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PETROGRAPHIC ANALYSIS OF TRACE FOSSIL *DESMOGRAPTON* FUCHS, 1895 FROM THE MIOCENE OF NORTHERN APENNINES (ITALY): A METHODOLOGY TO DETECT HYPICHNIAL FEATURES AND IMPLICATIONS ON THE GRAPHOGLYPTID ETHOLOGY

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Abstract. The trace fossil *Desmograption* Fuchs, 1895, as many other graphoglyptids, has been considered to be a typical pre-turbidite, three-dimensional burrow system formed in mud and preserved as a casting at the sole of turbidites. This classic interpretation was mostly based on hypichnial preservation, due to the lack of direct evidence (e.g. modern seafloor pictures) for pre-depositional or post-depositional origin. Due to the accidental series of processes invoked to explain the perfect hypichnial preservation of this delicate trace fossil, several doubts and questions have been raised. To try to clarify the sedimentary processes that lead this trace fossil to be preserved, 26 thin sections of *Desmograption dertonensis* Sacco, 1888 and *Desmograption ichthyforme* Macsotay, 1967 have been performed at sand/clay interface of thin-bedded sandstone turbidites in the Miocene marl deposits of Verghereto, Northern Apennines (Italy). Petrographic analysis of textures and grains of the burrow-filling sediments points out that most of the grains of burrows differ from those of overlying sand, being either more or less sorted and differ in composition and locally also in grain size. Burrows are occasionally characterised by an upper rim, more or less thick, enriched in glauconite, phosphates, pyrite or quartz. Axial cuts of the strings show that rim was involved in diagenetic compaction, squeezing and fluid migration modifying the original shape of the trace fossil. In pre-depositional conditions the oblique-oriented filling is the only explanation to preserve the upper rim of original mud, while compaction produced asymmetry in hypichnial tunnels. This petrographic approach, performed for the first time on this graphoglyptid genus, also elucidates the complex interaction of several taphonomic processes that led to the preservation of *Desmograption*. The application of a similar petrographic approach to other graphoglyptids could help to better understand their origin, ethology and their preservation processes.

Riassunto. La traccia fossile *Desmograption* Fuchs, 1895, come molti altri grafogliptidi di mare profondo, è comunemente considerata in letteratura una tipica struttura formatasi nel fango in condizione pre-

torbiditica e preservata a causa del riempimento da parte della sabbia in un deposito torbiditico. Questa classica interpretazione, basata soltanto sulla preservazione alla base degli strati, è dovuta alla mancanza di osservazioni dirette sui fondali marini profondi, utili per chiarire se si tratta realmente di un'attività pre- o post-deposizionale, operata da un organismo(i) sconosciuto. La mancanza di evidenze dirette pertanto non permette di avere la certezza dell'origine per tali strutture geometriche, e sono stati sollevati alcuni dubbi circa l'origine di queste tracce fossili. Al fine di fornire nuovi dati riguardanti la preservazione di questi grafogliptidi, sono stati analizzati, dal punto di vista petrografico, 26 esemplari di *Desmograption dertonensis* Sacco, 1888 e *Desmograption ichthyforme* Macsotay, 1967, provenienti da oltre 100 esemplari dell'area di Verghereto (Appennino Umbro-Romagnolo), dall'interfaccia sabbia/argilla di sottili torbiditi miocenici di frangia esterna. L'analisi petrografica, eseguita per la prima volta su esemplari di grafogliptidi, ha mostrato che la maggioranza dei clasti presenti all'interno dei tunnel potevano essere selezionati, a volte differendo in taglia e composizione rispetto al deposito arenitico circostante o superiore della torbidite. Inoltre, al tetto dei tunnel, sono talvolta preservati degli anelli argillosi scuri (*rim*s) arricchiti in glauconite, fosfati, pirite o quarzo che rimangono tuttora di difficile interpretazione. Essi potrebbero essere spiegati come relitti di fango preservati dal riempimento laterale o trasversale da parte della sabbia trasportata per singoli stadi (*steps*) dalla corrente di torbida. La forte asimmetria dei tunnels potrebbe essere poi stata indotta da compattazione tra la sabbia e il fango sottostante. Tuttavia il fenomeno richiede nuove indagini, ed un'ipotesi post-deposizionale all'interfaccia sabbia/pelite non è da escludersi. Lo studio petrografico dei *Desmograption* potrebbe essere il primo passo per riesaminare anche gli altri grafogliptidi e chiarire l'etologia di questo importante gruppo di tracce fossili di mare profondo.

Introduction

Graphoglyptids represent an important and diagnostic patterned trace fossil group, which is very com-

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mon in modern and ancient deep-water systems (Seilacher 2007). This group is characterised by three-dimensional burrow systems, usually preserved as bi-dimensional patterns, regular or irregular nets, radiating strings and uniramous, biramous or continuous meanders (Sacco 1888; Fuchs 1895; Seilacher 1962, 1977b, 1978, 2007; Książkiewicz 1977; Ekdale 1980; Miller 1991; Rona et al. 2003; Uchman 2004, 2007; Monaco 2008; Buatois & Mangano 2011, among others). Most of graphoglyptids occur as casts on the soles of deep-water, sandy turbidites of flysch deposits; however, examples from more proximal and considerably shallower terrigenous environments (e.g. Gierlowski-Kordesh & Ernst 1987; Uchman et al. 2004; Fürsich et al. 2007; Olivero et al. 2010) or from carbonate gravity flow deposits (e.g. Monaco & Uchman 1999; Milighetti et al. 2009; Uchman 1999) are also known. The preservation of graphoglyptids varies in Mesozoic and Cenozoic turbidite systems, following changes in depositional conditions of different sub-environments in the abyssal realm (e.g. *Nereites* ichnofacies, *Paleodictyon* ichnosubfacies) (Uchman 2007; Heard & Pickering 2008). Graphoglyptids have been, so far, interpreted as the result of burrower activity that did not actively backfill the tunnel but left them opened as a possible drainage system. The system of tunnels was probably a farming burrow system, developed to cultivate chemoautotroph organisms (e.g. bacteria) in the mucus lining that probably surrounded the tunnel wall (Seilacher 2007, cum ref.); this ethological behavior characterises the agrichnia.

Seilacher (2007), summarising the information recorded on graphoglyptids, pointed out that their smooth burrow surface and their sharp boundary might suggest a post-turbidite origin. However, tunnels passing into hypichnial furrows or continuing into the overlying sand have never been recorded. Furthermore, the recovery in the deep-sea muds of the living fossil *Paleodictyon nodosum* (Rona et al. 2003) has reinforced the idea that all graphoglyptids are pre-depositional trace fossils (Seilacher 2007). The tracemaker(s) remains still unknown (Swinbanks 1982). Seilacher (1977b) suggested that all graphoglyptids were dug in the background mud that contains mainly pelagic particles and that they could be preserved only when the turbidity current slightly eroded the uppermost part of the mud; the following sandy-turbidite deposition could cast and preserve these partially eroded and exposed tunnels. This hypothesis is also consistent with the fact that this fossil group is mostly found in distal or marginal turbidite facies (Seilacher 1977b; Heard & Pickering 2008; Monaco et al. 2012). Due to several factors that can influence the development and preservation of graphoglyptids, they have been considered good indicators of biogenic activity in the inter-turbidite time (Uchman 2007). The graphoglyptids are considered K-strategist

colonizers (Ekdale 1985; Uchman 1995) and their presence can suggest relatively stable conditions on the sea floor between depositions of turbidites (Uchman 2007).

As all the other graphoglyptids, the ichnogenus *Desmograpton* Fuchs, 1895, is considered pre-depositional or pre-turbidite ichnotaxon (Seilacher 1977b; McCann 1989; D'Alessandro 1980; Uchman 1995). Taphonomic features in many specimens from the northern Apennines show that a more complicated taphonomic history occurs than suggested by the classic hypothesis and an origin during the early stage of turbidite deposition can not be ruled out (Monaco & Checconi 2010a, b).

Thin section analysis and petrographic characterisation of graphoglyptids and of the sediment in which they are found have never been performed before, as macroscopic or magnifying lens analyses have been considered satisfactory. The aim of this study is to describe, through thin section analysis, the microfacies and the texture of sandy turbidite-beds and to compare it with the *Desmograpton*-filling sediments that are recorded at the base of the same beds.

Study area and geological setting

Desmograpton of this study has been collected at the soles of 1 to 8 cm-thick levels (those that are more rich of this ichnotaxon are 3 to 6 cm-thick) from the Miocene Verghereto Formation in the Verghereto area (Romagna-Tuscan Apennines). The Verghereto Formation is a very thick Early to Middle Miocene (probably Serravallian) marl unit that formed during a period of multi-phase tectonic activity that created foredeep system ridges and NW-SE oriented elongate basins in the Romagna-Tuscan-Umbrian sector of the Northern Apennines (Centamore et al. 2002). In the Verghereto area, the Verghereto Formation reaches its maximum thickness (up to 600 m) and includes sporadic, cm-thick sandstone and siltstone beds exhibiting a very high diversity in trace fossils (Monaco 2008; Monaco & Checconi 2008; Monaco et al. 2009; Milighetti et al. 2009). The cm-thick sandstone beds often contain asymmetrical current ripples, which are usually strongly reworked close to the bed base by hypichnial/endichnial trace fossils. These beds are interpreted as very distal turbidites that were reworked by bottom currents (Shanmugam 2001; Milighetti et al. 2009). In these beds, a very rich epichnial fauna occurs (Monaco & Checconi 2010a). The most common trace fossil is the hypichnial *Rutichnusrutis*, and is usually found with many *Desmograpton* specimens (Monaco 2011). For a detailed explanation of these deposits and their facies distribution, refer to Milighetti et al. (2009).

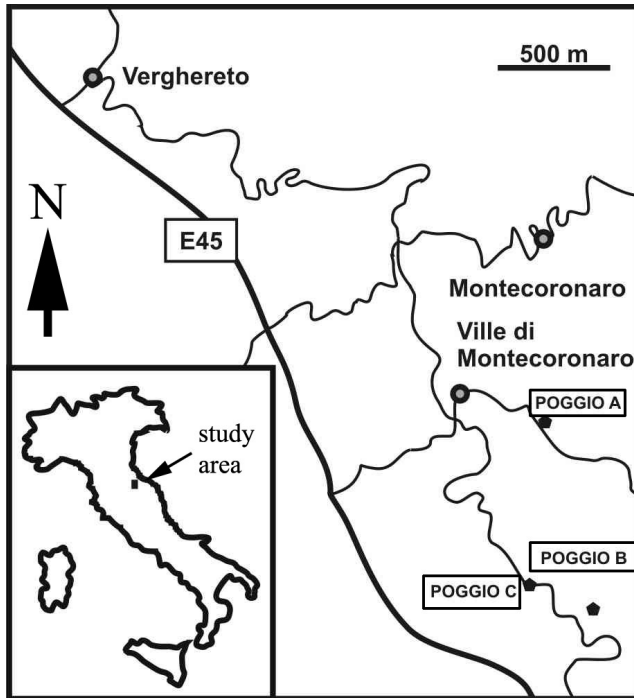


Fig. 1 - Study area and localization of the three sections with *Desmograption* (Poggio A Section, Poggio B Section, Poggio C Section).

Material and methods

In order to describe the petrographic features, 26 specimens of *Desmograption dertonensis* Sacco, 1888 and *Desmograption ichthyforme* Macsotay, 1967 were cut and analysed in thin section. They were selected from a group of about 100 specimens of *Desmograption* from the Verghereto area that are stored in the Biosedimentary Lab of Perugia University (Italy). These samples were collected at the Poggio A ichnofossil-lagerstätte (Monaco & Checconi 2010a) and at the Poggio C and B sections (Monaco 2011) (Fig.1).

Clay residues from the lower part of the sandy bed where removed with a hard plastic brush so that the hypichnial reliefs could be better exposed (Fig. 2). A few samples were not deeply washed to allow the thin section analysis of the clay layer texture.

Each sample was enclosed in a transparent resin, to preserve every element of the fragile trace fossil during the thin section preparation. The sandstone bed, containing the burrows, was always preserved in thin section due to the hard nature of the rock, whereas the underlying clay bed was only rarely preserved and generally disaggregated during sample preparation. Thin sections cuts were selected in order to show the different parts of the burrow (e.g. meanders, strings, shaft connections) in several orientations (Fig. 2). Oriented cuts of twenty-six specimens were examined using a transmitted light microscope and Dino Lite digital camera (from 7 to 200 magnifications, usually at 60X), to enhance textural characteristics of surface and filling of the trace fossil (Figs 3 to 8). The most representative quantitative parameters (string diameter, meander distribution and distance between strings) were also measured.

Results

Facies of the Verghereto Formation

Deposits of the Verghereto Formation in the studied area show alternations of very thin sandstone beds

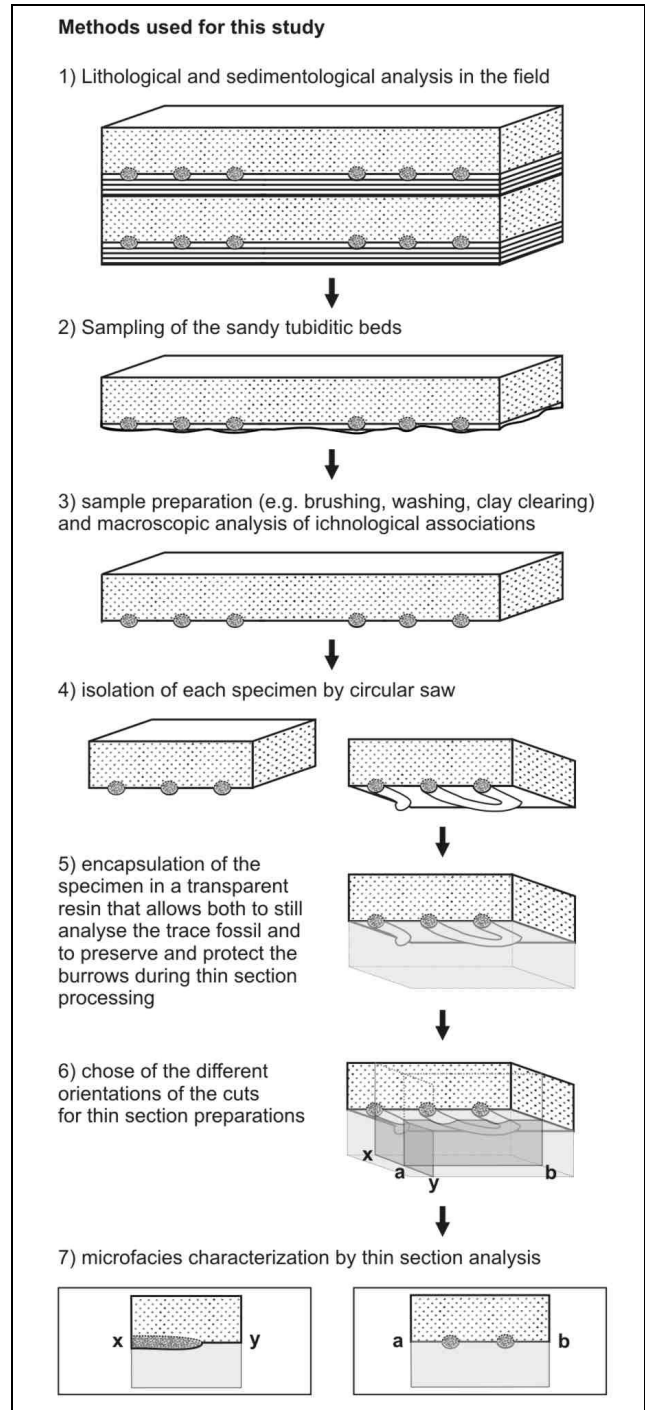


Fig. 2 - Methods used for the sampling and sample preparation for this study. After the sedimentological and lithological analyses in the field (1) samples have been collected (2) and prepared for the macroscopic analysis (3-4). The encapsulation of each *Desmograption* pattern in a transparent resin was necessary to protect the delicate burrows during thin section processing (5). Thin sections were prepared choosing different orientations in order to have representative views of the burrow system (6-7).

and very thick argillaceous layers. The latter are very homogeneous and no lamination or preferential grain orientation were visible in thin section. Clay minerals, scarce, rounded, silt to very fine sand-grade quartz

grains and scarce planktonic foraminifers are present in the claystone beds (see Pl. 1E).

Thin-bedded sandstone beds, 1 to 8 cm in thickness, are rhythmically arranged and usually are very similar to fine-grained and thin-bedded F9b Facies of Mutti (1992). These thin sandstones in the Vergereto area were probably very distal fringe lobe or overbank deposits, reworked by bottom currents, or storm-induced turbidite deposits (see description in Monaco & Checconi 2010a; Monaco 2011). Parallel to small-scale hummocky cross laminations and ripples are very common. The top is usually sharp, usually with ripples, but a cm-thick level of mud can be present and it is even strongly bioturbated (see epichnial assemblage in Monaco 2011).

Sandstone beds are characterised by immature, poorly sorted litharenites (*sensu* Folk 1974; Pettijohn et al. 1987). Grains are dominated by quartz, mica flakes and indeterminate clay minerals with subordinate glauconite, phosphates and very rare, partially dissolved, feldspars and carbonate clasts. Quartz represents the dominant component and occurs as sub-angular (ranging from 65% to 90% of the total fraction of quartz) and sub-rounded (ranging from 10% to 35%) grains in the fine- to medium-grained sand grade range. Coarse-grained sand grade quartz is much less common and occurs in few samples. The base of the sandstone beds is commonly characterised by relatively coarser, sand-size sediment, but several exceptions have been recorded at the sand-clay interface, where sand can be finer (Pl. 2A). In one sample, thin carbonate cement-filled vertical fractures are present (Pl. 2C). These fractures randomly occur in the bed and locally terminate at the *Desmograption* tunnels. For this reason they are interpreted as diagenetic fractures which do not represent an element of the trace fossil itself.

The sandstone beds contain a diverse taphonomic assemblage, comprising endichnial and hypichnial forms. Some endichnia creators tend to disturb depositional laminae (e.g., *Rutichnus*, *Halopoa* and, locally, *Ophiomorpha rudis*). Among these, *Rutichnus rutis* is the most abundant and produces endichnial deformations in the sand laminae, which are curved or irregularly arranged, forming bands, micro-convolute and “micro-patchy” structures (Monaco 2011, Fig. 3). In addition to *Desmograption*, other hypichnial structures are also very common; these include plug-shaped forms (e.g. *Bergaueria* and *Parahaentzschelinia*) and *Rutichnus rutis*, that occurs as convex to concave, mm-thick to cm-thick fin-shaped forms at the soles of turbidites (Monaco 2011).

Morphologic features of *Desmograption*

Desmograption is preserved as hypichnion with a horizontal burrow system, which is sub-parallel to the

bedding plane. Strings form a tunnel pattern, which is usually parallel or slightly divergent (depending on ichnospecies), departing from a central axial area where opposite meanders turn off with a characteristic undulating disposition (Monaco & Checconi 2010b). Strings in the studied samples range in diameter from 1 to 3 mm (exceptionally up to 10 mm where flattened) and the distance between the strings varies from a few millimeters (usually 0.5 mm to 3 mm) to few centimeters (maximum 2 cm). String varies in length from few up to 45 mm, are very discontinuous with either sharp or gradual interruptions of the string. Morphology and arrangement of meanders are one of the main taxonomic features at species level. In *Desmograption dertonensis* the apexes of semi-meanders are bent downward and quite distant to each other (up to 20 mm), whereas *Desmograption ichthyforme* shows angular and narrower semi-meanders and upward bending has been recorded. For a detailed analysis of other morphologic features (e.g. form of the axial area, shape of semi-meanders and string distribution) and taphonomy refer to Monaco & Checconi (2010b).

Relief and symmetry of tunnels

Thin section analyses revealed several *Desmograption* features: (1) the grades of relief from the basal host sandstone and consequently the interaction with the underlying clay, (2) the shape of the strings in cross section, (3) the composition of the upper rim and (4) the nature of the filling-sediment.

Desmograption tunnels show different grades of hyporelief, even when they belong to the same specimen (Fig. 3). Low relief is defined where the tunnel and only slightly meandering protuberances emerge from the sandstone bed (Fig. 3A). Semicircular (medium) relief is defined where half the perimeter bulges from the sandstone bed (Fig. 3B). High to very high relief is defined where the burrow only tangentially intersects the sandstone bed while the rest of it occurs within the clay layer (Fig. 3C). In some cases, the tunnel is detached from the sandstone bed and continues in the underlying mudstone, or is completely encased in the clay layer (Fig. 3D). This kind of relief mostly occurs in proximity to the apex of meanders, in particular where a meander is obliquely developed to the bedding plane, producing asymmetry (e.g. Monaco & Checconi 2010b). In a few specimens, however, this complete detachment has been recorded also for a straight string. In other cases, also tunnels are asymmetric and show a high relief (Fig. 3E). Where asymmetry is recorded, it is unidirectional and characterises more than one string of the same specimen. Burrows with a very high relief or which are semi-detached may show a neck narrower than the trace fossil that connects the tunnel to the host sand (Fig. 3F). Some features, such as the presence of a

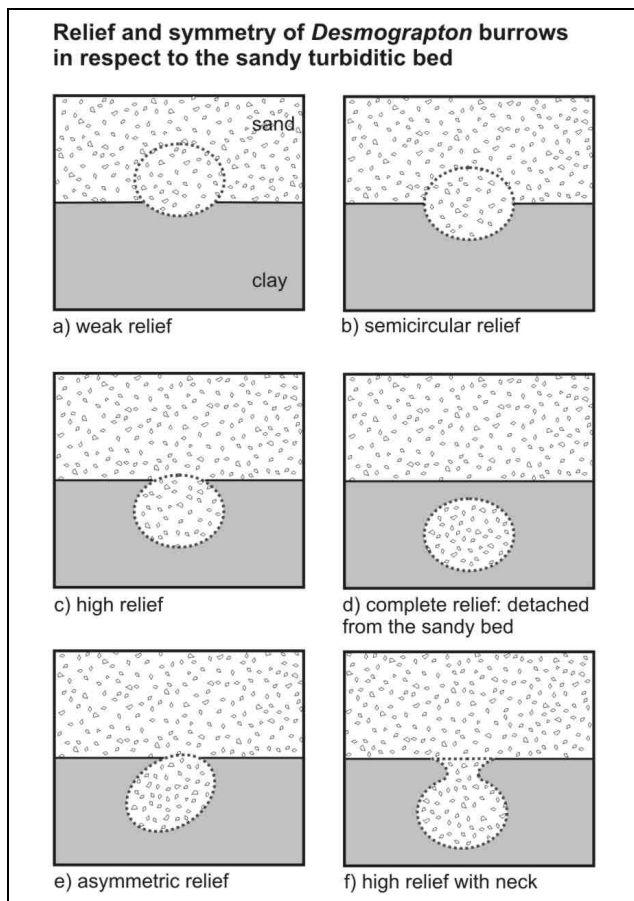


Fig. 3 - Relief and symmetry of *Desmograption* in respect to the sandy turbidite bed. *Desmograption* specimens are characterised by different hyporelieves: (a) weak; (b) semicircular; (c) high; (d) complete, when the burrow is entirely developed in the clay layer. Oriented compaction could contribute to create asymmetric tunnels (e). The presence of a neck that connects complete-relieved burrows with the sandy bed has been recorded (f), but its significance is still not clear. See text for detailed explanation.

neck or the asymmetry of the burrow, were not recordable by macroscopic analysis due to the small size of these burrow features.

Microfacies of *Desmograption*

Desmograption textures were found to vary considerably in some cases from those of the host sandstone bed and, furthermore, different textures were documented within strings of the same specimen. Four different microfacies textures have been identified that describe the sediment fill of the studied *Desmograption* specimens:

1. Microfacies 1 (M1): moderately sorted, very fine-grained sandstone rich in quartz. This texture is more enriched in clay minerals and the sand fraction is finer grained compared to the host sandstone bed (Pl. 2A). Pyrite is common within and around the burrow rim where it enhances the original burrow margin.

2. Microfacies 2 (M2): poorly sorted, fine- to medium-grained sandstone dominated by quartz. Clay

minerals and phosphates are almost completely absent from the burrow, but they are much more common in the host sandstone bed (Pl. 2C). Clay minerals and opaque grains (e.g. pyrite) are locally concentrated around the rim of the tunnel along the contact between the trace fossil and the overlying bed. This texture is generally slightly finer grained and more sorted than the host sandstone.

3. Microfacies 3 (M3): very poorly sorted, medium-grained sandstone rich in quartz grains. Very scarce components include pyrite, glauconite, carbonate clasts and clay. This texture is generally similar to the host sandstone (Pl. 2D).

4. Microfacies 4 (M4): a very poorly sorted, medium-grained quartz-rich sandstone with local concentrations of larger, sub-angular quartz grains within the burrow or at the neck that connects the burrow to the overlying sandstone bed (Pl. 1E). Clay minerals are scarce and pyrite, phosphates and carbonate clasts occur as rare accessory components. This texture is generally slightly coarser than the host sandstone bed.

Rim of the tunnel

The lower part of rim is sharp at the contact with the claystone bed and this sharpness is enhanced by the different lithologies of the sandy burrow-infilling sediment and the claystone. The upper part of the rim in the overlying host sandstone is an important new data, but cannot always be clearly distinguished (Fig. 4A). The rim of *Desmograption* can be occasionally enhanced by the concentration of (a) clay minerals along the rim (Fig. 4B-C; Pl. 2B); (b) pyrite and other opaque minerals (Fig. 4D; Pl. 2A); (c) coarse-grained quartz (Fig. 4E); (d) remarkable texture differences between the host sandstone and the burrow-filling sediments (Fig. 4F), as described in the paragraph above.

Discussion

Most graphoglyptids are included in the pre-depositional ichnofauna, which is characterised by organisms that colonize the deep-sea environment before the deposition of the sandy turbidite beds. The Seilacher (1977b, 2007) model invokes a complex and precise series of coincidental events for their preservation as hypichnial traces. The hypotheses on the origin and preservation described in the literature are, here below, compared and discussed with the data obtained in this study.

Presence of pyrite

Seilacher in many papers (1974, 1977a, b, 1978, 2007), hypothesised graphoglyptids to be characterised by a high specialised feeding behavior, which implies

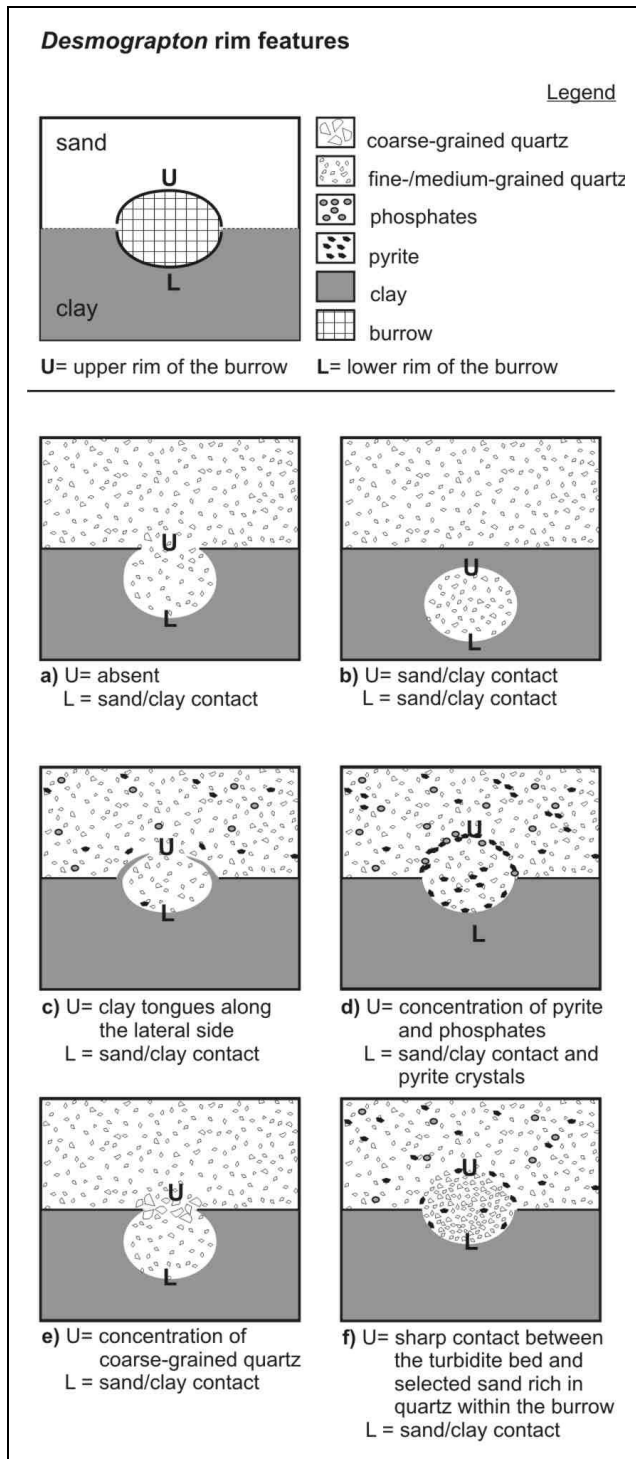


Fig. 4 - Rim features of *Desmograpton*. (a) Few recorded specimens do not show any rim with the overlying sand, while the lithological differences with the underlying clay layer create a sharp contact. If the tunnel was entirely developed in the clay layer (b), the rim is continuous and very sharp. Clay tongues and lips (c) may outline the lateral/upper side of the tunnel and they were formed at the sand/clay interval. (d) Pyrite and phosphate grains can be concentrated inside the burrow and along his rim. (e) Concentration of coarse-grained, selected quartz grains sometimes occurs along the contact between the tunnel and the overlying sand. (f) Selected quartz-sandstone can fill the burrow and pyrite crystal can occur along the rim.

the trapping of meiobenthos or cultivation of fungi and bacteria (e.g. “mushroom garden” model; Seilacher 1977a). Pyrite occurs in the studied sandstones as authigenic euhedral and more commonly anhedral small crystals (Pl. 2A). Locally pyrite is concentrated along the rim of the tunnels (Pl. 2A) and, in other cases, within the tunnel itself. This mineral is an indicator of the chemical processes and diagenetic stages that characterize the rock but, most importantly for this study, it commonly forms under reducing conditions replacing organic matter or in very close proximity to organic matter (Flügel 2004). Its presence around the burrow rim could be a relict of enrichment in organic matter. This feature cannot prove or controvert alone the “farming” (agricultural) behavior. The presence of residue organic matter around the burrow could, in fact, correspond either to organic mucus created by a specialised burrower around cultivation tunnels or to the organic fecal residue of a non-specialised burrower. When pyrite occurs along the burrow rim, it is occasionally common also within the trace fossil itself. This feature suggests that the burrow sediment includes residual organic (mucus?) material, which would be present not only along the burrow rim but also interiorly.

Casting or backfilling of the tunnel?

The petrographic features of the sediment filling of *Desmograpton*, such as the presence of a rim, different textures and distribution of minerals, do not clarify the doubts about whether *Desmograpton* is the result of casting due to sandy turbidite deposition or represents direct burrowing activity at the sand-clay interface. The most convincing explanation for the casting is the presence of opposite meanders that have little meaning in a possible process of continue backfilling. In favor of backfilling activity, on the contrary, are a lot of features, as the grain distribution, the different size of grains from outer sand and rim, which are poorly explained with the casting. The backfilling usually is characterised by meniscate structures that in the analysed *Desmograpton* specimens are lacking, although the small tunnel shape would have been not favorable for the formation of any backfilling microstructures. If *Desmograpton* was a cultivation burrow at the sand-clay interface, the “harvesting” could be done without necessarily producing a typical backfilling. Moreover, meniscate structures of backfilling are not always present or preserved in sand also in larger burrows, where the activity of post-turbidite meiofauna was very important (see Bromley 1996, among others).

In a recent work, Seilacher (2007) proposed that graphoglyptid tunnels could stay open for a long time due to their development in a compact mud and due to the presence of a strong mucus film. The mineral concentration and the sediment texture data obtained from

the thin sections analysis, therefore, do not allow to prove, or to rule out, that either *Desmograption* is the result of sand filling an open tunnel from above or a backfilled tunnel at the sand at the sand-clay interface.

Apparent fluting and crossing of pre-depositional marks

Examples of mini-flutes and mini-grooves, apparently crossed by not fluted *Desmograption*, are described in Monaco (2008, 2010b). Being the fluting the result of the turbiditic event, this feature would demonstrate a post-depositional development of *Desmograption*. However, these physical structures could probably represent marks due to bottom currents and the development of undisturbed *Desmograption* strings crossing them are considered to be subsequent to bottom currents before casting. In the ichnofossil-*lagerstätte*, Monaco & Checconi (2010a) debated the lack of fluted *Desmograption* commonly transversally oriented at the base of mini-flutes and mini-grooves, and suggested that this feature could be the result of multi-phase processes at the mud-sand interface.

Deformation and asymmetry

Squeezing of *Desmograption* tunnels and semi-meanders due compaction has been described before (e.g. Monaco 2008; Monaco & Checconi 2010a). Many of the studied specimens (about 70%) show an elongated elliptical structure. The squeezing is the first result of the vertical compaction of the sediment.

Another characteristic is the asymmetry. In half of the 26 specimens analysed in this paper an asymmetric relief has been found (Fig. 3E; Fig. 6). This asymmetry characterises all the strings attributable to the same tunnel mesh and is more evident in tunnels with higher relief. High to complete relief (Figs 3C, 3D, 3F) is related to the development of the burrow within the clay layer. Early diagenetic processes at the sand/-clay interface imply compaction and fluid (water) migration. Due to the higher percentage of intergranular voids, clay is subject to greater deformation than sand and can undergo a volume reduction of up to 70%. This explains why, in the same mesh, tunnels completely developed in the clay layer are more deformed than those developed at the sand-clay interface. If a transverse pressure causes oriented compaction of the sediment (e.g. associated with migration of fluids at the sand-clay interface), an oriented deformation can occur, producing tunnel asymmetry. The asymmetric preservation observed in some of the specimens analysed in this study (Pl. 1C-D) is comparable to the features interpreted by Seilacher (2007) as fluted graphoglyptids.

If the tunnels were fluted in pre-turbidite conditions, only exhumed tunnels would be deformed, while deeper tunnels (showing now a higher complete relief

with strong asymmetry in Pl. 1D-E) would remain buried and protected from deformation (e.g. in a typical flat sea floor). As a consequence, the occasional asymmetry of *Desmograption*, previously attributed to pre-turbidite fluting processes, could be also explained as the result of oriented deformation during compaction in early diagenesis (Fig. 6).

Relief and preservation

Preservation of graphoglyptid burrow systems depends mostly on physical agents (Seilacher 2007; Uchman 1995; Heard & Pickering 2008) and it is mainly evaluated through the sharpness and regularity of the hyporelief of the tunnels. Some of the specimens observed in thin section show a very good preservation even if their relief is very low. This has been recorded when the burrows are mainly preserved within the sandstone-bed, and the good preservation of the whole section of the burrow is visible only through the thin section analysis (e.g. Pl. 2B-C). Therefore, the relief cannot be the only parameter to measure the preservation quality of the tunnels, and only a petrographic study can define the preservation quality of *Desmograption*.

Energy of the environment

Graphoglyptids are considered to colonise mainly bathyal to abyssal environments (e.g. Wetzel 1983; Ekdale 1980; Gaillard 1991, among others). However, examples from shallower and high-energy environments are also been described (e.g. Gierlowski-Kordesh & Ernst 1987; Uchman et al. 2004; Olivero et al. 2010). In the Fuegian Andes (Argentina) Olivero et al. (2010) described channel and channel-levee deposits with a diverse graphoglyptid association at the base of thick-bedded turbidites associated with lenticular, channeled sandstone beds with a marked basal erosion surface. The Authors suggested that the preservation of graphoglyptids is remarkably good for these high-energy deposits. They attributed this feature to a combination of environmental conditions whereby gentle erosion resulting in exposure of the graphoglyptids galleries was followed by rapid casting of the galleries by the sandy turbidite. This accidental and casual series of events for the preservation of graphoglyptids is invoked by some authors (Seilacher 1962, 1977b, 2007; McCann & Pickerill 1988; Uchman 1995), due to the absence of evidence of a post-turbidite development of many graphoglyptids. Nevertheless, Seilacher (2007) refers to these events as a paradox.

Textural features of *Desmograption* burrows of this study do not exclude the alternative hypothesis that at least this ichnogenus, among other graphoglyptids, could develop during the initial phase of sand deposition. This hypothesis would more easily explain the

occurrence of very long and irregular tunnels at the base of turbidite deposits also in high-energy environments. The turbidite event would not affect the trace fossil in any way, since it would precede the development of the trace fossil.

In all cases the perfect preservation of graphoglyptids on the sole of sediment gravity flow deposits (not only turbidity currents but also debris and plastic flows, see discussion in Shanmugam 2001) should be verified by bed-by-bed sedimentological analyses, evaluating the erosional potential of different gravity flow events.

Trophic regime, nutrients and graphoglyptids

Deep-sea trace fossils can be very important indicators of the trophic conditions of the environment. Uchman (2007) suggested that the abundance of pre-depositional forms, especially relatively diverse graphoglyptids, would imply moderate oligotrophic and relatively stable conditions, which should occur during inter-turbidite times. Graphoglyptids are considered to be K-selected equilibrium strategists of colonization (Ekdale 1985; Uchman 1995, 2007). The hypothesis that *Desmograption* does not represent a pre-depositional trace-fossil would suggest that this ichnogenus should not be considered necessarily a K-strategist. The occurrence of other post-depositional burrows such as *Halopoa* (e.g. Milighetti et al. 2009; Monaco & Checconi 2010a) and *Rutichnus* (Monaco 2011), associated with *Desmograption*, indicates that burrowing organisms can feed on the abundant organic matter transported by currents (deep storms?). In many cm-thick beds *Desmo-*

graption and *Rutichnus* should represent expressions of a simultaneous activity of opportunistic organisms at the base of sand beds. *Halopoa* and *Rutichnus* that crosscut *Desmograption* have never been found, while doubtful evidences of *Desmograption* crosscutting other post-depositional trace fossils such as *Rutichnus* needs further analysis (Monaco & Checconi 2010b). If proved, this would suggest that *Desmograption* represents a “false” hypichnion (Monaco & Caracuel 2007), developed at the sand-clay interface like other larger and more complex opportunistic foraging feeders (r-strategist, e.g. *Rutichnus rutis*).

Suction (Seilacher) model and alternative taphonomic model for the development and preservation of *Desmograption*

Several questions are still open about the development, the timing and preservation of *Desmograption* and the other graphoglyptids. Seilacher (1977 b) theorises some processes that would lead to the preservation of pre-turbidite graphoglyptid meshes (the “suction” model, Fig. 6A). The suction effect, in the Seilacher model, is caused by the instant acceleration of the water related to the imminent arrival of the sandy turbidity current, eroding the unconsolidated surface at the top of the muddy bed (Fig. 5B, Figs. 6A). The following turbidity current then casts the exhumed tunnel system in mud as it deposits its sediment load (Fig. 5C). In this model, the burrow-filling deposit should consequently show no differences with the overlying sandy bed, being filled by the same isochronous depositional event. If the suction effect cannot affect the burrow system (devel-

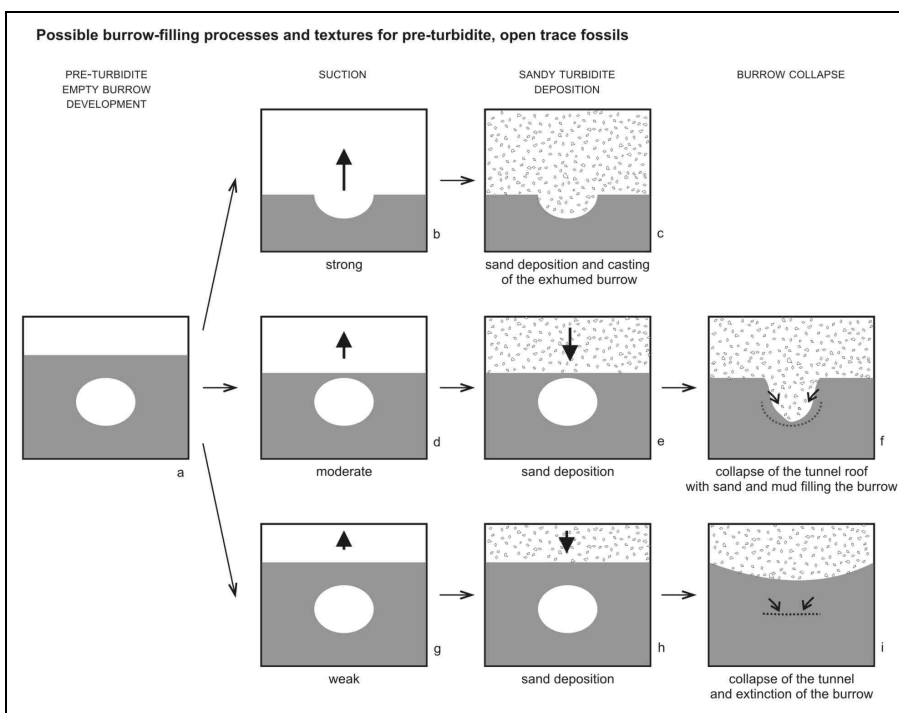


Fig. 5 - Pre-turbidite open tunnels (a) can be preserved as casts if, during a deep-water sandy turbidite deposition, the suction effect would erode the unconsolidated surface at the top of the muddy bed (b, d, g) and if the following turbidite cloud could cast the exhumed tunnel system (c). If the tunnel is not exhumed by the suction effect (e, h), its roof can collapse during the compaction, generating an irregular cast of the trace fossil (f) or its complete extinction (i). The casting of the exhumed tunnel cannot neither generate differences in texture and composition between the cast-filling sediment and the rest of the sandy bed (c) nor create any kind of rim around the burrow.

oped too deeply in the muddy bed), the weight of the sand during compaction should cause the collapse of the tunnel roof and the consequent filling of the trace fossil with sand (Fig. 5F), or should squeeze the empty burrow causing collapse extinction of the tunnel (Fig. 5I; Fig. 6A). Fluting can occur and it can asymmetrically erode the biogenic marks or completely erase them (Fig. 6A). The following turbidite deposition can cast any mark and biogenic or physical signature at the top of the clay layer (Fig. 6A). This casting process cannot create any difference in texture and/or composition between the cast-filling sediment and the rest of the sandy bed.

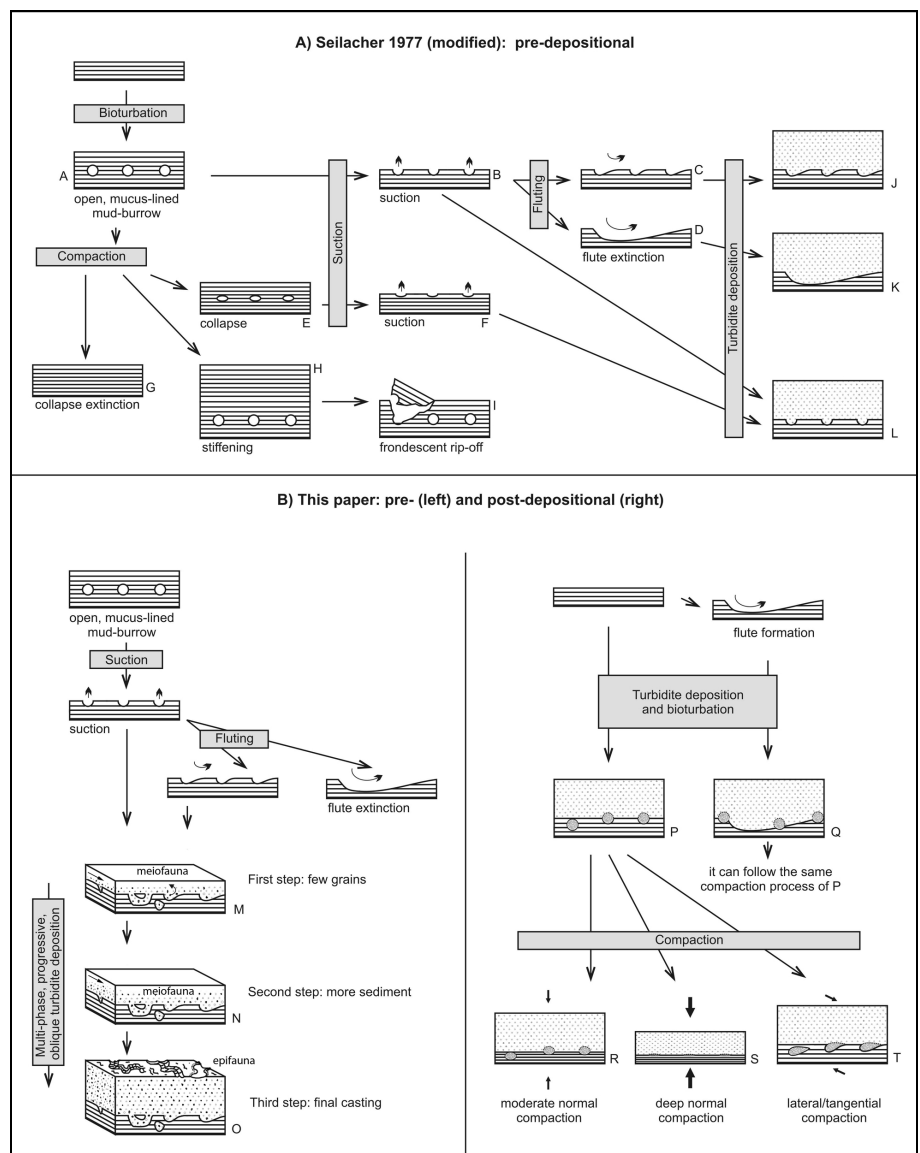
In this paper we propose two different models for the development and preservation of *Desmograption* burrows (Fig. 6, scheme B, left and right). The two models try to explain the presence of some of the parameters recorded in thin sections that can be hardly justified by the Seilacher model. These parameters include

the occasional presence of a rim surrounding *Desmograption* and the differences between the texture of burrow-filling sediment and the texture of the rest of the sandstone bed.

The two hypotheses are: (1) the *Desmograption* is pre-depositional, but the casting was not vertical and in a single phase, but follows steps of grain accumulations, that are transversally-oriented to preserve the upper rim, and (2) the *Desmograption* is a post-depositional trace fossil at sole of turbidite, probably formed during the first deposition (see the “false” hypichnia in Monaco & Caracuel 2007).

Hypothesis 1: the trace fossil is pre-depositional and the fillings oblique and multiphase (Fig. 6, scheme B, left). The way the casting takes place in cm-thick turbidites is not yet clear; it can not be excluded that the burial of sand is not single but it follows individual steps (multiphase turbidite) with small portions of grains transported by currents, with a delay in deposition

Fig. 6 - Comparison between the Seilacher “suction” model (scheme A, top) for the preservation of graphoglyptids suggested by Seilacher (2007), and two alternative models (scheme B, bottom left and right) for the preservation of *Desmograption* (refer to text for figure explanation).



(Fig. 6M-O). In any cases, to preserve the rim, is fundamental that the filling may take place transversely, obliquely with respect to the seabed. In this way, the granules are deposited “laterally” (grain-by-grain) leaving the rim preserved and the original pre-depositional mud intact; when the rim is thick it means that filling takes place in depth, away from the access point of the sand; this feature is typical of downward oriented meanders of *D. dertonensis*, less in *D. ichthyforme*. When no film occurs, tunnels are shallow and section shows the point of the sand input. In any case, the rim will be reduced by compaction. The role of meiofauna is important in this phase, producing a reworking in grain distribution (Fig. 6M-O).

Hypothesis 2: the trace fossil is post-depositional but develops at the sand/clay interface (“false hypichnion” Fig. 6, scheme B, right). According to the second hypothesis *Desmograption*-related burrowers colonized the sand/clay interface surface which can be either regular or irregular; some tunnels can slightly deviate from this horizontal surface and be dug only either in the sandy bed or in the clay layer. The burrowing activity (probably related to foraging) produces tunnels filled by sandy sediment that differs in texture and/or composition from the overlying sandy bed (Fig. 6P-Q). A compaction, which is perpendicular to bedding, can deform and squeeze *Desmograption* meshes symmetrically (Fig. 6R-S) or asymmetrically (Fig. 6T), similarly to fluted trace fossils; the two preservations, however, differ for the nature of the sediment and compaction direction.

These alternative models represent only a first attempt to justify the presence of some of the *Desmograption* parameters, recorded in thin section, that cannot be explained using the Seilacher model. A post-turbidite origin of *Desmograption* would explain the presence of a surrounding rim around this trace fossil if burial is rapid and vertical, explaining the recorded differences in textures between the sand of trace fossil and the outer sand. However, the data recorded in this study do not provide definite evidence for a post-turbidite origin of *Desmograption*. Further sedimentological and petrographic analyses of *Desmograption* specimens (and other graphoglyptids) from other localities are necessary in order to support or rule out the post-depositional hypothesis.

Conclusions

Twenty-six specimens of *Desmograption* from Cainozoic turbiditic deposits in the Verghereto area (Italy) have been analysed in thin section for microfacies and taphonomic characterisation.

1. *Desmograption* patterns develop mainly horizontally at the sole of very thin sandstone turbidite

beds. The burrow system shows mostly a horizontal distribution along the clay-sand interface, sub-parallel to the bedding plane. Some tunnels can oscillate and develop either in the sandstone or in the claystone. This creates different styles of hyporelief, which varies from incomplete to complete.

2. Burrow-filling sediment is usually enriched in pyrite. It occasionally differs, in terms of microfacies, both from the overlying sandstone bed and from the underlying clay bed.

PLATE 1

Desmograption hyporelief at the base of a turbidite bed, Poggio A Section, sample DSG3. Scale bar = 30 mm.

A) Merged thin section pictures (B-E) showing the textural and compositional features of the sandy bed and the related trace fossils along the transect X-Y about 50 mm long. The asymmetry of the burrows is attributed to oriented-oblique compaction. B-C) High relief, asymmetric *Desmograption* tunnel, filled by a very poorly sorted litharenite which is slightly coarser than the overlying sediment. D) Low- to medium-relief, asymmetric *Desmograption* tunnels, showing a poorly sorted litharenite similar to the one of the overlying sediment. E) *Desmograption* meander cut; the two sides of the same meander show different relief. A neck connects the very high- to complete-relief tunnels (extreme left and extreme right in the picture) with the sandy bed and the neck is filled by sorted, coarse-grained, angular quartz sandstone. Left tunnel is completely detached from the sandy bed being entirely surrounded within the clay layer; the right one is connected to the sandy bed by a neck filled by sorted, coarse-grained, angular quartz sandstone. Planktonic foraminiferal fragments are present in the claystone.

PLATE 2

A) Three types of low- to very-low reliefs in symmetric *Desmograption*. The two on the right are filled by a fine arenite to siltstone rich in clay minerals and pyrite. The tunnel on the left is filled by slightly coarser sediment, rich in clay minerals and it also shows a rim enriched in pyrite. The texture of the sandy bed is coarser, richer in quartz and considerably poorer in clay minerals. Sample DSG11. Scale bar = 5 mm. B) two *Desmograption* strings characterised by a rim enriched in darker clay minerals. The trace on the right shows a medium relief while the one on the left has a very low relief; the rim of this tunnel can be traced thanks to the enrichment in clay minerals around the burrow. Sample DSG11. Scale bar = 5 mm. C) Remarkable texture differences of the sandy bed and the burrow-infilling sediments: the burrow-filling deposits is characterised by an arenite that is more pale and homogeneous, richer in quartz and poorer in opaque minerals and clay minerals if compared to the texture of the sandy bed. A darker concentration of clay minerals enhances the rim of the burrow on the left. A diagenetic-induced fracture filled by calcite cement is present above the tunnel on the left. The burrow on the left shows a very good three-dimensional, elliptical preservation; however, its relief is very low as the tunnel is mostly preserved within the sandstone bed. Sample DSG51. Scale bar = 5 mm. D) High-relief, slightly asymmetric *Desmograption* tunnel, showing a very poorly selected, medium-grained sandstone rich in quartz grains heterogeneous in size; other very scarce components as pyrite, glauconite, carbonate clasts and clay occur. This texture is very similar to the one, which constitute the related sandy bed. Sample DSG51. Scale bar = 5 mm.

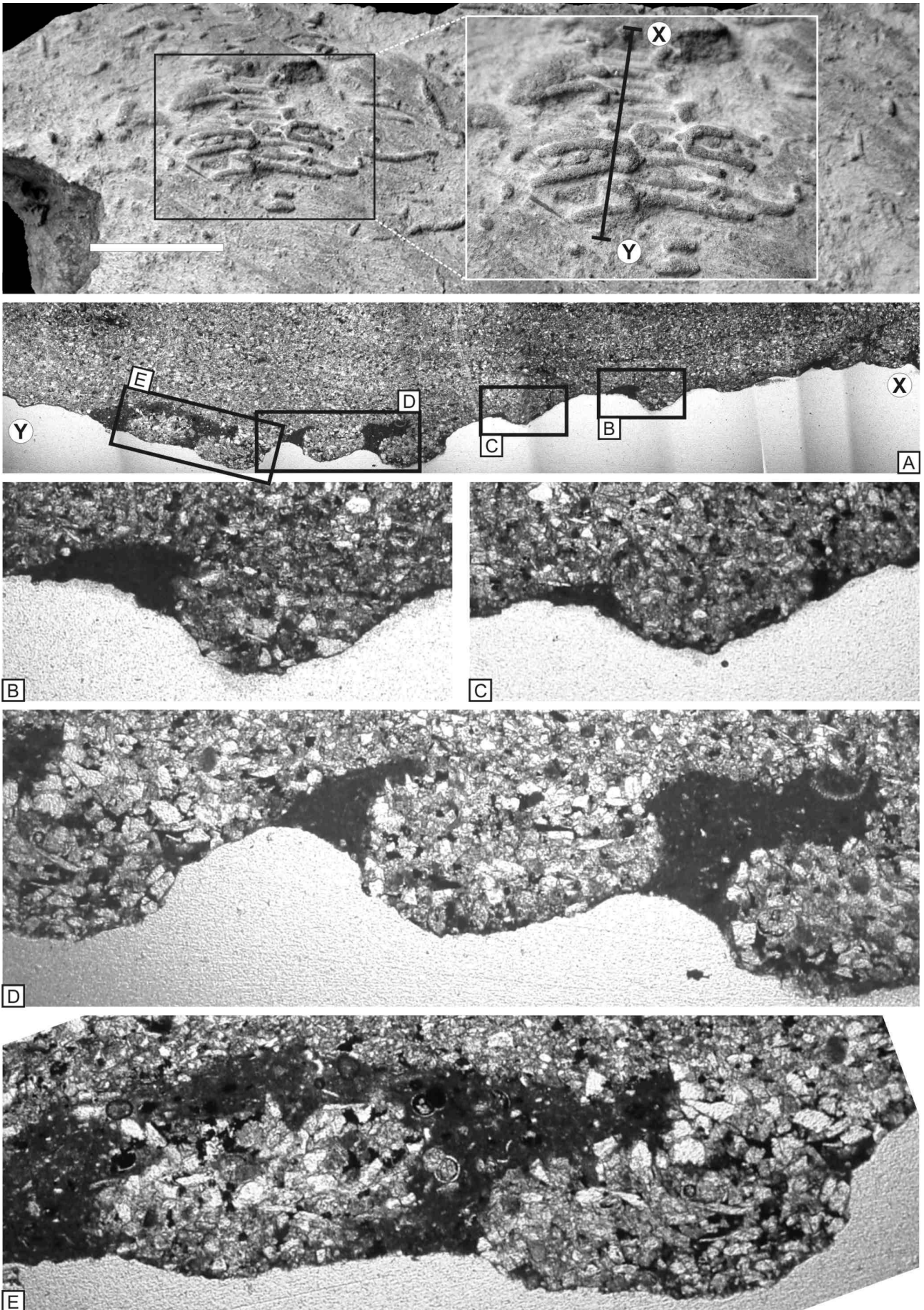


PLATE 1

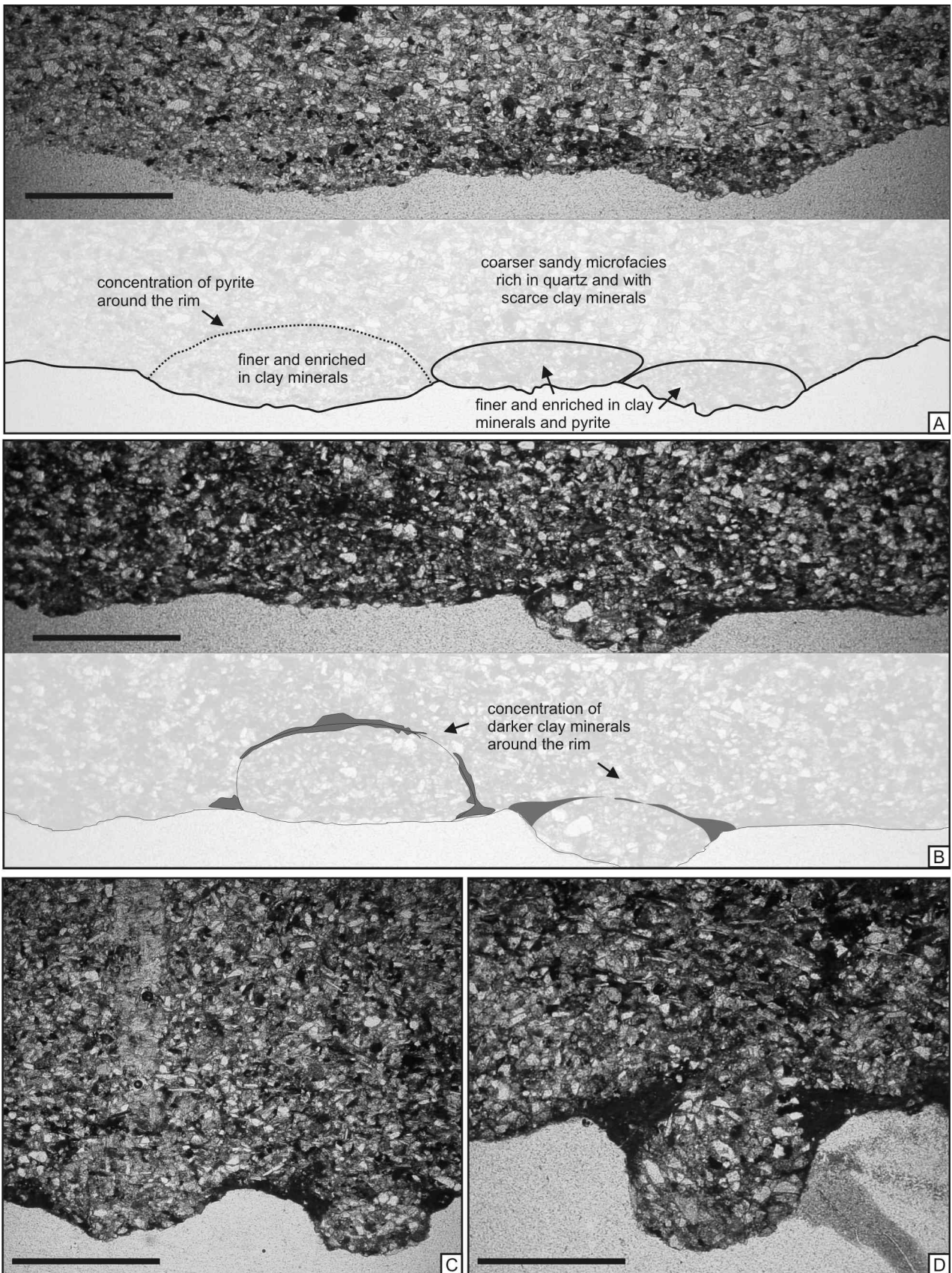


PLATE 2

3. The presence of a rim around several *Desmograption* burrows can coincide with concentrations of pyrite, phosphates, clay, or coarser-grained quartz. The occurrence of a rim represents a new feature that has not been previously described in the literature of *Desmograption* and many other graphoglyptids.

4. The presence of a rim and the differences in texture between the burrow-filling sediment and the surrounding sediment seem to be not explained by the typical “suction” model proposed by Seilacher (1977b) with a vertical, massive casting for the preservation of pre-turbidite graphoglyptids. In our study an oblique casting related to multiphase turbidite deposition seems a better solution. The hypothesis of a post-depositional origin for *Desmograption* has also been tentatively suggested, but the data recorded in this study do not provide definite evidence. Further studies are necessary to clarify the timing of *Desmograption* development compared to the turbiditic event.

5. Burrow deformation due to squeezing and oriented pressure occasionally generates compaction, flattening and asymmetry of the *Desmograption* mesh. This post-burrowing deformation seems to be comparable to features interpreted by Seilacher (2007) as post-burrowing fluting of graphoglyptids. Further analysis should verify if clear evidence of post-burrowing deformation related to oceanic flows is recorded in any *Desmograption* specimen.

6. Meiofauna or other micro-burrowers can re-work and move grains in tunnels of *Desmograption*, producing an upward transport of grains that induce variations in the burrow system and in sediment textures.

7. *Desmograption* mainly occurs in deep water thin-sandy turbidite deposits. The scarce recovery in shallower and higher energy deposits cannot be necessarily related to taphonomic and preservation processes. Trophic and ecologic factors seem still to be the main factors controlling its development. However, the absence of this ichnogenus in many deep-water turbidite deposits cannot be attributed only to erosion and extreme suction of the turbidite flow, but other factors need further explanation.

8. Some microfacies features of *Desmograption* are visible only in thin section and cannot be recorded with a standard macroscopic observation. The “suction” model suggested by Seilacher should be verified for all the other graphoglyptids (including the continuous strings in *Cosmorhappe*, *Helminthorhappe*, *Urohelminthoida*) with thin section analysis and other analyses (e.g. X-ray, fluorescence). The data obtained from these studies should help clarify the origin and preservation of *Desmograption* and of the other graphoglyptids. They would also contribute to detail the palaeoecological role and the palaeoenvironmental significance of the graphoglyptids in the fossil record.

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REFERENCES

- Bromley R. G. (1996) - Trace Fossils. Biology, Taphonomy and Application. London, Chapman & Hall, 316 pp.
- Buatois L. & Mángano M.G. (2011) - Ichnology, Organism-Substrate Interactions in Space and Time. Cambridge University Press, 358 pp.
- Centamore E., Fumanti F. & Nisio S. (2002) - The Central-Northern Apennines geological evolution from Triassic to Neogene time. *Boll. Soc. Geol. Ital.*, Vol. Spec. 1: 181-197.
- D’Alessandro A. (1980) - Prime osservazioni sull’ichnofauna miocenica della “Formazione di Gorgoglione” (Castelmezzano, Potenza). *Riv. It. Paleont. Strat.*, 86: 357-398.
- Ekdale A. A. (1980) - Graphoglyptid burrows in modern deep-sea sediment. *Science*, 207: 304-306.
- Ekdale A. A. (1985) - Paleoecology of the marine endobenthos. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 50: 63-81.
- Flügel E. (2004) - Microfacies of Carbonate Rocks. Springer-Verlag, Berlin, 976 pp.
- Folk R. (1974) - Petrology of sedimentary rocks. Hemphill Book Store, Austin, Texas, 170 pp.
- Fuchs T. (1895) - Studien über Fucoiden und Hieroglyphen. *Denkschr.k Ak. Wiss., Wien, Matem. Naturw. Kl.*, 62: 369-448.
- Fürsich F, Taheri J. & Wilmsen M. (2007) - New occurrences of the trace fossil *Palaedictyon* in shallow marine environments: examples from the Triassic-Jurassic of Iran. *Palaios*, 22: 424-432.

- Gaillard C. (1991) - Recent organism traces and ichnofacies on the deep-sea floor of New Caledonia, southwestern Pacific. *Palaios*, 6: 302-315.
- Gierlowski-Kordesh E & Ernst G. (1987) - A flysch trace fossil assemblage from the Upper Cretaceous shelf of Tanzania. In: G. Mathesis & Schandelmeier H. (Eds) - Current Research in African Earth Sciences: 217-221.
- Heard T. G. & Pickering K. T. (2008) - Trace fossils as diagnostic indicators of deep-marine environments, Middle Eocene Ainsa-Jaca basin, Spanish Pyrenees. *Sedimentology*, 55: 809-844.
- Książkiewicz M. (1977) - Trace fossils in the flysch of the Polish Carpathians. *Paleont. Pol.*, 36: 1-208.
- McCann T. (1989) - The ichnogenus *Desmograpton* from the Silurian of Wales - first record from the Paleozoic. *J. Paleontology*, 63: 950-953.
- McCann T. & Pickerill R. K. (1988) - Flysch trace fossils from the Cretaceous Kodiak Formation of Alaska. *J. Paleontol.*, 62: 330-348.
- Milighetti M., Monaco P. & Checconi A. (2009) - Caratteristiche sedimentologico-ichnologiche delle unità silicoclastiche oligo-mioceniche nel transetto Pratomagno-Verghereto, Appennino Settentrionale. *Ann. Univ. Ferrara, Museol. Sci. Natural.*, 5: 23-129.
- Miller W. (1991) - Paleoecology of graphoglyptids. *Ichnos*, 1: 305-312.
- Monaco P. (2008) - Taphonomic features of *Paleodictyon* and other graphoglyptid trace fossils in Oligo-Miocene thin-bedded turbidites of Northern Apennines flysch deposits (Italy). *Palaios*, 23: 667-682.
- Monaco P. (2011) - Morphologic variations of the trace fossil *Rutichnus* in cm-thick turbidites from the Verghereto Formation (Northern Apennines, Italy). *Riv. It. Paleont. Strat.*, 117: 161-172.
- Monaco P. & Caracuel J. E. (2007) - Il valore stratigrafico delle tracce fossili negli strato evento (*event bed*) del registro geologico: esempi significativi di ichtologia comportamentale dall'Italia e dalla Spagna. *Studi e Ricerche*, Museo "G. Zannato", Montecchio Maggiore (VI) 14: 43-60.
- Monaco P. & Checconi A. (2008) - Stratigraphic indications by trace fossils in Eocene to Miocene turbidites and hemipelagites of the Northern Apennines (Italy). In: M. Avanzini & F. Petti M. (Eds.) - Italian Ichnology - Proceedings of the Ichnology session of Geitalia 2007, VI Forum italiano di Scienze della Terra, Rimini - September 12-14, 2007. *Studi Trentini Sci. Nat., Acta Geologica*, 83(2008): 133-163.
- Monaco P. & Checconi A. (2010a) - Taphonomic aspects of the Miocene ichnofossil-*lagerstätte* from calcarenite turbiditic beds in the Verghereto Marls Formation (Northern Apennines, Italy). *Riv. It. Paleont. Strat.*, 116: 237-252.
- Monaco P. & Checconi A. (2010b) - Taphonomy of the graphoglyptid trace fossil *Desmograpton* Fuchs, 1895 at the sole of Miocene thin-bedded turbidites, Northern Apennines. *Boll. Soc. Paleont. It.*, 49: 163-172.
- Monaco P., Milighetti M. & Checconi A. (2009) - Ichnocoenoses in the Oligocene to Miocene foredeep basins (Northern Apennines, central Italy) and their relation to turbidite deposition. *Acta Geol. Pol.*, 60: 53-70.
- Monaco P., Rodríguez-Tovar F. & Uchman A. (2012) - Ich-nological analysis of lateral environmental heterogeneity within the Bonarelli level (uppermost Cenomanian) in the classic localities near Gubbio, central Apennines, Italy. *Palaios*, 27: 48-54.
- Monaco P. & Uchman A. (1999) - Deep-sea ichnoassemblages and ichnofabrics of the Eocene Scisti varicolori beds in the Trasimeno area, western Umbria, Italy. In: A. Farinacci & A. R. Lord (Eds) - Depositional Episodes and Bioevents. *Paleopelagos, Spec. Publ.*: 39-52. Univ. La Sapienza, Roma
- Mutti E. (1992). Turbidite sandstone. AGIP S.p.a., San Donato Milanese, 275 pp.
- Olivero E. B., Lopez M. I., Malumian N. & Torres Carbonell P. J. (2010) - Eocene graphoglyptids from shallow-marine, high energy, organic-rich, and bioturbated turbidites, Fuegian Andes, Argentina. *Acta Geol. Pol.*, 60: 77-91.
- Pettijohn F. J., Potter P. E. & Siever R. (1987) - Sands and Sandstones. Springer-Verlag, New York, 553 pp.
- Rona P., Seilacher A., Luginland H., Seilacher E., Vargas C. D., Vetriani C., Bernhard J. M., Sherrell R. M., Grassle J. F., Low S. & Lutz R. A. (2003) - *Paleodictyon*, a living fossil on the deepsea floor. *Eos Transactions AGU, Fall Meeting Suppl., Abstract OS32A-0241*, 84: 102.
- Sacco F. (1888) - Note di Paleocnologia italiana. *Atti Soc. Ital. Sci. Nat.*, 31: 151-192.
- Seilacher A. (1962) - Paleontological studies on turbidite sedimentation and erosion. *J. Geol.*, 70: 227-234.
- Seilacher A. (1974) - Flysch trace fossils: evolution of behavioural diversity in the deep-sea. *N. Jahrb. Geol. Paläontol. Monat.*, 4: 233-245.
- Seilacher A. (1977a) - Evolution of trace fossil communities. In: A. Hallam (Ed.) - Patterns of Evolution as Illustrated by the Fossil Record. Developments in Paleontology and Stratigraphy, Elsevier, 4: 359-376.
- Seilacher A. (1977b) - Pattern analysis of *Paleodictyon* and related trace fossils. In: T.P. Crimes & J.C. Harper (Eds), Trace Fossils 2. *Geol. J.*, Spec. Issue 9, London: 289-334.
- Seilacher A. (1978) - Use of trace fossil assemblages for recognizing depositional environments. SEPM, Short Course, 5: 167-181.
- Seilacher A. (2007) - Trace Fossil Analysis. Springer Verlag, Berlin, 226 pp.
- Shanmugam G. (2001) - Ten turbidite myths. *Earth-Sci. Rev.*, 58: 311-341.
- Swinbanks D.D. (1982) - *Paleodictyon*: the traces of infaunal Xenophyophores? *Science*, 218: 47-49.
- Uchman A. (1995) - Taxonomy and paleoecology of flysch trace fossils: the Marnoso-arenacea Formation and associated facies (Miocene, Northern Apennines, Italy). *Beringeria*, 15: 116 pp.

- Uchman A. (1999) - Ichnology of the Rhenodanubian Flysch (Lower Cretaceous-Eocene) in Austria and Germany. *Beringeria*, 25, 67-173.
- Uchman A. (2004) - Phanerozoic history of deep-sea trace fossils. In: McIlroy D. (Ed.) - The Application of Ichnology to Palaeoenvironmental and Stratigraphic Analysis. *Geol. Soc. London, Spec. Publ.*, 228:125-139.
- Uchman A. (2007) - Deep-sea Ichnology: development of major concepts. In: Miller III W. (Ed.) - Trace Fossils, Concepts, Problems, Prospects. Elsevier: 248-263.
- Uchman A., Janbu N. S. & Nemeč W. (2004) - Trace fossils in the Cretaceous-Eocene flysch of the Sinop-Boya-bat Basin, central Pontides, Turkey. *Ann. Soc. Geol. Pol.*, 74: 97-235.
- Wetzel A. (1983) - Biogenic structures in modern slope to deep sea sediments in the Sulu Sea Basin, Philippines. *Palaeogeogr., Palaeoclimatol., Palaeoecol.*, 42: 285-304.

