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# Análise morfológica e paleoecológica de icnofósseis atribuídos a tetrápodes não-arcossauros da Formação Botucatu (Cretáceo Inferior)

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Tese apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais da Universidade Federal de São Carlos, como parte dos requisitos para a obtenção do título de Doutor em Ciências, área de concentração em Ecologia e Recursos Naturais.

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# Índice

**Resumo**

Os icnofósseis, estudados pela paleoicnologia, são estruturas produzidas em decorrência de atividades comportamentais e fisiológicas dos organismos do passado. As pegadas, um dos tipos mais conhecidos de icnofósseis (bioturbações), são produzidas pela interação dos autopódios do animal com o substrato, sendo este último deformado no processo. O formato dos autopódios, as condições do substrato e o comportamento de locomoção do produtor influenciam diretamente na morfologia das pegadas. Durante o início do Cretáceo, um enorme paleodeserto de areia cobriu grandes extensões do território brasileiro, dando origem posteriormente aos arenitos eólicos da Formação Botucatu. Seu principal conteúdo fossilífero são as pegadas e escavações produzidas pelos animais (vertebrados e invertebrados) que viveram no paleodeserto, sendo a região do Município de Araraquara (Estado de São Paulo) a que apresenta a maior quantidade e diversidade de icnofósseis. O presente trabalho teve como principal objetivo a análise morfológica e paleoecológica de icnofósseis com afinidade a tetrápodes não-arcossauros provenientes da Formação Botucatu. As descrições das pegadas e pistas foram realizadas com base em parâmetros estabelecidos na literatura científica, como largura e comprimento das pegadas, passo oblíquo, passo duplo, ângulo de passo, largura da pista e rotação dos autopódios. Foram descritos e analisados diversos espécimes de pegadas de maior porte com afinidade a Synapsida, sendo definido um novo icnotáxon, *Aracoaraichnium leonardii*. Foi possível determinar que o produtor destas pegadas de maior porte pertencia a uma espécie diferente da produtora das pegadas de *Brasilichnium*, e não um estágio ontogenético avançado. Dessa forma, o produtor de *A. leonardii* representa um novo componente na estrutura ecológica do paleodeserto Botucatu. É inferido que os produtores deste icnotáxon poderiam se alimentar de invertebrados ou material vegetal, dependendo da disponibilidade dos recursos, sendo potenciais competidores dos produtores de *Brasilichnium*. Também foram descritas e analisadas pegadas com afinidade a Lepidosauria (lagartos). Tais pegadas são pentadáctilas, com dígitos curvos, sendo o dígito I direcionado para o interior da pista e oposto ao dígito V, que se encontra em uma posição posterolateral. São identificadas marcas atribuídas ao arraste e ao contato da cauda com o substrato. A atribuição icnotaxonômica foi realizada tentativamente ao icnogênero *Rhyncosauroides*, e futuras análises a partir de novos espécimes com melhor qualidade preservacional podem elucidar essa questão. A partir da análise das pistas foi possível identificar três comportamentos distintos de locomoção, sendo eles o deslocamento cursorial típico, um deslocamento onde as pegadas estão rotacionadas para mesma direção, divergindo da direção da pista, e um onde o produtor

faz momentos de parada. O reconhecimento de um novo produtor com afinidade a Lepidosauria aumenta a complexidade da teia ecológica da Formação Botucatu e contribuiu para o entendimento da distribuição e ocupação de nicho destes animais no Cretáceo Inferior.

**Palavras-chave:** Icnofóssil, pegadas fósseis, Tetrapoda, deserto, Cretáceo.

**Abstract**

Ichnofossils, studied by Paleoichnology, are structures produced as a result of behavioral and physiological activities of organisms of the past. Fossil tracks (footprints), one of the best-known types of ichnofossils (bioturbations), are produced by the interaction of the animal's autopods with the substrate, the latter being deformed in the process. The shape of the autopods, the conditions of the substrate and the locomotion behavior of the trackmaker directly influence the morphology of the tracks. During the beginning of the Cretaceous, a huge sandy paleodesert covered a large area of the Brazilian territory, giving rise later to the eolian sandstones of the Botucatu Formation. Its main fossiliferous content are the tracks and excavations produced by the animals (vertebrates and invertebrates) that lived in the paleodesert, being the region of the Municipality of Araraquara (São Paulo State) the one that presents the greatest quantity and diversity of ichnofossils. The present work had as main objective the morphological and paleoecological analysis of ichnofossils with affinity to non-archosaurian tetrapods from the Botucatu Formation. The descriptions of the tracks and trackways were carried out based on parameters established in the scientific literature, such as width and length of the tracks, oblique pace, stride, pace angulation, trackway width and rotation of the autopods. Several specimens of tracks with affinity to larger mammaliaformes have been described and analyzed, and a new ichnotaxon, *Aracoaraichnium leonardii*, has been defined. It was possible to determine that the trackmaker of these larger tracks belonged to a different species than the trackmaker of the *Brasilichnium* tracks, and not an advanced ontogenetic stage. In this way, the trackmaker of *A. leonardii* represents a new component in the ecological structure of the Botucatu paleodesert. It is inferred that the trackmakers of this ichnotaxon could feed on invertebrates or plant material, depending on the availability of resources, being potential competitors of the trackmakers of *Brasilichnium*. Tracks with affinity to Lepidosauria (lizards) were also described and analyzed for the first time. Such tracks are pentadactyl, with curved digits. The digit I is directed to the inside of the trackway and opposite the digit V, which is in a posterolateral position. Marks attributed to drag and contact of the tail on the substrate were identified. The icnotaxonomic attribution was tentatively made to the icnogenus *Rhyncosauroides*, and future analyzes based on new, better preserved specimens may elucidate this issue. From the analysis of the trackways, it was possible to identify three distinct locomotion behaviors, being the typical cursorial gait, a gait where the footprints are rotated in the same direction, diverging from the trackway's midline, and one where the producer makes stops. The recognition of a new trackmaker with a lizard-like affinity increases the complexity

of the ecological web of the Botucatu Formation and contributed to the understanding of the distribution and niche occupation of these animals in the Lower Cretaceous.

# 1. Introdução

## 1.1 Paleontologia

A Paleontologia pode ser definida, em termos gerais, como a ciência que estuda os organismos do passado. Essa definição pode ser diretamente entendida a partir do próprio termo Paleontologia, que é composto pelas palavras derivadas do grego *palaios*, *ontos* e *logos*, que significam, respectivamente, antigo, ser e estudo (Cassab, 2010). O conceito de passado, referente a um tempo que já passou, pode variar bastante dependendo do contexto em que ele é aplicado. Por exemplo, na História, os historiadores estão habituados a lidar com processos e acontecimentos do passado na escala de décadas a poucos milênios. Na Arqueologia, os arqueólogos aumentaram um pouco mais essa escala para dezenas de milhares de anos. Já na Geologia, processos e acontecimentos podem chegar a operar na escala de bilhões de anos, o que altera drasticamente a escala do tempo e a percepção do passado, sendo empregado o termo tempo geológico.

A idade do planeta Terra é estimada em aproximadamente 4,6 bilhões de anos, e a vida surgiu no planeta, provavelmente, no intervalo de tempo entre 4,0 e 3,5 bilhões de anos (Lepot, 2020). A vida como é conhecida hoje, em toda a sua diversidade funcional e de formas e tamanhos, é fruto de uma longa trajetória ao longo do tempo geológico marcada por eventos astronômicos, geológicos, climáticos e biológicos, que a modificaram desde seu surgimento até os dias atuais (Courtillot e Gaudemer, 1996; Cowen, 2013). Como a Paleontologia lida com os organismos do passado, e a vida tem uma história de bilhões de anos até o presente, a escala de tempo nesta ciência é muito ampla e pode variar em função do tipo de organismo que é estudado. Para ilustrar essa diferença na escala de tempo, pode-se contrastar trabalhos paleontológicos que lidam com grupos taxonômicos relativamente recentes, como o feito por Moura et al. (2019), na qual foi descrita uma nova espécie de pampaterídeo de poucos milhares de anos, com trabalhos que lidam com organismos que viveram há centenas de milhões de anos, como o realizado por Becker-Kerber et al. (2020), no qual foi descrita uma biota composta por organismos enigmáticos de aproximadamente 563 milhões de anos.

Para facilitar o entendimento da proporção e da escala do tempo geológico, é possível utilizar recursos didáticos que transformem, a partir de analogias, todo o tempo transcorrido desde a origem da Terra em outras medidas. Em Anelli (2010), enquanto os principais eventos geológicos e biológicos são descritos e o tempo geológico em que ocorreram são definidos, estes também são pontuados em um relógio. O princípio desse recurso didático é transformar

4,6 bilhões de anos em 24 horas a partir de cálculos simples, onde 4,6 bilhões de anos equivalem às 24 horas do dia. Dessa forma, é possível pontuar qualquer evento ou organismo do passado e comunicar de uma maneira que fique mais fácil a percepção da escala do tempo geológico.

Os organismos do passado, assim como os atuais, também tiveram os seus próprios ciclos de vida como nascimento, crescimento, interações ecológicas e morte. Ao longo de suas vidas, muitos vestígios de suas atividades biológicas foram produzidos e, com a morte, independente do motivo, também foram produzidos restos orgânicos de suas estruturas. Parte destes vestígios e restos foram incorporados à Litosfera por meio de um processo denominado de fossilização, que envolve uma série de etapas e reações químicas variadas que ocorrem com o recobrimento ou isolamento destes da superfície (Medeiros, 2010). É a partir destes restos orgânicos e vestígios, os fósseis, que os paleontólogos realizam diversos estudos por meio de metodologias científicas, e reconstroem cenários biológicos do passado (Seddon et al. 2014).

Portanto, o principal objeto de estudo da Paleontologia são os fósseis, de onde inúmeras informações são extraídas. Os restos corporais como ossos, dentes, conchas, escamas, troncos, flores, folhas, dentre outros, são classificados como somatofósseis, pois fazem parte da estrutura (*i.e.* corpo) do organismo, enquanto que os vestígios como pegadas, rastros, tocas, coprólitos, urólitos, ninhos e marcas de predação são classificados como icnofósseis, não fazendo parte do corpo do organismo, pois são produzidos em decorrência de diversas atividades comportamentais e fisiológicas.

A definição de fóssil pode variar bastante. Algumas mais simples podem definir que são restos e vestígios de mais de 11.000 anos, enquanto outras pontuam ainda que estes necessitam estar alterados quimicamente pela fossilização. No artigo 297 inciso I da Portaria N° 155 de 12 de Maio de 2016 do Departamento Nacional de Produção Mineral (DNPM), Brasil, fóssil é definido da seguinte maneira: "I - fóssil: resto, vestígio ou resultado da atividade de organismo que tenha mais de 11.000 anos ou, no caso de organismo extinto, sem limite de idade, preservados em sistemas naturais, tais como rochas, sedimentos, solos, cavidades, âmbar, gelo e outros, e que sejam destinados a Museus, Estabelecimentos de Ensino e outros fins científicos;". Esta definição de fóssil abrange tanto restos e vestígios, independentemente da idade e tipo de preservação, contanto que sejam atribuídos a organismos extintos e ocorram em sistemas naturais.

Os fósseis são os responsáveis por documentar a história da vida ao longo do tempo geológico. No entanto, existem lacunas no registro fóssil, pois a fossilização é um processo tendencioso e nem todas as espécies do passado tiveram seus registros preservados (Simões et

al. 2010). Além disso, as rochas sedimentares, principal meio onde são encontrados os fósseis, sofrem por processos de intemperismo, erosão e metamorfismo, que acabam por destruir o registro fóssil. O material biológico que foi preservado (*i.e* fossilizado), que sobreviveu ao tempo, e que foi coletado e analisado, é que será utilizado para os mais variados tipos de estudos e entendimento da biosfera pretérita (Behrensmeyer et al. 2000).

Atualmente, a Paleontologia pode ser subdividida em quatro grandes áreas de acordo com os tipos e natureza dos fósseis, sendo elas a Paleozoologia, a Paleobotânica, a Micropaleontologia e a Paleoicnologia, que será detalhada no próximo tópico. Na Paleozoologia, o objeto de estudo são os fósseis referentes aos animais, tanto vertebrados quanto invertebrados, na Paleobotânica o objeto de estudo são os fósseis das plantas e dos fungos, e na Micropaleontologia, o objeto de estudo são os fósseis microscópicos, ou microfósseis.

Em especial para as Ciências Biológicas, a Paleontologia permite reconstruir cenários bióticos do passado. Essas reconstruções podem ser realizadas em diversos níveis de escala e sob diferentes enfoques. Por exemplo, ao analisar uma assembléia fossilífera de determinada idade geológica, os paleontólogos podem buscar compreender aspectos paleoecológicos, paleobiogeográficos, evolutivos, dentre outros. Cada vez mais busca-se compreender aspectos paleobiológicos a respeito dos organismos, ao invés de apenas descrever uma nova forma taxonômica do passado. Mais recentemente, nas últimas décadas, uma série de técnicas analíticas químicas e de imagem vêm sendo desenvolvidas e refinadas conforme ocorrem avanços tecnológicos. Muitas dessas técnicas são empregadas na análise dos fósseis, permitindo com isso, explorar aspectos antes inimagináveis e responder questões de maneiras mais precisas (Riquelme et al. 2009; Delgado et al. 2014; Gomes et al. 2019).

## 1.2 Paleoicnologia

A Paleoicnologia, uma das subdivisões da Paleontologia, possui os seus próprios métodos e fundamentos, que vêm sendo definidos e refinados desde o seu surgimento como ciência (Souto, 2017). A palavra *ikhnos*, do grego, significa vestígio. Logo, a Paleoicnologia é o estudo dos vestígios antigos. Esta ciência é um dos campos que compõem a Icnologia (estudo dos vestígios), junto com um outro campo, denominado de Neoicnologia, que é o estudo dos vestígios atuais. São estudados, pela Icnologia como um todo, vestígios de animais vertebrados e invertebrados, de plantas, e de microrganismos.

Os icnofósseis, objeto de estudo de Paleoicnologia, são classificados de acordo com sua natureza e forma de produção em estruturas de biodeposição, bioturbações e bioerosões (Buatois e Mángano, 2011). As bioturbações, mais especificamente, são produzidas pela interação do corpo do organismo ou parte deste com o substrato, sendo as mais comuns as pegadas, os rastros e as escavações. Durante essa interação, parte da estrutura do substrato (*i.e.* sedimento inconsolidado) é rompida e remodelada, podendo este ser o leito ou à margem de um rio, lago ou mar, uma duna de areia, uma planície de inundação ou qualquer outro tipo de ambiente em que se tenha a deposição de sedimento (ambientes deposicionais marinhos, costeiros e continentais).

As bioturbações refletem os comportamentos dos organismos que as produziram e podem ser classificadas, a partir de critérios comportamentais, segundo um sistema de classificação proposto inicialmente por Seilacher (1953) para icnofósseis de invertebrados em ambientes deposicionais aquáticos. Neste sistema, existem cinco categorias de classificação dos comportamentos, sendo eles: vestígios de descanço (*cubichnia*), de locomoção (*repichnia*), de pastagem (*pascichnia*), de alimentação (*fodinichnia*) e de habitação (*domichnia*). Posteriormente, outras categorias e subcategorias comportamentais foram reconhecidas, descritas e revisadas (Bromley, 1990; Bromley, 1996).

Além de registrar diferentes comportamentos de organismos extintos, as bioturbações possuem outras características de alta relevância científica e importância para a Paleontologia. Muitos organismos de corpo mole possuem baixo potencial de fossilização e, devido a isso, em diversos casos, são sub-representados em assembleias fossilíferas (Simões et al. 2010). No entanto, quando em vida, tais organismos podem ter produzido bioturbações que ficaram preservadas, permitindo assim seu registro. As bioturbações não sofrem transporte como os somatofósseis, por exemplo, e por isso, sempre ocorrem *in situ*, ou seja, nos locais onde foram produzidas. Dessa forma, são bons indicadores paleoambientais (Carvalho e Leonardi, 2020). Também podem auxiliar no reconhecimento de topo e base de camadas sedimentares (Carvalho e Fernandes 2010).

No presente tópico será dada atenção especial a Paleocinologia de tetrápodes, com ênfase em pegadas fósseis. Tetrapoda é um grupo taxonômico com origem no período Devoniano (419,2 - 358,9 Ma) e que inclui, atualmente, anfíbios, répteis, aves e mamíferos (Benton, 2015). Pegadas fósseis já foram descritas para depósitos com idade variando do Devoniano (Qvarnström et al. 2018) ao Holoceno (McDonald et al. 2007), e ocorrem em uma grande diversidade de paleoambientes e são atribuídas aos mais variados grupos taxonômicos dentro de Tetrapoda.

A formação de pegadas envolve necessariamente o contato do autopódio do animal com o substrato. Este contato pode ser realizado pelos pés e pelas mãos, no caso de animais quadrúpedes, ou apenas pelos pés, no caso de animais bípedes. Quando mais de uma pegada ocorre em sequência, estas formam uma pista. As pistas têm o potencial de fornecer informações adicionais, como o modo de locomoção e a postura do produtor, indo além da morfologia dos autopódios registrada na pegada (Thulborn, 1990; Fernandes, 2017).

Todo o processo de produção até a fossilização de uma pegada começa com o autopódio deformando o substrato. O peso do animal precisa ser suficiente para deformar e moldar a camada de sedimento, por exemplo, areia e/ou lama, previamente depositada, no formato de seu autopódio. A umidade tem o potencial de tornar o substrato mais plástico, ou seja, mais moldável aos pés e/ou mãos do animal. Porém, se o substrato está saturado de água, a pegada adquire proporções exageradas e com contorno irreal (i.e. extramorfologia), pois os grãos sedimentares não possuem coesão suficiente para moldar de maneira precisa as reais dimensões dos autopódios (Gatesy et al. 1999).

Após a impressão do autopódio e formação da cavidade referente a pegada, esta pode ficar exposta ou ser coberta por nova camada de sedimento. O soterramento relativamente rápido garante que a pegada seja isolada de condições que possam alterar o seu formato ou mesmo destruí-la por completo, como fatores climáticos e pisoteio e retrabalhamento do substrato por outros animais (Laporte e Behrensmeyer, 1980). Assim como evidenciado por Carvalho et al. (2013) em pegadas de dinossauros terópodes do Cretáceo Inferior do Estado da Paraíba (Brasil), a presença de biofilmes formados por microrganismos podem auxiliar na preservação das pegadas no paleoambiente, pois estes mantêm o substrato coeso, diminuindo os efeitos da erosão. O acúmulo sucessivo de novas camadas faz com que ocorra o processo diagenético responsável por litificar as camadas de sedimento em rochas sedimentares, preservando assim as pegadas ali presentes (Thulborn. 1990). Quando as pegadas fósseis são encontradas e coletadas em rochas sedimentares, a deformação produzida pelo autopódio é o molde (*i.e.* epirelevo côncavo), e a camada superior que preencheu a deformação é o contra-molde (*i.e.* hiporelevo convexo). Tanto o molde como o contra-molde podem ser utilizados nos estudos paleocinológicos.

A dinâmica de formação de uma pegada envolve três principais fatores que influenciam no resultado morfológico desta, sendo eles o tipo de substrato, o comportamento de locomoção e o formato dos autopódios do produtor (*i.e.* taxonomia) (Falkingham, 2014). Dessa forma, o mesmo produtor pode produzir pegadas e pistas com morfologias distintas em função das condições do substrato, por exemplo, mais úmido, mais seco, mais ou menos consistente (Silva

et al. 2008), e em função do seu comportamento, por exemplo, andando, correndo, saltando, dentre outros (de Valais, 2009; Buck et al. 2017a). Em contrapartida, produtores taxonomicamente diferentes, mas que apresentem autopódios similares, podem produzir, sob as mesmas condições, pegadas com morfologia semelhante ou idêntica (Romilio e Salisbury, 2011).

O entendimento da dinâmica de produção e preservação das pegadas pode ser auxiliado por experimentos no campo da Neocinologia. Existem trabalhos que investigam esse processo a partir de condições controladas, produzindo assim resultados que podem ser comparados e aplicados na interpretação do registro paleoicnológico. Por exemplo, Brand (1996), utilizando uma salamandra, produziu pistas em uma ampla gama de condições variando no teor de umidade e inclinação em substrato arenoso. Os resultados produzidos por Brand (1996) auxiliam na interpretação de pegadas fósseis encontradas em paleoambientes eólicos. Também é possível analisar, por meio da Neoicnologia, aspectos relacionados ao comportamento dos animais e como eles podem produzir variações entre as pistas. Genise et al. (2009) analisaram a produção de diversas pistas de aves atuais observando o comportamento que era empregado. A partir destas análises, foi possível atribuir uma configuração geométrica de pista a determinado comportamento específico, com potencial para reconhecimento destes no registro icnofossilífero. Mais recentemente, Buck et al. (2017a) analisaram a produção de pistas em substrato arenoso em plano inclinado de um pequeno mamífero com capacidade de locomoção em saltos. Foi possível determinar, a partir dos resultados obtidos pelo experimento neoicnológico, diferenças na configuração das pistas e no formato das pegadas entre pistas sob diferentes tratamentos, facilitando assim a interpretação dos espécimes fósseis descritos de *Brasilichnium saltatorium*.

A descrição formal e hierarquizada de pegadas fósseis é realizada seguindo os princípios da icnotaxonomia, que é uma taxonomia paralela a classificação biológica clássica (Rindsberg, 2012), também binomial e em Latim, e devidamente reconhecida pelo Código Internacional de Nomenclatura Zoológica. São utilizadas características diagnósticas baseadas em critérios geométricos que possam ser diretamente observados e mensurados, o que permite uma sistematização para comparação entre diferentes espécimes (Demathieu & Demathieu, 2002). Normalmente, são utilizados dois níveis hierárquicos, o icnogênero e a icnoespécie. O táxon recebe o prefixo icno, o que permite a distinção e o reconhecimento como um icnofóssil. Deve-se ter em mente que o nome icnotaxonômico dado a determinada pegada não está associado a entidade taxonômica que a produziu, pois os icnofósseis e os fósseis corporais são classificados de maneiras independentes. Devido a icnotaxonomia ser baseada em critérios

morfológicos da estrutura em si, e não de quem a produziu, o mesmo organismo pode produzir diferentes estruturas que recebem nomes distintos, contanto que reflitam comportamentos diferenciados, ou diferentes organismos podem produzir a mesma estrutura, que receberá o mesmo nome taxonômico (Buatois e Mángano, 2013). Variações preservacionais já foram utilizadas erroneamente na criação de icnotáxons e posteriormente revisadas. Pode-se citar o trabalho de McKeever e Haubold (1996) e Lockley (2011), nos quais revisaram e sinonimizaram uma série de icnotáxons erigidos com base apenas em diferenças preservacionais, o que não é considerado como critério válido.

Para a descrição de pegadas e pistas são utilizados diversos parâmetros bem estabelecidos e que podem ser consultados em bibliografia especializada, como por exemplo Leonardi (1987), Thulborn (1990), Falkingham (2016) e Fernandes (2017). A descrição morfológica da pegada pode ser realizada, inicialmente, medindo o comprimento e a largura. Caso estejam preservadas marcas referentes aos dígitos, estes também podem ser descritos em termos de comprimento e largura, bem como ângulos interdigitais. As pistas indicam diretamente o modo e o comportamento de locomoção. Para acessar tais informações são mensurados o passo oblíquo, o passo completo e o ângulo de passo. A largura da pista também pode ser medida e utilizada na interpretação da postura do produtor. Marchetti et al. (2019) consideram que os parâmetros da pista também devem ser incluídos na diagnose dos icnotáxons, reforçando a classificação adotada por Buck et al. 2017a.

Uma das questões fundamentais envolvendo o estudo das pegadas fósseis é a identificação do produtor, que utiliza como base a descrição propriamente dita das pegadas e pistas. Isso pode ser feito comparando as pegadas com o registro de fósseis corporais dos autopódios, quando disponíveis. Deve-se levar em consideração a idade geológica do estrato onde as pegadas ocorrem, pois, inicialmente, é importante fazer comparações com somatofósseis de idade e localidades próximas. Também pode-se utilizar guias de identificação de pegadas atuais, que auxiliam no reconhecimento de morfologias características dos grandes grupos taxonômicos.

O potencial de estudo envolvendo as pegadas fósseis é bastante amplo. Trabalhos recentes têm produzido resultados que auxiliam na compreensão de padrões de distribuição e dispersão dos organismos, propondo assim modelos paleobiogeográficos, e na história de colonização de ambientes terrestres (Lagnaoui et al. 2019; Francischini et al. 2019; Marchetti et al. 2019; Marchetti et al. 2020). Por fim, existe uma complementação dos somatofósseis e dos icnofósseis. Por exemplo, Chen e Wilson (2015) inferiram, a partir da análise de diversos somatofósseis de mamíferos, modos de locomoção e a idade geológica em que estes surgiram.

No entanto, quando se busca informações também nos icnofósseis, o cenário pode ser diferente e mais completo. Chen e Wilson (2015) atribuem o surgimento da locomoção em saltos em mamíferos no Cretáceo (145 - 66 Ma), porém, sabemos, a partir de pistas fósseis, que tal modo de locomoção surgiu neste grupo, até o momento, no Jurássico (201,3 - 145 Ma) (de Valais, 2009).

**1.3 A Formação Botucatu e seus estudos paleontológicos**

Durante a maior parte da Era Mesozoica (251,9 – 66,0 Ma), grandes porções dos continentes experimentaram um evento de megadesertificação, tanto no Hemisfério Norte quanto no Hemisfério Sul (Almeida et al. 2012a). Um dos principais fatores que contribuíram para a predominância de um clima árido foi a aglutinação dos continentes no supercontinente Pangea durante o período Permiano (298,9 - 251.9 Ma) (Stampfli et al. 2013). Com essa configuração geográfica, grandes áreas ficaram sujeitas a severos déficits hídricos, ocorrendo assim o desenvolvimento de enormes paleodesertos de dunas (Parrish, 1993). Estes paleodesertos são atualmente reconhecidos e estudados a partir dos arenitos eólicos, que são os produtos da litificação da areia das dunas e, apresentam como principais características, estratificações cruzadas de médio a grande porte, ondulações de vento e grãos de sedimento bem selecionados (McKee, 1979).

No Brasil, a Bacia do Paraná, uma enorme bacia sedimentar intracratônica com aproximadamente 1,5 milhões de km$^2$, compreende, dentro dos seus 7 mil metros de espessura, diversos intervalos estratigráficos referentes a deposição eólica (Milani et al. 2007). Os arenitos eólicos mesozoicos mais antigos datam da transição permo-triássica, sendo pertencentes a Formação Pirambóia (Soares et al. 2008). Esta unidade geológica pode ser subdividida em três principais fácies, sendo elas lençóis de areia, interduna e duna e, com base na transição entre estas fácies, é possível inferir aumento na aridez ao longo da deposição (Dias e Scherer, 2008). Francischini et al. (2018) recentemente descreveram pegadas de tetrápodes para arenitos da Formação Pirambóia no Rio Grande do Sul que reforçam a natureza desértica da unidade. No Jurássico Superior, os estratos da Formação Guará, que afloram no oeste do Estado do Rio Grande Sul, indicam a ocorrência de condições áridas com base na intercalação de fácies de arenitos eólicos com arenitos fluviais (Scherer et al. 2000). Nesta unidade também foram descritas pegadas fósseis na fácies eólica, sendo estas atribuídas a dinossauros terópodes, saurópodes, ornitópodes (Dentzien-Dias et al. 2007) e anquilossauros (Francischini et al. 2017).

Com o passar do tempo ao longo da Era Mesozoica, infere-se que as condições de aridez aumentaram, atingindo o ápice durante a primeira parte do Cretáceo Inferior. Neste contexto, ocorreu a deposição dos arenitos eólicos da Formação Botucatu, que foi o maior paleodeserto de dunas já existente, margeando praticamente toda a extensão da Bacia do Paraná e ocorrendo também em outros países, como o Uruguai, Paraguai, Argentina e Namíbia (Scherer e Goldberg, 2007). Francischini et al. (2015) compararam as ocorrência de pegadas de dinossauros das formações Guará e Botucatu e, com base nestes dados, inferem maior aridez para a última unidade. Além destes dados, outros fatores reforçam essa interpretação, como a rara ocorrência de fácies que indiquem deposição aquosa.

No entanto, sabe-se que eventos pluviais aconteciam, principalmente na região de Araraquara e São Carlos, Estado de São Paulo, onde vários estratos apresentam pequenas crateras de impacto produzidas pelas gotas de água (Fernandes, 2005; Fernandes et al. 2014; Buck et al. 2015). Além disso, a ocorrência de abundante icnofauna também pode ser um fator para inferir maior disponibilidade de água na região de Araraquara. Com base nessas duas evidências, o paleoambiente da região de Araraquara, dominado por dunas de areia, pode ter sido pontuado por oásis em locais interdunas a partir do desenvolvimento de corpos d'água efêmeros, onde a fauna poderia buscar recursos. Na porção norte da Formação Botucatu, no Estado de Minas Gerais, foram descritos troncos de coníferas por Pires et al. (2011), o que também indica condições deposicionais mais úmidas. Já para o porção sul da unidade, Scherer (2000) inferem maior aridez. Até o momento, em comparação com a região do Município de Araraquara, nenhuma outra icnofauna da Formação Botucatu foi descrita em termos de diversidade e abundância, ou que mesmo chegasse próxima nestes quesitos.

Com o início da fragmentação do continente Gondwana a partir da Ativação Mesozoica e o início da separação da América do Sul e da África, que viria a resultar no surgimento do protoceano Atlântico Sul, um grande evento magmático ocorreu em grandes porções do território brasileiro durante o Eocretáceo (Almeida et al. 2012b). Neste contexto ocorreram os derrames de lava que deram origem aos basaltos da Formação Serra Geral, sendo um dos maiores episódios de extravasamento já registrados até o momento ao longo da história geológica da Terra, estimando-se uma cobertura de 75% da Bacia do Paraná (Almeida et al. 2012b).

Os derrames de lava estão assentados principalmente sobre os arenitos da Formação Botucatu, tendo sido importantes para a preservação das dunas e para a datação superior desta unidade (Scherer, 2000; Scherer, 2002). Juntas, as formações Botucatu e Serra Geral compreendem o Grupo São Bento (Scheneider et al. 1973). As condições desérticas

continuaram prevalecendo a partir do início e ao longo dos derrames, o que é explicitado pelo contato e entremeamento do basalto com o arenito (Scherer, 2000; Scherer, 2002). Datações dos basaltos já foram realizadas em diversos trabalhos, onde infere-se um intervalo de cerca de 1 - 2 Ma para o todo o evento magmático (e.g. Renne et al. 1992; Thiede e Vasconcelos, 2010; Pinto et al. 2011), ou um intervalo maior para os derrames com cerca de 10 Ma de duração (e.g. Turner et al. 1994; Stewart et al. 1996). Independente da interpretação, devido ao contato direto e entremeado da Formação Botucatu com a Formação Serra Geral, define-se como idade superior para esta primeira unidade o fim dos últimos derrames de lava, que encerram o ciclo deposicional do paleodeserto Botucatu e da Bacia do Paraná como um todo no Cretáceo Inferior. Já em relação a idade inferior da Formação Botucatu, não se sabe ao certo o início de sua deposição, uma vez que sua base ocorre em discordância com as unidades inferiores. Scherer (2002) utiliza o argumento de ausência de supersuperfícies dentro das sequências de arenitos para inferir um intervalo deposicional curto, estando inteiramente dentro do Cretáceo, porém, existe discussão se o paleodeserto teve seu início deposicional no Jurássico Superior.

Em termos paleontológicos, a Formação Botucatu é composta quase que exclusivamente por icnofósseis. Até o momento, nenhum somatofóssil de qualquer animal foi encontrado, sendo os icnofósseis atribuídos a tetrápodes e invertebrados a única maneira de se investigar e compreender os aspectos paleobiológicos destes grupos no paleodeserto Botucatu. O primeiro registro de um icnofóssil desta unidade compreende pegadas que foram reconhecidas pelo engenheiro de minas Joviano A. A. Pacheco em calçadas do Município de São Carlos (Estado de São Paulo) pavimentadas com o arenito Botucatu (Pacheco, 1913). Ainda na primeira metade da década do século XX, Huene (1931) descreveu uma das pistas previamente identificadas e a atribuiu a um provável cinodonte. Já na segunda metade da década, uma série de estudos sobre a icnofauna da Formação Botucatu começaram a ser desenvolvidos, focando na descrição de espécimes encontrados principalmente em pedreiras na região do Município de Araraquara (e.g. Leonardi, 1977; Leonardi, 1979; Leonardi, 1980; Leonardi e Godoy, 1980; Leonardi, 1981; Leonardi e Sarjeant, 1986; Fernandes et al. 1990; Leonardi e Oliveira, 1990). A grande quantidade e diversidade de morfotipos de pegadas encontradas revelou uma importância acentuada para a região de Araraquara, sendo denominada de Icnossítio do Ouro (Leonardi e Carvalho, 2002). Foram reconhecidos diversos morfotipos que foram atribuídos a diferentes produtores tetrápodes e invertebrados que serão discutidos adiante.

O primeiro icnotáxon formalmente descrito, e mais abundante para a Formação Botucatu, foi o icnogênero *Brasilichnium* (Leonardi, 1981), com a icnoespécie *Brasilichnium*

*elusivum*. O nome genérico *Brasilichnium* faz referência a pegadas brasileiras, enquanto que o nome específico faz alusão a dificuldade em se atribuir com clareza as pegadas a determinado produtor e ao aspecto bípede das pistas, mesmo tendo sido produzidas por um quadrúpede. Como este icnogênero era, até então, monoespecífico, as características diagnósticas da descrição original são aplicadas também para a icnoespécie. A diagnose apresentada em Leonardi (1981) inclui as seguintes características: pista de um animal pequeno e quadrúpede, ângulo de passo elevado, alto grau de heteropodia, marcas dos pés com contorno elíptico e maior no eixo transversal, eixo anteroposterior rotacionado para o interior da pista, pegadas pentadáctilas, com marcas dos dígitos curtas e sem garras, e dígito V maior em relação aos outros e com leve grau de abdução. As pistas foram tentativamente atribuídas a um "mamífero primitivo" de pequeno porte (Leonardi, 1981). Atualmente, a atribuição do produtor tem sido dentro do grupo dos Mammaliaformes (Leonardi e Carvalho, 2020), sem uma posição taxonômica precisa dentro deste.

Posteriormente, Fernandes e Carvalho (2008), com base em numerosos espécimes de *Brasilichnium* mais bem preservados do que os utilizados na descrição original realizada por Leonardi (1981), revisaram as características diagnósticas para este icnotáxon. A principal constatação realizada por Fernandes e Carvalho (2008) é a de que as pegadas de *Brasilichnium*, tanto das mãos quanto dos pés, são tetradáctilas, ao invés de pentadáctilas, e apresentam uma condição ectaxônica, com maior importância dos dígitos externos. Em relação à presença/ausência das marcas das mãos, foi observado que estas apareciam em valores de ângulo de passo entre 105° e 120°, indicando uma menor velocidade de locomoção e pistas mais largas, e quando as pegadas dos pés apresentavam rotação para o interior da pista. D'Orazi Porchetti et al., (2017a) avaliaram a presença/ausência das marcas das mãos em função da direção ascendente ou descendente em relação ao plano inclinado da paleoduna. Foi observado que quando o produtor descia o plano inclinado, as marcas das mãos eram claramente visíveis, possivelmente devido a distribuição de forças estar concentrada na porção anterior do animal (D'Orazi Porchetti et al., 2017a). Não foi observada relação entre a velocidade do produtor e a presença/ausência das marcas das mãos por D'Orazi Porchetti et al., (2017a). No entanto, ainda não está clara a questão de o motivo das marcas das mãos estarem presentes ou não quando o animal sobe o plano inclinado, sendo possível a sobreposição das pegadas das mãos pelas dos pés e/ou a formação das pegadas das mãos em subsuperfície, marcando assim, em camadas diferentes das pegadas dos pés (Leonardi, 1981; Fernandes e Carvalho, 2008).

Além da capacidade cursorial típica, o produtor das pegadas de *Brasilichnium* tinha a capacidade de locomoção saltatorial. É possível atestar essa capacidade e comportamento a

partir da análise de pistas atribuídas a este produtor e que apresentam uma configuração geométrica bastante característica. Em termos gerais, pistas associadas à locomoção saltatorial apresentam pegadas dos pés dispostas de maneira sub-paralela à paralela, onde os conjuntos destas configuram os ciclos de saltos. A primeira observação deste tipo de pista foi realizada por Leonardi (1977) e, em Leonardi (1981), estas foram atribuídas a uma variação locomotorial do mesmo produtor de *Brasilichnium*. Porém, apenas muitos anos depois pistas deste tipo de comportamento receberam a devida atenção (Buck et al. 2017a; D'Orazi Porchetti et al., 2017a).

Pistas com esse tipo de locomoção especializada e bastante distinta foram analisadas e classificadas por Buck et al. (2017a) como uma nova icnoespécie, denominada de *Brasilichnium saltatorium*. Foram descritas diversas pistas empregando este tipo de locomoção, tanto em direção ascendente quanto descendente em relação ao plano inclinado da paleoduna. A partir destas pistas, foi possível identificar diferenças que podem ocorrer nos parâmetros destas e das pegadas em virtude da direção do movimento. Alguns espécimes apresentam transições no modo de locomoção, o que está associado a mudança no comportamento. Tal mudança é refletida diretamente na geometria das pistas, e é bastante importante por mostrar que o mesmo animal pode produzir pistas classificadas como *B. elusivum* e *B. saltatorium*. Este tipo de locomoção saltatorial foi interpretado como uma possível resposta de fuga de predadores, perseguição de presas ou, ainda, para evitar contato prolongado com as areias quentes do deserto (Buck et al. 2017a).

Outro aspecto relacionado ao comportamento e que pode ser acessado pela análise das pistas é a possibilidade de gregarismo para os produtores de *Brasilichnium*. Rownland e Mercadante (2014), ao descreverem pegadas de *Brasilichnium* para o arenito Aztec (Jurássico Inferior) nos EUA, inferiram comportamento gregário para os produtores. Buck et al. (2016), ao analisar três lajes contendo duas pistas cada, também observaram essa possibilidade para os produtores da Formação Botucatu. As pistas apresentam as mesmas condições preservacionais, estão direcionadas para o mesmo sentido, sendo elas regularmente espaçadas, e apresentam parâmetros locomotoriais bastante semelhantes, indicando que podem ter sido produzidas dentro do mesmo intervalo de tempo por animais formando um grupo e, caminhando com o mesmo comportamento (Buck et al.2016).

O sistema ecológico da Formação Botucatu, além dos produtores de *Brasilichnium*, também apresentava uma segunda espécie de animal inferida como pertencente à linhagem evolutiva dos mamíferos. As pegadas, consideravelmente maiores que as de *Brasilichnium*, indicam um produtor de maiores proporções. Estas foram inicialmente ilustradas em Leonardi

(1980), sendo atribuídas tentativamente ao grupo Therapsida, mais especificamente a cinodontes ou dicinodontes, e foram denominadas de morfotipo "teromorfóide" (Leonardi e Godoy, 1980).

Tais pegadas de maior porte foram utilizadas como base por Leonardi e Godoy (1980) para estimar, inicialmente, uma idade triássica para a Formação Botucatu, usando como argumento de que linhagens evolutivas mais derivadas dos mamíferos foram pequenas durante o Jurássico e o Cretáceo. No entanto, posteriormente, foram descritas espécies de mamíferos de maior porte com base em somatofósseis, como por exemplo *Repenomamus giganticus*, do Cretáceo Inferior da China (Hu et al. 2005) e *Adalatherium hui*, do Cretáceo Superior de Madagascar (Krause et al. 2020). Dessa forma, as pegadas "termorfóides" da Formação Botucatu podem ter sido produzidas por organismos mais derivados, uma vez que o cenário evolutivo em relação aos tamanhos corporais dos mamíferos ainda não é tão bem compreendido.

Apesar do morfotipo "teromorfóide" ser conhecido a bastante a tempo (e.g. Leonardi e Godoy, 1980), apenas recentemente foram designadas classificações icnotaxonômicas para estas pegadas. Buck et al. (2017b) e D'Orazi Porchetti et al. (2017b) classificaram pegadas desse morfotipo (depositadas em diferentes coleções científicas) em diferentes níveis taxonômicos, como um novo icnogênero e uma nova icnoespécie de *Brasilichnium*, respectivamente. O segundo icnogênero atribuído a tetrápodes da Formação Botucatu foi batizado de *Aracoaraichnium*, até o momento monoespecífico com a icnoespécie *Aracoaraichnium leonardii* (Buck et al. 2017b). As pegadas apresentam contorno geral semelhante a *Brasilichnium*, porém, com diferenças nos dígitos, discussão que será mais aprofundada no capítulo 3 deste trabalho. A interpretação de pelo menos dois produtores com afinidade a mamíferos para a Formação Botucatu é sustentada, além da morfologia das pegadas, pela ausência de pegadas de tamanhos intermediários entre *Brasilichnium* e *Aracoaraichnium* (Buck et al. 2017b).

O registro paleoicnológico da Formação Botucatu também conta com uma série de pegadas atribuídas a dinossauros bípedes do grupo dos ornitópodes e dos terópodes (Leonardi, 1980; Leonardi e Godoy, 1986; Leonardi e Carvalho, 2002; Fernandes, 2005; Fernandes e Carvalho, 2007; Fernandes et al., 2011; Francischini et al., 2015; Manes et al., 2018a). Fernandes et al. (2011) reconhecem quatro morfotipos de pegadas de dinossauros Theropoda, sendo eles atribuídos a Coelurosauria (morfotipo I) e Carnosauria (morfotipos II, III e IV), sendo os predadores de topo do paleodeserto Botucatu. Os morfotipos atribuídos a Carnosauria

podem ser variações preservacionais em função de diferentes esforços locomotoriais ou diferentes características do substrato (Fernandes et al. 2011).

As pegadas atribuídas ao grupo dos Ornithopoda também apresentam diferentes morfotipos de tamanho e de forma, onde estes últimos podem estar associados a características preservacionais (Fernandes, 2005). Até o momento, as maiores pegadas fósseis da Formação Botucatu, bem como do Estado de São Paulo, são atribuídas ao grupo (Fernandes e Carvalho, 2007). Também atribuído ao grupo dos Ornithopoda foram descritas estruturas produzidas por extrusão líquida associadas a urina, denominadas de urólito, que são muito raras no registro icnofossilífero (Fernandes et al. 2004). A atribuição a produtor Ornithopoda foi realizada com base no tamanho da estrutura e das pegadas, sendo tais dinossauros os únicos compatíveis, e com base na comparação de estruturas atuais produzidas por urina de avestruz (Fernandes et al. 2004).

Em relação aos icnofósseis atribuídos a invertebrados, poucos estudos foram realizados dando especial atenção ao grupo. Embora já se tivesse conhecimento de icnofósseis como pistas e escavações produzidos por invertebrados (e.g. Pacheco, 1913; Leonardi, 1980; Leonardi e Sarjeant, 1986), a primeira identificação icnotaxonômica foi realizada por Fernandes et al. (1990), onde foram descritas escavações endoestratais atribuídas a *Taenidium*. O produtor foi interpretado como possíveis coleópteros e/ou anelídeos que escavavam o substrato arenoso em busca de alimento, produzindo assim os rastros (Fernandes et al. 1990).

Em diversos trabalhos posteriores e que lidam com a icnofauna da Formação Botucatu como um todo (e.g. Leonardi e Carvalho, 2002; Fernnades, 2005; Leonardi et al., 2007; Fernandes et al., 2014), os produtores invertebrados têm sido interpretados como artrópodes, pertencentes à Classe Insecta e Arachnida. As pistas espiestratais são atribuídas tentativamente aos icnogêneros *Hexapodichnus*, *Paleohelcura* e *Octopodichnus* (Fernandes e Fernandes, 2010; Peixoto e Fernandes, 2010; Sampaio, 2016), enquanto que as escavações endoestratais são atribuídas a *Ancorichnus*, *Arenicolites*, *Cochlichnus*, *Palaeophycus*, *Planolites*, *Scoyenia, Skolithos* e *Taenidium* (Fernandes et al. 1990; Peixoto et al. 2016; Manes et al. 2018b; Francischini et al. 2020). Riff et al. (2017) descreveram dois padrões de perfurações em lenhos fósseis da Formação Botucatu encontrados no Triângulo Mineiro, sendo atribuídas a atividade biológica de insetos xilófagos como cupins e besouros. Recentemente, Peixoto et al. (2020) descreveram pistas epiestratais, classificando-as como uma nova icnoespécie, denominada de *Paleohelcura araraquarensis*, e atribuindo-às provavelmente a um produtor Coleoptera.

## 2. Objetivo

Este trabalho tem como principal objetivo a análise de icnofósseis com afinidade a tetrápodes não-arcossauros provenientes da Formação Botucatu, para o entendimento da natureza dos diferentes morfotipos, dos aspectos locomotoriais, e dos aspectos paleoecológicos dos produtores.

## 2.1 Objetivos específicos

- Caracterizar  os morfotipos de pegadas fósseis com base em parâmetros morfológicos.
- Descrever as pistas fósseis com base em parâmetros locomotoriais.
- Designar icnotáxons para os diferentes morfotipos.
- Inferir, com base nos aspectos morfológicos e locomotoriais, os possíveis produtores das pistas.
- Determinar os aspectos paleoecológicos sobre os produtores inferidos, contribuindo assim para um melhor entendimento da ecologia do paleodeserto Botucatu.

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# A new ichnotaxon classification of large mammaliform trackways from the Lower Cretaceous Botucatu Formation, Paraná Basin, Brazil

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## ARTICLE INFO

## ABSTRACT

During the Early Cretaceous, a large area in Brazil and other South American countries was covered by an extensive paleoerg field, the Botucatu Desert. The Araraquara County (São Paulo State, Brazil) contains some of the most diverse ichnological assemblages in the Botucatu Formation. Mammaliform trace fossils from the Botucatu Formation are of great interest, as they may represent the only record of Lower Cretaceous Mammaliamorpha from Brazil. These trace fossils can be grouped into two distinct classes, based on the dimensions of the footprints. The larger morphotype is described and classified as a new ichnotaxon, Aracoaraichnium leonardii igen. nov. isp. nov., with a discussion of preservational features and paleoecological aspects. This morphotype can be differentiated from Brasilichnium Leonardi, 1981 by digit morphology, with digits III and IV being larger and sub-equal in size. The tracks are mesaxonic, unlike Brasilichnium, which is ectaxonic, and the stride is proportionally smaller, suggesting a trackmaker with shorter limbs in relation to body length. Another characteristic that reinforces the new ichnotaxon is the larger size of the footprints of Aracoaraichnium igen. nov. Footprints representing intermediate ontogenetic stages between Brasilichnium and the larger morphotype are not observed, suggesting that the two track types were made by different taxa. Compared with others tetrapod ichnotaxa, the new ichnotaxon is characterized by differences in the number and morphology of the digits, track morphology, the degree of heteropody, and locomotor parameters. Tracks with good preservation quality were likely originally produced in the humid subsurface, below the surficial dry sand layer. Tracks with smaller dimensions, and trackways with the presence or absence of the manus, may be due to variable degrees of impression into subsurface layers, and substrate heterogeneity. The Aracoaraichnium igen. nov. trackmakers probably inhabited areas near the desert, making occasional incursions into desert areas, while Brasilichnium trackmakers may have been mostly nocturnal residents of the desert environment.

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## 1. Introduction

During the Early Cretaceous (Neocomian), a large area in Brazil and adjacent South American countries was covered by the Botucatu Desert, an extensive paleoerg field (Milani et al., 2007). Several major groups of tetrapod animals lived in this environment, and records of their morphology and behavior are preserved as trace fossils in the sandstones of the Botucatu Formation (São Bento Group, Paraná Basin). Most ichnofossils from the Botucatu Formation were collected from quarries in and around Araraquara County (São Paulo State, Brazil), especially from the now-inactive São Bento quarry.

Trace fossils in the Botucatu Formation include theropod and ornithopod tracks, mammaliform footprints, insect and arachnid trails and burrows (Leonardi et al., 2007; Fernandes and Carvalho, 2007; Fernandes et al., 2011; Fernandes et al., 2014; Buck et al., 2017), and urolites (Fernandes et al., 2004). Although trace fossils are abundant, body fossils are rare in the Botucatu Formation, with the conifer logs found in the northern portion of Minas Gerais State being the only major example (Pires et al., 2011). Mammaliform trace fossils in the Botucatu Formation are of particular importance, because they may represent the only record of Mammaliamorpha from the Lower Cretaceous of Brazil.

Mammaliform tracks in the Botucatu Formation can be grouped into two distinct morphotypes. The first morphotype consists of smaller footprints, and was originally described by Leonardi (1981), who erected the ichnogenus Brasilichnium and ichnospecies B. elusivum Leonardi, 1981. Buck et al. (2017) later described a second ichnospecies,

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attributed to the same ichnogenus, based on similar footprints with a distinctly autopodial configuration in the trackways. The second morphotype is less well known. It consists of rare, larger mammaliform tracks, mentioned in passing by Leonardi and Oliveira (1990), Leonardi (1994), Leonardi and Carvalho (2002) and Leonardi et al. (2007). These trackways were informally described as having "an advanced gait with narrow gauge", and were preliminarily attributed to a tritylodontid trackmaker.

The larger mammaliform morphotype from the Botucatu Formation, which is not yet formally described, is similar in size and morphology to various other tetrapod footprints with synapsid affinities in the global ichnological record. For example, the ichnofamily Chelichnopodidae Lockley, 2011 encompasses two well-established ichnotaxa with very similar characteristics: Chelichnus, and Brasilichnium. Despite some analogous features, the larger mammaliform morphotype from the Botucatu Formation exhibits several differences, and represent a new ichnotaxon. The aim of this study is to describe and classify this larger mammaliform trackways, and to assess its preservational characteristics and paleoecological implications.

## 2. Materials and methods

### 2.1. Geologic context

The Botucatu Formation is part of an extensive continental paleoerg succession, comprising aeolian lithofacies. The strata are composed of fine- to medium-grained, well-sorted quartzose sandstones, with medium- to large-scale cross-bedding (Scherer and Goldberg, 2007). This unit is part of the Paraná Basin Gondwana III Supersequence, and is estimated to extend over an area of 1.5 million $km^2$ (Milani et al., 2007), covering the Brazilian states of Mato Grosso, Mato Grosso do Sul, Goiás, Minas Gerais, São Paulo, and Rio Grande do Sul. The erg deposits also extend into other South American countries (Uruguay and Paraguay), and are correlative with deposits in Africa (Namibia).

The age of the Botucatu Formation is still the subject of debate. During rifting of the supercontinent Gondwana, basaltic lava flows advanced over the Botucatu Desert, resulting in emplacement of the Serra Geral Formation. These basalts, which conformably overlie the sandstones of the Botucatu Formation (Scherer, 2002), were dated to 132 Ma using $^{40}Ar/^{39}Ar$ chronostratigraphy (Renne et al., 1992), and this can be confidently accepted as an upper age for the Botucatu Formation (Fig. 1). However, some uncertainty remains regarding the onset of Botucatu deposition. Here, we follow the interpretation of Scherer (2000), who argued that the desert sandstones
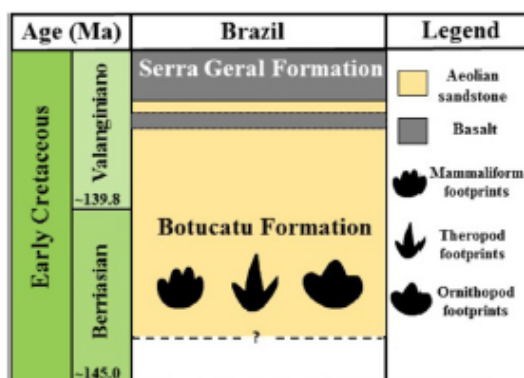
were deposited over a relatively short period of time (i.e., within hundreds of thousands of years), which would constrain the deposition of the Botucatu Formation exclusively to the Early Cretaceous.

The paleoenvironment of the Botucatu Desert, like many modern sandy deserts, consisted of an extensive field of medium to large aeolian dunes, interspersed with interdune valleys (Talbot, 1985; Mountney, 2004). The climate during deposition of the Botucatu Formation was probably hyper-arid, at least in the southern part of Brazil (Nowatzki and Kern, 2000; Scherer, 2000, 2002). In the interior of São Paulo State, several non-biogenic sedimentary structures (i.e., raindrop impressions, adhesion ripples, and desiccation cracks) indicate the presence of water during sedimentation, though carbonate lenses have not yet been identified (Buck et al., 2017).

### 2.2. Sampled material and ichnological methods

All tracks and trackways analyzed in this study were collected from the São Bento quarry, Araraquara County (21°49′03.4″ S and 48°04′22.9″ W), São Paulo State, Brazil (Fig. 2). The studied slabs are housed at the Laboratório de Paleoecologia e Paleoicnologia (LPP), of the Universidade Federal de São Carlos (UFSCar), and in the Coleção de Paleovertebrados, of the Museu Nacional (UFRJ). The São Bento quarry consists of a 20 m high and 100 m long paleodune deposit, displaying foresets with an average dip of 29° in a SSW direction. This quarry is currently inactive, but in past decades, sandstone was extracted for commercial purposes. This long-term exploitation allowed for the recovery of a large number of slabs containing ichnofossils.

Tracks and trackways were described following the conventions proposed by Leonardi (1987). The following parameters were measured for both the manus and pes: length and width of the tracks; length and width of the digits; rotation of the track in relation to the midline; stride length; oblique pace; pace angulation; external trackway width; and distance between pes and manus. We compare measurements from the new ichnotaxon described here to the measured parameters of Brasilichnium elusivum from Leonardi (1981) and Fernandes and Carvalho (2008). Freely available InStat3 software was used to apply the Student's $t$-test to these comparisons.

## 3. Results

### 3.1. Systematic paleoichnology

#### 3.1.1. Ichnofamily
Chelichnopodidae Lockley, 2011.

#### 3.1.2. Diagnosis
Lockley, 2011. Tetrapod trackways with mammal-like (synapsid) characteristics: complete manus and pes impressions rounded to transversely oval with manus slightly or significantly smaller than pes, showing the general pattern of a quadruped. Manus and pes with transversely oval heel pad and up to five short digit traces, but often with only three or four impressed. Trackway width, pace angulation, and pes and manus rotation variable.

#### 3.1.3. Included ichnogenera
Chelichnus Jardine, 1850 and Brasilichnium Leonardi, 1981.

#### 3.1.4. Ichnogenus
Aracoaraichnium igen. nov.

#### 3.1.5. Referred material
Holotype: LPP-IC-0015. Paratypes: LPP-IC-0016, LPP-IC-0017, LPP-IC-0018, LPP-IC-0019, LPP-IC-0020, LPP-IC-0021, LPP-IC-0022, LPP-IC-0023, LPP-IC-0024, LPP-IC-0025, LPP-IC-0026, LPP-IC-0027, MN4815-V.



Fig. 1. Stratigraphic framework of the Botucatu Formation in Brazil, showing tetrapod footprint occurrences.
Adapted from Francischini et al., 2015.

Fig. 2. Map of the Paraná Basin and surrounding areas in South America. Highlighted region shows Araraquara County, in São Paulo State, Brazil. Adapted from Fernandes et al., 2004.

### 3.1.6. Locality

São Bento quarry, Araraquara County, São Paulo State, Brazil. Geographic coordinates: 21°49′03.4″ S, 48°04′22.9″ W.

### 3.1.7. Horizon

Paraná Basin, São Bento Group, Botucatu Formation.

### 3.1.8. Repository

Trace fossil collection of the Laboratório de Paleoecologia e Paleoicnologia (LPP), Departamento de Ecologia e Biologia Evolutiva (DEBE), Universidade Federal de São Carlos (UFSCar), São Carlos municipality, São Paulo State, Brazil; and Coleção de Paleovertebrados, Museu Nacional (MN), Universidade Federal do Rio de Janeiro (UFRJ), Rio de Janeiro municipality, Rio de Janeiro State, Brazil.

### 3.1.9. Etymology

The generic name Aracoara refers to the name of Araraquara County (where the specimens were discovered) in the indigenous language, Tupi-Guarani, and means "place where the daylight lives". Ichnium means "little trace".

### 3.1.10. Diagnosis

Trackway of a quadruped characterized by walking locomotion. Narrow trackway with the interior margin of the pes very close to the midline. Footprints are semi-plantigrade, in a mesaxonic condition, with digits III and IV more anteriorly registered. Manus are significantly smaller than the pes. When manus are imprinted, they always register anterior to the pes in the locomotion cycle. Both manus and pes are tetradactyl, with short digits. The proximal traces of the digits are wide, but taper distally, ending in nail or claw traces. Digit III is the longest, followed by digit IV, which is sub-equal in length. Digits II and V are smaller, but also sub-equal to each other in length. Footprints are wider than they are long, with an oval heel pad, sometimes with the anteroposterior axis directed slightly inward. When the anteroposterior axis is directed inwards, it occurs for both the manus and pes in a similar degree. Tail impressions/drag are always absent.

### 3.1.11. Ichnospecies

Aracoaraichnium leonardii isp. nov. Figs. 3, 4, 5, 6, and 7.

### 3.1.12. Referred material, locality, horizon, repository and diagnosis

As for ichnogenus.

### 3.1.13. Etymology

The specific name refers to one of the most prominent researchers of Botucatu Formation trace fossils, Giuseppe Leonardi.

### 3.1.14. Description

A total of 14 sandstone slabs with recognizable ichnofossils were analyzed. Descriptive parameters for Aracoaraichnium leonardii igen. nov. isp. nov. are summarized in Table 1, and the holotype and paratypes are illustrated in Figs. 3, 4, 5, 6 and 7. The holotype, and specimens LPP-IC-0016, LPP-IC-0019, LPP-IC-0020, LPP-IC-0022, LPP-IC-0023, LPP-IC-0024, LPP-IC-0025, LPP-IC-0026, and LPP-IC-0027 are preserved in concave epirelief, some with sediment still inside the footprints. Specimens LPP-IC-0017, LPP-IC-0018, LPP-IC-0021, and MN4815-V, are instead preserved in convex hyporelief. Unfortunately, some slabs have only one or two isolated footprints. In these cases, it was not possible to measure locomotor parameters.

All of the trackways used in the description indicate typical walking locomotion (symmetric locomotion; Abourachid, 2003), and can be classified, following Seilacher (1953), as repichnia. The direction of movement in all trackways is interpreted as ascending an inclined paleodune, since sand arcs can only be seen in the posterior portion of the footprints.

Both pes and manus tracks have an elongated transverse axis, with a rounded posterior portion (oval heel pad). The footprints are defined as semi-plantigrade, as part of the palm can be observed in addition to the entire phalangeal portion of the foot. In the holotype specimen (LPP-IC-0015), the mean pes width and length are $6.1 \pm 0.4$ cm and $5 \pm 0.3$ cm respectively. The mean manus width and length are $2.2 \pm 0.7$ cm and $2 \pm 0.5$ cm respectively. Specimens LPP-IC-0019, LPP-IC-0020, LPP-IC-0022, and LPP-IC-0024 show values below this average. The difference can be interpreted as a result of the preservational characteristics discussed below.

In some specimens, it is possible to observe rotation of the anteroposterior axis towards the interior of the trackway, with an average angle of 12.9° for the pes. The manus and pes sets are rotated in a similar degree, suggesting a rotational parallelism between the two axes. For the hands it was possible to measure only a single angle

Fig. 3. *Aracoaraichnium leonardii* igen. nov. isp. nov. specimens. A. holotype LPP-IC-0015; B. first and second pes tracks of LPP-IC-0015; C. LPP-IC-0016; D. LPP-IC-0017; E. first pes track of LPP-IC-0017; F. LPP-IC-0018; G. fourth pes track of LPP-IC-0018. All scales are in centimeters. Direction of movement is towards the top of the photograph.

(11.8°), from the holotype specimen (LPP-IC-0015), because manus impressions are not always preserved, and those that are preserved often do not have a well-defined outline.

The average overall distance between manus and pes impressions (DMP) measured from the internal autopodium midpoint is 5.9 cm; the average distance between the anterior extremity of the pes and the posterior extremity of the manus (IDMP) is 2.7 cm. No overlap was observed between the anterior and posterior autopodia. It should be noted that IDMP was not measured in specimen LPP-IC-0021 due to the unclear contours of the manus and pes impressions, which are obscured by collapsed sediment. In specimen LPP-IC-0023, the contours of the impressions were clear, but the third set of autopodia showed no measureable internal distance; the posterior portion of the manus impression is aligned with the anterior portion of the pes impression, with no overlap. In specimens LPP-IC-0015, LPP-IC-0023, and MN4815-V the position of the manus varies along the trackway, being sometimes aligned with the anteroposterior axis of the pes, and sometimes displaced outwards.

The average trackway width is 12.7 cm for the pes and 13 cm for the manus. We consider *Aracoaraichnium leonardii* igen. nov. isp. nov. trackway to be narrow, because the inner margins of the pes impressions are either aligned with or very close to the midline of the

trackway. The width of the pes impressions represents about 38% of the total track width.

The mean values of the pes stride and oblique pace are 19.1 cm and 11.7 cm, respectively. Measurements for the manus are 18.7 cm and 13.8 cm, respectively. The mean values of the pes stride ranged from 15 cm (LPP-IC-0020) to 23.4 ± 0.4 cm (LPP-IC-0017), while the oblique pace ranged from 9 ± 1.3 cm (LPP-IC-0020) to 15 ± 1.6 cm (LPP-IC-0025). The mean values of the pace angle are 112.4 ± 12.7° for the pes and 88.8 ± 10° for the manus, which agree well with the measurements given by Leonardi et al. (2007). The lowest recorded mean value of pace angulation for the pes is 93 ± 1.9° (LPP-IC-0025), while the highest value is 131.1° ± 9.1° (LPP-IC-0024). The variation in these parameters may be related to particular aspects of locomotion on inclined planes; depending on the angle at which the animal climbed the paleodune, more or less effort would need to be exerted, causing observable variations in the trackway.

The length and width of the digits could only be measured in the holotype and a few other specimens (LPP-IC-0017, LPP-IC-0020, LPP-IC-0024, LPP-IC-0025, LPP-IC-0027, and MN4815-V). The pes and/or manus impressions in these specimens are especially well preserved, with digit contours reasonably well defined. The mean lengths and widths for each pes digit are: 1.1 cm and 1.3 cm respectively for digit
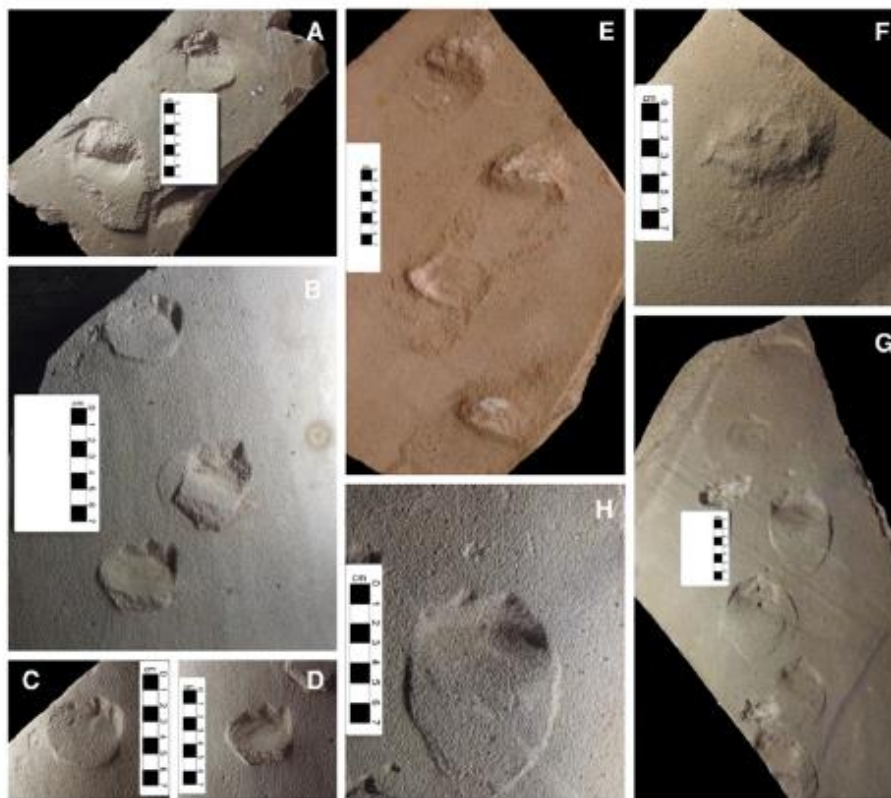
Fig. 4. *Aracoaraichnium leonardii* igen. nov. isp. nov. specimens. A. LPP-IC-0019; B. LPP-IC-0020; C–D. third and first pes tracks of LPP-IC-0020 respectively; E. LPP-IC-0021; F. fourth pes track of LPP-IC-0021; G. LPP-IC-0022; H. fourth pes track of LPP-IC-0022. All scales are in centimeters. Direction of movement is towards the top of the photograph.

II; 1.8 cm and 1.6 cm respectively for digit III; 1.5 cm and 1.4 cm respectively for digit IV; and 1 cm and 1.3 cm respectively for digit V. The manus digits were measured on the first impression in the holotype specimen, and have lengths and widths respectively of 0.6 cm and 0.6 cm for digit II; 1.1 cm and 1 cm for digit III; 0.6 cm and 0.5 cm for digit IV; and 0.5 cm and 0.6 cm for digit V. In specimen LPP-IC-0025, only the manus digits III and IV could be measured in the second and fourth impressions. The average length of manus digit IV on this track (1.9 cm) is higher than the average for manus digit III (1.7 cm), and differs from the holotype. This unusual condition (elongation and tapering of digit impressions) can possibly be explained by autopodium drag (Fig. 5F–G).

Digit III is the largest digit in both manus and pes impressions, followed by digit IV, with the two being sub-equal in size. The side digits (II and V) are smaller, and also sub-equal in size to one another. It should be noted that the digits are directed forward, aligned with the anteroposterior axis of the footprints, and can thus be characterized as mesaxonic. In some cases (e.g., specimen LPP-IC-0017, track 1) the digits are spread further apart, probably in response to a situation that required more support during locomotion. Curvature of the digits can be observed in some specimens, especially LPP-IC-0027.

Even in poorly preserved footprints, digit III shows the longest trace, followed by digit IV, in both manus and pes impressions. Remarkably, in many cases only the central digit traces (III and IV) are observable (specimens LPP-IC-0022, LPP-IC-0024 and LPP-IC-0025). This likely because, in addition to being the largest digits, these digits represent the point where the greatest drag force is exerted during locomotion.

In all footprints, both manus and pes impressions showed a maximum of four digits. The good state of preservation of some tracks suggests that the four imprinted digits represent the complete set. Specimens LPP-IC-0017, LPP-IC-0027, and MN4815-V can be referred to the pes, while the first impression (on the right side) of holotype LPP-IC-0015 can be distinguished as the manus. Another line of argument in support of the presence of four imprintable digits is the spatial arrangement of the digits themselves; external digits II and V coincide with the outer limits of the tracks along the transverse axis.

## 4. Discussion

### 4.1. Ichnotaxonomy and trackmaker affinity

Prior to this study, only two ichnotaxa from the Botucatu Formation had been formally described. Leonardi (1981) nominated the ichnogenus *Brasilichnium*, and ichnospecies *Brasilichnium elusivum*. He originally reported these small tracks as pentadactyl, with the trackways displaying cursorial locomotion, and attributed the tracks to a probable mammaliform producer. Fernandes and Carvalho (2008) later reviewed this ichnospecies, recognizing the tetradactyl of the pes and manus, and drawing some inferences about the presence or absence of anterior autopodial marks. More recently, Buck et al. (2017) described a second ichnospecies from the Botucatu Formation, *Brasilichnium saltatorium*. *B. saltatorium* also consists of small tetradactyl footprints, very similar to those of *Brasilichnium elusivum*, however, they display asymmetrical locomotion in distinct phases.

**Fig. 5.** *Aracoaraichnium leonardii* igen. nov. isp. nov. specimens. A. LPP-IC-0023; B. fourth pes/manus set of LPP-IC-0023; C. LPP-IC-0024; D. sixth pes track of LPP-IC-0024; E. LPP-IC-0025; F–G. fourth and second manus tracks of LPP-IC-0025 respectively. All scales are in centimeters. Direction of movement is towards the top of the photograph.

Buck et al. (2017) also attributed these tracks to a mammaliform producer.

Despite the amount of time that has passed since the first ichnotaxonomic descriptions from the Botucatu Formation were published, the larger mammaliform tracks from this unit have not been adequately classified. Leonardi (1980) mentioned this larger morphotype in a preliminary review of the Araraquara region's ichnofauna. Subsequent works have also mentioned these tracks, though without a complete ichnotaxonomic description (see Leonardi and Oliveira, 1990; Leonardi, 1994; Leonardi and Carvalho, 2002; and Leonardi et al., 2007). In these brief discussions, the trackways are described as narrow, with a pes angle of around 100° and a stride ranging from 15 to 50 cm. The footprints were described as semi-plantigrade and elliptical (with the transverse axis longer than the anteroposterior axis), with short digits. Characteristics such as the shape of the autopodia and the size of the digits in the present work agree well with these earlier studies. Fernandes and Corrêa (2007) mention that this morphotype is relatively rare, and the small number of samples collected by the authors over decades of work support this understanding.

Here, we identify the ichnogenus *Aracoaraichnium* igen. nov. as belonging to the Chelichnopodidae Lockley, 2011 ichnofamily. The new ichnogenus presents sufficient characteristics for such a designation, for example: heteropody, with the manus substantially smaller than

the pes; elliptical autopodium impressions, with an elongated transverse axis; quadupedal locomotion; short digits; and four distinct imprinted digits. *Aracoaraichnium* igen. nov. shares several similarities with two other ichnotaxa within Chelichnopodidae: *Chelichnus* and *Brasilichnium*. Nevertheless, there are sufficient morphological differences to justify designating it as a distinct ichnogenus.

The differences between *Aracoaraichnium* igen. nov. and *Chelichnus* are easily observed and defined. In the ichnogenus *Chelichnus*, the manus and pes are pentadactyl when preservation is complete. The degree of heteropody is also significantly lower in *Chelichnus* (i.e., the manus is only slightly smaller than pes; see McKeever and Haubold, 1996). *Chelichnus duncani* and *Chelichnus gigas* are the ichnospecies that most resemble *Aracoaraichnium leonardii* igen. nov. isp. nov. in their pes dimensions, however, the manus and pes of these ichnospecies show similar proportions, and both show pace angles of <90° (McKeever and Haubold, 1996; Krapovickas et al., 2014).

A long interval of time separates the occurrence of *Chelichnus* from that of *Aracoaraichnium* igen. nov. Until now, *Chelichnus* had only been identified in Permian aeolian deposits, in Europe (Germany; Scotland), North America (western U.S.A.), and South America (western Argentina). *Aracoaraichnium* igen. nov. has now been identified in the Neocomian-age aeolian deposits of the Botucatu Formation. The large

Fig. 6. *Aracoaraichnium leonardii* igen. nov. isp. nov. specimens. A. LPP-IC-0026; B. seventh manus track of LPP-IC-0026; C. MN4815-V; D. first and third pes tracks of MN4815-V. All scales are in centimeters. Direction of movement is towards the top of the photograph.

age gap in the occurrence of these traces suggests that the tracks were produced by different organisms.

Unlike *Chelichnus*, *Aracoaraichnium* igen. nov. and *Brasilichnium* occur in strata of the same age, and are even found in the same geologic unit. Furthermore, tracks of both ichnotaxa occur at the same locality (the São Bento quarry, Araraquara), in the same horizons. Footprints of both ichnotaxa are similar in some aspects: they have the same elliptical shape, with the transverse axis longer than the anteroposterior axis, and they share a similar length/width ratio. Comparing the length/width ratio of *Aracoaraichnium* igen. nov. (0.78 ± 0.09) to that
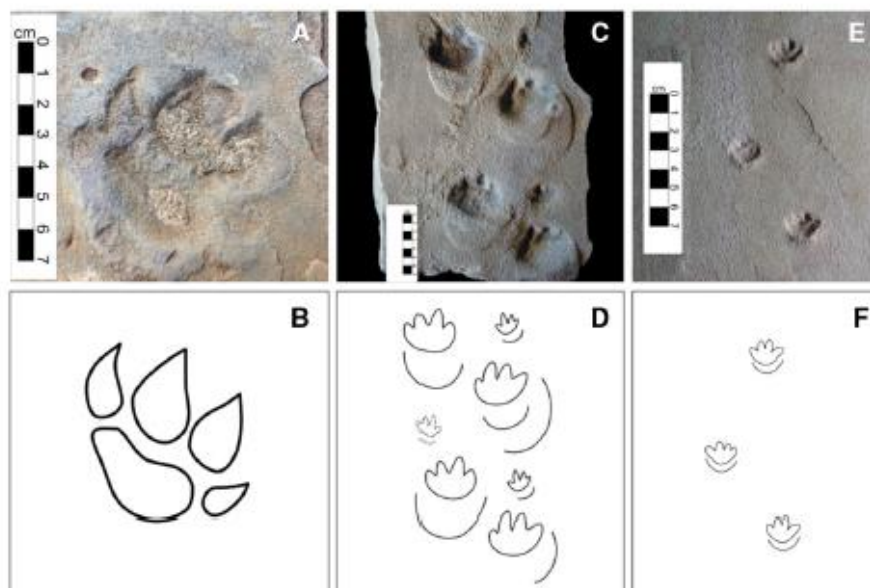


Fig. 7. A. LPP-IC-0027 (on the left side of the footprint, the feature that resembles a digit is interpreted as a broken sediment surface); B. schematic reconstruction from A; C. LPP-IC-0015 trackway; D. schematic reconstruction from C; E. *Brasilichnium elusivum* trackway; F. schematic reconstruction from E. Note the morphological differences between B–D and F. In panels B and D the footprints are mesaxonic, while in panel F the footprints are ectaxonic. All scales are in centimeters. All schematic reconstructions have the same scale as their respective photographs. Direction of movement is towards the top of the photograph.

**Table 1**
Parameters measured for *Aracoaraichnium leonardii* igen. nov. isp. nov.

| | Specimens | LPP-IC-0015 | LPP-IC-0016 | LPP-IC-0017 | LPP-IC-0018 | LPP-IC-0019 | LPP-IC-0020 | LPP-IC-0021 |
|---|---|---|---|---|---|---|---|---|
| Pes | Width (cm) | 6.1 ± 0.4 | 6.5 | 6.8 ± 0.5 | 6.7 ± 0.2 | 5 ± 1.6 | 4.5 ± 0.4 | 6.7 ± 0.2 |
| | Length (cm) | 5 ± 0.3 | 5 | 4.8 ± 0.1 | 5.7 ± 0.2 | 3.1 ± 1.2 | 3.6 ± 0.3 | 4.9 ± 0.4 |
| | L/W ratio | 0.86 ± 0.03 | 0.76 | 0.7 ± 0.04 | 0.85 ± 0.03 | 0.62 ± 0.03 | 0.79 ± 0.02 | 0.73 ± 0.04 |
| | Oblique pace (cm) | 10.7 ± 1.6 | – | 14.3 ± 0.4 | 12.6 ± 0.5 | 12.4 | 9 ± 1.3 | 11.5 ± 0.7 |
| | Stride length (cm) | 16.8 ± 0.7 | – | 23.4 ± 0.4 | 19.8 ± 0.6 | – | 15 | 19.7 ± 0.8 |
| | External width (cm) | 13.2 ± 0.4 | – | 14.8 ± 0.3 | 14.2 ± 0.4 | 13.4 | 9.4 | 12.5 ± 0.4 |
| | Pace angle (°) | 99.1 ± 2 | – | 108.1 ± 4.5 | 104.4 ± 4.3 | – | 112.7 | 121.2 ± 7.3 |
| | Rotation (°) | 16.7 ± 4.9 | – | – | – | – | – | – |
| Manus | Width (cm) | 2.2 ± 0.7 | – | – | – | – | – | 3.3 ± 0.4 |
| | Length (cm) | 2 ± 0.5 | – | – | – | – | – | 2.8 ± 0.3 |
| | L/W ratio | 0.87 ± 0.04 | – | – | – | – | – | 0.85 ± 0.02 |
| | Oblique pace (cm) | 13.1 ± 0.4 | – | – | – | – | – | 12.9 ± 0.3 |
| | Stride length (cm) | 17.2 ± 1 | – | – | – | – | – | 20.4 ± 1.1 |
| | External width (cm) | 12.3 ± 0.5 | – | – | – | – | – | 11.1 |
| | Pace angle (°) | 80.9 ± 5.7 | – | – | – | – | – | 103.6 ± 6.1 |
| | Rotation (°) | 11.8 | – | – | – | – | – | – |
| | DMP (cm) | 7 ± 0.9 | – | – | – | – | – | 4.3 ± 0.1 |
| | IDMP (cm) | 3.4 ± 0.9 | – | – | – | – | – | – |
| 1.0 | | | | | | | | |
| | Specimens | LPP-IC-0022 | LPP-IC-0023 | LPP-IC-0024 | LPP-IC-0025 | LPP-IC-0026 | LPP-IC-0027 | MN4815-V |
| Pes | Width (cm) | 5.8 ± 0.6 | 6.2 ± 0.2 | 4.8 ± 0.8 | 7.8 ± 0.9 | 6.7 ± 0.4 | 6.1 | 6.1 ± 0.1 |
| | Length (cm) | 4.5 ± 0.4 | 4.3 ± 0.05 | 4.3 ± 0.6 | 6.1 ± 0.6 | 5 ± 0.3 | 5.7 | 5.3 ± 0.1 |
| | L/W ratio | 0.77 ± 0.09 | 0.68 ± 0.01 | 0.9 ± 0.03 | 0.78 ± 0.04 | 0.74 ± 0.03 | 0.93 | 0.86 ± 0.02 |
| | Oblique pace (cm) | 10 ± 0.9 | 10.4 ± 0.8 | 10.7 ± 0.8 | 15 ± 1.6 | 12.9 ± 0.8 | – | 11.1 ± 1.2 |
| | Stride length (cm) | 18.1 ± 0.7 | 18.6 ± 0.4 | 19.4 ± 0.6 | 21 ± 0.8 | 21.8 ± 0.6 | – | 17 ± 0.6 |
| | External width (cm) | 10.8 ± 0.4 | 11 ± 0.7 | 9.3 ± 0.7 | 17.2 ± 6.2 | 13.5 ± 0.3 | – | 13.1 ± 0.1 |
| | Pace angle (°) | 126.6 ± 5.1 | 126.9 ± 6.6 | 131.1 ± 9.1 | 93 ± 1.9 | 112.7 ± 9.3 | – | 100.5 ± 0.2 |
| | Rotation (°) | – | 9.6 ± 1.4 | – | – | – | – | 12.4 ± 2.7 |
| Manus | Width (cm) | – | 3.9 ± 0.41 | – | 2.4 ± 0.9 | 3 ± 0.3 | – | 2.6 ± 1 |
| | Length (cm) | – | 3 ± 0.8 | – | 2.6 ± 1.1 | 2.8 ± 0.6 | – | 1.9 ± 0.3 |
| | L/W ratio | – | 0.79 ± 0.25 | – | 1.07 ± 0.06 | 0.92 ± 0.22 | – | 0.78 ± 0.22 |
| | Oblique pace (cm) | – | 12.5 ± 1 | – | 16.2 ± 1.5 | 14.7 ± 1.5 | – | 13.6 ± 0.4 |
| | Stride length (cm) | – | 18.5 ± 1 | – | 20.6 ± 1.2 | 22.2 ± 1.5 | – | 17.1 ± 0.7 |
| | External width (cm) | – | 12.7 ± 1.3 | – | 14.6 ± 5.4 | 14.7 ± 0.1 | – | 12.7 ± 0.4 |
| | Pace angle (°) | – | 96.7 ± 6.6 | – | 82.2 ± 4.9 | 90.8 ± 6.9 | – | 78.4 ± 2.1 |
| | Rotation (°) | – | – | – | – | – | – | – |
| | DMP (cm) | – | 4.2 ± 0.4 | – | 7.1 ± 0.2 | 5 ± 0.5 | – | 6.9 ± 0.9 |
| | IDMP (cm) | – | 1.1 ± 0.3 | – | 3.1 ± 0.4 | 1.8 ± 0.6 | – | 3.3 ± 1 |

Mean values are followed by standard deviation (in cm). Pace angle and rotation are in degrees. DMP: distance between manus and pes impressions; IDMP: distance between the anterior extremity of the pes and the posterior extremity of the manus.

of *Brasilichnium* (0.72 ± 0.1; Leonardi, 1981; Fernandes and Carvalho, 2008) yields a low P value of 0.07, which may not meet the threshold for significance. This index gives a general idea of the shape of the footprints, however, it must be noted that footprints dimensions can be affected by the characteristics of the substrate (Brand, 1996), which can introduce variations that do not reflect the real morphology of the track producers' autopodia.

Another feature shared between these two ichnotaxa is the presence of four digits on each autopodium. Because fully-preserved pes and manus imprints, presenting only four digits, exist for *Aracoaraichnium* igen. nov., the tetradactyly of the trackmaker can be verified. Fernandes and Carvalho (2008) suggested that if the producer of *Brasilichnium* had five digits per autopodium, digit I would have to have been in a higher position, where it would not mark the substrate during locomotion. This may have also been the case for the producer of *Aracoaraichnium* igen. nov.

Despite the generally similar shape of the footprints and the presence of four digits, certain diagnostic characteristics suggest that a different ichnotaxonomic classification is warranted (Fig. 7B, D, F). The footprints referred to *Brasilichnium* are ectaxonic, with digits IV and V more impressed and important during locomotion. In *Brasilichnium*, digit V shows a more prominent hypex relative to the other digits, with slight abduction (Leonardi, 1981; Fernandes and Carvalho, 2008). In contrast, *Aracoaraichnium* igen. nov. prints show that digits III and IV are most prominent, which characterizes the prints as mesaxonic. In *Aracoaraichnium* igen. nov., digit III is the longest, followed by digit IV, while digits II and V are substantially shorter. None of the

*Aracoaraichnium* igen. nov. tracks analyzed showed abduction of digit V, though the digits are spread out slightly in footprint 1 of specimen LPP-IC-0017. In addition to these differences, the digits of *Aracoaraichnium* igen. nov. are sometimes curved, as can be seen clearly in specimen LPP-IC-0027. This is not observed in *Brasilichnium* trackways. If *Brasilichnium* and *Aracoaraichnium* igen. nov. trackways were made by the same taxon, we would have to postulate a ontogenetic change in digit morphology, which in the absence of intermediate forms would be highly speculative. Therefore, we interpret the two track types as morphologically and ichnotaxonomically distinct.

Differences in locomotion between *Aracoaraichnium* igen. nov. and *Brasilichnium* can be inferred from their footprint length/stride ratios. The *Aracoaraichnium* igen. nov. producer had a proportionately shorter stride than the *Brasilichnium* trackmaker, with a mean footprint length/stride ratio of 0.25 ± 0.03 compared to a mean of 0.12 ± 0.02 for *Brasilichnium*. This difference is statistically significant at the $P < 0.05$ level. Krapovickas et al. (2014) obtained a similar result when comparing the same ratio in *C. duncani* (0.18; 0.25) and *C. gigas* (0.38), and used this result to infer anatomical differences between the trackmakers. Following the same line of reasoning, we propose that the *Aracoaraichnium* igen. nov. producer likely had shorter limbs in relation to its trunk length than the *Brasilichnium* producer. This shorter stride may also be reflected in the slightly smaller pace angle values obtained from *Aracoaraichnium* igen. nov.

The difference in size between *Aracoaraichnium* igen. nov. and *Brasilichnium* footprints also supports the classification into two distinct ichnotaxa adopted here. To date, no footprints with dimensions

intermediate between *Aracoaraichnium* igen. nov. and *Brasilichnium* have been found in the geologic unit in which both ichnotaxa co-occur. While one could argue that this is a result of insufficient sampling, hundreds of slabs containing ichnofossils have been collected from the São Bento quarry over a period of >10 years. Also, it is worth noting that the smallest footprints referred to *Aracoaraichnium* igen. nov. are still considerably larger than typical *Brasilichnium* footprints. Thus, the existence of two distinct track producers, belonging to two different species, is a more likely explanation for the two size classes than a single producer at two different ontogenetic stages.

Kubo and Benton (2009), comparing living and Permo-Triassic tetrapod tracks, proposed that limb posture is an important factor in determining the pace angle of trackways. The data collected by these authors indicate that extant mammals and birds (both of which display erect posture) have mean pace angles of 151.5° and 155.5°, respectively. In contrast, animals with a sprawling posture, such as lizards, have an average pace angle of 110°. The mean pace angle of *Aracoaraichnium* igen. nov. is 112.4°, suggesting a trackmaker with a sprawling posture. However, the maximum pace angle measured is 140.1° (for specimen LPP-IC-0024), and the mean values obtained from some specimens (126.6° for specimen LPP-IC-0022; 126.9° for specimen LPP-IC-23; 131.1° for specimen LPP-IC-0024) seems to indicate that this is not the case. The average value for *Brasilichnium elusivum* is 134.3°, based on the holotype specimen (Leonardi, 1981) and the tracks analyzed by Fernandes and Carvalho (2008). The minimum and maximum values of the mean pace angle measured for *Brasilichnium elusivum* are 105° and 159°, respectively. This large range of variation in pace angle observed in both ichnotaxa may be related to the particularities of locomotion on inclined planes. Future taphonomic and neoichnological studies may address this question in more detail.

Animals with an upright posture (i.e., a low femoral abduction angle) typically produce tracks with higher pace angle values than animals with a sprawling posture (Kubo and Osaki, 2009). Based on the relationships established by Kubo and Osaki (2009), tetrapods with pace angle values of 120° are estimated to have had femoral abduction angles around 13°. Taking this into account, it is likely that the *Aracoaraichnium leonardii* igen. nov. isp. nov. and *Brasilichnium* trackmakers had a semi-erect to erect posture, with low femoral abduction angles. This interpretation is in agreement with the inferred locomotor characteristics of the *Brasilichnium* trackmaker, which could use both walking and saltatorial gaits (Buck et al., 2017). A vertical position of the limbs relative to the body would be necessary during saltatorial locomotion.

Although *Aracoaraichnium* igen. nov. shares numerous similarities with *Chelichnus* and *Brasilichnium*, it is important to compare it with other quadrupedal tetrapod ichnotaxa. There are two Brazilian occurrences described by Silva et al. (2008a, 2008b) from the Upper Triassic Santa Maria Formation (Rio Grande do Sul State). Silva et al. (2008a) described the ichnospecies *Rhynchosauroides retroversipes* and Silva et al. (2008b) erected the ichnotaxon *Dicynodontipus protherioides*. Both ichnotaxa show autopodia with five digits, although the inferred producers are phylogenetically very distinct from one another, and the impressions are much smaller than *Aracoaraichnium* igen. nov. These ichnotaxa also display tail drag marks, which are never observed in *Aracoaraichnium* igen. nov. These characteristics are sufficient to clearly differentiate *Aracoaraichnium* igen. nov.

A comparison with ichnotaxa from other countries, which have not yet been identified in Brazil, serves to highlight the distinct characteristics of *Aracoaraichnium* igen. nov. *Aracoaraichnium* igen. nov. can generally be distinguished by the number of digits, though there are some cases where this is not a sufficient criterion. However, in these cases, autopodium and digit morphology are still sufficiently different to require a new classification. Nondinosauromorph archosauriform trackways, such as *Brachychirotherium*, *Chirotherium*, *Isochirotherium*, *Protochirotherium*, *Sphingopus*, and *Synaptichnium* are pentadactyl, and have pedal tracks with the fifth digit located posterolaterally to the first four digits (Demathieu and Demathieu, 2004; Kubo and Kubo,

2013). Nesbitt (2011) proposed that a hooked metatarsal V is an archosauriform, nondinosauromorph characteristic, indicating that the *Aracoaraichnium* igen. nov. producer did not belong to this group. Although there are some Pseudosuchia lineages that lost this characteristic, these groups were extinct by the Triassic (Nesbitt, 2011; Toljagić and Butler, 2013), and the elongated transverse axis of the footprints described here suggests that the *Aracoaraichnium* igen. nov. trackmaker had mammaliform affinities (de Valais, 2009).

Jurassic and Cretaceous ichnotaxa such as *Antipus*, *Batrachopus*, *Crocodylopodus*, and *Hatcherichnus* have crocodylomorph affinities. The *Batrachopus* and *Antipus* trackmakers had functionally tetradactyl feet, according to Lockley and Meyer (2004). Despite the similarity in the number of digits, in *Batrachopus* pes digits II and IV are sub-equal in size, and slightly smaller than digit III, while in *Aracoaraichnium* igen. nov. pes digits III and IV are sub-equal in size, and digit III is considerably larger. *Antipus* digits are also distinct, being much longer and slenderer than those of *Aracoaraichnium* igen. nov. Other distinct features of these ichnotaxa, which are not observed in *Aracoaraichnium* igen. nov., include: the presence of five digits in the manus; anteroposterior axis rotation relative to the outside of the trackway; and footprints that are longer than they are wide. *Crocodylopodus* is easily distinguishable because it has a pentadactyl pes. *Hatcherichnus* displays tetradactyl tracks, according to Foster and Lockley (1997), however, the trackmaker was clearly digitigrade, with digit III being the longest, followed by digit II. In *Hatcherichnus*, manus impressions are trydactyl, possibly due to taphonomic effects (Avanzini et al., 2010).

Comparisons can also be made to ichnotaxa attributed to Synapsida, which have a closer phylogenetic affinity to the inferred trackmaker of *Aracoaraichnium* igen. nov. While to date these ichnotaxa have not been found in Brazilian territory, they have been observed in both Triassic and Jurassic deposits in Argentina. Domnanovich and Marsciano (2006) re-evaluated a set of Argentinian Triassic ichnotaxa produced by trackmakers with nonmammalian therapsids affinity, including *Calibarichnus ayestarani*, *Palaciosichnus zettii*, *Gallegosichnus garridoi*, and *Stipanicichnus bonetti*. These ichnotaxa are characterized by marked homopody, a pes longer than it is wide, pentadactyl, and short digits that are similar in size. *Ameghinichnus* trackways in the Jurassic of Argentina display similar characteristics, with the exception that the footprints are wider than long (de Valais, 2009). *Dimetropus* (Romer and Price, 1940; Sacchi et al., 2014) and *Therapsipus* (Hunt et al., 1993; Lucas et al., 2003), two other ichnotaxa attributed to Synapsida, also display pentadactyly in both the manus and the pes. Xing et al. (2013) have also described mammal-like pentadactyl tracks from the Late Triassic Xujiahe Formation in China. These tracks are plantigrade, and the digit traces have blunt distal ends. All these characteristics are sufficient to differentiate these ichnotaxa from *Aracoaraichnium* igen. nov.



Fig. 8. *Aracoaraichnium leonardii* igen. nov. isp. nov. trackmaker reconstruction. Shows several inferred characteristics, such as relatively short limbs in relation to the trunk, pes and manus in the mesaxonic condition, and prominent digits III and IV (reconstruction by Aline M. Ghilardi).

Based on the autopodial morphology, gait, and locomotor characteristics of *Aracoaraichnium* igen. nov., we infer that the trackmaker belonged to the Mammaliamorpha. Its more specific affinities are uncertain, though it likely belonged to either the Tritylodontidae or a Mammaliaformes (Fig. 8).

### 4.2. Track preservation in the aeolian Botucatu Formation paleoenvironment

The nature of the substrate directly influences the formation and preservation of ichnological records. Certain characteristics of the substrate, such as its consistency and moisture content, can determine the preservation quality of the tracks produced. As Brand (1996) demonstrated through neoichnological experiments, as moisture in the sediment increases, the substrate becomes more cohesive, allowing for better preservation of footprints.

In dune deposits, where sand cohesion is usually very low, well-preserved footprints can be explained by the presence of moisture (Brand, 1996). Some of the tracks described in this work (LPP-IC-0015, LPP-IC-0017, MN4815-V), show autopodia with well-defined contours, and clearly delimited digits. Leonardi (1980) proposed that well-preserved footprints in aeolian deposits were likely produced at night and/or dawn, when the sand would be more cohesive due to the accumulation of dew. Another possibility is that the tracks were produced in a damp subsurface layer, as proposed by Fernandes (2005).

Mancuso et al. (2016) analyzed the preservation modes of Permian tetrapod tracks from aeolian deposits of the Los Reyunos Yacimiento Formation (Argentina), considering two main conditions for the substrate. In dry sand, footprints typically lacked precise definition, whereas in wet subsurface sand, digits impressions and claw drag traces were preserved. The interpretation that well-preserved footprints reflect the presence of interstitial water can be extended to the Botucatu Formation, which shares numerous similarities with the Los Reyunos Yacimiento Formation, and likely shows similar preservational modes.

Buck et al. (2017) concluded that precipitation events occurred in the Araraquara region (São Paulo State) during deposition of the Botucatu Formation. These events can be inferred from of the presence of non-biogenic sedimentary structures in the São Bento quarry, such as raindrop impressions, adhesion ripples, and desiccation cracks. Some of this meteoric water may have infiltrated into the sediment, raising the water table and facilitating the preservation of footprints with a high level of detail.

Subsurface footprint production may also explain other aspects of the observed taphonomy. The factors controlling the presence or absence of manus impressions in dune deposits is still poorly understood. Manus impressions are observed only in specimens LPP-IC-0015, LPP-IC-0021, LPP-IC-0023, LPP-IC-0025, LPP-IC-0026 and MN4815-V (all trackways progressing in an uphill direction). While progressing towards the top of a dune, the animal would have primarily used its hind limbs for support, while the anterior limbs would have played a subsidiary role (Fernandes, 2005). Thus, in thicker layers of sand, the hands may not have penetrated the substrate to the same degree as the feet, and may not have produced impressions in the deeper substrate layers. Another possibility, discussed by Lockley and Rice (1990) in relation to sauropod dinosaurs, is that manus tracks, due to their smaller surface area, exerted greater pressure on the substrate, making deeper imprints than pes tracks. If this were the case, in both interpretations we would expect manus and pes tracks to be recorded in different layers.

In some cases, the contours of individual footprints preserved within the trackways are poorly defined. Samples LPP-IC-0022 (Fig. 4G) and LPP-IC-0024 (Fig. 5C) clearly show these preservation failures, and the length and width of the autopodia show a high degree of variability. In specimen LPP-IC-0022, contours are difficult to discern from the fourth footprint forward, whereas in specimen LPP-IC-0024, the contours are unclear in footprints 2, 3 and 4. Such discontinuities can likely be explained by inhomogeneities in the substrate (Thulborn, 1990),

such as if the trace producer moved over an uneven layer of loose sand, or ripples in the sediment surface. In specimen LPP-IC-0020, a clear discontinuity can be observed in the proximal portion of the trackway.

Some autopodium prints are smaller, for example in specimens LPP-IC-0019 (Fig. 4A) and LPP-IC-0020 (Fig. 4B). While these prints could be interpreted to have been produced by smaller animals, in specimen LPP-IC-0019, the second footprint is substantially smaller than the first, indicating heterogeneity in the substrate. In specimen LPP-IC-0020, three successive footprints show smaller sizes compared to the other tracks described here, though they are similar in size to one another. This size disparity in specimen LPP-IC-0020 autopodia is likely due to the producer's feet entering the substrate, but only partially marking the subsurface sand layer.

It should be noted that in some footprints, even those with weakly delineated contours (LPP-IC-0022, LPP-IC-0024, MN4815-V), clearly show the main axis of the animal's autopodium. This occurs in both manus and pes impressions, providing evidence for the importance of digits III and IV during locomotion. As these are the longest digits, they penetrate deeper into the substrate, which favors preservation and can yield footprints that appear digitigrade (Milàn and Bromley, 2006).

Preservation is highly variable in aeolian environments, and the same animal may produce dissimilar tracks due to differences in the cohesion of the substrate (e.g. McKeever and Haubold, 1996; Lockley, 2011). Although the length/width ratio of the footprints described in this study varies considerably (0.62–0.93), they are interpreted to have been produced by the same species. This variation in morphology can be explained by substrate factors, as discussed above (e.g., cohesion, humidity, layer thickness), as well as by the direction of the animal's progression relative to the dune slope.

### 4.3. Implications for Botucatu Formation paleoecology

Recently, Krapovickas et al. (2016) reviewed the ichnological record in aeolian deposits over geological time. They were able to distinguish various phases of colonization in desert environments. The Botucatu Formation fits into phase 4 as defined by Krapovickas et al. (2016), presenting a well-established tetrapod fauna and invertebrate infauna.

Deserts comprise a mosaic of habitats in which ichnofossil occurrence is related to climatic conditions and resource availability (Krapovickas et al., 2016). The Araraquara region (as represented by the São Bento quarry specifically) shows an abundant and diverse ichnofauna, and is interpreted as a productive habitat, with moisture present during deposition (Fernandes et al., 2014; Buck et al., 2017). Buck et al. (2017) analyzed ichnocoenoses in the Botucatu Formation to infer trophic relationships among the fauna. They concluded that detritivorous organisms formed the base of the food chain, with theropod dinosaurs as apex predators.

Prior to this study, only one possible mammaliform from the Botucatu Desert paleoenvironment was formally described. Buck et al. (2017) inferred that this mammaliform was likely an intermediate consumer in the local ecological community. The present study expands the record of mammaliform trackmakers in the Botucatu Formation. Morphological differences in the autopodium, distinct locomotor characteristics, and the absence of intermediate-size footprints between *Aracoaraichnium* igen. nov. and *Brasilichnium*, all indicate that the two mammaliform ichnotaxa do not represent different ontogenetic stages of the same organism. The presence of small *Brasilichnium* tracks may indicate that young individuals were in fact living in the Botucatu Desert. This suggests that the *Brasilichnium* producer was a resident organism in this habitat, since the presence of juveniles suggests that reproduction was occurring in the desert environment. However, no tracks with significantly smaller dimensions (which would indicate young individuals) have yet been found for *Aracoaraichnium* igen. nov., despite extensive sampling over several

decades. This leads us to conclude that the *Aracoaraichnium* igen. nov. trackmaker probably made only sporadic incursions into the paleodesert.

Shenbrot et al. (1994) studied rodent communities in the modern deserts of North America and Asia, and observed that many species found in the desert do not reside there permanently, but instead live in more productive areas nearby, making sporadic incursions into the desert habitat. The *Aracoaraichnium* igen. nov. trackmakers may have made occasional forays into the desert in search of alternative food resources, such as invertebrates and/or plant material. *Brasilichnium* track producers likely selected from a range of food resources based on availability and nutritional requirements (Hadley and Szarek, 1981; Karasov, 1985). Assuming similar feeding habits, the two mammaliforms may have been direct competitors. Extant desert rodent species tend to compete more intensely when they have similar body sizes, and are less likely to coexist in the same habitat, as discussed by Bowers and Brown (1982). However, organisms with different body sizes may be able to coexist more easily, even with some overlap in their feeding niche. It is worth noting that during encounters between the two mammaliforms, the larger form (i.e. *Aracoaraichnium* igen. nov. trackmaker) would likely have prevailed in any antagonistic interactions. Both mammaliforms may have been preyed upon by the various theropod dinosaurs present in this paleoenvironment (Fernandes et al., 2011).

The activity of these animals likely followed patterns similar to those observed by Kronfeld-Schor et al. (2001). These researchers analyzed the energy consumption and water balance of two modern rodent species within genus *Acomys*, which coexist in rocky desert habitat in the Ein Gedi Natural Reserve of Israel. One species (*A. russatus*) engages in diurnal activity, while the other (*A. cahirinus*) is nocturnal. The nocturnal species expends more energy during the winter, for thermoregulation purposes, while the diurnal species uses more energy during the summer, due to the necessity of dissipating heat. No significant differences in osmotic regulation were observed between the two species, which may reflect physiological and behavioral adaptations for water preservation in *A. russatus*, which preferentially forages in shaded areas (Kronfeld-Schor et al., 2001). However, there are fundamental differences between rocky and sandy deserts; the Botucatu Formation was dominated by sandy dunes, and would have had little to no cover, except around rare oases. Thus, diurnal activity by mammaliform organisms would have presented significant thermoregulation and water balance problems. Predation pressure from theropod dinosaurs may have also favored nocturnal activity among the Botucatu Formation mammaliform community. Therefore, thermoregulation was likely the main energy expense for mammaliform organisms in the Botucatu Paleodesert, especially during cold winter nights. *Brasilichnium* producers, which were smaller desert residents, would have experienced more acute difficulties with thermoregulation. The presence of hair may have played an important role in insulating the mammaliform trackmakers, aiding in thermoregulation (Schmidt-Nielsen, 1997).

## 5. Conclusions

In this study, we describe a new ichnotaxon with mammaliform affinity from the Botucatu Formation, increasing the ichnodiversity of this unit. Although there are morphological similarities between *Brasilichnium* and *Aracoaraichnium* igen. nov. (i.e. tetradactyl, heteropody, greater length along the transverse axis of the footprints, and an oval heel pad), the new ichnogenus can be characterized as mesaxonic, with a greater length of digits III and IV, larger footprint dimensions (without intermediate size classes), and absence of abduction in digit V. The shared characteristics of *Brasilichnium* and *Aracoaraichnium* igen. nov. may reflect the phylogenic relationship of the trace producers. *Aracoaraichnium* igen. nov. can be differentiated from other well-known tetrapod ichnotaxa by digit and autopodium morphology, the number of digit traces, and the degree of heteropody.

Differences can also be observed between the locomotor parameters of *Brasilichnium* and *Aracoaraichnium* igen. nov. A proportionately shorter stride is observed in *Aracoaraichnium* igen. nov., which may indicate that the trace producer had relatively short limbs. Pace angle values indicate that the trace producer presented a semi-erect to erect posture, with a low degree of femoral abduction.

Some of the tracks described here have autopodia with smaller dimensions. This is interpreted as a taphonomic artifact, since the footprints were probably produced in the subsurface. A thick layer of dry surficial sand may have been present, which could have caused this effect. The existence of moderately well-preserved footprints can also be explained by the subsurface production model, in which subsurface sediments had a higher level of humidity. The presence or absence of manus impressions may reflect the relative effort exerted by the hind limbs as the animal ascended dunes in the paleoenvironment.

Since the ichnological evidence supports a distinct classification for the *Aracoaraichnium* igen. nov. tracks, the trackmaker is inferred to represent a newly recognized component of the Botucatu Formation paleocommunity. We infer that the *Brasilichnium* producer was a nocturnal resident of the paleodesert, while the *Aracoaraichnium* igen. nov. producer engaged in both diurnal and nocturnal excursions. The hypothesis that the *Aracoaraichnium* igen. nov. producer represents a different ontogenetic stage of the *Brasilichnium* trackmaker is rejected, due to the absence of footprints of intermediate sizes despite the extensive sampling of ichnofossils on Botucatu Formation slabs. The *Aracoaraichnium* igen. nov. producer may have fed on invertebrates and/or plant material, depending on their nutritional needs and food availability.

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**4. Sobre as pegadas com afinidade a Lepidosauria**

O trabalho apresentado a seguir será submetido à revista científica *Journal of South American Earth Sciences* (ISSN: 0895-9811).

**Lacertoid tracks from the Botucatu Formation (Lower Cretaceous) with different locomotory 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 fossil diversity of the Botucatu Formation is reported at the Ouro ichnosite, located at the Araraquara municipality region, São Paulo State, Brazil. The locality represents an area of greater humidity in the ancient desert, where a rich fauna lived in the past. 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 autopods and geometry of the trackways indicate an affinity with a lizard-like trackmaker. Furthermore, at least three different modes of locomotion were recognized for the trackmaker: a typical walking gait, a pause-walking gait, and sideways drifting. The current report suggests Lepidosauria 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 traces. However, considering the South American records of lepidosaurs, Iguania lizards are the most likely trackmakers. This may be one of the oldest Squamata records for South America, which bears important information about the ecology, evolution, and biogeography of the group during the Early Cretaceous.

## 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; Peixoto et al. 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 knowledge about Early Cretaceous desert ecosystems (Leonardi and Carvalho 2020).

Since the 19th century, the Botucatu sandstone has been exploited commercially and was largely used for urban paving. Nonetheless, most of the quarries are now deactivated and the very few that remain in activity exploit the material mainly for building finishes. The first sandstone slab with a tetrapod trackway from the Botucatu Formation was discovered by the mining engineer Joviano Pacheco in 1911. This trackway was first described in literature 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, having worked for many years to collect and describe local fossil materials. 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; Peixoto et al. 2020; Leonardi and Carvalho, 2020).

Despite the Botucatu Formation ichnofauna has been studied for almost forty years a unique track morphotype remained formally unknown until the present date. Herein we describe this new morphotype and its behavioral variations. Morphology and locomotory characteristics differentiate from all other known tracks from this unit. Among the observed features of this novel morphotype are footprints with digit V in posterolateral position and opposite to digit I associated 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 has affinities with Lepidosauria (Rynchocephalia + 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. This is the first lacertoid ichnofossil described for a Cretaceous eolian system and possibly one of the oldest records of Squamata in South America.

## 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 km² and outcrops in southern Brazil, Paraguay, northern Argentina, and Uruguay (Figure 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
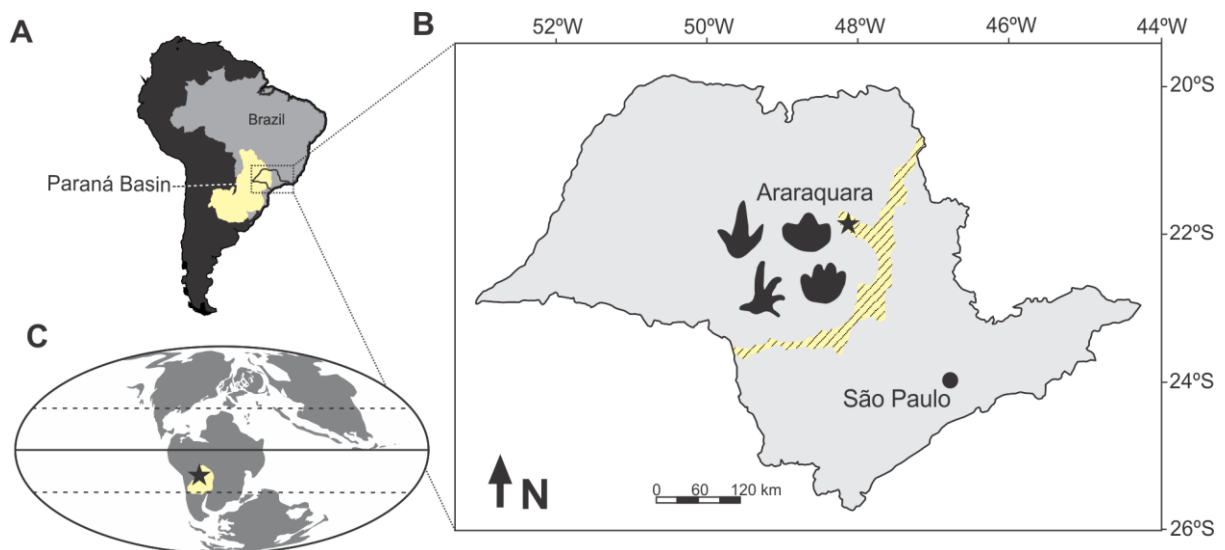
Mato Grosso do Sul (Scherer and Goldberg 2007).



Figure 1 - A, localization of the Paraná Basin in South America with 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 Araraquara site locality and the extent of the Botucatu Paleodesert. Paleogeographical reconstruction based on Scotese (2014). Paleodesert reconstruction following Scherer and Goldberg (2007). This figure derives from the original work of Fernandes et al (2004).

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 crossed stratifications and are interpreted as deposited in an eolian environment (Bigarella and Salamuni 1961; Salamuni and Bigarella 1967). The Botucatu Formation overlaps the fluvial-eolian deposits of Piramboia Formation and is covered by the magmatic extrusive rocks of the Serra Geral Formation (Figure 2).
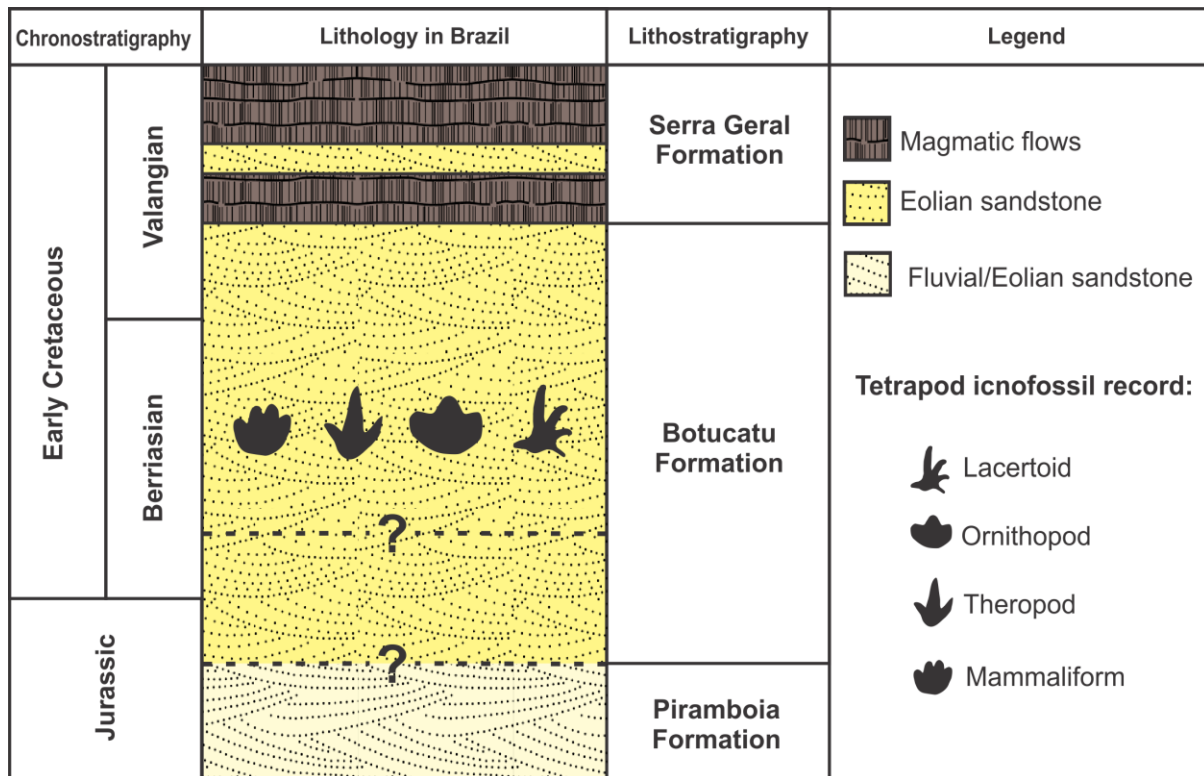
Figure 2 - Simplified stratigraphic column showing the lithology, chronostratigraphy, and contact relationships between the Piramboia, Botucatu, and Serra Geral units. This figure derives from Buck et al. (2017a) and Peixoto et al. (2020).

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 deserts (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 raindrops 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 the Minas Gerais State, coniferous wood fossils indicate an even wetter environment (Pires et al. 2011). Dendroclimatological analysis of these fossil plants 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 is possible to reckon that the extensive depositional range of the Botucatu Formation was under different climatic regimes resulting in some heterogeneity between deposits and their fossiliferous content.

Botucatu Formation age was subject to very different interpretations over time (Leonardi and Oliveira 1990; Bonaparte 1996). There is a consensus between authors assuming a relative age between the Late Jurassic and the Early Cretaceous for this unit (Renne et al. 1992; Turner et al. 1994; Scherer 2000; Tamrat and Ernesto 2006; Janasi et al. 2011). Scherer (2000), nonetheless, particularly infers a short interval for Botucatu Formation deposition. According to this author, it may be Berriasian to Valanginian in age (Lower Cretaceous), the upper limit being the last volcanic floods of the Serra Geral Formation, dated between 137 and 127 Ma (Turner et al. 1994). Those latter interdigitate and conformably overlie the Botucatu Formation and Scherer (2000)  presumes this was responsible for the preservation of the original desert dunes topography (Figure 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 Paleoecology and Paleoichnology (LPP) of the Department of Ecology and Evolutionary Biology (DEBE), Center for Biological and Health Sciences (CCBS), 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 *foreset* dune deposit of approximately 20m high and 100m long, while two specimens (LPP-IC-0041 and LPP-IC-0042) do not have precise information about the extraction location. Most of the Botucatu Formation specimens from the LPP collection do not have stratigraphic information because they were rescued from mining activity and were already removed from their original position when collected.

We followed the convention proposed by Leonardi (1987) for the terminology and description of the tracks and trackways. Pes length, width, length/width ratio, stride length, oblique pace, 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 analyzed material was compared with other trackways from the LPP collection and further specimens figured and described in the 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). The term 'lacertoid' is used here to refer to the footprint morphotype with characteristics

generally associated with Lepidosauria. The term 'lizard-like', in turn, is used to refer to a trackmaker with a body plan 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 its own registration number and, as each trackway is on its own 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 here are illustrated in Figures 3, 4, and 5. Macro photographs of footprints with digits impressions are in Figure 6.
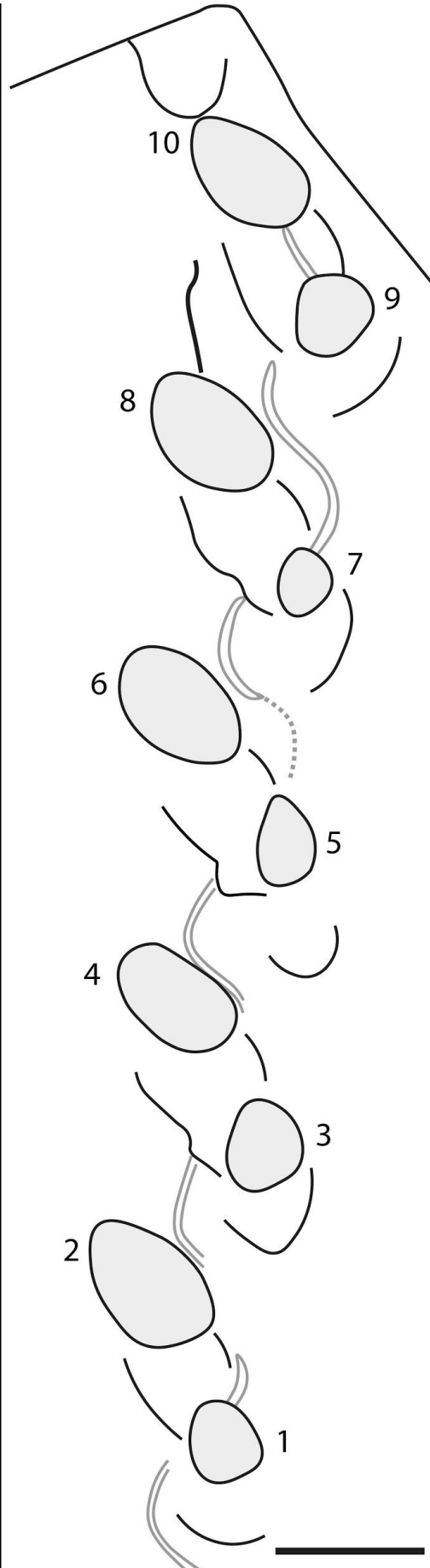
Figure 3 - A, photograph of specimen LPP-IC-0018. B, interpretative scheme of the specimen showing each footprint position (ellipses) in relation to the trackway midline axis. Note the alignment of the anteroposterior axis of all footprints and the divergence of these axes in relation to the trackway midline axis, a condition produced by side-walking on an inclined plane. The trackmaker walked from bottom to top.
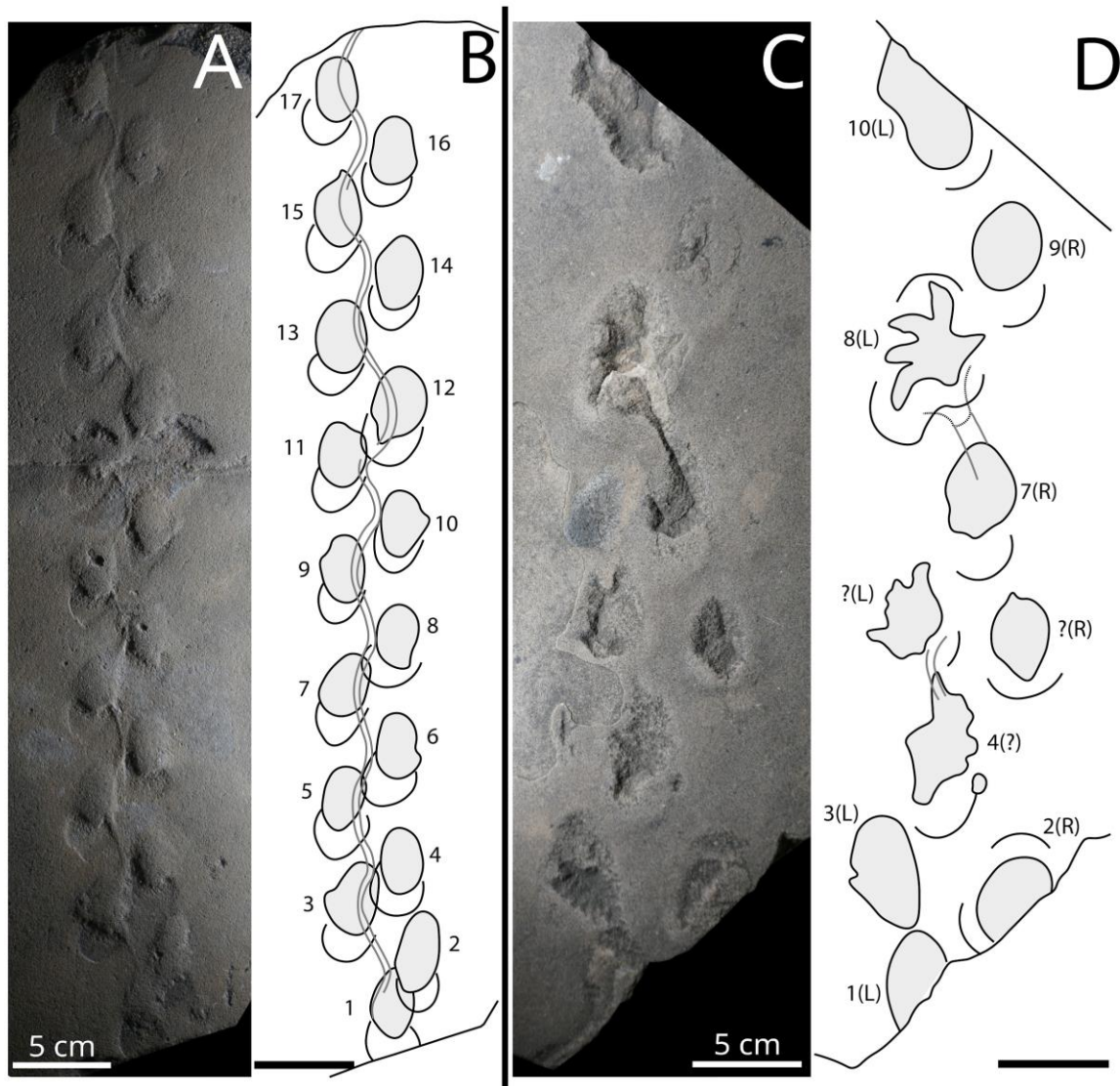


Figure 4 - Photography of specimens LPP-IC-0041 (A) and LPP-IC-0042 (C). B and D are the interpretative schemes for both specimens Note the anteroposterior axis of each footprint is nearly aligned with the trackway midline axis in both specimens. The trackmakers walked from bottom to top.
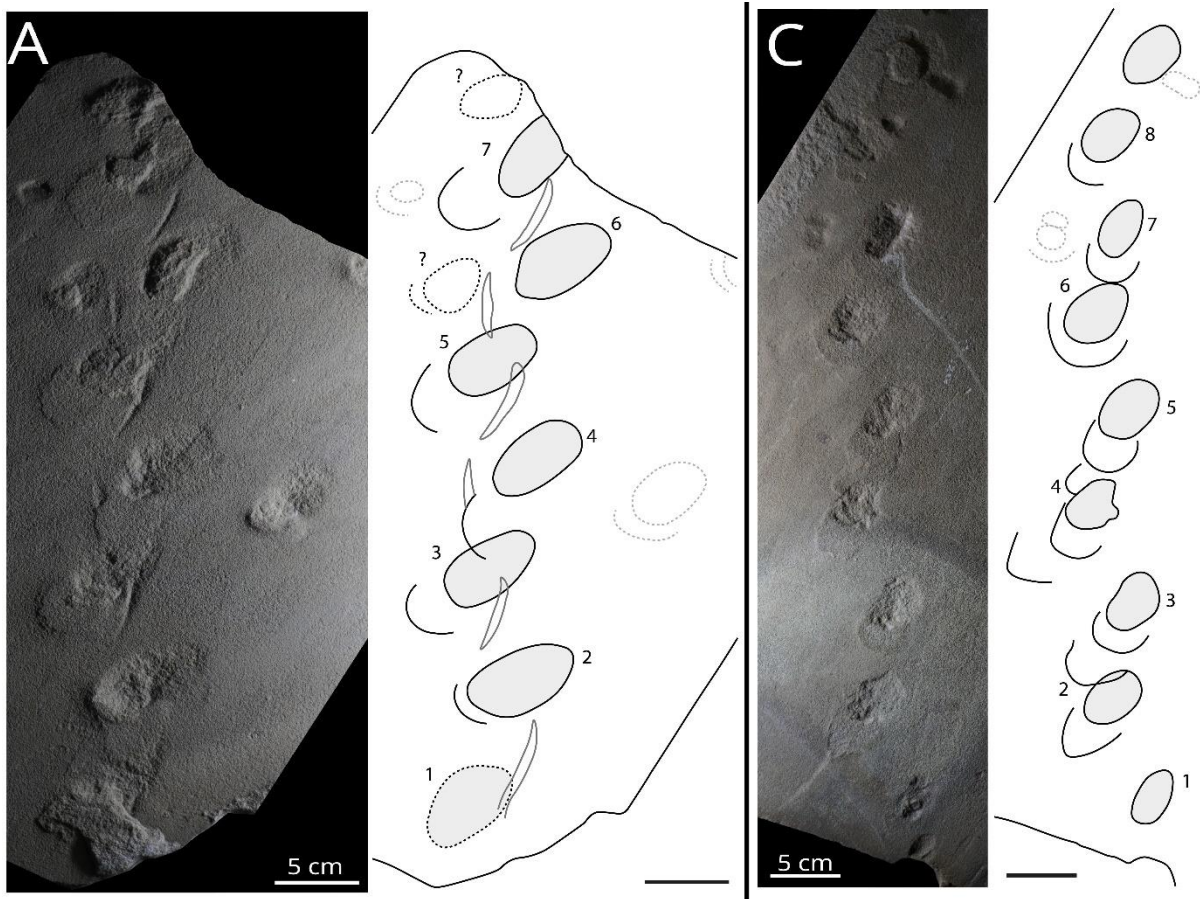
Figure 5 - Photograph of specimens LPP-IC-0043 (A) and LPP-IC-0044 (C). B and D are the interpretative schemes for both specimens. Note the anteroposterior axis of each footprint is nearly aligned with the trackway midline axis in both specimens. The trackmakers walked from bottom to top.
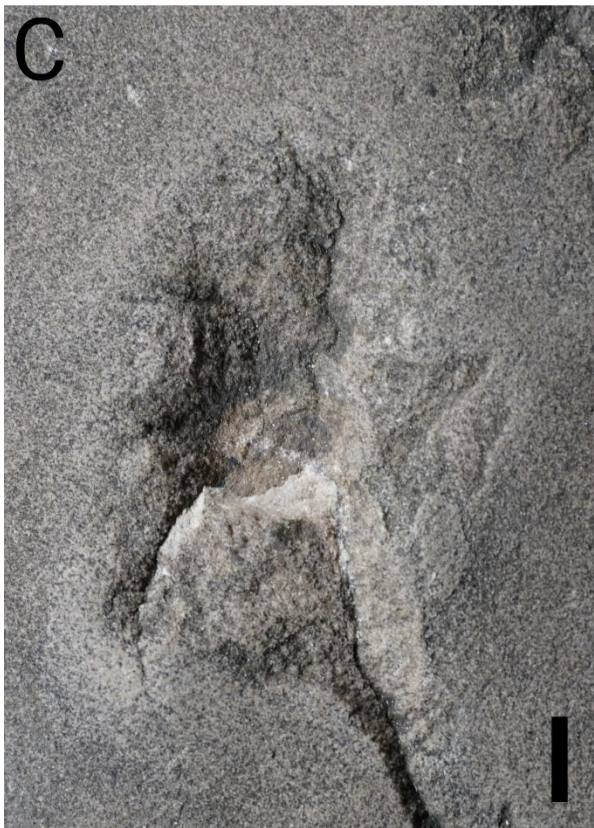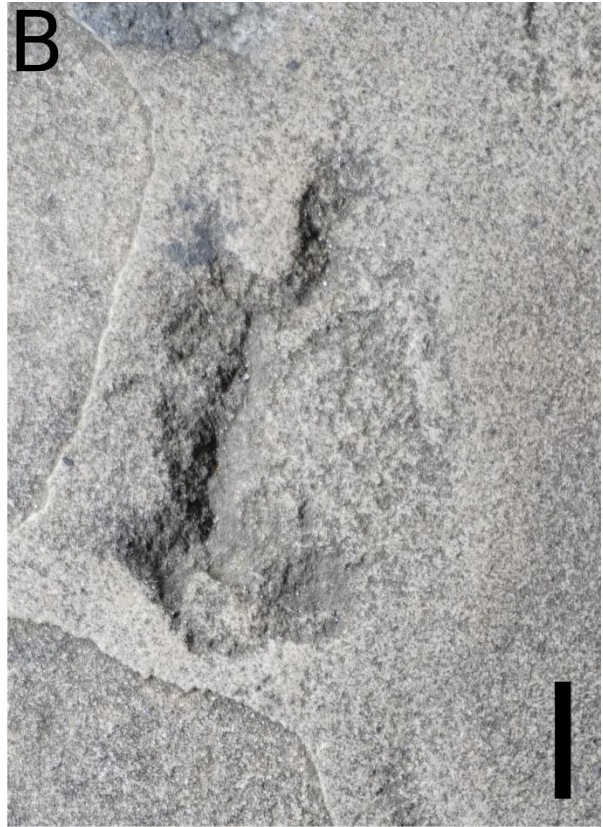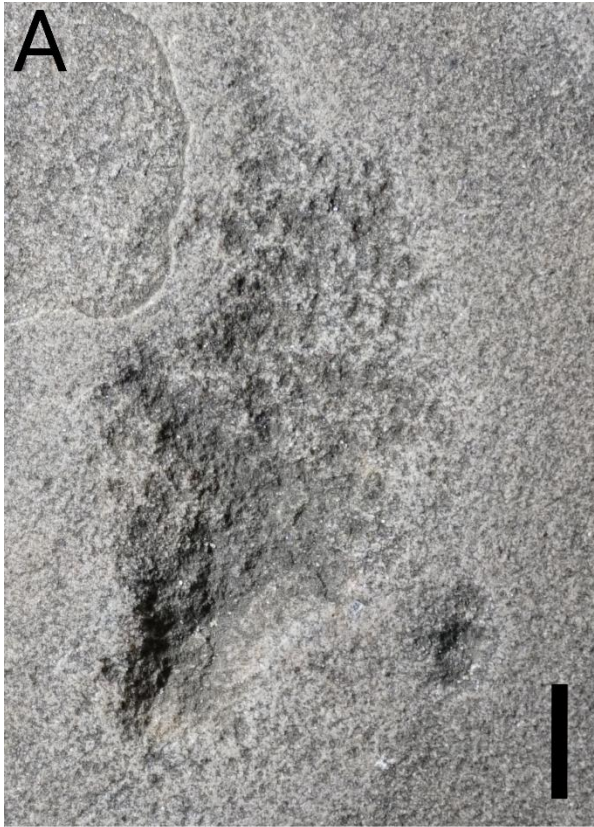
Figure 6 - Detailed macro photographs of the footprints with digits impressions in LPP-IC-0042 (A-C) and LPP-IC-0044 (D) A, Footprint 04. B, Footprint 05 or 06. C, Footprint 08. D, Footprint 04. Trackmakers walked from bottom to top. Scalebar 1 cm.

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.

Table 1. Mean values followed by standard deviation of morphological and locomotory parameters of lacertoid tracks and trackways. Width, length, oblique pace, stride, total 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 |
| Total 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 | $41 \pm 5.19$ | $25.98 \pm 6.52$ | $27.15 \pm 2.19$ | $48.21 \pm 6.69$ | $38.53 \pm 4.56$ |
|---|---|---|---|---|---|

Regarding the morphological details of the trackmaker's autopodium, only footprint 08 (left pes) of specimen LPP-IC-0042 has recognizable digit impressions (Figure 6, C). All other tracks have only elliptical contours and/or very few recognizable digit details (Figure 6, A, 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 (Figure 6, C). Digit II can be considered long and narrow. However, we can not distinguish the same feature for digits III, IV, and V since they apparently had their morphological characteristics altered during preservation. In the same specimen, footprints 04 and 05 or 06 (Figure 6, A and B), although not as well preserved as 08, seem to indicate the same morphology. It is possible to observe the presence of digits in similar positions to those of footprint 08. Footprint 04 of specimen LPP-IC-0044 (Figure 6, D) also has asymmetry and an elongate structure facing inwards 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 trackways grouping in 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, it is possible to observe tail marks crossing over some footprints impressions and/or other sedimentary structures. This 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 trackmaker's tail  touches the substrate. The length of the tail marks (*i.e.* continuity) varies with the locomotory 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 in one side of the trackway, possibly because this was the trackmaker's side closest to the dune slope.

The most recurring locomotory mode was side-walking or sideways-drifting (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, apparently, point against the dune slope. Footprint axes 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 is 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° ± 3.68, 38.53° ± 4.56, and 41° ± 5.19. The averages of the stride length and the pace angulation of the trackways showing this locomotory behavior are, respectively, 13.61 cm ± 0.38 and 140,07° ± 6.86 for LPP-IC-0043, 14.7 cm ± 0.57, and 147,9° ± 3.5 for LPP-IC-0044 and 10.65 cm ± 1 for LPP-IC-0018.

The other two locomotory behaviors observed are seen in specimens LPP-IC-0041 and LPP-IC-0042. LPP-IC-0041 trackway displays the typical walking gait, with mean values of stride length and pace angulation of 5.93 cm ± 0.44 and 94.18° ± 4.94, respectively. A sinuous tail drag can be observed along the entire trackway and has an average width of 0.33 cm ± 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° ± 6.52. Despite the low pace angulation, the trackway width mean is 5.35 cm ± 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 cm ± 1.13; stride: 11.34 cm; pace angulation: 128.8° ± 5.02), and a strange behavior, called here '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 rotated outwards in relation to the trackway, with values of 28.7° and 25.6° respectively. Between tracks 07 and 08, a grooved structure of 1.04 cm in width can be interpreted as a tail drag mark. It is not clear which of the footprints was produced after the 04, being only possible to determine left and right.

Regardless of the mode of locomotion, all tracks have a very low and elongated displacement rim, different from all other displacement rims of ichnogenera already known for this geological unity. This characteristic, conjointly with the footprint morphology, reinforces the interpretation of a new ichnogenus associated with a new trackmaker for the Botucatu Formation.

*4.2 Systematic Paleoichnology*

*Ichnofamily*

Rhyncosauroidea Haubold 1966

Type ichnospecies: *Rhynchosauroides rectipes* Maidwell, 1911.

cf. Rhynchosauroides isp. Maidwell 1911

*Diagnosis 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° to 148°, depending on the locomotory behavior. Pes may be rotated in the same direction due to a specific gait adopted. Manus not preserved or overprinted by the pes. Sinuous tail drags or tail impressions may occur.

*Referred material*

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

*Locality*

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

Geographic coordinates: 21°49′03.4″ S, 48°04′22.9″ W.

*Horizon*

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

*Repository*

Trace fossil collection of the Laboratory of Paleoecology and Paleoichnology (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.

*Ichnotaxonomic assignment*

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 ±0.09, is different from both *Brasilichnium* (0.72 ±0.1) and *Aracoaraichnium* (0.78 ±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 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 *Brasilichnium*, nor in *Aracoaraichnium* or in any dinosaur trackway described for the Botucatu Formation. Finally, the track's displacement rim is different from any track previously described in the current geological unity.

Since only one footprint (footprint 08 from LPP-IC-0042) preserves details of the digits morphology (Figure 6, C), it is difficult to confidently assign this morphotype to any existing ichnotaxon or even propose a new ichnospecies. 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. Thus, in this work, we chose to attribute the described tracks to Rhyncosauroidea ichnofamily and tentatively to *Rhyncosauroides* ichnogenus. The described footprints and *Rhyncosauroides* 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 the light of new, better-preserved specimens. Despite the general similarities mentioned above, digits seem more spread out in the morphotype herein described and pes rotation is also different (pes are rotated more outwards in relation to the trackway midline in the here described morphotype). These characteristics may vary, however, due to several aspects, such as substrate cohesion, surface slope, and trackmaker behavior.

## 5. Discussion

*5.1 Preservational features and different locomotory behaviors*

Leonardi et al (2007) attest that 90 to 95% of the Botucatu Formation footprints are of low quality, being only depressions on the substrate with no morphological details of the trackmakers autopodium preserved. The footprints described here can be considered of low quality since most of them have only the outline preserved. As evidenced 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 morphological details. This is a good explanation for the preservation of the trackways here described. Nonetheless, a certain amount of interstitial moisture, even if low, must have been present 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 trackway is very similar to Marchetti et al. (2019)'s trackway, 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. (2019) (see figure 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 autopods at higher speed locomotion (Kubo 2010; Diedrich 2005) or facultative bipedal behavior of the trackmakers, which will be discussed later in this topic.

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 production can generate larger traces (Brand 1996; Jackson et al.

2010). However, variation in extra morphology 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 track. 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 8 (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 in relation to the footprints preserved on the left side, which may be undertracks (Milàn 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 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, as well as they could vary under different modes of locomotion. Torso, tail, and limb length influences the way the animal moves, therefore it may also affect the type of tail marks it produces. The Botucatu Formation 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 or twice the body length. Due to the preservation of only the pes impressions, 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 position 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° ±4.94°) 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 ±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, called here 'paused-walking'. Footprints 02 and 03 are interpreted as left and right feet, being 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 tracksway, 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 and Caputo (2018) 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 Rowland and Caputo (2018) trackway, however, no signs of strong wind currents (*i.e.* wind ripples) were observed in any of the slabs analyzed. 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 sideway-walking, this behavior also could 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 assist locomotion using lateral movements of the tail. According to the proposal by Jagnandan 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 *Rynhcosauroides 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 footprints 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 described here 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 cf. *Rhynconsauroides* 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). 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, ornithopods, 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, possibly a lepidosaur (Figure 7), which had not been previously recognized as a component of the Botucatu paleodesert ecosystem, thus, increasing its diversity.



Figure 7 - Lizard-like trackmaker reconstruction (reconstruction by Júlio Lacerda).

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 have 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's 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) represent 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 for 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. In that way, 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 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 pontei* Júnior and Marques, 1997, *Olindalacerta brasiliensis* Evans and Yabumoto, 1998 and *Calanguban alamoi* Simões, Caldwell and Kellner, 2014 are the best-preserved lizard remains for the Mesozoic of Gondwana and are considered scleroglossan lizards. *C. alamoi* possibly has scincomorph affinities, while *T. pontei* and *O. brasiliensis* phylogenetic positions remain very controversial (Simões and Caldwell 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 deposited in 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 restrict taxonomic level within Squamata can be problematic. The structure of squamate autopods 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.

Simões et al. (2017) suggest a distribution pattern for lepidosaurs in the Cretaceous of South America, with Squamata dominating the northern and southeastern portion of Brazil, while sphenodontians would apparently be restricted to more southern latitudes, in Southernmost Brazil and Argentina. If this pattern truly represents the paleobiogeographic distribution of these groups and is not a result of collection and/or description bias, the lacertoid footprints of the Botucatu Formation most probably were produced by Squamata. 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 autopods is very common in desert-dwelling animals. Despite this difficulty, this new description increases the ecomorphotype diversity of the Botucatu paleodesert ecosystem and adds to the knowledge of Lepidosauria in the Mesozoic of Gondwana, indicating that representatives of the group were already well adapted to inhabiting desert environments during the very Early Cretaceous of the South American continent.

*5.3 Paleocological implication*

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 lepidosaur 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 (Louw 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 lepidosaur 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 lepidosaur 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 Guará 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 were occupying desert dune environments in Gondwana since the Early Cretaceous. Nowadays, only Squamata inhabit desert environments.

*5.4 Other comments*

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 (Lower Jurassic) (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 urgently needed. Several ichnogenera have been described (see examples in Avanzini and Renesto, 2002), some based on badly preserved materials, others poorly figured in the literature, with only a few details described. This makes a 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 has several similarities with *Rhynchosauroides* and was tentatively associated with this ichnogenus.

The new trackmaker was assigned to a lizard-like organism creature, possibly an iguanian or scleroglossan Squamata, although Rhynchocephalia cannot be fully discarded.

Despite being all produced by the same trackmaker, the trackways record variations in the pace angulation and footprint angle, reflecting different modes of locomotions. 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 trackways 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.

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**5. Considerações finais**

A Formação Botucatu é uma unidade geológica mundialmente famosa pelo seu registro de pegadas fósseis. Todo o conhecimento paleontológico desta unidade é majoritariamente produzido a partir de estudos icnológicos, como é o caso do presente trabalho. Até o momento, ainda não foram encontrados somatofósseis da fauna que esteve presente no paleodeserto Botucatu. No entanto, a análise morfológica das pegadas fósseis encontradas permite distinguir e determinar grupos taxonômicos que integraram o sistema ecológico pretérito, bem como entender os aspectos envolvidos na morfologia e preservação das pegadas e pistas. Dessa forma, o presente estudo contribui para um entendimento mais completo do cenário taxonômico e paleoecológico, pois analisa em mais detalhes pegadas atribuídas a um produtor mamaliforme de maior porte e descreve pela primeira vez pegadas atribuídas a produtores lepidossauros para a Formação Botucatu.

As pegadas atribuídas ao produtor mamaliforme de maior porte apresentam quatro dígitos curtos em condição mesaxônica e, a partir da descrição, foi estabelecido um novo icnotàxon denominado de *Aracoaraichnium leonardii*. Foi possível definir que os produtores das pegadas de *A. leonardii* não são estágios ontogenéticos avançados dos produtores das pegadas de *Brasilichnium*. A morfologia distinta dos autopódios e a ausência de tamanhos intermediários sustentam a existência de pelo menos duas espécies de produtores mamaliformes, sendo uma de menor porte, responsável pelas pegadas de *Brasilichnium*, e uma de maior porte, responsável pelas pegadas de *Aracoaraichnium*. As pegadas atribuídas a produtor com afinidade a Lepidosauria apresentam cinco dígitos curvos em condição ectaxônica, e foram atribuídas tentativamente ao icnogênero *Rhyncosauroides*. A partir da morfologia das pegadas e das pistas, pode-se inferir um produtor com uma morfologia geral de lagartos. Com o registro desses novos icnotáxons, a icnodiversidade de pegadas de tetrápodes da Formação Botucatu aumenta consideravelmente.

Foram investigados aspectos locomotoriais dos dois produtores com base nas pistas analisadas, sendo possível inferir comportamentos distintos. As pistas atribuídas a *Aracoaraichnium* apresentam proporção do comprimento das pegadas em relação ao passo duplo relativamente maior quando comparadas com as pistas atribuídas a *Brasilichnium*. Essa proporção pode ser utilizada para inferir que os produtores de *Aracoaraichnium* apresentavam membros relativamente mais curtos em relação ao tronco, ainda que estes estivessem em uma posição verticalizada, o que pode ser inferido a partir da largura das pistas. Já as pistas atribuídas a produtores com afinidade a lagartos apresentam maior variedade de

comportamentos, registrados na geometria das pistas. É observada locomoção cursorial típica, locomoção cursorial com momentos de parada do produtor, provavelmente para observar o ambiente, e um tipo de deslocamento onde as pegadas referentes aos pés estão alinhadas na mesma direção, divergindo da linha média da pista.

Em relação aos aspectos paleoecológicos, com a determinação de novos produtores, é possível inferir novas interações ecológicas. Em ambientes desérticos, a distribuição de recursos pode ocorrer de maneira localizada no espaço e pontualmente ao longo do tempo. Sendo assim, os organismos podem apresentar estratégias onívoras para a obtenção de alimento em função do que estiver disponível. Tendo esse padrão como base, os produtores de *Aracoaraichnium* poderiam se alimentar tanto de material vegetal ou de outros organismos, colocando-os como potenciais competidores de *Brasilichnium*, caso não houvesse diferenciação de nicho. Os produtores lagartos são interpretados como consumidores de artrópodes, podendo também se alimentar de indivíduos menores e jovens de mamaliformes, ou mesmo de ovos de dinossauros. Para evitar o calor excessivo durante o dia, estes poderiam passar parte do dia enterrados na areia.