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Sequestrichnia – an ethological category of marine trace fossils recording the collection and stowage of nutritional material within burrows

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ABSTRACT

Morphologically diverse trace fossils belonging to different ichnogenera share similar characteristics in that their producers: 1) sequester organic-rich sediment from the seafloor, or from suspension when plenty of benthic food is available; 2) transfer it downward; 3) stow it in a burrow; and 4) utilize it later during times when benthic food availability is restricted. Organic matter delivery to the seafloor is subject to pronounced seasonal fluctuations. Storage is optimal if the cache is located in anoxic sediment and beyond the reach of competing burrowers. Since the most reactive (i.e., nutritional) organic substances become oxidized first, refractory organic matter is enriched deeper in the substrate. If, however, reactive organic matter is brought in contact with refractory organic matter, priming may take place. Priming refers to enhanced microbial remineralization of refractory organic matter, typically up to 30%. This process is especially efficient where fresh organic matter is transferred into anoxic deposits. In addition, if an open burrow is produced within anoxic sediment, microbial activity is stimulated by the steep geochemical gradient between anoxic host sediment and oxygenated water in the lumen. The microbes and/or their metabolic products may also serve as food source. Consequently, stowing behaviour is an efficient nutritional and survival strategy for animals living in settings that experience strongly fluctuating delivery of benthic food, by conserving food resources during times of plenty to be used when starving.

KEY WORDS
Behaviour,
nutritional strategy,
cache,
seasonality,
deep sea.

RÉSUMÉ

Sequestrichnia – une catégorie éthologique de traces de fossiles marins signalant la collecte et le stockage de matériel nutritionnel dans des terriers.

Les ichnofossiles morphologiquement diversifiés appartenant à divers ichnogenres partagent des caractères comparables en ce sens que leurs producteurs : 1) séquestrent des sédiments riches en matières organiques du fond marin, ou bien en suspension lorsque la nourriture benthique est abondante ; 2) le transfèrent vers le bas ; 3) les stockent dans un terrier ; et 4) les utilisent plus tard lorsque la disponibilité de nourriture benthique est limitée. L'apport de matière organique au fond de la mer est soumis à des fluctuations saisonières prononcées. Le stockage est optimal si la cachette est située dans des sédiments anoxiques et hors de portée des fouisseurs concurrents. Étant donné que les substances organiques (i.e., nutriotionelles) sont oxydées en premier, la matière organique réfractaire est enrichit plus profondément dans le substrat. Toutefois, si la matière organique réactive est mise en contact avec la matière organique réfractaire à une reminéralisation microbienne accrue de la matière organique réfractaire, généralement jusqu'à 30 %, peut survenir. Ce processus est particulièrement efficace lorsque la matière organique fraîche est transférée dans des sédiments anoxiques. En outre, si un terrier ouvert est produit dans un sédiment anoxique, l'activité microbienne est stimulée par le fort gradient géochimique entre le sédiment hôte anoxique et l'eau oxygénée dans le lumen du tube. Les microbes et/ou leurs produits métaboliques peuvent également servir source de nourriture. Par conséquent, le comportement de stockage (Séquestrichnien) est une stratégie nutritionelle et de survie efficace pour les animaux vivant dans des environnements où la disponibilité de nourriture benthique fluctue fortement, car il permet de conserver les ressources alimentaires pendant des périodes d'abondance pour les utiliser en cas d'une famine.

MOTS CLÉS
Comportement,
stratégie alimentaire,
cachette,
saisonnalité,
mer profonde.

INTRODUCTION

Trace fossils record the behaviour of animals in the past (Abel 1935; Richter 1941). Commonly, the taxonomic affinity of the tracemakers is not known and their behaviour, therefore, must be deciphered from trace-fossil characteristics and habitat (e.g. Seilacher 2007). In this way, the main types of behaviour can be distinguished and ascribed to ethological categories such as domichnia, cubichnia, repichnia, pascichnia, fodinichnia, referring respectively to dwelling, resting, moving, vagile deposit or detritus feeding on the surface, and subsurface sediment feeding, as outlined, among others, by Seilacher (1953), Frey & Seilacher (1980), Bromley (1996) and Vallon *et al.* (2016). Some of the ethological categories are very broad and include several behavioural variants, such as repichnia for crawling on the surface, but also moving within the substrate. Ongoing research of trace fossils in combination with an increased understanding of physical, (geo)chemical and other environmental factors and biological responses to them in ancient and modern settings have yielded an increasingly detailed and differentiated view on the reaction of animals to their habitats, consequently, leading to the recognition of new behavioural categories. For instance, out of the well-established and broad category "fodinichnia" the category "agrichnia" was proposed for patterned graphoglyptid traces such as *Paleodictyon* Meneghini, 1850 (Ekdale *et al.* 1984). Agrichnia refer to subsurface farming of microbes or capturing of small invertebrates by the trace producer (Seilacher 1977a). In addition, the category "chemichnia" was established for such common trace fossils as *Chondrites* Sternberg, 1833 and *Trichichnus* Frey, 1970 (Bromley 1996); the producers of these burrows follow a chemosymbiotic style of nutrition while microbes or microbially processed compounds are utilized (e.g. Seilacher 1990). Furthermore, for trace fossils recording that their producers followed almost exactly a previous trace, the category of "sequorichnia" was introduced (Nara & Ikari 2011; Wetzel *et al.* 2020). Further behavioural categories have been proposed (see compilation, for instance, by Vallon *et al.* 2015) but since they are irrelevant to this paper they are not discussed here.

In the present study, the ethological category of trace fossils "sequestrichnia" is discussed. The establishment of this relatively new behavioural category is based on the observations that the producers of morphologically diverse trace fossils belonging to different ichnogenera and ichnofamilies sequester temporarily available organic-rich material on the sediment surface or from suspension and stow it in their burrows to be utilized during times of reduced benthic food availability. This concept was originally proposed by Uchman & Wetzel (2016) in a conference abstract and later applied to individual trace fossils (Uchman & Wetzel 2017; Jurkowska *et al.* 2018; Uchman & Rattazzi 2018; Uchman *et al.* 2019; Šamánek *et al.* 2022). Meanwhile the growing number of observations on trace fossils showing such a nutritional strategy as well as on modern counterparts impels us to address this type of behaviour and its environmental implications systematically. This is the purpose of the present paper.

BACKGROUND

Organic matter available on the seafloor fuels benthic life (e.g. Gage & Tyler 1991). In nearly all subaqueous environments, organic matter delivery to and deposition on the sediment surface fluctuates considerably due to seasonally varying primary production (e.g. Smith *et al.* 2002, 2018; Lutz *et al.* 2007). In addition, where water depth exceeds a few hundred metres, the amount of organic matter arriving on the seafloor decreases exponentially with water depth due to oxidation while settling through the water column (e.g. Suess 1980; Burdige 2006). The size and shape of the organic particles influence settling velocity, and hence the degree to which they become oxidized during transport; large, rapidly settling particles are less affected than small ones (e.g. Shaw *et al.* 2020). In the deep sea, days to weeks after a seasonal bloom in surface water organic matter arrives as detritus on the seafloor, the benthos experiences high food availability for a short period of several weeks to a few months, followed by low organic matter input for a longer time of several months or longer (e.g. Graf 1992; Smith *et al.* 2002). Commonly, organic matter is associated with the clay fraction due to adsorption on clay mineral surfaces and hydraulic sorting (e.g. Mayer 1999; Burdige 2006). At the sediment surface, a considerable proportion of organic matter is oxidized so long as it is located within the oxygenated zone (e.g. Smith *et al.* 1994, 2008; Tromp *et al.* 1995). Therefore, organic matter burial is strongly affected by sedimentation rate and only subordinately by primary production (e.g. Müller & Suess 1979; Stein 1991; Burdige 2007). Increasing sediment deposition, however, may dilute the organic matter content (e.g. Tyson 2001).

Two scenarios need to be distinguished concerning sedimentation rate. At sedimentation rates exceeding *c.* 2 cm kyr^{-1}, organic matter is buried and anoxic conditions develop within the deposits (e.g. Jung *et al.* 1997). Below the threshold value of 2 cm kyr^{-1}, sediment accumulation is so low that the deposits become completely oxidized, represented in the rock record by oceanic red beds barren of organic matter (e.g. Wagreich & Krenmayr 2005; see also Jung *et al.* 1997). As long as organic matter (i.e., benthic food) is available, animals bioturbate these deposits and enhance the flux of oxygen into the sediment, which in turn causes organic matter oxidation (e.g. Wetzel & Uchman 2018). Nonetheless, below the sediment surface low-oxygenated to slightly anoxic conditions may locally exist for some time in oceanic red beds (e.g. Hartmann 1979; Berner 1981; Myrow 1990). Such conditions prevail in the wide areas of the abyssal oceans.

When exposed to oxygen, the most reactive organic compounds are degraded first (e.g. Nierop *et al.* 2017). The reactive compounds are preferentially utilized by benthic animals because of the easily accessible nutritional value (e.g. Rullkötter 2006). The higher the organic matter delivery to the seafloor, the more intense is bioturbation (e.g. Boudreau 1998). Due to increasing bioturbation, the oxygenated zone is expanded and the residence time of organic matter therein (i.e., oxygen exposure time; Hartnett *et al.* 1998) becomes pro-

longed facilitating oxidation of organic matter (e.g. Smith & Rabouille 2002; Burdige 2006). In turn, the delivered fresh organic matter becomes dispersed within the surface mixed layer (e.g. Boudreau 1998) and thus, relatively diluted. In fine-grained, anoxic sediments, the oxic zone around burrows ventilated with oxygenated water remains relatively thin, on the order of 1-2 mm (e.g. Meysman *et al.* 2010); the steep geochemical gradient between tube water and host sediment stimulates microbial activity (e.g. Kristensen & Kostka 2005).

During bioturbation, relatively labile organic matter from the sediment surface is brought into close association with more refractory material deeper in the sediment over a wide range of time scales, depth scales, and geometries (e.g. Aller & Cochran 2019). For instance, organic particles of different reactivity and origin can be intermixed in a diffusion-like manner (Gerino *et al.* 1998; Meysman *et al.* 2003). Bringing together relatively labile and refractory organic matter by bioturbation promotes the phenomenon referred to as priming (Aller & Cochran 2019). Priming is defined as the enhanced microbial remineralization (conversion to CO_2) of otherwise low-reactive (refractory) organics in association with the decomposition of relatively reactive organic material in soils, aquatic sediments and natural waters (Löhnis 1926; Graf 1992; Hee *et al.* 2001). In particular, the input of fresh organic matter strongly stimulates microbial activity under anoxic conditions and in sediments relatively low in reactive organic matter; remineralization rates related to priming may reach *c.* 30% (van Nugteren *et al.* 2009). Even low amounts of organic matter buried below the oxygenated zone in the anoxic zone stimulate priming, and thus the activity of microbes; the microbes and/or their metabolic products represent a food source for burrowing animals (e.g. van Nugteren *et al.* 2009).

In addition, sequestered material can also be exploited indirectly, probably by solutions and ectoenzymes. The enzymes excreted by bacteria can be particularly active in burrows (Boetius 1995). This leads to the transformation of particulate organic matter into more labile or amorphous organic matter (cf. Boetius *et al.* 1996; Bélanger *et al.* 1997; Cao *et al.* 2013; Aller & Cochran 2019) that can be more easily taken up by the body surface of a burrowing animal. For instance, the flatworm *Paracatenula* Sterrer & Rieger, 1974, can absorb nutrition through its body surface (Jäckle *et al.* 2019). Some invertebrates stimulate the flow of pore water around their burrows by irrigation, and the nutritional organic matter can be leached (Brand *et al.* 2013), a process possibly also involving microbes, and utilized as food. All of this would reduce the energy-costly sediment reworking by body movements.

Organic matter available on the seafloor fuels benthic life. In oxygenated settings, benthic biomass decreases roughly exponentially with depth in sediment (e.g. Rex *et al.* 2006). The benthic animals get their nutrition in various ways; among them are opportunistic animals like holothurians that may respond immediately to the input of food and ingest organic-rich flocs as they arrive on the seafloor (e.g. Smith *et al.* 1986; Lauermann *et al.* 1997). Shallow-penetrating vagile echinoids that plough through the sediment and mix it as they feed within the surface mixed layer (e.g. Lohrer *et al.* 2004; Wetzel

2009). Some animals convey organic-rich material downward below the mixed layer (e.g. Jumars *et al.* 1990; Levin *et al.* 1997), a behaviour that is addressed in detail below.

GENERAL CONCEPT

The concept of stowing behaviour is rather simple: Animals collect organic-rich sediment or select organic particles on the sediment surface or from suspension, transport the material along their body or via their gut deep into the deposits and store it there to be utilized during periods of low food availability on the seafloor. Optimal storage conditions are accomplished if the sequestered material is not exposed to oxygenated water and if it is stowed below the intensely mixed zone, and thus below the reach of other animals competing for food. Although the general concept of sequestrichnia is simple, various trace-fossil producers have developed many ethological variants that differ in detail from one another and provide niche-related specialization as explained by the examples in the following.

Two general burrow morphologies are distinguished: spreite burrows and tubular open burrow systems. For each category an example is addressed in detail, whereas similar burrows of the same category are only briefly dealt with. In each case, principal aspects of burrow morphology, evidence of sequestration, and subsequent utilization of stowed material are outlined.

Spreite burrows

Ichnogenus *Zoophycos* Massalongo, 1855
(Fig. 1)

Zoophycos represents a regularly to irregularly coiled, simple to complex lobate spreite burrow that has shown changes in shape, size, and geometry through the Phanerozoic (e.g. Seilacher 1977b; later refined by Chamberlain 2000 and Zhang *et al.* 2015). For most *Zoophycos* older than the late Mesozoic, different ways of spreite production and behaviour are possible, including fodinichnial behaviour (e.g. Olivero & Gaillard 1996). In contrast, for Late Cretaceous to modern *Zoophycos,* sequestrichnial behaviour of the producers appears to be common. These are outlined here.

Evidence for sequestration of sediment on the seafloor is given by the colour of the spreite fill in combination with enlarged organic carbon values. The spreite consists of alternating lamellae containing host sediment and material likely sequestered on the seafloor and transferred downward; pellets may occur in both types of lamellae (Fig. 1). The sequestered sediment is commonly darker in greenish-grey host sediment or grey in reddish host sediment. In both cases, the organic carbon content of the spreite fill is higher than that of the host sediment; for example, the black spreite material of Paleocene *Zoophycos* (Gurnigel Flysch; Seligraben/Gurnigelbad, Switzerland) contains 1.1-1.7% C_{org} compared to 0.5-0.7% C_{org} in the green host sediment (see Wetzel & Uchman 1998: fig. 1d, e). In the Eocene of Arnakatxa Headland near Bilbao,

0.3-0.7% C_{org} occurs in grey spreite material and < 0.1% C_{org} in red limestone lutite alternations. However, in deep oceanic settings, also lighter material deposited during periods of enhanced nannoplankton productivity can be transferred downward (Fig. 1A). Other tracers, e.g. volcanic ash, also record a downward sediment transfer (e.g. Kotake 1991). For Pleistocene and Holocene *Zoophycos,* chronometric age data record a sequestration of surface material as the spreite fill is generally younger than the host sediment (e.g. Löwemark & Werner 2001; Leuschner *et al.* 2002; Küssner *et al.* 2018). In well-dated sediments, *Zoophycos* appears to be produced when environmental conditions switch to a starved sedimentation regime (Küssner *et al.* 2018) or during times of enhanced seasonality (e.g. Löwemark *et al.* 2006; Wetzel *et al.* 2011; Dorador *et al.* 2016).

The *Zoophycos* producer stows the sequestered material commonly in the form of mud lamellae or pellets in the spreite. Pellets, however, occur in both host and sequestered sediment, suggesting that they could have provided "seed" microbes housed in the gut to the spreite "bioreactor" (Fig. 1C). Therefore, a priming scenario appears realistic, in particular as subsequent lamellae overlap previous ones, indicating partial reworking and utilization of the spreite fill by the tracemaker (Fig. 1D). Since *Zoophycos* represents very likely a lifetime burrow of its producer (e.g. Wetzel & Werner 1980), the worm-like tracemaker probably took advantage of priming on a time scale of months to years.

Ichnogenus *Polykampton* Ooster, 1869

Polykampton occurring in Cretaceous (Albian) to Oligocene deposits represents a horizontal median tunnel with lateral spreite lobes, which alternate on either side of the tunnel and are slightly inclined to bedding; the tunnel runs within the interval of the spreite lobes or underneath (Uchman *et al.* 2019). *Polykampton* is produced: 1) in the sandy or muddy interval of (turbiditic) event beds; 2) along the mudstone-sandstone interface; or 3) across the sandstone-mudstone transition in turbiditic beds. The spreite and the main tunnel contain mud that is enriched in organic matter compared to the surrounding host sediment (C_{org} 3.05% vs 1.05%; Uchman *et al.* 2019). The mud was evidently introduced from above into the burrow. The organic content of spreite lobes could be a source of additional benthic food in the short term, just after organic-rich material was sequestered on the surface and stowed in spreite lobes. In addition, or alternatively, the producer could utilize organic matter when passing through the tunnel during the construction of a new lobe. By then, the sequestered organic-rich material might have already been altered to some degree by microbial activity.

Ichnogenus *Tubulichnium* Książkiewicz, 1977
(Fig. 2)

Tubulichnium is an oblique to horizontal, unbranched, blind-ending tube showing some internal organization due to slight vertical shift; the margins are densely lined with ellipsoidal
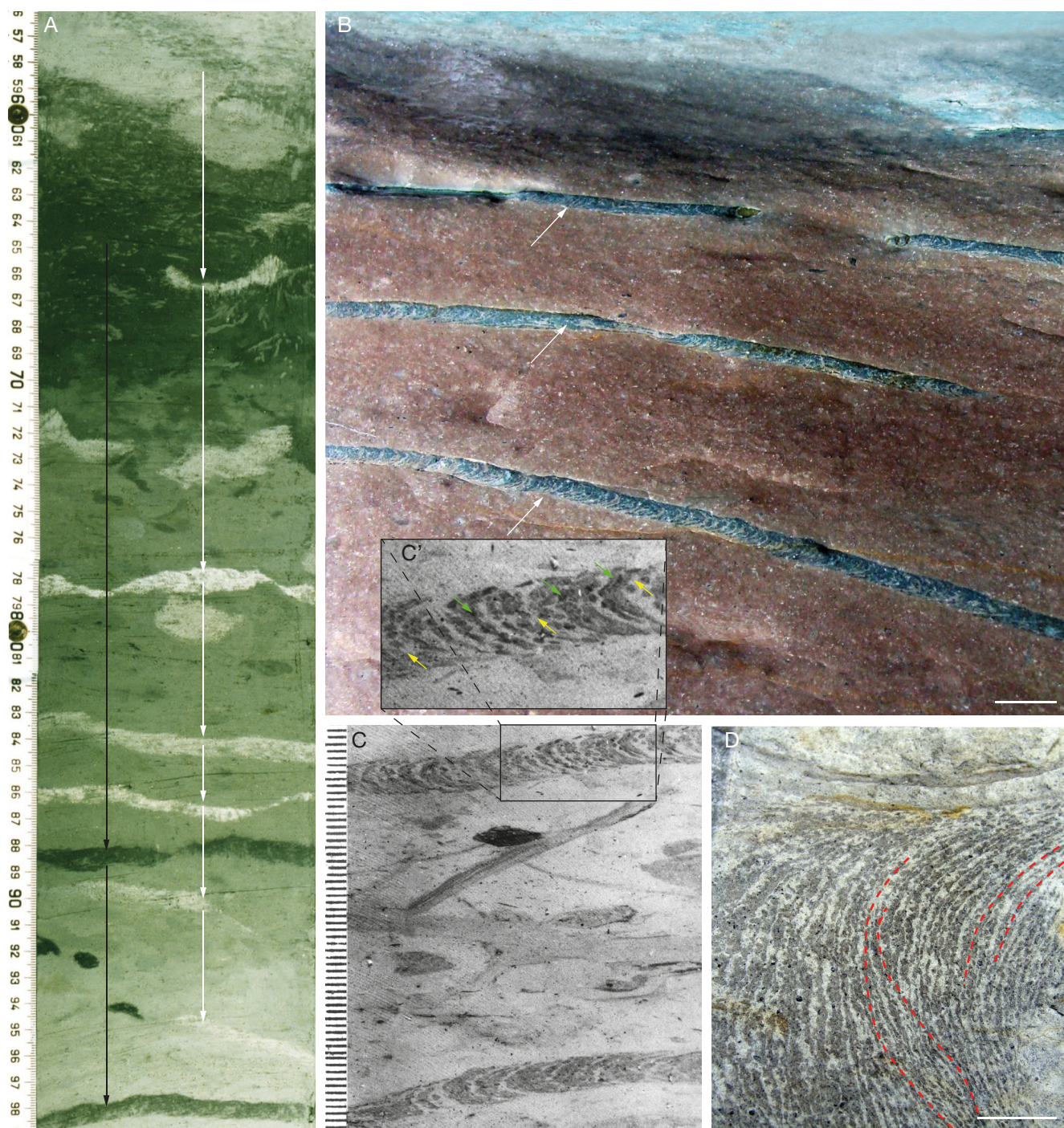
FIG. 1. — Sequestered and downward-transferred material in *Zoophycos* Massalongo, 1855: **A**, black mud and white nannofossil ooze displaced for > 26 (**black arrows**) and > 23 cm (**white arrows**) downward, respectively, as indicated by colour and composition of sediment (Institute of Geological Sciences Kiel, Germany, core 16867-3; 2.2°S, 5.1°E, 3894 m water depth, mid Atlantic; 16.56-16.99 m core depth); **B**, sequestered organic-rich grey sediment filling *Zoophycos* spreite (**white arrows**) produced in red pelagic mud (Maastrichtian, Zumaia, Spain); **C**, homogeneous and pelleted sequestered sediment alternating with host sediment in *Zoophycos* spreite; inset (**C'**) showing pellets occurring in both sequestered sediment (**green arrows**) and host sediment (**yellow arrows**) (DSDP Leg 93, Site 605, Core 16-4, 59.5-66.5 cm core depth; for details see Wetzel 1987); **D**, truncation of lamellae (marked with **red stippled lines**) in *Zoophycos* spreite in horizontal section, indicating reworking of previously emplaced material (Paleogene, Zumaia, Spain). Scale bars: 1 cm.

muddy pellets. The sequestration of material, which is then stowed in muddy laminae and pelleted fill, is documented by its composition: it contains *c.* 1.5% C_{org} and 20% $CaCO_3$ compared to *c.* 1.1% C_{org} and *c.* 26% $CaCO_3$ in the host sediment and 0.7% C_{org} and 12% $CaCO_3$ in the overlying mud in the studied Upper Cretaceous to Paleogene specimens (Uchman & Wetzel 2017). These data point to selective enrichment of organic-rich particles in the burrow. Microbial activity during priming may generate CO_2 that lowers alkalinity and fosters the dissolution of carbonate (van Nugteren *et al.* 2009).

Fig. 2. — *Tubulichnium* Książkiewicz, 1977 in turbiditic sand (Inoceramian Beds, Campanian-Paleocene, Magura Nappe, Słopnice, Poland): **A**, *Tubulichnium* penetrating down into turbidite sandstone; typical lining with mud pellets. Depression (surrounded by a **white stippled line**) resulting from sediment collapse after abandonment of the tube inhabited by the producer; **B**, **C**, traverse (**B**) and transverse oblique (**C**) sections of *Tubulichnium*. Pelletal laminae occurring at the 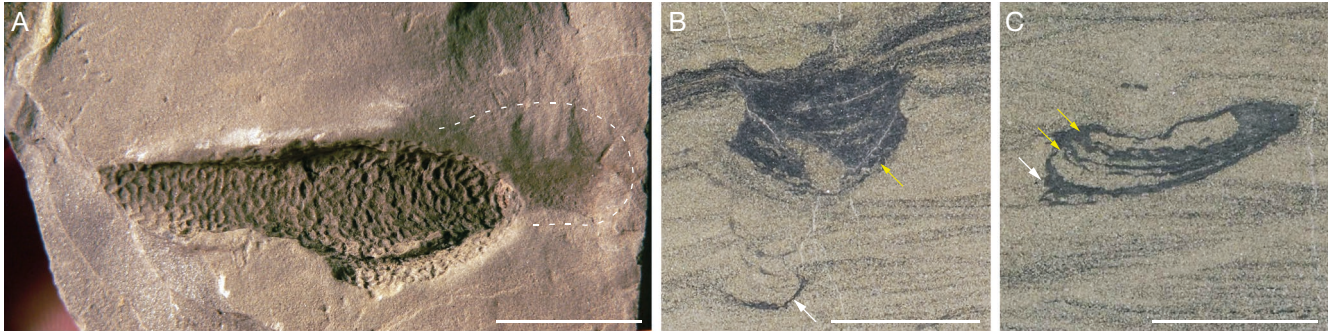base of the burrow (**white arrows**) and also in intermediate position (**yellow arrows**); local truncation of pellet-rich layers indicating subsequent, perhaps multiple reworking by the producer. Scale bars: 1 cm.

Although no clear spreite is developed, a partly laminated fill exhibiting local truncations (Fig. 2B, C) suggests utilization of the stowed material, as in the case of *Zoophycos*.

TUBULAR OPEN BURROW SYSTEMS

Ichnogenus *Cladichnus* D'Alessandro & Bromley, 1987

The *Cladichnus* burrow (Cretaceous-Eocene) consists of primary successively branched and radiating tubes, which contain a meniscate fill. These traces are preferentially constructed in anoxic sediments. New branches are produced roughly at the same level as previous ones, implying that appropriate conditions for stowing were encountered by the producer. In contrast, new branches constructed below or above may target stronger or weaker reducing conditions or represent a response to the downward or upward migration of the redox boundary.

Collection and transfer of surface material is recorded by the tubes' fill that was analyzed in detail for the ichnospecies *Cladichnus parallelum* Wetzel & Uchman, 2013, which contains 0.8% C_{org} and 0.3% $CaCO_3$ compared to 0.3% C_{org} and 64% $CaCO_3$ in the host sediment Cretaceous in age (Wetzel & Uchman 2013). The fill of the branches is interpreted to indicate priming that provided microbes (or their metabolic products) as an additional subsurface food source (cf. Mayer *et al.* 2001; van Nugteren *et al.* 2009).

Most likely, the trace producer ingested a considerable proportion of the filling material before emplacing the final, now meniscate fill. The arrangement of the branches has further implications. Branches at a level above the previous ones could allow utilization of upstreaming pore water, probably carrying nutritious compounds. Alternatively, a shift of the redox boundary may have caused the construction of new levels of open burrows.

Ichnogenus *Phymatoderma* Brongniart, 1849

Phymatoderma (Lower Jurassic-Pliocene) appears to be similar in some aspects to *Cladichnus* since it represents an actively filled burrow system consisting of numerous branches, which

deviate at a few levels from a common stem, diverging distally (e.g. Fu 1991; Izumi 2012). However, the producers tended to operate in a plane or only a few levels, less than in *Cladichnus*. In most cases, the branches are filled with pellets that are darker than the surrounding material (e.g. Uchman 1999), suggesting a higher content of organic matter that could foster enhanced microbial activity (e.g. Izumi *et al.* 2015). In black shales, in contrast, the pellets are lighter than the host sediment but document incorporation of surface detritus (Seilacher 1978; Izumi 2012).

Ichnogenus *Thalassinoides* Ehrenberg, 1944
(Fig. 3)

Crustaceans living in the modern deep South China Sea produce *Thalassinoides*-like burrows that document a sequestrichnial behaviour. Two kinds of burrows were encountered, which contained abundant foraminiferal tests stowed in greenish anoxic sediment. One burrow type contains benthic agglutinated foraminifera tests, which consist mainly of Pinatubo-1991 ash but were stowed below the ash in anoxic sediment (Kaminski & Wetzel 2004). The other kind of *Thalassinoides* occurs in water depths below the CCD; it exhibits a laminated fill consisting of calcareous planktonic foraminiferal tests that are stowed and preserved in the burrow, whereas they are already dissolved in the overlying hemipelagic sediment from which they originate (Wetzel & Unverricht 2013). The calcareous foraminiferal tests must have been stowed shortly after their deposition; otherwise they would show dissolution features. Partly truncated laminae in the burrow imply later reworking by the producer (Fig. 3).

Ichnogenus *Avetoichnus* Uchman & Rattazzi, 2011
(Fig. 4)

Avetoichnus (Paleocene-Oligocene) represents a mid-tier burrow consisting of a mostly horizontal to subhorizontal helix enveloping a central tube that was probably an open tunnel when the tracemaker lived. The tube contains grey mud, whereas the spiral is filled with black, probably

organic-rich mud that likely originated from the overlying pelagic sediment (Uchman & Rattazzi 2011). The tube resembles a pinched open burrow that truncates the inner edges of the helical turns, which were already filled with dark mud when the tunnel was still inhabited. Chemichnia like *Chondrites* co-occur with *Avetoichnus* (Fig. 4).

The colour of the helical fill suggests that it was displaced downward. Furthermore, the partial truncation of the inner turns of the spiral points to later reworking by the tracemaker. Very likely, the organic material in the spiral fostered the development of reducing conditions therein whereas the central tunnel was open and oxygenated water could be circulated through it by the inhabitant. Thus, a steep geochemical gradient developed across the tunnel margin between anoxic host sediment and oxic water in the lumen, a situation known to enhance microbial activity (e.g. Meysman *et al.* 2010). Thus, the trace-fossil producer sequestering organic-rich material on the seafloor appears to have constructed an organic-rich subsurface domain that rapidly became anoxic. Therefore, this trace is classified as a sequestrichnion.

OTHER POSSIBLE SEQUESTRICHNIA

The burial of labile organic matter in anoxic sediments deep below the surface mixed layer strongly suggests priming induced by the trace producers, probably wormlike animals such as echiurans, sipunculids, and polychaetes together with crustaceans. Besides utilizing the sequestered burrow fill directly as indicated by subsequent reworking, some trace-fossil producers burrowed down and construct a cache underneath a domain, which is already enriched in organic matter like seagrass or wood (e.g. Griffis & Suchanek 1991; Bojanowski & Wetzel 2024). From this perspective, some other trace fossils could also be sequestrichnia.

At least some specimens of the spreite burrow *Teichichnus zigzag* Frey & Bromley, 1985 occurring in Jurassic deposits record sequestrichnial behaviour (e.g. Wetzel *et al.* 2023). *Teichichnus zigzag* exhibits: 1) a spreite enriched in organic-rich material relative to the host sediment; 2) no reworking halo around the spreite (thus indicating that the organic matter was introduced from above); 3) lamellae produced later that systematically crosscut previously produced ones, and hence indicate reworking by the producer. It can thus be excluded that reworking represents a response to erosion of the sediment surface, because reworking of the spreite is locally restricted. Furthermore, in calm lagoonal bayfill deposits, *T. zigzag* is common (Knaust 2018). In these settings, hyperpycnal flows may provide organic matter. Therefore, a sequestrichnial behavior of the *T. zigzag* tracemakers in calm lagoonal settings is highly likely though it has not yet been demonstrated.

Other spreite burrows, for instance *Rhizocorallium commune* Schmid, 1876, are extensively filled with pellets. They were produced in dysoxic, low-energy mud (Knaust 2013), and could represent sequestrichnia. Unfortunately, TOC data of the spreite fill and host sediment are not available and, therefore, clear evidence of sequestrichnial behaviour is lacking although it is not unlikely.
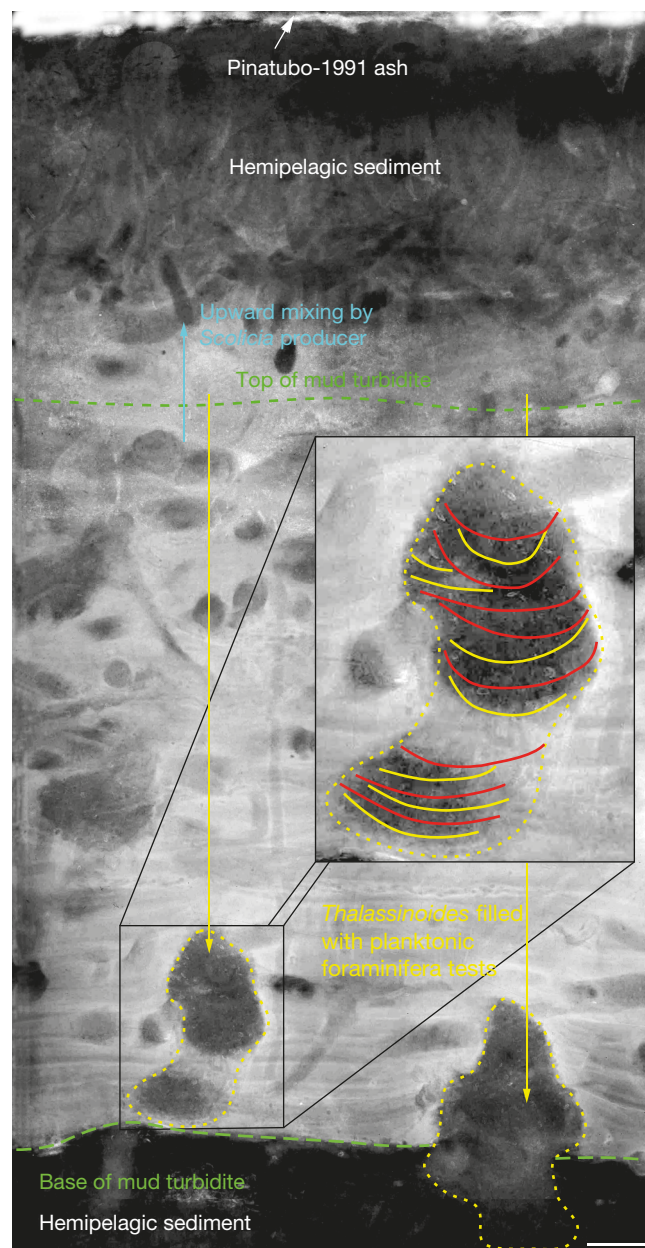
FIG. 3. — *Thalassinoides* Ehrenberg, 1944 filled with planktonic foraminifera tests (downward displacement marked by a **yellow arrow**) in a sub-CCD setting indicating rapid sequestration after deposition on the sea floor; inset showing local truncation (**red lines**) of laminae (**yellow lines**), indicating subsequent, probably multiple reworking by the producer. (RV Sonne cruise 114, core 27-1, 0-21 cm sediment depth; 15°45.00'N, 115°45.00'E, central South China Sea, 4220 m water depth; for details see Wetzel & Unverricht 2013). Scale bar: 1 cm.

Halimedides Lorenz von Liburnau, 1902, Cambrian (Series 2) to Recent in age, is a system of horizontal tunnels with chambers strung along it, not rarely in the context of poorly oxygenated deposits (Fernández-Martínez *et al.* 2021). When preserved in full relief, the chambers are filled with darker material than in the surrounding rock (e.g. Uchman 1999). The chambers, which have been interpreted as food caches (Gaillard & Olivero 2009; Lukeneder *et al.* 2012), could be good places for microbial processing of organic matter.

Lepidenteron mantelli (Geinitz, 1850) is a burrow in Upper Cretaceous marls of the deeper continental shelf. It is filled with sediment rich in plant material, which is strongly pyritized, foremost with pyrite framboids (Jurkowska *et al.* 2018). The plant material was actively collected, was a substrate for microbial activity and probably promoted priming. Therefore, this trace fossil could be partly sequestrichnial and partly chemichnial.

Gyrophyllites Glocker, 1841, Cambrian(?) and Early Ordovician to Cenozoic in age, is composed of a vertical to sub-vertical shaft with lateral, radial, petal-like lobes that may be repeatedly distributed at a few levels. The lobes may be filled with organic-rich material from the underlying or overlying bed, and their position at different levels was modulated by the migration of the redox boundary (Strzeboński & Uchman 2015; Muñoz *et al.* 2019). The fill of the lateral lobes could promote microbial processing including priming. However, in the case of *Gyrophyllites,* the mud appears to have been taken not only from the seafloor but also from of a bed beneath it, in cases where the proper mud was not present on the seafloor, in particular if a decelerating, low-erosive gravity flow rapidly deposited sand that covered and preserved the previous seafloor including the topmost organic-rich interval.

Some *Planolites* Nicholson, 1873 from Cretaceous marls was evidently filled actively with darker sediment from above (Locklair & Savrda 1998), possibly to induce priming. As *Planolites* can be produced by diverse organisms in a wide range of environments, only certain representatives of this ichnogenus might be sequestrichnia. Also, *Alcyonidiopsis* Massalongo, 1856, a simple, cylindrical burrow filled with pellets, commonly darker than the surrounding deposits, and known at least since the Ordovician (see Uchman 1999) can belong to sequestrichnia.

DISCUSSION

A synoptic comparison of the behavioural variants applied by burrowing animals that accomplish a sequestrichnial nutritional strategy helps to define the criteria to classify a trace as a sequestrichnion.

A deep burrow or part of a burrow is enriched in organic-rich matter, whereas the surrounding host sediment shows no indication of sorting or reworking related to that burrow, such as a halo consisting of sorted material. The material enriched in organic matter must have intentionally been introduced from above.

The downward-transferred, sequestered material contains sedimentary tracers that unequivocally originated from the contemporary seafloor, such as volcanic ash, microfossils (providing at least relative ages), tektites, etc.

Active fill is indicated by menisci or (spreite) lamellae or laminae.

Reworking of the sequestered material is recorded, for instance, by truncated menisci or lamellae.

Not all these criteria are met in any one ichnotaxon. For instance, even an evident sequestrichnion like *Zoophycos* does not meet all the above criteria. As shown in Figure 1A, the *Zoophycos* spreite is filled with material definitely derived from above, such as whitish nannofossil ooze, but is not enriched in organic matter. In this case, the large amount of coccoliths probably led to a dilution effect. Other doubtful cases may result from later oxidation of organic matter, in particular in the pelagic or hemipelagic oceanic red beds, which house *Zoophycos* with a red spreite surrounded by red host sediment, both low in C_{org} (< 0.1%; Wetzel & Uchman 2012: fig. 5F, G). In this case, the sedimentation rate was probably so low that the deposits were later completely oxidized, including the spreite.

The reworking of a previously formed burrow domain by the tracemaker becomes evident by crosscutting of subsequently produced burrow fill elements such as menisci, spreite lamellae, or the partially truncated helix of *Avetoichnus*. In contrast, for trace fossils like *Cladichnus,* reworking by the producer is not evident. However, it must be remembered that only the last phase of trace production is preserved in the sediment record. In the case of *Cladichnus,* it is possible that the lumen fill was reworked before the final fill was emplaced (see above), or the lumen fill acted as drainage for porewater enriched in reductant compounds that could be taken for nutrition if oxygen became available or symbionts were housed by the trace producer (implying combined sequestrichnial-chemichnial behaviour).

Microbial activity within the burrow fill is likely, but there is no test to determine whether it occurred during the life of the tracemaker or later. For instance, framboidal pyrite in the *Zoophycos* spreite has been interpreted to indicate microbial activity (e.g. Gong *et al.* 2007). It is not known, however, whether the sulphate-reducing microbes were already active during burrow production or later. Similarly, there is no proof that microbial activity was stimulated by the injection of labile organic matter to initiate priming. Nonetheless, priming occurs in every environment, and therefore is impossible to exclude from marine environments (see above, Background; van Nugteren *et al.* 2009). It appears that priming represents a very efficient way to develop main or additional food resources, because even low amounts of labile organic matter can enhance microbial activity considerably (e.g. van Nugteren *et al.* 2009).

Sequestrichnial behaviour has existed at least since the Cambrian (Series 2) as marked by the occurrence of *Halimedides* (Novis *et al.* 2022). Cambrian occurrences of *Gyrophyllites* are not obvious, but they are confirmed from the Early Ordovician (Muñoz *et al.* 2019). The occurrences of most other sequestrichnia are related to the Mesozoic Marine Revolution in the deep sea, one of the consequences of which was increased competition for food (Uchman 2004).

Environmental implications

Sequestrichnia evidently occur in settings characterized by short periods of organic matter deposition on the seafloor, for instance, after seasonal phytoplankton blooms in surface waters followed by a comparatively long period of low benthic food availability. Therefore, aside from pelagic environments, this behaviour is also appropriate in settings experiencing ephemeral deposition of organic-rich material and organic
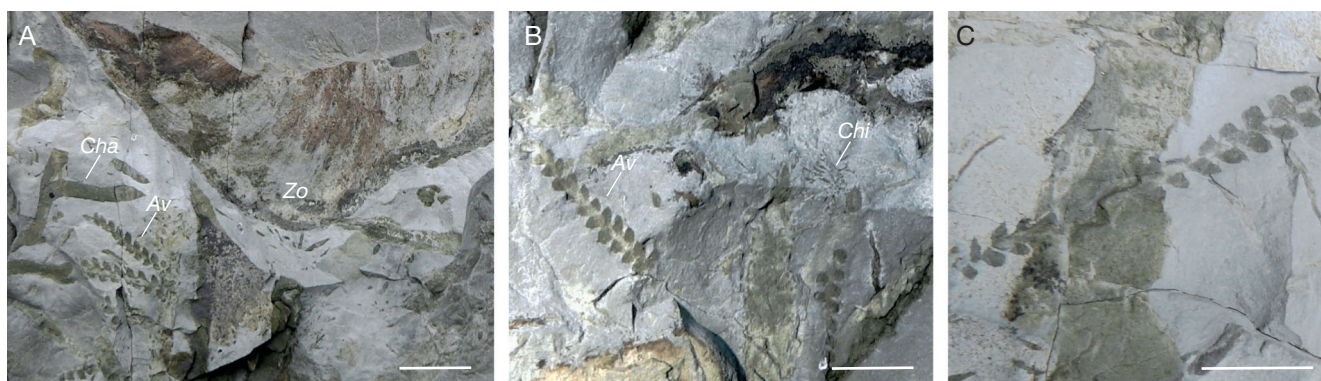
Fig. 4. — **A-C**, Field photographs of *Avetoichnus luisae* Uchman & Rattazzi, 2011 in the upper part of a turbiditic marl bed (Middle Eocene) at Zbludza, Magura Nappe, Polish Carpathians. Note that in **A**, *Avetoichnus* co-occurs with other sequestrichnia, i.e., *Zoophycos*. Abbreviations: **Av**, *Avetoichnus luisae*; **Cha**, *Chondrites affinis* (Sternberg, 1833); **Chi**, *Chondrites intricatus* (Brongniart, 1828); **Zo**, *Zoophycos* Massalongo, 1855. Scale bars: 1 cm.
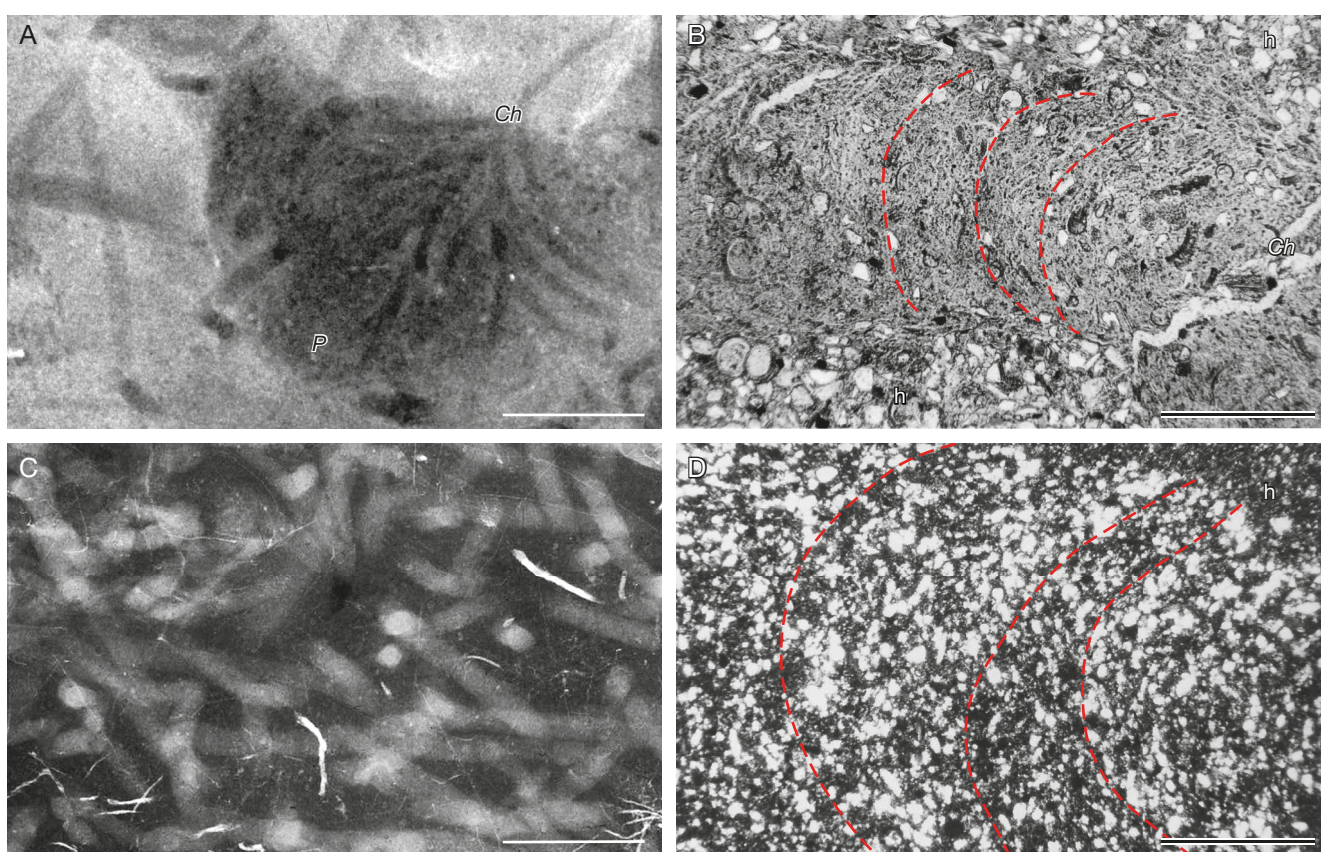

Fig. 5. — *Chondrites* Sternberg, 1833 exhibiting meniscate fill. Organic-rich mud arranged in menisci implies sequestrichnial behaviour of the producer: **A**, *Chondrites* filled with material finer than the host sediment (**ch**). *Chondrites* crosscuts *Planolites* Nicholson, 1873 (**P**). X-ray radiograph, negative: mud, dark; silt and sand, light. Institute of Geological Sciences Kiel, Germany, core 13250-1, 22-25 cm, 15°42.2'N, 17°32.7'W, 1680 m water depth (for details see Wetzel 1981); **B**, thin section of the *Chondrites* (**Ch**) shown in (**A**) filled with sediment finer than the host sediment (**h**), providing clear evidence of meniscate fill. Some menisci marked by **red broken line**. The same core as in **A**; **C**, *Chondrites* filled with material coarser than the host sediment. Organic-poor, silty fill arranged in menisci (see **D**) implies a chemichnial behaviour (for details see text). X-ray radiograph, negative: mud, dark; silt and sand, light. Institute of Geological Sciences Kiel, Germany, core 13239-1, 284-287 cm, 13°52.6'N, 18°18.8'W, 3156 m water depth (for details see Wetzel 1981); **D**, thin section of the *Chondrites* (**Ch**) shown in **C**, filled with sediment coarser than the fine-grained host sediment (**h**), providing clear evidence of meniscate fill (some menisci marked by **red broken line**). For further details see Wetzel (1981). Scale bars: A, C, 1 mm; B, D, 0.5 mm.

debris carried by mass flows or gravity currents to levee or overbank settings of deep-sea fans (e.g. Khripounoff *et al.* 2003; Vangriesheim *et al.* 2009; Mignard *et al.* 2017). As the amount of available benthic food settling to the seafloor decreases with water depth (see Background), sequestrichnial behaviour represents a more advantageous strategy with increasing water depth. Consequently, sequestrichnia occur typically in the *Zoophycos* and the *Nereites* ichnofacies.

Sequestrichnia are commonly emplaced in muddy sediment or in sand covered by mud. For the conservation of organic matter, a mud cover provides the advantage of having low permeability and diffusivity, hence the supply of electron acceptors for the oxidation of organic matter is limited. The stowing of organic-rich material deep within sediment, where oxygen is low or has already been consumed, is optimal for its conservation, in contrast to oxic conditions on or close to the seafloor. In both oxic and anoxic host sediments, the downward transfer of labile organic matter has a high potential to facilitate enhanced microbial activity since priming is not limited to either oxic or anoxic conditions (e.g. van Nugteren *et al.* 2009; Aller & Cochran 2019). Consequently, the animals producing sequestrichnia do some bioengineering by developing microenvironments in and around the cache wherein labile organic matter is stowed. In fact, such a cache represents the transition to chemichnia. The producers of the latter, however, are interpreted to feed on microbes or their metabolic products, and, importantly, they have not stimulated microbial activity by "injecting" labile organic matter (deep) into the sediment. However, the fill of *Chondrites* represents an ambiguous case because morphologically similar *Chondrites* can exhibit a meniscate or homogeneous fill, coarse or fine-grained, and even hollow burrows have been observed in Recent sediments (Wetzel 1981, 2008; Fig. 5). Only *Chondrites* showing a meniscate fill consisting of organic-rich mud suggests sequestrichnial behaviour, whereas coarse-grained fill or empty burrows may be typical of chemichnia.

Sequestrichnia considerably contribute to bioturbation as particles are transferred through considerable vertical distances ("non-local mixing", e.g. Boudreau 1986; Boudreau & Imboden 1987). Thus, sequestrichnial behaviour causes disturbance of the stratigraphic layering, including palaeoenvironmental and palaeoceanographic signals (e.g. Levin *et al.* 1997; Kaminski & Wetzel 2004).

Furthermore, geochemical processes are considerably affected by the transfer of labile organic matter downward by inducing priming at the cache site, and finally by the ventilation of the inhabited burrow by oxygenated water, which fosters enhanced microbial activity (e.g. Meysman *et al.* 2010).

CONCLUSIONS

Seasonally varying primary production affects wide regions of the oceans today and very likely did also in the past. In particular, in oligotrophic deep-sea settings, seasonal fluctuations in organic matter delivery require a survival strategy for the benthos. Sequestrichnia appear to record an appropriate behaviour of their producers: 1) collecting (labile) organic matter on the seafloor or from suspension; 2) transferring it downward; 3) stowing it in a subsurface cache; and 4) utilizing it during times of shortage in benthic food.

Sequestrichnia typically occupy a mid- to deep-tier position, commonly in anoxic sediment. The sequestered material is commonly stowed in anoxic sediment domains below the oxic surface mixed layer. Their fill is arranged in pellets, a spreite, menisci, or a mixture thereof.

The transfer of labile organic matter deep below the surface can considerably enhance the remineralization of organic matter by microbes, called priming; in turn, further nutritional organic compounds such as microbes and their metabolic products become available as food for the producers of sequestrichnia.

As the amount of available benthic food decreases with water depth, sequestrichnial behaviour becomes a more advantageous strategy with increasing water depth. Consequently, sequestrichnia occur typically in the *Zoophycos* and the *Nereites* ichnofacies.

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