

Ichnology, trace fossils and depositional environments

Preface to a Virtual Special Issue of the journal
Palaeogeography, Palaeoclimatology, Palaeoecology

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1. Introduction

The role of trace fossils has changed tremendously during the last decades, from “objects that were treated in standard palaeontology textbooks, at best, under “Miscellanea”, together with problematica, coprolites and pseudofossils useless as index fossils” (Seilacher, 2007, p. V), to a valuable tool in environmental analysis as indicated by the growing number of ichnological papers and textbooks published. This success stems mainly from the intimate connection of ichnology and sedimentology and the importance both fields have for palaeoenvironmental and basin analysis (e.g., MacEachern et al., 2009; Buatois and Mángano, 2011; Knaust and Bromley, 2012; Baucon and Neto de Carvalho, 2017; Knaust, 2017).

The multidisciplinary character of ichnology is intriguing and fascinating and attracts, besides ichnologists, in particular sedimentologists for several reasons. (1) Trace fossils and ichnofabrics are (fortunately) common features in sediments and sedimentary rocks and can easily be studied in outcrop and core. Even if biogenic sedimentary structures are not present, their absence has an environmental meaning. (2) Burrowing organisms sensitively respond to the conditions in their habitat and, in many instances, bioturbational structures represent better indicators of the environmental conditions than body fossils (e.g., Hertweck, 1972; Goldring, 1995). (3) Trace fossils and ichnofabrics are in situ ethologic structures and provide valuable insights into the ecology of benthic communities and dynamics of sedimentary systems. (4) Ichnofacies have a significant bearing on regional-scale studies.

Of course, there are various ways to utilize the ichnological inventory of sediments for environmental interpretation: **‘Key’ trace fossils** characterize specific habitat conditions, e.g., *Chondrites* occurs in dark, organic-rich deposits indicating anoxic pore waters and possibly lowered oxygenation of the bottom water (e.g., Bromley and Ekdale, 1984). **Trace fossil suites** represent a typical association within a defined ecologic context, such as colonization of event beds (e.g., Bromley, 1996) or surfaces of sequence stratigraphic relevance (e.g., Pemberton and MacEachern, 1995). **Ichnofacies** are recurring general assemblages that characterize a habitat in a general sense (Seilacher, 1967). The original five ichnofacies of Seilacher (1967) were later supplemented with more than ten additional ones (Buatois and Mángano, 2011; MacEachern et al., 2012), including ichnofacies for continental settings.

The content of trace fossils, their size, abundance, and penetration depth have high environmental meaning; for instance, when conditions deteriorate. In such a case, there is a trend to telescoping of tiers, decreasing of burrow size, penetration depth, degree of bioturbation, and an order of disappearance of ichnogenera. To integrate all these features, Bromley and Ekdale (1986) coined the term “ichnofabric” that comprises all aspects of the texture and internal structure of a sediment that result from bioturbation at all scales.

The field of ichnology is continuously evolving in so far as oceanographic, sedimentological, geochemical and microbial findings, to name a few, are integrated and evolving analytical techniques are applied to better understand the lively interface between biosphere, lithosphere, hydrosphere and/or atmosphere. Therefore, besides pure ichnological meetings held under the auspices of the International Ichnological Association (<https://www.ichnologicalassociation.org>), ichnological sessions have become a common part of sedimentologic congresses.

A session entitled “Ichnology, trace fossils, and depositional environments” was held at the 34th IAS Meeting of Sedimentology in Rome in 2019. It was intended to show new developments in ichnologic research and to illustrate the use of bioturbational structures in environmental analysis. A total of 11 oral contributions and 25 posters presented new findings and ideas at the interface between sedimentology and ichnology focusing on both investigations in the Recent and in the rock record and addressed (palaeo)biological, sedimentological, and geochemical aspects in addition. A subset of those presentations form the 16 contributions in this Special Issue of *Palaeogeography, Palaeoclimatology, Palaeoecology*, which cover depositional settings ranging from continental to abyssal and sediments Cambrian to Modern in age, showing various facets of ichnology. The present special issue is a “virtual issue” that is assembled from papers published in regular issues. This preface serves to show the overall structure of this collection of papers by introducing these contributions arranged by depositional environment from continental to deep-marine settings.

2. Continental environments

2.1. Water-level fluctuations in meandering-river floodplain deposits recorded by trace fossils

The advantages of an integrated ichnological-sedimentological approach are convincingly illustrated by a case study addressing Oligocene meandering-river deposits in the Swiss Molasse Basin (Lower Freshwater Molasse; Buatois et al., 2020, this volume). These deposits are excellently exposed and their sedimentary facies are well understood (e.g., Platt and Keller, 1992), but trace fossils provide additional information about the depositional environments and their short-term change after flooding events, in particular ‘flooded’ floodplain (= temporary pond), wet soil, desiccating conditions, and finally pedogenic overprint and caliche formation. Furthermore, root traces record the previously dense vegetation cover whereas other plant remains are rarely, if ever preserved due to the rather efficient oxidation of the floodplain deposits.

Depending on the (ground)water level, the meandering-river environments are characterized by trace-fossil suites belonging to the (1) *Mermia* ichnofacies (temporary pond situation; *Cochlichnus-Helminthoidichnites* suite), (2) *Scoyenia* ichnofacies (shallow groundwater level; *Taenidium* suite, including small root traces), and (3) *Camborygma* ichnofacies (*Camborygma* suite including large root traces; deep groundwater level). Composite ichnofabrics are common in these meandering river deposits and they document a colonization sequence in the given order by their cross-cutting relationships and record progressive lowering of the water table in overbank subenvironments that was rapid relative to sediment aggradation. In contrast, the

meander-belt sandstone is apparently not bioturbated and matches a statement of [Seilacher \(1963\)](#) about the low ichnodiversity in such freshwater deposits. Evidently, the degree of bioturbation increases away from the channel as it can be expected for decreasing energy and sedimentation rate and hence, more stable conditions. Frequency of depositional events was a first-order control on degree of bioturbation. Position of the water table and degree of substrate consolidation exerted considerable influence over the types of trace fossil assemblages produced.

3. Marginal-marine environments

3.1. Sea-level-modulated preservation of rhizoliths in an alluvial-marine transitional setting

In the past two decades, continental ichnology has experienced a significant growth as “ichnology moves out of the water” ([Genise et al., 2004](#); [Bromley et al., 2007](#)) with the application of continental ichnology to a variety of topics, including, among others, the definition of new archetypal ichnofacies, evaluation of evolutionary trends, application of trace fossils in the analysis of continental sedimentary environments, and the study of traces in soils and palaeosols ([Buatois and Mángano, 2011](#); [Genise, 2017](#)). Within this context, rhizoliths (plant root traces) provide relevant environmental information for the study of past terrestrial deposits.

Rhizoliths occurring in conglomerate and coarse sandstone deposits from the Lower Pliocene sedimentary infill of the intermontane Sorbas Basin (Almería, SE Spain) represent casts. Their infill consists of detrital grains, mobilized by downward percolating flows, arranged in concentric laminae showing differential cementation by micritic carbonate cement and variation in average grain size ([Esperante et al., 2021](#), this volume). The rhizoliths occur at the contact between alluvial and marine facies, the upper two of three conformable units arranged in a retrogradational stacking pattern, showing a direct relationship with sea-level dynamics. The contact is interpreted as a surface of subaerial exposure overlain by a marine flooding surface. This depositional context favoured the preservation of rhizoliths in such dynamic environment as an alluvial fan setting, where sediment mobility and high discharge events adversely impact growth of plants and preservation of their root traces.

This case study illustrates the stratigraphic value of root traces in sedimentary basin research as markers of composite discontinuity surfaces, and contributes to the understanding of sedimentation along the inner margin of a Mediterranean intermontane basin (Sorbas Basin) in the interval of deposition subsequent to the Messinian Salinity Crisis.

3.2. Plant and animal bioturbational structures in a quiescent bay or lagoonal setting

Animal trace fossils like tracks, trails, burrows and borings and plant trace fossils like rhizoliths are widely used in sedimentologic and palaeoecologic analyses ([Bromley, 1996](#); [MacEachern et al., 2012](#)). Rhizoliths are commonly present in palaeosols or aeolianites in terrestrial environments (e.g., [Retallack, 2001](#); [Gregory et al., 2006](#); [Kraus and Hasiotis, 2006](#)). Only a few investigations deal with rhizoliths in marginal-marine environments. The presence of both rhizoliths and animal traces, especially in a marginal-marine setting, can certainly result in confusion and derivative misinterpretations because of the morphological similarities between rhizoliths and animal burrows.

An integrative ichnological and sedimentologic study including body fossil data addresses the origin of the biogenic sedimentary structures in upper Middle Eocene strata of Wadi El-Hitan (UNESCO universal heritage area) in Egypt ([Abdel-Fattah and Gingras, 2020](#), this volume).

Three types of rhizoliths are recognized, which can be differentiated from animal-associated biogenic sedimentary structures on the basis of branching, size, orientation and internal structure. In addition, six common marine ichnogenera (*Ophiomorpha*, *Skolithos*, *Thalassinoides*, *Palaeophycus*, *Teichichnus* and *Taenidium*) have been found to co-occur. Facies characteristics, fossil content, rhizoliths and invertebrate trace-fossil suites reflect normal-marine to mildly brackish salinities associated with a quiescent bay margin or lagoon. Particularly, comparison between modern mangrove environments with the examined biogenic sedimentary structures supports the marginal marine mangrove-swamp origin.

3.3. Marine reptile traces recording earliest evidence of synchronous style of swimming

Marginal-marine deposits from the Triassic show frequently the intercalation of marine and terrestrially influenced deposits. The former mostly contain bones of marine reptiles, whereas the latter often exhibit footprints of terrestrial tetrapods. This, for example, is demonstrated for the Vossenveld Formation (Lower Muschelkalk Anisian) of Winterswijk, The Netherlands (Demathieu and Oosterink, 1983). Footprints of marine and semi-aquatic reptiles are rarely preserved due to their formation under shallow-water conditions with low preservation potential.

The Guanling Formation (Middle Triassic, Anisian-Ladinian) in southwestern China contains assemblages with abundant trackways, documenting subaqueous activities of swimming and bottom-walking marine diapsids. From the site near Anshun, Guizhou Province, Xing et al. (2020, this volume) describe two new ichnotaxa, *Dikoposichnus luopingensis* and *Anshunpes aquacursor* that suggest the co-occurrence of nothosaurian sauropterygians, placodonts and/or saurosphargids foraging in shallow-marine habitats that possibly were lagoons along the coast of the eastern Tethys. The new ichnotaxon *Anshunpes aquacursor* appears to be the first ichnological documentation of the swimming and “punting” movement of marine diapsid placodonts and/or saurosphargids, supporting the supposed lifestyle of these animals foraging in shallow, near-coast habitats of the Tethys Ocean.

3.4. Molting in Palaeozoic marginal-marine environments

Molting traces, so-called ecdysichnia (Vallon et al., 2015), of extinct, non-trilobite euarthropods were found in a very special environmental context (Mángano et al., 2021a, this volume); when they tried to get rid of their rigid cuticles and they searched for a substrate that provided some friction/rigidity suitable to strip off the hard body parts.

The euarthropods molted along consolidated mud covered by a thin, shifting sand veneer because when molted they are unprotected and represent an easy prey and therefore, attempt to hide within the sediment. The euarthropod molting traces are rather similar to the trilobite resting trace *Rusophycus*, but clearly differ from it in having a prominent median ridge (positive-hyporelief preservation) instead of an axial furrow because these euarthropods removed their hard body parts while scratching in supine position over the consolidated mud. These observations form the base to establish the new ichnogenus *Luancaia* (now *Luancaina*; Mángano et al., 2021b).

Noteworthy, the *Luancaina* producers preferred marginal-marine settings for their molting activities and evidently, they could tolerate severe salinity fluctuations. The preservation of these traces documents stressed environmental conditions because subsequent burrowers did not overprint them, as it would be expected in a full marine environment. Today, settings affected by strong salinity fluctuations and/or salinities lower than polyhaline (see below) experience low bioturbation. This case study nicely demonstrates that besides the introduction

of a new ichnogenus for molting, non-trilobite euarthropods, these trace fossils have a distinct ecologic meaning and helps to better understand the complexities of some marginal-marine settings, providing a more accurate environmental interpretation.

3.5. Bioturbation-enhanced heavy-mineral enrichment in estuarine point-bar deposits

Burrowing organisms record the environmental conditions within their habitat but in turn they change it by burrowing and irrigating the deposits, mixing and/or feeding the sediment, producing lined tubes or affecting the surface roughness and hence, the surface hydraulic properties (e.g., Santos et al., 2012).

For the Upper Cretaceous McMurray Oil Sands, Fustic et al. (2021, this volume) demonstrate that the change of the sediment surface properties by burrowing organisms led to the passive enrichment of heavy minerals, in particular zircons in open tubes produced in Inclined Heterolithic Strata (IHS; e.g., Hubbard et al., 2011). These zircon-rich deposits have several implications. With respect to exploration, they cause a high peak in gamma-ray logs that can easily be misinterpreted to represent a clay-rich bed having seal properties; only when applying spectral gamma-ray tools it becomes evident that the high gamma-ray peak is caused by uranium and thorium rather than potassium. Also other heavy minerals can become enriched due to bioturbation in IHS or even point bar deposits and hence, may form potential placer deposits (e.g., Miller and Orbock Miller, 2007). From the 'academic' point of view, the enrichment of zircons provides large grain populations suitable for age dating and provenance studies. With respect to the latter aspect, Fustic et al. (2021) nicely show that basement areas exhibiting prominent Appalachian (~400 Ma) and Grenville (~1100 Ma) orogeny and subordinately "Canadian Shield" signals acted as source areas of the studied deposits. The trace fossils encountered document that these HIS formed within the fluvial-marine transition zone (FMTZ) under estuarine conditions and thus, allow a rather distinct environmental interpretation of such deposits (e.g., Gingras et al., 2012).

3.6. Salinity and sedimentation dynamics in estuarine settings based on *Siphonichnus*

The fluvial-marine transition zone (FMTZ) represents a challenging habitat for organisms due to the environmental conditions that considerably vary in space and time such as extent of salt water intrusion, salinity, water turbidity, sedimentation rate, etc. Observations in modern settings for that the environmental conditions are fairly well known are of great use to refine the interpretations of the sediment record by using trace fossils (e.g., Dashtgard and La Croix, 2015; Wetzel et al., 2017). With respect to these aspects, the trace fossil *Siphonichnus* appears quite suitable as outlined by Wetzel and Unverricht (2020, this volume). *Siphonichnus* is produced by bivalves and represents an equilibrium as the producers respond by up- or downward movements to deposition or erosion, respectively (e.g., Zonneveld and Gingras, 2013; Knaust, 2015).

Siphonichnus occurs in rather high abundance in Holocene deposits filling the valley incised by the Red River into the Gulf of Tonkin during glacial times when the sea level was lowered. In particular, *Siphonichnus* is present in high abundance in polyhaline deposits (> 20 PSU [Practical Salinity Units]) that accumulated below the marine transgressive surface; above the latter, typically marine mollusc shells are present. Nonetheless, in the studied case, *Siphonichnus* occurs in marine deposits, but rarely. In lower-polyhaline deposits, *Siphonichnus* is rather small (< 1 cm burrow width), whereas in upper-polyhaline deposits it reaches >3 cm width. Some of the large *Siphonichnus* show vertical movements of up to 1 m up- and/or downward. The upper-polyhaline deposits are completely bioturbated and therefore, the extraordinary vertical extent of *Siphonichnus* specimens' are the only record of erosional or

depositional events of more than half a meter. Consequently, *Siphonichnus* size appears to be related to salinity and associated environmental factors (small – relatively low salinity, large – relatively high salinity) and erosion and deposition caused by (extraordinary) flood/discharge events and waning floods, respectively, which are recorded by vertical movements of the producing bivalves.

3.7. Relationships of bioturbation style to event beds and sedimentation rates in deltaic environments

Bioturbation of deltaic sediment is primarily a function of sediment accumulation rate, event frequency, substrate consistency, salinity variation, food availability, and oxygenation of the sea-floor and shallow subsurface (e.g., [Wheatcroft et al., 2007](#); [Bann et al., 2008](#); [Gingras et al., 2011](#)). Based on several North American deltaic systems, including modern and ancient examples, in which proximal accumulation in the delta and prodelta shelf clinofolds are particularly important, [Bhattacharya et al. \(2020, this volume\)](#) point out that the stratigraphic record consists of a series of event layers bounded by periods of slow or even zero deposition. The event beds are not of uniform thickness or character in space, and may be very discontinuous. When preserved, the intensity and type of burrowing represent a useful proxy to infer both the time span and the environmental conditions between and during events.

[Bhattacharya et al. \(2020\)](#) examine the nature and number of event beds preserved in heterolithic prodelta and delta-front strata in five proximal-accumulation-dominated (PAD) North American delta systems. Moreover, they explore the continuum between PAD, more distal deposits of mud belts and thicker subaqueous-delta clinofolds (SDC). The proximal portions of PAD and SDC systems typically show low degree of bioturbation that is dominated by simple vertical structures or ‘sediment-swimming’ structures, forming low-diversity suites that are typical of opportunistic exploitation by trophic generalists (r-selected behaviours). The bioturbation styles encountered in these deposits imply (1) high sedimentation rates, which preclude complete biogenic reworking, (2) high-frequency river floods and storm reworking, expressed by short colonization windows, (3) soupy substrates, likely reflecting formation of a prevailing fluid-mud lutocline, and (4) elevated turbidity near the sediment-water interface, which may cause further suppression of trace-making. All of the Cretaceous systems examined occur within thick muddy formations, which show a higher degree of bioturbation and higher trace-fossil diversities and hence, reflect lower sedimentation rates in more distal or deeper environments where river influence and physico-chemical stresses are lowered.

4. Shallow-marine environments

4.1. Bioerosion traces and palaeoenvironmental conditions in rocky shore settings

Rocky shores are commonly characterized by the *Entobia* subichnofacies of the *Trypanites* ichnofacies since the Jurassic ([Bromley and Asgaard, 1993a](#); [de Gibert et al., 2007](#)). [Łaska et al. \(2020, this volume\)](#), present a detailed bioerosion analysis of *Entobia* subichnofacies conducted on Pliocene shallow-marine deposits from the Agua Amarga Subbasin (Almería Province, SE Spain). An abundant and diverse bioerosion trace-fossil assemblage is typically present in a conglomerate and an overlying composite shell bed, both deposited in a shallow-marine setting. Borings in pebbles and cobbles of the conglomerate are produced mainly by bivalves (*Gastrochaenolites torpedo* and *G. lapidicus*), accompanied by the sponge boring *Entobia cateniformis* and the worm borings *Maeandropolydora? decipiens*, *M. cf. elegans*, *M. cf. high-energy*, nearshore marine setting at a rather low sedimentation rate. The composite shell bed contains both bioerosion and bioturbation structures. Borings in shells are dominated by *Entobia* (*E. cateniformis*, *E. geometrica*, *E. laquea*, *E. form A*) and subordinately by

Caulostrepsis, *Maeandropolydora* and (only in large *Ostrea* sp.) *Gastrochaenolites*. It represents the shallow shoreface environment with very low sedimentation to omission enabling colonization of the hard parts. The change from the conglomerate with bivalve borings to the overlying shell bed mainly with sponge borings records a deepening due to the transgression during the Pliocene.

4.2. Bioerosive structures on different substrates during a complex transgressive event

Bioerosion structures created by marine invertebrates are well-known to characterize shallow-water/coastal environments (Bromley and Asgaard, 1993a, 1993b; Taylor and Wilson, 2003). Bioerosion structures and their relationship with different types of substrate (corals, rockgrounds and shells) studied in coastal Miocene transgressive deposits (Alicante, southeastern Spain) reveal a multifaceted depositional and ecological scenario (Giannetti et al., 2020, this volume). Different ichnoassemblages related to the *Entobia* ichnofacies reveals variable exposure times and substrate conditions. Boring structures are mainly represented by *Gastrochaenolites*, *Entobia* and, more rarely, *Trypanites* and *Spirolites*? Different colonization patterns were identified, including truncated *Gastrochaenolites* and *Entobia* that are extensively developed on the Eocene rockground, small-sized *Entobia*, and superficial bioerosion on conglomerates and breccias, and *Gastrochaenolites hospitium* on corals.

The integration of ichnological, palaeoecological, and stratigraphic observations allow detecting and characterizing the different phases of the Miocene transgressive episode: (i) the initial phase corresponds to a long-term, slow transgression and the colonization of the Eocene rockground, the production of a wide planar surface, and the truncated *Gastrochaenolites-Entobia* assemblage, (ii) a second phase of limited duration documents a compartmentalization of the coastline into protected areas mainly colonized by oysters and more energetic ones where corals grew, and (iii) the final phase is characterized by a transgressive pulse leading to the establishment of a restricted inner platform followed by a slightly deeper sandy platform. During this phase, bioerosion of *Entobia* was limited to shells, while soft- and loose-ground burrows like *Ophiomorpha* were formed within the substrate.

4.3. Relationship of burrow size to tracemakers' population density, exemplified by *Bichordites*

Burrowing echinoids such *Echinocardium cordatum* producing the trace fossil *Bichordites* commonly occur in sandy deposits having a varying mud content. Based on long-term observations in modern sediments Buchanan (1966) found that at high population density the individual echinoids are smaller than at low population density. Seike et al. (2020, this volume) tested and verified this finding by studying a sediment layer that was homogenized 2011 by the Tohoku-Oki Mw 9.0 tsunami. Such an event layer represents an ideal situation to study the re-colonization by organisms with respect to size, abundance, faunal structure, penetration depth, etc. In the small study area (Funakoshi Bay, NE Japan), bioturbation by echinoids was so efficient that *Bichordites* burrows coin the actual sediment fabric. There is a clear linear relationship between population density of *Echinocardium cordatum* and size of *Bichordites* that decreases with increasing abundance due to the intraspecific competition for food within one habitat. A relation of burrow size and population density to organic matter content was not found. However, the applied geochemical measurements (TOC – total organic carbon, TN – total nitrogen) were not really appropriate to characterize benthic food (Seike et al., 2020).

A similar relationship between size and population density of *Echinocardium cordatum* was also found in the North Sea (Wieking and Kröncke, 2003; Kröncke, 2006). However, when comparing the size of *Echinocardium cordatum* in different habitats within the North Sea, larger echinoids were found to occur at sites characterized by high benthic-food quality whereas

smaller ones are present if benthic food quality is low. Food quality was evaluated from the content of phaeopigments and chlorophyll α in the sea urchins' gut (Wieking and Kröncke, 2003). Also the amount of mud was found to have a modulating effect as organic matter becomes enriched in the mud fraction due to its hydraulic equivalence. Furthermore, increasing mud content indicates net deposition and a “dilution” of the food of the surface-feeding *Echinocardium* by fine fraction including refractory organic matter.

At the first sight, the findings of Seike et al. (2020) and Kröncke (2006) appear to be contradictory, but in fact they are not. In *different* areas characterized by differing benthic food quality and quantity the echinoid faunas show different body size and population density structures, but within *one* habitat the population density is inversely related to trace (body) size (Buchanan, 1966; Kröncke, 2006; Seike et al., 2020). A similar relation was found for deep-sea sediments; in the South China Sea, in areas receiving high-quality benthic food large *Scolicia* (a trace fossil similar to *Bichordites* also produced by burrowing echinoids) are present, whereas in other areas where food quality is low *Scolicia* is small (Wetzel, 2008). In spite of these findings, further research is needed to differentiate the effects of grain size (mud content) from those of benthic food and to characterize the food source exploited by the various trace-fossil producing organisms.

4.4. Sedimentological and ichnological features of a hyperpycnite-dominated system

Hyperpycnal deposits (hyperpycnites) have been reported from different lacustrine and marine environments from coastal (mainly prodeltaic subenvironments), shallow-water to deep-water settings (Mulder et al., 2003; Steel et al., 2018). The ichnological characterization of hyperpycnites just started as there are only a few studies that show the variability of environmental context, but so far the absence of a unique ichnological pattern (Buatois et al., 2019).

In an outcrop and subsurface integrative sedimentological and ichnological analysis on a shallow-marine succession from the Upper Miocene of the Betic Cordillera (southern Spain), García-García et al. (2021, this volume) typified two types of sandbodies on the basis of their stratigraphic architecture, physical sedimentary structures, and ichnofacies in the fine-grained deposits embedding them. These deposits represent a sustained sandy, hyperpycnite-dominated system at the transition from a distal shallow-marine (prodelta) to offshore transition setting (below fair- and above storm-wave base). The lower sandstone body corresponds to channelized-lobate (cut-and-fill sequence) sandstones embedded into siltstones with dominant *Nereites* and *Phycosiphon* (*Nereites* ichnofacies). It is interpreted to have been deposited from distal hyperpycnites developed in an offshore setting. The upper sandstone body consists of lobate to channelized-top sandstones embedded into silty sands with dominant highly variable degree of bioturbation by *Taenidium* and *Schaubcylindrichnus* (depauperate *Cruziana* ichnofacies). It is interpreted to have formed by proximal marine sustained hyperpycnites in a prodelta setting. The studied succession is interpreted to represent the progradation of a sandy hyperpycnal system along a prodelta to starved offshore setting with high variability in grain-size, benthic food and oxygen content.

4.5. Modulation of shallow-marine benthic habitats and bioturbation by basin setting

The general configuration of marine basins and their morphology affects sediment delivery, ‘sediment caliper’, sedimentation rate, transfer processes of sediment and organic matter, as well as in combination with currents and circulation also oxygenation and in last consequence, the habitat of organisms. A case study addressing the Middle Jurassic Bardas Blancas Fm. in

the Neuquén Basin (Argentina) by Schwarz et al. (2021, this volume) provides an interesting example how basin setting affected sediment deposition and bioturbation.

The studied rift basin received large amounts of sand and also some fine-grained sediment (including organic material from rivers, directly or indirectly via fluvial-fertilized primary production) being transferred by storms and similar events to rather narrow depocenters being located not too far offshore. Due to sufficient benthic food availability the sediments there became completely bioturbated and hence, also show a rather uniform response in geophysical well logs. Similar deposits are known from the North Sea Central Graben (e.g., Gowland, 1996). In contrast, in other cases, the coastline is further away as, for example, in the Cretaceous epicontinental basin in central Europe that was surrounded by low-relief land, the amount of organic matter reaching the depocenters was rather low and the degree of bioturbation limited. Consequently, sediment transferred by storms to the depocenters exhibit primary sedimentary structures of, for instance, tempestites and may preserve *Paleodictyon* at the base of the event layers while the strata were only little bioturbated (Malekzadeh and Wetzel, 2020). *Paleodictyon* is otherwise well known to occur in deep-marine, often food restricted, turbiditic deposits (e.g., Uchman, 2003). As extreme, nearly unbioturbated, rapidly accumulated deposits in a Miocene back-arc setting have been described by Nara and Aikou (2016). These examples clearly show that the general context of a basin is essential to understand the relationships between sediment accumulation and bioturbation. Schwarz et al. (2021) provided an exciting case study for the importance of basin configuration and this enlightening investigation emphasized the role of ichnology in general environmental characterization and interpretation. When going in more detail, probably short-term environmental changes can be deciphered by analyzing the trace fossil suites and their size in such deposits.

5. Deep-ocean environments

5.1. Climatically induced changes in the ocean dynamics affected the deep-sea habitat

The Mediterranean Sea has been particularly sensitive to palaeoenvironmental changes because of its semi-enclosed nature, with limited connection with the Atlantic Ocean through the Strait of Gibraltar, and its location affected by northern and mid-latitudes as well as tropical climate systems. Particularly, during the Last Glacial Cycle (last ~130 kyr; Dansgaard et al., 1993), the Mediterranean Sea experienced rapid fluctuations in hydrographic conditions due to abrupt climatic changes in the Northern Hemisphere, which resulted from millennial-scale fluctuations, also affecting benthic habitat conditions. In the Alboran Basin (westernmost Mediterranean) in ODP Sites 976 and 977 deposits spanning the Last Glacial Cycle, a low/moderate diverse trace fossil assemblage consisting of common *Planolites*, *Chondrites* and *Thalassinoides*, and local *Scolicia* and *Zoophycos*, assigned to the *Zoophycos* ichnofacies exhibits long- and short-term cyclic fluctuations in ichnodiversity, degree of bioturbation, and size of trace fossils (Casanova-Arenillas et al., 2020, this volume). Correlation of the percentage of bioturbational sedimentary structures with other climate proxies, like alkenone sea-surface temperature records from that area and $\delta^{18}\text{O}$ profiles from Greenland shows a close relationship at both the long-term scale, over the Last Glacial Cycle, and the short-term, with fluctuations including the Heinrich Events, Younger Dryas and periods of organic-rich layer deposition.

Climatically induced changes and fluctuations in the ocean dynamics, which have a major incidence of the Western Mediterranean Deep Water, caused variations in environmental conditions such as oxygen and organic matter content on the deep-sea floor affecting the burrowing fauna.

5.2. Exploitation of nutrient-rich Palaeozoic event beds by *Dictyodora*

Dictyodora represents a trace fossil formed by deep-bulldozing organisms connected to the surface by a snorkeling siphon that produced a spreite having oblique to steeply inclined laminae while the whole burrow exhibits a meandering to spiral course. *Dictyodora* has stratigraphic significance as it occurs only in Palaeozoic deposits, mainly in deep-water event beds but also in prodelta sediments characterized by predominant episodic deposition. The newly studied, so far youngest *Dictyodora* specimens occur in Permian flysch together with *Arenicolites* and *Skolithos* (Zhang et al., 2020, this volume). These latter traces suggest some environmental similarities between the mentioned shallow- and deep-marine settings. The wall-like spreite of the Permian specimens as well as that of other specimens available to the authors (from the Carboniferous of Austria; see Seilacher, 2007, p. 82, 83) is enriched in fine-grained material compared to the host sediment and implies an active fill probably due to feeding and/or excreting activities via the siphon/snorkel (Zhang et al., 2020) as known for some modern organisms.

The occurrence of *Dictyodora* in shallow- as well deep-sea deposits and its association with *Arenicolites* and *Skolithos* implies (at least episodic) considerable deposition of nutritious material from suspension (e.g., Bromley, 1996) and explains the absence of graphoglyptids from such benthic-food rich settings. Relatively high sedimentation rate and frequency of depositional events probably favoured the preservation of organic matter and supported deposit- or surface-feeders following a complex nutritional strategy as expressed by the course of the *Dictyodora* producers, which may represent opportunistic, deep colonizers of an event bed (Zhang et al., 2020). The large size of the in terms of amplitude and wave length of the meandering Permian *Dictyodora* reaching in maximum 20 cm and 40 cm, respectively, could reflect the tendency to gigantism known for other animals before they disappeared from the fossil record.

5.3. Influence of variable benthic food availability in flysch on *Polykampton*

Polykampton consists of a central, mainly horizontal, slightly winding tunnel having rather narrow-spaced, petal-like lobes filled with fine-grained, organic-rich material on either side (Uchman et al., 2019). The studied specimens occur within a few tens of meters thick interval in Palaeogene muddy turbidites in the Lesser Caucasus (Georgia). *Polykampton* is interpreted as sequestrichnion; the producer collects organic-rich material on the sediment surface and stores it within the anoxic zone of the sediment to use it in times of low food availability (Wetzel and Uchman, 2016). The producer may directly use the stored material, but also indirectly after it has been processed by microbes as within the tunnel strongly reducing segments surrounded by organic-rich material and other ones alternate. Such an arrangement could be in favour of enhancing microbial activity when intermittently ventilated with oxygenated water as it has been described for some endobenthic animals in the Recent (e.g., Forster and Graf, 1992). Therefore, *Polykampton* documents a highly specialized behaviour indicating peculiar, probably long-term rather than annual, pronounced variations in food supply; otherwise *Polykampton* would be present more frequently because seasonal variations in primary productivity affect major parts of the world's oceans (e.g., Lutz et al., 2007). So far *Polykampton* was found only in Cretaceous and Cenozoic flysch deposits and it has been reported only rarely. Because of the striking similarities, Uchman et al. (2020, this volume) included the trace fossil *Dreginozoum* into *Polykampton*. *Dreginozoum* occurs in stratified event beds deposited in a regional depocenter within the Central European epicontinental basin during the late Cretaceous (Kappel, 2003). This example shows that further observations and studies are needed to decipher the environmental context of *Polykampton* within the *Nereites* ichnofacies in more detail.

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