosaur evolution. The new lagerpetid preserves the first skull, scapular and forelimb elements, plus associated vertebrae, known for the group, revealing how dinosaurs acquired several of their typical anatomical traits. Furthermore, a novel phylogenetic analysis shows the new dinosaur as the most basal Sauropodomorpha. Its plesiomorphic teeth, strictly adapted to faunivory, provide crucial data to infer the feeding behavior of the first dinosaurs.

RESULTS

Here we report one of the oldest (and the best preserved) associations of dinosaur and dinosaur precursor, respectively represented by new species of Lagerpetidae and Sauropodomorpha. There is evidence of four individuals in the association, two lagerpetids and two dinosaurs. The lagerpetids are represented by a

semi-articulated skeleton and a pair of fragmentary femora. As for the dinosaurs, a large articulated individual was preserved, together with smaller and non-duplicated bone elements that indicate the presence of another individual (either a juvenile or a smaller taxon). The two articulated specimens correspond to the type-specimens of the new taxa proposed below.

Systematic Paleontology

Locality, Stratigraphy, and Age

The specimens were collected side by side at the Buriol ravine (29°39'30.78"S; 53°26'08.97"W), São João do Polêsine-RS, Brazil; Almoa Member, Santa Maria Formation; Candelária Sequence, Paraná Basin [6]; *Hyperodapedon* Assemblage Zone, Carnian, Late Triassic [7].

Archosauria Cope, 1869 [8]

Dinosauriforma Benton, 1985 [9]

Lagerpetidae Arcucci, 1986 [10]

Ixalerpeton polesinensis gen. et sp. nov.

Holotype. ULBRA-PVT059. Partially articulated skeleton including skull roof, braincase, 23 pre-sacral, two sacral, and nine tail vertebrae, right scapula, left humerus, paired pelvic girdle, femur, tibia, and fibula (Figures 1A–1H and S1).

Etymology. The genus name combines the Greek words *ἵλαρος* (= leaping) and *ῥεπτόν* (= reptile). The specific epithet refers to São João do Polêsine, the town where the specimens were found.

Diagnosis. *Ixalerpeton polesinensis* differs from other Lagerpetidae by a unique suite of traits (autapomorphies marked with an asterisk): iliac antitrochanter, dorsoventrally deep distal end of the ischial shaft, pubis lacking ambiens process*, crest-shaped fourth trochanter, medial condyle of distal end of the femur with low angled craniomedial* and sharp angled caudomedial corners, and proximal end of the tibia with deep caudal groove.

Dinosauriformes Novas, 1992 [11]

Dinosauria Owen, 1842 [12]

Saurischia Seeley, 1887 [8]

Sauropodomorpha Huene, 1932 [13]

Buriolestes schultzi gen. et sp. nov.

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Figure 1. Skeletal Features of *Ixalerpeton polesinensis* and *Buriolestes schultzi*

(A–H) *I. polesinensis* (ULBRA-PVT059).

(A) Skeletal reconstruction.

(B) Skull roof.

(C) Braincase.

(D) Pre-sacral vertebrae.

(E) Sacral vertebrae.

(F) Humerus.

(G) Pelvis.

(H) Femur.

(I–P) *B. schultzi* (ULBRA-PVT280).

(I) Skeletal reconstruction.

(J) Skull.

(K) Humerus.

(L) Ilium.

(M) Ischium.

(N) Femur.

(O) Tibia and fibula proximal articulation.

(P) Epipodium and pes.

Some figured bones are still partially imbedded in the rock matrix, which has been digitally removed. See also [Figures S1](#) and [S2](#).

Abbreviations are as follows: a, astragalus; ac, acetabulum; bf, brevis fossa; d, dentary; dpc, deltopectoral crest; f, frontal; fi, fibula; fm, foramen magnum; ft, fourth trochanter; hy, hyoid apparatus; il, ilium; is, ischium; j, jugal; lt, lesser trochanter; m, maxilla; mcp, medial condyle projection; mt I, metatarsal I; p, parietal; pu, pubis; pm, premaxilla; pof, postfrontal; pp, paroccipital process; qj, quadratojugal; sa, surangular; so, supraoccipital; t, tibia.

Holotype. ULBRA-PVT280. Articulated skeleton including partial skull, few pre-sacral, three sacral, and 42 tail vertebrae, left scapula and forelimb lacking most of the manus, paired ilia and ischia, partial left pubis, and nearly complete left hind limb ([Figures 1I–1P](#) and [S2](#)).

Etymology. The genus name combines the Greek word ληστής (= robber) and the family name (Burio) of the type-locality owners. The specific epithet honors the paleontologist Cesar Schultz.

Diagnosis. *Buriolestes schultzi* differs from other sauropodomorphs by an autapomorphic caudal projection of the medial condyle of the tibia ([Figure 1O](#)), medial to the intercondylar notch; a full differential diagnosis is provided in the [Supplemental Experimental Procedures](#).

Descriptions

The parietal and frontal bones of *Ixalerpeton polesinensis* form a skull roof broader than that of most early dinosaurs. A large postfrontal fits laterally to the frontal, as more common to

non-archosaur archosauriforms [14]. Unlike dinosaurs [15], *I. polesinensis* retains a frontal not excavated by the supratemporal fossa and a post-temporal opening not reduced to a foramen-sized aperture. Medial to that, a notch in the supraoccipital indicates the path of the middle cerebral vein, which also laterally pierces the braincase, dorsal to the trigeminal foramen. The lateral braincase wall hosts the anterior tympanic recess [14, 16] and a shallow depression on the caudoventral surface of the parabasisphenoid (also seen in *Lewisuchus admixtus*, *Saturnalia tupiniquim*, and *Eodromaeus murphy*) that resembles the semilunar depression of non-archosaur archosauriforms [17]. Comparisons to other dinosauriforms [18–20] indicate that *I. polesinensis* preserves pre-sacral vertebrae 6–20, the first two of which are longer and may correspond to the last neck vertebrae. The trunk series starts with transitional morphologies, including a trapezoidal second vertebra as in *Marasuchus lilloensis* [20]. Unlike silesaurids [18] and most dinosaurs [15], the lateral surface of the neural arches lack laminae radiating from the apophyses, and the caudalmost vertebra lacks the cranially inclined neural spines described for *Lagerpeton chanarensis* [21]. The two-vertebrae sacrum fits the archosaur plesiomorphic pattern [14]. The ilium has a fully closed acetabulum, the caudal margin of which bears an antitrochanter. This is continuous to the ischial antitrochanter, which forms the entire acetabular margin of the bone, as in *L. chanarensis* [21]. *Ixalerpeton polesinensis* also shares an extensive ventromedial flange of the ischium with the latter taxon, forming the laminar symphysis and a deep articulation with the pubis. Its femur has various lagerpetid [5, 10] traits such as a large caudomedial tuber of the proximal portion, a lateral emargination ventral to the head, and a large tibiofibular crest separated from the lateral condyle by a deep groove. The fourth trochanter forms a large crest, differing from that of *Dromomeron* spp [10].

Buriolestes schultzi lacks usual sauropodomorph traits such as a reduced skull and an enlarged external naris [22]. As in all early dinosaurs [14], the frontal is excavated by the supratemporal fossa. A sharp ridge forms the ventral border of the antorbital fenestra, as is typical of neotheropods [23], but a subnasal gap and/or diastema is lacking in the premaxilla-maxilla junction. The dentary tip resembles those of other Carnian sauropodomorphs, with 2–3 large foramina and the ventrally sloping surface housing the first two teeth. Most teeth are caudally curved, with serrations (six per millimeter) forming straight angles to the crown margin, but these are not seen in the mesial carina of the elongate rostral teeth, a feature also reported for some neotheropods [23]. As typical of sauropodomorphs [24], the humerus is longer than 60% the length of the femur, and the deltopectoral crest extends for more than 40% of its length. The last of the three sacral vertebrae lacks dorsoventrally expanded ribs and, as in *Saturnalia tupiniquim* and *Plateosaurus engelhardti* [25], was surely incorporated from the tail series. The iliac preacetabular ala is short and dorsoventrally expanded, whereas the long postacetabular ala is ventrally excavated by a *brevis* fossa. The ventral margin of the acetabular wall is plesiomorphically straight [14], as in *Panphagia protos* and *S. tupiniquim*. The pubic shaft is straight, laminar, and slightly expanded at the distal end, lacking typical traits found in major dinosaur groups [15], e.g., sauropodomorph “apron,” theropod “boot,” ornithischian retroversion. The femoral head is expanded and kinked, as typical of

dinosaurs [15], but not completely inturned (states 304-2 and 305-1 in [14]). The iliofemoral musculature attaches to a subtle anterior trochanter and a marked trochanteric shelf. The tibia is slightly longer than the femur, but not as much as in early ornithischians and theropods, which also have an expanded outer malleolus [15], absent in *B. schultzi*. As in most non-theropod saurischians [15], the calcaneum is proximodistally flattened and has a reduced tuber. The third metatarsal is the longest, as is typical of dinosaurs [14], and the fifth element is proximally expanded. The distalmost of the 42 preserved tail vertebrae lack elongated prezygapophyses, differing from those of *Tawa hallae*, herrerasaurids, and neotheropods [14, 15].

DISCUSSION

A new phylogenetic analysis (see [Supplemental Experimental Procedures](#)) places *Ixalerpeton polesinensis* and *Buriolestes schultzi* respectively within Lagerpetidae and Sauropodomorpha (Figures 2 and S3). The joint record of sauropodomorphs and lagerpetids in the Santa Maria Formation matches a similar find in the coeval Ischigualasto Formation of Argentina [5]. Based on much more complete remains, the new discovery confirms that the co-occurrence between non-dinosaurian Dinosauriforms and dinosaurs was not restricted to later stages of the Triassic and to the northern parts of Pangaea, where silesaurids and lagerpetids have been found together with theropod dinosaurs [2, 3], reinforcing rapid replacement as a very unlikely scenario for the initial radiation of dinosaurs [2, 26, 27].

The discovery of *Ixalerpeton polesinensis* helps define traits of anatomical parts previously unknown for lagerpetids that are either unique to Dinosauriforms or diagnose less inclusive groups. For example, *I. polesinensis* bears an anterior tympanic recess in the braincase, as is typical of Dinosauriforms [14] and more recently also found out of the dinosaur line of archosaurs [28], but retains traits unknown to that group, such as a large post-temporal fenestra, a postfrontal bone, and a frontal not excavated by the supratemporal fossa [14]. Also, its glenoid faces slightly laterally, a plesiomorphic condition modified in Dinosauriforms to a fully caudally facing articulation [15]. On the contrary, its deltopectoral crest extending for more than 30% of the humerus demonstrates that this condition is plesiomorphic for Dinosauriforms.

Buriolestes schultzi adds to the recently found plethora of Carnian dinosaurs [22, 29–31], but its unique position as the sister taxon to all other sauropodomorphs helps clarify the sequence of character acquisition in the early evolution of the group. Sauropodomorphs share a ventrally bent dorsal margin of the dentary tip (usually with an inset first tooth) and a low mandibular articulation. Their humeri bear a long deltopectoral crest, particularly in the sister clade to *B. schultzi*. The sister clade to *Eoraptor lunensis* is characterized by a broader distal end of the humerus and the prevalence of teeth with leaf-shaped crowns and large denticles (four per millimeter). More caudal teeth with significantly shorter crowns are only seen in members of the clade formed by *Saturnalia tupiniquim*, *Chromogisaurus novasi*, *Panphagia protos*, and norian sauropodomorphs. Among these, *P. protos* has a skull that surpasses two-thirds of the femoral length, suggesting that it may represent an earlier split compared to *S. tupiniquim*.

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Figure 2. Time-Calibrated Phylogeny of Early Dinosauro-morphs

Simplified version of the strict consensus tree. See also Figure S3. Lagerpetidae, Dinosauria, Saurischia, Theropoda, and Sauropodomorpha are marked as color blocks. Numbered nodes represent Dinosauro-morphs (1), Dinosauriformes (2), Omithischia (3), Silesauridae (4), Herrerasauridae (5), Eusaurischia (6). Silhouettes represent the newly described *Ixalerpeton polesinensis* and *Buriolestes schultzi*. Stratigraphic ranges mark uncertainties about the age of the fossil occurrences, not the actual duration of the lineage.

Dental traits of *Buriolestes schultzi* are compatible with a faunivorous diet (Figure 3 and Supplemental Experimental Procedures), the animal probably preying on small vertebrates

and non-hardy-skeletonized invertebrates. Its discovery confirms that early members of the otherwise typically herbivorous Sauropodomorpha were likely predators. In consequence,

Figure 3. Dietary Preferences Represented on Early Dinosauriform Phylogenies

Hypothesis advocated here is shown in the left cladogram, with alternative arrangements shown on the right. Color of the branches represents reconstructed ancestral feeding habits of the lineages; green = herbivory and/or omnivory; black = ambiguous; orange = faunivory. Photographs illustrate (top to bottom) increasing levels of tooth adaptation toward herbivory and/or omnivory among eusaurischians. *Dracovenator* (BP/1/5278) and *Plateosaurus* (GPIT-18318a): left photograph scale bar represents 10 mm, right photograph total height = 3 mm; *Buriolestes* (ULBRA-PVT280) and *Pampadromaeus* (ULBRA-PVT016): left photograph scale bar represents 5 mm, left photograph total height = 1 mm.

regardless of the affinities of herrerasaurids and other putative theropods [26], our results consistently show faunivory as the ancestral diet of saurischian dinosaurs. Indeed, in the evolutionary hypothesis advocated here, the ancestor of all dinosaurs would also be faunivorous, with herbivory and/or omnivory appearing independently in Ornithischia (including silesaurids), the bulk of Sauropodomorpha, and later in various theropod groups [32]. Yet, alternative scenarios have to be considered, and the ancestral dinosaur diet is ambiguous if, for example, Silesauridae is both accepted as the sister group to dinosaurs and does not include *Lewisuchus admixtus* (Figure 3). In any case, new discoveries like *Ixalerpeton* and *Buriolestes* will continue to provide the kind of data necessary to ever more reliably test the patterns of early dinosaur evolution.

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and three figures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2016.09.040>.

AUTHOR CONTRIBUTIONS

Conceptualization, Supervision, and Project Administration, M.C.L., A.W.A.K., and S.F.C.; Methodology, Validation, and Formal Analysis, M.C.L., J.d.S.B., M.B., J.C.d.A.M., and R.T.M.; Investigation, M.C.L., S.F.C., J.d.S.B., M.B., J.C.d.A.M., and R.T.M.; Resources and Funding Acquisition, M.C.L. and S.F.C.; Data Curation, S.F.C., L.R.d.S., and B.J.B.; Writing – Original Draft, M.C.L., A.W.A.K., M.B., J.C.d.A.M., and R.T.M.; Writing – Review & Editing,

S.D.-d.-S., T.R., R.C., and A.B.; Visualization, M.C.L., S.F.C., M.B., and J.C.d.A.M.

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ANEXO 2

Um novo dinossauro de pequeno porte e afim aos terópodes do Triássico Superior da Formação Santa Maria, sul do Brasil

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Material suplementar: se encontra disponível no CD-ROM anexado ao final da Tese.

Síntese do anexo 2

A Formação Santa Maria, do Triássico Superior (Carniano superior) do sul do Brasil, abarca alguns dos mais antigos e seguros registros de dinossauros. No presente trabalho, é escrito um novo dinossauro saurísquio oriundo desta unidade estratigráfica, *Nhandumirim waldsangae* (LPRP/USP 0651), baseado em um esqueleto semi-articulado, incluindo vértebras truncais, sacrais e caudais, um chevron, ílio, fêmur, tíbia parcial, fíbula e metatarsais II e IV, bem como falanges ungueais e não ungueais do membro direito. O novo táxon difere dos demais dinossauiromorfos do Carniano por possuir uma combinação única de características anatômicas, algumas das quais são autapomórficas: centro caudal com quilhas ventrais longitudinais e proeminentes; brevis fossa que se estende por menos de três quartos da superfície ventral da ala pós-acetabular do ílio; trocânter dorsolateral terminando bem distal ao nível da cabeça do fêmur; porção distal da tíbia com uma tuberosidade que se estende mediolateralmente

na sua superfície cranial do osso, além de uma aba caudolateral de formato tabular; faceta articular semicircular craniomedialmente visível na fíbula distal; e metatarsal IV reto. Tais características claramente distinguem *Nhandumirim waldsangae* de *Saturnalia tupiniquim* e *Staurikosaurus pricei*, outros de dinossauros que foram coletados nas proximidades e praticamente no mesmo nível estratigráfico. Por mais que se trate de um indivíduo juvenil, as diferenças entre *Nhandumirim waldsangae* e as espécies supracitadas não podem ser atribuídas à ontogenia. A posição filogenética de *Nhandumirim waldsangae* sugere que ele represente um dos primeiros membros de Theropoda. Deste modo, *Nhandumirim waldsangae* mostra que alguns caracteres típicos de terópodos, como visto em *Coelophysis bauri* e *Lepidus praecisio*, já estavam presentes no início da evolução dos dinossauros e, possivelmente, representa o registro mais antigo do grupo para o Brasil..

**A new dinosaur with theropod affinities from the Late Triassic Santa Maria
Formation, South Brazil**

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RH: MARSOLA ET AL.—NEW DINOSAUR FROM CARNIAN OF BRAZIL

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ABSTRACT—The Late Triassic (Carnian) upper Santa Maria Formation of south Brazil has yielded some of the oldest unequivocal records of dinosaurs. Here, we describe a new saurischian dinosaur from this formation, *Nhandumirim waldsangae* gen. et sp. nov., based on a semi-articulated skeleton, including trunk, sacral, and caudal vertebrae, one chevron, right ilium, femur, partial tibia, fibula, and metatarsals II and IV, as well as ungual and non-ungual phalanges. The new taxon differs from all other Carnian dinossauromorphs through a unique combination of characters, some of which are autapomorphic: caudal centra with sharp longitudinal ventral keels; brevis fossa extending for less than three-quarters of the ventral surface of the postacetabular ala of the ilium; dorsolateral trochanter ending well distal to the level of the femoral head; distal part of the tibia with a mediolaterally extending tuberosity on its cranial surface and a tabular caudolateral flange; conspicuous craniomedially oriented semi-circular articular facet on the distal fibula; and a straight metatarsal IV. This clearly distinguishes *Nhandumirim waldsangae* from both *Saturnalia tupiniquim* and *Staurikosaurus pricei*, which were collected nearby and at a similar stratigraphic level. Despite being not fully-grown, the differences between *Nhandumirim waldsangae* and those saurischians cannot be attributed to ontogeny. The phylogenetic position of *Nhandumirim waldsangae* suggests that it represents one of the earliest members of Theropoda. *Nhandumirim waldsangae* shows that some typical theropod characters were already present early in dinosaur evolution, and possibly represents the oldest record of the group known in Brazil.

Introduction

Dinosaurs are a highly diverse group of archosaurs that emerged in the Late Triassic and are today represented only by the avian lineage. The oldest unequivocal dinosaur fossils are from Carnian deposits of Argentina and Brazil (southwestern Pangaea), which have yielded a diverse fauna of dinosauiromorphs (including dinosaurs), pseudosuchians, rhynchosaurs and therapsids (Langer, 2005b; Brusatte et al., 2008 a,b; 2010; Langer et al., 2010a; Martínez et al., 2012, 2016; Benton et al., 2014; Cabreira et al., 2016). Additional but less complete fossils from India and Zimbabwe suggest a wider palaeobiogeographic distribution for the earliest dinosaurs, with the group also occupying the eastern portion of south Pangea (Ezcurra, 2012).

With the exception of the Argentinean dinosaur *Pisanosaurus mertii*, traditionally interpreted as an ornithischian (Casamiquela, 1967; but see Agnolín and Rozadilla, 2017; Baron, 2017), the record of Carnian dinosaurs is restricted to saurischians (*sensu* Gauthier, 1986), with sauropodomorphs being the most speciose clade. Carnian sauropodomorphs are known from the Ischigualasto Formation of Argentina, including *Eoraptor lunensis* (Sereno et al., 1993), *Panphagia protos* (Martínez and Alcober, 2009) and *Chromogisaurus novasi* (Ezcurra, 2010), and the Santa Maria Formation of Brazil, encompassing *Saturnalia tupiniquim* (Langer et al., 1999), *Pampadromaeus barberenai* (Cabreira et al., 2011) and *Buriolestes schultzi* (Cabreira et al., 2016). These early sauropodomorphs comprise more than 50% of the taxonomic diversity of Carnian dinosaurs. Additional coeval saurischians include the herrerasaurids *Herrerasaurus ischigualastensis* (Reig, 1963), *Staurikosaurus pricei* (Colbert, 1970) and *Sanjuansaurus gordilloi* (Alcober and Martínez, 2010), which have been interpreted in different phylogenetic analyses either as theropods or non-

eusaurischian dinosaurs (e.g. Nesbitt and Ezcurra, 2015; Cabreira et al., 2016).

Eodromaeus murphii (Martínez et al., 2011) from the Ischigualasto Formation has been interpreted as a theropod by several authors (Martínez et al., 2011; Bittencourt et al., 2014; Nesbitt and Ezcurra, 2015), but was recently recovered as a non-eusaurischian dinosaur (Cabreira et al., 2016). Unambiguous theropods are more common in later Triassic (Norian) deposits, as seen in north Pangea dinosaur faunas, like in the Chinle Formation, that are dominated by coelophysids (e.g. Nesbitt et al., 2009; Ezcurra and Brusatte, 2011; Sues et al., 2011; Nesbitt and Ezcurra, 2015).

Here we describe a partial, semi-articulated skeleton of a not fully-grown dinosaur from the historic Waldsanga site (Langer, 2005a) of the Santa Maria Formation, south Brazil. This new specimen represents a new genus and species of saurischian dinosaur, and is tentatively assigned here to Theropoda, representing the oldest potential record of this group in Brazil.

Institutional Abbreviations—**AMNH FARB**, American Museum of Natural History, New York, U.S.A.; **BRSMG**, Bristol Museum and Art Gallery, Bristol, U.K.; **MB.R.**, Museum für Naturkunde, Berlin, Germany; **MCP**, Museu de Ciências e Tecnologia, PUCRS, Porto Alegre, Brazil; **LPRP/USP**, Laboratório de Paleontologia de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, Brazil; **NMMNHS**, New Mexico Museum of Natural History & Science, Albuquerque, U.S.A; **NMT**, National Museum of Tanzania, Dar es Salaam, Tanzania; **PULR**, Universidad Nacional de La Rioja, La Rioja, Argentina; **PVL**, Fundación Miguel Lillo, Tucumán, Argentina; **PVSJ**, Museo de Ciencias Naturales, San Juan, Argentina; **QG**, Natural History Museum of Zimbabwe, Bulawayo, Zimbabwe; **SAM-PK**, Iziko South African Museum, Cape Town, South Africa; **SMNS**, Staatliches Museum für Naturkunde, Stuttgart, Germany; **ULBRA**, Museu de Ciências Naturais, Universidade Luterana do Brasil, Canoas, Brazil.

Geological setting

The new specimen comes from deposits of the Alemoa Member of the Santa Maria Formation, at the site known as Waldsanga (Figure 1; Huene, 1942; Langer, 2005b; Langer et al., 2007) or Cerro da Alemoa (Da Rosa, 2004, 2015). The same site has also yielded the type specimens of the early sauropodomorph *Saturnalia tupiniquim* (Langer et al., 1999), the rauisuchian *Rauisuchus tiradentes* (Huene, 1942), and the cynodonts *Gomphodontosuchus brasiliensis* (Huene, 1928; Langer 2005a) and *Alemoatherium huebneri* (Martinelli et al., 2017). However, the most common fossils recovered from the site are rhynchosaurs of the genus *Hyperodapedon* (Langer et al., 2007)

Reddish, massive mudstones of the Alemoa Member compose the main lithology of the site, in contact with the yellowish to orange stratified sandstones of the overlying Caturrita Formation. The fine-grained beds of the Alemoa Member correspond to floodplain deposits, and are subdivided into lower, intermediate, and upper levels, whereas the coarser deposits of the Caturrita Formation represent ephemeral, high-energy channel and crevasse-splay deposits (Da Rosa, 2005, 2015). The lower and intermediate levels of the exposed Alemoa Member represent distal floodplain deposits, whereas the upper level represents a proximal floodplain (Da Rosa, 2005, 2015).

According to recent sequence stratigraphy studies (Horn et al., 2014), the strata exposed at the site belong to the Candelária Sequence, Santa Maria Supersequence (Santa Maria 2 Sequence of Zerkow et al., 2003), which includes the upper part of the Santa Maria Formation (Gordon, 1947) and the lower part of the Caturrita Formation (Andreis et al., 1980). Two assemblage zones (AZ) have been recognized within the

Candelária Sequence: the older *Hyperodapedon* AZ and the younger *Riograndia* AZ.

The occurrence of *Hyperodapedon* rhynchosaurs justifies correlating the site to the *Hyperodapedon* AZ.

Correlations with radioisotopically dated strata from the Ischigualasto Formation (Ischigualasto–Villa Unión Basin) in western Argentina (e.g., Martínez et al., 2011, 2012) that share a similar faunal association (e.g., Langer, 2005b; Langer et al., 2007) indicate that the *Hyperodapedon* AZ is late Carnian in age. This age is corroborated by detrital radiometric dating of the reddish mudstones at the level from which *Saturnalia tupiniquim* was collected, which has yielded a maximum age of c. 233 Ma (Langer et al., 2018).

Systematic paleontology

DINOSAURIFORMES Novas, 1992 sensu Nesbitt, 2011

DINOSAURIA Owen, 1842 sensu Padian and May, 1993

SAURISCHIA Seeley, 1887 sensu Gauthier, 1986

cf. THEROPODA Marsh, 1881 sensu Gauthier, 1986

NHANDUMIRIM WALDSANGAE, gen. et sp. nov.

(Figs. 2–15)

Holotype—LPRP/USP 0651, a partial postcranial skeleton (Fig. 2), consisting of three trunk vertebrae, two sacral vertebrae, seven caudal vertebrae, a chevron, pelvic and hindlimb bones from the right side of the body including an ilium, femur, partial tibia, fibula, metatarsals II and IV, ungual and non-ungual phalanges. The bones were found in close association within an area approximately 50 cm by 50 cm, and were

semi-articulated. Some fragmentary remains are not identifiable due to their incompleteness.

Etymology—The generic name combines the Portuguese derivatives of the indigenous Tupi-Guarani words *Nhandu* (running bird, common rhea) and *Mirim* (small), in reference to the size and inferred cursorial habits of the new dinosaur. The specific epithet name refers to the Waldsanga site, the historical outcrop (Langer, 2005a) that yielded this new species.

Type Locality and Horizon—Site known as Waldsanga (Huene, 1942; Langer et al., 2007) or Cerro da Alemoa (Da Rosa, 2004, 2015), at coordinates 29°41'51.86"S and 53°46'26.56"W, in the urban area of Santa Maria, Rio Grande do Sul State, southern Brazil. The new dinosaur comes from the upper levels of the Alemoa Member of the Santa Maria Formation, 1–1.5 m below the contact with the overlying Caturrita Formation, in the proximal floodplain deposits of the Candelária Sequence of the Santa Maria Supersequence (Zerfass et al., 2003; Horn et al., 2014).

Diagnosis—A saurischian dinosaur distinguished from all other Carnian dinosauromorphs by the following unique combination of autapomorphic characters: sharp longitudinal keels on the ventral surfaces of the proximal caudal centra; brevis fossa projecting for less than three-quarters of the length of the ventral surface of the iliac postacetabular ala; proximally short dorsolateral trochanter that terminates well distal to the level of the femoral head; distal tibia with a mediolaterally extending tuberosity on its cranial surface, in addition to a tabular-shaped caudolateral flange; conspicuous craniomedially oriented semi-circular articular facet on the distal fibula, probably related to the articulation of the lateral face of the ascending process of the astragalus; straight metatarsal IV.

Description

Axial Skeleton

Three caudal trunk vertebrae, two sacral vertebrae, with an isolated sacral rib, seven caudal vertebrae and a chevron have been recovered. For descriptive purposes, the trunk, sacral and caudal vertebrae will be sequentially numbered from the most cranial to the most caudal.

Trunk Vertebrae—Two trunk vertebrae (“1” and “3”) are known only from their centra, whereas a third (trunk vertebra “2”) also includes a poorly preserved neural arch (Figs. 3, 4). The vertebrae were arbitrarily ordered “1”–“3” based on their length: the longer elements are inferred to be more cranial, and the shorter more caudal. The absence of parapophyses, ventral keels, or chevron facets suggests that all three centra represent caudal trunk elements. The centra are spool-shaped and craniocaudally elongated in comparison with the typically craniocaudally compressed caudal trunk vertebrae of herrerasaurids (Novas, 1994; Bittencourt and Kellner, 2009). Their lateral surfaces have a craniocaudally oriented shallow depression, which is pierced by small nutrient foramina. The length:height ratios of vertebrae “1” to “3” rounds 1.4. Their articular faces are gently concave and rounded, but slightly taller than wide. Although the centra cannot be precisely oriented due to the absence of anatomical landmarks, the surface that we tentatively identify as the cranial articular surface of trunk vertebra “1” is notably shorter dorsoventrally than is the caudal articular surface.

Part of the neural arch is preserved in trunk vertebra “2” (Figs. 3B, 4). The prezygapophysis is short, not projecting beyond the cranial edge of the centrum. In cranial view, the articular surface of the prezygapophysis faces dorsomedially and articulates with the postzygapophysis at an angle of about 35 degrees to the horizontal.

The prezygodiapophyseal lamina reaches the prezygapophysis. Only a small part of the left transverse process is preserved, and it projects dorsolaterally. The caudal part of the left side of the neural arch preserves a well-developed fossa (the caudal chonos or postzygapophyseal centrodiapophyseal fossa of Wilson et al., 2011). This fossa is cranially bounded by a nearly vertical posterior centrodiapophyseal lamina (Wilson et al., 1999) so that the postzygapophyseal centrodiapophyseal fossa is only visible in lateral and caudal aspects. Cranial to this lamina, the badly preserved caudal portion of the medial chonos (or centrodiapophyseal fossa of Wilson et al., 2011) is visible. The postzygodiapophyseal lamina forms the dorsomedial border of the postzygapophyseal centrodiapophyseal fossa and contacts the posterior centrodiapophyseal lamina in its dorsalmost extension. The confluence between the left caudal pedicel of the neural arch and the roof of the neural canal forms the ventral margin of the postzygapophyseal centrodiapophyseal fossa. Postzygapophyses and possible hyposphene-hypantrum articulations are not preserved in the preserved trunk vertebrae.

Sacral Vertebrae—The recovered parts of the sacrum (Fig. 5) include an isolated and badly preserved centrum, the second primordial sacral vertebra still attached to its right rib, and an isolated left rib from the first primordial sacral vertebra. No remains of the neural arches were identified. Both preserved centra are craniocaudally short and robust. The isolated centrum is as long as wide, whereas that of the second sacral vertebra is slightly longer than wide. The ventral surfaces of the centra are less strongly concave in lateral view than those of the trunk and proximal caudal vertebrae. The recovered sacral vertebrae are not fused to one another, and there is no evidence for fusion of the sacral ribs with either the vertebra or the ilium. Several tiny nutrient foramina are present on the caudolateral half of the centrum of the second sacral vertebra. The articular surfaces of the centra are weakly concave and wider than

tall. In both sacral centra the cranial articular surface is broader transversely than is the caudal articular surface. The rib is firmly attached (but not fused) to the second sacral centrum, and there is a conspicuous swelling along the caudoventral margin of the articulation surface. The articulation surface with the rib occupies more than half of the craniocaudal length of the centrum. In contrast, in the isolated sacral centrum, the rib articulation surface is restricted to its cranial half.

The partial isolated rib from the first sacral vertebra (Fig. 5F, G) is mediolaterally wider than both recovered sacral centra. Those proportions are due to the iliac and sacral shortening in *Nhandumirin waldsangae* compared to other dinossauromorphs, such as *Saturnalia tupiniquim* (MCP-3845 PV). The rib is slightly concave and fan-shaped in dorsal aspect, being more dorsoventrally flattened along its incomplete cranial margin, whereas the lateral and caudal margins are confluent and form a gently curved profile. In lateral view, the rib has a smooth articular surface for the medial surface of ilium, and its cranial margin curves gently dorsally towards the contact with the transverse process (which is not preserved). This condition differs from the L-shaped cross section of the first sacral rib of *Saturnalia tupiniquim* (Langer, 2003).

The preserved right rib of the second sacral vertebra is missing its caudodorsal and cranioventral tips. The rib expands in dorsoventral height distally from the centrum, and its ventral surface is concave in cranial and caudal views. In dorsal and ventral views, the most cranial tip of the rib extends beyond the cranial limit of the centrum. In lateral view, the articular surface of the sacral rib expands dorsoventrally towards its caudal margin, i.e. it is narrower dorsoventrally at its cranial portion. The articular surface is smooth and slopes from cranioventrally to caudodorsally.

Caudal Vertebrae and Chevron—The seven recovered caudal vertebrae (Figs. 6, 7) are from different parts of the tail. They are generally more complete than those of the trunk and sacral series, preserving at least parts of the neural arch in all recovered elements. Caudal vertebrae “1”–“3” come from the first third of the tail, whereas vertebrae “4”–“5” represent mid-caudal vertebrae, and vertebrae “6”–“7” are distal caudal elements. The neurocentral suture is only visible in the three more proximal vertebrae, suggesting it is completely closed in more distal caudal vertebrae. The lateral surfaces of caudal centra “1”–“4” have shallow, proximodistally oriented, and distally positioned depressions, within each of which there are one or two tiny nutrient foramina. The caudal centra become increasingly elongate towards the distal part of the tail, changing from proximal caudal vertebrae with spool-shaped centra to distal caudal vertebrae with much more elongated centra. The length:height ratio of caudal centrum “1” is 1.0, increasing to 1.3 in caudal vertebrae “2”–“3”; 2 in caudal vertebrae “4”–“5”; and >3 in caudal vertebra “6”. The proximal and distal articular faces are round (caudal vertebrae “1”, “4”–“6”) or oval (caudal vertebrae “2”–“3”) in outline, and have concave surfaces with the proximal articular face always deeper than the distal. The ventral surfaces of caudal vertebrae “1”–“3” bear a craniocaudally extending keel. In caudal vertebra “1”, the keel is conspicuous only on the caudal half of the ventral surface of the centrum, is constricted at its midlength, and is laterally bounded by shallow excavations. The ventral keels of caudal vertebrae “2” and “3” lack the lateral excavations, but are stouter and extend for the whole ventral surface of the centrum.

Facets for chevron articulation are seen in caudal vertebrae “1”–“5”. Only the distal articulation for the chevron is present in caudal vertebra “1”. This suggests that this vertebra would have received the first chevron of the series, and therefore likely represents the first caudal vertebra. In caudal vertebra “1”, the area for the chevron

attachment includes two distinct articular facets. In caudal vertebrae “2”–“5” there are single, larger, continuous, and oval facets for the chevrons on both the proximal and distal articular facets of the centra.

The transverse processes are dorsolaterally directed in all caudal vertebrae. In caudal vertebra “1”–“3” they are also oriented caudolaterally in dorsal view, whereas in caudal vertebra “4” the transverse process is directed strictly laterally and forms a right angle with the centrum. Except for the cross-sectional morphology (see below), the precise length and shape of the transverse processes cannot be assessed in caudal vertebrae “1”–“3” due to damage. In caudal vertebra “4”, the transverse process is rectangular, and in caudal vertebra “5” it is reduced to a small bump. Transverse processes are absent in caudal vertebrae “6”–“7”. In cross-section, the transverse process is triangular in caudal vertebrae “1”–“2” and blade-like in caudal vertebrae “3”–“4”. The neural spine is best preserved in caudal vertebra “5”. It is parallelogram-shaped and its length is equal to two thirds of the centrum length. Its tip projects further distally than the distal border of the centrum. A preserved neural spine fragment of caudal vertebra “3” suggests that it is distally inclined.

The articular surfaces of the prezygapophyses face dorsomedially, whereas those of the postzygapophyses face ventrolaterally. The pre- and postzygapophyses articulate with one another at an angle of about 60° to the horizontal, except in caudal vertebra “1”, where the articulation is at 40° to the horizontal. The zygapophyseal articular surfaces of the caudal vertebrae are always set close to the vertebral body. Caudal vertebra “6” has stouter prezygapophyses than the preceding vertebrae, but they do not extend proximally far beyond the cranial centrum rim. Hyposphene-hypantra articulations are not present in the caudal vertebrae.

Two laminae are present on the neural arches of caudal vertebrae “1”–“4”. A faint prezygo-postzygapophyseal lamina (Ezcurra, 2010) extends along the dorsal surfaces of the neural arches of caudal vertebrae “3” and “4”, but does not reach either the pre- or the postzygapophyses. A more conspicuous lamina is present in caudal vertebrae “1”–“4”, in a similar position to the prezygodiapophyseal lamina of trunk vertebrae. In tail vertebrae “1”–“2”, this lamina forms the craniodorsal margin of a shallow concave surface, here interpreted as the prezygapophyseal parapodiapophyseal fossa (Wilson et al., 2011).

The only preserved chevron is isolated (Fig. 7G, H) and its position in the caudal column is uncertain. Its distal tip is missing, and the lateral edges of the proximal articulation are not preserved. The proximal articular surface is saddle-shaped and notably concave in cranial and caudal views. Cranially, the shaft has a subtle proximodistally extending sulcus near its proximal articulation, whereas in caudal view, the sulcus extends further distally and is deeper than its cranial counterpart. These sulci mark the openings for the haemal canal, but the exact shape of this canal cannot be described because the sulci are filled with matrix. The distal part of the chevron shaft is inclined caudally at 40° to the vertical in lateral view, and becomes mediolaterally narrower towards its distal end.

Appendicular Skeleton

Ilium—The ilium is incomplete (Fig. 8), lacking most of the dorsal lamina above the acetabulum, the caudal tip of the postacetabular ala, the cranial extension of the supraacetabular crest, and the lateroventral portion of the pubic peduncle.

The preacetabular ala does not extend cranially as far as the cranial edge of the pubic peduncle. The ala is subtriangular in lateral view, cranially directed, with a gently

rounded tip and a cranioventral margin that forms an angle of 80° with the dorsal margin. In dorsal view, the preacetabular ala arches laterally as it extends cranially. The angle formed by the pre- and postacetabular alae suggests that the iliac lamina was laterally concave, as seen in other dinosauriforms (Serenó and Arcucci, 1994; Novas, 1994; Langer, 2003; Martínez and Alcober, 2009). Muscle scars are present on the dorsal rim of the lateral surface of the preacetabular ala, and represent the insertion of the M. iliotibialis (Hutchinson, 2001a). The embayment between the preacetabular ala and the iliac body is cranially excavated by a dorsoventrally oriented and shallow preacetabular fossa (Hutchinson, 2001a; Langer et al., 2010b).

The dorsal margin of the supraacetabular crest is positioned at 47% of the dorsoventral height of the ilium and covers most of the craniocaudal extent of the acetabulum. The crest gently projects ventrolaterally, and the mediolaterally broadest point of the crest is located directly above the midpoint of the acetabulum. The ventral margin of the ilium is concave, indicating a perforated acetabulum. On the caudoventral portion of the acetabulum, the acetabular antitrochanter has a roughly squared outline, with several conspicuous, but low scars. The pubic peduncle has a cranioventrally facing articulation for the pubis. The ischiadic peduncle is columnar, with its caudodorsal and medial surfaces slightly flattened. It projects caudoventrally, with a concave caudal margin. The caudoventrally facing articular surface for the ischium is flat, rugose and suboval in outline and gently laterally deflected.

Two foramina pierce the ventrolateral margin of the ilium, at the cranial margin of the postacetabular ala. Caudal to these openings, a well-developed, but craniocaudally short brevis fossa occupies less than three-quarters of the length of the ventral margin of the postacetabular ala. The postacetabular ala is longer than the space between the pre- and postacetabular embayments. The ventrally oriented lateral wall of

the brevis fossa originates well caudal to both the supraacetabular crest and the ischiadic peduncle, whereas the medial wall of the brevis fossa expands medioventrally. The internal surface of the brevis fossa is rugose, and corresponds to the attachment area for the *M. caudofemoralis brevis* (Gatesy, 1990).

The dorsal lamina of the postacetabular ala is mediolaterally thin when compared to those of other Triassic dinosaurs (e.g., *Coelophysis bauri*, AMNH FARB 2708; *Saturnalia tupiniquim*, MCP 3845-PV; Langer et al., 2011b), and the same condition is observed for the dorsal lamina of the preacetabular ala. The entire lateral surface of the postacetabular ala is covered with muscle scars, which are caudal extensions of the scars present on the lateral surface of the preacetabular ala, and which are related to the insertion of *M. iliotibialis* (Hutchinson, 2001a; Langer, 2003; Langer, et al., 2010b).

The medial surface of the ilium bears a complex set of scars, including those for the sacral rib attachments. The scar of the first primordial sacral rib is rounded and L-shaped, with its apex pointing cranioventrally. Cranially, this scar nearly reaches the medial margin of the preacetabular fossa, but it is placed caudal to the base of the pubic peduncle. Its ventral margin parallels the ventral rim of the brevis fossa, and is continuous backwards to a point where it converges with the medial wall of that fossa. Along all its extension, this scar is slightly dorsally bowed, without any clear distinction of the articulation facets for the ribs of sacral vertebrae 2 and 3. Nevertheless, we presume that there were three sacral vertebrae in *Nhandumirim waldsangae*. This is based on the 4.6 cm length of the scars for the articulation of the sacral vertebrae on the ilium, whereas the total length of the two preserved sacral centra (1.5 and 1.4 cm, respectively) covers less than 65% of this length. Accordingly, the remaining space

would receive a third sacral vertebra, as seen in *Saturnalia tupiniquim* (MCP-3845 PV) (see Discussion).

Femur—The femur is nearly complete (Fig. 9) and slightly longer than twice the craniocaudal length of the ilium. At midshaft, the femur is subcircular in cross section, with a diameter of 1–1.2 cm. The bone wall thickness is approximately 20% of the femoral diameter, as measured on the cranial margin of the bone at the level of the distal end of the fourth trochanter. In addition to the thin bone wall, the femur is also remarkably slender: 12 cm long and 3.5 cm in circumference at midshaft (ratio = 3.4). Other early dinosaurs are more robust, such as *Saturnalia tupiniquim* (MCP 3844-PV), which has a femur that is 15 cm long and a midshaft circumference of 5 cm (ratio = 3). However, such differences would possibly be explained by allometric growth.

The femur is sigmoidal, particularly in cranial and caudal views, due to the cranial and medial bowing of the shaft and the inturned head. The femoral head is about one third wider mediolaterally than the femoral “neck” in cranial and caudal views, and more than twice mediolaterally longer than craniocaudally broad in proximal view. It is rugose and bears a distinct straight proximal groove which gently curves medially in its cranial extent and extends caudolaterally from the cranial margin of the head. Another faint and nearly mediolaterally extending ridge marks the cranial limit of the distally descending facies articularis antitrochanterica. The elevated caudal corner of the femoral head, or “greater trochanter”, forms a nearly right angle in caudal view. The medial tuber is well developed and rounded, occupying one third of the medial edge of the femoral head. Its caudal rim continues laterally as the ridge extending over the cranial margin of the facies articularis antitrochanterica. A medial ridge extends distally from the medial tuber. The medial tuber is separated from the craniomedial tuber by the concave and scarred ligament sulcus. This scarred area extends proximodistally parallel

to the medial ridge, and merges with a larger set of scars that surrounds the proximal portion of the fourth trochanter. The medial ridge is smooth, and caudally bounded by a shallow and somewhat concave surface distal to the fossa articularis antitrochanterica. This surface bears some roughly rounded small scars, and is caudodistally bounded by another proximodistally smooth ridge (Fig. 9C:‘oi’) that fades into the proximal slope of the fourth trochanter. This ridge possibly represents the insertion of the *M. obturatorius* (Langer, 2003).

The craniomedial tuber is well developed, rounded, medially projected, and larger than the medial tuber. Lateral to it, a small and rounded caudolateral tuber is present. The craniomedial tuber is distally bounded by a saddle-shaped notch that extends laterodistally, delimiting the scarred ventral emargination. Its scars merge medially with those of the ligament sulcus. The craniomedial surface of the femoral head (Langer and Ferigolo, 2013) bears muscle attachment scars, and is marked caudally by a sharp craniomedial crest (Bittencourt and Kellner, 2009). This crest extends distally from the cranio-lateral tuber, and fades away at the level of the cranial trochanter. An extensive, scarred flat surface is present along the whole lateral surface of the proximal end of the femur lateral to the aforementioned ridge. These scars are probably related to the dorsolateral ossification (sensu Piechowski et al., 2014) and the anterolateral scar (sensu Griffin and Nesbitt, 2016a). Although no clear association to any specific muscle insertion has been established, these scars may be related to the iliofemoral ligament (Griffin and Nesbitt, 2016a).

The cranial trochanter is a proximodistally oriented ridge that becomes distally broader, and then merges into the shaft at the level of the cranial limit of the fourth trochanter. The dorsolateral trochanter is a faint, proximodistally elongated ridge, which does not continue proximally to the level of the femoral head. It is essentially “short”, as

is the cranial trochanter. Muscles scars surround both trochanters, and although the trochanteric shelf is not present, these scars probably represent the attachment of *M. iliofemoralis externus* (see Hutchinson, 2001b). In cranial view, a smooth linea intermuscularis cranialis extends distally from the medial margin of the cranial trochanter, reaching the distal third of the shaft. In birds, this intermuscular line forms the border between *M. femorotibialis medialis*/*M. femorotibialis intermedius* and *M. femorotibialis externus* (Hutchinson, 2001b).

The fourth trochanter is set on the medial half of the shaft. It is a well-developed, rugose, and sinuous flange for the attachment of *M. caudofemoralis longus* (see Hutchinson, 2001b). Its proximal portion forms a low angle with the shaft, and has a sinuous outline in caudal view. It merges distally with the shaft, forming a steeper angle. Medial to the fourth trochanter, there is an oval depression, or fossa, that is also for insertion of *M. caudofemoralis longus* (Hutchinson, 2001b; Langer, 2003). The scar for the attachment of *M. caudofemoralis brevis* (Hutchinson, 2001b; Griffin and Nesbitt, 2016a) is rounded and proximolaterally located relative to the fourth trochanter.

The shaft of the distal third of the femur expands transversely and caudally. Along this portion of the bone, two longitudinally oriented intermuscular lines, the caudomedial and caudolateral lines (“femil” and “fclil” of Langer, 2003, respectively), form the borders of the distal femur. Between them, there is a well-developed, U-shaped popliteal fossa, bordered by low lateral and medial walls. In birds, the popliteal fossa corresponds to attachment of the *M. flexor cruris lateralis pars accessorius* (Hutchinson, 2001b). In cranial view, the distal quarter of the femur is straight and shows a distinct muscle scar on its laterocranial portion (“fdms” of Langer, 2003), as well as a set of scars that extend proximally from the distal margin of the femur, fading proximomedially at the level of the aforementioned scar. These two scarring areas may

correspond to the “unusual subcircular muscle scar” of *Herrerasaurus ischigualastensis* (Novas, 1994:406), later referred to as the craniomedial distal crest by Hutchinson (2001b).

The distal condyles are not well preserved and are offset medially due to a breakage. They are rugose and form a distal outline that is wider lateromedially than craniocaudally. The medial condyle comprises the whole medial half of the distal part of the femur, and is twice as long craniocaudally as it is wide. It is medially rounded, with a subtle caudal extension. In distal view, the medial condyle has a squared caudomedial corner, whereas the craniomedial and the caudolateral corners are rounded and separated from the lateral condyle by the sulcus intercondylaris. The sulcus intercondylaris extends craniocaudally for at least one third of the length of the medial condyle. Lateral to it, only a small and relatively uninformative portion of the lateral condyle is preserved. Although damaged, the crista tibiofibularis seems to be rounded, somewhat caudally expanded, and laterally directed. In addition, the crista tibiofibularis is separated from the lateral condyle by a smooth and concave surface in distal view, which extends proximally for about half of the length of the popliteal fossa.

Tibia—The bone is incomplete (Figs. 10, 11), crushed and missing its proximal quarter. The shaft is rod-like and circular in cross-section at midlength. The distal end is mediolaterally expanded and the articular surface is rugose. In distal view, the tibia is trapezoidal, with rounded corners and the cranial margin lateromedially broader than the caudal. In cranial view, a subtle mediolaterally expanded anterior diagonal tuberosity (Ezcurra and Brusatte, 2011; Nesbitt and Ezcurra, 2015) is visible. This tuberosity is closer to the medial corner, and exposed in medial, lateral, and distal views as a low lump. In lateral view, a proximodistally oriented groove extends proximally for about 10 mm. In distal view, this groove excavates laterally the tibia for about 20% of its

mediolateral width. The tibial facet for the ascending process of the astragalus is positioned cranial to the caudolateral flange. It is a well-developed surface, occupying half of the distal surface of the tibia. This facet forms an angle of about 25° with the distal margin of the tibia, suggesting that it would have articulated with a high and well-developed ascending process of the astragalus. The caudolateral flange of the tibia is tabular (Nesbitt and Ezcurra, 2015), but does not extend beyond the lateral limit of the cranial part of bone. Its mediolateral border bears a small mound-shaped projection that faces distally, which increases the distal extension of the bone. The tibia has a flat caudal surface, bearing medially a faint and proximodistally oriented ridge. Its caudomedial corner has a shallow notch that receives the caudomedial process of the astragalus. This notch has a rounded aspect in caudal and lateral views. In distal view, it fades laterally before the separation between the caudolateral flange and the facet for the astragalar ascending process.

Fibula—The fibula is more complete than tibia (Figs. 10, 11), albeit also crushed and lacking part of the cortical bone. It is nearly 10% longer than the femur, indicating that the epipodium was longer than the propodium in *Nhandumirim waldsangae*. Its proximal end is rugose and mediolaterally compressed, being three times longer craniocaudally than wide mediolaterally. The proximal end of the fibula is somewhat medially bowed, caudally expanded, and more than twice as wide as the shaft. In medial view, the first third of the fibula has a proximodistally-oriented scar for attachment of the M. iliofibularis (Langer, 2003) (Fig. 10C), which extends to the cranial surface of the bone, where it fades out. The proximal third of the lateral surface of the fibula is also scarred, and two small foramina are found on the medial surface of the bone near the midshaft. The shaft is straight and slender, and “D”-shaped in cross-section at midshaft, with a flatter medial surface.

The articular surface of the distal end of the fibula is rugose and flattened, forming a right angle to the long axis of the bone in lateral and medial views. The distal end is slightly mediolaterally expanded, whereas the craniocaudal length is twice that of the bone shaft. The cranial margin of the distal end is flat and nearly parallel to the shaft, whereas the caudal margin is caudally expanded. Scars are present on the medial side of the distal end of the fibula, and they may represent a ligamentous attachment to the tibia, as inferred for *Saturnalia tupiniquim* (Langer, 2003). The distal portion of the fibula also shows a distinct facet that occupies the cranial half of its medial side. This conspicuous facet extends proximally and has a semicircular shape both in medial and distal views. It probably articulated with the lateral face of the ascending process of the astragalus. In lateral view, the distal portion of the fibula is scarred for muscle insertion, and the bone surface is rugose and has an overall elliptical shape in distal view.

Pes—Only metatarsals II and IV of *Nhandumirim waldsangae* are preserved (Fig. 12). Although compressed in its proximal half, the length of metatarsal II indicates that the metapodium of *Nhandumirim waldsangae* is longer than half of the length of the propodium and epipodium.

The proximal end of metatarsal II is craniocaudally flattened. In proximal view, the long axis of the proximal end is rotated by about 20°, so that it is craniolaterally to caudomedially oriented. The proximal articular surface is planar, mediolaterally expanded, with nearly squared corners in proximal view. The craniomedial and caudolateral faces, for contact with metatarsals I and III, respectively, are flat and scarred. The shaft of metatarsal II is straight, and progressively expands lateromedially towards the distal end to form the distal condyles. The distal condyles have well-developed ligament pits, with the lateral deeper than the medial. Proximal to the ligament pits, the cranial surface of the metatarsal bears a raised surface, which has

conspicuous scars for ligamentous insertion and is best developed at the cranio-lateral margin of the bone. The lateral and medial distal condyles are subequal in length, but the former is more distally expanded than the latter. In distal view, the articular facet for the first phalanx is asymmetric: the cranial and lateral faces are flattened, whereas the caudal and medial surfaces are slightly concave, forming an angled caudomedial corner.

The proximal quarter of metatarsal IV is damaged. However, the bone was probably subequal in length to metatarsal II because, in medial and lateral views, the proximal part of the shaft has the proximal scars for articulation with metatarsals III and V. Metatarsal IV is straight, and its distal end also shows scars for ligament insertions. In distal view, its cranial face is somewhat convex, whereas the other surfaces are concave, with the corners forming acute angles. The caudolateral corner is drawn out into a subtriangular process in distal view. The condyles are asymmetrical, being craniocaudally longer than lateromedially wide. A shallow and mediolaterally oriented furrow is set caudal to the condyles and cranial to the caudolateral corner of the metatarsal II.

The pedal digits are represented by five non-ungual and three ungual phalanges (Fig. 13). However, as these elements were not preserved in articulation, both their position in the foot, and the phalangeal formula for *Nhandumirim waldsangae*, is uncertain.

One of the non-ungual phalanges, referred to as phalanx A (Fig. 13), is mediolaterally broader than the other preserved phalanges, and probably represents a first phalanx, as the outline of its proximal articulation is wider than high. In addition, the small dorsal intercondylar process suggests it would have articulated with a metatarsal. The other non-ungual phalanges have a proximal articulation that is about as high as wide, with a vertical ridge that separates the concave articular surface into

medial and lateral facets. This ridge is also present, but fainter, in phalanx A. In all non-ungual phalanges, the proximal half of the plantar surface is flattened and scarred for the insertion of the collateral and flexor ligaments. There are well-developed dorsal intercondylar processes. The process is not as well developed in phalanx A, which also bears fainter scars related to the insertion of the extensor ligaments.

A few foramina are seen on the shafts of the phalanges. A plantar-dorsal constriction is present in the distal half of the shaft, and forms a neck just proximal to the well-developed distal condyles. Pits for collateral ligaments are present on the lateral and medial margins of the distal condyles, and shallow pits for the extensor ligaments are also present. The distal articulation is ginglymoid, with separated condyles, although there is variation in shape. The articular surfaces of phalanges A and D are wider than high, whereas the articular surfaces of phalanges B and C (the distal condyles are missing in phalanx E) are nearly as wide as high.

The ungual phalanges have proximal articular surfaces that are higher than wide, also bearing a vertical ridge that separates medial and lateral articular facets. The dorsal intercondylar process is smaller than in the non-ungual phalanges, but its dorsal margin bears more clearly marked scars for the extensor ligaments. The flexor tubercles are well developed and mound like. The ungual phalanges are subtriangular in cross-section at midlength. They are curved, with their tips projected well beneath the base of the proximal articulation, but not as raptorial as in later theropods (see Rauhut, 2003). Attachment grooves for the ungual sheath are also present in both the medial and lateral sides of the unguals.

Osteohistology

Bone samples from the tibia and fibula (Fig. 14-15) were taken as close to the midshaft as possible, because this area preserves a larger amount of cortical tissue and growth markers (Francillon-Vieillot et al., 1990; Andrade and Sayão, 2014). The bones were measured, photographed and described for bone microstructure investigation before being sectioned, according to the methodology by Lamm (2013). The bone samples for histological slide preparation were taken from approximately 1cm of thickness. The sectioned samples were immersed in clear epoxy resin Resapol T-208 catalyzed with Butanox M50. They were cut with the aid of a micro rectify (Dremel 4000 with extender cable 225) coupled to a diamond disk, after they were left to dry. Then, the section assembly side was ground and polished in a metal polishing machine (AROPOL-E, AROTEC LTDA) using AROTEC abrasive grit (grit size 60 / P60, 120 / P120, 320 / P400, 1200 / P2500) to remove scratches from the block. After polishment, the blocks were glued on glass slides and thinned again, in order to make them translucent enough for observation of osteohistological structures through biological microscopy. All sections were examined and photographed in a light microscope (Zeiss Inc. Barcelona, Spain) equipped with an AxioCam camera with Axio Imager, after the histological slides were prepared. The M2 imaging software was used in the examination procedure.

The osteohistological terminology follows Francillon-Vieillot et al. (1990), except for the definition of laminar bone, for which we follow Stein and Prondvai (2014). General features of the cross-section are described from the endosteal margin to the periosteal surface.

Tibia—The compact cortex of the tibia is composed of laminar bone (Fig. 14), which occurs in long bones of several extinct and extant vertebrate groups (see Stein

and Prondvai, 2014). The low variation of lamina density and thickness observed here is consistent with principles of laminar bone (Hoffman et al., 2014). The vascular network has a homogeneous pattern for the entire transverse plane of the bone (Fig. 14C). It is composed of anastomosed vascular canals in a plexiform arrangement (Fig. 14E).

The medullary cavity and the inner portion of the cortex lack trabecular bone, differing from the pattern observed in *Silesaurus opolensis* in which the perimedullary region shows cancellous bone forming trabeculae (Fostowicz-Frelik and Sulej, 2010). In the inner cortex, the vascular canals extend all the way to the medullary cavity, with no deposition of inner circumferential lamellae. In this area the remodeling process is poor, indicating the beginning of the resorption process, marked by few erosion rooms and two primary osteons (Fig. 14D). The middle cortex exhibits two lines of arrested growth (LAGs), although no other growth marks as annuli, or zones are present. Despite rare in sauropods, the growth marks appear later in their ontogeny (see Sander et al., 2011). This is the contrary condition of early sauropodomorphs in which they have been recorded as annuli in *Plateosaurus engelhardti* (Sander and Klein, 2005; Klein and Sander, 2007), growth marks in *Massospondylus carinatus* (Chinsamy, 1993), and LAGs in *Thecodontosaurus antiquus* (de Riqclès et al., 2008, Cherry, 2002). Also, in other dinosauriforms, like *Silesaurus opolensis*, growth marks are broadly spread in different bones as annuli in the femur and tibia, and LAGs in the tibia (Fostowicz-Frelik and Sulej, 2010). The presence of two LAGs in *Nhandumirim waldsangae* shows two interruptions in its bone deposition, indicating two growth cycles at the moment of its death. The outer cortex presents the same pattern as the inner, with the vascular canals extending in the direction of the bone surface. There is no deposition of external lamellae, meaning that an external fundamental system is absent.

The observed pattern is consistent with primary tissues, represented by the plexiform arrangement of the vascular network. The bone deposition was rapid due to the presence of lamellar tissue and the plexiform vascular pattern, a common feature in dinosaurs and birds (e.g. Klein et al., 2012). This tissue is characterized by the interlaced presence of longitudinal, radial, and circular vascular channels (Lamm et al., 2013). The plexiform arrangement is common in sauropod dinosaurs, but not in Triassic sauropodomorphs (Stein and Prondvai, 2014). Due to this feature, the absence of internal and external lamellae and the beginning of bone remodeling, the holotype of *Nhandumirim waldsangae* represents an individual less advanced in ontogeny than reported for *Saturnalia tupiniquim* (paratype MCPV 3846; Stein, 2010) and *Asilisaurus kongwe* (Griffin & Nesbitt, 2016a). In *S. tupiniquim*, the bone has signs of remodeling marked by the presence of secondary osteons, in addition to two LAGs (Stein, 2010), the latter a similar condition of *N. waldsangae*. The deposition of internal circumferential lamellae on one part of the lamina may also be seen, indicating that MCPV 3846 is more advanced in ontogeny than the only specimen of *N. waldsangae*. As for *A. kongwe*, the main difference is the vascular pattern, which consists of longitudinal primary osteons surrounded by either parallel-fibered or woven bone, with the presence of an avascular region composed of parallel-fibered bone (Griffin & Nesbitt, 2016a). In *N. waldsangae*, longitudinal primary osteons with few anastomoses are present and restricted to the outer cortex. In addition, the presence of lamellae in *S. tupiniquim* indicates that the bone tissue of this taxon already records a decrease in deposition rate, consistent with bone maturity, whereas *A. kongwe* would be less advanced in its ontogeny, although already with signs of decreases in the rate of bone deposition. This differs from the condition presented *N. waldsangae*, indicating that this latter specimen was still growing rapidly at the time of its death, despite the presence of

LAGs. This evidence confirms that the high growth rates observed in Jurassic and Cretaceous dinosaurs (Curry, 1999; Horner et al., 2000, 2001; Sander, 1999, 2000; Erickson and Tumanova, 2000; Sander and Tückmantel, 2003; Sander et al., 2004; Erickson, 2005) were already present in dinosaurs during the Triassic.

Fibula—The bone exhibits the same osteohistological pattern as the tibia (Fig. 15). The beginning of bone remodeling is observed in the perimedullary region, with the formation of erosions rooms and a few secondary osteons (Fig. 15C-D). The vascularization is somewhat lower in the endosteal region, with more radial canals, fewer anastomoses. The radial canals are more common in the mesoperiosteal region. In the middle cortex, two lines of arrested growth are present (Fig. 15C), in position and numbers consistent with those present in the tibia. The vascular canals reach the external surface of the periosteal region without the formation of periosteal lamellae (i.e. an external fundamental system is absent).

The osteohistological pattern of *Nhandumirim waldsangae* differs from that of the fibula of *Asilisaurus kongwe*, which is composed mostly by coarse cancellous bone surrounded by a thin cortex of more compact bone (Griffin and Nesbitt, 2016a). Despite the presence of two LAGs in *N. waldsangae*, those differ from the unusual banded pattern of the outer cortex of the fibula in *A. kongwe* fibula. As no other fibula has yet been sampled among early dinosaurs, osteohistological patterns of this bone remain uncertain.

Comparatively, the general osteohistological features of *Nhandumirim waldsangae* are more similar with those of *Silesaurus opolensis*, with some distinctions most related to ontogeny. Both *N. waldsangae* and *S. opolensis* present the lamellar bone as the main osteohistological feature (Fostowicz-Frelik and Sulej, 2010), differing from the coarse cancellous bone with a thin compacted bone cortex of *Asilisaurus*

kongwe (Griffin and Nesbitt, 2016a), and the predominantly parallel-fibered bone of Ntaware Formation silesaurids (Peacock et al., 2017). LAGs are present in bones of the largest specimens of *S. opolensis* (Fostowicz-Frelik and Sulej, 2010), in both tibia and fibula of *N. waldsangae*, and absent in Ntaware Formation silesaurids femora (Peacock et al., 2017) and in *A. kongwe*, which have a banded pattern, not associated with growth marks (Griffin and Nesbitt, 2016a). Regarding the osteological maturity of *N. waldsangae*, *S. opolensis* and *A. kongwe*, the most remarkable difference between them is the presence of inner and outer circumferential lamellae in *S. opolensis* (Fostowicz-Frelik and Sulej, 2010), which is absent in the other two. This suggests that the larger specimen of *S. opolensis* was ontogenetically more mature than the *N. waldsangae* and *A. kongwe*. This evidence can be reinforced by the reduction of vascular channels and the absence of anastomoses in *S. opolensis*, whereas it is present in *N. waldsangae*.

Discussion

Comments on the Diagnosis of *Nhandumirim waldsangae*

Despite its incompleteness, the holotype of *Nhandumirim waldsangae* has potential autapomorphies, as well as a unique combination of characters that distinguishes it from other Triassic dinosauromorphs, supporting the recognition of a new genus and species for this specimen.

Regarding its vertebral column, *Nhandumirim waldsangae* has a sacrum comprising three vertebrae. Among early dinosaurs, the presence of three or more sacral vertebrae is plesiomorphic, but the homology of these elements to the primordial pair of sacral vertebrae has been the subject of extensive debate (e.g., Langer and Benton, 2006; Pol et al., 2011; Nesbitt, 2011). One of the paratypes of *Saturnalia tupiniquim*

(MCP 3845-PV) preserves a complete sacral series (Fig. 16), in which a trunk vertebra has been incorporated into the sacrum, and the first primordial sacral attaches caudal to the preacetabular ala of the ilium, medial to the caudal half of the iliac acetabulum. By comparison, the ilium of *Nhandumirim waldsangae* shows that the sacral rib of the first primordial sacral articulated with the ilium immediately caudal to the embayment between the preacetabular ala and pubic peduncle (Fig. 8E, F). This makes it unlikely that a trunk vertebra had been incorporated in the sacrum of *Nhandumirim waldsangae*. It is, however, unclear if the additional sacral vertebra in this latter species corresponds to the insertion of an element between the primordial pair (Nesbitt, 2011) or the incorporation of a caudal vertebra.

The ventral surfaces of the proximal caudal vertebrae in dinosauromorphs are plesiomorphically devoid of marked ornamentations. An exception is *Marasuchus lilloensis* (PVL 3871), the caudal vertebrae of which each bear a ventral longitudinal sulcus (Langer et al., 2013), resembling the condition in neotheropods such as *Dilophosaurus wetherilli* and “*Syntarsus*” *kayentakatae* (Tykoski, 2005). In addition, the proximal caudal vertebrae of the neotheropod *Dracoraptor hanigani* (Martill et al., 2016) bear subtle paired ventral keels. Among Triassic sauropodomorphs, the midcaudal vertebrae of *Panphagia protos* (PVSJ 874) and *Thecodontosaurus antiquus* (BRSMG Ca 7473) possess a shallow and broad ventral sulcus, as also seen in other dinosaur remains with uncertain affinities from the Carnian of south Brazil (Pretto et al., 2015). The proximal caudal vertebrae of *Efraasia minor* (SMNS 12667) resemble the first caudal vertebra of *Nhandumirim waldsangae* in having a ventral keel and lateral excavations, but these are restricted to the distal third of the centra, and more distal vertebrae seem to lack such keels. Accordingly, a ventral keel extending along the entire

length of the centrum of the proximal caudal vertebrae seems to be autapomorphic for *Nhandumirim waldsangae*.

Distal tail vertebrae with short zygapophyses, as seen in *Nhandumirim waldsangae*, are common among non-theropod dinossauromorphs, including the putative theropod *Eodromaeus murphi*. By contrast, in herrerasaurids and neotheropods, the zygapophyses are elongated (Rauhut, 2003; Tykoski, 2005).

The ilium of *Nhandumirim waldsangae* has a perforated acetabulum, a feature that is broadly acknowledged as a synapomorphy of Dinosauria (Brusatte et al., 2010; Langer et al., 2010a; Nesbitt, 2011). In addition, its iliac acetabulum (Fig. 17F) is deeper than in most early sauropodomorphs, such as *Panphagia protos* and *Saturnalia tupiniquim*, and is more similar to the condition in non-dinosaurian dinossauromorphs (Fig. 17A, B). Indeed, the earliest sauropodomorphs differ from *Nhandumirim waldsangae* in having an iliac acetabulum that is much shallower, being about twice as long craniocaudally as deep dorsoventrally (Fig. 17G), measured as the dorsoventral depth from the acetabular roof to the pubis-ischium contact.

Nhandumirim waldsangae has a well-developed brevis fossa on the iliac postacetabular ala, a feature that was hypothesized by Novas (1996) as a dinosaurian synapomorphy. However, recent discoveries revealed a more complex distribution of this feature among dinosauriforms. As pointed out by several authors (Fraser et al., 2002; Langer and Benton, 2006; Brusatte et al., 2010; Langer et al., 2010a; Nesbitt, 2011), a ventrally developed fossa is present in *Silesaurus opolensis*, whereas herrerasaurids, *Tawa hallae*, and a few early ornithischians lack this feature. Although a well-developed brevis fossa cannot be used to nest *Nhandumirim waldsangae* within Dinosauria, the presence of this feature does distinguish it from most non-dinosaurian dinossauromorphs, herrerasaurids, and some other dinosaurs. In saurischians with a well-

developed brevis fossa, the brevis shelf starts cranially as an inconspicuous ridge near to the iliac acetabulum, becoming more prominent along the postacetabular ala (e.g. Langer et al., 2010b). In *Nhandumirim waldsangae*, the ridge does not extend as close to the acetabulum, and the short brevis fossa does not contact the iliac body. This latter feature may represent another potential autapomorphy of the taxon.

The femur of *Nhandumirim waldsangae* differs from those of non-dinosaurian dinosauromorphs, including silesaurids, in possessing a unique combination of features, including: well-developed craniomedial tuber and femoral head; ventrally descending facies articularis antitrochanterica; angled greater trochanter; flanged fourth trochanter; and small crista tibiofibularis (Langer and Benton, 2006; Nesbitt, 2011; Langer et al., 2013).

Nesbitt (2011) discusses the presence of a groove on the proximal surface of the archosaur femur, highlighting that non-dinosaurian dinosauriforms have a deep and straight groove, which is also straight, but faint in sauropodomorphs, whereas it is distinctively curved in early neotheropods. The condition in *Nhandumirim waldsangae* differs from those two. It is deeper and somewhat curved compared to that of sauropodomorphs, but not as curved as in neotheropods. On the other hand, according to our first-hand observations, this feature has a more complex distribution among dinosaurs. Whereas some specimens of *Coelophysis bauri* clearly have a distinctive curved groove (e.g. NMMNHS 55344), this is much harder to identify in others (e.g. AMNH FARB 30618). In *Liliensternus liliensterni* (MB.R. 2175) the condition varies, with the left femur bearing a curved proximal groove and the right bone bearing a much straighter groove. Early sauropodomorphs also suggest some degree of variation in this feature. Rather than faint and straight, the proximal groove in one of the paratypes of *Saturnalia tupiniquim* (MCP 3846-PV) is deep and curved, resembling the condition in

N. waldsangae and *Buriolestes schultzi* (ULBRA-PVT280). Accordingly, we prefer to be more conservative and don't assume that *N. waldsangae* bear the neotheropod condition, stressing the need of a more comprehensive discussion of the definition and distribution of this character.

The dorsolateral trochanter of *Nhandumirim waldsangae* is potentially autapomorphic. It is set at the same level as the cranial trochanter, well below the level of the femoral head. Usually in saurischian dinosaurs, the dorsolateral trochanter is positioned well above the level of the cranial trochanter, as seen in *Saturnalia tupiniquim* (Langer, 2003), *Liliensternus liliensterni* (Langer and Benton, 2006; Nesbitt, 2011), and *Staurikosaurus pricei* (Bittencourt and Kellner, 2009). This is also the case in most ornithischians, in which, except in *Eocursor parvus* (see Butler, 2010), the dorsolateral trochanter is closely appressed to the greater trochanter (Norman, 2004; Langer and Benton, 2006).

The distal portion of the hindlimb epipodium of *Nhandumirim waldsangae* bears a unique set of theropod traits, which are uncommon among Carnian dinossauromorphs. In distal view, the tibia differs from those of almost all sauropodomorphs and herrerasaurids in its mediolaterally expanded profile. Early sauropodomorphs, such as *Saturnalia tupiniquim* and *Panphagia protos*, have a distal tibia profile that is nearly as wide transversely as long craniocaudally (Langer, 2003; Martínez and Alcober, 2009), as is also seen in *Eoraptor lunensis* (Sereno, 2012) and *Eodromaeus murphi* (PVSJ 562). *Herrerasaurus ischigualastensis* has a somewhat transversely expanded distal end of the tibia with a rounded cranial margin (Novas, 1994; PVL 2566), and *Staurikosaurus pricei*, and *Sanjuansaurus gordilloi* have a subcircular distal profile (Bittencourt and Kellner, 2009; Alcober and Martínez, 2010). On the contrary, non-heterodontosaurid ornithischians (Butler, 2010; Baron et al., 2017) and neotheropods

(Tykoski, 2005) share with *Nhandumirim waldsangae* a mediolaterally expanded distal end of the tibia.

Nesbitt and Ezcurra (2015) described the caudolateral flange (or posterolateral process) of the neotheropods *Zupaysaurus rougieri*, *Liliensternus liliensterni*, and *Coelophysis bauri* as tabular. A tabular caudolateral flange is more quadrangular than rounded, a shape resulting from a set of deflections. This is similar to the condition in *Nhandumirim waldsangae*, which also resembles neotheropods because it bears the anterior diagonal tuberosity on the cranial surface of the distal end of the tibia (Ezcurra and Brusatte, 2011). Among Carnian dinosauromorphs, the co-occurrence of a tabular caudolateral flange and the anterior diagonal tuberosity has so far been recognized only in the distal end of the tibia of *Nhandumirim waldsangae*.

The astragalus of many neotheropods has a prominent posteromedial process (or caudomedial process), as described for *Zupaysaurus rougieri* (Ezcurra and Novas, 2007). This process fits into a notch in the tibia, seen in the caudomedial corner of the distal surface of the bone. This condition is commonly found in neotheropods, such as “*Syntarsus*” *rhodesiensis* (holotype QG/1), as well as the “Petrified Forest theropod”, *Lepidus praecisio*, *Liliensternus liliensterni*, and *Tachiraptor admirabilis* (Padian, 1986; Ezcurra and Novas, 2007; Langer et al., 2014; Nesbitt and Ezcurra, 2015). The caudomedial notch is present in *Nhandumirim waldsangae*, *Eodromaeus murphi* (PVSJ 560, 562), *Guaibasaurus candelariensis* (Langer et al., 2011), and also in some sauropodomorphs, such as *Riojasaurus incertus* (PVL 3845, 4364; Ezcurra and Apaldetti, 2012) and *Coloradisaurus brevis* (Ezcurra and Apaldetti, 2012; Apaldetti et al., 2013).

The fibula of *Nhandumirim waldsangae* has an autapomorphic articular facet on the medial side of its distal end. This facet, which presumably marks the articulation

with the ascending process of the astragalus, was not observed in other early dinosaurs with a non-coossified tibiotarsus. In the fused tibiotarsus of some coelophysoids, the craniomedial corner of the distal fibula forms a flange and overlaps the cranial margin of the ascending process of the astragalus (see Rauhut, 2003; Tykoski, 2005; Ezcurra and Brusatte, 2011). This condition may prove to be homologous with that of *Nhandumirim waldsangae*, but the fusion of elements in coelophysoids hampers the proper evaluation of this feature.

The straight metatarsal IV of *Nhandumirim waldsangae* differs from the sigmoid elements of all well-known early dinosaurs. A similar condition is found in pseudosuchian archosaurs, pterosaurs and in *Lagerpeton chanarensis* and *Marasuchus lilloensis* (Serenio and Arcucci, 1993, 1994; Novas, 1996). Novas (1996) made the observation that metatarsal IV of dinosaurs tends to bow laterally along its distal half. Accordingly, we assume that a straight metatarsal IV represents an autapomorphic reversal of *Nhandumirim waldsangae* among dinosaurs, perhaps related to its small size.

Ontogeny and Taxonomic Validity of *Nhandumirim waldsangae*

The ontogenetic stage of *Nhandumirim waldsangae* is assessed based on (1) the tibia and fibula osteohistology (see above) and (2) the closure of neurocentral sutures. Osteohistology shows unmodified primary tissue as the main structural bony component. Anastomosed vascular canals abound, forming a plexiform arrangement, the beginning of the remodelling process composed by few erosion cavities aside primary osteons in both tibia and fibula and a few and small secondary osteons in the fibula. The medullary cavity and inner portion of the cortex lack trabecular bone and deposition of inner lamellae, as well as the external fundamental system in the outer cortex as well as growth marks like LAGs, annuli or zones. Also, the presence of two

LAGs in the middle cortex suggests that this individual has two years in the moment of his death. Despite the still controversial discussion about the presence of LAGs in sauropodomorphs, it indicates a temporary cessation of growth that has been shown to be deposited annually in extant vertebrates (Castanet and Smirina, 1990; Castanet et al., 1993, 2004). This pattern characterizes an individual still in full development, or a juvenile according to Sander et al. (2011). The closure of the neurocentral sutures only in caudal vertebrae also indicates that *Nhandumirim waldsangae* was not fully-grown. Irmis (2007) observed that pseudosuchians have a caudal–cranial sequence of neurocentral suture closure, but that bird-line archosaurs have a wider range of closure patterns. As such, a caudal–cranial sequence of neurocentral suture closure, although reported in some dinosaurs (Ikejiri, 2003; Irmis, 2007), cannot be assumed a priori for *Nhandumirim waldsangae*. However, the lack of neural arches in all but one of its trunk and sacral vertebrae suggests that the neurocentral sutures of these vertebrae were still open. On the other hand, the neural arches were preserved in all recovered caudal vertebrae of *Nhandumirim waldsangae*, with their neurocentral sutures closed. This suggests a caudal–cranial pattern of sutural closure in *Nhandumirim waldsangae*. According to this model, the holotype of *Nhandumirim waldsangae* would be regarded as an immature individual.

Because of its ontogenetic stage, *Nhandumirim waldsangae* might be thought to represent a juvenile of *Saturnalia tupiniquim* or *Staurikosaurus pricei*, other early saurischian dinosaurs found in the same beds, from the same or nearby sites. However, their morphological differences are noteworthy. *Nhandumirim waldsangae* differs from *Saturnalia tupiniquim* in the following traits: the presence of a ventral keel in the proximal caudal vertebrae; a short brevis fossa; no ridge connecting the brevis fossa to the iliac body and supracetabular crest; a perforated and deeper iliac acetabulum; a

caudoventrally oriented ischiadic peduncle of the ilium; femur more than twice the length of the ilium; femoral head more than twice as long as wide; a short dorsolateral trochanter; no trochanteric shelf; epipodium longer than the propodium; a mediolaterally expanded distal end of the tibia; tabular caudolateral flange; a caudomedial notch on the distal margin of the tibia; a flat caudodistal margin of the tibia; a craniomedial articular facet in the distal fibula; and a straight metatarsal IV.

Compared to *Staurikosaurus pricei*, *Nhandumirim waldsangae* has the following differences: craniocaudally longer caudal trunk vertebrae; a ventral keel in the proximal caudal vertebrae; short zygapophyses in distal caudal vertebrae; a postacetabular ala longer than the iliac body; a well-developed brevis fossa; a shorter pubic peduncle; femoral head more than twice as long craniocaudally as transversely wide; short dorsolateral trochanter; mediolaterally expanded distal end of the tibia; a tabular caudolateral flange of the tibia; a caudomedial notch in the distal articulation of the tibia; a flat caudodistal margin of the tibia; and a craniomedial articular facet in the distal portion of the fibula.

We consider it unlikely that the differences above can be explained solely by ontogeny. The most recent studies on skeletal variation throughout dinosauromorph growth reveal that morphological disparity among different ontogenetic stages is limited to a more restricted range of variation than that seen between *Nhandumirim waldsangae* and either *Saturnalia tupiniquim* or *Staurikosaurus pricei*. Piechowski et al. (2014) reported morphological variation possibly related to sexual dimorphism in *Silesaurus opolensis*, where additional ossification areas, such as the trochanteric shelf (or lateral ossification), were regarded as female traits. Griffin and Nesbitt (2016a) reported that several scars on the proximal end of the femur of the silesaurid *Asilisaurus kongwe* follow a consistent developmental order. Griffin and Nesbitt (2016b) showed that the

neotheropods *Coelophysis bauri* and “*Syntarsus*” *rhodesiensis* have both highly variable ontogenetic trajectories, where most of those variations (Griffin and Nesbitt, 2016b) are related to the presence of secondary ossifications and the fusion of elements in adult individuals. Compared to the ontogenetic trajectory inferred for *Asilisaurus kongwe* (Griffin and Nesbitt, 2016a), *Nhandumirim waldsangae* has features that better match those expected for mature individuals. Also, our understanding of the anatomy of *Nhandumirim waldsangae*, *Saturnalia tupiniquim* and *Staurikosaurus pricei* suggests that these dinosaurs have neither secondary ossifications nor fusion of elements such as those described for some neotheropods (Griffin and Nesbitt, 2016b). Consequently, most of those ontogenetic variations do not match the differences between *Nhandumirim waldsangae* and either *Saturnalia tupiniquim* or *Staurikosaurus pricei*, supporting the recognition of the former as a new early dinosaur species.

Phylogenetic Analyses and Implications

Nhandumirim waldsangae was scored in two recent phylogenetic data matrixes. Firstly, it was included in the dataset of Cabreira et al. (2016) to evaluate its relationships among early dinosauromorphs, and then it was included in the dataset of Nesbitt and Ezcurra (2015) to assess its possible theropod affinities.

Some scorings from the dataset of Cabreira et al. (2016) have been modified based on our own first-hand observations (Supplementary Data 1, Appendix 1S). Characters 256 and 257 of the modified Cabreira et al. (2016) dataset were taken from the datasets of Nesbitt and Ezcurra (2015) and Ezcurra and Brusatte (2011), respectively, because they describe features that are similarities between *Nhandumirim waldsangae* and some theropods. Character 248 from the Cabreira et al. (2016) dataset was excluded because it was considered uninformative, and a new character, number

258 of the modified Cabreira et al. (2016), was added (Supplementary Data 1, Appendix 2S). The modified Cabreira et al. (2016) data matrix is composed of 258 characters, 31 of which were ordered, and 44 taxa (Supplementary Data 1, Appendix 3S). The data matrix was analyzed in TNT 1.5 beta (Goloboff and Catalano, 2016). The heuristic search was performed under the following parameters: 10,000 replications of Wagner Trees (with random addition sequence); TBR (tree bi-section and reconnection) for branch swapping; hold = 20 (trees saved per replicate); and collapse of zero length branches according to “rule 1” of TNT (Goloboff et al., 2008).

The analysis resulted in 48 MPTs of 847 steps (Consistency Index = 0.348 and Retention Index = 0.639). The strict consensus tree (Fig. 18A) shows the same relationships outside Saurischia as those recovered by Cabreira et al. (2016). Saurischia is composed of two main clades, with Herrerasauria as the sister group of all other members of the group. *Daemonosaurus chauliodus*, *Tawa hallae* + *Chindesaurus bryansmalli* and *Eodromaeus murphi* are other saurischian dinosaurs outside Eusaurischia. *Guaibasaurus candelariensis* is recovered in two alternative positions: either outside Eusaurischia or within Sauropodomorpha. *Nhandumirim waldsangae* is found within Theropoda, as the sister taxon to a poorly resolved Neotheropoda (with a large polytomy including *Dilophosaurus wetherelli*, Petrified Forest Theropod, *Zupaysaurus rougieri*, *Liliensternus liliensterni* and coelophysoids). The relationships within Sauropodomorpha are the same as those of Cabreira et al. (2016). Bremer support values and bootstrap indices are generally low (Fig. 18A).

Based on the modified dataset of Cabreira et al. (2016), the position of *Nhandumirim waldsangae* within Theropoda is supported by three synapomorphies: a caudally extended ischiadic peduncle; a mediolaterally expanded distal end of the tibia;

and a tabular caudolateral flange of the tibia. This reveals that some typical neotheropod traits, previously only known in Norian taxa, first emerged during the Carnian.

A IterPCR analyses (Pol & Escapa, 2009) shows the Petrified Forest Theropod as the main floating taxon within Neotheropoda. Its pruning results in a polytomy including *Dilophosaurus wetherelli*, *Zupaysaurus rougieri*, and a clade where *Liliensternus liliensterni* is sister to coelophysoids.

The phylogenetic position of the problematic early dinosaur *Guaibasaurus candelariensis* (see Ezcurra, 2010; Langer et al., 2011) is different from that found by Cabreira et al. (2016). In the new analysis, its placement within Eusaurischia is supported by three synapomorphies: a short scapular blade, a more robust metacarpal I and an iliac supraacetabular crest with maximum breadth at the center of the acetabulum.

For the second analysis, some scorings were modified from the dataset of Nesbitt and Ezcurra (2015) (Supplementary Data 1, Appendix 4S), but no characters were edited or added. The data matrix was analyzed using the same search parameters described for the first analysis. This resulted in 48 MPTs each with a length of 1063 steps (Consistency Index = 0.386 and Retention Index = 0.685). Bremer support and bootstrap indexes are higher when compared to those of the first analysis (Fig. 18B). The strict consensus tree (Fig. 18B) is remarkably different from that presented by Nesbitt and Ezcurra (2015) for relationships within Saurischia, but the relationships outside of that clade match those found by those authors. The new topology shows two monophyletic groups, Sauropodomorpha and Theropoda (including *Tawa hallae*), in a large polytomy with *Nhandumirim waldsangae*, *Eodromaeus murphi*, *Eoraptor lunensis*, *Chindesaurus bryansmalli*, *Staurikosaurus pricei* and *Herrerasaurus ischigualastensis*. In this context, some characters seen both in *Nhandumirim*

waldsangae and in neotheropods, including the diagonal tuberosity on the anterior surface of the distal end of the tibia, the tabular caudolateral flange and the caudomedial notch on the distal end of the tibia are interpreted as homoplastic.

The IterPCR analyses (Pol and Escapa, 2009) identified *Nhandumirim waldsangae*, *Eodromaeus murphi* and *Chindesaurus bryansmalli* as the main floating taxa. When these taxa are pruned, the new strict consensus tree recovers *Eoraptor lunensis* as a saurischian, forming a polytomy with Sauropodomorpha and Theropoda, with Herrerasauridae found as sister group of all other members of the latter group. The analysis shows three possible positions for *Nhandumirim waldsangae*: as sister taxon to Saurischia (non-Eusaurischia); as sister taxon to *Eoraptor lunensis*, in a polytomy with Sauropodomorpha and Theropoda; or as an early theropod dinosaur, sister taxon to Herrerasauridae + *Tawa hallae* + Neotheropoda. The position of *Eodromaeus murphi* is ambiguous, with possible non-herrerasaurid theropod and Herrerasauridae affinities.

Further exploratory analyses were performed under the same search parameters described above, but enforcing constraints for the monophyly between *Nhandumirim waldsangae* and *Saturnalia tupiniquim*, and *Nhandumirim waldsangae* and *Staurikosaurus pricei*. The results show that 4 extra steps are needed to recover a *Nhandumirim waldsangae* + *Saturnalia tupiniquim* clade using both the modified matrixes of Cabreira et al. (2016) and Nesbitt and Ezcurra (2015). Using, the same data matrixes, 12 and 4 extra steps are needed to recover a clade comprising *Nhandumirim waldsangae* + *Staurikosaurus pricei*.

Conclusions

The last decade has witnessed a significant increase in the record of Carnian dinosaurs, with the discoveries of *Panphagia protos*, *Chromogisaurus novasi*, *Pampadromaeus barberenais*, and *Buriolestes schultzi*. These new discoveries support new models for the rise of dinosaurs, where the group, despite not being the most abundant faunal components, attained a noteworthy taxic diversity early in its evolutionary history (Brusatte et al., 2008a, b; Ezcurra, 2010; Benton et al., 2014).

Although incomplete, the skeletal remains of *Nhandumirim waldsangae* reveal a unique combination of potential autapomorphies, dinosauiromorph and saurischian symplesiomorphies, along with features previously considered to occur exclusively within coelophysoid dinosaurs. Probably due to this incompleteness, the phylogenetic analysis recovered uncertain relations for *Nhandumirim waldsangae*, but suggest a possible closer relationship with theropods than with sauropodomorph dinosaurs. These possible theropod affinities provide clues about the emergence of some coelophysoid anatomical traits. In addition, this would represent the oldest record of Theropoda known in Brazil.

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Figures

FIGURE 1. Geographic and geologic provenance of *Nhandumirim waldsangae* gen. et sp. nov. **A**, map of the Paraná Basin in South America; **B**, simplified geological map of the central portion of Rio Grande do Sul State (modified from Eltink et al., 2016), indicating Santa Maria (green star); **C**, location of selected outcrops in the eastern

outskirts of Santa Maria (modified from Da Rosa, 2014), indicating the
Waldsanga/Cerro da Alemoa site (green star); **D**, sedimentary log from the
Waldsanga/Cerro da Alemoa outcrop, indicating the provenance of the studied
specimen and other fossiliferous beds (modified from Da Rosa, 2005); **E**, photograph of
the outcrop, showing the channel and crevasse deposits (CH+CR) of the Caturrita
Formation, and the distal (FFd) and proximal floodplain deposits (FFp) of the Santa
Maria Formation, indicating the level where *Nhandumirim waldsangae* gen. et sp. nov.
was found. [planned for page width]

FIGURE 2. Silhouette depicting the preserved bones of *Nhandumirim waldsangae* gen.
et sp. nov. (LPRP/USP 0651). [planned for page width]

FIGURE 3. *Nhandumirim waldsangae* gen. et sp. nov. (LPRP/USP 0651). Trunk vertebrae “1”(A), “2” (B) and “3” (C) in right lateral (A) and left lateral (B–C) views.

Abbreviations: **dpr**, depression; **fm**, foramen; **lcp**, left caudal pedicel; **ns**, neural spine; **prz**, prezygapophysis; **tp**, transverse process. [planned for column width]

FIGURE 4. *Nhandumirim waldsangae* gen. et sp. nov. (LPRP/USP 0651). Partial neural arch of trunk vertebra “2” in (A) right lateral and (B) left caudolateral views.

Abbreviations: **cdf**, centrodiapophyseal fossa; **lcp**, left caudal pedicel; **nc**, neural canal; **pcdl**, posterior centrodiapophyseal lamina; **pocdf**, postzygapophyseal

centrodiapophyseal fossa; **podl**, postzygodiapophyseal lamina; **prdl**, prezygodiapophyseal lamina; **prz**, prezygapophysis. [planned for column width]

FIGURE 5. *Nhandumirim waldsangae* gen. et sp. nov. (LPRP/USP 0651). Sacral vertebrae. **A**, isolated centrum in ventral view. Second primordial sacral vertebral centrum in **(B)** ventral, **(C)** cranial, **(D)** right lateral and **(E)** caudal views. Left rib of first primordial sacral in **(F)** dorsal and **(G)** left lateral views. Dashed lines denote inferred limits of missing portions. **Abbreviations:** **fm**, foramen; **sr**, sacral rib; **srtp**, sacral rib and transverse process; **sw**, swelling. [planned for page width]

FIGURE 6. *Nhandumirim waldsangae* gen. et sp. nov. (LPRP/USP 0651). Caudal vertebrae “1” (A-D), “2” (E-H) and “3” (I-L) in (A, F and I) cranial, (B and J) caudal, (C, G and K) right lateral, (D) dorsal and (E, H and L) ventral views. **Abbreviations:** **dpr**, depression; **fca**, facet for chevron articulation; **fm**, foramen; **lm**, lamina; **nc**, neural canal; **ncs**, neurocentral suture; **ns**, neural spine; **poz**, postzygapophysis; **ppl**, prezygo-postzygopophyseal lamina; **prz**, prezygapophysis; **prpadf**, prezygapophyseal parapodiapophyseal fossa; **se**, shallow excavation; **tp**, transverse process; **vk**, ventral keel. [planned for page width]

FIGURE 7. *Nhandumirim waldsangae* gen. et sp. nov. (LPRP/USP 0651) Caudal vertebrae “4” (A-C), “5” (D), “6” (E), “7” (F) and chevron (G-H) in (A) cranial, (B) dorsal, (C-G) left lateral and (H) caudal views. **Abbreviations:** **dpr**, depression; **fca**, facet for chevron articulation; **lm**, lamina; **ns**, neural spine; **poz**, postzygapophysis; **ppl**, prezygo-postzygopophyseal lamina; **prz**, prezygapophysis. [planned for page width]

FIGURE 8. *Nhandumirim waldsangae* gen. et sp. nov. (LPRP/USP 0651). Right ilium in (A) cranial, (B) caudal, (C and D) lateral, (E and F) medial, (G) ventral and (H) dorsal views. D and F are outline drawings of C and E, respectively. Parts in black represent portions still covered by sediment; light gray represents scarred areas; dark gray represents articular facets of the peduncles; dashed lines represent the possible limits of missing parts; cross-hatched areas show broken parts. **Abbreviations:** 1st,

attachment scars for the first primordial sacral rib; **ac**, iliac acetabulum; **an**, acetabular antitrochanter; **brfo**, brevis fossa; **fm**, foramina; **imr**, iliac medial ridges; **ip**, ischiadic peduncle; **sac**, supracetabular crest; **poa**, postacetabular ala; **pp**, pubic peduncle; **pra**, preacetabular ala; **prf**, preacetabular fossa. [planned for page width]

FIGURE 9. *Nhandumirim waldsangae* gen. et sp. nov. (LPRP/USP 0651). Right femur in (A) cranial, (B) lateral, (C) caudal, (D) medial, (E) proximal, and (F) distal views.

Light gray indicate scarred areas, cross-hatched areas represent broken parts.

Abbreviations: 4th, fourth trochanter; **clt**, craniolateral tuber; **cmt**, craniomedial tuber; **cfbf**, fossa for caudofemoralis brevis; **cflf**, fossa for caudofemoralis longus; **ct**, cranial trochanter; **ctf**, crista tibiofibularis; **dlt**, dorsolateral trochanter; **faa**, facies articularis antitrochanterica; **fcil**, femoral caudolateral intermuscular line; **fcml**, femoral caudomedial intermuscular line; **fcmc**, femoral craniomedial crest; **fdms**, muscle scar on laterocranial distal femur; **fm**, foramen; “**gt**”, great trochanter; **lc**, lateral condyle; **lic**, linea intermuscularis cranialis; **ls**, ligament sulcus; **mc**, medial condyle; **mt**, medial tuber; **mr**, medial ridge; **oi**, obturatorius insertion; **pf**, popliteal fossa; **pg**, proximal groove; **si**, sulcus intercondylaris; **ssn**, saddle-shaped notch; **ve**, ventral emargination.

[planned for page width]

FIGURE 10. *Nhandumirim waldsangae* gen. et sp. nov. (LPRP/USP 0651). Right tibia (A and B) and fibula (C and D) in (A and C) cranial and (B and D) caudal views.

Abbreviations: **ifi**, iliofibularis insertion; **fm**, foramina; **pfms**, muscle scars on proximal fibula. [planned for column width]

FIGURE 11. *Nhandumirim waldsangae* gen. et sp. nov. (LPRP/USP 0651). Distal end and outline drawings of right tibia (A-E) and fibula (F and G) in (A) cranial, (B) lateral, (C) caudal, (D and G) medial and (E and F) distal views. **Abbreviations:** **adt**, anterior diagonal tuberosity; **clf**, caudolateral flange; **cmn**, caudomedial notch; **faap**, articular facet for the ascending process of the astragalus; **faf**, articular facet in distal fibula; **pdg**, proximodistally oriented groove; **pdr**, proximodistally oriented ridge; **tfl**, insertion area for the tibiofibular ligament. [planned for page width]

FIGURE 12. *Nhandumirim waldsangae* gen. et sp. nov. (LPRP/USP 0651). Right metatarsals II (A-F) and IV (G-K) in (A and G) cranial, (B and H) lateral, (C and I) caudal, (D and J) medial, (E) proximal and (F and K) distal views. Light grey indicates scarred areas, and cross-hatched areas represent broken portions. [planned for page width]

FIGURE 13. *Nhandumirim waldsangae* gen. et sp. nov. (LPRP/USP 0651). Right pedal phalanges in (A₁-H₁) dorsal, (A₂-H₂) lateral, (A₃-H₃) plantar, (A₄-H₄) medial, (A₅-H₅)

proximal and (A₆-D₆) distal views. Non-ungual phalanges 1-5 are respectively represented in A-E. F-G represent the unguals. [planned for page width]

FIGURE 14: General microstructural anatomy of the tibia of *Nhandumirim waldsangae* gen. et sp. nov. (LPRP/USP 0651). (A) Right tibia indicating the sampled area of the bone. (B) Cross section of the tibia with the squared areas detailed in (C-E). (C) View of the complete transect showing the osteohistological pattern of the tibia, with two lines of arrested growth in the middle cortex marked by white lines, and erosion cavities

indicating the beginning of remodelling process in the deep cortex. **(D)** Arrows point to secondary osteons, also marked by white lines. **(E)** Detail of the vascular arrangement, highlighting the vascular canals reaching the periosteal surface. Scale bars: 100mm **(B)**; 200µm **(C, E)**; 250µm **(D)**. **Abbreviations:** **er**, erosion cavities; **lag**, line of arrested growth; **vc**, vascular canals. [planned for page width]

FIGURE 15. General microstructural anatomy of the fibula of *Nhandumirim waldsangae* gen. et sp. nov. (LPRP/USP 0651). **(A)** Right fibula indicating the sampled area of the bone. **(B)** Cross section of the fibula with the square areas detailed in **(C-E)**. **(C)** View of the complete transect showing the osteohistological pattern of the fibula, composed by plexiform arrange of the vascular network. **(D)** Lines of arrested growth in the middle cortex marked by white lines. **(E)** Detail of the vascular arrangement, highlighting the vascular canals reaching the periosteal surface. Scale bars: 150mm **(B)**; 250µm **(C)**; 300µm **(D-E)**. **Abbreviations:** lag, line of arrested growth; **vc**, vascular canals. [planned for page width]

FIGURE 16. *Saturnalia tupiniquim* (MCP-3845 PV). Articulated sacrum and ilia in dorsal **(A)** view. **B.** Outline drawings represent the lateral aspect of the attachment scars of the sacral vertebra transverse processes and ribs in the right ilium. **Abbreviations:** **1st**, first primordial sacral vertebra; **2nd**, second primordial sacral vertebra; **ds**, dorsal vertebra incorporated to the sacrum. [planned for page width]

FIGURE 17. Lateral view of several early dinosauromorph ilia, showing the depth of the acetabulum. Dashed lines represent the possible limits of missing parts. **A**, *Asilisaurus kongwe* (NMT RB159, after Peacock et al., 2013); **B**, *Ixalerpeton polesinensis* (ULBRA-PVT059); **C**, *Eocursor parvus* (SAM-PK-K8025, after Butler, 2010); **D**, *Herrerasaurus ischigualastensis* (PVL 2566); **E**, *Coelophysis bauri* (AMNH FARB 2708); **F**, *Nhandumirim waldsangae* gen. et sp. nov. (LPRP/USP 0651); **G**, *Saturnalia tupiniquim* (MCP-3845 PV). Specimens scaled to the same acetabular length. [planned for page width]

FIGURE 18. Phylogenetic relationships of *Nhandumirim waldsangae* gen. et sp. nov. (LPRP/USP 0651) among early dinosauromorphs. **A**, Strict consensus of 48 MPTs found in the analysis of the data matrix of Cabreira et al (2016); **B**, Strict consensus of 48 MPTs found in the analysis of the data matrix of Nesbitt and Ezcurra (2015). Values at nodes are Bremer support and bootstrap proportions (above 50%). [planned for page width]

ANEXO 3

Materiais de sauropodomorfos e correlações bioestratigráficas da localidade tipo de *Sacisaurus*, Triássico Superior da Formação Caturrita, sul do Brasil

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Síntese do anexo 3

Sacisaurus agudoensis é o único salessaurídeo já reconhecido para a Supersequência Santa Maria. Todavia, a correlação entre sua localidade-tipo com outros sítios triássicos no Rio Grande do Sul é controversa. Em termos de idade, a ocorrência de *S. agudoensis* nestes estratos tampouco permite uma inferência mais precisa que Triássico Superior. O objetivo deste trabalho é a descrição de materiais de sauropodomorfos associados aos abundantes restos de *S. agudoensis*, e avaliar se o seu sinal filogenético pode ajudar a responder questão de correlação do sítio. De fato, a morfologia destes fósseis é mais condizente com a de sauropodomorfos pós-carnianos como *Pantydraco caducus* e *Unaysaurus tolentinoi* do que com espécies do Carniano, como *Saturnalia tupiniquim* e *Panphagia protos*, o que sugere uma idade mais nova ao depósito. Da mesma maneira, a anatomia dos dentes de cinodontes "brasilotontídeos" provenientes da mesma localidade e estrato parecem coincidir com as correlações sugeridas pelos sauropodomorfos descritos aqui.

**Sauropodomorph remains and correlation of the *Sacisaurus* site, Late Triassic
(Caturrita Formation) of southern Brazil**

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Abstract

Sacisaurus agudoensis is the only silesaurid known for the Triassic beds of the Santa Maria Supersequence and the correlation of its type-locality to the other Triassic deposits of south Brazil has always been controversial. In an attempt to improve this situation, a handful of dinosaur remains found associated to *S. agudoensis* are here described and compared. Their anatomy is more similar to that of Norian sauropodomorphs such as *Pantyraco caducus* and *Unaysaurus tolentinoi* than to that of Carnian taxa such as *Saturnalia tupiniquim* and *Pampadromaeus barberenai*. This resemblance suggests a younger (perhaps Norian) age to the *Sacisaurus* site, as also suggested by the record of *Riograndia*-like and brasilodontid cynodonts in the assemblage and local stratigraphic correlation that positions the site in the Caturrita Formation.

Key words: Dinosauria, Sauropodomorpha, Dinosauriformes, Santa Maria Supersequence, Caturrita Formation, biostratigraphy, Norian, South America.

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Introduction

The type-locality of the dinosauromorph *Sacisaurus agudoensis* Ferigolo and Langer, 2007, has been explored during 2000-2001 in a series of field works led by JF and the crew of Fundação Zoobotânica do Rio Grande do Sul, in the context of the IDB (Inter-American Development Bank) funded *Pró-Guaíba* Project. These unearthed the rich material attributed to *S. agudoensis*, as well as cynodont (Ribeiro et al. 2011) and other dinosaur remains (Langer and Ferigolo, 2013). The latter includes a handful of isolated bones, which are too large to represent the kind of animal supposedly sampled at its adult stage by the fossils attributed to *S. agudoensis*. The overlap of some of those

remains (i.e., ilium, femur) to bones of *S. agudoensis* indicates that they correspond to a different taxon, with further non-duplicated larger elements (i.e. ectopterygoid, neck vertebra, metatarsal I) also tentatively attributed to that taxon. This work aims at fully describing such specimens, inferring their phylogenetic affinities and signal for faunal correlation. Indeed, the correlation of the *Sacisaurus* site to other tetrapod-bearing localities of the Santa Maria and Caturrita formations is not strongly constrained. As such, we also attempt here to provide geological and biochronological data to more strongly define the stratigraphic position of that site.

Institutional abbreviations.— BPI, Evolutionary Studies Institute, Johannesburg, South Africa (formerly Bernard Price Institute); MB. R., Museum für Naturkunde, Berlin, Germany; MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MCP, Museu de Ciências e Tecnologia, PUCRS, Porto Alegre, Brazil; NHM, Natural History Museum, London, United Kingdom; PULR, Universidad Nacional de La Rioja, La Rioja, Argentina; PVSJ, Museo de Ciencias Naturales, San Juan, Argentina; SAM-PK, Iziko South African Museum, Cape Town, South Africa; SMNS, Staatliches Museum für Naturkunde, Stuttgart, Germany; UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; UFSM, Universidade Federal de Santa Maria, Santa Maria, Brazil; ULBRA, Museu de Ciências Naturais, Universidade Luterana do Brasil, Canoas, Brazil.

Geological Settings

The *Sacisaurus* site is located at 19°43'12'' S; 47°45'04'' W, inside the western urban area of city of Agudo, state of the Rio Grande do Sul, Brazil. Due to the urban expansion, the outcrop is now located on the western margin of Independência Street,

north to Concordia Avenue. Very few of the original outcrops remains, based on which a sedimentary profile is herein provided (Fig. 1A).

The profile is more than eight meters deep and composed of an intercalation of fluvial (CH) and overbank (CR) deposits. It starts with a fine sandstone where *ex situ* *Exaeretodon* fragments were recorded. Still in the first meter of the profile, reddish mudstones and a brownish fine sandstone are seen. The latter shows an upwards coarsening trend, with mud intraclasts at the top, forming a millimetric intraformational conglomerate. Above this conglomerate, there is an intercalation of reddish mudstones and greenish fine sandstones that preserved most fossils in the site. The rest of the profile is formed of yellowish to pinkish fine sandstones with millimetric intercalation of brown mudstones. These present a lobe or tabular geometry, are generally massive, but sometimes bear horizontal lamination and trough cross-bedding. Whereas the basal most levels represent traction and suspension deposition probably in an oxbow lake, the uppermost sandstones are linked to crevassing. These lithologies correspond to the Caturrita Formation (*sensu* Andreis et al. 1980), i.e. upper portion of the Candelária Sequence, Santa Maria Supersequence (*sensu* Horn et al. 2014).

Nearby outcrops allow for a better stratigraphic correlation (Fig. 1), as only crevasse deposits are recorded at “Ki–Delicia” and “ASERMA” sites. The slightly more distant, and much better known, Janner outcrop (Pretto et al. 2015) has equivalent lithologies at its top, whereas the highly fossiliferous reddish mudstones of the middle and lower part of the outcrop correspond to the Santa Maria Formation (Da Rosa, 2005, 2015).

Material

Bones of the larger dinosauiromorph found at the *Sacisaurus* site were not recovered articulated or closely associated, so that there is no clear evidence that they correspond to a single individual. This is corroborated by the preserved right and left femora, which share a very similar anatomy, but are of slightly different sizes. As a whole, the material have a similar taphonomic signature and includes a right ectopterygoid (MCN PV 10049), one cervical vertebra (MCN PV 10027), a right ilium (MCN PV10026), right (MCN PV10007) and left (MCN PV10008) femora, and a metatarsal I (MCN PV 10049). As mentioned above, the attribution of these specimens to the same taxon is tentative; based on their similar phylogenetic signal (discussed below) added of topotypic principles.

Comparative description

Ectopterygoid (MCN PV 10049).—The bone is nearly complete, missing only the rostral tip of the lateral process and the medial contour of the medial process (Fig. 2), precluding the proper assessment of its articulation with the pterygoid. As preserved, the ectopterygoid is slightly longer (rostrocaudally) than lateromedially wide. The lateral process is hook-shaped and arches rostrally, forming a pounded caudal margin with the medial process. Its lateral half flattens lateromedially, and it is dorsoventrally higher compared to its medial half. Its articulation with the jugal is marked by scars on the caudolateral margin. Although missing its rostral-most tip, it is clear that such articulation is tabular, differing from the T-shaped profile of *Plateosaurus engelhardti* (Prieto-Márquez and Norell, 2011). The medial half of the lateral process expands rostrocaudally towards the medial process, which is much longer rostrocaudally than the former.

The medial process is flange-like, dorsoventrally expanded, and bears a medially directed dorsal margin. Its ventral surface is excavated by a semicircular depression, which has been considered pneumatic and typical of theropods (e.g. Rauhut, 2003). Yet, Nesbitt (2011) notices that such feature just marks the articulation with the pterygoid, as seen in *Eoraptor lunensis*, *Pantyraco caducus*, *Plateosaurus engelhardti*, *Liliensternus liliensterni*, and *Coelophysis bauri*. The medial process has a long rostral projection resembling that of *Pa. caducus* (Yates, 2003; Galton and Kermack, 2010), and differing from that of “*Syntarsus*” *rhodesiensis* (Raath, 1977), *Allosaurus fragilis* (Nesbitt, 2011), *Pl. engelhardti* (Prieto-Márquez and Norell, 2011), and *Lesothosaurus diagnosticus* (Porro et al. 2015).

Neck vertebra (MCN PV 10027).—The only preserved vertebra (Fig. 3) is somewhat distorted and incomplete, missing the cranioventral portion of the centrum, the zigapophyses, the neural spine, and most of the parapophyses and diapophyses. Together, the dorsal position of the parapophyses in the centrum, the well-developed diapophyses, the elongated centrum, and the presence of a ventral keel, indicate that MCN PV 10027 represents a cervical vertebra, possibly from the caudal part (8th or 9th element) of the neck. For descriptive purposes, the laminae and fossae nomenclature of Wilson (1999, 2012) and Wilson et al. (2011) will be adopted.

The centrum has an elongated profile, at least three times longer than high, the ventral portion of which bears a stout ventral keel; only the caudal half of which its preserved. As such, the keel is mediolaterally thicker caudally, i.e. more than seven times thicker in its caudal portion than cranially at the middle of the centrum (Fig. 3B). That thicker portion projects further ventrally than the caudal articulation of the centrum. The surface surrounding that articulation is heavily scarred, mainly on its

ventral margin. In ventral view, the centrum is spool-shaped, with its caudal rim c.1.75 times wider than its middle portion. The caudal articular face of the centrum is deeply concave. In caudal view (Fig. 3C), it is exaggeratedly wider than high due taphonomic distortion. In lateral view, its margin is oblique to the long axis of the centrum, so that its ventral edge extends further caudally than the dorsal. The neurocentral suture is seen mainly along the caudal portion of the vertebra, suggesting an advanced closure stage. The dorsal surface of the centrum has a well-developed fossa (“fo” in Fig. 3), which is remarkably deep, dorsoventrally narrow, and craniocaudally elongated. Most of both parapophyses are missing due to breakages. Each is represented by a subtle and short oblique (cranioventrally to caudodorsally oriented) ridge set at the dorsal part of the cranial margin of the centrum, close to the neural arch, fading away caudodorsally in the direction of the “anterior centrodiapophyseal lamina”.

The neural arch bears well developed laminae and fossae. The cranial portion of the prezygodiapophyseal laminae is missing, but its well-developed caudal part is clearly seen in left lateral view (“prdl” in Fig. 3). This lamina roofs a deep prezygadiapophyseal centrodiapophyseal fossa and extends further laterally than the “anterior centrodiapophyseal lamina” (“acdl” in Fig. 3), which is short and does not reach the parapophysis. The centrodiapophyseal fossa is deep and craniocaudally elongated. It is set caudal to the prezygadiapophyseal centrodiapophyseal fossa, with its cranial half roofed by a lateroventrally directed, well-developed diapophysis, from the dorsal surface of which a well-developed postzygodiapophyseal lamina (“podl” in Fig. 3) arises. This lamina extends towards the base of the postzygapophysis (which is not preserved), marking the craniodorsal margin of a deep postzygadiapophyseal centrodiapophyseal fossa. The right of those fossae (Fig. 3E) is divided in two by a subtle ridge that expands cranioventrally from the middle of the postzygodiapophyseal

lamina. An equivalent ridge is, however absent from the left side of the vertebra. The postzygadiapophyseal centrodiapophyseal fossa also overlaps the caudal half of the centrodiapophyseal fossa dorsally. The “posterior centrodiapophyseal lamina” roofs the dorsal and caudal portions of the centrodiapophyseal fossa, also forming the whole ventral edge of the postzygadiapophyseal centrodiapophyseal fossa.

The dorsal surface of the neural arch (Fig. 3A) has several ridges, which are tentatively associated to the laminae of later saurischians. The cranial surface of the neural spine has a deep, dorsoventrally short and craniocaudally long “V”-shaped spinoprezygapophyseal fossa (“sprf” in Fig. 3) at the base. Its lateral margins are formed by subtle spinoprezygapophyseal laminae that reach the medial surface of the prezygapophyses, where they bifurcate. Another pair of ridges (“rdg1” in Fig. 3) form the lateral margin of the prezygapophyses, extending caudally along the dorsal surface of the neural arch to reach the lateral base of the neural spine caudal to the spinoprezygapophyseal fossa. Ventrolateral to that, there is another pair of faint craniocaudally directed ridges (“rdg2” in Fig. 3). Also, subparallel to the neural spine, a pair of inconspicuous low ridges (“eprl?” in Fig. 3) extend on the dorsal surface of the neural arch. Although its caudal end is missing, it most probably corresponds to the epipophyseal-prezygapophyseal lamina (Wilson, 2012).

Neck vertebrae with epipophyses have been regarded as a dinosaur synapomorphy (Langer and Benton, 2006; Nesbitt, 2011). Although the epipophyses are not preserved in MCN PV 10027, the ridge putatively related to the epipophyseal-prezygapophyseal lamina is an indirect evidence of their presence. A similar condition is seen in the 8th cervical vertebra of *Panphagia protos* (PVSJ 874), in which a craniomedially directed incipient ridge comes from the epiphysis. This condition is clearer in later saurischians, such as the sauropodomorphs *Adeopapposaurus mognai*

(PVSJ 610) and *Massospondylus carinatus* (BPI 4934; SAM PK K 388), and neotheropods like *Elaphrosaurus bambergi* (Rauhut and Carrano, 2016). No epipophyses are seen in the caudal cervical vertebrae of ornithischians (Sereno et al. 1993; Langer and Benton, 2006; Nesbitt, 2011), but these are seen in non-dinosauriform archosauriforms, as *Batrachotomus kupferzellensis* and *Tanystropheus longobardicus* (Langer and Benton, 2006; Nesbitt, 2011; Ezcurra, 2016). Yet, the morphology of MCN PV 10027, with well-developed fossae and laminae, stresses its closer resemblances to dinosaurs than to other archosaurs.

Carnian dinosaurs, such as *Eoraptor lunensis* (Sereno et al. 2012), *Panphagia protos* (Martínez and Alcober, 2009), and *Herrerasaurus ischigualastensis* (Sereno and Novas, 1993) lack the well-developed fossae and laminae seen in MCN PV 100027. These are also mostly absent in pseudosuchians, although deep fossae and prominent laminae are present in some poposaurids and crocodyliforms (Nesbitt, 2005, 2007; Wedel, 2007). Among later saurischians, neotheropods are widely recognized by their pneumatic vertebrae, as seen in early forms like *Coelophysis bauri* and *Liliensternus liliensterni* (see Benson et al. 2012). This condition is characterized by cervical vertebrae with well-developed laminae and deep fossae pierced by large foramina (Britt, 1993; O'Connor, 2006, 2007). On the other hand, early sauropodomorphs lack the deep fossae seen in neotheropods (Wedel, 2007; *Adeopapposaurus mognai*, PVSJ 610) and in MCN PV 100027, although the caudalmost vertebra of the cervical series of *Plateosaurus engelhardti* (SMNS 13200) has well-developed fossae and prezygodiapophyseal, centrodiapophyseal, and postzygodiapophyseal laminae, resembling the condition of MCN PV 100027. Neotheropods differs from MCN PV 100027 because they bear at least one pair of deep pleurocoels in the cranial portion of the centrum. As observed by Tykoski (2005), those pleurocoels are set either

caudodorsal or dorsal to the parapophyses. Although the cranial portion of the centrum of MCN PV 100027 is damaged, the remaining morphology does not suggest the presence of such a feature. Furthermore, a second pair of pleurocoels may be present caudal to the aforementioned, as in coelophysoids (Tykoski, 2005) and in *Elaphrosaurus bambergi* (Rauhut and Carrano, 2016), although not in *L. liliiensterni* (MB. R. 2175), but this is not seen in MCN PV 100027.

Ilium (MCN PV10026).—A right ilium (Fig. 4) is nearly complete, missing the cranial tip of the preacetabular ala, as well as small portions of the cranial part of the supracetabular crest, the cranioventral part of the acetabular medial wall, and the cranioventral part of the postacetabular ala. The iliac length suggests an individual smaller than those referred to *Saturnalia tupiniquim*, *Guaibasaurus candelariensis*, *Unaysaurus tolentinoi*, and *Pampadromaeus barberenai*. The preacetabular ala is subtriangular in lateral view and laterally directed due to the inwards arching of the entire blade (Fig.4C). Its shape resembles that seen in sauropodomorphs such as *Riojasaurus incertus* (PULR 56) and *Efraasia minor* (SMNS 12354), but clearly differs from that of other sauropodomorph remains from the Caturrita Formation (Bittencourt et al. 2012). The preacetabular ala is considerably shorter than the postacetabular ala and its cranial tip is set well caudal to the cranialmost edge of the pubic peduncle. Although the preacetabular ala of *Pantyraco caducus* (Yates, 2003) and *Leoneerasaurus taquetrensis* (Pol et al. 2011) extends cranial to the pubic peduncle, that structure is shorter in most early sauropodomorphs (Cooper, 1981; Benton et al. 2000; Langer, 2003; Rowe et al. 2011), unlike ornithischians and neotheropods. The preacetabular ala and the pubic peduncle are set at a right angle to one another in MCN PV10026. The concave area between them seems to harbor an incipient preacetabular fossa (“prf” in

Fig. 4), but this cannot be confirmed due to breakages. Dorsally, the preacetabular ala shows a slightly bulged lateral rugose muscle scar (“sc” in Fig. 4), related to the insertion of *M. iliotibialis* (Hutchinson, 2001a; Langer, 2003), which spans caudally along the dorsal edge of the iliac blade. It is caudally connected to a broad muscle attachment area at the caudal portion of the postacetabular ala.

The iliac blade is slightly higher than the height from the supracetabular crest to the ventralmost level of the iliac acetabulum. Its lateral surface, caudal to the preacetabular ala, bears two conspicuous depressions separated by a short, elevated area. The dorsal depression (“dd” in Fig. 4) is rounded and craniocaudally elongated, as well as larger than the lower one. It extends caudally as to almost reach the postacetabular ala, but its deepest point is immediately dorsal to the ventral depression. The latter (“vd” in Fig. 4) starts caudal to the preacetabular embayment, extending onto its maximal transverse depth right above the supraacetabular crest.

The postacetabular ala is stout and caudodorsally projected, giving a slightly sigmoidal aspect to the dorsal margin of the ilium in lateral/medial views. Its caudoventral portion bears a pair of longitudinal crests restricted to its caudal half. The medial of those (“vmc” in Fig. 4; “posteromedial lamina/shelf” of Ezcurra, 2010; “medial lamina/blade” of Martinez and Alcober, 2009) extends along the medial surface of the ilium, forming the dorsal margin of the attachment area for the second primordial sacral rib. Its mid-length is right dorsomedial to the caudal tip of the ventral margin of the postacetabular ala (“vmppoa” in Fig. 4), which extends caudally from the ischiadic peduncle. The medial margin of the *brevis* fossa (“brfo” in Fig. 4) is formed by those crests; the ventral margin of the postacetabular ala more cranially and the “medial crest” more caudally. Its lateral margin is, on the other hand, formed by the second, more lateral ridge (“vlc” in Fig. 4); i.e. the *brevis* shelf. The *brevis* fossa is shallow,

transversely and longitudinally broad, but craniocaudally shorter than in earlier sauropodomorphs like, *Saturnalia tupiniquim* (Langer, 2003), *Chromogisaurus novasi* (Ezcurra, 2010), and *Buriolestes scultzi* (Cabreira et al. 2016), resembling that of other sauropodomorphs, such as *Plateosaurus engelhardti* (SMNS 12950; 80664), *Massospondylus carinatus* (Cooper, 1981), and *Adeopapposaurus mognai* (Martínez, 2009). Likewise, such a reduced fossa *brevis* also differs from those of neotheropods (e.g. *Liliensternus liliensteni* MB. R. 2175) and early ornithischians (e.g. Baron et al. 2017).

The area between the supraacetabular crest and the postacetabular ala is concave, unlike that of earlier sauropodomorphs like *Chromogisaurus novasi* (Ezcurra, 2010), neotheropods (e.g. *Liliensternus liliensteni* MB. R. 2175), and some ornithischians (e.g. *Scelidosaurus harrisonii* NHM R 1111), which bears a ridge connecting the *brevis* shelf to the supraacetabular crest. The supraacetabular crest extends cranioventrally as a continuous flange from a rugose area at the level of the ischiadic peduncle, along the pubic peduncle, terminating near its articulation area. It is strongly expanded lateroventrally, but not as much as in theropods. Its point of maximal transverse breadth is above the center of the acetabulum, equally distant from the distal tips of the ischiadic and pubic peduncles. At this point, the supraacetabular crest is nearly set at the mid dorsoventral height of the ilium, unlike *Saturnalia* (MCP 3844-PV), *Pampadromaeus* (ULBRA-PVT016) *Panphagia* (PVSJ 874), *Chromogisaurus* (PVSJ 845) and *Buriolestes* (ULBRA-PVT280).

The acetabulum is as craniocaudally expanded as the length between the pre- and postacetabular embayments, and relatively deeper dorsoventrally than in early sauropodomorphs, e.g. *Saturnalia tupiniquim*, *Panphagia protos*, and *Chromogisaurus novasi* (Marsola et al. in review). Its medial wall is ventrally projected, the ventral

margin of which levels with the ventral tip of both ischiadic and pubic peduncles. This feature suggests a closed iliac acetabulum, unlike massospodylid and plateosaurid sauropodomorphs, neotheropods, and most ornithischians (see Baron et al. 2017), but similar to that of some non-dinosaur dinosauromorphs (Langer et al. 2013), *S. tupiniquim* (Langer, 2003), *P. protos* (Martínez and Alcober, 2009), and *Buriolestes schultzi* (Cabreira et al. 2016). There is a shallow ventral notch between the ischiadic peduncle and the ventral margin of the acetabulum, which sets the ventral limit of the ovoid dorsoventrally elongated antitrochanteric area of the acetabulum. The cranioventral portion of the acetabulum has a short vertical ridge forming an angle of 45° to the long axis of the pubic peduncle. As described in other dinosaurs (Langer et al. 2010), this ridge is set medially to the supraacetabular crest, producing a subtriangular ventral fossa (“vf” in Fig. 4) on the craniolateral corner of the acetabulum.

The pubic peduncle is as long as the extension between the pre- and postacetabular embayments. Its distal portion is dorsoventrally deeper and transversely narrower than the proximal. The craniodorsal surface bears a subtle ridge as seen in *Pampadromaeus barberenai* (ULBRA-PVT016). Medially the peduncle is mostly flat, with rugose distal areas for muscle attachment. Its articulation surface for the pubis faces cranioventrally, is somewhat rounded in outline and craniocaudally elongated, with the medial margin flatter than the lateral. The ischiadic peduncle is short and subtriangular, similar to that of *Saturnalia tupiniquim* (Langer, 2003). It is laterally bulged, producing a low mound-like process in ventral view that represents the acetabular antitrochanter. The articular surface for the ischium is caudoventrally facing, but lacks the caudal heel present in other sauropodomorphs, like *P. barberenai* (ULBRA-PVT016), *Riojasaurus incertus* (PULR 56), *Coloradisaurus brevis* (Apaldetti et al. 2013), and *Efraasia minor* (SMNS 12354).

The medial surface of the ilium has a complex anatomy, encompassing the concavities and crests that mark the articulation of the sacral vertebrae. Just caudal to the preacetabular embayment, a dorsoventrally elongated concavity (“tsr” in Fig. 4) is seen, cranially bounded by a vertical sharp ridge (“vr” in Fig. 4) formed by the medial edge of the preacetabular fossa. Its dorsal, ventral and caudal margins are formed by a gently elevated, continuous margin. Caudal to that, there is another concavity (“1st” in Fig. 4), which is rounded and craniocaudally longer than the former. The dorsal part of those concavities is formed by a continuous craniocaudally elongated depression that probably received the sacral transverse processes. Its dorsal margin is formed by a longitudinally oriented elevated margin, dorsal to which the medial iliac surface is marked by a spread rugose surface serving for muscle attachment sites, as is also the case of the surface bellow the articulation areas (“sc” in Fig. 4). More caudally, the medial surface of the postacetabular ala is marked by the “medial crest”, which extends cranially as a subtler ridge. This forms the medial margin of the caudal part of the *brevis* fossa, which is equally projected in *Thecodontosaurus antiquus* (BRSUG 23613), *Efraasia minor* (SMNS 12354), and *Plateosaurus engelhardti* (SMNS 12950), but less marked in *Massospondylus carinatus* (BPI 5238) and *Sarhsaurus aurifontanal* (TMM 43646-2). Dorsal to the “medial crest”, there is a longitudinal groove (“tp2nd” in Fig. 4) that received the transverse process of the second primordial sacral vertebra and merged cranially to the aforementioned “elongated depression”. The attachment site for the corresponding rib is a depressed subtriangular area (“r2nd” in Fig. 4) ventral to the “medial crest”. This arrangement matches that of dinosaurs in which two vertebrae form the bulk of the sacrum, as in *Saturnalia tupiniquim* (Langer, 2003) and *Staurikosaurus pricei* (Bittencourt and Kellner, 2009). Yet, it is also possible that the cranial, dorsoventrally elongate depression (“trs” in Fig. 4B) represents the articulation of the

rib of a trunk vertebra incorporated into the sacrum, as seen in one of the paratypes of *S. tupiniquim* (MCP 3845-PV; Marsola et al. in review).

Femora (MCN PV10007, MCN PV10008).—Even though the femora do not overlap (as they are from different sides) and share a very similar morphology, they probably represent two individuals, as size estimation suggests the right element comes from a considerably larger animal. In both femora, portions of the head and distal condyles are missing. As preserved, the right element (Fig. 6) is 14,75 cm long, whereas the left is 12,25 (Fig. 5). As reconstructed, the right femur would be nearly 15 cm and the left would measure between 13,5 – 14 cm. In any case, given their matching morphology, a single description will be provided below for both femora.

The femur has a sinuous shape produced by the craniomedial projection of the head and the cranial and medial bowing of the distal half of the shaft. The head fragment associated to the left femur (Figs. 5E-F) is typically dinosaurian in its transverse expansion, housing a rugose articular surface. Both the ligament sulcus and the lateral tuber are not as pronounced as in other dinosauriforms, such as *Sacisaurus agudoensis* (Langer and Ferigolo, 2013; MCN PV 10014), *Saturnalia tupiniquim* (MCP 3844-PV), *Buriolestes schultzi* (ULBRA-PVT280), and *Eodromaeus murphi* (PVSJ 562). The craniomedial tuber forms a rounded margin as seen perpendicular to the long axis of the head (Figs. 5E-F). The head-shaft transition is rounded and contiguous in those same views, its craniolateral surface being excavated by a subtle ventral emargination (“ve” in Fig. 5). There is no evidence of a groove on the proximal surface of the femur, and the caudal structures of the head, including the ‘greater trochanter’, have not been preserved.

The craniolateral surface of the proximal part of the femur has a rugose site for ligament attachment right distal to the articular surface, which extends ventrally as the intertrochanteric area. This area is laterally bound by the S-shaped dorsolateral trochanter, whereas the cranial trochanter is a cranially bulged, roughly triangular process, the rounded dorsal tip of which is well ventral to the femoral head. From the medial margin of the cranial trochanter, the *linea intermuscularis cranialis* (“lic” in Figs. 5-6) extends ventrally, bordering the medial and lateral surfaces of the shaft. Between the base of the cranial and the dorsolateral trochanter, there is a rugose and slightly elevated area (“mife” in Figs. 5-6) better seen in the left femur, which is probably the insertion site of *M. iliofemoralis externus* (Hutchinson, 2001b) and homologous to the trochanteric shelf.

As in herrerasaurids (Novas, 1994; Bittencourt and Kellner, 2009) and sauropodomorphs (Langer, 2004; Langer and Benton, 2006), the fourth trochanter of MCN PV10007 and PV10008 forms an asymmetrical flange, located on the caudal surface of the proximal half of the shaft. In lateral/medial views, it has the shape of an obtuse triangle, the longest edge of which projects caudoventrally from the shaft, forming a rounded apex on that same direction. In ornithischians, such as *Eocursor parvus* (Butler, 2010), the apex of the fourth trochanter is straighter and more distally projected, as to acquire a pendant shape. Equally different is the symmetrical and lower fourth trochanter of neotheropods, e.g. *Dilophosaurus* (Welles, 1984; UCMP 37302), and non-dinosaurian dinossauromorphs (Langer et al. 2013). In caudal view, the fourth trochanter has a slightly sinuous aspect and its lateral/medial outline shows that it is more expanded distally than proximally. The tip of the fourth trochanter is rounded, and its distal margin forms a nearly right angle to the long axis of the femur. In contrast, the distal margin of the fourth trochanter in ornithischians is strongly concave. A

proximodistally elongated and transversely broad fossa (“cflf” in Figs. 5-6), medially bound a ridge, is located medial to the fourth trochanter and represents the insertion of *M. caudofemoralis longus* (Hutchinson, 2001b; Langer, 2003). The shaft surface proximolateral to the fourth trochanter is also concave, encompassing a diagonally oriented oval rugose area (“cfbf” in Figs. 5-6) for the origin of *M. caudofemoralis brevis* (Hutchinson, 2001b; Griffin and Nesbitt, 2016). From the distal edge of the fourth trochanter, another intermuscular line extends distally along the caudomedial margin of the femoral shaft.

The femoral shaft expands transversely at the distal portion, but the exact morphology of the condyles cannot be evaluated due to its poor preservation. The popliteal fossa is enclosed by broad longitudinal ridges at the caudal surface of the distal part of the femur. The opposite (cranial) surface of the femur is not depressed, i.e. the flexor fossa seen in some saurischians, like neotheropods, is absent. However, that surface is scarred (“fdms” in Fig. 5) for muscle insertion as in *Herrerasaurus* (Novas, 1994) and *Saturnalia* (Langer, 2003).

Metatarsal I (MCN PV 10049).— Only the distal condyles of the left metatarsal I are preserved along with a small portion of the shaft (Fig. 7). The preserved part of the shaft is craniocaudally flattened, with a lateral margin wider than the medial, probably for articulation with metatarsal II, resulting in a subtriangular cross-section. The condyles expand lateromedially compared to the shaft, with the distal articulation being about one third wider than the preserved portion of the latter. The lateral condyle is much larger than the medial, also extending much more distally. It has a roughly triangular distal outline, with rounded corners, formed by lateral, craniomedial, and caudomedial margins. In the same view, the lateral margin of the condyle has a marked concavity,

arising from a well-developed ligament pit (“llp” in Fig. 7), and a laterally projecting caudolateral corner. The medial condyle is small, craniocaudally flattened, and caudomedially directed in distal view, forming a 45° angle to the lateromedial axis of the bone. This shape, along with the distal projection of the lateral condyle, produces a medial displacement of the first digit, as typical of sauropodomorphs as *Unaysaurus tolentinoi* (UFSM 11069), *Efraasia minor* (SMNS 12354), *Pantydraco caducus* (NHMUK RU P77/1), and *Leoneerasaurus taquetrensis* (Pol et al., 2011), but not in Carnian forms like *Saturnalia tupiniquim* (Langer, 2003) and *Pampadromaeus barberenai* (ULBRA-PVT016). Although the metatarsal I is also known for *Guaibasaurus candelariensis*, comparisons are hampered by its poor preservation (Langer et al., 2010). In neotheropods, like *Coelophysis bauri* (e.g. NMMNH P-42200; Rinehart et al. 2009), *Dilophosaurus wetherilli* (UCMP 37302), and *Sinraptor dongi* (Currie and Zhao, 1993), the medial condyle of metatarsal I is not as medially projected as in sauropodomorphs. This forms a craniocaudally deeper distal articular surface, therefore differing from MCN PV 10049. A condition like that of neotheropods is found in early ornithischians as *Abriktosaurus concors* (NHMUK RU B.54), *Lesothosaurus diagnosticus* (NHMUK RU B.17), and *Heterodontosaurus tucki* (SAM-PK K 1332). The craniomedial surface of the medial condyle bears a shallow ligament pit (“mlp” in Fig. 7), the craniolateral rim of which borders the lateral condyle. The caudolateral margin of the medial condyle forms the medial margin of a lateromedially wider than deep flexor fossa (“ff” in Fig. 7). Unlike that of *Plateosaurus engelhardti* (SMNS 13200 Z), and the above cited neotheropods and ornithischians, an equally wider than deep flexor fossa is present in the sauropodomorphs *U. tolentinoi* (UFSM 11069), *E. minor* (SMNS 12354), *Pan. caducus* (NHMUK RU P77/1), and *L. taquetrensis* (Pol et al. 2011). Both medial and lateral ligament pits are heavily scarred for ligament insertion.

Discussion

Correlations of the *Sacisaurus* site

The geological review provided here indicates that all fossil-bearing levels of the *Sacisaurus* site match the usual sandstone upward increase that regionally marks the Caturrita Formation (sensu Andreis et al. 1980) and that the entire site is above the neighboring mudstones of Janner site (Fig. 1). In palaeontological terms, although the lower levels of the site, which record *Exaeretodon*-like cynodonts (Ribeiro et al. 2011), have been roughly correlated to those of the Janner site (Langer et al., 2007; Langer and Ferigolo, 2013), a younger age has been tentatively assigned to the type-stratum of *S. agudoensis*, based on the presence of small, isolated postcanine teeth referred to the probainognathians *Riograndia guaibensis* and *Brasilitherium riograndensis* (Langer et al., 2007; Langer and Ferigolo, 2013). Indeed, their presence implies a correlation to the “*Riograndia* Assemblage Zone” of Soares et al. (2011; see also Bonaparte et al. 2010), which is younger than the “*Hyperodapedon* AZ” sampled from the Janner site. In this section, we first provide a brief revaluation of the cynodont teeth recovered from the same beds where all *S. agudoensis* specimens were found, followed by an attempt to more comprehensively position that locality into the biostratigraphic schemes for the Santa Maria Supersequence.

Cynodont teeth

The specimen previously referred to *Riograndia guaibensis* corresponds to an isolated postcanine (MCN-PV 10204) here interpreted as a left lower element (Figs. 8A-B). It has leaf-shaped crown with eight small cusps in mesiodistal line, which are the main features it shares with *R. guaibensis* (Bonaparte et al. 2001; Soares et al. 2011). The eight cusps have an asymmetrical distribution on the crown; the tallest cusp is preceded

by three mesial cups and followed by four distal cusps. The cusps are separated by shallow but long and curved (mesially convex) longitudinal (inter-cusp) grooves located on both lingual and labial sides. Following the curvature of the grooves, the main cusp and the four distal ones are slightly inclined backward. The cusps, especially the main and the mesial ones, have a marked ridge on their lingual surface. The distalmost cusp is located below the level of the mesialmost cusp and is slightly displaced lingually. The labial surface of the crown is convex and the lingual is concave, with the mesiolingual edge of the first cusp forming an elevated ridge. There is no conspicuous crown-root constriction, but the distal border is more concave than the mesial in this area. The latter is almost straight in labial/lingual views. The root is apically open and hollow, with a circular cross-section along all its extension.

In fact, MCN-PV 10204 resembles postcanine teeth of *Riograndia guaibensis* (Figs. 8C-D) in general aspect, but it is also reminiscent of the leaf-shaped crown morphology seen in several Triassic archosauromorph taxa, such as *Azendohsaurus*, *Revueltosaurus*, ornithischians, and sauropodomorphs (e.g., Flynn et al. 1999; Barret, 2000; Parker et al. 2005). Yet, none of the above archosauromorphs have teeth with the unique set of features of MCN-PV 10204, e.g. long and mesially convex inter-cusp grooves (= interdenticular sulci of Hendrickx et al. 2014) and crown with a concave lingual surface. Although, the postcanine teeth of *R. guaibensis* (e.g., UFRGS-PV-833-T; UFRGS-PV-1319-T) typically have more transversely narrow crowns, less developed (i.e. small) cusps and inter-cusp grooves, a considerably less concave lingual surface, and a more transversely flattened root with an incipient longitudinal groove, more conspicuously in the labial side (Figure 8C-D). Thus, the morphology of MCN-PV 10204 could fit to a more rostral *R. guaibensis* postcanine tooth, as more caudal teeth increase the cusp number up to 11 (e.g., UFRGS-PV-1319-T). However, a new

Riograndia-like cynodont, sister-taxon to *R. guaibensis*, has been recently reported from Janner site (Martinelli et al. 2016), which is typically included in the “*Hyperodapedon* AZ”, showing the occurrence of leaf-shape toothed cynodonts in faunas older than the “*Riograndia* AZ”. Therefore, the isolated tooth MCN-PV 10204 is here referred as a *Riograndia*-like taxon and it provides no compelling evidence that the stratigraphic level it comes from is younger than those corresponding to the “*Hyperodapedon* AZ” at the Janner site.

The specimens originally referred to *Brasilitherium riograndensis* include two isolated right lower postcanines (MCN-PV 10202, MCN-PV 10203). Their crown morphology is similar, but MCN-PV 10202 (Figs. 8E-F) is larger than MCN-PV 10203 (Figs. 8G-H). Given the crown complexity, they seem to be from the middle to caudal portions of the dental series, and MCN-PV 10202 is possibly from a more posterior position in the series than MCN-PV 10203. They are asymmetrical with a main cusp “a” followed by a large cusp “c” and a small cusp “d”. Cusp “b” is smaller than cusp “d” and placed lower in the crown than the remaining cusps. Cusps “a” to “d” are aligned, forming a sectorial crest, with conspicuous mesial and distal cutting edges connecting cusps, whereas cusp “b” is separated from cusp “a” by a concave notch. Both teeth have one mesiolabial and one mesiolingual accessory cusps (the latter possibly corresponding to cusp “e” of Crompton, 1974), located below the notch between cusps “a” and “b”. Consequently, in mesial view, cusp “b” is flanked by these two accessory cusps, as not seen in any *Brasilodon*-*Brasilitherium* specimens. A distolingual cingulum bears three cusps in MCN-PV 10102 and two discrete cusps in MCN-PV 10103. In MCN-PV 10102, the most distal cusp is broken at its base, but seems to be larger than the remaining elements. The more mesial cusp, near which the cingulum ends, could correspond to cusp “g”. In MCN-PV 10103, the distolingual cusps are considerably

larger. Particularly, the more mesially placed (just below the notch between cusps “a” and “c”) is acute and conspicuous, corresponding to cusp “g”. The root grooves are deep both lingually and labially. Particularly in MCN-PV 10103, it divides the root in two portions, with the distal one considerably larger mesiodistally and labiolingually, with a strongly convex distal wall.

In general aspect, MCN-PV 10202 and MCN-PV 10203 resemble more *Brasilitherium riograndensis* and *Brasilodon quadrangularis* than any other known probainognathians from South America (e.g., Bonaparte and Barberena, 2001; Martinelli et al. 2017a, b). They differ from the postcanine teeth of *Alemoatherium huebneri* because these lack a mesiolabial accessory cusp, their lingual cusps and cingulum are much less developed and cusp “d” is slightly smaller and lower positioned than cusp “b” (Martinelli et al. 2017a). Besides, *Prozostrodon brasiliensis* and *Botucaraitherium belarminoi* (Soares et al. 2014; Pacheco et al. 2017) postcanine teeth have a more continuous lingual cingulum, with a higher number of accessory cusps than MCN-PV 10202 and MCN-PV 10203. There are also subtle differences between these teeth and those of *Brasili. riograndensis* and *Brasilo. quadrangularis*. The caudal lower postcanine teeth of those two forms have an accessory distal cusp (distal to cusp “d”) not seen in MCN-PV 10202 and MCN-PV 10203. The distolingual accessory cusps of MCN-PV 10202 (at least three, including a larger distal cusp) and MCN-PV 10203 (two large cusps, the mesial corresponding to cusp “g”) are usually absent in the more caudal teeth of *Brasili. riograndensis* and *Brasilo. quadrangularis* and at least two cusps (“g” and accessory cusp) are present in their middle postcanine teeth (e.g., UFRGS-PV-603-T; UFRGS-PV-1043-T). Further, a mesiolabial cusp (in addition to mesial cusp “b” and the accessory mesiolingual cusp = cusp “e”) is not seen in any specimen of *Brasili. riograndensis* and *Brasilo. quadrangularis*, regardless the ontogenetic stage. Such

differences do not seem to represent intra-specific variations, as they are unknown in the large available sample of both *Brasili. riograndensis* and *Brasilo. quadrangularis* (Bonaparte et al. 2003, 2005; Martinelli et al. 2017a, b). Accordingly, although MCN-PV 10202 and MCN-PV 10203 clearly represent derived prozostroodontians closely related to the “brasilodontids” from the *Riograndia* AZ, the differences in their dentition better indicate a new, still poorly sampled taxon, the biostratigraphical significance of which it is still unknown.

The specimen MCN-PV 10205 includes an isolated left lower incisor 1 (Figure 9) similar to those of *Exaeretodon* spp (e.g., Abdala et al. 2002). The preserved portion is 28 mm tall, including most of the crown and a small portion of the root. It has an oval cross section at the base, longer labiolingually than mesiodistally. The labial surface is apicobasally convex with a relatively thick layer of enamel that defines mesial and distal cutting edges. The lingual surface is apicobasally concave, so that the tooth is overall slightly curved lingually. That surface is also transversally convex, forming a bulged central area along its entire length, which is separated from the distal cutting edge by an apicobasally oriented groove. An enamel layer is not seen in the lingual surface and the whole element exhibits evident postmortem weathering, with small, irregular pits. Although, the referral of an isolated incisor to any specific taxon is hardly feasible, the morphology of MCN-PV 10205 matches of that of gomphodontosuchine traversodontid incisor, in particular the genus *Exaeretodon*, which is typical of the *Hyperodapedon* AZ (Abdala et al. 2002; Soares et al. 2014) and very common at the Janner site. Therefore, MCN-PV 10203 also provides no evidence that the *Sacisaurus* type-stratum is younger than those referred to the “*Hyperodapedon* AZ” at the Janner site.

***Sacisaurus* site correlation**

Sacisaurus agudoensis is the only silesaurid from the Santa Maria Supersequence known to date based on a significant amount of material and does not help to correlate its type-locality to other Triassic sites in Rio Grande do Sul. In general terms, core-silesaurids (Cabreira et al. 2016) are known from both Carnian and Norian deposits (Langer et al. 2013), so that the occurrence of *S. agudoensis* does not help refining the age of the site more precisely than Late Triassic. As for the sauropodomorph remains described here, the anatomy of the recovered bones (especially the neck vertebra, ilium, and metatarsal) is more reminiscent of that seen in putatively younger (Norian) members of the group, such as *Pantyraco caducus* and *Unaysaurus tolentinoi*, than in Carnian sauropodomorphs such as *Saturnalia tupiniquim* and *Panphagia protos*. The isolated *Riograndia*- and *Exaeretodon*-like cynodont teeth do not help correlating the *Sacisaurus* site to either the top of the Alemoa Member or the base of the Caturrita Formation, as similar forms are found in both geological settings (Abdala et al. 2002; Ribeiro et al. 2011; Bittencourt et al. 2012; Martinelli et al. 2016). On the contrary, the record of “brasilotodontid” teeth seem to match that of the sauropodomorphs described here, as these cynodonts are until now restricted to the younger (Norian) “*Riograndia* AZ”. Yet, the resemblance of those same teeth to those of *Alemoatherium huebneri*, along with their differences relative to those of *Brasilitherium riograndensis* and *Brasilodon quadrangularis* precludes strong biostratigraphic inferences.

Put together, geological and palaeontological data indicate that the strata identified in the *Sacisaurus* site, with its recovered fauna, including the *Exaeretodon*-like gomphodontosuchinae traversodontids found in the sandstones below the type-stratum of *S. agudoensis*, are likely younger than those recovered from the Janner site. In lithostratigraphical terms, the fossil-bearing mudstones of the latter site are typical of

the Alemoa Member, matching those from other sites of the Santa Maria Supersequence that typically yield “*Hyperodapedon* AZ” faunas. In particular, the abundance of *Exaeretodon riograndensis* in the Janner site suggests that it belongs to younger faunas within the “*Hyperodapedon* AZ” (Langer et al. 2007; Pretto et al. 2015). On the contrary, the rocks exposed at the *Sacisaurus* site belong to the Caturrita Formation, which regionally overlaps the Alemoa Member, matching the signal provided by the sauropodomorph and “*brasilodontid*” fossils from the *S. agudoensis* type-stratum. Accordingly, the available data indicates a younger age for the *Sacisaurus* site relative of the entire “*Hyperodapedon* AZ”, so that the *Riograndia*-like teeth from the site could actually belong to *R. guaibensis*, which characterizes the younger “*Riograndia* AZ”. On the other hand, the *Exaeretodon*-like cynodonts found both at and below the *S. agudoensis* type-stratum indicates that traversodontids similar to that genus have extended their occurrence to strata younger than the “*Hyperodapedon* AZ”, as previously suggested by the presence of a small-sized form in “*Riograndia* AZ” deposits at the Poste site (Ribeiro et al. 2011), in the area of Candelaria (Bittencourt et al. 2012).

Conclusions

The specimens described here reveal the presence of a larger dinosauiromorph in the type-stratum of *Sacisaurus agudoensis*, most probably corresponding to a sauropodomorph dinosaur. Its anatomy resembles more that of Norian representatives of the group, such as *Pantyraco caducus* and *Unaysaurus tolentinoi* than that of Carnian taxa such as *Saturnalia tupiniquim* and *Pampadromaeus barberenai*. Together with local stratigraphic correlation and the presence of *brasilodontid* teeth in the fossil assemblage, this indicates a higher stratigraphic position and younger age for the

Sacisaurus site relative to the better sampled fauna of the neighboring Janner site. The fossiliferous layers of the latter correspond to the typical mudstones of the Santa Maria Formation, which yield the Carnian the “*Hyperodapedon* AZ”. These are regionally overlapped by the sandstones of the Caturrita Formation, which yield the Norian “*Riograndia* AZ” and correspond to the entire sequence exposed at the *Sacisaurus* site. Hence, a Norian age is, based on the available evidence, the best age estimate for *Sacisaurus agudoensis* and coeval fauna.

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and **(D)** Sedimentary profile of the *Sacisaurus* type-locality (star) and neighboring sites.

[planned for two-column width]

Figure 2. Right ectopterygoid MCN PV 10049 in **(A)** dorsal and **(B)** ventral views.

Abbreviations: **ja**, surface for jugal articulation; **lp**, lateral process; **mp**, medial process; **rp**, rostral projection of the medial process; **vd**, ventral depression on the medial process. Scale bar equals to 10 mm. [planned for one-column width]

Figure 3: Cervical vertebra MCN PV 10027 in (A) dorsal, (B) ventral, (C) caudal, (D) cranial, (E) right lateral and (F) left lateral views. The zoomed area in A shows the **epri**. Abbreviations: **acdl**, anterior centrodiapophyseal lamina; **cdf**, centrodiapophyseal fossa; **dp**, diapophysis; **epri**, epipophyseal-prezygapophyseal lamina; **fo**, fossa; **ncs**, neurocentral suture; **ns**, neural spine; **pcdl**, posterior centrodiapophyseal lamina; **pocdf**, postzygapophyseal centrodiapophyseal fossa; **podl**, postzygodiapophyseal lamina; **pp**, parapophysis; **ppr**, parapophyseal ridge; **prcdf**, prezygadiapophyseal centrodiapophyseal fossa; **prdl**, prezygodiapophyseal lamina; **rdg**, ridge; **sc**, muscle scars; **sprf**, spinoprezygapophyseal fossa; **sprl**, spinoprezygapophyseal lamina; **vk**, ventral keel. Scale bar equals to 10 mm. [planned for two-column width]

Figure 4. Right ilium MCN PV10026 in (A) lateral, (B) medial, (C) dorsal and (D) ventrocaudal views. Abbreviations: **1st**; attachment scars for the first primordial sacral vertebra; **ac**, iliac acetabulum; **amw**, acetabular medial wall; **an**, acetabular antitrochanter; **brfo**, brevis fossa; **dd**, dorsal depression; **imr**, iliac medial ridges; **ip**, ischiadic peduncle; **poa**, postacetabular ala; **pp**, pubic peduncle; **pra**, preacetabular ala; **prf**, preacetabular fossa; **r2nd**; attachment scars for the second primordial sacral vertebra rib; **sac**, supracetabular crest; **sc**, scars for muscle attachment; **tp2nd**; attachment scars for the second primordial sacral vertebra transverse process; **trs**, attachment scars for the trunk-sacral vertebra; **vd**, ventral depression; **vf**, ventral fossa; **vlc**, ventrolateral crest; **vmc**, ventromedial crest; **vmppoa**; ventral margin of the postacetabular ala; **vr**, vertical ridge. Scale bar equals to 20 mm. [planned for two-column width]

Figure 5. Left femur MCN PV10008 in (A) medial, (B) cranial, (C) lateral and (D) caudal views. **F** and **G** depict the head fragment in articulation with the rest of the bone in craniolateral and caudomedial views, respectively. Abbreviations: **4th**, fourth trochanter; **cmt**, craniomedial tuber; **cfbf**, fossa for caudofemoralis brevis; **cflf**, fossa for caudofemoralis longus; **ct**, cranial trochanter; **dlt**, dorsolateral trochanter; **fdms**, muscle scar on laterocranial distal femur; **lic**, linea intermuscularis cranialis; **ls**, ligament sulcus; **mife**: insertion site of *M. iliofemoralis externus*; **pf**, popliteal fossa; **ve**, ventral emargination. Scale bar equals to 20 mm. [planned for two-column width]

Figure 6. Right femur MCN PV10007 in (A) medial, (B) cranial, (C) lateral and (D) caudal views. Abbreviations: **4th**, fourth trochanter; **cfbf**, fossa for caudofemoralis brevis; **cflf**, fossa for caudofemoralis longus; **ct**, cranial trochanter; **dlt**, dorsolateral trochanter; **lic**, linea intermuscularis cranialis; **ls**, ligament sulcus; **mife**: insertion site of *M. iliofemoralis externus*; **pf**, popliteal fossa; **ve**, ventral emargination. Scale bar equals to 20 mm. [planned for two-column width]

Figure 7. Metatarsal I MCN PV 10049 in (A) cranial, (B) lateral, (C) caudal, (D) mediodistal and (E) distal views. Abbreviations: **ff**, flexor fossa; **lc**, lateral condyle; **llp**, lateral ligament pit; **mc**, medial condyle; **mlp**, medial ligament pit. Scale bar equals to 10 mm. [planned for one-column width]

Figure 8. Specimen MCN-PV 10204 (Agudo, *Sacisaurus* type-locality), isolated left lower postcanine tooth originally interpreted as belonging to *Riograndia* in labial (A) and lingual (B) views. *Riograndia guaibensis* from the *Riograndia* AZ (Faxinal do Soturno, Linha São Luiz site), anterior postcanines of specimen UFRGS-PV-833-T in lingual view (C) and of specimen UFRGS-PV-1319-T in labial view (D). Isolated right lower postcanines MCN-PV 10102 (E, F) and MCN-PV 10103 (G, H) from Agudo (*Sacisaurus* type-locality), originally referred to *Brasilitherium riograndensis*, in labial (E, G) and lingual (F, H) views. *Brasilodon quadrangularis*, from the *Riograndia* AZ (Faxinal do Soturno), detail of middle and posterior left lower postcanines (inverted for the figure) of specimen UFRGS-PV-603-T in labial (I) and lingual (J) views. Arrows indicate mesial side. Abbreviations: 4°, 8°, refer to cusp number; a, b, c, d, g, refer to the name of the lower cups; cin/ac, cingulum/accessory cusp or cusps; gr, groove on root; mla, mesiolabial cusp; mli (e), mesiolingual cusp; pc, postcanine tooth. [planned for one-column width]

Figure 9. Specimen MCN-PV 10205 from Agudo (*Sacisaurus* type-locality), isolated left lower incisor 1 of Traversodontidae (cf. *Exaeretodon* sp.) in lingual (**A**) and distal (**B**) views. [planned for one-column width]

ANEXO 4

Aumento da amostragem taxonômica sustenta a hipótese de que os dinossauros se originaram ao sul do Gondwana

Submetido como: **Marsola, J. C. A.**, Ferreira, G. S., Langer, M. C., Button, D. J., and Butler, R. J. Increases in sampling support the southern Gondwanan hypothesis for the origin of dinosaurs. *Proceeding of the Royal Society: B*.

Material suplementar: se encontra disponível no CD-ROM anexado ao final da Tese.

Síntese do anexo 4

Durante a maior parte do Mesozoico, os dinossauros dominaram os ecossistemas terrestres por todo o mundo, e mesmo com a extinção de boa parte do grupo, ainda persistem nos dias de hoje representados pelas aves. Esforços recentes para o melhor entendimento da origem dos dinossauros resultaram na descoberta de diversas novas espécies dos mais antigos membros do grupo e de outros dinossauiromorfos não-dinossauros. Além disso, novas análises filogenéticas destacaram as incertezas quanto às inter-relações das principais linhagens dinossaurianas (Sauropodomorpha, Theropoda e Ornithischia), e questionaram a hipótese tradicional de que o grupo tenha se originado na região sul do Gondwana, para então se dispersarem para todo Pangeia. Neste trabalho foi considerado um panorama histórico da pesquisa sobre a origem dos dinossauros para examinar o impacto de novas descobertas e de topologias divergentes na construção de hipóteses biogeográficas ao longo de 20 anos. Ademais, os resultados foram avaliados à luz de viéses de amostragem no registro fóssil. Nossos resultados

consistentemente otimizam a porção sul do Gondwana como a área ancestral dos Dinosauria, bem como de clados mais inclusivos, como Dinosauromorpha, e mostram que essa hipótese é robusta mesmo com o aumento da amostragem taxonômica e geográfica e com hipóteses filogenéticas conflitantes. Nossos resultados não encontraram nenhum suporte para a origem laurásiana dos dinossauros, como recentemente proposto, e sugerem que a origem do sul da Gondwana para os mesmos é a mais plausível, dado o atual conhecimento da diversidade dos primeiros dinossauros e dinossauromorfos não-dinossauros.

Increases in sampling support the southern Gondwanan hypothesis for the origin of dinosaurs

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Abstract

Dinosaurs were ubiquitous in terrestrial ecosystems through most of the Mesozoic and are still diversely represented in the modern fauna in the form of birds. Recent efforts to better understand the origins of the group have resulted in the discovery of many new species of early dinosaurs and their closest relatives (dinossauromorphs). In addition, recent re-examinations of early dinosaur phylogeny have highlighted uncertainties regarding the interrelationships of the main dinosaur lineages (Sauropodomorpha, Theropoda and Ornithischia), and questioned the traditional hypothesis that the group originated in South Gondwana and gradually dispersed over Pangaea. Here, we use a historical approach to examine the impact of new fossil discoveries and changing phylogenetic hypotheses on biogeographic scenarios for dinosaur origins over 20 years of research time, and analyse the results in the light of different fossil record sampling regimes. Our results consistently optimize South Gondwana as the ancestral area for Dinosauria, as well as for more inclusive clades including Dinossauromorpha, and show that this hypothesis is robust to increased taxonomic and geographic sampling and divergent phylogenetic results. Our results do not find any support for the recently proposed Laurasian origin of dinosaurs and suggest that a southern Gondwanan origin is by far the most plausible given our current knowledge of the diversity of early dinosaurs and non-dinosaurian dinossauromorphs.

1. Introduction

Dinosaurs dominated Mesozoic terrestrial ecosystems for more than 140 million years, and remain highly diverse today, in the form of birds. As such, dinosaurs represent an outstanding example of evolutionary success among terrestrial tetrapods, which is reflected by the broad scientific interest in the group. Recently, there has been intense debate over the origins, early evolutionary radiation, and rise to ecological dominance of the group, stimulated by new discoveries of early dinosaurs and closely related taxa [1-8], novel quantitative macroevolutionary analyses [9-12], and new geological data [13-16].

The discovery of many of the earliest known fossils of dinosaurs and their close relatives, non-dinosaurian dinosauiromorphs, in South America and other southern portions of the supercontinent Pangaea has led to the hypothesis that dinosaurs originated in this region [2, 17-18]. However, a recent high-profile reassessment of the early dinosaur evolutionary tree [19] not only challenged the long-standing classification of the three main dinosaur lineages [20-21], but also questioned the southern Gondwanan origin of the clade. Based solely on the observed palaeogeographical distribution of some of the closest relatives of Dinosauria in their phylogenetic hypothesis (i.e., the Late Triassic *Saltopus elginensis* and the Middle–Late Triassic Silesauridae, which were recovered in a polytomy with Dinosauria), Baron et al. [19, 22] proposed that dinosaurs may have originated in the northern part of Pangaea, referred to as Laurasia. However, this was suggested in the absence of any formal biogeographic analysis. Langer et al. [23] tested this hypothesis by running several quantitative biogeographical analyses to reconstruct ancestral areas, the results of which consistently recovered a southern Pangaeian (or Gondwanan) origin for dinosaurs. However, they only conducted these analyses for the Baron et al. [19] topology and did

not consider alternative phylogenetic scenarios (e.g. [8]), or the long-term robustness of these results to new fossil discoveries.

In this paper we aim to: (i) further test hypotheses about the ancestral distribution of dinosaurs using a broader range of quantitative biogeographical models and alternative phylogenetic hypotheses; (ii) test the stability of the biogeographic results over 20 years of additional scientific discoveries and new research that have dramatically changed our understanding of early dinosaur evolution; and (iii) discuss how biased palaeogeographic sampling of the fossil record might impact our scenarios for dinosaur origins.

2. Material and Methods

(a) Source trees and time scaling

We sampled trees from six independent phylogenetic analyses from the last 20 years, each of which dealt with the major diversity of early dinossauromorphs at the time they were published: (1) Sereno [24]; (2) Langer & Benton [25]; (3) Nesbitt et al. [2]; (4) Cabreira et al. [8]; (5) Baron et al. [19]; and (6) Langer et al. [23] (Figure 1). For the Baron et al. [19] dataset, we created three alternative topologies to explore the impact of the uncertain relationships between *Saltopus*, Silesauridae and Dinosauria found by that study. The three topologies differ in the following arrangements: A, *Saltopus* sister to Silesauridae + Dinosauria; B, *Saltopus* sister to Silesauridae; and C, *Saltopus* sister to Dinosauria. We pruned Cretaceous taxa from the chosen topologies, as their biogeographical range is beyond the scope of our study. Supraspecific taxa were replaced by specific representatives of the same clade in order to generate a more

explicit geographic distribution of terminal nodes. For example, in the topology of Sereno [24] we replaced Diplodocidae with *Diplodocus*.

Since the biogeographic methods employed here require fully-solved, time-calibrated topologies, we resolved all polytomies in the sampled trees according to the following procedure. For hypotheses resulting from many most parsimonious trees (MPTs; e.g. [23]), we first obtained a majority-rule consensus tree (cut-off = 50). The remaining polytomies were manually resolved using a standardised procedure suggested by previous studies, e.g. [26-27]. First, wherever possible we resolved polytomies to minimise biogeographic changes. For example, in a polytomy (*A,B,C*) where *A* and *B* share the same range, but *C* has a different range, we resolved *A+B* as sister-taxa to the exclusion of *C*. We further resolved polytomies based on relationships recovered in previous analyses. Finally, if polytomies remain, we chose the arrangement by randomly selecting one of the possible MPTs of that analysis. The dichotomous trees were then time-scaled using the R package *strap* [28], with branch lengths equally divided [10], and a minimum branch length of 1 Ma. Time ranges were based on the oldest and earliest dates of the stratigraphic stage (according to the International Chronostratigraphic Chart v. 2017/02) in which a taxon occurs, the latter data being gathered from the literature. For example, the first and last appearances of all Carnian taxa were considered as 237 and 227 Ma, respectively.

(b) Biogeographical analyses

In order to investigate the influence of phylogenetic uncertainty and sampling on ancestral distribution estimates for dinosaurs we conducted a series of stratified biogeographic analyses with the R package *BioGeoBEARS* [29] using the aforementioned phylogenetic trees. For each analysis, we ran two nested-models (M0

and M1; see below) of the likelihood-based models DEC (Dispersal-Extinction Cladogenesis [30-31]) and DIVALIKE (Dispersal-Vicariance Analysis [32]). Each taxon was scored for four biogeographic provinces as defined by Langer et al. [33]: South Gondwana (S), Equatorial Belt (B), Euramerica (A), and Trans-Uralian domains (T). We set a maximum range size of two areas. Even though our analyses are temporally restricted between the Middle Triassic to Middle Jurassic, a period during which no drastic palaeobiogeographical changes between the considered areas are supposed to have occurred, we conducted time-stratified analyses dividing the trees into two discrete periods: Middle Triassic to Norian (247.2–208.6 Ma) and Rhaetian to Middle Jurassic (208.5 Ma to the earliest tip of each tree). For each time stratum a dispersal multiplier matrix was specified to model the arrangement between the defined areas. To compare the effects of these assumptions, we followed the procedure of Poropat et al. [34] and conducted analyses with ‘*harsh*’ and ‘*relaxed*’ versions of the ‘*starting*’ dispersal multiplier matrices (see Supplementary Material), and also set the parameter w to be free in one of the models (M1; for M0 w is set to 1), in order to infer optimal dispersal multipliers during the analyses. It is important to consider that distinct models (e.g., DEC and DIVA) make specific assumptions about the biogeographic processes of range change. For that reason, the maximum-likelihood approach of *BioGeoBEARS* allowed us to test and choose the best fit model [35], using the likelihood-ratio test (LRT) and the weighted Akaike information criterion (AICc).

3. Results and discussion

(a) The inferred ancestral area for dinosaurs

With the sole exception of the ‘*starting*’ analysis of the Langer & Benton [25] tree, for which a joint distribution of South Gondwana and Euramerica was estimated for the

Dinosauria node, the best fit models (for LRT and AICc test results see the Electronic Supplementary Material) obtained from all our analyses support a strictly southern Gondwanan origin for dinosaurs (Table 1). Changing the dispersal multiplier matrices did not yield distinct estimates. Similarly, our results yield high support for South Gondwana as the ancestral area for other ornithodiran clades leading to the Dinosauria node. Whereas all analyses of the Nesbitt et al. [2] dataset and the ‘*starting*’ version of the Langer & Benton [25] dataset support a joint distribution of South Gondwana and Euramerica as the ancestral area for Dinosauromorpha, the clades Dinosauromorpha and Dinosauriformes are supported as originating in South Gondwana in all other analyses, including in those datasets that have the most extensive sampling of non-dinosaurian dinosauriforms, e.g. [8, 19, 23]. South Gondwana is also inferred as the ancestral area for the Silesauridae + Dinosauria clade in all analyses in which this sister-group relation is present (i.e. not in Sereno [24] or iteration C of the Baron et al. [19] dataset), with the exception of the ‘*harsh*’ analysis of the Langer & Benton [25] dataset. We note that the results for the Langer & Benton [25] tree may not be reliable due to the low taxon sampling of the tree and the short branches surrounding Dinosauria.

Our results do not therefore support the hypothesis of a Laurasian origin for Dinosauria as proposed by Baron et al. [19], regardless of which of their three alternative topologies ([19]: trees A, B and C) is employed. Although the problematic taxon *Saltopus elginensis* is known from Laurasia (late Carnian Lossiemouth Sandstone Formation of Scotland [36]), it is phylogenetically nested among South Gondwana taxa in all alternative hypotheses and occurs stratigraphically 10–15 million years later than the main splitting events along the dinosauromorph lineage leading up to the origin of dinosaurs. Likewise, although Baron et al. [19] noted that the Laurasian *Agnosphitys cromhallensis* was positioned as sister to other silesaurids in their results, this taxon is

known from the Rhaetian fissure fill deposits of southwest England, i.e. some 35–40 million years after the inferred origin of Silesauridae. All known Middle Triassic non-dinosaurian dinosauromorphs, as well as the only putative Middle Triassic dinosaur [4] are from South Gondwana and only from the Carnian onwards does their range expand into the northern hemisphere.

We conclude therefore, that the phylogenetic hypothesis proposed by Baron et al. [19] does not provide any significant support for a Laurasian origin of dinosaurs (Figure 2). Instead, all our results strongly support those of Nesbitt et al. [2] and Langer et al. [23] (Figure 2), in which southern Gondwana (“southern Pangaea” and “South America”, respectively, in their own terms) was also recovered as the ancestral area for dinosaurs. Furthermore, our analyses show that Ornithoscelida and Saurischia would also have originated in southern Gondwana in all possible versions of the Baron et al. [19] phylogenetic hypothesis.

(b) Historical patterns

Palaeontologists frequently use ancestral-area reconstruction approaches, such as those implemented by *BioGeoBEARS*, to infer ancestral ranges for clades and use these to make inferences about evolutionary histories, e.g. [26-27, 34]. However, they much more seldomly consider the robustness of those results to new fossil discoveries, which may include taxa from areas in which they were previously unsampled, and changes in phylogenetic hypothesis, which occur through the addition of more taxa and/or through changing topologies that result from new datasets or analytical approaches. For an ancestral range hypothesis to be considered well supported, it should be robust to such changes in the source data.

Here, we have provided a unique historical perspective on early dinosaur biogeography, by reconstructing ancestral areas for a series of alternative phylogenetic topologies taken from the last 20 years of research effort. Our key result – a South Gondwana origin for dinosaurs – has proved remarkably stable over two decades of new fossil discoveries and extensive phylogenetic research. Since the work of Sereno [24], 23 new Triassic dinosaurs and non-dinosaurian dinosauromorphs have been discovered and/or added to phylogenetic studies. This included new taxa from North America (e.g. [1-2, 37]), Europe [36, 38-39] and North Africa [40]. Yet, this greatly increased sampling has had few major impacts on models of early dinosaur biogeography, as the southern Gondwanan origin for the group is invariably supported as the best model throughout the research interval considered. We recommend using a similar historical perspective when estimating ancestral distributions of other clades, as a way of examining the support for biogeographical hypotheses.

Our results are also consistent despite highly divergent phylogenetic hypotheses for early dinosaurs. For example, Cabreira et al. [8] recovered the majority of silesaurids within Dinosauria, as a paraphyletic array of early ornithischians. Baron et al. [19, 22] proposed the unconventional clade Ornithoscelida, with Ornithischia as the sister-taxon of Theropoda, and herrerasaurids nested with sauropodomorphs within Saurischia, whereas Langer et al. [23] reiterated support for a traditional Ornithischia-Saurischia dichotomy at the base of Dinosauria. However, our results show that none of these conflicting rearrangements of the three main dinosaurian lineages (Sauropodomorpha, Theropoda, Ornithischia) and Silesauridae challenge the long-standing biogeographic hypothesis of a southern Gondwanan origin for dinosaurs.

(c) Sampling biases

A biogeographic hypothesis, such as the southern Gondwanan origin of Dinosauria, may be well supported through research time and under alternative phylogenetic topologies, but could still be flawed if fossil record sampling is highly heterogeneous. For example, if dinosaurs actually originated in the late Middle–earliest Late Triassic in Laurasia, and dispersed quickly across the globe, they might still be reconstructed as ancestrally from South Gondwana if that region is the only one from which terrestrial vertebrate fossils have been sampled in that time interval. Reconstructions of ancestral areas for fossil taxa should therefore always be considered within an explicit consideration of how the fossil record has been sampled spatially, and temporally, but this is rarely the case. Here, we briefly discuss fossil record sampling through the inferred origin and initial radiation of dinosaurs (Middle Triassic–early Late Triassic: Anisian–Carnian), and the implications for the South Gondwana origins hypothesis.

The earliest dinosauromorph body fossils, as well as the oldest putative dinosaur body fossil, are known from the Middle to earliest Late Triassic of South Gondwana, most notably from the Manda Beds of Tanzania [3-5] and the Chañares Formation of Argentina [41-44] (Figure 3). These represent two of the best-sampled stratigraphic units for terrestrial tetrapods in this interval, but Laurasian tetrapods of broadly comparable stratigraphic ages are known from various Laurasian localities, including the USA (Moenkopi Formation; e.g. Nesbitt [45]), the UK (Helsby Sandstone Formation; e.g. Coram et al. [46]), Russia (Donguz and Bukobay gorizonts; e.g. Gower & Sennikov [47]), Germany (Erfurt Formation; e.g. Schoch & Sues [48]) and China (Ermaying Formation; e.g. Sookias et al. [49]). To date, none of these Laurasian deposits have yielded dinosauromorph body fossils (Figure 3). Putative dinosauromorph footprint records have been reported from the Early–Middle Triassic of Laurasia [50],

but the taxonomic affinities of these occurrences remain controversial and difficult to confirm.

Similarly, the earliest definitive dinosaur body fossils are from the early Late Triassic (late Carnian) of Argentina and Brazil [6-8, 17-18, 51-54] (Figure 3). Although the dating of many Laurasian rock sequences of putatively similar age is controversial, those in Germany (e.g. [55]), Poland (e.g. [56]), North America (e.g. [57]), and the UK (e.g. [58]), have failed thus far to yield definite dinosaur remains, although the silesaurid *Silesaurus* is known from Poland [39], and the problematic *Saltopus* from the UK [36].

It remains possible that, as suggested by Baron et al. [22], better future sampling of Middle–early Late Triassic localities from Laurasia will overturn the South Gondwana hypothesis for dinosaur origins. However, these areas have been sampled by palaeontologists for >150 years and have so far failed to yield body fossils of Middle Triassic dinosauromorphs or early Late Triassic dinosaurs.

4. Conclusions

The last two decades have witnessed a great increase in the taxonomic sampling of Triassic dinosaurs and non-dinosaurian dinosauromorphs. Unearthed from different parts of the world, these new discoveries have helped palaeontologists to better understand not only the morphology and diversity of early dinosaurs, but also to develop new models for their rise. Along with these new finds, new phylogenetic hypotheses for early dinosaurs have been proposed. These have challenged conventional understanding of the relationships of the main dinosaurian lineages (e.g. [8, 19, 23]), and questioned the long-standing hypothesis of a southern Gondwanan origin for the clade [19, 23]. In this study, we have shown that even in the most divergent

phylogenetic hypotheses of early dinosaurs, a southern Gondwanan origin is strongly supported by quantitative biogeographic analyses. Additionally, we have demonstrated that South Gondwana is consistently supported as ancestral area in a range of phylogenies from the last 20 years, and has therefore been robust to increases in taxonomic, geographic and phylogenetic sampling. Although Middle–Late Triassic rock sequences worldwide have been sampled for decades, the oldest unequivocal dinosaur body fossil remains are still clustered in southern Gondwanan deposits. Given the present data, the South Gondwana hypothesis must therefore be considered the best-supported interpretation of the ancestral area for the rise of dinosaurs.

Data accessibility

R scripts, data and all results of the biogeographic analyses [will be] available as online supplementary information.

Authors' contributions

RJB conceived the study. JCAM collected data. JCAM, GSF, and DJB conducted analyses. JCAM, GSF and RJB wrote the paper. All authors revised and contributed comments to the final manuscript.

Competing interests

We declare no competing interests.

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Figures and Legends

Figure 1: Three phylogenetic topologies of early dinosaurs, showing the increased taxonomic and phylogenetic sampling of taxa since 1999. A. Sereno [24]. B. Langer & Benton [25]. C. Langer et al. [23]. Names in blue represent Jurassic taxa. Names in green represent taxa discovered from 1999–2009. Names in red represent taxa discovered from 2010–2017.

Figure 2: Ancestral area reconstruction for the time-calibrated trees of the best biogeographical models of the ‘starting’ versions of (A) Baron et al. ([19]: topology C)

(DIVA M0) and (B) Langer et al. [23] (DIVA M1). Pie charts depict the probabilities for ancestral areas of nodes. Rectangles next to the taxa indicate their temporal range and the colours indicate their area.

Figure 3: Palaeogeographical distribution in continental deposits of non-dinosauriomorph Tetrapoda, non-dinosaur Dinosauriomorpha and Dinosauria during the (A) Middle Triassic/early Carnian and (B) late Carnian.

Table 1: Best fit models for each analysed tree (all results are available in the supplementary information).

Tree	Distance multiplier	Best model	Ancestral Area for Dinosauria
Sereno, 1999	Starting	DIVA M1	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M1	South Gondwana
Langer & Benton, 2006	Starting	DEC M0	South Gondwana and Euramerica
	Harsh	DEC M1	South Gondwana
	Relaxed	DEC M1	South Gondwana
Nesbitt et al., 2009	Starting	DEC M0	South Gondwana
	Harsh	DEC M1	South Gondwana
	Relaxed	DEC M0	South Gondwana
Cabreira et al., 2016	Starting	DIVA M0	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M0	South Gondwana
Baron et al., 2017 A	Starting	DIVA M1	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M1	South Gondwana
Baron et al., 2017 B	Starting	DIVA M1	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M1	South Gondwana
Baron et al., 2017 C	Starting	DIVA M0	South Gondwana
	Harsh	DIVA M1	South Gondwana

Langer et al., 2017	Relaxed	DIVA M1	South Gondwana
	Starting	DIVA M1	South Gondwana
	Harsh	DIVA M1	South Gondwana
	Relaxed	DIVA M1	South Gondwana