



ABSTRACT BOOK

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TRISAUROPODISCUS: THE OLDEST BIRD-LIKE FOOTPRINTS (LATE TRIASSIC, SOUTHERN AFRICA)

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Footprint (track) morphology is the product of complex interactions between a trackmaker's anatomy and the substrate it interacts with. Consequently, fossil footprints can provide insight into ancient trackmakers' pedal anatomy, which is particularly useful for deep time intervals where understanding animal groups has historically relied upon limited fossil bone material. The tridactyl ichnogenus *Trisauropodiscus*, first documented from Late Triassic to Early Jurassic Karoo Supergroup strata in southern Africa by Paul Ellenberger and colleagues [¹⁻⁶], was posited by the authors to preserve a "proto-avian" affinity which, since its erection ~70 years ago, has been debated in the broader scientific community [e.g., ⁷]. Herein, we re-assess field material, collected cast material, published illustrations and photographs of *Trisauropodiscus* within a recently refined chronostratigraphic framework [⁸]. Utilising standard ichnological measurements (e.g., track length, track width, medial digit projection etc.) and landmark-based geometric morphometric analysis [^{9,10}]. To quantify track shape, we propose two distinct *Trisauropodiscus* morphotypes, of which one unequivocally resembles bird-like footprints. Morphotype I, which is similar to *Anomoepus* accepted to be attributed to ornithischian dinosaurs, preserves robust, rounded digits occasionally with pad impressions, is longer-than-wide and has a relatively narrower total digit divarication (Fig. 1A). Morphotype II, which is comparable to e.g., *Aquatilavipes*, *Avipedia*, *Quadridigitus* accepted to be attributed to fossil birds, preserves slender digits which lack pad impressions and taper to sharp tips, is wider-than-long, and has relatively wide total digit divarication (Fig. 1B). The bird-like nature of the Morphotype II footprints, known from multiple, well-provenanced Late Triassic and Early Jurassic southern African ichnosites [⁸] predates widely accepted, basal-most birds known from the global body fossil record by c. 60 million years [¹¹⁻¹⁴], with no possible trackmakers known from the local body fossil record. Although Morphotype II *Trisauropodiscus* strongly resembles Cenozoic and modern bird footprints, they are likely attributed to a yet-to-be found archosaur, but crucially demonstrate that the origin of a bird-like foot morphology is at least ~210 million years old.

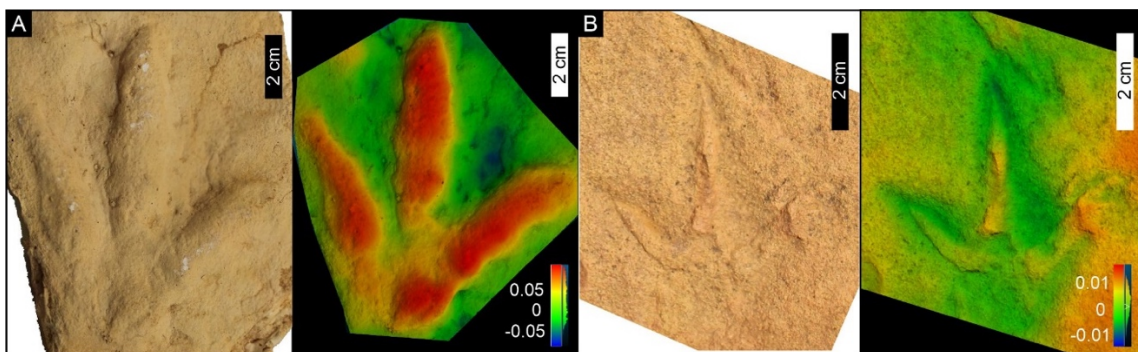


Fig. 1. Representative specimens of *Trisauropodiscus*. A. Morphotype I. B. Morphotype II. See [¹⁰] for details.

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ICHTNOLOGICAL CONTENT AND DEPOSITIONAL ENVIRONMENTS OF THE CARBONIFEROUS SUCCESSION AT THE AGUA DE LA PEÑA CREEK OF WESTERN ARGENTINA: EXPLORING THE GLACIAL TO POSTGLACIAL TRANSITION IN A MASS TRANSPORT INFLUENCED SETTING

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The outcropping Carboniferous succession in the Quebrada de Agua de la Peña, San Juan Province, Argentina, records the transition from glacial to postglacial conditions that prevailed during much of the Pennsylvanian in the western basins of Gondwana. These rocks, corresponding to the Bashkirian–Serpukhovian Guandacol Formation, make up about a 1100 m thick siliciclastic succession composed of diamictite, sandstone, mudstone (some bearing dropstones), and local conglomerate, that in places display a poorly diverse ichnofauna. Among these deposits, relatively thick (hundreds to several tens of meters) chaotic intervals with synsedimentary deformation associated with the development of mass transport complexes (MTC) stand out and occur interbedded with glacial to postglacial facies accumulated in situ. Regarding in situ facies occurrence and distribution, deposition took place partially filling available subaqueous topographic lows after the emplacement of the MTC. In this framework, the glacially influenced facies, characterized by diamictite, mudstone with dropstones, and thickening- and coarsening-upward packages of sandstone and mudstone (with and without dropstones), mainly reflect proglacial sedimentation, in connection with the development of subaqueous outwash fans and ice contact deltas. Monospecific trace-fossil suites comprising *Gordia marina* and *Gyrochorte* isp. occur in some sandstone bed tops deposited mainly from underflow currents and frontal splays. These surfaces exhibit low bedding plane bioturbation indexes (BPBI 1-3). On the other hand, the in situ postglacial deposits, mainly typified by coarsening- and thickening-upward packages of sandstone and mudstone, record deltaic sedimentation with the influence of waves and storms. These were deposited after the postglacial transgression that flooded the area. In these facies, particularly in some siltstone bed tops intercalated with silty claystone corresponding to prodelta deposits, a moderately diverse trace-fossil suite is recorded. This assemblage is composed of simple grazing trails, namely *Gordia marina*, *Mermia carickensis*, *Helminthoidichnites tenuis*, *Helminthopsis tenuis*, feeding traces such as *Treptichnus* isp., arthropod locomotion traces including *Orchosteropus atavus*, as well as undetermined trackways, and to lesser extent rosary trace fossils. These surfaces also display a relatively low BPBI (1-3). In addition, structures ascribed to *Skolithos* isp. were locally observed. Regarding the stratigraphic framework of the ichnofossil-bearing levels and associated facies (e.g. intercalating with MTC deposits) and their characteristics, it is possible to suggest subaqueous sedimentation in a final glacial to postglacial framework associated with the



development of unstable slopes and recurrent tectonic activity. In this scenario, trace-fossil suites provide valuable evidence of controlling environmental parameters, which are mainly related to stressors due to a complex interplay between the development of intermittent marine (brackish) conditions and the influence of important freshwater discharges from the feeder systems. Moreover, this situation may have been enhanced due to limited water circulation because of ponded conditions in the area, affecting negatively bottom oxygenation, therefore constraining and/or suppressing substrate colonization by the benthos. Overall, depositional systems, both glacially influenced and postglacial, would have evolved associated with an irregular coast, due to the emplacement of a MTC.

REASSESSMENT OF *ASTERIACITES* FROM THE LOWER CRETACEOUS APELEG FORMATION (SOUTHERN CHILE) AND A DISCUSSION ABOUT ITS PRODUCER

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Asteriacites von Schlotheim, 1820 is a relatively common ichnogenus attributed to asterozoans and has been recorded from Cambrian to Recent marine deposits, although its validity has been debated [1,2]. A recently emended diagnosis has settled the subject and provided morphometric parameters for the identification of the now three valid ichnospecies (*Asteriacites lumbricalis*, *A. stelliformis* and *A. quinquefolius*) [3]. In the Lower Cretaceous Apeleg Formation (Chilean Patagonia), *A. lumbricalis* was described almost two decades ago and ascribed to asteroids [4]. Recently, these specimens were reclassified as *A. stelliformis* based on photographs from the cited work, because the samples were considered lost [5]. In this work, new specimens of *Asteriacites* are described from this unit, and based on the previously mentioned emended diagnoses [3], an ichnotaxonomic discussion is presented. Additionally, the size range of each trace fossil was calculated to discuss the potential producers.

The Lower Cretaceous (Hauterivian–Aptian) Apeleg Formation in Chile is a marine unit with evidence of tidal and fluvial influence, mainly composed by greyish/green sandstones, some of which are part of heterolithic intervals that bear diverse and abundant trace fossils. *Asteriacites lumbricalis* and *Ophioichnus aysenensis* (= *Biformites zhadaensis*) were originally described from levels nearby the village of Ñirehuao, in the “Cerro Mirador” hill [4].

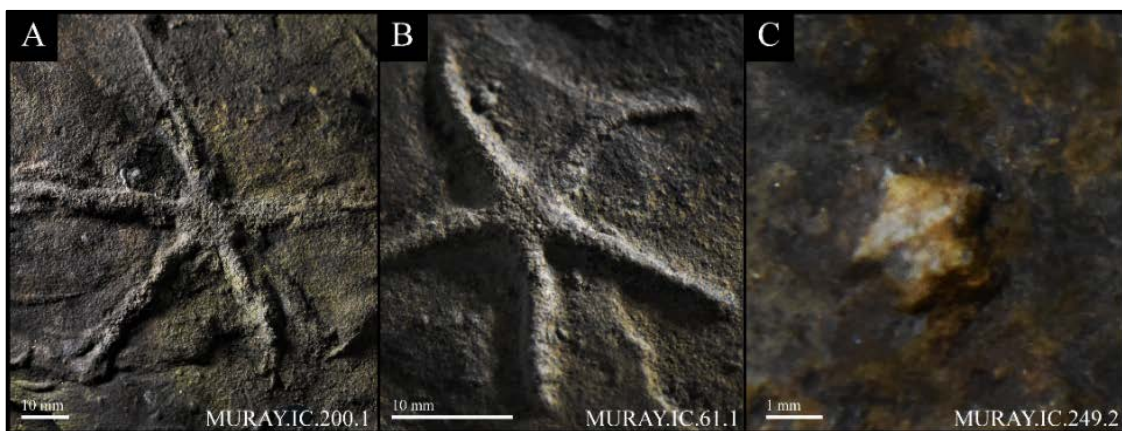


Fig. 1. Examples of well-preserved *Asteriacites* in the Apeleg Formation and its ichnospecific assignment using the emended diagnoses. A. *Asteriacites lumbricalis* (long arm imprints and central disc). B. *Asteriacites stelliformis* (arm imprints with a length/width ratio of more than 2) C. *Asteriacites quinquefolius* (wide arm imprints with a length/width ratio of less than two). Samples are housed in the collection of the Museo Regional de Aysén (MURAY).

From this locality, 248 new sandstone slabs were analyzed using the methodology included in the latest revision of the ichnogenus [3]. Examples from selected slabs with specimens preserved in positive hyporelief are shown here (Figs. 1, 2). All three ichnospecies of *Asteriacites* were identified (Fig. 1). The ichnospecific assignment is straightforward when the specimens are larger than 10 mm in diameter (Fig. 1). Some of the smallest specimens were assigned to *A. quinquefolius*. Many specimens of *A. stelliformis* are transitional to be classified as *A. quinquefolius*, because of their width/length arm ratio close to 2. Poorly preserved individuals remain indeterminate (indet.).

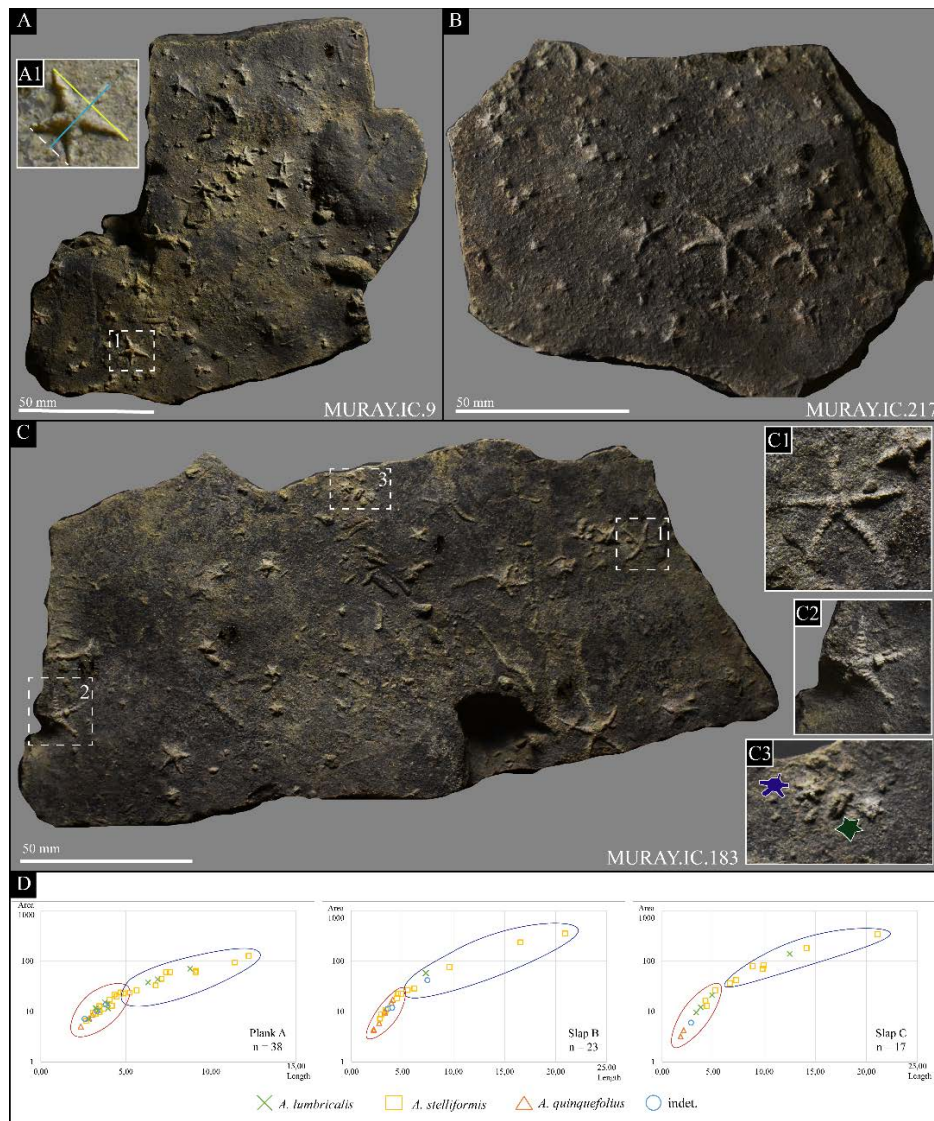


Fig. 2. A-C. Selected slabs with high concentrations of *Asteriacites*. D. Graphs plotting the measured values mentioned in the text for the same three slabs (A-C, from left to right). They include the ichnospecific assignment of each specimen. Two clusters are defined in each graph (red and blue), determined by the change slope. A1 is an example of how the measurements were taken. C1, *A. lumbricalis* with a smoothly notorious central disc and transverse sculpture on the arms. C2, *A. stelliformis* with transverse sculpture on the arms. C3, *A. lumbricalis* and *A. quinquefolius* together with a representation of their general shapes next to them. Samples are housed in the collection of the Museo Regional de Aysén (MURAY).

In extant ophiuroids, the diameter of the disc is the most used measure to differentiate ontogenetic stages within the same population [6,7]. However, this is not possible to replicate in this study considering that the disc is not necessarily preserved in all traces. Therefore, for the purpose of classifying groups of different sizes, another methodology was used. Each individual *Asteriacites* is selected and the measurement of the maximum length between opposite arms is



taken (Fig. 2A1, yellow line); then, a perpendicular line that defines the maximum width of the trace is drawn (Fig. 2A1, blue line) using the arm between the last measurement and the imaginary line that connect the end of the opposing arms (Fig. 2A1, white discontinuous line). A rectangular area comprising these continuous lines is then defined and calculated (Fig. 2A1). This area was then plotted against the maximum width (Fig. 2D).

The results indicate a similar trend in the three slabs: there are two main clusters (marked in red and blue) defined by the change in slope (Fig. 2D). *A. lumbricalis* and *A. stelliformis* fall together within the blue cluster. This group shows a higher dispersion. The presence of these two ichnospecies clustered together may indicate they are both formed by the same kind of producers: ophiuroids (brittle stars). This is coherent with the latest proposal for these ichnospecies [3] and is also supported by the transverse sculpture on the arm imprints, typical of ophiuroid traces [8], which in this case is present in specimens of both ichnospecies in the same slabs (Fig. 2C1-C2).

In the red clusters of slabs A and C, a large number of *A. lumbricalis*, *A. stelliformis* and *A. quinquefolius* fall together; this last ichnospecies has only been attributed to Asteroidea both through morphometric parameters [3] and type of sculpture [1]. In Recent brittle stars, juvenile characters often differ considerably from those in adults, including arm plates and radial shields which are related to the length of the arms [6]. The fact that specimens assignable to *A. quinquefolius* have a similar size (<5 mm) as those assigned to *A. lumbricalis* in the same layer and only within a few centimeters of distance (Fig. 2C3) could indicate they were produced by the same group of organisms, in this case, ophiuroids, especially when the attribution to ophiuroids in the case of these *A. lumbricalis* is unequivocal due to the type of sculpture.

In conclusion, the three ichnospecies of *Asteriacites* were found in the analyzed material from the Lower Cretaceous Apeleg Formation. In the case of smaller specimens, the results could be indicative of the arbitrariness of ichnospecific assignment through morphometric parameters and reinforces the relevance of sculpture in the attribution to producers [9]. The various specimens of *Asteriacites* identified in each of the studied slabs might have been produced by a population of ophiuroids in different stages of their ontogenetic development, which explains the difference in size and proportions.

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REVISION OF FOSSIL FOOTPRINTS *RHYNCHOSAUROIDES* MAIDWELL, 1911 FROM THE LATE TRIASSIC OF SOUTHERN OF BRAZIL

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The vertebrate fauna of Triassic of Rio Grande do Sul state is represented principally by rhynchosaurs, therapsids, and archosaurs (including dinosaurs). However, information regarding footprints produced by these organisms is scarce. The Predebon outcrop (São João do Polêsine municipality, Rio Grande do Sul state, Brazil) is unique by having rich data of Triassic tetrapod footprints of Santa Maria Supersequence. In the Predebon outcrop, body fossil record suggests a correlation with the *Hyperodapedon* Assemblage Zone (Carnian age) [1]. The ichnofauna of Predebon outcrop comprises the ichnotaxa *Grallator?* isp. (dinosaur trackmakers) [2], *Rhynchosauroides retroversipes*, *Rhynchosauroides* isp. (lepidosaur trackmakers) [3], and *Procolophonichnium nopcsai* (cynodont trackmakers) [4]. Recently, some footprints originally attributed to *Rhynchosauroides* were relocated to *Procolophonichnium* [5,6], also suggesting a change in the biological attribution. The present work reports an initial stage of ichnotaxonomical revision of *Rhynchosauroides* from Predebon outcrop. The analysis consists in the description of the qualitative and quantitative parameters of each track and trackway [7]. To support these analyses, the specimens will be scanned using photogrammetry and 3D modelling techniques [8], and depth maps with false colours will be produced. Recent studies [4] interpreted the Candelária Sequence as deposited by ephemeral braided rivers, sheet deltas, and ephemeral lakes, which indicates a humidity increase when compared to the lower sequences of the Santa Maria Supersequence. The presence of *Skolithos serratus* in the Predebon outcrop indicates the sediments were periodically exposed to air, with developed soil in desiccated-overbank deposits [9]. This kind of substrate makes it difficult for small organisms to move, causing them to slip and even sink in some cases (Fig. 1).

Due to substrate conditions, the footprint morphology may vary, making difficult its correct identification [4]. Preliminary analyses indicate that the footprints attributed to *R. retroversipes* and *Rhynchosauroides?* isp. (Fig. 2) [3] show morphologic characteristic similar to ichnospecies *P. nopcsai*, namely: (i) ectaxony absent, (ii) proportionally shorter and more robust digit impressions, where in *Rhynchosauroides* they are straight to curved outwards, (iii) semiplantigrade to plantigrade imprints, (iv) impressions of digits II-IV are grouped, whereas (v) imprints of digits I and V are placed in a proximal-lateral position but not separated from the others. This suggestion needs deep analyses for a better assignment to ichnogenus/ichnospecies.

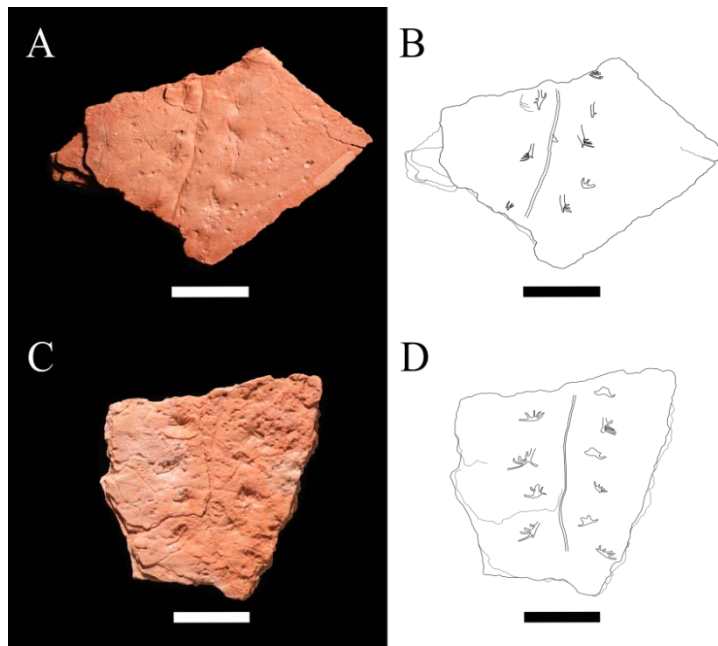


Fig. 1. Photographs and interpretative schemes of *Procolophonichnium nopcsai* specimens from Predebon outcrop [4]. Scales bars: 20 mm.

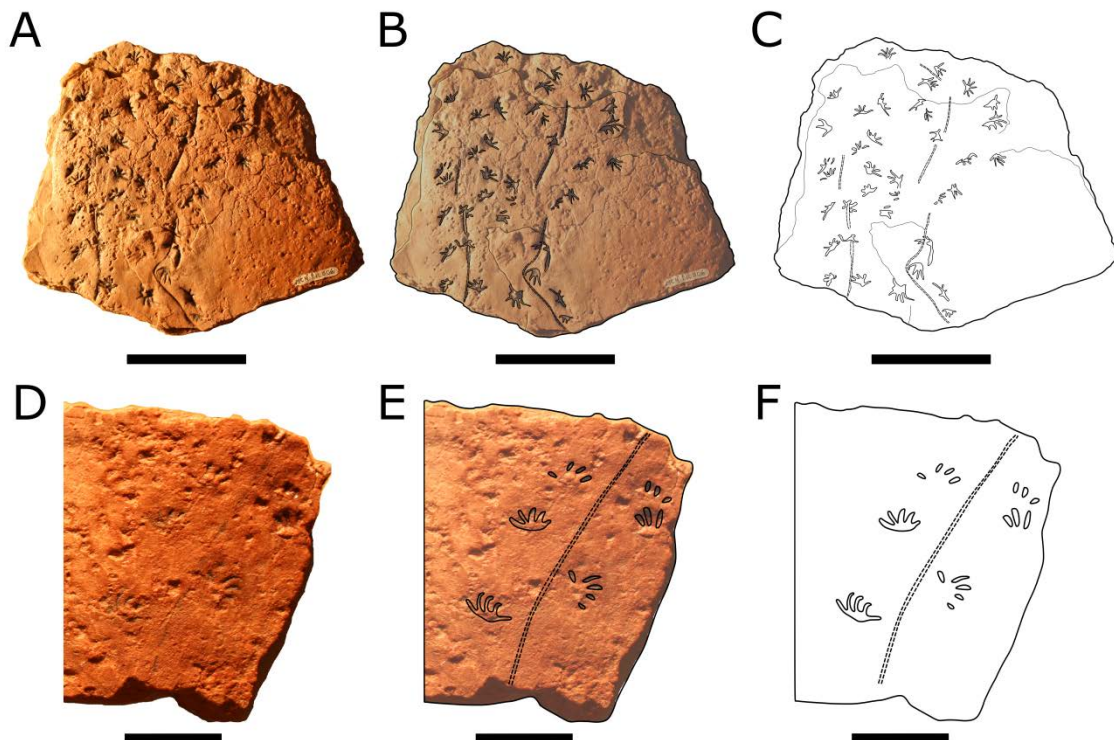


Fig. 2. Footprints from Predebon outcrop, photographs of specimens and interpretative schemes. A-C. *Rhynchosauroides retroversipes* (MCN-PIC.006) [3]; D-F. *Rhynchosauroides?* isp. (MCN-PIC.012) [3]. Scales bars: A-C = 50 mm; D-F = 20 mm.

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REVISION OF FOSSIL FOOTPRINTS FROM THE LATE PERMIAN OF SOUTHERN BRAZIL

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Some slabs from São Jerônimo da Serra outcrop (Passa Dois Group, Paraná Basin, Paraná state, Brazil), containing footprints have been reported in 2000 [1] and 2002 [2]. However, only in 2012 [3] they were classified more clearly. In the upper portion of the outcrop, siltstones with horizontal bedding appear, with small lenses of sand or clay. In this portion, some groups of fossils occur, such as fragments of sphenophyte stems, root marks, trace fossils, bivalve mollusks, isolated bones and scales of paleoniscid fishes and temnospondyl amphibian bones [3]. Three tetrapod ichnotaxa were described: *Procolophonichnium* isp. (procolophonid parareptiles and/or therapsids were the probable trackmakers), *Rhynchosauroides gangresci* (lepidosauromorph trackmakers) and *Dicynodontipus penugnu* (therapsid synapsids trackmakers). The analysis of the samples consisted of describing the qualitative and quantitative parameters relating to each footprint [4]; digitizing the specimens using photogrammetry and 3D modeling techniques [5]; making depth maps with false colors to help describe and interpret the data. In preliminary analyses based in photos available in [3], we hypothesize that the footprints attributed to *R. gangresci* (Figure 1A-C) show morphologic characteristic like ichnogenus *Dromopus* (Figure 1D-E), like (i) digits II-IV are grouped, whereas (ii) digits I and V are placed in a proximal-lateral position but not separated from the other digits, forming an angle greater than 100°. This hypothesis showed here need deep analyses for a better designation about ichnogenus/ichnospecies.

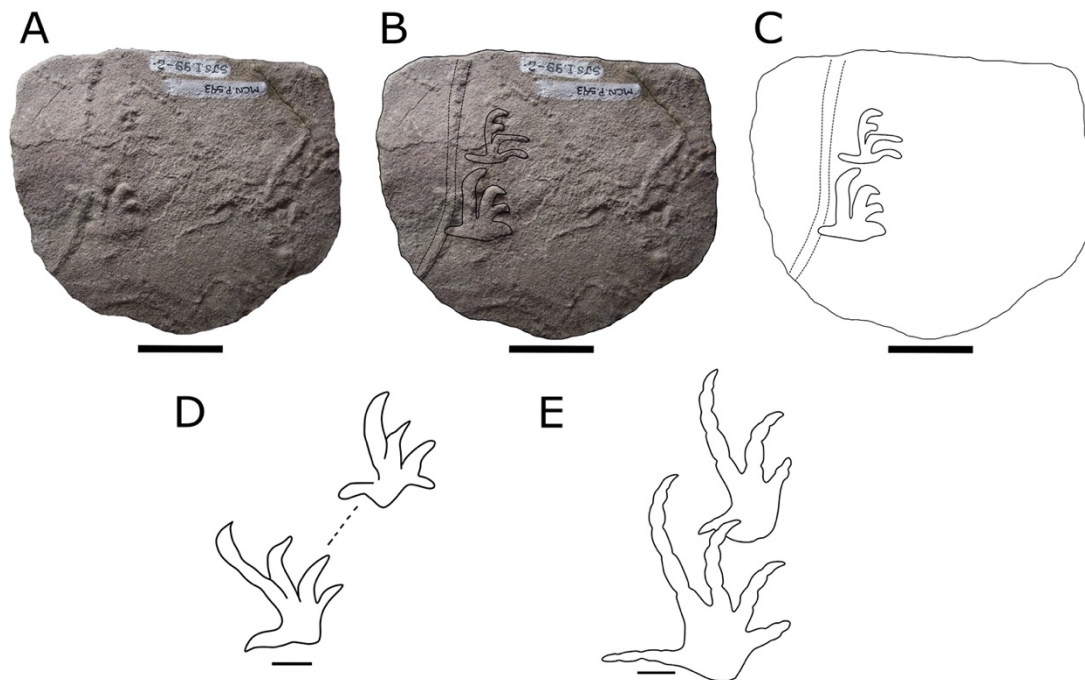


Fig. 1. A-C. Footprints from São Jerônimo da Serra outcrop, photographs of specimens and interpretative schemes. D-E, Sketches of *Dromopus lacertoides* [6]. Scale bars: A-C = 30 mm; D-E = 10 mm.



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EXCEPTIONALLY WELL-PRESERVED LARGE-SIZED BURROW SYSTEM FROM THE PLEISTOCENE OF NECOCHEA, BUENOS AIRES, ARGENTINA, AND ITS PUTATIVE PRODUCERS

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Large burrows are a common feature of the Upper Cenozoic of the Atlantic coast of South America, especially along the walls of cliffs of southeast Buenos Aires Province [1]. These burrows are usually preserved as ellipsoidal to semicircular in cross-section, have sharp edges, and are most frequently infilled, but occasionally are preserved totally or partially empty revealing original internal surfaces as they were millions of years ago. For large to very large excavations (from 0.8 up to 2 m in diameter), the possible producers have been interpreted mostly as xenarthrans, mainly cingulatan and ground sloths [2], based on their body sizes and their long-clawed forelimbs well-suited for digging. Claw marks inside these large burrows are a common feature that helps to identify possible producers [2]. In this contribution, we present an exceptionally well-preserved burrow system, recorded near Necochea in the southeast Buenos Aires Province, Argentina. The burrow system shows a vertical ellipsoidal entrance on the floor of 1.20 m wide and 0.8 m long, with claw marks preserved on one side (Fig 1). The preservation of the entrance can help to reconstruct the complete architecture of the burrow and the way in which the producer excavated the burrow. The animal started the digging towards the subsurface, removing soil with vertical descendent movements of the forelimbs. Preservation of clear claw marks indicates the sediment was compact and firm at that moment. After the burrow reached a depth of approximately 0.8 to 1 m, it became horizontal and developed in an L shape for approximately 26 m, located currently near the coastal cliff. Inside the burrow, there were also well-preserved claw marks. These marks are composed by three individual claws marks, that can be disposed in a rectilinear to semicircular fashion, usually clustered (Fig. 2). The presence of three claw marks, along the burrow’s diameter, could clarify the possible producer. Among ground sloths, glossotheres were too large to be considered producers of this burrow and, although scelidotheres were smaller in size, they showed a specialized hand bearing only two large ungual phalanges, so they could not be considered producers either. Among large cingulatan, pampatheres have a forelimb that displays three large ungual phalanx and showed body dimensions that are compatible with the burrow analyzed in this contribution. Pampatheres are recorded in the Cenozoic exposures of Buenos Aires coastal area, and indeed remains of them have been found inside burrows found in other areas of the same region. Therefore, in the case of the burrow system presented herein, pampatheres are proposed as possible producers, based on both body size and the phenetic correlation of the claw marks with the anatomy of the forelimb of these animals.



Fig. 1. Vertical entrance of the burrow system. Notice the claw marks on one side.



Fig. 2. Photogrammetric reconstruction of the inner walls of the burrow, showing several claw imprints. Scale bar = 1 m.

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BIOTURBATION AND BIOEROSION IN EXTERNAL ESTUARINE DEPOSITS IN SUBSURFACE, SPRINGHILL FORMATION, AUSTRAL-MAGALLANES BASIN, TIERRA DEL FUEGO, ARGENTINA

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Estuarine systems are complex transitional environments, with several sedimentary sub-environments that record a continuum of continental to marine processes. In the subsurface of the Tierra del Fuego province, which is the southernmost part of the Austral-Magallanes Basin, the Springhill Formation infills a hemigraben [1]. The Springhill Formation represents the first stage of marine transgression in the Austral-Magallanes Basin, and presents a variety of deposits ranging from fluvial, estuarine to open marine [2]. In this contribution, we describe the sedimentology and ichnology of the Springhill Formation, and we provide a paleoenvironmental reconstruction of the sequence. We also provide the first evidence of bioerosion within the Springhill Formation.

The studied interval is represented by 2 boreholes with 4 core samples, with a total of 29.52 m. length. From a sedimentological point of view, 11 sedimentary facies, dominated by sandstone, are described and grouped into 4 Facies Association: FA1 foreshore to upper shoreface, FA2 lower shoreface, FA3 lower shoreface with storm deposits, and FA4 inlets deposits. These environments represent only a subset of the environments of the Springhill Formation, corresponding to the late stage of hemigraben sedimentary infill. Most of the section described shows intense bioturbation (BI up to 6), and it displays a trace fossil association with *Ophiomorpha* isp., *Planolites* isp., *Asterosoma* isp., *Teichichnus* isp., *Thalassinoides* isp., *Haentzchellinia* isp., *Parahaentzchellinia* isp., *Rhizocorallium* isp., *Chondrites* isp., *Gyrolithes* isp., *Palaeophycus* isp., of the *Cruziana* ichnofacies, and another ichnoassociation characterized by *Macaronichnus* isp and *Ophiomorpha* isp. assigned to the *Skolithos* ichnofacies.

In some levels, abundant shell debris are observed. Therein are bivalves (with varying degrees of preservation), corals, and serpulidae tubes. The shelly levels are intensely bioturbated (Fig. 1A). The largest shells are commonly bioeroded, with borings identified as *Gastrochaeonolites* isp. and *Entobia* isp. are located in the thickest parts of the shells, sometimes in clusters, showing no preferential orientation (Fig. 1B). The presence of *Entobia* on the inner and outer parts of the shells, and the variable degree of preservation of the skeletal remains are evidence of time averaging of shell deposits (i.e., several biostratigraphical pathways that these bioclasts suffered before their final deposition) affording enough time to be bored the trace makers [3-4]. We infer those skeletal debris concentrations are reworked and redeposited by storms, in shoreface to offshore transition settings. Between storm events, a colonization window opens, allowing the benthic fauna to intensely bioturbate these deposits and exposed calcareous materials to boring.

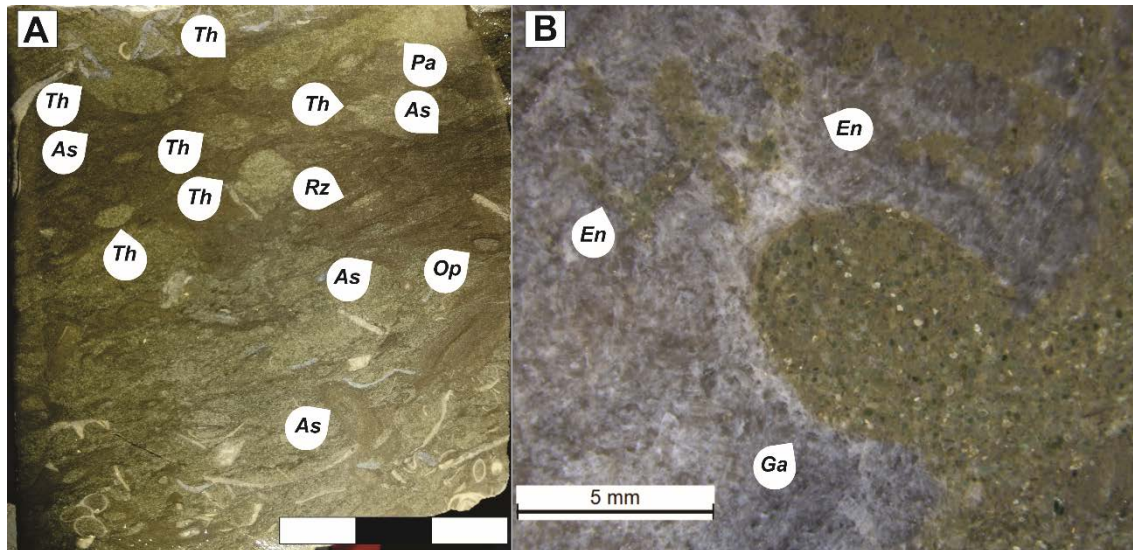


Fig. 1. A. General core view of intensely bioturbated storm deposits sand facies, with abundant skeletal fragments. B. Detail of a bioeroded shell. Abbreviations: As: *Asterosoma* isp., En: *Entobia* isp., Ga: *Gastrochaenolites* isp., Pa: *Palaeophycus* isp., Op: *Ophiomorpha* isp., Rz: *Rhizocorallium* isp., Th: *Thalassinoides* isp. Scale bar in A = 3 cm.

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ENVIRONMENTAL IMPLICATIONS OF ICHNOLOGICAL SITES, NORTH AND NORTHERN COASTS, BARREALES LAKE, NEUQUEN, ARGENTINA

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In memory of Dr. Jorge O. Calvo.

The ichnological sites located on the north and northeast coasts of Lake Barreales, 80 km northwest of the city of Neuquén (Fig. 1), is a relic of the environment where invertebrate and vertebrate organisms lived during the Upper Cretaceous period of the Neuquén Basin [^{1,2}].

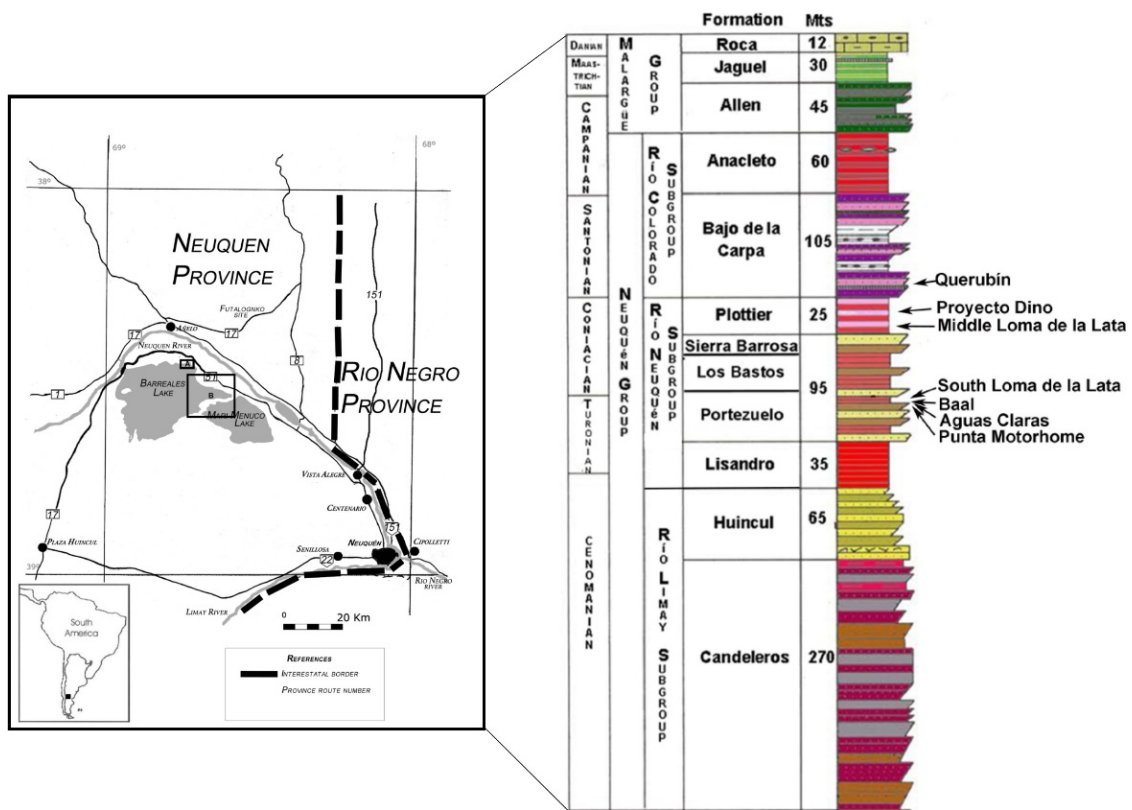


Fig. 1. Schematic stratigraphic profile of the Neuquén Group indicating the stratigraphic positions of the ichnological sites.

Trace fossils occur in Upper Cretaceous rocks of the Neuquén Group, specifically in the outcrops of the Portezuelo, Plottier, and Bajo de la Carpa Formations (Fig. 2).

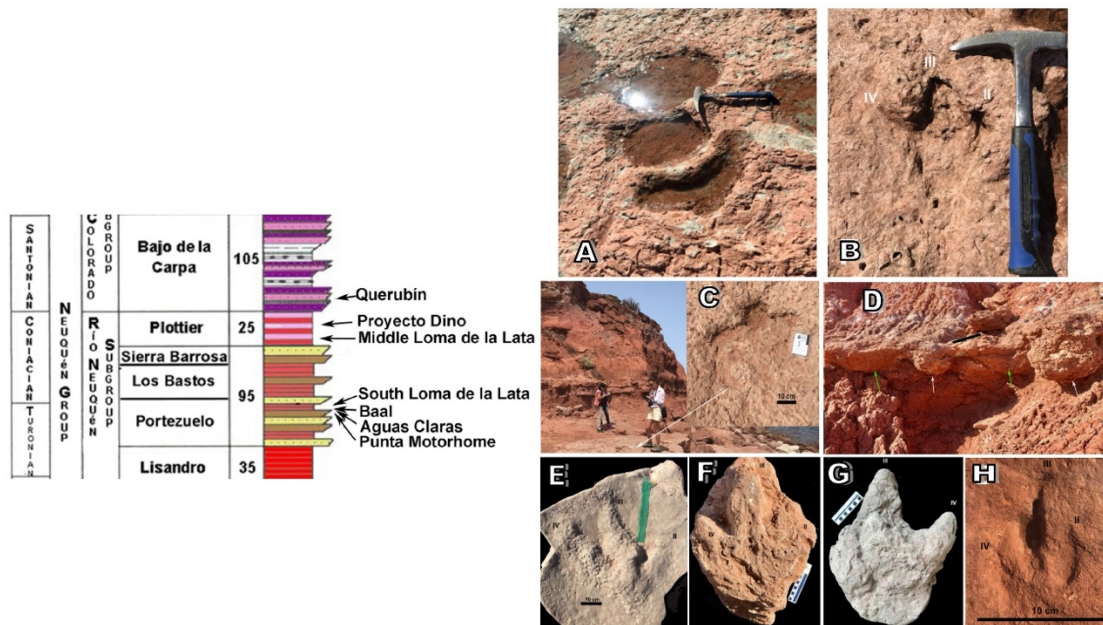


Fig. 2. A. The Querubin tracksite. Sauropod tracks of the Bajo de la Carpa Formation. B. The Querubin tracksite. Small theropod track. C. The Middle Loma de la Lata tracksite, ornithopod dinosaur rounded digit impressions of the Plottier Formation. D. Outcrops of the Plottier Formation with the sauropod dinosaur tracks at the Proyecto Dino site. E. The Punta Motorhome tracksite. Natural mold Theropod dinosaur track. F. Theropod dinosaur tracks from the Aguas Claras tracksite. G. Natural mold Theropod dinosaur track from Baal tracksite- H. The South Loma de la Lata tracksite. Small theropod track [3].

The Portezuelo Formation (Turonian–Coniacian) is composed of sandstones and siltstones whose thickness varies between 95 and 130 m. These deposits represent a high-energy fluvial system alternating with periods of stable conditions for the development of paleosols [4]. The Portezuelo Formation contains fossil traces of theropods associated with burrows of potentially suspensivorous organisms, such as *Skolithos*, represented by vertical shafts with preserved walls, 0.5 cm wide and up to 10 cm deep, excavated on fluvial channel bars.

The Plottier Formation (Coniacian) is composed of siltstones with intercalations of sandstones and conglomerates. Its thickness varies between 25 and 35 m. These deposits would have accumulated under a humid temperate climate with dry seasons in channeled meandering fluvial systems and floodplain deposits with abundant vegetation where paleosols developed. Rhizoliths, chemical nodules, and concretions indicate a mottled soil, formed by the alternation and superimposition of oxidation and reduction conditions. Traces of sauropods and ornithopods have been discovered in the sandstone beds, as well as traces left by detritivorous invertebrate organisms in the softground plains. The ichnodiversity is relatively low, and *Scoyenia* is recognized as the main ichnofacies [5].

The Bajo de la Carpa Formation (Santonian) is composed of coarse-grained sandstones, with reddish siltstones and claystones forming thin beds between the hard sandstone layers, deposited by a medium to high energy fluvial system [4]. The Bajo de la Carpa Formation can reach a thickness of 105 m. Traces of sauropods and theropods have been discovered, associated with *Skolithos* [5] and detritivorous organism burrows, representing the Ichnofacies *Scoyenia* [6], in horizontal planes with the presence of undulites, gradually decreasing in depth.

The analysis of trace fossils of this site allowed inferring the environmental conditions that prevailed during the organism-substrate interactions. The association of vertebrate ichnites with invertebrate burrows indicates the existence of softgrounds and deposition in a sub-aqueous floodplain. The greatest ichnological variability occurs in medium- to high-energy environments, while in low-energy environments paleosols developed. It has also been observed that oxygenation levels in general are higher in the sites where vertebrate traces associated with



Skolithos are found. Ichnodiversity and bioturbation intensity decrease towards the top in paleosol beds.

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FLAMINGO NEOICHOLOGY: STAMPING BEHAVIOR, BIOGENIC STRUCTURES, ENVIRONMENTAL CONTROLS AND PALEOENVIRONMENTAL MEANING

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Biogenic sedimentary structures provide important clues for determining the environmental conditions that prevailed during their record. Thus, accurate paleoenvironmental reconstructions largely depend on the study of the factors that control the behavior of bioturbators in modern settings [¹]. To contribute to this issue, we analyzed the environmental determinants of the stamping, a feeding technique used by extant flamingos that, while rotating around their axis (rotating stamping) produce characteristic structures consisting of a central mound of piled sediment surrounded by a peripheral trench excavated by foot trampling [^{2,3}] (Fig. 1). We compiled the available records of stamping behavior and rotating-stamping structures (ROT) from the literature and online video archives for all the modern flamingo species worldwide; these data were then analyzed using a set of descriptors including landforms, depositional environment, habitat type, water depth, water pH, salinity, tidal regime, climate, and season. Stamping behavior appears to be associated with shallow-keeled flamingos (genus *Phoenicopterus*), but little is known about deep-keeled species (genera *Phoenicoparrus* and *Phoeniconaias*), especially those from South America (*Phoenicoparrus andinus* and *Phoenicoparrus jamesi*). Our results indicate that flamingos tend to stomp more frequently in coastal environments, particularly brackish lagoons with very shallow water depths (~22 cm) and slightly alkaline waters (~7.8 pH) (Fig. 2). There was a preference for muddy substrates; thus, mudstones are the most likely lithologies where ROTs are expected to be found. The environmental characteristics associated with stamping behavior and to ROTs distribution contrasts with the global distribution pattern of fossil flamingo tracks (ichnogenera *Phoenicopterichnum* and *Culcitapeda*), which were mainly described from continental lacustrine deposits indicating high salinity and alkalinity [⁴⁻¹⁰]. Our results show that modern flamingos respond to a wide range of environmental factors to perform stamping behavior, as well as some species-specific idiosyncrasies. Because a single type of behavior exhibited such a variation, implying that the strict interpretation of highly alkaline and highly saline lake environments bearing flamingo-type fossil tracks (the proposed *Phoenicopterichnum* ichnosubfacies [¹⁰]) must be viewed with caution and supported by additional evidence. Despite being abundant with a good preservation potential, the ROTs have not yet been reported in the fossil record, possibly due to unknown diagenetic aspects, comparatively lower preservation potential of structures formed in coastal environments (compared to lake environments [¹¹]) or underestimation of these structures in the field by the possibility of being confused with other traces in similar environments, such as the nidification/feeding bowls of *Piscichnus*.

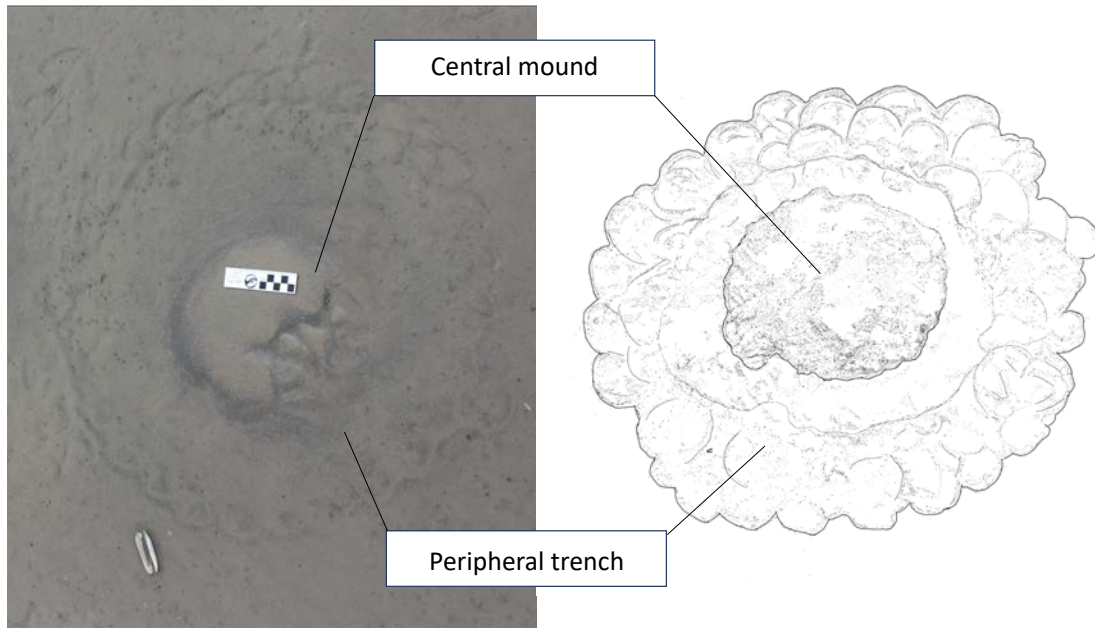


Fig. 1. Photograph example and schematic representation of rotating-stamping structure (ROT) registered by [the](#) Chilean flamingo (*Phoenicopterus chilensis*) in the Lagoa do Peixe National Park, Rio Grande do Sul, Brazil. Adapted from [3]. Scale = 10 cm.

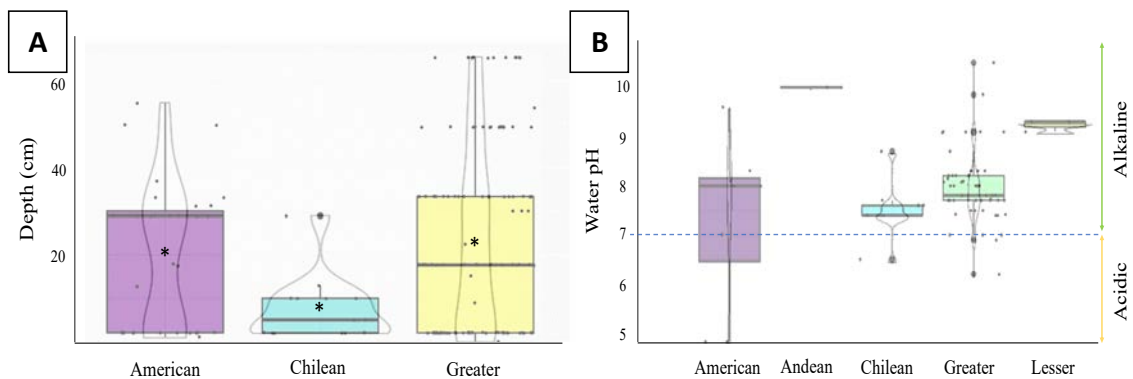


Fig. 2. Distribution of (A) water depth measurements (in centimeters) and (B) water pH values where flamingo species displayed the stamping behavior. An asterisk indicates the mean. Species: American flamingo (*Phoenicopterus ruber*), Andean flamingo (*Phoenicoparrus andinus*), Chilean flamingo (*Phoenicopterus chilensis*), Greater flamingo (*Phoenicopterus roseus*), Lesser flamingo (*Phoeniconaias minor*).

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CHALLENGES TO THE PALEOICHOLOGY RESEARCH ON THE TACUTU BASIN, CENTRAL/NORTHEAST AMAZONIA, RORAIMA (BRAZIL)

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The paleontological research in the State of Roraima (Brazil) is still recent, advancing only after the creation of the geology graduation course at the Universidade Federal de Roraima (UFRR) in 2006. Since then, more emphasis has been given to the Tacutu Basin, where, in addition to fossil wood [1], both invertebrate [2] and vertebrate [3] ichnofossils have been discovered. Currently, the ongoing work on paleoichnology is focused on dinosaur ichnofossils and preliminary results have already led to the discovery of numerous traces of sauropods (Fig. 1A). Theropod, ornithopod (Fig. 1B-D) and thyreophoran tracks have also been found. The rocks that contain these ichnofossils are sandstones and conglomerates of the Serra do Tucano Formation, which is estimated to be deposited between the Barremian and Albian ages [4]. These deposits crop out in the Brazilian side of the basin only [5] and are interpreted as an ancient fluvio-deltaic system [4,6,7]. In Guyana, the sedimentary rocks outcropping in the Tacutu Basin are understood as the Tacutu Formation (also referred to as Takutu Formation), mainly composed of siltstones and sandstones that were deposited in a shallow lacustrine environment and is stratigraphically positioned under the Serra do Tucano Formation, estimated to be deposited between the Berriasian and Barremian ages [4,6,8,9]. The Serra do Tucano Formation sandstones, however, are intensely weathered by lateritic processes when close to the surface, usually exposed in the form of fragmented and scattered sandstone blocks throughout the terrain (Fig. 1E), sometimes rolled over when in elevated regions. The laterization of these rocks, however, may have contributed to the tracks preservation since it added extra cohesion to the sandstone through the cementation of iron and aluminum oxides, thus preventing the tracks from being easily destroyed by the erosive processes active in the region. The dispersion of blocks throughout the terrain has made it challenging to correlate the tracks and to identify trails, as well as for stratigraphic correlations. Nevertheless, it is possible to find sets of pes and manus and evidence of sauropod trampling. The region presents an enormous potential for the occurrence of ichnofossils, given that only nine outcrops have been visited at different points on the Brazilian side of the Tacutu Basin and all of these outcrops have exhibited dinosaur ichnofossils with more than one major group of dinosaurs occurring per outcrop. This leads to the hypothesis that the still inaccessible outcrops may also contain fossilized traces. These outcrops are located in hills and plains. In plains, the largest site found spans for more than 6 km consisting of scattered blocks punctually throughout the terrain. However, a significant portion of landowners has not yet granted access to the areas and a substantial part of the potential sites is within indigenous territory, which directly collides with bureaucratic barriers. In addition to the presence of venomous fauna, the region's climate can also be inhospitable, ranging from heavy rainfall to intense sunlight, heat and winds, as the study area is located in a patch of Amazon savanna. This climate has been the primary challenging factor for photogrammetric data collection, whether using DSLR cameras or UAV. The available data has been collected by adapting photogrammetry techniques, resulting in satisfactory 3D and elevation models (Fig. 1B) for the preliminary results when using the software Meshroom (2019.2.0) [10]. Currently, the establishment of camps is still not possible as the work also lacks funding and voluntary collaborators.

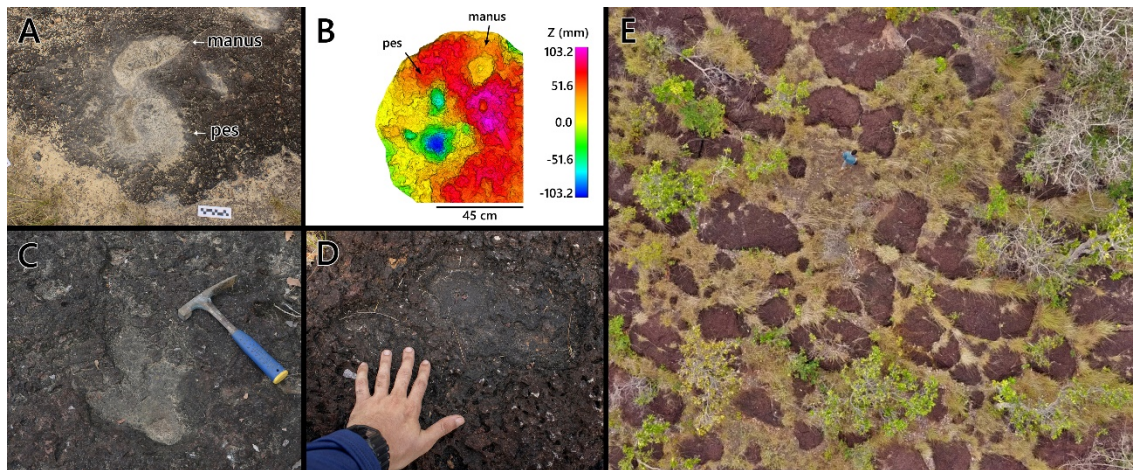


Fig. 1. A. Sauropod manus and pes tracks. B. Depthmap from a semi-digitigrade ornithopod pes and manus tracks. C. Semi-digitigrade ornithopod pes track. D. Digitigrade ornithopod pes track. E. Aerial perspective from the "Cascavel" site, composed of concretionary sandstone (Fe and Al oxides). Photo in E is a courtesy of Jorge Donizatti Pavani.

Therefore, arises the question: why study the paleoichnology of a complex and challenging region? The answer lies in the scarcity of information about dinosaurs in the Mesozoic not only in the Amazon region but throughout the north of South America. Additionally, there is a complete lack of Dinosauria occurrences in the northern/northeastern portion of South America represented by the State of Roraima. This study aims to fill this paleobiogeographic and paleoecological gap for the Early Cretaceous in the region. The richness of dinosaur ichnodiversity, along with its widespread occurrence on the Brazilian side of the Tacutu Basin could make it a unique location in the world. This potential uniqueness, coupled with future works on paleontology, may lead to the creation of the first geopark of Roraima, contributing to the identity of the Municipality of Bonfim (Roraima State) and allowing authorities to implement measures for the preservation of these ichnofossils, given that agricultural machinery traffic is widespread in the region, even in non-arable areas.

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POSSIBLE IN SITU DINOSAUR EXCREMENTS FROM THE SERRA DO TUCANO FORMATION (BARREMIAN–ALBIAN), TACUTU BASIN, RORAIMA, BRAZIL

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The Tacutu Basin is a Jurassic–Cretaceous rift-type basin located at the extreme north of Brazil (Roraima State) and extending into Guyana [1]. However, the sandstones, conglomerates, and mudstones that make up the Serra do Tucano Formation outcrop only on the Brazilian side of the basin [2] and are estimated to have an age between the Barremian and Albian [3]. Invertebrate ichnofossils have been recognized in sandstones and mudstones [4], and more recently, numerous dinosaur ichnofossils have been discovered widely distributed in the Serra do Tucano Formation on sandstones and conglomerates, such as tracks of sauropods, theropods, ornithopods, and thyreophorans [5], revealing a high diversity of dinosaurs in a paleoecological setting for the Lower Cretaceous of Roraima. However, the genesis of these ichnofossils is not yet fully understood, given that there are few studies on the Serra do Tucano Formation sedimentation and its diagenesis. The Serra do Tucano Formation is interpreted as an ancient fluvio-deltaic system with the presence of meandering channels [6]. Thus, it is possible that lacustrine bodies existed on the basin, along with the yet unknown influence of tides and marine incursions on the region's floodplain. While some ichnofossils may exhibit a good degree of preservation, most of them are poorly preserved and heavily weathered by lateritic processes, making more precise ichnotaxonomic classifications challenging. Thus, this study aims to enrich the discussion on the topic and contribute to the understanding of the paleoichnology of the Tacutu Basin, as the work is still in its early stages and many questions about the occurrence of the ichnofossils in the region remain unanswered, such as sauropod excavations and, especially, the occurrence of possible in situ fossilized excrements, where it is not clear whether they are coprolites or micturalites, a term to describe liquid evacuations [7,8]. Currently, three potential *in situ* fossilized excrements have been observed, allowing for the generation of elevation models derived from photogrammetric models, which, in turn, were produced by the software Meshroom 2019.2.0 [9]. The first one (st06-38) features a main elliptical depression with two internal elevations in the form of elliptical rings, leaving the center of the sample still as a depression, suggesting that it resulted from a concentrated fluid discharge, although it is not yet entirely clear if it is solely made by liquid evacuation. The second sample (st05-52) is also characterized by a depression with an elevation isolating the center of the sample, but with evidence of fluid flow towards its peripheral area, making the sample longer than wide, and thus, indicating the direction of discharge, allowing it to be characterized as a possible micturalite. Finally, the third sample (st01-03-01, Fig. 1) displays a prominent elliptical elevation surrounded by a depression, also showing signs of abundant fluid flow and oriented by the elevation of this sample, making it longer than wide. This feature may indicate that the elevation resulted from the remobilization of unconsolidated sediment during urine evacuation. However, it is also possible that the elevation itself is a coprolite that was evacuated after urine evacuation, justifying the overall sample shape with mixed characteristics of feces and urine, leading to the belief that at least some group of dinosaurs possessed a cloaca, although it is still early to arrive at more concrete conclusions. Furthermore, the hypothesis of mixed evacuation as a result of a gastric disease cannot be ruled out. The sandstone block that displays this ichnofossil also has at least two dinosaur tracks, one being a sauropod footprint filled with sand and the other, a partial and undetermined footprint that

clearly shows sediment deformation in the direction of the fossilized excrement, suggesting that the footprint was made after the evacuation. The only chemical analysis conducted so far on the elevation of this sample has been inconclusive, presenting mainly the metallic oxides expected for the rock cement (Mn, Fe, and Al oxides), with similar results for the first ichnofossil here described (st06-38).

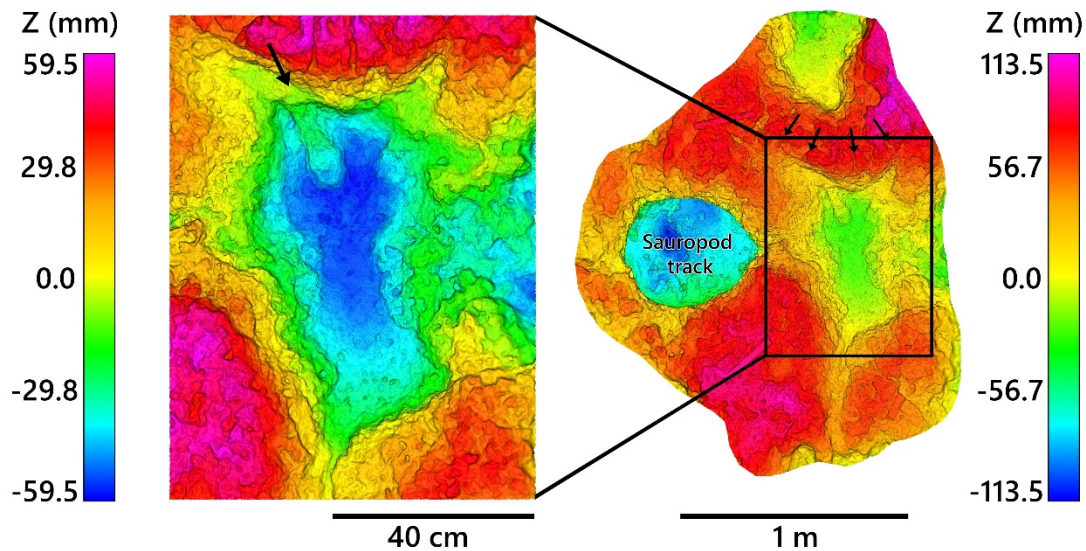


Fig. 1. Sample st01-03-01, showing mixed characteristics between liquid and solid evacuation. It is possible to notice at least two footprints on the sandstone block, one being a sauropod track filled with sand and, the other, a partial and undetermined footprint that was made after the evacuation. Arrows indicate the deformation direction (right) and flow origin (left).

The possibility of the samples presented here being pseudoichnofossils produced by diagenetic or weathering processes, while not ruled out, seems to be the least likely when elevation models are analyzed and when considered in the context of the outcrops, all of which feature dinosaur footprints. These footprints, in turn, do not exhibit characteristics similar to the potential fossilized excrements, making these three samples unique on the Serra do Tucano Formation. Now, there remains the need to conduct simulations and field observations on living counterparts, such as ostriches (*Struthio*), to provide a deeper understanding of sediment remobilization dynamics during Dinosauria evacuations.

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EVIDENCE OF SAUROPOD TRACKS AND OTHER TRACES IN THE BARREMIAN–ALBIAN FROM THE TACUTU BASIN, RORAIMA, BRAZIL

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Sauropod tracks have a widespread global distribution and occur throughout most of the Mesozoic and the entire Cretaceous period [1-5]. It is not surprising that they also occur on the Tacutu Basin, a rift-type basin located in the extreme north of Brazil (Roraima State) and part of Guyana, with a genesis linked to the opening process of the Atlantic [6,7]. These ichnofossils have a widespread occurrence on the Brazilian side of the basin, occurring on sandstones and conglomerates from Serra do Tucano Formation (Barremian–Albian), which was possibly deposited in a frankly continental environment, where the combination of sandy sediments, sporadic rain events, and channel overflow [8] would have allowed the formation and consolidation of the dinosaur footprints found in the region. Many dozens of these tracks have been found, with the majority still undescribed [9], representing only a small portion of the outcrops that potentially harbor ichnofossils. Other outcrops remain inaccessible. Sauropod tracks constitute the largest portion of the ichnofossils and have been characterized mainly based on their morphological features, as well-defined trackways have not yet been discovered, but only isolated footprints, trampling and sets of pes and manus. These fossilized traces often occur in association with theropod and ornithischian tracks, also part of an ongoing study. It is not yet possible to determine whether there was an influence of tides or marine incursions, but the data collected so far suggests that the fluvio-deltaic system hosted a diversified dinosaur fauna with an abundance of sauropods. This represents the first verifiable occurrence of Dinosauria in the central/northeastern region of the Amazonia. Although the Serra do Tucano Formation is associated with a savanna vegetation, conducting fieldwork in the region can still be challenging as the vegetation covers the outcrops, hiding a significant portion of the tracks and making rapid data collection using UAVs not possible. While the study is still on its early stages, it has provided an overall insight into the distribution of ichnofossils in the Tacutu Basin. However, some questions are still open. One of them concerns other ichnofossils that may occur in association. In this perspective, this work aims to present some fossilized sauropod tracks and other traces with doubtful characteristics, possibly related to overlapping footprints, nest excavations, or some other record of behavior not yet fully understood. The complex concretionary feature (Mn, Fe and Al) from the rocks of the Serra do Tucano Formation also hinders stratigraphic correlations between the outcrops and generally attributes a low degree of preservation to the ichnofossils. The depositional and diagenetic processes that originated the Serra do Tucano Formation are also poorly studied [10], adding to the challenges of understanding the ichnofossils taphonomy in the basin. Therefore, the preliminary results of this work help to better understand the deposition environment and paleoecological scenarios for the Lower Cretaceous of the Tacutu Basin. Additionally, it fills a paleobiogeographic gap regarding sauropods in the northern region of South America, as dinosaur remains found in this part of the globe are scarce and can be easily destroyed by intense weathering and erosive processes prevalent on the Amazonia.

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THE GIANT PALEOBURROWS FROM CAMINHOS DOS CÂNIONS DO SUL UNESCO GLOBAL GEOPARK

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South American paleoburrows (*paleotocas* or *paleocuevas*) are the common names for the ichnogenus *Megaichnos* Lopes et al., 2017 [1]. The ichnogenus, which are the largest ichnofossil known so far, whose galleries complexes can extend for hundreds of meters, can be divided in two ichnospecies: *M. minor* and *M. major*. Those huge galleries were excavated by extinct *Xenarthras* (Mammalia) [2] which inhabited South America during the Neogene and Quaternary. Once filled by sediments, those galleries are known as “crotovines”, using the same terminology as proposed by Chernyaev [3] for Russian deposits. The first interpretation of a giant paleoburrow was made by Ameghino, in 1908 [4], who wrote “structures similar to crotovines but without internal filling” [5]. More than a century after the first mention, giant paleoburrows are currently known through Brazil, Argentina, Uruguay, and Paraguay. However, its geographical and lithological distribution needs constant prospection, aiming a better comprehension regarding paleobiogeographical data and possible paleoethological bias.

The paleoburrows currently under prospection on *Caminhos dos Cânions do Sul* UNESCO Global Geopark (CCSUGG) compose its international relevance abiotic heritage, endorsed by UNESCO in 2022. The paleoburrows found in CCSUGG presents remarkable preservation and densification, whose galleries can reach up to 63 m in length, 4 m in height and 3 m in width. Claw marks, resting and turning chambers, and abrasion on the walls are noticed, so as inferences of native Americans occupations, such as lithic tools and graphism.

Geoparks are territories that possess abiotic diversity and aim for social development through the utilization of this diversity, assigning values to specific locations, the geosites. These elements are geomorphological, paleontological, mineralogical, petrological and hydrogeological features identified and inventoried in each area [6]. They can be assigned values such as scientific, educational and cultural. CCSUGG presents several geosites of international relevance, among them, the paleoburrows, which exhibit the mentioned values above.

This study was conducted in three stages. The first involved a literature review. In the second, field trips were conducted to prospect and investigate the possible ichnofossils, measure them, catalog, and record their characteristics on catalog charts. Finally, thematic maps were created, and the collected field information was standardized. Those processes and data acquisition still in progress.

The CCSUGG is situated in southern Brazil, at the border between the states of Santa Catarina and Rio Grande do Sul (Fig. 1) and encompasses deposits from the Paraná-Etendeka Sedimentary Basin and Quaternary sedimentary deposits. The oldest deposits in the Geopark area consist of sedimentary rocks from the Rio do Rasto Formation, which are overlaid by the eolian sandstones of the Botucatu Formation. The deposits of both formations are covered by the volcanic rocks of the Serra Geral Group, resulting in the erosive discontinuity that creates the canyons that give Geopark its name. The lowlands are composed by Quaternary alluvial plains and coastal sediments.

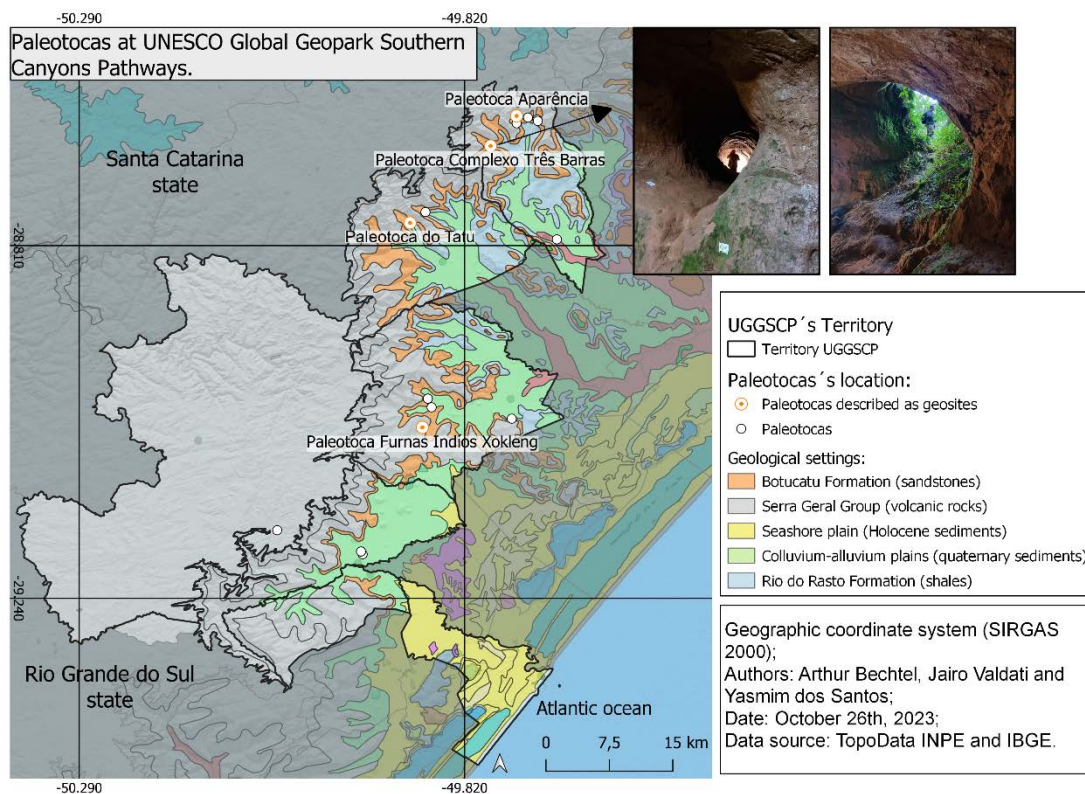


Fig. 1. Paleoburrows distribution at CCSUGG. The map includes the paleoburrows already considered as geosites and the lithology in which they occur, a relevant component for their preservation.

The CCSUGG territory has, currently, 24 cataloged giant paleoburrows. However, through communication with locals, at least 40 more are already known and waiting for its prospection. Among the already recognized giant paleoburrows from GMUCCS, four are recognized as UNESCO Geosites: Três Barras paleoburrow Complex (Fig. 1, 2A-B), Aparência paleoburrow (Fig. 2C-D), Toca do Tatu paleoburrow [7], and Índios Xokleng paleoburrow. For preservational care, only the first two are accessible for visitors. Twenty-three paleoburrows were excavated in sandstones of the Botucatu Formation and one in weathered basalts. The lowest altitude occurrence of paleoburrows cataloged in Botucatu Formation sandstones is 49 m (Alvorada I paleoburrow) and the highest is 432 m (Veisom paleoburrow). The only paleoburrow described so far in weathered basalt (Parque paleoburrow) is located at an elevation of 1032 m. The average altimetric elevation of paleoburrows present in the Botucatu Formation deposits is 235 m. Regarding paleoburrow dimensions, the largest single tunnel prospected so far is the Aparência paleoburrow, measuring 64 m in length, with an average width of 2.56 m and an average height of 1.40 m. The smallest are the Alvorada I and Escondida paleoburrows, with average widths below 1.30 m and average heights below 1 m. In terms of the number of galleries, seven paleoburrows are composed by two or more tunnels. The Três Barras paleoburrow complex have a remarkable density of 13 galleries, some of it partially lixiviated, whose could present more bifurcations. In other instances, the Molha Coco Alto paleoburrow has only two galleries, and others have a single gallery.

Based on the ichnotaxonomy of the South American Giant Paleoburrows, two species were recognized: *Megaicnhus major* and *Megaicnhus minor* [1]. Their diagnoses consider several aspects, such as tunnel shape and dimensions. *M. major* predominates in the CCSUGG study area, representing 20 of the 24 paleoburrows prospected so far. The other 4 paleoburrows have smaller dimensions and are considered as *M. minor*.

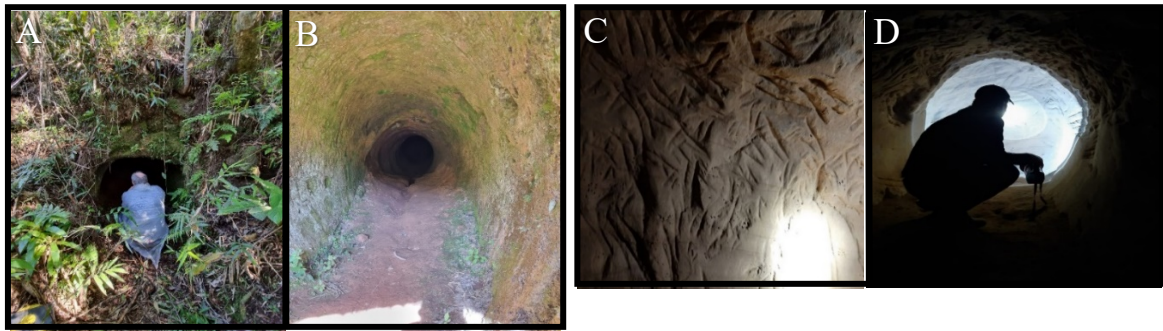


Fig. 2. Giant paleoburrows from the GMUCCS. A-B, “Três Barras” paleoburrows. C-D claws marks at “Aparência” paleoburrow. This paleoburrow received that name because the citizens reported some “visions” of indigenous people killed by colonizers.

The CCSUGG giant paleoburrows also presents remarkable aspects that must be considered, such as: (i) the sum of some tunnel complexes exceeding a hundred meters, and have entrances and galleries which allows to investigator or visitor to walk upright inside the ichnofossil; (ii) their unique preservation, once the step canyon morphology and topography, allow less water percolation, maintaining the unique integrity of the structures; (iii) the (re)occupation by various species through time, with current fauna highly adapted to cave environments (troglóbites) and larger animals like birds, *catetos* boars, *graxain* wild canines and even pumas, among others; (iv) the occupation by indigenous people who traversed, inhabited, and utilized these cavities; (v) the presence of archaeological records associated with the Laklaño-Xokleng Native Americans; (vi) sites where legends and stories are attributed by the inhabitants of the territory, thus conferring cultural value.

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USING PROCESS ICNNOLOGY TO ELUCIDATE OXYGEN FLUCUATIONS OVER THE CRETACEOUS OCEANIC ANOXIC EVENT 2 IN WESTERN CANADA

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Cretaceous oceanic anoxic events (OAEs) are an internationally recognized phenomenon resulting in globally correlated organic-rich horizons [¹⁻³]. Perhaps the most well-known of these events is OAE2, an ostensibly globally present organic-rich mudstone layer denoting the Cenomanian-Turonian boundary (~94 Ma). Despite the considerable literature pertaining to OAE events, in-depth trace fossil analyses spanning these intervals are limited. A well preserved, slabbed, and continuous 110m long drill core from the paleo-epicontinental Western Interior Seaway of western Canada provides an excellent opportunity to evaluate fine-detail ichnological characteristics before, during, and after the Canadian extent of the OAE2 (covering the Cenomanian Belle Fourche Formation and the Turonian Second White Specks (2WS) Formation). Historically, the lack of pervasive bioturbation throughout the Canadian OAE2 interval has been attributed to fluctuating and low depositional dissolved oxygen (DO₂) values [⁴⁻⁶]. The aim of this analysis is to elucidate physicochemical fluctuations, and specifically relative bottom water DO₂ fluctuations, over this supposed global anoxic event.

Millimeter scale sedimentological and ichnological observations were grouped into 10 cm interval 'data bins'. Binary values were used to record the presence or absence of a specific feature (presence of a feature = 1, absence = 0). This included discrete sedimentological features like current ripples and scour surfaces, and the presence or absence of a distinct ichnotaxon (Fig. 1). Additional ichnological data was summarized over 10 cm intervals, recording maximum burrow diameters (mm), diversity (number of individual ichnogenera), and both minimum and maximum bioturbation index (BI, 0-6^[7]) (Fig. 1). Individual ichnotaxa were combined into four ichnoguils (fugichnia, *Planolites*, *Phycosiphon*, *Chondrites*) (Fig. 1), providing insights into potential fluctuating oxygenation and other physicochemical factors over the length of the core. A relative oxygen curve ('relative DO₂ curve' in Fig. 1) was generated using the sum of maximum BI and size-diversity index (SDI; i.e., the product of maximum burrow diameter and diversity numbers) over an interval, scaled with total organic carbon (TOC) data (i.e., [BI+SDI]/TOC). The resulting curve shows that DO₂ available for burrowing organisms was permanently fluctuating, and only very rarely, if at all, reached persistent anoxia (a zero value) within the OAE2 event. Analysis of the ichnological characteristics and their interpreted oxygen reflections over the cored length reveal five distinct ichnological events (IEs; Fig. 1). Ichnological events tend to parallel the general major sedimentological shifts and internal formation boundaries and were further able to indicate surfaces commonly denoted on the basis of lithology alone (e.g., denote flooding surfaces; transition from IE1-IE2, and IE3-IE4). Ichnologic event analysis additionally identified an internal shift within the upper Second White Specks Formation (IE4-IE5), not identified during lithologic and geochemical (XRD) analysis [⁶].

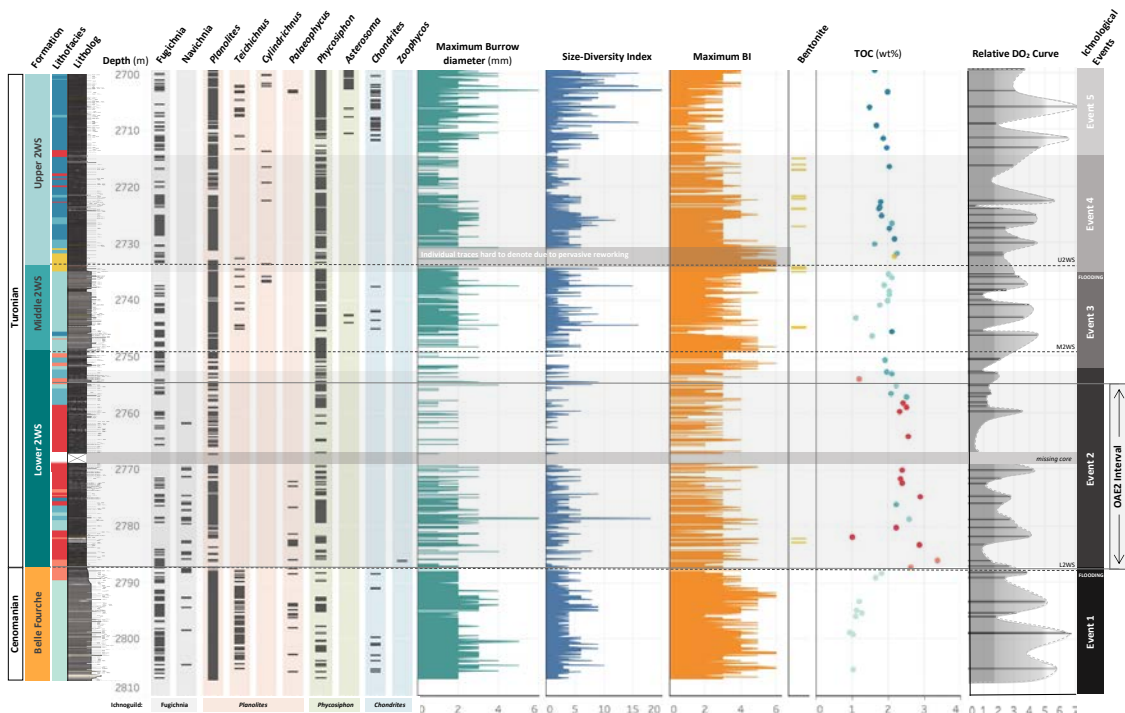


Fig. 1. Diagram illustrating several sets of ichnological data over the cored interval. Ichnogenera organized by their ichnoguild association (colored bars). Distinct ichnologic events denoted by alternating shaded intervals and greyscale bars to the right.

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SEQUESTRICHNIA CONTAINING STOWED BENTHIC FOOD CAUSE FORMATION OF “SILESIA DUMPLING” CONCRETIONS (BOOK CLIFFS, UTAH)

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Sequestrichnia refer to various, morphologically different trace fossils belonging to different ichnogenes, which share the same characteristics that their producers (i) sequester organic-rich material on the seafloor or from suspension when plenty of benthic food is available, (ii) transfer it downward, (iii) stow it into a burrow, and (iv) utilize it later during times when benthic food availability is restricted [1,2]. Storage is optimal if the cache is located in anoxic sediment and beyond the reach of competing burrowers. Since the most-reactive (= nutritional) organic substances are oxidized first [3], refractory organic matter becomes enriched deeper in sediment. If, however, reactive organic matter is brought in contact with refractory organic matter, priming may take place [4]. Priming is defined by the enhanced microbial remineralization (typically ~10–30%) of otherwise low-reactive (refractory) organics in association with the decomposition of relatively reactive organic material in soils, aquatic sediments and natural waters [5,6]. This process is especially efficient if fresh organic matter is transferred into anoxic deposits; even low amounts of organic matter buried below the oxygenated zone stimulate priming [7]. In addition, if an open-tube burrow is produced in fine-grained anoxic sediment, microbial activity is stimulated by the steep geochemical gradient between anoxic host sediment and oxygenated water in the tube [8]. Consequently, sequestrichnia stimulate microbial activity deep in – especially anoxic – sediment.

Calcite concretions recently found in a Cretaceous mudstone succession in Utah (USA) provide clear evidence of a sequestrichnial activity of burrowers in a shallow-marine epicontinental setting. These concretions are embedded in non-calcareous, silty and sandy mudstones of the Turonian (upper) part of the Tununk Shale Member [9] that were deposited on a storm-dominated inner shelf to distal lower shoreface at the western margin of the Western Interior Seaway during a sea-level lowstand [9]. Abundant wood chunks and bones in the mudstones document proximity to land. The concretions are sub-spherical and range from 15 to 35 cm in diameter. All specimens have a distinctive circular depression located at the side (Fig. 1A), so that the depression has a horizontal axis parallel to the bedding of the surrounding mudstone. Such morphology resembles that of “Silesian dumplings”, traditional dumplings of the Polish cuisine. From the depression a horizontal tube extends into the center, where an organic core, usually a well-preserved wood fragment, is present (Fig. 1B).

These tubes leading to the wood are interpreted as a root part of a Sequestrichnia burrow. The interiors of the concretions, especially the wood fragments, are cut by a dense network of septarian cracks (Fig. 1B), which indicates shrinkage caused by degradation of abundant microbial biomass inside the concretions [10]. Such amount of biomass could have been produced by microbial remineralization of refractory wood material, which seems to be in line with priming. Further evidence comes from isotope data, as the concretions exhibit depleted $\delta^{13}\text{C}$ values around -10‰. These values and the presence of framboidal pyrite of various sizes in the concretions suggest that the concretions formed under anoxic conditions, in the sulfate reduction diagenetic zone, although seawater-derived bicarbonate was also incorporated. The actual $\delta^{13}\text{C}$ values reflect the relative contribution of bicarbonate from two sources, (i) sulfate reduction (low $\delta^{13}\text{C}$ values) and (ii) seawater (high $\delta^{13}\text{C}$ values).

The lowest $\delta^{13}\text{C}$ values occur in the cores and calcite-cemented wood fragments and they increase outwards; the highest value was obtained in the infill of the tube. Such distribution of $\delta^{13}\text{C}$ values in combination with the internal structure of the concretions suggest that a steep geochemical gradient developed around the organic remains stored by the burrower in anoxic sediment, so that the organic matter served as the nucleation sites for the concretions [see ¹¹]. Organic C was microbially transformed to dissolved inorganic C through an anaerobic pathway (sulfate reduction), which favored carbonate oversaturation. Although we did not observe any continuation of the tube into the surrounding mudstone, the tube probably extended up to the sea floor (Fig. 2). These burrows acted as conduits allowing oxygenated seawater to percolate into the anoxic sediment restricting calcite precipitation around the burrow and resulting in the formation of the depression with the highest $\delta^{13}\text{C}$ values. Thus, the sequestrichnial activity supplied organic matter that fueled concretionary growth, but restricted calcite precipitation around the burrow, which is documented by the peculiar concretion morphology.

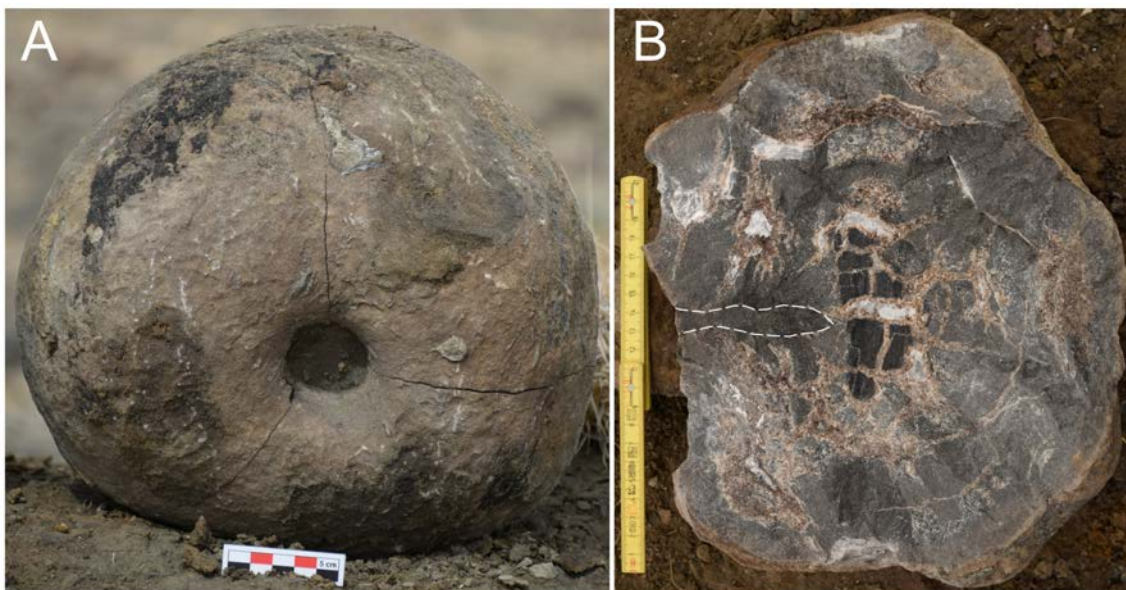


Fig. 1 Morphology and internal structure of the “Silesian dumpling” concretions. A. The circular depression is the not-cemented part of the burrow entering the concretion. B. Interior of a concretion showing heavily cracked wood fragment in the core (black), concretionary body (gray), and calcite spar filling the cracks (white and brown). The dashed line marks the tube that extends from the depression to the wood.

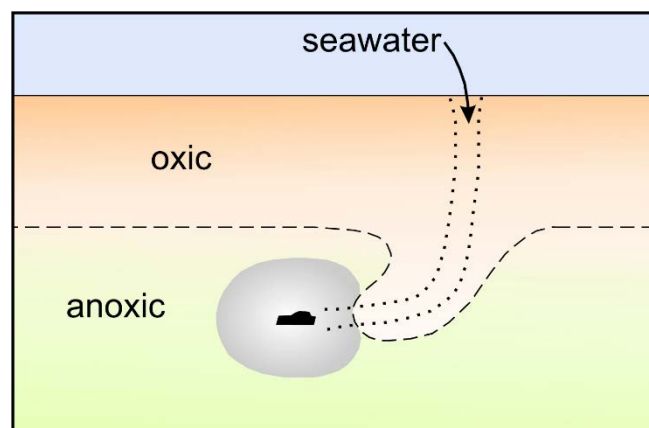


Fig. 2. A conceptual model of concretionary growth associated with a sequestrichnion. The dashed line marks the redox interface between oxic and anoxic conditions affected by the seawater percolating the burrow. The dotted line marks the burrow.



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EXPLORING THE ICHNOLOGICAL SIGNATURE OF MASS EXTINCTIONS

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The search for ichnological signatures of mass extinctions has experienced a steady growth since the publication of a seminal paper by Tony Ekdale and Richard Bromley in the mid-eighties. Mass extinctions were rapidly incorporated into evolutionary theory through their positioning as the so-called third tier in paleobiology by Steven Jay Gould. In recent years, mass extinctions are being seen from a new perspective given the current biodiversity crisis. Overall, despite the multiplicity of causes, ichnologic evaluation of mass extinctions suggests a set of relatively common responses from the marine benthos, resulting from typically a reduction in ichnodiversity, causing a decrease in the degree of bioturbation, reduction of bioturbation depth, burrow size reduction, dominance of simply constructed trace fossils in post-extinction strata, preferential survival of ichnotaxa produced by deposit feeders, and selective extinction in shallow-marine ecosystems. The severity of the mass extinction events essentially controls how pronounced were these effects, with the end-Permian mass extinction being the only event presently displaying evidence of the collapse of the mixed layer. Recent research also indicates that the ichnodiversity drop associated with the end-Permian event was not coincident with the extinction but occurred later in the Early Triassic. Sustained ichnodiversity levels across the boundary are thought to be the result of the opening of a taphonomic window that allowed preferential preservation of shallow tiers due to the disappearance of the mixed layer. Marked differences in the recovery time have also been noted with the end-Permian taking up to six million years for full re-establishment of the shallow-marine infauna. On the contrary, studies of post extinction deposits in the Chicxulub crater have revealed a re-establishment of the infaunal tiering structure within 30,000–45,000 years. The other so-called big five, the end-Ordovician, Late Devonian, and end-Triassic – as well as other extinction events of lower hierarchy – have received comparatively little attention. However, ongoing ichnological work is yielding insights into the dynamics of these events. Similarly, the ichnologic signature of mass extinctions on land has not been evaluated to the same extent than that of marine environments. Nevertheless, recent work suggests a decrease in the degree of bioturbation in the aftermath of the Capitanian and end-Permian events.



PALAEOENVIRONMENTAL RECONSTRUCTION OF A FINE–GRAINED TURBIDITE SYSTEM BASED ON ICHNOLOGICAL ANALYSIS: A CASE STUDY FROM TABERNAS BASIN (SE SPAIN)

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The Tabernas Basin in SE Spain is a frequently visited area for geoscientists due to its well exposed turbiditic deposits, widely studied as potential analogues for oil exploration. The filling of the basin comprises Serravallian to Messinian sediments from various settings, with turbidite deposits categorized into a sandy system, a muddy system, and a solitary channel system [1,2]. Despite numerous studies in the basin, the ichnological content has been somewhat overlooked [3,4,5]. Earlier contributions briefly mentioned some ichnogenera but lacked detailed ichnological analysis. Last year, a more precise ichnological study was published, focusing on one of the most representative sections of the muddy turbidite system from the basin. It described pre- and post-depositional trace fossils assemblages and discussed the evolution of fan deposition [6]. Here we present a more detailed analysis, examining five sections from the muddy turbidite system, allowing for a more complete paleoenvironmental reconstruction by interpreting different settings within the turbidite depositional system.

A total of 33 ichnospecies belonging to 20 ichnogenera have been identified. The pre-depositional trace fossils assemblage includes *Arenicolites* isp., *Chondrites intricatus*, *Chondrites* isp., *Nereites* isp., *Ophiomorpha annulata*, *Ophiomorpha* isp., *Ophiomorpha nodosa*, *Ophiomorpha rudis*, *Palaeophycus* isp., *Phycodes* isp., *Phycosiphon* isp., *Planolites* isp., *Scolicia* isp., *Scolicia prisca*, *Taenidium* isp., *Teichichnus* isp., *Thalassinoides* isp., *Thalassinoides suevicus* and *Zoophycos* isp.. Pre-depositional trace fossil assemblages encompass *Circulichnis* isp., *Cosmographaphe* isp., *Demograption* isp., *Helminthorhaphe* isp., *Helminthorhaphe japonica*, *Megagraption* isp., *Paleodictyon arvense*, *Paleodictyon majus*, *Paleodictyon maximum*, *Paleodictyon minimum*, *Paleodictyon miocenicum*, *Paleodictyon strozzii*, *Scolicia strozzii*, and *Urohelminthoida* isp.. The ichnological assemblage belongs to the *Nereites* ichnofacies, reflecting variations of *Ophiomorpha rudis* and *Paleodictyon* ichnosubfacies. Additionally, based on sedimentological characteristics, five distinct facies are differentiated: (i) massive mudstone; (ii) mudstone interbedded with thin sandstone beds; (iii) thin to thick beds associated with sandstones; (iv) very thick beds composed of conglomerates transitioning to fine sandstones; and (v) sandstones with mudstones showing slump structures.

Preliminary results show a clear zonation of facies in the basin based on grain size, also observed in the ichnological content. Coarser grained-size facies show more abundant post-depositional trace fossils and a relatively minor content of the pre-depositional assemblage compared to facies dominated by finer grained-size sediments. A clear trend is also registered in graphoglyptids, with smaller species more abundant in finer-grained facies. These variations allow characterizing different settings within the muddy turbidite system, according to particular paleoenvironmental conditions, which controlled the macrobenthic tracemaker community.

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ICHTNOLOGIC SIGNATURES OF DELTAIC TO SHALLOW MARINE GLACIAL ENVIRONMENTS FROM BASAL DEPOSITS OF THE ITARARÉ GROUP, PARANÁ BASIN (BRAZIL)

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The Itararé Group constitutes an important record of the Late Paleozoic Ice Age (LPIA) in southern Gondwana, with deposits associated with diverse depositional settings in shallow to marginal glacial-marine and glacial-lacustrine environments. Most of the trace fossils from the Itararé Group are represented by arthropod trackways and shallow invertebrate burrows preserved in thin-bedded rhythmites formed in continental settings and were interpreted as suites of *Mermia* and *Scoyenia* ichnofacies. In this study, we describe the basal deposits of the Itararé Group in the Tibagi region (Paraná State, S Brazil), aiming to (i) characterize the ichnofabrics preserved in the core well 2-GG-1-PR; and (ii) interpret the paleoecological conditions. Four ichnofabrics have been described: *Diplocraterion*, *Schaubcylindrichnus*, *Phycosiphon*, and *Teichichnus* (Fig. 1). The *Diplocraterion* ichnofabric is monotypic and is characterized by sharp-walled, U-shaped vertical burrows filled out with sandy material (Fig. 1D). It occurs in massive shale deposits and reflects the high cohesion of the substrate at the time of colonization [¹]. The *Schaubcylindrichnus* ichnofabric also occurs in shales but is polytypic, showing *Skolithos*, *Palaeophycus*, *Rhizocorallium*, and *Phycosiphon*, the two latter as subordinate burrows (Fig. 1B-C). The *Phycosiphon* and *Teichichnus* ichnofabrics occur in fine-grained, thin-bedded heterolithic beds. *Asterosoma* and *Palaeophycus* are commonly associated with *Phycosiphon* in the former (Fig. 1E-F) while *Phycosiphon*, *Rhizocorallium*, and *Palaeophycus* occur in the latter (Fig. 1G-I).

The set of ichnofabrics indicates the prevalence of marine conditions and suggest deposition in upper offshore settings, in the context of the *Cruziana* ichnofacies [²]. Short-term freshwater discharges during deglacial cycles might generated hyperpycnal flows that caused salinity fluctuations, reducing ichnodiversity. The low ichnodiversity of the ichnoassemblage registered in the basal portion of the core well 2-GG-1-PR is compatible with those described in marine prodelta settings [³]. However, the dominance of protrusive spreiten in the *Teichichnus* ichnofabric suggests the high sedimentation rates; this condition is consistent with more proximal settings than those represented by the *Phycosiphon* ichnofabric [³], suggesting colonization in a delta front [⁴]. The alternation of low to locally high bioturbation suggests alternations between brackish and fully marine conditions, with higher colonization rates under dominant polyhaline/stenohaline conditions.



Fig. 1. Fossil and trace fossils from studied well-core. A. Internal cast of a *Lingularia imbituensis* preserved in shale facies. B. *Schaubcylindrichnus* in massive mudstone (Sc). C. *Palaeophycus* in bedding plane representing (Pa). D. *Diplocraterion* in firmground (Di). E-F. *Phycosiphon* ichnofabric (Ph), *Asterosoma* (As), and *Palaeophycus* (Pa). G-I. *Teichichnus* ichnofabric represented by *Teichichnus* (Te), *Phycosiphon* (Ph), and *Rhizocorallium* (Rh).

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ICHTNOLOGICAL ANALYSIS OF CONTINENTAL DEPOSITS OF THE TAUBATÉ BASIN

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The Taubaté Basin is a sedimentary basin of Paleogene age that is part of the “Continental Rift of Southeast Brazil” derived from the evolution of the Brazilian continental margin [1]. The sedimentary infill is composed of alluvial fan and braided river deposits (Resende Formation), playa lake deposits (Tremembé Formation), and meandering river deposits (São Paulo Formation), which together represent the Taubaté Group. The reactivation of faults in the Taubaté Basin during the Miocene generate the deposits of the Itaquaquecetuba Formation (alluvial fan facies) and the Pindamonhangaba Formation (meandering fluvial facies). Trace fossils were barely mentioned in the literature in the Taubaté Basin, reported generically as biogenic structures [2]. This study focuses on characterize the biogenic structures of the Taubaté Basin, based on subsurface sampling, and to integrate sedimentological and ichnological data to provide paleoenvironmental interpretations.

The data described in this study came from a 697 m-long drill core, in which 11 lithofacies were recognized. Trace fossils are represented by the ichnogenera *Palaeophycus*, *Planolites*, and *Skolithos*, and body fossils of fish and plant also occur. The sedimentary succession shows intercalation of conglomeratic and sandstone facies with subordinate muddy intervals, representing alluvial fan deposits associated with fault edges and braided fluvial deposits, followed by shales with subordinate sandstone levels, representing lacustrine deposits (Fig. 1). *Palaeophycus* predominates in the sandstone and conglomeratic facies, suggesting colonization by opportunistic organisms, possibly during short colonization windows that allowed deposition of organic matter, in sparse mud facies. Simple horizontal burrows that resemble *Planolites* predominate in the muddy facies. *Skolithos* and *Macanopsis* are recorded mainly in the sandstone facies, and locally in the conglomeratic and muddy facies. The presence of *Skolithos* in these deposits suggests opportunistic colonization during higher energetic events, often associated with the colonization of sand bars.

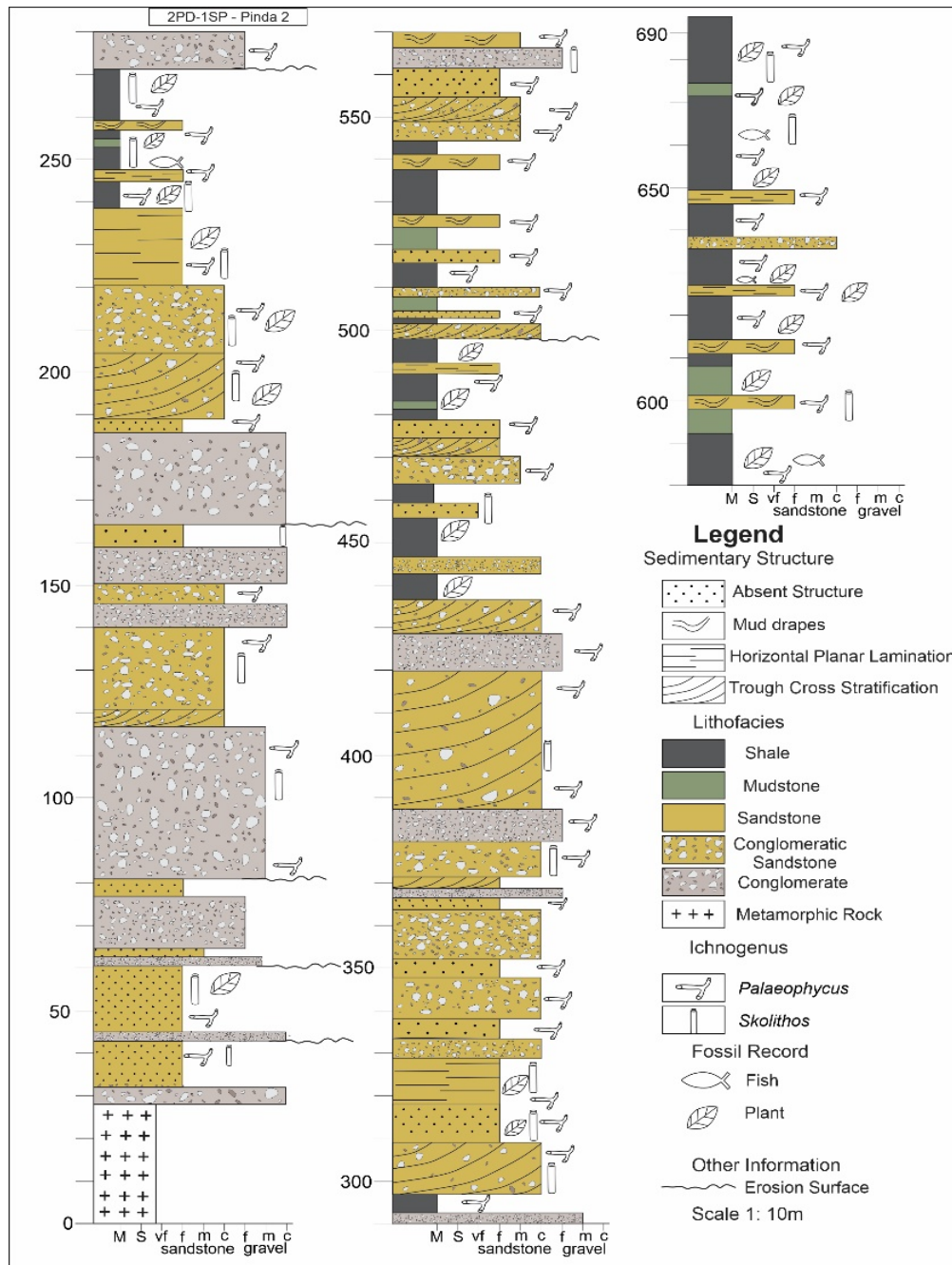


Fig. 1. Sedimentological log showing the trace fossil distribution in the studied well-core 2PD-1SP-Pinda 2.



Fig. 2. Biogenic structures described in well-core 2PD-ISP- Pinda 2. A. *Palaeophycus* in black shale facies (Fl). B. *Palaeophycus* in fine laminated sandstone facies with mud drapes (Hs). C. *Palaeophycus* in massive sandstone facies (Sm). D. *Palaeophycus* in fine sandstone facies with horizontal lamination (Sh). E. *Palaeophycus* in massive conglomeratic sandstone facies (Sg). F. *Palaeophycus* in stratified conglomeratic sandstone (Sgt). G. *Palaeophycus* in stratified matrix-supported conglomerate (Gt). H. *Skolithos* in fine, massive sandstone facies (Sm).

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AN EOCENE STORM- AND RIVER FLOOD-DOMINATED DELTA: ICHOLOGY AND SEDIMENTOLOGICAL SIGNATURES IN CORES, SAN JACINTO FOLD BELT, NW COLOMBIA

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Some Eocene reservoirs in the central part of the San Jacinto Fold Belt (NW Colombia) represent a succession deposited in marine and transitional environments. These deposits consist of sandstone and mudstone intervals that were cored in a stratigraphic well (A-stratigraphic well; 1832-1842 m interval). The resulting facies provide evidence of a deltaic system controlled by fluvial discharge and wave/storm energy. Parameters such as salinity, food supply, turbidity of the water, sedimentation rate, and flow types influenced the behavior of the benthic community, which are well expressed in the ichnological record, and which have affected the characteristics of the reservoir.

For this study, we grouped facies successions into three styles. Facies Style 1 consists of laminated mudstone layers with sandstone lenses, locally with low concentrations of organic matter. Mudstone layers are interbedded with thin, oscillatory rippled sandstone beds exhibiting sporadically distributed laminae of organic matter and soft-sediment deformation features. The grade of bioturbation is low (BI=0-3), with marine trace fossils such as *Nereites*, *Palaeophycus*, *Chondrites*, and *Phycosiphon*, intersected by *Thalassinoides*. This facies suggests the presence of fluvial-supplied mud through hypopycnal plumes or hyperpycnal flows. The thin sandstone layers correspond to short-lived storm events. These characteristics are interpreted to be indicative of a prodeltaic environment.

Facies Style 2 corresponds to laminated sandstone exhibiting cross-stratification, oscillatory lamination, parallel lamination, and hummocky cross-stratification, with concentrations of phytodetritus, and locally mud drapes on storm-generated beds. The grade of bioturbation is low (BI=0-2), with trace fossils such as *Thalassinoides* and *Ophiomorpha*, with some intervals displaying escape traces. The concentration of organic matter suggests phytodetrital pulses associated with fluvial discharge. During times of low river discharge, wave/storm reworking impacted bedforms, internal lamination, and the resulting trace fossil suites. These characteristics provide evidence of wave/storm action in a delta-front environment.

Facies Style 3 consists of unburrowed sandstone and mud-intraclast-rich conglomerate beds, displaying evidence of planar lamination, soft-sediment deformation, and subaqueous sediment gravity flows. These characteristics are associated with a significant influx of river sediment near the mouths of distributary channels.

Variations in the sedimentology and ichnology of the facies are crucial for understanding the behavior of benthic organisms in response to river sediment influx and wave/storm action across the deltaic system. Colonization by tracemakers producing *Thalassinoides* and *Ophiomorpha* was associated with low sedimentation rates in the delta-front, whereas in the prodeltaic systems, the presence of *Thalassinoides* was controlled by the rapid deposition of mud and elevated water turbidity. The ichnological characteristics of the reservoir improves the delimitation of porosity/permeability zones, which could be related to suites of deposit-feeding and/or dwelling structures and provide an additional perspective on hydrocarbon exploration in the area.

TRACKING PERMIAN VERTEBRATES THROUGH COPROLITES (RIO DO RASTO FORMATION, PARANÁ BASIN, BRAZIL)

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Coprolites are fossilized feces and represent one of the most informative sources about interactions between individuals in the fossil record [1]. The Rio do Rasto Formation is characterized by fluvial and lacustrine sedimentation deposited in the Paraná Basin during the Permian (Guadalupian–Lopingian) [2]. However, studies reporting coprolites from the Rio do Rasto Formation are mostly from the outcrop known as Coproland, in São Gabriel (Rio Grande do Sul), where more than 1,000 specimens were collected from the same mudstone layer [3]. Here we report the occurrence of 88 coprolites collected in 11 other outcrops from the Rio do Rasto Formation, in Rio Grande do Sul and Paraná states, southern Brazil (Fig. 1).

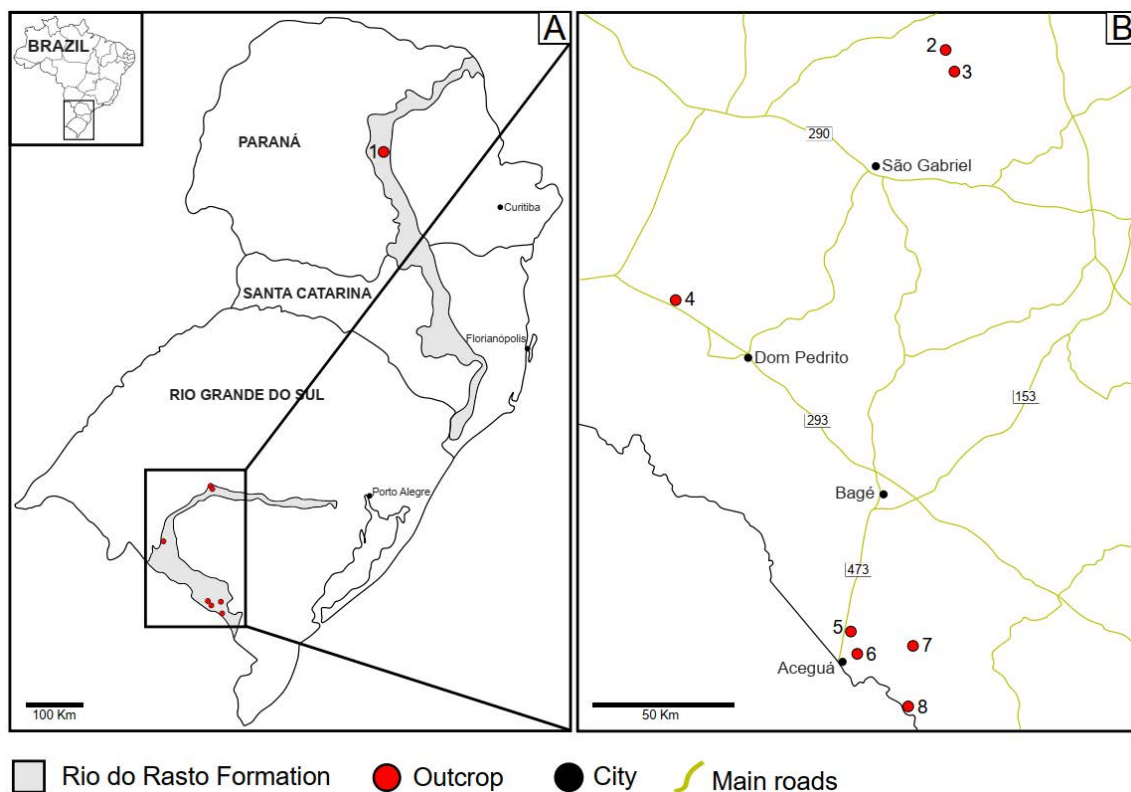


Fig. 1. Map indicating the outcrops where the coprolites were collected. A. Simplified map of the Rio do Rasto Formation, in the states of Paraná, Santa Catarina and Rio Grande do Sul, red dots indicate the outcrops in Paraná and Rio Grande do Sul. 1- Cândido de Abreu Outcrop. B. Detailed map indicating outcrops in the state of Rio Grande do Sul; 2- São José Farm; 3- Boqueirão Farm; 4- Nossa Senhora do Horto Farm; 5- Minuano Farm; 6- Santo Antônio Farm; 7- Invernada; 8- Nossa Senhora de Lourdes Farm.

The coprolites were classified by their morphotypes (heteropolar, amphipolar and non-spiral) and measurements were taken using a vernier caliper. Surface features and adhesion structures were observed using a stereomicroscope and petrographic thin sections were produced

to analyze the inclusions. The central portion of six coprolites were exposed and mounted on Al stubs, coated with Au and subjected to analysis under a JEOL JSN-6610LV Scanning Electron Microscope (SEM). In order to identify the chemical and mineralogical composition of the coprolites, Energy-dispersive X-ray spectroscopy (EDS) and X-ray powder diffraction analysis were conducted. Most of the coprolites present spiral morphologies: 11% are amphipolar, 23% are heteropolar and 26% are indeterminate spiral (despite being spiral it was not possible to classify them as amphipolar or heteropolar due to the fragmentation and/or the presence of concretions). The other 40% of the coprolites did not show evidence of spirals, being classified as non-spiral (Fig. 2).

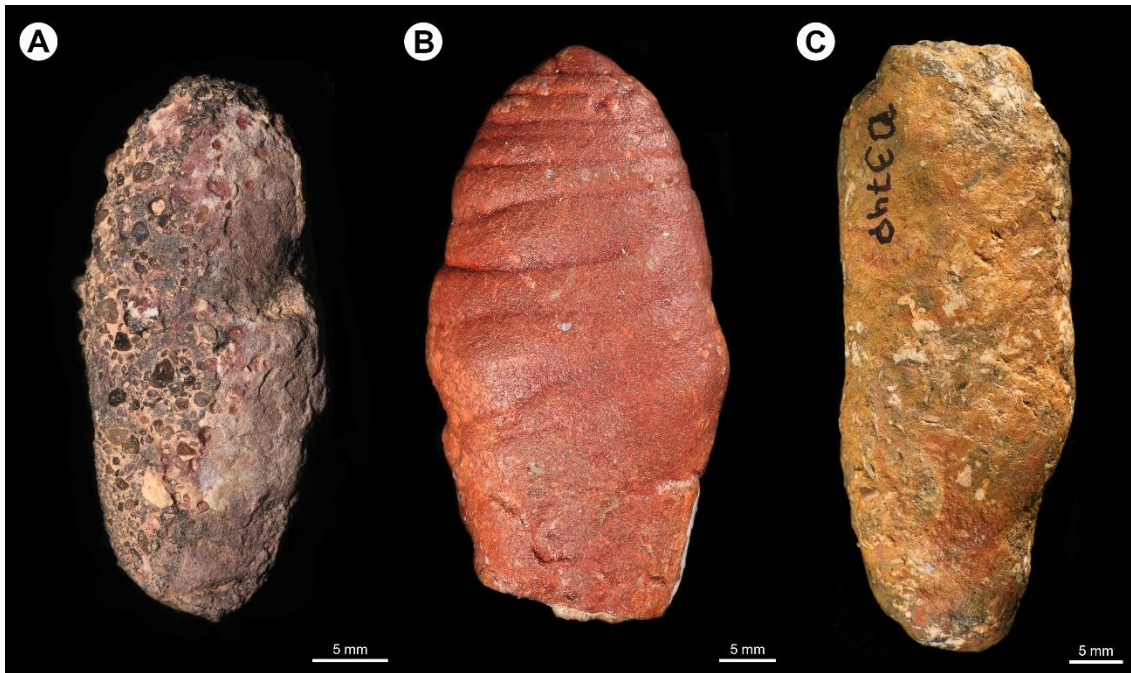


Fig. 2. Morphotypes identified. A. Amphipolar (UFRGS-PV-0371-P, Santo Antônio Farm). B. Heteropolar (UFRGS-PV-0535-P, Santo Antônio Farm). C. Non-spiral cylindrical (UFRGS-0374-P, Santo Antônio Farm).

Spiral feces are produced by animals that have spiral valves in the intestine, typical of non-tetrapod and non-teleost vertebrates, and present mainly in elasmobranchs and primitive bony fishes [3]. Therefore, the spiral coprolites here described were produced by fishes, probably sharks and lungfishes, and the non-spiral coprolites were probably produced by temnospondyl amphibians, very common in the Rio do Rasto Formation. Due to natural fragmentation of some coprolites, it was possible to analyze the inclusions in the interior and in the surface of the coprolites. Palaeonisciform fish scales (up to 314 in a single coprolite; Fig. 3A-B) were identified in most of the coprolites of all the morphotypes. Other inclusions as bone fragments, teeth, fish palatal bones and plant impressions were also found (Fig. 3C). The abundance of scales suggests a piscivorous diet for the producers of the coprolites. The plant impressions found in one of the non-spiral coprolites suggests an herbivorous or omnivorous diet.

The coprolites described represent an important source of information about the diversity of vertebrates in the Rio do Rasto Formation. The results are still preliminary, and more studies will be carried out to expand the knowledge regarding the paleoecological relationships during the Permian.

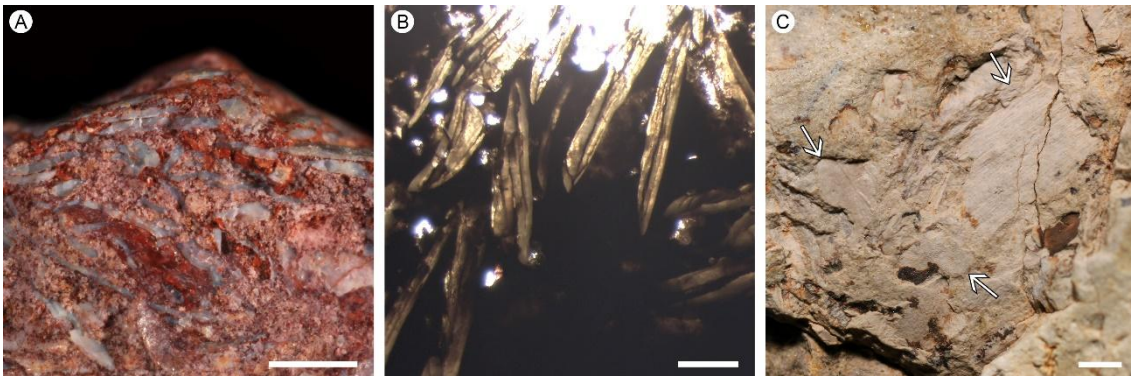


Fig. 3. Different identified inclusions. A. Fish scales (UFRGS-PV-0741c-P, Santo Antônio Farm). B. Thin section of a coprolite with scales (LGP-CSC-1363, Cândido de Abreu Outcrop). C. Plant impressions (UFRGS-0365b-P, Minuano Farm). Scale bars: A, C = 1 mm; B = 0.5 mm.

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ICHTNOLOGICAL ANALYSIS AS INDICATORS OF PHYSICO-CHEMICAL STRESSES IN WAVE TO TIDE-DOMINATED MIOCENE SHALLOW MARINE ENVIRONMENTS (ARGENTINE PATAGONIA)

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Ichnological features have emerged as invaluable tools for discerning diverse marine, marginal-marine, and river-influenced environments, as the ichnoassemblages characterizing their deposits can be frequently related to particular stress factors and their interactions. In this context, the Puerto Madryn Formation (Late Miocene–Pliocene) in NE Chubut (Argentine Patagonia) has undergone detailed integrative ichnological, including ichnofacies characterization, and sedimentological research, focusing on stacking patterns, bodies geometries and recurrent physical sedimentary structures, to interpret environmental (depositional and ecological) parameters affecting shallow marine systems. Particularly, a wave-dominated system underlying a tide-dominated system has been identified.

The wave-dominated system is characterized by tabular bodies that extend laterally for tens of kilometers, displaying fining- and coarsening-upward successions from mid- to lower shoreface to offshore-shelf environments. The ichnological assemblage allows for the characterization of the *Cruziana* ichnofacies, showcasing proximal, archetypal, and distal expressions. Internal variations within this ichnofacies are differentiated based on changes in oxygenation, nutrient levels, and sedimentation rates. In contrast, the tide-dominated system is distinguished by wide channel-shaped bodies filled with sandy to heterolithic facies, interpreted as deposits within the outer, middle, and inner/middle estuarine system. The ichnological assemblage in this setting can be assigned to both *Skolithos* and *Cruziana* ichnofacies. However, the application of ichnofacies in tidal systems is scrutinized due to the diverse scenarios arising from significant variations in energy and salinity conditions, water turbidity, and substrate consistency.

The integration of sedimentological and ichnological data facilitates the interpretation of complex and dynamic physico-chemical stresses, encompassing changing factors such as sedimentation rates, oxygen conditions, salinity, and nutrient availability. These stressors impact the diverse subenvironments within both wave- and tide-dominated systems in a variable way, influencing tracemaker communities. Notably, internal variations within specific subenvironments (such as the outer and middle estuary), may give rise to distinct ichnological features in response to temporal and spatial fluctuations in physico-chemical environmental conditions.



A PRELIMINARY ANALYSIS OF ENVIRONMENTAL AND ECOLOGICAL PREDICTORS OF FERN–ARTHROPOD INTERACTIONS IN THE SOUTHEASTERN ATLANTIC RAINFOREST, SOUTHERN BRAZIL

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Ferns are widely distributed in modern ecosystems and are an important resource for herbivorous insects. Insects present a major role in interacting with ferns, which leads to a richness of feeding guilds at levels comparable to those found in angiosperms [1]. Insect feeding guilds, such as external chewers and galls, are distributed heterogeneously on their host plants when considering environmental conditions and phylogeny [2]. For example, galling insects are more abundant in xeric than mesic conditions [3]. Concerning modern habitats, insects are more abundant in warm temperatures [4]. In the fossil record, damage type (DT) metrics such as the DT richness have shown a positive relationship with temperature [5,6] as well. In this work, preliminary results of modeling fern–arthropod interaction through environmental and ecological predictors are shown. The modern data are sampled from an elevational spectrum of localities in the southeastern Atlantic Rainforest, southern Brazil [7–9], where the environmental effects on the distribution of insect-induced DTs are analyzed.

Through a space- and time-controlled sampling, fern–arthropod interactions were surveyed in transects across elevations from 750 to 950 m in the upland locality [9] and, subsequently, at elevations from 13 to 14 m in the lowland locality [8], and an elevation of 632 m in the midland locality [7]. The ferns presented 43 DT analogs distributed across 24 fern species. Fern–arthropod interactions presented 21 DTs in the lowland locality [8], 19 DTs in the midland locality [7], and 17 DTs in the upland locality [9].

Generalized linear mixed models (GLMM) were used for modeling the environmental predictors of the fern–arthropod interaction in modern localities. Metrics such as the DT richness by fern species (presented in this work), DT frequencies (occurrence of DTs by fern species/total leaves sampled), and additional DT metrics (external feeding DTs, mining DTs, and galling DTs, all on fern species were tested as response variables. The models used the mean annual temperature (MAT) and mean annual precipitation (MAP) from the last 20 years as fixed effects, and the mean maximum leaf size (MLF) of ferns was used as an ecological fixed effect in the models. In addition, the localities [7–9] were added as a random effect in each model. All models were performed in R [10] and computed in the R Studio environment [11]. The packages used are in the published GLMM workflow [12], which presented a complete pre- and post-statistical assumption check for linear models. Response variables presented a different distribution of families and are used according to fitting statistical assumptions in the test models.

The models' estimation showed that DT richness by fern species presents a low positive relation with MAT and an even lower positive relation with MLF. MAP presented a low negative relation with DT richness, although this effect was higher than that of MLF (Fig. 1). Therefore, MAT presented a relatively low but positive effect on DT richness in the estimated statistically fitted models. MLF presented a lower positive relation with MAT than with DT richness, and a similarly low negative relationship with MAP.

Sampling fossil plant–insect interactions and the significance of DT metrics for ecological inferences have been discussed under different topics in the fossil record [13–16]. In all models tested, each fixed effect presented $P > 0.05$ (Table 1). There is a debate about whether P -values should be treated as a representation of statistical trust, and care for repeatability was suggested to be of more concern than distrust due to P -values [17]. Conversely, the high P -values

are likely caused by the small number of sampled leaves from each fern species. DT richness is a robust metric that encompasses all plants by locality and is traditionally treated as a metric that does not distinguish plant morphotypes in rarefaction tests [14]. Therefore, DT richness likely represents a practical way to assess a subset of the functional richness of herbivorous insects in the localities with a sufficient sample size [8,9]. This work shows a novel reproducible method in time and space, through an example of modern data for ecological inferences based on fossil plant-insect interaction metrics.

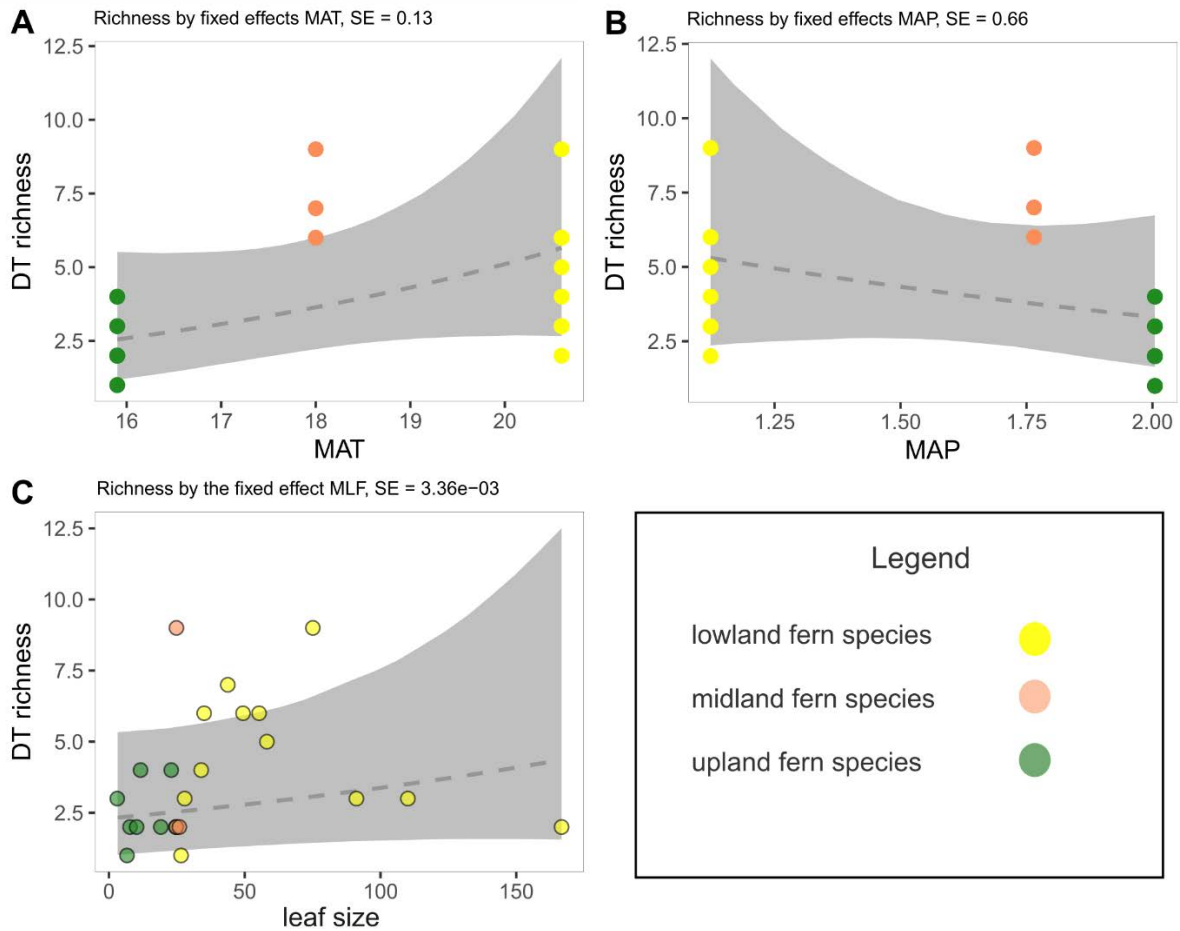


Fig. 1. DT richness by fern species counts as a function of mean annual temperature (MAT). A. Mean annual precipitation (MAP). B. Mean leaf size (MLF). C. Each point represents the number of DTs found by fern species plotted in different colors representing the localities. Mean model predictions (filled shades) and their 95% compatibility intervals (dashed lines) were derived from 2001 simulations of the posterior distribution of model parameters.



Table 1. Estimated relationships of mean annual temperature (MAT), mean annual precipitation (MAP), and mean leaf size (MLF) with DT richness on 14 fern species in elevations from 13 to 950 meters in the southern Atlantic Rainforest of Brazil.

Model = response variable ~ fixed effects	Distribution family	Coefficient	SE	z value	P-value
(1) DT richness ~	Hurdled Poisson	-1.86	2.32	-0.8	0.423
(1) MLF +		3.83E-03	3.32E-03	1.14	0.254
(1) MAT		0.17	0.13	1.35	0.177
(2) DT richness ~	Composite Poisson	2.18	1.11	1.97	0.049
(2) MLF +		3.17E-03	2.30E-03	1.38	0.168
(2) MAP		-0.53	0.66	-0.8	0.422

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INTEGRATION OF ICHNOLOGICAL AND PEDOLOGICAL INVESTIGATIONS REVEALS PREVALENCE OF SPECIFIC HYDROLOGIC REGIME AND ECOSYSTEM DURING THE EARLY PROGRESSIVELY WARMING AQUITANIAN CLIMATE IN THE KUTCH BASIN, GUJARAT, INDIA

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Recent study documents palaeosol facies in the Aquitanian Khari Nadi Formation (KNF) of the Kutch Basin [1]. Palaeosols identified within stratigraphy of KNF serve substantial evidences for subaerial exposure and stability of surface for considerable duration, thereby, raising doubt on the earlier hypothesis suggesting a steady deepening of the Kutch basin throughout the early Miocene interval. Integration of paleopedology and ichnoentomology is almost overwhelmingly lacking in the Indian stratigraphy. This emphasizes the need for such combined studies in formations like KNF, wherein conspicuously preserved termite nests and rhizoliths have been found. Therefore, the present work is focused on detailed identification of various termitic trace fossils and rhizolith patterns so as to have greater understanding of the nature and degree of pedogenesis and environmental set-up. Additionally, paleoclimate interpretations based on changes in continental trace-fossil suites and pedogenesis have been documented. The most prevalent burrow systems are *Termitichnus* and *Vondrichnus*, which can be distinguished by the presence or absence of variation in burrow diameter of the galleries [2] (Fig. 1A-B). *Termitichnus* ichnogenus here is represented by two ichnospecies: *T. simplicidens*, which lacks a discrete wall surrounding the chamber and is composed of simple burrows, and *T. qatranii*, which has a discrete wall around the chamber and consists of compound burrows (assembly of multiple simple burrows) located in peripheral boxwork. Apposition of chambers are common in both the isopteran ichnogenes (Fig. 1B, blue arrow). Herein, the most diagnostic is the distinct preservation of termite nests along-with rhizoliths; rather the former is accompanied with specific rhizolith patterns demonstrating a close relationship existing in a wetland ecosystem with high biodiversity comparable to mangrove ecosystem. The pedofeatures, in particular the rhizoliths, indicate changes in patterns of nestedness of faunal communities with fluctuating soil moisture. In general, rhizoliths are preserved in light brown-yellow to grey-colored pedocomplex, wherein each depletion zone is followed by a conspicuous purple-rust-colored zone due to the extensively coalesced purple-colored mottles. In this purple zone, grey rhizohalos show yellow-brown rims. Carbonaceous segregations and no calcareous segregation have been observed. The grey depletion zones abundantly contain the yellow-brown to red rhizotubules/accumulations with sand-filled rhizoliths. Throughout the pedocomplex, the yellow-brown- to red-coloured accumulations vary from masses to rhizocretions; the masses show extensive branching at finer scale towards the top of the profile. All this indicate prevalence of an imperfectly drained conditions under a specific ecosystem but also with an improving drainage condition with time due to fluctuation in soil moisture regime. The isopteran fecal pellets are preserved throughout as the spherical micropeds. The “partial Bioturbation Index” specific to the continental trace fossils (i.e., excluding the marine suites) increases up from 0 at the base of the formation to a laterally-variegated 2-5 in the lower-middle part. Likewise, a low yet marginally increasing-up isopteran and root ichnodiversity has been observed. Though the nature and degree of pedogenesis varies in the studied KNF section, the whole sequence uniformly preserves different stages of pedofeatures related to faunal activities, e.g., the termite nests with rhizolith patterns and presence of hydromorphic pedofeatures. The multiproxy dataset from the integration of pedological and

ichnological investigations clearly indicate pedoplasation of loose sediments due to extensive and exclusive pedoturbation under specific hydrologic regime favoured by the progressively warming Aquitanian paleoclimate.

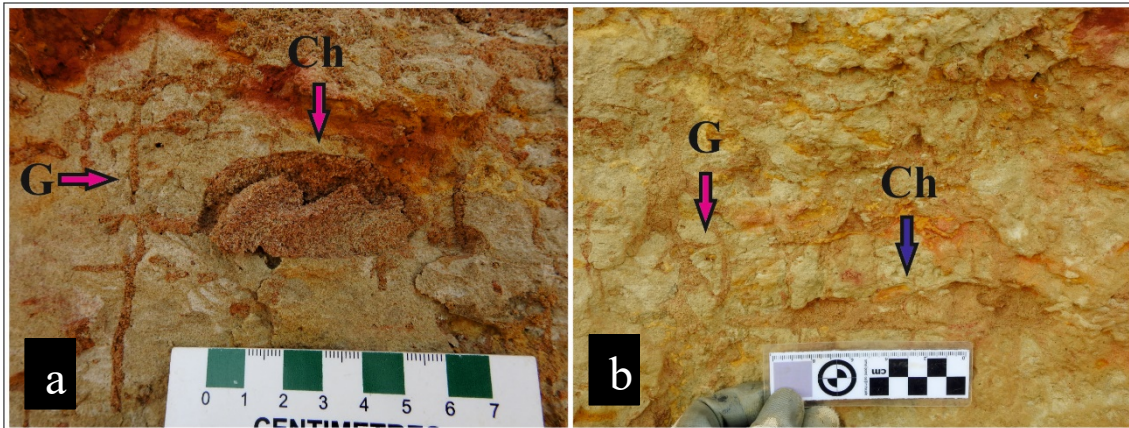


Fig. 1. Difference between two ichnogenera, viz., *Vondrichnus* isp. and *Termitichnus* isp., produced by termites. A. *Vondrichnus* isp. composed of chambers interconnected by galleries of similar diameter. B. Diameter of *Termitichnus* isp. gallery varying along the burrow length. Abbreviations: G = gallery; Ch = chamber. Blue arrow has been showed to mark the apposition of the chambers.

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COPROLITE RESEARCH: THE REWARDS AND CHALLENGES OF UNLOCKING INFORMATION HIDDEN WITHIN LITHIFIED FECES

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Coprolite research is burgeoning. Paleontologists are finding new coprolite assemblages all over the world and are examining specimens with different types of analytical and imaging technologies. Nevertheless, coprolites are still challenging to study. One of their most confounding features is that they can be highly variable in both morphology and composition. Fecal shapes have limited diagnostic value, so it is difficult to correlate coprolites with particular animals – or to determine whether specimens with different shapes were produced by one species or multiple animal taxa. Equally problematic is that dietary residues within coprolites may have been significantly altered by digestion and/or diagenesis. Despite these difficulties, well-preserved coprolites often retain recognizable biotic inclusions and may even include fossilized soft tissues. Furthermore, coprolites that lack identifiable contents still provide evidence of feeding activity and resource availability. Although coprolite evidence must be interpreted carefully, these fossils often reveal intriguing paleoecological information that is rarely available in body fossils. As such, most paleontologists are now aware that fossilized feces provide insights on ancient feeding behaviors, parasites, nutrient recycling, and other aspects of paleobiology.

On the other hand, the potential of coprolites to contribute unique temporal perspectives on ancient ecosystems is less appreciated. Coprolites essentially preserve dietary microcosms that represent short timescales – even though they are nested within the immensity of deep time. Such fossil snapshots are possible because mineralized coprolites contain biotic materials that were collected and ingested within a constrained period of time. After deposition, relatively rapid lithification helped prevent mixing of the fecal contents with younger or older materials. Because of their unusual taphonomic history, coprolites represent a form of ecosystem sampling on timescales of hours to days. At a minimum, the virtual absence of time-averaging verifies that organisms found within a coprolite truly coexisted in time and space. This is noteworthy because the contemporaneity of organisms within a sedimentary unit is often presumed without evidence – even though the sediments may represent a considerable time span.

Coprolites offer even more insightful information about short timescales when we can ascertain the season in which ancient feces were deposited. Animal diets reflect food availability and food choices; in most cases, food availability is ultimately controlled by the effects of phenological patterns on primary production (which fuels all secondary consumers). In turn, food availability helps guide animal movements across landscapes and determines when animals can reproduce. Because of these complex interactions, coprolite contents can shed light on temporal patterns in both environmental conditions and in the seasonal behavior of ancient animals. A coprolite assemblage from the Canadian High Arctic demonstrates the utility of fossil feces in analyzing seasonality in an ancient ecosystem. These diatom-packed marine coprolites were collected from a site that was located above the Arctic Circle in the Late Cretaceous. Because of limited winter light, Cretaceous phytoplankton would have been most abundant during seasons with ample daylight and substantial nutrient availability. Thus, the coprolite contents reveal how marine vertebrates exploited ancient seasonal plankton blooms. Moreover, organic geochemical analyses of biomarker proxies within these coprolites provide approximations of Late Cretaceous warm month temperatures rather than time-averaged estimates of mean annual temperatures.

Well-preserved coprolites offer a surprising repertoire of insights on different aspects of paleobiology. Although many analyses of fossil feces focus on evidence of trophic interactions, coprolites can also provide novel perspectives on our understanding of temporal patterns in ancient ecosystems. This is an unexpected and underappreciated aspect of the informative value of coprolites.



ON THE SYNONYMIIZATION OF *PALEOHELICURA TRIDACTYLA* WITH *STIARIA INTERMEDIA*: REANALYSIS OF ICHNOTAXOBASES

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Stiaria Smith, 1909 [¹] (typified by *Stiaria quadripedia* Smith, 1909) and *Paleohelcura* Gilmore, 1926 [²] (typified by *Paleohelcura tridactyla* Gilmore, 1926) are fossil trackways consisting of generally alternating series of three or four imprints and a narrow medial impression. The distinction of these ichnotaxa is problematic, requiring reexamination of the holotypes [^{3,4}]. *Stiaria intermedia* (Smith, 1909) has up to three imprints per series and a medial impression, while *Stiaria quadripedia* Smith, 1909 has up to four imprints per series and a medial impression [⁵]. *Paleohelcura tridactyla* Gilmore, 1926 has up to three imprints per series and sometimes a medial impression. The misinterpretation by Brady [⁶] of a small background depression as a fourth imprint in one *Paleohelcura* trackway has created ichnotaxonomical confusion, including some trackways with four-imprint series being mislabeled *Paleohelcura* when they should have been attributed to *Octopodichnus* Gilmore, 1927 [⁷] or *Stiaria quadripedia*. Since *Paleohelcura* properly has a maximum of three imprints per series, the existing question is whether *Paleohelcura tridactyla* should be regarded as a junior synonym of *Stiaria intermedia*. Conventionally, these two ichnotaxa have been considered distinct on the basis of external trackway width, series symmetry, and the presence of a medial impression. We have analyzed the type material and data for all the *Paleohelcura*-like and *S. intermedia*-like trackways in the available English published literature. We reviewed all the ichnotaxobases that could potentially serve to distinguish these two ichnotaxa, including external trackway width, the number of imprints per series, imprint morphology, medial impression, series morphology and symmetry, yet found no suitable parameters that could reliably distinguish them. An analysis of external trackway widths reveals the 20 mm external trackway width working rule-of-thumb should not be used, as it arbitrarily divides morphologically similar trackways constituting a continuous size range. Although such an ichnotaxonomic distinction may seem appealing for the interpretation of the producer and paleoenvironmental reasons, neither interpreted producer nor paleoenvironment are suitable ichnotaxobases [⁸]. We thus propose *P. tridactyla* be made a junior synonym of *S. intermedia*.

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IS A NEOTYPE NEEDED FOR *DIPLOPODICHNUS BIFORMIS* BRADY, 1947?

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Reexamination of the type material for *Diplopodichnus biformis* Brady, 1947 reveals that the type morphology is inconsistent with current usage. The type material comes from the Coconino Sandstone (Permian) in Arizona, USA. Located in the Museum of Northern Arizona (MNA; Flagstaff, AZ, USA), the “holotype” slab (MNA N3657) designated by Brady [¹] contains ternary and binary trails, and *D. biformis* was originally dimorphic. We concur with Keighley and Pickerill [²] in constraining the diagnosis of *Diplopodichnus* to two-grooved (not bilobed, trilobed, or tri-grooved) furrows. According to the golden wedge given by Keighley and Pickerill [²], a binary trail is assigned to *Diplopodichnus* if (i) the median ridge is at least the height of the surrounding sediment, and if (ii) the median ridge (central area) is at least as wide as the furrow width, otherwise the assignment falls to *Didymaulichnus* instead. While this distinction works well when the width of the median ridge is consistently wider or narrower than the furrow width, the ichnotaxonomy becomes less clear when the median ridge width is approximately the same as the furrow width and irregularly alternates between *Diplopodichnus* and *Didymaulichnus* morphologies, requiring the use of the compound ichnotaxon *Diplopodichnus* X *Didymaulichnus*. For more accurate taxonomic assignment, we implemented a “whole-trail” analytical approach. We created a 3D model of the “holotype” slab MNA N3657 (and other slabs containing binary trails in the Coconino Sandstone), and overlaid a false color relief filter to enhance the topology. We made digital measurements using FIJI (FIJI Is Just ImageJ) of the medial (i.e., central) ridge width (MRW) and area (MRA), as well as the mean groove width (MGW) and area (MGA). Widths were calculated based on the average taken of many linear measurements taken (in ~5 mm increments) along the length of the trail, while area was obtained as a second opinion by having ImageJ calculate the area of polygons drawn over the trail segments from the edges on either side of the ridge/groove at the surface level plane. For a third opinion, we visually identified and determined the percentage (%) of each trail corresponding with *Diplopodichnus* and *Didymaulichnus* morphologies (*Diplopodichnus* assigned if $MRW \geq MGW$). Each binary trail was then classified according to the criteria in Table 1. Close inspection and analysis of binary trails on MNA N3657 regrettably found the morphology of the trails, including the lectotype trail for *Diplopodichnus biformis* designated by Keighley and Pickerill [²] to fail the whole-trail criteria (Table 1) for assignment to *Diplopodichnus biformis*. The trails are either (mostly) *Didymaulichnus lyelli* or the compound trace fossil *Diplopodichnus biformis* X *Didymaulichnus lyelli*. In other words, the holotype and lectotype for *Diplopodichnus biformis* is invalid. There are two paths forward: (i) invalidate *Diplopodichnus biformis*, or (ii) propose a neotype. Option 1 would render all trails previously named *Diplopodichnus* nameless, requiring the assignment of a new name or expansion of an existing ichnotaxon. Considering that *Diplopodichnus biformis* is a well-known, widely used ichnotaxon since the turn of the century, invalidating *D. biformis* would create confusion and seriously destabilize the nomenclature of invertebrate fossil trails. Option 2 would require choosing a trail to propose as a neotype, and, according to articles 75 and 81 of the International Code of Zoological Nomenclature [³], submitting a case to the International Commission on Zoological Nomenclature requesting an exceptional new type fixation be made. Generally, neotype candidates should preferentially be selected from the type material (Coconino Sandstone); however, a thorough search of the relevant collections at the Museum of Northern Arizona and the Raymond M. Alf Museum of Paleontology (RAM; Claremont, CA, USA) for binary trails matching the morphology of *Diplopodichnus* in current usage, revealed no suitable fossil trails except perhaps for a couple very short trails on RAM 367. Barring any better specimens unknown to us, these two trails on RAM 367 seem to us to be the best candidates for



a *Diplopodichnus* neotype that the Coconino Sandstone has to offer. However, the short length and morphological/preservational variation of these RAM 367 trails does not make them ideal neotype candidates. This poster offers an opportunity for the ichnological community to see the evidence, discuss, and hopefully decide on the best path forward.

Table 1. Classification criteria for binary trails used in this study.

MRW / MGW	MRA / MGA	% <i>Diplopodichnus</i>	% <i>Didymaulichnus</i>	Classification
≥ 1	≥ 1	≥ 75%	≤ 25%	<i>Diplopodichnus biformis</i>
Any	Any	25% < x < 75%	25% < x < 75%	<i>Diplopodichnus X</i> <i>Didymaulichnus</i>
< 1	< 1	≤ 25%	≥ 75%	<i>Didymaulichnus lyelli</i>

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TRACKWAYS OF SCORPIONS, TARANTULAS, AND CRAYFISH PRODUCED EXPERIMENTALLY IN SUBAERIAL AND SUBAQUEOUS CONDITIONS COMPARED WITH *PALEOHELCURA* AND *OCTOPODICHNUS*

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There is a need for more comprehensive experimentation with invertebrates using quantitative analytical approaches to determine the effect of substrate conditions on surface trace morphology and evaluate the probability of certain invertebrates as fossil trackway producers. Sediments characterized by high pore-water contents and subaqueous substrates are rarely tested when experimenting with terrestrial producers, yet these overlooked conditions may limit the usefulness of neoichnological experiments for predicting the substrate water content conditions at the time of fossil trackway emplacement.

For the present study, we performed neoichnological experimentation on fine to very fine sand with six giant desert hairy scorpions (*Hadrurus arizonensis*), two Chilean rose tarantulas (*Grammostola rosea*), and four red swamp crayfish (*Procambarus clarkii*). The invertebrates performed a total of 473 runs (489 trackway segments analyzed) on dry, damp (~ 2-5% H₂O by weight), wet drying (~ 21-23% H₂O by weight), wet saturated, and subaqueous sand at horizontal (0°), shallow (~15°), and steep (~25°) slope angles, as each species was able (tarantulas floated when placed in water deeper than they could stand in). Photographs of the traces were used to make digital measurements in FIJI (an open-source image processing package based on ImageJ2). The trace morphometrics were recorded in spreadsheets. Trackways were quantitatively analyzed by examining single variable trends (for binary variables the presence and absence of trackway characteristics, and for ratio variables the maximum, median, and minimum values) across the five experimental sand water content conditions as well as the type material for the fossil trackways *Paleohelcura* Gilmore, 1926 [¹] and *Octopodichnus* Gilmore, 1927 [²] from the Coconino Sandstone and De Chelly Sandstone (lower Permian of northern Arizona, USA) [³] (e.g., Figure 1). To visualize the amount of overlap among the experimental water content conditions for each invertebrate species and relevant ichnotaxa in a multivariate context, we created nonmetric multidimensional scaling visualizations (N-MDS) using PAST3 (Paleontological Statistics software version 3) with a Gower dissimilarity matrix, allowing us to compare morphometric trends of many variables in a 2D coordinate plane. Trackways made in loose sand conditions (dry, wet saturated, and subaqueous sand) were easily distinguished from those made in stiffer wet drying and damp sand conditions. In loose sand, imprints were broad and deep, whereas imprints made in stiff sand were smaller, shallower, and sharply defined. On wet drying slopes, a stiffness gradient formed from saturated sand at the bottom of the slope to stiff, drying sand at the top: this produced a corresponding morphological gradient. Additionally, nonmetric multidimensional scaling visualizations show that trackway morphology can appear very similar in dry, wet saturated, and subaqueous conditions (the exception is that semi-swimming traces and current effects, when present, can make it easy to tell traces were produced underwater). Thus, care should be taken when using fossil trackway morphology in paleoenvironmental assessments of pore-water content. That said, detailed analysis of multiple trackways in each loose sand category revealed some differences. For example, there were relatively more multifid imprints in subaqueous sand than in dry or wet saturated sand. For crayfish, the width of internal marks produced (when present) were usually narrower underwater.

In addition to analysis of sand water content conditions, other findings cast doubt on the ability of these invertebrates to be the actual producers of *Paleohelcura* (which normally has three-imprint series) and *Octopodichnus* (which normally has four-imprint series) (Fig. 1). First, the tarantulas always made five-imprint series on dry sand (using their pedipalps in addition to



their legs) (Fig. 2A), while only sometimes setting down their pedipalps while walking in the other conditions. Second, the scorpions generally produced more four-imprint series than three-imprint series (Fig. 2B), with only 9/274 (3.3%) of analyzed trackway segments composed of only three-imprint series. Third, neither the scorpions or tarantulas produced bifid or trifid imprints (Fig. 2C) that were (relatively) as large as those found in *Octopodichnus*. Fourth, crayfish made wide tail-fan drag marks especially in wet saturated and dry sand conditions that tended to cover up more proximal imprints (Fig. 2D). These results suggest a need to explore other producer possibilities for *Paleohelcura* and *Octopodichnus* ichnites.

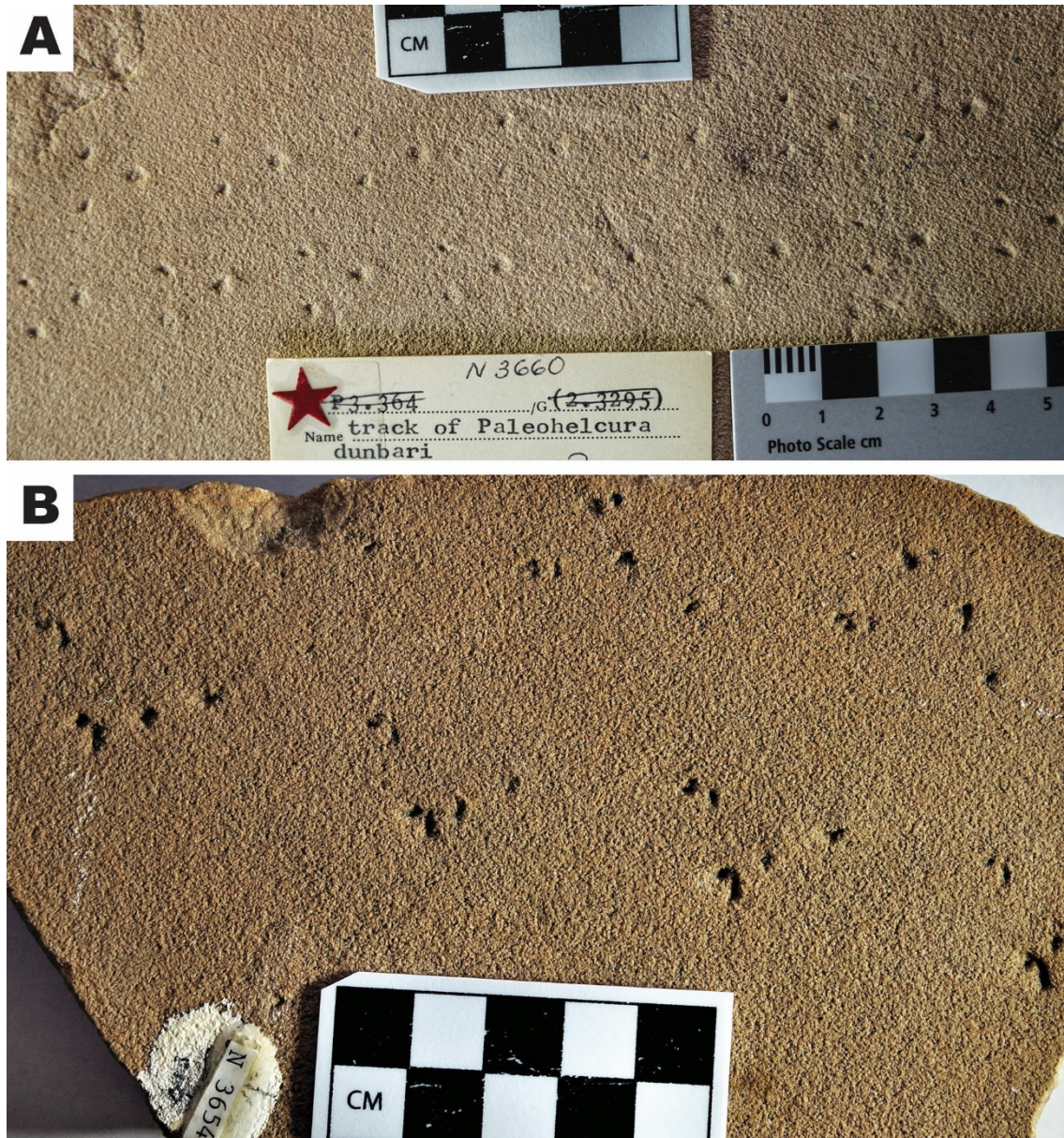


Fig. 1. Fossil trackways from the Coconino Sandstone (Permian, AZ, USA) from the Museum of Northern Arizona (MNA; Flagstaff, AZ, USA). A. MNA N3660, *Paleohelcura tridactyla* (=dunbari) Gilmore, 1926. B. MNA N3654, *Octopodichnus minor* Brady, 1947.

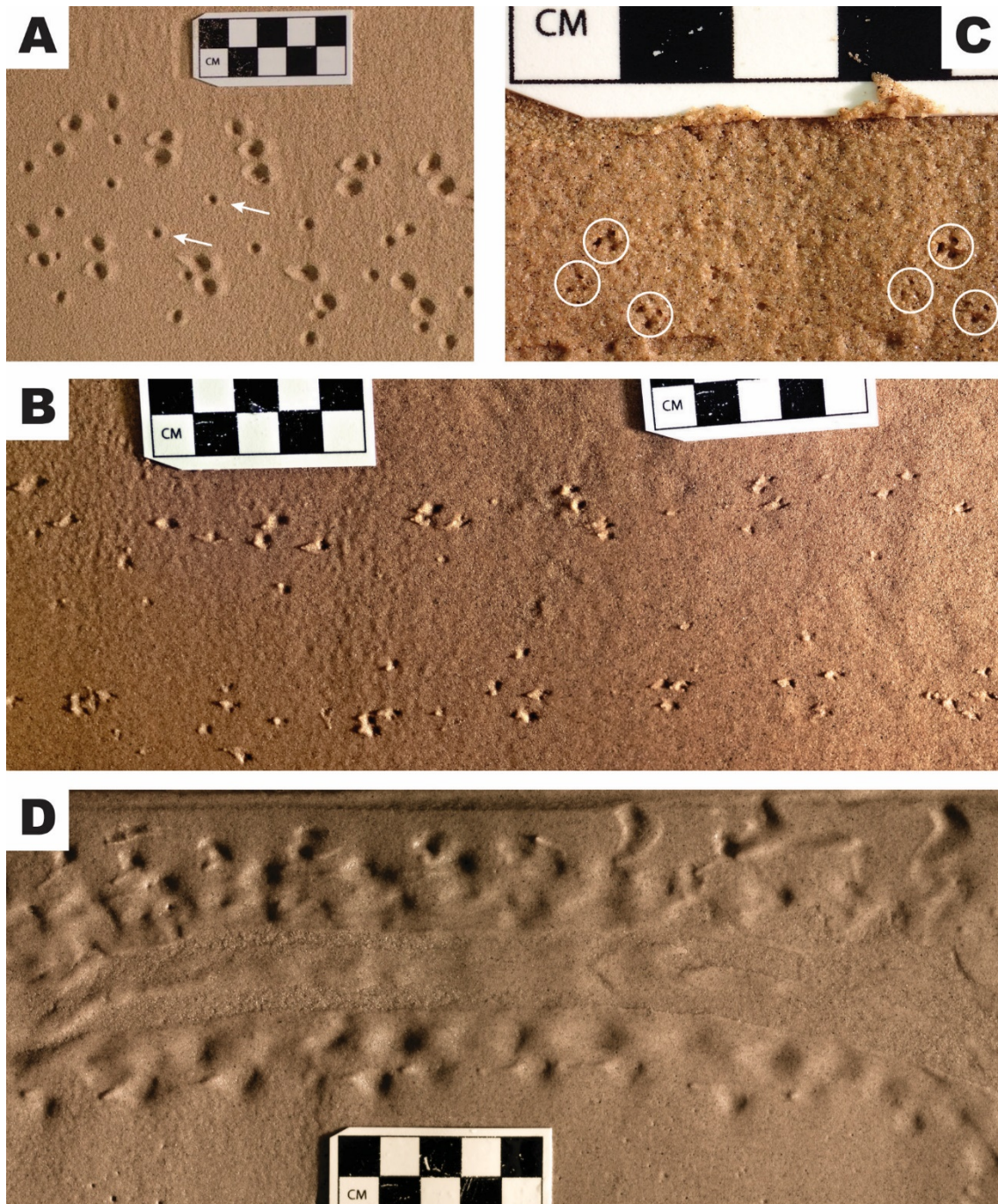


Fig. 2. Examples of experimental trackways produced in this study. A. Chilean rose tarantula trackway made in dry sand, walking uphill on a 15° slope; note the regular pedipalp imprints proximal to the walking leg imprints (white arrows). B. Giant desert scorpion trackway made in wet drying sand, walking uphill on a 25° slope. C. Close-up of scorpion trifold imprints made in stiff, wet drying sand, walking uphill on a 25° slope. D. Red swamp crayfish trackway made in wet saturated sand, walking uphill on a 15° slope; note the wide, medial impression caused by the crayfish's tail fan, covering up more proximal imprints on the left-hand side of the trackway.

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**BIOEROSION TRACES IN BONES FROM THE *SANTACRUZODON*
ASSEMBLAGE ZONE (EARLY CARNIAN, SANTA MARIA
SUPERSEQUENCE) AND THE ETHOLOGICAL DIVERSITY OF BONE
EXPLORATION BY INSECTS IN THE EARLY LATE TRIASSIC**

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Bioerosion traces produced by insects in bones are an important source of information regarding the structure and energy flow of past ecosystems, and the taphonomic history of vertebrate carcasses. They are direct evidence of interaction between insects and vertebrate remains and may contribute to the reconstruction of past environments, based on the identification of possible producers for the traces and the behaviors that generated them [^{1,2}]. Insect bioerosion is relatively common in bones from Jurassic to Quaternary [²⁻⁴], but Triassic examples are considerably rare and up until now have only been reported for the Brazilian Santa Maria Supersequence (SMS) [⁵⁻⁷], making this unit a crucial landmark for the study of the origin and evolution of bone exploration by insects. Here, we report new observations of already analyzed specimens [⁸] and new examples of bioerosion traces in bones from the SMS and discuss their importance in the understanding of ethological diversity of bone exploration by insects in the early Late Triassic.

The Middle–Upper Triassic SMS is a second-order depositional sequence restricted to the central region of the Rio Grande do Sul State. It is subdivided in four third-order sequences, being the Santa Cruz Sequence correspondent to the early Carnian [⁹]. Vertebrate fossil record of this sequence corresponds to the *Santacruzodon* Assemblage Zone (AZ) and comprises the bones analyzed here. This AZ is characterized by an extraordinary abundance of traversodontid cynodonts, especially *Santacruzodon hopsoni*, but its faunal content also includes other traversodontid and probainognathians cynodonts and non-dinosaurian archosauriforms [¹⁰]. Lithologically, the Santa Cruz Sequence presents conglomeratic sandstones with planar and trough-cross stratification at the base, representing a fluvial depositional system, overlaid by massive mudstones, representing loessic plains of eolian deposition, interbedded with coarse conglomeratic sandstones, interpreted as crevasse splays related to sporadic rainfall episodes [^{9, 10}].

Table 1. List of bioerosion morphotypes found in each specimen.

Specimen	Locality	Morphotype	Ichnotaxon
UFRGS-PV-0579-T	Schoenstatt	ornamented borings; trails	indeterminate; <i>Osteocallis</i>
UFRGS-PV-0589-T	Caixa de Abelhas	tube	indeterminate
UFRGS-PV-0871-T	Schoenstatt	Notch	cf. <i>Cuniculichnus</i>
MCP 4042-PV	Schoenstatt	Notch	cf. <i>Cuniculichnus</i>
MCP 4580-PV	Schoenstatt	Notch	cf. <i>Cuniculichnus</i>

The specimens come from the Schoenstatt Sanctuary (Santa Cruz do Sul municipality) and Caixa de Abelhas sites (Venâncio Aires municipality) and are housed in the collections of the Museu de Paleontologia da UFRGS Irajá Damiani Pinto (reference numbers UFRGS-PV-0579-T, UFRGS-PV-0589-T and UFRGS-PV-0871-T) and Museu de Ciências e Tecnologia da PUCRS (MCP 4042-PV and MCP 4580-PV). All fossils were analyzed with a stereomicroscope at

magnifications of 10x, 16x, 25x, and 40x, and photographed under different angles of lighting. UFRGS-PV-0579-T was analyzed with a scanning electron microscope at the CPGq-UFRGS. In total, ten traces were found and subdivided into four different morphotypes (Table 1): (i) ornamented borings: elongated, shallow to moderately deep depressions, ornamented with highly overlapping grooves, straight to arcuate, with no preferential orientation (Fig. 1B-D); (ii) trails: successions of straight to arcuate grooves attributable to the ichnogenus *Osteocallis* (Fig. 1E-F); (iii) notches: elongated borings with concave walls, rounded base and tapering ends, without bioglyphs, tentatively attributed to the ichnogenus *Cuniculichnus* (Fig. 1I); (iv) tubes: rounded borings that penetrate through the bone and are preserved as convex structures (Fig. 1G-H).

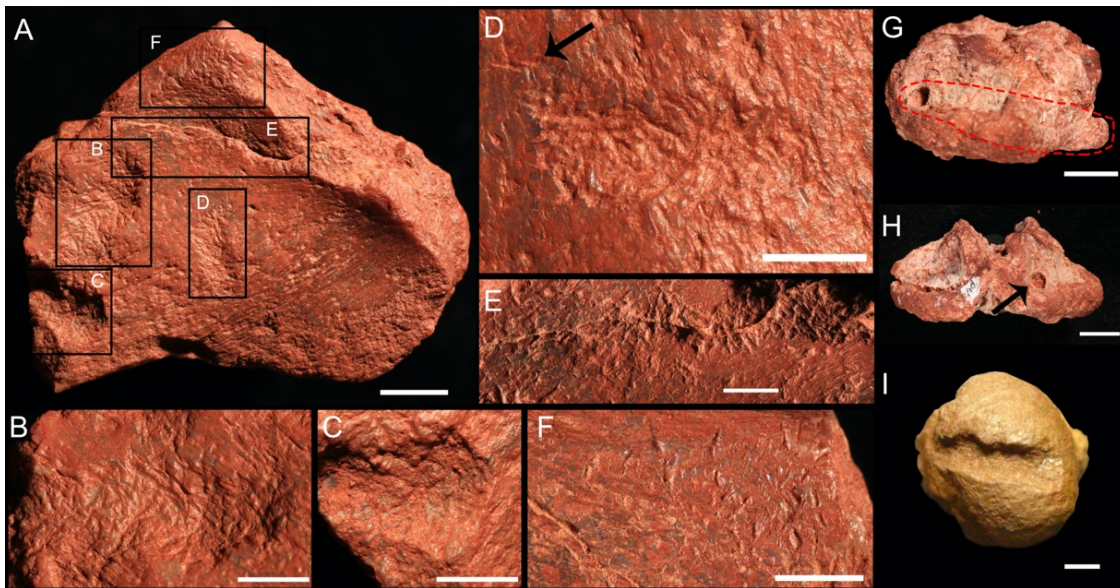


Fig. 1 – Examples of specimens from *Santacruzodon* AZ bearing bioerosion traces. A. General view of UFRGS-PV-0579-T highlighting the suite of traces on its surface. B-C. Ornamented borings showing grooves with no preferential orientation. D. Ornamented boring next to a small superficial trail of grooves (arrow). E-F. Trails of shallow grooves attributable to *Osteocallis*. G. Right lateral view of UFRGS-PV-0589-T showing the whole length of a tube (dashed lines). H. Dorsal view of UFRGS-PV-0589-T showing the rounded aperture of a tube (arrow). I. MCP 4580-PV showing a notch tentatively attributed to *Cuniculichnus*. Scale bars: A = 5 mm; B, C, E, F = 3 mm; D = 2 mm; G-H = 10 mm; I = 4 mm.

The traces described above are tentatively attributed to the action of insects due to the morphological similarity with bioerosion produced by modern insects in experiments and observations [11]. We understand that, even though research on modern bone bioerosion is still scarce, to this moment insects are the most likely producers of these traces, since there is no morphological correspondence between the traces and the bioerosion in bones produced by other organisms in continental settings, such as gastropods or even small vertebrates.

The specimen UFRGS-PV-0579-T exhibits a high density of traces on its surface, featuring two distinct morphotypes (Fig. 1A). Of particular interest is an ornamented boring that appears to extend from a small trail of shallow grooves (Fig. 1D). It is hypothesized that the trace producer may have initially grazed on the bone surface, superficially modifying it (forming a trail), before subsequently boring deeper into the bone, possibly exploring a region of interest. Previous discussions on the ethological interpretation of *Osteocallis* [12,13] remain inconclusive regarding whether its producer modified the bone itself or the overlying tissues. Nonetheless, the final nature of the borings is deemed unlikely, suggesting a potential association with *Osteocallis* as evidence of its inferred ethology. The behavioral origin of these traces, resembling incipient pupal chambers [14] or attempts to access internal nutrients [3], remains uncertain. While similar morphologies have been observed in experiments with dermestid beetles [11], the associated behavior remains undiscussed. Similarly, the interpretation of *Cuniculichnus* as pupal chambers lacks definitive ethological evidence due to the absence of experimental data and modern



analogues. Notably, the presence of *Cuniculichnus* in the early Late Triassic extends its occurrence by over 120 Ma, suggesting either rapid development of insect bone exploration or an even older origin. The tube found in UFRGS-PV-0589-T shares some morphological features with *Skolithos*, both being elongated structures with a rounded aperture. *Skolithos* is a fairly common trace in the SMS, and its occurrence in this unit has been attributed to the action of insects [15]. There is also a size correspondence in the diameter of both the tube and the *Skolithos* of SMS. It is possible that the behavior (and perhaps the producer) that generated the boring tube is the same that generated the *Skolithos* of SMS. However, this hypothesis still lacks enough evidence to be confirmed; therefore the origin of the tube remains uncertain.

Despite ongoing analysis of the ethological significance of these traces, the remarkable morphological diversity of bioerosion traces in the bones from *Santacruzodon* AZ hints at multiple behaviors or different producers, either taxonomically or ontogenetically diverse, or potentially indicating a highly specialized producer exploring bones in various ways. The proximity of the Santa Cruz Sequence to the Pinheiros-Chiniquá Sequence, which hosts the oldest records of insects bioerosion in bones, underscores the importance of the Brazilian Triassic in unravelling the origin and evolution of insects' bone exploration. Further research directed towards this subject promises to shed light on these intriguing questions.

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THE SIGNIFICANCE OF BENTHIC ECOSPACE COLONIZATION BASED ON THE ROECE AT THE CAMBRIAN SERIES 2–MIAOLINGIAN BOUNDARY, WESTERN HENAN PROVINCE

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The transition from the Cambrian Series 2 to the Miaolingian was a pivotal juncture in Earth's history, marking the onset of significant shifts in biodiversity and biomass dynamics during the Phanerozoic. Concurrently, profound transformations occurred in the alteration of sedimentary deposits by trace makers, reshaping benthic ecospace. This study employs ichnological and ecological methodologies to construct a comprehensive three-dimensional spatial model for ecospace occupation and ecosystem engineering within the Mantou Formation in western Henan Province, focusing on the transition between the Cambrian Series 2 and Miaolingian. A meticulous statistical analysis of 21 ichnogenera and 29 ichnospecies in the Mantou Formation revealed that, before the Redlichiid–Olenellid Extinction Carbon isotope Event (ROECE), the Member 1 of the Mantou Formation represents tidal flat deposition of siliceous clastic rocks interbedded with carbonate rocks and characterized by the development of sand-mud flats. The rock layers exhibit flaser and parallel bedding, and the surfaces of the mudstone layers display exposure features such as mud cracks. Due to the limited burrowing ability of metazoans at this time, it resulted in the occupation of only the surface, semi-infaunals, and shallow tier of ecological niches, with a lack of occupation in the middle and deep tiers (Fig. 1). The sedimentary substratum at the lower part of the Member 2 interval was occupied by microbial mats. Metazoans coexisted with microbial mats, which served as a food source. Wrinkle structures developed on the surface of thin-layered siltstones, with no signs of exposure seen at their base, suggesting that the sedimentary environment of this part was the intertidal zone. In the upper part of Member 2 of the Mantou Formation, there was a significant development of trace fossils of trilobite arthropods. At this time, the disturbance depth and abundance of metazoans increased significantly, and the ecological function has returned to the level before the extinction event. Due to a certain degree of consolidation of the sedimentary substratum, the trace fossils of trilobite arthropods were perfectly and finely preserved. Overall, the Member 2 of the Mantou Formation shows a continuous marine transgression process, with the sedimentary environment being an intertidal mud-sand flat deposition environment. In the Miaolingian Member 3 of the Mantou Formation, marine transgression peaked, mainly developing carbonate deposits in coastal shallow beach settings. In order to seeking more oxygen and food, metazoans have exploited and utilized the ecological niches in the middle and deep tiers. Due to frequent turbulence in this member of the water body, biotic occupation is less in the surface and semi-infaunal tiers in this member. In terms of sediment modification by metazoans, the disturbance by bioturbation in Member 1 of the Mantou Formation predominantly occurred in the shallow sediment layers, with an overall low degree of disturbance, but locally, disturbance intensity was high. In the lower part of Member 2 of the Mantou Formation, the decrease in the abundance of metazoans and the widespread development of microbial mats resulted in interactions between metazoans and microbial mats influencing sediment disturbance. Simultaneously, the development of microbes provides a food source for the revival of metazoans (Fig. 2). In the upper part of Member 2 of the Mantou Formation, the number of metazoans significantly increases, and the degree and depth of disturbance gradually grow. *Thalassinoides* and *Treptichnus*, with high ecosystem engineering impact values, massively occurs. In the Member 3 of the Mantou Formation, further strengthening of the disturbance of sediments by organisms occurs. Wide development of *Thalassinoides* happens in this member, and the bedding structure of the sediments is broken. After the

occurrence of the ROECE event, the trace makers with higher ecosystem engineering impact values have rapidly increased the depth and breadth of sediment disturbance, creating a large number of new ecological niches. This has significant meaning for the colonization of metazoans in benthic ecological niches.

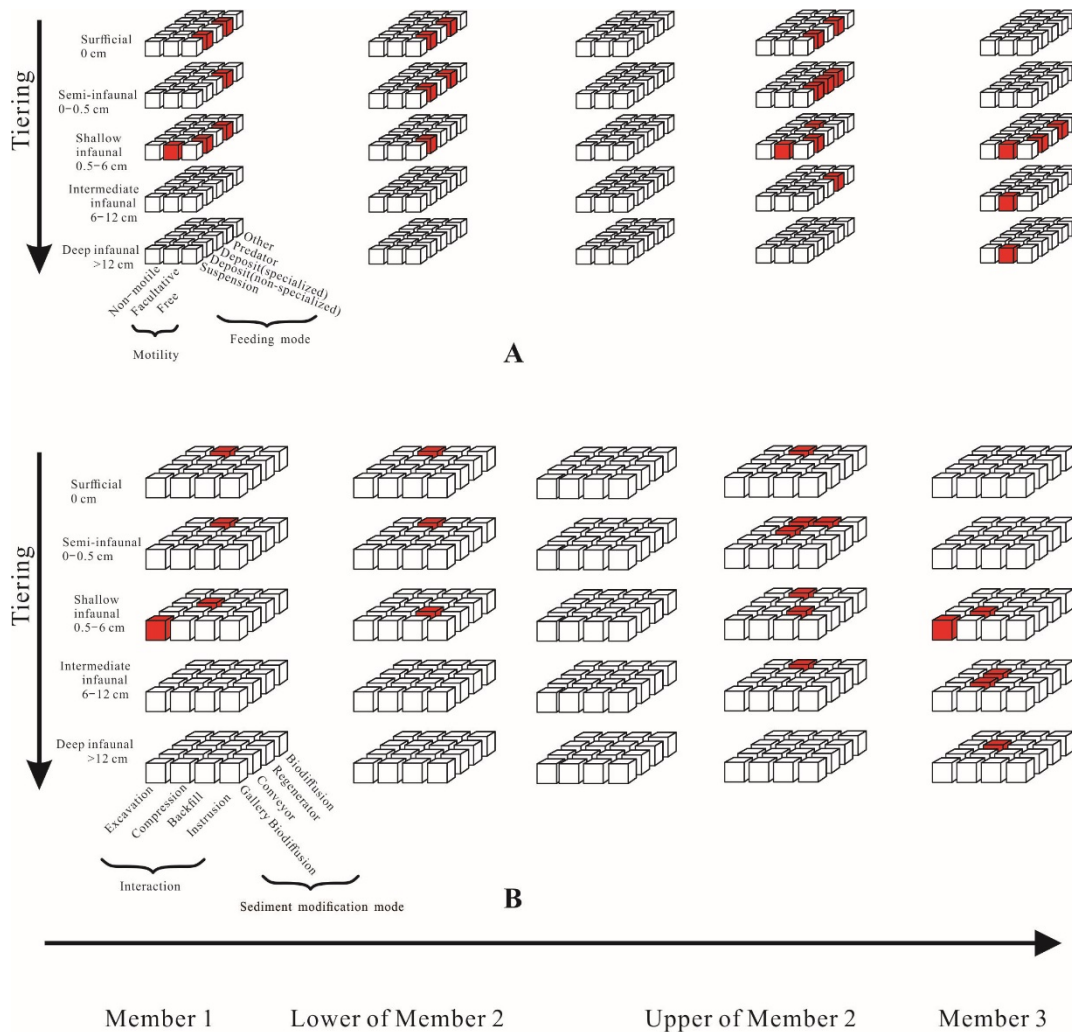


Fig. 1. Ecospace occupation and ecosystem engineering model of the Mantou Formation in western Henan Province. A. Ecospace occupation model. B. Ecosystem engineering model.

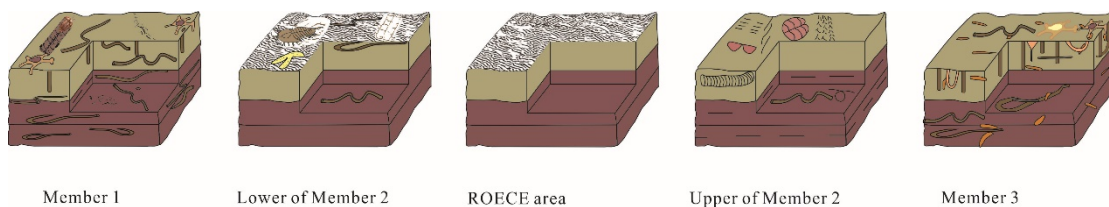


Fig. 2. Evolution of the sedimentary layer during the Cambrian Series 2–Miaolingian boundary, western Henan Province.



ICHTNOLOGICAL RESPONSE TO THE EOCENE HYPERTHERMAL EVENTS AS RECORDED IN THE ONSHORE KUTCH BASIN, INDIA

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The Eocene Epoch witnessed notable shifts in Earth's climate, featuring intermittent episodes of warming and cooling [1]. These Eocene global climatic aberrations, popularly known as the hyperthermal events include the Paleocene-Eocene Thermal Maximum (PETM) [1], Eocene Thermal Maximum 2 (ETM2) [1], Eocene Thermal Maximum 3 (ETM3) [1], Early Eocene Climatic Optimum (EECO) [1], Late Lutetian Thermal maximum (LLTM) [2], and Middle Eocene Climatic Optimum (MECO) [1]. The hyperthermal events have a significant impact on the marine and terrestrial biotic assemblages [3,4]. The behavioral traits of the endobenthic community in response to these climate changes are manifested in the ichnofossil suites [5]. Amongst all these hyperthermal events, the literature on ichnological signature of the PETM is scantily available. Furthermore, the trace-fossil studies associated to other Paleogene warming events are grossly underrepresented. This research investigates how the Eocene hyperthermal events affected the ichnological imprints from the onshore Cenozoic Kutch Basin situated in western India. The evidences of Eocene hyperthermal events are well-established in the Kutch Basin by carbon isotope analysis, authigenesis of glauconites, and the paleoecological responses of microfossils [6] (Fig. 1).

The Cenozoic Kutch Basin developed in a partially restricted-marginal to shallow-marine settings, and, at some places, in the supratidal terrestrial settings. The Eocene succession of Kutch consists of the Naredi, Harudi, and Fulra formations [7]. With the advent of Ypresian age, the deposition of the Naredi Formation (NF) occurred in a restricted marine setting on top of the Deccan volcanics and it records the first post-Mesozoic marine incursion in the basin. The NF, therefore, provides an ideal candidate for investigating an r-selection trace-fossil population with the reestablishment of the marine ecological niches afresh in the basin. The turning of era begins after the marine encroachment over a rugged volcanic terrain with the establishment of a restricted-marine setting in the shallowest part of the basin by depositing variegated shale beds. The lower shale units of NF are mostly devoid of trace fossils, except for the three intermittent bioturbated/bioeroded nodular/concretized horizons containing paucispecific firmground (*Thalassinoides* ichnofabric) to hardground (association of *Entobia* and *Gastrochaenolites*) ichnocoenoses. These impoverished suites of ichnofossils were influenced by oxygen-depleted bottom-water conditions as also evidenced by the fossil content. The hyperstressed to barren trace-fossil assemblages suggest eutrophic condition in a dysoxic environment that was inhospitable for the benthic organisms during ETM 2 and ETM 3. The upper half of the marine succession of NF is defined by a mixed-carbonate-siliciclastic succession, where bioturbation is restricted to the carbonate beds (with the *Cylindrichnus-Nummipera* and *Nummipera-Cylindrichnus* ichnofabrics) only and the shale units remain barren. The paucispecific trace-fossil assemblages of the Naredi carbonates show an increasing ichnoabundance from middle to top of the succession, thereby, revealing an ameliorating departure from the r-strategy of the infaunal benthic community under the influence of EECO. The transition culminates with complete bioturbation at the top of the marine Naredi succession, where the mid-tier *Thalassinoides suevicus* completely overprints the preexisting carbonate ichnofabrics. The amelioration of the benthic environment also marks a steady opening up and deepening of the sea along with a gradual transformation from eutrophy to oligotrophy as corroborated by the microfaunal assemblages. The marine succession of NF demonstrates an overall 3rd-order transgressive cycle during the ETMs 2 and 3 followed by a highstand systems tract during the EECO. Then, a Lutetian forced



regression breaks the continuity of the stratigraphic record of marine ichnofauna. Hence, the top of NF is defined by the pedogenized and lateritized terrestrial deposits containing a continental trace-fossil suite (*Camborygma*, lungfish aestivation burrows, *Macanopsis*, root traces) immediately below the subaerial unconformity separating the NF below and the fully marine Bartonian Harudi Formation (HF) above.

The HF marks the initial stage of the global Bartonian transgression. The mixed siliclastic-carbonate succession of HF represents transition of the restricted- to shallow-marine setting followed by a rapid further deepening. The MECO coincides with the deposition of a glauconite-rich shale stratum at the upper part of the HF. This mixed siliclastic-carbonate succession is bereft of trace fossils, except the three carbonate firmground/hardground horizons characterized by monospecific suites. These episodes of bioturbation/bioerosion demonstrate close association with the MECO. The *Balanoglossites* bearing shelly bivalve coquina bed has been deposited immediately before the initiation of MECO. The thin carbonate hardground, profoundly bioeroded with *Gastrochaenolites* coincides with the MECO. The nodular hardground overlying the foraminifera bearing glauconitic shale marks the end of MECO. This interval, particularly the bioeroded hardgrounds, demarcates a basin-wide sediment starvation making it a major condensed horizon after a glacioeustatic sea-level rise during the MECO. The HF is gradationally overlain by the Fulra Limestone (FL), which embodies the peak of Bartonian transgression and its ensuing highstand. The FL carbonates originating as the larger-benthic-foraminifera shoals show a recurrent and perhaps throughout occurrence of a *Thalassinoides* ichnofabric, where the burrow diameter and abundance gradually increase from bottom to top of the formation.

The ichnological and sedimentological data, therefore, indicate that, wherever developed, only a series of successive colonization ichnofaunal suites dominated this basin throughout the early and middle Eocene, as a reverberation of the transient climatic hyperthermal episodes and intermittent relative cooling. The climax as well as K-type population strategy in terms of ichnofossils can only be found in the much younger Oligocene deposits above the second major Priabonian-Rupelian subaerial unconformity in the onland Kutch Basin. Although the depositional settings and the relative sea-level change undoubtedly play a vital role in controlling the successive Eocene ichnocoenoses, the hyperthermal events directly and allogically dictated the relative sea-level change changes, depositional settings, and perhaps also indirectly influenced the ichnocoenoses by controlling the benthic dynamics in combination with the stressors offered by the depositional settings.

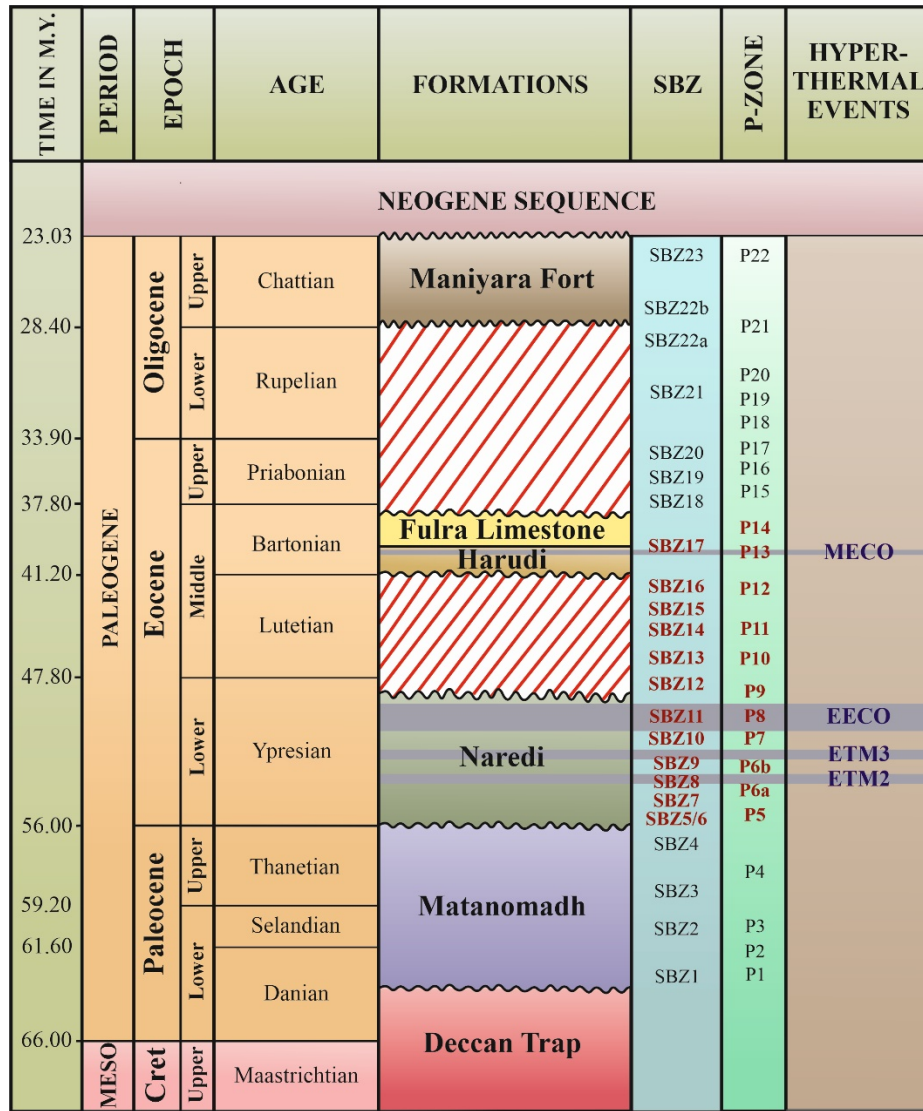


Fig. 1. Lithostratigraphy of Cenozoic Kutch Basin correlated with shallow benthic zones (SBZ), planktic foraminiferal zones (P-zones), and the Eocene hyperthermal events.

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ICHTNOLOGICAL RECORD CORRESPONDING TO THE MIDDLE EOCENE CLIMATIC OPTIMUM (MECO): A CASE STUDY FROM THE BARTONIAN KUTCH BASIN, WESTERN INDIA

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The Middle Eocene Climatic Optimum (MECO, ca. 40 Ma) [¹] represents a transitory interval of global warming characterized by a gradual 4°–6°C temperature increase of the oceans. This climatic aberration disrupted the long-term cooling episode extending from the middle to late Eocene. The MECO biostratigraphically corresponds to the upper interval of planktic foraminiferal zones E11–E12 and to the shallow benthic zone (SBZ) 17. The MECO coincides with the deposition of the Bartonian mixed siliciclastic-carbonate succession of the Kutch Basin from the western part of India. This case study aims to investigate the impact of MECO on the endobenthic community using ichnology as a proxy. The Bartonian Kutch succession consists of (i) the underlying marine green and grey shale and bioclastic limestone units defining the Harudi Formation, HF and (ii) the overlying Fulra Limestone, FL, deposited on a carbonate platform. The HF is bereft of trace fossils except in one bioturbated and two bioeroded hardground beds (Fig. 1). The shelly limestone bed or bivalve coquina bed at the middle part of the succession (underlain by grey shale and overlain by green shale) consists of a monospecific firmground ichnofabric characterized by *Balanoglossites triadicus* (BI 4) (Fig. 1A). The lower bioeroded bed constituting different ichnospecies of *Gastrochaenolites* is 2–3 cm thick and chocolate-colored carbonate hardground (Fig. 1B). The upper hardground horizon is characterized by a series of top-bioeroded (with *Gastrochaenolites*, *Entobia*, and *Oichnus*) carbonate nodules (10–20 cm diameter) – all containing the multigenerational septarian cracks (Fig. 1C). The upper hardground demarcates the top of the *Nummulites obtusus* coquina bed hosted by the middle green shale corresponding to E11. The basal part of the green shale corresponds to the MECO established earlier by a negative $\delta^{13}\text{C}_{\text{org}}$ isotopic excursion [²]. The upper bioeroded hardground demarcates a basin-wide sediment starvation making it a major condensed horizon following a glacioeustatic rise during the warming event. The MECO also prompted the deposition of shallow-marine platform carbonates of FL by accelerating a sharp rise in the sea-level and proliferation of diverse larger benthic foraminifera in warm oligotrophic sea-water [²].

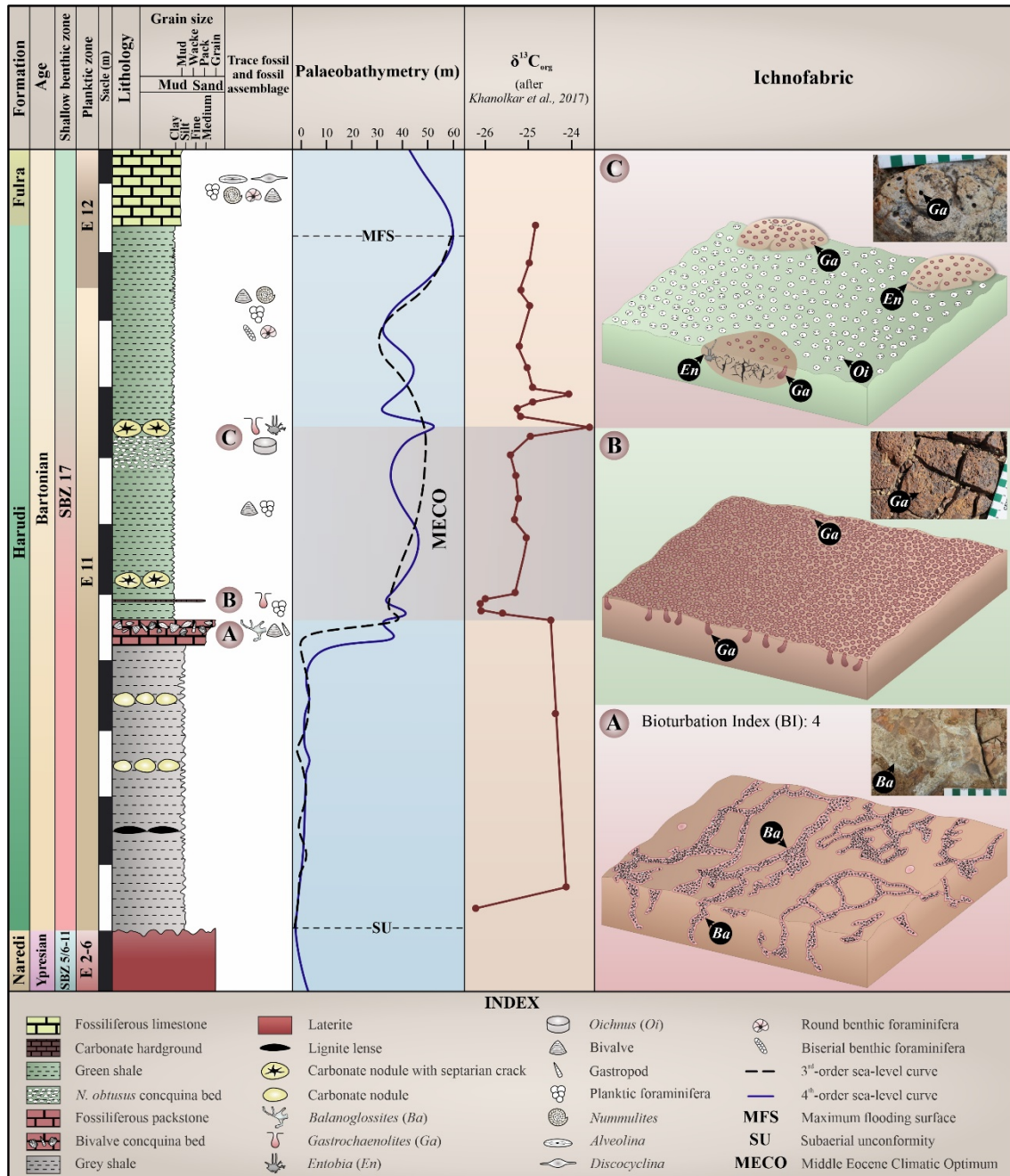


Fig. 1. Composite graphic lithology of Harudi Formation along with body-fossil and trace-fossil assemblages, biostratigraphic intervals, third-order [3] and fourth-order relative sea level curve, carbon isotopic characteristics [2], position of MECO, and ichnofabric of the trace-fossil assemblages. A. Monospecific *Balanoglossites* ichnofabric of the bivalve coquina bed. B. *Gastrochaenolites* bearing carbonate hardground. C. *Nummulites obtusus* bed and nodular hardground consisting of *Oichnus*, *Entobia*, and *Gastrochaenolites*.

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TAIWAN'S EVOLUTION AND ITS IMPACT ON THE ICNOLOGY OF SHALLOW-MARINE STRATA

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Late Miocene through early Pliocene shallow-marine sedimentary strata exposed along the Da'an River, Taiwan, form part of the fill of the Western Foreland Basin (paleo-Taiwan Strait), and the ichnology of these strata reflect the emergence and evolution of Taiwan. Taiwan emerged from the Pacific Ocean in the late Miocene as a result of collision between the Luzon Arc on the Philippine Sea Plate and the Eurasian Plate and the island continues to expand to the south and southwest through ongoing collision [^{1,2}]. Along the Da'an River, the late Miocene to early Pliocene Kueichulin Formation consists of shallow-marine strata dominated by robust and diverse trace fossil suites (Fig. 1A) [^{3,4}] suggesting seafloor conditions supported healthy infaunal communities and physical sediment reworking was minimal. The lower Kueichulin Formation is interpreted as being deposited in > 25 m water depth and when Taiwan was situated ~100 km to the northeast of its present position. Additionally, tidal flux was minimal and incipient-Taiwan provided partial protection from high-energy waves generated during tropical cyclones.

By the mid-Pliocene, shallow-marine strata record deposition in < 15 m water depth and preserve evidence of episodic sedimentation and extensive tidal reworking (Fig. 1B) [^{3,4}]. There is also a marked change in ichnological character from the early Pliocene to the mid-Pliocene as Taiwan propagated and expanded to the southwest. Tropical cyclones that regularly passed over the island began delivering huge sediment volumes to the Taiwan Strait, and post-storm sediment reworking via tides in the increasingly restricted waterway redistributed those sediments throughout the strait and to the adjacent seas. Ichnologically, mid-Pliocene and younger strata show a marked reduction in trace density, but not in size or diversity. The reduction in bioturbation intensity does not reflect changes in baseline ("normal") seafloor conditions, but instead reflects changes in the processes that controlled sedimentation. Specifically, as Taiwan expanded to the southwest, increasing sediment delivery to the Taiwan Strait and subsequent tidal reworking both: (i) increased erosion and redistribution of sediments colonized under normal seafloor conditions effectively limiting preservation of these beds; and (ii) increased sediment accumulation rates, which reduced the time available for seafloor colonization between sedimentation events.

The ichnological character of shallow-marine sedimentary strata exposed along the Da'an River demonstrate that the Taiwan Strait remained a favourable environment for infauna to thrive throughout emergence and growth of the island, and that changes in the trace assemblage reflect changing hydrodynamic conditions and episodic sedimentation. These findings reinforce the hypothesis that trace fossils are suitable, if not ideal, for distinguishing "normal" seafloor conditions from episodic, high-energy events, the latter of which commonly dominate the shallow-marine sedimentary record.

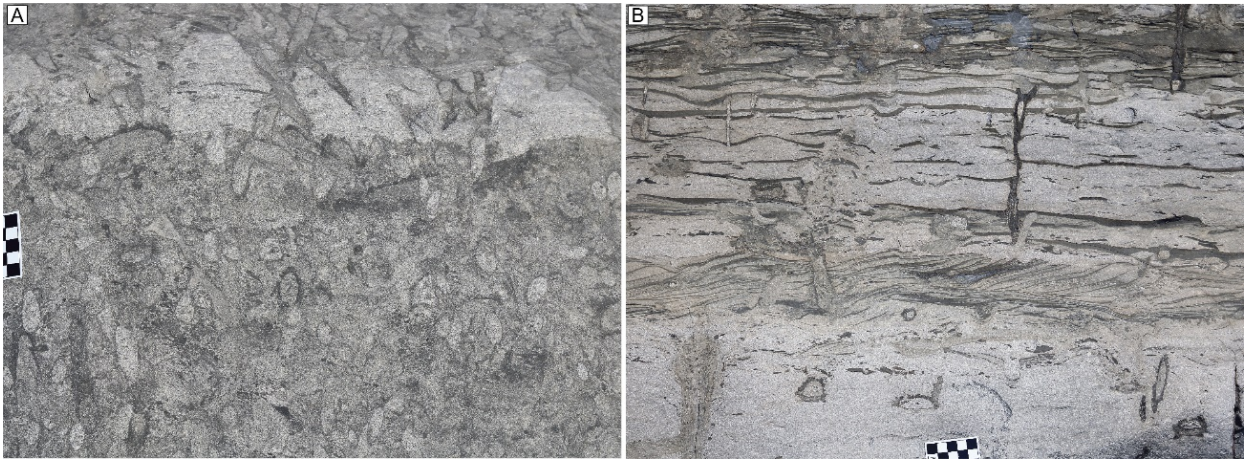


Fig. 1. A. Intense bioturbation of muddy sandstone with limited preservation of primary sedimentary structures. These strata record deposition in a healthy shelf setting with periodic storm reworking separated by extended periods of infaunal colonization. B. Trough cross-stratified muddy sandstone overlain by flaser through to lenticular bedded heterolithic strata. Bioturbation in this interval is much lower density, but trace fossils remain robust and diverse.

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JURASSIC DINOSAUR TRACKS IN BRAZIL: NEW RECORDS FROM THE GUARÁ FORMATION (UPPER JURASSIC, PARANÁ BASIN)

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In Brazil, the only dinosaur tracks known from the Jurassic period come from the Guar´a Formation [^{1,2}]. This formation is a large sedimentary sequence of fine-grained to conglomeratic sandstones of fluvial and aeolian origin. It extends from the west of the state of Paran´a to Uruguay, with known outcrops in the municipalities of Santana do Livramento and Ros´ario do Sul [³]. Tracks and trackways associated with theropods, sauropods, ornithopods and ankylosaurs have already been found in the Guar´a Formation deposits, in addition to vertebrate and invertebrate burrows [^{1,2}]. Due to the low cementation of its rocks, most materials can only be identified by the deformations in the sandstone layers, seen in plan view. Fine anatomical details, such as digit anatomy or claw marks, are difficult to distinguish, because what is currently exposed are undertracks (deformations in the sedimentary layers below the location of the original track, which were once eroded). Furthermore, many layers of aeolian sand sheets are bioturbated, which also makes track-trackmaker correlation difficult [^{1,2}]. In recent fieldwork, three new fossiliferous outcrops (Sanga do Torneado, Cerro Caver´a, and Saur´opodes) containing dinosaur tracks, preserved as concave epireliefs, and invertebrate burrows were found. Among the new records are the ichnogenera *Taenidium*, *Skolithos*, and *Arenicolites*, as well as tracks of theropod dinosaurs, including the first original track from the Guar´a Formation (UFRGS-PV-0207-G), and ornithopod, sauropod and, possibly, a new record of ankylosaur (UFRGS-PV-0208-G) tracks. For the original theropod track and the ankylosaurid track, photogrammetry and 3D modeling techniques were applied (Fig. 1), and the original theropod track was compared with other pedal materials from the Late Jurassic and adjacent time intervals through principal component analysis (PCA), with the aim of investigating the possible producer.

The left theropod track UFRGS-PV-0207-G has a very good degree of preservation (2.0 in the scale of Marchetti et al. [⁴]). This track is tridactyl and mesaxonic, 17.8 cm long and 16.7 cm wide (track length/width ratio: 1.08). The anterior triangle (AT) width is 14.81 cm and the length is 5.45 cm, with a AT length/width ratio of 0.368. The lengths of digits II, III and IV are respectively 10.18, 13.02 and 11.26 cm. The widths of digits II, III and IV are 4.4, 4.7 and 4.5 cm, respectively. The divarication angle between digits II and III is 20.4°, while between fingers III and IV it is 32.6°. The total divarication is 53°. The “heel” has an asymmetrical subtriangular shape. Width and length of the sole are 14.6 and 6.5 cm respectively. There is no evidence of a hallux. These characters approximate this track to the ichnogenera *Iberosauripus* Cobos et al., 2014 [⁵] and *Jurabrontes* Marty et al., 2017 [⁶]. Studies are still being carried out to obtain a correct ichnotaxonomic attribution. Unlike the other tracks in the formation, found on dirty roads and exposed to the erosion caused by vehicles, the track UFRGS-PV-0207-G was found in a creek, which allowed for less erosion and the preservation of the original layer where the track was produced, this being the only original track previously found in the Guar´a Formation. It can be seen that it is an original track, due to the excellent three-dimensional preservation, with well-preserved contours and fine details, such as claw marks and clear limits between the digits. In addition, we also obtained the second record of an ankylosaur track (UFRGS-PV-0208-G) from the Guar´a Formation. It is 23.7 cm long by 28.04 cm wide, with evident tetradactyly and paraxony. The lengths of digits I-IV are respectively 11.76, 12.16, 9.12 and 8.7 cm, and the widths of digits I, II, III and IV are 2.6, 3.4, 3.8 and 3.2 cm, respectively. The divarication angle between digits I-II is 25.0°, II-III is 7.2° and III-IV is 12.7°. The total divarication is 44.9°. Width and length of the sole are 19.19 and 8.4 cm respectively. Other features that suggest that this footprint

was produced by an ankylosaur are the radial arrangement of the digits, the wide sole, a slightly asymmetrical outline, and the approximate measurements of the digits in width and length. The generation of depth maps with false colors allowed a better visualization and interpretation of the track, highlighting the fine details, normally difficult to visualize. This track has great similarity with the ichnogenus *Metatetrapous*. This ichnotaxon has tetradactyl manus and pes. The pes are semiplantigrade and mesaxonic, with well-developed and separated digits I to IV [7], which fits with the track presented here. *Metatetrapous* was suggested as the potential ichnogenus of the first ankylosaurian tracks described for the Guar Formation [2], which is corroborated by the new finding.

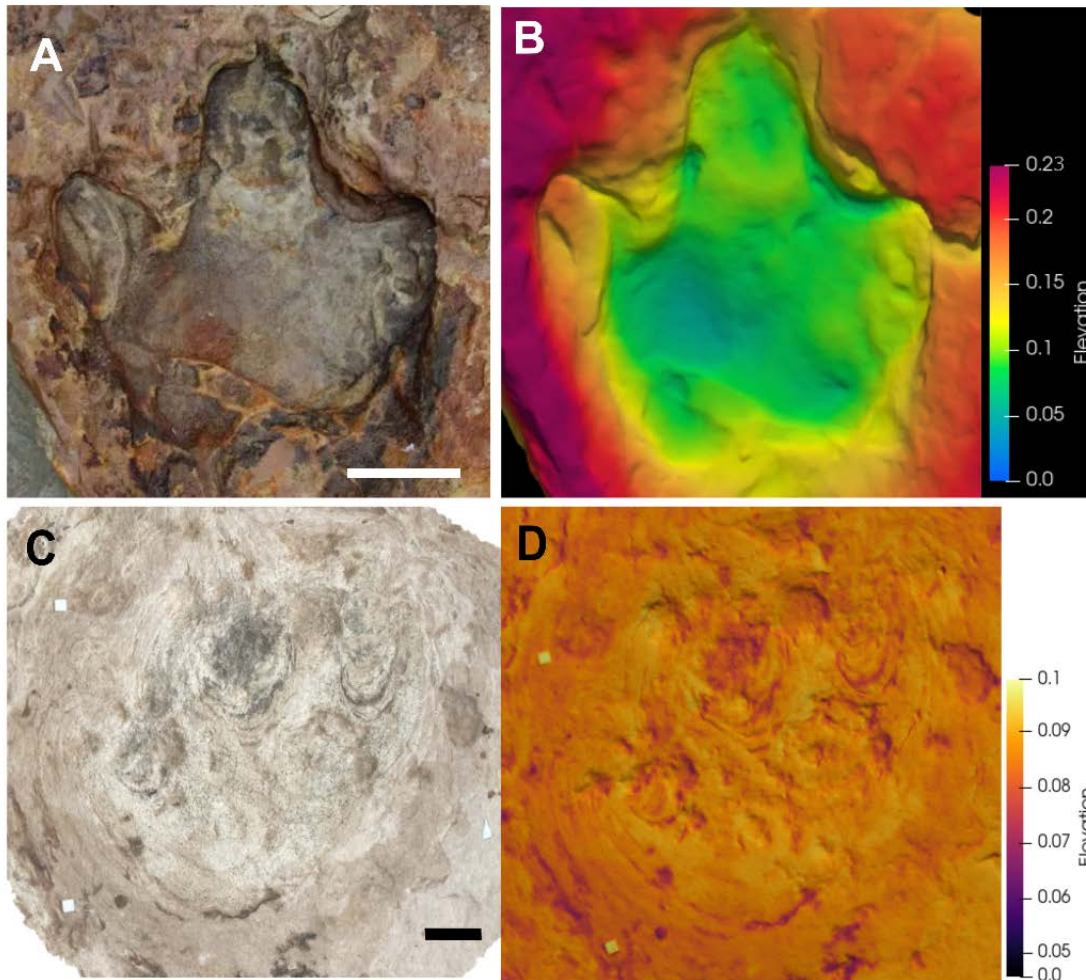


Fig. 1. A-B. Original theropod track UFRGS-PV-0207-G, with false-color depth map in B. C-D. Ankylosaur track UFRGS-PV-0208-G, with false-color depth map in D. Scale bars = 5 cm.

These new findings are of great scientific importance, as the Guar Formation holds unique information about the Jurassic ichnofauna of Western Gondwana. The universities and the municipal government of Rosrio do Sul intend to continue articulating ways to make the population aware of protecting the paleontological heritage of the municipality, as well as to enable new expeditions in search of fossil tracks in the region.

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ICHTNOLOGICAL APPROACH IN VERTISOLS OF THE SERRA DA GALGA MEMBER (UPPER CRETACEOUS, BRAZIL)

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The study and application of paleosols, in conjunction with ichnology, are still relatively unexplored as tools for paleoenvironmental and paleoecological reconstruction in the Brazilian intracontinental basins. Paleosols are common in the Serra da Galga Member (the upper unit of the Marília Formation, Maastrichtian of the Bauru Basin), whose deposits are essentially composed of conglomerates, sandstones, and mudstones accumulated in distributive fluvial settings [1]. These paleosols, interpreted as Vertisols, occur in floodplain architectural elements and show well-developed profiles and features related to poor drainage, wedge-shaped aggregates, slickensides, and clayey texture [2]. For the study, profile surveys were carried out in a key outcrop of the Serra da Galga Member, with 20 m high and 70 m long. Three Vertisols profiles varying from 75 to 132 cm in thickness, were described in detail. The horizons show clear or gradual boundaries, with smooth or wavy topography, and the predominant texture is a light greenish-gray loamy-sand. Pedogenic structures are characterized by fine to medium, angular to subangular blocky peds, and medium to coarse wedge-shaped associated to Mukkara microrelief. Moreover, redoximorphic features such as depletion and concentrations zones are diperse in 5-10% of the horizons. Bioturbation is observed, often filled with calcitic cementation, and is attributed to roots and soil-dwelling invertebrates. The plant traces are represented by: (i) white to gray, calcareous rhizcretions composed of powdery to solid calcite, exhibiting vertical and subvertical, linear and downward branching ranging from 1 to 15 cm in length and 0.2 to 6 cm in diameter; and (ii) rhizohaloes with circular and individual morphology and 2-9 cm in diameter, displaying a red external rim and a white central rim. Regarding the invertebrate burrows, the actively-filled burrows contain evidence of displacement with internal structure or meniscate sediment packets (*Taenidium* and *Planolites*), and the passively-filled ones are characterized by homogenous fill or crystalline spar fill (*Paleophycus* and *Skolithos*). These traces exhibit feeding (fodinichnia), dwelling (domichnia), and polychresichnia behaviors attributed to annelids, arthropods, and plants. Ichnodiversity is low throughout the section and bioturbation intensity is low to moderate (up to 3 in the bioturbation index), with a low tendency topward, indicating stressful conditions. The Vertisol profiles were developed under paleoprecipitation and paleotemperature ranging from 405 to 1136 mm/yr and 10.2 to 12.9°C, respectively, with mean values of 685 mm/yr and 11.4 °C, and standard errors of ±120 mm/yr and ± 0.83 °C. The values of the Köppen aridity index (MAP/MAT+33) indicate that all the horizons formed under subhumid to humid conditions. The presence of redoximorphic features, limited occurrence of calcium carbonate and rhizohalos through profile suggest a seasonal climate, with considerable paleoprecipitation and high-water saturation during the wet season and evaporative condition during the dry season. The relationship between the bioturbation index and saturation levels of the studied paleosols reveals an increase in redoximorphic features in horizons with a high trace density. This phenomenon is attributed to burrows and plant roots, which create soil macropores acting as permeable pathways, enhancing fluid flow. Consequently, this process leads to the movement and retention of base cations and water, resulting in redox depletions and concentrations. The soil-water profile, based on the distribution of studied trace fossils and their physiological moisture requirements, is represented by two behavioral groups reflecting different moisture zones: terraphilic organisms, which live above the water table, and hygrophilic organisms, which reside within the vadose zone. By analyzing the association between the bioturbation index, the concentration of ichnotaxa in each horizon, and the distribution of

ichnofossils according to soil moisture variation, the water saturation indexes control the frequency, density, and ichnodiversity observed in paleosols.

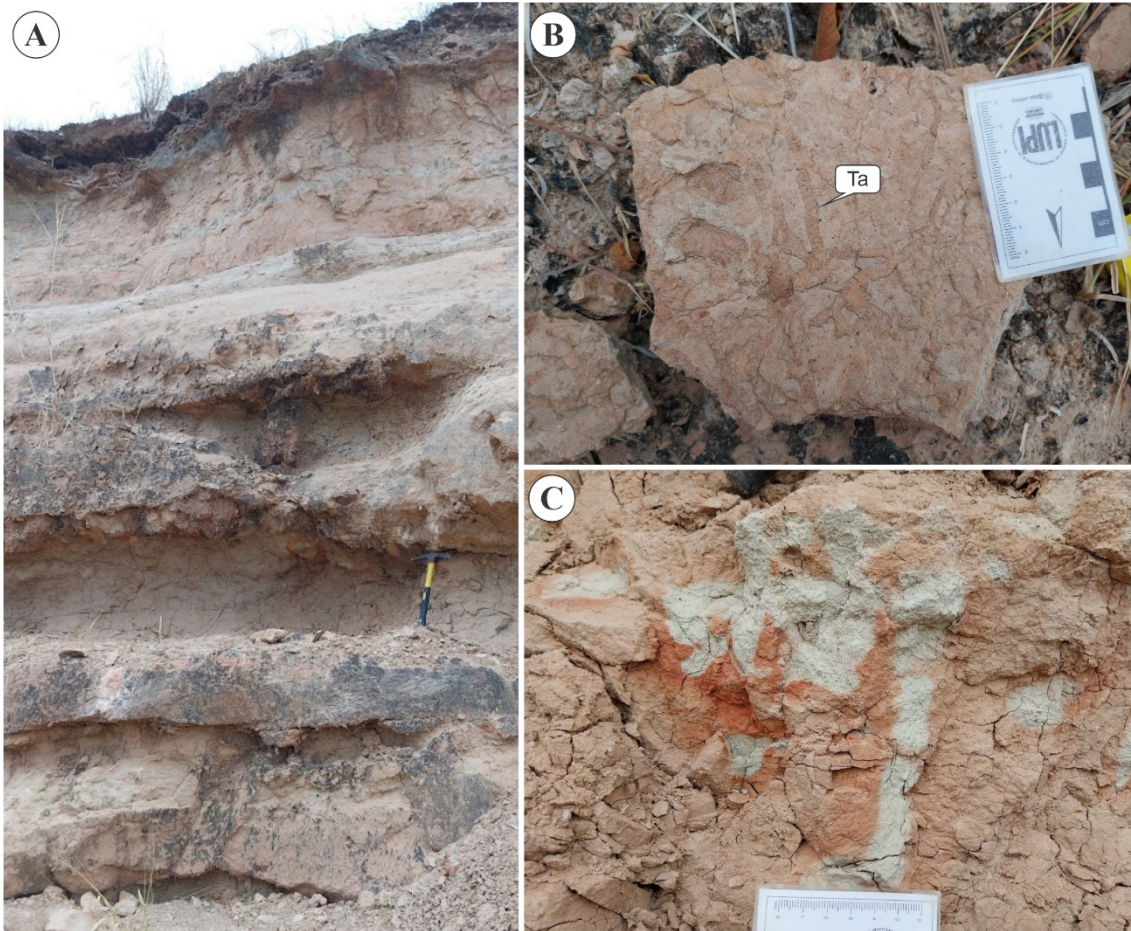


Fig. 1. Trace fossils from Serra da Galga Member. A. General view of studied outcrop. B. General view of burrows attributed to *Taenidium*. C. Occurrence of rhizohalos.

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THE USE OF PORTABLE AIR PERMEAMETERS IN THE STUDY OF BIOTURBATED ROCKS: PRELIMINARY RESULTS FROM *OPHIOMORPHA*

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In recent decades, numerous studies have demonstrated that trace fossils can impact certain petrophysical properties, such as porosity or permeability, in bioturbated deposits [1]. Different parts of some burrows (e.g., wall, fill) show distinct textural properties, having a notable influence in such petrophysical properties [2]. Typically, these studies are conducted either on rock samples or cores analyzed in laboratories. In terms of permeability, it is often measured from small samples, such as core plugs, using a permeameter, obtaining a single value for each sample. However, this ignores those textural heterogeneities that are associated to different parts of the burrows. When working with cores, the spot-permeameter is a commonly used method that allows obtaining a grid of permeability values for a short interval on a core-exposed surface, characterizing heterogeneities produced by bioturbation [3]. While these methods yield successful results, they require working with small samples or short core intervals and cannot be obtained in the field.

Here, we present and evaluate the use of portable air permeameters for studying permeability in bioturbated rocks as a potential tool to obtain point values directly from rock samples, both cores and outcrops. In the initial phase, we selected rock samples with *Ophiomorpha*, a trace fossil commonly associated with bioturbated reservoirs. Permeability was measured in rock samples at different stages: (i) directly in rock samples collected from outcrops; (ii) after cleaning; and (iii) on cut surfaces, to analyze how parameters such as dust, water content, or rugosity could affect permeability values obtained. Multiple points were measured for each sample, distinguishing between host rock, fill, and wall areas in point permeability values.

Additionally, core plugs were drilled and measured in the laboratory with a permeameter to compare values with those obtained using the portable permeameter. Preliminary results reveal that values obtained are accurate, especially when obtained from flat and clean surfaces. The use of a portable air permeameter is intriguing for characterizing permeability in bioturbated rocks. It provides values in just a few seconds from rock samples, cores, and outcrops, covering small areas and allowing the characterization of different parts of the burrow and the host rock.

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REVEALING RECENT SEDIMENTARY ENVIRONMENTS BASED ON BIOEROSION OF RELICT, UNBURIED SHELLS

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Taphonomical screening of unburied bioclastic remains is especially useful for discriminating actualistic taphofacies, based on the assumption that different environments lead to particular taphonomic routes [1,2]. The biological agents of postmortem destruction also depend on factors such as water energy, light exposure, sediment composition and sedimentation rate, which are nonlinearly distributed [3-6]. Therefore, a significant amount of taphonomic information relevant for environmental reconstructions can be obtained by screening bioerosion in dead substrates such as mollusk shells. In most cases, however, studies on taphonomic damage biologically originated are by far concentrated in tropical seas [3,7,8], generating a lack of studies on sub-tropical regions, which is the case in some Brazilian regions. Here, we focused on quantifying microendolithic damage present in mollusk and brachiopod shells recovered from the Southern Brazilian Shelf (SBS), using samples with depths ranging from 12 to 200 m, to test how much it varies according to differences in sedimentary and oceanographic parameters.

Samples were obtained using Van Veen grab dredge and Box-Corer samples during several oceanographic expeditions undertaken from 1975 to 1984 (Geomar VI, VII, XIII, XIV, XVIII, XXI and XXII) and in 1999 (REVIZEE), in an area ranging from parallel 27°S (near to Itajaí city) and parallel 34°S (near Chuí city). The SBS width varies around 130 to 200 km, and is heterogeneous, with sand dominating the shallow (up to depths of 60 m) settings and in northern region and muddy sediments predominating in the deep settings. In the southern area, mainly between isobaths 10 and 50 m, sand waves and elongated bioclastic deposits interrupt the usually smooth morphology [9]. This oceanographic region is marked by the confluence of warm Brazil current with Malvinas Current, which brings cold water with sub-Antarctic origin [10], both with variable intensity depending on the season of the year and the amount of freshwater discharge from the La Plata River. We analyzed shell remains from 13 samples evenly distributed in the area. The microendolithic damage present in shells were identified and the bioerosion pattern from each sample was evaluated together with oceanographic (salinity, temperature, current velocity) and sedimentological (grain size and composition) information. (The National Oceanographic Database – BNDO, an agency of the Brazilian Navy's Department of Hydrography and Navigation – DHN provided the raw data from each sampling station.)

A total of 2800 bioclasts were analyzed, and 1749 (~62.5%) were assignable to 35 genera of bivalve mollusks from 23 families, in addition to 29 brachiopods (~1%) and indeterminate fragments 1022 (~36.5%). 32 types of bioerosion traces were recognized, including 4 types of predation holes and one type of parasitism mark. The most frequent traces were: *Phormidium* isp., *Phytophora* isp., *Phytophora* isp. 2., *Entobia* isp., *Iramena* isp. and *Scolesia filosa* (Fig. 1). Less frequent traces were *Orthogonum* isp., *Gastrochaenolites* isp., *Gnathichnus pentax* and *Caulostrepsis taeniolar*. Several traces occur in a single locality, and most bioerosion traces had a very low frequency in each sample.

To test the relationship between microendolithic damage and environmental characteristics, we performed a Canonical Analysis of Proximity (CAP; Fig. 2). The Manhattan index was used, which is the most suitable for multivariate analyzes with taphonomic data, where varied ranges are obtained [11]. The relationship between the distribution of microendolytic taphonomic damage (relative frequency) present in the SBS and a series of environmental variables (standardized and normalized to adjust the numerical scale) were evaluated. The canonical variation, that is the relative amount of variation found in the bioerosion pattern

throughout the samples, and the sedimentary and oceanographic parameters indicate more than 85% of constrained variation. Most variation is contained in the first axis (42%), so the main variables that influence this damage are latitude, longitude, depth, and gravelly sediments. Microendolithic traces, such as *Orthogonum lineare*, *Phytophora* isp., and *Sarcomorpha* isp., among others, appear to be controlled preferentially by to latitude and longitude; the damage *Scolesia filosa* and *Fascichnus* isp. are more controlled by the environmental depth factor. *Pinnaceocladichnus* isp., *Iramena* isp., *Pennatichnus luceni*, and *Entobia* isp. show more correlation with gravel and sand substrates. *Phormidium* isp. occurs in samples richer in calcium carbonates. Other damages are preferentially controlled by the type of substrate and indeterminate fungi marks are associated with the presence of muddy substrates.

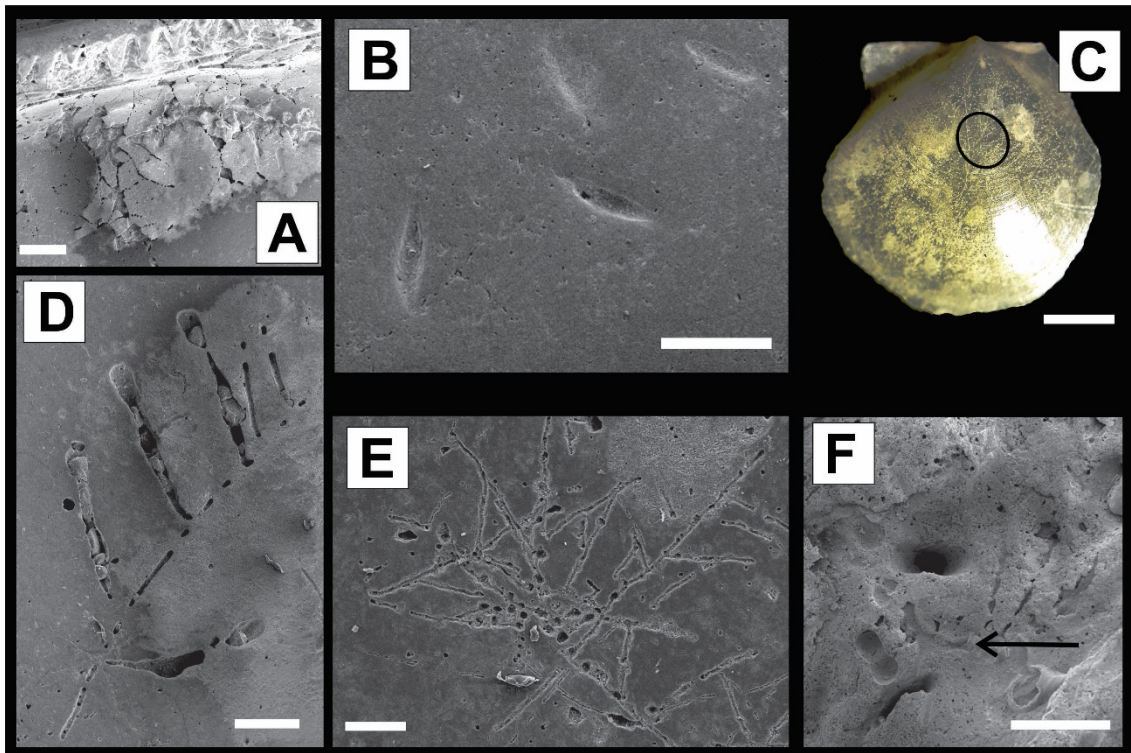


Fig. 1. Bioerosion traces (microendolithic traces) present on the continental shelf of Rio Grande do Sul. A. *Phormidium* isp. B. *Iramena* isp. C. *Phytophora* isp. D. *Pennatichnus moguerenica*. E. *Phormidium* isp. F. *Gastrochaenolites* isp. Scale bars: A, D = 200 μ m; B = 500 μ m; C, F = 1 mm; E = 50 μ m.

Endobiont organisms commonly feed on organic particles derived from surface planktonic productivity, therefore responding positively with primary productivity [3]. Fungi are heterotrophic beings that exploit organic matter by ‘drilling’ limestone substrates, including mollusk shells, and are completely independent of light exposure, inhabiting from intertidal to abyssal ocean depths [12]. In this work, several traces caused by fungi were correlated to depth and clay sediments. Other traces, produced by ctenostome bryozoans and clionid sponges have great relationship to gravel sediments, indicating also considerable planktonic productivity.

Cyanobacteria marks such as *Phormidium* were present in high intensity in all samples studied here, particularly in samples from high depths, far below the photic zone. Such traces (including but not restricted to *Phormidium*) indicate past environmental context that no longer exists in the sampled locality. Other from severe environmental changes, there is strong evidence [13] of intense temporal and spatial condensation (time-averaging) in the bathymetric range examined here. This is also consistent with interpretations of relative sea level variation during the Last Glacial Maximum: some samples at present depths of 135 m would easily be within the photic zone during the LGM, when the sea was 130 m below the present level [9].

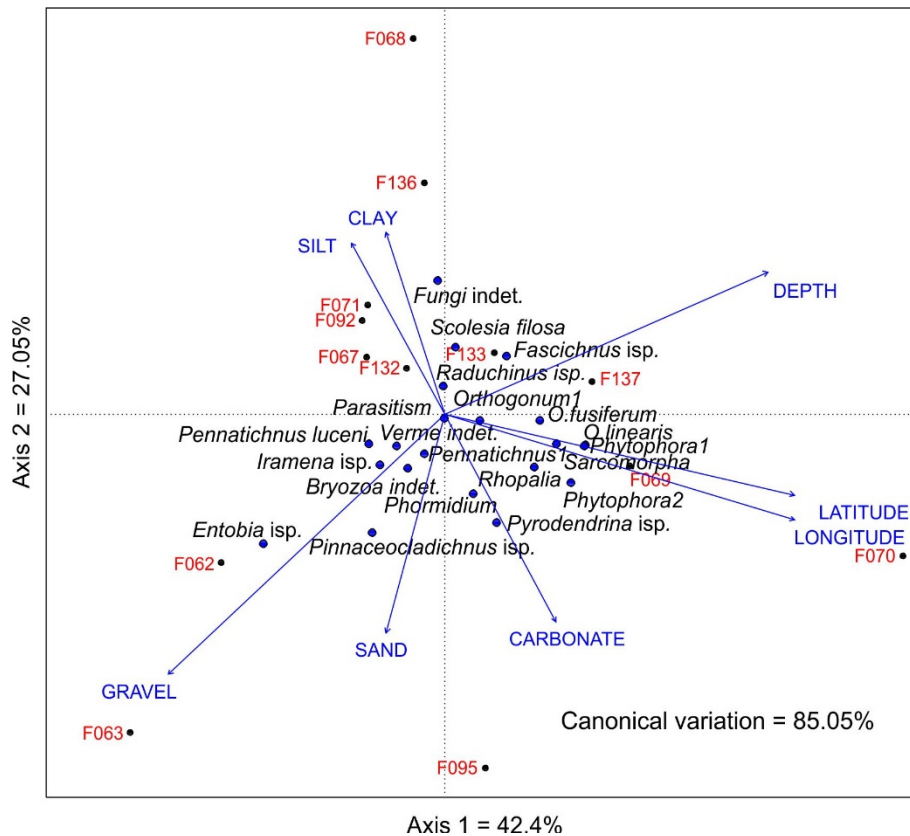


Fig. 2. Canonical Proximity Analysis, excluding damage of biogenic origin with very low frequencies. Axis 1 is significant using forward test for axes based on ANOVA model in R (function `anova.cca`; $F = 8.0502$, $p < 0.05$).

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CLAW-ONLY THEROPOD TRACKS IN THE EL MOLINO FORMATION, TOROTORO NATIONAL PARK, BOLIVIA

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Dinosaur tracks, including sauropod, theropod, thyreophoran and ornithopod prints, are abundant in the Upper Cretaceous (Maastrichtian) El Molino Formation, Bolivia [^{1,2}]. We studied the Carreras Pampa ichnosite on the outskirts of the town of Torotoro, within the Torotoro National Park. This ichnosite is very significant because of (i) the preservation of over fifteen thousand theropod tracks, the most significant number of dinosaur tracks from the same site known to date in the world; (ii) a wide variety of morphotypes of theropod tracks; (iii) a wide variety of styles of preservation; (iv) occurrence of many theropod trackways associated with tail drag traces; (v) clear predominant direction of trackway orientation (N-S and S-N, with subordinate E-W and W-E orientations); (vi) occurrence of many well-preserved theropod swim traces arranged in trackways; and (vii) association of bird tracks with theropod trackways.

The study area is within the Torotoro Syncline in the Bolivian Eastern Cordillera, in the Torotoro National Park (TTNP). In the TTNP, the Maastrichtian-Paleocene El Molino Formation consists of three members: (i) a lower member consisting of calcareous sandstones, carbonates and mudstones; (ii) a middle member dominated by thick uncemented turquoise and burgundy siltstones and green marls, alternating with thick layers of planar and cross-bedded oolitic and ostracod-rich fine grainstones and calcarenites, and minor evaporites, the thickness of the combined red siltstones and green marls increasing gradually upward; and (iii) an upper member consisting of alternating red and green mudstones, siltstones and calcarenites. The upper member is transitionally overlain by the Santa Lucía Formation, which consists mainly of brick-red mudstones and siltstones.

The tracksite consists of seven exposures (hereafter called sites) of the same layer characterized by similar track assemblages, lithology, and stratigraphic context. The seven exposures have been numbered 1 through 7, with sites 1-3 being continuous and separated from the rest of the sites by banks of partly eroded strata overlaying the trackbearing layer (Fig. 1). The bedding plane on which the studied tracks occur dips 2-4 degrees to the N-NW at sites 1 and 5-7, and 2-6 degrees to the N in sites 1-4. Wave ripples are extensive and well-preserved at site 3, irregularly distributed at sites 1-2 and 4, and absent at sites 5-7. Tracks were printed after the formation of the wave ripples.

Several styles of footprint preservation are observed at the Carreras Pampa ichnosite. With 'style of preservation,' we refer to the pattern of print impression determined by parameters such as distinctiveness and depth of the digits, shape and depth of the plantar/heel area, occurrence and depth of claw impressions, orientation of the digits, and presence of the impression of the hallux. In this study, we highlight a style of preservation in which tracks only show the print of the claw, with the trace of the rest of the autopodium either absent or barely distinguishable. The traces of the claws are preserved as round, elliptical or elongated indentations roughly arranged in an isosceles triangle, with approximately the exact distance between digits II and III and III and IV (Fig. 2). Some of the tracks show a very shallow outline of the plantar or the heel area, only visible at very low angle light. The position of the tracks in an alternating pattern of right and left sides confirms that these traces are vertebrate tracks. Occasionally, some tracks show a more conspicuous print of the digit, plantar and heel areas that are like the theropod tracks preserved on the tracksite, demonstrating the theropod nature of the traces. Based on the distance

between the preserved claw traces, the tracks are of small (10-20 cm) to medium (20-30 cm) length, made by theropods of 1.4-1.8 m of hip height.

These claw-only tracks occur on the same surface and near deeper tracks with digits and a fully printed plantar area. This suggests that the claw-only tracks were printed in a late stage of dewatering of the substrate when the sediment was firm but not dry. The presence of indentations in the substrate and posterior displacement rims in many claw prints suggest that the substrate was cohesive, and the distal ends of the toes with the claws were inserted into the sediment right before the animal withdrew its feet from the substrate. As the autopodia were lifted, they were sometimes pushed backward for the animal to gain thrust forward, thus pushing the cohesive sediment posteriorly, forming the expulsion rims.

The morphology and pattern of occurrence of the claw-only prints at the Carreras Pampa ichnosite match what Thulborn and Wade interpreted as tracks formed during the kick-off (K) phase observed at the Lark Quarry Environmental Park, western Queensland, Australia [3]. Those authors distinguish three phases during the trackmaker's step-cycle: T, or the touch-down phase when the foot makes contact with the substrate; W, the weight-bearing phase when the foot sinks deeper, leaving an impression; and K, the kick-off phase when the foot is released off the sediment. During the kick-off phase, the toes are lifted from the substrate, and in the process, the claws are incised into the sediment and pushed backward. In Carreras Pampa, that movement left puncture-like markings in the substrate, sometimes with rims of displaced sediment, most frequently in the posterior end of the indentations. Because of the high degree of firmness and cohesion of the sediment, in most tracks, the foot made no impression on the substrate during the T or the W phases, or the impression was very shallow. Only the claws left their impression because most of the animal's weight was supported by the distal part of the feet. Because digit III is the longest, frequently, its trace is the deepest and most developed; in some tracks, it is the only preserved. Thus, some of these trackways consist of tracks of three, two, or just one puncture-like marks alternating left and right sides.

At Carreras Pampa, this style of preservation is ubiquitous, with many entire trackways consisting exclusively of puncture-like markings, which the non-specialist easily misses.

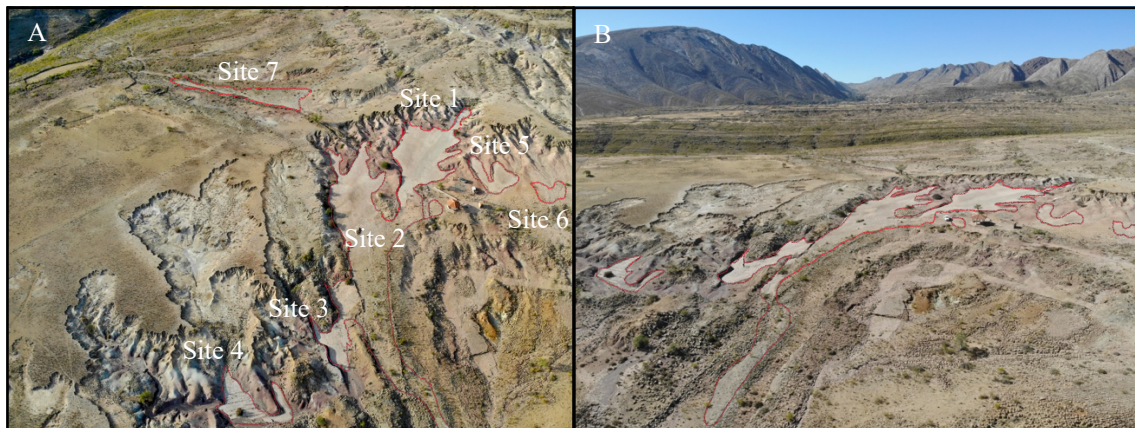


Fig. 1. A. View of the Carreras Pampa ichnosites with its seven areas of study. B. View of the Carreras Pampa ichnosite with the Torotoro Syncline in the background.

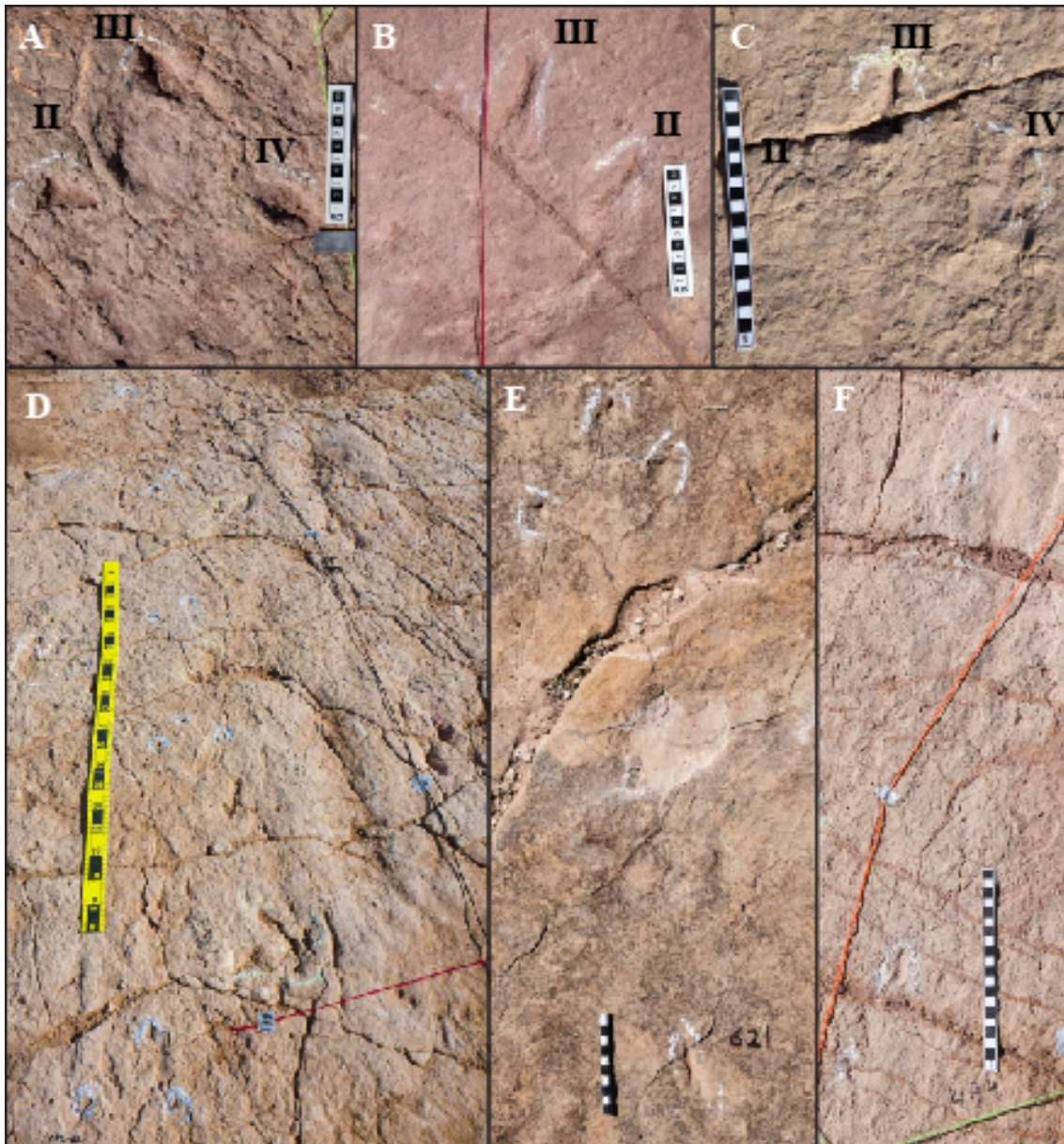


Fig. 2. Theropod tracks preserved as claw-only prints. A. Right track of trackway T22-2-36. B. Left track of trackway T22-2-53. C. Right track of trackway T22-128. D. Trackway CP6-62. The markings circled in blue chalk are the claw traces. Notice other tridactyl tracks marked with chalk. E. Trackway T22-2-621. F. Trackway T22-2-494.

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A NEW PROPOSAL FOR THE STUDY OF PALEOSYNECOLOGICAL RELATIONSHIPS BASED ON FOSSIL FOOTPRINT

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Paleoecological inferences based on fossil footprints have traditionally relied on morphological characters as ecological parameters. The classification of ecomorphotypes, e.g. webbed feet, based solely on morphological characters, carries the problem of implicitly accepting them as ecological equivalents [^{1,2}], all of them are aquatic birds assuming that they represent similar ecological roles, which does not always correspond to reality in nature. Body mass is a factor that influences the population density of birds [³] and their distribution range [⁴], making it an important variable when analyzing a community. In this work, we propose a more encompassing concept, the “ecoichnotype”, which combines traditional morphology and mass estimates. This concept can be applied in paleoecological models through a taxon-free ecomorphometric approach. Given that the ecological niche is an n-dimensional space [⁵], and that only morphological information is frequently analyzed in fossil footprints, the inclusion of mass adds a new dimension to the niche.

Analyses of avian footprints are carried out in two sites of the Vinchina Formation (Miocene, La Rioja Province), comparing them with each other. Both the Quebrada del Yeso and the Quebrada de La Troya record continental environments that have been the subject of geological and paleontological studies [⁶⁻⁸]. The tracking levels at Quebrada de La Troya correspond to an ephemeral lacustrine sub-environment, specifically playa-lake deposits. On the other hand, at Quebrada de La Troya the tracking levels represent meandering fluvial system and ephemeral lacustrine environments. In the Quebrada del Yeso, three ichnotaxa were identified: *Gragliavipes gavenskii*, *Phoenicopterichnus rector*, and cf. *Uhangrichnus* isp. and two unnamed morphotypes ascribed to Rheid and Rallids by Bonaparte 1965. In the Quebrada de la Troya, six were recognized: *Koreanaornis* isp., *Phoenicopterichnus rector*, *Gragliavipes gavenskii*, *Ardeipeda* isp., *Aramayoichnus* isp., and *Aramayoichnus chakana*. The decision was made to group *P. rector* and cf. *Uhangrichnus* isp. from both formations, as they represent a similar morphotype (tridactyl and webbed footprints) and estimated mass (between 3125 g and 3350 g). Despite their biological affinity and similar morphology, rheids are not considered equivalent between the sites because the mass calculated for the Quebrada de La Troya specimens is approximately 30% greater than that of the specimens from Quebrada del Yeso. In total, four ecoichnotypes were identified in Quebrada del Yeso and six in Quebrada de La Troya. Of these, two are shared between both sites, indicating a geographical/environmental pattern with species turnover [⁹]. The ichnodiversity and ecoichnotypes are summarized in Table 1. In the Quebrada del Yeso, where the more distal environments are less conducive to habitation due to high salinity [¹⁰], compared to Quebrada de la Troya, which has a higher supply of freshwater. This fact is reinforced by the shared affinity of the two groups with ibises and flamingos, which are known for their high environmental tolerance, allowing them to inhabit a broader range of environments.



Table 1. Summary of the ichnotaxa found at each site. The colors indicate ecoichnotypes.

Quebrada del Yeso	Quebrada de la Troya
<i>Gragliavipes gavenskii</i>	
Rheid morphotype	<i>Aramayoichnus chakana</i>
Rallid morphotype	<i>Aramayoichnus</i> isp.
<i>Phoenicopterichnus rector</i>	
cf. <i>Uhangrichnus</i>	<i>Ardeipeda</i> isp.
	<i>Koreanaornis</i> isp.

We suggest that our approach holds potential because both ecomorphotypes and ichnotaxonomy rely solely on the morphology of the footprint. Although these groups do not always coincide, they both use the same source of information. The size of a footprint is usually considered within the morphotypes, but it is not recommended as ichnotaxobase [11]. However, the size is directly linked to the total area of a footprint. Research conducted in last years [12] provides evidence that the area of a footprint would be directly linked to the mass of the producer, which gives the area of a footprint ecological relevance. From this perspective, given that the area (and possibly the size) of a footprint are not considered ichnotaxobases, the same ichnospecies can be considered as two different ecoichnospecies. For example, Rheids could be considered within the same ichnogenus, but differences in estimated masses group them into three different ecoichnotypes. An inverse case occurs with *P. rector* and cf. *Uhangrichnus*, where two different ichnogenera can be the same ecoichnotype, as their morphological characteristics and masses are similar.

In summary, the incorporation of body mass estimation offers a new dimension for differential analysis in vertebrate ichnology, introducing a parameter that has so far been overlooked. The ecoichnotype emerges as an innovative tool that opens a window to a new perspective for exploring synecological relationships in past ecosystems.

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MICROMORPHOLOGY OF MARINE INVERTEBRATE TRACE FOSSILS AND THEIR ETHOLOGICAL AND ICHNOTAXONOMIC IMPLICATIONS

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It is common for proposed paleobiological models for specific ichnotaxa to blend or associate concepts related to trace fossil production, basic feeding strategy, and biological affinities of the producers. These models persist in the literature as a whole, hindering the separation of partial interpretations (e.g., detailed interpretation of only the feeding strategy, or only the potential tracemaker) achievable through microscale studies of exceptionally preserved samples. Additionally, analyzing numerous specimens of the same ichnotaxon at different scales allows discussion of established ichnotaxobases due to the morphological variety involved, with the intention that morphologically based diagnoses present inferences about the tracemaker [1]. Micromorphological studies on current and fossil insect traces have yielded excellent results regarding producer behavior and biological affinity, along with ichnotaxonomic implications [2]. However, micromorphological studies on trace fossils produced by marine invertebrates with this scope are much scarcer, and include techniques such as petrography, scanning electron microscopy (SEM), X-ray microcomputed tomography, etc. [3-10]. These studies provide insights into the trace fossil production mode, potential tracemakers, substrate modification, and their consequences. For instance, in the case of *Nereites* MacLeay, some microscale features of analyzed specimens supported a construction differing from the typical worm-like organism model, aligning with other previous ideas, and also suggested an interpretation of an arthropod as tracemaker, a concept explored in previous neoichnological studies [6]. In the case of *Bolonia* Meunier, backfilling structures were interpreted as produced by the aboral and lateral spines of irregular echinoids, which worked together to compact the sediment anteroposteriorly and moved alternatively [10]. Here we present new results from the same line of research, describing and discussing the internal structure of examples of two other iconic ichnotaxa: *Ophiomorpha* Lundgren and *Dictyodora* Weiss. Exceptionally preserved examples of *Ophiomorpha* from Patagonian units (the Lower Cretaceous Agrio Formation and the Miocene Gaiman and Puerto Madryn formations), and of *Dictyodora* from the Silurian Gala Group (Scotland), were serially thin-sectioned. Transverse (vertical) and parallel (horizontal) to the bedding plane, or longitudinal and transverse to the main axis (depending on the ichnotaxon) sections were analyzed following previously used methods [3,6,10].

Ophiomorpha is one of the most globally recognized ichnogenera in marine deposits of various depths and age. Its ichnospecies are primarily classified based on pellet morphology. *Ophiomorpha irregulaire* Frey *et al.* exhibits conical or outwardly acute pellets with non-uniform sizes. The validity of this pellet morphology as diagnostic for *O. irregulaire* has been debated due to the possibility that these pellets are filled with sand-sized grains, enveloped by a layer of mud and organic material, and the conical appearance may result from an incomplete muddy rim [4,11].

This is supported by our results from Lower Cretaceous *Ophiomorpha*, where walls with coating rich in clays and organic matter bear pellets that appear flame-like but under microscopic analysis show reoriented grains that allow to infer their original spherical shape (Fig. 1A). Also, two types of organic matter were detected within the wall: discrete, dense organic particles of terrigenous affinity (mostly phytoclasts), and amorphous organic matter, mixed with the inorganic matrix. The presence of fermentation chambers [11] in some sectors is not disregarded. Additionally, the Miocene *Ophiomorpha*-rich deposits, described as composed by *O. nodosa* Lundgren, are now thought to include *O. nodosa* and *O. borneensis* Keij in intergradation, with a dominance of the latter. This implies the tracemaker was able to produce both type of pellets. The characteristic bilobed morphology of the pellets and its regular distribution is confirmed by what is observed in cross-section (Fig. 1B): the semi-spherical reworking by the tracemaker continues inside the wall, reinforcing the idea that these are originally bilobed pellets and not a taphonomical artifact. This material allows to speculate that *O. borneensis* might be more common than it is currently represented in the literature.

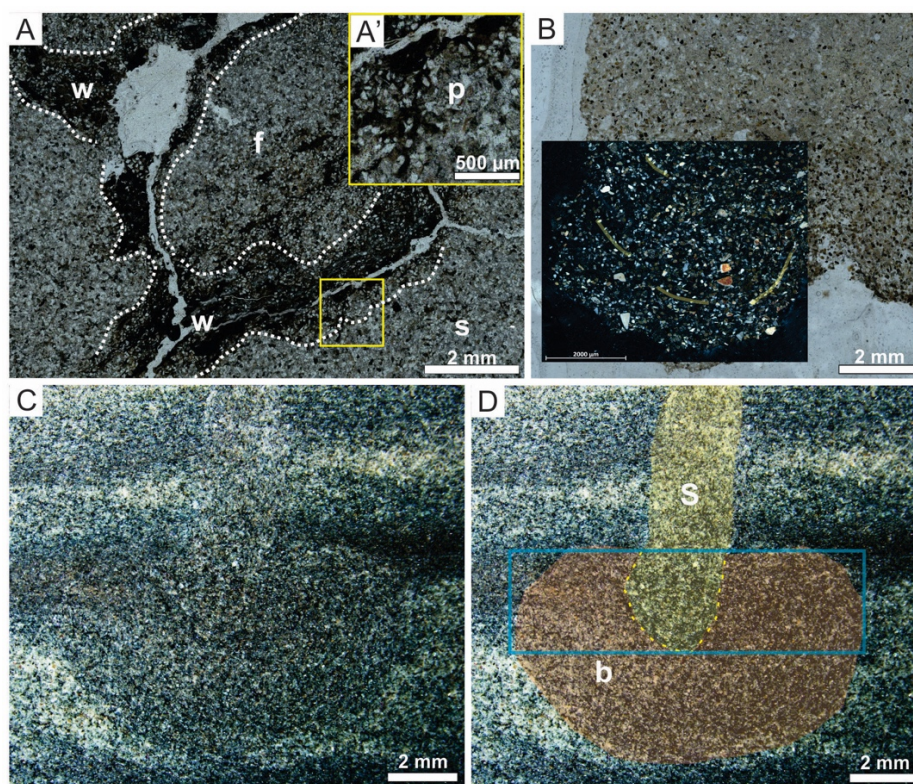


Fig. 1. A. Cross-section of main axis of *Ophiomorpha irregulaire* (CPBA 23328, UBA; Agrio Formation, Lower Cretaceous, Neuquén Basin) highlighting the wall in dotted white lines, and detail (yellow rectangle). A': Detail showing the original pellet morphology. B. Thin section of pelleted wall of *Ophiomorpha borneensis* (CNP-PIIC 1348, CENPAT; Gaiman Formation, Miocene). The section is parallel to the main axis of the burrow, showing bilobed pellet. One lobe of the pellet is shown with crossed nicols, and reoriented grains (transparent yellow lines) evidence that the semi-spherical reworking by the tracemaker continues inside the wall, reinforcing the idea that these are bilobed pellets. C. Vertical cross-section of *Dictyodora* (ABDUG Pal-10707, University of Aberdeen; Gala Group, Silurian, Scotland). D. Annotated version of C with the *spreite* (s) in yellow and the basal burrow (b) in orange. The dotted yellow line shows the area where they interconnect. The blue rectangle indicates the area that could explain the tripartite morphology seen in some samples, previously considered to be belong only to the basal burrow. Abbreviations: f = burrow fill; p = pellet; s = sandstone (bearing level); w = clay and organic matter-rich wall.

Dictyodora Weiss is a three-dimensional complex trace fossil characteristic of marine Paleozoic deposits recorded since the middle Cambrian. Its micromorphology under optical microscope has been illustrated [12,13] or very briefly described [14,15]; only one study illustrated part of the trace fossil under SEM [16]. Our preliminary results on Silurian samples include a thorough description of the internal structure of the area where the structures referred to as *spreite*



and basal burrow interconnect (Fig. 1C-D). In vertical cross-sections it is observed that the lowermost part of the *spreite* is surrounded by the uppermost and medial part of the basal burrow, in contrast with previous interpretations [17-19], allowing to discuss one of the possible interpretations of the *spreite*-producing structure as rigid [17]. The tripartite morphology of the basal burrow occasionally seen in samples [17,18] could be explained by this interconnection (Fig. 1D), supporting the necessity of a future diagnosis amendment [18].

More such studies are needed to challenge aspects of paleobiological/ethological models without necessarily completely discarding all ideas within them, and to discuss ichnotaxobases that do not depend but might rely on functional morphology.

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THE ICHNOGENUS *ZOOPHYCOS* AND THE FRASNIAN-FAMENNIAN BOUNDARY IN NORTH AMERICA: CAN WE USE TRACE FOSSILS TO CORRELATE ROCKS?

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The objective of the present work is to provide evidence that the first occurrence of the ichnogenus *Zoophycos* Massalongo, 1855 in black shales deposited in the North American Seaway (NAS) can be used to correlate the Frasnian-Famennian Boundary (FFB, Upper Devonian, c. 372 Ma). Thus, this research explores the use of ichnology as a biostratigraphic tool.

From the Middle Devonian to the Mississippian, most of the North American continent was covered by the epeiric NAS. It was bordered by orogens and the Laurentian Craton, and divided into several basins (from east to west: Appalachian, Michigan, Illinois, Iowa, Moose River-Huron Bay, Williston and Elk Point), separated from each other by submerged arches, with the Appalachian and Illinois basins being connected to the Rheic Ocean to the south via the Cumberland Sill. In this context, sedimentation processes in the NAS during the Frasnian and Famennian stages were dominated by deposition of thick black shale units (up to 100 m) comprising the Ohio, Chattanooga and New Albany shales, which evidence development of widespread marine anoxia.

In this research, we analyzed four cores representing sites in the Illinois Basin (n=3) and Appalachian Basin (n=1), and we compared our data with other sections in the literature from the Appalachian (n=2) and Moose River (n=1) basins. In the study units, the FFB is defined based on conodont biozones [1] and sequence stratigraphic correlations [2,3], representing a contact between highstand and transgressive systems tracts (Fig. 1).

Our results show dominance of black/dark-gray shales, with thin intercalations of greenish/light-gray shale or fine sandstone beds. Ichnological analysis allowed characterization of several ichnoassemblages (Fig. 1), with *Chondrites*, *Planolites*, *Zoophycos*, and vertical burrows in cases overprinting a mottled background, mostly occurring in light beds and penetrating downwards few cm.

In the lower Frasnian, all sections in the Illinois and Appalachian basins are dominated by shallow-tier ichnofabrics, indicating well-ventilated conditions during the deposition of sandstone and light-colored shale beds. However, a sudden turnover is recorded by a horizon consisting exclusively of *Zoophycos*, which transitions upwards in the Famennian to assemblages with scarce *Chondrites* or mottling and *Planolites* (Fig. 1). Occurrences of *Zoophycos* are also reported from sections in the Moose River [4] and Appalachian [5] basins, although the FFB-*Zoophycos* relationship is not well constrained there.

In all sections with well-defined biostratigraphic frameworks, the first occurrence (FO) of *Zoophycos* was nearly coincident with the FFB (0.5-8 m above) (Fig. 1). Therefore, the FO of *Zoophycos* within thick black shale successions can be tentatively used as a biostratigraphic indicator of the FFB in NAS sections lacking adequate biostratigraphic control.

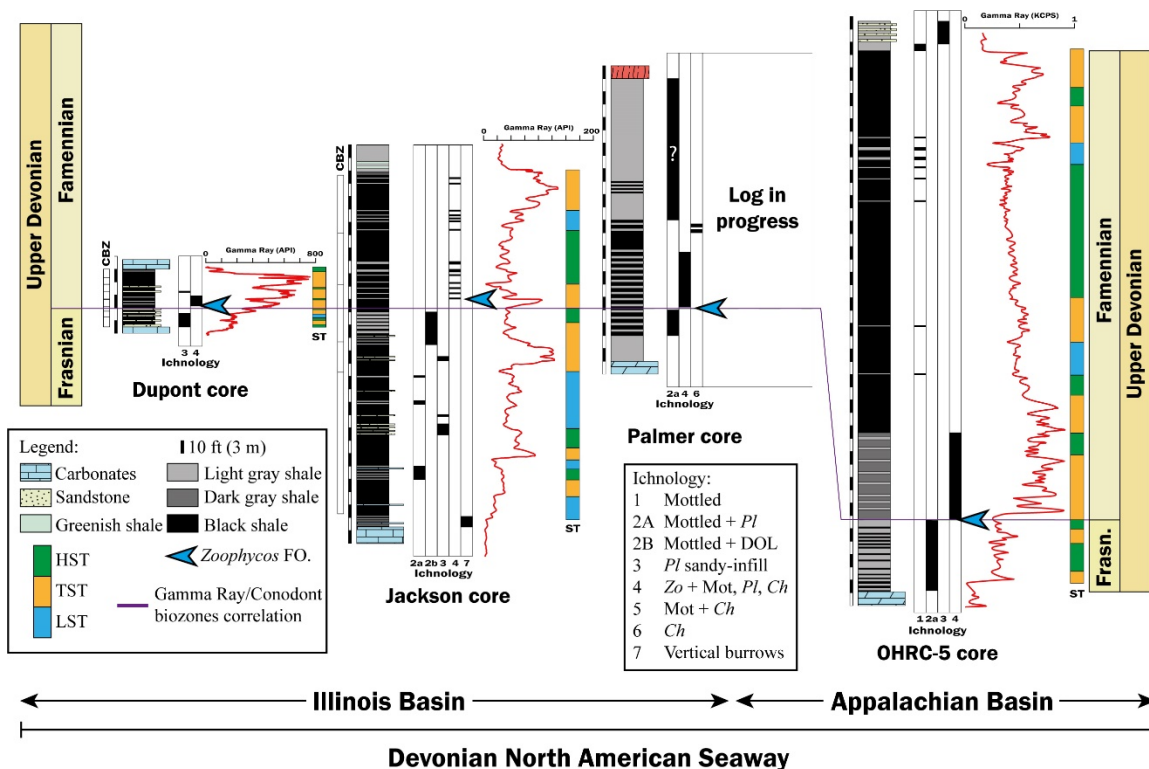


Fig. 1. Schematic stratigraphic columns of the studied cores. The Frasnian-Famennian Boundary is indicated by the purple line, after gamma ray logs, sequence systems tracts (ST) and conodont biozones (CBZ). Blue arrows indicate first occurrence (FO) of *Zoophycos*. HST: Highstand ST, TST: Transgressive ST, LST: Lowstand ST; *Ch*: *Chondrites*, DOL: dark-on-light burrows, *Mot*: mottled texture, *Pl*: *Planolites*, *Zo*: *Zoophycos*.

Notwithstanding, it should be noted that the presence of *Zoophycos* is linked to specific paleoenvironmental conditions, thus representing a caveat for this methodology. In shallower settings of the NAS, with high continental influence and short anoxic pulses, *Zoophycos* might not occur. This is the case for a section from the northern Appalachian Basin, near the Catskill Delta, where black shale beds are very thin (5-30 cm) [6], and relatively high-energy conditions and continental input of freshwater (deeper halocline) favored the presence of *Thalassinoides* around the FFB.

In conclusion, in the absence of adequate biostratigraphic control, the first occurrence of *Zoophycos* can be used to tentatively locate the FFB in black shale deposits of the Late Devonian North American Seaway.

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SUBSTRATE-CONTROLLED ICHNOFACIES AT THE PE0.0 BOUNDARY: AN EXAMPLE OF A RAVINEMENT SURFACE IN THE MIO-PLIOCENE, OCUCAJE DESERT, PERU

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The Eastern Pisco Basin in Southern Peru records a series of marine transgressive-regressive cycles characterized by thick layers of fine to very fine sandstones, diatomaceous and tuffaceous siltstones and claystones, bioclastic sandstones and phosphatic levels [1]. In Southern Peru, the boundary between the Chilcatay and Pisco formations (interformational -PE0.0-) corresponds to a discontinuity surface characterized by the presence of substrate-controlled ichnofacies, in particular *Glossifungites* and *Trypanites* ichnofacies. The present summary provides new ichnological (and sedimentological) data for both formations to understand the paleoenvironmental aspects involved.

The study area is located 350 km South of Lima, Peru, in the town of Ocucaje, where the Cerros Amara, Submarino, Buque, Buque Chico, Tres Pirámides, Zanjones, and Tinajones were surveyed. The work methodology consisted in the preparation of partial stratigraphic columns, carrying out an ichnological and sedimentological characterization of the PE0.0 surface.

The final section of the Chilcatay Formation in the study area is characterized, from base to top, by 10 m of coarse sandstones with fragmented bivalve and balanid remains, and the presence of *Thalassinoides* isp. This is followed by 15 m of fine massive sandstones with intercalations of carbonate sandstones. The last 5 m with massive yellowish-gray siltstones with abundant fish scales and millimetric levels of volcanic ash. The PE0.0 boundary corresponds to an erosional-irregular contact with a high degree of bioturbation and bioerosion affecting up to 50 cm depth. On this surface, the Pisco Formation begins with a matrix-supported conglomerate with a variable thickness of 5 to 25 cm, containing block-sized igneous clasts and amorphous silica (opal), phosphate nodules and carbonate intraclasts. Dispersed in a matrix of medium sandstone (arkose) with the presence of bivalve remains, balanomorph barnacles, elasmobranch teeth, cetacean bones, and wood. The igneous clasts, phosphate, and carbonate intraclasts are bioeroded throughout its surface. Over this level, massive layers of brown sandstones (40 to 50 m) with intercalations of carbonate and bioclastic sandstones are deposited.

The PE0.0 surface is characterized by the presence of three-dimensional network systems of bioturbation structures related to the activity of decapod crustaceans, reaching a depth of 50 cm and attributable to the ichnospecies *Spongeliomorpha iberica* and *Thalassinoides suevicus*. On the other hand, bioerosion structures related to the activity of lithophagous bivalves – *Gastrochaenolites lapidicus*, *G. turbinatus*, and *G. ornatus* – are very abundant. The fill of these structures consists of phosphate nodules and/or crystalline calcite and there are no cross-cut relationships between them suggesting a single colonization event. In contrast, the clasts in the basal layer of the Pisco Formation contain *Gastrochaenolites* isp., *Caulostrepsis cretacea*, *Maeandropolydora* isp., *Entobia* isp., and *Trypanites* isp. These affect the entire surface, overlap each other and are truncated, characteristics that suggest multiple colonization events and sufficient time for their formation. This ichnoassemblage characterizes the *Trypanites* ichnofacies product of the intense bioerosion of lithophagous bivalves (*Gastrochaenolites ornatus*, *G. turbinatus*, and *G. lapidicus*) [2], sipunculid polychaete worms (*Caulostrepsis cretacea* and *Maeandropolydora* isp.) [3], spionids (*Trypanites* isp.) [4,5], and clionaid sponges (*Entobia* isp.) (Fig.1).

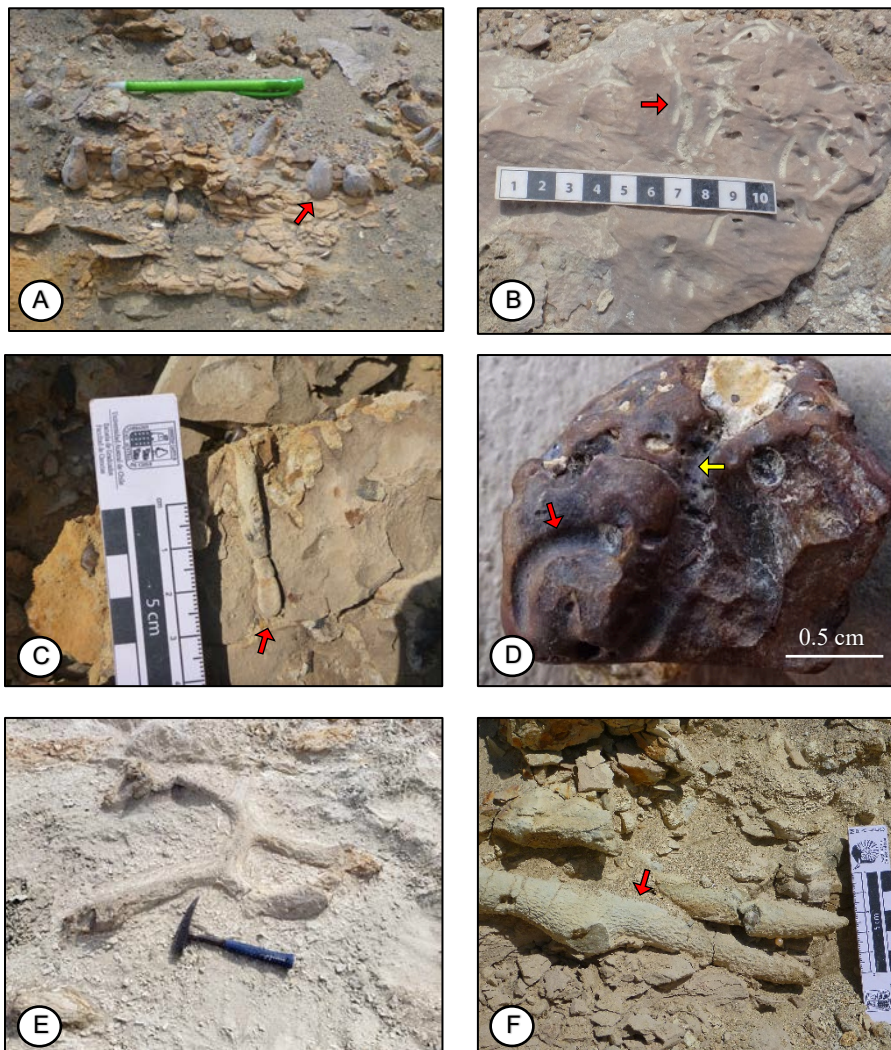


Fig. 1. Main traces in PE0.0 and basal layer of the Pisco Formation. A. Positive casts belonging to *Gastrochaenolites* isp. B. *Trypanites* isp. C. Positive cast of *Caulostrepsis* isp. D. *Meandropolydora* isp. (red arrow) and *Entobia* isp. (yellow arrow) E. *Thalassinoides suevicus*. F. *Spongiomorpha iberica*.

The events that led to the formation of the PE0.0 boundary surface can be divided into three main stages: (i) pre-discontinuity event, (ii) discontinuity surface, and (iii) post-discontinuity event.

The **pre-discontinuity event** corresponds to the deposition of the final facies of the Chilcatay Formation in a siliciclastic shoreface marine environment represented by massive sandstone layers and the presence of grayish siltstones in the offshore zone.

The **discontinuity surface** is the result of a significant low sea level and a superimposed ravinement event, corresponding to an intense process of abrasion and wave erosion during a transgressive process [6]. This surface is characterized by low sedimentation rates thus allowing the development of a depositional hiatus [7], a moment that is exploited by decapods organisms forming three-dimensional networks (ichnospecies *Thalassinoides suevicus* and *Spongiomorpha iberica*) and the presence of borings made by bivalves (ichnospecies *Gastrochaenolites lapidicus*, *G. ornatus*, and *G. turbinatus*). This ichnoassemblage represents the *Glossifungites* ichnofacies, which characterizes firm, semi-consolidated, dehydrated and non-lithified substrates. Contemporaneously, the reworked clasts or fragments (carbonate, siliceous or igneous) formed during the breaching process were a favorable substrate for the domicile of suspension-feeder organisms or passive predators, allowing the drilling action of bivalves, polychaetes and sponges (ichnospecies *Gastrochaenolites lapidicus*, *G. turbinatus*, *G. ornatus*, *G. torpedo*, *Trypanites* isp., *Caulostrepsis cretacea*, *Meandropolydora* isp., and *Entobia* isp.).



This ichnoassemblage represents the *Trypanites* ichnofacies, which characterizes hard, cemented, and lithified substrates.

The **post-discontinuity event** corresponding to the last major transgressive event in the basin with the deposition of the Pisco Formation. The ravinement process brought with it the formation of a basal lag deposit or transgressive conglomerate [⁸] characterized by the presence of phosphate nodules. The origin of these nodules would be associated with upwelling processes, a favorable environment for the precipitation of authigenic phosphate [⁹]. Sporadic high-energy processes allowed intraclasts to remain above or in the middle of these deposits, as well as fragments of invertebrates, vertebrates and trunk remains. Finally, the subsequent advance of the transgression allowed the deposition of powerful layers of massive sandstones.

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TETRADACTYL FOOTPRINTS FOUND IN LATE JURASSIC–EARLY CRETACEOUS TRANSITION IN THE GONDWANA WEST CONTINENTAL MARGIN, TARAPACÁ REGION, NORTHERN CHILE

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A new access road built for Teck Quebrada Blanca S.A., a copper mining company, located in the Tarapacá Region, Chile, crossing through the shallow marine Majala Formation facies and continental Chacarilla Formation facies (Late Jurassic-Early Cretaceous) [1], revealed a site called PK23, with fossil plant material and ichnites [2-4]. The facies analysis and the identification of the fossil wood, foliage and reproductive structures of halophytic conifers belonging to the Cheirolepidaceae family, suggest a deltaic margin environment with contributions of brackish waters [5,6].

In these formations, the different kinds of fossils are known, but they rarely have been found closely associated with each other, except for root marks and medium sized tridactyl dinosaur footprints (30-40 cm long) in the Chacarilla Canyon, site III [7].

Different biogenic structures recorded in sandstone levels were found at the PK23 locality, among them, three footprints (H1, H5, and H6) forming a bipedal trackway. H1 and H6 corresponds to tetradactyl right pedal impressions (Fig. 1), showing large digital divarication angles, and H1 has a tarsometatarsal trace (Fig. 1A-D). H5 morphology is not well defined, since it is a deep, collapsed footprint. This varied morphology within the trail, would be produced by the lateral viscosity variation of the substrate at the time the footprints were generated [8].

The record of Mesozoic tetradactyl footprints is relatively scarce, particularly in the Jurassic-Cretaceous transition [e.g. 9-12]. Therefore, we studied the morphological variations of an extensive footprint dataset, in which their producers have been already assigned, in order to place PK23 footprints within this morphospace.

We measured the digital divarication angles, which is the most stable character that remains recognizable in shallow to medium deep impressions representing the movement before kick-off stage [8,13], and applied Multivariate Analysis (PCA, Discriminant Analysis, Percentual Loading). Additionally, we build two hypothetical footprints from a 3D reconstruction of an articulated autopodium of a Late Jurassic tetradactyl dinosaur: *Chilesaurus diegosuarezi*, SNGM-1973 [14], to test for similarities.

Certainly, there is a low discriminant power for the multivariate analyses due to inherent variations of the digital divarication angles measured in footprints because of larger joint movement freedom, possible sediment collapse, as well as pedal anatomical diversity within tetradactyls, among other extramorphological features. Nonetheless, these analyzes highlight that the digit I mobility range in the fossil record, expressed as I-II divarication angle, is overall 5 times greater than the rest (Fig. 2B). Leaving aside the divergence angle between digit I and II, the PK23 tracks are plotting: (H6) Within indeterminate Dinosauria, and closer to Avialae; (H1) closer to Lepidosauria, Crocodylomorpha, Dinosauria indet., Theropoda and quadrupedal ornithischians. Both footprints further away from the virtual tracks of *Chilesaurus* (Fig. 2C). Therefore, we conclude that the producer of the PK23 footprints displays affinities with derived theropod pes, closer to birds and it is unlikely attributed to *C. diegosuarezi*.

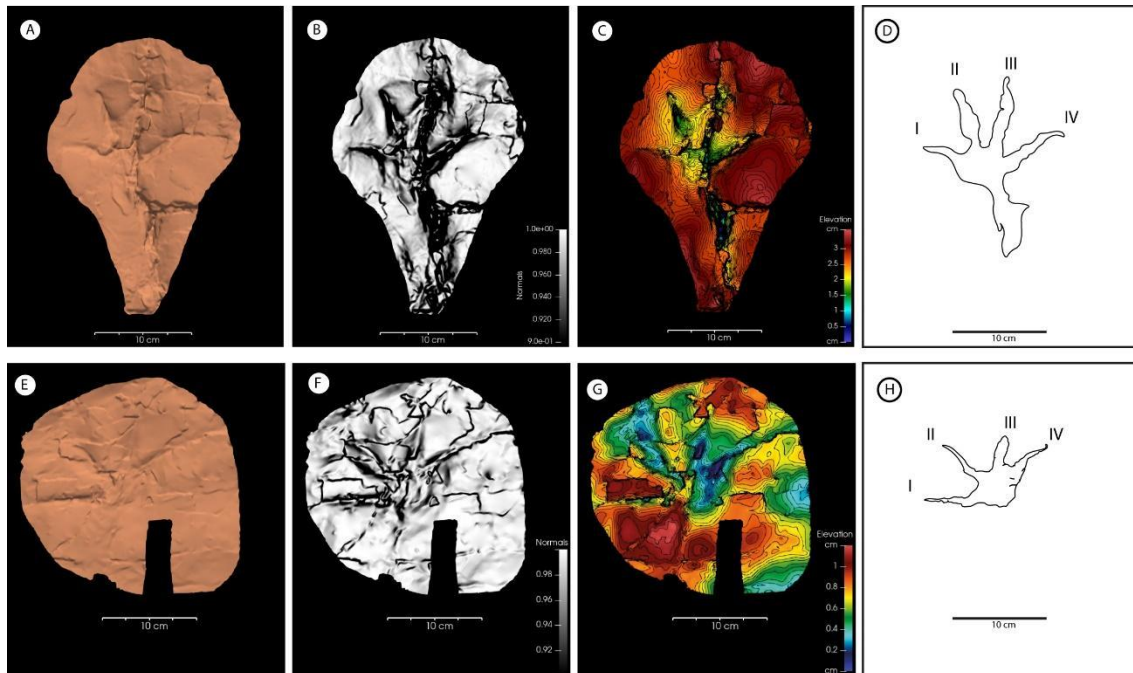


Fig. 1. PK23 tetradactyl footprints H1 (A-D) and H6 (E-H). Three-dimensional surface mesh (Go!Scan20; A and E); tilt graph mapping (Paraview 5.5; B and F), topographical map (Paraview 5.5; C and G) and footprint outline (Adobe Illustrator; D and H). Scale bars = 10 cm.

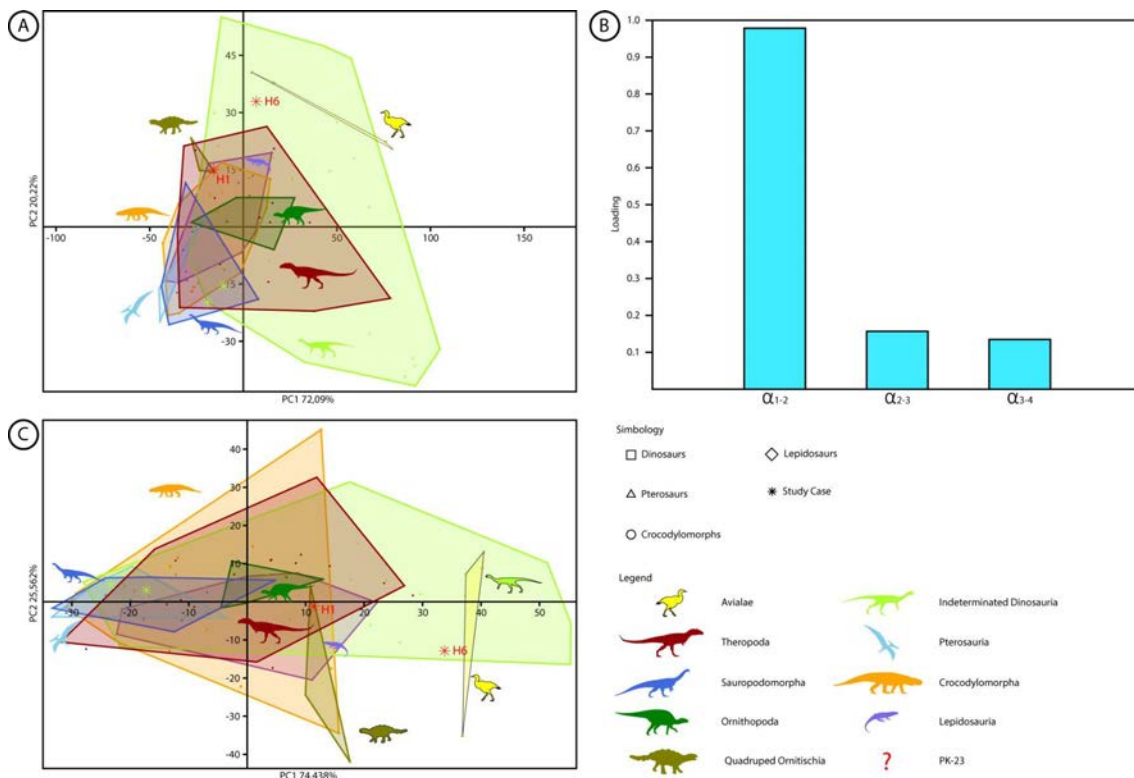


Fig. 2. Multivariate analysis of digital divarication angles. A. Principal Component Analysis between divarication angles I-II, II-III and III-IV showing high overlap of Dinosauria, Crocodylomorpha, Lepidosauria, Theropoda and Sauropodomorpha, while Pterosauria, quadrupedal ornithischia, Ornithopoda and Avialae are plotting further apart. B. Loading input is shown to mostly come from I-II divarication angle. C. Principal Component Analysis of divarication angles II-III and III-IV showing less overlap. The groups are better distributed than the previous analysis for Dinosauria, Crocodylomorpha, Lepidosauria, Theropoda and Sauropodomorpha, while Pterosauria, quadrupedal ornithischia, Ornithopoda and Avialae are plotting apart. H1 and H6 (red asterisk); *Chilesaurus* 3D modeled trackways (green asterisk).



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BIOEROSION PATTERN AS A PALEOENVIRONMENTAL PROXY: A CASE OF STUDY FROM QUATERNARY DEPOSITS FROM CENTRAL PATAGONIA (CHUBUT, ARGENTINA)

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Bioerosion is a valuable proxy for biotic parameters which allows us to infer paleoenvironmental and paleoclimatic changes over time. In Argentina, bioerosion analysis on marine Quaternary deposits increased in recent years [^{1,2}]. However, most ichnological studies are concentrated in the San Jorge Gulf [^{2,3}], one of the most productive regions of the Argentine Sea at present. Little is known about the deposits located in Patagonia north of the Gulf. To the north of Bahía Camarones (San Jorge Gulf, Central Patagonia, Argentina) is the Bahía Vera-Cabo Raso. It presents well-preserved deposits from the Jurassic to the Quaternary [^{3,4}]. However, ichnological analyses are scarce in this area, with only one bioerosion trace known from the Quaternary marine deposits [³]. Therefore, this work aims to ichnotaxonomic composition recorded in molluscan shells in the Bahía Vera-Cabo Raso area during the Quaternary and to discuss the differences in bioerosion patterns through time.

This area extends nearly 9 km from north to south and is located on the east coast of Chubut province, about 60 km north of Bahía Camarones (Chubut, Argentina; Fig. 1A). Beach ridge deposits periodically through shoreline progradation, each representing a certain time interval [³]. According to various authors [^{4,5,6}], this area presents parallel beach ridge deposits dating from the Late Quaternary to the present. The Pleistocene deposits include a sandy matrix-supported conglomerate with mollusc shells, followed by a level of fine-grained sandstones to medium-grained conglomerates with occasional or absent mollusc shells. Holocene deposits in Cabo Raso are characterised by fine to medium-grained sandy-conglomerates with mollusc shells, while Bahía Vera presents coarse-grained pebbly deposits without sands and scarce shells. For the Pleistocene and Holocene deposits, 4000 cm³ of bulk samples, containing biogenic and sedimentary material, were collected from fossiliferous levels in abandoned quarries. In both places, for the modern deposits, all complete mollusc shells found within a 1x1 m surface were collected. Once separated from the sedimentological content, the shells were washed with water and then with hydrogen peroxide (30% volume) using an ultrasonic cleaner. Later, they were observed under a binocular stereoscopic microscope. The absence/presence of bioerosion traces was recorded and separated according to the mollusc taxa and the age of the samples. Each sample represents an age (Modern, Mid-Holocene and Pleistocene), even when we can assume that a little time-averaging could be present, this does not disturb the general patterns interpreted. Only bioerosion traces produced by macroorganisms were considered. The identification of the bioerosion traces was based on the most recent diagnosis and emended diagnosis [⁷].

For Cabo Raso (Fig. 1B), a total of 524 mollusc shells were analysed, with 262 belonging to Gastropoda and 262 to Bivalvia, while for Bahía Vera, a total of 254 mollusc shells were analysed, 116 belongs to Gastropoda and 138 to Bivalvia (Fig. 1C). In the Holocene deposits from Bahía Vera, only shells from Gastropoda were found. A total of 15 ichnotaxa were recorded in the area: trace fossils produced by annelids (*Maeandropolydora* isp. and *Caulostrepsis* isp.), brachiopods (*Podichnus* isp.), bryozoans (*Finichnus* isp., *Iramena* isp., *Pennatichnus* isp., *Stellichnus* isp. and *Pinaceocladichnus* isp.), Cirripedia (*Centrichnus* isp. and *Rogerella* isp.), gastropods (*Caedichnus* isp., *Radulichnus* isp., *Renichnus* isp. and *Oichnus* isp.) and sponges

(*Entobia* isp.). The most abundant traces from the area are illustrated in Figure 1 (Fig. 1D-H). However, some differences in the ichnological content between Cabo Raso and Bahía Vera are important to consider.

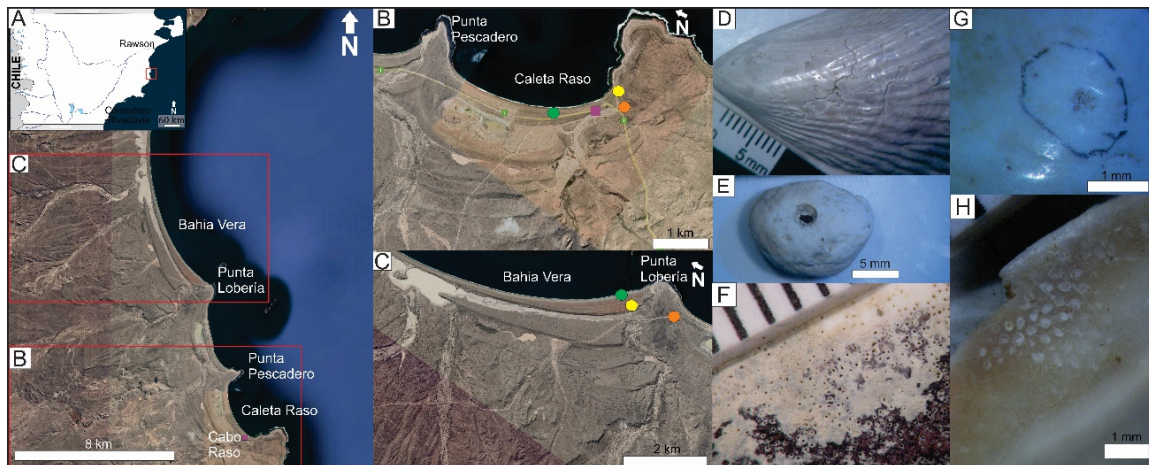


Fig. 1. Location of the study area in the northeast of Chubut (Patagonia). A. Satellite image of the area. B. Satellite image of Bahía Vera. C. Satellite image of Cabo Raso. Green point: modern deposits. Yellow point: Holocene deposits. Orange point: Pleistocene deposits. Violet Square: Cabo Raso locality. D-H. Examples of the most abundant bioerosion trace recorded in this area. D. *Maeandropolydora* isp., Modern, Bahía Vera. E. *Oichnus* isp., Pleistocene, Cabo Raso. F. *Iramena* isp., Pleistocene, Cabo Raso. G. *Podichnus* isp., Holocene, Cabo Raso. H. *Finichnus* isp., Holocene, Bahía Vera.

For Cabo Raso, mollusc shells from the Pleistocene deposits present a higher percentage of bioerosion (92 shells with bioerosion from 140 total shells). Considering all the samples, the most abundant ichnotaxa were: *Iramena* isp, *Podichnus* isp., *Finichnus* isp., *Maeandropolydora* isp. and *Oichnus* isp. However, *Finichnus* isp. was not recorded in the Holocene bulk samples. This is not the only difference through age. The number of ichnogenera in the Pleistocene and modern deposits is greater than in the Holocene deposits, where only four ichnotaxa were recorded. Based on the ethological categories, *Domichnia* predominated in all ages and *Pascichnia* was only present in Modern samples.

In Bahía Vera, the most abundant ichnotaxa taking into account all the samples from this zone are *Iramena* isp., *Renichnus* isp., *Maeandropolydora* isp. and *Finichnus* isp. However, there are differences between the samples of different ages. In the Pleistocene, only four ichnogenera were recorded (*Caedichnus* isp., *Iramena* isp., *Podichnus* isp. and *Pinaceocladichnus* isp.) and the number of ichnotaxa increased in the Holocene samples (from four to ten). Additionally, the mollusc shells from the Holocene present a higher percentage of bioerosion (26 shells with bioerosion from 35 total shells) and the modern samples show the highest ichnodiversity (14 ichnogenera). Considering the ethological categories, it is very similar to Cabo Raso: *Domichnia* is dominant across time and *Pascichnia* was only observed in the modern samples. The bioerosion pattern observed in the Quaternary deposits from the study area shows that there is not a great variation between Bahía Vera and Cabo Raso. However, some dissimilarities need to be discussed.

The Patagonian shelf extends from 38°S to 55°S and is influenced by the cold Malvinas current. It is well known the direct relationship between this current and the high levels of chlorophyll biomass (high nutrient) found in the Patagonian shelf [8]. Also, there is a well-defined Patagonian current generated by the interaction between the Magellan Strait's discharge and the Malvinas current to the South of 49°S [8]. This causes a decrease in the sea surface temperature (SST) and high productivity on the Patagonia coast [9]. Hence, it is possible to suggest that this environmental scenario in the area is responsible for the higher number of ichnogenera observed in the Modern samples in both places. The bioerosion pattern of Pleistocene deposits in Cabo Raso exhibits similarities with the modern bioerosion association (13 ichnotaxa in both ages). A comparable outcome was noted in the Quaternary bioerosion pattern from Bahía Camarones,



where the authors concluded that during the Pleistocene there was an active coastal front similar to the present [4]. It is possible that in the Cabo Raso locality, a similar scenario is occurring, i.e. a high-productivity environment. For the Pleistocene deposits in Bahía Vera, only 4 ichnotaxa were identified. However, the biogenic content of these deposits is very scarce (10 shells in total) and it is not possible to compare with the Pleistocene deposits of Cabo Raso and Bahía Camarones. Therefore, it is possible to suggest that the environmental scenarios in both ages were very similar.

Regarding the Holocene samples, both localities differ not only in the bioerosion association but also in the malacofauna association. As mentioned before, the Holocene deposits from Bahía Vera are conformed by coarse-grained pebbles while Cabo Raso presents fine to medium-grained sandy-conglomerates. This sedimentological difference is a response to different environmental energy between the studied places, i.e. Bahía Vera is a higher energy environment than Cabo Raso. In the mid-Holocene, a period of maximum warming called the Hypsithermal event occurred. This event increased the SST and weakened the oceanic anticyclones that provoked the increase in the energy of storms. The coastal sectors of Caleta Raso and Bahía Vera are very different; the former is a small embayment between two peaks, creating a protected zone from high-energy waves. In contrast, Bahía Vera is an open coast more affected by wave action. This difference might explain the absence of bivalve shells in samples from Bahía Vera. Also, Bahía Vera shows a higher bioerosion percentage and a higher number of ichnotaxa. A recent study of shells from lagoons in Africa suggests that higher bioerosion is enhanced by higher water energy [10].

In recent years, it has been demonstrated that the mollusc shells (and associated traces) preserved in the marine Quaternary deposits of Patagonia serve as a proxy for paleoenvironmental conditions [2,4]. This study not only reinforces this idea but also suggests that among the possible environmental factors, biological activities could be primarily determined by temperature and nutrient productivity [2,4,11].

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BETTER INTEGRATION OF ICHNOLOGY WITH INTERTIDAL FACIES MODELS

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Intertidal flats are fascinating. Unlike many depositional settings, intertidal zones can be visited during low tides, and most people have walked on an intertidal flat at some time or another. In spite of their accessibility, and indeed our sedimentological familiarity with them, intertidal flat deposits can be surprisingly difficult to identify in the rock record. The reason for this is largely due to insufficient models and recognition criteria for these sedimentologically variable settings.

In particular, proposed facies models for intertidal flat deposits minimize or even disregard bioturbation styles and distributions in intertidal zones. Rather, sedimentological characteristics, primarily manifest as heterolithic bedding, are heavily relied upon as diagnostic indicators of intertidal flat deposits. Additionally, existing intertidal flat models tend to disregard the sedimentological variability that results from geographic considerations, such as position within a bay or estuary, proximity to a fluvial source or – thinking of a much larger scale – latitude (i.e. tropical versus temperate versus polar). Finally, facies models for intertidal deposits have decidedly favored the characterization of macrotidal and even megatidal settings, skewing the overall view of intertidal flat sedimentology.

Using modern and ancient examples from sub polar, temperate, subtropical and tropical settings, we propose an interpretive framework that recognizes the importance of bioturbation for the identification of intertidal flat deposits. The main ichnological criteria for recognizing intertidal zones are:

1. In most shallow-marine settings, at least those which are characterized by progradational geomorphological entities, show lowered bioturbation intensities upwards (and landwards). This is a result of hydraulic energies increasing upwards causing increasingly shifting sediment substrates. In brackish to marine intertidal zones, bioturbation intensities tend to increase upwards: this is one of the few facies associations that exhibit this trend.
2. In micro- to mesotidal settings, subtidal units are sparsely to moderately burrowed whilst their tidal-flat counterparts exhibit very heightened bioturbation intensities with comparatively homogeneous burrow distributions. This results from a combination of a high-density population of infauna and slow rates of sediment aggradation.
3. Mud-dominated intertidal strata are normally highly bioturbated (typically BI 3 to 6) with bioturbation increasing in intensity upwards. Primary bedding, if preserved, is associated with tidal run-off creeks. Sand-dominated intertidal flats typically contain more abundant primary sedimentary structures. This is due to wave-reworking of the tidal flat, tidal-dune migration or the presence of variably scaled tidal run-off creeks. Within sandy intertidal flat deposits, BI ranges between 0 and 4, with rare beds displaying higher intensities of bioturbation.
4. Owing to their much more energetic nature, macrotidal subtidal deposits are normally unburrowed, and their intertidal counterparts are only sporadically burrowed with heterogeneous distributions.



5. In bays and estuaries, tidal currents, shallow waters, intertidal exposure, and close proximity to a marine source of abundant algae and plankton, commonly lead to an abundance of food such that consumable resources are available in the water column, on the sediment surface, and within the sediment. This leads to a scenario wherein two trophic adaptations occur: (i) some burrows (e.g., *Rosselia*, *Thalassinoides*, and *Palaeophycus* are constructed for trophic functions that differ from their marine counterparts; and, (ii) burrows of trophic generalists (e.g., *Teichichnus*, *Planolites*, *Cylindrichnus*, and *Skolithos*) dominate the trace-fossil suite.
6. In the rock record, assemblages indicative of polymodal resource exploitation are identifiable on the basis of their low diversities, high bioturbation intensities, and their trace-fossil composition. These features are similar to the characteristic trace assemblages that define the brackish-water model, suggesting that brackish-water stress and abundant food resources are conflated. Indeed, it may be that a common characteristic of many brackish-water locales is the presence of tidal currents coupled with a copious and regularly replenished food resource base. As such, low diversity, trophic generalist suites may be more closely allied with tidal resource distribution and storage than the presence of brackish water.
7. If the entire vertical succession is preserved, supratidal deposits overlie the intertidal units. The supratidal zone is commonly eluviated, locally massive appearing, contains rhizoliths, and displays rare trace fossils, including *Psilonichnus* and *Scoyenia*.
8. Due to the fluctuating positions of high and low tide levels, the shift from subtidal to intertidal, and then to supratidal sedimentation is marked by gradational changes in both sedimentology and ichnology. As a result, identifying an exact boundary that separates subtidal areas from intertidal zones can be challenging, and this difficulty is amplified in areas with larger tidal ranges.

Importantly, this synthesis ratifies some conclusions drawn by other researchers [e.g., 1,2]. Furthermore, the patterns described above are consistently observed in modern and ancient tidal environments. This paper will use the Lower Cretaceous McMurray Formation in Alberta, Canada, the Eocene Baronia Formation in Spain, Pleistocene and contemporary deposits in Willapa Bay, USA, and the current Gironde estuary as examples. Notably, there are exceptions in the Gironde estuary which will be explored further.

This presentation also considers, in some cases only hypothetically, the impact of latitudinal variations in these deposits. For example, decapod crustaceans are dominant in tropical to temperate settings. However, in tropical settings, these are represented by a mixture of shrimp and crabs: temperate intertidal flats are more likely dominated by shrimp. Moving northwards, decapods progressively shift to subtidal zones with the intertidal zone containing more annelids and isopods. Unfortunately, these trends are not fully worked out, and need more research to fully characterize.

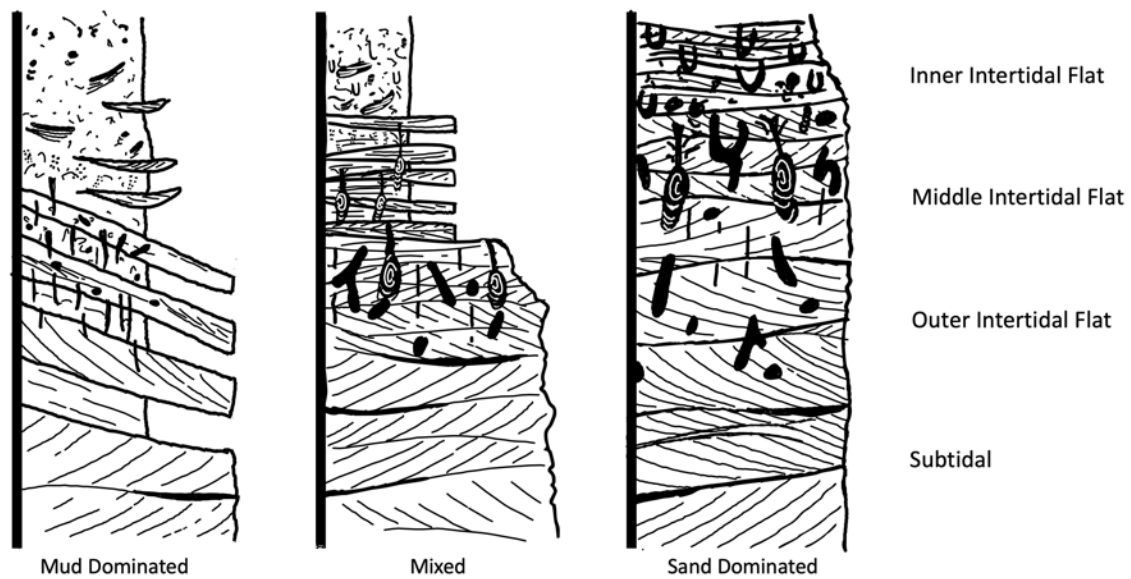


Fig. 1. An ichnological facies model for intertidal flat deposits needs to take into account several factors. These include grain size variability, tidal range, salinity and latitude. This diagram idealizes temperate zone mesotidal setting intertidal flats. The mud-dominated example emphasizes the burrows of mud-dwelling annelids and smaller clams. The sand-dominated examples show increasingly conspicuous bivalve and crustacean burrows. A simple example like this illustrates the potential complexities of intertidal facies models, and perhaps highlights that there is still research needed to fully characterize these settings.

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VARIABLE *OPHIOMORPHA* ICHNOFABRIC: IMPROVING THE UNDERSTANDING OF MOUTH BAR ENVIRONMENTS IN FAN-DELTA COMPLEX DEPOSITIONAL SETTINGS FROM THE UPPER CRETACEOUS OF NW SOUTH AMERICA

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Fan-delta deposits, an important sedimentary component of fan-delta complexes, are scarcely described in the ancient record because of the difficulty to distinguish them from other coarse-grained deposits (e.g., alluvial, fluvial, or deep marine). This handicap is overcome when a good record of physical/biogenic sedimentary structures or fossils unambiguously marks the influence of the receiving basin. However, this is usually not the case. During the Latest Cretaceous in Colombia, coarse-grained sedimentary systems were developed, associated with the uplift of mountain ranges linked to the collision with the Caribbean Plate. Not much is known about the sedimentary evolution of these systems.

Here, we present the *Ophiomorpha* ichnofabric record as a key proxy of marine influence within a generally fluvial-dominated system, improving the paleoenvironmental understanding and reconstructing animal-substrate interplay during the evolution of a fan-delta complex. The ichnological record, together with detailed sedimentological analysis, allows us to differentiate three *Ophiomorpha* ichnofabric types, distributed in four stratigraphic levels. The stratigraphic distribution of sedimentological and ichnological features points to distal alluvial environments towards the base, dominated by debris and sheet flows deposits and locally shallow braided channels, evolving upward into well-developed braided fluvial system whose facies arrangement is related to channel fills. Subsequently, a basinward migration of the sedimentary system is recorded through the occurrence of the first level with *Ophiomorpha* ichnofabric A, and then ichnofabrics A and B in levels 2 and 3, respectively, suggesting marine-influenced mouth bar settings. Toward the top, another steep basinward migration is evidenced by *Ophiomorpha* ichnofabric C in level 4, indicating wave-dominated processes in distal mouth-bar environments. The record of marine-influenced and dominated levels may indicate relative sea-level fluctuations related to local or autogenic processes at the basin scale. Furthermore, the present study demonstrates the capability of *Ophiomorpha* tracemakers to colonize challenging sedimentary environments.



WHEN THE SUN IS JUST RIGHT: A REMEMBRANCE OF PATRICK R. GETTY

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Fig. 1. Patrick R. Getty. Photograph by Andrew M. Bush.

Patrick Getty, who was a beloved member of the ichnological community for many years, passed away on 15 November 2021. He was a gifted educator, a prolific scientist, and a good friend (Fig. 1). Here, we remember Patrick and highlight some of his contributions to ichnology.

Patrick earned his A.A. degree from Springfield Technical Community College in Springfield, Massachusetts (USA), followed by a B.S. in Biology from the University of Massachusetts. Patrick loved dinosaurs, and his mentor at UMass, Margery Coombs, suggested that he do an undergraduate research project on a local dinosaur footprint assemblage. Thus began his career as an ichnologist, and he quickly became an expert in the fossils and rocks of the Hartford Basin. Patrick further refined his expertise while earning his M.S. from the Department of Geosciences at the University of Massachusetts, working with James “Whitey” Hagadorn of Amherst College on the enigmatic Cambrian trace fossil *Climactichnites* [1-3].

Patrick came to the University of Connecticut in 2007 as an instructor for the *Age of the Dinosaurs* course in the Geosciences program, and he began his Ph.D. the next year in Andrew Bush’s lab. His dissertation title – *Ichnology of Carboniferous and Jurassic Tetrapods and Insects* [4] – hints at his wide-ranging interests. After receiving his Ph.D. in 2014, Patrick worked as Visiting Assistant Professor in Geosciences at UConn for several years before joining the faculty of Collin College near Dallas, Texas.

Despite his relative youth, Patrick was widely respected as an ichnologist, paleontologist, and geologist. He had a keen eye for detail, a deep knowledge of the fossil record, and a careful, thorough approach to science [5-7]. Although dinosaurs were his first passion, he loved all trace fossils, eventually working on the taphonomy and interpretation of traces of insects, mollusks, amphibians, and fish [8-11]. Many of his papers reexamined classic sites and trace fossils, refining the taxonomy while adding insights on the identity, behavior, and ecology of the tracemakers [12-14]. Working at museums and sites in the Connecticut Valley region, he added his interpretations of the dinosaur behavior, as well as adding to knowledge of the food web at the time [15-21]. Patrick had the good fortune to regularly work with specimens in the Amherst College Museum of Natural History, especially those described by Edward Hitchcock (Fig. 2). His interpretations of

trace fossils were often buttressed by experimental trials and observations of living animals [22-29].



Fig. 2. Holotype of *Anomoepus curvatus* (Amherst College Museum of Natural History, ACM ich 52/10). Photo by PRG.

He loved leading field trips for students and for colleagues, including several focused on the trace fossil record of Connecticut and Massachusetts for the Geological Society of America and the New England Intercollegiate Geological Conference [30,31]. Patrick had a talent for finding traces in the most unlikely places “when the sun was just right”, as well as for locating long-neglected historical sites. Even the most casual excursion could turn into an impromptu public lecture if curious children (or adults) were in the vicinity. He was also interested in the history of ichnology, and in sharing that knowledge [32].

Patrick was devoted to his students, in the classroom and in the field. As a graduate student, he was already mentoring a suite of undergraduate research projects, many of which led to scientific publications. Examples include his reevaluation of *Lunulipes obscurus* with Sam Loeb [24] and his description of the Powder Hill dinosaur trackway site with Laurel Hardy [16]. As a popular lecturer, he has influenced many hundreds of students at several schools. He was also dedicated to public outreach and to making the geosciences a more welcoming discipline, both in his day-to-day life and by helping to organize the Geological Society of America’s annual LGBTQ+ social.

Patrick was a good colleague and friend, and he will be remembered for all he did for his students and colleagues, as well as for his research.

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THE PALEOENVIRONMENTAL SIGNIFICANCE OF VERTEBRATE COPROLITES IN POTIGUAR BASIN, BRAZIL

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This study aims to investigate the paleoenvironmental significance of vertebrate coprolites found in deposits of the Açu Formation (Potiguar Basin) in the east of the state of Ceará. The Açu Formation (Albian) corresponds to a coastal sedimentary sequence, characterized by lagoon-type depositional systems with estuarine channels [1].

The first coprolites were collected in 2015, through field works carried out by the Macrofósseis Laboratory – IGEO/UFRJ, when four collection points were mapped. Currently, 156 specimens were collected from sandy sediments of medium to coarse grain size, weakly consolidated, and are associated with numerous osteoclasts from fishes and reptiles (crocodilians, chelonians, and dinosaurs). The coprolites are morphologically characterized into three types, 80% being cylindrical and spiral-shaped pellets, 12% larger ovoid, and 65.8% undefined shape (Figs. 1, 2). Paleoenvironmental interpretations were carried out based on the analysis of structural aspects of coprolites and diagenesis.

The incorporation of coprolites into the sedimentary record always involves three aspects: animal diet, coprolite mass, and incorporation in the sedimentary record. These coprolites occur in clusters on the surface and loose in the sediment, in association with abrasion features characterized by breaks in one or both coprolite terminal portions, a polished surface, and different degrees of oxidation by oxides of iron and magnesium. These preservation state can be emphasized with the presence of physicochemically resistant elements such as teeth (crocodiles and dinosaurs), turtle shells, crocodile scutes, gar scales, and assorted small bone fragments.

The coprolite occurrence [2] associated with the condition of fossil elements, can help to explain the reason of a high number of coprolites of undefined shape and scarce presence of large specimens, which can be evidence of episodes with intense transport. However, last studies of bones, scales, and small teeth associated with coprolites [3] show the presence of eight kind of fish taxa. The existence of a diverse ichthyofauna can explain the high number of pellets found and suggests that the environmental settings might had been favorable to newly born fish whose produced these pellets. The distribution and reworking of coprolites as observed in the study area suggest paleoecological conditions that favored the formation of channel-lag concentrations.

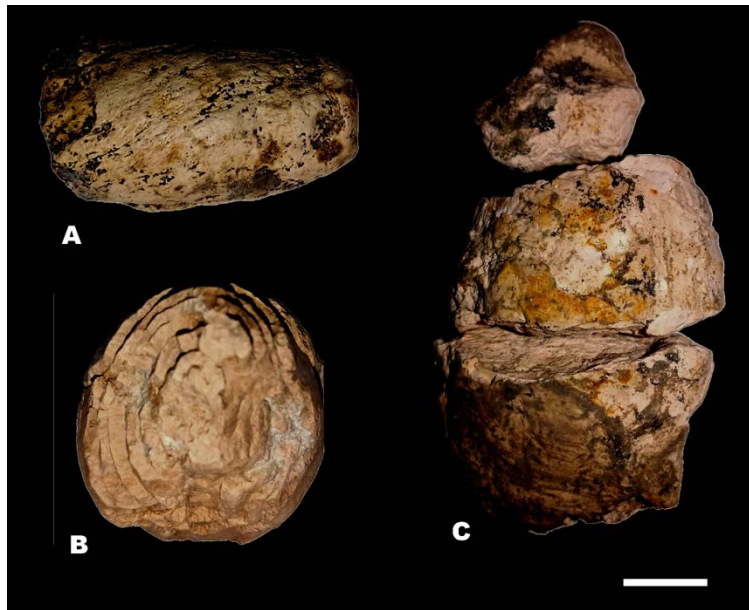


Fig. 1. The principal morphotypes of large coprolites: cylindrical (A), with internal spiral marks (B), and large ovoid with breaks (C). Scale bar = 1 cm.

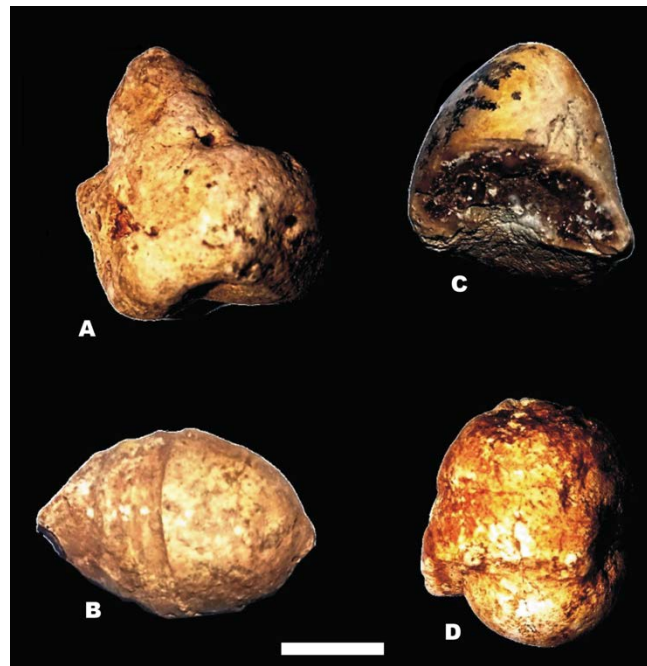


Fig. 2. The morphotypes of pellet coprolites: A. A section of cylindrical specimen. B. Small spiral. C. Terminal section of a cylindrical pellet. D. Ovoid specimen. Scale bar = 1 cm.

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DIAGENESIS AND PALEOENVIRONMENT CONDITIONS IN THE TRACE FOSSILS OF THE PIRABAS FORMATION

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The Pirabas Formation is composed of fossiliferous carbonates and siliciclastics, encompassing stratified and non-stratified biocalcitrudites, marls, calcilutites, and biohermites [1]. This formation displays diverse bedding structures, including parallel lamination, heterolithic and wavy-linen bedding, and low-angle and hummocky cross bedding [1]. The facies analysis indicates shallow marine platforms comprising lagoons, shoreface/foreshore, and mangrove paleoenvironments [1,2]. The Pirabas Formation displays a progradational depositional pattern with alternating inner/middle shelf deposits, tidal inlets, bioclastic barrier/front shoal deposits, and an internal platform comprising tidal flats and lagoon deposits (shallow and deep). These deposits form high frequency ascending shallowing cycles [3].

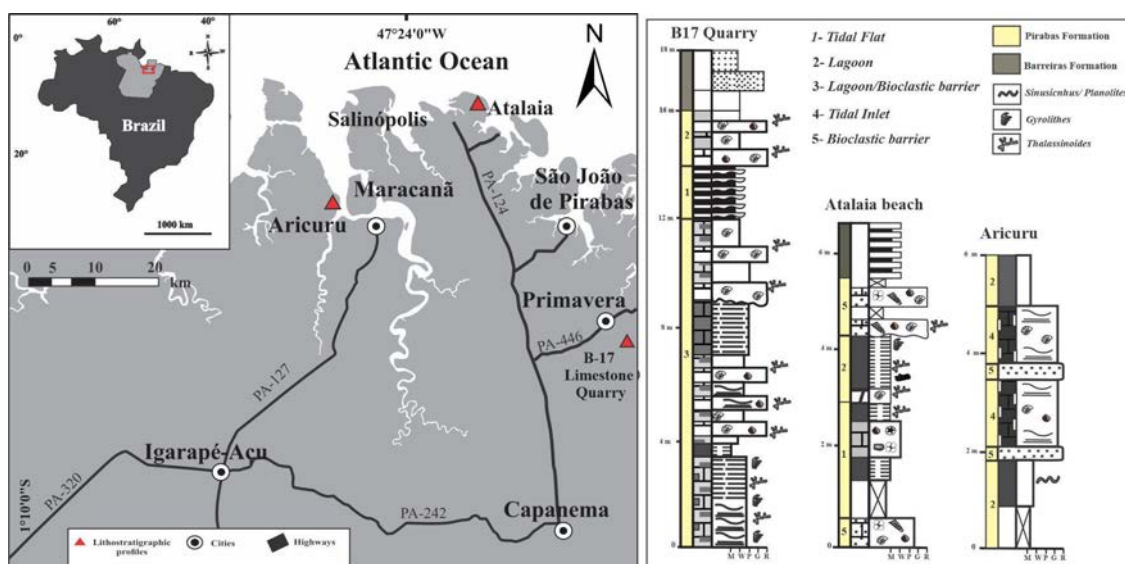


Fig. 1. Location map of the study area and profiles displaying the trace fossils of the Pirabas Formation.

Sedimentological and stratigraphic studies were conducted at three outcrops in the Salinópolis region: Atalaia Beach (0°35'37.48" S/47°18'50.49" W), Maracanã (Aricuru, 0°44'35.68" S/47°29'8.31" W), and Capanema (B-17 quarry, 01°02'48" S/47°09'18" W) (Fig. 1). During the fieldwork, stratigraphic profiles were created, and samples of trace fossils were collected whenever possible (ICGEO 209-218, 330). These trace fossils samples were subsequently gathered for petrographic, chemical, and mineralogical analyses. Thin sections were prepared for petrographic analysis to assess the main constituents of trace fossils' infill. XRD crystallographic analysis was conducted using the back-loading method with the X'Pert MPDPRO PANalytical diffractometer, equipped with a Cu anode ($\lambda=1.5406$), to obtain information about the chemical and mineralogical composition of the material. Subsequently, microstructure analyses using SEM/EDS were performed on both samples and thin sections, both of which underwent gold metallization. The acquisition of secondary electron images and EDS data (energy dispersive spectroscopy) was carried out using the Zeiss MEV equipment, model SIGMAVP, located at the Microanalysis Laboratory of the Geosciences Institute (IG) at UFPA.



Trace fossils found in carbonate-siliciclastic deposits exposed in outcrops of the Pirabas Formation in northern Brazil include *Gyrolithes*, *Thalassinoides*, and *Sinusichnus* [4,5]. These traces are associated with decapod crustaceans that inhabited the mangroves and lagoons of a carbonate shelf during the Miocene [1,2]. The presence of various types of mineralization is commonly found in association with bioturbated levels. This paper aims to elucidate the various types of minerals found in the burrows' infill, providing valuable insights into the geological processes and environmental conditions under which they were formed. Additionally, the objective is to enhance our understanding of the diagenetic processes linked to the presence of trace fossils in the Pirabas Formation.

Three distinct filling types (Fig. 2) were identified. The first type comprises microcrystalline calcite, abundant terrigenous grains, ostracod fragments, bryozoans, foraminifera, red algae, echinoderms, and interspersed with micrite laminae, as well as sparse bioclastic grains. This filling occurs in *Sinusichnus*, *Thalassinoides*, and *Gyrolithes* found in the lagoon facies deposits. The second type consists of microcrystalline siderite, ankerite, green algae, bivalves, and bryozoans. It occurs in *Thalassinoides* from lagoon deposits near the contact with the siliciclastic deposits of the Barreiras Formation. The core of these fillings is enriched in microcrystalline siderite, while ankerite predominates at its edges. The third type comprises framboidal pyrite and hematite, and predominantly found in deposits associated with mangroves. In these deposits, *Thalassinoides* galleries coexist with framboidal pyrites and hematite. According to the analyses conducted in this study, the burrows excavated by decapod crustaceans in the shallow marine settings represented by the Pirabas Formation support the interpretation that these deposits underwent processes related to early diagenesis. However, mineralogical distinctions can be observed in the trace fossils of lagoon deposits compared to those formed in mangroves.

The presence of trace fossils associated with the lagoon facies, filled with a matrix rich in microcrystalline calcite and bioclasts, suggests that these deposits were well oxygenated, indicating a high production of calcium bicarbonate. Decapod crustaceans, while creating burrows, introduced mucus, plant debris, and fecal material. The constant presence of these organisms in bioturbations created a contrast, with more oxygen-rich conditions inside the burrows, as opposed to the surrounding sediments where suboxic conditions prevailed. With the progression of burial, there was a change in the water conditions within the pores, allowing for the ideal availability of iron (Fe) and magnesium (Mg) ions. This change facilitated the suitable conditions for the replacement of calcite by ankerite [6].

The precipitation of siderite in the trace fossils of the Pirabas Formation may be associated with the presence of high concentrations of Fe^{2+} in the interstitial waters. This could be linked to terrigenous influxes into the lagoon, accompanied by the decomposition of organic matter by microorganisms near the water-sediment interface. Such activity triggers a sequence of organic matter decomposition processes involving oxidation, reduction of nitrate, Mn, Fe, and sulfate [7]. In the case of the Pirabas Formation lagoons, siderite forms in coastal sediments with tidal variations that promote the development of suboxic environments, leading to siderite precipitation [8].

Mangroves exhibit a complex geochemistry resulting from the interplay of biotic and abiotic factors in their sediments. Moreover, they boast a heightened concentration of organic matter and sulfate availability that fosters microbial activity. However, it is crucial to recognize that the upper layers of mangroves exhibit oxic conditions, whereas sediments beneath the water/sediment interface are anoxic [9]. The presence of pyrite and hematite in trace fossils of the mangrove deposits in the Pirabas Formations indicates that crustaceans transitioned from the more oxidizing substrate surface to deeper areas with reducing conditions. This transition led to framboidal pyrite precipitation through sulfate reduction by microorganisms interacting with organic matter in mangrove roots, as well as in traces fossilized with mucus, animal or plant remains [7,9]. These interactions facilitated the reduction of Fe^{2+} to Fe^{3+} . Bioturbation played a crucial role in promoting the reintroduction of oxygen in the deeper layers of the substrate. This

process, in turn, facilitated the exposure of pyrites, which underwent oxidation and transformed into hematite [9].

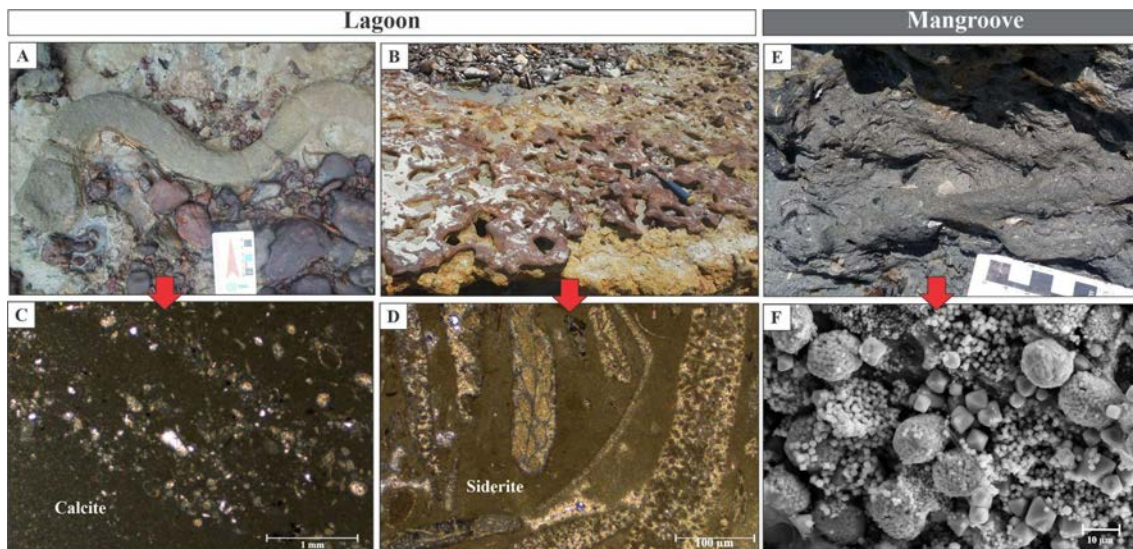


Fig. 2. The main types of trace fossil fillings in the Pirabas Formation are as follows. A-D. Composition of trace fossils from lagoons. E-F. Representation of framboidal pyrites in trace fossils belonging to mangrove deposits.

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PALEOECOLOGY OF THE EARLY PALEOZOIC AND THE ESTABLISHMENT OF THE PHANEROZOIC BIOSPHERE

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The early Paleozoic (538–252 Ma) witnessed the appearance of new ecosystems, with novel ecological niches and biotic interactions in comparison to Precambrian ecology. Biodiversity curves indicate substantial increases during two evolutionary breakthroughs, namely the Cambrian explosion and the Ordovician radiation. Trace fossils evaluate changes in animal-sediment interactions and offer an independent line of evidence from body fossils to decipher the nature of these evolutionary radiations. However, further detailed research needs to be done to assess how these global trends are expressed at a local scale. In this study, we compile large datasets from several units: the Chapel Island Formation (CIF, Ediacaran–Cambrian Age 2), the Random Formation (RF, Cambrian Age 2), the Armorican Sandstone Formation (ASF, Floian, Lower Ordovician), and the Kermur Formation (KF, Katian, Upper Ordovician). Trace-fossil occurrences and metrics are plotted in high-resolution sedimentary logs (reported at 1:40). Ichnologic metrics are: (i) vertical bioturbation (Bioturbation Index); (ii) bed surface bioturbation (Bedding Plane Bioturbation Index); (iii) trace-fossil width; and (iv) trace-fossil depth. Trace-fossil taxonomy follows modern standards with the use of ichnotaxobases and is supported by extensive literature reviews. Distinguishing between evolutionary and environmental cues is achieved through the generation of time-environment matrices. The base of the Fortunian (CIF) is characterized by a slight increase in bioturbation intensities and a burst in trace-fossil diversity and disparity, defining the establishment of a firmground ecology in shallow-marine environments. The Cambrian Age 2 (CIF and RF) corresponds to the development of fully bioturbated intervals of sediment and the establishment of a mixground ecology of modern aspect. Preliminary results from the studied Ordovician strata (ASF and KF) suggest that bioturbation levels remained high in shallow-marine environments and were mainly recorded as monospecific assemblages of millimeter-scale deposit feeders (i.e., *Planolites*) and/or the shallow infaunal activity of very large arthropods (tracemakers of *Cruziana* and *Rusophycus*, up to 15 cm wide). In addition, adequate environmental conditions allowed for new animal-sediment interactions to develop both in offshore (e.g., *Asterosoma*, diverse *Cruziana* and *Rusophycus* ichnospecies) and shoreface (e.g., *Daedalus*). Multidimensional cube analyses demonstrate that niche construction and ecosystem engineering expanded significantly during the middle Fortunian and remained complex through the Ordovician. In summary, this research contributes to the advancement and reinforcement of significant evolutionary trends by employing standardized investigative techniques and using an approach that seeks to effectively apply modern ecological concepts to the field of evolutionary paleoecology.



THE ICHNOGENUS *DICTYODORA* WEISS: AN ATTEMPT TO UNIFY TERMINOLOGY

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Dictyodora is a three-dimensional complex trace fossil characteristic of marine Paleozoic deposits recorded since the middle Cambrian [1]. According to the latest diagnosis [2], it is composed of a basal structure (lower margin) and a very thin structure (*spreite*) arranged perpendicular to the basal burrow showing a variable inclination. This structure appears as an irregular spiral or meandering "band", which corresponds to the intersection of the *spreite* with the planes parallel to the bedding [2]. Both structures were described as such in the last diagnosis [2]; however, they were called by different names in the literature. For example, the lower margin [2,3] has been referred to as the lower section [4] or basal burrow [5-7] or even as the lower part of the *spreite* [8]. Likewise, the *spreite* has been named as: striated vertical wall mural structure [9], narrow "wall" structure [6], dorsal vertical sediment curtain [10], crest-like or vertical wall [4,11], mid-dorsal vertical ridge [7], snorkel *spreite* [12]. Additionally, given the three-dimensional morphology of *Dictyodora*, the vertical, horizontal, and oblique preservations of each structure, and the different horizontal expressions (lower or higher horizontal sections) have also been given different names.

The *spreite* is the structure that is frequently preserved in different planes and bedding levels (Fig. 1). The horizontal expression of the *spreite* is the most recorded and has been described with a wide range of morphologies and used as the main ichnotaxobases to determine ichnospecies. Six ichnospecies are currently valid [4]: *Dictyodora liebeana* (Geinitz), *Dictyodora scotica* (M' Coy), *Dictyodora silurica* Yang and Hu, *Dictyodora tenuis* (M' Coy), *Dictyodora zimmermanni* Hundt and *Dictyodora atuelica* Pazos *et al.* The morphology of the horizontal expression of the *spreite* varies in the ichnospecies from regular to irregular meanders with one or more orders of sinuosity. In other cases, irregular non-meandriiform paths, and spiral meandriiform or spiral forms are distinguished (Fig. 2). The use of terms such as "wide", "loop", "regular" or "irregular" have different meanings depending on the author. For instance, the word loop has been used to describe a meander [13]. This heterogeneity in the use of descriptive terms (some even used the original descriptions/diagnoses) is another problem when comparing ichnospecies. Moreover, some of the diagnostic features of the ichnospecies are not mutually exclusive and are sometimes present in more than one ichnospecies. For example, *D. scotica* is distinguished by regular first-order meanders, although they may also be irregular according to the same authors [3]. Also, *D. silurica* has both regular and irregular meanders [14]. In the case of *D. tenuis*, the morphology of the meanders is irregular [5], but it has also been described as completely irregular or more or less regular [15]. Another case is that of *D. zimmermanni* where the shape of the meanders is either quite irregular [13] or is less regular than in *D. scotica* [16] or may have both morphologies [15]. As used so far, this character is not useful to differentiate ichnospecies. Similarly, the secondary sinuosity is also ambiguous, being described as absent for example in *D. zimmermanni* but it seems present when illustrated by the same authors [13], or it is not described in *D. silurica* but it is showed in the type material [14].

This variability in the terminology hampers a proper comparison between specimens and an ichnotaxonomic discussion. Therefore, it is important to find an agreement in the use of these terms. Although it is beyond the scope of this work to discuss and redefine the ichnospecific ichnotaxobases for *Dictyodora*, it is important to achieve a consensus on the descriptive terms. After the study of hundreds of specimens from Gondwana and Laurentia, to solve some of the

problems mentioned above, terms for each component and their respective morphologies are proposed (Fig.1).

The term “basal burrow” is proposed because “lower margin” and “tube” have not been used *in extenso* in the literature. Furthermore, the use of the term “tube” refers to a single cylindrical structure, and in some cases the basal burrow does not have a cylindrical morphology as a whole, but rather lenticular, ovoid and even trilobed. Moreover, the term *spreite* is preferred for the medial structure arranged perpendicularly and above the basal burrow, partly because it is the term used in the diagnosis [2], but mainly because it is a descriptive term, highlighting characteristics of the structure such as the delicate and fine striations observed in its lateral vertical sections. Furthermore, it is also the term used most extensively in the literature. Finally, this structure has a wide range of inclinations (40°–90°) and is not consistent with being called a ‘vertical structure’ in the strict sense of the term. Given the morphological range of the *spreite* depending on which part of its vertical extension is sectioned, to aid in the description three different sections are here proposed. The wider, *lower section*, where the basal burrow connects to the *spreite*, is observed only in vertical or oblique preservation of *Dictyodora*, which is not frequent. The *middle* and *upper sections* are defined in relation to the lower section and reflect the horizontal expressions of the *spreite* that are most commonly preserved. The use of the terms “upper” and “middle” is considered arbitrary and with the sole purpose of allowing comparison of the *spreite* when this structure changes morphologically vertically within the same specimen [17]. Additionally, different terms to describe the morphology of the trajectories of both the basal burrow and the horizontal expression of the *spreite* are proposed (Fig. 2).

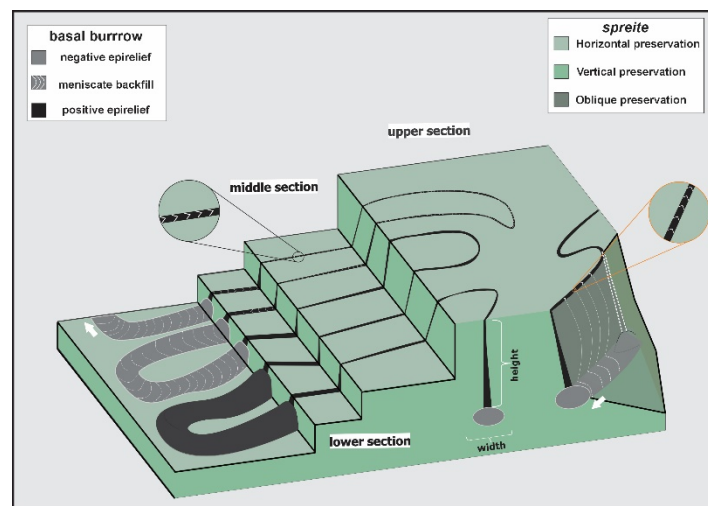


Fig. 1. Block diagram modified from a classical paper on *Dictyodora* [5] showing the three-dimensional nature of the ichnogenus, the different preservational expressions of the *spreite* and basal burrow, and some of the terminology proposed here.

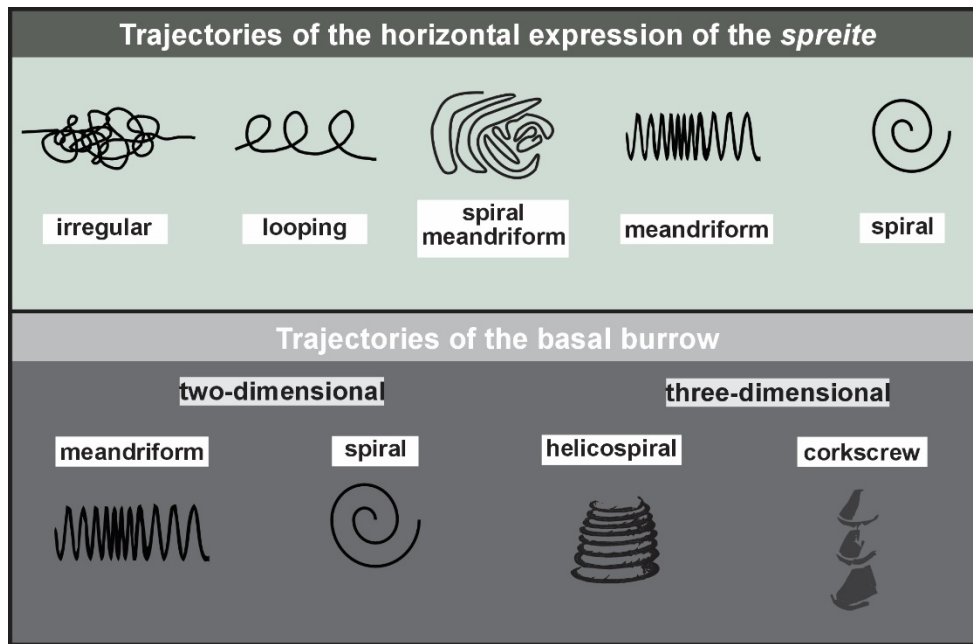


Fig. 2. Terminology to describe the trajectory of the horizontal expression of the *spreite* (useful for the three sections defined) and the basal burrow trajectories.

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A THREE-DIMENSIONAL MODEL OF *DICTYODORA* WEISS: NEW ICHNOTAXONOMICAL PERSPECTIVES

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Dictyodora is a complex three-dimensional Paleozoic marine ichnogenus that has been studied for more than a century. However, several problems for the diagnostic features as valid ichnotaxobases remain debatable at an ichnospecific level. *Dictyodora* is defined on the basis of two parts: an almost horizontal structure named lower margin (here named basal burrow) and a thin medial structure known as the *spreite* (Fig. 1). The latter is disposed angularly to the basal burrow with a variable inclination (e.g., 40 to 90°). The *spreite* is usually preserved as hypichnial epireliefs or epichnial hyporeliefs and is the most frequent feature preserved on a bedding plane. The morphological variations of the *spreite* have been used as a diagnostic characteristic at ichnospecific level [^{1,2}]. Numerous specimens analyzed from the middle Paleozoic (Silurian–Devonian) of Argentina (central-western Gondwana) recorded morphological transitions between ichnospecies, never reported before in the literature [³⁻⁶]. These records allow to point out several problems: most ichnospecies have an unclear diagnosis or vague descriptions; some diagnostic features are shared for more than one ichnospecies; and morphological intergradations assignable to different ichnospecies along a same specimen are observed. Moreover, intergradations between ichnospecies have been documented since the ichnogenus creation but never mentioned as such [^{7,8}].

In this work, new examples of intergradation involving also other ichnospecies of the ichnogenus *Dictyodora* are presented and studied in detail (Table 1). The specimens are recorded in a middle Paleozoic unit of Argentina. Those specimens reflect intergradation between most of *Dictyodora*'s ichnospecies. Some exceptions are the intergradation of *Dictyodora tenuis* (M' Coy) with *Dictyodora liebeana* (Geinitz), *Dictyodora silurica* Yang and Hu but also with *D. zimmermanni* Hundt. Notably, *D. silurica* is the only ichnospecies without intergradation with any another ichnospecies.

For instance, one of the specimens (IANIGLA-Icn 92) contains morphological features that show the *spreite* at different bedding planes. One of them is close to the basal burrow (level 1) and the other is more distant to the basal burrow (level 2) (Fig. 2). The three-dimensional reconstruction model documents variations in a vertical axis of the same structure between both levels. This model was obtained using photogrammetry techniques. The obtained images of the sample were processed using Meshroom Version 2021.1.0, and the open-source software Blender Version 3.3.1 was utilized for the interpretation and modeling of the final render. At level 1, the *spreite* presents a regular meandering trajectory with rounded or angular bends (archs), the latter being the most abundant, allowing this form to be assigned to *Dictyodora atuelica* Pazos *et al.* It continues laterally with regular meanders showing rounded archs assignable to *Dictyodora scotica* (M' Coy) and ends in smaller and irregular meanders characteristic of *D. tenuis*. Conversely, at level 2 the *spreite* presents a regular meandering pattern with predominantly rounded archs, assignable to *D. scotica*. The meanders continue with others showing angular archs, assignable to *D. atuelica*. Interestingly, it ends with regular meanders with rounded archs, typical of *D. scotica*. In conclusion intergradations are observed in both levels of the same specimen but involving different ichnospecies.

The numerous types and cases of intergradation observed in the material analyzed in this work but also in the revision of the literature regarding to intergradation between ichnospecies

belonging to *Dictyodora* allow to discuss diagnostic ichnotaxobases at ichnospecific level. The vertical variations (between levels 1 and 2) in the morphology of the *spreite* are not related to changes in the ethology of the producer. This suggests that most of the valid ichnospecies are the result of splitting in different ichnospecies the record of morphological variations, which may not be related to ethological changes. This invites to revise the ichnotaxobases used for differentiation of *Dictyodora* ichnospecies.

Table 1. Intergradation cases between *Dictyodora* ichnospecies. Those highlighted in green correspond to the material analyzed from the Río Seco de los Castaños Formation (San Rafael Block, Argentina) [6] while those highlighted in orange are those that were figured in the literature but not described as such.

	<i>D. atuelica</i>	<i>D. liebeana</i>	<i>D. scotica</i>	<i>D. silurica</i>	<i>D. tenuis</i>	<i>D. zimmermanni</i>
<i>D. atuelica</i>						
<i>D. liebeana</i>						
<i>D. scotica</i>						
<i>D. silurica</i>						
<i>D. tenuis</i>						
<i>D. zimmermanni</i>						

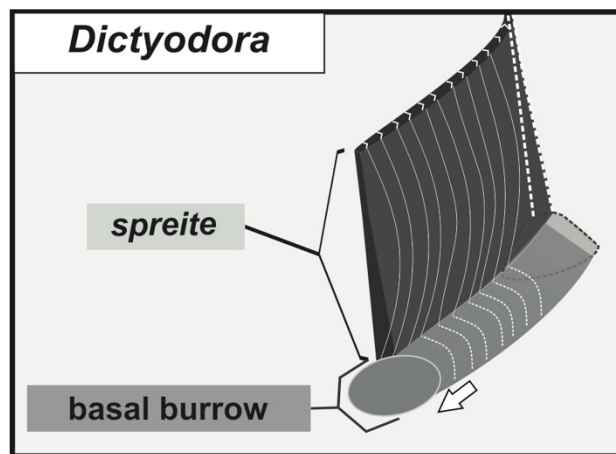


Fig. 1. Illustrative diagram of *Dictyodora* with its two components: basal burrow and the *spreite*.

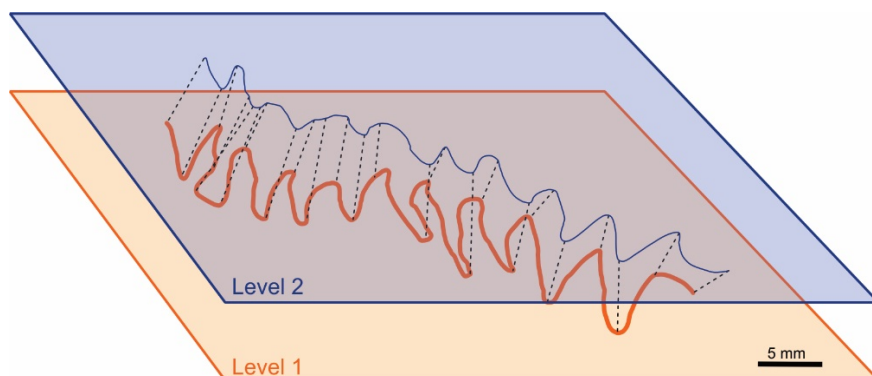


Fig. 2. Illustrative diagram of the specimen (IANIGLA-Icn 92) with transitional morphologies exposes in different levels (horizontal expressions of the *spreite*) both at the base (Level 1) and at the top (Level 2) of the slab.



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SPATIAL INTERACTIONS BETWEEN MICROBIAL MATS AND INTERTIDAL ORGANISMS, WILLAPA BAY, WASHINGTON, USA

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The “agronomic revolution” describes the transition from matgrounds to mixgrounds occurring during the early Cambrian, where microbial mats became limited to settings regarded as inhospitable to grazing and burrowing fauna [1-5]. Early evolutionary radiations in the Cambrian and Ordovician of new feeding strategies led to an increase in bioturbation [6]. The resulting increase in sediment mixing affected the nitrogen and phosphorous cycles, the transfer of organic carbon from the water column to the substrate, as well as solute transportation inside burrow systems (Fig. 1) [3,5,7]. Early animals are thought to have mainly used microbial mats as a source of food or oxygen [2]. Here, we posit that there may be additional benefits to colonization near the margins of a microbial mat (i.e., porewater micronutrients) and interrogate the assumption that bioturbation inhibits mat development.

The objective of this study is to characterize the interactions between microbial mats and organisms in a modern normal marine setting and compare to interactions preceding and following the agronomic revolution to better understand the evolution of these behaviours. Data were collected from the mesotidal, mesohaline intertidal flat of Willapa Bay, Washington, USA (Fig. 2). A transect of four data points was made between a heavily burrowed part of the tidal flat to a heavily matted part of the tidal flat. Porewater samples were collected using Rhizon samplers and analysed for pH and salinity as well as composition via inductively coupled plasma mass spectrometry (ICP-MS). A three-dimensional computer model was made of the intertidal flat using photos taken by an unmanned aerial vehicle using Agisoft Metashape software. Using a grid system, data including number of burrows, the presence or absence of a microbial mat, and elevation were collected from the model. Preliminary results show significantly fewer burrows in sample squares with microbial mat present than those without, possibly driven by elevation. Burrows are pervasive up to the margins of the microbial mat, suggesting that there are no impediments to bioturbation other than the mat cohesiveness, and perhaps there are even benefits to mat adjacency; there is perhaps an availability of porewater micronutrients that are otherwise unavailable in oxygenated bioturbated sediment. Iron, for example, was observed in relict burrows across the transect (Fig. 3) and precipitated from porewater samples — but only below the mat. The literature in general implies that the advent of bioturbation diminished the extent of microbial mats, but the interactions may in fact be more complex, with mats dictating bioturbation distributions at the intertidal margins.

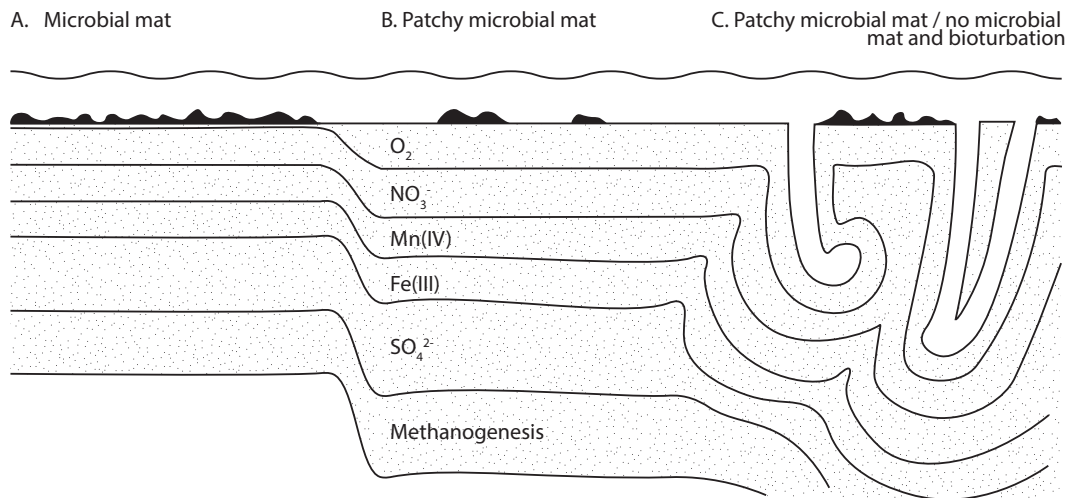


Fig. 1. A schematic representation of vertical zonation of electron acceptor used in sediments below microbial mats (A), patchy microbial mats (B), and in response to burrowing (C). Modified from [8,9].



Fig. 2. Location map and overview of the study area near Tokeland, Washington, USA at Willapa Bay showing the intertidal flat, tidal channels, burrowed interval, microbial mat, and salt marsh. The red box indicates the study area.

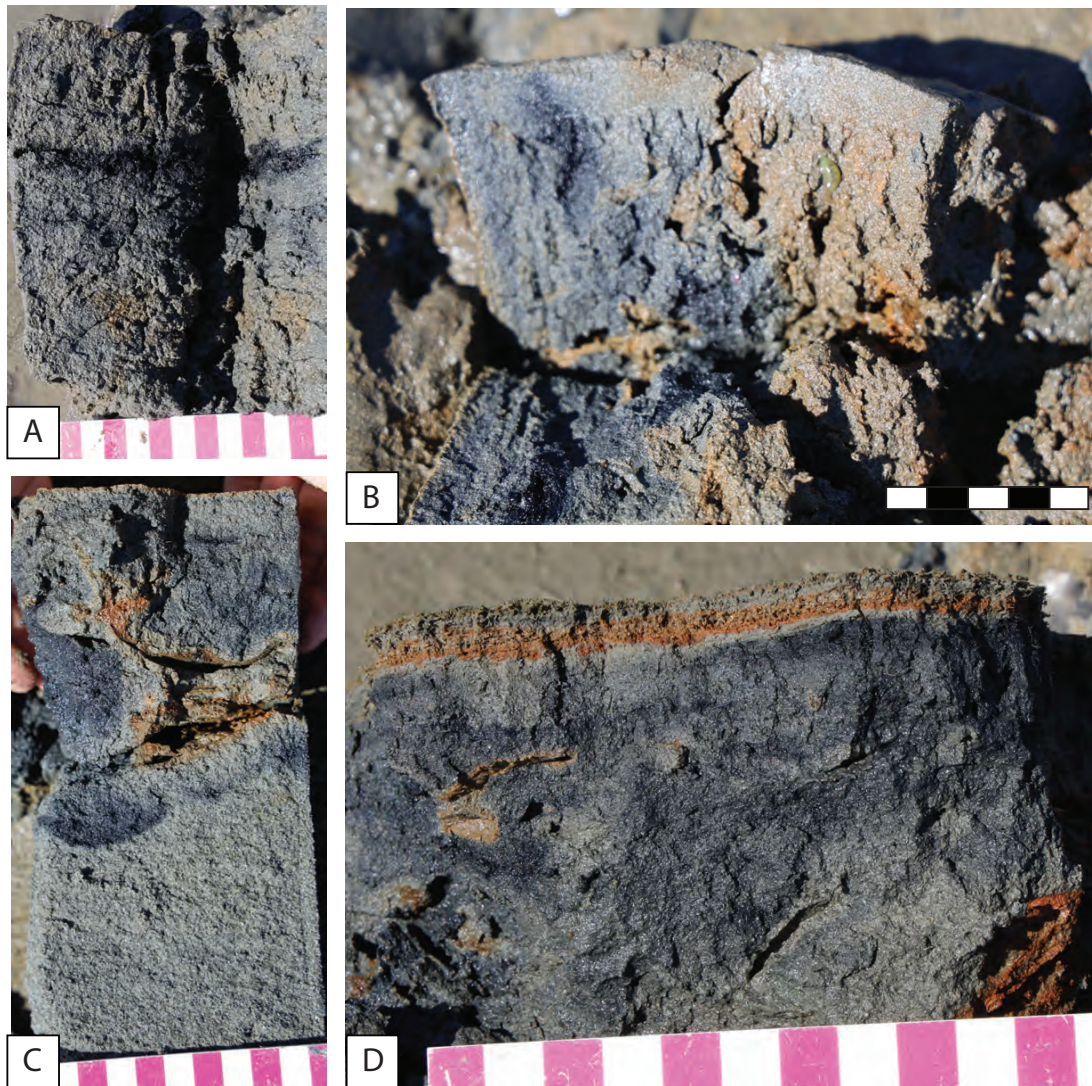


Fig. 3. Photos taken from each location of the transect at Willapa Bay. A Heavily burrowed upper layer of sediment with relict mat layer beneath. B. Partially burrowed and patchy mat location with nereid polychaete. C. Partially burrowed and patchy mat location with relict iron-rich burrow linings. D. Microbial mat location with rare burrowing showing laminated sediment beneath the mat.

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A QUIET WALK BY A LARGE THEROPOD DINOSAUR: A CASE STUDY OF THE LONGEST BIPEDAL TRACKWAY FROM THE CRETACEOUS OF PATAGONIA

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The Cenomanian Candeleros Formation exhibits one of the highest diversities of dinosaur tracks from the Late Cretaceous of Argentina [¹⁻⁴]. Here we report two exceptional trackways of bipedal animals from the El Chocón Medio locality (Candeleros Formation) in northwestern Patagonia, consisting of 30 and 13 successive tridactyl footprints (called here T1 and T2, respectively) (Fig. 1). Tracks of T1 and T2 are preserved in medium-grained sandstones from alluvial deposits and expressed as true tracks on the same tracking surface. T1 has a length of 40.4 m, and its footprints have an average length of 52.1 cm (a range of 50–60 cm in length), while T2 has a length of 15.6 m, and its footprints have an average length of 52.8 cm (a range of 51–55 cm in length). Strides displays constant values throughout both trackways, with T1 showing an average stride of 276.3 cm and T2 an average stride of 275.4 cm. These trackways are separated by about 75 m and are almost parallel showing a similar orientation, the last 10 tracks of T1 have a 76°N orientation while T2 has a 75°N orientation. Some indeterminate trackways of smaller size (less than 35 cm long) have also been recorded crossing almost perpendicularly to T2. No intra-trackway variation was recognized in T1 and T2, suggesting no changes in the substrate properties such a moisture content, along the tracking surface. Ichnospecies attributable to theropod dinosaurs known from the Candeleros Formation include: *Abelichnus astigarrae*, *Bressanichnus patagonicus*, *Deferrariischnium mapuchensis*, *Picunichnus benedettoi*, and *Candelerioichnus canalei* [¹⁻³]. The footprints studied here show several differences with all these ichnotaxa, and considering that they are poorly preserved, they were not assigned to any particular ichnotaxon. The Candeleros Formation presents one of the most diverse theropod faunas from the Cretaceous of South America, including carcharodontosaurids, abelisaurids, basal coelurosaurids, alvarezsaurids and dromaeosaurids [³]. However, taking into account their size, only a carcharodontosaurid or abelisaurid could have produced the current T1 and T2 footprints. Considering that the footprints of both parallel trackways have identical morphologies and sizes, the stride length and orientation of both trackways are similar, and that they are found in the same stratigraphic level, it is proposed that T1 and T2 would belong to the same large trackway. Thus, this trackway could reach 121 m in length, constituting the longest trackway documented of a large theropod in the Candeleros Formation and also in Patagonia. The longest known dinosaur trackway worldwide is that of a small theropod from the Late Cretaceous Cal Orcko tracksite of Bolivia, and it is 581 m long [^{5, 6}]. Although some trackways of large theropods have been documented, such as the 311 m trackway attributed to *Megalosauripus* from the Late Jurassic of Turkmenistan [^{7,8}], and the 180 m trackways from the Middle Jurassic White Limestone Formation of England [⁹], as far as we know no Cretaceous trackway of a large theropod as long as the one in the present study have been reported. Finally, the fact that the producer maintained the same constant speed throughout the entire trackway indicates a preferred walking gait that probably represents the energetic optima.

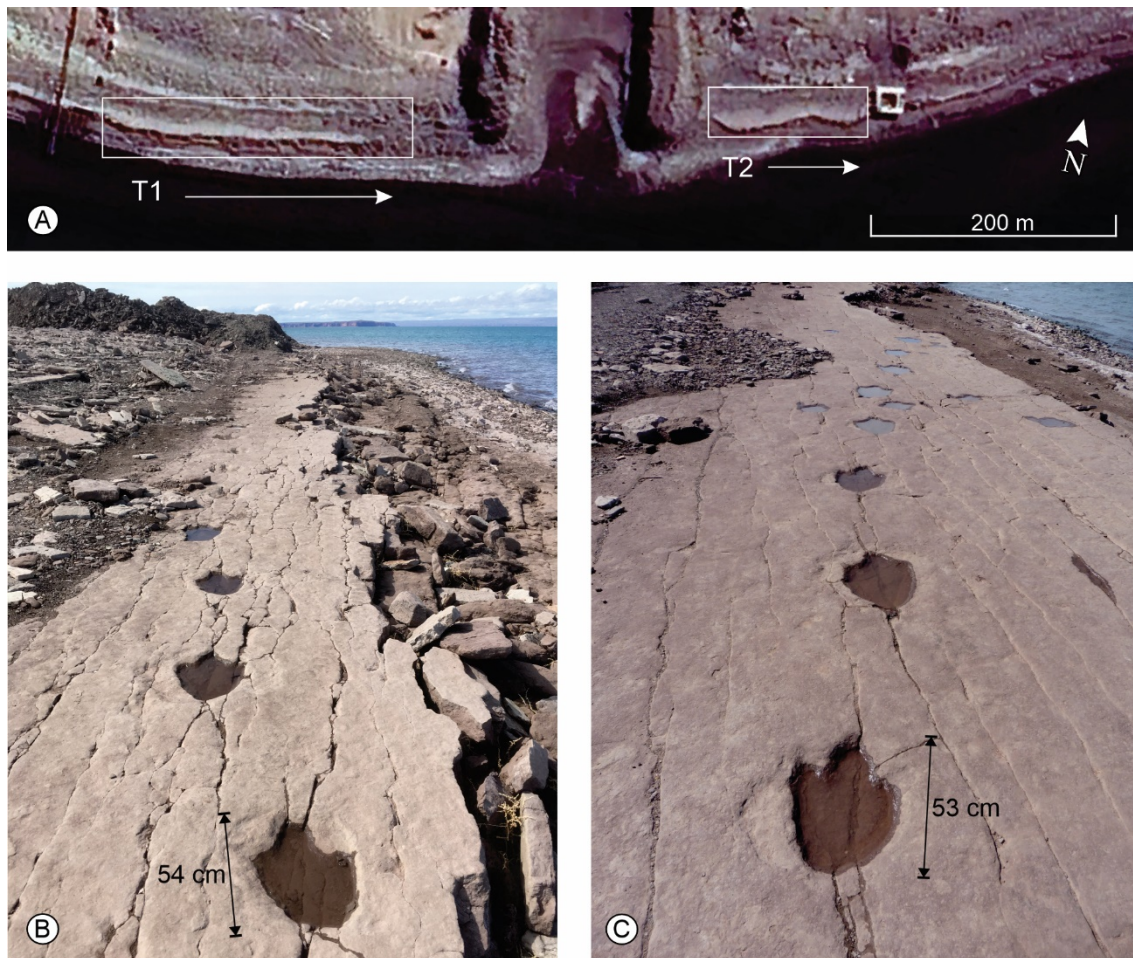


Fig. 1. A. Satellite image showing the track-bearing surfaces including the trackways T1 and T2. The white arrows indicate the orientation of both trackways. B. Trackway T1. C. Trackway T2.

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FIRST REPORT OF DEINONYCHOSAURIAN TRACKS FROM THE UPPER CRETACEOUS CANDELEROS FORMATION OF NORTHWESTERN PATAGONIA, ARGENTINA

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Several didactyl tracks from the Cenomanian Candeleros Formation (El Sauce locality, Neuquén Province, Argentina) are documented here. This record consists of at least six tracks preserved as negative epirelief in medium-grained sandstone from alluvial plain deposits. The tracks are strongly asymmetric, preserving only the impression of digits III and IV and a narrow and long claw mark corresponding to digit II. The tracks are between 9.6 and 10.3 cm long and between 4.8 and 5.9 cm wide. No clear trackway has been recognized, although five of the tracks have a similar orientation and only one is oriented in the opposite direction. Tracks do not preserve anatomical features, like digital pad impressions. The angle of divarication between the claw mark of digit II and the impression of digit III is considerably greater than the angle between the impressions of digits III–IV (e.g., in the best-preserved track the values are 16° and 9°, respectively). The Cretaceous record of didactyl tracks is poorly known in South America and has been assigned to dromaeosaurids (Deinonychosauria). It includes didactyl tracks documented in Bolivia from the Campanian Toro Toro Formation referred to as *Dromaeopodus?* isp. and undetermined tracks from the Maastrichtian El Molino Formation [^{1,2}]. Several ichnotaxa based on didactyl tracks and documented mainly in the Northern Hemisphere were related to deinonychosaurian theropods (e.g., *Menglongipus sinensis*, *Velociraptorichnus sichuanensis*, *Dromaeosauripus yongjingensis*, *Dromaeosauripus hamanensis*, *Dromaeopodus shandongensis*) [³⁻⁷]. The didactylid tracks from El Sauce show a smaller opening angle of digits III–IV than those of these ichnotaxa, except for *D. shandongensis* which displays similar values. Nevertheless, unlike the last ichnospecies, the tracks studied here do not preserve the impression of the phalangeal pads. In addition, none of these ichnotaxa have documented the claw mark of the digit II as in the present tracks. The deinonychosaurian fossil record of the Upper Cretaceous of Argentina is restricted to the Neuquén Basin and includes the Unenlagiinae dromaeosaurids: *Buitreraptor gonzalezorum* from the Cenomanian Candeleros Formation; *Unenlagia comahuensis*, *Unenlagia paynemili*, *Neuquenraptor argentinus* and *Pamparaptor micros* from the late Turonian–early Coniacian Portezuelo Formation; and *Austroraptor cabazai* from the Campanian–Maastrichtian Allen Formation [⁸⁻¹⁰]. Taking into account this fossil record and the size of their feet, it is likely that the producer of the tracks presented here was a medium-sized Unenlagiinae like *B. gonzalezorum*. Furthermore, these tracks show that the producer had a



developed ungual phalanx of digit II and the ability to rest it on the substrate, reflecting some kind of behavior (probably resting). Considering the above differences, the tracks were not assigned to any of the known ichnotaxa, and further studies are needed to determine if they correspond to a new ichnotaxon. The new findings from El Sauce improve not only our knowledge on the dromaeosaurids of northwestern Patagonia, but also increase the scarce deinonychosaurian track record of South America and particularly of the Cenomanian worldwide.

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GEOCHEMISTRY OF CALCRETISED FOSSIL TERMITARIA IN CALITZDORP (WESTERN CAPE, SOUTH AFRICA): NEST CONSTRUCTION BEHAVIOUR AND PALAEOCLIMATE PROXY POTENTIAL

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Termites demonstrate impressive adaptability to arid environments despite their requirement for humid living conditions [1]. This adaptability is manifested through the selective use of materials such as clays and silts (rich in exchangeable bases) and the construction of carefully designed nests that protect the termites from unfavourable subaerial conditions [2]. Here, we consider four subterranean fossil termitaria that have been replaced by calcite and dolomite, which have been dated to ~300 ka by U-Pb radiometric dating [3], from two localities 8 km apart, south of the town of Calitzdorp (Western Cape, South Africa). The macro-morphology of these unique and novel nests is the same at the two sites; they feature cylindrical bowl-shaped calcretised nests with thick walls (0.1–0.2 m thick) which vary in diameter (~0.5–1 m in diameter). The walls of the nest display horizontal shelving (i.e., tunnels) and vertical ramps connecting them. The underlying rocks vary from Quaternary calcretised alluvial sands to Devonian shale regolith. This study addresses two primary objectives: (i) assessing the geochemical composition of the nests relative to the nest-hosting sediments to discern if the termites were preferentially selecting building materials; and (ii) providing insights into the mid-Pleistocene palaeoclimate of the Western Cape, bridging a crucial gap in the local Quaternary palaeoclimate record. To achieve this, a dual approach is employed: firstly, a comprehensive analysis of the major and trace element geochemistry of the termitaria and the host lithologies; secondly, carbon and oxygen isotope data from the carbonates in the nest and calcretised lithologies are used to infer palaeoclimatic conditions at the time of calcretisation of the nest. At both localities, the nests are enriched in CaO, MgO, MnO, and P₂O₅, and depleted in K₂O, Fe₂O₃, Co, and Zn compared to the nest hosting sediments. The enrichment of exchangeable bases (CaO and MgO) and essential plant nutrients (MnO and P₂O₅) in the nests may signal preferential selection behaviour by the termites, enriching the nests in clays and organic matter [4]. Enrichment in CaO and MgO can be attributed to the presence of both calcrete and dolomite in the termitaria, respectively; however, elevated enrichment in the termitaria supports the hypothesis that termites are preferentially selecting Ca and Mg-rich materials like clays. Depletion in K₂O, also present in clay minerals, may result from a preference for Ca and Mg-rich clays introduced by termites or non-termite-related mechanisms like groundwater infiltration [5]. The depletion of Co and Zn in the nests may be attributed (i) the continual input of micronutrients (from decaying plant material) into the surrounding soil after the construction of the nest or (ii) an external source of soil which was poor in this material. The $\delta^{13}\text{C}$ value of the carbonate at both localities is similar (0 to -6‰), suggesting similar dominance of the C₄ vegetation. Semi-arid to arid conditions probably prevailed during carbonate precipitation, after the nest excavation, in the mid-Pleistocene. These geochemical results may potentially contribute valuable insights into ancient termite ecology and the palaeoclimate of the Western Cape (South Africa) during the middle Pleistocene.

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TAPHONOMY OF *TEREDOLITES LONGISSIMUS* FROM THE MAASTRICHTIAN–EOCENE OF THE ARAUCO BASIN, CHILE

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Teredolites has been used as a marker of paleoenvironmental conditions in paralic systems with marine influence and open sea environments, and in transgressive-regressive sequences [^{1,2}]. In the Arauco Basin (36°46' to 38°30' S), new records of fossil logs with *T. longissimus* allow inferring the paleoenvironmental conditions of the deposits but also present new evidence about its taphonomic process. This new material exhibits significant variability in the preservation, shape, and size of the traces among the different locations. This study focuses on the filling of the boreholes, of which at least 30% of the samples are mineralized by both calcium carbonates and silica, while the remaining 70% are filled by sediments. Its objective is to associate the occurrence/absence of mineralization with the taphonomic processes driven by the tracemakers and the type of deposit in which they are found.

The study area corresponds to a basin with predominantly siliciclastic sedimentation dominated by tectonostratigraphic and eustatic processes that generated a transgressive trend during the Late Cretaceous [³]. This is succeeded by episodes of transgression-regression alternations during the Paleogene. In this study, we analyzed samples from the Quiriquina Formation (upper Maastrichtian), Boca Lebu Formation (early Eocene), Trihueco Formation (middle Eocene), and Millongue Formation (middle to upper Eocene) [³]. The material was analyzed macroscopically with a digital magnifier and microscopically via thin section studies, alongside statistical assessments of the filling types associated with the borings.

The results show at least three types of mineralization in the borings, which can be grouped into: (i) recrystallization of the calcareous wall, (ii) a central phase with highly developed crystals, and (iii) an outer phase with poor crystal development. These phases can be identified regardless of the mineral composition filling the tubes. Thin sections reveal these three phases and also facilitate the identification of specific mineral species (Fig. 1).

In thin sections, the borings are observed to be filled with cemented clasts. Statistical analysis differentiates filling types according to the depositional context, such as transgressive shoreface, regressive shoreface, quiet bottom deposits represented by condensed sections, and settings impacted by hyperpycnal flows, as identified in subsurface deposits [¹]. The observed trend suggests that in lower-energy environments, the borings are predominantly filled with minerals, whereas turbulent flows result in almost complete sediment infill (Fig. 2). Within the same sample, it is common to find both filling types, although discerning a trend remains straightforward. Mixed fillings, frequently encountered, enhance the trace's utility as reliable geopetal indicators.

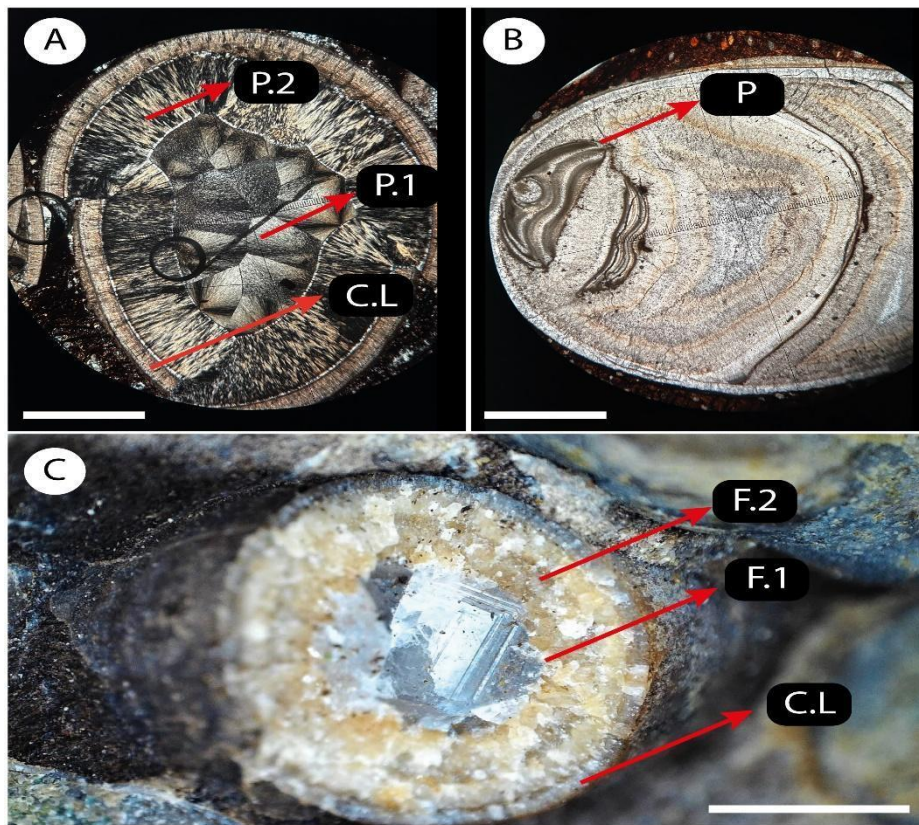


Fig. 1. A-B. Thin-section images of *Teredolites*; P.1: highly developed crystals phase; P.2: poor develop crystals phase; C.L: calcite lining; P: body fossils, pallets. C. Digital magnifier image of *Teredolites*. Scale bars: A-B = 0.5 mm; C = 4 mm.

T. longissimus is linked to mollusks from the Teredinidae family, wood borers with pallets [4,5]. These structures protect against predators and environmental changes, preventing sediment infill during early diagenesis and allowing later occupation by mineralizing fluids.

The previously noted mechanism [6] lacked an association with mineralization. This idea gains potential support from Ninon's findings [7], which document entire organisms, soft parts included, within silica-filled tubes. However, there are two proposed processes for sediment fillings: the absence of organisms in unoccupied borings, and a failure of closure mechanisms to block sediment entry in high-energy or turbulent environments. This challenges views like Serrano's [8], who argued that stress processes can be discerned through the presence or absence of pallets in sediment. Our study, however, has identified these structures across various deposit types, suggesting that filling type is a more critical factor.

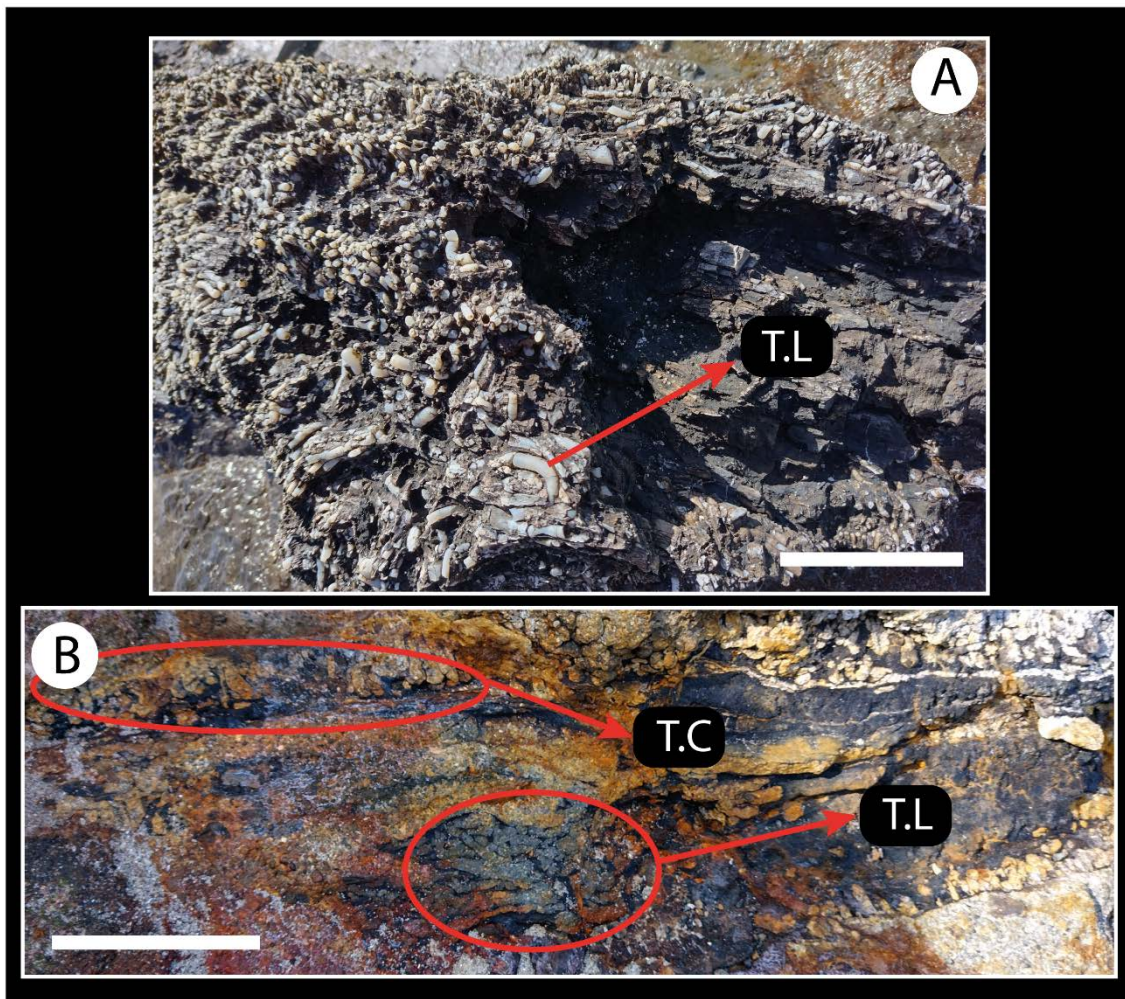


Fig. 2. A. *In situ* colonized fossil log with several mineralized tubes in a transgressive surface. B. *In situ* infested fossil log with all borings filled by sediment in a hyperpycnical flow deposit; T.L: *Teredolites longissimus*; T.C: *Teredolites clavatus*. Scale bars = 30 cm.

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VERTEBRATE FLOOD ESCAPE STRUCTURES INTERPRETED FROM FLUVIAL DEPOSITS OF THE WAPITI FORMATION, CANADA

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The Wapiti Formation of West-central Alberta, Canada, is a fluvial deposit of the Upper Cretaceous (Campanian-Maastrichtian) known for its rich record of vertebrate fossils [1]. Recent efforts in the Red Willow Falls area retrieved numerous well preserved trace fossils of animals and plants. Among those, there are enigmatic deformational structures left on the base of a sheet flood deposit formed within a flood plain environment. To understand and characterize the origin of these deformational structures, the sandstone blocks containing them were studied for their sedimentology, and the deformational features were photographed to be analyzed using 3D photogrammetry. As part of the analysis, trace fossils that occurred from the same locality were also described.

The sandstone blocks overlay a planar mud bed on an erosional contact marked by parting lineation. The sand layers are associated with planar tabular cross bedding and are devoid of bio- or rhizoturbation. The deformational structures are roughly triangular to fan-shaped and dig into the mudstone at a shallow angle (Fig. 1). They occur on the interface of the sand and the mud and do not crosscut the sedimentary fabric of the sandstone (Fig. 2). Some structures were well preserved that they displayed micron-scale parallel striae on their surfaces. These striae allowed for identifying the directions the deformations were being made.

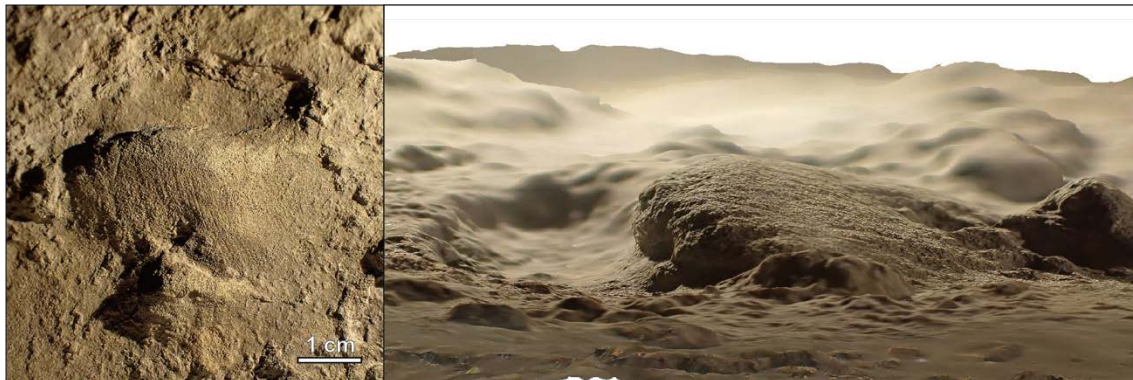


Fig. 1. Representative trace fossil from the Wapiti Formation viewed from above (left) and from the side (right). Notice the striae on the surface of the ichnite.

The overall morphology and the cross-current orientation of some of the deformational structures are incomparable to known physical sedimentary structures, making it likely that they originated through biogenic processes. The sizes of the ichnites also suggest that they are most likely of vertebrate origin. Many vertebrate tracks are aligned in trackways, which is not the case for the Wapiti trace fossils that occur more or less randomly. The random distribution of vertebrate tracks is a characteristic of swimming trace fossils where the trace makers make partial contact with the substrate [2]. The cross bedding in the sandstone supports the hypothesis that the area was submerged. Therefore, the enigmatic deformational structures from Red Willow Falls have been interpreted as vertebrate swimming trace fossils.

The sedimentology of the sands infilling the trace fossils indicates that the traces were emplaced on muddy substrate before the sands were deposited (Fig. 2). The preservation of fine striae on the surface of the ichnites also suggest that the deposition of sand was rapid and occurred right before or right as the traces were being made. Moreover, the striae on the trace fossil revealed that they occur in two distinct orientations: one occurs in the same direction as the paleoflow, which is interpreted from the cross bedding (Fig. 2); the others are perpendicular to that flow direction. These observations would suggest the following sequence of events: (i) A muddy fluvial overbank environment suffered a sudden flooding event, which led to surface erosion and formation of parting lineation; (ii) The trace making animal attempted to escape the flood first by moving against the current; (iii) In doing so, the trace maker kicked into the substrate leaving the ichnites found at Red Willow Falls; (iv) As the event progressed, the trace maker changed its course and moved perpendicular to the flow to escape the waters; (v) The swimming traces were buried by sand that got deposited as the flooding event died out forming a cast.

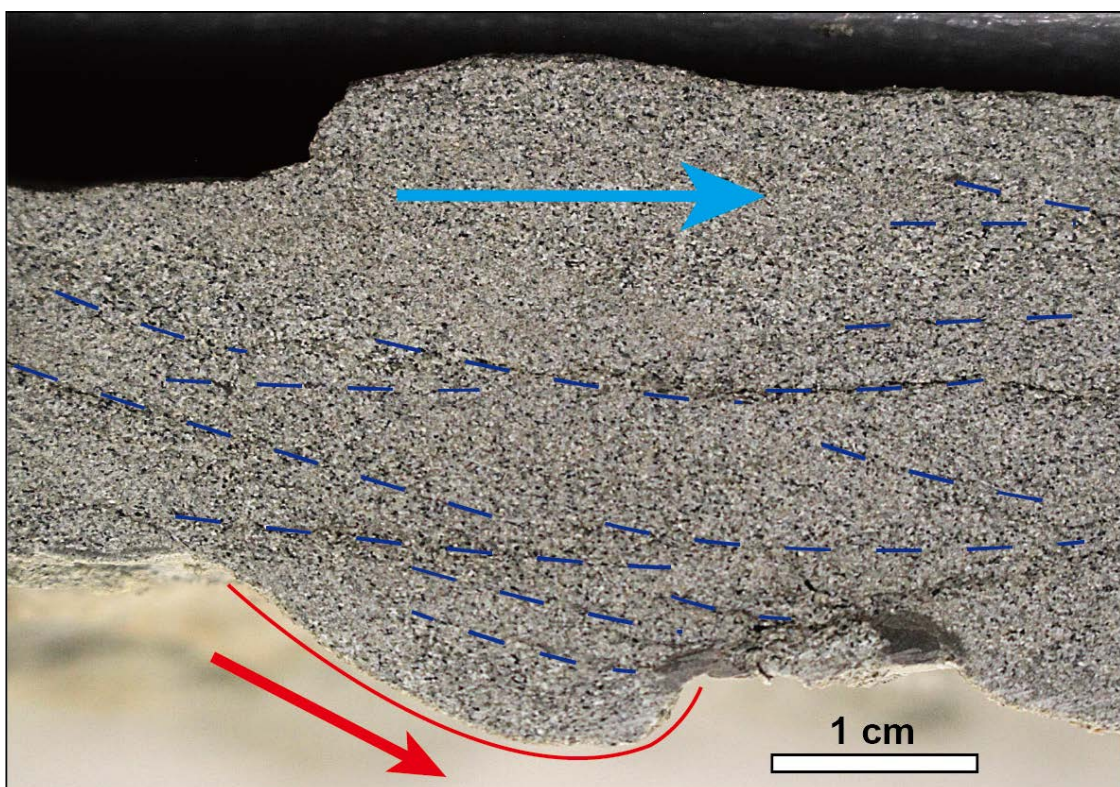


Fig. 2. A cross section of the sandstone block through one of the ichnites. The deformed area is indicated by a red line and some of the cross-bedding features are highlighted in blue. The paleoflow and trace formation occurred in the same direction.

The identity of the trace maker remains somewhat problematic. Based on the size, depositional environment, and vertebrate fossil record from the Wapiti Formation, the best candidate is turtles. In fact, morphologically similar vertebrate tracks from nearby locality have been interpreted as turtle tracks in the past [3]. Turtle fossils are also found in abundance from the Wapiti Formation [4]. However, the swim traces from Wapiti Formation lacks digital impressions, which are always present in other known turtle track fossils. Other possible trace makers include fishes and amphibians, but there are no known fish trace fossils comparable to the studied ichnites, and fossil record of amphibians are extremely poor in the Wapiti Formation. Still the vertebrate swim tracks from the Wapiti Formation provides a good example of how sedimentology can help identify vertebrate trace fossils, and how vertebrate ichnites can help interpret sedimentary events at a local scale.



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APPLICATIONS OF ICHNOLOGY IN PETROLEUM SYSTEMS – AN OVERVIEW

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Ichnological studies have been complementing sedimentological analyses in the exploration and production of hydrocarbons for some decades. Initially used as tool for facies interpretation [1], more recently ichnology has been applied to evaluate reservoir quality, predict and characterize source rock, constrain stratigraphic correlations, describe seal potential (e.g., unconformities) and to analyze the overburden (Fig. 1). Ichnofabric analysis has proven to be an invaluable tool in core description and the interpretation of depositional environments [2]. The identification of intervals with lowered bottom-water oxygenation by means of bioturbation combined with other proxies can aid in the identification of potential source-rock intervals. Likewise, various types of bounding surfaces can be recognized and described by their trace-fossil content. Discontinuity surfaces, omission surfaces and unconformities are hiatal surfaces with importance for sequence-stratigraphic interpretations. Together with sedimentary, diagenetic, and structural features, ichnological heterogeneities may have a positive or negative impact on reservoir quality and connectivity, depending on the kind of involved burrows. This information is equally important for identifying suitable formations for safe CO₂ storage. Advanced tools such as micro-CT scanning, thin-sectioning, digitalization, and small-scale modelling are effective in ichnological analyses.

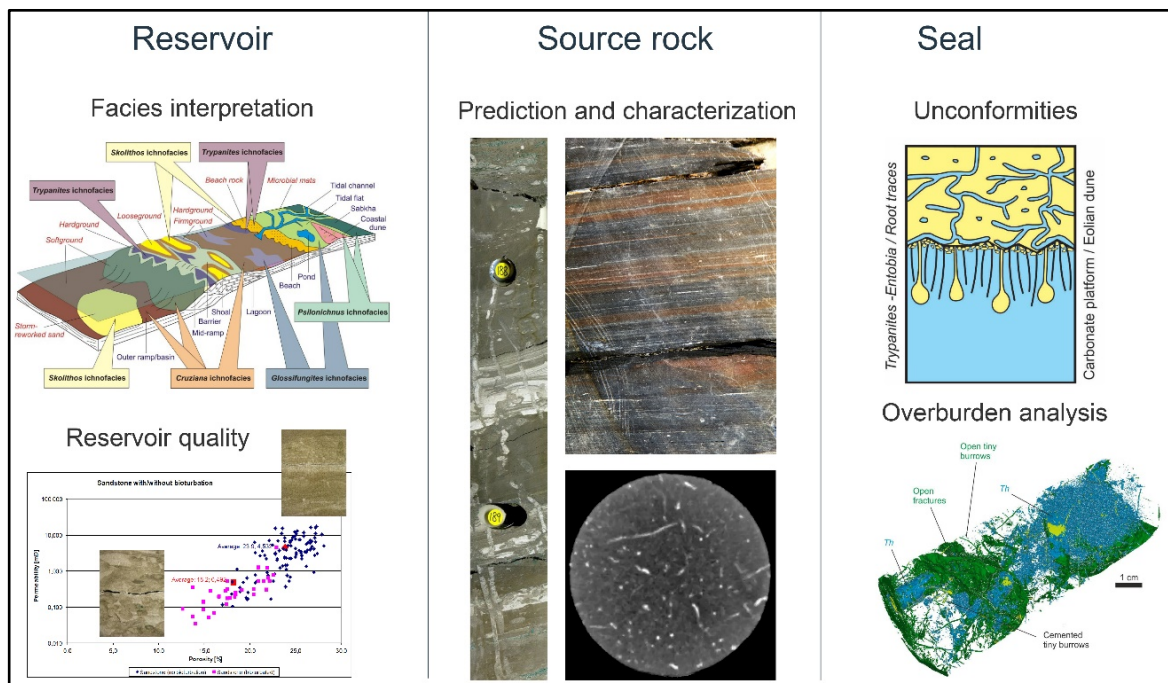


Fig. 1. Main applications of ichnological analysis in the prediction and characterization of petroleum systems.

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INSIGHTS INTO EARLY MAMMAL AND DINOSAUR LOCOMOTION, BEHAVIOR, AND ECOLOGY FROM MIDDLE JURASSIC TRACKWAYS OF LA MATILDE FORMATION, PATAGONIA

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The recent exploration of the Middle Jurassic La Matilde Formation (LMF) at Estancia Laguna Manantiales in Patagonia, Argentina, exposed two large tracking surfaces with more than 1000 well-preserved footprints. The unit records a diverse ichnofauna including traces of early mammals, dinosaurs, and invertebrates together with permineralized plant remains. This preservation facilitates the examination of interactions among the biogenic structures and their interplay with *in situ*-preserved body fossils. Consequently, it amplifies the opportunities for studying their behavioral, ecological, and locomotive dimensions revealed through the trackways.

LMF comprises primary and reworked siliceous volcanic sediments, predominantly consisting of tuff, lapilli stone, tuffaceous sandstones, and occasional occurrences of ignimbrites and breccias [1]. Our study is placed on its outcrops in northeastern Santa Cruz province, Argentina, and to the northwest of Parque Nacional Bosques Petrificados de Jaramillo. We searched expansive, well-exposed areas conducive to the observation of long trackways illustrating locomotion patterns and the interaction between ichnotaxa. During our fieldwork in 2022, we exposed two large surfaces within tracking levels previously investigated by Casamiquela [2,3] and de Valais [4,5], among others. The first exposed area (Museo Egidio Feruglio's quarry, MEFQ) is about 50 m² and records 10 long *Ameghinichnus patagonicus* trackways (100-350 cm) belonging to an early mammal that exhibits walking, bounding, and transitional gaits. We also recovered the trackways *Hexapodichnus casamiquelai*, attributed to an insect, the dinosaur footprints *Sarmientichnus scagliai*, and one unnamed trackway. Body fossils include converging roots and standing trunks of *Araucaria*, which were associated with impressions of raindrops and large circular depressions. The second exposed area is stratigraphically below the first one and was originally described by Casamiquela [2,3] (Casamiquela's quarry, CQ). This quarry contains more than 30 large blocks containing early mammal footprints, *A. patagonicus*, and the small theropod dinosaur footprint *Wildeichnus navesi*. We uncovered a large surface hosting a continuous trackway of more than 36 manus-pes pair of *Delatorrichnus goyenechei*, produced by a small dinosaur as well as short *Ameghinichnus* trackways.

Ameghinichnus patagonicus overwhelmingly dominates both tracking surfaces constituting 86% of the total footprints and trackways at CQ and 93% at MEFQ. Noteworthy, at both tracking surfaces, 60% of the trackways show a walking gait, while 40% exhibit bouncing



gaits. In CQ, 17% of these trackways display tail drag marks, evenly distributed between walking and bouncing gaits, with no digit drag marks. Notably, 80% of the trackways exhibit tails and digit drag marks at MEFQ, also evenly distributed between walking and bouncing gaits. In addition, in MEFQ 30% of the trackways include transitional gaits.

The consistent ratios of walking and bounding gaits across both sites suggest a persistent mode of locomotion. A noteworthy observation is that most trackways at MEF quarry exhibit tails and digit drags, presenting a contrast to Casamiquela's quarry, which features tail drag marks in a small proportion. The prevalence of pronounced tail and digit drag marks at the MEF quarry suggests an association with a substrate characterized by elevated water content. This aligns with the presence of large-sized and highly superimposed raindrop imprints and the identification of trackways exhibiting lower fidelity to the autopodium of the trackmaker compared to those in Casamiquela's quarry. Finally, a distinct zonation is observed, characterized by an external halo featuring large, densely superimposed raindrop imprints and poorly preserved trackways, alongside an internal halo showing well-preserved trackways, isolated regular-sized raindrop imprints, and *Araucaria* roots. We interpret this body fossil and ichnofossil association at MEF quarry to be a record of animals taking cover and sheltering under a tree during a storm or heavy rain.

Tail drag marks exhibit a lack of strict correlation with a specific gait, as they are evenly documented across both walking and bouncing gaits. In MEFQ tail impressions exhibit a deeper impression, likely attributed to the greater plasticity of the tuff layer influenced by elevated water content. This observation provides valuable insights into the locomotion dynamics and may suggest a morphological aspect of the trackmaker as the tail seems to be long enough to be forced to contact the ground despite the used gait.

Within the dinosaur tracks recovered, *Delatorrichnus goyenechei* represents 32%, *Wildeichnus navesi* 10%, and *Sarmientichnus scagliai* 8% of the total footprints and trackways on the CQ tracking surface, and one isolated *Sarmientichnus scagliai* at MEFQ. The *Delatorrichnus goyenechei* trackway, spanning approximately 450 cm, provided a unique opportunity to observe the persisting aspects of locomotion and body proportions of a dinosaur. It suggests an obligate quadrupedal dinosaur with a trunk length (gleno-acetabular) of approximately 35 cm long. The average pace angulation of the manus (172°) surpassed that of the pes (161°), indicating a lower femoral abduction angle. This suggests a more upright positioning of the forelimbs compared to the hindlimbs, highlighting both elongated forelimbs and hindlimbs in this Middle Jurassic dinosaur's body plan, which is not very frequently found. Our findings provide a unique opportunity for studying early mammals and dinosaurs' locomotion patterns, taxa interaction, and paleoecological and landscape dynamics during the Middle Jurassic of Patagonia.

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MAJOR QUESTIONS IN ARTHROPOD AND PATHOGEN HERBIVORY IN THE FOSSIL RECORD: A BRIEF ACCOUNT

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A central issue for the deep-time origin and evolution of arthropod and pathogen herbivory in the continental realm is how global processes and events have substantially affected the direction of herbivory for the three major elements of this system: the plant hosts, their herbivores, and the resulting interactions. The functional feeding group–damage type (FFG-DT) system was designed to address these important questions across time, space, and plant assemblages. Eight major questions have been identified that provide the coarsest grained view of the history of herbivory, yet also address fundamental patterns that have produced our herbivore-consuming green world. Tentative but brief answers are provided. The data come from FFGs and DTs recorded from fossil plant assemblages, some which are highlighted in Fig. 1.

How did herbivory originate on land? From the late Silurian to the Late Mississippian, a land flora was established that included nonvascular plants and vascular plants such as ferns and seed plants. This evidence supports spore consumption, borings, piercing and sucking, and pathogen damage on plant axes early in the Devonian and a small community of herbivores on liverworts [1]. Later in the Mississippian, feeding on leaves occurs [2]. Depending on the type of damage, minor to major time gaps exist between when a plant tissue or organ appears and when it is consumed [2].

What was the effect of the initial expansion of land plants on herbivores? An expansion of herbivory, especially piercing and sucking, occurred during the Early Pennsylvanian with the initial diversification of about 12 major insect lineages. During the Late Pennsylvanian, a diversified herbivore community of arthropods was established on marattialean ferns [3]; by latest Pennsylvanian, there is evidence for scale insects as well as physical and chemical antiherbivore defenses by medullosan seed ferns [4].

How did herbivores contend with the initial expansion of seed plants? In the early Permian, insect galls previously occurring on stems and rachises, shifted to targeting the foliage of seed plants [5]. Meanwhile, piercing and sucking increased in a second phase at the expense of chewing on seed-plant foliage [6]. By the end Permian, there was an increase of pathogenic damage on plants [7].

What effect did the end-Permian (P-Tr) ecological crisis have on the trajectory of herbivory? A substantial drop in the variety and intensity of herbivory followed the end-Permian ecological crisis, although Early Triassic plant assemblages are poorly represented. By late Middle Triassic, herbivory levels resumed to levels seen in the Late Permian [8].

What was herbivore life like in a world dominated by ferns and gymnosperms? The dramatic diversification of almost all herbivore functional feeding groups on ferns and gymnosperms during the Late Triassic [9] continued into the Jurassic and Early Cretaceous [10]. This amplification is illustrated the broad variety of mining on bennettitaleans, ginkgophytes, and conifers from the Middle Jurassic of China [11]. A gymnosperm-dominated plant assemblage of the Early Cretaceous shows extensive herbivory on single monodominant host species [12].

Did the initial rise of angiosperms provide new resources for herbivores? The style of herbivory on gymnosperm hosts changed during the later Early Cretaceous for emerging angiosperm plant assemblages that bore higher levels of herbivory on a few codominant host species but moderate levels on other hosts [7,13]. Ferns were minimally herbivorized during this



time interval. Immediately before the ecological crisis at the end-Cretaceous event, the richness and intensity of herbivory climbed to new levels [¹⁴], followed by drastic post-event reduction that took about 10 million years to equilibrate to end-Cretaceous levels [¹⁵]. An integrated community of insect and pathogen associations on the South American conifer *Agathis* survived for 68 m.y. on the same host genus in modern Malesia and adjacent Australia [¹⁶].

How did the Paleocene–Eocene Thermal Maximum and similar events affect herbivory? The Paleocene–Eocene Thermal Maximum at 55.8 Ma was the most dramatic, transient shift in temperature and CO₂ levels of the Cenozoic, associated with an increase in herbivory richness and intensity for many plant hosts and habitats [¹⁷]. After the PETM were other transient spikes in temperature and CO₂ levels that affected evergreen plant hosts in atypical ways, with heightened herbivory levels, a dramatic increase in galling, and a virtual absence of mining [¹⁸]. These features indicate a pattern typical of deciduous plant hosts. Many modern associations appear at this time.

When did modern herbivore associations occur? Modern, mostly specialized, associations appear during or by the Eocene, most of which have close counterparts in the modern world. Examples include coconut–pachymerine beetle seed predation, several dicot angiosperm–gall associations, and a conifer–leaf mine association. A few associations are older but most modern plant–insect interactions are more recent (Fig. 1).

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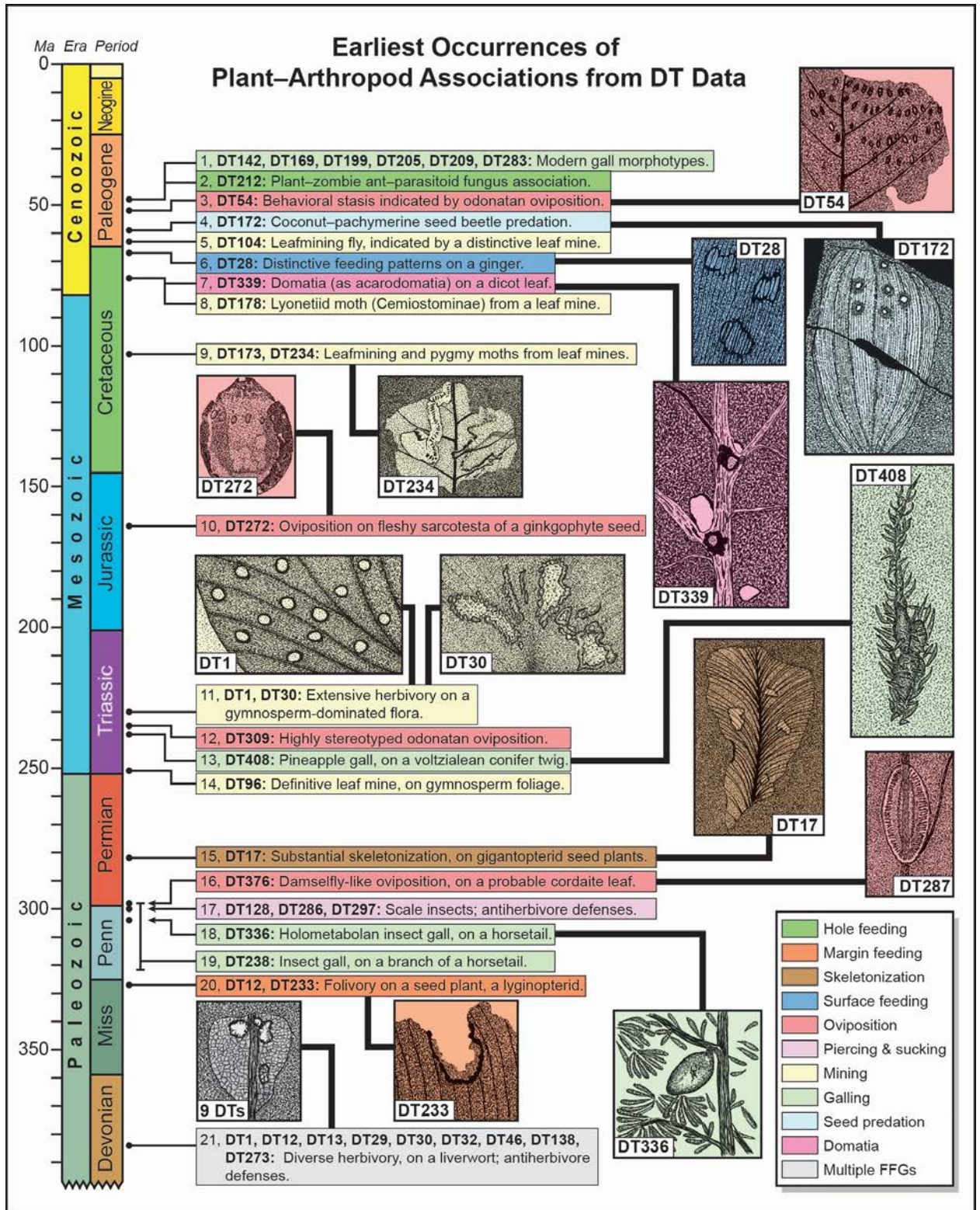


Fig. 1. Earliest occurrences of plant–arthropod associations in the fossil record from damage type (DT) data. From *Annual Review of Entomology*, reproduced with permission.



WORKSHOP WS_2: INSECT–PLANT INTERACTIONS NOTES

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Workshop WS_2 on Insect–Plant Interactions is organized in two sections. The first section is designed to provide a guide of how to collect, identify, and database herbivore induced damage on fossil and modern plants for understanding the paleobiology of herbivory. The second section uses various research tools to qualitatively and quantitatively assess data to discern patterns in the fossil record of herbivory and provide interpretations of those patterns.

How to Collect Damage-Type Data from Fossil and Modern Plant Assemblages

For fossil data, field collection of fossil plant material involves establishing a quarry in which a productive layer of fossil material is removed by using procedures ideally resembling that of what an archaeologist may use [^{1,2}]. However, outcrops of strata rarely provide such ideal conditions, owing to vagaries such as inclined dip of the strata, differential preservation of fossil bearing layers, lateral pinching out of productive layers, and excessive fracturing of the fossil material. There are five informal rules that are useful for excavation of an “average” quarry. First, keep the backwall of the quarry as vertical as possible. Second, remove fossiliferous rock slabs in a systematic fashion and transport them to a nearby site where they can be further split for processing. Third, keep the downslope talus rubble as far away from the excavated surface as possible. Fourth, keep the active quarry clean, removing unnecessary debris often with a brush with fine bristles. And fifth, after careful recognition of fossil plant material with a hand lens, isolate, label, and wrap and cushion with toilet paper those slabs to be placed in a container for transport to a lab. Censusing of all fossil material often is done at the outcrop¹ that includes fossil plant material sent back to the lab as well as material that is recorded (censused), then tossed and not sent to the lab for further investigation.

For modern data, the assessment of leaf herbivory may consider sampling methods from the point of view of a paleobiologist analyzing fossil leaves. This perspective mostly provides a comparison of modern and fossil DT metrics by considering equivalent sampling methods that might reproduce analogous taphonomic scenarios. For example, a census of modern plant–insect interactions can select a plant group and exclude others that likely would result in reliable inferences for interpreting similar scenarios in the fossil record [³]. Additionally, the composition of herbivorous arthropods from modern sites that are associated with leaf damage in live plants could be extended to the fossil record, albeit with the caution that some insects produce multiple external feeding DTs [⁴]. The sampling design of modern data relies on observing living plants and includes the possibility of finding active producers engaged in plant damage, which necessitates adding new methods to extract maximum information from a modern survey. Such a sampling design needs a variety of documentary techniques that are applied by neoecologists, such as photography (including a macro lens or similar equipment), filming, maintaining a notebook, and documentation of the spatial sampling area involving the ecological spectra, quadrats, and observations along a randomly selected trail that would include elevation and geographical coordinates. A pre-study of the vegetation in the sampling area is required by observing the surrounding areas to identify live arthropods and potential herbivorous insects. In addition, it is important to collect leaf samples for plant identification and record the number of leaves and plant individuals sampled, even if this information is unachievable in the fossil record.



To allow for spatial variability within the fossil plant assemblage [2], at least three quarries, preferably separated by several meters, should be excavated at the same stratigraphic level¹. Assessment of sample size is a major issue in herbivory studies [5,6]. Large sample sizes are best, and the more specimens the better, although limits to the number of specimens collected are generally reached based on the intactness of the plant fossils, the density of plant material encountered, and the spatial extent of the productive layers. For example, DT incidence on modern ferns suggests that they occur more frequently than in plants from fossil plant assemblages [3]. The low frequency of DT detection in fossil plants makes it important to have a large number of leaves in the analysis of plant–insect interactions [7]. The standard for nonangiosperm-dominated plant assemblages, although sometimes difficult to achieve, is a sample size of 2000 leaves [7], and all plant material, whether herbivorized or not should be collected. Care should be taken in the collection process, as often examples of herbivory are not readily recognizable in the field but become recognizable under the microscope in the lab. Furthermore, further splitting of slabs in the lab frequently reveal additional plant specimens. The standard for angiosperm leaves from Cretaceous and Cenozoic deposits is to collect and census 1000 leaves and leaflets that are minimally 50 percent complete [1].

During the survey of modern data, controlling the number of leaves sampled, DT occurrences, and time duration of analysis are a means of parameterizing the chance of DT detection in studies of fossil plant-insect interactions [3]. Therefore, all vegetative and reproductive structures require some observation to include any organism that may inhabit the foliage. Samples of arthropod behavior products associated with leaves are important for comparison to analogous examples in the fossil record. Lastly, besides collecting samples of leaf damage and associated structures, a critical observation of the full morphological variability of each incidence of damage is most important during the survey to avoid a partial description of the defining features of the damage.

Rock specimens and samples of modern leaf damage are best laid out on expansive surfaces in the laboratory where plant specimens can be databased. The structure of the database depends on the type of questions being asked regarding the fossil and modern material. A comprehensive Excel database would have plant Linnaean taxa or morphotypes along the rows of the left side of the data matrix, forming the first column, and the features of interest forming the second and following columns along the top of the data matrix. The first feature of interest is a listing of each damage type (DT) per column for each plant specimen. Some specimens may lack DTs whereas others may have multiple DTs that would require multiple columns. Other features requiring additional columns are the total and herbivorized surface area (if any) for each specimen; the feeding event occurrences (if any) for each DT of the specimen; and a measure of damage type functional breadth on the plant hosts, an index of host-plant specificity that is assigned to each DT as 1 (broad), 2 (intermediate), or 3 (narrow), retrospectively after the distribution of DTs on the plant hosts for the entire plant assemblage has been assessed. Other columns can include a photo log of which specimens have been photographed, and a comments field listing any unusual or notable aspects of the plant host or damage type.

Applications

The functional feeding group–damage type (FFG-DT) system is a method of documenting herbivory in the fossil and modern record (Fig. 1). Arthropod or pathogen damage on a plant is initially determined to be a member of one of five feeding classes: ectophytic, or external feeding; stylophytic (formerly ectoendophytic) or feeding by means of mouthpart stylets and ovipositors; endophytic, or internal feeding; pathogen, consisting of viral, bacterial, or fungal necroses; and the very rare domatia, comprised of ant or mite domiciles [8]. Each of these five feeding classes, in turn are divided into functional feeding groups (FFGs) [9,10]. For the ectophytic feeding class, the functional feeding groups are **hole feeding**, **margin feeding**, **skeletonization**, and **surface feeding**; for the stylophytic feeding class, the functional feeding groups are **piercing and sucking** and **oviposition**; for the endophytic feeding class the functional feeding groups are **mining**, **galling**, **seed predation**, and **borings**; for the pathogens feeding class, the functional



feeding group is solely **pathogens**; and for the domatia feeding class, the function feeding group is solely **domatia**. Currently, 427 damage types (DTs) are allocated to the 12 FFGs.

Six major metrics have been established to assess the richness and intensity of herbivory on fossil leaves, which can be quantified for individual plant taxa or for the bulk plant assemblage. The most used metrics are damage richness (or diversity), damage frequency, and damage functional breadth (or “specialization”), composition of the damage, herbivory index, and the most recent metric, feeding event occurrences [1,10,12]. **Damage richness** is the number of DTs observed once standardized for sample size. Often damage richness is assessed separately for mines, galls, and specialized damage. **Damage frequency** is the proportion of leaves with damage, but also can be expressed as a per taxon/morphotype basis. **Damage functional breadth** is a measure of the breadth of distribution of the DTs on the plant hosts and approximates “specialization”. **Damage composition** is a derivative metric that expresses the relative abundances of FFGs or DTs on the plant hosts that are ordinated in multidimensional space, frequently by nonmetric multidimensional scaling (NMDS). The **herbivory index** is the herbivorized plant surface area expressed as a fraction of the total plant surface area, which is calculated for each plant taxon/morphotype or for the entire plant assemblage. A **feeding event occurrence** is a single instance of an herbivore DT on a plant organ such as a leaf [11]. Feeding event occurrences is a fine-grained metric that can be used as links between DTs and plant hosts in bipartite networks, allowing the direct establishment of the interaction links between DTs and their host plant taxa/morphotypes [12]. It also should be noted that these metrics can be evaluated for the FFGs and DTs as well. For example, the herbivory index or amount of herbivorized surface area can be assessed for a particular FFG or DT.

There are many uses of the FFG-DT system to address major ecological and evolutionary questions in the history of herbivory, ranging from the unique ecological aspects of a specific DT association [9], to the extent of herbivore partitioning plant resources in a limited region during a limited time interval [12], to assessing the sweep of herbivory globally for extended geologic time [13]. At the most fundamental level, the establishment of a well-documented DT early in the fossil record can document the earliest known presence of a particular association, such as coconut-pachymerine beetle seed predation from the mid Paleocene of Colombia [14], or the existence of mite domatia in the Mesozoic [15]. The presence of the earliest DT of a leafmining fly mine can establish not only the earliest occurrence of the leafmining fly family Agromyzidae, but also the oldest occurrence of its encompassing clade, Schizophora [16], soon after the end-Cretaceous (K-Pg) ecological event. Other consequences involve certain mining DTs on early Lower Cretaceous angiosperms, indicating that, with phylogeny calibrations, that leaf-mining moths radiated tens of millions of years after their host plants [17], and that their plant-host spectrum has become progressively host specialized through geological time [11]. At a broader level, an ecologically integrated set of DTs representing several FFGs has been tracked through time, documenting the persistence of an ecological guild on the host conifer *Agathis* from the K-Pg interval in Patagonia to modern Malesia and Northern Australia [18].

Broader studies using plant and DT data extend globally and encompass crucial events of the Cenozoic. A series of studies initiated the study of broader patterns across multiple plant assemblages confined to the Paleogene [19,20], culminating in a study of the increase in herbivory during the Paleocene–Eocene Thermal Maximum in Western North America²¹. One such examination¹, using 66 plant-assemblage datasets representing 77,763 leaves from the Late Cretaceous to Pleistocene indicated that a linear correlation did not exist between geologic age and herbivory, albeit there was an effect of the K-Pg event on herbivory. However, there was an effect between paleolatitude, and importantly, temperature and herbivory [1], buttressed by other studies²². Many other studies of fossil and modern herbivory using the FFG-DT system have documented a variety of herbivory patterns on regional and global scales [4, 22, 23, 24].

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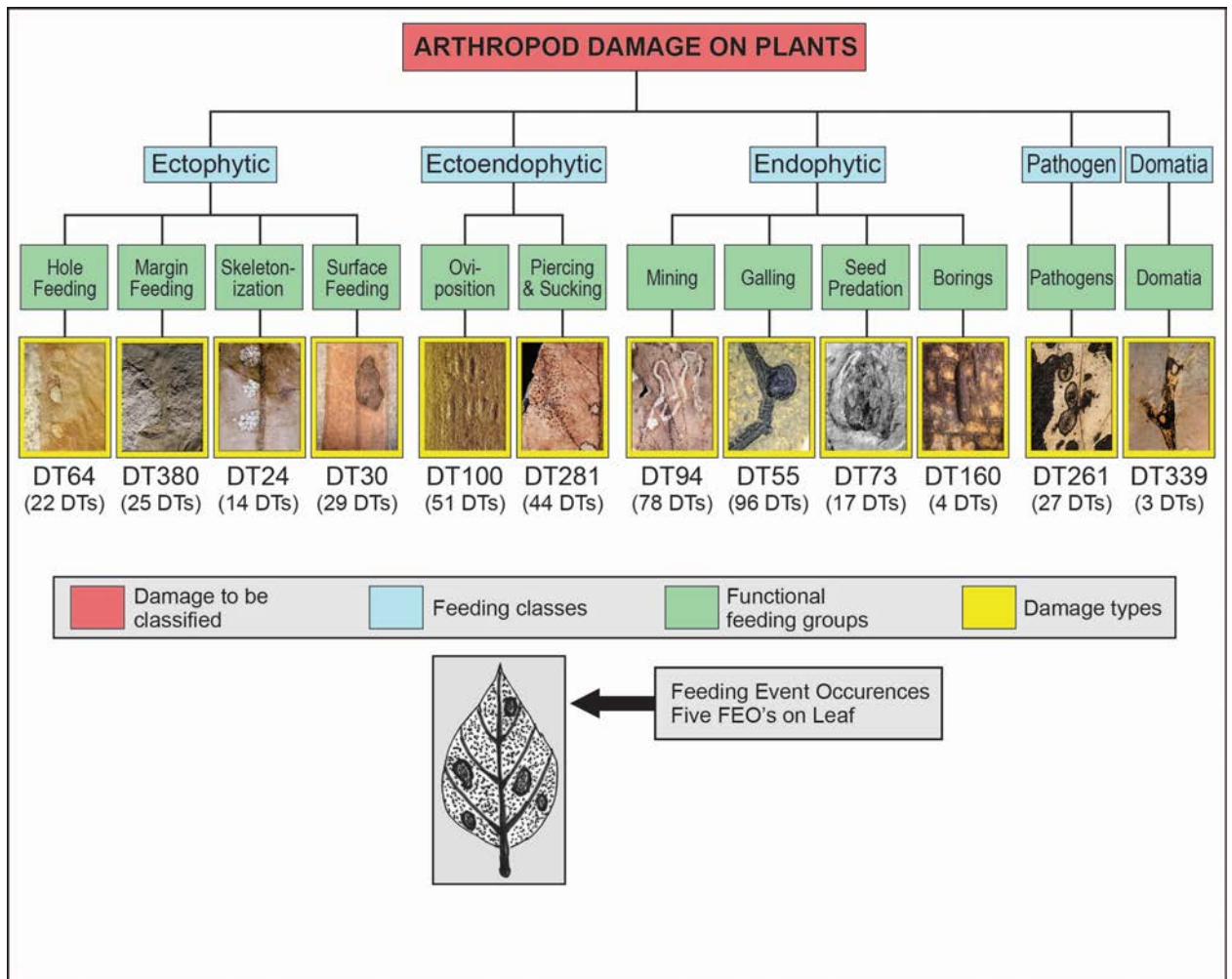


Fig. 1. The functional feeding group–damage type (FFG-DT) system for documenting and analyzing herbivory in the fossil record. Abbreviation: FEO, feeding event occurrences.



REPRESENTATION LEARNING AND ITS APPLICATIONS FOR THE QUANTITATIVE ANALYSIS OF TRACKS

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Artificial intelligence (AI) is one of the most promising emerging techniques in ichnology. So far, AI methods have been primarily used for classification tasks, such as for the differentiation of tracemaker groups [1], ichnotaxa, or bioturbation indexes [2]. However, the potential of AI goes far beyond simple classification and prediction. Here we explore the use of representation (or embedding) learning to visualize and analyze the relationships between shapes of dinosaur tracks based on images of footprint outlines. The results indicate broad overlap between many dinosaurian ichnotaxa, particularly theropods, suggesting oversplitting. Representation learning may be used to visually and statistically compare samples of trace fossils and to define ichnotaxa in a more objective and reproducible way.

The shape of a track is the result of the anatomy of the trackmaker, the substrate properties, the foot kinematics and behavior, and any alteration after track formation. However, vertebrate ichnotaxonomists are primarily concerned with trackmaker anatomy, and hence seek to define features (qualitative characteristics and quantitative measures) that, ideally, reflect anatomy but not the other sources of variation. Such anatomical features can then form the basis for ichnotaxonomy. This process can be translated to machine learning: An AI model trained to discriminate between tracks that we know were left by separate trackmaker taxa will learn anatomically relevant features while ignoring features that are not helpful for making these distinctions. These learned features, or representations, are simply an array of numbers (around 500 numbers in our analysis). A trained model will return these numbers (representations) for each provided track (including for new and unseen tracks). Two tracks with similar representations (small distance) can be assumed to be anatomically similar, while tracks with dissimilar representations (large distance) are anatomically dissimilar. Such distances can be used to determine whether or not two samples are (anatomically) distinct, and how much anatomical variation is present within a sample. Consequently, given a sufficient sample size, this approach may allow to detect differences in species composition and diversity through space and time.

The representations of a given set of tracks can be visualized as a scatter plot by reducing the representations to two dimensions (x and y). This could be done using the familiar principal component analysis (PCA), but more elaborate dimensionality reduction techniques such as UMAP (Uniform Manifold Approximation and Projection) are preferable. Both data that the model was trained on, and new data can be plotted this way. Such dimensionality reduction can also be used for cluster analysis that may form the basis for ichnotaxa definitions.

An important consideration is the format of the input data, which has to be a compromise between the amount of information that can be captured and the sample size required. Ideally, the model would be trained directly on 3D models or height maps, as these capture all relevant information and do not require the subjective interpretation of ambiguous track outlines. However, 3D models will contain a greater amount of irrelevant information or noise (such as the depth of the track, which primarily reflects the water content of the substrate rather than anatomy) that a model will need to learn to ignore, requiring larger sample sizes to do so. For now, we use black-and-white silhouettes of track outlines (32x32 px) that only capture the essence of the shapes while excluding much information that is less relevant. Our dataset consists of a total of 2022 silhouettes of tridactyl tracks belonging to modern birds (n=568), theropods (n=812), and ornithischians (n=642).



A number of different model architectures may be used for representation learning. We here use deep convolutional neural networks (DCNNs) trained to discriminate between known classes, where the output of the second last layer are the learned representations. While highly effective, the disadvantage of this approach is the necessity to define classes (in our case ichnotaxa) *a-priori*, which may not always reflect actual anatomical differences and could result in circular arguments. Another approach we tested involves the creation of pairs of tracks which we can assume to be of either the same biological species (positive pair) or of different species (negative pair) based on criteria such as the occurrence within a trackway (same species assumed) or the occurrence in largely different time epochs (different species assumed). These pairs are then fed to a Siamese neural network that aims to push the representations of negative pairs apart while bringing those of positive pairs closer together. A challenge with this approach is to find enough positive pairs to capture the full range of possible within-species variation.

Both the DCNN and Siamese neural network approaches show a separation between birds, theropods, and ornithischians (Fig. 1A). When the same model is used to plot just the tracks that have been assigned to ichnotaxa, some separation between these ichnotaxa is evident, especially between the elongated shapes of *Grallator*, *Jialingpus*, and *Anchisauripus* and the more robust ichnotaxa such as *Eubrontes* and *Megalosauripus*. However, ichnotaxa within these areas are overlapping in large parts, which applies especially to large theropod ichnotaxa like *Irenosauripus*, *Hispanosauropus*, *Therangospodus*, *Megalosauripus*, *Changpeipus*, *Eubrontes*, and *Kayentapus*, indicating oversplitting of ichnotaxa (Fig. 1B; note that only a subset of mentioned ichnotaxa is shown to obtain a more legible plot). Visual comparison of the images further demonstrates their similarity (Fig. 1C).

AI methods have several advantages over traditional qualitative and quantitative approaches. The direct reliance on images or even 3D models allow to capture the entire shape information, which is often difficult to quantify using measurements and landmarks. As measurements or landmarks are not required, subjectivity and measurement error are avoided. All possible shapes can be analyzed in a single analysis, while traditional approaches require that measures must be taken consistently in all examples, limiting the possible sample sizes. Finally, as the learned features are highly generalizable, it is possible to train models on modern taxa such as birds and then apply them to fossil taxa such as dinosaurs.

These methods also come with challenges, including the large sample sizes that are often required to obtain best results, especially where the input data is complex. It can also be challenging to formulate a correct training approach that allows the model to learn relevant features. In our case, training a model on pre-defined ichnotaxa runs into the issue of circularity. Our Siamese neural network approach, on the other hand, may not capture sufficient within-species variation, and therefore may incorporate irrelevant features. Last but not least, the learned representations are highly abstract, making it difficult to understand and interpret decisions made by the model.

However, there are also unexplored avenues to possibly overcome such issues. Often, only a small subset of tracks can be considered to be anatomically informative, and hence suitable for ichnotaxonomy. It is possible to classify the tracks based on their anatomical informativeness before the main analysis. This could be done based on the confidence score of the model when performing classification, or by using an independent model trained specifically to assess the anatomical fidelity of tracks. Another avenue for improvement is the training on multiple tracks of the same class at the same time – mirroring the approach of an ichnologist who looks at a series of tracks to determine which features are variable and which are potentially informative.

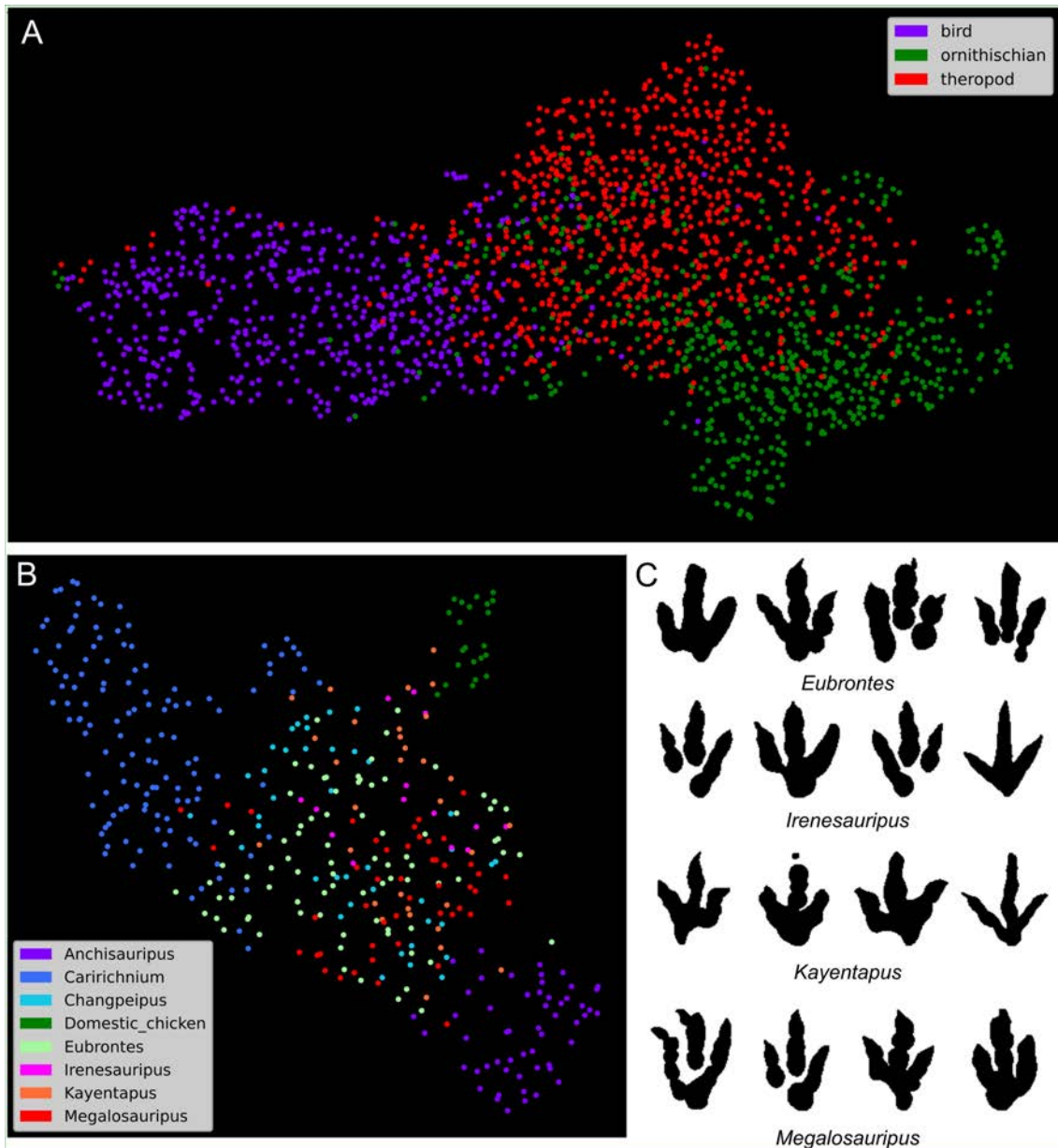


Fig. 1. A. Entire dataset plotted with UMAP based on a DCNN model, with birds, ornithischians, and theropods labeled. B. UMAP plot using the same model as in A, showing selected large theropod ichnotaxa as well as an ornithischian (*Caririchnium*, blue left), a bird (Domestic chicken, green top), and a small and elongated theropod (*Anchisauripus*, purple right). The selected large theropod ichnotaxa show broad overlap. C. Visual comparison of four large theropod ichnotaxa shown in B.

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**BRAZILIAN DINOSAUR AND MAMMAL TRACKS, AMONG CAIMANS AND
PIRANHAS, FROM THE FOREST TO THE SEMIARID**
Contribution to the formation and growth of a Vertebrate Ichnology School in Brazil

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There was once upon a time a somewhat crazy ichnologist vertebrate, who liked to look for fossil tracks where no other or few others had been. He liked being a paleontologist explorer. When I became professor of geological and paleontological chairs in the Federal University of Paraná at Curitiba (1975; in the very first team of professors at that new school of Geology), in the beginning, I often asked my colleagues: “Where are there vertebrate fossil tracks in Brazil?”. Almost everyone answered me “No fossil tracks in our Country”. However, I already knew from literature there was something. I started organizing expeditions, with funds from the National Research Council for Research (CNPq) and the support of the DNPM (the ancient Brazilian National Department of Mineral Production, actual Mining National Agency) and CPRM (Brazilian Geological Survey). I rediscovered the location of the Paraíba trackways in 1975 and discovered many completely new ones; I discovered the Botucatu sandstone quarries in Araraquara in 1976 and those of the Caiuá Group in 1977. In 1980, I found dinosaur tracks in the Marajó sub-basin in Pará. I then proposed to visit all the Phanerozoic sedimentary basins of Brazil in search of fossil footprints. I visited dozens of them, from the graben of Tacutu (Roraima State), in the extreme north of Amazonia, to the extreme south of the Paraná Basin, at the Chuí (Rio Grande do Sul State).

In some of these expeditions, often by canoe on Amazon rivers or in arid and very hot caatingas in the Northeast, or in the forests of Pará State, sometimes I found myself in every kind of adventure, even with bandits, caimans, and piranhas, as happened in the "romantic" expeditions of the nineteenth century. However, I've seen wonderful things.

Naturally I have worked in the area of Ichnology and Herpetology also in Italy and in several other countries, in six continents.

An important moment was the preparation (in 12 years and with four of the most important world ichnologists) of the “Glossary and Manual of Tetrapod Footprint Palaeoichnology”, widely used and quoted worldwide, until now, when we are preparing another, by colleagues Jens Lallensack and Peter Falkingham, who invited me to join them.

In the 1980s and 1990s I started working in all the countries of South America, and again Mexico and three Central American countries, in view of the preparation of the "Annotated Atlas of South America Tetrapod Footprints etc."

About 80 expeditions inside Brazil (1974-2023), about 125 publications on Brazilian material, including some books; active participation in many national and international congresses, and also informative work with press support, have contributed to making known in Brazil and in the world the treasures of the Brazilian Ichnology, and that of other countries.

Finally, what I appreciate most in my life is having taught to many young researchers, (in Brazil, in Italy and in other countries) to work with fossil tracks; and having contributed to form schools of tetrapod ichnology in some countries, especially in Brazil.



FIRST RECORD OF SHOREBIRD FOOTPRINTS IN THE EL MOLINO FORMATION (MAASTRICHTIAN), TOROTORO NATIONAL PARK, BOLIVIA

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The South American continent has a rich vertebrate ichnological record, including dinosaurs, birds and archosaurs. This is exemplified by the Upper Cretaceous El Molino Formation (EMF) in Torotoro National Park, Bolivia, which exhibits a well-preserved and extensive record of dinosaur tracks [1-2]. Over the past three decades, numerous avian tracks have been reported, often associated with tracks of other vertebrates as dinosaurs [3-6]. This study aims to describe the first record of Maastrichtian bird tracks in the El Molino Formation in the Torotoro National Park, Bolivia, within the Torotoro Syncline and situated in the northeast margin of the Central Andes.

The tracksite is an area of 8 m² and occurs in the lower member of the EMF, locally exposed as subhorizontal layers of massive calcareous sandstones showing 4 cm thick laminae without bedding structures on their surfaces (Fig. 1) and that are within a three-meter fining-upward succession of oolitic limestone, calcareous sandstones and massive marls. The sequence is interpreted as deposited in a shallow lacustrine environment. No trace fossils of invertebrates were found in the local stratigraphic section.

The study site was divided into three equal sectors, with each footprint traced using acetate sheet imprints. Measurements on bird footprints follow Leonardi (1987) [7]. Photos were taken with a digital camera and converted in orthorectified images, and a photogrammetric model of the entire site was generated and used to validate field measurements. A total of 225 bird tracks (TB23.2, TB23.3) were found as concave epireliefs in two levels of the tracksite, with a density of up to 108 tracks/m². They consist of 66 incomplete or poorly preserved tracks due to overprinting and 159 well-preserved tracks with all digits clearly identifiable. The tracks were classified into three distinctive morphotypes (Fig. 2) with their respective variations and one of them assigned tentatively to the ichnofamily Iognotornidae indet. Nine trackways were identified comprising 34 tracks, suggesting locomotion and foraging behavior, evidenced by possible pecking marks among the tracks and a zigzag stepping pattern. No preferred orientation of the trackways was identified (Fig. 2E).

Morphotype I (Fig. 2A) comprises 85 tracks, mostly tetradactyl, with an average FL=4.5±0.7 cm, F'L (including hallux)= 6.1±1.4 cm, FL/FW ratio of 0.71±0.1 and total divarication of 121°±13°. The tracks are morphologically anisodactyl and semi-symmetric regarding the axis of digit III (divarication II-III=62°; III-IV=61°), with a posterior medially oriented (divarication I-III=158°±10°), disconnected hallux (digit I) and a proximal web between digits III-IV. There is a high divarication-angle variation of this morphotype (average divarication II-IV =138°±12°), which consists of 15 tracks, mostly tridactyl, with straight and thick digits that occasionally are preserving heel impressions and less developed proximal webs. In total, five trackways show this morphotype. These tracks are assigned to the ichnofamily Iognotornidae indet. due to high variation in size, divarication and hallux morphology. This ichnofamily is defined by tetradactyl bird tracks that show prominent, posterior medially directed hallux impressions comprising about one-third of total track length. Hypex between digits III and IV is more

³/₄anteriorly situated than hypex between digits II and III, with the tendency for development of asymmetric, semipalmate web that is more strongly developed between digits III and IV. Digit divarication between II and IV averages at least 110°–120° wide. Step is typically short with a strong tendency towards inward rotation [8].

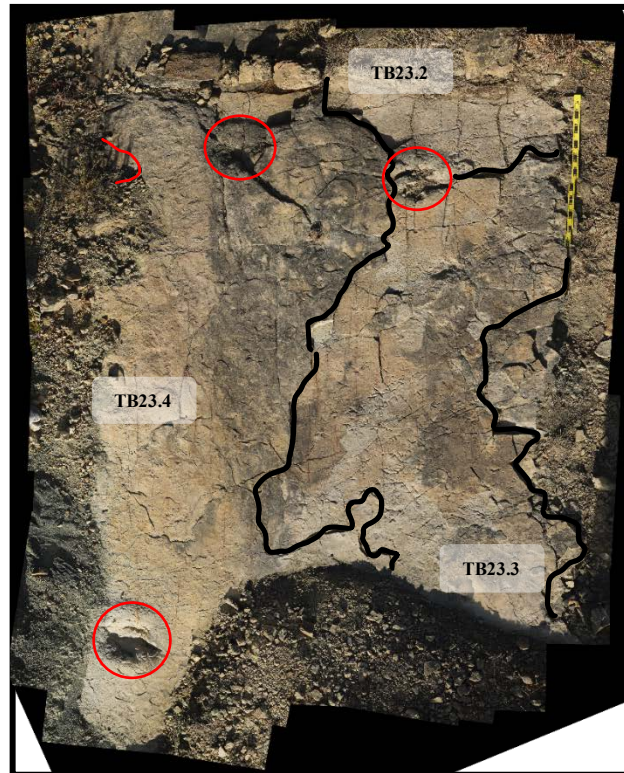


Fig. 1 Orthorectified image of the site. Dinosaur tracks highlighted in red. Margin of laminae delimited in black. Scale bar = 1m.

Morphotype II (Fig. 2B) consists of 38 tetradactyl tracks, medium-sized (average F'L= 6.8±1.8 cm), highly asymmetric by its lateral digit sizes and its interdigital angles (II-III= 44°; III-IV=71°). Its total divarication (II-IV) is 113°±19°. They show an anisodactyl morphology with a well-developed, connected and posteriorly to posterior medially oriented (divarication I-III = 163°±12°) hallux. In addition, there is no webbed impressions exhibited between their digits. 10 of these tracks occur in three trackways that exhibit wide and long steps with occasional stops. This morphotype has a small size variation that comprises 15 (average FL=3.3±0.7 cm) tetradactyl tracks, highlighted by its symmetry regarding to the axis of digit III. It has a posteriorly oriented hallux and high internal rotation characterize two identified trackways. It is suggested a possible ontogenetic growth stages among producers.

Morphotype III (Fig. 2C) comprises 13 isolated small tetradactyl tracks (average FL=2.2±0.2 cm; F'L(including hallux)=3.5±0.8 cm) with an anisodactyl and symmetric morphology regarding axis of digit III. It has a wide total divarication angle (average 138°±13°) and straight digits (in which lateral ones are thicker than digit III) of between 1.4-1.7 cm in length. Hallux is posterior to posterior medially oriented (divarication I- III=157°±12°).

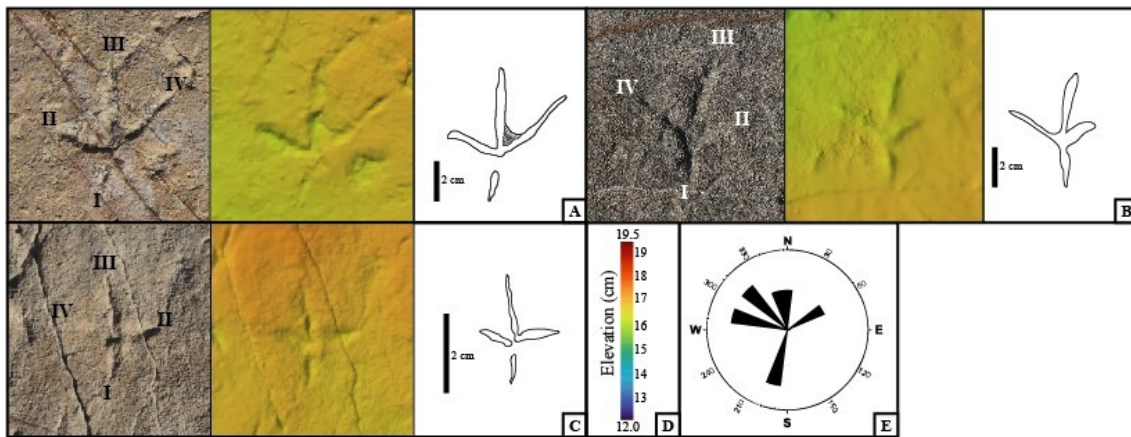


Fig. 2. Representative footprints of each morphotype described by their respective photography, photogrammetry image and diagram. Scale bars = 2 cm. A. Morphotype I. B. Morphotype II. C. Morphotype III. D. Elevation scale (cm). E. Rose diagram showing direction for each identified trackway.

In the upper level of the site (TB23.4), four deep theropod dinosaur tracks with claw drag marks and expulsion rims occur in an NNW-oriented trackway (Fig. 1). The substrate consists of medium to very fine-grained calcareous sandstone, formed through the early cementation of a muddy sediment, likely resulting from a mix of various sources. The lithology includes isolated ostracod valves, isolated ooids, and desiccation cracks within laminated layers. The inferred depositional setting is indicative of a lacustrine margin characterized by shallow water conditions, influenced by temporal fluctuations in water levels.

The morphological description of the tracks closely resembles both Cenozoic ichnotaxa and modern coastal bird tracks, suggesting convergence of these groups over time. The potential producers for morphotypes I and III are related to Charadriiformes, whereas for Morphotype II is related to Ciconiiformes. This finding enriches the trace fossil diversity in the El Molino Formation and Bolivia and provides additional paleontological evidence for the paleoecological relationships in the Upper Cretaceous of the Central Andes.

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INFLUENCE OF BIOTURBATION AND TRACE FOSSILS ON PALEOCLIMATIC TIME SERIES

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Our understanding of how the world responds to climate change is largely based on elaborate reconstructions using micropaleontological, geochemical, and isotopic proxies in marine sediment. The influence of the activities of benthic organism on the fidelity of these records, however, is routinely overlooked. In this contribution, I will highlight some of the worst errors and biases that bioturbation and deep-reaching burrowers can cause to paleoclimatic time series.

It is well known that the mixing of sediments near the sediment surface through bioturbation acts similar to a low-pass filter, reducing proxy signal amplitude and smoothing the record. In regions with low sedimentation rates, this up-mixing of older material and down-mixing of younger material can lead to large errors in radiocarbon dating. For example, in the Arctic Ocean, where sedimentation rates are often on the order of only millimeters or a few centimeters per thousand years, otoliths from Marine Isotope Stage 3 (57-29 ky) were found on the sediment surface of the sea floor [¹]. This mixing can also introduce significant shifts between different proxy signals if there are downcore differences in the abundance of the proxy carriers. Shifts in climate typically results in a shift in the faunal composition of microfossils, such as foraminifera. The mixing of the sediment would then shift more old foraminifera upwards for the species showing decreasing abundances and shift more young foraminifera downwards for the species showing an increasing abundance. This combined up- and downward shift of two proxy carriers originally situated in the exact same layer therefore can introduce a false gradient in isotope ratios or elemental composition between two species [²].

Deep-reaching burrows pose another threat to high-resolution paleoclimate reconstructions. Some organisms, such as the producers of *Zoophycos*, can pipe large amounts of sediment down into deeper layers, resulting in radiocarbon ages that are thousands, or even tens of thousands of years too old [3-5] (Küssner et al., 2018; Leuschner et al., 2002; Löwemark and Werner, 2001). Moreover, these down-piped foraminifera are often also better preserved compared to ambient foraminifera that may suffer from dissolution or authigenic calcite overgrowth, thereby making them an alluring target for paleoceanographers.

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THE ETHOLOGICAL ICHNO QUOTIENT (EIQ): A SEMI-QUANTITATIVE APPROACH TO ASSESS DEEP-MARINE TRACE FOSSILS IN CORE

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In unlithified, deep-marine sediment cores, it is often difficult to quantitatively assess variations in the amount and type of bioturbational structures and distinct burrows. Traditional bioturbation indices are often challenging to use because primary sedimentary structures are mostly hard to discern in fine-grained marine muds. Moreover, stratigraphic logs of bioturbation tend to be hard to read, and visual methods such as core logs with various symbols are often biased by the researchers' preferences. When assessing bioturbation intensity in a sediment core, we look into the collective abundance of traces. These traces, formed by organisms adapting to diverse environments, are generally categorized into ethological groups, which in turn can be used to indicate different habitat conditions prevailing when the organisms lived. This information then translates into paleoecological interpretations that can be contrasted against paleoenvironmental information obtained from geochemical or isotopic proxies. We here introduce the Ethological Ichno Quotient (EIQ) to establish a semi-quantitative measure reflecting the prevalence of diverse traces. This approach effectively summarizes behavioral variations and provides insights into the prevailing ecological conditions. In particular, we here demonstrate how a semi-quantitative assessment of the abundance of different traces and degree of bioturbation can be displayed in a way that efficiently summarizes different behaviors, but without overemphasizing the presence of individual traces.

The occurrence of trace fossils is recorded using a qualitative intensity scale ranging from absent (0), few (10), some (25), abundant (50), to dominating (100). The sum of all observed traces belonging to a specific ethological group is then continuously calculated for each depth interval. The rationale behind the quasi-logarithmic scale being that the occasional occurrence of several different individual trace fossils should not sum up to the equivalent of “abundant” or “dominating”. For example, the occurrence of one *Planolites*, one *Phycosiphon*, and one *Palaeophycos* in the same 5-cm interval now sums up to 30, approximately equal to “some” (25). Likewise, if we encountered four different trace fossils, each with an abundance of “some”, then the EIQ would sum up to 100, equal to one trace fossil dominating the fabric. The fact that the EIQ then conveniently sums up the intensity of different ethological groups of trace fossils (Fig. 1), therefore, facilitates the comparison to other geochemical, isotopic, micropaleontological, or paleoenvironmental proxies.

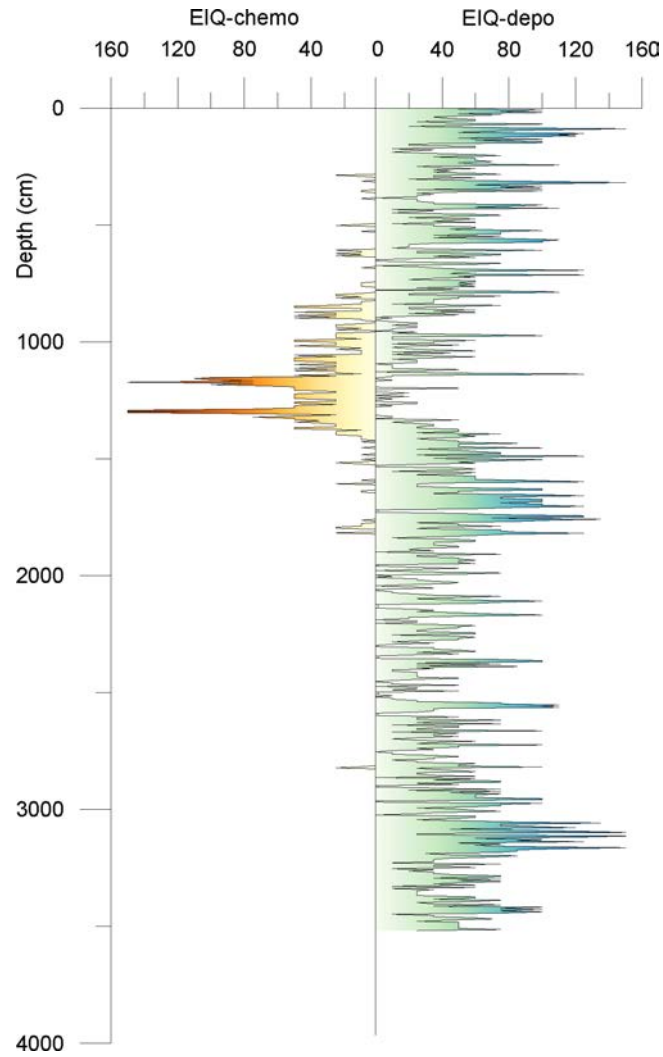


Fig. 1. Example showing variations in trace fossils representing chemosymbiotic vs. deposit feeding behaviors in a core from the continental margin off Taiwan. This semi-quantitative approach allows the relative importance of different ethological endobenthic groups to be visualized.

DEVONIAN TETRAPOD FOOTPRINTS AND THE ORIGIN AND EARLY EVOLUTION OF TETRAPODS

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A critical review of the reported Devonian tetrapod footprints indicates that there are only three records that can be verified as produced by a tetrapod [1]. These tracks include the oldest fossils of tetrapods. The tracks document that hindlimb-propelled, lateral-sequence walking by tetrapods with larger hindlimbs than forelimbs had appeared in the Middle Devonian. This calls into question whether the known Devonian tetrapod body fossils and their supposed sister group/ancestors, the tetrapodomorph fishes, which have larger forelimbs than hindlimbs, are the main line of tetrapod origins and evolution. The ichnology of Devonian tetrapod footprints thus mandates a rethink of current ideas about the origin and early evolution of tetrapods.

Multiple trackways from a Middle Devonian (Givetian) horizon of the Valentia Slate Formation on Valentia Island in southwestern Ireland were made along river margins in a freshwater setting [2]. Most impressive is a trackway of 150 footprints without median drag marks across a long, meandering path that extends for a course of about 10 m. This trackway shows both size differentiation of manus and pes footprints and an alternating trackway pattern (Fig. 1). The footprints are wider than long, and this may suggest a polydactyl trackmaker with forward-oriented digits.

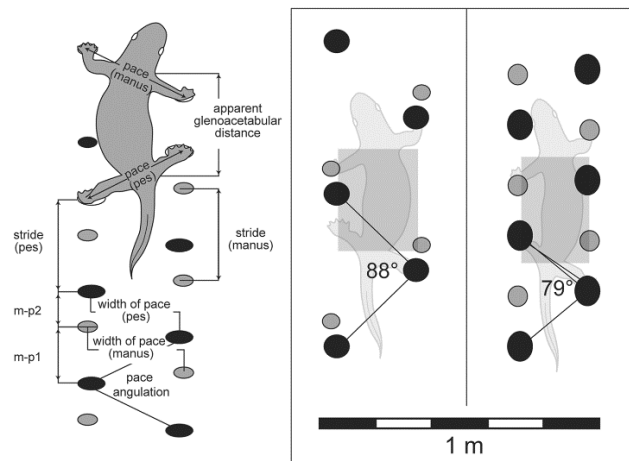


Fig.1. Interpretation of Middle Devonian trackways on Valentia Island, Ireland, showing lateral sequence walking by a tetrapod with a larger pes than manus. Modified from [2].

Tetrapod trackways from the Gnoa River in New South Wales, Australia are from nonmarine strata of fluvial origin of the Combyingbar Formation of Frasnian age [3]. Here, two trackways show alternating trackway patterns, differentiation (by size) of the manus (smaller) and pes (larger) and, in some imprints, evident digit impressions. One preserves overstepped, broad and short manus impressions smaller than pes impressions that are longer than wide. Some of the manus and pes impressions have at least five, short and blunt, laterally-directed digit imprints.

A tetrapod trackway from the Upper Old Red Sandstone of Easter Ross in northern Scotland may be of Devonian age [4]. The footprint-bearing stratum is part of an eolian sabkha deposit, so the footprints were impressed subaerially. The footprints form an alternating trackway

of three steps in which inferred manus and pes imprints can be differentiated (manus much smaller than pes).

The Middle Devonian tetrapod trackways from Valentia Island in Ireland are the oldest fossils of tetrapods, so they provide an important datum that places tetrapod origins during the Middle Devonian, or earlier. Bona fide Devonian tetrapod footprints are from nonmarine facies, so they do not support a marginal marine origin of tetrapods. They indicate lateral sequence walking and pelvic-limb-propelled, fully terrestrial (subaerial) locomotion in freshwater environments by at least some Devonian tetrapods.

Note that the purported tetrapod tracks from the Middle Devonian Zachełmie locality in Poland [^{5,6}], supposedly from lacustrine sediments [⁷], are not tetrapod tracks, but instead fish nests [¹]. The supposed lacustrine sediments were originally interpreted as nearshore marine (they include dolomites with conodonts), so their interpretation as lacustrine is questionable.

The tetrapodomorph fishes, the supposed sister taxon to tetrapods, such as *Panderichthys* and *Tiktaalik*, have robust pectoral fins, much larger than their hind fins, quite different from the larger pelvic limbs of tetrapods (Fig. 2). There is thus a marked disconnect between the locomotory apparatus of terrestrial tetrapods, driven by hindlimb propulsion, and that of their supposed nearest relatives, driven by forelimb propulsion. The footprint record suggests this evolutionary gap had already been bridged by the Middle Devonian.

The transition from fins to limbs is widely regarded to have taken place in the aquatic realm. In other words, Devonian tetrapods are regarded as primarily aquatic. Indeed, the limbs of *Ichthyostega* and *Acanthostega* have been seen as relatively inflexible paddles that were unlikely to have left the kinds of Devonian trackways attributed to tetrapods [⁸].

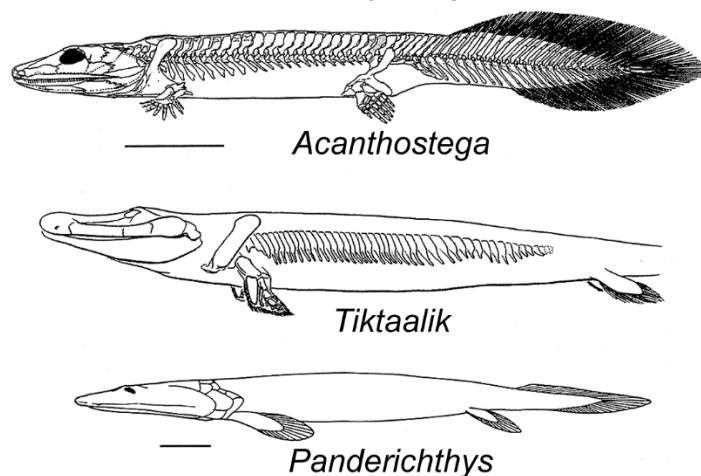


Fig. 2. Lateral views of skeletons and body outlines of selected tetrapodomorph fishes and a Devonian tetrapod (*Acanthostega*). After [¹]. Scale bars = 10 cm.

Bona fide Devonian tetrapod footprints indicate an alternating pattern of limb-supported locomotion by a tetrapod with a larger hindfoot than forefoot (Fig. 1). This is the characteristic pattern of quadrupedal locomotion of post-Devonian tetrapods. The Devonian tetrapod footprint record thus indicates such locomotion was possible at least some of the time by some Devonian tetrapods. Body fossils of these Devonian tetrapods await discovery.

There is thus a considerable morphological gap between the locomotory apparatus of fully terrestrial tetrapods, driven by hindlimb propulsion, and that of their supposed nearest relatives, driven by forelimb propulsion. For the tetrapodomorph fishes to be closely related, if not ancestral to tetrapods, a major reversal in relative limb sizes needed to have taken place. Instead, it is more likely that the supposed close relationship of the tetrapodomorph fishes to tetrapods is an example of how cladistic analysis fails to identify convergence. Indeed, the known “stem tetrapods” and their supposed closest relatives, the tetrapodomorph fishes, likely do



not represent the main line of tetrapod evolution but instead are groups convergent on many tetrapod morphological features.

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LOWER MISSISSIPPIAN TRACE FOSSILS FROM BLUE BEACH, NOVA SCOTIA, CANADA, PROVIDE IMPORTANT INSIGHT INTO LOCAL PALEOENVIRONMENTS AND THE EARLY EVOLUTION OF TETRAPODS

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The Lower Mississippian Blue Beach and Hurd Creek members of the Horton Bluff Formation at Blue Beach, Nova Scotia, Canada, yield an extensive fossil record, including the earliest terrestrial tetrapod fauna, several taxa of associated fishes, nonmarine and marine invertebrates, and an early flora containing nearshore and terrestrial plants. Trace fossils from Blue Beach are diverse invertebrate traces and the earliest large assemblage of bona fide pentadactyl tetrapod footprints and trackways. Sedimentary structures, microbially-induced sedimentary structures and some problematic structures are also present in the Blue Beach deposit (Fig. 1).



Fig. 1. Outcrops of the Blue Beach Member (foreground) and Hurd Creek Member (cliff) at Blue Beach.

Invertebrate traces are assigned to the following ichnotaxa: *Arborichnus* new ichnospecies; *Cruziana problematica* Schindewolf (Fig. 2); *Dendroidichnites irregulare* Holub and Kozur; *Diplichnites gouldi* Gevers, Frakes, Edwards and Marzolf; *Diplopodichnus biformis* Brady; *Gordia marina* Emmons; *Helminthopsis abeli* Książkiewicz; *Hexapodichnus horrens* Hitchcock; *Kouphichnium lithographicum* Nopsca; *Lockeia siliquaria* James; *Margaritichnus reptilis* Bandel; *Monomorphichnus podolicus* Uchman, Drygant, Paszkowski, Porębski and Turnau and *M. cf. M. bilinearis* Smith; *Oniscoidichnus* isp.; *Palaeophycus tubularis* Hall; *Palmichnium macdonaldi* Braddy; *Protichnites* isp.; *Protovirgularia dichotoma* M'Coy; *Rusophycus carbonarius* Dawson (Fig. 2); *Selenichnites rossendalensis* Hardy; *Siphonichnus* isp.; *Stiallia pilosa* Smith; and *Stiaria intermedia* Smith. These ichnotaxa are characteristic of the *Cruziana* ichnofacies of marginal marine environments. They provide strong support for

identifying a marine embayment, not a freshwater lake (as was long identified), as the depositional setting of the Blue Beach and Hurd Creek members of the Horton Bluff Formation.

Vertebrate ichnotaxa present at Blue Beach are new ichnotaxa of rhizodontid trails and resting traces; *Undichna britannica* Higgs; *Undichna* isp.; new temnospondyl resting and activity traces; *Attenosaurus subulensis* Aldrich in Aldrich and Jones; *Batrachichnus salamandroides* Geinitz; *Characichnos* isp.; *Hylopus hardingi* Dawson; *Limnopus heterodactylus* King; and *Pseudobradypus* new ichnospecies. The tetrapod footprint ichnotaxa are characteristic of the *Batrachichnus* ichnofacies, which is consistent with a coastal paleoenvironment. The tetrapod footprints from Blue Beach represent small and large temnospondyl and reptiliomorph (“anthracosaur” or “embolomere”) trackmakers. However, only some of the reptiliomorph trackmakers may be represented by tetrapod body fossils from Blue Beach, which are of reptiliomorphs, whatcheriids, crassigyrinids and “stem tetrapods” (acanthostegids, ichthyostegids and tulerpetontids). The Blue Beach temnospondyl footprints are the oldest fossils of temnospondyls and are of large and small ichnotaxa, likely indicating an already developed diversity of temnospondyls.

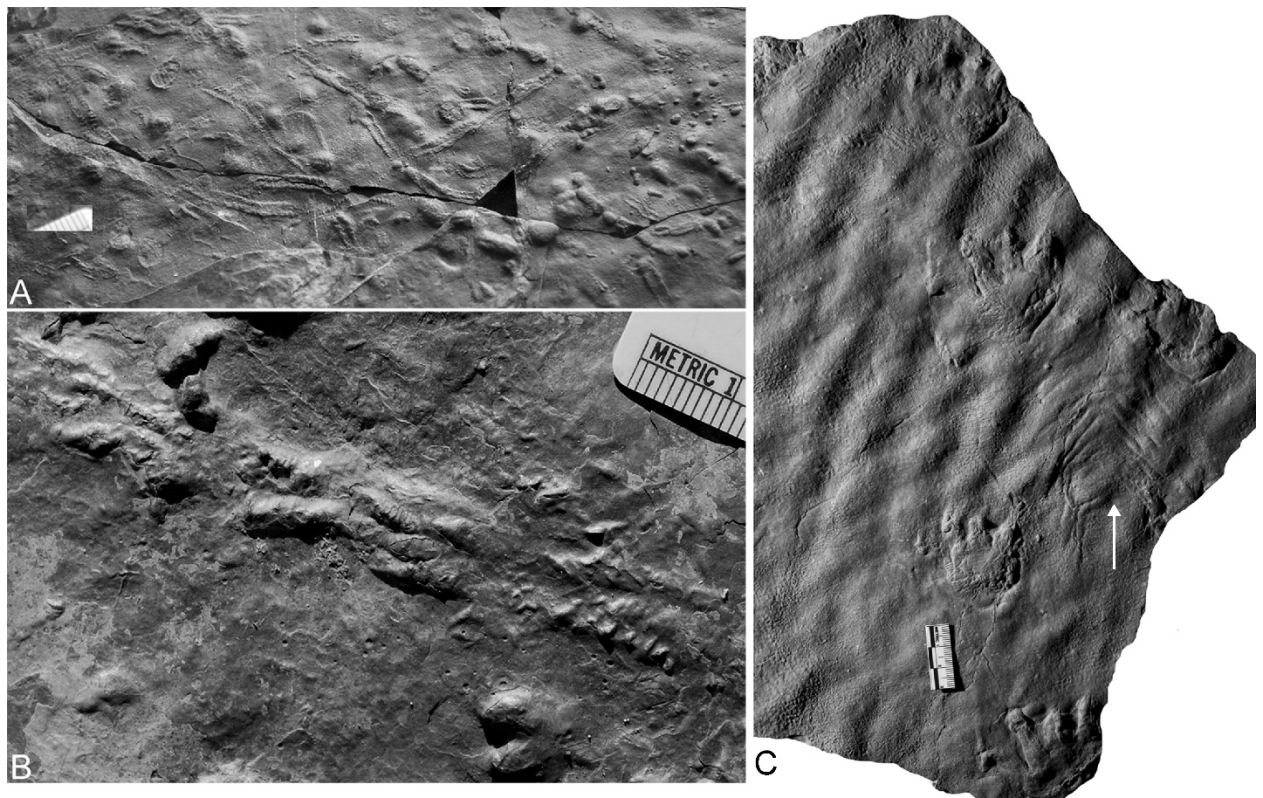


Fig. 2. The trace fossils *Cruziana* and *Rusophycus* (A-B) dominate the invertebrate ichnoassemblage at Blue Beach. *Limnopus* (C), temnospondyl amphibian footprints (here associated with the chevron-shaped mark of the thorax, arrow), are the oldest record of temnospondyls. Scales in mm.

The tetrapod footprints from Blue Beach are those of pentadactyl, lateral-sequence walking quadrupeds that used hindlimb propulsion. Such footprints are known from a few Devonian records, including the oldest tetrapod fossils, which are Middle Devonian (Givetian) trackways from Ireland. Devonian tetrapods known from body fossils and their closest relatives among the tetrapodomorph fishes did not make the kind of footprints found at Blue Beach. The Blue Beach tetrapod footprints thus were made by tetrapods largely not known from the local body fossil record, which indicates that a significant portion of early Carboniferous tetrapod diversity remains to be discovered.



INFAUNAL RESPONSE DURING THE END-PERMIAN MASS EXTINCTION: EVIDENCE FROM TRACE FOSSILS

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The end-Permian Mass Extinction (EPME) has caused the largest loss of biodiversity in the Phanerozoic. The mechanism and tempo of this event remain to be explored, with focus on what factors controlling the timing of recovery and whether the recovery process between low and mid- to high latitude regions is diachronous or not. During the last few decades, Permian–Triassic trace fossils have been studied intensively to understand the timing and process of EPME and subsequent biotic recovery. This is because trace fossils represent behaviors of both skeletonized and soft bodied organisms, and their preservation was not affected by the same taphonomic constrains that may have biased the body-fossil record. Analyses of secular changes in ichnodiversity, ichnodisparity, and tiering structure from the late Permian to the Middle Triassic show that global ichnodiversity and ichnodisparity maintained their levels during the EPME. A sharp decrease of both ichnodiversity and ichnodisparity, however, occurred in the Dienerian. The maintained high ichnodiversity in Griesbachian interval is in contrast with the great loss of body fossils at that time. This discrepancy between body- and trace-fossil diversity is interpreted to be the result of taphonomic effects of trace fossils by the resurgence of widespread microbial matgrounds and firmgrounds in the Griesbachian. Such substrate changes aided the preservation of surficial, semi-infaunal, and shallow-tier trace fossils, which is indicated by an unusual dominance of shallower tiers in the Griesbachian. Our study indicates that the EPME strongly affected the sediment mixed layer, allowing the preservation of shallower tier trace fossils. A further analysis of trends on ichnodiversity and ichnodisparity between low- and mid- to high latitude regions suggests that infaunal organisms from mid- to high latitude regions were more resilient to the extinction scenario. Furthermore, the maintained number of occupied categories of ecospace and ecosystem engineering in these regions suggests a faster recovery of infaunal organisms compared with those at low latitude regions. Our study reinforces the significance of trace fossils on evaluating the response of organisms to environmental extremes in critical intervals of deep time on Earth.



SEILACHERIAN ICHNOFACIES FOR DYNAMIC MARINE ENVIRONMENTS

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Development of new Seilacherian ichnofacies for complex dynamic marine depositional settings has proven challenging. Demonstrating temporal and geographic recurrence requires integration of numerous ancient examples and (where possible) characterization of many modern analogues. Additionally, unlike most previous marine-related ichnofacies that were founded on relatively stable environments, sedimentologically dynamic environments such as deltas and marginal marine paralic systems are subject to spatial and temporal variations in physical energy, depositional rate, water turbidity, salinity, oxygenation, and benthic communities. Such variations invariably lead to marked changes in beds and bedset thickness distributions, the types of physical stratification, bioturbation intensities, and the composition and distribution of trace fossil suites.

Many marine environments are typified by relatively stable depositional conditions, manifest by generally uniform substrate types, marine salinities, physical energy, depositional rates and food delivery styles. As such, the resulting facies commonly show broadly consistent trace fossil suites, with uniformly distributed bioturbation and narrow ranges of bioturbation intensity. Intercalated event beds, where they occur, record short-lived excursions from these conditions, are generally infrequent, and typically reflect a consistent origin (e.g., tempestites in shallow water or turbidites in deeper water). Under such scenarios, post-event suites are distinctive and stand in marked contrast to the ambient pre-event suites by which these archetypal ichnofacies are recognized. Such scenarios typify suites of the *Skolithos*, *Cruziana*, *Zoophycos* and *Nereites* ichnofacies.

Highly dynamic environments, by contrast, experience pronounced variations in most if not all of the above parameters, resulting in a complex juxtaposition of discrete suites that record an array of faunal responses to these persistently changing physico-chemical conditions. As a result, the facies of these environments display marked variations in the trace fossil suites, sporadically distributed burrowing and wide ranges in bioturbation intensity. Three new ichnofacies (*Phycosiphon*, *Rosselia* and *Teichichnus* ichnofacies) [¹⁻³] are adopted to express shallow-marine depositional environments characterized by recurring physico-chemical stress as a result of generally rapid but variable deposition rates, temporal changes in physical energy, fluctuations in water turbidity, significant accumulation of fluid mud, variability in substrate consistency, and fluctuations in salinity.

Suites of the *Phycosiphon* Ichnofacies (Fig. 1A) are typified by pronounced changes in ethological characteristics, bioturbation intensities, and faunal colonization patterns, which record the complex interactions of fully marine basinal conditions with fluvial-sediment influx in distal, low-energy marine environments situated below fairweather wave base. Fully marine trace fossil suites are juxtaposed at the bed and bedset scales with low-diversity suites dominated by facies-crossing elements. Numerous intercalated mudstone beds are unburrowed, possess navichnia, or show top-down colonization patterns, and are interpreted to be of fluid-mud origin. Most traces are assigned to mobile deposit-feeding, sessile deposit-feeding, surface grazing, and domiciles for deposit feeding or carnivory. Subordinate behaviours reflect escape, sediment-swimming, and re-equilibration. These juxtaposed suites point to short-term but recurring alternations between

low-energy, stable marine conditions and episodes of elevated physico-chemical stress, consistent with prodeltaic environments.

Suites of the *Rosselia* Ichnofacies (Fig. 1B) occur in beds and bedsets showing variable bioturbation intensities and sporadically distributed bioturbation recording high-energy, episodic deposition of sandstone-dominated heterolithic marine successions. BI values are variable in both sandstone and mudstone beds, and generally decline upwards concomitantly with sandstone content. Facies are dominated by event-bed style deposition. Pre-event suites typically reflect normal marine conditions, albeit generally with a paucity or absence of vertical dwellings, which normally have a positive correlation with suspension feeding. Rather, most dwelling structures are related to deposit-feeding behaviours or carnivory, interpreted to be the response to elevated water turbidity associated with fluvial sediment influx. Mobile deposit-feeding and surface detritus feeding structures form persistent elements of most suites. Post-event suites are typically sporadically distributed and where present, record top-down colonization made up of low-diversity, strongly facies-crossing elements. Fugichnia and re-equilibrichnia are common components, particularly where deposition rates are both episodic and elevated. Fluid-mud layers commonly mantle the event beds, shielding them from colonization and leading to reduced BI values. Most intercalated mud beds are unburrowed or contain navichnia.

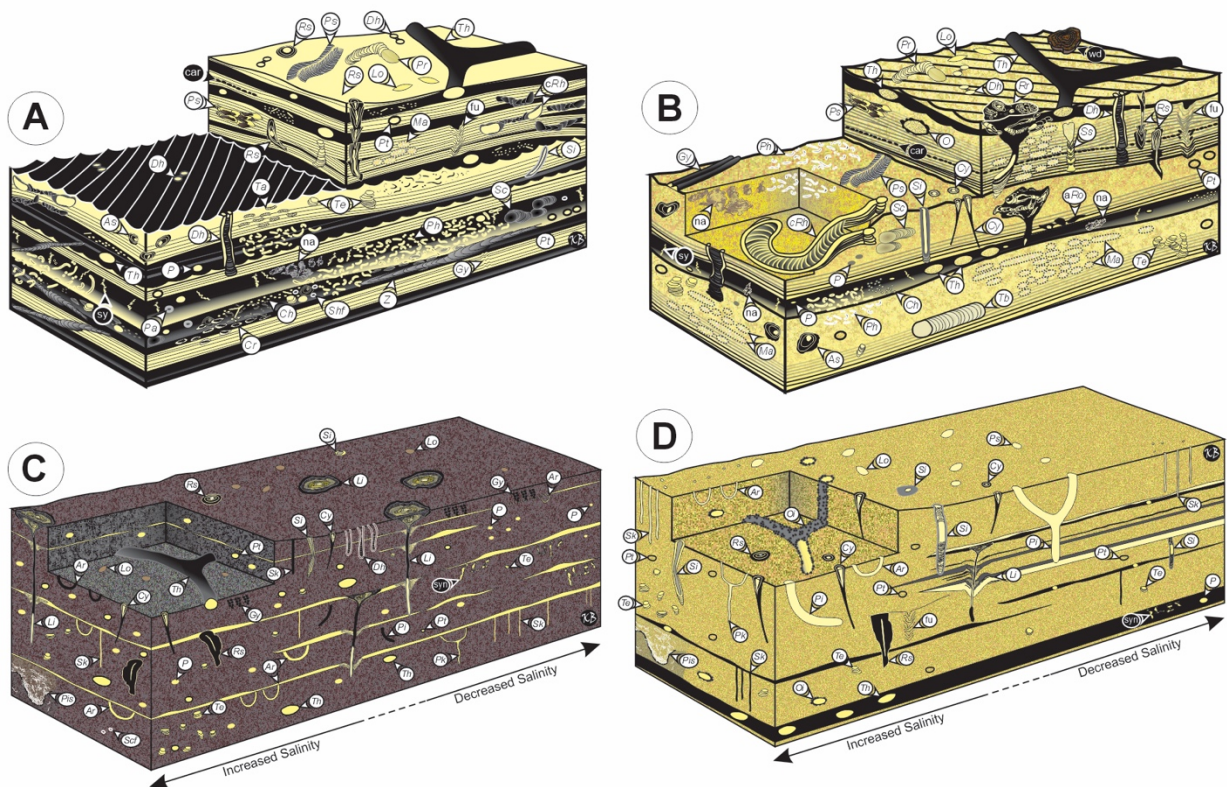


Fig. 1. Block diagrams of the (A) *Phycosiphon*, (B) *Rosselia* and (C, D) *Teichichnus* ichnofacies, used to characterize the range of physico-chemical conditions and resulting animal-sediment relations in facies of prodeltaic, delta-front and brackish-water paralic settings, respectively [1-3].

Suites of the *Teichichnus* Ichnofacies (Fig. 1C-D) show most of the same evidence of physico-chemical stress as outlined above, with the exception that they record persistent salinity reduction and so generally lack intercalated beds containing fully marine ichnogenera. Brackish-water settings are dominated by euryhaline-tolerant species resulting from osmoregulation-related selective pressures that reduce diversity and promote infaunal strategies. Faunas adopt r-selected strategies, characterized by rapid colonization, high population densities, and monospecific assemblages. Tides provide abundant food through transport of organic matter, sedimentation during slack-water periods, and proximity to marine environments. This increased food



availability favors trophic generalists using various feeding behaviors to exploit both intrastratal and surficial resources. Accordingly, the *Teichichnus* Ichnofacies is recognized by reduced trace fossil diversity, smaller trace sizes, dominance of trophic generalist behaviors, sporadic distribution of trace fossils, locally elevated bioturbation intensities, and opportunistic colonization. Importantly, this ichnofacies is characterized by predominantly facies-crossing trace fossils associated with surface deposit feeding, intrastratal deposit feeding, and localized filter feeding.

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PENETRATIVE BIOTURBATION IN MIDDLE CAMBRIAN BURGESS SHALE-TYPE DEPOSITS: THE CASE OF MARBLE CANYON

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Marble Canyon at Yoho National Park in the Canadian Rockies is host to abundant and exquisitely preserved diverse soft-bodied organisms dominated by arthropods, hemichordate, and lophophorates [^{1,2}]. Burgess Shale-type (BST) deposits are typically characterized by the pristine preservation of sedimentary fabrics in the absence of pervasive and extensive, penetrative bioturbation. Notably, trace fossils from Marble Canyon display unique features not associated with classic Burgess Shale-type localities. The ichnofossiliferous interval at Marble Canyon, which occurs in the upper part of the middle Cambrian Thick Stephen Formation, is characterized by the local recurrence of high-density, low-diversity assemblages of discrete, relatively large size (average 0.85 mm wide) trace fossils, resulting in penetrative bioturbation (up to 28 mm deep) and significant disturbance of the primary fabric. Although relatively extensive at outcrop scale, the assemblages tend to decrease in density or disappear laterally in hundreds of meters. These high-density trace-fossil assemblages (i.e, densely bioturbated horizons, BI=3–4, locally 5) occur a few meters below the primary soft-bodied fossil-bearing interval [^{1,2}]. In cross-section views, trace fossils display a complex spreite whose general morphology is hard to reconstruct. These biogenic structures are also recorded as hypichnial ridges, epichnial grooves, or full reliefs at lithologic interfaces, revealing subtle lithological changes between laminae. CT-scans show a palimpsest ichnofabric involving two basic morphologies: shallow U-shaped burrows and semispherical pits. Fossiliferous intervals and highly bioturbated horizons are interbedded with slides, slumps, and synsedimentary faulting indicating deposition in a relatively steep slope. Absence of wave- or storm-generated sedimentary structures indicates deposition below storm wave base. Integrated sedimentologic and ichnologic analysis suggests recurrent colonization events by opportunistic tracemakers possibly enabled by improved oxygen conditions at an unstable muddy slope along the front of the Cathedral Escarpment at Marble Canyon. This ichnofauna and its associated facies allow to revisit the issue of the role of oxygen in BST deposits and to expand our understanding of opportunistic assemblages in physically stressed Cambrian environments.

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TRACE FOSSILS FROM THE LOWER CAMBRIAN CRANBROOK LAGERSTÄTTE OF BRITISH COLUMBIA, CANADA: EXPLORING ANIMAL-SUBSTRATE INTERACTIONS IN BURGESS SHALE-TYPE DEPOSITS

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The lower Cambrian Cranbrook Lagerstätte (Series 2, Stage 4) occurs within the Eager Formation of British Columbia, Canada, representing one of the oldest Burgess Shale-type deposits in North America. The succession consists of claystone intercalated with normally graded mudstone having medium silt to very fine sand and disarticulated skeletal debris delineating laminae near the bed bases. Well known for its olenelloid trilobites and soft-bodied fossils, such as *Tuzoia* and *Anomalocaris*, the site also contains trace fossils, commonly forming low-diversity and low-density suites. Bioturbation intensity in cross-section is low. Trace fossils display significant persistence through the quarry section. *Helminthoidichnites tenuis*, *Palaeophycus tubularis*, *Diplocraterion* isp., *?Arenicolites* isp., and large finger-like structures represent the majority of the trace fossils identified. *Cochlichnus* isp., *Helminthopsis* isp., *Teichichnus rectus*, and *Treptichnus* isp. are comparatively rare. *Bergaueria* isp. shows only very local occurrence of relatively high density. *Diplichnites* occurs in at least two stratigraphic levels that display microbially induced sedimentary structures (MISS). Several *Tuzoia* specimens are associated with *Helminthoidichnites tenuis*, which are not confined to the carapaces, representing incidental associations. Notably, *Tuzoia* specimens are locally modified by overprinting burrows (i.e. taphonomic association). The Cranbrook ichnofauna was dominated by worms, with arthropods being remarkably less common. The rarity of arthropod trackways is likely due to the absence of well-developed bedding plane surfaces and lithologic interfaces that typically enhance their visualization. Overall, the Cranbrook trace fossil assemblages do not display a well-defined tiering structure. Two broad assemblages recur through the studied interval. The *Helminthoidichnites tenuis* assemblage consists of *Helminthoidichnites tenuis*, *Helminthopsis* isp., *Palaeophycus tubularis*, and *Diplichnites* isp. The *Diplocraterion* isp. assemblage is typically monospecific to very low diversity, and is commonly associated to finger-like structures and/or local presence of *P. tubularis* and *?Arenicolites* isp. The finger-like structures contain small (2-3 mm) disarticulated or broken trilobite sclerites (mainly cephalae) and, less commonly, fine sand. These structures are somewhat reminiscent of ribbon-like, elongate aggregates interpreted as coprolites or gut contents of endobenthic predators, such as priapulid worms, in other Burgess Shale-type deposits. However, in the Cranbrook Lagerstätte, these structures are most likely passively infilled burrows. Dwelling burrows containing trilobite fragments and/or coarser grains than the host rock suggest significant sediment bypass and trapping of transported grains within the burrows, which is consistent with the presence of normally graded mudstone interpreted as deposited from turbidity currents. Other ichnotaxa are rare and cannot be assigned to a particular assemblage. The Cranbrook ichnofauna records the activities of a surficial epifauna and a shallow-tier infauna that colonized the sea bottoms during short colonization windows between episodic flows and inhabited a relatively well-oxygenated shelf environment (i.e., below storm wave base).



BIOEROSION STRUCTURES FOUND IN SHELLS OF *MACTRA ISABELLEANA* D'ORBIGNY, 1846 (MOLLUSCA: BIVALVIA) FROM THE COASTAL PLAIN OF RIO GRANDE DO SUL, BRAZIL

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Mollusk shells commonly serve as substrate and food for several groups of marine invertebrates, such as bryozoans, annelids, and even other mollusks, which use them as housing, refuge or feeding [¹]. In the Rio Grande do Sul Coastal Plain (RSCP), accumulations of biodepositional gravel, known as “Concheiros”, are found, formed mainly by bones, teeth and shells of mollusk. Those concentrations were previously in submerged deposits, later remobilized by the action of storms and deposited on the beach face [¹], where shells are commonly found with traces left by various organisms. These accumulations are represented by shells of different ages and may be composed of fossil and recent specimens [²]. The RSCP was formed by the deposition of reworked sediments from the Pelotas Basin, during the Neogene and Quaternary [^{1,3}]. It is a wide plain, on average 100 km wide, and elongated, stretching from Torres to Chuí (620 km), geographically oriented in the NE-SW direction [^{3,4}]. *Mactra isabelleana* d'Orbigny, 1846 is a very common and dominant marine bivalve (Mollusca, Bivalvia, Mactridae) on the southern coast of Rio Grande do Sul and Uruguay, with a known distribution from southeastern Brazil (Cabo Frio, Rio de Janeiro) to San Antonio Oeste, Río Negro province, Argentina [⁵]. Inhabits sandy and muddy bottoms, up to maximum depths of 25 m [^{1,7,8}]. For this reason, they are often used as a substrate and food for various organisms. Therefore, the present work aims to identify the types of bioerosion found in the shells of *M. isabelleana* from RSCP, as well as their possible tracemakers. To this end, the malacological collection of the Laboratório de Geologia e Paleontologia (LGP) at FURG, composed of bivalves and gastropods collected at RSCP was analyzed. Totaling 552 disarticulated valves (both right and left) *M. isabelleana* shells were analyzed for the presence or absence of bioerosions and to which ichnogenus they belong, with the help of previous studies [^{1,9-11}]. The maximum length and height were measured. The specimens analyzed ranged between 3.06 and 57.28 mm (25.63 mm ± 0.59) in length and 2.42 and 46.67 mm (20.03 mm ± 0.48) in height. Of these shells, 35.6% (197/552) showed at least one type of bioerosion. The most found ichnogenus was *Caulostrepsis* (192/197, 97.5%). Then, shells with bioerosion of the *Iramena* type (11/197, 5.6%), *Pennatichnus* (05/197, 2.5%) and the presence of the ichnogenus *Oichnus* (02/197, 1.0%) were observed (Fig. 1). The ichnogenus *Caulostrepsis* is produced by spionid polychaetes, which excavate U-shaped tunnels in shells [^{1,8}]. The ichnogenus *Iramena* and *Pennatichnus* are caused by Ctenostomate bryozoans, which produce tunnel systems with openings on the surface, the first with an irregular pattern of openings and the second with an axial pattern, similar to the shape of a feather [^{9,12}]. All these bioerosions are classified in the same ethological category, Domichnia, consisting of permanent housing structures of sessile or semi-sessile species, generally suspension feeders [⁹]. Considering the dynamics of the beaches in the south of Rio Grande do Sul, the depth of occurrence of *M. isabelleana*, as well as the large amount of suspended material and phytoplankton activity, these bioerosion patterns are consistent to the environment. Additionally, in several shells, it was observed that, associated with the bioerosions on the external surface caused by spionid polychaetes, there are internal anomalous growth structures, showing that the mollusk was alive when it was used as a substrate [¹¹]. It is also very common to observe accumulations of these shells with the valves still attached on the beach, sometimes with the presence of a soft part, current imports, as can be seen in Fig. 2. On the other hand, the ichnogenus *Oichnus* is classified as Praedichnia, being the result of predation on the

organism. This ichnogenus has a circular, semicircular shape borings perpendicular to the substrate, made by mollusks [13].

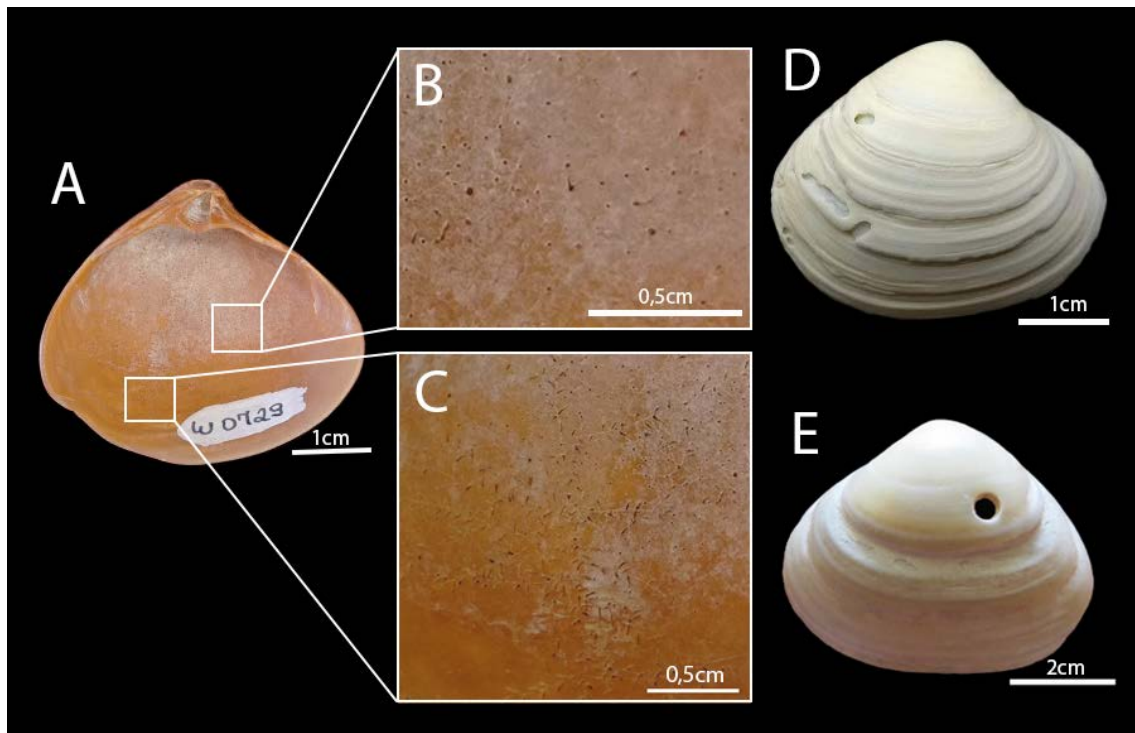


Fig. 1. Bioerosions in shells of *Mactra isabelleana*. A-C. Valve with the presence of *Iramena* (B) and *Pennatichnus* (C). D. Shell with the presence of *Caulostrepsis*. E. Shell with the ichnogenus *Oichnus*.



Fig. 2. Accumulation of *Mactra isabelleana* shells present on Concheiros Beach. Some specimens have the valves still articulated.



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**BIOEROSIONS ON SHELLS OF *ZIDONA DUFRESNII* DONOVAN, 1823
(CAENOGASTROPODA: VOLUTIDAE) FROM CASSINO BEACH,
SOUTHERN BRAZIL**

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Biological traces identified in fossil remains can provide a reliable record of ecological interactions between organisms, which can be associated, for example, with predation, parasitism and commensalism [1]. Among the groups of marine invertebrates, bivalves and gastropods, commonly act as hosts and have excellent preservation potential [1]. *Zidona dufresnii* (Caenogastropoda: Volutidae) is a common gastropod that inhabits the western coast of the Southern Atlantic Ocean, at 35 to 60 m depth in sandy bottoms from Rio de Janeiro, Brazil (22°S) to Patagonian waters, San Matias Gulf, Argentina (42°S) [2,3]. This study analyzed *Z. dufresnii* collected in the Cassino Beach, located in the Rio Grande do Sul Coastal Plain (RSCP) to identify the different types of bioerosion preserved in his shells. Cassino Beach is located at south of the plain, just after the mouth of Lagoa dos Patos, and is a dissipative beach, with fine sand, a gentle slope and a wide beach face [4]. Due to the orientation of the coast, swell waves, generated in southern latitudes, and wind-generated waves produced by strong spring-summer sea breezes are dominant. The average significant wave height is 1.5 m, however, in storm events, which generally occur in the autumn-winter period, waves can exceed 2 m, and the average sea level along the coast can reach at 1.3 m. These events can disturb the bottom where there are submerged deposits, containing bones and shells, and deposit them on the beach face [1]. To identify the most frequent bioerosion structures and their possible causes, all *Z. dufresnii* shells were analyzed with the aid of a stereomicroscope when necessary. The bioerosive structures found were compared with the literature to identify the structure taxa [1, 5-8]. In total, 226 *Z. dufresnii* shells were analyzed, of which 173 (76.5%) showed bioerosion and in 111 specimens (49.1%) more than one associated ichnogenus was found (Fig. 1). The predominant bioerosion was *Caulostrepsis* (146/226, 64.6%), which is characterized by a U-shaped tunnel excavated by spionid polychaetes [6]. The second most abundant ichnogenus was *Iramena* (98/226, 43.3%), produced by ctenostomate bryozoans, presenting a system of tunnels little bifurcated with irregularly pattern with rounded apertures opening into a main cavity [5,8]. *Pennatichnus* bioerosion (59/226, 26.1%) also result of the interaction of ctenostomate bryozoans, but with a tunnel system with axial openings towards the surface with a shape similar to a feather [7,8]. The ichnogenus *Finichnus*, produced by cheilostome bryozoans (35/226, 15.4%), presenting groups of elliptics or pear-shaped shallow pits [9]. The ichnogenus *Entobia*, produced by clionid sponges, composed of interconnected galleries parallel to the surface, with network-shaped perforations and which, in most cases, covers the entire shell [10], was found (19/226, 8.4%). *Podichnus*, a bioerosion also of fixation (Fixichnia) - like *Finichnus* - resulting from the dissolution of carbonate on the surface of the shell caused by Pedunculate Brachiopods, was observed (10/226, 4.42%). This structure is shaped like a compact group of small, shallow pits [11]. The ichnogenes *Gastrochaenolites* and *Oichnus*, both produced by mollusks, were present in one shell (1/226, 0.4%) each. The ichnogenes *Gastrochaenolites* (a club-shaped perforation, where the apertural region is narrower than the main chamber, and can be circular, oval or dumbbell-shaped) is produced by Mytiladae Bivalves [12], which use the shell of *Z. dufresnii* as a substrate for permanent housing (Domichnia) – as well as *Caulostrepsis*, *Iramena*, *Pennatichnus* and *Entobia*. While *Oichnus*, characterized by circular perforation perpendicular to the substrate drilling the surface [13], is a trace left by Carnivorous Gastropods by the act of predation (Praedichnia). It can be noted that the majority of bioerosions found are in the ecological category Domichnia and Fixichnia, caused by sessile or

semi-sessile and suspension-eating organisms, which use the mollusk shell as a substrate, given that there is no presence of rocks or consolidated sediment in this region. The abundance of these organisms is consistent with the environmental conditions where *Z. dufresnii* lives, where there is a lot of organic matter in suspension and shallow depth, with food available for the filter feeders. However, trace that show evidence of predatory evidence (Praedichnia) occurred in only one of the shells analyzed, which may indicate that *Z. dufresnii* is not an organism that is easily preyed upon by other mollusks or that does not inhabit the same environment. These data are still preliminary, as the study is in its initial phase. More collections will be carried out on Cassino Beach to better understand the ecological interactions of these organisms with *Z. dufresnii*.

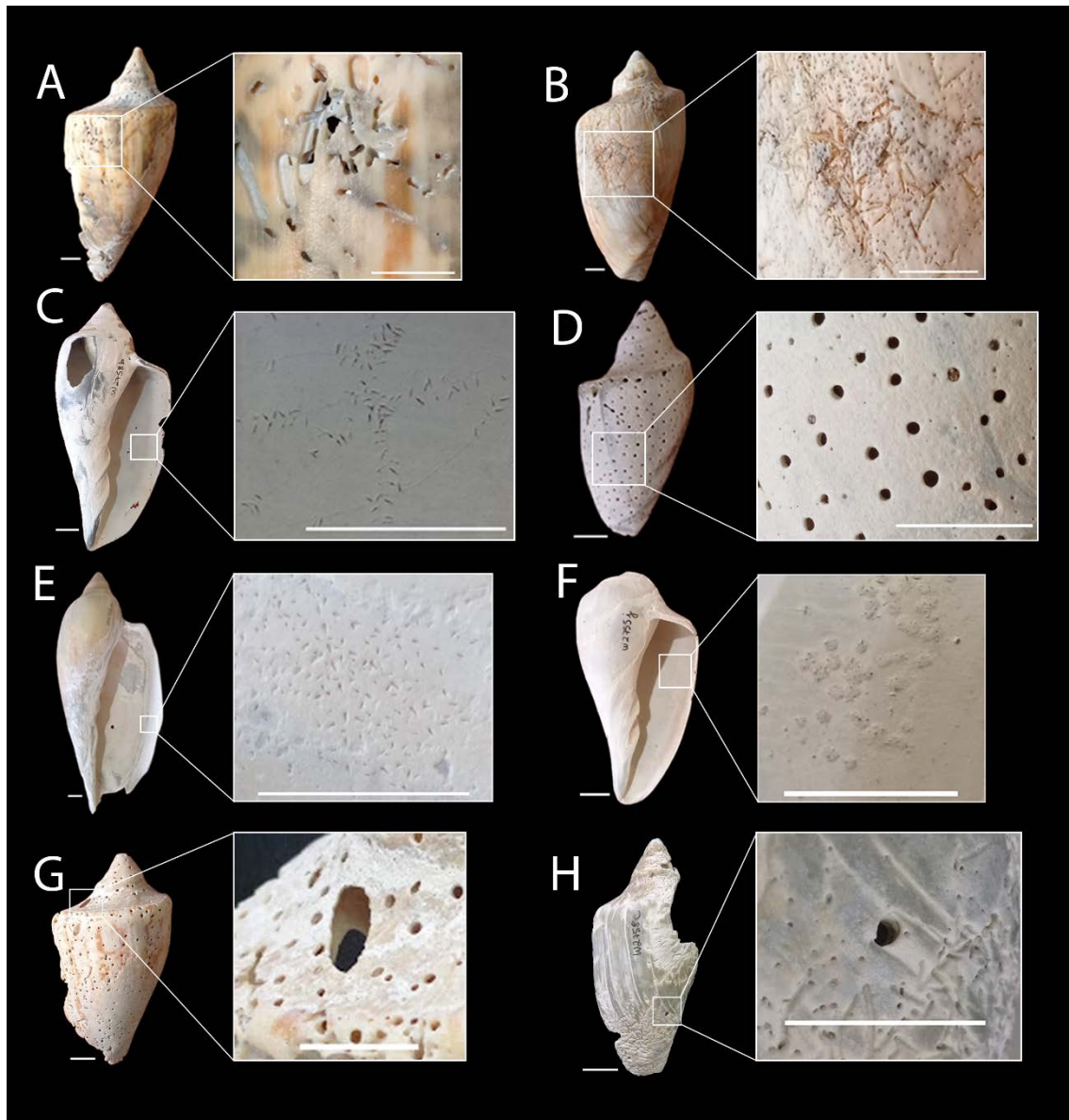


Fig. 1. Shells of *Z. dufresnii* with the presence of bioerosion. A. *Caulostrepsis* isp. B. *Iramena* isp. C. *Pennatichnus* isp. D. *Entobia* isp. E. *Finichnu* isp. F. *Podichnus* isp. G. *Gastrochaenolites* isp. H. *Oichnus* isp. Scale bar = 1 cm.

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POPULAR ICHNOLOGY: TOWARD A PUBLIC AWARENESS OF OUR SCIENCE

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Ichnology is probably among the oldest of sciences, whether developed through the practice of tracking animals or indigenous societies' recognition of trace fossils as signs of pre-human lives. Nevertheless, public awareness of ichnology is less than that of other sciences. One limiting factor for ichnology has been its relatively recent inclusion as a subset of geology or paleontology. Geology itself is already overshadowed somewhat by physics, chemistry, biology, and computer sciences, with the most attention given to human-health issues and technological innovations. Ichnology is further classified as a lesser part of paleontology, which in educational institutions translates into a niche status. Hence even university-educated people may not know of ichnology, nor would they know its scientific importance and presence in everyday life.

One proposed solution for increasing a public awareness of ichnology is for ichnologists to identify and communicate how their science connects with non-ichnologists' lives. One of the easiest avenues for introducing basic ichnological concepts is through neoichnology, in which available substrates and modern tracemaker behaviors result in many visible and interpretable traces. For example, wherever plants and herbivorous or wood-boring insects live, insects impart traces in leaves and wood. Insect and bird nests are other common ichnological examples that also demonstrate how traces animal behaviors can be linked to seasonal behaviors. Even urban environments have a variety of traces preserved in cemented walkways that host "pre-fossilized" trackways of domestic animals and humans. As for paleoichnology, the enduring and near-universal popularity of dinosaurs provides an opportunity to teach and learn about dinosaur tracks and their trace fossils.

Strategies for how ichnologists can communicate ichnology and connect it a broader public is thus multi-faceted. For those of us who teach in educational institutions, we can act on a local level by including more ichnological concepts and examples in our teaching and public engagement. As for researchers, we can partner with paleontological artists ("paleoartists"), science writers, poets, and other creative people skilled at conveying scientific ideas in appealing ways. Of course, the internet became an outlet for ichnology via websites starting in the 1990s, followed by blogging and other forms of social media. These online spaces then provided potentially large stages for publicly accessible discussions of traces and trace fossils. Social media further provided outlets for ichnologists to interact directly with the public on traces and trace fossils, whether as individuals or through moderated discussion groups. Adult books about ichnology written for general audiences are yet another way to spread the word about our science, although these may take years. However, children's books featuring dinosaur tracks, dinosaur coprolites, or modern animal tracks are perhaps the most effective means for sparking ichnological awareness at an early age. Still, ichnological outreach with the longest-lasting educational impacts are probably best served by creating preserves with publicly accessible trace fossils, such as dinosaur tracksites in Portugal, Spain, Republic of Korea, China, Australia, and the United States. Such "ichnoparks" are also intertwined with conservation ethics, ensuring that these scientific and educational resources are available in perpetuity.

In these efforts to effectively spread the word about ichnology for us and for all, we must also heed two rules. First, our communications about ichnology must employ effective narratives. This approach means that we present factual information about traces and trace fossils while also showing how traces both new and old can inspire compelling stories. Second, ichnology must become more inclusive by acknowledging and remedying limitations imposed by previous societal and political systems. For instance, recent efforts in decolonizing paleontology should at



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a minimum acknowledge that trace fossils are oftentimes preserved and evident in colonized landscapes. Where these two rules can come together is through indigenous traditions that may have already created and perpetuated intriguing stories connected to trace fossils. Perhaps most importantly, inclusion means rejecting past structures that limited our science to only a privileged few, and increasing opportunities for a wide range of voices to participate in our science, truly bringing it closer to the ideal of “One Ichnology.”



RECENTLY DISCOVERED INVERTEBRATE AND VERTEBRATE TRACE FOSSILS IN CIRCUMPOLAR CONTINENTAL FACIES OF THE WONTHAGGI FORMATION (EARLY CRETACEOUS) IN VICTORIA, AUSTRALIA, AND THEIR PALEONTOLOGICAL IMPORTANCE

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The Wonthaggi Formation (Early Cretaceous: Valanginian–Aptian) of Victoria, Australia, which is composed of alluvial and fluvial clastic lithofacies deposited in rift valleys at ~75° S paleolatitude, preserves a well-documented body fossil assemblage that includes gymnosperms, angiosperms, insects and other arthropods, fishes, temnospondyls, turtles, plesiosaurs, dinosaurs, and mammals [^{1,2}]. However, Wonthaggi trace fossils were previously represented by only a few invertebrate burrows and non-avian theropod tracks [^{3,4}]. Hence, we are gratified to report a variety of trace fossils in the Wonthaggi Formation discovered since 2020 that significantly advance our understanding of Early Cretaceous circumpolar continental ecosystems in Australia and elsewhere.

Newly diagnosed invertebrate trace fossils consist of arthropod trackways attributed to pterygote insects (*Lithographus*) and possibly crayfish (?*Siskemia*) on floodplain siltstones. Other arthropod trace fossils include abundant and small cylindrical pellets with hexagonal cross-sections matching *Microcarpolithes*, interpreted as fossil feces of drywood termites (Isoptera, Kalotermitidae). These pellets, along with smaller coprolites credited to xylophagous mites (Acari), were concentrated in a probable termite-nest chamber inside a >1 m wide gymnosperm trunk. Vertebrate trace fossils are represented by non-avian and avian dinosaur tracks preserved on floodplain siltstones and sandstones, and a large burrow system in an overbank deposit. Most non-avian dinosaur tracks are 30–47 cm long and made by large theropods (1.2–1.9 m hip heights), but also include those of small ornithopods (40–48 cm hip heights). Avian footprints are tridactyl or tetradactyl (with hallux) and range from 6.5–14 cm wide, with thin digits relative to track lengths, wide divarication angles, and sharp claw imprints. Lastly, the large burrow system hints at a previously unknown vertebrate tracemaker. This burrow system covers an area of about 30 m² and consists of interconnected horizontal tunnels, a spiral ramp, chambers, and vertical shafts. Horizontal tunnels are as much as 4.3 m long, whereas tunnel and shaft widths are 20–28 cm wide, with cross-sectional areas of nearly 500 cm².

In terms of their paleontological importance, the Wonthaggi insect trackways, crayfish trackway, termite coprolites and nest structure, and mite coprolites are the first known from the Cretaceous of Australia, and the oldest. The termite and mite trace fossils also indicate xylophagous arthropods were adapted to polar forests during the Early Cretaceous. The Wonthaggi avian tracks are the oldest in Gondwana, while also showing a diverse avifauna lived in polar environments then and perhaps migrated seasonally. The presence of large non-avian theropods, small ornithopods, and burrowing vertebrates in these environments further point to



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varied ecological niches for vertebrates in their ecosystems. In summary, these new finds of Wonthaggi trace fossils greatly enhance our understanding of Early Cretaceous life in continental polar environments of Australia.

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ICHTNOLOGY AND PALEOENVIRONMENTS OF THE SERRA GRANDE GROUP AT THE NORTHEASTERN PORTION OF THE PARNAÍBA BASIN, NE BRAZIL

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The Lower Paleozoic of the intracratonic basins in northern and northeastern Brazil is characterized by extensive glacial deposits that record the Silurian glaciation of West Gondwana. This glaciation was followed by a marine transgression that flooded the Solimões, Amazonas, and Parnaíba basins, forming thin but extensive layers of black shales. In the Parnaíba Basin, this period is recorded in the siliciclastic rocks of the Serra Grande Group, which comprises the following formations: (i) Ipu Formation, composed of sandstones with pebbles, glacial diamictites, and fine to coarse sandstones, documenting the short-duration Llandovery glaciation [^{1,2}]; (ii) Tianguá Formation, composed of dark gray, bioturbated, sideritic, and carbonate-rich shales, intercalated with fine to medium sandstones, siltstones, and shales deposited during the post-glacial transgression still in the Llandovery [^{1,3}]; (iii) Jaicós Formation, consisting of coarse sandstones with pebbles that mark the transgressive-regressive cycle of the Serra Grande Group, interpreted as the record of braided fluvial systems that settled in the basin during sea-level fall [³].

These paleoclimatic and paleoenvironmental changes strongly influenced sedimentary dynamics and substrate colonization by benthic organisms. To investigate these effects on the Silurian biota, ichnotaxonomic identification, ethological classification, ichnodiversity analysis, and quantification of bioturbation were conducted. The studied outcrops are located on the Serra de Ibiapaba between the regions of Cocal, State of Piauí, and Crateús, Ipueiras, and Viçosa of Ceará, State of Ceará. Twelve sedimentary facies arranged in five facies associations (FA) were described. FA 1 represent deposition in fluvio-glacial settings and constitute the Ipu Formation. The Tianguá Formation comprises deposits of offshore (FA 2), delta front (FA 3), and foreshore/shoreface (FA 4), and the fluvial deposits of FA 5 characterize the Jaicós Formation. Trace fossils occur only in delta front and foreshore/shoreface deposits. In the delta front facies association, *Arenicolites* isp., *Arthropycus linearis*, *Beaconites antarcticus*, *Beaconites coronus*, *Planolites* isp., *Planolites montanus*, *Skolithos linearis*, and *Skolithos* isp. are present. In the foreshore/shoreface facies association, *Arthropycus alleghaniensis*, *Cruziana* isp., *Diplocraterion* isp., *Heimdallia?*, *Lockeia siliquaria*, *Palaeophycus striatus*, *Palaeophycus tubularis*, *Protovirgularia rugosa*, *Rusophycus* isp, *Torrowangea?*, as well as indeterminate meniscate burrows, horizontal tubes, and trace fossils with internal concentric lamination that were not possible to classify due to the difficulty in accessing the outcrop.

The glaciomarine facies of the Ipu Formation indicate high sedimentation rates, high energy, and rapid transition to offshore conditions, which could be stressful for benthic organisms inhabiting periglacial regions, explaining the absence of ichnofossils. Stressful conditions may also have extended to the deposition of black and gray shales at the base of the Tianguá Formation. Organic geochemistry data suggest reducing environmental conditions during the deposition of these shales [⁴], explaining the absence of ichnofossils. Thus, substrate colonization during the early Paleozoic sedimentation in the basin could have been challenging primarily due to hydrodynamic factors. Paleoenvironmental conditions begin to change with the formation of deltaic and shoreline deposits. In the Tianguá Formation, deltaic facies form coarsening-upward cycles exhibiting relatively low diverse and locally abundant ichnofossils. The intensity of



bioturbation in layers with *Arthropycus* and *Skolithos* at the base of the coarsening-upward cycles is approximately 50% (BI=4) [5] and is distributed heterogeneously regularly, suggesting periods of regular variation in local physicochemical conditions [6]. In this scenario, *A. lateralis* producers would intensively exploit the clayey substrate for food at the base of the cycles during calmer periods, covered by sediments during deltaic lobe advances in high sedimentation rate periods. The substrate would sporadically be occupied by suspension-feeding organisms, generating spaced *Skolithos* and *Arenicolites* (BI=2), suggesting high sedimentation rates limiting substrate occupation. The deltaic ichnofacies are poorly diversified, with only five ichnogenera identified. These traces also show few architectural design variations, with the presence of horizontal burrows with horizontal to vertical branches (*Arthropycus*), vertical unbranched burrows (*Skolithos*), vertical single U-shaped burrows (*Arenicolites*), simple actively filled (massive) horizontal structures (*Planolites*), and simple actively filled (meniscate) horizontal structures (*Beaconites*). Thus, these characteristics suggest paleoenvironmental stress, possibly caused by high sedimentation rates discharge from the rivers feeding the delta.

The foreshore and shoreface deposits (Tianguá Formation) show few variations in sedimentation rates and the present influence of storm and wave action. Storm action played a significant role in changing the pattern of distribution and intensity of bioturbation. In the initial tens of meters, the distribution of bioturbations is regular but heterogeneous, with intercalations between layers intensely bioturbated (BI=4) and layers without bioturbations with preserved sedimentary structures (BI=0). This distribution suggests colonization events punctuated by less favorable conditions for infauna occurring in tide-influenced environments, seasonal/annual variations, or long-term climatic cycles [6]. The appearance of storm facies towards the top coincides with the increased intensity and regularity of horizontal bioturbation, predominantly by components of the *Cruziana* Ichnofacies. Exhibits storm layers without bioturbation interbedded with layers intensely bioturbated by resident fauna (BI=6) during fair weather periods, as often observed in shoreface deposits affected by "intermediate energy" storms [7,8].

In the marine deposits, animals appear to take advantage of regular colonization windows even under the influence of swash-backwash action and storm waves to colonize the marine substrate in various ways. The ichnofossil assemblage in these marine deposits is more diverse in terms of ichnospecies and architectural designs than the deltaic facies, with the presence of horizontal burrows with horizontal to vertical branches (*A. alleghaniensis*), bilobate trails (*Cruziana*), vertical single U-shaped burrows (*Diplocraterion*), burrows with complex vertically oriented spreiten (*Heimdallia*), isolated oval to almond-shaped burrows (*L. siliquaria*), passively filled horizontal burrows (*P. striatus* and *P. tubularis*), chevronate trails (*Protovirgularia rugosa*), bilaterally symmetrical short, scratched impressions and burrows (*Rusophycus*), and simple actively filled (massive) horizontal structures (*Torrowangea?*). This suggests environmentally less stressful conditions.

The transitional and marine sedimentation ends with a regional sea-level fall, rejuvenating fluvial currents and partially eroding deltaic and shoreline deposits for hundreds of kilometers. In the studied region, the fluvial deposits of the Jaicós Formation are found only at the top of the outcrops in the form of thick layers of coarse sandstones and conglomerates, with no observed bioturbation. Locally, *Lockeia* and *Skolithos* were observed in the finer facies of this unit [9].

The integration of facies analysis, stratigraphy, and ichnology allows for a detailed understanding of the depositional and palaeoecological conditions of the Serra Grande Group in the eastern portion of the Parnaíba Basin. The Ipu Formation in the study area is characterized by fluvial and glacial facies that record the Llandovery glaciation in the basin. Due to stressful conditions related to hydrodynamic variations caused by the advance and retreat of glaciers, bioturbating organisms should have been rare, or their traces were not preserved. The post-glacial marine transgression formed an extensive epicontinental sea, initially giving rise to the black-to-gray shales of the Tianguá Formation, where, due to reducing conditions at the sediment-water interface, substrate colonization was not possible. Environmental conditions changed with the establishment of deltaic and shoreline deposits, providing greater opportunities for substrate



colonization by burrowing organisms. In foreshore deposits, taphonomic factors may have played a significant role in preserving surface traces, which would otherwise be eroded during swash-backwash processes and normal wave action. In shoreface deposits, storm wave action controlled the diversity and distribution of ichnofossils. The epicontinental sea began to retreat during the Devonian, exposing a wide area to the east of the Parnaíba Basin and establishing braided fluvial channels.

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RHIZOLITHS: BODY FOSSILS, TRACE FOSSILS OR BOTH?

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Root system development produce bioturbation structures at all scales resulting from the growth and development of the plant anchoring system. There is an intrinsic difficulty in distinguishing the resulting structure as a body fossil or a trace fossil, in some cases complicated by diagenetic modifications, that can be produced during root development or postdate it. Very little is known about rhizolith or root trace [1] formation and preservation, which can give important insights in their nature and significance. Plant roots move and compress soil particles just as animal producers do thus producing bioturbation [2]. This statement implies that, independent of the preservation type (cast, molds) or diagenetic modifications (concretionary or diffuse cementation, and/or color change), and the scale of modifications (rootlets or tree root), root generated structures are trace fossils. A particular case can be made for specimens preserving organic matter including fully carbonized and/or mineralized plant tissues for considering them body fossils [2], but bioturbation is present, even in this case. We are referring to the same biogenic sedimentary structure, even if the body of the producer is preserved (e.g., coalified root cast) or not. It is herein proposed that except those root structures that preserve a substantial amount of any form of preserved organic matter, which are considered body fossils, all other root-generated structures be considered trace fossils. In consequence, there is no need to demonstrate a formation process in several steps (e.g., [2]) to be considered a trace fossil. We also advocate the use of rhizolith, a general descriptive term for all these structures, deeply entrenched in the ichnologic and sedimentologic literature. Diagenetic processes can affect any type of trace fossil, but this is not necessarily considered a factor that change the status as an ichnofossil. Cementation in root traces is commonly linked to interactions among the root, the soil, and microorganisms in the rhizosphere. This process can even start during the life of the plant [3] or very close to the death of the plant (Fig. 1). In nonmarine settings, the presence of cementation is a feature that distinguishes root traces from animal burrows (that commonly are devoid of cementation). In addition to the architectural pattern, the composition of the root cast or cement of root traces is also very useful in the paleocological and paleoenvironmental interpretation of these biogenic sedimentary structures, as they commonly result from early diagenetic processes. Another aspect raised by a recent proposal [2], suggest that root systems do not develop a recurrent morphological pattern, instead they result in indistinct blurring of existing stratification. We disagree with this conclusion. As recognized from the botanical literature [4] and observed in fossil examples, root systems do have different architectural patterns resulting from soil hydrological constraints and those typical of the plant types. Examples includes adventitious root traces (Fig. 2A-B), strongly branched subvertical (Fig. 2D) and tap root traces (Fig. 2C). Fossil root systems can also produce a modification of the primary sedimentary structure, thus resulting in an ichnofabric where identification of discrete structures can be difficult, as with many other ichnofabrics. To conclude, it is proposed that all root-generated structures be treated as trace fossils except those that contain a significant proportion of preserved organic matter, which are considered body fossils. We also encourage the use of binomial nomenclature to name morphologically distinctive and repetitive root trace fossils.

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Fig. 1. Recent dead root in alluvial sediments (white arrow) with incipient carbonate cementation (black arrow). Salta Province, Argentina.

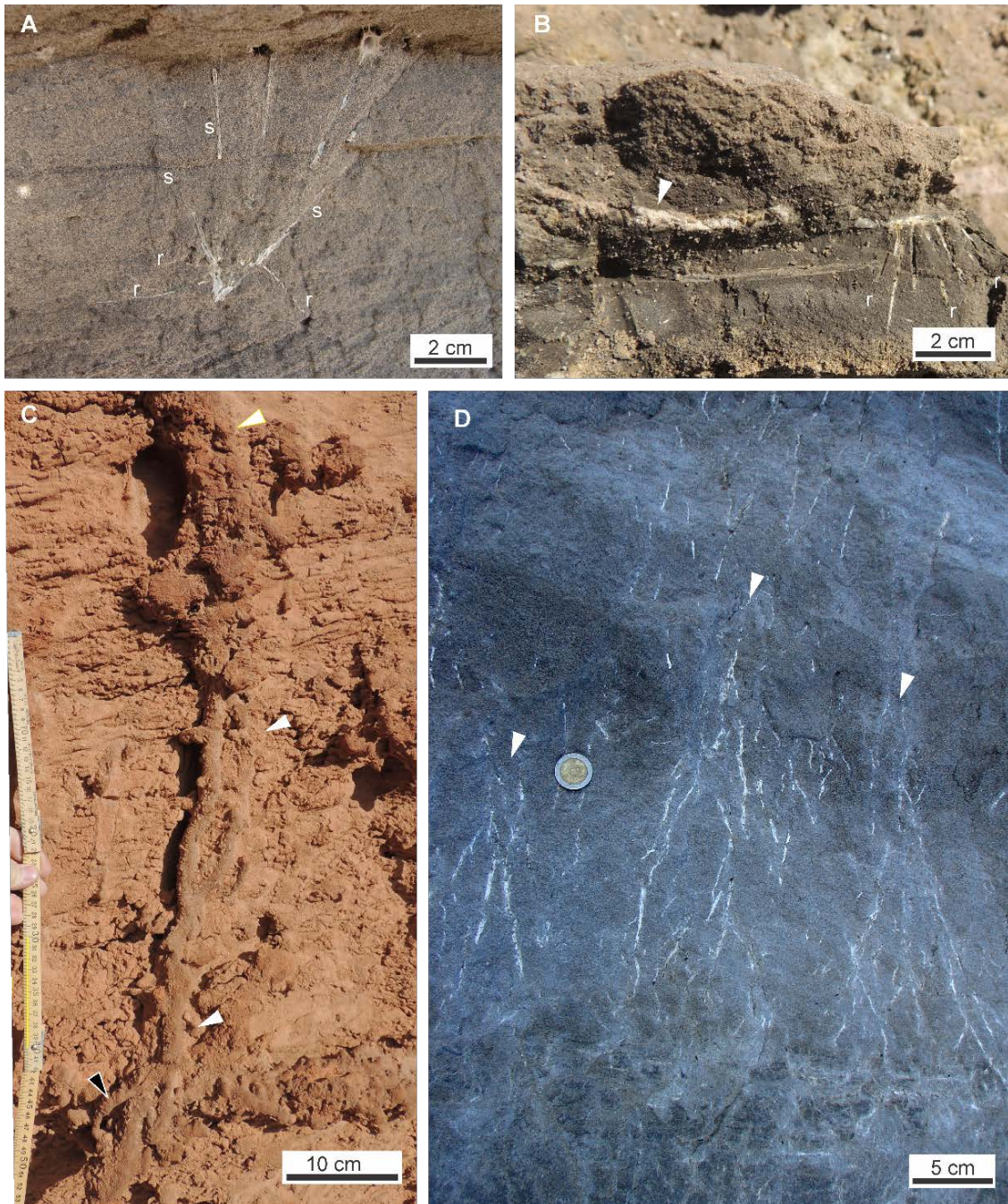


Fig. 2. Examples of fossil root system architecture. A. Isolated system with adventitious root traces (r) arising from stem traces (s). B. Subhorizontal rhizomatous stem trace (arrowed) with adventitious root traces (r) arising from a knot. C. Subvertical tap root system (white arrows) with distal branching (black arrow). D. Three tap root-like systems (arrows) with marked branching of the main root trace and uniform arrangement of secondary root traces. A, B and D are from the Upper Miocene-Pliocene Río Negro Formation, Río Negro Province; and C from the Upper Oligocene-Upper Miocene Angastaco Formation, Salta Province, both from Argentina.



ICHNOTAXONOMY OF FOSSIL VERTEBRATE BURROWS: A REVIEW

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The scientific study of vertebrate burrows apparently started with the description of the “gigantic fossils” from the Miocene of Nebraska that Barbour [1] named *Daimonelix*. This was the first (ichno)genus of vertebrate burrows that provoked an extended debate about the origin and nature of the structure. Studies on vertebrate burrows were revived about fifty years later with the discovery and description of subvertical burrows with lungfish remains, even articulated ones, especially in the Permian of USA, that were interpreted as lungfish aestivation burrows. The seminal chapter by Voorhies [2] summarized the current knowledge on extant and fossil vertebrate burrows and related the apparent dearth of fossil vertebrate burrows, to a bias in the description, suggesting that they were much more common than perceived. In the last two decades of the XX century, three new ichnogenera were proposed: *Ichnogyrus*, *Piscichnus* and *Cornulatichnus*. About 70% of the ichnotaxa of vertebrate burrows (n= 20) were erected in the last twenty years, starting with the description of amphibian aestivation burrows under the ichnogenus *Torridorefugium* [3]. This contribution reviews all the proposed ichnogenera and comments on their ichnotaxonomic status. In addition, the criteria for the ichnotaxonomic treatment are proposed both at the ichnogenus and ichnospecies level (Table 1). Among the 20 proposed ichnogenera, only 14 are considered available, including: *Alezichnos*, *Cornulatichnus*, *Daimonelix*, *Katarrhedrites*, *Maneraichnus*, *Megaichnus*, *Nagtuichnus*, *Natatorichnus*, *Piscichnus*, *Redondarefugium*, *Reniformichnus*, *Torridorefugium*, *Yaviichnus* and (probably) *Tambia*. Examples of ichnogenera that are not considered available includes *Cynodontipus* and *Ichnogyrus*. *Cynodontipus* was proposed to represent a supposed isolated and incomplete fossil footprint of a Triassic hairy therapsid [4]. The ichnogenus has been reinterpreted as representing a procolophonid burrow and the supposed hair traces as sets of claw traces [5]. Accepting the vertebrate burrow interpretation, the surface ornamentation is not enough to describe a burrow system, but also features like overall architecture are necessary. In consequence, *Cynodontipus* is considered a *nomem dubium*. *Ichnogyrus* (erected for a tight and straight helical structure represented by a single loose specimen) was the second to be formally proposed among vertebrate burrows, and probably marks the revival for interest on this type of structures. The authors [6] identified a discrete structure with a differential diagnosis. The interpretation of the structure as the filling of once open burrow is contradictory due to the closeness of the whorls and absence of bioglyphs. Successive whorls use part of the space of the former, in consequence, there would be no space for their wall. There is no known similar structure produced by an extant animal, although some analogous remains were described from Cretaceous rocks of England [7] and Australia, as “Dinocochlea”. The latter was reinterpreted as a helical concretion, on the basis of findings of similar structures in the Mississippian of Alaska [8]. In consequence, the most parsimonious interpretation is that *Ichnogyrus* is an inorganic structure of concretionary origin, and the name is considered a *nomen nudum*. An analysis of the stratigraphic distribution of proposed valid ichnogenera suggest that the Oligocene-Miocene (especially the Miocene) is the interval with more named ichnogenera, essentially related to mammals and, in many cases, to rodents. *Piscichnus* is the ichnogenus with the greater stratigraphic range: from the Middle Devonian to the Holocene, and is also represented in nonmarine and shallow marine settings. It is estimated that, since 1970, approximately 180 papers dealing with vertebrate burrows were published, with about 80% released in the last twenty years. For the next decades, we envisage the continued recognition of new vertebrate burrow morphologies and advances in the stratigraphic, sedimentologic and paleoecological utility of this type of trace fossil.



Table 1. Ichnotaxobases for fossil vertebrate burrows. The order in the table is related to the hierarchy of the morphologic features.

Generic ichnotaxobases	Specific ichnotaxobases
Overall architecture of the burrow system (distinguishing between ramps, subhorizontal branched systems and spiral systems).	Type of primary surface ornamentation (digging traces), including overall pattern of claw/tooth traces, number of claw/tooth traces on sets, width of sets of claw/tooth traces.
Morphology of the cross-sectional shape of tunnels (distinguishing between subcircular, flattened elliptical and vertical elliptical; and including the vertical diameter/horizontal diameter ratio as a useful measure).	Type and density of secondary surface ornamentation (ornamentation of biogenic origin not resulting from the digging by the producer).
Presence/absence of bilobed bottom.	Details of the burrow system architecture (e.g., type of ramification, angle of ramification, ramp inclination).
Presence/absence of chambers (including the chamber volume/tunnel volume ratio).	Location of chambers (lateral, terminal, bilateral, at a ramification).
Number of levels.	Chamber filling (e.g., droppings, plant material, fur, sediment).
Presence/absence of closed circuits.	Tunnel or ramp size, especially as expressed by the horizontal diameter.
Type of burrow filling (active vs. passive).	

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REVISITING THE LOWER PALEOZOIC ICHNOSTRATIGRAPHIC MODELS BASED ON THE BRAZILIAN RECORD

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Ichnofossils are still controversial as biostratigraphic markers due to the broad temporal occurrence of most ichnotaxa. However, certain groups with complex behavioral programs and limited temporal intervals have been used in models to determine relative ages [^{1,2}], such as the Proterozoic–Cambrian limit (the Treptichnus pedom Zone [³]. For the Paleozoic, “cruzianiform” and “arthrophycid” ichnospecies make up, respectively, the Cruziana and Arthropycid stratigraphy models [⁴⁻⁷], which correlate strata and allow estimating relative ages in shallow-marine settings. Cruziana stratigraphy uses ichnospecies with stratigraphic ranges that vary from the Furongian to the Mississippian, and the model has been proposed mainly for Gondwana [^{4,6}]. This stratigraphic scheme has most of its records in the Ordovician, but Cruziana acacensis appears to be a useful index of Llandoveryan deposits [⁶]. Arthropycus occurs mainly in the Ordovician and Silurian, having a more cosmopolitan distribution, with records in Gondwana and Laurasia from the Cambrian to the Carboniferous [⁵⁻⁸]. However, these two models are still questioned by the absence of independent chrono- or biostratigraphic controls, besides the local distribution of some Cruziana ichnospecies [^{1,8}]. Also, there were a few other ichnotaxa restricted to lower Paleozoic deposits with stratigraphic value than Cruziana, Rusophycus, or arthropycid burrows that were not considered in these models. Recently, we proposed a broader ichnostratigraphic model [⁹] (Fig. 1), based on data from early Paleozoic Brazilian deposits well-calibrated by biostratigraphy. Most of the Brazilian ichnological record of stratigraphic value is concentrated in Silurian–Devonian beds of the Amazonas, Parnaíba, and Paraná basins (Fig. 2) dated by chitinozoans, miospores, and acritarchs [⁹]. Arthropycus alleghaniensis is the most common stratigraphic ichnomarker, occurring in the three basins [⁹⁻¹²]. Cruziana acacensis occurs in the Parnaíba and Paraná basins [⁹⁻¹¹] and show high potential to occur in the Amazonas Basin. These two ichnospecies occur exclusively in deposits dated as Llandovery by chitinozoa, miospores, and acritarchs in the Brazilian basins [⁹]. The Silurian ichnological record from Brazil also reveals other ichnotaxa with potential biostratigraphic value, such as Heimdallia chatwinni, which occurs in the Parnaíba and Paraná basins, and Musculopodus sedentarius in the Parnaíba Basin [^{9,11,13}]. The presence of these ichnospecies in the same strata where C. acacensis and A. alleghaniensis occur reinforces their Llandoveryan age. Bifungites is common in the deposits of all three basins, and particularly abundant in the Eifelian–Givetian deposits. Except for one record from the Middle to Late Jurassic [¹⁴], the global distribution of Bifungites is concentrated in Cambrian to Mississippian deposits [⁹]. All ichnotaxa described here present enough distinctive characteristics and a narrow temporal range of occurrence, meeting the criteria to be considered stratigraphic ichnomarkers. Therefore, the proposal of a broader model that includes all these ichnospecies with biostratigraphic value will enhance the use of trace fossils to date lower Paleozoic strata. This model significantly enriches our understanding of the spatio-temporal distribution of biostratigraphically significant ichnotaxa and corroborates that certain groups of ichnofossils are useful as a relative proxy for age delimitation. This new scheme holds promise for improving global stratigraphy, especially when other biostratigraphic data are not available.



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NEW RECORD OF THE ICHNOGENUS *TAOTEICHNUS* FOR THE PLEISTOCENE OF SOUTH AMERICA

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Bones constitute an important substrate in which various organisms produce modifications as a result of different activities (e.g., feeding, locomotion, attachment). The crucial aspect of identifying tracemakers in the fossil record lies in its significance for understanding various factors, including seasonality and microenvironmental/climatic conditions in ancient ecosystems. This process enhances taphonomic reconstructions, providing valuable insights into the ecological and environmental dynamics of the past. Of the numerous ichnotaxa described to date, only about 8% correspond to bone substrates, the majority of which are attributed to different groups of invertebrates [1], particularly insects, specifically representatives from various orders such as Dermestidae, Tenebrionidae, Calliphoridae, Tineidae, and Termitidae [2]. Within the fossil record, these modifications are relatively rare but hold significant ecological value, as they enable the characterization of environmental conditions and the behaviour of insects associated with vertebrate remains [3].

With a few exceptions, the identity of the producer is often not retained alongside its trace fossil, making the identification of the organism that created the trace more challenging. This is further complicated by the fact that similar traces may be produced by different organisms [4]. Therefore, determining the identity of the producer requires careful comparisons with modern examples [5].

Given the diversity of ecological niches occupied by these invertebrates as bioeroding agents, Parkinson [6] argued that accurately identifying tracemakers in the fossil record is crucial for understanding aspects such as seasonality and microenvironmental/climatic conditions in ancient ecosystems, thereby enhancing taphonomic reconstructions. These aspects have received less attention compared to the applications of ichnology in paleoenvironmental reconstructions [7]. On the other hand, it is equally important to distinguish and correctly interpret post-mortem modification processes and agents of vertebrate remains to obtain a comprehensive understanding of the taphonomic overprints in the fossil record [8]. In the context of vertebrate fossil remains, the analysis of bone modifications allows us to infer specific stages of the decomposition process. This study analyses and compares trace fossils recorded on an undetermined Pleistocene skeletal specimen of a terrestrial vertebrate deposited in the Paleontological Collection of the "Florentino Ameghino" Provincial Museum of Natural Sciences in the city of Santa Fe, Argentina. The specimen, deposited as MFA-G-PV1164, originates from the banks of the Salado del Norte River near the town of Emilia (Santa Fe Province). The material comes from deposits composed of consolidated silt. Deposits are massive to laminated at the base, with an increased concentration of clays towards the upper interval. The upper part of this deposit is structured in the form of horizontal sheets with sub-horizontal carbonate plates and vertical partitions formed by rhizoconcretions, along with crack fillings with secondary carbonates [9]. Absolute ages for these deposits range from 46.5 ± 3.2 ka to 25.8 ± 2.2 ka BP, a period characterized by humid conditions [10]. The bone material exhibits surface cracking, a result of prolonged exposure to weathering agents.

The identified bioerosion trace fossils comprise galleries with a semi-circular to elliptical cross-section, randomly distributed over a large part of the bone surface and locally penetrating inside. Bioglyphs arranged transversely to the gallery axis can be observed on the walls. The average diameter of the galleries is 3.4 mm, reaching a length of 9.72 mm in one case. The morphology of the analyzed trace fossils is like those previously recorded in the Pleistocene Río Bermejo Formation (20 ka) in Formosa Province [11], attributed to *Taoteichnus* [12], with the exception that they do not exhibit the typical Y-shaped branching described for this ichnogenus and have a higher areal density, covering almost the entire surface. Regarding the average diameter, it is slightly larger than that obtained for the trace fossils from Formosa (3.23 mm) (Fig. 1). Concerning the original measurements by Xing et al. [12] for materials from the Luafeng Formation (Lower Jurassic) in China, unfortunately, a proper comparison is not possible as they only reported minimum and maximum values of the observed diameters. However, the measurements obtained in both Pleistocene materials from Argentina mostly fall within the values reported by the mentioned authors. On the other hand, the diameter obtained by Paz [13] for similar galleries recorded in the Santa María Supergroup (Upper Triassic) in Rio Grande do Sul (Brazil) is significantly smaller than those mentioned earlier. However, since only one average is mentioned, this could represent a bias.

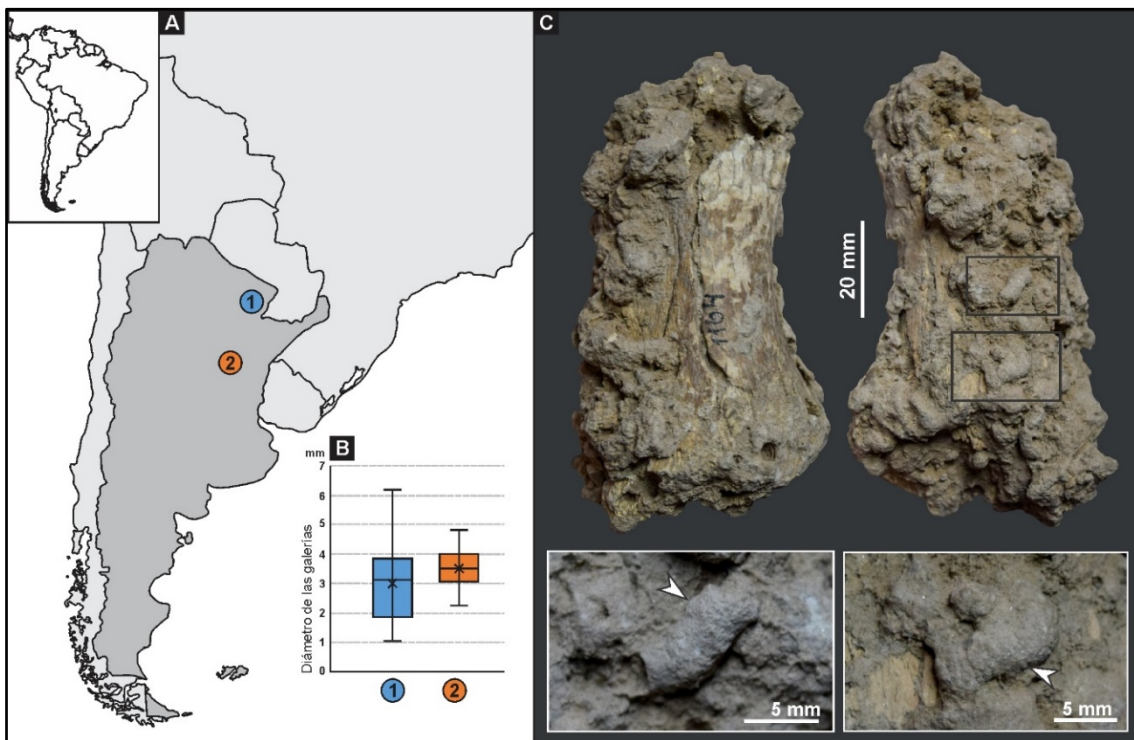


Fig. 1. A. Geographical origin of Pleistocene records of the ichnogenus *Taoteichnus*: 1. Río Bermejo, Formosa Province; 2. Río Salado del Norte, Santa Fé Province. B. Comparative graph between the diameters of *Taoteichnus* galleries from both fossiliferous localities. C. Photographs, in anterior and posterior views, of the bone fragment with traces recovered in the province of Santa Fe, with a detailed view of the chambers. The arrows indicate scratches on the gallery walls.

In summary, the morphology, diameter, and arrangement of galleries and perforations on the associated bone substrate from the Pleistocene of the province of Santa Fe are very similar to those assigned to the ichnogenus *Taoteichnus* in various materials ranging from the Late Triassic to the Late Pleistocene. There are some differences, such as the branching type, which Paz [13] has used to propose a possible new ichnospecies for the Upper Triassic of Brazil. However, given the scarcity of materials, these features are likely not of taxonomic value but simple variations. The studied trace fossils exhibit a marked morphological similarity to subaerial feeding galleries constructed by subterranean termites. Specifically, this behaviour (possibly seasonal) of utilizing decomposing vertebrate carcasses as a nutrient source and constructing galleries is a known but



poorly documented feeding supplement in some species of neotropical xylophagous termites. In this context, Thorne and Kimsey [14] proposed the argument that termites face challenges in satisfying their nitrogen requirements solely through a cellulose-based diet. As a result, certain termite species adapt by making physiological or behavioral adjustments to enhance their nitrogen supply. In light of this, the presence of galleries that specifically penetrate the spongy bone suggests that the bones were utilized as a food source, indicating a purposeful and not casual or incidental manipulation. Detailed observations suggest that perforations and exploration into the medullary spaces occurred within these galleries. Over time, under favorable microenvironmental conditions, the entire bone covered by such galleries is eventually destroyed.

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A MULTIPLE ICHNOCOENOSIS FROM EARLY CRETACEOUS CONTINENTAL DEPOSITS OF NORTHERN CHILE (CHACARILLA FORMATION, ATACAMA DESERT)

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The skeletal record of Chilean dinosaurs includes sauropods, theropods, ornithopods and thyreophorans [1]. The track record however consists only of isolated reports from the Late Jurassic/Early Cretaceous [2]. In 2022, a field campaign explored the area of the Quebrada de Huatacondo (Tarapacá Basin) where an ornithopod trackway and an isolated theropod track had been registered. First results indicate the presence of 12 different tracklevels in the Late Jurassic Majala and Early Cretaceous Chacarilla Formations. The siliciclastic sediments of both formations were interpreted as being deposits of meandering rivers [3].

We recorded minute, intermediate-sized and large theropod tracks, as well as sauropods and many trampled surfaces; the reported large ornithopods trackway [2], however shows long metatarsal impressions and is therefore assigned to theropods [4]. This implies that the supposed age of the Majala Formation is not necessarily Cretaceous as was suggested [2] (on the base of the occurrence of ornithopods). The sedimentary succession of the Majala and the Chacarilla Formation is made up of more than 1000 m of cross-bedded fine sand- and siltstones with mud cracks, ripple marks and occasional invertebrate traces (e.g., *Planolites*, *Ophiomorpha*) and we propose that they have been deposited in a distal alluvial plain under arid to semi-humid conditions, respectively.

Both formations have been explored in a second field campaign, in 2023, in the Quebrada de Arcas (Tarapacá Basin), where we could rely on reports from mapping geologists. The Majala Fm consists mainly of strongly folded evaporites and sandstones with no clear track-bearing surfaces. However, within the Chacarilla Fm we could observe 20 new tracklevels, 8 on surfaces and 12 in cross sections. The sedimentary succession is steeply inclined (700), and many of the levels spotted with binoculars have been explored with a UAS (DJI Mavic 3 Pro, and DJI Mavic Air 2), because the rock was too friable to climb and set up bolts. Occasionally, surfaces display burrows of crayfish (*Ophiomorpha*; see Fig. 2), traces of nematods (*Cochlichnus*) and of moving bivalves. The Chacarilla Fm. consist of a more than 300-m-thick stack of thickening-upward cycles of sand- and siltstones with mud cracks and ripple marks. It was deposited on a distal alluvial plain in a synrift back-arc basin under semi-arid to humid conditions.



Fig. 1. Surface in the lower part of the Chacarilla Formation (?Early Cretaceous; Tracklevel QA 1) in the middle part of the Quebrada de Arcas (Tarapacá Basin) showing two trackways of medium sized sauropods (arrows and coauthors for scale on the left side).



Fig. 2. Surface in the lower part of the Majala Formation (?Late Jurassic; Tracklevel MAJ 6) in Quebrada de Hutacondo (Tarapacá Basin) showing a pellet filled burrow attributed to *Ophiomorpha*.

Tridactyl tracks of different sizes (FL from 15 to 63 cm) show long slender digits and were left by medium- to large-sized theropods. Several levels with oval and crescent shaped tracks of quadruped dinosaurs are assigned to sauropods (FL from 30 to 60 cm) with a strong heteropody (1:4; Fig. 1). Another surface shows two theropods, a large one and a smaller one, walking more or less side by side (Fig. 3). One specific level has a surface with ripple marks and displays faint prints of a sauropod that are overgrown by a pustulous microbial mat before drying up (mud cracks). The highest level (QA20) in the sedimentary sequence shows a surface of appr.

120 m² with more than 80 individual tracks forming at least two trackways that were left by small sauropods (pes length: 35 cm).

The geochemical composition of the sampled sedimentary rocks equals an almost upper crustal composition with distinct formation-specific differences between sand- and siltstones of the Majala and Chacarilla Formations: Rocks of the Majala Fm are slightly enriched in Cr, Ni and Cu, whereas rocks of the Chacarilla Fm show slight differences in elemental composition between the base and the top part. Summarizing the preliminary results, changes in the geochemistry between the two formations can already be clarified. With the complementary new data of the Quebrada Arca, the paleo-environmental conditions of the region can be reconstructed in a promising way. Additional U-Pb dating of the formations will provide desirable age constraints of deposition and provenance to set up an overall picture of the Late Jurassic to Early Cretaceous paleo-environment in Northern Chile. We hope that these differences will help to pin-point the limit between the two formations [5].

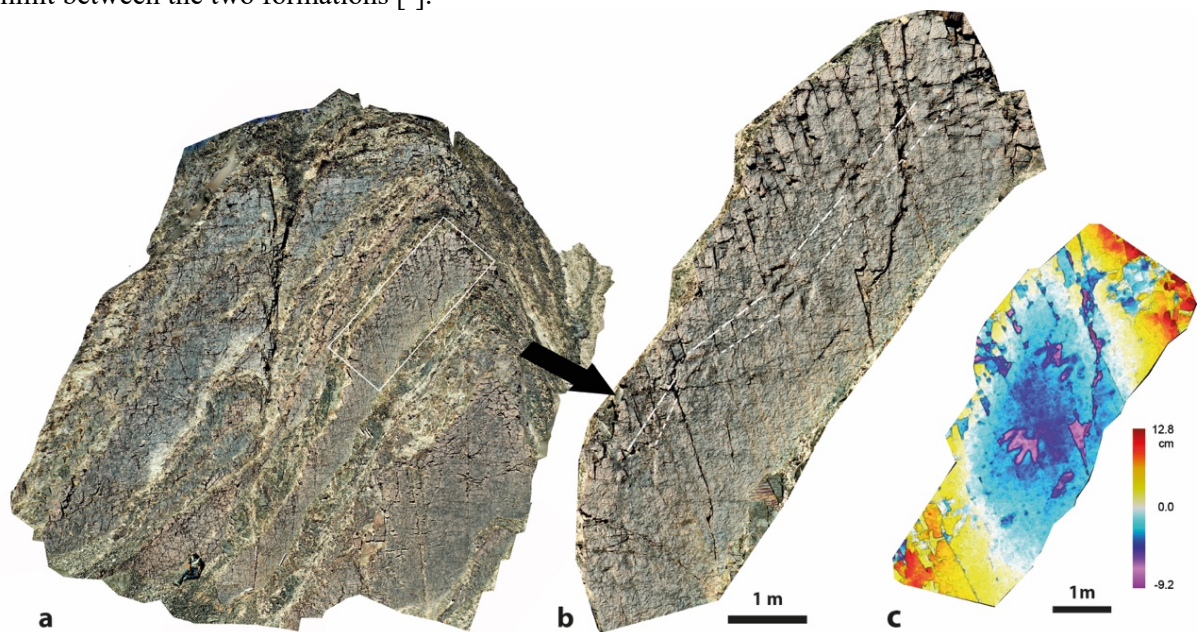


Fig. 3. Surface in the upper part of the Chacarilla Formation (?Early Cretaceous; Tracklevel QA 17) in the Quebrada de Arcas (Calama Basin). A. Overview and situation of B with geologist for scale. B. Two parallel trackways of theropods close to each other. C. False color depth model.

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DEEP-SEA NEOICHOLOGY: NEW INSIGHTS

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Detailed deep-sea neoichnological studies have increased in number during the last decades, mainly through advances in visual instrumentation used to observe this underexplored environment. The appearance of new technology has enabled the acquisition of highly detailed images over large-scale areas of the deep-sea floor, and the subsequent characterization of biogenic traces (lebensspuren) and trace makers. Here, we provide three examples of recent deep-sea neoichnological studies which helped us to assess the relationship between environmental conditions and neoichnological information and then its potential application to paleoichnology (trace fossils).

Example 1: A comparative ichnological analysis was conducted between a small abyssal hill (50 m elevation) and the surrounding abyssal plain; such seafloor features are known to generate substantial environmental heterogeneity with effects on the benthic faunal community of the Porcupine Abyssal Plain (c. 4850 m depth), Northeast Atlantic. Based on X-ray data from two box cores, we observed that topographically-enhanced near-bottom currents over the hill likely produce significant changes in depositional dynamics and sediment properties (e.g., grain size), and control bioturbational sedimentary structures (i.e., traces and biodeformational structures). Neoichnological analyses allowed the characterization of sediment mixed layers with different attributes. Our results highlight the complexity of deep-sea environments, demonstrating that substantive changes in bioturbational sedimentary assemblages can be related to local (km-scale) environmental heterogeneity (e.g., subtle topographic variations) rather than regional-scale spatio-temporal environmental variations (e.g., sea level changes, oxygenation events). Considering the vast global extent of abyssal hill terrain, we suggest that their influence on the paleoichnological record is usually overlooked, and it would be necessary to pay more attention to these heterogeneities in paleoenvironmental reconstructions.

Example 2: Lebensspuren are common features of deep-sea landscapes, being more abundant than their tracemakers, rendering them promising proxies for inferring biodiversity. In the literature, the density-diversity relationships between lebensspuren and benthic fauna remain unclear and contradicting correlations have been proposed (i.e., negative, positive, or even null correlations). We present a study where lebensspuren and benthic fauna were characterized taxonomically at eight deep-sea stations in the Kuril Kamchatka Trench area. Diversity correlation was observed at specific stations, showing both negative and positive correlations depending on (i) the number of unknown tracemakers (especially significant for dwelling lebensspuren), (ii) the multiple origins of particular lebensspuren, and (iii) the tracemakers producing different lebensspuren. Lebensspuren and total faunal density were not correlated. However, lebensspuren density was either positively or negatively correlated with tracemaker densities, depending on the lebensspuren morphotypes. A positive correlation was observed for resting lebensspuren, while negative correlations were observed for locomotion-feeding lebensspuren. Thus, lebensspuren diversity may be a good proxy for tracemaker biodiversity when the lebensspuren-tracemaker relationship can be reliably characterized. Lebensspuren-density correlations vary depending on the specific lebensspuren residence time, tracemaker



density and associated behaviour. We suggest that lebensspuren density and diversity correlations should be related specifically to tracemakers rather than to the benthic fauna in general. On a global scale, abiotic (e.g., hydrodynamics, substrate consistency) and other biotic (e.g., microbial degradation) factors may also play an important role.

Example 3: Deep-sea benthic communities are strongly controlled by the quantity and quality of organic matter sinking from the ocean surface. The intensity of the bioturbation has long been linked with organic matter and measured as a diffusive process by considering the vertical particle reworking (endobenthic bioturbation), disregarding the seafloor horizontal mixing (epibenthic bioturbation). Here, a novel approach to quantify horizontal mixing is presented: Seafloor Bioturbation Intensity (SBI). SBI quantification was based on seafloor image datasets from eight stations associated to different environmental conditions in the north-western Pacific (e.g., Chl.- α , silicate). To calculate SBI, we characterized the area occupied by all different types of lebensspuren related to epibenthic bioturbation, tracemakers and their ingested sediment thickness. Our results showed a negative correlation between organic matter and SBI. It is demonstrated that lebensspuren morphotypes contributed differently to SBI. Not all morphotypes — and, by extension, their corresponding tracemakers — are equally controlled by the same environmental factors. This research reveals a negative relationship between SBI and organic matter content that conflicts with the traditionally held view on vertical bioturbation intensity, where a dominant positive correlation is expected. Thus, when determining the long-term relation between epibenthic fauna and bioturbation intensity, other environmental variables need to be considered rather than exclusively organic carbon content. We emphasize the importance of characterizing horizontal bioturbation for approaching global biogeochemical cycles and conservational strategies.

These three study cases show the complexity of the deep-sea, proving that abyssal environments are more heterogenic than initially believed. Therefore, neoichnological analysis that provide quantitative feedbacks into the tracemaker and lebensspuren relationship would give critical knowledge for interpreting the deep-sea trace fossil record.

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NEW TETRAPOD TRACKWAYS IN THE COCONINO SANDSTONE, GRAND CANYON NATIONAL PARK, AZ

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The behavior of early Permian tetrapods is not well understood, however the ichnological record can provide evidence for it. The Coconino Sandstone (southwestern USA) preserves many tetrapod tracks made by amniote and anamniote vertebrates including the youngest record of the ichnogenus *Ichniotherium* [1]. Trackways of *Ichniotherium sphaerodactylum* have been previously identified from loose blocks of Coconino Sandstone and some poorly preserved in situ tracks just below the South Rim of Grand Canyon National Park (GRCA) and along the Mogollon Rim in Northern Arizona [2]. Here, we introduce a new, significant locality in a Coconino Sandstone layer outcropping below the North Rim at GRCA that contains at least 15 trackways preserved in situ on a 20° foreset surface of an eolian dune which may belong to the ichnogenus *Ichniotherium* (Fig. 1).

The Coconino Sandstone was deposited as an eolian desert erg during the early Permian (Kungurian: Cisuralian) and crops out in Southwestern United States [1]. At GRCA, the Coconino Sandstone is often exposed as sheer cliffs containing large-scale crossbedding and sits between the underlying Permian Hermit Formation and overlying the Permian Toroweap Formation. In some areas, the Coconino Sandstone may contain rare interdunal deposits [2]. Vertebrate ichnogenes reported in this unit include *Amphisauropus*, cf. *Dromopus*, cf. *Erpetopus*, *Ichniotherium*, *Tambachichnium*, and *Varanopus*, besides other undetermined tracks [3].

An 84m-thick stratigraphic section was measured at the new locality. 15 trackways were documented on five different horizons near the middle of the full section. Loose blocks of Coconino Sandstone containing tracks preserved as natural casts were also documented and matched up to the *in situ* trackway molds. One of these loose blocks containing trackway casts was collected for further analysis. Three separate photogrammetry models showing elevation range were created where most trackways are present. Trackway lengths were measured, with the longest being 5.1 meters and the shortest being 1.2 meters. These trackways show typical features of upslope locomotion, such as very short pace, low asymmetry, deeper expulsion rims proximally and sliding traces parallel to the direction of progression. The trackways generally are parallel to each other and go in the same direction, with minimal overlap. Since this is observed on the same surfaces, this can potentially indicate aggregation behavior. The morphology of these tracks is similar to *Ichniotherium*, in which case the number of parallel trackways present on this outcrop may indicate herding behavior of diadectomorph reptiliomorphs, which has not been previously reported and acquires an important meaning in consideration of its occurrence in deserts, being the diadectomorphs anamniotes.



Fig. 1. An NPS photograph of the newly discovered locality showing the outcrop containing multiple in situ vertebrate trackways within the Coconino Sandstone at Grand Canyon National Park.

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SUITE OF BIOEROSION TRACE FOSSILS ON NEW TURTLE MATERIAL FROM THE EARLY PALEOCENE SALAMANCA FORMATION, ARGENTINA

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The earliest Paleocene Salamanca Formation [1] is located within the Golfo San Jorge Basin, Chubut Province, Patagonia, Argentina. Outcrops of the Salamanca Formation represent a low energy coastal transitional environment subject to tidal influence. The Paleocene is marked by progradation of shallow- and marginal-marine systems resulting in the accumulation of shallowing-upward, tidally influenced, nearshore to fluviodeltaic deposits overlain by a marine flooding surface, subsequently followed by coastal swamp deposits [2,3]. The Salamanca Formation is well known for its paleofauna, which includes invertebrates and vertebrates comprising a diverse array of mammals [4], alligatorids [5,6], and turtles [7]. Herein, we describe several chelid, pan-chelid, and indeterminate turtle plastron and carapace fragments housed at the Museo Paleontológico Egidio Feruglio (Trelew, Chubut) that exhibit bioerosion trace fossils from the Punta Peligro-El Gauchito area in southeastern Chubut Province. Various morphologies of trace fossils are observed on these turtle fossils including tunnels, shallow pits, furrows, and holes. The holes and pits are vertical, furrows are horizontal, and tunnels range in orientation from vertical to horizontal, penetrating bone tissue including both cortical and spongy tissues. The trace fossils are restricted to the outermost layer of the shell. Assignment of trace makers of bioerosion trace fossils on the Salamanca turtle material was done through the application of osteic bioerosion trace fossil ichnotaxobases [8] and comparison with previously published examples of bioeroded fossil turtles from the Jurassic [9], Cretaceous [10], and Paleogene [11]. The most likely trace makers for the tunnels, pits, and furrows are continental invertebrates, likely insects with well-developed mouthparts, and aquatic ectoparasites, possibly leeches, ticks, or flukes. The large holes are mostly likely attributed to caimanine alligatorids. These osteic bioerosion trace fossils indicate various periods of subaerial exposure and subaqueous conditions prior to final burial. Some of the turtle specimens were bioeroded prior to disarticulation and show evidence of postmortem weathering, most likely due to hydraulic transportation. The presence of osteic bioerosion trace fossils seems to suggest terrestrial and aquatic trace makers at multiple stages of the taphonomic pathway of these turtle specimens, which is consistent with the transitional setting indicated for these deposits.

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IMAGING BIOGENIC STRUCTURES FROM BARKLEY CANYON (NORTHEAST PACIFIC, WESTERN CANADA): RECONSTRUCTING BENTHIC RESPONSE TO DEEP-MARINE TIDALLY DRIVEN CURRENTS

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Submarine canyons represent deep, large-scale topographic features incised into continental margins. This morphology allows them to funnel and transport nutrients from coastal and shelf areas to diverse mega- and macrobenthic communities in the deep-sea. The Barkley Canyon, off British Columbia, Canada, is a mid-slope submarine canyon, reaching up to 2660 m depth in the Cascadia Basin. This site has seasonal changes in flow regime that alter the transport of oxygen, nutrients, and particulate carbon in the canyon. At this site, nutrient input is predominantly delivered along bottom tidally driven and downwelling currents, which deliver fresh phytodetritus to the seafloor. A well-established oxygen minimum zone (OMZ) between 600 m and 1200 m depth in the canyon affects the size, diversity, and distribution of the benthic fauna. Regional distribution of fauna is also affected by seasonal conditions; organisms like *Chioneocetes tanneri* (Tanner crab) exhibit ontogenetic migration patterns through the canyon based on seasonality. While past studies have addressed the benthic community in this region, works focusing on bioturbation and biogenic structures have received comparatively less attention. Video and turbidity sensor data provided by Ocean Networks Canada's NEPTUNE observatory located at the canyon axis (985 m deep) allows the study of modern biogenic structures to get a better understanding of the composition and community structure. Through detailed video observations of periods with varying levels of turbidity, the impact of deep-marine tidally driven currents and the response of the benthos can be assessed. At times of low turbidity with an average of 0.27 NTU (June 25, 2018–March 27, 2019), a dense occurrence of burrow openings (approximately 90/m²) showing surrounding rims, inferred to have been formed by polychaetes, has been observed. In contrast, these features were absent from the sea bottom at times of high turbidity where averages reached 0.40 NTU (June 17, 2016–December 26, 2017). The increase in energy and high sediment supply linked to the arrival of the currents may have been detrimental to the establishment of polychaete worm populations. Oval shallow depressions recording the resting impressions of *Chioneocetes tanneri* (Tanner crab) and occasional feeding traces of *Anoplopoma fimbria* (Sablefish) representing incipient *Osculichnus* generate an irregular pitted topography. Substrate conditions around the canyon axis site are heterogeneous with a top tier of muddy, organic-rich, fluffy sediment and patches of a lower layer of compacted sediment which is locally exhumed by the erosive nature of the turbulent flow. Ichnologic studies of modern submarine canyons involving the use of continuous videos may provide valuable information on changes at the community level (e.g. megafaunal composition and density) in physically controlled settings and best assess the effects of deoxygenation, high turbidity, or high energy erosional events. A better understanding of bioturbation in modern submarine canyons is essential to build up models that reconstruct physical processes and biogenic responses in these environments in the fossil record.



REFINING *CRUZIANA* STRATIGRAPHY: THE CASE OF TRANSITIONAL ICHNOTAXA IN THE LOWER PALEOZOIC OF NORTHWESTERN ARGENTINA

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The Central Andean Basin comprising northwestern Argentina, northern Chile, western Bolivia, and southern Perú is well known for the presence of highly fossiliferous upper Cambrian–Lower Ordovician rocks. The occurrence of both body and trace fossils in the same outcrops allows to better constrain the age of animal–substrate interactions. The aim of this contribution is to evaluate the transition between the *Cruziana semiplicata* and *Cruziana rugosa* groups based on the presence of trace and body fossils. The biostratigraphy based on trilobites, conodonts, graptolites and chitinozoans in the basin is well established at high resolution [^{1–6}]. Also, the presence of the *Cruziana semiplicata* and *Cruziana rugosa* groups has been extensively documented (see [⁷] and references therein, and [⁸]). The main trilobite authorship suspects are olenids and asaphids (*Neoparabolina* and *Ogygynus* for the Argentina specimens) for the *C. semiplicata* and *C. rugosa* groups respectively (see [⁹]). During the Tremadocian–Floian transition, a significant trilobite faunal turnover took place in northwest Argentina, as evidenced by the replacement of olenids by asaphids (see [¹⁰] and references therein). This is coincident by a turnover of trilobite trace fossils as illustrated by the replacement of the *Cruziana semiplicata* by the *Cruziana rugosa* groups in the same region [^{7, 11–12}].

The stratigraphic range of the *Cruziana rugosa* group (i.e., *C. rugosa rugosa*, *C. rugosa furcifera*, and *C. rugosa goldfussi*) have been traditionally considered Lower Ordovician indicators, but specimens from Bolivia triggered the debate about their younger range [⁸]. As a result, the *C. rugosa* group is now considered as Ordovician in age without further precision. On the other hand, the distinctive ichnospecies *Cruziana semiplicata* tends to be considered an upper Cambrian (Furongian)–Tremadocian indicator. In turn, *Cruziana tortworthi* and *C. breadstoni* were proposed as “transitional ichnotaxa” signaling Tremadocian strata in other Gondwana regions [^{11, 13, 14}]. These last two ichnotaxa display morphologic features from both *C. semiplicata* (e.g. external fine scratch imprints and marginal ridge) and *C. rugosa* (e.g., deeper, regular, subparallel, multiple sets of scratch imprints). Particularly, the Rupasca Member (early late Tremadocian age; *Bryograptus kjerulfi* graptolite Biozone/*Bienvillia tetragonalis* trilobite Biozone) of the Santa Rosita Formation is host to *C. semiplicata*, directly associated with *C. tortworthi* and *C. breadstoni*. These deposits are restricted to the upper part of the *B. tetragonalis* Biozone according to the revised concept of Meroi Arcerito et al. [¹]. A low diversity trilobite association dominated by the olenid *Leptoplastides granulosis* (Harrington) and with the asaphid *Asaphellus stenorachis* (Harrington) as a subordinate element occur in *Cruziana*-bearing strata. Finally, the presence of these “transitional ichnotaxa” in these well-defined age strata allow us to conclude that the trilobite trace fossils of the Rupasca Member are key to provide new precision on *Cruziana* stratigraphy for the Tremadocian.



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QUANTITATIVE CHARACTERIZATION OF 3D PORE STRUCTURES AND PERCOLATION CHARACTERISTICS IN BIOTURBATED RESERVOIR MEDIA BASED ON X-RAY MICRO-CT: A CASE STUDY OF THE NEOGENE SANYA FORMATION IN THE QIONGDONGNAN BASIN, NORTHERN SOUTH CHINA SEA

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Organisms alter the primary texture of sediments, leading to alteration in petrophysical properties between the fills and host sediments, which affects reservoir properties and fluid flow characteristics [1,2]. In this paper, the three plugs (S1, S2, and S3) selected were all derived from cores from the Sanya Formation in the Qiongdongnan Basin. The content of *Ophiomorpha* in the three selected plugs varied, with about 75% by volume of *Ophiomorpha* in the S1 plug, about 60% by volume of *Ophiomorpha* in the S2 plug, and about 50% by volume of *Ophiomorpha* in the S3 plug. The 3D scanned data volume of the three selected plugs was obtained using the X-ray microscope (Zeiss Xradia 510 Versa) (XRM) to scan the rock plugs in the Key Laboratory of Paleomagnetic and Palaeotectonic Reconstruction, Institute of Geomechanics, Chinese Academy of Geological Sciences, and a 3D pore structure model was established. The geometric characteristics of the microscopic pore structure were quantitatively and visually characterized by a modified maximal ball algorithm [3,4], and connectivity analysis of the pore structure was carried out. Next, numerical simulations of the percolation characteristics of the analyzed bioturbated reservoir samples were performed using digital core software (Avizo) and multi-physics field simulation software (Comsol). The results show that: (i) 3D pore structures reveal that pore volume, pore area, pore equivalent radius, throat area, throat equivalent radius and throat length have a large distribution range; among them, the pore volume has the largest distribution range, which can vary by 6 orders of magnitude, indicating that the pore size distribution of the bioturbated reservoir is uneven and has strong heterogeneous characteristics; (ii) the connected pore structure is very complex, and as the equivalent radius of connected pore increases, the coordination number also gradually increases, the better the connectivity. Finally, numerical percolation simulation results also suggested that larger connected pore space plays a key role in the effective permeability of the reservoir. This study has important implications for analyzing the modification effect of bioturbation on oil and gas reservoirs and enhancing production and recovery in the study area.

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TOWARDS A METHOD TO ESTIMATE MIXED LAYER BIOTURBATION INTENSITY IN MUD-RICH SUCCESSIONS

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The marine profile can be subdivided from top to bottom into mixed, transition, and historic layers. The former two represent the layer of homogeneous rapid mixing and the layer of heterogeneous mixing containing discrete traces, respectively. The historic layer occurs below the transition layer and constitutes a zone of inactive bioturbation containing the fossilized record of tiering. Droser and Bottjer [1] and Taylor and Goldring [2] after Reineck [3] proposed the two most widely used semi-quantitative methods to assess degree of bioturbation in vertical cross-section views. These methods are based on the preservation of biogenic structures emplaced in the mixed and transition layers overprinting the primary fabric. However, neither of these methods discriminate between different degrees of mixed layer bioturbation. As an example, a bed representing a fully bioturbated mixed layer bed would have the maximum index (5 or 6) of traditional methods even if all its grains were displaced once or several times.

Neglecting mixed layer bioturbation is acceptable for most analysis of heterolithic and sandstone-dominated successions displaying exquisitely preserved trace fossils available for examination. Yet, in mudstone-rich successions lacking or showing scarce discrete trace fossils emplaced in transition layers, mixed layer bioturbation is the most important recognizable biogenic signal to assess degree of bioturbation. In organic-rich muddy substrates, for instance, high organic carbon loads make specialized feeding superfluous, precluding the genesis of discrete traces, whereas soupy substrates foster the formation of biodeformational structures over distinct trace fossils [4].

In such muddy systems, traditional methods to quantify the degree of bioturbation are of little use. Low sedimentation rates typical of these depositional environments allow for complete homogenization of the primary fabric, and therefore, mostly maximum bioturbation indexes are recorded. Researchers have recognized this problem for a long time and opted to use simple descriptive approaches [5] or measure bed thickness [6] to characterize mixed layer bioturbation intensity.

There is a need to establish a common language between the ichnological community by creating a method to estimate mixed layer bioturbation. Studies of ancient muddy successions suggest that the transition between absent and present macrofauna is constituted by meiofaunally reworked muds ("cryptobioturbated mudstone" [7], which is not the same as the concept of cryptobioturbated sandstone). For example, data from the Upper Jurassic–Lower Cretaceous Vaca Muerta Formation of Argentina indicate that meiofauna-rich ichnocoenoses having 1–2 mm burrow sizes and 1–15 mm penetration depths generate what has been called cryptobioturbated mudstone [8]. Such meiofaunal transition will have a different impact upon the mixed layer than macrofaunal bioturbation and will therefore leave a distinctive signal in the fossilized rock fabric. Generating a methodology to estimate mixed layer bioturbation in mud-rich successions could provide a starting point to characterize the environmental variability of intervals lacking discrete trace fossils and improve ichnofabric description of intervals with trace fossils.

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ICHNOFAUNA OF A CAMBRIAN–ORDOVICIAN DELTA COMPLEX: THE LOS CABOS GROUP OF ASTURIAS, SPAIN

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The Los Cabos Group comprises 3000–4500 m-thick middle Cambrian to Lower Ordovician shallow-marine deposits in Asturias, Spain [¹], constituting distal deposits of the well-known "Armorican Quartzite" of Iberia and France. The formation holds enormous potential to analyze paleoecological controls and the evolution of trace fossils in mud-rich shallow-marine areas due to its great thickness and prolonged time span. Moreover, it contains an impressive record of animal-substrate interactions that have been intensively studied in the seventies [²]. However, deltaic and sediment-gravity flow facies were overlooked in previous analyses [³], and therefore, there is a need to consider this riverine influence on the development of the Los Cabos ichnofauna.

For this purpose, we undertook a sedimentologic and ichnologic analysis of the most complete and less tectonically affected succession of the Los Cabos Group (>5000 m of section, between the towns of Barcia and Cadavedo). Trace fossils were analysed in detail in terms of their morphology (and related ichnotaxobases), size, and ethology. Bioturbation intensity was assessed as well.

A preliminary sedimentologic analysis indicates that the succession contains storm- and flood-influenced deltaic and tide-dominated shallow-marine deposits. The storm- and flood-influenced deltaic deposits are characterized by thin- to thick-bedded, massive and normal-graded, mudstone and very fine-grained quartz and lithic greywacke; and combined-flow, current-, and wave-ripple cross-laminated, hummocky and swaley cross-stratified, planar, trough, and low-angle cross-bedded, and horizontal-laminated, very fine-grained quartz and lithic greywacke, siltstone and very fine- to fine-grained quartz arenite. The mudstone and greywacke show mudstone and arenite intraclasts, slump folds, arenite and mudstone pseudonodules, convolute bedding, ball and pillow structures, and load casts. Bioturbation index is 0 to 3, and *Bifungites*, *Cruziana*, *Monomorphichnus*, *Planolites*, *Rusophycus*, *Skolithos*, and *Teichichnus* occur.

The tide-dominated shallow-marine deposits consist of very thin- to medium-bedded, massive and horizontal-laminated mudstone; and current-ripple and low-angle cross-laminated, planar and trough cross-bedded, and horizontal-laminated very fine- to fine-grained quartz arenite with abundant very thin mud drapes. Mudstone and arenite are typically interbedded as lenticular, wavy and flaser heterolithic successions or as sand-rich intervals. Bioturbation index is 0 to 5, and *Arenicolites*, *Diplocraterion*, *Lingulichnus*, *Planolites*, and *Rosselia* are observed.

Preliminary results indicate the presence of two trace-fossil assemblages. The storm- and flood-influenced assemblage contains a larger proportion of horizontal trace fossils over vertical structures, whereas the opposite is true in the tide-dominated intervals. This trend could be related to the detrimental effect of high-water turbidity in deltaic systems upon filter feeding organisms that create vertical trace fossils. Further ichnologic work will improve our understanding of stress



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factors controlling the ichnofauna, generate a comprehensive depositional model of the Cabos Group, and help to delineate patterns of evolutionary significance in Cambrian-Ordovician strata.

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DEEP-SEA UPPER ORDOVICIAN *LINGULICHNUS VERTICALIS* AND THEIR ASSOCIATED BODY FOSSILS SUGGEST AN EARLY COLONIZATION OF PROXIMAL TURBIDITE SYSTEMS

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High-energy zones of deep-marine systems such as channel-levee complexes and proximal areas of turbidite splays may show the development of the *Ophiomorpha rudis* ichnosubfacies of the *Nereites* Ichnofacies, dominated by callianassid shrimp burrows [¹]. However, this ichnosubfacies was not established in the deep sea until the Late Jurassic. During the early and mid Paleozoic, high-energy deep-marine areas were typically barren or display low levels of bioturbation [²]. These areas probably remained sparsely bioturbated until the Late Jurassic, although a comprehensive evolutionary review of this subenvironment is currently needed.

An unusual, dense occurrence of *Lingulichnus verticalis* and their associated brachiopod body fossils (lingulides) is recorded in an Upper Ordovician channel-overbank complex in Spain, constituting the first report of *Lingulichnus* from deep-marine environments [³]. The study area is in the Frejulfe beach, Asturias, Spain, and belongs to the West Asturian-Leonese Zone, a Variscan tectonostratigraphic domain of the Paleozoic Iberian Massif. The trace fossils were found in the Agüeira Formation, a 300–3000 m-thick turbiditic sandstone, siltstone, and mudstone succession interpreted as a submarine fan [^{4,5}].

The study interval (35 m thick) preserves fining- and thinning-upward channel and overbank deposits. The channel deposits comprise 10–100 cm-thick, massive, and parallel- to sinusoidal-laminated, very fine-grained sandstone. Bioturbation index is typically 0 and rarely 1–2, with *Lingulichnus verticalis* and *Phycosiphon incertum*. The overbank deposits consist of 1–20 cm-thick, climbing-ripple to current-ripple cross-laminated, and parallel-laminated, very fine-grained sandstone to siltstone, interbedded with mudstone. It contains *Lingulichnus verticalis*, *Nereites* isp., *Phycosiphon incertum*, and *Planolites* isp., generating a bioturbation index of 1–3 and rarely 4 or 5. Calcium phosphate and poorly preserved pyrite-replaced lingulides (10–55 mm in length and 3–25 mm in width) occur in both deposits.

Lingulichnus verticalis [⁶] consists of oblique (35–45° of inclination) to rarely vertical, passively filled burrows showing a lower rounded to ellipsoidal structure (1–20 mm diameter), and an upper, straight, tubular structure (1–5 mm wide and 10–65 mm long) surrounded by concave-up, cone-in-cone spreite (1–13 mm diameter). Rarely, the upper structure has spade morphology. Plan views are ovoid to oval with rounded and pointed edges. The lower structure is typically preserved in mudstone (hemipelagite), below sandstone or siltstone (turbidite), whereas the upper structure is preserved in sandstone or siltstone (turbidite). Lingulides occur below the spreite of, or laterally associated to *Lingulichnus verticalis* with their anterior end facing up.

Ellipsoidal burrow cross-section, cone-in-cone spreite, and the existence of spade morphologies suggest the trace fossil can be attributed to *Lingulichnus* Hakes, 1976, a dwelling,



equilibrium, and escape structure of lingulide brachiopods. The burrows are inclined in the direction of cleavage, indicating that tilting is produced by tectonic deformation and supporting an assignment to *Lingulichnus verticalis*. Escape behaviour is inferred from the specimens crosscutting thin-bedded turbidites. Dwelling behaviour can be interpreted from the examples where the lingulide is preserved below the burrow, as it represents an organism that retracted into its burrow during a high hydrodynamic energy event and was unable to reposition to the surface after sedimentation and burial associated with the high energy event. Equilibrium behaviour is interpreted in spreite observed within mudstone, indicating gradual vertical migration on a slowly accreting seafloor.

The present report expands the variety of behaviours and feeding styles in early Paleozoic deep-marine environments and the bathymetric range of *Lingulichnus*. The abundance of lingulide trace fossils may reflect an environment rich in suspended food due to the occurrence of continuous bottom currents. As lingulides are opportunistic organisms adapted to stressed, relatively high-energy environments such as intertidal settings [7], both their suspension-feeding strategy and the ability to burrow responding to erosion and rapid sedimentation probably enabled lingulide populations to thrive in these unusual proximal settings of the deep sea.

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ICHOLOGY OF A TRUE SUBSTRATE IN A CRETACEOUS EPHEMERAL POND, NEUQUÉN BASIN, ARGENTINA

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In the last decade, there has been a growing interest in the study of bedding planes, particularly those candidates to be true substrates, capturing the attention of sedimentologists. A true substrate records the sediment-water/air interphase at the time of deposition [1], resulting in an archive of processes that occurred during a very brief taphonomic window, where stasis prevailed [1,2]. During this period, microbial activity occurs and provides substrate resistance preventing later erosion. In this scenario, trace fossils assist in the identification of true substrates. These trace fossils must be disregarded as undertraces, and other sedimentary structures like certain ripple types and desiccation cracks are also documented in the candidate surface. Other accompanying indicators, such as microbially induced sedimentary structures (MISS) [3], are usually present. In the Cretaceous of the Neuquén Basin, on a biostabilized surface in the Agrío Formation, trace fossils with delicate features exquisitely preserved, along with water level marks and steeply inclined lee-side ripples, supported a true substrate interpretation [4]. Later studies on the same surface, in physical continuity with the previously studied channel, documented current ripples preserved on a gently inclined plane (channel border), that extends almost horizontally and contains tracks of slipping dinosaurs on a biostabilized surface [5]. This true substrate allowed the reconstruction of a marginal-marine scene documented in a short taphonomic window.

In the nonmarine Candeleros Formation, a narrow-gauge sauropod trackway with rims presents almost undisturbed ripples on top due to biostabilization suggesting a true substrate [6]. We study here other surface documented in the same nonmarine stratigraphic unit where the previous works [6] suggested arid conditions based on halite pseudomorphs, adhesion and wind ripples, together with widespread mud cracks in iron rich cemented fine-grained sandstones and mudstones. The herein studied surface covers an area of approximately 120 m², but the exact limits are unknown due to covering by overlying beds. The area represents a very shallow unfilled exposed depression, specifically a shallow ephemeral pond. Ephemeral ponds, usually not considered in the study of trace fossils assemblages or icnofacies analysis, are extremely shallow bodies of waters often found in flat areas, frequently linked to fluvial plains, and their permanence depends on climate conditions. Within the pond, sedimentary structures and bioturbation vary in location and type. Ripples and desiccation cracks are dominant, and vertebrate tracks prevail over invertebrate trace fossils. The combined study of sedimentary structures and trace fossils indicates different stages in the pond's evolution until complete dryness. The earliest stage documents a shallow water level, where wave ripples some with flat-topped crests (Fig. 1A), and others with abrupt changes in axis suggest some emerged areas (Fig.1B). This stage implies recurrent biostabilization, documented by pockets with multidirectional ripples (Fig. 1A). In some cases, invertebrate trace fossils are partially covered by ripples or are found in flat areas intensely affected by desiccation cracks. The invertebrate trace fossils documented in patches with ripples consist of curved or radiate probing projections departing from a center, reaching 5 cm in length

along their longest axis. They are assigned to *Oldhamia* Forbes with the ichnospecies *O. curvata* Lindholm and Casey and *O. radiata* Forbes. The latter is more abundant. This new finding constitutes the first record of the ichnogenus in nonmarine deposits in the world. Similarly to Cambrian marine records of Ireland, *Arenicolites* Salter is also documented [7], and the possibility of the same producer cannot be disregarded.

The final stage involves the complete dryness of the pond, marked by the presence of numerous desiccation cracks. In some areas, classical mud cracks with sandstone infilling were observed (Fig. 1C). However, the most frequently observed cracks exhibit a pattern consistent with the desiccation of biostabilized surfaces. They include irregular, tortuous, incipient, and reticulated cracks, exposed horizontally or irregularly turned upward (Fig. 2A), forming areas of uneven topography with local variations in the cracking pattern related to biostabilized surfaces.



Fig. 1. A. Wave ripples, flat-topped and multidirectional pocket; B. Ripples with changing axis and flattened, incipient cracking in down-left area; C. Mud cracks with sandy infilling.

The intermediate stage marks a period of stasis with progressive changes in substrate moisture, which is only recognizable solely through the record of imparted tracks on the surface. A sauropod-inferred trackway and isolated tracks were produced prior to cracking (Fig. 2B), and the observed rims are irregular, suggesting a high level of moisture. Some isolated tracks without rims but deeply imprinted probably record a more advanced stage of dryness. It is essential to note that the entire area with many sauropod tracks is scarcely cracked. Theropod tracks imparted on the surface are crucial to understand the progressive dryness of biostabilized areas, documenting the shortest taphonomic window in the entire evolution of the substrate. They include different morphological variants and sizes. Firstly, in a small area without cracks, an isolated grallatorid-type track quite deeply impressed on the surface presents sharp borders (Fig. 2C), suggesting a still wet substrate. The question arises: why just one track? Close to the track, most of the surface is cracked, indicating that the dinosaur mostly walked on a surface with less moisture and in a more advanced state of dryness and only in a wet patch the track was well recorded. A second type of theropod track consists of larger ones forming a challenging-to-follow trackway, presenting wider and larger digit impressions than the first type. Finally, an extremely flat and the largest tridactylar track (Fig. 2D), isolated, is almost topographically indistinguishable from the surrounding area. A possible explanation for the noted differences in the track preservation is related to progressive dryness but variations in the speed and size of the producer might have resulted in different pressure on the substrate. Interestingly, very shallow oval hollows are observed in almost all areas of the exposed surface. They are interpreted as transmitted sauropod tracks (undertracks), spectacularly preserved in vertical section in overlying beds, with some of them in contact with the studied surface.

The studied surface is an excellent example of a true substrate but also a clear palimpsest in the sense of Davies and Shillito [2], comprising a series of abiotic and biotic processes that show the complexity of a “blink” in the geological record. This work also emphasizes the need of sedimentological analysis focused on the substrate during the study of vertebrate tracks and trackways.

In conclusion, this work documents that true substrates may result in excellent archives of their moisture variations. On those surfaces, vertebrate tracks provide crucial information not

only about intermediate stages in pond evolution but also regarding the ichnofauna diversity that is higher than in any other part of the stratigraphic unit.

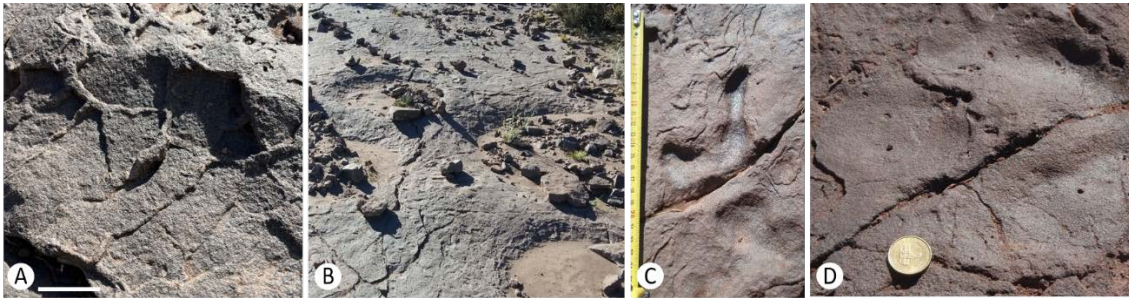


Fig. 2. A. Turned upward cracked surface, scale bar = 5 cm; B. Sauropod trackway with discrete rims and cracking; C. Gallatorid-type track deeply imparted on the surface; D. Flat theropod track, coin for scale = 2.5 cm.

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INSIGHTS ABOUT ANCIENT DUNE DESERT PALEOECOLOGY BASED ON INVERTEBRATE TRACE FOSSILS OF THE BOTUCATU FORMATION (EARLY CRETACEOUS, BRAZIL)

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The amount of animal biomass in modern dune deserts is tied to the primary productivity in the area, steadily increasing when the water input increases, whether by rain or fog [¹⁻³]. There is evidence that life in ancient deserts followed the same ecological strategy [⁴⁻⁶]. Here we analyzed the invertebrate trace fossils in the Botucatu Formation to test this hypothesis. The Botucatu Formation (Paraná Basin) is the Brazilian geological record of a large sand sea (Botucatu Paleodesert) developed under an arid climate in mid-south Gondwana during the latest Jurassic–Early Cretaceous [^{7,8}]. No animal body fossils were ever found, but the paleodesert fauna can be indirectly accessed by their trace fossils, which beyond the diversity, also provide information about paleoecology [⁶].

The Botucatu Formation crops out along the entire contour of the Paraná Basin, with correlative units in Argentina, Uruguay, Paraguay, and Namibia [^{8,9}]. The Botucatu Formation in Brazil is overlaid by the Late Jurassic units Guará Formation (southern) and Piramboia Formation (northern) [¹⁰]. This is overlaid by the extrusive magmatic rocks of the Serra Geral Group, dating around 134 Ma [¹¹⁻¹³], which gives the upper age for the Botucatu Formation. For this work, we analyzed the trace fossils in outcrops of São Bento quarry, Araraquara (São Paulo State), an area part of the Ouro Ichnosite, well known by its trace fossils, mainly those of tetrapods [^{14,15}].

Invertebrate trace fossils in the Botucatu Formation are rare and scattered. However, in the São Bento quarry, we track occurrences of *Skolithos* isp. and undetermined horizontal traces occurring scattered but also in highly bioturbated beds. These beds are in cross-bedded sandstones that we interpreted as the upper part of the paleodunes slipface, which demises the influence of the water table or a wet interdune, if any. Based on comparisons with modern dune deserts, we interpret the highly bioturbated beds as the response of the invertebrate fauna to episodic wet events, probably rains. When a moisture threshold is attained, it triggers invertebrate proliferation recorded as highly bioturbated beds.

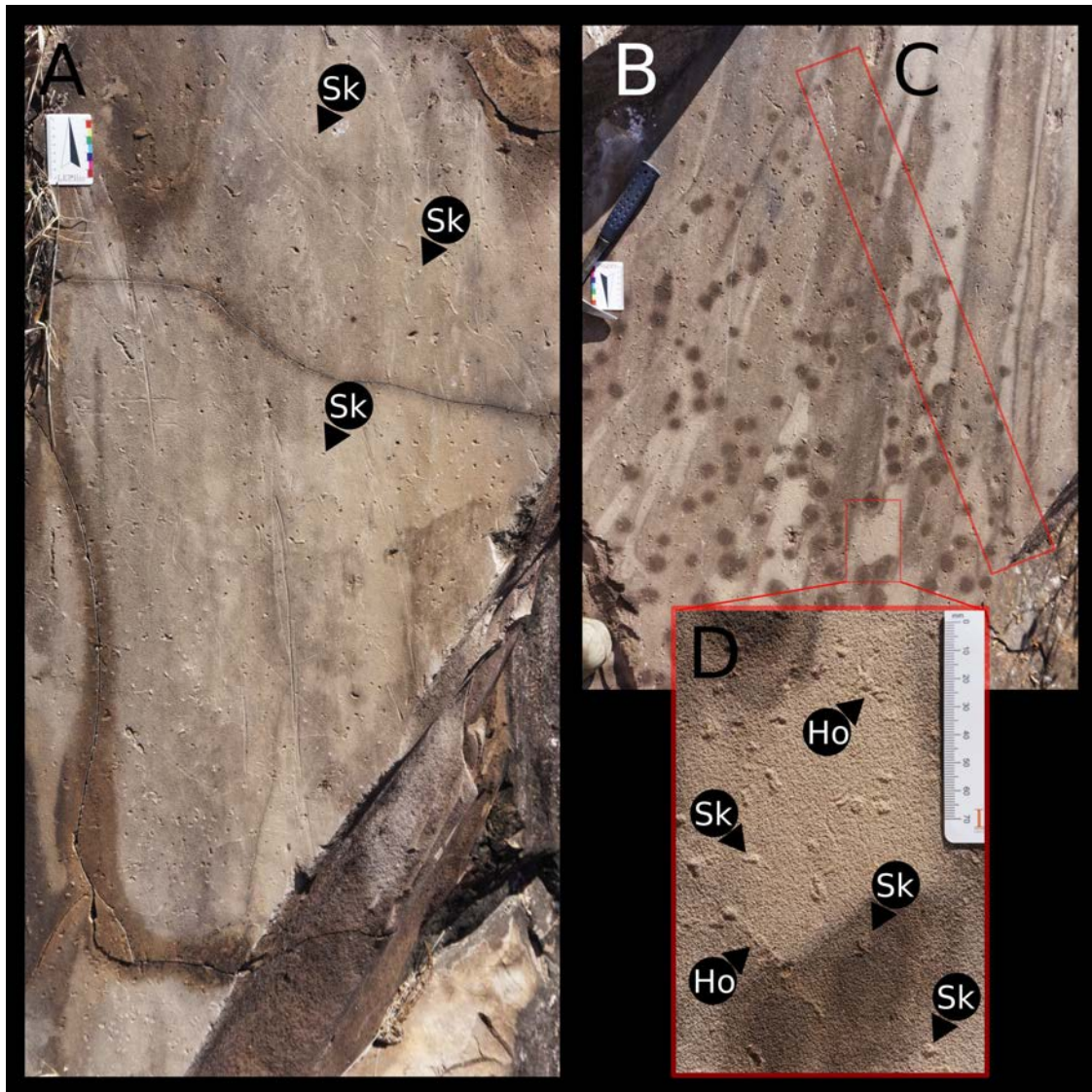


Fig. 1. Botucatu Formation bioturbated beds in São Bento quarry (Araraquara, SP). A. Bioturbated bedding plane with high concentration of *Skolithos* isp.; B. Bioturbated bed bearing *Skolithos* isp., and undetermined horizontal traces. C. Tetrapod trackway; D. Detail of the invertebrate burrows in the bioturbated bed. Abbreviations: Sk: *Skolithos* isp., Ho: Undetermined horizontal traces.

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A LIMULID PARADISE IN THE ASTURIAN JURASSIC (N SPAIN)

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Xiphosurid trackways are very scarce at the Spanish fossil record, only were reported several references about the Carboniferous of Palencia [^{1,2}], Asturias [³] and Ciudad Real [⁴], and the Triassic of Lérida [⁵] and Barcelona [⁶]. Here we present abundant limulid trackways from the Kimmeridgian (Upper Jurassic) of Asturias (N Spain). All of them were found at the “Dinosaur Coast” and some of them are housed at the Jurassic Museum of Asturias (MUJA).

The trackways are preserved, both as concave epireliefs and convex hiporeliefs, in loose sandstone blocks from the Lastres Formation. This latter, about 400 m thick, is characterized by alternations of sandstones, marlstones and mudstones related to fluvial-dominated deltas which were deposited in the margin of a shelf lagoon.

The morphology of the Asturian trackways reveals at least five different behaviours: resting, ploughing, crawling, walking and running. Resting traces (Fig. 1A-B) consist of impressions of the body outline. It is possible to recognize the prosoma and the telson, and sometimes the opisthosoma. They are the most scarce of all. Ploughing traces (Fig. 1C) consist of a series of deep, crescent-shaped impressions superimposed on each other in the direction of the limulid movement. They are produced by repeated pressing of the prosoma in the sediment. Crawling trackways are formed by the walking legs (Fig. 1D-E). The impressions of the legs III-V are shorter and simpler than pusher ones. The morphology of the pusher prints is not well defined. In this kind of trackways, the walking leg impressions show a high angle respect to midline and the stride is short. The telson drag mark is present and usually continuous. This type of trackways indicates that the body was in contact with the substrate. Walking trackways are formed by the walking leg imprints (Fig. 1E), but contrary to crawling traces, the walking leg impressions have a low angle respect to midline and the stride is higher. Telson’s drag mark is not present, which would indicate that the limulid moved with its body raised from the substrate. Running trackways are composed of the pusher imprints (Fig. 1F), in this case well defined, which show a long stride. Pusher prints are tetradactyl on the anterior edge and have an elongated bifid posterior impression. The only criterion to recognize running locomotion is a long stride, since the trackways formed only by pusher prints with a short stride can represent undertracks [⁷].

The resting traces are assigned to *Selenichnites* isp., the scarcest ichnogenus in Asturias, the ploughing traces are assigned to *Crescentichnus* isp., and the crawling, walking and running traces are assigned to *Kouphichnium* isp., the most abundant ichnogenus in this region.

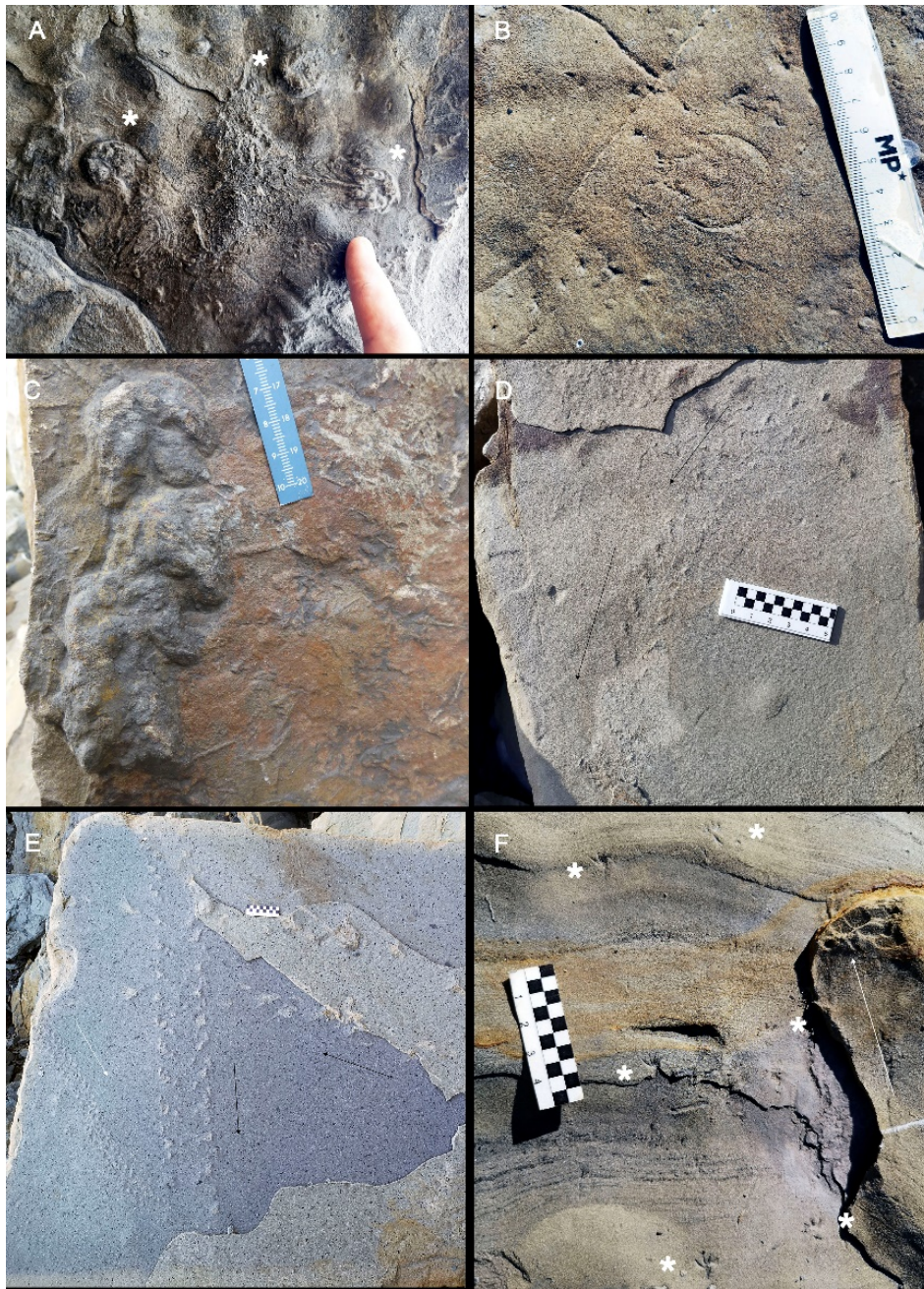


Fig. 1. Trackways showing different behaviour of limulids. A. Resting traces indicated by asterisk. Note the impressions of prosoma and telson. B. Resting trace showing the prosoma and opisthosoma. Note the lack of telson imprint and the preservation of genal spines and terminal projection traces. C. Ploughing traces. D. Crawling (white arrow) and walking traces (black arrows). E. Crawling traces. F. Running traces associated to ripple marks. Only the pusher prints are preserved. Note the bifid posterior impression in the right tracks.

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INFORMATION REVOLUTIONS IN THE HISTORY OF LIFE: THE EVOLUTION OF THE “IMMENSE WORLD”

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To a first approximation, ichnology is the science of animal movement in the fossil record. It is critical, therefore, to understand how movement and its controls have evolved over deep time. The movement ecology paradigm [1] provides a framework for describing the shifts that have occurred. The key elements of the paradigm are [2]: (i) *the external environment* – the presence and distribution of resources, competitors, predators, mates, etc.; (ii) *navigation capacity* – the ability to sense and process information about the external environment, to determine where and whether to move; (iii) *motion capacity* – how the animal can move, based on its biomechanical abilities; (iv) *internal states* – the why move component, based on the physiological and/or psychological requirements of an organism. It is the interactions of these elements that control movement. All of these components have developed over the history of life, as external environments have changed, and life has evolved. Implicit in this is that each organism has its own perceptual world, its own unique subset of environmental signals that it perceives and reacts to. This perceptual or subjective world was termed the *Umwelt* by von Uexküll [3]. Organisms occupying the same physical space can perceive non-overlapping aspects of it and thus have utterly different *Umwelten*. Yong has called the incredible diversity of *Umwelten* in the modern day “An Immense World” [4]. In terms of movement, the *Umwelt* encompasses the navigation capacity, as well as aspects of the internal state and the motion capacity. The basic hypothesis here is that as the variety and complexity of potential environmental signals increased over time, the abilities of organisms to receive and react to these signals also increased, i.e., the diversity of *Umwelten* also grew. These increases are largely co-evolutionary, as the richness of signals, the potential information content of the environment, is mainly driven by the diversity of biological signal producers. Episodes of increase in the complexity of the spatial and temporal information landscape and in organisms’ ability to perceive and act on it, *information revolutions* [5], thus parallel other major transitions in the history of life.

Probable information revolutions were:

(i) The origin of microbial life. Chemoreception was the earliest ability to appear, with bacterial and archaeal species detecting and responding to a vast array of chemical signals, including those from nutrients and toxins, pH and oxygen concentrations, and those emitted by conspecifics, with the signals detected being specific to each species [6]. A form of mechanoreception is used by those that attach to surfaces [7]. Other known senses include photoreception [8] and magnetoreception [9]. Microbes move in response to these signals, either stochastically using flagella, in water born species, or gliding on surfaces [10-12]. Their minute size limits them to moving in response to changes in signal gradients over time [13] and prevents signal localization within their bodies.

(ii) The appearance of single-celled eukaryotes. Although bigger than microbes, protists still predominantly use chemoreception [14] and are limited by their small size to detect gradients. They are large enough, however, to produce physically separated chemical or photoreceptors, allowing more efficient movements [13] using cilia or pseudopodia.

(iii) The major jump in information and its usage occurred with the advent of animals, probably beginning in the Ediacaran [15] and accelerating during the Cambrian [5, 16]. Key innovations included larger size, so that animals could now detect odor plumes (rather than gradients), fluid movements, and sound [17]; the polarization of sense organs in bilaterians associated with movement, perhaps leading to a major increase in cognition [18]; the ability to have movement of sense organs, such as antennae and eyes, detached from movement of the



whole body; and the formation of image forming eyes. Information could now come from sources well removed from the body, a major increase in the sensory range.

(iv) The conquest of the land. Profound changes in the transmission of environmental signals occurred with the transition of water to air as a medium [19]. Visual range greatly increased [20]. Major changes occurred in the composition of odorants [21] and the propagation of sound. Heat detection became possible. Among vertebrates, these were probably tied to major increases in brain size and complexity and the ability to separately move the head. [18,19] The development of forests greatly increased the three-dimensional complexity of the terrestrial world and the necessity to create more complex neural maps.

(v) The origin of angiosperms. The origin of flowers led to a huge increase in the diversity of odorants and in the range of colors in the terrestrial environment, possibly promoting olfaction [22] and vision [23] of both insects and vertebrates.

Over geologic time, the diversity of environmental signals that organisms receive and their abilities to move in response to them have increased. Interpreting the behavior underlying the production of trace fossils requires understanding the Umwelt of the tracemakers.

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NUMMULITES TEST TAPHONOMY: INSIGHTS FROM OLIGOCENE DEPOSITS OF THE KUTCH BASIN, GUJARAT, INDIA

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Larger benthic foraminifera (LBF) serve as informative markers for diverse shallow-marine sclerobionts [1] in the low sedimentation regimes [2,3]. Investigating these carbonate substrate communities within a paleoenvironmental and taphonomic framework provides an understanding of the interaction of sclerobionts with live or dead foraminiferal tests. In this investigation, we integrate a comprehensive examination of bioerosion, encrustation, predation, ethology and their implications for paleoenvironments. Our aim is to highlight the taphonomic pathways of nummulite accumulations from the basal member of the Oligocene (Chattian) Maniyara Fort Formation in the Kutch Basin of Gujarat. To understand the processes and interactions affecting these fossilized foraminiferal tests, we have employed various analytical techniques, including field observations, thin-section petrography, SEM and micro-CT. Approximately 91% of the studied specimens were affected by borers and/or encrusters.

Morphological analysis of different bioerosion structures preserved on *Nummulites* tests (Fig. 1A-B) are attributed to the activity of clionid sponges (*Entobia megastoma*), polychaete annelids (*Trypanites* isp. and *Maeandropolydora sulcans*), gastropods (*Radulichmus* isp.), sharks (*Linichnus bromleyi*) and algal microborings, along with corrosion pits and fractures. Regarding encrusting traces, bivalves (Ostreids), polychaete annelids (serpulids), rotaliid foraminifera (megalospheric *Nummulites*) and bryozoans have been recognized (Fig. 1C). The microborings created by sponges and polychaete worms are primarily attributed to domichnial activities, whereas exploratory bite marks from sharks and grazing traces from gastropods are attributed to praedichnial and pascichnial behaviors, respectively. The exceptional preservation and distinct morphology, as revealed through the micro-CT scan coupled with 3D modeling, greatly assisted in the identifying microborings of sponge, worm and algal borings within the *Nummulites* test. The taphonomic characteristics of bioeroded and encrusted *Nummulites* can serve as valuable paleoecological indicators of deposition under conditions of low to moderate sedimentation rates. The presence of both, non-bioeroded and bioeroded/encrusted tests, the prevalence of thick-bedded nummulite packstone and grainstone, and the abundance of larger and flat *Nummulites* spp., as well as the presence of non-preferred imbrications, together with the reported ichnological assemblage, collectively suggest an autochthonous to parautochthonous nature of the nummulite accumulation. This likely occurred in a shallow-marine environment, potentially within a middle to inner carbonate ramp. The present study contributes to our understanding and comparison of different carbonate-platform environments belonging to the paleomarine ecosystems and the processes that have shaped the Oligocene fossil record in the Kutch Basin.

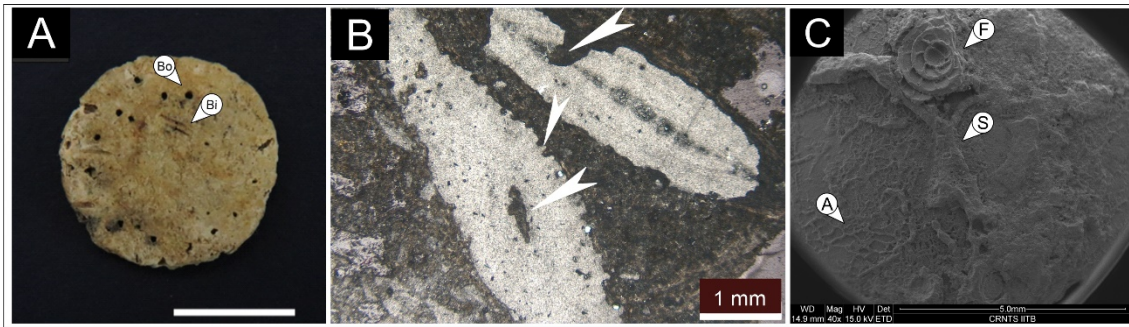


Fig. 1. A. *Nummulites* test showing bioerosional features (Bo- Boring, Bi- Praedichnial bite marks); B. Photomicrograph of transverse section of *Nummulites* with microborings along the margins and across the tests (white arrow); C. Longitudinal view, SEM image, showing encrusting foraminifera (F), serpulid encrustation (S) and algal microborings (A).

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PRECAMBRIAN TRACE FOSSILS OF SLIME MOLDS

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Slime molds (Amoebozoa, Mycetozoa) are free-living microscopic amoebae common in soils. The amoebae live on bacteria and fungi dispersed in soils but have the startling ability to aggregate into a multicellular, sluglike grex, and migrate to more fertile patches [1]. They go a short distance (<18 cm) and form a stalk to elevate a sporangium, which then bursts to release spores (Fig. 1). The grex trail up to 1 cm wide includes transverse marks superficially like backfills, but they are convex in direction of movement, where the front rim bites into sediment, so the opposite of backfills. The trails also have levees and taper strongly as a thin initial stream of amoebae merge into a wider grex. This taper and short lengths, distinguish slime mold trails from fossil trails of worms and other animals, which are parallel sided and almost always extend off the edge of slabs. Microscopic amoebae would not be expected to leave much of a fossil record, but grex trails have been found in paleosols as old as Paleoproterozoic (1.9 ± 0.1 Ga) in the Stirling Quartzite of Western Australia (Fig. 2). These were within streamside alluvial paleosols (Fluvents) in a region of desert paleosols (hyperarid Gypsids). Along with paleosol fungi such as Paleoproterozoic (2.2 ± 0.1 Ga) *Diskagma buttoni* [3], *Myxomitodes* is evidence of eukaryotic life on land much earlier than in the sea [2]. Aerobic, eukaryotic soil microbiomes replaced Archean, anaerobic, prokaryotic soil microbiomes of actinobacteria, purple sulfur bacteria, sulfur-reducing bacteria, and methanogens, best known from the 3.0 Ga Farrel Quartzite of Western Australia [4]. *Lamonte trevallis* is another likely slime mold trail of Ediacaran (550 Ma) age from intertidal paleosols of the Shibantan Formation of Hubei, China [5]. Differences between slime mold and worm trails are subtle, and a more detailed fossil record of slime molds may emerge from re-examination of Precambrian and Phanerozoic fossil trails.

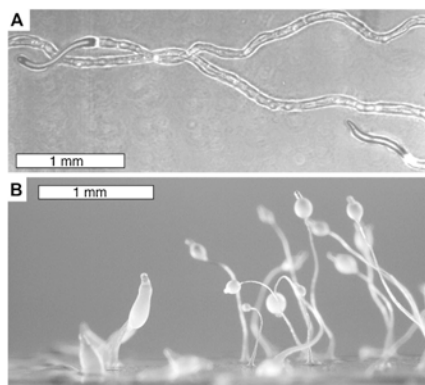


Fig. 1. Slug (grex) and trails in agar (A) and sporocarps (B) of the living slime mold (*Amoebozoa*, *Mycetozoa*) *Dictyostelium discoideum* [3].

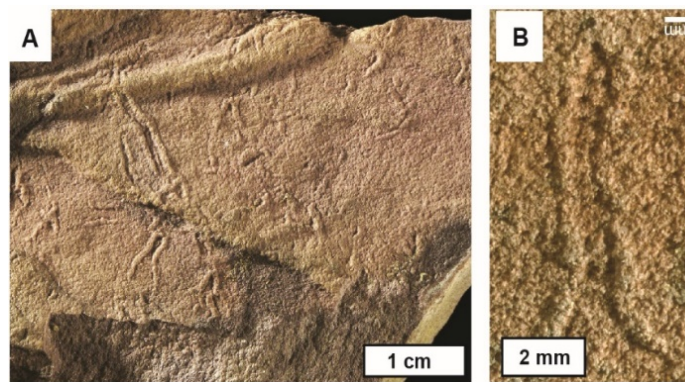


Fig. 2. Fossils paleosol of from Paleoproterozoic (1.9 ± 0.1 Ga), Stirling Range Formation, *Myxomitodes stirlingensis* at 53.8 m on Barnett Peak, Stirling Range, Western Australia [2].

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BURROW SIZE AND FOOD SUPPLY IN THE DEEP SEA

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Food is one of the most important limiting factors for living organisms in the deep sea. Ancient food supply can be proxied by several methods, such as the rate of sedimentation and total organic carbon. The two sets of data are well correlated with each other and also with maximum burrow size. These data were obtained from Deep Sea Drilling Project Legs 64 to 81 during the 1980s. In total, 2.3 km of hydraulic piston cores from the Atlantic and eastern Pacific Oceans were studied. The hydraulic piston technique was then new and offer an unparalleled opportunity for study of deep-sea Cenozoic ichnofacies due to recovery of long cores (up to 300 m) with relatively little distortion caused by core-liner drag. Use of these young cores allows close comparison of modern and fossil burrow distribution and preservation, particularly because abyssal water depths have changed little since the Pliocene.

Two burrow assemblages (“Abyssal” and “Bathyal,” in practice overlapping somewhat in water depth) are recognized based on abundance and diversity of ichnospecies. These presumably correspond to the lower tiers of the *Nereites* and *Zoophycos* ichnofacies, respectively; however, the upper tiers are rarely preserved in the cores, and much remains obscure about modern burrows in the deep sea. The Abyssal Assemblage includes thin *Chondrites* (usually less than 1 mm in lumen width), *Cylindrichnus*, *Trichichnus*, thin *Thalassinoides* (usually < 2 cm in lumen width) and “reduction burrows.” The Bathyal Assemblage comprises the same ichnotaxa, plus thick, recurved *Chondrites* (lumen \geq 2 mm wide), *Skolithos*, *Teichichnus*, thick *Thalassinoides* (lumen \leq 5 cm wide), *Lophoctenium*, and *Zoophycos*, which are rare to absent in the Abyssal Assemblage. Burrows tend to be larger in the Bathyal Assemblage as well as more diverse.

Assemblages correlate with factors such as sedimentation rate, water depth, and organic carbon content. The Abyssal Assemblage occurs mostly in sediments deposited at very low rates (0 to 3 cm ka⁻¹) at abyssal depths (3.0 to 4.5 km), with very low organic carbon contents (0.0 to 0.67%). The Bathyal Assemblage occurs mostly in sediments deposited at slightly higher rates (5 to 13 cm ka⁻¹) at bathyal to upper abyssal depths (0.6 to 3.7 km), with higher organic carbon contents (0.2 to 4.3%). These relationships are probably due ultimately to higher food supply at bathyal sites than at abyssal sites.



NEW THEROPOD TRACKS FROM CANDELEROS FORMATION IN PICÚN LEUFÚ (NEUQUÉN PROVINCE, ARGENTINA): PALEOBIOLOGICAL ASPECTS

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In memory of Dr. Jorge O. Calvo.

Lower sections of the Candeleros Formation (Albian–lower Cenomanian, Neuquén Group) outcrop at the Bajada de la Peta site, located at the southwestern end of Lake Ezequiel Ramos Mexía, 15 km east of Picún Leufú (Neuquén, Argentina). This site presents several ichnological records assigned mainly to theropod and sauropod dinosaurs [^{1,2}]. Recent works have allowed us to expand the ichnological record with the discovery of new tracks preserved in positive epirrelief and mold.

The track-bearing surface is composed of medium to fine sandstone facies of yellowish-brown color. Although the depositional environment for these levels is varied, depending on the sector of the basin being studied, the Bajada de la Peta deposits are interpreted as alluvial plain environments associated with wide mudflats with the presence of ephemeral channels of little development [²].

In this work we analyze a new trackway, which is formed only by three tridactyl tracks preserved in a block detached from the outcrop due to water erosion of the lake. The tracks present conspicuous characteristics corresponding to different pedal structures of the trackmaker such as claw impressions, pads, heel and digit orientation, as well as preserved interdigital spaces, which evidences an excellent state of preservation.

The tracks are asymmetrical and present straight and robust digits (II-III-IV), they are oriented anteriorly and present very reduced interdigital spaces (8°-10°). Digit III is the largest, followed by digit IV. The impressions of digital pads are remarkable, counting two impressions in digits II and IV, and three impressions in digit III. All the tracks present impressions of the ungual phalanges. The heel-pad is formed by three impressions, being the central impression the largest. We interpret that these impressions may correspond to the distal ends of the metatarsals, which do not form a single impression. The heel-pad is small in relation to the total size of the track (1/3). Tracks are 20 cm long and 11 cm wide. All digits were measured considering the heel-pad. Digit II has a length of 15 cm and forms an angle of 45° with respect to digit IV and 10° with respect to digit III. Digit IV has a length of 17 cm and has an angle of 8° with respect to digit III.

The trackway is formed by two tracks corresponding to the left foot and one to the right. The distance between consecutive tracks is approximately 52 cm, the stride length is 103 cm and

the pace angulation is 160°. Following the formula proposed by Alexander [3], the speed of displacement was estimated at 1.5 km/h.

The features described above allow us to assign the tracks studied to a small theropod dinosaur. The theropod record of the Candeleros Formation is varied, with taxa belonging to Alvarezsauridae, Unenlaginae, Abelisauridae and Carcharodontosauridae. The described morphology of the studied tracks is more congruent with the autopod anatomy of taxa belonging to Alvarezsauridae and Abelisauridae, however, it is not possible to assign the trackmaker to one of these clades.

Regarding to the Picún Leufú ichnological record, the tracks studied present some similarities with those described for *Picunichnus benedettoi* and *Candelerioichnus canalei* [1,2]. With *P. benedettoi* it shares the relation of the heel-pad to the total length of the track, low interdigital angles and the general morphology of the digital pads. However, it has considerably more elongated digits II and IV. In addition, anteromedial and anterolateral orientations are observed for digits II and IV in *Picunichnus*, respectively, a condition that differs from the tracks studied. It should be noted that some characteristics of *Picunichnus* may be due to taphonomic artifacts resulting from the deformation generated in deep tracks formed on saturated substrates. In addition, *Picunichnus* presents the imprint of the digit I, which is unusual in the record. The autopodial anatomy of derived theropods evidences that digit I is dorsally located and, because of its small size, does not reach the lower half of the diaphysis of the metatarsals so it is generally not imprinted in the track. As suggested [4], we consider that what allowed the imprinting of digit I was due to the *Picunichnus* trackmaker walking on a saturated substrate.

On the other hand, some similarities with *C. canalei* are also observed, particularly with those preserved in Cerrito del Bote [2], which present low interdigital angles and digits II and IV relatively more elongated than those of *Picunichnus*. However, the material described here presents a digit IV considerably longer than digit II.

In this context, tracks described present differences with the known ichnotaxa and require a more detailed study. For this purpose, it is also necessary to analyze the pedal morphology of the available skeletal remains, in order to better understand which are the anatomical aspects and which are the taphonomic factors that modify the preserved morphologies.



Fig. 1. New trackway (MMPL-Pv12) composed of three tracks found at the Bajada de la Peta site (Picún Leufú, Neuquén, Argentina).



Fig. 2. Track H 2, corresponding to the right foot impression of the trackmaker of trackway MMPL-Pv12, a small-sized theropod; digits II, III and IV, claw impression (in III and IV), pads, heel and digit orientation are observed.

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THE FIRST RECORD OF PTEROSAUR FOOTPRINTS FROM PERU

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Pterosaur footprints were found in association with large theropod dinosaur footprints in a new locality, herein named Querulpa-2, that crops out closely to a widely known thematic park, at Querulpa Chico, Arequipa Department, southern Peru. Regarding the age, it seems to be located very close to the contact between the Late Jurassic (Tithonian) sediments of the Gramadal Formation and the Early Cretaceous (Berriasian) sediments of the Hualhuani Formation. Two different stratigraphic levels, preserving pterosaur and theropod footprints, are recognized (Fig. 1A). Pterosaur footprints are mainly represented by manus impressions (Fig. 1B-F), pes impressions are scarce, and trackways are apparent.

Manus have the typical pterosaurian configuration being tridactyl, with a short digit I, a slightly longer digit II, and digit III being the longest. Manus impressions, in the lower level, have a mean length of 6.6 cm and a mean width of 4.2 cm. The mean angle of divarication between digits I and II is 42.8° and between digits II and III is 52°. One manus seems to preserve a sharp and short claw impression in digit I (Fig. 1D). A small pterosaur hand is over impressed on a larger hand; it is perhaps suggestive of the presence of a mixed-age group of pterosaurs. Manus impressions in the upper level are slightly larger than those in the lower level; one measures 10.7 cm in length and 5.9 cm in width; in this case the angle of divarication between digits I and II is 19°, and between digits II and III is 60° (Fig. 1E).

There are few partial pes impressions; however, a complete one (Fig. 1G) is tetradactyl, with an elongate plantar area and a rounded heel. It is 8.9 cm in length, 1.3 cm in width at the heel area, and 2.9 cm at the widest anterior area. One of the digits, herein assumed as Digit I, is robust and bears a short sub-triangular claw, with a constriction at its base; the middle digits, II and III, are longer; digit II is robust as well, while digit III is slender with a rounded distal end; digit IV is short with a rounded distal end. Digit I is separated from digits II to IV by a wide, concave, hypex.

Currently, there are two pterosaurian ichnofamilies that include pterodactyloid footprints [1]; the ichnofamily Pteraichnidae includes the genera *Pteraichnus* Stokes (1957) and *Purbeckopus* Delair (1963), and the ichnofamily Agadirichnidae, includes the ichnogenera *Haenamichnus* Hwang et al. (2002) and *Agadirichnus* Ambroggi and Lapparent (1954). Agadirichnidae is defined based on large-sized footprints, with pes impressions ranging from 7.7-17.0 cm for *Agadirichnus*, and reaching 34.0 cm for *Haenamichnus*; pes impressions are long and slender, and manus impressions massive.

The conspicuous morphology, of the pterosaurian pes from Peru, with an elongated plantar impression, clearly differs from that present in the ichnospecies attributed to Pteraichnidae; however, it recalls the morphological traits of Agadirichnidae. Even more, this elongated pes morphology has been related to members of Azhdarchidae [2].

So far, the only non-dinosaurian vertebrate fossil footprints from the Mesozoic of Peru are related to Chirotheriidae [3]; in this way, it represents the first record of pterosaur footprints from Peru, and the second record from South America, preceded only by pterosaurian footprints recorded from the Cretaceous of Argentina [4,5]. The age for these footprints must be defined, however, at the moment, represents the oldest record of pterosaur footprints in South America.

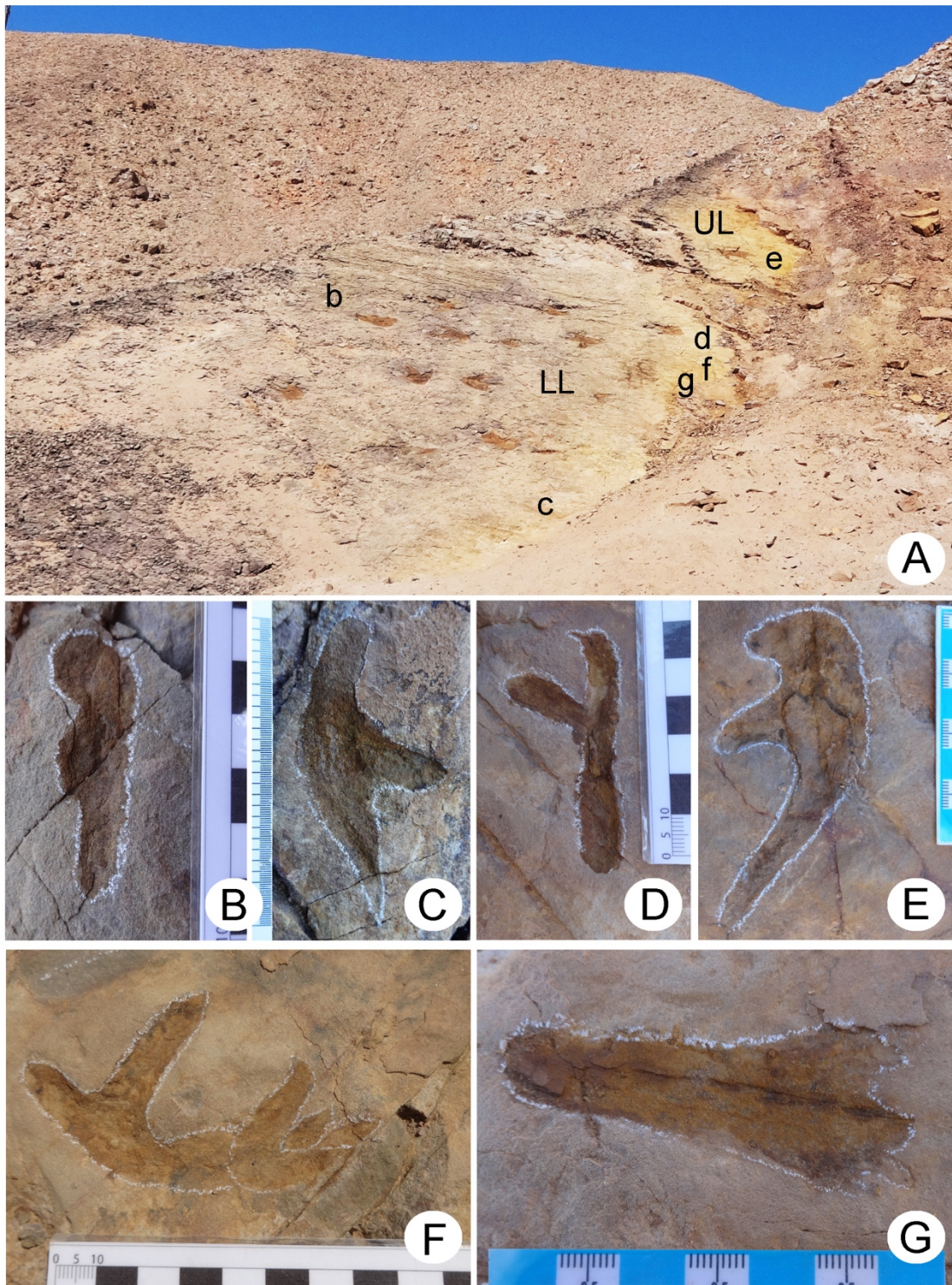


Fig. 1. A. Panoramic view of the new tracksite (Querulpa-2) in the Department of Arequipa, southern Peru, the most distinctive features on the surface are theropod footprints. B. Left hand with short digit impressions. C. Right hand. D. Left hand impression with a probable claw impression in digit I. E. Left hand impression from the upper level. F. Right manus impression overstep by a smaller right hand. G. Pes impression from the lower level. Abbreviations: b-g = approximate location of the footprints shown in B-G; LL, lower level; UL, upper level. Scales in centimeters.

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INTEGRATIVE ICHNOLOGICAL AND SEDIMENTOLOGICAL APPROACH: CONTOURITES AND PALEO-GATEWAYS RECONSTRUCTIONS

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Closing and opening of oceanic paleo-gateways have strongly influenced the tectono-stratigraphic and sedimentary evolution of basins, affecting global ocean circulation, climate, sedimentary processes, and living biota. Paleo-gateways govern the regional and global expression of first-order hydrological, climatic, and environmental changes, and are also critical for the exchange of water, heat, salt, and nutrients between oceans and seas. Areas adjacent to paleo-gateways tend to have the highest bottom current velocities and are therefore characterized by bottom current deposits (i.e., contourites) [^{1,2}], which record the oceanic gateways evolution. Better characterization of bottom current processes and deposits will therefore shed light on gateways evolution and related paleo-environmental (i.e., depositional and ecological) conditions.

The evolution of paleo-gateways determines variations in paleo-environmental conditions that affects trace maker communities and subsequently biogenic structures. With respect to paleo-gateways, bottom currents and their associated contourites deposits have been approached through trace fossil studies. In the last years, ichnological and sedimentological studies of contourites have increased significantly, demonstrating their relevance for the characterization and differentiation of these facies from other deepwater sedimentary facies [³⁻⁵]. Regardless of the consensus on the relevance of bioturbation in contourite characterization, ichnological data can advance the understanding of contourite sedimentary facies for a wide range of applications. In this context, an integrative ichnological and sedimentological approach proves to be a useful strategy for a better understanding of contourites and then paleo-gateways.

In this research examples of ichnological and sedimentological analyses on contourites are presented from the Late Miocene deposits in Morocco associated with the Rifian Corridor [⁶], and from late Eocene to middle Miocene deposits in Cyprus associated with the evolution of the nearby Indian Gateway [^{7,8}] to assess: (i) the role of deep-water ocean paleo-gateways in influencing benthic ecosystems and associated trace makers, and (ii) the strengths of ichnological analysis as a tool for improving knowledge about paleo-gateways.

During the Late Miocene, the Atlantic Ocean and the Mediterranean Sea were in part connected by the Rifian Corridor (Morocco). Outcrops from Morocco are associated with a contourite channel system related to the dense paleo-Mediterranean Outflow Water in the Rifian Corridor. Deposits consist of turbidites intercalated between deep-sea mudstones (i.e., hemipelagites and drift deposits), channelized sandstone contourite facies, and shallow marine sandstones. Contourites deposits in Morocco reveals that: (i) *Macaronichnus segregatis degiberti* abundance in sandier deposits was related to distance from the core of bottom currents in relation to changes in energy and organic matter availability [⁹], and (ii) ichnofacies distribution was controlled by Rifian Corridor paleogeography and paleo-MOW location [¹⁰].

In Cyprus, the opening of the nearby Indian Gateways influenced late Eocene to middle Miocene deep-marine deposition. Here, the outcrops provide a unique example of carbonate contourites, interstratify with pelagic/hemipelagic, turbidite, reworked turbidites and mass-transport deposits. Two long-term contourite depositional systems developed: a late Eocene system consisting primarily of finer-grained contourites, and a latest Oligocene to middle



Miocene system dominated by coarser-grained contourites. Results from these contourite deposits reveal: (i) ichnological features allow to identified variations in substrate consistency and minor hiatuses associated with intermittent bottom currents on the contourite bi-gradational sequence (i.e., muddy-sandy-muddy) [¹¹], and (ii) variations in ichnofabrics allowed the recognition of interactions between deep-water processes [¹²].

Thus, these two examples from contourites on Morocco and Cyprus demonstrate that integrative ichnological and sedimentological analysis represents a useful tool to discriminate deepwater deposits, to decode paleoceanographic processes and their variability, environmental and sedimentary changes, and to improve knowledge of the evolution of paleo-gateways. The ichnological analysis revealed a strong influence of food supply, flow velocity, and seafloor heterogeneity, and a high incidence of hydrodynamic energy, which affected trace maker communities during the evolution of paleo-gateways, bottom currents, and associated deposits (i.e., contourites).

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NEOGENE AND EXTANT CAPYBARA FOOTPRINTS: *PORCELLUSIGNUM CONCLUDATOR* REVISITED

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The vertebrate ichnotaxon *Porcellusignum concludator* Angulo and Casamiquela, 1982 was defined for the Neogene Río Negro Formation (Río Negro province, Argentina) and has been recognized with different criteria by several authors. The purpose of this contribution is to review the ichnotaxon to clarify its identification in the type area and formation, as well as to document additional findings in the Late Miocene Las Flores Formation (San Juan Province). In addition, the fossil material was compared with extant capybara footprints. In the original description [1] the ichnotaxon was characterized as isolated footprints, essentially tridactyl (not excluding some tetradactyl impressions), with punctiform digit imprints, connected by an arcuate segment, and approximately 10.5 cm long. However, subsequent studies [2,3] in the same unit recognized that this ichnotaxon shows tridactyl pes and tetradactyl manus prints. The pes is 8.5 cm long and 9 cm wide and the manus is 9.5 cm long and 10 cm wide. Additionally, these studies described the morphology as digitigrade and noted the presence of a rounded palmar impression. These tracks were assigned to Hydrocoeridae and are comparable to extant capybaras. In Argentina, the stratigraphic record of capybaras is documented since the Early Miocene [4].

This study was based on observations on *Porcellusignum concludator* from the type unit, the Río Negro Formation (Upper Miocene-Lower Pliocene). These trace fossils were documented in a sedimentary paleoenvironment of interdune lakes. Additionally, an analysis was conducted on footprints from the Museo de Ciencias Naturales, Universidad Nacional de San Juan (specimen PVSJ 855) from the Upper Miocene Las Flores Formation). This unit is essentially lacustrine. To compare with the fossil material, extant capybara footprints and trackways produced on sandy substrates were photographed.

The ichnotaxon is represented by abundant topotypic material including a single quadrupedal trackway composed by seven footprints and several isolated footprints or manus-pes sets. All the material was preserved in negative hyporelief. The 1.38 m long trackway was slightly curved, narrow (trackway breadth = 0.18 m) and composed of alternating tetradactyl manus and tridactyl pes prints, with the former in the left side and the latter on the right side. Manus prints were rotated inward (18°), whereas pes prints were roughly parallel to the midline. The manus are paraxonic and semiplantigrade to plantigrade, with four short digit imprints with blunt tips, and a rounded “heel”. Manus prints are wider than they are long, with an average length of 7.5 cm (n=14) and an average width of 9.3 cm. The average total divarication is 88°. The pes is functionally tridactyl and mesaxonic, although deeper footprints have a shallow imprint of a fourth digit. Pes prints are digitigrade to semiplantigrade with a shallowly imprinted rear end. Pes prints are slightly wider than long with an average length of 7.5 cm (n = 11) and average width of 7.8 cm (n= 13), and the corresponding footprint length/width ratio is 0.97. Average total divarication is 81° (n = 6). Footprints are commonly deeply set (Fig. 1A-B).

The specimen from the Las Flores Formation is a 50 cm long, straight, and narrow (15 cm wide) trackway composed of three consecutive manus-pes sets and two incomplete prints. The manus print exhibits an outward rotation of 20°, while the pes prints also show an outward rotation of 10°. Manus are paraxonic, semiplantigrade to plantigrade, with four short digits ending in rounded tips and a subrounded heel. The manus are wider than they are long, with an average



length and width of 4.1 and 6.2 cm, respectively. The total divarication is 150°. The pes are functionally tridactyl and mesaxonic. The pes are wider than they are long, with an average length of 5.4 cm and an average width of 6.1 cm. The average total divarication is 71°. Footprints are commonly deeply set (Fig. 1C). This material was referred to a mammal of the family Hegetotheridae [5].

Extant capybara footprints included up to 300 cm long and 30 cm wide trackways and isolated manus pes sets. The trackway consists of manus-pes pairs, with the manus positioned behind the pes. The manus impression exhibits an outward rotation of 6°, while the pes impressions also show an outward rotation of 20°. The manus print is paraxonic and plantigrade and have four short digits with rounded tips and a subrounded heel. In general, the digits are connected to the palm pad, with the greatest depth of the impressions observed in the palm pad and the distal region of digits III, IV, V. In contrast, digit II is disconnected from the palm pad and is shallower, sometimes are absent. The manus print is wider than long, with an average length and width of 9.5 and 11.8 cm, respectively. The total divarication is 126°. The pes print is functionally tridactyl and mesaxonic, with a notch in the posterior margin. In general, the digits are discontinuously connected to the palm pad. The greatest depth of the footprints is observed in the palm pad and the distal region of digits II, III, and IV. The pes print is slightly wider than long, with an average length of 11.2 cm and an average width of 11.3 cm (Fig. 1D).

Comparison of material of *P. conculcator* from the type area, similar material from the San Juan Province, and extant capybara footprints, reveals morphological similarities, suggesting a common or related producer. All of them exhibit an organization in manus-pes pairs, composed of tridactyl pes and tetradactyl manus prints. Additionally, the manus shows a rounded heel with short digits that have rounded distal terminations. Another shared characteristic is the ratio of length to width of the footprints, always wider than long. In both feet and hands, this ratio is approximately 0.94 and 0.77, respectively. Notable differences are identified, such as divarication, foot postures (plantigrade-digitigrade), and posterior foot morphology (rounded in the fossil record vs. concave in the present). These differences are likely strongly influenced by the type of substrate in which the organism left its traces. Fossil footprints are typically found in lacustrine mudflats (high water saturation), while fresh footprints are found in sandy substrates with lower water saturation. These substrate characteristics could have affected the stability of the producer, influencing its posture, depth of prints, variation of the interdigital angle, and consequently, the formation of the footprints. Dimensional differences can possibly be attributed to a change in producer size, either due to different ontogenic stages or generic differences.

The combination of morphological features such as a quadrupedal trackway, coexistence of tridactyl and tetradactyl footprints, rounded palmar pads, and digits with rounded and deep distal ends in a swampy sedimentary environment are distinctive features of *Porcellusignum conculcator*. The most likely producer is an organism belonging to Hydrocoeridae. In addition, features such as foot posture, divarication, and the registration of digit II suggest different forms of adaptation and behavior of the producer, depending primarily on the type of substrate it inhabits.

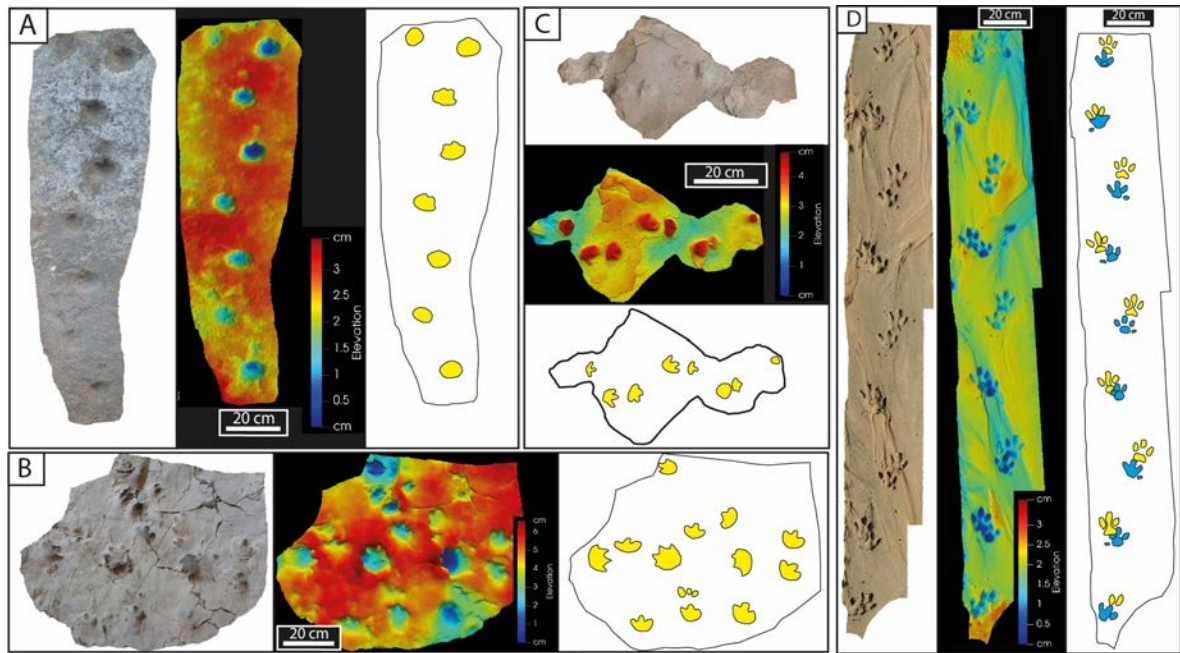


Fig. 1. A-B. Orthomosaic, digital elevation model and interpretative diagram of *Porcellisignum conculcator* from the Rio Negro Formation. C. Orthomosaic, digital elevation model, and interpretative diagram of *Porcellisignum* isp. from Las Flores Formation. D. Digital elevation model and interpretative diagram of extant capibara footprints.

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**BIOEROSION IN *PACHYCYMBIOLA BRASILIANA* (LAMARCK, 1811)
SHELLS FROM THE RIO GRANDE DO SUL COASTAL PLAIN
(QUATERNARY)**

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Bioerosion, i.e., the breakdown of hard substrates by organisms, is a major structuring force that modifies past and present ecological communities and ecosystem functions [1]. Because of that, it is a useful tool for studies on paleoclimatic, paleoceanographic, and changes in productivity [2]. *Pachycymbiola brasiliiana* is one of the most common gastropods in southern Brazil, being recorded in subtropical fossil deposits from the Pleistocene and Holocene [3]. Its distribution covers the coastal area between Rio de Janeiro, Brazil and Río Negro, Argentina, (23°S and 41°S) [4,5], inhabiting shallow waters from 8 to 70 m deep, frequently appearing in shallower waters, or even on the beach, when hundreds of live specimens and shells are swept away by storms [4,6]. It is common for studies about bioerosion preserved in mollusc shells from the South Atlantic to report their presence in *P. brasiliiana* [7-11]. However, there is no study that characterizes ecological interactions between bioeroders and *P. brasiliiana*. The only information about its ecology is that it is a carnivorous species, mainly predated bivalves [12]. The aim of this study is to characterize the bioerosion structures found on *P. brasiliiana* from Rio Grande do Sul Coastal Plain (RSCP). The study is based on 380 *P. brasiliiana* shells were collected together in a shell accumulation at the Cassino Beach. The shells are deposited in the LGP (Laboratório de Geologia e Paleontologia, Universidade Federal do Rio Grande - FURG). Cassino is a dissipative beach and the increase in wave energy during storms reworks fossils and shells from the paleolines of beaches drowned during the Holocene transgression [13,14], which occasionally promotes the deposition of shell banks on the beach. *P. brasiliiana* is often present in these shell accumulations. The shells were examined with the naked eye and with the aid of a stereoscopic microscope to identify bioerosion structures at the ichnogenus level. Seven ichnogenera from two different ethological categories were identified (Fig. 1). The same shell frequently has more than one bioerosion structure. In some cases, the same shell presents more than one ichnogenus (Fig. 1D-G, J-K). Only 24% of the shells do not have bioerosion structures. The most abundant ethological category was dominichia (Table 1), which bioerosion attributed to dwelling of filter-feeding and detritivorous organisms. The most common trace fossil found on *P. brasiliiana* is *Caulostrepsis*, occurring in 73% of the shells (Table 1). This abundance has never been found in *P. brasiliiana* before. *Entobia* is usually very common in *P. brasiliiana* [11], but in this sample its presence corresponds to only 3,15% of the shells. This study presents preliminary results of an ongoing master's degree research. Because of this, more analyzes are needed to make inferences about ecological relationships with *P. brasiliiana*.

Table 1. Bioerosions found in *P. brasiliiana* from CPRS, ethological category, ichnogenus, producers, and presence in the sample.

Ethological Category	Ichnogenus	Producer	Presence in the sample (n=380)
Domichnia	<i>Caulostrepsis</i> (Clarke, 1908)	Spionid polychaetes	278 (73%)
	<i>Iramena</i> (Boekschoten, 1970)	Ctenostomate bryozoans	78 (20.52%)
	<i>Gastrochaenolites</i> (Leymerie, 1842)	Mytilidae bivalves	16 (4,21%)
	<i>Entobia</i> (Bronn, 1838)	Clionid sponges	12 (3,15%)
	<i>Pennaticismus</i> (Mayoral, 1988)	Ctenostomate bryozoans	11 (2,89%)
Fixchnia	<i>Finichnus</i> (Taylor, 2012)	Cheilostome bryozoans	3 (0,78%)
	<i>Podichnus</i> (Bromley & Surlyk, 1973)	Pedunculate brachiopods	1 (0,26%)

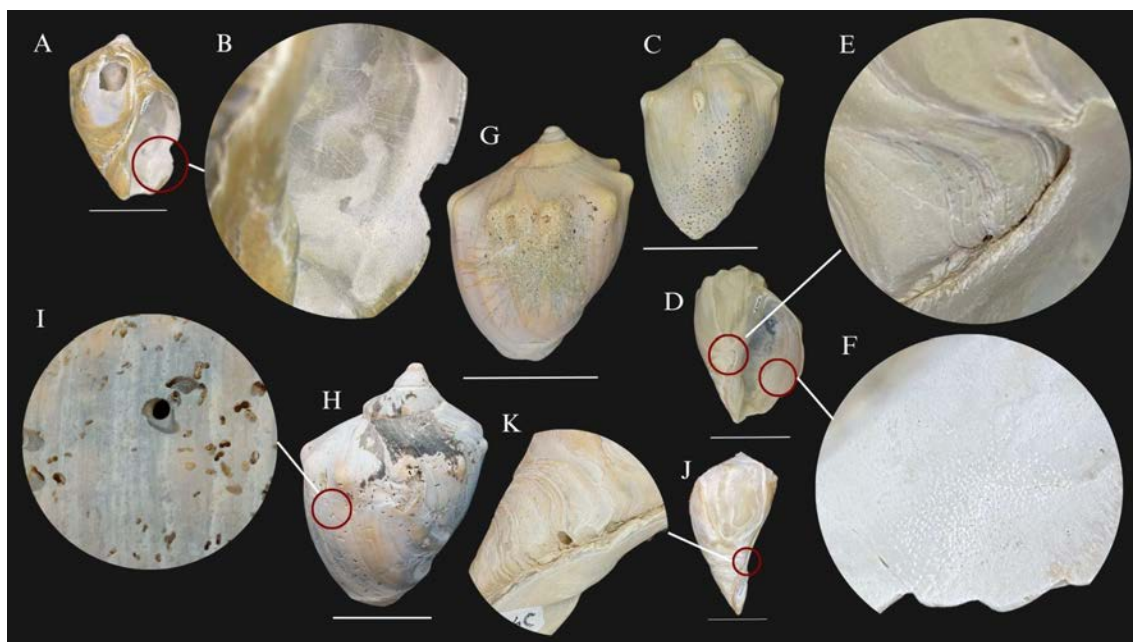


Fig. 1. Bioerosion structures found on *P. brasiliiana*. A-B. *Finichnus* (sample LGPW2748F). C. *Entobia* (sample LGPW2751D). D-F. *Podichnus* and *Pennaticismus* (sample LGPW2751G). G: *Iramena* and *Caulostrepsis* (sample LGPW2743K). H-I. *Gastrochaenolites* and *Caulostrepsis* (sample LGP2775K). J-K. *Gastrochaenolites* (sample 2744E). Scale bars = 5 cm.

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PLANT-ARTHROPOD AND PATHOGEN INTERACTIONS IN NORTH-CENTRAL GONDWANA

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Permian plant-arthropod interactions in Brazil are reported on leaves and seeds from the Permian Cisuralian to Guadalupian [¹⁻⁴]. The Paraná Basin is the only Permian basin in Brazil that has a record of these interactions. Nevertheless, the Parnaíba Basin, located in northern Brazil, shows an extraordinary record of Permian plants [⁵] and, consequently, constitutes potential material to find plant-arthropod interactions. This study aims to report for the first time arthropod herbivory and pathogen interactions in early Permian plant fossils recovered from the Pedra de Fogo Formation, located in the Parnaíba Basin. The study material is deposited at the fossil collections of the University of São Paulo at Ribeirão Preto (São Paulo State) and the Federal University of Piauí (Piauí State). All specimens were examined under a stereomicroscope to identify the host morphotaxon, and to evaluate the presence of damage. We used the *Guide to Insect (and Other) Damage Types on Compressed Plant Fossils* [⁶] to identify the presence of herbivory. As a result, 399 specimens were analyzed, including callipterid seed fern and fern fronds, sphenopsid stems and leaflets, seeds, and woody stems, all preserved as impressions. The most abundant taxon was *Rhachiphyllum* sp. with 143 specimens, followed by sphenopsid stems with 85 specimens. We found 22 specimens with at least one instance of herbivory, representing 5.51% of the plant assemblage, and 28 damage occurrences. In southern Permian localities from the Paraná Basin, the frequency of damage reaches up to 8% of the assemblages [^{7,8}], consistent with our findings. Herbivory was observed in 19 *Rhachiphyllum* sp. fronds, two woody stems, and one sphenopsid stem. In total, we recorded seven functional feeding groups (FFGs) consisting of margin feeding, surface feeding, skeletonization, piercing and sucking, galling, borings, and pathogens (Table 1). Whereas other researchers found oviposition and seed predation [^{3,7}] in Paleozoic floras, this study did not find any record of these FFGs. A total of 13 damage types (DTs) were identified, of which the most abundant were margin feeding DT13 and DT12, and galling DT80 (Table 1) that varied from 14.28% to 17.86%. Other damage types were less frequent with less than 10.71%. Other Paleozoic plant assemblages in Gondwana also had an elevated number of DT12 and DT13 [^{7,9,10}]. The present study will contribute to an understanding of the differences in herbivory from different regions in Gondwana by comparing the results obtained from a north-central Parnaíba Basin with ones from a southeast Paraná Basin, in Brazil.



Table 1. Functional feeding groups and damage types found at the plant assemblage from the Pedra de Fogo Formation.

Functional Feeding Group	Damage Type	Damage occurrences	Percentage
Margin Feeding	DT12	4	14.28%
	DT13	5	17.86%
	DT14	2	7.15%
MF Total		11	
Surface Feeding	DT103	1	3.57%
	DT108	1	3.57%
SF Total		2	
Skeletonization	DT16	1	3.57%
SK Total		1	
Piercing and Sucking	DT183	1	3.57%
	DT46	3	10.71%
	DT48	2	7.15%
PS Total		6	
Galling	DT80	5	17.86%
	DT87	1	3.57%
GA Total		6	
Pathogens	DT174	1	3.57%
PA Total		1	
Borings	DT284	1	3.57%
WB Total		1	
Grand Total		28	100%

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PALEOENVIRONMENTAL INSIGHTS FROM THE PURGATOIRE DINOSAUR TRACKSITE (MORRISON FORMATION, USA): A STUDY OF BED 1

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^{3†} In Memoriam

The Purgatoire dinosaur tracksite in southeastern Colorado is a key site for unraveling dinosaur behavior in carbonate wetland settings of the lower Morrison Formation. At the Purgatoire dinosaur tracksite, several bedding plane exposures (Beds 1–4) hold > 2,000 dinosaur footprints contributing to our global Late Jurassic ichnological heritage [^{1,2}]. In this study, we focus on the investigation of the lowermost track-bearing unit, Bed 1. This track-bearing bed, in conjunction with the associated sedimentology and body fossil evidence, paints a picture of a larger lacustrine setting. Previously, it was described as a trample ground with the interaction between sauropods and unionid bivalves [¹]. Here, we clarify these relationships and detail new evidence of invertebrate activity and the interaction between plants and animals adjacent to a lake shoreline.



Fig. 1. Oblique view of the section at the Purgatoire site (co-authors as scales on Bed 1)

Purgatoire Bed 1, analyzed through sedimentological and ichnological techniques, reveals tabular, laterally continuous, massive bioclastic wackestones overlying thin, laminated dark shales, suggesting a wetland-lake system. The sedimentological features, along with charophytes and various body fossils (fish remains, unionid bivalves, gastropods, conchostrachans), align with this classification. However, rootlet traces, vadose silt, and microkarstification (via thin-section analysis) indicate periodic subaerial exposure and partial



pedogenesis. During the latter times, the presence of sauropod and tridactyl tracks and trackways are recorded across the unit and indicate animals utilizing the lake shoreline.

Sauropod tracks attributed to *Parabrontopodus* isp. exhibit convex epireliefs lacking anatomical fidelity or deep 'dinoturbations', infilled with wackestone, and disrupting laminated shales. Dinoturbation structures average 22 cm in depth and are noticeable in cross-sectional reliefs. Preservation in Bed 1 is impacted by both substrate consistency and plants, with the latter appearing now as fragmentary impressions of Sphenophytes (*Equisetum* sp.) associated with sauropod tracks. Unionid bivalves are found in association with Bed 1 sauropod tracks. Despite a limited sample area and the unionids not being in typical life positions, the absence of crushing or breakage, and no orientated dispersion, suggests they were unlikely to be trampled or pushed by sauropods directly. Tridactyl traces (concave epireliefs), attributed to *Megalosauripus* isp., were discovered on Bed 1. Only a single track had been previously reported and considered similar to Morrison theropod footprints at Higbee and Fruita tracksites [1]. Additionally, newly discovered invertebrate burrows in Bed 1, resembling *Camborygma* isp., are also documented and highlight the diversity of organisms bioturbating Bed 1.

In conclusion, the study of Bed 1 at the Purgatoire dinosaur tracksite adds valuable insights into the paleoenvironmental dynamics of a shallow lacustrine setting during the Morrison Formation times. The diverse biota and their associations contribute significantly to our understanding of this ecosystem.

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ICHTNOLOGIC ANALYSIS OF THE PINDAMONHANGABA FORMATION: SIGNATURE OF A MEANDERING FLUVIAL SYSTEM DOMINATED BY ARTHROPOD COLONIZATION

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The Taubaté Basin is located in the Central Segment of the Southeast Brazilian Rift Continental System (RCSB) and presents itself as an elongate, depressed feature with a maximum dimension of 170 km in the eastern state of São Paulo. The basin's sedimentation originated typically from continental processes and underwent pre-rift (Paleogene) and post-rift phases. The sedimentary sequence of the Taubaté Group includes the Resende Formation, deposited in alluvial fan environments associated with braided fluvial systems; the Tremembé Formation, featuring a shallow lake environment (with an increase in water depth towards the top); and the São Paulo Formation, with deposits of meandering fluvial systems, representing the syn-rift sequence. Above these, there is the Pindamonhangaba Formation, characterized by meandering fluvial systems and post-rift sedimentation. Although well studied from a sedimentological perspective, the units of this basin have not previously been analyzed from an ichnological view. The objective of this study is to characterize the ichnoassociations of the Pindamonhangaba Formation using a paleoecological approach. To achieve this, a literature revision was conducted, followed by field data collection, including the creation of a sedimentological section at a 1:20 scale and the description of *in-situ* trace fossils. The study area is an outcrop in the city of Taubaté. A section approximately 33 m thick was analyzed, predominantly composed of muddy facies with pedogenized features intercalated with sandy bars. In the bars, simple trace fossils, either vertical or horizontal, predominate, attributed to *Skolithos* and *Palaeophycus* respectively. The suite of paleosols is more diverse, with simple structures present (*Skolithos* and *Palaeophycus*) as well as structures exhibiting horizontal to inclined excavation with meniscate filling, with or without an evident wall, attributed to *Beaconites* and *Taenidium* respectively. At the top of the section, dense and grouped, vertically oriented excavations occur, attributed to *Termitichnus*. The occurrence of meniscate trace fossils associated with simpler ones in a suite of low diversity is a typical expression of the *Scoyenia* ichnofacies. On the other hand, the relatively low diversity of structures produced by termites suggests the *Termitichnus* ichnofacies for the top of the section. In this regard, the transition from *Scoyenia* to *Termitichnus* ichnofacies indicates higher relative humidity within the paleosols at the top of the section [1], potentially influenced by climatic improvement during the Miocene.

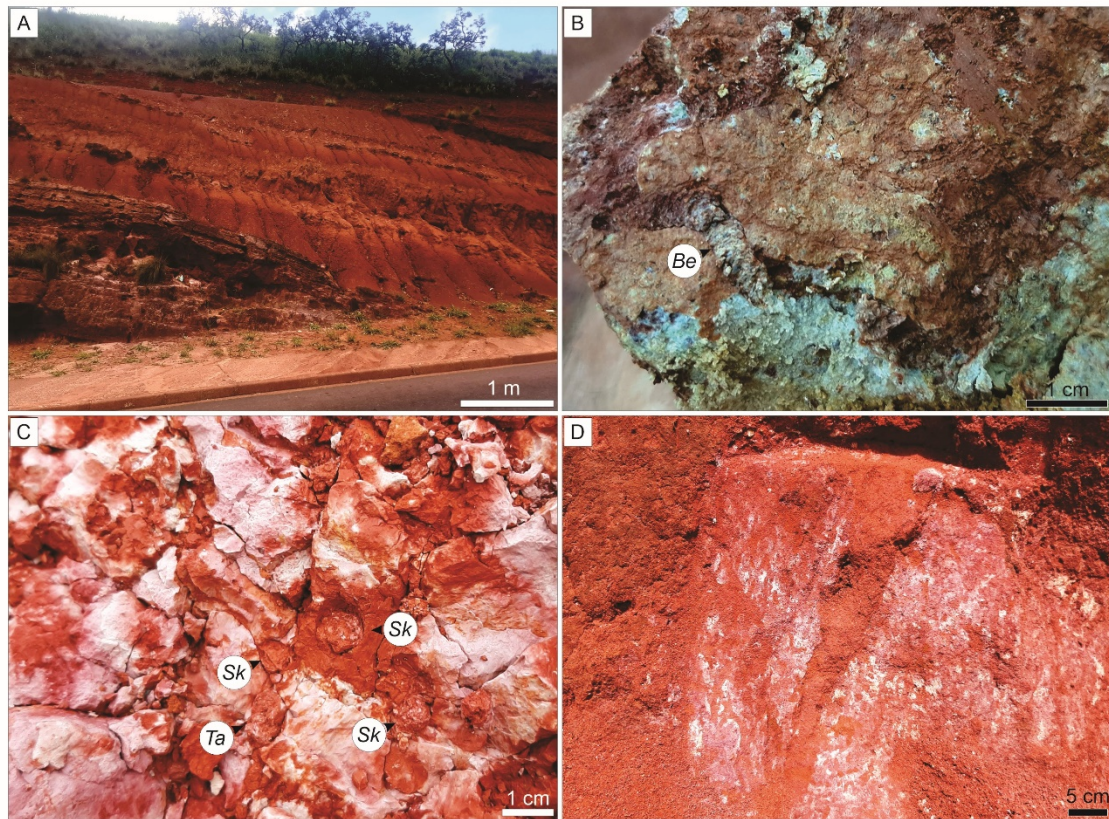


Fig. 1. Trace fossils from Pindamonhangaba Formation. A. General view of studied outcrop. B. Detail of *Beaconites* (*Be*). C. Detail of *Skolithos* (*Sk*) and *Taenidium* (*Ta*). D. General view of dense burrows ramifying from a central shaft, attributed to *Termitichnus*.

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NEOICHOLOGICAL ANALYSIS OF MOLE CRICKET BURROWS: IMPLICATIONS OF SUBSTRATE MOISTURE CHANGES ON PRESERVATION AND MORPHOLOGY

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The morphology and architectural design of trace fossils are strongly influenced by substrate characteristics, organism anatomy, and burrowing behavior. In this study, we explore the influence of substrate moisture on preservation variants of horizontal to subhorizontal mole cricket burrows and discuss its correspondence to previously described ichnogenera. Field observations were conducted on clayey and sandy substrates; burrows were described and photographed *in situ*, and laboratory analyses were performed on collected samples to better visualize the morphologies. Mole cricket burrows consist of branched, straight to sinuous tunnels with circular to semicircular cross sections, and exhibit distinctive features on the inner walls that are influenced by substrate moisture and texture (Fig. 1). Morphotypes were identified based on substrate characteristics, including well-developed pelletized roofs, subtle scratch traces, collapsed roofs, and lateral fringes. Understanding the impact of substrate moisture changes on the preservation and morphology of mole cricket burrows is essential for interpreting trace fossils in paleoenvironmental reconstructions. Mole cricket burrows share similarities with *Sphaerapus*, influenced by substrate conditions and digging behavior, though *Sphaerapus* lacks scratch traces present in mole-cricket burrows. In contrast, *Protovirgularia*, found in various environments, result from the rhythmic locomotion of cleft-foot protobranch bivalves, producing chevron-shaped trails anchored within sediment layers. The basal portion of the mole cricket burrow can resemble *Protovirgularia* if the burrows are produced (i) in plastic substrates and have the pelletized roofs eroded, and (ii) in muddy substrates when the burrow reaches the underlying sandy level (Fig. 2). Besides providing insights into the modes of preservation and substrate conditions of mole cricket burrows, this study also compares their preservation variants with those of *Protovirgularia* and *Sphaerapus*.

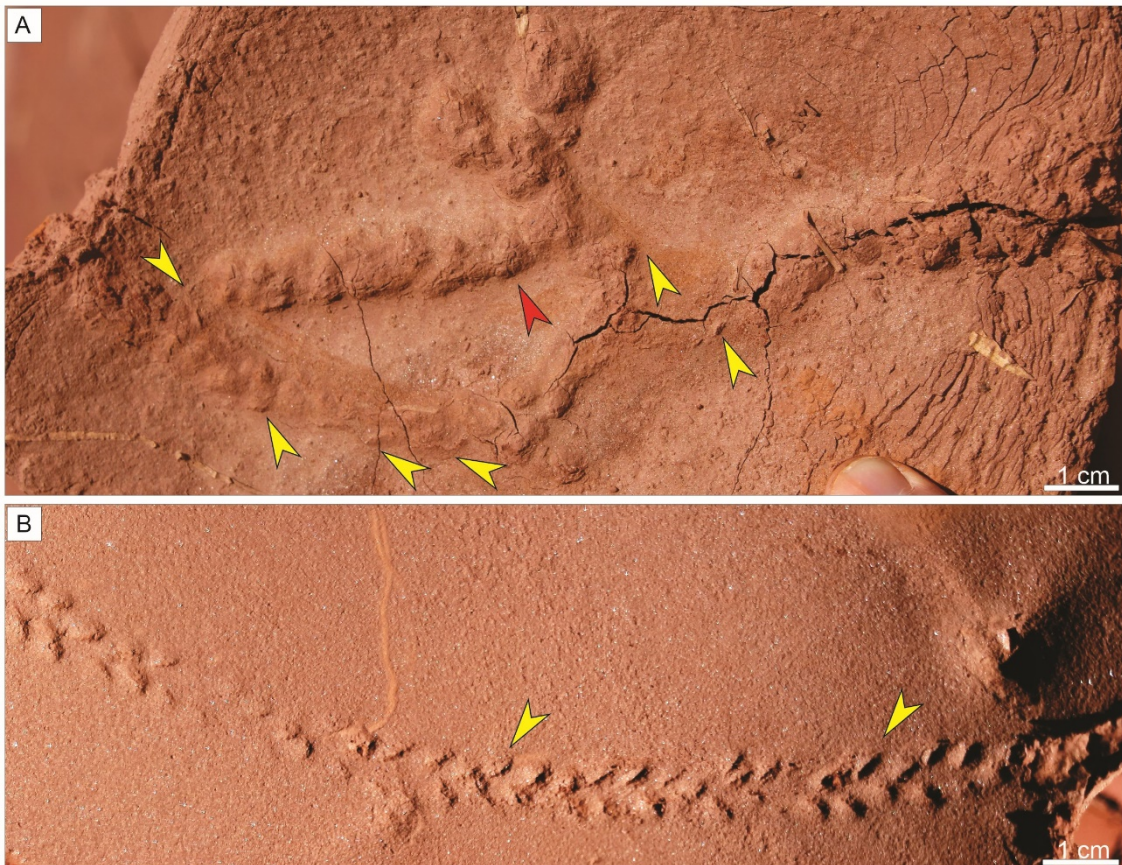


Fig. 1. Mole cricket burrows in a modern lake margin. A. The three-dimensional structure with variable levels of depth in the substrate; yellow arrows highlight deeper positions of the burrow, while the red arrow indicates shallower full relief structures. B. Undertrace (eroded ruff) of the mole cricket burrow, generating a structure that resembles a trail with well-developed chevron-like pattern, forming acute angles towards the burrow's main axis (yellow arrow).

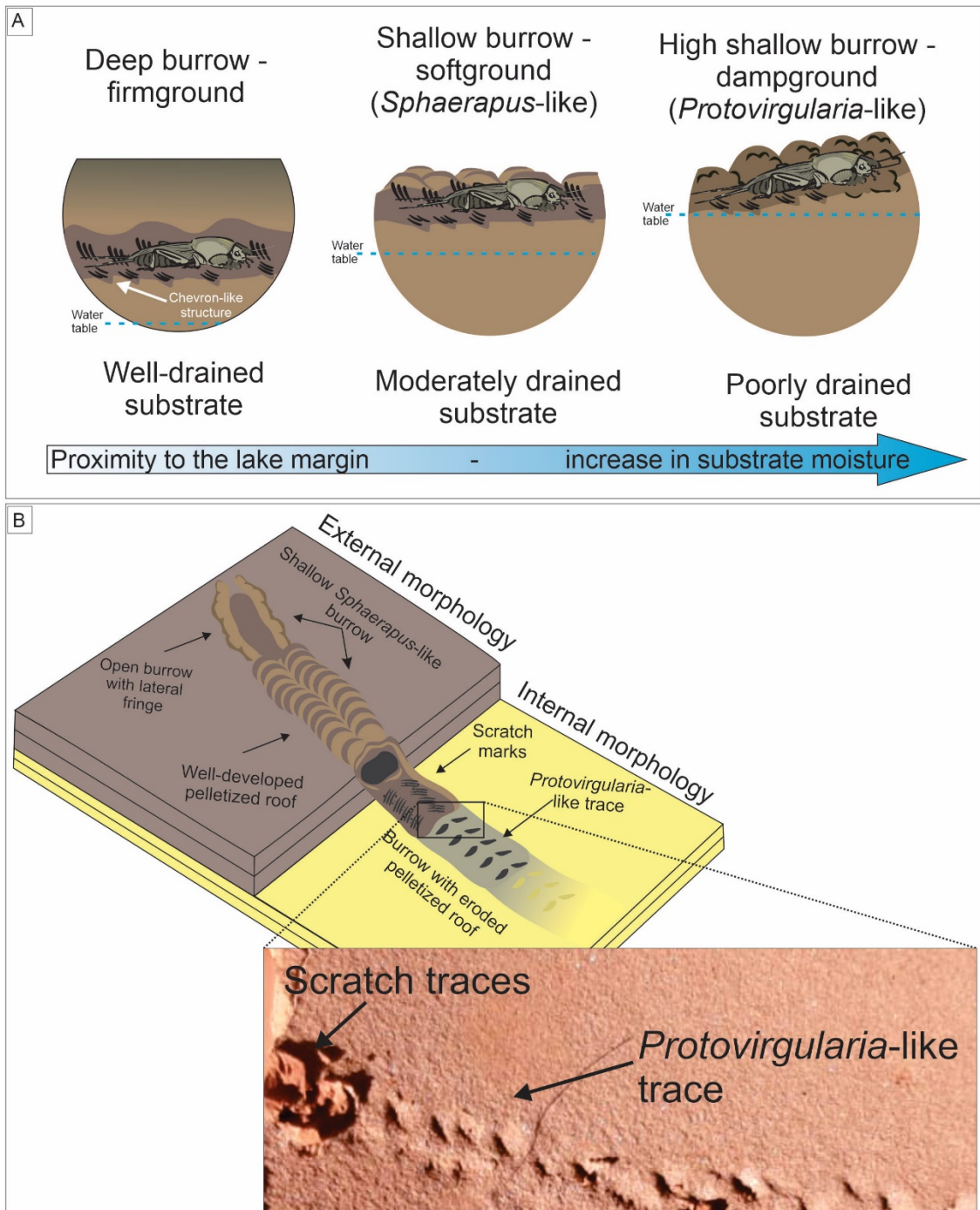


Fig. 2. The role of substrate properties in controlling mole cricket burrow morphotypes. A. Distribution of different morphotypes in relation to moisture at lake edges; note that the chevron-like pattern (*Protovirgularia*-like) can be preserved in well drained or poorly drained settings, depending on the depth of the burrow. B. Relationships between different preservational morphotypes and their similarities with *Protovirgularia* and *Sphaerapus*; note that the *Sphaerapus* morphology correspond to the tree-dimensional burrow, while the *Protovirgularia* morphology is the negative epirelief of the burrow's bottom.



ICHTNOLOGICAL ANALYSIS AND PALEOENVIRONMENTAL INFERENCES OF THE NEOGENE MEANDERING FLUVIAL DEPOSITS (FLORIANO FORMATION, SE BRAZIL)

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The sedimentary basins in the “Continental Rift of Southeastern Brazil” (CRSB) provides an opportunity for ichnological analyses due to its well-established facies relationships and paleoenvironmental interpretations. This study reports invertebrate trace fossils from the Neogene fluvial deposits (Floriano Formation) and applies integrated ichnological and facies analyses to reconstruct the environmental conditions recorded in this lithostratigraphic unit. Fieldworks revealed a rich ichnofauna in the Floriano Formation, whose facies associations have been interpreted as indicative of meandering river environments. Four sedimentary facies were identified, including bioturbated sandstone, horizontally stratified sandstone, laminated sandstone, and mudstone. Six ichnogenera were identified, *Arenicolites*, *Beaconites*, *Camborygma*, *Palaeophycus*, *Skolithos*, and *Taenidium*. Those ichnogenera occur as *Skolithos*, *Taenidium*, and *Beaconites* ichnocoenoses. The *Skolithos* ichnocoenosis is primarily represented within sand bar deposits, indicating arthropod colonization in abandoned channels. The *Taenidium* ichnocoenosis, observed within mudstone layers and presenting *Camborygma* burrows, suggests transitional environments between aquatic and subaerial conditions, locally with high-water table levels. The *Beaconites* ichnocoenosis indicates changes in substrate consistency associated with progressive desiccation and extended exposure time. Therefore, the identified ichnocoenoses, combined with the analysis of physical sedimentary structures suggest generally humid conditions during colonization by invertebrates of the meandering river deposits of the Floriano Formation.

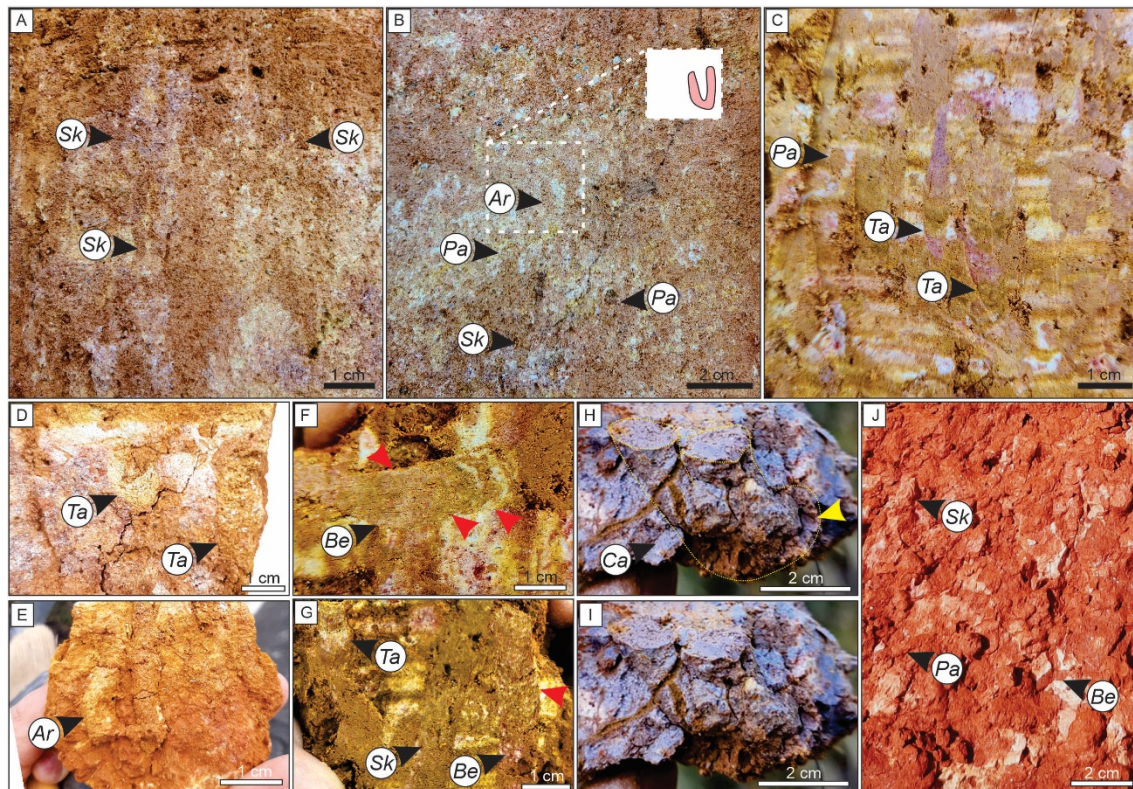


Fig. 1. Trace fossils from the studied section. A-B. The *Skolithos* ichnocoenosis with *Skolithos* (*Sk*), *Arenicolites* (*Ar*), and *Palaeophycus* (*Pa*). C-I. The *Taenidium* ichnocoenosis with *Taenidium* (*Ta*), *Beaconites* (*Be*), and *Camborygma* (*Ca*) – the yellow arrow indicated the lateral chamber. H. The *Beaconites* ichnocoenosis with *Skolithos* (*Sk*), *Beaconites* (*Be*), and *Palaeophycus* (*Pa*).

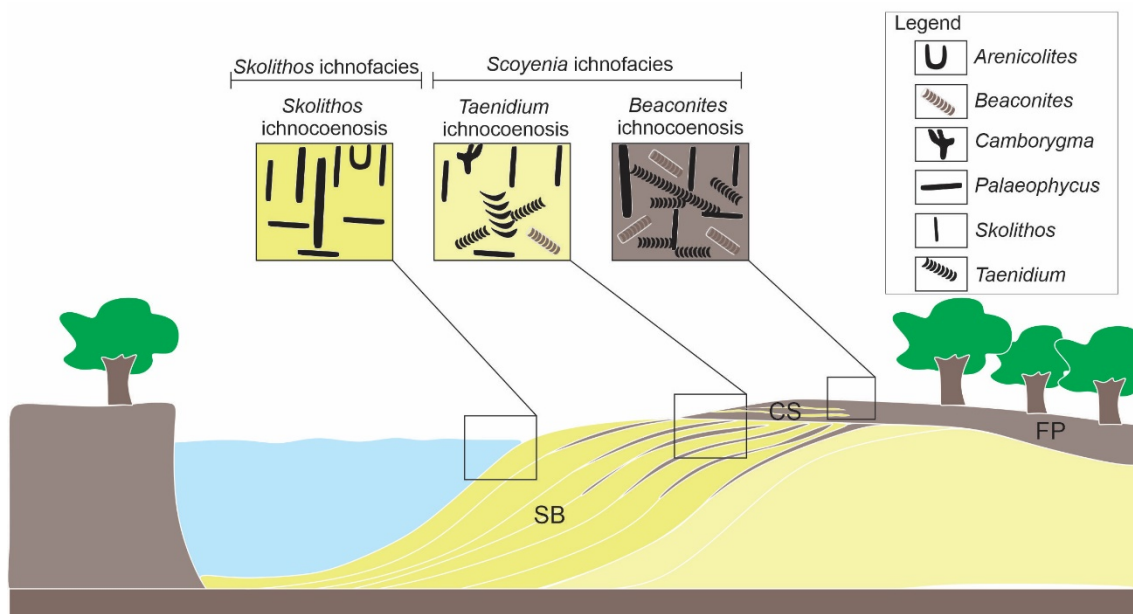


Fig. 2. Idealized distribution of the ichnocoenoses in the meandering river system represented by Floriano Formation, Resende Basin. Abbreviations: SB = sand bars; CS = crevasse splays; FP = floodplain mudstones.



MULTIPLE-*RUSOPHYCUS* ASSEMBLAGE FROM THE PARNAÍBA BASIN (NE BRAZIL) REFLECTS TRILOBITES AS TRACEMAKERS AND THEIR MOLTING BEHAVIOR

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Trilobites inhabited most environments of Paleozoic seas, ranging from estuaries to continental slopes, and were globally distributed. Although their functional morphology and phylogenetic relations are established by well-preserved body fossils, the behavior of trilobites has received less attention. Three well-known trace fossils are interpreted to be produced by trilobitomorphs when preserved in Paleozoic rocks, *Rusophycus* (a resting trace), *Cruziana* (a furrowing trace), and *Diplichnites* (a locomotion trace). Those trace fossils unveil some aspects of trilobite behavior, but they were not investigated to test paleoecologic strategies based on morphometric parameters. This study uses *Rusophycus* to investigate the paleoecologic strategies of trilobites in storm-dominated shallow marine deposits of the Pimenteira and Cabeças formations (Middle to Upper Devonian, Parnaíba Basin, Brazil). A detailed analysis of *Rusophycus* was conducted in a section that represents the transition between the Pimenteira and Cabeças formations (Parnaíba Basin). The width and length of the *Rusophycus* were measured, and statistical analyses were performed to understand the population characteristics. Relatively small-sized *Rusophycus* are dominant in these deposits, suggesting the dominance of young tracemakers and inferred r-strategist populations. The here reported multiple-*Rusophycus* assemblage reveals paleoecologic strategies of the population, crosscutting relationships with shallow-tier trace fossils such as *Bergaueria*, *Palaeophycus*, and *Protopaleodictyon* (Fig. 1) suggest that *Rusophycus* is a deep-tier burrow. The main reason for deep burrowing might be protection during ecdysis. Thus, the random distribution, lack of hunting evidence, and depth of *Rusophycus* suggest molting activity in storm-influenced deposits of the Pimenteira Formation, probably by calmoniids or homalonotids (Fig. 2).

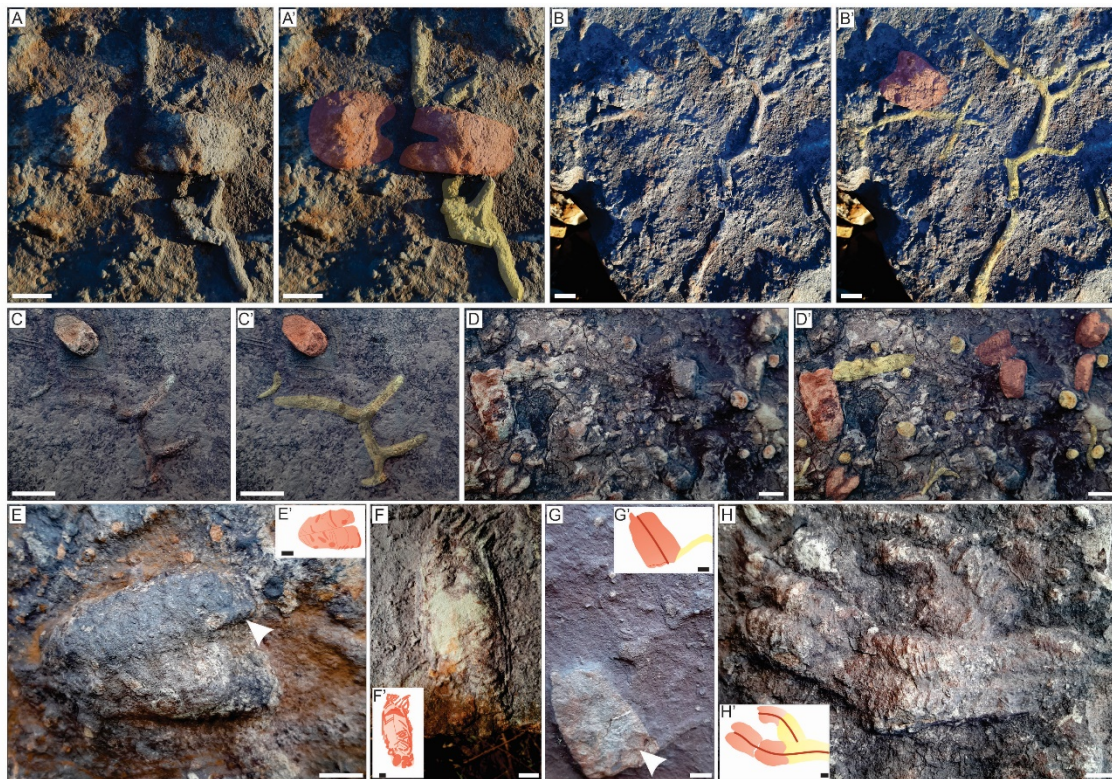


Fig. 1. Details of *Rusophycus* from the studied section. A-C, A'-C'. *Rusophycus* (highlighted in red) in association with *Protopaleodyction* (highlighted in yellow). D-D'. *Rusophycus* (highlighted in red) in association with *Bergaueria* and *Palaeophycus* (highlighted in yellow). E-G, E'-G'. Detail of the morphology of *Rusophycus*. *Rusophycus* also overlaps *Palaeophycus* (white arrow) in E-G. H-H'. *Rusophycus* (highlighted in red) in association with *Cruziana* (highlighted in yellow). Scale bars = 2 cm.

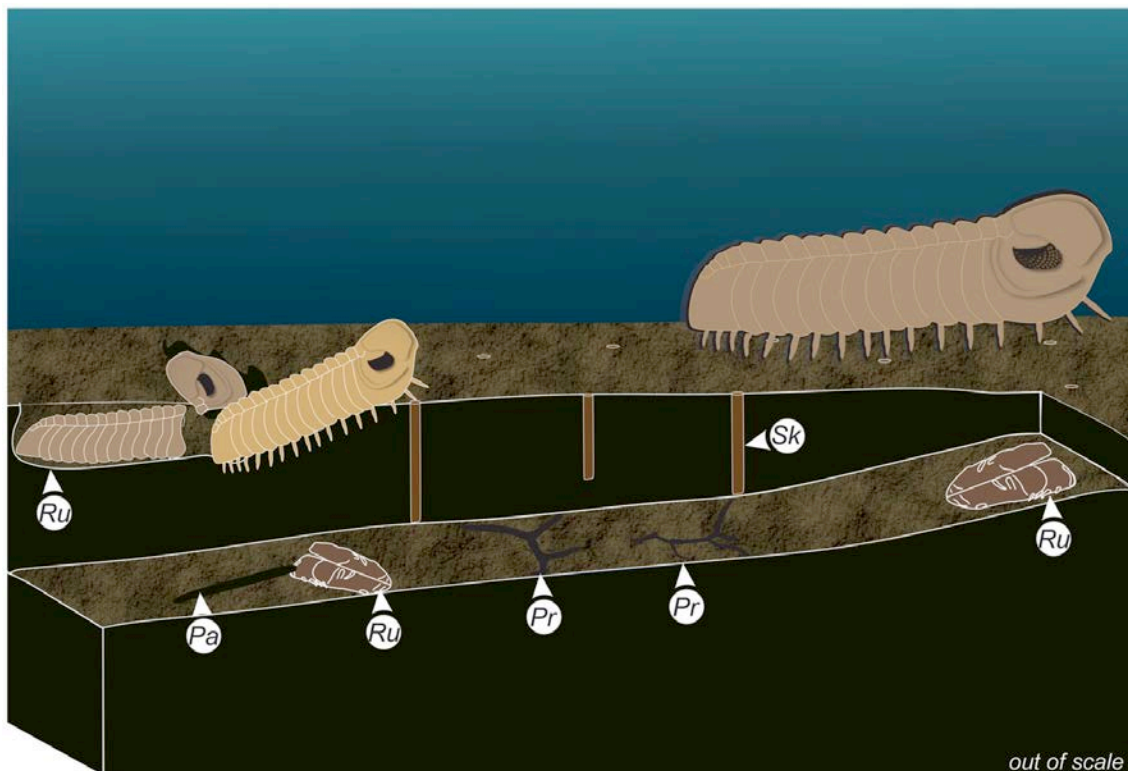


Fig. 2. Reconstitution of the molting strategy of trilobites while producing *Rusophycus*, and tier relation of commonly associated trace fossils. *Pr*, *Protopaleodyction*; *Ru*, *Rusophycus*; *Sk*, *Skolithos*.



NEOICHOLOGY ON MARINE DEPOSITS – BEACHES, SHOREFACES, AND DEEP-SEA FLOORS

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Biological sediment mixing, or bioturbation, is one of the most critical controls on biogeochemical cycling and vertical sediment redistribution in seafloor environments. Analysis of modern bioturbation structures also provides useful information on the paleoecology of trace fossils. Here, I present some of our neoichnological achievements on temperate beaches, shorefaces, and deep-sea floors.

Sandy beaches: this environment is characterized by deposit-feeding traces of opheliid polychaete (modern counterpart of *Macaronichnus*) and burrow of ghost crabs (modern counterpart of *Psilonichnus*). The vertical distribution range and shape of *Macaronichnus* represent sea-level [1] and beach morphodynamics (erosion and deposition states) [2], respectively. The presence of *Macaronichnus* on beaches of the tropical region can be used as an indicator of the upwelling of cold, nutrient-rich waters [3].

Shoreface: Burrows of the upogeniid shrimps (modern counterparts of *Ophiomorpha* and *Parmaichnus*) densely occur in the lower shoreface setting (water depth: >8 m). The burrow's dense occurrence means intensive filter-feeding of the tracemaker, affecting coastal water column conditions [4]. Burrows of the spatangoid echinoderm (modern counterparts of *Bichordites*) are also common in the shoreface with a small impact of freshwater discharge [5]. Burrows of the garden eel, such as *Gorgasia taiwanensis*, are seen on the sandy seafloor, where a constant bottom current occurs [6].

Deep-sea floor: This environment is well known for geometrical complex traces [7]. The deep-sea bandfish *Acanthocephala limbata* produces the geometric pattern of burrow openings, although the ecological role of the pattern is unclear [8]. Burrow casting in the deep-sea floor is possible [9] and can solve the enigma of the deep-sea burrows produced by invertebrates and vertebrates.

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CHARACTERISTICS AND SEDIMENTARY ENVIRONMENT OF ICHNOFOSSELS OF THE LOWER PERMIAN TAIYUAN FORMATION IN THE XIANGNING AREA, EASTERN MARGIN OF THE ORDOS BASIN

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The Taiyuan Formation is well exposed in the Gancaoshan zone, Xiangning County, on the eastern margin of the Ordos Basin in China. It is a set of coal-bearing strata composed of a mixture of carbonate and terrigenous clastic rocks. In this work, we analyze the composition and distribution characteristics of ichnofossils and their sedimentary environment in the area. Multi-layer tempestites and mixed tidal flat deposits were found in the outcrop profile of the carbonate rocks (L2, L3, L4, L5), and fourteen ichnogenera and seven ichnospecies were recognized. Four types of ichnoassemblages (Fig. 1) and their sedimentary environment models were established: Type A is the *Zoophycos* with light gray fillings-*Planolites* ichnoassemblage, formed in a mixed tidal flat environment; Type B is the *Zoophycos* with gray fillings-*Taenidium* ichnoassemblage, occurring in a rich oxygen sedimentary environment in the upper zone of the shallow sea (usually between the low tide line and the storm wave base); Type C is the *Zoophycos* with grayish-yellow fillings-bioturbation structure ichnoassemblage, produced in a dysaerobic sedimentary environment in the middle zone of the shallow sea (between the storm wave base and redox interface); Type D is the *Zoophycos* with black fillings-*Teichichnus* ichnoassemblage, developed in an anoxic sedimentary environment in the lower zone of the shallow sea (commonly located near or below the redox interface). This analysis provides ichnologic information for studying the sedimentary environments of the Ordos Basin and a scientific basis for exploring and developing late Paleozoic fossil energy resources.

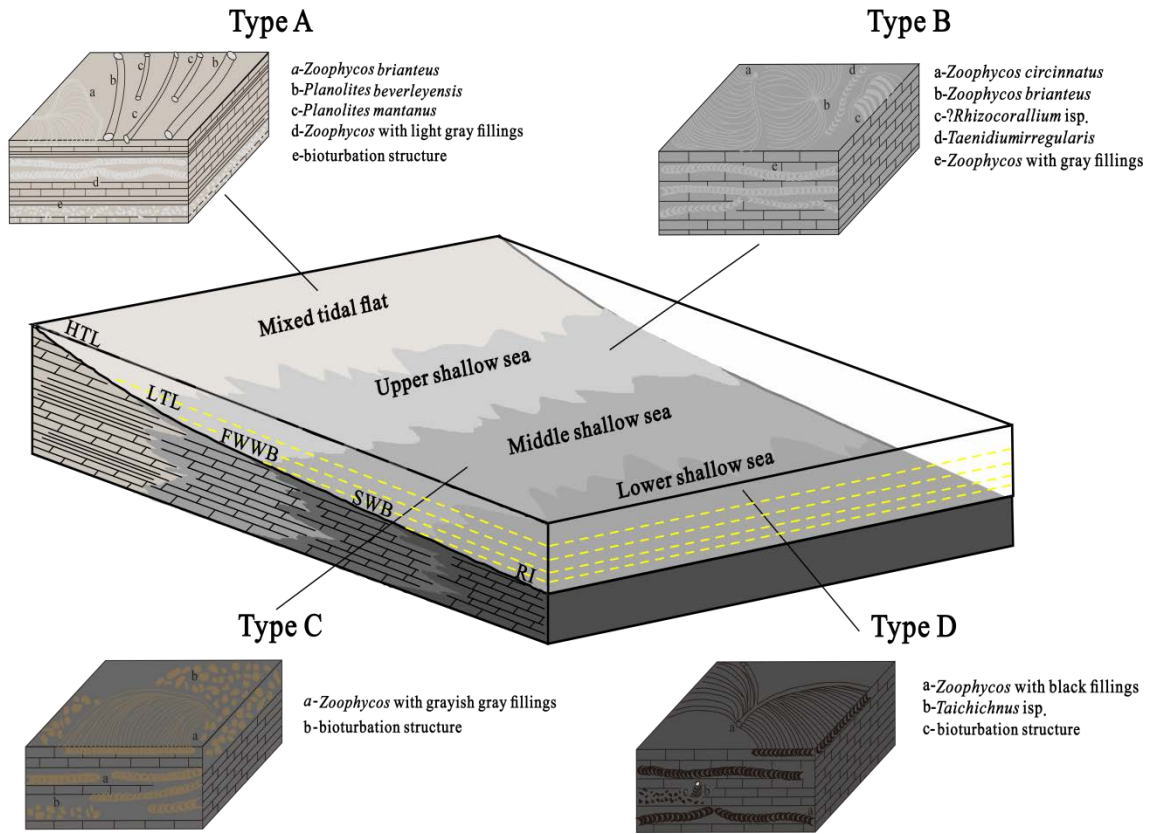


Fig.1. Ichnoassemblage types and their distribution model of sedimentary environment in the Taiyuan Formation. Abbreviations: HTL-high tide line; LTL-low tide line; SWB-storm wave base; FWWB-fair-weather wave base; RI-redox interface.



SIGNIFICANCE OF OUTCROP MORPHOLOGY AND TRUE SUBSTRATES FOR ICHNOLOGY

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Field-based analysis of sedimentary strata and their constituent ichnofaunas is highly reliant on available exposure of rock outcrop. The physical shape and structure of geological exposures places intrinsic biases upon any observations which can be made of the rocks: for example, the gathering of particular measurements can be impeded or abetted, or the outcrop may be variably suited to the observations of vertical profiles or horizontal bedding planes. The information contained within a bedding surface is different to that contained within a vertical stratigraphic section: both aspects may be available but provide different focal lengths in terms of recorded time and space scales. The presence or absence of bedding surfaces at a given outcrop, or within a formation as a whole, is particularly significant in ichnological studies [^{1,2}], as epifaunal trace fossils can most often only be observed upon these surfaces (unlike infaunal trace fossils that can be seen in both bedding plane and vertical exposures, as they are 3-D constructions that must intersect with vertical and horizontal planes).

Whilst it is well understood that observations of trace fossils in well core have inherent limits and biases, equivalent biases dependent on outcrop geomorphology are often overlooked and infrequently discussed in scientific publications. However, the limits imposed by outcrop geomorphology can play an even more significant role, as whilst the inherent limits of core studies are consistent across all studies, those associated with outcrop geomorphology can vary drastically depending on specific outcrop traits at different locations. This can limit comparability of previous studies when it is uncertain how outcrop biases have affected observations, interpretations, and trace fossil censuses.

To remedy this, in this presentation we will: (i) summarise the treatment of outcrop geomorphology effects on ichnological observations in previous ichnological literature; (ii) discuss the significance of True Substrate theory to ichnological problems [^{1,2}]. True substrates are defined as “sedimentary bedding planes that demonstrably existed at the sediment–water or sediment–air interface at the time of deposition, as evidenced by features such as ripple marks or trace fossils” [¹]; (iii) present a widely applicable method for characterizing outcrops based upon their geomorphology, and how these different morphotypes may differently influence observations. This develops a methodology first employed in a study of the Tumblagooda Sandstone [³], and built upon in subsequent studies [⁴], to explain how the variable outcrop morphologies typically linked with different facies associations may be partly responsible for the very different ichnological signatures of these associations.

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TRACE-FOSSIL DISTRIBUTION AND HIGH-RESOLUTION SEQUENCE STRATIGRAPHY OF THE CLAYSTONE MEMBER, BURDIGALIAN CHHASRA FORMATION, KUTCH BASIN, WESTERN INDIA

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The Burdigalian Chhasra Formation (CF) is established as a characteristic mixed siliciclastic and bioclastic carbonate system. The formation is subdivided into the older Claystone Member (CM) and the younger Siltstone Member (SM), although the monikers might be lithological misnomers. Together defining a 3rd-order early Miocene sequence, the CM along with its underlying Aquitanian Khari Nadi Formation (KNF) developed in a transgressive systems tract (TST), whereas its ensuing highstand systems tract (HST) is represented by the SM [¹⁻³]. However, this study emphasizes establishing a comprehensive and detailed, high-resolution sequence stratigraphy for the CF by integrating the sedimentological and ichnological characteristics. Along the Kankawati River valley, both the KNF and CF crop out. The CM succession commences at its unconformable contact with the underlying KNF demarcated by a monospecific firmground *Thalassinoides* suite (BI 4) (Fig. 1). The subaerial unconformity developed at the top of KNF is directly modified during the subsequent transgression creating a co-planar surface, *sensu* [⁴]. The surface is a transgressive ravinement surface with a 15 cm thick lag deposit. The lag concentration deposit at the base of CM indicates the onset of transgression and the subsequent development of wave/tide ravinement surfaces overlying the paleosol bed of the older KNF. The monospecific *Teichichnus* suite (BI 3) in the mudstone of the lower part of the CM indicates marine incursion and sedimentation likely under a brackish-water condition. The overlying sand-dominated heterolithic facies are typified by the prevailing assemblage of *Rosselia*, *Planolites*, *Bergaueria*, *Skolithos*, *Diplocraterion*, *Cylindrichnus*, and *Fugichnia* representing the archetypal *Rosselia* Ichnofacies (BI 3) (Fig. 2). The ensuing 4th-order-deepening of the basin is evidenced by the dominance of biostromal carbonates intercalated by mudstone facies (Fig. 1). A monospecific *Thalassinoides* colonization suite (BI 5 at the base to 0 at the top) characterizes the storm-influenced biostromes. The large-scale gutter casts (30-40 cm in depth and width) (Fig. 1) are observed in the upper part of the CM, which are filled with hummocky/swaley cross-laminated medium-grained sands. This erosional surface marks the Basal Surface of Forced Regression (BSFR) (Fig. 1). The gutter casts are overlain by a transgressive lag deposit bed containing bioclasts of molluscs, bioturbated with monospecific *Thalassinoides* suite suggesting another transgressive event. Ca. 8 m-thick younger interval remains unexposed in the study area. At the base of the following younger exposed interval, a ca. 80-100 cm-thick pedogenized layer (point C in Fig. 1) suggests another regressive event. This subaerial unconformity is overlain by a transgressive lag deposit defining it to be another co-planar surface [⁵]. The same biostromal limestone-mudstone intercalation overlies the transgressive lag deposit.

The sedimentologic, bioclastic, and trace-fossil distributions within the CM collectively point toward a tidally-influenced subtidal, shallow-marine, upper-shoreface to offshore-transition depositional settings with moderate to low sediment supply within a 3rd-order transgressive trend with intermittent regressive events triggering 4th-order sequence-stratigraphic changes influencing the lithofacies assemblages and the corresponding trace-fossil suites.

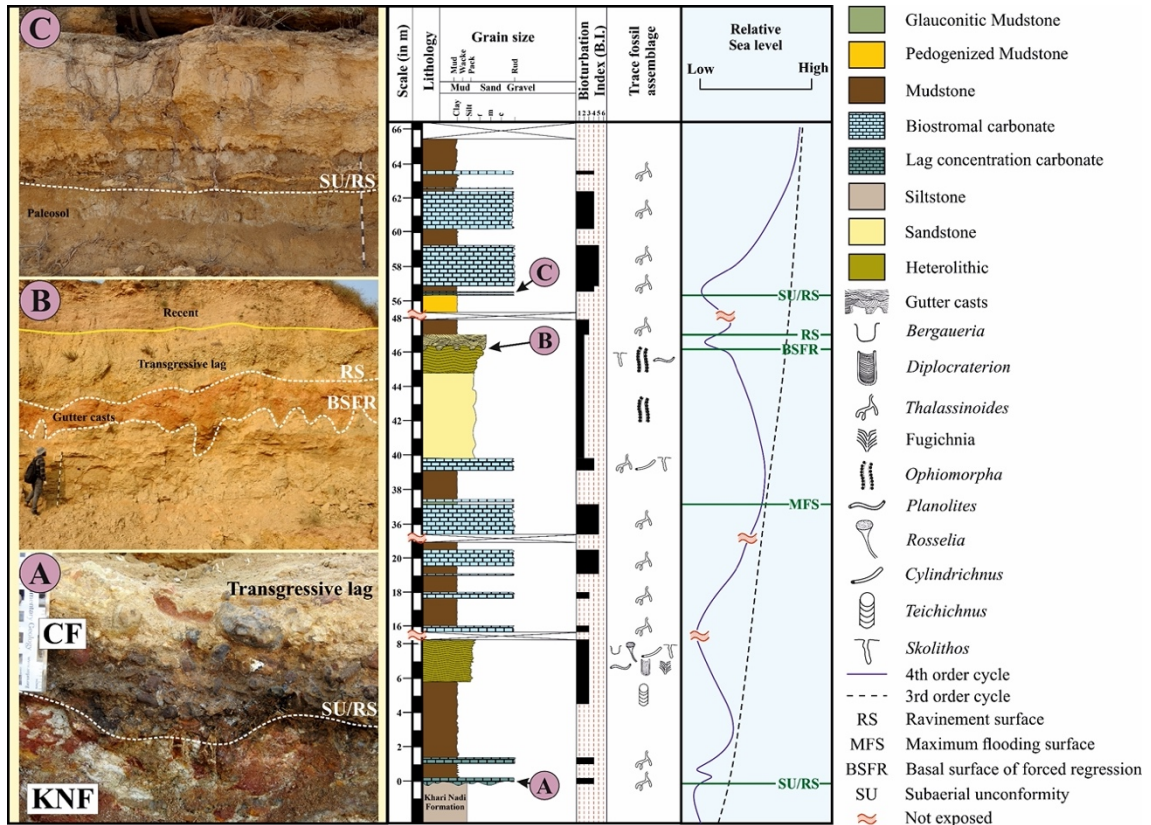


Fig. 1. High-resolution sequence stratigraphic hierarchy and relative sea level curve during the early Miocene as recorded within the Claystone Member, Chhasra Formation, Kutch Basin.

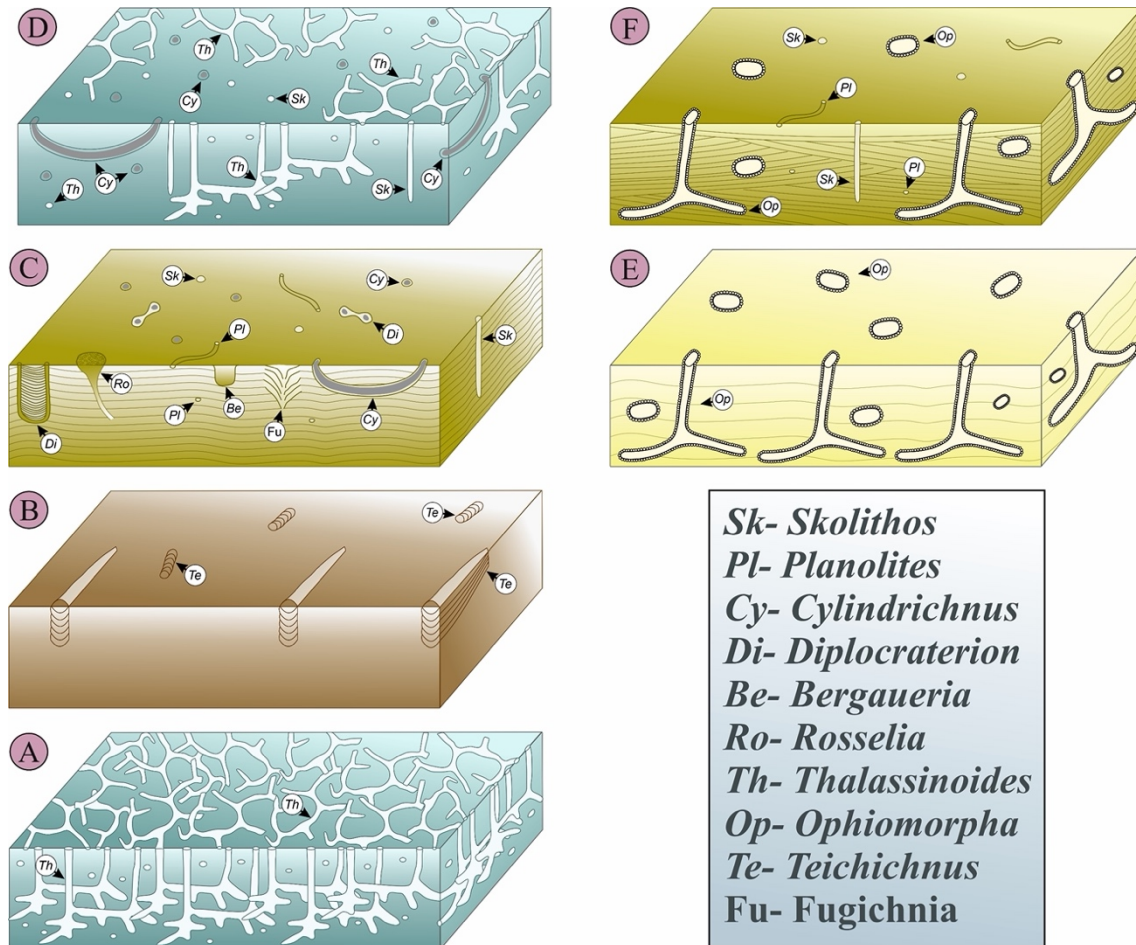


Fig. 2. Ichnofabrics of the Claystone Member. A. Monospecific *Th*-ichnofabric. B. Monospecific *Te*-ichnofabric. C. *Ro*-, *Pl*-, *Di*-, *Be*-, *Cy*-, *Sk*-, *Fu*-ichnofabrics. D. *Th*-, *Cy*-, *Sk*-ichnofabrics. E. Monospecific *Op*-ichnofabric. F. *Op*-, *Pl*-, *Sk*-ichnofabrics.

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CRETACEOUS COPROLITE RECORD IN THE ARARIPE BASIN, BRAZIL

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The Cretaceous Santana Group strata of the Araripe Basin contain an important ichnofossil record with exceptional fossil preservation. The purpose of this work is to report an overview of the vertebrate coprolites and bone balls from the Santana Group and new evidence of their paleobiological context. The Santana Group is a thick sequence of limestones and shales outcropping on the Araripe plateau in, northeast Brazil thought to have been deposited in large, virtually landlocked lagoon, during the Early Cretaceous and organized into three lithologic units: Crato (lower), Ipubi (middle) and Romualdo (upper), where fishes are the most dominant group in the fossil assemblages. The morphological features, description, chemical analysis, and thin sections of the coprolites can provide a potential method to obtain behavioral information on this fossil biota.

The Santana Group strata host exceptional fossil, whose sedimentary history is closely linked to the opening of the South Atlantic Sea and the breakup of South America and Africa [^{1,2}]. Systematic excavations of the Santana sediments have taken place since the end of the nineteenth century [³⁻⁵]. Nowadays, Santana limestone and claystone is exposed in various outcrops in many quarries at the margin of the basin. Numerous well-preserved fossils have been recovered, among them insects, crustaceans, fishes (Chondrichthyes, Coelacanth, Osteichthyes), frogs, crocodylians, chelonians, pterosaurs, dinosaurs, and plants [^{6,7}]. The vertebrate coprolites from the Santana Group are the main ichnofossil remains present in these deposits, and they were reported in the early 20th century, and during the last years they have received more attention and have been better investigated.

The fossil material was collected in systematic excavations and is housed in the collection of Departamento de Ciências Naturais of the Universidade do Estado do Rio de Janeiro and Departamento de Geologia of the Universidade Federal do Rio de Janeiro. The inside structure of the coprolites was observed through perpendicular thin section of the length long axis by use of a saw; 10 mm thick sections were glued on a glass slide, and the ground sections were observed in transmitted and polarized light, and with a scanning electron microscope. For determination of mineral and chemical composition powder detached by a drill from the host sediment and the coprolite matrix were analyzed by spectrographic x-ray diffraction (DRX) and x-ray fluorescence (FRX) to determine mineral and elemental composition.

The vertebrate coprolites and bone balls preserved in these units reveal an autochthonous condition with three-dimensional preservation of morphology with cylindrical or oval-shape, and rare spiral shapes. The coprolite matrix exhibits hardness or softness in consistency, and some specimens externally have transverse grooves produced by the excretory process. The coprolites and bone balls in the Romualdo Formation are preserved by cementation in isolated carbonate nodules, and in the Crato and Ipubi formations, most of the specimens were preserved by compression inside the sediment layers.

Some of the specimens possess internal small cavities that probably resulted from microbial processes. The thin sections showed the presence of food remains inside of the coprolite matrix with a very fine-grained groundmass of disarticulated bone fragments, arthropods carapaces, worms structures, and planktonic shells (Fig. 1). Also, in the coprolites from the Ipubi and Romualdo units, concentrations of ostracods of the genus *Pattersonocypris*, are present around and inside of the coprolite mass.

The measurements of spectroscopy analysis for the FDX reveals a great number of peaks that can be identified as crystalline planes of a phase of calcium carbonate or calcite, CaCO₃, and calcium hydroxyapatite (Ca₁₀(PO₄)₆(OH)₂). The FRX analysis identifies a dominant

concentration of calcium and phosphate and the minor presence of sulfur, iron, and manganese elements in the coprolite matrix (Table 1).

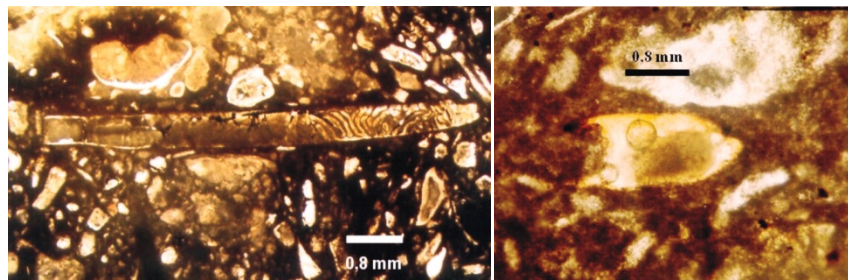


Fig. 1. Two well preserved inclusions of Romualdo coprolites shown by thin sections under transmitted light; note on the left side a worm body and on the right side a radiolarian shell.

Table 1. The chemical composition (per cent) by x-ray fluorescence analysis of host sediment (left side) and coprolites (right side) of the Santana Group, 1-Romualdo, coprolite: UFRJ/DG 103-IcV; 2- Ipubi, coprolite: UFRJ/DG 179-IcV, 3- Crato, coprolite: UNIRIO/LIBA 70-Ic.

Samples	1	2	3
Elements			
SiO ₂	4.56/0.80	21.06/0.34	0.80/0.75
TiO ₂	0.01/0.00	0.39/0.00	0.58/0.00
Al ₂ O ₃	2.06/0.01	7.47/0.01	0.16/0.01
Fe ₂ O ₃	1.71/0.51	6.16/0.23	0.86/0.57
MgO	0.00/0.64	2.14/0.98	2.20/0.00
CaO	70.70/66.41	17.75/72.02	53.60/67.86
MnO ₂	0.80/1.03	0.01/0.46	0.18/1.11
P ₂ O ₅	0.00/9.48	1.09/0.16	0.38/9.56
SO ₃	0.01/0.59	0.01/0.67	0.25/0.62
K ₂ O	0.01/0.0	1.27/0.01	0.73/0.0
ZrO ₂	0.01/0.0	0.01/0.0	0.07/0.0

The Santana Group also reveals the dominant presence of fossils of brackish and associated marine fish in the units where these coprolites are preserved. The difference in composition between the host sediment and fossilized excrement indicates a partial substitution of the fossil structure by elements present in the depositional environment. The coprolite preservation of the Ipubi Formation, deposited in thin layers of black shale, and in the Crato Formation, preserved in claystone, are similar to those described for the Pennsylvanian in the United States [8], and the Late Jurassic of Nusplingen in Germany [9], in both cases associated with a dominantly fish assemblage.

The cylindrical and ovoid-shaped coprolites with sizes on the order of 3.0 to 6.0 cm long and 1.5 to 7.0 cm wide, and the different mass consistency, if compared with fresh coprolites from extant fishes, verifies that in these communities coexisted producers of different size and feeding behavior with detritivorous or, omnivorous, or carnivorous diet. The bone balls are found free in the sediment with white color and measured widths between 4.0 to 9.0 cm.

We conclude that of these ichnofossil records of the Santana Group strata reflect changes in food web diversity of these communities during the Early Cretaceous. The coprolites were smaller and less numerous in the Crato and Ipubi strata due to stressful environmental factors, however in the Romualdo strata, where episodes of marine transgressions are registered, the ichnofossil diversity increased, and this factor allowed us to understand how the environmental changes really affect these paleocommunities.



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PRELIMINARY STUDIES ON NEW SAUROPOD TRACKS FROM THE UPPER CRETACEOUS (BAJO DE LA CARPA FORMATION) AT QUERUBÍN TRACKSITE, NEUQUÉN PROVINCE, ARGENTINA

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In memory of Dr. Jorge O. Calvo.

The Querubín site is located in the Santonian Bajo de la Carpa Formation. It was discovered in 2010 by Silvia Cuevas, who observed several circular depressions on the bedding surface. Posteriorly, a study carried out by paleontologist Dr. Jorge Calvo and collaborators identified these structures as sauropod tracks. In addition, theropod and possibly iguanodontids tracks were identified, as well as invertebrate fossil remains [^{1,2}]. This site, which we refer to as Sector A, is located on the east coast of Los Barreales Lake, 80 km northwest of Neuquén city (38°31'5.6/0.8" S; 68°40'48.1/42.2" W).

In this communication, we describe preliminarily a new set of tracks found on the bedding surface I of Sector B (Fig. 1) which is located on the coast (38°31'8.15"S, 68°40'42.56"O) near Sector A. In 2022, during the development of the doctoral thesis of the first author [³], a first trip and field work was made to the new sector with traces of Querubín tracksite, with the aim of carrying out comparative studies with sauropod tracksites from Agua del Choique (Mendoza, Argentina). The Sector B has an area of 250 m² in which c.a. 70 sauropod tracks are preserved. As in Sector A [²], tracks are irregularly distributed, forming a trampling surface which makes it difficult to identify possible trackways. Although the tracks are well preserved, the track-bearing surface (L-1) is subject to erosion caused by lake waves and seasonal lake flooding. This process continuously reveals new dinosaur tracks and invertebrate traces but, unfortunately, also can cause entire blocks to be lost prior to study. Therefore, the field conditions are complex and are subject to variation of the lake level.

The objective of the Querubín tracksite research project is to analyze the new tracks in the Sector B in their paleobiological, taphonomical, and paleoenvironmental aspects. In addition, given the constant erosion and weathering and consequent loss of fossils and data, three-dimensional models and casts will be made as a heritage protection objective. In order to achieve this, the following tasks were performed: (i) evaluate the preservation state of the tracks in the Sector B; (ii) uncover and prepare the track-bearing surface of the Bajo de la Carpa Formation; (iii) measure, map, and photograph the tracks; and (iv) take photographs following specific protocols for photogrammetric modeling.

The Querubín tracksite is composed of four track-bearing surfaces (L-1, L-2, L-3, and L-4) and all of them are intensively bioturbated both by vertebrates (sauropods and theropods) and invertebrates (Fig. 2) [²]. All tracks are on gray-green, medium-to fine-grained sandstone facies belonging of the lower section of the Bajo de la Carpa Formation [⁴]. The paleoenvironment has

been interpreted as a meandering river and tracks were left on its adjacent floodplains [2]. Following the stratigraphic column of the Querubín tracksite made by Calvo and collaborators [2], the tracks of the Sector B are preserved on L-1. In this sector, two areas have been differentiated: one of them, located to the north, with eroded tracks, and other one located to the south, with the best-preserved tracks and which are described in this study.



Fig. 1. The new sauropod tracks at Querubín tracksite (Sector B), located on the east coast of Los Barreales Lake.

Tracks are deep (≤ 30 cm) and show large displacement rims. While two well-preserved manus-pes sets have been identified, the majority are pedal tracks. The morphology of the pes tracks is variable, ranging from circular to subtriangular contour. The size of the pes tracks is also variable. The two pedal tracks corresponding to the manus-pes sets measure 68.7 cm long by 53.7 cm wide and 46.6 cm long by 37.5 cm wide. Regarding the manus tracks, they have a symmetrical kidney shape with a straight or nearly straight posterior contour. The two manual tracks identified measure 22.1 cm long by 46.4 cm wide and 23.5 cm long by 29.8 cm wide. The manus-pes distances are 27.5 cm and 25.8 cm, respectively. In both manual and pedal tracks, no detail marks such as claws, digits or skin are observed.

Although it is possible to observe at least three trackways, the arrangement of the sequences of tracks is quite chaotic, so it is deduced that the tracks belong to more than one animal that stepped on the surface. This inference is also supported by the fact that the trackways also present tracks of different sizes, which are often very close to each other or even strangely elongated, evidencing a possible overlapping. Manual and pedal tracks are located away from the midline of the trackway and are therefore described as wide-gauge trackway [5]. Tracks from Sector B are similar to those of Sector A [2]. Given the features of the tracks and trackways, and the fact that titanosaurs are the only sauropods that lived since the Coniacian in South America [6], the tracks from Sector B of Querubín tracksite are assigned to titanosaurs.

Sector B of the Querubín tracksite is also a site of high potential for taphonomic studies to better understand the sub-environments in which the titanosaurs lived [7]. In addition, in this

site it is possible to see, both in cross section and in zenithal view, the different strata immediately below and above of the L-1 track-bearing surface. The study of the different undertracks that are clearly visible at the lower levels, is extremely useful to make descriptions and interpretations of the three-dimensional nature of the tracks, and to better understand the influence of substrate conditions, locomotion and anatomy, on track morphology.

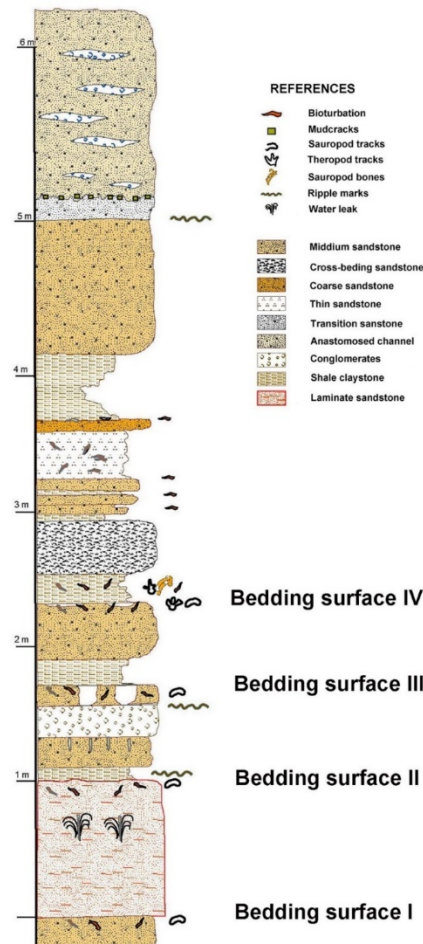


Fig. 2. The stratigraphic column of the Querubín tracksite corresponding to the lower section of the Bajo de la Carpa Formation (Santonian), indicating the four track-bearing surfaces (modified from [2]).

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WHERE DID THE ORDOVICIAN BIOEROSIONAL REVOLUTION BEGIN?

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Macroboring organisms have evolved and changed through the Phanerozoic. The major rise in the diversity of macroboring ichnofossils took place during the Middle and Late Ordovician and was termed the "Ordovician Bioerosion Revolution". In 2004, Mikuláš and Dronov [1] expressed the opinion that the Baltic region was the birthplace of bioerosion. Wilson and Palmer [2] reported seven bioerosional ichnogenera from the Ordovician. A decade later, eleven Ordovician bioerosional ichnogenera were listed by Mángano et al. [3].

During the Ordovician and Silurian, Baltoscandia was covered by a shallow epeiric sea. The sedimentary basin was influenced by changes in sea level, climate, and depositional conditions that favoured precipitation of carbonates. Carbonate sedimentation commenced during the latest Floian in the cool epicontinental basin and ended up in a restricted tropical sea in late Přidoli. The resulting rock succession was highly condensed; thus, hardgrounds and omission surfaces are numerous, and bioerosion is common.

The main goal of this study is to summarise and discuss the distribution and diversity patterns of bioerosion in the region. Data was collected by systematically reviewing previous literature and paleontological collections. In recent years, new material has been obtained intensively. *Trypanites* is the earliest bioerosional trace in Baltica, which appeared in the Cambrian stage 3. *Oichnus* occurs in obolid shells from the Cambrian–Ordovician boundary beds. The Ordovician succession of the Baltic region hosts thirteen macroboring ichnogenera: *Trypanites*, *Gastrochaenolites*, *Sulcolithos*, *Tremichnus*, *Pinaceocladichnus*, *Palaeosabella*, *Sanctum*, *Petroxestes*, *Oichnus*, *Caedichnus*, *Osprioneides?*, *Entobia?*, and *Gnathichnus?*. From the Silurian, only six macroboring genera are recorded: *Trypanites*, *Osprioneides*, *Sulcolithus*, *Pinaceocladichnus*, *Tremichnus*, and *Palaeosabella?*. *Balanoglossites*, the trace-maker of which demonstrated the ability to bioerode, is common in the Ordovician, and has also been recorded from the Silurian. Moreover, several undescribed macroborings occur within hardgrounds and biogenic substrates. The most common ichnogenus in Baltica is *Trypanites*; its trace-maker community was diverse and has changed over time. The genus is represented at least by two ichnospecies: shallow *T. sozialis* and elongated *T. weisei*.

Trypanites and *Gastrochaenolites* appear below the Early–Middle Ordovician boundary. A rich assemblage of macrobioerosional traces including *Trypanites*, *Gastrochaenolites* and *Sulcolithus* occurs on Dapingian hardgrounds, and only a few finds are related to biogenic substrates. A major change in the bioerosion took place in the Upper Ordovician. Since early Sandbian, the boring diversity and intensity have been related to different shelly fossils, and nine ichnogenera are reported. The trace-makers strongly preferred substrates with a homogeneous and dense texture. In the Sandbian and early Katian, macrobioerosional traces occurred mainly on bryozoans, as well as brachiopods. In the upper Katian, these traces occurred on tabulate corals (heliolitines) and bryozoans, as well as rugosans and stromatoporoids. In the Silurian, these macroborings are predominantly found in stromatoporoids with fewer occurrences associated with heliolitines and rugosans.

The sudden increase in the diversity of bioerosion and bioclastrations in Baltica took place in the Sandbian, and eight ichnogenera have already been reported. During the same time interval (late Sandbian and early Katian), the first tropical reefs appeared in the region, though



the diversification of bioerosional traces is not related to the development of reefs. The Sandbian was characterised by high bioproduction and diversity of macro- and microfauna in Baltica, associated with coastal upwelling and nutrient input from volcanic ash. There was intensive diversification of bryozoans, and oversized colonies of trepostomes are common in the Sandbian sediments of Estonia.

In general, our data shows that the available volume of hard substrates controls the ichnodiversity on lithic and biogenic substrates [4]. In the pre-Hirnantian Ordovician, there is a link between the diversity of bioerosional traces and the size of body fossils. Large Hirnantian corals and lower Rhuddanian stromatoporoids do not bear bioerosion, pointing to the strong influence of the end-Ordovician extinction on various bioeroding taxa in Baltica. During the Silurian, the community of bioeroding organisms recovered; however, it never reached the diversity seen in the Upper Ordovician.

The data from the study corroborates that Baltica was the birthplace of bioerosion. A diverse assemblage of macrobioerosional traces and intensity of borings shows that the Ordovician Bioerosion Revolution had begun in Baltica.

The rapid diversification of bioerosional traces in the region was probably a combination of multiple global and regional factors. The major global factors were the seawater chemistry and oxygenation, stability of the sea level and increasing phytoplankton availability. The main regional drivers supporting the diversity of bioeroding organisms were the nutrient-rich, well-oxygenated epeiric sea and unusually low sedimentation.

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ICHTNOLOGY OF THE SINEMURIAN–TOARCIAN BASINAL DEPOSITS FROM THE MOCHRAS DRILL CORE, CARDIGAN BAY BASIN, UK, AND ITS APPLICATION TO INTERPRETATION OF OXYGENATION CHANGES AND CYCLOSTRATIGRAPHY

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The continuous Sinemurian–Toarcian section of the Llanbedr (Mochras Farm) Borehole in the Cardigan Bay Basin, UK, comprises heavily bioturbated hemipelagic calcareous mudstones, wackestones/siltstones and subordinate packstones/sandstones. Several beds show bigradational grain-size trends and sedimentary structures typical of contourites. Most of them show a transition from massive, organic-rich calcareous mudstone to siltstone or very fine-grained sandstone with shallow-water bioclasts, and back to the massive mudstone. Many layers of siltstone/very fine-grained sandstone/calcareenite show pinstripe lamination and small current ripples, which are usually partly disturbed by bioturbation. The contourites were hypothesized to have been deposited by thermohaline-driven geostrophic contour currents flowing between the Boreal Ocean and Peri-Tethys through the NE-SW trending, narrow and relatively deep Cardigan Bay Strait.

The siltstone/very fine-grained sandstone/calcareenite beds contain the most diverse and best visible trace fossils. Trace fossils are strongly dominated by *Phycosiphon incertum* represented by four morphotypes (Ph1–Ph4), which were produced by opportunistic colonizers. The dwelling and deposit-feeding structures, such as *Thalassinoides*, *Schaubcylindrichnus*, and *Teichichnus*, are relatively common. They are accompanied by *Trichichnus*, which is a deep-tier trace fossil chemichnion produced by filamentous sulfide-oxidizing bacteria with a high tolerance for dysoxia, less common *Zoophycos* (fodinichnion), *Planolites* (pascichnion), *Palaeophycus* (pascichnion), *Lockeia* (cubichnion), and rare dwelling structures, such as cf. *Polykladichnus*, *Siphonichnus*, *Monocraterion*, *Arenicolites*, and *Skolithos*. Contrary to existing views that *Phycosiphon* is generally uncommon in contourites, the contourite deposits in Mochras are strongly dominated by *P. incertum*. The trace fossil assemblage resembles the *Zoophycos* ichnofacies, but the eponymous ichnotaxon is uncommon. The intensive bioturbation is conditioned by a relatively stable supply of organic-rich sediment and oxygen [^{1,2}].

The contourites in the Toarcian succession are more frequently base- or top-cut than in the Pliensbachian, which suggests fewer stable conditions in the depositional system. The system was distinctly disturbed at the Pliensbachian–Toarcian transition and at the beginning of the negative carbon-isotope excursion (To-CIE) marking the Toarcian Oceanic Anoxic Event (T-OAE), where the bioturbation was less intensive, *Phycosiphon* is less abundant, and *Trichichnus* is more common. However, anoxia marked by unbioturbated laminated mudstones is marginally developed, and the peak and recovery phase of the negative excursion of the anoxic event is characterized loss of *Trichichnus* and better oxygenated sea-floor conditions. The Pliensbachian–Toarcian boundary event appears to be a significant palaeoceanographic turning point, starting a CaCO₃ decline with the most severe oxygen depletion, stronger than during the T-OAE (but dysoxic, not anoxic). This can have been caused by the extreme climate warming during the To-CIE, which may have enhanced and caused a reversal in the direction of deep marine circulation, improving oxygenation of the sea floor. A minor dysoxic event also occurred in the latest Thouarsense and Dispansum zones.



Ichnological and lithological signals suggest repetitive fluctuations in benthic conditions attributed to a hierarchy of orbital cycles (precession and obliquity [4th order], short eccentricity [3rd order], long eccentricity [2nd order], and Earth–Mars secular resonance [1st order]). Spectral analysis of binary data for ichnotaxa appearances gives high confidence in orbital signals in accord with previous work based on geochemical time series [3]. This allows refined estimation of ammonite zone lengths.

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VARIATIONS IN THE ORIENTATION OF *TAENIDIUM* IN FLUVIAL PALEOSOLS DEPOSITS: CAÑADÓN SECO FORMATION, UPPER CRETACEOUS, GOLFO SAN JORGE BASIN, ARGENTINA

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Fluvial systems are composed of a wide variety of subenvironments that are characterized by different sedimentary and biological processes (trace fossils). Floodplains are the place where pedogenic and bioturbation processes have their maximum expression [1]. Soil development depends on the interaction of the five soil-forming factors (parent material, climate, organisms, topographic relief and time). These factors in turn are linked to intrinsic characteristics of the system, such as the sedimentation rate, the variation of the water table and the organisms that inhabit the fluvial system [2]. Aiming to understand the modifications of the biological action and its relationship with the lateral variations within a fluvial system, a detailed study of 149 m of core samples of the Cañadón Seco Formation was carried out, coming from three wells on the southern flank of the Golfo San Jorge Basin. Twenty-nine sedimentary facies were defined and grouped into four facies associations: (i) Channel, (ii) Crevasse channel, (iii) Crevasse-splay, and (iv) Floodplain. From the pedological point of view, two pedotypes were described: (i) Pedotype 1: greenish gray to reddish colored, with rhizoliths, mottles and reddish and black nodules, structureless, massive interpreted as Inceptisols-like paleosols, and (ii) Pedotype 2: greenish gray to reddish colored, with rhizoliths, mottles, nodules, slickensides, angular and wedge-shaped peds, interpreted as Vertisols/Vertic Inceptisols-like paleosols. The trace fossils observed are: *Taenidium* isp., *Camborygma* isp., *Planolites* isp., as well as rhizoliths and escape traces, suggesting an ichnocoenosis of the *Scoyenia* ichnofacies. The dominant trace fossil in the entire succession is *Taenidium* isp. (Fig. 1), which in continental environments represent the activity of insect larvae that live in unsaturated vadose zones [3]. Variations in the orientation of the *Taenidium* isp. specimens were observed, such as (i) horizontal, (ii) vertically ascending, and (iii) vertically descending (Fig. 2). These orientations correspond to producer's responses to keep them in the vadose zone, that is, unsaturated humid conditions. It is interpreted that when the *Taenidium* are horizontal, the water table is stabilized. When they are vertically ascending, that behavior responds to a rise in the water table, while when they are vertically descending that reflect a descent in the water table (Fig. 2) [4]. In this way, the behavior of *Taenidium* producers shows seasonal fluctuations in the water table related to seasonal rainfall and/or fluvial discharge, which is in line with the development of seasonal paleosols with vertic pedofeatures. The variations observed in the stacking of the facies associations of the different core samples correspond to autocyclic processes of a low gradient fluvial system, that is, avulsions of the main channels towards the lowland regions. The paleoenvironment inferred for the entire studied section corresponds to a high sinuosity meandering fluvial system in a seasonal climate.

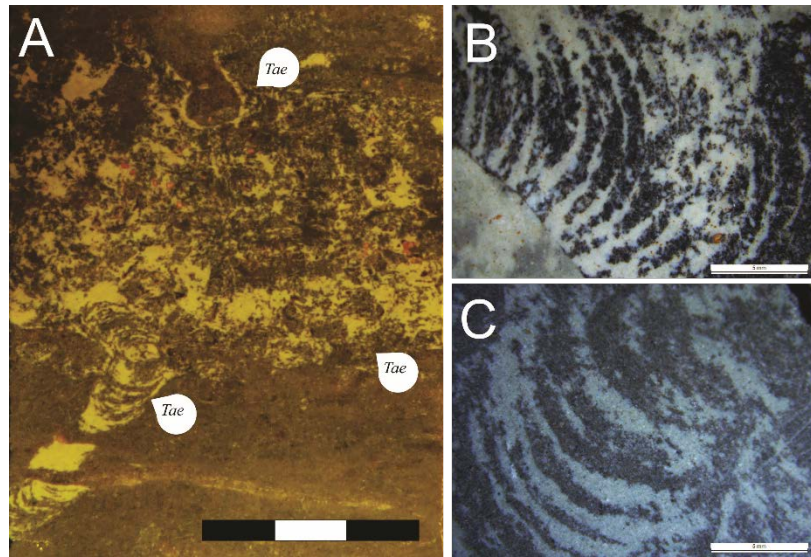


Fig. 1. A. *Taenidium* isp in core sample showing different orientation and bioturbation index, B-C. Detail of meniscate-backfilled burrows. Scale bars: A = 3 cm; B-C = 5 mm.

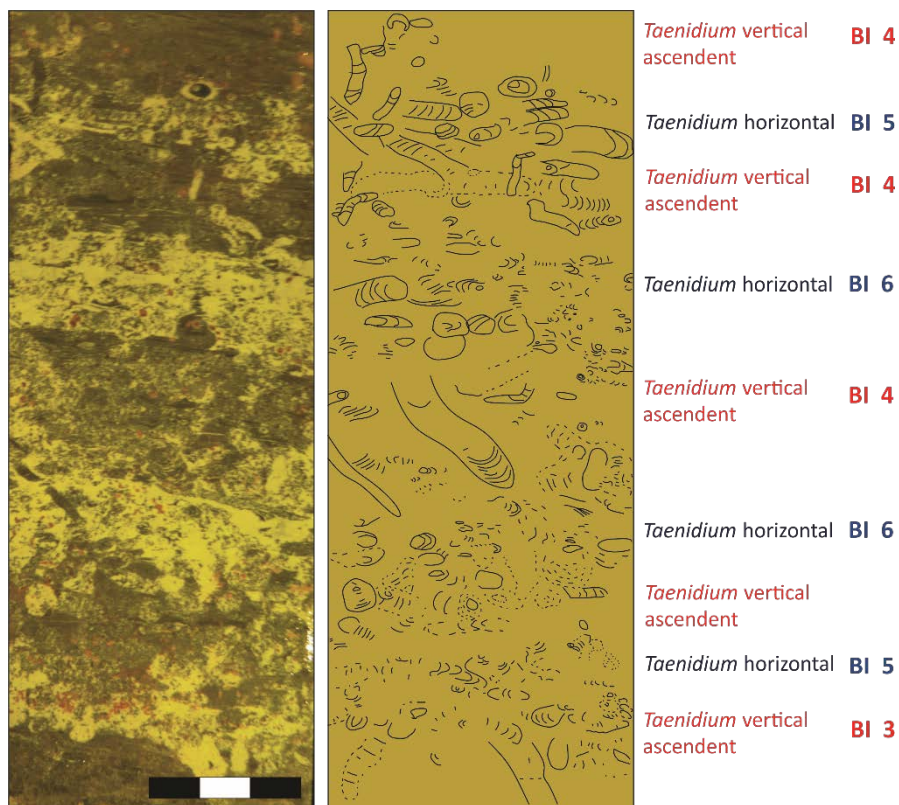


Fig. 2. Variation in distribution, orientation, and bioturbation index (BI) of *Taenidium* isp. in core sample from fluvial palaeosols deposits.

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BIOEROSION ON TERRESTRIAL TURTLE CARAPACE FROM THE LATE PLEISTOCENE SOPAS FORMATION, NORTHERN URUGUAY

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The research of bioerosion in bones has a longstanding tradition in archaeology but has gained recent conceptual development within ichnology. While fossil bioeroded bone records in Uruguay are primarily limited to scavenging and possibly pupation traces on glyptodont remains [1], this study presents bioerosion structures with distinct ichnotaxobases found on remains of a giant terrestrial turtle. The studied material (FCDPI 9863) consists of a marginal carapace plate of a giant land turtle, probably belonging to the genus *Chelonoidis* Fitzinger, 1835, and an unidentified isolated fragment of bone (FCDPI 9865). The material comes from Paso del Buey Negro, on the Arapey Chico River, in Salto County, northern region of Uruguay. Despite having been found as floats, the stratigraphic position of these remains corresponds to the Sopas Formation, which is composed of sandstones, siltstones, and bears levels with paleosols, where abundant vertebrate remains and other trace fossils as *Taenidium* and *Castrichnus* are also found. The origin of the Sopas Fm. is related to fluvial deposition and subsequent edaphization in some levels. Vertebrates found in this unit suggest different paleoenvironments such as grasslands, riparian forest and freshwater bodies and streams. The age of this stratigraphic unit ranges from the Late Pleistocene to the early Holocene. There are OSL datings for the locality of the studied material corresponding to $36.9 \pm 6.5\text{ky}$ [2]. The turtle plates and other bone fragments exhibit bioerosion structures characterized by nonbranching sinuous furrows on the bone surface transitioning to true borings penetrating beyond the cortical bone. These subcylindrical structures, with subcircular cross-sections and diameters up to 9 mm, contain infills composed of bone chips arranged in menisci. The bone chips were identified by the presence of osteons. The infills of furrows protrude from the bone surface.

Both furrows and penetrative borings, although made by the same trace maker, differ in origin. Penetrative borings indicate direct bone penetration, while furrows and their infills suggest a distinct behavior of crawling along the bone-sediment interface, akin to *Amphifaoichnus* and *Taotieichnus*, two ichnogenera associated with bioerosion structures on bone surfaces.

The distinctive morphological and behavioral characteristics of the Uruguayan material's bioerosion structures, particularly the active infill composed of bone chips arranged in menisci [3], signify postmortem production. Morphological and taphonomic analyses suggest these structures are the result of scavenging organisms, possibly insects with robust mouthparts capable of fragmenting bone and arranging it into menisci.

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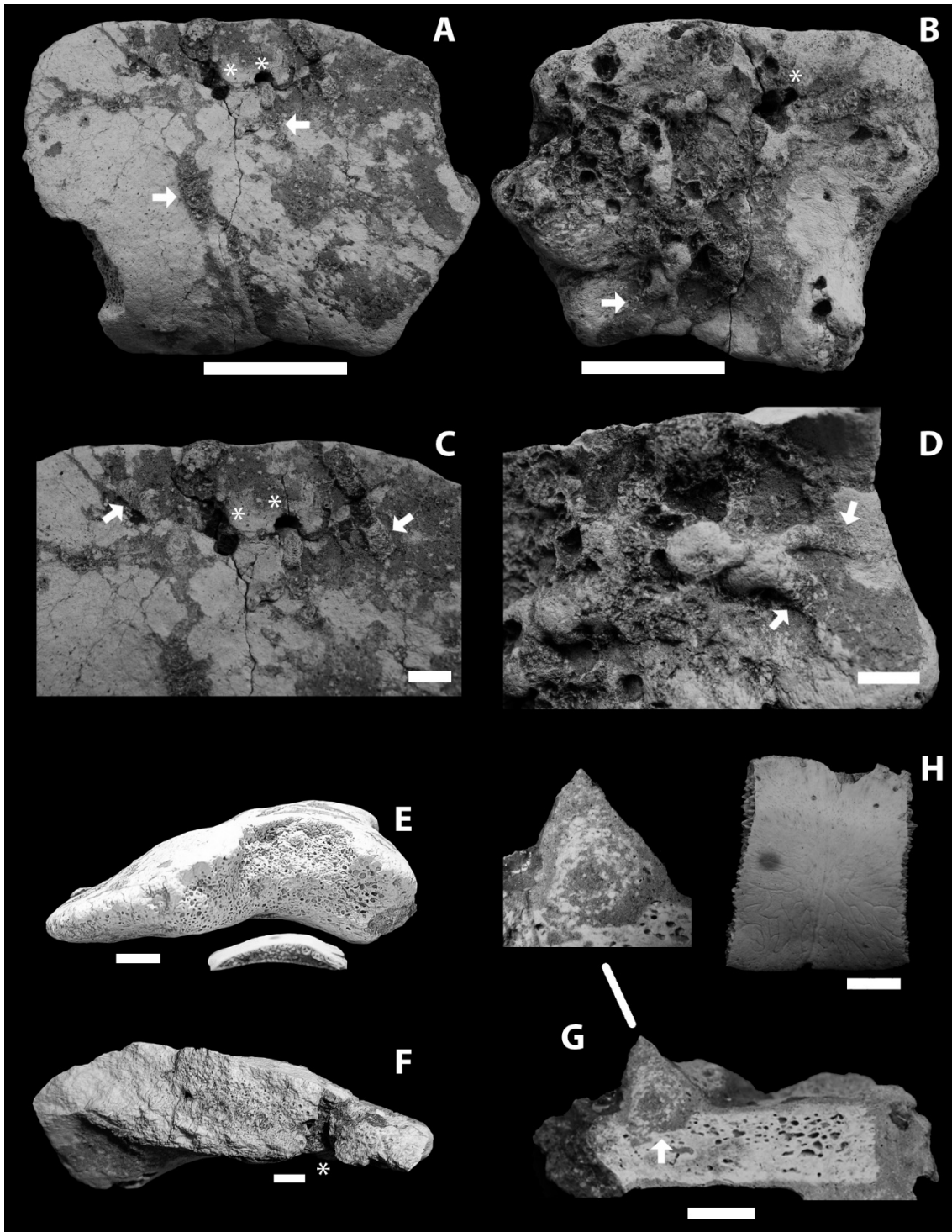


Fig. 1. A-F, Marginal plate of *Chelonoidis* isp. FCDPI 9863 with furrows (→) and borings (*). A. External side. B. Internal side. C. Detail of furrows and borings with meniscate infill, external side. D. Detail of furrows with meniscate infill, internal side. E. Cross section through the thickness of the plate compared to a recent freshwater turtle. F. cross section of the plate showing penetrative boring along its whole thickness. G. Section of an isolated bone fragment, FCDPI 9865, showing a furrow in cross section with its infill. In the inset bone chips can be seen as part of the infill. H, Marginal plate of a recent freshwater turtle for comparison, external view. Scale bars: A-B = 5 cm; C-H = 1 cm.



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***PSAMMICHNITES GIGAS CIRCULARIS* ICHNOZONE IN THE LOWER CAMBRIAN OF PIN VALLEY, SPITI HIMALAYA AND ITS BIOSTRATIGRAPHIC SIGNIFICANCE**

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The Cambrian outcrops of the Kunzam La Formation are well exposed along the Pin valley (Spiti, Himalaya) from Muth to Baldur localities, India, yet their trace and body fossils are poorly documented from this valley. The only known trilobite biozone from the Pin valley is *Oryctocephalus indicus*, which occurs just below the Cambro-Ordovician angular unconformity at Shian locality in Pin valley [1]. The present work is an addition to the Lower Cambrian biostratigraphy of the Pin Valley. The *Psammichnites gigas circularis* ichnozone in Pin Valley is recognized and its correlation from Kashmir to Kinnaur region is discussed. The Pin valley lies in the Spiti region of Himachal Pradesh and geologically constitute part of the Tethyan Himalayan belt. Cambrian outcrops in the Himalayas are known from the Tethyan and Lesser Himalayan belt, and the Cambrian biozonation is available from Parahio valley of Spiti region [2]. The Cambrian rocks in the Tethyan Himalaya are interpreted to be deposited in shallow marine, storm-dominated nearshore to offshore setting [3].

Recent investigations in the Pin valley between the Mud and Baldur locality, precisely on the outcrops exposed on the left bank of the Pin River just opposite to Shian locality, yield abundant specimens of *Psammichnites gigas circularis* in medium-grained sandstone of the Kunzam La Formation (Fig. 1). Stratigraphically, the outcrops lie nearly 160 meters below the base of the *O. indicus* biozone (Wuliuan, Miaolingian) and falls in late part of the Series 2/Stage 4. Eighteen large sandstone blocks were studied. *Psammichnites gigas circularis* are large bilobate burrows preserved on top of sandstone beds, featuring a distinct sinusoidal median furrow, moderately convex, forming isolated loops and showcasing either scribbling or meandering paths (Fig. 1a-f). Each individual loop displays variations in the convexity of lobes and the width of the median furrow, with convexity ranging from high to low. In some specimens, the median furrow follows a smooth path, while others exhibit collapsed features along its course, a defining characteristic of *Psammichnites gigas circularis*. Additionally, in some specimens the lobes undergo a change in thickness, thicker to thinner during the course of the path. The length of burrows is 25-52 cm, and the width is 2-7.5 cm. Notably, the bilobate traces intersect (Fig. 1a-e) and depicts large loop-shaped structures (Fig. 1f), resembling semi-circles. At the points where the bilobate trace fossils intersect, they appear raised from the surface in comparison to the overall length of the path.

In the Cambrian of the Himalayas, *Psammichnites* is a biostratigraphically significant trace fossil [4-6] and two ichnosubspecies level ichnozones (i.e., younger *Psammichnites gigas gigas* and older *Psammichnites gigas circularis*) are identified in Series 2/Stage 4 of Zanskar (Ladakh), Chandra valley (Lahaul and Spiti), Parahio valley (Spiti) and Tidong valley (Kinnaur) [4-5,7]. Demarcation of *Psammichnites gigas circularis* ichnozone in Pin valley is significant as it links the rocks and ichnozones of the Spiti region with Kinnaur region, the latter being poorly explored area in the Himalayas.

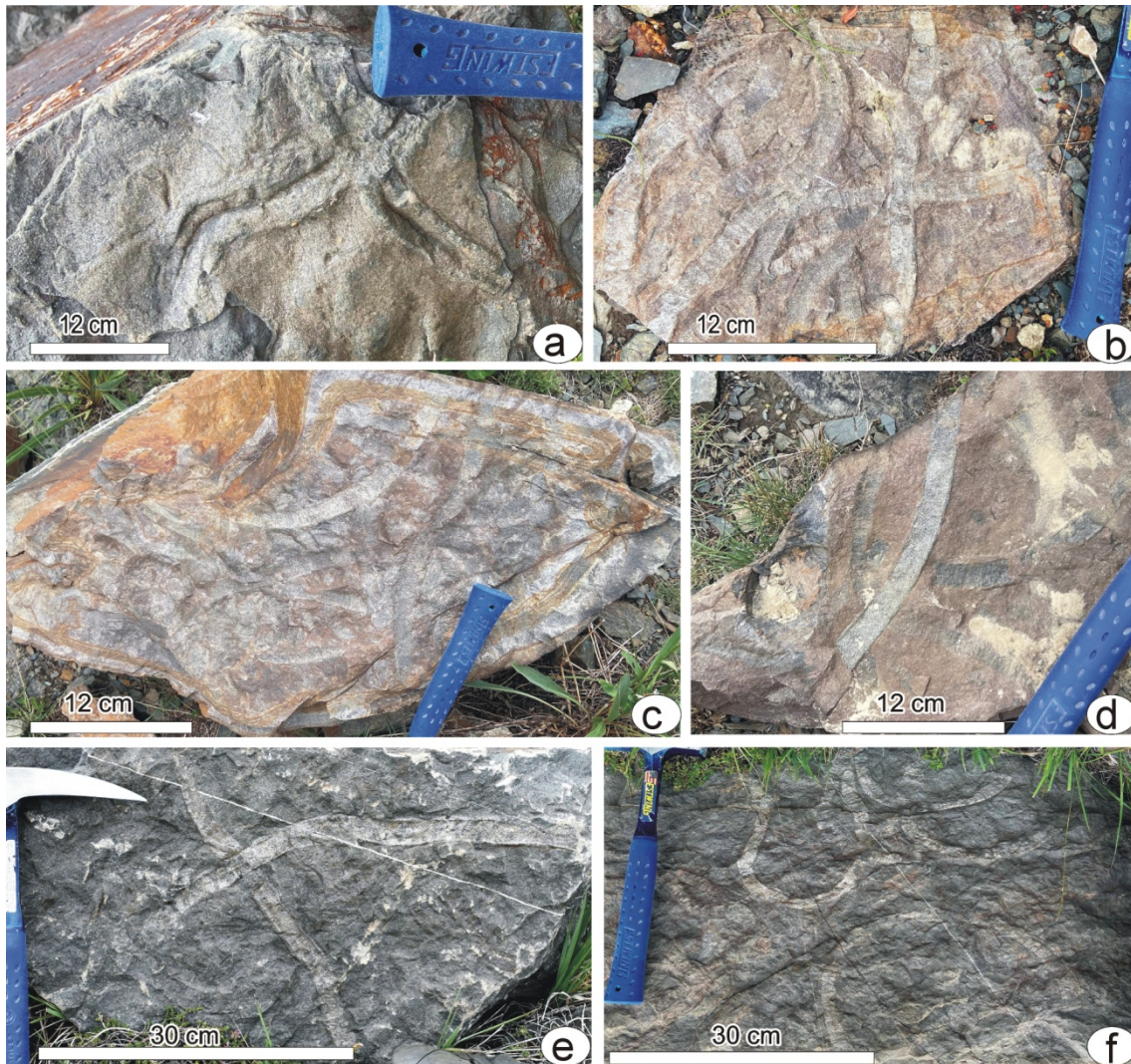


Fig. 1. Gregarious, crossing-over and densely packed *Psammichnites gigas circularis* from the Cambrian Series 2/ Stage 4 of Kunzam La Formation, Pin Valley, Spiti Himalaya.

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HOW SMOOTHNESS OF TRACE FOSSILS INFORMS ON EVOLUTION OF LOCOMOTION, BODY PLANS, AND NAVIGATIONAL CAPABILITIES DURING THE EDIACARAN–CAMBRIAN TRANSITION

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Trace fossils provide a unique insight into the evolution of early animals during the Neoproterozoic–Phanerozoic transition, when abundant simple horizontal trace fossils are recorded. During this critical interval, the smoothness (i.e., whether there exist abrupt turns along the curve) of horizontal trace fossils significantly increased, indicating the advent of profound anatomical and behavioural innovations. However, this has not been quantified before. We propose several new quantitative metrics, including smoothness criterion, minimum normalized curvature radius, kurtosis of normalized curvature, and energy spectral density, which are used to calibrate the change of smoothness of trace fossils, such as *Gordia*, *Helminthopsis*, *Helminthoidichnites*, and *Cochlichnus*, during the Ediacaran–Cambrian transition. According to these metrics, we have classified trace fossils into non-smooth, regional-smooth, and smooth ones, corresponding to random creeping, gliding, and peristalsis/undulation, respectively. The first massive occurrence of regional-smooth trace fossils at terminal Ediacaran (Fig. 1) offers uncontroversial evidence on the activities of mobile bilaterians. The increase of locomotory efficiency, sensory range, and navigational capabilities can also be quantitatively inferred by different definitions of smoothness. Finally, these metrics may also contribute to develop quantitative approaches to ichnotaxonomy.

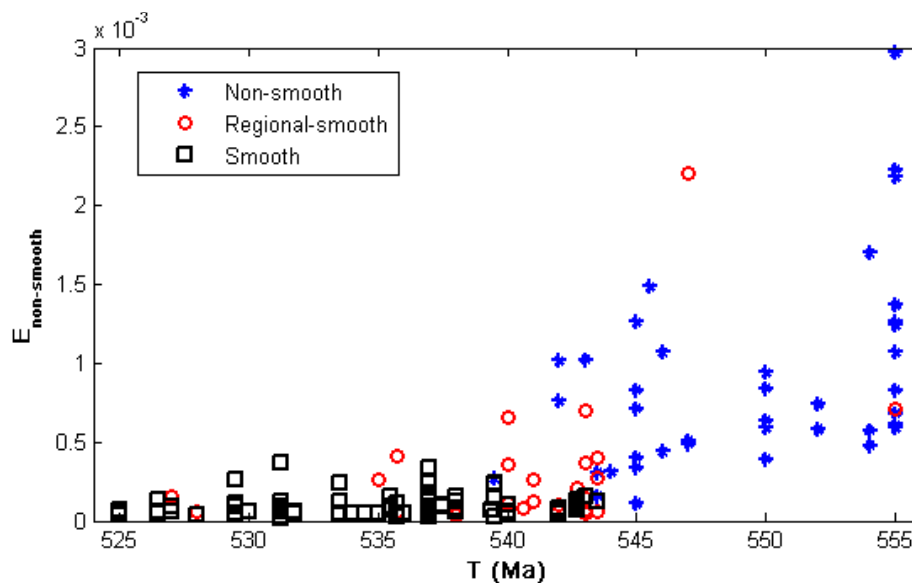


Fig. 1. The energy consumption for small-scale non-smooth locomotion decreased exponentially through time. The first massive appearance of regional-smooth traces was around the terminal Ediacaran.



ECOLOGICAL INSIGHTS FROM TRACE FOSSILS OF THE LOWER DEVONIAN TALACASTO FORMATION, ARGENTINEAN PRECORDILLERA

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The Precordillera is a peripheral foreland basin included within the Cuyania composite terrane of western Argentina. The Lower Devonian (Lochkovian–Emsian) Talacasto Formation in the Central Precordillera consists primarily of siltstone and very fine-grained sandstone formed in a wave-dominated shallow-marine setting. This unit provides paleoecologic insights at a period characterized by repeated biotic crises. This formation shows a thickening and deepening trend from approximately 100 m (shelf to upper shoreface facies) in the south to over 1000 m thick (shelf to lower shoreface facies) in the northern area. This contribution aims to decipher the benthic ecology of shallow-marine settings in Southwest Gondwana through the analysis of trace-fossil assemblages, integrating sedimentologic and paleontologic datasets. Four different sections, covering 78 km along dip (S-N), were logged, namely Quebrada Poblete Sur (QPS), Quebrada de Talacasto (QT), Río Las Casitas (RLC), and Loma de Los Piojos (LLP). Three trace-fossil assemblages are identified in the Talacasto Formation. In ascending stratigraphic order, these are: (1) *Palaeophycus* assemblage (PA), including *Palaeophycus tubularis*, *Palaeophycus heberti*, and *Helminthopsis* sp., (2) *Phycosiphon-Zoophycos* assemblage (PZA), comprising *Phycosiphon incertum*, *Zoophycos* sp., *Nereites missouriensis*, *Chondrites* sp., *Palaeophycus striatus*, *Palaeophycus tubularis*, and *Palaeophycus heberti?*, and (3) *Rosselia* assemblage (RA), containing *Rosselia socialis*, *Skolithos* sp., *Arenicolites* sp., and *Palaeophycus* sp. The first assemblage (PA), recognized in the lowermost interval of the QPS section, is preserved in sparsely bioturbated (BI=2), black, parallel-laminated mudstone representing a shelf subenvironment. The tracemakers are most likely worm-like organisms, probably polychaetes. This assemblage reflects overall low hydrodynamic energy and a relatively shallow redox discontinuity surface. The PZA is typically found in thoroughly bioturbated (BI=5-6) mixed siltstone and very fine-grained sandstone (lower offshore) and wave-ripple cross-laminated very fine-grained sandstone (upper offshore) that characterize the northern sections (RLC and LLP). However, it is also present in shallower-water deposits, represented by very fine- to fine-grained sandstone (lower/middle shoreface) in the southern sections (QT and QPS). *Chondrites* and *Zoophycos* are typical of dysoxic/anoxic sediment, but the presence of *Phycosiphon incertum* and *Nereites missouriensis* requires oxygenated interstitial waters. Although this trace-fossil assemblage is present in the same sedimentary facies, not all ichnotaxa are found in the same beds. *Chondrites* sp. typically forms monospecific suites and more rarely is accompanied by *Zoophycos* sp. *Phycosiphon incertum* may be present either forming monospecific suites or commonly accompanied by *Zoophycos* sp. and *Nereites missouriensis*. This association may be linked to a shallow redox discontinuity surface, as well. The diverse record of brachiopods, trilobites, and crinoids indicates well-oxygenated bottom waters. The extremely high degree of bioturbation (BI=5-6) in the finer-grained deposits indicates a very low sedimentation rate that allowed long colonization windows. This is supported by the presence of the bivalve *Ptychopteria*



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sp. and the preservation of semi-articulated trilobites and crinoids. Additionally, the dominance of *Pascichnia* and *Fodinichnia* may indicate high food supply. Furthermore, the hydrodynamic conditions would have been calm between storm events. Finally, the RA includes mid-tier detritus and suspension-feeding trace fossils and is dominated by *Rosselia socialis*. This trace-fossil assemblage is present in amalgamated hummocky cross-stratified very fine-grained sandstone indicative of a lower/middle shoreface both in LLP and RLC. The tracemakers inhabited permanent dwelling structures that were re-established after successive event of erosion and sedimentation above the fair-weather wave base. RA is associated with high hydrodynamic energy and high sedimentation rate. The distal *Cruziana* Ichnofacies is typically present in offshore deposits (such as LLP and RLC sections). However, its presence in the sandstone deposits of the lower shoreface (QT and QPS sections) may imply an anomalous onshore expansion of this ichnofacies.



CHEMICHNIAL BEHAVIOR OF (SOME) CHONDRITES PRODUCERS DOCUMENTED BY EXHUMED, STILL SOFT, METHANE-DERIVED CONCRETIONS

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Chondrites was found to characterize lowered oxygenation because of its pioneering role during oxygenation phases in organic-rich, commonly laminated “black shales” formed under oxygen-deficient conditions [1]. Later, the deep position of *Chondrites* in tiered sequences of burrows observed in Late Quaternary anoxic deep-sea sediments was related to bottom-water oxygen content $\geq 0.2 \text{ mlO}_2/\text{L}$ [2]. Correspondingly in the rock record, specific trace fossils disappear from telescoping or appear in expanding bioturbation tiers in response to decreasing or increasing oxygenation, respectively, while *Chondrites* typically occurs in a deep tier [3]. This concept was further elaborated into so-called Oxygen-Related Ichnocoenoses (ORI; [4]). Then, the *Chondrites* producers were interpreted to take advantage of chemosymbiosis [5]. This hypothesis was based on the similar burrow pattern, mainly the branching angle, of *Thyasira*, a bivalve following a chemosymbiotic lifestyle while utilizing H_2S [6,7]. In the following, the new behavioral category “chemichnia” was introduced for *Chondrites* [8]. The interpretation of *Chondrites* as chemichnion has so far been purely based on (i) its occurrence in oxygen-deficient sediment, (ii) the not really striking similarity in burrow pattern – the thyasirid burrows are at best *Chondrites*-like [9] – and (iii) framboidal pyrite within *Chondrites* that is indicative of microbial activity [9]. These microbes, however, were active after the *Chondrites* fill has been emplaced. Thus, direct geochemical evidence of a chemichnial behavior of (some) *Chondrites* producers is lacking except those, which are today produced in anoxic sediments since they contain Pinatubo-1991 ash [10].

Concretions recently found in a Middle Jurassic mudrock succession in SW Germany provide clear evidence of a chemichnial behavior of *Chondrites* producers, which burrowed into these carbonate concretions, which originally formed in mud, then underwent reworking and became embedded in a hummocky-cross-stratified, sandy tempestite (Fig. 1). The detrital material in the concretion is clay and silt, whereas the *Chondrites* tubes, which penetrate the concretions, are filled with sand originating from the surrounding tempestite. This indicates that the concretions were still soft to stiff when displaced and, hence, in an early stage of formation (see [11]). The concretions are cemented by carbonate derived from (i) anaerobic oxidation of methane (AOM) and (ii) organoclastic sulfate reduction (OSR) as recorded by $\delta^{13}\text{C}$ values $< -25\%$ and between -25 and -15% , respectively [12]. The host sandstone is cemented by calcite displaying $\delta^{13}\text{C}$ values of ~ -8 to -2% and, thus, precipitated from a different fluid than the calcite forming the concretions (Fig. 2). The *Chondrites* tubes are sparse in the host sandstone whereas they cluster along and within the concretions wherein they are abundant (Figs. 1, 2). The sand fill of the *Chondrites* tubes is cemented by calcite, which shows $\delta^{13}\text{C}$ values ranging from -31 to -18% typical of AOM and OSR, respectively, likely affected by admixed sea-water bicarbonate (Fig. 2) [13]. The *Chondrites* tubes do not show a lining or a reaction halo around them (Fig. 2). Thus, it appears that no (thick) biofilm developed along the *Chondrites* tubes, which could be expected in case of an agrichnial behavior fostering the growth of microbes along the tubes.

These data and observations are best explained by a chemichnial and not an agrichnial behavior of the *Chondrites* producers. They might have utilized reduced chemical compounds collected from the pore water via the tube system. Although biogenic methane is possible, reduced sulfur species are more likely, because they are produced through both AOM and OSR, and

Chondrites were also observed in carbonate concretions formed in the OSR zone (without AOM involved) [14]. However, to be purely adapted to utilize only methane is rather unlikely, because in many instances, the methane-containing zone is located below the maximum burrowing depth of the *Chondrites* producers [12,15]. Thus, the maximum depth of penetration could have been limited to the sulfate-methane transition zone.

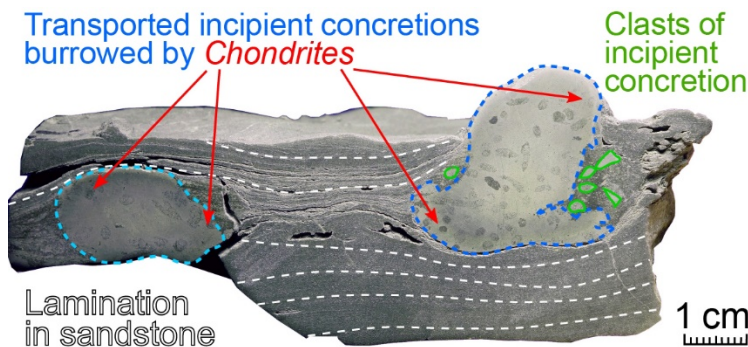


Fig. 1. Sandy tempestitute containing reworked carbonate concretions, which were exploited by *Chondrites* producers. Note, within the concretions, *Chondrites* tubes are abundant, whereas they are sparse to absent in the sandy tempestitute. Small clasts dismembered from the concretion attest for its weak cementation during reworking, but *Chondrites* tubes are not affected by compaction and record ongoing carbonate cementation.

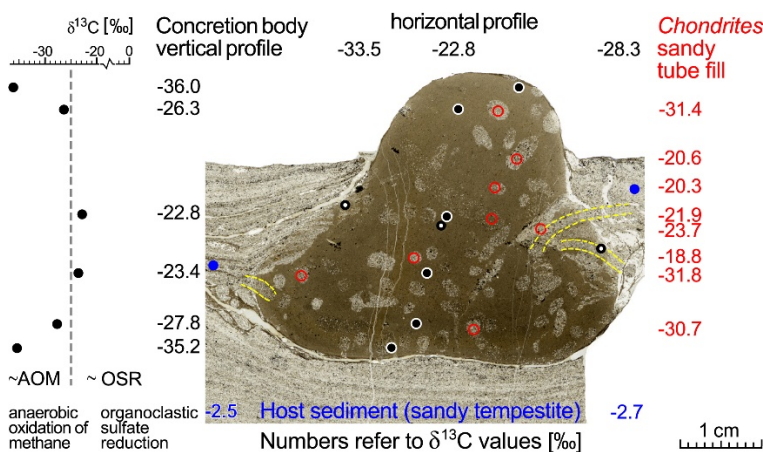


Fig. 2. *Chondrites* produced in a reworked, at that time still soft-to-stiff, carbonate concretion embedded in a fine-sandy tempestitute. The concretion body contains mud whereas the *Chondrites* fill is identical to the sandy host sediment; some *Chondrites* tubes continue from the sandy host sediment into the concretion (between yellow broken lines). The $\delta^{13}\text{C}$ values in the concretion body and the *Chondrites* fill record carbonate precipitation due to (organoclastic) sulfate reduction and anaerobic oxidation of methane, which occurred before and continued after the concretions underwent reworking.

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GYMNOSPERM INSECT MINES FROM THE MIDDLE JURASSIC OF NORTHEASTERN CHINA INDICATE AN EXPANSION OF EARLY MINING EVOLUTION

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The associations between plants and insects shifted considerably from the expansion seen on gymnosperm-dominated plant assemblages of the Late Triassic, such as the Molteno Biome of the Karoo Basin in South Africa, to substantially altered plant–insect associations on new, gymnosperm-dominated and emergent angiosperm-dominated plant assemblages of the Early Cretaceous [1–5]. The Jurassic Period was the interval bracketed between these two diversification events for which very little is known. Yet the Jurassic must have been crucial for the initial appearance and early colonization of new plant hosts by a variety of functional feeding groups, such as surface feeding, piercing and sucking, galling, seed predation, pathogens, but especially leaf miners. Although no diverse, abundant, and well sampled plant assemblage of significance has been comprehensively examined for plant–insect associations, nevertheless an ongoing study of one such plant assemblage has recovered a variety of plant–arthropod (and pathogen) associations representing an insight into the plant associations with insects during this intervening time interval. Unlike a few previous studies describing single interactions from the Jurassic [6], our comprehensive approach has examined bulk plant assemblage of somewhat more than 2000 plant specimens of the Yanliao Biota from the Daohugou locality of the Jiulongshan Formation, Middle Jurassic (Callovian, 165 Ma), of Northeastern China [7]. Data from this deposit currently is being analyzed, of which the mining functional feeding group displays elevated diversity and implications for the early ecological evolution of this group of internally feeding insects. In addition to the variety of associations such as herbivory, pollination, mimicry, and chemical and physical antiherbivore defenses [7,8], the role of mining provides a rare window into the intricate relationships between a plant host and its often obligate insect consumer of internal tissues. Mining previously has not been reported from the Yanliao Biota and this report [9] provides timely data on a topic that is very poorly known.

Mining typically occurs on foliage and is a type of herbivory by which an insect larva of a holometabolous insect consumes the live internal tissues of its plant host from within [5,9–11]. The mining functional feeding group appeared relatively late in the fossil record, lacking a Paleozoic presence, and has an earliest definitive occurrence from the Early Triassic of Russia [12]. Although there is an elevated richness of mine damage types (DTs) from the Late Triassic Molteno Formation of South Africa [1–3], Jurassic occurrences consist of two unconvincing examples of leaf mines from the Early and Middle Jurassic from specimens described by Edirisooriya and Dharmagunawardhane [13] and Santos et al. [14], respectively. Nevertheless, a definitive, moth-like, serpentine mine occurs on leaves of a pteridosperm from the Late Jurassic of Queensland, Australia [15,16].

We investigated Yanliao mines and their host plants, focusing on detailed mine features, mode of larval feeding, and documentation of which internal plant tissues were consumed. We used the standard functional feeding group–damage type system of categorizing mining damage.

From the 2014 plant specimens at the Daohugou fossil site, we discovered 27 occurrences of mines on 14 specimens that resulted in eight, new, mine DTs present on six genera of bennettitalean, ginkgoalean, and pinalean gymnosperms. The richness of these structurally distinctive mines provide evidence for a suite of diverse mines that fill the gap between the Late Triassic and Early Cretaceous (Fig. 1).

Three conclusions result from this study. First, the Daohugou mid-Mesozoic mines are structurally conservative and track plant-host anatomy rather than plant phylogeny. Second, likely makers of these mines, based on three lines of evidence, were from an early lineage of tenthedrinoid sawflies, three early lineages of polyphagan beetles, and four early lineages of monotrystian moths. Third, the nutrition hypothesis, which would suggest that Middle Jurassic miners had greater access to more nutritious, inner tissues of newly emerging gymnosperm lineages, best explains the evolution of mining during the pre-angiospermous, mid Mesozoic (Fig. 2).

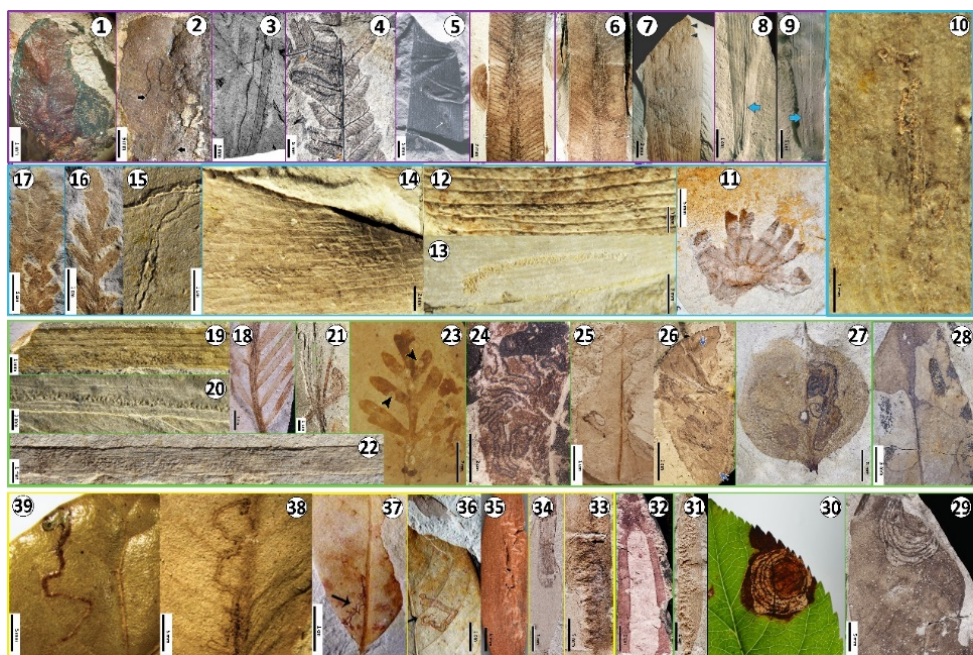


Fig. 1. Mesozoic mines on a variety of vascular plant hosts [9].



Fig. 2. Leaf-mining community of gymnosperms and their patterns of herbivory, documented from the Daohugou plant assemblage of the Middle Jurassic Jiulongshan Formation, Northeastern, China [9], as rendered by Xiaoran Zuo.



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A NEW LOOK AT THE LATE JURASSIC THEROPOD TRACK RECORD FROM CHILE

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The bone record of non-avian dinosaurs from Chile consists of sauropods, theropods, ornithopods, and rare thyreophorans [1]. However, the ichnological record plays a significant role in supplementing and enlarging the Chilean dinosaur record. Rich track-bearing levels, with a Late Jurassic to Early Cretaceous age (J/K), are known mainly from northern Chile in a 200 km North-South belt from the Quebrada Chacarilla (Tarapacá Region) to the San Salvador River (Antofagasta Region). However, Mesozoic vertebrate footprints are heavily understudied, and the published record is rather sketchy. Published tracksites located in this belt include, the Quebrada Chacarilla [2], the Quebrada de Arcas, and San Salvador River [3].

During May 2022, a two-week survey was conducted in the Quebrada Huatacondo in Northern Chile. During this field campaign, several new levels with dinosaur footprints in the Majala Formation (Oxfordian?–Kimmeridgian) were discovered; there, the application of modern digitalization techniques, such as close-range and drone photogrammetry, were implemented for the first time in the country [4].

The section of the Majala Formation consists of a 200-m sequence of sand- and siltstones interspersed with millimetric to centimetric very fine to medium silty sandstone which are situated in the middle to the upper part of this stratigraphic unit. In this section, five levels were recorded confirming the presence of at least four trackways of large theropods (footprint lengths from 40 to 55 cm) (Fig. 1) and one outcrop with more than 20 footprints of minute to small theropods (footprint lengths from 8 to 13 cm) (Fig. 2).

There is no skeletal record of theropods in northern Chile that could help to assign the tracks to possible producers. Thus, the only fossil record of this group from the Late Jurassic in northern Chile are their trace fossils. However, when comparing track sizes from Huatacondo with other theropod tracks from the Tarapacá Basin (e.g., Quebrada Chacarilla, Río San Salvador), their dimensions and morphology are very similar (footprint lengths ranging from 38 to 55 cm, hip height from 195 to 240 cm). Other tracks from the Quebrada Huatacondo are substantially smaller (average footprint lengths of 11.7 cm and average hip height of 52 cm) than the others (footprint lengths ranging from 16 to 20 cm, hip height from 70 to 90 cm).

Coeval localities in South America, like Botucatu Formation in Brazil [5], the Castellón Formation in Bolivia [6], and the Baños del Flaco Formation in Chile [7], show that the small theropod footprints are similar in terms of footprint lengths (8 to 12.5 cm) and hip height (45 to 55 cm) in both Brazil and Bolivia. However, in the Quebrada Huatacondo, the PI/Pw ratio is greater than 1, unlike in the other localities. The Baños del Flaco Formation yields medium-sized theropod tracks (Average PI = 24, average hip height = 107 cm) and small tracks (Average PI = 18, average hip height = 80 cm). Thus, the tracks in Quebrada Huatacondo represent the smallest Late Jurassic theropods on the southwestern margin of Gondwana.

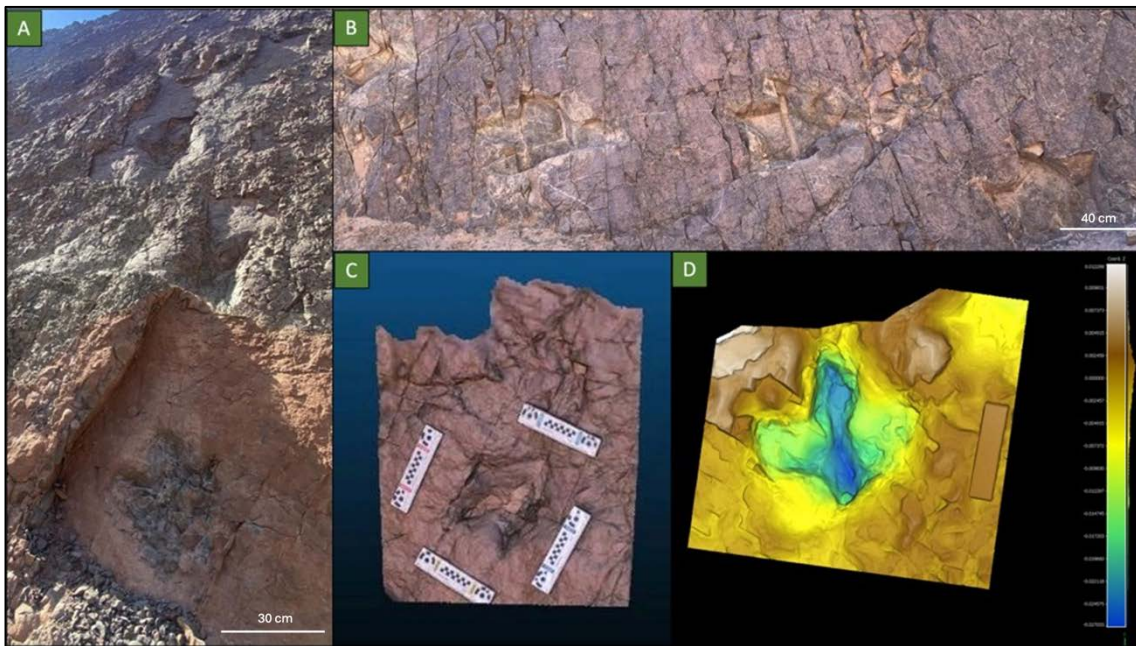


Fig. 1. Some examples of large theropod footprints from the Majala Formation in the Quebrada Huatacondo discovered during the May 2022 campaign. A-B. Photographs of tracks and trackway. C. A 3D model of two theropod footprints. D. False color depth map of a tridactyl track.

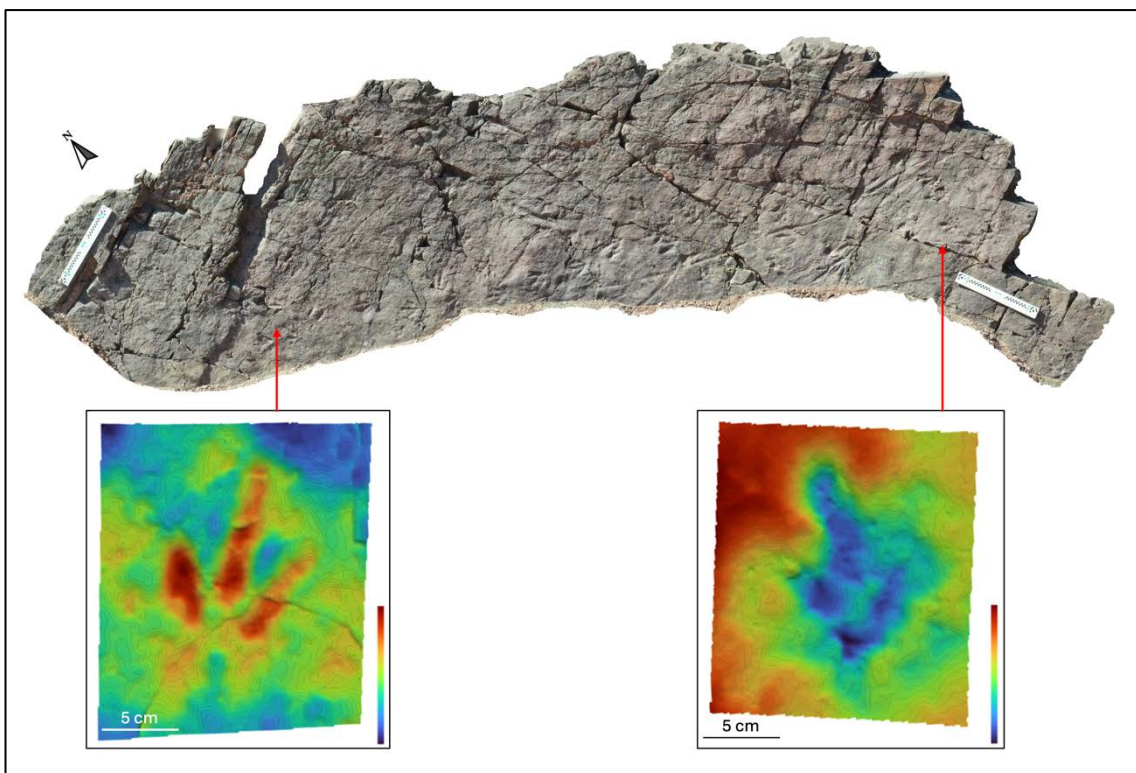


Fig. 2. Surface with trackways of small theropods from Quebrada Huatacondo (Majala Formation), and two 3D models of some of the footprints.

If we consider the PI/Pw ratio with the anterior triangle (AT) length-width ratio of the tracks in Quebrada Huatacondo and compare them with known ichnotaxa from the Late Jurassic [8], The large tridactyl tracks show similarities with Laurasian ichnotaxa *Megalosauripus* and



Jurabrontes, while the smaller with *Janlingpus*. Given their preservation, however, a clear ichnotaxonomical attribution is, at this stage, premature.

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GLOSSIFUNGITES ICNOFACIES RELATED TO STRATIGRAPHIC DISCONTINUITIES OF MESOZOIC–CENOZOIC DEPOSITS IN THE ARAUCO BASIN, CENTRAL CHILE

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The Arauco Basin (Central Chile) is located in the coastal forearc domain of the Andean active margin of the South American Plate and corresponds to a part of the raised platform. It hosts a ~2300 m thick Maastrichtian–Holocene sedimentary succession [1]. Although sedimentological characterizations of stratigraphic units have been relatively well studied, the contact relationships between these units lack research.

Within the Arauco Basin, five discordant tectonostratigraphic sequences have been recognized [1]. From base to top, these are: (S1) Late Cretaceous (Santonian–Maastrichtian); (S2) Paleocene–Middle Eocene; (S3) Lower Miocene; (S4) Pliocene–Pleistocene; and (S5) Pleistocene–Holocene, which correlate to the Quiriquina Formation, Lebu Group, Ranquil Formation, Tubul Formation, and Cañete Formation, respectively. Each of these sequences is separated by sedimentary hiatuses spanning different time intervals [3]. In this context, this study focuses on the trace fossils recognized from the four discontinuities throughout the Mesozoic–Cenozoic. The base of the entire sedimentary sequence overlies an unconformity to Paleozoic metamorphic basement rocks, in which *Gastrochaenolites* isp. have been reported [2].

Four discontinuity surfaces were recognized, characterized by the following features: SB1, local colonization with *Gastrochaenolites ornatus* and *Rhizocorallium* isp.; SB2, *Gastrochaenolites*; SB3, scarce and local presence of *Gastrochaenolites*; and SB4, local presence of *Gastrochaenolites* in bimodal sizes. Generally, the specimens recognized on the discontinuity surfaces exhibit passive infill and vertical disposition. The lithologies associated with the discontinuities range from shale to medium-grained sandstone. All the colonized surfaces here studied, was generated in a coastal marine environment during an important sea-level fall leading to the exhumation and erosion, conforming a sequence boundary. Subsequently, during a sea level rise, these surfaces, constituted as firmgrounds, were colonized during the early periods of transgression, giving rise to the conditions required for the development of the *Glossifungites* Ichnofacies. Differences in size and diameter of *Gastrochaenolithes* suggest a complex colonization history associated with paleoenvironmental stress.

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THE YOUNGEST *DICTYODORA* FROM THE LATE PERMIAN DEEP SEA IN WEST QINLING, CENTRAL CHINA

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Dictyodora Weiss, 1884 has been generally considered an ichnogenus with restricted temporal ranges from the Cambrian to the Mississippian. Until now, there have been no reports of *Dictyodora* after the Mississippian. Here, we report well-preserved and abundant *Dictyodora* from deep-sea sediments of the Lopingian Maomaolong Formation in West Qinling, central China, which is hitherto the youngest occurrence of *Dictyodora* and extends its stratigraphic range to the Late Permian. Two ichnospecies of *Dictyodora* are distinguished in the study area: *D. zimmermanni* and *D. cf. scotica*. Unlike the small-sized *Dictyodora* in pre-Pennsylvanian deposits, the three-dimensional morphology of *Dictyodora* studied herein shows singular amplitudes and longer limbs with clearly inclined walls and basal burrows. The described *Dictyodora* is interpreted to be made by a soft-bodied worm-like organism with a snorkel-like organ, in similarity to other *Dictyodora* documented in previous studies. Detailed systematic ichnological features of *Dictyodora* ichnotaxobase, as well as SEM and EDS results indicate that the described *Dictyodora* is not simply a respiration structure made during locomotion of the trace maker but results from its active filling by the trace maker. *Dictyodora* is probably not a good indicator of deep-marine environment in the Paleozoic. Our dataset indicates that *Dictyodora* originated in shallow-marine environments in the early Cambrian, then migrated into the deep sea in Ordovician time and marginal-marine environments in the Wenlock, and finally got restricted to deep-marine environments in the Carboniferous and Permian. Detailed comparison with global biotic-environmental changes suggests that the evolutionary trend of *Dictyodora* is multiply affected by the Great Ordovician Biodiversification Event, the close of the Iapetus and Rheic oceans, and the Late Devonian and end-Permian mass extinctions. Both *Psammichnites* and *Dictyodora* are structures made by organisms with snorkel-like organs, and both were eliminated during the end-Permian mass extinction.