



A NEW NANOID TITANOSAUR (DINOSAURIA: SAUROPODA) FROM THE UPPER CRETACEOUS OF BRAZIL

BRUNO A. NAVARRO^{1,2,3}
ALINE M. GHILARDI^{3,4}
TITO AURELIANO^{3,4,5}
VERÓNICA DÍEZ DÍAZ^{6,7}
KAMILA L. N. BANDEIRA⁸
ANDRÉ G. S. CATTARUZZI²

FABIANO V. IORI^{9,10}
ARIEL M. MARTINE¹¹
ALBERTO B. CARVALHO²
LUIZ E. ANELLI¹²
MARCELO A. FERNANDES³
HUSSAM ZAHER²

¹Programa de Pós-Graduação em Zoologia, Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão (Travessa 14) 321, 05508-090 São Paulo, SP, Brazil.

²Laboratório de Paleontologia e Herpetologia, Museu de Zoologia, Universidade de São Paulo, Avenida Nazaré 481, 04263-000 São Paulo, SP, Brazil.

³Laboratório de Paleoeecologia e Paleocnologia, Departamento de Ecologia e Biologia Evolutiva, Universidade Federal de São Carlos, Rodovia Washington Luís (SP-310) km 235, 13565-905 São Carlos, SP, Brazil.

⁴Departamento de Geologia, Universidade Federal do Rio Grande do Norte, Rua das Engenharías s/n, Lagoa Nova, 59078-970 Natal, RN, Brazil.

⁵Institute of Geosciences, University of Campinas, Rua Carlos Gomes 250, 13083-855 Campinas, SP, Brazil.

⁶Museum für Naturkunde, Leibniz-Institut für Evolutions-und Biodiversitätsforschung, Invalidenstraße 43, 10115 Berlin, Germany.

⁷Institut für Biologie, Humboldt Universität, Invalidenstraße 42, 10117 Berlin, Germany.

⁸Laboratório de Sistemática e Tafonomia de Répteis Fósseis, Departamento de Geologia e Paleontologia, Museu Nacional, Universidade Federal do Rio de Janeiro s/n, 20940-040 Rio de Janeiro, RJ, Brazil.

⁹Museu de Paleontologia “Prof. Antônio Celso de Arruda Campos”, Centro de Artes, Praça do Centenário, 15910-000 Monte Alto, SP, Brazil.

¹⁰Museu de Paleontologia “Pedro Candolo”, Estação Cultura, Praça Farmacêutico Bruno Garisto, 15890-000 Uchoa, SP, Brazil.

¹¹Centro de Ciências Humanas e da Educação, Universidade Estadual do Norte do Paraná, Rua Padre de Melo 1200, 86400-000 Jacarezinho, PR, Brazil.

¹²Departamento de Geologia Sedimentar e Ambiental, Instituto de Geociências, Universidade de São Paulo, Rua do Lago, 562, 05508-080 São Paulo, SP, Brazil.

Submitted: 27 October 2021 - **Accepted:** 25 August 2022 - **Published:** 15 September 2022

To cite this article: Bruno A. Navarro, Aline M. Ghilardi, Tito Aureliano, Verónica Díez Díaz, Kamila L. N. Bandeira, André G. S. Cattaruzzi, Fabiano V. Iori, Ariel M. Martine, Alberto B. Carvalho, Luiz E. Anelli, Marcelo A. Fernandes, and Hussam Zaher (2022). A new nanoid titanosaur (Dinosauria: Sauropoda) from the Upper Cretaceous of Brazil. *Ameghiniana* 59(5), 317–354.

To link to this article: <http://dx.doi.org/10.5710/AMGH.25.08.2022.3477>

PLEASE SCROLL DOWN FOR ARTICLE

NEW NEOBATRACHIA FROM THE LATE CRETACEOUS OF BRAZIL

A geologically older, less ossified species of *Baurubatrachus* reveals new osteological information that provides novel characters.

NEW NANOID TITANOSAUR FROM THE UPPER CRETACEOUS OF BRAZIL

A new saltasaurine from the Bauru Basin brings new clues in the evolutionary history of the last titanosaurs.

NEW PHOCIDAE FROM THE LATE MIOCENE–PLIOCENE OF CHILE

The southernmost occurrence of a fossil seal is recorded from the South Pacific Ocean from Guafo Island in Chilean Patagonia.

A NEW NANOID TITANOSAUR (DINOSAURIA: SAUROPODA) FROM THE UPPER CRETACEOUS OF BRAZIL

BRUNO A. NAVARRO^{1,2,3}, ALINE M. GHILARDI^{3,4}, TITO AURELIANO^{3,4,5}, VERÔNICA DÍEZ DÍAZ^{6,7}, KAMILA L. N. BANDEIRA⁸, ANDRÉ G. S. CATTARUZZI², FABIANO V. IORI^{9,10}, ARIEL M. MARTINE¹¹, ALBERTO B. CARVALHO², LUIZ E. ANELLI¹², MARCELO A. FERNANDES³, AND HUSSAM ZAHER²

¹Programa de Pós-Graduação em Zoologia, Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão (Travessa 14) 321, 05508-090 São Paulo, SP, Brazil. brunonavarro@alumni.usp.br

²Laboratório de Paleontologia e Herpetologia, Museu de Zoologia, Universidade de São Paulo, Avenida Nazaré 481, 04263-000 São Paulo, SP, Brazil. andrecattaruzzi@gmail.com; albertbc3@gmail.com; hussam.zaher@gmail.com

³Laboratório de Paleocologia e Paleocnologia, Departamento de Ecologia e Biologia Evolutiva, Universidade Federal de São Carlos, Rodovia Washington Luís (SP-310) km 235, 13565-905 São Carlos, SP, Brazil. marcelicno@yahoo.com.br

⁴Departamento de Geologia, Universidade Federal do Rio Grande do Norte, Rua das Engenharias s/n, Lagoa Nova, 59078-970 Natal, RN, Brazil. alinemghilardi1@gmail.com

⁵Institute of Geosciences, University of Campinas, Rua Carlos Gomes 250, 13083-855 Campinas, SP, Brazil. aureliano.tito@gmail.com

⁶Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung, Invalidenstraße 43, 10115 Berlin, Germany. diezdiaz.veronica@gmail.com

⁷Institut für Biologie, Humboldt Universität, Invalidenstraße 42, 10117 Berlin, Germany.

⁸Laboratório de Sistemática e Tafonomia de Répteis Fósseis, Departamento de Geologia e Paleontologia, Museu Nacional, Universidade Federal do Rio de Janeiro s/n, 20940-040 Rio de Janeiro, RJ, Brazil. kamila.bandeira@mn.ufrj.br

⁹Museu de Paleontologia “Prof. Antônio Celso de Arruda Campos”, Centro de Artes, Praça do Centenário, 15910-000 Monte Alto, SP, Brazil. biano.iori@gmail.com

¹⁰Museu de Paleontologia “Pedro Candolo”, Estação Cultura, Praça Farmacêutico Bruno Garisto, 15890-000 Uchoa, SP, Brazil.

¹¹Centro de Ciências Humanas e da Educação, Universidade Estadual do Norte do Paraná, Rua Padre de Melo 1200, 86400-000 Jacarezinho, PR, Brazil. arielmilanimartine@gmail.com

¹²Departamento de Geologia Sedimentar e Ambiental, Instituto de Geociências, Universidade de São Paulo, Rua do Lago, 562, 05508-080 São Paulo, SP, Brazil. anelli@usp.br

Abstract. Titanosaurian sauropods are known to exhibit remarkable body size disparity, with some taxa famed for nearing the zenith of terrestrial vertebrate body size. Here, we describe a new titanosaurian – *Ibirania parva* gen. et sp. nov. – from the Upper Cretaceous (Santonian–Campanian) São José do Rio Preto Formation of Bauru Basin, in which represents one of the smallest sauropods known to date. The new taxon is diagnosed by seven autapomorphies and had an estimated body length of 5.7 m. Histological and μ CT scan analyses showed that this new taxon is represented by skeletally mature individuals, which had attained somatic maturity prior to death. Phylogenetic analyses recovered the new taxon deeply nested within Saltasaurinae, a clade previously known by small-sized forms. *Ibirania parva* gen. et sp. nov. brings new information indicating that the body size reduction in some titanosaurians could be driven by recurrent ecophysiological settings, present in South America prior to the diversity peak attained by the group during the Campanian–Maastrichtian.

Key words. Bauru Basin. Growth Patterns. Histology. Nanism. Saltasauridae. São José do Rio Preto Formation.

Resumen. UN NUEVO TITANOSAURIO ENANO (DINOSAURIA: SAUROPODA) DEL CRETÁCICO SUPERIOR DE BRASIL. Los saurópodos titanosaurios son conocidos por mostrar una notable disparidad de tamaño corporal, con algunos taxones famosos por acercarse al cenit del tamaño corporal de un vertebrado terrestre. En este trabajo se describe un nuevo titanosaurio – *Ibirania parva* gen. et sp. nov. – del Cretácico Superior (Santoniano–Campaniano) de la Formación São José do Rio Preto de la Cuenca Bauru, el cual representa uno de los saurópodos más pequeños conocidos hasta la fecha. El nuevo taxón se puede diagnosticar gracias a siete autapomorfías y tenía una longitud corporal estimada de 5.7 m. Los análisis histológicos y de microtomografía computarizada muestran que este nuevo taxón está representado por individuos esqueléticamente maduros, que habrían alcanzado la madurez somática antes de la muerte. Los análisis filogenéticos han recuperado la inclusión del nuevo taxón dentro de Saltasaurinae, un clado previamente conocido por formas de pequeño tamaño. *Ibirania parva* gen. et sp. nov. arroja nueva información indicando que la disminución del tamaño corporal en algunos titanosaurios podría estar impulsado por escenarios ecofisiográficos recurrentes, presentes en América del Sur antes del pico de diversidad alcanzado por el grupo durante el Campaniano–Maastrichtiano.

Palabras clave. Cuenca Bauru. Patrones de crecimiento. Histología. Enanismo. Saltasauridae. Formación São José do Rio Preto.

TITANOSAURIA is a clade of neosauropods with a remarkable diversity and worldwide distribution (Curry Rogers, 2005; Wilson, 2006b; García *et al.*, 2015; González Riga *et al.*, 2019). They are known to exhibit conspicuous body size disparity marked by the occurrence of giant (*e.g.*, Bonaparte & Coria, 1993; Novas *et al.*, 2005; Lacovara *et al.*, 2014; González Riga *et al.*, 2016; Carballido *et al.*, 2017) and nanoid taxa (*e.g.*, Stein *et al.*, 2010; Klein *et al.*, 2012; Díez-Díaz *et al.*, 2013b; Curry Rogers & Kulik, 2018; Díez-Díaz *et al.*, 2018). Titanosaurians represent the most typical large-bodied herbivorous faunal component in the Late Cretaceous biotas from the southern continents (Powell, 2003; Upchurch *et al.*, 2004; Tomaselli *et al.*, 2021). Nonetheless, they are also present in Laurasia, with some forms from the Early Cretaceous (Dal Sasso *et al.*, 2016; Averianov & Skutschas, 2017; Averianov & Efimov, 2018; Mannion *et al.*, 2019).

Titanosaurian fossils from Brazil have been known since the late nineteenth century (Derby, 1895; Woodward, 1910; Pacheco, 1913; Huene, 1931). Most specimens were recovered in the northwestern region of the São Paulo State and within the “Triângulo Mineiro” region of the Minas Gerais State. Both regions encompass the Upper Cretaceous continental deposits of the Bauru Basin (Batezelli, 2015; Fernandes & Ribeiro, 2015; Menegazzo *et al.*, 2016) in which, alongside notosuchians, titanosaurians are the most common vertebrate occurrences (Santucci & Bertini, 2001; Pol *et al.*, 2014; Bandeira *et al.*, 2018). Ten titanosaur taxa have been recognized in these strata until now (see Gil *et al.*, 2020) and, beyond the named forms, the Bauru Basin titanosaur record also includes: isolated and associated appendicular and axial remains (*e.g.*, Campos & Kellner, 1999; Santucci & Bertini, 2001; Santucci, 2002; Azevedo *et al.*, 2007; Lopes & Buchmann, 2008; Silva Jr *et al.*, 2017), isolated teeth (Candeiro *et al.*, 2006), few cranial bones (Martinelli *et al.*, 2015), and eggs and eggshells assigned to Megaloolithidae and Faveoolithidae oofamilies (Magalhães-Ribeiro, 2002; Grellet-Tinner & Zaher, 2007). Most of these finds lack a more specific taxonomic assessment (*e.g.*, Bertini *et al.*, 2001; Santucci, 2008), hampering major associations between axial and appendicular morphotypes.

Another particularity about the titanosaurian fauna from the Bauru Basin is the small body size displayed by most of the described species. The Bauru Basin titanosaurians (*e.g.*, *Gondwanatitan faustoi*, *Trigonosaurus pricei*, *Brasilotitan*

nemophagus) were relatively smaller than other forms reported from coeval localities, usually displaying sizes similar to found in insular nanoid taxa. Even if some taxa, such as *Arrudatitan maximus*, *Uberabatitan ribeiroi*, and *Austroposeidon magnificus*, are represented by large-sized individuals (20–25 m in length; Bandeira *et al.*, 2016; Silva Jr *et al.*, 2019, 2021), most of Bauru Basin titanosaur specimens exhibit small to median sizes, ranging between 8–12 m in body length (Kellner & Azevedo, 1999; Campos *et al.*, 2005; Kellner *et al.*, 2005; Machado *et al.*, 2013). For example, none of the known taxa reached the large sizes of their contemporary Argentinian species, such as *Puertasaurus reuili*, *Dreadnoughtus schrani*, and *Notocolossus gonzalezparejasi* (Novas *et al.*, 2005; Lacovara *et al.*, 2014; González Riga *et al.*, 2016). This pattern raises interesting questions about the titanosaurian fauna from Bauru Basin, especially when compared with other correlated Gondwanan occurrences: (i) was nanism triggered by the environmental stress that prevailed in the region during the end of the Cretaceous? or (ii) was nanism related to a taphonomical bias? (see Bandeira *et al.*, 2018). No hypotheses have been previously proposed to explain this singular pattern.

Here we describe a new titanosaurian taxon from the Upper Cretaceous (Santonian–Campanian) São José do Rio Preto Formation. The new taxon is represented by associated axial and appendicular remains recovered in a single outcrop located at Sítio dos Irmãos Garcia, in Vila Ventura, Ibirá Municipality, in northeastern São Paulo State, Brazil (Fig. 1). This new taxon not only represents one of the smallest sauropods described to-date but, according to our expanded phylogenetic analysis, also represents to the first unequivocal saltasaurine titanosaurian reported for Brazil. We performed a histological analysis to assess growth patterns that could explain the putative occurrence of a nanoid taxon outside typical insular habitats. We further discuss if such pattern is driven by phylogenetic trends, paleoecological dynamics, or corresponds to a response to the ecophysiological settings represented in the Upper Cretaceous of the Bauru Basin.

Institutional abbreviations. BIBE, Big Bend National Park, Texas, USA; CPPLIP, Complexo Paleontológico de Peirópolis Llewellyn Ivor Price, Uberaba, Brazil; DGM, Departamento de Geologia e Mineralogia, Companhia de Pesquisa de Recursos Minerais, Rio de Janeiro, Brazil; INPC, Instituto Nacional de

Patrimônio Cultural, Loja, Ecuador; **LPP**, Laboratório de Paleoeologia e Paleicnologia, Universidade Federal de São Carlos, Brazil; **MACN**, Museo Argentino de Ciencias Naturales

Bernardino Rivadavia, Buenos Aires, Argentina; **MAL**, Malawi Department of Antiquities, Lilongwe and Nguludi, Malawi; **MAU**, Museo Municipal Argentino Urquiza, Rincón de los

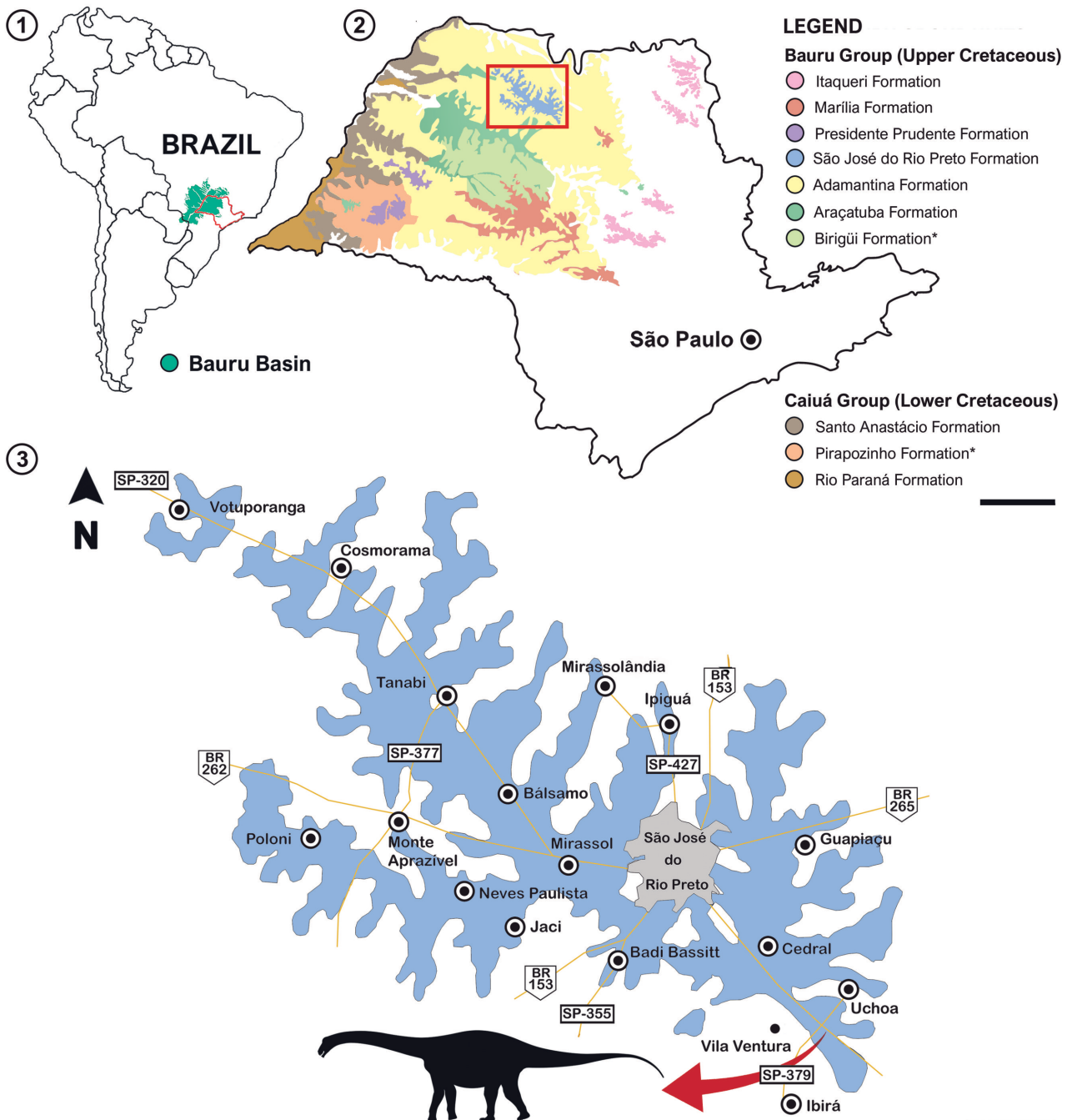


Figure 1. Geographic and geological context of Bauru Basin (modified from Delcourt & Iori, 2018). 1, Bauru Basin deposits in the South America, which the red outline represents the São Paulo State; 2, distribution map and stratigraphic hierarchy adopted in this study for the Bauru Basin units at the São Paulo State (modified from Menegazzo *et al.*, 2016). The red square denotes the region that has collected the specimens studied here. Asterisks mark the subsurface locations; 3, distribution map of São José do Rio Preto Formation in the north-western region of the São Paulo State. The red arrow shows the location of the outcrop that has yielded the *Ibirania parva* gen. et sp. nov. specimens. Yellow lines represent federal (BR) and state (SP) highways.

Sauces, Argentina; **MCNA**, Museo de Ciencias Naturales de Álava, Vitoria-Gasteiz, Spain; **MCS**, Museo de Cinco Saltos, Cinco Saltos, Argentina; **MCT**, Museu de Ciências da Terra, Companhia de Pesquisa de Recursos Minerais, Rio de Janeiro, Brazil; **MLP**, Museo de La Plata, La Plata, Argentina; **MN**, Museu Nacional, Universidade Federal do Rio de Janeiro, Brazil; **MPCA**, Museo Provincial Carlos Ameghino, Cipolletti, Argentina; **MPMA**, Museu de Paleontologia Prof. Antonio Celso de Arruda Campos, Monte Alto, Brazil; **MPPC**, Museu de Paleontologia Pedro Candolo, Uchoa, Brazil; **MZSP**, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; **NHM**, Natural History Museum, London, United Kingdom; **PVL**, Instituto Miguel Lillo, San Miguel de Tucumán, Argentina; **UTPL**, Universidad Técnica Particular de Loja, Ecuador; **YM**, Yamana locality collection, Loja, Ecuador.

Anatomical abbreviations. **ACDL**, anterior centrodiapophyseal lamina; **CDF**, centrodiapophyseal fossa; **CPOL**, centropostzygapophyseal lamina; **CPRL**, centroprezygapophyseal lamina; **EPRL**, epipophyseal-prezygapophyseal lamina; **lat. CPOL**, lateral centropostzygapophyseal lamina; **lat. CPRL**, lateral centroprezygapophyseal lamina; **lat. SPOL**, lateral spinopostzygapophyseal lamina; **med. CPOL**, medial centropostzygapophyseal lamina; **med. CPRL**, medial centroprezygapophyseal lamina; **med. SPOL**, medial spinopostzygapophyseal lamina; **PACDF**, parapophyseal-centrodiapophyseal fossa; **PCDL**, posterior centrodiapophyseal lamina; **PCPL**, posterior centroparapophyseal lamina; **POCDF**, posterior centrodiapophyseal fossa; **PODL**, postzygodiapophyseal lamina; **POSF**, postspinal fossa; **POSL**, postspinal lamina; **PPDL**, paradiapophyseal lamina; **PRDF**, prezygodiapophyseal fossa; **PRDL**, prezygodiapophyseal lamina; **PRPL**, prezygoparapophyseal lamina; **PRSDF**, prezygapophyseal-spinodiapophyseal fossa; **PRPADF**, prezygapophyseal-paradiapophyseal fossa; **PRSF**, prespinal fossa; **PRSL**, prespinal lamina; **SPDL**, spinodiapophyseal lamina; **SPOL**, spinopostzygapophyseal lamina; **SPRL**, spinoprezygapophyseal lamina; **TPOF**, intrapostzygapophyseal fossa; **TPOL**, intrapostzygapophyseal lamina; **TPRL**, intraprezygapophyseal lamina.

MATERIALS AND METHODS

Materials

At least four specimens of the new taxon are known from a single horizon. Both axial and appendicular remains

are preserved. Axial remains of the new taxon comprise fragmentary-to-moderately preserved elements. The most complete elements have their approximate position in the axial column established primarily by the position of zygapophyses, by the elevation of parapophyses relative to the diapophyses, and the neural spine inclination and development when preserved (Gallina, 2011).

The appendicular elements associated with the new taxon consist of a fragmentary right radius and ulna, the distal half of a right metacarpal, diaphyseal fragments of a right and a nearly fully preserved left fibula, and an almost complete left metatarsal. Intense pre- and post-diagenetic weathering obliterated several morphological traits, which hampered comparisons. Nevertheless, the specimens were useful to estimate limb heights and to histological sampling.

We compared the new taxon primarily with the type specimens of Brazilian titanosaurs that share overlapping elements, including *Gondwanatitan faustoi* (MN 4111-V), *Baurutitan britoi* (MCT 1490-R), *Trigonosaurus pricei* (MCT 1488-R, 1719-R), *Maxakalisaurus topai* (MN 5013-V), *Uberabatitan ribeiroi* (CPPLIP-0494, 1019, 1032, 1068, 1077, 1107, 1108), and *Tapuiasaurus macedoi* (MZSP-PV 807). Additional comparisons were made with a set of undescribed titanosaurian specimens from the Bauru Basin (DGM 775-R; MCT 1487-R, 1616-R, 1619-R, 1621-R; CPPLIP 0036, 0037, 0110, 0111, 0361, 0458) and with the closely related taxa *Neuquensaurus australis* (MCS-Pv 5), *Saltasaurus loricatus* (PVL 4017), *Rocasaurus muniozi* (MPCA-Pv 46, 858, 859, 860), *Bonatitan reigi* (MACN-Pv RN 821, 1061), *Yamanasaurus lojaensis* (YM-UTPL-002, YM-INPC-014–017), and an unnamed from Angostura Colorada Formation (MACN-Pv RN 233). Further comparisons were extended to *Malawisaurus dixeyi* (MAL-180, 239, 243, 245, 278, 280, 283), *Overosaurus paradasorum* (MAU-Pv-CO-439), and some small-sized titanosaurian taxa from Europe, such as *Magyarosaurus dacus* (NHM-R.3861 and R.4896) and *Lirainosaurus astibiae* (MCNA 7442, 7443, 7445, 1882, 2207, 2208, 2211, 7451, 7452, 7454, 7455, 7457, 7458, 8605–8607, 9647, 13388, 13851, 13853, 13854, 13857, 14435–14455). First-hand observations on these specimens were conducted by BAN, KLNB, and VDD (see Supplementary Online Information).

Methods

Computed Tomography (CT) Imagery. The holotypic posterior dorsal vertebra (LPP-PV-0200) was tomographed using a Philips Diamond Select Brilliance CT 16-slice medical scanner with more than 200 slices and a voxel size of 0.75 mm at the HU-UFSCar. Acceleration voltage varied between 90 and 120 kV in a current of 367 mA. We followed the methodology applied by Aureliano *et al.* (2020) to process the data and generate the three-dimensional reconstruction with the software 3D Slicer © v4.10 (Fedorov *et al.*, 2012) and CloudCompare © v2.9.1.

The μ CT-scanning procedures applied to LPP-PV-200 were performed on the Phoenix v|tome|x M 300 (General Electric Measurement & Control Solutions, Wunstorf, Germany). This equipment is a 300-kV μ -focus X-ray source installed at the Laboratório de Microtomografia of the Museu de Zoologia, Universidade de São Paulo, Brazil. X-ray projection images were set at 333 ms of time of exposure per image, in one slow 360 degrees stepwise rotation of the sample, with 4000 images, voltage 220 kV, current 250 μ A, and voxel size resolution 146 μ m. A beam hardening correction filter was used to reduce artifacts, using the factor of six (values varying from zero to 10).

Data processing was executed using a high-performed workstation model HP Z820 with an eight-core Intel Xeon © 2.20GHz, with 128 GB of RAM memory, run on Microsoft Windows 7 Ultimate © 64-bit operating system. The reconstruction of acquired raw data was performed using the GE system-supplied software phoenix datos|x reconstruction v. 2.3.0 (General Electric Measurement & Control Solutions, Wunstorf, Germany). Three-dimensional editions as well as the analysis of the reconstructed data were performed using the software VGStudio MAX © V2.2.3 64 bits (Volume Graphics GmbH, Heidelberg, Germany).

Thin Section Sampling. Samples were taken from the holotype (LPP-PV-0202) and a referred specimen (LPP-PV-0043) of *Ibirania parva*, n. gen., n. sp., to evaluate growth patterns. Specimens were tomographed prior to sectioning. We used Epoxiglass © 1.504 resin to embed the fossil, following standard procedures to prepare the thin sections (*sensu* Lamm, 2013). Samples were ground to a thickness of approximately 40 to 60 μ m. Thin sections were observed and photographed using a petrographic ZEISS © Axioscope microscope with an AxioCam MRc 5 camera attached and

imaging by the software ZEISS © Application Suite v. 4.4. Samples measurements were taken through ImageJ v.1.8. The Histological Ontogenetic Stage (**HOS**) of the specimen was established and comparisons were made with the published literature (*e.g.*, Klein & Sander, 2008; Stein *et al.*, 2010; Company, 2011; Klein *et al.*, 2012; Curry Rogers *et al.*, 2016; Díez-Díaz *et al.*, 2018). Furthermore, we also applied the ‘three-front model’ suggested by Mitchell and Sander (2014), as an additional approach to infer ontogenetic maturity in these specimens.

Data archiving. High-resolution μ CT-scan reconstructions and thin section images of specimens used in this study are available at MorphoBank (<https://www.morphobank.org>), project ID 4184.

Measurements. Axial and appendicular materials were measured using digital calipers and measuring tape. Vertebral measurements included total height, centrum length, width, and height, the height of the neural arch and spine, as well as the Elongation Index (**EI**). The EI represents the centrum length divided by the mean average value of the posterior mediolateral width and dorsoventral height. Measurements of all axial materials are available in Table 1. The Eccentricity Index (**EI**) was calculated for appendicular bones, corresponding to the mid-shaft mediolateral breadth divided by the anteroposterior breadth (Wilson & Carrano, 1999). The Robustness Index (**RI**) has been calculated as the average of the greatest widths, as preserved, of the proximal and distal ends, and the mid-shaft divided by the preserved length of the element in question (Wilson & Upchurch, 2003). Measurements of all appendicular materials are available in Table 2.

Anatomical and Directional Terminology. We used for anatomical structures and their orientations the traditional “Romerian” terminology instead of the veterinarian and avian alternatives, as proposed by Wilson (2006a). For the identification and designation of vertebral laminae and fossae we follow the landmark-based scheme proposed by Wilson (1999, 2012) and Wilson *et al.* (2011), respectively. For internal pneumatic bony tissues, we follow the nomenclature proposed by Wedel *et al.* (2000) and Wedel (2003, 2007).

Phylogenetic Analysis. We investigated the phylogenetic relationships of the new taxon within Titanosauria using the recently published dataset of Carballido *et al.* (2017) as

TABLE 1. Selected measurements of axial bones of *Ibirania parva* gen. et sp. nov. in millimeters (mm).

Material	Specimen	Acronym	TH	CL	CW	CH	NAH	NSH	EI
Middle cervical centrum	Referred	MPPC 02-012	-	251*	132*	136*	-	-	0,53
Posteriormost cervical vertebra	Referred	MPMA 08-0049/02	171*	191*	106*	63*	106*	-	0,44
Anteriormost dorsal vertebra	Referred	MPMA 08-0050/01	194*	200*	121*	88*	129*	93*	0,52
Anterior dorsal neural arch	Referred	MPPC 02-013	-	-	-	-	120*	-	-
Anterior dorsal neural arch	Referred	MPPC 00-023	-	-	-	-	79*	-	-
Middle dorsal centrum	Referred	MPPC 02-005	-	203*	133*	131*	-	-	0,65
Posterior dorsal vertebra	Holotype	LPP-PV-0200	271	175*	85*	93*	186	116	0,51
First caudal centrum	Holotype	LPP-PV-0204	-	138*	53*	72*	-	-	0,45
Middle caudal vertebra	Referred	MPMA 08-0060/07	116	89	62	70	46*	35*	0,74
Middle caudal neural arch	Holotype	LPP-PV-0206	-	-	-	-	70*	67*	-
Posterior caudal centrum	Holotype	LPP-PV-0205	-	54*	33*	32	-	-	0,60

An asterisk (*) marks the measurements based only on preserved portions, while a dash (-) denotes when the region is not preserved or indicates measurements that could not be taken. Abbreviations: **TH**, Total Height; **CL**, Centrum Length; **CW**, Centrum Width; **CH**, Centrum Height; **EI**, Elongation Index; **NAH**, Neural Arch Height (measured from dorsal surface of the centrum to the top of neural spine); **NSH**, Neural Spine Height (measured from the intrapostzygapophyseal lamina to the top of neural spine).

modified by Filippi *et al.* (2019), Carballido *et al.* (2020), and Hechenleitner *et al.* (2020). We further expanded both taxon sampling and character sets based on new information available, and scoring modifications based on our new observations. The complete list of modifications, scorings, and support analyses are provided in the Supplementary Online Information. Character scorings were made on Mesquite v3.61 (Maddison & Maddison, 2011) and exported in both .NEX and .TNT formats.

The resulting dataset encompassed 114 taxa and 435 characters. Characters scored included 88 from the skull, 20 from the mandible, 14 from teeth, 37 from the cervical series, 64 from the dorsal series, four from the cervical and dorsal ribs, six from the sacral vertebrae, 62 from the caudal series, six from the chevrons, 26 from the pectoral girdle, 29 from the forelimb, 25 from the pelvic girdle, 53 from the hind limb, and one from the dermal skeleton. We followed Carballido *et al.* (2017) in treating 24 multistate characters as ordered (14, 61, 100, 102, 109, 115, 127, 132, 135, 136, 166, 179, 195, 256, 259, 276, 277, 278, 279, 299, 303, 346, 352, 354). Taxon sampling included 64 terminal taxa in the

outgroup and 50 terminal taxa in the ingroup. Unstable taxa were detected using the ‘*iterpcr*’ method in TNT (Pol & Escapa, 2009). This allowed to recover the following eight highly unstable rogue taxa, all with fragmentary morphologies: *Isanosaurus attavipachi*, *Rayososaurus agrioensis*, *Lusotitan atalaiensis*, *Padillasaurus leivaensis*, *Malarguesaurus florenciae*, *Quetecsaurus rusconii*, *Drusilasaura deseadensis* and *Garrigatitan meridionalis*. They were subsequently removed from the matrix, resulting in the present dataset used in this study (*i.e.*, 435 chars for 106 terminals).

The reduced dataset was analyzed using equally weighted parsimony in TNT v1.5 (Goloboff *et al.*, 2008). We conducted the analysis with the “New Technology Search”, using the command “*xmult=hits 100*”. Under this command, Sectorial Search, Ratchet, Drift, and Tree Fusing algorithms are applied together with the traditional search procedures, such as Wagner Trees, Tree Branch Reconnection (**TBR**) and Subtree-Pruning-Regrafting algorithms, to find the Minimum Length Trees (**MLTs**). A final round of TBR branch swapping was applied to the optimal trees obtained at the end of the replicates by using the command “*bb*”, to find all

TABLE 2. Selected measurements of appendicular bones of *Ibirania parva* gen. et sp. nov. in millimeters (mm).

Material	Side	Specimen	Acronym	TH	APB	MLB	PW	DW	MSC	ECI	RI
Radius	Right	Holotype	LPP-PV-0203	256*	56	33	-	71*	140	0,59	0,25
Ulna	Right	Holotype	LPP-PV-0202	223*	66	40	95*	78*	130	0,61	0,36
Metacarpal	Right	Holotype	LPP-PV-0201	112*	29	27	-	47	32	0,93	0,34
Metatarsal	Left	Holotype	LPP-PV-0207	108	38	20	63	51	76	0,53	0,47
Fibula	Right	Referred	LPP-PV-0043	139*	65	48	-	-	167	0,74	-
Fibula	Left	Referred	MPMA 09-0001/99	434*	66	48	112*	86*	178	0,73	0,20

An asterisk (*) marks the measurements based only on preserved portions, while a dash (-) denotes when the region is not preserved or indicates measurements that could not be taken. Abbreviations: **TH**, Total Length; **APB**, Anteroposterior Breadth; **MLB**, Mediolateral Breadth; **PW**, Proximal Width; **DW**, Distal Width; **MSC**, Mid-Shaft Circumference; **ECI**, Eccentricity Index; **RI**, Robustness Index.

the Most Parsimonious Trees (**MPTs**). A maximum of 100000 MPTs was set to be saved in memory. For the construction of a strict consensus tree, zero length branches were collapsed (collapsing rule 3) if they lacked support under any of the most parsimonious reconstructions (Fig. 1 in Supplementary Online Information).

Node supports for the MPT's were calculated using Bootstrap and Jackknife (Felsenstein, 1985), and Bremer (Decay Index; Bremer, 1994). Resampling support analyses consisted in 1000 pseudoreplicates in TNT with the same tree search strategy employed for the parsimony analysis, in which the resulting trees were summarized through absolute and GC frequencies. Bremer support was calculated using the TNT script "*bremsup.run*" that combines heuristic searches of suboptimal trees allied to tree searches under negative constraints (Fig. 2 in Supplementary Online Information).

The obtained topologies were processed in FigTree v1.4.2 and the R v4.0.3 (available at <https://www.r-project.org/>). The strict consensus was temporally scaled in the R software, using the "*ape*", "*strap*" and "*phytools*" packages, and followed the method described by Ruta *et al.* (2006) (see Fig. 3 in Supplementary Online Information).

Phylogenetic Definitions. The phylogenetic definitions used in this study are summarized in the Supplementary Online Information. Newly proposed clade definitions were regis-

tered at RegNum platform (<https://www.phyloregnum.org/>) of the International Code of Phylogenetic Nomenclature (PhyloCode; Cantino & de Queiroz, 2020). Following article 6, recommendation 6.1A from the Phylonyms (de Queiroz *et al.*, 2020), all clades established under this code are italicized (see Supplementary Online Information).

SYSTEMATIC PALEONTOLOGY

DINOSAURIA Owen, 1842

SAUROPODA Marsh, 1878

NEOSAUROPODA Bonaparte, 1986

MACRONARIA Wilson & Sereno, 1998

TITANOSAURIA Bonaparte & Coria, 1993

LITHOSTROTIA Upchurch, Barrett & Dodson, 2004

EUTITANOSAURIA Sanz, Powell, Le Loeuff, Martínez &

Pereda Suberbiola, 1999

SALTASAUROIDEA Powell, 1992

SALTASAURIDAE Powell, 1992

SALTASAURINAE Powell, 1992

Ibirania gen. nov.

LSID urn:lsid:zoobank.org:act:1E4BCAB6-7D37-4199-9667-1BBA61489EEF

Type species. *Ibirania parva* sp. nov. from the late Santonian to early Campanian (Upper Cretaceous) of São José do Rio Preto Formation, Bauru Basin at Ibirá Municipality, São Paulo State, Brazil (Fig. 2).

Diagnosis. As for type and only known species, by monotypy.

Ibirania parva sp. nov.

Figures 1–13; Tables 1, 2

LSID urn:lsid:zoobank.org:act:3E8A5EC8-0E0B-4351-A454-02746D2ECC1A

Etymology. The generic epithet is a combination of the name “Ibirá”—the municipality in which the specimens were found—with “*ania*”, a modified form of the Greek word “*planía*” (meaning “wander”). The name Ibirá is a Portuguese derivative from the Tupi word “*ybyrá*”, which means “tree” or “wood.” Thus, the name of this new genus, means “Ibirá wanderer” or even “tree wanderer” in allusion to its browser feeding behavior. The specific epithet “*parva*” – a feminine substantive – is derived from the Latin word “*parvus*,” which means small or little, in reference to the nanism exhibited by this form.

Holotype. The holotype of *Ibirania parva* consists of disarticulated but associated postcranial remains of a single individual (Fig. 3), including: a moderately preserved posterior dorsal vertebra (LPP-PV-0200), partial anterior (LPP-PV-0204) and posterior caudal centra (LPP-PV-0205), partial neural arch of a mid-caudal vertebra (LPP-PV-0206), fragmentary radius (LPP-PV-0203) and ulna (LPP-PV-0202), the distal half of a metacarpal (LPP-PV-0201), and a nearly complete metatarsal (LPP-PV-0207). All materials are referred to the same individual because they were found on the same layer and in close association, lacking overlapping elements (see Figs. 4–5 in Supplementary Online Information). In addition, all the bones exhibit similar diagenetic features (e.g., ferruginous impregnations and moderate oxidation), compatible size (reconstructed size of the radius 367 mm, ulna 364 mm, and metacarpal 242 mm), and they are the only titanosaurian material found at this stratum. Besides the proximity of the bone remains, the forelimb materials are all from the right side and their taphonomic signature (e.g., lacking most of the proximal portions) support the view that these pertained to the same individual.

Referred material. Additional individuals (Fig. 3) recovered from adjacent outcrops are assigned as referred specimens of *Ibirania parva*. They consist of a fragmentary cervical centrum (MPPC 02-012), a nearly preserved posteriormost cervical vertebra (MPMA 08-0049/02), a partial anterior dorsal vertebra (MPMA 08-0050/01), two partial neural arches of

probable anterior dorsal vertebrae (MPPC 02-013 and MPPC 00-023), a mid-dorsal centra (MPPC 02-005), a complete mid-caudal vertebra (MPMA 08-0060/07), diaphyseal fragments of a fibula (LPP-PV-0043), and a nearly complete fibula (MPMA 09-0001/99). These specimens are associated with this taxon because they share the autapomorphies that diagnose the holotype, similar diagenetic features, and were found close to this specimen at the same horizon (see Figs. 4 and 6–8 in Supplementary Online Information).

Repositories. The holotype (LPP-PV-0200–0207), referred specimen (LPP-PV-0043), and histological samples are deposited at the Laboratório de Paleoecologia e Paleoicnologia (LPP) of the Departamento de Ecologia e Biologia Evolutiva, Universidade Federal de São Carlos (UFSCar), São Carlos Municipality, São Paulo State, Brazil. The remaining referred specimens (MPMA 08-0049/01–02, 08-0060/07, 09-0001/99; MPPC 00-023, 02-005, 02-012, 02-013) are deposited in two institutions: Museu de Paleontologia de Monte Alto ‘Professor Antônio Celso de Arruda Campos’ (MPMA), Monte Alto Municipality, and Museu de Paleontologia ‘Pedro Candolo’ (MPPC), Uchoa Municipality, São Paulo State.

Geographic occurrence. The holotype was collected in a single outcrop (Figs. 1–2; see Figs. 4–5 in Supplementary Online Information), located at Sítio dos Irmãos Garcia (Garcia Brothers Farm), near the Washington Luis State Highway (SP-310) in Vila Ventura, Ibirá Municipality, north-eastern São Paulo State, Brazil. The referred specimens were collected in coeval levels (altimetric height equals 493 m) from outcrops around Vila Ventura District. GPS coordinates of these localities are deposited in their respective collections (LPP, MPMA, and MPPC) and are available upon request.

Stratigraphic occurrence. All individuals assigned to *Ibirania parva* were collected in brownish to pinkish layers of massive conglomeratic sandstones (Fig. 2). These facies are characterized by trough-cross bedding stratification and high carbonate cementation, with minor intercalation of mudstone lenses and shale pellets, typical of the São José do Rio Preto Formation (*sensu* Fernandes & Ribeiro, 2015; Menegazzo *et al.*, 2016; see Fig. 4 in Supplementary Online Information) and may comprise the lower level from this unit based on their stratigraphic correlations. Previous mi-

cropaleontological and correlated radiometric data constrain these horizons in a late Santonian to early Campanian age (Dias Brito *et al.*, 2001; Castro *et al.*, 2018; see Geological Settings in the Supplementary Online Information). Isotopic data suggest an arid to semi-arid paleoenvironment ($\delta^{18}\text{O} = -5.98$ and $\delta^{13}\text{C} = -6.26$; Dias Brito *et al.*, 2001).

Diagnosis. *Ibirania parva* represents a small-sized saltasaurine titanosaurian that can be distinguished from all other titanosaurian taxa by the following autapomorphies: (1) dorsal vertebrae with thick (almost “rod-shaped”) PRSL bearing an additional prominent crest at mid-height; (2) dorsal vertebrae with thick SPRL that surpasses half of PRSL height. In the anterior elements the SPRL extends parallelly to the PRSL, whereas in the posterior ones they

merge in the lateral surface of PRSL, not extending beyond their ventral end as a tripartite laminae; (3) posterior dorsal vertebrae with subparallel anterior SPDL and posterior SPDL, with the medial extremity of posterior SPDL projecting dorsally beyond the level of the anterior lamina, and forming a ventral contact with incipient aliform processes; (4) single CPRL in posterior dorsal vertebrae with expanded dorsal and ventral extremities, forming a thin anterolateral rim to the CPRF; (5) posterior dorsal vertebrae with a SPOL bearing two rami (med. SPOL and lat. SPOL), with the lateral one being forked due to the presence of an enlarged pneumatic foramen, forming two branches, and the medial one forming part of a median posterior ridge; (6) mid-caudal centra with a ventral hollow, but lacking longitudinal bony



Figure 2. Fossil-bearing site at Vila Ventura District, Ibirá Municipality, São Paulo State. **1**, general view of the outcrops in a pasture area and its various rock levels. The yellow star indicates the exact point where the holotypic specimen of *Ibirania parva* gen. et sp. nov. was recovered. The referred specimens were collected at the same stratigraphic level; **2**, rock section showing all lithofacies occurring in these outcrops; **3**, transition from Facies B2 (massive sandstones) to Facies A (conglomeratic sandstones) and its non-concordant contact; **4**, detail of Facies A (conglomeratic sandstones).

septa or ventrolateral ridges; (7) ulna bearing a distinctive muscular pit on the posteromedial surface of its distal half.

Our phylogenetic analysis further recovered the following additional potential autapomorphies: presence of the SPRL on entirely dorsal series (Char. 162 and 163: 0→1); divided CPOL on mid- and posterior dorsal neural arches (Char. 191: 0→1); mid- and posterior dorsal neural arches lacking the ACPL and PRPL (Chars. 192 and 193: 1→0); ventral contact of SPDL and SPOL in mid- and posterior dorsal neural arches (Chars. 203: 1→0); a med. SPOL present and forming part of the median posterior ridge on posterior dorsal neural arches (Char. 205: 0→1); laminar neural spine on posterior dorsal neural arches narrower transversely than anteroposteriorly (Char. 208: 2→0); anterior caudal centra ventrally convex (Chars. 233: 1→0); incipient ventral extension of the TPRL, not reaching the aperture of neural canal (Char. 428: 0→1).

Comparative diagnosis. *Ibirania parva* can be further distinguished from other South American titanosaurs by the following combination of plesiomorphic and apomorphic characters. Putative additional autapomorphies are marked with an asterisk (*). Some characters shared between the holotype and referred specimens are discussed, allowing the association of both materials as belonging to the same taxon.

The cervicodorsal vertebrae of *Ibirania parva* are characterized by their anteroposteriorly elongated centra (Tab. 1). The posteriormost cervical centrum bears a conspicuous dor-

sal notch in the cotyle, similar to the one found in *Europasaurus holgeri* Sander *et al.*, 2006 (Carballido & Sander, 2014) and *Rocasaurus muniozi* Salgado & Azpilicueta, 2000. Postzygapophyses of the posteriormost cervical vertebrae bear a stout “pillar-like” epiphysis but, like in other saltasaurines (e.g., *Rocasaurus muniozi*), apparently lack an EPRL, as present in other titanosaurs such as *Uberabatitan ribeiroi* Salgado & Carvalho, 2008 and *Brasilotitan nemophagus* Machado *et al.*, 2013 (Salgado & Azpilicueta, 2000; Silva Jr *et al.*, 2019). Like the posterior dorsal vertebrae, the posteriormost cervical vertebrae apparently possess a SPOL that is divided into two rami (med. SPOL and lat. SPOL) and presents a large dorsomedial pneumatic foramen in the anterior portion of the POCDF, as in *Saltasaurus loricatus* Bonaparte & Powell, 1980 and *Rocasaurus muniozi* (Zurriaguz & Powell, 2015).

The anterior dorsal vertebrae exhibit tapered and low neural spines, as in *Trigonosaurus pricei* Campos *et al.*, 2005, *Overosaurus paradasorum* Coria *et al.*, 2013, *Pitekunsaurus macayai* Filippi & Garrido, 2008, and *Muyelensaurus pecheni* Calvo *et al.*, 2007. However, in contrast to these taxa, the anterior dorsal vertebrae of *Ibirania parva* bear a well-developed SPRL and a broad and deeper POSF. The dorsal vertebrae referred to *Ibirania parva* possess a thick POSL along most of the posterior face of the neural spine, unlike *Uberabatitan ribeiroi* and *Isisaurus colberti* Jain & Bandyopadhyay, 1997. The anterior and posterior dorsal vertebrae of *Ibirania parva* also share a well-developed PODL but lack a

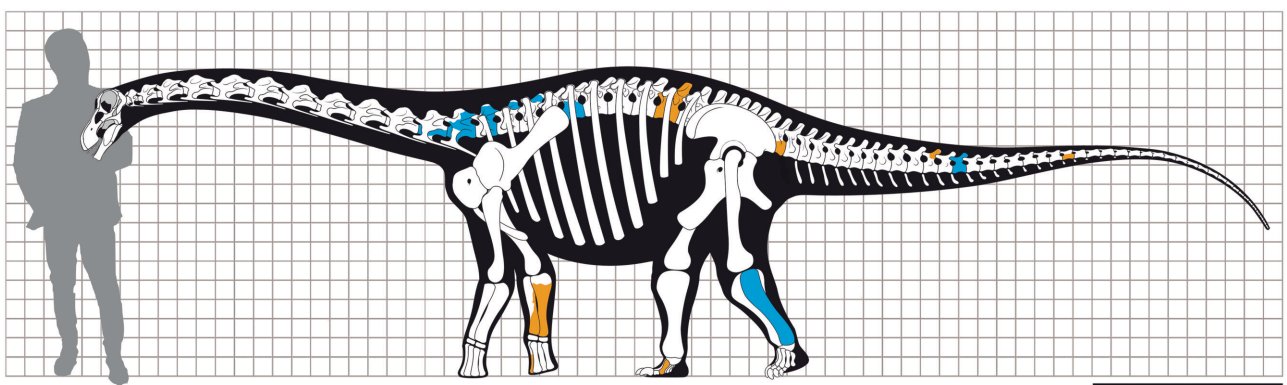


Figure 3. Skeletal reconstruction of *Ibirania parva* gen. et sp. nov., based on the body proportions of the holotypic specimen. Recovered bone elements (colored) and missing bones (white) were reconstructed through comparisons with closely related taxa. Color key: orange elements represent the holotype (LPP-PV-0200 to 0207*); blue elements represent the referred specimens (MPMA 08-0049/02, 08-0050/01, 08-0060/07, 09-0001/99; MPPC 02-005, 02-012, 00-013, 00-023). The asterisk marks a reversed element for a better visualization. Scale bar equals 1 m, human silhouette displays 1.8 m.

hyposphene-hypantrum complex and a dorsal notch on the cotyle. Unlike the posterior dorsal vertebrae, the PRSL and POSL of *Ibirania parva* anterior dorsal vertebrae bear smooth ventral bulges (*).

The posterior dorsal vertebra is characterized by lacking an ACPL (*), a PRPL (*), and bearing prezygapophyseal articular facets that tapers medioventrally (subtriangular in shape) (*), and sharp postzygapophyseal borders that taper dorsolaterally (*). Like *Trigonosaurus pricei*, a pronounced bulge is present below the TPRL, but in *Ibirania parva* it is more beveled anteriorly and pierced by a small foramen. The PPDL is slender and well-developed, as in *Bonatitan reigi* Martinelli & Forasiepi, 2004 and *Lirainosaurus astibiae* Sanz *et al.*, 1999 (Díez-Díaz *et al.*, 2013a; Salgado *et al.*, 2015). The aliform processes are rudimentary and are not formed by an extension of the SPDL, being more perpendicular in respect to the vertical axis of the neural spine. This condition differs from some titanosaurs, such as *Argentinosaurus huiculensis* Bonaparte & Coria, 1993, *Patagotitan mayorum* Carballido *et al.*, 2017, and *Saltasaurus loricatus* (Zurriaguz & Powell, 2015).

The lateral aspect of the neural spine is marked by pneumatic foramina, with an enlarged foramen present below the lat. SPOL, like the condition found in *Saltasaurus loricatus*. A deep and excavated POCDF is present, ventrally surrounded by an anterior expansion of the lat. CPOL that connects with the PCDL, a condition shared with posterior dorsal vertebrae referred to *Malawisaurus dixeyi* Jacobs *et al.* 1993 (Gomani, 2005) and CPPLIP 0494. A large “V-shaped” pneumatic foramen in the POCDF is present, as in *Saltasaurus loricatus*. Posterior dorsal vertebrae also display a columnar med. CPOL that is slightly forked on its dorsal portion by a median groove (*), like the anterior dorsal vertebrae of *Mendozasaurus neguyelap* González Riga, 2003 (González Riga *et al.*, 2018).

The first caudal centrum of *Ibirania parva* displays a biconvex-type articulation as observed in other saltasaurids, such as *Yamanasaurus lojaensis* Apesteguía *et al.*, 2020, *Neuquensaurus australis* Lydekker, 1893, *Alamosaurus sanjuanensis* Gilmore, 1922 (Gilmore, 1946), and *Baurutitan britoi* Kellner *et al.*, 2005. The first caudal centrum of *Ibirania parva* is anteroposteriorly elongated, differing from the condition present in cf. *Antarctosaurus wichmannianus* Huene, 1929 and *Pellegrinisaurus powelli* Salgado, 1996, which exhibit

anteroposteriorly shortened biconvex centra. Pneumaticity in the caudal series is like *Saltasaurus loricatus* and *Rocasaurus muniozi*, in which the internal somphospondylous tissue reaches the mid- to posterior elements (Zurriaguz & Cerda, 2017). The mid-caudal neural arches exhibit posterodorsally inclined neural spines, as in other saltasaurines, lacking the postzygapophyseal bony processes present in *Rinconosaurus caudamirus* Calvo & González Riga, 2003, *Muyelensaurus pecheni*, *Bonitasaura salgadoi* Apesteguía, 2004, and *Uberabatitan ribeiroi* (Gallina & Apesteguía, 2015).

The appendicular material of *Ibirania parva*, although fragmentary, displays robust profiles (Tab. 2), like other saltasaurids. The radius appears to expand distally, as in several macronarians (Upchurch *et al.*, 2015), and the ulna has a triradiate “D-shaped” cross section on mid-shaft. The lateral trochanter of the fibula is incipient and vertically placed (*), differently from other titanosaurs, such as *Laplatasaurus araukanicus* Huene, 1929 and *Uberabatitan ribeiroi* (Gallina & Otero, 2015).

Ontogenetic assessment. Holotypic and referred specimens of *Ibirania parva* are represented by skeletally mature individuals, based on morphological and osteohistological approaches. The ontogenetic assessment was established following the HOS parameters of Klein and Sander (2008) for long-bone tissue types, and the ‘three-front-model’ of Mitchell and Sander (2014) for ontogenetic maturity (see below).

DESCRIPTION AND COMPARISONS

Axial Skeleton

Posteriormost cervical vertebra. Referred posteriormost cervical vertebra (MPMA 08-0049/02; Fig. 4) is partially preserved, missing the anterior part of the neural spine, prezygapophyses, diapophyses, and most of the right side. The centrum, as preserved, is anteroposteriorly elongated (Tab. 1) and is distorted obliquely in the left side (Fig. 4.1–4.4). The condyle is abraded by transport before the complete burial, preserving in the right side only the internal surface of the pleurocoelic cavity and a small portion of the parapophysis, which is also visible in the anterior view (Fig. 4.1, 4.2). Laterally, the pleurocoelic cavities are present as deep fossae without well-defined edges, differing from the condition present in *Saltasaurus loricatus*. However, in the referred mid-to-posterior centrum (MPPC 02-012), it is

possible to observe a small well-defined pneumatopore on the left side. Additionally, MPPC 02-012 also preserves marked striations in the ventral path of the left fossa that extends laterally (see Fig. 6 in Supplementary Online Information), possibly related to the development of insertion points of diverticula. Internally, the somphospondylous tissue of both cervical elements is arranged into large “honeycomb-shaped” cells (Fig. 4.5; Fig. 6 in Supplementary Online Information). The ventral surface of the cervical centrum of MPMA 08-0049/02, although exhibiting an oblique distortion, is almost flat transversally (Fig. 4.6). Posteriorly and dorsally, the cotyle bears a well-marked dorsal notch.

The neural arch only preserves a portion of its left side (Fig. 4.1–4.4), displaying well-developed and thick laminae. Part of a stout and single CPRL is visible in anterior and lateral views and is strongly projected anterodorsally. However, it is not at the same level as the diapophyses as seen in *Saltasaurus loricatus* and *Neuquensaurus australis* (see Fig. 7 in Supplementary Online Information). The anterodorsal end of the prezygapophysis is not fully preserved, but apparently lacks the posteroventral processes on the lateral surface. A PRDF is present, exhibiting an “U-shaped” ventral outline. The extension of PRDF cannot be assessed due to the fragmentary condition of the dorsal end of the PRDL and the absence of preserved diapophyses. The left diapophysis, although not fully preserved, is supported by a thick ACDL and by a thickened posterior PCDL. The PCDL dorsally borders a longitudinally elongated and deep CDF, like *Trigonosaurus pricei* (see Fig. 7 in Supplementary Online Information). The PODL is damaged but, within the PCDL, delimit a deep and ellipsoid shaped POCDF. A tall foramen pierces the dorsomedial surface of the anterior portion of POCDF.

The preserved postzygapophysis extends posterolaterally to the cotyle edge (Fig. 4.2–4.4). The articular surface is anteroposteriorly broader than that of the preserved prezygapophysis and, as in *Rocasaurus muniozi*, the angle of articulation is posteroventrally oriented around 30° (see Fig. 7 in Supplementary Online Information). This condition differs from that in other saltasaurines, such as *Neuquensaurus australis* and *Saltasaurus loricatus*, in which the articular surfaces of postzygapophyses are strongly angled, reaching more than 45° (see Fig. 7 in Supplementary Online Information). Dorsally, the postzygapophysis bears a stout and pil-

lar-like epipophysis, but there are no signs of an EPRL, as in the posterior cervical vertebrae of *Saltasaurus loricatus* (PVL 4017-7). In turn, the postzygapophysis is connected to the preserved left lateral part of the neural spine by thick SPOL, which is split, as in dorsal elements (see below), into two segments: the lateral and medial SPOL. The former is visible only in the lateral aspect, whereas the latter is visible in both lateral and posterior views and probably contacts ventromedially with the TPOL. From below, the postzygapophysis is supported by a wide CPOL, which apparently becomes bifid dorsally, as in the dorsal elements. The medial ramus of the CPOL contacts the TPOL instead of the postzygapophysis, as in *Rocasaurus muniozi* (MPCA-Pv 859), but in *Ibirania parva* these laminae possibly create a paired TPOF (Fig. 4.4). The neural spine is very damaged, hampering major observations and comparisons of structure development, such as the POSL and the POSF.

Anterior dorsal vertebrae. Anterior dorsal elements of *Ibirania parva* include two neural arch fragments (MPPC 02-013 and MPPC 00-023; see Fig. 8 in Supplementary Online Information) and a partially preserved anteriormost dorsal vertebra (MPMA 08-0050/01; Fig. 5). The position of these partial neural arches was established through the preserved laminae and the general shape. MPPC 02-013 and MPPC 00-023 only preserve the anterior part, lacking most of the neural spines. MPMA 08-0050/01 lacks the left anteroventral region of the centrum, portions of the neural spine, and transverse processes. Both were designated as referred specimens of *Ibirania parva*, because they exhibit some of the autapomorphies present in the posterior dorsal material of the holotype (LPP-PV-0200).

The anterior surface of MPPC 02-013 and MPPC 00-023 preserves a thick PRSL, as seen in *Notocolossus gonzalezparejasi* (González Riga *et al.*, 2016). This lamina extends through the entire neural spine in both elements, and in MPPC 00-023, it is accompanied by prominent SPRLs, as in *Uberabatitan ribeiroi* (Silva Jr *et al.*, 2019). However, in *Ibirania parva* the SPRL are closer to the PRSL than in other titanosaurs (see Fig. 9 in Supplementary Online Information). Above the SPRL, an incipient crest can be observed on the PRSL of MPPC 02-013 (Fig. 7 in Supplementary Online Information). In MPPC 02-013, the ventral portion of PRSL increases into a broad profile, as in MPMA 08-0050/01 and in *Patagotitan mayorum*, differing

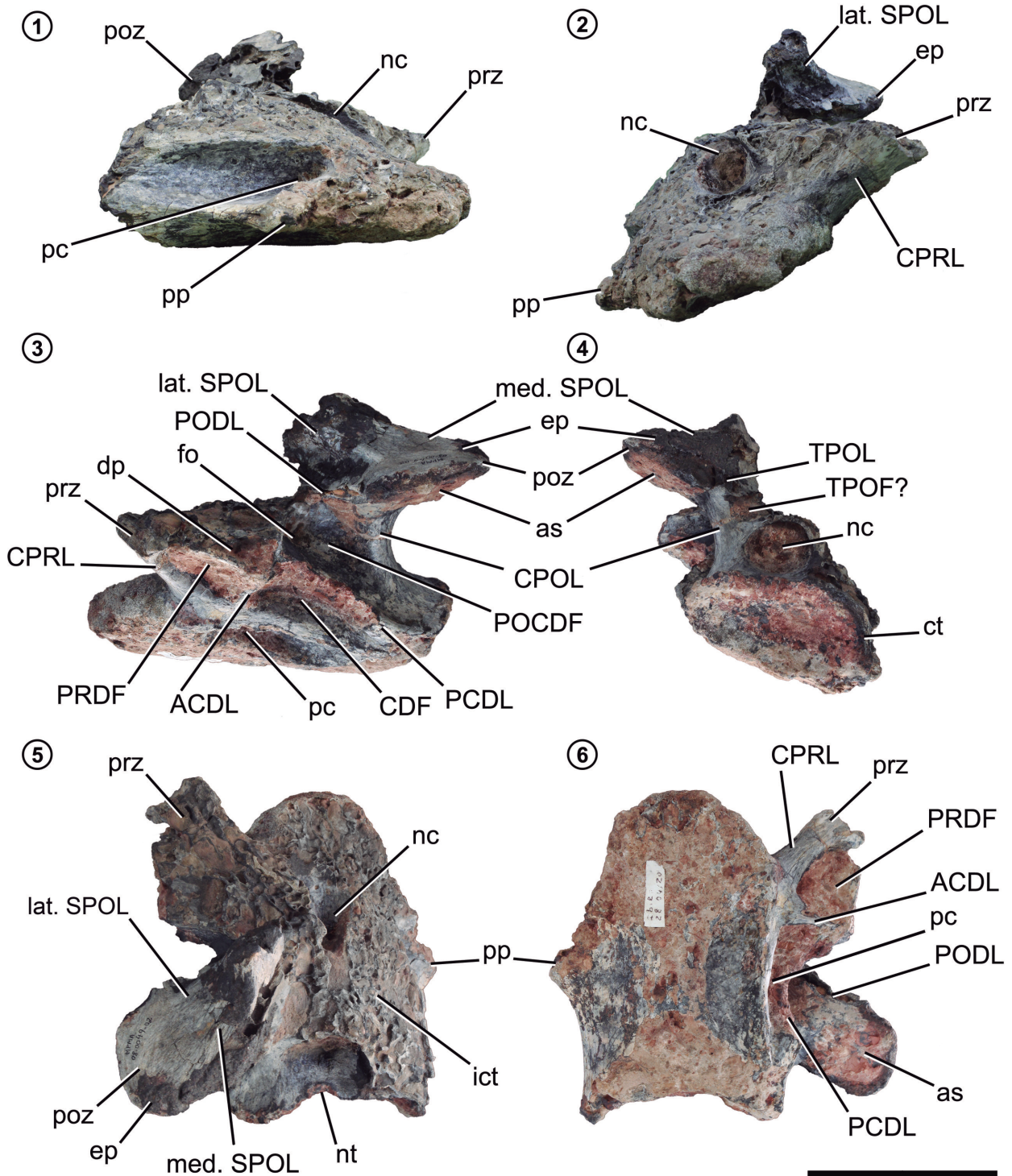
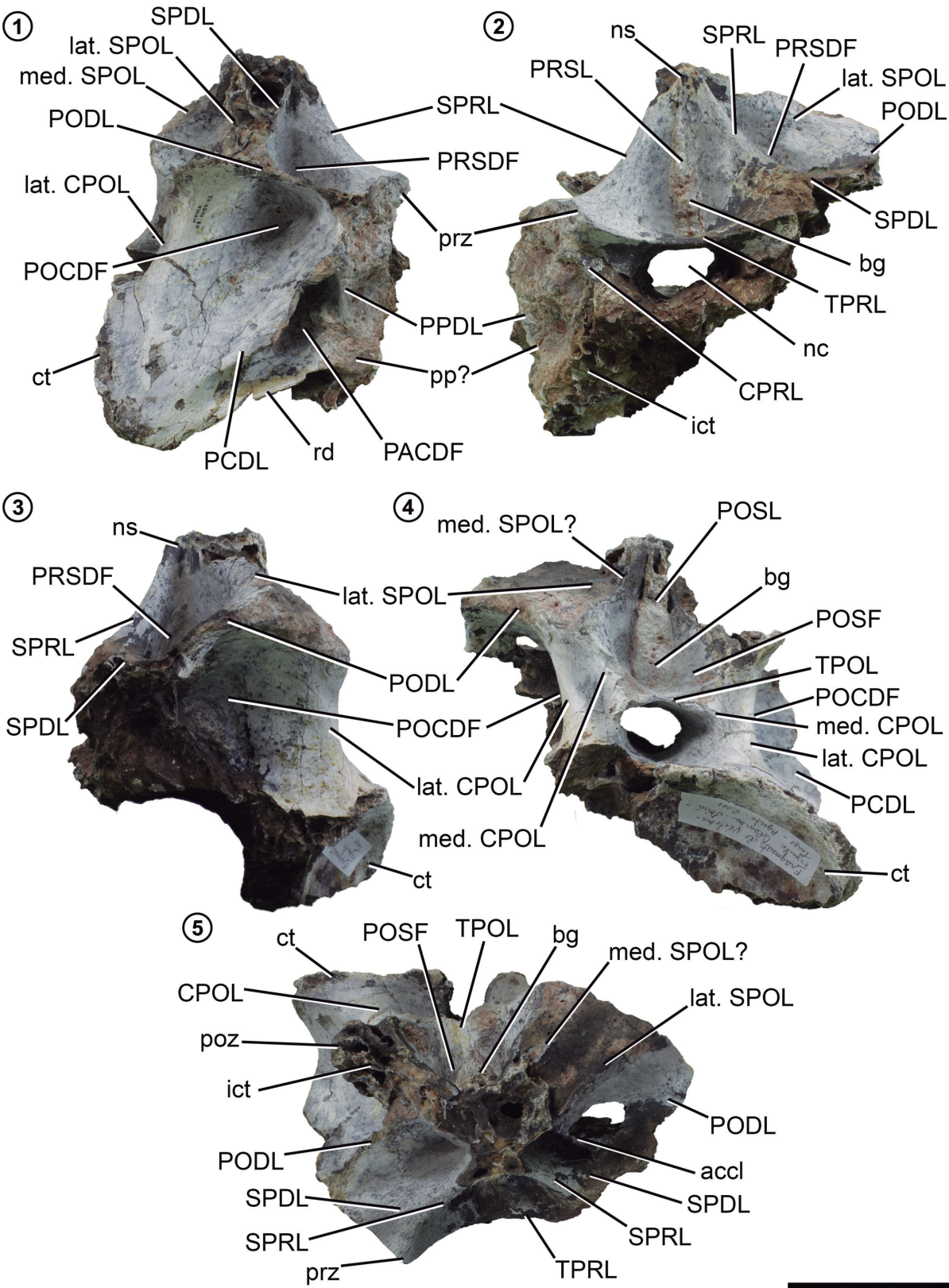


Figure 4. Referred posteriormost cervical vertebra of *Ibirania parva* gen. et sp. nov. (MPMA 08-0049-02). 1, right lateral view; 2, anterior view; 3, left lateral view; 4, posterior view; 5, dorsal view; 6, ventral view. Anatomical abbreviations: ACDL, anterior centrodiapophyseal lamina; as, articular surface; CDF, centrodiapophyseal fossa; CPOL, centropostzygapophyseal lamina; CPRL, centroprezygapophyseal lamina; ct, cotyle; dp, diapophysis; ep, epiphysis; fo, foramen; ict, internal camellate tissue; lat. SPOL, lateral spinopostzygapophyseal lamina; med. SPOL, medial spinopostzygapophyseal lamina; nc, neural canal; nt, notch; pc, pleurocoel; PCDL, posterior centrodiapophyseal lamina; POCDF, posterior centrodiapophyseal fossa; PODL, postzygodiapophyseal lamina; poz, postzygapophysis; pp, parapophysis; PRDF, prezygodiapophyseal fossa; prz, prezygapophysis; TPOL, intrapostzygapophyseal lamina; TPOF, intrapostzygapophyseal fossa. Scale bar equals 10 cm.



from the tripartite condition of *Mendozasaurus neguyelap* (González Riga *et al.*, 2018). Only a small part of the SPDL is preserved on both neural arches, showing that the neural spine, although not fully preserved, possesses subparallel lateral margins that slightly converge on the dorsal end. In addition, the SPDL shows no signs of split on its preserved portion, with diapophyses developing slightly laterally than upward as in *Trigonosaurus pricei* and *Overosaurus paradasorum* (Campos *et al.*, 2005; Coria *et al.*, 2013).

The most complete anterior dorsal (MPMA 08-0050/01) represents either the first or second dorsal vertebra, given that its parapophysis stands slightly above the level of the preserved anterior margin of the pleurocoel (Fig. 5.1). Except for a minor part of the right lateral side, the centrum is strongly displaced to the right side and crushed sagittally, revealing the “honeycomb-like” internal tissue with large cells. The zygapophyses and diapophyses are not preserved, but their probable positions can be assessed through associated laminae. The prezygapophyses are bounded by a sharp and thin TPRL that is well developed anteriorly (Fig. 5.2, 5.5). Ventrally, a thick single CPRL is preserved on the right side, bordering a shallow CPRF. This condition differs from that present in *Saltasaurus loricatus*, in which the CPRL is divided into two distinct rami (*i.e.*, lat. CPRL and med. CPRL; see Fig. 9 in Supplementary Online Information). Posterodorsally, the prezygapophyses are linked to the neural spine by a strongly developed SPRL, which accompanies the curvature of the neural spine (Fig. 5.2). Together with the SPRL, the PODL and lateral SPOL delimit a broad and deep PRSDF (Fig. 5.3), which on the left side is internally divided by a small accessory lamina (Fig. 5.4) that connects the lateral SPOL to the possible medial end of the SPDL. This laminae-fossae pattern could be homologous to the condition seen in the mid-cervical vertebrae of *Rapetosaurus krausei*, *Uberabatitan ribeiroi*, and DGM Series A (MCT 1487-

R), in which the EPRL extends across the SDF and divide it into two secondary depressions (Curry Rogers, 2009; Wilson, 2012; Silva Jr *et al.*, 2019). However, this accessory lamina has an asymmetrical development, and the absence of other axial elements sharing its presence hampers a better assessment of how this feature develops along the dorsal series.

The transverse processes are not preserved, except for the right parapophysis. A sharp ridge extends posteriorly to the parapophysis and reaches the ventrolateral margin of the cotyle (Fig. 5.1), as in the first dorsal vertebra of *Trigonosaurus pricei* and MCT 1487-R. However, this could represent a taphonomical artifact due to the extremely damaged condition displayed by the preserved centrum and could be related to the anterodorsal margin of the pleurocoel. In lateral view, a very damaged vertical PPDL is present, bounding a deep, triangular-shaped PACDF with the PCDL and posteroventral ridge of the parapophysis. The PCDL is present as a slender lamina that develops also posteroventrally, above the posteroventral ridge of the parapophysis. The PODL are strongly laterally developed, forming an extensive posterodorsal roof to the POCDF (Fig. 5.3–5.5). This fossa is trapezoidal in shape, and extremely deep on its medial face. No evident signs of a SPDL are observable on its proximal end. Nonetheless, the SPRL appears to widen distally, and appears bifurcated into a posterior ramus that could correspond to a SPDL (Fig. 5.5).

The neural spine appears to lack only its dorsal surface (Fig. 5.2, 5.5), displaying lateral margins that gently curve toward its dorsal end and creating a tapered and low profile to the neural spine like the one present in *Trigonosaurus pricei*, *Notocolossus gonzalezparejasi*, and other titanosaurs (see Fig. 9 in Supplementary Online Information). However, the neural spine in *Ibirania parva* apparently does not strongly project posteriorly as in these taxa, resembling more the

Figure 5. Referred anteriormost (first or second) dorsal vertebra of *Ibirania parva* gen. et sp. nov. (MPMA 08-0050-01). 1, right lateral view; 2, anterior view; 3, left lateral view; 4, posterior view; 5, dorsal view. Anatomical abbreviations: **accl**, accessory lamina; **bg**, bulge; **CPRL**, centro-prezygapophyseal lamina; **ct**, cotyle; **ict**, internal camellate tissue; **lat. CPOL**, lateral centropostzygapophyseal lamina; **lat. SPOL**, lateral spinopostzygapophyseal lamina; **med. CPOL**, medial centropostzygapophyseal lamina; **med. SPOL**, medial spinopostzygapophyseal lamina; **nc**, neural canal; **ns**, neural spine; **PACDF**, parapophyseal-centrodiapophyseal fossa; **PCDL**, posterior centrodiapophyseal lamina; **POCDF**, postzygapophyseal-centrodiapophyseal fossa; **PODL**, postzygodiapophyseal lamina; **POSF**, postspinal fossa; **POSL**, postspinal lamina; **poz**, postzygapophysis; **pp**, parapophysis; **PPDL**, paradiapophyseal lamina; **PRSDF**, prezygapophyseal-spinodiapophyseal fossa; **PRSL**, prespinal lamina; **prz**, prezygapophysis; **rd**, ridge; **SPDL**, spinodiapophyseal lamina; **SPRL**, spinoprezygapophyseal lamina; **TPOL**, intrapostzygapophyseal lamina; **TPRL**, intraprezygapophyseal lamina. Scale bar equals 10 cm.

straight condition present in *Isisaurus colberti* (Jain & Bandyopadhyay, 1997) and saltasaurines (Zurriaguz & Powell, 2015). A stout PRSL is present through the entire extension of the neural spine. This lamina slightly expands ventrally in a smooth ellipsoid bulge as in *Patagotitan mayorum* (see Fig. 9 in Supplementary Online Information). Likewise, the posterior surface of the neural spine bears a stout POSL along all its height, also displaying a bulge that increases ventrally and a broad elliptical POSF with its ventral surface extending close to the cotyle margin due to a strong development of the TPOL (Fig. 5.4, 5.5).

As with the last cervical and posterior dorsal elements, the CPOL is dorsally divided into lateral and medial rami in the anterior dorsal vertebra. The postzygapophyses are not fully preserved in this element, but the lateral CPOL extends ventrolaterally below their insertion point. In turn, the medial CPOL extends posterodorsally and merges with the TPOL. The CPOL split in *Ibirania parva* differs from that present in other titanosaurs, such as *Mendozasaurus neguyelap*. In *Ibirania parva* the bipartite CPOL lacks a fossa between its medial and lateral rami, which the medial being more developed than the lateral ramus (Fig. 5.4). By contrast, in *Mendozasaurus neguyelap* the split is marked with the development of a small triangular fossa which, although it occurs asymmetrically, the lateral branch is more developed than the medial one. The SPOL is very damaged but appears to be stout. In dorsal view this lamina also is divided into two segments, with the lateral ramus being visible anteriorly and laterally, whereas the medial one is visible only in posterior view and approaches the dorsal extremity of the POSL.

Posterior dorsal vertebrae. Two mid-to-posterior dorsal elements were recovered, including a referred centrum (MPPC 02-015; Fig. 10 in Supplementary Online Information) and the near-complete holotypic vertebra (LPP-PV-0200; Fig. 6). As observed in several other titanosaurs, the mid-to-posterior dorsal centra of *Ibirania parva* are higher than wide in cross section, compressed transversely, strongly opisthocelous, and anteroposteriorly elongated (Fig. 6.1, 6.3, 6.6). This morphology differs from some Brazilian titanosaurs (e.g., *Tapuiasaurus macedoi*), which display mid- to posterior dorsal centra that are as wide as high and anteroposteriorly short (Zaher *et al.*, 2011). The cotyle in *Ibirania parva* possesses a sub quadrangular out-

line (Fig. 6.4) differing from the circular shape present in some saltasaurine titanosaurs (e.g., *Saltasaurus loricatus*, *Rocasaurus muniozi*). However, mid- to posterior dorsal centra of *Ibirania parva* lacks the strong dorsoventral compression shared by several Brazilian titanosaurs, such as *Trigonosaurus pricei* and *Uberabatitan ribeiroi* (Campos *et al.*, 2005; Salgado & Carvalho, 2008). In addition, *Ibirania parva* mid- to posterior dorsal centra lack a ventral keel (Fig. 6.6) as in *Barrosasaurus casamiquelai* (Salgado & Coria, 2009). As in other titanosaurs, the mid- to posterior dorsal centra exhibit the characteristic narrow and deep pneumatopores with acuminate posterior border (Fig. 6.1, 6.3), which are enclosed medially by a thin bony septum (Fig. 11 in Supplementary Online Information). The left surface of the posterior dorsal centrum is partially eroded, allowing the observation of a highly pneumatized internal tissue with a complex somphospondylous system, which the trabeculae of the internal cells are formed by typical spongy bone tissue (Fig. 11 in Supplementary Online Information).

The neural arch pedicel height on LPP-PV-0200, from the dorsal border of the cotyle until to the ventral limit of the TPOL, is subequal than to centrum height (Fig. 6.4). The neural spine is relatively low and strongly inclined relative to the vertical axis of the vertebra (*ca.* 45°), in which its posterodorsal tip surpasses the level of the cotyle edge (Fig. 6.5). In addition, the lateral surface of the neural spine features a series of small pneumatic wrinkles (Fig. 11 in Supplementary Online Information). The distal parts of the diapophyses and parapophyses are not preserved, and the left prezygapophysis is missing. The right prezygapophysis is damaged anteriorly, but it preserves an expanded laminar border on the articular surface, like the condition present in dorsal vertebrae attributed to *Malawisaurus dixeyi* (Gomani, 2005). However, in *Ibirania parva* that laminar border tapers medially (Fig. 6.3) whereas in *Malawisaurus dixeyi* it has a rounded outline. Hyposphene-hypantrum articulations are not present in *Ibirania parva* (Fig. 6.2).

In anterior view, the prezygapophysis is ventrally supported by a thin and sharply developed CPRL that widens both ventrally and dorsally. This lamina smoothly merges ventrally to the prezygapophysis and forms an accentuated lateral rim for the CPRF (Fig. 6.2, 6.3; see Fig. 11 in Supplementary Online Information). This pattern appears to be unique to *Ibirania parva*, because other titanosaurs ex-

hibit restricted CPRF above the neural canal (e.g., *Uberabatitan ribeiroi*, *Maxakalisaurus topai*, *Tapuiasaurus macedoi*; Fig. 12 in Supplementary Online Information). The CPRF in these taxa is developed between a dorsal splitting of CPRL, where its lateral ramus is expanded laterally, sometimes merging with the ACPL – absent on the posterior dorsal of *Ibirania parva* – and contacting below prezygapophyses. By contrast, the medial ramus connects to a ventral ramus of the TPRL above the neural canal or directly ventrally to the

prezygapophyses, as in the unnamed titanosaurian DGM 775-R and *Barrosasaurus casamiquelai*. *Ibirania parva* likewise differs from the condition shared by *Lirainosaurus astibiae*, *Trigonosaurus pricei*, *Overosaurus paradasorum*, *Muyelensaurus pecheni*, and, in part, *Bonitasaura salgadoi*, in which the CPRL and the ventral ramus of TPRL do not fully enclose the CPRF laterally and medially (see Fig. 12 in Supplementary Online Information). *Ibirania parva* CPRL-CPRF morphology also differs from the condition, present in *Opisthocoelicaudia*

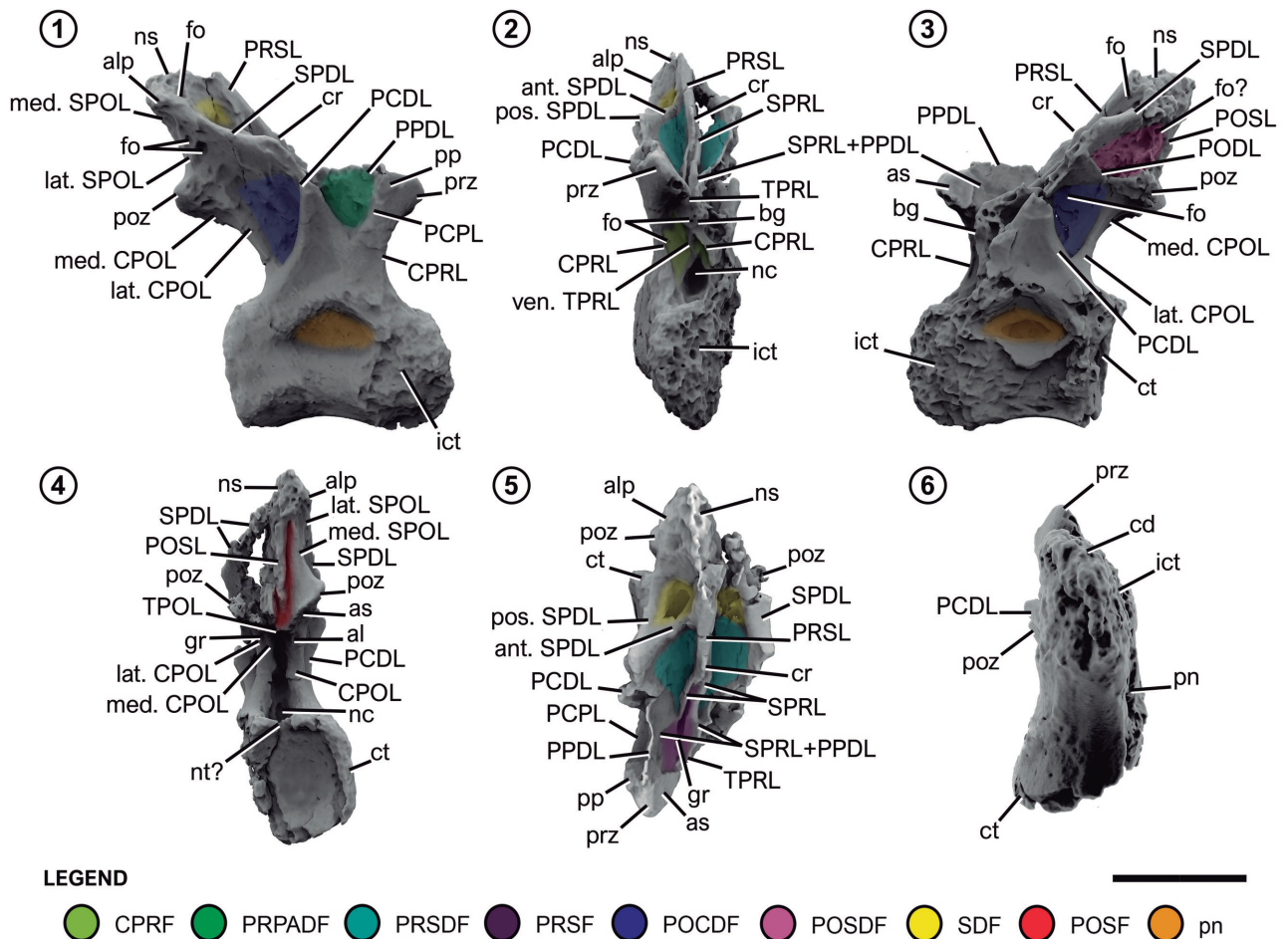


Figure 6. Posterior dorsal vertebra of *Ibirania parva* gen. et sp. nov. holotype (LPP-PV-0200). 1, right lateral view; 2, anterior view; 3, left lateral view; 4, posterior view; 5, dorsal view; 6, ventral view. Anatomical abbreviations: **al**, additional lamina; **alp**, aliform process; **ant. SPDL**, anterior spinodiapophyseal lamina; **as**, articular surface; **bg**, bulge; **cr**, crest; **CPRF**, centroprezygapophyseal lamina; **CPRL**, centroprezygapophyseal lamina; **ct**, cotyle; **fo**, foramina; **gr**, groove; **ict**, internal camellate tissue; **lat. CPOL**, lateral centropostzygapophyseal lamina; **lat. SPOL**, lateral spinopostzygapophyseal lamina; **nc**, neural canal; **nt?**, notch; **ns**, neural spine; **med. CPOL**, medial centropostzygapophyseal lamina; **med. SPOL**, medial spinopostzygapophyseal lamina; **PCDL**, posterior centrodiapophyseal lamina; **PCPL**, posterior centroparapophyseal lamina; **pn**, pneumatopore; **POCDF**, postzygapophyseal-centrodiapophyseal fossa; **PODL**, postzygodiapophyseal lamina; **POSDF**, postzygapophyseal-spinodiapophyseal fossa; **POSF**, postspinal fossa; **POSL**, postspinal lamina; **pos. SPDL**, posterior spinodiapophyseal lamina; **poz**, postzygapophysis; **pp**, parapophysis; **PPDL**, paradiapophyseal lamina; **PRPADF**, prezygapophyseal-paradiapophyseal fossa; **PRSDF**, prezygapophyseal-spinodiapophyseal fossa; **PRSF**, prespinal fossa; **PRSL**, prespinal lamina; **prz**, prezygapophysis; **SDF**, spinodiapophyseal fossa; **SPRL**, spinoprezygapophyseal lamina; **TPRL**, ventral intraprezygapophyseal lamina; **TPOL**, intrapostzygapophyseal lamina; **ven. TPRL**, ventral ramus of the intraprezygapophyseal lamina. Scale bar equals 10 cm.

skarzynskii, *Epachthosaurus sciuttoi*, *Dreadnoughtus schrani*, and *Elaltitan lilloi*, which the CPRL and ACPL are merged in a thick single lamina that forms pedicels in the neural arch, resulting in a deeper undivided CPRF (Fig. 12 in Supplementary Online Information). On the other hand, some titanosaurs from Peirópolis (CPPLIP-0035) and saltasaurines such as *Neuquensaurus australis* and *Saltasaurus loricatus* exhibit a similar morphology to *Ibirania parva*, differing by the CPRL developed that are widened and flat, as well as in the presence of a ventral ramus of the TPRL and/or additional internal pneumatopores on CPRF (see Fig. 12 in Supplementary Online Information).

The lateral borders of the neural canal in *Ibirania parva* are laminar, but there is no contact with the ventral ramus of the TPRL. The latter slightly extends vertically above the neural canal and ends dorsally in a “pendant-shaped” bulge, which is anteriorly flattened and pierced by a small foramen. The dorsal ramus of the TPRL extends posteriorly, where it becomes the border for a single and medially placed elongated sulcus that extends anteroventrally to the PRSL. Additionally, the dorsal surface of the TPRL converges with the posterior end of the SPRL, forming accessory laminae in both sides of the PRSL. These accessory PRSL does not expand laterally from its ventral portion – as in *Uberabatitan ribeiroi* – but extends over half of its length (see Fig. 11 in Supplementary Online Information). The PRSL is well developed and robust, almost “rod-shaped”, bearing a rugose crest at its mid-height (Fig. 6.2, 6.5). This morphology is interpreted here as another autapomorphic condition of *Ibirania parva*. Like the PRSL, the POSL is thick and is present along the entire height of the neural spine.

Parapophyses and diapophyses are incomplete, but their position can be inferred from associated laminae. The latter project more dorsally than dorsolaterally, as in other saltasaurines (Zurriaguz & Powell, 2015). As mentioned above, the ACPL is absent, whereas the PCPL is well-developed and extends posteriorly close to the dorsal margin of cotyle, like the anterior dorsal vertebrae (MPMA 08-0050/01). The PCPL with the PCDL delineates a deeper PRPADF, as in *Bonatitan reigi* (Salgado *et al.*, 2015), and is medially surrounded by a thin and well-developed PPD. Ventral to this fossa, the surface is mostly flat and featureless. The diapophyses are supported by a robust PCDL. The anterior portion extends anteroventrally but does not

reach the dorsal border of the centrum. The posterior ramus is highly conspicuous and projects anterodorsally from the posterior border of the centrum. It is softly curved and then becomes straighter dorsally, closer to the diapophysis, with its lateral surfaces almost flat. A shallow depression is present on the widened end of the PCDL (Fig. 6.1, 6.3), differing from the condition present in other saltasaurines, such as *Saltasaurus loricatus*, *Neuquensaurus australis*, and *Rocasaurus muniozi*, which possess an excavated CDF (Zurriaguz & Powell, 2015).

The SPDL is bifurcated, as in several lithostrotians (*e.g.*, *Bonitasaura*, *Rapetosaurus*), exhibiting an anterior and a posterior ramus (Salgado *et al.*, 1997; Salgado & Powell, 2010). The split of SPDL occurs proximally, differing from some taxa such as *Trigonosaurus pricei*, which an incipient split occurs nearer to the diapophyses than to the neural spine. In *Ibirania parva*, both SPDL rami are robust and border a dorsally opened and deep SDF, unlike other saltasaurines such as *Neuquensaurus australis* and *Saltasaurus loricatus*. The anterior ramus of the SPDL is closely appressed to the neural spine, and then extends laterally, converging with the posterior ramus of the SPDL. In turn, the posterior ramus projects more posterodorsally than the anterior one, interpreted here as an autapomorphic condition (Fig. 6.2). Its medial end is curved ventrally to an incipient aliform process, without contribution to the latter. The aliform process is reduced and damaged, but its base seems oriented perpendicular to the neural spine axis (Fig. 6.1). Laterally the main SPDL is almost horizontal, bearing a convex dorsal surface.

The postzygapophysis has a wide articular surface. Its posterior border tapers and slightly curves dorsally, forming a sharp posterior corner (Fig. 6.1). *Ibirania parva* possesses two SPOLs, medially and laterally contacting the postzygapophysis to the neural spine. Paired SPOL are typical of non-titanosaurian sauropods, such as rebbachisaurids (Wilson, 1999, 2012), but can also appear in some titanosaurs (*e.g.*, *Lirainosaurus astibiae*, *Bonitasaura salgadoi*). In *Ibirania parva* the medial lamina, with the POSL, forms a restricted POSF shaped as a vertical trough (Fig. 11 in Supplementary Online Information). The lateral lamina bifurcates dorsally, into rami directed anterodorsally in an area marked by pneumatic wrinkles (Fig. 6.1, 6.4). This split is produced by the development of an enlarged pneumatic foramen anteriorly and between the lat. SPOL ramus (Fig.

11 in Supplementary Online Information). The TPOL, although is not fully preserved, appears to exhibit a nearly “U-shape” and projects posteriorly as far the postzygapophyses.

Ibirania parva displays a thin PODL, which is preserved only on the left side (Fig. 6.1, 6.3). This lamina is present in *Andesaurus delgadoi*, *Epachthosaurus sciuttoii*, *Rapetosaurus krausei*, *Overosaurus paradasorum*, *Neuquensaurus australis*, and *Saltasaurus loricatus* (Salgado et al., 2005; Salgado & Powell, 2010; Zurriaguz & Powell, 2015), but absent in *Opisthocoelicaudia skarzynskii*, *Muyelensaurus pecheni*, *Ampelosaurus atacis*, *Lirainosaurus astibiae*, *Rocasaurus muniozi*, and *Bonatitan reigi*.

As in the posteriormost cervical and anteriormost dorsal vertebrae, the medial CPOL are dorsally bipartite, but in the mid- to posterior dorsal vertebra the laminae development is asymmetric (Fig. 6.4). In the left medial CPOL, the lateral and medial rami are equally developed and separated by a shallow vertical groove. However, a conspicuous additional ridge between the two rami marks the right medial CPOL complex. The medial CPOL are straight, delimiting a single and deep CPOF. Unfortunately, the fragmentary condition of this fossa prevents the confirmation of a ventral ramus of the TPOL, as present in *Bonitasaura salgadoi*, *Rocasaurus muniozi*, and *Bonatitan reigi*. The lateral CPOL forms a prominent rim through most of its length, but it expands anteroventrally and merges with the posterodistal end of the PCDL, forming a continuous ventral ridge to the POCDF, as in *Malawisaurus dixeyi*. With the PODL, the PCDL and the lateral CPOL delimit a ventrally excavated POCDF. In *Ibirania parva* the POCDF is better preserved on the left side of the neural arch, where it shows an enlarged “V-shaped” foramen anteroventral to the PODL (Fig. 6.3), a feature only shared with *Saltasaurus loricatus*. The absence of such foramen on the right side of the neural arch could be explained either by asymmetric development or by the collapse of the PODL due to the lateral diagenetic compression. The presence of several foramina along the cervicodorsal neural arches and the complex camellate pattern in the centra indicate strong pneumaticity in *Ibirania parva*.

Caudal vertebrae. Four caudal vertebrae were associated with the *Ibirania parva*: three (LPP-PV 0204–0206) were recovered with the rest of the material assigned to the holotype and one (MPMA 08-0060/07) was found in adjacent

outcrops. The latter shares with the holotype of *Ibirania parva* a short prezygapophysis and a low, posterodorsally projecting neural spine, differing in that way from other caudal morphotypes from the same unit (Navarro et al., unpublished data).

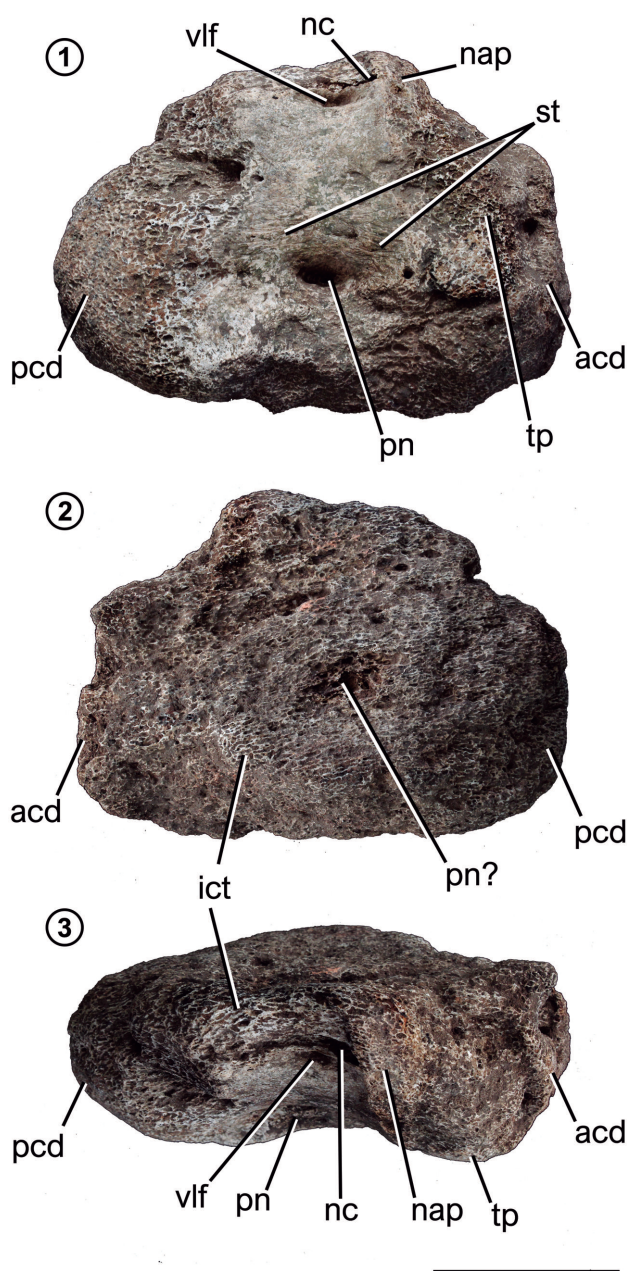


Figure 7. Biconvex first caudal centrum of *Ibirania parva* gen. et sp. nov. holotype (LPP-PV-0204). 1, right lateral view; 2, left lateral view; 3, dorsal view. Anatomical abbreviations: acd, anterior condyle; ict, internal camellate tissue; nap, neural arch pedicel; nc, neural canal; pcd, posterior condyle; pn, pneumatopore; st, striae; tp, transverse process; vlf, ventrolateral fossa. Scale bar equals 10 cm.

LPP-PV-0204 (Fig. 7) consists of a partially preserved first caudal centrum (or last sacral according to D’Emic & Wilson, 2011). This element possesses a biconvex articulation, as in *Neuquensaurus australis*, *Antarctosaurus wichmanianus*, *Alamosaurus sanjuanensis*, *Pellegrinisaurus powelli*, and *Baurutitan britoi*. The giant titanosaurian *Dreadnoughtus schrani* has been also interpreted as possessing a biconvex centrum in the first caudal vertebra (Lacovara *et al.*, 2014), but the presence of wide ventrolateral transverse processes and a flat anterior portion of the centra suggest that this element in fact corresponds to a non-biconvex sixth sacral vertebra. In addition, the preserved sacrum of *Dreadnoughtus schrani* was recovered articulated to its caudal series and displays only five sacral elements (see supplementary figures 13 and 14 of Lacovara *et al.*, 2014).

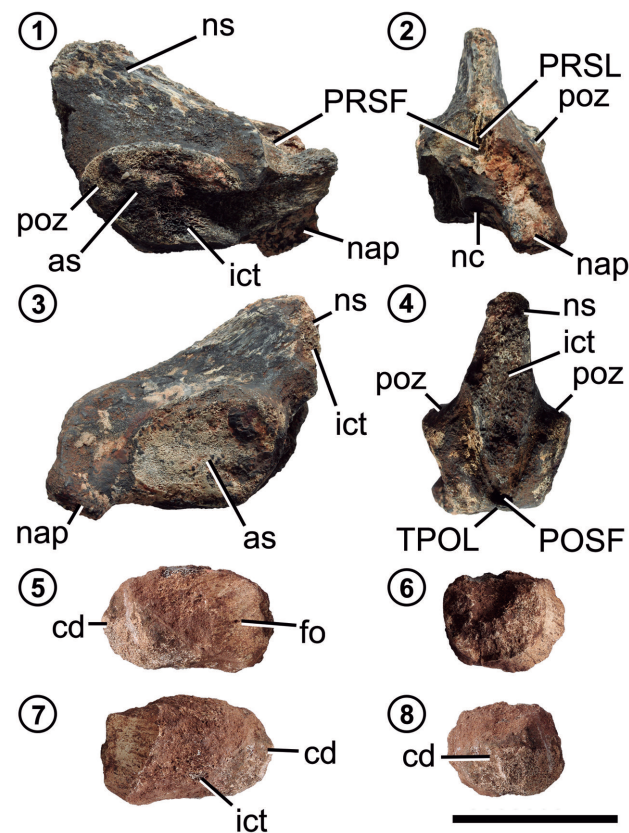


Figure 8. Partial middle caudal neural arch and posterior caudal centrum of *Ibirania parva* gen. et sp. nov. holotype (LPP-PV-0206 and LPP-PV-0205, respectively). 1, 5, right lateral view; 2, 6, anterior view; 3, 7, left lateral view; 4, 8, posterior view. Anatomical abbreviations: as, articular surface; cd, condyle; fo, foramen; ict, internal camellate tissue; nap, neural arch pedicel; nc, neural canal; ns, neural spine; POSF, postspinal fossa; poz, postzygapophysis; PRSF, prespinal fossa; PRSL, prespinal lamina; TPOL, intrapostzygapophyseal lamina. Scale bar equals 5 cm.

The first caudal centrum *Ibirania parva* shares with *Saltasaurus loricatus* a small pneumatopore on the lateral surface of the centra (Fig. 7.1), indicating a conspicuous internal pneumatization on anterior caudal vertebrae (Zurriaguz & Cerda, 2017). Dorsally, the pneumatopore bears several smooth stripes, which may be associated with the development of diverticula. The left lateral side is badly preserved (Fig. 7.2), allowing the view of a somphospondylous internal tissue with small-sized cells. Most of the neural arch is absent due to recent weathering (Fig. 7.1, 7.3), preserving solely a damaged ventral end of transverse processes on the right side and parts of the neural arch pedicel, where neurocentral joints are not visible in the periosteum. The preserved part of neural arch pedicel bears a conspicuous lateral fossa with a rounded shape. Although damaged, the centrum also displays a marked constriction at its mid-length (Fig. 7.3).

The holotypic middle neural arch (LPP-PV-0206) only preserves its dorsal portion, lacking the prezygapophyses (Fig. 8). In anterior view, a marked PRSF is present bearing an incipient ventral PRSL. The neural spine is low, transversely compressed and strongly posterodorsally projected as in other saltasaurines (Fig. 8.1, 8.3). Posteriorly, the neural spine displays a broad POSF that is filled by a wide POSL on the entire preserved dorsoventral extension (Fig. 8.4), as in *Saltasaurus loricatus*, *Bonatitan reigi* (Martinelli & Forasiepi, 2004; Zurriaguz & Cerda, 2017), and MPMA 08-0060/07. The postzygapophyses are flat, lacking postzygapophyseal bony processes and laterally developed hyposphenal ridges.

The partial posterior centrum (LPP-PV-0205) is badly preserved, lacking most of its anterior portion and the whole neural arch (Fig. 8.5, 8.8). As in MPMA 08-0060-07, the centrum is strongly procoelous and as wide as high, slightly dorsoventrally compressed (quadrangular in shape). Unlike some saltasaurines such as some *Neuquensaurus* specimens, which have an internal pneumatization in the caudal series restricted to the middle caudal elements, in *Ibirania parva* this pattern appears to reach the most posterior elements. LPP-PV-0205 preserves a somphospondylous internal tissue similar to that in *Saltasaurus loricatus* and *Rocasaurus muniozi* (Zurriaguz & Cerda, 2017).

The referred mid- to posterior caudal element (MPMA 08-0060/07) is nearly complete (Fig. 9). The centrum has a quadrangular shape (as wide as high) in anterior view, being

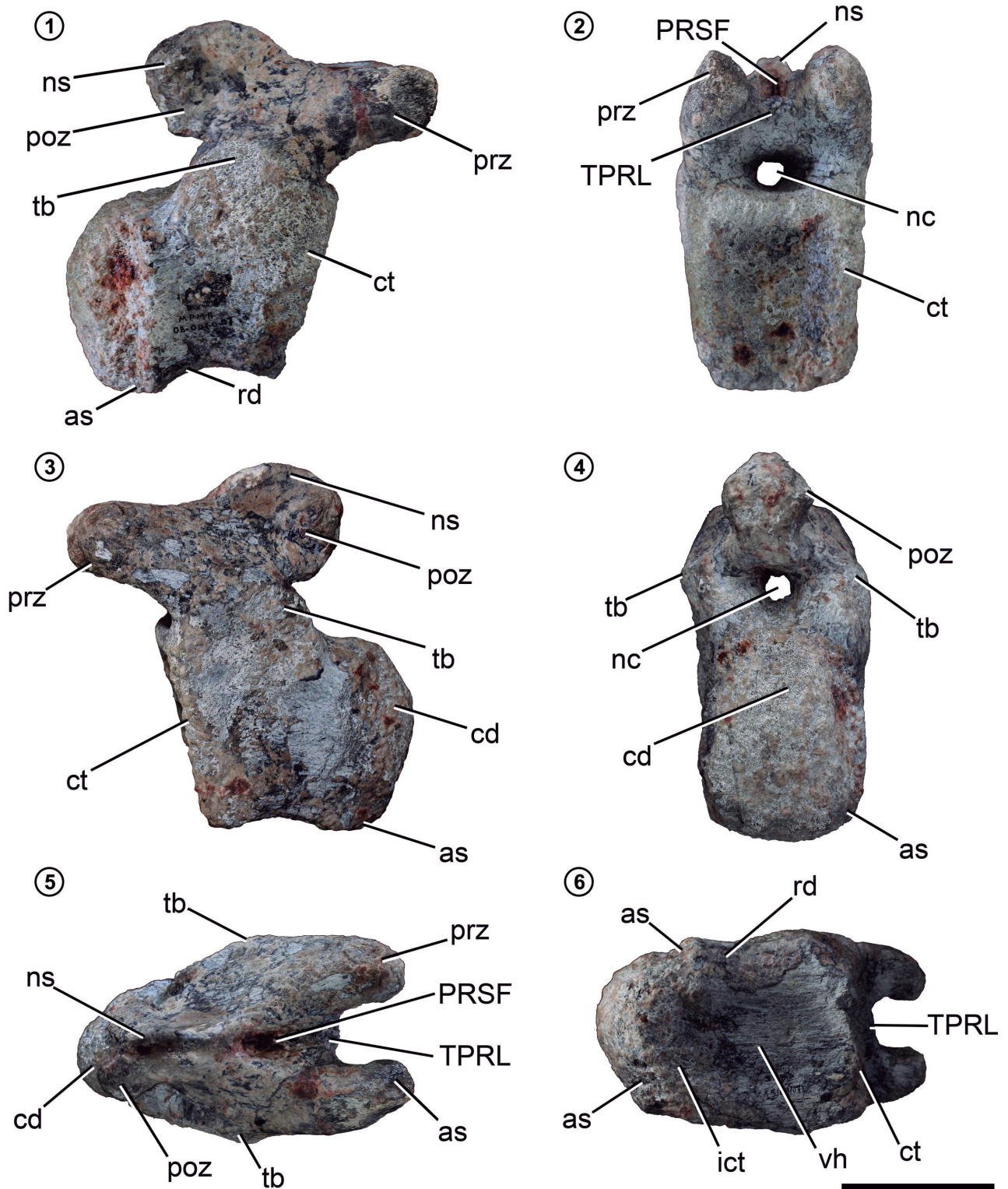
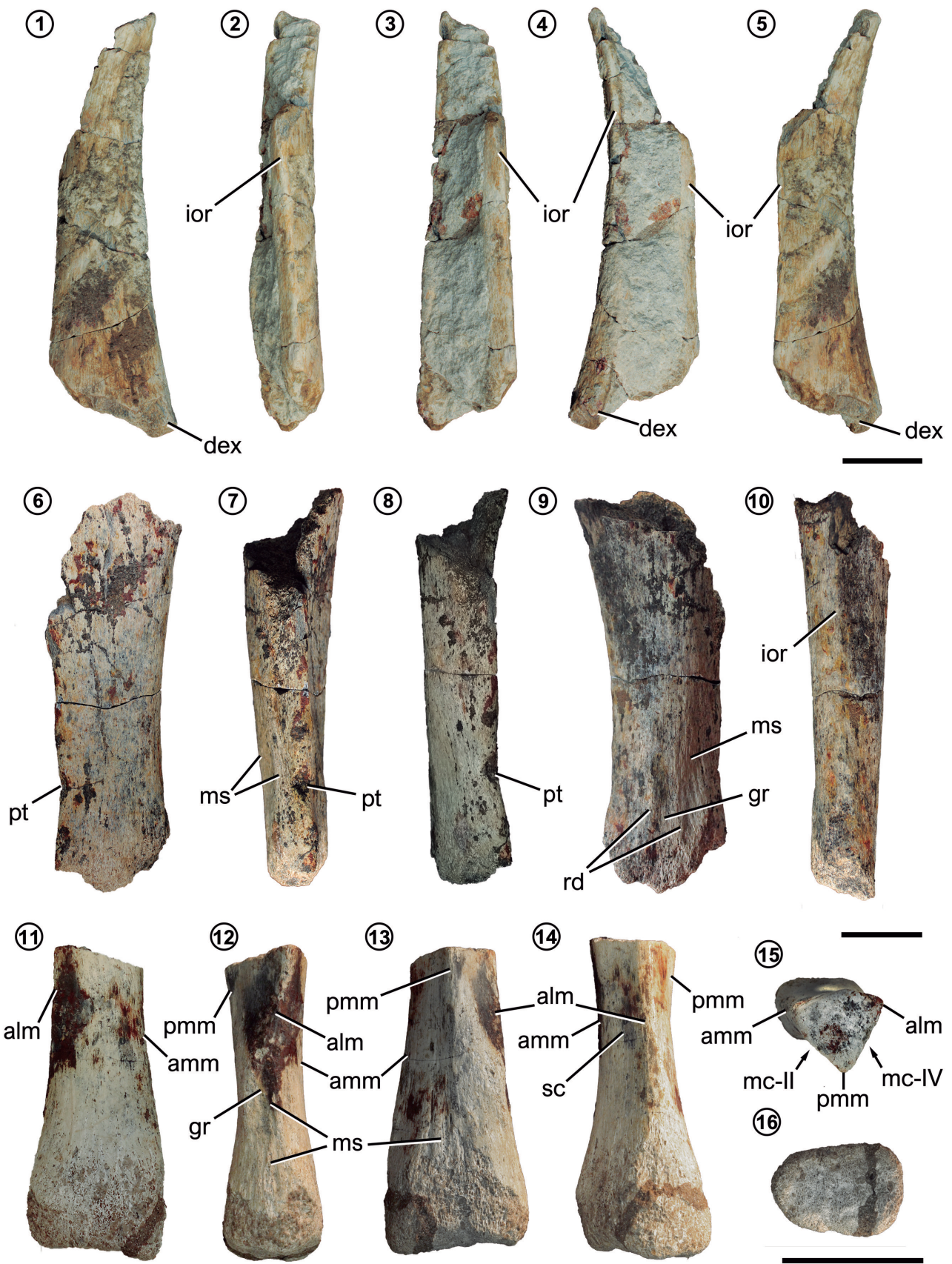


Figure 9. Referred middle caudal vertebra of *Ibirania parva* gen. et sp. nov. (MPMA 08-0060-07). 1, right lateral view; 2, anterior view; 3, left lateral view; 4, posterior view; 5, dorsal view; 6, ventral view. Anatomical abbreviations: as, articular surface; cd, condyle; ct, cotyle; ict, internal camellate tissue; nc, neural canal; ns, neural spine; poz, postzygapophysis; PRSF, prespinal fossa; prz, prezygapophysis; rd, ridge; TPRL, intraprezygapophyseal lamina. Scale bar equals 5 cm.



anteroposteriorly short, strongly procoelous, and lacking marked lateral depressions. *Ibirania parva* bears an anteriorly deflected cotyle margin in lateral view (Fig. 9.1, 9.3), as present in *Gondwanatitan faustoi*, *Uberabatitan ribeiroi*, the holotype of *Neuquensaurus australis* (MLP-Ly 4 - 5), and *Rocasaurus muniozi* (MPCA-Pv 58). As in *Baurutitan britoi*, the centrum preserves incipient tuberosities posterolaterally (Fig. 9.3–9.5) that are reminiscent of the transverse processes where the *M. ilioischiocaudalis* inserts (Díez-Díaz *et al.*, 2020). On the lateral and ventral surface of the centrum, it is possible to visualize an elaborate somphospondylous internal tissue. A shallow and transversely wide ventral hollow is present (Fig. 9.6) as in most saltasaurids (Sanz *et al.*, 1999; Salgado & Azpilicueta, 2000), but lacking a median bony septum as seen in *Rocasaurus muniozi* and *Saltasaurus loricatus* (Zurriaguz *et al.*, 2017). *Ibirania parva* mid- to posterior caudal vertebra also lacks prominent ventrolateral ridges. The neural arch is low and with short prezygapophyses, as in *Bonatitan reigi* (Martinelli & Forasiepi, 2004). However, the prezygapophyses are robust, slightly curved medially (Fig. 9.1, 9.5), with the articular surfaces strongly obliquely oriented. The SPRL and TPRL are well marked and thick, mainly the latter, bordering a deep PRSF. The TPRL develops anteriorly, projecting beyond the cotyle margin (Fig. 9.6). As in LPP-PV-0206, the PRSL of MPMA 08-0060/07 is almost absent, and the neural spine is low and strongly posterodorsally projected, bearing a ventrally broad POSL filling the posterior surface. The postzygapophyses are flat, with an outline that tapers posterodorsally, lacking postzygapophyseal bony processes and laterally developed hyposphenal ridges laterally developed present in rincosaurians and *Epachthosaurus sciuttoi* (Martínez *et al.*, 2004; Calvo *et al.*, 2007).

Appendicular skeleton

Radius. LPP-PV-0203 (Fig. 10.1–10.5) is a fragmentary diaphyseal bone lacking most of its anteromedial surface and

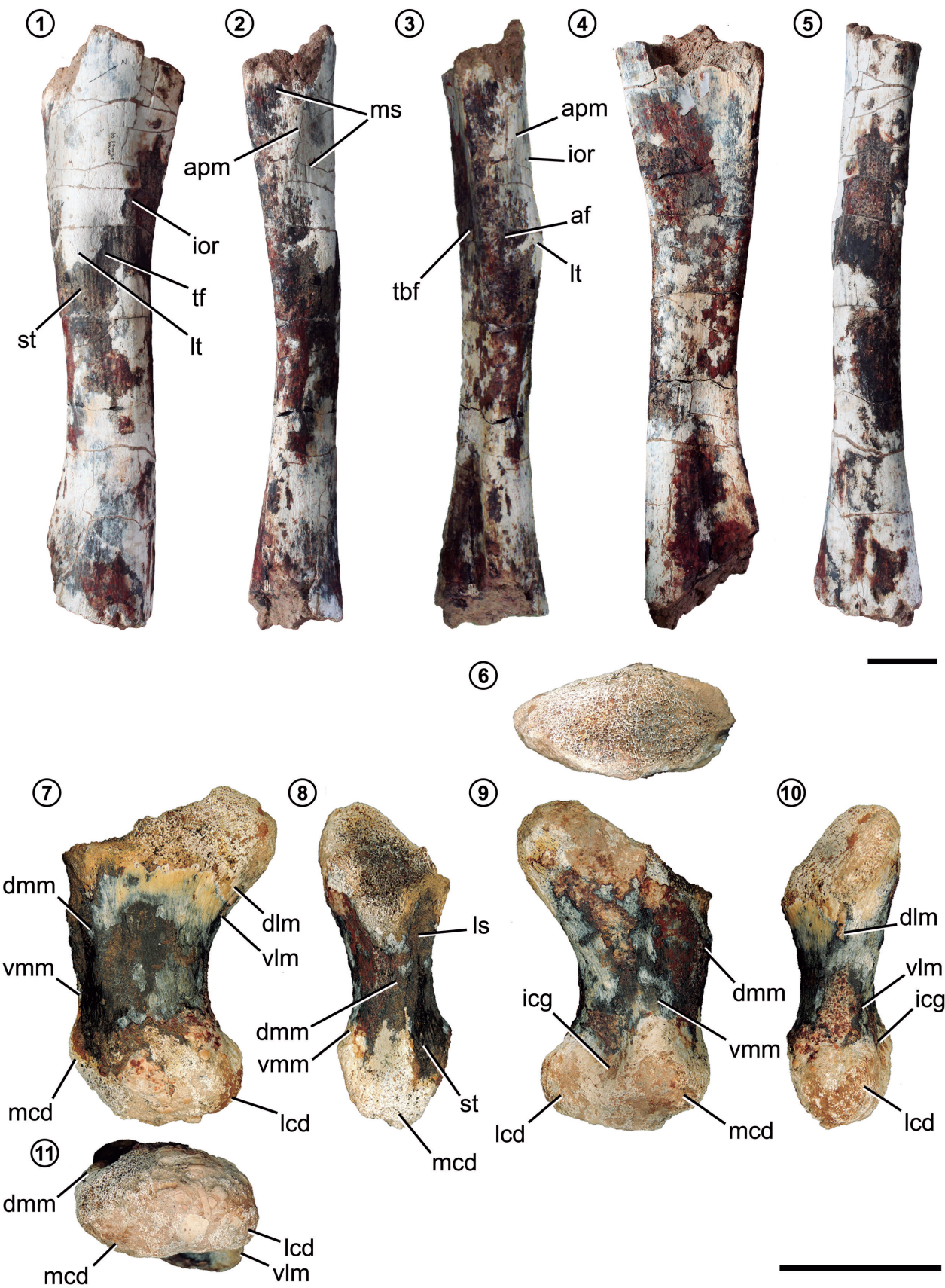
proximal half (Fig. 10.2, 10.4). This element is identified as the distal half of a right radius due to its ellipsoid shape at mid-section. Only the anterolateral and posterolateral surfaces of the diaphyseal region are preserved, bearing a slightly convex profile. As in *Yamanasaurus lojaensis*, it is not possible to recognize interosseous ridges over the diaphysis, as expected for the posterior surface (Apesteguía *et al.*, 2020). In turn, the posteromedial margin displays a thick ridge, continuous with the rest of the bone margin, which gradually expands transversely towards its distal end (Fig. 10.1). Given its fragmentary condition, we cannot assess if it had an obliquely oriented ventral margin or expanded ends, as in other saltasaurines (Powell, 1992).

Ulna. The holotype of *Ibirania parva* also preserves a fragmentary right ulna (LPP-PV-0202; Fig. 10.6–10.10) lacking its extremities. Its identification was based on the comparison with appendicular materials from other titanosaurs and the characteristic “D-shaped” diaphyseal cross section, for which some histological samples were prepared (see below). The proximal end exhibits a very fragmentary condition, not preserving an olecranon, or the anteromedial and anterolateral processes; the distal end is only slightly abraded.

The proximal portion appears to be wide, consistent with the typical tri-radiate shape. The radial fossa consists of a flattened area, lacking interosseous ridges. In the posterior view, in turn, the bone exhibits a convex profile, and the distal end preserves two parallel ridges directed proximodistally (Fig. 10.9), possibly representing muscular scars for the *M. flexor carpi ulnaris* (Borsuk-Białynicka, 1977). Additionally, there is an ellipsoid pit located close to the distal end, visible in the posterolateral view, which probably served as the insertion point of the radial ligament. This latter condition appears autapomorphic to *Ibirania parva*, although the hypothesis that such trait may correspond to pathology cannot be dismissed.

The diaphyseal shape has straight lateral and medial

Figure 10. Forelimb bones of *Ibirania parva* gen. et sp. nov. holotype. Partial right radius (LPP-PV-0203) in 1, lateral view; 2, anterolateral view; 3, anteromedial view; 4, medial view; 5, posteromedial view; partial right ulna (LPP-PV-0202) in 6, lateral view; 7, posterolateral view; 8, posteromedial view; 9, medial view; 10, anteromedial view; distal half of metacarpal III (LPP-PV-0201) in 11, lateral view; 12, anterolateral view; 13, medial view; 14, posteromedial view; 15, midshaft in cross section view; 16, distal view. Anatomical abbreviations: **alm**, anterolateral margin; **amm**, anteromedial margin; **dex**, distal end expansion; **gr**, groove; **ior**, interosseous ridge; **mc**, metacarpal; **ms**, muscular scar; **pmm**, posteromedial margin; **pt**, pit; **rd**, ridge; **sc**, sulcus. Scale bars equals 5 cm.



margins, with the beginning of the expansion marked by the slight development of the lateral and medial processes. This could mean, although not preserved, that the proximal end was not as expanded as in other titanosaurians (e.g., *Diamantinasaurus matildae*, *Elaltitan lilloi*, *Epachthosaurus sciuttoi*, *Opisthocoelicaudia skarzynskii*). The profile present in the ulna of *Ibirania parva* differs from the slender nature of some titanosaurians, such as *Rapetosaurus krausei* (Curry Rogers, 2009) and *Narambuenatitan palomoi* (Filippi et al., 2011), resembling the robust condition of *Neuquensaurus australis* and other saltasaurines (Otero, 2010; Tab. 2).

Metacarpal. The distal half of a right metacarpal III (LPP-PV-0201; Fig. 10.11–10.16) was identified due to the triangular-shaped cross section at the mid-shaft (Fig. 10.13) and through comparisons with other taxa that preserve more complete manual material, including *Argyrosaurus superbus*, *Elaltitan lilloi*, *Neuquensaurus australis*, *Diamantinasaurus matildae*, *Opisthocoelicaudia skarzynskii*, *Mansourasaurus shahinae*, and *Angolatitan adamastor* (Huene, 1929; Borsuk-Białynicka, 1977; Otero, 2010; Mateus et al., 2011; Mannion & Otero, 2012; Poropat et al., 2015; Sallam et al., 2018). It has a pronounced “V-shaped” depression with marked ridges on the posterolateral facet of the mid-shaft and converges distally. This depression extends mediolaterally and laterodistally, accompanying an interosseous ridge (Fig. 10.12). These ridges could represent scars of the ligaments that kept digits II and IV tightly bound. The distal end is rectangular in shape (Fig. 10.16) and lacks the “U-shaped” groove or articular condyles on the anterior surface, indicating that the manus of *Ibirania parva* probably lacked phalanges.

Fibula. Some diaphyseal fragments of a fibula (LPP-PV-0043), assigned to a referred individual, were recovered near the holotype stratum. The bone exhibits a slight “D-shaped” profile in cross section and bears an incipient lateral trochanter, which is partially preserved. Aureliano et al. (2021a) described the histological profile of this element and

the pathological alterations caused by acute osteomyelitis and parasitic infections as well.

The left fibula of *Ibirania parva* (MPMA 09-0001/99; Fig. 11.1–11.5) is a slender bone only missing parts of its proximal and distal ends. Nonetheless, the proximal end is seemingly more anteroposteriorly expanded than the distal one (Fig. 11.1, 11.4). The anterolateral margin in the proximal end is gently convex, and a possible tibial scar can be present (Fig. 11.2). The midshaft on lateral view differs from the straighter condition of *Laplatasaurus araukanicus*, *Uberabatitan ribeiroi*, and *Mendozasaurus neguyelap* (see Fig. 13 in Supplementary Online Information). The lateral trochanter is slightly developed, present as a smooth tuberosity, as in the pathological specimen LPP-PV-0043. In addition, the lateral trochanter is in line with the proximodistal axis of the diaphysis, possibly corresponding to an autapomorphy of *Ibirania parva*.

The lateral trochanter is located above the mid-length of the bone (Fig. 11.3) as in *Dreadnoughtus schrani* and *Neuquensaurus australis* and differing from *Rapetosaurus krausei*, in which the lateral trochanter is positioned at the mid-height of the fibula. In *Ibirania parva*, the trochanter is oriented from the anteroproximal to posterodistal faces, as in several titanosaurians (González Riga et al., 2019), with a longitudinal and shallow trochanteric fossa dividing it into two segments. However, the lateral trochanter is less prominent than in these taxa. In medial view, a wide and shallow tibial fossa is present proximally. The fibula exhibits a slight sigmoid profile, due to the presence of a concave anteromedial margin close to the distal end. Nevertheless, this outline is less pronounced than the sigmoid profile exhibited in *Epachthosaurus sciuttoi* and much more gracile than the observed in *Dreadnoughtus schrani*. The preserved portion of the distal end expands mediolaterally (Fig. 11.5), giving a smooth excavated fossa that projects towards its mid-length.

Metatarsal. A probable metatarsal I (LPP-PV-0207; Fig.

Figure 11. Hind limb bones of *Ibirania parva* gen. et sp. nov.: referred left fibula (MPMA 09-0001/99) in 1, lateral view; 2, posterior view; 3, posteromedial view; 4, medial view; 5, anteromedial view; holotypic left metatarsal I (LPP-PV-0207) in 6, proximal view; 7, dorsal view; 8, lateral view; 9, ventral view; 10, medial view; 11, distal views. Anatomical abbreviations: af, anterior fossa; apm, anteroproximal margin; dlm, dorso-lateral margin; dmm, dorsomedial margin; icg, intercondylar groove; ior, interosseous ridge; lcd, lateral condyle; ls, lateral sulcus; lt, lateral trochanter; mcd, medial condyle; st, striae; tbf, tibial fossa; tf, trochanteric fossa; vlm, ventrolateral margin; vmm, ventromedial margin. Scale bars equals 5 cm.

11.6–11.11) is preserved, based in comparison with more complete pedes (e.g., *Mendozasaurus neguyelap*, *Notocolossus gonzalezparejasi*). This bone is proximodistally elongated when compared to other titanosaurs like *Opisthocoelicaudia skarzynskii* and the Naashoibito pes referred to *Alamosaurus sanjuanensis* (D'Emic *et al.*, 2011). Preserved portions of the proximal and distal ends indicate they were transversely expanded. The proximal articular surface slopes ventromedially as in *Dreadnoughtus schrani*, *Rapetosaurus krausei*, and *Notocolossus gonzalezparejasi*. The metatarsal shows a slightly concave lateral border with a subtle lateral ridge. In medial view (Fig. 11.6, 11.7), a delicate medial ridge appears at mid-length and shows a poorly pronounced sigmoidal lateral edge. In posterior view (Fig. 11.9), a minor but accentuated intercondylar groove appears delimiting transversely the distal articular surface. The dorsal surface of the distal end is slightly twisted medially but, in dorsal view, the lateral margins exhibit a strong lateral deflection, and the articular surface broadly convex mediolaterally (Fig. 11.6, 11.11).

OSTEOHISTOLOGY

Skeletochronology of *Ibirania parva*

The holotypic ulna shows no macroscopic damage on its surface, but thin sections reveal truncated osteons all over the external bone perimeter (Fig. 12.1). Truncation was caused by pre-burial and/or post-exhumation transport. The presence of sandstone grains infilling cavities (mostly between trabeculae) supports a pre-burial transportation hypothesis (Fig. 12.2). The abundance of oxide minerals laterally on the surface and infilling vacant spaces in the periosteum indicates post-exhumation weathering. Despite all these destructive taphonomic features, the microstructure is well-preserved, and histology could be assessed (Fig. 12.1–12.6).

The extent and type of vascularization is consistent across thin sections. The entire cortex has been secondarily remodeled into dense Haversian bone (Type G to Type H bone tissue *sensu* Klein & Sander, 2008; Sander *et al.*, 2011; also see Fig. 14 in Supplementary Online Information), lacking an interstitial laminar primary bone (Modified Laminar Bone *sensu* Klein *et al.*, 2012) as present in some *Magyarosaurus* specimens, *Ampelosaurus atacis*, and *Rapetosaurus krausei* (Stein *et al.*, 2010; Curry Rogers *et al.*,

2016). Two (possibly three) generations of secondary osteons overlap one another (Fig. 12.2). These latter are longitudinally arranged and vary remarkably in size (ranging from 89–254 μm) and shape. Each secondary osteon contains up to five layers of centripetally deposited lamellar bone. Abundant and large resorption cavities throughout the mid-cortex is indicative of intense bone remodeling at the time of death. Lines of Arrested Growth (**LAGs**) have not been identified in *Ibirania parva* thin sections, differing from *Neuquensaurus australis* (Cerdeña & Salgado, 2011). This condition is not uncommon in derived titanosaurs (e.g., Woodward & Lehman, 2009; Company, 2011; Klein *et al.*, 2012; Ghilardi *et al.*, 2016), being more related to the life history of an individual rather than a developmental pattern (Curry Rogers & Kulik, 2018; González *et al.*, 2020). However, there is no evidence of an External Fundamental System (or Outer Circumferential Layer), indicative of growth cessation. By contrast, although most of the outermost cortex of *Ibirania parva* consists of a dense Haversian bone, the secondary osteons are horizontally organized, in non-uniform subparallel patterns (see Fig. 14 in Supplementary Online Information).

Nonetheless, the secondary osteons located in the middle cortex are chaotically arranged and obliteration increases towards the medullary cavity. The medullary cavity of the ulna is reduced and filled with cancellous bone (Fig. 12.5), given the cortex displays an ‘average thickness’ ($\text{CT}/\text{CaM} = 0.058$; *sensu* Mitchell & Sander, 2014). Applying the three-front model of Mitchell and Sander (2014) to the anterior area of the bone, a “senescent” status was achieved with this specimen, with both Apposition Front and the Resorption Front exhibiting slow rates (Fig. 12.6).

PHYLOGENETIC ANALYSIS

Phylogenetic relationships of *Ibirania parva*

Our phylogenetic analysis resulted in 258 MLTs of 1840 steps ($\text{CI} = 0.309$ / $\text{RI} = 0.692$), showing a well-resolved topology with the best score being hit 100 times. TBR branch swapping of these 258 trees found additional optimal trees, yielding a total of 1080 MPTs. A strict consensus of these is shown in Figure 13. The complete topology recovered, as well as Bremer, bootstrap, and jackknife support values for the consensus tree are given as Supplementary Online Information. A list of unambiguous synapomorphies

supporting the nodes of the strict consensus of Figure 13 is also provided as Supplementary Online Information.

Branch support values for most macronarian nodes received low to moderate support values (Table 3). Except *Lithostrotia* (2), other more inclusive taxa of the ingroup (e.g., *Titanosauria*, *Eutitanosauria*) exhibit only a low Bremer support (1). One of the few clades with higher support values in our analysis corresponds to the *Saltosaurinae*, in which *Ibirania parva* was retrieved, with a Bremer value of 3

and bootstrap and jackknife of 70 and 85, respectively. *Saltosauridae* (*sensu* Sereno, 1998), on the other hand, was recovered as monophyletic, but received a Bremer of 2 and was not statistically supported by bootstrap and jackknife values. *Ibirania parva* was recovered as the sister taxon of a new clade within *Saltosaurinae*, which includes the Argentinian taxa *Bonatitan reigi* and *Rocasaurus muniozi*, although they also clustered with low support values (Bremer of 2 and jackknife of 54). Nonetheless, our analysis corroborates

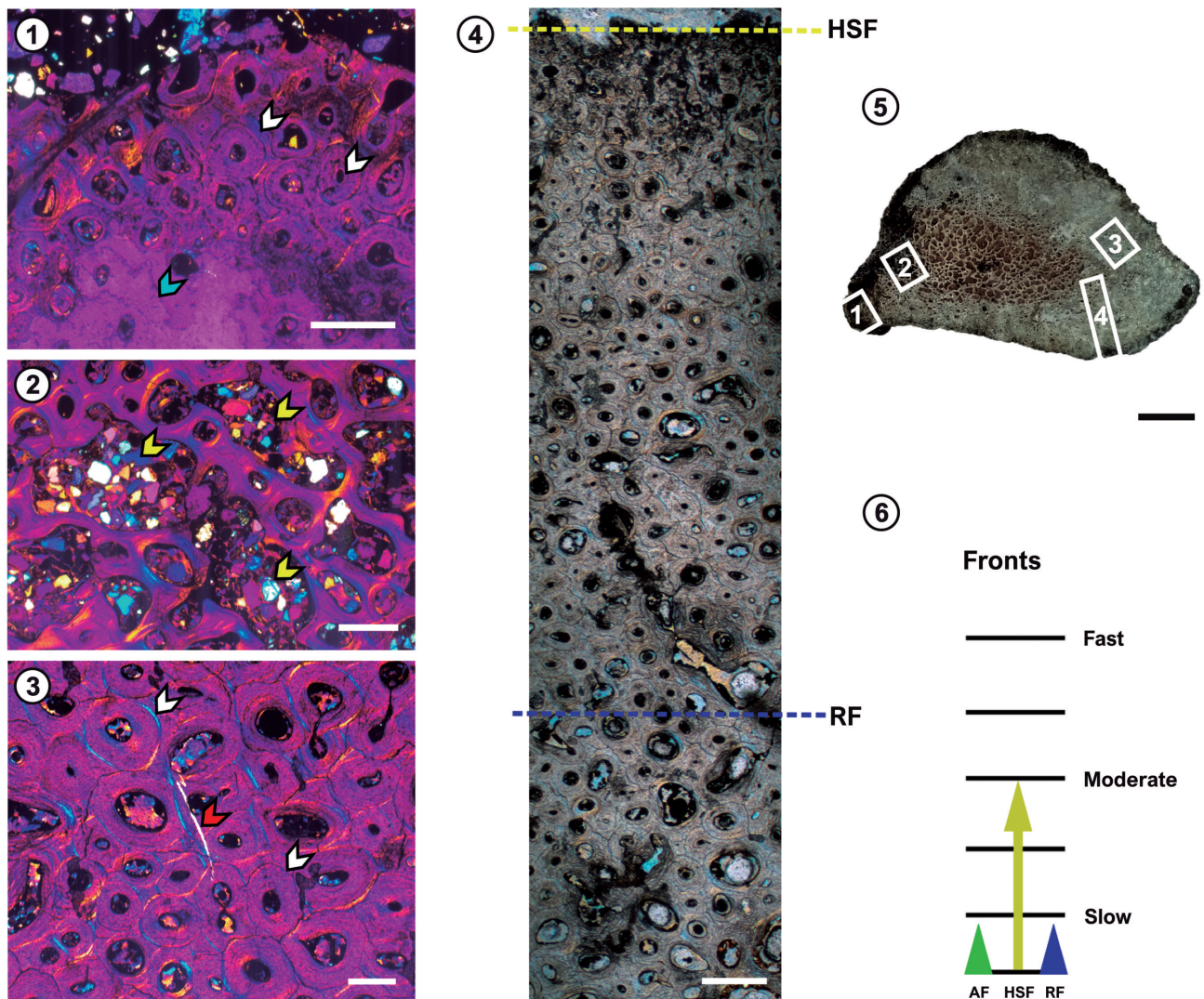


Figure 12. Osteohistology of *Ibirania parva* gen. et sp. nov. holotypic ulna (LPP-PV-0202). 1, Chaotically arranged secondary bone tissue (white arrows) in anterolateral cortical surface. There are up to five centripetally deposited Haversian layers around osteons. Note that a portion of the outer cortex was obliterated post diagenesis (blue arrow); 2, Sandstone grains (yellow arrows) infilling medullary spongiosa anterolaterally; 3, Haversian osteons in mid-cortex medially. There are at least two generations of secondary osteons overlapping each other. Red arrow points to potential Sharpey's fibers; 4, Profile at the medial portion of the shaft. Marked bone deposition fronts according to Mitchell and Sander (2014); 5, Mid cross section of the ulna with the location of 1–4 samples; 6, Three-front model indicating a "senescent" ontogenetic status according to Mitchell and Sander (2014). Abbreviations: AF, Apposition Front; HSF, Haversian Front; RF, Resorption Front. Images were taken under polarized light with crossed nicols in 1–3 and parallel nicols in 4. Scale bar in 1, 2 equals 500 μ m; 3 equals 200 μ m; 4 equals 400 μ m; and 5 equals 1 cm.

that *Ibirania parva* was a saltasaurine titanosaurian, and the first unequivocally known from Brazil – although some authors have also considered other taxa as putative members

of this group in the past (e.g., *Maxakalisaurus topai*; Kellner *et al.*, 2006).

Saltasauridae, recovered here for the first time with

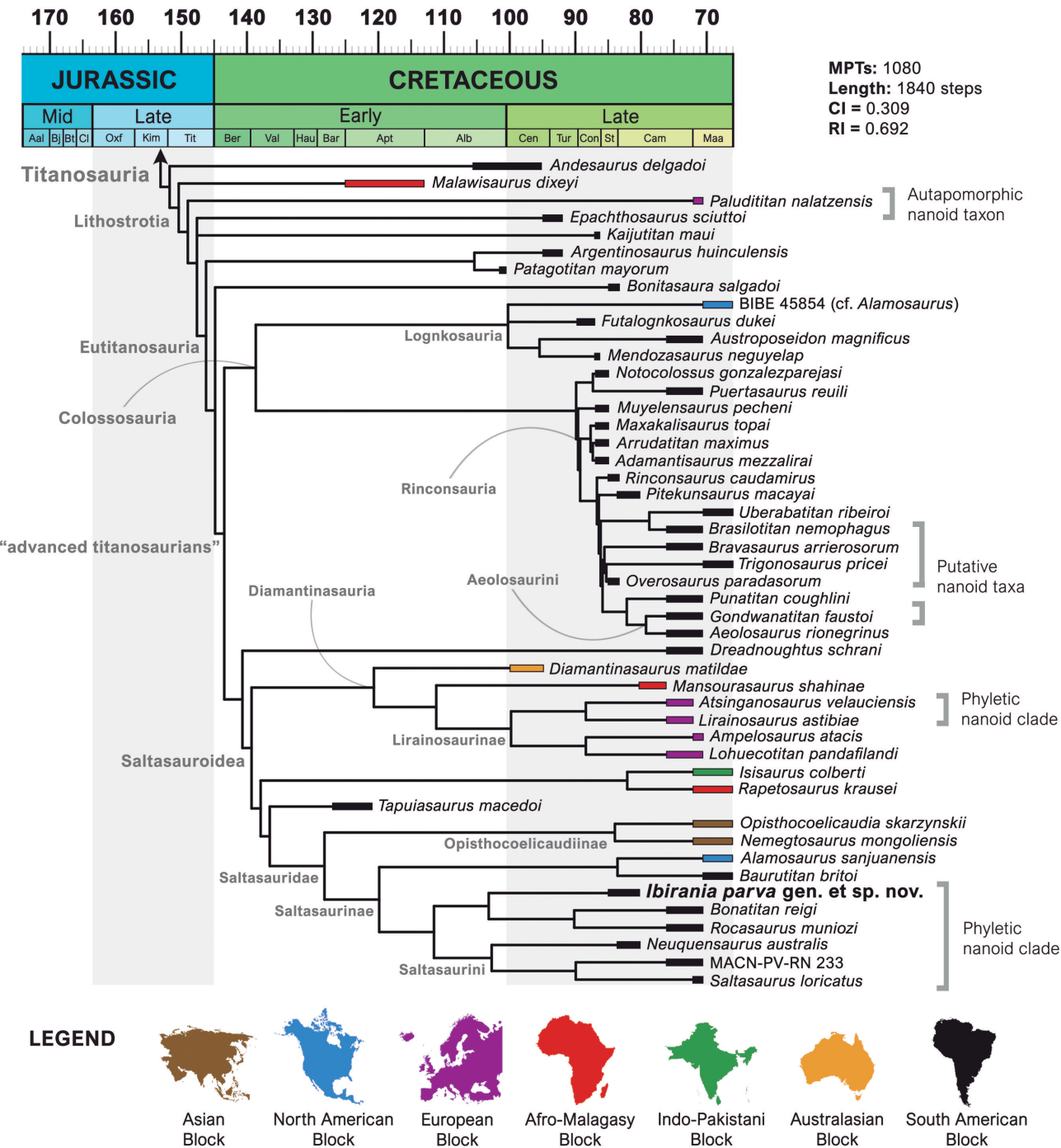


Figure 13. Temporally calibrated strict consensus tree depicting the phylogenetic affinities of *Ibirania parva* gen. et sp. nov. within Titanosauria and the occurrence of nanoid taxa in the group. Colored thick bars represent temporal range of terminal taxa (see Supplementary Online Information) and their spatial distribution according to the key provided in the figure. Age abbreviations: Aal, Aalenian; Alb, Albian; Apt, Aptian; Bar, Barremian; Ber, Berriasian; Bj, Bajocian; Bt, Bathonian; Cam, Campanian; Cen, Cenomanian; Cl, Callovian; Con, Coniacian; Hau, Hauterivian; Kim, Kimmeridgian; Maa, Maastrichtian; Oxf, Oxfordian; St, Santonian; Tit, Tithonian; Tur, Turonian; Val, Valanginian.

TABLE 3. Node support values of the main macronarian clades.

Nodes	Br.	Bt.	Jk.
Macronaria	3	66	83
Somphospondyli	2	-	-
Titanosauriformes	2	-	-
Brachiosauridae	2	-	-
Titanosauria	1	-	-
Lithostrotia	2	-	-
Eutitanosauria	1	-	-
Colossosauria	1	-	-
Lognkosauria	1	-	-
Rinconsauria	1	-	-
Aeolosaurini	1	60	63
Saltasauroidae	1	-	-
Diamantinasauria	1	-	-
Lirainosaurinae	1	-	-
Saltosauridae	2	-	-
Opisthocoelicaudiinae	3	74	78
Saltosaurinae	2	52	69
Saltosaurini	3	70	85

A dash (-) denotes when a node support is not recovered. Abbreviations: **Br.**, Bremer (Decay Index); **Bt.**, Bootstrap; **Jk.**, Jackknife.

Baurutitan britoi and *Bonatitan reigi*, is supported by six unambiguous synapomorphies: middle to posterior dorsal centra with slightly concave ventral surfaces, sometimes with one or two crests (Char. 178: 1→2); neural canal of middle and posterior dorsal vertebrae enclosed in a deep fossa in anterior view (Char. 183: 0→1); middle and posterior dorsal centra with a ventral keel (Char. 186: 0→1); posterior dorsal neural arches with expanded PCDL ventral end (Char. 209: 1→0); and opisthocoelous anterior caudal centra (except for the first) (Char. 231: 3→5, Char. 430: 2→0). Some of these synapomorphies, especially the two latter, indicate that the morphology displayed by *Opisthocoelicaudia skarzynskii* is the plesiomorphic condition for saltasaurids, being consistent with the acquisition of a seventh vertebra (representing the biconvex second sacro-

caudal element) observed in the sacrum of saltasaurines.

Saltosaurinae was recovered encompassing a clade formed by *Baurutitan britoi* and *Alamosaurus sanjuanensis* (two synapomorphies), and a more inclusive clade formed by *Ibirania parva*, *Bonatitan reigi*, and *Rocasaurus muniozi*, plus Saltosaurini (three synapomorphies). Synapomorphies uniting *Ibirania parva* with the clade formed by *Bonatitan reigi* and *Rocasaurus muniozi* include the presence of a small notch in the dorsal margin of the posterior cervical cotyle (Char. 133: 0→1), middle and posterior cervical vertebrae with the CPOL dorsally divided, with the medial part contacting the TPOL (Char. 144:0→1), and the anterior face of middle caudal centra strongly inclined anteriorly (Char. 255: 0→1). The clade composed by *Bonatitan reigi* and *Rocasaurus muniozi* is supported by only one unambiguous synapomorphy: middle caudal centra quadrangular-shaped, flattened ventrally and laterally (Char. 250: 1→2).

In addition, we recovered a monophyletic Saltosaurini, with *Neuquensaurus australis* as sister group of the clade formed by the unnamed saltosaurine from Angostura Colorada Formation (MACN PV RN-233) and *Saltasaurus loricatus*. This clade is supported by five unambiguous synapomorphies, all related to the femoral and caudal musculature: neural spines of the posterior caudal vertebrae strongly displaced posteriorly (Char. 258: 0→1); the ratio of centrum length to centrum height in the middle caudal vertebra is 2 or higher (Char. 259: 0→1); presence of a concave kink on the ventral margin of the ilium preacetabular processes (Char. 330: 0→1); a longitudinal ridge on the anterior face of the femur (Char. 349: 0→1); anterior crest in the proximal end of fibula absent or poorly developed (Char. 370: 1→0).

Titanosauria was recovered with the following unambiguous synapomorphies: dorsal vertebrae with smooth and narrow single PRSL (Char. 165: 1→2); and middle to posterior dorsal centra with ventral surface convex transversely (Char. 177: 1→0). Lithostrotia was recovered outside of Eutitanosauria (as in Hechenleitner *et al.*, 2020) and supported by two synapomorphies: strongly procoelous anterior caudal centra (excluding the first ones) (Char. 231: 2→3); and the absence of ventrolateral ridges on anterior and mid caudal centra (Char. 234: 1→0). Finally, Eutitanosauria is characterized by the change of platycoelous to slightly procoelous condition in the caudal

centra (Char. 231: 1→2); and chevrons with a deep haemal canal, approximately 50% of the chevron length (Char. 270: 0→1).

In our analysis, we also recovered the recently established clades Lirainosaurinae (Díez-Díaz *et al.*, 2018), Colossosauria (González Riga *et al.*, 2019), and Diamantinasauria (Poropat *et al.*, 2021). Additionally, some other results are consistent with previous analyses, such as *Mansourasaurus* as the sister group of Lirainosaurinae (Sallam *et al.*, 2018) and aeolosaurines more closely related to Rinconsauria than saltasaurines (Calvo *et al.*, 2007). However, there are conspicuous differences in the given topology when compared to previous iterations of this matrix (*i.e.*, Filippi *et al.*, 2019; Carballido *et al.*, 2020; Hechenleitner *et al.*, 2020), possibly reflecting the significant increase in taxon sampling. For example, some taxa such as *Bonitasaura salgadoi* is positioned as more closely related to the giant eutitanosaurs from the Early and early Late Cretaceous than to other “advanced titanosaurs”—here represented by colossosaurs and saltasauroids—, and Diamantinasauria was recovered in a more derived position, nested into Saltasauroidae, rather in a basal position in Lithostrotia.

Colossosauria monophyly is recovered through two unambiguous synapomorphies, but with the differences as follow: *Austroposeidon magnificus* is a member of Lognkosauria and sister taxon of *Mendozasaurus neguyelap*, supported by seven synapomorphies, as well as the cervical series referred to *Alamosaurus sanjuanensis* (BIBE 45854), supported by three synapomorphies; *Patagotitan mayorum* and *Argentinosaurus huinculensis* form a clade outside Lognkosauria, as well as *Puertasaurus reuili* and *Notocolossus gonzalezparejasi* (supported by five synapomorphies). In addition, the latter clade composes the sister group of Rinconsauria (supported by three synapomorphies); *Trigonosaurus pricei* is the sister taxon of *Overosaurus paradasorum*, forming monophyletic group outside Aeolosaurini (two synapomorphies), as well as *Uberabatitan ribeiroi* and *Brasilotitan nemophagus* (three synapomorphies), and the group formed by *Maxakalisaurus topai* plus *Adamantisaurus mezzalirai* and *Arrudatitan maximus* (three synapomorphies).

The calibrated topology indicates that Rinconsauria represents an endemic group of South American

colossosaurs whose adaptative radiation occurred after the Cenomanian–Turonian faunal turnover event. By contrast, saltasaurids were retrieved in close relation with globally distributed taxa, forming the clade Saltasauroidae, in which some minor apical groups such as Saltasaurinae, Opisthocoelicaudiinae, and Lirainosaurinae, become endemic due to the isolation of landmasses during the Campanian–Maastrichtian interval. The clade formed by these groups is supported by seven synapomorphies: prezygapophyses of middle cervical vertebrae do not extend beyond the anterior margin of the centrum (Char. 147: 1→0); SPRL not contacting the lateral margins of the neural spine of cervical vertebrae (Char. 151: 0→1); anterior and middle dorsal neural spines, lacking a SPRL (reversed in *Ibirania parva*) (Char. 162: 1→0); middle and posterior dorsal with the anterior face entirely surrounded by the neural arch (Char. 183: 1→0); anterior and middle caudal vertebrae bearing ventrolateral ridges and ventral longitudinal hollows (Char. 234: 0→1, Char. 251: 0→1); and humeral distal condyles exposed on the anterior portion of the shaft (Char. 305: 0→1).

DISCUSSION

Ibirania parva – a nanoid taxon or an immature?

Although Titanosauria includes giant species, Brazilian titanosaur taxa such as *Gondwanatitan faustoi*, *Trigonosaurus pricei*, *Brasilotitan nemophagus*, and now *Ibirania parva*, are smaller-bodied than their Gondwanan or South American relatives. Below, we review osteological and histological data supporting their ontogenetic age estimate. We further discuss phylogenetic implications and factors that may have influenced the reduction of body size in *Ibirania parva*.

Osteological evidence. The degree of neurocentral suture closure in vertebrae has been widely used as a relative parameter of archosaurian somatic maturity (see Griffin *et al.*, 2021). Nonetheless, the closure of the neurocentral suture as the main parameter of somatic maturity is a labile proxy, given different patterns in the way of the neurocentral suture is fused have been documented both fossil and extant archosaurs (*e.g.*, posterior towards anterior elements, anterior towards posterior elements; Brochu, 1996; Woodruff *et al.*, 2017). Thus, its usage in low sample sets (*i.e.*, only two or fewer axial regions are preserved) should be taken with caution if it is not complemented by internal anatomy data,

such as CT scan imagery or histological thin sections (Irmis, 2007). Fortunately, cervical, dorsal, and caudal material is known for *Ibirania parva*, allowing safely inference of its somatic maturity.

Although some of such modules of the axial skeleton of *Ibirania parva* exhibit fragmentary conditions, most of the elements have been preserved with the centra fused to their neural arches. Externally, neurocentral sutures are not visible in the vertebrae of *Ibirania parva* (see Figs. 4–7), indicating they are fully fused. CT scan slices also support this inference (see Fig. 15 in the Supplementary Online Information), in which the internal camellate trabeculae appear continuous. Axial materials of *Ibirania parva* also display additional external and internal traits indicative of mature individuals, such as a high degree of internal pneumaticity development (Aureliano et al., 2021b) and neural arches with well-developed laminae and fossae.

These patterns differ from other small-sized and immature individuals, such as the referred to *Rocasaurus muniozi*, *Bonatitan reigi*, and *Bonitasaura salgadoi* (Salgado & Azpilicueta, 2000; Gallina & Apesteguía, 2015; Salgado et al., 2015), in which many of the preserved dorsal and caudal neural arches and centra are detached at the neurocentral suture, sometimes exhibiting a rudimentary development or slightly marked neural arch laminae.

Histological evidence. Titanosaurians are widely known in literature due to display a more secondarily remodeled cortical bone tissue compared to other neosauropods (Stein et al., 2010; Company, 2011; Klein et al., 2012; Cerda et al., 2017), and the thin sections of *Ibirania parva* exhibit this pattern. Padian et al. (2016) demonstrated that the cortex of epipodial bones (i.e., radii, ulnae, tibiae, and fibulae) are more secondarily remodeled within the same individual than propodial bones, such as the humerus or the femur. This pattern could be explained due to higher stress loading exerted in epipodial, mesopodial, and metapodial bones than in the propodial ones. A similar tissue pattern was also observed both in the ulna and humerus of the Iberian nanoid titanosaurian *Lirainosaurus astibiae* (Company, 2011). Therefore, the proximal limb bones of *Ibirania parva* could also have this tissue adaptation.

As in *Magyarosaurus* (Mitchell & Sander, 2014), the strong remodeling in the cortex of *Ibirania parva* was caused by the slowdown of the Resorption Front, whereas the

Haversian Front is constant across several taxa (Klein et al., 2012; Mitchell & Sander, 2014). By reducing the speed of the Resorption Front, *Ibirania parva* adapted their long bones with a thick cortex and small medullary volume allowing this taxon to support an axial loading regime similarly to *Magyarosaurus* and *Lirainosaurus astibiae*. This pattern cannot be observed in the nanoid macronarian *Europasaurus holgeri* or in *Rapetosaurus krausei*, in which a predominantly fibrolamellar bone tissue is present in the cortex (Sander et al., 2006; Curry Rogers et al., 2016).

Other titanosaurs such as *Ampelosaurus ataxis* and *Alamosaurus sanjuanensis* also exhibit a greater amount of Haversian bone when compared to other neosauropods, such as *Apatosaurus* (Company, 2011; Klein et al., 2012; Mitchell & Sander, 2014). However, the extreme abundance of this type of tissue observed in *Ibirania parva* resembles the condition found in *Lirainosaurus astibiae* and *Magyarosaurus*, rather than any other sampled titanosaurian in literature, including the small-bodied Patagonian saltosaurine *Neuquensaurus australis*, which displays several LAGs (Cerda & Salgado, 2011). Thus, an effect of analogous environmental conditions, for example, shared by *Ibirania parva* and the insular nanoid titanosaurs from Europe could convergently culminate in similar decreased apposition growth in these taxa.

The extreme remodeling activity obliterates completely the primary bone tissue in the samples of the *Ibirania parva* ulna, suggesting that this individual had long ceased appositional growth at its moment of death, exhibiting a late HOS (at least HOS 13 from Klein & Sander, 2008). *Ibirania parva* exhibit HOS 14, based on the presence of up to five generations of secondary osteons (Stein et al., 2010; see Fig. 11.1, 11.2, 11.4 in Supplementary Online Information). Furthermore, applying to the anterior area of the bone the three-front model of Mitchell and Sander (2014), a “senescent” status is reinforced for this taxon (Fig. 12).

The small body size of *Ibirania parva* and its implications

Although body size increase seemingly to be a general trend in Sauropodomorpha throughout the Mesozoic Era (phyletic gigantism *sensu* Gould & Macfadden, 2004; Sander & Clauss, 2008), episodes of nanism have evolved multiple times and in different sauropod lineages during the Jurassic

and Cretaceous (e.g., Stein *et al.*, 2010; Carballido & Sander, 2014). Different evolutionary processes could be associated with these events (see de Souza & Santucci, 2014; Van der Geer *et al.*, 2016), including biotic or abiotic pressures, or even a combination of both. These include “island miniaturization” (e.g., Benton *et al.*, 2010; Weishampel *et al.*, 2010; Csiki-Sava *et al.*, 2015) as well as niche segregation and adaptability to a specific feeding strategy (see Whitlock, 2011; Button *et al.*, 2014, 2016; Otero *et al.*, 2021).

In South America, saltasaurines display a conspicuous reduction in their body sizes, which has been explained as either a response to geographical restriction to a vast north-south coastal corridor of the Andean region in the latest Cretaceous (Apesteguía, 2002; Leanza *et al.*, 2004; Apesteguía *et al.*, 2020) or to occupation of new and restricted environments formerly occupied by diplodocoid sauropods (Powell, 2003; Cerda *et al.*, 2012).

Our cladistic analysis recovered *Ibirania parva* within Saltasauridae (Fig. 13), in the less inclusive clade Saltosaurinae and as the sister taxon of a group composed of the small-bodied *Rocasaurus muniozi* and *Bonatitan reigi*. Thus, the small size exhibited by *Ibirania parva* would have been inherited from a common ancestor shared by *Rocasaurus* and *Bonatitan*. Phyletic and autapomorphic nanism have already been proposed in other titanosaurs (e.g., *Magyarosaurus dacus*, *Lirainosaurus astibiae*, *Atsinganosaurus velauciensis*) from the ancient Ibero-Armorican Island and the Hațeg Archipelago biota, from the Campanian–Maastrichtian strata of Europe (Stein *et al.*, 2010; Klein *et al.*, 2012; Díez-Díaz *et al.*, 2013b; Díez-Díaz *et al.*, 2018). Except for *Magyarosaurus*, a possible autapomorphic nanoid, these taxa comprise an endemic clade of European titanosaurs (Lirainosaurinae) that includes phyletic nanoid forms, and their phylogenetic relationships indicate that they are related to the South American saltasaurids, composing a more inclusive group identified here as Saltasauroida.

By contrast, *Ibirania parva* was recovered in a slightly older (Santonian–Campanian) continental geological unit, the intracratonic Bauru Basin, differing from other South American or European saltasauroid occurrences, which are found in deposits with marine influence. For this reason, a nanism occurrence driven by insularity pressures (*sensu stricto*) can be excluded in this taxon. If the other

saltasaurines from South America represent true island-nanoid taxa, the occurrence of *Ibirania parva* could indicate a putative phyletic nanism trend, which could be intensified in other saltasauroids due to insularity pressures.

The inferred paleoenvironmental conditions in the São José do Rio Preto Formation may have created selective pressures analogous to those occurring in some typical insular habitats (i.e., differential resource supply and effects of area size; Van der Geer *et al.*, 2016). The small size acquired by some vertebrate forms in these habitats, such as the new taxon presented here, could have been a way to compensate for the implied constraints during prolonged episodes of aridity.

CONCLUSIONS

Specimens of small-sized titanosaurian morphotype of the Upper Cretaceous São José do Rio Preto Formation display a set of autapomorphies—and a unique combination of characters as well—that differentiate it from other titanosaurs, supporting the presence of a new taxon in the Bauru Basin: *Ibirania parva*. The fully-grown somphospondylous internal bone tissue associated with a high laminae and fossae development, plus the absence of visible neurocentral sutures in the axial remains, indicates a late ontogenetic stage to the type and referred specimens of this new taxon. Additional μ CT scan and histological data from holotypic materials also support this assignment (Type G and H bone tissues, ranging from the HOS 13–14), ruling out the possibility that the small size exhibited by *Ibirania parva* specimens are due they belonged to immature individuals.

Phylogenetic analyses retrieved *Ibirania parva* deeply nested in Saltasauridae, as a member of its less inclusive clade Saltosaurinae and sister-group to the clade formed by the Patagonian species *Rocasaurus muniozi* and *Bonatitan reigi*. Some taxa included in Saltosaurinae are already known by displaying a noticeable reduction on its body sizes, being *Ibirania parva* the first identified as a nanoid taxon through histological data.

The geological evidence from Vila Ventura fossil-bearing sites allows us to infer the possible paleoenvironmental and paleoecological dynamics from this ecosystem, which was established there during the late Santonian to early Campanian time-interval (Late Cretaceous). The scenario in

question corresponds to a braided fluvial system of a flood-plain, under the strong influence of well-marked seasonality and predominantly arid climate. This environment could acquire peculiar ecophysiological settings during the dry seasons, causing different selective pressures in the resident biota. We propose that the presence of nanoid taxa outside an insular environment may be explained by a probable phyletic nanism trend.

The nanism observed in *Ibirania parva* is associated with the evolution of an endemic fauna in response to the stressed environment conditions of São José do Rio Preto Formation, characterized by prolonged drought periods. *Ibirania parva* represents the first unequivocal nanoid titanosaur reported from South America at this point and indicates the occurrence of nanism processes also in non-insular environments driven by recurring climatic and ecophysiological patterns.

ACKNOWLEDGMENTS

We thank the following colleagues for allowing access to the specimens deposited under their care: R. Machado, R. C. Silva (MCT/DGM of CPRM-RJ), L. Barbosa, S. A. K. Azevedo (MN-UFRJ), S. A. S. Tavares (MPMA), L. S. Paschoa (MPPC), T. S. Marinho, J. C. G. Silva Jr., L. C. B. Ribeiro (CPPLIP-UFTM), J. C. Corral, J. Alonso (MCNA), B. Madarieta (MVHMC-UPV), F. Ortega (UNED), J. Le Loeuff (MDE), G. Garcia, X. Valentin (UP), S. Maidment, P. Barrett (NHM), and V. Codrea (UBB). We are grateful to V. Zurriaguz (CONICET-URN), P. Mocho (IDL-UL), D. Pol (CONICET-MEF), and J. A. Wilson Mantilla (MP-UMICH) for providing photographs of important specimens and whose comments and suggestions enhanced the conceptualization of this manuscript. The authors are also indebted to S. Lages (UFMG) for his reconstructions of the specimens studied here, to L. B. dos R. Fernandes for her collaboration in collecting part of the fossil material, and to P. Morgato for preparing the thin sections. CT scan imagery was possible through the staff efforts of the Laboratório Multiusuário de Processamento de Imagens de Microtomografia Computadorizada de Alta Resolução (MZ-USP) and of the Laboratório de Tomografia Computadorizada do Instituto Médico Legal de São Paulo. We would like to acknowledge P. Saldiva, M. P. Santos, E. Cardoso, and the rest of the FM-USP team for conducting the fossil tomography. We are grateful to reviewers C. Griffin and C. Woodruff and the editor J. A. Wilson Mantilla, whose comments and suggestions greatly improved this paper. This work was supported by scholarships from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES - Financial Code #001 to BAN and AMG), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq fellow # 130.280/2018-6 to BAN and # CNPq 131.777/2018-1 to TA), and by a research grant from Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP proc. 2011/50206-9 to HZ). The authors are also deeply grateful to *Colecionadores de Ossos*TM and their Crowdfunder's, for supporting part of the costs and analyses. The TNT software v1.5 was made freely available through the Willi Hennig Society (<http://www.lillo.org.ar/phylogeny/tnt/>). This paper was originally intended to be published in a special volume of the Anais da Academia Brasileira de Ciências honoring Diogenes De Almeida Campos but had to be withdrawn after final

acceptance due to technical issues. Nevertheless, we would like to express our gratitude for the profound and enduring contribution given by Dr. D. Campos to Brazilian Palaeontology.

REFERENCES

- Apesteguía, S. (2002). Greater Gondwana and the Kawas Sea coastal tetrapod fauna (Campanian–Maastrichtian). *Boletim do 6º Simpósio sobre o Cretáceo do Brasil / 2º Simposio sobre el Cretácico de América del Sur* (pp. 1–6). São Pedro.
- Apesteguía, S. (2004). *Bonitasaura salgadoi* gen. et sp. nov.: a beaked sauropod from the Late Cretaceous of Patagonia. *Naturwissenschaften*, 91(10), 493–497.
- Apesteguía, S., Soto Luzuriaga, J. E., Gallina, P. A., Granda, J. T., & Guaman Jamarillo, G. A. (2020). The first dinosaur remains from the Cretaceous of Ecuador. *Cretaceous Research*, 108, 104345.
- Aureliano, T., Ghilardi, A. M., Silva Jr., J. C. G., Martinelli, A. G., Borges Ribeiro, L. C., Marinho, T. S., Fernandes, M. A., Ricardi-Branco, F., & Sander, P. M. (2020). Influence of taphonomy on histological evidence for vertebral pneumaticity in an Upper Cretaceous titanosaur from South America. *Cretaceous Research*, 108, 104337.
- Aureliano, T., Nascimento, C. S., Fernandes, M. A., Ricardi-Branco, F., & Ghilardi, A. M. (2021a). Blood parasites and acute osteomyelitis in a non-avian dinosaur (Sauropoda, Titanosauria) from the Upper Cretaceous Adamantina Formation, Bauru basin, Southeast Brazil. *Cretaceous Research*, 118, 104672.
- Aureliano, T., Ghilardi, A. M., Navarro, B. A., Fernandes, M. A., Ricardi-Branco, F., & Wedel, M. J. (2021b). Exquisite air sac histological traces in a hyperpneumatized nanoid sauropod dinosaur from South America. *Scientific Reports*, 11, 24207.
- Averianov, A. O., & Efimov, V. (2018). The oldest titanosaurian sauropod of the Northern Hemisphere. *Biological Communications*, 63(3), 145–162.
- Averianov, A. O., & Skutschas, P. P. (2017). A new lithostrotian titanosaur (Dinosauria, Sauropoda) from the Early Cretaceous of Transbaikalia, Russia. *Biological Communications*, 62(1), 6–18.
- Azevedo, R. P. F., Candeiro, C. R. A., & Bergqvist, L. P. (2007). Primeiro Registro de Pós-cranianos de Titanosauria (Sauropoda) no Município de Alfredo Marcondes/ SP, Formação Adamantina (Turoniano–Santoniano), Bacia Bauru. *Anuário do Instituto de Geociências*, 30, 112–118.
- Bandeira, K. L. N., Brum, A. S., Pêgas, R. V., Cidade, G. M., Holgado, B., Cidade, A., & Souza, R. G. (2018). The Baurusuchidae vs Theropoda record in the Bauru Group (Upper Cretaceous, Brazil): a taphonomic perspective. *Journal of Iberian Geology*, 44(1), 25–54.
- Bandeira, K. L. N., Simbras, F. M., Machado, E. B., Campos, D. A., Oliveira, G. R., & Kellner, A. W. A. (2016). A new giant Titanosauria (Dinosauria: Sauropoda) from the Late Cretaceous Bauru Group, Brazil. *Plos One*, 11, e0163373.
- Batezelli, A. (2015). Continental systems tracts of the Brazilian Cretaceous Bauru Basin and their relationship with the tectonic and climatic evolution of South America. *Basin Research*, 29(S1), 1–25.
- Benton, M. J., Csiki, Z., Grigorescu, D., Redelstorff, R., Sander, P. M., Stein, K., & Weishampel, D. B. (2010). Dinosaurs and the island rule: The dwarfed dinosaurs from Hateg Island. *Palaeogeography Palaeoclimatology Palaeoecology*, 293(3–4), 438–454.
- Bertini, R. J., Santucci, R. M., & Arruda-Campos, A. C. (2001). Titanossauros (Sauropoda, Saurischia) no Cretáceo Superior continental (Formação Marília, Membro Echaporã) de Monte Alto, Estado de São Paulo, e correlação com formas associadas

- do Triângulo Mineiro. *Geociências*, 20(1–2), 93–103.
- Bonaparte, J. F. (1986). Les dinosaures (Carnosaurés, Allosauridés, Sauropodes, Cétosauridés) du Jurassique moyen de Cerro Córdo (Chubut, Argentine). *Annales de Paléontologie*, 72(4), 325–386.
- Bonaparte, J. F., & Coria, R. A. (1993). Un nuevo y gigantesco saurópodo titanosaurio de la Formación Río Limay (Albiano-Cenomaniense) de la Provincia del Neuquén, Argentina. *Ameghiniana*, 30(3), 271–282.
- Bonaparte, J. F., & Powell, J. E. (1980). A continental assemblage of tetrapods 389 from the Upper Cretaceous beds of El Brete, northwestern Argentina (Sauropoda-Coelurosauria-Carnosauria-Aves). *Mémoires de la Société Géologique de France, nouvelle série*, 139, 19–28.
- Borsuk-Białynicka, M. (1977). A new camarasaurid sauropod *Opisthocoelecaudia skarzynskii*, gen. n., sp. n. from the Upper Cretaceous of Mongolia. *Palaeontologia Polonica*, 37, 1–64.
- Bremer, K. (1994). Branch support and tree stability. *Cladistics*, 10(3), 295–304.
- Brochu, C. A. (1996). Closure of neurocentral sutures during crocodilian ontogeny: implications for maturity assessment in fossil archosaurs. *Journal of Vertebrate Paleontology*, 16(1), 49–62.
- Button, D. J., Barrett, P. M., & Rayfield, E. J. (2016). Comparative cranial myology and biomechanics of *Plateosaurus* and *Camarasaurus* and evolution of the sauropod feeding apparatus. *Palaeontology*, 59(6), 887–913.
- Button, D. J., Rayfield, E. J., & Barrett, P. M. (2014). Cranial biomechanics underpins high sauropod diversity in resource-poor environments. *Proceedings of the Royal Society B*, 281(1795), 20142114.
- Calvo, J. O., & González Riga, B. J. (2003). *Rinconsaurus caudamirus* gen. et sp. nov., a new titanosaurid (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia, Argentina. *Revista Geológica de Chile*, 30(2), 333–353.
- Calvo, J., González Riga, B., & Porfiri, J. D. (2007). A new titanosaur sauropod from the Late Cretaceous of Neuquén, Patagonia, Argentina. *Arquivos do Museu Nacional (Rio de Janeiro)*, 65(4), 485–504.
- Campos, D. A., & Kellner, A. W. A. (1999). On some sauropod (Titanosauridae) pelvises from the continental Cretaceous of Brazil. *Proceedings of the Second Gondwanan Dinosaur Symposium*, 15, 143–166.
- Campos, D. A., Kellner, A. W. A., Bertini, R. J., & Santucci, R. M. (2005). On a titanosaurid (Dinosauria, Sauropoda) vertebral column from the Bauru group, Late Cretaceous of Brazil. *Arquivos do Museu Nacional (Rio de Janeiro)*, 63(3), 565–593.
- Candeiro, C. R. A., Martinelli, A. G., Avilla, L. S., & Rich, T. H. (2006). Tetrapods from the Upper Cretaceous (Turonian–Maastrichtian) Bauru Group of Brazil: a reappraisal. *Cretaceous Research*, 27(6), 923–946.
- Cantino, P. D., & de Queiroz, K. (2020). *PhyloCode: a phylogenetic code of biological nomenclature*. CRC Press.
- Carballido, J. L., Pol, D., Otero, A., Cerda, I., Salgado, L., Garrido, A., Ramezani, J., Cúneo, N. R., & Krause, J. M. (2017). A new giant titanosaur sheds light on body mass evolution among sauropod dinosaurs. *Proceedings of the Royal Society B*, 284(1860), 20171219.
- Carballido, J. L., & Sander, P. M. (2014). Postcranial axial skeleton of *Europasaurus holgeri* (Dinosauria, Sauropoda) from the Upper Jurassic of Germany: implications for sauropod ontogeny and phylogenetic relationships of basal Macronaria. *Journal of Systematic Palaeontology*, 12(3), 335–387.
- Carballido, J. L., Scheil, M., Knötschke, N., & Sander, P. M. (2020). The appendicular skeleton of the dwarf macronarian sauropod *Europasaurus holgeri* from the Late Jurassic of Germany and a re-evaluation of its systematic affinities. *Journal of Systematic Palaeontology*, 18(9), 739–781.
- Castro, M. C., Goin, F. J., Ortiz-Jaureguizar, E., Vieytes, E. C., Tsukui, K., Ramezani, J., Batezelli, A., Marsola, J. C. A., & Langer, M. C. (2018). A Late Cretaceous mammal from Brazil and the first radioisotopic age for the Bauru Group. *Royal Society Open Science*, 5(5), 180482.
- Cerda, I., Chinsamy, A., Pol, D., Apaldetti, C., Otero, A., Powell, J. E., & Martínez, R. N. (2017). Novel insight into the origin of the growth dynamics in sauropod dinosaurs. *Plos One*, 12(6), e0179707.
- Cerda, I., & Salgado, L. (2011). Bone microstructure of the upper cretaceous titanosaur sauropod *Neuquensaurus australis* Lydekker, 1893. *Ameghiniana, Suplemento Resúmenes*, 48(4), R98–R99.
- Cerda, I., Salgado, L., & Powell, J. E. (2012). Extreme postcranial pneumaticity in sauropod dinosaurs from South America. *Paläontologische Zeitschrift*, 86(4), 441–449.
- Company, J. (2011). Bone histology of the titanosaur *Lirinosaurus astibiae* (Dinosauria: Sauropoda) from the latest Cretaceous of Spain. *Naturwissenschaften*, 98(1), 67–78.
- Coria, R. A., Filippi, L. S., Chiappe, L., García, R., & Arcucci, A. B. (2013). *Overosaurus paradasorum* gen. et sp. nov., a new sauropod dinosaur (Titanosauria: Lithostrotia) from the Late Cretaceous of Neuquén, Patagonia, Argentina. *Zootaxa*, 3683, 357–376.
- Csiki-Sava, Z., Buffetaut, E., Osi, A., Pereda Suberbiola, X., & Brusatte, S. L. (2015). Island life in the Cretaceous - faunal composition, biogeography, evolution, and extinction of land-living vertebrates on the Late Cretaceous European archipelago. *ZooKeys*, 469, 1–161.
- Curry Rogers, K. (2005). Titanosauria: a phylogenetic overview. In K. Curry Rogers, & J. A. Wilson (Eds.), *The Sauropods: Evolution and Paleobiology* (pp. 50–103). University of California Press.
- Curry Rogers, K. (2009). The postcranial osteology of *Rapetosaurus krausei* (Sauropoda: Titanosauria) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, 29(4), 1046–1086.
- Curry Rogers, K., & Kulik, Z. (2018). Osteohistology of *Rapetosaurus krausei* (sauropoda: titanosauria) from the upper cretaceous of Madagascar. *Journal of Vertebrate Paleontology*, 38(3), 1–24.
- Curry Rogers, K., Whitney, M., D’Emic, M., & Bagley, B. (2016). Precocity in a tiny titanosaur from the Cretaceous of Madagascar. *Science*, 352(6284), 450–453.
- D’Emic, M. D., & Wilson, J. A. (2011). New remains attributable to the holotype of *Neuquensaurus australis* (Dinosauria: Sauropoda): implications for saltasaurine systematics. *Acta Palaeontologica Polonica*, 56(1), 61–73.
- D’Emic, M. D., Wilson, J. A., & Williamson, T. E. (2011). A Sauropod Dinosaur Pes from the Latest Cretaceous of North America and the Validity of *Alamosaurus sanjuanensis* (Sauropoda, Titanosauria). *Journal of Vertebrate Paleontology*, 31(5), 1072–1079.
- Dal Sasso, C., Pierangelini, G., Famiani, F., Cau, A., & Nicosia, U. (2016). First sauropod bones from Italy offer new insights on the radiation of Titanosauria between Africa and Europe. *Cretaceous Research*, 64, 88–109.
- de Queiroz, A., Cantino, P. D., & Gauthier, J. (Eds.) (2020). *Phylonoms: a companion to the PhyloCode*. CRC Press.
- de Souza, L. M., & Santucci, R. M. (2014). Body size evolution in Titanosauriformes (Sauropoda, Macronaria). *Journal of Evolutionary Biology*, 27(9), 2001–2012.
- Delcourt, R., & Iori, F. V. (2018). A new Abelisauridae (Dinosauria: Theropoda) from São José do Rio Preto Formation, Upper

- Cretaceous of Brazil and comments on the Bauru Group fauna. *Historical Biology*, 32(3), 1–8.
- Derby, A. O. (1895). Notas sobre a geologia e paleontologia de Matto Grosso. *Arquivos do Museu Nacional (Rio de Janeiro)*, 9, 59–88.
- Dias Brito, D., Musacchio, E. A., Castro, J. C., Maranhão, M. S. A. S., Suárez, J. M., & Rodrigues, R. (2001). Grupo Bauru: Uma unidade continental do Cretáceo do Brasil – Conceções baseadas em dados micropaleontológicos, isotópicos e estratigráficos. *Revue de Paléobiologie*, 20(1), 245–304.
- Díez-Díaz, V., Demuth, O. E., Schwarz, D., & Mallison, H. (2020). The tail of the Late Jurassic sauropod *Giraffatitan brancai*: digital reconstruction of its epaxial and hypaxial musculature, and Implications for tail biomechanics. *Frontiers in Earth Science*, 8, 160.
- Díez-Díaz, V., Garcia, G., Pereda Suberbiola, X., Jentgen-Ceschino, B., Stein, K., Godefroit, P., & Valentin, F. (2018). The titanosaurian dinosaur *Atsinganosaurus velauciensis* (Sauropoda) from the Upper Cretaceous of southern France: new material, phylogenetic affinities, and palaeobiogeographical implications. *Cretaceous Research*, 91, 429–456.
- Díez-Díaz, V., Pereda Suberbiola, X., & Sanz, J. L. (2013a). The axial skeleton of the titanosaur *Lirainosaurus astibiae* (Dinosauria: Sauropoda) from the latest Cretaceous of Spain. *Cretaceous Research*, 43, 145–160.
- Díez-Díaz, V., Pereda Suberbiola, X., & Sanz, J. L. (2013b). *Lirainosaurus astibiae*: new insights into the best known European titanosaur. *European Association of Vertebrate Palaeontologists 11th Annual Meeting* (pp. 36). Villers-sur-Mer.
- Fedorov, A., Beichel, R., Kalpathy Cramer, J., Finet, J., Fillion-Robin, J.-C., Pujol, S., Bauer, C., Jennings, D., Fennessy, F., Sonka, M., Buatti, J., Aylward, S., Miller, J. V., Pieper, S., & Kikinis, R. (2012). 3D Slicer as an image computing platform for the Quantitative Imaging Network. *Magnetic Resonance Imaging*, 30(9), 1323–1341.
- Felsenstein, J. (1985). Phylogenies and the comparative method. *American Naturalist*, 125(1), 1–15.
- Fernandes, L. A., & Ribeiro, C. M. M. (2015). Evolution and palaeoenvironment of the Bauru Basin (upper Cretaceous, Brazil). *Journal of South American Earth Sciences*, 61, 71–90.
- Filippi, L. S., García, R., & Garrido, A. (2011). A new titanosaur sauropod dinosaur from the Upper Cretaceous of North Patagonia, Argentina. *Acta Palaeontologica Polonica*, 56(3), 505–520.
- Filippi, L. S., & Garrido, A. (2008). *Pitekunsaurus macayai* gen. et sp. nov., nuevo titanosaurio (Saurischia, Sauropoda) del Cretácico Superior de la Cuenca Neuquina, Argentina. *Ameghiniana*, 45(3), 575–590.
- Filippi, L. S., Salgado, L., & Garrido, A. (2019). A new giant basal titanosaur sauropod in the Upper Cretaceous (Coniacian) of the Neuquén Basin, Argentina. *Cretaceous Research*, 100, 61–81.
- Gallina, P. (2011). Notes on the axial skeleton of the titanosaur *Bonitasaura salgadoi* (Dinosauria–Sauropoda). *Anais da Academia Brasileira de Ciências*, 83(1), 235–246.
- Gallina, P., & Apesteguía, S. (2015). Postcranial anatomy of *Bonitasaura salgadoi* (Sauropoda, Titanosauria) from the Late Cretaceous of Patagonia. *Journal of Vertebrate Paleontology*, 35(3), e924957.
- Gallina, P., & Otero, A. (2015). Reassessment of *Laplatasaurus araukanicus* (Sauropoda: Titanosauria) from the Upper Cretaceous of Patagonia, Argentina. *Ameghiniana*, 52(5), 487–501.
- García, R. A., Salgado, L., Fernández, M. S., Cerda, I. A., Paulina Carabajal, A., Otero, A., Coria, R. A., & Fiorelli, L. E. (2015). Paleobiology of titanosaurs: reproduction, development, histology, pneumaticity, locomotion and neuroanatomy from the South American fossil record. *Ameghiniana*, 52(1), 29–68.
- Ghilardi, A. M., Aureliano, T., Duque, R. R., Fernandes, M. A., Barreto, A. M., & Chinsamy, A. (2016). A new titanosaur from the Lower Cretaceous of Brazil. *Cretaceous Research*, 67, 16–24.
- Gil, L. M., Bandeira, K. L. N., Brusatte, S. L., Pereira, P. V. L. G., Kuhn, C. E. S., de Souza, A. B., Hirooka, S. S., & Candeiro, C. R. A. (2020). New records of Titanosauria (Dinosauria: Sauropoda) from the Upper Cretaceous of Mid-Western Brazil (Mato Grosso). *Journal of South American Earth Sciences*, 101, 102596.
- Gilmore, C. W. (1922). A new sauropod dinosaur from the Ojo Alamo Formation of New Mexico. *Smithsonian Miscellaneous Collections*, 72(14), 1–9.
- Gilmore, C. W. (1946). Reptilian fauna of the North Horn Formation of central Utah. *U.S. Government Printing Office*, 210-C, 1–53.
- Goloboff, P. A., Farris, J. S., & Nixon, K. C. (2008). TNT, a free program for phylogenetic analysis. *Cladistics*, 24(5), 774–786.
- Gomani, E. M. (2005). Sauropod dinosaurs from the early Cretaceous of Malawi, Africa. *Palaeontologia Electronica*, 8(1), 1–37.
- González, R., Cerda, I. A., Filippi, L. S., & Salgado, L. (2020). Early growth dynamics of titanosaur sauropods inferred from bone histology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 537, 109404.
- González Riga, B. J. (2003). A new titanosaur (Dinosauria, Sauropoda) from the Upper Cretaceous of Mendoza province, Argentina. *Ameghiniana*, 40(2), 155–172.
- González Riga, B., Lamanna, M., Ortiz David, L., Calvo, J., & Coria, J. P. (2016). A gigantic new dinosaur from Argentina and the evolution of the sauropod hind foot. *Scientific Reports*, 6(1), 19165.
- González Riga, B., Lamanna, M., Otero, A., Ortiz David, L., & Kellner, A. W. A. (2019). An overview of the appendicular skeletal anatomy of South American titanosaurian sauropods, with definition of a newly recognized clade. *Anais da Academia Brasileira de Ciências*, 91(2), e20180374.
- González Riga, B., Mannion, P. D., Poropat, S., Ortiz David, L., & Coria, J. (2018). Osteology of the Late Cretaceous Argentinean sauropod dinosaur *Mendozasaurus neguyelap*: implications for basal titanosaur relationships. *Zoological Journal of the Linnean Society*, 184(1), 136–181.
- Gould, S. J., & Macfadden, B. J. (2004). Gigantism, dwarfism, and Cope's rule: "nothing in evolution makes sense without a phylogeny". *Bulletin of the American Museum of Natural History*, 285, 219–237.
- Grellet-Tinner, G., & Zaher, H. (2007). Taxonomic identification of the Megaloolithid egg and eggshells from the Cretaceous Bauru Basin (Minas Gerais, Brazil): comparison with the Auca Mahuevo (Argentina) Titanosaurid eggs. *Papéis Avulsos de Zoologia*, 47, 105–112.
- Griffin, C. T., Stocker, M. R., Colleary, C., Stefanic, C. M., Lessner, E. J., Riegler, M., Formoso, K., Koeller, K., & Nesbitt, S. J. (2021). Assessing ontogenetic maturity in extinct saurian reptiles. *Biological Reviews*, 96(2), 470–525.
- Hechenleitner, E. M., Leuzinger, L., Martinelli, A. G., Rocher, S., Fiorelli, L. E., Taborda, J. R., & Salgado, L. (2020). Two Late Cretaceous sauropods reveal titanosaurian dispersal across South America. *Communications Biology*, 3, 622.
- Huene, F. v. (1929). Los saurísquios y ornitisquios del Cretáceo Argentino. *Anales del Museo de La Plata*, 3, 1–196.
- Huene, F. v. (1931). Verschiedene Mesozoisches Wirbeltierreste Aus Südamerika. *Neues Jahrbuch Mineralogie, Geologie, Paläontologie*, 66 (B), 181–191.
- Irmis, R. B. (2007). Axial skeleton ontogeny in the Parasuchia (Archosauria: Pseudosuchia) and its implications for ontogenetic determination in archosaurs. *Journal of Vertebrate Paleontology*,

- 27(2), 350–361.
- Jacobs, L., Winkler, D. A., Downs, W. R., & Gomani, E. M. (1993). New material of an Early Cretaceous titanosaurid dinosaur from Malawi. *Palaeontology*, 36(3), 523–523.
- Jain, S. L., & Bandyopadhyay, S. (1997). New titanosaurid (Dinosauria: Sauropoda) from the Late Cretaceous of central India. *Journal of Vertebrate Paleontology*, 17(1), 114–136.
- Kellner, A. W. A., & Azevedo, S. A. K. (1999). A new sauropod dinosaur (Titanosauria) from the Late Cretaceous of Brazil. *Proceedings of the Second Gondwanan Dinosaur Symposium*, 15, 111–142.
- Kellner, A. W. A., Campos, D. A., de Azevedo, S., Trotta, M. M., Henriques, D., Craik, M., & de Paula Silva, H. (2006). On a new titanosaur sauropod from the Bauru Group, Late Cretaceous of Brazil. *Boletim do Museu Nacional*, 74, 1–31.
- Kellner, A. W. A., Campos, D. A., & Trotta, M. M. (2005). Description of a titanosaurid caudal series from the Bauru Group, Late Cretaceous of Brazil. *Arquivos do Museu Nacional (Rio de Janeiro)*, 63(3), 529–564.
- Klein, D. C., & Sander, P. M. (2008). Ontogenetic stages in the long bone histology of sauropod dinosaurs. *Paleobiology*, 34(2), 247–263.
- Klein, N., Sander, P. M., Stein, K., Le Loeuff, J., Carballido, J. L., & Buffetaut, E. (2012). Modified laminar bone in *Ampelosaurus atacis* and other titanosaurs (Sauropoda): Implications for life history and physiology. *Plos One*, 7(5), e36907.
- Lacovara, K., Lamanna, M., Ibiricu, L., Poole, J. C., Schroeter, E. R., Ullmann, P. V., Voegelé, K. K., Boles, Z. M., Egerton, V. M., Harris, J. D., Martínez, R. D., & Novas, F. E. (2014). A Gigantic, Exceptionally Complete Titanosaurian Sauropod Dinosaur from Southern Patagonia, Argentina. *Scientific Reports*, 4, 6196.
- Lamm, E. T. (2013). Preparation and Sectioning of Specimens. In K. Padian, & E. T. Lamm (Eds.), *Bone histology of fossil tetrapods: advancing methods, analysis, and interpretation* (pp. 55–160). University of California Press.
- Leanza, H. A., Apesteguía, S., Novas, F., & de la Fuente, M. (2004). Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. *Cretaceous Research*, 25, 61–87.
- Lopes, R. P., & Buchmann, F. S. C. (2008). Fossils of titanosaurs (Dinosauria, Sauropoda) from a new outcrop in Triângulo Mineiro, southeastern Brazil. *Revista Brasileira de Paleontologia*, 11(1), 51–58.
- Lydekker, R. (1893). Contributions to the study of the fossil vertebrates of Argentina. I, the dinosaurs of Patagonia. *Anales del Museo de La Plata, Paleontología*, 2, 1–14.
- Machado, E. B., Avilla, L. S., Nava, W. R., Campos, D. A., & Kellner, A. W. A. (2013). A new titanosaur sauropod from the Late Cretaceous of Brazil. *Zootaxa*, 3701(3), 301–321.
- Maddison, W. P., & Maddison, D. R. (2011). *Mesquite: A Modular System for Evolutionary Analysis*. In (Version 3.61) <http://mesquiteproject.org>
- Magalhães-Ribeiro, C. M. (2002). Ovo e fragmentos de cascas de ovos de dinossauros, provenientes da região de Peirópolis, Uberaba, Minas Gerais. *Arquivos do Museu Nacional (Rio de Janeiro)*, 60(3), 223–228.
- Mannion, P. D., & Otero, A. (2012). A reappraisal of the Late Cretaceous Argentinean sauropod dinosaur *Argyrosaurus superbus*, with a description of a new titanosaur genus. *Journal of Vertebrate Paleontology*, 32(3), 614–638.
- Mannion, P. D., Upchurch, P., Jin, X., & Zheng, W. (2019). New information on the Cretaceous sauropod dinosaurs of Zhejiang Province, China: impact on Laurasian titanosauriform phylogeny and biogeography. *Royal Society Open Science*, 6(8), 191057.
- Marsh, O. C. (1878). Principal characters of American Jurassic dinosaurs, Part I. *American Journal of Science* (series 3), 16, 411–416.
- Martinelli, A. G., & Forasiepi, A. M. (2004). Late Cretaceous vertebrates from Bajo de Santa Rosa (Allen Formation), Río Negro Province, Argentina, with the description of a new sauropod dinosaur (Titanosauridae). *Revista del Museo Argentino de Ciencias Naturales, Nueva Serie*, 6(2), 257–305.
- Martinelli, A. G., Marinho, T. S., Filippi, L. S., Ribeiro, L. C., Fonseca Ferraz, M. L. d., Cavellani, C. L., & Teixeira, V. D. P. A. (2015). Cranial bones and atlas of titanosaurs (Dinosauria, Sauropoda) from Late Cretaceous (Bauru Group) of Uberaba, Minas Gerais State, Brazil. *Journal of South American Earth Sciences*, 61, 164–170.
- Martínez, R. D., Giménez, O., Rodríguez, J., Luna, M., & Lamanna, M. C. (2004). An articulated specimen of the basal titanosaurian (Dinosauria: Sauropoda) *Epachthosaurus sciutoi* from the early Late Cretaceous Bajo Barreal Formation of Chubut province, Argentina. *Journal of vertebrate Paleontology*, 24(1), 107–120.
- Mateus, O., Jacobs, L. L., Schulp, A. S., Polcyn, M. J., Tavares, T., Buta Neto, A., Morais, M. M., & Antunes, M. T. (2011). *Angolatitan adamastor*, a new sauropod dinosaur and the first record from Angola. *Anais da Academia Brasileira de Ciências*, 83(1), 221–233.
- Menegazzo, M. C., Catuneanu, O., & Chang, H. K. (2016). The South American retroarc foreland system: the development of the Bauru Basin in the back-bulge province. *Marine and Petroleum Geology*, 73, 131–156.
- Mitchell, J., & Sander, P. M. (2014). The three-front model: a developmental explanation of long bone diaphyseal histology of Sauropoda. *Biological Journal of the Linnean Society*, 112(4), 765–781.
- Novas, F., Salgado, L., Calvo, J., & Agnolín, F. L. (2005). Giant titanosaur (Dinosauria, Sauropoda) from the Late Cretaceous of Patagonia. *Revista del Museo Argentino de Ciencias Naturales, Nueva Serie*, 7(1), 37–41.
- Otero, A. (2010). The appendicular skeleton of *Neuquensaurus*, a Late Cretaceous saltasaurine sauropod from Patagonia, Argentina. *Acta Palaeontologica Polonica*, 55(3), 299–326.
- Otero, A., Carballido, J. L., Salgado, L., Canudo, J.-I., & Garrido, A. (2021). Report of a giant titanosaur sauropod from the Upper Cretaceous of Neuquén Province, Argentina. *Cretaceous Research*, 122, 104754.
- Owen, R. (1842). Report on British Fossil Reptiles. Part 2. Report - *British Association for the Advancement of Science*, 11, 60e204.
- Pacheco, J. A. (1913). Notas sobre a geologia do vale do Rio Grande a partir da foz do Rio Pardo até sua confluência com o Rio Paranaíba. *Boletim da Comissão Geográfica e Geológica do Estado de São Paulo*, 1, 33–38.
- Padian, K., Werning, S., & Horner, J. R. (2016). A hypothesis of differential secondary bone formation in dinosaurs. *Comptes Rendus Palevol*, 15(1–2), 40–48.
- Pol, D., & Escapa, I. H. (2009). Unstable taxa in cladistic analysis: identification and the assessment of relevant characters. *Cladistics*, 25(5), 515–527.
- Pol, D., Nascimento, P. M., Carvalho, A. B., Riccomini, C., Pires-Domingues, R. A., & Zaher, H. (2014). A new notosuchian from the Late Cretaceous of Brazil and the phylogeny of advanced notosuchians. *Plos One*, 9(4), e93105.
- Poropat, S. F., Kundrát, M., Mannion, P. D., Upchurch, P., Tischler, T. R., & Elliott, D. A. (2021). Second specimen of the Late Cretaceous Australian sauropod dinosaur *Diamantinasaurus matildae* provides new anatomical information on the skull and neck of early titanosaurs. *Zoological Journal of the Linnean Society*, 192(2), 610–674.

- Poropat, S. F., Upchurch, P., Mannion, P. D., Hocknull, S. A., Kear, B., Sloan, T., Sinapius, G. H. K., & Elliott, D. (2015). Revision of the sauropod dinosaur *Diamantinasaurus matildae* Hocknull et al. 2009 from the middle Cretaceous of Australia: implications for Gondwanan titanosauriform dispersal. *Gondwana Research*, 27(3), 995–1033.
- Powell, J. E. (1992). Osteología de *Saltasaurus loricatus* (Sauropoda–Titanosauridae) del Cretácico Superior del noroeste Argentino. In J. L. Sanz, & A. D. Buscalioni (Eds.), *Los Dinosaurios y Su Entorno Biotico: Actas del Segundo Curso de Paleontología in Cuenca* (pp. 165–230). Instituto “Juan de Valdes”.
- Powell, J. E. (2003). Revision of South American titanosaurid dinosaurs: paleobiological, palaeobiogeographical and phylogenetic aspects. *Records of the Queen Victoria Museum*, 111, 1–173.
- Ruta, M., Wagner, P. J., & Coates, M. I. (2006). Evolutionary patterns in early tetrapods. I. Rapid initial diversification followed by decrease in rates of character change. *Proceedings of the Royal Society B*, 273(1598), 2017–2111.
- Salgado, L. (1996). *Pellegrinisaurus powelli* nov. gen. et sp. (Sauropoda, Titanosauridae) from the Upper Cretaceous of Lago Pellegrini, northwestern Patagonia, Argentina. *Ameghiniana*, 33(4), 355–365.
- Salgado, L., Apesteguía, S., & Heredia, S. E. (2005). A new specimen of *Neuquensaurus australis*, a Late Cretaceous saltasaurine titanosaur from north Patagonia. *Journal of Vertebrate Paleontology*, 25(3), 623–634.
- Salgado, L., & Azpilicueta, C. (2000). A new saltasaurine dinosaur (Sauropoda, Titanosauridae) from the Rio Negro Province (Allen Formation, Upper Cretaceous), Patagonia, Argentina. *Ameghiniana*, 37(3), 259–264.
- Salgado, L., & Carvalho, I. S. (2008). *Uberabatitan ribeiroi*, a new titanosaur from the Marília Formation (Bauru Group, Upper Cretaceous), Minas Gerais, Brazil. *Palaeontology*, 51(4), 881–901.
- Salgado, L., & Coria, R. A. (2009). *Barrosasaurus casamiquelai* gen. et sp. nov., a new titanosaur (Dinosauria, Sauropoda) from the Anacleto Formation (Late Cretaceous: early Campanian) of Sierra Barrosa (Neuquén, Argentina). *Zootaxa*, 2222, 1–16.
- Salgado, L., & Powell, J. E. (2010). Reassessment of the vertebral laminae in some South American titanosaurian sauropods. *Journal of Vertebrate Paleontology*, 30(6), 1760–1772.
- Salgado, L., Coria, R. A., & Calvo, J. (1997). Evolution of titanosaurid sauropods. I: phylogenetic analysis based on the postcranial evidence. *Ameghiniana*, 34(1), 3–32.
- Salgado, L., Gallina, P., & Paulina Carabajal, A. (2015). Redescription of *Bonatitan reigi* (Sauropoda: Titanosauria), from the Campanian–Maastrichtian of the Rio Negro Province (Argentina). *Historical Biology*, 27(5), 525–548.
- Sallam, H. M., Gorscak, E., O'Connor, P. M., El-Dawoudi, I. A., El-Sayed, S., Saber, S. S., Kora, M. A., Sertich, J. W., Seiffert, E. R., & Lamanna, M. C. (2018). New Egyptian sauropod reveals Late Cretaceous dinosaur dispersal between Europe and Africa. *Nature Ecology and Evolution*, 2, 445–451.
- Sander, P. M., & Clauss, M. (2008). Sauropod gigantism. *Science*, 322(5899), 200–201.
- Sander, P. M., Klein, N., Stein, K., & Wings, O. (2011). Sauropod bone histology and its implications for sauropod biology. In N. Klein, K. Remes, C. Gee, & P. M. Sander (Eds.), *Biology of the Sauropod Dinosaurs: Understanding the Life of Giants* (pp. 276–302). Indiana University Press.
- Sander, P. M., Mateus, O., Lavent, T., & Knötschke, N. (2006). Bone histology indicates insular dwarfism in a new Late Jurassic sauropod dinosaur. *Nature*, 441(7094), 739–741.
- Santucci, R. M. (2002). *Revisão dos Titanosauridae (Saurischia, Sauropoda) do Cretáceo Superior continental da Bacia Bauru* (Dissertação de Mestrado, Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, Rio Claro).
- Santucci, R. M. (2008). First titanosaur (Saurischia, Sauropoda) axial remains from the Uberaba Formation, Upper Cretaceous, Bauru Group, Brazil. *Historical Biology*, 20(3), 165–173.
- Santucci, R. M., & Bertini, R. J. (2001). Distribuição paleogeográfica e biocronológica dos titanossauros (Saurischia, Sauropoda) do Grupo Bauru, Cretáceo Superior do sudeste brasileiro. *Revista Brasileira de Geociências*, 31(3), 307–314.
- Sanz, J., Powell, J. E., Le Loeuff, J., Martínez, R., & Pereda Suberbiola, X. (1999). Sauropod remains from the Upper Cretaceous of Laño (northcentral Spain). Titanosaur phylogenetic relationships. *Estudios del Museo de Ciencias Naturales de Alava*, 14(Número Especial 1), 235–255.
- Sereno, P. C. (1998). A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. *Neues Jahrbuch Fur Geologie Und Palaontologie-Abhandlungen*, 210(1), 41–83.
- Silva Jr., J. C. G., Marinho, T. S., Martinelli, A. G., & Langer, M. C. (2019). Osteology and systematics of *Uberabatitan ribeiroi* (Dinosauria; Sauropoda): a Late Cretaceous titanosaur from Minas Gerais, Brazil. *Zootaxa*, 4577, 401–438.
- Silva Jr., J. C., Martinelli, A. G., Iori, F. V., Marinho, T. S., Hechenleitner, E. M., & Langer, M. C. (2021). Reassessment of *Aeolosaurus maximus*, a titanosaur dinosaur from the Late Cretaceous of Southeastern Brazil. *Historical Biology*, 34(3), 1–9.
- Silva Jr., J. C. G., Martinelli, A. G., Ribeiro, L. C., & Marinho, T. S. (2017). Description of a juvenile titanosaurian dinosaur from the Upper Cretaceous of Brazil. *Cretaceous Research*, 76, 19–27.
- Stein, K., Csiki, Z., Rogers, K. C., Weishampel, D. B., Redelstorff, R., Carbadillo, J. L., & Sander, P. M. (2010). Small body size and extreme cortical bone remodeling indicate phyletic dwarfism in *Magyarosaurus dacus* (Sauropoda: Titanosauria). *Proceedings of the National Academy of Sciences*, 107(20), 9258–9263.
- Tomaselli, M. B., Ortiz David, L., & González Riga, B. (2021). Paleoenvironmental contexts of South American Cretaceous sauropod tracks. *Journal of South American Earth Sciences*, 110(Suppl. 2), 103393.
- Upchurch, P., Barrett, P. M., & Dodson, P. (2004). Sauropoda. In D. B. Weishampel, P. Dodson, & H. Osmólska (Eds.), *The Dinosauria (Second Edition)* (pp. 259–322). University of California Press.
- Upchurch, P., Mannion, P. D., & Taylor, M. P. (2015). The anatomy and phylogenetic relationships of “*Pelorosaurus*” *becklesii* (Neosauropoda, Macronaria) from the Early Cretaceous of England. *Plos One*, 10(6), e0125819.
- Van der Geer, A. A. E., Van den Bergh, G. D., Lyras, G. A., Prasetyo, U. W., Due, R. A., Setiyabudi, E., & Drinia, H. (2016). The effect of area and isolation on insular dwarf proboscideans. *Journal of Biogeography*, 43(8), 1656–1666.
- Wedel, M. J. (2003). The evolution of vertebral pneumaticity in sauropod dinosaurs. *Journal of Vertebrate Paleontology*, 23(2), 344–357.
- Wedel, M. J. (2007). What pneumaticity tells us about prosauropods, and vice versa. *Special Papers in Palaeontology*, 77, 207–222.
- Wedel, M. J., Cifelli, R. L., & Sanders, R. K. (2000). Osteology, paleobiology, and relationships of the sauropod dinosaur *Sauroposeidon*. *Acta Palaeontologica Polonica*, 45(4), 343–388.
- Weishampel, D. B., Csiki, Z., Benton, M. J., Grigorescu, D., & Codrea, V. (2010). Palaeobiogeographic relationships of the Hateg biota—Between isolation and innovation. *Palaeogeography*

- Palaeoclimatology Palaeoecology*, 293(3–4), 419–437.
- Whitlock, J. A. (2011). Inferences of diplodocoid (Sauropoda: Dinosauria) feeding behavior from snout shape and microwear analyses. *Plos One*, 6(4), e18304.
- Wilson, J. A. (1999). A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. *Journal of Vertebrate Paleontology*, 19(4), 639–653.
- Wilson, J. A. (2006a). Anatomical nomenclature of fossil vertebrates: standardized terms or lingua franca? *Journal of Vertebrate Paleontology*, 26(3), 511–551.
- Wilson, J. A. (2006b). An Overview of titanosaur evolution and phylogeny. *Actas de las III Jornadas sobre Dinosaurios y su Entorno* (pp. 169–190). Burgos.
- Wilson, J. A. (2012). New vertebral laminae and patterns of serial variation in vertebral laminae of sauropod dinosaurs. *Contributions from the Museum of Paleontology, the University of Michigan*, 32(7), 91–110.
- Wilson, J. A., & Carrano, M. T. (1999). Titanosaurs and the origin of “wide-gauge” trackways: A biomechanical and systematic perspective on sauropod locomotion. *Paleobiology*, 25(2), 252–267.
- Wilson, J. A., D’Emic, D. M., Ikejiri, T., Moacdieh, E. M., & Whitlock, J. A. (2011). A nomenclature for vertebral fossae in sauropods and other saurischian dinosaurs. *Plos One*, 6(2), e17114.
- Wilson, J. A., & Sereno, P. C. (1998). Early evolution and higher-level phylogeny of sauropod dinosaurs. *Journal of Vertebrate Paleontology*, 18(S2), 1–79.
- Wilson, J. A., & Upchurch, P. (2003). A revision of *Titanosaurus Lydekker* (Dinosauria - Sauropoda), the first dinosaur genus with a “Gondwanan” distribution. *Journal of Systematic Palaeontology*, 1(3), 125–160.
- Woodruff, D. C., Fowler, D. W., & Horner, J. R. (2017). A new multi-faceted framework for deciphering diplodocid ontogeny. *Palaeontologia Electronica* 20.3.43A: 1–53.
- Woodward, A. S. (1910). On a tooth of a Triassic dinosaur from Sao Paulo, Brazil. *Report of the British Association for the Advancement of Science*, 79(1909), 483.
- Woodward, H. N., & Lehman, T. M. (2009). Bone histology and microanatomy of *Alamosaurus sanjuanensis* (Sauropoda: Titanosauria) from the Maastrichtian of Big Bend National Park, Texas. *Journal of Vertebrate Paleontology*, 29(3), 807–821.
- Zaher, H., Pol, D., Carvalho, A. B., Nascimento, P. M., Riccomini, C., Larson, P. L., Juarez-Valieri, R., Pires Domingues, R. A., Da Silva Jr., N. J., & Campos, D. A. (2011). A Complete Skull of an Early Cretaceous Sauropod and the Evolution of Advanced Titanosaurians. *Plos One*, 6(2), e16663.
- Zurriaguz, V., & Cerda, J. I. (2017). Caudal pneumaticity in derived titanosaurs (Dinosauria: Sauropoda). *Cretaceous Research*, 73, 14–24.
- Zurriaguz, V., Martinelli, A. G., Rougier, G. W., & Ezcurra, M. D. (2017). A saltasaurine titanosaur (Sauropoda: Titanosauriformes) from the Angostura Colorado Formation (upper Campanian, Cretaceous) of northwestern Patagonia, Argentina. *Cretaceous Research*, 75, 101–114.
- Zurriaguz, V., & Powell, J. E. (2015). New contributions to the presacral osteology of *Saltasaurus loricatus* (Sauropoda, Titanosauria) from the Upper Cretaceous of northern Argentina. *Cretaceous Research*, 54, 283–300.

Editorial Note: Both this work and the nomenclatural acts it contains have been registered in the ZooBank. The work is permanently archived in the Online Archives LOCKSS and Portico.
 LSID urn:lsid:zoobank.org:pub:8B578EFC-D121-420C-AED8-5E836AC6E179

doi: 10.5710/AMGH.25.08.2022.3477

Submitted: 27 October 2021

Accepted: 25 August 2022

Published: 15 September 2022