

First dinosaur ichnofauna from the Bauru Group indicates Cenomanian–Turonian events led to an ‘Ornithischian Hiatus’ in the Upper Cretaceous of Southeast Brazil

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ABSTRACT

The Cenomanian–Turonian interval represents a critical period of faunal change during the Late Cretaceous. Although the main causes of this turnover are contentious, it is undeniable that these global events significantly influenced the last stages of dinosaur evolution. The Bauru Group in southeastern Brazil is known for its rich body-fossil record of crocodyliform and dinosaur remains, representing a key geological unit for understanding the evolution of continental biotas in the Upper Cretaceous of Gondwana. However, the ichnological record in these units is scarce, primarily consisting of invertebrate burrows and rare tetrapod traces. This study focuses on the newly discovered tracksite within the Cenomanian–Turonian Santo Anastácio Formation, marking the first dinosaur ichnofauna identified in the Bauru Group. The new ichnocoenosis includes four theropod morphotypes, a quadrupedal and a small bipedal ornithischian, bipedal and graviportal ornithopods, and a small, narrow-gauged sauropod trackmaker. These tracks provide new insights into the dinosaur faunas during the Cenomanian–Turonian interval and highlight the existence of clades not previously identified in the Bauru Group, particularly ornithischians. The absence of body fossils of these taxa in the younger strata of the Bauru Group indicates that the successive environmental fluctuations during the Cenomanian–Turonian may have been responsible for regional extinctions or migration of these animals to higher latitudes. This ecological shift might have allowed specialized crocodyliforms like sphagesaurians to fill the niches left by small herbivorous dinosaurs in the Bauru Group, while titanosaurs dominate the medium-to-large herbivore roles in these ancient ecosystems.

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1. Introduction

The Bauru Group hosts the richest assemblage of fossil vertebrates from southeastern Brazil and plays an important role in understanding the evolution of continental biotas during the Upper Cretaceous in South America (Bertini et al., 1993; Candeiro and Rich 2010; Apesteguía et al., 2013; Langer et al., 2022). Several localities

within the Bauru Group feature a prolific tetrapod body-fossil record (Candeiro et al., 2006), in particular the fossil-sites of Monte Alto, Presidente Prudente, and General Salgado in São Paulo State (Mezzalana 1989; Suárez 2002; Carvalho et al., 2013), as well as Campina Verde and Uberaba-Peirópolis in the Triângulo Mineiro region, Minas Gerais State (Ribeiro and Carvalho 2009; Martinelli and Teixeira 2015).

In this context, the fossil-bearing sites in the General Salgado region of northwestern São Paulo State have become prominent hotspots for the collection of well-preserved, articulated specimens (Fig. 1A–C), with a particular abundance of crocodyliforms (Brandt Neto et al., 1991; Bertini et al., 1999; Arruda et al., 2004). These

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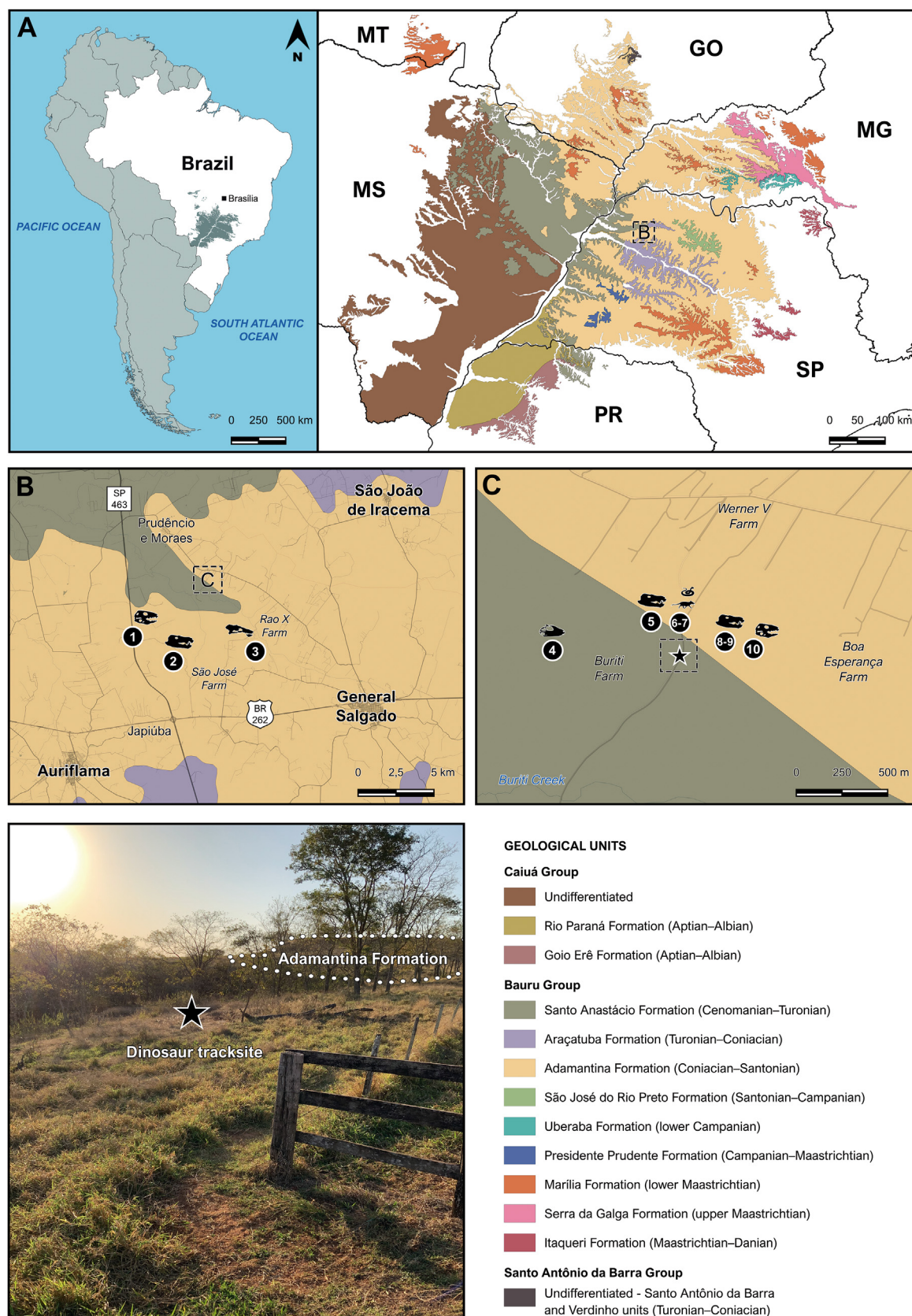


Fig. 1. Geographic location of the fossil sites in the General Salgado area. Dashed squares indicate enlarged areas. **A**, map of the Bauru Supersequence in South America and in Central Brazil; **B–C**, fossil sites in the General Salgado area and its known tetrapod taxa: (1), *Caipirasuchus attenboroughi* (LAPEISA-0001; Ruiz et al., 2021); (2), *Campinasuchus dinizi* (UFRJ-DG 402-R; Darlim et al., 2021); (3), *Armadillosuchus arrudai* (UFRJ-DG 303-R and MPMA-64-0001-04; Marinho and Carvalho 2009); (4), *Gondwanasuchus scabrosus* (UFRJ-DG 408-R; Marinho et al., 2013); (5), *Baurusuchus salgadoensis* (MPMA 62-0001-02; Carvalho et al., 2005); (6), *Brasilestes stardusti* (LPRP/USP 0751; Castro et al., 2018); (7), “Anilioid”

specimens have been found in three main sites (Buriti, São José and Rao X farms) of the middle Coniacian deposits of the Adamantina Formation, that yielded numerous specimens of baurusuchids (e.g., *Baurusuchus salgadoensis* [Carvalho et al., 2005](#); *Baurusuchus albertoi* [Nascimento and Zaher, 2010](#); *Gondwanasuchus scabrosus* [Marinho et al., 2013](#); *Aplestosuchus sordidus* [Godoy et al., 2014](#)) and sphaesaurids (e.g., *Armadillosuchus arrudai* [Marinho and Carvalho, 2009](#); *Caipirasuchus stenognathus* [Pol et al., 2014](#)).

The fossil assemblage recovered from the General Salgado region also includes remains of small tetrapods, notably humeri of a neobatrachian, plastron and shell fragments of podocnemidoid turtles ([Freitas et al., 2023](#)), vertebrae attributed to an alethinophidian “anilioid” snake ([Zaher et al., 2003](#)), and mammal teeth, including the putative tribosphenidan *Brasilestes stardusti* ([Castro et al., 2018](#); but see [Rougier et al., 2021](#)). Conversely, dinosaur remains in the General Salgado region are scarce, consisting only of sauropod and theropod tooth crowns and an isolated sauropod rib (e.g., [Vasconcellos et al., 2008](#)), which were recovered on the outskirts of the Auriflama municipality ([Fig. 1B](#)).

Regarding ichnological evidence within the Bauru Group, most identified trace fossils are invertebrate burrows and excavations (e.g., [Fernandes and Carvalho 2006](#)), or root traces (e.g., [Do Nascimento et al., 2019](#)). Despite the relative abundance of tetrapod body fossils, ichnological data for tetrapods is sparse. Notable occurrences include several coprolites (e.g., [Souto 2008](#)), bite marks (e.g., [Reis et al., 2022](#)), gastroliths (e.g., [Vasconcellos and Carvalho 2010](#)), and a variety of eggshells and egg clutches attributed to testudines ([Azevedo et al., 2000](#); [Carvalho et al., 2014](#); [Marsola et al., 2014a](#)), crocodyliforms ([Magalhães Ribeiro et al., 2006](#); [De Oliveira et al., 2011](#)), sauropods ([Price 1951](#); [Magalhães Ribeiro 2002](#); [Fiorelli et al., 2022](#)), and theropods ([Kellner et al., 1998](#)), including avialans ([Marsola et al., 2014b](#)). Dinosaur tracks are particularly rare, with the only significant discovery being two partial theropod tracks from the Marília Formation in Minas Gerais State yet to be published ([Bertolucci 2020](#)).

In this study, we present the first dinosaur tracksite within the Bauru Group, located at the renowned paleontological site Buriti Farm ([Fig. 1C–D](#)). Unlike the previously documented fossil findings from this site, the newly identified ichnocoenosis is preserved within the Santo Anastácio Formation (Cenomanian–Turonian). This finding expands our understanding of the faunal content and paleoenvironmental conditions of the area during the early stages of the Bauru Group, providing the first evidence of ornithischians in this unit. Additionally, we examine the notable absence of similar faunal components in the upper strata of the Bauru Group and explore the paleoecological implications of this discovery for understanding faunal turnovers during the early Late Cretaceous.

2. Geological background and stratigraphical framework

The Bauru Supersequence (*sensu* [Arai and Dias-Brito 2023](#)) represents an extensive inner sag in the Paraná Basin, covering ca. 380,000 km² of southeast Brazil and part of Paraguay ([Menegazzo et al., 2016](#)). The origin of this geological unit is linked with the isostatic overloading of the Paraná-Etendeka lava flows, attributed to the thermomechanical subsidence resulting from the Gondwanan Rifting during the Early Cretaceous ([Riccomini 1997](#); [Milani et al., 2007](#); [Carneiro et al., 2012](#)). The sedimentary infilling of the Bauru Supersequence reaches a maximum thickness of approximately 300 m and is primarily composed of sandy sequence deposited under arid to semiarid climatic conditions ([Fernandes](#)

and [Basilici 2009](#); [Basilici and Sgarbi 2012](#); [Batezelli and Ladeira 2016](#); [Blanco et al., 2021](#)). However, different interpretations of its sedimentary succession have created challenges in establishing a consistent chrono- and lithostratigraphic framework for this unit. This disagreement stems from the lack of integration between different methodological approaches in the proposed stratigraphic schemes, hampering the recognition of certain units in the field or their correlation with previously identified fossiliferous horizons ([Pires-Domingues et al., 2007](#)).

A general consensus exists that the Bauru Supersequence can be divided into two main units, the Caiuá and Bauru sequences, which are regionally separated by erosional unconformities ([Paula e Silva et al., 2005](#); [Batezelli 2015](#)). The Caiuá Sequence (CS) comprises fluvial and aeolian sandstones deposited in erg conditions, while the Bauru Sequence (BS) consists of mudstones, siltstones, and sandstones that were deposited in more humid environments, including palustrine, fluvial, and alluvial system tracts ([Fernandes and Coimbra 2000](#)). However, there is a lack of consensus regarding the lithostratigraphic hierarchy of these units. They have been variously interpreted as groups of the Paraná Basin (e.g., [Soares et al., 1980](#); [Paula e Silva et al., 2009](#); [Arai and Dias-Brito 2023](#)), as distinct groups of a single new basin, termed the Bauru Basin (e.g., [Fernandes and Coimbra 1996](#); [Menegazzo et al., 2016](#)), or as forming separate, individualized basins known as the Caiuá and Bauru basins (e.g., [Fúlfaro et al., 1999a](#); [Batezelli 2010](#)).

The delimitation and nomenclature of the formations within the Bauru Supersequence also remain contentious. The BS is traditionally arranged from the base to the top as follows: Araçatuba, Adamantina and Marília formations. Meanwhile, the CS traditionally comprises the Rio Paraná, Goio Erê and Santo Anastácio formations ([Soares et al., 1980](#); [Fernandes and Coimbra 1994](#); [Batezelli et al., 2003](#)). Additional units have been proposed for both sequences, including the Uberaba, Verdinho, Santo Antônio, São Carlos, and the Serra da Galga formations, although these are restricted to specific regions ([Castro et al., 2002](#); [Sgarbi et al., 2004](#); [Soares et al., 2021](#)). [Fernandes and Coimbra \(2000\)](#) provided a revised stratigraphic framework for the BS units, considering lateral variations and environmental differences in their deposition, particularly in the Adamantina Formation. They subdivided this formation into regional units: the Presidente Prudente, São José do Rio Preto and Vale do Rio do Peixe formations. However, nearly all lithofacies previously attributed to the Adamantina Formation are encompassed by the latter, which, according to the Brazilian Stratigraphic Code, does not justify a name change (see [Petri et al., 1986](#)). Alternatively, [Paula e Silva et al. \(2005; 2009\)](#) used geophysical profiles and core-drilling samples to identify two new subsurface units in the Bauru Supersequence in São Paulo State, named the Pirapozinho (CS) and Birigüi (BS) formations. Like early interpretations (e.g., [Soares et al., 1980](#)), these authors do not distinguish between the Rio Paraná and Goio Erê formations, treating them as a single unit termed the Caiuá Formation. Furthermore, they classify the Santo Anastácio Formation as part of the BS, based on the presence of local unconformities with other units of the CS, which is followed by this work.

Concerning fossil occurrences, the BS units shelter one of the richest vertebrate records of the Brazilian Cretaceous (see [Candeiro and Rich 2010](#); [Menegazzo et al., 2016](#); [Langer et al., 2022](#) and references therein). In contrast, the CS is characterized by sparse fossil occurrences from a few localities, mainly coming from the Rio Paraná and Goio Erê formations ([Leonardi 1977](#); [Fittipaldi et al., 1989](#); [Fernandes et al., 2009](#); [Manzig et al., 2014](#); [Menegazzo](#)

snake vertebrae (MZSP-PV 1400; [Zaher et al., 2003](#)); (8), *Baurusuchus albertoi* (MZSP-PV 140; [Nascimento and Zaher 2010](#)); (9), *Aplestosuchus sordidus* (LPRP/USP 0229a; [Godoy et al., 2014](#)); (10), *Caipirasuchus stenognathus* (MZSP-PV 139; [Pol et al., 2014](#)). A black star indicates the location of the new dinosaur tracksite described in this study (20°34'2.77"S 50°28'3.83"W).

et al., 2015; Simões et al., 2015; Langer et al., 2019; Kellner et al., 2019; Ruiz et al., 2021; De Souza et al., 2021; Pêgas 2024), precluding major stratigraphic refinements.

Rock exposures of the Bauru Supersequence in São Paulo State are predominantly represented by the units of the BS, with the Adamantina Formation being particularly extensive and covering nearly half of the state's territory (Fig. 1A). In contrast, units commonly associated with the CS are more restricted and primarily consist of deposits of the Santo Anastácio Formation. The Santo Anastácio Formation is characterized by amalgamated sandstone beds, typically massive, with decimeter-thick tabular strata of very fine-to medium-grained, quartzitic and subarkosic sandstones, which occasionally contain siltclay fractions, nodules and calcite concretions (Fernandes and Coimbra 1994; Fúlfaró et al., 1999b). The grains are poorly sorted, ranging from sub-rounded to subangular, and are often coated with iron oxides, imparting a purplish to reddish aspect to the rocks. The newly described ichnocoenosis is located within the mapped area of the Santo Anastácio Formation (*sensu* Fernandes 2004) and is attributed to this unit based on its lithological features, which correspond to those documented in the literature (Fig. 2). Moreover, the facies of the Santo Anastácio Formation are distinctly different from those described for the Adamantina Formation, which is also present in adjacent outcrops in this locality (Fig. 1D).

The depositional context of the Santo Anastácio Formation is a topic of extensive debate. Soares et al. (1980) argue that its deposition primarily occurred within intertwined fluvial systems. In contrast, Fernandes and Coimbra (1994; 2000) suggest that the unit comprises sand sheet deposits accumulated in broad marginal plains of dune complexes, occasionally influenced by sporadic rainwater runoff. According to Paula Silva et al. (2009), these deposits are linked to aeolian systems, formed through the reworking of pre-existing fluvial deposits. Alternatively, Fúlfaró et al. (1999b) propose that the entire Santo Anastácio Formation represents a paleosol developed at the top of the CS. Given the diversity of these perspectives, we adopt a composite model of fluvial-aeolian deposition for this unit, recognizing that each interpretation may contribute complementary aspects of the formation's depositional history.

The age of the Santo Anastácio Formation is also subject of ongoing debate and remains uncertain. Stratigraphically, this formation is positioned beneath the BS and above the CS, separated from these units by erosional unconformities (referred to as surfaces S1 and S2 *sensu* Paula e Silva et al., 2009; and K1 *sensu* Batezelli 2015). Batezelli (2010; 2015) and Menegazzo et al. (2016) proposed a Cenomanian age for the Santo Anastácio Formation based on its stratigraphic relationships. In contrast, Arai and Dias-Brito (2023) suggested that it spans the Turonian to Coniacian interval, based on the maximum ages of the overlying Araçatuba and Adamantina formations. Absolute ages of the Paraná-Etendeka magmatism ($\sim 134.5 \pm 0.5$ Ma; see Rossetti et al., 2018) and the presence of tapejarid pterosaurs in the Goio Erê Formation (Manzig et al., 2014; Kellner et al., 2019) suggest a post-Barremian age for the CS, likely dating from the Aptian to Albian. Conversely, the BS is dated from the Turonian to the Maastriichtian, based on ostracods, charophytes and associated vertebrate fauna (Dias-Brito et al., 2001; Fernandes and Magalhães Ribeiro 2015; Menegazzo et al., 2016). High-precision radioisotopic U–Pb dating of detrital zircons provides a maximum depositional age of 90 ± 21 Ma (late Turonian) for the Araçatuba Formation (Dias et al., 2021) and 87.8 ± 0.12 Ma (middle Coniacian) for the Adamantina Formation (Castro et al., 2018). Given this evidence, and after reviewing the available data, we support a Cenomanian–Turonian age (~ 97 – 93 Ma) for the Santo Anastácio Formation (see Fig. S1).

3. Methodology

3.1. Data acquisition and analysis

The track-bearing layer was uncovered through the careful removal of debris flows (<10 cm), exposing the footprints. These footprints were then outlined with chalk to enhance visibility. Photographs were taken under natural light conditions using both an iPad 10 Pro © and a professional camera Nikon D50 ©. Tracing maps were developed and subsequently converted to digital format in Adobe Photoshop (2024) © for detailed analysis. Linear measurements were performed *in-situ*, directly from the footprint impressions, using a measuring tape and following standard ichnological conventions (e.g., Leonardi et al., 1987; Thulborn 1990; Miller 2007; Sedorko and Francischini 2021). Concerning the terms applied to describe the axony patterns in vertebrate tracks, we followed the revised terminology proposed by Romano et al. (2020).

Given that footprints formed in seasonal environments often show some degree of distortion due to the variations of plasticity in the sedimentary substrate (e.g., Porchetti et al., 2017), the preserved length of the footprint may not correspond precisely to the original length of the trackmaker's autopodium. Consequently, the measurements should be considered approximations, and any estimates derived from them were treated here as extrapolations ($\approx$). Firstly, the preserved footprint length (FL) was used to estimate the trackmaker hip height (H), employing the allometric equations described by Thulborn (1984) and Thulborn and Wade (1984).

To estimate the hip heights (H) of theropod trackmakers, we applied the following equations: (i) $H \approx 3.06FL^{1.14}$, used to estimate H for small-sized trackmakers; (ii) $H \approx 4.15FL + 28.52$, used for mid-to large-sized trackmakers; and (iii) $H \approx 3.49(1.5FL)^{1.02}$, which is used for functional monodactyl trackmakers, where digit III is approximately twice as the length of digits II and IV. For estimating the hip heights (H) of ornithopod trackmakers, we employed the following equations: (iv) $H \approx 3.97FL^{1.08}$, used for cursorial forms; (v) $H \approx 5.06FL^{1.07}$, used for graviportal forms; and (vi) $H \approx 3.76FL^{1.16}$ serves as a general estimate of H for this group (Thulborn 1984). The sizes of bipedal trackmakers were further categorized according to the size classes proposed by Marty et al. (2018), which are based on the maximum length of the footprints: minute-sized ($FL < 10$ cm), small-sized (FL between 10 and 20 cm), medium-sized (FL between 21 and 30 cm), large-sized (FL between 31 and 50 cm) and giant-sized ($FL > 50$ cm).

In contrast, estimating dimensions for quadrupedal dinosaur footprints presents notable challenges, primarily due to the broad plantar area observed in many groups (see González-Riga 2011). Despite these inherent uncertainties, we undertook the calculation of hip height estimates for quadrupedal tracks using two specific equations: (vii) $H \approx 4FW$ and (viii) $H \approx 5.9FL$. The first equation proposed by Lockley (1986), uses the footprint width (FW), while the second, proposed by Thulborn (1990), employs the footprint length (FL). For the partial sauropod trackway, we also applied the equation developed by González-Riga (2011), expressed as (ix) $H \approx 4.586FL$.

Average H values were computed for each footprint and, subsequently, means were determined for each limb. These limb averages were further used to calculate estimates for body length, gait, and relative speeds of partial trackways. For estimating trackmaker body lengths (without considering neck and tail lengths), we used the method based on the ratio of gleno-acetabular distance to hip height (GAD/H) as proposed by Mazzetta and Blanco (2001). To determine gait metrics, two methods were adopted: the first involves dividing stride length by the estimated hip height (λ/H), and the second divides stride length by its pace length (λ/PL). According to the classification made by Thulborn and Wade (1984), these metrics allow the raking of

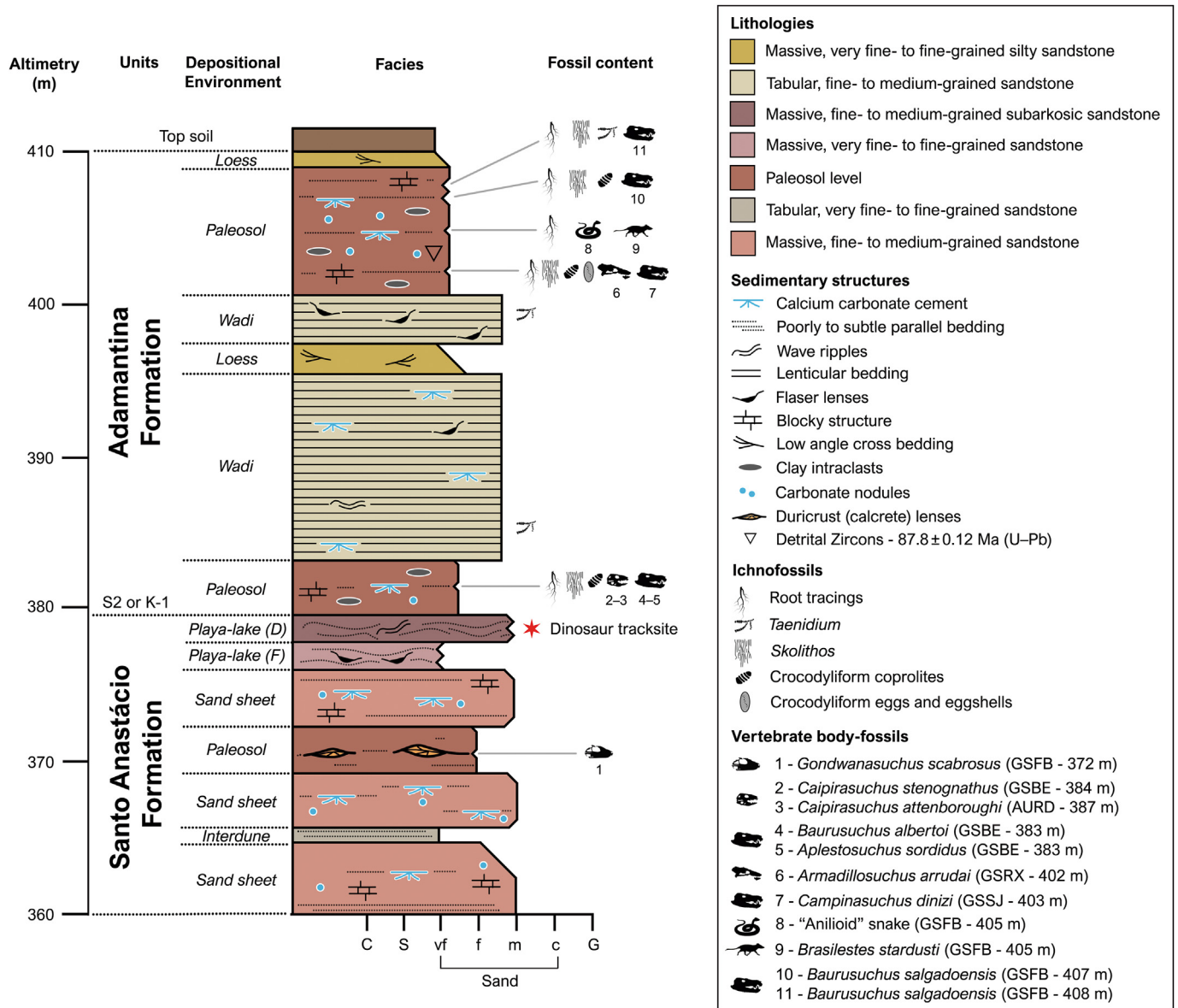


Fig. 2. Stratigraphic section in the General Salgado area. Sedimentary succession and position of the fossil content were based on field observations of the Santo Anastácio Formation (Cenomanian–Turonian) and correlated with the geologic columns of the Adamantina Formation (middle Coniacian) provided by [Carvalho et al. \(2013\)](#) and [Castro et al. \(2018\)](#). Depositional environments followed the models proposed by [Basilici and Sgarbi \(2012\)](#). Vertebrate body-fossils were positioned in the column based on altimetry acquired at fossil sites (in parentheses). The new tracksite laid in a stratum formed during the drying phase of a playa-lake system (D), which overlies a layer deposited under flooding phase (F). Abbreviations: AURD, road near Auriflâma; GSBE, General Salgado - Boa Esperança Farm; GSFB, General Salgado - Buriti Farm; GSRX, General Salgado - Rao X Farm; GSSJ, General Salgado - São José Farm.

dinosaur gaits into three categories: “walking” (gait values less than 2.0), “trotting” (gait values ranging from 2.0 to 2.9), and “running” (gait values exceeding 2.9).

To further characterize the relative speeds (V) of these trackmakers, we employed the equation proposed by [Alexander \(1976\)](#) as revised by [Thulborn \(1984; 1990\)](#): $(x) V \approx 0.25 G^{0.5} \lambda^{1.67} H^{-1.17}$. In this equation, G is the constant acceleration of free fall (9.8 ms^{-2}), and λ represents the stride length in centimeters. This formulation allows for the estimation of the trackmaker’s speed in meters per second.

3.2. Ichnotaxonomy

Although parataxonomy has been extensively applied in the study of trace fossils, we have chosen not to adhere the traditional assignment of ichnofamilies to dinosaur tracks (e.g. *Grallatoridae*, *Iguanodontopodidae*). This approach often carries

significant biological implications and can potentially lead to misinterpretations by conflating ichnotaxa with taxa defined by body fossils. Instead, we have analyzed the trackmakers and classified them within the current phylogenetic framework of Dinosauria. While we refrained from assigning ichnofamilies, the use of ichnogenera remains valuable for establishing correlations with other ichnofaunas and ichnofacies and is employed here for comparative purposes. In our analysis, each trackmaker is associated with suprageneric taxa based on its inferred autopodial anatomy, considering the temporal and geographic ranges of the assigned clades ([Carrano and Wilson 2001](#)).

3.3. Abbreviations

AC, Hitchcock Ichnology Collection, Pratt Museum of Amherst College, Amherst, Massachusetts, USA; AÇPI, Açu - Fazenda dos

Pingos tracksite, Açú, Rio Grande do Norte, Brazil; **ALBA**, Alcântara - Praia da Baronesa tracksite, Alcântara, Maranhão, Brazil; **CICC**, Cianorte - Córrego Catingueiro tracksite, Cianorte, Paraná, Brazil; **GSFB**, General Salgado - Fazenda Buriti tracksite, General Salgado, São Paulo, Brazil; **IGM**, Mongolian Institute of Geology, Ulaan Bataar, Mongolia; **LAPEISA**, Laboratório de Paleontologia e Evolução de Ilha Solteira, Universidade Estadual Paulista 'Julio de Mesquita Filho', Ilha Solteira, São Paulo, Brazil; **LPP-IC**, Laboratory of Paleoecology and Paleoichnology, Universidade Federal de São Carlos, São Carlos, São Paulo, Brazil; **LPRP/USP**, Laboratório de Paleontologia de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, São Paulo, Brazil; **MLP**, Museo de La Plata, La Plata, Buenos Aires, Argentina; **MOR**, Museum of the Rockies, Bozeman, Montana, USA; **MPA**, Material Paleontológico de Araraquara, São Carlos, São Paulo, Brazil; **MPCN-PV**, Museo Patagónico de Ciencias Naturales, General Roca, Río Negro, Argentina; **MPCO.V**, Vertebrate collection, Museu de Paleontologia de Cruzeiro do Oeste, Cruzeiro do Oeste, Paraná, Brazil; **MPMA**, Museu de Paleontologia de Monte Alto 'Prof. Antonio Celso de Arruda Campos', Monte Alto, São Paulo, Brazil; **MUC-Pv**, Museo de Geología y Paleontología, Universidad Nacional del Comahue, Neuquén, Argentina; **MZSP-PV**, Paleovertebrate collection, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; **PPUH**, Porto Primavera - Usina Hidroelétrica tracksite, Rosana, São Paulo, Brazil; **QM F**, Queensland Museum Fossil, Brisbane, Queensland, Australia; **SLIM**, São Luís - Ilha do Medo tracksite, São Luís, Maranhão, Brazil; **SOES**, Sousa - Fazenda Estreito tracksite, Sousa, Paraíba, Brazil; **SOPP**, Sousa - Passagem das Pedras tracksite, Sousa, Paraíba, Brazil; **UFRJ-DG**, Reptiles collection, Departamento de Geologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil.

4. Description of the ichnocoenosis

The newly discovered ichnocoenosis (GSFB) was identified by AAG in December 2022 at Buriti Farm, located in the Prudêncio e Moraes District of General Salgado Municipality, in the northwestern region of São Paulo State, Brazil. The track-bearing layer is situated in a ravine along the lateral banks of a farm road, exposed at an elevation between 379 and 380 m. This layer is isolated, with no direct stratigraphic contact with the overlying Adamantina Formation (Figs. 1–2). The footprints were preserved within a centimeter-thick layer of subarkosic, fine to medium-grained sandstone that exhibits a purplish coloration and is characterized by highly siliceous cementation. The slab containing the tracks was partially covered by soil and rests horizontally upon a decimeter-thick, tabular layer of very fine to fine-grained reddish sandstone that is highly cemented and features small oxide concretions and calcite lenses.

The preserved ichnological assemblage includes tracks and undertracks in a concave epirelief representing a minimum of 11 different individuals (GSFB-01–11), distributed in a relatively small surface area of 3 m². This assemblage comprises two well-preserved isolated footprints, 14 partial footprints (primarily undertracks), and three partial trackways (Fig. 3). Due to significant weathering observed at the outcrop, efforts were made in August 2023 to collect some parts of the slab, currently housed in the Museu de Zoologia da Universidade de São Paulo, Brazil (MZSP-PV 1336a–d; see supplementary data).

4.1. Morphology of the tracks

4.1.1. GSFB-01

Based on their proportions, represents probable consecutive footprints of the left and right feet and both are orientated to the west (Fig. 4). The left footprint shows only the proximal part of the plantar pad and is almost completely covered by sediment. In

contrast, the right one is a well-defined tridactyl footprint overlying another track (GSFB-02). In both impressions of GSFB-01, the plantar pad has similar dimensions (Table 1) and has the rear margin is indented by a posteromedial notch, forming incipient heel-like bulges. Some regions of the plantar pad surface show multiple small and rounded pits, especially in the right footprint, which may correspond to a negative skin impression of reticulated scales (Fig. 4C; see Hendrickx et al., 2022). The right footprint is digitigrade and mesaxonic with rounded hypexes, particularly the digits II–III, each terminating in well-marked but relatively short unguals, and lacks a hallux impression. In general, the GSFB-01 tracks are longer than wide (length-to-width ratio equal to 1.84), with digit III impression 1.5 times longer and more robust than outer digits. Digit II is a narrow impression, slightly shorter (13.4 cm) than digit IV (14.5 cm). Digit IV impression is almost completely infilled, but it is more divaricated (30.7°) than digit II (26.3°) and slightly recurved medially in relation to the median axis of the footprint.

4.1.2. GSFB-02

Comprises a partial impression of the left pes and an undertrack of the right pes, both orientated to the west and probably made by the same individual. The left pes only retains the impression of digit III, which is superimposed by the right foot of GSFB-01 (Fig. 4). Like the latter track, the digit III of GSFB-02 appears robust and has a well-defined but short ungual with an acute hypex. The undertrack of the right pes was delineated by the relative position of the preserved ungual marks and is about 40 % smaller than GSFB-01 (Table 1). The impression is tridactyl, digitigrade and mesaxonic, lacking a hallux impression. Digit IV is slightly longer (11.3 cm) than digit II (10.2 cm), but significantly smaller than digit III (± 12.5 cm). Digit III appears to be 50 % less elongated than GSFB-01, ruling out the possibility that it originates from the same individual. The plantar pad also features a rear margin that is indented by a posteromedial notch but appears less pronounced than in GSFB-01. Like the latter track, GSFB-02 exhibit similar length-to-width ratio values (1.81), as well as an angle of divarication between digits (31°).

4.1.3. GSFB-03

Consists of two consecutive partial tracks, oriented to S–SW. Both are tridactyl, digitigrade, and mesaxonic. These footprints are preserved as faintly marked impressions, mostly preserving their right side (Fig. 5), indicating that they likely represent undertracks of the left and right pes of a same individual. Although poorly preserved, its general shape and dimensions could be accessed based on the preserved portions of some digits and ungual marks. Both left and right pes exhibit similar sizes (Table 1). In general, GSFB-03 tracks appear longer than wide, with a length-to-width ratio of 1.75–1.76. The plantar pad is broad, and its proximal portion is almost convex in-shape, lacking notches or heel-like bulges. Digits II and IV are subequal in length, with digit III slightly longer than outer digits (around 15 %), but all appear slender and display slightly acute hypexes. The unguals are well-marked in the substrate. Nonetheless, they appear to be proximodistally short and slightly broader in respect to other similar tracks in this ichnocoenosis (e.g., GSFB-01).

4.1.4. GSFB-04

Includes small partial impressions of the left and right pes, orientated to W–SW, probable made by the same individual (Fig. 5). Although partially preserved, GSFB-04 tracks appear to be tridactyl, digitigrade, and mesaxonic, lacking hallux marks. Based on preserved portions of both footprints, GSFB-04 appear longer than wide, with a length-to-width ratio averaging 1.82–1.93. The

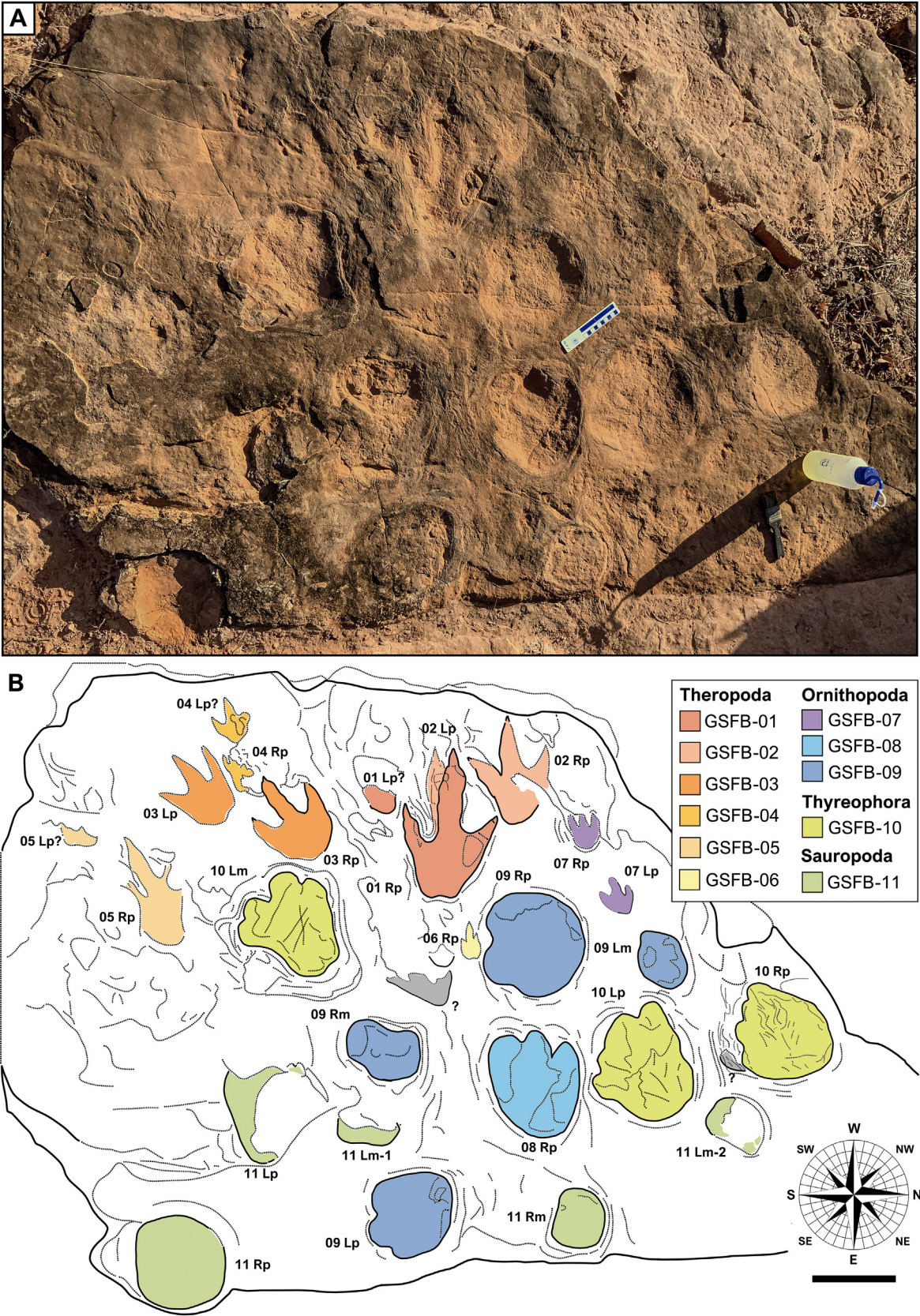


Fig. 3. Tracksite at the Buriti farm. **A**, dinoturbated slab under natural light; **B**, interpretative outline drawing with the ichnites separated by colors, indicating each individual in the ichnocoenosis. Dotted lines represent reconstructed parts of the track silhouettes and the main surface distortions in the sedimentary substrate, while solid lines silhouettes correspond to well-preserved tracks. Abbreviations: L, left; m, manus; p, pes; R, right. Scale bar equals 20 cm.

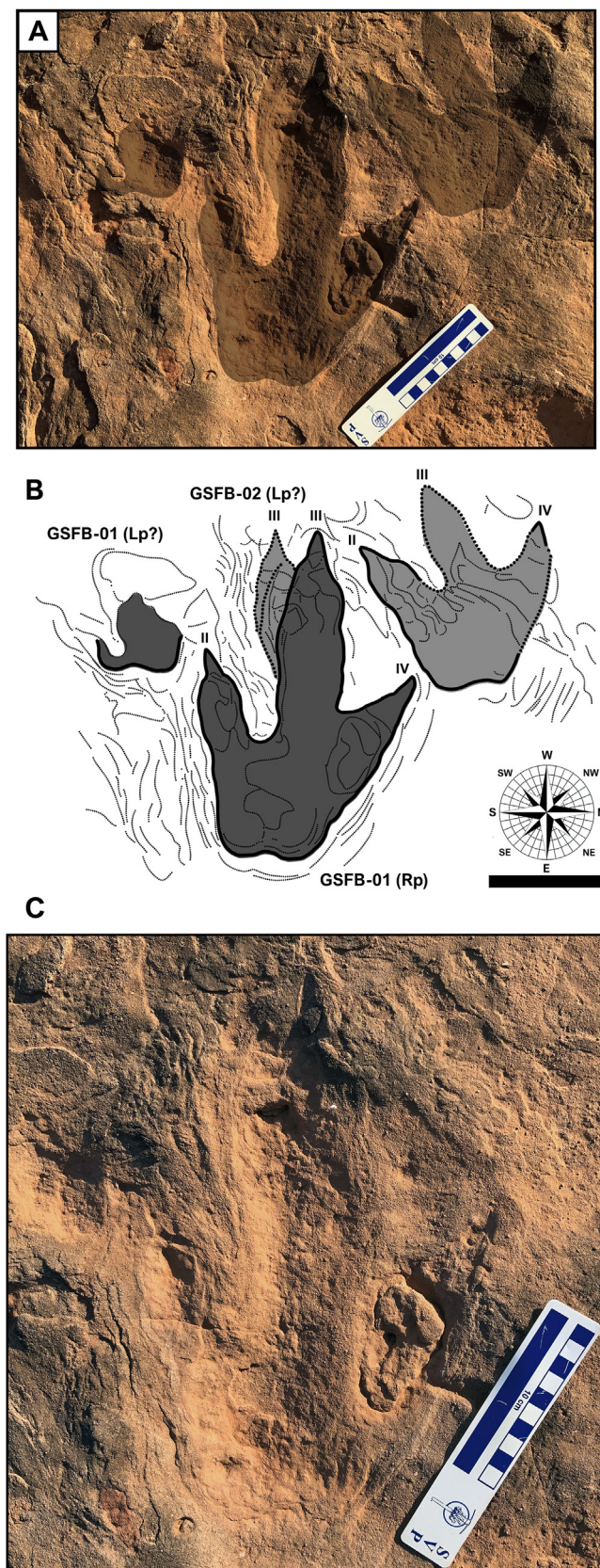


Fig. 4. Theropod tracks and undertracks (GSFB-01 and GSFB-02). **A**, dinoturbated slab with shaded footprints; **B**, interpretative outline drawing. Dark grey represents well-defined tracks and light grey indicate undertracks. Large-dotted lines represent reconstructed parts of the track silhouettes, while small-dotted lines correspond to surface distortions in the sedimentary substrate. Roman numerals indicate the position

right pes is almost covered with sediment, mainly exposing the digit IV. The left pes is almost fully exposed, particularly in the digits III and IV. Digit II is faintly impressed and the plantar pad is partially infilled with sediment, hindering detailed descriptions. Preserved digits III and IV on both footprints display acute hypexes and have an angle of divarication ranging 27.3° – 28.7° , being also subequal in size (Table 1). In contrast, the angle between digits II–III appear more pronounced (37.2°).

4.1.5. GSFB-05

Comprises poorly preserved consecutive undertracks of the left and right pes, both orientated to W–SW. The right impression preserves only its proximal portion, while in the left one, although incomplete, it is possible to discern both digits and the plantar portion (Fig. 5). The left footprint is tridactyl, digitigrade and mesaxonic, and exhibits acute hypexes. It appears longer than wide (Table 1), displaying a high length-to-width ratio value (1.90), likewise other tracks in this ichnocoenosis (GSFB-04). By contrast, the angle of divarication of outer digits in respect to the digit III is less pronounced than in other similar tracks, averaging 22° – 29° .

4.1.6. GSFB-06

Corresponds to an isolated right footprint orientated to the west, completely infilled, of a small functionally monodactylous trackmaker (Fig. 6). The footprint is tridactyl, digitigrade and mesaxonic, with digit III very robust in respect to the outer digits and concerning 75 % of the total length of the footprint (Table 1). In addition, GSFB-06 exhibits the highest length-to-width-ratio values in the ichnocoenosis (2.09). Both digits exhibit acute hypexes, with the unguals appearing long and well-developed. The angle divarication of outer digits is similar to other tracks (e.g., GSFB-05), averaging 24° – 29° , with digit IV slightly longer than digit II, but less robust than the former. The plantar portion is almost circular and features a rear margin indented by an incipient posteromedial notch but lacking developed heel-like bulges.

4.1.7. GSFB-07

Consists of two partially covered and poorly preserved consecutive footprints, oriented to W–SW (Fig. 7). Both are tridactyl, digitigrade, mesaxonic, and made by a small-sized trackmaker (Table 2). Footprint impressions seem slightly longer than wide, with length-to-width-ratio averaging 1.56–1.58. The plantar pads display a convex, nearly ‘V-shaped’ rear margin, lacking marked notches. The medial portion appears slightly more pronounced posteriorly than the lateral side, probably due to development of heel-like bulges. Digits are subequal in length and splayed, forming an arc wider than the plantar pad. All digits exhibit rounded hypexes with pointed, proximodistally short unguals. The angle of divarication between digits is high when compared to other tracks (see above), ranging from 30° – 34° in the digits II–III and 38° – 43° in digits III–IV.

4.1.8. GSFB-08

Includes an isolated but well-preserved footprint, probably the right one based on the development of left digit (Fig. 8). The track is tridactyl, digitigrade, mesaxonic and longer than wide (Table 2) and orientated to the west. The plantar pad exhibits a “U-shaped” rear margin, with a length-to-width ratio of 1.70. The digits are short and have rounded hypexes, with the angle of divarication of the outer digits being less than 29° . Although partially covered, the

of each digit; **C**, detail of GSFB-01 (MZSP-PV 1336a), depicting several small, rounded pits in the plantar surface. Abbreviations: L, left; p, pes; R, right. Scale bar equals 10 cm.

Table 1
Footprint measurements and estimated hip height (*H*) for theropod tracks and undertracks (in cm).

Measures	GSFB-01	GSFB-02	GSFB-03		GSFB-04		GSFB-05	GSFB-06
	R pes	R pes	R pes	L pes	R pes	L pes	R pes	R pes
Maximum proximodistal length (<i>FL</i>)	29.4	19.0*	25.7	23.8	14.3	13.1*	21.9*	8.6
Digit II, maximum proximodistal length	13.4	10.2	13.9	13.5	6.6	—	13.2*	3.4
Digit III, maximum proximodistal length	22.0	12.5*	17.9	17.5	10.0	10.7*	10.1*	6.6
Digit IV, maximum proximodistal length	14.5	11.3	13.5	12.4	9.1	8.7	15.1	3.9
Maximum distance between digits II–IV	18.8	16.0	17.4	16.6	—	—	15.1*	4.4
Maximum width of the plantar portion (<i>W</i>)	16.0	10.5*	14.7*	13.5*	7.4*	7.2*	11.5	4.1
Angle of divarication between digits II–III	26.3°	31.6°	40.5°	39.3°	37.2°	—	22.8°	29.2°
Angle of divarication between digits III–IV	30.7°	31.0°	43.1°	40.3°	28.7°	27.3°	29.1°	24.4°
Length-to-Width ratio (<i>FL</i> / <i>W</i>)	1.84	1.81	1.75	1.76	1.93	1.82	1.90	2.09
<i>H</i> estimate for small-bodied forms	144.26	88.06	124.00	113.56	63.30	57.27	103.02	35.80
<i>H</i> estimate for large-bodied forms	150.41	107.58	135.26	127.33	87.70	82.72	119.24	—
<i>H</i> estimate for monodactylous forms	—	—	—	—	—	—	—	47.66
Average <i>H</i> values	147.33	97.82	129.63	120.45	75.50	69.99	111.13	41.73
Mean			125.04		72.75			

An asterisk (*) marks the measurements based on preserved portions, while a dash (–) denotes when the region is not preserved or indicates measurements that could not be taken. Abbreviations: L, left; R, right.

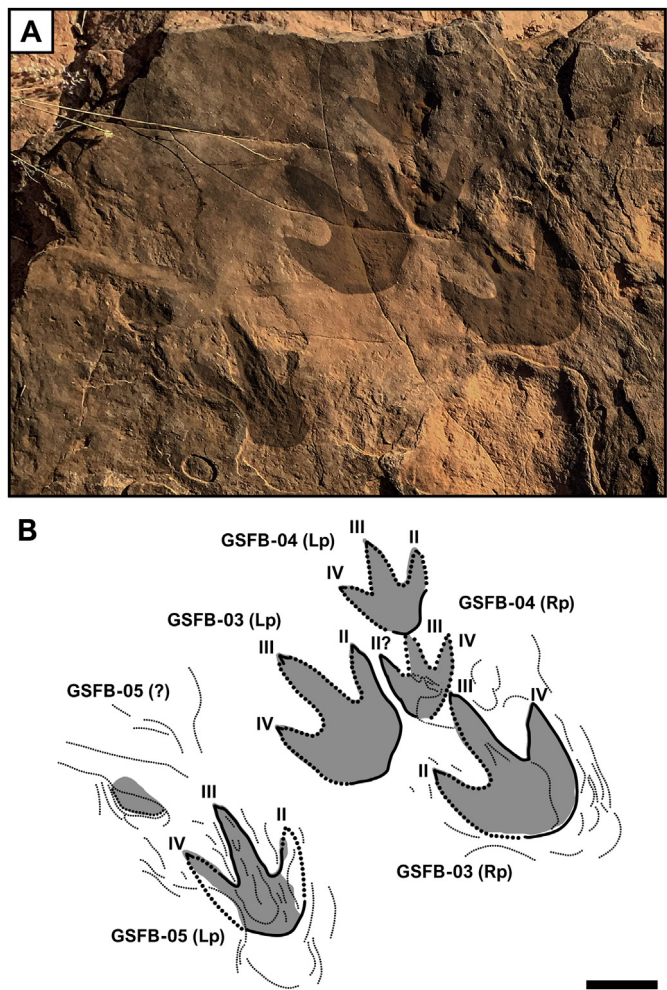


Fig. 5. Partial theropod tracks and undertracks (GSFB-03 to GSFB-05). **A**, dinoturbated slab with shaded footprints; **B**, interpretative outline drawing. Large-dotted lines represent reconstructed parts of the track silhouettes, while small-dotted lines correspond to surface distortions in the sedimentary substrate. Roman numerals indicate the position of each digit. Abbreviations: L, left; p, pes; R, right. Scale bar equals 10 cm.

internal digit appears broader and slightly longer than the other digits, resembling a hoof-like toe, and the median and right digits are almost equally wide. The left digit likely corresponds to the inner digit (II) since it is more developed in large bipedal animals due to gravitational supporting of the body mass (Hildebrand and Goslow 1998). The pad of median digit (III) is broad and subequal in width to the posterior rear margin. In contrast, the outer digit (IV) is anteroposteriorly shorter than the other digits, reaching about 75 % of the breadth from median digit.

4.1.9. GSFB-09

Consists of a partial trackway containing four consecutive footprints orientated S–SE (Fig. 9A). They comprise paired footprints of manus and pes of a graviportal trackmaker, two of them (right manus and left pes) infilled with sediment (Fig. 9B, E). The manus tracks are almost elliptical, wider than long (Table 2) and show no impressions of pollex. However, both have heel-like projections on the posteromedial edge (Fig. 9B–C) and are slightly rotated negatively (~37°). Tracks from pes are as long as wide, tridactyl, digitigrade and mesaxonic. The plantar pad exhibits a broad rounded rear margin, with a length-to-width ratio averaging 1.46 (right pes in a probable stepping move; Fig. 9D) to 1.58 (left pes in a probable lifting move; Fig. 9E). Digits have wide and rounded hypexes, with digit III being longer than the outer digits. In addition, digit III in both feet appears to be a hoof-like toe and broader than the outer digits, with digit IV slightly longer than digit II. The angle of divarication with digit II varies little (44.5° on the right pes and 47.7° on the left pes), while between digits III–IV it varies strongly (53.6° on the left pes and 34.4° on the right pes).

4.1.10. GSFB-10

Comprises a partial trackway in S–SW direction with three non-consecutive footprints of a quadrupedal trackmaker (Fig. 10A). All footprints are tetradactyl and have short hypexes, nearly rounded distally. GSFB-10 tracks are semiplantigrade and as long as wide (Table 3), with a length-to-width ratio ranging 1.0–1.1. The plantar pads are broad, and bears round rear margins. One of the footprints (Fig. 10B) have a ‘U-shaped’ rear margin, slightly narrower posteriorly (Fig. 10B) than the others (Fig. 10C–D). This footprint is paraxonic and strongly rotated negatively (~60°), with the angle of divarication between digits I–II and digits III–IV equal (21°).

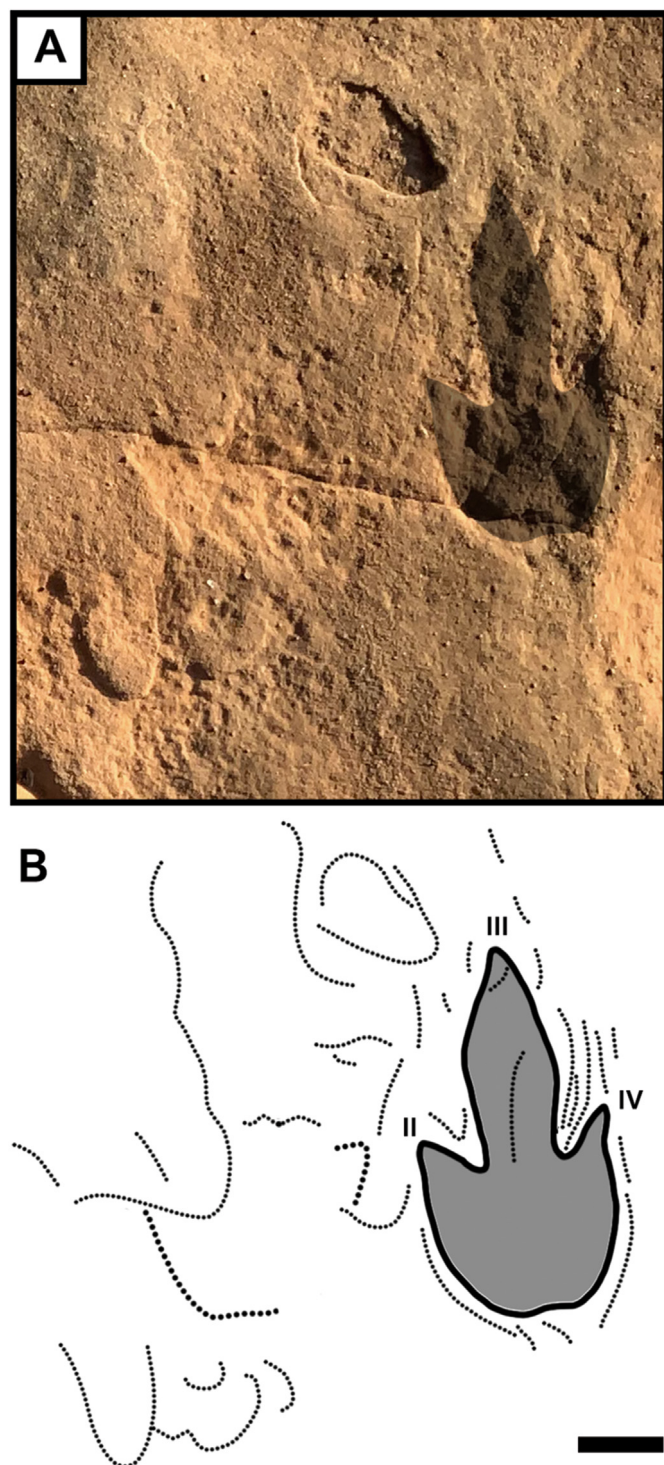


Fig. 6. Track of a minute-sized theropod (GSFB-06). **A**, dinoturbated slab with shaded footprint; **B**, interpretative outline drawing. Large-dotted lines represent reconstructed parts of the track silhouettes, while small-dotted lines correspond to surface distortions in the sedimentary substrate. Roman numerals indicate the position of each digit. Scale bar equals 2 cm.

However, the angle of divarication between the digits II and III is notably high (33°) in this footprint, being those digits apparently marked by a notch (Fig. 10B). In contrast, both posterior footprints lack a median notch. They are also negatively rotated, but to a lesser degree than the anterior footprint ($\sim 40^\circ$). Paraxony in the posterior impressions are also more incipient, with a divarication between

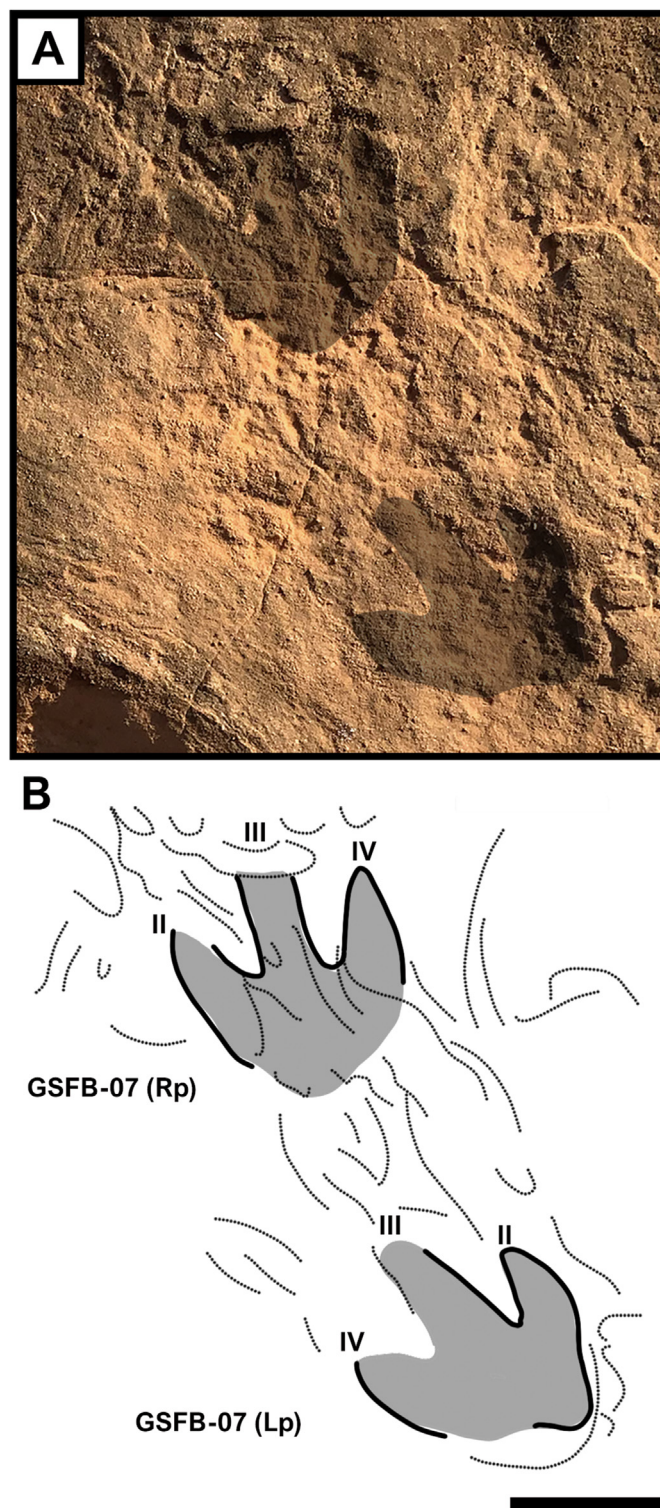


Fig. 7. Partial track and undertrack of a small-sized bipedal ornithomorph (GSFB-07). **A**, dinoturbated slab with shaded footprint; **B**, interpretative outline drawing. Solid lines represent reconstructed parts of the track silhouettes, while dotted lines correspond to surface distortions in the sedimentary substrate. Roman numerals indicate the position of each digit. Abbreviations: L, left; p, pes; R, right. Scale bar equals 5 cm.

digits I–II averaging 22° – 32° , in digits II–III 28° – 37° and between digits III–IV 14° – 16° . The anterior footprint probably corresponds to a manus impression, based on the morphology of its digits and comparisons with similar footprints (see below in section 4.2.2.4.).

Table 2Footprint measurements and estimated hip height (*H*) for ornithopod tracks and undertracks (in cm).

Measures	GSFB-07		GSFB-08		GSFB-09		L pes
	R pes	L pes	R pes	R manus	L manus	R pes	
Maximum proximodistal length (<i>FL</i>)	8.5	8.9	25.7	14.8	12.3	26.2	23.0
Digit II, maximum proximodistal length	6.3	4.1*	15.2	12.0	7.9*	13.4	10.3
Digit III, maximum proximodistal length	6.3	6.5	14.4	10.7	10.8	15.2	13.5
Digit IV, maximum proximodistal length	5.5*	4.7*	13.7	10.4	7.0*	14.0	12.9
Maximum distance between digits II–IV	6.8	6.4	16.8	18.8	15.3	20.0	17.1
Maximum width of the plantar portion (<i>W</i>)	5.4	5.7	15.1	11.8	9.9*	17.9	14.6
Angle of divarication between digits II–III	30.5°	38.8°	28.4°	—	—	44.5°	47.7°
Angle of divarication between digits III–IV	34.7°	43.6°	28.9°	—	—	53.6°	34.4°
Length-to-Width ratio (<i>FL/W</i>)	1.58	1.56	1.70	1.25	1.24	1.46	1.58
<i>H</i> estimate for cursorial forms	40.15	42.24	—	—	—	—	—
<i>H</i> estimate for graviportal forms	—	—	163.22	—	—	166.96	145.28
General <i>H</i> estimate	45.13	47.66	162.45	85.84	69.10	166.49	143.18
Average <i>H</i> values	42.64	44.95	162.83	—	—	166.72	144.23
Mean	43.80	—	—	77.47	—	155.48	—

An asterisk (*) marks the measurements based on preserved portions, while a dash (—) denotes when the region is not preserved or indicates measurements that could not be taken. Abbreviations: L, left; R, right.

The similarity in dimensions between this and the more posterior footprints, identified here as pes impressions, is attributed to taphonomic factors due to the trackmaker's displacement effort in a more plastic substrate, evidenced by the fluidization marks bordering the footprint.

4.1.11. GSFB-11

Corresponds to a partial trackway moving in a N–NW direction (Fig. 11A). All footprints are semi-circular and almost 'D-shaped', as long as wide, lacking major morphological details or marks from digits (Fig. 11A–B). The trackway consists of five footprints that exhibit a conspicuous heteropody: two corresponding to impressions from pes, and three correspond to tracks of manus. Two of them are partially covered by the substrate and one footprint from manus is entirely infilled by sediment (Fig. 11C). However, both appear to have been laid on the same surface, suggesting that they were probably made by the same individual. The left footprints from manus are strongly rotated positively (43°–86°) while the right footprint is notably less rotated (33°). All of them lacks pollex impressions and have a length-to-width ratio averaging 0.80–0.90. The two pedal footprints dip further into the substrate compared to some of the manual tracks (Fig. 11B) and are about twice as long as the manus tracks (Table 3), with a length-to-width ratio equal to 0.96.

4.2. Identity of the trackmakers

The trackmakers within the GSFB ichnocoenosis can be attributed to the principal dinosaur lineages: Ornithischia, Theropoda, and Sauropoda. Within these lineages, distinct morphotypes have been identified based on their morphological and morphometric differences. Using the track measurements provided in Tables 1–3, we inferred the height of the hip-joint of each individual. Estimated heights indicate a predominance of medium to large-sized trackmakers in the Santo Anastácio Formation ichnofauna (Fig. 12), with only two small morphotypes being present (GSFB-06 and GSFB-07).

4.2.1. Theropoda

Theropods are the most distinctive group within the GSFB ichnocoenosis and comprise half of the identified tracks. The six individuals attributable to theropod trackmakers (GSFB-01–GSFB-06) exhibit tridactyl and mesaxononic footprints, in general longer than wide, with proximodistally elongated hypoxes terminating in sharp unguals. These footprints have been classified into four

distinct morphotypes (1–4) based on the relative sizes of the digits, the angle of divarication between digits, and the length-to-width ratios of the tracks, as well as by comparisons with other ichnotaxa and preserved theropod feet.

4.2.1.1. Morphotype 1. Morphotype 1 includes medium-to large-sized trackmakers, with estimated hip heights averaging 147 cm for GSFB-01 and 97.8 cm for GSFB-02 (Fig. 12A). This morphotype is characterized with a narrow proximally plantar area, with a rear margin indented by a median notch. Digit III is notably longer and more robust than the outer digits, with digit IV being relatively longer, more recurved medially, and more closely appressed to digit III compared to digit II (see Table 1). Additionally, the angle of divarication between the digit's ranges from 26° to 31°, and the length-to-width ratio averages between 1.80 and 1.90.

Mid-to large-bodied theropod trackmakers are commonly associated with the ichnogenus *Eubrontes* (e.g., Leonardi 1994; Lockley and Meyer 2000; Da Silva et al., 2012; Manes et al., 2021). The extensive temporal range of their occurrences, spanning from the Early Jurassic to the Early Cretaceous, suggests that *Eubrontes* might represent a 'wastebasket' ichnotaxon. *Eubrontes*-type tracks are characterized by large functionally tridactyl footprints (*FL* > 25 cm) with a relatively short digit III, divarication of outer digits averaging 25°–40°, a broad plantar area, and an infrequently impressed hallux (Olsen et al., 1998, p. 590). While Morphotype 1 shares with *Eubrontes* a narrow plantar pad mildly indented by a median notch, it differs in that the outer digits are nearly equal in length and diverge laterally from the midline of the footprint in the latter (Fig. 13A–C).

Morphotype 1 is similar to other theropod track occurrences from the Cenomanian of northeastern Brazil (Carvalho 2001) and Argentina, such as *Abelichnus astigarrae* (Calvo 1991; Calvo and Rivera 2018), where digit IV is slightly longer than digit II and appressed to the digit III (Fig. 13D–E). This condition aligns with the pedal morphology seen in Avetheropoda, such as carnosaurians and coelurosaurians, where the non-ungual pedal phalanges in digit IV are more elongated proximodistally than in Ceratosauria (Fig. 14I–J; Carrano 2007; Carrano et al., 2012). The estimated hip heights of Morphotype 1 correspond to medium-sized theropod trackmakers, thus excluding the possibility that these footprints were produced by small coelurosaurians.

In the Cenomanian–Turonian, body fossils of medium to large-sized avetheropods in Brazil include isolated carcharodontosaurid and megaraptoran vertebrae from the Açu Formation in Rio Grande

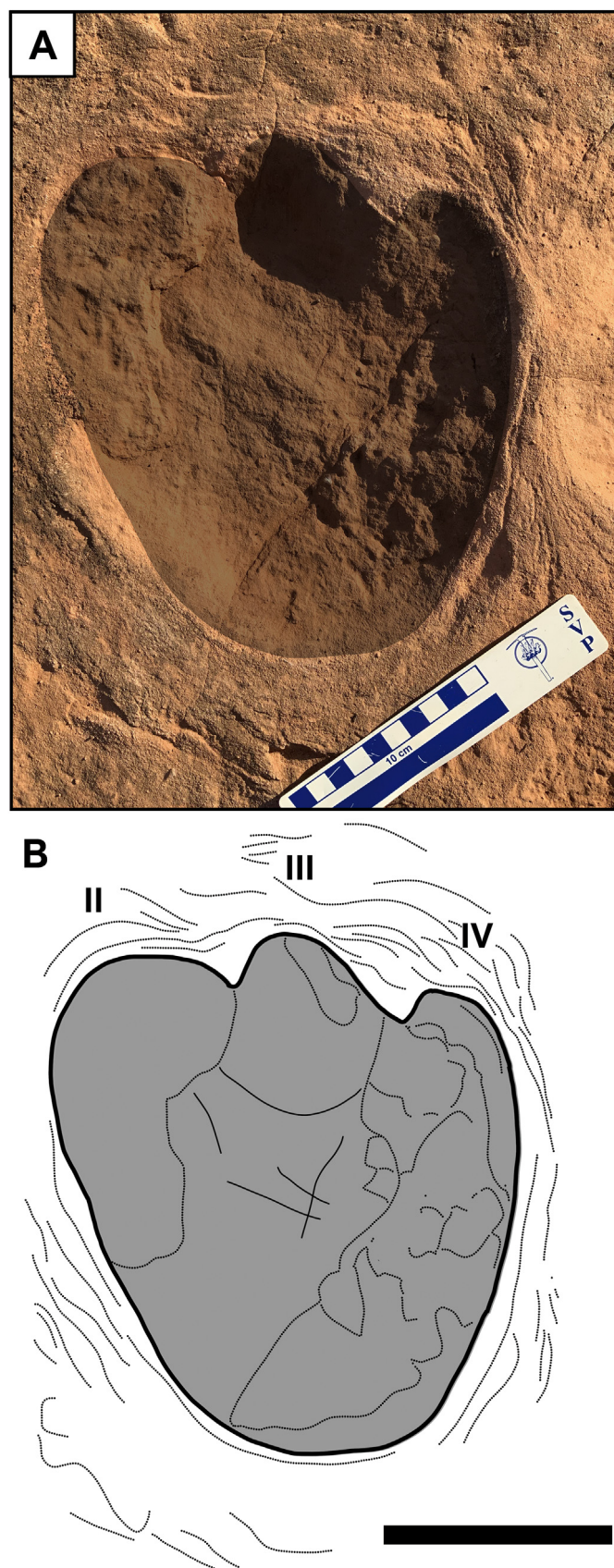


Fig. 8. Isolated track of a medium-sized bipedal ornithopod (GSFB-08, MZSP-PV 1336-b). **A**, dinoturbated slab with shaded footprint; **B**, interpretative outline drawing, with dotted lines exhibiting the main surface distortions in the

do Norte State (Pereira et al., 2020), isolated bones and multiple carcharodontosaurid teeth from the Alcântara Formation in Maranhão State (Medeiros et al., 2014). Although several teeth and a fragmentary left maxilla recovered from the Bauru Group were initially attributed to this group (e.g., Candeiro et al., 2004; Candeiro et al., 2006; De Azevedo et al., 2013), these specimens have been currently reinterpreted as belonging to abelisaurids (Delcourt and Grillo 2018; Delcourt et al., 2020; Giaretta et al., 2024). Nevertheless, none of these occurrences preserve pedal elements, restricting further comparisons.

In Argentina, the group is represented by middle-sized megaraptorans like *Aoniraptor libertatem* and *Gualicho shinyae*, and large-bodied carcharodontosaurids such as *Mapusaurus rosae* and *Taurovenator violantei* from the Huincul Formation, as well as *Giganotosaurus carolinii* from the Candeleros Formation (Coria and Salgado 1995; Coria and Currie 2006; Motta et al., 2016; Apesteguía et al., 2016). Notably, *Gualicho shinyae* preserves a nearly complete left foot, showing remarkable similarities with tracks of Morphotype 1 (Fig. 13I), suggesting that their trackmakers likely correspond to related forms. This is expected given megaraptorans were also present in the Upper Cretaceous of Brazil (e.g., Méndez et al., 2012; Martinelli et al., 2013; Salles et al., 2017).

4.2.1.2. Morphotype 2. Morphotype 2 (GSFB-03) corresponds to a medium-sized trackmaker, with estimated hip heights averaging 127–135 cm (Table 1). This morphotype differs from Morphotype 1 in several key aspects, particularly in the development of the outer digits, which are of equal lengths. In this morphotype, digit III is slightly longer than digits II and IV, which are subequal in length. Tracks from Morphotype 2 are characterized by a length-to-width ratio of 1.75–1.76, a broad plantar pad without a proximomedial notch or heel-like bulges in the rear margin, and an angle of divarication between digits ranging from 39° to 43°. Moreover, both tracks in this morphotype lack an impression of the hallux, and the unguals are proximodistally shorter compared to those in Morphotype 1. These features also set Morphotype 2 apart from *Eubrontes*-like tracks (Fig. 13C). Additionally, the outer digits in Morphotype 2 are straight and uncurved, despite the high angle of divarication from the median line (Fig. 13F–H), resembling the condition seen in *Bressanichnus patagonicus* from the Candeleros Formation (Calvo 1991; Calvo and Rivera 2018).

When compared to medium-sized theropod taxa, the morphological traits exhibited by *Bressanichnus* and Morphotype 2 are consistent with those found in preserved pes of abelisaurid ceratosaurs (Fig. 13J). Abelisauridae is a diverse group of theropod dinosaurs known for their extremely reduced forelimbs and heavily sculptured, short, and high skulls (Novas et al., 2013). The temporal distribution of abelisaurids spans from the Middle Jurassic to the Late Cretaceous, being particularly abundant in South America after the Cenomanian (Pol and Rauhut 2012; Zaher et al., 2020). Contemporary occurrences of medium-sized abelisaurids, comparable to the trackmaker of Morphotype 2, include taxa such as the brachyrostrans *Ilokelesia aguadagrandensis*, *Skorpiovenator bustingorryi* and *Tralkasaurus cuyi*, all from the Huincul Formation (Coria and Salgado 1998; Canale et al., 2009; Cerroni et al., 2020). The former taxon, *Ilokelesia aguadagrandensis*, is particularly similar in size to the trackmaker associated with Morphotype 2 (Fig. 12A).

4.2.1.3. Morphotype 3. Morphotype 3 is represented by the partial tracks and undertracks of GSFB-04 and GSFB-05. The trackmakers correspond to small-to medium-sized individuals (Fig. 12A). The

sedimentary substrate. Roman numerals indicate the position of each digit. Scale bar equals 10 cm.

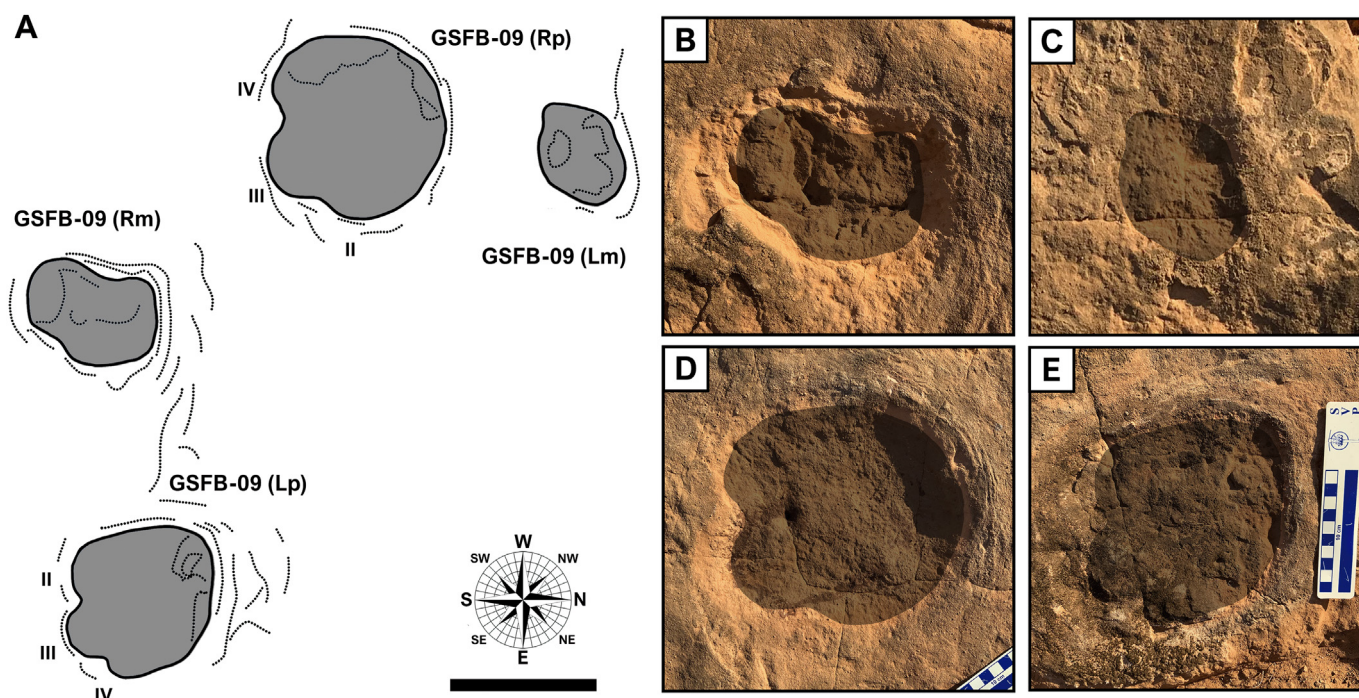


Fig. 9. Partial trackway of a graviportal ornithomorph (GSFB-09). **A**, interpretative outline drawing, with dotted lines exhibiting the main surface distortions in the sedimentary substrate; **B**, shaded detail of the left manus impression; **C**, shaded detail of the right manus impression; **D**, shaded detail of the right pes impression; **E**, shaded detail of the infilled left pes impression. Roman numerals indicate the position of each digit. Abbreviations: L, left; m, manus; p, pes; pmh, posteromedial heel; R, right. Scale bars equal 20 cm (A) and 10 cm (B–E).

estimated hip height for GSFB-04 ranges from 57 to 63 cm using equation (i) and 82–87 cm using equation (ii), while GSFB-05 has an estimated hip height averaging between 103 and 119 cm. Although these tracks are poorly preserved, the shared characteristics suggest they belong to single morphotype. These features include a high length-to-width ratio (approximately 1.90) and an angle of divarication between digits ranging from 22° to 29° .

Compared to other morphotypes found in the locality, the development of digit III in Morphotype 3 is similar to that observed in Morphotype 1, with digit IV being slightly more developed than digit II, and digit III being slightly longer than the outer digits (Table 1). However, the plantar pad of Morphotype 3 lacks the median notch and heel-like bulges characteristic of Morphotype 1, instead resembling the morphology seen in Morphotype 2 (Fig. 5). Despite these similarities, the angle of divarication between digits and length-to-width ratios of Morphotype 3 differ significantly from those of other trackmakers at the site. Given these distinct features, two potential classifications for Morphotype 3 arise: (i) the footprints may belong to juvenile individuals of Morphotype 1 or Morphotype 2; or (ii) they could represent a different type of theropod trackmaker. Due to the fragmentary nature of these tracks, we classify them as a distinct morphotype with uncertain affinities, tentatively identified as an indeterminate Theropoda.

4.2.1.4. Morphotype 4. Morphotype 4 is represented by the isolated track GSFB-06. The footprint dimensions suggest it was produced by a minute individual (Table 1), with estimated hip heights ranging from 35 to 47 cm and a body length of approximately 1.0–1.5 m (Fig. 12A). This morphotype is characterized by digit III being twice as long as the outer digits, a low angle of divarication between the digits (24° – 29°), and, similar to Morphotype 1, digit IV being slightly longer than digit II. The high length-to-width ratio (2.0) and the overall morphology of Morphotype 4 are consistent with functionally monodactylous trackmakers (Fig. 14).

Comparable monodactyl footprints have been documented in the Botucatu Formation, including the ichnotaxon *Farlowichnus rapidus* (Leonardi et al., 2024), and in the Candeleros Formation, represented by *Picunichnus benedettoi* and *Deferrariischnium mapuchensis* (Calvo 1991; Calvo and Mazzetta 2004; Calvo and Rivera 2018). *Farlowichnus rapidus* is a common theropod ichnotaxon from the Botucatu Formation and has been associated to noasaurid trackmakers (Leonardi and Carvalho 2002; Fernandes et al., 2010). Several similarities have been noted between this ichnotaxon and the noasaurid *Vespersaurus paranaensis* from the overlying Rio Paraná Formation (Langer et al., 2019). However, the pedal anatomy of *Vespersaurus* contrasts with that of *Farlowichnus* in the development of outer digits, being both digits nearly equal in length in *Vespersaurus* (Fig. 14H). The unguals in *Vespersaurus* are sharp and longer than wide, differing from the broader unguals inferred for *Farlowichnus* and Morphotype 4. Despite the plastic deformation common in footprints from aeolian deposits (Porchetti et al., 2017; Langer et al., 2019), the autopodium of *Vespersaurus* more closely resembles coeval theropod tracks from the Rio Paraná Formation (Leonardi 1977; Fernandes et al., 2009) than those of *Farlowichnus* and Morphotype 4 (Fig. 14E–F).

Morphotype 4 differs from *Farlowichnus* tracks in the development of digit III, which is proximally broad and nearly triangular (pendant-shaped) in the latter ichnotaxon (Fig. 14A–B). Additionally, the rear margin of the plantar pad is hemispherical in *Farlowichnus*, differing from the slightly bilobated condition of the Morphotype 4. The Morphotype 4 exhibit greater similarity to the conditions seen in *Picunichnus* and *Deferrariischnium* (Fig. 14C–D), which digit III these ichnotaxa are more proximodistally elongated, and the rear margin is slightly indented by a notch as in *Picunichnus*.

The asymmetrical arrangement of the outer digits in Morphotype 4 aligns with the pedal anatomy of coelurosaurians, particularly alvarezsaurids (Figure 14G; e.g., Turner et al., 2009; Hone

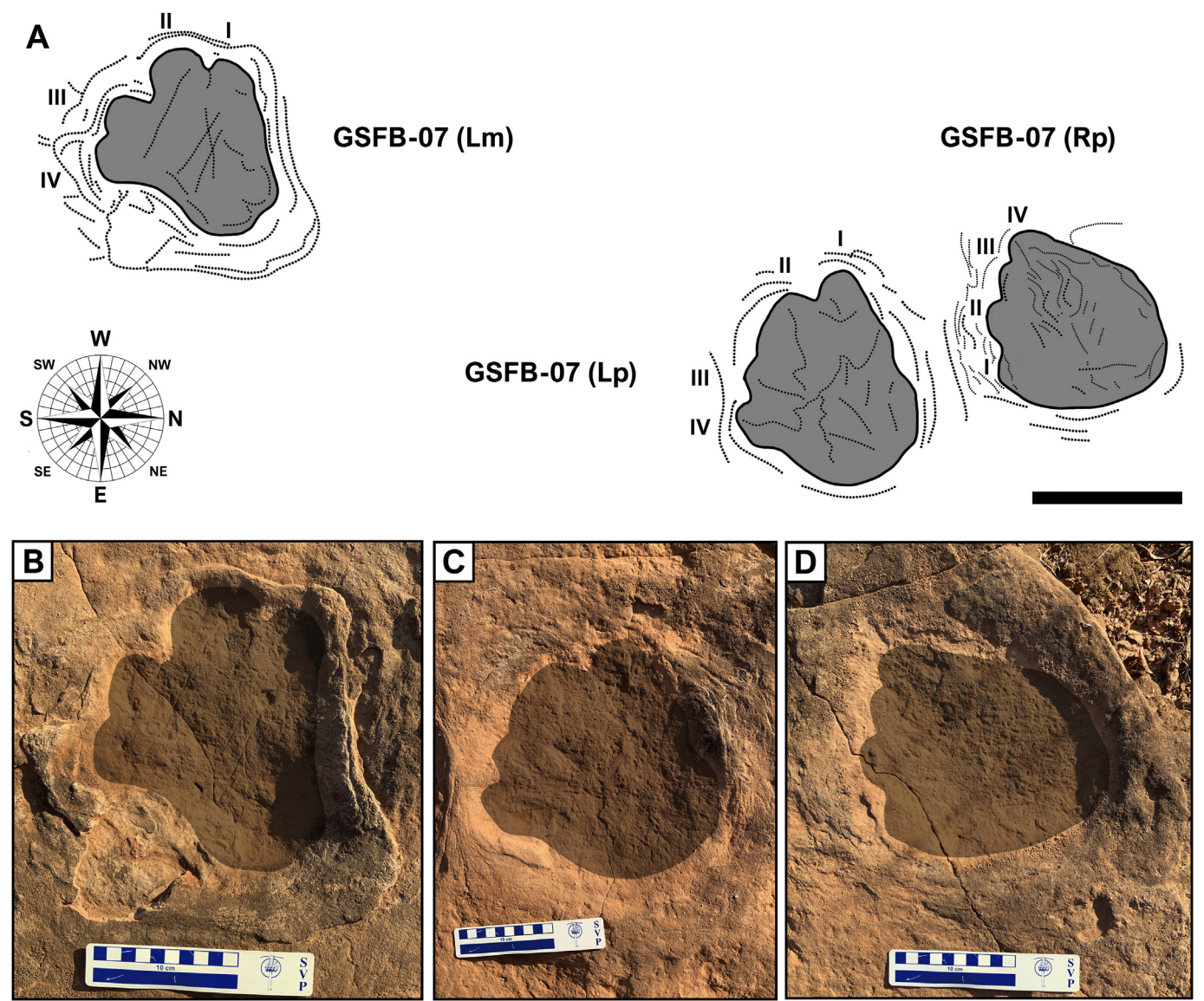


Fig. 10. Partial trackway of a quadrupedal ornithischian (GSFB-10, MZSP-PV 1336-b-c). **A**, interpretative outline drawing, with dotted lines exhibiting the main surface distortions in the sedimentary substrate; **B**, shaded detail of the left manus impression; **C**, shaded detail of the left pes impression; **D**, shaded detail of the right pes impression. Roman numerals indicate the position of each digit. Abbreviations: L, left; m, manus; p, pes; R, right. Scale bars equal 20 cm (A) and 10 cm (B–D).

Table 3
Footprint measurements and estimated hip height (*H*) of the quadrupedal trackmakers (in cm).

Measures	GSFB-10			GSFB-11				
	L manus	L pes	R pes	L manus-1	L manus-2	R manus	L pes	R pes
Maximum proximodistal length (<i>FL</i>)	24.7	26.3	24.7	11.2*	11.6*	13.9	21.2*	21.3
Maximum mediolateral width (<i>FW</i>)	23.7	26.2	22.0	14.1	14.7	14.0	22.2*	22.2
Maximum width of the plantar portion (<i>W</i>)	13.3	17.3	16.8	14.0	13.3	13.8	19.3	19.3
Angle of divarication between digits I-II	21.2°	32.3°	22.6°	—	—	—	—	—
Angle of divarication between digits II-III	33.0°	37.5°	28.1°	—	—	—	—	—
Angle of divarication between digits III-IV	21.7°	16.5°	14.8°	—	—	—	—	—
Length-to-Width ratio (<i>FL</i> / <i>FW</i>)	1.04	1.00	1.13	0.80	0.79	0.93	0.96	0.96
<i>H</i> estimate <i>sensu</i> Lockley (1986)	95.00	104.76	87.88	56.24	58.68	55.84	88.68	88.80
<i>H</i> estimate <i>sensu</i> Thulborn (1990)	145.73	154.88	145.85	66.02	68.62	76.64	124.96	125.79
<i>H</i> estimate <i>sensu</i> González-Riga (2011)	—	120.38	113.37	—	—	—	97.13	97.77
Average <i>H</i> values	120.37	126.67	115.70	61.13	63.65	66.24	103.59	104.12
Mean		121.19		63.67			103.86	

An asterisk (*) marks the measurements based on preserved portions, while a dash (—) denotes when the region is not preserved or indicates measurements that could not be taken. Abbreviations: L, left; R, right.

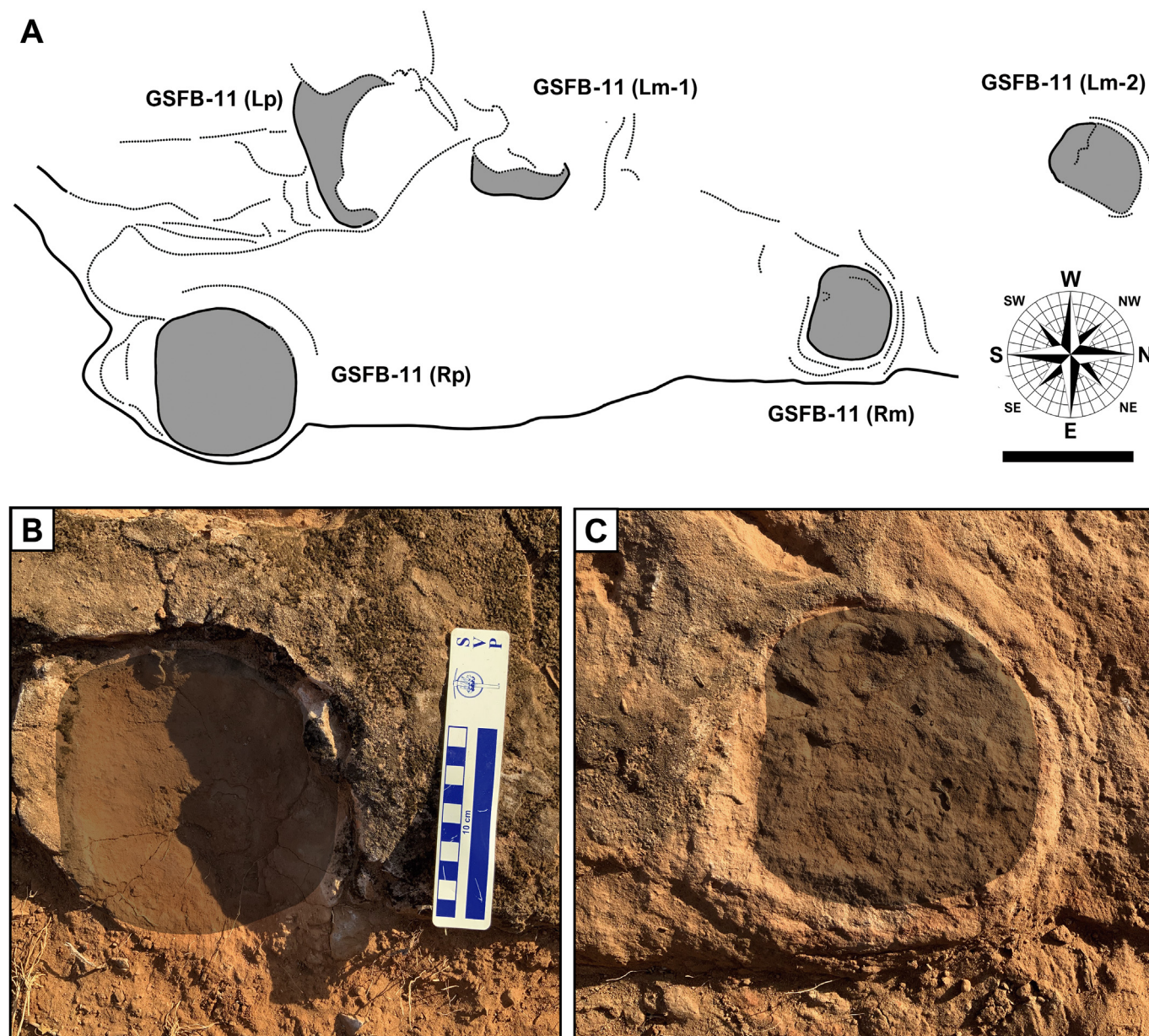


Fig. 11. Partial sauropod trackway (GSFB-11, MZSP-PV 1336-d). **A**, interpretative outline drawing, with dotted lines representing reconstructed parts of the track silhouettes and the main surface distortions in the sedimentary substrate; **B**, shaded detail of the right pes impression; **C**, shaded detail of the infilled left manus impression. Abbreviations: L, left; m, manus; p, pes; R, right. Scale bars equal 20 cm (A) and 10 cm (B).

et al., 2012). Alvarezsauroid theropods are widespread and, except for *Haplocheirus sollers*, are predominantly found in Upper Cretaceous deposits (Choiniere et al., 2010; Xu et al., 2011), with South American records preceding those from the Northern Hemisphere (Averianov and Sues 2017). The body proportions of Morphotype 4 are compatible with those of contemporary alvarezsauroids from Argentina, such as *Alnashetri cerropoliciensis* from the Candeleros Formation (Makovicky et al., 2012).

4.2.2. Ornithischia

Four individuals were identified as probable ornithischian trackmakers (GSFB-07– GSFB-10). These tracks are characterized by being mediolaterally wider than anteroposteriorly long, with convex heels and rounded, proximodistally short hypoxes. Each individual represents a distinct morphotype, differing on their size,

posture, degree of heteropody and axony patterns. Morphotypes were classified based on the trackmaker's stance, overall morphology, digit formula, and digit development, as well as through comparisons with other ichnotaxa from the literature.

4.2.2.1. Small Bipedal Morphotype. The partial tracks of GSFB-07 are attributed to a minute bipedal ornithischian given they are wider than its as anteroposteriorly long, although they are also tridactyl and have digits relatively elongated. Based on the track sizes (Table 2), the estimated hip height for the trackmaker averages between 45 and 47 cm, and the body length ranges from 1.5 to 2 m (Fig. 12B). These body proportions are comparable to those of some ornithischian specimens from South America, such as the ornithopod *Gasparinisaura cincosaltensis* (Salgado et al., 1997), and the basal thyreophoran *Jakapil kaniukura* (Riguetti et al., 2022a).

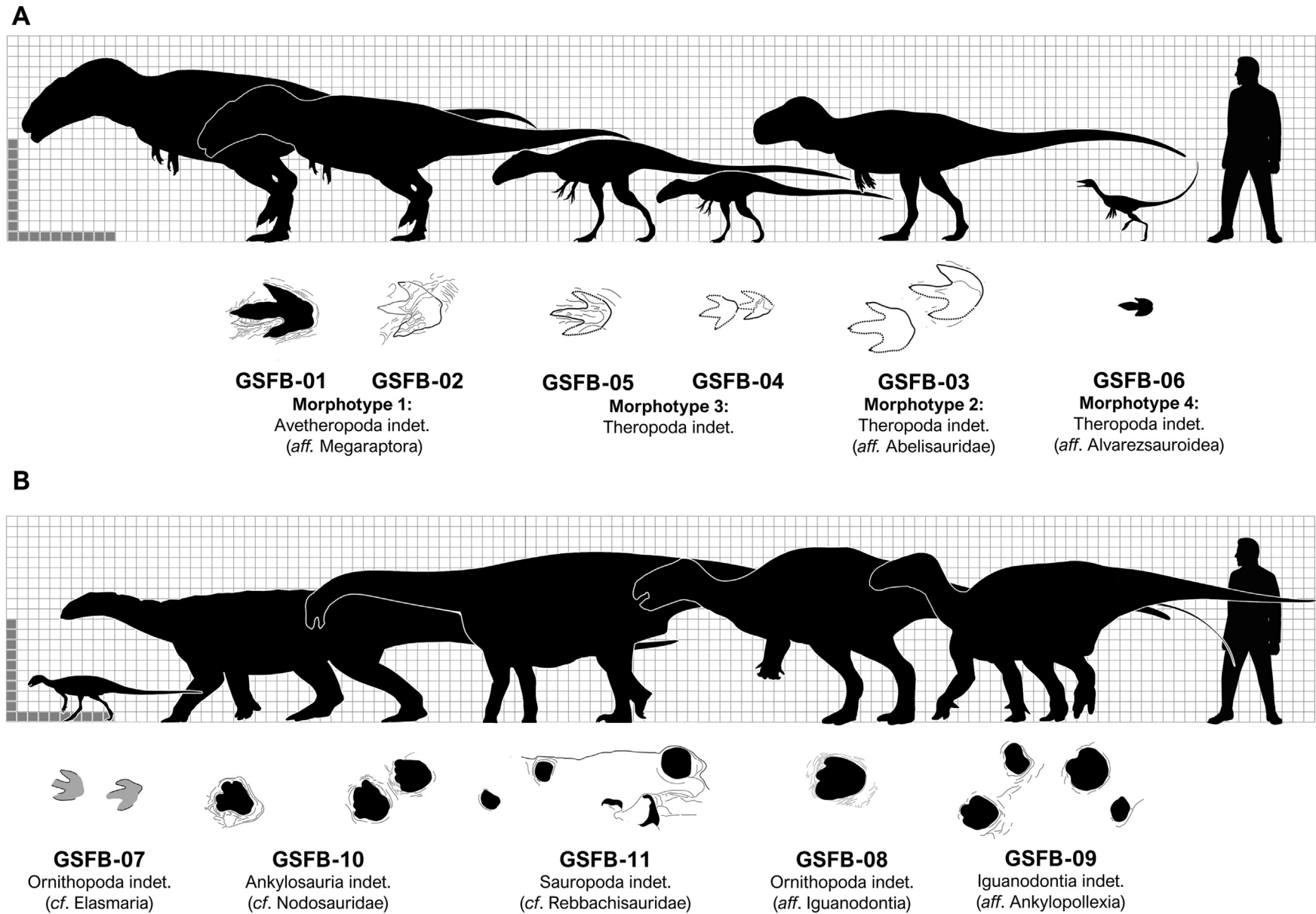


Fig. 12. Comparative body size scale of the Buriti Farm trackmakers. **A**, theropod trackmakers; **B**, ornithischian and sauropod trackmakers. Dimensions based on hip height estimates (see [Tables 1–3](#)). Filled tracks correspond to well-preserved footprints, while the unfilled ones comprise partial tracks and undertracks. Scale bars equal 100 cm. Human silhouette equals 180 cm.

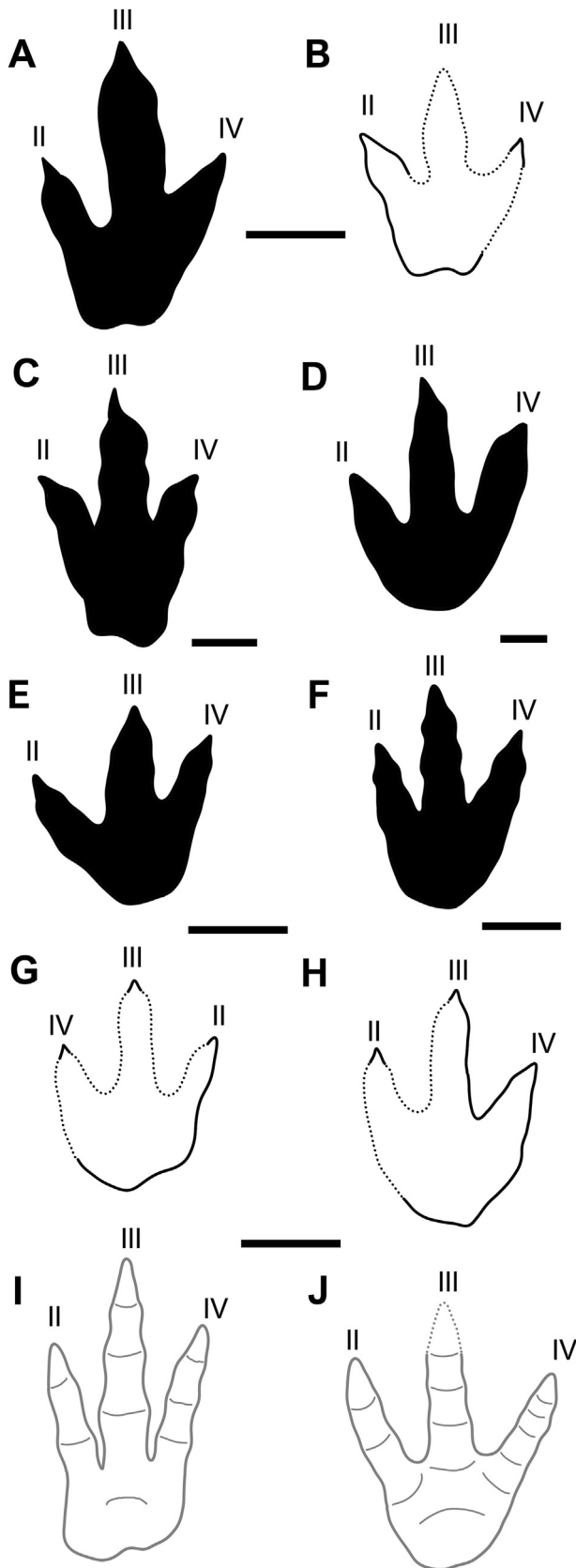


Fig. 13. Outline drawings from selected medium-to-large-sized theropod dinosaurs. **A–B,** right tracks of GSFB-01 (MZSP-PV 1336-a) and GSFB-02 (Morphotype 1); **C,** right track of *Eubrontes giganteus* (AC 15/3; redrawn from Olsen et al., 1998, fig. 5); **D,** left track of *Abelichnus astigarrae* (MUC-Pv 74 reversed; redrawn from Calvo and Rivera 2018, fig. 3); **E,** right theropod track from the Alcántara Formation (ALBA-

However, the pedal anatomy of the latter taxon is unknown, limiting further comparisons.

In the Upper Cretaceous of Gondwana, small ornithischians are primarily represented by the endemic clade Elasmaria, with several specimens reported from Argentina (Rozadilla et al., 2021). Other notable elasmarian occurrences in Gondwanan localities include *Fulgurotherium australe* and *Weewarrasaurus pobeni* from the Albian–Cenomanian Griman Creek Formation of Australia (Huene 1932; Bell et al., 2018). Cenomanian–Turonian elasmarian occurrences from South America include *Loncosaurus argentinus* from the Mata Amarilla Formation (Coria and Salgado 1996), *Notohypsilophodon comodorensis* from the Lower Bajo Barreal Formation (Ibárricu et al., 2014), *Anabisetia saldiviai* from the Cerro Lisandro Formation (Coria and Calvo 2002), and more recently *Chakisaurus nekul* from the Huincul Formation (Nogueira et al., 2024).

Small ornithopod footprints are less common compared to those of larger ornithopod trackmakers, particularly beyond the Botucatu Formation (Díaz Martínez et al., 2015; Francischini et al., 2015). The GSFB-07 tracks share similarities with *Wintonopus latomorum* (Fig. 15A–B), a small ornithopod-type track from the same horizons as *Fulgurotherium* and *Weewarrasaurus* (Thulborn and Wade 1984). Similar to the Australian ichnogenus, in the GSFB-07 tracks the plantar pads are convex and slightly anteroposteriorly longer medially than laterally. Digit impressions in both tracks are sub-equal and splayed, generally mediolaterally broad and have blunt, nearly rounded hypoxes. Considering the minute size of the trackmaker, the absence of a hoof-like digit III on both GSFB-07 tracks, as well as comparing with preserved pedal elements (Fig. 15C), we associate their trackmaker with a probable small elasmarian ornithopod, a group present in Brazil since the Lower Cretaceous (Bandeira et al., 2024).

4.2.2.2. Large Bipedal Morphotype. This morphotype includes the isolated track GSFB-08, attributed to a medium-to large-sized individual with an estimated hip height averaging 162 and 163 cm (Fig. 12B). These dimensions closely align with those of the theropod Morphotype 1 (Tables 1 and 2). The GSFB-08 track is associated with a bipedal iguanodontian trackmaker, distinguished by a broader, hoof-like digit II, a low angle of divarication between the outer digits (Figs. 8, 15D), and a U-shaped heel.

The ichnological record of bipedal iguanodontians is notably abundant from Upper Jurassic to Lower Cretaceous strata of Brazil, primarily in the northeastern region (Leonardi 1994; Leonardi and Carvalho 2021). Two ichnotaxa are particularly well-documented: *Sousaichnium pricei* (Fig. 15E) and *Staurichnium diogenis*, both from the Sousa Formation in Paraíba State (Leonardi 1979). Although less common, bipedal iguanodontian tracks have also been reported from southern and southeastern Brazil (Fig. 15F), specifically in the Guará and Botucatu formations (Dentzien-Dias et al., 2007; Fernandes and Carvalho 2007; Francischini et al., 2015). GSFB-08 differs from these records in the size of the footprints and the development of digit II.

Up to now, contemporary material includes isolated iguanodontian tracks from the Açu Formation in Rio Grande do Norte State (Leonardi et al., 2021) and from the Candeleros Formation (Fig. 15G–I), where two ichnotaxa have been described: *Limayichnus major* and *Sousaichnium monetiae* (Calvo 1991; Calvo and Rivera

12; redrawn from Carvalho 2001, fig. 6); **F,** left track of *Bressanichnus patagonicus* (MUC-Pv 60 reversed; redrawn from Calvo and Rivera 2018, fig. 4); **G–H,** left and right tracks of GSFB-03 (Morphotype 2), respectively; **I,** ventral contour of *Gualicho shinyae* right foot (MPCN-PV 0001; redrawn from Apesteguía et al., 2016, fig. 13); **J,** ventral contour of *Majungasaurus crenatissimus* left foot (reversed; redrawn from Carrano 2007, fig. 11). Roman numerals indicate the position of each digit. Scale bars equal 10 cm.

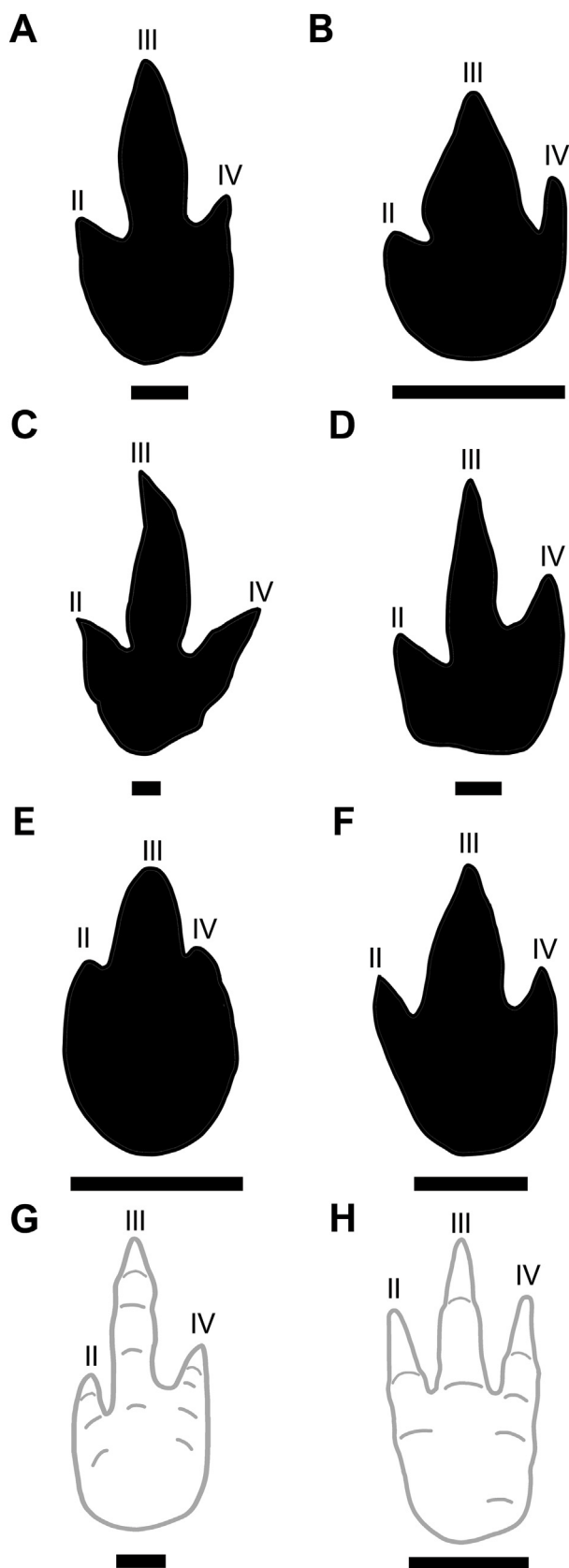


Fig. 14. Outline drawings from selected small-to-medium-sized theropod dinosaurs. **A**, right track of GSFB-06 (Morphotype 4); **B**, right track of *Farlowichnus rapidus* (LPP-IC-0200; redrawn from Leonardi et al., 2024, fig. 4); **C**, right track of *Deferariischnium mapuchensis* (MUC-Pv 97; redrawn from Calvo and Rivera 2018, fig. 6); **D**, right track of *Picunichnus benedettoi* (MUC-Pv 72; redrawn from Calvo and Rivera

2018). GSFB-08 differs from these ichnotaxa in both the dimensions of footprints, being proximodistally longer than mediolaterally wide, and the development of digits, particularly the digit II. Regarding coeval bone remains of iguanodontians in South America, they are also quite rare. They primarily consist of isolated appendicular elements from the Candeleros Formation in Argentina (Coria et al., 2007) and two partial teeth from the Guichón Formation in Uruguay (Huene 1934; Soto et al., 2012). Although additional coeval iguanodontian records are known from other Gondwanan localities, such as Australia (e.g., *Fostoria dhimbangunmal*, *Muttaborrasaurus langdoni*; Bell et al., 2019), the pedal anatomy of these occurrences remains unknown. This scarcity of skeletal material hampers detailed comparisons with the GSFB-08 tracks.

4.2.2.3. Graviportal Morphotype. This morphotype, represented by the partial trackway GSFB-09, is attributed to a graviportal iguanodontian trackmaker. Given the overall morphology of the tracks and stance, the trackmaker of GSFB-09 likely corresponds to an ankylopollexian (Fig. 12B). This morphotype is characterized by ellipsoid-shaped manus footprints that are slightly negatively rotated and lack impressions of pollexes. The pedes footprints are broad, as long as wide, tridactyl, and exhibit a hoof-like digit III (Fig. 15J). The GSFB-09 trackway was made by a medium-to large-sized individual with similar dimensions to the bipedal iguanodontian morphotype (GSFB-08; see Table 2), with estimated hip heights averaging 69–85 cm for the forelimbs and 144–166 cm for the hind limbs, with an overall body length of approximately 438 cm (Table 4). GSFB-09 differs from this morphotype in the posture, in the rear margin shape and development of digit II, suggesting the presence of two iguanodontian forms within the Santo Anastácio Formation. However, the possibility that such features could correspond to extramorphological variations cannot be entirely ruled out due to the absence of additional footprints from GSFB-08.

Similarly to the bipedal forms, tracks from graviportal iguanodontians in Brazil are more commonly found in the Upper Jurassic to Lower Cretaceous strata of the northeastern region of the country (Leonardi 1994; Leonardi and Carvalho 2021). The only described ichnotaxon from this region is *Caririchnium magnificum* from the Antenor Navarro Formation of Paraíba State (Leonardi 1984). The manus impressions of GSFB-09 are similar to *Caririchnium magnificum*, which features a rectilinear medial margin accompanied by a mild posteromedial heel-like bulge (Fig. 15K). However, GSFB-09 differs from *Caririchnium* in the digit development, which are broad and unseparated, and the overall shape of the pedal tracks, which are longer than wide in the latter ichnotaxon. Additionally, GSFB-09 does not exhibit a sole in the pedal pads, which are diagnostic of *Caririchnium* tracks (Díaz-Martínez et al., 2015).

In terms of body fossils, ankylopollexians in Brazil are known from axial remains collected in the Berriasian–Barremian Salvador and Marfim formations of Bahia State (Bandeira et al., 2024). Contemporary body fossil material only includes isolated caudal vertebrae from the Alcântara Formation in Maranhão State, initially associated with a *Ouranosaurus*-like form (Novas 2009). Compared to the complete pes of other iguanodontians, GSFB-09 differs in the

2018, fig. 8); **E**, right theropod track from Cianorte tracksite (CICC-04; redrawn from Leonardi 1977, fig. 10); **F**, right theropod track from Porto Primavera tracksite (PPUH-01; redrawn from Fernandes et al., 2009, fig. 7); **G**, ventral contour of *Kolghuva* left foot (IGM 100/2011; redrawn from Turner et al., 2009, fig. 2); **H**, ventral contour of *Vespersaurus paranaensis* right foot (MPCO.V 0065d1; redrawn from photos ceded by L. Vidal). Roman numerals indicate the position of each digit. Scale bars equal 2 cm.

development of digit III from the Venice specimen of *Ouranosaurus nigeriensis* (MSNVE 3714), which non-ungual phalanges are more proximodistally longer and lacks a broad, hoof-like ungual (Bertoazzo et al., 2017: fig. 18). In contrast, the features present in GSFB-09, such as a short digit III resembling metatarsal III and a broad ungual III-4, are similar to the condition observed in saurolophine hadrosaurids like *Brachylophosaurus* (Gierliński and Sabath 2008: fig. 7C). As with the other iguanodontian footprint described here, the absence of pedal elements within coeval taxa precludes further comparisons.

4.2.2.4. Quadrupedal morphotype. GSFB-10 represents a quadrupedal morphotype. Hip height estimates suggest that the GSFB-10 trackmaker was a medium to-large-sized individual, with limb heights averaging 120–121 cm and an overall body length of about 560 cm (Tables 3 and 4). Unlike sauropod trackmakers, GSFB-10 exhibits a low degree of heteropody, characterized by paraxonic tetradactylous tracks with short, nearly rounded hypoxes, “U-shaped” rear, and strongly negative rotation. This combination of features allows us to associate GSFB-10 with a thyreophoran trackmaker (Thulborn 1990). Given the early Late Cretaceous age inferred for the Santo Anastácio Formation and the tetradactyl condition of the trackmaker, it is more likely attributable to an ankylosaurian rather than a stegosaurian (Fig. 12B), whose occurrences are controversial in this interval (Maidment et al., 2008).

Ankylosauria traditionally includes two main groups: Nodosauridae and Ankylosauridae (e.g., Thompson et al., 2012). Recent analyses suggest that Gondwanan ankylosaurs form an endemic clade named Parankylosauria (Soto-Acuña et al., 2021), which is the sister taxon to the clade composed of these families (Euankylosauria). In terms of autopodial anatomy, nodosaurids typically have tetradactylous manus and pes (Fig. 16A–C), while parankylosaurians and ankylosaurids usually exhibit pentadactylous manus and tetradactylous pedes (Fig. 16E–F). Based on the morphology observed in GSFB-10 tracks, they were likely produced by a nodosaurid trackmaker (Thulborn 1990).

Nodosaurids are widespread in the Cenomanian of Laurasia, with several records from North America (e.g., Carpenter et al., 1999), Asia (e.g., Hawakaya et al., 2005), and Europe (e.g., Vullo et al., 2007; Blows 2014). Although some Gondwanan records were previously assigned to nodosaurids (e.g., Arbour and Currie 2016), this classification is now considered contentious due to conflicting phylogenetic hypotheses (e.g., Soto-Acuña et al., 2021). The fossil record of South American ankylosaurians is generally sparse compared to other ornithischian groups (Pereda-Suberbiola et al., 2015; Bandeira et al., 2024). Most occurrences have been found in the Campanian–Maastrichtian units of Argentina, Bolivia, and Chile (see Riguetti et al., 2022b and references therein), with coeval Gondwanan occurrences limited to an isolated thoracic dermal scute from the Puerto Yeruá Formation in Argentina (De Valais et al., 2003) and a single, isolated tooth from the Kem Kem Beds in Morocco (Ibrahim et al., 2020).

Apart from a supposed ‘dermal spike’ from Colina (northeast São Paulo State) reported by Huene (1931), which is currently lost, body fossils of Late Cretaceous ankylosaurians are unknown in Brazil. Brazilian occurrences are limited to partial trackways from the Upper Jurassic Guarú and Corda formations (Leonardi 1978; Francischini et al., 2017), and putative tracks from the Lower Cretaceous Antenor Navarro Formation (Leonardi 1994; Leonardi and Carvalho 2021). Contemporary partial trackways from quadrupedal ornithischians have also been reported in the Alcântara Formation of Maranhão State, in northeast Brazil (Carvalho 2001). Some of these exhibit tridactyl manus associated with tetradactyl pes (Fig. 16D), leading some authors to assign its trackmakers to putative ceratopsians (Novas 2009).

Compared to ichnotaxa typically associated with ankylosaurians, GSFB-10 differs of *Ligabueichnium* from the Campanian Toro Toro Formation of Bolivia and the widespread *Tetrapodosaurus* (Fig. 16E), as both have pentadactyl manus impressions with significant superposition of the manus by the pes, as well as tetradactyl pes impressions with a strongly reduced sole pad with a V-shaped rear margin (Riguetti et al., 2021). GSFB-10 shares notable features with *Metatetrapous valdensis*, an ichnogenus related to ankylosaurians from the Upper Berriasian Obernkirchen Member of the Bückeberg Formation in Germany, and with unnamed ankylosaurian tracks from the Coniacian–Santonian Frontier Formation in the USA (Hornung and Reich 2014; Panasci et al., 2024). Like these tracks (Figure 16B, F), the manus impression in GSFB-10 is slightly longer than wide, tetradactyl and with well-splayed digits, preserving an elongated, ‘U-shaped’ posterior rear margin. However, GSFB-10 differs in the format of the digits, which are proximodistally shorter and mediolaterally broader than the former tracks, also lacking marks from unguals.

4.2.3. Sauropoda

GSFB-11 represents the only morphotype associated with a sauropod trackmaker, contrasting with the abundant body-fossil record of sauropods found in the upper units of the Bauru Group (Brusatte et al., 2017). The spacing between GSFB-11 footprints suggests they were produced by a narrow-gauged trackmaker (Lockley et al., 1994a). During the Cenomanian–Turonian, narrow-gauged sauropods were represented by rebbachisaurid diplodocoids, a group abundant in South America (Salgado et al., 2022). Therefore, given the size of the trackmaker, the general morphology of the tracks, and the chronostratigraphic and paleobiogeographic context, we consider that GSFB-11 was likely produced by a small-sized rebbachisaurid. Wide-gauge trackways are associated with titanosauriforms given that only this group possesses specializations in the appendicular skeleton associated with this type of locomotion, such as femora with an acute angle between the proximodistal axis and the distal condyles, a strongly eccentric femoral diaphysis cross-section (at least 150 % wider mediolaterally than anteroposteriorly), and a beveled lateral bulge (Fig. 11A; Wilson and Carrano 1999).

Although GSFB-11 exhibit conspicuous heteropody, it clearly differs from the typical titanosauriform-type tracks such as *Brontopodus birdi* and *Titanopodus mendozaensis*, which often have eccentrically crescentic, wider than long manus footprints and pedal footprints that are longer than wide (Fig. 17A–C), frequently showing unguals marks in the pedal digits (Lockley et al., 1994b; González Riga and Calvo 2009). In contrast, the GSFB-11 trackmaker shares characteristics with giant-sized narrow-gauge ichnotaxa like *Parabrontopodus mcintoshi* and *Sauropodichnus giganteus* (Fig. 17D–E), featuring almost “D-shaped” tracks that are as long as they are wide. The estimated hip heights of GSFB-11 suggests that it belonged to a small-bodied sauropod trackmaker, with approximately 900 cm in body length (Table 3). This body-size is comparable to contemporaneous rebbachisaurid forms such as *Itapeuasaurus cajapiensis* from the Alcântara Formation in northeastern Brazil (Fig. 12B; Lindoso et al., 2019), and *Katepensaurus goicoecheai* from the Bajo Barreal Formation of Argentina (Ibárcicu et al., 2013). However, the absence of similar footprints at the tracksite makes it challenging to determine whether these tracks were made by a small adult individual or by an immature individual (Leonardi 1981).

4.3. Paleoenvironmental interpretation

The depositional setting of the Santo Anastácio Formation has been subject to varying interpretations (see Section 2). Some

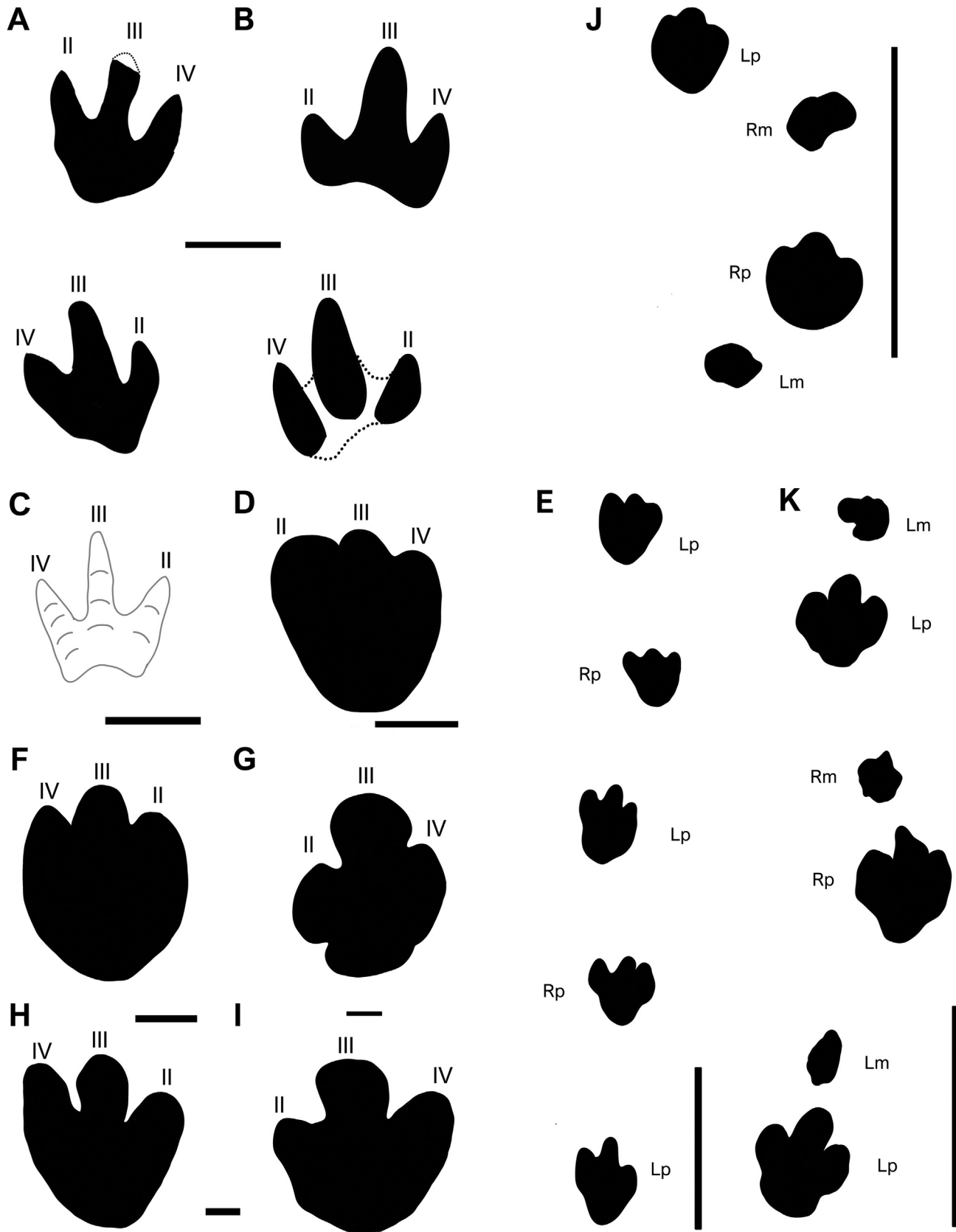


Fig. 15. Outline drawings from selected ornithopod dinosaurs. **A**, left and right tracks of GSFb-07; **B**, left and right tracks of *Wintonopus latomorum* (QM F10322/B; redrawn from Thulborn and Wade 1984, fig. 13A–B); **C**, elasmarian foot contour based on *Gasparinisaura cincosaltensis* (MUCPv-214; Salgado et al., 1997) and *Trinisaura santamartensis* (MLP 08-III-1-1; Coria et al., 2013); **D**, right track of GSFb-08 (MZSP-PV 1336-b); **E**, type trackway of *Sousaichnium pricei* (SOPP-1; redrawn from Leonardi 1994, fig. 12–1); **F**, left track of an unnamed large iguanodontian from the Botucatu Formation (MPA-334; Fernandes and Carvalho 2007); **G**, right track of an unnamed iguanodontian from the Açú Formation (AÇPI 4; redrawn from Leonardi et al., 2021, fig. 4); **H**, left track of *Sousaichnium monettae* (MUCPv-71; redrawn from Calvo and Rivera 2018, fig. 19); **I**, right track of *Limayichnus major*

authors propose a strict aeolian deposition (e.g., [Fernandes and Coimbra 2000](#); [Fernandes and Magalhães Ribeiro 2015](#)), while others suggest that an intertwined fluvial system was the predominant environment (e.g., [Soares et al., 1980](#); [Paula e Silva et al., 2009](#)). The presence of some tetrapod fossils within this unit, such as aquatic turtles, supports the hypothesis of deposition within a fluvial context (see [Menegazzo et al., 2015](#)). Nevertheless, the sedimentology of the GSFB ichnocoenosis indicates the existence of ephemeral water bodies heavily influenced by sand sheet deposits ([Fig. 2](#)), characteristic of playa-lake facies in arid to semi-arid environments (see [Basilici and Sgarbi 2012](#)).

Despite the notable aeolian influence within the Santo Anastácio Formation, evidence of fluidization in the substrate (see [Figs. 4–7, 10](#)) suggests that the surface where footprints were formed was periodically subjected to varying water levels. This resulted in footprints being differentially preserved, with some tracks only faintly impressed and others deeply embedded into the sedimentary substrate and completely infilled. The prevalence of medium-to large-bodied trackmakers suggests that resources were available in this paleoenvironment, such as vegetated areas and water supply, at least on a seasonal basis. Consequently, the GSFB ichnocoenosis likely represents a “feeding zone” for the local fauna ([Fig. 18](#)). On the other hand, the estimated gait speeds ([Table 4](#)) imply that this ichnocoenosis may have been a recurring pathway used by migrating herds, possibly in search of perennial water sources during dry seasons. The high density of trackmaker per square meter (3.6 trackmakers/m²) and the preferential orientation of the tracks ([Table 5](#)) indicate that many individuals were converging towards a common point, likely a primary water body. Although direct evidence of behavior is absent, this pattern suggests that the ichnocoenosis may reflect a congregation area for animals, emphasizing the critical role of water sources in shaping the local paleoecology.

5. Discussion

5.1. Stratigraphic and paleobiogeographic implications

In the General Salgado area, most of the fossil discoveries originate from paleosol levels of the Adamantina Formation ([Fig. 2](#); e.g., [Vasconcellos and Carvalho 2010](#); [Carvalho et al., 2013](#); [Castro et al., 2018](#)). These deposits have yielded a tetrapod fauna predominantly composed of crocodyliforms, with numerous specimens exhibiting near-complete skeletons and a high degree of articulation ([Arruda et al., 2004](#); but see [Bandeira et al., 2018](#) for a taphonomic perspective). In contrast, fossil discoveries are notably scarce in the Santo Anastácio Formation. Tetrapod specimens from this unit are confined to a few isolated localities, which significantly hampers efforts to establish robust stratigraphic correlations and refinements on the formation's age.

Early discoveries in the Santo Anastácio Formation include incomplete postcranial remains of a putative crocodyliform specimen found in Pereira Barreto municipality, probable baurusuchids from General Salgado municipality, and an unnamed turtle carapace from the Rubinéia municipality, all in São Paulo State ([Fittipaldi et al., 1989](#); [Agostinho 2009](#); [Menegazzo et al., 2015](#)). According to [Menegazzo et al. \(2015, p. 26\)](#), the occurrence of podocnemidoid turtles in the Santo Anastácio Formation suggests a Late Cretaceous age for this unit. This age determination is based on comparisons with the stratigraphic ranges of related taxa, such as “*Bauruemys brasiliensis*” and “*Cambaremys langertoni*”, which are

Table 4
Estimated body lengths and relative speeds of some trackmakers from the Santo Anastácio Formation.

Measures	GSFB-09	GSFB-10	GSFB-11
Pace length (in cm)	70.21	25.82	38.98
Gleno-acetabular distance (in cm)	68.14	67.98	93.62
Body length estimate (GAD/H)	0.44	0.56	0.90
Average hip height (in cm)	155.48	121.19	103.86
Stride length (in cm)	91.43	89.83	93.20
Gait estimate 1 (λ/H)	1	1	1
Gait estimate 2 (λ/PL)	1.30	3.48	2.39
Relative speeds (in km/h)	2.57	3.34	4.25

found in the overlying Adamantina and Serra da Galga formations ([Kischlat 1994](#); [De França and Langer 2005](#); [Romano et al., 2013](#)), and *Portezueloemys patagonica*, known from the Turonian–Coniacian Portezuelo Formation of the Neuquén Basin ([de la Fuente 2003](#)). Similarly, the potential presence of baurusuchids in the Santo Anastácio Formation suggests that this unit is likely contemporaneous with the upper strata of the Bauru Group, particularly the Adamantina Formation. While baurusuchids are typical tetrapod components of the Adamantina Formation, it is important to note that tracks from this group are absent in the ichnocoenosis described in this study.

More recently, [Ruiz et al. \(2021\)](#) described the sphagesaurid *Caipirasuchus attenboroughi* based on a specimen collected along the road between the municipalities of Auriflama and General Salgado ([Fig. 1B](#)). The genus *Caipirasuchus* has been previously documented in the overlying Adamantina Formation (e.g., [Iori and Carvalho 2011](#); [Iori et al., 2016](#); [Martinelli et al., 2018](#); [Iori et al., 2024](#)), with notable occurrences including *Caipirasuchus stenognathus* in the General Salgado area ([Pol et al., 2014](#)). [Ruiz et al. \(2021\)](#) initially associated the discovery of *Caipirasuchus attenboroughi* with the Santo Anastácio Formation, based on lithological differences from the Adamantina Formation. They suggested that these two formations might be temporally correlated ([Ruiz et al., 2021, p. 18](#)). However, upon closer examination of the type locality, it was determined that the strata yielding the remains of *Caipirasuchus attenboroughi* are actually linked to the paleosol levels of the Adamantina Formation, indicating that these deposits are potentially contemporaneous with those containing *Caipirasuchus stenognathus* ([Figs. 1–2](#)).

Another crocodyliform occurrence potentially associated to the Santo Anastácio Formation is *Gondwanasuchus scabrosus*. Although initially associated with the Adamantina Formation, this taxon was discovered in paleosol layers beneath the track-bearing level described in this study ([Fig. 2](#)). *Gondwanasuchus scabrosus* is among the smallest baurusuchids documented to date ([Marinho et al., 2013](#)) and is often considered a basal member of this clade (e.g., [Godoy et al., 2014](#)), which is consistent with its proposed new stratigraphic placement. Despite this, the presence of marked sutures and well-developed orbits in *Gondwanasuchus scabrosus* suggests it was in an early ontogenetic stage (e.g., [Geroto and Bertini 2012](#); [Dos Santos et al., 2024](#)). This juvenile status raises the possibility that it may represent a semaphoront of a yet undescribed taxon (see [Agostinho 2009](#)), hampering the clear recognition of its systematic position within Baurusuchidae.

Early fossil discoveries from the Santo Anastácio Formation have consistently suggested a Late Cretaceous age for this unit. This is in stark contrast to the Early Cretaceous ages attributed to the Caiuá Group, primarily inferred from the presence of tapejarid pterosaurs

(MUCPv-67; redrawn from [Calvo 1991, fig. 4](#)); **J**, partial trackway of GSFB-09; **K**, type trackway of *Caririchnium magnificum* (SOES-9; redrawn from [Leonardi 1984, fig. 8](#)). Roman numerals indicate the position of each digit. Abbreviations: L, left; m, manus; p, pes; R, right. Scale bars equal 10 cm (A–D, F–I) and 100 cm (E, J–K).

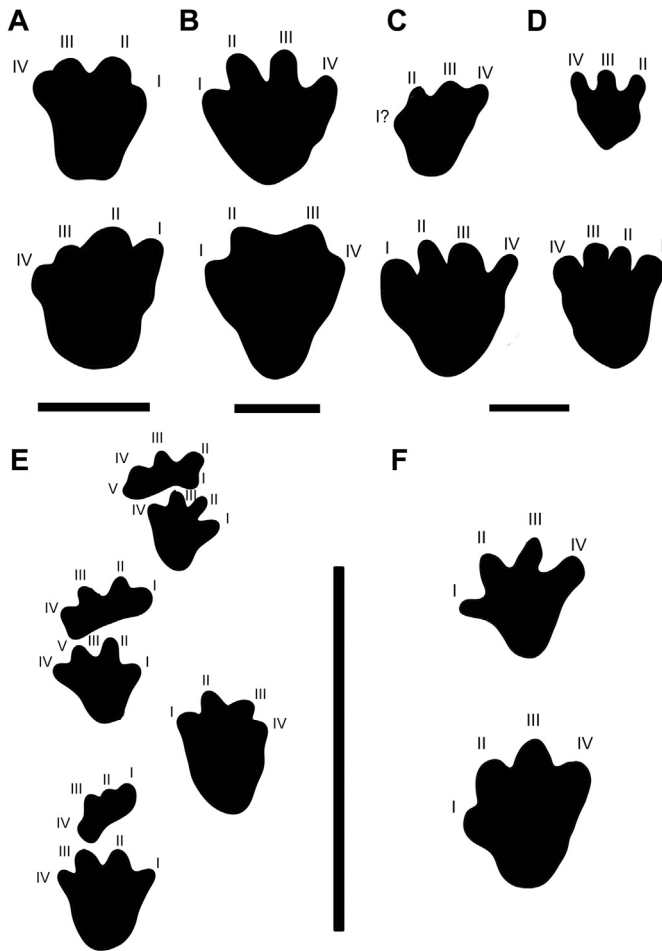


Fig. 16. Outline drawings from selected quadrupedal ornithischian dinosaurs. **A**, left manus (above) and pes (below) tracks of GSFb-10 (MZSP-PV 1336-b-c); **B**, right manus and pes tracks of an unnamed ankylosaur from the Frontier Formation (MOR 1644 2 and MOR 11768 2; redrawn from Panasci et al., 2024, fig. 10); **C**, right manus and pes tracks of a putative ankylosaur from the Alcántara Formation (SLIM 06-07; redrawn from Carvalho 2001, fig. 5C); **D**, left manus and pes tracks of a putative ceratopsian from the Alcántara Formation (SLIM 05-08; redrawn from Carvalho 2001, fig. 5C); **E**, partial trackway of *Tetrapodosaurus borealis* (redrawn from Lockley et al., 2021, fig. 2); **F**, partial trackway of *Metatetrapos valdensis* (redrawn from Hornung and Reich 2014, fig. 7). Roman numerals indicate the position of each digit. Scale bars equal 10 cm (A–D) and 100 cm (E–F).

(e.g., Batezelli 2010; Batezelli 2015; Menegazzo et al., 2016; Arai and Dias-Brito 2023). The dinosaur tracksite described here is a rare and significant find, as most dinosaur tracks at southeastern Brazil are typically discovered in Upper Jurassic and Lower Cretaceous aeolian deposits, such as those of the Guará, Botucatu, and Rio Paraná formations (Leonardi 1994; Dentzien-Dias et al., 2007; Francischini et al., 2015). Although these earlier units contain some tracks of large-sized trackmakers (e.g., Fernandes and Carvalho 2007), the majority of the tracks identified suggest a predominance of small-sized fauna adapted to desert environments (e.g., Fernandes et al., 2009; Fernandes et al., 2014; Francischini et al., 2017), with *Brasielichnium* and *Farlowichnus* typical ichnotaxa from these horizons (e.g., Fernandes and Carvalho 2008; Fernandes et al., 2010; Buck et al., 2016; Buck et al., 2017; Porchetti et al., 2017; Francischini et al., 2022). The absence of such track types in the Santo Anastácio Formation (at least until now) highlights possible differences with the Lower Cretaceous ichnofacies of southeastern Brazil, underscoring unique paleoenvironmental and faunal characteristics of this unit.

Dinosaur tracks within the Santo Anastácio Formation reveal a diverse ichnofauna previously unknown, predominantly composed

of medium-to large-sized trackmakers (Fig. 12). These findings provide crucial insights into the environmental reconstruction and faunal composition of this unit (Fig. 18). The faunal assemblage of Santo Anastácio Formation exhibits notable similarities with other middle Cretaceous deposits from Gondwana (Fig. 19), facilitating comparisons and the establishment of stratigraphic correlations with contemporary South American units (see Supplementary data).

Like the geological units in northeast Brazil, Uruguay, and Argentina, the ichnofauna of the Santo Anastácio Formation shares common components typical of the Cenomanian–Turonian interval. This assemblage includes probable abelisaurid, megaraptoran, and alvarezsaurid theropods (e.g., Makovicky et al., 2012; Cerroni et al., 2020; Pereira et al., 2020), rebbachisaurid sauropods (e.g., Ibiricu et al., 2013; Lindoso et al., 2019), along with elasmarian (e.g., Coria and Salgado 1996; Ibiricu et al., 2014; Nogueira et al., 2024), ankylosaurian (e.g., Carvalho 2001; De Valais et al., 2003), and iguanodontian ornithischians (e.g., Calvo 1991; Coria et al., 2007; Soto et al., 2012; Leonardi et al., 2021). Furthermore, comparing the GSFb ichnofauna and the previously described fossil occurrences of the Santo Anastácio Formation with tetrapod assemblages from the Neuquén Basin, the faunal content aligns this unit with the Limayan Faunachron (Leanza et al., 2004).

5.2. Paleocological significance of the Santo Anastácio ichnofauna

Remarkably, most of the trackmakers identified in the GSFb ichnofauna have not been previously detected as body-fossils in the upper units of the Bauru Group (Coniacian–Maastrichtian), such as ornithischians, rebbachisaurids, and some theropod groups (Fig. 19). By the latest Cretaceous, dinosaur assemblages in South America were primarily composed of titanosaurian sauropods (Gallina et al., 2022; Santucci and Filippi 2022), small to medium-sized abelisauroids (noasaurids and abelisaurids), and a diverse array of tetanurans, such as megaraptorans, alvarezsaurids, unenlagiids and several paravians (Novas et al., 2013), with abelisauroids and titanosaurians emerging as dominant faunal components (Ibiricu et al., 2020; Delcourt et al., 2020). Typical ‘middle-Cretaceous’ faunal components, such as rebbachisaurids, spinosaurids, and carcharodontosaurians, became globally extinct after the Turonian at latest, and possibly earlier, near the end of the Cenomanian, being the exact timing of their disappearance poorly constrained (see Barrett et al., 2009). Thus, the absence of some of these taxa in the upper units of the Bauru Group is consistent with this faunal turnover.

However, apart from the putative thyreophoran ‘dermal spike’ reported by Huene (1931), ornithischian bone fossils are also absent in the upper Bauru Group strata. Contemporary deposits in South America feature a varied ichnological and osteological record of ornithischians post-Turonian interval, including ankylosaurians, elasmarians, hadrosaurids, and even putative ceratopsians (see Rozadilla et al., 2021). In contrast, the paleoecosystems of the upper Bauru Group exhibit a crocodyliform-dominated fauna (e.g., Godoy et al., 2014, fig. 10; Reis et al., 2022, fig. 5). Some hypotheses suggest that crocodyliform groups like baurusuchids may have occupied ecological niches typically held by theropod dinosaurs (e.g., Riff and Kellner 2011), although potential biases in the fossil record explain the abundance of their records and challenge the notion that baurusuchids outcompeted theropods (Bandeira et al., 2018). Like other archosaurs, such as theropods and pterosaurians, the absence of ornithischians in the upper Bauru Group can be explained by the fact that the group inhabited regions that were not conducive to their preservation. Nevertheless, the lack of ornithischian teeth in the abundant dentary records of crocodyliforms and theropods in the upper Bauru units is noteworthy and has yet to reveal any occurrence of this group (Ribeiro et al., 2023).

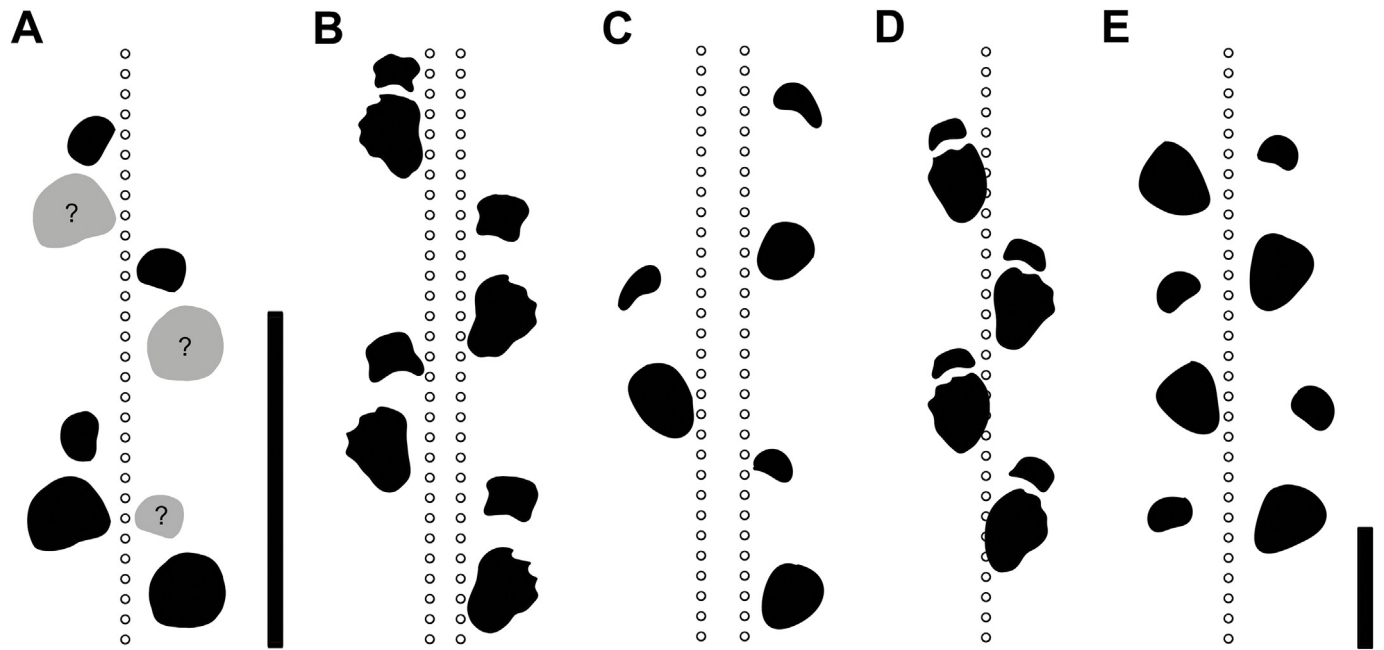


Fig. 17. Outline drawings from selected sauropod dinosaurs. **A**, partial trackway of GSPB-11 (MZSP-PV 1336-d); **B**, trackway of *Brontopodus birdi* (redrawn from Lockley et al., 1994a, fig. 1); **C**, trackway of *Parabrontopodus mcintoshii* (redrawn from Lockley et al., 1994a, fig. 3); **D**, trackway of *Titanopodus mendozaensis* (redrawn from Gonzalez Riga and Calvo 2009, fig. 4); **E**, trackway of *Sauropodichnus giganteus* (redrawn from Calvo and Rivera 2018, fig. 14). Dotted lines indicate the gauge axis. Scale bars equal 100 cm.

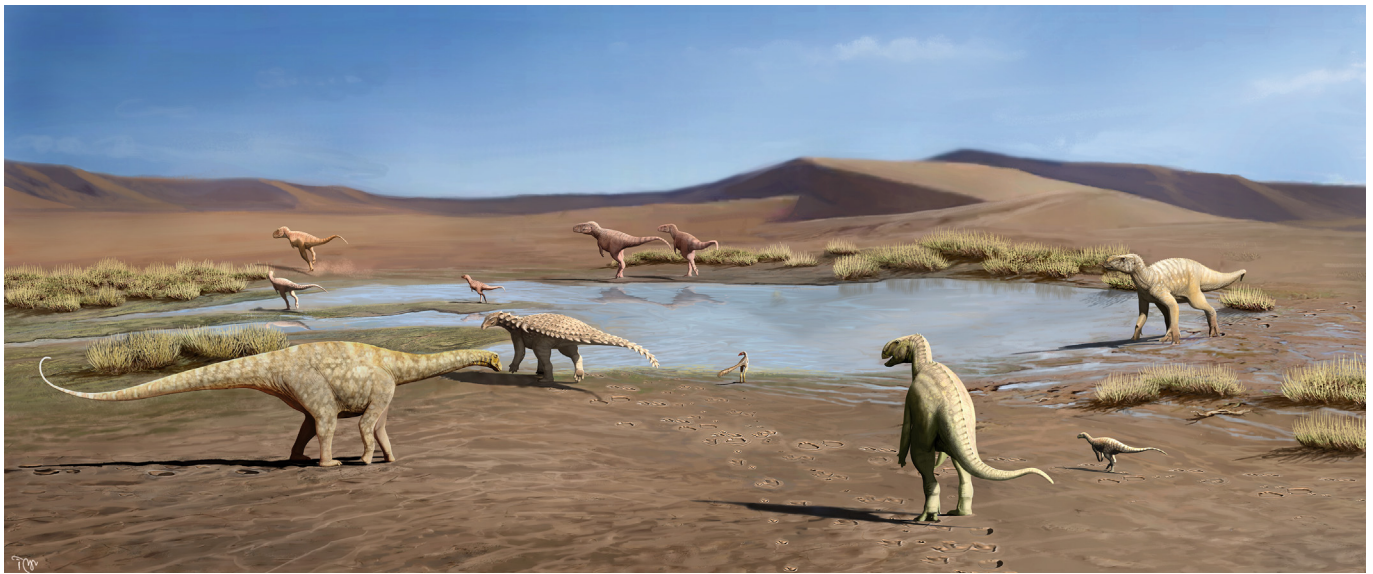


Fig. 18. Paleoenvironmental reconstruction of the Cenomanian–Turonian Santo Anastácio Formation at Buriti Farm. While the illustration represents collectively all the putative trackmakers, no evidence suggests social behavior or interaction among these animals, which probably crossed the area at different times. Artwork by Matheus F. Gadelha.

It is reasonable to infer that the successive environmental fluctuations during the latest Cenomanian–earliest Turonian interval—and their subsequent effects as well—had immediate impacts on distribution of dinosaur populations (Fig. 20). The Cenomanian/Turonian boundary is characterized by events of climatic instability, such as the Oceanic Anoxic Event 2 (OAE2; also called the Bonarelli Event), and the Plenus Cold Event (PCE). The OAE2 represents a major perturbation of carbon cycle during the late Cenomanian (~93–94 Ma), indicated by significant carbon burial and positive $\delta^{13}\text{C}$ excursion, and has been associated with heightened volcanic activity and greenhouse gas emissions that led to shifts in oceanic

productivity and deoxygenation (Schlanger and Jenkyns 1976; Kuroda et al., 2007; Turgeon and Creaser 2008; Jenkyns 2010). The PCE corresponds to a transient cooling episode in the latest Cenomanian (~40 kyr; Jarvis et al., 2011), documented by a positive oxygen-isotope excursion and southward migration of endemic, marine boreal macrofauna (Jefferies 1962; Jeans et al., 1991; Gale and Christensen 1996; O'Connor et al., 2010; Jenkyns et al., 2017). These climatic perturbations during the Cenomanian–Turonian transition triggered the onset of the Cretaceous Thermal Maximum (CTM), one of the warmest intervals in the Phanerozoic (Arthur et al., 1988; Barclay et al., 2010; Huber et al., 2018). The CTM represents a

Table 5
Preferential orientation in displacement of the trackmakers.

Track	Trackmaker type	Orientation
GSFB-01	Theropoda	W
GSFB-02	Theropoda	W-SW
GSFB-03	Theropoda	SW
GSFB-04	Theropoda	SW-W
GSFB-05	Theropoda	SW
GSFB-06	Theropoda	W
GSFB-07	Ornithopoda	W-SW
GSFB-08	Ornithopoda	W
GSFB-09	Ornithopoda	SE
GSFB-10	Thyreophora	S-SW
GSFB-11	Sauropoda	N

prolonged phase of elevated global temperatures, peaking in the earliest Turonian, which surface-ocean temperatures exceeded 30 °C in the tropical regions (Forster et al., 2007; Scotese et al., 2021).

In continental ecosystems, as response to global warmth, these environmental disruptions led to the establishment of an open, savanna-like vegetation at tropical regions, primarily composed of deciduous dry/warm shrublands (Heimhofer et al., 2018). On the other hand, distribution patterns of ornithischian dinosaurs towards the end of the Cretaceous seem to reflect palaeolatitudinal controls driven by climatic settings (e.g., Chiarenza et al., 2022), with some lineages like ankylosaurians and hadrosaurids favoring more temperate and humid environments (see Arbour et al., 2016;

Ibircu et al., 2021). The Bauru Group, located at paleolatitudes within the “Southern Hot Arid Belt” post-Turonian interval (Chumakov 1995), experienced episodic aridity with seasonal, short intervals of increased humidity (Fig. 2), as evidenced by the alternating aeolian sand sheets, paleosol levels, and channel deposits in the northern sector of the Adamantina Formation (Basilici and Dal’ Bó 2010). In the southeastern region, by contrast, the absence of channel deposits and a prolonged hiatus between depositional cycles indicate a general retrogradation of fluvial distributary systems triggered by reduced precipitation (see Dias-Brito et al., 2001; Basilici et al., 2016). Therefore, it is plausible that successive climatic shifts in the Cenomanian–Turonian interval and concomitant floristic changes affected faunal distributions, resulting on regional extinctions or forcing susceptible organisms to migrate to more favorable areas.

Notwithstanding, the groups that flourished after the middle Cretaceous extinction events varied regionally, despite the likely global scale of faunal turnover, indicating a faunal provinciality during the Campanian–Maastrichtian (e.g., Coria and Salgado 2005; Cullen and Evans 2016; Maidment et al., 2021). Crocodyli-forms were remarkably abundant in the upper units of the Bauru Group, particularly sphagesaurians (Iori et al., 2024). Their cranio-dental anatomy suggests a conspicuous herbivorous diet in this group, including propalinal movements, side alternation during chewing, and oblique tooth-to-tooth occlusion (Iori and Carvalho 2018). In addition, sphagesaurian teeth show several convergences with ornithischians, such as lanceolate molariform tooth

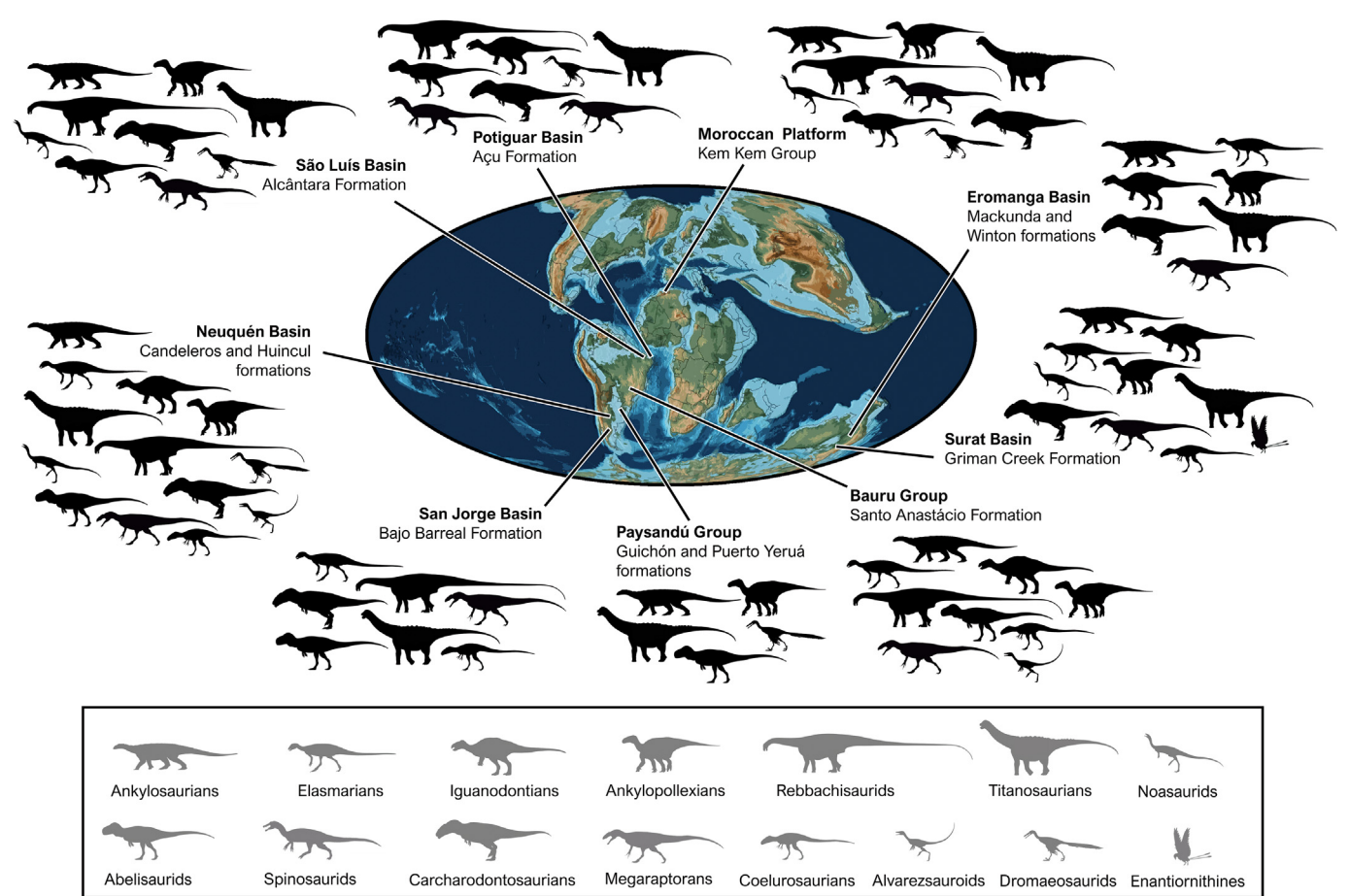


Fig. 19. Main dinosaur assemblages during the Cenomanian–Turonian (middle Cretaceous) in Gondwana. Taxon occurrences were acquired at the Paleobiology Database (<https://paleobiodb.org>). Paleogeographic reconstruction modified from Scotese (2016).

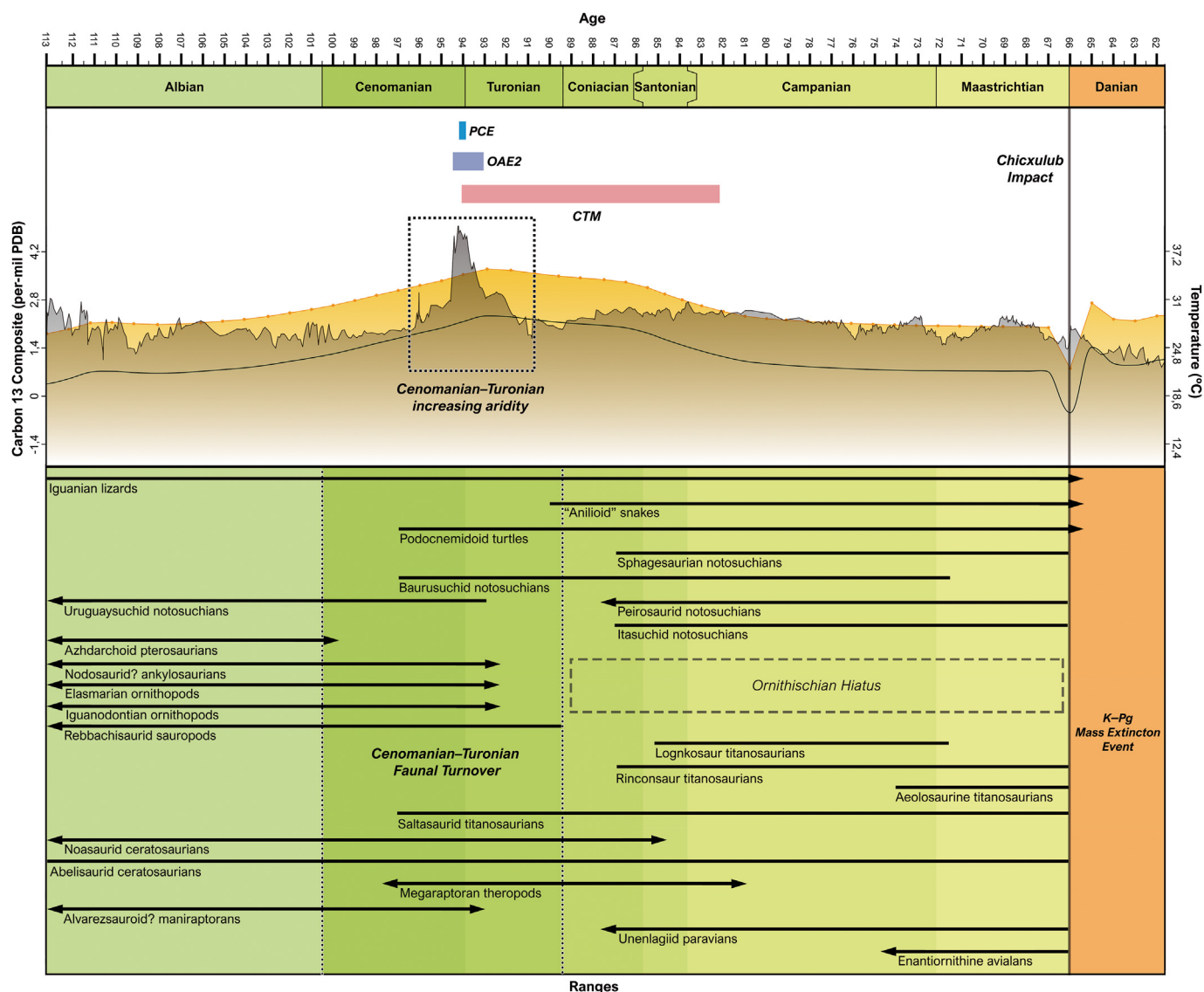


Fig. 20. Chronostratigraphic distribution of reptile groups in South America, focusing on record of the Chaco-Paraná Basin and contrasted with major environmental perturbations in the early Late Cretaceous: Oceanic Anoxic Event 2 (OAE2; following [Jenkyns 2010](#); [O'Connor et al., 2020](#)), Plenus Cold Event (PCE; following [Jarvis et al., 2011](#)) and the Cretaceous Thermal Maximum (CTM; following [Huber et al., 2018](#)). The grey area exhibit aridity shifts based on $\delta^{13}\text{C}$ data presented by [Cramer and Jarvis \(2020\)](#). The yellow area exhibits mean of global temperatures, with tropical (dotted orange line) and global (black line) average temperatures based on $\delta^{18}\text{O}$ levels presented by [Scotese et al. \(2021\)](#). Detailed taxon occurrences are summarized in the Supplementary Material (Fig. S1). Chart produced with TSCreator 8.0 (<https://timescalecreator.org/>), following the Geologic Time Scale 2020 ([Gradstein et al., 2020](#)).

crowns with 'fan-like' ridges forming well-developed carinae (e.g., [Nobre and Carvalho 2006](#)).

Thus, the presumed local extinction of ornithischians in southeast Brazil could have provided ecological opportunities for sphagesaurians to occupy niches of small-sized primary consumers previously held by thyreophorans and ornithopods, while titanosaur sauropods prevailed as medium to large-bodied herbivores in the upper Bauru Group. Similar faunal patterns are observed in other Upper Cretaceous units of Gondwana, such as the Lameta and Maevarano formations, where omnivorous/herbivorous crocodyliforms were present, yet ornithischian records are doubtful or absent (e.g., [Buckley et al., 2000](#); [Krause et al., 2006](#); [Halliday et al., 2020](#)).

6. Conclusions

The GSFB ichnofauna represents the first documented dinosaur tracksite within the Bauru Group and specifically within the Santo

Anastácio Formation (Cenomanian–Turonian). This ichnocoenosis includes four distinct theropod morphotypes, comprising putative abelisaurid, megaraptoran, and alvarezsaurid trackmakers. Additionally, it features a small bipedal ornithischian, likely an elasmarian, an ankylosaurian with nodosaurid affinities, both bipedal and a graviportal iguanodontians, and a small, narrow-gauged sauropod trackmaker, presumably a rebbachisaurid. The faunal content of this ichnocoenosis exhibits remarkable similarities to contemporaneous deposits across South America, particularly those from the Chaco-Paraná Basin (e.g., Guichón and Puerto Yerúa formations) and Neuquén Basin (Candeleros and Huincul formations).

The discovery of dinosaur tracks in the Santo Anastácio Formation reveals the presence of groups not previously identified in the Bauru Group through body fossils, such as ankylosaurians, elasmarians, and iguanodontians. The 'Ornithischian Hiatus' in the upper strata of the Bauru Group may reflect the global faunal turnover event in the Cenomanian–Turonian interval, followed by the onset of an intense greenhouse climate that persisted until

the early Campanian (~82 Ma). This period led to significant floristic changes in continental ecosystems and influenced the distribution of dinosaur populations toward the end of the Cretaceous.

Geological data suggest recurrent episodes of increasing aridity in the upper Bauru units (Coniacian–Maastrichtian), which likely prompted the regional extinction or successive migration of ornithischian fauna to higher latitudes during the early stages of the Bauru Group. This faunal shift could have allowed specialized crocodyliform lineages, like sphagesaurians, to occupy the niches of small-sized primary consumers, previously filled by thyreophorans and ornithopods. Concurrently, several lineages of titanosaurs dominated the role of medium-to large-sized herbivores in these paleoecosystems, while baurusuchids and abelisauroids led as apex predators.

Furthermore, the distinct pattern of crocodyliform occurrences in the immediate overlying units, such as the Araçatuba and Adamantina formations, suggests that the predominance of these faunal components in the Upper Bauru Group units may not solely be due to taphonomic biases. Instead, it may indicate genuine biogeographic provincialism, warranting further investigation. The dinosaur tracks from the Santo Anastácio Formation address significant gaps in our understanding of faunal composition and paleoenvironmental conditions during the early stages of the Bauru Group and enhance our comprehension of biotic changes during the early Late Cretaceous.

CRedit authorship contribution statement

Bruno A. Navarro: Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation, Conceptualization. **Arioaldo A. Giarretta:** Writing – review & editing, Visualization, Validation, Conceptualization. **Marcelo A. Fernandes:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Formal analysis. **Alberto B. Carvalho:** Writing – review & editing, Visualization, Validation, Data curation. **Hussam Zaher:** Writing – review & editing, Visualization, Validation, Supervision, Resources, Project administration, Funding acquisition, Data curation, Conceptualization.

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Declaration of competing interest

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

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Data availability

Data will be made available on request.

References

- Agostinho, M.B., 2009. Reconhecimento geológico (Formações Santo Anastácio e Adamantina) e paleobiológico (Mesoeucrocodylia Baurusuchidae e Sphagesauridae) na região noroeste do estado de São Paulo [master's thesis]. Rio Claro: Universidade Estadual Paulista (UNESP). <http://acervodigital.unesp.br/handle/11449/92903>.
- Alexander, R.M., 1976. Estimates of speeds of dinosaurs. *Nature* 261 (5556), 129–130. <https://doi.org/10.1038/261129a0>.
- Apesteguía, S., Gallina, P.A., Gianechini, F.A., Soto, M., Perea, D., 2013. Dinosaurios cretácicos del Triángulo Minero (Grupo Baurú, Brasil), el Grupo Paysandú (Uruguay Occidental) y la Cuenca Neuquina (Grupo Neuquén, Argentina). In: Candeiro, C.R., dos, A., Avilla, L., dos, S. (Eds.), *Fósseis de vertebrados e plantas do período dos dinossauros na região do Triângulo Mineiro*. Rio de Janeiro: Letra Capital, pp. 185–141.
- Apesteguía, S., Smith, N.D., Valieri, R.J., Makovicky, P.J., 2016. An unusual new theropod with a didactyl manus from the Upper Cretaceous of Patagonia, Argentina. *PLoS One* 11 (7), e0157793. <https://doi.org/10.1371/journal.pone.0157793>.
- Arai, M., Dias-Brito, D., 2023. Supersequência Bauru (Cretáceo da Bacia do Paraná): Revisão estratigráfica com base em dados paleontológicos recentes. *Derbyana* 44. <https://doi.org/10.14295/derb.v44.800>.
- Arbour, V.M., Currie, P.J., 2016. Systematics, phylogeny and palaeobiogeography of the ankylosaurid dinosaurs. *Journal of Systematic Palaeontology* 14 (5), 385–444. <https://doi.org/10.1080/14772019.2015.1059985>.
- Arbour, V.M., Zanno, L., Gates, T., 2016. Ankylosaurian dinosaur palaeoenvironmental associations were influenced by extirpation, sea-level fluctuation, and geodispersal. *Palaeogeography, Palaeoclimatology, Palaeoecology* 449. <https://doi.org/10.1016/j.palaeo.2016.02.033>.
- Arruda, J.T., Carvalho, I. de S., Vasconcellos, F.M. de, 2004. Baurusuquídeos da Bacia Bauru (Cretáceo Superior, Brasil). *An Inst Geociências* 27, 64–74. https://doi.org/10.11137/2004_0_64-74.
- Arthur, M.A., Dean, W.E., Pratt, L.M., 1988. Geochemical and climatic effects of increased marine organic carbon burial at the Cenomanian/Turonian boundary. *Nature* 335 (6192), 714–717. <https://doi.org/10.1038/335714a0>.
- Averianov, A., Sues, H.-D., 2017. The oldest record of Alvarezsauridae (Dinosauria: Theropoda) in the Northern Hemisphere. *PLoS One* 12 (10), e0186254. <https://doi.org/10.1371/journal.pone.0186254>.
- Azevedo, S.A.K.D., Gallo, V., Ferigolo, J., 2000. A possible chelonian egg from the Brazilian late cretaceous. *Anais da Academia Brasileira de Ciências* 72, 187–193. <https://doi.org/10.1590/S0001-37652000000200007>.
- Bandeira, K.L.N., Brum, A.S., Pêgas, R.V., Cidade, G.M., Holgado, B., Cidade, A., De Souza, R.G., 2018. The Baurusuchidae vs Theropoda record in the Bauru Group (Upper Cretaceous, Brazil): a taphonomic perspective. *Journal of Iberian Geology* 44 (1), 25–54. <https://doi.org/10.1007/s41513-018-0048-4>.
- Bandeira, K.L.N., Navarro, B.A., Pêgas, R.V., Brilhante, N.S., Brum, A.S., De Souza, L.G., Da Silva, R.C., Gallo, V., 2024. A reassessment of the historical fossil findings from Bahia State (Northeast Brazil) reveals a diversified dinosaur fauna in the Lower Cretaceous of South America. *Historical Biology* 36 (5), 1–42. <https://doi.org/10.1080/08912963.2024.2318406>.
- Barclay, R.S., McElwain, J.C., Sageman, B.B., 2010. Carbon sequestration activated by a volcanic CO2 pulse during Ocean Anoxic Event 2. *Nature Geoscience* 3 (3), 205–208. <https://doi.org/10.1038/ngeo757>.
- Barrett, P.M., McGowan, A.J., Page, V., 2009. Dinosaur diversity and the rock record. *Proc R Soc B Biol Sci* 276 (1667), 2667–2674. <https://doi.org/10.1098/rspb.2009.0352>.
- Basilici, G., Dal' Bó, P.F.F., 2010. Anatomy and controlling factors of a Late Cretaceous Aeolian sand sheet: The Marília and the Adamantina formations, NW Bauru Basin, Brazil. *Sedimentary Geology* 226 (1), 71–93. <https://doi.org/10.1016/j.sedgeo.2010.02.010>.
- Basilici, G., Sgarbi, G.N., 2012. A Sub-bacia Bauru: um sistema continental entre deserto e cerrado. In: Hasui, Y., De Almeida, F.F.M., Carneiro, C.D.R., Bartorelli, A. (Eds.), *Geologia do Brasil*. São Paulo: Beca, pp. 520–543.
- Basilici, G., Dal' Bó, P.F.F., de Oliveira, E.F., 2016. Distribution of palaeosols and deposits in the temporal evolution of a semiarid fluvial distributary system (Bauru Group, Upper Cretaceous, SE Brazil). *Sedimentary Geology* 341, 245–264. <https://doi.org/10.1016/j.sedgeo.2016.04.014>.
- Batezelli, A., 2010. Arcabouço tectono-estratigráfico e evolução das Bacias Caiuá e Bauru no Sudeste brasileiro. *Brazilian Journal of Genetics* 40, 265–285. <https://doi.org/10.25249/0375-7536.2010402265285>.
- Batezelli, A., 2015. Continental systems tracts of the Brazilian Cretaceous Bauru Basin and their relationship with the tectonic and climatic evolution of South America. *Basin Research* 29 (S1), 1–25. <https://doi.org/10.1111/bre.12128>.
- Batezelli, A., Ladeira, F.S.B., 2016. Stratigraphic framework and evolution of the Cretaceous continental sequences of the Bauru, Sanfranciscana, and Parecis basins, Brazil. *J South Am Earth Sci* 65, 1–24. <https://doi.org/10.1016/j.jsames.2015.11.005>.
- Batezelli, A., Saad, A., Etchebehere, M.L.C., Perinotto, A., Fulfaro, V.J., 2003. Análise estratigráfica aplicada a Formação Araçatuba (Grupo Bauru - KS) no Centro-Oeste do Estado de São Paulo. *Geociências* 22, 5–19.

- Bell, P.R., Herne, M.C., Brougham, T., Smith, E.T., 2018. Ornithopod diversity in the Griman Creek Formation (Cenomanian), New South Wales, Australia. *PeerJ* 6, e6008. <https://doi.org/10.7717/peerj.6008>.
- Bell, P.R., Brougham, T., Herne, M.C., Frauenfelder, T., Smith, E.T., 2019. *Fostoria dhimbangummal*, gen. et sp. nov., a new iguanodontian (Dinosauria, Ornithopoda) from the mid-Cretaceous of Lightning Ridge, New South Wales, Australia. *Journal of Vertebrate Paleontology* 39 (1). <https://doi.org/10.1080/02724634.2019.1564757>.
- Bertini, R.J., Marshall, L.G., Gayet, M., Brito, P., 1993. Vertebrate faunas from the Adamantina and Marília formations (Upper Bauru Group, Late Cretaceous, Brazil) in their stratigraphic and paleobiogeographic context. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen* 188 (1), 71–101.
- Bertini, R., Manzini, F., Brandt Neto, M., 1999. Novas ocorrências de Baurusuchidae (Sebecosuchia: Crocodylomorpha) na região de General Salgado, Formação Adamantina (Cretáceo Superior) do Grupo Bauru na região noroeste do Estado de São Paulo. *Acta Geologica Leopoldensia* 23, 29–38.
- Bertolucci, J.C., 2020. Novos registros de icnofósseis para o Grupo Bauru (Cretáceo Superior) no Triângulo Mineiro [Monograph]. Uberlândia: Universidade Federal de Uberlândia, p. 42.
- Bertoza, F., Dalla Vecchia, F., Fabbri, M., 2017. The Venice specimen of *Ouranosaurus nigeriensis* (Dinosauria, Ornithopoda). *PeerJ* 5. <https://doi.org/10.7717/peerj.3403>.
- Blanco, L.A.D., Batezelli, A., Ladeira, F.S.B., 2021. Paleoenvironmental and paleoclimatic reconstruction of Lower to Upper Cretaceous sequences of the Bauru Basin based on paleosol geochemistry and mineralogical analyses. *Palaeogeography, Palaeoclimatology, Palaeoecology* 569, 110328. <https://doi.org/10.1016/j.palaeo.2021.110328>.
- Blows, W.T., 2014. Notice of nodosaur (Dinosauria, Ankylosauria) remains from the mid-Cretaceous of Cambridge, England, with comments on cervical half-ring armour. *Proceedings of the Geologists' Association* 125 (1), 56–62. <https://doi.org/10.1016/j.pgeola.2013.07.001>.
- Brandt Neto, M., Barcha, S.F., Manzini, F.F., Brighetti, J.M.P., 1991. Nova ocorrência de crocodilianos na região do Noroeste do Estado de São Paulo. *Geociências* 10 (1), 191–203.
- Brusatte, S.L., Candeiro, C.R.A., Simbras, F.M., 2017. The last dinosaurs of Brazil: The Bauru Group and its implications for the end-Cretaceous mass extinction. *Anais da Academia Brasileira de Ciências* 89, 1465–1485. <https://doi.org/10.1590/0001-3765201702160918>.
- Buck, P.V., Ghilardi, A.M., Fernandes, L.B.R., Fernandes, M.A., 2017. A new ichnotaxon classification of large mammaliform trackways from the Lower Cretaceous Botucatu Formation, Paraná Basin, Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology* 485, 377–388. <https://doi.org/10.1016/j.palaeo.2017.06.027>.
- Buck, P., Ghilardi, A., Peixoto, B., Fernandes, L., Fernandes, M., 2016. A new tetrapod ichnotaxon from Botucatu Formation, Lower Cretaceous (Neocomian), Brazil, with comments on fossil track preservation on inclined planes and local paleoecology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 466. <https://doi.org/10.1016/j.palaeo.2016.11.009>.
- Buckley, G.A., Brochu, C.A., Krause, D.W., Pol, D., 2000. A pug-nosed crocodyliform from the Late Cretaceous of Madagascar. *Nature* 405 (6789), 941–944. <https://doi.org/10.1038/35016061>.
- Calvo, J., 1991. Huellas de dinosaurios en la Formación Río Limay (Albiano-Cenomaniano?). *Picún Leufú, Provincia del Neuquén, República Argentina (Ornithischia-Saurischia: Sauropoda-Theropoda)*. *Ameghiniana* 28, 241–258.
- Calvo, J., Mazzetta, G., 2004. New findings of dinosaur tracks in the Candeleros Formation (Albian-Cenomanian), Picún Leufú, Neuquén, Argentina. *Ameghiniana* 41, 545–554.
- Calvo, J., Rivera, C., 2018. Huellas de dinosaurios en la costa oeste del embalse Ezequiel Ramos Mexía y alrededores (Cretácico Superior, Provincia de Neuquén, República Argentina). *Boletín Soc Geol Mex* 70. <https://doi.org/10.18268/BSGM2018v70n2a11>.
- Canale, J.L., Scanferla, C.A., Agnolín, F.L., Novas, F.E., 2009. New carnivorous dinosaur from the Late Cretaceous of NW Patagonia and the evolution of abelisaurid theropods. *Naturwissenschaften* 96 (3), 409–414. <https://doi.org/10.1007/s00114-008-0487-4>.
- Candeiro, C.R.A., Rich, T., 2010. Overview of the Late Cretaceous Biota of the western São Paulo State, Brazil, Bauru Group. *J South Am Earth Sci* 29 (2), 346–353. <https://doi.org/10.1016/j.jsames.2009.08.001>.
- Candeiro, C.R.A., Abranches, C.T., Abrantes, E.A., Avilla, L.S., Martins, V.C., Moreira, A.L., Torres, S.R., Bergqvist, L.P., 2004. Dinosaurs remains from western São Paulo state, Brazil (Bauru Basin, Adamantina Formation, Upper Cretaceous). *J South Am Earth Sci* 18 (1), 1–10. <https://doi.org/10.1016/j.jsames.2004.08.004>.
- Candeiro, C.R.A., Martinelli, A.G., Avilla, L.S., Rich, T.H., 2006. Tetrapods from the Upper Cretaceous (Turonian–Maastrichtian) Bauru Group of Brazil: a reappraisal. *Cretaceous Research* 27 (6), 923–946. <https://doi.org/10.1016/j.cretres.2006.05.002>.
- Carneiro, C.D.R., de Almeida, F.F.M., Hasui, Y., Zalán, P.V., Teixeira, J.B.G., 2012. Estágios evolutivos do Brasil no Fanerozoico. In: Hasui, Y., De Almeida, F.F.M., Carneiro, C.D.R., Bartorelli, A. (Eds.), *Geologia do Brasil*. São Paulo: Beca, pp. 131–136.
- Carpenter, K., Kirkland, J., Burge, D., Bird, J., 1999. Ankylosaurs (Dinosauria: Ornithischia) of the Cedar Mountain Formation, Utah, and their stratigraphic distribution. *Utah Geol Surv Misc Publ* 99, 244–251.
- Carrano, M.T., 2007. The appendicular skeleton of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology* 27 (Suppl. 2), 163–179. [https://doi.org/10.1671/0272-4634\(2007\)27\[163:TASOMC\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2007)27[163:TASOMC]2.0.CO;2).
- Carrano, M.T., Wilson, J.A., 2001. Taxon distributions and the tetrapod track record. *Paleobiology* 27 (3), 564–582.
- Carrano, M.T., Benson, R.B.J., Sampson, S.D., 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). *Journal of Systematic Palaeontology* 10, 211–300. <https://doi.org/10.1080/14772019.2011.630927>.
- Carvalho, I., 2001. Pegadas de dinossauros em depósitos estuários (Cenomaniano) da Bacia Bauru de São Luís (MA), Brasil. In: Rossetti, D., de, F., Góes, A.M., Truelsenbrodt, W. (Eds.), *O Cretáceo Na Bacia São Luís-Grajaú*. Belém: Museu Paraense Emílio Goeldi, pp. 245–264.
- Carvalho, I. de S., Arruda Campos, A. de C., Henrique Nobre, P., 2005. *Baurusuchus salgadoensis*, a New Crocodylomorpha from the Bauru Basin (Cretaceous), Brazil. *Gondwana Research* 8 (1), 11–30. [https://doi.org/10.1016/S1342-937X\(05\)70259-8](https://doi.org/10.1016/S1342-937X(05)70259-8).
- Carvalho, I., Vasconcellos, F., Marinho, T., Nobre, P., Campos, A., Arruda, J., 2013. Répteis Fósseis de General Salgado, SP Registro de transformações ambientais na Bacia Bauru durante o Cretáceo. In: Winge, M., Schobbenhaus, C., Souza, C.R. de G., Fernandes, A.C.S., Berbert-Born, M., Sallun Filho, W., De Queiroz, E.T. (Eds.), *Sítios Geológicos e Paleontológicos do Brasil SIGEP*, vol. 3. Serviço Geológico do Brasil - CPRM, Brasília, pp. 211–224. <https://doi.org/10.13140/2.1.2890.8488>.
- Carvalho, L., Grillo, O., Azevedo, S., Paula, P., 2014. Ovos de crocodilomorfos: primeiro registro para o afloramento de Pirapozinho (SP), Cretáceo Superior. In: *Paleodest. Vitória: Sociedade Brasileira de Paleontologia*, p. 45.
- Castro, J., Dias-Brito, D., Arai, M., Rodrigues, R., Musacchio, E., 2002. Formação São Carlos: uma nova unidade para o Grupo Bauru (Cretáceo continental do Brasil). In: *Bol Resumos. São Pedro: Sociedade Brasileira de Geologia*, pp. 351–357.
- Castro, M.C., Goin, F.J., Ortiz-Jaureguizar, E., Vieytes, E.C., Tsukui, K., Ramezani, J., Batezelli, A., Marsola, J.C.A., Langer, M.C., 2018. A Late Cretaceous mammal from Brazil and the first radioisotopic age for the Bauru Group. *Royal Society Open Science* 5 (5), 180482. <https://doi.org/10.1098/rsos.180482>.
- Cerroni, M.A., Motta, M.J., Agnolín, F.L., Aranciaga Rolando, A.M., Brissón Egli, F., Novas, F.E., 2020. A new abelisaurid from the Huincul Formation (Cenomanian-Turonian; Upper Cretaceous) of Río Negro province, Argentina. *J South Am Earth Sci* 98, 102445. <https://doi.org/10.1016/j.jsames.2019.102445>.
- Chiarenza, A.A., Mannion, P.D., Farnsworth, A., Carrano, M.T., Varela, S., 2022. Climatic constraints on the biogeographic history of Mesozoic dinosaurs. *Current Biology* 32 (3), 570–585.e3. <https://doi.org/10.1016/j.cub.2021.11.061>.
- Choiniere, J.N., Xu, X., Clark, J.M., Forster, C.A., Guo, Y., Han, F., 2010. A basal alvarezsaurid theropod from the early Late Jurassic of Xinjiang, China. *Science* 327 (5965), 571–574. <https://doi.org/10.1126/science.1182143>.
- Chumakov, N., 1995. Climatic zones in the middle of the Cretaceous Period. *Stratigraphy and Geological Correlation* 3, 3–14.
- Coria, R.A., Calvo, J.O., 2002. A new iguanodontian ornithopod from Neuquén Basin, Patagonia, Argentina. *Journal of Vertebrate Paleontology* 22 (3), 503–509. [https://doi.org/10.1671/0272-4634\(2002\)022\[0503:ANIOFN\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2002)022[0503:ANIOFN]2.0.CO;2).
- Coria, R.A., Currie, P.J., 2006. A new carcharodontosaurid (Dinosauria, Theropoda) from the Upper Cretaceous of Argentina. *Geodiversitas* 28 (1), 71–118.
- Coria, R.A., Salgado, L., 1995. A new giant carnivorous dinosaur from the Cretaceous of Patagonia. *Nature* 377 (6546), 224–226. <https://doi.org/10.1038/377224a0>.
- Coria, R., Salgado, L., 1996. “*Loncosaurus argentinus*” Ameghino, 1899 (Ornithischia, Ornithopoda): A revised description with comments on its phylogenetic relationships. *Ameghiniana* 33, 373–376.
- Coria, R.A., Salgado, L., 1998. A Basal Abelisauria Novas, 1992 (Theropoda-Ceratosauroidea) from the Cretaceous of Patagonia, Argentina. *Gaia* 15, 89–102.
- Coria, R.A., Salgado, L., 2005. Mid-Cretaceous turnover of saurischian dinosaur communities: evidence from the Neuquén Basin. *Geol Soc Lond Spec Publ* 252 (1), 317–327. <https://doi.org/10.1144/GSL.SP.2005.252.01.16>.
- Coria, R.A., Cambiaso, A.V., Salgado, L., 2007. New records of basal ornithomimid dinosaurs in the Cretaceous of North Patagonia. *Ameghiniana* 44 (2), 473–477.
- Coria, R.A., Moly, J.J., Reguero, M., Santillana, S., Marensi, S., 2013. A new ornithomimid (Dinosauria; Ornithischia) from Antarctica. *Cretaceous Research* 41, 186–193. <https://doi.org/10.1016/j.cretres.2012.12.004>.
- Cramer, B.D., Jarvis, I., 2020. Chapter 11 - Carbon Isotope Stratigraphy. In: Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M. (Eds.), *Geol Time Scale 2020*. Elsevier, Amsterdam, pp. 309–343. <https://doi.org/10.1016/B978-0-12-824360-2.00011-5>.
- Cullen, T.M., Evans, D., 2016. Palaeoenvironmental drivers of vertebrate community composition in the Belly River Group (Campanian) of Alberta, Canada, with implications for dinosaur biogeography. *BMC Ecology* 16. <https://doi.org/10.1186/s12898-016-0106-8>.
- Da Silva, R.C., Barboni, R., Dutra, T., Godoy, M.M., Binotto, R.B., 2012. Footprints of large theropod dinosaurs and implications on the age of Triassic biotas from Southern Brazil. *J South Am Earth Sci* 39, 16–23. <https://doi.org/10.1016/j.jsames.2012.06.017>.
- Darlim, G., Carvalho, I. de S., Tavares, S.A.S., Langer, M.C., 2021. A new *Pissarrachampsinae* specimen from the Bauru Basin, Brazil, adds data to the understanding of the Baurusuchidae (Mesoeucrocodylia, Notosuchia) distribution in the Late Cretaceous of South America. *Cretaceous Research* 128, 104969. <https://doi.org/10.1016/j.cretres.2021.104969>.
- De Azevedo, R.P.F., Simbras, F.M., Furtado, M.R., Candeiro, C.R.A., Bergqvist, L.P., 2013. First Brazilian carcharodontosaurid and other new theropod dinosaur fossils from the Campanian–Maastrichtian Presidente Prudente Formation, São Paulo State, southeastern Brazil. *Cretaceous Research* 40, 131–142. <https://doi.org/10.1016/j.cretres.2012.06.004>.

- De França, M.A.G., Langer, M.C., 2005. A new freshwater turtle (Reptilia, Pleurodira, Podocnemidae) from the Upper Cretaceous (Maastrichtian) of Minas Gerais, Brazil. *Geodiversitas* 27 (3), 391–411.
- de la Fuente, M.S., 2003. Two new pleurodiran turtles from the Portezuelo Formation (Upper Cretaceous) of Northern Patagonia, Argentina. *Journal of Paleontology* 77 (3), 559–575.
- De Oliveira, C.E.M., Santucci, R.M., Andrade, M.B., Fúlvaro, V.J., Basílio, J.A.F., Benton, M.J., 2011. Crocodylomorph eggs and eggshells from the Adamantina Formation (Bauru Group), Upper Cretaceous of Brazil. *Palaeontology* 54 (2), 309–321. <https://doi.org/10.1111/j.1475-4983.2010.01028.x>.
- De Souza, G.A., Soares, M.B., Weinschütz, L.C., Wilner, E., Lopes, R.T., de Araújo, O.M.O., Kellner, A.W.A., 2021. The first edentulous ceratopsian from South America. *Scientific Reports* 11 (1), 22281. <https://doi.org/10.1038/s41598-021-01312-4>.
- De Valais, S., Apesteguía, S., Udrizur Sauthier, D., 2003. Nuevas evidencias de dinosaurios de la Formación Puerto Yeraú (Cretácico), Provincia de Entre Ríos, Argentina. *Ameghiniana* 40, 507–511.
- Delcourt, R., Grillo, O.N., 2018. Reassessment of a fragmentary maxilla attributed to Carcharodontosauridae from Presidente Prudente Formation, Brazil. *Cretaceous Research* 84, 515–524. <https://doi.org/10.1016/j.cretres.2017.09.008>.
- Delcourt, R., Brilhante, N.S., Grillo, O.N., Ghilardi, A.M., Augusta, B.G., Ricardi-Branco, F., 2020. Carcharodontosauridae theropod tooth crowns from the Upper Cretaceous (Bauru Basin) of Brazil: A reassessment of isolated elements and its implications to palaeobiogeography of the group. *Palaeogeography, Palaeoclimatology, Palaeoecology* 556, 109870. <https://doi.org/10.1016/j.palaeo.2020.109870>.
- Dentzien-Dias, P.C., Schultz, C.L., Scherer, C.M.S., Lavina, E.L.C., 2007. The trace fossil record from the Guará Formation (Upper Jurassic?), Southern Brazil. *Arq Mus Nac Rio Jan.* 65 (4), 585–600.
- Dias, A.N.C., Chemale, F., Candeiro, C.R.A., Lana, C.C., Guadagnin, F., Sales, A.S.W., 2021. Unraveling multiple tectonic events and source areas in the intracratonic Bauru Basin through combined zircon geo and thermochronological studies. *J South Am Earth Sci* 106, 103061. <https://doi.org/10.1016/j.jsames.2020.103061>.
- Dias-Brito, D., Musacchio, E.A., de Castro, J.C., Maranhão, M.S.A.S., Suárez, J.M., Rodrigues, R., 2001. The Bauru Group: A continental Cretaceous unit in Brazil – Concepts based on micropaleontological, oxygen isotope and stratigraphical data. *Revue de Paleobiologie* 20 (1), 245–304.
- Díaz Martínez, I., Pereda Suberbiola, X., Pérez-Lorente, F., Canudo, J., 2015. Ichnotaxonomic Review of Large Ornithomimid Dinosaur Tracks: Temporal and Geographic Implications. *PLoS One*. <https://doi.org/10.1371/journal.pone.0115477>.
- Do Nascimento, D.L., Batezelli, A., Ladeira, F.S.B., 2019. The paleoecological and paleoenvironmental importance of root traces: Plant distribution and topographic significance of root patterns in Upper Cretaceous paleosols. *Catena* 172, 789–806. <https://doi.org/10.1016/j.catena.2018.09.040>.
- Dos Santos, D.M., De Carvalho, J.C., De Oliveira, C.E.M., De Andrade, M.B., Santucci, R.M., 2024. Cranial and postcranial anatomy of a juvenile baurusuchid (Notosuchia, Crocodylomorpha) and the taxonomical implications of ontogeny. *The Anatomical Record*. <https://doi.org/10.1002/ar.25419> ar.25419.
- Fernandes, L., 2004. Mapa litoestratigráfico da parte oriental da Bacia Bauru (PR, SP, MG), escala 1:1.000.000. *Boletim Paranaense de Geociências* 55. <https://doi.org/10.5380/geo.v55i0.4283>.
- Fernandes, L.A., Basili, G., 2009. Transition of ephemeral palustrine to aeolian deposits in a continental arid – semi-arid environment (Upper Cretaceous Bauru Basin, Brazil). *Cretaceous Research* 30 (3), 605–614. <https://doi.org/10.1016/j.cretres.2008.12.002>.
- Fernandes, A.C.S., Carvalho, I.D.S., 2006. Invertebrate Ichnofossils from the Adamantina Formation (Bauru Basin, Late Cretaceous), Brazil. *Revista Brasileira de Paleontologia* 9, 211–220. <https://doi.org/10.4072/rbp.2006.2.05>.
- Fernandes, M.A., Carvalho, I.D.S., 2007. Pegadas fósseis da Formação Botucatu (Jurássico Superior-Cretáceo Inferior): o registro de um grande dinossauro Ornithomida na Bacia do Paraná. In: *Anais. Búzios: Sociedade Brasileira de Paleontologia*, p. 238.
- Fernandes, M.A., Carvalho, I.D.S., 2008. Diagnostic revision for the mesozoic tetrapod ichnospecies *Brasilichnium elusivum* (Leonardi, 1981) (Mammalia) from the Botucatu Formation, Paraná Basin, Brasil. *Ameghiniana* 45, 167–173.
- Fernandes, L.A., Coimbra, A.M., 1994. O Grupo Caiuá (Ks): revisão estratigráfica e contexto deposicional. *Revista Brasileira de Geociências* 24 (3), 164–176.
- Fernandes, L.A., Coimbra, A.M., 1996. A Bacia Bauru (Cretáceo Superior, Brasil). *Anais da Academia Brasileira de Ciências* 68 (2), 195–205.
- Fernandes, L.A., Coimbra, A.M., 2000. Revisão estratigráfica da parte oriental da Bacia Bauru (Neocretáceo). *Revista Brasileira de Geociências* 30 (4), 717–728.
- Fernandes, L.A., Magalhães Ribeiro, C.M., 2015. Evolution and palaeoenvironment of the Bauru Basin (Upper Cretaceous, Brazil). *J South Am Earth Sci* 61, 71–90. <https://doi.org/10.1016/j.jsames.2014.11.007>.
- Fernandes, L.A., Sedor, F.A., Da Silva, R.C., Da Silva, L.R., Azevedo, A.A., Siqueira, A.G., 2009. Icnofósseis da Usina Porto Primavera, SP: Rastros de dinossauros e de mamíferos em rochas do deserto neocretáceo Caiuá. In: Winge, M., Schobbenhaus, C., Souza, C.R. de G., Fernandes, A.C.S., Berbert-Born, M., De Queiroz, E.T., Campos, D. de A. (Eds.), *Sítios Geológicos e Paleontológicos do Brasil (SIGEP)*, vol. 2. Serviço Geológico do Brasil - CPRM, Brasília, pp. 479–488.
- Fernandes, M., Ghilardi, A., Carvalho, I., Leonardi, G., 2010. Pegadas de dinossauros Theropoda do Paleodéserto Botucatu (Jurássico Superior-Cretáceo Inferior) da Bacia do Paraná. In: *Paleontol Cenários Vida*, fourth ed. Interciência, Rio de Janeiro, pp. 609–621.
- Fernandes, M.A., Ghilardi, A.M., Carvalho, I. de S., 2014. Paleodéserto Botucatu: inferências ambientais e climáticas com base na ocorrência de icnofósseis. In: Carvalho, I., de S., Garcia, M.J., Lana, C.C., Strohschoen, O. (Eds.), *Paleontologia Cenários de Vida: Paleoclimas*, fifth ed. Interciência, Rio de Janeiro, pp. 71–80.
- Fiorelli, L.E., Martinelli, A.G., Da Silva, J.L., Hechenleitner, E.M., Soares, M.V.T., Silva Junior, J.C.G., Silva, J.C.D., Borges, É.M.R., Ribeiro, L.C.B., Marconato, A., et al., 2022. First titanosaur dinosaur nesting site from the Late Cretaceous of Brazil. *Scientific Reports* 2022, 5091. <https://doi.org/10.1038/s41598-022-09125-9>.
- Fittipaldi, F.C., Fernandes, L.A., Simões, M.G., Coimbra, A.M., 1989. Primeira ocorrência de tetrapódes na Formação Santo Anastácio (Cretáceo da Bacia do Paraná). In: *Resumos*, vol. 16. Sociedade Brasileira de Zoologia, João Pessoa, pp. 89–90.
- Forster, A., Schouten, S., Moriya, K., Wilson, P.A., Sinninghe Damsté, J.S., 2007. Tropical warming and intermittent cooling during the Cenomanian/Turonian oceanic anoxic event 2: Sea surface temperature records from the equatorial Atlantic. *Paleoceanography* 22 (1). <https://doi.org/10.1029/2006PA001349>.
- Francischini, H., Dentzien-Dias, P.C., Fernandes, M.A., Schultz, C.L., 2015. Dinosaur ichnofauna of the Upper Jurassic/Lower Cretaceous of the Paraná Basin (Brazil and Uruguay). *J South Am Earth Sci* 63, 180–190. <https://doi.org/10.1016/j.jsames.2015.07.016>.
- Francischini, H., Sales, M., Schultz, C., Dentzien-Dias, P., 2017. The presence of ankylosaur tracks in the Guará Formation (Brazil) and remarks on the spatial and temporal distribution of Late Jurassic dinosaurs. *Ichnos* 25. <https://doi.org/10.1080/10420940.2017.1337573>.
- Francischini, H., Sipp, G., Barcelos-Silveira, A., Schultz, C., Dentzien-Dias, P., 2022. Revisiting the southernmost occurrence of *Brasilichnium elusivum* Leonardi, 1981 with comments on the tetrapod track record of eolian environments. *Revista Brasileira de Paleontologia* 25, 249–254. <https://doi.org/10.4072/rbp.2022.4.01>.
- Freitas, R.C., Batezelli, A., Muniz, F.P., Ribeiro, D.C., Ruiz, J.V., Alves, Y.M., Geroto, C., Castro, M.C., Barbosa, G.G., Langer, M.C., Montefeltro, F.C., 2023. A microvertebrate assemblage from the Adamantina Formation (Bauru Group, Upper Cretaceous) in São Paulo State, Brazil. *Cretaceous Research* 150, 105589. <https://doi.org/10.1016/j.cretres.2023.105589>.
- Fúlvaro, V., Etchebehere, M. de C., Perinotto, J., de J., Saad, A., 1999a. Bacia Caiuá: uma nova bacia cretácea na Bacia do Paraná. In: *Bol Resumos*, vol. 5. Sociedade Brasileira de Geologia, Serra Negra, pp. 439–442.
- Fúlvaro, V., Etchebehere, M. de C., Perinotto, J., de J., Saad, A., 1999b. Santo Anastácio: um geossolo cretácico na Bacia Caiuá. In: *Bol Resumos*, vol. 5. Sociedade Brasileira de Geologia, Serra Negra, pp. 125–130.
- Gale, A.S., Christensen, W.K., 1996. Occurrence of the belemnite *Actinocamax plenus* in the Cenomanian of SE France and its significance. *Bulletin of the Geological Society of Denmark* 43 (1), 68–77.
- Gallina, P.A., Gonzalez Riga, B.J., Ortiz, David L., 2022. Time for Giants: Titanosaurs from the Berriasian–Santonian Age. In: *South Am Sauropodomorph Dinosaurs Rec Divers Evol*. Springer International Publishing, Cham, pp. 299–340. https://doi.org/10.1007/978-3-030-95959-3_9.
- Geroto, C.F.C., Bertini, R.J., 2012. Descrição de um espécime juvenil de Baurusuchidae (Crocodyliformes: Mesoeucrocodylia) do Grupo Bauru (Neocretáceo): considerações preliminares sobre ontogenia. *Rev Inst Geológico* 33 (2), 13–29. <https://doi.org/10.5935/0100-929X.20120007>.
- Giaretta, A.A., Rodrigues, S.C., Buck, P.V., 2014. A new geographical record of Abelisauridae (Theropoda, Dinosauria) for the Bauru Group (Upper Cretaceous). *J South Am Earth Sci* 133, 104722. <https://doi.org/10.1016/j.jsames.2023.104722>.
- Gierlinski, G.D., Sabath, K., 2008. Stegosaurian footprints from the Morrison Formation of Utah and their implications for interpreting other ornithischian tracks. *Oryctos* 8, 29–46.
- Godoy, P.L., Montefeltro, F.C., Norell, M.A., Langer, M.C., 2014. An additional baurusuchid from the Cretaceous of Brazil with evidence of interspecific predation among Crocodyliformes. *PLoS One* 9 (5), e97138. <https://doi.org/10.1371/journal.pone.0097138>.
- Gonzalez Riga, B., Calvo, J., 2009. A new wide-gauge sauropod track site from the Late cretaceous of Mendoza, Neuquén Basin, Argentina. *Palaeontology* 52 (3), 631–640. <https://doi.org/10.1111/j.1475-4983.2009.00869.x>.
- González Riga, B.J., Calvo, J.O., 2009. A new wide-gauge sauropod track site from the Late Cretaceous of Mendoza, Neuquén Basin, Argentina. *Palaeontology* 52 (3), 631–640. <https://doi.org/10.1111/j.1475-4983.2009.00869.x>.
- González-Riga, B.J., 2011. Speeds and stance of titanosaur sauropods: analysis of *Titanopus* tracks from the Late Cretaceous of Mendoza, Argentina. *Anais da Academia Brasileira de Ciências* 83 (1), 279–290. <https://doi.org/10.1590/S0001-37652011005000002>.
- Gradstein, F.M., Ogg, J.G., Schmitz, M.D., Ogg, G.M., 2020. *Geologic time scale 2020*. Elsevier.
- Halliday, T.J.D., Holroyd, P.A., Gheerbrant, E., Prasad, G.V.R., Scanferla, A., Beck, R.M.D., Krause, D.W., Goswami, A., 2020. Leaving Gondwana: The Changing Position of the Indian Subcontinent in the Global Faunal Network. In: Prasad, G.V.R., Patnaik, R. (Eds.), *Biol Consequences Plate Tecton New Perspect Post-Gondwana Break-Up—A Tribute Ashok Sahni*. Springer International Publishing, Cham, pp. 227–249. https://doi.org/10.1007/978-3-030-49753-8_9.
- Hawakaya, H., Manabe, M., Carpenter, K., 2005. Nodosaurid ankylosaur from the Cenomanian of Japan. *Journal of Vertebrate Paleontology* 25 (1), 240–245. [https://doi.org/10.1671/0272-4634\(2005\)025\[0240:NAFTCO\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2005)025[0240:NAFTCO]2.0.CO;2).
- Heimhofer, U., Wucherpfennig, N., Adatte, T., Schouten, S., Schneebeli-Hermann, E., Gardin, S., Keller, G., Kentsch, S., Kujau, A., 2018. Vegetation response to exceptional global warmth during Oceanic Anoxic Event 2. *Nature Communications* 9 (1), 3832. <https://doi.org/10.1038/s41467-018-06319-6>.

- Hendrickx, C., Bell, P.R., Pittman, M., Milner, A.R.C., Cuesta, E., O'Connor, J., Loewen, M., Currie, P.J., Mateus, O., Kaye, T.G., Delcourt, R., 2022. Morphology and distribution of scales, dermal ossifications, and other non-feather integumentary structures in non-avian theropod dinosaurs. *Biological Reviews* 97 (3), 960–1004. <https://doi.org/10.1111/brv.12829>.
- Hildebrand, M., Goslow, G.E., 1998. *Analysis of vertebrate structure*, fifth ed. Wiley, New York.
- Hone, D.W.E., Choiniere, J.N., Tan, Q., Xu, X., 2012. An articulated pes from a small parvicursorine alvarezsaurid dinosaur from Inner Mongolia, China. *Acta Palaeontologica Polonica* 58 (3), 453–458. <https://doi.org/10.4202/app.2011.0127>.
- Hornung, J.J., Reich, M., 2014. *Metatetrapodus valdensis* Nopcsa, 1923 and the presence of ankylosaur tracks (Dinosauria: Thyreophora) in the Berriasian (Early Cretaceous) of Northwestern Germany. *Ichnos* 21 (1), 1–18. <https://doi.org/10.1080/10420940.2013.873720>.
- Huber, B.T., MacLeod, K.G., Watkins, D.K., Coffin, M.F., 2018. The rise and fall of the Cretaceous Hot Greenhouse climate. *Global and Planetary Change* 167, 1–23. <https://doi.org/10.1016/j.gloplacha.2018.04.004>.
- Huene, F von, 1931. Verschiedene mesozoische Wirbeltierreste aus Südamerika. *Neuen Jahrb Für Mineral Geol Paläontol Beil-Bd* 66, 181–198.
- Huene, F von, 1932. Die fossil Reptil-Ordnung Saurischia, ihre Entwicklung und Geschichte. *Monogr Zur Geol Palaeontol Ser* 1 (1–2), 1–361, 4.
- Huene, F von, 1934. Nuevos dientes de Saurios del Cretáceo del Uruguay. *Bol Inst Geológico Urug* 21, 13–20.
- Ibárricu, L.M., Casal, G.A., Martínez, R.D., Lamanna, M.C., Luna, M., Salgado, L., 2013. *Katapsaurus goicoecheai*, gen. et sp. nov., a Late Cretaceous rebbachisaurid (Sauropoda, Diplodocoidea) from central Patagonia, Argentina. *Journal of Vertebrate Paleontology* 33 (6), 1351–1366. <https://doi.org/10.1080/02724634.2013.776562>.
- Ibárricu, L.M., Martínez, R.D., Luna, A., Casal, G.A., 2014. A reappraisal of *Notohypsilophodon comodorensis* (Ornithischia: Ornithopoda) from the Late Cretaceous of Patagonia, Argentina. *Zootaxa* 3786 (4). <https://doi.org/10.11646/zootaxa.3786.4.1>.
- Ibárricu, L.M., Casal, G.A., Martínez, R.D., Alvarez, B.N., Poropat, S.F., 2020. New materials and an overview of Cretaceous vertebrates from the Chubut Group of the Golfo San Jorge Basin, central Patagonia, Argentina. *J South Am Earth Sci* 98, 102460. <https://doi.org/10.1016/j.jsames.2019.102460>.
- Ibárricu, L.M., Casal, G.A., Alvarez, B.N., De Sosa Tomas, A., Lamanna, M.C., Cruzado-Caballero, P., 2021. New hadrosaurid (Dinosauria: Ornithopoda) fossils from the uppermost Cretaceous of central Patagonia and the influence of paleoenvironment on South American hadrosaur distribution. *J South Am Earth Sci* 110, 103369. <https://doi.org/10.1016/j.jsames.2021.103369>.
- Ibrahim, N., Sereno, P.C., Varricchio, D.J., Martill, D.M., Dutheil, D.B., Unwin, D.M., Baidder, L., Larsson, H.C.E., Zouhri, S., Kaoukaya, A., 2020. Geology and paleontology of the Upper Cretaceous Kem Kem Group of eastern Morocco. *ZooKeys* 928, 1–216. <https://doi.org/10.3897/zookeys.928.47517>.
- Iori, F.V., Carvalho, I.S., 2011. *Caipirasuchus paulistanus*, a new sphagesaurid (Crocodylomorpha, Mesoeucrocodylia) from the Adamantina Formation (Upper Cretaceous, Turonian–Santonian), Bauru Basin, Brazil. *Journal of Vertebrate Paleontology* 31 (6), 1255–1264. <https://doi.org/10.1080/02724634.2011.602777>.
- Iori, F.V., Carvalho, I. de S., 2018. The Cretaceous crocodyliform *Caipirasuchus*: behavioral feeding mechanisms. *Cretaceous Research* 84, 181–187. <https://doi.org/10.1016/j.cretres.2017.11.023>.
- Iori, F.V., de Souza Carvalho, I., da Silva Marinho, T., 2016. Postcranial skeletons of *Caipirasuchus* (Crocodyliformes, Notosuchia, Sphagesauridae) from the Upper Cretaceous (Turonian–Santonian) of the Bauru Basin, Brazil. *Cretaceous Research* 60, 109–120. <https://doi.org/10.1016/j.cretres.2015.11.017>.
- Iori, F.V., Ghilardi, A.M., Fernandes, M.A., Dias, W.A.F., 2024. A new species of vocalizing crocodyliform (Notosuchia, Sphagesauridae) from the Late Cretaceous of Brazil. *Historical Biology* 1–12. <https://doi.org/10.1080/08912963.2024.2364332> (D.R.).
- Jarvis, I., Lignum, J.S., Gröcke, D.R., Jenkyns, H.C., Pearce, M.A., 2011. Black shale deposition, atmospheric CO₂ drawdown, and cooling during the Cenomanian–Turonian Oceanic Anoxic Event. *Paleoceanography* 26 (3). <https://doi.org/10.1029/2010PA002081>.
- Jones, C., Long, D., Hall, M., Bland, D., Cornford, C., 1991. The geochemistry of the Plenus Marls at Dover, England: evidence of fluctuating oceanographic conditions and of glacial control during the development of the Cenomanian–Turonian $\delta^{13}\text{C}$ anomaly. *Geological Magazine* 128 (6), 603–632.
- Jefferies, R., 1962. The palaeoecology of the *Actinocamax plenus* subzone (lowest Turonian) in the Anglo-Paris Basin. *Palaeontology* 4 (4), 609–647.
- Jenkyns, H.C., 2010. Geochemistry of oceanic anoxic events. *Geochemistry, Geophysics, Geosystems* 11 (3). <https://doi.org/10.1029/2009GC002788>.
- Jenkyns, H.C., Dickson, A.J., Ruhl, M., van den Boorn, S.H.J.M., 2017. Basalt-seawater interaction, the Plenus Cold Event, enhanced weathering and geochemical change: deconstructing Oceanic Anoxic Event 2 (Cenomanian–Turonian, Late Cretaceous). *Sedimentology* 64 (1), 16–43. <https://doi.org/10.1111/sed.12305>.
- Kellner, A., Campos, D., De Azevedo, S., Carvalho, L., 1998. Theropod dinosaur eggs from the continental Upper Cretaceous of Minas Gerais. *Journal of Vertebrate Paleontology* 18 (3), 55A.
- Kellner, A.W.A., Weinschutz, L., Holgado, B., Bantim, R., Sayão, J., 2019. A new toothless pterosaur (Pterodactyloidea) from Southern Brazil with insights into the paleoecology of a Cretaceous desert. *Anais da Academia Brasileira de Ciências* 91. <https://doi.org/10.1590/0001-3765201920190768>.
- Kischlat, E., 1994. Observações sobre *Podocnemis elegans* Suarez (Chelonii, Pleurodira, Podocnemididae) do Neocretáceo do Brasil. *Acta Geologica Leopoldensia* 17, 345–351.
- Krause, D.W., O'Connor, P.M., Rogers, K.C., Sampson, S.D., Buckley, G.A., Rogers, R.R., 2006. Late Cretaceous terrestrial vertebrates from Madagascar: implications for Latin American biogeography. *Annals of the Missouri Botanical Garden* 93 (2), 178–208. [https://doi.org/10.3417/0026-6493\(2006\)93\[178:LCTVFM\]2.0.CO;2](https://doi.org/10.3417/0026-6493(2006)93[178:LCTVFM]2.0.CO;2).
- Kuroda, J., Ogawa, N.O., Tanimizu, M., Coffin, M.F., Tokuyama, H., Kitazato, H., Ohkouchi, N., 2007. Contemporaneous massive subaerial volcanism and late Cretaceous Oceanic Anoxic Event 2. *Earth and Planetary Science Letters* 256 (1), 211–223. <https://doi.org/10.1016/j.epsl.2007.01.027>.
- Langer, M., Martins, N., Manzig, P., Ferreira, G., Marsola, J., Fortes, E., Lima, R., Sant'ana, L., Vidal, L., Lorençato, R., Ezcurra, M., 2019. A new desert-dwelling dinosaur (Theropoda, Noasaurinae) from the Cretaceous of south Brazil. *Scientific Reports* 9. <https://doi.org/10.1038/s41598-019-45306-9>.
- Langer, M., Delcourt, R., Montefeltro, F. C., Silva Júnior, J. C.G., Soler, M. G., Ferreira, G. S., Ruiz, J. V., Barcelos, L. A., Onary, S., Marsola, J. C.A., et al., 2022. The Bauru Basin in São Paulo and its tetrapods. *Derbyana* 43. <https://doi.org/10.14295/derbv43.776>.
- Leanza, H.A., Apesteguía, S., Novas, F.E., de la Fuente, M.S., 2004. Cretaceous terrestrial beds from the Neuquén Basin (Argentina) and their tetrapod assemblages. *Cretaceous Research* 25 (1), 61–87. <https://doi.org/10.1016/j.cretres.2003.10.005>.
- Leonardi, G., 1977. Two new ichnofaunas, vertebrates and invertebrates, in the eolian Cretaceous sandstones of the Caiuá Formation in northwest Paraná. In: *Atas. São Paulo: Sociedade Brasileira de Geologia*, pp. 112–128.
- Leonardi, G., 1978. Ornithischian trackways of the Corda Formation (Jurassic), Goiás, Brazil. In: *Actas. Buenos Aires: Asociación Paleontológica Argentina*, pp. 215–222.
- Leonardi, G., 1979. Nota preliminar sobre seis pistas de dinossauros Ornithischia da Bacia do Rio do Peixe, em Sousa, Paraíba, Brasil. *Anais da Academia Brasileira de Ciências* 51, 501–516.
- Leonardi, G., 1981. Ichnological data on the rarity of young in Northeast Brazil dinosaurian populations. *Anais da Academia Brasileira de Ciências* 53, 345–346.
- Leonardi, G., 1984. Le impronte fossili di dinosauri (with the holotypes of the ichnogen. *Caririchnium* and *Ligabueichnium*). In: Bonaparte, J.F., Colbert, E.H., Currie, P.J., De Ricques, A., Kielan-Jaworowska, Z., Leonardi, G., Morello, N., Taguet, P. (Eds.), *Sulle Orme Dei Dinosauri*. Venezia: Erizzo, pp. 163–186.
- Leonardi, G., 1994. Annotated atlas of South America tetrapod footprints (Devonian to Holocene) with an appendix on Mexico and Central America. *Serviço Geológico do Brasil - CPRM, Brasília*.
- Leonardi, G., Carvalho, I. de S., 2002. Jazigo Icnofossilífero do Ouro (Araraquara), SP. Ricas pistas de tetrapodes do Jurássico. In: Schobbenhaus, C., Campos, D. de A., Queiroz, E., Winge, M., Berbert-Born, M. (Eds.), *Sítios Geológicos E Paleontológicos Bras SIGEP*, vol. 1. Brasília, pp. 39–48.
- Leonardi, G., Carvalho, I. de S., 2021. Dinosaur Tracks from Brazil: A Lost World of Gondwana. Indiana University Press, Bloomington. <https://doi.org/10.2307/j.ctv21hrh1>.
- Leonardi, G., Casamiquela, R., Demathieu, G., Haubold, H., Sarjeant, W., 1987. *Glossary and Manual of Tetrapod Footprint Palaeoichnology*. Serviço Geológico do Brasil - CPRM, Brasília.
- Leonardi, G., Dos Santos, M.D.F.C.F., Barbosa, F.H.D.S., 2021. First dinosaur tracks from the Açú Formation, Potiguar Basin (mid-Cretaceous of Brazil). *Anais da Academia Brasileira de Ciências* 93 (Suppl. 2), e20210635. <https://doi.org/10.1590/0001-3765202120210635>.
- Leonardi, G., Fernandes, M.A., Carvalho, I. de S., Schutzer, J.B., Silva, R.C. da, 2024. *Farlowichnus rapidus* new ichnogen., new ichnosp.: A speedy and small theropod in the Early Cretaceous Botucatu paleodesert (Paraná Basin), Brazil. *Cretaceous Research* 153, 105720. <https://doi.org/10.1016/j.cretres.2023.105720>.
- Lindoso, R.M., Medeiros, M.A.A., Carvalho, I. de S., Pereira, A.A., Mendes, I.D., Iori, F.V., Sousa, E.P., Arcanjo, S.H.S., Silva, T.C.M., 2019. A new rebbachisaurid (Sauropoda: Diplodocoidea) from the middle Cretaceous of northern Brazil. *Cretaceous Research* 104, 104191. <https://doi.org/10.1016/j.cretres.2019.104191>.
- Lockley, M.G., 1986. A guide to dinosaur tracksites of the Colorado Plateau and American Southwest. *Univ Colo Denver Geol Dep Mag* 1, 1–56.
- Lockley, M.G., Meyer, C., 2000. *Dinosaur tracks and other fossil footprints of Europe*. Columbia University Press, New York.
- Lockley, M., Farlow, J., Meyer, C., 1994a. *Brontopodus* and *Parabrontopodus* ichnogen. nov. and the significance of wide- and narrow-gauge sauropod trackways. *Gaia* 10, 135–146.
- Lockley, M., Meyer, C., Hunt, A., Lucas, S., 1994b. The distribution of sauropod tracks and trackmakers. *Gaia* 10, 233–248.
- Lockley, M.G., Kim, K.S., Lim, J.D., 2021. *Tetrapodosaurus* trackways from the Cretaceous of Colorado and Canada: observations on variability in ankylosaurian gaits. *N M Mus Nat Hist Sci Bull* 82 (7), 227–235.
- Magalhães Ribeiro, C.M., 2002. Ovo e fragmentos de cascas de ovos de dinossauros, provenientes da região de Peirópolis, Uberaba, Minas Gerais. *Arquivos do Museu Nacional* 60 (3), 223–228.
- Magalhães Ribeiro, C.M., Carvalho, I. de S., Nava, W.R., 2006. Ovos de crocodilomorfos da Formação Araçatuba (Bacia Bauru, Cretáceo Superior), Brasil. In: Gallo, V., Brito, P.M.M., Silva, H.M.A., Figueiredo, F.J. (Eds.), *Paleontologia de Vertebrados: Grandes temas e contribuições científicas*. Interciência, Rio de Janeiro, pp. 285–292.
- Maidment, S., Norman, D., Barrett, P., Upchurch, P., 2008. Systematics and phylogeny of Stegosauria (Dinosauria: Ornithischia). *Journal of Systematic Palaeontology* 6, 1815–1821. <https://doi.org/10.1017/S1477201908002459>.

- Maidment, S.C.R., Dean, C.D., Mansergh, R.I., Butler, R.J., 2021. Deep-time biodiversity patterns and the dinosaurian fossil record of the Late Cretaceous Western Interior, North America. *Proc R Soc B Biol Sci* 288 (1953), 20210692. <https://doi.org/10.1098/rspb.2021.0692>.
- Makovicky, P.J., Apesteguía, S., Gianechini, F.A., 2012. A new coelurosaurian theropod from the La Buitrera Fossil Locality of Río Negro, Argentina. *Fieldiana Life Earth Sci.* 5, 90–98. <https://doi.org/10.3158/2158-5520-5.1.90>.
- Manes, M.L. de, Silva, R.C. da, Scheffler, S.M., 2021. Dinosaurs and rivers on the edge of a desert: A first recognition of fluvial deposits associated to the Botucatu Formation (Jurassic/Cretaceous), Brazil. *J South Am Earth Sci.* 110, 103339. <https://doi.org/10.1016/j.jsames.2021.103339>.
- Manzig, P.C., Kellner, A.W.A., Weinschütz, L.C., Fragoso, C.E., Vega, C.S., Guimarães, G.B., Godoy, L.C., Luccardo, A., Ricetti, J.H.Z., Moura, C.C. de, 2014. Discovery of a rare pterosaur bone bed in a Cretaceous desert with insights on ontogeny and behavior of flying reptiles. *PLoS One* 9 (8), e100005. <https://doi.org/10.1371/journal.pone.0100005>.
- Marinho, T.S., Carvalho, I.S., 2009. An armadillo-like sphagesaurid crocodyliform from the Late Cretaceous of Brazil. *J South Am Earth Sci* 27 (1), 36–41. <https://doi.org/10.1016/j.jsames.2008.11.005>.
- Marinho, T. da S., Iori, F.V., Carvalho, I. de S., Vasconcellos, F.M. de, 2013. *Gondwanasuchus scabrosus* gen. et sp. nov., a new terrestrial predatory crocodyliform (Mesoeucrocodylia: Baurusuchidae) from the Late Cretaceous Bauru Basin of Brazil. *Cretaceous Research* 44, 104–111. <https://doi.org/10.1016/j.cretres.2013.03.010>.
- Marsola, J.C.D.A., Grellet-Tinner, G., Montefeltro, F.C., Langer, M.C., 2014. The first Pan-Podocnemididae turtle egg from the Presidente Prudente Formation (Late Cretaceous, Bauru Group), Brazil. *Zootaxa* 3872 (2), 187–194. <https://doi.org/10.11646/zootaxa.3872.2.5>.
- Marsola, J.C.D.A., Grellet-Tinner, G., Montefeltro, F.C., Sayão, J.M., Hsiou, A.S., Langer, M.C., 2014. The first fossil avian egg from Brazil. *Alcheringa: An Australasian Journal of Paleontology* 38 (4), 563–567. <https://doi.org/10.1080/03115518.2014.926449>.
- Martinelli, A.G., Teixeira, V.P.A., 2015. The Late Cretaceous vertebrate record from the Bauru Group in the Triângulo Mineiro, southeastern Brazil. *Boletim Geológico y Minero* 126 (1), 129–158.
- Martinelli, A.G., Ribeiro, L.C.B., Méndez, A.H., Neto, F., Cavellani, C., Felix, Ferraz, Teixeira, V., 2013. Insight on the theropod fauna from the Uberaba Formation (Bauru Group), Minas Gerais State: New megaraptoran specimen from the Late Cretaceous of Brazil. *Rivista Italiana di Paleontologia e Stratigrafia* 119, 205–214. <https://doi.org/10.13130/2039-4942/6035>.
- Martinelli, A., Marinho, T., Iori, F., Ribeiro, L., 2018. The first *Caipirasuchus* (Mesoeucrocodylia, Notosuchia) from the Late Cretaceous of Minas Gerais, Brazil: New insights on sphagesaurid anatomy and taxonomy. *PeerJ* 6. <https://doi.org/10.7717/peerj.5594>.
- Marty, D., Belvedere, M., Razzolini, N.L., Lockley, M.G., Paratte, G., Cattin, M., Lovis, C., Meyer, C.A., 2018. The tracks of giant theropods (*Jurabrontes curtulensis* ichnogen. & ichnosp. nov.) from the Late Jurassic of NW Switzerland: palaeoecological & palaeogeographical implications. *Historical Biology* 30 (7), 928–956. <https://doi.org/10.1080/08912963.2017.1324438>.
- Mazzetta, G.V., Blanco, R.E., 2001. Speeds of dinosaurs from the Albian-Cenomanian of Patagonia and sauropod stance and gait. *Acta Palaeontologica Polonica* 46 (2), 235–246.
- Medeiros, M.A., Lindoso, R.M., Mendes, I.D., Carvalho, I. de S., 2014. The Cretaceous (Cenomanian) continental record of the Laje do Coringa flagstone (Alcântara Formation), northeastern South America. *J South Am Earth Sci* 53, 50–58. <https://doi.org/10.1016/j.jsames.2014.04.002>.
- Méndez, A.H., Novas, F.E., Iori, F.V., 2012. First record of Megaraptora (Theropoda, Neovenatoridae) from Brazil. *Comptes Rendus Palevol* 11 (4), 251–256. <https://doi.org/10.1016/j.crpv.2011.12.007>.
- Menegazzo, M.C., Bertini, R.J., Manzini, F.F., 2015. A new turtle from the Upper Cretaceous Bauru Group of Brazil, updated phylogeny and implications for age of the Santo Anastácio Formation. *J South Am Earth Sci* 58, 18–32. <https://doi.org/10.1016/j.jsames.2014.12.008>.
- Menegazzo, M.C., Catuneanu, O., Chang, H.K., 2016. The South American retroarc foreland system: The development of the Bauru Basin in the back-bulge province. *Marine and Petroleum Geology* 73, 131–156. <https://doi.org/10.1016/j.marpetgeo.2016.02.027>.
- Mezzalana, S., 1989. Os fósseis do Estado de São Paulo. *Bol Inst Geológico Estado São Paulo* 45 (2), 1–141.
- Milani, E.J., Melo, J.H.G. de, Souza, P.A. de, Fernandes, L.A., França, A.B., 2007. Bacia do Paraná. *Boletim de Geociências da Petrobras* 15, 265–287.
- Miller, W.C. (Ed.), 2007. *Trace fossils: concepts, problems, prospects*, first ed. Elsevier, Amsterdam, Netherlands.
- Motta, M., Aranciaga Rolando, A., Rozadilla, S., Agnolín, F., Chimento, N., Brissón Egli, F., Novas, F., 2016. New theropod fauna from the Upper Cretaceous (Huincul Formation) of Northwestern Patagonia, Argentina. *N M Mus Nat Hist Sci Bull* 71.
- Nascimento, P.M., Zaher, H., 2010. A new species of *Baurusuchus* (Crocodyliformes, Mesoeucrocodylia) from the Upper Cretaceous of Brazil, with the first complete postcranial skeleton described for the family Baurusuchidae. *Papéis Avulsos de Zoologia* 50, 323–361. <https://doi.org/10.1590/S0031-10492010002100001>.
- Nobre, P.H., Carvalho, I.D.S., 2006. *Adamantinasuchus navae*: A new Gondwanan Crocodylomorpha (Mesoeucrocodylia) from the Late Cretaceous of Brazil. *Gondwana Research* 10 (3–4), 370–378. <https://doi.org/10.1016/j.jgr.2006.05.008>.
- Nogueira, R.A., Rozadilla, S., Agnolín, F.L., García Marsà, J.A., Motta, M.J., Novas, F.E., 2024. A new ornithomimid from the Upper Cretaceous (Huincul Formation) of northwestern Patagonia, Argentina: Implications on elasmarian postcranial anatomy. *Cretaceous Research* 159, 105874. <https://doi.org/10.1016/j.cretres.2024.105874>.
- Novas, F.E., 2009. *The age of dinosaurs in South America*. Indiana University Press, Bloomington.
- Novas, F.E., Agnolín, F.L., Ezcurra, M.D., Porfiri, J., Canale, J.L., 2013. Evolution of the carnivorous dinosaurs during the Cretaceous: The evidence from Patagonia. *Cretaceous Research* 45, 174–215. <https://doi.org/10.1016/j.cretres.2013.04.001>.
- Olsen, P.E., Smith, J.B., McDonald, N.G., 1998. *Type Material of the Type Species of the Classic Theropod Footprint Genera Eubrontes, Anchisauripus, and Grallator* (Early Jurassic, Hartford and Deerfield Basins, Connecticut and Massachusetts, U.S.A.). *Journal of Vertebrate Paleontology* 18 (3), 586–601.
- O'Connor, L.K., Jenkyns, H.C., Robinson, S.A., Remmelzwaal, S.R.C., Batenburg, S.J., Parkinson, J.J., Gale, A.S., 2020. A Re-evaluation of the Plenus Cold Event, and the Links Between CO₂, Temperature, and Seawater Chemistry During OAE 2. *Paleoceanography and Paleoclimatology* 35 (4), e2019PA003631. <https://doi.org/10.1029/2019PA003631>.
- Panasci, G., Varricchio, D.J., Martin, A.J., Dyman, T., 2024. Dinosaur tracks from the Frontier Formation, Montana: preservation, distribution and palaeoecological significance for the middle Cretaceous terrestrial ecosystems of North America. *Historical Biology* 36 (4), 796–819. <https://doi.org/10.1080/08912963.2023.2184692>.
- Paula e Silva, F. de, Chang, H.K., Caetano-Chang, M.R., 2005. Estratigrafia de sub-superfície do Grupo Bauru (K) no Estado de São Paulo. *Revista Brasileira de Geociências* 35, 77–88. <https://doi.org/10.25249/0375-7536.20053517788>.
- Paula e Silva, F. de, Chang, H.K., Caetano-Chang, M.R., 2009. Sedimentation of the Cretaceous Bauru Group in São Paulo, Paraná Basin, Brazil. *J South Am Earth Sci* 28 (1), 25–39. <https://doi.org/10.1016/j.jsames.2009.02.008>.
- Pêgas, R.V., 2024. A taxonomic note on the tapejarid pterosaurs from the Pterosaur Graveyard site (Caiuá Group, Early Cretaceous of Southern Brazil): evidence for the presence of two species. *Historical Biology* 0 (0), 1–22. <https://doi.org/10.1080/08912963.2024.2355664>.
- Pereda-Suberbiola, X., Díaz-Martínez, I., Salgado, L., de Valais, S., 2015. Síntesis del registro fósil de dinosaurios tireóforos en Gondwana. *Publ Electrónica Asoc Paleontológica Argent.* 15 (1), 90–107.
- Pereira, P.V.L.G.C., Ribeiro, T.B., Brusatte, S.L., Candeiro, C.R., dos, A., Marinho, T. da S., Bergqvist, L.P., 2020. Theropod (Dinosauria) diversity from the Aquí Formation (mid-Cretaceous), Potiguar Basin, Northeast Brazil. *Cretaceous Research* 114, 104517. <https://doi.org/10.1016/j.cretres.2020.104517>.
- Petri, S., Coimbra, A.M., Amaral, G., Ojeda, H.A., Fúlforo, V.J., Ponçano, W.L., 1986. Código brasileiro de nomenclatura estratigráfica e guia de nomenclatura estratigráfica. *Revista Brasileira de Geociências* 16 (4), 370–415. <https://doi.org/10.25249/0375-7536.1986370415>.
- Pires-Domingues, R.A., Nascimento, P.M., Simões, M.G., Riccomini, C., Zaher, H., 2007. Implicações dos dados geológicos, fossilíferos e tafonômicos nas reconstruções da fauna de vertebrados da Bacia Bauru: uma abordagem integrada. In: Carvalho I de S., Cassab, R., de, C.T., Schwanke, C., Carvalho, M. de A., Fernandes, A.C.S., Rodrigues, M.A. da C., De Carvalho, M.S.S., Arai, M., Oliveira, M.E.Q. (Eds.), *Paleontologia Cenários de Vida*, first ed. Interciência, Rio de Janeiro, pp. 273–284.
- Pol, D., Rauhut, O.W.M., 2012. A Middle Jurassic abelisaurid from Patagonia and the early diversification of theropod dinosaurs. *Proc R Soc B Biol Sci* 279 (1741), 3170–3175. <https://doi.org/10.1098/rspb.2012.0660>.
- Pol, D., Nascimento, P.M., Carvalho, A.B., Riccomini, C., Pires-Domingues, R.A., Zaher, H., 2014. A new notosuchian from the Late Cretaceous of Brazil and the phylogeny of Advanced Notosuchians. *PLoS One* 9 (4), e93105. <https://doi.org/10.1371/journal.pone.0093105>.
- Porchetti, S.D., Bertini, R.J., Langer, M.C., 2017. Proposal for ichnotaxonomic allocation of therapsid footprints from the Botucatu Formation (Brazil). *Ichnos* 25, 192–207. <https://doi.org/10.1080/10420940.2017.1308929>.
- Price, L.L., 1951. Ovo de dinossauro na formação Bauru, do estado de Minas Gerais. *Notas Prelim Div Geol Mineral.* 53, 1–7.
- Reis, L.F.D.S., Ghilardi, A., Fernandes, M., 2022. Bite traces in a sauropod rib from the Upper Cretaceous São José do Rio Preto Formation (Bauru Basin), Brazil. *Historical Biology* 35. <https://doi.org/10.1080/08912963.2022.2090248>.
- Ribeiro, L.C.B., Carvalho, I. de S., 2009. Sítio Peirópolis e Serra da Galga, Uberaba, MG: Terra dos dinossauros do Brasil. In: Sítios Geológicos e Paleontológicos do Brasil (SIGEP), vol. 1. Serviço Geológico do Brasil – CPRM, Brasília, pp. 1–13.
- Ribeiro, T.B., Brito, P.M.M., Gomes da Costa Pereira, P.V.L., 2023. The predominance of teeth in the non-avian dinosaur record from Cretaceous Brazil: a review. *Historical Biology* 1–16. <https://doi.org/10.1080/08912963.2023.2238965>.
- Riccomini, C., 1997. Arcabouço estrutural e aspectos do tectonismo gerador e deformador da Bacia Bauru no Estado de São Paulo. *Revista Brasileira de Geociências* 27, 153–162. <https://doi.org/10.25249/0375-7536.1997153162>.
- Riff, D., Kellner, A.W.A., 2011. Baurusuchid crocodyliforms as theropod mimics: clues from the skull and appendicular morphology of *Stratiotosuchus maxhechti* (Upper Cretaceous of Brazil). *Zoological Journal of the Linnean Society* 163 (s1), S37–S56. <https://doi.org/10.1111/j.1096-3642.2011.00713.x>.
- Riguetti, F.J., Apesteguía, S., Pereda-Suberbiola, X., 2022. A new Cretaceous thyreophoran from Patagonia supports a South American lineage of armoured dinosaurs. *Scientific Reports* 12 (1), 11621. <https://doi.org/10.1038/s41598-022-15535-6>.

- Riguetti, F.J., Citton, P., Apesteguía, S., Zaccarias, G.G., Pereda-Suberbiola, X., 2021. New ankylosaurian trackways (cf. *Tetrapodosaurus*) from an uppermost Cretaceous level of the El Molino Formation of Bolivia. *Cretaceous Research* 124, 104810. <https://doi.org/10.1016/j.cretres.2021.104810>.
- Riguetti, F.J., Pereda-Suberbiola, X., Ponce, D., Salgado, L., Apesteguía, S., Rozadilla, S., Arbour, V., 2022. A new small-bodied ankylosaurian dinosaur from the Upper Cretaceous of North Patagonia (Rio Negro Province, Argentina). *Journal of Systematic Palaeontology* 20 (1), 2137441. <https://doi.org/10.1080/14772019.2022.2137441>.
- Romano, P.S., Oliveira, G.R., de Azevedo, S., Kellner, A.A., de Almeida Campos, D., 2013. New information about *Pelomedusoides* (Testudines: Pleurodira) from the Cretaceous of Brazil. In: Brinkman, D. (Ed.), *Morphology and Evolution of Turtles*. Springer, London, pp. 261–275.
- Romano, M., Citton, P., Avanzini, M., 2020. A review of the concepts of 'axony' and their bearing on tetrapod ichnology. *Historical Biology* 32 (5), 611–619. <https://doi.org/10.1080/08912963.2018.1516766>.
- Rossetti, L., Lima, E.F., Waichel, B.L., Hole, M.J., Simões, M.S., Scherer, C.M.S., 2018. Lithostratigraphy and volcanology of the Serra Geral Group, Paraná-Etendeka Igneous Province in Southern Brazil: Towards a formal stratigraphical framework. *Journal of Volcanology and Geothermal Research* 355, 98–114. <https://doi.org/10.1016/j.jvolgeores.2017.05.008>.
- Rougier, G.W., Martinelli, A.G., Forasiepi, A.M., 2021. The South American Mesozoic record and early evolution of mammals. In: Rougier, G.W., Martinelli, A.G., Forasiepi, A.M. (Eds.), *Mesozoic Mammals from South America and their fore-runners*, Springer Earth System Sciences. Springer, Cham, pp. 345–388. https://doi.org/10.1007/978-3-030-63862-7_10.
- Rozadilla, S., Agnolín, F., Manabe, M., Tsuihiji, T., Novas, F.E., 2021. Ornithischian remains from the Chorrillo Formation (Upper Cretaceous), southern Patagonia, Argentina, and their implications on ornithischian paleobiogeography in the Southern Hemisphere. *Cretaceous Research* 125, 104881. <https://doi.org/10.1016/j.cretres.2021.104881>.
- Ruiz, J., Bronzati, M., Ferreira, G., Martins, K., Queiroz, M.V., Langer, M., Montefeltro, F., 2021. A new species of *Caipirasuchus* (Notosuchia, Sphagesauridae) from the Late Cretaceous of Brazil and the evolutionary history of Sphagesauria. *Journal of Systematic Palaeontology* 19. <https://doi.org/10.1080/14772019.2021.1888815>.
- Sales, M.A.F., Martinelli, A.G., Francischini, H., Rubert, R.R., Marconato, L., Soares, M.B., Schultz, C.L., 2017. New dinosaur remains and the tetrapod fauna from the Upper Cretaceous of Mato Grosso State, central Brazil. *Historical Biology* 30 (5), 661–676. <https://doi.org/10.1080/08912963.2017.1315414>.
- Salgado, L., Coria, R.A., Heredia, S.E., 1997. New materials of *Gasparinisaura cincosalensis* (Ornithischia, Ornithomimidae) from the Upper Cretaceous of Argentina. *Journal of Paleontology* 71 (5), 933–940. <https://doi.org/10.1017/S0022336000035861>.
- Salgado, L., Gallina, P.A., Lerzo, L.N., Canudo, J.I., 2022. Highly specialized diplodocoids: The Rebbachisauridae. In: Otero, A., Carballido, J.L., Pol, D. (Eds.), *South Am Sauropodomorph Dinosaurs Rec Divers Evol*. Springer International Publishing, Cham, pp. 165–208. https://doi.org/10.1007/978-3-030-95959-3_5.
- Santucci, R.M., Filippi, L.S., 2022. Last Titans: Titanosaurs from the Campanian–Maastrichtian age. In: Otero, A., Carballido, J.L., Pol, D. (Eds.), *South Am Sauropodomorph Dinosaurs Rec Divers Evol*. Springer International Publishing, Cham, pp. 341–391. https://doi.org/10.1007/978-3-030-95959-3_10.
- Schlanger, S.O., Jenkyns, H.C., 1976. Cretaceous oceanic anoxic events: causes and consequences. *Geologie en Mijnbouw* 55 (3–4), 179–184.
- Scotese, C., 2016. PALEOMAP PaleoAtlas for GPlates and the PaleoData Plotter Program. Evanston: University of Illinois. <https://doi.org/10.13140/RG.2.2.34367.00166>.
- Scotese, C.R., Song, H., Mills, B.J.W., van der Meer, D.G., 2021. Phanerozoic paleotemperatures: The earth's changing climate during the last 540 million years. *Earth-Science Reviews* 215, 103503. <https://doi.org/10.1016/j.earscirev.2021.103503>.
- Sedorko, D., Francischini, H. (Eds.), 2021. *Icnologia: interações entre organismos e substratos*. Editora CRV, Curitiba.
- Sgarbi, P.B.A., Heaman, L.M., Gaspar, J.C., 2004. U–Pb perovskite ages for Brazilian kamafugitic rocks: further support for a temporal link to a mantle plume hot-spot track. *J South Am Earth Sci* 16 (8), 715–724. <https://doi.org/10.1016/j.jsames.2003.12.005>.
- Simões, T.R., Wilner, E., Caldwell, M.W., Weinschütz, L.C., Kellner, A.W.A., 2015. A stem acrodontan lizard in the Cretaceous of Brazil revises early lizard evolution in Gondwana. *Nature Communications* 6 (1), 8149. <https://doi.org/10.1038/ncomms9149>.
- Soares, P., Landim, P.M.B., Fúlvaro, V.J., Neto, A.F., 1980. Ensaio de caracterização estratigráfica do Cretáceo no Estado de São Paulo: Grupo Bauru. *Revista Brasileira de Geociências* 10, 177–185. <https://doi.org/10.25249/0375-7536.1980177185>.
- Soares, M.V.T., Basile, G., Marinho, T. da S., Martinelli, A.G., Marconato, A., Mountney, N.P., Colombero, L., Mesquita, Á.F., Vasques, J.T., Abrantes Junior, F.R., Ribeiro, L.C.B., 2021. Sedimentology of a distributive fluvial system: The Serra da Galga Formation, a new lithostratigraphic unit (Upper Cretaceous, Bauru Basin, Brazil). *Geological Journal* 56 (2), 951–975. <https://doi.org/10.1002/gj.3987>.
- Soto, M., Perea, D., Cambiaso, A., 2012. First sauropod (Dinosauria: Saurischia) remains from the Guichón Formation, Late Cretaceous of Uruguay. *J South Am Earth Sci* 33 (1), 68–79. <https://doi.org/10.1016/j.jsames.2011.08.003>.
- Soto-Acuña, S., Vargas, A.O., Kaluza, J., Leppe, M.A., Botelho, J.F., Palma-Liberona, J., Simon-Gutstein, C., Fernández, R.A., Ortiz, H., Milla, V., et al., 2021. Bizarre tail weaponry in a transitional ankylosaur from subantarctic Chile. *Nature* 600 (7888), 259–263. <https://doi.org/10.1038/s41586-021-04147-1>.
- Souto, P.R. de F., 2008. *Coprólitos do Brasil: Principais ocorrências e estudo*. Rio de Janeiro: Publitt.
- Suárez, J.M., 2002. Sítio Fossilífero de Pirapozinho, SP: Extraordinário depósito de quelônios do Cretáceo. In: Schobbenhaus, C., Campos, D., de A., De Queiroz, E.T., Winge, M., Berbert-Born, M. (Eds.), *Sítios Geológicos e Paleontológicos do Brasil (SIGEP)*, vol. 1. Serviço Geológico do Brasil - CPRM, Brasília.
- Thompson, R.S., Parish, J.C., Maidment, S.C.R., Barrett, P.M., 2012. Phylogeny of the ankylosaurian dinosaurs (Ornithischia: Thyreophora). *Journal of Systematic Palaeontology* 10 (2), 301–312. <https://doi.org/10.1080/14772019.2011.569091>.
- Thulborn, R.A., 1984. Preferred gaits of bipedal dinosaurs. *Alcheringa: An Australasian Journal of Palaeontology* 8 (3), 243–252. <https://doi.org/10.1080/03115518408618947>.
- Thulborn, R.A., 1990. *Dinosaur tracks*. Chapman & Hall, London.
- Thulborn, R.A., Wade, M., 1984. Dinosaur trackways in the Winton Formation (mid-Cretaceous) of Queensland. *Mem Qld Mus* 21 (2), 413–517.
- Turgeon, S.C., Creaser, R.A., 2008. Cretaceous oceanic anoxic event 2 triggered by a massive magmatic episode. *Nature* 454, 323–326. <https://doi.org/10.1038/nature07076>.
- Turner, A.H., Nesbitt, S.J., Norell, M.A., 2009. A large alvarezsaurid from the Late Cretaceous of Mongolia. *American Museum Novitates* 3648, 1–14. <https://doi.org/10.1206/639.1>.
- Vasconcellos, F., Carvalho, I., 2010. Paleontological assemblage associated with *Bauriusuchus salgadoensis* remains, a Bauriusuchidae Mesoeucrocodylia from the Bauru Basin, Brazil (Late Cretaceous). *N M Mus Nat Hist Sci Bull* 51, 227–237.
- Vasconcellos, F.M. de, Marinho, T. da S., Iori, F.V., Morato, L., 2008. First dinosaur remains from General Salgado surroundings (Adamantina Formation, Bauru Basin -Late Cretaceous), São Paulo State, Brazil. In: Senra, M.C.E., Barreiro, R.M.C. (Eds.), *Livro Resumos*. Rio de Janeiro.
- Vullo, R., Neraudeau, D., Lenglet, T., 2007. Dinosaur teeth from the Cenomanian of Charentes, Western France: evidence for a mixed Laurasian-Gondwanan assemblage. *Journal of Vertebrate Paleontology* 27 (4), 931–943. [https://doi.org/10.1671/0272-4634\(2007\)27\[931:DTFTCO\]2.0.CO;2](https://doi.org/10.1671/0272-4634(2007)27[931:DTFTCO]2.0.CO;2).
- Wilson, J.A., Carrano, M.T., 1999. Titanosaurs and the origin of “wide-gauge” trackways: A biomechanical and systematic perspective on sauropod locomotion. *Paleobiology* 25 (2), 252–267. <https://doi.org/10.1017/S0094837300026543>.
- Xu, X., Upchurch, P., Ma, Q., Pittman, M., Choiniere, J., Sullivan, C., Hone, D.W.E., Tan, Q., Tan, L., Xiao, D., Han, F., 2011. Osteology of the alvarezsaurid *Linhensykus monodactylus* from the Upper Cretaceous Wulansuhai Formation of Inner Mongolia, China, and comments on alvarezsaurid biogeography. *Acta Palaeontologica Polonica*. <https://doi.org/10.4202/app.2011.0083>.
- Zaher, H., Langer, M., Fara, E., Carvalho, I., Arruda, J.T., 2003. A mais antiga serpente (Anilioidea) brasileira: Cretáceo Superior do Grupo Bauru, General Salgado, SP. In: *Paleontol Em Destaque*, vol. 18. Ribeirão Preto, pp. 50–51.
- Zaher, H., Pol, D., Navarro, B.A., Delcourt, R., Carvalho, A.B., 2020. An Early Cretaceous theropod dinosaur from Brazil sheds light on the cranial evolution of the Abelisauridae. *Comptes Rendus Palevol* (6). <https://doi.org/10.5852/cr-palevol2020v19a6>.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.cretres.2024.106075>.