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# *Farlowichnus rapidus* new ichnogen., new ichnosp.: A speedy and small theropod in the Early Cretaceous Botucatu paleodesert (Paraná Basin), Brazil

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A B S T R A C T

The Botucatu Formation (Paraná Basin, Brazil and the southern neighboring countries) comprises one of the richest tetrapod ichnological deposits of the Lower Cretaceous in South America. The ichnofossils are found in reddish sandstones lithofacies -interpreted to be dune and interdune deposits. The sandstones of Botucatu Formation originally covered a surface estimated in at least 1,300,000 km$^2$, the largest known fossil desert in the Earth's history. The distribution area of the Botucatu paleodesert presents one of the world's largest megatracksites. The tetrapod ichnofauna from the Botucatu Formation comprises minor bipedal dinosaur tracks (almost all attributable to theropods, with one exception, a doubt ornithopod trackway) along with many thousands of footprints of early mammals, and a single trackway of a lacertiform reptile. Among the bipedal dinosaur footprints, the most common and typical are considered theropod tracks, with long strides and high step angle and always with an acuminate termination. These trackways are straight and very narrow, with long strides and step angles showing high values. The footprints have a relatively large and very wide III digit and small, short, pointed, bladelike outer digits. The most special characteristic is that the II digit is longer and more important than the IV digit. Because of this morphology, the general outline of the footprint often reminds that of a waterdrop and, although it is structurally tridactyl, it usually looks like functionally monodactylous. These tracks are herein assigned to small theropods adapted to desert life with a prevalently cursorial gait, probably ancestors of clades such as noasaurs and velocisaurs. Due its unique morphological aspects it is defined a new ichnogenus and ichnospecies, *Farlowichnus rapidus* new ichnogen., new ichnosp.
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## 1. Introduction

Although the aeolian environment is frequently, and wrongly, considered inadequate for track preservation, taphonomic events linked to moist dunes and the presence of microbial mats (Carvalho et al., 2013) foster a good geological context for an early diagenesis of the sediments. The diversity of Botucatu Formation ichnofauna including early mammals, theropods, one case of a large ornithopod trackway, in addition to invertebrate trace fossils, is worldwide known (Leonardi and Carvalho, 2021a) and allows an overview of the arid terrestrial ecosystems during the Early Cretaceous (Figure 1).

The tetrapod tracks from the Botucatu ichnosites (also found on the sidewalks of the town) are very abundant, although frequently poor on quality (M−1 to M−2 morphological preservation quality,

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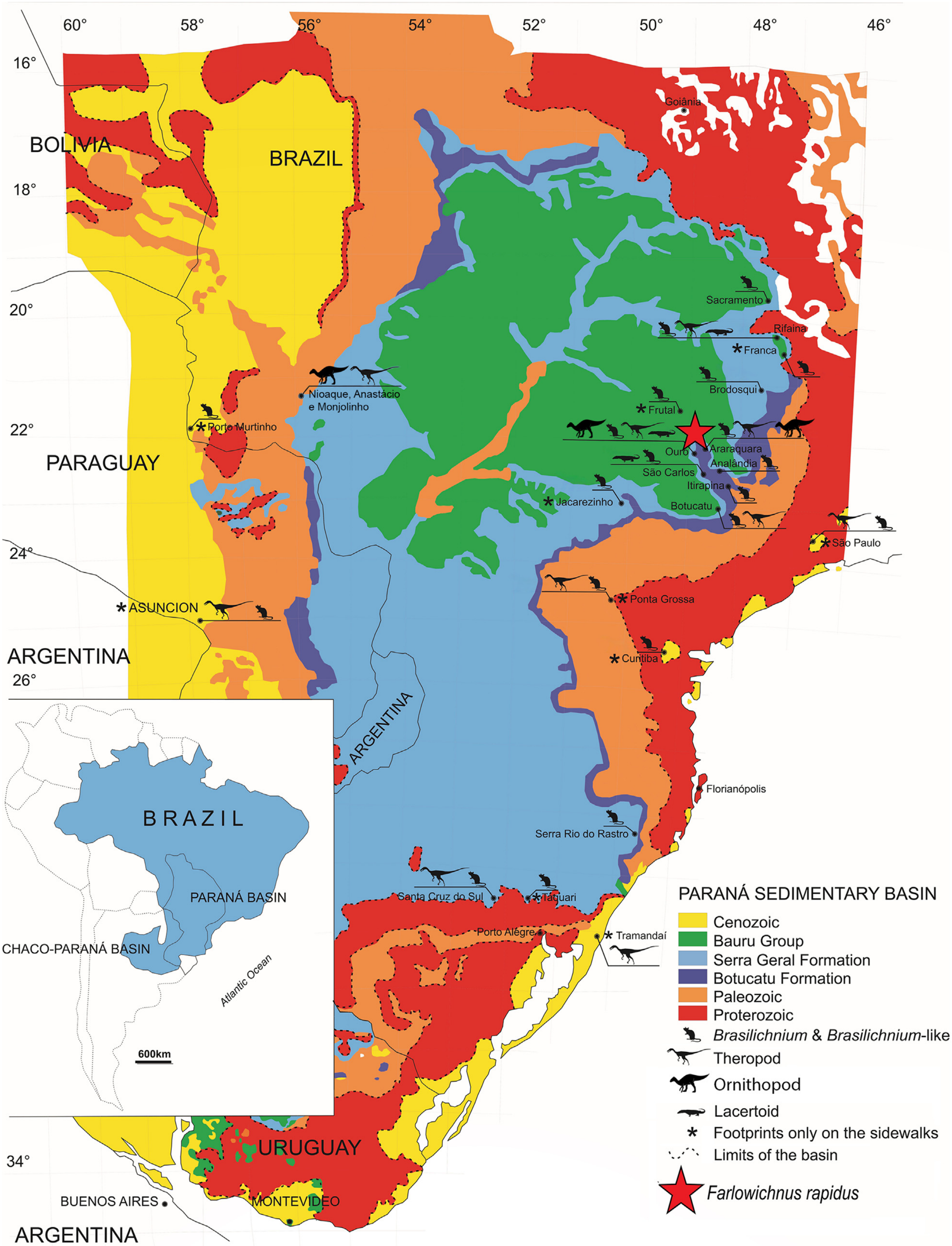


**Fig. 1.** Geological map of Paraná Basin with the distribution of Botucatu Formation fossil tracks. The red star indicates the location area of *Farlowichnus rapidus* new ichnogen., new ichnosp., theropod tracks from Botucatu Formation (modified from Leonardi and Carvalho, 2021a).

sensu Belvedere and Farlow, 2016; Marchetti et al., 2019). The footprints are often a rounded or elliptical cavity (convexity in the counter prints or natural casts) furnishing no morphological details. However, the parameters of such tracks frequently enable them to be classified, despite their poor quality. Detail identifications and descriptions are subject to the better specimens (M−3 as for their morphological preservation quality).

The ichnofauna from the Botucatu ichnosites shows about 8 different types of bipedal and functionally tridactylous dinosaur tracks, with an elevated pace angulation, up to 180°. They are represented by trackways and isolated footprints. A number of these theropod tracks have been mentioned and illustrated (Leonardi, 1980, 1994; Leonardi and Godoy, 1980; Leonardi and Oliveira, 1990; Leonardi and Carvalho, 2002; and especially Fernandes et al., 2011), but never thoroughly classified, named or formally attributed to a trackmaker.

Among these theropod trackways, a small one from the Botucatu Formation ichnosites is tridactylous, but often appears functionally almost monodactylous. The naming of this last form, which is the most typical and common among the dinosaur tracks in the Botucatu Formation, is the subject of this paper.

In the Botucatu Formation about ten distinct morphologies are attributed to mammals, with walking, running, hopping and galloping tracks. Among these tracks, the most abundant was classified as *Brasilichnium elusivum* Leonardi (1981). Other ichnogenera and ichnospecies attributed to mammals are *Brasilichnium saltatorium* Buck, Ghilardi, Peixoto, Fernandes, Fernandes (2017); *Aracoaraichnium leonardii* Buck, Ghilardi, Fernandes, Fernandes (2017); *Brasilichnium anaiti* D'Orazi Porchetti, Bertini, Langer, 2017. This tetrapod ichnofauna is associated with invertebrate trails and burrows, mainly considered produced by arthropods (arachnids and insects, adults or larvae). There is also an urolite, a liquid dinosaur excretion (Fernandes et al., 2004).

A widespread impression is that the past and current deserts are environments of death. However, nowadays as in the past, life was and is able to adapt in these extremely arid environments. In fact, however, in the Botucatu paleodesert the body fossils are extremely rare, just some silicified logs of ancient Conypherophyta (Pires et al., 2011) were found, and no animal body fossil. But as demonstrated through the ichnological data, the Botucatu paleodesert was inhabited by many animals, usually rather small. The tetrapod tracks indicate the presence of a biped dinosaur fauna, almost all small-sized theropods, possibly living around ponds or wadi areas.

The biota of this complex environment is known mainly from trace fossils from the Araraquara region, São Paulo State, but there are many other occurrences in São Paulo, Paraná, Santa Catarina, Rio Grande do Sul and Mato Grosso do Sul states, Brazil. There are tracks of a small lizard-like reptile trackway, small and medium-sized mammals, small and medium-sized theropod dinosaurs and one ornithopod of medium to large-size (Buck et al., 2017a, 2017b, 2022; D'Orazi Porchetti et al., 2017; Fernandes, 2005; Fernandes and Carvalho, 2007, 2008; Fernandes et al., 1988, 1990, 2004, 2011; Francischini et al., 2015, 2020, 2022; Leonardi, 1977, 1980, 1981, 1989, 1994; Leonardi and Godoy, 1980; Leonardi and Sarjeant, 1986; Leonardi and Oliveira, 1990; Leonardi and Carvalho, 2021a; Manes et al., 2021; Peixoto et al., 2020). Among the valid tetrapod ichnotaxa are *Brasilichnium elusivum*, *Brasilichnium saltatorium*, *Aracoaraichnium leonardii*, *Brasilichnium anaiti* and cf. *Eubrontes* isp. (Leonardi, 1981; Buck et al., 2017a, b; D'Orazi Porchetti et al., 2017; Manes et al., 2021). There are also invertebrate trace fossils such as *Ancorichnus*, *Arenicolites*, *Beaconites*, *Hexapodichnus*, *Octopodichnus*, *Paleohelcura*, *Scoyenia*, *Skolithos* and *Taenidium* (Faccini et al., 1989; Fernandes et al., 1990, 2002; Fernandes and Fernandes, 2010; Peixoto and Fernandes, 2010).

Among the bipedal dinosaur footprints from the Botucatu Formation, the most common are theropods, recognizable as such because of the very high step angle and the digits with an acuminate termination. One of them differ from all known theropod tracks and the purpose of this study is to name and to interpret the possible trackmaker.

The Botucatu Formation is a Lower Cretaceous deposit (Berriasian-Hauterivian) of desertic environments. The preserved footprints indicate animals of small to medium-size. The theropod tracks found in this formation are probably related to the fossil that have already been found in the Gondwana supercontinent. Among them the most common are the clade Abelisauroidea, and more particularly the Noasauridae Bonaparte and Powell, 1980, which has expanded to include numerous other Cretaceous Gondwanan forms from South America, Africa, Madagascar, India, Australia and Europe (Langer et al., 2019). They are small to medium-sized dinosaurs with necks, arms, and skulls relatively longer than those of other abelisauroid clades (Barbosa et al., 2023). Little is yet known about their biology, metabolism, and even their diet, a probably varied diet because they have teeth of different types and there are also edentulous specimens (Langer et al., 2019).

### 1.1. Institutional abbreviations

LPP - IC - Laboratory of Paleoecology and Paleoichnology of the Federal University of Sao Carlos-UFSCar, São Carlos, São Paulo, Brazil.

IC - Ichnofossils.

MCT - Museu das Ciências da Terra, C.P.R.M., Serviço Geológico do Brasil, Rio de Janeiro.

UFRJ DG − Macrofossil Collection, Rio de Janeiro Federal University, Brazil.

## 2. Geological, stratigraphical and paleoenvironmental settings

The Ouro ichnosite (one of the Botucatu ichnosites) is located in the State of São Paulo, in the Municipality of Araraquara, 4 Km E of the Ouro former railway station, approximately 8 km ESE from the Araraquara downtown. There are there several abandoned sandstone quarries, the main one being called São Bento quarry, located at 21°49′03.4″S and 48°04′22.9″W. These sandstones constitute the Botucatu Formation, an important stratigraphic unity that extends along a stretch of the Brazilian territory comprised between the states of Minas Gerais and Rio Grande do Sul, on the east border, and in the states of Mato Grosso and Goiás, on the west border of the Paraná Basin. The outcrops are distributed on a roughly circular route of about 4500 km. These sandstones are almost always silicified and therefore hard, making it a very suitable building material.

The Botucatu Formation comprises Lower Cretaceous (Berriasian-Hauterivian) reddish to yellowish aeolian sandstones, mainly constituted of fine to medium grain size sandstones, with rounded to subrounded quartz grains, moderately selected and with almost no matrix. These sandstones originally covered an estimated surface of at least 1,300,000 km$^2$. It is interpreted as the largest known desert in the world history, with a large number of invertebrate and tetrapod ichnosites. From the paleontological point of view, the sandstones of the Botucatu Formation despite having no animal body fossils, present a large amount of fossil tetrapod tracks.

These sandstones are found in a succession of thick tangential cross-stratification, peculiar to transverse dunes (Fúlfaro and Petri, 1988). These beds are interpreted as paleo ergs similar to great sand seas as the Sahara Desert (Scherer and Goldberg, 2007; Holz et al., 2008). The dominant direction of the aeolian paleocurrents are N−S in the north portion of the basin and SW-NE to South, originating a confluence zone near the parallel 24°S. This suggests that the deposition was controlled by a wind pattern characteristic of monsoons (Scherer, 2000; Scherer and Goldberg, 2007; Perea et al., 2009). In the lower portion of the Botucatu Formation can occur mudstones, muddy sandstones and conglomeratic sandstones with lenticular and tabular geometries, cross-stratifications and convolute structures interpreted as the deposition in a fluvial-aeolian environments (Rocha-Campos and Farjallat, 1966; Schneider et al., 1974; Manes et al., 2021).

The lithofacies from this lithostratigraphic unit are interpreted as foreset and interdune facies deposits of large dunes, an inland desert, with high sand supply (Leonardi, 1980; Leonardi et al., 2007; Milani et al., 2007; Carvalho, 2022). In this way there was the establishment of a paleoerg, that overpass the phreatic level changes, allowing the interdune areas to always keep dry (Caetano-Chang, 1997; Carvalho, 2022). Despite this environmental condition of the Botucatu paleodesert, some small lakes, probably ephemeral (Almeida, 1950; Paraguassu, 1970), should have existed, especially in areas where the tetrapod ichnofauna is abundant (Carvalho, 2022; Carvalho and Leonardi, 2021).

The upper portion of the Botucatu sandstones is interbedded with the lava flows of Serra Geral Formation, including evidence of the interaction between unconsolidated sandstones and the lava, in a context of fissural volcanism (Holz et al., 2008). The basalts of Serra Geral Formation are dated between 127 and 137 Ma (Scherer and Lavina, 2006), allowing to establish the upper limit of Botucatu Formation in 132 Ma, analogous to the basaltic province of Etendeka, in north-western Namibia, Africa (Holz et al., 2008). The study of Brückmann et al. (2014) demonstrated that the oldest aeolian deposits present the age of 134.5 $^{+/-}$ 2.1 Ma.

The Botucatu paleodesert was established during a specific continental paleogeography under a strong global warming episode that allowed the origin of wide aeolian systems throughout the Gondwana continent during the Late Jurassic and Early Cretaceous (Mountney et al., 1999; Scherer and Lavina, 2006; Veiga and Spalletti, 2007; Price et al., 2018). These environmental factors resulted in the deposition of the sands of the Botucatu Formation and the origin of the largest known aeolian system (more than 1,300,000 km$^2$), embracing almost all the Paraná Basin (Figure 1), including the Western of Paraguay and Northeastern Argentina (Fernandes et al., 2014).

## 3. Ichnosystematics

The fossil trackways described in this study are unique in morphology, so it is formally erected a new ichnotaxon (an ichnogenus and ichnospecies).

***Farlowichnus*** new ichnogen.

*Type species* - *Farlowichnus rapidus* new ichnogen. new ichnosp. (Figures 2, 3, 4)
*Holotype* — LPP-IC-0200 (Figures 2, 3)

*Type locality* — São Bento Quarry, district of Ouro, Municipality of Araraquara, São Paulo, Brazil.

*Derivatio nominis* - The name of this ichnogenus is dedicated to the remarkable paleontologist and ichnologist James (Jim) O. Farlow, Emeritus Professor of Geology as well as Adjunct Professor of Biology, at the Department of Geosciences, Indiana—Purdue University at Fort Wayne, Indiana, USA; as a sign of high esteem and gratitude for his outstanding contribution to tetrapod ichnology.

*Diagnosis* — This trackway has a very high step angle, long paces and strides and a very narrow internal and external trackway width (Table 1). The internal width values are always negative. The stride length/footprint length ratio is high. The footprints are almost parallel or only slightly divergent from the midline; in this last case, they show low positive and negative track rotations. No tail marks or drags are visible.

The footprints are tridactylous, strongly mesaxonic, with low digital divergence (inherently narrow divergence), acute hypices. No hallux is visible. They are longer than they are wide. The posterior margin of the pes is U-shaped. The anterior apex of the Weems triangle (anterior triangle) subtends an acute angle. The footprint contour presents a waterdrop-like appearance, especially when the outer digits are very close to central digit. An evident heterodactyly is observed, with the digit III being wide, long and relevant, usually with a triangular outline, outer digits (II and IV) proportionally very short (digit III/digit II free length ratio of 1.8; and digit III/digit IV free length ratio of 3.5 in the holotype).

The II digit is longer (almost the double) than the IV. So that the digit free lengths are III > II > IV (Table 3). The claw marks of digit III are often slightly turned inward. The third digit is always very wide at its base, and then goes progressively sharpening towards the tip. Often, however, it swells slightly soon after the hypices. The outer digits are more often triangular more rarely, rather elongated, with parallel margins, and always with an acuminate termination. The digits II are narrow and deep, with a blade-like aspect in the holotype. The proximal notch of digit II is rarely evident. The most striking feature of the outer digits is that the medial (or preaxial) digits are considerably more developed, that is, longer and more clearly imprinted, than the lateral (or postaxial) digits, both in the left and right foot.

The area of the anterior triangle (AT) is rather greater than the area of the backfoot triangle (BFT). These tracks are theropod footprints, *sensu* Masrour et al. (2023).

***Farlowichnus rapidus*** new ichnogen. new ichnosp.

*Holotype* — LPP-IC-0200. A slab with one trackway of four footprints, housed in the Laboratory of Paleoecology and Paleoichnology of the Federal University of São Carlos - UFSCar, São Carlos, São Paulo, Brazil. (Figure 2, 3, 4; Tables 1—3).

*1st Paratype* - LPP-IC-0231, housed in the Museum of Science of São Carlos “Prof. Mário Tolentino”, São Carlos, São Paulo, Brazil (Figure 5A, 6A).

*2nd Paratype* - MCT-R-1954, housed in the Museum of Earth Sciences of the Geologic Service of Brazil, Urca, Rio de Janeiro, Brazil (Figure 5B, 6B).

*Housed collection*
- Holotype and the first paratype: Laboratory of Paleoecology and Paleoichnology of the Federal University of Sao Carlos-UFSCar, São Carlos, São Paulo, Brazil (Figure 5A, 6A).
- Second paratype: Museum of Earth Sciences of the Geological Service of Brazil, Rio de Janeiro, Brazil (Figure 5B, 6B).

*Type locality* — São Bento Quarry, district of Ouro, Municipality of Araraquara, São Paulo, Brazil (Cf. Figure 1).

*Stratigraphic unit and horizon* — Botucatu Formation, São Bento Group; Lower Cretaceous, Berriasian—Hauterivian

*Derivatio nominis* — The Latin name of the ichnospecies epithet means an agile and with a usually running gait and a cursorial lifestyle theropod trackmaker, crossing the dunes that nowadays are at Araraquara county, São Bento quarry and others quarries and localities.

*Diagnosis of the ichnospecies* - the same of the ichnogenus

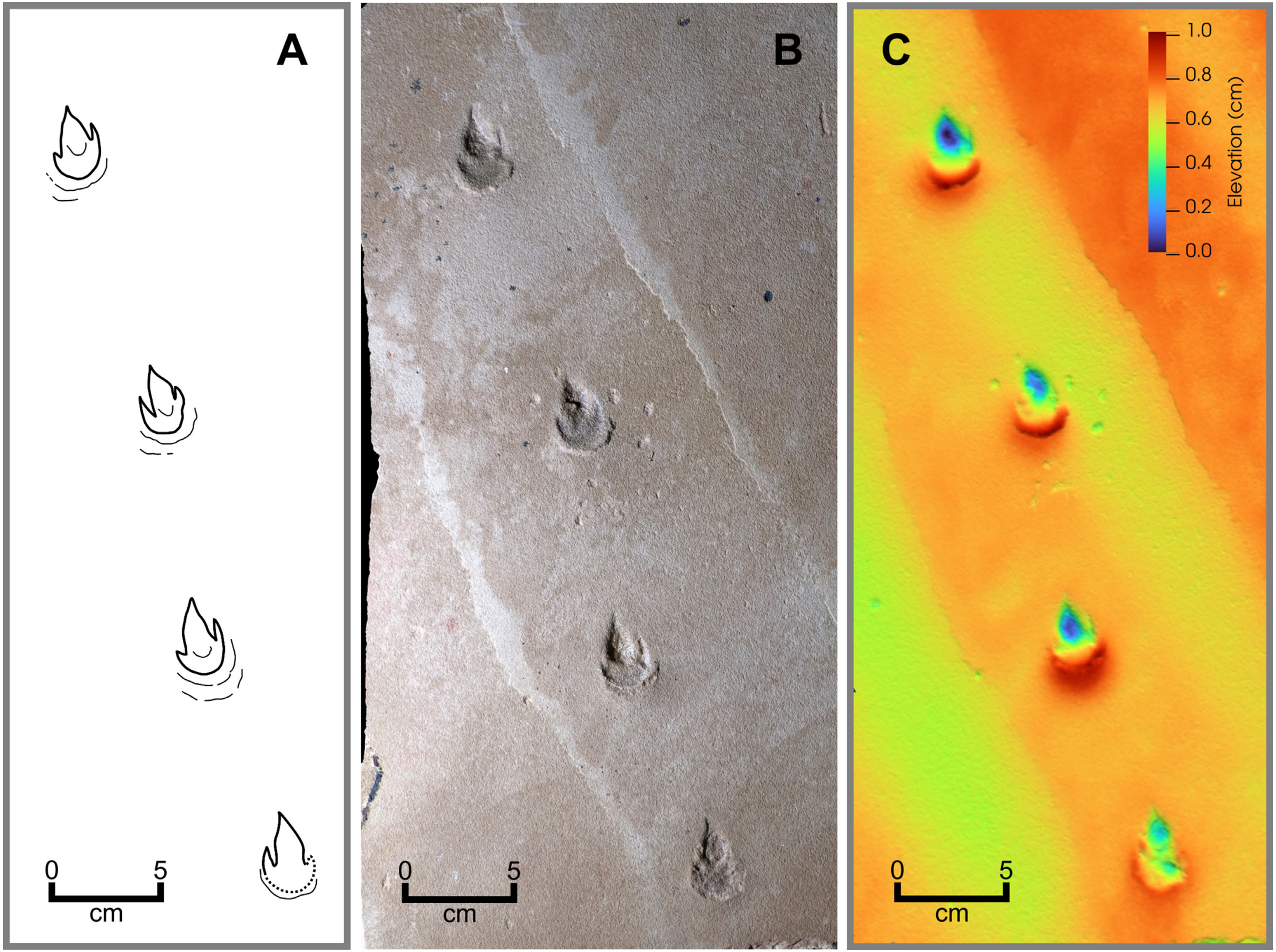


**Fig. 2.** A. Interpretive drawing of the sample LPP-IC-0200, holotype, with the waterdrop shape of the footprints; B. Photographic detail of the track, showing the tridactyl footprints with the two smaller outer digits II and IV, and the longest and larger digit III; C. Photogrammetric detail of the *Farlowichnus rapidus* new ichnogen., new ichnosp. Note the low eolian ripples, characteristically present on the downwind side, on the surface of the dune foresets.

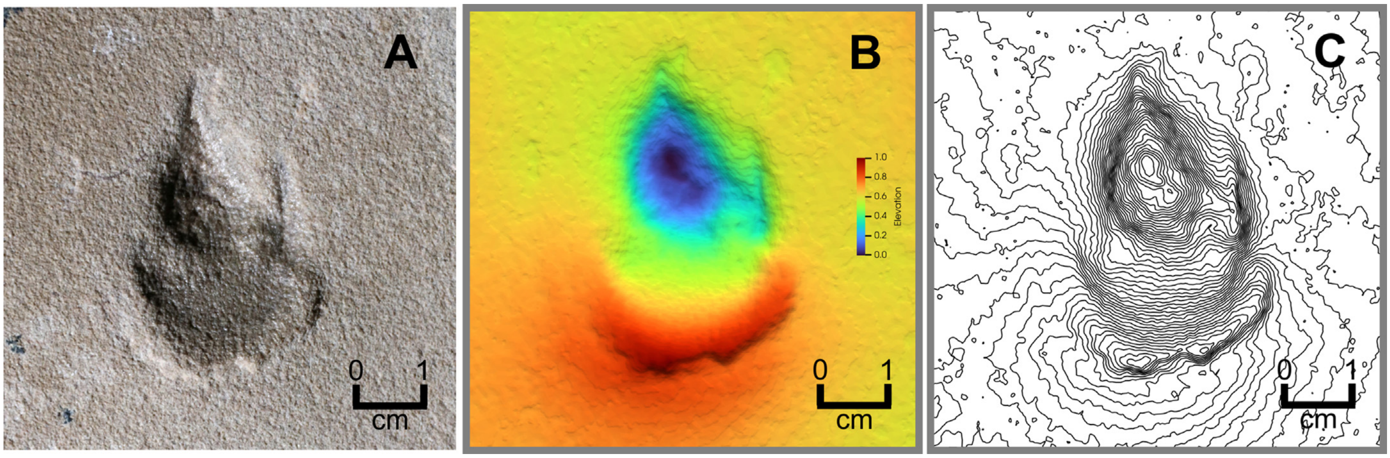


**Fig. 3.** The fourth footprint of the trackway, referring to the left foot of the small theropod, in the sample LPP-IC-0200. A. Photographic detail of the tridactyl footprint with the two smaller outer digits II and IV, and the longest and larger digit III; B. Detail in photogrammetry technique, of the same footprint of the holotype of *Farlowichnus rapidus* new ichnogen., new ichnosp.; C. Topographic image of the holotype's fourth footprint, showing in comparison digit II larger than digit IV.

## 4. Description

The dominant size of the third digit, which constituted the main source of the foot support, probably allows to consider this foot and the corresponding footprint to be of almost functionally monodactyl type. It should be noted that this large, triangular shape, but with a narrower base, of digit III is a rather constant characteristic, and one cannot think that it depends on the behavior of the animal or on the different consistency of the substrate (Falkingham, 2016), since this, in this formation, is always eolian sand of the dune foresets. One cannot apply to this new form the variability observed in other cases, as can be seen for example in Xing et al. (2021, fig. 9). Note also that these are not penetrative tracks, as those illustrated in Gatesy and Falkingham (2020). The direct examination of these footprints indicates that the shape of this digit III, as well as the two external digits, depend on the anatomical shape of the trackmaker's toes, and not on of the trackmaker's behavior or substrate properties.

The average foot index (length-to-width ratio) is 1.78 in holotype (Table 2). As for the Weems triangle (Weems, 1992) or anterior triangle (AT) (Table 3), the average digit III projection is 1.52 cm and the track span is 2.03 cm in the holotype. Despite the considerable length of the projection of digit III (AT length), the average AT ratio: digit III extension/track span is 0.74 in the holotype and 0.9 in the first paratype. These are medium values, in relation to other common theropod footprints, probably because the base of the AT is very long, because it is inclined to the axis of the footprint, due to the strong inequality between the length of the digit II and that of the digit IV. In the first paratype these values are respectively 5.6 cm and 6.4 cm. For the backfoot triangle, the average backfoot length (Lockley, 2009; Farlow, 2018) is 2.09 cm in the holotype and 6.2 cm in the first paratype. The average ratio: digit III extension/backfoot length is 0.73 in the holotype; and 0.95 in the first paratype (Tables 1–3).

As for the proximal portion of the footprints, there are no “plantar” pads, and in particular, any impression of tarsal or metatarsals pads is not noticeable. As for digital pads, neither of the arthral type nor of the mesarthral type are observed. We observe only, but not always, a long pad that covers almost all the digit III, up to the terminal claw (exclusive). All three digits are acuminated, but only in digit III (not always, but clearly in holotype) the claw mark is well recognizable and morphologically distinct from the body of the digit. The outer digits are usually pointing forward, but somehow, they are turned slightly inward, due to having the inner margin straight and the rounded outer margin curved inward.

The footprints are always accompanied by a crescent-shaped sandstone ridge, a special type of displacement rim, characteristic of the dune environment (Figures 2–7). These crescents are always present in the direction of the foreset dip, representing the sand displaced by the animal's foot during its progress across the slopes of a dune. In fact, the crescent-like convex epirelief that always accompanies one edge of the footprints, corresponds to the sand pushed by the foot of the animal, and in the case of drier sand, by the proper gravity force, but always following the maximum dip direction (Leonardi, 1980; Leonardi and Carvalho, 2021a, b). The peculiar shape and structure of this displacement rim partly depend on the pressure exerted by the trackmaker's foot, and partly by the effect of the gravity force on the loose sand. Some of these crescent-like displacement rims are long (along an axis parallel to the dip), and some of them are shorter, which indicates different makeup of the superficial sand laminae and/or different speed of the trackmaker or different pressure of the feet of the trackmaker on the sand.

In the case of this new theropod ichnotaxon, it is also noticed that, in relation to the crescents of mammalian footprints (such as those of *Brasilichnium*), the ridges of the crescent displacement rim are comparatively higher and often less extensive.

Some footprints show interdigital wedges of sand between the digits, probably accumulated in the entry movement of the foot, pushing forward (Figure 2C; cf. Leonardi and Carvalho, 2021b; Masrour et al., 2023).

## 5. The trackmaker

The tracks *Farlowichnus rapidus* new ichnogen., new ichnosp., with its peculiar characteristics described above, are very different from all the other known theropod tracks. Glut (2003) and Leonardi and Carvalho (2021b) presented all ichnogenera attributable to dinosaurs, in an annotated list, excluding class Aves (living and fossil) and “including all commonly accepted ichnogenera, but also ichnogenera that are now considered invalid, doubtful (*nomen dubium*), or were not formally published (*nomen nudum*)” (Glut, 2003). Among them, there are about 52 ichnogenera attributable to non-avian theropods.

The maker of these tracks presented here, and here called *Farlowichnus rapidus* new ichnogen. new ichnosp., clearly belonged to

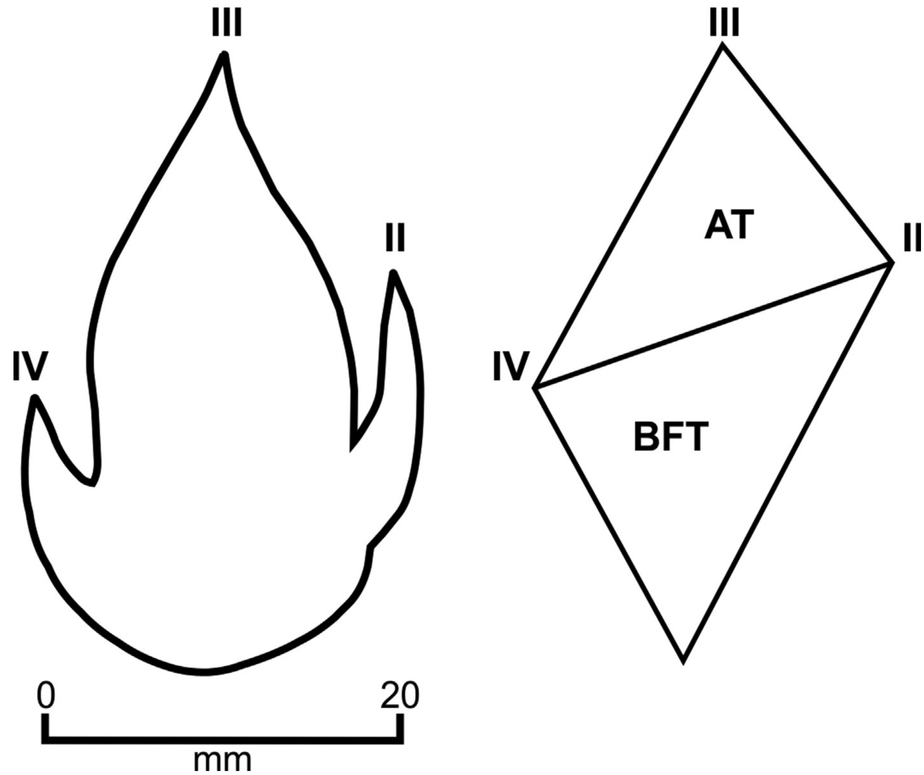


**Fig. 4.** Schematic outline of the fourth footprint of the holotype trackway, referring to a left footprint of the small theropod, in the sample LPP-IC-0200, and the corresponding triangles: AT triangle (anterior triangle or Weems triangle) and BFT triangle (backfoot triangle). Note the obliquity of the line that separates the two adjacent triangles, which highlights the greater development of digits II than the digits IV. It should also be noted that the upper angle of the AT is acute (70°) thus underlining the strong mesaxony of the footprints of this new form.

**Table 1**
Trackway parameters of LPP-IC-200, holotype of *Farlowichnus rapidus*.

| LPP-IC- 200/N° | Stride (cm) | Step Angle | External Width (cm) | Internal Width (cm) | LPP-IC- 0200/N° | Oblique Pace (cm) |
|---|---|---|---|---|---|---|
| 1–3 | 22.50 | 170° 30′ | 3.60 | −0.90 | 1–2 | 11.20 |
| 2–4 | 24.30 | 172° | 3.20 | −1.10 | 2–3 | 11.30 |
| | | | | | 3–4 | 13.00 |
| n | 2 | 2 | 2 | 2 | n | 3 |
| min | 22.50 | 172° | 3.20 | −1.10 | min | 11.20 |
| max | 24.30 | 170° 30′ | 3.60 | −0.90 | max | 13.00 |
| M | 23.40 | 171° 15′ | 3.40 | −1.00 | M | 11.83 |
| $\sigma_{n-1}$ | 1.273 | 1.060 | 0.283 | 0.141 | $\sigma_{n-1}$ | 1.116 |

**Table 2**
Footprint parameters of LPP-IC-0200, holotype of *Farlowichnus rapidus*.

| LPP-IC- 200/N° | Footprint Length (cm) | Footprint Width (cm) | Index FL/FW | Divergence of Footprints from Midline |
|---|---|---|---|---|
| 1 | 4.20 | 2.40 | 1.75 | 6° |
| 2 | 4.10 | 2.30 | 1.78 | −7° |
| 3 | 3.80 | 2.10 | 1.81 | −5° |
| 4 | 3.95 | 2.20 | 1.80 | 5° |
| n | 4 | 4 | 4 | 4 |
| min | 3.80 | 2.10 | 1.75 | −7° |
| max | 4.20 | 2.40 | 1.75 | 6° |
| M | 4.00 | 2.25 | 1.78 | −1° |
| $\sigma_{n-1}$ | 0.175 | 0.129 | 0.026 | 6.702 |

a theropod, as demonstrated because of the high step-angle, the internal width of the trackways having always negative values; and the presence of acuminated digits and claw clearly visible on the digit III. On the other hand, the footprints differ from those of many other theropods mainly due to the fact that digits II are longer than digits IV, unlike the other theropod tracks recorded in Table IV, and the theropods in general, with minor exceptions. As an exception, such a scale of lengths of the digits (III > II > IV) is also found, for example, in *Majungasaurus crenatissimus* Carrano (2007), a Noasaurinae theropod of the Late Cretaceous of Madagascar: its pedal digits show the scale III > II > IV, with a proportion of 10 > 9 > 7. Relative digit length is of primary importance in defining track

**Table 3**
Measurements from digits of holotype LPP-IC-200 of *Farlowichnus rapidus*.

| LPP-IC-200/N° | Free length of digit (cm) | | | Width of digit at its base (cm) | | | Toe III ext. (cm) | Track span (cm) | Back foot length (cm) | Ratio Toe III ext./Track span | Ratio Toe III ext./Back foot length |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | II | III | IV | II | III | IV | – | – | – | – | – |
| 1 | 1.20 | 3.10 | – | 0.45 | 1.40 | – | 1.90 | 2.20 | 2.07 | 0.86 | 0.92 |
| 2 | 1.30 | 2.30 | 0.40 | 0.30 | 1.40 | 0.40 | 1.73 | 2.30 | 2.10 | 0.75 | 0.82 |
| 3 | 1.50 | 2.10 | 1.05 | 0.50 | 1.10 | 0.35 | 1.13 | 1.86 | 2.10 | 0.61 | 0.54 |
| 4 | 1.20 | 2.00 | 0.90 | 0.30 | 1.40 | 0.30 | 1.36 | 2.20 | 2.10 | 0.62 | 0.65 |
| – | – | – | – | – | – | – | – | – | – | – | – |
| n | 4 | 4 | 3 | 4 | 4 | 3 | 4 | 4 | 4 | 4 | 4 |
| min | 1.20 | 2.00 | 0.40 | 0.30 | 1.10 | 0.30 | 1.13 | 1.86 | 1.86 | 0.61 | 0.54 |
| max | 1.50 | 3.10 | 1.05 | 0.50 | 1.40 | 0.40 | 1.90 | 2.30 | 2.30 | 0.86 | 0.92 |
| M | 1.35 | 2.37 | 0.73 | 0.39 | 1.32 | 0.35 | 1.53 | 2.14 | 2.14 | 0.74 | 0.73 |
| $\sigma_{n-1}$ | 0.141 | 0.499 | 0.340 | 0.103 | 0.150 | 0.050 | 0.228 | 0.193 | 0.015 | 0.119 | 0.170 |

morphology (Lockley, 2009, p. 426), and its belonging. Moreover, this difference in the ratio between the relative length of the digits II and IV, as well as the scale of digit lengths (here III > II > IV instead of III > IV > II, which is more normal in theropods) does not seem an unacceptable phenomenon. These are, deep down, the tracks of a theropod that lived in Gondwana, in a distant environment and clearly separated from the others ones, in an immense desert (with a surface corresponding to ~35% of the surface of the current Sahara Desert). This, in all probability, as was to be expected, had a fauna with endemic elements.

In particular, the characteristics that distinguish this new form from the others are the posterior margin of the pes that is always wide and rounded, and the external digits that are usually close to finger III, often slightly curved inward. This gives the footprints an outline reminiscent of a waterdrop. The evident heterodactyly is a very special character, with the digit III being very wide, long, physically and functionally relevant. The set of this wide middle digit and the other two, the outer ones, which were often leaning on it, created a kind of functional monodactyly, which supposedly helped the animal to adapt to a dune-desert life. Moreover, in the strongly mesaxonic tracks the anterior triangle is most elongate when the divarication is least (Lockley, 2009). However, it should be noted that digit divarication shall be considered as an extrinsic (non-morphological) variable (Ibidem). Another main reason to consider this tracks a new form is especially the rare feature of having the digit II longer than the IV (Figure 3). In addition, the digits II are so narrow and deep that they have sometimes a blade-like aspect, especially in the holotype. The most striking feature of the external digits is that the medial (or preaxial) digits are considerably more developed, that is, longer and more clearly imprinted, than the lateral (or postaxial) ones (Table 4).

According to Lallensack et al. (2016, 2020) and Farlow (1989, 2018), when digit III is very long and digits II and IV are proportionately very short, this indicates cursoriality. This feature is very pronounced in the emu and in the ornithomimosaur *Gallimimus*. The ostrich is very instructive here: it is didactyl, and only digit III is used for propulsion, while digit IV is short and merely serves as an outrigger to stabilize the animal while running.

The characteristics and numerical parameters of its trackways and footprints, examined and measured in about twenty trackways, indicate that the trackmaker of *Farlowichnus rapidus* nov. ichnogen. and nov. ichnosp. was a small, cursorial theropod, related to a Gondwanan theropod family, possibly the ancestral theropods of clades such as noasaurids or velocisaurids. Leonardi (1977) and Langer et al. (2019) suggested that similar tracks from the Botucatu Formation are also found in the Caiuá Group (Early Cretaceous, Aptian-Albian, 133-120 Ma), interpreting the recurrence of a similar desert-dwelling fauna. These authors also observed that the functionally monodactyl theropod footprints from the Botucatu Formation, Caiuá Group (Paraná Basin) and La Matilde Formation (Argentina; Casamiquela, 1964) are consistent with the foot morphology of *Vespersaurus paranaensis*. If we consider that the trackmaker of *Farlowichnus rapidus* nov. ichnogen. and nov. ichnosp. was similar to *Vespersaurus paranaensis*, then it would be a small, cursorial, generalist predator (Barbosa et al., 2023) (Figure 7), capable of feeding on small tetrapods, such as small or medium mammals, such as *Brasilichnium*; as well as on arthropods and likely on small reptiles; probably not discarding the carrion.

More in detail, like the foot of *Vespersaurus paranaensis*, also that corresponding to *Farlowichnus rapidus* new ichnogen. new ichnosp., has an uncommon morphology. The fact that its pedal ray III has the main supporting function in walking or running gait, would then probably depend on laterally compressed metatarsals II and IV, such as those of *V. paranaensis* (or also, for example, the II one of the Sidi Daoui small-sized, gracile abelisaurid of Morocco, of Longrich et al., 2023) so that the central element (metatarsus III) would have borne most of the body load during locomotion. Besides, similar conditions (Langer et al., 2019) are present in other Noasaurinae.

As for the pedal digits of *V. paranaensis*, the widest base of the ungual phalanx III, as in other small dinosaurs of the aforementioned family, is consistent with the condition provided for a bearing phalanx; and corresponds to the greater width of the digit III of *Farlowichnus rapidus* new ichnogen. new ichnosp.

In contrast, the claws of the digits II and IV of *V. paranaensis* are strongly laterally compressed, and form a sharp ventral edge, not corresponding to a bearing phalanx; however consistent with the blade-like shape of the outer digits of tracks *Farlowichnus rapidus* new ichnogen. new ichnosp. In addition, the pedal digits II and IV of *V. paranaensis*, especially when compared to the general condition of theropods, are shortened compared to the digit III, exactly as *in Farlowichnus rapidus* new ichnogen. new ichnosp.

One can also notice another point of convergence: as the pedal claws of *V. paranaensis* (and other Noasaurinae) have the sole not arcuate, so it also results for the tracks *Farlowichnus rapidus*. The impressions of the tips of their digits are never separated from the impressions of the corresponding digits, as happens not rare in the footprints of carnivores, dinosaurs or not. Langer et al. (2019) suggest that these aspects indicate that *V. paranaensis* may have been a functionally monodactylous animal, with only one central wide toe, with the character of a digit bearing the main weight of the animal's body, flanked by thin outer digits, kept very close. As a result, the same authors continue, we are in the presence of a previously unregistered anatomical adaptation among the archosaurs, although – as they propose – previously mentioned by the tracks of the same geological unit that gave

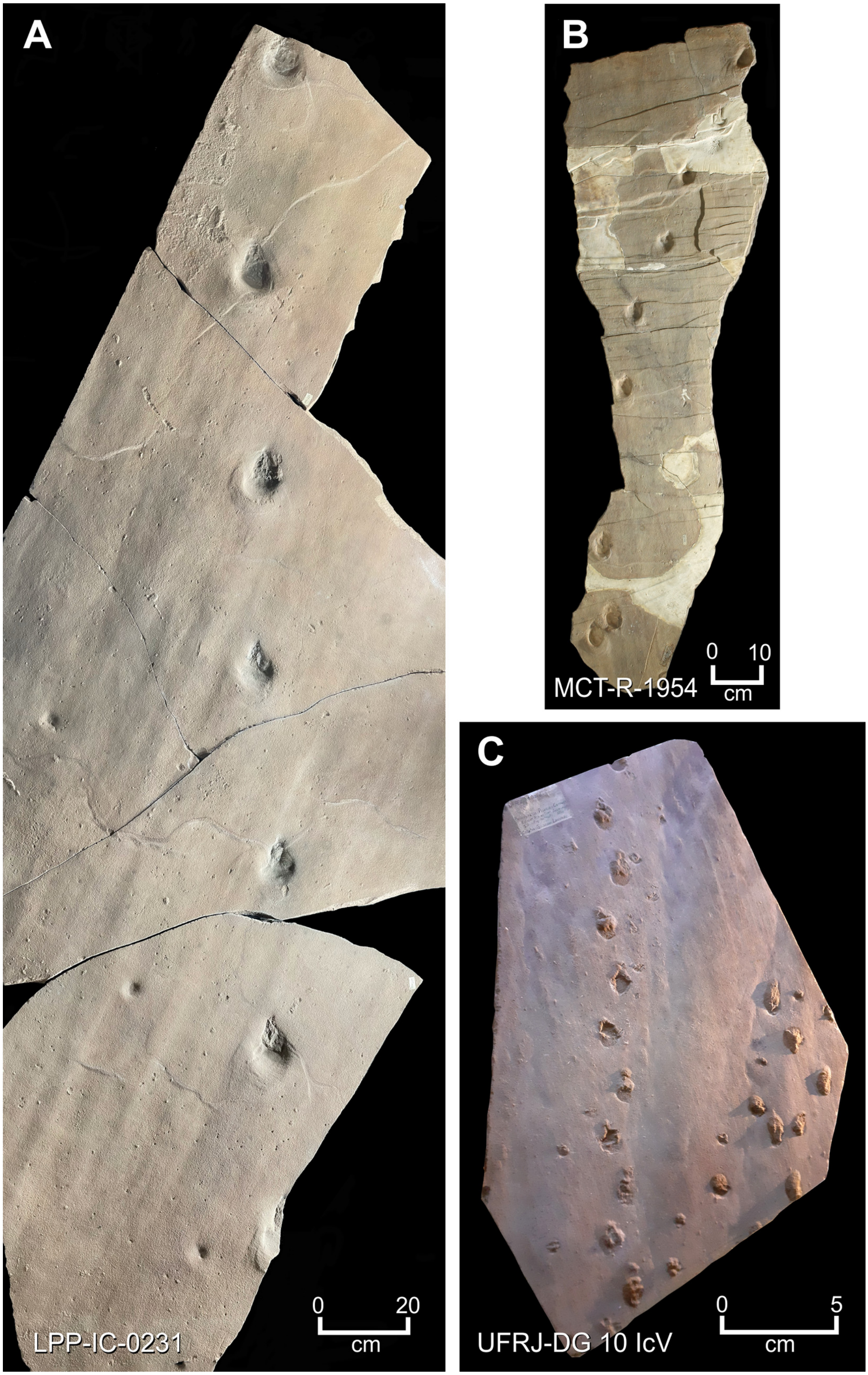


**Fig. 5.** Photographs of the paratypes and of another trackway of *Farlowichnus rapidus* new ichnogen., new ichnosp.;. A. 1st Paratype LPP-IC-0231 and B. 2nd Paratype MCT-R-1954. C. Sample UFRJ-DG 10 IcV, showing the same morphological pattern of the waterdrop shape of the *Farlowichnus rapidus* new ichnogen., new ichnosp. trackways.

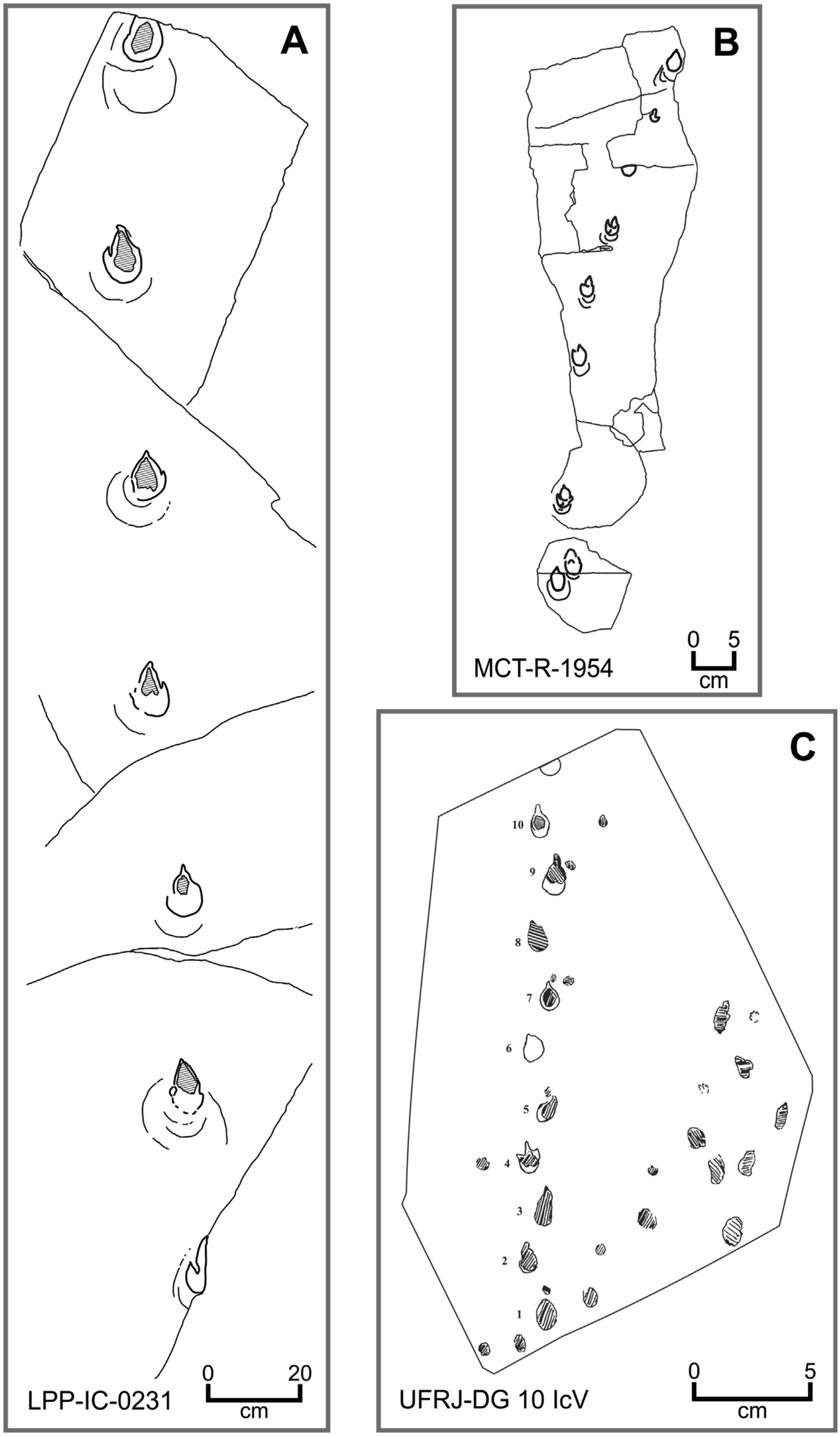


**Fig. 6.** Interpretive drawings of the paratypes and of another trackway, as above. A. 1st Paratype LPP-IC-0231 and B. 2nd Paratype MCT-R-1954. C. Sample UFRJ-DG 10 IcV, of the *Farlowichnus rapidus* new ichnogen., new ichnosp. trackways. The cracked part, inside the footprints, corresponds to the sedimentary infilling of the upper layer of detached rock.


**Fig. 7.** Reconstruction of the living environmental scenery of the trackmaker of *Farlowichnus rapidus* new ichnogen., new ichnosp. The trackmaker of the holotype, represented here by the theropod, may have had about 1.5 m in length (Art by Guilherme Gehr).

**Table 4**
Comparison between the ratio: mean length of the digit IV/mean length of the digit II, in some theropod tracks.

| In mm | Average length of the digit II | Average length of the digit III | Average length of the digit IV | Ratio: mean length of the digit IV/mean length of the II. | Scale of lengths of digits |
|---|---|---|---|---|---|
| *Grallator* igen., Late Jurassic of Spain, (Castanera et al., 2016). | 25 individuals = 57.2 | 25 individuals = 111.3 | 25 individuals = 68 | 1.19 | III > IV > II in mm |
| *Eubrontes*, several species, from L. Jurassic of New England, the first 20 specimens from Table A8.1 (Farlow, 2018). | 20 individuals = 71.20 | 20 individuals = 107.05 | 20 individuals = 103.68 | 1.45 | III > IV > II in mm |
| *Kayentapus minor*, the 12 specimens from Table A8.1 (Farlow, 2018). | 12 individuals = 127.9 | 12 individuals = 165.5 | 12 individuals = 148.57 | 1.16 | III > IV > II in mm |
| Theropod tracks (31 individuals) from Lower Cretaceous, Rio do Peixe Basins, Brazil, (Leonardi and Carvalho, 2021b). | 31 individuals = 140.0 | 31 individuals = 178 | 31 individuals = 175.8 | 1.26 | III > IV > II in mm |
| Average of all the data of the above mentioned theropod tracks | 98 individuals = 99.07 | 98 individuals = 140.46 | 98 individuals = 124.01 | 1,25 | III > IV > II in mm |
| *Anomoepus*, diverse species (non theropod), 20 individuals from Table A8.1 (Farlow, 2018). | 20 individuals = 38.67 | 20 individuals = 56.3 | 20 individuals = 59.96 | 1.55 | IV > III > II in mm |
| All the theropod footprints (39) we attribute to *Farlowichnus*, which we could measure. | Mean length of these 12 footprints = 12.7 | Mean length of these 17 footprints = 35.9 | Mean length of these 10 footprints = 8.8 | 0.69 | III > II > IV in mm |

*V. paranaensis*, that is the theropod tracks of the Brazilian Caiuá Group (Leonardi, 1977).

Langer et al. (2019) finally suggest also that the gap in the record of body fossils of Noasaurinae from the Late Jurassic to the Early Cretaceous may have been tied to the progressive drying up of the central part of the supercontinent Gondwana, just at the time when the great desert corresponding to the Botucatu Formation existed. In this time, this family could gradually had adapted and specialized in dwelling in the desert environment. This setting, not normally suitable for the preservation of bones, in exchange would have preserved the impressions of their feet. The tracks of the new genus and species presented here, could just come to complete, in some way, the gap mentioned above.

It seems that in this case we need not resort to interpreting this new form through a phenomenon of heterochrony, or judging it as just a phase of the ontogenetic development (Lockley, 2009), given that in the specimens of *Farlowichnus rapidus* new ichnogen. new ichnosp., there are specimens of a whole series of progressively larger dimensions, the length of their footprints being represented within a range of 19.4–112 mm.

Finally, to get an idea of the size of the maker of these tracks, when compared, for example, with *Noasaurus leali* Bonaparte and Powell (1980), the trackmaker of the holotype trackway (LPP-IC-0200) and the second paratype trackway (MCT-R-1954) may have had about 1.5 m in length, of which at least half were attributable to the long tail (Cf. Figure 7); and a weight of about 12–15 kg (cf. Paul, 2010). The trackmaker of the first paratype, which has much longer footprints (average length 11.2 cm), could proportionally reach 3 m or 3.5 m in length, and a proportionally greater weight.

We also attribute to this new form the following *in situ* specimens found at São Bento Quarry, a very long trackway of more than 20 footprints, concave epirelief (Leonardi and Carvalho, 2021a); Catingueiro creek, Cianorte, Paraná, Brazil, some specimens of this ichnomorphotype (Leonardi, 1977). These are from the Caiuá Group, Rio Paraná Formation, probably Aptian-Albian (Langer et al., 2019).

The *ex-situ* specimens are the samples MCT-R-1953 that comprises one trackway with 3 footprints, convex hyporelief, from São Bento quarry. Sample LPP-IC-0201, a trackway with 5 footprints, one of them with digits, medium quality, concave epirelief. Sample LPP-IC-0202, a slab with two trackways, respectively with 4 and 2 footprints, of medium quality associated with *Skolithos,* preserved as concave epirelief. Sample LPP-IC-0203, a trackway with three footprints, preserved as convex hyporelief, one of good quality. Sample LPP-IC-0204, a trackway with 5 footprints, two of them good quality, preserved as convex hyporelief. Sample LPP-IC-0205, a slab with a long trackway with 8 footprints, poor quality, preserved as concave epirelief. It is important because it belongs to the smallest trackmaker of this morphotype. This trackway is associated with two trackways of different kind of mammalian trackways. Sample LPP-IC-0206 with one isolated large and deep footprint, preserved as concave epirelief. Sample LPP-IC-0207, a slab with a short trackway 3 footprints of medium quality, with infilling, preserved as concave epirelief. At Museu Arqueológico e Paleontológico de Araraquara-MAPA, Araraquara, São Paulo, Brazil, there is a slab from the São Bento quarry with *Farlowichnus rapidus* nov. ichnogen. and nov. ichnosp. tracks. The flagstones of the Botucatu Formation (from the quarries of Araraquara), that cover the pillars of the front side of the cathedral of São Carlos, shows some examples of trackways of this new taxon (Leonardi and Godoy, 1980). Sample UFRJ-DG 10-IcV – Macrofossil Collection, Rio de Janeiro Federal University, Brazil. A trackway with 11 footprints and some isolated footprints of other individuals, concave epirelief (Figure 4C). Sample UFRJ-DG 13-IcV - Macrofossil Collection, Rio de Janeiro Federal University, Brazil, that presents one isolated footprint, poor quality, concave epirelief. At Paleontology Museum "Prof. Antonio Celso de Arruda Campos", Monte Alto, São Paulo, Brazil, a slab probably proceeding from Araraquara, with a trackway. At the Department of Biology, Universidade Federal do Espírito Santo-UFES, Vitória, ES, Brazil, a slab (ARSB 400) with two trackways of this morphotype, accompanied by two mammalian trackways and two arthropod trails.

## 6. Conclusions

Herein, we have described a new ichnogenus and a new ichnospecies for tracks attributed to a theropod from Botucatu Formation, based on its trackways and footprints morphologies. This new ichnotaxon presents peculiar anatomical aspects of the autopodia that indicates a species adapted to the large dry sand dunes of the Botucatu paleodesert.

A large number of trackways and other kinds of traces of animal activities, related to tetrapods and invertebrates from the Botucatu Formation (Lower Cretaceous) had already been formally classified or had received an ichnospecies designation. No dinosaur track, however, had received an ichnological name, probably by the fact that the dinosaur tracks in this lithostratigraphic unit are much less numerous when compared with those of the early mammals. Herein, a new taxon has been established for a theropod, the dinosaur that in the sandstones of the Botucatu Formation left more numerous trackways.

The *Farlowichnus rapidus* new ichnogen. new ichnosp. indicates a peculiar gait of a cursorial Early Cretaceous Gondwanan small theropod. The patterns of footprint preservation show a unique foot morphology, in which digits II and IV are very small when compared with a prominent and large digit III. There is also a variance in length between the outer digits, the digit II generally being almost double-sized than the digit IV. not an ordinary situation in theropod feet. Digit II are narrow and deep, sometimes with a blade-like aspect, and due this outline, the general morphology of the footprint often remembers that of a waterdrop. All three digits are pointed, but only on digit III the claw is clearly recognizable and protruding. The trackways are straight, very narrow, with long strides and step angle shows high values. The tracks of *Farlowichnus rapidus* new ichnogen. new ichnosp. are assigned to small theropods adapted to desert life with mainly cursorial gait, probably precursors of clades such as noasaurs and velocisaurs. The distinct pattern of the autopodia with a stronger digit III could be an adaptation to life in the dry and soft sands of the Botucatu paleodesert.

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## Data availability

Data will be made available on request.

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