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REVISITING THE SOUTHERNMOST OCCURRENCE OF *BRASILICHNIUM ELUSIVUM* LEONARDI, 1981 WITH COMMENTS ON THE TETRAPOD TRACK RECORD OF EOLIAN ENVIRONMENTS

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ABSTRACT – Mammalian lineage is deep rooted in Mesozoic, with several taxa and ichnotaxa described worldwide. One of the most prolific mammaliaform ichnospecies is *Brasilichnium elusivum*, which is extremely abundant in the Lower Cretaceous Botucatu Formation of the Brazilian Paraná Basin, as well as in other Mesozoic ichnofaunas of North America and Africa. In this contribution, we revisited the proposed southernmost occurrence of *B. elusivum* using both classical and photogrammetric (3D digitization) approaches. The flagstone containing the studied material was found *ex situ*, in a sidewalk at Santa Cruz do Sul Municipality (the Rio Grande do Sul State, Brazil), and the results of the performed analysis showed that the tracks cannot be assigned to any ichnotaxon. Lastly, some significant issues related to ichnological research of *ex situ* track-bearing flagstones and large eolian deposits are discussed.

Keywords: Early Cretaceous, Botucatu Formation, mesozoic mammals, South America, vertebrate ichnology.

RESUMO – A linhagem mamaliana está profundamente enraizada no Mesozoico, com diversos táxons e icnotáxons descritos em todo mundo. Uma das icnoespécies mais prolíficas de mamaliaformes é *Brasilichnium elusivum*, que é extremamente abundante na Formação Botucatu, Cretáceo Inferior da Bacia do Paraná, Brasil, assim como em outras icnofaunas mesozoicas da América do Norte e da África. Nesta contribuição, nós revisitamos a suposta ocorrência mais meridional de *B. elusivum* usando abordagens clássicas e de fotogrametria (digitalização em 3D). A laje contendo tal material foi encontrada *ex situ*, em uma calçada no Município de Santa Cruz do Sul (Estado do Rio Grande do Sul, Brasil) e os resultados das análises realizadas mostraram que ele não pode ser atribuído a nenhum icnotáxon. Por fim, alguns tópicos importantes relacionados à pesquisa icnológica de lajes *ex situ* e grandes depósitos eólicos são discutidos.

Palavras-chave: Eocretáceo, Formação Botucatu, mamíferos mesozoicos, América do Sul, icnologia de vertebrados.

INTRODUCTION

The evolution of the mammalian lineage goes back further to the late Paleozoic, with the origin of cynodonts. Mammaliamorph cynodonts diverged in Late Triassic and true mammals become diversified and cosmopolite in Middle Jurassic (*e.g.*, Grossnickle *et al.*, 2019). Though the evolution of true mammal characters (such as typical mammalian middle ear, diphyodonty, and craniomandibular suspension composed just of the squamosal-dentary articulation) is well known due to a sequence of transitional forms, the mammalian Mesozoic record is still incomplete and fragmentary when compared to the Cenozoic, especially considering postcranial elements (Chimento *et al.*, 2016; Abdala *et al.*, 2020; Rougier *et al.*, 2021, and references cited by them). With respect to this, trace fossils provide important and reliable data, not only complementing the osteological record, but also introducing new and unique information regarding the evolution of the locomotion patterns (Casamiquela, 1961; Rainforth & Lockley, 1996; de Valais, 2009; Buck *et al.*, 2017), paleoecology (Kuznetsov & Panyutina, 2018), and geographic distribution (Leonardi, 1981; Leonardi & Carvalho, 2021a, b) of mammals in the Mesozoic. Mesozoic mammal and mammal-like tracks and trackways are not rare and can be assigned to the ichnogenera *Procolophonichnium*, *Ameghinichnus*, and *Brasilichnium*, besides several other less expressive ichnotaxa (*e.g.*, Casamiquela, 1961; Ellenberger, 1972; Leonardi, 1981; de Valais, 2009; Mateus *et al.*, 2017; Klein & Lucas, 2021).

Among the Mesozoic track record, *Brasilichnium* is an interesting case of tracks produced by a desert-dwelling animal, being one of the oldest evidences of asymmetrical gaits, heteropody and functional tetradactyly among the mammalian lineage. The attribution of this ichnogenus to a true mammal, however, was not always unambiguous and some authors considered it as related to non-mammalian therapsids or to tritylodont cynodonts (Huene, 1931; Leonardi, 1980, 1981; Leonardi *et al.*, 2007). Indeed, the correlation between *Brasilichnium* and a least inclusive

biological taxon is still precarious because this ichnogenus seems to occur in a wide time span, from the Late Triassic to the Late Cretaceous (Lockley & Hunt, 1995; Lucas et al., 2010; Lockley, 2011), and few functionally tetradactyl mammaliaforms have been found in this interval so far. This lack of precise correlation and apparent wide geographic and temporal distribution can be derived from the assignment of some undiagnostic material to Brasilichnium. Consequently, inappropriate ichnotaxonomic assignments prevent the correct circumscription of the spatiotemporal distribution of the ichnotaxon and its trackmakers. In this paper, we aim to reassess one of the trackways preserved in the slab UFRGS-PV-0067-K (previously assigned to Brasilichnium elusivum) and discuss the methodological traps related to the attribution of tetrapod tracks produced in eolian settings to a particular biological taxon, focusing on the presumed southernmost occurrence of Brasilichnium in the Early Cretaceous of Brazil (Figure 1).

Institutional abbreviations. UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

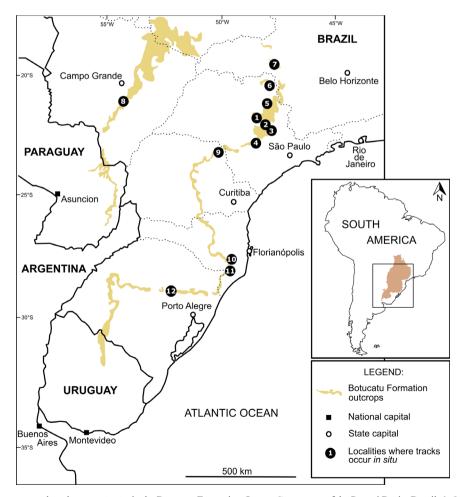


Figure 1. Localities where tetrapod tracks occur *in situ* in the Botucatu Formation, Lower Cretaceous of the Paraná Basin, Brazil: 1, Ouro Ichnosite (Califórnia, Cerrito Novo, Cerrito Velho, Corpedras, Santa Águeda, São Bento and São Domingos quarries), Araraquara Municipality. 2, Itaguaçú Quarry, São Carlos Municipality. 3, Nova América Farm, Analândia Municipality. 4, Botucatu Hill. 5, Visconde Quarry, Brodósqui Municipality. 6, Chave do Calixto Quarry, Rifaina Municipality. 7, Unnamed quarries, Sacramento Municipality. 8, Nioaque riverbank, Nioaque Municipality. 9, Unnamed quarries, Jacarezinho Municipality. 10, Rio do Rastro Hill. 11, Unnamed inselberg in the Southern Santa Catarina State. 12, Adolf Kessler Quarry, Santa Cruz do Sul Municipality (but see the text for discussion).

MATERIAL AND METHODS

The specimen studied here is a track-bearing sandstone slab collected by the ichnologists Dr. Giuseppe Leonardi and Dr. William A.S. Sarjeant in November 1983 from a sidewalk in the downtown Santa Cruz do Sul city, in the Rio Grande do Sul State, southern Brazil (Figure 2; Leonardi & Sarjeant, 1986; Leonardi, 1994). The entire sandstone slab was removed by the UFRGS staff and housed in the Cretaceous vertebrate collection of the Museu de Paleontologia da UFRGS Irajá Damiani Pinto under the collection number UFRGS-PV-0067-K. This slab is composed of silicified, medium-grained sandstone, originally interpreted as coming from the Adolf Kessler Quarry, from the Lower Cretaceous Botucatu Formation (Leonardi, 1994). There are no other sedimentary structures besides the tetrapod tracks.

A digital photogrammetric model of the slab UFRGS-PV-0067-K was produced following the methodology proposed by Mallison & Wings (2014). 245 photos (resolution: 5,184x3,456 / 72 dpi) were taken using a Canon EOS Rebel T6 digital camera, a 50 mm Yongnuo lens and a turntable. The model was generated by the software Agisoft Metashape Pro (Educational License) in a high resolution, being then realigned using Meshlab (v. 2020.02). The color topographic profile was built with Paraview (v. 5.8.0), using 80 contour lines. For comparison purposes, a silicon rubber cast was also produced.

For ichnotaxonomic analysis, we used the Brasilichnium elusivum revised diagnosis proposed by Fernandes & Carvalho (2008), which includes the following characters: trackway of a quadruped animal; mean gleno-acetabular distance of 7.5 cm; manus considerably smaller than the pes; manus-pes distance increases as the speed decreases; pace angulation relatively high for a quadruped; heteropody directly proportional to the *pes* positive rotation (values $> 75^{\circ}$); longitudinal axis of the pes parallel to the trackway axis; heteropody not evident when pace angulation is $> 125^\circ$; pes elliptical with larger axis almost transversal and anteroposterior axis slightly directed inwards; short, often rounded digits, with possible 2-3-3-3-3 phalangeal formula; the posterior tracks are ectaxonic, tetradactyl (digits II-V) and semiplantigrade; pedal digit V is slightly abducted, showing a high hypex; anterior tracks with at least four clawed digits; tail drag traces always absent.

RESULTS

The slab UFRGS-PV-0067-K bears two almost parallel trackways (UFRGS-PV-0067-Ka and UFRGS-PV-0067-Kb)

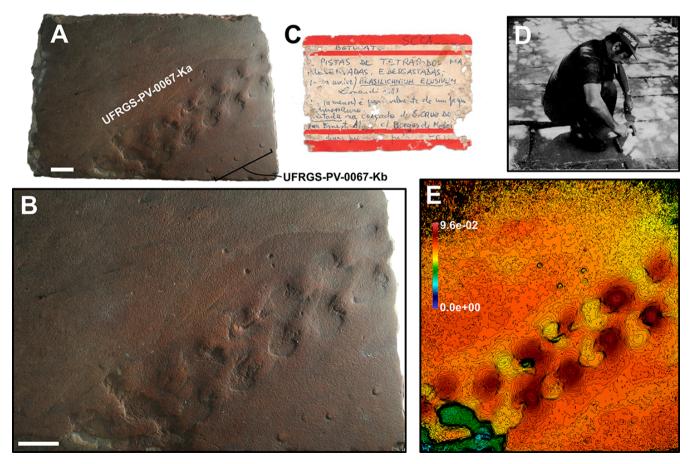


Figure 2. A–B, tetrapod track-bearing sandstone slab UFRGS-PV-0067-K. C, catalog card with the original interpretation of the tracks. D, Mr. Valdor Ochagávia da Costa collecting the referred slab on the Santa Cruz do Sul sidewalk. Modified from Leonardi & Sarjeant (1986). E, False color depth map of the trackways. Scale bars = 5 cm.

preserved as convex hyporeliefs and separated by 7.5 cm from each other. One of the trackways (UFRGS-PV-0067-Kb; Figures 2A–B) is composed of five circular tracks of diminutive size (means: 1.75 cm length and 0.65 cm width). The mean pace angulation is 142.36°. Means of the oblique pace and stride lengths are, respectively, 3.32 cm and 6.28 cm. The internal trackway width is very narrow, being negative in some parts of the trackway. This trackway was formerly described as being produced by a theropod dinosaur (Leonardi, 1994).

UFRGS-PV-0067-Ka is the trackway regarded as *Brasilichnium elusivum* by Leonardi (1994) and composed of 11 roughly circular tracks. Although the lack of morphological details in this trackway prevented us from properly attributing the tracks to *manus* or *pedes*, the wide gauge (external trackway width: 7.6–8.5 cm; internal trackway width: 1.3–2.5 cm) and pace angulation (mean: 70.87°) indicated that the trackmaker was a quadrupedal animal. The mean length of the oblique pace is 5.5 cm, and the mean stride length is 6.3 cm.

Crescent-shaped displacement rims are associated with all these tracks, indicating that the trackways were produced in an oblique substrate. These rims also indicated that both trackways are oriented in the same direction. No digits or claw traces were preserved, as well as any diagnostic character (ichnotaxobase) that could be used for classification purposes. The circular to elliptical outline of the tracks, on the other hand, characterize preservational grades of 0.0p to 0.0c according to the scale proposed by Marchetti *et al.* (2019a), which is not reliable for ichnotaxonomy. Based on the poor preservation, we interpret both trackways preserved on UFRGS-PV-0067-K as indeterminate and are cautious in attributing them to a specific trackmaker.

DISCUSSION

The assumption of the presence of *Brasilichnium elusivum* (UFRGS-PV-0067-Ka; here interpreted as indeterminate tetrapod tracks) in a flagstone (putatively from the Botucatu Formation) found at Santa Cruz do Sul sidewalks allowed the proposition of a southernmost Early Cretaceous ichnofauna containing this mammalian ichnotaxon, in addition to an indeterminate, diminutive dinosaur trackway (UFRGS-PV-0067-Kb) by Leonardi (1994) and subsequent works (*e.g.*, Leonardi & Carvalho, 2021a). However, based on the three points discussed below, we argue that this record must be seen with caution.

Firstly, even though the Ouro Ichnosite area has been historically quarried for the exploitation of the Botucatu flagstone (Fernandes *et al.*, 2008; Francischini *et al.*, 2020), other quarries occur in further regions of the São Paulo State (Fig. 1; see also Leonardi, 1977), providing flagstones to pave numerous urban areas in the entire state, including at regions where the Botucatu Formation does not crop out (*e.g.*, Leonardi & Carvalho, 2021a). Therefore, there is no solid evidence that flagstones quarried in certain municipalities are used to pave exclusively in their own urban areas or, in the opposite situation, that flagstones found on sidewalks of a particular city came from quarries in its surroundings. For example, Botucatu flagstones were used for paving several localities in São Paulo city (Leonardi & Carvalho, 2002, 2021a), far more than 250 km from Araraquara. Applying this argument for the Rio Grande do Sul State, there is no direct evidence that the Santa Cruz do Sul flagstones were quarried from the Adolf Kessler Quarry or even that they came from only one outcrop/quarry of Botucatu Formation. As a result, considering the UFRGS-PV-0067-K as evidence of a local ichnofauna of the Botucatu Formation at Santa Cruz do Sul can be misleading.

A second point is the latent depositional diachronism present in large eolian deserts. Scherer (2000) stated that there are no supersurfaces within the eolian strata of the Botucatu Formation, which means that the preserved eolian deposits of this unit usually correspond to a single eolian accumulation. On the other hand, the preservation of the dunes was controlled by fissural, tholeiitic to alkaline lava floods, which compose the Serra Geral Group of the Paraná-Etendeka Large Igneous Province (PELIP) and advanced over the Botucatu dunes from south to north. Scherer (2000) argued that diachronism in the Botucatu-Serra Geral system (in the Rio Grande do Sul area) is insignificant, due to the relatively short duration of the lava flows, being constrained to 1 Ma (Baksi, 2018) to 4 Ma (Rossetti et al., 2018) interval. However, the precise age and the duration of the lava flows of the entire PELIP are still debatable, because of methodological discrepancies and alteration in the samples (Cañón-Tapia, 2018 and references therein). Consequently, the use of the PELIP rocks as a datum for inferring the age of the deposition for the entire Botucatu Formation needs more support. Furthermore, even when the Botucatu desert age is considered short, it is possible that different track-bearing outcrops represent different biological generations of trackmakers, reflecting some degree of temporal diachronism among these faunas. Therefore, considering the track record within this unit as a single, contemporaneous (ichno)fauna could be a conceptual trap and reduce the evolutionary history of the occupation of the desert environments during the Mesozoic to a short and single time interval.

The third argument is regarding the attribution a priori of the ex situ flagstone UFRGS-PV-0067-K to the Botucatu Formation. In Arizona and the surrounding states of the USA southwest, there are several units representing eolian deserts and coastal dunes of the Permian age. Namely, DeChelly, Coconino, and Glorieta formations comprise a set of eolian, interfingered facies representing the evolution of desert settings during the Cisuralian (early Permian). The ichnofaunas preserved in them are very similar to each other in composition, although there are differences in the proportion of some ichnotaxa (Marchetti et al., 2019b and references therein), consequently, only one slab is not necessarily representative of the whole ichnofauna of each one of those paleoenvironments. Similarly, several other eolian or fluvio-eolian units have been recognized in the Paraná Basin, some of which were recently dismembered from the original conception of the Botucatu Formation by Gonzaga

de Campos (1889). The Guará (Scherer & Lavina, 2005) and Pirambóia (Soares, 1975, but see also Lavina *et al.*, 1993 and Soares *et al.*, 2008) formations, as well as the Pedreira Sandstone (Nowatsky & Kern, 2000), are composed of eolian, fluvial and lacustrine deposits related to the development of wet desert systems through the Mesozoic of the Paraná Basin. Together with the Botucatu Formation, all the abovementioned eolianites crop out in the eastern-central Rio Grande do Sul, being able to provide flagstones for paving urban sidewalks. Particularly, the Pedreira Sandstone (Upper Jurassic; Brückmann *et al.*, 2019) is commercially explored for this purpose and could be an alternative hypothesis for the origin of the slab UFRGS-PV-0067-K.

FINAL REMARKS

Based on the arguments provided above, we are aware that UFRGS-PV-0067-K could not be coming from the Botucatu Formation, contrarily to the proposed by previous papers. But, even if this stratigraphical source is proved to be correct, it is not a direct indication that the Santa Cruz do Sul ichnofauna is contemporary to the classical ichnofaunas found on the northeastern border of the Paraná Basin (i.e., the Ouro Ichnosite in Araraquara surroundings). Lastly, classical and photogrammetry-based analyses of UFRGS-PV-0067-K indicated that both trackways present on this slab cannot be unambiguously attributed to any specific trackmaker or classified in a particular ichnotaxon, due to the lack of well-preserved morphological characteristics. Consequently, we dissent from the original ichnotaxonomical proposition and claim for further data in order to better understand the spatiotemporal distribution of tetrapods in the Early Cretaceous Botucatu erg.

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