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Bite traces in a sauropod rib from the Upper Cretaceous São José do Rio Preto Formation (Bauru Basin), Brazil

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ABSTRACT

By studying fossil bite traces, we can reconstruct the behaviour of extinct organisms and better understand past communities, environments, and ecosystems. In this paper, we analyse bite traces on a fragmented sauropod rib from the Upper Cretaceous of the Bauru Basin, southeastern Brazil. The fossil was collected in the Ibirá municipality, São Paulo State, in the strata of the São José do Rio Preto Formation (Santonian-?Maastrichtian). The analysed specimen displays nine tooth drag traces on its external surface, produced by six or seven biting events. The traces consist of shallow linear grooves, with tapered ends and a serrated or smooth edge morphology. They can be classified as *Linichnus serratus, Linichnus bromleyi*, and *Knethichnus parallelum* and were produced by an organism with ziphodont dentition, probably an Abelisauridae. This work adds to the knowledge of the Bauru Basin palaeoecology and palaeobiology and expands the record of Mordichnia of Gondwana.

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Bioerosion; Theropoda; Crocodylomorpha; Ibirá; Praedichnia; Mordichnia

Introduction

Bite traces on bone surfaces can provide important information about ecological relationships in ancient ecosystems. In addition to revealing the past existence of intra and interspecific interactions, they can help, for example, to determine the feeding behaviour of extinct organisms, the manner of prey selection by predators, and can also be used as taphonomic indicators (Jacobsen 1998; D'Amore and Blumenschine 2012; Hone et al. 2018; Drumheller et al. 2020).

Bite traces on dinosaur bones have been found and described in various localities around the world, in strata of different ages, and interpreted as the result of cannibalism (Rogers et al. 2003; McLain et al. 2018; Drumheller et al. 2020; Dalman and Lucas 2021), predation or necrophagy (Currie and Jacobsen 1995; Robinson et al. 2015; Drumheller et al. 2020; Brown et al. 2021), play (Rothschild 2015), intraspecific aggression (Peterson et al. 2009), among others (Brown et al. 2021). Each published paper on the subject enriches our understanding of dinosaur ethology and their past ecological relationships.

Here we describe tooth traces associated with a ziphodont bite maker found on a sauropod rib from the São José do Rio Preto Formation (Upper Cretaceous), Bauru Basin, southeast Brazil. The traces described here confirm a trophic relationship often inferred for this geological context but which had yet no direct evidence formally described. This expands the palaeoecological and palaeobiological understanding of the basin and also adds to the knowledge of the Cretaceous dinosaur communities of western Gondwana.

Geological context

The Bauru Basin has a maximum thickness of 300 metres and an estimated area of 370,000 km^2, distributed mainly in the western part of the Brazilian states of São Paulo and Minas Gerais, in southeastern Brazil. In addition, it also extends into the northwestern Paraná State and southern Goiás State (Fernandes and Coimbra 1996) (Figure 1(a)). It is subdivided into two groups, the Caiuá and Bauru, often referred to as chrono-correlated and deposited during the Late Cretaceous (Fernandes and Coimbra 1996, 2000). More recently, however, this view has been challenged and there is currently a lack of consensus on the onset of the basin sedimentation, which may have taken place as early as the Early Cretaceous (Menegazzo et al. 2016; Batezelli 2017).

According to Fernandes and Coimbra (2000) and Fernandes and Ribeiro (2015), the Caiuá Group is essentially aeolian and would be composed of the Rio Paraná, Goio Erê, and Santo Anastácio formations. In turn, the Bauru Group is essentially fluvial and would be composed of the Uberaba, Vale do Rio do Peixe (VRP), Araçatuba, São José do Rio Preto (SJRP), Presidente Prudente (PP) and Marília formations. More recently the Marília Formation has been subdivided into Marília and Serra da Galga formations considering differences observed in strata from the northeastern portion of the basin (Soares et al. 2020).

The history of definitions and redefinitions of the Bauru Basin lithostratigraphy is very long and complex and to this day there is no consensus among authors (e.g., Soares et al. 1980, 2020; Suguio 1981; Fernandes and Coimbra 1996, 2000; Batezelli et al. 2003; Paula E Silva et al. 2003, 2005, 2006, 2009; Batezelli 2010; Fernandes and Ribeiro 2015). The proposal by Fernandes and Coimbra (2000), reinforced by Fernandes and Ribeiro (2015), is used here because, in our view, it best describes the lithological differences observed in the Ibirá region.

The SJRP Formation, the focus of the present study, is essentially formed by sandstones, often conglomeratic, accumulated in channel bars and fluvial plains of wide and shallow interbedded systems (Fernandes 2004). This unit belongs to the former Adamantina

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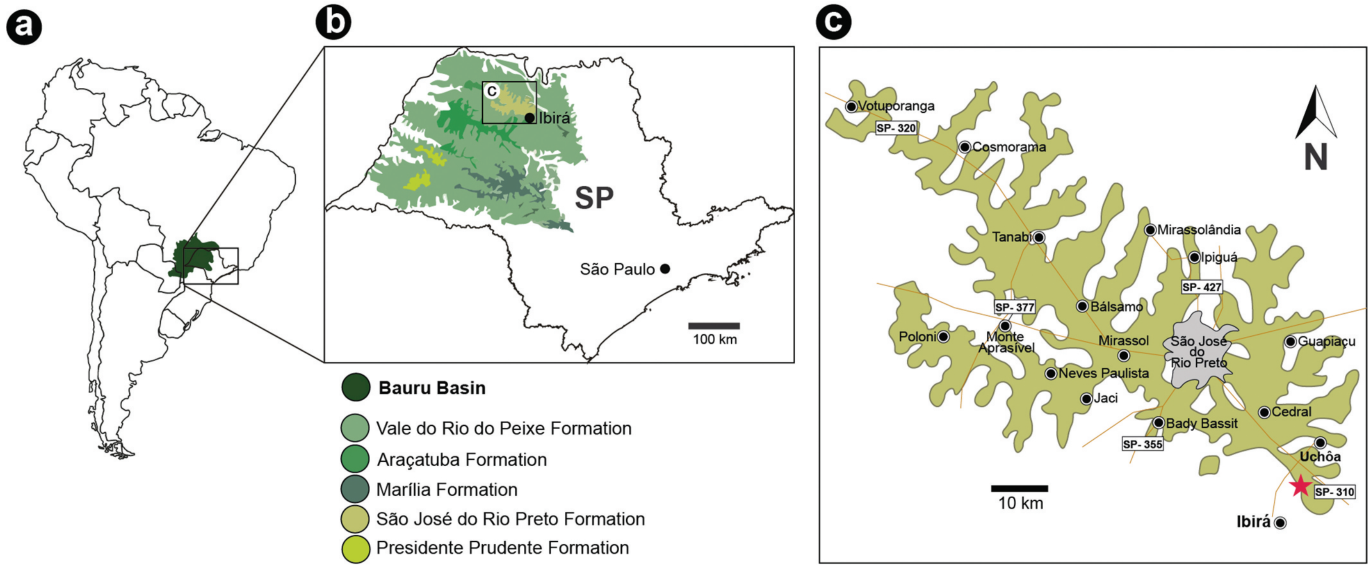

Figure 1. (a) Location of the Bauru Basin in South America. (b) Outcropping rocks of Bauru Group in São Paulo State. (c) São José do Rio Preto Formation context. The location where the fossil was found is marked by a red star. Modified from Delcourt and Iori (2018)

Formation, proposed by Soares et al. (1980), dismembered by Fernandes and Coimbra (2000), and is present in the highest regions of the São José do Rio Preto municipality, north of the Tietê River in São Paulo state (Fernandes and Coimbra 2000; Fernandes 2004) (Figure 1(b,c)). The estimated age for the SJRP Formation is Santonian or Santonian-Maastrichtian (Dias-Brito et al. 2001; Castro et al. 2018). It would be chronocorrelated with part of the former Marília Formation and its upper portion with the PP Formation (Fernandes and Coimbra 2000; Fernandes 2004; Fernandes and Ribeiro 2015

The fossil record of the SJRP Formation is abundant but mostly fragmentary, mainly occurring in the conglomeratic strata, where bone fragments and other bioclasts are very common (Fernandes and Coimbra 2000). Its fossil register includes microfossils (Dias-Brito et al. 2001); molluscs (Mezzalira 1974); vertebrate and invertebrate ichnofossils (Fernandes 2006; Souto 2010; Sperança et al. 2017); rhizoliths (Fernandes and Ribeiro 2015); teeth and bones of dinosaurs (Theropoda and Titanosauria) and Crocodyliformes (Arid and Vizotto 1963; Mezzalira 1989; Montefeltro et al. 2009; Iori et al. 2011; Marinho and Iori 2011; Méndez et al. 2014; Delcourt and Iori 2018; Pinheiro et al. 2018; Fernandes et al. 2019; Aureliano et al. 2021a, 2021b); in addition to fish, amphibian and chelonian remains (Mezzalira 1989; Ghilardi and Fernandes 2007; Paschoa et al. 2019; Hermanson et al. 2020). Most of the SJRP Formation fossils are disarticulated and fragmented (Fernandes and Coimbra 2000). For a more extensive listing of the Bauru Group fossils, see Fernandes and Ribeiro (2015) and Menegazzo et al. (2015).

Specifically in the region of the Ibirá municipality, São Paulo State, the source area of the material here described, the fossil record is abundant and known at least since the 1960s (Arid and Vizotto 1963). It mostly consists of teeth and isolated bones of dinosaurs and Crocodyliformes, disarticulated fragments of Testudines carapace, fish scales, coprolites, and isolated anuran bones (Ghilardi and Fernandes 2007; Ghilardi 2008; Montefeltro et al. 2009; Iori and Carvalho 2011; Marinho and Iori 2011; Delcourt and Iori 2018; Paschoa et al. 2019; Fernandes et al. 2019; Aureliano et al. 2021a, 2021b).

Bite traces in Bauru Basin fossils

One of the first records of bite traces described for the Bauru Basin was presented by Avilla et al. (2004). The authors describe an almost complete articulated tail of a Baurusuchidae (Crocodyliformes) with shallow circular punctures on the osteoderms. The fossil was found in the VRP Formation and the punctures were interpreted as bite traces of another Crocodylomorpha. As the traces show signs of regeneration and the fossil was mostly articulated, the authors interpreted them as the result of social interaction between the organisms involved, probably intraspecific combat.

After that, Kellner et al. (2006) mention and figure bite traces in the holotype material of *Maxakalisaurus topai*, also found in the VRP Formation. From the image available (see Kellner et al. 2006), (Figure 3), it is possible to observe at least three relatively deep oval punctures on a bone fragment, produced by large teeth with some labial-lingual compression. The authors suggest that the traces may be the result of necrophagy by theropod dinosaurs since isolated teeth of these animals were found in the same deposit. Similarly, Machado et al. (2013) also mention and figure the occurrence of several punctures interpreted as possible bite traces on the surface of an ilium fragment of *Brasilotitan nemophagus*, found in the PP Formation. From the image available (Machado et al. 2013, Figure 12) it is possible to observe several shallow circular traces distributed on the surface of the specimen. The authors highlight the need for further examination to confirm its ichnological nature.

Vasconcellos and Carvalho (2010) then, describe and try to interpret bite traces in a study that addresses the palaeoichnological assembly associated with *Baurusuchus salgadoensis* specimens found in the General Salgado municipality area, São Paulo State, VRP Formation. The described traces were identified in the holotype material of *B. salgadoensis* and consist of several circular to elliptical punctures, shallow to deep, located preferentially in the nasal and maxillary bones of the specimen. The authors suggest that this may be evidence of intraspecific competition or attempted predation by theropod dinosaurs. They exclude necrophagy because the traces show signs of regeneration.

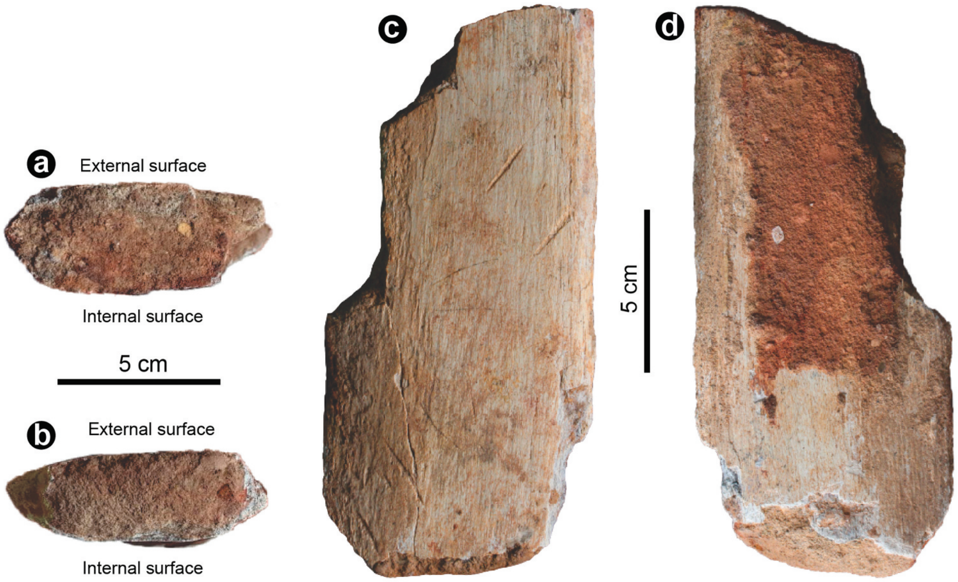

Figure 2. Specimen LPP-PV-208. (a) Proximal view. (b) Distal view. (c) External surface. (d) Internal surface.

Shortly after, Marinho and Iori (2011) described a large titanosaur osteoderm from the SJRP Formation, found in the Ibirá municipality area, São Paulo state. The authors identified three possible bite traces attributed to a large Crocodylomorpha or a theropod dinosaur. They consist of circular to elliptical relatively deep punctures, which led the authors to conjecture about the protective function of osteoderms in titanosaurs.

Furthermore, Araújo-Júnior and Marinho (2013) described bite traces on the pubis of a partially articulated Baurusuchidae specimen found in the VRP Formation. The traces consist of several shallow grooves, more or less parallel to each other and perpendicular to the long axis of the bone. The traces were interpreted as the result of scavenging.

More recently, Paes-Neto et al. (2018) described an epiphysis of a sauropod long bone from the Serra da Galga Formation with sub-elliptical punctures interpreted as possible bite traces. The authors, however, did not rule out bioerosion by insects. Finally, PVLGC et al. (2021) described a distal epiphysis of a sauropod fibula from the PP Formation, with several bite traces. These are mostly circular punctures of varying size and depths but some shallow grooves were also described. The authors interpreted the traces as a product of necrophagy by Itasuchidae crocodylomorphs.

Material and methods

The material analysed in this work is a fragmentary rib of an indeterminate sauropod under the register number LPP-PV-208. The specimen is currently housed at the Laboratory of Palaeoecology and Palaeoichnology (LPP) of the Universidade Federal de São Carlos (UFSCar), São Carlos municipality, São Paulo State, Brazil. The fragmentary rib was collected between 2005 and 2010, in the surroundings of Ibirá municipality, western São Paulo State, during one of the field works conducted under the coordination of MAF. The site where the material was collected is located at the coordinates 20°58'39.8 "S and 49°14'15.3"W, and is called "Sítio dos Irmãos Garcia", although also known as "Sítio Vaca Morta".

An analogical pachymeter was used to obtain the trace measures, including length, maximum width, and distance between traces. Measurements were made three times and the mean values were used as the final results. Some traces are interrupted, so we measured the length of their separate portions, as well as their total length.

We used a Canon EOS model 6D camera, with lenses 50 mm 1.4 and 100 mm 2.8, to acquire images. The specimen was illuminated with a spotlight at approximately 45°, providing better contrast and visualisation of the traces. For the detailed images, we photographed the specimen under the same lighting conditions with an Olympus SZ40 stereomicroscope using 40x magnification. This allowed us to identify features not observed with the naked eye.

The software Adobe Illustrator and Adobe Photoshop were used to make the figures. The contrast and brightness of the images were adjusted, when necessary, to facilitate the visualisation of the traces.

The terminology proposed by Seilacher (1953) was adopted, in which the term 'trace' is used to refer to modifications derived from biological activities, as opposed to the term 'mark'. Furthermore, we used the ichnotaxobases of Pirrone et al. (2014) and the classification of bite traces proposed by Hone and Watabe (2010), where: 'punctures' are deep tooth traces that penetrate the cortex of the bone; 'bite and drag' are traces in which the teeth have been sunk into the surface of the bone, penetrating the cortex and then pulled through it; and 'drag' are traces in which the teeth only touch the surface of the bone, without breaking through the cortex, and are pulled through it, leaving surface grooves.

To classify the curvature of traces, we used the proposal by D'Amore and Blumensehine (2009), and, finally, for ichnotaxonomy, we considered the recent review for bioerosion traces published by Wisshak et al. (2019).

Results

Description of the specimen

Specimen LPP-PV-208 (Figure 2) has a length of approximately 18 cm and a maximum width of 8.5 cm. It is a meso-distal fragment of a proximal dorsal rib of a sauropod. This can be stated due to the specimen size and oval distal and proximal D-shaped cross-section (see Waskow and Sander 2014). Furthermore, plank-shaped ribs are typical of Titanosauriformes (Wilson 2002). This is the most probable identification since all sauropods described from the Bauru

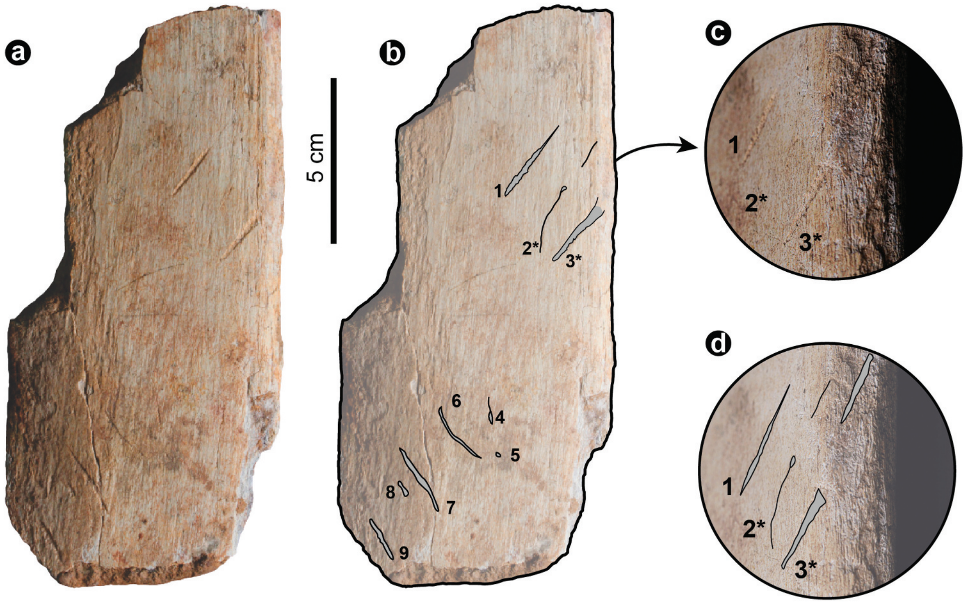

Figure 3. Bite traces identified on specimen LPP-PV-208. (a) Overview of the external surface of LPP-PV-208. (b) Highlight of the identified bite traces. (c) Detail showing continuity of trace 3 in the lateral side of the specimen. (d) Line drawing of traces observed in c. The traces indicated with "*" are composite.

Basin so far belong to this clade (e.g., Machado et al. 2013; Bandeira et al. 2016). Moreover, only Titanosauriformes survived until the latest Cretaceous (Upchurch and Barret 2004).

Description of the traces

On the external surface of the analysed specimen, we could identify at least 9 linear shallow grooves, interpreted as tooth traces (Figures 2(c) and Figure 3). They do not penetrate the cortex of the bone, therefore are considered here as drag traces. They were likely produced between six or seven distinct biting events. As there is still sediment adhered to about ⅔ of the inner part of the specimen (Figure 2(d)), it was not possible to analyse the presence of traces in this region. However, in the exposed inner area no recognisable traces were found. There are also some linear and irregular marks on the external surface of the specimen, which may be interpreted as trampling marks or post-diagenetic features. These were not considered or described in this study.

In the proximal part of the external surface of the specimen, we identified three bite traces (traces 1, 2, and 3), all positioned diagonally (between 50° and 85°) to the longitudinal axis of the specimen. These traces can be seen in Figure 3 and Figure 4 and their respective measurements are shown in Table 1. They are described below.

Trace 1 – a straight shallow groove (drag trace), with tapered, V-shaped, ends, 19.66 mm long and 1.75 mm wide (Figure 4(a,d)). It is positioned at 55° to the longitudinal axis of the specimen and has a serrated morphology, associated with the rupture of superficial bone fibres during tooth dragging. It is also possible to observe a positive relief in one of the borders, a feature associated with the plastic deformation of bone fibres by the pressure of the tooth against the bone surface during contact.

Trace 2 – a curved superficial groove (drag trace), divided into two parts, evidencing an interruption in the tooth contact with the bone surface during its formation (Figure 4(a,e)). It is sigmoid-shaped, very superficial, consisting only of a thin drag line on the bone surface. Its angle to the longitudinal axis of the specimen varies from 60 to 85°, with a curvature between 45 and 90°. The longest part of the trace measures 20.18 mm in length and presents variable depth and width, whereas the shortest part of the trace, located closer to the rib border, measures 7.59 mm in length. The total length of the trace (including its interruption) is 39.96 mm.

Trace 3 – a rectilinear shallow groove (drag trace), divided into two parts, extending from the lateral portion of the rib to its external surface (Figure 4(a,b,f)). Its total length is 49.70 mm and it has V-shaped tapering ends. This trace is positioned at 55° to the longitudinal axis of the specimen, has a similar depth to trace 1, and also has a serrated morphology. Its maximum width is approximately 1.95 mm. This compound trace is shortly interrupted near the edge of the rib. Its shortest part is located at the lateral surface of the specimen, while the longest is on the external surface of the rib, parallel to trace 1.

Traces 1 and 3 are straight, parallel to each other, have serrated edges, and similar depths. Trace 2, on the other hand, is at a different angle and displays a sigmoid curvature, denoting a movement of the head of the bite maker during its formation. We interpret that traces 1 and 3 were produced during the same bite event, whereas trace 2 would have been generated in a different one.

According to the way the bone fibres were ruptured and deformed in traces 1 and 3 (see Figure 4(b)), it is also possible to state that these traces were produced from the proximal outer portion of the rib, distally to its centre.

In the distal portion of the external surface of specimen LPP-PV-208, we identified six additional bite traces (traces 4, 5, 6, 7, 8, and 9), all positioned diagonally to the longest axis of the specimen, between 40° and 80°. These traces can be seen in Figure 3 and Figure 4 and their respective measurements are gathered in Table 1. They are described below.

Trace 4 – a short shallow linear groove (drag trace) with V-shaped tapering ends (Figure 4(c,g)). Its length is 8.35 mm and its maximum width is 1.10 mm. One of its edges is smooth and the other has evidence of scraping of the tooth serrated carinae, extending for 1.10 mm, at an angle of 40° to the main axis of the trace.

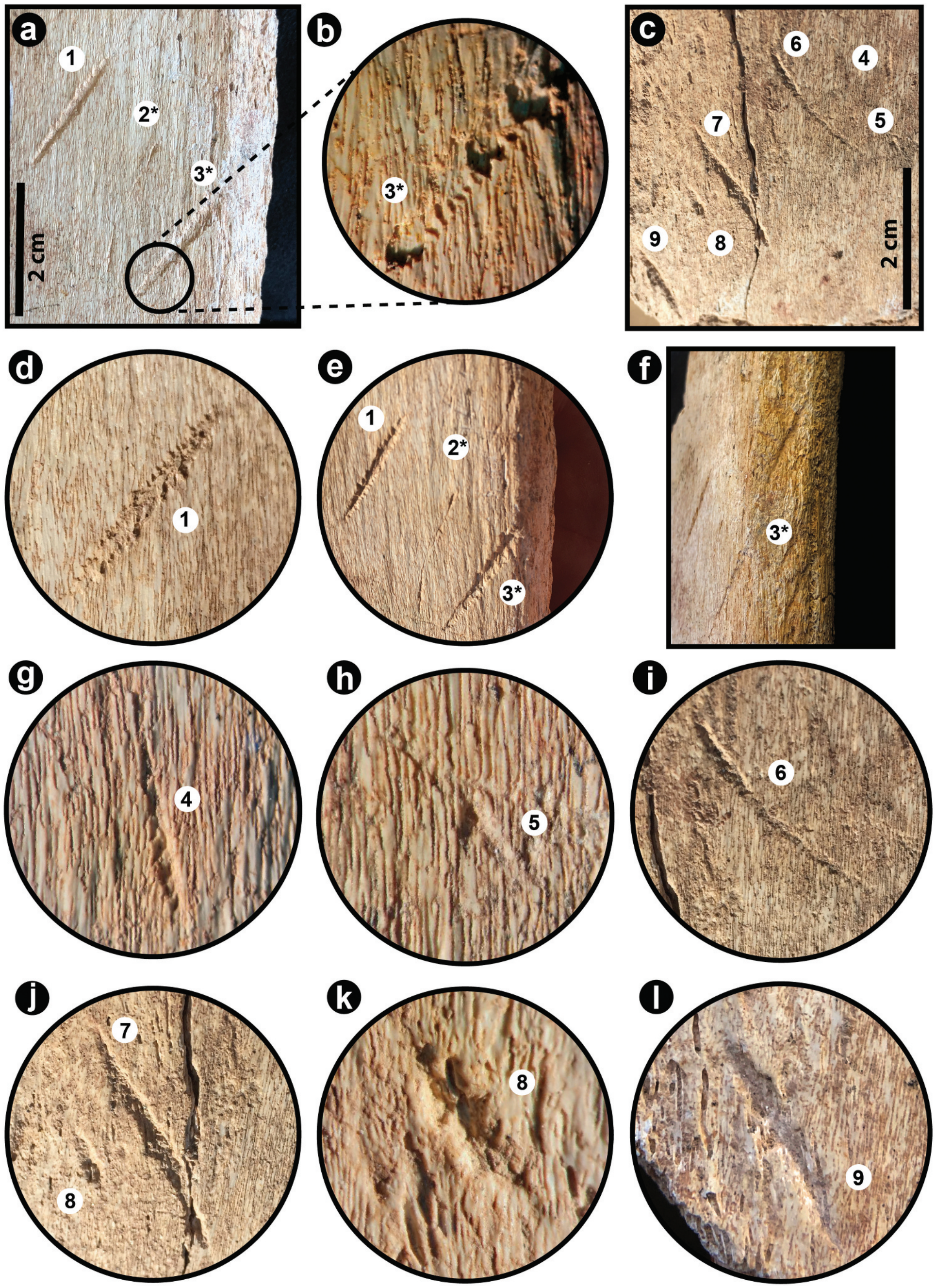

Figure 4. Traces 1 to 9. (a) Overview of the proximal part of the specimen LPP-PV-208. (b) Detail of trace 3, showing the serrated borders. (c) Overview of the distal part of the specimen LPP-PV-208. (d-l) Traces 1 to 9, respectively. The traces indicated with "*" are composite.

Table 1. Total length, maximum width, angle, and morphology of the traces identified in specimen LPP-PV-208. The traces indicated with "*" are composite.

Traces	1	2*	3*	4	5	6	7	8	9
Total length (mm)	19.66	39.96	49.70	8.35	2.42	20.16	23.10	4.64	15.27
Maximum Width (mm)	1.75	-	1.95	1.10	1.04	0.67	1.42	1.10	1.45
Angle	50°	50°	60° to 85°	80°		40° to 80°	55°	60°	55°
Edges	Serrated	Smooth	Serrated	Smooth	Smooth	Mostly Smooth	Smooth	Smoothly Serrated	Smoothly Serrated

Trace 5 – a very short shallow linear groove (drag trace), about 2.42 mm in length and 1.04 mm in maximum width (Figure 4(c,h)), with V-shaped tapering ends. It is positioned at 55° to the longitudinal axis of the specimen and has smooth edges.

Trace 6 – a curved linear groove (drag trace), with 20.16 mm in length and 0.67 mm in maximum width, with V-shaped tapering ends (Figure 4(c,i)). Its axis varies between 40 and 80° to the longitudinal axis of the specimen, with curvature between 45 and 90°. Its edges are mostly smooth, but serrations can be observed on its distal part.

Table 2. Distance between traces produced during the same bite.

Traces	1–3	7–9
Distance (mm)	22.99	19.59

Trace 7 – a linear groove (drag trace), with a length of 23.10 mm and a maximum width of 1.42 mm, practically straight, with its main axis at approximately 55° to the longitudinal axis of the specimen and V-shaped tapering ends (Figure 4(c,j)). This trace is deeper when compared to traces 4, 5, 6, and 8. Its edges are smooth.

Trace 8 – a very short groove (drag trace), with V-shaped tapered ends, a length of 4.64 mm, a maximum width of 1.10 mm, and smoothly serrated edges (Figure 4(c,k)). It is also possible to observe that one of the borders is in positive relief, denoting the plastic deformation of the superficial bone fibres, due to the pressure of the tooth on the bone surface.

Trace 9 – a linear groove (drag trace), 15.27 mm long, with a maximum width of 1.45 mm and V-shaped tapering ends. This trace is practically straight and has smoothly serrated edges (Figure 4(c,l)). Its main axis is at approximately 55° to the longitudinal axis of the specimen and its depth is similar to that of trace 6.

Since traces 7 and 9 are very similar in morphology and have coinciding angles, we consider they were produced during the same biting event. Traces 4 and 5, in turn, would have been produced in independent biting events and traces 6 and 8 do not allow us to interpret whether they belong to unique or independent biting events. Thus, this set of six traces, located in the most distal portion of the specimen, would have been generated between 4 and 5 distinct biting events.

Inter-trace spacing

The distances between traces interpreted as having been produced during the same bite are shown in Table 2.

Discussion

Ichnotaxonomical comparisons

The traces described here can be classified as belonging to the ichnofamily Machichnidae (Wisshak et al. 2019), which includes 'punctures to grooves, both of somewhat irregular outline, often in sets, in bone'. This ichnofamily is associated with the ethological category of Praedichnia (i.e., predation or scavenging traces; Ekdale 1985), subcategory Mordichnia (bite traces on bones; Müller 1962), and includes the ichnogenera (*Knethichnus* Jacobsen and Bromley 2009, *Linichnus* Jacobsen and Bromley 2009, *Machichnus* Mikuláš et al. 2006, *Mandaodonites* Cruickshank 1986, and *Nihilichnus;* Mikuláš, Kadlecová, Fejfar and Dvorák 2006). Besides these, other ichnogenera associated with bite traces were described, such as '*Heterodontichnites*' (Rinehart et al. 2006) and '*Brutalichnus*' (Mikuláš et al. 2006), however, the former was considered a junior synonym of *Mandaodonites* and the latter *nomen nudum* (Wisshak et al. 2019).

Nihilichnus includes 'roughly triangular, circular or ovoid holes or external pits, occurring solitarily or in groups, which may show recurring patterns' and *Mandaodonites* includes 'perforations of a dentition composed of conical teeth of various sizes, producing a sigmoid curve when printed on resistant substrates'. *Nihilichnus* characterises very well the traces figured and/or described by Avilla et al. (2004), Kellner et al. (2006), Vasconcellos and Carvalho (2010), Marinho and Iori (2011), Machado et al. (2013), PVLGC et al. (2021) and even Paes-Neto et al. (2018), but not the traces presented here.

Machichnus in turn, is characterised by 'shallow serial, parallel or subparallel grooves', arcuate in cross-section. This ichnogenus represents gnawing traces, which mainly affect the edges of the substrate. Although the traces described here consist of linear grooves, they are not serial nor arcuate in cross-section. Similarly, they also differ from the gnawing furrows recently described by Brown et al. (2021).

The traces described here, however, share the same characteristics of (*Linichnus* Jacobsen and Bromley 2009), including (*Linichnus serratus* Jacobsen and Bromley 2009 and *Linichnus bromleyi*; Muñiz et al. 2020), and are therefore classified as such. The diagnosis of *L. serratus* is 'single elongated groove of biogenic origin on skeletal material (e.g., bones, teeth). The groove, U- or V-shaped in transverse section, may only affect the surface of the bone, or bone-fibres may be cut through, recurved, or broken within the groove. The groove has a serrated morphology'. Traces 1 and 3 fit well in this description. The other traces, however, do not. Jacobsen and Bromley (2009) already observed that there could be a variation within *Linichnus* but only recently Muñiz et al. (2020) formalised the description of a second ichnospecies: *L. bromleyi*. The diagnosis of *L. bromleyi* is '*Linichnus* with a non-serrated edge', which describes well traces 2 and 4–9.

Besides the ichnogenus *Linichnus*, trace 4 also presents a feature similar to (*Knethichnus parallelum* Jacobsen and Bromley 2009), whose diagnosis consists of 'scraping structures in which serration traces extend as parallel grooves leading in some cases away from an initial groove'. Although subtle, it is possible to perceive a short dragging of the tooth serrated carina on the left margin of this trace.

Compared to the bite traces already described for the Bauru Basin, the traces presented here share some similarities to those of Araújo-Júnior and Marinho (2013), which are also dragging traces, probably *L. bromleyi*. Since the authors do not describe details of the morphology of the grooves, it is not possible to know for sure whether they have a serrated morphology. From the image (Figure 4 of Araújo-Júnior and Marinho 2013) it is only possible to recognise that they do not have tapered ends, which is different from what we observe here. Moreover, they also occur in a greater density (at least 50 linear traces were identified in an area of a few -cm^2), most have a curvature between 45 and 90° and some intersect each other, which evidences a different generating behaviour (perhaps gnawing?), and/or a distinct trace maker.

Identity of the bite maker

As the traces are relatively narrow (especially trace 2) and have tapered, V-shaped, ends, we can interpret a bite maker with very pointed teeth and/or teeth with a high degree of labial-lingual compression. In addition, the scraping trace of the carinae observed in trace 4 indicates that it had teeth with serrated carinae. The trace maker would therefore have a ziphodont dentition. Ziphodont dentition is characterised by long rows of relatively uniform, distally curved, labio-lingually compressed teeth with serrations present or absent (Benton 2004; D'Amore and Blumensehine 2009).

In the Bauru Basin, there are two groups of predators and potential bite makers that could have produced the traces observed in LPP-PV-208: theropod dinosaurs, including Abelisauridae, Megaraptora, and Coelurosauria; and Crocodyliformes, including large Notosuchia and Itasuchidae (e.g., Carvalho et al. 2005; Iori et al. 2011; Méndez et al. 2012; Delcourt and Grillo 2014; Delcourt and Iori 2018; Pinheiro et al. 2018). Each of these groups has specific dental features and different stratigraphic occurrences, which allows us to try to determine the probable responsible for the described traces.

According to Bandeira et al. (2018), Baurusuchidae (Notosuchia) is the second-best represented tetrapod clade in the Bauru Basin, with several species already found. All members of this group share a tall and robust skull, with heterodont ziphodont dentition, serrated carinae, and a reduction in the number of teeth (Carvalho et al. 2005). To date, however, no records of Baurusuchidae have been described in the SJRP Formation. Moreover, records of bites possibly attributed to Baurusuchidae have already been described by Avilla et al. (2004) and Vasconcellos and Carvalho (2010), and these have a distinct pattern from what is observed here.

The only record of Notosuchia from the SJRP Formation includes small omnivorous forms, with multicusped teeth (Montefeltro et al. 2009), probably related to 'advanced notosuchians' (Marinho et al. 2022). It is possible to discard them as bite makers by their size and also by the peculiar characteristics of their teeth (i.e., bulbous low crowns, slightly transversely flattened, apically opened with accessory cusps and discrete smooth carinae).

Although there are no records of Baurusuchidae and other large Notosuchia in the SJRP Formation, there is abundant evidence of other faunivorous Crocodyliformes, such as the Itasuchidae. These include semi-aquatic forms, represented locally by *Roxochampsa* and *Pepesuchus*. The dentition of Itasuchidae shows some labial-lingual compression, but very incipient. The teeth of *Roxochampsa* have obtuse tips (Pinheiro et al. 2018), which can exclude them as potential trace makers. *Pepesuchus*, on the other hand, has relatively pointed teeth, but like *Roxochampsa* has a 'crocodyloid occlusion' (Pinheiro et al. 2018), which would make it difficult to produce the traces presented here. In this way, we could also exclude them as potential trace makers. In addition, PVLGC et al. (2021) describe bite traces attributed to Itasuchidae, including punctures and possible drag traces, which are very different from the ones described here. Moreover, feeding traits of Crocodyliformes generally include circular or ovoid puncture marks, shallow or deep, associated or not with grooves. This is closely linked to the group's differentiated feeding behaviour, especially, their way of manipulating food (e.g., Njau and Blumenschine 2006; Noto et al. 2012; Boyd et al. 2013; Pujos and Salas-Gismondi 2020).

Based on the current evidence, we could exclude the hypothesis that the traces found in LPP-PV-208 would have been produced by Crocodyliformes from the Bauru Basin. This leads us to the second group of possible bite makers, the theropod dinosaurs. Isolated teeth of theropod dinosaurs are very common in the fossil record of the SJRP Formation and the variety of morphotypes indicates the presence of different groups of these organisms (Ghilardi and Fernandes 2011; Delcourt et al. 2020). In the Ibirá region, bone remains of possible Megaraptora and Abelisauridae have already been found (Méndez et al. 2012; Delcourt and Iori 2018), as well as teeth attributed to Maniraptora indet. and Unenlagiinae (Ghilardi and Fernandes 2011). The teeth of Unenlagiinae described so far do not have serrated carinae, which alone would exclude them as potential bite makers. Furthermore, the size of the teeth attributed to them is not compatible with the traces observed in LPP-PV-208. The teeth of Maniraptora indet. are also too small, making Abelisauridae and Megaraptora the most likely bite makers. The species of Abelisauridae known from the Ibirá region, *Thanos simonattoi*, was a medium-sized Abelisauridae, about 5.5 m long, whereas the possible Megaraptora collected in the same region would have a slightly larger size (Méndez et al. 2012; Delcourt and Iori 2018).

Abelisauridae, according to Bandeira et al. (2018), is the third most representative vertebrate group in the Bauru Basin. Abelisauridae includes robust, medium to large forms with relatively short skulls and reduced forelimbs (Bonaparte 1991; Sampson and Witmer 2007; Ruiz et al. 2011; Delcourt 2018). They have narrow teeth of variable labial-lingual compression and oval cross-section, with well-developed mesial and distal serrated carinae (Smith 2007; Delcourt et al. 2020). Megaraptora, on the other hand, have considerably smaller representativeness in the Bauru Basin, and its identification is still questioned by some authors (Motta et al. 2016; Delcourt and Iori 2018; Porfiri et al. 2018). The only records would be a caudal vertebra found in the SJRP Formation and another from the Uberaba Formation, identified as Megaraptora mainly due to its pneumaticity (Méndez et al. 2012; Martinelli et al. 2013). Megaraptora includes medium to large theropods, with proportionally large and robust forelimbs, elongated claws, and an elongated and narrow snout (Porfiri et al. 2007, 2014). Their teeth are distinguished from those of the Abelisauridae for being strongly recurved distally (Hendrickx et al. 2020).

Some bite traces already described in the literature, associated with theropods, have many similarities with those found in LPP-PV-208, which helps to reinforce the identification of a theropod bite maker (e.g., Rogers et al. 2003; Rivera-Sylva et al. 2012; Robinson et al. 2015; Augustin et al. 2020). The distinction between Abelisauridae and Megaraptora, on the other hand, is more difficult, as bite traces conclusively produced by Megaraptora have not yet been described. However, one would expect that, since they possess more distally curved teeth, Megaraptora would leave more mesial carinae scrapping traces. As this is not the case in the material here described, we conclude that the bite maker would most likely be an Abelisauridae. Furthermore, the traces seen in LPP-PV-208 share many similarities with that described by Rogers et al. (2003), which would reinforce a bite maker with Abelisauridae affinities.

Remarks on intertooth distance

The distance between teeth can help indicate the size of the bite maker and also give more clues about its possible phylogenetic affinity (e.g., Rogers et al. 2003; Brown et al. 2021). However, the spacing between the teeth can vary in many ways, so caution is needed (Hone and Chure 2018).

In the case reported here, there is no theropod cranial material from the SJRP Formation that allows direct comparison of intertooh distance. The only Theropoda cranial materials described for the Bauru Basin are the fragment of Abelisauridae maxilla from the PP Formation (Azevedo et al. 2013; Delcourt and Grillo 2018) and the partials maxilla and dentary of Unenlagiinae from the Marília Formation (Brum et al. 2021). The Abelisauridae maxilla has a completely preserved crown and 5 alveoli. By the proportions, the specimen represents a form of Abelisauridae larger than *Skorpiovenator* and *Majungasaurus*. The interdental distance of the specimen would be between 2 and 3 cm, which is equivalent to what is found here. Conversely, the material of Unenlagiinae described by Brum et al. (2021) has an interdental distance of about 1 cm, and the teeth lack serrations, being of a probable piscivorous form.

The PP Formation is chronocorrelated with the SJRP Formation. They were continuous in the past, only formed in different environmental contexts (Fernandes and Ribeiro 2015). It is possible that the same large theropod taxon is present in both units, as the Crocodyliformes *Pepesuchus*, found in both (Campos et al. 2011; Iori and Carvalho 2011).

As mentioned, it is problematic to try to identify the bite maker phylogenetic affinity by means of intertooth distance. For example, it is difficult to identify which teeth of the trace maker have contacted the bone surface. Hone and Chure (2018) note that feeding traces of theropods can generally be attributed to premaxillary teeth, as these provide greater control while feeding. However, the high intertooth distance found in LPP-PV-208 bite traces may indicate that they were produced either by maxillary or dentary teeth, as the distance between these is usually greater (e.g., Smith 2007). Distinct degrees of tooth wear and different phases of tooth eruption can affect the distance between traces left on a surface, which results in an overestimated intertooth distance value. Also, changes in head angulation are capable of altering the spacing between traces, which can lead the intertooth distance to be underestimated (Hone and Chure 2018). The difference in inter-trace distance between traces 1 and 3 and traces 7 and 9 may be a reflection of the second case but the first problem is more complex. Theropods continually lost their teeth and could grow new ones. Thus, irregularities in the tooth line could occur as the theropod lost some teeth and/or new teeth were growing. For this reason, we cannot rule out that the features described here were produced by premaxillary teeth, nor can we make a secure phylogenetic and/or size inference of the bite maker based solely on that.

Bite maker behaviour

It was possible to determine that at least six or seven different biting events left traces in LPP-PV-208. It is not possible, however, to determine the order in which they occurred but they were probably generated by the same bite maker since they share similarities and are very close together.

At least two of the described traces (2 and 3) evidence an interruption in the contact of the tooth with the bone surface during its formation. In the case of trace 2, this may reflect 1) a change in bite pressure along the tooth drag on the bone surface, 2) a movement of the predator’s head during the bite, 3) the encounter of resistance by some tissue soft attached to the bone during the tooth drag, or 4) the movement of the prey as it defends itself and tries to escape from the predator. We sustain that, in this case, the first three hypotheses are more plausible, considering the anatomical location of the bites. Trace 2 presents a sigmoid curvature, which may indicate that the interruption was caused by the head movement of the predator. Also, there is a variation in the trace depth and width, which can be caused either by variation in bite pressure or also by head movement. In the case of trace 3, the interruption can be explained simply by the transition of the tooth contact from the side of the rib to the external surface of it.

The curvatures of traces 2 and 6 suggest that they were probably formed by a medial-caudal movement of the head of the bite maker. In this movement, the jaw and teeth of the carnivore are positioned perpendicular to the body of the prey. The animal then moves its head laterally, then caudally, returning the head to a perpendicular position to the carcase. This movement helps to tear the flesh and/or skin of the prey (D’Amore and Blumensehine 2009). Also, the superficiality of traces 2 and 6 indicates that the teeth would have been further away from the bone during incidental contact.

The other traces found in LPP-PV-208 do not present curvature, i.e., they are straight or practically straight. The simple act of “pulling” the meat for defleshing during biting is capable of generating straight tooth traces or clusters of subparallel traces (Hone and Chure 2018). The subparallel trace clustering pattern involves the production of traces by teeth of the same tooth line (mandibular and/or maxillary) during the same bite event (D’Amore and Blumensehine 2009). As already argued, this would likely be the case for traces 1 and 3 and traces 7 and 9.

Trace 4, in its turn, evidence that the head of the bite maker was at a different angle to the rib surface when the bite was taken, perhaps laterally and/or frontally included, or that the trace maker changed the angle of the head during the bite (see D’Amore and Blumenschine 2012). The subtle scraping of the serrated carinae observed on one edge of this trace help support this assertion. Furthermore, the angle of trace 4 to the longitudinal axis of the rib is quite different from the others, approximately 80°, while the angle of the other traces varies mainly between 50 and 60°.

Unlike traces 1 and 3, most traces located distally in the specimen have smooth edges. Bite makers can generate different traces depending on several factors (see D’Amore and Blumensehine 2009; D’Amore and Blumenschine 2012). In the case of trace 4, its smooth morphology can be explained by the dragging of the tooth aligned to the bone fibres. Nonetheless, the angle and force applied to the bite, besides the characteristics of the bone, among others, can also generate variation in the edge morphology (Muñiz et al. 2020). It is particularly notable that traces 8 and 9 have edges with smooth serrations. This could be a simple taphonomic variation, due to different bone plasticity in response to a determinate biting force, for example, or it could mean that these wounds have undergone some regeneration. To affirm that there was regeneration it would be necessary to carry out a histological analysis. If these injuries have undergone regeneration, they were necessarily inflicted in an earlier event than traces 1 and 3, which do not show any signs of bone tissue recovery. This observation would be interesting as it could demonstrate that this anatomical region was commonly exploited as a vulnerable spot by the predator.

According to Filippi and Bellardini (2021), it would be possible to differentiate between bite traces produced by predation and necrophagy. According to these authors, necrophagy traces generally include concentrations of carnivore teeth traces on specific parts of certain bones and are often associated with some degree of disarticulation of skeletal elements. The condition of the specimen described here indicates that it was buried and fossilised when already fragmented and disarticulated. However, taking into account the sedimentary environment of the SJRP Formation (fluvial of interlaced channels), the disarticulation and fragmentation could be explained simply by hydric transportation. This is a common condition in fossils of the unit. Now, as the traces described here are superficial, some show no evidence of regeneration, and there are no signs that the prey resisted the bite maker behaviour, we interpret that they most likely originated *post mortem*, from a necrophagic behaviour. It is possible that the trace maker was responsible for taking down the sauropod but this cannot be stated based on the pieces of evidence available here.

Palaeoecological implications

The palaeofauna of the SJRP Formation has been more broadly studied in the last decades and records of several organisms have been recently described. This has greatly increased our understanding of the Bauru Basin palaeofauna and stratigraphy. Although the trophic relationship between Abelisauridae and Sauropoda has already been previously inferred for the basin (e.g., Kellner et al. 2006; Godoy et al. 2014), the evidence presented here confirms this interaction and also adds details on how this interaction occurred. Considering the already known record for the SJRP Formation,

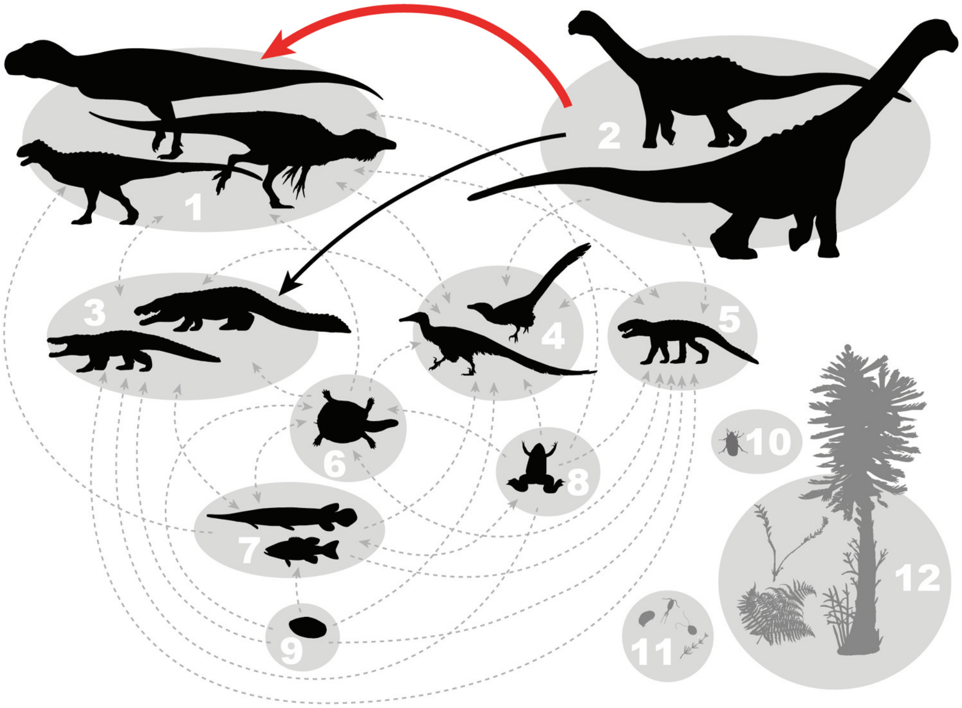

Figure 5. Reconstruction of the SJRP Formation trophic web. The solid red arrow indicates the direct relationship described in this paper. 1. Abelisauridae and Megaraptora; 2. Titanosauriformes; 3. Itasuchidae; 4. Maniraptora; 5. Notosuchia; 6. Chelonia; 7. Fishes; 8. Anura; 9. Molluscs; 10. Terrestrial invertebrates; 11. Freshwater zooplankton and algae; 12. Terrestrial plants. In grey are the group of organisms that would be the base of this ecosystem, some not yet represented by body fossils.

Abelisauridae, along with Megaraptora, would be the top predators of the unit, while Itasuchidae and maniraptoran dinosaurs would be intermediate predators in this ecosystem. Titanosauriformes occupied the medium and large herbivore niches, while small Notosuchia occupied the niche of smaller herbivores/omnivores. Amphibians, chelonians, fishes, and invertebrates would be the primary to tertiary consumers and terrestrial and aquatic plants would be at the base of this ecosystem. So far records of ornithischian dinosaurs have not been found in the basin, even after decades of exploration. This makes the structure of this ecosystem different from any other fossil locality in the world.

Figure 5 represents a trophic web of the unit, based on the records found so far, highlighting the specific trophic relationship reported here.

Remarks on Bauru Basin's tooth traces previously described

Most of the works published so far on bite traces from the Bauru Basin do not adopt an ichnotaxonomic approach, only the papers by Paes-Neto et al. (2018) and PVLGC et al. (2021). Furthermore, in the case of Kellner et al. (2006) and Machado et al. (2013), the traces are only shortly mentioned, as the papers have other objectives that do not include the description of tooth traces.

It is possible, however, based on the images and descriptions provided by previous authors, to make the ichnotaxonomic identification of some of the bite traces mentioned or described so far. As previously stated, the traces described by Avilla et al. (2004), Kellner et al. (2006), Vasconcellos and Carvalho (2010), Marinho and Iori (2011), and Machado et al. (2013) have characteristics that allow us to associate them to ichnogenus *Nihilichnus*. Nevertheless, the traits presented by Kellner et al. (2006) and Machado et al. (2013) should first be better analysed to confirm their ichnological origin.

Regarding the putative bite traces presented by Paes-Neto et al. (2018), their attempted association with "*Brutalichnus*" should now be disregarded. We agree with Wisshak et al. (2019) that the ichnogenus should be considered *nomen nudum*. Nevertheless, the traces described by Paes-Neto et al. (2018) present some features similar to *Nihilichnus*, and if its Praedichnia nature is confirmed, it should be associated with it. We agree with the authors, however, in their interpretation that the traces may actually be the result of invertebrate bioerosion. Furthermore, it is also possible that they are the product of dissolution. Therefore, specific analyses, such as computed tomography or palaeohistological thin sections, would be necessary to confirm its ichnological nature.

PVLGC et al. (2021), in turn, assume that the traces they described present similarities with *Nihilichnus*, but conclude that the traces would be attributed to *Mandaodonites* based on their age. We disagree with PVLGC et al. (2021), first, because the traces presented by them do not have the diagnostic sigmoid curvature of *Mandaodonites*, and second, because the occurrence of fossil traces should not be limited by time. The same fossil traces can be produced by organisms of distinct biological affinities over geological time and this is why fossil traces usually have a broad stratigraphic range: because they reflect behaviours rather than specific groups of organisms (Buatois and Mángano 2011). Thus, we consider that the stratigraphic occurrence is not a good justification for disregarding the association to *Nihilichnus* and suggest that they should be recognised as this ichnogenus.

As for the bite traces described by Araújo-Júnior and Marinho (2013), these present similarities to *Linichnus bromleyi*, however, as already pointed out, the available description and images are not sufficient to identify all the diagnostic features and, therefore, the material should be reanalysed and redescribed.

The ichnological approach and especially the ichnotaxonomical identification is important to systematise palaeoichnological knowledge. It facilitates comparisons with other fossil deposits and should be maintained in future work.

Conclusions

The specimen LPP-PV-208 is a fragmentary rib of a Titanosauriformes indet. with a series of tooth traces produced by a bite maker with ziphodont dentition. The traces have characteristics that allow associating them with the ichnospecies *Linichnus serratus, Linichnus bromleyi*, and *Knethichnus parallelum* and reflect a probable necrophagic behaviour of a medium to large-sized Abelisauridae.

The material described reveals more information of the feeding behaviour of a probable Abelisauridae from the Bauru Basin and evidences of the direct relationship between two dinosaur clades present in the SJRP Formation, often interpreted as predator and prey but which had no conclusive evidence of interaction formally described.

This is the first formally described record of *Linichnus* and *Knethichnus* for Brazil, although similar material was already mentioned in literature. This adds to the knowledge of fossil bite traces from Brazil and expands the Mordichnia record of Gondwana.

We suggest that more attention should be given to fossil bite traces and strongly encourage future descriptions to adopt an ichnological approach for a better systematisation of ichnological knowledge.

Finally, Abelisauridae, along with Megaraptora, occupied the top of the food chain in the ancient SJRP Formation palaeoecosystem, while Titanosauriformes occupied the medium to large herbivore niches. So far ornithischian dinosaurs have not been found in this context, even after decades of exploration. This makes the Bauru Basin a unique late Cretaceous palaeoecosystem.

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