

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/363398888>

A glimpse into ancient food storage: Sequestrichnia and associated nucleocave Chondrites from Eocene deep-sea deposits

Article in *Acta Palaeontologica Polonica* · September 2022

DOI: 10.4202/app.00965.2021

CITATIONS

0

READS

84

4 authors, including:



Jaroslav Šamánek

Masaryk University

9 PUBLICATIONS 19 CITATIONS

[SEE PROFILE](#)



Lothar Herbert Vallon

Østsjællands Museum

23 PUBLICATIONS 200 CITATIONS

[SEE PROFILE](#)



Radek Mikuláš

The Czech Academy of Sciences

169 PUBLICATIONS 2,082 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Ichonology of Tertiary marine deposits of the Czech Republic [View project](#)



Lower Paleozoic rocks of Spiti-Kinnaur (North Western) Himalaya, India [View project](#)

A glimpse into ancient food storage: Sequestrichnia and associated nucleocave *Chondrites* from Eocene deep-sea deposits

JAROSLAV ŠAMÁNEK, LOTHAR H. VALLON, RADEK MIKULÁŠ, and MICHAL VACHEK



Šamánek, J., Vallon, L.H., Mikuláš, R., and Vachek, M. 2022. A glimpse into ancient food storage: Sequestrichnia and associated nucleocave *Chondrites* from Eocene deep-sea deposits. *Acta Palaeontologica Polonica* 67 (3): 767–779.

The old brickyard Velká nad Veličkou in the Czech Republic offers a unique insight into an Eocene deep-sea ichno-assemblage that is dominated by sequestrichnia. Secondary use of such food-stowing was made by the tracemaker of *Chondrites intricatus* as evidenced by its frequent penetration of the trace fossil *Zoophycos brianteus* and its occurrence preferentially on the surface of *Zoophycos* spreiten. Here, the *Chondrites* tracemaker presumably exploited the nutrient-enriched micro-environment (nucleocave). This close interrelations between *Chondrites* and *Zoophycos* support the hypothesis of a sequestrichnial behaviour of the *Zoophycos* producer. The studied locality also yields *Helminthopsis tenuis*, *Tubulichnium mediterranensis*, *Scolicia strozzii*, ?*Dactylodites* isp., *Megagraption irregulare*, and *Planolites* isp.

Key words: *Zoophycos*, trace fossils, deep-marine, flysch, Bílé Karpaty Unit, Outer Western Carpathians, Czech Republic.

Jaroslav Šamánek [samanej.j@mail.muni.cz], Department of Geological Sciences, Faculty of Science, Masaryk University, Kotlářská 267/2, 611 37 Brno, Czech Republic.

Lothar H. Vallon [kv@oesm.dk], Geomuseum Faxe, Østsjælland Museum, Rådhusvej 2, DK-4640 Faxe, Denmark.

Radek Mikuláš [mikulas@gli.cas.cz], Institute of Geology of the Czech Academy of Sciences, Rozvojová 269, 165 02 Praha 6, Czech Republic.

Michal Vachek [michal.vachek66@gmail.com], State Land Office, Bratislavská 1/6, 695 01 Hodonín, Czech Republic.

Received 16 December 2021, accepted 11 April 2022, available online 8 September 2022.

Copyright © 2022 J. Šamánek et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License (for details please see <http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

At first glance, deep-tier trace fossils such as various ichno-species of *Zoophycos*, *Chondrites*, *Spirophyton*, *Polykampton*, and *Pilichnus* reflect a feeding behaviour. On closer inspection, however, the ethology of these trace fossil makers becomes more complicated as frequently discussed in recent years. A thorough investigation led Uchman and Wetzel (2016) to introduce a new ethological group—sequestrichnia or food-storage or stowing traces. Stowing behaviour is predominantly applied by tracemakers in deep-sea settings, where food availability fluctuates seasonally or episodically. When highly nutritious material is deposited, the tracemakers collect it on the sediment surface and stow it in deep-tiers where shallow deposit feeders cannot reach it and where little- or not oxygenated porewater favours the preservation of organic matter (Uchman and Wetzel 2016; for shallower environments see also Bromley 1996: 100–101,

fig. 4.25; Seilacher 2007: 54, pl. 18). Sequestration was further analysed in the ichnogenera *Polykampton* (Uchman and Rattazzi 2017; Uchman et al. 2019, 2020) and *Tubulichnium* (Uchman and Wetzel 2017). Additionally, Jurkowska et al. (2018) discussed food storage in *Lepidenteron mantelli* and Rodríguez-Tovar et al. (2019) in the ichnogenus *Halimedes*.

The trace fossil *Chondrites* records a wide variety of behaviour of its producers, living in anoxic (Bromley and Ekdale 1984) or oxic settings (Wetzel and Uchman 2012), showing either a deposit feeding, farming, or chemosymbiotic behaviour (e.g., Fu 1991, Baucon et al. 2020). In particular, deep-tier *Chondrites* ispp. appear to follow a chemosymbiotic strategy that can be utilised in order to identify trace fossils applying stowing behaviour (sequestrichnia), which became reworked by the *Chondrites*-producer. In this context, the Velká nad Veličkou locality (Eocene of the Carpathian Flysch Belt, Czech Republic) where *Chondrites* and supposed sequestrichnial ichnogenera occur in close relationship within a specific bed is of particular interest. The

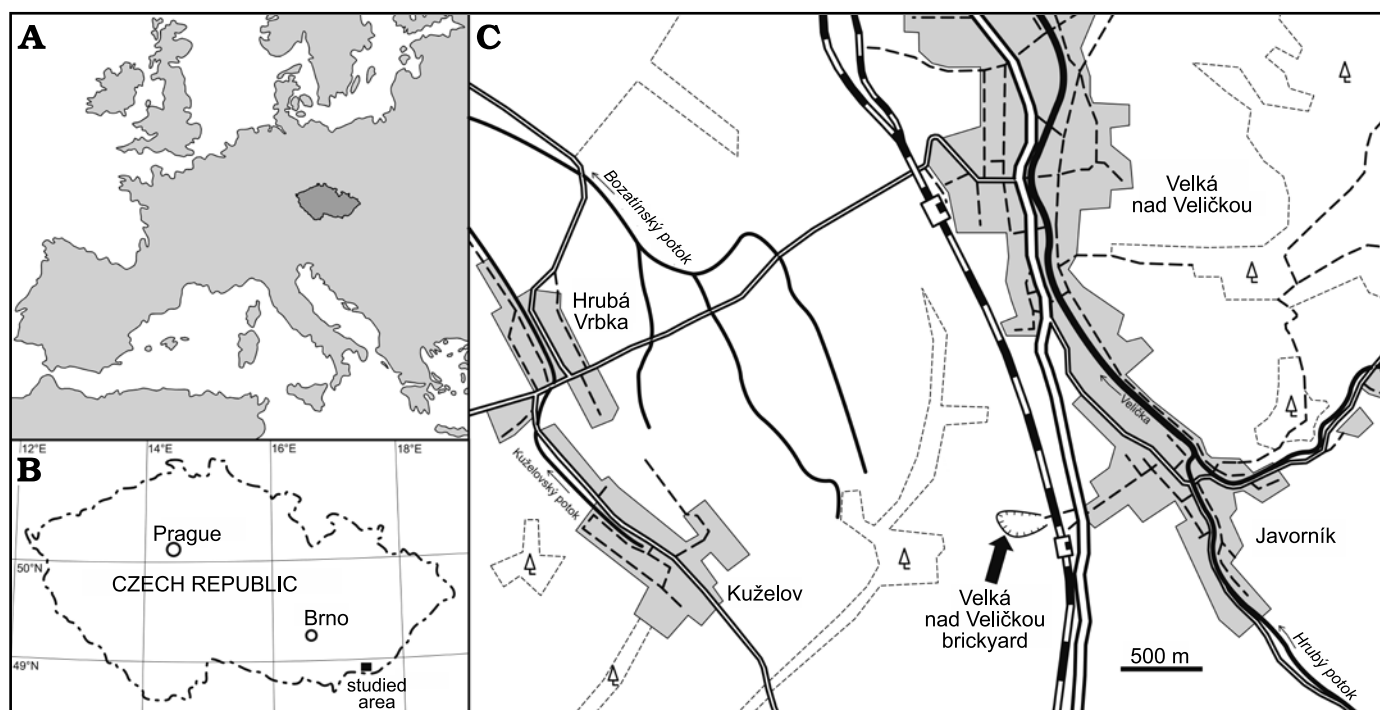


Fig. 1. Location of the studied area in Europe (A) and the Czech Republic (B). Schematic map of the studied locality (C).

aim of the present paper is to describe this distinct ichnoassemblage in which both food-storage and chemosymbiotic behaviours were applied in dependence upon each other.

Institutional abbreviations.—ICN, Natural History Museum of Verona, Italy; MZM, Moravian Museum, Brno, Czech Republic; Z, City Museum in Strážnice, Czech Republic.

Geological setting

The old brickyard Velká nad Veličkou (formerly known as the Javorník brickyard; 48°51'41.067"N, 17°31'4.278"E) is located near the Javorník nad Veličkou railway station in the south-eastern part of Moravia (Czech Republic), close to the border with the Slovak Republic (Fig. 1). The quarrying ceased in 1993 and since 2013 the locality is protected by law as a natural monument.

The outcrop is the stratotype of the Kuželov Formation of the Hluk Facies of the Bílé Karpaty Unit (Stráník et al. 1995). The Kuželov Formation is dominated by greenish, brownish, and reddish foliated claystone with intercalated mainly thin-bedded, laminated sandstone beds. Strongly lithified marl beds (in Czech “pelokarbonát”) are a diagnostic feature of the Kuželov Formation. The formation is about 250 m thick and represents sediments deposited in a distal part of a deep-sea turbidity fan from the late Paleocene to the early Eocene (Stráník et al. 1995). From the studied locality, Bubík (1995) described an assemblage of agglutinated foraminifera that is dominated by tubular forms indicative for depths of the lower slope. Index fossil for the Planktonic Foraminifera Zone P6 and the

Nannoplankton Zone NP10, i.e., *Rheophax elongatus* provided an early Eocene age (see Bubík 1995; Stráník et al. 1995). The Kuželov Formation is underlain by the Nivnice Formation or Paleocene–Eocene variegated beds (Stráník et al. 1995). There are neither indications of shallowing during the sedimentation of the Kuželov Formation nor of discontinuous sedimentation. The overlying sediments have been eroded (Bubík 1995).

So far, the only ichnological study of the outcrop was a brief mention in an unpublished Ph.D. thesis by Němcová (1973) written in Czech; she described *Rhabdoglyphus grossheimi* and a new, but invalid ichnospecies, *Spirophycus ornatus*. Although she did not mention the exact collection point, the specimens must derive from a more sandy part of the quarry considering the lithology of the depicted samples.

Material and methods

The studied material was collected exclusively at the old brickyard Velká nad Veličkou. Most of the trace fossils come from a 170 mm thick, moderately bioturbated bed (further referred to as *Zoophycos* Bed) in the southern part of the outcrop (Fig. 2). The strata are tectonically tilted and inclined at an angle of 45°. The *Zoophycos* Bed yields trace fossils mostly preserved in full relief within the strongly lithified marl. Their infill derives from an overlying 50 mm thick siltstone layer. Thus, we may presume that this siltstone bed was deposited before (or during) the production of the observed trace fossils.

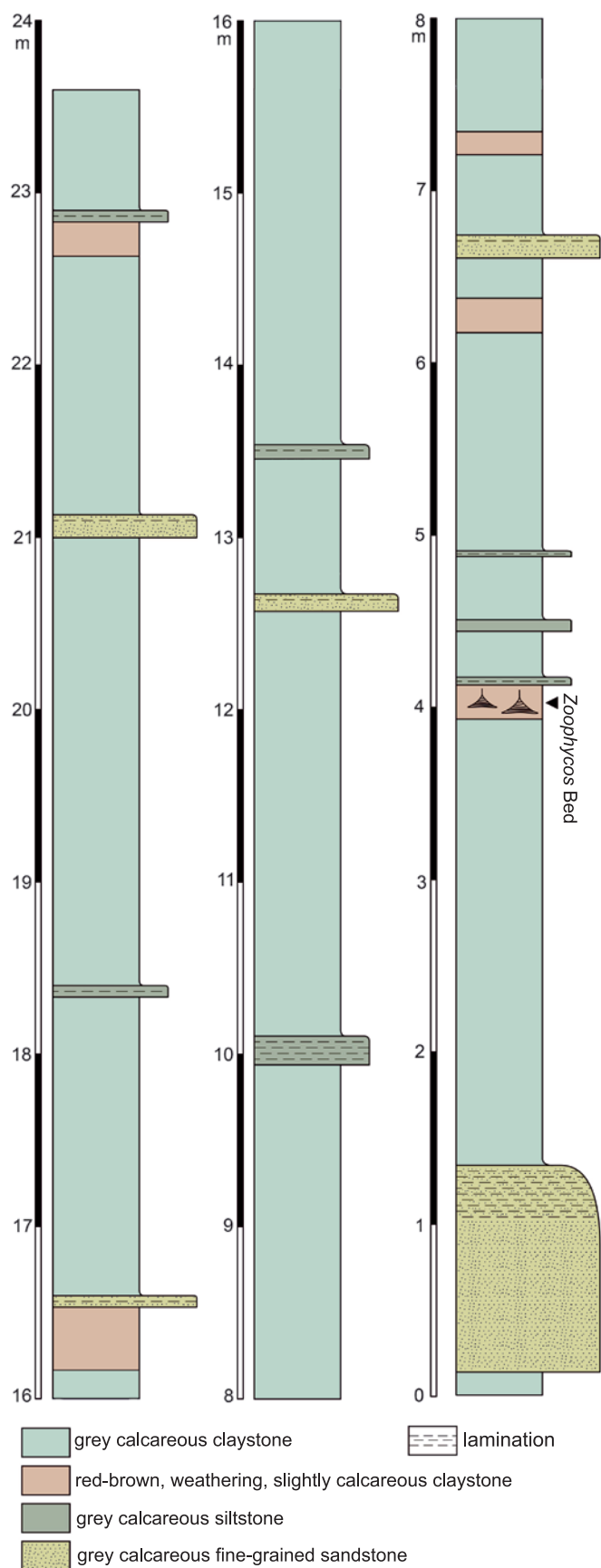


Fig. 2. Stratigraphic position of the *Zoophycos* Bed in the southern part of the studied locality.

Additional trace fossil material was collected from the talus. These trace fossils do not display the unique preservational features (see below) as the specimens in the *Zoophycos* Bed and are derived from other strata.

Measurements introduced by Wetzel and Bromley (1996) were used for *Helminthopsis tenuis*.

The herein described specimens are housed in the collection of the Moravian Museum, Brno, Czech Republic (MZM) under the inventory numbers Ge 32946-32961 and the City Museum in Strážnice, Czech Republic under the inventory number Z 69.

Systematic palaeoichnology

The ichnogenera are arranged according to the morphological system by Buatois et al. (2017).

Simple horizontal trails

Ichnogenus *Helminthopsis* Wetzel and Bromley, 1996

Type ichnospecies: *Helminthopsis hieroglyphica* Wetzel and Bromley, 1996, Ganei, Switzerland, Paleocene–lower Eocene.

Helminthopsis tenuis Książkiewicz, 1968

Fig. 3.

Material.—Single large specimen on a sandstone slab, collected from talus (MZM Ge 32946) from Velká nad Veličkou, Czech Republic, Eocene.

Description.—Incomplete specimen of an unbranched, horizontal burrow with a fairly constant diameter of about 10 mm and a somewhat rectangular cross-section. Preserved



Fig. 3. Simple horizontal trail *Helminthopsis tenuis* Książkiewicz, 1968, MZM Ge 32946, from Velká nad Veličkou, Czech Republic, Eocene.

as convex hyporelief with a passive, structureless fill (no pellets were observed). Burrow segments are rarely straight and often slightly wiggly. Two meanders, one wide and one narrow, are preserved. The broad meander is 120 mm wide and 86.6 mm high, the narrow one measures 61.3 mm in width and 80 mm in height. The burrow possesses a partially preserved median furrow.

Remarks.—Wetzel and Bromley (1996) interpreted *Helminthopsis* as feeding burrows constructed in shallow depths of sediments probably rich in benthic food. Although collected from talus, the trace fossil might therefore have been constructed within a layer that was deposited in times of nutrition-rich sedimentation. Thus, it might have been constructed by a shallow tier tracemaker that the producers of sequestrichnia aimed to avoid (cf. Uchman and Wetzel 2016).

Stratigraphic and geographic range.—Ediacaran to Recent (Buatois et al. 2014; Kundal et al. 2022); worldwide.

Simple actively filled (massive) horizontal to oblique structures

Ichnogenus *Planolites* Nicholson, 1873

Type ichnospecies: *Planolites beverleyensis* (Billings, 1862), near Beverley in the township of Bastard, Ontario, Canada, Potsdam Sandstone, Cambrian.

Planolites isp.

Material.—Six specimens on 2 samples collected from the siltstone layer overlying the *Zoophycos* Bed (MZM Ge 32948) from Velká nad Veličkou, Czech Republic, Eocene.

Description.—Near-surface, unbranched, cylindrical burrows with a smooth wall and no lining, preserved as positive hyporelief. Course of burrow generally horizontal but undulating vertically. Occurring in two different size ranges; the smaller one is about 1 mm wide and preserved over a length of about 30 mm, the larger type has a constant width of about 5 mm and is preserved for lengths between 30 to 80 mm. The latter size variant is more common.

Simple, actively filled (pelletoidal) horizontal to oblique structures

Ichnogenus *Tubulichnium* Książkiewicz, 1977

Type ichnospecies: *Tubulichnium incertum* Książkiewicz, 1977, Gurnigel Nappe in the Fribourgian Alps, Switzerland, Maastrichtian–lower Palaeogene.

Remarks.—Originally described as *Tubotomaculum* García-Ramos, Mángano, Buatois, and Rodríguez-Tovar, 2014, the ichnogenus was considered a junior synonym of *Tubulichnium* Książkiewicz, 1977, by Uchman and Wetzel (2017) and its only ichnospecies *Tubotomaculum mediterraneus* García-Ramos, Mángano, Buatois, and Rodríguez-Tovar, 2014, was transferred to *Tubulichnium* by Uchman and Wetzel (2017).

Tubulichnium mediterraneus (García-Ramos, Mángano, Buatois, and Rodríguez-Tovar, 2014)

Fig. 4.

Material.—In the field, about 200 observed, usually partially preserved specimens, derived from the *Zoophycos* Bed; 113 collected (owing to the large number of specimens, inventorying was done in lots: MZM Ge 32958 (figured herein), MZM Ge 32959 (not figured) from Velká nad Veličkou, Czech Republic, Eocene.

Description.—All *Tubulichnium mediterraneus* specimens were observed in mid-tier position within the *Zoophycos* Bed as horizontal, unbranched burrows with no obvious connection to the surface. The burrows have a fairly straight to slightly winding course and blind endings. The diameter of the burrows is fairly constant in the range of 4.4 to 13.5 mm, but irregular swellings occur along the burrow. The burrows are lined with elongated, small, 1 mm long and 0.4 mm wide, silty pellets consisting of material derived from the overlying siltstone layer. The maximal preserved length is 60 mm. Larger burrows of probably higher ichnogenic stages display a spindle-like morphology and often retrusive, vertical spreiten with oblique lamellae. Burrows are often colour-enhanced by manganese- or/and iron-rich oxides.

Remarks.—*Tubulichnium mediterraneus* is relatively common in Cretaceous to Eocene strata in the Mediterranean and occurs according to García-Ramos et al. (2014) often in association with *Rotundusichnium zumayensis* Plička, 1989, *Zoophycos* isp., *Chondrites* isp., *Gyrophylites* isp., and *Stelloglyphus llicoensis* Le Roux, Nielsen, and Henríquez, 2008. Other occurrences are restricted to the Miocene of Borneo (Seilacher 2007; García-Ramos et al. 2014). *Tubulichnium* was interpreted by Uchman and Wetzel (2017) to represent a sequestrichnion.

Stratigraphic and geographic range.—Upper Cretaceous to Miocene (García-Ramos et al. 2014); probably worldwide.

Complex actively filled horizontal structures

Ichnogenus *Scolicia* de Quatrefages, 1849

Type ichnospecies: *Scolicia prisca* Quatrefages, 1849, Donostia-San Sebastián, Guipuscoa, Spain, Paleogene.

Scolicia strozzii (Savi and Meneghini, 1850)

Fig. 5.

Material.—Single specimen collected in the talus (MZM Ge 32949) from Velká nad Veličkou, Czech Republic, Eocene.

Description.—Only a small section of a guided meander is preserved as bilobate positive hyporelief with a median groove. The burrow is 40 mm wide and each of the two limbs has a length of about 95 mm. Most of the original internal structures have been destroyed by small indetermined burrows.

Stratigraphic and geographic range.—Tithonian to Recent (Tchoumatchenco and Uchman 2001); probably worldwide.

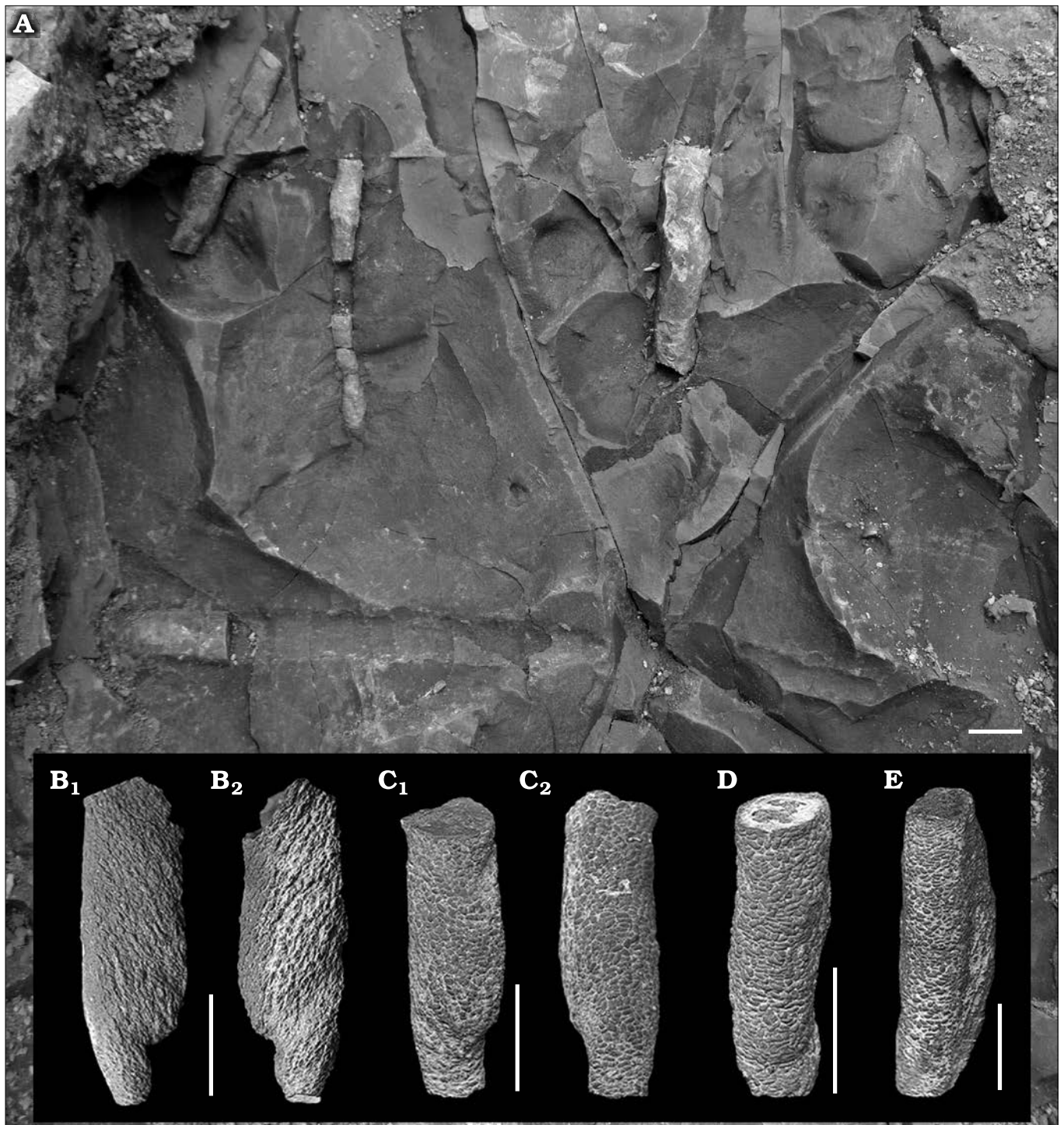


Fig. 4. Simple, actively filled (pelletoidal) horizontal to oblique structure *Tubulichnium mediterraneus* (García-Ramos, Mángano, Buatois, and Rodríguez-Tovar, 2014), from Velká nad Veličkou, Czech Republic, Eocene. **A.** Field photo of in situ specimens. **B–E.** MZM Ge 32958, partially preserved burrows with clearly visible spindle-like shape and pelletal infill. Same specimens from different angles (**B**₁ and **B**₂; **C**₁ and **C**₂). Scale bars 10 mm.

Radial to rosette structures

Ichnogenus *Dactyloidites* Hall, 1866

Type ichnospecies: *Dactyloidites asteroides* (Fitch, 1850), New York, USA, Granville Formation, Cambrian.

Remarks.—*Dactyloidites* is an ichnogenus that deserves further investigations. It was synonymized with *Haentz-*

schelinia Vialov, 1964, and with *Brooksella* Walcott, 1896 (Fürsich and Bromley 1985; Pickerill et al. 1993; Wilmsen and Niebuhr 2014; Boyd and McIlroy 2016). *Brooksella* was later re-described as a body fossil by Ciampaglio et al. (2006). Wilmsen and Niebuhr (2014) revisited the type material of *Dactyloidites otto* and discussed the synonymisation of *Haentzschelinia* and *Dactyloidites*. They concluded

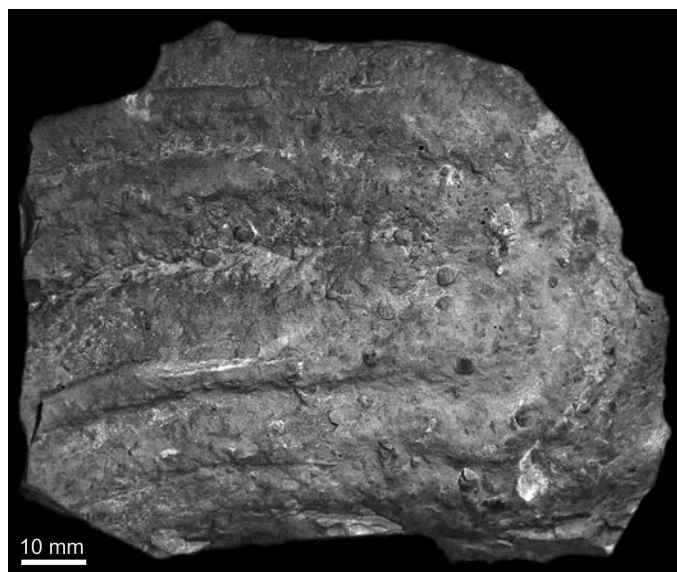


Fig. 5. Complex actively filled horizontal structure *Scolicia strozzii* (Savi and Meneghini, 1850) MZM Ge 32949, from Velká nad Veličkou, Czech Republic, Eocene.

(in accordance with Fürsich and Bromley 1985) that there is no valid argument to use *Haentzschelina* as separate ichnogenus. However, *Haentzschelina* is still retained as separate ichnogenus by some authors and since its defence by Vialov (1989), *Haentzschelina* was mainly used for more radial forms (e.g., Belaústegui et al. 2015; Muñoz et al. 2019) and for post-Palaeozoic forms, although a certain time range is not regarded as ichnotaxobase. Recently, Boyd and McIlroy (2016) described a new ichnospecies of *Dactyloidites* and emended the diagnosis of this ichnogenus.

?*Dactyloidites* isp.

Fig. 6.

Material.—Eight incomplete traces (MZM Ge 32950–32957) from the *Zoophycos* Bed, about 30 more observed in the field, from Velká nad Veličkou, Czech Republic, Eocene. In average, 10–15 specimens occur on one square metre, usually arranged in groups with individual burrows about 50–100 mm apart.

Description.—Burrow system with numerous cylindrical galleries radiating from a centre creating radial or fan-like structures up to 70 mm in diameter. Individual tunnels have a constant diameter of about 1 mm. They are commonly unbranched and rarely bifurcating at acute angles near their blind tapering endings. The individual J-shaped tunnels usually form multiple layers and are not lined or coated with pellets. The burrows are circular in cross-section and do not overlap. Unlike the specimens that are usually referred to *Dactyloidites*, the central axis of the observed specimens consists of multiple, steeply inclined to subvertical shafts; the parts of shafts connecting the galleries with the surface were not observed.

Remarks.—Species of at least four different ichnogenera are similar to the studied material: *Asterosoma* Otto, 1854,

Phycodes Richter, 1850, *Phymatoderma* Brongniart, 1849, and *Dactyloidites* Hall, 1886. However, none of the first three fits perfectly. Species of *Asterosoma* have a concentrically layered wall around a passively filled lumen. Some of our more fan-like specimens resemble *Phycodes auduni* Dam, 1990, or *Phycodes bromleyi* Dam, 1990. However, the ichnospecies of *Phycodes* are best restricted to burrows having a (sub-)quadrate cross-section (Seilacher 2000). Ichnospecies of *Phymatoderma* are irregularly branched, and pellets frequently occur (e.g., Izumi and Yoshizawa 2016). Multiple shafts are not found in any ichnospecies of *Dactyloidites*. Nevertheless, the defined ichnotaxobases for *Dactyloidites* matches the studied material best. The ichnogenus *Dactyloidites* comprises five valid ichnospecies: *Dactyloidites otto* (Geinitz, 1849), *Dactyloidites asteroides* Fitch, 1850, and *Dactyloidites cabanasi* (Meléndez in Cabanás, 1966), exhibit simple, less radiating morphotypes, whereas *Dactyloidites peniculus* D'Alessandro and Bromley, 1986, and *Dactyloidites jordii* Boyd and McIlroy, 2016, represent more complex radiating burrows with multiple layers of tunnels that sometimes are overlapping.

The studied material of ?*Dactyloidites* isp. from the Velká nad Veličkou shares similarities with more densely radiating ichnospecies. *Dactyloidites peniculus* D'Alessandro and Bromley, 1986, occurs as a radial pile or brush-like structure. The studied material is distinguishable from *D. peniculus* by presence of dichotomous branching tunnels running from the central shaft without lining or pelleted structure. *Dactyloidites jordii* Boyd and McIlroy, 2016, has a bilateral symmetry, exhibits multiple orders of branching, and the burrows display an n-shaped cross-section. In contrast, the studied material has radial or bilateral symmetry (in the case of fan-like morphotypes), exhibits only first order branching, and the cross-section of tunnels is circular. Furthermore, it also shares similarities with *D. otto* (*Haentzschelina otto* sensu Seilacher 2008) such as dichotomous branching of tunnels and a fan to radial outline.

Burrows with helicoidal spreiten

Ichnogenus *Zoophycos* Massalongo, 1855

Type ichnospecies: *Zoophycos brianteus* Massalongo, 1855, Livorno, Tuscany (Italy), Upper Cretaceous.

Zoophycos brianteus Massalongo, 1855

Fig. 7A₁.

Material.—Three nearly complete specimens from the *Zoophycos* Bed (MZM Ge 32960, MZM Ge 32961; Z 69) from Velká nad Veličkou, Czech Republic, Eocene.

Description.—The three studied, almost complete specimens exhibit the typical spreite of *Zoophycos* helically coiled around a vertical axis. Both sinistral and dextral helices were observed, and the structures were constructed from top to bottom. The spirals' diameters increase downward. The first has a nearly circular outline, the second is rather oval, and the last one is slightly lobate. The largest

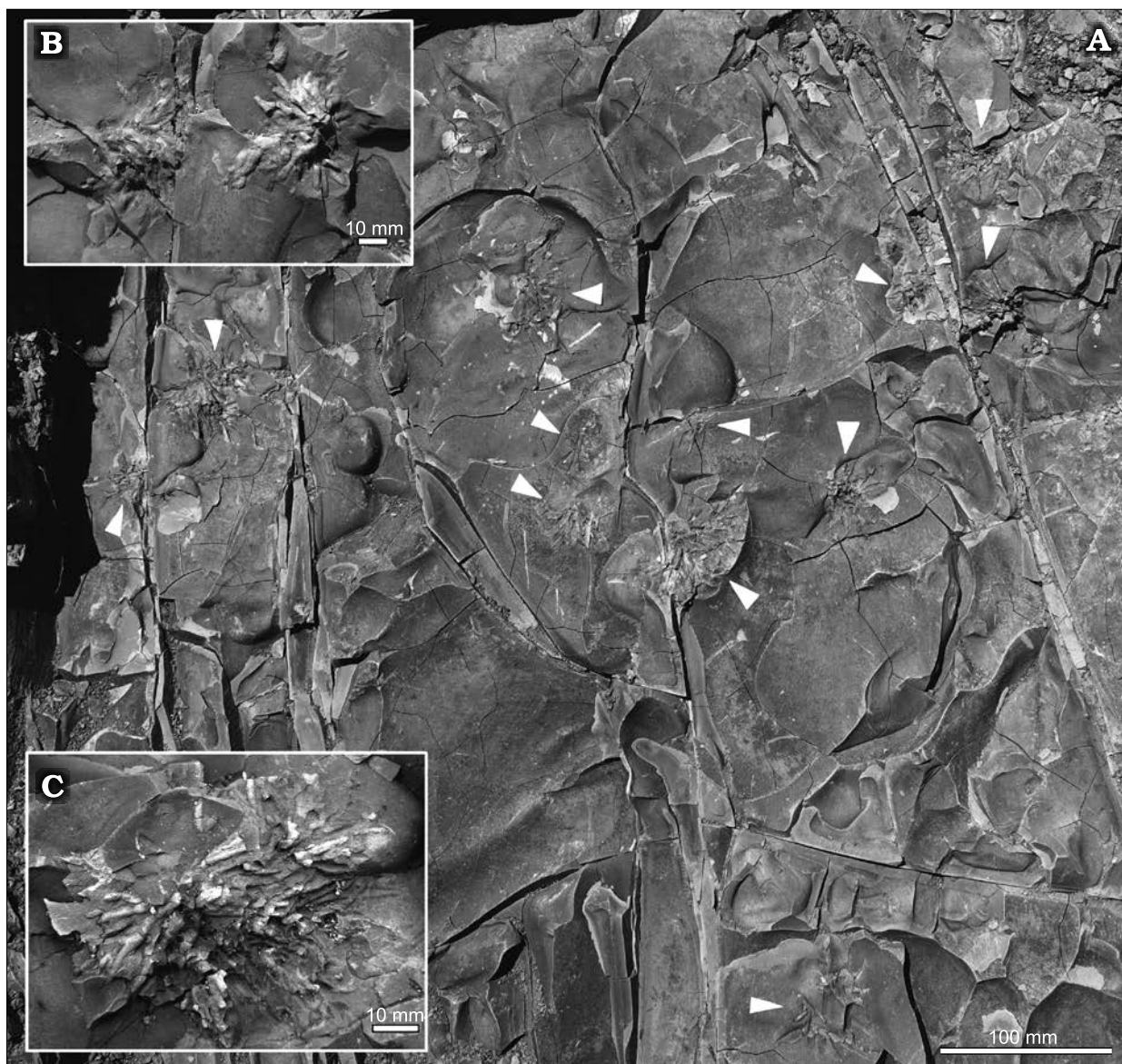


Fig. 6. Radial to rosette structures ?*Dactyloidites* isp., from Velká nad Veličkou, Czech Republic, Eocene. A–C. Field photos of in situ specimen (indicated by arrows, A), close ups (B, C).

diameters of the three specimens measure 139 mm, 167 mm, and 225 mm respectively. They penetrate from the top of the *Zoophycos* Bed for about 150 mm with a total height of the *Zoophycos* spreite whorls of about 40 mm each. In vertical sections, each spreite-whorl is bent concave upwards with both limits (marginal tunnel and contact at the centre) being roughly at the same level. The thickness of the spreite increases from 2.8 mm at the top whorl to up to 6.4 mm as a maximum. This maximal thickness is already reached about halfway through the burrow's vertical extension. From there on, the spreite thickness does not increase further. An inner, not bioturbated area with a subcircular cross-section is present having a diameter 7.6–8.5 mm. A central shaft has not been observed. In all specimens, the marginal (unlined) tunnel is well developed as well as primary and secondary lamellae of the spreite. The maximal distance between two

subsequent primary lamellae increases from the top to the bottom of the helix. On the surfaces of the whorls, faecal pellets have been observed. They have an elongate ellipsoidal to slightly ovoid or capsule-like shape. Their size is fairly constant in all specimens; ranging 0.8–1.4 mm in length and 0.4–0.5 mm in width. With depth protrusion, these faecal pellets increase in size.

Remarks.—Olivero (2007) redescribed the specimens of the three proposed *Zoophycos*-species by Massalongo, 1855. He selected lectotypes and a new type ichnospecies of *Zoophycos* since the originally designated type ichnospecies constitutes rather a fossil alga than a trace fossil (Olivero 2007). The studied specimens match with the redescription of *Zoophycos brianteus* by Olivero (2007).

In general, two ways of construction exist in *Zoophycos*, from top to bottom or from bottom to top. This can be inferred

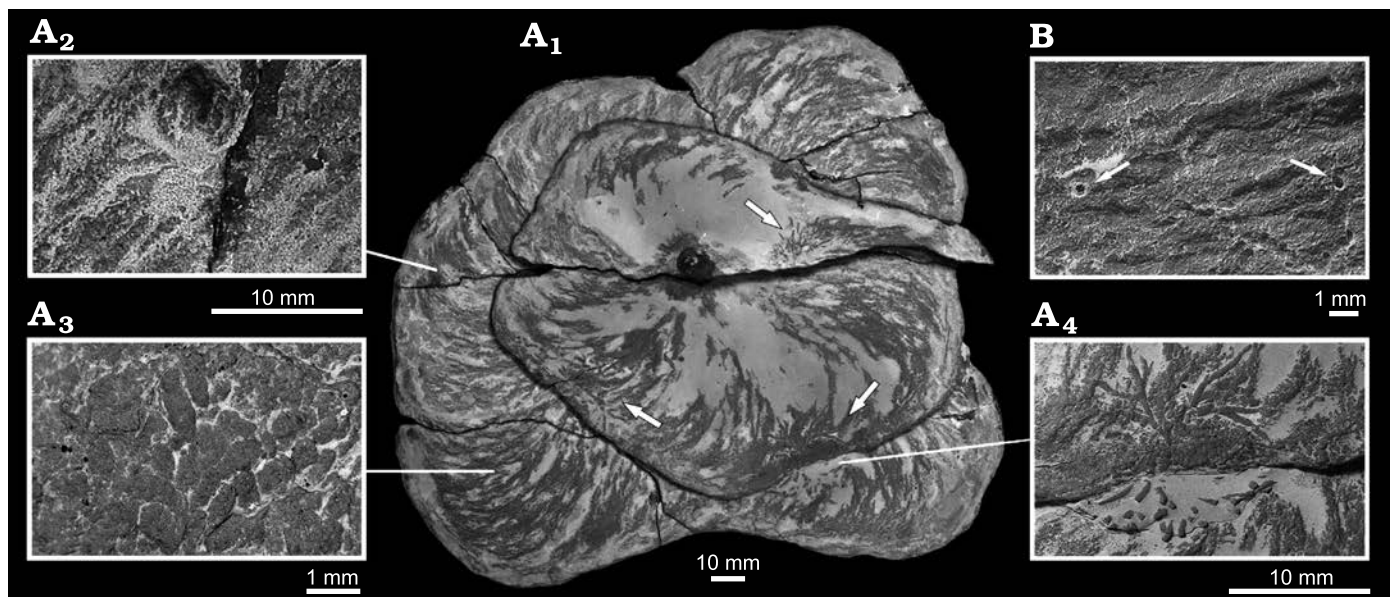


Fig. 7. *Zoophycos brianteus* Massalongo, 1855, with *Chondrites intricatus* (Brongniart, 1823). A. MZM Ge 32960, from Velká nad Veličkou, Czech Republic, Eocene. A₁, bottom two coils of *Z. brianteus*, arrows mark specimens of *Ch. intricatus*; A₂, cylindrical structure penetrating a *Z. brianteus* spreite; A₃, pellets on the surface of the spreite; A₄, *Ch. intricatus* on the surface of a spreite. B. MZM Ge 32961, from Velká nad Veličkou, Eocene, minute shafts cross-cutting a *Z. brianteus* spreite, note the diagenetic halo around the shafts.

by the convex side of the lamellae within the spreite (Olivero and Gaillard 1996). According to the findings by Olivero and Gaillard (1996, 2007), the bottom to top mode of building seems to be more common but the (lecto-)type material of *Zoophycos brianteus* (ICN1, ICN2, ICN3, ICN4) seems to be constructed from top to bottom (see Olivero 2007).

For the studied specimens, ichnogenetic stages (Belaústegui et al. 2016) are transitional but a growth of the tracemaker during construction can be inferred owing to increases of spreite thickness, diameter of the whorls, pellet size, dimensions of the marginal tunnel etc. (cf. Kotake 1989). The tracemaker seems to have reached adult size before the structure was completed.

All specimens exhibit a continuous spreite with mixture of silty material and pellets (Fig. 7A₃) indicating an active downward-movement of overlying more nutritious material into the nutrition-poor *Zoophycos* Bed. The deposition of faecal pellets within the structure points towards a sequestration behaviour (cf. Uchman and Wetzel 2016, 2017). The tracemaker purposely stowed material in order to either re-digest it or to utilise it indirectly by consuming microbes cultivated on it or their processed compounds. The same behaviour by a Recent *Zoophycos*-tracemaker was observed by Wetzel et al. (2011).

Some individual coils of the largest specimen are cross-cut by younger shafts of an undetermined trace fossils with a diameter up to 10 mm (Fig. 7A₂). On the spreite surfaces, several specimens of *Chondrites intricatus* (Fig. 7A₄) and minute circular shafts (diameter less than 1 mm) occur (Fig. 7B).

Stratigraphic and geographic range—Lower Permian to Recent (Hu et al. 2010); worldwide.

Burrows with shaft or bunch with downwards radiating probes

Ichnogenus *Chondrites* Sternberg, 1833

Type ichnospecies: *Chondrites targionii* (Brongniart, 1828), locality and age unknown.

Chondrites intricatus (Brongniart, 1823)

Fig. 7A₄.

Material.—12 specimens on the surface of the above mentioned *Zoophycos brianteus* specimens (MZM Ge 32960, MZM Ge 32961; Z 69), 3 isolated specimens observed in sediment (collected in situ from the *Zoophycos* Bed) from Velká nad Veličkou, Czech Republic, Eocene.

Description.—Regularly branching, small, dendritic burrow systems covering an area of up to 90 mm², with numerous minute branches, less than 1 mm in diameter, usually preserved in close contact with both upper and lower surfaces of *Zoophycos* spreite/whorls; isolated occurrence of *Chondrites intricatus* in the surrounding claystone is rare.

Remarks.—All above described *Zoophycos brianteus* specimens are pierced by minute vertical shafts filled with pyrite having a diagenetic halo (Fig. 7B). The diameter of these shafts is in the same size-range as the diameter of the individual branches of *Chondrites intricatus* (less than 1 mm). Thus, these shafts may represent connections of the branched section of *Chondrites* with the ancient water-sediment interface.

Stratigraphic and geographic range—Lower Silurian (Rindsberg and Chown 1986) to Recent; worldwide.

Regular to irregular network graphoglyptids

Ichnogenus *Megagraption* Książkiewicz, 1968

Type ichnospecies: *Megagraption irregulare* Książkiewicz, 1968, Berest near Grybów, Beloveža Beds, Poland, lower Eocene.

Megagraption irregulare Książkiewicz, 1968

Fig. 8.

Material.—Single incomplete specimen (MZM Ge 32947) collected from the talus, preserved as positive hyporelief from Velká nad Veličkou, Czech Republic, Eocene.

Description.—Trace fossil commonly preserved as hypichnial irregular nets. *Megagraption* with meshes bordered by only slightly winding strings, which commonly branch at approximately right angles. The incomplete specimen is confined by the edges of the slab and has a length of 150 mm and a width of 60 mm with a tunnel diameter of 1 mm. It consists of an irregular network of winding galleries, which branch at approximately 90°. Branching occurs only on the convex sides of the winding galleries.

Remarks.—*Megagraption irregulare* occurs from Silurian (Crimes and Crossley 1991) to Miocene (D'Alessandro 1982) in deep-sea, mainly flysch deposits. For more in-depth discussion on *Megagraption*, see Uchman (1998).

Stratigraphic and geographic range—Lower–Middle Ordovician to Miocene (Uchman et al. 2005); worldwide.

Discussion

The studied trace fossils from the old brickyard Velká nad Veličkou belong to the *Zoophycos* ichnofacies and represent a deep-sea flysch ichnoassemblage (see also Ekdale and Bromley 1984) confirming previous bathymetric interpretations of a lower slope setting based on agglutinated foraminifera (Bubík 1995). It is dominated by *Zoophycos brianteus*, *Chondrites intricatus*, *?Dactyloidites* isp., and *Tubulichnium mediterraneis*. The studied *Zoophycos* Bed (Fig. 9) yielded mid- to deep-tier trace fossils and most tracemakers applied food-stowing behaviour (sequestrichnia). Shallow or surface traces are preserved in the overlying siltstone layer and are represented by *Planolites* isp. The interrelationships of these near-surface burrows and the trace fossils in the *Zoophycos* Bed are difficult to evaluate because no cross-cuts or avoidance behaviour could be observed. Given the fact that these are near-surface burrows and most of the trace fossils of the *Zoophycos* Bed are mid- to deep tier burrows, it can be assumed that all these traces were made simultaneously. The upper mid-tier ichnosuite is represented by *T. mediterraneis* and the lower mid-tier by *?Dactyloidites* isp. Finally, the deepest tier is represented by *Chondrites intricatus* and *Zoophycos brianteus*, the biggest *Zoophycos*, however, already has its first whorl in the lower mid-tier. Considering that the *Z. brianteus* whorls were cross-cut by minute vertical shafts and intricate networks

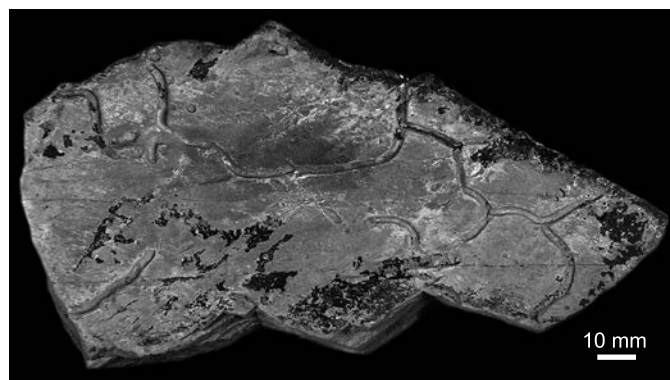


Fig. 8. Regular to irregular network graphoglyptid *Megagraption irregulare* Książkiewicz, 1968, MZM Ge 32947, from Velká nad Veličkou, Czech Republic, Eocene.

of *Chondrites intricatus*, the latter were the last constructed ichnotaxa in the ichnoassemblage.

When proposing the new ethological category “sequestrichnia” for stowing traces, Uchman and Wetzel (2016) listed common morphologies for trace fossils belonging to this ethological category. They also described the strategies applied by the tracemakers in order to stow food items. For the studied *Z. brianteus* specimens, most of the described strategies can be recognized: (i) The trace fossils are embedded within an organic-poor sediment (the *Zoophycos* Bed), which is overlain by an organic-rich layer (siltstone); (ii) The traces within the *Zoophycos* Bed are actively filled with material originating from the organic-rich stratum above and this material was transferred deep below the water sediment-interface keeping it out of reach of the shallower living bioturbators and probably also to preserve it in an anoxic environment. In the studied case, this fill is deposited as pellets and within the spreiten (compare Uchman and Wetzel 2016; see also Bromley 1991). During times of nutritional scarcity, the tracemakers remobilize the food from their storage either indirectly by solutions or ectoenzymes or directly by reworking and re-digestion. This “recycling-diet” was probably enriched in microbes growing within the active fill (cf. Jurkowska et al. 2017).

Similarly to *Zoophycos brianteus*, *Chondrites intricatus* is filled with the silty material deriving from the overlying stratum (except the shafts probably belonging to *Chondrites*). The preferred and close contact suggests that the *Zoophycos* structures represented a favourable (micro-) environment for the *Chondrites* tracemakers to exploit (compare Uchman and Wetzel 1999; Mikuláš et al. 2012; Rodríguez-Tovar et al. 2019). *Chondrites* has repeatedly been interpreted as chemichnion (for summary see Fu 1991; Bromley 1996; Vallon et al. 2016) and the diagenetic halos around the penetrating minute shafts together with their pyritic core, support a chemichnial behaviour. Chemichnia are produced by tracemakers that live in symbiosis with chemoautotrophic bacteria. Hence, their burrows need to serve both the needs of the oxygen-dependent tracemaker and its sulphate-reducing bacteria. The burrows, therefore, commonly exhibit an upper part where the tracemaker lives (usually not preserved

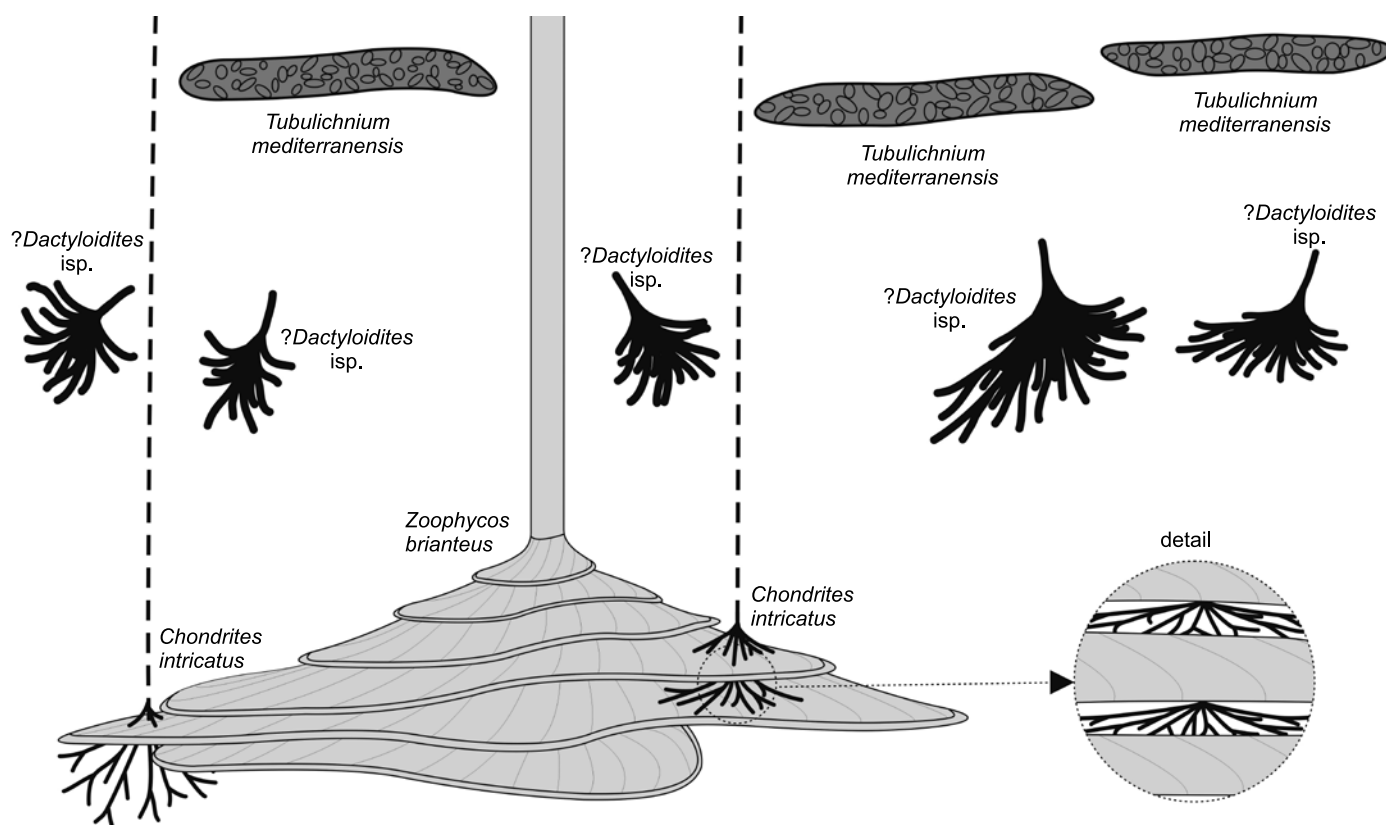


Fig. 9. Tiering of the *Zoophycos* Bed at Velká nad Veličkou, Czech Republic, Eocene. Upper tier dominated by *Tubulichnium mediterraneus*, mid-tier dominated by *?Dactyloidites* isp., lower tier dominated by *Zoophycos brianteus* and interacting nucleocave *Chondrites intricatus* (enlargement).

in the fossil record) and a lower part reaching down into the anoxic area of the sediment as for instance shown for modern sediments by Wetzel (2008: fig. 5D). Here sulphide- or ammonium-rich porewaters are mined which are essential for respiration of the symbiont-microbes (Seilacher 1990; Kędzierski et al. 2015). Although *Chondrites intricatus* may also appear isolated within the *Zoophycos* Bed, their preferred occurrence in-between individual *Z. brianteus* whorls points to favourable conditions for the *Chondrites* tracemakers in this nucleocave micro-environment. The faecal pellets within the *Z. brianteus* spreite probably enriched the already anoxic sediments with additional metabolic products locally, intensifying the sulphide- or ammonium-rich porewater. Because the *Z. brianteus* whorls were filled with the silty material from above, they might have acted as reservoir of pore water enriched in sulphide owing to their coarser grain size and more open pore-space compared to the surrounding mud. In the studied material from Velká nad Veličkou, the individual *Chondrites* tracemakers repeatedly exploited the same *Z. brianteus* specimen in the same manner. Once a reservoir was depleted, the trace-maker burrowed deeper through the coil and exploited a new source. Although the two ichnogenera *Zoophycos* and *Chondrites* are very common, are frequently reported together and have a large stratigraphic range (e.g., Vinn et al. 2020 and references herein), we do not know of any similar interaction as reported herein.

The ichnogenus *Tubulichnium* is present in Triassic to Oligocene deposits and it occurs together with trace fossils typical of the *Nereites* ichnofacies (Uchman and Wetzel 2017). *Tubulichnium rectum* occupies a relatively deep tier in depths between 30 and 65 mm (Uchman and Wetzel 2017) although García-Ramos et al. (2014) treated *T. mediterraneus* as a structure formed in a shallower tier. Proposed cache behaviour of *T. mediterraneus* (García-Ramos et al. 2014) corresponds with the sequestration interpretation by Uchman and Wetzel (2017). The possible tracemakers are under discussion. For *T. rectum* a vermiform animal (Uchman and Wetzel 2017) was proposed in contrast to crustacean trace-maker of *T. mediterraneus* (García-Ramos et al. 2014).

The ichnogenus *Dactyloidites* usually occurs in shallow, sandy marine to brackish environments (D'Alessandro and Bromley 1986; Agirrezabala and Gibert 2004; Uchman and Pervesler 2007; Boyd and McIlroy 2016) whereas the studied specimens derive from a deep-sea environment. The studied material is therefore in concordance with the type ichnospecies *Dactyloidites asteroides* (Fitch, 1850) (see Hall 1886; cf. Landing 2012) from the Granville Formation, New York, USA, which was interpreted to derive from a lower slope environment (Donald H. Goldstein, personal communication 2021). Although recent deep-sea radial burrows were reported (Huggett 1987; Gaillard 1991; Bett et al. 1995; Turnewitsch et al. 2000; Bell et al. 2013), all the structures were observed on the sediment surface. The studied material shows distinct

infaunal features similarly to burrows of *Arenicola marina* (Linnaeus, 1758) reported by Rijken (1979). He noticed that the stimulus for this atypical behaviour of *A. marina* is the presence of nutrient-rich sediment at living depth. Despite *A. marina* is an inhabitant of shallow seas, this hypothesis can be applied to deep-sea environments as well. Further, the presence of plant remains within or in close contact with *Dactyloidites otto* was repeatedly reported (see Agirrezabala and Gibert 2004; and references therein). This behaviour of incorporating plant material has been interpreted as farming (agrichnia) by Agirrezabala and Gibert (2004). Alternatively, this and our observations of deep-marine *Dactyloidites* isp. may also point to sequestration (e.g., stacked J-shape burrows combined with pellet deposition). The studied deep-sea material further supports this interpretation as these infaunal burrows were actively filled with silty material from the layer above the *Zoophycos* Bed.

Conclusions

The Velká nad Veličkou brickyard exemplifies deep-sea flysch sedimentation with uniquely preserved trace fossils and a relatively rich ichnoassemblage. The *Zoophycos* Bed offers a rare glimpse into the ecology of deep-sea dwellers and their feeding strategies, that mostly applied the recently recognised behaviour of sequestration. *Chondrites intricatus* burrows occur in close contact with *Zoophycos brianteus*, in particular to the spreite whorls inferring a highly specialised behaviour of the *Chondrites intricatus* tracemakers. This is interpreted as an opportunistic exploitation of a nucleocave environment with sulphide- or ammonium-rich pore waters. *Dactyloidites* isp. in the Velká nad Veličkou brickyard outcrop contributes to the broader knowledge about this ichnogenus. The studied material represents a deep-sea environment (like its type ichnospecies) whereas most *Dactyloidites* ichnospecies are reported from shallow-marine settings.

Acknowledgements

We are greatly thankful to Arden. R. Bashforth (Natural History Museum of Denmark, Copenhagen, Denmark) for access to Dam's material deposited at the museum. We would also like to thank Michał Stachacz (Kraków, Poland), Donald H. Goldstein (University of Connecticut, Storrs, USA), and Andrew K. Rindsberg (University of West Alabama, Livingston, USA) for discussions and providing further information or hardly accessible literature and improving language. Christian Klug (University of Zürich, Switzerland) translated the French passage. Alfred Uchman (Jagiellonian University, Kraków, Poland), Olev Vinn (University of Tartu, Estonia), and Andreas Wetzel (University of Basel, Switzerland) provided helpful and constructive comments on the manuscript with their reviews. JŠ acknowledges research project MUNI/A/1394/2021. RM was supported by the Institute of Geology of the Czech Academy of Sciences No. RVO 679 858 31 and the Czech Science Foundation (Project No. 18-05935S).

References

- Agirrezabala, L.M. and Gibert, J.M. de 2004. Paleodepth and paleoenvironment of *Dactyloidites otto* (Geinitz, 1849) from Lower Cretaceous deltaic deposits (Basque-Cantabrian Basin, West Pyrenees). *Palaios* 19: 276–291.
- Baucon, A., Bednarz, M., Dufour, S., Felletti, F., Malgesini, G., de Carvalho, C.N., Niklas, K. J., Wehrmann, A., Batstone, R., Bernardini, F., Briguglio, A., Cabella, R., Cavalazzi, B., Ferretti, A., Zanzerl, H., and McIlroy, D. 2020. Ethology of the trace fossil *Chondrites*: Form, function and environment. *Earth-Science Reviews* 202: 102989.
- Belaústegui, Z., Doménech, R., and Martinell, J. 2015. Trace fossils of the Middle Miocene of the El Camp de Tarragona Basin (NE Spain). In: D. McIlroy (ed.), *Ichnology: Papers from Ichnia III. Geological Association of Canada, Miscellaneous Publication* 9: 15–30.
- Belaústegui, Z., Muñiz, F., Mángano, M.G., Buatois, L.A., Doménech, R., and Martinell, J. 2016. *Lepeichnus giberti* igen. nov. isp. nov. from the upper Miocene of Lepe (Huelva, SW Spain): Evidence for its origin and development with proposal of a new concept, ichnogeny. *Palaeogeography, Palaeoclimatology, Palaeoecology* 452: 80–89.
- Bell, J.B., Jones, D.O.B., and Alt, C.H.S. 2013. Lebensspuren of the bathyal Mid-Atlantic Ridge. *Deep-Sea Research Part II: Topical Studies in Oceanography* 98: 341–351.
- Bett, B.J., Rice, A.L., and Thurston, M.H. 1995. A quantitative photographic survey of “spoke-burrow” type lebensspuren on the Cape Verde abyssal plain. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 80 (2): 153–170.
- Billings, E. 1862. New species of fossils from different parts of the Lower, Middle and Upper Silurian rocks of Canada. In: E. Billings (ed.), *Palaeozoic Fossils, Vol. 1 (for 1861–1865)*, 96–168. Geological Survey Canada, Montreal.
- Boyd, C. and McIlroy, D. 2016. Three-dimensional morphology and palaeobiology of the trace fossil *Dactyloidites jordii* nov. isp. from the Carboniferous of England. *Geobios* 49: 257–264.
- Bromley, R.G. 1991. *Zoophycos*: strip mine, refuse dump, cache or sewage farm? *Lethaia* 24: 460–462.
- Bromley, R.G. 1996. *Trace Fossils: Biology, Taphonomy and Applications*. Second edition. 361 pp. Chapman & Hall, London.
- Bromley, R.G. and Ekdale, A.A. 1984. *Chondrites*: a trace fossil indicator of anoxia in sediments. *Science* 224: 872–874.
- Brongniart, A.T. 1823. Observations sur les Fucoids. *Mémoires de la Société d'Histoire Naturelle de Paris* 1: 301–320.
- Brongniart, A.T. 1828. *Histoire des végétaux fossiles ou recherches botaniques et géologiques sur les végétaux renfermés dans les diverses couches du globe*. 488 pp. G. Dufour & E. D'Ocagne, Paris.
- Brongniart, A.T. 1849. Tableau des genres de végétaux fossiles considérés sous le point de vue de leur classification botanique et de leur distribution géologique. *Dictionnaire universel d'histoire naturelle* 13: 1–27 (152–176).
- Buatois, L.A., Narbonne, G.M., Mángano, M.G., Carmona, N.B., and Mýrow, P. 2014. Ediacaran matground ecology persisted into the earliest Cambrian. *Nature Communications* 5: 3544.
- Buatois, L.A., Wisshak, M., Wilson, M.A., and Mángano, M.G. 2017. Categories of architectural designs in trace fossils: A measure of ichnodisparity. *Earth-Science Reviews* 164: 102–181.
- Bubík, M. 1995. Cretaceous to Paleogene agglutinated foraminifera of the Bílé Karpaty unit (West Carpathians, Czech Republic). In: M.A. Kaminski, S. Geroch, and M.A. Gasiński (eds.), *Proceedings of the Fourth International Workshop on Agglutinated Foraminifera*, Kraków, Poland, September 12–19, 1993. *Grzybowski Foundation Special Publication* 3: 71–116.
- Cabanás, G. 1966. Notas estratigráficas de la provincia de Córdoba. Con una nota sobre un nuevo fósil del Cambriano por Bermudo Meléndez. *Notas y Comunicaciones del Instituto Geológico y Minero de España* 90: 77–84.
- Ciampaglio, C.N., Babcock, L.E., Wellman, C.L., York, A.R., and Brunswick, H.K. 2006. Phylogenetic affinities and taphonomy of *Brooksella*

- from the Cambrian of Georgia and Alabama, USA. *Palaeoworld* 15: 256–265.
- Crimes, T.P. and Crossley, J.D. 1991. A diverse ichnofauna from Silurian flysch of the Aberystwyth Grist Formation, Wales. *Geological Journal* 26: 27–64.
- D'Alessandro, A. 1982. Processi tafonomici e distribuzione delle tracce fossili nel Flysch di Gorgolione (Appennino Meridionale). *Rivista Italiana di Paleontologia e Stratigrafia* 87: 511–560.
- D'Alessandro, A. and Bromley, R.G. 1986. Trace fossils in Pleistocene sandy deposits from Gravina area Southern Italy. *Rivista Italiana di Paleontologia e Stratigrafia* 92: 67–102.
- Dam, G. 1990. Taxonomy of trace fossils from the shallow marine Lower Jurassic Neill Klint Formation, East Greenland. *Bulletin of the Geological Society of Denmark* 38: 119–144.
- Ekdale, A.A. and Bromley, R.G. 1984. Comparative ichnology of shelf-sea and deep-sea chalk. *Journal of Paleontology* 58: 322–332.
- Fitch, A. 1850. A historical, topographical and agricultural survey of the County of Washington. Part 5. *New York Agricultural Society, Transactions* 9 (for 1849): 753–944.
- Fu, S. 1991. Funktion, Verhalten und Einteilung fucoider und lophoctenider Lebensspuren. *Courier Forschungsinstitut Senckenberg* 135: 1–79.
- Fürsich, F.T. and Bromley, R.G. 1985. Behavioural interpretation of a rosetted spreite trace fossil: *Dactyloidites otto* (Geinitz). *Lethaia* 18: 199–207.
- Gaillard, C. 1991. Recent organism traces and ichnofacies on the deep-sea floor off New Caledonia, Southwestern Pacific. *Palaaios* 6: 302–315.
- García-Ramos, J.C., Mángano, M.G., Buatois, L.A., and Rodríguez-Tovar, F.J. 2014. The ichnogenus *Tubotomaculum*: an enigmatic pellet-filled structure from upper Cretaceous to Miocene deep-marine deposits of Southern Spain. *Journal of Paleontology* 88: 1189–1198.
- Geinitz, H.B. 1849. *Das Quadersandsteingebirge oder Kreidegebirge in Deutschland*. 292 pp. Craz and Gerlach, Freiberg.
- Hall, J. 1886. Note on some obscure organisms in the roofing slate of Washington County, New York. *New York State Museum of Natural History, Annual Report* 39: 1–160.
- Hu, B., Song, H., Liu, S., and Zhang, L. 2010. Sedimentary facies, ichnofossils and storm deposits in the Lower Permian Taiyuan Formation, Jiaozuo city, Henan Province, Central China. *Acta Geologica Polonica* 60: 45–52.
- Huggett, Q.J. 1987. Mapping of hemipelagic versus turbiditic muds by feeding traces observed in deep-sea photographs. In: P.P.E. Weaver and J. Thomson (eds.), *Geology and Geochemistry of Abyssal Plains. Geological Society Special Publication* 31: 105–112.
- Izumi, K. and Yoshizawa, K. 2016. Star-shaped trace fossils and Phymatoderma from Neogene deep-sea deposits in central Japan: probable echiuran feeding and fecal traces. *Journal of Paleontology* 90: 1169–1180.
- Jurkowska A., Uchman, A., and Banaś, M. 2017. Life beneath ammonite shells—A unique Late Cretaceous habitat for the trace maker of *Chondrites* and its impact on taphonomy of the shells. *Cretaceous Research* 72: 151–160.
- Jurkowska, A., Uchman, A., and Świerczewska-Gładysz, E. 2018. A record of sequestration of plant material by marine burrowing animals as a new feeding strategy under oligotrophic conditions evidenced by pyrite microtextures. *Palaaios* 33: 312–322.
- Kędzierski, M., Uchman, A., Sawłowicz, Z., and Briguglio, A. 2015. Fossilized bioelectric wire—the trace fossil *Trichichnus*. *Biogeosciences* 12: 2301–2309.
- Kotake, N. 1989. Paleoeecology of the *Zoophycos* producers. *Lethaia* 22: 327–341.
- Książkiewicz, M. 1968. On some problematic organic traces from the Flysch of the Polish Carpathians, Part 3. *Rocznik Polskiego Towarzystwa Geologicznego* 38: 3–17.
- Książkiewicz, M. 1977. Trace fossils in the Flysch of the Polish Carpathians. *Acta Palaeontologica Polonica* 36: 1–208.
- Kundal, S.N., Kundal, P., Kumar, S., Chowdhary, N., and Prasad, G.V.R. 2022. Late Pliocene–Early Pleistocene ichnofauna from bentonitized tuff band and associated mudstone horizons, Jammu and Kashmir, India, and their palaeoenvironmental implications. *Arabian Journal of Geosciences* 15: 269.
- Landing, E. 2012. The great American carbonate bank in eastern Laurentia: Its births, deaths, and linkage to paleoceanic oxygenation (Early Cambrian–Late Ordovician). In: J.R. Derby, R.D. Fritz, S.A. Longacre, W.A. Morgan, and C.A. Sternbach (eds.), *The Great American Carbonate Bank: The Geology and Economic Resources of the Cambrian–Ordovician Sauk Megasequence of Laurentia. AAPG Memoir* 98: 451–492.
- Le Roux, J.P., Nielsen, S.N., and Henríquez, Á. 2008. Depositional environment of *Stelloglyphus llicoensis* isp. nov.: a new radial trace fossil from the Neogene Ranquil Formation, south-central Chile. *Revista Geológica de Chile* 35: 307–319.
- Linnaeus, C. 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tenth edition*. 824 pp. Laurentius Salvius, Holmiae.
- Massalonga, A. 1855. *Zoophycos, novum genus plantarum fossilium*. 52 pp. Typis Antonellianis, Veronae.
- Mikuláš, R., Fatka, O., and Szabad, M. 2012. Paleoeecologic implications of ichnofossils associated with slightly skeletonized body fossils, middle Cambrian of the Barrandian Area, Czech Republic. *Ichnos* 19: 199–210.
- Muñoz, D.F., Mángano, M.G., and Buatois, L.A. 2019. Unravelling Phanerozoic evolution of radial to rosette trace fossils. *Lethaia* 52: 350–369.
- Němcová, A. 1973. *Klasifikace a význam bioglyfů při výzkumu sedimentů karpatského flyše*. 124 pp. Unpublished Ph.D. Thesis, Faculty of Science, Jan Evangelista Purkyně University (Masaryk University), Brno.
- Nicholson, H.A. 1873. Contributions to the study of the errant annelids of the older Palaeozoic rock. *Proceedings of the Royal Society of London* 21: 288–290.
- Olivero, D. 2007. *Zoophycos* and the role of type specimens in ichnotaxonomy. In: W. Miller III. (ed.), *Trace Fossils: Concepts, Problems, Prospects*, 219–231. Elsevier, Amsterdam.
- Olivero, D. and Gaillard, C. 1996. Paleoeecology of Jurassic *Zoophycos* from south-eastern France. *Ichnos* 4: 249–260.
- Olivero, D. and Gaillard, C. 2007. A constructional model for *Zoophycos*, In: W. Miller III. (ed.), *Trace Fossils: Concepts, Problems, Prospects*, 466–477. Elsevier, Amsterdam.
- Otto, E. von 1854. *Additamente zur Flora des Quadergebirges in Sachsen. 2. Heft*. 54 pp. G. Mayer, Leipzig.
- Pickerill, R.K., Donovan, S.K., and Dixon, H.L. 1993. The trace fossil *Dactyloidites otto* (Geinitz, 1849) from the Neogene August Town Formation of South-Central Jamaica. *Journal of Paleontology* 67: 1070–1074.
- Plička, M. 1989. *Rotundusichnium zumayensis* ichnog. n. a new trace fossil from the Outer Carpathian Flysch of West Slovakia (Czechoslovakia). *Západné Karpaty, séria paleontológia* 13: 69–79.
- Quatrefages, M.A. de 1849. Note sur la *Scolicia prisca* (A. de Q.) Annelide fossile de la Craie. *Annales des Sciences Naturelles, 3 série, Zoologie* 12: 265–266.
- Richter, R. 1850. Aus der Thüringischen Grauwacke. *Zeitschrift der Deutschen Geologischen Gesellschaft* 2: 198–206.
- Rijken, M. 1979. Food and food uptake in *Arenicola marina*. *Netherlands Journal of Sea Research* 13: 406–421.
- Rindsberg, A.K. and Chowns, T.M. 1986. Ringgold Gap: Progradational sequences in the Ordovician and Silurian of northwest Georgia. In: T.L. Neathery (ed.), *Geology of North America, Geological Society of America Centennial Field Guide, Vol. 6*, 159–162. Southeastern Section of the Geological Society of America, Boulder.
- Rodríguez-Tovar, F.J., Míguez-Salas, O., Dorador, J., and Duarte, L.V. 2019. Opportunistic behaviour after the Torcian Oceanic Anoxic Event: The trace fossil *Halimedes*. *Palaeogeography, Palaeoclimatology, Palaeoecology* 520: 240–250.
- Savi, P. and Meneghini, G.G. 1850. *Osservazioni stratigrafiche e paleontologiche concernenti la geologia della Toscana e dei Paesi Limitrofi*. 259 pp. Stemparia Granducale, Firenze.

- Seilacher, A. 1990. Aberrations in bivalve evolution related to photo- and chemosymbiosis. *Historical Biology* 3: 289–311.
- Seilacher, A. 2000. Ordovician and Silurian arthropycid ichnostratigraphy. In: M.A. Sola and D. Worsley (eds.), *Geological Exploration in Murzuq Basin*, 237–258. Elsevier, Amsterdam.
- Seilacher, A. 2007. *Trace Fossil Analysis*. 226 pp. Springer-Verlag, Berlin.
- Seilacher, A. 2008. *Fossil Art: An Exhibition of the Geologisches Institut, Tübingen University, Germany*. 98 pp. CBM-publishing, Laasby.
- Sternberg, G. K. 1833. *Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt. IV Heft*. 48 pp. C.E. Brenck, Regensburg.
- Stránik, Z., Bubík, M., Krejčí, O., Marschalko, R., Švábenická, L., and Vujta, M. 1995. New Lithostratigraphy of the Hluk Development of the Bílé Karpaty unit. *Geologické práce, Správy* 100: 57–69.
- Tchoumatchenco, P. and Uchman, A. 2001. The oldest deep-sea *Ophiomorpha* and *Scotocia* and associated trace fossils from the Upper Jurassic–Lower Cretaceous deep-water turbidite deposits of SW Bulgaria. *Palaeogeography, Palaeoclimatology, Palaeoecology* 169: 85–99.
- Turnewitsch, R., Witte, U., and Graf, G. 2000. Bioturbation in the abyssal Arabian Sea influence of fauna and food supply. *Deep-Sea Research Part II: Topical Studies in Oceanography* 47: 2877–2911.
- Uchman, A. 1998. Taxonomy and ethology of flysch trace fossils: revision of the Marian Książkiewicz collection and studies of complementary material. *Annales Societatis Geologorum Poloniae* 68: 105–218.
- Uchman, A. and Pervesler, P. 2007. Palaeobiological and palaeoenvironmental significance of the Pliocene trace fossil *Dactyloidites peniculus*. *Acta Palaeontologica Polonica* 52: 799–808.
- Uchman, A. and Rattazzi, B. 2017. The trace fossil *Polykampton cabellae* isp. nov. from the Pagliaro Formation (Paleocene), Northern Apennines, Italy: A record of nutritional sediment sequestration by a deep sea invertebrate. *Ichnos* 25: 1–10.
- Uchman, A. and Wetzel, A. 1999. An aberrant, helicoidal trace fossil *Chondrites* Sternberg. *Palaeogeography, Palaeoclimatology, Palaeoecology* 146: 165–169.
- Uchman, A. and Wetzel, A. 2016. Sequestrichnia—a new ethological category of trace fossils in oligotrophic deep-sea environments. In: A. Bacon, C.N. de Carvalho, and J. Rodrigues (eds.), *Ichnia 2016. Abstract Book*, 190. UNESCO Geopark Naturtejo/International Ichnological Association, Castelo Branco.
- Uchman, A. and Wetzel, A. 2017. Hidden subsurface garden on own faeces—the trace fossil *Tubulichnium rectum* (Fischer-Ooster, 1858) from the Cretaceous–Palaeogene deep-sea sediments. *Palaeontologia Electronica* 20.2.40A: 1–18.
- Uchman, A., Hanken, N.-M., and Binns, R. 2005. Ordovician bathyal trace fossils from metasiliciclastics in Central Norway and their sedimentological and paleogeographical implications. *Ichnos* 12: 105–133.
- Uchman, A., Lebanidze, Z., Beridze, T., Kobakhidze, N., Lobzhanidze, K., Khutsishvili, S., Chagelishvili, R., Makadze, D., Koiava, K., and Khundadze, N. 2020. Abundant trace fossil *Polykampton* in Palaeogene deep-sea flysch deposits of the Lesser Caucasus in Georgia: Palaeoecological and palaeoenvironmental implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 558: 109958.
- Uchman, A., Wetzel, A., and Rattazzi, B. 2019. Alternating stripmining and sequestration in deep-sea sediments: The trace fossil *Polykampton*—an ecologic and ichnotaxonomic evaluation. *Palaeontologia Electronica* 22.2.21A: 1–18.
- Vallon, L.H., Rindsberg, A.K., and Bromley, R.G. 2016. An updated classification of animal behaviour preserved in substrates. *Geodinamica Acta* 28: 5–20.
- Vialov, O.S. 1964. Star-shaped hieroglyphs from the Triassic of north-eastern Siberia [in Russian with English summary]. *Geologičeskij i Geofizika* 5: 112–115.
- Vialov, O.S. 1989. Paleochronological studies [in Russian with English summary]. *Paleontologičeskij Sbornik* 26: 72–78.
- Vinn, O., Bendella, M., Benyoucef, M., Zhang, L.-J., Bouchemla, I., Ferré, B., and Lagnaoui, A. 2020. Abundant *Zoophycos* and *Chondrites* from the Messinian (Upper Miocene) of northwest Algeria. *Journal of African Earth Sciences* 171: 103921.
- Walcott, C.D. 1896. Fossil jellyfishes from the Middle Cambrian terrane. *Proceedings of the United States National Museum* 18: 611–615.
- Wetzel, A. 2008. Recent bioturbation in the deep South China Sea: A uniformitarian ichnologic approach. *Palaios* 23: 601–615.
- Wetzel, A. and Bromley, R.G. 1996. Re-evaluation of the ichnogenus *Helminthopsis*—A new look at the type material. *Palaeontology* 39: 1–19.
- Wetzel, A. and Uchman, A. 2012. Hemipelagic and pelagic basin plains. In: D. Knaust and R.G. Bromley (eds.), *Trace fossils as indicators of sedimentary environments. Developments in Sedimentology* 64: 673–701.
- Wetzel, A., Tjallingii, R., and Wiesner, M.G. 2011. Bioturbational structures record environmental changes in the upwelling area off Vietnam (South China Sea) for the last 150,000 years. *Palaeogeography, Palaeoclimatology, Palaeoecology* 311: 256–267.
- Wilmsen, M. and Niebuhr, B. 2014. The rosetted trace fossil *Dactyloidites otto* (Geinitz, 1849) from the Cenomanian (Upper Cretaceous) of Saxony and Bavaria (Germany): ichnotaxonomic remarks and palaeoenvironmental implications. *Paläontologische Zeitschrift* 88: 123–138.