



Ichnological analysis: A tool to characterize deep-marine processes and sediments

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ABSTRACT

The deep-marine environment is a complex setting in which numerous processes—settling of pelagic and hemipelagic particles in the water column, sediment gravity flows (downslope density currents; turbid flows), and bottom currents—determine sediment deposition, hence a variety of facies including pelagites/hemipelagites, contourites, turbidites and hyperpycnites. Characterization and differentiation among deep-sea facies is a challenge, and numerous features may be highlighted to this end: sedimentary structures, geochemical data, micropaleontological information, etc. Ichnological information has become a valuable, yet in some cases controversial, proxy, being in most of cases understudied. This paper gathers the existing ichnological information regarding the most frequent deep-sea facies—from those in which ichnological analyses are numerous and detailed (e.g. pelagites/hemipelagites and turbidites), to those for which ichnological information is lacking or imprecise (hyperpycnites and contourites). This review analyses palaeoenvironmental (i.e., ecological and depositional) conditions associated with deep-sea sedimentary processes, influence of these changes on the tracemaker community, and associated ichnological properties. A detailed characterization of trace fossil assemblages, ichnofabrics and ichnofacies is presented. Special attention is paid to variations in trace fossil features, approached through sedimentary facies models and the outcrop/core scale. Similarities and differences among deep-sea facies are underlined to facilitate differentiation. Pelagic/hemipelagic sediments are completely bioturbated, showing biodeformational structures and trace fossils, being characterized by composite ichnofabrics. The trace fossil assemblage of muddy pelagites and hemipelagites is mainly assigned to the *Zoophycos* ichnofacies, and locally to the distal expression of the *Cruziana* ichnofacies. Turbidites are colonized mostly from the top, determining an uppermost part that is entirely bioturbated, the spotty layer; below it lies the elite layer, characterized by deep-tier trace fossils. Turbidite beds pertain to two different groups of burrows, either “pre-depositional”, mainly graphoglyptids, or “post-depositional” traces. Turbidite deposits are mostly characterized by the *Nereites* ichnofacies, with differentiation of three ichnosubfacies according to the different parts of the turbiditic systems and the associated palaeoenvironmental conditions. There are no major differences in the trace fossil content of the hyperpycnite facies and the classical post-depositional turbidite, nor in the pelagic/hemipelagic sediments, except for a lower ichnodiversity in the hyperpycnites. Trace fossil assemblages of distal hyperpycnites are mainly assigned to the *Nereites* ichnofacies, while graphoglyptids are scarce or absent. Ichnological features vary within contourites, largely related to palaeoenvironmental conditions, depositional setting, and type of contourite. Ichnodiversity and abundance can be high, especially for mud-silty contourites. The ichnological features of mud-silty contourites are similar to those of the pelagic/hemipelagic sediments (the tiering structure probably being more complex in pelagic/hemipelagic) or to the upper part of the muddy turbidites (contourites probably being more continuously bioturbated). No single archetypal ichnofacies would characterize contourites, mainly assigned to the *Zoophycos* and *Cruziana* ichnofacies.

1. Introduction. The deep-sea environment

The deep-marine environment is a complex setting where sediment deposition depends on numerous processes (e.g., [Hüneke and Mulder,](#)

[2011](#); [Pickering and Hiscott, 2016](#)). Three main sedimentary processes in deep-water environments are 1) the settling of pelagic and hemipelagic particles in the water column, 2) sediment gravity flows (downslope density currents; turbid flows), and 3) bottom currents

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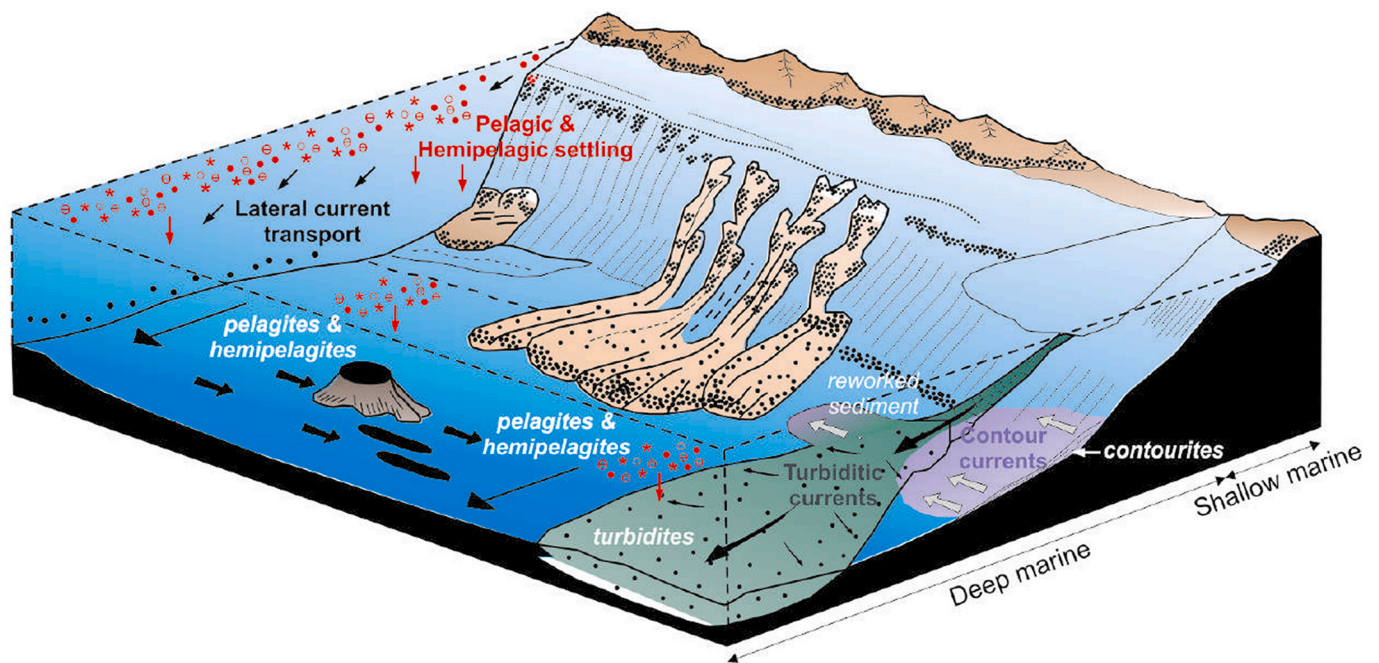


Fig. 1. Depositional processes and sediment distribution in the deep-sea. Simplified from Einsele (2000) and Rebesco et al. (2014).

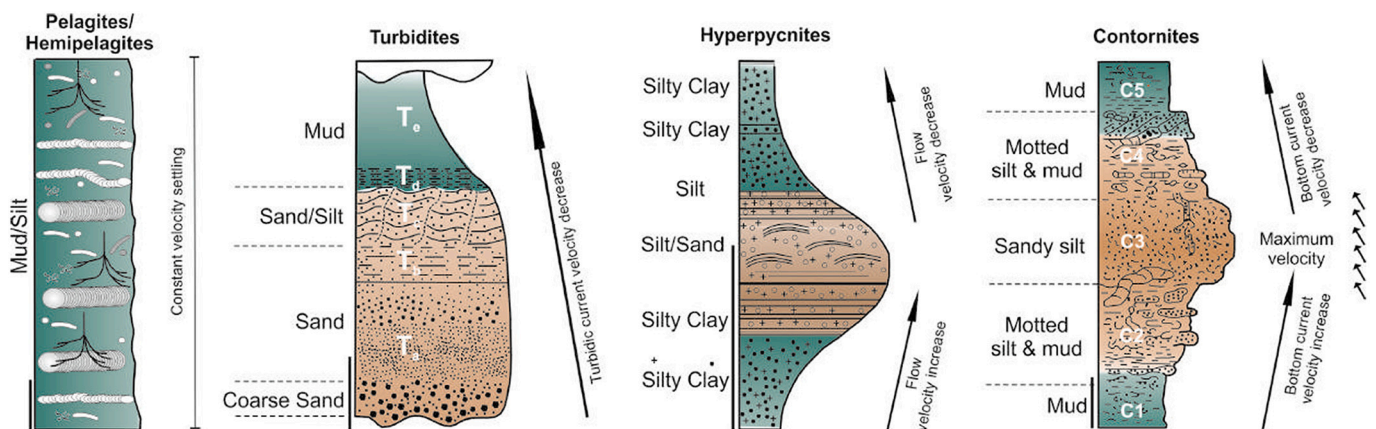


Fig. 2. Facies models for pelagites/hemipelagites, turbidites, hyperpycnites, and contourites with indication of current velocity. Based on Bouma (1962), Gonthier et al. (1984), Mulder et al. (2002), and Rebesco et al. (2014). Scale = 10 cm.

(mainly alongslope flow) (Hüneke and Mulder, 2011; Rebesco et al., 2014; Pickering and Hiscott, 2016; de Castro et al., 2020a, 2020b, 2021; Stow and Smillie, 2020; Fig. 1). There is significant scientific and economic interest in the distinction of deep-water facies owing to their impact on the formation of hydrocarbon reservoirs (Viana, 2008; Mutti and Carminatti, 2012; Mutti et al., 2014; Sansom, 2018; Fonesu et al., 2020; Fuhrmann et al., 2020), as well as their usefulness for palaeoclimatic and palaeoceanographic studies (Rebesco et al., 2014; de Castro et al., 2020b; Thiéblemont et al., 2020). Deep-water facies play an important role in slope stability and related geohazards (Laberg and Camerlenghi, 2008; Miramontes et al., 2018; Teixeira et al., 2019) and in the sustainability of deep-sea ecosystems (Hebbeln et al., 2016; Lozano et al., 2020).

End-member deposits in the deep-sea environment may arise from a single, predominant process, whereas more varied deposits can form due to the interaction of processes determining mixed/hybrid sedimentary facies. In the latter case, multiple features and deposits may be built by the interplay of bottom current entrainment and winnowing, turbidity current overspill, and continuous hemipelagic settling. Characteristic

facies models have been proposed for end-member deposits and mixed/hybrid facies over the years (i.e., Bouma, 1962; Faugères et al., 1984; Gonthier et al., 1984; Stow and Faugères, 2008; Mulder et al., 2002, 2008; Mutti, 2011; de Castro et al., 2020a, 2020b, 2021; Stow and Smillie, 2020; Fig. 2). Against this background, the differentiation and characterization of deep-marine sediments, based on valid diagnostic criteria, looms as a challenge.

Trace fossil analysis has emerged in 21st century as a powerful indicator of palaeoenvironmental evolution and associated changes. It now stands as a pivotal element supporting sedimentological and stratigraphic interpretations, thus a key in sedimentary basin research (Knaust and Bromley, 2012). The axis of ichnological studies resides in the relationship between trace fossils and palaeoenvironmental conditions. Tracemaker behaviour records the response to biotic and abiotic factors (e.g., salinity, oxygen, nutrients, hydrodynamic energy, rate of sedimentation, and substrate, among others; Mángano and Buatois, 2012). This is why ichnological analysis helps identify and characterize deep-sea sediments such as pelagic, gravitational, and bottom current deposits. Ichnological information is now included in many studies as a

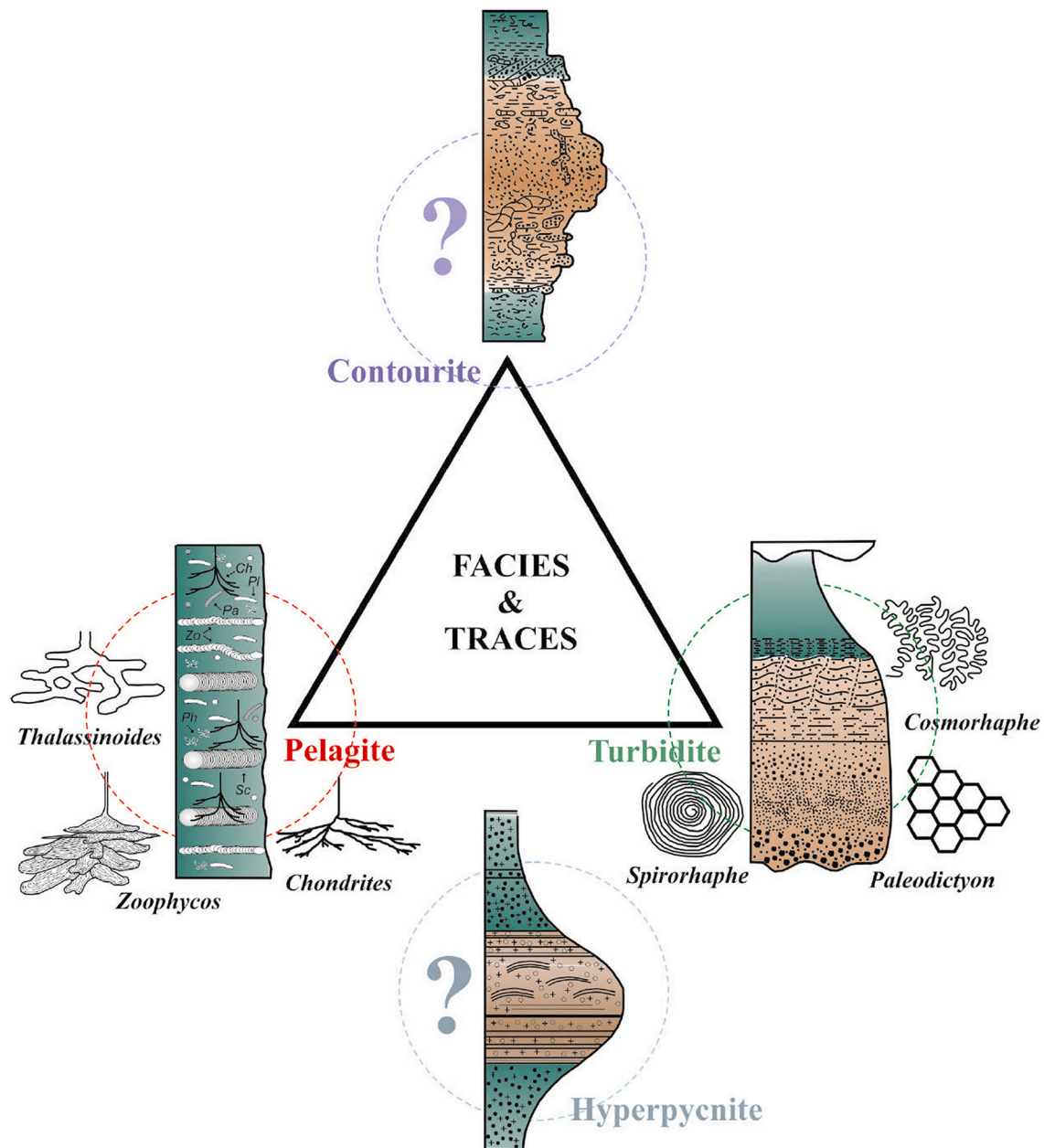


Fig. 3. Facies models and main trace fossils for deep-sea facies, reflecting the absence of characteristic trace fossils from contourites and hyperpycnites. Note: *Chondrites* (Ch), *Palaeophycus* (Pa), *Planolites* (Pl), *Phycosiphon* (Ph), *Scolicia* (Sc), and *Zoophycos* (Zo).

criterion to discern pelagites/hemipelagites, contourites, turbidites and hyperpycnites (e.g., Mulder et al., 2002; Ponce et al., 2007; Wetzel et al., 2008; Rodríguez-Tovar and Hernández-Molina, 2018; Buatois et al., 2019), confirming the variability of cases (Fig. 2). However, there are not reviews available in which detailed and recent ichnological information on all these deep-sea facies is compiled, being usually dispersed in the literature.

The aim of this paper is not to discuss deep-sea sedimentation in terms of processes and deposits, which might be a controversial endeavor. Rather, the focus is a review on the ichnological record of deep-sea sediments as a significant tool to improve characterization of deep-sea deposits and the processes involved, in view of ecological features and depositional conditions. Current understanding and usage of the ichnological approach in deep-sea sediment research is summarized, with an emphasis on hemipelagites/pelagites, turbidites, hyperpycnites, and contourites, indicating diagnostic features as well as limits

in its application. This review will be specially useful for those non-specialists in ichnology trying to use the ichnological record as a tool for deep-sea sedimentary basin research.

2. Bioturbation in hemipelagites/turbidites/hyperpycnites/contourites: Previous ideas

Distinguishing between hemipelagites, turbidites, hyperpycnites and contourites is no easy matter, and numerous criteria have been proposed for this purpose. Among the criteria, bioturbation and trace fossils are considered important attributes, or even diagnostic features, of particular deep-sea facies (Mulder et al., 2001, 2002, 2003; Wetzel et al., 2008; Stow and Smillie, 2020; Fig. 3). Because they reflect the behaviour of producers, trace fossils provide meaningful information on ecological and depositional parameters that affect the tracemaker community, in some cases determined by the sedimentary processes involved.

Table 1
Ichnological features in hemipelagites, turbidites, hyperpycnites, and contourites in papers comparing deep-sea facies.

	Hemipelagite	Turbidite		Hyperpycnite	Contourite	
		Muddy	Sandy		Muddy	Sandy
Mulder et al. (2002, 2003)		Absent to intense ¹ Few ²		Absent to intense ¹ Few ²	Thorough and intense ¹ Many ²	
Wetzel et al. (2008)	Continuous ¹ Dependent on organic matter flux (average) ³ Complete reworking normal ⁴		Post-depositional ¹ Normally low, dependent on local conditions ³ Complete reworking rare ⁴		Continuous, syn- and post-depositional ¹ Very high ³ Complete reworking normal ⁴	
Stow and Smillie (2020)	Pervasive, high-intensity and diverse under normal oxygenated conditions ¹ Complete bioturbational mottling is more common under slow rates of deposition ⁴ <i>Zoophycos</i> and <i>Nereites</i> ²		Top-down “ichnofacies”, reworking the upper parts of a bed while leaving the lower parts unaffected ¹		Pervasive, well-developed common throughout the beds ¹	Less than in fine-grained ¹
					<i>Glossifungites</i> ²	<i>Glossifungites</i> ²
			Distinctive “ichnofacies” for different turbidite settings ²			

Note: 1 (bioturbation), 2 (ichnofacies), 3 (bioturbation rate), 4 (degree of bioturbation). The term “ichnofacies” is not usually used in the usual ichnological sense.

Palaеоenvironmental conditions such as sedimentation rate, hydrodynamic energy, substrate consistency, bottom water oxygenation, salinity or food availability can be interpreted in light of the trace fossil assemblage (Ekdale et al., 1984; Buatois and Mángano, 2011; Knaust and Bromley, 2012). Thus, ichnological features serves to characterize deep-marine processes and sediments. However, only a few papers comparing deep-sea facies include ichnological information (Table 1).

Mulder et al. (2001) indicated that the hyperpycnal turbidite and the contourite can be differentiated according to the presence of bioturbation; the contourite sequence is bioturbated, the hyperpycnal turbidite is not. Later, Mulder et al. (2002) referred to the variability of ichnofacies (ichnotaxa?) among facies; contourite sequences are always bioturbated with various ichnofacies, whereas turbidite sequences might not be. Accordingly, Table 1 of Mulder et al. (2002), subsequently used in other papers (table 7 of Mulder et al., 2003), sets the criteria for a turbidite sequence (Bouma-like), hyperpycnal turbidite sequence (hyperpycnite) and contourite sequence, including data on bioturbation and ichnofacies. Similar criteria may characterize the turbidite sequence (Bouma-like) and the hyperpycnal turbidite sequence (hyperpycnite), having absent to abundant bioturbation structures and a few ichnofacies, while the contourite sequence shows thorough and abundant bioturbation structures and many ichnofacies (Mulder et al., 2002).

Wetzel et al. (2008) present a study of bioturbation focusing on contourites, comparing bioturbation in sandy turbidites and sandy contourites (Table 11.1 in Wetzel et al., 2008), as well as in hemipelagites, muddy turbidites and muddy contourites (Table 11.2 in Wetzel et al., 2008). In contourites, bioturbation is generally stronger. The rate of bioturbation (rate of burrow production) is moreover very high in sandy contourites when compared to turbidites, leading to complete or near-complete reworking of the sediment. Biodeformational structures are common, and the trace fossil assemblage is quite varied. Regarding muddy contourites, the authors indicated that as for their coarse-grained counterparts, there was not a definitive ichnofacies association and tiering structure, but there are certain distinctive characteristics. Bioturbation is strong and continuous, leading to complete reworking of the sediment, with a generally varied trace-fossil assemblage. The rate of

bioturbation is typically high, but can vary with fluctuations in sedimentation rate and the supply of organic matter. Periodically higher bottom-current velocities may lead to a silty or sandy horizon and/or to a non-deposition horizon, together with associated vertical and U-shaped burrows.

Shanmugam (2018a) offered a very general analysis of bioturbation and trace fossils in deep-water contourites, turbidites, and hyperpycnites, concluding that “the presence of ichnological signatures in the ancient sedimentary record is irrelevant for interpreting deep-water deposits as a product of a specific process.”

Stow and Smillie (2020) presented a review of the distinction between turbidites, contourites and hemipelagites, by analysing diverse features, including bioturbation, with some data on ichnotaxa and ichnofacies. However, since the ichnofacies concept was probably not applied in the usual ichnological sense (e.g., *Phycosiphon* or *Thalassinoides* ichnofacies), some data must be considered with caution. At the small scale (field, borehole and laboratory analysis): a) turbidites generally show intermittent episodes of bioturbation in between events, and burrows penetrate from the top of a turbidite bed downwards; b) contourites, especially finer-grained facies, show persistent and pervasive bioturbation structures, while sandy contourites show less bioturbation structures; and c) hemipelagites generally show pervasive, tiered and diverse trace fossils.

3. Ichnological record in pelagites and hemipelagites

Pelagic settling and hemipelagic deposition are the background depositional processes in the deep-sea environment. Pelagic settling refers to the vertical settling under the influence of gravity by which primary biogenic material and very fine-grained terrigenous or other detritus in the surface waters fall continuously and slowly (usually <1 cm/ka) to the seafloor (Stow and Smillie, 2020). Pelagic sediments commonly contain <25% terrigenous material in the fraction ≥5 μm, their median grain size being ≤5 μm, apart from authigenic minerals and skeletons of microfossils (Einsle, 2000). There are three types of pelagic sediments (Einsle, 2000): a) pelagic (silty) clays and claystones

Table 2
Main trace fossils and ichnofacies in deep-sea facies.

	Hemipelagite	Turbidite	Hyperpycnite	Contourite	
				Muddy	Sandy
Frequent ichnotaxa	<i>Asterosoma</i> , <i>Chondrites</i> , <i>Nereites</i> , <i>Palaeophycus</i> , <i>Phycosiphon</i> , <i>Planolites</i> , <i>Scolicia</i> , <i>Spirophyton</i> , <i>Taenidium</i> , <i>Teichichnus</i> , <i>Thalassinoides</i> , <i>Trichichnus</i> and <i>Zoophycos</i>	Post-depositional <i>Chondrites</i> , <i>Dictyodora</i> , <i>Nereites</i> , <i>Ophiomorpha</i> , <i>Palaeophycus</i> , <i>Phycosiphon</i> , <i>Planolites</i> , <i>Scolicia</i> , <i>Thalassinoides</i> , <i>Trichichnus</i> , and <i>Zoophycos</i> Pre-depositional graphoglyptids as <i>Cosmorhapha</i> , <i>Helminthorhapha</i> , <i>Lorenzina</i> , <i>Megagraption</i> , <i>Paleodictyon</i> , <i>Spirorhapha</i> , and non-graphoglyptids, e.g. <i>Spirophycus</i> , and <i>Scolicia</i>	<i>Chondrites</i> , <i>Diplocraterion</i> , <i>Gordia</i> , <i>Nereites</i> , <i>Ophiomorpha</i> , <i>Paradictyodora</i> , <i>Phycodes</i> , <i>Phycosiphon</i> , <i>Phymatoderma</i> , <i>Protovirgularia</i> , <i>Scolicia</i> , <i>Tasselia</i> , and <i>Zoophycos</i> Near absence of graphoglyptids	<i>Chondrites</i> , <i>Palaeophycus</i> , <i>Planolites</i> , <i>Thalassinoides</i> , and <i>Zoophycos</i> . <i>Phycosiphon</i> , <i>Scolicia</i> , and <i>Taenidium</i> . <i>Mycellia</i>	Clastic <i>Macaronichnus</i> , <i>Parahaentzschelina</i> , <i>Planolites</i> , <i>Scolicia</i> , <i>Thalassinoides</i> Calcareous <i>Gyrolithes</i> , <i>Palaeophycus</i> , <i>Planolites</i> , <i>Phycosiphon</i> , <i>Planolites</i> , <i>Scolicia</i> , <i>Taenidium</i> , <i>Teichichnus</i> , and <i>Thalassinoides</i>
Ichnofacies	<i>Zoophycos</i> ichnofacies (frequent) Distal <i>Cruziana</i> ichnofacies	<i>Nereites</i> ichnofacies: <i>Ophiomorpha rudis</i> , <i>Paleodictyon</i> , and <i>Nereites</i> ichnosubfacies	<i>Nereites</i> ichnofacies: <i>Ophiomorpha rudis</i> , and <i>Nereites</i> ichnosubfacies		<i>Zoophycos</i> ichnofacies, Distal-archetypal-proximal <i>Cruziana</i> ichnofacies, <i>Glossifungites</i> ichnofacies

containing $\leq 30\%$ CaCO_3 and biogenic SiO_2 (calcareous clays or siliceous clays and claystones); b) calcareous oozes, marls and marlstones, chalk and pelagic limestones ($\text{CaCO}_3 \geq 30\%$); and c) siliceous oozes, silicified claystones, porcellanite, diatomites, radiolarites, chert ($\text{SiO}_2 \geq 30\%$).

Hemipelagic deposition involves both vertical settling and slow lateral advection through the water column. The driving forces behind lateral advection include the inertia of river plumes (both within the water column and at the surface), glacial meltwater diffusion, turbid layer plumes, internal tides and waves, and other slowly moving mid-water currents (Stow and Smillie, 2020). Hemipelagic deposition is a continuous process, showing variable rates of deposition (2–20 cm/ka) depending on the nature of biogenic and terrigenous input (Stow and Smillie, 2020). Hemipelagic sediments (i.e., hemipelagites) are fine-grained sediments containing a large proportion of terrigenous silt and clay. At least 25% of their grain size fraction $\geq 5 \mu\text{m}$ is terrigenous and volcanogenic, or else derives from shallow-marine sediments (Einsele, 2000). There are three types of hemipelagic sediments (Einsele, 2000): a) terrigenous muds and mudstones (CaCO_3 content $\leq 30\%$); b) volcanogenic muds (predominantly volcanic ash, CaCO_3 content $\leq 30\%$); and c) calcareous muds and marlstones (CaCO_3 content $\geq 30\%$). A particular case of pelagic/hemipelagic sediments would be organic rich layers (i.e., black shales, sapropels, ORLs), containing relatively high amounts of organic matter. Hemipelagic and pelagic sediments are frequently redeposited and partially mixed with shallow-water material by gravity mass movements, and they may be winnowed and reworked by deep bottom currents (Einsele, 2000).

3.1. Ichnological signature of pelagic and hemipelagic sediments

Detailed ichnological analyses on pelagic and hemipelagic sediments have been conducted in the last decades, allowing for a precise ichnological characterization of these facies, mainly favoured by the integration of information from modern and ancient deep-sea sediments (e.g., Chamberlain and Clark, 1973; Ekdale, 1977, 1985; Wetzel, 1991, 2010; Savrda et al., 2001; see Wetzel and Uchman, 2012 for a review). As a rule, deep-sea sediments continuously accumulating in an oxygenated setting are completely bioturbated (Uchman and Wetzel, 2011 and references therein). In this case, two main types of bioturbational sedimentary structures can be differentiated: biodeformational structures, showing no distinct outline and not displaying a recurrent geometry that might permit their classification; and trace fossils, with sharp outlines and characteristic recurrent geometries allowing their ichnotaxonomical classification (Uchman and Wetzel, 2011; Wetzel and Uchman, 2012).

In general, trace fossil assemblages in pelagic and hemipelagic

sediments are abundant and diverse, the most frequent ichnotaxa being *Asterosoma*, *Chondrites*, *Nereites*, *Palaeophycus*, *Phycosiphon*, *Planolites*, *Scolicia*, *Spirophyton*, *Taenidium*, *Teichichnus*, *Thalassinoides*, *Trichichnus* and *Zoophycos* (Wetzel and Uchman, 2012; Table 2, Fig. 4).

3.2. Ichnofacies and trace fossil assemblage

A trace fossil assemblage of muddy pelagites and hemipelagites would be mainly assigned to the *Zoophycos* ichnofacies (Table 2, Fig. 12), which is typified by the ichnogenera *Zoophycos*, *Phycosiphon* and *Chondrites* (Wetzel and Uchman, 2012). The *Zoophycos* ichnofacies ideally is found in circalittoral to bathyal, quiet-water marine muds or muddy sands, below the storm wave base, particularly in shelfal to slope areas (MacEachern et al., 2007, 2012; Buatois and Mángano, 2011, Fig. 12). Settings are generally free of turbidity flows and subject to oxygen deficiencies. The trace fossil assemblage is characterized by: i) low diversity, though individual traces may be abundant; ii) grazing and feeding structures produced by deposit feeders; iii) shallow and deep tier structures; and iv) horizontal to gently inclined spreiten structures (MacEachern et al., 2007).

We cannot discard local assignment to the distal expression of the *Cruziana* ichnofacies as transitional between the archetypal *Cruziana* ichnofacies and the archetypal *Zoophycos* ichnofacies in a basinward direction (MacEachern et al., 2007; Table 2, Fig. 12). Distal expressions of the *Cruziana* ichnofacies are associated with muddy siltstone and silty mudstones, reflecting soft, cohesive substrates under persistently quiescent fully marine conditions (MacEachern et al., 2007). Trace fossil assemblages from both the distal expressions of the *Cruziana* ichnofacies and the *Zoophycos* ichnofacies are quite similar, with suites appearing impoverished in the latter (MacEachern et al., 2007).

3.3. Ichnofabrics

As indicated above, deep-sea pelagic and hemipelagic sediments continuously accumulating in an oxygenated setting are completely bioturbated, consisting of biodeformational structures and abundant and diverse trace fossils. In this case, hemipelagic and pelagic sediments are characterized by the so-called “composite ichnofabrics” (Ekdale and Bromley, 1983, 1991; Bromley and Ekdale, 1986), generated by the superimposition of different (successive) suites of biogenic structures (Ekdale et al., 2012). Two main types of composite ichnofabrics have been defined (Savrda, 2016): “autocomposite ichnofabrics” are those characterized by a single ichnocoenosis, and self-generated by a particular assemblage of tracemakers, whereas “heterocomposite ichnofabrics” comprise two or more different ichnocoenoses (Fig. 5).

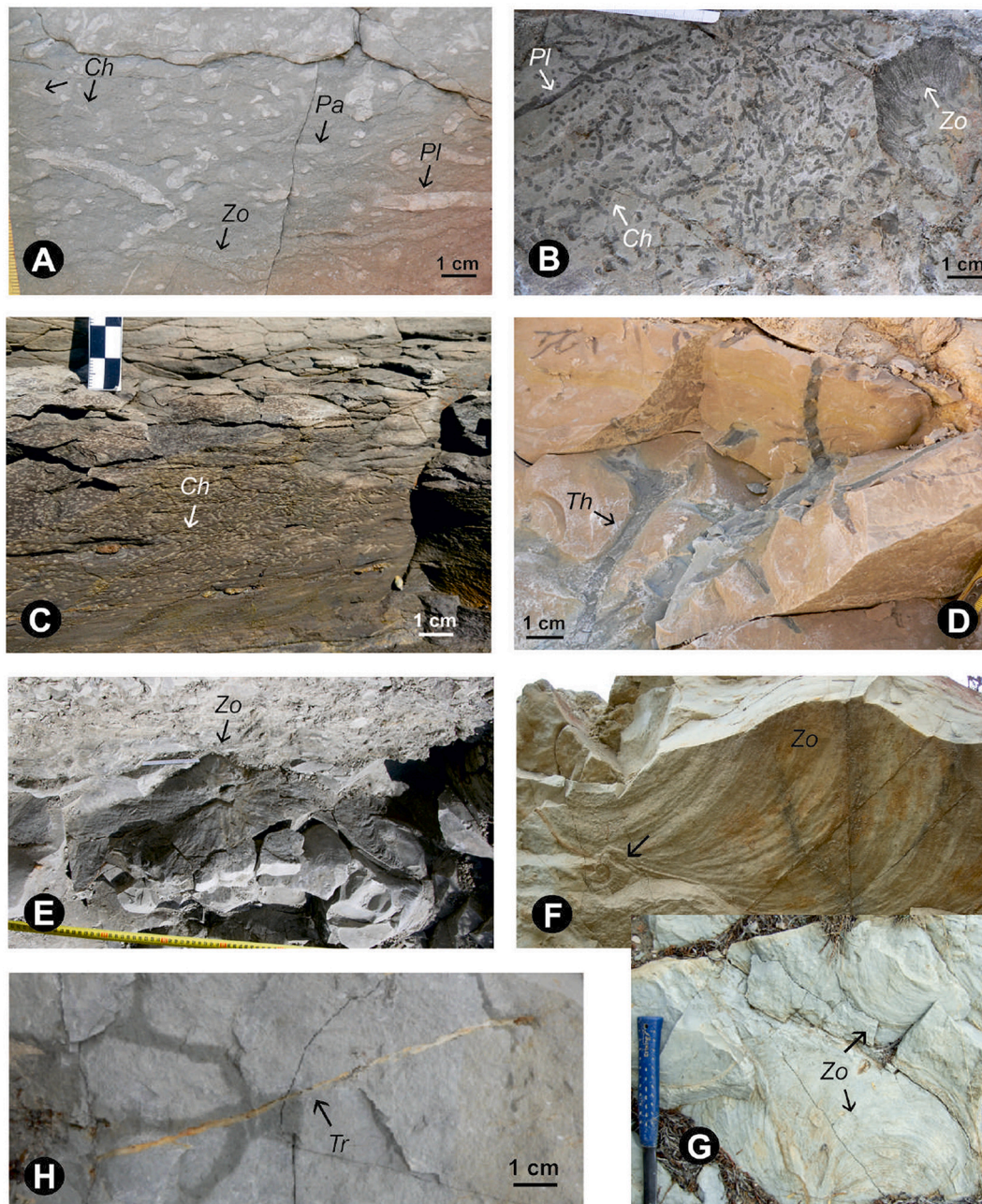


Fig. 4. Trace fossils from pelagites/hemipelagites. **A)** Composite ichnofabric showing *Chondrites* (*Ch*), *Palaeophycus* (*Pa*), *Planolites* (*Pl*), and *Zoophycos* (*Zo*) (Cretaceous/Palaeogene transition at Bidart, Spain). **B)** *Chondrites* (*Ch*), *Planolites* (*Pl*), and *Zoophycos* (*Zo*) (Cretaceous/Paleogene transition at Caravaca, Spain). **C)** *Chondrites* (*Ch*) in organic matter rich sediments (Toarcian at the Lastres section, Spain). **D)** *Thalassinoides* (*Th*) (Cretaceous/Palaeogene transition at Bidart, Spain). **E)** *Zoophycos* (*Zo*) (Cretaceous/Paleogene transition at Caravaca, Spain). **F, G)** *Zoophycos* (*Zo*) (Hauterivian at Río Argos section, Spain). Note ammonites (black arrow). **H)** *Trichichnus* (*Tr*) (Hauterivian, Río Argos section, Spain).

Characterization of autocomposite ichnofabrics can prove complicated, especially when the color and composition of the host sediment is similar to that of the trace fossil infill, impeding a clear differentiation. In this case, to improve the visibility of ichnological features and hence the characterization of composite ichnofabrics, the use of image processing techniques is especially useful, as recently shown for deep-sea pelagic calcilitites from the Petra Tou Romiou section in Cyprus (Miguez-Salas and Rodríguez-Tovar, 2019a; Miguez-Salas et al., 2019; Rodríguez-Tovar et al., 2020) (Fig. 5).

3.4. Environmental conditions and benthic habitat during pelagic/hemipelagic settling

The main palaeoecological factors affecting burrowing communities of pelagic and hemipelagic settings are organic-matter supply, sedimentation rate and oxygenation interrelating in a variable manner, depending on the particular case. The burial velocity of organic-matter generally depends on the sedimentation rate, influencing the exposure time of organic matter to oxygen, and then affecting the oxygenation in bottom and pore waters. An illustrative schematic representation by Wetzel (2010) reflects the variable implications of seasonal organic matter deposition, resulting in oxygenation within the sediment, effects

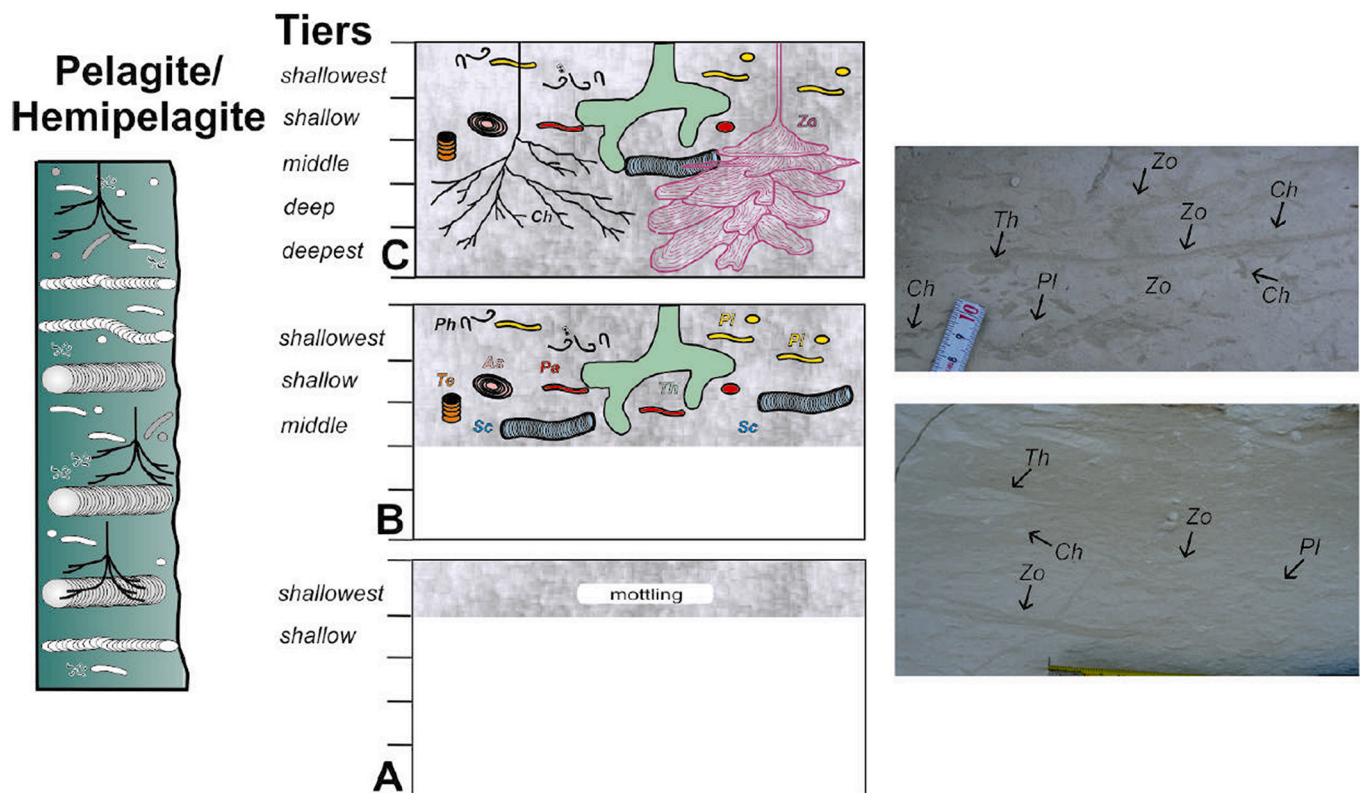


Fig. 5. Tiering evolution from A to C, showing frequent differentiated traces during deposition of pelagic/hemipelagic sediments. Images for composite ichnofabric showing cross-cutting relationships. Note: *Asterosoma* (As), *Chondrites* (Ch), *Palaeophycus* (Pa), *Planolites* (Pl), *Phycosiphon* (Ph), *Teichichnus* (Te), *Thalassinoides* (Th), *Scolicia* (Sc), and *Zoophycos* (Zo).

on the redox boundary, and a possible influence on the *Nereites* producers. On this basis, a more detailed response on the part of burrowing organisms in deep-marine hemipelagic settings to changing environmental factors—including bottom and pore water oxygenation, sedimentation rate, and organic-carbon (C_{org}) content within sediment—is presented, in relation to burrow diameter, numbers and position of tiers and tentative ichnofabric, and including ichnotaxa such as *Chondrites*, *Planolites*, *Scolicia*, *Teichichnus*, *Thalassinoides*, and *Zoophycos* (Uchman and Wetzel, 2011; Wetzel and Uchman, 2012). In short, the sedimentation rate controls the burial of organic matter, and then vertical extension and composition of tiers. Under an increasing sedimentation rate, the vertical extension of tiers may increase, and deeply penetrating burrows may be dominant in deep tiers; whereas in the case of reduced sediment input, the penetration depth tends to decrease. When sediment input is drastically reduced, little organic matter is buried and the substrate tends to stiffen, as indicated by ichnological features (Uchman and Wetzel, 2011; Wetzel and Uchman, 2012; Uchman et al., 2013). As stated by these authors, the relationship between organic-matter content and sedimentation rate cannot be clearly distinguished and directly evaluated. Nonetheless, very high availability of benthic food under well-oxygenated conditions would determine a bioturbated texture characterized by biodeformational structures usually >2 cm in diameter and the absence of well-preserved (discrete) burrows (Uchman and Wetzel, 2011; Wetzel and Uchman, 2012). Fluctuations in food supply among pelagites and hemipelagites have been interpreted based on the ichnological features of particular ichnotaxa such as *Nereites* (Wetzel, 2010), *Scolicia* (Kröncke, 2006; Wetzel, 2008; Wetzel and Uchman, 2018) or *Zoophycos* (Dorador et al., 2016 and references therein). With respect to oxygenation, a clear relationship has been described between ichnological features and the oxygen content of bottom/pore waters (see Rodríguez-Tovar, 2021 for a recent review). Four redox facies—oxic (8–2 mL/L), dysoxic (2–0.2 mL/L), suboxic (0.2–>0 mL/L), and anoxic

(0 mL/L)—correspond to the biofacies terms aerobic, dysaerobic, quasi-anaerobic and anaerobic, respectively (Tyson and Pearson, 1991). The lower limit of dysoxic and dysaerobic at 0.2 mL/L marks the end of bioturbation (Tyson and Pearson, 1991). These authors also indicated that the exaerobic biofacies, consisting of laminated strata but containing in situ epibenthic macroinvertebrate body fossils, yet without bioturbation (Savrda and Bottjer, 1987, 1991), may in part correspond to the quasi-anaerobic biofacies, but probably does not form part of the normal sequence in most shelf settings. In the model proposed by Savrda and Bottjer (1986, 1987, 1989, 1991) for pelagic and hemipelagic sediments unaffected by sediment gravity flows, a decrease in oxygenation from the aerobic to anaerobic facies is reflected in the ichnological features by decreasing ichnodiversity, density, burrow size, burrowing depth, and complexity of tiering structures.

3.5. Final remarks

1. Dominant palaeoecological factors in pelagic and hemipelagic settings are organic-matter supply, sedimentation rate, and oxygenation, interrelating with and affecting the tracemaker community in a variable fashion.
2. As a rule, pelagic and hemipelagic sediments continuously accumulating in an oxygenated setting are completely bioturbated, showing biodeformational structures and trace fossils. Trace fossil assemblages in pelagic and hemipelagic sediments are abundant and diverse, the most frequent ichnotaxa being *Asterosoma*, *Chondrites*, *Nereites*, *Palaeophycus*, *Phycosiphon*, *Planolites*, *Scolicia*, *Spirophyton*, *Taenidium*, *Teichichnus*, *Thalassinoides*, *Trichichnus*, and *Zoophycos*.
3. The trace fossil assemblage of muddy pelagites and hemipelagites could be mainly assigned to the *Zoophycos* ichnofacies, although we cannot discard a local assignment to the distal expression of the *Cruziana* ichnofacies.

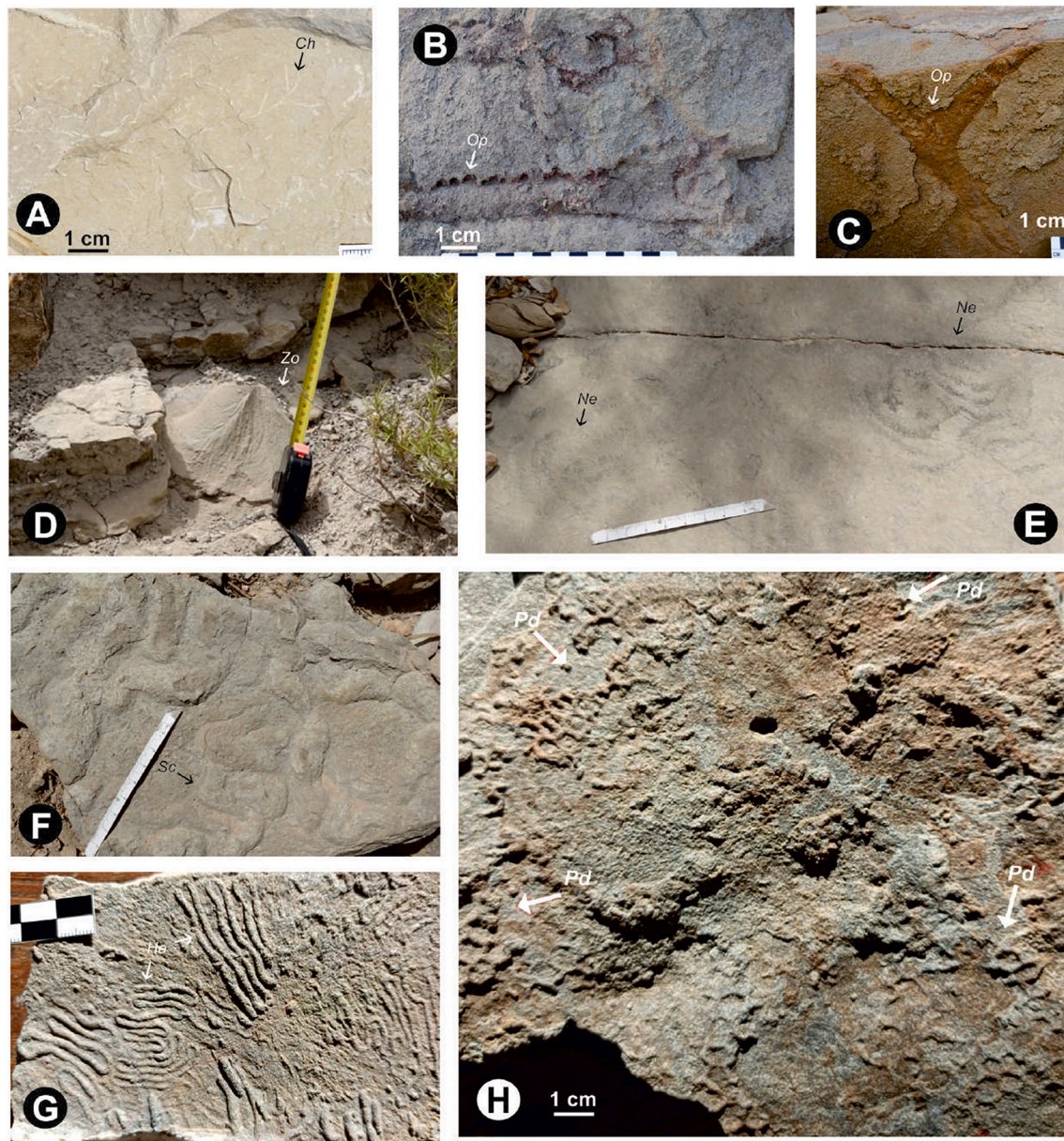


Fig. 6. Trace fossils from turbidites. Post-depositional: A) *Chondrites* (*Ch*) (lower Paleogene at Río Gor, Spain). B, C) *Ophiomorpha* (*Op*) (Miocene, Tabernas Basin, Spain). D) *Zoophycos* (*Zo*) (lower Paleogene at Río Gor, Spain). E) *Nereites* (*Ne*) (lower Paleogene at Río Gor, Spain). Pre-depositional: F) *Scolicia* (*Sc*) (lower Paleogene at Río Gor, Spain). H) Different forms of *Paleodictyon* (*Pd*) (Miocene, Tabernas Basin, Spain). G) *Helminthorhaphe* (*He*) (Miocene, Tabernas Basin, Spain).

4. Pelagic and hemipelagic sediments are characterized by composite ichnofabrics, generated by the superimposition of different (successive) suites of biogenic structures. The development of composite ichnofabrics may reveal the progressive upward migration of a single, tiered benthic community during continuous sediment accretion (autocomposite ichnofabrics), or the successive occupation of the sediment by multiple communities of organisms in response to autogenic or allogenic changes in environmental conditions within a depositional system (heterocomposite ichnofabrics).

4. Ichnological record in turbidites

Turbidites refers to deposits of turbidity currents (Sanders, 1965). This simple definition embraces, however, an important discussion from its beginning to the present insofar as the processes involved and the resulting products. A detailed revision can be found in the book by Pickering and Hiscott (2016), who analyze the relationship between

turbidity currents and other sediment gravity flows, variability within turbidity currents, and internal characteristics of turbidites. Their review presents different interpretations, underlining the importance of the topic and numerous contradictory matters (for general overviews see also Shanmugam, 2002, 2021). At the outcrop scale, the Bouma (1962) intervals are the most commonly applied model for a turbidite bed, even though Pickering and Hiscott (2016) reconsider the ideal Bouma sequence consisting of five divisions (T_a to T_e). Here data and information from ichnological analyses conducted on turbidites are presented without discussion about the conception of turbidites in the original ichnological papers.

4.1. Ichnological signature of turbidites

Ichnological analyses on turbidites are numerous, giving rise to a detailed characterization of ichnological properties in classical turbidites (Uchman, 1995, 1998, 1999, 2001; Heard and Pickering, 2008;

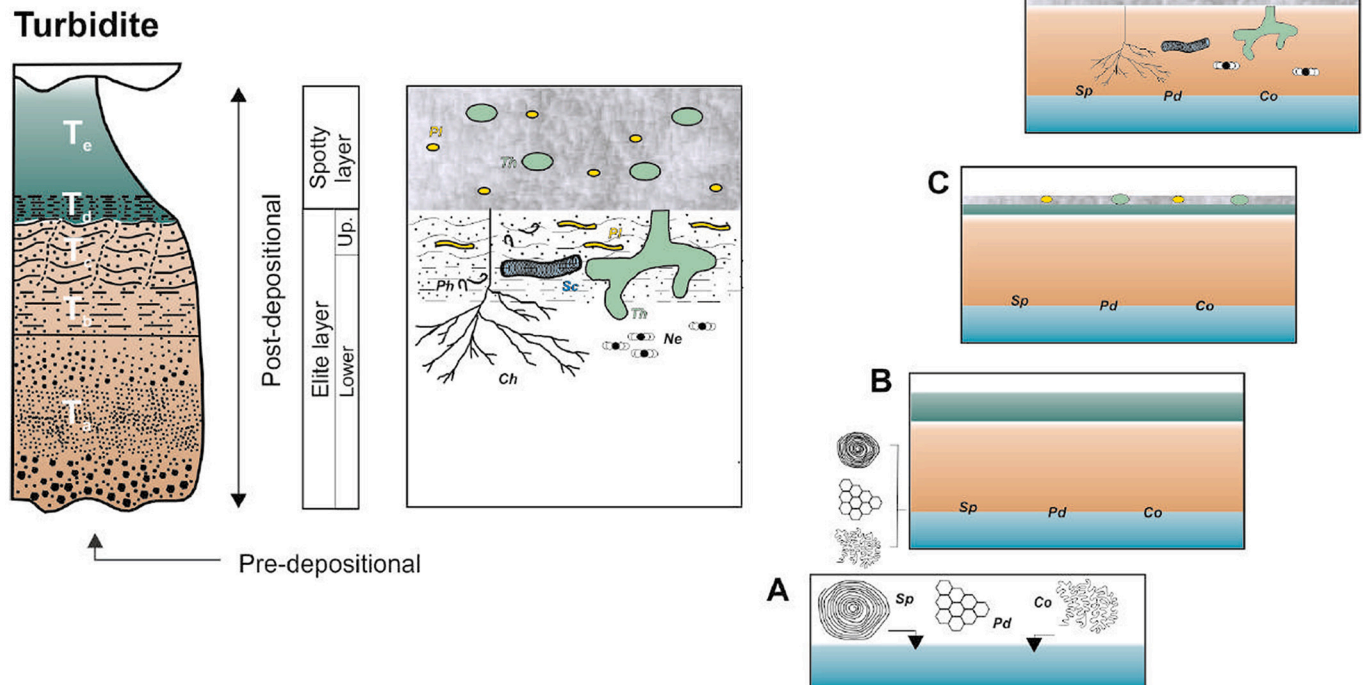


Fig. 7. Distribution of trace fossils (pre- and post-depositional) in a turbidite bed, with differentiation between the spotty and the elite (lower and upper) layers (based on Uchman, 1999). Evolution of bioturbation during deposition of turbiditic sediments: A) Pre-depositional traces on the seafloor of pelagic sediment, B) Deposition of turbidite sediments (pre-depositional traces on the sole of turbiditic bed), C) Post-depositional bioturbation on the upper part (spotty layer) of the turbiditic bed, and D) Post-depositional traces on the elite layer of the turbiditic bed. Note: *Chondrites* (Ch), *Cosmorhaphe* (Co), *Nereites* (Ne), *Palaeodictyon* (Pd), *Planolites* (Pl), *Phycosiphon* (Ph), *Thalassinoides* (Th), *Scolicia* (Sc), and *Spirorhaphe* (Sp).

Rodríguez-Tovar et al., 2010, 2016; Uchman and Wetzel, 2011, 2012; Heard et al., 2014). As a rule, two different groups of burrows are distinguished in light of turbidity currents and consequently turbidite beds, either “pre-depositional” or “post-depositional” (Książkiewicz, 1954; Seilacher, 1962; Leszczyński, 1993) (Table 2, Fig. 6). Pre-depositional burrows refer to those produced prior to the deposition of a turbidite, in the background sediment; not rarely, they consist of highly organized and often delicate burrows known as “graphoglyptids” (Fuchs, 1895), normally produced by shallow burrowing organisms, mostly mud dwellers. Post-depositional assemblages consist of deeply penetrating trace fossils, related to the colonization of previously deposited turbiditic sands-muds, including (Table 2): *Chondrites*, *Dicthyodora*, *Nereites*, *Palaeophycus*, *Phycosiphon*, *Planolites*, *Scolicia*, *Thalassinoides*, *Trichichnus*, and *Zoophycos* (Uchman and Wetzel, 2011).

Graphoglyptids are mainly preserved as semi-relief due to the scouring and casting of shallow burrow systems; they are common, but never abundant, on the soles of sandy turbidites (see Uchman and Wetzel, 2011, 2012 and references therein for discussion of graphoglyptids). Some frequent ichnogenera of pre-depositional burrows are graphoglyptids as *Cosmorhaphe*, *Helminthorhaphe*, *Lorenzina*, *Megagraption*, *Paleodictyon*, *Spirorhaphe*, and non-graphoglyptids as *Spirorhynchus* and *Scolicia* (Table 2).

4.2. Ichnofacies

Trace fossil assemblages from turbidite deposits are mostly assigned to the *Nereites* ichnofacies (Table 2, Fig. 12), which typically includes trace fossils forming diverse meanders, spirals and nets pertaining mostly to graphoglyptids. The *Nereites* ichnofacies is not uniform. Three ichnosubfacies have been established in view of different parts of the turbiditic systems and the associated palaeoenvironmental conditions (Table 2, Fig. 12). Thus, the *Ophiomorpha rudis* ichnosubfacies is linked

to thick-bedded sandstones in channels and proximal lobes (Uchman, 2001, 2009), the *Paleodictyon* ichnosubfacies to more sandy ‘normal’ flysch, and the *Nereites* ichnosubfacies to mud-rich distal flysch (Seilacher, 1974). The *Ophiomorpha rudis*–*Paleodictyon*–*Nereites* ichnosubfacies may express a bathymetric trend from inner to outer fan, and a nonbathymetric trend from channel axis, then levee, to overbank or inter-channel areas (Uchman and Wetzel, 2012).

4.3. Ichnofabrics

Turbidites are deposited very rapidly overall, but speed depends on the divisions. According to data included in Pickering and Hiscott (2016), the time it takes to deposit divisions T_a to T_c of a turbidite bed are in the range of minutes to hours, while the rest of divisions (T_d and T_e) require greater time, in the range of weeks/months or even longer (Uchman and Wetzel, 2011, 2012; Fig. 7). The very rapid deposition of divisions T_a to T_c impedes coetaneous bioturbation, which can occur during deposition of division T_e or the upper part of T_d . Thus, turbidites are colonized mostly from the top of the turbidite bed. Basically, two intervals can be discerned in the turbiditic bed, a spotty layer and an elite layer (see detailed descriptions in Uchman, 1999; Uchman and Wetzel, 2011, 2012; Fig. 7). The spotty layer is entirely bioturbated, occupying the uppermost part of a turbidite bed, commonly corresponding to the upper part of T_d and the entire T_e Bouma’s intervals (Uchman, 1999). The spotty layer usually has oval spots, corresponding to cross-sections of trace fossils —commonly *Planolites* and *Thalassinoides*— of a different color than the indistinctly mottled background, though other cases can be also noted (Uchman, 1999). Below the spotty layer, in a distinct (because of the lithological contrast) or gradational boundary (due to intense bioturbation) lies the elite layer (Uchman and Wetzel, 2011, 2012). Trace fossils in the elite layer are the most eye-catching, corresponding to deep-tier trace fossils (Uchman,

1999). In most marly turbidites, these deep-tier elite traces are *Chondrites*, *Planolites*, *Nereites*, *Phycosiphon*, and *Scolicia* (Uchman and Wetzel, 2011, 2012). Trace fossils from the elite layer overprint the totally or almost totally bioturbated background in the upper part (upper elite layer), and the background of primary sedimentary structures in the lower part (lower elite layer) (Uchman, 1999; Uchman and Wetzel, 2011, 2012). Some burrows penetrate below turbidites to form the so-called exichnial elite layer (Uchman, 1999). Wetzel and Uchman (2001) presented a model of sequential colonization in turbidites showing the distribution of trace fossils in the different turbidite divisions according to oxygenation and the amount of food in the turbiditic sediments (Uchman and Wetzel, 2011, 2012). In this model *Phycosiphon* and *Halopoa* were formed at an early stage in well-oxygenated sediments, then *Nereites* were produced by trace makers just above the newly formed redox boundary, and finally *Chondrites* formed in an oxygen-restricted environment of the new turbidite or even deeper levels into the sediment (Wetzel and Uchman, 2001).

4.4. Environmental conditions and benthic habitat during turbidity currents

Different environmental (ecological and depositional) conditions before and after turbidite currents determine tracemaker behaviour and ichnoassemblages. Trace fossils associated with turbidites mainly represent two population strategies: opportunistic (r-selected) and equilibrium (K-selected) (Ekdale, 1985). K-selected ichnotaxa are produced by animals adapted to a stable environment with low or moderate ecological stress. They usually reproduce slowly, showing high taxonomic diversity but relatively low abundance. Tracemakers of r-selected trace fossils, in turn, are adapted to instability and high environmental stress, having high-reproduction rates, rapid growth rates, broad environmental tolerances and generalized feeding habits, and showing low diversity (Uchman, 1999; Uchman and Wetzel, 2011; Pickering and Hiscott, 2016). The pre-depositional graphoglyptids are a typical example of K-selected forms. The specialized farming behaviour (agrichnia) of graphoglyptid producers, as well as the small size of the tunnel networks, can be mainly interpreted as adaptation to nutrient-poor conditions. The efficient means of feeding by graphoglyptid tracemakers, cultivating bacteria (i.e., trace makers living in symbiosis with chemoautotrophic bacteria; chemichnia, Bromley, 1996; Vallon et al., 2016), is an adaptation to nutrient-poor, stable environments (Seilacher, 1977; Miller III, 1991; Uchman, 1999). Collection of nutritional sediment in the burrow system, beyond the range of other possible consumers (i.e., sequestrichnia; Wetzel and Uchman, 2016), in cases accompanied by chemichnial activity, is also a good adaptation to food deficiency between episodes of organic-rich sediment supply. Post-depositional trace fossils are mostly r-selected forms (Tunis and Uchman, 1996), as with the typical *Ophiomorpha* producers, burrowing deep into the turbidite beds to exploit buried nutrients that cannot be reached by smaller organisms (Pickering and Hiscott, 2016). The ratio between r-selected versus K-selected ichnotaxa may therefore vary in a given basin in response to environmental changes such as oxygenation, sedimentation rate, grain size, etc. (Tunis and Uchman, 1996; Uchman, 1991, 1992, 2004; Uchman and Wetzel, 2011).

4.5. Final remarks

1. Turbidites are colonized mostly from the top downward, determining two different intervals in the turbidite bed. The uppermost part, the spotty layer, corresponding to the upper part of T_d and the entire T_e Bouma's divisions, is entirely bioturbated. It is characterized by oval spots against a mottled background. Below the spotty layer is the elite layer, characterized by deep-tier trace fossils (Uchman, 1999). Trace fossils from the elite layer overprint the totally or almost totally bioturbated background of the upper part

(upper elite layer), and the background of primary sedimentary structures in the lower part (lower elite layer).

2. As a rule, turbidite beds are characterized by two different groups of burrows, either the pre-depositional or post-depositional traces. The pre-depositional burrows are produced prior to the deposition of a turbidite, in the background sediment, and mainly consist of highly organized, often delicate burrows known as "graphoglyptids". Graphoglyptids are common on the soles of sandy turbidites. Post-depositional assemblages consist of deeply penetrating traces fossils, including *Chondrites*, *Dictyodora*, *Nereites*, *Palaeophycus*, *Phycosiphon*, *Planolites*, *Scolicia*, *Thalassinoides*, *Trichichnus*, and *Zoophycos*.
3. The specialized farming behaviour (agrichnia) of graphoglyptid tracemakers as well as the small size of the tunnel networks would mainly point to adaptation to nutrient-poor conditions, reflecting an equilibrium (K-selected) strategy. Post-depositional trace fossils are mostly r-selected forms.
4. Turbidite deposits are largely characterized by the *Nereites* ichnofacies, which typically includes trace fossils forming diverse meanders, spirals, and nets, belonging mostly to the graphoglyptid group. Three ichnosubfacies can be differentiated under the *Nereites* ichnofacies, according to the different parts of the turbiditic systems and the associated palaeoenvironmental conditions: the *Ophiomorpha rudis* ichnosubfacies for thick-bedded sandstones in channels and proximal lobes, the *Paleodictyon* ichnosubfacies for more sandy 'normal' flysch, and the *Nereites* ichnosubfacies for mud-rich distal flysch.

5. Ichnological record in hyperpycnites

In recent years, hyperpycnal flows and the resulting deposits (hyperpycnites) have been acknowledged as significant processes and sediments occurring in deep-sea environments (see Zavala and Arcuri, 2016; Zavala, 2020). Hyperpycnal flow occurs when a relatively dense land-derived gravity flow enters a marine or lacustrine water reservoir; the density of the incoming flow is higher than that of the water in the reservoir (Zavala, 2020). According to Mulder et al. (2003), hyperpycnal flows form in the marine environment when river discharge enters the ocean with suspended concentrations in excess of 36 kg m^{-3} due to buoyancy considerations, or as little as $1\text{--}5 \text{ kg m}^{-3}$ when convective instability is considered. Depending on the characteristics of the parent flow (flow duration and flow rheology) and basin salinity, the resulting deposits (hyperpycnites) are highly variable (Zavala, 2020). Following Mulder et al. (2003), "a hyperpycnal process means that riverine material, except what is eroded on the seafloor, is transported directly to the marine environment, the continental shelf and slope or to the abyss, by a turbulent flow initially containing fresh water". Thus, hyperpycnal systems in marine settings can develop in coastal, shallow- and deep-water environments. Hyperpycnites are basically extrabasinal turbidites having distinctive and —to date— poorly known facies characteristics (Zavala and Arcuri, 2016).

The most widely accepted version of a hyperpycnal-type sequence is a fine-grained deposit composed of a coarsening-upward basal unit deposited in the waxing period of discharge, and a top fining-up unit deposited during the waning period of discharge (Mulder and Alexander, 2001; Mulder et al., 2001, 2002, 2003; Mulder, 2011; Mulder and Chapron, 2011; Fig. 2). The lower sequence is not always preserved, making it difficult to distinguish hyperpycnites from classical turbidites (Mulder and Chapron, 2011). The common occurrence of organic debris of continental origin at the base of deposits is an indicator of hyperpycnites. Hyperpycnal flow deposits can be quite complex (Zavala, 2018, 2020). The definition of the hyperpycnal flows and the corresponding hyperpycnites is controversial, and the processes involved and diagnostic features are still a matter of discussion (Mulder et al., 2002; Zavala and Arcuri, 2016; Shanmugam, 2018b, 2021; Zavala, 2019, 2020; Van Loon et al., 2019).

Hyperpycnite

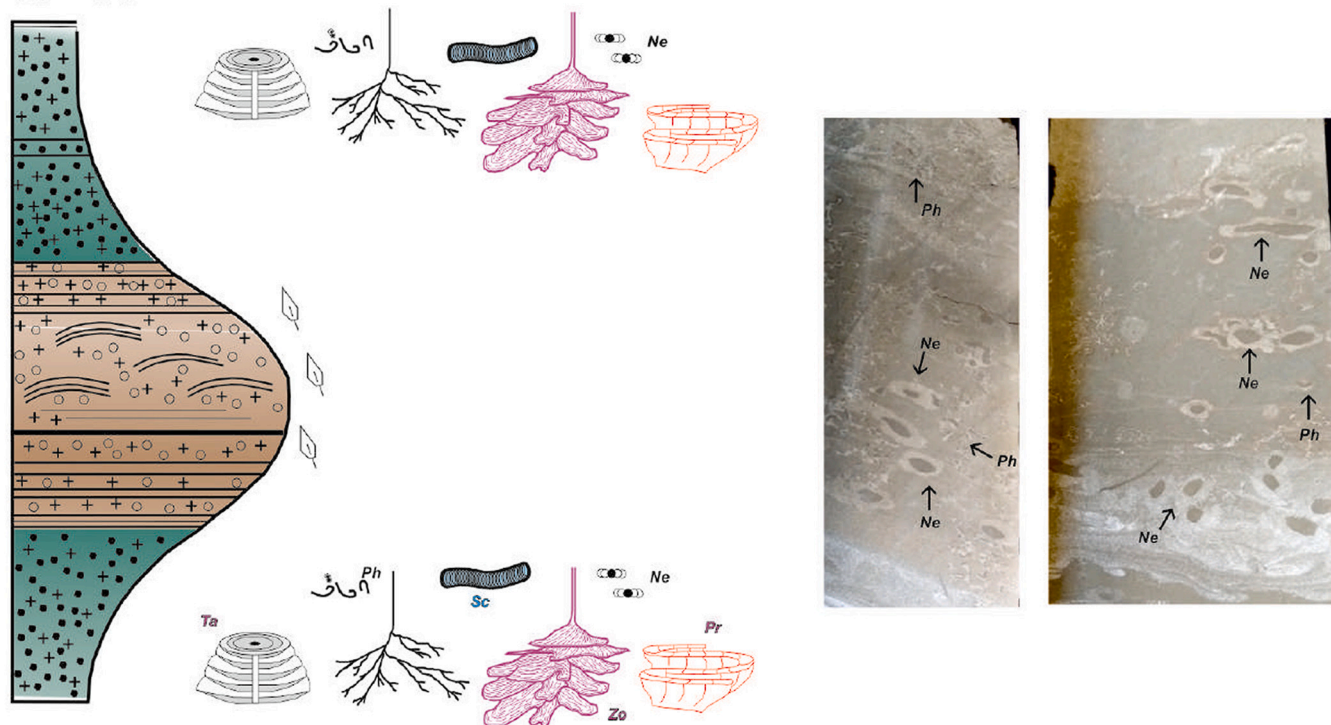


Fig. 8. Trace fossils at the lower and upper parts of hyperpycnite beds and images with particular ichnotaxa. Note: *Chondrites* (Ch), *Nereites* (Ne), *Physcosiphon* (Ph), *Pradictyodora* (Pr), *Scolicia* (Sc), *Spirorhaphes* (Sp), and *Tasselias* (Ta).

5.1. Bioturbation in hyperpycnites

Hyperpycnal flows determine significant changes in palaeoenvironmental conditions, such as rapid fluctuations in the rate of sedimentation, variations in salinity related to fresh-water discharge, oxygen depletion associated with input of phytodetritus, and rapid changes in substrate type and consistency (Buatois et al., 2019). Such changes are not constant throughout the depositional area, instead showing variability along the depositional dip and strike profiles (Buatois et al., 2019). Particularly in modern and ancient deep-marine environments, lower salinity (Yang et al., 2018 and references therein), enrichment in organic matter (Wetzel, 2008), and even massive benthic litter (Pierdomenico et al., 2019) have been recognized. In most cases, these changes affect the benthic habitat significantly, determining variations in ichnological features of the living community.

Hyperpycnal processes induce longer-term (days, weeks or months) changes than surge-type turbidite flows (minutes, hours) in depositional and ecological conditions (i.e., hydrodynamic energy, rate of sedimentation, grain size, salinity, and nutrient availability, among others) (Zavala, 2020). The ethological response of the tracemaker community to these changes could therefore be used to characterize and differentiate hyperpycnites from (surge-type) turbidite flows (García-García et al., 2021). Yet this is no simple matter; as revealed in previous ichnological studies, in some cases there is great similarity between the trace fossil content of the classical turbidites and the hyperpycnites (e.g., Ponce et al., 2007; Carmona and Ponce, 2011).

Ichnological characterization of hyperpycnites is still in early stages when compared with similar studies of pelagic/hemipelagic or turbiditic sediments. The existing studies on hyperpycnites documenting biogenic structures tend to refer to deltas (MacEachern et al., 2005; Bhattacharya and MacEachern, 2009; Buatois et al., 2011; Canale et al., 2015, 2016; Dasgupta et al., 2016a, 2016b; Bhattacharya et al., 2020), and less often to lakes (Buatois and Mángano, 1993, 1995, 1998) or deep-marine systems (Ponce et al., 2007; Wetzel, 2008; Carmona and Ponce, 2011;

Ponce and Carmona, 2011). Despite these ichnological studies, as stated in Buatois et al. (2019), we lack particular ichnological signatures, trace fossil assemblages or ichnofacies characterizing hyperpycnites, or explaining their variability according to different palaeoenvironmental settings. More detailed ichnological studies on hyperpycnites are therefore necessary in order to enhance characterization of the primary and secondary processes, the associated palaeoenvironmental changes, and the resulting deposits.

Ichnological information on hyperpycnites from deep-marine systems has been obtained from both modern (Wetzel, 2008) and ancient settings (Ponce et al., 2007; Wetzel, 2008; Olivero et al., 2010; Carmona and Ponce, 2011; Ponce and Carmona, 2011; García-García et al., 2021).

5.2. Modern hyperpycnites

The Pinatubo 1991 ash accumulation is overlain by multiple brownish mud layers, interpreted as having a hyperpycnal origin, from strong monsoonal precipitation (Wetzel, 2008). Plant debris and even wood suggest a terrestrial source. These brownish muds contain some organic material (0.1%–0.2% Corg). They are characterized by a small ichnofauna; *Diplocraterion*-like spreiten, cf. *Lapispira*, and unnamed tubes have been observed. The muds form the media for recolonization of the 1991 ash layer —pioneer fauna colonized the hyperpycnal mud deposits. The presence of cf. *Lapispira* and *Diplocraterion*-like forms and the small size of the traces within the hyperpycnites support this deduction. Depending on the thickness of the hyperpycnites, bioturbation is more or less intense. Generally, colonization of the hyperpycnites occurred shortly after deposition. The immediate colonization of the hyperpycnites is favoured by a grain-size composition similar to that of the background sediment and benthic food content (0.2%–0.4% Corg). Some organic matter was entrained when hyperpycnal suspension currents flowed down the continental slope, now dispersed within the hyperpycnite. The organic matter in these layers is, therefore, labile yet sufficient to support small-sized infauna (Wetzel, 2008).

5.3. Ancient deep-marine hyperpycnites

5.3.1. Trace fossil assemblage

Detailed ichnological analyses of ancient hyperpycnites from distal settings are relatively scarce (Carmona and Ponce, 2011; Ponce and Carmona, 2011; García-García et al., 2021). Carmona and Ponce (2011) indicate that for Miocene deep-marine hyperpycnites, in the distal setting, the ichnofossils occur mainly in heterolithic intervals developed at the base and top of the hyperpycnal lobe deposits, showing high abundance and low to moderate diversity (Fig. 8). In these heterolithic facies the ichnoassemblage is dominated by deposit-feeding traces, mainly *Scolicia*, *Nereites*, and *Phycosiphon* (Carmona and Ponce, 2011; Ponce and Carmona, 2011). The fairly sandy heteroliths show discrete intervals completely bioturbated with *Scolicia* and *Nereites*, probably reflecting periods of normal marine salinity and high food content. Intervals with abundant *Phycosiphon*, *Nereites*, and subordinate *Tasselia*, commonly registered in fine-grained heteroliths and massive mudstones, would also indicate full-marine conditions, although the patchy distribution of traces suggests fluctuations in salinity and organic input (Carmona and Ponce, 2011). Sporadically, at the top of the muddy intervals, *Gyrophyllites*, *Thalassinoides*, *Chondrites*, *Paradictyodora*, and *Phycodes*, among others, are observed. Punctually, in some isolated sandstone beds, pre-event trace fossils such as *Paleodictyon* and *Helicolithus* represent a low-diverse graphoglyptid suite (Carmona and Ponce, 2011; Ponce and Carmona, 2011). García-García et al. (2021) recently revealed the presence of upper Miocene highly bioturbated channelized-lobe sediments with dominant *Nereites* and *Phycosiphon*, together with *Chondrites*, interpreted as distal hyperpycnites developed in offshore settings (Fig. 8).

Noteworthy is the uncommon presence of graphoglyptids, typical traces from turbidites, in hyperpycnal deposits. Their rarity may stem from a combination of ecological and taphonomic reasons (Buatois et al., 2019). From an ecological point of view, graphoglyptids represent sophisticated feeding strategies (farming and trapping) in settings with limited food supply; thus the increased food supply in connection with hyperpycnal flows may have prevented this behaviour, favouring the development of feeding and grazing traces of deposit feeders. Taphonomically, graphoglyptids, as pre-depositional traces, are preserved in the soles of the overlapped turbidite beds, so that the absence of turbidity currents prevents their preservation.

5.3.2. Ichnofacies

Trace fossil assemblages of distal hyperpycnites have been mainly assigned to the *Nereites* ichnofacies, differentiating between the *Ophiomorpha rudis* and *Nereites* ichnosubfacies, according to the particular areas of the hyperpycnal system—high-energy, proximal channelized and levee areas, and low-energy middle to distal zones, respectively (Buatois et al., 2019; García-García et al., 2021). The general absence of graphoglyptids allows one to discard the *Paleodictyon* ichnosubfacies (Table 2).

5.3.3. Environmental conditions and benthic habitat

Environmental (ecological and depositional) conditions affecting tracemaker communities in a deep-sea setting are of particular importance when associated with hyperpycnal flows. According to Carmona and Ponce (2011), fluctuations in hydraulic energy and sedimentation rate are moderate but nonetheless strong, and oxygen concentration appears to be quite normal. Therefore, the input of organic matter and fluctuations in salinity would be the main palaeoecological factors affecting the infaunal communities and determining trace fossil features associated with hyperpycnal systems in a deep-sea setting. Generally, the presence of totally bioturbated intervals by deposit-feeding organisms, such as those producing *Scolicia*, *Nereites*, and *Phycosiphon*, reveals generalized normal marine salinity conditions and a large amount of organic material, except for brief episodes of freshwater influx that suggest fluctuations in salinity, sediment and organic input, as signaled

by the patchy distribution of these trace fossil suites (Carmona and Ponce, 2011). The presence of these deposit-feeding organisms could mark an opportunistic population strategy related to a large amount of organic material (Carmona and Ponce, 2011), as observed in modern hyperpycnal deposits (Wetzel, 2008). In the case studied by García-García et al. (2021), highly bioturbated packages with *Nereites* and *Phycosiphon* assigned to the *Nereites* ichnofacies reveal local increases of benthic food and good oxygenation on the sea-floor or within the first centimeters of the substrate. In turn, the low trace fossil diversity could indicate a relatively unstable setting presumably linked to the variable area influenced by hyperpycnal flows in distal prodelta to offshore transition settings.

5.4. Final remarks

1. Hyperpycnal flows generate various stress factors in deep-sea setting; the input of organic matter and fluctuations in salinity being the main palaeoecological factors affecting the infaunal communities.
2. Ichnoassemblages of the deep-marine hyperpycnite successions reflect colonization by opportunistic organisms, forming communities that are commonly impoverished, and poorly to moderately diverse, showing patchy distribution and often weakly developed tiering structures.
3. The trace fossil assemblage is dominated by deposit-feeding traces, mainly *Scolicia*, *Nereites*, and *Phycosiphon*. Common ichnogenera in these deposits are *Chondrites*, *Paradictyodora*, *Phymatoderma*, *Protovirgularia*, *Tasselia*, and *Zoophycos*. Significant is the absence or uncommon presence of graphoglyptids.
4. There are no major differences in the trace fossil content between the hyperpycnite facies associations, the classical post-depositional turbidite and the pelagic/hemipelagic sediments, except for low ichnodiversity in the hyperpycnites.
5. Trace fossil assemblages of distal hyperpycnites have been mainly assigned to the *Nereites* ichnofacies, differentiating between the *Ophiomorpha rudis* and *Nereites* ichnosubfacies, and discarding the *Paleodictyon* ichnosubfacies.

6. Ichnological record in contourites

The term “contourites” refers to sediments deposited by or significantly affected by the action of bottom currents (Stow et al., 2002; Rebesco et al., 2014). As underlined by Rebesco et al. (2014), the term contourites was originally proposed for sediments deposited in the deep sea by contour-parallel thermohaline currents, but has subsequently been extended to designate a larger spectrum of sediments affected to some degree by different current types.

Early papers already proposed a model for muddy contourite facies (Gonthier et al., 1984; Faugères et al., 1984; Stow and Holbrook, 1984; Fig. 2). In this “standard” facies model, a vertical sequence consists of three main facies: homogeneous mud, mottled silt and mud, and sandy silt, arranged in coarsening-upward or fining-upward cycles (negatively/positively graded). Accordingly, contourites were thought to have resulted from a continuous process, giving rise to a characteristic bigradational vertical facies array tied to shifts in the energy of the bottom current (weak to strong, to weak again). This model has met with wide acceptance, with only minor modifications, the main one probably being the proposal by Stow et al. (2002), later adopted in Stow (2005) and Stow and Faugères (2008). These authors introduced interval divisions (C1 to C5) as well as amendments concerning variations for partial contourite sequences (Rebesco et al., 2014; Shanmugam, 2017; Fig. 2). The most noteworthy change appeared in the contourite facies model presented in Shanmugam (2017), with reference to Stow and Faugères (2008): the indication of “± hiatuses” within C3, the middle sandy contourite division. Recently, detailed trace-fossil analysis of bigradational sequences of sand-dominated contourites in Petra Tou Romiou section (Cyprus) clearly supports that sedimentation processes

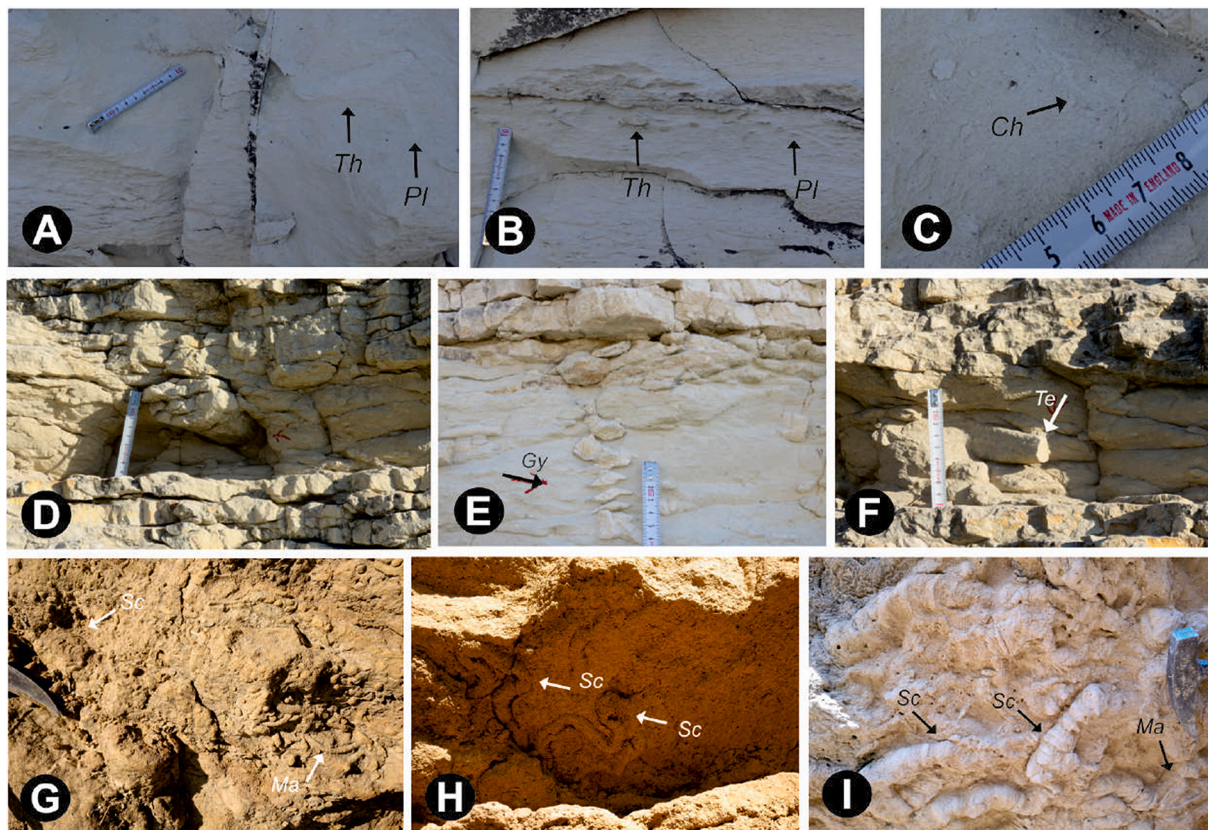


Fig. 9. Trace fossils from contourites. A-C) Calcareous muddy contourites with *Chondrites* (Ch), *Planolites* (Pl), and *Thalassinoides* (Th) (Eocene at Petra Tou Romiou, Cyprus). D-E) Calcareous sandy contourites with *Chondrites* (Ch), *Planolites* (Pl) and *Thalassinoides* (Th) (D), *Gyrolithes* (Gy) (E) and *Teichichnus* (Te) (F) (Eocene-Miocene at Petra Tou Romiou, Cyprus). G-I) Clastic sandy contourites with *Macaronichnus* (Ma), and *Scolicia* (Sc) (Miocene at the Rifian Corridor, Morocco).

were discontinuous during contourite deposition—in contrast to the formerly accepted notion that sediment accumulation induced by the bottom current is an uninterrupted process, with a gradually changing flow velocity related to the bigradational sequence formation (Rodríguez-Tovar et al., 2019; Fig. 2).

6.1. Bioturbation in contourites

The relationship between contourites and bioturbation has always been a controversial topic (see Rodríguez-Tovar and Hernández-Molina, 2018). At one extreme, initial papers describing contourites and most subsequent research treat bioturbation as a reliable diagnostic criterion when differentiating contourites from other deep-water deposits (Lowell and Stow, 1981; Gonthier et al., 1984; Chough and Hesse, 1985; Stow et al., 1986, 1998; Faugères and Stow, 1993; Mulder et al., 2001, 2002, 2013; Wetzel et al., 2008). At the other extreme, some studies interpret bioturbation as a secondary order feature in contourites, even absent in some cases, assigning greater importance to other sedimentary physical features (Shanmugam et al., 1993; Shanmugam, 2017; Martín-Chivelet et al., 2003, 2008). Between both extreme positions, certain authors indicate that the significance of bioturbation is variable depending on the context—bioturbation is a diagnostic feature of muddy/silty contourites, while in sand-dominated contourite deposits the primary sedimentary traction structures would be the main diagnostic feature (Rebesco et al., 2014). Regardless of this lack of consensus concerning bioturbation as a diagnostic criterion, ichnological data are known to provide valuable information to improve characterization of contourites and the bottom current processes involved, and to discern them from associated deep-sea facies.

Since the recent review by Rodríguez-Tovar and Hernández-Molina (2018) “*Ichnological analysis of contourites: Past, present and future*”,

detailed ichnological studies on contourites have increased significantly, entailing different types of contourites in outcrop and core examples (see an update in Rodríguez-Tovar et al., 2021, in press).

6.2. Trace fossil assemblages

Outcrop and core studies on contourite facies allow for characterization of trace fossil assemblages, showing variations between types of contourites, particularly between muddy and sandy, calcareous and clastic contourites (Rodríguez-Tovar et al., 2021, in press; Table 2, Fig. 9).

Muddy contourites, both calcareous and clastic, are usually characterized as highly bioturbated deposits having a common indistinct mottled appearance (Rodríguez-Tovar and Hernández-Molina, 2018). Trace fossil assemblage diversity as observed in muddy contourites comprises recurrent ichnogenera: *Chondrites*, *Palaeophycus*, *Planolites*, *Thalassinoides*, and *Zoophycos*. Other frequent ichnogenera are *Phycosiphon*, *Scolicia*, and *Taenidium*, together with *Mycellia*. Trace fossil abundance and diversity in muddy contourites should be similar to those registered in pelagic and hemipelagic deposits.

In clastic sandy contourites, traction sedimentary structures become dominant (Rebesco et al., 2014), but in some cases these deposits are bioturbated throughout and can appear as massive (structureless). Core examples reveal the presence of common *Thalassinoides*, *Planolites*, and sub-vertical burrows. In the past year, two ichnological studies on sandy clastic contourite deposits from Late Miocene Rifian Corridor outcrops (Morocco) have shown trace fossil assemblages of high abundance and low ichnodiversity, *Scolicia*, *Parahaentzschelinia*, and *Macaronichnus* being common ichnogenera (Míguez-Salas et al., 2020; Míguez-Salas and Rodríguez-Tovar, 2021).

In calcareous sandy contourites, meanwhile, primary sedimentary

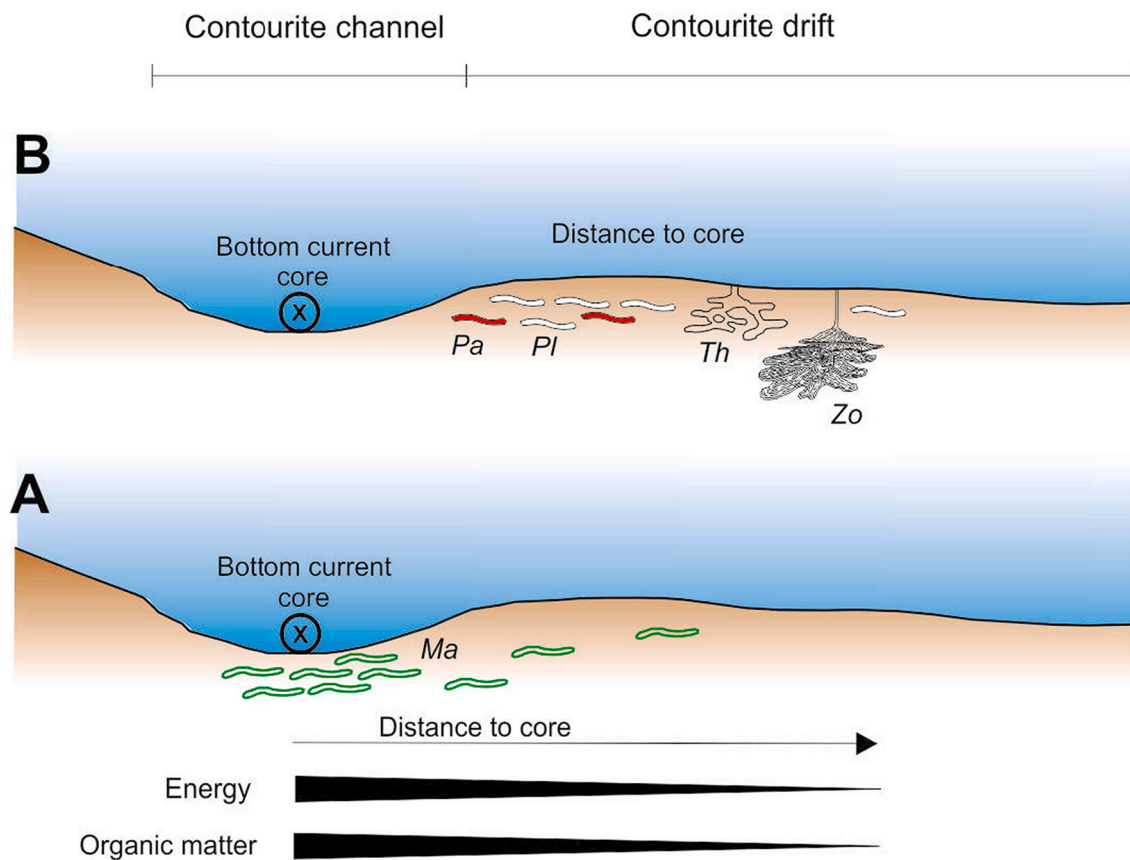


Fig. 10. Variations in ichnological features from distance to the core of bottom currents in relation to changes in energy and organic matter availability. A) Variations in trace fossil assemblages with *Palaeophycus* (Pa), *Planolites* (Pl), *Thalassinoides* (Th), and *Zoophycos* (Zo) (based on Dorador et al., 2019). B) Changes in density of *Macaronichnus segregatis degiberti* (Ma) (based on Míguez-Salas and Rodríguez-Tovar, 2019b).

structures are commonly affected and disturbed by bioturbation. Ichnological analysis conducted on cores shows as recurrent ichnogenera *Palaeophycus*, *Phycosiphon*, *Planolites*, *Scolicia*, *Taenidium*, and *Thalassinoides* (Rasmussen and Surlyk, 2012; Reolid and Betzler, 2019). The study of outcrop analogues from late Oligocene and early Miocene calcareous contourites in southern Cyprus (Petra Tou Romiou type outcrop and Agios Konstantinos section) records abundant *Planolites* and *Thalassinoides* together with common *Gyrolithes* and *Teichichnus*. The trace fossil assemblage diversity observed in carbonate drifts so far can be considered slightly higher than that in siliciclastic contourites. Nevertheless, compared to other marine deposits, diversity is clearly lower.

6.3. Archetypal ichnofacies in contourites

The possibility of recognizing a typical trace fossil assemblage and then defining specific archetypal ichnofacies for contourites is difficult. In recent years, a few research papers about ichnofacies in contourites from outcrop and core have been presented (Table 2, Fig. 12). Ichnological analysis of the carbonate contourite drift at the Petra Tou Romiou outcrop (Cyprus) permits assignment of the trace fossil assemblages to the *Zoophycos* ichnofacies associated with chalky calcilutite sediments, and the distal-archetypal-proximal *Cruziana* ichnofacies related to sandy contouritic facies (Míguez-Salas and Rodríguez-Tovar, 2019b). In the sandy contouritic drift of the Rifian Corridor (Morocco), the impoverished proximal *Cruziana* ichnofacies (MacEachern et al., 2012) was tentatively assigned (Míguez-Salas et al., 2020; Míguez-Salas and Rodríguez-Tovar, 2021). Occasionally, in association with strong bottom currents, non-deposition horizons and stiff- to hardgrounds, a typical *Glossifungites* ichnofacies is developed (Wetzel et al., 2008; Stow

and Smillie, 2020).

Core analysis of the carbonate drift from the Maldives, and comparison to other carbonate drifts points to the *Cruziana* and *Zoophycos* ichnofacies as the main one from carbonate drifts (Reolid and Betzler, 2019).

6.4. Environmental conditions and benthic habitat

According to the trace fossil assemblages in contourites, changes in temperature and salinity related to bottom currents may be discarded as major limiting factors inducing significant variations in the macrobenthic tracemaker communities. Similarly, because contour currents are typically associated with well-oxygenated water masses (Wetzel et al., 2008), oxygenation may not be a limiting factor for benthic habitats affected by bottom currents.

Nonetheless, bottom currents are characterized by high energy flows, hence the capacity to produce extensive accumulations of sediments (Rebesco et al., 2014). Hydrodynamic energy and rate of sedimentation would accordingly constitute two major impact factors influencing the benthic habitat due to bottom current activity. Changes in bottom-current velocity and the consequences (e.g., erosion, non-deposition, and variable rate of deposition) can produce changes in substrate features that could have a major impact on the benthic habitat (Wetzel et al., 2008). Moreover, benthic food is usually limited in the deep-sea environment, determining an important influence on the benthic biota. Bottom currents may carry a considerable amount of particulate organic matter into deep-marine environments (e.g., Thistle et al., 1985; Lucchi and Rebesco, 2007; Wetzel et al., 2008; Rebesco et al., 2014). For these reasons, a complex interaction between factors including hydrodynamic energy, rate of sedimentation/erosion and

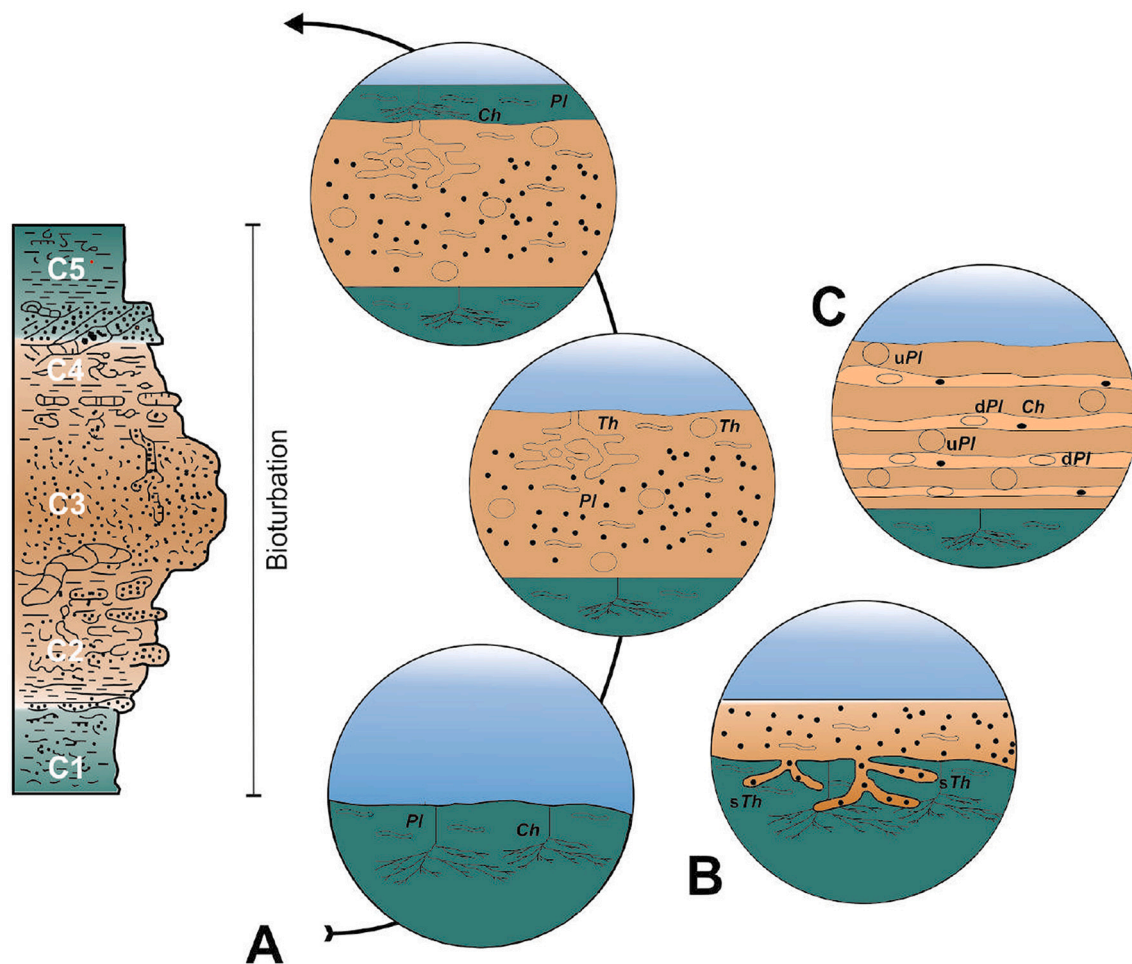


Fig. 11. Different cases of development of bioturbation during contourrite deposition. **A)** Continuous deposition without significant hiatuses, **B)** Erosion or long-term non-deposition between divisions C1 to C2, yielding indurated discontinuity surfaces, where overlain by sand allowing the presence of a typical *Glossifungites* ichnofacies (based on [Wetzel et al., 2008](#)), **C)** Variations in trace fossil composition and shape of burrows between compacted and non-compacted layers, revealing variations in substrate consistency during deposition of the calcarenite beds of division C3 associated with intermittent bottom current processes (based on [Rodríguez-Tovar et al., 2019](#)). Note:

Chondrites (Ch), *Planolites* (Pl), deformed *Planolites* (dPl), undeformed *Planolites* (uPl), *Thalassinoides* (Th), stiff substrate *Thalassinoides* (sTh).

benthic food flux can influence the macrobenthic tracemaker community in terms of diversity, abundance, size of organisms, and behaviour, determining variations in the ichnological features at different scales.

At the regional scale, in the range of contourrite drifts, bottom currents induce variations in composition and behaviour of tracemakers—as revealed by ichnological features—that can affect the complete trace fossil assemblage or particular ichnotaxa. The carbonate contourrite drift at the Petra Tou Romiou outcrop (Cyprus) records an ichnofacies replacement, from the *Zoophycos* ichnofacies to the *Cruziana* ichnofacies, suggesting a relative sea level fall, in turn determining a change toward proximal and shallower depositional settings and increased bottom-current flow velocity ([Miguez-Salas and Rodríguez-Tovar, 2019b](#)). This is also reflected by ichnological features: the presence of vertical burrows, the near absence of traces (e.g., *Gyrolithes* and *Ophiomorpha*) produced by filter feeding organisms, and the presence of traces such as *Thalassinoides*, together with *Teichichnus* which are produced by larger deposit feeders ([Miguez-Salas and Rodríguez-Tovar, 2019b](#)). Characteristic of the sandy contouritic drift of the Rifian Corridor (Morocco) is the abundant, locally exclusive, presence of the trace fossil *Macaronichnus segregatis degiberti*, revealing greater density near the sandstone units associated with contouritic channels (sides and axis), while abundance decreases progressively aside from the channels ([Fig. 10A](#)). The presence of *M. s. degiberti* only locally in studied bottom

current deposits was interpreted as revealing the interplay between food supply, flow velocity, and seafloor heterogeneity ([Miguez-Salas et al., 2020, 2021](#)). The proposed interpretation linked the record of dense *Macaronichnus* ichnoassemblages in the contourrite sediments to high nutrient supply provided by ancient bottom currents, further supported by the record of *Scolicia* ([Miguez-Salas et al., 2020, 2021](#)); abundance and size usually increase in conjunction with a higher amount of benthic food (see [Wetzel et al., 2008](#)).

An ichnological study of cores collected along the NW Iberian Margin confirms systematic variation in ichnological content across proximal to distal depocenters within a large-scale elongated contourrite drift ([Dorado et al., 2019](#)). Sedimentation rate and organic matter availability are higher in areas proximal to the core of the bottom current, where organic matter is rapidly buried. This prevents oxidation and makes organic matter available for shallow tier tracemakers (i.e., *Palaeophycus* producers). In distal settings, sedimentation rate and organic matter availability is lower. The organic matter is rapidly oxidized at the surface, favouring development of middle and deep tier tracemakers—those showing activity from a few to some tens of centimeters down within the substrate, transporting organic matter to deeper layers of the sediment (i.e., *Zoophycos* producers) ([Fig. 10B](#)).

At a shorter-scale range, ichnological analysis points to variations in bottom current features during contourrite deposition according to the

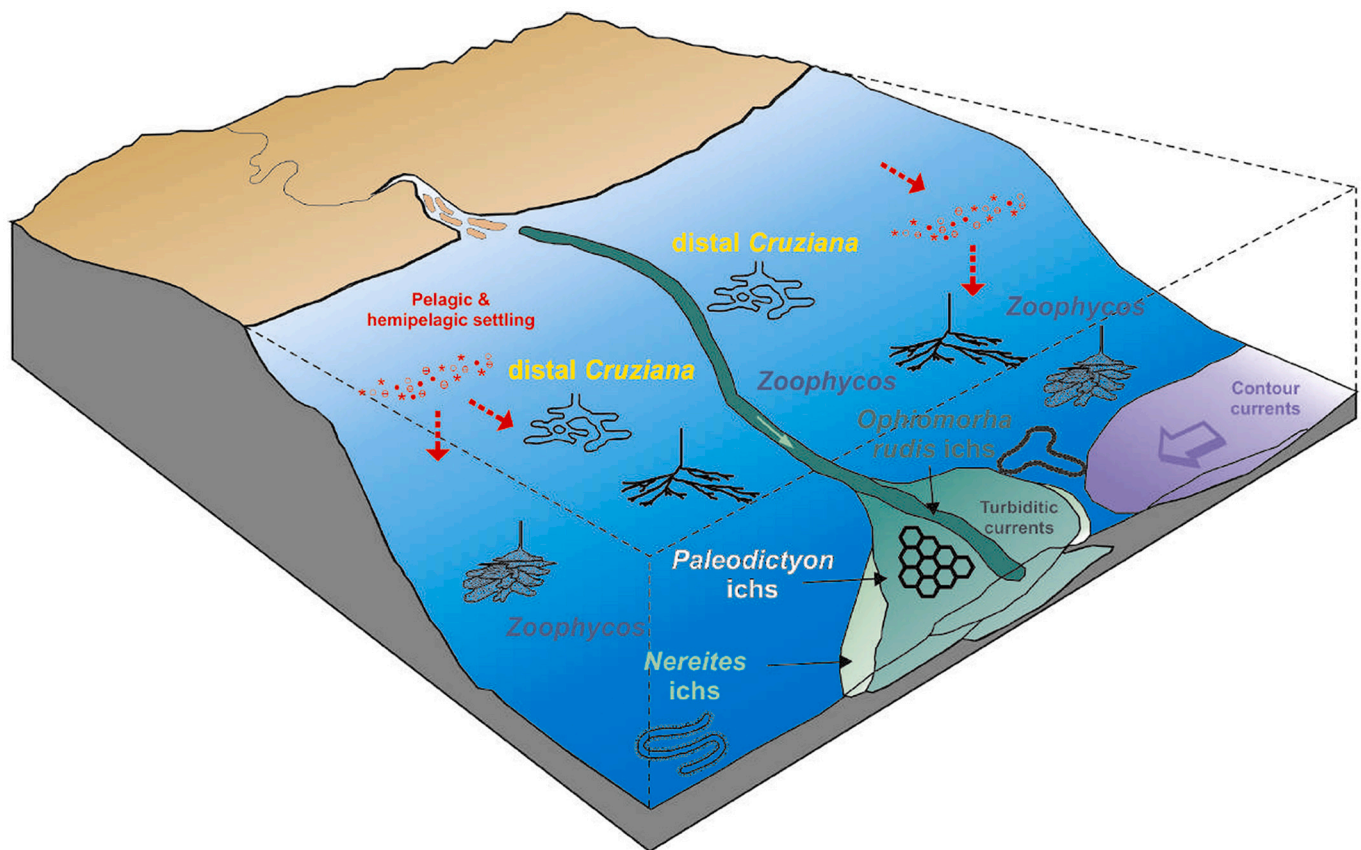


Fig. 12. Distribution of ichnofacies (distal *Cruziana*, *Nereites*, and *Zoophycos*) and ichnosubfacies (*Nereites*, *Ophiomorpha rudis* and *Paleodictyon*), with representation of typical ichnotaxa, in the deep-sea environment (based on Callow et al., 2014 from McIlroy, 2004).

contourite facies model scale (Rodríguez-Tovar et al., 2019). According to the traditional contourite facies model, contourites result from a continuous process, giving rise to a characteristic bigradational vertical facies array related to shifts in the energy of the bottom current (weak to strong, to weak again) (Fig. 11A). Certain modifications have been proposed with regard to this model, however. Thus, the presence of stiff-to hardground trace fossils can reveal deep erosion or long-term non-deposition, yielding indurated discontinuity surfaces; where overlain by sand, they would allow the presence of the archetypal *Glossifungites* ichnofacies (Wetzel et al., 2008; Fig. 11B). Such discontinuities could be related to the hiatuses indicated by Shanmugam (2017) in the C3 division (Fig. 11B). In greater detail, through ichnological analysis of bigradational sequences of the sand-dominated calcareous contourites from the Petra Tou Romiou type section (southern Cyprus), minor hiatuses were recognized (Rodríguez-Tovar et al., 2019). Ichnological features such as length, shape, diameter, and orientation of individual burrow segments, the configuration of burrow systems, as well as external features, fill material, and taphonomy, were studied. Variations in the trace fossil composition and shape of burrows between compacted and non-compacted layers was interpreted as revealing variations in substrate consistency during deposition of the calcarenite beds associated with intermittent bottom current processes governing contourite deposition, and minor hiatuses (Fig. 11C). This conclusion opposes the traditional notion that sediment accumulation induced by the bottom current is an uninterrupted, continuous process, with a gradually changing flow velocity related to the bigradational sequence formation (e.g., from the first models in Faugères et al., 1984; Gonthier et al., 1984; Stow and Holbrook, 1984; see Rebesco et al., 2014, and references therein). Discontinuous deposition and interruption in sedimentation during deposition of the bigradational contourite sequence have likewise been recognized based on recent ichnological analysis of cores from

the Gulf of Cadiz contourite depositional system (de Castro et al., 2020a, 2020b).

6.5. Final remarks

1. Bottom currents determine a complex interaction between hydrodynamic energy, rate of sedimentation/erosion and benthic food flux influencing the macrobenthic tracemaker community and then determining variations in the ichnological features.
2. As a rule, ichnological features such as ichnoassemblage, ichnodiversity and abundance vary in contourites, related in response to palaeoenvironmental conditions, depositional setting and type of contourite.
3. Ichnodiversity and abundance can be high, especially for mud-silty contourites. Ichnological features from mud-silty contourites are similar to those of the pelagic/hemipelagic sediments (the tiering structure probably being more complex in pelagic/hemipelagic) or the upper part of the muddy turbidites (contourites probably being more continuously bioturbated).
4. There is no unique archetypal ichnofacies characterizing contourites; contouritic facies can be related to several ichnofacies (i.e., mainly *Zoophycos* and *Cruziana* ichnofacies).
5. The traditional interpretation of the contourite facies model as the result of a continuous process, giving rise to a characteristic bigradational vertical facies array related to shifts in the energy of the bottom current (weak to strong, to weak again), must be reconsidered based on the presence of minor internal discontinuities revealing discontinuous deposition and interruption in sedimentation.

6.6. Final remarks

Trace fossil analysis has proven to be a useful tool in sedimentary basin research, especially when characterizing palaeoenvironmental (i. e., ecological and depositional) conditions. Ichnological information can be used as a proxy for the recognition and differentiation of deep-sea sedimentary facies as hemipelagites/pelagites, turbidites, hyperpynites, and contourites. Irrespective of bioturbation as a diagnostic feature of particular deep-sea facies, the possibility of interpreting environmental parameters such as hydrodynamic energy, rate of sedimentation, oxygenation, and nutrient availability, among others, will improve our knowledge of deep-sea sedimentary processes (i. e., pelagic/hemipelagic settling, downslope, and bottom currents) and their final products (pelagites/hemipelagites, hyperpynites, turbidites, and contourites). Ichnological features refine previously proposed facies models, improving outcrop/core scale analyses, with special attention to trace fossil assemblages, ichnodiversity, and the abundance of traces, reinforcing the application of the ichnofabric approach and the ichnofacies model. Facies as profusely studied as pelagites/hemipelagites and turbidites reveal diagnostic ichnofabrics, trace fossil assemblages, and ichnofacies; less known ones such as hyperpynites and contourites show variability in ichnological properties, thus far impeding, up to date, conclusive characterization. In some cases, similar ichnological properties are indicative of different facies from variable depositional processes —e.g. pelagites/hemipelagites, muddy contourites, and muddy turbidites— but even in these cases, detailed ichnological analyses facilitate differentiation.

Declaration of Competing Interest

The author declares that he has no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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