



## Lacertoid tracks from the Botucatu Formation (Lower Cretaceous) with different locomotor behaviors: A new trackmaker with novel paleoecological implications

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### ABSTRACT

The Botucatu Formation (Paraná Basin) is an eolian deposit that represents an extensive paleoerg that existed in the south-central Gondwana during the Early Cretaceous. The fossil record of the unit is almost exclusively constituted of ichnofossils, including numerous tracks and burrows of vertebrates and invertebrates. The greatest trace fossil diversity of the Botucatu Formation is reported at the Ouro ichnosite, located in the Araraquara municipality region, São Paulo State, Brazil. This site comprises a faunal-rich setting of greater humidity in the ancient desert. In this work, a new footprint morphotype is reported for the Ouro ichnosite. Five trackways including tracks with an elongated anteroposterior axis associated with tail drag marks are described. The morphology of the autopodia and geometry of the trackways indicate an affinity with a lizard-like trackmaker. Furthermore, at least three different modes of locomotion were recognized: a typical walking gait, a pause-walking gait, and sideways drifting. The current report suggests Lepidosauria may have inhabited the ancient Botucatu desert, a group never reported before in this geological context. This finding expands the knowledge about the Botucatu Formation paleofauna and adds more complexity to its ecological network. Squamata and Sphenodontia are plausible candidates to have produced the described fossil tracks.

### 1. Introduction

The Botucatu Formation fossil record is mainly composed of vertebrate and invertebrate tracks, trails, and burrows produced in an extensive eolian environment, which covered a large area of South America and Africa during the late Mesozoic (Leonardi and Sarjeant, 1986; Leonardi and Carvalho, 2002; Leonardi et al., 2007; Fernandes and Carvalho, 2007; Fernandes et al., 2011; Fernandes et al., 2014; Buck et al., 2017a; Buck et al., 2017b; D' Orazi Porchetti et al., 2017a, D'

Orazi Porchetti et al., 2017b; Peixoto, 2020). The most significant ichnofossil diversity from this geological unit comes from the 'Ouro Ichnosite', located in the Araraquara municipality region, Southeast Brazil (Leonardi and Carvalho, 2002). This locality is one of the most important Gondwanan ichnofossil sites and has provided great insight into Early Cretaceous (Berriasian-Valangian) desert ecosystems (Leonardi and Carvalho, 2020).

Since the 19th century, the Botucatu sandstone has been exploited commercially and was largely used for urban paving. The first sandstone

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slab with a tetrapod trackway from the Botucatu Formation was discovered by the mining engineer Joviano Pacheco in 1911. This trackway was first described by [Huene \(1931\)](#), but only decades later was better interpreted by [Leonardi \(1980\)](#). It was Giuseppe Leonardi who actually motivated studies with the unit's ichnofossils. He collected and described local fossil materials for many years. After he left Brazil, studies continued to be carried out and many discoveries have been and are still being made over the years (e.g. [Fernandes et al., 2004](#); [Fernandes and Carvalho, 2007](#); [Fernandes et al., 2011](#); [Fernandes et al., 2014](#); [Buck et al., 2017a](#); [Buck et al., 2017b](#); [D'Orazzi Porchetti et al., 2017a](#); [D'Orazzi Porchetti et al., 2017b](#); [Peixoto et al., 2020](#); [Leonardi and Carvalho, 2020](#)).

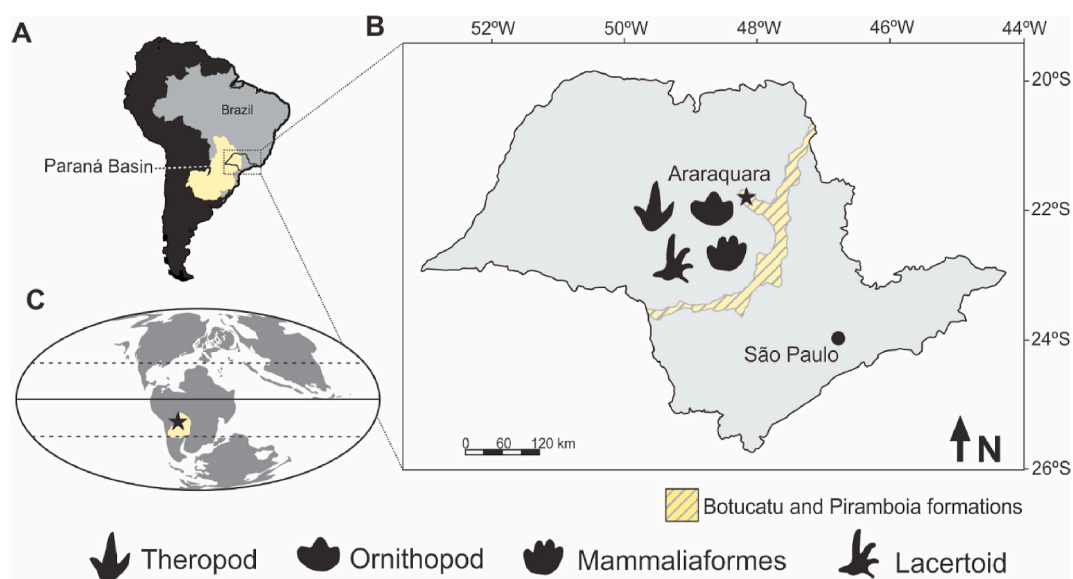
Despite the abundance of knowledge provided by the Botucatu Formation ichnofauna over the decades, a rare and distinctive track morphotype remained formally unknown. Herein we describe this new morphotype and its behavioral variations. Morphology and locomotory characteristics differentiate it from all other known tracks from this unit. Among the observed features of this novel morphotype are footprints with digit V in the posterolateral position and opposite to digit I associated with tail drag marks. These characteristics allow the interpretation of a new trackmaker for the Botucatu paleodesert with novel paleoecological and paleobiogeographic implications. The new trackmaker, a lizard-like tetrapod, probably has affinities with Lepidosauria (Rhynchocephalia + Squamata), presenting autopodia with general lizard-like characteristics, supported by the analysis and comparison with modern and fossil lacertoid tracks and trackways. Several Lepidosauria body fossils have already been described for the Triassic, Jurassic, and Cretaceous of South America, attesting to the presence of the group in the western portion of Gondwana at this time interval ([Estes and Price, 1973](#); [Bonfim-Júnior and Marques, 1997](#); [Evans and Yabumoto, 1998](#); [Apesteguía and Novas, 2003](#); [Bonaparte and Sues, 2006](#); [Nava and Martinelli, 2011](#); [Brizuela and Albino, 2011](#); [Apesteguía and Jones, 2012](#); [Martínez et al., 2013](#); [Simões et al., 2014](#); [Simões et al., 2015](#); [Hsiou et al., 2019](#); [Vivar et al., 2020](#); [Bittencourt et al., 2020](#)). Lepidosauria is a living group that characteristically includes desert dweller species and the current record adds information about the clade's ecology, evolution, and locomotory behavior in this type of environment. These are the first lacertoid tracks described for a Cretaceous eolian system.

## 2. Geological context

The Botucatu Formation integrates the Gondwana III Supersequence of the Paraná Basin, an immense South American intracratonic basin with a sedimentary record extending from the Upper Ordovician to the Cretaceous ([Milani et al., 2007](#)). The Botucatu Formation covers an area of more than 1,500,000 km<sup>2</sup> and outcrops in southern Brazil, Paraguay, northern Argentina, and Uruguay ([Fig. 1](#)). Rocks associated with the same sedimentary context also occur in Namibia and South Africa. In Brazil, the Botucatu Formation is found in the states of Rio Grande do Sul, Santa Catarina, Paraná, São Paulo, Minas Gerais, Goiás, Mato Grosso, and Mato Grosso do Sul ([Scherer and Goldberg, 2007](#)).

Botucatu Formation quartzitic sandstones are fine to medium textured with well-sorted rounded grains, and absent or nearly absent mineral content other than quartz. They bear medium to large cross-stratification and are interpreted as deposited in an eolian environment ([Bigarella and Salamuni, 1961](#); [Salamuni and Bigarella, 1967](#)). The Botucatu Formation overlaps the Middle to Late Jurassic fluvial-eolian deposits of Piramboia Formation ([Christofoletti et al., 2021](#)) and is covered by the magmatic extrusive rocks of the Serra Geral Formation ([Milani et al., 2007](#)) ([Fig. 2](#)).

The Botucatu Formation paleoenvironment can be characterized by the presence of dune fields with interdune valleys (see [Talbot, 1985](#) and [Mountney, 2004](#)) composing an immense *paleoerg*, similar to what is observed in current sand seas ([Scherer, 2000](#); [Leonardi et al., 2007](#); [Fernandes et al., 2014](#)). Climate during deposition is interpreted as arid or hyperarid. In the southern portion of the paleodesert, a hyperarid climate is inferred by [Nowatzki and Kern, 2000](#) and [Scherer \(2000\)](#). Nonetheless, in the northeastern portion between the states of São Paulo and Minas Gerais, climatic conditions are recognized as more humid. In the Araraquara region, São Paulo State, sedimentary structures associated with pluvial episodes such as raindrop imprints and adhesion ripples have been identified ([Fernandes et al., 2014](#); [Buck et al., 2017a Fig. 3](#)). The large number of tracks found in the same region can also be an indicator of a local milder climate ([Fernandes et al., 2014](#)). Increased humidity, even if seasonal, might have allowed the establishment of a rich paleofauna represented nowadays by the Ouro ichnosite diverse ichnocoenosis ([Fernandes et al., 2014](#)). Further north, in Minas Gerais State, coniferous wood fossils indicate an even wetter environment ([Pires et al., 2011](#)). Dendroclimatological analysis of these fossil plants



**Fig. 1.** A, localization of the Paraná Basin (yellow) in South America displaying the occurrence of the Botucatu and Piramboia formations in the State of São Paulo, southeast Brazil (B). C, Early Cretaceous (Berriasian) continental setting with the 'Ouro ichnosite' locality and the extent of the Botucatu Paleodesert. Paleogeographic reconstruction based on [Scotese \(2014\)](#). Paleodesert reconstruction following [Scherer and Goldberg \(2007\)](#). Modified from [Fernandes et al. \(2004\)](#).

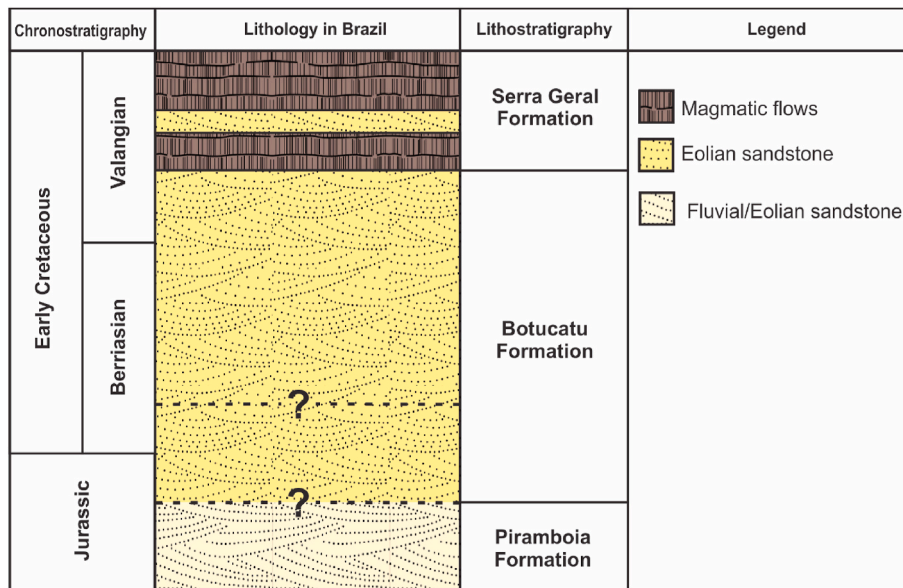


Fig. 2. Simplified stratigraphic column showing the lithology, chronostratigraphy, and contact relationships between the Piramboia, Botucatu, and Serra Geral units. This figure was adapted from Buck et al. (2017a) and Peixoto et al. (2020).

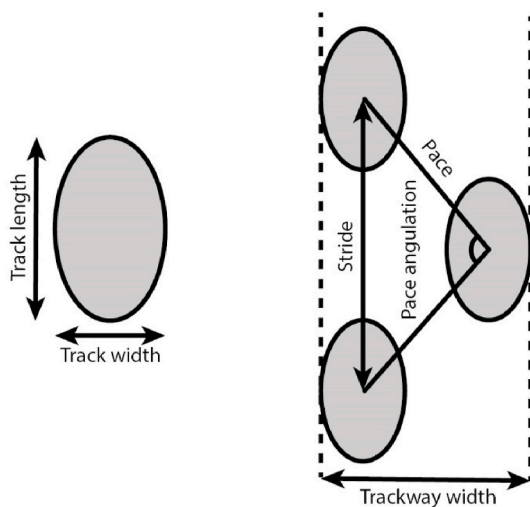


Fig. 3. Measures obtained for the ichnological analyses following Leonardi (1987).

indicates they were growing with some degree of seasonal water stress, which led the authors to infer a semi-desert arid paleoenvironment (Pires et al., 2011). Therefore, it can be considered that the extensive depositional range of the Botucatu Formation was under different climatic regimes resulting in some heterogeneity between deposits and their fossiliferous content.

The Botucatu Formation age range consensus is from the Late Jurassic, according to paleomagnetic data (Tamrat and Ernesto, 2006) to the Early Cretaceous, being this upper limit given by the radiometric dating of the Serra Geral volcanic flows (Valanginian) that interdigitate the upper part of the deposit and conformably overlie the Botucatu Formation (Renne et al., 1992; Turner et al., 1994; Scherer, 2000; Janasi et al., 2011). Scherer (2000) presumes they were responsible for the preservation of the original desert dunes' topography (Fig. 2).

### 3. Materials and methods

#### 3.1. Provenance and description of the specimens

In the present study, five trackways are described. They are housed in the Laboratory of Paleocology and Paleoichnology (LPP) of the Department of Ecology and Evolutionary Biology (DEBE), Center for Biological and Health Sciences (CCBS) of the Federal University of São Carlos (UFSCar), São Carlos municipality, São Paulo State, Brazil. Each trackway is preserved in a distinct sandstone slab designated as LPP-IC-0018, LPP-IC-0041, LPP-IC-0042, LPP-IC-0043, LPP-IC-0044.

All slabs are from the Ouro Ichnosite, a complex of quarries located in the Araraquara county region (São Paulo State, Brazil). Three specimens (LPP-IC-0018, LPP-IC-0043, and LPP-IC-0044) were collected in the São Bento quarry (21°49'03.4"S and 48°04'22.9"W), a dune foreset deposit of approximately 20m high and 100m long, while two specimens (LPP-IC-0041 and LPP-IC-0042) do not have precise provenance information. Most of the Botucatu Formation specimens from the LPP collection do not have precise stratigraphic information because they were already removed from their original stacking when rescued from mining activity.

We followed the convention proposed by Leonardi (1987) for the terminology and description of the tracks and trackways (Fig. 3). Pes length, width, length/width ratio, stride length, oblique pace, trackway width, tracks rotation and pace angulation were measured. Tracks superimposed by other tracks and/or sedimentary structures, as well as footprints with vague outlines were not measured to avoid possible errors in interpretation. The studied material was compared with other trackways from the LPP collection and with specimens described and illustrated in the scientific literature.

Linear morphological measurements of the tracks were made using calipers accurate to 0.1 mm and angles were measured using photographs and the freeware ImageJ (Schneider et al., 2012). Finally, the term 'lacertoid' is used to refer to the footprint morphotype, which displays characteristics generally associated with Lepidosauria and the term 'lizard-like' is used to refer to the trackmaker body plan, which is similar to lizards.



## 4. Results

### 4.1. Description of the specimens

A total of five trackways with lacertoid tracks were recognized and described, one in each different sandstone slab. Each of the slabs received a registration number. Since each trackway is on a single slab, we can refer to these directly as their registration number.

Specimens LPP-IC-0018 and LPP-IC-0041 trackways are preserved as convex hyporelief and specimens LPP-IC-0042, LPP-IC-0043, and LPP-IC-0044 trackways are preserved as concave epirelief.

The morphological and locomotory parameters of the lacertoid tracks and trackways analyzed can be seen in Table 1. All trackways described are illustrated in Figs. 4–6. Macro photographs of footprints with digit impressions are shown in Fig. 7.

The size of the footprints varies from 2.44 cm ± 0.19 in width and 3.7 cm ± 0.26 in length, to 4.14 cm ± 0.29 in width and 6.71 cm ± 0.24 in length for specimens LPP-IC-0041 and LPP-IC-0043, respectively. All other specimens have intermediate values. The general morphology can be described as “tracks with elongated anteroposterior axis”, which makes it possible to group all of them in the same morphotype. The footprints are all interpreted as produced by the trackmaker’s pes.

Regarding the morphological details of the trackmaker’s autopodium, only footprint 08 (left pes) of specimen LPP-IC-0042 has recognizable digit impressions (Fig. 7, C). All other tracks have only elliptical contours and/or very few recognizable digit details (Fig. 7A and B, and D). Footprint 08 of specimen LPP-IC-0042 is asymmetric, ectaxonic, semi-plantigrade, and functionally pentadactyl. Digits II, III, IV, and V are curved outwards while digit I faces inwards. Digit V is in a posterolateral position and is opposite to digit I (Fig. 7, C). Digit II can be considered long and narrow. However, we cannot distinguish the same feature for digits III, IV, and V as their morphology was apparently altered during preservation. In the same specimen, footprints 04 and 05 or 06 (Fig. 7A and B), although not as well preserved as 08, seem to indicate the same morphology. The presence of digits in similar positions to those of footprint 08 can be observed. Footprint 04 of specimen LPP-IC-0044 (Fig. 7, D) also has asymmetry and an elongated structure facing inwards towards the trackway, which was interpreted here as digit I, as it is in the same position of digit I in footprint 08 of specimen LPP-IC-0042. These shared characteristics reinforce the trackway grouping within the same morphotype.

We identified three distinct locomotory behaviors in the analyzed trackways: The typical walking gait with constant velocity (LPP-IC-0041); a paused-walking gait (LPP-IC-0042); and a sideways-drifting (LPP-IC-0018, LPP-IC-0043, and LPP-IC-0044).

Another feature is the presence of sinuous structures related to tail drag and tail impressions (see Kim and Lockley, 2013 for terminology and definition). Such structures are interpreted as locomotion traces and occur continuously (LPP-IC-0041), discontinuously (LPP-IC-0018, LPP-IC-0042, and LPP-IC-0043), or are completely absent (LPP-IC-0044). In some cases, tail marks crossing over some footprint impressions and/or other sedimentary structures can be observed. This



Fig. 4. A, photograph of specimen LPP-IC-0018. B, interpretative scheme of the specimen showing each pes position (ellipses) in relation to the trackway midline axis. Note the alignment of the anteroposterior axis of all footprints and the divergence of these axes in relation to the trackway midline axis, a condition produced by side-walking on an inclined plane. Footprints are numbered in sequence, from the bottom to the top of the figure.

indicates they were produced after the footprint, as it naturally occurs for tail marks. The width of the tail marks varies according to the trackmaker’s size, and it also depends on which portion of the tail

Table 1

Mean values followed by standard deviation of morphological and locomotory parameters of lacertoid tracks and trackways. Width, length, oblique pace, stride, trackway width, and tail mark width are in centimeters. Pace angulation and track rotation are in degrees.

Parameters	LPP-IC-0018	LPP-IC-0041	LPP-IC-0042	LPP-IC-0043	LPP-IC-0044
Width	3.19 ± 0.24	2.44 ± 0.19	3.36 ± 0.49	4.14 ± 0.29	3.33 ± 0.42
Length	5.13 ± 0.06	3.7 ± 0.26	5.33 ± 0.9	6.71 ± 0.24	4.64 ± 0.56
L/W ratio	1.61 ± 0.12	1.52 ± 0.12	1.58 ± 0.19	1.64 ± 0.12	1.41 ± 0.06
Oblique pace	–	4.02 ± 0.5	6.6 ± 1.13	7.17 ± 0.44	7.68 ± 0.53
Stride	10.65 ± 0.99	5.93 ± 0.44	11.34	13.61 ± 0.38	14.7 ± 0.57
Pace angulation	–	94.18 ± 4.94	128.8	140.07 ± 6.86	147.9 ± 3.5
Trackway width	–	5.35 ± 0.24	8.26 ± 1.66	8.59 ± 0.31	6.27 ± 0.37
Tail mark width	0.5 ± 0.19	0.32 ± 0.04	1.04	0.87 ± 0.16	–
Track rotation	41 ± 5.19	25.98 ± 6.52	27.15 ± 2.19	48.21 ± 6.69	38.53 ± 4.56



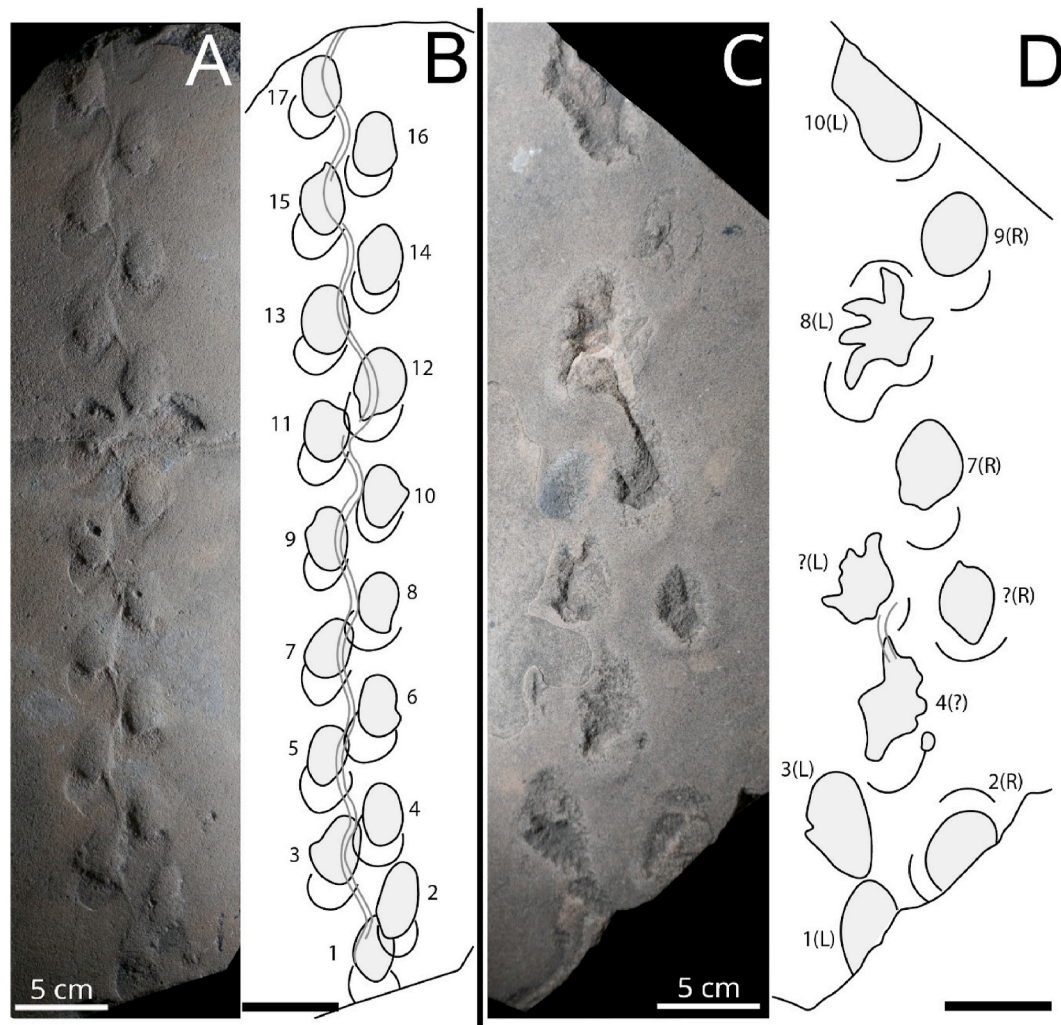


Fig. 5. Photography of specimens LPP-IC-0041 (A) and LPP-IC-0042 (C). B and D are the interpretative schemes for both specimens. Note the anteroposterior axis of each footprint is nearly aligned with the trackway midline axis in both specimens. Footprints are numbered in sequence, from the bottom to the top of the figure.

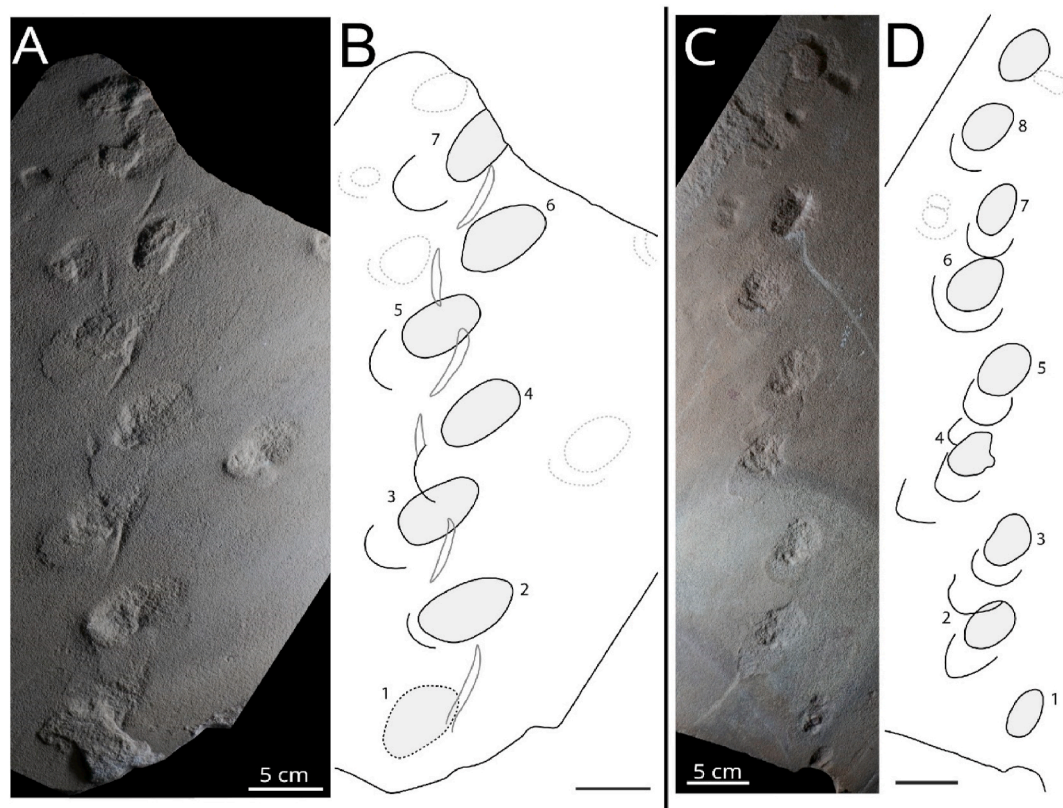
touches the substrate. The length of the tail marks (*i.e.* continuity) varies with the locomotor behavior observed. In specimen LPP-IC-0043, the distal part of the trackmaker's tail touched the substrate leaving sinuous sub-rounded marks, tapered distally. In specimens LPP-IC-0018 and LPP-IC-0041, tail impressions tend to drag on one side of the trackway, possibly because this was the trackmaker's side closest to the dune slope.

The most recurring locomotor mode was side-walking or sideways-drifting (Rowland et al., 2020) (seen in specimens LPP-IC-0018, LPP-IC-0043, and LPP-IC-0044). In this case, anteroposterior axes of both the left and right footprints are facing the same direction and point against the dune slope. The footprint axis direction is not aligned with the midline axis of the trackway. Consequently, it does not align with the direction of movement, indicating the trackmaker's body was rotated in relation to the direction of the trackway. The average rotation in specimens LPP-IC-0043, LPP-IC-0044, and LPP-IC-0018 are, respectively,  $45.83^\circ \pm 3.68$ ,  $38.53^\circ \pm 4.56$ , and  $41^\circ \pm 5.19$ . The average of the stride length and the pace angulation of the trackways showing this locomotor behavior are, respectively,  $13.61 \text{ cm} \pm 0.38$  and  $140.07^\circ \pm 6.86$  for LPP-IC-0043,  $14.7 \text{ cm} \pm 0.57$ , and  $147.9^\circ \pm 3.5$  for LPP-IC-0044 and  $10.65 \text{ cm} \pm 1$  for LPP-IC-0018.

The other two locomotor behaviors observed are seen in specimens LPP-IC-0041 and LPP-IC-0042. LPP-IC-0041 displays the typical quadrupedal walking gait, with mean values of stride length and pace angulation of  $5.93 \text{ cm} \pm 0.44$  and  $94.18^\circ \pm 4.94$ , respectively. A sinuous tail drag can be observed along the entire trackway and has an average

width of  $0.33 \text{ cm} \pm 0.04$ . Some footprints on the left side (the trackmaker's side closer to the dune slope) rotate inwards, with an average value of  $25.98^\circ \pm 6.52$ . Despite the low pace angulation, the trackway width mean is  $5.35 \text{ cm} \pm 0.24$ . The trackway observed in specimen LPP-IC-0042, in turn, displays both the typical walking gait, observed from footprint 07 onwards (pace:  $6.6 \text{ cm} \pm 1.13$ ; stride:  $11.34 \text{ cm}$ ; pace angulation:  $128.8^\circ \pm 5.02$ ), and a strange behavior here called 'paused-walking gait'. The latter occurs between tracks 01 and 06 and can be described by irregular steps, in which footprints 02 and 03, and 05, and 06 are parallel or subparallel, and the pace does not advance. Thus, the parameters of this part of the trackway do not seem to represent locomotion. Footprints 02 and 03 are outwardly rotated in relation to the trackway, with values of  $28.7^\circ$  and  $25.6^\circ$  respectively. Between tracks 07 and 08, a grooved structure of  $1.04 \text{ cm}$  in width can be interpreted as a tail drag mark. It is not clear which of the footprints was produced after the 04, and it is only possible to determine left and right.

Regardless of the locomotion mode, all tracks have a very low and elongated displacement rim, different from all other displacement rims of ichnogenus already known for this geological unit, suggesting a different locomotor effort in relation to trackmakers interpreted until now. The footprint morphology reinforces the interpretation of an ichnogenus hitherto not reported for the Botucatu Formation and a new trackmaker in the paleoecological context.



**Fig. 6.** Photograph of specimens LPP-IC-0043 (A) and LPP-IC-0044 (C). B and D are the interpretative schemes for both specimens. Note the alignment of the anteroposterior axis of all footprints and the divergence of these axes in relation to the trackway midline axis, a condition produced by side-walking on an inclined plane. Footprints are numbered in sequence, from the bottom to the top of the figure.

## 4.2. Ichnotaxonomic discussion

### 4.2.1. Morphological characteristics of lacertoid tracks from the Botucatu Formation

Asymmetrical tracks with semi-plantigrade functionally pentadactyl pes. Footprints elongated on the anteroposterior axis with a length around 5 cm and width around 3.3 cm. Spread out digits. Digits I and V facing opposite directions. Digit V in a posterolateral position. Digit I facing inwards the trackway. Digits II-IV curved. Digit II pointing forward and digits III and IV pointing outwards the trackway midline. Hypex between digits I and II broad. Pace angulation ranging from  $94^\circ$  to  $148^\circ$ , depending on the locomotory behavior. Pes may be rotated in the same direction due to the specific gait adopted. Manus not preserved or overprinted by the pes. Sinuous tail drags or tail impressions may occur.

### 4.2.2. Referred material

LPP-IC-0018, LPP-IC-0041, LPP-IC-0042, LPP-IC-0043 and LPP-IC-0044.

### 4.2.3. Locality

Ouro ichnosite, São Bento quarry, Araraquara county, São Paulo State, Brazil.

Geographic coordinates:  $21^\circ 49' 03.4''$  S,  $48^\circ 04' 22.9''$  W.

### 4.2.4. Horizon

Eolian facies of the Botucatu Formation, São Bento Group, Paraná Basin.

### 4.2.5. Repository

Trace fossil collection of the Laboratory of Paleocology and Paleotechnology (LPP), Department of Ecology and Evolutionary Biology

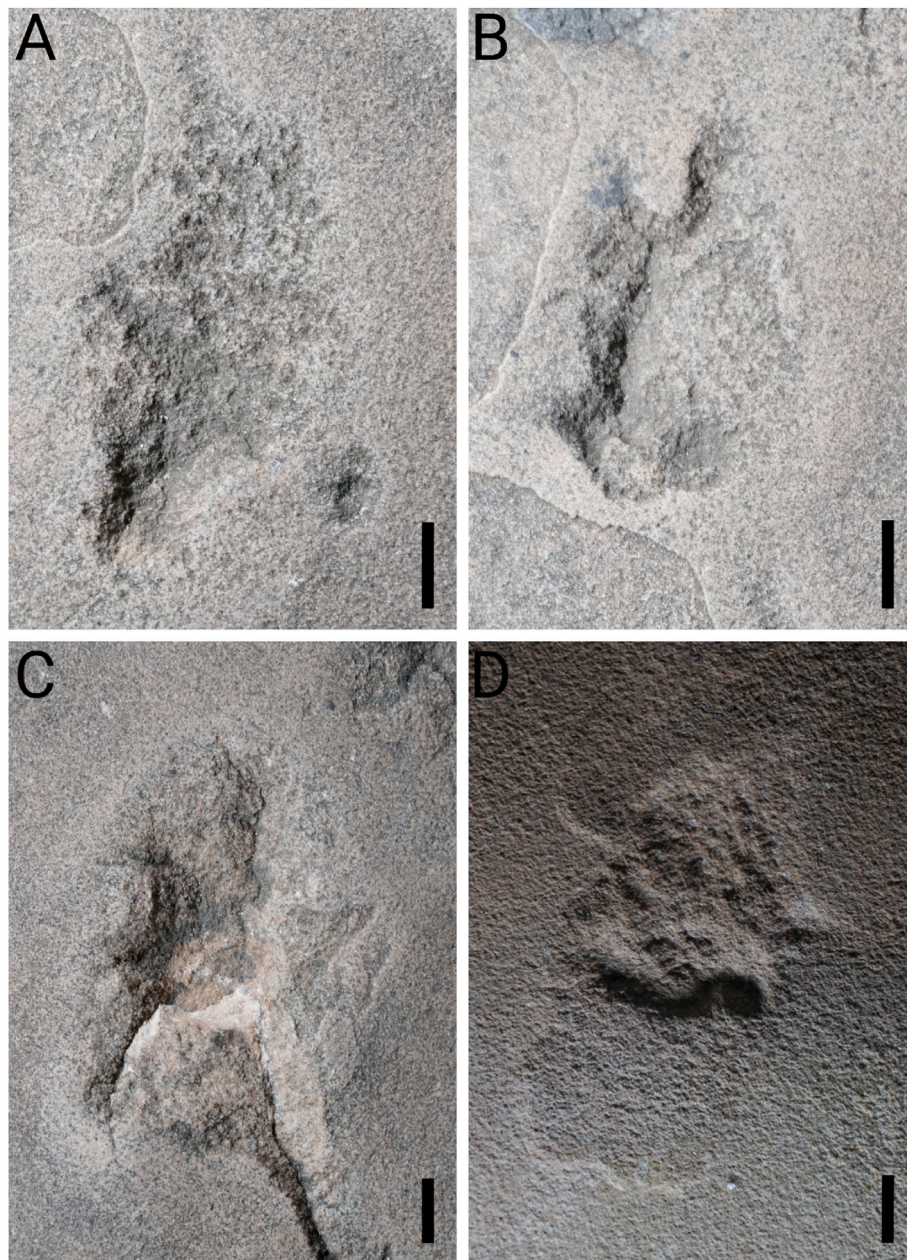
(DEBE) of the Center for Biological and Health Sciences (CCBS) of the Federal University of São Carlos (UFSCar), São Carlos, São Paulo State, Brazil.

### 4.2.6. Comparison with other ichnotaxa

The observed track morphotype (*i.e.* functionally pentadactyl asymmetric footprints with curved and opposite digits) is unprecedented in the Botucatu Formation. The tracks' anteroposterior elongation, with an average length/width ratio of  $1.54 \pm 0.09$ , is different from both *Brasilichnium* ( $0.72 \pm 0.1$ ) and *Aracoaraichnium* ( $0.78 \pm 0.09$ ) (see Buck et al., 2017a; Buck et al., 2017b). When compared with Botucatu Formation theropod tracks, in turn, the general outline of the footprints is similar (length/width ratio between 1 and 1.7 for dinosaurs) but dinosaur trackways have a higher pace angulation (see Fernandes et al., 2011). The currently described trackways indicate a quadrupedal trackmaker excluding the possibility of a theropod producer. Sinuous tail drag marks or even tail impressions were not observed in either *Brasilichnium*, nor in *Aracoaraichnium* or in any dinosaur trackway described for the Botucatu Formation.

Since only one footprint (footprint 08 from LPP-IC-0042) preserves details of the digit morphology (Fig. 7, C), it is difficult to confidently assign this morphotype to any existing ichnotaxon or even propose a new ichnospecies. The digit width and length and interdigital angle variation are unknown or difficult to determine for the current morphotype and these are parameters often used to recognize ichnospecies. The absence of manus impressions further limits the classification. The described footprints and *Rhynchosauroides* share the following characteristics: asymmetrical tracks with an elongated anteroposterior axis, curved and slender digits, with digit I opposite to V in posterolateral position. A revision may be required in the future in light of new, better-preserved specimens. Despite the general similarities mentioned above, the digits seem more spread out in the morphotype herein described and





**Fig. 7.** Detailed macro photographs of the footprints with digit impressions in LPP-IC-0042 (A–C) and LPP-IC-0044 (D) A, Footprint 04. B, Footprint 05 or 06. C, Footprint 08. D, Footprint 04. Trackmakers walked from bottom to top. Scale Bar 1 cm.

pes rotation is also different (pes are rotated more outwards in relation to the trackway midline in the described morphotype). These characteristics may vary in response to several variables, such as substrate cohesion, surface slope, and trackmaker behavior.

#### 4.3. Ichnofaunal association

All slabs have an ichnofaunistic association, except for LPP-IC-0042. On LPP-IC-0018 two tetrapod trackways other than the lacertoid can be identified. One was described by Buck et al. (2017b) as *Aracoarachnium leonardii* and the other can be identified as *Brasilichnium elusivum*. The latter overlaps the lacertoid trackway on its anterior portion. LPP-IC-0041 has two different sized *Brasilichnium*, both on the right side of the lacertoid trackway. LPP-IC-0043, in turn, has several tetrapod trackways. On the right side of the lacertoid, a descending *Brasilichnium* specimen is recorded. It overlaps the second lacertoid footprint. On the

left side of the lacertoid tracks there is a *Brasilichnium* trackway in an upward direction and, finally, on both sides, there are sequences of small footprints tentatively attributed to theropod dinosaurs. For last, on LPP-IC-0044 trackways classified as *Brasilichnium* can be observed on both sides of the lacertoid trackway.

## 5. Discussion

### 5.1. Preservational features and different locomotor behaviors

The coarse sandy sediment of eolian deposits and its moisture content influence the footprint and other bioturbations morphology, with sharper details better preserved if the sediment was wetter during the trace fossil production (Loope 2006, 2008; Milán and Bromley, 2006; Milan and Loope 2007; Jackson et al. (2010); Buck et al., 2017a; Marchetti et al., 2019a; Peixoto et al., 2020). Leonardi et al. (2007) attest



that 90–95% of the Botucatu Formation footprints are of low quality, consisting only of depressions on the substrate with no morphological details of the trackmakers' autopodium. According [Belvedere and Farlow \(2016\)](#) and [Marchetti et al. \(2019b\)](#) preservation scales, most of the footprints described here can be considered of poor quality, with only the outline preserved, different from the tracks described by [Kim et al. \(2019\)](#). Footprints 04, 05 or 06 and 08 of the LPP-IC-0042 slab and footprint 04 of the LPP-IC-0044 slab are slightly better preserved, bearing subtle digit imprints. As observed by [Jackson et al. \(2010\)](#), when the trackmaker's autopodium is removed from a dry sandy substrate, the sediment collapses due to the lack of cohesion, thus destroying and/or hiding the imprint of the autopodium's details. This is a good explanation for the preservation of the trackways described here. Nonetheless, a certain amount of interstitial moisture, even if low, must have been available in the substrate at the time the footprints were produced. A few tracks have digit impressions and very sharp and clear tail marks that could only have been preserved under some degree of substrate moisture (see [Mancuso et al., 2016](#)). Variation in tracks' preservation within the same trackway can also be observed in some lacertoid tracks described by [Chure et al. \(2014\)](#). In specimens depicted in [Figs. 4C and 5](#) of [Chure et al. \(2014\)](#), the quality of preservation and the presence of digits varies within the same trackway similar to the specimens analyzed here. Besides that, also similar to our specimens, the manus impressions are not visible or preserved.

Regarding the "absence" of manus impressions in the Botucatu Formation lacertoid trackways, a few possible explanations must be considered: 1) they have not been preserved; 2) they were overprinted by the pes prints; 3) trackmakers were moving bipedally. Specimen LPP-IC-0041 lacertoid trackway is very similar to the one of [Marchetti et al. \(2019a\)](#) obtained through a neoichnological experiment with a lizard moving quadrupedally on an inclined sand surface. The direction of movement reported in the aforementioned experiment is close to parallel to the surface's slope and the reported tracks have low pace angulation with a continuous tail drag mark associated. In the final portion of the trackway obtained by [Marchetti et al. \(2019a\)](#) (see [Fig. 5A](#)), it is not possible to distinguish pes and manus tracks due to the collapse of the sandy substrate. This condition is very similar to what is observed in specimen LPP-IC-0041. Additionally, [Fornós et al. \(2002\)](#) argue trackmakers ascending inclined planes take shorter steps (stride), which favors the overlap of manus and pes prints. Therefore, the dry sand collapse and the partial/total overlap of pes and manus prints due to the trackmaker's effort to ascend the dune may have, together, acted to form homopod trackways. The homopody seen in specimen LPP-IC-0042 can also be interpreted as the result of overprinting, while the trackways preserved in specimens LPP-IC-0018, LPP-IC-0043, and LPP-IC-0044 can either have been produced by the superposition of the autopodia at higher speed locomotion ([Kubo, 2010](#); [Diedrich, 2005](#)) or facultative bipedal behavior of the trackmakers, which will be discussed later in this topic.

The differences in track's length and width observed in this work can reflect either trackmakers' different sizes and/or are the result of extramorphology. Specimen LPP-IC-0043, for example, has the largest footprints among the analyzed specimens. Low cohesion of the sand grains at the time of the trackway formation can generate larger tracks ([Brand, 1996](#); [Jackson et al., 2010](#)). However, variation in extramorphology can also be a product of the trackmaker's higher speeds, which is usually followed by a change in the pace angulation ([Brand, 1996](#)). A distinct pace angulation is detected in specimens LPP-IC-0018, LPP-IC-0043, and LPP-IC-0044, for example.

Variation in the displacement rims can also be a product of differences in substrate moisture and/or trackmaker's speed. Tracks observed in specimens LPP-IC-0018, LPP-IC-0043, and LPP-IC-0044 have very low and elongated displacement rims that partially cover the previous tracks. This reinforces the interpretation of a faster locomotion behavior and/or low moisture content of the substrate at the time of the tracks' formation ([Brand, 1996](#)).

Specimen LPP-IC-0041 displacement rims are shorter and together with the low and consistent pace angulation and the continuous sinuous tail drag mark associated may indicate that the trackmaker was moving slower, but at constant velocity. Specimen LPP-IC-0042 trackway, in turn, has the most subtle displacement rims, which could indicate tracks are preserved on subsurface (undertracks) or produced on a less inclined plane. The preservation of the five digits in footprint 08 (attested by the displacement rim around each digit), and the partial preservation of the digits in footprints 04 and 06, are also indicative of higher humidity of the substrate. It can also be inferred that this trackway was produced on a somewhat irregular substrate since footprints 05, 07, and 09 on the right side have smaller dimensions when compared to the footprints preserved on the left side, which may be undertracks ([Milán and Bromley, 2006](#)).

Behavioral variation can also be attested by the trackways' geometry and associated structures. The presence/absence of tail marks and the orientation of the tracks in relation to the direction of movement are further indicatives of distinct behaviors preserved in the analyzed specimens. [Diedrich \(2005\)](#) and [Kubo \(2010\)](#) observed a tendency of lizard-like trackmakers to keep their tail suspended while at higher speeds and to drag it on the substrate at lower speeds. For dinosaurs, [Kim and Lockley \(2013\)](#) found similar results and attested the preservation of these structures could be directly influenced by the individual behavior of the producers. [Kubo \(2010\)](#) also noted that straight or sinuous tails drag marks could be produced by distinct trackmakers and that they could vary under different modes of locomotion. Torso, tail, and limb length influence the way the animal moves, therefore it may also affect the type of tail marks it produces. The Botucatu Formation lizard-like trackmaker left sinuous tail dragging marks on the substrate when at lower speeds and no marks or intermittent tail impressions (suspended tail) while at higher speeds. In specimen LPP-IC-0042, the presence of a sinuous tail dragging structure was expected, however, as discussed by [Kim and Lockley \(2013\)](#), an individual behavior might have affected the resulting trackway or the absence of this feature would reinforce the undertrack preservation previously suggested.

[Holst et al. \(1970\)](#) carried out neoichnological experiments with several lizards and a young crocodile varying in body size. They concluded a long tail (twice the length of the body) was responsible for producing a narrow continuous and straight tail dragging mark, while a short tail (same length of the body) produced sinuous interrupted tail marks. Based on specimens LPP-IC-0041 and LPP-IC-0018 that present a sinuous continuous tail dragging mark and an almost continuous tail drag mark, respectively, one can infer a possible trackmaker with a tail length between once and twice the body length. Due to the preservation of only the pes impressions, the glenoacetabular distance could not be estimated.

Structures attributed to body dragging or 'belly dragging' (see [Kubo, 2010](#); [Bernardi and Avanzini, 2011](#); [Curth et al., 2014](#) for definition) were not observed. Dragging the ventral portion of the animal's body is associated with a sprawled posture and, consequently, low pace angulation ([Kubo and Ozaki, 2009](#)). Specimen LPP-IC-0041 trackway, with typical cursorial gait, has the lowest pace angulation ( $94.18^\circ \pm 4.94^\circ$ ) and the lowest stride length/footprint length ratio (1.6), characteristics of a typical sprawling gait. However, the analysis of this trackway shows a narrow gauge (trackway width of  $5.35 \pm 0.24$  cm). This and the absence of structures associated with a sprawling posture ('belly walking'), such as claw drag marks (during swing phase) and body dragging marks, indicate a 'high walk'. In deserts, 'high walk' may be an adaptation to life on hot substrates, thus keeping vital organs away from the excessive heat of the sand surface by means of a more erect posture and possibly longer limbs ([Costa, 2012](#)).

Specimen LPP-IC-0042 shows a very distinct locomotion behavior from footprint 01 to 06, here called 'paused-walking'. Footprints 02 and 03 are interpreted as left and right feet aligned and rotated almost symmetrically, reflecting a position adopted by the trackmaker when it stopped. This may have recorded a moment when the trackmaker

slowed down to observe its surrounding environment. Until footprint 06, strides are short, but from there on, the trackmaker adopts the typical cursorial locomotion. This records a change in the animal behavior along the trackway, different from the other specimens walking at a constant velocity (e.g. LPP-IC-0041).

Another mode of locomotion recorded is sideways-walking observed in specimens LPP-IC-0018, LPP-IC-0043, and LPP-IC-0044, associated here with a higher travel speed. Rowland et al. (2020) recently described a trackway from an eolian environment where the footprints are facing the same direction, diverging about 40° from the trackway midline. They tentatively attributed this stance to strong winds pushing the animal while it was crossing the dune. The specimens described here have similar footprint rotation to the one described by Rowland et al. (2020), however no signs of strong wind currents (i.e. wind ripples). This type of behavior is apparently adopted in response to the oblique ascending movement in relation to the dune slope. It occurs in eolian environments of different ages and is displayed by different trackmakers (e.g. Brand and Tang, 1991; Lockley et al., 1992; Loope, 1992; Fornós et al., 2002; Loope and Milàn, 2016). It is noteworthy that some of the left footprints of specimen LPP-IC-0041 are rotated inwards the trackway and opposite to the displacement rim. Although the mode of locomotion of LPP-IC-0041 is not sideways-walking, this behavior could also be a balance response due to the dune slope.

Increasing speed is indicated by higher stride values between specimens LPP-IC-0018, LPP-IC-0043, and LPP-IC-0044, respectively, and accordingly, tail marks change from semi-continuous (LPP-IC-0018), to intermittent (LPP-IC-0043), to completely absent (LPP-IC-0044). This is probably because tail suspension generates better balance and assists locomotion using lateral movements of the tail. According to the proposal by Jagannadan and Higham (2017), lateral movements of the tail can facilitate the rotation of the pelvic girdle, thus allowing greater hind limbs stride length and greater pace angulation (Kubo and Ozaki, 2009). Such tail lateral movements could be responsible for the absence or partial preservation of tail marks, which would be produced in brief moments when the tip of the tail touched the substrate. Avanzini and Renesto (2002) found tail marks are less observed on tracks with higher pace angulation and conclude at higher speeds *Rhynchosauroides tirolicus* trackmaker's tail would remain suspended.

Another possibility is that LPP-IC-0018, LPP-IC-0043, and LPP-IC-0044 trackways were produced during bipedal locomotion. Silva et al. (2008) raised the hypothesis of this type of locomotion for a trackway with lacertoid morphology from the Triassic of Brazil, in which only the pes imprints were recorded and the stride values were superior to other similar trackways presenting manus impressions. This would indicate a greater speed of the trackmaker while bipedal. The specimen described by Silva et al. (2008) is similar to specimens LPP-IC-0018 and LPP-IC-0043 lacertoid trackways and bear tail marks associated. Lee et al. (2018) also interpreted lacertoid trackways from the Lower Cretaceous (Aptian-early Albian) as bipedal. They likewise had high strides but no tail marks. During a modern lizard bipedal locomotion study, Snyder (1962) identified that *Amphibolurus cristatus* could either leave or not tail marks on the substrate. Leonardi (1975), in turn, described higher stride and pace angles in bipedal locomotion of *Tupinambis teguixin* and attested it usually leaves intermittent curved tail marks on the substrate. Finally, Rocha-Barbosa et al., 2008 also identified tail marks produced during bipedal locomotion of *Tropidurus torquatus*. The presence or absence of tail marks on the trackways of specimens LPP-IC-0018, LPP-IC-0043, and LPP-IC-0044 does not preclude the interpretation of bipedal locomotion. Variation may be related to individual body and tail posture adopted during this type of behavior.

On the other hand, as discussed before, Botucatu Formation's lizard-like trackmaker did not have a very long tail. This contrasts with Snyder's (1962) observation that modern lizards with specialized bipedal locomotion usually have relatively long tails. Thus, LPP-IC-0018 and LPP-IC-0043 trackways may indicate a case of

bipedalism associated with tail marks, where the trackmaker is not fully specialized in bipedal locomotion (see discussion in Silva et al., 2008). Clemente (2014) discusses and reinforces the hypothesis of exaptation for the appearance of bipedalism in lizards. According to this author, bipedalism in lizards would have occurred primarily as a consequence of lifting the front portion of the body due to the acceleration of movement. Thus, the lacertoid trackways observed in specimens LPP-IC-0018, LPP-IC-0043, and LPP-IC-0044 could represent cases in which the animal raised the front portion of the body due to acceleration (e.g. Reed, 1956; Kinsey and McBrayer, 2018). This behavior is identified in several modern lizard species that live in open environments such as deserts (Snyder, 1962; Irschick and Jayne, 1998). By adopting this posture, they can increase even more their locomotion speed (Irschick and Jayne, 1998) and/or expand environmental perception (Kohlsdorf and Biewener, 2006), consequently guaranteeing higher success rates when escaping predators.

## 5.2. Trackmaker identity

Before our work, Botucatu Formation tetrapod trackmakers included different groups of theropods, ornithomorphs, and Mammaliaformes (Leonardi, 1980; Leonardi and Oliveira, 1990; Fernandes and Carvalho, 2007; Fernandes et al., 2011; Fernandes et al., 2014; Buck et al., 2017a; Buck et al., 2017b; Leonardi and Carvalho, 2020). The tracks here attributed to a lacertoid morphotype indicate a new producer, a lizard-like, probably a lepidosaur (Fig. 8), which had not been previously recognized as a component of the Botucatu paleodesert ecosystem, thus increasing its diversity.

Kubo (2010) listed some typical lizard tracks' features, which support our interpretation, such as functionally pentadactyl feet with curved digits, digit I opposite to V, with digit V directed in a posterolateral position. Kubo (2010) also highlights lizard footprints present increasing digit length from digit I to IV. Unfortunately, this feature could not be adequately measured in the analyzed specimens due to their low quality of track preservation. Even so, in footprint 08 of LPP-IC-0042, there is an increase in digit length between digits I and II respectively. Besides all that, there are also the associated tail marks, which further support lizard-like producers.

We can try to infer the trackmakers' affinities within the Order Lepidosauria by comparing chronocorrelated records. The Squamata *Gueragama sulamericana* Simões, Wilner, Caldwell, Weinschütz and Kellner (2015) (Iguania, Acrodonta) was described from the sandstones of the Goio-Erê Formation (Caiuá Group, Bauru Basin), Upper Cretaceous (Turonian-Campanian), Cruzeiro do Oeste municipality (Paraná State, Brazil). This geological unit represents an arid eolian paleoenvironment, and together with the Rio Paraná and Santo Anastácio formations (Caiuá Group, Bauru Basin) constitute the Caiuá paleodesert (Fernandes and Coimbra, 2017). Despite the time gap separating the Botucatu Formation and the Caiuá Group, they are in the same tectonic context (Basilici et al., 2012). The Caiuá paleodesert may be the depositional continuation of the Botucatu paleodesert, yet more humid, after the lava flows of the Serra Geral Formation (Batezelli, 2010; Menegazzo et al., 2016). Dinosaur and mammaliform footprints (*Brasilichnium*) have already been recorded in the Rio Paraná Formation (Caiuá Group) (Leonardi, 1977; Fernandes et al., 2009), showing that the lineages persisted in the same region after the magmatic event. Thus, trackmakers with close phylogenetic affinities may have inhabited the Caiuá and the Botucatu paleodesert alike. This makes Iguania lizards and possibly even the *Gueragama* lineage likely candidates for the Botucatu Formation trackmaker. Two other fossil Iguania were described for the Bauru Basin context. *Brasiliguana prudentes* Nava and Martinelli (2011) was described in the Adamantina Formation (Turonian-Santonian) context and *Pristiguana brasiliensis* Estes and Price (1973) was found in rocks from the Marília Formation (Campanian-Maastrichtian). These occurrences, despite being in a different paleoenvironmental context, attest to the presence of iguanids within the area that was once the





Fig. 8. Lizard-like trackmaker reconstruction (reconstruction by Julio Lacerda).

depositional range of the Botucatu paleodesert.

Another four Mesozoic lizard species have been described in Brazil. Three are from the Crato Formation (Lower Cretaceous, Aptian-Albian), Araripe Basin, southern Ceará State, Northeast Brazil (Bonfim-Júnior and Marques, 1997; Evans and Yabumoto, 1998; Simões, 2012; Simões et al., 2015), and one is from the Quiricó Formation (Lower Cretaceous, Valanginian-Early Aptian), Sanfranciscana Basin, Minas Gerais State, Southeast Brazil (Bittencourt et al., 2020). *Tijubina ponteii* Júnior and Marques, 1997, *Olindalacerta brasiliensis* Evans and Yabumoto (1998) and *Calanguban alamoii* Simões, Caldwell and Kellner (2014) are the best-preserved lizard remains for the Mesozoic of Gondwana and are considered scleroglossan lizards. *C. alamoii* possibly has scincomorph affinities, while *T. ponteii* and *O. brasiliensis* phylogenetic positions remain very controversial (Simões et al., 2017). *Neokotus sanfranciscanus* Bittencourt, Simões, Caldwell and Langer (2020), in turn, is interpreted as a Paramecellodidae, being the oldest known South American lizard body fossil (Bittencourt et al., 2020). Its remains were collected in the lowest Quiricó Formation strata, interpreted as a shallow lacustrine environment. The age of the lower levels of the Quiricó Formation coincides with the upper levels of the Botucatu Formation, indicating this family of lizards was present in the continent at the time of the Botucatu Formation deposition. The ichnofossils described here may be older and from another tectonic context, but still, this group of lizards is a good candidate.

Determining the trackmaker at a more restricted taxonomic level within Squamata can be problematic. The structure of squamate autopodia can be highly convergent in species inhabiting the same type of environment (Daza et al., 2016) and, according to Kubo (2010), despite his small sampling, there was no strong correlation between the morphology of footprints and phylogeny. This makes it more difficult to determine the producer of the lacertoid tracks. Some general morphotypes, however, can be excluded, such as forms with zygodactyl feet and groups with a very elongated torso and tail.

Rhynchocephalia might also be good candidates for the trackmakers. During the Cretaceous, unlike Laurasia, representatives of the group

were present in several locations in Gondwana (Sues and Reisz, 1995; Evans and Sigogneau-Russell, 1997; Ross et al., 1999; Evans et al., 2001; Apesteguía and Novas, 2003; Apesteguía and Jones, 2012; Gentil et al., 2019). In Brazil, until now, the record of Rhynchocephalia is restricted to the Triassic of Rio Grande do Sul State (Santa Maria Supersequence, Paraná Basin), being represented by *Clevosaurus brasiliensis* Bonaparte and Sues (2006), *Clevosaurus hadroprodon* sp. (Hsiou et al., 2019) and *Lanceirosphenodon ferigoloi* Vivar, Martinelli, Hsiou and Soares (2020). Besides that, there are the *Rhynchosauroides* tracks that Silva et al. (2008) attributed to the group.

The absence of body fossils in the Botucatu Formation remains an impediment to the reconstruction of a more phylogenetically accurate scenario since adaptive convergence of autopodia is very common in desert-dwelling animals. Despite this difficulty, this new description increases the ecological diversity of the Botucatu paleodesert ecosystem and adds the possibility that lepidosaurians were not only present there but already well adapted to inhabiting desert environments during the very Early Cretaceous of the South American continent.

### 5.3. Paleoeological implications

The description of a new footprint morphotype assigned to a distinct trackmaker increases the ecological complexity of the Botucatu Formation ecosystem. A new node and novel ecological interactions must be added to the inferred trophic web (see Buck et al., 2017a). The Botucatu paleodesert lizard-like trackmaker could have been an herbivore, an omnivore, or a carnivore since modern lizards have various feeding behaviors (McBrayer, 2007). Most modern lizards are mainly carnivorous, sit-and-wait, or ambush foragers that consume largely terrestrial invertebrates, particularly insects (Pianka and Vitt, 2003; McBrayer, 2007). The preferred feeding strategy of modern desert lizards, however, seems to be omnivory, where species consume variable proportions of vegetation including seeds along with insects (Louv and Holm, 1972; Robinson and Barrows, 2013). Desert dune environments can be very harsh. They are stressed by the scarcity of resources, which



depend on rainfall. Some living desert lizards consume plant material seasonally with increased rainfall, while during droughts the main food resource is insects (Robinson and Barrows, 2013). Regarding the foraging strategy, desert lizards can be sit-and-wait or widely foragers and this seems to be strongly linked to phylogeny, although some reversions have occurred (Vitt and Pianka, 2007). Vitt and Pianka (2007) identified almost without exception that iguanians ambush their prey. They rely on visual prey detection and capture food via lingual prehension, preferably consuming ants, other Hymenoptera, beetles, and bugs. Scleroglossans, in turn, were found to be wide foragers and consume prey items rarely consumed by iguanians. After the first split in squamate phylogeny (about 200 Ma) they acquired chemical prey discrimination and switched from the ancestral tongue prehension to jaw prehension (Vitt and Pianka, 2005; Huey and Pianka, 2007). Vitt and Pianka (2007) found modern Scincoidea feed mainly on termites, while varanids preferentially eat spiders and vertebrates. Teiids and gymnophthalmids, in turn, consume orthopterans and centipedes. Vitt and Pianka (2007) finally conclude wide foraging, chemical prey discrimination, and jaw prehension introduced a new food resource base for scleroglossans, providing them access to sedentary and hidden prey that were and are unavailable to iguanians.

Probably the Botucatu paleodesert lizard-like trackmaker fed mostly on arthropods, such as insects and/or arachnids. Arthropods are recorded by various traces in the eolian sandstones of the Botucatu Formation and are part of the typical detritus-based food web (Leonardi et al., 2007; Peixoto et al., 2020). Taking into account the size of the Botucatu Formation lizard-like trackmaker, it could also have fed on dinosaur neonates and eggs, as well as juvenile Mammaliaformes. The consumption of vertebrates and eggs, however, is a very specialized behavior only seen in a few groups of modern and extinct lizards (McBrayer, 2007). The new class of trackmaker is inferred as a secondary consumer and potential competitor of Mammaliaformes. Both groups could have preyed on the same food items and depending on their size and the lepidosaurian phylogenetic affinity, they could also have preyed on each other. Niche segregation possibly occurred, with the selection of preferred prey by one group or another or even temporal segregation in the desert environment. Typically, ectothermic organisms in deserts are diurnal, while small mammals are mostly nocturnal. Metabolic rates of ectotherms are lower also resulting in less need to acquire food.

As inferred for *Gueragama sulamericana* (Simões et al., 2015), the Botucatu Formation lizard-like trackmaker could also have spent part of the day in burrows to avoid extreme conditions. Body thermal regulation through fossorial behavior is an efficient strategy for desert environments and is used by several current species (Holm, 1973). The periods of greatest activity could have been in the morning and/or at dusk (Louw and Holm, 1972; Holm, 1973; Porter et al., 1973; Grant and Dunham, 1990) when solar radiation is weaker and the temperature is lower but sufficient to allow ectotherms activity. In contrast, during the night when it is colder, ectotherm trackmakers probably remained sheltered. Until now, tetrapod burrows have not been registered for the Botucatu Formation but these structures were reported in the underlying eolian deposits of the Upper Jurassic Guara Formation (Rio Grande do Sul State, Brazil) (Dentzien-Dias et al., 2012). Future fieldwork can find such structures, confirming this paleoecological interpretation.

The current record is very important from an ecological point of view, as it shows that representatives of Lepidosauria may have occupied desert dune environments in Gondwana since the Early Cretaceous. Nowadays, only Squamata among lepidosaurians inhabit desert environments.

#### 5.4. Additional comments

Co-occurrence of lizard-like and mammaliaform tracks in dune deposits was reported in Permian of North America and Europe (Haubold et al., 1995) and in Late Triassic–Early Jurassic Navajo and Nugget

sandstone in the USA (Faul and Roberts, 1951; Haubold, 1971; Albers, 1975; Lockley and Hunt, 1995; Lockley et al., 2011; Chure et al., 2014). Regarding the abundance of lacertoids trackways in the Botucatu sandstone, they are much rarer than *Brasilichnium* tracks. Traces of mammal-like trackmakers are also much more common than lacertoid tracks in the Nugget Sandstone (Albers, 1975; Lockley et al., 2011; Chure et al., 2014). Trackmaker's behavioral differences may explain this pattern. The low frequency could reflect the behavior of sit-and-wait foraging strategy for the lizard-like trackmaker and an active widely foraging for the mammal-like trackmaker. Other possibilities are smaller populations of lizard-like trackmakers and/or preservational issues.

Finally, a thorough review of ichnotaxa related to lacertoid morphotypes is necessary. Kim et al., (2019) reviewed some ichnotaxa of lizard-like tracks, but many ichnogenera have been described (see examples in Avanzini and Renesto, 2002); some based on poorly preserved specimens and others on poorly figured specimens. This makes comparison very difficult. Since this was not the focus of this work, we preferred to use more commonly adopted classifications.

## 6. Conclusions

A new tetrapod track morphotype was identified and described for the Botucatu Formation. It shares some characteristics with *Rhynchosauroides* and was tentatively associated with this ichnogenus. The position of the tracks along the trackway and the morphology of some better preserved footprints allowed the identification of the trackmaker as a lizard-like animal.

Despite being all produced by the same trackmaker, the trackways described here record variations in the pace angulation and footprint angle, reflecting different modes of locomotion. These are: a typical cursorial gait with constant velocity; a cursorial gait recording a pause (the 'paused-walking'), and side-walking on an inclined plane. The analysis of this trackway diversity shows how morphological characteristics of the tracks and trackways vary depending on the locomotory behavior adopted (e.g. presence of tail marks).

This work increased the knowledge about the Botucatu paleodesert fauna, its trophic ecology, and the ichnodiversity of this geological unit. It also advanced our understanding of desert ecosystems' evolution.

### CRedit authorship contribution statement

**Pedro Victor Buck:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Validation, Writing – original draft, Writing – review & editing. **Aline Marcelle Ghilardi:** Conceptualization, Funding acquisition, Investigation, Visualization, Writing – original draft, Writing – review & editing. **Bernardo de C.P. e M. Peixoto:** Funding acquisition, Investigation, Visualization, Writing – review & editing. **Tito Aureliano:** Investigation, Visualization, Writing – review & editing. **Marcelo Adorna Fernandes:** Conceptualization, Formal analysis, Investigation, Methodology, Resources, Supervision, Writing – review & editing.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## References

- Albers, S.H., 1975. Paleoenvironment of the Upper Triassic-Lower Jurassic Nugget Sandstone Near Heber, Utah. Doctoral dissertation. Department of Geology and Geophysics, University of Utah.
- Apesteigua, S., Novas, F.E., 2003. Large Cretaceous sphenodontian from Patagonia provides insight into lepidosaur evolution in Gondwana. *Nature* 425 (6958), 609–612. <https://doi.org/10.1038/nature01995>.
- Apesteigua, S., Jones, M.E.H., 2012. A late cretaceous “tuatara” (Lepidosauria: sphenodontinae) from south America. *Cretac. Res.* 34, 154–160.
- Avanzini, M., Renesto, S., 2002. A review of Rhynchosauroides tirolicus Abel, 1926 ichnospecies (Middle Triassic: anisian-Ladinian) and some inferences on Rhynchosauroides trackmaker. *Riv. Ital. Paleontol. Stratigr.* 108 (1) <https://doi.org/10.13130/2039-4942/5453>.
- Basilici, G., Sgarbi, G.N., Dal’Bó, P.F.F., Hasui, Y., 2012. A Sub-bacia Bauru: um sistema continental entre deserto e cerrado. *Geologia do Brasil Beca*, pp. 520–543.
- Batezelli, A., 2010. Arcaibouço tectono-estratigráfico e evolução das Bacias Caiuá e Bauru no Sudeste brasileiro. *Rev. Bras. Geociências* 40, 265–285.
- Belvedere, M., Farlow, J.O., 2016. A numerical scale for quantifying the quality of preservation of vertebrate tracks. In: Falkingham, P.L., Marty, D., Richter, A. (Eds.), *Dinosaur Tracks: the Next Steps*. Indiana University Press, Bloomington, pp. 92–98 chap. 6.
- Bernardi, M., Avanzini, M., 2011. Locomotor behavior in early reptiles: insights from an unusual *Erpetopus* trackway. *J. Paleontol.* 85 (5), 925–929.
- Bigarella, J.J., Salamuni, R., 1961. Early Mesozoic wind patterns as suggested by dune bedding in the Botucatu Sandstone of Brazil and Uruguay. *Geol. Soc. Am. Bull.* 72 (7), 1089–1105.
- Bittencourt, J.S., Simões, T.R., Caldwell, M.W., Langer, M.C., 2020. Discovery of the oldest South American fossil lizard illustrates the cosmopolitanism of early South American squamates. *Nat. Commun.* 3 (1), 1–11. <https://doi.org/10.1038/s42003-020-0926-0>.
- Bonaparte, J.F., Sues, H.D., 2006. A new species of *Clevosaurus* (Lepidosauria: Rhynchocephalia) from the upper triassic of Rio grande do Sul, Brazil. *Palaentology* 49 (4), 917–923.
- Bonfim-Júnior, F. de C., Marques, R.B., 1997. Um novo lagarto do Cretáceo do Brasil (Lepidosauria, Squamata, Lacertilia-Formação Santana, Aptiano da Bacia do Araripe), vol. 20. *Anuário do Instituto de Geociências*, pp. 233–340.
- Brand, L.R., 1996. Variations in salamander trackways resulting from substrate differences. *J. Paleontol.* 70 (6), 1004–1010.
- Brand, L.R., Tang, T., 1991. Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona: evidence for underwater origin. *Geology* 19 (12), 1201–1204.
- Brizuela, S., Albino, A., 2011. A scincomorpha lizard from the campanian of patagonia. *Cretac. Res.* 32 (6), 781–785.
- Buck, P.V., Ghilardi, A.M., Peixoto, B.C.P.M., Fernandes, L.B., dos, R., Fernandes, M.A., 2017a. A new tetrapod ichnotaxon from Botucatu Formation, Lower Cretaceous (Neocomian), Brazil, with comments on fossil track preservation on inclined planes and local paleoecology. *Palaeoogeogr. Palaeoeclimatol. Palaeoecol.* 466, 21–37.
- Buck, P.V., Ghilardi, A.M., Fernandes, L.B., dos, R., Fernandes, M.A., 2017b. A new ichnotaxon classification of large mammaliaform trackways from the Lower Cretaceous Botucatu Formation, Paraná Basin, Brazil. *Palaeoogeogr. Palaeoeclimatol. Palaeoecol.* 485, 377–388.
- Chure, D.J., Good, T.R., Engelmann, G.F., Lockley, M.G., Lucas, S.G., 2014. A forgotten collection of vertebrate and invertebrate ichnofossils from the Nugget sandstone (? Late triassic–? Early jurassic), near heber, wasatch county, Utah. In: *Fossil Footprints of Western North America: New Mexico Museum of Natural History and Science Bulletin*, 62, pp. 181–196.
- Christofletti, B., Peixoto, B.C.P.M., Warren, L.V., Inglez, L., Fernandes, M.A., Alessandretti, L., Alexandre de Jesus Perinotto, J., Simões, M.G., Assine, M.L., 2021. Dinos among the dunes: dinoturbation in the pirambóia formation (Paraná Basin), São Paulo state and comments on cross-section tracks. *J. S. Am. Earth Sci.* 109, 103252. <https://doi.org/10.1016/j.jsames.2021.103252>.
- Clemente, C.J., 2014. The evolution of bipedal running in lizards suggests a consequential origin may be exploited in later lineages. *Evolution* 68 (8), 2171–2183. <https://doi.org/10.1111/evo.12447>.
- Costa, G., 2012. *Behavioural Adaptations of Desert Animals*. Springer Science & Business Media.
- Curth, S., Fischer, M.S., Nyakatura, J.A., 2014. Ichnology of an extant belly-dragging lizard—analogs to early reptile locomotion? *Ichnos* 21 (1), 32–43. <https://doi.org/10.1080/10420940.2013.877006>.
- Daza, J.D., Stanley, E.L., Wagner, P., Bauer, A.M., Grimaldi, D.A., 2016. Mid-Cretaceous amber fossils illuminate the past diversity of tropical lizards. *Sci. Adv.* 2 (3) <https://doi.org/10.1126/sciadv.1501080>.
- Dentzien-Dias, P.C., Figueiredo, A.E.Q., Mesa, V., Perea, D., Schultz, C.L., 2012. Vertebrate footprints and burrows from the upper jurassic of Brazil and Uruguay. *Ichnology of Latin America—selected papers. Sociedade Brasileira de Paleontologia, Série Monografias* 2, 129–139.
- Diedrich, C., 2005. Actupaleontological trackway experiments with Iguana on intertidal flat carbonates of the Arabian Gulf—a comparison to fossil *Rhynchosauroides* tracks of Triassic carbonate tidal flat megatracksites in the European Germanic Basin. *Maritima* 35 (2), 203–220.
- D’Orazi Porchetti, S., Bertini, R.J., Langer, M.C., 2017a. Walking, running, hopping: analysis of gait variability and locomotor skills in *Brasilichnium leonardi*, with inferences on trackmaker identification. *Palaeoogeogr. Palaeoeclimatol. Palaeoecol.* 465, 14–29. <https://doi.org/10.1016/j.palaeo.2016.10.009>.
- D’Orazi Porchetti, S., Bertini, R.J., Langer, M.C., 2017b. Proposal for ichnotaxonomic allocation of therapsid footprints from the Botucatu Formation (Brazil). *Ichnos* 25, 192–207. <https://doi.org/10.1080/10420940.2017.1308929>.
- Estes, R., Price, L.L., 1973. Iguanid lizard from the upper cretaceous of Brazil. *Science* 180 (4087), 748–751. <https://doi.org/10.1126/science.180.4087.748>.
- Evans, S.E., Prasad, G.V.R., Manhas, B.K., 2001. Rhynchocephalians (diapsida: Lepidosauria) from the jurassic kota formation of India. *Zool. J. Linn. Soc.* 133 (3), 309–334.
- Evans, S.E., Sigogneau-Russell, D., 1997. New sphenodontians (diapsida: Lepidosauria: Rhynchocephalia) from the early cretaceous of North Africa. *J. Vertebr. Paleontol.* 17 (1), 45–51. <https://doi.org/10.1080/02724634.1997.10010952>.
- Evans, S.E., Yabumoto, Y., 1998. A lizard from the early cretaceous Crato Formation, Araripe Basin, Brazil. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 349–364.
- Faul, H., Roberts, W.A., 1951. New fossil footprints from the Navajo(?) sandstone of Colorado. *J. Paleontol.* 25 (3), 266–274. <https://www.jstor.org/stable/1299922>.
- Fernandes, L.A., Coimbra, A.M., 2017. O Grupo Caiuá (Ks): revisão estratigráfica e contexto deposicional. *Rev. Bras. Geociências* 24 (3), 164–176.
- Fernandes, L.A., Sedor, F.A., Silva, R.C., Silva, L.R., Azevedo, A.A., Siqueira, A.G., 2009. Icnofósseis da Usina Porto Primavera, SP: rastros de dinossauros e de mamíferos em rochas do deserto Neocretáceo. In: *Sítios Geológicos e Paleontológicos do Brasil. CPRM-Serviço Geológico do Brasil, Brasília*, pp. 479–488.
- Fernandes, M.A., Carvalho, L.S., 2007. Pegadas fósseis da Formação Botucatu (Jurássico Superior-Cretáceo Inferior): o registro de um grande dinossauro Ornithopoda na Bacia do Paraná. In: Carvalho, L.S., et al. (Eds.), *Paleontologia: Cenários de Vida. Rio de Janeiro*, vol. 1. Interciência, Rio de Janeiro, pp. 417–424.
- Fernandes, M.A., Fernandes, L.B., dos, R., Souto, P.D.F., 2004. Occurrence of urolites related to dinosaurs in the lower cretaceous of the Botucatu Formation, Paraná Basin, São Paulo state, Brazil. *Rev. Bras. Paleontol.* 7 (2), 263–268.
- Fernandes, M.A., Ghilardi, A.M., Carvalho, L.S., Leonardi, G., 2011. Pegadas de dinossauros Theropoda do Paleodeserto Botucatu (Jurássico Superior-Cretáceo Inferior) da Bacia do Paraná. In: Carvalho, L.S., et al. (Eds.), *Paleontologia: Cenários de Vida*, vol. 4. Interciência, Rio de Janeiro, pp. 609–620.
- Fernandes, M.A., Ghilardi, A.M., Carvalho, L.S., 2014. Paleodeserto Botucatu: inferências ambientais e climáticas com base na ocorrência de icnofósseis. In: *Paleontologia: Cenários de Vida—Paleoclimas*, vol. 5. Interciência, Rio de Janeiro, pp. 71–80.
- Fornós, J.J., Bromley, R.G., Clemmensen, L.B., Rodriguez-Perea, A., 2002. Tracks and trackways of myotragus balearicus bate (artiodactyla, caprinae) in pleistocene aeolianites from mallorca (balearic islands, western mediterranean). *Palaeoogeography. Palaeoeclimatol. Palaeoecol.* 180 (4), 277–313. [https://doi.org/10.1016/S0031-0182\(01\)00431-X](https://doi.org/10.1016/S0031-0182(01)00431-X).
- Gentil, A.R., Agnolin, F.L., Marsà, J.A.G., Motta, M.J., Novas, F.E., 2019. Bridging the gap: sphenodont remains from the turonian (upper cretaceous) of patagonia. *Palaebiol. Infer. Cretaceous. Res.* 98, 72–83. <https://doi.org/10.1016/j.cretres.2019.01.016>.
- Grant, B.W., Dunham, A.E., 1990. Elevational covariation in environmental constraints and life histories of the desert lizard *Sceloporus merriami*. *Ecology* 71 (5), 1765–1776. <https://doi.org/10.2307/1937584>.
- Haubold, H., 1971. *Ichnia Amphibiorum et Reptiliorum Fossilium. Handbuch der Paläoherpetologie* 18, 1–124.
- Haubold, H., Lockley, M.G., Hunt, A.P., Lucas, S.G., 1995. Lacertoid footprints from permian dune sandstones, cornberg and DeChelly sandstones. In: Lucas, S.G., Heckert, A.B. (Eds.), *Early Permian Footprints and Facies*. New Mexico Museum of Natural History and Science, Bulletin, vol. 6, pp. 235–244.
- Holm, E., 1973. The influence of constant temperatures upon the circadian rhythm of the Namib desert dune lizard *Aporosaura anchietae* Bocage. *Madoqua* 2 (2), 33–41.
- Holst, H.K.H., Smit, J., Veenstra, E., 1970. Lacertoid footprints from early middle Triassic at Haarmühle, near alstatte, w-Germany. *Proc. K. Ned. Akad. Wet. Ser. B Phys. Sci.* 73 (2), 157.
- Hsiou, A.S., Nydam, R.L., Simões, T.R., Pretto, F.A., Onary, S., Martinelli, A.G., Liparini, A., Martínez, P.R.R., de, V., Soares, M.B., Schultz, C.L., Caldwell, M.W., 2019. A new clevosaurid from the Triassic (Carnian) of Brazil and the rise of sphenodontians in Gondwana. *Sci. Rep.* 9 (1), 1–12. <https://doi.org/10.1038/s41598-019-48297-9>.
- Huene, F.V., 1931. *Verschiedene mesozoische Wirbeltierreste aus Südamerika. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Beilagen*, Bd 66, 181–198.
- Huey, R.M.B., Pianka, E.R., 2007. Historical introduction: on widely foraging for Kalahari Lizards. In: Reilly, S.M., et al. (Eds.), *Lizard Ecology*. Cambridge University Press, pp. 1–10. <https://doi.org/10.1017/CBO9780511752438.002>.
- Irschick, D.J., Jayne, B.C., 1998. Effects of incline on speed, acceleration, body posture and hindlimb kinematics in two species of lizard *Callisaurus draconoides* and *Uma scoparia*. *J. Exp. Biol.* 201 (2), 273–287.
- Jackson, S.J., Whyte, M.A., Romano, M., 2010. Range of experimental dinosaur (Hypsilophodon foxii) footprints due to variation in sand consistency: how wet was the track? *Ichnos* 17 (3), 197–214. <https://doi.org/10.1080/10420940.2010.510026>.
- Jagnandan, K., Higham, T.E., 2017. Lateral movements of a massive tail influence gecko locomotion: an integrative study comparing tail restriction and autotomy. *Sci. Rep.* 7 (1), 1–8. <https://doi.org/10.1038/s41598-017-11484-7>.

- Janasi, V. de A., Freitas, V.A., Heaman, L.H., 2011. The onset of flood basalt volcanism, Northern Paraná Basin, Brazil: a precise U–Pb baddeleyite/zircon age for a Chapecó-type dacite. *Earth Planet Sci. Lett.* 302 (1–2), 147–153. <https://doi.org/10.1016/j.epsl.2010.12.005>.
- Kim, J.Y., Lockley, M.G., 2013. Review of dinosaur tail traces. *Ichnos* 20 (3), 129–141. <https://doi.org/10.1080/10420940.2013.817405>.
- Kim, K.S., Lim, J.D., Lockley, M.G., M, G., Kim, D.H., Pinuela, L., Yoo, J.S., 2019. Largest Cretaceous lizard track assemblage, new morphotypes and longest trackways comprise diverse components of an exceptional. Korean Konservat-Lagerstätten ichnofauna Scientific Reports 9, 13278. <https://doi.org/10.1038/s41598-019-49442-0>.
- Kinsey, C.T., McBrayer, L.D., 2018. Forelimb position affects facultative bipedal locomotion in lizards. *J. Exp. Biol.* 221 (24) <https://doi.org/10.1242/jeb.185975>.
- Kohlsdorf, T., Biewener, A.A., 2006. Negotiating obstacles: running kinematics of the lizard *Sceloporus malachiticus*. *J. Zool.* 270 (2), 359–371.
- Kubo, T., 2010. Extant lizard tracks: variation and implications for paleoichnology. *Ichnos* 17 (3), 187–196. <https://doi.org/10.1080/10420940.2010.502500>.
- Kubo, T., Ozaki, M., 2009. Does pace angulation correlate with limb posture? *Palaeogeography, Palaeoclimatology, Palaeoecology* 275 (1–4), 54–58. <https://doi.org/10.1016/j.palaeo.2009.02.001>.
- Lee, H.J., Lee, Y.N., Fiorillo, A.R., Lü, J., 2018. Lizards ran bipedally 110 million years ago. *Sci. Rep.* 8 (1), 1–7. <https://doi.org/10.1038/s41598-018-20809-z>.
- Leonardi, G., 1975. Trackways of the south American lizard *Tupinambis teguixin* (Linnaeus 1758), lacertilia, teiidae. *Anais Academia Brasileira de Ciências* 47, 301–310.
- Leonardi, G., 1977. Two New Ichnofaunas (Vertebrates and Invertebrates) in the Eolian Cretaceous Sandstone of the Caiuá Formation in Northwest Paraná. *Atas do I Simpósio de Geologia Regional, São Paulo*, pp. 112–128.
- Leonardi, G., 1980. On the discovery of an abundant ichno-fauna (vertebrates and invertebrates) in the Botucatu Formation s.s. in Araraquara, São Paulo, Brazil. *An Acad. Bras Ciências* 52 (3), 559–567.
- Leonardi, G., 1987. Glossary and Manual of Tetrapod Footprint Palaeoichnology, p. 75p.
- Leonardi, G., Carvalho, I.S., 2002. Jazigo Icnofossilífero do Ouro-Araraquara (SP): ricas pistas de tetrapodes do Jurássico. In: Schobbenhaus, C., et al. (Eds.), *Sítios Geológicos e Paleontológicos do Brasil*, vol. 1. DNPM/CPRM/SIGEP, Brasília.
- Leonardi, G., Carvalho, I.D., Fernandes, M.A., 2007. The desert ichnofauna from Botucatu Formation (upper jurassic-lower cretaceous), Brazil. In: Carvalho, I.S., et al. (Eds.), *Paleontologia: Cenários de Vida*, vol. 1. Interciência, Rio de Janeiro, pp. 371–383.
- Leonardi, G., Oliveira, F.H., 1990. A revision of the Triassic and Jurassic tetrapod footprints of Argentina and a new approach on the age and meaning of the Botucatu Formation footprints (Brazil). *Rev. Bras. Geociências* 20 (1), 216–229. <https://doi.org/10.5327/rbg.v20i1.331>.
- Leonardi, G., Sarjeant, W.A.S., 1986. Footprints representing a new Mesozoic vertebrate fauna from Brazil. *Mod. Geol.* 10, 73–84.
- Leonardi, G., Carvalho, I. de S., 2020. Review of the early mammal *Brasilichnium* and *brasilichnium*-like tracks from the lower cretaceous of South America. *J. S. Am. Earth Sci.* 102940. <https://doi.org/10.1016/j.jsames.2020.102940>.
- Lockley, M.G., Loope, D.B., Brand, L.R., 1992. Comment and reply on 'fossil vertebrate footprints in the coconino sandstone (permian) of northern Arizona: evidence for underwater origin. *Geology* 20 (7), 666–670.
- Lockley, M.G., Hunt, A.P., 1995. *Dinosaur Tracks and Other Fossil Footprints of the Western United States*. Columbia University Press, p. 338p.
- Lockley, M.G., Tedrow, A.R., Chamberlain, K.C., Minter, N.J., Lim, J.D., 2011. Footprints and invertebrate traces from a new site in the Nugget Sandstone (Lower Jurassic) of Idaho: implications for life in the northern reaches of the great Navajo-Nugget erg system in the western USA. *Fossil Record* 3, 344–356.
- Loope, D.B., Milàn, J., 2016. Dinosaur tracks in eolian strata: new insights into track formation, walking kinetics and trackmaker behavior. In: Falkingham, P.L., et al. (Eds.), *Dinosaur Tracks: the Next Steps*, pp. 359–365.
- Loope, D.B., 1992. Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona—evidence for underwater origin—comment. *Geology* 20 (7), 667–668.
- Loope, D.B., 2006. Burrows dug by large vertebrates into rain-moistened, Middle Jurassic sand dunes. *J. Geol.* 114, 753–762. <https://doi.org/10.1086/507618>.
- Loope, D.B., 2008. Life beneath the surfaces of active jurassic dunes: burrows from the entrada sandstone of South-central Utah. *Palaios* 23, 411–419. <https://doi.org/10.2110/palo.2006.p06-133r>.
- Louw, G.N., Holm, E., 1972. Physiological, morphological and behavioural adaptations of Namib desert lizard *Aporosaura anchietae* (Bocage). *Madoqua* 2 (1), 67–85.
- Mancuso, A.C., Krapovickas, V., Marsicano, C., Benavente, C., Benedito, D., De La Fuente, M., Ottone, E.G., 2016. Tetrapod tracks taphonomy in eolian facies from the Permian of Argentina. *Palaios* 31 (8), 374–388. <https://doi.org/10.2110/palo.2015.077>.
- Marchetti, L., Voigt, S., Lucas, S.G., Francischini, H., Dentzien-Dias, P., Sacchi, R., Mangiancotti, M., Scali, S., Gazzola, A., Ronchi, A., Millhouse, A., 2019a. Tetrapod ichnotaxonomy in eolian paleoenvironments (Coconino and De Chelly formations, Arizona) and late Cisuralian (Permian) sauropsid radiation. *Earth Sci. Rev.* 190, 148–170. <https://doi.org/10.1016/j.earscirev.2018.12.011>.
- Marchetti, L., Belvedere, M., Voigt, S., Klein, H., Castanera, D., Díaz-Martínez, I., Marty, D., Xing, L., Feola, S., Melchor, R.N., Farlow, J.O., 2019b. Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present. *Earth Sci. Rev.* 193, 109–145. <https://doi.org/10.1016/j.earscirev.2019.04.008>.
- Martínez, R.N., Apaldetti, C., Colombi, C.E., Praderio, A., Fernandez, E., Malnis, P.S., Correa, G.A., Abelin, D., Alcober, O., 2013. A new sphenodontian (Lepidosauria: Rhynchocephalia) from the Late Triassic of Argentina and the early origin of the herbivore opisthodontians. *Proceedings of the Royal Society B: Biological Sciences* 280 (1772), 20132057. <https://doi.org/10.1098/rspb.2013.2057>.
- McBrayer, L.D., 2007. *Lizard Ecology*. Cambridge University Press.
- Milani, E.J., Rangel, H.D., Bueno, G.V., Stica, J.M., Winter, W.R., Caixeta, J.M., Neto, O. P., 2007. *Bacias sedimentares brasileiras: cartas estratigráficas. Anexo ao Boletim de Geociências da Petrobrás* 15 (1), 183–205.
- Milàn, J., Bromley, R.G., 2006. True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 231 (3–4), 253–264. <https://doi.org/10.1016/j.palaeo.2004.12.022>.
- Milàn, J., Loope, D.B., 2007. Preservation and erosion of theropod tracks in eolian deposits: examples from the Middle Jurassic Entrada Sandstone, Utah, U.S.A. *J. Geol.* 115, 375–386. <https://doi.org/10.1086/512758>.
- Mountney, N.P., 2004. Feature: The sedimentary signature of deserts and their response to environmental change. *Geol. Today* 20 (3), 101–106. <https://doi.org/10.1111/j.1365-2451.2004.00458.x>.
- Nava, W.R., Martinelli, A.G., 2011. A new squamate lizard from the Upper Cretaceous Adamantina Formation (Bauru Group), São Paulo State, Brazil. *An Acad. Bras Ciências* 83 (1), 291–299. <https://doi.org/10.1590/s0001-37652011000100017>.
- Nowatzki, C.H., Kern, H.P., 2000. The eolianites between Sanga do Cabral and Botucatu formations in Rio Grande do Sul State, Brazil. *An Acad. Bras Ciências* 72 (2), 247–256. <https://doi.org/10.1590/s0001-3765200000200010>.
- Peixoto, B., de, C.P.E.M., Mángano, M., Minter, G., Fernandes, N.J., L.B.dos, R., Fernandes, M.A., 2020. A New Insect Trackway from the Upper Jurassic-Lower Cretaceous Eolian Sandstones of São Paulo State. Implications for Reconstructing Desert Palaeoecology, Brazil. <https://doi.org/10.7717/peerj.8880>. PeerJ, 8, e8880.
- Pianka, E.R., Vitt, L.J., 2003. *Lizards: Windows to the Evolution of Diversity*. University of California Press.
- Pires, E.F., Guerra-Sommer, M., Scherer, dos Santos, dos Santos, C.M., Cardoso, A.R., 2011. Early Cretaceous coniferous woods from a *paleoerg* (Paraná Basin, Brazil). *E. J. S. Am. Earth Sci.* 32 (1), 96–109. <https://doi.org/10.1016/j.jsames.2011.04.001>.
- Porter, W.P., Mitchell, J.W., Beckman, W.A., DeWitt, C.B., 1973. Behavioral implications of mechanistic ecology. *Oecologia* 13 (1), 1–54.
- Reed, C.A., 1956. Temporary bipedal locomotion in the lizard *Agama caucasica* in Iraq. *Herpetologica* 12 (2), 128–128.
- Renne, P.R., Ernesto, M., Pacca, I.G., Coe, R.S., Glen, J.M., Prévot, M., Perrin, M., 1992. The age of Paraná flood volcanism, rifting of Gondwanaland, and the Jurassic-Cretaceous boundary. *Science* 258 (5084), 975–979. <https://doi.org/10.1126/science.258.5084.975>.
- Robinson, M.D., Barrows, C.W., 2013. Namibian and North American sand-diving lizards. *J. Arid Environ.* 93, 116–125. <https://doi.org/10.1016/j.jaridenv.2012.08.003>.
- Rocha-Barbosa, O., Loguercio, M.F.C., Velloso, A.L.R., Bonates, A.C.C., 2008. Bipedal locomotion in *Tropidurus torquatus* (Wied, 1820) and *Liolaemus lutzae* Mertens, 1938. *Braz. J. Biol.* 68 (3), 649–655. <https://doi.org/10.1590/s1519-69842008000300024>.
- Ross, C.F., Sues, H.D., De Klerk, W.J., 1999. Lepidosaurian remains from the Lower Cretaceous Kirkwood Formation of South Africa. *J. Vertebr. Paleontol.* 19 (1), 21–27. <https://doi.org/10.1080/02724634.1999.10011119>.
- Rowland, S.M., Caputo, M.V., Jensen, Z.A., 2020. Early adaptation to eolian sand dunes by basal amniotes is documented in two Pennsylvanian Grand Canyon trackways. *PLoS One* 15 (8), e0237636. <https://doi.org/10.1371/journal.pone.0237636>.
- Salamuni, R., Bigarella, J.J., 1967. The Botucatu Formation. *Problems in Brazilian Gondwana Geology*. Curitiba, PR, Brazil, pp. 197–206.
- Scherer, C.M.S., 2000. Eolian dunes of the Botucatu Formation (Cretaceous) in southernmost Brazil: morphology and origin. *Sediment. Geol.* 137 (1–2), 63–84. [https://doi.org/10.1016/S0037-0738\(00\)00135-4](https://doi.org/10.1016/S0037-0738(00)00135-4).
- Scherer, C.M., Goldberg, K., 2007. Palaeowind patterns during the latest Jurassic–earliest Cretaceous in Gondwana: evidence from aeolian cross-strata of the Botucatu Formation, Brazil. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 250 (1–4), 89–100.
- Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 Years of Image Analysis. *Nat. Methods* 9, 671–675.
- 2 Scotese, C.R., 2014. *Atlas of Early Cretaceous Paleogeographic Maps, PALEOMAP Atlas for ArcGIS*, vol. 2. ResearchGate Academia. The Cretaceous, Maps 16–22, Mollweide Projection.
- Silva, R.C., Ferigolo, J., de Souza Carvalho, I., Fernandes, A.C.S., 2008. Lacertoid footprints from the Upper Triassic (Santa Maria Formation) of Southern Brazil. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 262 (3–4), 140–156. <https://doi.org/10.1016/j.palaeo.2008.02.006>.
- Simões, T.R., 2012. Redescription of *Tijubina ponteii*, an Early Cretaceous lizard (Reptilia: Squamata) from the Crato Formation of Brazil. *An Acad. Bras Ciências* 84 (1), 79–94. <https://doi.org/10.1590/s0001-37652012000100008>.
- Simões, T.R., Caldwell, M.W., Kellner, A.W., 2014. A new Early Cretaceous lizard species from Brazil, and the phylogenetic position of the oldest known South American squamates. *J. Syst. Paleontol.* 13 (7), 601–614. <https://doi.org/10.1080/14772019.2014.947342>.
- Simões, T.R., Wilner, E., Caldwell, M.W., Weinschütz, L.C., Kellner, A.W., 2015. A stem acrodontan lizard in the Cretaceous of Brazil revises early lizard evolution in Gondwana. *Nat. Commun.* 6 (1), 1–8. <https://doi.org/10.1038/ncomms9149>.
- Simões, T.R., Caldwell, M.W., Weinschütz, L.C., Wilner, E., Kellner, A.W., 2017. Mesozoic lizards from Brazil and their role in early squamate evolution in South America. *J. Herpetol.* 51 (3), 307–315.
- Snyder, R.C., 1962. Adaptations for Bipedal Locomotion of Lizards. *American Zoologist*, pp. 191–203.
- Sues, H.D., Reisz, R.R., 1995. First record of the early Mesozoic sphenodontian *Clevosaurus* (Lepidosauria: Rhynchocephalia) from the Southern Hemisphere. *J. Paleontol.* 123–126.



- Talbot, M.R., 1985. Major bounding surfaces in aeolian sandstones—a climatic model. *Sedimentology* 32 (2), 257–265.
- Tamrat, E., Ernesto, M., 2006. Paleomagnetic constraints on the age of the Botucatu Formation in Rio Grande do Sul, Southern Brazil. *An Acad. Bras Ciências* 78 (3), 591–605. <https://doi.org/10.1590/s0001-37652006000300016>.
- Turner, S., Regelous, M., Kelley, S., Hawkesworth, C., Mantovani, M., 1994. Magmatism and continental break-up in the South Atlantic: high precision 40Ar-39Ar geochronology. *Earth Planet Sci. Lett.* 121 (3–4), 333–348. [https://doi.org/10.1016/0012-821X\(94\)90076-0](https://doi.org/10.1016/0012-821X(94)90076-0).
- Vivar, P.R.R., Martinelli, A.G., Hsiou, A.S., Soares, M.B., 2020. A New Rhynchocephalian from the Late Triassic of Southern Brazil Enhances Eusphenodontian Diversity. *J. Syst. Paleontol.* 18 (13) <https://doi.org/10.1080/14772019.2020.1732488>.
- Vitt, L.J., Pianka, E.R., 2005. Deep history impacts present-day ecology and biodiversity. *Proc. Natl. Acad. Sci. Unit. States Am.* 102 (22), 7877–7881. <https://doi.org/10.1073/pnas.0501104102>.
- Vitt, L.J., Pianka, E.R., 2007. Feeding ecology in the natural world. In: Reilly, S.M., et al. (Eds.), *Lizard Ecology: the Evolutionary Consequences of Foraging Mode*. Cambridge University Press, pp. 141–172.