



OPEN The record of *Scalichnus* ichnofabrics in ancient fluvial settings and its paleoecological significance

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Bivalves are a dominant group of benthic invertebrates in freshwater ecosystems playing significant ecological roles in fluvial and marginal lacustrine environments. Despite being active burrowers, the traces left by freshwater bivalve mollusks are less studied and documented than those of their marine counterparts, both in modern and ancient records. In this study, we provide a detailed description of a bivalve ichnofabric primarily characterized by *Scalichnus* found in fluvial deposits of the Cretaceous Exu Formation, Araripe Basin, northeastern Brazil. Most preserved traces exhibit menisci or irregular concave-upwards laminae at the base of the oval chamber, indicating upward displacement in response to sediment aggradation. Additionally, the presence of stacked *Scalichnus* in the sandbars suggests that bivalves repositioned themselves upward in the substrate during episodic or seasonal sediment accumulation. In some cases, stacked *Scalichnus* extend over 60 cm, indicating multiple aggradation events under low deposition rates, which likely allowed the animals to survive these depositional changes. In this context, the preservation of *Scalichnus* ichnofabrics is associated with variations in sedimentation rates driven by climatic seasonality. These fluctuations likely required the upward repositioning of the bivalves in response to substrate aggradation.

Keywords Bioturbation, Freshwater mollusks, Climate seasonality, Continental ichnology

Bivalve mollusks are a dominant group of benthic invertebrates in freshwater ecosystems, playing significant ecological roles in fluvial and marginal lacustrine environments^{1,2}. Adapted to various lifestyles, they are primarily infaunal or semi-infaunal suspension feeders, burrowing into substrates using their specialized foot^{3,4}. Whether adopting a shallow to deep infaunal or semi-infaunal mode of life, their ability to move up and down through the substrate is crucial for maintaining their siphons openings at the sediment-water interface^{5,6}. Although bivalve mollusks are active burrowers, the traces left by freshwater bivalve species are less studied and documented than those of their marine counterparts in both modern and ancient records. Marine and coastal settings have provided extensive evidence of trace fossils produced by bivalve mollusks since the Paleozoic^{7,8}, while records in coeval continental environments are comparatively scarce. The primary trace fossils attributed to bivalves in non-marine environments include locomotion and resting traces from the ichnogenera *Ptychoplasma*, *Lockeia*, and *Scalichnus*, as well as V-shaped traces^{9–13}. In transitional and marine settings, composite burrows indicative of downward or upward shell movement are common. These structures often belong to the ichnofamily Siphonichnidae, including the ichnogenus *Scalichnus*^{14–17}. However, *Scalichnus* or *Scalichnus*-like traces are barely recorded in continental paleoenvironments compared to other ichnogenera, such as *Lockeia*. In this study, we present a detailed comprehensive description of bivalve mollusk ichnofabrics, primarily characterized by *Scalichnus*-like structures, identified in the fluvial deposits of the Cretaceous Exu Formation, Araripe Basin, northeastern Brazil. This geological unit is notably deficient in macroscopic body fossils, highlighting the importance of trace fossils for paleoenvironmental and paleoecological interpretations. Our goals are to describe these trace fossils and discuss the paleoecological significance of their record in fluvial

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environments. To achieve this, we analyzed the nature of the *Scalichnus*-dominated paleoichnocoenosis and inferred its paleoenvironmental controls within the substrate colonization windows.

Geological settings

The Mesozoic Araripe Basin is the most extensive among the interior basins of northeastern Brazil, covering an area of ~9,000 km² (Fig. 1A). The basin is situated between the Potiguar, Parnaíba, and Tucano-Jatobá basins in the Central Domain (Transversal Zone) of the Precambrian Borborema Province¹⁸. Geological evolution comprises four stratigraphic sequences that are limited by regional unconformities associated with different tectono-stratigraphic phases, as follows: (i) the fluvio-lacustrine pre-rift; (ii) the fluvio-lacustrine syn-rift; (iii) the transitional to marine post-rift I; and (iv) the fluvial post-rift II^{19–21}. The rift and initial post-rift I sequences were generated by strike-slip tectonic reactivation of basement structures of the Precambrian Borborema Province during the Late Jurassic–Early Cretaceous, in the context of the Gondwana break-up and subsequent South Atlantic Ocean opening^{21–23}. Overlying unconformably the oldest strata, the two post-rift sequences crop out in the escarpments of the Araripe Plateau/Chapada, an east-west elongated tableland whose flat top dips slightly to W²⁴. The Aptian–Albian transitional/marine Santana Group (post-rift I sequence) comprises the Barbalha, Crato, Ipubi, and Romualdo formations. The Araripe Group (post-rift II sequence) encompasses the Araripina and Exu formations^{25–28}. Regional stratigraphic correlations with the Açu and Itapecuru formations of the Potiguar and Parnaíba basins suggest Albian to Cenomanian ages for the Araripe Group²¹.

The Exu Formation, whose trace fossils are studied herein, is an up to 240 m-thick siliciclastic unit cropping out at the upper part of the Araripe Plateau. The unit rests unconformably on the Romualdo and Araripina formations and on Precambrian crystalline rocks. Fining-upward cycles varying from immature pebbly- to coarse-grained cross-bedded sandstone with paleocurrents towards to west predominate throughout the unit^{19,28} (Fig. 1B–I). Massive and bioturbated sandstones and interbedded mudstones can be present, mainly in the western part of the basin, suggesting the occurrence of channel fill and floodplain deposits (Fig. 1J). Indeed, the Exu Formation was deposited in fluvial environments with unconfined and low-sinuosity channels. Contrary to the underlying marine fossil-rich Cretaceous units of the Araripe Basin²¹ the fossil record of the Exu Formation is meager, and biostratigraphic relevant macro- and microfossils are lacking. The depositional tract of Exu Formation shows no evidence of marine incursions^{19,21} and overall continental sedimentation with sediment supply from highlands located at East of the Araripe Basin²⁵ as suggested by paleocurrent data (Fig. 1A). Reworked rudist bivalves reported from a subjacent section referred as lower Exu Formation²⁸ belongs, in fact, to the underlying Araripina Formation. The Exu Formation deposits crop out in steep escarpments bordering the Araripe Plateau, whose top is a flat, erosional paleosurface covered by ferricretes and silcrettes²⁴. The plateau exhumed with the Exu Formation represents only a small segment of the extensive distributive fluvial system that was active during the Albian–Cenomanian interval.

Results

Sedimentary facies

The deposits studied of the Exu Formation correspond to a 40 m-long and a 24 m-thick exposed sedimentary succession. The section comprises three facies succession bounded by internal discontinuities (Fig. 2A–E), composed of five recurrent sedimentary facies: bioturbated sandstone (Sb), horizontally stratified sandstone (Sh), trough cross-bedded sandstone (St), matrix supported polymictic conglomerate (Gm), and trough stratified conglomerate (Gt) (Table 1). The facies succession 1 comprises a 7 m-thick succession composed of 0.2 to 0.5 m-thick sets of granule- to pebble-conglomerate (Gm) (Fig. 3A) that grade into medium- to poorly preserved coarse-grained cross-bedded, and massive sandstone (St, and Sb) (Fig. 3B, C). The sandstone sets are dm-thick and bounded by nearly horizontal erosive surfaces, which are frequently poorly preserved due to redoximorphic features, such as Liesegang bands and mottles (Fig. 3D). The contact between cosets is erosional, and paved by thin layers of quartz pebbles (Fig. 3E). Overall, sedimentary structures exhibit poor preservation with predominance of massive sandstone (Sb), with the recognition of coarse-grained cross-bedded sandstone (St) often indicated by the presence of granules within foresets or iron concentration along the structures (see Fig. 3F). *Scalichnus* isp. and *Taenidium barretti* are the most common trace fossils in this succession. *Lockeia* isp. occurs locally.

Facies successions 2 and 3 together are more than 15 m thick and are composed of granule- to pebble-conglomerate of Gm and Gt facies that pass upward gradationally to pebbly- to medium-grained sandstone (St, Sp, Sh facies). These deposits are organized in m-thick cosets with a fining-upward trend with scour and fill structures with irregular erosional surfaces composed of Gm facies at the base (Fig. 4A–G). These deposits are lenticular and amalgamated sand bodies with thickness that ranges from 0.3 m to 1.5 m. A transition from parallel laminated sandstone to conglomerate and cross-bedded sandstone is observed at the base of the sand bodies (Fig. 4C). When well preserved, the bottom boundary is incisional and erosive, with slightly concave-up bases composed of Gm and St facies. *Scalichnus* isp. in the main component of the ichnofabric in facies succession 2 and 3, crosscutting the St and Sh facies (Fig. 4G–H).

Interpretation. The sedimentary succession of the Exu Formation in the study area reflects the cyclic development of mobile, erosion-dominated fluvial-bar complexes with low sinuosity. These bar complexes are characterized by bedload-dominated transport, which incises and erodes pre-existing channel and adjacent floodplain deposits, leading to stacked lateral and vertical bar deposits^{31,32}. A common feature is the occurrence of sets composed by matrix-supported Gm lithofacies changing to St lithofacies at the base of the sand bars, indicative of large, sinuous 3D subaqueous dunes migration (bedload transportation)³³. The erosive bottom boundary forms slightly concave-up bases, typical of the aggradational infill of multi-story bar aggradation deposits composed of conglomerates and sandstones with cross-bedding and planar bedding structures^{33,34}.

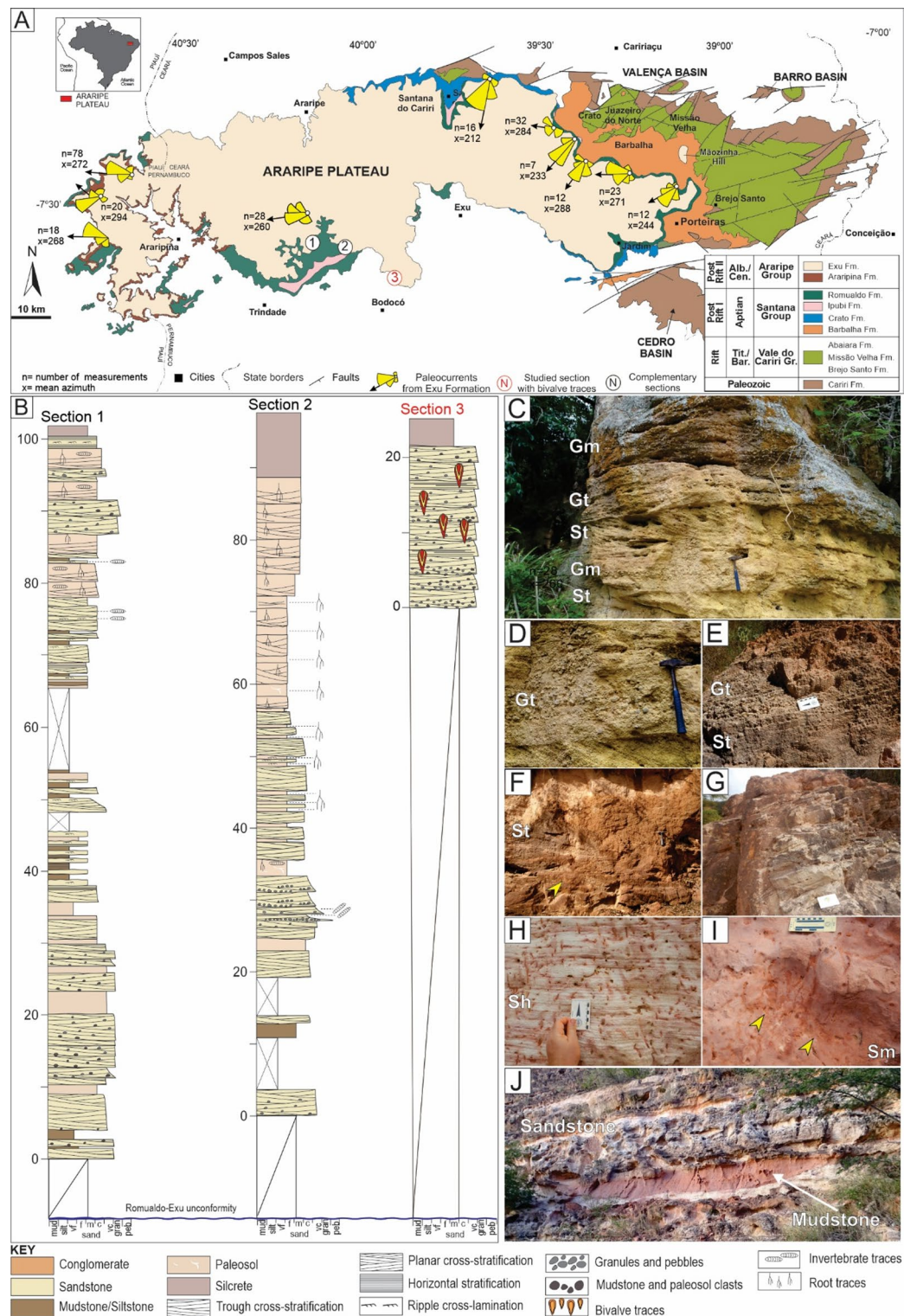


Fig. 1. (A) Location of the study area in the Araripe Basin, NE Brazil. Adapted from Assine (2007)²¹; Lorenso (2021)²⁹ and Rodrigues et al., (2022)³⁰. Paleocurrent data from Assine (1994)²⁰. (B) Composite image of the described sections in study area. Adapted from Lorenso (2021)²⁹. (C–J) Details of facies described throughout the study area. Sb – massive or bioturbated sandstone; Sh – horizontally stratified sandstone; St – trough cross-bedded sandstone; Gm – matrix supported polymictic conglomerate; Gt – trough stratified conglomerate (Gt); Fm – massive mudstone; Fl – laminated mudstone. The map and columns was generated using the software CorelDRAW 2021(<https://www.coreldraw.com/>).

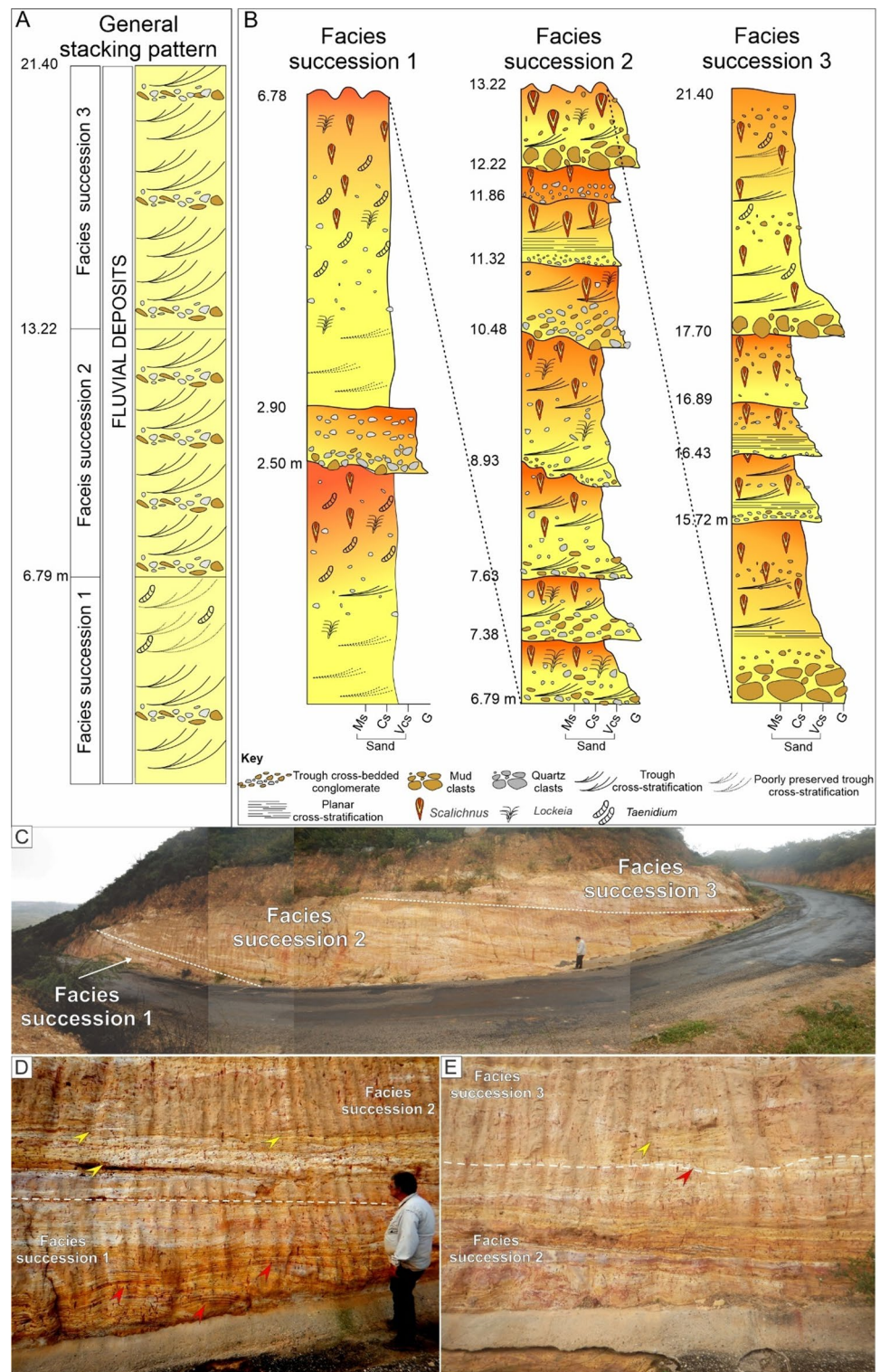


Fig. 2. (A) General sedimentary log of the studied section. (B) Detailed sections of three facies succession described. Note the increase in preservation of sedimentary structures and occurrence of conglomerates towards the top. (C) General aspects of studied section and their facies succession. (D) Facies succession 1 and 2. Yellow arrowhead highlight occurrence of St lithofacies. Red arrowheads indicate the occurrence of Liesegang bands in Facies succession (1) Dashed lines indicate the limit between facies successions 1 and (2) (E) Facies successions 2 and (3) Yellow arrowhead highlight occurrence of St lithofacies. Red arrowheads indicate irregular contact between facies successions 2 and 3.

Code	Descriptions
Sb	Medium- to very coarse-grained/conglomeratic, structureless, bioturbated sandstone with reddish-yellowish-purplish colors. Granule and pebble size quartz and mud clasts occur dispersed in the sets
Sh	Medium- to very coarse-grained sandstone with parallel stratification forming cosets with 0.5 to 0.8 m in thickness. Planar crossbedding occasionally marked by quartz clasts at the base of sets
St	Coarse- to very coarse-grained sandstone, locally conglomeratic, with through cross-stratification forming cosets with 1.0 to 1.5 m in thickness and a fining-upward trend
Gm	Conglomerate with coarse-grained sandy matrix composed of rounded to angular pebbles of quartz and mud clasts with 0.5 to 20 cm in diameter
Gt	Conglomerate composed of angular pebbles of quartz 0.5 to 10 cm showing trough crossbedding and forming sets with 20 to 40 cm in thickness

Table 1. Facies descriptions and interpretations of outcrops with bivalve trace fossils.

Transition from lower to upper flow regimes are marked by the presence of Sh facies, while scour surfaces are associated with flow reactivation events, likely corresponding to seasonal peaks in discharge during high energy events^{35,36}. The presence of mud clasts further indicates the erosion and reworking of floodplain deposits or channel-fill mud deposits formed after channel abandonment and energy reduction³⁷. The primary difference between facies succession 1 and facies succession 2 and 3 lies in environmental energy levels and sedimentation rates. Facies succession 1 is dominated by massive and poorly preserved cross-bedded sandstone beds, while the successions 2 and 3 display well-preserved sedimentary structures and intraformational pebble-sized conglomerates, indicative of increase in energy conditions. As energy levels increase in facies successions 2 and 3, there is also a notable rise in the occurrence of bivalve trace fossils, suggesting a strong correlation between environmental energy and the preservation of ichnofossils.

Trace fossils

The trace fossil assemblage registered in the study area is almost chiefly composed of bivalve mollusk burrows representing the ichnogenera *Scalichnus* and *Lockeia*, with subordinate occurrence of *Taenidium* and escape traces.

Ichnofamily Siphonichnidae Knaust, 2015.
Ichnogenus *Scalichnus* Hanken et al., 2001.
Scalichnus isp.

Description: Vertical to oblique sack-like burrows with a thick inorganic lining and one or two vertical tubes at the top (Fig. 5A-D). The burrow varies between 2 and 8 cm in diameter and 4 to 20 cm in length, and, in some cases, the walls exhibit disturbed and compressed zones, with irregular or disrupted boundaries (Figs. 5E and 6A). The burrows are filled with heterogeneous, poorly sorted, yellowish, and reddish coarse to very coarse sand material and centimetric clasts collapsed inside the burrows (Fig. 6B-C). In some cases, poorly developed menisci or irregular concave-upwards and convex-downwards laminae are present at the bottom of the traces (Fig. 6D-E). In bedding-plane view, the burrow shows a sub-circular to circular cross section, where one or two small siphon tubes and a disturbed zone can be seen in the upper part of the burrow (i.e., the siphonal region) (Fig. 6F-H). The inorganic material that forms the thick reddish mantle around siphon is organized in two discrete zones and is composed of finer-grained sand than that forming the surrounding matrix (Fig. 7A-D).

Remarks: These traces occur at the tops of sets that crosscut the St and Sp facies and occasionally within conglomerates (Gm facies) (Fig. 8A-C). In some instances, they exhibit a distinctive “star-shaped” structure (Fig. 8D-E). These are the most abundant traces in the studied deposits forming a dense ichnofabric [bioturbation scale (BS) 5–6] with ≥ 30 specimens per quadrat (50 × 50 cm²). Despite the smaller size compared to those generally recorded in marine settings, the sack-like morphology, the presence of menisci or irregular concave-upward laminae at the base, and the occurrence of siphon tubes with thick lining at the top fulfill the ichnotaxobases of *Scalichnus* at the ichnogenus level^{14–17,37,38}. *Scalichnus* is usually interpreted as produced by *Panopea* (e.g., *P. fausaji*, *P. japonica*)^{14,17,37,38} but was also attributed to the burrows made by *Tagelus plebeius*³⁸. The producer of the *Scalichnus* in fluvial settings is unknown.

Scalichnus has been interpreted as an escape or equilibrium trace^{15,16}. The presence of disturbed zones with irregular and/or disrupted walls in the described specimens supports its interpretation as reflecting equilibrium behavior. However, *Scalichnus* combining also resting/dwelling behaviors, as the sack-like morphology represents the place occupied by the bivalve inside the substrate. It reflects the activity of filtering-feeding bivalves capable of vertical movement within the substrate to avoid burial events³⁹. In vertical section, the dwelling chamber of *Scalichnus* can resemble *Conichnus conicus* Männil, 1966 when siphon traces are absent. However, *C. conicus* lacks the sack-like morphology and rounded base observed¹³ which was in the specimens from the Exu Formation. When siphon tubes are preserved, *Scalichnus* may resemble *Siphonichnus*¹⁵ but the latter is distinguished by its vertically orientated siphon tubes and the absence of longitudinal lining¹⁶.

Lockeia James, 1879.
Lockeia isp.

Description: Isolated, sack-like burrows having oval or almond-shaped cross sections oriented vertical to oblique to the bedding plane. Compressional structures that deform the surrounding bed may be seen (Fig. 9A-D). In plan view, the traces occur as shafts with concave epirelief or almond-shaped burrows filled with sandy material (Fig. 9E-F). The burrows are 2 to 5 cm wide and 7 to 20 cm long.

Remarks: *Lockeia* is interpreted as a shallow-tier resting trace left by bivalves and is commonly found in both marine and non-marine aquatic settings^{7,40}. The trace is produced by both cleft- and wedge-foot bivalves^{41,42}.

Taenidium Heer, 1877.

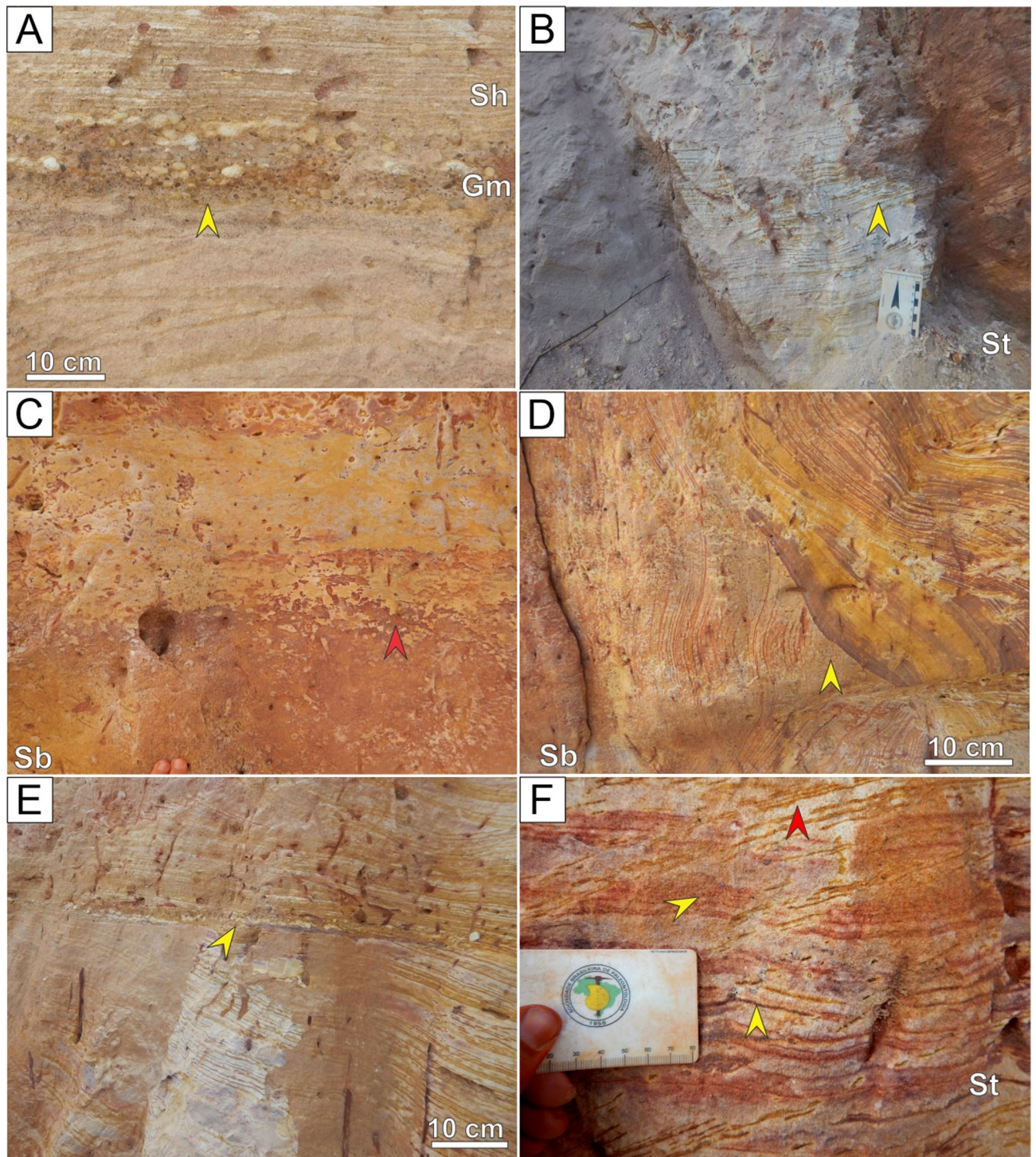


Fig. 3. (A) Gm facies (yellow arrowheads) are associated with Sb facies with a fining upward trend. (B) Poorly preserved St facies (yellow arrowheads). (C,D) Sb facies associated with liesegang bands. (E) Transition between cosets. Note the occurrence of clasts (yellow arrowhead) marking the transition. (F) Poorly preserved St facies indicated by clasts and iron concentration (yellow arrowhead).

Taenidium barretti (Bradshaw, 1981).

Description Unbranched, unlined, cylindrical to slightly ellipsoidal burrows with a meniscate infill, oriented horizontal to vertical to bedding (Fig. 10A-B). The menisci are heterogeneous and filled with medium to coarse sand grains, showing alternation of yellowish, whitish, and purplish colors (Fig. 10C-F). Menisci width vary from 1 to 23 mm and are loosely packed. The burrow diameter ranges from 8 to 20 mm and remains constant within individual specimens. The lengths range from 30 to 150 mm. The morphology of the menisci remains consistent regardless of the burrow orientation.

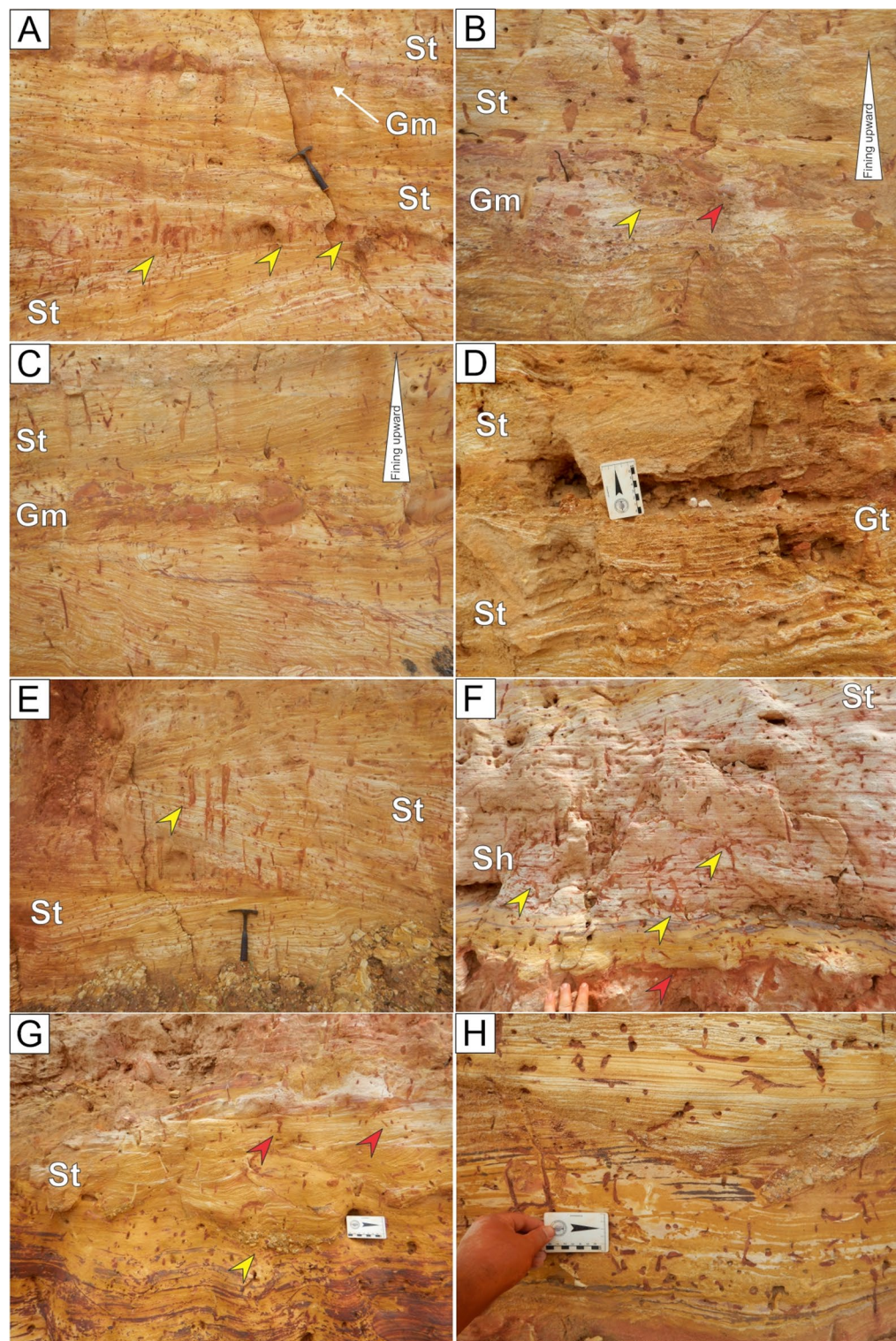


Fig. 4. (A,B) St and Gm facies with a fining-upward trend. The yellow arrowhead indicates the Gm facies. (C) Sets of bioturbated St facies with fining upward trend. (D) Gt facies. (E) St facies. Note bivalve trace fossils cross-cutting the St facies (yellow arrowhead). (F) Sh facies associated with conglomerate (yellow arrows). (G,H) Scour surfaces marked by Gm facies (yellow arrowhead).

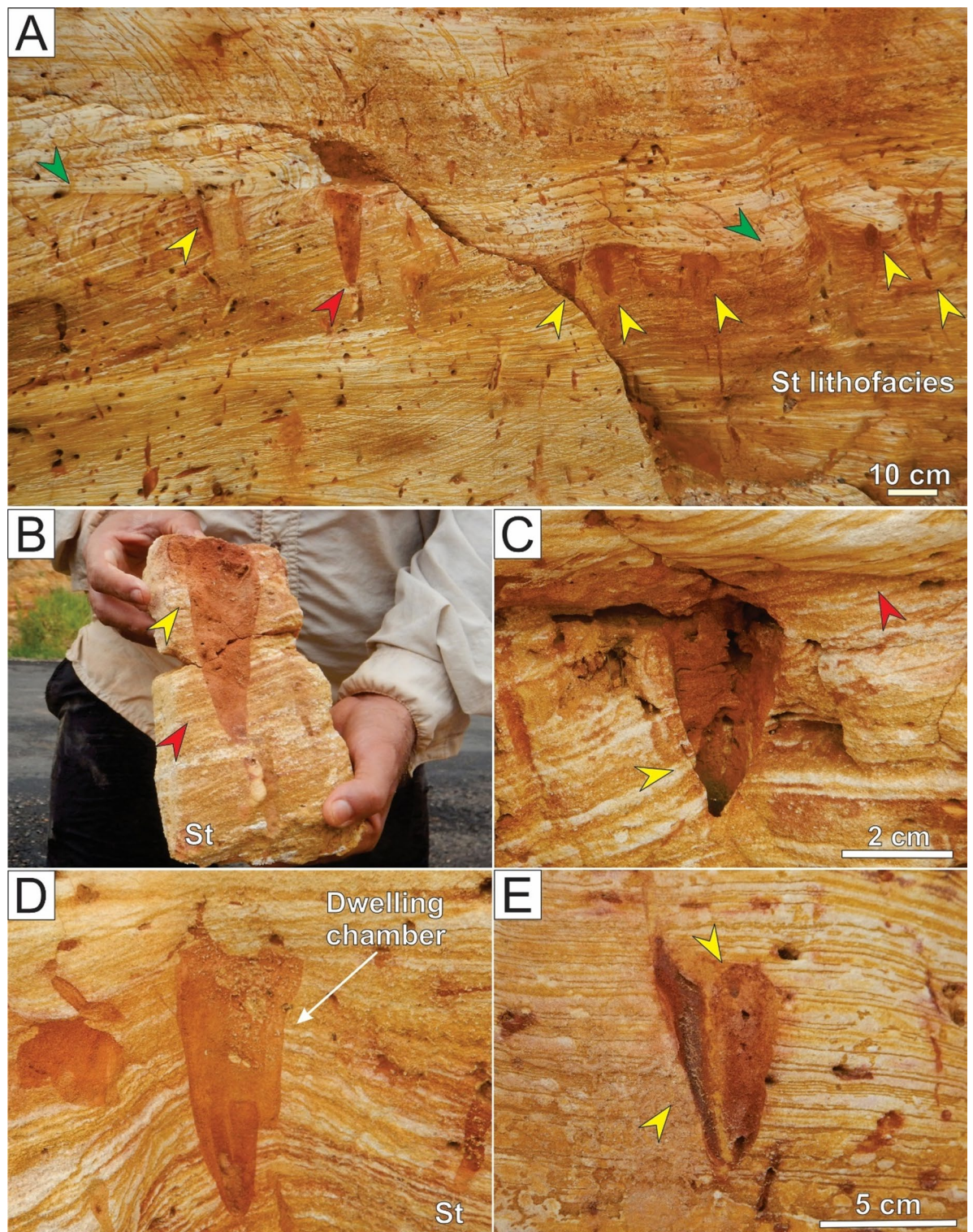


Fig. 5. (A) *Scalichnus* isp. cross-cutting St facies. Note the diverse occurrence associated with the same sandbar (yellow arrowhead). Red arrow indicates the occurrence of a large *Scalichnus*. Note the surface that limits the occurrence of *Scalichnus* (green arrowhead). (B–D) Detail of dwelling chambers (yellow arrows) cross-cutting the St facies (red arrowhead). (E) Thick-lined *Scalichnus* showing sharp contact with the substrate (yellow arrowhead).

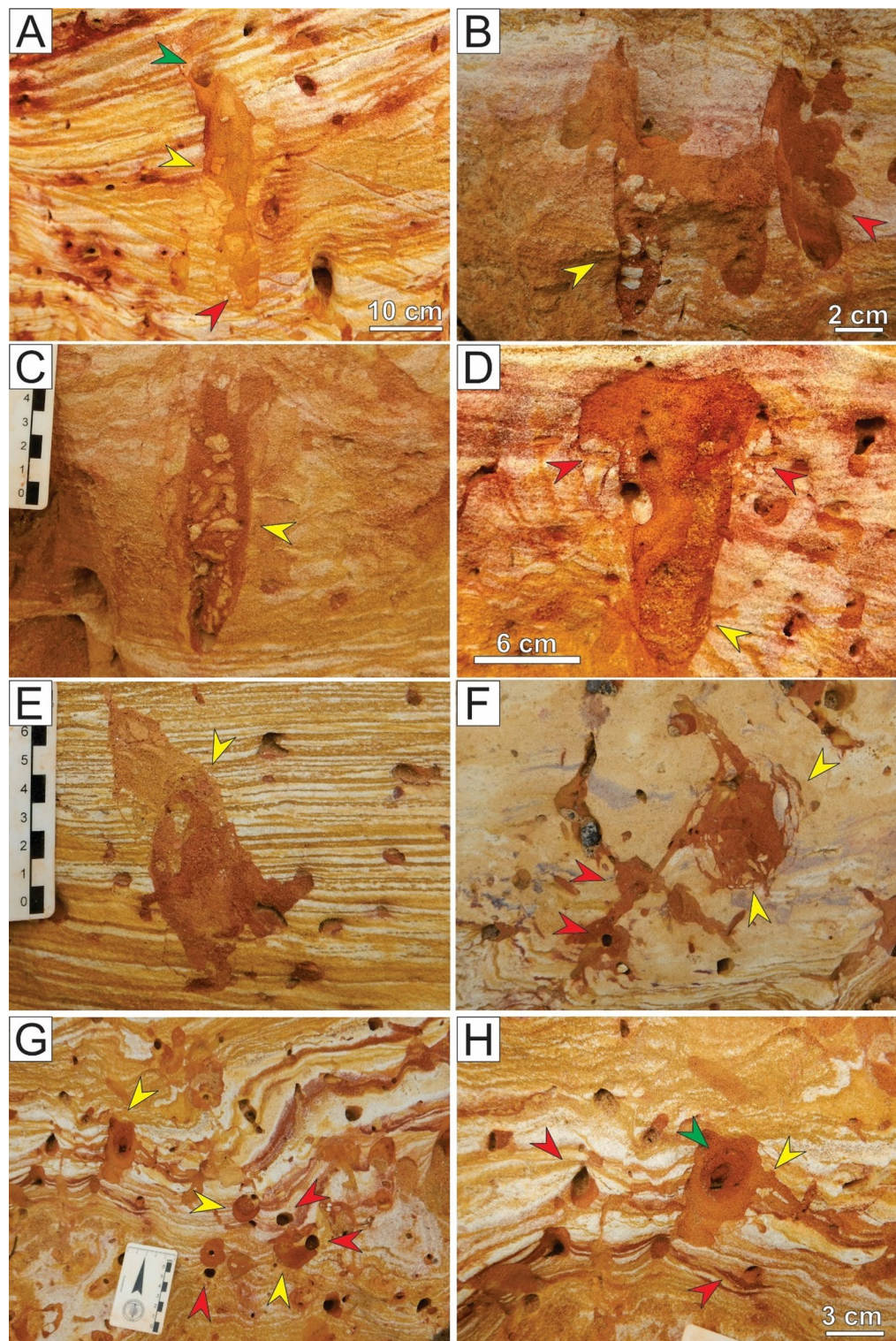


Fig. 6. (A–C) *Scalichnus* showing irregular burrow border (red arrowhead) and filled with substrate clasts (yellow arrowhead). The green arrow highlights the siphon's tube. (D) *Scalichnus* with menisci showing concave-upward laminae (yellow arrowhead). Red arrows highlight the irregular borders and sharp contact with the substrate. (E) *Scalichnus* with menisci showing convex downwards laminae (yellow arrowhead). (F–H) *Scalichnus* in plan view. Note the irregular border (yellow arrowhead). Red arrowheads indicate the occurrence of the siphon's tubes. The green arrowhead highlights the thick lining in *Scalichnus*.

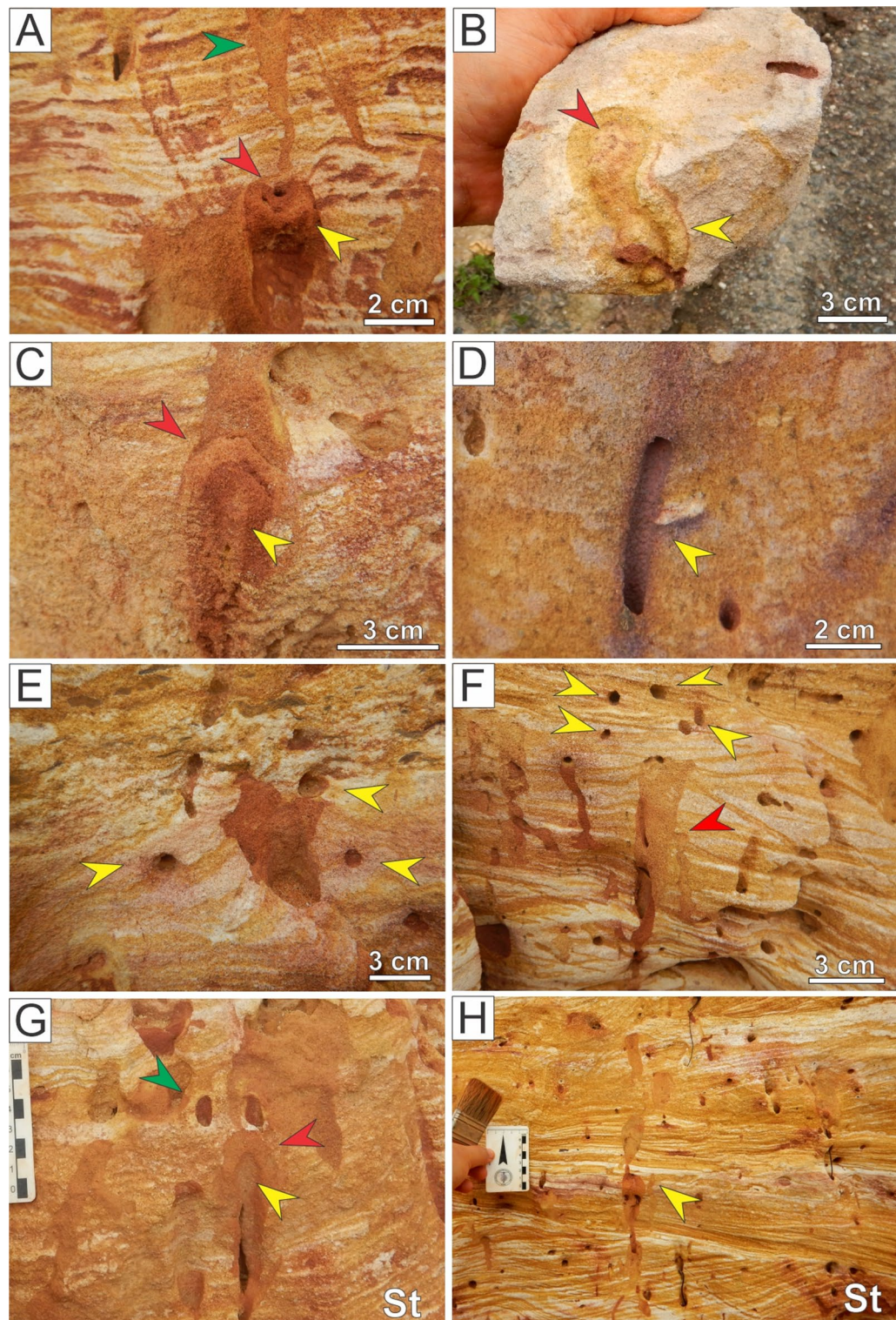


Fig. 7. (A–C) Thick-lined tube associated with *Scalichnus* (yellow arrowhead). Note the core (red arrowhead) and the mantle (yellow arrowhead) that comprise the burrow lining. The green arrowhead indicates the trace continuation above. (D) Thick-lined siphon tube that resembles *Skolithos*. (E,F) *Scalichnus* with different tubes probably associated with changes in siphon position in the substrate. (G) Thick-lined siphon tube with core (yellow arrowhead) and mantle (red arrowhead). The green arrow indicates the different siphon's positions. (H) Stacked *Scalichnus* indicating upward repositioning of the bivalve in the substrate.

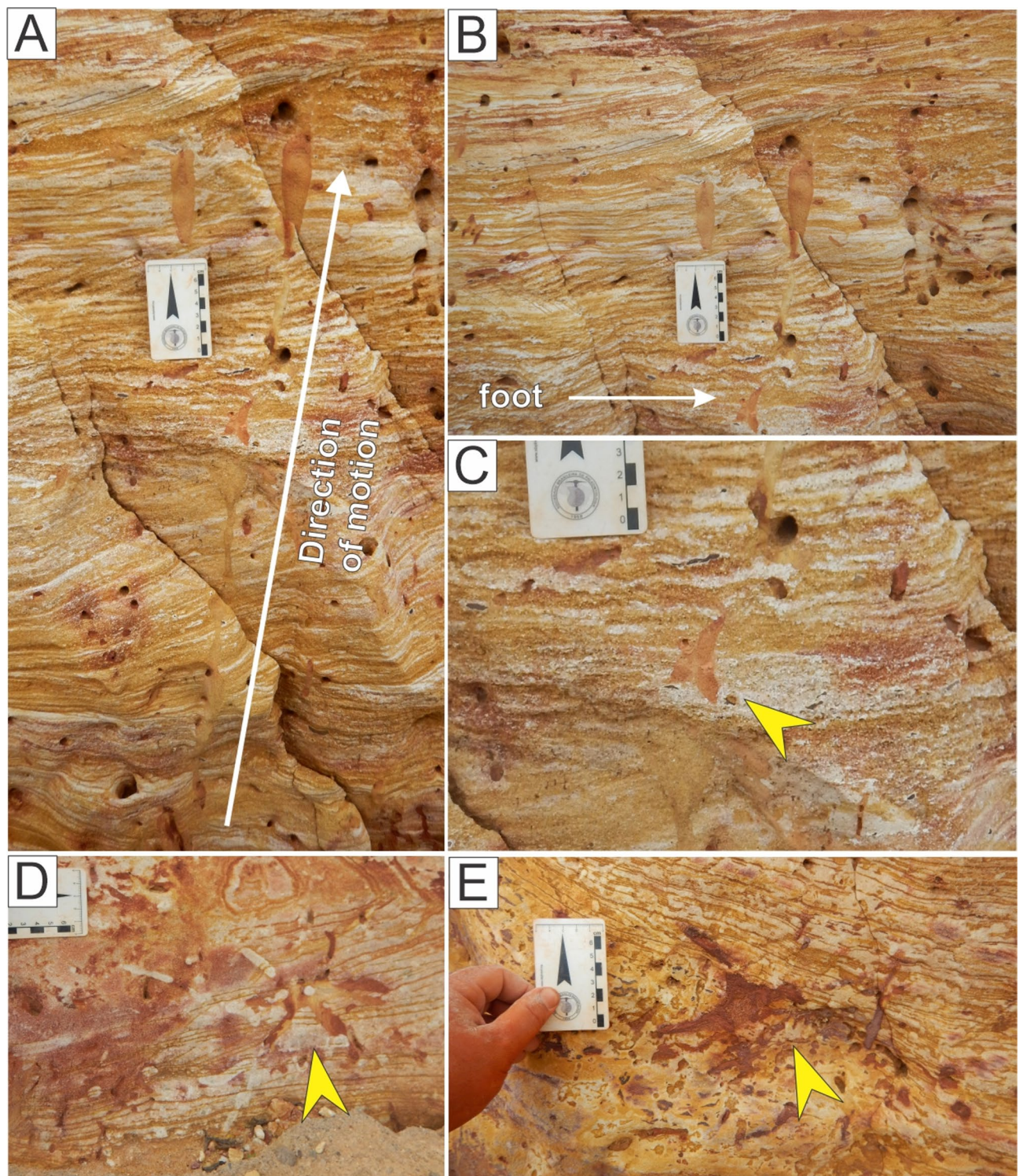


Fig. 8. (A) Long stacked *Scalichnus* (~50 cm) with preserved bivalve foot trace. (B,C) Detail of the foot trace. (D,E) Complex deformed structures associated with *Scalichnus*.

Remarks: The previously mentioned characteristics fulfill the ichnotaxobases of *Taenidium barretti*^{43–46}. Despite the weathering of the studied deposits, the diagnostic features are clearly observed in a few specimens (Fig. 10C–D). In most cases, *Taenidium* was identified based on changes in color resulting from redoximorphic features. *Taenidium barretti* is commonly found in moist to wet substrates within continental settings and is interpreted as feeding burrows produced by millipedes and beetle larvae^{44,45,47–49}.

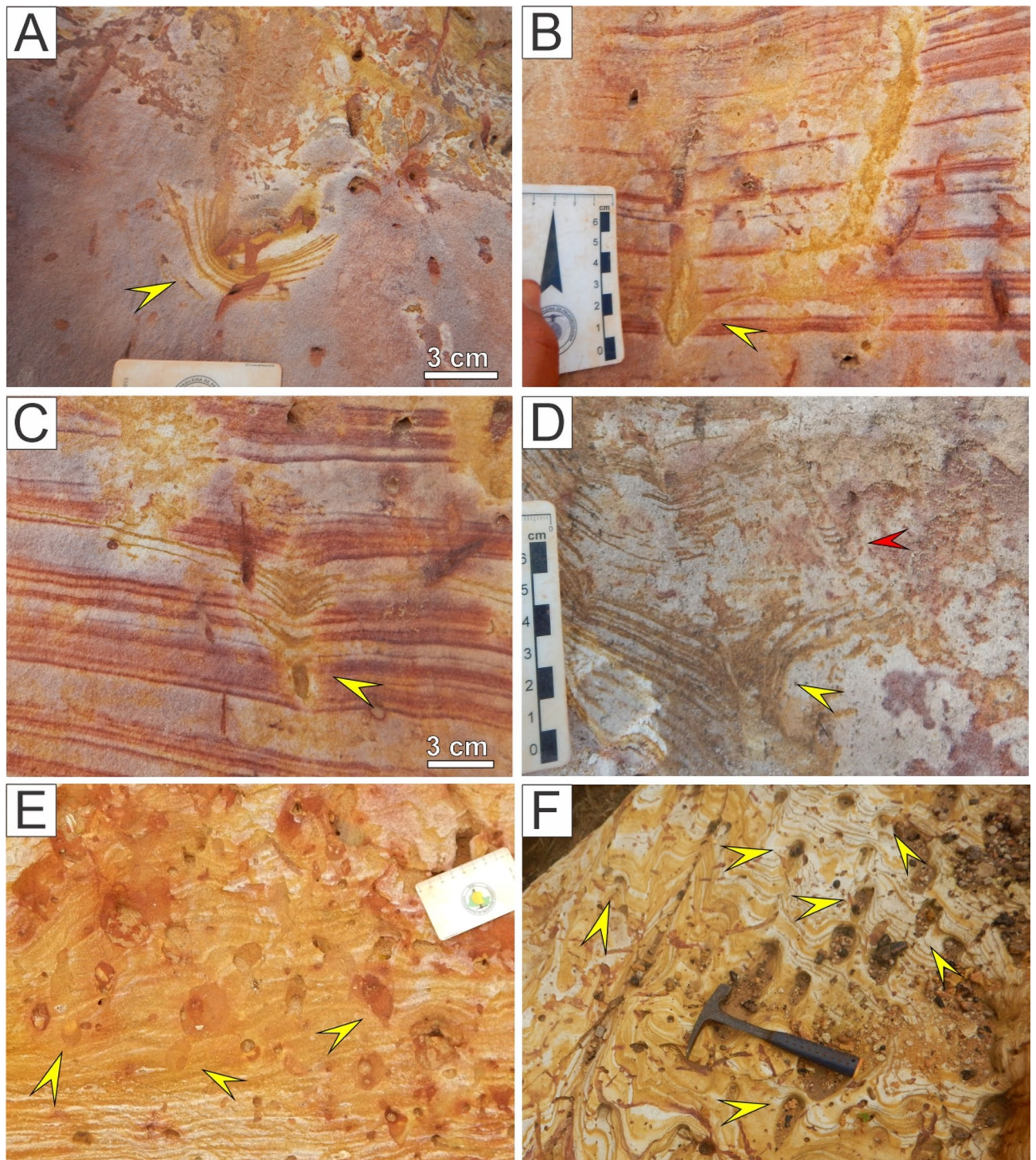


Fig. 9. (A–D) *Lockeia* isp. in the longitudinal cross section (yellow arrow). Red arrows indicate the presence of *Taenidium barretti* and *Lockeia* isp. in plain view (yellow arrowhead). (E,F) *Lockeia* isp. in transverse cross section.

Trace fossil suites

The Taenidium-Scalichnus suite

This suite occurs in facies succession 1 and is characterized by the occurrence of *Taenidium barretti*, *Scalichnus* isp., and subordinate *Lockeia* isp. forming low to moderate bioturbation (BS 2–3). Although very common in Brazilian Mesozoic continental deposits^{42,49,50}, the occurrence of *Taenidium* in the Exu Formation is discrete (BS 2–3) and concentrated in the finer-grained beds (St and Sb facies) of the facies succession 1. *Scalichnus* isp. also occurs in Sb facies but is never crossed by *T. barretti* and vice versa. This preservation mode suggests

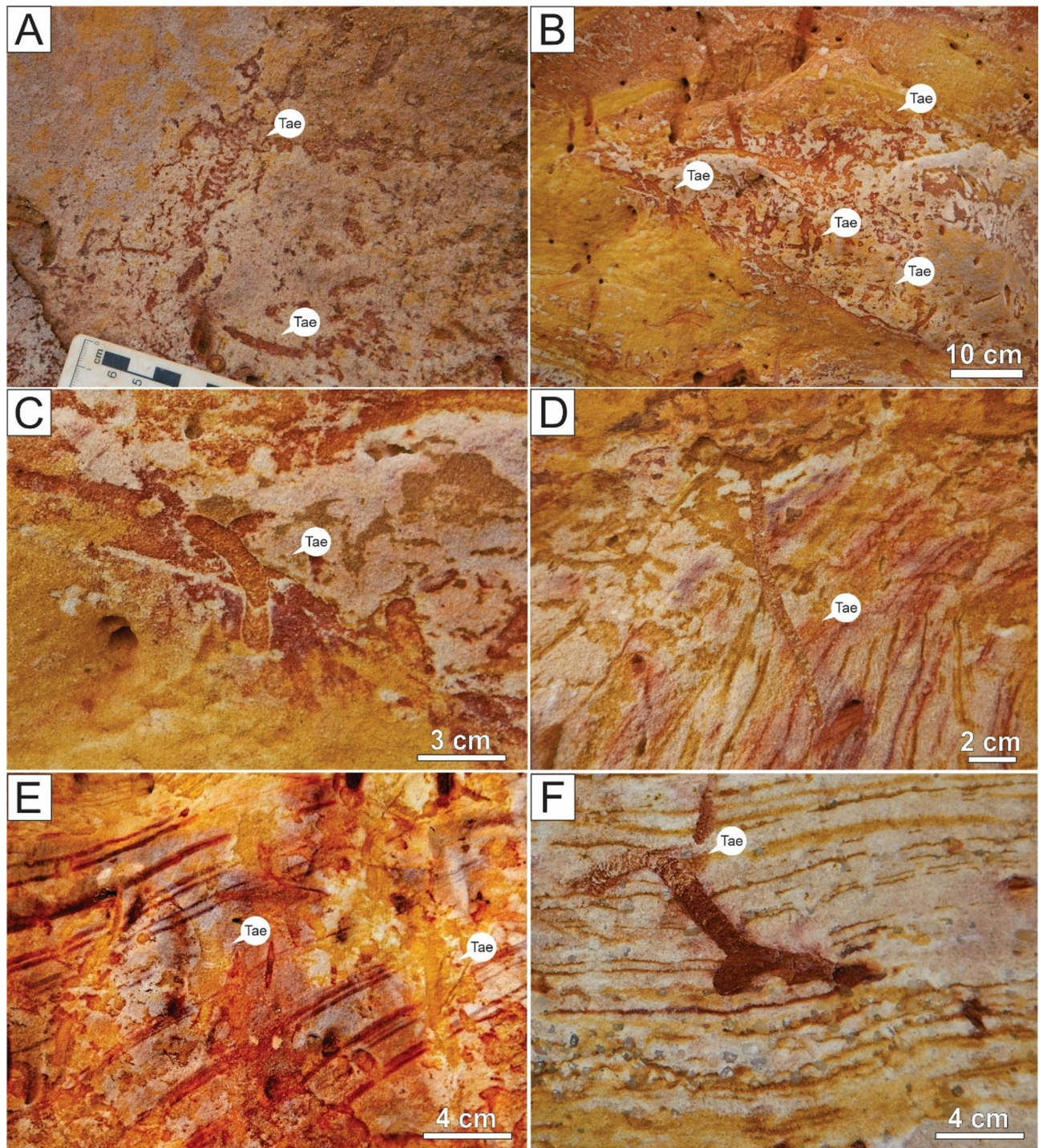


Fig. 10. (A,B) Poorly preserved *T. barretti*. (C,D) Well-preserved *T. barretti* with clear menisci. (E,F) Poorly preserved *T. barretti* enhanced by redoximorphic features.

colonization of different tiers and, possibly, changes in sediment accumulation. *Scalichnus* isp. and subordinate *Lockeia* isp. represent more perennial endobenthic populations inhabiting shallow tiers of the fluvial bars. *T. barretti*, otherwise, suggests the exploration of the uppermost substrate surface during aggradation periods under a low sedimentation rate regime. The abundance of Fe and the lise-gang rings present in the beds bearing *T. barretti* reinforce a potential short time event of subaerial substrate exposure. *T. barretti* is a common ichnotaxa in moist to wet substrates of fluvial settings with low erosion and sedimentation rates^{12,51}. Although *Scalichnus* has not been reported yet in non-marine settings, resting/dwelling and equilibrium/escape burrows made by bivalve mollusks are also common in river and delta bars and floodplains^{52,53}.

In this scenario, the presence of *T. barretti* suggests oscillations in the water table, creating colonization windows that alternated between aquatic and terrestrial environments. These conditions allowed bioturbation by insects or worm-like invertebrates^{54,55}. However, the absence of rhizoliths, paleosols, and mud cracks indicates very short periods of substrate exposure and the persistence of wet conditions⁴⁵. Consequently, the occurrence of *Taenidium* isp. in this suite likely reflects opportunistic colonization events, potentially controlled by climate seasonality.

The Scalichnus suite

This suite encompasses a dense (BS 5–6) occurrence of *Scalichnus* isp. in facies successions 2 and 3, with subordinate presence of *Lockeia* isp. Large populations of infaunal bivalves colonized the top of the sand bars in active channels, cross-cutting the primary sedimentary fabric. The monotypic nature of bivalve burrows and the dominance of *Scalichnus* in this suite possibly result from increased sedimentation rates and/or the frequency of river discharges during the deposition of facies successions 2 and 3, which limited substrate colonization by other organisms. The presence of *Scalichnus* isp. variants representing escape burrows further support the dominance of higher sedimentation rates compared to facies succession 1. Bioturbated deposits in active fluvial channels often exhibit monospecific suites, predominantly composed of dwelling traces left by suspension feeders⁵⁶.

Discussion

Tracemaker and paleogeographic context

Trace fossils often provide critical insights not revealed by body fossil or in their absence, as seen in the Exu Formation deposits^{7,56}. To date, the ichnofabric reported here represents the first documented evidence of ancient life in these beds. This is also the first record of *Scalichnus* in freshwater settings, as previous occurrences are exclusively associated with marine paleoenvironments^{14–17,37,38,57}. Although the exact taxonomic affinity of the bivalve group responsible for these traces remains uncertain, unionid bivalves would be the most likely because they are the most common burrowing freshwater mollusks since the Devonian⁵⁸. Nevertheless, the burrows described here exhibit longer siphons like observed in marine and coastal settings than those observed in extant unionid bivalves, raising questions about their producer, and the possibility of marine influence in the deposition of the Exu Formation. However, the paleogeographic context of the Araripe Basin through the Albian–Cenomanian rules out any influence of the sea during the Exu Formation.

The studied outcrop containing *Scalichnus* encompasses the well-documented fluvial facies of the Exu Formation which are associated with a large distributive fluvial system under semi-arid conditions without any evidence of marine influence^{19–21,25,27,59}. The fluvial paleocurrent trends of the Exu Formation deposits are also well established, showing a predominant westward depositional dip toward the Parnaíba Basin (Fig. 1A), likely influenced by regional uplift processes in the eastern Borborema Province during the Albian^{19,20,60,61}. The sedimentary data from this work also confirm that the facies and successions of the Exu Formation were deposited in a high energy fluvial system with bedload-dominated sediment transport and characterized by unconfined channels at the western side of the basin^{62–66}. Fining-upward trends, low-angle crossbedding, and parallel stratification reflect multiple flood events that transported sandbars, driven by transient flow energy associated with seasonal variations³⁵. No evidence of marine incursions or marine-influenced processes is observed in these beds.

Marine incursions into the Araripe Basin occurred during the Aptian–Albian and had ceased following the deposition of the Romualdo Formation (transgressive and regressive cycles, Fig. 1A), which has been extensively studied due to its rich fossil record^{30,67–73}. Following the deposition of the Romualdo Formation, continental conditions became established in the Araripe Basin, as evidenced by fluvial deposits and paleosols within the overlying Araripe Formation²⁷.

Paleogeographic reconstructions indicate that during deposition of the Exu Formation, the paleo-São Francisco River estuary was positioned ~735 km northwest in coastline along the equatorial margin, maintaining significant distance from marine influence. This is corroborated by the fluvial-marine deposits recorded in the Alcântara Formation (Albian–Cenomanian, Grajaú Basin), which comprises a distinct depositional system tract showing tidal channels, lagoon and shallow marine deposits^{74,75}.

Regarding the inference that the trace maker was a unionid bivalve, two key questions arise. First, the presence of elongated siphons in the described *Scalichnus* is typically associated with marine bivalves, rather than freshwater forms. However, as previously established, there is no evidence of marine influence in the Exu Formation, suggesting that the burrows were produced by a freshwater bivalve. Based on the findings of this study, the most parsimonious interpretation is that the tracemaker of the described *Scalichnus* was a freshwater bivalve. Therefore, accordingly, the ichnofauna of the Exu Formation may be interpreted as a freshwater bivalve-dominated endobenthic ichnocoenosis (comprising *Scalichnus* isp. and *Lockeia* isp.), with occasional arthropod traces (*Taenidium barretti*) occurring in facies succession 1, likely associated with shallower water conditions and substrate dewatering.

In the fluvial deposits of the Exu Formation, *Scalichnus* isp. represents traces of dwelling, equilibrium, and escape behaviors⁶². The vertical tubes associated with *Scalichnus* isp. likely represent traces from upward-oriented bivalve siphons. Multiple tubes connected to a single dwelling chamber (Fig. 7E–G) suggest that the mollusk altered its siphon orientation without abandoning the burrow. Freshwater bivalves burrow using a muscular “hatchet foot” in a push-and-pull motion^{3,4,51} which involves rhythmic foot shape changes for anchorage and locomotion⁶⁶. Most traces preserved in the Exu Formation show menisci or irregular concave-up laminae at the base of oval chambers, indicating upward displacement in response to sediment aggradation^{15,76}. Stacked *Scalichnus*, extending over 60 cm in some cases, can indicate repeated sedimentation events allowing bivalves to reposition during episodic or seasonal sediment accumulation (Figs. 7H and 8A–C). Each chamber likely represents a stable period followed by a depositional event. In this context, the preservation of *Scalichnus*

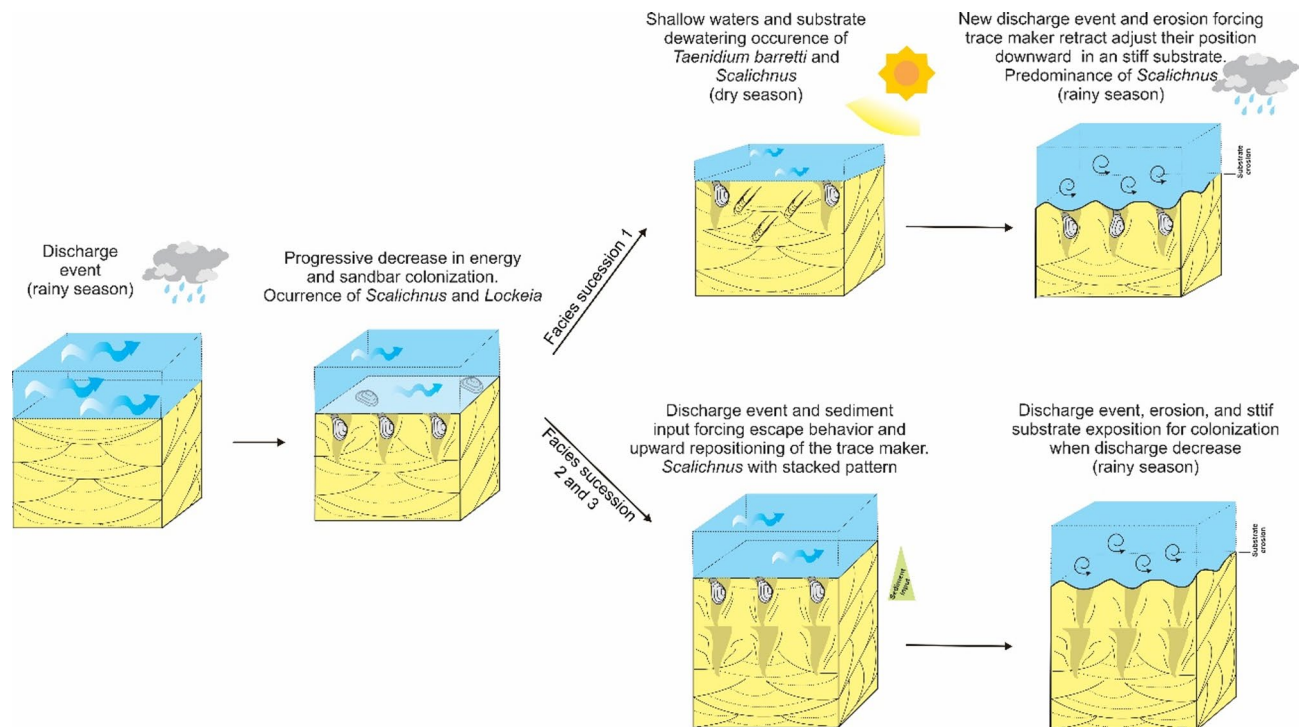


Fig. 11. Taphonomic pathways and environmental distribution of *Scalichnus* due to changes in discharge conditions in response to climatic seasonality. The figure was generated using the software CorelDRAW 2021 (<https://www.coreldraw.com/>).

ichnofabrics reflects variations in sedimentation rates driven by climatic seasonality, forcing burrowers to adapt to aggradation. Evidence of disturbed zones and disrupted walls in *Scalichnus* suggests burrowing in stiff substrates exposed by flood erosion. Sharp chamber-substrate contacts and burrow wall clasts further support this interpretation.

The *Scalichnus-Lockeia* association suggests periods of environmental stability, while the significant displacement observed in trace fossils indicates short-term stress, possibly due to seasonal discharge variations⁵. *Scalichnus*-rich beds truncated by conglomerates further imply dynamic hydrological conditions influenced by discharge events. High bioturbation in *Scalichnus* suites suggests dense mollusk populations, consistent with modern freshwater bivalves in low-shear-stress settings⁴ with periods of slow discharge velocity. The presence of traces of varying sizes within the same bed indicates multiple colonization events and specimens at different ontogenetic stages.

Distinct colonization windows differentiate the *Taenidium-Scalichnus* suite (FA-1), representing progressive shoaling, from *Scalichnus* suites in facies successions 2 and 3, which suggest long-term colonization under stable conditions interrupted by changes in fluvial discharge (year or decadal scales) (Fig. 11). Extensive bioturbation in sandbars probably reflects discharge seasonality, with colonization occurring during periods of reduced flow intensity after rainy seasons. Another possibility is the changes in fluvial dynamics, such as channel migration.

The absence of paleosols and rhizoliths, coupled with carbonate cementation, indicates short subaerial exposure marked by *T. barretti*⁴⁵. The outcrops studied do not show any evidence of regional climatic changes, therefore, the autogenic fluvial processes driven by climatic seasonality likely controlled trace fossil distribution, creating colonization opportunities on subaqueous dunes after aggradation⁵⁸.

Modern freshwater bivalves require perennial, well-oxygenated, low-turbidity waters with stable streambeds^{1,4,77,78}. Their glochidial larval stage depends on fish hosts for dispersal, emphasizing the need for persistent water bodies⁷⁹. Therefore, it is probable that despite evidence of seasonality in the trace fossil assemblages, the fluvial system was perennial, exhibiting a reduction in its marginal extent during dry seasons as observed in modern semiarid environments. However, due to the scarcity of data, and considering the common channel unconfinement towards west, it is difficult to determine the distance between the described ichnofabrics in alluvial plain and the main channel.

Taphonomic processes favoring fossil preservation differ from those of body fossils. Diagenetic mineral precipitation along burrow walls often enhances trace visibility^{80,81} as seen in the iron-rich walls of *Scalichnus* in the Exu Formation. Hematite precipitation likely resulted from increased substrate permeability due to burrowing. Additionally, bioturbation structures facilitated selective mineralization, with iron-rich features indicating oxidative conditions and substrate dewatering. Redox features suggest organic matter presence and substrate drainage variations⁸² likely linked to periodic water table oscillations. These processes may reduce water pH, leading to shell dissolution⁸³ explaining the abundance of bivalve traces without shell preservation. Coarse sandstones and conglomerates further highlight high-energy conditions that constrain body fossil preservation.

All this evidence supports the previously mentioned ghost taxa hypothesis, in which the body fossils were not preserved.

Conclusions

The occurrence of *Scalichnus* in the Exu Formation represents the first well-documented record of this ichnogenus in a fluvial setting. No evidence of marine incursions has been identified in these deposits. Although unionid bivalves are the most common burrowing freshwater bivalve in both modern and fossil records, the precise taxonomic identity of the trace-making bivalve remains uncertain due to the evidence of a long siphoned-bivalve. The preservation of *Scalichnus* ichnofabrics is likely influenced by variations in sedimentation rates driven by climatic seasonality. The observed stacked patterns and escape traces suggest recurring sedimentation events that compelled the trace producers to burrow upward in response to aggradation. Disturbed zones and disrupted walls in *Scalichnus* indicate excavation in a firm substrate, likely following erosion events truncated the tops of sandbars. Moreover, the highly bioturbated sandbars (i.e., in-channel bioturbation) reflect variations in discharge events, where reduced flow intensity after the rainy season created conditions conducive to the colonization of riverbed deposits. These stable post-erosion conditions allowed for the establishment of subaqueous dune communities. Thus, the primary factor controlling the occurrence of *Scalichnus* is climatic seasonality. This driver, regulates autogenic processes within the channels, creating periodic opportunities for the colonization of the substrate following discharge events.

Materials and methods

The bivalve mollusk burrows were recorded in surface deposits exposed near Bodocó city (7°36'54.43"S 39°57'7.77"O), Pernambuco State, Brazil (Fig. 1A). The outcrop extends approximately 40 m laterally (Fig. 2A, B). Detailed facies description followed the methodology outlined by Miall³³ focusing on lithology, bed geometry, and sedimentary structures. Associated facies were grouped into three distinct facies successions based on Walker⁸⁴. Photographic panels and vertical columnar sections were elaborated to document external architecture, geometry, and bounding surfaces, aiding interpretations of depositional processes. Trace fossils were described and photographed in the field. In the laboratory, collected samples were analyzed using high-resolution photographs, which were edited in Adobe Photoshop to enhance contrast, brightness, and vibrance, allowing better visualization of ichnofabric details according to Dorador & Rodríguez-Tovar⁸⁵. Ichnotaxonomic classification adhered to Bromley⁷ guidelines, using ichnotaxobases such as morphology, branching patterns, burrow boundaries, and filling material. Additional parameters included burrow dimensions, density, cross-cutting relationships, and preservational type. The bioturbated area was quantified using the bioturbation scale (BS) of Reineck⁸⁶ ranging from 0 (no bioturbation) to 6 (homogenized sediment with no apparent primary sedimentary structures).

Data availability

Data will be made available upon request. Please contact Diego Nascimento (dih.sapo@gmail.com).

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Author contributions

D.L.N., F.S.B.L. and M.A. data curation, conceptualization and writing original draft. R.G.N. and M.G.S. conceptualization and writing original draft.

Declarations

Competing interests

The authors declare no competing interests.

Publication consent

All participant of this article provided the consent to publish.

Additional information

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