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Bichordites-dominated ichnofabrics from Spanish Pliocene calcarenites: traces of marine life in migrating dunes

Weronika ŁASKA[1, 2, *], Shannon HSIEH[3], Francisco J. RODRÍGUEZ-TOVAR[4] and Alfred UCHMAN[1]

[1] Jagiellonian University, Faculty of Geography and Geology, Institute of Geological Sciences, Gronostajowa 3a, 30-387 Kraków, Poland; ORCID: 0000-0001-5034-5240 [W.Ł.], 0000-0002-0591-777X [A.U.]

[2] University of Warsaw, Institute of Evolutionary Biology, Faculty of Biology, Biological and Chemical Research Centre, Żwirki i Wigury 101, 02-089 Warszawa, Poland

[3] email: shannonhsieh1@gmail.com, ORCID: 0000-0002-8074-547X

[4] Universidad de Granada, Departamento de Estratigrafía y Paleontología, Facultad de Ciencias, 18002 Granada, Spain; ORCID: 0000-0002-1400-2715

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A series of Pliocene ichnofabrics is described from the Cuevas Formation, Almería-Níjar Basin of south-eastern Spain, where a thick, cross-stratified, mixed bioclastic-siliciclastic succession is exposed along a laterally continuous section. It records the dynamic conditions of ancient subaqueous dunes during their deposition and the activities of organisms colonizing them. The ichnofabrics are dominated by *Bichordites*, traces likely made by burrowing sea urchins adapted to live in shifting sand. Ichnofabrics range from those showing weak bioturbation with little else but *Bichordites* (representing high-energy, continuously migrating dunes) to ichnofabrics featuring a high degree of bioturbation containing a low to moderately diverse ichnofauna (representing more physically stable environments where organisms could gather food in less agitated waters). Strong burrowers like the *Bichordites* producers could have acted as ecosystem engineers. *Piscichnus* producers may have preyed on benthic sand-dune organisms. The non-uniform distribution of ichnotaxa in these Pliocene sand dunes, alongside previous studies, suggests that these ancient bioturbating communities may have been similar to those in modern seas.

Key words: sea urchins, marine strait, palaeoecology, macrobenthic ecosystem, spatial distribution, biotic interactions.

INTRODUCTION

Shallow seas are characterized by sandy deposits that shift and change dynamically or rhythmically in response to hydraulic conditions forming various bedforms, including sand ripples, subaqueous dunes and sand ridges (Jordan, 1962; Allen, 1980; Borsje et al., 2009; Cheng et al., 2021). Among the most dynamic large-scale bedforms are tidal sand waves, with wavelengths of several hundreds of metres and heights of several metres, which can migrate as much as tens of metres per year (Borsje et al., 2009; Cheng et al., 2021). Although such dynamic bedform environments may initially appear barren of marine life, they are in reality habitats for benthic organisms that have adapted to these conditions.

Organisms moving, interacting with each other, and responding to sediment mobilization due to tidal currents and wave action often modify the substrate in distinctive ways. The traces and undeterminable bioturbation structures they left behind, though often temporary, can be preserved under favourable conditions and enter the geological record, offering valuable insights into past ecological and depositional conditions.

Ancient marine sand ridges and sand wave complexes are well documented from many geological periods and regions, ranging from the early Paleozoic of Argentina to the Carboniferous of England and the Cretaceous Western Interior Seaway in North America to the Cenozoic Mediterranean (Pryor and Amaral, 1971; Bouma et al., 1982; Rice and Shurr, 1983; Slatt, 1984; Brenner and Martinsen, 1990; Mángano et al., 1996; Nielsen and Johannessen, 2008; Olariu et al., 2012; Chiarella et al., 2016; Longhitano et al., 2021); many of these deposits show some evidence of bioturbation, including the presence of ichnofossils, consistent with a long-standing history of benthic life within them. Heterogeneity in the trace fossil distributions within such ancient dunes has been studied. For instance, Olariu et al. (2012) examined the Lower Eocene Baronia Formation in Spain and found that in siliciclastic cross-stratified

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* Corresponding author, e-mail: wn.laska@uw.edu.pl

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sandstone, bioturbation varied among dune bottomsets and foresets; the differences in bioturbation intensity and ichnological diversity were attributed to different dune migration rates.

Similar *Bichordites*-dominated ichnofabrics and ichnoassemblages have been documented from Neogene and Quaternary calcarenites, arenites and other sandstones representing subaqueous dune deposits and similar unstable substrates (Colella and D'Alessandro, 1988; D'Alessandro, 2004; Gibert and Goldring, 2007, 2008; Aguirre et al., 2010; Caruso et al., 2011; Nara, 2014; Caruso and Monaco, 2015; Baucon et al., 2020). The ichnoassemblages documented consist primarily of *Bichordites* and other traces attributed to sea urchins, including *Scolicia*, accompanied by *Macaronichnus*, *Planolites*, *Palaeophycus*, *Rosselia*, *Skolithos* and *Piscichnus*, among others. Although *Bichordites* and associated ichnotaxa are well-described and used as palaeoenvironmental indicators, few studies have examined in detail the heterogeneity in their distribution and associations within different parts of a sand wave complex or compared them to living communities in sand-wave ecosystems. For example, Nara (2014) described the ichnotaxa from a Pleistocene *Bichordites*-dominated ichnofabric and their distribution across bottomsets, foresets, and topsets of large-scale trough cross-bedded sandstones in the Ichijiku Formation of the Boso Peninsula, Japan. D'Alessandro and Uchman (2007) discussed how *Bichordites* and *Bichordites*-*Rosselia* ichnoassemblages were related to habitats with differing levels of seafloor stability in a Pleistocene section in Italy.

This paper provides an in-depth, large-scale examination of lateral and vertical heterogeneities in *Bichordites*-dominated ichnofabrics across sand wave complexes, based on an ichnological and sedimentological field study conducted on a cross-stratified Pliocene Río Alías strait-fill succession, exposed in the Almería-Níjar Basin of southeastern Spain. In contrast to previous studies on the strait succession, which primarily noted the presence of bioturbation structures and identified only *Scolicia* as an ichnotaxon (Dabrio, 1986–1987; Sola et al., 2024), our study provides a comprehensive description of the full suite of ichnotaxa within one of the key sections representing the Río Alías Strait. This detailed analysis highlights the diversity of trace fossils present, offering insights into the palaeoenvironmental conditions and the benthic community structure that existed within this ancient tidally influenced strait. Combining physical sedimentary structure data with trace fossil information, the ichnological evidence of benthic community zonation in these deposits was examined; this enables comparisons with analogous modern counterparts, offering a novel perspective not previously addressed in other studies.

GEOLOGICAL SETTING

The study area is located in the northeastern part of the Almería-Níjar Basin (Fig. 1), also known as the Níjar Basin (e.g., Dabrio, 1986–1987; Aguirre and Sánchez-Almazo, 2004; Fortuin and Dabrio, 2008). This elongated depression is oriented SW-NE and is one of several Neogene outer intermontane Mediterranean-linked basins in SE Spain, like the Vera, Sorbas and Tabernas basins (Fig. 1A). These basins are situated within the Internal Zone of the Betic Cordillera, the westernmost limit of the Alpine Mediterranean Belt (e.g., Salé et al., 2012; Sola et al., 2017).

The formation and separation of these basins, including the Almería-Níjar Basin, were driven by tectonic uplift of the Betic Cordillera mountain ranges. Notable uplifts include the Sierra de Gádor, the Sierra Alhamilla during the latest Tortonian, the Sierra Cabrera during the latest Messinian, and the Cabo de Gata volcanic province during the Miocene–Pliocene transition (e.g., Martín and Braga, 1996; Aguirre, 1998; Braga et al., 2003a, b; Aguirre et al., 2008). This tectonic uplift also led to the formation of the Río Alías Strait in the Early Pliocene, located at the northeastern end of the Almería-Níjar Basin. This strait was a marine corridor, ~12 km long and up to 2 km wide, connecting the basin with the Mediterranean Sea (Sola et al., 2024).

During the Neogene, ongoing tectonic processes considerably affected sedimentation in these basins, which were gradually infilled with predominantly shallow-marine to continental sediments supplied from the adjacent emergent topography. In the latest early Pliocene, the development of the El Argamasón delta system in the northeastern part of the Almería-Níjar Basin led to the occlusion of this strait (Aguirre et al., 2008). During this same period, the Almería-Níjar Basin and the adjacent Carboneras Basin, initially separated by a volcanic elevation, coalesced and were connected by straits formed at the shortest distance between the two basins in the El Castillico area (Braga et al., 2003a, b; Martín et al., 2003, 2004; Aguirre et al., 2008, 2012; Aguirre, 2017).

The Almería-Níjar Basin contains a Miocene–Pleistocene infill composed of several units separated by unconformities. The Lower Pliocene deposits onlap the irregular surface bounding upper Messinian strata, which were excavated by the early Pliocene transgression, as well as the metamorphic rocks of the Betic Cordillera and volcanic rocks of the Sierra de Gata (Aguirre, 1998, 2017; Braga et al., 2003a, b; Martín et al., 2003, 2004). These deposits exhibit diverse facies, predominantly of mixed siliciclastic-carbonate and siliciclastic deposits (e.g., Aguirre, 1998, 2017; Braga et al., 2003a, b). Major deltas developed along the basin margins include the Abrioja delta in the northwest corner (Postma, 1979, 1983), the El Barranquete delta in the ESE part (Boorsma, 1992), and the El Argamasón delta at the northeastern edge. All of them provided siliciclastic material from the erosion of the Betic metamorphic basement and volcanic rocks of the Sierra de Gata region (Aguirre, 1998, 2017) to the Almería-Níjar Basin. In shallow platform areas sheltered from terrigenous input, carbonates including bioclastic calcarenites and calcirudites formed in the northern Palmo de Salas, the Gafares-El Argamasón areas, and the western margins of the Almería-Níjar Basin (Aguirre, 1998, 2017).

The late Pliocene deposits, characterized by siliciclastic strata and temperate coral banks with *Cladocora caespitosa* (Linnaeus, 1767), are found exclusively in the central Almería-Níjar Basin. This restricted occurrence is due to tectonic uplift and a relative drop of sea level, which maintained marine conditions only in this central area. Quaternary sands and conglomerates, deposited in alluvial fans and beach environments, represent the final sedimentary infill of the basin (Goy and Zazo, 1986; Aguirre, 1998).

GENERAL DESCRIPTION OF THE SECTION STUDIED

The study area is located near the El Argamasón hamlet in Almería Province, southeastern Spain (Fig. 1). The section investigated, here referred to as Río Alías, is exposed in the deep river-cut gorge of Río Alías, near Cortijo del Molino de Abajo, ~1 km south-east of El Argamasón (GPS coordinates: N36°56.713', W01°55.611'). The strata studied commence ~650 m west of the bridge to the village of El Argamasón and extend laterally for 1000 m, initially in a southwest direction, then turning northwest. This river-cut section is deeply incised

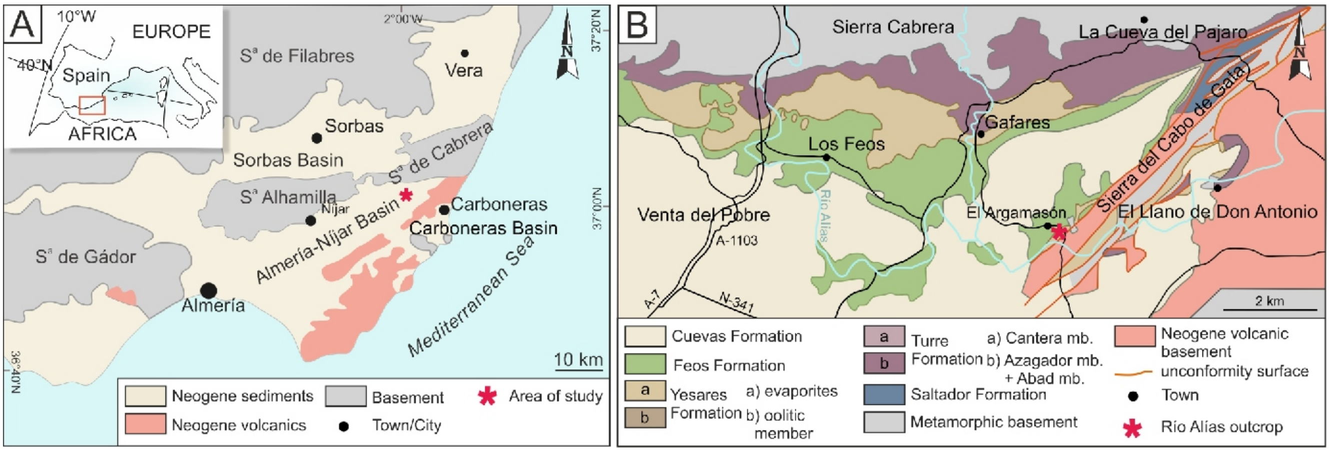

Fig. 1. Location and simplified geological map of the Eastern Betic region (A, B) in Almería Province with the study area indicated, showing the Almería-Níjar Basin and other Neogene basins (A) and the main strike-slip faults controlling their evolution (modified from Martín et al., 1996 and Salé et al., 2012)

into Lower Pliocene deposits, part of the Río Alías Strait's infill (Sola et al., 2024). The strait infill consists of mixed carbonate-siliciclastic deposits, with siliciclastic material sourced from deltas that transported sediments mostly eroded from the Sierra Cabrera relief, located to the north (Sola et al., 2024).

The Pliocene succession starts with shallow-marine calcarenites, sandstones and conglomerates, which formed due to the progradation of shelf-talus and fan-delta systems (Dabrio et al., 1986–1987). As this study concentrates on Lower Pliocene calcarenites yielding the trace fossil assemblage, the overlying deposits are not further addressed.

In the Río Alías section, the exposed calcarenites represent a portion of the Cuevas Formation (Salé et al., 2012), corresponding to the Lower Pliocene to the lowermost Upper Pliocene Unit I defined by Aguirre (1998). They rest on yellow to greyish siltstones and marls, with a sharp contact between them exposed in the cliffs adjacent to the river valley (Blum, 2007).

METHODS

The data and material for this study were collected during field campaigns in March 2019. Most of the ichnofossils were observed, measured, and photographed in the field. Descriptions of the size and morphology of the ichnotaxa were made and their abundance was noted; in decreasing order, traces were generally described as “abundant” if they were found in high numbers in all beds investigated, “common” if seen in all beds but not necessarily in large numbers, “uncommon” if not found in all beds, and “rare” if only present in a minority of beds. The bioturbation intensity was qualitatively assessed based on 2D images, following the scheme provided by Taylor and Goldring (1993). The Taylor and Goldring (1993) bioturbation scale (Bioturbation Index; BI = 0–6) is non-linear and assesses the disruption of primary sedimentary structures by burrowing organisms, ranging from no visible bioturbation (BI = 0), through minimal (BI = 1–2), moderate (BI = 3–4), to intense or complete bioturbation with heavily homogenized sediment (BI = 5–6). Due to the significant ambiguity and inconsistency in the terminology used for classifying subaqueous bedforms of different scales, the classification scheme proposed by Ashley (1990) was used for this study. “Dunes” include forms such as sand waves or megaripples, as they are related to similar hydraulic energies in lower flow-regime conditions despite their differences in size and morphology. Unmanned Aerial Systems (UAS) drones were used to study the spatial relationships between bedforms and trace fossils exposed in steep cliffs along the Río Alías. Thin sections were made to investigate the microfacies and fossil content of the dominant lithologies. In order to statistically measure components, the point counting technique (600 points) was applied using *JMicroVision v1.3.3* on the stitched large images of thin sections. Large images were photographed with a *Nikon Eclipse 50i* polarizing microscope equipped with a *Nikon DS-Fi1* digital camera.

RESULTS

LITHOLOGY

The calcarenites of the Río Alías section (Fig. 2) are buff-yellow in colour, fine- to medium- and coarse-grained and composed of fine, moderately to poorly sorted carbonate grains mixed in various proportions with siliciclastic grains which consist of monocrystalline to polycrystalline quartz. Based on thin section analysis, skeletal components are dominated by echinoderm fragments and calcareous red algae, accompanied in varying proportions by foraminifera, bryozoans, bivalve fragments and barnacles. Well-developed planar and trough cross-stratification is the predominant sedimentary structure of the calcarenites (Dabrio, 1986–1987; Sola et al., 2024). The thickness of cross-stratified sets varies from 0.2 m to 1 m, locally up to 4 m. Each set forms a tabular or gently lenticular body with planar or slightly curved bounding surfaces that are generally traceable laterally for up to 30 m. Bounding surfaces are either sharp or gradational, and they are often marked by burrows. Bed-sets occur individually or are arranged in stacked cosets grouped into monotonous, mostly 2 to 8 m thick successions, overlying or laterally interfingering with different-scale planar and trough cross-bedded calcarenites. Foresets are concave-upwards, transitioning into tangential, rarely angular toesets and in some instances into thinner and finer-grained bottomsets commonly with poorly defined contacts between foresets and bottomsets. The majority of foresets dip to the east, though there are localized intercalations of cross-sets (sets of cross-stratified beds) dipping to the west (Dabrio, 1986–1987). Compound cross-stratification is common, with

Fig. 2. Panoramic view of part of a Río Alías exposure showing large-scale cross-stratification of calcarenites (note people for scale) generated by migrating sand dunes

smaller foresets superimposed on larger ones, descending along the lee side. Concave-up reactivation surfaces, truncating and dividing foresets into distinct packages, are spaced irregularly and are frequently marked by bioturbation. Cross-sets show significant variation in bioturbation, ranging from completely unburrowed to sparsely or thoroughly bioturbated (for details see Section 4.3). Locally, fine- to medium-grained, pervasively bioturbated calcarenite lenses are intercalated within the cross-stratified calcarenites, reaching thicknesses of up to 1 metre and extending laterally for several metres. In these lenses, bioturbation has largely obliterated the physical sedimentary structures, leaving only sporadic traces of parallel lamination in some beds.

Dabrio (1986–1987) and Sola et al. (2024) interpreted these deposits as formed by migrating 2D and 3D subaqueous dunes of varying sizes, shaped by complex and unsteady currents. The dominant flow direction was east to west, with occasional subordinate flows in the opposite direction. These alternating high- and low-energy phases were driven mostly by tidal currents and, when funneled through a narrow strait connecting the Almería-Níjar Basin with the Mediterranean Sea, the flow was accelerated and controlled dune evolution and migration (Sola et al., 2024), directly affecting habitat stability of the benthos. Omission and reactivation surfaces are often marked by bioturbation structures. These reflect periods of reduced energy and cessation of bed material movement, indicating the unsteady nature of the flow. The presence of reactivation surfaces, tidal bundles of bioclastic and siliciclastic laminae together with bidirectional (herringbone) cross-stratification was interpreted as suggesting flow reversals associated with tidal activity (Sola et al., 2024). According to Sola et al. (2024), the water depth of the Río Alías Strait during the Early Pliocene, estimated from subaqueous dune foreset heights, ranged from ~20 to 65 m, consistent with typical microtidal straits and reflecting significant tidal influence on sediment transport.

ICHNOTAXONOMY AND DESCRIPTION OF *BICHORDITES* AND ASSOCIATED TRACE FOSSILS

Asterosoma isp.
(Fig. 3)

Description. – Endichnial burrow system characterized by a bundle (at least two) of vertical to oblique elongated bulbous structures. The structures are 32–224 mm (mean = 46 mm) long and 9–48 mm (mean = 25 mm) wide. Each structure extends upwards and outwards from a central common point, creating a radiating pattern (Fig. 3). The bulbous structures are slightly to markedly arched. They exhibit a small cylindrical inner central tube with a concentric lining characterized by a swelling in the middle to terminal regions, contributing to their bulbous morphology. They taper at one or both ends. The lining is distinguishable by its brighter colour compared to the central tube and host rock, which are of similar colours. The bulbs are better preserved due to preferential cementation of the lining and often protrude out of the weathered bed.

Remarks. – Burrows similar to those described herein, characterized by bundled, upwardly radiating, bulbous and lined tubes, have been reported from Lower-Middle Jurassic marginal marine deposits of the Sorthat Formation in Denmark and attributed to *Asterosoma* isp. (Bromley and Uchman, 2003), and from the Miocene siliciclastic rocks of the Grund Formation in northern Lower Austria (Molasse Basin) and attributed to *Asterosoma radiciforme* von Otto, 1854 (Pervesler and Uchman, 2004).

According to Knaust (2021), the type species *Asterosoma radiciforme* von Otto, 1854, exhibits passive filling rather than concentric lamination, and thus the lined burrows with upwardly radiating bulbous structures, previously grouped under

Fig. 3. *Asterosoma* isp. in calcarenites, Río Alías section, field photographs
A–C – vertically to obliquely oriented lined bulbs of *Asterosoma* isp.

Asterosoma, are more compatible with and should be ascribed to *Rosselia*. However, the arguments that the radially arranged bulbs of *A. radiciforme*, covered with wrinkles, are passively filled are not convincing. The radial arrangement suggests a significant behavioural activity that does not align with any specific ichnospecies within the *Rosselia* group. Some of the specimens resemble *Rosselia prolifera* (Forunier et al., 1980), originally *Polycylindrichnus prolifer* Forunier et al., 1980 (see description in Knaust, 2021), due to the preserved bulbous structures which form a Y shape; however, these specimens are incomplete. Since the ichnogenus *Asterosoma* is pending reevaluation to determine whether to exclude or include the lined forms, the burrows reported here, showing greater morphological similarity to this ichnogenus, are assigned to *Asterosoma* isp. *Lamellaecylindrica ludwigae* (Schlirf, 2000), originally *Asterosoma ludwigae* Schlirf, 2000, also presents lined burrows with bulbous extensions radiating from an elongate burrow (Knaust, 2021). However, unlike the radiating bulbous burrows studied here, *L. ludwigae* is distinguished by downwards rather than upwards branching.

Bichordites monastiriensis Plaziat and Mahmoudi, 1988
(Figs. 4 and 5B–F)

Description. – Horizontal, straight to winding complex burrow, showing a characteristic meniscate backfill and a central core. It measures 28–89 mm (mean = 54 mm) in diameter, with a maximum observed length of 109.5 cm (mean = 35 cm). Within one burrow, the diameter is constant, or there is a slight change in diameter along its course faintly tapering toward its end. The dorsal (top) and often the ventral (base) surface of the burrows show a bilobate to subquadrate profile in transverse cross-section formed by parallel lobes, separated by an axial groove (Fig. 4B, D, E). Notably, there is considerable variability in the morphological preservation (*sensu* Marchetti et al., 2019), both within individual burrows and among them. The upper portion of the backfill menisci, arranged in a *Laminites*-type pattern (referenced in Uchman, 1995), may be absent or poorly defined, often preserved incompletely and limited to a part of the trace fossil (Fig. 5B). Frequently, the upper half of the menisci is weathered away and entirely missing (Fig. 4C), while the lower, typically better-cemented portion remains intact. However, the base of the lower portion also weathers away and is often entirely absent (Fig. 4A). In most specimens observed on bedding planes, the peripheral portion of the meniscate fill is entirely weathered away, leaving the better-lithified, preferentially preserved central core, which is located approximately below the central axis or closer to the basal part. The core may display transverse irregular annulations, which are indicative of weathered edges of the meniscate backfill (Fig. 4B, D, F). In some specimens, the central core is formed by a tube, ovoid to heart-shaped in cross-section and filled with massive sediment, often slightly more compacted and lighter than the surrounding part of the burrow (Fig. 4D). In one case, a vertically oriented structure seen in transverse section is preserved above the burrow (Fig. 4E); it gradually widens towards the top, forming a funnel shape; it possibly represents the respiratory shaft connecting the burrow with the sediment-water interface (as noted in Bromley and Asgaard, 1975; Bromley et al., 1997).

Remarks. – *Bichordites* is interpreted as a locomotion-feeding trace fossil, which is distinguished from *Scolicia* by having a single drainage tube, whereas the latter bears a pair of tubes (e.g., Plaziat and Mahmoudi, 1988; Uchman, 1995). *Bichordites* is described in the literature as being produced by detrivore, irregular spatangoids of the genus *Echinocardium* (family Loveniidae), including *E. cordatum* Pennant, 1777 (Bromley and Asgaard, 1975), foremost *E. mediterraneum* (Bromley et al., 1997), *Euaptagus,* including *Eupatagus ornatus* (family Eupatagidae) (Bernardi et al., 2010), or possibly *Maretia* (family Maretiidae) (Gibert and Goldring, 2008; Villegas-Martín and Netto, 2017). However, none of the spatangoids have been observed in life position within a burrow in the exposure studied.

Bivalve burrow
(Fig. 5A)

Description. – This vertically oriented endichnial structure is characterized by two distinct parts: a heart-shaped base obliquely oriented towards the foreset from which emanates a very long narrow tube representing the upper part (Fig. 5A). This tube cross-cuts the foreset laminae and connects the lower part with the bedding plane which represents the previous seafloor. The heart-shaped base measures 62 mm in length and 37 mm in width, and the upper cylindrical part is 530 mm long and has a diameter of 22 mm. The burrow infill is similar to the host bed; occasionally, remnants of lining composed of lighter material occur in some areas. Notably, no protrusive or retrusive spreiten were observed.

Remarks. – This structure shares features consistent with those observed in modern bivalve burrows as depicted in X-radiographs of *in situ* specimens (Zonneveld and Gingras, 2013, fig. 1A; Wetzel and Unverricht, 2020, figs. 6–10). The heart-shaped base presumably served as the dwelling chamber; the bivalve shell possibly dissolved during post-depositional diagenesis, whereas the long tube is interpreted as the trace of the siphon.

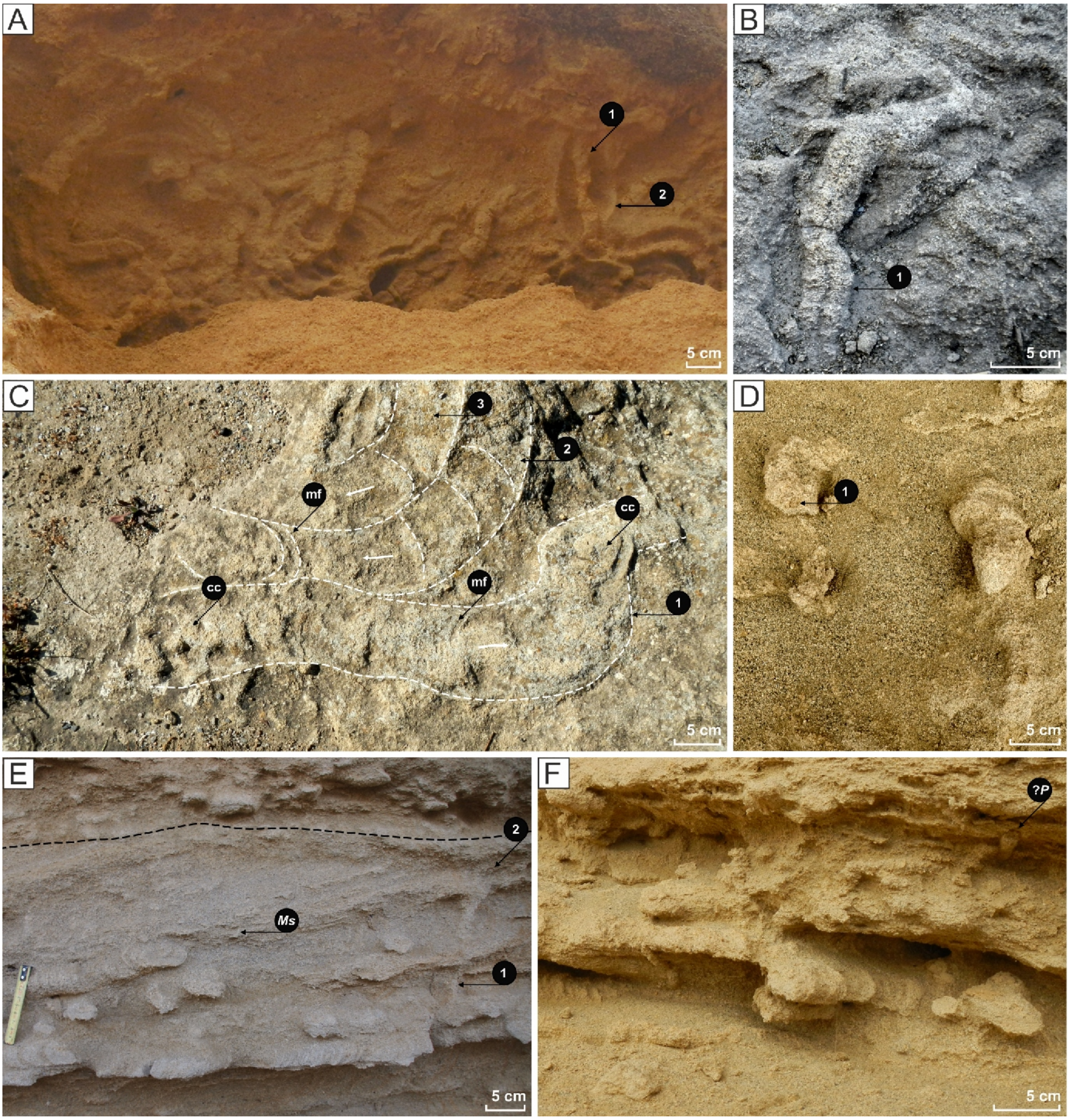

Fig. 4. Field photographs of *Bichordites monastiriensis* from the Pliocene of the Río Alías section, illustrating details of its morphology

A – weathered bedding plane with several specimens of *B. monastiriensis*. Arrows indicate fragments of burrows where less cemented parts, including the part of the meniscate fill together with the burrow floor, are selectively weathered away, leaving the strongly cemented central core (arrow 1) and a margin of depression after weathering out of the meniscate envelope (arrow 2); **B** – endichnial *B. monastiriensis* (false epichnia) viewed from above, showing well-cemented sediment surrounding the central core. Arrow 1 points to a part of *B. monastiriensis* with weathered margins of the meniscate backfill and a bilobate central core; **C** – three examples of *B. monastiriensis* (1, 2, and 3 outlined with a white, dashed line) showing the central core (cc) and meniscate filling (mf). The concavity of the menisci indicates the direction of movement of the tracemakers (white arrows); **D** – meniscate *B. monastiriensis*. Arrow 1 points to the darker central canal within the central core; **E** – *Bichordites* ichnofabric II with abundant *B. monastiriensis*, locally accompanied by *Macaronichnus segregatis* (*Ms*), present within the foresets of trough cross-bedded calcarenites. Arrows 1 and 2 point to a conical structure over *B. monastiriensis* that widens toward the top, seen in longitudinal section, and interpreted as a possible shaft funnel. The black dashed line marks the bounding surface. Note that the overlying calcarenite exhibits a higher intensity of bioturbation, characteristic of *Bichordites* ichnofabric III; **F –** close-up of cross-set with *B. monastiriensis*, accompanied by ?*Palaeophycus* isp. (?*P*), *Bichordites* ichnofabric II

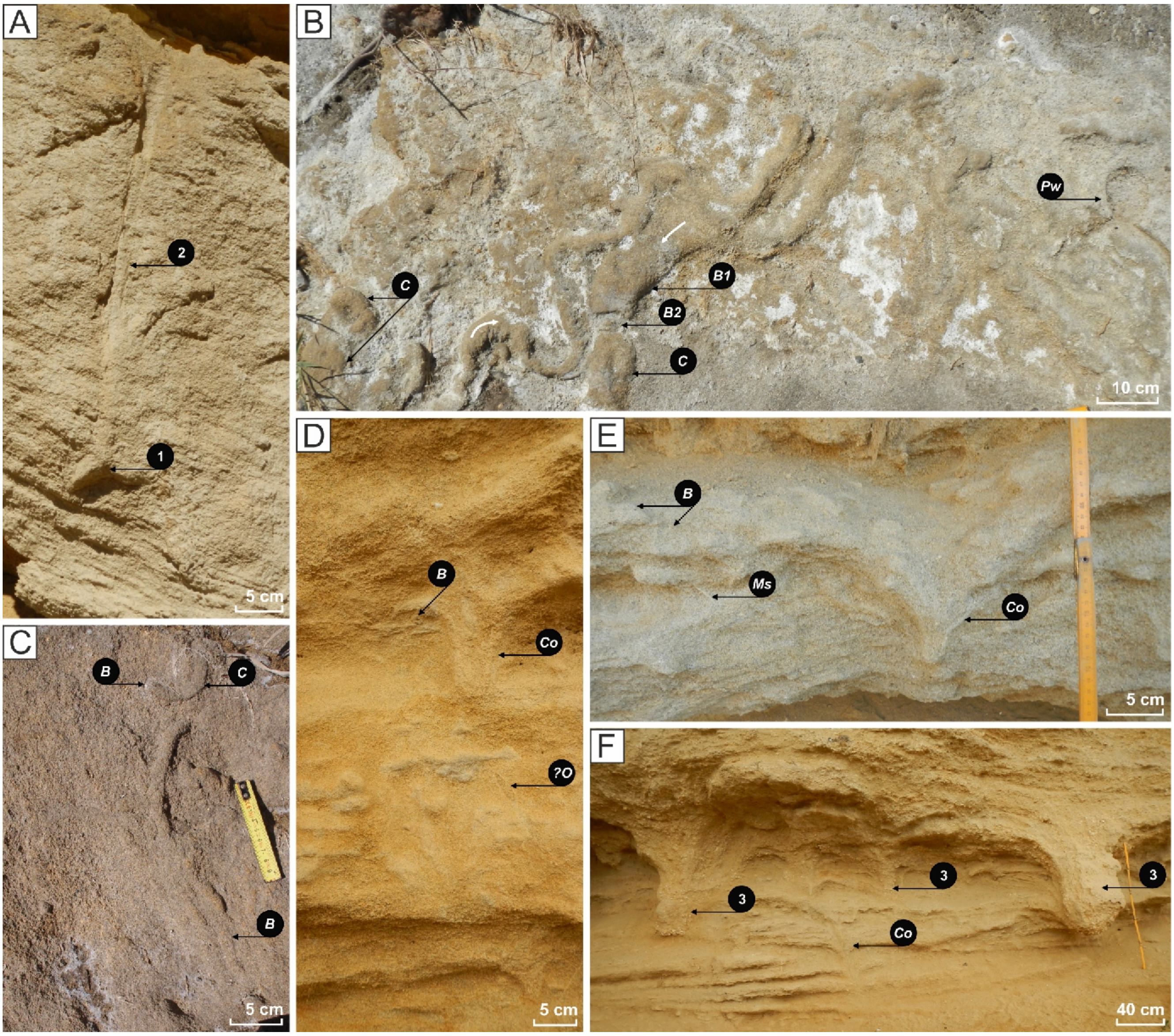

Fig. 5. Trace fossils from the Pliocene of the Río Alías section, field photographs

A – bivalve burrow, arrow 1 points to a heart-shaped base interpreted as the possible dwelling chamber and arrow 2 points to the elongated tube interpreted as the trace of the siphon; **B, C –** *Bichordites* ichnofabric II, weathered surface of foreset showing false epichnia of *Cardioichnus* isp. (*C*) associated with *B. monastiriensis* and *Piscichnus waitemata* (*Pw*) seen from above. *Cardioichnus* (*C*) is preserved at the end of the gently curving burrow of *Bichordites* in the *Lamnites* type preservation mode (*B1*) that in a short distance is weathered away, showing the inner, annulated core (*B2*). Arrows show the direction of movement of the spatangoid during burrowing; **D–F –** *Bichordites* ichnofabric II*,* *Conichnus* isp. (*Co*) and other unknown, large conical structures (3) in association with *B. monastiriensis* (*B*), ?*Ophiomorpha nodosa* (?*O*), and *Macaronichnus segregatis* (*Ms*) cross-cutting or present along the foresets

Cardioichnus isp.
(Fig. 5B, C)

Description. – A distinct heart-shaped mound consisting of two slightly elongated, bilaterally symmetrical lobes separated by a centrally placed, dorsal, roundish or V-shaped depression (Fig. 5B, C). The lobes are generally rounded, with a slightly flattened ventral (base) surface and a rounded dorsal (top) surface. The trace is 33–73 mm (mean = 59 mm) wide and 57–122 mm (mean = 91 mm) long.

This trace occurs as a full-relief endichnion or false epichnion (endichnia exposed due to weathering). In full-relief preservation, sediment surrounding the upper portion or margins of the trace appears partially weathered-out, indicating a lesser degree of lithification typical of trace fossils produced by heart urchins. In false epichnia preservation, they lie horizontally or obliquely at around 40° to the surface of the host bed, sticking out of the weathered host foresets (Fig. 5B). Some specimens occur at the end of *Bichordites* isp. (Fig. 5C).

Remarks. – Due to poor preservation, specimens lack characteristic features allowing assignment at the ichnospecies level. *Cardioichnus* is considered as a resting trace (cubichnion) of irregular echinoids belonging to spatangoids (e.g., Smith and Crimes, 1983; Plaziat and Mahmoudi, 1988; Mayoral and Muñiz, 2001; Kappus and Lucas, 2019).

Conichnus isp.
(Fig. 5D–F)

Description. – An endichnial burrow characterized by its conical, downward-tapering shape with a rounded base, vertically to sub-vertically oriented to the bedding planes (Fig. 5D–F). These burrows are longer than they are wide, reaching up to 485 mm in length and 73 mm in diameter. They are commonly observed on vertical exposed faces where the internal structure of the burrow is seen in longitudinal section. The infill appears structureless or exhibits concentric lamination, which is convex-down, U- to slightly V-shaped in vertical section. *Conichnus* may cut through or deflect adjacent laminae within the host bed, locally causing deformation of the underlying deposits.

Remarks. – *Conichnus* is attributed to sea-anemones or similar organisms and is thought to be their resting or dwelling structures (e.g., Shinn, 1968; Frey and Howard, 1981; Pollard et al., 1993; Savrda, 2002). Morphological variations in *Conichnus* are likely influenced by behavioural adaptations to changing local environmental conditions. Burrows exhibiting retrusive laminae are interpreted as escape or equilibrium structures formed during sediment aggradation (e.g., Shinn, 1968; Gibert et al., 1998; Savrda, 2002; Buck and Goldring, 2003; Abad et al., 2006; Gingras et al., 2011; Mata et al., 2012; Desai and Saklani, 2015; Klug and Hoffmann, 2018; Patel et al., 2018).

Cylindrichnus concentricus Toots in Howard, 1966
(Fig. 6A, B)

Description. – A simple endichnial burrow composed of a central, concentrically lined tube that bends downwards, forming an arch or wide U-shape (Fig. 6A, B). The limbs of the U or the arch are oriented obliquely and the elongated base of the U or the arch is horizontal. Towards the aperture, the lining gradually increases in thickness, resulting in a slightly conical morphology of the burrow near the aperture. The fill of the central tube is similar to the host rock, whereas the lining is composed of light, muddy laminae. The burrow is typically up to 170 mm long. It is circular to elliptical in cross-section, ranging in diameter from 20 to 26 mm.

Remarks. – Most observed burrows are incomplete. *Cylindrichnus concentricus* shares similarities with *R. socialis* in having a central core lined by concentric layers but differs in its arcuate U-shape geometry and two openings to the seafloor (Ekdale and Harding, 2015; Knaust, 2021), in contrast to the typically vertical or inclined *R. socialis*.

Cylindrichnus concentricus is commonly attributed to detritus-feeding organisms inhabiting U-shaped burrows, which likely gathered food from the seafloor using tentacles. These organisms may have then incorporated fine-grained material into the walls of their burrows (e.g., Belaústegui and Gibert, 2013). Present-day analogs of such traces are associated with terebellid polychaetes, such as *Amphitrite ornata* (see Aller and Yingst, 1978), *Neoamphitrite figulus* (see Schäfer, 1956, 1972), or *Cirriforma luxuriosa* (see Zorn et al., 2007). Additionally, Goldring (1996) suggested decapod crustaceans as possible tracemakers, as they have been found in association with concentrically laminated, bow-shaped burrows.

Macaronichnus segregatis Clifton and Thompson, 1978
(Figs. 5E, 6C, D, F–H and 7A, D, H)

Description. – A horizontal through oblique to vertical, straight to gently contorted cylindrical, smooth cylinder, circular in cross-section, with a diameter of 1.2–5.4 mm (mean 2.8 mm) and traced for a maximum distance of 97.4 mm (mean 27.2 mm). It is composed of a core enhanced in light grains, while dark grains (like those in the host rock) are enriched in the surrounding mantle. It occurs gregariously, often in the fill of *Piscichnus waitemata* (Fig. 7A, B).

Remarks. – Most of the observed specimens display all typical features of *Macaronichnus segregatis*; however, some of them lack the darker mantle. Thin cylinders, mostly about 2–3 mm in diameter, correspond to the size of the ichnosubspecies *M. segregatis segregatis*. According to the size-distribution model proposed by Seike et al. (2011), *M. s. segregatis* is exclusive to shallow-marine foreshore environments, in contrast to *M. segregatis degiberti*, mostly distinguished by its larger size with diameters up to 15 mm (Rodríguez-Tovar and Aguirre, 2014). In the section analysed, only a few specimens have a diameter >3 mm.

M. segregatis degiberti shows a wide environmental distribution from tidal channels, tidal sand bars, tidal sand ridges, the upper–lower shoreface, and continental shelf to deep-marine settings (e.g., Nara and Seike, 2019; Miguez-Salas et al., 2021; Rodríguez-Tovar and García-García, 2023), except in the high-energy foreshore (Nara and Seike, 2019). Nevertheless, the smaller *Macaronichnus segregatis* has also been recorded from deeper environments, marine channel systems, and the neritic to upper bathyal realm, showing that tube diameter does not depend on water depth and should be used with caution as an indicator (Knaust, 2017; Giannetti et al., 2018). According to Quiroz et al. (2010, 2019), the presence of *M. segregatis* in tropical environments is associated with nutrient-rich and cold waters related to upwelling and enhanced primary productivity that had been considered as major factors controlling the distribution of *Macaronichnus.* Generally, *M. segregatis* tends to occur at intermediate and high latitudes, rarely at lower latitudes (Clifton and Thompson, 1978; Pearson et al., 2013; Nara and Seike, 2019; Quiroz et al., 2019; Olivero and López-Cabrera, 2020).

Macaronichnus segregatis has been commonly interpreted as a pascichnion produced by selective deposit-feeding opheliid polychaetes such as *Ophelia limacina* Rathke, 1843, *Thoracophelia mucronata* Treadwell, 1914 (formerly assigned to *Euzonus*), or the travisid polychaete *Travisia* (producer of *M. s. giberti*), which feed on the epigranular microbial biomass on sand particles (Clifton and Thompson, 1978; Gingras et al., 2002; Nara and Seike, 2004; Dafoe et al., 2008a, b; Pemberton et al., 2012; Nara and Seike, 2019).

Ophiomorpha nodosa Lundgren, 1891
(Fig. 6D, E)

Description. – Vertical to slightly oblique, mostly straight, rarely slightly curved, walled tubes with occasional branching at 120° (Fig. 6D, E). Walls show a poorly developed knobby appearance. They are lined with material in a lighter colour than the burrow fill, which is identical to the surrounding ma-

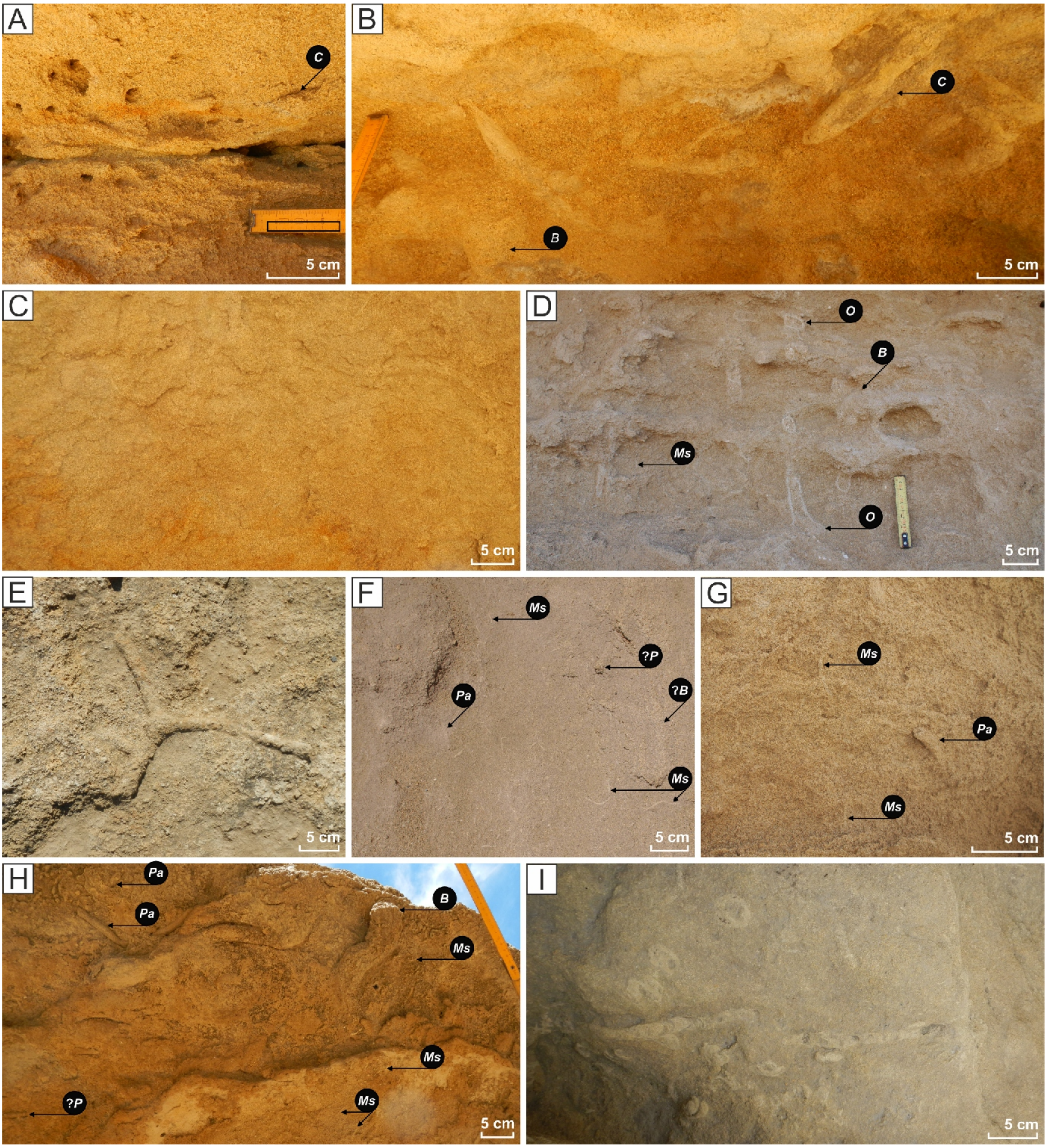

Fig. 6. Other trace fossils from the Pliocene of the Río Alías section, field photographs

A, B – widely arched concentric tube of *Cylindrichnus concentricus* (*C*) cutting a totally bioturbated background with light mottles and poorly preserved *B. monastiriensis*; **C** – *M. segregatis* poorly contrasting with the background sediment; **D** – deep-tier *Ophiomorpha nodosa* (*O*) cutting through densely bioturbated calcarenites with poorly preserved, partially destroyed *Bichordites monastiriensis* (*B*) and *Macaronichnus segregatis* (*Ms*); **E** – branched fragment of *O. nodosa* featuring knobby ornamentation of the wall; **F, G** – light-coloured *M. segregatis* in association with ?*Planolites* isp. (?*P*), *Palaeophycus* isp. (*Pa*) and ?*B. monastiriensis* (?*B*); **H** – weathered bedding plane with several specimens of *B. monastiriensis* (*B*)*, Palaeophycus* isp. (*Pa*), and *M. segregatis* (*Ms*); **I** – *Patagonichnus* isp.

trix. The tunnels are circular to slightly oval in cross-section, having a 12–41 mm (mean = 23 mm) diameter including the lining. Most burrows are vertical to the bedding plane; horizontal elements are rare. Enlargements at branching points are observed (Fig. 6E). Tunnels up to 542 mm long were observed.

Remarks. – *Ophiomorpha nodosa* is described as being produced by suspension-feeding decapod crustaceans such as callianassids (e.g., Knaust, 2017).

Palaeophycus isp.
(Figs. 6F–H and 7B)

Description. – A simple, straight to gently curved, elongate, cylindrical burrow, up to 210 mm long, with a thin lining. It is circular to sub-circular in cross section, up to 14 mm in diameter. The material filling the burrow closely resembles the surrounding sediment. The trace is preserved as full relief or epirelief.

Remarks: *Palaeophycus* is interpreted as a dwelling structure of a predatory or suspension-feeding worm-like organism (Pemberton and Frey, 1982; Knaust, 2017). The characteristic lined wall distinguishes it from *Planolites* (Pemberton and Frey, 1982).

Patagonichnus isp.
(Fig. 6I)

Description. – An endichnial compound trace fossil observed on weathered upper bedding planes. It comprises many closely spaced mud-lined tubes up to 446 mm long, visible only in cross-section, along with horizontal structures displaying meniscate backfilled laminae. In cross-section, the tubes are circular to elliptical, up to 29 to 41 mm (mean = 35 mm) in diameter. The tubes are walled and filled with sediment similar to the host rock. Their walls are voluminous and display eccentric or concentric lamination made of light, muddy material. The backfilled structures, occasionally in contact with the lined tubes, follow a slightly winding course; the backfill is composed of the same muddy material as the concentric and eccentric lining of the tube wall.

Remarks. – The intricate geometry is characteristic of the ichnogenus *Patagonichnus*. However, partial preservation prevents further ichnospecific assignment. When viewed individually, the mud-lined tubes of the specimens analysed resemble *Rosselia socialis*, but the complexity and presence of horizontal structures with meniscate backfills distinguish them from that ichnospecies. *Patagonichnus* is possibly produced due to the feeding activity of gregarious polychaetes (Olivero and López Cabrera, 2005).

Piscichnus waitemata Gregory, 1991
(Figs. 5B, 7A, B, G and 11D)

Description. – In longitudinal section, the burrow appears as bowl- to sack-shaped depressions (concave epireliefs), which are circular to oval in bedding plane view. These depressions range in diameter from 77 to 350 mm (mean = 179 mm). Typically, they have steep-sloped margins and can reach up to 378 mm in depth, with an average of 187 mm. The material infilling depressions slightly differs in colour and structure from the surrounding sediment and is mostly massive and often bioturbated by *Macaronichnus segregatis* Clifton and Thompson, 1978 (Fig. 7A) and subordinately by *Ophiomorpha nodosa* and *Rosselia socialis* (Fig. 11D). *P. waitemata* is present either isolated or in localized clusters where specimens are typically spaced a few centimetres apart.

Remarks. – *Piscichnus waitemata* is interpreted as a praedichnion produced by bottom-feeding rays or other fish that create pits by flapping their pectoral fins or expelling a water jet through their mouths to expose prey (Gregory et al., 1979; Gregory, 1991; Gingras et al., 2007; Pearson et al., 2007; Löwemark, 2015; Uchman et al., 2018, 2020; Nielsen et al., 2020).

Planolites isp.
(Fig. 6F, H and 7C)

Description. – A simple, cylindrical straight to gently curved, unlined burrow, circular in cross-section, 4–13 mm (mean = 10 mm) in diameter, with an observed length reaching 152 mm (mean = 73 mm). It is preserved as either full relief or epirelief. The fill resembles the surrounding sediment, though it may be slightly coarser and brighter.

Remarks. – Distinctively, the absence of a wall lining differentiates *Planolites* isp. from other trace fossils such as the lined, passively filled *Palaeophycus* and actively filled *Macaronichnus*. *Planolites* is interpreted as a pascichnion produced by actively burrowing and feeding worm-like deposit feeders such as annelids, hemichordates, and priapulids (Osgood, 1970; Pemberton and Frey, 1982; Fillion and Pickerill, 1990; Keighley and Pickerill, 1995; Knaust, 2017). Additionally, arthropods (e.g., crustaceans) and molluscs (e.g., bivalves) are also considered as potential tracemakers (Knaust, 2017).

Rosselia socialis Dahmer, 1937
(Fig. 7D–H)

Description. – An endichnial, vertically to obliquely (40–60°) oriented structure, which typically occurs either individually or in clusters of two or three specimens found in close proximity (Fig. 7E–G). *R. socialis* is characterized by a central tubular shaft enveloped by a concentric lining that flares outwards in the upper part, close to the upper bedding plane, giving it a characteristic spindle- or funnel-shaped morphology. The burrow measures 62–254 mm (mean = 138 mm) in length and 20–97 mm (mean = 48 mm) in width at the upper, swollen, flared part. The central shaft has a circular to elliptical cross-section and maintains a uniform diameter within one burrow of 10–21 mm (mean = 14 mm). It is filled with sediment resembling in colour the surrounding host rock. In contrast, the lining of the shaft appears notably brighter (Fig. 7D). The lining in the upper part of the burrow, as seen in weathered, cross- or oblique-sections, displays distinct concentric laminae composed of alternating light, muddy (fine-grained) laminae, and darker-coloured, sandier (coarser-grained) laminae. However, in most specimens, these concentric laminae are less distinct and appear blurred. The lining shows preferential diagenetic cementation and is well-preserved, sticking prominently out of weathered bed surfaces (Fig. 7D–H). Specimens of vertically stacked spindle-shaped structures representing equilibrichnia

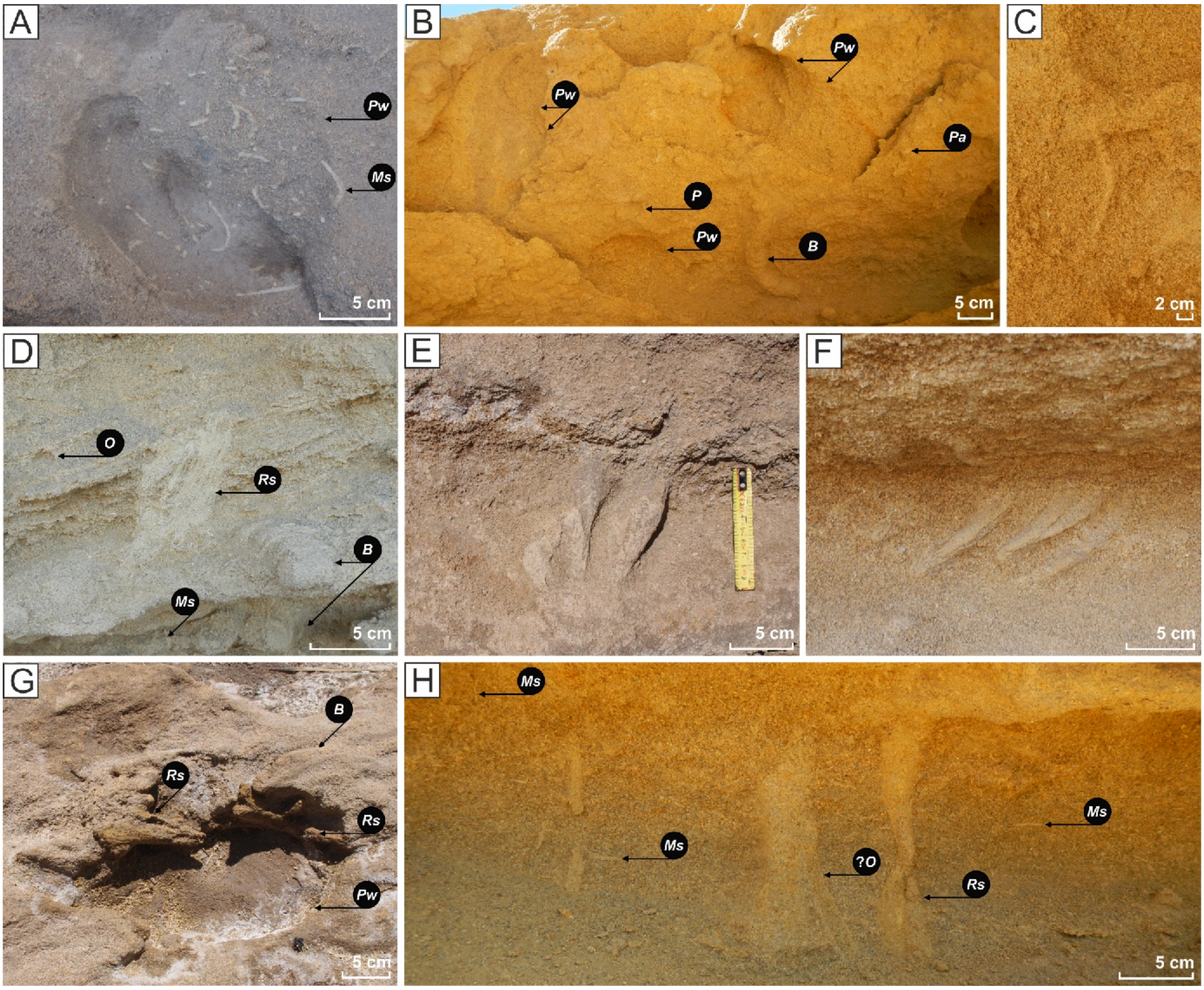

Fig. 7. More trace fossils from the Pliocene of the Río Alías section, field photographs

A – horizontal section of *Piscichnus waitemata* (*Pw*) with *M. segregatis* (*Ms*) in the filling, weathered bedding plane; **B –** weathered bedding plane with several specimens of *B. monastiriensis* (*B*) in association with *Palaeophycus* isp. (*Pa*), *Planolites* isp. (*P*), *M. segregatis* (*Ms*), and aggregation of *P. waitemata* (*Pw*); **C –** *Planolites* isp.; **D –** the bulb-like part of *Rosselia socialis* (*Rs*) seen in oblique section, showing light-coloured concentric lamellae oriented obliquely to the foreset plane, present in association with *Bichordites monastiriensis* (*B*), *Macaronichnus segregatis* (*Ms*), and *Ophiomorpha nodosa* (*O*) constituting *Bichordites* ichnofabric II; **E, F –** clusters of *R. socialis* oriented obliquely to vertically to the bedding plane of totally bioturbated calcarenites. Note the erosive truncations of upper part of the specimens; **G –** *Bichordites* ichnofabric II, obliquely oriented *R. socialis* partially within *Piscichnus waitemata* (*Pw*) observed on the weathered surface of foresets in association with *B. monastiriensis* (*B*); **H –** *Bichordites* ichnofabric III, vertically stacked spindles of *R. socialis* in association with ?*O. nodosa* (?*O*) and *M. segregatis* (*Ms*) penetrating a homogenized background

are rarely present (Fig. 7H). In some morphological variants of *R. socialis,* the spindle- or funnel-shaped upper parts are missing. These elongated forms consist of vertically stacked central tubes, which are only slightly swollen in the upper part.

Remarks. – Some of the burrows examined with less robust conical flare of the proximal part resemble *Cylindrichnus concentricus* in partial preservation, having steeply inclined downward-tapering limbs. However, the complete U was not observed.

The spindle-shaped specimens represent the original burrow morphology of *Rosselia socialis*. In contrast, those with an upper part characterized by a funnel shape have possibly been truncated by erosion (e.g., Nara, 1995, 1997, 2002; Frieling, 2007). Specimens with only the shaft preserved likely represent remnants of deeply eroded burrows (e.g., Uchman and Krenmayr, 1995; Schlirf et al., 2002; Frieling; 2007; Netto et al., 2014). Specimens with bulbous parts point to substrate stabilization under low-energy conditions for an extended period, allowing the tracemaker to gradually incorporate considerable amounts of material into the burrow wall, forming concentric laminae composed of finer grains around the shafts. According to Liou et al. (2022), each lamina represents one feeding season of the producer. This implies that the longer the organism occupies the substrate in the same position, the thicker the lining becomes, resulting in a more bulbous termination of the structures. The elongated, vertically stacked *Rosselia* specimens are interpreted to be a result of the tracemaker's upward movement to adjust its life position in response to sedimenta-

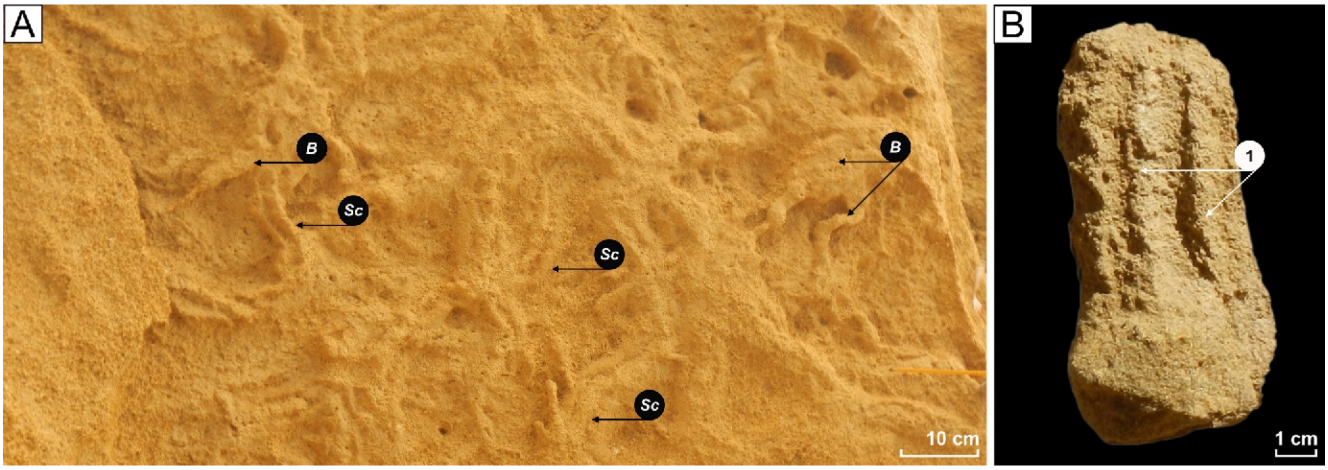

Fig. 8. Echinoid trace fossils from the Pliocene of the Río Alías section, field photographs

A – weathered bedding plane with several specimens of *Scolicia* isp. (*Sc*) and *Bichordites monastiriensis* (*B*); **B –** longitudinal view of the ventral side of *Scolicia* isp. showing a pair of cylindrical strings of sediment (1)

tion, which can be associated with depositional events, often preceded by erosion (e.g., Nara, 1997; Frieling, 2007). Their final morphology is influenced by factors such as changes in sedimentation rate, duration of sedimentation pauses (substrate stabilization), frequency of depositional events, and whether the event deposition was preceded by erosion (e.g., Nara, 1995, 2002; Uchman and Krenmayr, 1995; Frieling, 2007).

Rosselia socialis is interpreted as a feeding and dwelling structure. The probable tracemaker of *Rosselia* is a detritus-feeding terebellid polychaete that inhabits a tube, collects material from the seafloor using tentacles, and after digestion, deposits fecal material around the tube, leading to the formation of the observed concentric lining (see Nara, 1995 and citations therein). Burrows resembling *R. socialis* are also constructed by polychaetes belonging to the families Spionidae and Cyrratulidae (Gingras et al., 1999, 2008; Zorn et al., 2007; Olivero et al., 2012; Duperron and Scasso, 2020). Other inferred producers of *R. socialis* are thalassinidean shrimps (Rindsberg and Gastaldo, 1990), annelids, and sea anemones (Suganuma et al., 1994).

Scolicia isp.
(Fig. 8)

Description. – A long, horizontal, straight to meandering burrow, typically bilobed, with a meniscate backfill (Fig. 8A, B). The structure has an oblong outline and is 52–70 mm (mean = 59 mm) wide, with observed lengths of up to 72.7 cm (mean = 36.9 cm). It is commonly preserved as endichnion, exposed by weathering (false epichnion), whose most notable characteristic feature is a pair of parallel, cylindrical, ridges running along the ventral part of the burrow; the ridges are separated by an almost flat to concave-up surface (Fig. 8B). This trace fossil is randomly distributed, with local high-density patches.

Remarks. – *Scolicia* has been interpreted as a locomotion and feeding trace produced by spatangoids (Bernardi et al., 2010), similar to *Bichordites* but having two ventral ridges. Nara et al. (2020) reported a new ichnospecies, *Scolicia shirahamensis*, which in addition to the two ventral ridges referred to as drainage tubes, also possesses a third central core, potentially of fecal origin. *Moira lachesinella* Mortensen, 1930 (Spatangoida, Schizasteridae) is known to produce traces similar to *S. shirahamensis* (Nara et al., 2020).

Conical structures
(Fig. 5F)

Description. – These are vertically oriented, large, and vary in shape from reverse cone-shaped to sack-shaped with a rounded apical terminus (Fig. 5F). They range in length from 316 mm to 1139 mm (mean = 583 mm) and in width from 113 mm to 785 mm (mean = 422 mm). Typically, the internal fill is structureless, composed predominantly of coarse-grained sediment derived from the overlying stratum. At the bottom of these structures, shell debris, primarily oysters, is commonly found, and in some instances, this is mixed with bioeroded carbonate clasts. Across the burrow margins of some specimens, downward deflections of the surrounding laminae are observed.

Remarks. – The size of the structures partly corresponds to *Scalichnus*, but the internal structure is different (Zonneveld and Gingras, 2013).

ICHNOASSEMBLAGE, THE *BICHORDITES* ICHNOFABRIC ASSOCIATION

Within the deposits studied, 12 ichnotaxa were recorded, with a striking dominance of *Bichordites monastiriensis*. This ichnotaxon co-occurs with *Macaronichnus segregatis* and *Piscichnus waitemata* and less frequently with *Scolicia* isp. and *Cardioichnus* isp. Other accompanying traces are rarer and scattered across the succession. These include: (1) *Ophiomorpha nodosa*, (2) *Rosselia socialis*, (3) *Asterosoma* isp., (4) *Cylindrichnus* isp., (5) *Conichnus* isp., (6) *Planolites* isp., (7) *Palaeophycus* isp., (8) *Patagonichnus* isp., and (9) bivalve burrows and (10) conical structures. *Patagonichnus* isp. and bivalve burrows were recorded only once.

The continuous exposure allowed the evaluation of the vertical and lateral variability in bioturbation intensity, ranging from no perceptible bioturbation (Bioturbation Index, BI = 0) to nearly complete or complete bioturbation (BI = 4–5). Bioturbation in-

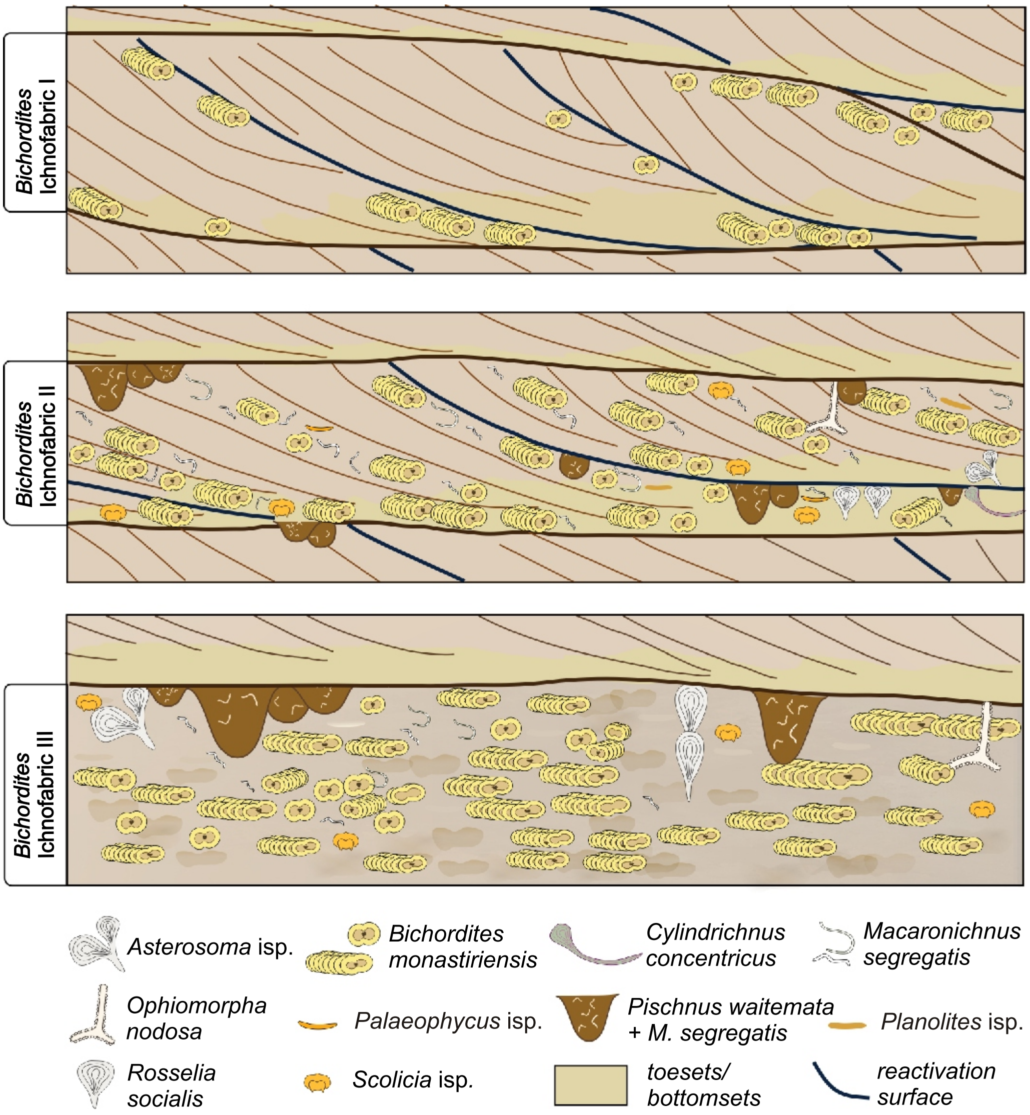

Fig. 9. Schematic illustration of the *Bichordites* ichnofabric I, *Bichordites* ichnofabric II, and *Bichordites* ichnofabric III, showing the distribution of trace fossils in the cross-bedded and massive, fully bioturbated calcarenites of the Cuevas Formation (not to scale)

tensity and the distribution of ichnotaxa vary significantly laterally, on a scale of metres, leading to distinctive patchiness in ichnofabrics (*sensu* McIlroy et al., 2007). Wherever the beds are bioturbated, *Bichordites* is present and mostly volumetrically dominant. By contrast, the distribution of other ichnotaxa is inconsistent, and their relative abundance varies laterally within the same bed.

The distribution and occurrence of less common ichnotaxa, particularly those interpreted as suspension feeders within a community dominated by deposit feeders, may indicate variations in hydrodynamic conditions (McIlroy, 2007). Based on bioturbation intensity, the composition of the trace fossil association, the proportion of other ichnotaxa, tiering, and the spatial relationship of bioturbation structures to primary physical sedimentary structures, three types of *Bichordites* ichnofabrics recurring along the exposure are distinguished (Fig. 9).

Bichordites ichnofabric I
(Figs. 9 and 10)

The ichnofabric is monospecific and formed by unevenly distributed shallow-tier *Bichordites monastiriensis*; this is expressed in the variable bioturbation intensity ranging from BI = 0 to BI = 1. Primary sedimentary structures are very well preserved and comprise medium- and large-scale trough- and planar cross-bedding, up to 4 m thick. Rare, bioturbated intervals with *Bichordites* occur irregularly along the base of the cross-bedded sets, in the toeset/bottomset regions. Foresets are rarely bioturbated with *Bichordites*; however, when bioturbation structures do occur, they are generally found in foresets that have been truncated by reactivation surfaces.

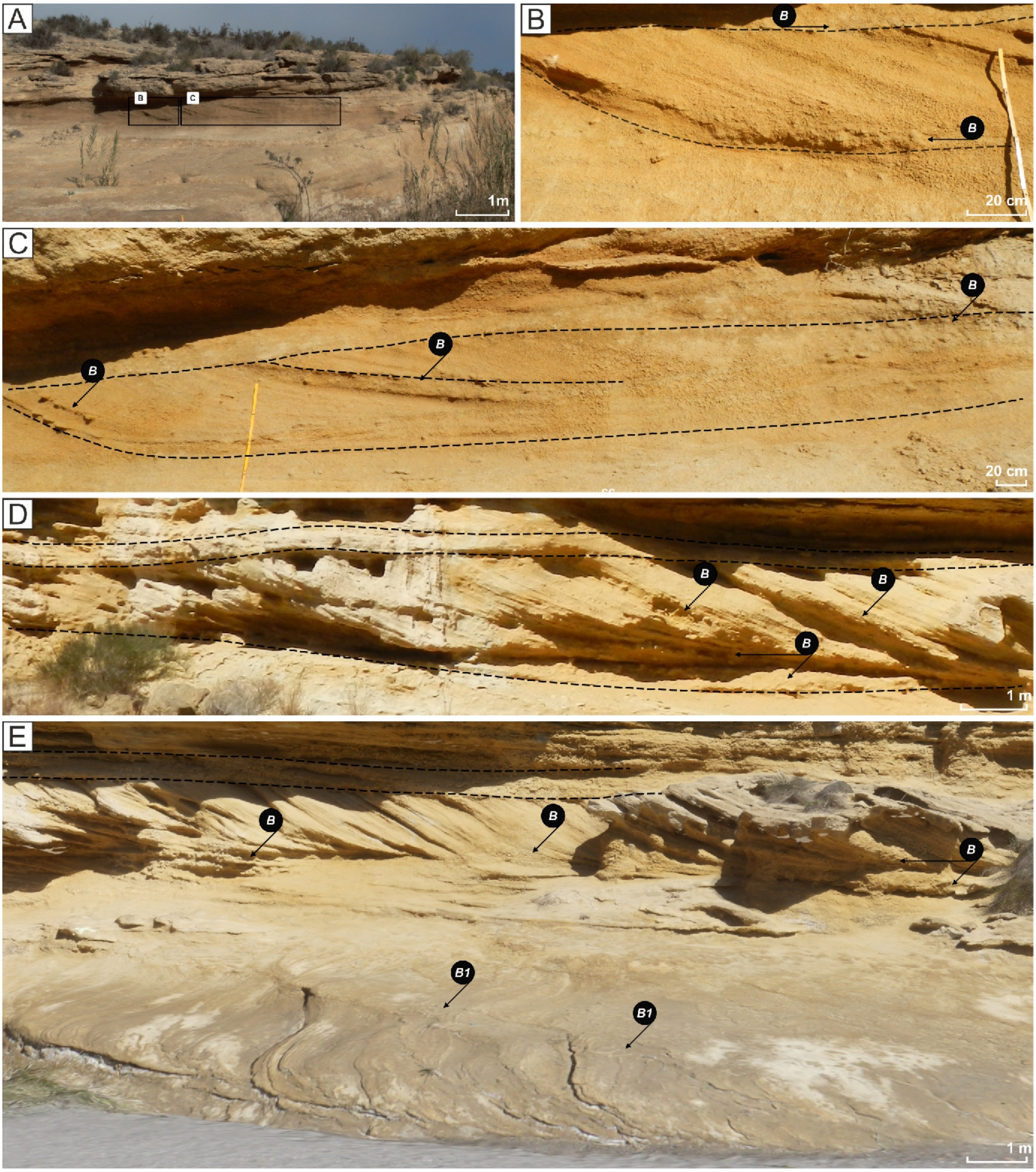

Fig. 10. ***Bichordites*** **ichnofabric I viewed in vertical cross-section**

A–E – cross-bedding showing unidirectional foresets with tangential contacts and sporadic distribution of patches of indistinct *Bichordites monastiriensis* (*B*). Arrows show zones of its presence along toesets/bottomsets, along foresets and along the bedding surfaces. Note that a large portion of cross-stratification is preserved. Black rectangles in A indicate the locations shown in more detail in B and C. In E note the patches consisting of *Bichordites monastiriensis* (*B1*) neighbouring areas devoid of burrows seen on weathered bedding plane

Bichordites ichnofabric II
(Figs. 4E, F, 5B–F, 7D, G, 9, 11A–C, F and 12)

This is the prevalent ichnofabric, occurring in both tabular- and trough-cross-stratified calcarenites, each ranging in thickness from 10 to 100 cm. *Bichordites monastiriensis* dominates but bioturbation intensity is characteristically higher than *Bichordites* ichnofabric I. The vertical and lateral distribution of trace fossils and their relation to the primary sedimentary structures are still visible. A notable feature is the considerable lateral heterogeneity of bioturbation intensity and spatial zonation of co-occurring ichnotaxa, with distinct associations for foresets, toesets/bottomsets, and bounding surfaces.

In the cross-sets, intervals of moderately to intensely bioturbated (BI = 3–6) and weakly to non-bioturbated (BI = 0–1) foresets irregularly alternate. Burrows are distinctly crowded in foresets below the reactivation surfaces. In bioturbated foresets, *Bichordites* dominates. These abundant sinusoidal traces align sub-parallel to foreset planes, forming a 'bedding-parallel' fabric. Commonly *Macaronichnus segregatis* and rarely *Piscichnus waitemata*, *Conichnus,* and escape structures contribute to this dense association in foresets. *M. segregatis* appears as fine, pale strings, variably oriented, mostly subparallel but also oblique to vertical to bedding. *P. waitemata* is typically found as single burrows or aggregated in clusters of 3 to 5 individuals, often nested. Within the filling of *P. waitemata*, *M. segregatis* is common. Within the foreset, burrows are randomly distributed, as is particularly evident on weathered foreset planes where bioturbated patches neighbour areas devoid of burrows. Distinct bioturbated horizons occur in the toesets, often transitioning tangentially into thin bottomsets. These toesets/bottomsets are moderately to highly burrowed (BI = 3–4) and contain abundant *B. monastiriensis*, common to uncommon *Macaronichnus segregatis*, rare *Planolites*, *Palaeophycus*, *Scolicia* isp., *Rosselia socialis*, *Cylindrichnus concentricus,* and *Asterosoma* isp. Vertically oriented, deeper-tier *Rosselia socialis*, and *Asterosoma* isp., if present, occur as individuals or in clusters of up to three, locally cross-cutting *B. monastiriensis*.

On the upper bounding surface, trace fossils are patchily distributed. *P. waitemata* is common, and *Ophiomorpha nodosa*, *R. socialis*, *Asterosoma* isp., and *C. concentricus* are rare. These trace fossils extend down vertically, cross-cutting the foreset from the top. They are commonly truncated by the erosive bases of successive cosets.

Bichordites ichnofabric III
(Figs. 4E, 7H, 9, 11D–F and 12)

The ichnofabric is rare and often intercalated with the *Bichordites* ichnofabric II. It occurs in small to medium-scale beds of calcarenites, mostly of lenticular geometry with limited lateral continuity of up to 15 m. A high degree of bioturbation (BI = 4–6) is characteristic of the ichnofabric, and primary sedimentary structures are rare to absent. In domains not entirely obliterated by bioturbation, slight appearances of parallel lamination and/or cross-bedding can be observed. Ichnodiversity is low to moderate, ranging from two to five ichnotaxa. *Bichordites monastiriensis* is abundant and accompanied commonly and uncommonly by *Macaronichnus segregatis* and *Piscichnus waitemata*, with rare *Scolicia* isp., *Rosselia socialis, Cylindrichnus concentricus*, *Asterosoma* isp., and *Ophiomorpha nodosa*. The rare ichnotaxa are mostly present as isolated individuals, rarely occurring in groups of two or three. There are intervals where the fabric is constituted by poorly to well-preserved, superimposed (vertically stacked), and moderately to densely packed, horizontal, parallel running traces of *B. monastiriensis*, along which rare white spots of *M. segregatis* occur. More frequently, the ichnofabric displays complex overprinting: stacked shallow traces of *B. monastiriensis* and *M. segregatis* or homogenized fabric with randomly distributed light mottles resembling outlines of spatangoid burrows are crosscut by distinct, well-preserved traces, commonly *P. waitemata* and rarely by deep-tier, lined *Asterosoma* isp., *C. concentricus, O. nodosa,* or *R. socialis* (including vertically stacked forms). These traces extend vertically to obliquely downwards from the upper bounding surface. *P. waitemata* occurs as individuals or in clusters, similarly as in *Bichordites* ichnofabric II.

DISCUSSION

VARIABILITY IN DEGREE OF BIOTURBATION BETWEEN THE BEDS

The development of ichnofabrics is governed by a complex interplay of physico-chemical and biological factors such as ethology (behaviour) and community structure, grain size, sedimentation rate, oxygenation, salinity, and organic matter content (Ekdale, 1985; Droser and Bottjer, 1993; Gibert and Ekdale, 2002; Taylor et al., 2003). The succession housing the three types of *Bichordites* ichnofabrics was interpreted as deposits of migrating subaqueous dunes within an ancient marine strait (Dabrio, 1986–1987; Sola et al., 2024). The major factors potentially affecting bioturbation in such dunes are considered below.

At the study site, salinity and oxygen levels were likely not limiting factors for the benthic fauna. The presence of *Bichordites monastiriensis*, a trace fossil produced by stenohaline echinoids such as *Echinocardium cordatum* suggests fully marine conditions (e.g., Bromley and Asgaard, 1975). Furthermore, spatangoid echinoids are a reliable indicator of aerobic conditions on the sea floor (Ekdale, 1988; Bromley et al., 1995), excluding oxygen deficiency as a limiting factor.

Sediment movement in migrating bedforms follows a cyclic process of transport and sediment stabilization, known as 'periodic' sediment shift. The duration of each phase in this cycle varies based on bedform size and the prevailing hydrodynamic conditions (Zlatanović et al., 2017). Burrowing organisms likely face challenges inhabiting unstable substrates during transport phases, with colonization windows – defined as periods available for benthic colonization (Pollard et al., 1993) – limited to brief intervals of stability in between them.

Sedimentary structures at the study site indicate high, fluctuating hydrodynamic energy, impacting sediment mobility, that likely served as the most significant environmental stressor. In straits with strong, variable currents, rapid deposition and erosion shape the timing and extent of benthic colonization. The vertical and lateral variability in the scale and type of cross-stratification suggests deposition occurred under conditions of frequent changes in current speed, with intermittent periods of stability providing limited opportunities for colonization, as mirrored in the ichnofabrics.

Bichordites ichnofabric I likely formed in an environment characterized by short-lived colonization windows (e.g., Pemberton et al., 1992; Hofmann et al., 2012), with long intervals between them. This is suggested by the monospecific occur-

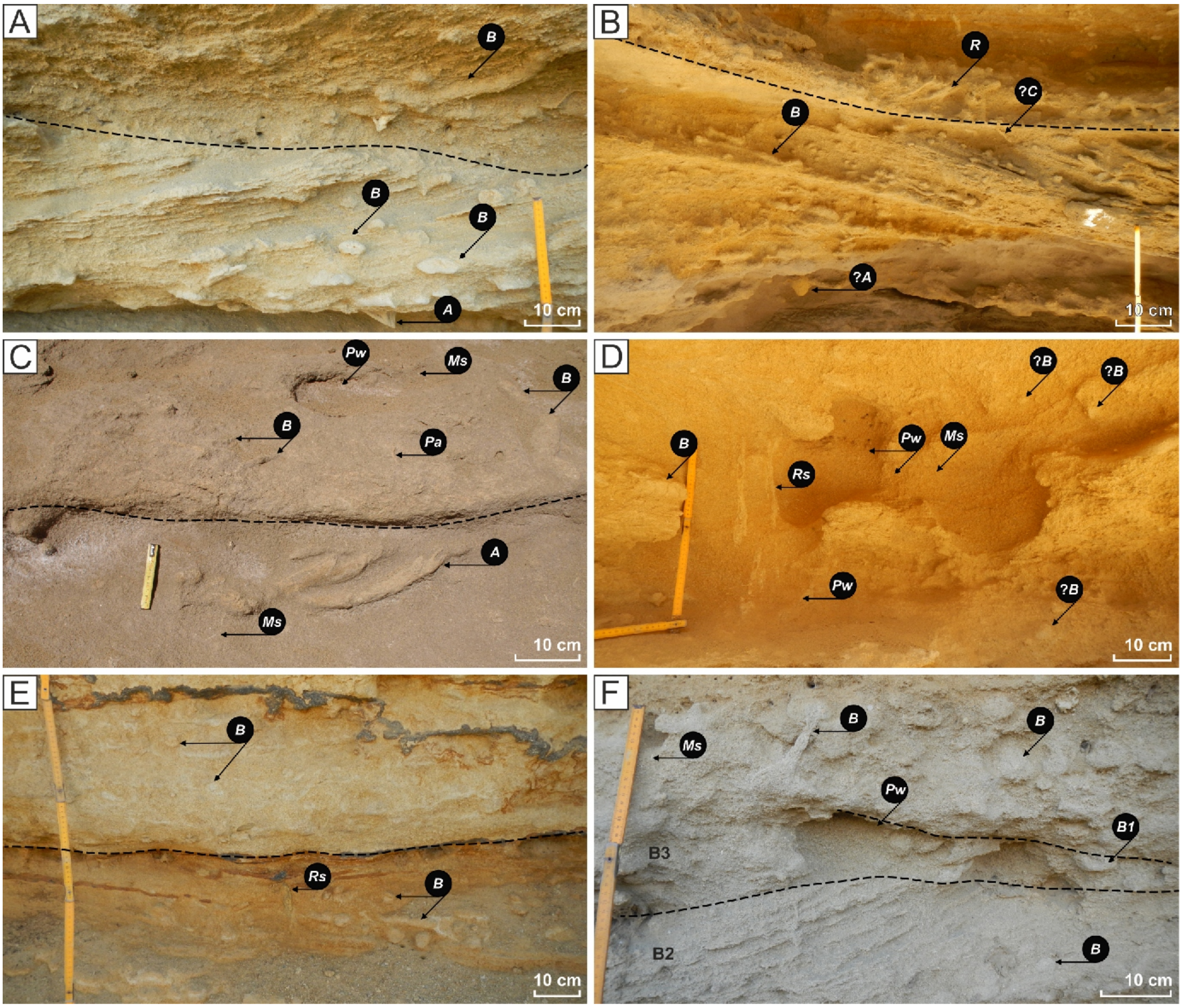

Fig. 11. *Bichordites* ichnofabric II (A–C, F) and *Bichordites* ichnofabric III (D–F) viewed in vertical cross section

A, B – cross-bedded calcarenites showing lateral heterogeneity in bioturbation, where bioturbated foresets show a dominance of *Bichordites monastiriensis* (*B*) aligned sub-parallely to foreset planes accompanied by *Macaronichnus segregatis* (*Ms*). Note presence of vertical and subvertical ?*Cylindrichnus* (?*C*), *Asterosoma* isp. (?*A*) and *Rosselia* isp. (*R*) in the toeset and bottomset; **C –** weathered bedding plane view with *B. monastiriensis* (*B*), *M. segregatis* (*Ms), Rosselia socialis* (Rs), *Piscichnus waitemata* (*Pw*), *Palaeophycus* (*Pa*) and *Asterosoma* isp. (A); **D, E –** multi-tiered composite *Bichordites* ichnofabric III constituted by poorly preserved *B. monastiriensis* (*B*), *M. segregatis* (*Ms*), *Rosselia socialis* (*Rs*) seen on an almost completely homogenized background with randomly distributed light mottles resembling outlines of spatangoid burrows (?*B*) cross-cut by *P. waitemata* (*Pw*), *R. socialis* (*Rs*). In D note vertically stacked *M. segregatis* and *R. socialis* within the *P. waitemata*.; **F –** Contact between *Bichordites* ichnofabric II (BII) and *Bichordites* ichnofabric III (BIII). Note vertical stacking of shallow traces of *B. monastiriensis* (*B*) with subordinate *M. segregatis* (*Ms*), *P. waitemata* (*Pw*) constituting *Bichordites* ichnofabric III. Dashed lines delinate erosional surface separating two beds

rence of spatangoid burrows and their scattered distribution in small, isolated domains along well-preserved foresets and toesets/bottomsets in large-scale trough cross-bedded calcarenites (Gibert and Goldring, 2008; Hofmann et al., 2012). The prolonged periods of elevated sedimentation, likely driven by continuous 2D- and 3D-dune migration, created highly stressed environments, as suggested by the low ichnodiversity and low levels of bioturbation (Ekdale, 1985; Gingras et al., 2011). Under such conditions, only organisms with specialized behaviours, such as rapid burrowers, could successfully colonize (Baucon et al., 2020). The brief colonization windows prevented the development of a stable, complex benthic community, instead favouring opportunistic spatangoid echinoids capable of quickly burrowing during short-lived stable conditions between depositional events. Overall, the low bioturbation intensity reflects these harsh environmental conditions and limited macrobenthic activity.

Compared to *Bichordites* ichnofabric I, the notably higher bioturbation intensity of *Bichordites* ichnofabric II reflects longer periods of colonization and bioturbation. Despite a high degree of bioturbation, the primary sedimentary fabric is preserved due to the bedding-parallel distribution of *B. monastiriensis*. The small to medium-scale 2D tabular cross-stratified and 3D trough cross-stratified calcarenites that house *Bichordites*

Fig. 12. *Bichordites* ichnofabrics II (B2) and III (B3) viewed in vertical cross-section and their spatial relation

Sand-dune related stacked 2D and 3D cross-beds of different scale. Note large scale cross-bedding sitting on the trough erosional surface scoured in pre-existing sets of 2D and 3D calcarenites. *P. waitemata* (outlined with white lines) that is typically found as single burrows or in clusters distributed along boundary surfaces and reactivation surfaces (black lines)

ichnofabric II point to intermediate energy conditions (e.g., Allen, 1980), implying lower net sedimentation rates. The lateral heterogeneity in bioturbation structures reflects fluctuations in local environmental conditions. The irregularly alternating bioturbated and non-bioturbated foresets reflect the episodic nature of sedimentary processes driven by the periodic migration of small and medium 2D and 3D dunes. Periods of reduced energy led to relative sediment stability, enabling bioturbation mainly in foresets and bottomsets. These colonization events were repeatedly interrupted by increases in energy and sedimentation, which destabilized the environment, resulting in less bioturbated or non-bioturbated foresets. The balance between sediment deposition and periods of stability allowed for the development of a more complex bioturbating community in various parts of the dune structures, recorded by a diversity of traces. *Rosselia* and other trace fossils possessing a thick lining are interpreted to point to relatively long-term occupation when compared to incidental traces of deposit feeders such as *Bichordites* and *Macaronichnus* (cf. Taylor et al., 2003). Their presence in toeset/bottomset zones and rarely on the upper bounding surface indicates the presence of suspension feeders in a community dominated by deposit feeders, pointing to more stable conditions in at least some parts of the dune fields, foremost troughs. Gingras et al. (2008) showed that suspension-feeding animals burrow into the sediment at a slower rate compared to deposit feeders, with volumetric burrowing rates ranging from 0.01 and 0.15 cm per hour, whereas deposit-feeding animals displace 10 to 100 times more sediment than suspension feeders. The spatial separation between the trace fossils could be related to some tracemakers' preference for specific sediment characteristics (Goldring et al., 2007). Due to the availability of organic material and the stability of sediments when compared to the stoss slopes in present-day dunes, steep lee slopes (foresets) of dunes tend to be biodiversity hotspots, providing habitat for a variety of species (Cheng et al., 2021). The quickly colonizing deposit feeders, including *Bichordites* and *Macaronichnus* producers, probably benefited from the organic-rich sediments (Miguez-Salas et al., 2021). Organisms producing lined traces, such as *Rosselia socialis*, *Cylindrichnus concentricus*, and *Asterosoma*, likely inhabited troughs where they utilized finer sediments and organic matter (that accumulate in high quantity due to reduced current speeds) to construct burrow linings that provided burrow stability in the otherwise unstable substrate (Goldring et al., 2007). The truncation of the upper parts of these traces suggests that colonization was followed by erosion before their burial by the migrating dunes.

Bichordites ichnofabric III records the longest colonization window among the three ichnofabrics. This is suggested by the presence of vertical traces such as *Piscichnus waitemata* and deeper-tier burrows such as *Rosselia socialis*, *Cylindrichnus concentricus*, *Asterosoma* isp., or *Ophiomorpha nodosa*. The latter traces cross-cut the mottled background with differently preserved shallow-tier *B. monastiriensis* and *Macaronichnus segregatis*, and indicate multiple (at least two) colonization events. The shallow-tier traces of *B. monastiriensis* and *M. segregatis*, and other bioturbation structures preserved as mottling, were possibly emplaced just after deposition, with the cross-cutting ones emplaced later. Such a composite ichnofabric with overprinting points to a stable environment with extended periods of low-energy conditions, decreased sedimentation rates, and bedform movement fostering longer colonization windows and more intense and deeper bioturbation. This pattern is consistent with findings by Gingras et al. (2011), who noted that high bioturbation intensities are difficult to achieve unless sedimentation rates are at least sporadically low. Also, equilibrium forms of *R. socialis* indicate long periods of occupation and persistent usage of the structure during animal growth and sediment accumulation on the surface.

Previous work by Nara (2014), Colella and D'Alessandro (1988), D'Alessandro and Massari (1997), D'Alessandro et al. (2004), Gibert and Goldring (2007, 2008), and Aguirre et al.

(2010), among others, documented similar ichnofabrics and ichnofabric associations from Neogene and Quaternary sand waves, particularly those dominated by *Bichordites* or *Scolicia*. These studies underlined the impact of fluctuating hydrodynamic energy on bioturbation patterns, suggesting spatangoid echinoid traces as indicators of shifting substrates. Like the study site, some of these previous studies addressed seaways or straits. Miguez-Salas et al. (2021) described an ichnoassemblage with predominant *Macaronichnus* and *Scolicia* resembling a proximal expression of the *Cruziana* ichnofacies; they discussed how the energetic conditions in the deeper-water late Miocene Rifian Corridor, as a gateway, could have caused lowered ichnodiversity. Nara (2014) described the *Bichordites* ichnofabric as occurring primarily in the foresets of sand waves, as in the section studied. His study highlights how varying current strengths influenced the distribution of burrows and intensity of bioturbation, supporting the idea that alternating periods and different areas of high and low energy could foster the development of distinct ichnofabrics similar to those observed in the Río Alías strait.

STRESS ADAPTATION STRATEGIES AND TOLERANCE OF SHIFTING SUBSTRATES INFERRED FROM OBSERVED TRACE FOSSILS

The dominant *Bichordites monastiriensis* and subordinate *Scolicia* components of the ichnoassemblage were likely produced by spatangoid sea urchins, rapid bioturbators that move around horizontally and vertically on and in seafloor sediments. *Bichordites* dominates in the foresets. Its tracemakers were able to keep pace with rapid sedimentation. Saitoh and Kanazawa (2012) studied the morphological and behavioural adaptations to shallow-water environments of six spatangoid species in a protected bay that is usually calm except for storms. There, ripple marks around 5 cm high with 20–30 cm wavelength were seen on the seafloors shallower than 10 m and, in places, at 10–18 m depths during winter and early spring. They described some spatangoids as being able to burrow deeply in fine- or coarse-grained sand to survive storms, whereas the specialized spatangoid species *Lovenia elongata* could quickly reposition itself after disturbance despite burrowing shallowly in the sediment. Buchanan (1966) found that littoral populations of *Echinocardium cordatum* burrowed to depths of 15 cm and could move through the sand at a speed of 6–8 cm/h, whereas offshore populations burrowed more shallowly and moved more slowly through the sediment. Gibert and Goldring (2008: table 1) summarized data on the burrowing speeds of various modern spatangoids belonging to different families; many spatangoids can burrow at least a few centimetres per hour or day, while burrowing depth ranges from being only partly buried to 10–30 cm. Lohrer et al. (2005: fig. 5) found that *Echinocardium* populations likely reworked the upper sediment column once every 3–5 days, which exceeded the frequency of mixing by physical processes like storms capable of stirring the upper 5 cm of sediment.

Other trace fossils represent more sedentary animals that remain in one place and adjust their position vertically in response to sedimentation, for instance *Conichnus* and *Rosselia*. For example, Savrda (2002) and Abad et al. (2006) described specimens of *Conichnus* exhibiting marginal and internal fabrics linked to initial penetration of substrate, retrusive movement, escape behaviour, burrow abandonment, and protrusive equilibrium movement. Savrda (2002), using apparent neap-spring tidal cyclicity expressed in lithofacies to interpret sedimentation rates, estimated that aggradation of around 1 cm/day or less led to retrusive migration but rapid foreset deposition of >5 cm/day led to tracemaker escape.

In the study section, *Rosselia socialis* also shows equilibrium-related features. Across the Phanerozoic, *Rosselia* has been found in shallow-marine habitats such as deltaic or storm-influenced shoreface settings (Nara, 2002; Nara and Haga, 2007; Baniak et al., 2014; Netto et al., 2014; MacEachern and Bann, 2020; Bayet-Goll et al., 2021, 2022; Liou et al., 2022). Buatois et al. (2016) considered *Rosselia* ichnofabrics from the Ordovician to reflect infaunal polychaete communities capable of synchronous equilibrium behaviour, occupying sandy, high-energy places.

Besides *Rosselia socialis*, most of the other trace fossils of El Argamasón have a lining, like *Ophiomorpha nodosa, Cylindrichnus concentricus, Palaeophycus,* and *Asterosoma*. They may also relate to burrow strengthening or stability under shifting substrate conditions, as discussed in detail by Zorn et al. (2010) and Gingras et al. (2011), though the authors also mention that lining production can have other reasons.

Planolites is a common, simple, unlined, horizontal trace found in various settings, making it challenging to infer specific adaptations of the tracemaker. However, some *Planolites* have been described as pioneer traces, for example, in deltaic deposits (Goldring, 1995).

ECOSYSTEM ENGINEERING AND BIOTIC INTERACTIONS INFERRED IN THE SHIFTING, SANDY HABITATS

Once sand-dwelling organisms colonize the substrate, biological interactions, in addition to physical constraints or factors, also play a crucial role in shaping the community by either facilitating or inhibiting the ways of life of other organisms. Particularly prominent is the bulldozing behaviour of sea urchins that can disturb or foster other marine life. Bulldozing effects prevent colonization of other, less mobile organisms and destroy their traces (e.g., Thayer, 1979; Wetzel, 1981; D'Alessandro and Uchman, 2007). The lining of *Rosselia socialis* found in association with *Bichordites* was considered to be potential protection against such kinds of disturbance (D'Alessandro and Uchman, 2007).

Another example of ecosystem engineering would come from the rays and other fish producing *Piscichnus*; these animals are involved in major biogeomorphological interactions with sea-bottom habitats, influencing both the physical substrate and the macrobenthos as they feed and rest (O'Shea et al., 2011; Flowers et al., 2021; Nauta et al., 2024). *Piscichnus* has previously been found associated with similar types of ichnofossils seen at the study site (Nara, 2014; Dominici et al., 2017; Uchman et al., 2018). Many species of ray live on sandy seafloors and feed on epi- and endo- benthic animals such as crustaceans, polychaetes, molluscs, echinoderms, and fish (Michael, 1993; Ellis et al., 1996; Collins et al., 2007; Sommerville et al., 2011; Last et al., 2016; Rastgoo et al., 2018). At the study site, *Piscichnus* tracemakers very likely did the same. Löwemark (2015) and Uchman et al. (2018) mentioned how spatial and cross-cutting relationships between *Piscichnus* and crustacean burrows like *Ophiomorpha* suggest targeted hunting by rays. Also at the study site, such interactions are recorded as *Piscichnus* cross-cuts both *Rosselia* and *Ophiomorpha*. Although Löwemark (2015) study suggested that rays favoured thalassinoid crustaceans and worms while echinoid body fossils were found intact with no visible signs of predation, rays can sometimes feed on sea urchins; Uchman et al. (2018) noted cross-cutting of *Bichordites* by *Piscichnus*. Although we did not observe any *Piscichnus* cross-cutting the ends of *Bichordites*, the crowding of *Bichordites* in the sections studied may have obscured such interactions. Grun (2016) described a predatory attack on the spatangoid *Meoma ventricosa* by a stingray, which made several stops on a sand flat, producing 'ray holes' in the sediment to uncover prey, and documented the crushed remains of the sea urchin's test left behind at the feeding site.

In the section studied, *Macaronichnus segregatis* occurs in the foresets with *Bichordites monastriensis.* Olivero and López Cabrera (2020) described a dense association of *Macaronichnus* occurring with *Bichordites* at the base of a compound Miocene tidal bar in Tierra del Fuego. These authors, as well as Kotake (2007), Seike et al. (2011), and Nara and Seike (2019), described how the presence and density of *Macaronichnus* are limited by the degree of substrate compaction, reasoning that the travisiid polychaetes, inferred to have made *M. s. degiberti*, struggled to burrow in firmer substrates. Therefore, both observations at the study site and the previous studies suggest that bulldozing by sea urchins like *Echinocardium* might facilitate colonization of the *Macaronichnus* tracemaker. Production of pits by rays, wherein loose material accumulates, could have a similar effect. Previously, Kotake (2007) reported small, densely packed *Macaronichnus* inside the fill of *Piscichnus*, considering that the *Macaronichnus* producer used it as a new, temporary habitat, which also enhanced preservation of the trace. In modern settings, studies have examined the impact of ray feeding pits on benthic communities, which may include negative effects on some taxa that are eaten or disturbed but positive ones on others through habitat restructuring and material accumulating in pits (Thrush et al., 1991; Cross and Curran, 2004; Heithaus et al., 2010; Flowers et al., 2021; Barnes and Cottrell, 2024; Nauta et al., 2024). For instance, early-colonizing species such as small amphipods can utilize the organic matter inside pits (VanBlaricom, 1982; Heithaus et al., 2010). Thrush et al. (1991) found rapid colonization in bivalve and polychaete-dominated communities after feeding distubances by rays, noting that ray pits quickly filled with sediment similar to that of the surrounding sandflat. These authors suggested that the ability of community residents to actively move or tolerate passive transport into nearby disturbed areas sustains the population density and structure in those communities.

In the ichnofossil record, both the *Bichordites-Macaronichnus* and *Piscichnus-Macaronichnus* associations may reflect strong, actively moving bioturbators whose actions helped other sand-dwelling animals to settle in, dig new burrows, and feed more easily, even if they initially caused disturbance (or predation) within the community.

VARIABILITY IN BIOTURBATION WITHIN THE FOSSIL DUNES; COMPARISON TO MODERN ANALOGUES

In the foresets studied, the tops of *Bichordites* as well as *Macaronichnus* and rarely *Piscichnus* are cut by erosion that is also recorded by the erosional surface dividing the sets of lamination. However, the top bounding surfaces mark the presence of *Piscichnus*, *Ophiomorpha*, *Rosselia,* and other traces also occur in bottomsets/toesets. The non-uniform, patchy distribution of trace fossils observed in the ichnofabric studied matches observations of modern organisms producing similar burrows in present-day sand waves. The data from the study site and modern analogues suggest lateral and vertical zonation of habitats occupied by infauna with different feeding modes limited by physical conditions as well as disturbance by other organisms.

Differences in bioturbation have been found to be linked to physical habitats within sand waves driving seascape community structure in modern settings (Damveld et al., 2018; Cheng et al., 2021). These can be compared to examples from the geological past like the section studied and others (Colella and D'Alessandro, 1988; D'Alessandro and Massari, 1997; D'Alessandro et al., 2004; Gibert and Goldring, 2007, 2008; Aguirre et al., 2010; Nara, 2014). Damveld et al. (2018) used video transects to reveal a greater abundance of epibenthos and endobenthos in sand wave troughs, where there are less abundant and more irregularly shaped ripples; they consider the sheltered nature of the troughs and the deposition of organic matter to be favourable to the benthos. Cheng et al. (2021) collected box cores within a transect line in the North Sea and similarly found strong heterogeneity within the habitats, with greater individual, biomass, and taxon densities on the steeper slopes of sand waves. The steep slope hosted 53 taxa and most of the communities of the gentle slope, crest, and troughs were subsets of the steep slope community. Although the communities along a sandwave were diverse, over 90% of total biomass came from echinoids (mainly *Echinocardium cordatum*), of which 80% was concentrated on the steep slope. The steeper slopes containing more crawlers and surficial modifiers matches observations at the study sites that *Bichordites* dominates the ichnoassemblage, particularly in the foresets. Cheng et al. (2021) considered the steep slopes to be more destabilized by motile bioturbators, and thus, to be more under biotic control than the gentle slopes, which were controlled mainly by physical forces. Strong bioturbators such as echinoids may exclude other taxa, such as tube-dwelling worms, by mixing sediments. However, as ecosystem engineers, they also have complex effects on biogeochemistry and physical habitats (Lohrer et al., 2004, 2005), potentially boosting biodiversity by benefiting other organisms. In the case studied, this is reflected in the ichnofossil record, where the *Macaronichnus* tracemaker appears to favour sediments loosened by the *Bichordites* tracemaker.

In contrast to the bulldozing by echinoids inferred in the *Bichordites*-dominated foresets of the study site, there may have been habitat partitioning so that areas that were previously quieter troughs could be dominated by animals that pick up food that accumulates there. Among such animals were the producers of *Rosselia* and others, which were inferred to have lined burrows that could also be physically stabilized against disturbance. Overall, these comparisons suggest that ecosystems in dynamic sandy seabeds similar to those in the present day would have existed by the Pliocene, if not earlier in the Neogene.

HETEROGENEITY IN ICHNOASSEMBLAGES

A major finding of this study is the notable variation in ichnofossil diversity and abundance over just a few metres as well as across entire dune complexes, spanning tens to hundreds of metres. In fact, ichnoassemblages can vary significantly depending on the scale of observation. Most studies, due to practical limitations, focus on smaller, accessible areas, which may not fully represent larger surfaces or outcrops (Marenco and Hagadorn, 2019; Shillito and Gougeon, 2023). While spatial heterogeneity has long been recognized in modern landscape ecology, its role in ichnology has only recently gained attention by attributing it to a combination of biotic and physical processes, such as ecosystem engineering (Buatois and Mángano, 2011) and habitat partitioning, including microhabitat use. For example, Dashtgard (2011) conducted a neoichnological study on invertebrate burrows in the tidal flats of Boundary Bay, British Columbia, and found considerable variation in trace diversity and burrow density across the area. Some of this variation was linked to physicochemical factors, whereas other patterns arose from bed-scale tiering related to the inherent heterogeneity of infaunal communities rather than to changes in environmental conditions. Modern studies of benthic communities, such as those by Dashtgard (2011), Damveld et al. (2018), and Cheng et al. (2021), along with this study's findings in Pliocene dunes, suggest that future research exploring ichnoassemblage variation across multiple spatial scales could help differentiate microhabitat-driven bioturbation patterns from broader environmental controls in depositional settings such as seaways, straits, and tidal flats.

CONCLUSIONS

The Pliocene section studied in the Almería-Níjar Basin, southern Spain, offers a rare opportunity to study large-scale subaqueous dune deposits and their ichnoassemblages. Three distinct types of *Bichordites*-dominated ichnofabrics were distinguished, each varying in bioturbation intensity and ichnodiversity. These variations are inferred to reflect differences in hydraulic energy levels and the duration of colonization windows. *Bichordites* ichnofabric I is characterized by low bioturbation intensity and is almost exclusively dominated by *Bichordites*, suggesting a high-energy environment with a limited colonization window. *Bichordites* ichnofabric II is similarly dominated by *Bichordites*, but exhibits greater bioturbation intensity and a slight increase in ichnodiversity, indicating a longer colonization window and less extreme hydraulic conditions. *Bichordites* ichnofabric III is distinguished by ubiquitous bioturbation structures and low to moderate ichnodiversity, with *Bichordites* accompanied by other trace fossils, suggesting the longest colonization window. These ichnofabrics provide new insights into how benthic organisms interacted with dynamic, migrating sand waves and the environmental factors that influenced bioturbation intensity and ichnodiversity.

Evidently, laterally continuous exposures are essential for understanding spatial heterogeneity in ichnofossil distributions, as smaller-scale observations may overlook significant variations. The use of drones for mapping extensive exposures also proved to be valuable for accessing and analyzing complex sedimentary structures, suggesting future research can benefit from such technologies.

Comparisons between these Pliocene *Bichordites*-dominated ichnoassemblages and modern sand-wave settings highlight similarities in local habitat partitioning across crests, slopes, and troughs, which are dominated by bulldozing sea urchins acting as ecosystem engineers. This type of microhabitat partitioning, influenced by both physical variation and interactions between organisms (e.g., disturbance or facilitation), may often be overlooked when focusing solely on broader-scale physical environmental controls on variation in ichnoassemblages. Also, the dominance of bioturbators, such as sea urchins, in both settings emphasizes the role of physical and biological processes in shaping benthic communities, past and present. Furthermore, integration of both microhabitat and large-scale environmental perspectives is needed for analysing ichnoassemblage variation.

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REFERENCES

Abad, M., Ruiz, F., Pendón, J.G., Tosquella, J., González-Regalado, M.L., 2006. Estructuras de escape y equilibrio asociadas a *Conichnus conicus* como indicadores de tasas de sedimentación variables en medios litorales tortonienses del SO de España. Geobios, **39**: 1–11; https://doi.org/10.1016/j.geobios.2004.07.001

Aguirre, J., 1998. El Plioceno del SE de la Península Ibérica (provincia de Almería). Síntesis estratigráfica, sedimentaria, bioestratigráfica y paleogeográfica. Revista de la Sociedad Geológica de España, **11**: 297–315.

Aguirre, J., 2017. *Amusium cristatum* shell beds in the lower Pliocene deposits of Almería-Níjar Basin (SE Spain). Spanish Journal of Palaeontology, **32**: 3–16; https://doi.org/10.7203/sjp.32.1.16985

Aguirre, J., Sánchez-Almazo, I.M., 2004. The Messinian post-evaporitic deposits of the Gafares area (Almerýěa-Nýějar basin, SE Spain). A new view of the "Lago-Mare" facies. Sedimentary Geology, **168**: 71–95; https://doi.org/10.1016/j.sedgeo.2004.03.004

Aguirre, J., Martín, J.M., Braga, J.C., Betzler, C., Berning, B.B., Buckeridge, J.S., 2008. Densely-packed concentrations of sessile barnacles (Cirripedia: Sessilia) from the early Pliocene of SE Spain. Facies, **54**: 193–206; https://doi.org/10.1007/s10347-007-0132-2

Aguirre, J., Gibert, J.M.de, Puga-Bernabéu, A., 2010. Proximal–distal ichnofabric changes in a siliciclastic shelf, Early Pliocene, Guadalquivir Basin, southwest Spain. Palaeogeography, Palaeoclimatology, Palaeoecology, **291**: 328–337; https://doi.org/10.1016/j.palaeo.2010.03.004

Aguirre, J., Braga, J.C., Martín, J.M., Betzler, C., 2012. Palaeoenvironmental and stratigraphic significance of Pliocene rhodolith beds and coralline algal bioconstructions from the Carboneras Basin (SE Spain). Geodiversitas, **34**: 115–136; https://doi.org/10.5252/g2012n1a7

Allen, J.R.L., 1980. Sand waves: a model of origin and internal structure. Sedimentary Geology, **26**: 281–328; https://doi.org/10.1016/0037-0738(80)90022-6

Aller, R.C., Yingst, J.Y., 1978. Biogeochemistry of tube-dwellings: a study of the sedentary polychaete *Amphitrite ornata* (Leidy). Journal of Marine Research, **36**: 201–254; https://elischolar.library.yale.edu/journal_of_marine_research/1429

Ashley, G.M., 1990. Classification of large-scale subaqueous bedforms; a new look at an old problem. Journal of Sedimentary Research, **60**: 160–172; https://doi.org/10.2110/jsr.60.160

Baniak, G.M., Gingras, M.K., Burns, B.A., Pemberton, G.S., 2014. An example of a highly bioturbated, storm-influenced shoreface deposit: Upper Jurassic Ula Formation, Norwegian North Sea. Sedimentology, **61**: 1261–1285; https://doi.org/10.1111/sed.12100

Barnes, R.S., Cottrell, L.G., 2024. Do stingray feeding pits enhance intertidal macrobenthic biodiversity? Hydrobiologia, **851**: 3403–3412; https://doi.org/10.1007/s10750-024-05504-7

Baucon, A., Piazza, M., Cabella, R., Bonci, M.C., Capponi, L., de Carvalho, C.N., Briguglio, A., 2020. Buildings that 'speak': Ichnological geoheritage in 1930s buildings in Piazza della Vittoria (Genova, Italy). Geoheritage, **12**: 1–22; https://doi.org/10.1007/s12371-020-00496-x

Bayet-Goll, A., Knaust, D., Daraei, M., Bahrami, N., Bagheri, F., 2021. *Rosselia* ichnofabrics from the Lower Ordovician of the Alborz Mountains (northern Iran): palaeoecology, palaeobiology and sedimentology. Palaeobiodiversity and Palaeoenvironments, **102**: 103–128; https://doi.org/10.1007/s12549-021-00493-0

Bayet-Goll, A., Buatois, L.A., Mángano, M.G., Daraei, M., 2022. The interplay of environmental constraints and bioturbation on matground development along the marine depositional profile during the Ordovician Radiation. Geobiology, **20**: 233–270; https://doi.org/10.1111/gbi.12473

Belaústegui, Z., Gibert, J.M. de, 2013. Bow-shaped, concentrically laminated polychaete burrows: a *Cylindrichnus concentricus* ichnofabric from the Miocene of Tarragona, NE Spain. Palaeogeography, Palaeoclimatology, Palaeoecology, **381**: 119–127; https://doi.org/10.1016/j.palaeo.2013.04.021

Bernardi, M., Boschele, S., Ferretti, P., Avanzini, M., 2010. Echinoid burrow *Bichordites monastiriensis* from the Oligocene of NE Italy. Acta Palaeontologica Polonica, **55**: 479–486; https://doi.org/10.4202/app.2009.0064

Blum, A.J, 2007. Controls on long-term drainage development of the Carboneras basin, SE Spain. Ph.D. thesis, University of Plymouth.

Boorsma, L.J., 1992. Syn-tectonic sedimentation in a Neogene strike-slip basin containing a staked Gilbert-type delta (SE Spain). Sedimentary Geology, **81**: 105–123; https://doi.org/10.1016/0037-0738(92)90059-Z

Borsje, B.W., de Vries, M.B., Bouma, T.J., Besio, G., Hulscher, S.J., Herman, P.M., 2009. Modeling bio-geomorphological influences for offshore sandwaves. Continental Shelf Research, **29**: 1289–1301; https://doi.org/10.1016/j.csr.2009.02.008

Bouma, A.H., Berryhill, H.L., Brenner, R.L., Knebel, H.J., 1982. Continental shelf and epicontinental seaways. AAPG Memoir, **31**: 281–327; https://doi.org/10.1306/M31424C10

Braga, J.C., Martín, J.M., Betzler, C., Aguirre, J., 2003a. Spit-platform temperate carbonates: The origin of landward downlapping beds along a basin margin (lower Pliocene, Carboneras Basin, SE Spain). Sedimentology, **50**: 553–563; https://doi.org/10.1046/j.1365-3091.2003.00564.x

Braga, J.C., Martín, J.M., Quesada, C., 2003b. Patterns and average rates of late Neogene-Recent uplift of the Betic Cordillera, SE Spain. Geomorphology, **50**: 3–26; https://doi.org/10.1016/S0169-555X(02)00205-2

Brenner, R.L., Martinsen, O.J., 1990. The fossil sandstone – a shallow marine sand wave complex in the Namurian of Cumbria and North Yorkshire, England. Proceedings of the Yorkshire Geological Society, **48**: 149–162; https://doi.org/10.1144/pygs.48.2.149

Bromley, R.G., Asgaard, U., 1975. Sediment structures produced by a spatangoid echinoid: a problem of preservation. Bulletin of the Geological Society of Denmark, **24**: 261–281; https://doi.org/10.1016/S0016-7878(97)80026-0

Bromley, R.G., Uchman, A., 2003. Trace fossils from the Lower and Middle Jurassic marginal marine deposits of the Sorthat Formation, Bornholm, Denmark. Bulletin of the Geological Society of Denmark, **52**: 185–208.

Bromley, R.G., Jensen, M., Asgaard, U., 1995. Spatangoid echinoids: deep-tier trace fossils and chemosymbiosis. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **195**: 25–35; https://doi.org/10.1127/njgpa/195/1995/25

Bromley, R.G., Asgaard, U., Jensen, M., 1997. Experimental study of sediment structures created by a spatangoid echinoid, *Echinocardium mediterraneum*. Proceedings of the Geologists' Association, **108**: 183–189; https://doi.org/10.1016/S0016-7878(97)80026-0

Buatois, L.A., Mángano, M.G., 2011. Ichnology: Organism-Substrate Interactions in Space and Time. Cambridge University Press, Cambridge.

Buatois, L.A., García-Ramos, J.C., Piñuela, L., Mángano, M.G., Rodríguez-Tovar, F.J., 2016. *Rosselia socialis* from the Ordovician of Asturias (northern Spain) and the early evolution of equilibrium behavior in polychaetes. Ichnos, **23**: 147–155; https://doi.org/10.1080/10420940.2015.1132213

Buchanan, J.B., 1966. The biology of *Echinocardium cordatum* [Echinodermata: Spatangoidea] from different habitats. Journal of the Marine Biological Association of the United Kingdom, **46**: 97–114; https://doi.org/10.1017/S0025315400017574

Buck, S.G., Goldring, R., 2003. Conical sedimentary structures, trace fossils or not? Observations, experiments, and review. Journal of Sedimentary Research, **73**: 338–353; https://doi.org/10.1306/091602730338

Caruso, C., Sonnino, M., Uchman, A., 2011. Trace fossils in the Pleistocene arenites outcropping nearby the village of Bombile (southern Ionian Calabria). Rendiconti Online SGI, **17**: 59–61; https://doi.org/10.3301/ROL.2011.23

Caruso, C., Monaco, P., 2015. *Bichordites monastiriensis* ichnofabric from the Pleistocene shallow-marine sandstones at Le Castella (Crotone), Ionian Calabria, southern Italy. Rivista Italiana di Paleontologia e Stratigrafia, **121**: 381–397.

Cheng, C.H., Borsje, B.W., Beauchard, O., O'Flynn, S., Ysebaert, T., Soetaert, K., 2021. Small-scale macrobenthic community structure along asymmetrical sand waves in an underwater seascape. Marine Ecology, **42**, e12657; https://doi.org/10.1111/maec.12657

Chiarella, D., Moretti, M., Longhitano, S.G., Muto, F., 2016. Deformed cross-stratified deposits in the Early Pleistocene tidally-dominated Catanzaro strait-fill succession, Calabrian Arc (Southern Italy): triggering mechanisms and environmental significance. Sedimentary Geology, **344**: 277–289; https://doi.org/10.1016/j.sedgeo.2016.05.003

Clifton, H.E., Thompson, J.K., 1978. *Macaronichnus segregatis*: a feeding structure of shallow marine polychaetes. Journal of Sedimentary Research, **48**: 1293–1302; https://doi.org/10.1306/212F7667-2B24-11D7-8648000102C1865D

Colella, A., D'Alessandro, A., 1988. Sand waves, *Echinocardium* traces and their bathyal depositional setting (Monte Torre Palaeostrait, Plio-Pleistocene, southern Italy). Sedimentology, **35**: 219–237; https://doi.org/10.1111/j.1365-3091.1988.tb00946.x

Collins, A.B., Heupel, M.R., Hueter, R.E., Motta, P.J., 2007. Hard prey specialists or opportunistic generalists? An examination of the diet of the cownose ray, *Rhinoptera bonasus*. Marine and Freshwater Research, **58**: 135–144; https://doi.org/10.1071/MF05227

Cross, R.E., Curran, M.C., 2004. Recovery of meiofauna in intertidal feeding pits created by rays. Southeastern Naturalist, **3**: 219–230; https://doi.org/10.1656/1528-7092(2004)003[0219:ROMIIF]2.0.CO;2

Dabrio, C.J., 1986–1987. Las "sand waves" calcareníticas del Río Alías (Mioplioceno de la Cuenca de Níjar, Almería). Acta Geológica Hispánica, **21**: 159–166.

Dafoe, L.T., Gingras, M.K., Pemberton, S.G., 2008a. Determining *Euzonus mucronata* burrowing rates with application to ancient *Macaronichnus segregatis* tracemakers. Ichnos, **15**: 78–90; https://doi.org/10.1080/10420940802016475

Dafoe, L.T., Gingras, M.K., Pemberton, S.G., 2008b. Analysis of mineral segregation in *Euzonus mucronata* burrow structures: one possible method in the construction of ancient *Macaronichnus segregatis*. Ichnos, **15**: 91–102; https://doi.org/10.1080/10420940802016582

D'Alessandro, A., Massari, F., 1997. Pliocene and Pleistocene depositional environments in the Pesculuse area (Salento, Italy). Rivista Italiana di Paleontologia e Stratigrafia, **103**: 221–258; https://doi.org/10.54103/2039-4942/13450

D'Alessandro, A., Massari, F., Davaud, E., Ghibaudo, G., 2004. Pliocene–Pleistocene sequences bounded by subaerial unconformities within foramol ramp calcarenites and mixed deposits (Salento, SE Italy). Sedimentary Geology, **166**: 89–144; https://doi.org/10.1016/j.sedgeo.2003.11.017

D'Alessandro, A., Uchman, A., 2007. *Bichordites* and *Bichordites-Rosselia* ichnoassemblages from the Lower Pleistocene Tursi Sandstone (southern Italy). SEPM Special Publications, **88**: 213–221; https://doi.org/10.2110/pec.07.88.0213

Damveld, J.H., van der Reijden, K.J., Cheng, C., Koop, L., Haaksma, L.R., Walsh, C.A., Soetaert, K., Borsje, B.W., Govers, L.L., Roos, P.C., Olff, H., 2018. Video transects reveal that tidal sand waves affect the spatial distribution of benthic organisms and sand ripples. Geophysical Research Letters, **45**: 11–837; https://doi.org/10.1029/2018GL079858

Dashtgard, S.E., 2011. Linking invertebrate burrow distributions (neoichnology) to physicochemical stresses on a sandy tidal flat: implications for the rock record. Sedimentology, **58**: 1303–1325; https://doi.org/10.1111/j.1365-3091.2010.01210.x

Desai, B.G., Saklani, R.D., 2015. Palaeocommunity dynamics and behavioral analysis of *Conichnus*: Bhuj formation (Lower Cretaceous), Kachchh-India. Ichnos, **22**: 43–55; https://doi.org/10.1080/10420940.2014.995377

Dominici, S., Benvenuti, M., Garilli, V., Uchman, A., Pollina, F., 2017. Stratigraphic palaeobiology around the Pliocene-Pleistocene boundary at Altavilla Milicia (Sicily, Italy). In: EGU General Assembly Conference Abstracts, 11667.

Duperron, M., Scasso, R.A., 2020. Petrographic analysis of crowded *Rosselia* ichnofabrics from the Tremadocian of Northwestern Argentina: ethologic meaning and diagenesis. Revista de la Asociación Geológica Argentina, **77**: 335–352.

Droser, M.L., Bottjer, D.J., 1993. Trends and patterns of Phanerozoic ichnofabrics. Annual Review of Earth and Planetary Sciences, **21**: 205–225; https://doi.org/10.1146/annurev.ea.21.050193.001225

Ekdale, A.A., 1985. Paleoecology of the marine endobenthos. Palaeogeography, Palaeoclimatology, Palaeoecology, **50**: 63–81; https://doi.org/10.1016/S0031-0182(85)80006-7

Ekdale, A.A., 1988. Pitfalls of paleobathymetric interpretations based on trace fossil assemblages. Palaios, **3**: 464–472; https://doi.org/10.2307/3514720

Ekdale, A.A., Harding, S.C., 2015. *Cylindrichnus concentricus* Toots in Howard, 1966 (trace fossil) in its type locality, Upper Cretaceous, Wyoming. Annales Societatis Geologorum Poloniae, **85**: 427–432; https://doi.org/10.14241/asgp.2015.018

Ellis, J.R., Pawson, M.G., Shackley, S.E., 1996. The comparative feeding ecology of six species of shark and four species of ray (Elasmobranchii) in the north-east Atlantic. Journal of the Marine Biological Association of the United Kingdom, **76**: 89–106.

Fillion, D., Pickerill, R.K., 1990. Ichnology of the upper Cambrian? to lower Ordovician Bell Island and Wabana groups of eastern Newfoundland, Canada. Palaeontographica Canadiana, **7**: 1–119.

Flowers, K.I., Heithaus, M.R., Papastamatiou, Y.P., 2021. Buried in the sand: Uncovering the ecological roles and importance of rays. Fish and Fisheries, **22**: 105–127; https://doi.org/10.1111/faf.12508

Fortuin, A.R., Dabrio, C.J., 2008. Evidence for Late Messinian seismites, Níjar Basin, south-east Spain. Sedimentology, **55**: 1595–1622; https://doi.org/10.1111/j.1365-3091.2008.00959.x

Frey, R.W., Howard, J.D., 1981. *Conichnus* and *Schaubcylindrichnus*: redefined trace fossils from the Upper Cretaceous of the Western Interior. Journal of Paleontology, **55**: 800–804.

Frieling, D., 2007. *Rosselia socialis* in the Upper Marine Molasse of southwestern Germany. Facies, **53**: 479–492; https://doi.org/10.1007/s10347-007-0117-1

Fu, S., Werner, F., 2000. Distribution, ecology and taphonomy of the organism trace, *Scolicia*, in northeast Atlantic deep-sea sediments. Palaeogeography, Palaeoclimatology, Palaeoecology, **156**: 289–300; https://doi.org/10.1016/S0031-0182(99)00146-7

Giannetti, A., Baeza-Carratalá, J.F., Soria-Mingorance, J.M., Dulai, A., Tent-Manclús, J.E., Peral-Lozano, J., 2018. New paleobiogeographical and paleoenvironmental insight through the Tortonian brachiopod and ichnofauna assemblages from the Mediterranean-Atlantic seaway (Guadix Basin, SE Spain). Facies, **64**, 24; https://doi.org/10.1007/s10347-018-0536-1

Giannetti, A., Monaco, P., Falces-Delgado, S., La Iacona, F.G., Corbí, H., 2019. Taphonomy, ichnology, and palaeoecology to distinguish event beds in varied shallow-water settings (Betic Cordillera, SE Spain). Journal of Iberian Geology, **45**: 47–61; https://doi.org/10.1007/s41513-018-0094-y

Gibert, J.M.de, Da Silva, C.M., Cachao, M., 1998. Icnofábrica de *Ophiomorpha*/*Conichnus* en el Mioceno inferior de Cristo de Rei (Almada, Portugal). Implicaciones paleoambientales. Revista Española de Paleontología, **13**: 251–259.

Gibert, J.M.de, Ekdale, A.A., 2002. Ichnology of a restricted epicontinental sea, Arapien Shale, Middle Jurassic, Utah, USA. Palaeogeography, Palaeoclimatology, Palaeoecology, **183**: 275–286; https://doi.org/10.1016/S0031-0182(01)00491-6

Gibert, J.M.de, Goldring, R., 2007. An ichnofabric approach to the depositional interpretation of the intensely burrowed Bateig Limestone, Miocene, SE Spain. Sedimentary Geology, **194**: 1–16; https://doi.org/10.1016/j.sedgeo.2006.04.008

Gibert, J.M.de, Goldring, R., 2008. Spatangoid-produced ichnofabrics (Bateig Limestone, Miocene, Spain) and the preservation of spatangoid trace fossils. Palaeogeography, Palaeoclimatology, Palaeoecology, **270**: 299–310; https://doi.org/10.1016/j.palaeo.2008.01.031

Gingras, M.K., Pemberton, S.G., Saunders, T., Clifton, H.E., 1999. The ichnology of modern and Pleistocene brackish-water deposits at Willapa Bay, Washington; variability in estuarine settings. Palaios, **14**: 352–374; https://doi.org/10.2307/3515462

Gingras, M.K., MacMillan, B., Balcom, B.J., Saunders, T., Pemberton, S.G., 2002. Using magnetic resonance imaging and petrographic techniques to understand the textural attributes and porosity distribution in *Macaronichnus*-burrowed sandstone. Journal of Sedimentary Research, **72**: 552–558; https://doi.org/10.1306/122901720552

Gingras, M.K., Armitage, I.A., Pemberton, S.G., Clifton, H.E., 2007. Pleistocene walrus herds in the Olympic Peninsula area: trace-fossil evidence of predation by hydraulic jetting. Palaios, **22**: 539–545; https://doi.org/10.2110/palo.2005.p05-120r

Gingras, M.K., Dashtgard, S.E., MacEachern, J.A., Pemberton, S.G., 2008. Biology of shallow marine ichnology: a modern perspective. Aquatic Biology, **2**: 255–268; https://doi.org/10.3354/ab00055

Gingras, M.K., MacEachern, J.A., Dashtgard, S.E., 2011. Process ichnology and the elucidation of physico-chemical stress. Sedimentary Geology, **237**: 115–134; https://doi.org/10.1016/j.sedgeo.2011.02.006

Goldring, R., 1995. Organisms and the substrate: response and effect. Geological Society Special Publications, **83**: 151–180; https://doi.org/10.1144/GSL.SP.1995.083.01.09

Goldring, R., 1996. The sedimentological significance of concentrically laminated burrows from Lower Cretaceous Ca-bentonites, Oxfordshire. Journal of the Geological Society, **153**: 255–263; https://doi.org/10.1144/gsjgs.153.2.0255

Goldring, R., Codée, G.C., Pollard, J.E., 2007. Climatic control of marine trace fossil distribution. In: Trace Fossils: Concepts, Problems, Prospects (ed. W. Miller, III): 159–171. Elsevier. London; https://doi.org/10.1016/B978-044452949-7/50136-4

Goy, J.L., Zazo, C., 1986. Synthesis of the Quaternary in the Almeria littoral neotectonic activity and its morphologic features, western Betics, Spain. Tectonophysics, **130**: 259–270; https://doi.org/10.1016/0040-1951(86)90116-2

Gregory, M.R., Ballance, P.F., Gibson, G.W., Ayling, A.M., 1979. On how some rays (Elasmobranchia) excavate feeding depressions by jetting water. Journal of Sedimentary Research, **49**: 1125–1129; https://doi.org/10.1306/212F78C9-2B24-11D7-8648000102C1865D

Gregory, M.R., 1991. New trace fossils from the Miocene of Northland, New Zealand: *Rorschachichnus amoeba* and *Piscichnus waitemata*. Ichnos, **1**: 195–205; https://doi.org/10.1080/10420949109386352

Grun, T.B., 2016. Echinoid test damage by a stingray predator. Lethaia, **49**: 285–286; https://doi.org/10.1111/let.12165

Heithaus, M.R., Frid, A., Vaudo, J.J., Worm, B., Wirsing, A.J., 2010. Unraveling the ecological importance of elasmobranchs. In: Sharks and their relatives II, CRC Press: 627–654; https://doi.org/10.1201/9781420080483

Hofmann, R., Mángano, M.G., Elicki, O., Shinaq, R., 2012. Paleoecologic and biostratigraphic significance of trace fossils from shallow-to marginal-marine environments from the Middle Cambrian (Stage 5) of Jordan. Journal of Paleontology, **86**: 931–955; https://doi.org/10.1666/11-129R1.1

Jordan, G.F., 1962. Large submarine sand waves: their orientation and form are influenced by some of the same factors that shape desert sand dunes. Science, **136**: 839–848.

Kappus, E.J., Lucas, S.G., 2019. Ichnologic note a new ichnospecies of *Cardioichnus* from the Cretaceous (Albian) of New Mexico. Ichnos, **26**: 127–133; https://doi.org/10.1080/10420940.2018.1482215

Keighley, D.G., Pickerill, R.K., 1995. Commentary: The ichnotaxa *Palaeophycus* and *Planolites*: Historical perspectives and recommendations. Ichnos, **3**: 301–309; https://doi.org/10.1080/10420949509386400

Klug, C., Hoffmann, R., 2018. Early Devonian actiniarian trace fossils (*Conichnus conicus*) from the Anti-Atlas of Morocco. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **290**: 65–74.

Knaust, D., 2017. Atlas of Trace Fossils in Well Core. Appearance, Taxonomy and Interpretation. Springer, Cham; https://doi.org/10.1007/978-3-319-49837-9

Knaust, D., 2021. *Rosselichnidae* ifam. nov.: burrows with concentric, spiral or eccentric lamination. Papers in Palaeontology, **7**: 1847–1875; https://doi.org/10.1002/spp2.1367

Kotake, N., 2007. *Macaronichnus* isp. associated with *Piscichnus waitemata* in the Miocene of Yonaguni-jima Island, Southwest Japan. In: Trace Fossils Concepts, Problems, Prospects (ed. W.M Miller, III): 492–501. Elsevier, Amsterdam; https://doi.org/10.1016/B978-044452949-7/50156-X

Last, P.R., White, W.T., de Carvalho, M.R., Séret, B., Stehmann, M.F.W., Naylor, G.J.P., 2016. Rays of the World. Melbourne: CSIRO Publishing & Cornell University Press; https://doi.org/10.1080/17451000.2017.1336246

Liou, Y.H., Löwemark, L., Wang, P.L., Dashtgard, S., 2022. Geochemical signatures of sedimentary and diagenetic processes in the trace fossil *Rosselia* from the Pliocene in Taiwan. Scientific Reports, **12**, 22316; https://doi.org/10.1038/s41598-022-26772-0

Lohrer, A.M., Thrush, S.F., Gibbs, M.M., 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. Nature, **431**: 1092–1095; https://doi.org/10.1038/nature03042

Lohrer, A.M., Thrush, S.F., Hunt, L., Hancock, N., Lundquist, C., 2005. Rapid reworking of subtidal sediments by burrowing spatangoid urchins. Journal of Experimental Marine Biology and Ecology, **321**: 155–169; https://doi.org/10.1016/j.jembe.2005.02.002

Longhitano, S.G., Rossi, V.M., Chiarella, D., Mellere, D., Tropeano, M., Dalrymple, R.W., Steel, R.J., Nappi, A., Olita, F., 2021. Anatomy of a mixed bioclastic–siliciclastic regressive tidal sand ridge: Facies-based case study from the lower Pleistocene Siderno Strait, southern Italy. Sedimentology, **68:** 2293–2333; https://doi.org/10.1111/sed.12853

Löwemark, L., 2015. Evidence for targeted elasmobranch predation on thalassinidean shrimp in the Miocene Taliao Formation, NE Taiwan. Lethaia, **48**: 227–234; https://doi.org/10.1111/let.12101

MacEachern, J.A., Bann, K.L., 2020. The *Phycosiphon* Ichnofacies and the *Rosselia* Ichnofacies: Two new ichnofacies for marine deltaic environments. Journal of Sedimentary Research, **90**: 855–886; https://doi.org/10.2110/jsr.2020.41

Mángano, M.G., Buatois, L.A., Aceñolaza, G.F., 1996. Trace fossils and sedimentary facies from a Late Cambrian-Early Ordovician tide-dominated shelf (Santa Rosita Formation, northwest Argentina): implications for ichnofacies models of shallow marine successions. Ichnos, **5**: 53–88;l https://doi.org/10.1080/10420949609386406

Marchetti, L., Belvedere, M., Voigt, S., Klein, H., Castanera, D., Díaz-Martínez, I., Marty, D., Xing, L., Feola, S., Melchor, R.N., Farlow, J.O., 2019. Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present. Earth-Science Reviews, **193**: 109–145; https://doi.org/10.1016/j.earscirev.2019.04.008

Marenco, K.N., Hagadorn, J.W., 2019. Big bedding planes: outcrop size and spatial heterogeneity influence trace fossil analyses. Palaeogeography, Palaeoclimatology, Palaeoecology, **513**: 14–24; https://doi.org/10.1016/j.palaeo.2018.08.008

Martín J.M., Braga J.C., 1996. Tectonic signals in the Messinian stratigraphy of the Sorbas basin (Almería, SE Spain). In: Tertiary basins of Spain: the stratigraphic record of crustal kinematics. World and Regional Geology Series (eds. P.F. Friend and C.J. Dabrio), **6**: 387–391. Cambridge University Press, Cambridge.

Martín, J.M., Braga, J.C., Betzler, C., 2003. Late Neogene-recent uplift of the Cabo de Gata volcanic province, Almería, SE Spain. Geomorphology, **50**: 27–42; https://doi.org/10.1016/S0169-555X(02)00206-4

Martín, J.M., Braga, J.C., Aguirre, J., Betzler, C., 2004. Contrasting models of temperate carbonate sedimentation in a small Mediterranean embayment: The Pliocene Carboneras Basin, SE Spain. Journal of the Geological Society **161**: 387–399; https://doi.org/10.1144/0016-764903-044

Mata, S.A., Corsetti, C.L., Corsetti, F.A., Awramik, S.M., Bottjer, D.J., 2012. Lower Cambrian anemone burrows from the upper member of the Wood Canyon Formation, Death Valley region, United States: palaeoecological and palaeoenvironmental significance. Palaios, **27**: 594–606; https://doi.org/10.2110/palo.2012.p12-016r

Mayoral E., Muñiz, F., 2001. New Ichnospecies of *Cardioichnus* from the Miocene of the Guadalquivir Basin, Huelva, Spain, Ichnos, **8**: 69–76; https://doi.org/10.1080/10420940109380174

McIlroy, D., 2007. Lateral variability in shallow marine ichnofabrics: implications for the ichnofabric analysis method. Journal of the Geological Society, **164**: 359–369; https://doi.org/10.1144/0016-76492005-101

Michael, S.W., 1993. Reef sharks and rays of the world: a guide to their identification, behavior, and ecology, Annapolis, MD. ProStar Publications; https://doi.org/10.1017/s0025315400034998

Miguez-Salas, O., Rodríguez-Tovar, F.J., de Weger, W., 2021. The Late Miocene Rifian corridor as a natural laboratory to explore a case of ichnofacies distribution in ancient gateways. Scientific Reports, **11**, 4198; https://doi.org/10.1038/s41598-021-83820-x

Nara, M., 1995. *Rosselia socialis*: a dwelling structure of a probable terebellid polychaete. Lethaia, **28**: 171–178; https://doi.org/10.1111/j.1502-3931.1995.tb01610.x

Nara, M., 1997. High-resolution analytical method for event sedimentation using *Rosselia socialis*. Palaios, **12**: 489–494; https://doi.org/10.2307/3515386

Nara, M., 2002. Crowded *Rosselia socialis* in Pleistocene inner shelf deposits: benthic paleoecology during rapid sea-level rise. Palaios, **17**: 268–276; https://doi.org/10.1669/0883-1351(2002)017<0268:CRSIPI>2.0.CO;2

Nara, M., 2014. The *Bichordites* ichnofabric in the Pleistocene ocean current-generated sand ridge complex. Spanish Journal of Palaeontology, **29**: 191–202; https://doi.org/10.7203/sjp.29.2.17801

Nara, M., Haga, M., 2007. The youngest record of trace fossil *Rosselia socialis*: occurrence in the Holocene shallow marine deposits of Japan. Paleontological Research, **11**: 21–27; https://doi.org/10.2517/1342-8144(2007)11[21:TYROTF]2.0.CO;2

Nara, M., Seike, K., 2004. *Macaronichnus segregatis*-like traces found in the modern foreshore sediments of the Kujukurihama Coast, Japan (in Japanese with English abstract). Journal of the Geological Society of Japan, **110**: 545–551; https://doi.org/10.5575/geosoc.110.545

Nara, M., Seike, K., 2019. Palaeoecology of *Macaronichnus segregatis degiberti*: Reconstructing the infaunal lives of the travisiid polychaetes. Palaeogeography, Palaeoclimatology, Palaeoecology, **516**: 284–294; https://doi.org/10.1016/j.palaeo.2018.12.011

Nara, M., Seno'o, M., Yamaoka, Y., 2020. *Scolicia shirahamensis* isp. nov.: a triple-corded *scolicia* and its ichnological implications. Ichnos, **27**: 300–306; https://doi.org/10.1080/10420940.2020.1744580

Nauta, J., Leurs, G., Nieuwenhuis, B.O., Mathijssen, D.R., Olff, H., Bouma, T.J., van der Wal, D., Hijner, N., Regalla, A., Pontes, S.L., Govers, L.L., 2024. Bioturbation by benthic stingrays alters the biogeomorphology of tidal flats. Ecosystems, **27**: 493–507; https://doi.org/10.1007/s10021-024-00901-4

Netto, R.G., Tognoli, F.M., Assine, M.L., Nara, M., 2014. Crowded *Rosselia* ichnofabric in the Early Devonian of Brazil: an example of strategic behavior. Palaeogeography, Palaeoclimatology, Palaeoecology, **395**: 107–113; https://doi.org/10.1016/j.palaeo.2013.12.032

Nielsen, J.K., Nara, M., Jacobsen, A.R., 2020. Bowl-shaped structures in a Pleistocene clastic carbonate wedge on the Island of Rhodes, Greece. Ichnos, **27**: 326–333; https://doi.org/10.1080/10420940.2020.1744582

Nielsen, L.H., Johannessen, P.N., 2008. Are some isolated shelf sandstone ridges in the Cretaceous Western Interior Seaway transgressed, detached spit systems? SEPM Special Publication, **90**: 333–354; https://doi.org/10.2110/pec.08.90.0333

Olariu, C., Steel, R.J., Dalrymple, R.W., Gingras, M.K., 2012. Tidal dunes versus tidal bars: the sedimentological and architectural characteristics of compound dunes in a tidal seaway, the lower Baronia Sandstone (Lower Eocene), Ager Basin, Spain. Sedimentary Geology, **279**: 134–155; https://doi.org/10.1016/j.sedgeo.2012.07.018

Olivero, E.B., López Cabrera, M.I., 2005. *Patagonichnus*: a new trace fossil from the Miocene of Patagonia. A probable fodinichnion of gregarious polychaetes. Ameghiniana, **42**: 277–294.

Olivero, E.B., López Cabrera, M.I., Ercolano, B., Pittaluga, S., Lizarralde, Z., 2012. Caught in fraganti: actual and Holocene, crowded *Rosselia*-like mud-lined tubes produced by spionid polychates. Ameghiniana, **49** (4), Suplemento – Resúmenes: R152; https://doi.org/10.5710/AMGH.v49i4.5

Olivero, E.B., López Cabrera, M.I., 2020. A new shallow-marine, high-latitude record of the trace fossil *Macaronichnus* in Miocene, reworked delta-front clinoforms, Punta Basílica, Tierra Del Fuego, Argentina. Ichnos, **27**: 369–383; https://doi.org/10.1080/10420940.2020.1755854

Osgood, R.G.Jr., 1970. Trace fossils of the Cincinnati area. Palaeontographica Americana, **6**: 276–439.

O'Shea, O.R., Thums, M., Van Keulen, M., Meekan, M., 2011. Bioturbation by stingrays at Ningaloo reef, Western Australia. Marine and Freshwater Research, **63**: 189–197; https://doi.org/10.1071/MF11180

Patel, S.J., Shitole, A.D.. Joseph, J.K., 2018. Plug Shaped Burrows *Conichnus-Conostichus* from the Late Cretaceous of Bagh Group, Gujarat, Western India. Journal of the Geological Society of India, **91**: 41–46; https://doi.org/10.1007/s12594-018-0818-9

Pearson, N.J., Gingras, M.K., Armitage, I.A., Pemberton, S.G., 2007. Significance of Atlantic sturgeon feeding excavations, Mary's Point, Bay of Fundy, New Brunswick, Canada. Palaios, **22**: 457–464; https://doi.org/10.2110/palo.2005.p05-121r

Pearson, N.J., Mángano, M.G., Buatois, L.A., Casadío, S., Raising, M.R., 2013. Environmental variability of *Macaronichnus* ichnofabrics in Eocene tidal-embayment deposits of southern Patagonia, Argentina. Lethaia, **46**: 341–354; https://doi.org/10.1111/let.12012

Pemberton, S.G., Frey, R.W., 1982. Trace fossil nomenclature and the *Planolites-Palaeophycus* dilemma. Journal of Paleontology, **56**: 843–881.

Pemberton, S.G., MacEachern, J.A., Dashtgard, S.E., Bann, K.L., Gingras, M.K., Zonneveld, J.-P., 2012. Shoreface, Developments in Sedimentology, **64**: 563–603.

Pervesler, P., Uchman, A., 2004. Ichnofossils from the type area of the Grund Formation (Miocene, Lower Badenian) in northern Lower Austria (Molasse Basin). Geologica Carpathica, **55**: 103–110.

Plaziat, J.C., Mahmoudi, M., 1988. Trace fossils attributed to burrowing echinoids: A revision including new ichnogenus and ichnospecies. Geobios, **21**: 209–233; https://doi.org/10.1016/S0016-6995(88)80019-6

Pollard, J.E., Goldring, R., Buck, S.G., 1993. Ichnofabrics containing *Ophiomorpha*: significance in shallow-water facies interpretation. Journal of the Geological Society, **150**: 149–164; https://doi.org/10.1144/gsjgs.150.1.0149

Postma, G. 1979. Preliminary note on a significant sequence in conglomeratic flows of a mass-transport dominated fan-delta (lower Pliocene, Almeria Basin, SE Spain). Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Serie B, **82**: 465–471.

Postma, G. 1983. Water-escape structures in the context of a depositional model of a mass flow dominated conglomeratic fan-delta (Abrioja Formation, Pliocene, Almeria Basin, SE Spain). Sedimentology, **30**: 91–103; https://doi.org/10.1111/j.1365-3091.1983.tb00652.x

Pryor, W.A., Amaral, E.J., 1971. Large-scale cross-stratification in the St. Peter Sandstone. GSA Bulletin, **82**: 239–244; https://doi.org/10.1130/0016-7606(1971)82[239:LCITSP]2.0.CO;

Quiroz, L.I., Buatois, L.A., Mángano, M.G., Jaramillo, C.A., Santiago, N., 2010. Is the trace fossil *Macaronichnus segregatis* an indicator of temperate to cold waters? Exploring the paradox of its occurrence in tropical coasts. Geology, **38**: 651–654; https://doi.org/10.1130/G30140.1

Quiroz, L.I., Buatois, L.A., Seike, K., Mángano, M.G., Jaramillo, C., Sellers, A.J., 2019. The search for an elusive worm in the tropics, the past as a key to the present, and reverse uniformitarianism. Scientific Reports, **9**, 18402; https://doi.org/10.1130/G30140.1

Rastgoo, A.R., Navarro, J., Valinassab, T., 2018. Comparative diets of sympatric batoid elasmobranchs in the Gulf of Oman. Aquatic Biology, **27**: 35–41; https://doi.org/10.3354/ab00694

Rice, D.D., Shurr, G.W., 1983. Patterns of sedimentation and paleography across the Western Interior Seaway during time of deposition of Upper Cretaceous sandstones and equivalent rocks. In: Mesozoic Paleogeography of the West-Central United States (eds. M.W. Reynolds and E.D. Dolly): 337–358. The Rocky Mountain Section, Society of Economic Paleontologists and Mineralogists, Denver.

Rindsberg, A.K., Gastaldo, R.A., 1990. New insight on ichnogenus *Rosselia* (Cretaceous and Holocene, Alabama). Journal of the Alabama Academy of Science, **61**, 154.

Rodríguez-Tovar, F.J., Aguirre, J., 2014. Is *Macaronichnus* an exclusively small, horizontal and unbranched structure? *Macaronichnus segregatis degiberti* isubsp. nov. Spanish Journal of Palaeontology, **29**: 131–142; https://doi.org/10.7203/sjp.29.2.17682

Rodríguez-Tovar, F.J., García-García, F., 2023. *Macaronichnus* 'co-occurrence' in offshore transition settings: discussing the role of tidal versus fluid muds influence. Geobios, **80**: 73–82; https://doi.org/10.1016/j.geobios.2023.07.001

Saitoh, M., Kanazawa, K.I., 2012. Adaptative morphology for living in shallow water environments in spatangoid echinoids. Zoosymposia, **7**: 255–265; https://doi.org/10.11646/zoosymposia.7.1.24

Salé, S.O., Gennari, R., Lugli, S., Manzi, V., Roveri, M., 2012. Tectonic and climatic control on the Late Messinian sedimentary evolution of the Nijar Basin (Betic Cordillera, Southern Spain). Basin Research, **24**: 314–337; https://doi.org/10.1111/j.1365-2117.2011.00527.x

Savrda, C., 2002. Equilibrium responses reflected in a large *Conichnus* (Upper Cretaceous Eutaw formation, Alabama, USA). Ichnos, **9**: 33–40; https://doi.org/10.1080/10420940190034058

Schäfer, W., 1956. Wirkungen der Benthos-Organismen auf den jungen Schichtverband. Senckenbergiana Lethaea, **37**: 183–263.

Schäfer, W., 1972. Ecology and Palaeoecology of Marine Environments. Oliver & Boyd, Edinburgh.

Schlirf, M., Uchman, A., 2005. Revision of the ichnogenus *Sabellarifex* Richter, 1921 and its relationship to *Skolithos* Haldeman, 1840 and *Polykladichnus* Fürsich, 1981. Journal of Systematic Palaeontology, **3**: 115–131; https://doi.org/10.1017/S1477201905001550

Seike, K., Yanagishima, S.I., Nara, M., Sasaki, T., 2011. Large *Macaronichnus* in modern shoreface sediments: Identification of the producer, the mode of formation, and paleoenvironmental implications. Palaeogeography, Palaeoclimatology, Palaeoecology, **311**: 224–229; https://doi.org/10.1016/j.palaeo.2011.08.023

Shillito, A.P., Gougeon, R., 2023. Identifying and accounting for outcrop constraints on observations in field-based ichnological studies. Ichnos, **30**: 269–282; https://doi.org/10.1080/10420940.2024.2330417

Shinn, E.A., 1968. Burrowing in recent lime sediments of Florida and the Bahamas. Journal of Paleontology, **42**: 879–894.

Slatt, R.M., 1984. Continental shelf topography: key to understanding distribution of shelf sand-ridge deposits from Cretaceous Western Interior Seaway. AAPG Bulletin, **68**: 1107–1120; https://doi.org/10.1306/AD4616DD-16F7-11D7-8645000102C1865D

Smith, A.B., Crimes, T.P., 1983. Trace fossils formed by heart urchins – a study of *Scolicia* and related traces. Lethaia, **16**: 79–92; https://doi.org/10.1111/j.1502-3931.1983.tb02001.x

Sola, F., Puga-Bernabéu, Á., Aguirre, J., Braga, J.C., 2017. Heterozoan carbonate deposition on a steep basement escarpment (Late Miocene, Almería, south-east Spain). Sedimentology, **64**: 1107–1131; https://doi.org/10.1111/sed.12343

Sola, F., Puga-Bernabéu, Á., Braga, J.C., 2024. Tidally influenced deposits in the Río Alías Strait connecting a marginal basin with the Mediterranean Sea (Pliocene, South-East Spain). The Depositional Record, **00**: 1–30; https://doi.org/10.1002/dep2.303

Sommerville, E., Platell, M.E., White, W.T., Jones, A.A., Potter, I.C., 2011. Partitioning of food resources by four abundant, co-occurring elasmobranch species: relationships between diet and both body size and season. Marine and Freshwater Research, **62**: 54–65; https://doi.org/10.1016/S0022-0981(01)00257-X

Suganuma, K., Omori, M., Hirakoso, S., Ryuugasaki Collaborative Research Group, 1994. On the Ichnogen. *Rosselia*, fossil burrows found from the Kamiiwahashi Formation, in the district of Tokizaki, Edosaki-machi, Ryuugasaki City, Ibaraki Prefecture (in Japanese with English summary). Journal of Fossil Research, **26**: 61–68.

Thrush, S.F., Pridmore, R.D., Hewitt, J.E., Cummings, V.J., 1991. Impact of ray feeding disturbances on sandflat macrobenthos: Do communities dominated by polychaetes or shellfish respond differently? Marine Ecology Progress Series, **69**: 245–252.

Thayer, C.W., 1979. Biological bulldozers and the evolution of marine benthic communities. Science, **203**: 458–461; https://doi.org/10.1126/science.203.4379.45

Taylor, A.M., Goldring, R., 1993. Description and analysis of bioturbation and ichnofabric. Journal of the Geological Society, **150**: 141–148; https://doi.org/10.1144/gsjgs.150.1.014

Taylor, A., Goldring, R., Gowland, S., 2003. Analysis and application of ichnofabrics. Earth-Science Reviews, **60**: 227–259; https://doi.org/10.1016/S0012-8252(02)00105-8

Uchman, A., 1995. Taxonomy and palaeoecology of flysch trace fossils: the Marnoso-arenacea Formation and associated facies (Miocene, Northern Apennines, Italy). Beringeria, **15**: 1–115.

Uchman, A., Krenmayr, H.G., 1995. Trace fossils from lower Miocene (Ottnangian) molasse deposits of Upper Austria. Paläontologische Zeitschrift, **69**: 503–524; https://doi.org/10.1007/BF02987810

Uchman, A., Torres, P., Johnson, M.E., Berning, B., Ramalho, R.S., Rebelo, A.C., Melo, C.S., Baptista, L., Madeira, P., Cordeiro, R., Avila, S.P., 2018. Feeding traces of recent ray fish and occurrences of the trace fossil *Piscichnus waitemata* from the Pliocene of Santa Maria Island, Azores (Northeast Atlantic). Palaios, **33**: 361–375; https://doi.org/10.2110/palo.2018.027

Uchman, A., Johnson, M.E., Ramalho, R.S., Quartau, R., Berning, B., Hipólito, A., Melo, C.S., Rebelo, A.C., Cordeiro, R., Ávila, S.P., 2020. Neogene marine sediments and biota encapsulated between lava flows on Santa Maria Island (Azores, north-east Atlantic): an interplay between sedimentary, erosional and volcanic processes. Sedimentology, **67**: 3595–3618; https://doi.org/10.1111/sed.12763

VanBlaricom, G.R., 1982. Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. Ecological Monographs, **52**: 283–305; https://doi.org/10.2307/2937332

Villegas-Martín, J., Netto, R.G., 2017. *Bichordites* from the early Eocene of Cuba: significance in the evolutionary history of the spatangoids. Journal of South American Earth Sciences, **80**: 404–410; https://doi.org/10.1016/j.jsames.2017.10.008

Wetzel, A., 1981. Ökologische und stratigraphische Bedeutung biogener Gefüge in quartären Sedimenten am NW-afrikanischen Kontinentalrand. “Meteor” Forschungs-Ergebnisse, C **34**: 1–47.

Wetzel, A., Unverricht, D., 2020. Sediment dynamics of estuarine Holocene incised-valley fill deposits recorded by *Siphonichnus* (ancient Red River, Gulf of Tonkin). Palaeogeography, Palaeoclimatology, Palaeoecology, **560**, 110041; https://10.1016/j.palaeo. 2020.110041

Zlatanović, S., Fabian, J., Mendoza-Lera, C., Woodward, K.B., Premke, K., Mutz, M., 2017. Periodic sediment shift in migrating ripples influences benthic microbial activity. Water Resources Research, **53**: 4741–4755; https://doi.org/10.1002/2017WR020656

Zonneveld, J.-P., Gingras, M.K., 2013. The ichnotaxonomy of vertically oriented, bivalve-generated equilibrichnia. Journal of Paleontology, **87**: 243–253; https://doi.org/10.1666/11-064R1.1

Zorn, M.E., Muehlenbachs, K., Gingras, M.G., Konhauser, K.O., Pemberton, S.G., Evoy, R. 2007. Stable isotopic analysis reveals evidence for groundwater-sediment-animal interactions in a marginal-marine setting. Palaios, **22**: 546–553; https://doi.org/10.2110/palo.2006.p06-023r

Zorn, M.E., Gingras, M.K., Pemberton, S.G., 2010. Variation in burrow-wall micromorphologies of select intertidal invertebrates along the Pacific northwest coast, USA: behavioral and diagenetic implications. Palaios, **25**: 59–72; https://doi.org/10.2110/palo.2009.p09-026r