Radial Domichnia–Fodinichnia ichnofossil from the Lower Cretaceous of San Andrés (Santander, Colombia)

Icnofósil radial Domichnia–Fodinichnia del Cretácico inferior en San Andrés (Santander, Colombia)

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Highlights

- A previously undescribed radial trace fossil from the Lower Cretaceous Aguardiente Formation (Colombia) is documented.
- Artificial intelligence–assisted three-dimensional reconstruction provided enhanced visualization of the specimen's internal architecture and stratified gallery system.
- Morphological, similarity, and parsimony analyses indicate that the trace fossil cannot be confidently assigned to any established radial ichnogenus.

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Palabras clave:

Formación Aguardiente; icnofósil radial; Domichnia–Fodinichnia; Polychaeta; Cretácico Inferior; Santander.

ABSTRACT

Introduction. Burrow and tunnel systems preserved in sandy and muddy marine substrates are commonly associated with the behavioral activities of polychaete worms and other benthic invertebrates, providing relevant ethological information in sedimentary records. **Objectives.** This study aims to *i)* describe the morphological and ethological characteristics of a radial ichnofossil, *ii)* evaluate its possible correspondence with previously established radial ichnogenera, and *iii)* propose paleoecological interpretations of the trace-making organism and its depositional environment. **Materials and Methods.** A detached sandstone block from the Aguardiente Formation (Albian–Cenomanian, Lower Cretaceous) was examined along the banks of the Hisgaura River, San Andrés municipality (Santander, Colombia). The trace architecture was documented through high-resolution photography, digital image processing, and artificial intelligence–assisted three-dimensional reconstruction to enhance visualization of its morphology and internal organization. UPGMA–Jaccard similarity and parsimony analyses were applied to assess relationships with other radial and rosette ichnogenera. **Results.** The specimen is preserved in full relief and consists of a central ellipsoidal chamber from which slightly sinuous tubular galleries radiate, locally arranged in superposed tiers. Similarity analysis groups the structure with *Arenituba*, *Guanshanichnus*, and *Hartsellea*. Parsimony analysis recovered a single most-parsimonious tree (length = 32 steps; CI = 0.34; RI = 0.7) in which the specimen forms part of a clade characterized primarily by branched galleries and shallow-marine occurrence. **Conclusions.** The structure records ethological evidence of a benthic organism inhabiting sandy shallow-marine environments. Diagnostic differences preclude confident assignment to any previously established radial ichnogenus.

RESUMEN

Introducción. Los sistemas de madrigueras y galerías preservados en sustratos marinos arenosos y fangosos están comúnmente asociados con las actividades comportamentales de poliquetos y otros invertebrados bentónicos, aportando información etológica relevante en el registro sedimentario. **Objetivos.** Este estudio tiene como objetivos: *i)* describir las características morfológicas y etológicas de un icnofósil radial, *ii)* evaluar su posible correspondencia con icnogéneros radiales previamente establecidos, y *iii)* proponer interpretaciones paleoecológicas del organismo constructor y de su ambiente de depósito. **Materiales y Métodos.** Se examinó un bloque desprendido de arenisca de la Formación Aguardiente (Albiano–Cenomaniano, Cretácico Inferior), localizado en la ribera del río Hisgaura, municipio de San Andrés (Santander, Colombia). La arquitectura de la traza fue documentada mediante fotografía de alta resolución, procesamiento digital de imágenes y reconstrucción tridimensional asistida por inteligencia artificial para mejorar la visualización de su morfología y organización interna. Se aplicaron análisis de similitud UPGMA–Jaccard y análisis de parsimonia para evaluar relaciones con otros icnogéneros radiales y en roseta. **Resultados.** El espécimen se preserva en relieve completo y consiste en una cámara central elipsoidal desde la cual irradian galerías tubulares ligeramente sinuosas, localmente dispuestas en niveles superpuestos. El análisis de similitud agrupa la estructura con *Arenituba*, *Guanshanichnus* y *Hartsellea*. El análisis de parsimonia recuperó un único cladograma más parsimonioso (longitud = 32 pasos; CI = 0,34; RI = 0,7), en el que el espécimen forma parte de un clado caracterizado principalmente por galerías ramificadas y desarrollo en ambientes marinos someros. **Conclusiones.** La estructura registra evidencia etológica de un organismo bentónico que habitaba ambientes marinos arenosos someros. Las diferencias diagnósticas impiden su asignación confiable a un icnogénero radial previamente establecido.

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INTRODUCCIÓN

Polychaetes, commonly referred to as bristle worms due to the presence of chaetae, play a significant role in coastal ecology and marine ecosystems, as well as in paleontology and sedimentology, because of their influence on sedimentary processes and the recycling of organic matter(1). Variations in the diversity and population density of these organisms may reflect changes in physical and chemical environmental parameters. Consequently, they are widely used as indicators of shoreline stability, contamination levels, and both present and past environmental conditions(2). The biological activities of polychaetes contribute to marine ecosystems in multiple ways: they stabilize and rework sediments, construct habitats for other marine organisms, promote biodiversity by forming dense colonies, serve as a food source for other species due to their high protein content, and regulate populations of other invertebrates(3-4). Their paleontological record is also relatively abundant in terms of behavioral evidence and life modes, making them a key group in ichnological research. Ichnology is the discipline devoted to the study of trace fossils preserved as sedimentary structures produced by biological activity, including footprints, burrows, borings, fecal pellets, and other biogenic structures. Marks that do not reflect behavioral function are excluded from ichnological analysis. Trace fossils representing ethological activity may be regarded simultaneously as paleontological and sedimentological entities, supporting and complementing interpretations derived from both disciplines within sedimentary geology(5). Ichnology occupies a conceptual crossroads between paleontology (and biology) and sedimentology (and stratigraphy). Trace fossils link paleontology and sedimentology in ways that most body fossils cannot. In this context, ichnological research provides dynamic connections among multiple fields. The analysis of specific ichnofaunas yields significant contributions to paleoecology, sedimentology, sequence stratigraphy, reservoir characterization, diagenesis, paleoclimatology, paleoceanography, biostratigraphy, evolutionary paleoecology, paleoanthropology, and archaeology(6). Moreover, trace fossils are commonly more abundant in lithological units where body fossils are scarce(6). In Colombia, the paleontological record of polychaetes has traditionally been limited to members of the family Serpulidae, whose calcareous tubular fossils are commonly found attached to bivalve or gastropod shells. More recently, Duque et al.(7-8) reported two polychaete species from the Upper Cretaceous Conejo Formation: a representative of the family Pectinariidae characterized by an agglutinated tube constructed from sand grains and shell fragments, and the species *Protopholoe colombiana* (Order: Capitellida), distinguished by a prostomium lacking appendages and the absence of palps. The objective of this study is to describe a biogenic structure preserved in shallow-marine sandstones and to evaluate its morphological and ethological affinities with radial or rosette-shaped ichnogenera documented in the literature.

MATERIALS AND METHODS

Study Area. The trace fossil described herein was documented in 2019 during a field excursion conducted within the framework of a Paleontology course at Universidad de Santander (UDES). The structure occurs on a detached (rolled) sandstone block of the Aguardiente Formation (Cretaceous: Albian–Cenomanian), exposed along the bank of the Hisgaura River in the municipality of San Andrés, Santander, Colombia (N 6.782353°; W 72.842428°) (**Figure 1**). Due to its considerable weight, the block was not collected and was left in situ. Therefore, detailed field notes and photographic records were obtained for subsequent analysis.

The geological units exposed in the study area include the Tibú-Mercedes Formation and the Aguardiente Formation, as well as younger travertine deposits containing plant fossil remains (**Figure 2**). According to Caballero and Sierra(9), the Tibú-Mercedes Formation in the San Andrés area is characterized by a high proportion of calcareous rocks, expressed as limestones, calcareous-cemented sandstones, and calcareous mudstones.

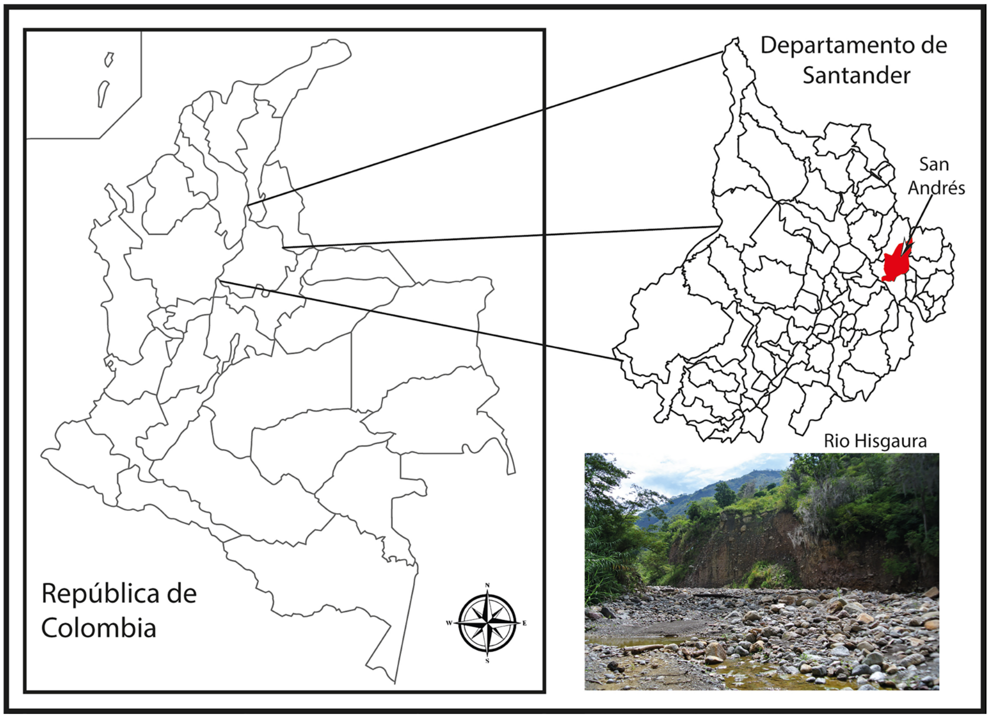


Figure 1. Hisgaura River in the municipality of San Andrés, Santander, Colombia.

In the study area, the Aguardiente Formation consists predominantly of medium- to very coarse-grained white quartz arenites with cross-stratification and glauconitic levels at the base of the unit; conglomerates composed of quartz granules with shell molds; and subordinate light gray fissile sandy mudstones. The formation is mainly sandy, quartz-rich, and well indurated, with partings filled by micaceous and carbonaceous material that in some strata is widely disseminated, locally darkening the sandstones.

The Aguardiente Formation represents a littoral depositional environment consistent with a barrier-island system, including tidal channels and lagoonal tidal flats, with facies associated with tidal inlet, flood-tidal delta, ebb-tidal delta, tidal flat, and lagoon settings(9).


Calcareous rocks (Tibú-Mercedes Formation)
Sandstones (Aguardiente Formation)
Quaternary travertines

Figure 2. Rocks and fossils found at the Hisgaura River study site.

Photographic Analysis. Because the trace fossil was not collected, analysis was based exclusively on two-dimensional photographic documentation. Digital image-processing techniques were applied to generate a pseudo-relief representation and a depth map, which facilitated: *i)* Enhancement of morphological details; *ii)* Evaluation of illumination and shadow patterns and *iii)* Simulation of three-dimensional perspectives Adobe® Photoshop® software was used to convert the original color images to grayscale. From these, a depth map was constructed. Additionally, an oblique-view relief image with lateral illumination and a red–blue stereoscopic image were generated to enhance visualization of spatial relationships within the structure.

Three- Dimensional Reconstruction Using Artificial Intelligence. For exploratory visualization, a three-dimensional reconstruction was generated from two-dimensional images using the Tripo 3D AI platform (https://studio.tripo3d.ai/home), limited free version. The grayscale image processed in Adobe® Photoshop® served as input for the reconstruction. The platform produces a triangulated mesh model that is subsequently textured to enhance visualization. The generated files were exported in OBJ format for three-dimensional viewing and in GLB format for potential 3D printing. It should be noted that AI-generated models do not provide metrically precise reconstructions but preserve the principal geometric characteristics of the trace fossil.

Morphometric Analysis. Measurements of gallery width and length were obtained using the public-domain software ImageJ 1.54g (http://imagej.org).

Cluster and Parsimony Analyses. A binary character matrix (**Table 1**) was constructed based on the descriptions of radial and rosette-shaped ichnogenera provided by Muñoz et al.(10) The ichnogenera *Asterichnites*, *Cycloichnus*, *Rotamedusa*, and *Sphaerichnus* were excluded because they do not conform to models of radially arranged structures originating from a central chamber or a vertical central axis. A dendrogram was generated using the UPGMA algorithm and the Jaccard similarity index, both appropriate for binary datasets. Additionally, a cladogram derived from parsimony analysis was constructed using a heuristic search with subtree pruning and regrafting (SPR) and unordered characters. All analyses were performed using the PAST (Paleontological Statistics Software Package for Education and Data Analysis), (https://www.nhm.uio.no/english/research/resources/past/).

Seriation. To determine the chronological distribution and stratigraphic occurrence of the ichnogenera, a seriation analysis was conducted in PAST based on a binary matrix incorporating the ichnogenera and geological time intervals. This procedure allowed identification of the ichnogenus selected as the outgroup for the parsimony analysis.

RESULTS

Observations. The trace fossil displays a central chamber from which radial tunnels or galleries extend. The galleries have an average diameter of 2.9 mm (n = 18) and exhibit moderate sinuosity. The central chamber measures 1.78 and 1.39 cm in diameter. The radial galleries reach an average length of 4 cm (n = 6) (**Figure 3**). In several galleries that have detached from the host rock, impressions of quasi-square internal segments are visible. In other cases, semicircular structures are observed in the terminal portions of the tunnels (**Figure 4**). A schematic representation of the tubular system (**Figure 5A**) indicates superposition of galleries at different vertical levels. To facilitate interpretation of this spatial arrangement, (**Figure 5B**), illustrates the inferred stratification of the galleries. The uppermost galleries are interpreted as the oldest. For descriptive purposes, the vertical arrangement was arbitrarily divided into four levels in order to simplify representation of the behavioral pattern of the trace-making organism.

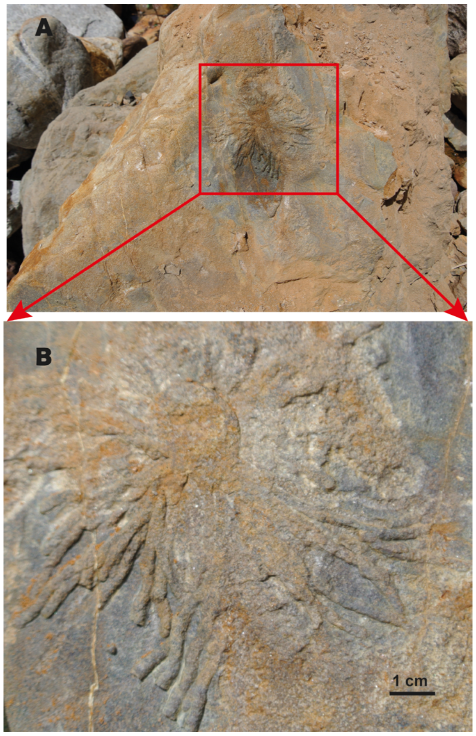


Figure 3. Overview and structural details of the trace fossil. (**A**) General view; (**B**) Detailed view highlighting its structure.

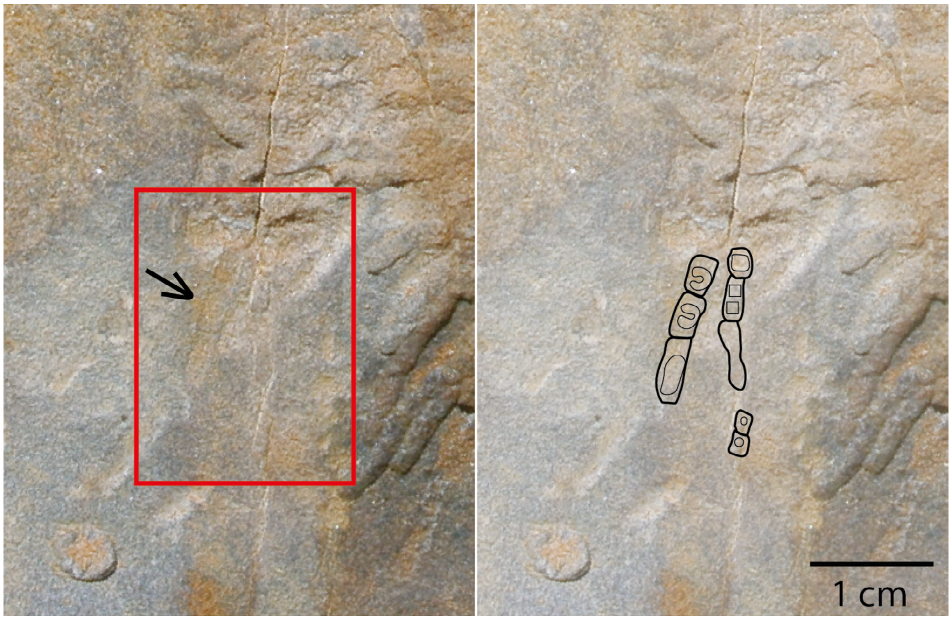


Figure 4. Detail of elongated structures showing internal modular divisions and semicircular terminal features.

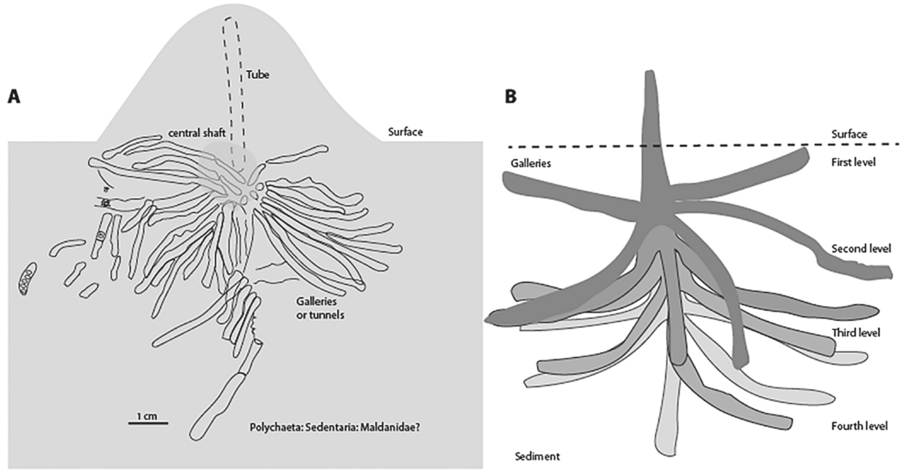


Figure 5. General schematics. (**A**) Field detail of the trace fossil. (**B**) Interpretative reconstruction of vertically stacked galleries.

Photographic Analysis. Two-dimensional photographic analysis highlights the sinuosity of the galleries and the vertical stacking of successive phases of biological activity. Conversion of the original image to grayscale followed by application of an emboss filter at an angle of 135° allowed construction of a relief map (**Figure 6B**), providing a visual approximation of depth variations within both the galleries and the central chamber. The inclined relief representation (**Figure 6C**) and the stereoscopic inclined relief image (**Figure 6D**) generate an apparent three-dimensional effect, supporting the interpretation of stratified gallery construction associated with repeated feeding activity.

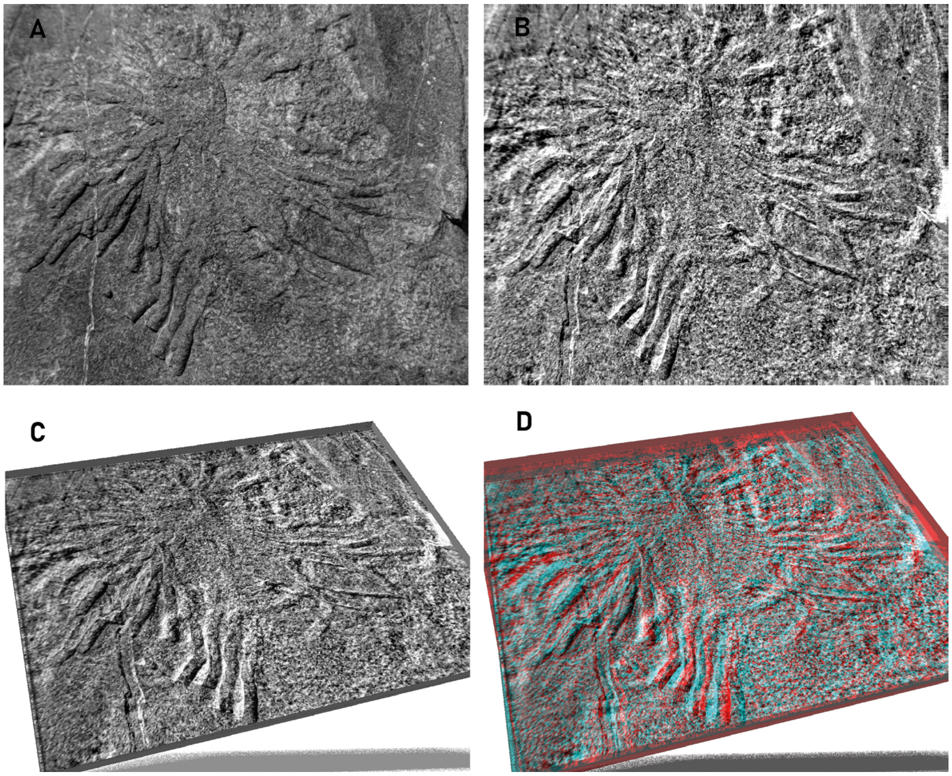


Figure 6. Two-dimensional image processing. (**A**) Grayscale image. (**B**) Relief map. (**C**) Inclined relief map. (**D**) Stereoscopic inclined relief map (pseudo-3D).

Three-Dimensional Reconstruction Using Artificial Intelligence. Reconstruction of the fossil structure using the Tripo 3D AI platform (**Figure 7**) allowed clearer visualization of the horizontal and vertical spatial distribution of the galleries. Although the reconstruction is not metrically exact, it preserves the principal morphological characteristics of the trace fossil. No artificial structural artifacts are evident. However, the algorithm generated a dome-like vertical relief of the overall structure, likely as a computational solution to accommodate the stacked gallery geometry. The triangulated mesh generated by the AI platform and the textured model are shown in (**Figure 7A–B**), respectively. The texture enhances contrast between light and shadow and facilitates recognition of morphological features. Comparison between the grayscale two-dimensional image and the textured three-dimensional reconstruction (**Figure 7C–D**) demonstrates strong correspondence in overall geometry and gallery arrangement.

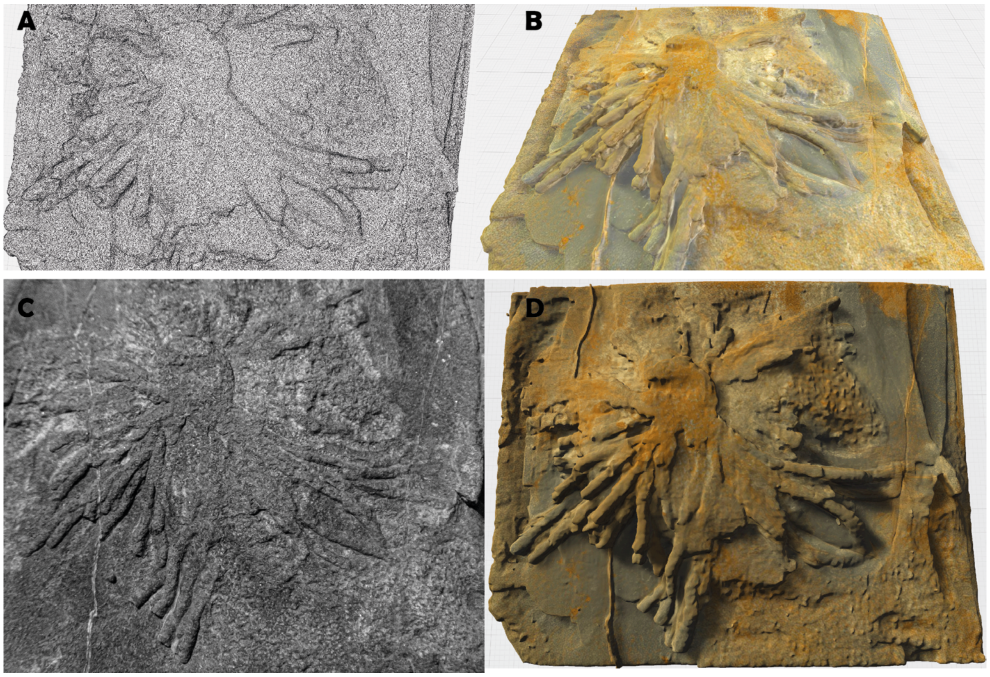


Figure 7. Three-dimensional reconstruction using artificial intelligence. (**A**) Triangular mesh. (**B**) Textured mesh. (**C**) Grayscale 2D image. (**D**) Textured 3D reconstruction.

Based on the morphological characteristics observed in the trace fossil and on the combined analysis of two-dimensional imagery, pseudo-relief models, and AI-assisted reconstruction, the structure is interpreted as an ethological trace produced by an organism inhabiting sandy substrate. The organism likely occupied a central chamber and constructed a vertical shaft from which sinuous galleries extended subhorizontally, locally penetrating deeper into the surrounding sediment.

Morphological Identification Key. For morphological identification of the biogenic structure, a comparative dichotomous key was constructed based on the concise morphological descriptions and illustrations of radial and rosette-shaped trace-fossil genera compiled by Muñoz et al.(10) Its purpose is comparative and operational, intended to evaluate the morphological affinity of the studied specimen rather than to provide a comprehensive systematic revision of these groups.

Dichotomous Key for Radial, Rosette-Shaped, and Related Ichnotaxa

1a.	Structure clearly subcircular or spherical, with radial lobes and/or axial extensions.	**2**
1b.	Structure clearly radiate, with ray-like elements or galleries (rosette-shaped, palmated, or radially arranged), or with galleries/tunnels radiating from a central point	**3**
2a.	Spherical or nearly spherical structure with radial lobes and no internal spreiten; possible deposit/excremental function	***Sphaerichnus***
2b.	Subcircular structure with a central depression and two concentric ridges covered by radial costae	***Rotamedusa***
3a.	Presence of a shaft (tube) or clearly identifiable central chamber from which galleries, tubes, or rays radiate	**4**
3b.	Absence of a shaft (vertical axis); rosette-, star-, or radially netted structure without an evident central tube	**10**
4a.	Central shaft with radial galleries displaying menisci or annulations	**5**
4b.	Central shaft with radial galleries lacking menisci or annulations	**7**
5a.	Burrow branching upward from a central axis, palmated distribution; tube walls lined and meniscate or with transverse backfill	***Hartsellea***
5b.	Burrow with radially distributed tunnels, branched or unbranched	**6**
6a.	Burrow with annulated or moniliform tunnels composed of meniscate segments, forming successive and irregular branching systems in radial distribution	***Cladichnus***
6b.	Broad central shaft with narrow horizontal radial tunnels exhibiting meniscate structures and sandy coatings of pelleted annuli	***Phoebichnus***
7a.	Vertical central shaft with radial tubes, branched or unbranched, horizontal or subhorizontal, forming palmated or stellate rosette-like structures and galleries with spreiten (laminae)	***Dactyloidites***
7b.	Central shaft with short radial galleries or a different pattern; includes funnel-shaped burrows	**8**
8a.	Inverted funnel-shaped structure with annular corridor connected to the surface by multiple vertical shafts.	***Heliochone***
8b.	Structure not funnel-shaped; galleries extending from a central axis in horizontal radial arrangement or curving upward	**9**
9a.	Central shaft with vertically radiating tunnels bearing non-overlapping spreiten; in plan view, tunnels radially distributed without merging	***Haentzschelinia***
9b.	Curved tunnels arranged in a fan-like or radial pattern, becoming horizontal in a descending pattern from a vertical axis	***Scotolithus***
10a.	Sinuous galleries or tunnels, branched or unbranched, forming a radial rosette-like biostructure	**11**
10b.	Straight galleries or tunnels, or arranged in concentric semicircles	**21**
11a.	Galleries ornamented with transverse ridges or mammillated appearance	***Clematischnia***
11b.	Galleries smooth or finely annulated	**12**
12a.	Structure with rosette-shaped galleries covering all radial quadrants	**13**
12b.	Structure with galleries not covering all radial quadrants	**22**
13a.	Presence of central knobs or nodules with multiple narrow radial tunnels	***Capodistria***
13b.	Absence of central knobs	**14**
14a.	Cone-shaped burrow composed of small, irregular, backfilled tubes, vertical and oblique; in plan view, tunnel openings radially distributed without merging	***Parahaentzschelinia***
14b.	Rosette-shaped burrow	**15**
15a.	Galleries branched or bifurcated	**16**
15b.	Galleries unbranched and not bifurcated	**18**
16a.	Central structure from which smooth or finely annulated tubes or galleries originate, irregular, branched or unbranched, coated or filled with sand	***Arenituba***
16b.	Central structure from which smooth tubes originate, exhibiting bifurcations	**17**
17a.	Structure from which numerous thin radiating tunnels (rays) arise, bifurcated; short vertical burrow	***Guanshanichnus***
17b.	Defined central area with radial crest-like convexities, some bifurcating centrifugally	***Radiichnus***
18a.	Narrow, densely spaced galleries forming a multi-tiered rosette pattern	***Stelloglyphus***
18b.	Separated galleries arranged in a radial pattern	**19**
19a.	Stellate form with unbranched rays and radial retrusive spreiten	***Asterichnus***
19b.	Looser stellate form, tubes or rays lacking spreiten	**20**
20a.	Defined central area; horizontal or subhorizontal club-shaped lobed tubes, unbranched, originating from a central point, sometimes at multiple levels	***Gyrophyllites***
20b.	No defined central area; elliptical ray-like tunnels radiating from a poorly defined central region	***Volkichnium***
21a.	Exactly eight sharp grooves or rays radiating from an unmarked central zone; small accumulations of matrix at the inner ends (star-shaped appearance)	***Asterichnites***
21b.	Galleries arranged in concentric semicircles distributed around a central axis	***Cycloichnus***
22a.	Bilobate galleries with random radiate pattern and passive infill	***Dactylophycus***
22b.	Galleries not bilobate	**23**
23a.	Biserial feather-like (feathering) pattern, without defined central axis, with needle-like branching resembling conifer needles or a feather	***Taxichnites***
23b.	Non-feathered pattern; arched tunnels or tunnels penetrating a funnel-shaped structure	**24**
24a.	Funnel-shaped burrow penetrated by a central tube and smaller tubes extending into the sediment from the base of the funnel	***Monocraterion***
24b.	Burrow not funnel-shaped; flattened arched galleries nearly touching distally and radiating from the center, lacking spreite	***Bifasciculus***

Upon application of the dichotomous key to the studied specimen, the presence of a central chamber or axial shaft with radially arranged galleries directs the identification toward ichnogenera characterized by structures with a central shaft. The absence of well-developed menisci and the morphology of the tunnels—relatively thick, sinuous, locally branched, and sand-filled—place the specimen within the group of ichnogenera that includes *Arenituba*, *Guanshanichnus*, and related taxa. However, detailed comparison with published descriptions and illustrations reveals significant morphological discrepancies, particularly in the diameter and configuration of the radiating elements, thereby precluding an unequivocal assignment to any of these established ichnogenera.

Analytical Approach. The comparative analysis was based on discrete morphological, architectural, behavioral, and paleoenvironmental characters derived from published descriptions of radial and rosette-shaped ichnotaxa. Only characters that contributed to analytical consistency were retained; therefore, character numbering is non-consecutive. All characters were treated as binary (0/1). Character definitions and coding scheme are summarized in (Table 1). The resulting data matrix used for cluster and parsimony analyses is presented in (Table 2).

Table 1. Character definitions and binary coding scheme

Character	Category	Description	State 0	State 1
2	Architecture	Development of central chamber	Poorly developed or absent	Well defined
3	Behavioral / Tiering	Relative depth of the gallery system within the sediment	Shallow	Deep
4	Paleoenvironmental	Environmental distribution range (shallow –deep settings)	Broad	Restricted
5	Paleoenvironmental	Occurrence in deep -water environments	Present	Absent
6	Behavioral	Presence of spreiten (curved laminae produced by systematic sediment reworking)	Absent	Present
7	Architecture	Branching pattern of galleries	Simple	Branched
8	Architecture	Gallery geometry	Straight	Sinuous
9	Architecture	Funnel-shaped burrow morphology	Absent	Present
10	Architecture	Dominant orientation of gallery development	Horizontal	Vertical
11	Architecture	Vertical stratification of galleries	Single-tiered	Multi-tiered
12	Architecture	Overall gallery morphology	Uniform	Palmated, club-shaped, semicircular, or related forms

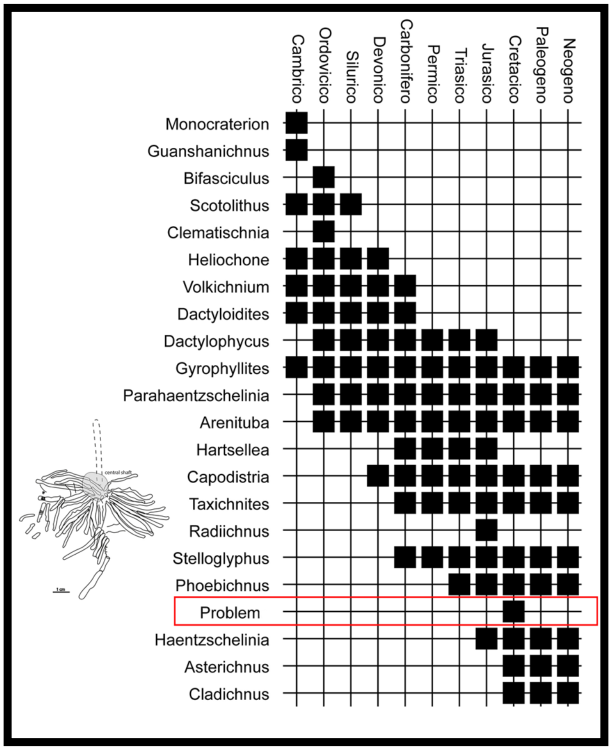
Table 2. Binary character matrix used for cluster and parsimony analyses

Ichnogenera	2	3	4	5	6	7	8	9	10	11	12
Gyrophyllites	0	0	0	0	0	0	0	0	0	1	0
Volkichnium	0	0	0	0	0	0	0	0	0	0	0
Arenituba	1	0	0	0	0	1	1	0	0	0	0
Asterichnus	0	0	0	0	1	0	0	0	0	0	1
Bifasciculus	0	0	1	0	0	0	1	0	0	0	0
Capodistria	1	0	1	0	0	0	1	0	0	0	1
Cladichnus	0	0	0	0	0	1	1	0	0	0	1
Clematischnia	1	0	1	1	0	1	1	0	0	0	1
Dactyloidites	1	1	0	1	1	0	0	0	0	1	1
Dactylophycus	0	0	0	1	0	1	0	0	0	0	0
Guanshanichnus	1	0	0	1	0	1	1	0	0	0	0
Haentzschelinia	1	1	0	1	1	0	0	0	1	1	1
Hartsellea	1	0	1	1	0	1	1	0	1	0	0
Heliochone	1	0	1	0	0	0	0	1	1	1	1
Monocraterion	1	0	1	1	0	0	1	1	1	1	1
Parahaentzschelinia	1	0	0	1	0	0	0	1	1	1	1
Phoebichnus	1	0	0	0	0	0	0	0	0	0	1
Radiichnus	0	0	1	1	0	1	1	0	0	0	0
Scotolithus	0	0	1	1	0	0	1	0	0	0	0
Stelloglyphus	0	0	0	0	0	0	0	0	0	0	1
Taxichnites	0	0	1	0	0	1	0	0	1	0	1
San Andrés trace fossil (Problem)	**1**	**0**	**1**	**1**	**0**	**1**	**1**	**0**	**0**	**1**	**0**

Note. Character numbering is non-consecutive because only those characters that contributed to analytical consistency were retained in the final matrix.

Seriation, Similarity, and Parsimony. The seriation analysis illustrates the temporal distribution of the radial and rosette ichnogenera across geological periods, indicating that *Gyrophyllites* is the most persistent ichnogenus since the Cambrian (**Figure 8**). For this reason, *Gyrophyllites* was selected as the outgroup in the parsimony analysis. This decision was also methodological, as the parsimony algorithm implemented in PAST designates the first row in the data matrix as the outgroup for tree construction.

The UPGMA–Jaccard similarity analysis based on the data in (**Table 2**), produced a dendrogram with a cophenetic correlation coefficient of 0.8. The San Andrés trace fossil (**Figure 9B**) clusters within the group comprising *Arenituba*, *Guanshanichnus*, *Hartsellea*, and *Radiichnus*, showing closest affinity to *Hartsellea* and *Clematischnia*. A comparable relationship is observed in the parsimony analysis, which yielded a single most-parsimonious cladogram with a tree length of 32 steps, a consistency index (CI) of 0.34, and a retention index (RI) of 0.7 (**Figure 9A**). In this topology, the San Andrés trace fossil forms part of the clade ((((((San Andrés trace fossil, Clematischnia) Hartsellea) (Dactylophycus, Radiichnus) Guanshanichnus) Arenituba) Cladichnus).



	Cambrico	Ordovicico	Silurico	Devonico	Carbonifero	Permico	Triasico	Jurasico	Cretacico	Paleogeno	Neogeno
Monocraterion	■										
Guanshanichnus	■										
Bifasciculus		■									
Scotolithus	■	■	■								
Clematischnia		■									
Heliochone	■	■	■	■							
Volkichnium	■	■	■	■	■						
Dactyloidites	■	■	■	■	■						
Dactylophycus		■	■	■	■	■	■	■			
Gyrophyllites	■	■	■	■	■	■	■	■	■	■	■
Parahaentzschelinia		■	■	■	■	■	■	■	■	■	■
Arenituba		■	■	■	■	■	■	■	■	■	■
Hartsellea					■	■	■	■			
Capodistria				■	■	■	■	■	■	■	■
Taxichnites					■	■	■	■	■	■	■
Radiichnus								■			
Stelloglyphus					■	■	■	■	■	■	■
Phoebichnus							■	■	■	■	■
Problem									■		
Haentzschelinia								■	■	■	■
Asterichnus									■	■	■
Cladichnus									■	■	■

Figure 8. Temporal seriation analysis of radial and rosette ichnogenera.

This clade is supported primarily by the presence of branched galleries. Excluding *Arenituba* and *Cladichnus*, the subclade (((((San Andrés trace fossil, Clematischnia) Hartsellea) (Dactylophycus, Radiichnus) Guanshanichnus) is additionally characterized by preferential development in shallow marine environments. It is important to emphasize that parsimony analysis in this context does not evaluate phylogenetic relationships among organisms but rather serves as a heuristic tool to assess morphological and ethological similarity among trace-fossil architectures. The relatively low CI (0.34) indicates a high degree of homoplasy in structural patterns, which is expected because similar burrow architectures may evolve independently in unrelated organisms under comparable environmental conditions. Therefore, CI values are not necessarily indicative of poor analytical quality in ichnological studies. The RI value (0.7) suggests moderate structural congruence among characters within the proposed topology. However, it must be noted that the number of characters included in the analysis is limited, and the units analyzed are behavioral structures rather than organisms. Trace fossils represent responses to environmental constraints and may be constructed by different taxa that converge on similar architectural solutions. Based on the comparative, similarity, and parsimony analyses, the San Andrés trace fossil cannot be confidently assigned to any established radial ichnogenus. From an ethological perspective, the structure reflects both dwelling and feeding behavior, and is therefore classified within the Domichnia–Fodinichnia category. The studied specimen shares with *Guanshanichnus glockerichnoides* the development of a multi-tiered residential structure composed of superposed galleries(9). However, the radial elements differ markedly in morphology.

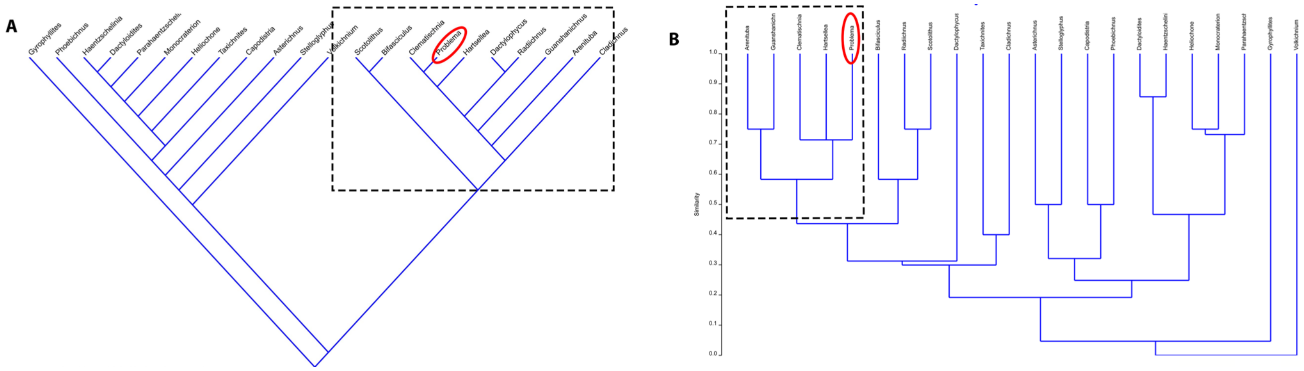


Figure 9. Similarity and parsimony analyses. (**A**) Parsimony cladogram. (**B**) UPGMA–Jaccard similarity dendrogram.

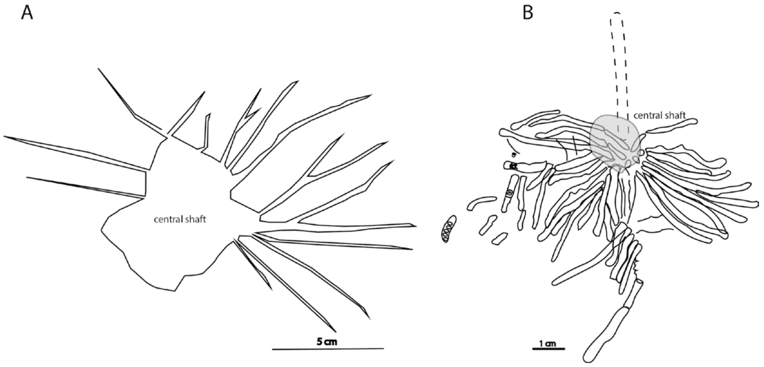


Figure 10. Morphological comparison between *Guanshanichnus glockerichnoides* and the San Andrés trace fossil. (**A**) Redrawn from **Figure 6A** of Weber et al.(11) (**B**) General schematic of the studied specimen. Note the thin, pointed radial elements in *G. glockerichnoides* compared with the thicker tubular galleries of the studied trace fossil.

DISCUSSION

Ichnotaxonomy: The identification of trace fossils—and particularly of their tracemakers—is inherently complex. Soft-bodied organisms lacking hard skeletal elements have low preservation potential, reducing the likelihood of direct body-fossil association. Exceptional fossil deposits such as the Burgess Shale and Chengjiang Lagerstätten demonstrate that under special taphonomic conditions soft tissues may be preserved with remarkable fidelity. However, the depositional environment of the studied specimen does not correspond to such preservational settings. The taxonomy of animal-derived fossils and ichnofossils is regulated by the International Code of Zoological Nomenclature (ICZN). The assignment of an ichnotaxon at the ichnospecies level ideally requires a clear morphological diagnosis, although it does not necessarily require certainty regarding the biological producer(6). A recurring difficulty arises from the fact that similar ethological structures may be produced independently by different species—even belonging to distinct higher taxa—thereby complicating taxonomic attribution. The ICZN (Articles 10.3 and 13.3) establishes the conditions for availability and validity of names proposed for collective groups and ichnotaxa. In particular, names proposed for ichnotaxa are treated as family-, genus-, or species-group names depending on their original establishment, and generic names published after 1930 must be accompanied by fixation of a type species. When a new ichnogenus or ichnospecies is proposed, it must represent a morphologically discrete and diagnosable unit distinct from previously established taxa. A classic example of trace–producer linkage is *Thalassinoides suevicus*, whose burrow systems were found associated with chela fragments of crustaceans (*Hoploparia dentata* and *H. longimana*) in Lower Cretaceous deposits of central Crimea(12). The specimen analyzed herein presents a significant interpretative challenge requiring high-level zoological and paleontological expertise. Consensus among consulted geoscientists supports interpretation as a trace fossil, whereas specialists in marine invertebrates expressed divergent views regarding the identity of the possible tracemaker.

Taxonomic Discernment: The specimen exhibits a sandy structural consistency and is non-calcareous in nature. Following a detailed analysis of its morphology, the following taxonomic conclusions have been derived: *i)* Cnidarians and Bryozoans: Its belonging to a cnidarian colony is ruled out due to the absence of polyps, coralites, or septa. Likewise, the lack of characteristic apertures allows for the exclusion of bryozoans; *ii)* Macroalgae: The hypothesis of an algal thallus has been dismissed. The mode of preservation does not correspond to carbonaceous compression (typical of non-calcified macroalgae) but rather shows the properties of a sedimentary infill; *iii)* Structural Differentiation: The specimen lacks the internal network of medullary and cortical tubes that would define genera such as Codium. Therefore, the evidence suggests it is a trace fossil (ichnofossil) rather than an algal organism. Regarding the small pinnate structures located at one end of the central chamber, these have been excluded from the main analysis of the radiate body. It is considered that they could be intrusive elements from other organisms or independent structures unrelated to the main unit.

Expert Opinions. The taxonomic nature of the specimen has generated a technical debate among specialists from various disciplines, primarily divided into two perspectives: ichnological and zoological interpretation: *i) Ichnological Analysis (Trace Fossil).* Several experts agree that the general morphology is consistent with a trace fossil. The following comparative observations have been made: Differentiation from *Guanshanichnus glockerichnoides*: Although a structural similarity exists, the specimen under study presents thicker, septate, or knotty rays, some of which are branched. This contrasts with *G. glockerichnoides*, whose rays are thinner, tapered, and exhibit terminal bi- or trifurcations, allowing for its exclusion from this ichnospecies (**Figure 10**). Technical Consensus: There is general agreement that the structure functions as a record of biological activity (trace), although the need for deeper morphological and biological analysis to precisely determine its affinity is emphasized. *ii) Zoological Analysis (Body Fossil).* From the perspective of marine zoology and invertebrate morphology, affinities with living organisms have been proposed: Polychaetes: This option was initially evaluated but discarded because the specimen's "segmented" tentacles do not match the known morphology of this group. Anthozoans and Holothuroids: A possible relationship with tube-dwelling anemones (Ceriantharia) or sea cucumbers (Holothuroidea) has been suggested. This hypothesis is supported by the presence of a robust cylindrical body located beneath the appendages, as well as the correspondence in size range and proportions with extant taxa. This diversity of criteria underscores the complexity of the specimen. It exhibits significant morphological ambiguity, combining characteristics typical of radial ichnological structures with elements reminiscent of the tentacular appendages of modern organisms.

Paleoecological Interpretation: The available evidence supports interpretation of the structure as an ethological trace produced by a benthic marine organism inhabiting sandy, shallow-marine to possibly intertidal environments, as suggested by grain size and sedimentological context. The abundance of radial galleries and their vertical stacking indicate sustained exploratory and feeding activity. In polychaete analogs—particularly maldanids—tube construction and modification are closely related to food availability. Limited organic content may promote deeper vertical excavation, whereas nutrient-rich substrates favor horizontal feeding structures. A polychaete tracemaker, functionally comparable to modern maldanids such as *Clymenella*, represents the most consistent behavioral analog. Comparisons with modern maldanid polychaetes are therefore informative. This genus constructs tubes up to 20 cm long and feeds on detritus, protozoans, and diatoms within the sediment (13-14). Maldanids may continuously construct or modify tubes throughout life(15) and are capable of absorbing dissolved organic matter(16). The vertical stratification and multiplicity of galleries observed in the San Andrés trace fossil suggest prolonged occupation of the burrow system and sustained feeding activity.

Taxonomic Position of the Specimen: Based on comparative morphology and the exploratory key, the specimen shows closest affinity to *Arenituba* and *Guanshanichnus*, but differs from *Arenituba* in mode of preservation (epirelief versus full relief) and from *Guanshanichnus* in the diameter and morphology of the radial galleries, which are thicker and more sinuous in the San Andrés trace fossil. Similarity and parsimony analyses place the specimen within a morpho-ecological grouping including *Scotolithus*, *Dactylophycus*, *Hartsellea*, *Clematischnia*, *Radiichnus*, *Guanshanichnus*, *Arenituba*, *Cladichnus*, and *Capodistria*. At present, the structure is reported solely from an ethological standpoint as a dwelling and feeding system (Domichnia–Fodinichnia), pending further field exploration and discovery of additional specimens.

CONCLUSIONS

Observations, image analyses, similarity clustering, and parsimony assessment indicate that: the specimen represents ethological evidence of a benthic organism that constructed successive radial tunnels from a central chamber, forming a multi-tiered burrow system. A polychaete exhibiting behavioral patterns comparable to modern maldanids such as *Clymenella* is considered the most consistent functional analog of the tracemaker. The described ichnological record cannot be confidently assigned to any established radial ichnogenus. Similarity and parsimony analyses place the specimen closest to *Hartsellea*, *Guanshanichnus*, and *Arenituba*, forming a morpho-ecological clade ((((((San Andrés trace fossil, *Clematischnia*) *Hartsellea*) (*Dactylophycus*, *Radiichnus*) *Guanshanichnus*) *Arenituba*) *Cladichnus*). The trace fossil has not been previously described and therefore contributes significantly to paleoecological interpretation of the Aguardiente Formation.

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ETHICAL CONSIDERATIONS

This research was based exclusively on the analysis of previously exposed geological material and photographic documentation. It did not involve the manipulation of living organisms or the collection of biological or geological samples. Therefore, approval from an institutional research ethics committee was not required.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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