

# Current Biology

## A Unique Late Triassic Dinosauromorph Assemblage Reveals Dinosaur Ancestral Anatomy and Diet

### Highlights

- Two new fossil species are described: a sauropodomorph and a lagerpetid
- These come from one of the oldest dinosaur-bearing rock units of the world
- The new lagerpetid reveals how dinosaurs acquired their typical anatomical traits
- The new sauropodomorph is the only known strictly faunivorous member of the group

### Authors

Sergio Furtado Cabreira,  
Alexander Wilhelm Armin Kellner,  
Sérgio Dias-da-Silva, ...,  
Rodrigo Carrilho, André Brodt,  
Max Cardoso Langer

### Correspondence

mclanger@ffclrp.usp.br

### In Brief

Cabreira et al. report one of the best preserved associations of dinosaur and dinosaur precursor known so far. The new sauropodomorph and lagerpetid were found at the same excavation in south Brazil, from one of the oldest (Late Triassic, ca. 230 Ma) rock units with dinosaur remains, shedding light on the ancestral anatomy and diet of dinosaurs.



# A Unique Late Triassic Dinosauromorph Assemblage Reveals Dinosaur Ancestral Anatomy and Diet

Sergio Furtado Cabreira,<sup>1</sup> Alexander Wilhelm Armin Kellner,<sup>2</sup> Sérgio Dias-da-Silva,<sup>3</sup> Lúcio Roberto da Silva,<sup>1,3</sup> Mario Bronzati,<sup>4</sup> Júlio Cesar de Almeida Marsola,<sup>5,6</sup> Rodrigo Temp Müller,<sup>3</sup> Jonathas de Souza Bittencourt,<sup>7</sup> Brunna Jul'Armando Batista,<sup>1</sup> Tiago Raugust,<sup>8</sup> Rodrigo Carrilho,<sup>9</sup> André Brodt,<sup>9</sup> and Max Cardoso Langer<sup>5,10,\*</sup>

<sup>1</sup>Museu de Ciências Naturais, Universidade Luterana do Brasil, Canoas-RS 92425-900, Brazil

<sup>2</sup>Departamento de Geologia e Paleontologia, Museu Nacional-UFRJ, Rio de Janeiro-RJ 20940-040, Brazil

<sup>3</sup>Centro de Apoio à Pesquisa Paleontológica, Universidade Federal de Santa Maria, Santa Maria-RS 97105-900, Brazil

<sup>4</sup>Ludwig-Maximilians-Universität and Bayerische Staatssammlung für Paläontologie und Geologie, Munich 80333, Germany

<sup>5</sup>Laboratório de Paleontologia, FFCLRP, Universidade de São Paulo, Ribeirão Preto-SP 14040-901, Brazil

<sup>6</sup>School of Geography, Earth and Environmental Sciences, University of Birmingham, Birmingham B15 2TT, UK

<sup>7</sup>Departamento de Geologia, Universidade Federal de Minas Gerais, Belo Horizonte-MG 31270-901, Brazil

<sup>8</sup>Instituto Federal de Educação Ciência e Tecnologia Catarinense, Concórdia-SC 89700-000, Brazil

<sup>9</sup>Centro Universitário La Salle, Canoas-RS 92010-000, Brazil

<sup>10</sup>Lead Contact

\*Correspondence: [mclanger@ffclrp.usp.br](mailto:mclanger@ffclrp.usp.br)

<http://dx.doi.org/10.1016/j.cub.2016.09.040>

## SUMMARY

Dinosauromorpha 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 dinosauromorph 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; Alemoa Member, Santa Maria Formation; Candelária Sequence, Paraná Basin [6]; *Hyperodapedon* Assemblage Zone, Carnian, Late Triassic [7].

Archosauria Cope, 1869 [8]

Dinosauromorpha 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 *ιξαλος* (= leaping) and *ερπετόν* (= 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.

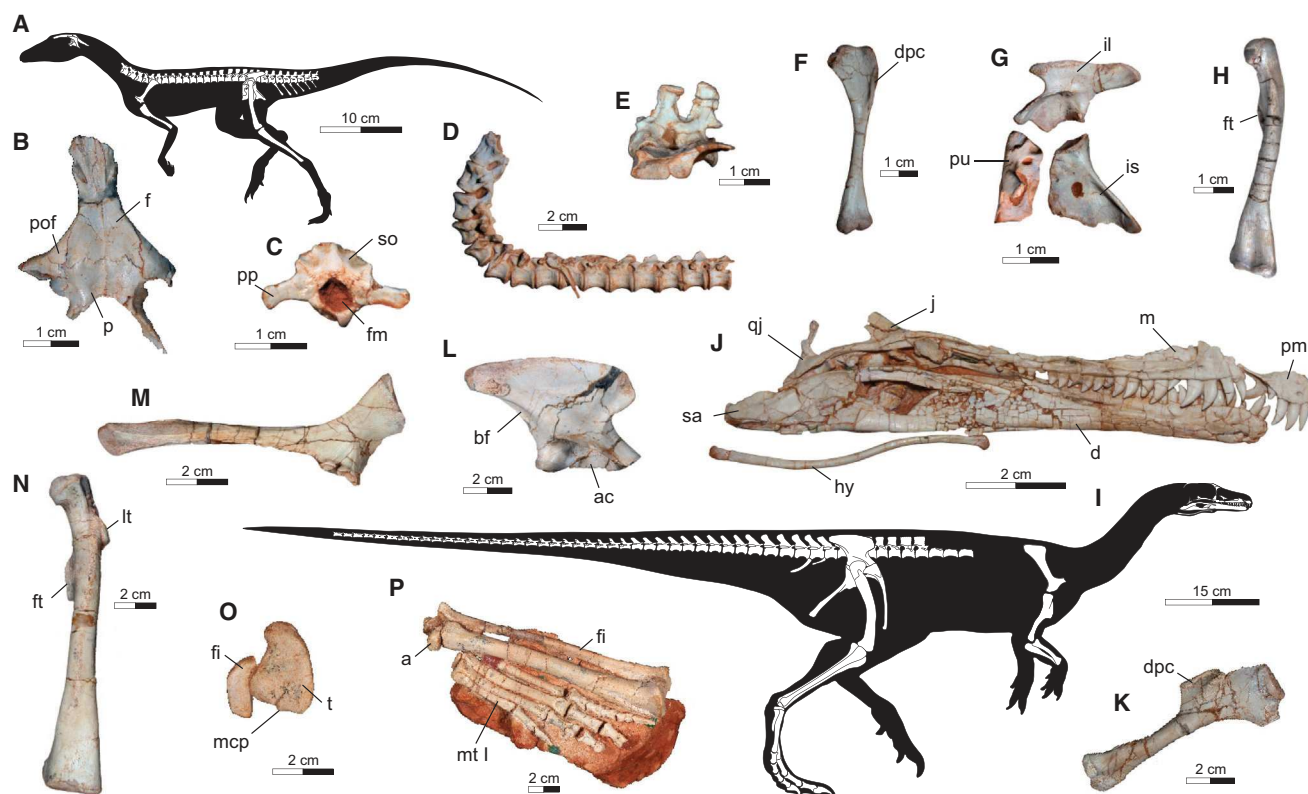
Dinosauriformes Novas, 1992 [11]

Dinosauria Owen, 1842 [12]

Saurischia Seeley, 1887 [8]

Sauropodomorpha Huene, 1932 [13]

*Buriolestes schultzi* gen. et sp. nov.



**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 11–1P](#) and [S2](#)).

**Etymology.** The genus name combines the Greek word ληστής (= robber) and the family name (Buriol) 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 archosauromorphs [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 dinosauromorphs [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 subnarial 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

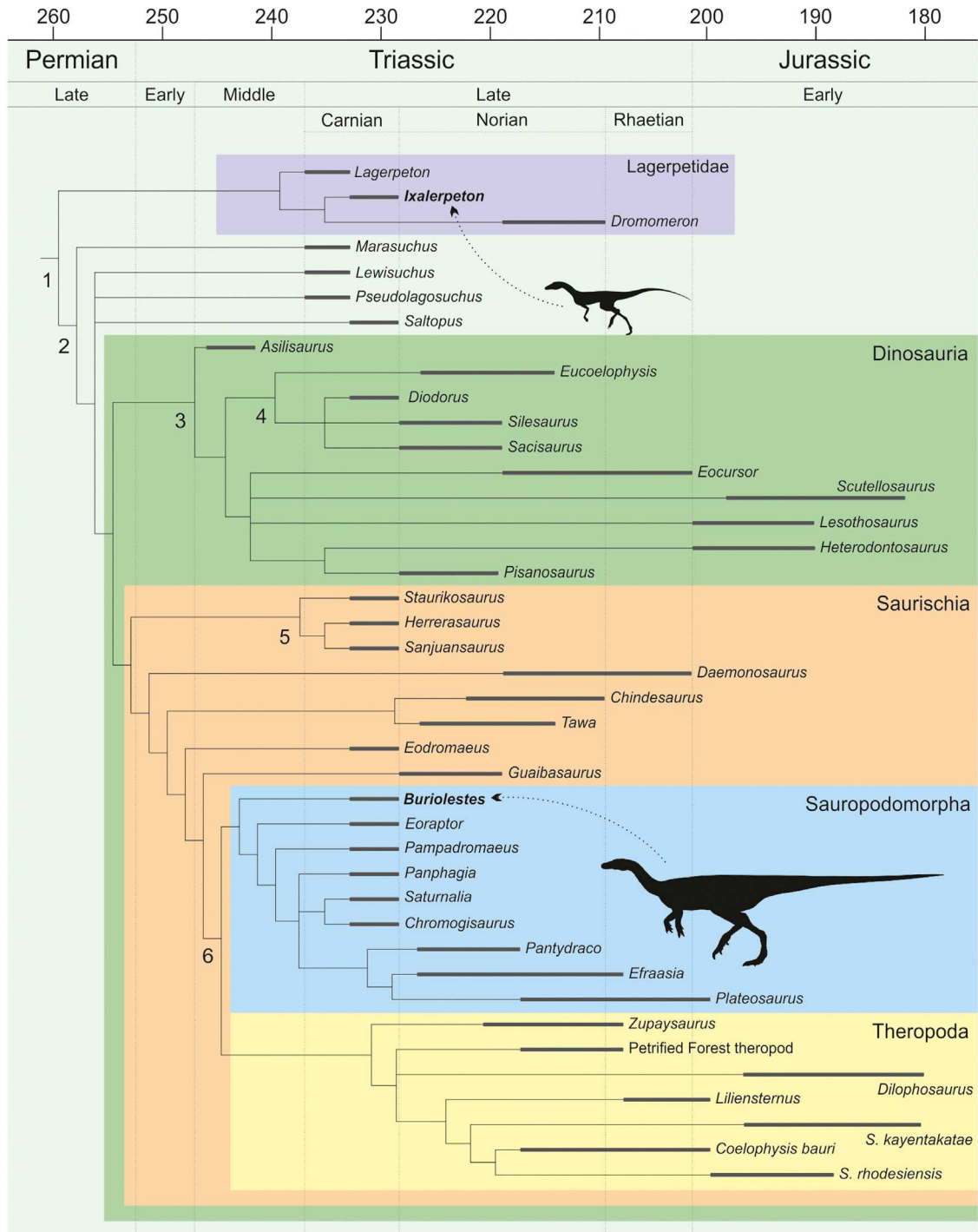
dinosaurs [15], but not completely inturned (states 304-2 and 305-1 in [14]). The iliofemoral musculature attaches to a subtle anterior trochanter and a marked trochanteric shelf. The tibia is slightly longer than the femur, but not as much as in early ornithischians and theropods, which also have an 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 Dinosauroomorpha 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 Dinosauroomorpha or diagnose less inclusive groups. For example, *I. polesinensis* bears an anterior tympanic recess in the braincase, as is typical of Dinosauriformes [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 Dinosauriformes 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 Dinosauroomorpha.

*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 slit compared to *S. tupiniquim*.



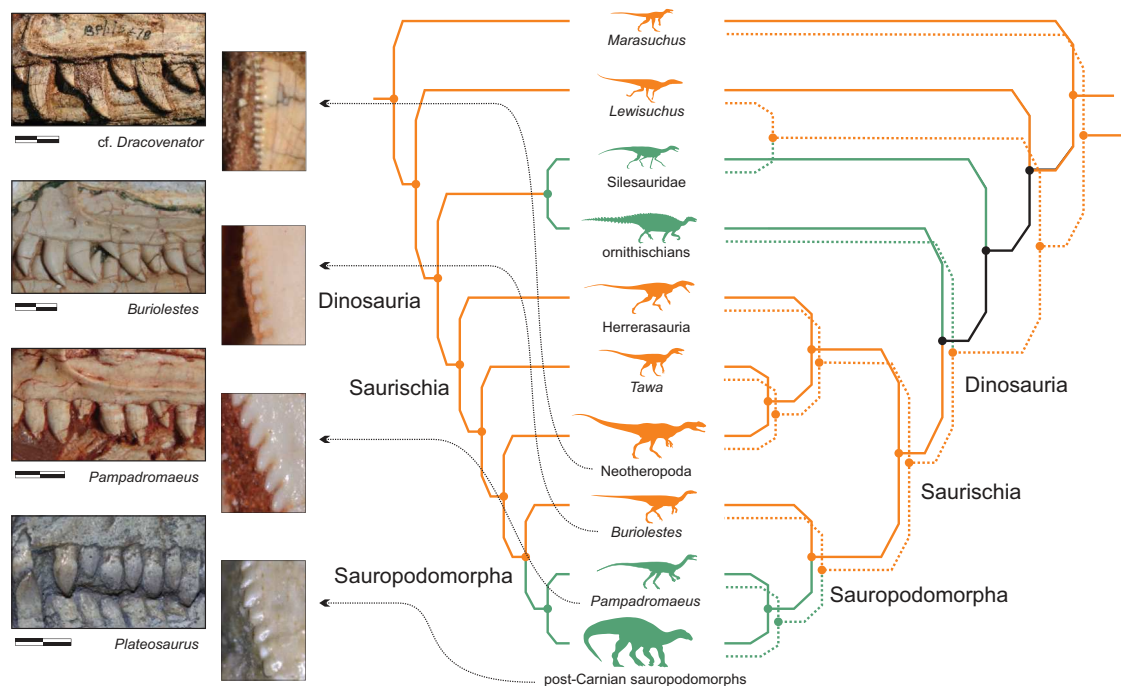
**Figure 2. Time-Calibrated Phylogeny of Early Dinosauriforms**

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 Dinosauriomorpha (1), Dinosauriformes (2), Ornithischia (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-hardily-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.

#### ACKNOWLEDGMENTS

The authors thank Luiz F. Lopes (UFRGS) for the photographic work. This study was supported by the following grants: FAPESP #2014/03825-3 to M.C.L.; FAPERJ #E-26/202.893/2015 and CNPq #304780/2013-8 to A.W.A.K.; FAPESP #2013/23114-1 to J.C.d.A.M.; and CNPq #246610/2012-3 to M.B.

Received: August 9, 2016

Revised: September 15, 2016

Accepted: September 21, 2016

Published: November 10, 2016

#### REFERENCES

- Langer, M.C., Nesbitt, S.J., Bittencourt, J.S., and Irmis, R.B. (2013). Non-dinosaurian Dinosauriforms. *Geol. Soc. Spec. Publ.* 379, 157–186.
- Irmis, R.B., Nesbitt, S.J., Padian, K., Smith, N.D., Turner, A.H., Woody, D., and Downs, A. (2007). A Late Triassic dinosauriform assemblage from New Mexico and the rise of dinosaurs. *Science* 317, 358–361.
- Niedzwiedzki, G., Brusatte, S.L., Sulej, T., and Butler, R.J. (2014). Basal dinosauriform and theropod dinosaurs from the mid–Late Norian (Late Triassic) of Poland: implications for triassic dinosaur evolution and distribution. *Palaeontol.* 57, 1121–1142.
- Da Rosa, A.A. (2014). Geological context of the dinosauriform-bearing outcrops from the Triassic of Southern Brazil. *J. S. Am. Earth Sci.* 61, 108–119.

5. Martínez, R.N., Apaldetti, C., Alcober, O.A., Colombi, C.E., Sereno, P.C., Fernandez, E., Santi Malnis, P., Correa, G.A., and Abelin, D. (2013). Vertebrate succession in the Ischigualasto Formation. *J. Vertebr. Paleontol.* 32 (suppl. 6), 10–30.
6. Horn, B.L.D., Melo, T.P., Schultz, C.L., Philipp, R.P., Kloss, H.P., and Goldberg, K. (2014). A new third-order sequence stratigraphic framework applied to the Triassic of the Paraná Basin, Rio Grande do Sul, Brazil, based on structural, stratigraphic and paleontological data. *J. S. Am. Earth Sci.* 55, 123–132.
7. Langer, M.C., Ribeiro, A.M., Schultz, C.L., and Ferigolo, J. (2007). The continental tetrapod-bearing Triassic of South Brazil. *New Mexico Mus. Nat. Hist. Sci. Bull.* 47, 201–218.
8. Gauthier, J. (1986). Saurischian monophyly and the origin of birds. *Mem. California Acad. Sci.* 8, 1–55.
9. Sereno, P.C. (1991). Basal archosaurs: phylogenetic relationships and functional implications. *Mem. Soc. Vert. Paleontol.* 2, 1–53.
10. Nesbitt, S.J., Irmis, R.B., Parker, W.G., Smith, N.D., Turner, A.H., and Rowe, T. (2009). Hindlimb osteology and distribution of basal dinosauriforms from the Late Triassic of North America. *J. Vertebr. Paleontol.* 29, 498–516.
11. Novas, F.E. (1992). Phylogenetic relationships of the basal dinosaurs, the Herreriasauridae. *Palaeontol.* 35, 51–62.
12. Padian, K., and May, C.L. (1993). The earliest dinosaurs. *New Mexico Mus. Nat. Hist. Sci. Bull.* 3, 379–381.
13. Upchurch, P. (1997). Sauropodomorpha. In *Encyclopedia of Dinosaurs*, P.J. Currie, and K. Padian, eds. (Academic Press), pp. 658–660.
14. Nesbitt, S.J. (2011). The early evolution of archosaurs: relationships and the origin of major clades. *Bull. Am. Mus. Nat. Hist.* 352, 1–292.
15. Langer, M.C., and Benton, M.J. (2006). Early dinosaurs: a phylogenetic study. *J. Syst. Palaeontology* 4, 309–358.
16. Witmer, L.M. (1997). Craniofacial air sinus systems. In *Encyclopedia of Dinosaurs*, P.J. Currie, and K. Padian, eds. (Academic Press), pp. 151–159.
17. Ezcurra, M.D. (2016). The phylogenetic relationships of basal archosauriforms, with an emphasis on the systematics of proterosuchian archosauriforms. *PeerJ* 4, e1778.
18. Dzik, J. (2003). A beaked herbivorous archosaur with dinosaur affinities from the early Late Triassic of Poland. *J. Vertebr. Paleontol.* 23, 556–574.
19. Bittencourt, J.S., Arcucci, A.B., Marsicano, C.A., and Langer, M.C. (2014). Osteology of the Middle Triassic archosaur *Lewisuchus admixtus* Romer (Chañares Formation, Argentina), its inclusivity, and relationships among early dinosauriforms. *J. Syst. Palaeontology* 13, 189–219.
20. Sereno, P.C., and Arcucci, A.B. (1994). Dinosaurian precursors from the Middle Triassic of Argentina: *Marasuchus lilloensis*, n. gen. *J. Vertebr. Paleontol.* 14, 53–73.
21. Sereno, P.C., and Arcucci, A.B. (1994). Dinosaurian precursors from the Middle Triassic of Argentina: *Lagerpeton chanarensis*. *J. Vertebr. Paleontol.* 13, 385–399.
22. Sereno, P.C., Martínez, R.N., and Alcober, O.A. (2013). Osteology of *Eoraptor lunensis* (Dinosauria, Sauropodomorpha). *J. Vert. Paleontol.* 32 (sup. 1), 83–179.
23. Yates, A.M. (2005). A new theropod dinosaur from the Early Jurassic of South Africa and its implication for the early evolution of theropods. *Palaeont. Afr.* 41, 105–122.
24. Yates, A.M. (2007). The first complete skull of the Triassic dinosaur *Melanorosaurus* Haughton (Sauropodomorpha: Anchisauria). *Spec. Pap. Palaeontol.* 77, 9–55.
25. Pol, D., Garrido, A., and Cerda, I.A. (2011). A new sauropodomorph dinosaur from the Early Jurassic of Patagonia and the origin and evolution of the sauropod-type sacrum. *PLoS ONE* 6, e14572.
26. Brusatte, S.L., Nesbitt, S.J., Irmis, R.B., Butler, R.J., Benton, M.J., and Norell, M.A. (2010). The origin and early radiation of dinosaurs. *Earth Sci. Rev.* 101, 68–100.
27. Benton, M.J., Forth, J., and Langer, M.C. (2014). Models for the rise of the dinosaurs. *Curr. Biol.* 24, R87–R95.
28. Sobral, G., Sookias, R.B., Bhullar, B.-A.S., Smith, R., Butler, R.J., and Müller, J. (2016). New information on the braincase and inner ear of *Euparkeria capensis* Broom: implications for diapsid and archosaur evolution. *R Soc Open Sci* 3, 160072.
29. Ezcurra, M.D. (2010). A new early dinosaur (Saurischia: Sauropodomorpha) from the Late Triassic of Argentina: a reassessment of dinosaur origin and phylogeny. *J. Syst. Palaeontology* 8, 371–425.
30. Martínez, R.N., and Alcober, O.A. (2009). A basal sauropodomorph (Dinosauria: Saurischia) from the Ischigualasto Formation (Triassic, Carnian) and the early evolution of Sauropodomorpha. *PLoS ONE* 4, e4397.
31. Cabreira, S.F., Schultz, C.L., Bittencourt, J.S., Soares, M.B., Fortier, D.C., Silva, L.R., and Langer, M.C. (2011). New stem-sauropodomorph (Dinosauria, Saurischia) from the Triassic of Brazil. *Naturwissenschaften* 98, 1035–1040.
32. Zanno, L.E., and Makovicky, P.J. (2011). Herbivorous ecomorphology and specialization patterns in theropod dinosaur evolution. *Proc. Natl. Acad. Sci. USA* 108, 232–237.