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A small abelisaurid caudal vertebra from the Bauru Basin, Presidente Prudente Formation (Late Cretaceous), Brazil adds information about the diversity and distribution of theropods in central South America

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ABSTRACT

Abelisauridae is a diverse clade of theropod dinosaurs, geographically well-distributed especially in the southern continents during the Cretaceous. The record of abelisaurids in South America comes mainly from Patagonia, whereas in Brazil they are mostly represented by numerous dental crowns and isolated bones, with few formally named species, mostly coming from the Late Cretaceous beds of the Bauru Group. In this contribution, we describe a small abelisaurid mid-caudal vertebra (LPRP/USP L0020) from the Presidente Prudente Formation, Bauru Group. LPRP/USP L0020 bears several abelisaurid features, such as an almost flat ventral surface, a poorly constrict centrum, lack of pneumatization, and distally positioned transverse processes. Body length estimation suggest that LPRP/USP L0020 belonged to a roughly 3.4 m long adult animal, representing one of the smallest known abelisaurids. The discovery of LPRP/USP L0020 indicates that Late Cretaceous abelisaurids from central South America were more diverse in body size than previously known, and possibly as diverse as their Patagonian counterparts.

1. Introduction

Abelisauridae is a large and diverse group of theropod dinosaurs known by having very distally reduced forearms, shortened and thick skulls, which are broadly distributed in the southern continents from the Middle Jurassic to the Late Cretaceous (Carrano and Sampson, 2008; Delcourt, 2018; Novas et al., 2013; Zaher et al., 2020), with sparce records in Europe (Tortosa et al., 2014). The knowledge about this group comes mainly from Patagonia, with several described species (Novas et al., 2013), and Madagascar, which yielded many specimens of *Majungasaurus crenatissimus* (Krause et al., 2007). In Brazil, abelisaurid remains are mostly composed of dental crowns and usually correspond to medium and large animals (Delcourt et al., 2020a). Although few species have been named (Delcourt and Iori, 2018; Iori et al., 2021; Kellner and Campos, 2002; Zaher et al., 2020), the increasing record of the group indicates that, despite the poor preservation (Bandeira et al., 2018), it could be as diverse in south-central Brazil as in Patagonia.

The general morphology of abelisaurids is rather peculiar compared to that of other theropods by having extremely short skulls and almost vestigial arms (Bonaparte et al., 1990; Canale et al., 2009; Delcourt, 2018; Sampson and Witmer, 2007), but the caudal vertebrae of the South American abelisaurids are also peculiar. Their transverse processes can be anteroposteriorly or only anteriorly projected, increasing the rigidity of the tail (Méndez, 2014; Persons and Currie, 2011). In general, vertebral length has a strong correlation with body length, representing an adequate proxy for size estimates of incomplete specimens (Grillo and Delcourt, 2017). In turn, dimensional estimates can help understanding the diversity of past environments (e.g., Canale et al., 2016).

In the present contribution, we describe a middle caudal vertebra of a small abelisaurid from the Bauru Basin, which helps to understand the diversity and distribution of this group in central South America.

2. Institutional abbreviations

DGM, Divisão de Geologia e Mineralogia, extint section of Departamento Nacional de Produção Mineral (DNPM), currently Agência Nacional de Mineração (ANM), Rio de Janeiro, Brazil; **FMNH**, Field Museum of Natural History, Chicago, IL, USA; **LPRP/USP**, Labo-

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ratório de Paleontologia de Ribeirão Preto, Ribeirão Preto, Brazil; **MMCh-PV**, Museo Paleontológico "Ernesto Bachmann" Villa El Chocón, Neuquén, Argentina.

3. Geological settings

The Bauru Basin occupies an area of nearly 370,000 km^2 in southern central South America (Fernandes and Ribeiro, 2015) in paleolatitudes compatible with the "Southern Hot Arid Belt" (Chumakov, 1995). Its sedimentary infilling, i.e., Bauru Supersequence (Milani et al., 2007), covers the Valanginian-Aptian basalts of the Serra Geral Formation (Bruckmann et al., 2014) and is subdivided into the Caiuá and Bauru groups, mostly deposited, respectively, in eolic and alluvial-fluvial environments (Batezelli, 2015). The age of both groups is disputed, with some authors suggesting that they are isochrones (Fernandes and Ribeiro, 2015). Yet, a more traditional proposal, in which the Caiuá Group is older than the Bauru Group, has been corroborated by more recent works (e.g., Menegazzo et al., 2016; Batezelli, 2015).

Starting with the division of the Bauru Group into the Caiuá, Santo Anastácio, Adamantina, and Marilia Formations (Soares et al., 1980), recent studies did not reach an agreement concerning the subdivision and age of those deposits, although it is relatively consensual that all their upper units belong to the Late Cretaceous (Batezelli, 2015; Castro et al., 2018; Fernandes and Coimbra, 2000; Fernandes and Ribeiro, 2015; Menegazzo et al., 2016; Pinheiro et al., 2018). According to those studies, the Bauru Group deposits cropping out in western São Paulo state have been variously assigned to the Vale do Rio do Peixe (i.e., Adamantina), Araçatuba, Marília, Presidente Prudente, and São José do Rio Preto formations. Whereas the former unit was assigned a post-Turonian (≤87.8 Ma) maximal age using high-precision U–Pb geochronology (Castro et al., 2018), the latter three are usually placed upper in the proposed stratigraphic schemes (Fernandes and Ribeiro, 2015; Pinheiro et al., 2018), so that "Campanian-Maastrichtian" represents a reasonable age approximation, which is in agreement with some biotratigraphic proposals (Menegazzo et al., 2016; Pinheiro et al., 2018). A post-Turonian age for the deposition of the Bauru Group is also consistent with the lack of unambiguous records of Carcharodontosauridae, a theropod group that gets extinct during that Stage in Patagonia (Meso et al., 2021).

The isolated caudal vertebra described here (LPRP/USP L0020) cames from "Chácara Califórnia" (21°47′28″ S; 50°51′46″ W), a small farm located in the eastern surroundings of Osvaldo Cruz, São Paulo (Fig. 1). It was found in 2010, along with turtle and crocodilian remains, during the excavation of a well. According to the local farmers, the fossils were recovered about 20 m deep, whereas sauropod remains were found on the surface nearby (Fig. 1). Following recent works (Fernandes and Ribeiro, 2015; Pinheiro et al., 2018), Osvaldo Cruz is within the surface exposure area of the Presidente Prudente Formation, as corroborated by some recent *in situ* evaluations (A. Batezelli, pers. com.).

4. Systematic paleontology

Dinosauria Owen, 1842.
Theropoda Marsh, 1881.
Ceratosauria Marsh, 1884.
Abelisauroidea Bonaparte and Novas, 1985.
Abelisauridae Bonaparte and Novas, 1985.
Abelisauridae indet.

5. Description and comparisons

The isolated caudal vertebra (LPRP/USP L0020) is relatively well preserved, although it lacks the neural spine, the zygapophyseal processes, and the distal end of the transverse processes (Fig. 2). Its surface is well preserved, showing muscle scars as usually happens in vertebrate fossils from the Bauru Basin (e.g., Brum et al., 2018; Delcourt and Iori, 2018; Langer et al., 2019). There is no apparent shape distortion, but the borders of the proximal and distal articular facets are slightly abraded. The total length of the centrum is 57.34 mm; proximal width and height are 28.42 mm and 24.75 mm, respectively; whereas

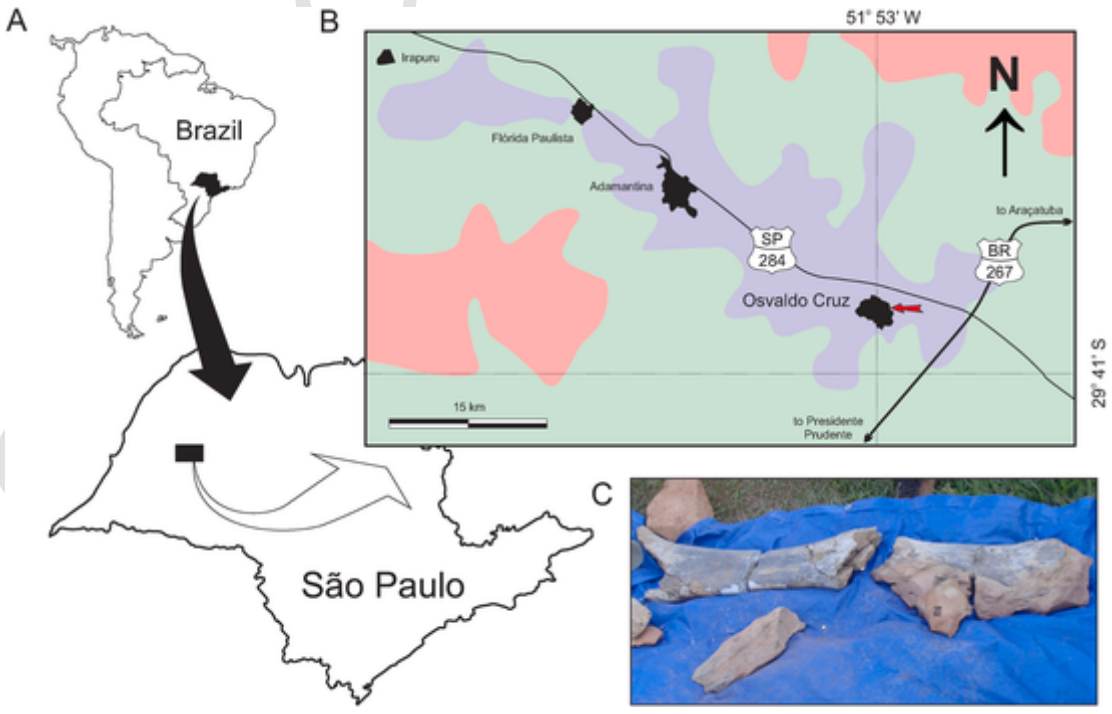

Fig. 1. Location and fossils from "Chácara California". A, location of the site in maps of South America, Brazil, and São Paulo state. B, Surface exposure map (from Fernandes and Ribeiro, 2015) of the Bauru Group units in the area the fossiliferous site, indicated by red arrow (purple, green, and orange shading mark, respectively, the Presidente Prudente, Vale do Rio do Peixe, and Araçatuba formations). C. sauropod remain found at the surface near the fossiliferous site.

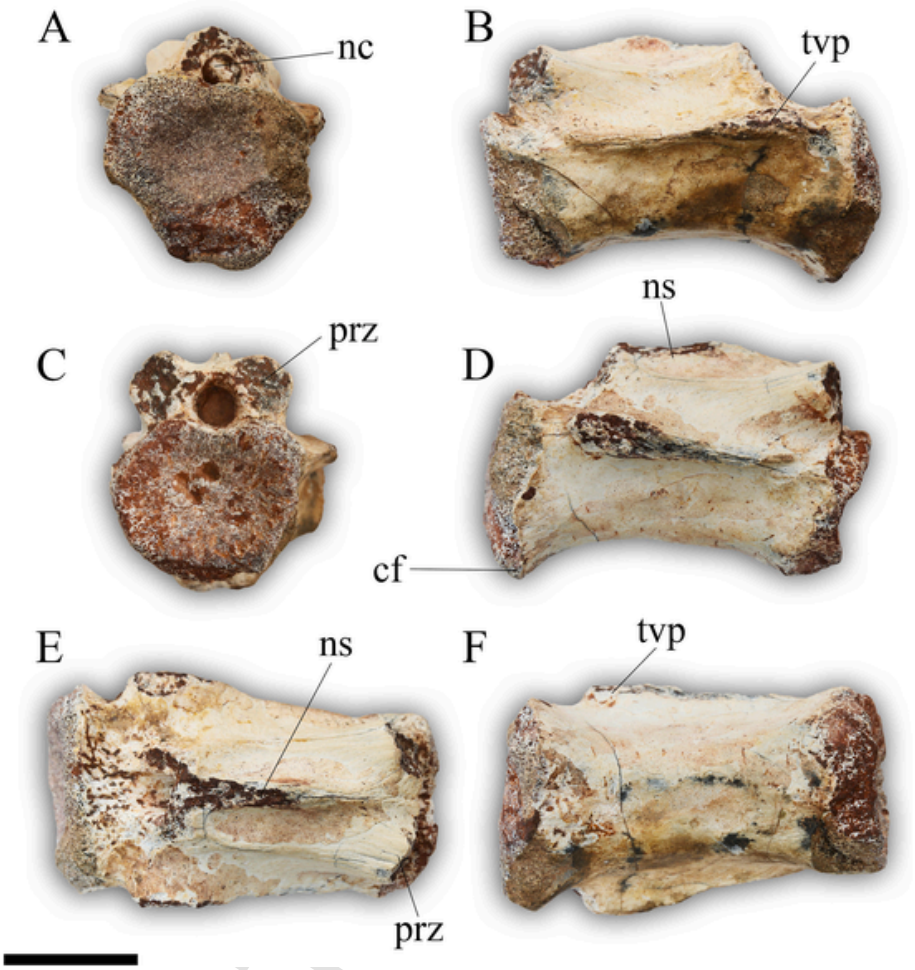

Fig. 2. Middle caudal vertebra LPPR/USP L0020 in distal (A), left lateral (B), proximal (C), right lateral (D), dorsal (E), and ventral (F) views. Abbreviations: cf, chevron facet; nc, neural canal; ns, neural spine; prz, prezygapophysis; tvp, tranverse process. Scale bar equals 20 mm.

distal width and height are 31.37 mm and 27.47 mm, respectively. The total height of the vertebra, as preserved, is 40.32 mm.

The centrum is amphicoelous, almost twice longer than tall with sub-circular articular facets. Such proportions suggest that the vertebra belongs to the middle position in the tail, probably distal or near the 14th vertebra, as seen in *Maj. crenatissimus* (FMNH PR 2100; O'Connor, 2007). The distal articulation for the chevron ends more ventrally than the proximal. There is no pneumatization on the lateral surfaces and the neurocentral suture is barely visible. The ventral surface is almost flat, as seen in *Ekrixinatosaurus novasi*, *Aucasaurus garridoi*, *Masiakasaurus knopfleri* (FMNH PR 2126), and *Elaphrosaurus bambergi* (Rauhut and Carrano, 2016), differing from the condition in *Eoabelisaurus mefi*, in which that surface is more rounded in the middle caudal vertebrae, as well as in *Ilokelesia aguadagrandensis* (Coria and Salgado, 1998) and *Vespersaurus paranaensis* (Langer et al., 2019), which the ventral surface is more concave. In ventral view, the centrum is not constricted, as seen in the middle caudal vertebrae of Noasauridae, such as *Mas. knopfleri* (FMNH PR 2126), *Ve. paranaensis* (Langer et al., 2019), and *El. bambergi* (Rauhut and Carrano, 2016), a feature that could be potentially synapomorphic for the group. On the contrary, LPRP/USP L0020 has an only slightly constricted centrum, as in Abelisauridae, such as *Eo. mefi*, *Maj. crenatissimus* (FMNH PR 2100), and *I. aguadagrandensis*. The articular facets are subcircular, with the distal slightly wider than tall, as seen in *Mas. knopfleri* (FMNH PR 2126). This condition differs from those of *Eo. mefi* and *Maj. crenatissimus* (FMNH PR 2100; O'Connor, 2007), which have almost circular distal facets.

The transverse processes are not fully preserved, but are placed in the distal half of the centrum and directed laterally, as in *Maj. crenatissimus* (FMNH PR 2100; O'Connor, 2007) and *Viavenator exxoni* (Filippi et al., 2018). Because their distal ends are incomplete, it is not possible to verify if they are anteroposteriorly expanded as in the other South American taxa, or if they taper as in *Maj. crenatissimus* (Méndez, 2014). Nevertheless, due to their short cross section, it seems that they were not laterally elongated, but short as in *Vi. exxoni* (Filippi et al., 2018). The position of the transverse processes also resembles that of *Mas. knopfleri* (FMNH PR 2126), although the processes are proportionally larger in this taxon than in *Maj. crenatissimus* (FMNH PR 2100) and LPRP/USP L0020. In *Ceratosaurus nasicornis*, *Aucasaurus garridoi*, *Ek. novasi*, *I. aguadagrandensis* (Méndez, 2014), *Eo. mefi*, *El. bambergi* (Rauhut and Carrano, 2016), and *Deltadromeus agilis* (Sereno et al., 1996) the transverse processes are placed in the proximodistal middle of the vertebra.

The zygapophyseal processes are not fully preserved, missing their distal ends. However, due to their thick cross section, we can assume that they were elongated and may have well surpassed the centrum border, as in other abelisauroids, such as *Maj. crenatissimus* (FMNH PR 2100; O'Connor, 2007), *Mas. knopfleri* (FMNH PR 2126), and possibly *Vi. exxoni* (Filippi et al., 2018). This condition differs from that of *C. nasicornis*, which has short postzygapophyses extending just slightly beyond the centrum (Madsen and Welles, 2000). As expected for theropod middle caudal vertebrae, there is no evidence of hyposphene-hypanthrum articulations. The spinopostzygapophyseal fossa (sensu Wilson et al., 2011) is proximodistally elongated, slightly deeper in its

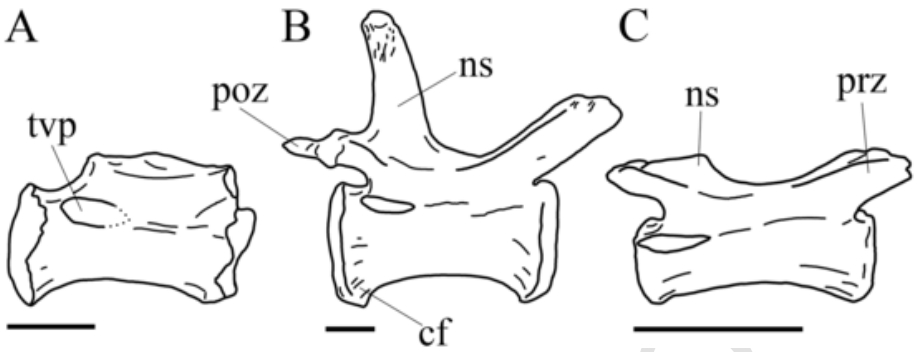

Fig. 3. Schematic drawings of the middle caudal vertebrae of LPR/USP L0020 (A), *Majungasaurus crenatissimus* (FMNH PR 2100), and *Masiakasaurus knopfleri* (FMNH PR 2126) in right lateral views. Abbreviations: cf, chevron facet; ns, neural spine; poz, postzygapophysis; prz, prezygapophysis; tvp, transverse process. Scale bars equal 20 mm.

distal portion, at the base of neural spine, as seen in several taxa, such as *Mas. knopfleri* (FMNH PR 2126), *D. agilis*, *Eo. mefi*, and *Maj. crenatissimus* (FMNH PR 2100).

The neural canal is circular in cross section and quite small compared with the articular surface of the centrum, such as in *C. nasicornis*, *El. bambergi*, *Eo. mefi*, *Maj. crenatissimus* (FMNH PR 2100). Instead, in *Ve. paranaensis* and *Mas. knopfleri* (FMNH PR 2126), the proportion between the neural canal and the centrum surface is smaller in both proximal and distal views.

6. Discussion

6.1. Taxonomic affinities

The record of non-avian theropods in the Bauru Basin is mostly composed by abelisauroid body fossils (de Souza et al., 2021; Delcourt and Iori, 2018; Iori et al., 2021; Langer et al., 2019), including numerous dental crowns (Delcourt et al., 2020b; Delcourt and Grillo, 2018; Ghilardi and Fernandes, 2011). Other theropod groups are rare, including undetermined (Delcourt and Grillo, 2014; Machado et al., 2008) and Unenlagiini (Brum et al., 2021; Candeiro et al., 2012) maniraptoriforms, as well as megaraptorans (Martinelli et al., 2013; Méndez et al., 2012).

Compared to the non-abelisauroid theropods know for the Bauru Basin, LPRP/USP L0020 lacks the pleurocoels of the middle and distal caudal centra of megaraptorans (Martinelli et al., 2013; Méndez et al., 2012). It also differs from the undetermined maniraptoriform DGM 930-R by lacking lateral foramina and having a flat ventral surface (Delcourt and Grillo, 2014) and from Unenlagiini middle caudal vertebrae by not having a very constricted and elongated centrum (Motta et al., 2016).

The taxonomic affinity of LPRP/USP L0020 to Abelisauridae is supported by several similarities it shares with other members of the group with preserved middle caudal vertebrae, such as an almost flat ventral surface, a poorly constrict centrum, lack of pneumatization, and distally placed transverse processes. Although the almost flat ventral surface and distal position of the transverse process are shared with noasaurids such as *Mas. knopfleri* (FMNH PR 2126), its proportions and general shape are typical of abelisaurids. Indeed, LPRP/USP L0020 and the 14th caudal of *Maj. crenatissimus* (FMNH PR 2100; O'Connor, 2007) are almost undistinguishable, although the latter is ca. 1.6 times longer than the former, suggesting that the Brazilian taxon was slightly smaller (Fig. 3). The neurocentral suture of LPRP/USP L0020 is faint and fully closed, suggesting that this abelisaurid could have reached full somatic growth at the time of its death.

6.2. Body size and the theropod diversity from the Bauru Group

Grillo and Delcourt (2017) used an allometric coefficient to estimate the body length of abelisauroid theropods, and a similar study was performed by Currie (2003) to assess the allometry of Asian and North American tyrannosaurids. Grillo and Delcourt (2017) found that the length of all studied vertebral centra developed isometrically and are strongly corelated with body length. Given the availability of material, the authors used caudal vertebrae 1–6 for their estimates, but we may assume that middle caudal vertebrae (such as LPRP/USP L0020) works for body-length approximations in abelisauroids. In this case, considering the mean body length (Grillo and Delcourt, 2017) and length of the 14th caudal centrum of *Maj. crenatissimus* (FMNH PR 2100; (O'Connor, 2007), LPRP/USP L0020 would belong to an animal around 3.4 m long, representing one of the smallest known abelisaurids. The specimen MMCh-PV 69, from the Late Cretaceous Candeleros Formation, northwest Patagonia, Argentina, has been estimated with a body mass of roughly 240 kg (Canale et al., 2016). Although its body length was not estimated (Canale et al., 2016), its mass is similar to that of *Herrerasaurus ischigualastensis* (~292 kg; Campione et al., 2014), which can reach between 3 and 5 m long (Langer, 2004). Also, the middle-sized *Niebla antiqua* (ca. 4-4.5 m) from Allen Formation, Patagonia, has a near body length of LPRP/USP L0020 (Rolando et al., 2021). These values suggest that MMCh-PV 69, *N. antiqua* and LPRP/USP L0200 could have a similar body size.

LPRP/USP L0020 corresponds to an abelisaurid slightly smaller (Fig. 4) than the mid-sized representatives of the group recovered in the Bauru Group, such as the ca. 4 m long "Cambará abelisauroid" (Grillo and Delcourt, 2017; Machado et al., 2013), the ca. 5 m long *Kurupi itaata* (Iori et al., 2021), and the 6 m long *Thanos simonattoi* (Delcourt and Iori, 2018). *Pycnonemosaurus nevesi*, from the Late Cretaceous of the Parecis Group (Delcourt, 2017), is significantly larger, nearly reaching 9 m (Grillo and Delcourt, 2017).

The record of medium to large sized theropods in the Late Cretaceous of the Bauru Group mainly includes abelisaurids, with the group largely represented by dental crowns (Delcourt et al., 2020a). This pattern may either result from abelisaurids replacing teeth more frequently (D'Emic et al., 2019), or because they were actually more abundant than other theropods (Bandeira et al., 2018). Although increased recently, the record of megaraptors in the Bauru Group is still restricted to few isolated vertebral centra (Martinelli et al., 2013; Méndez et al., 2012; Sales et al., 2018), suggesting they were not as abundant in central South America as in the southernmost part of the continent (Lamanna et al., 2020). This provincialism might have been driven by paleoclimatic conditions, what is partially consistent with the record of megaraptors in colder environments (Benson et al., 2012; Lamanna et al., 2020; Novas et al., 2019).

Fig. 4. Hypothetical representation of the Abelisauridae LPRP/USP L0020 during the Late Cretaceous of the Bauru Basin, Brazil. The environmental condition of central South America is regarded as semiarid; note the Podocnemidae turtle at first plane. Art by Johnny Pauly Vieira (Mingau).

7. Conclusion

The caudal vertebra of a small theropod (LPRP/USP L0020) from the Presidente Prudente Formation, Late Cretaceous of Brazil, bears several abelisaurid features, such as an almost flat ventral surface, a poorly constrict centrum, lack of pneumatization, and distally placed transverse processes. LPRP/USP L00220 is virtually undistinguishable from the 14th caudal vertebra of *Maj. crenatissimus* (FMNH PR 2100), suggesting a near position in the tail. LPRP/USP L0020 belonged to an animal roughly 3.4 m long, i.e., one of the smallest known abelisaurids. Its discovery increases the record of abelisaurids in the Bauru Group and corroborates the idea that this group was more abundant and diverse than other theropods in central South America during the Late Cretaceous.

CRediT authorship contribution statement

Rafael Delcourt: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Max Cardoso Langer:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Rafael Delcourt reports financial support was provided by State of Sao Paulo Reuter Foundation.

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